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AN ANALYSIS OF GEOGRAPHICAL VARIATION IN WESTERN NORTH AMERICAN MENZIESIA (ERICACEAE)

James C. Hickman and Michael P. Johnson

The boreal shrub genus *Menziesia* J. E. Smith consists of four species in Japan and two rather closely related species in North America, one occupying the Appalachian region and the other, *M. ferruginea* Smith (1791), occupying coastal and mountainous areas throughout the moist regions of western North America. All members of the genus are found in mesic habitats. Occasionally they constitute the dominant understory vegetation, especially in coastal bogs and forests and at lake margins in areas of high rainfall or persistent fog or mist.

The western populations were originally described as two separate species. *M. ferruginea* Smith included the coastal populations, and *M. glabella* Gray (1878), a less pubescent and glandular form, occurred in the Rocky Mountains. Intermediate specimens, subsequently collected in the Cascade Range, led Peck (1941) to consider the Cascade and Rocky Mountain plants together as *M. ferruginea* var. *glabella* (Gray) Peck. Calder and Taylor (1965) have recently made the combination *M. ferruginea* ssp. *glabella.*

The pubescence characters used to differentiate the two entities lack the geographical coherence suggested by the proposed systems of classification. The purpose of this study is to examine more carefully and discuss the geographical differentiation within *M. ferruginea.*

Methods

A total of 143 herbarium specimens was studied from throughout the range of the species. In so far as can be determined, each represents a distinct population. The geographical range of the species has been divided into seven areas on the basis of physiography, climate, geology and political boundaries (Detling, 1948). The areas are: 1, the Alaskan coast; 2, the Canadian coast; 3, the United States coast from Washington to northern California; 4, the northern Cascade Mountains from British Columbia to the Columbia River; 5, the southern Cascade Mountains of Oregon; 6, the Canadian Rocky Mountains; and 7, the Rocky Mountains of the United States as far south as Wyoming. The localities and areas are shown in Fig. 1.

The only well-defined geographical discontinuity between areas occurs in central British Columbia. It isolates the Rocky Mountain populations from all others. The coastal areas are essentially continuous from northern California to the Kenai Peninsula and merge with the Cascade areas through the Manning Park-Mt. Seymour area in southwestern British Columbia. In this instance the line between areas was drawn on geological grounds, keeping the volcanic Cascades as an entity.

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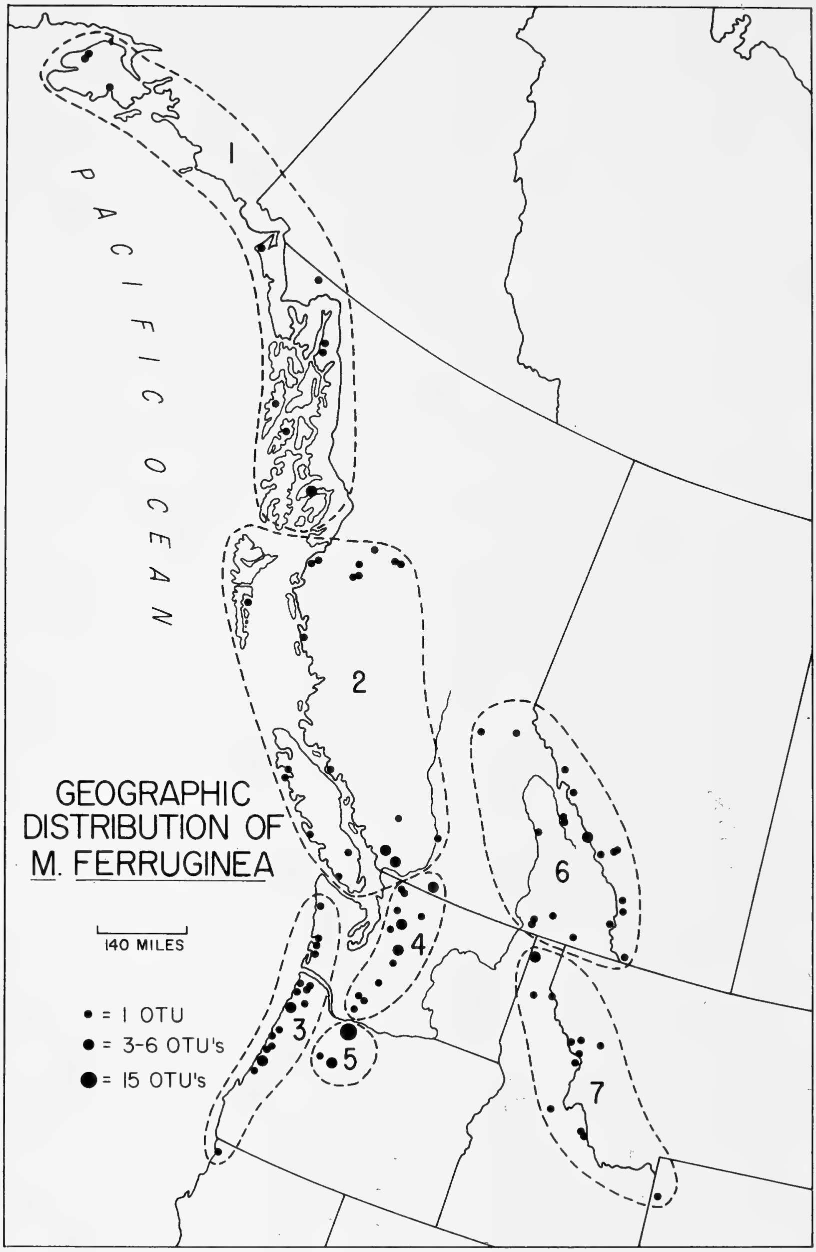

Fig. 1. The localities of analyzed specimens and the boundaries of the geographical sample areas: 1, Alaskan coast; 2, Canadian coast; 3, United States coast; 4, northern Cascade Mountains; 5, southern Cascade Mountains; 6, Canadian Rocky Mountains; 7, United States Rocky Mountains.

Twenty-nine characters were measured. They included leaf tip shape and density and length of glandular and puberulent hairs on the young stem, pedicel, calyx and carpels. For both the upper and lower leaf surfaces, density and length of subulate, glandular and puberulent hairs were measured. Two other characters were derived by summing the densities of subulate and glandular hairs for both surfaces, giving a measure of total leaf pubescence. All leaf density measurements for subulate and glandular hairs were made by superimposing a grid over the leaf surface and counting all those hairs that fell completely within the grid, as well as those along two adjacent sides which had their points of attachment within the grid. Densities of hairs on stems and petioles were measured by counting the number of hair bases visible on a 1 mm segment taken immediately proximal to the oldest leaf, and 1 mm below the calyx, respectively. The puberulent hairs were too small to be counted by these methods, and their densities were approximated by measuring the distance of several hairs to their nearest neighbors. The average distance was then converted to a density measurement. All measurements of length were made with a micrometer. The leaf tip shape index resulted from numerically grading a minimum of ten leaves per specimen from round (1) to acuminate (8).

Sokal and Sneath (1963) suggest using no fewer than sixty characters in numerical taxonomic studies. However, this study concerns subspecific variation, necessitating analysis of a large number of individuals, and the number of characters consequently had to be sacrificed. Ehrlich and Ehrlich (1967) have shown that classifications of butterflies based on small subsets of characters are highly and significantly correlated with the classification based on the total characters sampled. This has also been demonstrated in plants by Johnson and Holm (1968). Although sufficient data are not available to generalize this phenomenon, we might accordingly expect the narrow character set we have chosen to significantly approximate the total variation pattern in *M. ferruginea.*

The variation in each character was analyzed by comparing the means for that character in all paired combinations among the seven areas using analysis of variance (F tests). Multivariate analysis was made following the methodology of Sokal and Sneath (1963). Each herbarium specimen was taken as an operational taxonomic unit and compared with every other OTU to construct two matrices of similarity measures between the OTU's. Taxonomic distance and product moment correlation coefficients were the similarity measures employed. All characters were standardized such that the mean for each is zero with a variance of one. Each matrix was clustered using the unweighted pair-group method with arithmetic means. A phenogram was constructed from each cluster analysis.

RESULTS

For all characters measured, the variation within any one geographi-

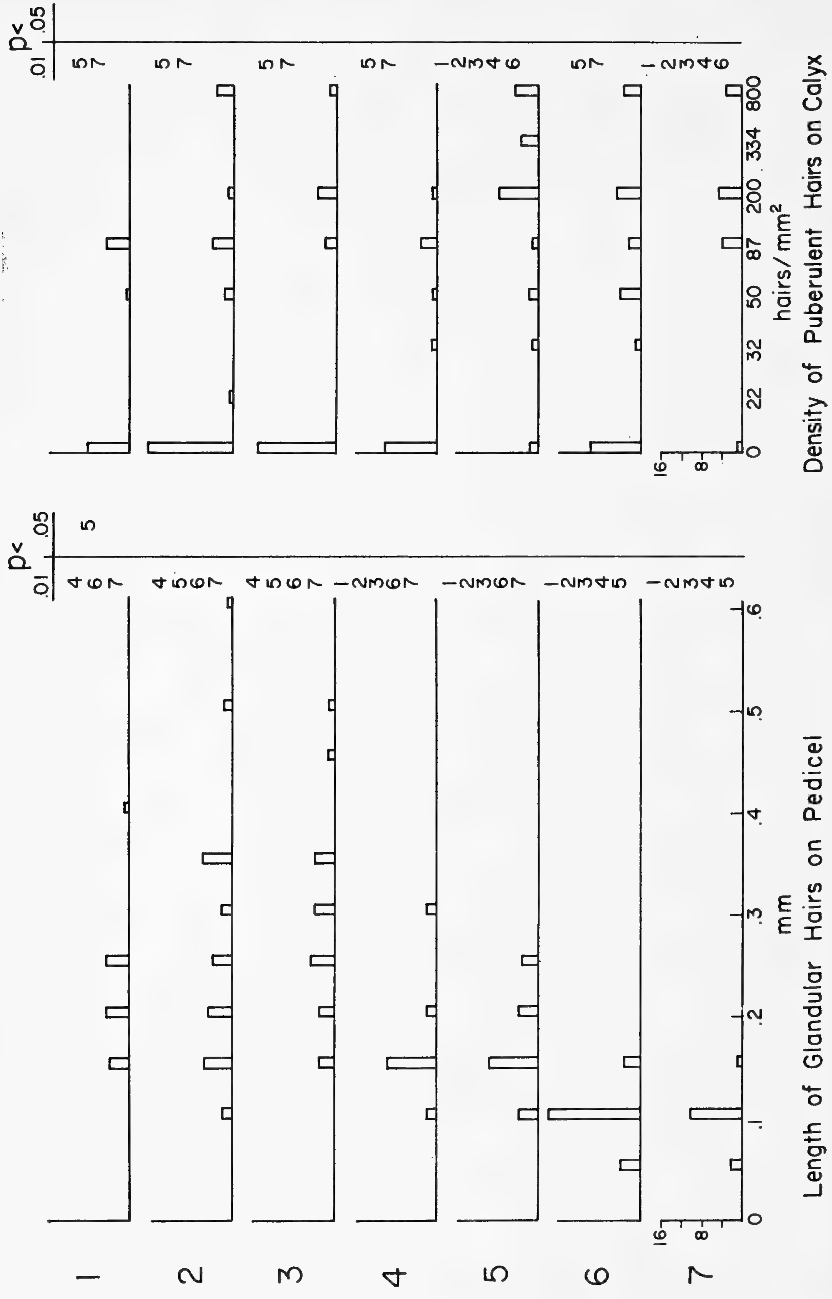

FIG. 2. Character state distributions for four characters for the seven areas (fig. 1). To the right of each histogram are given all areas which differ significantly for that character at the five and one percent levels based on the F test.

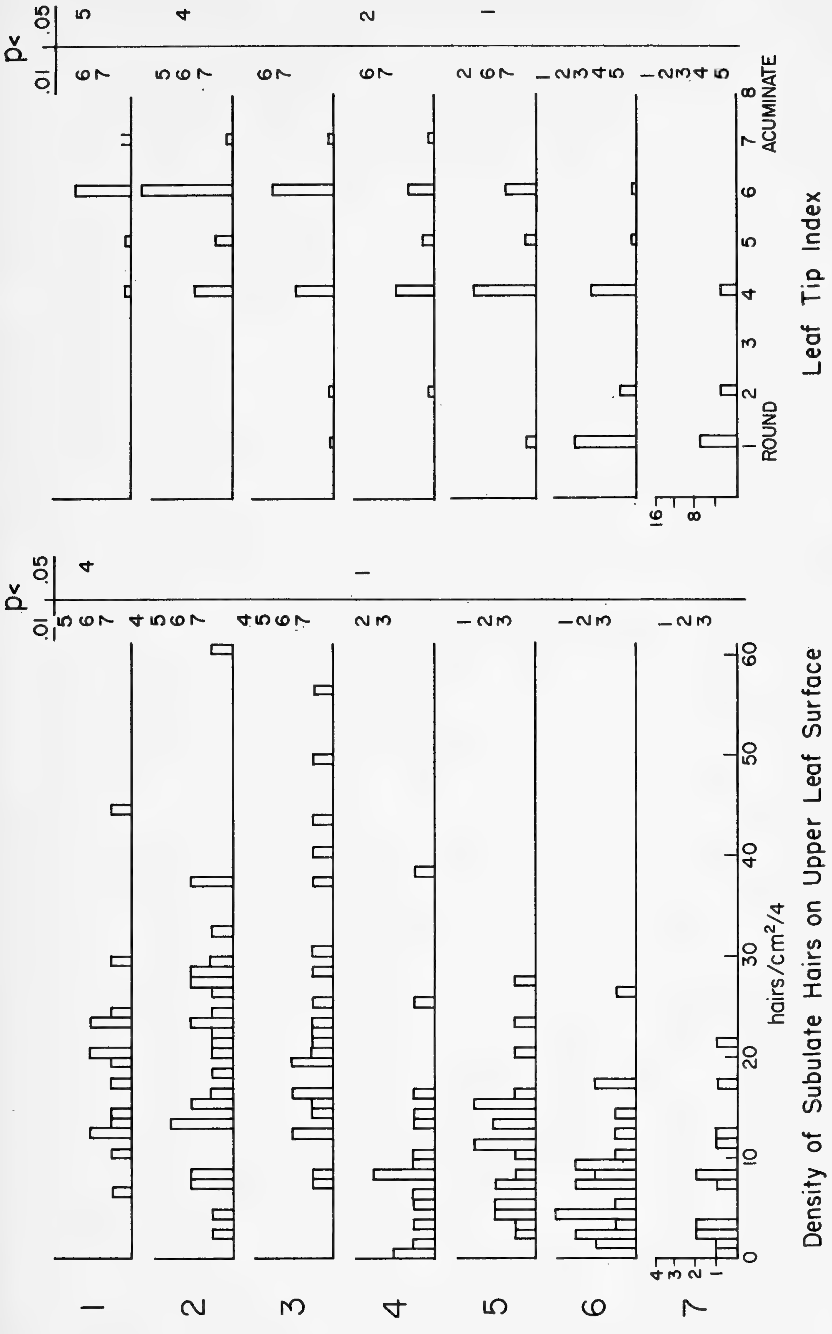

Fig. 2 continued.

TABLE I. A List of Those Characters for Which There Are Numerous Significant Differences Between Geographical Areas in Paired Combinations. Also Given Are the General Geographical Patterns of Variation of These Characters.

Character	*Description of Variation Pattern*
Density of subulate hairs on upper leaf surface	Decreasing clinally inland; Cascade and Rocky Mountains similar (fig. 2)
Total density of hairs on upper leaf surface	Decreasing clinally south and inland, but reversed in the Rocky Mountains
Length of subulate hairs on upper leaf surface	Decreasing clinally south and inland
Length of glandular hairs on upper leaf surface	Decreasing clinally south and inland
Density of glandular hairs on lower leaf surface	Decreasing clinally south and inland, but reversed in the Rocky Mountains
Length of glandular hairs on lower leaf surface	Unclear, generally decreasing south and inland
Density of glandular hairs on young stem	Decreasing clinally south and inland, but reversed in the Rocky Mountains
Length of glandular hairs on young stem	Increasing clinally south on coast, decreasing inland
Density of puberulent hairs on pedicel	Increasing clinally south and inland; southern Cascade and U.S. Rocky Mountains similar
Length of glandular hairs on pedicel	Decreasing clinally inland; three groups: Coast, Cascades and Rocky Mountains (fig. 2)
Density of puberulent hairs on calyx	Two groups, no clinal change: southern Cascades and Rocky Mountains similar (fig. 2)
Length of longest cilium on calyx	Increasing clinally south and inland, but reversed in the Rocky Mountains
Density of puberulent hairs on carpel	Coast constant; others increasing south and inland
Density of glandular hairs on carpel	Coast constant; others increasing south and inland
Length of glandular hairs on carpel	Not clinal: Coast lowest; Cascades highest; Rocky Mountains intermediate
Leaf tip index	Decreasing clinally south and inland; jump downscale (to roundness) at Rocky Mountains (fig. 2)

cal area overlaps the variation in all other areas. A series of histograms of four characters for each of the seven areas is given in Fig. 2. Also included are code numbers for those areas which differ significantly from the area-character under consideration. Significance at $p < .05$ and $p < .01$ is based on the F test between the means. Those characters which exhibit significant differences between samples in several paired combinations are given in Table I, with descriptions of the patterns of character variation.

For character sets involving size, such as those used in this study, Sokal and Sneath (1963) suggest that a correlation coefficient gives a better measure of similarity than taxonomic distance. As predicted, in the phenogram based on taxonomic distance, several geographically unrelated and morphologically diverse specimens clustered with one another or with the major clusters only at unusually high levels. Since these individuals are extreme for one or more measurements, it seems that the clustering pattern here is adversely affected by characters involving size. For this reason, we consider the phenogram based on correlation coefficients to be the more appropriate measure of similarity, and further discussion will pertain to it.

The OTU's fall into three large clusters which we refer to as Rocky Mountain, Cascade and Coastal (fig. 3). The Rocky Mountain cluster is the most homogeneous: it contains Rocky Mountain OTU's almost exclusively, and almost every Rocky Mountain OTU is included in it. The Cascade and Coastal clusters are heterogeneous. They contain a predominance of OTU's from the areas for which they are named, but also include a significant number of OTU's from other areas. The Cascade and Rocky Mountain clusters show greater affinity to one another than either does to the Coastal cluster.

Discussion

The patterns of variation of characters in Table I show an independence, or "discordance." Regarding the problem of concordance and discordance at subspecific levels, Ehrlich and Holm (1964, p. 166) state that "with discordance predominaitng, subspecies recognized on the basis of one or a few convenient characters would not be evolutionary units. They would be simply units of convenience for filing specimens."

Figure 2 presents a fraction of the original data and demonstrates some of the more important variation patterns in detail. The density of subulate hairs on the upper leaf surface is the most readily observed character for differentiating the described *M. ferruginea* var. *glabella* (Gray) Peck from the more pubescent typical *M. ferruginea* of coastal regions. This character shows a clinal decrease inland, with the Rocky Mountain and Cascade populations varying as a unit. The coastal populations form another quite distinct statistical unit. This character, taken alone, would indicate that Peck was correct in stating that the var. *glabella* should include both Rocky Mountain and Cascade plants (1941). If we consider leaf tip shape, however, another pattern becomes apparent. The coastal and Cascade specimens show a clinal increase in roundness of the leaf tip as one progresses south and inland. The Rocky Mountain plants show a sharp break from all the other populations, having for the most part quite round leaf tips. This pattern, if taken alone, would lead one to consider the Rocky Mountain form to constitute the most nearly distinct subspecific unit. The length of glandular hairs on the pedicel exhibits yet another pattern of variation. Here all

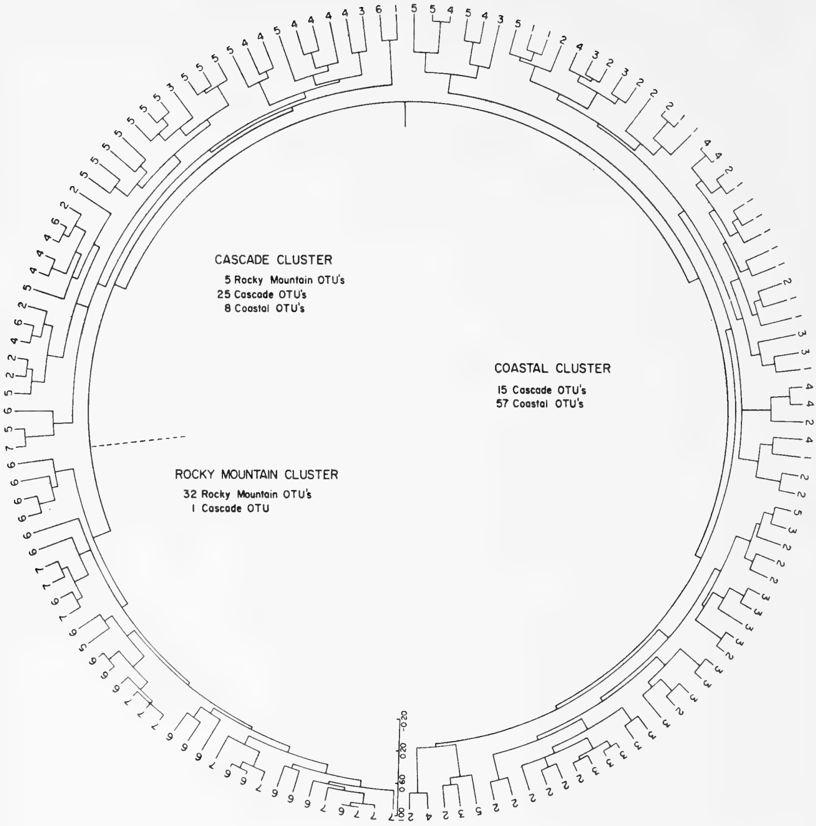

FIG. 3. Phenocycle resulting from the cluster analysis of the matrix of correlation coefficients. The OTU's are labeled as to the geographical area from which they came (fig. 1). A summary of the constituents of each of the major clusters is given. A dotted line marks the boundary between the Cascade and Rocky Mountain clusters.

of the three major groups of populations are significantly different from one another, with the cline again decreasing inland. Although the clines for these three characters are generally similar, their relative expressions follow different patterns, and they must thus be considered discordant characters.

Hitchcock, *et al.* (1959) state the range of *M. ferruginea* var. *glabella* (Gray) Peck as follows: "Rocky Mts., Alta. and B.C. to Wyo., westward to e. Wash. and Oreg. and down the Columbia to Mt. Hood and Mt. Adams, where the two varieties freely interbreed." The only specimen from the Columbia Plateau Province of which we are aware was collected at Twin Lakes, in northeastern Washington (Ferry Co.). This collection came to our attention too late to be included in the analyses. In fact, *Menziesia* seems to be poorly collected throughout the critical western part of the Rocky Mountain areas. However, some indirect evidence supporting Hitchcock's statement is found by referring to the density of puberulent hairs on the calyx in Fig. 2. The Oregon Cascade and United States Rocky Mountain areas form a single statistical population, separate from all others, being the only areas in which the mode for this character is not zero. The pattern of variation for this character would certainly indicate some degree of gene flow across the Columbia Plateau or the northern Great Basin in the present or recent geologic past.

The foregoing comments necessitate a more detailed consideration of the probable migrational history of the genus in western North America. It appears from present distributions of member species and by analogy with ecologically similar species which have left a paleontological record that *Menziesia* has migrated southward from an originally boreal distribution with the increasingly temperate climate in this region during the first half of the Tertiary. In the Ericaceae, generic distinctions on the basis of pollen morphology are difficult, and direct evidence of *Menziesia's* migrational routes are lacking (Hansen, 1947; 1955; Heusser, 1960). The following discussion assumes that *Menziesia* has a similar migrational history to other boreal species whose pollen records have been studied.

In Wisconsin Pleistocene times, glaciers formed in the mountains of British Columbia, which led to the development of more massive piedmont glaciers and finally to a virtually continuous ice sheet that covered all of western Canada and the northern half of Washington and parts of Idaho and Montana. Alpine valley glaciers and piedmont glaciers also formed in the mountain ranges much farther to the south (Flint, 1945; 1957). The interior of Alaska and the more westerly portions of the Yukon Territory were not covered by the ice sheet. This area must have acted as a refugium for many boreal species during the Wisconsin glacial period. The western North American ice sheet was thickest and persisted the longest in central British Columbia where it had no direct outlets (Flint, 1957); *Menziesia* is today absent from this area. It seems likely that this is due not only to the long persistence of Wisconsin ice, but to the warming and drying trend which immediately followed the melting of the glaciers and culminated about 6,000 years ago (Hansen, 1947; 1955) making the area climatically unsuitable for *Menziesia.*

It also seems likely that during glacial periods *Menziesia* occupied much area in the southern Cascades and the Great Basin where it has not been able to persist. Certain present distributions support this hypothesis. *Menziesia* commonly co-occurs with *Chamaecyparis nootkatensis* (Lamb.) Spach along the coasts of British Columbia and Alaska. The two also co-occur at the southernmost montane locality known for *Menziesia,* in the Oregon Cascades (*J. C. Hickman 492-4,* ORE.; *J. C. Hickman 492-5,* ORE). Several collections of *Chamaecyparis* have also been taken from an evidently relictual population of large trees in the Aldrich Mountains of east-central Oregon (*A. Cronquist 7646,* DS; *O. V. Mathews,* 1940 DS). These collections may indicate that cool, moist conditions prevailed during the Pleistocene in much of what is now semi-arid region between the Cascade and Rocky Mountains, and that *Menziesia* could have been widely distributed through this area.

The interrelationships among the populations have also been analyzed by computing phenetic similarity (fig. 3). On the lower clustering levels the complexity of patterns is the most striking characteristic. This is not true for the Rocky Mountain areas, however, indicating that they constitute the least variable grouping. Other small clusters show great geographical diversity in their members: OTU's cluster first with a member of the same area in only one third of the instances. It is the higher clustering levels that should be expected to indicate possible subspecific taxonomic divisions. The Rocky Mountain populations and the bulk of the Cascade populations cluster in a large group, parallel to the large group of coastal forms with which the remainder of the Cascade individuals are more closely allied. Here the homogeneity of the Rocky Mountain cluster does not imply that these plants constitute the most distinct grouping. It is not surprising that the Cascade and Rocky Mountain materials are phenetically similar since these two areas probably have greater environmental similarities than has either with the coastal area. That the Coastal cluster contains numerous OTU's from the Cascade area (and the converse) suggests the possibility of greater or more recent gene flow between them. This is supported by the present geographical continuity between the coastal and Cascade areas at Manning Park and the possibility of more southerly connections in the recent geologic past as suggested by Detling (1954; 1958).

Conclusions

The variation pattern in *Menziesia ferruginea* is complex. Univariate and multivariate analyses show that no single character nor set of characters studied can be used to separate individuals into geographically or ecologically coherent categories. Thus, the erection of subspecific taxa is inappropriate and inadequate for describing this pattern. It must rather be explained in terms of migrational history, past and present gene flow, and adaptations to existing environments. These factors have led to an overlapping and partially discordant complex of morphological clines from north to south and from the coast to the Rocky Mountains. We suggest that in future works botanists consider *M. ferruginea* Smith var. *glabella* (Gray) Peck to be a later synonym for *M. ferruginea* Smith.

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THE DISTRIBUTION OF PINACEAE IN AND NEAR NORTHERN NEVADA

William B. Critchfield and Gordon L. Allenbaugh

Introduction

More than 50 years ago G. B. Sudworth (1913) observed: "Contrary to popular belief, our present knowledge and published records of the geographic range of North American trees is still very incomplete." This statement remains true today for much of the interior West, particularly the semi-arid Great Basin. Although the botanical exploration of this region began over a century ago, information about the distribution of native trees is still sketchy and inaccurate. This is true even of the Pinaceae, although most of the trees in this family are readily identifiable and are among the most conspicuous elements of the vegetation.

One reason for this lack of information is the unique topography of the Great Basin, which is made up of many smaller basins with interior drainage. Tree growth is mostly confined to the numerous isolated mountain ranges, called basin ranges. These ranges, usually oriented north and south and typically much longer than wide, occupy about half the total area of the Great Basin (Fenneman, 1931). The intervening valleys, which sometimes contain playas or playa lakes, are usually treeless. Many of the basin ranges are rather inaccessible, and plant collections from some of them are few or nonexistent.

Throughout much of the Great Basin three pines, *Pinus monophylla, P. flexilis,* and *P. aristata,* are among the dominant elements of the montane vegetation (Billings, 1951). Toward the north and northwest, however, they disappear and other members of the Pinaceae appear as outliers of the coniferous forests that border the northern Great Basin. This transitional area is the region covered by this paper (fig. 1). It includes much of the northern Great Basin and a physiographically similar portion of the Snake River drainage (southeastern Idaho and adjoining parts of Oregon and Nevada). This paper reports several extensions of species ranges, summarizes what is currently known about the distribution of the Pinaceae in this region, and reviews the events that may have brought about the present "insular" distribution of these conifers.

Sources of Information

The first detailed maps of these conifers were those of Sudworth (1913; 1916; 1918). His original working maps, which are on file at the Washington Office of the U. S. Forest Service, have been helpful in establishing the sources of his information. Revised versions of Sudworth's maps were published by the Forest Service in 1938 (Munns, 1938). Recently, revised distribution maps of all of the Pinaceae of this region have been published (Fowells, 1965; Critchfield and Little, 1966).

The Idaho ranges of these species have also been mapped by Johnson (1966).

The principal descriptions of the distribution of the Pinaceae in this region are those of Billings (1954) and Little (1956). Parts of the region were covered by Sudworth (1908) and Holmgren (1942).

Unpublished sources of information include field observations and specimens in several herbaria. Our collections are not cited in the text, but the localities that we visited are indicated in Fig. 1. Specimens from these localities are in the conifer herbarium of the Institute of Forest Genetics, Placerville, California (IFGP: Critchfield, 1966), and some of them are duplicated in these herbaria: US, USFS, and MSC. Several government agencies which have supplied us with information and collections are cited in the text by these abbreviations: Forest Service, U. S. Department of Agriculture (FS); Bureau of Land Management, U. S. Department of the Interior (BLM); and Nevada State Fish and Game Commission (NFG).

The contributions of several individuals and agencies are referred to in the text. We also wish to thank J. R. Griffin, E. L. Little, Jr., and J. L. Jenkinson for their help.

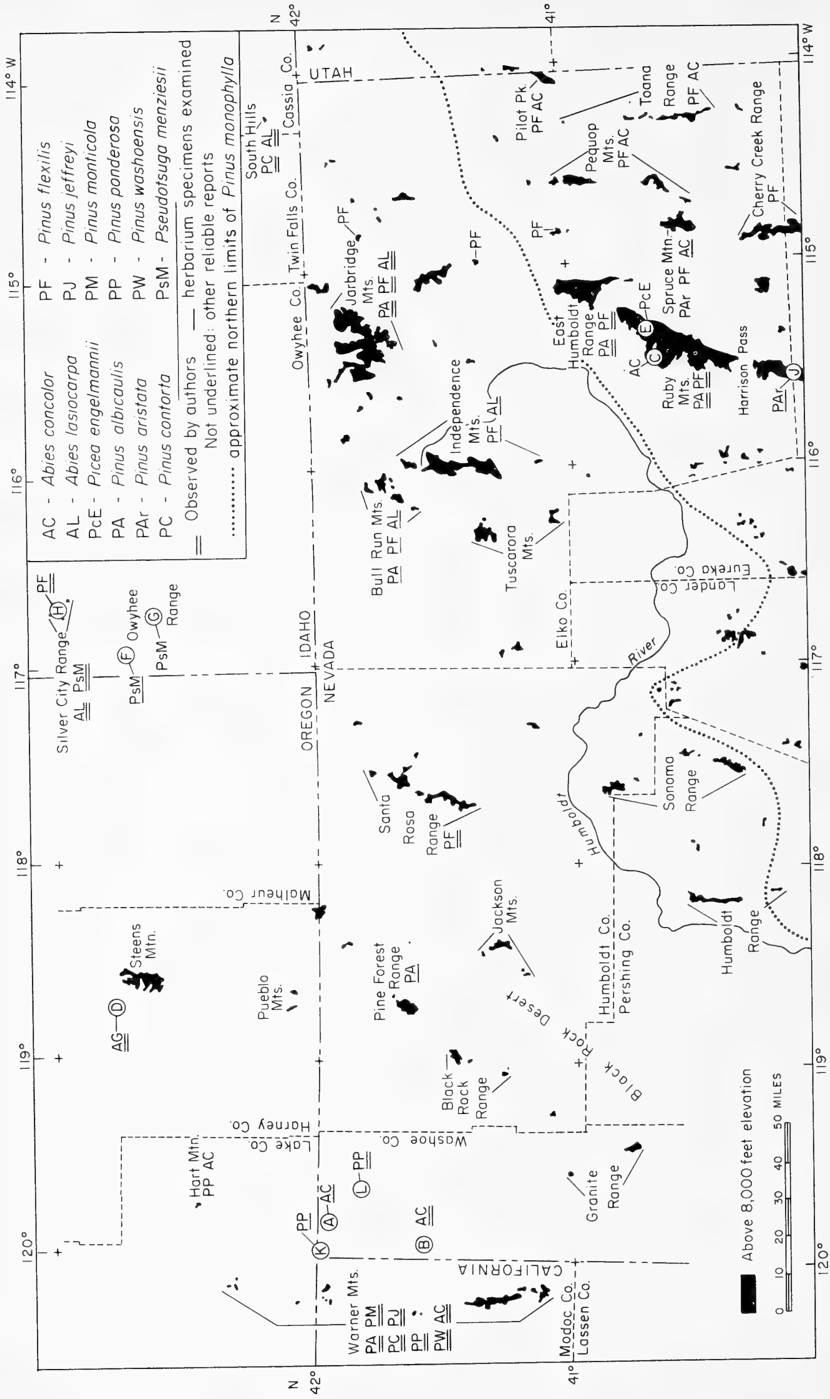
THE DISTRIBUTION OF SPECIES

ABIES CONCOLOR (Gord. & Glend.) Lindl. White fir. Both California white fir and Rocky Mountain white fir extend into widely separated parts of this region. The former is sometimes called *A. lowiana* (Gord.) A Murr. or *A. concolor* var. *lowiana* (Gord.) Lemm. to distinguish it from Rocky Mountain white fir, which extends from the southern Rocky Mountains into the eastern and southern parts of the Great Basin. These two geographically separated strains differ in morphology, but their status as separate taxa is not universally recognized.

It has been known for many years that California white fir grows in the Warner Mountains of northeastern California and southern Oregon and in the nearby Hart Mountain area of southern Oregon (Sudworth, 1908). White fir is one of the commonest trees in the mixed-conifer forest of the Sierra Nevada and southern Cascade Mountains, and the forests of the Warner Mountains are an impoverished eastward extension of this vegetation type.

East of the Warner Mountains, several unreported outliers of white fir grow in a range of low mountains in the northwestern corner of Nevada. These mountains do not have a generally accepted name now, but in the past they have been called the East Warner Mountains. This range is separated from the Warner Mountains by Surprise Valley and from the mountains to the east by Long and Coleman Valleys.

Near the northern end of the range, just west of Coleman Valley and a few miles south of the Oregon border, are two fairly extensive creek-bottom stands of white fir about two miles apart (fig. 1A: 41°57.7′ N Lat, 119°50.0′ W Long, and 41°56.4′, 119°49.5′). They are growing at


AC - Abies concolor
AL - Abies lasiocarpa
PcE - Picea engelmannii
PA - Pinus albicaulis
PAr - Pinus aristata
PC - Pinus contorta
PF - Pinus flexilis
PJ - Pinus jeffreyi
PM - Pinus monticola
PP - Pinus ponderosa
PW - Pinus washoensis
PsM - Pseudotsuga menziesii
Observed by authors — herbarium specimens examined
Not underlined: other reliable reports
approximate northern limits of Pinus monophylla
114° W
115°
116°
117°
118°
119°
120°
42° N
41°
UTAH
IDAHO
NEVADA
OREGON
CALIFORNIA
Cassia Co.
Twin Falls Co.
Owyhee Co.
Malheur Co.
Harney Co.
Lake Co.
Washoe Co.
Modoc Co.
Lassen Co.
Elko Co.
Eureka Co.
Lander Co.
Humboldt Co.
Pershing Co.
South Hills PC AL
Jarbridge Mts. PA PF AL
PF
Pilot Pk. PF AC
Toana Range PF AC
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Cherry Creek Range PF
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Granite Range
Warner Mts. PA PM PC PJ PP PW AC
Above 8,000 feet elevation
0 10 20 30 40 50 MILES

5500–6800 ft along spring-fed streams which flow eastward into Coleman Valley (BLM). J. C. Fremont's first expedition may have passed within sight of these stands when it entered Nevada through Coleman Valley early in 1844. The first and only botanists known to have visited them are F. V. Coville and J. B. Leiberg, who collected white fir in this vicinity in 1896 (Coleman Valley, *Coville & Leiberg 119,* US).

Twenty-five miles to the south is a third and much smaller outlier growing around a spring at the head of Forty-nine Canyon (fig. 1B: 41°35.2′ N Lat, 119°54.9′ W Long, 6000 ft elev.). This grove, also reported to us by BLM, is within sight of Nevada State Highway 8A. It consists of 10 large trees and several times as many seedlings and saplings. The largest trees range up to 4 ft in diameter at breast height, and are at least 200–300 years old.

These outliers of California white fir are separated by more than 200 miles from the northwestern limits of Rocky Mountain white fir (fig. 1). The latter is present in the higher ranges of east-central and southern Nevada (Billings, 1954; Little, 1956), and extends north into southern Elko County. There it grows on Pilot Peak (NFG, BLM), in the Toana Range (NFG; A. H. Holmgren, pers. comm.), in the Pequop Mountains (NFG), and on Spruce Mountain (*Zavarin 723–737,* IFGP). A single stand in the northern Ruby Mountains (fig. 1C) is located at an elevation of about 8500 ft in Seitz Canyon, at 40°39′ N Lat, 115°28′ W Long (FS).

Older distribution maps erroneously show white fir in many of the mountain ranges of northern Elko Co., south-central Idaho, and northwestern Utah (Sudworth, 1916; and Munns, 1938). The most recent map of the species still shows it on one of these ranges—the South Hills, in Idaho (Fowells, 1965). The presence of white fir north of southern Elko Co. has not been verified, and this error may have originated from confusion between this species and *Abies lasiocarpa.*

ABIES GRANDIS (Dougl.) Lindl. Grand fir. The typical form of grand fir, which ranges from northern California to western Montana, does not enter or even approach the Great Basin. In the southern part of its range, however, grand fir appears to intergrade with white fir through a broad zone extending from northwestern California to western Idaho. This intermediate form extends into the northwestern Great Basin. The only representative of the Pinaceae in the southeastern corner of Oregon, it is present in a single locality on the west slope of Steens Mountain (fig. 1D).

Although this stand is not shown on distribution maps or listed in floras, its existence has been known for many years. F. V. Coville visited it in 1896 (*Coville 598,* US). An early geological report on Steens Mountain probably referred to this stand in the following statement: "A few pines, firs, junipers, and cottonwoods grow in the deep canyons on its west slope" (Russell, 1903). In another geological report Waring (1909),

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FIG. 1. The distribution of Pinaceae in northern Nevada and adjacent areas. Circled letters A to L are localities mentioned in the text.

commenting on the remarkable absence of timber on this range, noted as one of the exceptions "a small group of firs in one canyon." In 1938, O. V. Matthews collected wood samples of the fir, which he called *A. concolor* (Anon, 1944).

The Steens Mountain fir grows along the banks of Big and Little Fir Creeks and on the north-facing slopes of their canyons. The stand extends a short distance below the point where they join to form a stream known as Mud or Fir Canyon Creek. The main stand ranges in elevation from 5900 to 6200 ft, and covers an estimated 30–40 acres (42°47′ N Lat, 118°43′ W Long). About a mile to the south is an outlier consisting of a few trees (BLM).

The Steens Mountain stand is nearly equidistant from *A. concolor* in south-central Oregon and the intermediate populations of the Blue Mountains to the north. We have grouped it with *A. grandis* because it is morphologically similar to the Blue Mountains fir, which at present is commonly classed with *A. grandis* (Fowells, 1965).

ABIES LASIOCARPA (Hook.) Nutt. Subalpine fir. This high-elevation tree extends westward from the Wasatch Mountains into the Great Basin at least as far as the Deep Creek Range, just southeast of the region considered here (McMillan, 1948). It is absent from the isolated ranges in the northern Great Basin, but in the northern part of Elko Co. it is one of the commonest trees in the mountains that form the divide between the Great Basin and the Snake River drainage. It grows in the Bull Run and Jarbidge Mountains, and in the Independence Mountains it extends at least as far south as the Jack Peak area at 41°30′ N Lat (FS). Subalpine fir is also a common tree on two ranges north of this divide—the Silver City Range and the South Hills (fig. 1). From the South Hills this fir extends eastward to the Wasatch and Rocky Mountains.

Abies lasiocarpa may be the fir that Sereno Watson encountered in the extreme northwestern corner of Utah on King's 1867–68 Fortieth Parallel Expedition. Watson crossed the northern end of the Goose Creek Mountains, which extend southwest from this corner of Utah into Nevada. In some of the moist canyons, he found a tree that he called *A. grandis* (Watson, 1871). His description does not fit any of the western firs, but *A. lasiocarpa* is the only fir on the nearby ranges, including the Albion Mountains (FS) and South Hills to the north and the Raft River Mountains to the east (Preece, 1950).

A report of *A. lasiocarpa* on Steens Mountain (Bailey, 1936) is probably a mistake. Bailey's table 7 lists it in the Hudsonian zone of this range, but in the text he notes that the aridity of Steens Mountain eliminates all of the trees characteristic of the Hudsonian zone.

PICEA ENGELMANNII Parry. Engelmann spruce. This species—the only spruce of the northern Great Basin—is common north and east of this region. It extends west from the Rocky Mountains to the Raft River Mountains (Preece, 1950) and the Albion Mountains (FS). It stops short of the South Hills in southern Idaho, although it is often shown there (Munns, 1938; Johnson, 1966; Fowells, 1965). Farther south, another salient extends westward from the Wasatch Mountains to the Deep Creek Mountains (McMillan, 1948) and the nearby high ranges of eastern Nevada (Billings, 1954; Little, 1956).

In the region treated here, Engelmann spruce is definitely known in only one locality, the head of Thorpe Creek in the northern Ruby Mountains (FS). This stand is located at an elevation of 9–10,000 ft at 40°42′ N Lat, 115°20′ W Long (fig. 1E). There may be other small outliers in this range, however. Sereno Watson, the first botanist to visit the Ruby Mountains, noted that "in some of the high western canyons there is a dense growth of *Abies* [*Picea*] *engelmannii*" (Watson, 1871). He traveled extensively in the southern and central Ruby Mountains, and his routes are shown on the map accompanying his account. Since the northernmost point that Watson visited was nearly 10 miles south of Thorpe Canyon, the stands of Engelmann spruce that he found may have been overlooked since 1868.

Watson called the Ruby Mountains the "East Humboldt Mountains." The later change of names has caused a great deal of confusion, since two other ranges in northern Nevada are sometimes called the East Humboldt Mountains at present. One of them, a northward extension of the Ruby Mountains, was called the Clover Mountains by Watson. The other range, located east of the Humboldt Mountains in Pershing County, is called the East Humboldt or East Range. (Watson referred to it as the Pah-Ute Mountains.) A Pershing County outlier of *P. engelmannii* shown by Munns (1938) can probably be attributed to this change in place names.

Engelmann spruce is also sometimes shown in the Silver City Range (Munns, 1938; Fowells, 1965). This southern Idaho occurrence has not been verified, and is probably in error.

PSEUDOTSUGA MENZIESII (Mirb.) Franco. Douglas fir. Of the two generally recognized geographic races of this species, only the Rocky Mountain Douglas fir (var. *glauca* (Beissn.) Franco) extends into this region. The Pacific Douglas fir (var. *menziesii*) reaches its eastern limits west of the Warner Mountains.

Rocky Mountain Douglas fir, like Engelmann spruce, extends west from the Wasatch and Rocky Mountains in two salients. In the north it reaches the Raft River Mountains (Preece, 1950) and the Albion Mountains (FS). Like Engelmann spruce, Douglas fir stops short of the South Hills, although it is generally mapped there (Sudworth, 1918; Fowells, 1965; Johnson, 1966). The southern salient extends westward from the Wasatch Mountains to the Deep Creek Range (McMillan, 1948) and the higher ranges of east-central Nevada (Billings, 1954; Little, 1956). Unlike Engelmann spruce, Douglas fir is not known to extend north into Elko Co., although Sudworth (1918) and Munns (1938) showed it in the Ruby Mountains on the basis of an unpublished report accompanying Sudworth's original working map of this species ("Ruby Mountains at Harrisons Pass, scarce").

The only known stands of Douglas fir in this region are in southwestern Idaho. It is a common tree in the Silver City Range, sometimes considered part of the Owyhee Range. Two other sizable but previously unreported outliers are present in the Owyhee Range to the south (BLM; fig. 1F, G). Around South Mountain (42°45′ N Lat, 116°55′ W Long) this species is distributed rather widely, with a much smaller patch (100–200 acres) about 12 miles to the southeast (42°38′, 116°42′).

Douglas fir has also been reported in the mountains of northern Elko Co. (Billings, 1954; Little, 1956; Fowells, 1965), but we consider this occurrence doubtful. These reports are based on specimens collected on Cobb Creek and Merritt Mountain, south and northeast of Mountain City (*Nichols & Lund 373, 453,* RENO). However, Forest Service and other local informants are unanimous in stating that they have never seen Douglas fir growing in nature anywhere in these mountains.

PINUS MONTICOLA Dougl. Western white pine. This pine is widely distributed north and west of the Great Basin. It enters the region considered here only at its western edge, in the Warner Mountains. It was first encountered on the higher peaks of this range by C. Hart Merriam in 1896 (Sargent, 1897).

PINUS ALBICAULIS Engelm. Whitebark pine. This pine is characteristic of high elevations, extending to timberline, in the high mountains west and north of this region and in the Warner Mountains. It is also unexpectedly common in several mountain ranges of northern Nevada. Its presence there was not reported until recently, although it has occasionally been collected in this region during the past 70 years. One reason that *P. albicaulis* has been generally overlooked is its close similarity to *P. flexilis,* which is much more widely distributed in the Great Basin region. The two species differ greatly in their cones, but the rather fragile cones of *P. albicaulis* are nearly always destroyed by birds or small mammals as they approach maturity or soon thereafter. Vegetatively these two white pines are much alike; a reported difference in the number and distribution of resin canals in the needles of trees in southern Montana and western Wyoming (Ericson, 1964) does not hold true in Canada (Brayshaw, 1965) or northern Nevada.

The presence of whitebark pine in the higher parts of the Warner Mountains has been known since C. H. Merriam found it there in 1896 (Sargent, 1897). Sudworth (1913) and Munns (1938) did not record it elsewhere in this region. Their maps show it in two localities to the east, the Albion Mountains of Idaho and the Wasatch Mountains east of Salt Lake City, but we have been unable to verify either of these occurrences. Holmgren (1942) did not list whitebark pine in his flora of northeastern Nevada. Billings (1954) reported "vegetative specimens (probably authentic) . . . from . . . Pine Mountain in Humboldt County."

We have not been able to locate a Pine Mountain in Humboldt Co., but there is a Pine Mountain in northern Elko Co. (41°46′ N Lat, 115°37′ W Long). Authentic *P. albicaulis* has been collected there (*Hitchcock 1177,* US), and this may be the locality to which Billings referred.

The first report that whitebark pine is widely distributed in northern Nevada was that of Little (1956). He recorded it in the Pine Forest Range of Humboldt Co., and the Jarbidge Mountains, Ruby Mountains, and Pine Mountain, all in Elko Co. In addition to these areas, it is now known to occur in the East Humboldt Range and the Bull Run Mountains, both in Elko Co. (fig. 1).

Whitebark pine is the only pine of the Pine Forest Range. This stand is far removed from any other stand of this species—at least 70 miles east of the Warner Mountains and nearly twice that distance west of the nearest stands in northern Elko Co. Presumably this is the pine referred to in an early geological report: "The Pine Forest Mountains are covered over a limited area with a forest of yellow pine, from which this range derives its name" (Russell, 1885). Whitebark pine was collected here in 1896 (*Streator 1015,* US) and 1901 (*Griffiths & Morris 225,* US), but these collections were overlooked for more than 50 years. The pine of the Pine Forest Range was identified as "*Pinus flexilis* (?)" by Taylor (1912), a zoologist who did extensive field work in this area. His identification was based partly on foliage, "no cones being at hand," and partly on geographic and zonal considerations. One of Taylor's photographs of this pine was included in Hall's comprehensive treatment of the mammals of Nevada, captioned "limber pines in the Pine Forest Mountains" (Hall, 1946, plate 2b). The identification of this pine as *P. albicaulis* by Little (1956) is the first mention in the botanical and forestry literature of this or any other pine in these mountains. The Pine Forest stand was visited a few years ago by A. Cronquist, who noted that the pines are confined to the granitic rocks that make up the core of this range (pers. comm.).

In the Jarbidge Mountains of northern Elko Co., *P. albicaulis* is the only common pine; *P. flexilis* is present but rare. In this region *P. albicaulis* reaches much lower elevations than it does at the same latitude in California. It grows from as low as 6400 ft in the valley of the Jarbidge River to above 10,000 ft in the Jarbidge Mountains to the east. It is known to extend as far northeast as Pole Creek, at about 41°55′ N Lat, 115°15′ W Long (*Nelson & McBride 2070,* US, A). Its range in northern Elko Co. has recently been extended as far west as the Bull Run Mountains, where it was collected by S. A. Scott (FS) at 41°42′ N Lat, 116°08′ W Long, 8600 ft elevation (*Scott,* 1965, IFGP). This species has not yet been reported from the Independence Mountains, a higher southward extension of the Bull Run Mountains.

South of the Humboldt River *P. albicaulis* appears in the connected Ruby and East Humboldt Ranges. Around Angel Lake, at 8400 ft in the East Humboldts, it is intermingled with *P. flexilis*. In the Ruby Mountains we have seen it at the head of Lamoille Canyon, a U-shaped glaciated valley which penetrates deeply into the northern part of the range. Below 8500 ft we saw only *P. flexilis,* but above that elevation *P. albicaulis* is the more common of these two pines. Both species are still present at 10,000 ft on the crest of the range south of Lamoille Canyon. *P. albicaulis* extends at least as far south as Green Mountain, at 40°23′ N Lat (FS), but it has not yet been reported in that part of the Ruby Mountains south of Harrison Pass. At Green Mountain it reaches its southermost known limit in the region east of the Sierra Nevada.

PINUS FLEXILIS James. Limber pine. This pine, one of the characteristic trees of the basin ranges, is present on the higher mountains throughout most of Nevada except the extreme western part (Billings, 1954; Little, 1956). Holmgren (1942) reported that it is frequent in the higher mountains of Elko Co. Most distribution maps (Sudworth, 1913; Munns, 1938; Little, 1949) show it in the mountains of Elko Co. and in the Warner Mountains of California.

Limber pine is widespread in the eastern part of this region. It was collected in the Ruby Mountains by Sereno Watson nearly a century ago ("East Humboldt Mountains," *Watson 1113,* US). Holmgren (1942) noted limber pine on Spruce Mountain, at the southern end of the Pequop Mountains (fig. 1). Here, according to R. D. Wright (pers. comm.), it is mixed with bristlecone pine *(P. aristata)* in an extensive forest that extends from 9000 ft to the top of the mountain.

In the northern part of Elko Co., limber pine is present in the Independence Mountains (*Kinnaman 21,* FS), Bull Run Mountains (*Scott,* 1965, IFGP), Pine Mountain (*Hitchcock 1176,* US), and the Jarbidge Mountains, where it is quite rare. We found only two small groves in the valley of the Jarbidge River, one growing on a rocky outcrop on the canyon wall (41°48′ N Lat, 115°24′ W Long), and the other on the bank of the river (41°55′, 115°25′).

Elsewhere in Elko Co. limber pine is present in most of the higher mountains (fig. 1). For this information we are indebted to L. W. Hoskins (NFG, pers. comm.).

North and east of this corner of Nevada the distribution of limber pine is sporadic. It is absent from the South Hills, but is frequent at higher elevations in the Raft River Mountains (Preece, 1950), and is present in the Albion Mountains (Johnson, 1966). In the Silver City Range of southwestern Idaho, only two trees of this species have been found (fig. 1H). They are growing near the top of War Eagle Mountain at 8100 ft elevation, 42°59′ N Lat, 116°40′ W Long (W. H. Baker, pers. comm.).

In the western half of this region, limber pine is present only in the Santa Rosa Range of eastern Humboldt Co. It does not appear to have been reported from this range before, although it is not uncommon. It grows in scattered patches near the crest of the mountains.

Limber pine is shown in the Warner Mountains on many distribution maps of this species. This error can be attributed to an early misidentification of some other five-needled pine, probably western white pine. Excerpts from a 1903 report by Filibert Roth on the Warner Mountains Forest Reserve, which are on file at the Washington Office of the Forest Service, mention the appearance of limber pine with lodgepole pine at 7000 ft. It is not likely that Roth confused whitebark and limber pines, since he noted elsewhere that whitebark pine is common above 7500 ft. Western white pine, the only other white pine present in the Warners, is a more likely candidate for this persistent but erroneous extension of limber pine's range into northern California.

Pinus aristata Engelm. Bristlecone pine. Like limber pine, bristlecone pine is a characteristic tree of the basin ranges, but it is neither as common nor as widespread as limber pine. From the southern Rocky Mountains and the mountains of southern Utah it extends west to the Deep Creek Range (McMillan, 1948) and the higher mountains of eastern and central Nevada (Billings, 1954; Little, 1956). In northern Nevada it is known to occur on Sherman Mountain, at the southern end of the Ruby Mountains (fig. 1J; Little, 1956), and on Spruce Mountain in southern Elko Co. (Holmgren, 1942). On these two mountains bristlecone pine reaches its northwestern known limits. It was first collected in the Ruby Mountains— presumably on Sherman Mountain—by Watson in 1868 ("East Humboldt Mountains," *Watson 1112,* US), and it has since been collected on Sherman Mountain by others (*Hitchcock & Martin 5686,* POM). On Spruce Mountain, the upper slopes are occupied by an extensive forest of this species and limber pine.

Bristlecone pine was also mapped in the East Humboldt Range of Pershing Co. by Munns (1938). This erroneous range extension can be attributed to Watson's specimen from the "East Humboldt Mountains," later called the Ruby Mountains.

Pinus monophylla Torr. & Frem. Singleleaf pinyon. This species is the commonest member of the Pinaceae throughout much of the Great Basin. Mixed with juniper (usually *Juniperus osteosperma* (Torr.) Little), it occupies a broad woodland belt on the lower slopes of the mountains in the central and southern Great Basin. In north-central Nevada, it reaches its known northern limits south of the Humboldt River (fig. 1), although older maps often show it north of the river in Elko Co. (Sudworth, 1913; Munns, 1938; Little, 1949). East of the Nevada-Utah border it extends much farther north to the Raft River Mountains (Preece, 1950) and southern Idaho (Johnson, 1966). Its range in Nevada is shown in detail by Critchfield and Little (1966).

Pinus contorta Dougl. Lodgepole pine. Two geographic races of this widespread and variable species enter this region at places more than 300 miles apart. The open-cone Sierra Nevada-Cascade race, which has been called *P. contorta* ssp. *murrayana* (Balf.) Critchfield (Critchfield, 1957), grows in the Warner Mountains. The Rocky Mountain race (*P. contorta* ssp. *latifolia* (Engelm.) Critchfield), which often has serotinous cones, occurs in the mountains of southern Idaho as far west as the South Hills, where it is a common tree. In the South Hills area lodgepole pine stops a few miles short of the Nevada border (FS), although it is sometimes shown in the northeastern corner of that state (Munns, 1938). Nor does this species extend south from Idaho to the Raft River Mountains of northwestern Utah (Preece, 1950; FS), although it is shown there on the most recent maps (Fowells, 1965; Critchfield and Little, 1966).

PINUS JEFFREYI Grev. & Balf. Jeffrey pine. This primarily California species extends into this region only in the Warner Mountains. Although Sudworth (1908) recorded Jeffrey pine "at the sources of the Pitt [Pit] River," which originates in the Warners, it was not shown in the northeastern corner of California on older distribution maps (Sudworth, 1913; Munns, 1938; Little, 1949). The species is locally common in the southern Warner Mountains, and recent maps all record it there (Haller, 1962; Fowells, 1965; Critchfield and Little, 1966).

PINUS WASHOENSIS Mason & Stockwell. Washoe pine. This close relative of ponderosa pine is distributed along the western edge of the Great Basin in a few scattered localities from Lake Tahoe north. It enters the region that we are concerned with only in the Warner Mountains (Haller, 1961), where it intergrades with ponderosa pine. Haller, (1965) has suggested that hybridization between the Pacific and Rocky Mountain races of ponderosa pine may have played a role in the origin of this doubtfully distinct species.

PINUS PONDEROSA Laws. Ponderosa pine. One of the most wide-ranging trees in western North America, this species is unexpectedly absent from a large area in the center of its range, including nearly all of the northern Great Basin, northern Utah, southern and eastern Idaho, western Wyoming, and southwestern Montana. The many occurrences shown in this central region by Munns (1938) all appear to be in error. Baker and Korstian (1931) attributed this large gap in the range of ponderosa to a deficiency of moisture in the early part of the growing season.

The Rocky Mountain race of ponderosa pine (*P. ponderosa* var. *scopulorum* Engelm.) does not enter the region considered here, although it is present not far south in the mountains of eastern and southern Nevada (Billings, 1954; Little, 1956). The Pacific race extends east to the Warner Mountains and the Hart Mountain area of southern Oregon (Sargent, 1897; Sudworth, 1908). It is also present in northwestern Nevada in two localities that have not previously been reported.

One of these Nevada outliers (fig. 1K) is within a few miles of the ponderosa stands in and near the Warner Mountains. In the extreme northwestern corner of the state (41°59.5′ N Lat, 119°58.0′ W Long), a scattered stand of this species grows along Twenty-mile Creek at an elevation of about 5000 ft (BLM). It extends downstream a short distance into Oregon.

The other and much smaller outlier in northwestern Nevada is at least

20 miles from the nearest known ponderosa pine (fig. 1L). This grove, located on the west slope of Bald Mountain in the Sheldon National Antelope Refuge, was reported to us by O. V. Deming of the Fish and Wildlife Service, U. S. Department of the Interior (pers. comm.). It is growing at an elevation of 6500 ft at 41°50.0′ N Lat, 119°38.5′ W Long. It consists of one large tree (43 inches dbh, about 50 ft high) at least 300 years old, three smaller trees from 9 to 35 ft high and ranging in age up to about 70 years, and a large number of scrubby seedlings. Except for a few seedlings, the entire colony is confined to an outcropping of whitish rhyolitic sand which appears to be extremely infertile. The isolation of this grove and the distribution of tree ages suggest that all of the younger trees in the colony are descendants of the single old tree.

Discussion

The Pinaceae has a long history in the northern Great Basin. The four genera represented in this region today, *Abies, Picea, Pseudotsuga,* and *Pinus,* were present here 40 million years ago. All are elements of the Eocene flora of the Copper Basin, near the Jarbidge Mountains in northern Elko Co., Nevada (Axelrod, 1966). Several contemporary species are represented by closely similar fossil species in this conifer-rich flora: *Abies grandis* or *A. concolor* (*A. sonomensis* Axelrod), *Picea engelmannii* (*P. lahontense* MacGinitie), *Pseudotsuga menziesii* (*P. sonomensis* Dorf), *Pinus aristata* (?) (*P. crossii* Knowlton), and *P. ponderosa* (*P. harneyana* Chaney & Axelrod). During the ensuing Miocene epoch, several of these fossil species were also widespread on the Columbia Plateau north of the Great Basin (Chaney, 1959).

The highly discontinuous and sporadic distribution of the Pinaceae in this region today may have been influenced by events of the much more recent Pleistocene epoch. During Pleistocene times the climate of the Great Basin was periodically cooler and wetter than it is now, and these climatic cycles are widely believed to have caused major changes in plant distribution (Morrison, 1965). Lake Lahontan, a Pleistocene lake that covered much of northwestern Nevada during the pluvial periods, may have acted as a barrier to plant migration. The southern shoreline of the lake during the last pluvial period coincides rather closely with the present northern limits of *Pinus monophylla* (cf. Morrison, 1965, fig. 1; cf. Critchfield and Little, 1966, map 16). The northern arms of the lake, which extended to the Oregon border, may have restricted east-west migration. Cordilleran elements of the Pinaceae are confined to the region east of the lake. Their westernmost representative is *Pinus flexilis* in the Santa Rosa Range, just east of the Lake Lahontan shoreline. West of the shoreline, in northwestern Nevada, the outliers of the Pinaceae all have Pacific affinities with the possible exception of the *Pinus albicaulis* stand in the Pine Forest Range.

A lake the size of Lahontan could not have been more than a partial barrier to east-west migration across the Great Basin, however. It cannot entirely account for evidences of long-term separation between eastern and western elements of the Pinaceae in this region. Four of the most widespread species considered here have U-shaped ranges that border the northern Great Basin on the east, north, and west. All four, *Abies concolor, Pseudotsuga menziesii, Pinus ponderosa,* and *Pinus contorta,* are differentiated into well-defined geographic races on opposite sides of the Great Basin. It is improbable that these races met without mixing during the pluvials, since the eastern and western races of *Pinus ponderosa* and of *Abies concolor* have proved to be highly compatible in crosses made at the Institute of Forest Genetics, Placerville, California. Nor is it likely that these races have evolved as recently as the last pluvial, which is estimated to have been about 20,000 years ago (Martin, 1963). Both the long generation interval of these trees and the geographic extent of their races argue against this possibility. The alternative is that the Great Basin long antedates the late Pleistocene as a barrier between Pacific and Cordilleran segments of these conifers.

This conclusion is hard to reconcile with recent evidence of drastic vertical and latitudinal plant migrations in the Great Basin and the Southwest during the late Pleistocene. This evidence, much of it from analyses of fossil pollen in the Southwest, has recently been reviewed by Martin and Mehringer (1965). It supports the view that the disjunct distributions of the montane conifers considered here are remnants of former continuous distribution across the intervening basins.

A different interpretation of comparable patterns of distribution has been advanced by Wells (1966) and Wells and Berger (1967). Their investigations of late-Pleistocene macrofossils preserved in wood rat middens in west Texas and the southern Great Basin have failed to uncover any evidence of substantial downward displacement of high-montane conifers during the last pluvial period. They attribute the disjunct and sporadic distribution of these species to long-distance transport of propagules, rather than former continuity. This view of Pleistocene vegetational history provides some support for our interpretation of the Great Basin as a long-term barrier in the evolutionary history of these coniferous species.

Two range extensions in this region have been reported since this article was prepared. S. A. Scott (FS) has collected *Pinus albicaulis* in the Jack Peak area (41°30′ N Lat), extending the range of this species to the Independence Mountains (*S. A. Scott,* 1967, IFGP). C. W. Ferguson of the University of Arizona has found an extensive stand of *Pinus aristata* near the summit of Pearl Peak in the Ruby Mountains (Deseret News, Salt Lake City, Utah; Dec. 12, 1968), 7–8 miles north of the stand on Sherman Mountain.

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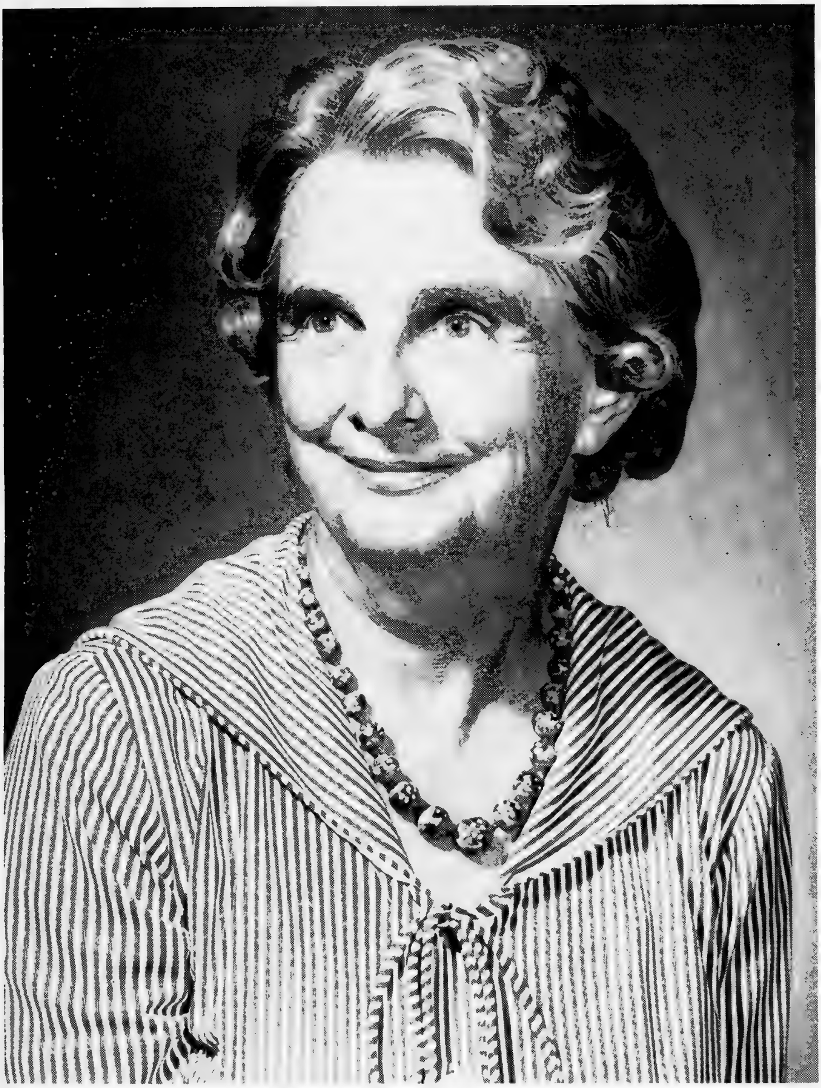
LAURA M. LORRAINE, 1904–1968

ROXANA S. FERRIS

To be a good botanical collector does not mean that one must be a professional botanist. The aesthetic enjoyment of seeing nature undisturbed and a desire to know something about the plants of meadows, streams and forests stimulated Laura Lorraine to collect flowers to satisfy this curiosity. During her college years at Stanford University, where she received her Bachelor's and Master's degrees in Romance Languages, she took a course on the classification of flowering plants with Dr. L. R. Abrams, a course designed for both botanical and non-botanical students. From this background of laboratory and field work, she acquired a most rewarding hobby.

Our many botanical excursions together were profitable as well as pleasant and extensive collections were added to the Dudley Herbarium at Stanford. The specimens were collected in Northern California or the Sierra Nevada. One of the pack trips in the Sierra yielded a new *Lewisia* —*Lewisia sierrae,* collected at the headwaters of the south fork of the San Joaquin.



Laura Lorraine was born in Michigan, December 12, 1904 and died in Sebastopol, California, February 5, 1968. After receiving her master's degree in 1926, she became a teacher at the Analy High School in Sebastopol, and with the exception of a 3-year leave of absence, held that post until her death. The leave was spent in New York as Executive Director of the National Business and Professional Women. Her administrative abilities were also evidenced during her long tenure at Analy High School by her work with the California Scholarship Federation, at the state as well as local level.

Dudley Herbarium, Stanford University

REVIEWS

The Population Bomb. By Paul R. Ehrlich. xiv + 223 pp., Ballantine Books, New York. 1968. $.95.

An argument of extreme importance for biologists and the future of mankind is raging within the rapidly-growing profession of futurology. One pole is represented by Kahn and Wiener, who argue in *The Year 2000: A Framework for Speculation on the Next Thirty-Three Years* that despite great increases in the world population, a trouble-free world is the most likely prospect for the next few decades. The opposite pole is represented by the book under review. A very large number of experts is lined up on both sides, and it is important to understand why reasonably well-informed people can have such remarkably different points of view. We will consider the basic issues in Ehrlich's book and explain why his critics err when they take issue with him.

1. The most basic contention Ehrlich makes is that there will be large-scale starvation in the world in about a decade, involving considerably more than the present 3½ million deaths per annum from this cause. Related to this point, he contends that family planning has been a failure, the impressive new strains of the cereal grains may lead to a variety of serious problems resulting in lower production than expected, and the maximum amount of animal protein we can get from the world's oceans is only about double the present annual catch. The optimists point out, on the other hand, that world rice production rose 12% in 1967, the take from the oceans increased sharply in Japan and Norway last year, and family planning can work, because the birth rate per capita is dropping sharply in the U. S. and elsewhere. In this bewildering barrage of facts, claims, and counterclaims, who is right? In general, there are three explanations for the discrepancies: successes tend to be well publicized, whereas typically only the real experts know about failures or omens of doom; there is a widespread tendency to underestimate the complexity of many problems, so that important factors are ignored in making predictions; and finally, many of the "experts" in this whole complex of problems are in fact only experts on one aspect. Physicists may not realize how little they know about epidemiology, and agronomists may overestimate their grasp of the current situation in fisheries, for example. In the case of the cereal grains, while the success with new strains is well known, the international crisis developing because of pesticide resistance in cotton pests is not. In general, few people grasp the basic ecological facts about pesticides: they generally produce a less serious long-term effect on the populations of pests than on the populations of parasites and predators that would normally control the pests, because of higher initial pest densities; as spray calendars draw on a greater variety of chemicals, cross-resistance to a wide variety of chemicals develops in the pests, so that there is rapid selection for pests that can withstand anything that can be used against them; and no matter what the details are of a control program, the long-term consequences of pest buildup are likely to be worse where the largest possible acreage is planted to the same species and variety. One of the best-informed books available on the future for cereal grains is Paddock and Paddock's *Famine 1975!,* for which the title gives the plot.

Two lines of argument support Ehrlich's contention that oceanic production cannot be enormously increased: a theoretical argument and one based on the history of exploited marine resources. The former is that much of the world's oceans are aquatic deserts because of inadequate upwelling of minerals, and further, since we typically harvest predators, there is great thermodynamic conversion inefficiency in harvesting food pyramids several steps removed from incident solar energy. Also, it would take too many calories per calorie obtained to make seiving plankton out of sea water a profitable activity in most parts of the oceans. The historical argument is that given the current economic demand for animal protein and the long experience exploiting most major oceanic stocks, how is it that many of these have shown an actual decline in yield over the last several decades if we have only begun to tap the resource?

The magnitude of the impending population-unplanned family catastrophe can best be grasped by studying a typical village in an underdeveloped country in detail, as in Gilbert Etienne's *Studies in Indian Agriculture*. To a considerable extent it has been possible to prevent massive catastrophe up to the present by increasing the proportion of all available land under cultivation. However, just about all land that could possibly be cultivated is now under cultivation, yet the population keeps increasing. Thus, mass famine can only be averted by increasing yield per acre, but thermodynamic realities impose an upper asymptote on this figure.

2. Ehrlich notes that pandemics may be a great problem in the near future, a point not made by many experts. The fact is that plague, for example, could break out on a fearful scale in India. Precisely those conditions that allowed a resurgence of plague in India in the 1940's are found there again: large numbers of rats per person moving freely through warehouses full of American grain shipments, with inadequate efforts being made to kill the rats or board up holes. Plague can explode with such speed that it could overwhelm public health organizations.

3. Ehrlich notes that we are seriously polluting the planet. The magnitude of this problem is not well known. Smog from Los Angeles is having a serious effect on plants far to the east of the surrounding mountains, and some authorities state that it is now causing enormous losses in agricultural productivity. Emphysema death rates are among the most rapidly rising variables on earth.

In general, it appears that more familiarity with existing data would show that it is Ehrlich's critics who err, not Ehrlich.—KENNETH E. F. WATT, Department of Zoology, University of California, Davis.

Rocky Mountain Flora. By WILLIAM A. WEBER. vii + 437 pp., 346 fig. University of Colorado Press, Boulder. 1967. $9.40.

"This book, a revision of the *Handbook of Plants of the Colorado Front Range,* culminates twenty years of intensive field and laboratory studies of the Rocky Mountain flora." It is a field guide to the "Ferns, conifers, and flowering plants of the Southern Rocky Mountains from Pikes Peak to Rocky Mountain National Park and from the plains to the Continental Divide. . . . Over 1,500 kinds of plants [1,400 species, cf. p. 2] are keyed and classified. The book is small enough to be carried in a rucksack [but not a pocket], and only a hand magnifier is needed to make the necessary examinations."

The introductory pages include a tantalizing review of why the vegetation of the Front Range is more than a "green blur." Weber points out that the flora of the Southern Rockies includes some taxa that are circumpolar; reoccur in the mountains of Central Asia; or are Tertiary relicts. The paragraphs on "Plant Geography" lead one to expect an important digest, but instead one is abandoned with a parsimonious list of examples on p. 6 and a reference to an earlier paper (Weber, W. A. 1965. Plant geography in the southern Rocky Mountains. *In* H. E. Wright, Jr., and D. F. Frey (editors). The Quaternary of the United States. Princeton Univ. Press, New Jersey.) which will not be available to many for whom this book is intended. This list, which could have kindled a lot of interest, is disappointing inasmuch as extraterritorial occurrences in the text frequently are neglected. None of the three endemics mentioned on p. 6 is clearly indicated in the text as not occurring elsewhere; one of these, *Aletes acaulis,* also occurs in New Mexico and Texas and must have been a mistake for *A. anisatus*. The selection of *Aralia racemosa* as an example of an "Eastern Woodland-prairie" cognate ought to have been explained as this species is not otherwise included in this book.

The remainder of the book is organized like its predecessor, as a continuous series of keys without the interjection of descriptions and the frills of endless measurements and literature citations. The first key leads to helpful categories such as Parasites (here including saprophytes), Aquatics, Vines, Monocots, Woody Dicots, and

Herbaceous Dicots. The families (and their genera) are arranged alphabetically within major groups, with the monocots appearing last. This is very practical for rapid finding of family and genus. The genera of Compositae are strictly alphabetical, but the grasses are arranged by tribe. Short commentaries on field observations are frequent with conscientious attention to ecology and distribution within the Front Range. Occasional synonyms are given and there are references to the second edition of the *Handbook* when there has been a change in name.

The illustrations by C. F. Yocom are an asset. The introduction and glossary use 78 of the 346 figures; thus, about 18 percent of the taxa are illustrated. The supplemental dissections or blow-ups shown beside the main drawings, which could have been helpful to beginners, are nowhere explained.

Weber has succeeded in presenting a handy and attractive two-fisted means for finding names of plants in the Front Range. The area where generally applicable is substantially greater than that of the Front Range; but both the area and the style are similar to those of the author's earlier *Handbook* and it would have seemed appropriate for this to have been the illustrated third edition without change of title. This volume distills much personal experience and is a welcome addition to the books on plants of the Rocky Mountains.—WALLACE R. ERNST, Smithsonian Institution, Washington, D. C.

Taxonomy of Flowering Plants. 2nd ed. By C. L. PORTER. ix + 472 pp., 400 plates (311 individual and sets of line drawings, 88 black & white photographs, 1 color photograph). W. H. Freeman and Company, San Francisco. 1967. $6.75.

The second edition of this popular text, now in a more readable print, is basically the same as the first edition, with few significant changes, but with numerous small refinements. Since Mooring's discriminating review of the contents and format of the first edition (Madroño 16:171–172) could apply equally appropriately to the second edition, this brief review pertains primarily to the refinements in the second edition.

In Part I, which deals with History, Principles and Methods, a brief discussion of chemical and numerical taxonomy has been added to the chapter on Concepts of Taxa. 63 additional entries are found in the lists of references at the end of chapters; charts have been improved in format, and boldface type has been substituted for italics wherever definitions occur. Part II, which covers "Selected Orders and Families of Monocotyledons" includes several additional examples of certain taxa plus three subclass descriptions. In Part III, which deals with "Selected Orders and Families of Dicotyledons," further examples of taxa, along with keys to the families of the Ranales and the "Tribes of the Asteraceae (Compositae)," have been added. A floral diagram has been corrected, and a qualifying statement on the Apetalae has been inserted.

Throughout the book, illustrations have been renumbered in groups with parts a, b, c, etc., instead of each individual illustration being numbered consecutively; several black and white photographs have been added, and the clarity of most of the photographs has been improved.

The second edition, like the first, contains few errors, and, despite minor reservations about the author's continued use of Fabaceae, Lamiaceae, etc., instead of traditional family names, impresses this reviewer as being an excellent text, if not the best available, for introductory taxonomy courses, especially those of less than a year's duration. The clear floral diagrams and line drawings will also be found very useful in lengthier introductory courses, but instructors would probably want to supplement the material on history and principles in such instances.—KINGSLEY R. STERN, Department of Biological Sciences, Chico State College, Chico, California.

Handbook of Northwestern Plants. By Helen M. Gilkey and La Rea M. Dennis. 505 pp., illustrated. Oregon State University Bookstores, Inc., Corvallis, Oregon 97331. 1967. $7.00.

Those of us who were botanically weaned on Gilkey's "Handbook of Northwest Flowering Plants" will welcome this edition of a most useful guide to the more conspicuous vascular plants of the Pacific Northwest. In this recent revision, Dr. Gilkey has been ably aided by La Rea Dennis, assistant curator of the Oregon State University Herbarium. The keys are easy to use and the illustrations are good. The concise descriptions of the plants are often accompanied by comments that make the book interesting browsing. However, although I agree that the flower of *Calypso bulbosa* has a "delicate lovely fragrance," I still remain to be convinced that it is the stems and leaves of *Lysichitum americanum* that are responsible for its skunk-like odor rather than its "pleasantly fragrant" flowers.

The present edition of the book represents a substantial revision over earlier ones. It is about 100 pages longer than the previous edition; this increased length is due not only to the use of larger type, but also to the inclusion of additional taxa. The book now includes vascular cryptogams, although earlier versions did not. This expanded coverage accounts for the altered title. Illustrations of various species also have been added, and the reproduction of most illustrations is superior to that in earlier editions. Nomenclature changes are evident throughout the work: the former *Baeria maritima* is now found as *Lasthenia minor* subspecies *maritima; Cacaliopsis* is a *Luina;* and in many other genera recent monographic work has been utilized. Errors seem to be few. For example, although *Oxalis stricta* is keyed out, a description of the species is missing from the text.

The authors have done a good job in selecting species to be included in this handbook, since it is not intended to be comprehensive. Readers are told to use other references for identification of grasses and sedges. Weeds are particularly prominent in the book, perhaps because they are likely to be picked up by amateurs or agriculturalists. Although this book will appeal to amateur botanists or novices, it will be of use to professionals in the region as well. Its small size makes it truly a handbook; its simplicity of style and ease of usage insure its wide adoption by northwesterners interested in naming the plants around them.—Robert Ornduff, Department of Botany, University of California, Berkeley.

NOTES AND NEWS

Zoe. A small reside of back numbers of the biological journal, *Zoe,* published by T. S. and Katharine Brandegee from 1890 until 1908 is available from the Herbarium, Department of Botany, University of California, Berkeley. No charge will be made except for postage. From Vol. I, numbers 1–4, 6, 8–10, and 12 are missing; from Vol. II, numbers 1 and 2 are missing; Vols. III and IV are complete; and from Vol. V, number 1 is missing.

New Distribution Record for Claytonia nevadensis from Northwestern California.—Chambers (Leafl. West. Bot. 10:1–8. 1963) reviewed the known distribution of *Claytonia nevadensis* Wats. citing specimens from a number of collections in the Sierra Nevada, the Mt. Lassen area and Steens Mountain in southeastern Oregon. In the summer of 1967 I collected this species in Trinity Co., Calif., apparently a new westward distribution record. The plants were found growing in dense clumps on wet, gravelly soil below the permanent ice field on the north side of Thompson Peak at an elevation of 7800 ft. There were several colonies observed in the immediate area. The specimens collected are deposited in the Herbarium of Humboldt State College (HSC), *Ferlatte 907,* August 11, 1967.—William J. Ferlatte, Division of Biological Sciences, Humboldt State College, Arcata, Calif.

NEW PUBLICATIONS

Evolution of the Fern Genus Osmunda. By C. N. MILLER, JR. Contributions from the Museum of Paleontology, University of Michigan, 21:139–203. 1967.

The Book of Grass, An Anthology on Indian Hemp. Edited by GEORGE ANDREWS and SIMON VINKENOOG. xiv + 242 pp. Grove Press, New York. 1967. $5.00.

The Lupines of Canada and Alaska. By DAVID B. DUNN and JOHN M. GILLETT. 89 pp. Canada Department of Agriculture, Research Branch, Monograph No. 2. 1966.

Key to the Native Trees of Canada. By T. C. BRAYSHAW. xix + 43 pp., illus. Bull. 125, Department of Forestry. Queen's Printer, Ottawa. 1961. $0.50.

The Ancient Bristlecone Pine Forest. Edited by RUSS and ANNE JOHNSON. 44 pp., illus. Chalfant Press, Inc., Bishop, Calif. 1966. $1.25.

Agrostology. By W. EDWIN BOOTH. vi + 222 pp., illus. The Endowment and Research Foundation, Montana State University, Bozeman, Montana. 1964.

Flora of the Cabeza Prieta Game Range. By NORMAN M. SIMMONS. Journal of the Arizona Academy of Sciences 4(2):93–104. 1966.

John Torey, A Story of North American Botany. By ANDREW DENNY ROGERS III. xiii + 352 pp. (Facsimile of the edition of 1942.) Hafner Publishing Co., 31 E. 10th St., New York. 1967. $7.50.

The Wild Flowers of California. By MARY ELIZBETH PARSONS, with a new table of changes in nomenclature by ROXANA S. FERRIS. cvi + 425 pp. (Facsimile of the edition of 1907.) Dover Publications, New York. 1966. $2.25, paper.

Plants and Civilization. By HERBERT G. BAKER. vii + 183 pp., illus. Wadsworth Publishing Co., Belmont, Calif. 1965.

A History of Botany in West Virginia. By WHELDON BOONE. xi + 196 pp., illus. McClain Printing Co., Parsons, West Virginia. 1965. $6.00. A very interesting little book full of biographical information about the professional and amateur botanists who have worked in West Virginia.

Place Names of Shasta County. By GERTRUDE A. STEGER, revised by HELEN HINCKLEY JONES. 71 pp. La Siesta Press, Glendale, California. 1966.

Notes on the Vegetation Zones of Western Canada, with Special Reference to the Forests of Wells Gray Park, British Columbia. By LEENA HÄMET-AHTI. Annales Botanici Fennici 2:274–300. 1965.

Plants of the White Mountains, California and Nevada. By ROBERT M. LLOYD and RICHARD S. MITCHELL. iv. + 60 pp., mimeographed. Department of Botany and White Mountain Research Station, University of California, Berkeley. Revised edition, 1966.

An English-Classical Dictionary for the Use of Taxonomists. By ROBERT S. WOODS. xiv + 331 pp. Pomona College, Claremont, California, 1966.

A Dictionary of the Flowering Plants and Ferns. By J. C. WILLIS, revised by H. K. AIRY SHAW. xxii + 1214 + liii pp. Cambridge University Press. 7th edition, 1966.

Flora of Peru. Solanaceae. By DONOVAN S. CORRELL. Botanical Series Field Museum of Natural History 13, part V-B(2):271–458. 1967.

Skyline Landscape of the San Francisco Peninsula Cities. By KATHRYN STEDMAN. 36 pp. The Council for Foothill Planning and Research, P.O. Box 11511, Palo Alto, California. 1966.

Skyline Scenic Parkway, San Francisco to Monterey, California. 24 pp. Loma Prieta Chapter, Sierra Club. 1966.

Exploring Our Baylands. By DIANE R. CONRADSON and HOWARD KING. 60 pp. Palo Alto Chamber of Commerce, Palo Alto, California. 1966.

A WEST AMERICAN JOURNAL OF BOTANY

A quarterly journal devoted to the publication of botanical research, observation, and history. Back volumes may be obtained from the Secretary at $12.00 per volume. Single numbers of Volumes 1 and 2 may be obtained at $1.00 and of Volumes 3 through 18 at $1.50. Some numbers are in short supply and are not available separately.

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

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

Abbreviations of botanical journals should follow those in *Botanico-Periodicum-Huntianum* (Hunt Botanical Library, Carnegie-Mellon University, Pittsburgh, Pennsylvania, 1968).

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MADROÑO

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THE XEROPHYTIC CUCURBITA OF NORTHWESTERN MEXICO AND SOUTHWESTERN UNITED STATES

W. P. Bemis and Thomas W. Whitaker

The genus *Cucurbita* is indigenous to the American continents. The center of origin probably is the tropical and semitropical regions of southern Mexico (Whitaker and Bemis, 1964). In the hot, arid deserts of northwestern Mexico and southwestern United States there occur a group of xerophytic species, possibly derivatives of populations from mesic ancestors that became adapted to climatic changes toward greater aridity. These species essentially are isolated geographically from other species of *Cucurbita,* and are well adapted to the highly specialized habitat to which they are currently restricted.

The restricted xerophytic species are *C. cylindrata* Bailey, *C. cordata* Wats., *C. palmata* Wats., and *C. digitata* Gray. Although a fifth species, the wide ranging and variable *C. foetidissima* HBK., is *truly xerophytic,* it is only distantly related to the four restricted species. Another species, *C. pedatifolia* Bailey from central Mexico, has some strong xerophytic characters, and may represent a transitional stage to the xerophytic condition. This paper is concerned with some of the biological characteristics of the restricted species that fit them for their specialized environment and their genetical relationships to each other and to other species of *Cucurbita.*

RANGE AND HABITAT

These species are confined to the extreme southwestern portions of the United States and adjacent Mexico. This area comprises some of the hottest and most arid locations on the North American continent. The general area is characterized not only by low average rainfall but by relatively prolonged precipitation-free periods; 6 to 10 consecutive months without rainfall are not unusual. At Bahia de Los Angeles in Baja California, Mexico, where *C. cordata* has been collected, a rain-free period of 23 consecutive months has been recorded (Hastings, 1964).

The xerophytic species must be well adapted to their rugged environment in order to survive. These species generally grow in loose, gravelly, well-drained soils below 4,000 feet elevation. The banks or the flood plains of dry, sandy washes are favorite habitats. Such habitats are normally free of stringent competition from other species, and because of their location are likely to receive relatively more moisture than other locations in this uncongenial environment.

Figure 1 shows the range or collection sites of the four species. *Cucurbita cylindrata* is found only in Baja California, mostly in Baja California del Sur, or in about the middle portion of the peninsula. *Cucurbita cordata* has been found only around Bahia de Los Angeles in Baja Cali-

MADROÑO, Vol. 20, No. 2, pp. 33–80. August 11, 1969.

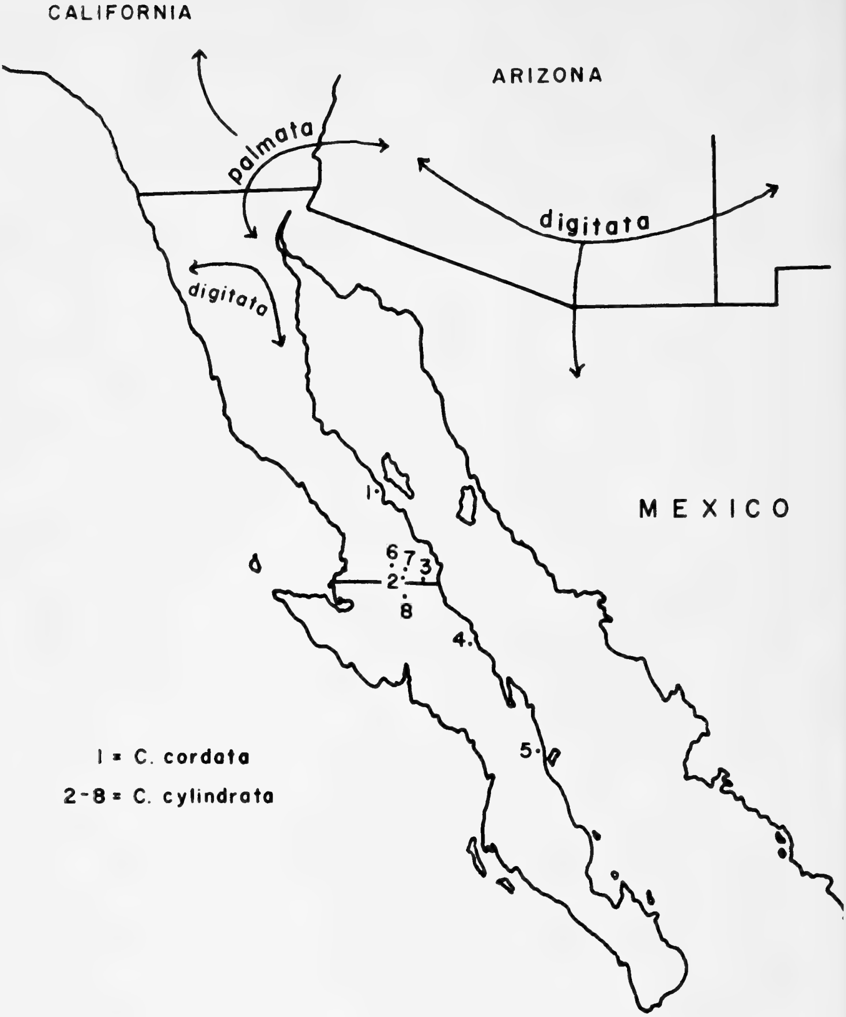
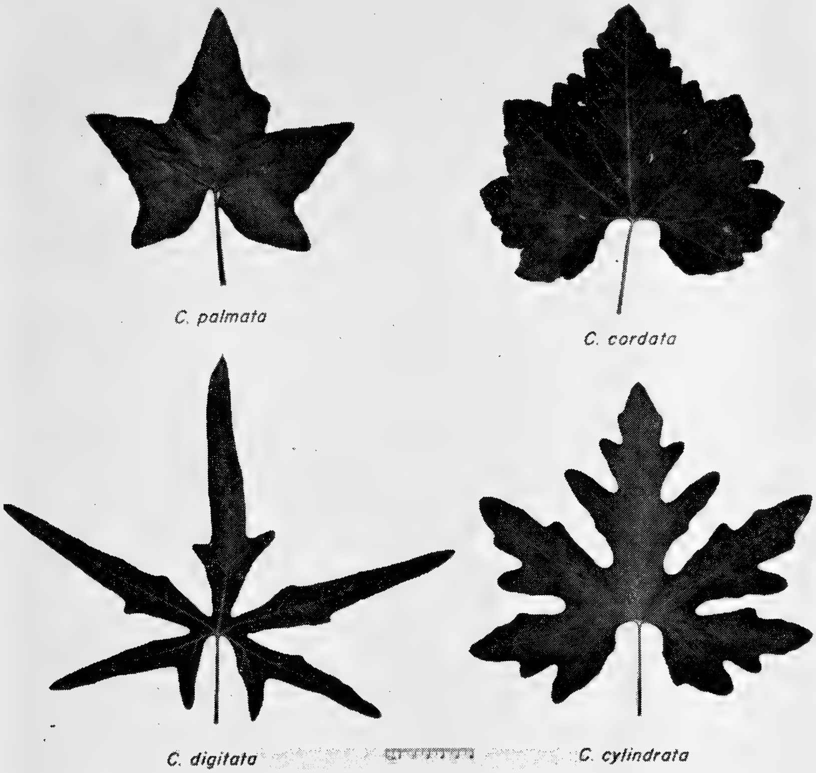


FIG. 1. Distribution of *Cucurbita palmata, C. digitata, C. cordata* and *C. cylindrata.*

fornia del Norte. It may be that *C. cylindrata* and *C. cordata* are sympatric in the central portion of Baja California. This suggestion, however, requires confirming data from more thorough botanical exploration of the peninsula.

The ranges of *C. palmata* and *C. digitata* are more extensive. *Cucurbita palmata* extends from the northeastern portion of Baja California through California into the San Joaquin Valley and lower portions of the Salinas Valley and eastward to near the Colorado River. *Cucurbita digitata* extends from northern Sonora, Mexico, into southern Arizona and New



C. palmata

C. cordata

C. digitata

C. cylindrata

FIG. 2. Typical shape of mature leaves of *Cucurbita palmata, C. cordata, C. digitata* and *C. cylindrata*.

Mexico. *Cucurbita digitata* also is found at higher elevations in northern Baja California. The ranges of *C. digitata* in southern Arizona and northern Baja California are separated by *C. palmata*. These two species are sympatric at the periphery of their ranges and in these locations interspecific hybridization between them was observed (Bemis and Whitaker, 1965).

MORPHOLOGICAL DIFFERENCES

A numerical taxonomic study was conducted by Rhodes, *et al.* (1967) in which 93 plant characters were scored for 21 different species of *Cucurbita*. The four xerophytic species clustered together at a significant level in the eight different statistical techniques that were employed. This indicates a relatively close morphological relationship between them when compared with other species of *Cucurbita*. There are, however, morphological differences among the four xerophytic species.

The most obvious differences among these four species are the shapes of the leaf blades. The first 2 to 4 true leaves of the seedlings (juvenile leaves) are similar in appearance in all four species. The older leaves, however, are quite different (fig. 2). In *Cucurbita digitata* the narrow lanceolate lobes extend almost to the base of the leaf blade; in *C. palmata* the lobes are broad, and about twice as long as they are wide; in *C. cordata* the leaf lobes are again broad extending about one-third the depth of the blade; and finally in *C. cylindrata* the lobes are deep, narrow and obtuse.

There are many other subtle differences between these four species. Among the more marked dissimilarities are the size and shape of the large storage roots. *Cucurbita digitata* has a large turnip-shaped taproot; in *C. palmata* the storage root is stout, fusiform, and bifurcated or even trifurcated a few inches below the crown. *Cucurbita cordata* and *C. cylindrata* each have large fusiform roots. Dittmer and Talley (1964) suggest that the roots of the xerophytic *Cucurbita* are adapted for extracting the moisture from the soil to a depth of not greater than 4 feet. Root penetration is such that there is no possibility of obtaining moisture from deep subsurface water tables. Excluded from this source of moisture, the root system by means of highly developed laterals is well adapted for gathering and storing moisture from the upper 4 feet of soil, and retaining it for an indefinite period of time.

The small gourd-like pepos produced on the vines are similar in shape for each of the xerophytic species, being nearly round. All are distinctly striped but their color patterns differ as follows:

C. cylindrata	Dark green	not yellow at maturity
C. cordata	Gray green	not yellow at maturity
C. palmata	Diffuse green mottle	yellow at maturity
C. digitata	Clear green mottle	yellow at maturity

The fresh weight of the pepos range from 150 to 330 grams with *C. cylindrata* usually having the smallest pepos of the four species. The pepo rind is thin, but relatively hard. The narrow band of white flesh is fibrous and when exposed to the desert environment dries into a network of fibers. The pepos are five-carpelate except for *C. digitata* which has three to five with a mean of 4.5 ± .8 carpels. This characteristic of five carpels (consistent for *C. cordata, C. cylindrata* and *C. palmata*) is unique in the genus inasmuch as all of the other species of *Cucurbita* are predominantly tri-carpellate. The five carpel character is basically recessive but not completely so because the F_1 hybrids between *C. moschata* × *C. digitata* and *C. moschata* × *C. palmata* produce pepos with carpel numbers of 3.4 ± .6 and 3.6 ± .8, respectively. *Cucurbita moschata* Duch. ex Poir. is consistently tri-carpellate (Bemis, 1963).

A single pepo often contains more than 500 seeds. The seeds of *C. cordata* and *C. cylindrata* are smaller than those of *C. digitata* and *C.*

palmata. Room dry weight of 100 seeds for the species is 2.8 ± .3, 2.8 ± .7 and 5.4 ± .5, 4.9 ± .7 grams, respectively. The seed shape and seed coat color are similar for all four species.

The rate of pepo enlargement is rapid for these xerophytic species. The mean diameter of the ovary of *C. palmata* at the time of pollination is 1.6 cm. The rate of enlargement follows a typical sigmoid growth curve which begins to decrease in rate about the 8th day after pollination. The mean maximum pepo diameter of 7.0 cm. was reached on the 12th day after pollination. The rate of seed development (weight), however, is slower than the rate of pepo enlargement. Maximum seed weight is not reached until 34 days after pollination (Ba-Amer, 1967).

REPRODUCTION

Observations in the field, experimental garden, and greenhouse suggest that the vegetative method of reproduction in the xerophytic *Cucurbita* is the most common. Each node of a runner is capable of producing adventitious roots, especially if covered with soil. In time the intervening internodes decay. The net result is a group of vegetatively produced plants surrounding a mother plant, and the entire community forms a roughly circular colony. For example, from a single plant of *C. foetidissima* in the experimental garden, a colony of about 705 individual plants was vegetatively produced within the course of three growing seasons.

Our observations in the field suggest that plants of the xerophytic *Cucurbita* regularly produce quantities of ripe fruit with numerous viable seeds, but few seedlings and even fewer mature plants originate from this source. The seeds are an attractive and nutritious source of food for desert animals, particularly rodents. It is evident that only a few seeds survive their depredations. Those that do survive and become young seedlings are vulnerable to browsing mammals, insect attacks, and drought. Thus sexual reproduction is erratic, undependable, and only infrequently results in a mature plant.

The seeds exhibit delayed dormancy apparently associated with the relatively tough seed coat. Some seeds from a mature fruit, properly ripened, will germinate readily, while others do not unless the seed coat is removed. This delayed dormancy may have significance for the survival of the species, but the phenomenon is not well understood.

These observations suggest that the xerophytic *Cucurbita* are adapted to cope reproductively with the rugged environment mainly through a modified version of conventional vegetative reproduction. Such a system allows only limited genetic variation.

POLLINATORS

Paul D. Hurd, Jr., and his colleagues have made important monographic studies of squash bees of the genera *Peponapis* and *Xenoglossa* (Hurd and Linsley, 1964; 1966). Females in species of these genera are specifically dependent upon particular species of *Cucurbita* for their pollen nutrition. Thus species limitation of these insects for pollen becomes a powerful taxonomic tool for studying species relations in the *Cucurbita*. Hurd informs us that it is indeed unusual to find a species-to-species relationship of plants and insects within a single genus of plants. This relationship permits a new approach to the systematics of *Cucurbita*. Already some exciting results are commencing to appear.

Squash bees restricted to *Cucurbita palmata* and *C. digitata* for their pollen supplies are *Peponapis timberlakei, Xenoglossa angustior* and *X. strenua*. Hurd has no data for the Baja California species, *C. cordata* and *C. cylindrata,* but he judges from the distribution of squash bees in this area that the same bee species as those dependent upon *C. palmata* and *C. digitata* will also need *C. cordata* and *C. cylindrata* for their pollen economy, with one exception. For those in the southern half of the peninsula, *X. angustior* would be replaced by the endemic *X. mustelina.* As would be expected, a number of species of squash bees are dependent upon the widely ranging *C. foetidissima* as follows: *Peponapis pruinosa, P. smithii, Xenoglossa angustior, X. kansensis, X. patricia* and *X. strenua.*

These observations reinforce support for a close relationship between the four xerophytic species from California, Arizona, and Baja California, and the wide divergence of *C. foetidissima* from this group.

COMPATIBILITY

The four xerophytic species of *Cucurbita* hybridize readily in all combinations with little if any decrease in fertility in the F_1 plants. The F_1 plants have great vegetative vigor, are self-fertile, and fertile in backcrosses to the parent species.

Where these species are sympatric they tend to hybridize, usually along the perimeter of their range as we have shown for *Cucurbita palmata* and *C. digitata* (Bemis and Whitaker, 1965). It is probable that future botanical exploration in Baja California will uncover a similar situation where the ranges of *C. cordata* and *C. cylindrata* overlap in about the central portion of the peninsula.

The chromosome number of these four xerophytic species is $n = 20$. This number is consistent for all species of *Cucurbita* examined thus far. The homology of their respective chromosome complements was verified by cytological examination of *C. cylindrata, C. digitata, C. palmata* and their reciprocal F_1 hybrids (Groff & Bemis, 1967a). Occasional univalents were observed, but their frequency was the same whether they occurred in a species, or a species hybrid. Hybrids with *C. cordata* were not examined cytologically, but the fertility of the hybrids suggests that its chromosome complement is homologous with the other three species.

Extensive attempts to hybridize these species with other *Cucurbita* yielded few or no seeds. The only success recorded was with *Cucurbita moschata,* a cultivated species, when it was used as the pistillate parent in matings with *C. digitata* and *C. palmata*. The partially developed embryos from these matings were artificially cultured in order to produce the hybrid plants (Bemis & Nelson, 1963). The hybrids were vegetatively vigorous, but completely sterile. Sixty-three pollen mother cells at MI were examined from the F_1 hybrid *C. moschata* × *C. digitata* and the frequency of univalents was 36.4 ± 2.9, $2\mathbf{n} = 40$ (Groff and Bemis, 1967b). These observations suggest an almost complete lack of chromosome homology between these xerophytic species and *C. moschata.*

BIOCHEMISTRY

Some significant biochemical information relating to the four xerophytic species of *Cucurbita* has been recorded by Chisholm and Hopkins (1966), and confirmed and expanded by Bemis, *et al.* (1967). In a chemical analysis of the seeds of *C. digitata* and *C. palmata* Chisholm and Hopkins found the conjugated fatty acid, punicic acid, in relatively large amounts (17%—*C. digitata*; 11%—*C. palmata*). They state: "*C. digitata* and *C. palmata* are believed to be the only plants native to North America that have been shown to produce punicic acid."

Bemis, *et al.* (1967) added *C. cordata* with 8.99% punicic acid, and a recent analysis of *C. cylindrata* seeds shows this taxon to have 21.4% punicic acid. *Cucurbita foetidissima* had only .36% punicic acid, while in 12 other species of *Cucurbita* the punicic acid ranged from .05% to .33%. This unique occurrence of punicic acid in significant amounts in the seeds of the four xerophytic *Cucurbita* and its virtual absence in seeds of other *Cucurbita,* including the xerophytic *C. foetidissima,* again signifies the close relationship of this group of species.

DISCUSSION

The xerophytic *Cucurbita* species, *C. cylindrata, C. cordata, C. digitata* and *C. palmata* represent an extreme evolutionary divergence in the genus. If our assumption is correct that the center of distribution of *Cucurbita* is the tropical and semitropical region of southern Mexico, then the xerophytic *Cucurbita* are terminal ecotypes adapted and apparently restricted to the hot, dry environments of the deserts in western North America. The evolution of the xerophytic *Cucurbita* from the mesophytic progenitors probably is recent. Evidence for this is that the chromosome number has remained constant, the monoecious character of the plants and the simple inflorescence also have remained constant; but more important is the limited compatibility that still exists with the cultivated species, *C. moschata.*

The morphological characters of the xerophytic *Cucurbita* are either unique for the species or are extreme modifications of certain characters. Among the unique characters are the consistent five-carpelate nature of the pepos with the exception of *C. digitata* which still has some variation. The other species of *Cucurbita* are predominantly tri-carpellate. The pistillate and staminate flowers differ from those of mesophytic species. The pistillate flowers have a pronounced tubular corolla which encloses a long style with a five-lobed compound stigma. The staminate flowers are also tubular enclosing a long fused anther column.

The flowers are conveniently adapted to protect the solitary squash bees which inhabit the flowers on the day they blossom. The symbiotic relationship between species of *Cucurbita* and certain of the squash bees is unusual. The bees are dependent upon the *Cucurbita* for their pollen nutrition. This need for food from a specific group of plants restricts the distribution of the insects.

The large storage roots of the xerophytic species represent an extreme modification of the tuberculate root of transitional species such as *C. pedatifolia*. The development of the tuberous roots has resulted in the perennial nature of the xerophytic species and the predominantly vegetative mode of reproduction, which in turn restricts the genetic variation because of reduced sexual reproduction. Likewise the relatively high amounts of punicic acid in the seeds found only in the four xerophytic species suggests a close genetic relationship.

The wide ranging *C. foetidissima,* while having xerophytic properties, is not adapted to the extremes of environment of the four species discussed here. Differences in morphological and biochemical characters, specific pollinators, and incompatibility suggest that *C. foetidissima* and the other four xerophytic species diverged at an early date in the evolution of the genus.

The evidence presented in this report probably would lead the trained taxonomist to consider these four taxa as subspecies, if the similarities are considered more significant than the differences between them. In our opinion the subspecies category would be satisfactory.

Summary and Conclusions

1. *Cucurbita cordata, C. cylindrata, C. palmata,* and *C. digitata* are adapted to the hot arid regions of the Sonoran desert, primarily through a modification of their root systems.
2. Modification of the root system has led to a change in growth habit from annual to perennial, and to an efficient system of vegetative reproduction which in effect restricts genetic variation.
3. These four species are cross compatible and have many morphological similarities.
4. Two of the four species are specific pollen hosts for three species of squash bees, *Peponapis timberlakei, Xenoglossa angustior,* and *X. strenua*. Host specificity of squash bees is a highly sophisticated measurement of relationship among *Cucurbita* species.
5. Certain morphological and biochemical characters unique in the genus separate them from other species of *Cucurbita*. The extreme nature of the habitat they occupy suggests they are terminal ecotypes.
6. Limited compatibility with *C. moschata* relates these species to the annual, mesophytic, cultivated members of the genus.

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SOME NEW SPECIES, NEW COMBINATIONS, AND NEW RECORDS OF RED ALGAE FROM THE PACIFIC COAST

Isabella A. Abbott

The algae described in this paper come from two Pacific Coast areas where intensive collections have been made, the Monterey Peninsula, California (Smith, 1944; Hollenberg and Abbott, 1966) and Coos Bay, Oregon (Doty, 1947). This paper forms a part of a continuing study by the author of red algae, particularly from the Monterey area, and of studies of other new taxa with George J. Hollenberg (Hollenberg and Abbott, 1965; 1966; 1968).

Three species of Delesseriaceae (Ceramiales) are here newly described: *Nitophyllum dotyi* from Oregon, *N. cincinnatum* from California and *Cryptopleura rosacea* from California. *Nitophyllum hollenbergii* (Delesseriaceae) is a transfer from *Myriogramme*. In the Gigartinales, *Ozophora* J. Agardh (Phyllophoraceae) is reinstated with *O. californica* J. Agardh as the type species, and *O. latifolia* and *O. norrisii* as newly described. *Chondrus ocellatus* Holmes (Gigartinaceae), known from northern Japan, is reported from Sunset Bay, near Cape Arago, Oregon, and is the first species of this genus to be reported from the eastern Pacific since Kylin (1928) removed *Chondrus affinis* Harvey to *Rhodoglossum*.

Specimens without an herbarium abbreviation are at the Hopkins Marine Station. Abbreviations for herbaria are the standard ones and the following ones: GMS, Gilbert M. Smith algae herbarium at the Hopkins Marine Station, and MSD, collection of Maxwell S. Doty, University of Hawaii. Collecting numbers, except where preceded by a name, are those of the author. Color names which are capitalized in the description are those of Ridgeway (1915).

Nitophyllum hollenbergii (Kylin) Abbott, comb. nov. *Myriogramme hollenbergii* Kylin, Acta Univ. Lund. 27(11): 32, pl. 11. 1941.

Nitophyllum is distinguished from *Myriogramme* on very technical grounds. Vegetatively they are for the most part monostromatic and lack veins of any kind except perhaps basally. One of the reproductive differences emphasized by Kylin (1956) is the terminal carpospores of *Nitophyllum*, whereas those of *Myriogramme* are in chains.

The lectotype of *M. hollenbergi, Hollenberg 2854,* GMS, which is cystocarpic shows carpospores that are terminal.

Other reference in the literature to *Myriogramme hollenbergii* are Smith (1944), Dawson (1962), and Norris and West 1966).

Distribution: British Columbia, Vancouver I.; Washington, near Smith I., Partridge Bank off Whidbey I. Oregon, Tegula Bay, south of Cape Arago, *Doty 25764,* MSD. Several new collections from Monterey, California, were made in the vicinity of the previously known localities (Smith, 1944). Dawson (1962) has reported this species from La Jolla, California, and Isla Magdalena, Baja California.

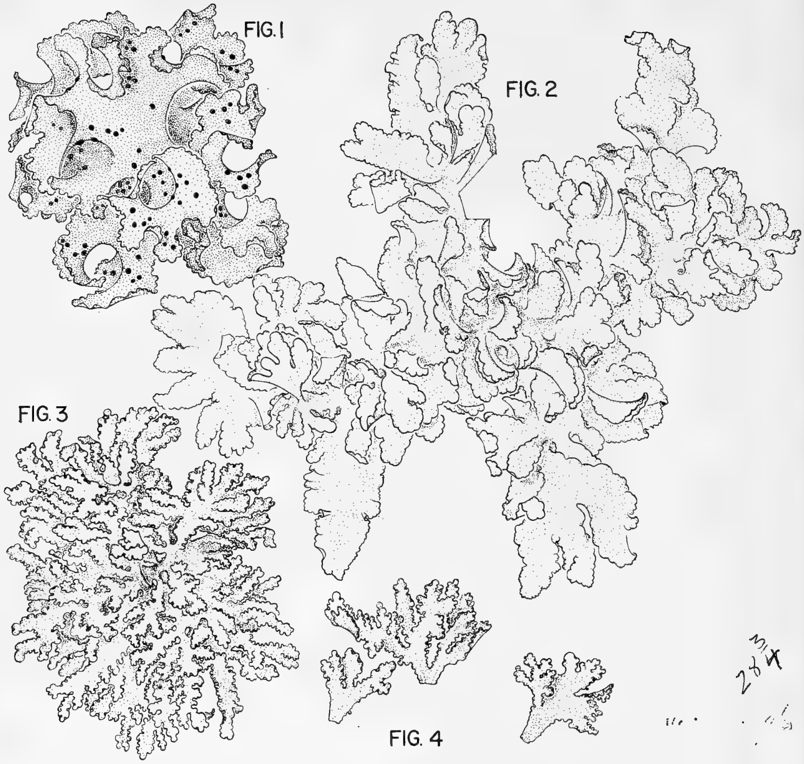
Nitophyllum cincinnatum Abbott, sp. nov. Fig. 1. Thallus (in algis corallineis) epiphyticus, membranaceus, per hapteron parvum, et secundo gradu per extensiones paxilliformes cellularum thalli inferiorum affixus, usque ad 6 cm alt., lobatus, lobis in circulis cristatis aggregatis, omni lobo cuneato, latitudine apicum aequa altitudinis thalli aut dimidio breviore; interdum prolifero, marginibus crebre corrugatis, corrugatienibus crispatis, et undulatis et fimbriatis. Thallus monostromaticus, sine venis microscopicis, rubro-purpureus. Cystocarpi 1.0–1.5 mm diam., gonimoblastus sporas unicas terminales, 25–28 × 12–15 u habens. Sori tetrasporangiales c. 0.5 mm diam., longiores quam lati, in centro altiores quam ad margines.

Thallus epiphytic on corallines, membranous, attached by a small holdfast and secondarily by occasional peg-like extensions of the lower thallus, up to 6 cm high, lobed, lobes occurring in circular to trumpet-shaped groups, each lobe cuneate, the width of the tops equal to or one-half the height, occasionally proliferous, with densely ruffled margins, the ruffles crisp, both undulate and fimbriate. Thallus monostromatic, with no microscopic veins. Color when fresh reddish-orange (Russet Vinaceous to Sorghum Brown), reddish purple when dry (Deep Corinthian Purple). Cystocarps 1.0 to 1.5 mm across, gonimoblast with single terminal spores, 25–28 by 12.5 μ. Tetrasporangial sori about 0.5 mm in diameter, longer than wide, and center higher than at the edges.

Holotype: California, Monterey County, cast ashore at the south end of Carmel Beach, *Abbott 2029*, May 12, 1961, GMS, 6 specimens tetrasporangial, 2 cystocarpic on 1 sheet.

Other specimens: California, San Mateo Co., attached at 15 ft lepth off Moss Beach, *4130*, on *Calliarthron;* Monterey Co., at 20–25 ft depth off Whaler's Cove, Pt. Lobos State Reserve Park, *4135*, on *Calliarthron;* Monterey Co., *4138*, US; *4129*, WTU; *4141*, UC; *4134*, UCSB; *4130*, MSD; *4131* MSD.

Nitophyllum cincinnatum is named for the deep ruffling and curling of the thallus. When first collected, it seemed to match the description of *N. mirabile* Kylin (1925) from the Friday Harbor region, but an examination of specimens of that species showed that the deep ruffling and size of the new species were different from the northern species. *Nitophyllum mirabile,* further, is a relatively flat blade with undulate margins, whereas *N. cincinnatum* is funnel or trumpet shaped, resembling in form the medusoid genus *Haliclystus*. As described, it is the only species of *Nitophyllum* of this shape on this coast, *N. mirabile* being a broad flat blade with ruffled margins, *N. northii* strap-shaped without ruffles, and *N. hollenbergii* small broad blades, without a modified margin.



Figs. 1–4. *Nitophyllum* sp. and *Cryptopleura rosacae:* 1. habit of *Nitophyllum cincinnatum* showing cystocarps on the crisp, ruffled lobes of the thallus, × ¾; 2. *Nitophyllum dotyi,* the type specimen which is a cystocarpic thallus, × ¾; 3–4, *Cryptopleura rosacea;* 3, habit of *Abbott 4190,* the type specimen, showing the lobes arranged in clumps which are characteristic of this species, × ½; 4, three segments in detail, showing dense ruffling on margins, × 1.

Nitophyllum dotyi Abbott, sp. nov. Fig. 2. Thallus 8 cm alt., membranaceus, roseus, in aliquot lobos primarios divisu, omni lobo ad dimidum altitudinis loborum primariorum vicissim diviso, marginibus undulatis proliferisque. Thallus omnio monostromaticus, nisi ad basem, sine venis micro-aut macroscopicis. Cystocarpi 300–500 μ lat., carposporae terminales, ellipticae ad obovatas, 1.5–2.0 plo longiores quam latae. Tetrasporangia spermatangiaque non visa.

Thallus 8 cm tall, membranous, rose-red (Rocelin Purple to Deep Helebore Red), divided into several primary lobes, each lobe divided again to one-half the depth of the primary lobes, the margins undulate and proliferous. Monostromatic except basally, without microscopic veins. Cystacarps 300–500 μ wide, carpospores terminal, 45–60 by 30 μ, elliptical to obovate, up to twice longer than broad. Tetrasporangia and spermatangia not seen.

Holotype: Oregon, Coos Co., Lighthouse Beach, Cape Arago, *Ethel I. Sanborn,* July 11, 1926, UC552380. Regretfully known only from the holotype, this species can be placed without question in this genus, as each procarp contains only one carpogonial branch and one group of sterile cells, the carpospores are terminal, and the thallus is without veins.

It differs from the other *Nitophyllum* species on this coast by being larger, more lobed, and more strongly proliferous. In fact, this species resembles some of the proliferous forms of *Hymenena setchellii* more than it does any species of *Nitophyllum,* but lacks the microscopic veins present in *Hymenena,* and is a more delicate thallus.

Nitophyllum dotyi is named in honor of Maxwell S. Doty of the University of Hawaii in recognition of his major contribution to the knowledge of the Oregon marine algal flora, and the marine flora of the Pacific Coast.

Cryptopleura rosacea Abbott, sp. nov. Figs. 3, 4. Thalli 5–10 cm alt. lobos taeniaformes flabellato et ramosos, qui segmenta taeniaformia 2–3 cm long. ferunt, habentes; margines segmentorum crebre crenati, omni crena c. 0.5 cm long. cacumina obtusa ad spathulata habente. Partes inferiores venas macroscopicas non perspicuas, partes superiores venas microscopicas praebentes. Partes thalli inferiores polystromaticae, partes superiores et margines monostromaticae. Cystocarpi per loborum superficiem sparsi, carposporas terminales habentes.

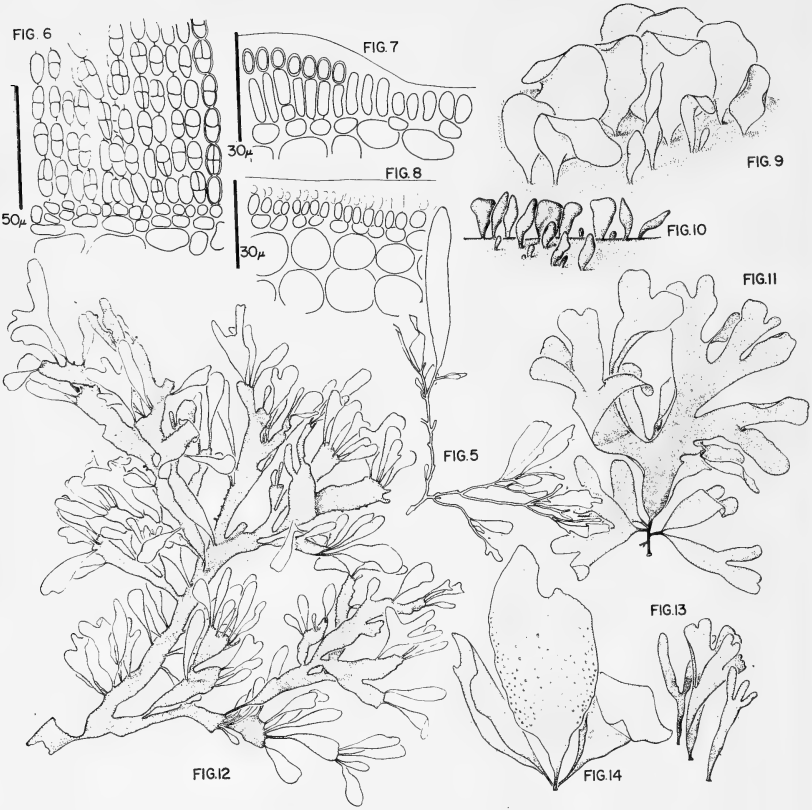
Thalli 5–10 cm tall, in a crisp clump, with branched flabellate, ribbon-like lobes bearing ribbon-like segments 2–3 cm long, with densely scalloped margins, each scallop about 0.5 cm long, segments with blunt to spathulate tips. Thallus a deep rose-red (Indian Lake to Dahlia Crimson). Lower portions with indistinct macroscopic veins, upper portions with microscopic veins. Lower portions of thallus polystromatic, upper portions and margins monostromatic. Cystocarps few in the main segments, 1.0–1.5 mm wide, somewhat flat; gonimoblasts with terminal carpospores.

Holotype: California, Monterey Co., cast ashore at the south end of Carmel Beach, *Abbott 4190,* May 5, 1965, GMS.

Other specimens: From the type locality, *4191,* May 19, 1965, UC; *4192,* June 19, 1965; *4193,* April 25, 1965; *4194,* May 7, 1966.

In general form, this newly described species of *Cryptopleura* resembles the illustration of *C. dichotoma* Gardner (1927) but Gardner's description of size of thallus, width of blades, branching of segments, character of the margins and color of the thallus is different from these in *C. rosacea,* the latter species being taller, having wider blades, branches flabellate, with ruffly margins, and of a brighter color. Since *C. dichotoma* is known only from the type specimen, no further comparisons can be made.

Cryptopleura rosacea is smaller and a more splender species than *C. lobulifera* or *C. brevis,* as well as differing in color, width of segments



Figs. 5–14. 5–12, *Ozophora* species; 5, habit of *Ozophora clevelandii* (the type specimen of *Phyllophora clevelandii*), showing prominent stipes and linear blades characteristic of this species, × ½; 6, tetrasporangial nemathecia of *O. clevelandii* showing chains of tetrasporangia arranged in a nemathecium on the surface of the thallus; 7, monosporangia of *O. clevelandii,* arranged in a nemathecium on the surface of the thallus; 8, spermatangial sorus of *O. latifolia,* occurring on special leaflets; 9, spermatangial leaflets which occur in clusters near the midline of the blades of the thallus of *O. clevelandii* (similar in other species of *Ozophora*), × 1; 10, cystocarpic papillae of *O. clevelandii,* × 1; 11, habit of the type specimen of *O. latifolia,* showing broad flabellae dichotomously branched, and an inconspicuous stipe, both characteristic of this species, × ⅓; 12, habit of cystocarpic thallus of the type specimen of *O. norrisii,* showing repeated branching, the last orders of branches with slender, delicate stipes which ar characteristic of this species. Basal portion missing, × ⅓; 13–14, *Chondrus ocellatus;* 13, erect, tufted, little-branched, furrowed thalli known as *C. ocellatus* f. *parvus* which resemble *Rhodoglossum affine,* × ⅞; 4, broad, short, blade-like form close to *C. ocellatus* f. *ocellatus* and resembling depauperate specimens of *Iridaea flaccida,* × ⅞.

and density of ruffling of the margins. It appears to be a subtidal species, as it has not been collected intertidally.

OZOPHORA J. Agardh (1892) with *O. californica* as the only species, was described from the Golden Gate (San Francisco) California, and was transferred by Kylin (1931) to *Phyllophora*. Dawson (1961) restricted the northern specimens described by Smith (1944, as *Phyllophora clevelandii* Farlow) to *P. californica,* reserving for the specimens from Santa Barbara south the name of *P. clevelandii*. Examination of the type specimen of *O. californica* in the Agardh herbarium shows the cystocarpic material to be identical with the more recently collected material in the northern California area. Richard E. Norris of the University of Washington some years ago called to my attention the peculiar spermatangial leaflike proliferations of this entity. Detailed studies of these and other reproductive structures show that these specimens cannot be allied with *Phyllophora* where the spermatangia occur in cavities on the surface of the thallus, and where the cystocarps are borne on leaflike proliferations. It therefore seems advisable to present a more adequate description of *Ozophora*.

Thallus erect, with one to several fronds arising from a disc-like holdfast, with or without several cylindrical stipes, upper portions producing irregularly linear to wedge-shaped blades with stipes, or branching dichotomously in blade-like segments; if not stipitate, then main axis and subsequent branches blade-like, sometimes with proliferous stipitate bladelets and ultimately forming broad, blunt tips. New growth and regeneration common in various parts of the thallus, at first appearing as small ear-like lateral proliferations. Medulla parenchymatous, with a narrow 2–3 layered cortex. Spermatangia in thin cordate leaflets clustered on the surfaces of the thallus, toward the mid-line, or marginal, the spermatangia occurring in a colorless superficial band on the surface of the leaflets. Cystocarps in simple cylindrical or fusiform proliferations (papillae) the cystocarps bulging out the median portion on the proliferations. Carpospores small, in clusters separated by sterile filaments. Asexual thalli with monospores (undivided tetraspores?) in superficial blisters or in small marginal warts. Tetrasporangia in surface nemathecia, the sporangia in chains, cruciately divided.

Ozophora is clearly related to *Phyllophora* on the basis of the vegetative structure, having a parenchymatous medulla and narrow cortex, and in reproduction, having tetrasporangia in superficial nemathecia, the tetrasporangia (fig. 6) borne in chains. These characters are also shared with *Petroglossum* Hollenberg (1943). *Petroglossum* differs from *Phyllophora* in having spermatangial sori continuous with the surface of the thallus and although spermatangial sori are continuous (fig. 8) in *Ozophora,* they are in special (fig. 9) leaflets, whereas in *Phyllophora,* in contrast, spermatangia are in pit-like cavities. *Petroglossum* and *Phyllophora* bear cystocarps in leaflets; *Ozophora* has cystocarps (fig. 9) in papillae. If the asexual sori of the three species of *Ozophora* are sometimes monosporangial (assuming that these are not undivided tetrasporangia), these are suggestive of the modified life cycle shown by *Ahnfeltia plicata* in the Phyllophoraceae.

Ozophora clevelandii (Farlow) Abbott, comb. nov. Figs. 5, 6, 7, 9, 10. *Phyllophora clevelandii* Farlow, Proc. Amer. Acad. Arts 2: 368. 1875. *Ozophora californica* Agardh, Analecta algologica, 82. 1892. *Phyllophora california* (Agardh) Kylin, Acta Univ. Lund. 27(11): 34, pl. 20, fig. 50. 1931. *Phyllophora submaritimus* Dawson, Allan Hancock Found. Publ. Occas. Pap. 8: 6, figs. 17, 18. 1949.

Thalli 10–28 cm high, frequently overgrown by encrusting bryozoans, hydroids, and barnacles, several clindrical wiry stipes (fig. 5) up to half the height of the thallus arising from a disc-shaped, woody holdfast, the linear or spathulate blades occasionally furcate, on short stipes if on the second or third order of branches, blades 0.5 to 2.0 cm wide, up to 15 cm long, occasionally proliferous (regenerative) at the tips, which are otherwise blunt. Cystocarps on papillae (fig. 10) borne on the central portion of both surfaces of the blades, sometimes spreading to the margins but not marginal; spermatangial leaflets in clusters (fig. 9) at the center of the blades; monosporangia (fig. 7) (undivided tetrasporangia?) in blister-like nemathecia on the surface of the blades; tetrasporangia (fig. 6) in superficial nemathecia, in chains, cruciately divided.

Holotype of *Ozophora californica:* California, San Francisco, from the Golden Gate, no. 25365, LD, a fragmented thallus which is cystocarpic. Another specimen, no. 25364, LD, from Unalaska, is said to be this species but it is too fragmentary to identify.

Holotype of *Phyllophora clevelandii:* California, San Diego Co., San Diego, *Daniel Cleveland,* Dec. 1874, FH.

Other specimens: California, Marin Co., cast ashore at Duxbury Reef, *4216,* Dec. 27, 1967; Santa Cruz Co., cast ashore at Davenport, *Hair & Nicholson,* July 16, 1965; Monterey Co., *Hollenberg 3934,* July 16, 1939; cast ashore at Moss Beach, *4177; 4178,* MSD; *4179; 4209;* cast ashore 3 miles north of San Simeon, *4180,* GMS, UC, WTU; *4181,* GMS, MSD, UCSB; San Luis Obispo Co., cast ashore at Shell Beach, *4183,* June 4, 1966; *4184,* Oct. 22, 1967, GMS, MSD.

Additional references to *Ozophora clevelandii* are Smith (1944) and Dawson, 1949. Additional references to *Phyllophora californica* are Dawson (1958; 1961).

Distribution: from Duxbury Reef, Marin Co., through central California, Channel Islands, and reported by Dawson (1961) from several Pacific Mexico localities.

Ozophora clevelandii is usually collected in the drift, and there usually as fragments. Such specimens usually resemble various forms of *Prionitis,* particularly *P. andersonii,* and without experience with these two taxa would be easy to confuse with the latter. Likewise, *O. latifolia* (described below) is also found cast ashore, but except for possible confusion with *Rhodymenia pacifica,* is more easily defined as a separate entity from other red algae. In part, these associations are a reflection of the main differences between these two species of *Ozophora,* namely, that the conspicuous cylindrical stipes (fig. 5) with broadly linear blades of *O. clevelandii* remind one of *Prionitis* and the broad foliar segments of *O. latifolia* (with basal portions lacking) remind one of *Rhodymenia pacifica.* The intact thalli of *O. latifolia* (fig. 11) obtained by dredging or diving show only very short stipes less than 2 cm high, whereas stipes may be one-half the total height of the thallus in *O. clevelandii.* Because more collections are now available than when Dawson (1949, 1961) drew up his descriptions of the southern California and Pacific Mexico *Phyllophora* species, it is clear that on vegetative grounds *Phyllophora submaritimus* Dawson is the same as *Ozophora clevelandii* although no fertile material of the southern taxon is known.

The holotype of *Phyllophora clevelandii* (fig. 5) bears that designation in the hand and initials of F. S. Collins. It is represented by two bleached, sterile specimens, obviously parts of the same thallus. On the same sheet is another specimen, different from these two and bearing tetrasporangia (fig. 6) in chains. Two packets are also on this sheet, one from Santa Cruz collected by C. L. Anderson is also tetrasporangial; the second, from San Francisco, collected by N. L. Gardner is cystocarpic. The tetrasporangial nemathecia are oval and on the surface of the thallus, and resemble the nemathecia which bear monosporangia of the more recently collected thalli. The cystocarps of the Gardner specimen are in fusiform proliferations or papillae similar to those of the type specimen of *Ozophora californica.* Although sterile, the type specimen of *Phyllophora clevelandii* is of the shape, size, and structure of the specimen illustrated by Smith (1944), which is accepted here as identical.

Phyllophora clevelandii is described by Dawson (1961) as having tetrasporangia on small leaflets borne on the surface of the blades; since these are borne in a different place than the reported monospores and tetrasporangia borne in nemathecia on the surface of the thallus in *Ozophora,* it is concluded that some of his specimens are different from *O. clevelandii,* and thus probably not *Ozophora.*

Ozophora latifolia Abbott, sp. nov. Figs. 8, 11. Thallus usque ad 30 cm alt., cum aut sine stipite brevi cylindrico; axis principalis complanatus, laminiformis, 2.5–3.0 cm lat. irregulariter ad regulariter dichotome flabellate ramosus, aut segmenta prolifera stipitata 7–10 cm long., 1.0–2.0 cm lat., e margine axis principalis producta, habens. Sectiones transversae complanatae, medullam achromaticam parenchymatiformem et filamenta corticalia photosynthetica, e 3–4 stratis constantia, habentes. Spermatangia in proliferationibus cordatis laminiformibus, in fasciculis in superficie segmentorum ordinatis, spermatangiis superficie proliferationum complanatis. Cystocarpi in proliferationibus e superficiei laminarium cylindricis ad fusiformes ad teretes, simplicibus aut semel-ramosis facti, massa carposporarum media, inflationem parvam efficiente. Thalli asexuales monosporici, monosporae (tetrasporae no divisae?) in excrescentiis marginlibus, aut in nematheciis pustuliformibus in segmentis factae.

Thallus up to 30 cm tall, brick red when fresh, drying to a rusty-red, with or without a short, cylindrical stipe less than 2 cm high, main axis flattened and blade-like, 2.5 to 3.0 cm wide, irregularly to regularly dichotomously flabellately branched (fig. 11), or with stipitate proliferous segments 7–10 cm long and 1.0 to 2.0 cm wide produced from the margin of the main axis. Cross sections flattened, with a colorless parenchyma-like medulla and photosynthetic cortical filaments of 3–4 layers. Spermatangia in pink cordate leafllike proliferations 1–2 mm high and 1–3 mm broad, arranged in clusters on the surface of the segments, the spermatangia forming a continuous, colorless band (fig. 8), on the surface of the leaflets. Cystocarps borne in simple or once-branched cylindrical to fusiform and terete proliferations (papillae), 1 to rarely 2 mm high, from the surface of the blades, and occasionally fringing the margins; carpospore mass median in section, and making a small swelling in the proliferation, internally filling the entire center of the medulla. Carpospores small and ovate, about 10 by 7 μ arranged in small clusters separated by sterile filaments. The asexual thalli monosporangial, monosporangia (undivided tetrasporangia?) produced in marginal outgrowths, or in blister-like nemathecia on the segments (branches of the second order).

Holotype: California, Monterey Co., dredged at 50–60 ft depth, north of Coastguard breakwater off Monterey, *Abbott 4172,* July 31, 1964, GMS, spermatangial and cystocarpic plants on 1 sheet.

Other specimens: Oregon, Lincoln Co., from Seal Rocks, *Doty 2664.* California, San Mateo Co., at 10 ft depth off Pigeon Pt, *4146;* Monterey Co., 29 specimens variously distributed to: GMS, MSD, UC, UCSB, US, WTU; San Luis Obispo Co., Shell Beach, 3 specimens distributed to: GMS, MSD, WTU; Santa Barbara Co., Santa Barbara, *Peattie 28,* SBM.

Thalli of *O. latifolia* are taller, the segments longer and broader and more branched than those of *O. clevelandii.* The chief differences are in the possession of longer and more prominent stipes and linear blades of the latter species.

Ozophora latifolia is named for its broad axis, blades and thallus segments.

Ozophora norrisii Abbott, sp. nov. Fig. 12. Thalli subaestuales, usque ad saltem 20 cm alt. (thallo altissimo fracto), hapteron discoideum parvum, stipitem delicatum, et axem principalem foliarem habentes; axis principalis axe secondarios latitudine quasi aequos, ad tertiam quartamque ordinem conferte ramosos, pinnatim irregulariterque efficiens.

Laminae proliferae simplices ad spathulatas ad divaricate furcatas, in omni ordine ramificationis, 1–3 cm long., ad 1 cm lat., in stipitibus delicatis tenuibusque sitae. Cystocarpi in papillis secundum margines orientibus siti; foliola spermatangialia marginalia; monosporangia in nematheciis pustuliformibus in superficie laminarum orientibus sita.

Thalli up to at least 20 cm tall, from a small discoid holdfast and a delicate stipe, with a foliar main axis which gives rise pinnately, flabellately, and irregularly to secondary axes of nearly the same width, and branching closely to the third and fourth order. Simple to spathulate to divaricately forked proliferous bladelets on all orders of branching, 1–3 cm long, up to 1 cm wide, on delicate slender stipes. Cystocarps on papillae borne along the margins; spermatangial leaflets marginal; monosporangia (undivided tetrasporangia?) in blister-like nemathecia on blade surfaces.

Holotype: Washington, San Juan Co., dredged in 40 ft depth Partridge Pt., west of Whidbey I., *Norris 4952,* July 27, 1964, GMS-holotype, WTU.

Other specimens: Washington, San Juan Co., dredged off Salmon Bank, southwest of San Juan I., *Norris 4803,* July 16, 1964, WTU, spermatangia; *Norris 5167,* Feb. 13, 1965, cystocarpic; at type locality, *Norris, 5214,* July 6, 1965, cystocarpic, spermatangial, sporangial, dredged in 30–35 ft.

Ozophora norrisii has a thinner thallus than the other two species in the genus. It also branches more profusely, the third and higher orders of branches being distinguished by very delicate stipes. Furthermore, spermatangial leaflets are marginal in location. In general form, it is similar to *Petroglossum pacificum* Hollenberg (1943, fig. 4) but 3–4 times the size of this species, and lacks the crustose base of *Petroglossum pacificum*. With *O. latifolia,* it shares a short, inconspicuous stipe.

Ozophora norrisii is named in honor of Richard E. Norris of the University of Washington who first called attention to the peculiar reproductive structures of this genus.

CHONDRUS OCELLATUS Holmes f. PARVUS Mikami, Sci. Pap. Inst. Algol. Res. Fac. Sci. Hokkaido Imp. Univ. 5: 233, pl. 3, fig. 1. 1965. Fig. 13, 14.

Thalli saxicolous, olive green to brown, tufted in two growth forms, one (fig. 13) 0.5 to 1 cm high from a short, stout holdfast and stipe, upper portion of flabellae dichotomously branched once or twice, furrowed with blunt, obtuse tips, but otherwise smooth, with edges raised at the margins; the other (fig. 14) type foliar, with almost no stipe to stipes of 1 cm high, the blades expanding and 2.5 to 3 cm broad, with broad rounded tips, and up to 5 cm high.

Monoecious. Spermatangia produced laterally near the tips of the cortical filaments, less than 2 μ wide. Cystocarps up to 1 mm wide, scattered over the median portions of the blades, internally with no "Faserhulle" (special medullary filaments which surround the cystocarp). Tetrasporangia arising from accessory branches of the medullary filaments, 28 by 35 μ associated in flat to ovate internal sori.

Distribution: Oregon, Coos Co., at 3.5–4 ft tide level, below *Endocladia* zone, Sunset Bay, near Cape Arago, *Norris 5359,* July 20, 1967, GMS, MSD, WTU. The Japanese locality for this form is Shimonoseki, Yamaguchi Prefecture, south central Japan. Forma *ocellaltus* is found throughout Honshu and its type locality is Shimoda, Shizuoka Prefecture.

Chondrus, as understood by modern workers, is not known on the Pacific Coast of North America, previous reports having been shown to be species of *Rhodoglossum* and other genera. Therefore, to find a representative of *Chondrus,* and to be able to ally it with a known species is rather a surprise. Although these specimens, on casual inspection, resemble *Rhodoglossum affine* and depauperate *Iridaea* specimens, close study of the reproductive structures shows conclusively that this is a species of *Chondrus*. The two strongest characteristics shown are: no "Faserhulle" which is present in the 3 other genera of Gigartinaceae on this coast, namely, *Rhodoglossum, Gigartina* and *Iridaea;* and tetrasporangia arising from accessory branches of the medullary filaments, which only *Iridaea* of the other genera shares. The specimens show a remarkable resemblance to those illustrated in Plate 3, fig. 1 of Mikami (1965), and some of them grade into what Mikami (1965) considers to be f. *ocellatus,* being somewhat taller and more robust than the average for f. *parvus*.

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A NEW NAME FOR A SPECIES OF POLYPODIUM FROM NORTHWESTERN NORTH AMERICA

Frank A. Lang

A biosystematic study of the *Polypodium vulgare* complex in the Pacific Northwest (Lang, 1965) has shown that there are three cytotypes present in the area from Alaska south along the Pacific Coast to central California and east to the Rocky Mountains that are apparently involved evolutionally with each other.

One, represented by *P. glycyrrhiza* D. C. Eaton, is uniformly diploid ($\mathbf{n} = 37$) throughout its range and is morphologically, ecologically, and geographically distinct from another species in the area, *P. hesperium* Maxon.

Cytological investigations on *P. hesperium* have shown that this species is composed of two cytotypes, one diploid ($\mathbf{n} = 37$) and one tetraploid ($\mathbf{n} = 74$) (Evans, 1963; Knobloch, 1962; Lang, 1965; Lloyd, 1963, Manton, 1950).

The distinctive coastal species *P. scouleri* Hook and Grev. is also present in the study area but is not considered here as it does not appear to have played a role in the present problem.

The two cytotypes included in *P. hesperium* are quite distinct and separable on a number of points (Table 1). It is felt that these differences are such as to warrant their recognition as distinct species.

TABLE I. CHARACTERS DISTINGUISHING THE TWO CYTOTYPES OF P. HESPERIUM

	Tetraploid	*Diploid*
Chromosome number	**n** = 74	**n** = 37
Frond shape	oblong	oblong
Segment shape	acute to obtuse	obtuse
Sorus shape	oval	circular
Sorus location	median	marginal (near margin than midrib)
Paraphyses	very rare	common
Rhizome pruinose	—	+
Rhizome taste	licorice	acrid
Scale strip	absent	±
New fronds	summer	spring
Geographical distribution	interior (mostly east of Cascade Mountains)	Western mountains

Since the two cytotypes included in *P. hesperium* are recognized as two distinct species, it thus becomes necessary to establish to which cytotype the epithet *hesperium* properly belongs, the diploid or the tetraploid. *Polypodium hesperium* Maxon is the oldest available name which must be used for one or the other of the two cytotypes.

The type specimen of *P. hesperium* was compared morphologically with a range of both diploid and tetraploid specimens from throughout the Northwest, and chromosome determinations were made on topotype material. This comparison makes it clear that the tetraploid cytotype agrees very closely with the type specimen of *P. hesperium* Maxon. Among other features in common, both have oval sori located midway between the costa and segment margin, and a sweet licorice-like rhizome, as mentioned by Maxon (1900) in his original description. The diploid cytotype, on the other hand, has circular sori near the segment margin and an acrid tasting rhizome. The geographical distributions give further evidence that the holotype of *P. hesperium* is tetraploid since, as far as is known, the diploid cytotype does not occur in the area of its type locality. A collecting trip to the type locality of *P. hesperium* in Coyote Canyon, Lake Chelan, Washington, yielded several isolated colonies of *Polypodium*. They were essentially similar in morphology and all plants on which chromosome counts were made proved to be tetraploid (**n** = 74). On the basis of the evidence there is little doubt that the tetraploid should bear the name *P. hesperium* Maxon.

The restriction of *P. hesperium* to the tetraploid cytotype apparently leaves the diploid cytotype without a name. There are, however, several possible names in the literature which should be considered.

One epithet that might apply is *P. amorphum* Suksdorf, the type specimen of which was collected at the base of a shady cliff in Dog Creek Canyon, Skamania Co., Washington, in the region of the Columbia River Gorge. On the basis of a photograph in Frye (1934), examination of the type specimen and Suksdorf's description, this species has some features in common with the diploid cytotype, viz., a thin slender pruinose rhizome with typical scales and circular marginal sori with paraphyses. In morphology of the frond, *P. amorphum* is very variable with mostly semicircular frond segments and bifurcate frond tips. The diploid cytotype does not agree with it in these features.

In the fall of 1967 and again in the spring of 1968, I made two trips to Dog Creek to collect topotype material of *P. amorphum*. Dog Creek flows through a narrow percipitous canyon in a series of waterfalls, some up to 30 ft. high. The first trip involved a search of the lower reaches of the canyon from its mouth at the Columbia River to a point one-half mile upstream. Here further upstream search became impossible because of a high waterfall with no safe way around it. The only *Polypodium* found on this part of the stream was *P. glycyrrhiza*. Several additional attempts by others (Slater, 1964; pers. comm.) at the lower end of the canyon to re-collect *P. amorphum* have also failed.

The upper part of the canyon was reached on the second trip after a steep four and one-half mile hike up Dog Mountain and down a tributary stream to Dog Creek. Here it was discovered that Dog Creek and the tributary meet at the botom of an inaccessible box canyon after a vertical fall of about 75 feet. Specimens of the diploid cytotype were seen growing, out of reach, from the underside of the overhanging cliffs. None of these plants appeared to be similar to *P. amorphum*. A search upstream from the head of the box canyon yielded only *P. glycyrrhiza*.

Since Suksdorf was about 70 years old when *P. amorphum* was first collected in 1925 and was under a doctor's order not to make extended collecting trips (Weber, 1944), it seems likely that he collected his type specimen from the lower end of the canyon. Weber (pers. comm.) concurs with this evaluation and states that Suksdorf definitely did not have an assistant to collect for him in the field. In making up specimens for distribution, Suksdorf returned to the type locality three times; in doing so he probably collected most of the existing plants, any survivors having subsequently died out. *Polypodium amorphum* seems to be an example of the "sports" that occasionally occur in various fern species with its unusual frond segments and bifurcate frond tips. In all probability *P. amorphum* is no longer an extant taxon due mainly to the zeal of its author.

Article 71 of the 1966 edition of International Code of Botanical Nomenclature states that a name must be rejected if it is based on a monstrosity. If one accepts that a monstrosity, in the botanical sense, is a plant that deviates greatly from the natural form or character, is abnormal, or is malformed, then *P. amorphum* must be rejected, since *P. amorphum* does deviate greatly from natural form (compare the phtograph of the type of *P. amorphum* in Frye (1934) Fig. LVIII, with the drawing of the diploid cytotype of *P. hesperium,* Fig. LVII, 3 and 4, in Frye). If one accepts that it is merely a sport of the diploid cytotype of *P. hesperium* s.l., it is in any event abnormal in morphology when compared to most members of the *P. vulgare* complex.

One of the problems with Article 71, as pointed out by Davis and Heywood (1965), is that it fails to define a monstrosity. The definition given above is based on the 1966 edition of Webster's New Collegiate Dictionary. One of the examples of the application of Article 71 given in the rules refers to the orchid genus *Uropedium,* a peloric form with the third sepal (labellum) resembling the other two. The generic name, *Uropedium,* according to the rules, is based on a monstrosity and "must therefore be rejected." The monstrosity is now referred to as *Phragmipedium caudatum* (Lindl.) Rolfe.

If *P. amorphum* was a plant that represented a morphological extreme along a more or less continuous line of variation in the diploid cytotype of *P. hesperium* s.l., then it would be difficult to reject the name under Article 71. Article 7, note 1, states that the nomenclatural type is not necessarily the most representative element of a taxon; it is merely that element with which the name is permanently associated. An exception to this is when a name is based on a monstrosity (Benson 1962).

Since *P. amorphum* shows a very clear morphological discontinuity from the rest of the diploids in *P. hesperium* s.l., apparently no worse than the example of *Uropedium,* Article 71 makes the rejection of the epithet *amorphum* mandatory if the Code is to be followed. Of all the specimens examined in this study, none have approached the morphology of *P. amorphum.* In all probability the form arose only once and is now extinct.

Shivas (1961) has rejected the epithet *cambricum* for the European diploid *P. australe* Fee on the basis that *P. cambricum* L. is based on a monstrosity.

I accept a similar view that *P. amorphum* is based on a monstrosity and must be rejected under Article 71.

Several varietal names should be considered on the basis of Recommendation 60a of the Code. *P. vulgare* var. *columbianum* Gilbert cannot be used for the diploid cytotype since it is apparently a synonym of the tetraploid *P. hesperium.* All of the plants examined from the general area of the type locality, the Arrow Lakes in British Columbia, appear to be tetraploid; the diploid has not been found in the interior. Photographs of the type specimen indicate that it was probably tetraploid, also they agree closely with the type specimen of *P. hesperium* and with known tetraploid plants. In any case, the new combination *P. columbianum* for the diploid would be illegitimate since it would be a later homonym of *P. columbianum* Baker.

Clute (1910) described *Polypodium vulgare* var. *perpusillum* from Mount Lemon, Arizona and gave the following brief description: "Fronds one to four inches long, one-half to three-quarters of an inch wide deminishing below, pinnules oblong, obtuse, about eight pairs; sori medium size, numerous, near margin than midrib." This description more or less fits the diploid cytotype, especially the sori being near the margin than the midrib. Unfortunately, Clute's type specimen has not been located nor has topotype material been available for examination. The description is not precise enough to state with certainty that it is the same as the diploid cytotype of *P. hesperium* s.l.

In view of this the writer does not feel justified in taking up Clute's varietal epithet of *perpusillum* for the diploid cytotype, and so the new name *Polypodium montense* is proposed. Quantitative measurements are presented in following manner to display best their variability. Using stipe length as an example the shortest stipe measured was (8 mm long) (80% of all stipes measured were from 28 to 100 mm long, the average stipe length being 58 mm long) (the longest stipe was 142 mm long).

Polypodium montense F. A. Lang, nom. nov. *Polypodium amorphum* Suksdorf, Werdenia 1: 16, 1927. Holotype: Dog Creek Canyon, near Cooks, Skamania Co., Washington, *Suksdorf 11667,* WS.

Rhizoma repens, amarum, 3–5 mm per medium, saepe pruinosum, paleaseum; squamae rhizomatum atrobrunneae vel castaneae, saepe axe centrali cellularum fuscatarum, anguste ovatae vel ovatae, saepe constrictae supra fundo, usque 5 mm longae, plerumque apicibus capillaribus, crasse dentatis, cellulis grandibus circa 25 numero trans squamam paulo supra fundo; frondes circa 130 mm longae, maxima longitudine circa 300 mm; stipites graciles, (8) (28–*58*–100) (142) mm longi; laminae coriaceae vel membranaceae, oblongae, (18) (46–*81*–122) (190) mm longae, (11) (17–*24*–30) (45) mm latae; laciniae oblongae vel abovatae, apicibus obtusis vel raro acutis, marginibus integris vel cernulatis, (5) (9–*13*–17) (25) mm longae, (3) (4–*6*–7) (12) mm latae, latitudine longitudini collata ut una pars duabus partibus confertur (1.2) (1.8–*2.3*–3.0) (3.6); venis liberis, semal atque iterum; hydathodi parvae, rotundae, paucis cellulis; sorus circularis, propior margini quam costae; paraphyses multae; chromosomatum numerus **n = 37, 2n = 74.** Holotype: Cheakamus River, British Columbia, *Lang 211,* UBC.

Rhizome creeping, acrid, 3–5 mm in diameter, often pruinose, paleaceous; rhizome scales dark brown to castaeus, often with a central strip of darkly colored cells, narrowly ovate to obovate, often constricted above point of attachment, to 5 mm long, usually with a capillary tip, margin coarsely toothed, cells large, ca. 25 in number across scale just above point of attachment; frond averaging 130 mm long; max. ca. 300 mm long; stipe slender, (8) (28–*58*–100) (142) mm long; blades coriaceous to membraneous, oblong (18) (46–*81*–122) (190) mm long, (11) (17–*24*–30) (45) mm wide; segments oblong to obovate, tips obtuse to

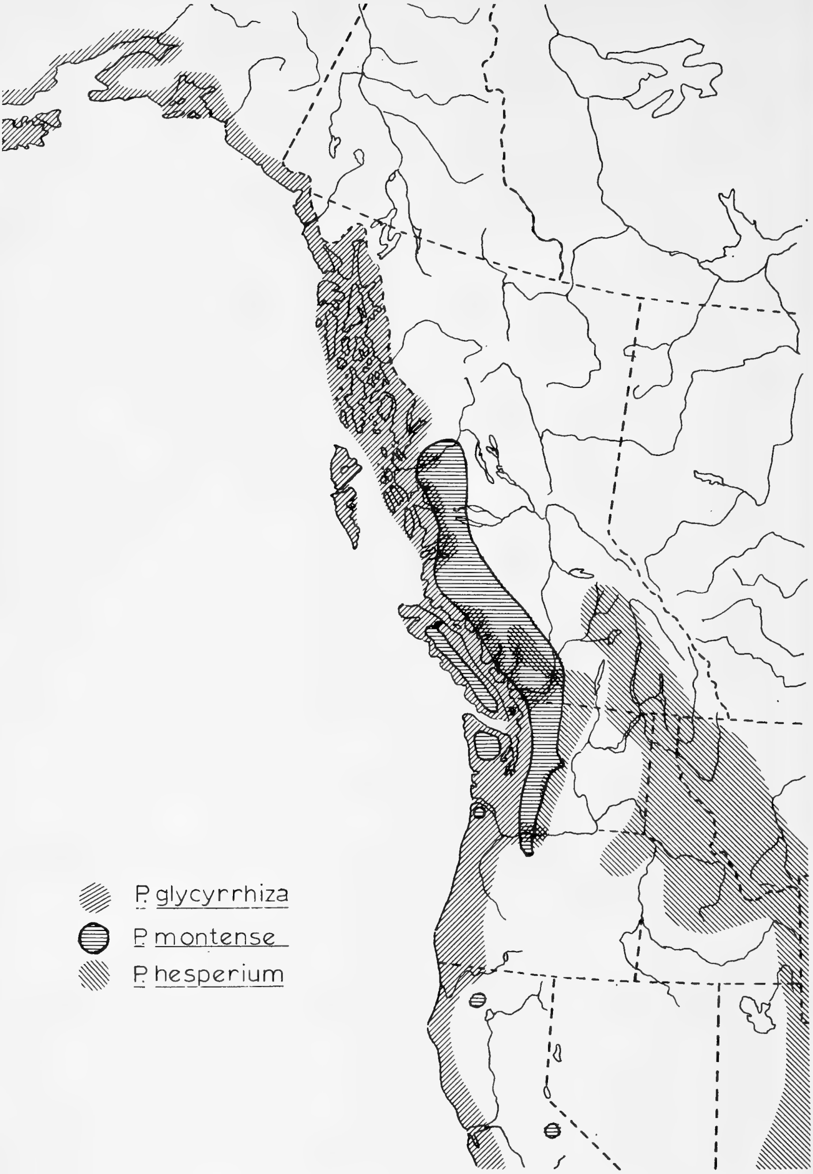

FIG. 1. Distribution of *Polypodium* in northwestern North America.

rarely acute, margin entire to crenulate, (5) (9–*13*–17) (25) mm long, (3) (4–*6*–7) (12) mm wide, ratio of length to width (1.2) (1.8–*2.3*–3.0) (3.6); hydathodes small, round, few-celled; veins free, forking 1–*2* times; sorus circular, nearer the margin than the costa; paraphyses many; chromosome number **n = 37, 2n = 74.**

New fronds produced from late April to June; found growing in rock crevices in mountains from central Coast Range in British Columbia south through the Cascade Mountains in Washington to Oregon and the Sierra Nevada Range in California, in the Olympic Mountains and Wenatchee Mountains of Washington and the Northern Coast Range of Oregon, usually at high elevations but descending to bottoms of river valleys.

The geographical distribution of *P. montense* is based on specimens from the following herbaria, UBC, UC, V, and WTU. Figure 1 shows the distribution of *P. montense, P. hesperium* and *P. glycyrrhiza* in Northwestern North America. *Polypodium montense* is apparently absent from the Mount Hood region of Oregon south to the Sierra Nevada Mountains in California.

A few herbarium specimens from the mountains of Northeastern Colorado, the Laramie Hills of southeast Wyoming and some of the high mountains of Arizona appear to be *P. montense.* The majority of specimens from the Rocky Mountain Region, however, are apparently the tetraploid *P. hesperium.*

Polypodium montense is closely related to *P. virginianum* L. of Eastern North America, sharing many features in common with it, but differing in its obtuse frond segments and geographical distribution. The possible role of *P. montense* in the parentage of the tetraploid cytotype of *P. virginianum* has already been discussed (Lloyd and Lang, 1964).

I would like to express my thanks to T. M. C. Taylor for his invaluable aid, to William Reid of the University of Washington for his help with the Latin description, and to Southern Oregon College for partial financial support.

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THE PYGMY FOREST-PODSOL ECOSYSTEM AND ITS DUNE ASSOCIATES OF THE MENDOCINO COAST

H. JENNY, R. J. ARKLEY, and A. M. SCHULTZ

INTRODUCTION

Along the Mendocino coast some twenty irregular patches of pygmy forest, dominated by stunted cane-like cypresses (*Cupressus pygmaea*) and dwarfed bishop (*Pinus muricata*) and Bolander pines (*Pinus contorta* ssp. *bolanderi*), are surrounded by belts of tall bishop pines and shore pines (*Pinus contorta*) and by luxurious regional forests containing giant redwoods (*Sequoia sempervirens*) and Douglas firs (*Pseudotsuga menziesii*). This striking forest differentiation, marked by floristic endemism, has fascinated botanists ever since Bolander's early explorations over a century ago.

Bishop and Bolander pines, but not the shore pine, are closed-cone pines. Mason (1934) approached the problem of the origin of the coastal closed-cone pine forests from a broad point of view. Looking for natural barriers that would conserve pines, he ruled out—correctly we think—local climates, topographic constellations and especially country rock, as there are no serpentines, quartzites or other rock extremes. Mason then searched for a water barrier and assumed, in analogy with the fossil and living forests on Santa Cruz I. off Santa Barbara, that the coastal strips used to be Tertiary pine-populated islands that later united with the mainland and preserved their unique flora against infiltration from the continental forest. Just how the aggressive invaders from the regional redwood and Douglas fir forest were kept at bay during hundreds of thousands of years could not be explained. A good account of Mason's ideas is given by Cain (1944) and more recently by Langenheim and Durham (1963).

The possible role of soils in the floral discontinuities of the greater Fort Bragg area came into focus with the work of the Mendocino County Soil and Vegetation Survey during the late forties, and by the subsequent studies of Gardner and Bradshaw (1954) and Mason's student McMillan (1956; 1964).

NEED FOR AN ECOSYSTEM CONCEPT

When it was discovered that pygmy forest grows on podsol soil, known locally as Blacklock soil, having a white, bleached surface horizon and an iron-cemented hardpan below it, naturalists indulged in an apparent *circulus vitiosus*. On field trips the professors of botany would tell their students that the podsol soil is the cause of the unusaul assortment of plant species, whereas the visiting professors of pedology (soil science) would attribute—in the light of classical podsol theory—the soil horizon features to the acid-producing vegetation. While it is true that a species individual responds to its soil niche, it is also true that it modifies that niche, which, in turn, reacts upon the individual. A broader approach is called for, the joint development of soil, vegetation and animal life with their mutual interrelated feedbacks (Jenny, 1961). It is embodied in the concept of the ecosystem.

ECOSYSTEMS RELATED TO LAND FORMS

During Pleistocene times, when the continental glaciers formed and melted, the world-wide sea level sank and rose. The rising sea cut *terraces* into the prevailing graywacke sandstone rock. The retreating sea covered these platforms with beach sands, gravels and clays. Tectonic forces elevated the terraces. In this light, the higher terraces in the Mendocino area most likely are the older terraces.

Detailed field work between Navarro River and Fort Bragg led Gardner (1967) to assign terrace levels at altitudes of 100 ft., 175 ft., 300 ft., 425 ft. and 650 ft., corresponding to first, second, third, fourth and fifth terraces. These are the major terraces, according to our observations. The measurements do not refer to the actual terrace surfaces but to the hidden, buried "nickpoints" where terrace floor and sea cliff meet. Invariably, the pygmy forests and their associated extreme podsols are extensive on the three upper terraces (fig. 1).

The nearly level terraces are dissected by rivers that flow from the inland graywacke *mountains* westward to the sea. *Hill* and *canyon slopes* are continually being rejuvenated by a combination of slow geologic erosion (back cutting) and sandstone weathering. The slopes, mostly steep, are covered with impressive regional forests rich in redwoods and Douglas firs.

Besides these terraces, mountains and canyons a fourth landscape feature assumes prominence, the *sand dunes*. Wind is presently blowing graywacke-type sand from the beach up on to the adjacent higher first terrace, thereby placing fresh dune sand upon older, weathered and plant-covered beach deposit. What is happening today apparently happened in the past, for extensive sand dunes rest on all terraces. On the higher plateaus they have undergone intensive weathering and produced Noyo soils, but dune size and shape are largely preserved. Most important, the dunes on the lower terraces carry redwood and Douglas fir, those on the higher mainly bishop pines.

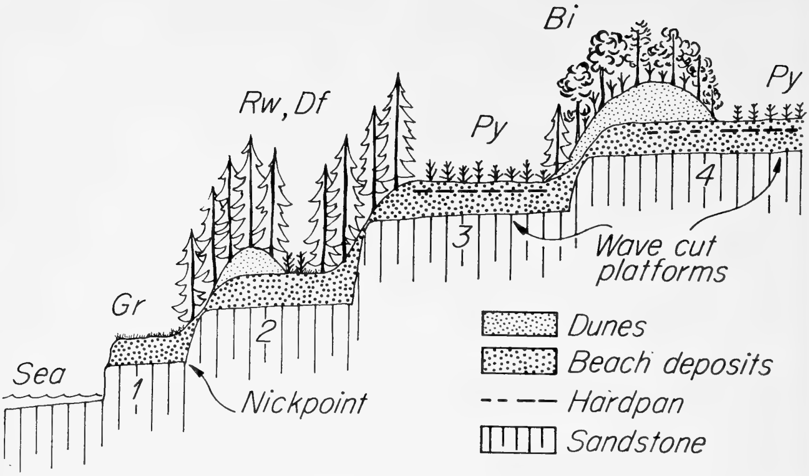

FIG. 1. Schematic arrangement of four marine terraces (1, 2, 3, 4) Fort Bragg area, with a young dune on second and very old dune on fourth terrace. Gr. = grassland, Rw, Df = redwood-Douglass fir forest, Bi = bishop pine forest, Py = pygmy forest. Horizontal distance is 3 miles, vertical distance 500 ft. above sea level.

To sum up, there is, then, a remarkable and fortunate mineralogical uniformity in the soil parent materials which are the initial states of the various forest soil ecosystems. They are either weathering graywacke sandstone or sandstone-derived beach materials and dunes. And though the land-form features fail to be uniquely reflected in vegetation discontinuities, they nevertheless bring out clearly the convergence of narrow endemism and dwarfism upon the higher and hence older land surfaces (*vetusta surfaces*). Their strongly podsolized soils provide niches for closed-cone pines and these niches also govern size and shape of the trees, tall bishop pines on Noyo soil and puny dwarfs on Blacklock soil.

THE PYGMY FOREST-PODSOL ECOSYSTEM

Among the various forest soil ecosystems along the coast the pygmy-podsol type has received most attention.

Vegetation mosiac. Extreme pygmy forest is species-poor and space-unsaturated, with as much as 25 per cent of the ground area bare or covered with colonies of lichen. Slender cypresses and gnarled and twisted bishop-and Bolander pines, many decades old and some passing the century mark, are only 1.5–3 m tall. Their trunk thicknesses do not exceed the diameter of a human wrist or arm.

Bolander pine was recognized as a distinct taxon, *Pinus bolanderi* Parl. by McMillan (1956). Critchfield (1957) designated it as a subspecies of *P. contorta.* Its leaves are narrowed, devoid of resin canals and the cones are heavier and asymmetrical. Unlike *P. contorta,* they are serotinous (closed-cone), a feature confirmed by plantings at the Institute of Forest Genetics, Placerville, California (personal communication by W. B. Critchfield). According to E. G. Linsley (personal communication) the cones harbor a longhorned beetle (*Paratimia conicola*) not observed on *P. contorta* but known from closed-cone pines in the dry interior Coast Range foothills (*P. attenuata*). Bolander pine is an advanced stage of ecotypic differentiation.It is an "edaphic" ecotype conforming to Turesson's definition.

Likewise dwarfed are the prominent ericaceous shrub companions, like *Ledum glandulosum* (Labrador-tea), *Rhododendron macrophyllum*) (rose-bay), *Gaultheria shallon* (salal), the two *Arctostaphylos* (manzanita) species, *nummularia* and *columbiana,* and *Vaccinium ovatum* (huckleberry). Trees and shrubs exhibit die-back symptoms and fungus-gall infestations suggestive of specific nutrient deficiencies. Indeed, chemical analysis of pine needles registers deplorable shortages of potassium, calcium, magnesium, and phosphorus (analyses by A. Ulrich).

The dwarf extremes are interspersed with clusters and thickets of taller pines and cypresses, in the 6–12m range, still with no signs of redwood or Douglas fir, though these giants prosper a short distance away. Occasionally, a statuesque bishop pine as high as 21m towers amidst the dwarfs.

Soil profile features. For an explanation of this living mosaic we must take a look at the underlying *Blacklock podsol* soil (fig. 2), a Typic Sideraquod. It is easier said than done. It takes two people with a sharp auger two to three hours to penetrate the dark-gray, 4-inch thick surface layer (A1 horizon), the 14-inch-thick bleached, white A2 horizon, and the concrete-like hardpan B-horizon (Bmir) which occupies the depth interval of about 18–30 inches. Below the pan is rusty, mottled sand or sandy loam, weakly cemented in places. At a depth of 5–10 ft. unaltered sandy beach material (C-horizon) is reached. It rests at 10–20 ft. on the impervious, sea-cut platform of hard sandstone.

The Blacklock surface soil is extremely acid, pH 2.8–3.9, one of the most acid soils known anywhere. It is low in available nitrogen and phosphorous, demonstrated already by McMillan (1956), and in potassium and micronutrients, as ascertained by elaborate pot tests in the greenhouses at Berkeley. The supply of the nutritionally important exchangeable calcium (Ca), magnesium (Mg) and potassium (K), expressed as milliequivalents in 100 g oven-dry soil, is exceedingly low. Above the hardpan the sum of these bases (Ca + Mg + K) is less than 1 meg/100g.

In stratified and finer textured beach materials of the old terraces a dense clay pan with up to 61% clay may occur instead of the iron cemented hardpan. It too acts as an effective impediment to root penetration. The bases are likewise low and mineral acidity is high. We are naming this soil *Aborigine.* A multitude of brown iron streaks and patches tint and mottle its clays.

FIG. 2. Pygmy forest—podsol ecosystem. Cane-like *Cupressus pygmaea* growing on Blacklock soil showing surface humus horizon on white bleached A2 horizon which rests on iron hardpan. Water table is at 66 cm depth. Photo R. A. Gardner.

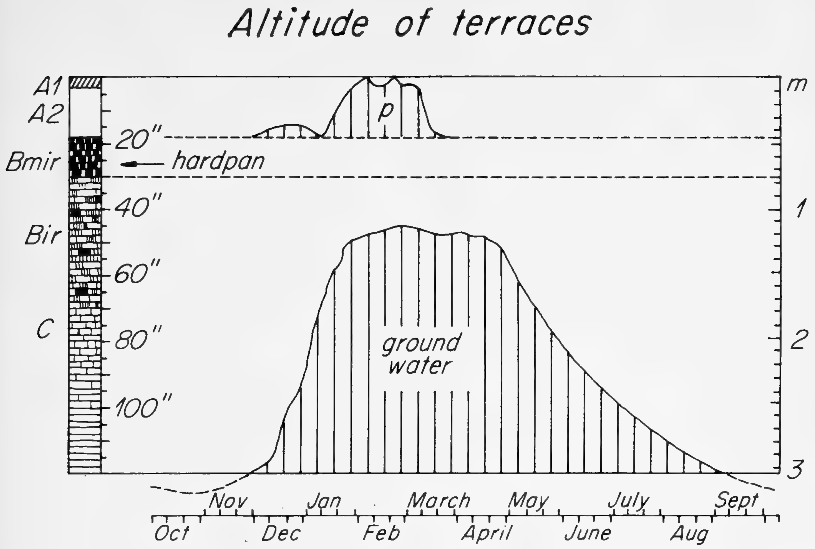

FIG. 3. Fluctuating water tables in Blacklock soil. Profile horizons indicated on left. During fall the water table is below 10 ft. After winter rains start a perched water table p above the hardpan is formed. The deep ground water table rises slowly to maximum height in February. During prolonged rains it may reach the hardpan. Mean annual precipitation is 38 inches.

Water regimen. If a 10 foot test hole is dug in the fall season, no free water is encountered. In early November, following the first 5–8 inches of winter rains, water begins to pile up on the basal rock plane and a rising groundwater table is set in motion. Long before it reaches the upper strata, water accumulates above the hardpan layer creating a second, perched water table (fig. 3) that floods the entire surface soil. In late spring the surface water table disappears by evapotranspiration and seepage. The soil down to the hardpan dries out, hardens and imparts extreme xeric conditions. In depressions and low places wetness persists throughout the rainless summer, giving rise to small sphagnum bogs. By October 1st, the descending ground water table has receded below the 10 ft.mark. Judging from about 40 permanent installations the rate of descent varies substantially among sites. Its correlation with the vegetation pattern has not yet been undertaken.

Podsolization process. As said, during the rainy season the surface soil is terribly wet and water stands in puddles and ponds. Its color is coffee brown from dissolved acid humus substances, their acidity originating from the carboxyl groups of pine needles and ericaceous leaves. The chelates of the humus combine with iron and other metals made accessible by weathering and render them mobile. Prior to and during hardpan formation the metal chelates (Fe, Mn) percolated and diffused into the subsoil, thereby bleaching and impoverishing the surface soil and leaving behind a snow white, thixotropic A2 horizon. This is podsolization. For reasons not yet fully understood, even though European investigators succeeded in imitating the process in the laboratory, iron may be precipitated in the subsoil as colloidal iron hydroxide. Its positive charge combines, according to a prominent theory, with the negatively charged soil particles cementing them together to an iron hardpan (Bmir of Blacklock). According to R. Tüxen (personal comment to Jenny) and Bloomfield (1965), iron migration is sensitive to the floristic composition of the plant cover. The process offers a promising challenge to an ecosystem-oriented biochemist.

Enclaves and borders. Within the pygmy forest area the taller pine and cypress thickets previously mentioned occupy fine textured (more clay, less sand) beach deposits but their clayey B-horizon is more permeable to roots than the severe Aborigine clay pan. The base status of lower horizons may be relatively high. The origin of this soil diversity is still obscure. One of the lone, impressive bishop pines surrounded by dwarfs had its root system exposed by chiseling away the hard A2 and indurated Bmir horizons. Surprisingly, an enormous tap root penetrated the hardpan and extended into the permeable deeper strata. Maybe there had been a crack or blemish in the pan, or the root was endowed with an exceptional supply of iron-dissolving chelates.

Seen from a distance, the change from pygmy to regional forest is very sharp. Vegetation appears discontinuous. Looking at the boundary more closely, 30–100 ft. wide transition zones (ecotones) disclose modulations of soils and plants. Where the canyon of Jug Handle Creek cuts into the fourth terrace (fig. 4) the drainage pattern is altered, the surface soil is deeper and moist in summer, and the hardpan is partially or entirely absent. At another site, an old sand dune rises rather abruptly above the pygmy plain. Its deep, weel drained soils offer a foothold to tall trees and thereby maintain a sharp vegetational contrast.

Multiple causes. In ecological parlance "edaphic causes" shape the appearance of vegetation. The adjective edaphic pertains to soil and its parent material. For Blacklock soil, what are the specific causes of endemism and dwarfism? Is it wetness in winter, dryness in summer, fluctuating water table, or is it oxidation or reduction, or harmful nitrite formation associated with the water regimen? Or, is it the impenetrable hardpan, either as a physical obstacle or as an unfavorable chemical environment? Or, is it high acidity or its related aluminum toxicity, or any one or all of the deficient nutrient elements in the spectrum of soil fertility? There is an enormous multiplicity of "causes," for thousands of soil properties are interrelated among each other, and with countless properties of the root system, and with enzymatic reactions and metabolic pathways inside the plant. It is a truly multivariate statistical problem, and we are approaching it in this light. We selected operationally soil variables that are amenable to manipulation and that are largely in-

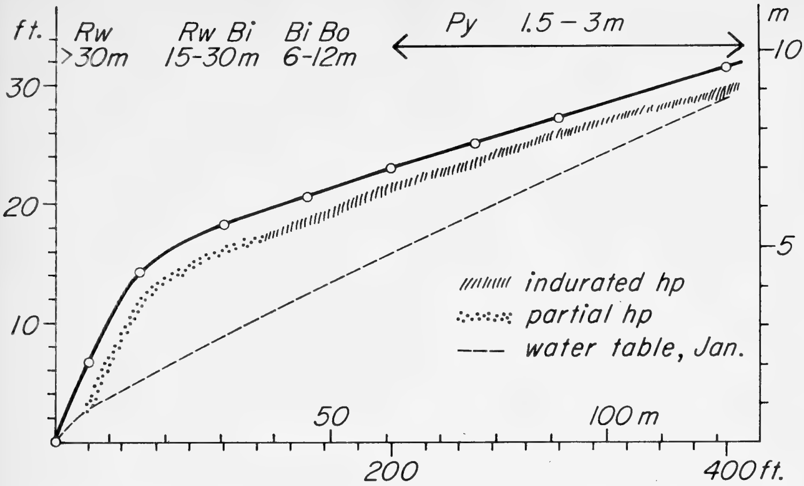

FIG. 4. Transition from pygmy (Py) forest on fourth terrace to regional forest in Jug Handle canyon. Circles indicate profile sites; water table as of Jan. 17; tree height in meters; Rw = redwood, Bi = bishop pine, Bo = Bolander pine. Vertical scale magnified.

dependent of each other (non-collinear). Thus, we initiated large-scale field experimentation on drainage with deep and shallow drains, randomized fertilization and breaking up of hardpan. So far, after a year's work, growth increments have been small, as one might expect for dwarfs. Mean elongation of five marked twigs on each of 80 pine trees was more than twice that of 80 cypresses. Also, elongations were larger on drained than undrained sites.

At any rate, this formidable array of soil attributes resulting from system evolution puts a tremendous strain on higher organisms. Redwood and Douglas fir do not grow and cypress and pines barely survive.

GENESIS OF ECOSYSTEM AND ITS SIGNIFICANCE FOR ENDEMISM AND DWARFISM

The staircase of terraces carpeted with beach materials and dune sand offers beautiful illustrations of ecosystem genesis. *The dune sequence* shall be taken up first.

On the lowest terrace, *recent dunes,* if bare, are still moving inland. Stabilization is brought about by colonizers, including lupines and *P. contorta* and *P. muricata.* The pines are able to endure strong salty winds, dry crests and winter-wet depressions. Slowly soil fertility is being built up.

Further away from the coast, as near Inglenook, the dunes on the second terrace (Lv-sites) are thousands of years old, but no C-14 dates are on hand. Dunes on the third terrace, Nm sites southeast of Cleone, might have been blown at the end of the last inter-glacial period or sometime thereafter. In all these *young dunes* oxidation has converted the originally drab, gray color of the recent dunes into a warm, rich brown. The minerals have weathered moderately, clay in amounts of 10–20% has been formed, and the exchangeable bases Ca + Mg + K are present in full measure, especially in the surface horizons (fig. 5). Acidity is around pH 5, considered advantageous for forest growth. All sites are covered with magnificent forest of redwoods, Douglas fir, grand fir (*Abies grandis*) and some western hemlock (*Tsuga heterophylla*). The soils abound in total nitrogen and in mildly acid humus, as exemplified by the carbon (C) – curve Lv in Fig. 6. These organic soil properties were not present at ecosystem time zero, the fresh dune, rather they are feed-back derivatives of the plant mantle on the one hand and the active microbial soil population — including the crucial nitrogen-fixers — on the other.

On the fourth and fifth terraces *very old dunes* are clearly recognizable. Sites specifically studied are labelled as Wi at 410 ft. altitude along Willits Road, and Dr at 560 ft. at the east end of Gibney Lane. The dunes are strongly weathered to great depth. The soils, known as Noyo, have podsolic features with a conspicuous, bleached, whitish A2 horizon underlain by yellow-brown, clay-rich B-horizons. The deeper subsoils may exhibit red-white reticulate mottling, a sign of profound chemical alteration. There is no hardpan though isolated iron concretions and cementations may appear in its place. During winter, water tables may be observed at depths greater than 10 feet.

The base content (Ca + Mg + K) is low (fig. 5, Wi, Dr), and soil reaction is sour, pH being around 4. Instead of mere humus acidity, as in Lv, Noyo's has a strong component of aluminum-rich clay acidity, said to be harmful to root growth. To a depth of 4 inches organic matter is enriched, but below that surface strip it drops to low magnitudes (fig. 6, Dr).

The dominant vegetation consists of sizable bishop pines, up to a century old, an isolated redwood tree here and there, and dense 1.5–3m tall underbrush of ericaceous species, joined by wax mytle (*Myrica californica*) and chinquapin (*Castanopsis chrysophylla*).

To summarize, the dune sequence expresses the transformation of the inert, fresh dune into a giant-tree ecosystem with an abundance of mild humus, a rich supply of bases, and advantageous quantities of soil acidity. This forest belongs to the major climax associations of the Coast Range (Heusser, 1960). Further soil transformations enhanced mineral acidity, depleted the stock of bases by leaching, and drained the humus reservoir to one-half by virtue of altered litter fall and soil microbe assembly. Gradually, the habitat became Noyo soil and the lush regional forest was displaced by endemic stands of closed-cone pine. From a utilitarian point of view, such as a lumberman's, the ecosystem deteriorated. If climax is defined (Cain, 1944) as a terminal plant community which is in dynamic equilibrium with the prevailing climate, then bishop pine rather than redwood forest would be climax on the dune. It explains in

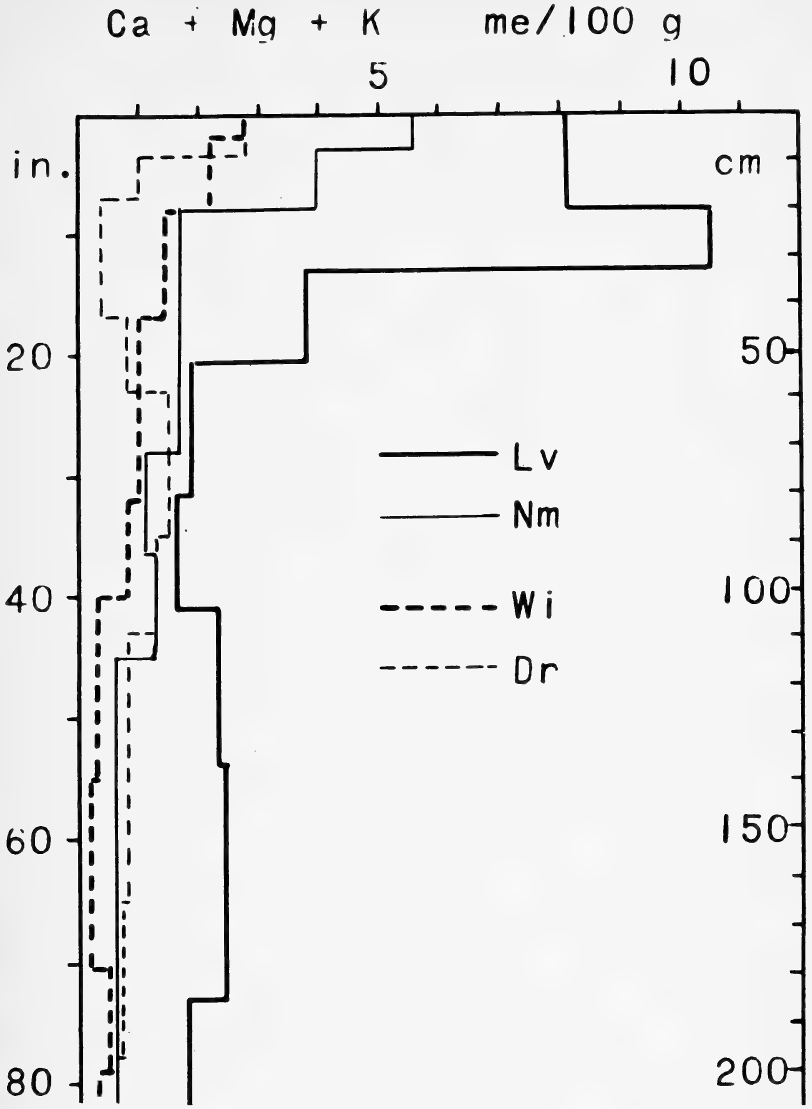

FIG. 5. Soil-depth curves of sum of exchangeable bases (me. of Ca + Mg + K in 100 grams of soil) for sand dunes of various ages. Lv is the youngest, Dr the oldest dune.

part the perpetuation of pine forests along the coast.

The parallel genesis of the *terrace soils* proper is accompanied by vegetation diversification of spectacular extent. New state factors entering into play are sluggish surface drainage, seasonal high water table, and texture extremes of beach materials ranging from sands to clays. When these materials were deposited their exchangeable bases had been in

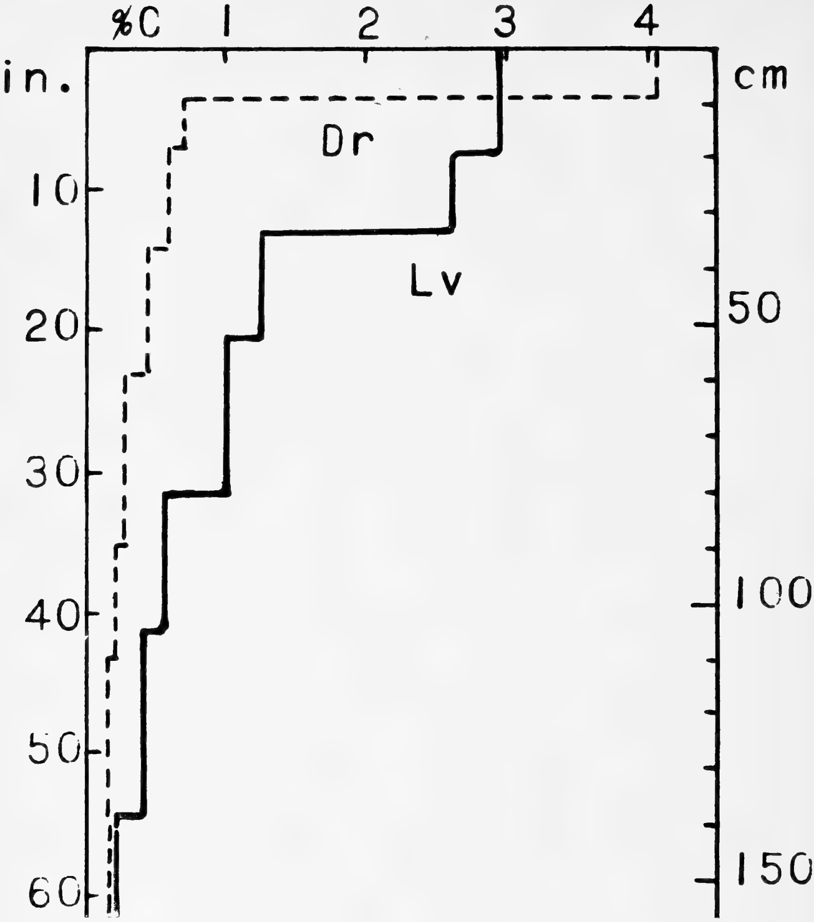

FIG. 6. Soil organic matter (mainly humus) expressed as percentage of organic carbon, in young (Lv) and very old (Dr) dunes in relation to soil depth.

chemical equilibrium with sea water which enriched their sodium content.

The *first terrace* supports grasslands and pine forests. Few redwoods, Douglas firs or hemlocks are seen. It appears that these trees cannot bear the local sea-salt and sodium challenge of air and soil. Under bishop pine in a sandy matrix Gardner (1967) sampled near Cleone a profile having a weakly bleached A2 horizon resting on a rusty colored sandy hardpan of weak cementation. It may be considered a precursor to Blacklock soil, the more so as its base content is relatively high.

East of Fort Bragg, the expansive *second terrace* displays wide ecosystem diversity. There are patches of tall redwoods on finer textured soil lacking wetness and A2 horizon but possessing an iron-stained clayey B. It might be a precursor to Aborigine soil. Nearby are tall, slender redwoods and hemlocks on waterlogged soil with A2 and iron concretions. Not far from it dense mixed stands of 12–18 m tall cypresses and bishop pines with an occasional redwood tree grow on bleached soil with iron nodule concretions. Last but not least, there is a tract of Blacklock soil with dwarfy forest devoid of commercial timber species.

On the *third and higher terraces* pygmy forest with pines and cypresses of various degrees of dwarfism is associated with Blacklock and Aborigine soils, as mentioned. In their sand fractions Gardner (1967) counted the slowly weathering potassium feldspar crystals (F) and the highly resistnet quartz grains (Q). In Fig. 7 the half circles on the vertical axis denote F/Q ratios of recent dune and beach materials. The white dots characterize the C-horizons of Blacklock soils on various terraces. In spite of the scatter of points, the trend (dashed line) confirms the mineralogical uniformity of the parent materials. Their mean is 17.5 K-feldspars per 100 quartz grains.

The black dots record F/Q of the Blacklock A2 horizons. The profiles of the older surfaces display exceedingly low ratios, less than 0.0003 for the fifth terrace. They signify far-gone weathering and they establish antiquity of soils, and, therewith, stability of the land forms. Moreover, the declining curve, in approaching zero, defines a terminal steady state condition. Barring a catastrophic change in state factors, we cannot visualize progression except perhaps for the trees getting more dwarfy.

It is tempting to view the evolution of the podsol ecosystems as an approximation to a monotone time-sequence operating in the cool and humid oceanic climate of the Fort Bragg area under conditions of tolerable salt influx. The initial state, the landscape situation at the start, comprises dune and terrace plus its biotic factor, the latter defined as the pool of species available to the site.

Today's biotic factor is made up of the germules offered by the regional forest and the coastal scrub and grasslands with an admixture of pine diaspores, particularly bishop-, shore- and Bolander pines. For the old Noyo, Blacklock and Aborigine soils the initial biotic factor might have included the Pleistocene ancestors of the pines. As the generations of seeds sprouted and grew the ensuing tree growth and vegetation differentiation responded to niche-creating soil development. Specifically, the emergence of dwarfism, severe ecotypes and local endemism became a consequence of orderly system evolution. It is not known on what soil type or types bishop pine evolved its genetic constitution, but that of Bolander pine presumably developed in conjunction with Blacklock and Aborigine soil genesis.

Natural vegetation sequences of the order of magnitude here envisioned are customarily attributed to a climatic shift. While we do recognize climatic changes in the Mendocino area, we do not believe them to be critical. Even if effective moisture had been doubled or reduced, it would have merely temporarily accelerated or retarded the long-time podsolic trend that molded both phenotype and genotype.

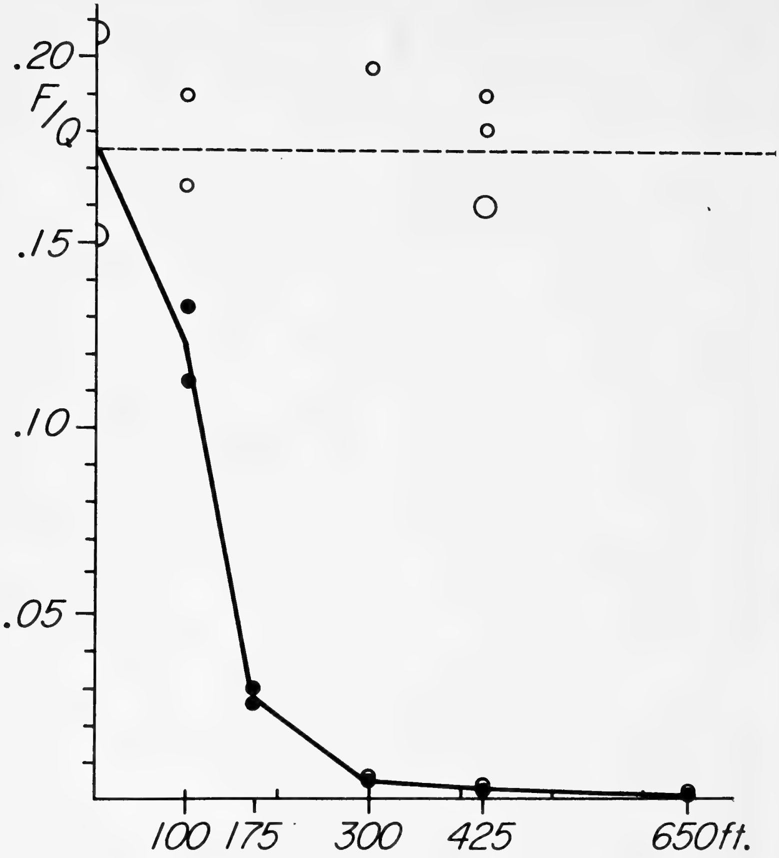

FIG. 7. Ratios of per cent K-feldspar (F) and per cent quartz (Q) in the sand fractions of parent materials (white dots) and in Blacklock A2 horizons (black dots). Parent material averages 17.5 feldspar to 100 quartz grains. The lower the ratios the more weathering has occurred.

THE AGE PROBLEM OF THE PODSOL ECOSYSTEM

Heusser (1960) published a pollen profile of a boggy site in the pygmy forest southeast of Fort Bragg. Bolander pine was prominent throughout the span of some 6,000 years. Redwood can be traced to much earlier periods as buried trees are frequently encountered by well drillers. A log was found at 16 ft. depth at the base of the Nm dune which sits on the front edge of the third terrace.

If the origin of the first terrace is correctly interpreted, its cutting was completed at the onset of the Wisconsin glaciation, some 100,000 years ago. If the higher terraces are also linked to glacial periods, time spans up to one million and more years could be involved (middle or early Pleistocene). These estimates pertain to the rock-cut terrace platforms.

Owing to erosion and deposition, the soils on a terrace might be younger than the platform itself. Also, since the classic podsols of northern Europe are all post-glacial, podsolization is a relatively fast process. Still, none of the German and Scandinavian profiles and their plant cover even approaches the extreme hardpan and dwarfism of the Mendocino Blacklock ecosystem.

The low F/Q quotients of Fig. 7 prove advanced age of soils but they do not elucidate the age of the profile features, specifically of the hardpan. In a clever piece of detective work, Gardner (1967) answered the query for site Wi where an extensive old dune rests on the fourth terrace. It was blown in when the sea level stood at the third terrace. Gardner dug a vertical shaft into the dune. At 13 ft. depth the deeply weathered mantle faded rapidly into unaltered dune material, its slip faces still intact. Their inclinations were identical with those of today's fresh dunes, and so was their orientation as to wind direction. At 20 ft., at the unweathered base of the dune, a light-gray horizon was underlain by a rusty-streaked, irregularly cemented hardpan, the two strata identifying a Blacklock precursor. No wood remains showed up.

Podsolization on the high terrace must have started prior to dune deposition, and though the process became arrested under the dune, it continued outside, for Blacklock exists there now. Gardner (1967) devised a speculative mathematical model of the weathering process that predicted a soil age of about a million years on the highest terrace. The order of magnitude seems plausible.

To conclude, not only the terraces themselves but their soil profiles too possess a venerable age For how long today's Blacklock and Aborigine profiles have capped the terrace mantle is not known. Because of its age and extreme features the pygmy forest-podsol ecosystem is unique in the temperate region, and it comes as close to a terminal steady-state system with balanced inputs and outputs as can be expected to be found in nature. It deserves further intensive investigation. To do so, suitable sites must be protected as scientific reserves. It is an urgent task that demands highest priority (Jenny, 1960).

SUMMARY

1. Along the coast of northern California, the higher, older marine terraces carry pygmy forest, and the associated old sand dunes are covered with bishop pines. The lower, younger terraces and dunes support grasslands, pines, and redwood-Douglas fir forest.

2. Pygmy forest consists of small cypresses (*Cupressus pygmaea*), dwarfed, closed-cone pines (*Pinus muricata* and *P. contorta* ssp. *bolanderi*) and stunted ericaceous associates, growing on extreme podsol soil having a bleached, white A2-horizon underlain by an indurated iron hardpan. During millennia vegetation and soil have evolved together (pygmy forest-podsol ecosystem).

3. Two sequences of podsolization are envisioned, both starting on

sandy parent materials: a. *Dunes.* Younger dunes, in contrast to unaltered recent dunes, are slightly weathered. They are high in bases and humus, low in clay acidity and they support luxurious redwood-Douglas fir forest. Continual weathering and leaching in the cool and humid oceanic climate impoverishes the soil and augments acidity. Through time the regional forest is gradually replaced by endemic bishop pines. b. *Terraces.* On the level plateaus with high, fluctuating water tables the podsolic processes are intensified, resulting in hardpans and clay pans and soil conditions that produce dwarfism, narrow endemism and pronounced ecotypic differentiation.

4. Geologic considerations and soil weathering indices provide age estimates of several hundred thousand years. The pygmy forest and its podsol soil comes as close to a terminal steady-state ecosystem as can be expected to be found in nature. Adequate preservation is urgent.

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NEW RECORDS OF MYXOMYCETES FROM OREGON. I.

Dwayne H. Curtis

A moderate amount of information has appeared in the literature dealing with slime molds of Oregon. At the present time, using only the species concepts accepted by Martin (1949), 188 species of Myxomycetes have been recorded from the state. The most extensive investigation, covering a period of more than twenty years, was conducted by Peck and Gilbert (1931). They collected primarily in northwestern Oregon from the western slope of the Cascades south to the Three Sisters Mountains, and the upper northern third of the Willamette Valley including the Coast Mountains. In 1932, Martin reported the occurrence of a new species from Oregon. In recent years only a few species have been added to the list. Two new species have been described by Kowalski (1966, 1968), and I (Curtis, 1968) reported *Barbeyella minutissima* Meylan from southern Oregon.

During the summers of 1966 and 1967, I collected in Crater Lake National Park in the south, central part of the state. Most of the specimens were obtained from moist decaying wood near the melting snow in the months of June and July. Later in the year, the slime molds were collected from duff, bark, fallen twigs and decaying wood. All my collections were taken at altitudes from 4,000 to 7,500 feet. In this paper, 8 species of Myxomycetes are listed as new to the state in the sense that no report of their occurrence in Oregon has been previously published. This brings the total number of slime molds found in the state to 196 species.

All collections have been deposited in the University of Iowa Herbarium, Iowa City, Iowa, and specimens in the Trichiaceae, Physaraceae and Didymiaceae have been deposited in the Crater Lake National Park Herbarium, Crater Lake, Oregon. The numbers used for the collections are my own and in this report indicate only those specimens given to the University of Iowa Herbarium.

LICEACEAE

Licea pusilla Schrad. On decayed coniferous wood 0.2 miles north of Park Headquarters, 6,500 feet, *6,* June 15, 1966. A limited number of sporangia were found in one collection. They are purplish-brown, sessile, and dehisce by preformed lobes. This exceedingly tiny species was reported by Kowalski (1966a) recently from California. Previously it had only been found as far west as Iowa, and is considered rare.

RETICULARIACEAE

Lycogala flavofuscum (Ehrenb.) Rost. I obtained only one aethalium on the side of a dead, barkless stump about 4 feet above the ground on the east side of Kerr Valley, 6,500 feet, *52,* July 28, 1966. The aethalium is about 15 mm in diameter, ochraceous-grey and the spores are buff in mass.

DIANEMACEAE

Dianema Andersoni Morgan. One collection on decayed wood, about 2 miles north of Park Headquarters, 6,800 feet, *1067,* July 14, 1967. The sporangia are sessile, 0.6–0.8 mm in diameter. This Myxomycete has been reported from Washington, British Columbia, and more recently from California (Kowalski and Curtis, 1968). It is considered rare.

TRICHIACEAE

Trichia affinis De Bary. Five collections on bark and decayed wood, one near White Horse Creek and Highway 62, 5,800 feet; two near Park Headquarters, 6,500 feet, *45, 69;* one on the east side of Kerr Valley, 6,500 feet; and one in the vicinity of the Vidae Falls Springs, 6,800 feet. The sporangia are 0.5—1 mm in diameter, crowded, and bright golden-yellow.

Hemitrichia montana (Morgan) Macbr. My collections, *67, 835, 857, 1064,* indicate that this species is ubiquitous throughout the park at elevations from 6,000 to 7,000 feet. It is so common that I am convinced that perhaps it was reported by Peck and Gilbert (1931) under another name. Hagelstein (1944) uses it synonymously with *Hemitrichia clavata* (Pers.) Rost. This common species may be sessile to short stalked with a translucent, shining peridium. The color is variable from a bright ochraceous-orange to a dark greenish-olive.

PHYSARACEAE

Physarum auripigmentum G. W. Martin. Twelve collections, frequently found beneath layers of decayed wood on fallen logs, at altitudes from 4,400 to 6,800 feet, *1006, 1022, 1090, 1100,* primarily from the Rim Village area south to lower Annie Creek, found throughout the summer months in both 1966 and 1967. The sporangia are readily recognized since they are 0.4–0.6 mm in diameter and greenish to bright yellow.

DIDYMIACEAE

Diderma deplanatum Fries. Eleven collections on decayed wood, taken from the Rim Village area southward to the south Park Entrance, North Rim road and Kerr Valley, at elevations from 6,000 to 7,000 feet, *762, 955, 1031, 1105,* June and July, 1967. The sporangia are white, sessile and 1–1.5 mm in diameter. They are very fragile and lose their peridium readily.

Diderma nigrum Kowalski. One collection, on coniferous twigs about 2 miles south of Park Headquarters, 6,200 feet, *1041,* July 10, 1967. This rare Myxomycete was recently described by Kowalski (1968). The sporangial dehiscence is star-shaped, revealing the white inner sporangial walls and black capillitium.

I am indebted to Donald T. Kowalski for verifying the determinations and for his assistance through the course of this investigation. This study was supported in part by the Chico State College Foundation, grant GU-1627.

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REVIEWS

The Evolution and Classification of Flowering Plants. By Arthur Cronquist. x + 396 pp. Houghton Mifflin Co., Boston, 1968. Price $6.95.

In an invited paper presented at meetings commemorating the 50th anniversary of the Botanical Society of America, held at the University of Connecticut in 1956, this reviewer had the temerity to suggest that, "there seems to be rather general agreement that sufficient evidence to formulate a really new, thorough-going, and generally satisfactory phylogenetic arrangement of flowering plants is not yet available." (Amer. J. Bot. 44: 88–92. 1957.) Later in the same meetings, however, two new systems for at least part of the angiosperms were presented by Herbert F. Copeland (Madroño 14: 1–9. 1957) and Arthur Cronquist (Bull. Jard. Bot. Etat 27: 13–40. 1957), respectively, and Robert F. Thorne announced that he was working toward the same goal (Aliso 6: 57–66. 1968). I do not recall that any of us were then aware of the work of Takhtajan, which has subsequently assumed such major importance.

The present volume is the outgrowth of that original Cronquist paper and is an attempt to devise a general classification of angiosperms responsive to all presently available pertinent information. The scope and variety of this information and its application are impressive. It ranges from the more traditional morphology and anatomy of the flower, fruit, and vegetative body, to pollen, embryology, and biochemical characteristics. The author is especially partial to type of nectary, nuclear constitution of pollen grains, details of ovular structure, nature of seminal food reserves, distribution of vessels, and type of stomatal apparatus, among other features.

Cronquist emphasizes that while taxonomy is necessarily based on multiple correlation of characters, a proper taxonomic system must also reflect (albeit muddily) evolutionary relationships, and that development of taxonomy and the unraveling of phylogeny each influences and strengthens the other. "A phylogenetic scheme which provides for all the available information and hangs together without serious internal contradictions is regarded as not only satisfactory but also something of a triumph." His classification is essentially one of consensus, in which he attempts to capitalize on the various natural groupings that have been achieved in the past. It is interesting to note how numerous these are on various levels. He asserts that if the requirement of a strictly single (monophyletic) origin for groups is not insisted upon too strictly, much of the apparent conflict between phylogeny and taxonomy disappears. He thinks the occurrence of evolutionary parallelism is itself an indicator of relationships and should be taken into account. The evidence for the adaptive significance of many of the character combinations that distinguish orders and families leaves him distinctly unsatisfied, and he repeatedly wonders aloud if the unfashionable concept of "evolutionary momentum" (orthogenesis?) may not play a role where selective impetus is obscure or undemonstrated.

He believes that angiosperms are a monophyletic group with ancestors somewhere in the seed ferns, and that the primitive flowering plants were woody and probably arborescent dicotyledons with magnolian/ranalian characteristics. Monocotyledons must have been derived from aquatic dicotyledons which had lost their cambium and hence the capacity to produce secondary growth and vessels in the normal way; monocot leaves developed from modification of a bladeless petiole. Consistent with his emphasis on consensus, Cronquist has adopted in major outline the system proposed by Takhtajan (Taxon 13: 160–164. 1954). The angiosperms (re-christened Magnoliphyta by Cronquist) are divided into dicots (Magnoliatae) and monocots (Liliatae). The dicotyledons are construed as consisting of 6 subclasses—Magnoliidae, Hamamelidae, Caryophyllidae. Dilleniidae, Rosidae, and Asteridae—and the monocotyledons as comprising 4 subclasses—Alismatidae, Commelinidae, Arecidae, and Liliidae. Whereas Takhtajan admitted 61 orders of dicots and 21 orders of monocots for a total of 82, Cronquist accepts 56 orders of the former group and 18 of the latter for a total of 74. Thorne, incidentally, eschews subclasses but recognizes 19 superorders and 43 orders of dicots and 5 superorders and 11 orders of monocots for a total of 54 orders. Although a good many differences in treatment do in fact exist between the first two of these arrangements, and even more between them and the last, the similarities are vastly more striking than are the differences. As Cronquist remarks, "We are all—or nearly all—Besseyans." It appears that we may be in danger of becoming Takhtajanians, as well.

Cronquist provides keys to the subclasses, to the orders, and to the component families. These must obviously allow for many exceptions, but they are useful. The selective bibliography accompanying the discussion of each order should prove to be even more useful. The writing is clear, concise, and positive, but the difficulties with various taxonomic dispositions and the possibility of alternative choices are pointed out frankly. The really fascinating aspect of the book is the opportunity afforded in the running discussions of orders to find out what has happened to the groups of one's particular interest. If there is any danger in the treatment, it is that so many of the long-standing controversies and indecisions seem to have been resolved so easily and logically. It should be rewarding to see whether consensus widens or diminishes as other books involving comparable schemes of classification appear, as they surely will. For the present, Cronquist has given us a very useful, well written, and stimulating volume in an uncrowded field of endeavor. —Lincoln Constance, Department of Botany, University of California, Berkeley.

Flora of Alaska and Neighboring Territories. By Eric Hultén. xxii + 1008 pp., illustrated. Stanford Univ. Press. 1968. $35.00.

Eric Hultén's preeminence among students of the Alaskan flora is a present-day example of how floristics research in a state or region tends to be dominated, for long periods of time, by the outstanding work of a single individual. Although Professor Hultén's principal interests, by his own admission, have been in the phytogeography of circumboreal floras, he has contributed to taxonomy such important references as the Flora of Kamchatka (1927–1930), Flora of the Aleutian Islands (1937, 1960), and Flora of Alaska and Yukon (1941–1950). As those who have used these books know, their purpose was to document scientifically the literature, collections, nomenclature and distribution of arctic plants; and descriptions, illustrations and keys are generally lacking.

In a charmingly personal preface to the present book, Hultén tells how he decided to prepare what would be ". . . a flora of another character . . . one that would serve a larger public." This work, Flora of Alaska and Neighboring Territories, is in all respects a great achievement. As a manual its primary purpose is that of plant identification, and this is accomplished through concise keys, descriptions and illustrations of all the species and most infraspecific taxa of Alaskan higher plants (spermatophytes and vascular cryptogams). Other essentials are also included—keys to families and genera, a glossary of terms, a list of botanical authorities, and bibliography. Especially remarkable, however, is the book's content of phytogeographical information, given in paired range maps for each taxon—a dot map of the area covered by the manual, and an outline map of each entity's complete circumpolar range. These are Hultén's unique contributions, derived from more than 40 years of study of boreal floras and they add a highly useful dimension that is rarely found in regional floristic manuals.

Alaska is a very large place, and a large book is required to do justice to it. What are the statistics of this flora? The area covered is Alaska, including the Aleutian Islands, Yukon Territory, the northwest tip of British Columbia, and the Chukchi Peninsula of Sibera—a total of 1,022,400 square miles. In it are, "Some 1,974 distinct, taxonomically named plants, belonging to 1,559 species, 412 genera,, and 89 families . . ." The book also mentions hundreds of hybrids and over 200 closely related taxa occurring in neighboring boral regions. Not only are there large latitudinal and altitudinal differences within this area, but the land is geologically complex and includes major sections that were free of ice during the last two glacial maxima. The importance of its central position in the migration route between the Old and the New Worlds hardly needs mentioning. What better vantage point is there to view, in panorama, the history and relationships of northern plant species?

"A general condition of the flora of this region is that the morphological variation of a given taxon is greater in Alaska than in other parts of its range." Hultén's taxonomic approach to this complex flora makes use of two traditional tools: a conservative view of species, and a concept of subspecies as the major morphologically recognizable, geographical divisions of a species. Because the author has so extensively revised the nomenclature of the flora, particularly at the subspecific level, every reviewer will find much to comment on in groups he knows at first hand. Species that we in the Pacific Northwest have recognized as distinct may run northward and intergrade with others in Alaska or elsewhere in the arctic. As a result we find, for example, *Populus trichocarpa* made a subspecies of *P. balsamifera, 'Beckmannia syzigachne"* submerged in an asiatic subspecies of *B. erucaeformis,* and *Phyllodoce glanduliflora* reduced to a subspecies of *P. aleutica.* Even more notable is Hultén's synonymizing of *Aster foliaceus* with *A. subspicatus*; the types of both of these are Alaskan and rather similar, but farther south the names are applied to two very distinct entities. Although such unions appear justified, one wonders about other cases where evidence of intergradation is slighted and the plants are kept as distinct species. *Tiarella trifoliata* and *T. unifoliata* were shown by Kern to be interfertile and intergrading, yet they are recognized here as species. *Amelanchier florida* was placed by Hitchcock as a subspecies of *A. alnifolia* on the basis of their evident intergradation, and they are not convincingly distinguished by Hultén's descriptions and illustrations. In *Saxifraga,* intergradation is admitted between *S. davurica* and *S. unalaschcensis,* yet they are kept as species. A similar relationship seems to exist between *Hieracium triste* and *H. gracile,* which nonetheless are not merged by Hultén. Very minor differences, principally of pubescence, appear to mark the two species recognized in *Romanzoffia* as well as the three of *Douglasia,* whose geographical relationships resemble those of subspecies.

Some interesting changes in generic alignments can be noted, but forunately these are minimal. The treatment is conservative in groups like *Lycopodium, Claytonia,* and *Chrysanthemum-Tanacetum. Minuartia* is divided from *Arenaria, Podagrostis* from *Argostis,* and *Platanthera* from *Habenaria,* however. Hultén's conservative handling of apomictic and hybridizing groups is important in reducing the number of named microspecies. In the difficult genus *Salix* there are 56 taxa described, in *Antennaria* there are 19, in *Arnica* 17, and in *Taraxacum* only 11.

Many of the author's nomenclatural changes appear to be derived from a rather long paper published in Arkiv för Botanik, in 1967. Not having this paper available, I have only noted a few of what appear to me to be unusual selections of names for this flora. *Alnus oregona* should be *A. rubra* Bong., for example, the *Betula-Alnus rubra* of Marshall being no homonym of the latter name. *Stachys emersonii* is used by Hultén, although from Epling's examination of the type it appears that *S. mexicana* Benth. is an earlier name for this species. Finally, *Echinopanax* is used in place of *Oplopanax,* although A. C. Smith, in the Flora of North America, states that the former is a *nomen nudum.* The editorial work on this book is, overall, so excellently done that it is mere nit-picking to call attention to minor errors. In a few cases, however, illustrations seem to be significantly at variance with plant descriptions; these were noticed for *Ranunculus trichophyllus* var. *trichophyllus,* where floating leaves are not lacking from the drawing, for *Amelanchier,* where the key leaf-shape differences are not apparent, and for *Linnaea borealis* ssp. *longiflora,* whose leaves are hardly "elliptical, acute." On the range maps, the circumpolar distribution of *Papaver nudicaule* is omitted, as is the occurrence on the Gaspé Peninsula of *Agoseris aurantiaca.*

This review would be incomplete without the simple statement that Flora of Alaska is a beautiful book! The difficult job of arranging keys, drawings, maps and text has been solved with neatness and economy of space. Luxurious additions are the physiographic maps on the end-boards and a section of superb colored plates from photographs by the author. Among many small but helpful details in the book are the habitat notes and information on type localities provided for all taxa, an index of common names, and pronunciation guides for the scientific names. With such careful attention to details evident throughout the work, two omissions stand out quite noticeably—there are no generic descriptions and no index to synonyms. The latter would have helped this reviewer discover how the genus *Youngia* came to be lost, before he noticed that its only North American species, *Y. americana,* resides on page 956 in the synonymy of *Crepis nana.*

It will be apparent to all who use this book that the Alaskan flora contains a goldmine of biosystematic problems that have hardly been touched. Hultén has brought to a high level of refinement the taxonomic knowledge that can be gained from morphological and geographical evidence, but the genetic, cytological and biochemical information necessary for a total synthesis of relationship is largely lacking. The difficulties of integrating biosystematic data with existing morphological categories are already clear from what is known of the cytotaxonomy of such "difficult" groups as *Epilobium angustifolium* (Mosquin), *Calamagrostis canadensis* (Löve, Mitchell, and others) and *Achillea millefolium,* sens. lat. (Ehrendorfer, Mulligan and Basset). The flora of Alaska will amply repay careful study by generations of future botanists, all of whom will be indebted to Eric Hultén for this landmark in the botany of North America. —KENTON L. CHAMBERS, Oregon State University, Corvallis.

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NEOGENE FLORISTIC AND VEGETATIONAL HISTORY OF THE PACIFIC NORTHWEST

Jack A. Wolfe

The Neogene fossil plant assemblages of the Pacific Northwest are more numerous and more completely studied than the Neogene assemblages of any other area of North America (fig. 1). Most of the work has been based on the study of plant megafossils—particularly leaves—which provide a valid basis for the reconstruction of lineages and hence floristic history. The increasing body of palynologic data, on the other hand, provides an insight into vegetational history, which is difficult to reconstruct from megafossils that represent largely the specialized streamside and lakeside vegetation. Both megafossil and microfossil assemblages typically represent ligneous plants, although microfossil assemblages include more representatives of herbaceous plants than do megafossil assemblages. This report will thus primarily concern woody plants.

By piecing together lineages and by analyzing the vegetational types in which the lineages have lived, it is possible to understand the development of vegetation in terms of its floristic elements. Proponents of various "geofloral" concepts have unfortunately confused flora and vegetation, which inherently leads to a confusion of floristic and vegetational history. It is extremely improbable from the genetic and physiological viewpoint that many lineages could have remained in association throughout the Tertiary; that is, that a given vegetational type remained floristically unchanged (Mason, 1947; MacGinitie, 1962; Wolfe, 1964). Recent work has indeed shown that many "Madro-Tertiary" elements in Nevada represent lineages that were present earlier in the mesic Miocene vegetation of the Pacific Northwest (Wolfe, 1964). Work in Alaska has also shown that the concept of an "Arcto-Tertiary Geoflora" is invalid (Wolfe, et al., 1966; Wolfe, 1966; 1969; Wolfe and Leopold, 1967; Wahrhafting, et al., 1969; Hopkins, et al., in press). The discussion of the Neogene of the Pacific Northwest involves an understanding of the history not only of that area but of much of northwestern North America.

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Publication of this paper has been authorized by the Director, U.S. Geological Survey.

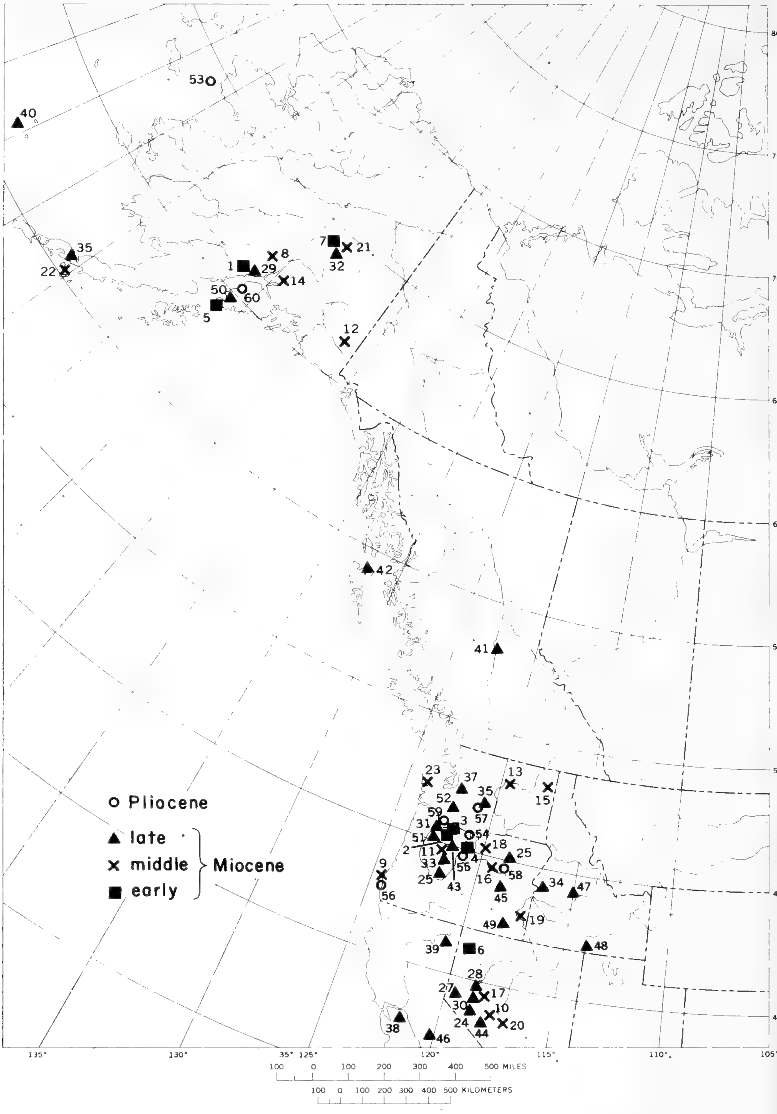

FIG. 1. Location of some Neogene and early Pleistocene assemblages in northwestern North America. Numbers correspond to assemblages as follows:

Early Miocene

1. Capps Glacier
2. Collawash
3. Eagle Creek
4. Maupin
5. Seldovia Point
6. Upper Cedarville
7. Upper Healy Creek

METHODS OF DETERMINING VEGETATION

The paleobotanist, after completing identification of the fossils from a given assemblage or series of assemblages, has at least a partial list of the flora. The significance of such a list in terms of vegetation is not agreed on by all paleobotanists. Most poleobotanists working on Tertiary assemblages of western North America have used a two-fold approach to determine vegetation: 1, a strict application of uniformitarianism to the tolerances of a given lineage, genus, or family (i.e., tolerances have not changed through time), and 2, counts of the megafossils.

That lineages have had different tolerances in the past than at present should be obvious from theoretical considerations. Assuming that the dicotyledons, for example, at one time evolved in a limited area that had a limited number of habitats and climates, during the spread outward from such an area the organisms in any lineage would have met new environmental conditions; the same reasoning can be applied to the lineages comprising any genus or subgenus. The fact that the dicotyledons today occupy an extremely wide range of habitats is an indication that lineages are capable of adapting to new environmental conditions. The fossil record in fact supports such a concept of changing tolerances: one lineage of *Pterocarya,* for example, first appears in North America during the Eocene in subtropical and tropical forests (Wolfe, 1968). During the Oligocene, the lineage is represented in tropical forest during the early part of that epoch, but by the late Oligocene it was present in warm temperate vege-

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Middle Miocene

8. Cache Creek
9. Cape Blanco
10. Fingerrock
11. Fish Creek
12. Frederika
13. Grand Coulee
14. Houston
15. Latah
16. Mascall
17. Middlegate
18. Monument
19. Rockville
20. San Antonio
21. Suntrana
22. Unga Island
23. Wishkaw River

Late Miocene

24. Aldrich Station
25. Blue Mountains
26. Brock Road
27. Chalk Hills
28. Chloropagus
29. Chuitna River
30. Fallon
31. Faraday
32. Grubstake
33. Hidden Lake
34. Hog Creek
35. Lower Ellensburg
36. Marble Point
37. Mashel
38. Neroly
39. Pit River
40. Pribilof Canyon
41. Quesnell
42. Skonun
43. Skunk Creek
44. Stewart Spring
45. Stinking Water
46. Table Mountain
47. Thorn Creek
48. Trapper Creek
49. Trout Creek
50. Type Homerian
51. Weyerhauser
52. Wilkes

Pliocene and early Pleistocene

53. Bering Platform
54. Dalles
55. Deschutes
56. Elk River
57. Middle Ellensburg
58. Rattlesnake
59. Troutdale
60. Type Clamgulchian

tation (Wolfe, 1959). During the early and middle Miocene, the lineage participated in the Mixed Mesophytic forest, and during the late Miocene the lineage is represented only in conifer forest. *Pterocarya* is today represented only in broad-leaved deciduous forests. In most instances, of course, tolerances of the Neogene representatives of a given genus or lineage probably more closely approximate the present tolerances of the genus or lineage than do the Paleogene represntativs. Note, however, that *Chamaecyparis nootkatensis* participated in vegetation that represents a conifer-live oak association during the late Miocene in southwestern Nevada (Wolfe, 1964); clearly *C. nootkatensis* included during the late Miocene physiological races that are no longer extant. Uniformitarianism should be applied cautiously to vegetational reconstructions.

If, of course, the "associational method" of determining the flora is utilized, such anomalous associations as that of *Chamaecyparis nootkatensis* and *Quercus chrysolepsis* will not be known. The "holotype" of the associational method of determination (Cain, 1944, p. 43) is in fact an excellent demonstration of the weakness of the method. Knowlton (1902) originally described *Cinnamomum bendirei* from the Bridge Creek assemblage of Oregon. Chaney (1927), however, interpreted this assemblage as a redwood forest and thus considered *Cinnamomum* an incongruous element. He therefore transferred Knowlton's species to *Philadelphus,* which would be expected in a redwood forest. Brown (1940) pointed out that the leaves morphologically could not be *Philadelphus* but had the diagnostic characters of Lauraceae; he thus transferred the species to *Sassafras.* This transfer was ignored by Chaney (194b, p. 350), who still considered that *Philadelphus* was a better choice for a redwood forest. After the discovery of the living *Metasequoia* and the realization that the Bridge Creek assemblage contained not *Sequoia* but rather *Metasequoia,* Chaney (1952) accepted Brown's transfer of the species to *Sassafras.* The leaves, however, have the small areoles lacking branched, freely ending veinlets and the continuous marginal vein of *Cinnamomum, Lindera,* and *Neolitsea; Sassafras* has large areoles intruded by branching veinlets and lacks a marginal vein (Wolfe, 1960). Knowlton's determination was more valid than either Chaney's or Brown's.

The second widely used method of reconstructing past vegetation is through the use of leaf counts. The basic assumption of this method is that the representation of leaves in a fossil bed is proportional to the representation of the plants that bore them in the ancient forets. Chaney (1959) has discussed the variables affecting such an assumption, and was forced to the conclusion (p. 46) that the assumption was perhaps valid only for generalities. Without any statistical basis, Chaney (1959, p. 46) stated: "I believe that any species that has provided as much as one-fifteenth [about 7 percent] of the record of foliage and fruit in a fossil flora must have been numerous enough to be considered abundant in the forest . . ." Whether Chaney's belief is valid is, of course, unknown.

It is extremely doubtful that the relative representation of plant megafossils is significant in reconstructing ancient vegetation. Megafossil assemblages contain an overrepresentation of fluviatile and lacustrine species that grew at or near the site of deposition (MacGinitie, 1953, p. 46; Fægri and Iversen, 1964, p. 39). As yet, no one has demonstrated any sizable correlation between the relative representation of organisms and the relative representation of their larger organs either on the forest floor or at the sites of deposition. One attempt to do so is that of Chaney (1924). The correlation coefficients he obtained were indeed sufficiently high to indicate that leaf counts might be valuable in reconstructions of vegetation. The only species for which Chaney gave the raw data is *Alnus rubra* [= *A. oregona*], the coefficient computed was 0.49. Note, however, that negative matches, situations in which neither organisms or remains of this species were found, were included in the computations. Such an inclusion hardly seems justifiable; the coefficient would be even higher if a worker included negative matches from Nevada, where the species does not grow. Recomputation of the correlation coefficient after elimination of all negative matches yields a coefficient of 0.35, i.e., very close to a universe in which no correlation exists. I conclude that although there is a slight correlation, it is insufficient for leaf counts to be considered useful in the reconstruction of vegetation.

Fossil leaves are, however, not entirely useless in determining vegetation. The physiognomic features of foliage are largely independent of taxonomy and appear to be highly sensitive to the environment (Richards, 1952, p. 154). The correlation between vegetational types and the leaf margin—whether entire or nonentire—is striking (Bailey and Sinnott, 1915, 1916). Several paleobotanists have applied this correlation to vegetational interpretations of fossil assemblages. In general, in a mesic climate, the percentages of species that have entire margined leaves can be correlated to vegetational type as follows:

76+	Tropical Rain forest
57–75	Paratropical Rain forest (extratropical rain forest of Wang, 1961; Subtropical Rain forest of Richards, 1952)
40–56	Subtropical forest
10–35	Temperate forest

Summer dryness and extreme winter low temperatures increase the percentage for the temperate forest; this increase is probably related to the physiological aridity of both far northern and truly arid climates. In Alaska, for example, the leaf margin percentage is 42, but a large number of the woody dicot species that have entire margins are thick- and small-leaved Ericaceae. The leaves of species of mid latitude, arid environments show similar adaptations. A consideration of leaf size should, therefore, be considered along with the type of leaf margin.

For Neogene assemblages, the microfossil assemblages are probably an excellent source of data for reconstructions of vegetation. Microfossil assemblages do not, insofar as the pollen of woody plants is concerned, represent local vegetation only; the pollen rain of a given region appears to be rather uniform and reflects the predominant vegetation type in the region (Davis and Goodlett, 1960). The variables affecting the interpretation of a pollen diagram have been and are being investigated; corrective factors that take into account many of the variables have been proposed (see for example, Fægri and Iversen, 1964, p. 99–123). Although some of the variables, for example, amount of pollen production, may have changed for various genera, the comparison of two approximately isochronous spectra or diagrams should yield a reasonable idea of the distribution of vegetational types during that interval of time. It should be emphasized, however, that interpretation of a single spectrum can be highly misleading; in a region of active volcanism, for example, one major eruption could drastically change the regional vegetation and hence pollen rain. Reconstruction of even a short diagram through several feet of section should help eliminate the effect of such short term changes in vegetation.

EFFECT OF ALTITUDE

Some workers have argued that previous interpretations of vegetational and floristic history in the Pacific Northwest have failed to take into account the varying altitudes at which the fossil assemblages lived. Thus Axelrod (1964) considered that a particular group of assemblages from the Pacific Northwest is isochronous and of middle Miocene age; these assemblages purportedly show a strong floristic and vegetational zonation according to altitude. The only method of testing the validity of Axelrod's conclusion is to demonstrate the contemporaneity of the assemblages. Various data—mammalian, radiometric, diatom, freshwater molluscan, and stratigraphic—all of which are high reliable for determining relative ages in the Neogene rocks of the Pacific Northwest, are available for several of these assemblages:

Assemblage	Basis for age assignment	Altitude[5]	Probable "absolute" age
Trapper Creek	diatoms, mollusks, stratigraphy[1]	3,000 ft.	11–12 m.y.
Trout Creek	radiometric[2]	2,300	13.1 m.y.
Mascall	radiometric[2]	1,500	15.4 m.y.
Upper Cedarville	radiometric[2]	1,100	19.8 m.y.
Rockville ("Succor Creek," in part)	radiometric[2]	600	16.7 m.y.
Grand Coulee	radiometric[4]	250	15.7–16.8 m.y.
Latah	radiometric[3,4]	250	15.5–20.6 m.y.

[1] Mapel and Hail, 1959.
[2] Evernden and James, 1964.
[3] Obradovich, unpub. data.
[4] Gray and Kittleman, 1967.
[5] Axelrod, 1964.

These data illustrate that age, not altitude, is the important factor. The early Miocene Upper Cedarville flora represents a cool time interval as compared with the warmer ("lower altitude") middle Miocene assemblages such as the Grand Coulee, Latah, Mascall, and Rockville (Wolfe and Hopkins, 1967). The age of the Upper Cedarville has been a matter of considerable discussion. I (1964), for example, have considered this assemblage to be of late Miocene age. The problem arises from the fact that LaMotte (1936) included in this flora material from '49 Camp, where the early Miocene radiometric age was obtained, and from the Pit River area many miles to the east. The Pit River assemblage contains *Platanus dissecta* Lesq., which is a typically late Miocene species. The Upper Cedarville ('49 Camp) and Pit River are here considered as distinct floras. The Rockville-Succor Creek problem is analogous to that of the Upper Cedarville-Pit River. The Succor Creek (late Miocene) and Rockville (middle Miocene) assemblages are here considered as distinct.

The late Miocene assemblages likewise represent a cooler time interval than do the middle Miocene assemblages. These middle and late Miocene assemblages do show a gradation from lower to higher, but this gradation is stratigraphic and not altitudinal.

EARLY MIOCENE

The concept of early Miocene varies from one paleontological discipline to another. The mammalian workers use the term Arikareean for this interval; radiometric dates indicate a duration for the Arikareean from about 21 to 25 or 26 million years ago (Evernden, et al., 1964). The foraminiferal workers, on the other hand, consider their Saucesian Stage to be basal early Miocene, and the base of this stage has a radiometric age of 22.5 million years (Turner, 1968). The moluscan paleontologists consider their Vaqueros "stage" to be of earliest middle Miocene age and this is thought to be equivalent in the foraminiferal sequence to the Saucesian stage. The base of the Miocene in western North America thus can be placed from about 23 to 28 million years, depending on which biostratigraphic framework is accepted. The only plant assemblages in this time interval (early Miocene) that have radiometric dates are the small Maupin assemblage, the upper member of the John Day Formation, which is younger than 23 million years (Evernden, et al., 1964) and the Upper Cedarville with an age of 19.8 million years (Evernden and James, 1964). These assemblages are, on paleobotanical grounds, correlative to the Miocene zone 2 of Wolfe (1962) and to the lower part of the Seldovian Stage of the paleobotanical geochronology. The lower Seldovian assemblages which are the oldest under consideration here may thus not be basal Miocene and may represent only the later part, 19 to 23 or 24 million years, of the early Miocene.

The known lower Seldovian assemblages are well represented in Alaska and in conterminous United States. In Alaska, they include the Seldovia Point, Capps Glacier, and Upper Healy Creek assemblages (Wolfe, et al., 1966; Wolfe, 1966; Wahrhaftig, et al., 1969). A total of about 70 megafossil entities is known, and the pollen floras have also been extensively studied. In conterminous United States, aside from the Maupin (Wolfe, unpublished data) and Upper Cedarville (LaMotte, 1936), lower Seldovian assemblages include the Collawash (Wolfe, unpublished data) and Eagle Creek (Chaney, 1920). Approximately 160 megafossil entitles are known, but, except for the Collawash, the microfossil assemblages apparently have not been studied.

The Alaskan assemblages are preserved in rocks that, for the most part, were deposited in large coal basins at low altitudes. The Upper Healy Creek beds were deposited at least 300 miles from the coast, and the Capps Glacier assemblage may have been only about 100 to 150 miles from the coast. The Seldovia Point assemblage was nearer to the coast than the other two assemblages but the beds containing their assemblage were deposited in a valley in an area of moderate relief (Wolfe, et al., 1966).

The topographic setting of the assemblages in Oregon is known with reasonable certainty. The basalts of the Columbia River Group buried and thus preserved some of the early Miocene topography in northwestern Oregon. At the time, the Cascades were probably more than 1,500 feet in height (Peck, et al., 1964, p. 28); the Collawash beds are at about the altitude at which the basalts thinned out against the range. To the north, in the area of Eagle Creek deposition, the basalts attain a thickness of about 2,500 feet. The distribution and thickness of the basalts thus indicates that the Eagle Creek assemblage probably was in a broad valley not far above sea level, whereas the Collawash assemblage was at about 2,500 feet elevation on the northern margin of the Cascade Range in Oregon. The original elevation of the Maupin assemblage is somewhat uncertain, but the small size of the assemblage makes its vegetational and floristic significance impossible to evaluate at this time.

The original elevation of the Upper Cedarville beds is extremely uncertain; certainly northwestern Nevada had a considerable elevation even in the early Miocene, but an altitudinal interpretation based on geologic data would be highly conjectural.

FLORA. The lower Seldovian flora is known to contain at least 180 megafossil species, and, combined with the microfossil floras, over 200 species are represented. The flora is particularly rich in species of Taxodiaceae, Salicaceae, Juglandaceae, Betulaceae, Fagaceae, Rosaceae, and Aceraceae; also typically present are *Ulmas, Zelkova, Cocculus, Liquidambar,* and *Platanus.*

The sources of many lineages in the lower Seldovian floras are known with reasonable certainty. One source is earlier vegetation of the Pacific Northwest; the lineages occurred in vegetation that represented Paratropical Rain forests, i.e., similar to the vegetation of lowland Taiwan and Hong Kong, or Subtropical forests. These lineages have displayed a considerable adaptability to changes in climate. Another source is the Paleogene temperate to marginally subtropical upland assemblages along the Rocky Mountains (Wolfe, 1960); some of these lineages had already appeared in the Pacific Northwest by the time that temperate vegetation occupied this area in the later Oligocene. A third, although minor, source is represented by lineages that first appear in the later Oligocene temperate vegetation of Alaska.

The lineages of Fagaceae for the most part are of unknown descent. One of the particularly striking features of Miocene as compared with older floras is the presence of "lobed" oaks, particularly the black oaks. The black "lobed" oaks are apparently restricted to North America, although Chelebaeva (1968) has referred a fragmentary specimen from the middle Miocene of Kamchatka to this group. The predecessors of the "lobed" black oaks must almost certainly be within the other members of the subgenus *Erythrobalanus*, and possibly forms such as *Quercus peritula* Cocker. from the marginally subtropical Florissant assemblage of the early Oligocene of the Rocky Mountains or *Q. pregrahamii* MacG. from the subtropical Weaverville assemblage of the late Oligocene of California may be ancestral. The origin of the "lobed" white oaks is even more problematic. MacGinitie (1953) considers the subgeneric assignment of the Florissant *Q. lyratiformis* Cocker. to be dubious, and this is the only pre-Miocene material from North America known to me that has been referred to *Leucobalanus*. The close relationship between the extant east American and the Miocene west American members of *Leucobalanus* indicates the probability that there was a common source in the Oligocene of the Rocky Mountains.

Some regional floristic differentiation is apparent in the early Miocene of northwestern North America. Most species of Salicaceae, for example, are distinct between Alaska and the Pacific Northwest. Rosaceae are more diverse in the Pacific Northwest and Lauraceae are unknown in Alaska. The Alaskan flora has a definite Asian element that did not reach the Pacific Northwest: *Acer fatisiifolia, A. ezoanum, Kalopanax, Ulmus longifolia, Populus reniformis*. More than half the known Alaskan lower Seldovian species are, however, also known in the Pacific Northwest, thus indicating that the two areas should be considered as parts of the same floristic province during the early Miocene.

Altitudinal zonation of the flora in the Pacific Northwest does not appear to have been pronounced during the early Miocene. Most species known from the low altitude Eagle Creek flora are also known in the upland Collawash flora. Considering the little latitudinal floristic zonation during the early Miocene, it should be expected that altitudinal floristic zonation would also be slight.

VEGETATION. The vegetation of the early Seldovian of northwestern North America was broad-leved deciduous. An apparently continuous deciduous forest extended from Japan and northern China north into

Alaska and south into the Pacific Northwest. Evergreens were an important part of this forest; coniferous evergreens became increasingly important in the north and broad-leaved evergreens in the south.

The Alaskan pollen assemblanges from the Cook Inlet region indicate that locally the conifers such as *Picea* were present in the lowland forest—presumably because of the cool summers (Wolfe and Leopold, 1967). In the interior of Alaska, however, only deciduous conifers of Taxodiaceae appeared in significant numbers with the broad-leaved deciduous plants. Broad-leaved evergreens were apparently rare in Alaska. The leaf margin percentage for the Alaskan lower Seldovian flora is 15, i.e., similar to that for the temperate forest of the Mid-Atlantic Staes and the northern border of the Mixed Mesophytic forest in China today.

In the Pacific Northwest, broad-leaved evergreens were more diverse and include: *Quercus, Magnolia, Cinnamomum, Litsea, Persea, Umbellularia, Exbucklandia, Cercocarpus, Lyonothamnus, Garrya*, and *Arbutus*. The leaf margin percentage for a large assemblage such as the Collawash is 25, i.e., similar to that for the region occupied by the Mixed Mesophytic forest in central China. The pollen assemblages from the Collawash beds contain only minor amounts of *Picea*, indicating that coniferous forest was not present even at 2,500 feet altitude. In eastern Asia today the Mixed Mesophytic forets has a latitudinal range of about 14°, but in western North America this vegetational type spanned at least 25° of latitude; even in the early Miocene latitudinal zonation of vegetation was much less pronounced than today.

MIDDLE MIOCENE

In this report, the term middle Miocene denotes an interval from about 14 or 15 to about 19 million years age. This interval is equivalent to the Hemingfordian and early Barstovian ages of the mammalian paleontologists. Assemblages of this age in Alaska include the Unga Island (locs. P9978, P9993 of Burk, 1965), Suntrana (Wahrhaftig, et al., 1969), two assemblages in the Kenai formation, the Houston and Cache Creek (Wolfe, et al., 1966) and the Frederika (Wolfe, unpublished data). In the Pacific Northwest, assemblages of this age include the Fish Creek, Cape Blanco, Wishkaw River, and Monument (Wolfe, unpublished data), as well as published assemblages such as the Latah (see Chaney and Axelrod, 1959, for list of references), Grand Coullee (Berry, 1931), Mascall (Chaney and Axelrod, 1959), and Rockville (Graham, 1965), which is, in part, the Succor Creek flora of some authors. In Nevada, only two middle Miocene assemblages have been described, the Middlegate (Axelrod, 1956) and the Fingerrock (Wolfe, 1964); an additional assemblage is known from the San Antonio Range (Wolfe, unpublished data) and three other assemblages are currently under study by Axelrod. In central California, no assemblages of middle Miocene age have been thoroughly studied.

The depositional setting of the assemblages from Alaska is, with one exception, lowland. The exception is the Frederika, which is preserved in beds that were deposited in an area of considerable relief. These beds were formed in part because of the damming of the drainage by the first extrusion of the Wrangell lavas (E. M. MacKevett, pers. comm., March 1969).

In the Pacific Northwest, both the Wishkaw River and Cape Blanco assemblages occur in intertonguing marine-nonmarine rocks, and hence represent coastal lowland vegetation. The Fish Creek assemblage occurs in beds that overlie the basalts of the Columbia River Group; presumably the Fish Creek assemblage lived at about the same elevation as the early Miocene Collawash assemblage, i.e., about 2,500 feet. In eastern Oregon, the Monument assemblage, which occurs in beds that are pre-Columbia River Group but post-John Day Formation, probably grew in a region of little relief. The Mascall assemblage probably grew in an upland basin surrounded by considerable relief, to judge from the thick volcanic sequence that grades laterally into the Mascall Formation (Thayer and Brown, 1966). The Latah assemblage occurs in lake beds that were formed by the damming of the drainage by the lavas of the Columbia River Group (Pardee and Bryan, 1926). Pardee and Bryan suggest that the lavas, which are much thicker to the east and south than it is now, i.e., higher than 1,500 to 2,000 feet (A. B. Griggs, pers. the Latah region by a chain of hills; the lavas finally attained a thickness sufficient to flow over the hills and ended deposition of the Latah. Several miles to the east of the Latah basin, the lavas lap onto the old granitic highland. These data indicate that the Latah Formation was deposited in an upland basin; if anything, the Latah basin was higher than it is now, i.e., highe rthan 1,500 to 2,000 feet (A. B. Griggs, pers. comm., March 1969). Geologic data bearing on the original altitude of the Rockville and the Middle Miocene assemblages from Nevada is lacking, although it is presumed that these regions were uplands of at least moderate elevation.

Flora. The flora of the middle Miocene (upper Seldovian) in Alaska and the Pacific Northwest differs little from that of the early Miocene. An almost complete generic list for the early and middle Miocene is given in Table 1. Almost all lineages in the late Seldovian were also represented in the early Seldovian. Some groups, e.g., Salicaceae, were more diverse in Alaska during the late Seldovian than during the early Seldovian, and possibly this represents diversification of the family. Pinaceae are better represented in the megafossil floras than previously, particularly late in the middle Miocene. A fir related to the extant *Abies bracteata* has an earlier record in the upland conifer forests of the Oligo-Miocene of the Rocky Mountains and makes its first appearance in the Pacific Northwest during the middle Miocene.

In Alaska one of the few upland assemblages of Miocene age, the assemblages from the middle Miocene Frederika Formation, contains a diversity of Pinaceae in contrast to the lowland Alaskan assemblages. Included in the Frederika assemblage are *Abies, Picea, Pinus,* and *Tsuga,* which are accompanied by *Pterocarya, Fagus, Ulmus,* and *Acer.*

Over 230 species and 110 genera of presumed ligneous plants are now known in the early and middle Miocene of northwestern North America. Considering the incompleteness of the fossil record, the richness is impressive. Despite extensive search, about 20 species with highly distinctive leaves from the Collawash assemblage have yet to be identified; it is conceivable that some of the leaves belong to extinct genera analogous to the epibiotic and/or monotypic genera of the extant Mixed Mesophytic forest of eastern Asia.

TABLE 1. COMPOSITION OF THE EARLY AND MIDDLE MIOCENE FLORA OF NORTHWESTERN NORTH AMERICA.

"p" denotes a record based largely or entirely on pollen. PNW = Pacific Northwest.

	No. species	Alaska	PNW		No. species	Alaska	PNW
Ginkgo	1	1	1	*Celtis*	1	0	1
Cephalotaxus	1	0	1	*Ulmus*	4	2	3
Abies	4	2p	3	*Zelkova*	1	1	1
aff. *Cedrus*	1	p	1	*Schoepfia/Anacolosa*	1p	0	1p
Keteleeria	1	0	1	*Aristolochia*	1	0	1
Picea	2	1	2	*Cercidiphyllum*	1	1	1
Pinus	3	2	3	*Clematis*	2	0	2
Pseudotsuga	1	p	1	*Mahonia*	3	0	3
Tsuga	1	3p	0	*Cocculus*	1	1	1
Chamaecyparis	1	1	0	*Liriodendron*	1	0	1
Fokienia	1	p	1	*Magnolia*	1	0	1
Calocedrus	1	0	1	*"Laurophyllum"*	6	0	6
Thuja	1	1	1	*Cinnamomophyllum*	1	0	1
Cunninghamia	1	0	1	*Sassafras*	1	0	1
Glyptostrobus	2	1	1	*Hydrangea*	1	1	1
Metasequoia	1	1	1	*Itea*	1?	p	p
Sequoia	1	1	1	*Exbucklandia*	1	0	1
Taxodium	1	1	1	*Fothergilla*	1	1	1
Populus	12	7	6	*Liquidambar*	1	1	1
Salix	13	8	6	*Platanus*	1	1	1
Comptonia	1	1	0	*Amelanchier*	2	0	2
Carya	4	3	4	*Cercocarpus*	1	0	1
Juglans	2	1	1	*Crataegus*	3	1	3
Pterocarya	4	3	4	*Holodiscus*	1	0	1
Alnut	7	5	7	*Lyonothamnus*	1	0	1
Betula	3	2	2	*Prunus*	3	1	3
Ostrya	3	2	1	aff. *Peraphyllum*	1	0	1
Ostryopsis	1	1	0	*Pyrus*	1	0	1
Castanea	1	0	1	*Rosa*	1	0	1
Castanopsis	1	0	1	*Rubus*	1	0	1
Fagus	7	2	5	*Sorbus*	2	1	1
Quercus	11	3	10	*Spiraea*	1	1	0

	No. species	Alaska	PNW		No. species	Alaska	PNW
Albizzia	1	0	1	*Xylonagra*	1	0	1p
Cercis	1	0	1	*Gordonia*	1	0	1
Cladrastis	1	1	1	*Idesia*	1	0	1
Gymnocladus	1	0	1	*Shepherdia*	1	1	0
Sophora	1	0	1	*Cornus*	2	0	2
Ptelea	1	0	1	*Nyssa*	1	1	1
Ailanthus	1	0	1	*Oreopanax*	1	0	1
Cedrela	1	0	1	*Alangium*	1	1	0
Rhus	1	0	1	*Clethra*	1	0	1
Toxicodendron	1	0	1	*Arbutus*	2	0	2
Pistacia	1	0	1	*Leucothoe*	1	0	1
Ilex	4	p	4	*Rhododendron*	2	1	1
Acer	12	7	8	*Diospyros*	1	0	1
Aesculus	2?	1	1	*Kalopanax*	1	1	0
Allophylus	1	0	1	*Halesia*	1	0	1
Ceanothus	1	0	1	*Fraxinus*	3	1	3
Colubrina	1	0	1	*Catalpa*	1	0	1
Karwinskia	1	0	1	*Diervilla*	1p	1p	0
Sageretia	1	0	1	*Symphoricarpos*	1	1	0
Zizyphus	1	0	1	*Sambucus*	1	0	1
Vitis	4	1	3	*Viburnum*	1?	p	1
Tilia	3	1	2	*Clerodendrum*	1	0	1

Noteworthy in this flora is a so-called Madro-Tertiary element. Included in this category are:

Quercus (part), *Juglans (Rhysocaryon), Mahonia, Cercocarpus, Lyonothamnus,* aff. *Peraphyllum, Ceanothus, Colubrina, Karwinskia, Garrya, Xylonagra,* and *Arbutus.*

Note that most of these genera formed an important part in the upland forest of the late Miocene of Nevada; although they have been termed 'Madro-Tertiary" by some workers, i.e., the lineages supposedly migrated northward into Nevada during the Neogene, the history of the lineages indicate that they were derived from a mesic forest of the Pacific Northwest during the middle to late Miocene interval.

The sources of the Mixed Mesophytic forest of the Miocene of western North America have been briefly touched on in this report (see also discussion by Wolfe, 1969). One significant element that contains both evergreen and deciduous broad-leaved plants was derived at various times during the later Paleogene from the evergreen broad-leaved forests. Several lineages representing genera such as *Quercus* (species that have "unlobed" leaves), *Alnus, Carya, Pterocarya, Magnolia, Cocculus, Cinnamomophyllum, Persea,* and other genera of the *"Laurophyllum"* type; *Liquidambar;* and *Platanus,* can be traced from the Paratropical Rain or Subtropical forests of the Eocene and earlier Oligocene into the temperate vegetation of the Miocene. A second and major element that primarily contains deciduous broad-leaved plants was derived during the Eocene and earlier Oligocene from the temperate to marginally subtropical vegetation that lived in the uplands, especially the Rocky Mountains. Lineages that display such a distribution represent, for example, *Populus, Salix, Sassafras, Amelanchier, Cercocarpus, Crataegus, Sorbus,* and *Acer*. A third but minor element was derived from the temperate vegetation of the later Oligocene of Alaska; most of these lineages represent Salicaceae or Betulaceae. Many of the lineages from these various sources diversified after entering the Mixed Mesophytic forest; members of Salicaceae, Judlandaceae, and Rosaceae, exemplify such a pattern.

VEGETATION. As in the early Miocene, the vegetation of northwestern North America was largely broad-leaved deciduous forest. Some zonation of vegetation is evident because broad-leaved evergreens, except for Ericaceae, were absent from Alaska but formed a significant element in the Pacific Northwest. Upland vegetation in the Northwest had only a minor element in Pinaceae, but in Alaska conifers of this family were dominant in the uplands.

The middle Miocene was warmer than the early Miocene. This is indicated by comparing the leaf margin percentages of the upland Collawash assemblage, 25, with those of the upland Fish Creek, 31, and Latah, 32, assemblages. Although the percentages for the Collawash and Latah are not strikingly different, the large size of both assemblages indicates that statistically the percentages are highly reliable. The warming could have brought subtropical vegetation farther north along the coast, and indeed the Cape Blanco assemblage has a leaf margin percentage of 35, which is closely approaching subtropical.

In reference to probable altitudes of the assemblages from central and southwestern Nevada, note that the leaf margin percentage for the San Antonio, Middlegate, and Fingerrock assemblages combined is 19. This is considerably less than the percentages for upland Oregon assemblages such as the Mascall or Fish Creek. Broad-leaved evergreens such as *Exbucklandia, Magnolia,* and Lauraceae are lacking in Nevada. I think it highly probable that the Nevada assemblages must have been significantly higher than the known middle Miocene assemblages from the Pacific Northwest, some of which grew at altitudes of at least 2,500 feet, i.e., the Nevada assemblages probably lived at altitudes of 4,000 to 5,000 feet or more. This suggestion takes into account the fact that not only do the Nevada assemblages appear to represent a cooler vegetation than that of the Pacific Northwest, but also that the Nevada assemblages are farther south than those in the Northwest.

LATE MIOCENE

The term late Miocene as used in this report represents the later part of the Barstovian and all the early Clarendonian mammalian ages. In terms of available radiometric ages, this interval lasted from about 14 to about 10 million years ago. Assemblages for which independent ages are available are, in Alaska, the Grubstake (Wahrhaftig and others, 1969), Pribilof Canyon (Hopkins, et al., in press), and Marble Point (locs. P5182, P9990 of Burk, 1965). The largest assemblages, however, are those from the Kenai Formation—the Chuitna River and those from the type section of the Homerian Stage (Wolfe, 1966). In British Columbia, late Miocene assemblages includes the Skonun (Martin and Rouse, 1966) and the Quesnel (Peil, unpublished data). In the Pacific Northwest this interval is represented by the Mashel, Wilkes, Faraday, Weyerhauser, Skunk Creek, Hidden Lake, and Brock Road assemblages (Wolfe, unpublished data), and by many previously published assemblages: Lower Ellensburg (Smiley, 1963), Stinking Water (Chaney and Axelrod, 1959), Blue Mountains (Chaney and Axelrod, 1959), Trout Creek (Graham, 1965), Thorn Creek (Smith, 1941), Trapper Creek (Axelrod, 1964), Hog Creek (Dorf, 1936), and Pit River (LaMotte, 1936). Not included in this discussion is the small assemblage from the Payette Formation. In Nevada, late Miocene assemblages include the Cloropagus, Fallon, and Aldrich Station (Axelrod, 1956), Chalk Hills (Axelrod, 1962), and Stewart Spring (Wolfe, 1964). In central California, only two late Miocene assemblages have been studied: the Table Mountain (Condit, 1944) and the Neroly (Condit, 1938).

In all instances, the Alaskan late Miocene assemblages represent lowland vegetation, as interpreted from the geologic data. Some were coastal (Pribilof Canyon, Marble Point), some were slightly interior (Chuitna River and type Homerian), and one was several hundred miles in the interior (Grubstake). The Skonun assemblage from the Queen Charlotte Islands was obtained from predominantly marine beds, and thus can be considered coastal lowland. The original altitude of the Quesnel assemblage is unknown, except that this area of British Columbia probably had at least moderate elevation during the late Miocene.

The Pacific Northwest assemblages represent both lowland and upland. The Mashel, Wilkes, Faraday, and Weyerhauser assemblages come from the Puget-Willamette lowland, and geologic evidence does not indicate that during the late Miocene this area was at a different altitude than today. During the late Miocene, the High Cascade Range had not yet developed, the Western Cascades being the only significant upland between the eastern and western Pacific Northwest. The fact that a few thousand feet of middle to late Miocene basalt did not override the Cascade Range in southern Washington is an indication that the Western Cascade Range there had at least moderate elevation, 3,000 feet, at the time of extrusion of the basalts. A chain of volcanoes formed the crest of this range in the central and northern parts of the Cascades in Oregon (Peck, et al., 1964, p. 31). Note that the Brock Road assemblage was situated near the crest of the range, whereas the Skunk Creek and Hidden Lake assemblages were east of the crest. All are now west of the crest of the present Cascades.

The topographic setting of the assemblages from eastern Oregon and Idaho cannot be precisely determined. The Hog Creek assemblage was probably in a broad valley of the ancestral Snake River. All the other assemblages, however, were in a broad sense upland. Geologic data are likewise imprecise in interpreting the original altitude of the Nevada assemblages, although they too were upland.

In California, the Table Mountain assemblage, which is now in the foothills of the Sierra Nevada, probably was lower than the present altitude, ca. 2,000 feet. The Neroly assemblage occurs in an intertonguing maine-nonmarine section, and was thus coastal.

FLORA. After the middle Miocene, many genera and species of the Mixed Mesophytic forest became extinct in northwestern North America, and are not found even in the lowland regions west of the Cascade Range; the Faraday, Weyerhauser, Wilkes, and Mashel assemblages represent the flora of the Puget-Willamette lowland. Notably lacking in these assemblages are genera such as *Castanea, Schoepfia/Anacolosa, Cercidiphyllum, Cocculus, Magnolia, Cinnamomophyllum, Laurophyllum, Exbucklandia,* and many others that were present even in the upland early and middle Miocene. Specific diversity within genera such as *Carya, Fagus,* and *Quercus* was also less in the late than in the early to middle Miocene.

Floristic provincialism was more pronounced during the late Miocene than earlier in the Neogene. A similarity matrix was constructed (table 2) based on comparison of the specific composition of the megafossil assemblages. Five groupings are apparent: Alaska, Columbia Plateau-Cascade Range, Nevada, Puget-Willamette, and California. The first three floristically intergrade. Alaska and Nevada had floras that were more closely related than were the floras of Nevada and California or Nevada and the Puget-Willamette area.

Late Miocene assemblages, particularly those in Alaska, display a greater diversity of *Salix* and Ericaceae than earlier assemblages. From Alaska south to the Columbia Plateau and Nevada conifers were better represented than before. The "Madro-Tertiary" elements were largely restricted to Nevada.

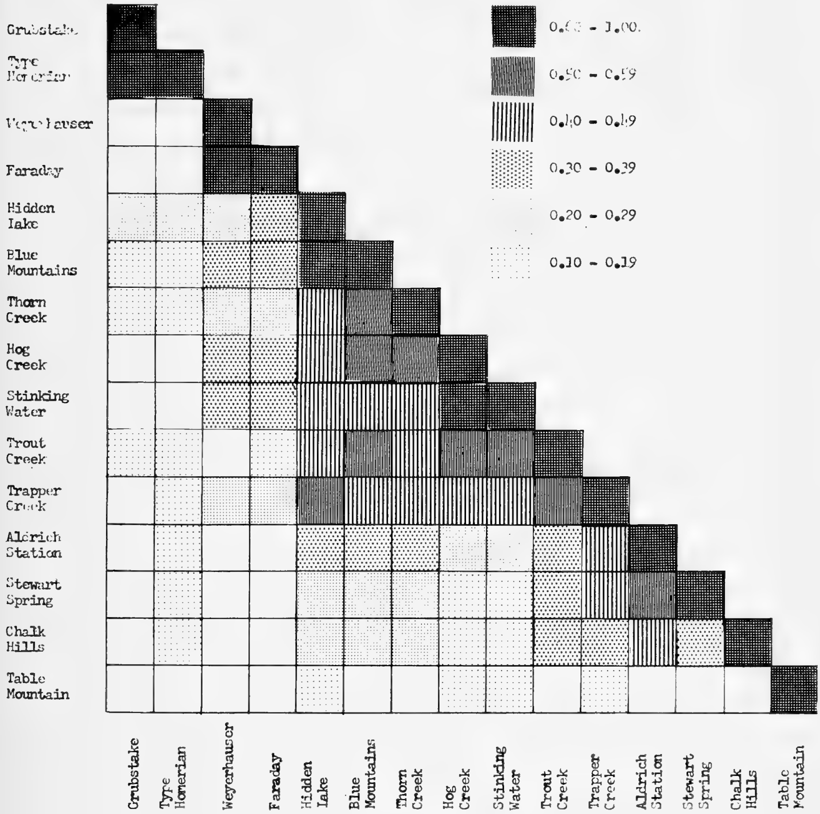
The group that suffered most extinction is composed of lineages that were derived from the paratropical and subtropical vegetation during the later Neogene. The Mixed Mesophytic elements that were derived from the upland assemblages of the Paleogene Rocky Mountains were proportionately better represented in the late than in the early or middle Miocene. Notable exceptions, however, are some lineages of Juglandaceae, Betulaceae, *Liquidambar,* and *Platanus,* all of which were of paratropical or subtropical extraction. These long-ranging lineages were also widely distributed in the Mixed Mesophytic forest and thus probably had broader tolerances than many of their associates.

TABLE 2. SIMILARITY MATRIX OF SOME LATE MIOCENE MEGAFOSSIL ASSEMBLAGES IN NORTHWESTERN NORTH AMERICA.

Coefficient of similarity (or association) is that of Dice and Sørensen as given in Sokal and Sneath (1963, p. 129):

$$S_D = 2n_{JK}/(2n_{JK} + u)$$

where S_D = coefficient of similarity, n_{JK} = number of positive matches, and u = number of negative matches.



The modern aspect of the late Miocene flora is clear. Not only were many exant lineages represented, but in some instances the extant species was represented. Note, however, that many late Miocene lineages have not survived to the present day. One particularly significant example is the lineage represented by aff. *Cedus;* this lineage is represented by cone scales in which the seeds were born entirely on the cone scale as in *Cedrus* but that had a long subtending bract as in *Abies*. At the four localities at which these cone scales have been found, pollen samples typically display an abundance of *Cedrus*-like pollen and presumably the two organs represent the same genus.

It is noteworthy that in the late Miocene some related lineages had attained certain distribution patterns which have been largely maintained to this day, and some lineages had attained a restricted distribution either west or east of the Cascade Range. Thus the lineages of *Alnus incana, Betula papyrifera,* and *B. occidentalis* are known only from assemblages that lived to the east of the late Miocene crest of the Cascade Range; the lineages to which *A. oregona* and *A. rhombifolia* belong were, on the other hand, represented only west of the Cascades. In reference to north-south distribution, the probable ancestor of *Holodiscus dumosus* occurs in assemblages that were east and south of the assemblages in which the probable ancestor of *H. discolor* is represented. The lineage of *Betula papyrifera* was largely northern and the lineage of *B. occidentalis* was largely southern. However, some lineages, e.g., that to which *Quercus kelloggi* belongs, were represented both east and west of the Cascades, whereas these lineages are today entirely western.

VEGETATION. The leaf margin percentages for both the Alaska and Nevada assemblages are approximately 30, whereas those for the Puget-Willamette and Columbia Plateau assemblages range from 14 to 24, typically about 17 to 21. The high percentage for Alaska, combined with the small size of the leaves, is interpreted as representing an approach to cold, and hence physiologically arid, conditions; the present percentage for Alaska is 42. In Nevada, however, a summer dry climate had probably set in, which is of course physiologically arid (Wolfe and Hopkins, 1967). Percentages similar to those for Alaska have been obtained for the modern vegetation of the Pacific Northwest. The Puget-Willamette assemblages were probably analogous to the vegetation of the Middle Atlantic states, i.e., temperate broad-leaved deciduous forest.

The extensive amount of pollen data allows an excellent understanding of vegetational regions during the late Miocene (fig. 2). The Alaskan assemblages represent a cool conifer forest, which was floristically more diverse than the present boreal forest. Broad-leaved deciduous plants, other than Betulaceae and Salicaceae, were represented, although sparsely. The Skonun assemblage shows some similarity to the Alaskan assemblages in the high representation of Betulaceae, but the moderate representation of Juglandaceae and Fagaceae indicate a mixed conifer broad-leaved deciduous forest. The Skonun-Mashel-Weyerhauser-Faraday spectra intergrade from the mixed forest in the northern lowlands to a broad-leaved deciduous forest in the southern lowlands. Juglandaceae, Fagaceae, and *Liquidambar* appear to have been the major constituents of the more southern forest. This could be designated a hickory-oak-beech assemblage.

The vegetational differences between the Willamette lowland and the higher elevations in the Cascade Range can be readily determined from the pollen spectra (fig. 3). All upland spectra have large amounts of Pinaceae, particularly aff. *Cedrus* and *Picea,* whereas, except for

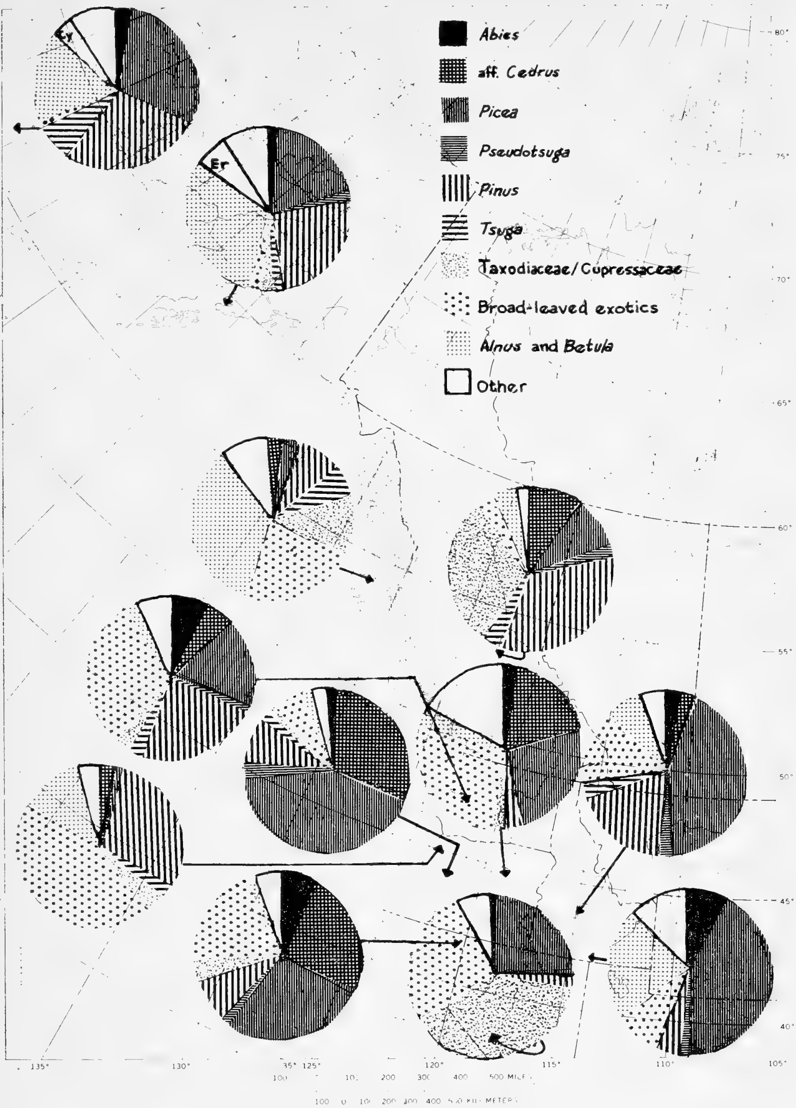
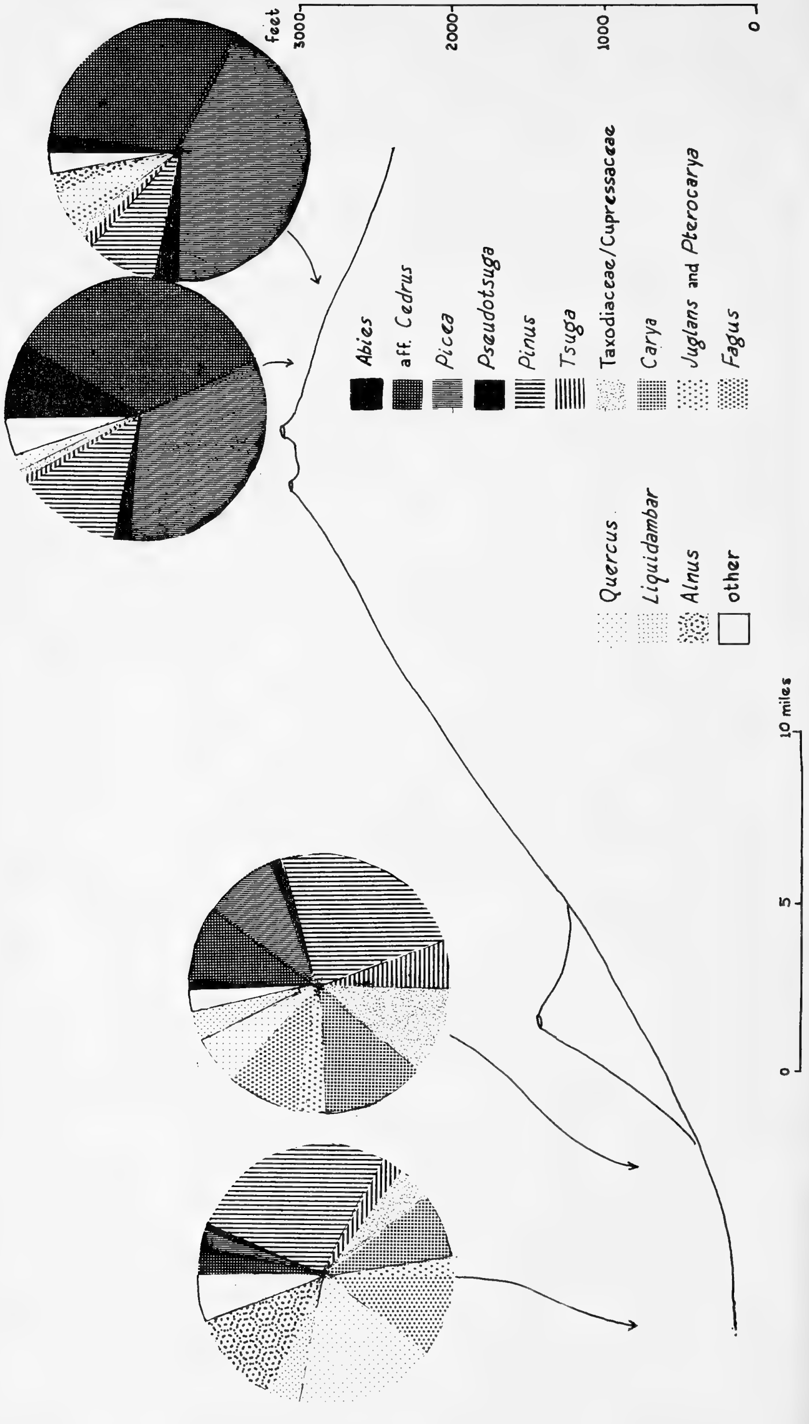


FIG. 2. Pollen spectra of some late Miocene assemblages in northwestern North America. The following assemblages are included (number preceding corresponds to figure 1; numbers in parentheses indicate number of samples and total grains counted): 25. Blue Mountains (2:600); 33. Hidden Lake (7:2112); 37. Mashel (1:300); 39. Pit River (1:300); 40. Pribilof Canyon (2:600); 41. Quesnel (1:430); 42. Skonun (10:1575); 44. Stewart Spring (1:300; 47. Thorn Creek (1:300); 48. Trapper Creek (1:300); 50. Type Homerian (6:1027); 51. Weyerhauser (3:964); Data for Quesnel furnished by K. M. Piel and data for Skonun from Martin and Rouse (1966). Some conifers are too sparsely represented in some spectra to be included in this illustration. Most of the solid black segment in Mashel spectrum represents *Keteleeria*. In the Pribilof Canyon spectrum Cy = Cyperaceae and Gramineae and in the Type Homerian spectrum Er = Ericales.


feet
3000
2000
1000
0
Abies
aff. Cedrus
Picea
Pseudotsuga
Pinus
Tsuga
Taxodiaceae/Cupressaceae
Carya
Juglans and Pterocarya
Fagus
Quercus
Liquidambar
Alnus
other
0
5
10 miles

Pinus, Pinaceae are a minor element in the lowalnd spectra. Broad-leaved deciduous trees, notably members of Juglandaceae, Fagaceae, and *Liquidambar,* are dominant in the Weyerhauser spectrum and rare in the upland spectra. The Faraday spectrum is in some respects transitional between the Weyerhauser and the upland spectra. This transitional character could be expected because of the proximity to the site of deposition of the Faraday beds of a volcano that was active during the late Miocene (Peck, et al., 1964). The pollen profile for the Faraday beds displays a marked decrease in pollen of Pinaceae immediately above an ash layer; presumably the eruption of the ash from the local volcano resulted in the death of many Pinaceae that grew on the slopes of the volcano. Note that *Tsuga,* primarily *T. heterophylla* type, attains its highest relative abundance in the Faraday spectrum; *Tsuga* may have been a prominent member of the forest at altitudes intermediate between the Faraday and Hidden Lake sites of deposition.

The upland conifer forest, which can be characterized as a spruce-cedar forest, occupied a broad area from central British Columbia south to northeastern California and east to the mountains of Idaho. The Trapper Creek assemblages appears to be intermediate between the spruce-cedar association and the Nevada vegetation, as indicated in the Trapper Creek by the paucity of aff. *Cedrus* and the presence of *Ephedra, Sarcobatus,* and *Artemesia.* Axelrod (1964, p. 65) has suggested that the presence of *Ephedra* and *Sarcobatus* reported earlier from Trapper Creek (Leopold, *in* Mapel and Hail, 1959) was due to modern contamination. An additional sample, with which great care was taken to eliminate and prevent contamination, has also yielded these pollen types. There is no reasonable basis for the exclusion of these genera from the Trapper Creek flora.

The megafossil assemblages from Nevada have been characterized as representing a spruce-live oak-cedar (*Chamaecyparis,* not aff. *Cedrus*) association (Wolfe, 1964). The pollen assemblages from Stewart Spring that are now under study by H. E. Schorn confirms such an interpretation.

Judging both mega- and microfossil data, the following associations appear to have occupied northwestern North America during the late Miocene:

Alaska. Conifer forest of *Abies grandis, Picea sitchensis, P. glauca, Pinus monticola,* and *Tsuga heterophylla,* accompanied by *Betula papyrifera,* i.e., a birch-pine forest. Streamside vegetation largely Salicaceae and *Alnus.* Undergrowth largely Rosaceae and Ericaceae.

FIG. 3. Pollen spectra of some late Miocene assemblages in the Willamette Valley and Cascade Range of Oregon. Profile of Western Cascade Range is hypothetical but based on available geologic data (Peck, et al., 1965; D. L. Peck, pers. comm.). Assemblages are, from left to right (numbers in parentheses indicate number of samples and total grains counted): Weyerhauser (3:964), Faraday 28:7757), Skunk Creek (1:300) a,nd Hidden Lake (7:2112). Small amounts of *Keteleeria* are included in the *Abies* totals.

Columbia Plateau-Cascade Range. Conifer forest of*Abies concolor, Abies magnifica,* aff. *Cedrus, Keteleeria, Picea breweriana, P. magna, Pinus monticola, P. ponderosa, Tsuga heterophylla, Thuja plicata,* and *Sequoia sempervirens,* accompanied by *Betula papyrifera, Quercus chrysolepis, Ulmus* spp., *Acer* spp., and *Arbutus idahoensis,* i.e., a spruce-cedar forest. Streamside vegetation largely Salicaceae, *Alnus,* and *Platanus.* Undergrowth mostly Rosaceae.

Nevada. Conifer forest of *Abies concolor, Picea breweriana, Picea magna, Chamaecyparis, nootkatensis, Tsuga heterophylla,* accompanied by *Quercus chrysolepsis,* i.e., a spruce-cedar-live oak forest. Streamside vegetation largely Salicaceae. Undergrowth mostly Rosaceae.

Puget-Willamette lowland. Broad-leaved deciduous forest of *Carya bendirei, Fagus, Quercus deflexiloba, Liquidambar,* and *Arbutus,* accompanied by *Thuja plicata* and *Sequoia sempervirens,* i.e., a hickory-oak-beech forest. Streamside vegetation largely Salicaceae and Betulaceae. Undergrowth mostly Rosaceae and Ericaceae. Locally, a *Taxodium-Nyssa* association persisted.

Central California—mixed broad-leaved evergreen and deciduous woodland of *Quercus chrysolepis, Castanopsis, Carya, Persea,* and *Arbutus,* accompanied by *Pinus* (closed-cone), i.e., a live oak-madrone woodland. Streamside vegetation mostly Salicaceae. Undergrowth mostly Rosaceae and Ericaceae. Locally, a *Taxodium-Nyssa* association persisted.

Pliocene and Early Pleistocene

From about 10 to 2 or 3 million years ago, the fossil record in northwestern North America is notably poor. Pliocene assemblages are known in Alaska: the Type Clamgulchian, represented by many large collections from the Kenai Formation, and several assemblages from the Bering platform area (Hopkins, et al., 1960; Wolfe, unpublished data) that are probably of late Pliocene and/or early Pleistocene age. In the Pacific Northwest, Pliocene assemblages are represented by the Troutdale (Chaney, 1944b), Dalles (Chaney, 1944a), Middle Ellensburg (Smiley, 1963), and Deschutes (Chaney, 1938). One early Pleistocene assemblage is known from the Cape Blanco area (Wolfe unpublished data). Pliocene assemblages from regions south of the Pacific Northwest appear to have little to contribute to an understanding of the vegetation or flora of the Northwest.

The topographic setting of all the known Alaskan Pliocene and early Pleistocene assemblages is coastal lowland. The Troutdale assemblage in Oregon is the only Pliocene assemblage known from the Puget-Willamette lowland. The assemblages from eastern Washington and Oregon probably were at moderate elevations. The assemblage from the Elk River beds at Cape Blanco was obtained from rocks that are predominately marine.

Flora. Compared to the Miocene, the Pliocene flora was depauperate. In Alaska, nearly all the broad-leaved deciduous trees had become extinct; note, however, that *Glyptostrobus,* which today is the most tropical member of Taxodiaceae, persisted into the Type Clamgulchian assemblage. Salicaceae and two species in the Betulaceae were the primary constituents of the Alaskan ligneous dicotyledonous flora, and Pinaceae are well represented by *Picea* and *Pinus* in the microfossil assemblages.

In the Northwest, the flora still contained some broad-leaved deciduous elements now exotic to the region, such as *Pterocarya, Ulmus, Platanus,* and *Aesculus.* Some of these exotics, e.g., *Ulmus,* are known in the Deschutes assemblage (Wolfe, unpublished data), which is only five to six million years old (Evernden and James, 1964). By the early Pleistocene, however, broad-leaved exotics were apparently almost extinct in the Northwest. The Elk River assemblage contains some *Platanus,* but otherwise the flora has a modern aspect.

The known megafossil species in the Northwestern Pliocene and Pleistocene assemblages are primarily members of lineages that were present in this region during the Miocene. No significant amount of migration of woody lineages into the region appears to have taken place during the Pliocene, although the fossil record is sufficiently poor to emphasize "appears." As noted in the discussion of the late Miocene flora, the flora of the Pacific Northwest was modern in aspect by the late Miocene.

VEGETATION. The character of the vegetation in the Northwest during the Pliocene is not clear, largely because of the lack of pollen assemblages and the small size of the megafossil assemblages. The leaf margin percentages for both the Troutdale and Middle Ellensburg show a definite increase compared to the Faraday and Lower Ellensburg. This change was not, therefore, the result of orogenic activity, because the Faraday-Troutdale sequence is west of the Cascade Range. The increase in leaf margin percentages is probably due to the onset of a definite summer dry climate in the Pacific Northwest (Wolfe and Hopkins, 1967). This change would account for the extinction of many lineages, e.g., those of *Carya, Fagus, Liquidambar,* and some of *Acer.* The persistence of *Ulmus* east of the Cascade Range should not be surprising, because some Asian species of the genus have proved to be highly successful in cultivation on the Columbia Plateau.

The Troutdale assemblage does not indicate a cooler climate than that of the late Miocene, despite the probable change to summer dry conditions. The extinction of various lineages by the end of the late Miocene can be readily explained in terms of the changed precipitation regime. Insofar as known, the Troutdale assemblage could represent broad-leaved deciduous forest derived from the late Miocene vegetation. None of the Troutdale localities have yielded records of Pinaceae more diverse than the Pinaceae of, for example, the Weyerhauser assemblage.

The Ellensburg assemblages (Smiley, 1963) may offer a clue as to the direction of temperature changes. The late Miocene Lower Ellensburg assemblage lacks Lauraceae except for *Sassafras,* whereas the early Pliocene Upper Ellensburg assemblage contains *Persea.* Similarly, the Middle Ellensburg assemblage contains ligneous legumes lacking in the Lower Ellensburg. Although the evidence is not conclusive, the early Pliocene may have been somewhat warmer than the late Miocene in the Pacific Northwest.

The Deschutes assemblage indicates that by the later Pliocene, conifer forest was probably not present near the sites of deposition; the late Miocene rocks, however, consistently contain some megafossils of Pinaceae. This absence of Pinaceae in the Pliocene megafossil assemblages may reflect the increasing aridity from the rain shadow created by the accretion of the High Cascades. The conifer forest would thus be restricted to higher elevations away from the sites of deposition. Clearly, however, much more paleobotanical, especially palynologic, data are needed for an understanding of the vegetation of the Columbia Plateau during the Pliocene.

ORIGINS OF THE MODERN FLORA AND VEGETATION

From the preceding discussion, it is clear that many phylads and lineages now extant in the Pacific Northwest were present in this region prior to the Pleistocene and were in fact present in the Miocene. Several of the lineages were at one time members of the summer wet Mixed Mesophytic forest and have since adapted to summer dry conditions. Extant species that have such a history in the Pacific Northwest include: *Populus tremuloides, P. trichocarpa, Salix commutata, S. fluviatilis, S. lasiandra, S. lasiolepis, Quercus garryana, Q. kelloggi, Alnus rhombifolia, A. rubra, Betula occidentalis, Castanopsis chrysophylla, Celtis douglassi, Clematis columbiana, Mahonia aquifolium, M. repens, M. nervosa, Amelanchier alnifolia, Cercocarpus montanus, Crataegus douglassi, Holodiscus discolor, Osmaronia cerasiformis, Peraphyllum ramoisissimum, Prunus demissa, Sorbus scopulina, Spiraea, densiflora, Toxicodendron radicans, Acer grandidentatum, A. glabrum, A. macrophyllum, A. negundo, Ceanothus velutinus, Arbutus menziesi, Leucothoe davisae, Rhododendron occidentalis, Cornus nuttalli, Garrya elliptica, Shepherdia utilis,* and *Sambucus glauca.*

Some of the extant species, however, appear to have entered the Pacific Northwest after the extinction of the Mixed Mesophytic forest, i.e., after the middle Miocene. Some appear to have entered from the north, because their first fossil records are in the Miocene or Pliocene of Alaska; note that this does not mean that the lineages are of northern origin but may have evolved in Eurasia and migrated through Alaska. Included are: *Salix barclayi, S. scouleriana, S. hookeriana, S. glauca, S. monticola, S. piperi, Myrica californica, Alnus, incana, A. sinuata, Ribes triste, Prunus subcordata, Rubus idaeus, Acer circinnatum, Gaultheria shallon, Vaccinium alaskaense,* and *Symphoricarpos albus.*

The majority of these species live today in the mountains of the

Pacific Northwest, although some, particularly *Salix hookeriana* and its allies, are lowland species. These willows apparently attained a coastal distribution from Cook Inlet south to western Washington during the later Miocene. Some lineages may have entered the Pacific Northwest from the south. *Peraphyllum,* for example, was a member of the Mixed Mesophytic forest in the Northwest, but the only late Miocene record of the genus is in Nevada; when summer dry climates prevailed in the Northwest at the close of the Miocene, lineages such as *Peraphyllum* may have reentered from the south. Most "Madro-Tertiary" elements in the modern flora of the Northwest may have followed such a pattern.

The known Tertiary vegetation of the Pacific Northwest does not closely match the modern vegetation floristically. The deciduous broad-leaved forest of the late Miocene western lowlands has survived in a highly modified form in the Willamette and Rogue River valleys. At least 50 percent of the late Miocene species of this vegetation, however, no longer participate in this forest type. Most have become regionally extinct, but others, for example, *Leucothoe* aff. *L. davisae,* are today montane species.

The late Miocene conifer forest of the Columbia Plateau-Cascade region has also been highly modified since 10 million years ago. The area perhaps floristically most closely related to this vegetation is the present Siskiyou Mountains and adjacent areas. In this region, most of the late Miocene conifer species have survived, including some of the associated ligneous dicotyledons. Again, however, at least 50 percent of the late Miocene species associated with the conifer forest no longer participate in this extant forest type. Although extinction accounts for much of the floristic change, some of the lineages, e.g., those to which *Quercus chrysolepis* sensu stricto (excluding *Q. vaccinifolia*) and *Plantanus racemosa* belong, are no longer part of the conifer forest. The primary difference, however, between the late Miocene and modern conifer forest of the Northwest is that *Pseudotsuga* did not play as significant a role in the vegetation as it does today. Hansen's (1949) data indicate that *Pseudotsuga* pollen in the pollen rain occurs in about the same percentage as the percentage of *Pseudotsuga* in the surrounding forest as measured in basal area. Pollen of *Pseudoteuga* is, however, not abundant in any Neogene pollen assemblage known to me in the Northwest. Even the early Pleistocene assemblages at Cape Blanco have low amounts of *Pseudotsuga* (Wolfe, unpublished data), whereas interglacial deposits of the Puget lowland (Leopold, unpublished data) contain large quantities of the genus. It appears, therefore, that the dominance of *Pseudotsuga* in the present conifer forest of the Northwest was attained during the middle or late Pleistocene.

Note also that, since the late Miocene, the conifer forest has received some immigrants from the north as well as incorporating some elements from the late Miocene broad-leaved forest. To the latter group probably belong: *Arbutus menziesi, Leucothoe davisae,* and *Rhododendron macrophyllum.*

The conifer forest of the late Miocene of Alaska has, of course, suffered from extensive extinction. Vegetationally, this conifer forest is probably most like that of southern British Columbia, and there are also strong floristic similarities. The apparent absence of *Acer* and *Rhododendron (Rhododendron)* coupled with the presence of *Pterocarya* and *Ulmus* in the Alaskan late Miocene, however, indicate that as a vegetational and flloristic unit the Alaskan late Miocene forest did not migrate southward.

The floristic changes that have occurred in the vegetation of the Pacific Northwest during the Neogene indicate strongly that the present associations are also most probably transitory. As Mason (1947) has noted, the association must be continually redefined at each point in time because of the coincidental nature of associations.

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ECOLOGIC PLANT GEOGRAPHY OF THE PACIFIC NORTHWEST

R. DAUBENMIRE

The purpose of this phytogeographic sketch is to provide an introduction to the natural vegetation of the Pacific Northwest for the use of botanists from other areas who will be attending the XI International Botanical Congress in Seattle in 1969. Attention will be centered on the State of Washington, with secondary emphasis on the adjoining areas. If my friends in British Columbia feel that I have slighted their Province, this is more a consequence of maps terminating at the international border than of any intent of mine to confine attention to the "Pacific Northwest,"—a nationalistic and ambiguous though useful term, which I shall not try to define!

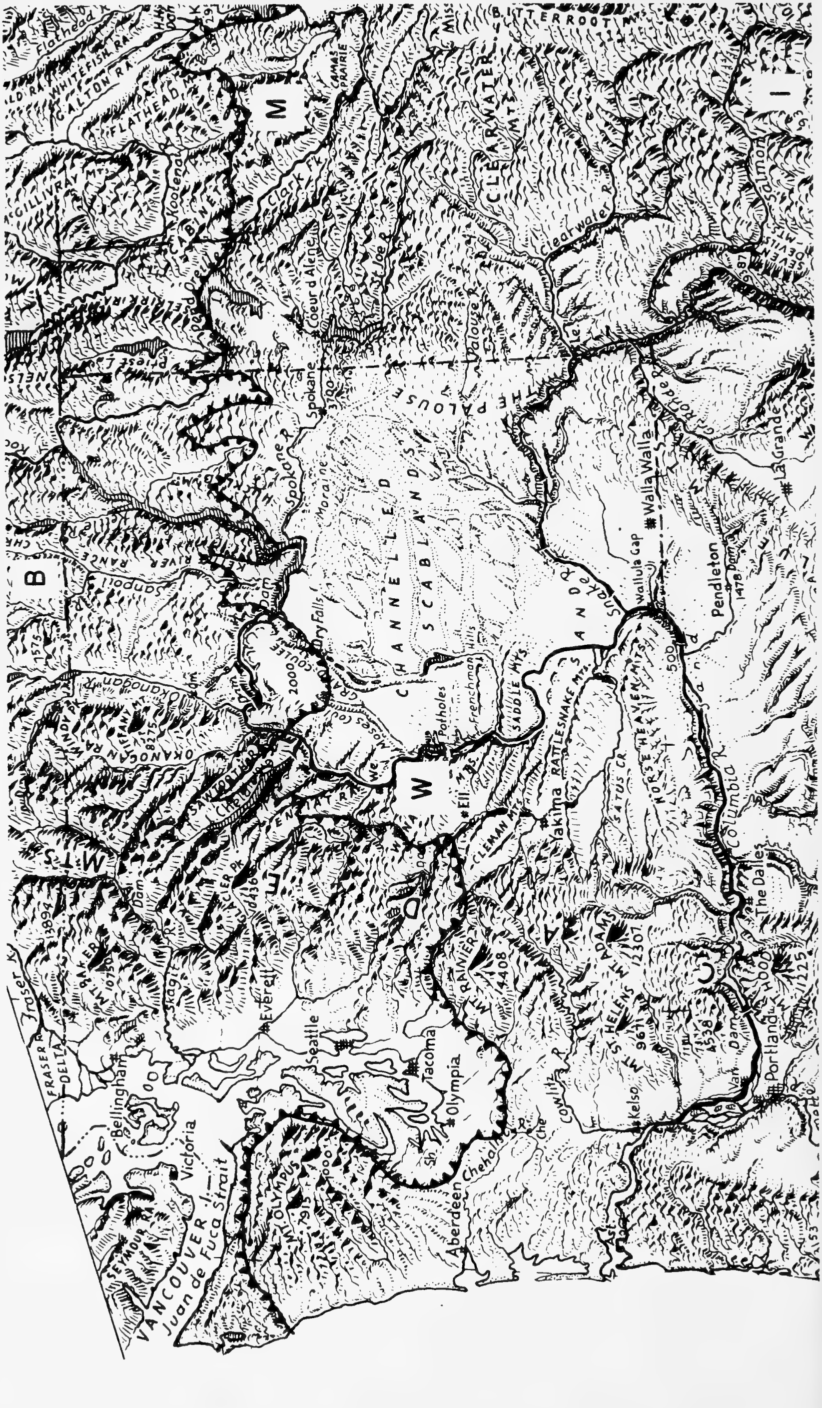
The visitor, like some of us who reside here, may be appalled by the scarcity of natural vegetation in a region which was opened up by white explorers as late as 1805 (the Lewis and Clark expedition). Nevertheless the account is centered on remnants of natural vegetation with the intent of helping the visitor recognize some of the common types and see how they fit into a regional pattern.

THE LAND SURFACE

The Rocky Mountains (only a limited fringe of them shows at the right edge and upper half of fig. 1) are the oldest of our major mountain systems, the uplifting and folding that first gave them definition having taken place well back in the Cenozoic Era. Their rocks are partly granitic and partly sedimentary, and show a wide variation in the degree of metamorphism, but neither chemically nor physically do they present extreme conditions that h ave been acclaimed of much phytogeographic importance.

Later in the Cenozoic another major geologic event of interest to us here was the building up of a great basaltic plateau of some 26,000,000 ha^2 in extent that covered the non-mountainous parts of eastern Washington, eastern Oregon, and southern Idaho. Layers of the columnar basalt that comprise this plateau are conspicuous features of canyon walls throughout the plateau region.

In Pliocene time the Cascades were uplifted, these mountains reaching considerable height and thereby stimulating so much rainfall that their basaltic veneer was in large part soon eroded away exposing the intrusive core. Since basalt gives rise to much more fertile soil than acid igneous rocks, there are some significant botanical differences to be observed in going from basaltic to granitic areas. For example, from Mt. Rainier southward basalt is the prevailing rock still mantling the Cascades, whereas northward acid igneous rocks outcrop. The ubiquity of *Purshia*


Flathead
WHITEFISH RA.
GALTON RA.
FLATHEAD
M
CAMAS PRAIRIE
BITTERROOT MTS.
CLEARWATER MTS.
I
Salmon
SEVEN DEVILS MTS.
Clearwater R.
St. Joe R.
Coeur d'Alene
Clark Fk.
Kootenai
CABINET MTS.
SELKIRK
Pend Oreille
Priest L.
NELSON
Spokane
3100
Spokane R.
Palouse R.
THE PALOUSE
CHANNELED SCABLANDS
Moraine
Dry Falls
GRAND COULEE
2000
Dam
Sanpoil
KETTLE RIVER RANGE
B
1575
Okanogan R.
OKANOGAN RA.
WINDY PK.
TIFFANY MT.
8275
Chelan
W
Moses Cou.
Potholes
Frenchman Hills
SADDLE MTS.
CLEMAN MTS.
Yakima
RATTLESNAKE MTS.
SATUS CR.
HORSE HEAVEN MTS.
Snake R.
Wallula Gap
Walla Walla
Pendleton
1478
La Grande
Grande Ronde R.
500
Columbia R.
The Dalles
MT. HOOD
11225
Portland
Vancouver
Dam
4538
MT. ST. HELENS
9671
Kelso
Cowlitz R.
MT. ADAMS
12307
MT. RAINIER
14408
Tacoma
Olympia
Seattle
Everett
Skagit
MT. BAKER
10750
13894
GLACIER PK.
10436
Fraser R.
FRASER DELTA
Bellingham
Victoria
VANCOUVER I.
Juan de Fuca Strait
SEYMOUR
MT. OLYMPUS
7915
Aberdeen
Chehalis R.


STANLEY VAL.
SAWTOOTH MTS.
SOLDIER MTS.
Camas
Bruneau R.
LONG VAL.
Payette 2180
Payette R.
Dam
Boise R.
Boise
8406
5000-6000
OWYHEE RA.
Owyhee R.
Dam
Malheur R.
Powder R.
Baker
ELKHORN RIDGE
GREENHORN MT.
STRAWBERRY MTS. 9600
ALDRICH MTS.
Burns
Malheur L.
STEENS MTS.
9354
PINE FOREST MTS.
SANTA ROSA RA.
PARADISE V.
Shore of L. Lahontan
Quinn R.
N
John Day R.
UMATILLA
Picture Gorge
OCHOCO MTS.
Crooked R.
O
SANDY DESERT
5000±
GREAT
Hart Mtn. 8030
ABERT RIM
Summer L.
L.
WARNER RA.
Goose L.
Alturas
Madras
Rim
Deschutes R.
Bend 3620
LAVA
Paulina Mts.
Walker Ra.
Mt. Thielsen 9180
Crater L.
JEFFERSON 10495
Craters
5800
THREE SISTERS 10354
Klamath Falls
LANGELL VAL.
MODOC LAVA BEDS
C
SHASTA 14162
Salem
160
Corvallis
Alb.
Eugene
420
Roseburg
Medford
Klamath R.
4097
9038
Mar.

tridentata in the igneous foothills, in contrast with its restriction to a few special habitats in the basalt area to the south is correlaed with this geologic discontinuity.

In Fig. 1 a chain of low mountains is shown following the Pacific shoreline. These are the Coast Ranges. They are well developed in southwestern Oregon where they merge with the Cascades, but otherwise they are quite low in Oregon and Washington with the outstanding exception of the Olympic Mountains. To the north in British Columbia they again become imposing features of the land.

Continental glaciation terminated in Washington and northern Idaho (fig. 1), leaving the area to the north mantled with glacial till. In places melt waters flowing outward from the ice cut great chasms in the basalt flows, and elsewhere washed the surface clean in broad drinageways, depositing large sheets of gravel and sand farther downstream.

Vulcanism during the late Cenozoic raised a string of spectacular volcanic peaks far above the general level of the Cascade crest from British Columbia to California, but spectacular as these peaks are, their major significance for ecology lies in the ejecta spread over the landscape when two of them erupted.

In approximately 12,000 B.C. Glacier Peak, situated a little to the northwest of the center of Washington in Fig. 1, erupted and winds at that time spread fine white ash over considerable area to its leeward. Then in 6600 B.C. the stupendous explosion of Mt. Mazama, in the southwest quarter of Oregon in Fig. 1, gave rise to a blanket of materials so deep and extensive as to dwarf the Glacier Peak event. (Crater Lake now occupies the vent where Mt. Mazama exploded.) Fine white ash fanned out eastward and northward over most of the Pacific Northwest, extending well into British Columbia and Montana, to provide a valuable marker in sediments that has been generally useful in geochronology, archaeology and the correlation of fossil sequences in bogs. In the more immediate vicinity of Mt. Mazama coarse pumice was deposited to great depths, smothering pre-existing vegetation and providing a substrate that supports highly distinctive vegetation even today. For example, *Pinus contorta,* nearly everywhere a seral tree in the mountains, is the only tree that can grow over a large portion of the pumice area, and here it maintains reproduction as a climax dominant.

In some period prior to the last (Wisconsin) glaciation there were several episodes of loess accumulation on the basaltic plateau between

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FIG. 1. Physiography of Washington and Oregon, with adjoining parts of British Columbia, Idaho, Nevada and California. These state and province names have been indicated only by centrally placed letters, respectively: W, O, BC, I, N and C. The ornamented line crossing the map in the approximate latitude of central Washington indicates the southern limits of the last (Wisconsin) continental glaciation. Areas subjected to mountain glaciation are not indicated. Map reproduced through the courtesy of Edwin Raisz and the publishers of W. W. Atwood's "Physiographic provinces of North America."

the Cascades and the Rockies. The volcanic ash which fell later became incorporated with this loess, or in places was washed into hollows. On the forest-covered mountain slopes the ash was trapped and fixed where it fell, giving the forest of northern Idaho in particular a relatively complete cover of fine-textured fertile material (usually very fine sandy loam) so that the occurrence of thin stony soil is not so important a factor in forest ecology there as in most mountain areas of western North America. Down on the basal plain in Washington, the loess mantle with its incorporated ash was in places stripped away in the path of extensive Wisconsin glacial floods, so that desert-like areas of bare basalt became exposed. These areas which support sparse vegetation mainly of dwarf shrubs and the tiny caespitose grass *Poa secunda,* are labelled "channelled scablands" in Fig. 1.

Other botanically significant geologic features which are more localized are the outcroppings of serpentine (southwestern Oregon and the east slope of the Cascades in central Washington), recent outpourings of lava (locally in the Cascades of Washington and Oregon, and especially in Craters of the Moon National Monument in southern Idaho), and cones of coarse ejecta that dot the landscape in central Oregon, and form Mt. St. Helens in Washington.

CLIMATE

Far greater climatic complexity is encountered in the surroudings of these meetings than has characterized the areas where most of the preceding congresses have convened. All of those areas had diversity resulting from the latitudinal climatic gradient, and some had a significant superimposed gradient, usually extending more or less at right angles, that involved degrees of oceanicity or continentality. But it would be difficult to find a match for the intensification of the north-south climatic gradient that results from the strong influence of the Westerlies that are centered approximately on the Canada-United States border, or a match for the steepness of the oceanic-continental gradient that results from massive mountains rising to height of several thousand meters within a few km of tidewater.

When the topographic map (fig. 1) is compared with the precipitation map (fig. 2), the "approach effect" is clearly shown by the high precipitation on lowlands as the Westerlies approach major mountain masses from the southwest. A sizable area in the lowlands to the southwest of the Olympic Mountains has precipitation in excess of 2,540 mm a year. Quinault Ranger Station has an average annual value of 3,414 mm. It is in this general area that cryptogamic epiphytes are so spectacularly developed, and a trip up the Hoh or Quinault Valleys is eminently worthwhile to see the phenomenon. The approach effect is again evident along the west base of the Cascades and even along the west base of the Rockies across the arid intermountain trough.

The effect of mountains on precipitation also has its negative aspect, the creation of a relatively dry rain shadow along the leeward base of each of the major mountain masses. To the northeast of the Olympic Mountains a weak but well-defined rain shadow provides many more sunny days at places like Sequim than in surrounding areas, with the influence clearly discernible even in Seattle and on the nearby islands in Puget Sound. The most pronounced rainshadow is along the eastern base of the Cascades in central Washington. In the Yakima Valley the mean annual precipitation drops as low as 175 mm within easy sight of heavy forests of mesophytic conifers that encircle the glacier-clad slopes of Mount Rainier where precipitation is at least 2,972 mm. Both the rainshadow and the approach effect are well illustrated (from British Columbia to Oregon) by both weather statistics and the resultant vegetation patterns.

Not only does our precipitation vary greatly from one place to another but its unequal distribution throughout the year is botanically important. Each summer the belt of the Westerlies recedes northward, and failing to drag heavy supplies of moisture inland at this season, the summers are left remarkably short of precipitation. Where the annual sum is low, the shortage becomes critical, and those who visit the rainshadow at the east flank of the Cascades will experience weather that for a few months in summer remind one of true desert conditions. Only the coolness and shortness of summers west of the Cascades (the spring and autumn seasons are quite long) keep drouth from reaching serious proportions there.

Winter rains are gentle and almost mistlike, often accompanied by heavy cloud and fog that bedevil air transportation. Coastal areas get only half the possible hours of sunshine. In summer convectional showers are so rare that storm-induced erosion is not severe. Strangers seeing the wheatlands of southeastern Washington (the "Palouse" in fig. 1) for the first time are usually amazed at the sight of cultivated slopes so steep that self-levelling harvesting machines are used, and the trucks that service them frequently overturn. Such slopes are not cultivatable under rainfall conditions that prevail toward the center of the continent.

Along the coast the frost-free season is approximately 250 days long, and snow is rather ephemeral, whereas in the mountains frost is likely any day in summer and snowbanks may persist throughout the summer even in the subalpine forest belt.

In winter a high pressure system forces Arctic air masses southward down the plain east of the Rockies and often this air spills over the mountains westward to temporarily overwhelm the oceanic character of the climate between the Rockies and the Cascades. These sudden cold spells are very damaging to fruit trees and ornamentals (all aliens), and sometimes even the native plants are damaged. The Columbia Gorge is large enough to allow oceanic influences to penetrate inland readily, and often cold air influences extend farthest west down this gorge. At its western extremity many trees are flag-shaped in consequence of ice storms in winter when cold air pours westward down the valley, and at the eastern extremity they are flag-shaped in the opposite direction by the pressure of winds blowing eastward while branches are actively growing.

SOILS

In discussing "the land surface" the general character of the parent materials for soils has been indicated. In Fig. 3 the types of profiles that might be expected on deep loams of undulating topography are shown. These zonal soils are closely related to the pattern of rainfall, but since there are large areas of steep topography in which surface materials are moved by gravity from time to time, the large areas of parent material of geologically recent origin (sand and gravel, bare rock, volcanic ejecta, desiccated lake beds, etc.), the map units are highly complex mixtures of azonal, intrazonal, and zonal soils.

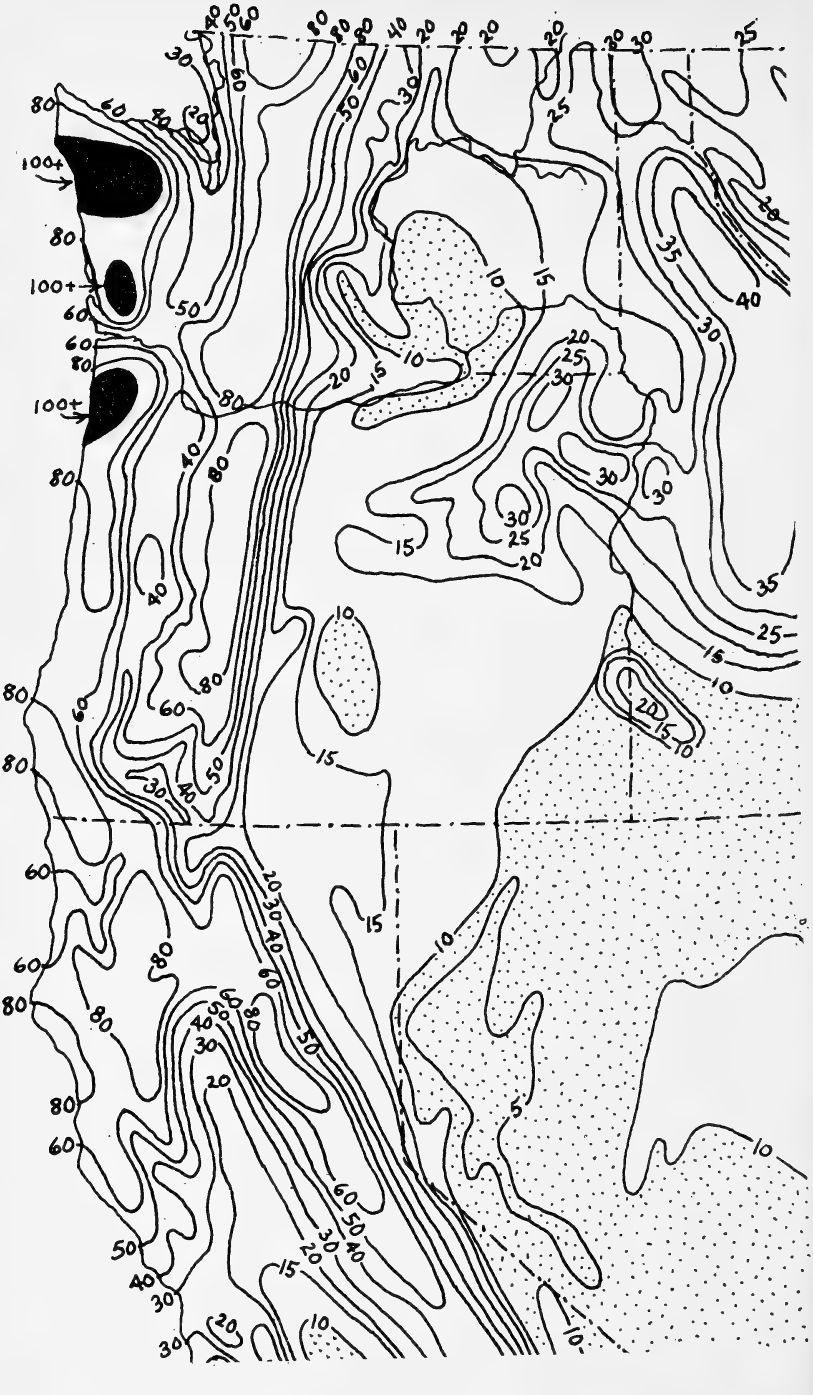
ALPINE VEGETATION

Where the mountains rise so high that heat is no longer adequate to allow the development of the tree life-form, the vegetation of the treeless area is called alpine tundra (figs. 4, 5). Near the coast the elevation of this ecologically critical level is about 900 m in west central British Columbia, rising to about 2,700 m at the southern end of the Cascade Mountains in California. Eastward in the more continental climates of the Rocky Mountains the critical level is about 800 m higher at equivalent latitudes. Although this timberline is relatively stable, one can frequently see evidence of trees having invaded contiguous areas of herbaceous vegetation, with most of the invasion having taken place during the very dry period in the early 1930's.

In the highest part of the alpine region glaciers and lichen-covered rock debris dominate the landscapes, whereas down next to timberline lush meadows dominated by forbs (*Lupinus, Castilleja, Valeriana, Pedicularis, Anemone*) mixed with graminoids, or by low shrubs (*Empetrum nigrum, Luetkea pectinata, Phyllodoce, Cassiope*) prevail. At intermediate elevations there are stony fell fields where the plant cover is incomplete and cushion plants exemplified by the holarctic *Silene acaulis* are best developed. Mid- to late July is approximately the height of the flowering season for alpine plants in west central North America. The communities they form have been well studied only in Montana.

SUBALPINE FORESTS

The forests just below upper timberline differ considerably on either side of a line drawn a little east of the divide of the Cascades (figs. 4, 5). East of this line *Abies lasiocarpa* and *Picea engelmannii* are the conspicuous species in old-growth stands. Since they are geologically recent derivatives of *Abies balsamea* and *Picea glauca,* which characterize the transcontinental taiga belt, the term montana taiga has been applied to subalpine forests of the Rockies. Climatic similarity, i.e., heat budgets marginal for tree development, is another point of similarity that is synecologically significant.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Undergrowth plants in this forest likewise bespeak strong affinity with the far North, e.g., *Cornus canadensis, Linnaea borealis, Pyrola* ssp., and *Sorbus scopulina*. In the vicinity of the Canada-United States border *Menziesia ferruginea* and *Xerophyllum tenax* usually dominate over all other undergrowth species. Elsewhere a widespread type has the dwarf *Vaccinium scoparium* as the chief ground cover.

Following fire or logging the first generation forests are typically composed of *Pinus contorta, P. albicaulis, P. monticola,* and *Larix occidentalis* in varying proportions. *Abies lasiocarpa* and *Picea engelmannii* sometimes invade simultaneously but usually they are late-comers.
Nearly everywhere the *Abies* slowly increases at the expense of all others, ultimately dominating the climax, except in the few localities where *Tsuga mertensiana* occurs. There the *Tsuga* proves the best competitor. In the krummholz at upper timberline, where the severe climate keeps the tree cover so open that differences in shade-tolerance are not critical, *Abies lasiocarpa* and *Pinus albicaulis* or *P. flevilis* are the main species.

Subalpine forests of the Cascade crest and the few high mountains still closer to the ocean might be bracketed under the term montane taiga only by virtue of their heat budget, since floristic affinities with the transcontinental taiga are essentially nil. Although *Abies lasiocarpa* makes a limited penetration into the strongly oceanic climates, reaching even to the Olympic Mountains, *Picea engelmannii* does not follow it, and instead the major climax dominants there are *Abies amabilis, A. magnifica, Tsuga mertensiana, and Chamaecyparis nootkatensis*. Beneath these trees the common plants include *Menziesia ferruginea, Rhododendron albiflorum, Xerophyllum tenax, Vaccinium ovalifolium, V. membranaceum, Pachistima myrsinites,* and *Pyrola* spp.

Conspicuous trees in the initial regeneration that follows deforestation are *Pseudotsuga menziesii, Larix occidentalis, Abies procera, A. lasiocarpa, Pinus contorta, P. monticola,* and *P. albicaulis*. The last- mentioned becomes especially prominent with *Tsuga mertensiana* in the krummholz at upper timberline.

MONTANE AND LOWLAND FORESTS CHARACTERISTIC OF WET OCEANIC CLIMATES

In the region about Seattle natural forest succession usually trends toward the dominance of *Tsuga heterophylla* on well-drained mineral soil. *Acer circinata* and *Cornus nuttallii* are common understory trees. Beneath these trees the two most significant dominants, both evergreen, are *Polystichum munitum* on relatively moist sites or *Gaultheria shallon* on soils having a slight tendency toward dryness. Other common species, most conspicuous under intermediate moisture conditions, are *Berberis nervosa, Clintonia uniflora, Cornus canadensis, Phegopteris dryopteris, Ribes sanguineum,* and *Rubus spectabilis*.

FIG. 2. Mean annual precipitation in inches. Areas with more than 2,540 mm and less than 254 mm have been shaded for emphasis (after Kincer, 1922).


GREAT SOIL GROUPS, MAINLY:
A - SIEROZEM
B - BROWN
C - CHESTNUT
D - CHERNOZEM & PRAIRIE
E - NON-CALCIC BROWN
F - BROWN PODZOLIC, GRAY BROWN PODZOLIC, GRAY WOODED, WESTERN BROWN FOREST & PODZOL
G - REDDISH BROWN LATERITIC
H - ALPINE TURF
I - GRUMUSOL
J - SOLONCHAK & SOLONETZ
K - ALLUVIAL & HUMIC GLEY
L - REGOSOL
M - LITHOSOL

In somewhat swampy situtions *Thuja plicata* maintains dominance indefinitely, and the conspicuous undergrowth plants include *Oplopanax horridum, Athyrium filix-foemina,* and *Lysichiton, americanum.* In valleys too dry for *Tsuga* or *Thuja, Abies grandis* is the climax dominant.

The vegetation as a whole has a lush aspect, with many of the broad-leaved trees, shrubs, and herbs evergreen, as are nearly all the coniferous trees.

Owing to the high incidence of fires in the past, the uplands are most usually dominated by coastal ecotypes of *Psuedotsuga menziesii,* which is the most valuable forest tree of the region and the mainstay of its important forest industry. Old virgin stands of this tree, already established when white man first arrived but no longer common outside national parks, contained individuals up to 127 m tall, with butt diameters up to 7.6 m. *Alnus rubra* is another seral species that is highly aggressive on disturbed land. This is the largest species in its genus and is extensively used for furniture. On recently cut-over lands *Pteridium aquilinum* or the alien *Cytisus scoparius* commonly determine the physiognomy until the first seral forest gets established. In southwestern Oregon *Ulex europea* plays this role.

On moist but not swampy terraces *Acer macrophyllum* is quite common, this tree being an especially good "host" for *Selaginella oregana* which so copiously festoons its branches on the windward side of the Olympic Mountains (especially in the Hoh and Quinault Valleys). *Populus trichocarpa, Rhamnus purshiana,* and *Fraxinus oregana* are other broad-leaved trees common on stream terraces.

Picea sitchensis is mainly confined to a very narrow strip along the open ocean where it plays a climax role under moderate salt spray influence, but becomes seral to *Tsuga* on sandy soils slightly farther back from the ocean. Other trees that are found only close to the ocean are a salt-tolerant ecotype of *Pinus contorta* that is most common on dunes or bogs, and *Chamaecyparis lawsoniana* which is seral to *Tsuga heterophylla* in the Coast Ranges of southern Oregon. Forest along the coast is frequently interrupted by dunes supporting such characteristic species as *Elymus mollis, Carex macrocephala, Lupinus littoralis, Abronia latifolia, Poa macrantha,* and *Lathyrus littoralis,* or by tidewater marshes in which *Distichlis spicata* and *Salicornia pacifica* are the dominants.

Coniferous forests quite similar to those described as characteristic of uplands and swamps back from the influence of sand and salt spray continue from near sea level up the mountains to the lower limits of the subalpine belt, and from British Columbia to southern Oregon, with a disjunct area reappearing on the seaward slope of the major mountain ranges in northern Idaho, northern Montana and southeastern British

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FIG. 3. Principal soil regions. Only the characteristic zonal soil present in each map unit has been indicated (after Various Authors, 1964).

Columbia ("cool moist forests" in figs. 4 and 5). In this inland extension the most notable differences are (1) the substitution of *Pinus monticola* and *Larix occidentalis* as the prevailing seral trees, and (2) the absence of *Gaultheria shallon* and scarcity of *Polystichum munitum* in the undergrowth. In place of these one finds mainly *Clintonia uniflora, Tiarella unifoliata, Phegopteris dryopteris, Viola orbiculata,* and *Vaccinium membranaceum,* all of which occur in the coastal segment, but are overshadowed there by the more conspicuous *Gaultheria, Polystichum, Berberis nervosa,* etc.

The major climax dominants of upland forests in the interior are segregated, with *Tsuga heterophyla* in the most moist situations. *Thuja plicata* in less moist places (but a seral tree on *Tsuga* sites), and *Abies grandis* on soils tending to be drouthy.

Immediately after a fire destroys forests in this group a rich variety of shrubs invades the landscape, and until a new forest canopy develops, this shrubbery provides an abundance of winter browse for deer and wapiti which abound in the area.

Along the coast a related but evidently distinct forest area is one in which *Sequoia sempervirens* dominates, this area extending as a narrow strip from the southwest extremity of Oregon to a little south of San Francisco Bay (see its delimitation in fig. 4). One living *Sequoia* meassured at 117 m tall is thought to be the tallest tree left standing in North America. Pure stands of this species characterize floodplains but on contiguous hillsides *Lithocarpus densiflora, Abies grandis,* and *Pseudotsuga menziesii* form a lower tree stratum. The most abundant plants of the forest floor include *Oxalis rubra, Polystichum munitum, Berberis nervosa, Gaultheria shallon,* and *Vaccinium* spp. *Thuja* and *Tsuga heterophylla* are sparingly represented in the *Sequoia* area.

The southern and inland limits of the *Sequoia sempervirens* forest are associated with the limits of frequent summer fog which results from warm breezes blowing landward across very cold water along the coast.

Forests Characteristic of Moderately Dry to Dry Climates

Soils of the subalpine forests remain moist throughout summer, except perhaps in the top 20 cm or so, and the same is true of those forests below in which *Tsuga, Thuja* or *Abies grandis* are climax dominants. But in passing from the *Abies grandis* areas into land where the soils regularly dry several to many decimeters deep there is a clear ecologic discontinuity. Here *Pseudotsuga menziesii* (or ecologic equivalents) remains free from competition from more shade-tolerant species and so can persist as a major climax dominant, if not the only one. It is desirable to consider separately three geographic subdivisions of this *Pseudotsuga* belt.

In the Willamette Valley of central Oregon (fig. 4) the Douglas fir forest is distinctive for the abundance of *Quercus garryana,* a low deciduous tree which is usually seral to *Pseudotsuga,* but may form pure climax stands in certain relatively dry sites. Small areas in which the *Quercus* plays much the same role also occur on the gravelly outwash plain in Washington southward of Olympia and Tacoma. The deciduous *Holodiscus discolor* is a characteristic shrub of the Douglas fir forest.

Another distinctive segment of what is here referred to as the *Pseudotsuga* belt occurs in the mountains of south central Oregon, extending from there southward in an inverted V-shaped area (delimited in fig. 4) on both sides of the interior valley of California. In this area *Pseudotsuga* is variously associated with *Libocedrus decurrens* and *Abies concolor. Pinus ponderosa, P. jeffreyi, P. lambertiana,* and *Sequoiadendron giganteum* are all seral trees here. The last mentioned is famous for its massive trung, which grows to a diameter of 11 m and a height of 100 m, thus dwarfing the climax trees of shorter stature and life-span that grow around it. *Sequoiadendron* trunks may have more than 3500 xylem layers.

Another distinctive feature of this southern Oregon-California sector of Douglas fir belt is the abundance of evergreen sclerophyllous shrubs in the undergrowth. These increase conspicuously in early stage of regeneration cycles following deforestation.

A third subdivision of the Douglas fir belt has more distinctly continental climates, occurring on the east-facing slopes of the Cascades, thence eastward in the foothills across the breadth of the Rockies. Here *Pseudotsuga* is the sole climax dominant on zonal soils, with seral trees including *Pinus ponderosa, P. contorta, Larix occidentalis,* and *Populus tremuloides*. In the undergrowth one of the following usually dominates the physiognomy: *Calamagrostis rubescens, Physocarpus malvaceus, Holodiscus discolor* or *Symphoricarpos albus*. On the east flank of the Cascades, *Pinus contorta* is the only conifer that can form forests on large areas of coarse pumice in what appears to be the equivalent climatic belt.

Progressing down the moisture gradient into areas drier than *Pseudotsuga* can tolerate, one sometimes comes abruptly onto steppe on the basal plain, but elsewhere one or two distinctive forest belts may intervene.

If the Douglas fir belt gives way to another forest belt, the later is typically dominated by *Pinus ponderosa* growing in pure stands. These climax pine stands contain a wide variety of undergrowth types depending on variation in climate, aspect or soil, all of which still allow the pine, and only this pine, to form the tree stratum. Some of the undergrowth plants that are locally conspicuous are *Purshia tridentata, Physocarpus malvaceus, Symphoricarpos albus, Festuca idahoensis, F. scabrella, Agropyron spicatum, Stipa comata,* and *Aristida longiseta*. In certain of these forest types the pine grows slowly and is subject to attack and deformation by the parasitic *Arceuthobium campylopodum*, but elsewhere it grows rapidly and provides one of our most valuable timbers. The best growth of the tree, however, is in higher zones where *Pseudotsuga* and *Abies grandis* are climax.

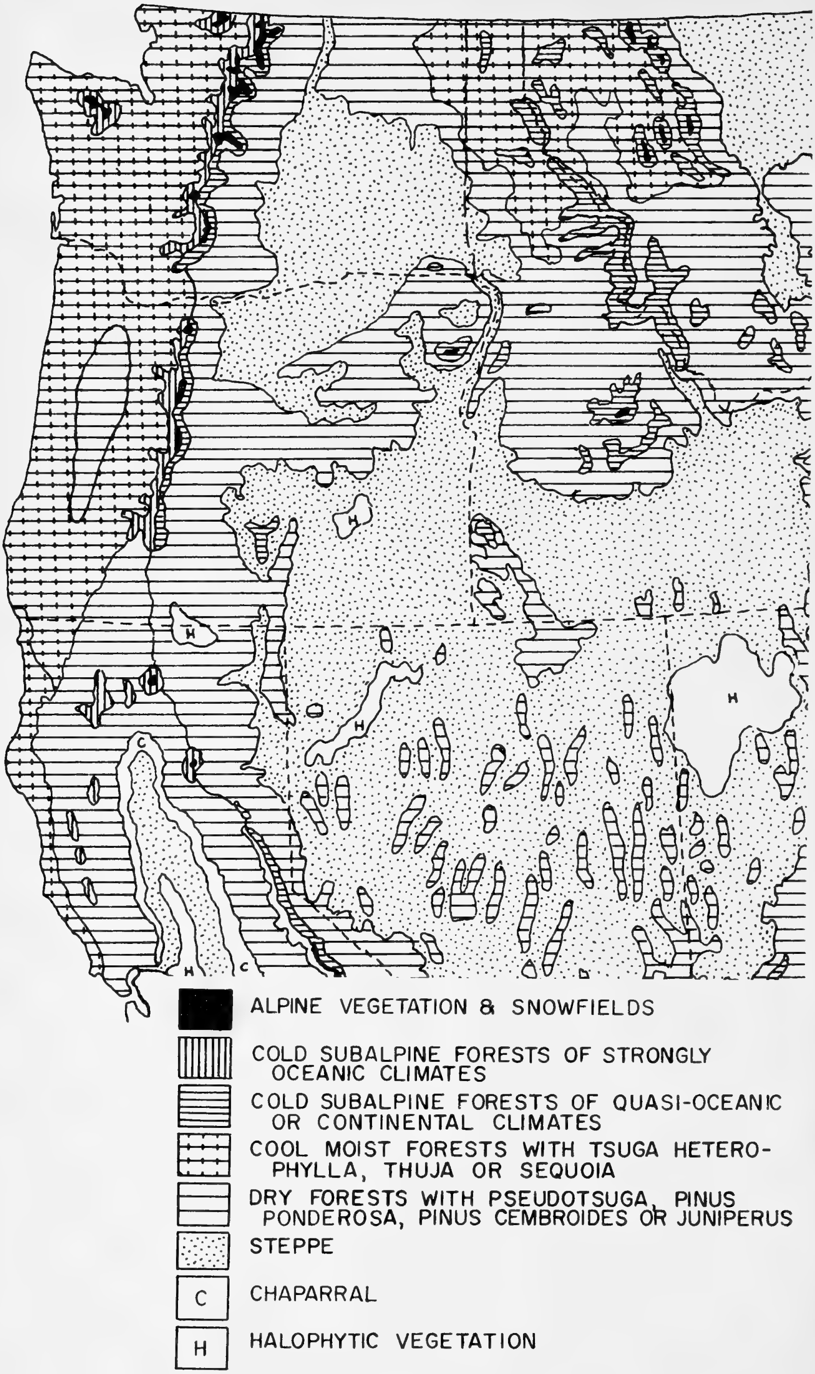

Fig. 4. Vegetation of northwestern U.S.A. (after Shantz & Zon, 1924).

FIG. 5. Vegetation of British Columbia (after Rowe, 1959).

Again as one reaches the lower and drier limit of the *Pinus ponderosa* belt, he may come out onto an unforested basal plain, or he may have one more forest belt to pass through. The last is perhaps better characterized as woodland savanna, for the species of *Juniperus* (*J. scopulorum, J. occidentalis, J. osteospermum*) and *Pinus flexilis* which comprise this type are only a few meters tall and rarely form a closed canopy. This lowest conifer belt is fairly well developed in western Montana, and more locally represented in southern Idaho, and in central Oregon (where the pine does not occur).

On the west side of the Rockies in Washington and British Columbia, groves of *Populus tremuloides* become a conspicuous feature of landscapes in the margin of the steppe, where they are confined to locally moist places.

Chaparral Vegetation

Chaparral vegetation in North America (corresponding to maquis, garigue, fynbos and mallee in other parts of the world) is rather easily divided into three physiognomic categories: scrub (up to 2 m tall), woodland and savanna. All three types are well represented about the margin of the great valley in central California (fig. 4), and the first two extend in fragmentary fashion into southern Oregon.

Chaparral scrub in which *Ceanothus cuneatus, Arctostaphylos viscida, A. canescens, Cercocarpus betuloides, Eriodictyon californicum, Garrya fremontii, Rhamnus californica,* and *Rhus triloba* are major species is locally well represented east of the Coast Ranges in the upper Rogue River Valley of Oregon, with a trace still farther north in the Umpqua River Valley. This scrub occupies a belt marginal to what was originally a small area of steppe, (all too small to show in fig. 4), with *Quercus garryana, Pinus ponderosa* and *Pseudotsuga menziesii* in progressively wetter situations.

Relatively dry ridge summits in southwestern Oregon are in places dominated by *Lithocarpus densiflora* and *Arbutus menziesii* growing as low forest trees with *Rhododendron macrophyllum* forming a tall shrub layer beneath. Stands of this character may be interpreted as the northerly limits of chaparral woodland, which is floristically much more complex southward.

Steppe Vegetation

The low-lying unforested areas between the Cascades and the Rockies are often referred to as "desert" by the local populace. But the few months of intensive summer heat and drouth, combined with the occurrence of cacti, rattlesnakes, scorpions, and tarantulas that perhaps suggest this classification to the layman, do not impress the plant geographer as strongly as does the moderately heavy to heavy stand of perennial grass that grew nearly everywhere before the era of domestic livestock. The term steppe is more appropriate to the botanist.

A good grass cover is possible on practically all soils throughout the arid parts of the Pacific Northwest, for despite the low rainfall, nearly all of it falls in winter when evapotranspiration is feeble and much of the water can percolate deep enough to get below the reach of direct evaporation into the air, thus providing water to sustain a vigorous spurt of vegetative and flowering activity as temperature rises in spring. Summer is mostly a period of aestivation with more plants inactive at this season than in mid-winter. East of the divide of the Rockies most of the rain falls in summer, and the steppe grasses there delay their activity accordingly.

On zonal soils in the steppes of the Pacific Northwest the most characteristic dominants are *Agropyron spictaum, Festuca idahoensis, F. scabrella* (chiefly in British Columbia), and *Poa secunda*. On sandy soils these species are replaced by *Stipa comata, Oryzopsis hymenoides, Agropyron dasystachyum,* and *Sporobolus cryptandrus*.

The driest parts of the intermountain trough from Central British Columbia to central Oregon, together with practically all the intermountain area farther south, originally supported conspicuous but low-growing gray-leaved shrubs that formed a layer well above the grasses, making the term shrub-steppe applicable to this area. Over most of the shrub-steppe *Artemisia tridentata* was the outstanding representative of this shrub layer, with the monotony somewhat relieved locally by other shrubs such as *Chrysothamnus nauseosus, C. viscidiflorus, Tetradymia canescens, Grayia spinosa, Purshia tridentata,* and *Gutierrezia sarothrae*. All these shrubs are deep-rooted, and except for *Grayia* they retain their leaves through the dry summers, with *Artemisia* holding its leaves throughout the year. Herbaceous plants, for the most part the same species as in contiguous steppe lacking shrubs, go into aestivation in midsummer as moisture in the upper meter or more of the profile is used up.

Perennial forbs (*Arnica, Balsamorhiza, Castilleja, Crepis, Geranium, Lupinus, Potentilla,* etc.) are conspicuous in both steppe and shrub-steppe in inverse ratio to the degree of aridity, i.e., they achieve their maximum importance in communities just below lower timberline.

Three cacti occur in the Pacific Northwest—*Opuntia polyacantha* (most widespread), *O. fragilis,* and *Pediocactus simpsonii.*

Over most of the intermountain steppe area the most aggressive plant to assume dominance as grazing eliminates native perennials is the alien *Bromus tectorum*. In the less arid eastern fringe of the steppe it is locally moist enough for *Poa pratensis* to take over this role. In the Great Basin area the noxious alien *Halogeton glomeratus* is relatively more conspicuous in this role.

In eastern Washington and northern Oregon thin stony soils overlying basalt outcroppings are abundant and these support a wide variety of special communities in nearly all of which the tiny perennial *Poa secunda* is the chief grass, with one or more species of dwarf shrubs conspicuous.

Artemisia rigida is the most widespread of these dwarf shrubs, but several species of *Eriogonum* are also common.

Other special soil types in the steppe region support communities in which one of the following is the characteristic dominant: *Eurotia lanata, Artemisia arbuscula, A. nova,* and *Atriplex nuttallii.*

Saline basins in the Great Basin of Utah and Nevada support a rich assortment of halophytic shrubs, forbs, and grasses. The major halophytes here, roughly in order in increasing tolerance of wetness and salinity, are: *Salicornia rubra, Allenrolfea occidentalis, Suaeda depressa, S. intermedia, Distichlis stricta, Atriplex patula, A. argentea, Sporobolus airoides, Puccinellia airoides, Triglochin maritima, Bassia hyssopifolia, Sarcobatus vermiculatus, Atriplex confertifolia, A. nuttallii,* and *Kochia americana.* Northward only a few of this group play the role of major dominants. Here in the north *Distichlis stricta* is ubiquitous. In some places it is associated with *Elymus cinereus,* a coarse caespitose grass growing about 2 m tall, and elsewhere with *Sarcobatus vermiculatus,* a succulent-leaved chenopodiaceous shrub. Marshes in which *Typha latifolia* and *Scirpus* spp. cover large areas are conspicuous in south central Oregon.

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SOIL DIVERSITY AND THE DISTRIBUTION OF PLANTS, WITH EXAMPLES FROM WESTERN NORTH AMERICA

A. R. KRUCKEBERG

Discontinuity of pattern and form is an ubiquitous feature of living things. All along the scale of organizational complexity, from cell to ecosystem, some degree of environmental hiatus separates the elements of a system. Mitochondria are discreet entities separated from one another by the microenvironments of dissimilar subcellular phases. At a higher level, individuals of the same population are not confluent; time, space, chance and inhospitable habitats contrive to maintain temporary or partial discontinuities. But it is at the level of the species that isolation is most apparent and evolutionarily significant. The modern Darwinist sees the immense diversity in the organic world as resulting from the interactions over geological time of the variant heredities of organisms, the natural selection of adapted variants, and the manifold factors which promote the isolation of those adapted variants. Evolution of our present diverse biota without discontinuity is unthinkable.

The discontinuities in the physical environment which isolate populations and species, though richly unlimited in degree and permuting interaction, can be reduced to but two broad groups: climatological and geological. In other words, the limits to distribution of kinds of organisms are largely imposed by differences in climate or geology, or both. That climate is primary in controlling the broad distribution of organisms is undisputed. Tolerance spans of terrestrial organisms are chiefly limitations in reaction to stressful levels of moisture and temperature. Within areas of broad climatic similarity, though, geological variability provides the major source of regional biotic diversity. The contribution of geological phenomena to vegetational discontinuity takes a number of forms. Variations in topography, in mineral content and physical properties of parent rock account for most of the regional differentiation brought about by geological processes. When microclimatic and biotic features act in concert with geology, the mosaic of habitats is greatly enriched.

The soils derived from parent rocks owe their distinct qualities to a set of interacting factors. Hans Jenny (1941) characterizes the soil formation process as a set of variables in a functional array. In Jenny's formula, $s = f(cl, o, r, p, t)$, there are five independent variables that define the soil system: climate (cl), organisms (o), topography (r), rock type or parent material (p), and time (t). If all but one factor, say p (parent material), remain constant, then variations in the end product (soil) are due to differences in parent material.

It is this one variable, parent material (p), that will be the central theme of this review of soil diversity and plant distribution. The Jenny formulation, however, reminds us that the biological properties of soils cannot be analyzed one factor at a time. When we abstract just parent material from the total soil ecosystem, we achieve manageable simplicity only at the expense of setting aside the interacting whole system. Our primary concern will be to examine the possible effects of chemical variations of parent material and soil on plant distribution. Such chemical diversity will condition the kind and amount of mineral nutrients available to the vegetation. To paraphrase Jenny's factorial approach, we can ask: Other factors being equal, what effects do differences in soil mineral content have on the distribution of plants?

Soils can control the distribution of plants in other ways, however, and we will look briefly at some of these. The physical properties of soil and parent material, weathering processes, soil microclimate, and those properties uniquely induced by the biota are also the domain of the edaphic factor complex; they will be touched upon wherever appropriate.

Though we may be operating at a microcosmal level where other environmental influences might vastly overshadow the effects of soil chemical differences, such differences can be dramatically effective in altering plant distribution. Examples to follow will support this contention. I will offer evidence to support two general hypotheses that bear on the probable interactions between mineralogical composition of parent material and discontinuities of plant distribution.

First Hypothesis: Given a regional climatic framework, much of the plant species diversity and discontinuity in the region is governed by variations in soil chemistry, and thus by specific variations in the mineralogy of rock substrates.

Second Hypothesis: Speciation within a regionally contiguous genus is largely a response to environmental discontinuity within the confluent area. Sharp discontinuities in soil chemistry can serve as isolating phenomena to bring about species diversification.

Historical Background

We can scarcely doubt that discerning humans through the ages have been aware of sharp vegetational discontinuities arising from differences in soil. Geological and vegetational diversity go hand in hand in regions around the Mediterranean and the near east, the scene of Man's agricultural beginnings. A much later record from the Age of New World Exploration specifically ties vegetation to soil. Columbus is said to have capitalized on a specific soil-plant association when he had to replace a mast on a ship of his first fleet (Buck, 1949). The story goes that he was counselled to choose a log o f pine growing on red soil in nearby Cuba; the red limonitic soils of Cuba are known to be high in iron and to have furnished durable timbers.

Correlations between substrate and vegetation really became a part of botanical science much later—in the 19th cenutry. It was the young and alert Austrian botanist, Franz Unger, who first emphasized the significance of geological formation for plant distribution. From the pen of the master botanist-naturalist, Anton Kerner von Marilaun, we get an intriguing accunt of the patterning of vegetation that set Unger to develop his concept of the chemical concept of plant distribution. I quote from the English version of Kerner's *Natural History of Plants,* (Kerner and Oliver, 1902): "The little town of Kitzbuhel, in the Northeast Tyrol, has a very remarkable position. On the north rises the Wilde or Vorder Kaiser, a limestone chain of mountains with steep, pale, furrowed sides, and on the south the Rettenstein group, a chain of dark slate mountains whose slopes are clothed far up with a green covering. The contrast presented by the landscape in its main features is also to be seen in the vegetation of these two mountain chains. On the limestone may be seen patches of turf composed of low stiff Sedges, Saxifrages whose formal rosettes and cushions overgrow the ledges and steps of the rugged limestone, the yellow-flowered Auricula, the Rock-rose-flowered Rhododendron, and white-flowered Cinquefoil adorning the gullies, dark groups of Mountain Pines bordered with bushes of Alpine Rose; and opposed to these on the slate mountains are carpets of thick turf composed of the Mat-grasses sprinkled with Bell-flowers, *Arnica montana* and other Composites, groups of Alpine Alder and bushes of the rust-colored Alpine Rose—these are the contrasts in the plant-covering which would strike even a cursory observer, and would lead a naturalist to ask what could have been the cause. No wonder that the enthusiastic Botanist, Franz Unger, was fascinated by this remarkable phenomenon in the vegetable world. In his thirtieth year, furnished with a comprehensive scientific training, he came as a doctor to Kitzbuhel, and with youthful ardour he used every hour of leisure from his professional duties in the investigation of the geological, climatic and botanical conditions of his new locality, devoting his fullest attention to the relations between the plants and the rocks forming their substratum. The result of his study was his work, published in 1836, on the Influence of Soil on the Distribution of Plants as shown in the Vegetation of the North-east, Tyrol, which marked an epoch in questions of this sort. The terminology introduced in the book found rapid entrance into the botanical works of the time. Unger divided the plants of the district accordingly to their occurrence on one or other of the substratums—in which lime and silica respectively predominated—into (1) those which grow and flourish on limestone only; (2) those which prefer limestone, but which will grow on other soils; (3) those which grow and flourish on silica only; and (4) those which, whilst preferring silica, will grow on other soils."

Until the advent of modern soil science, arguments pro and con for Franz Unger's chemical theory of plant-soil relationships persisted without the full understanding of the nature of plant mineral nutrition. The essence of Unger's view—that mineral content of soils is the primary edaphic influence on plant distribution—is vindicated by contemporary soil chemistry. Qualitative and quantitative differences in elemental (ionic) content of both the exchange complex and the soil solution do cause selective responses in the composition of vegetation cover as I will relate shortly.

Parent material of whatever sort, igneous, metamorphic, sedimentary rocks, and organic materials, become soil by weathering. Through the action of temperature changes, wind abrasion, water and other chemical agents, as well as biological influences, rocks weather to those textural and particle size classes of materials that constitute mineral soil. Mineral soil, then, is a mixture of particles ranging downward in size from rock fragments through gravel and sand to silt and clay. The most reactive phase for plants is the colloidal clay fraction. Ionic exchange between root systems and the soil is mediated by clay colloids. Major and minor elements required for plant growth are adsorbed on clay colloid surfaces. Since weathering frees primary minerals to generate secondary clay minerals and to participate in ion exchange, it is to be expected that the mineralogical composition of the weathering parent material will determine the quality of the reactive mineral content of soils.

The diversity of the geologic parent materials available at the earth's surface for soil formation is vast and rich. The range of rock types is derived from variations in both mineralogical content and mode of origin. Thus, at one end of the spectrum are the acid rocks, rich in feldspars (silicates of K, Na, Al and Ca). Acid rocks exist as granites (batholithic or intrusive igneous), rhyolites (volcanic surface flows), or as schists and gneisses (metamorphics), or as consolidated sediments (sandstones, etc.). Omitting the broad range of transitional members along the scale from acid to basic rocks, we come to the other end of the spectrum. Here are the ultrabasic rocks, chiefly of iron-magnesium silicates, plentiful and worldwide in distribution. Both igneous and metamorphic types occur; common examples of ultrabasics are peridotite and serpentinite.

Plant Responses to Differences in Chemical Composition of Soil and Underlying Parent Material

How sensitive is the plant to variations in chemical content of soils? For cultivated plants, man's agricultural experience is rich and his skillful manipulations of crops and soils have had bountiful returns. Application of macro- and micronutrient fertilizers is a cornerstone of good farm practice. But what of natural vegetation and its response to chemical variations in soil? Positive evidence is clear for peculiar vegetational and floristic displays on a number of truly abnormal soils. The term "abnormal" signifies 1, the abundant occurrence in soils of one or more elements rarely found in such excessive amounts in agricultural soils, or 2, the absence of one or more of the essential plant nutrients usually available in cultivated soils, or yet 3, some combination of these exceptional elemental constitutions. However, I would repeat my earlier "disclaimer". Soil as a part of the living ecosystem is the product of many interactions, both biotic and environmental. To say that a soil is abnormal and gives rise to exceptional vegetational responses due to mineral composition is valid to the extent that of all the soil forming influences, the quality of parent material is primary in its effect on plant growth.

I will present examples largely from the "abnormal" group of soils. Not only are the vegetational responses so striking, but their careful study may reveal guidelines for determining the chemical effects that may exist for plants on more normal, yet chemically variable, soils.

"Abnormal" (Azonal) Soils

Soils and Vegetation of Limestone and Dolomite

It was the stark contrasts in vegetation between limestone and slate slopes in the Tyrolean Alps that led Franz Unger (1836) to his chemical theory of edaphic restriction. Striking differences in physiognomy, species composition, and plant morphology are associated with rocks rich in calcium carbonate. Examples of contrasts between calciphile and calciphobe elements of a regional flora abound in the early European literature. Plants favoring limestone soils are *calciphiles* or *calcicoles;* plants avoiding limestone soils are *calciphobes* or *calcifuges*. The occurrence of vicariism (selective replacement of closely related species or varieties on contrasting soils) is frequent. It will suffice to give one or two examples of contrasts in floristic composition to reveal the nature of the vegetational discontinuity caused by limestone.

The remarkable flora on vast outcrops of limestone and chalk in Great Britain has fascinated botanists and naturalists for decades. This sustained interest is delightfully recounted in two modern books, "Wild Flowers of the Chalk and Limestone," by J. E. Louseley (1950), and "Downs and Dunes, Their Plant Life and its Environment," by E. J. Salisbury (1952). Only a fragmentary account of the rich chalk and lime floras can be given here. The gamut in degree of constancy of species to soils derived from rocks rich in calcium carbonate begins on the side of the rare and obligate lime inhabitants such as the two orchids, *Orchis simia,* monkey orchid, and *O. militaris,* military orchid, and *Helianthemum polifolium,* white rockrose. Franz Unger (1836, p. 168) would have called such exacting plants "bodenstet" (or "soil-fast"). The other extreme, plants common not only on limestone, but on other soils, he referred to as "bodenvag" (or "soil-wanderer") species. In addition, limestones and chalks in Britain have their share of calcifuges—plants that avoid the calcareous substrates. Foxglove, *Digitalis purpurea,* and broom, *Sarothamnus scoparius,* though widespread, are conspicuously absent from these soils. Louseley says of the two species, ". . . (they) are such excellent soil indicators that on train journeys it is often easy to tell immediately when the railroad line leaves chalk or limestone by their presence on the railway banks." Ericaceous species, long known to gardeners for their aversion to limestone, are equally discriminating members of the natural vegetation. Only where the chalks are surface-leached and an acid humus has developed can species of the heath family get a local toehold on lime.

Limestone vegetation in other parts of the world is no less remarkable for possessing a high proportion of indicator species. For example, the geology of Japan and Taiwan is especially rich in calcareous deposits. The botanical composition of 63 limestone outcrops (Shimizu, 1962), were categorized in grades of fidelity, the degree to which a species is restricted to a particular community type. There are 75 species in Fidelity Class 5 ("exclusives"—high restriction to limestone); this class contains a large number of ferns, shrubs, and herbaceous perennials, but few trees. The next Fidelity classes, 4 and 3, ("selectives" and "preferents") with 48 and 112 species respectively, add considerably to the total floristic richness of the calcicolous floras.

There is no question, then, that limestone parent materials have exerted a profound selection on regional floras, resulting in unique vegetational composition, physiognomy, and soil formation. It remains now to look at possible physiological explanations of accommodation to limestone.

Physiological explanations of preference for, or avoidance of, limestone soils are not wholly satisfying. Obscuring the search for answers are a number of complicating ecological and soil chemistry factors. Do calcicoles require a medium high in calcium or are they merely able to tolerate high calcium in exchange for a release from greater competition stress on non-calcareous soils? Is the limestone effect one of pH preference or more fundamentally a nutritional problem? The high pH values generated by some limestone soils no doubt exert strong side effects on the availability of other elements, e.g., iron, aluminum, manganese, phosphate. A physiological approach has been fruitful in the case of differences in calcium preference of grasses in the genus *Agrostis* (Clarkson, 1965). Of four species of *Agrostis* grown in controlled solution cultures of various calcium regimes, the well-marked calcifuge species, *A. setacea,* has a significantly different capacity for calcium uptake. The results for the three calcicole and one calcifuge species appear to be related to differences in the capacities of their active transport system—the metabolically controlled mechanism for moving ions from soil to root interior. The calcifuge species, *A. setacea,* seems to have a calcium transport system of lower capacity than the other three. The ecological assessment of these results would appear to be that a calcifuge species may have an inherently lower threshold to calcium uptake.

A now classic study of a calcicole-calcifuge species pair by A. C. Tansley, pioneer British ecologist, has a timely and contemporary message for anyone studying the effects of a single soil variable on plant distribution. Tansley (1917) demonstrated that species interactions greatly altered the effect of soil type on plant growth. The two bedstraws, *Galium saxatile* and *G. sylvestre,* were grown in pure and mixed stands on acid peat and calcareous soils. "Both species can establish and maintain themselves—at least for some years—on either soil," but "the calcicole species is handicapped as a result of growing on acid peat and therefore is reduced to subordinate position in competition with its calcifuge rival, which is less handicapped," and ". . . the calcifuge species *(Galium saxatile)* is heavily handicapped especially in the seedling stage, as a direct effect of growing on calcareous soil, and is thus unable to compete effectively with its calcicole congener, *Galium sylvestre*." Tansley's work emphasizes the obvious but often overlooked danger of reading too much ecological significance into results obtained from plants studied in artificial isolation. The current research on plant competition by John Harper (1967) and his associates in Britain underscores the importance of variability in plant response as influenced by biotic interaction.

Lists of species pairs, calcicole versus calcifuge, imply that taxonomically recognizable kinds of plants have different tolerances and that the members of a given pair may be closely related. Though there may be some question as to the advisability of giving such vicariads taxonomic recognition, there is no doubt that there are interpopulational differences to an edaphic factor such as limestone. In pursuit of this possibility, it has now been amply demonstrated that species occupying a diverse array of edaphic habitats have responded genetically to variant selective agents of the soil; i.e., such species exhibit ecotypic differentiation. Working with *Trifolium repens,* a species with wide edaphic range, genecologists in Britain have found intraspecific variation in tolerance to calcareous and acid soils. Snaydon (1962) concludes that, ". . . the wide edaphic range of *T. repens* is due, at least in part, to the presence within the species of specifically adapted physiological types." When such intraspecific but interpopulational differences include morphological characters, and when the contrasting edaphic factors act as isolating barriers, both taxonomic separation and microevolutionary divergence are demonstrable.

It is too simple to hope for a one-to-one correspondence between the chemical nature of a calcareous substrate and a selective action on the potential flora the rock may support. Species which may be highly restricted to limestone in one area may be indifferent to such substrates elsewhere along their range. This is likely the case for the peculiar floristic composition of the Convict Creek basin in the Sierra Nevada of California. Major and Bamberg (1963) describe a remarkable aggregation of geographically disjunct species in the basin. Several taxa, otherwise found only far to the east or north, occur on a narrow band of marble in the basin; this highly distinctive calcareous substrate intrudes locally at Convict Creek, the monotonous granodiorite of the Sierras. It appears that the locally arid outcrops and the contrasting moist seeps provide habitats not otherwise available on the high eastern slope of the massif. The high calcium content of the marble is thus only secondary or even irrelevant to the local occurrence of the disjunct species.

The end result of interactions between substrate and floristic composition can be clearcut: the patterning of vegetation we see can then be di-

FIG. 1. Mosaic of vegetation types in the White Mountains, California. Sagebrush on sandstone and bristlecone pines on dolomite. Photograph taken by Albert Hill and furnished by Harold Mooney.

rectly related to the distribution of the parent materials. But when one is led to sort out the properties of the environment which yield the floristic end product, the story becomes complex. Take a recent case, that of the clearly substrate-oriented distribution of bristlecone pine, *Pinus aristata,* of the White Mountains in eastern California. The pines, now acclaimed the real patriarchs of the plant world, occur chiefly on dolomitic limestone, whereas sagebrush is dominant in adjacent granitic and sandstone soils (fig. 1). Physiological ecologists (Wright and Mooney, 1965) find that it is the interaction of physical, nutritional and biotic factors that lead to the complementary distribution of the pine and sagebrush *(Artemisia tridentata)* dominants. The light-colored dolomitic soils are moist and cool, and yet are highly deficient in phosphates. Sagebrush is excluded from the dolomite by the phosphorus deficiency, and reciprocally the pines prefer the cooler, moister dolomites, while tolerating the low phosphorus status. The temperature-moisture difference and the phosphorous deficiency thereby effect a competitive relationship which results in the visible substrate-oriented patterning of vegetation.

Vegetation on Acid Soils

The story of vegetation on limestone tells us that the plant response runs the gamut from narrow calcicolous restriction through broad tolerance or indifference to clear avoidance of the substrate. Such an array of responses largely repeats itself whenever exceptional chemically limiting edaphic responses occur. At the risk of being too inclusive, I want to examine this range of plant response for other chemically unique substrates. For most of them only limited discussion is possible. The mere catalog of other unusual substrates is intriguing in itself. Thus, to use low pH as a crude basis for compilation, there are the highly acid soils induced by a variety of exceptional parent materials: Aluminum-rich bauxites or terra rossa soils of the tropics, silica-rich soils (sands, diatomaceous earths, slates, laterites, etc.), hydrothermally altered volcanics (rich in sulfates), and the soils of lead mine tailings and zinc deposits.

Studies prior to 1957 on the effects of aluminum on plant life led to the generalizations, 1, that soils with high Al may restrict dicot weed competition in grass pastures, 2, that on Al-rich soils there are three levels of Al uptake: a, plants requiring aluminum ions in their metabolism, b, plants known as "aluminum accumulators," which concentrate Al ions in plant tissues with visible but non-lethal effects, and c, plants which are tolerant of Al but collect little or only small percentages of Al in their tissues, and 3, that certain plant families or genera either require Al for normal growth, e.g., Ericaceae, Moraceae, Ferns, and Lycopodiaceae, or are accumulators of Al (*Carpinus,* Rubiaceae, and Melastomaceae). Several of these generalizations have now been put to the test of careful field observation by Howard and Proctor (1957). A major portion of the lowland land surface of Jamaica contains aluminum-rich bauxite deposits. Although agriculturally poor, the bauxitic areas do support a mixture of cultivated crops and a native vegetation in varying stages of secondary succession. Since undisturbed vegetation on bauxite is in remote areas and as yet unsampled, studies on the effects of Al on vegetation were restricted to disturbed sites. The authors concluded: "it appears that the bauxite flora of Jamaica consists of plants which are unaffected by aluminum and tolerant of its presence . . . to the present we have found no species characteristic of bauxite soils, nor have we demonstrated that the vegetation of adjacent areas currently not found on the bauxite deposits will not grow on the bauxite soils. To the contrary, the invasion of plants from adjacent areas on barren, mined-out pits and the plantations established in these pits indicate that factors other than the concentration of aluminum will control the success or failure of these species on bauxite." At this point we would have to conclude the effects of Al on floristic pattern and vegetation are unresolved.

Highly acid and infertile soils underlain by sands and other siliceous substrates often support unique plant assemblages. The pine barrens of New Jersey, the shale barrens of the Appalachians, and possibly the coastal sands of the Carolinas are eastern representatives of the type. Notable in the West are the Mendocino barrens and the laterites-sericitis schists in the Sierra Nevada foothills of California, while in the

Great Basin's desert and mountain country the hydrothermally altered volcanics create local vegetational discontinuities.

Just back of the Pacific coastline in Mendocino Co., California, is a dissected sandstone plateau which supports that most remarkable vegetation, the "pygmy forest" (Jenny, et al., 1969). In its most extreme representation a dense growth of cane-like dwarfed individuals of *Cupressus pygmaea* and *Pinus bolanderi,* not over eight feet tall, cover the ashy gray podsolic soils. Notable associates of the pygmy conifers are several ericaceous shrubs. Of the latter, *Arctostaphylos nummularia* is endemic to the pygmy forests and is one of the three rare acid-soil endemics in the section Schizococcus. Since other species of conifers occur on exceptional soils, the possibility exists that there are features in common among several atypical (non-zonal) soil types in California that yield unusual floras. The general conclusions from thorough field study, greenhouse culture work (mineral nutrition) and laboratory analysis of soils and plant material (McMillan, 1956) merit our attention. Two problems needed explanation: 1, the restricted distribution of *Cupressus* species on a variety of exceptional soil types including the Mendocino acid barrens, and 2, the anomaly of good growth of cypress seedlings on fertile and infertile soils in greenhouse culture. McMillan suggests 1, that edaphic restriction of native plants is not tied to a particular nutritional requirement provided solely by the unique substrate; 2, some common physiological tolerance, e.g., to low calcium availability, may be the basis of generic differentiation in *Cupressus* but not so for other genera of similar edaphic predisposition, and 3, that the pine barren plant community is an array of species that results from "the overlapping of different tolerance ranges of the component individuals for environmental conditions presented by a particular habitat."

In the Great Basin region of the West, broad expanses of sagebrush, juniper, and saltbrush desert are occasionally interrupted by isolated stands of yellow pine and other disjunct subordinate species. These remarkable floristic islands are usually found to be growing on local nonzonal soils of exceptional nutrient characteristics. In both Nevada and Utah, such restricted isolates of vegetation occur on highly acid soils derived from hydrothermally altered lavas and volcanics. Billings (1950) found that the altered andesites northwest of Reno were "very deficient in exchangeable bases, phosphorous, and nitrogen as compared to" adjacent zonal soils supporting pinyon-juniper and sagebrush. Billings concluded that "the pine stands are relicts which have remained because of the inability of sagebrush zone dominants to invade these mineral-deficient soils."

The vegetation of desert "islands" of altered volcanics in Utah substantiate Billings' views on the casual nature of the floristic isolation. Salisbury (1964) adds to the total picture by suggesting that succession to zonal soils typical of the regional climate can occur under the influence of the vegetation itself especially through humus accumulation and eventual plant succession . . . even on these altered volcanics of low pH. The soil profiles from extreme (non-zonal) to zonal sites show an amelioration of the pH and nutrient status of the soil. Leaching of the undesirable elements and the biological addition of essential nutrients appears to achieve the successional change. We would predict, however, that succession to zonal status could be achieved only under ideal conditions of topography, moisture and vegetation cover. Steep slopes of altered andesite with high runoff would undoubtedly persist as non-zonal, sterile soils. In fact, we could generalize to say that severe topography coupled with exceptional parent material will permanently arrest soil formation at the azonal or skeletal state; the biological consequence would be the persistence of a pioneer, edaphically specialized endemic flora.

The last example of non-zonal acid soil and its influence on plant distribution is not only fascinating in its own right, but fosters some far-reaching generalizations. The remarkable restrictions of *Arctostaphylos myrtifolia* in almost pure stands to Eocene laterite and to sericitic schists in the Sierra Nevada foothills of California has been thoroughly studied by Gankin and Major (1964). Near Ione and San Andreas a non-zonal acid heath association abruptly interposes itself within the regional climax vegetation. The Ione manzanita occurs often in dense heath-like stands on substrates of low base status, low fertility, of exceptionally low pH values, 2.0 to 3.95, and of high soluble aluminum values. It is contended that it is the high soil acidity and high aluminum content which exert such a strong selective inclusion-exclusion effect on the regional flora. After citing a number of other examples of edaphically controlled endemism and disjunct distributions, the authors seek a common cause (p. 803): "The above examples could be expanded, evidently indefinitely. Once this principle of disjunct and endemic plant occurrence on non-zonal sites is accepted, examples become almost too numerous. In all these cases,, explanations of why the rare plants occur where they do in terms of plant physiological reactions are completely lacking. Judging from the cases cited, they would have to be conflicting. The only explanation which fits the diversity of facts—that is, plants occurring at higher or lower altitudes than normal, in wetter habitats or drier, with less calcium or more—is in terms of plant competition. All the cases fit the conclusion that rare or disjunct (non-zonal) plants can occur in a given area where competition is decreased by some kind of extraordinary soil parent material or other continuously effective disturbance of climax vegetation development." With that conclusion I would concur, but would at the same time suggest that the competition hypothesis opens up still another "Pandora's Box" of complex biotic interactions. Competition, like endemism, soil infertility, and pH, is as yet a rather vague concept, at least in contemporary plant ecology. Attempts to analyze "competition" and to test its complex nature are only recently gaining fruitful momentum.

Soils and Vegetation on Serpentine and other Ultramafic Rocks

The last and certainly most spectacular "abnormal" (azonal) soil to be discussed is that derived from serpentine and other ferromagnesian rocks. The plant life on such soils has held particular fascination for generations of botanists. On nearly every major land mass of the world, ferromagnesian (ultramafic) outcrops weather to soils that exert a profound selective influence on the regional flora. Stark contrasts between the barrenness of ultramafic and the comparative luxuriance of adjacent non-ultramafic sites, as well as the pronounced differences in species composition are familiar and striking features of this discontinuity in vegetation dominated by geology. Although the most celebrated manifestations of ultramafic vegetation are in Europe (the "dead" Alps, the Balkan Peninsula and northern Sweden) and North America (central California to Oregon and Washington, and the Gaspé Peninsula) other areas, both tropical and temperate, show tell-tale vegetational responses to these soils. Cuba, New Caledonia, New Guinea, New Zealand, and Japan also have notable areas of serpentine and related rocks which in turn support unique floras (Krause, 1958; Whittaker, *et al.,* 1954).

Before turning to the floristics and ecology of serpentines, we should set the scene. I propose to use the word "serpentine" broadly to encompass all ultramafic rocks and soils weathering from them. The term "ultramafic" (or "ultrabasic") embraces those rock types in which the mineralogical composition is largely in the form of silicates of iron and magnesium, as exemplified by the mineral, olivine. The commonest ultramafics are the igneous rocks, peridotite and dunite, and their metamorphic derivative, serpentine. Soils weathering from such rocks are high in magnesium and low in calcium; because of other minerals, pyroxene, amphibole, chromite, etc., in additional to the crucial olivine, the soils may also contain unusually high amounts of nickel and chromium. A secondary biological effect during soil genesis is the common deficiency in nitrogen and phosphorus. Serpentine soils are both unfit for most agriculture and highly selective for native plant species. The calcium-magnesium ratio of much less than 1.0 is considered to be a crucial selective soil factor for the distribution of plant species. Serpentine usually has both a physiognomic as well as a taxonomic effect on plant life. Serpentine vegetation is sparse, with much intervening barren ground; dwarfing and xerophytism are common. Species composition is both depauperized and often unique; endemism and range disjunction are frequently the most outstanding floristic attributes.

Both because they are spectacular samples of serpentine vegetation and are reasonably representative of temperate zone ultramafics, I will confin my discussion to the serpentines of western North America. For convenience, we can distinguish three physiographic regions in which serpentines abundantly occur: 1, the Central California Coast Ranges—Sierra Nevada foothills area, 2, the Klamath-Siskiyou area, and 3, the Northern Cascades—Wenatchee Mountain areas. We will look first at

FIG. 2. Outcrop of serpentine overlooking meadow of mixed alluvium, three miles northeast of Middletown, California.

the vegetational and floristic responses, then at the genotypic reactions of populations to serpentine, and finally develop hypotheses to account for the evolution and adaptation to the serpentine habitat. All along the north-to-south transect, especially from Douglas Co. in Oregon, to San Luis Obispo Co. in California, abundant and often extensive ultramafic outcrops serve to further complicate the already intricate environmental mosaic. The North Bay counties (Napa, Lake, Marin and Sonoma) of central California afford an ideal locale in which to sample the central Californian version of the vegetational discontinuities associated with serpentine outcrops (fig. 2). The serpentines here stand in sharp contrast to the adjacent non-serpentine sites which support largely wide-ranging woody dominants of either the oak woodland, mixed conifer, or chaparral type. Such sclerophyllous shrubs as *Quercus durata, Ceanothus jepsonii, Garrya congdonii,* and even the small coniferous trees, *Cupressus sargentii,* and *C. macnabiana,* are unmistakable "indicator' species because of their typical restriction to and numerical dominance on serpentine soils. It is not these dominant woody species, however, which have made

Californian serpentines celebrated as a source of rare and endeimc plants. The transient spring flora of the dry serpentine hills still continues to be a source of "new or otherwise noteworthy" additions to the California flora. From the time of E. L. Greene and W. L. Jepson to recent collecting by Freed Hoffman, John Thomas Howell, John Morrison, Helen Sharsmith and others, the list of herbaceous rarities endemic to serpentine has grown and continues to grow. A genus of crucifers, *Streptanthus,* is particularly rich in serpentine forms and well serves as an example of wholesale evolutionary diversification on this selective substrate. At least 12 species in California and southern Oregon occur on serpentine: for example, *S. niger,* Tiburon Peninsula; *S. batrachopus,* Mount Tamalpais; *S. insignis,* San Benito Co.; *S. polygaloides,* Sierran foothills; *S. hesperidis* and *S. brachiatus,* Lake Co.; and *S. morrisonii,* upper Austin Creek, Sonoma Co. A few are just as obligate on serpentine but of wider range: *S. howellii.* Siskiyou Mts.; and *S. barbatus, S. breweri, S. barbiger,* and *S. drepanoides,* Napa to Trinity counties. Still others have a broader edaphic tolerance and occur both on and off serpentine: *S. glandulosus,* San Luis Obispo Co. to southern Oregon; and *S. tortuosus,* Sierra Nevada—Coast Range-Siskiyou triangle, though some named intraspecific taxa appear to be local serpentine endemics. Populations of *S. glandulosus* when grown on test serpentine soil proved to be most instructive in the quest for an explanation of serpentine restriction (Kruckeberg, 1951). Collections from non-serpentine sites were clearly intolerant of serpentine soil, while morphologically indistinguishable serpentine samples grew vigorously on the same test soil. Infraspecific variation in physiological tolerance is clearly demonstrated here and expands the idea of ecotypic differentiation of species beyond climatic response to that on soil differences. *Streptanthus glandulosus* is therefore interpreted as a species originally possessing several edaphic biotypes and that through time non-serpentine biotypes have been gradually eliminated. Ultimately its fate may be that of its obligate serpentine endemic relatives, restricted to serpentine. I would concur with Gankin and Major (1964) that it is the 'pressure' of competition—though its action unspecified as yet—that reduces biotype diversity and forces ultimate confinement to serpentine. In this sense then, some of the narrow endemics of *Streptanthus* appear to be "depleted" species. Biotype depletion need not be the prelude to extinction, however. Having found refuge as edaphic specialists on serpentine, diversification within the serpentine environment may ensue. This seems to have ben the speciational history in at least three subsections, *Insignes, Pulchelli,* and *Hesperides,* of the genus.

When we move from the xeric chaparral-covered serpentines of California to the more mesic serpentine habitats in the Siskiyou Mountains to the North, we find a definite shift in composition of vegetation. Though the contrast between serpentine and non-serpentine plant associations is often as striking as those to the South, both species and life-form composition are clearly different. Annuals and chaparral shrub species no longer dominate the ultrabasic landscape. Rather, it is the particular blend of widely spaced conifers and intervening broadleaved shrub and herbaceous layers that characterize the mountainous serpentines the Siskiyous. The forest-shrub complex on serpentine (Whittaker, 1960) gives way abruptly to climax (?) montane mixed coniferous forests on neighboring non-serpentine soils. Repeating the character of the highly acid non-zonal soils discussed earlier is the occurrence of open mixed stands of conifers, often stunted, composed in part of species not common on adjacent "normal" soils. The occurrence of certain conifers on serpentine appears to be the result of altitudinal and/or geographical extensions of more typical ranges of the species. *Pinus jeffreyi,* Jeffrey pine, and *P. attenuata,* knobcone pine, fit this category of disjunct distributions, repeating here in the Siskiyous what is notable about their distributions elsewhere in the far West.

Most remarkable is the shrub cover of Siskiyou serpentines. Nearly every taxon of the sclerophyllous shrub layer is a varietal xeromorph of a species more typically of mesophytic and arborescent habit. Whittaker has observed example after example of these "trees-turned-shrubs," or mesic-turned-xeric shrub. "*Quercus chrysolepis* is represented on serpentine by var. *vaccinifolia,* the most abundant single shrub species there; *Lithocarpus densiflora* is represented by var. *echinoides, Umbellularia californica* by an unnamed shrubby variant, and *Castanopsis chrysophylla* by var. *minor* (uncommon in the study area). *Quercus garryana* occurs on serpentine as the shrubby var. *breweri.* Among other trees and shrubs a series of congeneric pairs appear in non-serpentine and serpentine floras with the serpentine species in each case of smaller stature: *Amelanchier florida* and *A. gracilis, Garrya fremontii* and *G. buxifolia, Rhamnus purshiana* and *R. california occidentalis, Holodiscus discolor* and *H. dumosus, Ceanothus integerrimus* and *C. pumilus,* and *Berberis nervosa* and *B. pumila.*"

Local moist seeps at the base of serpentine-peridotite slopes are havens for some of the most spectacular of the Siskiyou endemics: *Cypripedium californicum, Rudbeckia californica, Darlingtonia californica, Trillium rivale, Lilum bolanderi,* and *L. occidentale.* There is no doubt that the rich endemism of the Siskiyou Mountains can be correlated in large part to the "insular" occurrence of ultrabasic rocks.

Contrasts between serpentine plant life of the Siskiyous and that of western and central Washington are muffled by the presence in both of a coniferous forest cover. Yet species differences between the two areas are truly sharp. The most telling contrast is in the reduction in species diversity on the Washington ultrabasics. Though there are remarkable species discontinuities and edaphic restrictions in the state, the serpentine flora is markedly depauperate compared to that on the Siskiyou and Californian serpentines. But before we deal in specifics, let me set the physiographic scene for display of plants on ultrabasics in Washington.

Ultramafics in the state occur in two major settings (Kruckeberg,

Fig. 3. Barren serpentine slopes within coniferous forest type, headwaters of Boulder Creek in Cle Elum River drainage, Wenatchee Mountains, Washington.

1969). The largest exposure is in montane portions of Kittitas and adjacent Chelan counties. The sites are all in the Wenatchee Mountains which form an easterly extending spur of the Cascade Range. The outcrops occur either as peridotite, dunite, or serpentine; exposures of the rock may be massive, of many square miles in extent, or very local (fig. 3). Old altered volcanics (greenstones), sedimentary rocks, gneisses and schists, as well as acid igneous granodiorite border or even interfinger with the ultramafics. The region is thus lithologically rich and complex. The terrain is rugged, with steep slopes and high ridges that culminate in the ultramafic peaks, Earl, Navaho, and Ingalls, from 5000 to 7000 feet altitude. The clearest and most spectacular contact between ultramafic and non-ferromagnesian rock types is along upper Ingalls Creek where the east boundary of peridotite at the creek abruptly gives way to the massive granodiorite of the Stuart Range.

All of the Wenatchee Mountains ultramafics occur in areas of coniferous forest. At altitudes from 2400 to 4000 feet, the forest consists of open stands of Douglas fir, yellow pine, and western white pine; this forest type grades insensibly upward into a mixture of subalpine fir, mountain hemlock and whitebark pine. The stand are invariably open, the barren slopes between the scattered trees lightly populated with grasses and forbs, some of which are highly characteristic of ultramafic soils.

The next largest series of ultramafic occurrences in Washington is in the northwestern counties of Snohomish, Skagit, San Juan, and Whatcom. The most outstanding of these is Twin Sisters Mountain, a westerly outlier of the northern Cascades; it is pure dunite, an igneous ultramafic composed primarily of the mineral olivine. Rock of similar origin occurs locally at low elevations to the west; Fidalgo Island and Cypress Island have the most extensive of this series of ultramafic outcrops.

The vegetation on the Twin Sisters dunite contrasts strikingly with that on the adjacent non-ferromagnesian parent materials. The luxuriance of the Humid Transition forest abruptly gives way to stunted Douglas fir, lodgepole pine, western white pine and shrubby *Juniperus communis*. The insular ultramafics also support conifers, largely Douglas fir, *Pinus contorta,* and *J. scopulorum.*

The coniferous forest on ferromagnesian substrates is by no means dense and continuous. The trees are largely stunted and widely spaced; often on steep, stony serpentinized outcrops there are no trees present. On such barren, continuously eroding slopes, as well as on talus, in rock fissures and on sparsely forested slopes, one is almost sure to find a representation of species restricted to the ferromagnesian soils and rock.

The flora of the Wenatchee Mountains has received the lion's share of my attention. The serpentines of this rugged range support a depauperate flora, a shifting, variable mosaic of both indicator-endemics and wide-ranging edaphically indifferent ("bodenvag") species. The ultramafic rocks at the same time exert a pronounced exclusion effect on much of the regional flora on adjacent non-serpentine habitats. From field records of observations on 36 serpentine and 30 non-serpentine sites a picture of partial floristic discontinuity has emerged and yields fruitful generalizations on the effects on the flora of these northern ultramafic soils. 1. Extreme barren serpentine habitats are depauperized in species number, especially in species of the tree and shrub life form. Such serpentine barrens within the coniferous forest biome appear as though the alpine and timberline zones have been eccentrically displaced downward in altitude. 2. There are indeed endemic and indicator species on Washington serpentines. These are: *Polystichum mohrioides lemmonii, Cheilanthes siliquosa, Poa curtifolia, Eriogonum pyrolaefolium coryphaeum, Arenaria obtusiloba, Claytonia megarhiza nivalis, Anemone drummondii, Thlaspi alpestre, Ivesia tweedyi, Lomatium cuspidatum, Douglasia dentata nivalis,* and *Chaenactis thompsonii.* These twelve species are strong indicators of serpentine; all are herbaceous (two ferns, a grass and nine dicot forbs). 3. Conifers for the most part do not show any marked edaphic preferences. I have observed certain low to mid-montane coniferous species to occur at higher altitudes on serpentine: *Pinus contorta latifolia,* lodgepole pine; *P. ponderosa,* yellow pine; *P. monticola,* western white pine; and *Taxus brevifolia,* western yew. On massive dunite of the more westerly Twin Sisters Mountain, lodgepole pine is the dominant timberline tree; it is unknown in this role elsewhere in the Pacific Northwest. A reverse displacement occurs for the three other conifers. *Pinus albicaulis,* whitebark pine; *Abies lasiocarpa,* subalpine fir; and the shrubby *Juniperus communis* occur at lower than normal elevations on serpentine.

With respect to the flora on nearby non-serpentine soils, it is clear that a large number of species (35) avoid serpentine. This "serpentinophobia" is most evident where serpentine rocks contact other rock types such as granite, greenstone, sandstone, etc. For some plants, avoidance of serpentine becomes a family or generic matter. Though rich in species in the Pacific Northwest, the genus Penstemon fails to occur on serpentine. The Ranunculaceae, Saxifragaceae, Leguminosae, Rosaeae, and Ericaceae are conspicuous by their scarcity or absence on serpentine.

In Washington as in other parts of the world, some elements of the regional flora appear to act indifferently to serpentine. The soil-wanderers (bodenvag species) in Washington form a conspicuous element of the flora, especially since most are conifers. There is no doubt though that species of this category often are responding genetically to the serpentine habitat. Ecotypic differentiation into serpentine tolerant strains has been demonstrated for Washington serpentine flora just as clearly as for the Californian examples (Kruckeberg, 1967). Nine of the 18 bodenvag species tested clearly showed differences in serpentine tolerance. Six showed signs of the same phenomenon, while only three species failed to show ecotypic variation. The clearest responses were with herbaceous perennials, e.g., *Achillea lanulosa, Fragaria virginiana, Prunella vulgaris,* and *Rumex acetosella.* The two latter species are especially noteworthy inasmuch as they are introduced species on serpentine. They have respondd adaptively to selection for serpentine tolerance probably within the last 50–75 years. At first it appeared that coniferous bodenvag species were not ecotypically differentiated. Only after a long period of growth (2 years) has it been possible to detect ecotypic response in lodgepole pine, *P. contorta latifolia.*

The most faithful indicators of Washington serpentines are two ferns, *Cheilanthes siliquosa,* rock brake, and *Polystichum mohrioides* var. *lemmonii,* (Kruckeberg, 1964). The *Cheilanthes* rarely fails to appear on even the most isolated and smallest ultrabasic outcrop, and at all altitudes from sea level to timberline. Though restricted to higher altitudes the *Polystichum* is just as reliable an indicator. One is led to assume that spores of these serpentinophytes are widely dispersed or at least in a regionally chain mail fashion, but only do they establish populations following germination on soils of ultramafic origin. The distribution of *C. siliquosa* spans the North American continent from the Gaspé of Quebec to British Columbia and thence to central California and nearly always its discontinuous range coincides with the outcropping of ultramafics.

"Normal" (Zonal) Soils

Admittedly arbitrary is the antithesis—normal versus abnormal soils.

Yet to the extent that climate or parent material are primary in determining the quality of a soil, the distinction is justified. We would, therefore, expect that normal soils will be characterized by properties derived from other parent materials. In other words, given a range of unexceptional parent materials in a region of similar climate, all normal soils would be nearly alike, converging on common properties due to the overriding effects of the regional climate. The vegetational response to a single soil type on differing parent materials should be homogeneity, other factors being the same.

Does this in fact ever occur? A test of this progression to sameness of soil from different parent materials could only be made under ideal conditions. For example, chemically similar and "normal" parent materials of varied origin, e.g., volcanic, intrusive, metamorphic and sedimentary rocks would be expected to have weathered over the same periods of time, would have to be subjected to the same succession of biota and would have to be compared under similar topographic sites. The concurrence of all of these seems unlikely. Even where the properties of the differing parent materials are not extreme, physically or chemically, soil and vegetation differences are likely to exist. Two of the examples cited earlier can be brought to bear on this point. According to Wright and Mooney (1965), it is the dolomite which is the preferred substrate for the White Mountain bristlecone pine. The sandstone and granite both support the sagebrush dominant and much of the subordinate vegetation. Yet the species composition on the two latter substrates does differ: between the two more normal rock types there are substrate preferences by the flora.

Whittaker's (1960) study of soil preferences by the flora of the Siskiyou Mountain included comparisons between two rock types, diorite and gabbro, less extreme than serpentine-peridotite. Soils derived from diorite and gabbro are much alike chemically. Assuming uniform soil forming factors other than parent materials, the two parent materials should support rather similar vegetation. On the contrary, differences in vegetational composition still do occur and are substrate-dependent. Even dominant tree species show differential responses; species on the gabbro occur with greater frequency on more mesic sites. Whittaker generalizes this "shift toward the mesic" as a common trend associated with change toward substrates higher in ferromagnesian minerals.

It is therefore likely that whenever geological diversity exists in mountainous regions there will be corresponding floristic diversity. The more extreme the lithological differences, the greater the differences in flora. Substrate dependence will more likely be minimal in areas of minimal topographic relief and/or on alluvial substrates. The latter condition appears to hold for the Pacific Northwest where valley alluvium from volcanics, sedimentaries, or granodiorites supports the same climax coniferous forest—including much the same species in the subordinate vegetation. Still another possibility exists: several vegetation types on a single and local substrate. Wells (1962) finds this to be true in the central Californian coastal vegetation. He attributes this kind of vegetational heterogeneity to a history of fire, grazing and other disturbances.

Other Soil Properties Affecting Plant Distribution

Once formed from parent material by the processes of weathering, soil comes into it own as a substrate which can develop unique properties independent of its mineralogical origin. The interplay between organism and soil introduces new dimensions and creates new properties. Two significant attributes of soil that affect plant distribution in remarkable ways are currently under vigorous and fruitful scrutiny. The first of these, soil microtopography, is usually intrinsic to soil and can vary apart from the activity of associated biota. The other influential soil property is the presence in soils of substances of biological origin that promote or inhibit growth. Studies of these two properties are providing unexpected insights into the basic ecological problem of competition (interference) and evoke possible mechanisms for such ecological phenomena as a succession, spatial pattern, endemism, etc.

Soil Microtopography

The fate of seed, once shed from the parent plant, is largely a matter of chance. Where a seed is deposited will be a primary determinant of germination. Even dispersal to a suitable soil or organic substrate is not enough to ensure success. From the "ant's eyeview" the surface of the substrate can be mountainously irregular; and to the seed, major differences in soil microtopography may spell the difference between a favorable microenvironment for germination and failure. Harper, *et al.* (1965) has studied the effect of microtopography on germination and has emphasized germination on "safe" versus "unsafe" germination sites as a potent control of plant populations. Their earlier experiments (Harper, 1961) were done with seed of annual grasses, *Bromus* species, sown on two contrasting soil surfaces. On a uniformly rough surface, irregular clumps of soil about ½ inch in diameter, there was a linear increase in germination with increase in sowing density. But on a soil of regular surface, checked by drying into smooth sectors bounded by cracks, germination failed to increase beyond a rather low density. Clearly the rough surface provided "many more potential germination sites" than did the smooth one. Only those seed that landed in the crevices germinated and there the number of "safe" sites was limited! Harper, *et al.* (1965) greatly elaborated on this theme by using a variety of species of differing seed size and increasing the variety of soil surfaces. There is no question but that the physical heterogeneity of soil surfaces provides a range of microhabitats both suitable and unsuitable for germination. The probable effect of "safe" microsite may be to provide suitable moisture and temperature conditions for germination. The effectiveness of soil pathogens on reducing seedling survival must also depend on the quality of the particular microsite.

Variations in soil microtopography are the product of soil-forming factors. This idea can be formalized in terms of Jenny's soil-forming factor equation ($s = (cl, o, r, p, t)$) where "s" now is "soil microtopography." We can draw from Harper's work some rather far-reaching inferences which bear upon competition, succession and plant distribution. 1. Different species will respond uniquely to different configurations of soil microsites and thereby create local differences in species distribution. 2. Microsite variations decrease the pressure of interspecific interference, if the species have distinct safe site preferences. 3. Changes in microsite through time from bare mineral soil through various successional stages will result in the selection for different species at each stage of the seral sequence. The concept of "safe" site thus is pregnant with experimental strategems for studying a species niche, plant distribution, and the dynamics of vegetation.

Soil Inhibitors

The effect of a metabolite of one species on the survival and/or competitive ability of another is well known to the protistan (microbial) and aquatic animal ecologist. That an equivalent interaction mediated by soil intake-output of metabolites can occur in higher plants thus appears most reasonable. Though repeatedly suggested ever since the time of Liebig, the possibility of promotion or inhibition of growth by metabolites which pass from plant to plant via the soil has only occasionally been given serious attention. Paradoxically the botanist who now finds good evidence for the phenomenon was in the position of having to deny the ecological effectiveness of the first modern case of allelopathy, the effect of plants on each other through their metabolites. Muller (1953) could not substantiate under field conditions the inhibitory effect of metabolites of *Encelia,* a desert shrub, on other plants which had been found in laboratory tests of leachates. The inconclusive nature of antibiotic effects of plant-on-plant is attributed to the differences between natural conditions in the field, dilution, microbial decomposition, soil sequestering of leachates, etc., and the more concentrated doses combined with ideal though artificial conditions in laboratory experiments. More recently Muller and his associates (1964; 1965), have developed incontrovertible evidence for the inhibition of vegetation by volatile terpenes given off by species of *Salvia* and *Artemisia* in the California coastal sage community. The causal basis, toxicity of terpenes, for swaths or perimeters of sterile ground around the sage species has been confirmed in laboratory studies. The suppression is greatest against annual grassland species. Moreover the toxic effect of the terpenes can be retained by the soil for several months. Natural inhibitors can have a far-reaching effect on floristic composition. A substance produced by the shrub by chamise, *Adenostema fasciculatum,* excludes species of grass, which in turn would otherwise exclude *Dodecatheon clevelandii,* a shrub-tolerant herb. Thus this two-step biochemical exclusion creates an inhibitor-induced association of the chamise with the *Dodecatheon.*

The deposition in soil and recycling of organic metabolites is now well established. A wide range of secondary metabolic products of plants, carbohydrates, amino acids, organic acids, volatiles, alkaloids, etc., can be recovered in the tissue of plants grown on substrates, soils or culture solutions, that contain the substances (Grummer, 1961; Tukey, 1962; Winter, 1961). Evaluation of the ecological role of such exogenous substances confronts the same problem of complex factor interaction that persistently vexes the ecologist. A laboratory test of toxicity may not be complemented by positive evidence of toxicity in the field. Differences in concentration, unavailability of exudate-leachate due to adsorption or microbial activity, rainfall-temperature effects, all may lessen or negate the influence of the metabolite. Despite these reservations, it is becoming increasingly clear that interference phenomena, and in turn, pattern and distribution of species in communities, even the effective niche of a plant species, can be importantly influenced by organic compounds cycled through the plant-soil-plant system.

Evolutionary Consequences of Variations in Soils

Plants are ever responsive to differences in their environment that occur over spans of time and space. The effective level of response is the population. The outcome of organism-environment interaction is either adaptive response through natural selection or failure to colonize the habitat, and hence, exclusion or extinction. Variations in soils, then, as significant parts of the fabric in the environmental mosaic, operate as agents of natural selection. Discontinuity of the soil features will further act to isolate adaptive variants. The result of such interactions can be discerned at various hierarchical levels and will be expressed in a variety of modes. Microevolutionary reaction to soil differences will take the form of degrees of ecotypic differentiation, the development of broad genotypic tolerance, or ecological exclusion. The origin of species restricted to edaphically unique habitats is a higher order of evolutionary divergence. Raven (1964) has invoked the concept of catastrophic selection to account for diversification of edaphic specialists. Rapid selection of exceptional genotypes under the stringent environment of azonal soils is presumed to lead to fixation of unique, incipient populations. When soil and biological discontinuities become congruent, isolation and species formation then are promoted. Examples of evolutionary change up to the level of species as occasioned by the selective action of soil differences have been presented above in the section on "abnormal" soils.

Would we not expect some degree of edaphic preference to be expressed in still higher levels of the taxonomic system? Could not sections of genera, entire genera, or even families show in substantial degree singular edaphic restrictions? Such expression of specificity can be induced by climate and is a major ingredient of speciation in the direction of adaptive radiation or extinction. The high incidence of the genus *Streptan-*

thus to serpentine, many caryophylls to ultrabasics, Ericaceae to acid soils, Cyperaceae to water-logged soils, genera of the Chenopodiaceae and Amaranthaceae to nitrogenous or saline soils are all suggestive of edaphic specialization. We would contend then, that soil, as is climate, is a potent selective agency in securing evolutionary change.

Plants as Indicators of Mineral Deposits

The non-random distribution and abundance of plant populations in a circumscribed habitat is the expression of one or more of a set of environmental controls. It is as though the unique composition of a flora is telling the observer that some factor is having an overriding effect on the composition of the plant cover. Plants which act as assay organisms for some environmental component are called indicator species. The recognition of plant indicators has been a traditional approach to the study of environmental restraints on plant distribution. Ecologists, agriculturalists, foresters and range managers all use the sensitivity of plants to environment in attempting to control or manage vegetation.

Plant indicators have been exploited in yet another way—prospecting for mineral deposits. Deposits of a variety of minerals have been located by searches in the field for the tell-tale displays of eccentric patterns of plant occurrences or equally startling absences of occurrences. It is when the indicator plants are found to contain unusual quantities of some mineral element that the geobotanical prospector strikes it rich. Biogeochemical methods have now become standard practice for search for ore deposits in the United States, Canada, Scandinavia, the U.S.S.R. and elsewhere.

Let me relate a personal anecdote as a prologue to the description of some of the results that the method has produced. During his nightly rounds of our department, a faithful janitor would customarily linger in the herbarium. Our suspicions were aroused by his preoccupation with the contents of the herbarium cases, a conduct most unlikely for one of his limited talents. His predilection for dried plants was, however, genuine. He was scanning the contents of every case with a Geiger counter, in the hope that somewhere in our Pacific Northwest collection, his counter would begin ticking at a runaway accelerated rate. His actions told us that he was looking for uranium, at that time a much soughtafter element. The outcome of his effort was, alas, unsuccessful, though the intent was perfectly justified. Uranium deposits could be located by this method!

More systematic and successful have been the operations of the Geochemical Prospecting Methods Division of the U.S. Geological Survey. Helen Cannon of the U.S. Geological Survey has published (1960) a comprehensive review of geobotanical prospecting for ore bodies. Although she points out that the recognition of absences of vegetation, or unusual changes in appearance of plants also can yield "strikes," it is the plant indicator approach that concerns us here.

The list of minerals which plant indicators can disclose reads like a miner's "Eldorado": A conservative compilation would contain boron, copper, gypsum, iron, lead, phosphorus, selenium, silver, uranium and zinc. The copper indicators are both abundant and unusually reliable. They "belong" mainly to three plant groups: the Caryophyllaceae or pink family, the Labiatae or mint family, and the mosses. These copper deposits have been located in Sweden by simply examining localities from which the herbarium specimens of the "copper mosses" had been collected. The copper indicators, *Elsholtzia haichowensis* from China, *Acrocephalus robertii* from Katanga, and *Ocimium homblei* from Rhodesia all belong to the mint family and are very useful in prospecting. The blue-flowered *Ocimium homblei* will not grow in soil containing less than 100 parts of copper per million. The distribution of this plant has led to the discovery of several ore deposits and is currently being mapped in both Northern and Southern Rhodesia by the Rhodesian Selection Trust (Cannon, 1960).

The well-known affinity of members of the loco-weed genus, *Astragalus,* for selenium has led to uranium discoveries, since the occurrence of the two elements is often highly correlated. A good example of the plant indicator method comes from the work of Cannon's group in western United States. Several species, grasses, legumes, and composites, in the shadscale–juniper vegetation of the Yellow Cat area in Grand Co., Utah, proved to be consistent indicators of selenium. In this particular area, selenium and molybdenum are useful pathfinder elements in prospecting for uranium and vanadium. On mineralized soil indicator species contained 6 to 11 times the amount of uranium found in unmineralized ground.

As biogeochemistry becomes more sophisticated in technique, we would predict additional rewarding mineral discoveries. Edaphic plant ecology is certain to contribute to future mineral prospecting and as well, should reap rewards for the student of plant distribution.

Epilogue

It is axiomatic in biology that complexity through factor interactions breeds exceptions to consistent trends and that the analytic approach at the community level must momentarily disregard complex interactions. Our singling out of the soil factor in plant distribution has been just such an over-simplification. The dwelling place of a particular species or assemblage of species is the result of past and ongoing interplay between biota and environment.

In this paper, we have taken the view that soil characteristics can often have the dominating local or even regional impact of determining distribution and/or pattern of plants in associations. Edaphic plant ecology, then, becomes one useful key to the understanding of discontinuity in vegetation.

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PHYTOGEOGRAPHY OF NORTHWESTERN NORTH AMERICA: BRYOPHYTES AND VASCULAR PLANTS

W. B. Schofield

INTRODUCTION

Within northwestern North America there are a number of fairly natural phytogeographic regions, each characterized by a series of endemic and associated species with common affinities. The present survey does not attempt to discuss all of these regions or to give exhaustive lists of the flora that characterizes them. This study can be considered very preliminary, to be amplified and improved with additional floristic information and of detailed preparation of distribution maps. Those of Hultén (1968) emphasize the importance of such maps.

Subspecific categories are not considered here. Although several species are represented in western North America by endemic subspcies, this is not indicated in the discussion.

In the present discussion the region covered is as follows: Alaska and Yukon, British Columbia and the Rocky Mountains portion of Alberta, and also including the area of Hitchcock, *et al.,* (1955–1969), *Vascular Plants of the Pacific Northwest:* "Washington State, the northern half of Oregon (approximately north of the 44th parallel), Idaho north of the Snake River Plains, the mountainous portion of Montana, and an indefinite southern fringe of British Columbia." For the distribution of the vascular plants, therefore, the basic sources have been Hultén (1968), Hitchcock, *et al.* (1955–1969), Henry (1915), and Eastham (1947). Reference has been made also to the introductory portions of Davis (1952), Peck (1941), Piper (1906), and Calder and Taylor (1968). For the mosses the basic source of distributional data has been Grout (1928–1939), although these data have been considerably expanded. For the hepatics Frye and Clark (1937–1947) and Arnell (1956) have provided general information, greatly amplified by more recent literature.

The region covered is phytogeographically complex. It occupies an area somewhat more than one third the area of Europe. The climate varies from arctic to temperate, from oceanic to continental, from extremely humid to arid. Latitude ranges from north of the Arctic circle (to somewhat beyond 71°N) southward to approximately 44°N, and longtitude from 170°E to approximately 113°E. The elevation ascends from sea-level to 20,320 ft., Mt. McKinley, Alaska, with numerous mountain chains possessing peaks more than 10,000 ft. high. The geologic substrata are equally complex, and widely dispersed through various climatic extremes. Vegetation ranges from arctic and alpine tundras through boreal coniferous, montane coniferous, humid coastal coniferous and drier coniferous forests, and arid grassland to semidesert. This is discussed by Daubenmire (1969).

Besides these factors, the present composition of the flora has been moulded by historical circumstances. A major factor determining the present ranges of species was the Pleistocene glaciations and the intervening interglacials. Associated with climatic changes were variations in the position and nature of corridors of migration, thus leading to expansion or restriction of floral boundaries. The flora available preceding the Pleistocene glaciations is discussed by Wolfe and Leopold (1967) and Wolfe (1969).

In Alaska and Yukon there existed, during the Pleistocene glaciations, large unglaciated areas that served as refugia for the flora. This flora consisted largely of circumboreal and circumpolar species, but also possessed taxa surviving from floras of the more distant past, some of them possibly from Tertiary time. These taxa are discussed in detail later. Smaller unglaciated areas existed also in the Queen Charlotte Islands, British Columbia, and possibly at higher elevations in the Rocky Mountains of Canada.

South of the boundary of the continental glaciers, a considerable portion of Idaho, Washington and Oregon has been colonized by plants for many millions of years. Post-Pleistocene and recent variations in the vegetational composition are discussed by Heusser (1960; 1965). Colinvaux (1967) has summarized the Quaternary vegetational history of arctic Alaska.

Phytogeographic examination of the vascular flora of northwestern North America appears to have lagged behind floristic studies. Although Asa Gray (1859) compared the flora of western North America with that of Japan, and Gray and Hooker (1880) analyzed the Rocky Mountain flora, it is Piper (1906) who first attempted to summarize all of the floristic elements. Harshberger (1911) also analyzed floristic elements, but concentrated on floristic composition of the vegetation instead of the ranges of the species that make up the flora. Peck (1941) has also summarized the floristic composition of vegetational areas in Oregon, noting phytogeographic affinities. Weber (1965) has discussed the phytogeography of the southern Rocky Mountains.

Although several studies of the phytogeography of California have appeared (summarized in Stebbins and Major, 1965), the only other major analysis of the total vascular flora of an extensive area in Western North America is that of Cooper (1936) in his analysis of the strand and dune flora of the Pacific coast. Unfortunately Detling did not complete his comprehensive study of the flora of the Pacific Northwest, but fragments of the manuscript have been published (Detling, 1968). Northward, in Alaska, Hultén has published numerous studies, first his beautiful synthetic study (1937) and culminating in his recent *Flora of Alaska and Neighboring Territories* (1968). His atlases of vascular plant distributions (1958; 1962) have also contributed considerably to the understanding of the ranges of plants in the boreal and arctic portions of the Northern Hemisphere. Another publication of similar significance is that of Meusel, *et al.* (1965). Distribution maps illustrating ranges of arctic and boreal species in Canada have been published by Raup (1947), Raymond (1950), and Porsild (1955; 1957; 1958; 1966), and are particularly important in understanding taxa of circumboreal and circumarctic distribution. In many cases these maps have shown that earlier interpretation of species as disjunct have resulted from inadequate collection. The check-list of Porsild and Cody (1968) adds further such evidence, amplified somewhat in Cody and Porsild (1968).

A general phytogeographic synthesis for the bryoflora has not appeared previously. Herzog (1926) has briefly summarized the affinities of the bryoflora of western North America, with a concentration on endemism. Irmscher (1929) has discussed disjunctions, and makes reference to western North American mosses. The most complete summaries of bryophyte floristic elements are included in Evans (1914), Koch (1954; 1956), Steere (1959; 1965), Persson (1949), Iwatsuki (1958), Schofield (1965; 1968a; 1968b), and Ireland and Schofield (1967). The maps of Szweykowski (1961–1969) are highly important in understanding the distribution of circumboreal hepatics.

In the following discussion the flora is treated initially by major phytogeographic elements. Within each of these, more detailed distributional patterns are considered. In each section hepatics are treated first, followed by mosses and vascular plants. For the bryophytes the order of taxa is basically that of Arnell (1965) for the hepatics, Crum, *et al.* (1965) for the mosses, Hitchcock, *et al.* (1955–1969) for the vascular plants peculiar to the region of that flora and Hultén (1968) for Alaskan and other species of northern distribution.

ENDEMISM

In this category are treated those taxa that are either restricted to the area of the study or extend into it, but are western North American endemics. The latter designation includes taxa that are confined mainly to areas in or west of the Rocky Mountains, infrequently extending eastward in the prairies or, occasionally, to the Black Hills of South Dakota.

ENDEMIC GENERA

In the bryophytes, although the number of endemic genera is not great, northwestern North America shows greater richness than the remainder of North America, north of Mexico. In the hepatics there is the Family Gyrothyraceae with the genus *Gyrothyra* Howe (Schuster, 1955) which occurs from coastal northern California northward to south coastal Alaska. This taxon has undoubtedly increased in abundance with the increase in disturbance by man. It is particularly abundant on roadside silts and clays.

Endemic moss genera include: *Crumia* Schof., *Roellia* Kindb., *Leucolepis* Lindb., *Pseudobraunia* (Lesq. & James) Broth., *Alsia* Sull., *Dendroalsia* Britt., *Bestia* Broth., *Tripterocladium* (Müll.) Kindb., *Trachybryum* (Broth.) Schof., and *Rhytidiopsis* Broth.

Of these genera *Roellia, Trachybryum,* and *Rhytidiopsis* are confined largely to subalpine elevations, although *Trachybryum* sometimes descends to sea level and is occasionally associated with the oak woodland from northern California to southwestern British Columbia. *Leucolepis* is widespread at all elevations. *Pseudobraunia, Alsia, Dendroalsia, Bestia,* and *Tripterocladium* are predominantly of lower elevations and occur mainly west of the Cascade Mountains. *Crumia* is more widespread (Schofield, 1966), being restricted by its calcareous seepage habitat rather than by elevation. It it noteworthy that all endemic moss genera except *Pseudobraunia* and *Tripterocladium* are dioecious and none possess any special gemmae for vegetative reproduction, yet most show very wide geographic range and often occur in great abundance.

In the vascular flora generic endemism is particularly notable.

Gramineae: *Pleuropogon* R.Br. and *Scribneria* Hack.

Liliaceae: *Camassia* Lindl., *Leucocrinum* Nutt., and *Scoliopus* Torr.

Orchidaceae: *Eburophyton* Heller.

Chenopodiaceae: *Grayia* H. & A., *Nitrophila* Wats., and *Sarcobatus* Nees.

Portulacaceae: *Calyptridium* Nutt., *Lewisia* Pursh, and *Spraguea* Torr.

Berberidaceae: *Vancouveria* Morr. & Dec.

Papaveraceae: *Canbya* Parry, *Eschscholtzia* Cham., and *Meconella* Nutt.

Cruciferae: *Anelsonia* Macbr. & Pays., *Athysanus* Greene, *Caulanthus* Wats., *Chlorocambe* Rydb., *Idahoa* Nels. & Macbr., *Phoenicaulis* Nutt., *Physaria* (Nutt.) Gray, *Polyctenium* Greene, *Schoenocrambe* Greene, *Stanleya* Nutt., *Streptanthella* Rydb., *Thelypodium* Endl., and *Thysanocarpus* Hook.

Sarraceniaceae: *Darlingtonia* Torr.

Saxifragaceae: *Bolandra* Gray, *Conimitella* Rydb., *Elmera* Rydb., *Lithophragma* Nutt., *Peltiphyllum* Engl., *Suksdorfia* Gray, *Telesonix* Raf., *Tellima* R.Br., and *Tolmiea* T. & G.

Hydrangeaceae: *Whipplea* Torr.

Rosaceae: *Chamaebatiaria* (Porter) Maxim., *Kelseya* (Wats.) Rydb., *Luetkea* Bong., *Osmaronia* Greene, *Peraphyllum* Nutt., *Petrophytum* (Nutt.) Rydb., and *Purshia* DC.

Umbelliferae: *Orogenia* Wats., *Perideridia* Reichenb., *Rhysopterus* Coult. & Rose, and *Sphenosciadium* Gray.

Cactaceae: *Pediocactus* Britt. & Rose.

Malvaceae: *Sidalcea* Gray.

Euphorbiaceae: *Eremocarpus* Benth.

Ericaceae: *Allotropa* Torr. & Gray, *Cladothamnus* Bong., *Hemitomes* Gray, *Pityopus* Small, and *Pleuricospora* Gray.

Primulaceae: *Douglasia* Lindb.

Polemoniaceae: *Eriastrum* Woot. & Standl., *Gymnosteris* Greene, *Langloisia* Greene *Leptodactylon* H. & A., and *Linanthastrum* Ewan.

Hydrophyllaceae: *Ellisia* L., *Hesperochiron* Wats., and *Romanzoffia* Cham.

Boraginaceae: *Coldenia* L., and *Dasynotus* Johnst.

Scrophulariaceae: *Chionophila* Benth., *Cordylanthus* Nutt., *Mimetanthe* Greene, *Synthyris* Benth., and *Tonella* Nutt.

Valerianaceae: *Plectritis* DC.

Campanulaceae: *Downingia* Torr., *Githopsis* Nutt., *Heterocodon* Mitt., *Howellia* Gray, and *Porterella* Torr.

Compositae: *Apargidium* T. & G., *Bahia,* Laq., *Balsamorhiza* Nutt., *Blepharipappus* Hook., *Chaenactis* DC., *Chrysothamnus* Nutt., *Crocidium* Hook., *Dimeresia* Gray, *Eatonella* Gray, *Enceliopsis* (Gray) Nels., *Eriophyllum* Laq., *Hulsea* Torr. & Gray, *Luinia* Benth., *Madia* Mol., *Raillardella* Benth., *Rigiopappus* Gray, and *Wyethia* Nutt.

More than half of these genera are monotypic. Many are widespread, *Camassia, Sarcobatus, Eschscholtzia, Lewisia, Romanzoffia, Lithophragma, Luetkea, Apargidium,* etc., where others, *Scribneria, Chlorocambe, Darlingtonia,* etc., are highly restricted in their range. Of particular interest is the fact that there are no endemic genera of Pteridophytes or Gymnosperms. A number of families are especially rich in endemic genera: Cruciferae (13 genera), Saxifragaceae (19 genera), Rosaceae (7 genera) and Compositae (17 genera). Many of these genera are restricted to rather arid regions, although a number are of alpine and subalpine habitats and others are of forests at lower elevations. As in the bryophytes, most of the genera are clearly distinct from related genera.

Since there is such a richness of endemic species, these are treated here in relation to thir distribution pattern in the region.

Species Endemism

Widespread at Elevations Below Subalpine

These species are conspicuous elements of both flora and vegetation. The vascular plants give the vegetation its physiognomic character and the bryophytes tend to dominate that flora in other strata. Within such a wide range many species are environmentally restricted. For example, some bryophytes are consistently on perennially dry and exposed rock surfaces while others are confined to rocks perennially inundated. The forest is entirely of endemic trees and mainly of endemic shrubs, and the herbaceous vegetation is dominated by endemic species. Most of the species do not extend beyond the crests of the Rocky Mountains and many disappear with the boundary to the boreal coniferous forest of northern latitudes or the arid portions of the interior regions. Thus the widespread element is found in regions of relatively high precipitation on both the coast and lower elevations of the coastal mountains and also at lower elevations of the mountains west of the Rockies. Many of the species extend southward along the coast as far south as the southern limits of the coastal redwood forest (*Sequoia sempervirens* (Don) Endl.) in California and occasionally at lower elevations of the Sierra Nevada.

Within this same geographic area are other floristic elements; these are discussed elsewhere in this paper. Their phytogeographic significance is great, but their contribution to the vegetational cover is generally smaller than that of the endemic species, particularly in the vascular flora.

The distributions of the hepatics are not well understood since collection has been rather limited: *Gyrothyra underwoodiana* Howe., *Plectocolea rubra* (Gottsche) Evans, *Scapania americana* Müll., *Bazzania ambigua* (Lindenb.) Trevis., *Radula bolanderi* Gottsche, *Porella roellii* Steph., *P. navicularis* (Lehm. & Lindenb.) Lindb., *Frullania nisquallensis* Sull., and *F. franciscana* Howe.

Among the mosses the details are somewhat clearer and the representation of endemic taxa is somewhat greater: *Sphagnum mendocinum* Sull. & Lesq., *Atrichum selwynii* Aust., *Pogonatum macounii* (Kindb.) Kindb. & Mac., *Ditrichum ambiguum* Best, *D. schimperi* (Lesq.) Kunze, *Dicranella* n. sp., *Amphidium californicum* (Hampe) Broth., *Dicranum howellii* Ren. & Card., *Barbula rubiginosa* Mitt., *Scouleria aquatica* Hook., *Racomitrium depressum* Lesq., *R. varium* (Mitt.) Lesq. & James, *Pohlia longibracteata* Broth., *Leucolepis menziesii* (Hook.) Steere, *Plagiomnium insigne* (Mitt.) Koponen, *P. venustum* (Mitt.) Koponen, *Rhizomnium glabrescens* (Kindb.) Koponen, *Ulota megalospora* Vent., *U. obtusiuscula* Müll. & Kindb., *Orthotrichum consimile* Mitt., *Fontinalis neomexicana* Sull. & Lesq., *F. patula* Card., *Dichelyma uncinatum* Mitt., *Neckera douglasii* Hook., *Porotrichum bigelovii* (Sull.) Kindb., *Thamnobryum leibergii* (Britt.) Nieuwl., *Isothecium stoloniferum* (Hook.) Brid., *Claopodium bolanderi* Best, *Homalothecium fulgescens* (Mitt.) Lawt. *Brachythecium frigidum* (Müll.) Besch., B. *lamprochryseum* Müll. & Kindb., *Eurhynchium oreganum* (Sull.) Jaeg. & Sauerb., *Scleropodium obtusifolium* (Hook.) Kindb., and *Hypnum circinale* Hook.

These bryophytes occupy a diversity of habitats but the majority are epiphytic on tree trunks and occur less commonly on rock. The remainder occupy various habitats, from splashed rock faces, for example *Scouleria aquatica* and *Scleropodium obtusifolium;* humid cliff bases, on rock or on soil, *Pogonatum macounii, Pohlia longibracteata, Porotrichum bigelovii,* and *Thamnobryum leibergii;* rotten logs or forest floor, *Dicranum howellii* and *Brachythecium frigidum;* or aquatic *Sphagnum mendocinum* and *Fontinalis neomexicana.*

A number of species that have a wide range but are rare are:

Hepatics: *Blepharostoma arachnoideum* Howe, *Jungermannia allenii* Clark, *Plectocolea rubra* (Gottsche.) Evans, and *Sphaerocarpos hians* Haynes.

Mosses: *Fissidens ventricosus* Lesq., *F. pauperculus* Howe, *Crumia latifolia* (Kindb.) Schof., *Scouleria marginata* Britt., *Brotherella roellii* (Ren. & Card.) Fleisch., and *Triperocladium leucocladulum* (Müll.) Kindb.

Based on their present ecology and distribution it can be inferred that during glaciation, the bulk of these species persisted largely south of the glacial boundary, probably in forested environments. The relative scarcity of most of them in unglaciated Alaska indicates that they did not persist there. A number of these species have probably increased in abundance in recent times, largely with the expansion of the available habitat, chief among these are *Gyrothyra underwoodiana,* an undescribed *Dicranella,* and *Pohlia longibracteata,* all of which frequently abound on moist road-cuts. Many others have probably been greatly restricted by the elimination of their forest habitat, although gross distributional pattern probably has not been greatly altered.

The vascular flora of this widespread distribution is large. The woody elements of this flora characterize the vegetation. Since these taxa are endemic, the impression of great endemism results in spite of the very considerable number of circumboreal and circumpolar species that make up the total flora. The following list is far from complete, but will serve to illustrate the diversity of taxa present:

Polypodiaceae: *Polystichum munitum* (Kaulf.) Presl, *Polypodium glycyrhiza* Eat., and *P. hesperium* Maxon.

Taxaceae: *Taxus brevifolia* Nutt.

Pinaceae: *Pinus contorta* Dougl., *Picea sitchensis* (Bong.) Carr., *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla* (Raf.) Sarg., and *Abies grandis* (Dougl.) Lindl.

Cupressaceae: *Chamaecyparis nootkatensis* (Lamb.) Spach.

Juncaceae: *Juncus brachyphyllus* Wieg. and *J. oreganus* Wats.

Liliaceae: *Clintonia uniflora* (Schult.) Kunth, *Disporum hookeri* (Torr.) Nichols, *Erythronium oreganum* Appleg., *E. revolutum* Sm., *Trillium ovatum* Pursh, *Veratrum californicum* Durand, and *Zygadenus elegans* Pursh.

Orchidaceae: *Cypripedium montanum* Dougl. and *Listera caurina* Piper.

Poaceae: *Agropyron spicatum* (Pursh.) Scribn. & Sm., *Agrostis aequivalvis* Trin., *A. diegoensis* Vasey, *A. idahoensis* Nash., *A. microphylla* Steud., *Bromus pacificus* Shear, *Elymus innovatus* Beal, *Festuca idahoensis* Elmer, *F. subulata* Trin., *Glyceria elata* (Nash.) Hitchc., *Melica subulata* (Griseb.) Scribn., *Poa laxiflora* Buckl., *P. stenantha* Trin., and *Trisetum cernuum* Trin.

Cyperaceae: *Carex atrostachya* Olney, *C. preslii* Steud., *C. phaeocephala* Piper, *C. petasata* Desv., *C. microptera* Mack., *C. laeviculmis* Meinsch., *C. phyllomanica* Boott., *C. scopulorum* Holm, *C. kelloggii* Boott., and *C. sitchensis* Prescott.

Araceae: *Lysichiton americanum* Hult. & St. John.

Salicaceae: *Salix lasiandra* Benth., *S. scouleriana* Benth., and *S. sitchensis* Sanson.

Betulaceae: *Alnus rhombifolia* Nutt. and *A. rubra* Bong.

Aristolochiaceae: *Asarum caudatum* Lindl.

Portulacaceae: *Montia parvifolia* (Moc.) Greene and *M. sibirica* (L.) Howell.

Caryophyllaceae: *Silene menziesii* Hook.

Ranunculaceae: *Aconitum columbianum* Nutt., *Aquilegia formosa* Fisch., *Coptis asplenifolia* Salisb., *Ranunculus alismaefolius* Geyer, *R. occidentalis* Nutt., and *Thalictrum occidentale* Gray.

Berberidaceae: *Berberis aquifolium* Pursh.

Saxifragaceae: *Boykinia elata* (Nutt.) Greene, *Heuchera cylindria* Dougl., *H. glabra* Willd., *H. micrantha* Dougl., *Mitella trifida* Grah., *Saxifraga ferruginea* Grah., *Tellima grandiflora* (Pursh.) Dougl., *Tiarella trifoliata* L., *Tolmiea menziesii* (Pursh.) T. & G., *Ribes bracteosum* Dougl., and *R. laxiflorum* Pursh.

Rosaceae: *Holodiscus discolor* (Pursh.) Maxim., *Osmaronia cerasiformis* (T. & G.) Greene, *Physocarpus capitatus* (Pursh.) Kuntze, *Potentilla glandulosa* Lindl., *P. gracilis* Dougl., *Prunus emaginata* (Dougl.) Walpers, *Pyrus fusca* Raf., *Rosa gymnocarpa* Nutt., *R. nutkana* Presl., *Rubus lasiococcus* Gray, *R. leucodermis* Dougl., *R. nivalis* Dougl., and *Spiraea douglasii* Hook.

Leguminosae: *Lathyrus nevadensis* Wats., *Lotus purshianus* (Benth.) Clements & Clements, *Lupinus lepidus* Dougl., and *L. polyphyllus* Lindl.

Oxalidaceae: *Oxalis oregana* Nutt.

Celastraceae: *Pachystima mysinites* (Pursh) Raf.

Aceraceae: *Acer circinatum* Pursh and *A. glabrum* Torr.

Balsaminiaceae: *Impatiens ecalcarata* Blank.

Rhamnaceae: *Ceanothus sanguineus* Pursh and *Rhamnus purshiana* DC.

Hypericaceae: *Hypericum anagalloides* C. & S.

Violaceae: *Viola purpurea* Kell.

Onagraceae: *Boisduvalia densiflora* (Lindl.) Wats., *Epilobium glaberrimum* Barbey, *E. luteum* Pursh, and *E. minutum* Lindl.

Cornaceae: *Cornus nuttallii* Aud.

Ericaceae: *Allotropa virgata* T. & G., *Chimaphila menziesii* (R.Br.) Spreng., *Gaultheria shallon* Pursh, *Menziesia ferruginea* Sm., *Pleuricospora fimbriolata* Gray, *Pyrola aphylla* Sm., *P. dentata* Sm., *P. picta* Sm., *Vaccinium alaskaense* Howell, and *V. parvifolium* Sm.

Primulaceae: *Dodecatheon jeffreyi* van Houtte.

Gentianaceae: *Gentiana sceptrum* Griseb. and *G. douglasiana* Bong.

Convolvulaceae: *Cuscuta occidentalis* Millspaugh.

Hydrophyllaceae: *Romanzoffia sitchensis* Bong.

Caprifoliaceae: *Lonicera ciliosa* (Pursh) DC.

Campanulaceae: *Heterocodon rariflorum* Nutt.

Compositae: *Agoseris grandiflora* (Nutt.) Greene, *Antennaria anaphaloides,* Rydb., *A. corymbosa* Nels., *A. dimorpha* (Nutt.) T. & G., *Arnica amplexicaulis* Nutt., *A. diversifolia* Greene, *A. latifolia* Bong., *Aster subspicatus* Nees, *Microseris laciniata* (Hook.) Schultz-Bip., and *Prenanthes alata* (Hook.) Dietr.

Subalpine and Alpine

Besides possessing a flora containing rich representation of circumpolar species, the mountains of northwestern North America have many bryophyte and vascular plant endemics. The woody flora is essentially endemic but not confined to the mountains while endemism decreases in the herbs and bryophytes. The subalpine forest probably possesses more endemic bryophytes than the alpine portion, but in the vascular flora endemism increases in alpine areas. While some mountains serve as islands of endemism for vascular plants, the bryophytes are not so confined. This is in spite of very narrow environment restriction of many of them. Most of these bryophytes produce numerous sporophytes annually although several are dioicous. Special vegetative reproductive organs are not known for any of the endemic alpine bryophytes.

In the following discussion the widespread subalpine and alpine species are treated first and various mountains are noted with their endemic floras.

1. Widespread subalpine and alpine

Hepatics: *Macrodiplophyllum imbricatum* (Howe) Perss.

Mosses: *Oligotrichum parallelum* (Mitt.) Kindb., *Polytrichadelphus lyallii* Mitt., *Buxbaumia piperi* Best, *Ditrichum montanum* Leib., *Trematodon boasii* Schof., *Dicranoweisia roellii* Kindb., *Dicranum pallidisetum* (Bailey) Irel., *Grimmia atricha* Müll. & Kindb., *Pohlia columbica* (Kindb.) Andr., *Roellia roellii* (Broth.) Crum, *Lescuraea baileyi* (Best & Grout) Lawt., *L. atricha* (Kindb.) Lawt., *L. stenophylla* (Ren. & Card.) Kindb., *Heterocladium procurrens* (Mitt.) Rau. & Herv., *Hygrohypnum bestii* (Ren. & Bryhn.) Holz., *Trachybryum megaptilum* (Sull.) Schof., *Brachythecium leibergii* Grout, *B. hylotapetum* Hig. & Hig., and *Rhytidiopsis robusta* (Hook.) Broth.

Vascular Plants:

Polypodiaceae: *Pellaea bridgesii* Hook.

Pinaceae: *Larix occidentalis* Nutt., *L. lyallii* Parl., *Pinus albicaulis* Engelm., *P. flexilis* James, *P. monticola* Dougl., *Tsuga mertensiana*

(Bong.) Sarg., *Abies amabilis* (Dougl.) Forbes, *A. lasiocarpa* (Hook.) Nutt., and *Picea engelmannii* Parry.

Cupressaceae: *Juniperus occidentalis* Hook.

Juncaceae: *Juncus drummondii* Mey., *J. mertensianus* Bong., *J. parryi* Engelm., and *J. regelii* Buch.

Cyperaceae: *Carex anthoxanthea* Presl., *C. circinnata* Mey., *C. nigricans* Mey., *C. albonigra* Mack., *C. atrata* L., *C. mertensii* Prescott, and *C. petricosa* Desv.

Liliaceae: *Allium validum* Wats., *Erythronium grandiflorum* Pursh, *E. montanum* Wats., *Lilium columbianum* Hanson, *Stenanthium occidentale* Gray, and *Xerophyllum tenax* (Pursh) Nutt.

Orchidaceae: *Cypripedium montanum* Dougl.

Poaceae: *Agrostis humilis* Vasey, *A. thurberiana* Hitchc., *A. variabilis* Rydb., *Bromus sitchensis* Trin., *B. suksdorfii* Vasey, *Calamagrostis tweedyi* (Scribn.) Scribn., *Festuca viridula* Vasey, *Melica spectabilis* Scribn., *Oryzopsis exigua* Thurb., *Poa bolanderi* Vasey, *P. curta* Rydb., *P. curtifolia* Scribn., *P. gracillima* Vasey, *P. grayana* Vasey, *P. lettermanii* Vasey, *P. nervosa* (Hock.) Vasey, *P. reflexa* Vasey & Scribn., and *P. suksdorfii* (Beal) Vasey.

Salicaceae: *Salix barclayi* Anderss., *S. barrattiana* Hook., *S. cascadensis* Cockerell, *S. dodgeana* Rydb., *S. geyeriana* Anderss., *S. nivalis* Hook., *S. tweedyi* (Bebb) Ball, and *S. wolfii* Bebb.

Polygonaceae: *Eriogonum androsaceum* Benth., *E. chrysops* Rydb., *E. pyrolifolium* Hook., *Polygonum bistortoides* Pursh, *P. minimum* Wats., *P. newberryi* Small, *P. phytolaccifolium* Meisn., and *Rumex paucifolius* Nutt.

Caryophyllaceae: *Silene parryi* (Wats.) Hitchc. & Maguire, *S. scaposa* Robins., *S. scouleri* Hook., and *Stellaria jamesiana* Torr.

Ranunculaceae: *Aquilegia jonesii* Parry, *Caltha biflora* D.C., *C. leptosepala* D.C., *Delphinium glareosum* Greene, *D. glaucum* Wats., *D. occidentale* Wats., *Ranunculus cardiophyllus* Hook., *R. cooleyae* Vasey & Rose, *R. eschscholtzii* Schlecht., *R. inamoenus* Greene, and *R. verecundus* Robins.

Papaveraceae: *Papaver pygmaeum* Rydb.

Fumariaceae: *Dicentra uniflora* Kell.

Cruciferae: *Anelsonia eurycarpa* (Gray) Macbr. & Pays., *Arabis furcata* Wats., *A. lyallii* Wats., *A. microphylla* Nutt., *A. platyperma* Gray, *Cardamine breweri* Wats., *Chlorocrambe hastata* (Wats.) Rydb., *Draba apiculata* Hitchc., *D. aurea* Vahl., *D. crassifolia* Nutt., *D. densifolia* Nutt., *D. incerta* Pays., *D. lonchocarpa* Rydb., *D. paysonii* Macbr., *D. praealta* Greene, *D. stenoloba* Ledeb., and *D. ventosa* Gray.

Crassulaceae: *Sedum oregonense* (Wats.) Peck.

Saxifragaceae: *Elmera racemosa* (Wats.) Rydb., *Leptarrhena pyrolifolia* (Don) R. Br., *Mitella breweri* Gray, *Parnassia fimbriata* Konig., *Saxifraga arguta* Don, *S. chrysantha* Gray, *S. debilis* Engelm., *S. occi-*

dentalis Wats., *S. oregana* Howell, *S. tolmiei* T. & G., *Telesonix jamesii* (Torr.) Raf., *Ribes howellii* Greene, *R. mogoelonicum* Greene, and *R. montigenum* McClatchie.

Rosaceae: *Ivesia gordoni* (Hook.) T. & G., *I. tweedyi* Rydb., *Kelseya uniflora* (Wats.) Rydb., *Luetkea pectinata* (Pursh) Kuntze, *Potentilla brevifolia* Nutt., *P. drummondii* Lehm., *P. flabellifolia* Hook., *P. hookeriana* Lehm., *Rubus pedatus* Sm., *Sanguisorba sitchensis* Meyer, and *Spiraea densiflora* Nutt.

Leguminosae: *Astragalus cottonii* Jones, *A. tegetarius* Wats., *A. whitneyi* Gray, *Hedysarum occidentale* Greene, *Oxytropis parryi* Gray, *Trifolium beckwithii* Brew., *T. dasyphyllum* T. & G., *T. nanum* Torr., and *T. parryi* Gray.

Haloragidaceae: *Hippuris montana* Ledeb.

Umbelliferae: *Angelica roseana* Henderson.

Ericaceae: *Cassiope mertensiana* (Bong.) Don, *Gaultheria humifusa* (Grah.) Rydb., *G. ovatifolia* Gray, *Phyllodoce empetriformis* (Sw.) Don, *Rhododendron albiflorum* Hook., and *Vaccinium membranaceum* Dougl.

Gentianaceae: *Gentiana calycosa* Griseb.

Polemoniaceae: *Polemonium elegans* Greene.

Boraginaceae: *Cryptantha nubigena* (Greene) Pays.

Scrophulariaceae: *Castilleja applegatei* Fern., *C. parviflora* Bong., *C. rhexifolia* Rydb., *Mimulus lewisii* Pursh, *Pedicularis bracteosa* Benth., *P. contorta* Benth., *P. cystopteridifolia* Rydb., *P. ornithorhyncha* Benth., and *Pentstemon davidsonii* Greene.

Valerianaceae: *Valeriana acutiloba* Rydb.

Compositae: *Antennaria lanata* (Hook.) Greene, *A. mollis* Hook., *A. nevadensis* Gray, *Arnica michauxiana* Bess., *A. scopulorum* Gray, *A. alpigenus* (T. & G.) Gray, *Chaenactis alpina* (Gray) Jones, *Erigeron asperugineus* (Eat.) Gray, *E. lanatus* Hook., *E. leiomerus* Gray, *E. simplex* Greene, *E. ursinus* D. C. Eat., *E. vagus* Payson, *Haplopappus lyallii* Gray, *H. pygmaeus* (T. & G.) Gray, *Hulsea algida* Gray, *Saussurea americana* Eat., *Senecio megacephalus* Nutt., *S. subnudus* DC., and *S. werneriifolius* Gray.

2. A number of mountain areas posses their endemic species

a. Rocky Mountains (mainly)

Vascular Plants: *Juncus hallii* Engelm., *J. tweedyi* Rydb., *Allium brevistylum* Wats., *Draba crassa* Rydb., *Sedum debile* Wats., *Conimitella williamsii* (Eat.) Rydb., *Trifolium haydenii* Porter, *Primula parryi* Gray, *Phacelia lyallii* (Gray) Rydb., *Synthyris canbyi* Pennell, *Cirsium tweedyi* Rydb., *Erigeron pallens* Cronq., *Hymenoxys grandiflora* (T. & G.) Parker, and *Townsendia spathulata* Nutt.

b. Cascade Mountains (principally)

Mosses: *Pohlia cardotii* (Ren.) Broth.

Vascular Plants: *Silene suksdorfii* Robins., *Draba aureola* Wats., *Physaria alpestris* Suksd., *Smelowskia ovalis* Jones, *Tauschia stricklandii* (Coult. & Rose) Math. & Const., *Castilleja cryptantha* Greenm., *C. rupicola* Piper, *C. suksdorfii* Gray, *Pedicularis rainierensis* Pennell & Warren, *Aster gormanii* (Piper) Blake, *Erigeron cascadensis* Heller, *Hulsea nana* Gray, *Luinia nardosmia* (Gray) Cronq. and *L. stricta* (Greene) Rob.

c. Olympic Mountains

Vascular Plants: *Petrophytum hendersonii* (Canby) Rydb., *Viola flettii* Piper, *Campanula piperi* Howell, *Aster paucicapitatus* Rob., *Erigeron flettii* Jones, and *Senecio websteri* Greenm.

d. Cascade Mountains, Coast and Insular Mountains, and Olympic Mountains

Mosses: *Dichodontium olympicum* Ren. & Card. and *Grimmia olympica* Britt.

Vascular Plants: *Delphinium glareosum* Greene, *Erysimum arenicola* Wats., *Smelowskia divergens* Wats., *Vaccinium deliciosum* Piper, *Arnica nevadensis* Gray, and *Senecio flettii* Wieg.

e. Wenatchee Mountains

Vascular Plants: *Silene seelyi* Morton & Thompson, *Delphinium viridescens* Leiberg, *D. xantholeucum* Piper, *Lomatium cuspidatum* Math. & Const., *Valeriana columbiana* Piper, *Chaenactis ramosa* Stockwell, and *C. thompsonii* Cronq.

f. Wallowa Mountains (sometimes also in Blue Mountains)

Vascular Plants: *Lomatium greenmanii* Mathias, *L. oreganum* Coult. & Rose, *Castilleja chrysantha* Greenm., *C. fraterna* Greenm., *C. glandulifera* Pennell, *C. owenbeyana* Pennell, *C. rubida* Piper, *Pentstemon spathulatus* Pennell, and *Senecio porteri* Greene.

There are numerous other subalpine and alpine endemics, in a number of cases of very restricted distribution. The majority of the endemics are of circumpolar genera and many are especially rich in species, for example, *Salix, Arabis, Draba, Saxifraga, Trifolium, Castilleja, Pedicularis, Erigeron,* and *Senecio.* Although many of these genera are notoriously polymorphic, the endemic species tend to be remarkably distinct. Since many of the species are ecologically restricted, their discovery is often by chance, and thus their total distribution through mountainous western North America is not thoroughly known. Considerable botanical exploration even in presumably well-known mountain areas, remains to be done.

Dry Interior Plans

East of the Cascade and Coastal Mountains and west of the Rocky Mountains there extends a lowland trough lying in the rain shadow of the coastward mountains. This drier region possesses a vegetation that is composed predominantly of species endemic to western North America. Many range southward into the cold deserts and some even to the warmer arid regions as far south as Mexico. Many are found also east of the Rocky mountains and the northern limits are largely in central British Columbia, although occasionally some species extend into Yukon and Alaska. Endemism is highest in perennial herbs although some are woody or annual. No endemic hepatics have been reported and few mosses, although little careful bryological exploration has been made in this area.

Bryophytes: *Barbula andreaeoides* Kindb., *B. platyneura* Müll. & Kindb., *Pottia nevadensis* Card. & Thér., *Grimmia calyptrata* Hook., *Funaria americana* Lindb., and *Orthotrichum hallii* Sull. & Lesq.

Vascular Plants

Pinaceae: *Pinus ponderosa* Dougl. and *P. flexilis* James.

Lilliaceae: *Allium nevadense* Wats. *Fritillaria pudica* (Pursh) Spreng., and *Leucocrinum montanum* Nutt.

Iridaceae: *Iris chrysophylla* Howell and *Calochortus bruneaunis* Nels. & Macbr.

Poaceae: *Danthonia parryi* Scribn., *D. unispicata* Munro, *Melica bulbosa* Geyer, *M. fugax* Boland., *Muhlenbergia andina* (Nutt.) Hitchc., *Stipa lettermanii* Vasey, *S. thurberiana* Piper, and *Trisetum wolfii* Vasey.

Ulmaceae: *Celtis douglasii* Planch.

Polygonaceae: *Chorizanthe brevicornu* Torr., *C. watsoni* T. & G., *Eriogonum angulosum* Benth., *E. caespitosum* Nutt., *E. cernuum* Nutt., *E. chrysocephalum* Gray, *E. deflexum* Torr., *E. douglasii* Benth., *E. elatum* Dougl., *E. heracleoides* Nutt., *E. microthecum* Nutt., *E. niveum* Dougl., *E. sphaerocephalum* Dougl., *E. thymoides* Benth., and *Polygonum austiniae* Greene.

Chenopodiaceae: *Atriplex truncata* (Torr.) Gray, *Grayia spinosa* (Hook.) Moq., *Kochia americana* Wats., *Monolepis pusilla* Torr., *M. spathulata* Gray, *Nitrophila occidentalis* (Moq.) Wats., *Salicornia rubra* Nels., *Sarcobatus vermiculatus* (Hook.) Torr., *Suaeda intermedia* Wats., and *S. spalding*ii Wats.

Amaranthaceae: *Amaranthus californicus* (Moq.) Wats.

Portulacaceae: *Calyptridium roseum* Wats., *Lewisia rediviva* Pursh, and *Talinum spinescens* Torr.

Caryophyllaceae: *Arenaria aculeata* Wats., *A. franklinii* Dougl., *A. hookeri* Nutt., *A. pusilla* Wats., *Silene douglasii* Hook., *S. oregana* Wats., and *S. spaldingii* Wats.

Paeoniaceae: *Paeonia brownii* Dougl.

Ranunculaceae: *Clematis hirsutissima* Pursh, *C. ligusticifolia* Nutt., *Delphinium andersonii* Gray, *D. depauperatum* Nutt., *D. glaucescens* Rydb., *D. multiplex* (Ewan) Hitchc., *D. stachydeum* (Gray) Nels. & Macbr., *Myosurus aristatus* Benth., *Ranunculus andersonii* Gray, *R. jovis* Nels., and *R. reconditus* Nels. & Macbr.

Papaveraceae: *Canbya aurea* Wats.

Cruciferae: *Arabis cobrensis* Jones, *A. cusickii* Wats., *A. lignifera* Nels., *Caulanthus crassicaulis* (Torr.) Wats., *C. pilosus* Wats., *Draba douglasii* Gray, *Erysimum occidentale* (Wats.) Robins., *Idahoa scapigera* (Hook.) Nels. & Macbr., *Lepidium dictyotum* Gray, *Lesquerella douglasii* Wats., *L. kingii* Wats., *Phoenicaulis cheiranthoides* Nutt., *Physaria didymocarpa* (Hook.) Gray, *Polyctenium fremontii* (Wats.) Greene, *Schoenocrambe linifolia* (Nutt.) Greene, *Stanleya tomentosa* Parry, *S. viridifolia* Nutt., *Streptanthella longirostris* (Wats.) Rydb., *Thelypodium integrifolium* (Nutt.) Endl., and *T. sagittatum* (Nutt.) Endl.

Saxifragaceae: *Lithophragma parviflora* (Hook.) Nutt., *L. tenella* Nutt., *Ribes aureum* Pursh, and *R. velutinum* Greene.

Rosaceae: *Cercocarpus ledifolius* Nutt., *Chamaebatiaria millefolium* (Torr.) Maxim., *Holodiscus dumosus* (Hook.) Heller, *Peraphyllum ramosissimum* Nutt., and *Purshia tridentata* (Pursh) D.C.

Leguminosae: *Astragalus adanus* Nels., *A. argophyllus* Nutt., *A. arthurii* Jones, *A. atratus* Wats., *A. calycosus* Torr., *A. casei* Gray, *A. cibarius* Sheld., *A. collinus* Dougl., *A. convallarius* Greene, *A. curvicarpus* (Sheld.) Macbr., *A. cusickii* Gray, *A. filipes* Torr., *A. geyeri* Gray, *A. howellii* Gray, *A. inflexus* Dougl., *A. leibergii* Jones, *A. lyallii* Gray, *A. malacus* Gray, *A. microcystis* Gray, *A. newberryi* Gray, *A. nudisiliquus* Nels., *A. obscurus* Wats., *A. palousensis* Porter, *A. reventus* Gray, *A. salmonis* Jones, *A. scaphoides* Jones, *A. sinuatus* Piper, *A. spaldingii* Gray, *A. speirocarpus* Gray, *A. stenophyllus* T. & G., *A. succumbens* Dougl., *A. tegetarioides* Jones, *A. toanus* Jones, *A. tweedyi* Canby, *A. umbraticus* Sheld., *Lathyrus lanszwertii* Kell., *L. pauciflorus* Fern., *L. rigidus* White, *Lupinus caudatus* Kell., *L. holosericeus* Nutt., *L. laxiflorus* Dougl., *L. sabinii* Dougl., *L. saxosus* Howell, *L. wyethii* Wats., *Oxytropis lagopus* Nutt., *Petalostemon ornatum* Dougl., *Trifolium gymnocarpon* Nutt., *T. macrocephalum* Pursh, and *T. thompsonii* Morton.

Malvaceae: *Iliamna longisepala* (Torr.) Wiggins, *Sidalcea neomexicana* Gray, *S. oregana* (Nutt.) Gray, *Sphaeralcea grossulariifolia* (H. & A.) Rydb., and *S. munroana* (Dougl.) Spach.

Violaceae: *Viola beckwithii* T. & G. and *V. trinervata* Howell.

Loasaceae: *Mentzelia albicaulis* Dougl., *M. dispersa* Wats., and *M. laevicaulis* (Dougl.) T. & G.

Cactaceae: *Pediocactus simpsonii* (Engelm.) Britt. & Rose.

Onagraceae: *Oenethera alyssoides* H. & A., *O. andina* Nutt., *O. boothii* Dougl., *O. claviformis* Torr. & Frem., *O. deltoides* Torr. & Frem., *O. minor* (Nels.) Munz, *O. palmeri* Wats., *O. scapoidea* Nutt., and *O. tanacetifolia* T. & G.

Umbelliferae: *Lomatium canbyi* Coult. & Rose, *L. farinosum* (Hook.) Coult. & Rose, *L. gormanii* (Howell) Coult. & Rose, *L. hambleniae* Math. & Const., *L. nudicaule* (Pursh) Coult. & Rose, *L. watsonii* Coult. & Rose, and *Tauschia hooveri* Math. & Const.

Gentianaceae: *Frasera montana* Mulford.

Polemoniaceae: *Gilia minutiflora* Benth., *Gymnosteris nudicaulis* (H. & A.) Greene, *G. parvula* Heller, *Linanthus pharnaceoides* (Benth.) Greene, *Phlox aculeata* Nels., and *P. caespitosa* Nutt.

Hydrophyllaceae: *Hesperochiron californicus* (Benth.) Wats., *Nama aretioides* (H. & A.) Brand, *N. densum* Lemmon, and *Phacelia bicolor* Torr.

Boraginaceae: *P. glandulifera* Piper, *Cryptantha scoparia* Nels., *C. simulans* Greene, *Hackelia arida* (Piper) Johnst., *H. ciliata* (Dougl.) Johnst., *H. patens* (Nutt.) Johnst., *Pectocarya setosa* Gray, and *Plagiobothrys harknessii* (Greene) Nels & Macbr.

Scrophulariaceae: *Castilleja angustifolia* (Nutt.) Don, *C. cervina* Greenm., *C. chromosa* Nels., *C. exilis* Nels., *C. flava* Wats., *C. inverta* (Nels. & Macbr.) Pennell & Ownbey, *C. linariifolia* Benth., *C. longispica* Nels., *C. lutescens* (Greenm.) Rydb., *C. oresbia* Greenm., *C. pallescens* (Gray) Greenm., *C. rustica* Piper, *C. thompsonii* Pennell, *C. xanthotricha* Pennell, *Cordylanthus capitatus* Nutt., *C. ramosus* Nutt., *Mimulus cusickii* (Greene) Piper, *Orthocarpus barbatus* Cotton, *Pentstemon acuminatus* Dougl., *P. barrettiae* Gray, *P. cinicola* Keck, *P. cusickii* Gray, *P. cyaneus* Pennell, *P. gairdneri* Hook., *P. humilis* Nutt., *P. laetus* Gray, *P. lemhiensis* (Keck) Keck & Cronq., *P. peckii* Pennell, *P. pumilus* Nutt., *P. radicosus* Nels., *P. rydbergii* Nels., *P. seorsus* (Nels.) Keck, and *P. speciosus* Dougl.

Orobanchaceae: *Orobanche californica* S. & S.

Compositae: *Antennaria geyeri* Gray, *Artemisia tridentata* Nutt., *A. tripartita* Rydb., *Brickellia microphylla* (Nutt.) Gray, *B. oblongifolia* Nutt., *Cirsium magnificum* (Nels.) Petr., *C. utahense* Petr., *Eatonella nivea* (Eat.) Gray, *Erigeron aphanactis* (Gray) Greene, *E. chrysopsidis* Gray, *E. linearis* (Hook.) Piper, *E. piperianus* Cronq., *E. poliospermus* Gray, *Haplopappus stenophyllus* Gray, *Madia minima* (Gray) Keck, *Rigiopappus leptocladus* Gray, *Stephanomeria exigua* Nutt., and *S. lactucina* Gray.

Californian

A distinctive element in the flora of southwestern British Columbia occupies the so-called "Mediterranean" climatic portion of Southern Vancouver Island, the islands of the southern Strait of Georgia and the headlands of the adjacent mainland. The species occupy sites that are edaphically similar to those occupied by the same taxa further south to California in more conspicuously Mediterranean climates, and where they are more widespread. All species are restricted to west of the Cascade Mountains, occupy drier sites, but are not maritime. This element possibly extended its range northward from California or Oregon to southern British Columbia during the Hypsithermal Interval and fragments persist only in edaphically suitable sites although the general climate of the region is unfavourable.

It is equally possible that the species have entered the region by expanding their range stepwise via the available edaphically suitable sites, and no Hypsithermal Interval need be involved as an initiating cause. The element is conspicuous both in the bryoflora and vascular flora and is represented by both western North American endemics and by species of wider world distribution, but whose restriction is essentially to Mediterranean climates. This element is discussed briefly by Schofield (1965; 1968a; 1968b), and Ireland and Schofield (1967).

Hepatics: *Fossombronia longiseta* Aust. and *Frullania californica* (Aust.) Evans.

Hornworts: *Anthoceros hallii* Aust.

Mosses: *Fissidens ventricosus* Lesq., *Ditrichum ambiguum* Best, *Pleuridium bolanderi* Müll., *Timmiella crassinervis* (Hampe) Koch, *Tortula amplexa* (Lesq.) Steere, *T. bolanderi* (Lesq.) Howe, *Physcomitrium megalocarpum* Kindb., *Ptychomitrium gardneri* Lesq., *Orthotrichum papillosum* Hampe, *Pseudobraunia californica* (Lesq.) Broth., *Alsia californica* (Hook. & Arnott.) Sull., *Dendroalsia abietina* (Hook.) Britt., *Bestia vancouveriensis* (Kindb.) Wijk. & Marg., *Isothecium cristatum* (Hampe) Robins., *Homalothecium nuttallii* (Wils.) Jaeg. & Sauerb., *H. pinnatifidum* (Sull. & Lesq.) Lawt., and *H. arenarium* (Lesq.) Lawt.

Vascular Plants: *Carex brevicaulis* Mack., *Juncus bolanderi* Engelm., *Brodiaea congesta* Smith, *Allium crenulatum* Wieg., *Disporum smithii* (Hook.) Piper, *Erythronium oreganum* Appleg., *E. revolutum* Smith, *Sisyrinchium douglasii* Dietr., *Habenaria elegans* Lindl., *Poa confinis* Vasey, *Quercus garryana* Dougl., *Montia diffusa* (Nutt.) Greene, *Delphinium menziesii* D.C., *Ranunculus lobbii* (Hiern) Gray, *Berberis nervosa* Pursh, *Meconella oregana* Nutt., *Corydalis scouleri* Hook., *Ribes sanguineum* Pursh, *Rosa pisocarpa* Gray, *Lotus micranthus* Benth., *Lupinus bicolor* Lindl., *Trifolium oliganthum* Steud., *Rhus diversiloba* T. & G., *Viola howellii* Gray, *V. sempervirens* Greene, *Clarkia amoena* (Lehm.) Nels. & Macbr., *Lomatium utriculatum* (Nutt.) Coult. & Rose, *Arbutus menziesii* Pursh, *Arctostaphylos columbiana* Piper, *Vaccinium ovatum* Pursh, *Dodecatheon hendersonii* Gray, *Navarretia squarrosa* (Esch.) H. & A., *Hydrophyllum tenuipes* Heller, *Amsinckia spectabilis* F. & M., *Castilleja levisecta* Greenm., *Mimulus alsinoides* Dougl., *Orthocarpus attenuatus* Gray, *O. pusillus* Benth., *Galium cymosum* Wieg., *Plectritis congesta* (Lindl.) D.C., *Valeriana scouleri* Rydb., *Balsamorhiza deltoidea* Nutt., *Madia madioides* (Nutt.) Greene, *Microseris bigelovii* (Gray) Schultz-Bip., and *Senecio macounii* Greene.

Other vascular plants, probably of the same element, extend northward to the Puget Sound area in Washington, and occur southward to California between the coastal mountains and the Cascades. The following are representative: *Castanopsis chrysophylla* (Dougl.) D.C., *Are-*

naria paludicola Robins., *Anemone deltoidea* Hook., *Vancouveria hexandra* (Hook.) Morr. & Dec., *Lupinus albicaulis* Dougl., and *Trifolium gracilentum* T. & G.

Other elements, representing the same general distribution, extend as far north as the Columbia Gorge, thence southward into California. Still others have a restricted distribution in central Oregon: *Brodiaea hendersonii* Wats., *Pleuropogon oregonus* Chase, *Delphinium leucophaeum* Greene, *Isopyrum hallii* Gray, *Stanleya confertifolia* (Robins.) Howell, *Sidalcea campestris* Greene, *Lomatium bradshawii* (Rose) Math. & Const., and *L. hallii* (Wats.) Coult. & Rose.

Maritime

A number of species are confined to the sea-coast, mainly to sandy shores, the latter elements having been discussed by Cooper (1936):

Polypodium scouleri Hook. & Grev., *Juncus leseurii* Bol., *Agrostis longiligula* Hitchc., *A. pallens* Trin., *Calamagrostis crassiglumis* Thurb., *C. nutkaensis* (Presl) Steud., *Poa confinis* Vasey, *P. howellii* Vasey & Scribn., *P. macrantha* Vasey, *P. pachypholis* Piper, *Salix hookeriana* Barr., *Abronia latifolia* Eschsch., *A. umbellata* Lam., *Sagina crassicaulis* Wats., *Spergularia macrotheca* (Hornem.) Heynh., *Thelypodium lasiophyllum* (H. & A.) Greene, *Sedum spathulifolium* Hook., *Saxifraga marshallii* Greene, *Filipendula occidentalis* (Wats.) Howell, *Potentilla pacifica* Howell, *Sanguisorba menziesii* Rydb., *Lathyrus littoralis* (Nutt.) Endl., *Lupinus littoralis* Dougl., *Vicia gigantea* Hook., *Sidalcea hendersonii* Wats., *S. hirtipes* Hitchc., *Angelica hendersonii* Coult. & Rose, *Conioselinum pacificum* (Wats.) Coult & Rose, *Lilaeopsis occidentalis* Coult. & Rose, *Sanicula arctopoides* H. & A., *S. bipinnatifida* Dougl., *Garrya elliptica* Dougl., *Romanzoffia tracyi* Jeps., *Castilleja litoralis* Pennell, *Orthocarpus castillejoides* Benth., *Boschniackia hookeri* Walpers, *Plantago macrocarpa* C. & S., *Lasthenia minor* (D.C.) Ornduff, *Erigeron glaucus* Ker, *Ambrosia chamissonis* (Less.) Greene, *Jaumea carnosa* (Less.) Gray, and *Senecio bolanderi* Gray.

All of these species are not equally widespread, *Poa pachypholis* being restricted to the type locality. Others extend from California to Alaska: *Calamagrostis nutkatensis, Sagina crassicaulis, Pontentilla pacifica, Vicia gigantea, Conioselinum pacificum,* and *Plantago macrocarpa.* Still others extend from southern British Columbia to California: *Salix hookeriana, Abronia latifolia, Spergularia macrantha, Sidalcea hendersonii,* and *Sanicula arctopoides,* etc. A number extend from Oregon to California: *Saxifraga marshallii, Garrya elliptica, Castilleja litoralis, Erigeron glaucus,* and *Senecio bolanderi.*

Alaska and Yukon

A considerable portion of Alaska and Yukon escaped glaciation during the Pleistocene and served as a refugium for plants. Hultén (1937;

1968) and Porsild (1951; 1966) have been the principal contributors to the knowledge of this flora and Hultén (1937; 1968) in particular, has discussed history of the flora. Although many species have expanded their ranges well beyond the boundaries of Alaska and Yukon, many others continue to be restricted to areas near the refugia.

Steere has done considerable bryological field work in Alaska and has discussed this in various papers (Steere, 1938; 1958a; 1959, Schuster & Steere, 1968) and has contributed most of the information concerning Alaskan bryophyte endemics but many of his data remain unpublished. Persson (1946a; 1946b; 1947; 1949, 1952a; 1946b; 1962; 1968) has contributed richly to the knowledge of the bryoflora of the region. Although his data have yielded no new information concerning the endemics, his detailed discussions have considerably clarified the bryogeography. Other publications concerning the bryophytes of Alaska are Evans (1900; 1901; 1914), Howe (1901), Williams (1901; 1903), Cardot and Thériot (1902), Cardot (1906), Holzinger and Frye (1921), Bartram (1938), Clark and Frye (1942; 1946; 1948), Harvill (1947; 1950), Stair (1947; 1948), Thomas (1952), Sherrard (1955; 1957), Ando, Persson and Sherrard (1957), Steere and Schofield (1956), Persson and Gjaervoll (1957; 1961), Persson and Weber (1958), Schuster and Steere (1958), Iwatsuki and Sharp (1967; 1968) and Hattori and Sharp (1968). The most complete bryogeographic summaries are by Evans (1914), Persson (1949) and Steere (1953; 1965).

Among the bryophytes the *Hygrolejeunea* has closest affinities with tropical species, the *Pterigoneurum* is largely a genus of arid regions, the *Frullania* is doubtfully distinct from the widely distributed North American endemic *F. bolanderi,* and the *Trichodon,* of close affinity with a circumboreal species, is known from a single collection and is therefore not well understood. The *Oligotrichum* is clearly distinct, and is not closely related to any western North American species.

Hepatics: *Frullania chilcootensis* Steph., *Hygrolejeunea alaskana* Schuster & Steere.

Mosses: *Oligotrichum falcatum* Steere, *Trichodon borealis* Williams, and *Pterigoneurum arcticum* Steere.

Vascular Plants.

Poaceae: *Arctagrostis poaeoides* Nash, *Poa eyerdamii* Hult., *Puccinellia triflora* Swallen, *P. interior* Sorens., and *Agrophyron yukonense* Scribn. & Merr.

Cyperaceae: *Carex jacob-peteri* Hult. and *C. microchaeta* Holm.

Salicaceae: *Salix setchelliana* Ball, *S. stolonifera* Cov., *S. arctolitoralis* Hult., and *S. athabascensis* Raup.

Betulaceae: *Betula kenaica* Evans.

Polygonaceae: *Polygonum alaskanum* (Small) Wright.

Chenopodiaceae: *Atriplex drymarioides* Standl. and *A. alaskensis* Wats.

Portulacaceae: *Claytonia bostockii* Porsild and *C. scammaniana* Hult.

Caryophyllaceae: *Stellaria alaskana* Hult. and *Melandrium macrospermum* Porsild.

Ranunculaceae: *Ranunculus turneri* Greene.

Papaveraceae: *Papaver walpolei* Porsild.

Cruciferae: *Thlaspi arcticum* Porsild, *Draba exalata* Ekman, *D. maxima* Hult., *D. olgiviensis* Hult., *Smelowskia pyriformis* Drury & Rollins, *S. borealis* (Greene) Drury & Rollins, *Erysimum angustatum* Rydb., and *Braya bartlettiana* Jordal.

Saxifragaceae: *Boykinia richardsonii* (Hook.) Gray, *Saxifraga spicata* Don, and *S. reflexa* Hook.

Leguminosae: *Lupinus kuschei* Eastw., *Astragalus polaris* Benth., *A. nutzotinensis* Rousseau, *A. williamsii* Rydb., *Oxytropis kokrinensis* Porsild, *O. scammaniana* Hult., *O. huddlesonii* Porsild, *O. glaberrima* Hult., *O. kobukensis* Welsh, *O. koyukukensis* Porsild, and *O. sheldonensis* Porsild.

Umbelliferae: *Podistera yukonensis* Math. & Const.

Primulaceae: *Douglasia arctica* Hook., *D. gormani* Constance, and *Androsace alaskana* Cov. & Standl.

Gentianaceae: *Gentiana platypetala* Griseb.

Hydrophyllaceae: *Phacelia mollis* Macbr., *Romanzoffia sitchensis* Bong., and *R. unalaschensis* Cham.

Boraginaceae: *Eritrichium splendens* Kearney and *Mertensia drummondii* (Lehm.) Don.

Scrophulariaceae: *Pentstemon gormani* Greene, *Synthyris borealis* Pennell, *Castilleja unalaschcensis* (C. & S.) Malte, *C. hyetophila* Pennell, *C. chrymactis* Pennell, *C. yukonis* Pennell, *C. annua* Pennell, *C. villosissima* Penell, and *Rhinanthus arcticus* (Sterneck) Pennell.

Campanulaceae: *Campanula aurita* Greene.

Compositae: *Haplopappus macleanii* Brandegee, *Aster yukonensis* Cronq., *Erigeron purpuratus* Greene, *E. hyperboreus* Greene, *Antennaria pallida* Nels., *A. stolonifera* Porsild, *A. alborosea* Porsild & Porsild, *A. leuchippi* Porsild, *Artemisia alaskana* Rydb., *Senecio yukonensis* Porsild, *S. hyperborealis* Grumm., *S. sheldonensis* Porsild, *Saussurea angustifolia* (Willd.) D.C., and *Taraxacum carneocoloratum* Nels.

Most of the species are, predictably, of polymorphic circumpolar genera, but the presence of a species of *Boykinia* suggests that it is a Tertiary relict (Hultén, 1968). The endemics are most richly represented in alpine and subalpine habitats, but a number are maritime and others in forests, testifying to the diversity or habitats available in the Pleistocene refugia.

Aleutian Islands

Tatewaki (1963) has suggested "Hultenia" to designate the phytogeographic area encompassed by the Aleutian and Commander Islands. He indicates that both flora and vegetation merit the recognition of this area and gives a detailed analysis of the floristic composition and affinities. He notes a "marked difference between the (flora of) the Commander Islands and the Aleutian Islands. There is a decided floristic depression between the first and second district." The Commander Islands flora is clearly of the Eastern Asiatic floristic Region while the Aleutian Islands are of the North American floristic Region. He terms the line between these "Tatewaki's Line." This arch of islands is envisioned as a migratory route, serving as a stepping stone corridor for the expansion of Asiatic species eastward and North American species westward. Ample floristic evidence is presented to support this concept.

No bryophyte endemics have yet been reported for the area although unpublished results of Z. Iwatsuki and A. J. Sharp suggest that such species may be present.

Except for the *Polystichum* all vascular plants are derivative species of arctic and alpine areas. The *Polystichum* has its affinities with Himalayan and Chinese species. The remaining species may be relatively "young," belonging to notoriously polymorphic genera in some cases to *Taraxacum, Draba,* and *Artemisia.*

Tatewaki notes the following: *Polystichum aleuticum* Christens., *Calamagrostis bracteolata* Vassiliev, *Elymus aleuticus* Hult., *Cerastium aleuticum* Hult., *Draba aleutica* Ekman, *Artemisia aleutica* Hult., *Taraxacum chromocarpum* Hagl., *T. eyerdamii* Hagl., and *T. oncophorum* Hagl.

Although noted for the Aleutian Islands by Tatewaki, Hultén (1968) does not indicate the presence of the *Elymus* or the *Taraxacum* species. In this flora however, the following species are essentially restricted to the Aleutian Islands, although in all cases these species extend also to the Alaskan mainland as well: *Poa hispidula* Vasey, *Poa turneri* Scribn., *Salix cyclophylla* Rydb., and *Gentiana aleutica* C. & S.

The Queen Charlotte Islands

The Queen Charlotte Islands of British Columbia have served as a refugium for a number of species, both endemics and disjunct fragments of a flora of pre-glacial times. The higher elevations, at least, escaped glaciation, and the affinities of many bryophytes and vascular plants imply that they are pre-Pleistocene relicts. Calder and Taylor (1968) have thoroughly treated the vascular flora and Persson (1958), and Schofield (1962; 1965; 1966b; 1968a; 1968b) have provided preliminary notes concerning the bryophytes.

Among the bryophytes only the endemic *Acanthocladium carlottae* Schof. has been described although there remain undescribed species of *Seligeria, Brotherella, Acanthocladium,* and *Mastopoma* (?). The latter three genera suggest a montane flora of a subtropical latitude, the relationship of each of the species being largely with the Malaysian area, and suggesting great antiquity. There is a rich representation in the Islands of species showing affinities either with East Asia or Western Europe. These are discussed later under these disjunct elements.

The endemic vascular plants are confined largely to higher elevations or to habitats of lower elevations on the flanks of the mountains. The bryophyte disjuncts and endemics show a similar restriction. In all cases relationships of the undescribed taxa is with taxa of distant unglaciated areas rather than with those of adjacent glaciated areas, emphasizing that the species are probably pre-glacial relicts.

Vascular Plants: *Isopyrum savilei* Calder & Taylor, *Saxifraga taylori* Calder & Savile, *Geum schofieldii* Calder & Taylor, *Ligusticum calderi* Math. & Const., and *Senecio newcombei* Greene.

Columbia River Gorge

Piper (1906) noted that the gorge of the Columbia River and valleys of adjacent tributaries served as an area of endemism. He noted that 16 species were endemic to the gorge. Since that time many have either been found to be more widespread or have slipped into the synonymy of more widespread species. Detling (1958), in discussing the flora of the gorge noted 7 species endemic to the gorge. *Douglasia laevigata* Gray is more widespread, and thus should be excluded. Perusal of Hitchcock, *et al.* (1955–1969) indicates that 17 species are indeed endemic to the Columbia River Gorge, although a number do extend sometimes into the Wilamette Valley or into some of the tributary watercourses of the Columbia River.

Detling (1958) suggests that the gorge served as a corridor of migration for both lowland and highland species, supporting this concept by noting disjunctions of species in the gorge and in these other areas. He suggests that the lowland migrations probably occurred during the Hypsithermal and that the montane elements migrated downwards from higher elevations during the Pleistocene refrigeration. The endemics, fragments of these floras, are suggested to be relics, restricted in their range by rather narrow environmental tolerance. Unfortunately no experimental evidence is available to support or refute this hypothesis.

A single bryophyte has been noted as endemic to the Columbia River Gorge (Hermann & Lawton, 1968): *Desmatodon columbianus* Hermann & Lawt.

Vascular Plants: *Agrostis howellii* Scribn., *Calamagrostis howellii* Vasey, *Poa leibergii* Scribn., *Allium robbinsii* Henderson, *A. pleianthum* Wats., *Salix fluviatilis* Nutt., *Bolandra oregana* Wats., *Sullivantia oregana* Wats., *Astragalus diaphanus* Dougl., *Eryngium petiolatum* Hook., *Lomatium columbianum* Math. & Const., *L. laevigatum* (Nutt.) Coult. & Rose, *Cryptantha leucophaea* (Dougl.) Pays., *Pentstemon barrettae* Gray, *Erigeron howellii* Gray, *E. oreganus* Gray, and *Hieracium longiberbe* Howell.

BOREAL

The Boreal flora is composed of four elements of particular significance: circumboreal, circumboreal maritime, boreal American, and circumboreal through anthropogenic introduction. In the boreal bryoflora the North American vegetation is dominated by circumboreal species, with remarkably few endemic taxa while in the vascular flora the conspicuous elements of the vegetation are endemic to North America, thus all tree species and most shrubby species are endemic to North America (exception: *Alnus crispa*). Many circumboreal bryophytes and herbaceous vascular plants are also conspicuous elements in the Arctic flora. Many of these species extend their ranges southward in the mountains as far as Arizona, and, in some cases, into Mexico. The woody species, on the other hand, are largely supplanted southward by western North American endemics, even in the Northern Rocky Mountains.

Circumboreal

Hepatics: *Riccardia sinuata* (Dick.) Trevis., *R. pinguis* (L.) Gray, *Pellia endiviifolia* (Dicks.) Dumort., *P. neesiana* (Gottsche.) Limpr., *P. epiphylla* (L.) Lindb., *Metzgeria conjugata* Lindb., *Moerckia flotoviana* (Nees.) Schiffn., *Blasia pusilla* L., *Fossombronia dumortieri* (Hüb. & Genth.) Lindb., *Ptilidium ciliare* (L.) Hampe, *P. pulcherrimum* (Web.) Hampe, *Lepidozia reptans* (L.) Dumort., *Bazzania trilobata* (L.) Gray, *B. tricrenata* (Wg.) Trevis., *Calypogeia neesiana* (Mass. & Carest.) Müll., *C. sphagnicola* (Arn. & Perss.) Warnst. & Loeske, *C. trichomanis* (L.) Corda, *C. fissa* (L.) Raddi, *C. suecica* (Arn. & Perss.) Müll., *Cephaloziella elachista* (Jack.) Schiffn., *C. hampeana* (Nees.) Schiffn., *C. rubella* (Nees.) Douin, *Anastrophyllum michauxii* (Web.) Buch., *Barbilophozia barbata* (Schmid.) Loeske, *B. lycopodioides* (Wallr.) Loeske, *Gymnocolea inflata* (Huds.) Dumort., *Jamesoniella autumnalis* (D.C.) Steph., *Jungermannia lanceolata* Schrad., *J. pumila* With., *J. atrovirens* Dumort., *J. tristis* Nees., *J. sphaerocarpa* Hook., *Leiocolea heterocolpos* (Thed.) Buch., *L. gillmanii* (Aust.) Evans, *Lophozia excisa* (Dicks.) Dumort., *L. marchica* (Nees.) Steph., *L. incisa* (Schrad.) Dumort., *Mylia taylori* (Hook.) Gray, *M. anomala* (Hook.) Gray, *Nardia scalaris* (Schrad.) Gray, *N. geoscyphus* (DeNot.) Lindb., *Orthocaulis kunzeanus* (Hüb.) Buch., *Plectocolea obovata* (Nees.) Mitt., *P. hyalina* (Lyell) Mitt., *Sphenolobus minutus* (Crantz.) Steph., *Lophocolea heterophylla* (Schrad.) Dumort., *L. minor* Nees., *L. cuspidata* (Nees.) Limpr., *Chiloscyphus polyanthos* (L.) Corda, *Harpanthus scutatus* (Web. & Mohr.) Spr., *Geocalyx graveolens* (Schrad.) Nees., *Plagiochila asplenioides* (L.) Dumort., *Diplophyllum taxifolium* (Wahl.) Dumort., *D. albicans* (L.) Dumort., *Scapania irrigua* (Nees.) Dumort., *S. paludicola* Loeske & Müll., *S. umbrosa* (Schrad.) Dumort., *S. undulata* (L.) Dumort., *Cephalozia bicuspidata* (L.) Dumort., *C. connivens* (Dicks.) Spr., *C. catenulata* (Hüb.) Lindb., *C.*

media Lindb., *C. macounii* Aust., *Cladopodiella fluitans* (Nees.) Spr., *Odontoschisma denudatum* (Nees) Dumort., *O. elongatum* (Lindb.) Evans, *Gymnomitrion concinnatum* Corda, *Marsupella sphacelata* (Gies.) Lindb., *M. sparsifolia* (Lindb.) Dumort., *M. emarginata* (Ehrh.) Dumort., *Radula complanata* (L.) Dumort., *Porella platyphylla* (L.) Lindb., *Preissia quadrata* (Scop.) Nees., *Conocephalum conicum* (L.) Dumort., *Reboulia hemispherica* (L.) Raddi, *Riccia sorocarpa* Bisch., *R. crystallina* L., *R. fluitans* L., and *Ricciocarpus natans* (L.) Corda.

Mosses: *Sphagnum nemoreum* Scop., *S. rubellum* Wils., *S. fimbriatum* Wils., *S. fuscum* (Schimp.) Klinggr., *S. girgensohnii* Russ., *S. papillosum* Lindb., *S. squarrosum* Crome., *Andreaea rupestris* Hedw., *Fissidens adianthoides* Hedw., *F. bryoides* Hedw., *F. osmundioides* Hedw., *Trichodon cylindricus* (Hedw.) Schimp., *Ditrichum heteromallum* (Hedw.) Britt., *Distichium capillaceum* (Hedw.) B.S.G., *Blindia acuta* (Hedw.) B.S.G., *Trematodon ambiguus* (Hedw.) Hornsch., *Dicranella heteromalla* (Hedw.) Schimp., *D. rufescens* (With.) Schimp., *D. varia* (Hedw.) Schimp., *Dicranodontium denudatum* (Brid.) Britt., *Amphidium lapponicum* (Hedw.) Schimp., *Dichondontium pellucidum* (Hedw.) Schimp., *Oncophorus wahlenbergii* Brid., *Kiaeria starkei* (Web. & Mohr.) Hag., *Dicranum elongatum* Schleich., *D. fuscescens* Turn., *D. scoparium* Hedw., *Encalypta ciliata* Hedw., *E. vulgaris* Hedw., *Tortella fragilis* (Hook.) Limpr., *T. tortuosa* (Hedw.) Limpr., *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen, *Barbula convoluta* Hedw., *B. unguiculata* Hedw., *Pottia heimii* (Hedw.) Fürnr., *Tortula mucronifolia* Schwaegr., *T. norvegica* (Web.) Wahlenb., *T. ruralis* (Hedw.) Gaertn., Mey., & Scherb., *Grimmia alpicola* Hedw., *G. apocarpa* Hedw., *Racomitrium aciculare* (Hedw.) Brid., *R. canescens* (Hedw.) Brid., *R. lanuginosum* (Hedw.) Brid., *Tayloria lingulata* (Dicks.) Lindb., *Tetraplodon angustatus* (Hedw.) B.S.G., *Splachnum ampullaceum* Hedw., *Tetraphis pellucida* Hedw., *Pohlia nutans* (Hedw.) Lindb., *P. wahlenbergii* (Web. & Mohr.) Andr., *Leptobryum pyriforme* (Hedw.) Wils., *Bryum pallens* Sw., *Plagiomnium affine* (Bland.) Koponen, *Mnium spinulosum* (Voit.) Schwaegr., *Aulacomnium palustre* (Hedw.) Schwaegr., *Meesea trifaria* Crum, Steere, & Anderson, *Paludella squarrosa* (Hedw.) Brid., *Catascopium nigritum* (Hedw.) Brid., *Plagiopus oederiana* (Sw.) Limpr., *Philonotis fontana* (Hedw.) Brid., *Timmia austriaca* Hedw., *Orthotrichum obtusifolium* Brid., *O. speciosum* Nees., *Ulota phyllantha* Brid., *Fontinalis antipyretica* Hedw., *Climacium dendroides* (Hedw.) Web. & Mohr., *Neckera pennata* Hedw., *Myurella julacea* (Schwaegr.) B.S.G., *Leskea polycarpa* Hedw., *Thuidium recognitum* (Hedw.) Lindb., *Abietinella abietina* (Hedw.) Fleisch., *Cratoneuron filicinum* (Hedw.) Spruce, *Campylium stellatum* (Hedw.) Jens., *Leptodictyum riparium* (Hedw.) Warnst., *Amblystegium serpens* (Hedw.) B.S.G., *Drepanocladus aduncus* (Hedw.) Warnst., *D. uncinatus* (Hedw.) Warnst., *Hygrohypnum luridum* (Hedw.) Jenn., *Calliergon cordifolium* (Hedw.) Kindb., *Scor-*

pidium scorpioides (Hedw.) Limpr., *Tomenthypnum nitens* (Hedw.) Loeske, *Brachythecium albicans* (Hedw.) B.S.G., *B. plumosum* (Hedw.) B.S.G., *Eurhynchium praelongum* (Hedw.) B.S.G., *E. pulchellum* (Hedw.) Jenn., *Pterigynandrum filiforme* Hedw., *Orthothecium chryseum* (Schwaegr.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., *Plagiothecium denticulatum* (Hedw.) B.S.G., *Pylaisiella polyantha* (Hedw.) Grout, *Hypnum callichrom* Funck., *H. revolutum* (Mitt.) Lindb., *Isopterygium pulchellum* (Hedw.) Jaeg. & Sauerb., *Ptilium crista-castrensis* (Hedw.) DeNot., *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *Hylocomium splendens* (Hedw.) B.S.G., *Atrichum undulatum* (Hedw.) Beauv., *Pogonatum alpinum* (Hedw.) Rohl., *P. urnigerum* (Hedw.) Beauv., and *Polytrichum piliferum* Hedw.

Vascular Plants.

Lycopodiaceae: *Lycopodium annotinum* L. and *L. clavatum* L.

Selaginellaceae: *Selaginella selaginioides* (L.) Link.

Equisetaceae: *Equisetum variegatum* Schleich., *E. fluviatile* L., and *E. arvense* L.

Ophioglossaceae: *Botrychium lunaria* (L.) Sw.

Polypodiaceae: *Pteridium aquilinum* (L.) Kuhn, *Thelypteris phegopteris* (L.) Slosson, *Athyrium filix-femina* (L.) Roth., *Cystoperis fragilis* (L.) Bernh., *Woodsia ilvensis* (L.) R.Br., *Dryopteris dilatata* (Hoffm.) Gray, and *Gymnocarpium dryopteris* (L.) Newm.

Cupressaceae: *Juniperus communis* L.

Typhaceae: *Typha latifolia* L.

Sparganiaceae: *Sparganium augustifolium* Michx.

Potamogetonaceae: *Potamogeton natans* L., *P. gramineus* L., and *P. filiformis* Pers.

Scheuchzeriaceae: *Scheuchzeria palustris* L.

Poaceae: *Phalaris arundinacea* L., *Hierochloe odorata* (L.) Wahlenb., *Alopocurus aequalis* Sobol., *Cinna latifolia* (Trev.) Griseb., *Agrostis borealis* Hartm., *Calamagrostis neglecta* (Ehrh.) Gaertn., Mey., & Scherb., *Trisetum spicatum* (L.) Richter, *Beckmannia erucaeformis* (L.) Host, *Poa glauca* Vahl, *P. palustris* L., *Glyceria maxima* (Hartm.) Holmb., and *Bromus inermis* Leyss.

Cyperaceae: *Eriophorum angustifolium* Honck., *Trichophorum caespitosum* (L.) Hartm., *Eleocharis uniglumis* (Link.) Schult., *Rhynchospora alba* (L.) Vahl., *Carex pauciflora* Lightf., *C. diandra* Schrank, *C. canescens* L., *C. disperma* Dew., *C. limosa* L., and *C. rostrata* Stokes.

Araceae: *Calla palustris* L.

Juncaceae: *Juncus alpinus* Vill., *J. articulatus L.,* and *Luzula parviflora* (Ehr.) Desv.

Orchidaceae: *Cypripedium calceolus* L., *Listera cordata* (L.) R.Br., *Platanthera obtusata* (Pursh) Lindb., *Goodyera repens* (L.) R.Br., *Corrallorhiza trifida* Chatelain, and *Calypso bulbosa* (L.) Richb. f.

Salicaceae: *Salix phylicifolia* L.

Myricaceae: *Myrica gale* L.

Betulaceae: *Betula nana* L.

Polygonaceae: *Koenigia islandica* L. and *Polygonum amphibium* L.

Caryophyllaceae: *Chenopodium glaucum* L., *Stellaria longifolia* Muhl., *S. calycantha* (Ledeb.) Bong., *Cerastium arvense* L., *Sagina nodosa* (L.) Fenzl., and *Moehringia lateriflora* (L.) Fenzl.

Ceratophyllaceae: *Ceratophyllum demersum* L.

Ranunculaceae: *Caltha palustris* L., *Ranunculus trichophyllus* Chaix., and *R. sceleratus* L.

Cruciferae: *Subularia aquatica* L., *Cardamine pratensis* L., and *Arabis hirsuta* (L.) Scop.

Droseraceae: *Drosera rotundifolia* L.

Crassulaceae: *Sedum rosea* (L.) Scop.

Rosaceae: *Rubus chamaemorus* L., *Potentilla palustris* (L.) Scop., *P. fruticosa* L., and *Sanguisorba officinalis* L.

Leguminosae: *Hedysarum alpinum* L.

Linaceae: *Linum perenne* L.

Callitrichaceae: *Callitriche hermaproditica* L.

Violaceae: *Viola selkirkii* Pursh.

Onagraceae: *Epilobium angustifolium* L., *E. palustre* L., and *Circaea alpina* L.

Haloragidaceae: *Myriophyllum verticellatum* L.

Cornaceae: *Cornus suecica* L.

Ericaceae: *Pyrola secunda* L., *Moneses uniflora* (L.) Gray, *Monotropa hypopitys* L., *Empetrum nigrum* L., *Ledum palustre* L., *Andromeda polifolia* L., *Chamaedaphne calyculata* (L.) Moench., *Arctostaphylos uva-ursi* (L.) Spreng., *Vaccinium vitis-idaea* L., *V. uliginosum* L., and *Oxycoccus microcarpus* Turcz.

Primulacaceae: *Androsace septentrionalis* L., and *Lysimachia thyrsiflora* L.

Labiatae: *Scutellaria galericulata* L., *Stachys palustris* L., and *Mentha arvensis* L.

Scrophulariaceae: *Limosella aquatica* L. and *Veronica scutellata* L.

Lentibulariaceae: *Utricularia intermedia* Hayne and *U. vulgaris* L.

Rubiaceae: *Galium boreale* L. and *G. triflorum* Michx.

Caprifoliaceae: *Sambucus racemosa* L. and *Linnaea borealis* L.

Campanulaceae: *Campanula rotundifolia* L.

Compositae: *Erigeron acris* L. and *Senecio congestus* (R.Br.) D.C.

Circumboreal Maritime

No hepatics are restricted to sea-shores although several tolerate some salinity. Among the mosses only two are essentially restricted to maritime habitats, both occurring on rocks affected by salt spray: *Grimmia maritima* Turn. and *Ulota phyllantha* Brid. Other mosses are tolerant of salt spray, but are not restricted to such habitats.

Among the vascular plants are a number of obligate halophytes. In some cases these are found away from the sea-coast, but generally in saline or alkaline environments. In North America there are some exceptions, e.g., *Lathyrus maritimus* in the Great Lakes area, *Armeria maritima* in the Rocky Mountains.

Vascular Plants: *Zostera marina* L., *Ruppia spiralis* L., *Calamagrostis deschampsioides* Trin., *Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Elymus arenarius* L., *Corex glareosa* Wahlenb., *C. mackenziei* Krecz., *Stellaria humifusa* Rottb., *Honckenya peploides* (L.) Ehrh., *Cochlearia officinalis* L., *Potentilla egedii* Wormsk., *Lathyrus maritimus* L., *Hippuris tetraphylla* L. f., *Ligusticum scoticum* L., *Armeria maritima* (Mill.) Willd., *Mertensia maritima* (L.) Gray, and *Tripleurospermum phaeocephalum* (Rupr.) Pobed.

Boreal American

This element is composed of endemic species of wide distribution in northern North America. The number and vegetational importance of endemic bryophytes of this distribution pattern is not significant but the vascular plants, particularly woody species, are main components of the vegetation.

Hepatics: *Plectocolea obscura* Evans is the only species that can be placed here and even this species is uncertain, being reported from Northeastern United States and Oregon. The latter record needs verification.

Mosses: *Seligeria campylopoda* Kindb., *Grimmia dupretii* Ther., *Physcomitrium immersum* Sull., *Philonotis americana* Dism., and *Climacium americanum* Brid.

Few of these species are common, the exceptions being *Philonotis americana* and *Climacium americanum*. The others are infrequent and in rather specialized habitats.

Vascular Plants (dominant or conspicuous elements of the vegetation are designated by an asterisk).

Pinaceae: *Pinus banksiana* Lamb.,* *Larix laricina* (DuRoi) Koch.,* *Picea glauca* (Moench.) Voss.,* and *P. mariana* (Mill.) Britt., Sterns., Pogg.*

Cupressaceae: *Juniperus horizontalis* Moench.*

Sparganiaceae: *Sparganium eurycarpum* Engelm. and *S. multipedunculatum* (Morong.) Rydb.

Potamogetonaceae: *Potamogeton epihydrus* Raf. and *P. foliosus* Raf.

Alismataceae: *Sagittaria cuneata* Sheld.

Poaceae: *Oryzopsis pungens* (Torr.) Hitchc., *Muhlenbergia richardsonis* (Willd.) Trin., *M. glomerata* (Willd.) Trev., *Agrostis geminata* Trin., *Calamagrostis canadensis* (Michx.) Beauv.,* *Danthonia spicata* (L.) Beauv., *Sphenopholis intermedia* (Rydb.) Rydb., *Glyceria borealis* (Nash) Batchelder, *G. striata* (Lam.) Hitchc., *Festuca saximontana*

Rydb., *Agropyron smithii* Rydb., *A. subsecundum* (Link.) Hitchc., and *A. pauciflorum* (Schwein.) Hitchc.

Cyperaceae: *Eriophorum viridi-carinatum* (Engelm.) Fern., *Scirpus subterminalis* Torr., *S. americanus* Pers., *S. paludosus* Nels., *S. validus* Vahl.,* *S. microcarpus* Presl., *Carex leptalea* Wahlenb., *C. bebbii* Olney, *C. crawfordii* Fern., *C. aenea* Fern., *C. arcta* Boott, *C. interior* Bailey, *C. deweyana* Schwein., *C. aurea* Nutt., *C. garberi* Fern., *C. deflexa* Hornem., *C. concinna* R.Br., *C. eburnea* Brott, and *C. lanuginosa* Michx.

Juncaceae: *Juncus nodosus* L.

Liliaceae: *Smilacina racemosa* (L.) Desf. and *S. stellata* (L.) Desf.

Iridaceae: *Sisyrinchium montanum* Greene.

Orchidaceae: *Amerorchis rotundifolia* (Banks) Hult., *Platanthera orbiculata* (Pursh) Lindb., *P. dilatata* (Pursh) Lindb., *Listera convallarioides* (Sw.) Nutt., and *Corallorhiza maculata* Raf.

Salicaceae: *Populus balsamifera* L.,* *P. tremuloides* Michx.,* *Salix arctophila* Cockerell.,* *S. brachycarpa* Nutt., *S. pedicellaris* Pursh, *S. mackenzieana* Barratt, *S. myrtillifolia* Anderss., *S. candida* Flügge, and *S. interior* Rowlee.

Betulaceae: *Betula glandulosa* Michx.* and *B. papyrifera* Marsh.*

Urticaceae: *Urtica gracilis* Ait.

Santalaceae: *Geocaulon lividum* (Richards.) Fern.

Polygonaceae: *Rumex fenestratus* Greene, *Polygonum pennsylvanicum* L., and *P. achoreum* Blake.

Caryophyllaceae: *Arenaria dawsonensis* (Britt.) Mattf.

Nymphaeaceae: *Nuphar variegatum* Engelm.

Ranunculaceae: *Actaea rubra* (Ait.) Willd., *Anemone multifida* Poir., *Ranunculus abortivus* L., *R. pennsylvanicus* L. f., and, *R. macounii* Britt.

Fumariaceae: *Corydalis aurea* Willd. and *C. sempervirens* (L.) Pers.

Cruciferae: *Rorippa obtusa* (Nutt.) Britt., *Cardamine pennsylvanica* Muhl., *Draba aurea* Vahl., *Descurainia richardsonii* (Sweet) Schulz, *Arabis arenicola* (Richards.) Gelert, and *Erysimum inconspicum* (Wats.) MacM.

Saxifragaceae: *Saxifraga tricuspidata* Rottb., *Ribes oxycanthoides* L., *R. hudsonianum* Richards., and *R. glandulosum* Grauer.

Rosaceae: *Rubus pubescens* Raf., *R. arcticus* L., *Fragaria virginiana* Duchesne, *Potentilla vahliana* Lehm., *P. argentea* Pursh, and *P. pennsylvanica* L.

Leguminosae: *Oxytropis deflexa* (Pall.) D.C., *Hedysarum mackenziei* Richards. and *Vicia americana* Mühl.

Geraniaceae: *Geranium bicknellii* Britt.

Violaceae: *Viola adunca* Sm. and *V. renifolia* Gray.

Elaeagnaceae: *Shepherdia canadensis* (L.) Nutt.* and *Elaeagnus commutata* Bernh.

Onagraceae: *Epilobium leptophyllum* Raf.

Umbelliferae: *Cicuta bulbifera* L.

Ericaceae: *Ledum groenlandicum* Oeder,* *Kalmia polifolia* Wang., and *Vaccinium caespitosum* Michx.

Primulaceae: *Primula mistassinica* Michx.

Apocynaceae: *Apocynum androsaemifolium* L.

Labiatae: *Dracocephalum parviflorum* Nutt.

Scrophulariaceae: *Euphrasia disjuncta* Fern. & Wieg. and *Pedicularis groenlandica* Retz.

Rubiaceae: *Galium brandegei* Gray.

Caprifoliaceae: *Viburnum edule* (Michx.) Raf., *Symphoriocarpus albus* (L.) Blake,* and *Lonicera involucrata* (Richards.) Banks.

Compositae: *Solidago multiradiata* Ait., *S. canadensis* L., *Aster laevis* L., *A. junciformis* L., *Erigeron compositus* Pursh, *E. hyssopifolius* Michx., *E. elatus* Greene, *E. philadelphicus* L., *Antennaria pulcherrima* (Hook.) Greene, *Achillea lanulosa* Nutt., *Artemisia canadensis* Michx., *Petasites sagittatus* (Banks) Gray, *Senecio pauciflorus* Pursh, *S. pauperculus* Michx., *Taraxacum lacerum* Greene, and *Lactuca biennis* (Moench.) Fern.

Circumboreal by Anthropogenic Introduction

In the bryophytes it is rather difficult to determine anthropogenic introductions since such a high proportion of the species show a natural circumboreal distribution. Certainly the distribution of many circumboreal species have been anthropogenically expanded by destruction of competing native vascular plants and by clearing sites, but in many cases, if abandoned by man, such sites revert to a covering of vascular plant vegetation and thus bryophytes are eliminated. In cities, however, a number of presumably introduced species do persist in gardens and on stone or concrete walls, and sometimes as lawn weeds. Most of the species are also natural elements of the local flora, thus invasion of the urban sites cannot be confidently attributed to anthropogenic introduction. Among such bryophytes are:

Hepatics: *Blasia pusilla* L. and *Marchantia polymorpha* L.

Mosses: *Ceratodon purpureus* (Hedw.) Brid., *Dicranoweisia cirrata* (Hedw.) Lindb., *Barbula vinealis* Brid., *Pottia truncata* (Hedw.) Fürnr., *Tortula ruralis* Hedw., *T. muralis* Hedw., *Grimmia apocarpa* Hedw., *Funaria hygrometrica* Hedw., *Pohlia annotina* (Hedw.) Lindb., *Leptobryum pyriforme* (Hedw.) Wils., *Bryum argenteum* Hedw., *Calliergonella cuspidata* (Hedw) Loeske, *Brachythecium albicans* (Hedw.) B.S.G., *Eurhynchium praelongum* (Hedw.) B.S.G., and *Rhytidiadelphus squarrosus* (Hedw.) Warnst.

It should be noted that most of these bryophytes are common elements of the natural circumboreal flora, but their invasion of anthropogenic environments has considerably expanded their local ranges. The vascular plants, on the other hand, are mainly accidental introductions and in many cases are noxious weeds of arable land. Many species were introduced first in eastern North America and have expanded their ranges westward with the activity of man. Many were introduced in ship's ballast, others with seeds of domestic crops and a number have escaped from cultivation.

Vascular Plants

Poaceae: *Anthoxanthum odoratum* L., *Phleum pratense* L., *Alopecurus pratensis* L., *Agrostis tenuis* Sibth., *A. stolonifera* L., *Holcus lanatus* L., *Avena fatua* L., *A. sativa* L., *Arrhenatherum elatius* (L.) Presl & Presl, *Dactylis glomerata* L., *Poa trivialis* L., *P. pratensis* L., *P. annua* L., *Festuca arundinacea* Schreb., *Bromus tectorum* L., *B. secalinus* L., *Lolium perenne* L., *L. tementulum* L., *Agropyron pecteniforme* Roem. & Schult., and *A. repens* (L.) Beauv.

Urticaceae: *Urtica urens* L.

Polygonaceae: *Rumex acetosella* L., *R. acetosa* L., *R. obtusifolius* L., *R. crispus* L., *Polygonum convolvulus* L., *P. persicaria* L., *P. hydropiper* L., and *P. aviculare* L.

Chenopodiaceae: *Chenopodium rubrum* L. and *C. album* L.

Caryophyllaceae: *Stellaria media* (L.) Vill., *Spergularia rubra* (L.) Presl & Presl, *Agrostemma githago* L., *Melandrium noctiflorum* (L.) Fries, and *Vaccaria pyramidata* Medic.

Ranunculaceae: *Ranunculus repens* L. and *R. acris* L.

Papaveraceae: *Papaver rhoeas* L.

Cruciferae: *Lepidium sativum* L., *Thlaspi arvense* L., *Sisyrinchium officinale* (L.) Scop., *S. altissimum* L., *Sinapsis arvensis* L., *Brassica juncea* (L.) Czern., *B. rapa* L., *Raphanus sativus* L., *Rorippa nasturtium-aquaticum* (L.) Hayek., *Capsella bursa-pastoris* (L.) Medic., *Neslia paniculata* (L.) Desv., *Descurainia sophia* (L.) Prantl, *Turritis glabra* L., *Erysimum cheiranthoides* L., andd *Hesperis matronalis* L.

Leguminosae: *Medicago sativa* L., *M. lupulina* L., *Melilotus officinalis* (L.) Lam., *M. albus* Desv., *Trifolium hybridum* L., *T. repens* L., *T. pratense* L., *Vicia angustifolia* (L.) Reichard., and *V. cracca* L.

Gerianaceae: *Geranium robertianum* L.

Umbelliferae: *Pastinaca sativa* L.

Boraginaceae: *Lappula myosotis* Moench. and *Myosotis palustris* L.

Labiatae: *Nepeta cataria* L., *Glechoma hederacea* L., and *Galeopsis bifida* Boenn.

Scrophulariaceae: *Linaria vulgaris* Mill., *Veronica anagallis-aquatica* L., *V. persica* Poir., and *V. arvensis* L.

Plantaginaceae: *Plantago lanceolata* L. and *P. major* L.

Compositae: *Gnaphalium uliginosum* L., *Anthemis cotula* L., *Matricaria matricarioides* (Less.) Porter, *Tripleurospermum inodorum* (L.) Schultz-Bip., *Chrysanthemum vulgare* (L.) Bernh., *Senecio vulgaris* L., *Cirsium arvense* (L.) Scop., *C. vulgare* (Savi) Ten., *Leontodon autumnalis* L., *Taraxacum officinale* Weber, and *Crepis tectorum* L.

CIRCUMARCTIC

A number of species are restricted to arctic regions, rarely extending into the subarctic. Steere (1953; 1965) has discussed the bryogeographic element and Porsild (1957) has noted vascular plants of this distributional type.

Hepatics: *Mesoptychia sahlbergii* (Lindb., & Arn.) Evans, *Lophozia latifolia* Schuster, and *Plagiochila arctica* Bryhn. & Kaalas.

Musci: *Psilopilum laevigatum* (Wahlenb.) Limpr., *Distichium hagenii* Ryan, *Blindia polaris* (Berggr.) Hag., *Haplodon wormskjoldii* (Hornem.) R.Br., *Tetraplodon paradoxus* (R.Br.) Hagen, *Pohlia crudoides* (Sull. & Lesq.) Broth., *Bryum wrightii* Sull., *Cyrtomnium hymenophyllum* (B.S.G.) Holmen, *Cinclidium latifolium* Lindb., *C. subrotundum* Lindb., and *Aulacomnium acuminatum* (Lindb. & Arn.) Par.

Vascular Plants: *Arctagrostis latifolia* (R.Br.) Griseb., *Colpodium vahlianum* (Liebm.) Nevski, *Arctophila fulva* (Trin.) Anderss., *Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Agropyron boreale* (Turcz.) Drobov, *Eriophorum triste* (T. Fries) Löve & Hadac, *Carex subspathacea Wormskj., C. adelostoma* Krecz., *C. krausei* Beocl, *Luzula arctica* Blytt., *Salix arctica* Pall., *Cerastium regelii* Ostenf., *Minuartia strictat* (Sw.) Kiern., *Ranunculus confervoides* (Fries) Fries, *R. pallasii* Schlecht., *R. lapponicus* L., *R. sulphureus* Soland., *Cochlearia officinalis* L., *Eutrema edwardsii* R.Br., *Draba subcapitata* Simm., *D. micropetala* Hook., *D. alpina* L., *D. macrocarpa* Adams, *Braya purpurascens* (R.Br.) Bunge, *Saxifraga hieracifolia* Waldst. & Kit., *S. foliolosa* R.Br., *Potentilla hyparctica* Malt, *P. pulchella* R.Br., *Dryas octopetala* L., *Pyrola grandiflora* Radius, *Cassiope tetragona* (L.) Dvn., *Lomatogonium rotatum* (L.) Fries., *Pedicularis lapponica* L., and *Erigeron eriocephalus* Vahl.

ARCTIC-ALPINE

Hultén (1937) has suggested that, for species of this distributional pattern, Arctic-Montane is more appropriate, since this does not imply that the species are present in the European Alps. Although this is true, the term alpine has been used traditionally in a more general way, denoting any montane area above tree line. Arctic-alpine, as generally used, indicates that a species is widespread in Arctic regions, i.e., north of tree-line, and extends southward in higher elevations of mountains or in sites edaphically equivalent (cliffs, bogs, headlands, etc.). It has been shown (Mooney and Billings, 1961; Mooney and Johnson, 1965) that, among the flowering plants, the alpine populations of arctic alpine species represent ecotypes in those species that have been experimentally examined. It is possible that the bryophytes of this distribution also possess ecotypes. In the bryophytes, however, vegetative reproduction decreases selection and thus segregation of ecotypes is greatly impeded. Persistence of bryophytes in microenvironments that closely match the macroenvironment of arctic regions would also work against the type of selection that leads to alpine ecotypes in vascular plants.

Hepatics: *Anthelia julacea* (L.) Dumort., *A. juratzkana* (Limpr.) Trevis, *Cephaloziella arctica* Bryhn. & Douin, *Arnellia fennica* (Gottsche.) Lindb., *Isopaches bicrenatus* (Schmid.) Buch., *Leiocolea badensis* (Gottsche.) Joerg., *L. bantriensis* (Hook.) Joerg., *L. muelleri* (Nees.) Joerg., *Lophozia longiflora* (Nees.) Schiffn., *L. ventricosa* (Dicks.) Dumort., *L. alpestris* (Schleich.) Evans, *L. wenzelii* (Nees.) Steph., *L. longidens* (Lindb.) Macoun, *Orthocaulis binsteadii* (Kaal.) Buch., *O. attenuatus* (Mart.) Evans, *O. quadrilobus* (Lindb.) Buch., *Saccobasis polita* (Nees.) Buch., *Tritomaria exsecta* (Schmid.) Schiffn., *T. exsectiformis* (Breidler) Schiffn., *T. quinquedentata* (Huds.) Buch., *Harpanthus flotowianus* Nees., *Scapania cuspiduligera* (Nees.) Müll., *S. uglinosa* (Sw.) Dumort., *S. subalpina* (Nees.) Dumort., *S. paludosa* (Müll.) Müll., *Cephalozia pleniceps* (Aust.) Lindb., *C. ambigua* Mass., *C. striatula* Jens., *Pleuroclada albescens* (Hook.) Spr.,*Gymnomitrion coralloides* Nees., *Marchantia alpestris* Nees., *Mannia pilosa* (Hornem.) Frye & Clark, *Asterella ludwigii* (Schwaegr.) Underw., *Peltolepis quadrata* (Sauter) Müll., *Clevea hyalina* (Sommerf.) Lindb., and *Sauteria alpina* Nees.

Mosses: *Trematodon brevicollis* Hornsch., *Arctoa fulvella* (Dicks.) B.S.G., *Dicranum acutifolium* (Lindb. & Arn.) Jens., *D. elongatum* Schleich., *Encalypta affinis* Hedw. f., *E. brevicolla* (B.S.G.) Bruch., *Molendoa tenuinervis* Limpr., *Barbula icmadophila* Schimp., *Didymodon rufus* Lor., *Pottia heimii* (Hedw.) Fürn., *Stegonia latifolia* (Schwaegr.) Vent., *Desmatodon systylius* B.S.G., *D. laureri* (Schulz.) B.S.G., *Voitia nivalis* Hornsch., *Tayloria froelichiana* (Hedw.) Lindb., *T. splachnoides* (Schleich.) Hook.,*Pohlia schimperi* (C.M.) Andr., *P. drummondii* (C.M.) Andr. *Plagiobryum demissum* (Hoppe & Hornsch.) Lindb., *Bryum obtusifolium* Lindb., *Mnium blyttii* B.S.G., *Cyrtomnium hymenophylloides* (Hüb.) Koponen, *Cinclidium stygium* Sw., *Aulacomnium turgidum* (Wahl.) Schwaegr., *Amblyodon dealbatus* (Hedw.) B.S.G., *Conostomum tetragonum* (Hedw.) Lindb., *Bartramia ithyphylla* Brid., *Myurella tenerrima* (Brid.) Lindb., *Drepanocladus tundrae* (H. Arnell) Loeske, *Cirriphyllum cirrosum* (Schwaegr.) Grout, *Hypnum bambergeri* Schimp., *H. vaucheri* Lesq., *H. procerrimum* Mol., and *Rhytidium rugosum* (Hedw.) Kindb.

Vascular Plants: *Huperzia selago* (L.) Bernh., *Lycopodium alpinum* L., *Woodsia alpina* (Bolton) Gray, *Hierochloe alpina* (Sw.) Roem. & Schult., *Phleum commutatum* Gandoger, *Alopecurus alpinus* Sm., *Phippsia algida* (Soland.) R.Br., *Poa alpina* L., *P. arctica* R.Br., *Eriophorum scheuchzeri* Hoppe, *Kobresia myosuroides* (Vill.) Fiori & Paol., *K. simpliciuscula* (Wahlenb.) Mack., *Carex capitata* Soland., *C. microglochin* Wahlenb., *C. bicolor* All., *C. glacialis* Mack., *C. misandra* R.Br., *Juncus biglumis* L., *Luzula confusa* Lindeb., *L. spicata* (L.) D.C. *Tofieldia pusilla* (Michx.) Pers., *Salix reticulata* L., *Oxyria digyna* (L.) Hill, *Polygonum viviparum* L., *Sagina saginoides* (L.) Karst., *Minuartia rubella* (Wahlenb.) Graebn., *Silene acaulis* L., *Melandrium apetalum* (L.) Fenzl., *Ranunculus hyperboreus* Rottb., *R. nivalis* L., *Thalictrum alpinum* L., *Cardamine bellidiflora* L., *Draba nivalis* Liljebl., *D. fladnizensis* Wulf., *Erysimum pallasii* (Pursh) Fern., *Saxifraga oppositifolia* L., *S. flagellaris* Willd., *S. nivalis* L., *S. caespitosa* L., *Parnassia palustris* L., *Sibbaldia procumbens* L., *Astragalus eucosmus* Robins., *A. alpinus* L., *Oxytropis campestris* (L.) D.C., *Epilobium latifolium* L., *E. hornemannii* Rchb., *Rhododendron lapponicum* (L.) Wahlenb., *Loiseleuria procumbens* (L.) Desv., *Phyllodoce caerulea* (L.) Bab., *Arctostaphylos alpina* (L.) Spreng., *Diapensia lapponica* L., *Pedicularis sudetica* Willd., *Pinguicula vulgaris* L., *Campanula uniflora* L., *Achillea borealis* Bong., *Arnica alpina* (L.) Olin, *Taraxacum ceratophorum* (Ledeb.) D.C., and *Crepis nana* Richards.

CIRCUMALPINE

A number of plants are predominantly alpine in distribution, and not essentially arctic, although occasionally they are found in mountainous parts of the arctic. These species occur in many mountain ranges throughout the Northern Hemisphere, sometimes extending to edaphically suitable sites associated with cliffs, canyons, and river gorges. It is possible that a number of the bryophytes may ultimately prove to be arctic-alpine in distribution, but current information would place them in the present category.

Hepatics: *Haplomitrium hookeri* (Sm.) Nees., *Jungermannia cordifolia* Hook., *Nardia compressa* (Hook.) Gray, *Tritomaria scitula* (Tayl.) Joerg., *Cephalozia leucantha* Spr., *Hygrobiella laxiflora* (Hook.) Spr., *Marsupella brevissima* (Dumort.) Grolle, and *Gymnomitrion obtusum* (Lindb.) Pears.

Mosses: *Oreas martiana* (Hoppe & Hornsch.) Brid., *Aongstroemia longipes* (Sommerf.) B.S.G., *Oligotrichum hercynicum* (Hedw.) Lam. & D.C., *Grimmia mollis* B.S.G., *Oedipodium griffithianum* (Dicks.) Schwaegr., *Hygrohypnum smithii* (Swartz.) Broth., *H. alpestre* (Hedw.) Loeske, *Calliergon stramineum* (Wahl.) Kindb., *Brachythecium turgidum* B.S.G., and *B. collinum* (Schleich.) B.S.G.

Vascular Plants: *Athyrium distentifolium* Tausch., *Cystopteris montana* (Lam.) Bernh., *Vahlodea atropurpurea* (Wahlenb.) Fries, *Lloydia serotina* (L.) Rchb., *Sagina saginoides* (L.) Karst., *Anemone narcissiflora* L., *Thalictrum alpinum* L., *Sibbaldia procumbens* L., *Myosotis alpestris* Schmidt, *Aster alpinus* L., *Senecio fuscatus* (Jord. & Fourr.) Hayek., and *S. resedifolius* Less.

Many of the bryophytes are widespread in mountainous western North America and absent from Eastern North America: *Moerckia blyttii, Nardia compressa, Hygrobiella laxiflora, Oreas martiana, Aongstroemia longipes,* etc., which is the case also for several vascular plants: *Lloydia serotina, Myosotis alpestris, Senecio fuscatus,* and *Aster alpinus.*

DISCONTINUOUS DISTRIBUTIONS

In the flora of northwestern North America there are several striking disjunct elements. For most local disjunctions the details are presently not apparent, particularly in the bryoflora. Only further collections will expose these if they do exist. For the more dramatic disjunctions, however, the evidence is clear and, in many cases, the species involved are environmentally restricted. Thus the western European disjuncts in western North America are predominantly confined to oceanic environments and are unlikely to be found across North America since the environment is unavailable there. The situation for coastal and semi-arid elements with affinities in southern South America is similar.

Western American Bicentric Alpine

A number of species, independent of their gross distributional pattern, show a disjunction within western North America suggesting that in this geographic area, at least, the Pleistocene glaciations eradicated the intervening portions of their range, leaving only those portions that survived and later expanded outward from their glacial refuges. Since suitable habitats are available in the intervening areas it must be assumed that the species are in some way prevented from merging the two western American fragments of their distribution. All species showing this pattern are alpine; they are segregated here under their general distributional element. Weber (1965) has discussed this disjunction for the Southern Rocky Mountains.

1. Arctic-alpine: *Alopecurus alpinus* Sm., *Poa vaseyochloa* Scribn., *Salix polaris* Wahlenb., *Minuartia biflora* (L.) Schinz. & Thell., *Saxifraga hirculus* L., *S. foliolosa* R.Br., and *Gentiana tenella* Rottb.

2. Endemic Western American alpine: *Poa nevadensis* Vasey, *Salix dodgeana* Rydb., *Silene douglasii* Hook., *Draba densifolia* Nutt., *Arabis lemmonii* Wats., *Potentilla virgulata* Nels., *Phlox hoodii* Richards., *Townsendia hookeri* Beaman, *Erigeron pumilus* Nutt., and *Artemisia cana* Pursh.

3. Circumarctic: *Phippsia algida* (Soland.) R.Br., *Carex rupestris* All., and *Draba fladnizensis* Wulf.

4. Circumalpine: *Swertia perennis* L.

5. Eurasia—Western American: *Silene repens* Patrin., *Anemone narcissiflora L., Viola biflora* L., and *Gentiana algida* Pall.

6. Asia—Western American: *Kobresia sibirica* Turcz., *Ranunculus gelidus* Karel & Kiril, *Smelowskia calycina* (Steph.) Mey., *Bupleurum triradiatum* Adams, and *Androsace filiformis* Retz.

Details of bryophyte distributions are presently insufficient to determine whether this distribution pattern is followed by these plants.

Affinities with Asia

This floristic element has probably received more attention than any other in the geographic region under consideration. Gray (1859) had noted the relationships in the vascular flora and these have been treated in greater detail by Hultén (1928; 1937), Hara (1939), Li (1952(, Tatewaki (1963) and briefly by Schofield (1965). The bryoflora has been considered in greatest detail by Persson (1946a; 1946b; 1947; 1052a; 1952b; 1958; 1962; 1963). Other discussions have been by Holzinger & Frye (1921), Persson and Gjaervoll (1957; 1961), Persson and Weber (1958), Steere (1959), Steere and Schofield (1956), Steere and Schuster (1960), Schofield (1965; 1966; 1968a; 1968b) and Iwatsuki and Sharp (1967; 1968). Other floristic treatments are also included in the literature cited, and it is from these that the following details have been derived.

The Asiatic affinities can be segregated into several distinct elements: Amphi–Beringian, North Pacific, East Asian–North American and Eurasian–Western American. Further subdivisions could be made, particularly in the vascular flora. In the bryoflora, however, even many of the above categories are not clearly demonstrable.

Amphi-Beringian

In this element are included species found on both sides of the Bering sea, extending into Siberia on the Asian side and into Alaska in North America. Some species found in China have also be included. In all cases the distribution appears to expand both eastward and westward from the Bering Sea area.

Hepatics: *Pseudolepicolea fryei* Perss. (Grolle & Ando), *Ascidota bleblepharophylla* Mass., and *Radula prolifera* Arnell.

Pseudolepicolea fryei is also found in a single locality on the west coast of Hudson Bay (Schuster, 1966).

Mosses: *Gollania turgens* (C. Müll.) Ando might be placed here, although its distribution is in mountains of Alaska and locally in China.

Vascular Plants:

Selaginellaceae: *Selaginella siberica* (Milde) Huron.

Poaceae: *Agrostis trinii* Turcz., *Calamagrostis holmii* Lange, *Koeleria asiatica* Domin., *Poa lanata* Scribn. & Merr., *P. malacantha* Kom., *P. pseudoabbreviata* Roshev., *Colpodium wrightii* Scribn. & Merr., *Puccinellia borealis* Swallen, *P. geniculata* (Turcz.) Krecz., and *Agropyron macrourum* (Turcz.) Drobov.

Cyperaceae: *Carex lugens* Holm., *C. podocarpa* Clarke, and *C. nesophila* Holm.

Juncaceae: *Luzula rufescens* Fisch. and *L. tundricola* Gorodk.

Salicaceae: *Salix phlebophylla* Anderss., *S. rotundifolia* Trautv., *S. sphenophylla* Skvortz., *S. fuscescens* Anderss., *S. ovalifolia* Trautv., *S. chamissonis* Anderss., and *S. pulchra* Cham.

Polygonaceae: *Rumex arcticus* Trautv. and *R. sibiricus* Hult.

Portulacaceae: *Claytonia tuberosa* Pall., *C. acutifolia* Pall., and *C. sarmentosa* Mey.

Caryophyllaceae: *Cerastium maximum* L., *C. jenisejense* Hult., *Minuartia arctica* (Stev.) Aschers. & Graebn., *M. yukonensis* Hult., *A. chamissonis* Maguire, *Wilhelmsia physodes* (Fisch.) McNeill, *Melandrium taylorae* (Robins.) Tolm., and *M. taimyrense* Tolm.

Ranunculaceae: *Delphinium brachycentrum* Ledeb. and *Aconitum delphinifolium* D.C.

Fumariaceae: *Corydalis pauciflora* (Steph.) Pers.

Cruciferae: *Cardamine hyperborea* Schulz, *C. microphylla* Adams, *C. purpurea* C. & S., *Draba caesia* Adams, *D. eschscholtzii* Pohle, *D. pilosa* D.C., *D. pseudopilosa* Pohle, *D. stenopetala* Trautv., *D. kamtschatica* (Ledeb.) Bush., and *D. chamissonis* Don.

Saxifragaceae: *Saxifraga eschscholtzii* Sternb., *S. serpyllifolia* Pursh, *S. exilis* Steph., *S. nudicaulis* Don., *S. davurica* Willd., *S. unalaschensis* Sternb. and *Chrysosplenium wrightii* Fr. & Sav.

Rosaceae: *Spiraea beauverdiana* Schneid. and *Potentilla elegans* C. & S.

Leguminosae: *Astragalus umbellatus* Bunge, *Oxytropis mertensiana* Turcz., and *O. arctica* R.Br.

Umbelliferae: *Cnidium ajanense* (Regel & Tiling) Drude and *C. cnidiifolium* (Turcz.) Schischk.

Primulaceae: *Primula tschuktschorum* Kjellm., *P. cuneifolia* Ledeb., *P. borealis* Duby, *Douglasia ochotensis* (Willd.) Hook., and *Dodecatheon frigidum* C. & S.

Gentianaceae: *Gentiana barbata* Froel. and *G. glauca* Pall.

Polemoniaceae: *Phlox sibirica* L., *Eritrichium aretioides* (Cham.) D.C., and *E. chamissonis* D.C.

Scrophulariaceae: *Lagotis glauca* Gaertn., *Castilleja elegans* Malte, *C. caudata* (Pennell) Rebr., and *C. hyperborea* Pennell.

Orobanchaceae: *Boschniakia rossica* (C. & S.) Fedtsch.

Plantaginaceae: *Plantago canescens* Adams.

Valerianaceae: *Valeriana capitata* Pall.

Compositae: *Artemisia globularia* Bess., *A. glomerata* Ledeb., *A. senjavinensis* Bess., *A. laciniatiformis* Kom., *A. furcata* Bieb., *Arnica lessingii* Greene, *A. frigida* Mey., *Senecio atropurpureus* (Ledeb.) Fedtsch., *Saussurea nuda* Ledeb., *S. viscida* Hult, *Taraxacum lateritium* Dahlst., and *T. kamtschaticum* Dahlst.

North Pacific

In this category are placed species that range around the North Pacific Basin. In most cases the species do not extend into continental regions. It seems likely that many of these species did not expand their range via the Bering land bridge, but by the Aleutian Chain. In other cases these species appear to be ancient relict populations of Tertiary times. Several species persist in regions where they survived the Pleistocene and preceding glaciations. In others of wider range, the species have expanded since glaciation, but from their refugia on either side of the Pacific.

Hepatics: *Takakia lepidozioides* Hatt. & Inoue, *T. ceratophylla* (Hook.) Grolle, *Herberta himalayana* (Steph.) Miller, *Ptilidium californicum* (Aust.) Underw., *Bazzania ambigua* Lindenb., *Lepidozia filamentosa* (Lehm. & Lindenb.) Gottsche, Lindenb., & Nees, *Chandonanthus hirtellus* (Web.) Mitt., *C. pusillus* Steph., *Gymnomitrion pacificum* Grolle, *Macrodiplophyllum plicatum* (Lindb.) Perss., *M. microdontum* (Mitt.) Perss., *Scapania bolanderi* Aust., *Plagiochila satoi* Hatt., *P. rhizophora* Hatt., *P. semidecurrens* Lehm. & Lindenb., *Porella vernicosa* Lindb., *Radula obtusiloba* Steph., *R. auriculata* Steph., *Cololejeunea macounii* (Spruce) Evans, and *Apotreubia nana* (Hatt. & Inoue) Hatt. & Mizut.

Mosses: *Sphagnum guwassanense* Warnst., *S. subobesum* Warnst., *Oligotrichum parallelum* (Mitt.) Kindb., *O. aligerum* Mitt., *Bartramiopsis lyellii* (James) Kindb., *Pogonatum laterale* (Brid.) Brid., *Pohlia columbica* (Kindb.) Andr., *Trachycystis flagellaris* (Sull. & Lesq.) Lindb., *Rhizomnium nudum* (Williams) Koponen, *Ulota japonica* (Sull. & Lesq.) Mitt., *U. repens* Mitt., *Climacium japonicum* Lindb., *Pleuroziopsis ruthenica* (Weinm.) Kindb., *Bryhnia hultenii* Bart., *Myuroclada maximowiczii* (Borosz.) Steere & Schof., *Campylium adscendens* (Lindb.) Perss., *Hypnum subimponens* Lesq., *H. dieckii* Ren. & Card., *Claopodium crispifolium* (Hook.) Ren. & Card., *C. pellucinerve* (Mitt.) Best., *Lescuraea julacea* Besch. & Card., *Hypopterygium fauriei* Besch., and *Habrodon leucotrichus* (Mitt.) Perss.

Vascular Plants (those marked with an * are maritime): *Mecodium wrightii* (Bosch.) Copeland, *Deschampsia beringensis* Hult., *Poa macrocalyx* Trautv. & Mey.,* *Puccinellia pumila* (Vasey) Hitchc.,* *P. hultenii* Swallen,* *P. kamtschatica* Holmb.,* *Carex macrocephala* Willd.,* *C. elusinoides* Turcz., *C. ramenskii* Kom., *C. gmelini* H. & A.,* *C. macrochaeta* Mey., *C. spectabilis* Wew., *Juncus ensifolius* Wikstr., *J. mertensianus* Bong., *Fritillaria camschatcensis* (L.) Ker.-Gawl., *Maianthemum dilatatum* (How.) Nels. & MacBr., *Streptopus streptopoides* (Ledeb.) Frye & Rigg., *Dactylorhiza aristata* (Fisch.) Soo., *Platanthera convallariifolia* (Fisch.) Lindb., *P. chorisiana* (Cham.) Rchb., *Atriplex gmelinii*

Mey.,* *Stellaria ruscifolia* Pall., *Cerastium fischerianum* Ser., *Sagina crassicaulis* Wats.,* *Minuartia macrocarpa* (Pursh) Ostenf., *Aconitum maximum* Pall., *Ranunculus eschscholtzii* Schlecht., *Oxygraphis glacialis* (Fisch.) Bunge, *Papaver alboroseum* Hult., *Cardamine umbellata* Greene, *Draba borealis* D.C., *D. hyperborea* (L.) Desv., *Saxifraga bronchialis* L., *S. bracteata* Don, *Rubus pedatus* Sm., *R. spectabilis* Pursh, *Geum calthifolium* Menzies, *G. rossii* (R.Br.) Ser., *G. pentapetalum* (L.) Makino, *Sanguisorba stipulata* Raf., *Geranium erianthum* D.C., *Viola langsdorfii* Fisch., *Epilobium behringianum* Haussk., *E. sertulatum* Haussk., *Angelica genuflexa* Nutt., *Rhododendron camtschaticum* Pall., *Phyllodoce aleutica* (Spreng.) Heller, *Cassiope stelleriana* (Pall.) D.C., *C. lycopodioides* (Pall.) Don, *Fauria crista-galli* (Menzies) Makino, *Plagiobothrys orientalis* (L.) Johnston, *Pentstemon fruticosus* (Pursh) Greene, *Veronica stelleri* Pall., *Euphrasia mollis* (Ledeb.) Wettst., *Pedicularis chamissonis* Stev., *Pinguicula macroceras* Link., and *Hieracium triste* Willd.

A number of vascular plant genera are present only in East Asia and Western North Amreica, but are represented by different species in each of the areas: *Pseudotsuga, Phyllospadix, Lysichiton, Castanopsis, Achlys,* and *Echinopanax.*

East Asia–North American

A number of species of vascular plants are widespread in North Americt, particularly in boreal and arctic regions and extend into the eastern portion of Asia, occasionally westward nearly to Europe. The only bryophyte of comparable range appears to be the moss *Hypnum plicatulum* (Lindb.) Jaeg. & Sauerb.

Vascular Plants: *Lycopodium obscurum* L., *Hierochloe pauciflora* R.B., *Calamagrostis purpurascens* R.Br., *Danthonia intermedia* Vasey, *Schizachne purpurascens* (Torr.) Swallen, *Bromus ciliatus* L.,*Elymus mollis* Trin., *Eriophorum callitrix* Cham., *Carex stipata* Muhl., *C. viridula* Michx., *C. membranacea* Hook., *Smilacina trifolia* (L.) Desf., *Salix fuscescens* Anderss., *S. alaxensis* (Anderss.) Cov., *S. depressa* L., *Alnus crispa* (Ait.) Pursh, *Stellaria longipes* Goldie, *S. edwardsii* R.Br., *Cerastium beeringianum* C. & S., *Brasenia schreberi* Gmel., *Caltha natans*, Pall., *Coptis trifolia* (L.) Salisb., *Anemone richardsonii* Hook., *A. parviflora* Michx., *Rorippa hispida* (Desv.) Britt., *Lesquerella arctica* (Wormsk.) Wats., *Arabis lyrata* L., *A. drummondii* Gray, *A. divaricarpa* Nels., *A. holboellii* Hornem., *Mitella nuda* L., *Parnassia kotzebuei* C. & S., *Ribes lacustre* (Pers.) Poir., *R. triste* Pall., *Geum macrophyllum* Willd., *Oxytropis nigrescens* (Pall.) Fisch., *Sium suave* Walt., *Conioselinum chinense* (L.) B.S.G., *Angelica lucida* L., *Heracleum lanatum* Michx., *Cornus canadensis* L., *Pyrola asarifolia* Michx., *Monotropa uniflora* L., *Arctostaphylos rubra* (Rehd. & Wilson) Fern., *Lycopus lucidus* Turcz., *L. uniflorus* Michx., *Veronica americana* Schwein., *Pedicularis labradorica* Wirsing., *P. langsdorfii* Fisch., *P. capitata* Adams., *Galium kamtchaticum*

Steller., *Antennaria friesiana* (Trautv.) Ekman, *Anaphalis margaritacea* (L.) B. & H., *Artemisia frigida* Willd., *Petasites palmatus* (Ait.) Gray, *Senecio resedifolius* Less., and *S. pseudo-arnica* Less.

Eurasia–Western America

A number of species are widespread through both Asia and Europe, either in the arctic or in boreal regions, sometimes both, and extend into western North America. In most cases these plants do not extend east of the Rocky Mountains, but in some cases reach the west coast of Hudson Bay or the Great Lakes region. These are represented by only vascular plants.

Cryptogramma crispa (L.) R.Br., *Thelypteris limbosperma* (All.) Fuchs., *Ruppia spiralis* L., *Agrostis clavata* Trin., *Scolochloa festucacea* (Willd.) Link., *Carex obtusata* Lilj., *C. pyrenaica* Wahlenb., *C. lapponica* Lang., *C. rhynchophysa* Mey., *Cypripedium guttatum* Sw., *Hammarbya paludosa* (L.) Ktze., *Salix hastata* L., *Rumex graminifolius* Lamb, *Silene repens* Patrin, *Anemone narcissiflora* L., *Pulsatilla patens* (L.) Mill., *Thalictrum minus* L., *Aruncus sylvester* Kostel, *Hedysarum hedysaroides* (L.) Schinz & Thell., *Impatiens noli-tangere* L., *Viola biflora* L., *V. epipsila* Ledeb., *Ligusticum mutellinoides* (Crantz.) Willar, *Primula sibirica* Jacq., *Androsace chamaejasme* Host, *A. filiformis* Retz., *Trientalis europaea* L., *Gentiana algida* Pall., *G. prostrata* Haenke, *Swertia perennis* L., *Polemonium acutiflorum* Willd., *P. boreale* Adams, *Myosotis alpestris* Schmidt, *Pedicularis verticellata* L., *P. oederi* Vahl, *Aster alpinus* L., *A. sibiricus* L., *Artemisia laciniata* Willd., *Petasites frigidus* (L.) Franck., and *Senecio fuscatus* (Jord. & Fourr.) Hayek.

Western North America—Southern Hemisphere Disjunctions

In the western North American flora two different discontinuities are exhibited by species that reappear in the Southern Hemisphere: bi-polar disjuncts and Pacific North American–South American disjuncts.

Bipolar Disjuncts

Du-Rietz (1940) has thoroughly discussed the problem of bipolar plant distribution, summarizing both pertinent literature and basic information. A bipolar disjunct pattern is that in which species occur in the temperate Northern Hemisphere, and again in the temperate Southern Hemisphere but are essentially absent from tropical latitudes.

To explain this pattern DuRietz (1940) concluded that "it seems necessary to look for epeirogenetic transtropical highland bridges older than the mountain-chains of the Alpine Orogen. Such highland bridges may have existed not only in Africa, but also bordering the transtropical Alpine geosynclines (i.e. the Andean and the Malaysian geosynclines), partly passing over present deep sea bottom."

In many cases the plants of this disjunction are circumboreal in the Northern Hemisphere, several being ubiquitous through that range.

Sainsbury (1952) briefly discussed some of the mosses of New Zealand that showed this distributional pattern. The discussions of Martin (1946; 1949; 1952a; 1952b) have also contributed to the understanding of this disjunction.

Hepatics: *Fossombronia pusilla* (L.) Dum., *Metzgeria furcata* (L.) Dum., *Moerckia blyttii* (Moerch.) Brockm., *Anthelia juratzkana* (Limpr.) Trevis, *Ptilidium ciliare* (L.) Hampe., *Barbilophozia hatcheri* (Evans) Loeske, *Jungermannia cordifolia* Hook., *Orthocaulis floerkei* (Web. & Mohr.) Buch., and *Diplophyllum obtusifolium* (Hook.) Dumort.

Mosses: *Sphagnum centrale* C. Jens., *S. fimbriatum* Wils., *S. magellanicum* Brid., *S. palustre* L., *S. papillosum* Lindb., *S. subnitens* Russow & Warnst., *Andreaea rupestris* Hedw., *Tetrodontium brownianum* (Dicks.) Schwaegr., *Pogonatum alpinum* (Hedw.) Röhl., *Polytrichum formosum* Hedw., *Buxbaumia aphylla* Hedw., *Fissidens adianthoides* Hedw.,*Ditrichum flexicaule* (Schwaegr.) Hampe, *Saelania glaucescens* (Hedw.) Broth., *Dicranum scoparium* Hedw., *Pottia heimii* (Hedw.) Fürnr., *Desmatodon convolutus* (Brid.) Grout, *Tortula muralis* Hedw., *T. papillosa* Wils., *T. laevipila* (Brid.) Schwaegr., *Encalypta vulgaris* Hedw., *Grimmia donniana* Sm., *G. trichophylla* Grev., *Racomitrium lanuginosum* (Hedw.) Brid., *Funaria microstoma* B.S.G., *Tetraplodon mnioides* (Hedw.) B.S.G., *Bryum angustirete* Kindb., *B. pseudotriquetrum* (Hedw.) Gaertn., Mey. & Scherb., *B. caespiticium* Hedk., *B. microerythrocarpum* C. Müll. & Kindb., *Aulacomnium palustre* (Hedw.) Schwaegr., *Bartramia halleriana* Hedw., *B. pomiformis* Hedw., *B. ithyphylla* Brid., *Orthotrichum alpestre* Hornsch., *Climacium dendroides* (Hedw.) Web. & Mohr., *Neckera pennata* Hedw., *Campylium polygamum* (B.S.G.) Jens., *Leptodictyon riparium* (Hedw.) Warnst., *Drepanocladus uncinatus* (Hedw.) Warnst., *Calliergon cordifolium* (Hedw.) Kindb., *C. sarmentosum* (Wahlenb.) Kindb., *Calliergonella cuspidata* (Ren.) Grout, *Brachythecium albicans* (Hedw.) B.S.G., *B. plumosum* (Hedw.) B.S.G., *B. rutabulum* (Hedw.) B.S.G., *B. salebrosum* (Web. & Mohr) B.S.G., *B. velutinum* (Hedw.) B.S.G., *Eurhynchium praelongum* (Hedw.) B.S.G., *Pleurozium schreberi* (Brid.) Mitt., *Plagiothecium denticulatum* (Hedw.) B.S.G., *P. roeseanum* B.S.G., *Hypnum revolutum* (Mitt.) Lindb.,*Isopterygium pulchellum* (Hedw.) Jaeg. & Sauerb., and *Hylocomium splendens* (Hedw.) B.S.G.

Vascular Plants:*Botrychium lunaria* (L.) Sw., *Pteridium aquilinum* (L.) Kuhn., *Asplenium trichomanes* L., *Potamogeton filiformis* Pers., *P. praelongus* Wulf., *P. natans* L., *Triglochin palustris* L., *Vahlodea atropurpurea* (Wahl.) Fries., *Carex buxbaumii* Wahl., *C. capitata* Soland., *C. canescens* L., *C. diandra* Schrank, *C. lachenalii* Schkuhr., *C. magellanica* Lam., *C. microglochin* Wahl., *C. pyrenaica* Wahl., *Juncus filiformis* L., *Koenigia islandica* L., *Chenopodium glaucum* L., *Montia fontana* L., *Honkenia peploides* (L.) Ehrh., *Anemone multifida* Poir, *Cochlearia officinalis* L., *Gentiana prostrata* Kaenke, and *Hieracium gracile* Hook.

Pacific North American—South American Disjuncts

In arid and coastal areas of Pacific North America are a number of species that reappear again in South America in Argentina and Chile, generally as elements of the same environment. These species have attracted the attention of a number of botanists: Gray and Hooker (1880), Bray (1898; 1900), Campbell (1944), Campbell and Wiggins (1947), Raven and Lewis (1959), and Cruden (1966). In a symposium concerning this disjunction, Raven (1963) provided the summary. In the same publication were detailed studies of particular species by Chambers (1963), Constance (1963), Heckard (1963), and Ornduff (1963).

No information concerning bryophytes was included and the details concerning the bryoflora are inadequate to make any valid generalizations.

Raven (1963) suggests the following theory to explain this disjunction: "The great majority of the plants reached their disjunct areas by long-distance dispersal relatively recently. For the bipolar species, the Pleistocene seems the most likely time of dispersal, for the temperate species, the late Pliocene or Pleistocene, and for the desert species, excluding those that have differentiated from common ancestors that spanned the tropics, no time has probably been more likely than the recent past. Both bipolar and temperate disjuncts have come mostly from the north and are almost entirely herbaceous. The desert disjuncts, on the other hand, often appear to have originated in the south, or have diverged from a common tropical ancestor. Many of them are woody."

As was noted earlier, DuRietz (1940) did not hold this opinion. Cruden (1966) also suggests another alternative, noting that for the examples given by Raven, birds could not have served as the dispersal agents and no other agency is likely for such great distances. He suggests that birds, other than shorebirds, may have been important in stepwise dispersal of the species for relatively short distances. "Mountain hopping provides a reasonable explanation for the movement of a large segment of the parental gene pool across the tropics through the buildup of large intermediate populations."

Unfortunately such mountains have not been available during the time suggested and one would be forced to imply a change in the ecology of the species during "migration" and reversion to the original ecological requirements on "arrival."

Species exhibiting this disjunction are (those marked * are essentially maritime): *Palleae atropurpurea* (L.) Link, *Lilaea scilloides* (Poir.) Haum., *Triglochin concinna* Burtt—Davy,* *Agrostis idahoensis,* Nash, *Bromus trinii* Desv., *Danthonia californica* Boland., *Deschampsia danthonioides* (Trin.) Munro, *D. elongata* (Hook.) Munro, *Festuca megalura* Nutt., *Poa stenantha* Trin., *P. secunda* Pres, *Carex* *praegracilis* Boott, *Scirpus cernuus* Vahl.,* *S. nevadensis* Pers., *Juncus leseurii* Boland,* *Calandrinia ciliata* (R. & P.) D.C., *Oxytheca dendroidea* Nutt., *Polygonum punctatum* Ell., *Cardionema ramosissima* (Weinm.) Nels. & Macbr.,* *Anemone multifida* Poir., *Myosurus apetalus* Gay, *Lepidium nitidum* Nutt., *Fragaria chiloensis* (L.) Duch.,* *Trifolium macraei* H. & A., T. *microdon* H. & A., *Boisduvalia glabella* (Nutt.) Walpers, *Gayophytum humile* Juss., *G. diffusum* T. & G., *Osmorhiza chilensis* H. & A., *O. depauperata* Phil., *Sanicula crassicaulis* Poepp., *S. graveolens* Poepp., *Microsteris gracilis* (Hook.) Greene, *Polemonium micranthum* Benth., *Coldenia nuttallii* Hook., *Cryptantha circumscissa* (H. & A.) Johnst., *Heliotropium curassavicum* L., *Lappula redowskii* (Hornem.) Greenm., *Plectocarya linearis* (R. & P.) D.C., *Plagiobothrys scouleri* (H. & A.) Johnst., *Veronica peregrina* L., *Plantago patagonica* Jacq., *Convolvulus soldanella* L.,* *Ambrosia chamissonis* (Less.) Greene,* *Madia gracilis* (Sm.) Keck., *M. sativa* Mol., and *Psilocarphus brevissimus* Nutt.

Western North America—Western Europe

Most of the species of this element are oceanic in their distribution although a number are alpine. In both cases they appear to be persistent remnants of a circumboreal flora, possibly dating back as early as Tertiary time. To imply long-distance dispersal from Europe is illogical since suitable habitats for the species also exist in eastern North America, but the species do not occur there. Evans (1900), and Persson (1949) have discussed this element in the hepatics in particular, and Schofield (1965; 1968a; 1968b) has considered all bryophytes. The vascular flora of this disjunction was briefly discussed by Schofield (1965). Several of the species are widespread and abundant in both parts of their range, others are highly restricted.

Hepatics: *Herberta straminea* (Dumort.) Trevis, *Mastigophora woodsii* (Hook.) Nees., *Bazzania pearsonii* Steph., *Cephaloziella phyllacantha* (Mass. & Carest.) Müll., *C. turneri* (Hook.) Müull., *Anastrepta orcadensis* (Hook.) Schiffn., *Anastrophyllum donianum* (Hook.) Spr., *A. assimile* (Mitt.) Steph., *Gymnocolea acutiloba* (Kaal.) Müll., *Jungermannia caespiticia* Lindenb., *Plagiochila major* (Nees.) Arnell, *Diplophyllum obtusifolium* (Hook.) Dum., *Scapania scandica* (Arn. & Bach.) MacVicar, *Marsupella alpina* (Gottsche.) *Bernet., M. brevissima* (Dumort.) Grolle, *M. commutata* (Dumort.) Grolle, *Pleurozia purpurea* (Lightf.) Lindb., *Porella cordaeana* (Hueb.) Evans., *Metzgeria fruticulosa* (Dicks.) Evans., *Moerckia blyttii* (Moerch.) Brockm., and *Bucegia romanica* Radian.

Among the hepatics, and several of the mosses, a number of species are found in scattered localities in mountainous Japan and in the Himalayas.

Mosses: *Andreaea nivalis* Hook., *Ditrichum zonatum* (Brid.) Kindb., *Cynodontium jenneri* (Schimp.) Stirt., *Kiaeria falcata* (Hedw.) Hag., *Dicranum tauricum* Sapeh., *D. spadiceum* Zett., *Dicranodontium uncinatum* (Harv.) Jaeg., *Campylopus schwarzii* Schimp., *C. schimperi* Milde, *C. subulatus* Milde, *Paraleucobryum enerve* (Thed.) Loeske, *Encalypta affinis* Hedw., f., *E. longicollis* Bruch., *Leptodontium recurvifolium* (Tayl.) Lindb., *Barbula vinealis* Brid., *Geheebia gigantea* (Funck.) Boul., *Pottia lanceolata* (Hedw.) Müll., *Tortula subulata* Hedw., *T. laevipila* (Brid.) Schwaegr., *T. latifolia* (Spreng.) Hartm., *T. princeps* DeNot., *Grimmia pulvinata* (Hedw.) Sm., *G. decipiens* (Schultz.) Lindb., *G. hartmannii* Schimp., *Micromitrium tenerum* (B.S. G.) Crosby, *Funaria muhlenbergii* Hedw. f., *Tayloria hornschuchiana* (Gre. & Arn.) Lindb., *T. froelichiana* (Hedw.) Mitt., *Pohlia erecta* Lindb., *P. vexans* (Limpr.) Lindb. f., *P. gracilis* (B.S.G.) Lindb., *Epipterygium tozeri* (Grev.) Lindb., *Bryum miniatum* Lesq., *B. canariense* Brid., *Bartramia halleriana* Hedw., *Zygodon rupestris* (C. Hartm.) Milde, *Z. gracilis* Wils., *Orthotrichum rupestre* Schleich., *O. laevigatum* Zett., *O. speciosum* Nees., *O. rivulare* Turn., *O. cupulatum* Brid., *O. alpestre* Hornsch., *O. tenellum* Bruch., *O. pulchellum* Brunt., *Antitrichia curtipendula* (Hedw.) Brid., *Pterogonium gracile* (Hedw.) Sm., *Neckera menziesii* Hook., *Hookeria lucens* (Hedw.) Sm., *Fabronia pusilla* Raddi, *Lescuraea stenophylla* (Ren. & Card.) Kindb., *Drepanocladus trichophyllus* (Warnst.) Podp., *Hygrohypnum molle* (Hedw.) Loeske, *Calliergon megalophyllum* Mik., *Brachythecium trachypodium* (Funch) B. & S., *B. tromsoense* (Kaur. & Arn.) Limpr., *Scleropodium caespitans* (Müll.) L. Koch., *S. tourettei* (Brid.) Koch., *Plagiothecium piliferum* (Sw.) B.S.G., *P. platyphyllum* Mönk., and *P. undulatum* (Hedw.) B.S.G.

Vascular Plants: *Equisetum telmateia* Ehrh., *Blechnum spicant* (L.) Roth, *Thelypteris oreopteris* (Ehrh.) Slosson, *Carex stenophylla* Wahlenb., *C. foetida* All., and *Saxifraga adscendens* L., also the vicariant species (the European in parentheses): *Anemone drummondii* Wats. (*A. baldensis* L.), *Pulsatilla occidentalis* (Wils.) Freyn. (*A. alpinus* (L.) Debartre), *Trifolium nanum* Torr. (*T. alpinum* L.), and *Astragalus goniatus* Nutt. (*A. danicus* Retz.).

Cordilleran Disjuncts in Eastern America

Fernald (1924; 1925), in his discussion of vascular plant distribution in northeastern North America, noted a conspicuous element of western North American affinity. Many of these species are North American endemics, while others show a broken circumboreal distribution, or in some cases, affinities with Asia. In all of these, however, there is a marked disjunction between northeastern North America and Western North America. In many the western North American portion of the distribution does not extend beyond the Rocky Mountain chain.

Since the publication of the earlier papers, Fernald (1926; 1933); 1935; 1942) published the results of his considerable field-work further emphasizing this element. His explorations concentrated on areas in eastern North America that had previously yielded disjuncts and in which he located further taxa of this distribution pattern. These regions included Newfoundland, Gaspé and the shores of Lake Superior. Most frequently these plants occur in river canyons or at high elevations. Thus, many of the species appear to be part of a broken circumalpine or circumboreal distribution, or are species endemic to mountains of North America. The contributions of Marie-Victorin (1935; 1938), in his explorations of the islands of the St. Lawrence River, Anticosti and Mingan Islands, contributed further information concerning this disjunction. Abbe (1936) briefly discussed cordilleran disjuncts in Labrador peninsula, noting that they are few in number and that in many the ranges are not as interrupted as was previously assumed.

Further discussions of this element are those of Stebbins (1935), Wynne-Edwards (1937; 1939), Griggs (1940), Raymond (1950), Scoggan (1950), Böcher (1951), Butters & Abbe (1953), Rousseau (1953), Rune (1953; 1954), Dutilly, Lepage and Duman (1958), Schuster (1958), and Schofield (1959). The check-list of Newfoundland vascular plants of Rouleau (1956) is also a valuable source of basic information, as is that of Porsild and Cody (1968) for Mackenzie District.

Explanations for this disjunction are rather varied. The basic problems have been threefold: the inadequacy of details of glaciation in the pertinent areas in eastern America, the ecology of the disjuncts in their eastern outposts, and the uncertainties concerning the total ranges of the species due to inadequate collections from intervening areas. Changes in the status of these avenues of information have led to changes in the theory explaining the plant disjunctions.

Fernald (1925) felt that "Cordilleran" and particularly arctic-alpine species in eastern North America had survived on nunataks during the Pleistocene glaciations. The nunataks he considered to be essentially coincident with the areas rich in these disjunct plants. Arguments against this hypothesis have been strongest and most convincing concerning the arctic-alpine elements. Wynne-Edwards (1937; 1939), Rousseau (1950) and Dammann (1965) have noted that these species could certainly have immigrated into their present sites following glaciation and now persist in only those microclimatic sites that are not invaded by the general flora that is more adapted to the macroclimate.

Stebbins (1935) suggested that each disjunct "migrated eastward in post-glacial times, following near the front of the retreating ice-sheet. Widespread, though local, in its western distribution, it becomes rarer and rarer eastward, with a more limited range north and south, until at its eastern limit there are (few) widely separated stations for it."

Abbe (1936) to explain the presence of this element in Labrador, where the cordilleran taxa are largely now near sea-level suggested: "Possibly then, the balance of all factors were such that in areas, as at the heads of fiords, protected from wind, warmed by occasional föhn winds and by the action of direct insolation, and with melt-water available from the ice-fields above, plants may have survived through the peak of Wisconsin glaciation in the lee of the Torngat Mountains in northeastern Labrador."

Wynne-Edwards (1937) suggested what is termed by Victorin (1938) the "rainbow hypothesis": "Some of these plants have wide limits of climatic tolerance, occurring through a wide latitudinal range, in which case their American distribution takes the form of an arch spanning the continent from the Cordillera to the St. Lawrence by way of the Arctic, while others are more confined, the hardiest occupying the crown of the arch and least hardy its two ends, whereby their ranges are disrupted into western and eastern centres."

Griggs (1940), to explain the distribution of rare plants, suggested that, for disjuncts: "rare plants have been eliminated from the older adjacent barren areas by competition with the more competent common vegetation but persist in the refuges more recently opened to colonization because the ecological succession there has not run quite so far as elsewhere." This would assume a continuity in the past distribution of the disjunct species.

Rousseau (1950) summarizes his explanation as follows: "(a) some (of the Cordilleran disjuncts) . . . could be indifferent arctic alpine plants, now absent from the Arctic proper through elimination by various historical factors (b) The remaining species after this elimination could be considered, at least hypothetically, as pre-glacial plants, though this is not the only probable explanation (c) The remaining species could, as well, be considered as simply alpine species, living on alpine formations constituted after the recess of the glacier. The plants could have taken shelter there during the "pre-sylvatic period," after having travelled from the Canadian Rockies to the Gaspé Peninsula, along the "Arctic Corridor" bordering the receding continental glacier. During glaciation these plants in the Rockies could have sought refuge either south of the glacier or on nunataks. The relicts would then be preglacial in the Rockies and postglacial in Gaspé."

Gaspé has been explored bryologically by both F. Leblanc and J. Kucyniak but the results have not yet been published. From the extensive bryological collections made in Newfoundland, Tuomikoski has published results only on the hepatics (Buch & Tuomikoski, 1955). In this paper he notes only two "Cordilleran" hepatics: *Frullania bolanderi* Aust. and *Cephalozia catenulata* (Hueb.) Spruce. He notes, however, that a number of species show this disjunct pattern in North America although they belong to the circumboreal element. These species are widely distributed through eastern North American, extend westwards frequently to the Great Lakes and southward in the Appalachian Mountains, but are absent until west of the Rocky Mountains in many cases. They are therefore excluded here as "Cordilleran disjuncts" largely because they represent a different distributional pattern to those discussed arlier.

Steere (1937; 1938) drew attention to the bryophytes to Cordilleran disjunction in the Great Lakes areas. Schuster (1958) provided further information for this region.

Of the hepatics cited by Steere (1937; 1938), Schuster (1958) suggested that they could not be considered Cordilleran but were of much wider distribution, being found in intervening areas. He suggested that those that have not been collected in intervening areas are largely inconspicuous and will undoubtedly be found with further exploration.

It seems possible that the mosses may be similarly distributed, but the presently known ranges would support Steere's contention that they are Cordilleran disjuncts: *Racomitrium patens* (Hedw.) Hübn., *Grimmia hartmannii* Schimp., *Lescuraea incurvata* (Hedw.) Lawt., and *Hygrohypnum molle* (Schimp.) Loeske. It should be noted that these mosses are essentially circumboreal in their world-wide distribution.

The Cordilleran disjunct vascular plants can be divided into three categories (those marked with an asterisk are maritime).

1. Endemic to North America: *Cheilanthes siliquosa* Maxon, *Woodsia oregana* Eat., *Polystichum scopulinum* (Eat.) Maxon, *Poa canbyi* (Scribn.) Piper, *Festuca scabrella* Torr., *Agropyron violaceum* (Hornem.) Lange, *Eleocharis nitida* Fern., *Carex filifolia* Nutt., *Goodyera oblongifolia* Raf., *Platanthera unalaschensis* (Spreng.) Kurtz., *Salix vestita* Pursh, *Polygonum fowleri* Robins.,* *Salicornia virginica* L.,* *Minuartia obtusiloba* (Rydb.) House, *Spergularia canadensis* (Pers.) Don,* *Dryas drummondii* Richards., *Vaccinium ovalifolium* Sm., *Campanula latisepala* Hult., and *Arnica cordifolia* Hook., *A. mollis* Hook., and *Cirsium foliosum* (Hook.) D.C.

2. East Asian—western American—Eastern American disjunct: *Potamogeton subsibiricus* Hagstr., *Poa eminens* Presl,* *Eleocharis kamtschatica* (Mey.) Kom.,* *Carex lyngbaei* Hornem.,* *C. stylosa* Mey., *C. franklinii* Boott, *Juncus ensifolius* Wikstr., *Epilobium glandulosum* Lehm., *Conioselinum chinense* (L.) B.S.P., *Angelica lucida* L., *Galium kamtschaticum* Steller, *Arnica frigida* Mey., *Senecio resedifolius* Less., and *S. pseudo-arnica* Less.

3. Essentially circumboreal, but in North America with western North America and eastern America disjunction: *Lycopodium inundatum* L., *Athyrium distentifolium* Tausch., *Cystopteris montana* (Lam.) Bernh., *Polystichum lonchitis* (L.) Roth., *P. braunii* (Spenn.) Fee., *Trichophorum pumilum* (Vahl.) Schinz. & Thell., *Thalictrum alpinum* L., *Ligusticum scothicum* L., and *Cornus suecica* L.

In summary, there is a marked disjunct Cordilleran element in the flora of eastern North America, centered largely around the Gulf of St. Lawrence region and the Great Lakes. The species are largely alpine in distribution and ecology although several are maritime. In most cases they are restricted to sites relatively free from invasion by the species that dominate the general local vegetation, and are essentially in sites at a persistent pioneering phase.

The most plausible explanation of their disjunction is that the eastern representatives are remnants of a more widespread flora of the past, possibly of pre-Pleistocene arctic-alpine distribution in North America. The Pleistocene glaciations can be assumed to have eliminated the north-central portion of the range, but since habitats were available in northeastern and western North America the species survived, probably south of the glacial boundary, but possibly in nunataks or coastal refuges, moving to their present sites following retreat of the ice sheet but being eliminated from their Pleistocene refugium by the encroaching vegetation and by a succession toward more mesophytic temperate vegetation. Evidence for nunataks and refugia in eastern North America has been disputed.

SUMMARY

The flora of northwestern North America is composed of a rich representation of endemics, both in genera and species. Highest concentration of these is in areas that are environmentally diverse and escaped the Pleistocene glaciations. Although the glaciated areas also possess many endemics, their flora tends to be dominated by circumboreal taxa, greatest in Alaska and northern British Columbia, and decreasing southward.

That much of the western North American flora is a fragment of a more widespread flora of Eurasian affinities appears indisputable. Why, in many cases, these taxa have not extended their range across North America, or remain as persistent remnants in suitable environments on both sides of the continents, can probably never be adequately explained. Reconstruction of the climatic and accompanying geologic events as reflected by the records of past floras will considerably aid in the proposition of a working hypothesis. However, new information will always make necessary modification of the historical details that have led to present distributions.

In vascular plants, in particular, the ranges of taxa have been greatly altered by man's activities. The introduction of exotic species of vascular plants has also greatly affected the species that formed the native flora that preceded the advent of man. The effects of aboriginal man on plant introductions have never been adequately studied.

In bryophytes such introductions are presumed to be relatively infrequent but man's influence on distribution patterns has been drastic in environments that are readily exploited by man. Since bryophytes are frequently found in rather extreme environments and persist in small microclimatic sites, they may remain while the more vulnerable vascular flora succumbs. Thus the bryophytes serve as a valuable tool to interpret past floristic history. From the hypotheses derived from bryophyte distributions one can extrapolate to vascular plant distributions.

The bryoflora of western North America consists of a considerably higher percentage of elements of circumboreal distribution than does the vascular flora. The presence of remarkably wide disjuncts is also generally more conspicuous in the bryophytes than in the vascular flora. This is emphasized by disjunction of species of western Europe—western North America and also of a number of species of southeast Asia—western North America. Especially notable about these taxa is the fact that most lack sexual reproduction and have no special means of asexual reproduction. To explain their distribution based on chance long distance dispersal is hazardous and creates more problems than it solves.

Bipolar distributions and affinities with South America imply a past continuity of floras, although attempts have been made to explain this disjunction by long-distance dispersal.

The Cordilleran disjuncts in eastern North America are considered to be fragments of the continuous flora; the time of the continuity is uncertain.

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A NEW SPECIES OF CASTILLEJA FROM THE SOUTHERN SIERRA NEVADA

Lawrence R. Heckard and Rimo Bacigalupi

Castilleja praeterita, Heckard and Bacigalupi, sp. nov. (fig. 1, a-h). Planta perennis omnino praesertim insuper septatim villoso-hirsuta, caulibus costato-angulatis 1–3.5 dm altis, insuper adscendente ramosis plerumque pluribus ex radice lignosa arcuato-adscendentibus. Folia 3–5 cm longa, linearia vel lineari-lanceolata, obtusa vel acuminata, superiora in lobis duobus (interdum 4) angustissimis adscendentibus dissecta. Inflorescentia angusta, conferta, villosa glanduloso-puberulentaque, 1.5–2 cm lata, demum 8–14 cm longa, bracteis eius plerumque 1.5–2 cm longis, 5–8 mm latis, parte centrali oblonga, ad basem versus paulo angustata, ad apicem truncato-rotundatum versus sensim latescente, lobis lateralibus plerumque duobus angustatis adscendentibusque apice rotundatis ex medio instructa. Calyx 14–18 mm longus, plus minusve quadrangularis, sagittaliter aequaliterque 7–11 mm fissus, lobis terminalibus duobus in quoque latere 0.5–2 mm longis, acutis vel rotundatis, quam latis paulo longioribus. Corolla 13–16 mm longa, calyci plus minusve aequilonga vel paulo exserta, galea ca. 1.5 mm longa, dorso minute puberulenta, labio inferiore ca. 1.5 mm longo, sacculis tribus angustis conniventibus, apice brevissime in lobulis involutis apiculatisque ca. 0.5 mm longis terminantibus instructo. Inflorescentiae quod ad colorem attinet bimodales: bracteae calycesque aut pallide virides, ad apices versus citrini, galeae dorso viridis membranis lateralibus stramineis; aut ei glaucescentes, ad apices versus lateriti vel plerumque ei omnino pallide phoenicei, galeae membranis lateralibus violaceo-porphyreis.

Perennial with one to several (to 15) arcuate-ascending annual costate-angulate stems arising from a woody root-crown. Stems 1–3.5 dm tall, occasionally with subordinate ascending branches arising mostly above their mid-points. Stems and leaves villous-hirsute with septate trichomes throughout, occasionally with some inconspicuous glandular trichomes, becoming increasingly villous just below and in the inflorescence. Leaves 3–5 cm long and 2–5 mm broad, linear to linear-lanceolate or narrowly oblong, blunt or attenuate to a pointed tip, the lower entire and nearly petioleless, the upper sessile, broadened below a pair (rarely 2 pairs) of much narrower, divergent or ascending lobes. Inflorescence villous and glandular-puberulent, dense and narrow, 1.5–2 cm broad, becoming 8–14 cm long, the bracts and calyces scaberulous towards the tips. Bracts shorter and broader than the upper leaves, 15–20 (to 25) mm long, 5–8 mm broad, with a pair (rarely 2 pairs) of narrow lobes with rounded or apiculate apices ascending from near the middle, the much broader central lobe oblong but slightly narrowed be-

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Madroño, Vol. 20, No. 4, pp. 209–240. March 25, 1970.

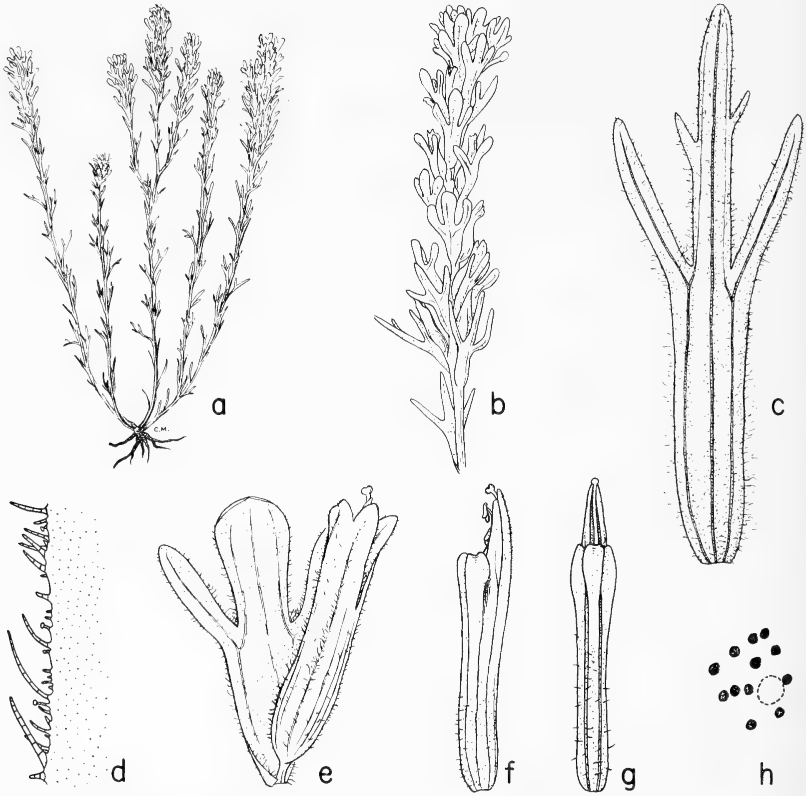

FIG. 1, *Castilleja praeterita:* a, habit, × 1/6; b, inflorescence, × ½; leaf, × 2; d, detail of bract margin, × 10; e, bract and flower, × 2; f, corolla, side view, × 2; g, corolla, front view, × 2; h, chromosomes, n = 12, prophase II, × 800 *(Bacigalupi & Heckard 9213)*. Drawings a-g are from the type collection, *Bacigalupi & Heckard 9190*.

low and with a broadened truncate or truncately rounded distal portion. Pedicels 1–2 mm long. Calyx 14–18 mm long, somewhat quadrangulate, the corners formed by four major veins, cleft medianly 7–11 mm, laterally 0.5–2 mm into lobes which are a little longer than broad and either pointed or rounded and sometimes apiculate. Corolla 13–16 mm long, included or exserted 1–2 mm beyond the calyx, its tube glabrous or sparsely pilose (the trichomes sometimes gland-tipped) along the ventral and lateral surfaces, its galea ca. 5 mm long, minutely puberulent along the back, its lower lip ca. 1.5 mm long, formed of 3 narrow pouches, the outer folds of which are connivent and each of which terminates in an inconspicuous incurving hooded and apiculate lobe. Inflorescence of two color-forms: (1) bracts and calyces pale green and tipped with lemon yellow, the corolla with the membranous lateral flaps of the galea yellowish white; (2) bracts and calyces grayish green and tipped with pale brick red, or often pale reddish with anthocyanin pigment throughout, the corollas with the lateral flaps of the galea maroon-purple; the back of the galea and lower lip green in both forms but the lower lip of the second color-form often suffused with dull purple. Anther-pairs sparsely pilose along the dehisced margins, connivent at anthesis and forming a tier in the opening between the lateral margins of the galea, later separating, the dimorphic anther-cells of the upper anther-pair ca. 1.5–2 mm and 1.0–1.5 mm long respectively, the lower anther-pair with the corresponding cells ca. 0.3 mm shorter. Stigma capitate but very shallowly bilobed, a little over 0.5 mm broad, protruding 0–2 mm beyond the galea at anthesis. Ovary cylindric-ovoid, 2–2.5 mm long, maturing into a many-seeded capsule ca. 8–10 mm long. Seeds 1–1.5 mm long and 0.75 mm broad, variously angled, with a tan, reticulate outer testa. Chromosome number: **n = 12.**

Type. *Bacigalupi & Heckard 9190,* northern edge of Horse Meadow on Salmon Creek, about 7 air miles east southeast of Fairview, southern Sierra Nevada, Tulare Co., California, elevation 7400 ft., Aug. 10, 1966, **n = 12** (JEPS-holotype; isotypes to be distributed).

Other representative specimens (UC or JEPS unless otherwise indicated): Tulare Co.: Big (Brown) Meadow, ca. 3 miles southeast of Horse Meadow, *Bacigalupi & Heckard 9206* (chromosome voucher: **n = 12**); Monache Meadows, *Munz 15067* (RSA); Bakeoven Meadows, *Howell 26764* (CAS, DS); southwest of Templeton Meadow, *C. N. Smith 1515*; Tunnel to Ramshaw Meadow, *Howell 25909* (CAS, UC); Little Whitney Meadow, *Ferris & Lorraine 10779*; Cottonwood Pass, *Peirson,* Aug. 8, 1911; north of Crabtree Meadows, *Raven 7594*; below Timberline Lake, *Robbins 3623*. Inyo Co.: Horseshoe Meadow, *Bacigalupi & Heckard 9212* (chromosome voucher: **n = 12**); above Cottonwood Sawmill, canyon of Cottonwood Creek, *Bacigalupi & Heckard 9213* (chromosome voucher: **n = 12**); Cottonwood Lakes, *Alexander & Kellogg 3315*.

The specific name of this species comes from the Latin word, *praeterita,* meaning overlooked, neglected, or passed by without notice.

Usually associated with and probably parasitic on the roots of *Artemisia rothrockii* and, less frequently, with *Artemisia tridentata* (*Bacigalupi 9213*); dryish, sandy or rocky slopes, commonly bordering meadows; in areas of *Pinus contorta* ssp. *murrayana;* elevation 7,400–11,000 ft.

It will be seen that the cited specimens fall into two groups—a southern one which includes the type of the species, and a more northerly one—between which there is a gap of approximately 24 air miles. Whether this interval represents an actual gap in distribution or merely reflects minimal collecting in this area is conjectural.

There are some morphological differences between the northern and southern populations of *C. praeterita*. The two southern populations (Big, formerly Brown, Meadow and Horse Meadow) consistently have the yellow inflorescence with yellow-tipped bracts and calyces rather than the pale brick red inflorescence which predominates in northern populations. There is also a tendency in these southern populations for the plants to be larger in all respects, including bracts and floral parts. Especially noticeable is the broader inflorescence. Chromosome counts indicate that these differences are not related to level of polyploidy as samples both from southern populations and from two of the northern populations all proved to be diploid.

Although collections of this species have been accumulating in herbaria over the past seventy years, they have either remained unidentified or have been incorrectly referred to *Castilleja pilosa* (Wats.) Rydb. The superficial resemblance to *C. pilosa* may be attributed to similarities in habit, foliage, and indument. *Castilleja pilosa* is sharply differentiated from *C. praeterita,* however, by its calyx, which is more or less equally 4-cleft rather than relatively deeply slit only in its sagittal plane, as in most castillejas. The 4-cleft calyx has been used by some taxonomists (Watson, 1871; Gray, 1878; Jepson, 1925) as a basis for referring *C. pilosa* and closely related species to *Orthocarpus*.

Judging from the absence of annotations on collections of *C. praeterita* in California herbaria (CAS, DS, JEPS, RSA, UC), it would seem that Pennell never saw specimens of our new species. Had he done so, he doubtless would have devised a scheme of subgeneric subdivisions very different from the one he proposed in 1951. *Castilleja praeterita* has a lower lip somewhat pouched but less than half the length of the galea, a combination of characters which precludes its inclusion in any of the 19 sections proposed by Pennell (1951) or as modified by Ownbey (1959). The nearest affinity would seem to be with sections *Chrysanthae* and *Pallescentes,* but the teeth of the lower corolla-lip are far less developed than in most members of those groups, being reduced to mere apiculations. The nature of the apex of the calyx-lobes is used by Pennell to separate section *Chrysanthae* (lobes obtuse) from section *Pallescentes* (lobes acute). Shape of apex of the calyx-lobes of *C. praeterita* varies considerably and hence is of doubtful value in relating the species to either of these two sections. The calyx-lobes of *C. praeterita* are never linear-triangular (as in most species of section *Pallescentes*), but are broader and conform more closely with section *Chrysanthae.* On the other hand, *C. praeterita* occupies ecological sites quite different from the moist meadows preferred by all species of section *Chrysanthae:* it favors drier and better drained slopes surrounding the lower portions of mountain meadows, a habitat more similar to that occupied by species of section *Pallescentes.* In view of these points of non-conformity, one might be tempted to propose a new section to accommodate *C. praeterita,* but we believe there is need for a complete re-evaluation of the sections as proposed by Pennell (1951). Noel Holmgren (1968) is in agreement with this opinion and has not given nomenclatural recognition to superspecific groupings. He suggests that the reticulate nature of species relationships has resulted from speciation through hybridization between members of relatively unrelated groups. A program of artificial hybridizations currently in progress (Heckard, 1964) indicates that hybridization is indeed possible not only between quite unrelated species, but even between members of differing polyploid levels.

Our conclusion is that there are no species particularly closely related to *Castilleja praeterita*. The very short apiculate teeth of the lower corolla-lip occur in no species of either section *Chrysanthae* or *Pallescentes*. The only species which approaches this reduced condition of teeth is *C. culbertsonii* (section *Chrysanthae*), where the teeth, though still longer than those of *C. praeterita,* are reduced to about 0.5 mm in length. Despite this floral similarity, the sum of characters does not indicate a close relationship between the two species. The only other species of *Castilleja* which, to our knowledge, has the teeth of the lower lip as reduced as in *C. praeterita* is *C. cinerea* Gray. This restricted endemic of arid, sagebrush slopes at elevations above 6,000 ft. in the San Bernardino Mts. has a deeply 4-cleft calyx which places it far from *C. praeterita* and among the *Orthocarpus*-like species.

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NOTES AND NEWS

MADROÑO. Starting with the January 1970 issue (Vol. 20, No. 5), *Madroño* will be increased to 48 pages per issue from the current 32. An increasing number of submitted papers and the recent demise of two California journals, *Leaflets of Western Botany* and the *Contributions from the Dudley Herbarium*, makes this desirable. Unfortunately, it will be necessary to increase the subscription rate to *Madroño* and the dues to the Society as follows: institutional subscriptions, $12.00 per year and individual membership, $8.00 per year. Student membership remains at $4.00 per year.

TWO NEW SPECIES OF UMBELLIFERAE FROM THE SOUTHWESTERN UNITED STATES

Mildred E. Mathias, Lincoln Constance, and William L. Theobald

For a number of years the senior authors have recognized the existence of anomalous populations of Umbelliferae in western Texas and adjacent New Mexico. Herbarium specimens of these puzzling plants, usually in flower or immature fruit, have been referred to *Pseudocymopterus montanus,* a polymorphic "catch-all." A restudy of the Umbelliferae for the treatment of the family for the Manual of the Texas Flora has necessitated a review of these discordant elements. Adequate fruiting material is now filed in herbaria and it is apparent that recognition of two species is warranted, one referrable to *Aletes* and the other to *Pseudocymopterus.*

Aletes filifolius Mathias, Constance, and Theobald, sp. nov. Fig. 1. Plantae acaules vel caulescentes; foliis ternato-pinnatisectis, divisionibus filiformibus, 0.5–5.6 cm longis; pedunculis 7–38 cm longis, foliis longioribus; involucri bracteis plerumque nullis; radiis 4–21, 6–20 mm longis, involucelli bracteolis linearis vel lanceolatis; pedicellis 6–15, 1.5–5 mm longis; calycis dentes evidentibus, lanceolatis; umbelluli fructis 2–10, oblongis vel ovoideo-oblongis, 2.4–8 mm longis, 1.8–4 mm latis, costis prominentis et alatis, alis suberosis; vittae plerumque in valleculis solitariae, in commissuri 2.

Plants 2–4 dm tall, caespitose from a branching woody root crowned with old leaf sheaths, acaulescent or with 1–2 stem leaves; leaves petiolate, broadly ovate in general outline; blades 2.5–20 cm long, 2.5–14 cm broad, ternately-pinnately decompound, the ultimate divisions filiform, 0.5–5.6 cm long, 1–2 mm broad; petioles 2.5–15 cm long; peduncles 7–38 cm long, longer than the leaves, scaberulent at the base of the umbel; bracts of involucre usually wanting; rays 4–21, 6–20 mm long, spreading-ascending; bractlets of involucel linear to lanceolate, 2–5 mm long, free to slightly connate at base, rarely reduced to one; pedicels 6–15, 1.5–5 mm long; calyx-teeth evident, lanceolate; petals yellow, ovate with a narrower inflexed apex; styles slender, spreading, stylopodium lacking; disk present; fruits in each umbellet 2–10, oblong to ovoid-oblong, 2.4–8 mm long, 1.8–4 mm broad, the dorsal and lateral ribs prominent and corky-winged, wings pale yellow to white, rarely inconspicuous; vittae large, mostly solitary in the intervals, 2 on the commissure; seed subterete in transection, at times slightly channeled under the vittae; the face more or less plane; sclerenchymatous cells inconspicuous.

Type: Moist soil on ledge along stream, north fork, North McKittrick Canyon, Guadalupe Mts., Culberson Co., Texas, 18 Aug. 1946, *Correll 13961* (US 2178785–holotype, LL-isotype).

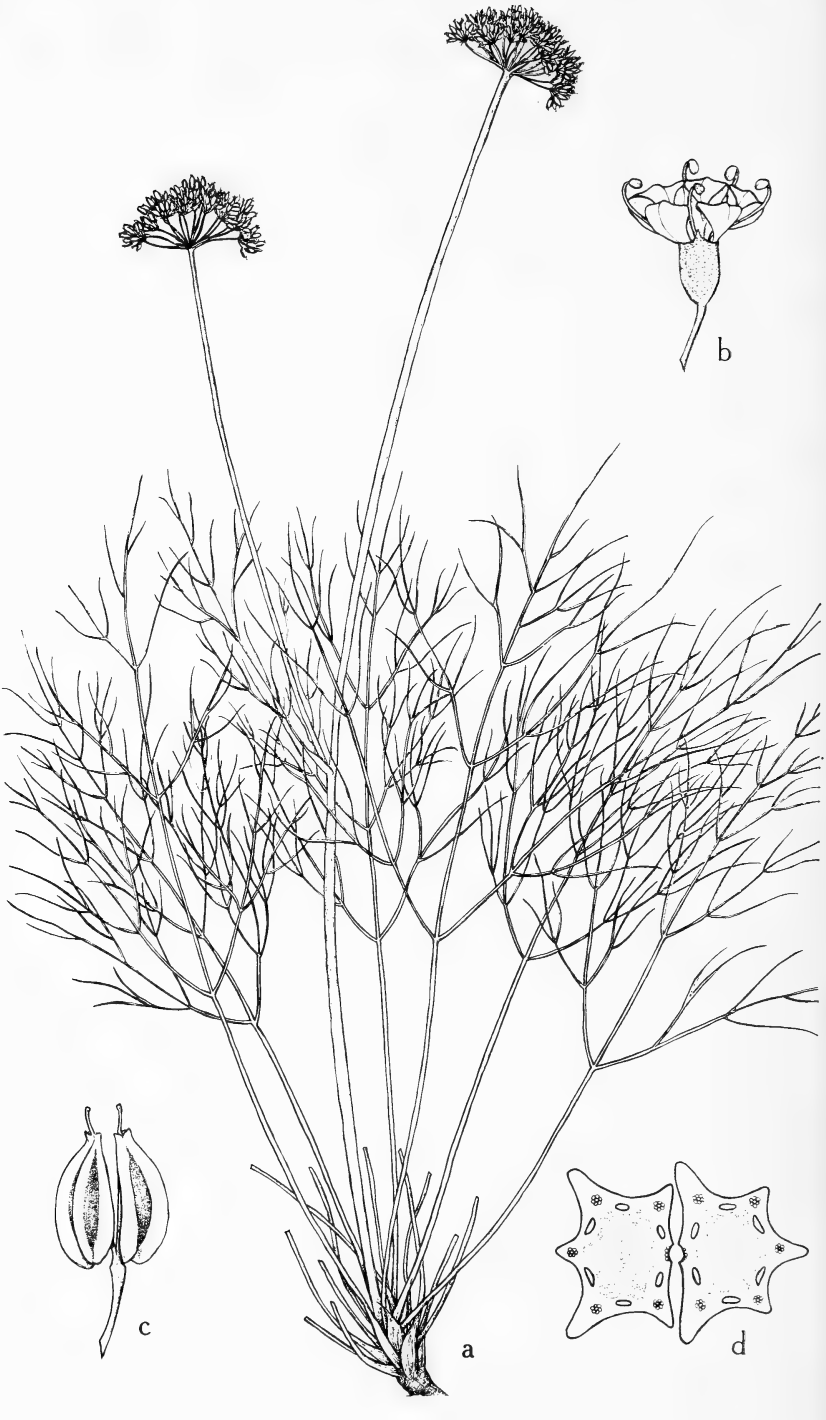
Distribution: Mountains of western Texas and southern and south-central New Mexico.

Representative Specimens. TEXAS: Brewster Co.: frequent on limestone north slopes of Altuda Mt., 10 mi SE of Alpine, Del Norte Mts., 4500 ft., 8 June 1948, *Warnock 7833* (LL, MICH, SMU, UC); abundant near top of Baldy Peak, Glass Mts., 13 July 1940, *Warnock W297* (UC). Culberson Co.: moist shaded bluffs, upper McKittrick Canyon, Guadalupe Mts., 2140 m, 22 July 1931, *Moore & Steyermark 3573* (GH, MICH, MO, UC, US); scarce among boulders, bed of 1st narrow canyon off west side of North McKittrick Canyon, Guadalupe Mts., 1575 m, 16 July 1945, *McVaugh 7413* (LL, MICH, UC); vicinity of Frijole Post Office, 5000-9500 ft, 4 Aug. 1930, *Grassl 166* (MICH); Pine Springs Canyon, Guadalupe Mts., 7 Sept. 1961, *Correll & Johnston 24272* (LL); numerous and scattered on the banks and in the bed of the creek in Pine Spring Canyon and north McKittrick Canyon, 6800 ft, 2 June 1949, *Hinckley & Hinckley 11* (US); McKittrick Can., 28 June 1939, *Lehman* (GH); growing in sand about rock, narrow canyon floor, North Fork of McKittrick Canyon, Guadalupe Mts., 25 July 1957, *Correll & Johnstone 18496* (LL). Jeff Davis Co.: dry rocky places, Little Aguja Canyon, Davis Mts., 1765 m, 17 June 1931, *Moore & Steyermark 3136* (GH, MO, UC).

NEW MEXICO: Dona Ana Co.: deep east-west canyon above Dripping Springs, 6300–7300 ft, 28 July 1952, *Dunn 8436* (UC); Filmore Canyon, Organ Mountains, 26 May 1905, *Wooton* (UC, US); Van Patten's, Organ Mts., 9 June 1906, *Standley* (MO, US), 16 July 1902, *Wooton* (US), 29 Aug. 1894, *Wooton* (US). Eddy Co.: Carlsbad, 4 June 1924, *Lee 154* (US). Grant Co.: Big Hatchet Mts., 17 May 1892, *Mearns 39* (US); Sycamore Creek, 13 Aug. 1902, *Wooton* (US). Socorro Co.: lower valley of Tulerosa River, 30 Aug. 1905, *Hough* (US).

The genus *Aletes* was revised recently by Theobald, Tseng, and Mathias (1964) who recognized five species occurring in the southwestern United States. *Aletes filifolius* is readily distinguishable from the other members of the genus on the basis of habit and basic leaf pattern. It is the only caulescent species, usually with one or two stem leaves, and a ternately-pinnately decompound leaf blade. The other five members of the genus are acaulescent and have pinnate or bipinnate leaves. Nevertheless, on the basis of other vegetative characteristics, and especially in floral and fruit characters, all of these taxa form a distinct and coherent genus.

Aletes acaulis, the most widespread taxon and type species of the genus, also occurs in western Texas. Both it and *A. filifolius* are known from similar habitats on canyon slopes, canyon bottoms, and in rocky crevices in the mountains and in several instances have been reported from the same vicinity. As noted above they are readily distinguishable from each other by their foliage characters.


b
c
a
d

It is expected that *A. filifolius* will be recorded from adjacent Mexico. Several collections from that area are possibly referable to it but confirmation must await the collection of more mature fruiting material.

Pseudocymopterus longiradiatus Mathias, Constance, and Theobald, sp. nov. Fig. 2. Plantae caulescentes, foliis caulis 1–3, ternato-pinnatisectis, divisionibus ovatis vel oblongis, lobatis, lobis obovatis vel lineari-oblongis, 2–14 mm longis; pedunculis 13–49 cm longis, foliis longioribus; radii 8–18, patentibus, 17–58 mm longis, pedicellis 12–25, 2–6 mm longis; umbelluli fructis 2–12, ovoideo-oblongis vel oblongis, 6–9 mm longis, costis lateralibus late alatis, alis membranaceis vel spongiosis; vittae in valleculis solitariae, in commissuris 2.

Plants 3–9 dm tall from a long taproot, caulescent with 1–3 stem leaves, rarely acaulescent; leaves petiolate, ovate-oblong to broadly ovate in general outline, 4.5–15 cm long, 3.5–13 cm broad, ternate-pinnately decompound; the ultimate divisions ovate to oblong in outline, pinnately lobed to parted, the lobes obovate to linear-oblong, 2–14 mm long, 1.5–4 mm broad, acute to distinctly acuminate; petioles 4.5–15 cm long; peduncles terminal or axillary, 13–49 cm long, longer than the leaves, scaberulent to hirtellous-pubescent at the base of the umbel; bracts of involucre usually wanting; rays 8–18, 17–58 mm long, spreading; bractlets of involucel linear-lanceolate, 3–11 mm long, free to slightly connate at base, longer or shorter than the flowers; pedicels 12–25, 2–6 mm long; calyx teeth evident, ovate to deltoid, often with a pale or colored margin; petals pale cream-yellow, ovate with a narrower inflexed apex; styles slender, spreading, stylopodium lacking; disk present; fruits in each umbellet 2–12, ovoid-oblong to oblong, 6–9 mm long, 3–5 mm broad, flattened dorsally or appearing terete due to wings, wings membranous or spongy, linear to triangular in transection; vittae large, solitary in the intervals, 2 on the commissure; the seed face more or less plane; sclerenchymatous cells absent.

Type: In sandy soil under maples and oaks by dry stream bank, Upper McKittrick Canyon, 6000 ft, Guadalupe Mts., Culberson Co., Texas, 22 June 1947, *Meyer & Meyer 2186* (UC 758246–holotype; MO–isotype).

Distribution: Mountains of western Texas and southern New Mexico.

Representative specimens. TEXAS: Brewster Co.: infrequent on northeast limestone slopes of Mt. Ord, 15 mi S of Alpine, Gage Estate, 4650 ft, 23 May 1949, *Warnock & Turner 8645* (LL). Culberson Co.: wooded bluff, locally abundant, 1st narrow canyon off west side of North McKittrick Canyon, Guadalupe Mts., 1575 m, 16 July 1945, *McVaugh 7414* (LL, UC); moist soil in cool canyon, Guadalupe Mountains, steep canyon on southeast slope of Pine Top Mountain, 15 Aug.

FIG. 1. *Aletes filifolius:* a, habit, × ½; b, flower at anthesis, × 10; c, mature fruit, lateral view, × 5; d, mature fruit, transection, × 8.

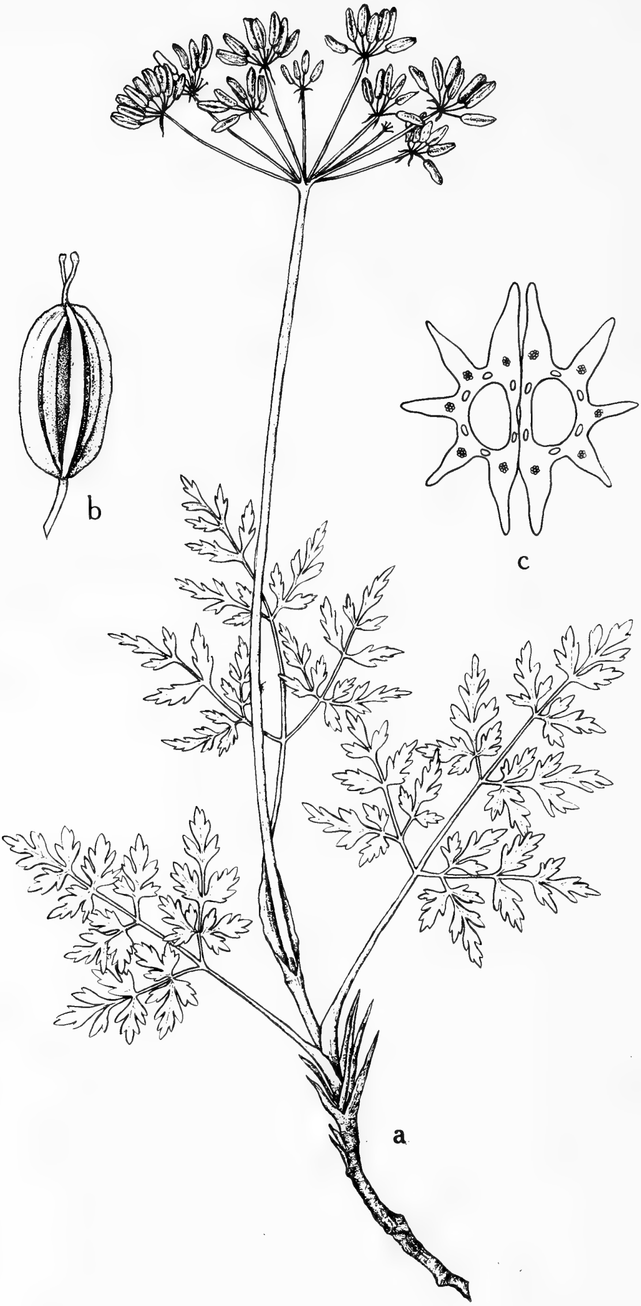


FIG. 2. *Pseudocymopterus longiradiatus:* a, habit, × ½; b, mature fruit, dorsal view, × 3; c, mature fruit, transection, × 8.

1946, *Correll 13904* (LL); under maples, south fork of McKittrick Canyon, Guadalupe Mountains, 30 April 1962, *Correll & Ogden 25055* (LL); under oaks, South Fork of McKittrick Canyon, Guadalupe Mts., 2 July 1958, *Correll & Johnstone 19161* (LL); crevices of cliffs, north-facing canyon, about 9 miles north of Van Horn, 24 April 1961, *Correll & Rollins 23805* (LL); on flats, vicinity of Frijole Post Office, 8000 ft, 10 Aug. 1930, *Grassl 134* (MICH); woods near spring, canyon, east side of Guadalupe Peak, 7500–8000 ft, 29 May-4 June 1912, *Chase 5980* (MICH). Jeff Davis Co.: dry grassy shaded canyon slope, Little Aguja Canyon, Davis Mountains, 1550 m, 17 June 1931, *Moore & Steyermark 3131* (GH, MICH, MO, UC); abundant on slopes in shaded bottom, branch canyon to east just above pass, Wild Rose Pass, about 15 mi NE of Ft. Davis, 10 April 1947, *McVaugh 7891* (MICH).

NEW MEXICO: Otero Co.: west of Mt. Park in an old apple orchard surrounded by pinyons and rather dense oak thicket about 12 ft. tall, along the road to Cloudcroft, ca 6800 ft, 28 June 1952, *Dunn 8097* (LA); Alamo (Lincoln) National Forest, Haynes Canyon, in forest of Douglas spruce and rock pine, 10 Aug. 1911, *Barlow* (MO).

Pseudocymopterus has been a difficult genus to delimit. For a number of years it has been treated as monotypic with the single highly variable species, *P. montanus*. Studies now in progress indicate that several taxa may warrant recognition within this complex. *Pseudocymopterus longiradiatus* can be distinguished by the much longer rays, the larger fruit with larger vittae, and the ternate-pinnately decompound leaves. *Pseudocymopterus montanus* in western Texas is reported only from Mt. Livermore at elevations from 6000 to 8000 feet while *P. longiradiatus* occurs at generally lower elevations in both the Davis and Guadalupe Mountains.

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AGROSTIS PERENNANS (POACEAE), A REMOTE DISJUNCTION IN THE PACIFIC NORTHWEST

Curt G. Carlbom

Agrostis perennans (Walt.) Tuckerm. is an extremely polymorphic taxon in the eastern United States, with many different ecotypic and morphological forms having been described. While it has been reported from all states east of the Mississippi River and three states immediately to the west (*Hitchcock,* 1950), I am reporting it here for the first time from the Pacific Northwest.

A collection of an *Agrostis* (*Carlbom Ac-73,* OSC) from a mesic, semishaded site in the dense coastal *Pseudotsuga—Tsuga* forest approximately two miles east of Copalis, Washington, and an early Thomas Howell collection from Tillamook, Oregon (*Howell, s.n.,* 1884, ORE), identical to it, were compared with a range of specimens from the eastern United States, including ten holotypes of names considered synonyms with *A. perennans* by Hitchcock. These two western collections were identical with the eastern material in the usual spikelet characters as well as in the trichodium-net development.

Five S_1 plants (OSC) and cloned material of *Ac-73* were morphologically indistinguishable from one another when grown under uniform garden conditions. Cytological studies of meiosis in pollen mother cells of *Ac-73* and two S_1 plants revealed no meiotic irregularities, with normal bivalent pairing (21 II) in all cells investigated. The haploid chromosome number, $\mathbf{n} = \mathbf{21}$, agrees with root-tip counts ($\mathbf{2n} = \mathbf{42}$) reported by Björkman (1960) for collections of *A. perennans* from eastern Canada.

Agrostis perennans is possibly a relict species in the Pacific Northwest, having had previously a more or less continuous east-west distribution as late as the Pleistocene.

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A MUTANT OF LITHOCARPUS DENSIFLORUS

John M. Tucker, William E. Sundahl, and Dale O. Hall

A peculiar, low, shrubby, oak-like plant was discovered by Dale Hall in January, 1962, on the Challenge Experimental Forest (which is maintained by the Pacific Southwest Forest and Range Experiment Station, Berkeley) approximately one mile north of Challenge, Yuba Co., California. It was quite unlike any species known to the senior author and did not appear to be a hybrid of any California oak.

About 25 more were found a few weeks later. They were about 1 to 1½ feet tall and were located in a strip 100 feet long and 50 feet wide. Many of these new seedlings had germinated in squirrels' seed caches. There was about one "odd oak" in each group of five to 15 seedlings, the others being tanoak. About half of the "odd oak" seedlings in these caches eventually died.

Some of the remaining plants were transplanted to pots. One was brought to Davis; however, it soon died. Another, in a container with its native soil, was brought to Davis in February, 1964. This one survived, although its growth has been extremely slow. Altogether, there are about 20 of these plants living that we know of. They have been found in several different places, about 2 miles apart (fig. 1). All were in close proximity to *Lithocarpus densiflorus*. A brief note, and a photograph of one of them, appeared in the Sacramento Bee (p. 10, County Life Section), July 21, 1963 (by Melvin Gagnon, at that time a staff writer for the Bee).

Still another occurrence came to our attention recently (after this manuscript had been submitted for publication). Two individuals—one reportedly 8 feet tall (*Smith No. 91,* DAV), which is larger than any we have seen—were noted at 2150 feet elevation, center of Sec. 10, T. 18 N., R. 7 E., in Yuba Co., by B. F. Smith, Sept. 20, 1968.

Close inspection in the field with regard to possible parent trees, and re-examination of fine morphological details, led us to suspect that these peculiar little plants must be odd forms of *Lithocarpus densiflorus*. Although radically different from typical arborescent forms of this species in size, stature, and leaf form (fig. 2), they are very similar in certain other characters such as leaf pubescence and form of the stipules.

The several sites where these plants have been discovered so far lie between 2,150 and 3,425 feet elevation in the ponderosa pine belt (Transition Zone). Here the dominant vegetation is a forest of *Pinus ponderosa, Pinus lambertiana, Pseudotsuga menziesii, Abies concolor, Libocedrus decurrens, Arbutus menziesii, Quercus kelloggii, Lithocarpus densiflorus, Acer macrophyllum, Cornus nuttallii,* and occasionally other woody species.

At first, it was considered that these plants might be monosomics or trisomics. Squash preparations were made on several occasions in a search for visible chromosomal aberrations. All such attempts were unsuccessful.

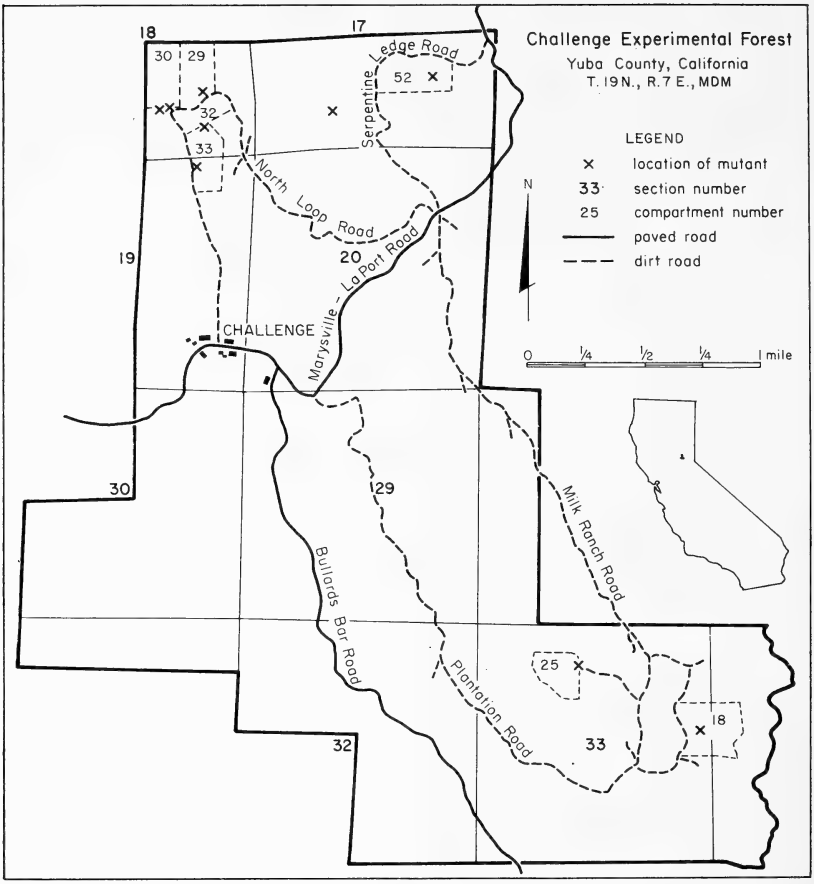

FIG. 1. Location of tanoak mutants.

A more likely hypothesis was advanced by Robert M. Echols, Geneticist, Pacific Southwest Forest and Range Experiment Station. He suggested that we are dealing with a sublethal recessive mutation. If this is true, the rather frequent occurrence of these odd plants over an area more than two miles in extent indicates that this mutation spread, and at present, occurs with a fairly high frequency in the heterozygous condition. A tree heterozygous for the mutation would appear to be a normal tanoak, yet could be expected to produce an occasional homozygous recessive acorn due to pollination by some other heterozygous tree nearby, or possibly by selfing. With this thought in mind, acorns were collected from several normal-appearing trees in the vicinity of the mutants, and germinated at Davis during the fall of 1965.

From a total of 45 acorns that germinated (which represents the progeny of five different trees), it was apparent that one seedling was a mutant

FIG. 2. A large shrubby mutant of *Lithocarpus densiflorus.*

(fig. 3). This was in the progeny of tree number 0-5. There can be no doubt, therefore, that these peculiar little plants are forms of *Lithocarpus densiflorus,* and, provided the hypothesis is correct, it is thus established that tree number 0-5 is heterozygous.

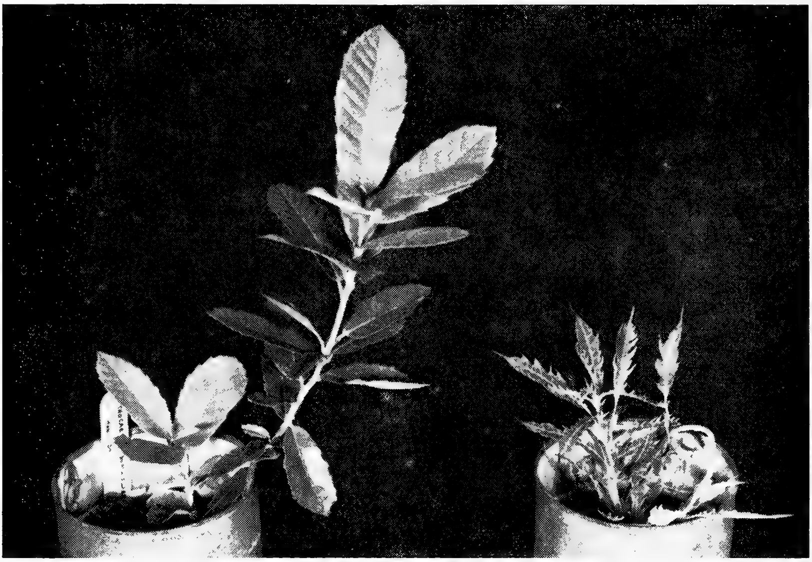

FIG. 3. Progeny from *Lithocarpus densiflorus* parent tree 0-5—a normal-appearing seedling (left), and the mutant (right).

A program of experimental self-pollination may well be attempted. If a sizeable number of experimentally-produced acorns can thus be obtained, we would be in an excellent position to test our hypothesis that the aberrant forms are the result of a single gene mutation. If, on germination, approximately ¼ of them proved to be mutant forms and ¾ normal, the hypothesis would be confirmed. A strikingly different ratio would require some other explanation.

If the tree proves to be completely self-incompatible, an attempt could be made to locate a second heterozygous tanoak by progeny tests similar to those already carried out. A series of controlled crosses, using the two trees as parents, would then be attempted. In this way we may make a small contribution to the knowledge available for the genus *Lithocarpus*.

Since this distinctive mutant is so different from typical *L. densiflorus*, a formal taxonomic designation is justified. Although this case does not seem to be adequately accommodated by the present International Code of Botanical Nomenclature, it seems logical to us to accord it the status of forma.

Lithocarpus densiflorus f. **attenuato-dentatus** Tucker, Sundahl, and Hall, f. nov. A Lithocarpo densifloro tipico foliis lineari-oblongis apicibus anguste, acuminatis, ad basem versus cuneatis, marginibus attenuato-dentatis, dentibus exilibus discedit.

Small woody plants, the largest to ca. 8 feet in height; although commonly with a single stem or trunk from the base, tending to become branched, spreading, and shrub-like; twigs slender and persistently gray hirsute-tomentose; buds hirsute; leaves to 13 cm long and 1.5 cm wide, linear-oblong, apex narrowly acuminate, sub-aristate, base narrowly cuneate, margins minutely and irregularly revolute, attenuate-dentate, the teeth narrow, sub-aristate, and directed forward; upper surface glabrous, dark green and slightly glossy, lower surface pale green, dull, and sparsely stellate-pubescent; secondary veins 6–9 on a side; petiole 10–15 mm long, sparsely stellate to glabrate, the petiole and midrib (especially on the under side of the leaf) yellowish; stipules caducous, linear, 7–8 mm long, lightly hirsute. No flowers or fruit have been observed.

Holotype: California, Yuba Co., Challenge Experimental Forest, ca. 1 mile N of Challenge, elevation 2675 ft., *J. M. Tucker* s. n., May 22, 1963 (DAV).

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CHROMOSOME NUMBERS IN SOME NORTH AMERICAN SPECIES OF THE GENUS CIRSIUM. II. WESTERN UNITED STATES

Gerald B. Ownbey and Yu-tseng Hsi

As was suggested in the previous paper of this series (Ownbey and Hsi, 1963), chromosome numbers in the North American species of *Cirsium* may contribute substantially to an understanding of the taxonomy and evolution of the genus. At the very least they will be of significant value in the initial arrangement of the species into alliances which will with certain reservations represent natural groups. Our experience to date indicates that morphologically similar species now grouped together frequently have the same or only slightly varying chromosome numbers.

Due to the small and intergrading sizes of the chromosomes of *Cirsium,* i.e., 0.6–3.0 microns in length when fully contracted in the species discussed here, it has not been possible adequately to characterize the karyotypes of the species examined. It is safe to assume that at least one pair of satellite chromosomes can be observed in all species and frequently one or two additional satellite chromosomes are seen. Karyotype evolution in *Cirsium* may lead either to a loss or gain in numbers, but reduction in numbers seems to be the rule. It is usually assumed that 17 is the primitive number in the genome as the preponderance of living species have retained this number. Accessory chromosomes, when present, cannot be identified morphologically in our preparations and for this reason it has been concluded that they are intact or nearly so. A few examples of chromosomal fragments have also been seen.

All of the chromosomal data recorded here is based upon the study of root tip preparations. With few exceptions the root tips were obtained from 7–14 day old seedlings grown under sterile conditions in the laboratory.

Counts for *Cirsium acanthodontum, C. rydbergii, C. utahense, C. wallowense, C. pastoris* and *C. arizonicum* are published here for the first time. Earlier counts for the remaining species have been published as follows: *C. brevistylum,* Moore & Frankton (1962); *C. scopulorum,* Moore & Frankton (1965); *C. tweedyi,* Moore & Frankton (1965); *C. coloradense,* Ownbey & Hsi (1963, under *C. foliosum*), Moore & Frankton (1967); *C. scariosum,* Ownbey & Hsi (1963, under *C. foliosum*), Moore & Frankton (1967); *C. tioganum,* Ownbey & Hsi (1963, under *C. foliosum*), Moore & Frankton (1967); *C. ochrocentrum,* Hsi (1960), Ownbey & Hsi (1963); *C. undulatum,* Hsi (1960), Frankton & Moore (1961), Ownbey & Hsi (1963); *C. subniveum,* Ownbey & Hsi (1963); *C. californicum,* Moore & Frankton (1963); *C. occidentale,* Moore & Frankton (1963). The new counts for these species agree closely with the earlier ones except that greater variation in the number of accessory chromosomes is sometimes reported here.

We have arranged the species in the text in the sequence and in the groups proposed by Petrak (1917). Species not known to Petrak, viz., *C. acanthodontum* Blake, *C. brevistylum* Cronq., *C. subniveum* Rydb., *C. wallowense* Peck and *C. pastoris* Howell, are placed in the groups to which they appear to be most closely allied. All American thistles, both native and introduced, belong to the subgenus *Eucirsium.*

Sect. *Echenais,* Subsect. *Americana*

Cirsium acanthodontum Blake. **2n = 32** (2 plants). Oregon, Curry Co., 11.7 miles N of Agness, *Ownbey & Ownbey 3054,* MIN. This collection came from near the type locality.

Sect. *Onotrophe,* Subsect. *Crassifolia*

Cirsium rydbergii Petrak. **2n = 34** (1 plant). Utah, Grand Co., Salt Wash, about one-half mile N of Turnbow Cabin, Arches National Monument, *Welsh & Moore 2742,* MIN.

Subsect. *Minutiflora*

Cirsium brevistylum Cronq. **2n = 34** (3 plants). Oregon, Coos Co., 15.5 miles N of Agness, *Ownbey & Ownbey 3055,* MIN.

Subsect. *Globosa*

Cirsium scopulorum (Greene) Cock. **2n = 34, 35, 36, 37.** Colorado, Clear Creek Co., Mt. Evans, alt. ca. 11,000 ft., *Ownbey 3671,* MIN, **2n = 34** (4 plants), **2n = 35,** (1 plant), **2n = 36** (2 plants), **2n = 37** (4 plants).

Cirsium tweedyi (Rydb.) Petrak. **2n = 34** (1 plant). Wyoming, Yellowstone National Park, Sylvan Pass, *Ownbey & Ownbey 3071,* MIN.

Subsect. *Acaulia*

Cirsium coloradense (Rydb.) Cock. **2n = 34, 36?** Colorado, La Plata Co., 21.9 miles E of Durango, Route 160, alt. ca. 7200 ft., *Ownbey & Hsi 2642,* MIN, **2n = 34** (2 plants), **2n = 36?** (2 plants).

Cirsium scariosum Nutt. **2n = 34, 36.** Idaho, Clark Co., 2.4 miles N of Spencer, *Ownbey & Ownbey 3067,* MIN, **2n = 36** (1 plant); Montana, Powell Co., 5 miles SW of Avon, *Ownbey & Hsi 2908,* MIN, **2n = 34** (3 plants), **2n = 36?** (1 plant); Wyoming, Johnson Co., 13.5 miles W of Buffalo, Route 16, *Ownbey & Ownbey 3030,* MIN, **2n = 34** (1 plant).

Cirsium tioganum (Congd.) Petrak. **2n = 34** (1 plant). Colorado, Jackson Co., 1.3 miles N of Walden, *Ownbey & Ownbey 1497,* MIN.

Cirsium canescens Nutt. × *C. tioganum* (Congd.) Petrak. **2n = 34** (2 plants). Colorado, Jackson Co., 1.3 miles N of Walden, *Ownbey & Ownbey 1497a,* MIN. The data for this hybrid were earlier published by Ownbey & Hsi (1963) under *C. canescens* Nutt. × *C. foliosum* (Hook.) DC.

Subsect. *Acanthophylla*

Cirsium ochrocentrum Gray. **2n = 32, 34.** Arizona, Apache Co., 3 miles N of Concho, *Baker & Baker 2512,* MIN, **2n = 32** (2 plants), **2n = 34** (4 plants); Texas, Tom Green Co., 4.4 miles NE of Tankersly *Ownbey & Baker 2994,* MIN, **2n = 32** (7 plants). The Arizona collection represents the southwestern race of the species distinguished by its scarlet-red corollas and scarcely decurrent leaves. The Texas collection also appears to represent a recognizable race having unusually small heads, phyllaries and phyllary spines.

Cirsium undulatum (Nutt.) Spreng. **2n = 26** (4 plants). Texas, Terrell Co., Independence Creek bottoms near Pecos River, *Demaree 48442,* MIN. This collection comes from the southern periphrey of the range of *C. undulatum.* It differs morphologically from typical material in having extensively branched stems and small heads. The phyllaries and anthers are also smaller than usual for the species.

Subsect. *Campylophylla*

Cirsium subniveum Rydb. **2n = 34, 35, 36.** Idaho, Bonneville Co., 0.5 mile W of the Snake River bridge, just W of Swan Valley, *Ownbey & Ownbey 3043,* MIN, **2n = 34** (2 plants), **2n = 36** (1 plant); Lincoln Co., 19 miles S of Carey, Route 26, *Ownbey & Ownbey 3046,* MIN, **2n = 34** (3 plants); same locality, *Ownbey & Ownbey 3047,* MIN, **2n = 35** (2 plants). The voucher for *Ownbey & Ownbey 3047* was aberrant in having glabrous and shining upper surface of the leaves and in the broadly auriculate bases of the principal cauline leaves. The other voucher specimens cited compare closely with the type specimen of *C. subniveum* (*Nelson 1070,* US).

Cirsium utahense Petrak. **2n = 30, 32.** Arizona, Coconino Co., along Route 180, about 30 miles NW of Flagstaff, *Baker & Baker 2511,* MIN, **2n = 32** (5 plants); Yavapai Co., between Cordis Junction and Mayer, *Deaver 5962,* MIN, **2n = 30** (2 plants). The distinctions between *C. utahense* and *C neomexicanum* are not always clear but, following the treatment of *Cirsium* by Howell (1960) for the Pacific States, the voucher specimens are identified as *C. utahense.* The voucher of *Baker & Baker 2511* is not typical *C. utahense* in being more thinly pubescent throughout and in having basal and cauline leaves remotely pinnatifid, the segments lanceolate.

Cirsium wallowense Peck. **2n = 34** (4 plants). Oregon, Wallowa Co., 31 miles N of Enterprise, *Ownbey & Ownbey 3060,* MIN.

Cirsium californicum Gray. **2n = 28, 29, 30.** California, Mariposa Co., Route 41, Yosemite National Park, 11.8 miles N of the junction of the road to Mariposa Grove, *Baker & Baker 2503,* MIN, **2n = 28** (4 plants), **2n = 29** (1 plant), **2n = 30** (2 plants).

Cirsium occidentale (Nutt.) Jepson. **2n = 28, 29, 30.** California, Marin Co., along Mt. Tamalpais road, 0.2 mile beyond Mt. Tamalpais State Park, *Baker & Baker 2493,* MIN. **2n = 28** (2 plants), **2n = 29** (1 plant), **2n = 30** (5 plants).

Cirsium pastoris Howell. **2n = 30, 31, 32, 33.** California, Mendocino Co., 1.6 miles N of Cummings, *Baker & Baker 2491,* MIN, **2n = 30** (1 plant), **2n = 32** (2 plants), **2n = 33** (1 plant); Oregon, Josephine Co., 10 miles N of Grants Pass, Route 99, *Ownbey & Ownbey 3058,* MIN, **2n = 30** (1 plant, **2n = 31** (1 plant), **2n = 32** (5 plants), **2n = 33** (1 plant).

Sect. *Erythrolaena,* Subsect. *Subcoriacea*

Cirsium arizonicum (Gray) Petrak. **2n = 30** (5 plants). Arizona, Coconino Co., a few miles NE of Strawberry on the Long Valley road, *Baker & Baker 2509,* MIN.

This study was supported by National Science Foundation grants G9071 and GB2727 made to the senior author. We wish to thank the following people for supplying us with collections of *Cirsium* seeds and vouchers used in these studies: Gary R. Baker, Chester F. Deaver and S. L. Welsh. We are indebted to Mrs. Siu–tsun Hsi for many excellent cytological preparations.

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A NEW COPROPHILOUS SPECIES OF CALONEMA (MYXOMYCETES)

Donald T. Kowalski

At present, the genus *Calonema* is monotypic, the single species being *C. aureum* Morgan. It is very similar to the genus *Oligonema*. The only difference between the two genera is that in *Oligonema* the capillitium is composed of short, free elaters, while in *Calonema* it consists of long threads more or less united into a net. Some authors, like Lister (1925) and Hagelstein (1944), believed that *C. aureum* was nothing more than a form of *Oligonema flavidum* Peck. They both retained *Calonema* in their monographs, however, but only for the sake of convenience.

The species to be described below is common on cow dung throughout the Sacramento Valley, wherever natural forage is present. It fruits abundantly in cavities embedded in the dung or on the lower surface in contact with the soil. Since both of these niches are characterized by a high relative humidity, almost all of the collections consist of perfectly matured sporangia.

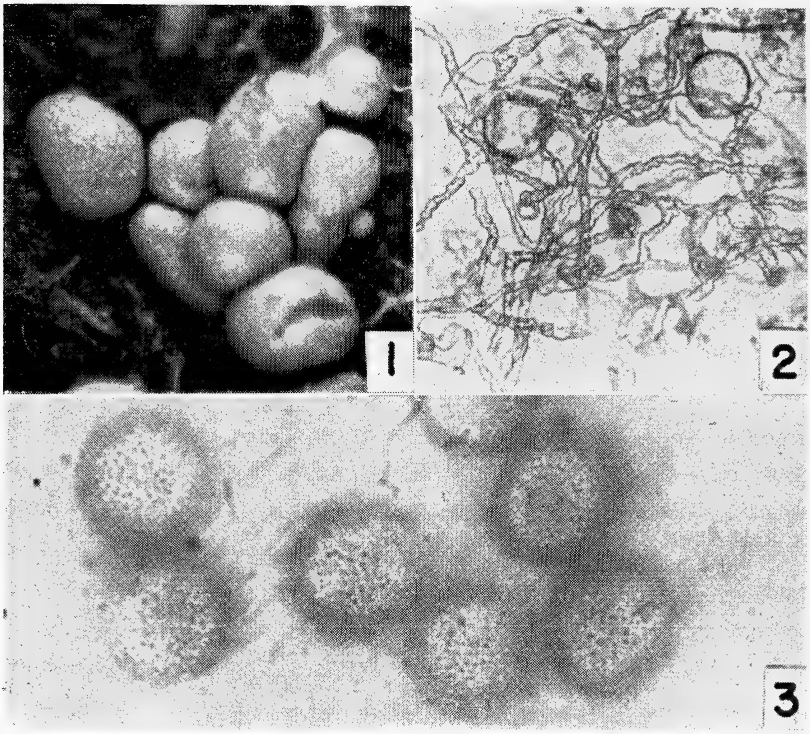
Calonema luteolum Kowalski, sp. nov. Sporangiis dissipatis, gregariis vel agglomeratis, sessilibus, globosis vel subglobosis, 0.1–0.5 mm diam; peridio simplici, membranaceo, luteo, iridescenti; capillitio luteo, filamentis ramosis et anastomosis formandis reticulum, laevigatus, tubularis, 2.0 μ crassis; sporis globosis, spinulosis, luteis, 12–13 μ diam; plamodio ignoto.

Type. Near intersection of Butte Creek and U.S. Highway 99E, 2 miles south of Chico, Butte Co., California, April 22, 1967, *D. T. Kowalski 5998* (IA-holotype, MICH, TEX.).

Collections examined: *Kowalski 2554, 5362, 5393, 5400, 5407, 5420, 5508, 5514, 5521, 5526, 5529, 5536, 5540, 5544, 5549, 5552, 5613, 5614, 5620, 5623, 5625, 5636, 5639, 5992, 5993, 5994, 5995, 5996, 5997, 5998.*

This species is known from the Sacramento Valley of California, where it is found only on cow dung.

Sporangia (fig. 1) scattered, clustered, to often heaped, sessile, irregularly shaped, globose or subglobose, occasionally slightly elongated, 0.1–0.5 mm in diameter; peridium single, thin, membranous, transparent, spores clearly visible through the peridium, iridescent, smooth, entirely lacking any distinctive markings, brilliant yellow; hypothallus lacking; capillitium (fig. 2) composed of branching and anastomosing tubular threads, forming a distinct net, threads of uniform thickness, averaging about 2.0 μ thick, weakly attached to the peridium over the entire surface, surface of threads smooth or minutely ornamented, but completely lacking any sign of spiral ornamentation, internal thickenings present, dividing up the threads into numerous chambers 1–4 μ in diameter, yellow, few free ends, but when free ends present, not noticeably in-



FIGS. 1–3. *Calonema luteolum:* 1, sporangia, × 33; 2, capillitium, × 670; 3, spores, × 1440.

flated; spores (fig. 3) globose, spinulose, yellow in mass, bright yellow by transmitted light, 12–13 μ in diameter; plasmodium unknown.

This species is easy to identify in the field. The restricted nature of the substrate and the fact that the sporangia are bright yellow and form in small heaped clusters is distinctive. The major microscopic characteristics are the smooth capillitium, forming a distinct reticulum, and the spinulose spores, 12–13 microns in diameter. It can easily be separated from *C. aureum* on these features. *Calonema aureum* also has a reticulate capillitium, but its surface bears rings or fragmentary spirals. In none of the 30 collections listed above, did I observe any rings or spirals on the capillitium of *C. luteolum.* The major difference, however, is that *C. aureum* has spores which are 13–15 microns in diameter and they bear a distinct, coarse reticulum.

Whether or not *C. luteolum* belongs in the genus *Calonema* is debatable. While it has characteristics resembling *Calonema,* in other ways it is similar to the genus *Perichaena.* It resembles *Perichaena* in regards to the capillitium and spores. The capillitium of *Perichaena* is also reticulate and lacks rings or spirals and the spores of this genus are never reticulate, being either minutely warted or spinulose. Species of *Perichaena,* however, have a two-layered peridium and the sporangia, while they may be clustered, are never heaped. *Calonema luteolum* is similar to the genera *Calonema* and *Oligonema* in that in both of these genera the peridium is single, membranous and often iridescent and the sporangia can be heaped. It differs from these genera, however, in that their capillitium often has spiral markings and the spores are reticulate, while *C. luteolum* has a smooth capillitium and spinulose spores.

The problem arises in deciding which characteristics are the most important taxonomically, or, which characteristics are the most important in showing phylogenetic relationships, I believe the presence of a single peridium and heaped sporangia indicate that the affinities of *C. luteolum* are with *Calonema* and *Oligonema* even though the capillitial and spore characteristics are reminiscent of the genus *Perichaena.* Perhaps this is one area in which cultural studies can be of immense importance in determining evolutionary relationships.

This study was supported by the National Science Foundation (Grant GB-5799).

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A NEW CAMPANULA FROM NORTHERN CALIFORNIA

LAWRENCE R. HECKARD

An undescribed *Campanula* has turned up in area where one would not have expected to find a new species of flowering plants—Castle Crags, the spectacular and conspicuous mass of spires and domes which rises 4,000 ft. above the Sacramento River southwest of Dunsmuir. A trail in Castle Crags State Park leads up to and among the granitic pinnacles where the *Campanula* grows fairly abundantly in the crevices of sloping and even vertical walls. The plant was first collected in 1948 by the late Freed Hoffman whose private herbarium was given to the University of California. The specimen, identified as *C. scabrella,* came to my attention in connection with a review of the genus *Campanula* in California. I am pleased to name this plant for Stanwyn G. Shetler of the Smithsonian Institution, Washington, D.C., student of *Campanula* and author of a useful conspectus of the genus in North America.

Campanula shetleri Heckard, sp. nov. Fig. 1. Herba perennis rosulata dense caespitosa tota scabro-hispidula; folia breve spathulata paribus dentium oppositorum duobus instructa; caules floriferi 2–5 cm alti,

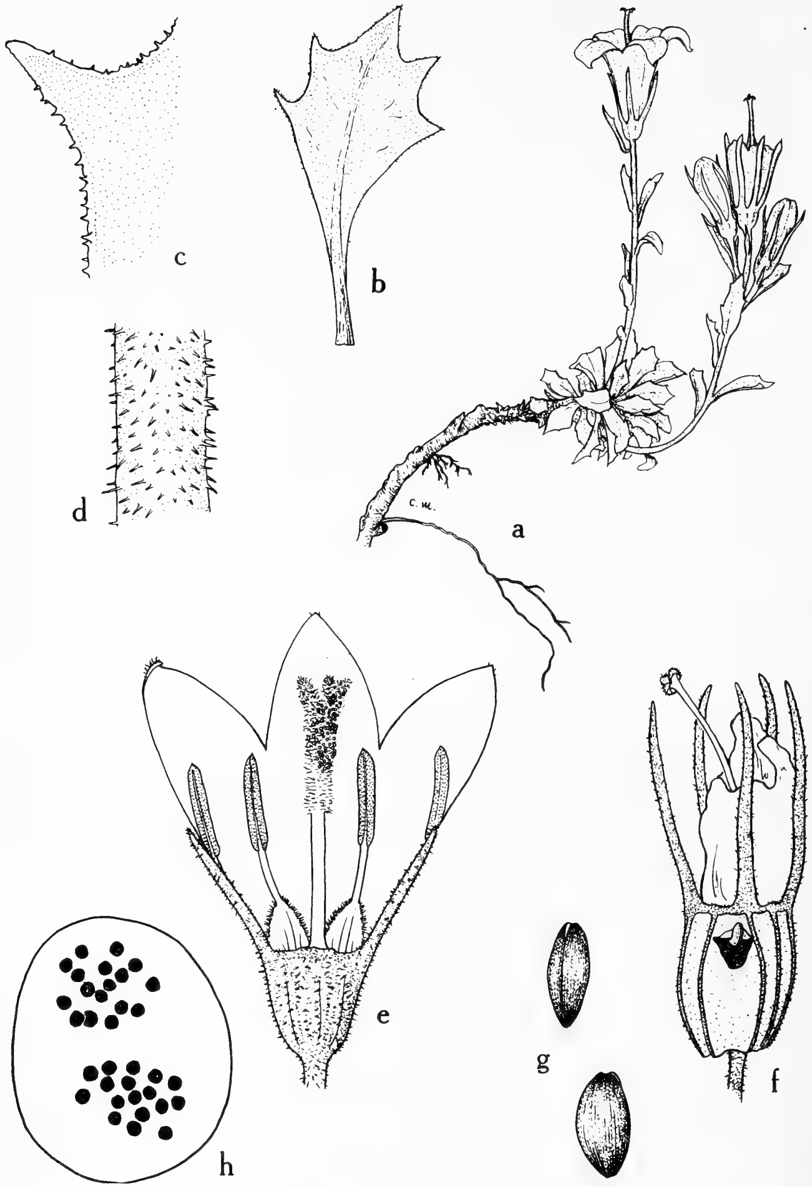

FIG. 1. *Campanula shetleri:* a, habit, × 1½; b, rosette leaf, × 3; c, detail of leaf lobe, × 10; d, detail of peduncle, × 20; e, flower, × 5; f, flower at fruiting stage showing the pore of dehiscence, × 5; g, seed, ×15; h, meiotic chromosomes (camera lucida of MII, *Heckard 1524*), n = 17, ca. × 1300. (Voucher specimens for the drawings: a-e, *Heckard 1524*; f,g, *Heckard 1731*).

inflorescentiis 1–5-floribus terminantes; corolla infundibuliformis 9–10.5 mm longa, ore similiter lata lobis eius ovato-deltoideis 4.5–5 mm longis, quam tubo leviter brevioribus; hypanthium cupulatum super medium latissimum lobis eius integris subulatis; capsulae pori in partem eius super medium collocati.

Mat-forming perennial with densely clustered rosulate shoots arising from long and slender, sparingly branched underground stems with adventitious roots arising singly or in clusters in axillary regions where the inflorescence-branches have abscissed; rosettes with loose to dense clusters of spirally arranged leaves, the stem clothed below for varying distances with withered leaves or leaf-bases, some rosettes giving rise in the leaf-axils to 1 to 3 flowering shoots; rosette-leaves scabrous-hispidulous throughout, the lamina short-spatulate (roughly hexagonal), about 6–7 mm long and 4–5 mm broad, with 2 pairs of opposite teeth, the apex cuneate with a sharp to blunt tip, the base also cuneate, tapering gradually into a short petiole 1–2 mm long; flowering shoots ascending to erect, 2–5 cm high, bearing few to ca 15 leaves which are gradually reduced towards the shoot-apex, the herbage scabrous-hispidulous throughout, the cauline trichomes slightly retrorse; inflorescence with one terminal flower or also with 1–2 (4) later-opening flowers each borne on a short pedicel 1–4 mm long, the pedicels axillary in the uppermost leaves (bracts) and bearing usually 2 sub-opposite or 1 subulate bracteole(s) about 2 mm long; calyx-lobes subulate, entire, densely hispidulous, 4–5 mm long in anthesis, lengthening in fruit to 5–6 mm; corolla pale blue to nearly white, glabrous except for a few small pointed trichomes (similar to those of the herbage) on the outer face at the tip of the corolla-lobe, funnelform, 9–10.5 mm long and about as broad distally, the lobes ovate-deltoid and acute, spreading and becoming recurved, 4.5–5 mm long, slightly shorter than the tube; anthers glabrous, narrow-oblong, 2.5–3 mm long; filaments 2–2.5 mm long, the basal portion ovate-deltoid and ciliate, ca. 1.5 mm long, slightly exceeding the linear distal portion; style about as long as the corolla, 7–8 mm long in anthesis, papillose on the upper one-third, the 3 stigmata each 1 mm long, becoming strongly recurved after anthesis; hypanthium cup-shaped (2–2.5 mm in diam.), scabrous-hipidulous throughout, 2–3 mm long and usually slightly narrower, broadest above the middle; capsule erect, broadly to narrowly cylindric or somewhat urceolate with broadened base, 3–4.5 mm long and 3–4 mm broad, often longer than broad, rounded and irregularly 3-lobed at base, opening just above the middle by three valves; seed just less than 1 mm long, ovoid to ellipsoid with a slight crest, somewhat 3-angled with the 2 broader sides flattened, the third rounded, the seed coat smooth, shining, amber in color; chromosome number: **n = 17.**

Holotype. CALIFORNIA. Shasta Co.: Castle Crags State Park, along trail to Castle Dome, ca. 4200 ft; forming mats in cracks of north- and northeast-facing granite cliffs, *Heckard & Bacigalupi 1524,* 14 June 1966 (JEPS).

Other specimens examined: CALIFORNIA. Shasta Co.: trail to summit of Castle Crags, almost at timber line, *Hoffman 2644* (UC); 0.2 mile south of Castle Dome, 4700 ft., *Heckard 1525, 1731* (JEPS). Siskiyou Co.: north-facing cliffs at Little Castle Lake, ca. 6000 ft., *Roderick,* 1 Sept. 1967 (JEPS).

The plants grow in granitic detritus and humus accumulated in the crevices and cracks of steep and even vertical north- and northeast-facing cliffs. Associated crevice-plants are *Penstemon newberryi* ssp. *berryi, Heuchera merriamii,* and *Ivesia gordonii,* while the most common and conspicuous trees and shrubs of the surrounding area are *Pinus ponderosa, Quercus chrysolepis, Lithocarpus densiflora* var. *echinoides,* and *Arctostaphylos patula.* A few individuals of *Picea breweriana,* a species restricted to the mountains of northern California and southern Oregon, are present. Although *C. shetleri* grows near and above the apparent timberline of Castle Crags, it should be considered a part of the Yellow-Pine Forest community of Munz and Keck (Munz and Keck, 1949; Munz, 1959) since timberline in the crags is probably largely controlled by the granitic substrate and steepness of the topography.

The new species has a known range of less than 4 miles, but it should be looked for on other unexplored granitic peaks in the general region. The limited distribution of *C. shetleri* is not unique in this genus. Shetler (1963) points out that several North American campanulas are highly localized.

Shetler (1963) divides the 16 *Campanula* species restricted to North America into 5 species-groups based on habit and habitat. *Campanula shetleri* has its closest affinity with group 2, the arctic-alpine endemics, consisting of 5 species from western North America. Strictly speaking, the relatively low elevation (4,000–6,000 ft.) occupied by *C. shetlerii* would not qualify it as an endemic of the arctic-alpine zone. The addition of *C. shetleri* to the group thus makes the group-name less appropriate. The species most similar to *C. shetleri* is another narrow endemic, *C. piperi* of the Olympic Mountains in Washington, nearly 500 air-miles distant. *Campanula piperi* occupies a rock-crevice habitat similar to that of *C. shetleri* but in the arctic-alpine zone. In general, *C. shetleri* is much smaller in almost all respects than *C. piperi,* a comparison which includes all flower-parts such as anthers, stigmata, and hypanthium. Several additional well-defined morphological differences between the two species are listed in Table 1. Both species have the same chromosome number of **n = 17.**

Two other species in the arctic-alpine group, *C. wilkinsiana* and *C. scabrella,* are of some interest because, although rare in California, they occur within a short distance of *C. shetleri* on neighboring mountains.

Campanula wilkinsiana is a rather narrow endemic of the Salmon-

Table 1. A Comparison of the Principal Morphological Differences between Campanula shetleri and C. piperi

	C. shetleri	*C. piperi*
Height	To 5 cm	To 10 cm
Indument	Scabrous-hispidulous throughout, the trichomes up to 0.2 mm long.	Finely scabrous-hirtellous in upper portions (calyx-lobes, hypanthium, upper stem and cauline leaves); trichomes less than 0.1 mm long. Rosette leaves glabrous.
Leaves	Short-spatulate, to 1 cm long, dentate with 2 pairs of teeth.	Oblanceolate-spatulate, 1.5–3 cm long, serrate-dentate with 3–6 pairs of teeth.
Calyx-lobes	Narrowly triangular (subulate), 4–6 mm long, entire.	Triangular, 5–10 mm long, occasionally with 1 or more sharp teeth.
Corolla	Pale blue to whitish, about 10 mm long, lobes the same length as or slightly shorter than tube.	Blue (rarely white), 12–16 mm long, lobes almost twice as long as tube.

Trinity Mts. and Mt. Shasta, the latter only 15 air-miles from Castle Crags. Ecologically, it differs from *C. shetleri* in that it grows in spring or streamside sites. Morphologically, *C. wilkinsiana* differs in being a much larger, completely glabrous plant lacking a conspicuous rosette and characterized by obovate to elliptic leaves which are serrate in their upper halves. Moreover, it has deep blue corollas up to 15 mm long terminating stems which are leafless in the upper portion.

The other neighbor, *C. scabrella,* a plant of western Montana to Washington and southward, grows abundantly on Mt. Eddy just 10 air-miles north of Castle Crags. This species, which forms small mats on talus slopes at elevations of 8–9,000 ft., is amply distinct from *C. shetleri* in its entire oblanceolate leaves, herbage with grayish puberulence, and a capsule which opens near the summit.

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NOTES AND NEWS

PROPOSED CALIFORNIA TREE ATLAS. For several years I have been compiling detailed distributional maps in collaboration with W. B. Critchfield. Eighty-six tree species native to California, and adjacent fringes of Nevada, are included. This U.S. Forest Service project is largely based on Vegetation Type Map Survey, Soil Vegetation Survey, and Forest Survey sources. Much of the data has been available for decades but never in a convenient form. For some species the available Forest Service data yield relatively complete maps. For others the coverage is marginal, and we need help.

In 1970 working copies of the new compilations should be available for all species. I hope to place copies for review in the larger botanical centers in California. Several sets will be circulated to interested individuals. This note is a plea to those kind hearted souls who have unpublished tree distribution items stored away. Perhaps some of you can contact me before publication ot the final atlas. Unpublicized tree records from any part of the state, even for the more obvious species, would help. But data about specific range limits or isolated colonies in Lassen, Modoc, Napa, Siskiyou, Trinity counties and all of the Mojave region would be particularly helpful.—JAMES R. GRIFFIN, Hastings Reservation, Carmel Valley, California 93924.

THE CLASSIFICATION SOCIETY. The annual meeting of The Classification Society, North American Branch, will be held April 8–9, 1970 at Battelle Memorial Institute, Columbus, Ohio. For further details, write the Program Chairman, Doctor Joseph Kruskal, Bell Telephone Laboratories, Murray Hill, New Jersey 07994.

The Classification Society, founded in Great Britain in 1964, has as its main purpose the promotion of cooperation and interchange of views and information among those interested in the principles and practice of pattern recognition and classification in any discipline that uses them. As a result, its membership includes anthropologists, biologists, computer and information specialists, geologists, librarians, linguists, psychologists, soil scientists and others.

The Society seeks to provide unique services to its members. These include symposia on classification that are not discipline-constrained and a project under consideration that will result in a bibliography of articles dealing with the theoretical and applied aspects of classification. Supplements to the original bibliography would be issued periodically.

Business of the Society is conducted by a Committee elected by the membership. The Society recently organized into two branches, The European Branch and the North American Branch. Other branches will be organized as the need arises. Current membership numbers around 300, divided equally between the two branches. Annual dues are U.S. $3.00 and entitle members to receive copies of the Bulletin of the Society, which contains contributions of both a formal and informal nature. Membership applications may be obtained from the Secretary, Doctor Theodore J. Crovello, Department of Biology, The University of Notre Dame, Notre Dame, Indiana 46556, or from Doctor J. Willmott, Department of Computation, University of York, Heslington, York, England.

REVIEWS

Flora Europaea. Edited by T. G. TUTIN, V. H. HEYWOOD, N. A. BURGES, D. M. MOORE, D. H. VALENTINE, S. M. WALTERS, and D. A. WEBB. Vol. 2. Rosaceae to Umbelliferae, xxvii + 455 pp., 5 maps. Cambridge University Press. 28 February 1969 ["1968"]. $23.50.

The Editorial Organization of the *Flora Europaea* project produced Vol. 1, Lycopodiaceae to Platanaceae, in 1964 after approximately eight years of existence (reviewed, Madroño 18: 62–63. 1965). This second volume, about five years later, continues the botanical synthesis in English for the multilingual region between the Atlantic and the Ural Mountains. The project is expected to be completed in a total of four volumes. Although this work is intended for use in Europe it is applicable, at least in part, because of the extensive distribution of many genera and species, throughout the Northern Hemisphere and to whatever European plants are cultivated or naturalized. Appendices explain abbreviations of author's names and titles of references for Vol. 2. Each volume has its own fold out maps, English-Latin vocabulary, and index and can be used independently.

Volume 2 treats 50 families including Rosaceae, Leguminosae, and Umbelliferae, respectively with 35, 74, and 110 genera. The number of species keyed out for some of the larger genera are 75 species for *Rubus*, 118 for *Alchemilla*, 133 for *Astragalus*, 99 for *Trifolium*, 105 for *Euphorbia*, and 92 for *Viola*. Reconsideration of some generic points of view has returned *Dasiphora fruticosa* to *Potentilla*, thus differing from *Flora USSR*, and happily has reunited *Cornus* permitting respectful disregard for *Thelycrania* and *Chamaepericlymenum*, thus differing from the *Flora of the British Isles*. Inclusion of persistent introductions reveals, astonishingly, that *Gunnera tinctoria* is locally naturalized in western Europe. Eleven species of *Eucalyptus* have been included although there is no mention that they reproduce.

The only deficiency worth commenting on concerns the failure to give generic citations and to indicate the type species for the genera. This would amount to a statement established from the original description of the name of the species on which the genus was founded. Admittedly this sometimes is very complicated but authors having delt with a genus taxonomically surely are in a better position to express an opinion on generic type species than normally is possible for the staff members of the Index Nominum Genericorum project.

The clearly stated, indented keys with numbered couplets, the condensation of vast numbers of synonyms, all clearly indexed, the annotations on variation and problem situations appearing on every page, mark *Flora Europaea* as an important taxonomic summation. Perhaps only one of many small steps forward for Mankind of 1969, the continuation of this flora is a great step forward for botanists, many of whom will turn to these volumes for purposes other than to identify unknown specimens of European plants.—WALLACE R. ERNST, Smithsonian Institution, Washington, D.C.

Plant Taxonomy. By V. H. HEYWOOD. iv + 60 pp., illustrated. St. Martin's Press, New York. 1967.

This book is an outline of the current field of plant taxonomy and is intended for beginning biology students. The author attempts not only to present the scientific and theoretical basis for plant taxonomy, but also tries to give an overview of modern research methods in this area of biology. Although the topics represent a rather complete survey of plant taxonomy (e.g., populations and species, cytotaxonomy, biochemical systematics, numerical taxonomy, etc.), the discussion and the accompanying examples of these topics are uneven in quality and often incomplete. For example, the discussion of natural selection found on page 26 fails to make any mention of the important contributions population genetics has made in helping us to define and understand this most important biological phenomenon. Also at times the author assumes of the beginning biology student a greater biological background than is reasonable to expect and as a result the significance of many conclusions that are drawn are cryptic to the student. In general, I feel that the book, because of its brevity, falls short of its expectations.—DENNIS R. PARNELL, California State College, Hayward.

Vascular Plants of the Pacific Northwest. By C. LEO HITCHCOCK, ARTHUR CRONQUIST, MARION OWNBEY, and J. W. THOMPSON. Part 1, 914 pp., illustrated. University of Washington Press. 1969. $25.00.

Publication of this part of *Vascular Plants of the Pacific Northwest* marks completion of this outstanding contribution to floristic knowledge of North America. Fourteen years have been required for the conclusion of the serial publication of this flora, which was initiated in 1955. This span of time is remarkably short when one considers its coverage and the fact that many less ambitious works have seriously faltered or expired before consummation. This most recent part—actually Part 1 of the series—includes vascular cryptogams, gymnosperms, and monocotyledons. In addition, it contains an index of the plant families, genera, and common names covered by parts 1–5 and the species covered in Part 1. Also included are an un-illustrated glossary and an unexpected and somewhat immured vegetative key to aquatic vascular plants (mostly at the family level) which precedes the treatment of the monocots. There is a modest "Additions and Corrections" section which lists recent records for the area (some of which are accompanied by illustrations), nomenclatural changes, alterations of ranges, or other comments relvant to portions already published. This section of the work is particularly interesting for its documentation of weedy species that have been recorded recently in the Pacific Northwest. The bulk of Part 1 is occupied by treatments of the Cyperaceae and Gramineae, two families which have made my own taxonomic existence more complex than I would like. However, the fine illustrations that accompany the descriptions of each species in both families have convinced me that genera and species do exist in both of them and, furthermore, that it is probably possible for an informed amateur to determine the Northwestern members of these specialized and enigmatic families with relative ease. The vegetative key to the grasses (and to aquatic plants) will be of particular value to biologists concerned with range and wildlife management.

Anyone traveling in Britain or Europe will probably see far more Pacific Northwestern native plants in cultivation there than he will see grown in their natural range. One feature of this flora which perhaps I have underemphasized in my reviews of the earlier numbers of this series is the very valuable commentary on the horticultural merits and demerits of the indigens of the region. These advisory comments have been provided largely by C. L. Hitchcock, whose extensive experience with the cultivation of northwestern natives is well known to horticulturalists in the Seattle area. Gardeners are counseled of the virtues of potential cultigens such as *Scoliopus, Camassia,* and *Allium* spp.; warned against failure with some of the attractive but difficult species of *Erythronium, Fritillaria,* and *Calochortus;* cautioned against the aggressiveness of *Maianthemum dilatatum;* and admonished in strong terms against picking *Trillium* or depleting the rapidly diminishing populations of *Calypso* and *Cypripedium.*

Experts in the families covered by Part 1 doubtless would find some cause for criticism of "their" genera or families (e.g., why *Libocedrus* and not *Calocedrus*?), but I encountered little with which I had serious disagreement. Although this part is the most expensive of the series, the cost per page is considerably less than that of its predecessors! Having been weaned botanically in the Pacific Northwest and in the institution which might be considered the home of this project I cannot claim to be objective in my assessment of this flora. The superb standards of conception and execution which have characterized this project since its inception have persisted until its completion. The authors deserve our congratulations and warm praise for providing such a durable and scholarly treatment of the vascular plants of the Pacific Northwest.—ROBERT ORNDUFF, University of California, Berkeley.

Supplement to A California Flora. By PHILIP A. MUNZ. iv + 224 pp. University of California Press, Berkeley and Los Angeles. 1968. $7.00.

The appearance of a 224-page supplement to a flora of California is an event of interest to all botanists interested in the plants of North America. The size of the supplement attests to the amount of work that has been done on the plants of the state in the decade since the publication of the original work. On the other hand, this very size likewise makes the use of the supplement inconvenient. One wishes that a new edition of the Flora could have been prepared instead, but since that was apparently not possible, the supplement is a welcome substitute.

Most of the material in the supplement has to do with changes proposed in revisions and other monographic works that have appeared since 1959. Unfortunately, as in the original Flora, bibliographical citations are abbreviated to the point where they are of limited value. Thus the name of a worker may refer to a publication, a personal communication, or even a specimen, and the status of the date which sometimes follows the name is of comparably uncertain origin. There is no printed bibliography, and the reader will often not be able to distinguish the possibilities given above. On the other hand, the addition of a bibliography would have made the Supplement even longer, and, for those with a thorough working knowledge of the California flora, the brief references given here will be of some use in indicating the sources of the statements given.

In addition, range extensions, new chromosome numbers, and other new information is given for hundreds of species. The format is convenient and the information presented is easily integrated with that in the flora, and the supplement itself is nearly free of typographical errors. There is a useful index, and the sturdy, attractive volume is well printed and bound.

In connection with the supplement, it is of interest to draw attention to two articles that provided statistical analyses of the material in the original book: Smith, Gladys L. and Anita M. Noldeke, "A statistical report on A California Flora," Leafl. West. Bot. 9: 117–123. 1960., and Noldeke, Anita M. and J. T. Howell, "Endemism and A California Flora," Leafl. West. Bot. 9: 124–127. 1960. These papers reveal that 162 families, 1075 genera, 5675 species, 1586 additional subspecies and varieties, and 443 taxa of indefinite status were reported in the Flora, with the largest families being Compositae (822 species), Gramineae (449 species), and Leguminosae (372 species), and the largest genera being *Carex* (144 species), *Astragalus* (93 species), *Phacelia* (87 species), *Lupinus* (82 species), and *Eriogonum* and *Mimulus* (77 species each).

Nearly 30 per cent of the native species were endemic to California, as compared with about 40 per cent reported by W. L. Jepson in his (1925) *Manual of the Flowering Plants of California*. The reduction appears to be due largely to the successful abandonment of Jepson's highly provincial view of the plants of California, as well as to extensive and intensive exploration just beyond the borders of the State, especially in Baja California and Oregon. Nevertheless, California still has an extraordinarily high proportion of endemics for a continental area, and were the proportion of endemism computed for the entire "California floristic province," which excludes the desert areas of California but includes portions of the three neighboring states, the proportion would be much higher.

As the number of naturalized species represented in the flora of California creeps inexorably upward, dozens of recently reported genera, including for example *Pteris, Cyrtomium, Viscum, Gunnera, Rhagadiolus, Boussingaultia, Halodule,* and *Apera,* are listed in this Supplement, as is the family Aponogetonaceae. It is becoming increasingly obvious that if future works are to provide a balanced account of the plants of the State, that we shall have to reexamine our standards for inclusion or exclusion of weedy plants; old records of species that did not persist, for example, should presumably not continue to be listed.

In the Supplement, the family Balsaminaceae is reported from California for the first time, on the basis of a native and an introduced species; the same appears to be true for Loganiaceae, as *Buddleia utahensis* Cov. was accidentally omitted from the Flora itself. The Koeberliniaceae are likewise added to the flora of the State on the basis of a recently published record of *Koeberlinia spinosa* Zucc. in the Chocolate Mts. of Imperial County. *Kobresia* and *Bensoniella (Bensonia)* are recently reported genera of native plants, and outstanding native species added to the flora of the State during the past decade include *Lycopodium inundatum* L., *Abies amabilis* (Dougl.) Forbes, *Saxifraga caespitosa* L., *Rubus nivalis* Dougl., and *Juncus marginatus* Rostk. Thus as in recent decades, nearly all of the additions to the flora of the State come from the geologically complex and floristically rich ranges of northern California, and, to a lesser extent, from the Sierra Nevada. This strongly suggests that the flora of central and southern California is relatively well known.

Floristic work among the plants of California, in part spurred by the appearance of the Flora, has been extensive, with genera such as *Streptanthus* and *Galium* continuing to receive a great deal of attention, and critical recently described species being listed in such genera as *Polystichum, Silene, Opuntia, Monardella,* and *Nemacladus.* Recent generic segregates such as *Calocedrus, Chrysolepis,* and *Munzothamnus* are recognized in the Supplement. A few new combinations, new varieties, and at least one new species (*Layia ziegleri* Munz) are presented in the work itself.

An entirely new treatment of the genus *Eriogonum,* based on notes by James L. Reveal, is incorporated directly into the Supplement. This 40-page synopsis indicates that 104 species are now known from the State, in comparison with the 77 listed in the Flora. The new treatment is an excellent contribution which should greatly aid students of the genus, and incorporates much new information. It is much more monographic in scope than most of the Flora, containing numerous critical notes. As such, the work on *Eriogonum* stand in sharp contrast, for example, to the scattered notes on *Arctostaphylos* summarized here. In the latter group, a variety of workers have continued to present new combinations and new taxa without ever approaching the overall view of the group necessary to achieve taxonomic synthesis. A useful taxonomic system for a complex group such as *Arctostaphylos* will never be built up of such blocks, and indeed, the overall pattern of variation tends to become more and more obscure as the new taxa are proliferated. It is greatly to be hoped that some of the studies of this genus now under progress will eventually provide a new synthesis, based on a sound understanding of the biology of the plants, that will make possible an appreciation of this most critical and interesting genus, whose history is inextricably bound up with that of the floristic associations with which it occurs.—Peter H. Raven, Department of Biological Sciences, Stanford University.

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JOHN H. THOMAS, Editor

October 25, 1969

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A NEW SPECIES AND SOME NEW COMBINATIONS IN CALYLOPHUS (ONAGRACEAE)

Howard F. Towner and Peter H. Raven

The evolution and breeding systems of the genus *Calylophus* have been the subject of dissertation research by the senior author for the past three years. Information from this work has led to a biosystematic study and a taxonomic revision of the genus, which will be published in the near future. The present paper is intended to validate our new combinations and a new species in advance of their use in the forthcoming *Manual of the Vascular Plants of Texas* by Donovan S. Correll and Marshall C. Johnston. The research on *Calylophus* has been supported by National Institutes of Health graduate research fellowship 2-FO1-GM-32,708-02 to the senior author and by National Sience Foundation research grant GB-7949X to the junior author.

Calylophus encompasses two former subgenera of *Oenothera* which were recognized by their peltate or discoid stigmas, and in our treatment will consist of five species. The only monograph concerned with those species has been that of Munz (1929). In it were recognized four species of *Oenothera* subg. *Salpingia* and one of subg. *"Calylophis."* Recent unification of these taxa as the genus *Calylophus* by Raven (1964) created a small, cohesive group of species which showed more affinity to such genera as *Gaura* and *Clarkia* than to other species formerly referred to *Oenothera*. This change was followed by Shinners in his treatment of the Texas species of *Calylophus* (1964). Shinners attempted to draw new taxonomic lines between infraspecific groups, and he reduced a number of taxa to synonomy or varietal status. Munz's contribution to the *North American Flora* (1965) retained the traditional generic alignment of the Onagreae, with *Calylophus* included in *Oenthera*. Most of the forms in the subgenus *Salpingia* were accorded specific rank.

Our investigation has resulted in a view of the *Calylophus hartwegii* group which agrees with Shinners' treatment in regarding it as an assemblage of intergrading infraspecific taxa. Several minor differences appear between the two discussions. First, we prefer to use the rank subspecies as the only infraspecific taxon, for reasons presented by Raven (1969). The entities within *C. hartwegii* intergrade, but retain their identities over large geographical ranges. They are thus major forms which are best dealt with by according them subspecific status. Secondly, we recognize *C. hartwegii fendleri,* which constitutes a distinctive series of populations distributed over a definite eco-geographical range. The third difference, to be fully treated in the forthcoming revision, consists of small changes in the boundaries between taxonomic

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entities. According to our study, there is no justification at present for distinguishing between two major groupings within this complex, such as *O. greggii* and *O. hartwegii* in the sense of Munz (1929). Intergradation occurs between nearly any two forms which come into contact. A reticulate pattern of phenetic and crossing relationships is evident, so the only logical approach is to place all of the forms in *C. hartwegii.*

The *Calylophus serrulatus* group, like the *C. hartwegii* complex, has never been well understood, either in a biological or taxonomic sense. We have discovered that this assemblage includes one outcrossing self-incompatible species, *C. drummondianus,* and two species which are self-pollinating complex structural heterozygotes. The interpretation of this group was particularly difficult in the past, since the three species often exhibit parallel patterns of geographical variation. It is not surprising, therefore, that this situation has led to widely differing taxonomic treatments.

CALYLOPHUS Spach, Hist. Veg. Phan. 4: 349. 1835. *Meriolix* Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819; nomen nudum. Raf., J. Phys. Chim. Hist. Nat. Arts 89: 259. 1819; nomen nudum. Walp., Repert. 2: 79. 1843. *Calylophus* Spach, Hist. Veg. Phan. 4: 349. 1835. *Calylophis* Spach, Nouv. Ann. Mus. Hist. Nat. III. 4: 337. 1835. *Oenothera* subg. *Calylophis* (Spach) T. & G., Fl. North Amer. 1: 501. 1840. *Oenothera* subg. *Salpingia* T. & G., Fl. North Amer. 1: 501. 1840. Type: *O. lavandulaefolia* T. & G. = *Calylophus hartwegii* ssp. *lavandulifolius* (T. & G.) Towner & Raven. *Salpingia* (T. & G.) Raimann, in Engler & Prantl, Naturl. Pflanzenfam. III. 7: 217. 1893; non Mart. 1828. *Galpinsia* Britt., Mem. Torrey Bot. Club 5: 236. 1894.

Perennial herbs, sometimes with slightly woody lower stems and base. Flowers actinomorphic, borne in axils of upper leaves, opening near sunset, in mid-afternoon, or near sunrise; hypanthial tube well-developed; petals yellow, fading pink or orange in some species. Stigma peltate to discoid or globose-peltate, sometimes shallowly 4-lobed. Gametic chromosome numbers, **n = 7, 14.** Three of the five species are self-incompatible; two are self-compatible.

Type. *Calylophus nuttallii* Spach. *C. serrulatus* (Nutt.) Raven. Five species will be recognized in this paper and in the forthcoming revision. They occur throughout the Great Plains from southern Canada to Texas, and from the Great Basin and Southwest to north-central Mexico. The genus is vaguely divisable into groups corresponding to *Oenothera* subg. *Calylophus* and *Salpingia,* but the characters used to distinguish them, namely sepal midrib height and hypanthial tube length, vary within each complex. This separation may be used with caution in keys, however no sectional division has been made because of the variability and the small size of the genus.

Calylophus hartwegii (Benth.) Raven, *Brittonia* 16: 286. 1964. *Oenothera hartwegii* Benth., Pl. Hartw. 5. 1839

Calylopus hartwegii ssp. **lavandulifolius** (T. &. G.) Towner & Raven, comb. nov. *Oenothera lavandulaefolia* T. & G., Fl. North Amer. 1: 501. 1840.

Calylophus hartwegii ssp. **fendleri** (Gray) Towner & Raven, comb. nov. *Oenothera fendleri* Gray, Mem. Amer. Acad. Arts II. 4: 45. 1849.

Calylophus hartwegii ssp. **pubescens** (Gray) Towner & Raven, comb. nov. *Oenothera greggii* var. *pubescens* Gray, Pl. Wright. 1: 72. 1852.

Calylophus hartwegii ssp. **filifolius** (Eastw.) Towner & Raven, comb. nov. *Oenothera tubicula* var. *filifolia* Eastw., Proc. Calif. Acad. Sci. III. 1: 72. 1897.

Calylophus hartwegii ssp. **toumeyi** (Small) Towner & Raven, comb. nov. *Galpinsia toumeyi* Small, Bull. Torrey Bot. Club 25: 317. 1898.

Calylophus hartwegii ssp. **maccartii** (Shinners) Towner & Raven, comb. nov. *Calylophus hartwegii* var. *maccartii* Shinners, Sida 1: 343. 1964.

Calylophus tubicula (Gray) Raven, Brittonia 16: 286. 1964. *Oenothera tubicula* Gray, Pl. Wright. 1: 71. 1852.

Calylophus serrulatus (Nutt.) Raven, Brittonia 16: 286. 1964 (published in error as *Calylophus serrulata,* since the gender of *Calyophus* is masculine). *Oenothera serrulata* Nutt., Gen. North Amer. Pl. 1: 246. 1818.

Calylophus drummondianus Spach, Ann. Sci. Nat. Bot. II. 4: 272. 1835 (published as *Calylophis drummondiana*).

Calylophus drummondianus ssp. **berlandieri** (Spach) Towner & Raven, comb. nov. *Calylophis berlandieri* Spach, Ann. Sci. Nat. Bot. II. 4: 273. 1835.

Calylophus australis Towner & Raven, sp. nov. A *Calylopho serrulato* similis, pubescentia sparsa trichomatibus crassis saepe incurvatis differt; foliis oblanceolatis, interdum linearibus, longissimis 15–35 mm longis, 1–4 mm latis, plerumque grosse serratis; petalibus 7–13 mm longis; arenosum "Texas Gulf Coast" secus. Herba suberecta vel effusa, 1.5–5 dm. alta, simplex vel basi ramosa. Folia longissima pubescentia sparsa appressa sursum deorsumque, linearia vel oblanceolata, sub-integra vel grosse serrata, subsessilia, sursum deminuta solum exigue. Tubus hypanthii infundibuliformis, basi tubularis, in sectione transversali subquadratus, costibus 4 prominentibus, 6–12 mm longus, apice 4–9 mm diametro, extus subglaber vel sparse pubescens, intus glaber. Sepala ovata, 4–7 mm longa, exigue vel manifeste costata, apicibus subulatis 0.2–1 mm longis. Petala obovata vel obcordata, saepa vadose incisurata, 7–13 mm longa lataque. Stamina biseriata, filamenta epipetalorum 3–6 mm longa, episepalorum ca. 2–4 mm longa; anthera 2–4 mm longa. Stylus 8–15 mm longus, glaber; stigma discoideum, subquadratum, infra subsulcatum, 1–2 diametro, antheris circumdatum. Capsula cylindrica, sessilis, 12–28 mm longa, 1-2 mm crassa, sparse pubescens. Semina brunnea, 0.7–1 mm longa, ovoidea, acute angulata, extremitate unustantum lateribusque complanata, subgranulosa. Autogama. Numerus chromosomaticus gameticus, $n = 7$.

Type. Texas. Cameron Co: On Texas route 4, 2.8 miles west of end of road at Boca Chica. Large population along low ridge at roadside, ca. 100 yards from tidal sandflat. *Towner 187,* May 29, 1969 (DS 612434-holotype, RSA, TEX, US). Chromosome determination of holotype: $\mathbf{n} = 7$ (ring of 14 at meiotic metaphase I).

Distribution. Occasional on sand and shell-hash soils along Texas Gulf Coast, on shores of bays, and on offshore islands. Occurs from Brazos and Galveston counties south to the Mexican border. Expected from northern coast of Tamaulipas. Seventy-four specimens from the the following herbaria have been examined during the course of this study: ARIZ, DS, F, GH, LL, MO, NEB, NY, OKL, OKLA, PH, POM, RSA, SMU, TEX, US, WTU.

Vouchers for chromosome counts. Texas. Aransas Co.: 1.3 miles west of Copano Village, *Towner 182* (DS), 1 plant with probable ring of 14 and 1 plant with 1_{II} and probable ring of 12; 5.8 miles southeast of Aransas Pass on State Highway 361, *Raven & Gregory 19393* (DS), 2 plants with ring of 14 grown from seed at Stanford. Cameron Co.: Texas Route 4, 2.5 miles west of end of road at Boca Chica, *Towner 188* (DS), 1 plant with probable ring of 14 and 1 plant with 1_{II} and probable ring of 12. Jackson Co.: Texas Highway 35, 11.2 miles west of Palacios, *Towner 175* (DS), one plant with 1_{II}, ring of 12, and 1_{II} of diminutive chromsomes. Matagorda Co.: 6.5 miles south of Matagorda on road to coast (Farm Road 2031), *Towner 174* (DS), probable ring of 14. San Patricio Co.: 3.5 miles south of Ingleside on Farm Road 1069, ca. ½ mile from Corpus Christi Bay, *Towner 184* (DS), 2 plants with ring of 14.

The new species, like *Calylophus serrulatus,* differs from *C. drummondianus* in its smaller flowers, self-compatibility, and pollen sterility of 30-60%. The small-flowered species are complex structural heterozygotes, their 14 chromosomes normally forming a ring at diakinesis. Some individuals of both species exhibit one pair and a ring of 12. Both

C. australis and *C. serrulatus* seem to be derived from *C. drummondianus,* which has normal chromosome pairing during meiosis. They also seem to have arisen independently from *C. drummondianus,* as suggested by their phenetic affinities and geographical ranges.

Calylophus drummondianus ssp. *berlandieri* and *C. australis* are very similar vegetatively, and their flower sizes occasionally overlap. Because of this and their occasional sympatry, some herbarium material is difficult to identify. Unopened buds may be removed from the sheets, and the pollen can be stained and checked for fertility. This method can be used to assign most doubtful specimens to one of the two taxa. Berlandier's type, although from typical *C. australis* habitat, proved to have highly fertile pollen. Thus it was assigned to *C. drummondianus,* and a new type was required for the structural heterozygote.

Calylophus australis differs from *C. serrulatus* primarily in the short, thick, sparse stem hairs, versus the fine, appressed, dense canescence of the latter species. There are some plants from eastern Texas which have the pubescence of *C. australis,* but have longer leaves and taller stature. *Calylophus australis* has short, usually coarsely serrate leaves, and is sub-erect. *Calylophus serrulatus* has a wide range of leaf dimensions, but the margins are coarsely serrate only in specimens whose leaf size exceeds that of *C. australis*. *Calylophus serrulatus* occurs throughout the Great Plains, occupying a wide range of soil types, while *C. australis* is endemic to sandy soil, generally along the southern coast of Texas. The two species seem to come into contact only in inland eastern Texas. In Brazos and Madison counties, the populations are *australis*-like, and in neighboring counties to the north the plants combine the pubescence of *C. australis* and the large leaves of eastern *C. serrulatus*. These intermediate populations seem to be isolated slightly from the main distributions of the two species. They may be occupying an area of former hybridization or they may be further autogamous derivatives of *C. drummondianus*.

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TWO NEW SPECIES AND SOME NOMENCLATURAL CHANGES IN OENOTHERA SUBG. HARTMANNIA (ONAGRACEAE)

Peter H. Raven and Dennis R. Parnell

For the past three years, we have been engaged in a detailed biosystematic investigation of *Oenothera* subg. *Hartmannia.* At this time, it appears desirable to record some of our findings which affect the names in the group so that these names will be available for other publications. This work has been supported by a series of grants from the National Science Foundation, most recently by GB-7879X.

Oenothera platanorum Raven & Parnell, sp. nov. Herba perennis basi pauci- vel multiramosa, radice crassa, 0.5–5.6 dm alta, strigulosa. Folia anguste elliptica vel elliptica, raro anguste ovata, subserrata vel subintegria; folia basalia rosulata, 1–7 cm longa, 4–14 cm lata, interdum sinuato-pinnatifida, subglabria vel strigulosa praesertim ad nervos costamque; folia caulina 1.2–5 cm longa, 3–11 mm lata; petiolum 3–32 mm longum. Inflorescentia erecta. Sepala sub anthesi connata, apicibus sublatis ad 1.5 mm longis, 7.5–11.5 mm longa, 1.5–2 mm lata, strigulosa. Petala rosea, 8–14 mm longa, 8–12.5 mm lata. Filamenta 4–9 mm longa; antherae 2.5–3.5 mm longae. Lobi stigmatis 2–4 mm longi. Stylus 12–19 mm longus. Tubus hypanthii 9–14 mm longus, apice 1.5–3 mm diametro, extus strigulosus. Capsula clavata vel anguste obovoidea, 9–14 mm longa, 3–4 mm crassa, 4-angulata, in quoque angulo vulvulaque costa prominente, loculae subdistinctae; pedicellus 4–15 mm longus. Semina dilute brunnea, 0.7–0.9 mm longa, 0.3–0.5 mm crassa, anguste obovoidea vel interdum ovoidea, ad columnam persistentem centralem affixa. Numerus chromosomaticus gameticus, **n** = **7.**

Type. ~~Texas~~. Cochise Co: Near Fort Huachuca. *Lemmon 2704,* May 1846 (F 99335-holotype, F, G, GH, US).

Additional specimens examined. ARIZONA. Cochise Co.: Fort Huachuca, base of Huachuca Mts., *Mearns 1527* (US); near Fort Huachucha, *Wilcox 190* (US); Bear Creek Huachuca Mts., *Goodding 272* (RSA); Garden Canyon, Huachuca Mts., *Kearney & Peebles 14070* (GH, US); Huachuca Mts., *Holkner 1662* (DS, US), *Toumey* in 1894 (GH, US); Hereford, *Jones* in 1947 (POM). Gila Co.: Rio San Carlos, *Mohr 269* (US). Pima Co.: Fort Lowell, Tucson, *Thornber 457* (DS, MO, US). Pinal Co.: near Sacaton, *Harrison 1778* (US). Santa Cruz Co.: Sycamore Canyon, *Mason 1685* (MEX); near Canelo, *Arnold* in 1938 (DS, GH).

This proposed new species is most closely related to the widespread *rosea* L'Hér. ex Ait., to which it is superficially similar. In that species, however, the hypanthial tube is only 5–7 mm long and the petals only 5–8 mm long and 4–6.5 mm wide. More importantly, *O. rosea* is a complex structural heterozygote, the chromosomes forming a ring of 14 at meiotic metaphase I (Raven and Parnell, unpubl.), whereas *O. platanorum,* as determined by an examination of 3 plants grown from the progeny of *Parnell 1031,* from Sycamore Canyon, Santa Cruz Co., Arizona, forms 7 bivalents at meiotic metaphase I. Like other complex structural heterozygotes in Onagraceae, *O. rosea* has only 40–60 per cent stainable pollen, *O. platanorum* normally more than 95 per cent. Although it is at present known only from southern Arizona, *O. platanorum* will doubtless eventually be discovered in adjacent northern Mexico, since it occurs within a few miles of the international border.

Oenothera texensis Raven & Parnell, sp. nov. Herba perennis erecta 2.5–5 dm alta, basi pauci- vel multiramosa, radice crassa, strgulosa sparse hirsutaque. Folia elliptica vel anguste ovata, raro ovata, serrulata vel sinuato-pinnatifida (praesertim basalia), subglabria vel sparse strigulosa praesertim ad nervos costamque, raro dense hirsuta, 2.5–4 cm longa, 8–18 mm lata; petiolum 4–21 mm longa. Inflorescentia erecta. Sepala sub anthesi connata, apicibus subulatis ad 2 mm longis, 15–18 mm longa, 2–4 mm lata, strigulosa. Petala rosea, 12–21 mm longa, 10–20 mm lata. Filamenta 9–13 mm longa; antherae 3.5–6 mm longae. Lobi stigmatus 3.5–6 mm longi. Tubus hypanthii 15–21 mm longus, apice 3–4 mm diametro, extus dense strigulosa. Capsula obovoidea, 8.5–14 mm longa, 3.5–6 mm crassa, valde 4-angulata, in quoque angulo valvulaque costa prominente, loculae subdistinctae; pedicellus 7–12 mm longus. Semina delute brunnea, 0.8–1 mm longa, 0.2–0.3 mm crassa, obovoidea vel ovoidea, ad columnam persistentem centralem affixa. Numerus chromosomaticus gameticus, **n** = **7.**

Type. Texas. Jeff Davis Co: Upper Limpia Canyon near Mt. Livermore, *Ferris* & *Duncan 2539* (DS 124606-holotype, MO), July 9-12, 1921.

Additional specimens examined. TEXAS. Jeff Davis Co.: Limpia Canyon, *Nealley 145* (F); Fort Davis, *Young* in 1918 (US); 5 miles n w of McDonald Observatory, *Innes & Moon 1141* (GH, TEX); Davis Mts., *Palmer 34376* (US).

MEXICO. Coahuila. Santa Rosa Mts., *Marsh 1375* (TEX); Sierra del Carmen, Cañon de Sentenela on Hacienda Piedra Blanca, *Wynd & Mueller 513* (MICH, S); Muzquiz, *Marsh 643* (TEX). Sinaloa. Ocurahui, Sierra Surotato, *Gentry 6343* (MICH). Tamulipas. Summit of Cerro Zamora, Sierra de San Carlos, *Bartlett 13750* (MICH); Mesa de Tierra, vicinity of San Jose, *Bartlett 10452* (MICH).

Oenothera texensis differs markedly from both *O. rosea* and *O. platanorum,* its closest relatives, in its much larger flowers. Like *O. platanorum,* it regularly forms seven bivalents at meiotic metaphase I (determined in an examination of four plants from the progeny of *Parnell 1029,* from along stream bed, 6.2 miles north of city limit of Fort Davis, Jeff Davis Co., Texas); and also like that species, it regularly has 95 per cent or more stainable pollen.

OENOTHERA EPILOBIIFOLIA H.B.K. ssp. EPILOBIIFOLIA, Nov. Gen. & Sp. 6: 92. 1823. *O. multicaulis* R. & P. var. *tarquensis* sensu Munz, Amer. J. Bot. 19: 757. 1932; North Amer. Fl. II. 5: 81. 1965, pro parte; non *O. tarquensis* H.B.K., Nov. Gen. & Sp. 6: 91. 1823.

OENOTHERA EPILOBIFOLIA ssp. **cuprea** (Schlecht.) Raven & Parnell, comb. nov. *O. cuprea* Schlecht., Linnaea 12: 269. 1838. *O. multicaulis* R. & P. var. *tarquensis* sensu Munz, Amer. J. Bot. 19: 757. 1932; North Amer. Fl. 11. 5: 81. 1965, pro parte; non *O. tarquensis* H.B.K., Nov. Gen. & Sp. 6: 91. 1823.

In this subspecies, which is found from central Mexico to Costa Rica and again in southern Colombia, the yellow petals at anthesis have a bright red blotch in the lower third to half; in ssp. *epilobiifolia,* they are entirely yellow. *Oenothera epilobiifolia* ssp. *epilobiifolia* is found in central and northern Colombia and adjacent Venezuela. In both subspecies, the petals fade red after fertilization.

OENOTHERA MULTICAULIS R. & P., Fl. Peruv. 3: 80, t. 317. 1802. *O. tarquensis* H. B. K., Nov. Gen. & Sp. 6: 91. 1823. *O. multicaulis* var. *tarquensis* (H. B. K.) Munz & Johnston, Contr. Gray Herb. 75: 18. 1925.

Our unpublished investigations have shown that this species, in the sense of Munz (Amer. J. Bot. 19: 755–765. 1932), consists of two biological entities. One of these, corresponding largely to his var. *typica,* is a complex structural heterozygote which regularly forms a ring of 14 chromsomes at meiotic metaphase I and is best known from high elevations in Peru and Bolivia. This relatively small-flowered species also ranges north to Ecuador, however, and as shown by a comparison between recent collections from the Río Tarquí (Valley of the Río Tarquí, a few km s. of Cuena, *Giles 43a*) and the type of *O. tarquensis* H. B. K. (P), includes that entity. The oldest available name for the larger-flowered, bivalent-forming species in then *O. epilopiifolia,* but it corresponds largely to the entity that has been known as *O. multicaulis* var. *tarquensis* (H. B. K.) Munz & Johnston. Like other complex structural heterozygotes in Onagraceae, *O. multicaulis* forms only 40 to 60 per cent stainable pollen, whereas in *O. epilobiifolia* the plants regularly have 95 per cent or more stainable pollen. A few popualtions in southern Ecuador and Peru which are evidently not complex structural heterozygotes are currently under investigation.

OENOTHERA KUNTHIANA (Spach) Munz, Am. J. Bot. 19: 759. 1932. *Hartmannia domingensis* Urban & Ekman, Ark. Bot. 23A: 28. 1931. *Oenothera domingensis* (Urban & Ekman) Munz, North Amer. Fl. II. 5: 82. 1965.

An examination of the holotype of *Hartmannia domingensis* (S) has shown it to be referable to this widely distributed complex structural heterozygote (Raven and Parnell, unpubl.). It has hitherto been compared with *O. rosea,* to which it is only distantly related, and this has led to its continued recognition as a species.

OENOTHERA SPECIOSA Nutt., Jour. Acad. Nat. Sci. Philadelphia 2: 119. 1821. *O. delessertiana* Steud., Nom. Bot. ed. 2. 2: 206. 1841. *O. speciosa* var. *childsii* (Bailey) Munz, Leafl. W. Bot. 2: 87. 1935.

Although populations of this species from north Texas northward are often diploid (**n** = 7), with white flowers that open at sunset, whereas those from central Texas southward and also common in cultivation and occasionally established elsewhere are usually tetraploid (**n** = **14**), with rose-purple flowers that open near sunrise, intensive studies in the field have shown that these correlations do not always hold true (Raven and Parnell, unpubl.). It seems best, therefore, to group all of these plants in one species, without subdivision, and to describe the characteristics of particular populations of interest rather than to accord them distinctive Latin names.

SUMMARY

Critical remarks on *Oenothera* subg. *Hartmannia* are presented. Two new species, *O. platanorum* and *O. texensis,* which for bivalents at meiotic metaphase I, are segregated from the complex structural heterozygote, *O. rosea,* which forms a ring of 14 chromosomes at meiotic metaphase I. The pair-forming *O. epilobiifolia* (*O. multicaulis* var. *tarquensis* of most authors) is segregated from the complex structural heterozygote *O. multicaulis,* whereas *O. domingensis* is synonymized with *O. kunthiana* and *O. delessertiana* with *O. speciosa.* With these changes, we currently recognize the following species of subg. *Hartmannia* as valid: *O. seifrizii* Mung, *O. epilobiifolia* HBK., *O. multicaulis* R. & P., *O. tetraptera* Cav., *O. kunthiana* (Spach) Munz, *O. deserticola* (Loesener) Munz, *O. purpusii* Munz, *O. texensis* Raven & Parnell, *O. platanorum* Raven & Parnell, *O. rosea* L'Her. ex Ait., and *O. speciosa* Nutt. All of these species are diploid (**n** = **7**) except for the last, in which autotetraploids (n = 14) occur commonly: and all of the diploids form bivalents at meiotic metaphase I except for *O. kunthiana, O. multicaulis,* and *O. rosea,* which are complex structural heterozygotes. *Oenothera speciosa* is self-incompatible, all the others are self-compatible, with varying degree of out crossing.

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(Editorial note. The following series of papers dealing with the Galápagos Islands are published together here in anticipation of the *Flora of the Galápagos Islands* being edited by Ira L. Wiggins and Duncan M. Porter. — J. H. T.)

STUDIES ON PLANTS OF THE GALÁPAGOS ISLANDS. I. NEW SPECIES AND COBINATIONS

Ira L. Wiggins

Galium galapagoense Wiggins, sp. nov. Herba gracillima pluribus caulibus e basi communi tenuibus quadrangulis adscentibus vel scandentibus usque 1 m longi sparse scaberulis. Folia plerumque 4-verticillata 3—7 cm distantia; lamina membranaceo-herbacea elliptica vel obovato-elliptica apice rotundata breviter apiculata basi sub cuneata, utrinque sparse pilosa margina scabra, 5—17 mm longa, 2—9 mm lata. Flores minuti sessile in cymis axillaribus paucifloris dispositi; ovarium subglobosum unicate pilose 0.6—0.8 mm diamentiens; corolla rotata flavescens in lacinias 4 ovatas acuminatus 1 mm longas divisa; stamina paullum infra faucem inserta, filamentia brevissime, antherae parvae rotundato-ellipsoidae vix 0.3 mm longae; stylus 1—1.4 mm longus in ramulis 2 breves subdivergentus corolla laciniis circa dimidio breviores divisus; stigmatibus capitatis coronatis. Fructus subglobosus 1.5—2 mm diametiens ruber breve papillatus.

Holotype. Ecuador. Isla Santa Cruz. Flanks of Cerro Copa, near center of island, altitude about 570 m. *Sigvard Horneman 2,* Feb. 8, 1964 (DS).

This species is unlike any of the known species of *Galium* on the mainland of South America, particularly in that the dichasium has each terminal flower sessile between the subtending leaves, and with the slender branches of the next order of the inflorescence arising in the axils between the leaves and the terminal flower. This system of branching and flowering repeats itself two to four times in each axillary dichasium. The arrangement is totally unlike that in *Relbunium,* to which the plant was referred by Stewart (Proc. Calif. Acad. Sci. IV. 1: 146. 1911). Occasionally one of the axillary branches in a dichasium fails to develop, and then the morphologically terminal flower appears to be axillary to a leaf borne on a straight branch.

The minute flowers are distinctive, also, for they are no more than 2—2.4 mm wide when fully open, and the cup is about 1 mm deep.

The leaves are distinctly 3-nerved, and generally are considerably thinner than those of *Galium ferrugineum* Krause, to which it would key in Macbride's *Flora of Peru* (Field Mus. Nat. Hist., Bot. Ser. 13(6): 260. 1936). *Galium ferrugineum* has 1-nerved leaves, with pinnately arranged secondary veins, and the tissue is much more coriaceous than that in *G. galapense.*

Galium has not been reported, as such, from the Archipiélago de Colón by earier workers.

Passiflora colinvauxii Wiggins, sp. nov. Herba scandens sparsim puberula mox glabra, caule angulato; stipulae setaceae falcatae 2—4 mm longae; folia membrancea bilobata integra trinervia 3—5 cm longa 7—16 cm lata basi rotundata vel subtruncata, lobis oblongo-lanceolatis divaricatis acutis vel obtusis lobo medio obsoleto vel brevissimo, petiolo gracili eglanduloso; bracteae setaceae librae integrae falcatae; tubus calycis cupulatus 6—7 mm latus glaber, sepalis late oblongis 6—7 mm longis 3—4 mm latis apice rotundatis; petalae albae membranaceae 2—2.5 mm latae 3.5—6 mm longae anguste oblongae; corona biseriata, filamentis purpureis vel apicem albis, exterioribus longioribus; operculum membranaceum plicatum incurvatum breviter fimbriatum. Ovarium ovoideum glabrum; fructus anguste ovoideus 3—4 cm longus 1.5—2 cm latus glaber; semina ovoidea-lenticularia 2—2.5 mm longa ca 2 mm lata minute corrugata fusca.

Holotype. Ecuador. Isla Santa Cruz. In treeless region en rounte to El Chato (west of village of Bella Vista). *Paul A. Colinvaux 443,* July 30, 1966 (DS).

The label on the holotype further states, "Creeping plant, covering large areas of ground and climbing on trees. Flowers white, fruits green."

This species is strikingly different from the other two passifloras known to occur on the Galápagos Islands, both in the broad, lunate leaves and in the narrowly ovoid fruits. The ocelae at the base of the leaf blade are rather conspicuous, but the herbage is eglandular, and no glands occur on the petioles.

Sicyocaulis Wiggins, gen. nov. Cucurbitaceae. Herba graciles scandentes radice perennante. Folia integra vel plus minusve lobata; petiolus gracilis quam lamina paullo brevior. Cirrhi bifidi vel rarissime simplices. Flores monoici minuti lutei. Flores masculi pedicellati ad apices racemorum dispositi; pedunculis gracilibus foliis duplo longioribus. Receptaculum complanatum latum. Sepala dentiformia minuta. Corolla profunde 5-partida segmentis ovatis vel lanceolatis integris. Stamina 4, filamentis connatis basi tubo receptaculii inserta; antherae oblongae omnes biloculares in capitulum subglobosum conniventes. Pistillodeum nullum. Flores feminei pedicellati solitarii vel 2—3 ad bases racemorum dispositi, perianthium ut in mare. Staminodia nulla. Ovarium ovoideum unilocularis, stylus gracilis in stigmata non profunde bifida divisus; ovulum unum pendens. Fructus ovoideus rostratus ad basem parce minutusque spinulosus. Semen solitarium oblongus compressum testa firma laevis vel ad apicem minute tuberculata.

This plant keys out to the vicinity of *Sicyos* in Hutchinson (Gen. Fl. Pl. 2: 411. 1967) and at first glance resembles that genus. But the flowers are much smaller than any I have seen in that genus, the pistillate flowers are not gathered into heads of several flowers, each flower being slenderly pedicellate. Further, the forward-pointing, few spines at the base of the fruit are quite unlike the radiating, numerous bristles common on the fruits of *Sicyos*.

Neither can it be placed in the genus *Frantzia,* for that genus has the female flowers borne singly in the axils, or paired in that position with a male flower. In contrast, our plant has the pistillate flowers borne on slender pedicels at or near the base of the flowering part of the racemes, these always being long-stalked and the flowers removced a considerable distance from the stem on which the peduncle is borne.

Type species. *Sicyocaulis pentagonus* Wiggins.

Sicyocaulis pentagonus Wiggins, sp. nov. Plantae monoicae scandens 3—5 m altae; rami gracillimi angulatosulcati sparse puberula vel subglabra internodia 1—2 dm longa; cirrhi bifidi graciles elongati glabri ramis 10—25 cm longis; folia alterna, petiolis gracilibus 2—8 (—10) cm longis, laminae minute scaberulae, cordato quinquelobae 2—12 cm logae et latae, sinu basali 2—3 cm profundo; inflorescentiae racemosae 1—5 cm longae elongatae; pedicelli 3—6 mm longi filiformes ad apicem clavatos; sepals minute; lobi corollae oblongi 0.6—1 mm longi 0.4—0.6 mm lati acuti vel minute apiculati flavascentes glabri; columna staminum gracilis 1—1.4 mm alta antheris ca 0.6 mm longis interne ad columnam adnatis externe libris; fructus ovoideus 10—15 mm longus 4—5 mm latus rostratus rostello 2.5—3 mm longo, fructu supra basin sparce spinoso parallelo ad axem.

Holotype. Ecuador. Isla Santa Cruz. Along trail about 1 km south of Bella Vista, along trail from Bahía Académia, altitude about 225 m. *I. L. Wiggins 18679,* Feb. 21, 1964 (DS).

Plantago paralias Decne. var. **pumila** (Hook.f.) Wiggins, comb. nov. *P. tomentosa* Lam. var. *?pumila* Hook.f., Trans, Linn. Soc. Lond. 20: 194. 1847.

Hooker's specimen was inadequate, consisting only of three or four very depauperate plants that scarcely showed the characters needed to make an identification. Its relationship, as disclosed by more and larger plants collected in 1964, clearly show its relationship with *Plantago paralias*. Known from Islas San Cristóbal, Santa Cruz and Santa Maria.

Vallesia glabra (Cav.) Link var. **pubescens** (Anderss.) Wiggins, comb. nov. *V. pubescens* Anderss., Kongl. Svensk. Vet.-Akad. Handl. 1853: 195. 1855.

Differing from var. *glabra* only in having a fine, closely arranged, erect indument of simple, non-glandular hairs on the twigs, petioles, inflorescences and under surfaces of leaf blades, and certainly not worthy of a higher nomenclatoral rank.

Known only from the Galápagos Islands and there occurring on at least six of the islands. Plants from Central America sometimes approach this, but have fewer hairs on the young vegetation.

Division of Systematic Biology, Stanford University

A NEW COMBINATION IN TRICHONEURA FROM THE GALÁPAGOS ISLANDS

John R. Reeder and Charlotte G. Reeder

Trichoneura lindleyana (Kunth) Ekman var. **albemarlensis** (Robins. & Greenm.) Reeder & Reeder, comb. nov. *Leptochloa albemarlensis* Robins. & Greenm., Amer. J. Sci. III. 50:145. 1895.

Known from Islas Genovesa, Isabela, Pinta, San Salvador, Santa Cruz, and Santa María.

Department of Botany, University of Wyoming, Laramie

A NEW COMBINATION IN CHAMAESYCE FROM THE GALÁPAGOS ISLANDS

Derek Burch

Chamaesyce **nummularia** (Hook. f.) Burch var. **glabra** (Robins. & Greenm.) Burch, comb. nov. Amer. J. Sci. III. 50:144. 1895. *Euphorbia nummularia* var. *glabra* Robins. & Greenm., Amer. J. Sci. III. 50: 144. 1895.

Differs from var. *nummularia* only in being completely glabrous.

Known only from Isla Santa María. Recollected by Uno Eliasson in 1966 and 1967 and apparently well established at altitudes of 5–15 m at Las Cuevas and at Black Beach.

University of South Florida, Tampa

NEW COMBINATIONS IN THE CYPERACEAE OF THE GALÁPAGOS ISLANDS

Tetsuo Koyama

Cyperus polystachyos Rottböll ssp. **holosericeus** (Link) T. Koyama, comb. nov. *C. holosericeus* Link, Hort. Berol. 1:317. 1827. *C. microdontus* Torr., Lyceum Nat. Hist. New York 3:255. 1836. *C. gatesii* Torr., Lyceum Nat. Hist. New York 3:255. 1836. *C. microdontus* var. *texensis* Torr., Lyceum Nat. Hist. New York 3:430. 1836. *C. fugax* Liebm., Vidensk. Selsk. Skr. Kjoeb. ser. 5. 196. 1851. *C. inconspicuus* Liebm., Viednsk. Selsk. Skr. Kjoeb. ser. 5. 197. 1851. *C. liebmannii* Steudel, Syn. Pl. Glumac. 2:7. 1854. *C. texensis* Steudel, Syn. Pl. Glumac. 2:9. 1854. *C. polystachyos* var. *leptostachyus* Böckeler, Linnaea 35:478. 1868. *C. polystachyos* var. *laxiflorus* C. B. Clarke, in Urban, Symbol. Antill. 2(1):17. 1900. *C. polystachyos* var. *leptostachyus* f. *inconspicuus* Kükenth., in Engler, Pflanzenreich IV. 20:372. 1936. *C. polystachyos* var. *leptostachyus* f. *fugax* Kükenth., in Engler, Pflanzenreich IV. 20:372. 1936. *C. polystachyos* var. *texensis* Fernald, Rhodora 41:530. 1939.

In the Galápagos Islands, known only from Isla San Salvador.

Cyperus virens Michx. ssp. **drummondii** (Torr. & Hook.) T. Koyama, comb. nov. *C. drummondii* Torr. & Hook., Lyceum Nat. Hist. New York 3:437. 1836. *C. virens* var. *drummondii* Kükenth., in Engler, Pflanzenrecih IV. 20. 181. 1936. *C. surinamensis* sensu Anderss., Kongl. Vetensk. Acad. Handl. 1853:153. 1855; sensu Robins., Proc. Amer. Acad. Arts 30:129. 1902; sensu Eliasson, Svensk. Bot. Tidskr. 59:478. 1965, non Rottböll.

In the Galápagos Islands known from Islas San Cristóbal and Santa Cruz.

Rhynchospora nervosa (Vahl) Böckeler ssp. **ciliata** (Vahl) T. Koyoma, comb. nov. *Dichomena ciliata* Vahl, Enum Pl. 2:246. 1806. *R. ciliata* Kükenth., Bot. Jahrb. Syst. 56 (Beibl. 125):16. 1921. *R. nervosa* var. *ciliata* Kükenth., Bot. Jahrb. Syst. 75:295. 1951.

Known in the Galápagos Islands from Islas Isabela, San Cristóbal, and Santa Cruz.

New York Botanical Garden, Bronx

A NEW VARIETY OF OPUNTIA MEGASPERMA FROM THE GALÁPAGOS ISLANDS

J. Lundh

Opuntia megasperma Howell var. **mesophytica** J. Lundh, var. nov. Plantae arborescentes vertice apertae; articuli caulium atrovirides; spinae 2.5–3.9 cm longae aureofulvae albescentes apicem fuscae; flores parvi 6–8 cm longi; fructus parvi 4–6 cm longi.

Plants more or less arborescent, with open crowns and slender, vertical branches 2–6 m tall; trunk up to 40 cm in diameter, brownish; larger terminal joints dark green becoming gray-green, obovate to elongate, 12–20 cm long, 5.5–9.5 cm wide, 0.8–1.7 cm thick; leaves 3–7 mm long; areoles ovate, 1.5–2 mm in diameter, typically 1.8–2.2 cm apart; spines often nearly absent, golden brown and banded, becoming bone white with a rather dark tip, 1–17 per areole, 2.5–3.9 cm long, 0.5–1 mm in diameter basally; flowers about 6 cm in diameter, 6–8 cm long; fruits 4–6 cm long, 2.7–3.6 cm in diameter; seeds 7–10 mm long, 5–8 mm wide, 2–4 mm thick.

Holotype. Chatham Island (Isla San Cristóbal), Galápagos Islands, Ecuador, *J. Lundh s. n.*, in 1962 (AHFH).

Known only from the western end of Isla San Cristóbal, where it has been collected by Lundh and by E. F. Anderson.

NEW COMBINATIONS IN THE COMPOSITAE OF THE GALÁPAGOS ISLANDS

ARTHUR CRONQUIST

DARWINIOTHAMUS TENUIFOLIUS (Hook. f.) Harling var. **glabriusculus** (Stewart) Cronquist, comb. nov. *Erigeron lancifolius* var. *glabriusculus* Stewart, Proc. Calif. Acad. Sci. IV. 1:151. 1911. *E. lancifolius* Hook. f., Trans. Linn. Soc. London 20:208. 1847. *E. tenuifolius ssp. lancifolius* Solbrig, Contr. Gray Herb. 191:43. 1962. *D. lancifolius* Harling. Acta Horti Berg. 20(3):115. 1962.

Known only from Isla Isabela.

DARWINIOTHAMNUS TENUIFOLIUS (Hook. f.) Harling var. **glandulosus** (Harling) Cronquist, comb. nov. *D. lancifolius* ssp. *glandulosus* Harling, Acta Horti Berg. 20(3):117. 1962.

Known only from Islas Fernandina and Isabela.

POROPHYLLUM RUDERALE (Jacq.) Cass. var. **macrocephalum** (DC.) Cronquist, comb. nov. *P. macrocephalum* DC., Prodr. 5:648. 1836. *P. ruderale* ssp. *macrocephalum* R. R. Jhtn., Univ. Kansas Sci. Bull. 48:233. 1969.

In the Galápagos, known from 11 islands. A widespread weed.

PSEUDOLEPHANTOPUS **spiralis** (Less.) Cronquist, comb. nov. *Distreptus spiralis* Less., Linnaea 6:690. 1831. *Spirochaeta funckii* Turcz., Bull. Soc. Imp. Naturalistes Moscou 24:167. 1851. *Chaetospira funckii* Blake, J. Wash. Acad. Sci. 25:331. 1935. *P. funckii* Philipson, J. Bot. 76:301. 1938.

Theer is a small problem about the typification of *Pseudelephantopus spiralis,* inasmuch as the original publication of *Distreptus spiralis* Less. gave the locality as Jamaica. The species is not otherwise known there, although it is found occasionally in the Lesser Antilles and is widespread on the South American mainland. However, the description is so clearly that of the present species that it seems necessary to take up Lessing's epithet.

In the Galapagos Islands known from a single collection (*Wiggins & Porter 632,* DS), taken at an altitude of about 570 m on Isla Santa Cruz.

Lecocarpus is a genus of three closely allied species, endemic to the Galápagos Islands. Two of the species have usually been referred to the related genus *Acanthospermum,* but the unity of the group is obvious and has often been remarked. In the course of my work I learned that Tod F. Stuessy, then a graduate student at the University of Texas had independently arrived at similar conclusions in connection with his study of *Acanthospermum.* Accordingly, the necessary new combinations are attributed here to Cronquist and Stuessy. As this manuscript goes to press (June 1970) we have learned that Uno Eliasson would have made the combination *L. lecocarpoides,* had we not done so.

LECOCARPUS **lecocarpoides** (Robins. & Greenmn.) Cronquist & Stuessy, comb. nov. *Acanthospermum lecocarpoides* Robins. & Greenm., Amer. J. Sci. III. 50. 141. 1895.

LECOCARPUS **leptolobus** (Blake) Cronquist & Steussy, comb. nov., *Acanthospermum leptolobum* Blake, J. Wash. Acad. Sci. 12:204. 1922.

New York Botanical Garden, Bronx

NEW COMBINATIONS AND TAXA IN THE CACTACEAE OF THE GALÁPAGOS ISLANDS

EDWARD F. ANDERSON and DAVID L. WALKINGTON

JASMINOCEREUS THOUARSII (Weber) Backeb. var. **delicatus** (Dawson) Anderson & Walkington, comb. nov. *J. howellii* Dawson, J. Cact. Succ. Soc. Amer. 34:71. 1962. *J. howellii* var. *delicatus* Dawson, J. Cact. Succ. Soc. Amer. 34:71. 1962.

Known from Islas Bartolomé, San Salvador, and Santa Cruz.

JASMINOCEREUS THOUARSII (Weber) Backeb. var. **sclerocarpus** (K. Sch.) Anderson & Walkington, comb. nov. *Cereus sclerocarpus* K. Sch. in Robins., Proc. Amer. Acad. Arts 38:179. 1902. *J. sclerocarpus* Backeb., Jahrb. Deutsch. Kakteen-Ges. 2:24. 1944.

Known from Islas Fernandina and Isabela.

OPUNTIA ECHIOS Howell var. **zacana** (Howell) Anderson & Walkington, comb. nov. *O. zacana* Howell, Proc. Calif. Acad. Sci. IV. 21:48. 1933. *O. galapageia* Hensl. var. *zacana* Backeb., Cactaceae 1:562. 1958.

Known only from tiny Isla Seymour, off the northeast segment of Isla Santa Cruz.

OPUNTIA GALAPAGEIA Hensl. var **profusa** Anderson & Walkington, var. nov. Habitus variabilis; folia parva, usque ad 4 mm longa; trichomata numerosa; spinae non valde dimorphe nec pungentes; fructus profusi 17–25 mm longi, 22–27 mm diametro, spinas raro ferens.

Plants variable, mostly prostrate, or shrubby to arborescent, 1–3 m tall; trunk, when present, flaky and reddish; larger terminal joints 21–38 cm long, 18–26 cm wide, 1.8–2.7 cm thick; leaves small, up to 4 mm long; areoles 4–6 mm in diameter, typically 2.2–3.3 cm apart; spines bristly, pungent only on new stem joints; fruits greenish, becoming yellow-green to brown, with glochids on some, without spines, nearly globose, 1.7–2.5 cm long, 2.2–2.7 cm in diameter, with a deep, small, greenish brown umbilicus, the fruits often profuse, up to 82 on a single joint; seeds 2–3 mm long, 1.5–2 mm wide, 1 mm thick.

Holotype. Northwest corner of Isla Rábida, Galápagos Islands, Ecuador, *Anderson 2546* (RSA).

Occurring from near sea level to about 100 m elevation on Isla Rábida, the only island from which it is known.

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NOTES ON GALÁPAGOS EUPHORBIACEAE

Grady L. Webster

Croton

As noted by a number of observers (especially Stewart, Proc. Cal. Acad. Sci. IV. 1:206–209, 215–216. 1911), plants of *Croton* are an important component of the woody vegetation of the Galápagos at both low and high elevations; and in the arid zones *Croton* may be the vegetational dominant. Although Andersson (Kongl. Svenska Freg. Eugenies Resa, Bot. 105, 106. 1857) recognized six species of Galápagos *Croton,* Mueller Argoviensis (DC., Prodr. 15(2):604–606. 1866) amalgamated all of the Galápagos taxa into the single species *Croton scouleri,* and later workers such as Robinson and Stewart have followed Mueller's circumscription.

Svenson (Amer. J. Bot. 33:458–460. 1946) not only treated all the Galápagos Crotons as a single species, but combined *C. scouleri* with the South American species *C. rivinifolius* HBK. There is certainly a striking resemblance between these two species, and Svenson may be correct in postulating that the Galápagos taxa were derived by long-distance dispersal from Ecuadorian populations of *C. rivinifolius*. However, the Galápagos plants differ from the mainland ones in a number of respects, especially in the seeds, which are smooth to pitted rather than ribbed as in *C. rivinifolius* and related species. Consequently, it seems best to follow Mueller and retain *C. scouleri* as a distinct polytypic species endemic to the Galápagos. The system of subspecific taxa presented here to some extent resembles that of J. T. Howell, who examined and annotated a large number of collections, but did not publish his conclusions.

The variation in Galápagos *Croton* is still not satisfactorily understood despite the rather considerable number of collections made of these common plants. Unfortunately, many collectors have not carefully noted the habitat conditions or even the altitude at which specimens were taken, so that it is difficult to establish the ecological status of the various proposed taxa. Most of the characters of the taxa recognized here appear to represent segments of altitudinal clines, and only future work can establish whether or not sufficient discontinuities exist to justify maintaining discrete taxa. Inter–island variation is on the whole less well-defined than altitudinal intra–island variation, but one population at least appears to have a distinct seed size. Nevertheless, even seed size is not consistently diagnostic. It is possible that when the local populations are more thoroughly collected any attempt to recognize varieties within the species will have to be abandoned.

The Galápagos populations of *Croton* may be summarized as follows.

Croton scouleri Hook. f., Trans. Linn. Soc. London 20:188. 1947. Lectotype, Isla San Salvador (James), *Scouler* (K-n. v., A-isotype fragment).

The populations of this species endemic to the Galápagos are here classified into four rather ill-defined varieties.

CROTON SCOULERI var. SCOULERI. *C. macraei* Hook. f., Trans. Linn. Soc. London 20: 188. 1847. Type, Isla Isabela (Albemarle), *Macrae* (K-n. v.). *C. albescens* Anderss., Kongl. Vetensk. Acad. Handl. 1853: 242. 1855. Type, Isla Santa María (Charles), in 'locis editioribus umbrosis', *Andersson 208* (A-fragment of type from S.). *C. incanus* Anders., Kongl. Vetensk. Acad. Handl. 1853:243. 1855 (non *C. incanus* HBK.). Type, Isla San Salvador (James), in 'locis siccis', *Andersson* (GH-isotype). *C. scouleri* var. *glabriusculus* Stewart, Proc. Calif. Acad. Sci. IV. 1:89. 1911. Type, Isla Pinta (Abingdon), 1000–1650 ft., *Stewart 1834* (CAS). *C. scouleri* var. *castellanus* Svenson, Amer. J. Bot. 22:239. 1935. Type, Isla Genovesa (Tower), *Snodgrass* & *Heller* (GH-n. v.; no collection of Snodgrass and Heller from Genovesa was seen among the Gray Herbarium specimens, and Svenson may have based the name on the Genovesa collection of Baur).

Illustrations. Svenson, Amer. J. Bot. 22: pl. 4, figs. 1–3; pl. 9, figs 1, 2. 1935.

The majority of lowland *Croton* populations belong to this highly diverse variety. The variation in leaf shape from narrowly linear to elliptic is so striking that all previous authors have accepted the narrow-leaved variant as either a species, *C. macraei,* or a variety. However, this foliar variation appears to be at least partly related to an altitudinal cline, linear-leaved plants in the lowlands being replaced by broad-leaved ones at higher elevations. At some localities (Academy Bay, Isla Santa Cruz) narrow- and broad-leaved forms evidently occur in the same population. The transition between the extremes is so continuous that it seems quite impractical to recognize the narrow-leaved plants as a distinct variety. These stenophyllous variants must be classified only at the rank of forma.

CROTON SCOULERI f. **macraei** (Hook. f.) Webster, comb. nov., based on *C. macraei* Hook. f., cited above.

It is possible that the littoral populations with broad densely stellate leaves, designated as var. *castellanus* by Svenson, may prove to merit varietal recognition, particularly if they prove to be characterized by large seed size (see discussion under var. *darwinii*). However, on the basis of presently available specimens no useful diagnostic characters can be found. The only other outstanding variant of var. *scouleri* is the plant from Isla Pinta described as var. *glabriusculus* by Stewart. The type specimen *(Stewart 1834)* is indeed unique in having stellate hairs with one very long branch on the upper leaf surfaces. However, other specimens from Isla Pinta do not show this character, so the taxon described by Stewart does not appear to make up a discrete population. It may be conveniently referred to at the rank of forma.

CROTON SCOULERI f. **glabriusculus** (Stewart) Webster, comb. nov., based on *C. scouleri* var. *glabriusculus* Stewart, cited above.

CROTON SCOULERI var. **darwinii** Webster, var. nov. Frutex vel arbuscula foliis rotundatis depresso-stellatis, seminibus 3.9–4.5 mm longis.

Type. Isla Darwin (Culpepper), *J. R. Hendrickson* H-7, Jan. 29, 1964 (DS–holotype).

This variety is apparently restricted to the two small northernmost islands, Darwin and Wolf. Some forms of var. *scouleri* are similar in leaf shape and pubescence, but these have smaller seeds (2.6–3.6 mm long). One problematical collection from Isla Daphne (*Pool 290,* BKL) has large seeds over 5 mm long but is vegetatively similar to plants described from Genovesa and elsewhere by Svenson as var. *castellanus.* Although Svenson's variety has here been synonymized with var. *scouleri,* it might prove to be characterized by large seed size, and it is possible that var. *darwinii* would then fall into synonymy under var. *castellanus.* However, until more complete collections are available, this possibility must remain only hypothetical. The plants from Isla Darwin and Isla Wolf in any event have a characteristic aspect, and in the present rudimentary state of our knowledge it seems most reasonable to treat them as a distinct variety.

CROTON SCOULERI var. BREVIFOLIUS (Anderss.) Muell.-Arg., in DC., Prodr. 15(2): 605. 1866. *C. brevifolius* Anderss., Kongl. Vetensk. Acad. Handl. 1853:105. 1855. Type, Isla Santa María (Charles), *Andersson 206* (A-fragment of type from S).

As here circumscribed, this variety is restricted to higher altitudes on Isla Santa María. Although Stewart (Proc. Calif. Acad. Sci. IV. 1:88–89. 1911) recorded this variety from a large number of islands, most of the collections cited are here referred to var. *scouleri.* As presently understood, var. *brevifolius* may be distinguished from var. *scouleri* by the loose tomentum on the undersides of the leaves, and from vars. *darwinii* and *grandifolius* by its smaller seeds.

CROTON SCOULERI var. GRANDIFOLIUS Muell. Arg., in DC., Prodr. 15(2):605. 1866. Type, Isla San Salvador (James), *Darwin* (CGE-isotype, K-holotype–n. v.).

Illustration. Svenson, Amer. J. Bot. 22:272, pl. 4, fig. 5. 1935.

Most plants of Galápagos *Croton* with large leaves (at least 5 cm long and 3 cm broad) may be assigned to this variety, which is recorded from higher altitudes on Isla Isabela, Isla San Cristóbal, Isla Santa Cruz, and Isla San Salvador. In general, specimens of var. *grandifolius* are easily distinguished from those of vars. *darwinii* and *scouleri* by the larger leaves with flocculent tomentum beneath. It is much more difficult to find good diagnostic characters to separate var. *grandifolius* from var. *brevifolius,* although the leaves are usually smaller in the latter. Some specimens from Isla Santa María (*Howell 9312, Stewart 1837*) overlap var. *grandifolius* in size. The seeds of var. *grandifolius* on Isla Santa Cruz appear to be larger, but the seeds of the large-leaved populations on Isabela, San Cristóbal, and San Salvador are still unknown. Until fruiting collections are available, varietal assignment of the specimens from those three islands must remain provisional.

ACALYPHA

In his synopsis of Galápagos *Acalypha*, Robinson (Proc. Amer. Acad. Arts 38: 161–165. 1902) recognized no less than 13 species, including four described by himself. Pax and Hoffmann (Pflanzenreich IV. 147 (XVI): 30–31, 132–134. 1924) accepted all 13 of Robinson's species and placed them into two widely separated taxa: 'sect.' *Phleoideae* in 'ser.' *Polygynae-Acrogynae*, and 'sect.' *Cuspidatae* in 'ser.' *Oligogynae*. This disposition, apparently made on the basis of position of spikes, terminal or axillary, resulted in a completely artificial arrangement of taxa and is wholly untenable, however the species may be circumscribed.

The treatments of Robinson and of Pax and Hoffmann contrast strongly with the earlier one of Mueller Argoviensis, who treated all of the Galápagos taxa of *Acalypha* known to him as seven varieties of the single species *A. parvula*. A detailed analysis of the much larger number of specimens now available shows that Mueller was justified in lumping together under *A. parvula* many of the populations of plants with glandular trichomes. However, the populations of plants with more densely pubescent leaves and stems lacking glandular trichomes do not appear to intergrade with members of the *A. parvula* complex on the several islands where they are sympatric. These non-glandular plants are therefore accepted as distinct species. The newly described *A. wigginsii* is to some extent intermediate between *A. parvula* and *A. sericea* and is sympatric with them on Isla Santa Cruz. The classification thus adopted here, with five species and several varieties, represents a rather unstable compromise between the previous schemes. It, like its predecessors, may have to be extensively remodeled when better population samples are available of these still rather poorly understood taxa.

Glandular trichomes absent or nearly so; young stems densely villose-hirsute

ACALYPHA SERICEA Anderss., Kongl. Vetensk. Acad. Handl. 1853:238. 1855.

This is the most widespread and variable non-glandular species, corresponding to *A. parvula* in the glandular taxa. The species comprises 3 fairly well-marked varieties differing in mean size of leaves, staminate spikes, and seeds.

ACALYPHA SERICEA Anderss. var. SERICEA. *A. parvula* γ *pubescens* Muell.-Arg., Linnaea 34:47. 1865; in. DC., Prodr. 15(2):878. 1866. Type, Isla Isabela, 'locis lapidosis regionis inferioris insulae Albemarle', *Andersson* (S-n. v.). The type locality was originally cited as Isla San

Cristöbal (Chatham), but was corrected in Andersson's later treatment (Kongl. Svenska Freg. Eugenies Resa, Bot. 103. 1857).

Leaves 1–2 (–3) cm long, with mostly 10–15 teeth per side; staminate spikes mostly 3–15 mm long; seeds 1.0–1.2 mm long. Recorded from Marchena (Bindloe) and Pinta (Abingdon); some specimens from Abingdon are unusually glandular and somewhat approach *A. parvula.*

Acalypha sericea Anderss. var. **indefessus** Webster, var. nov. Suffrutex caulibus villosulis eglandulosis, foliis 2.5–5.5 longis, dentibus lateribus c. 15–25, spicis masculis plerumque 5–15 mm longis, seminibus 1.2–1.3 mm longis.

Type. Isla Santa Cruz (Indefatigable), along 'new road' from Bahia Academy to Bella Vista, transition zone, *Wiggins 18672,* Feb. 9, 1964, (DS-holotype). Other collections examined, all from the general locality, include *Fournier 243* (DAV), *Taylor TT59* (CAS), and *Wiggins 18492* (DS).

Endemic to Isla Santa Cruz, in relatively mesic vegetation between 100 and 200 m. The plants resemble var *baurii* from San Cristóbal in aspect, but have much shorter staminate spikes and styles; the larger seeds and leaves (with more teeth per side) provide differential features from var. *sericea.*

Acalypha sericea Anderss. var. **baurrii** (Robins. & Greenm.) Webster, comb. nov. *A. baurii* Robins. & Greenm., Amer. J. Sci. 50:144. 1895. Type, Isla San Cristóbal (Chatam), southwest end, middle region, *Baur 285* (GH).

Leaves mostly 4–6 cm long, with 23–31 teeth per side; staminate spikes 30–60 mm long; seeds 1.2 mm long. Known only from the type collection on San Cristóbal.

Acalypha flaccida Hook. f., Trans. Linn. Soc. London 20:186. 1847. *A. parvula η flaccida* Muell.-Arg., Linnaea 34:48. 1865; in DC., Prodr. 15(2): 878. 1866. Type, Isla San Salvador (James), *Darwin* (CGE).

Known only from the type collection; very similar to *A. sericea* in appearance, but with much smaller, non-hispidulous pistillate bracts in strictly axillary spikes.

Acalypha velutina Hook. f., Trans. Linn. Soc. London 20:186. 1847. *A. parvula γ pubescens ϐ velutina* Muell.-Arg., Linnaea 34:48. 1865; in DC., Prodr. 15(2):878. 1866. Type, Isla Santa María (Charles), *Darwin* (CGE). The variety recognized by Hooker, *A. velutina β minor* (Trans. Linn. Soc. London 20:187. 1847), also based on a Darwin collection from Charles (CGE), is only a small-leaved form of no taxonomic importance.

Very similar to some forms of *A. sericea,* but differing in the axillary spikes and distinctly bullate-rugose leaves. Endemic to Isla Santa María.

Glandular trichomes present, at least on pistillate bracts

Acalypha wigginsii Webster, sp. nov. Annua erecta, caule dense glanduloso-tomentello; foliis ovatis basi cordatis obtuse dentatis 2–7 cm longis, strigoso-hirsutis glandulosisve; spicis axillaribus, parte mascula 1.5–10 mm longa; calycis masculis glabris; involucris foemineis 2–3, 2–floris, ad mediam 6–10-lobis, glandulosis, parce hirsutis; seminibus 1.3–1.5 mm longis.

Type. Isla Santa Cruz (Indefatigable), north slope of Mt. Crocker, alt. ca. 860 m, *Wiggins & Porter 663,* Feb. 18, 1967 (DS–holotype). Additional collections examined, Mt. Crocker, *Wiggins & Porter 665* (DS); Gebirge im Innern, *Schimpff 96* (CAS, MO); among rocks in moist zone, south slope of mountain, alt. 1000 ft., *Svenson 96* (BRKL).

This species is known only from Isla Santa Cruz, where it appears to be restricted to higher altitudes in the mountainous interior. The completely glabrous staminate calyces and large stipules distinguish it from the many taxa of the *A. parvula* complex, while the glandular pubescence sets it apart from the large-leaved species related to *A. sericea.*

ACALYPHA PARVULA Hook. f., Trans. Linn. Soc. London, 20:185. 1847.

All of the small-leaved populations of Galápagos *Acalypha* with glandlar pubescence are referred to this single protean species. As Robinson noted, these plants include annuals and perrenials, erect and prostrate forms, with striking differences in the spikes. His decision to recognize nine species in this complex cannot be followed, because these various marked characters vary in a largely uncorrelated manner from island to island without showing any clear geographic separations. A number of the taxa may be treated as varieties, in approximately the circumscriptions of Mueller, but it must be admitted that these are difficult to distinguish in practice and may not be natural units. The four varieties recognized here are extensively sympatric, and further study may show that they are simply arbitrary assemblages of plants selected from a mosaic of clinal and microgeographic variation.

ACALYPHA PARVULA Hook. f. var PARVULA. Type, Isla Isabela (Albemarle), *Macrae* (K-n. v.). *A. cordifolia* Hook. f., Trans. Linn. Soc. London 20:187. Type, Isla Santa María (Charles), *Darwin* (CGE). *A. diffusa* Anderss., Kongl. Vetensk. Acad. Handl. 1853:240. 1855. Type, Isla Isabela (Albemarle), 'in locis siccissimis', *Andersson* (GH-isotype). *A. spicata* Anderss., Kongl. Vetensk. Acad. Handl. 1853:239. 1854. Type, Isla San Cristóbal (Chatham), *Andersson* (GH-isotype). *A. parvula β cordifolia* Muell.-Arg., Linnaea 34:47. 1865; in D.C., Prodr. 15(2):877. 1866. *A. albemarlensis* Robins., Proc. Amer. Acad. Arts 38:163. 1902. Type, Isla Isabela (Albemarle), Tagus Cove, alt. 1220 m, *Snodgrass & Heller 885* (GH-holotype).

This variety is the most widespread and diverse taxon of Galápagos *Acalypha.* It is recorded from Fernandina, Isabela, Pinzón, San Cristóbal, Santa Cruz, Santa Fé, and Santa María. Only on Española and San Salvador does it appear to be lacking from the larger central islands. Various forms of var. *parvula* are difficult to separate from other varieties of

A. parvula, and sometimes even from specimens of *A. sericea.* However, in the majority of instances the populations included here may be recognized by the axillary pistillate spikes, distinctly glandular erect stems, seeds 1.1 mm long or less, and leaves scarcely exceeding 2 cm long.

ACALYPHA PARVULA var. RENIFORMIS (Hook. f.) Muell.-Arg., Linnaea 34:48. 1865; in DC., Prodr. 15 (2):878. 1866. *A. reniformis* Hook. f., Trans. Linn. Soc. London 20:187. 1847. Type, Isla Santa María (Charles), *Darwin* (CGE). *A. adamsii* Robins., Proc. Amer. Acad. Arts 38:161. 1902. Type, Isla San Cristóbal (Chatham), southwest end, middle region, *Baur 282,* June 1891 (GH).

Stems often prostrate, usually not densely glandular; terminal spikes usually present; pistillate bracts mostly subsessile; seeds small (0.9–1.1 mm long). Recorded from Española, Pinzón, Rábida, San Cristóbal, San Salvador, Santa Cruz, Santa Fé, and Santa María.

ACALYPHA PARVULA Hook. f. var. STROBILIFERA (Hook. f.) Muell.-Arg., Linnaea 34:47. 1865; in DC., Prodr. 15(2):877. 1866. *A. strobilifera* Hook. f., Trans. Linn. Soc. London 20:187. 1847. Type, Isla San Cristóbal (Chatham), *Darwin* (CGE). *A. parvula* α *procumbens* Muell.-Arg., Linnaea 34:48. 1865; in DC., Prodr. 15(2):878. 1866.

Stems usually glandular, spikes terminal or axillary; pistillate bracts usually pedunculate; seeds mostly large (1.2–1.5 mm long). Recorded from Daphne, San Cristóbal and Santa Cruz, common in the vicinity of Academy Bay on the latter island.

ACALYPHA PARVULA Hook. f. var. **chathamensis** (Robins.) Webster, comb. nov. *A. chathamensis* Robins., Proc. Amer. Acad. Arts 38:163. 1902. Type, Isla San Cristóbal (Chatham), *Snodgrass & Heller 541* (GH-lectotype, DS-isotype).

Stems erect, glandular; leaves larger (2.5–4.5 cm long) than in most other forms of *A. parvula*; spikes axillary; seeds small (1.0–1.1 mm long). Endemic to San Cristóbal, where it is known from only one other collection (*Snodgrass & Heller 540,* DS, GH). In aspect, specimens of var. *chathamensis* suggest *A. sericea* var. *baurii,* which also occurs on San Cristóbal; but the glandular and non-velutinous indumentum definitely places them within *A. parvula.*

I wish to thank the curators of the herbaria at Stanford, Harvard, the Brooklyn Botanical Garden, and Cambridge for their generosity in loaning critical specimens. The Darwin collections from the herbarium at Cambridge (CGE) are duplicates of those at Kew examined by Hooker; since the specimens at Kew were not seen, no attempt was made to specify whether the collections at CGE are syntypes or isotypes.

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NOMENCLATURAL CHANGES AND NEW SUBSPECIES IN THE CENTROSPERMAE OF THE GALÁPAGOS ISLANDS

UNO ELIASSON

ALTERNANTHERA FILIFOLIA (Hook. f.) Howell ssp. **glaucescens** (Hook. f.) Eliasson, comb. nov. *Bucholtzia glaucescens* Hook. f., Trans. Linn. Soc. London 20:191. 1847. *Telanthera glaucescens* Moq. in D.C., Prodr. 13:369. 1849. *T. strictiuscula* Anderss., Kongl. Vetensk. Acad. Handl. 1853:166. 1855. *T. angustata* Anderss., Kongl. Svenska Vetenskapsakad. Handl. 1857:61. 1861. *Achyranthes glaucescens* Standley, J. Wash. Acad. Sci. 5:74. 1915. *A. strictiuscula* Standley, J. Wash. Acad. Sci. 5:75. 1915. *Alternanthera glaucescens* Howell, Proc. Calif. Acad. Sci. IV. 21:104. 1933. *A. glaucescens* f. *strictiuscula* Howell, Proc. Calif. Acad. Sci. IV. 21:105. 1933.

This subspecies apparently is restricted to Isla San Cristóbal.

ALTERNANTHERA FILIFOLIA (Hook. f.) Howell ssp. **microcephala** Eliasson, ssp. nov. *A. glaucescens* f. *strictiuscula* sensu Eliasson, Svensk. Bot. Tidskr. 60:143. 1966, not Howell, 1933.

Caules non multos ramos dimittentes, tenues, nonnumquam subglauci; internodia 5–8 cm longa; folia inferiora linearia vel lineariolanceolata, 3–4 cm longa, 2–7 mm lata, glabra; folia superiora filiformia vel linearia, 2–4 cm longa, 0.5–1 mm lata, glabra; capitula superior parte plantae pauca, terminalia vel in brevibus pedunculis axillaribus posita, rotundata, diametro 3–4 mm; flores laxe imbricati, apicibus rectis.

Holotype. Bahía Sullivan, 170 m, Isla San Salvador, Ecuador, *Inga & Uno Eliasson 1393* (S).

Apparently restricted to Isla Bartolomé and to the adjacent areas of Isla San Salvador.

ALTERNANTHERA FILIFOLIA (Hook. f.) Howell ssp. **nudicaulis** (Hook. f.) Eliasson, comb. nov. *Bucholtzia nudicaulis* Hook. f., Trans. Linn. Soc. Lond. 20:191. 1847. *Telanthera nudicaulis* Moq. in DC., Prodr. 13:369. 1849. *Achyranthes nudicaulis* Standley, J. Wash. Acad. Sci. 5:74. 1915. *Alternanthera nudicaulis* Christoph., Nyt Mag. Naturvidensk. 70: 73. 1931.

Known only from Isla Santa María.

ALTERNANTHERA FILIFOLIA (Hook. f.) Howell ssp. **pintensis** Eliasson, ssp. nov.

Caules admodum ramosi, superiore saltem parte trichomatibus albis subramosis praediti; internodia 3–5 (–7) cm longa; folia oblanceolata vel oblongo-lanceolata, 2–3 (–6) cm longa, 4–7 (–15) mm lata, praesertim infra trichomatibus albis stellatis praedita; capitula solitaria vel 2–7–glomerata, ovoidea vel cylindrica, 5–8 mm longa, 3–4 mm lata;

flores admodum dense imbricati sed apicibus liberis rectis; flores trichomatibus densis subflavis simplicibus praediti.

Intermediate in characters between *A. filifolia* ssp. *nudicaulis* and *A. snodgrassii.*

Holotype. At an altitude of about 200 m, Isla Pinta, Galápagos Islands, Ecuador, *Inga & Uno Eliasson 2151* (s).

Known only from Isla Pinta.

ALTERNANTHERA FILIFOLIA (Hook. f.) Howell ssp. **rabidensis** Eliasson, ssp. nov.

Caules et rami superiore parte trichomatibus simplicibus albis praediti; internodia 2–5 cm longa; folia oblanceolata, 2–3 cm longa, 4–7 (–10) mm lata, praesertim infra trichomatibus simplicibus albis praedita; capitula solitaria vel 2–4—glomerata, rotundata vel cylindrica, 4–10 mm longa, 3–4 mm lata; flores laxe imbricati apicibus leviter incurvatis; flores trichomatibus subflavis simplicibus praediti.

Holotype. On top of island, at an altitude of about 390 m. Isla Rábida, Ecuador, *Inga & Uno Eliasson 1414* (S).

Known only from Isla Rábida.

FROELICHIA NUDICAULIS Hook. f. ssp. **lanigera** (Anderss.) Eliasson, comb. nov. *F. lanigera* Anderss., Kongl. Svenska Vetenskapsakad. Handl. 1857:63. 1861. *F. lanata* Anderss., Kongl. Svenska Vetenskapsakad. Handl. 1857: pl. 3, fi. 1. 1861. *F. scoparia* Robins., Proc. Amer. Acad. Arts 38:136. 1902. *F. lanigera* ssp. *scoparia* Howell, Proc. Calif. Acad. Sci. IV. 21:116. 1933.

Occurring on fresh lava fields, especially at high altiudtes, on Islands Fernandina and Isabela.

MOLLUGO FLAVESCENS Anderss. ssp. **gracillima** (Anderss.) Eliasson, comb. nov. *M. gracillima* Anderss., Kongl. Vetensk. Akad. Handl. 1853: 226. 1855. *M. gracilis* Anderss., Kongl. Svenska Vetenskapsakad. Handl. 1857: pl. 15, fig. 3. 1861. *M. gracillima* Anderss. ssp. *latifolia* Howell, Proc. Calif. Acad. Sci. IV. 21:17. 1933. *M. flavescens* Anderss. ssp. *angustifolia* Howell, Proc. Calif. Acad. Sci. IV. 21:18. 1933. *M. flavescens* Anderss. ssp. *intermedia* Howell, Proc. Calif. Acad. Sci. IV. 21.18. 1933.

MOLLUGO FLAVESCENS Anderss. ssp. **insularis** (Howell) Eliasson, comb. nov. *M. insularis* Howell, Proc. Calif. Acad. Sci. IV. 21:19. 1933.

Known only from Islas San Cristóbal and Santa María.

MOLLUGO FLAVESCENS Anderss. ssp. **striata** (Howell) Eliasson, comb. nov. *M. striata* Howell, Proc. Calif. Acad. Sci. IV. 21:19. 1933.

Known only from the type collection (*Stewart 1477,* CAS), from Isla Wolf.

Mollugo floriana (Robins.) Howell ssp. **santacruziana** (Christoph.) Eliasson, comb. nov. *M. snodgrassii* Robins. var. *santacruciana* Christoph., Nyt Mag. Naturvidensk. 70:75. 1931.

Known only from the type collection, taken at "Academy Bay," Isla Santa Cruz (*Rorud 1230*).

Anredera **ramosa** (Moq.) Eliasson, comb. nov. *Tandonia ramosa* Moq., in D.C. Prodr. 13:227. 1849. *Boussingaultia ramosa* Hemsley, Biol. Centr.-Amer. 3:27. 1882. *B. baselloides* in Galápagos literature, not H.B.K., 1825.

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A NEW SPECIES OF POLYGONUM (POLYGONACEAE)

Jerrold Coolidge

During the course of study in preparing a revision Section *Avicularia* of the genus *Polygonum,* (Coolidge, 1964) a group of specimens were found which possessed charateristics distinct enough to warrant description as a new species.

Polygonum triandrous Coolidge, sp. nov. Herba annualis; erecta; 1 vel 4 dm longa; folia lineari-lanceolata vel linearia, 2 vel 4 cm longa; inflorenscentia axillaris; 2 vel 3 flores in axilla foliorum; flores erectae, 2 vel 3.5 cm longae, virides marfinibus roseis vel albis; stamina 3; achenium ovoideum, 3 mm longum, atrum, glabrum.

Annual; erect, glabrous except glaucescent or scurfy at nodes; stem 1 to 4 dm long, terete, branched from the base or throughout; leaves linear-lanceolate or linear, 2 to 4 cm long, 3 to 5 mm wide, revolute or flat, light green, glaucous on upper surface, acute, midvein prominent, articulation to ocrea conspicuous; ocrea 2-parted when young, lacerate with age, silvery with reddish-brown base, 4 to 5 mm long; pedicels stout, 2 mm long; inflorescence axillary, 2 to 3 flowers in the axils throughout the length of stem; articulated with the flower at the flower base, flower and fruit erect, 3 to 3.5 mm long, green with pink or white margins; calyx segments ovate, obtuse, 5 -parted to near the base; stamens 3, 1.5 mm long, anthers white, filaments dilated gradually; style 0.1 to 0.2 mm long, 3-cleft to near the base; achene ovoid, 3 mm long, black, smooth and shining (fig. 1).

Type. Idaho: Blaine Co., along trail to Hyndman Peak, *W. H. Baker 11005* (ID-holotype, ARIZ, MONTU, NY, OSC, RM, UC, WS, WTU).

Numerous collections of *P. triandrous* from herbaria throughout the western states have been examined. In most cases, it has been identified as *P. sawatchense* Small and does appear to be most closely allied with

FIG. 1. Photograph of type of *Polygonum triandrous.*

this species. It differs in having narrower leaves below, the upper leaves of a more bracteate nature and the most apparent difference, the presence of only three stamens. *Polygonum triandrous* may be distinguished from other related species by the following key:

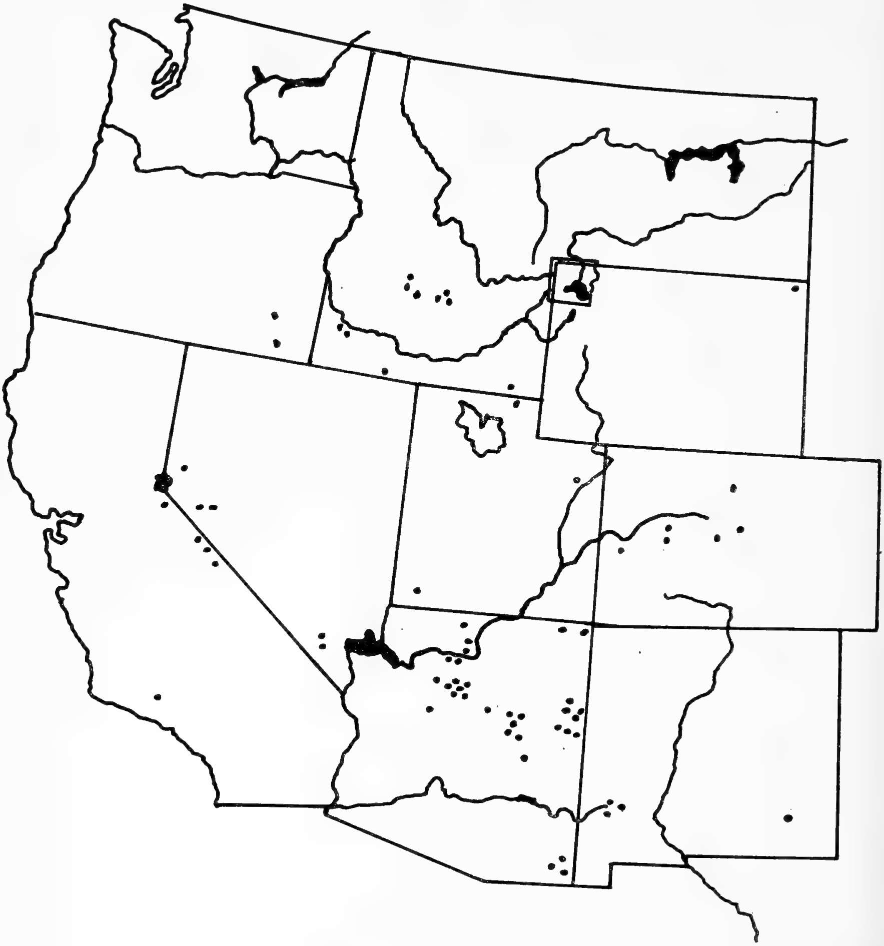

FIG. 2. Distribution of *Polygonum triandrous* in western North America.

Leaf size somewhat reduced upward, lanceolate, liner
Leaves linear, linear-lanceolate
Stamens 3 . . . . *P. triandrous* Coolidge
Stamens 8 . . . . *P. tenue* Michx.
Leaves lanceolate . . . . *P. sawatchense* Small
Leaf size about the same throughout, ovate, obovate
Flowers few in axils, remote . . . . . . *P. minimum* Wats.
Flowers several in axils, congested . . . . *P. cascadense* Baker

The known range includes areas within the Colorado Plateau, New Mexican Highlands, Rocgy Mountains, Columbia Plateau, Great Basin and the Sierra Nevada (fig. 2). The distributional pattern of this species would indicate a probable origin in central Arizona, radiating into all western states except perhaps, Washington and Montana.

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CHROMOSOME NUMBERS AND A PROPOSAL FOR CLASSIFICATION IN SISYRINCHIUM (IRIDACEAE)

THEODORE MOSQUIN

INTRODUCTION

The classification of North American *Sisyrinchium* has been highly unsatisfactory for many decades. For example, it is difficult with the aid of standard floras such as Abrams (1923), Fernald (1950), Gleason (1952), and Munz (1959) to identify many collections of this genus from regions covered by these floras. One reason for this difficulty is that plants of this genus are notoriously lacking in qualitative differences such as are necessary to distinguish species. A second reason is that regional floras which deal with different or confluent parts of the continent have continued to follow traditional and local classifications. The existing disagreements concerning the occurence and the nature of phenotypic discontinuities illustrates the need for a reappraisal of variability not only by the use of techniques of modern taxonomy but by examination of variation on a continent-wide basis. The present paper brings together some field, herbarium, published, and laboratory observations on correlations between morphology, chromosome numbers, ecology, and geography of plants of this genus from populations throughout much of the North American distribution area.

The *Sisyrinchium* populations considered in this paper comprise the widely distributed, small-flowered perennials in which the anther filaments are united in a tube. Excluded are the annuals of Texas and adjacent regions which have been discussed recently by Shinners (1962). Also excluded are the large-flowered perennials of Mexico and the Caribbean Islands as well as the large-flowered and very distinctive *S. douglasii* Dietr. of western North America. So defined, the plants commented on in this paper range from Greenland to Alaska and south to Florida, Texas, and California and may extend into Mexico.

Directly relevant to their classification and an outstanding feature of the *Sisyrinchium* populations considered here is that a high degree of self-pollination appears to be a characteristic feature (Knuth, 1909; Ingram, 1967; Table 1). Table 1 shows the results of an experiment designed to determine the potential for automatic self-pollination in a tetraploid poupulation growing under natural conditions near Banff,

TABLE 1. SEED SET RESULTING FROM ARTIFICIAL BAGGING EXPERIMENTS IN WILD PLANTS OF SISYRINCHIUM BERMUDIANA

Data from a 12-ploid population about 6 miles west of Banff, Alberta, Canada (vouchers *Mosquin & Seaborn 7048* and *7164,* DAO).

Number of individual plant	Number of capsules on inflorescence	Number of seeds per capsule	Number of seeds in control capsules (adjacent plants)
7048–1	3	3; 26; 8	16
7048–2	2	3; 16	33
7048–3	2	6; 6	20
7048–4	1	32	30
7048–5	3	3; 5; 25	24
7048–6	1	1	28

Alberta. The pollination bags used in this experiment were white and highly porous. They were made from synthetic material especially designed for tree-breeding work in the field and do not deteriorate under usual field conditions. The plants were bagged on June 25 and the data collected on July 29, 1968. The bagged plants of this population, isolated from insects, produced nearly 45% seed set as compared with the controls. There can be no doubt, therefore, not only that these plants were self-compatible but that they are highly homozygous. A consideration of the morphological effects of self-pollination (Stebbins, 1957) reads like a description of the variation pattern of wild populations considered here. Thus local populations are highly uniform morphologically, while conspicuous differences often occur between geographically isolated colonies. Intermediates are common between character extremes. Morphologically very similar plants occur in widely separated places, for example on the American northwest coast and in the Appalachian region, and again in Greenland and the western United States.

Another feature of the *Sisyrinchium* populations considered here is polyploidy, an important evolutionary mechanism. To date the numbers **2n = 16, 32, 64, 82, 84, 88, 90,** and **96** have been reported among these plants (Bowden, 1945; Löve and Löve, 1958; 1961; Lewis and Oliver, 1961; Oliver and Lewis, 1962; Clapman, et al.; 1962; Böcher, 1966; Oliver, 1966; Ingram, 1967; table 2). It is possible, therefore, that in some places chromosome numbers might provide the necessary key for discovering corresponding morphological breaks.

In closely related species, differences in chromosome numbers are frequently reflected in differences in pollen grain size. This is, however, not so in *Sisyrinchium,* where I have found that tetraploids may have pollen as large as the 12-ploids. It is of interest that Böcher (1966) in

TABLE 2. CHROMOSOME NUMBERS.

Sisyrinchium arenicola Bicknell. **2n = 32**: NORTH CAROLINA, Moore Co., 2.7 mi S of Pine Bluff, *Mosquin & Mosquin 5935* (COLO, DAO).

S. bellum Wats. **n = 16**: CALIFORNIA, San Diego Co., Santa Yysabel, *Mosquin & Snow* 3974 (COLO,, DAO); several mi W of San Pasqual, *Mosquin & Snow 3975* (COLO, DAO). **2n = ca 90** CALIFORNIA, Inyo Co., 6.7 mi W of the Lee Vining Junction along Tioga Pass Hwy, *Mosquin 4780* (COLO, DAO, DS, UAC).

S. bermudiana L. **2n = 32**: ALBERTA, about 6 miles west of Banff, *Mosquin & Seaborn 7164.* CALIFORNIA, Plumas Co., about 2 mi SE of Graegle, *Mosquin & Gillett 5305* (COLO, DAO). ***n = 16***: NEVADA, Lyon Co., road to Virginia City near Hwy 50, *Gillett & Moulds 12700* (COLO, DAO). **2n = ca 64**: MONTANA, Meagher Co., Ringling, *Mosquin & Gillett 5226* (DAO); Missoula Co., 13.9 mi W of Lolo, *Mosquin & Gillett 5262* (DAO). TEXAS, Van Zandt Co., 12.7 mi E of Terrell, *Mosquin & Mosquin 5469* (DAO, DS); Galveston Co., Galveston Island, near SW tip of the Island, about 22 mi SW of Galveston, *Mosquin & Mosquin 5529* (DAO). **2n = 96**: ALBERTA, 7.5 mi S of the Trans Canada Hwy, along road to Kananaskis Lakes, *Mosquin & Benn 5185* (COLO, DAO, UAC). BRITISH COLUMBIA, 7.7 mi E of Galloway (no voucher). CALIFORNIA, Sierra Co., along road from State Hwy 89 to Independence Lake (DAO). MONTANA, Cascade Co., 15 mi E of Great Falls, *Mosquin & Gillett 5215* (DAO); Jefferson Co., 1.5 mi E of Pipestone Pass, *Mosquin & Gillett 5261* (COLO, DAO, UAC). NEW BRUNSWICK, Restigouche Co., 20 mi NE of Kedgwick, *Mosquin & Spicer 6374* (DAO). ONTARIO, Norfolk Co., Turkey Point, *Bowden 138–55* (DAO); Carleton Co., 3 mi SW of North Gower, *Mosquin & Frankton 6519* (DAO). QUEBEC, Bonaventure Co., 1 mi W of Nouvelle, *Mosquin & Spicer 6366* (DAO); Gaspe Co., at lodge about 2 mi N of Mt. Albert, *Mosquin & Spicer 5997* (DAO); 9 mi W of Petite Vallee, *Mosquin & Spicer 6346* (COLO, DAO); Rimouski Co., about 6 mi SW of Ste. Flavia, *Mosquin & Spicer 5997* (COLO, DAO); Stanstead Co., about 5 mi due E of Fitch Bay, *Mosquin & Spicer 6338* (DAO). SOUTH DAKOTA, Pennington Co., 1.9 mi NE of Hill City, *Mosquin & Mulligan 5148* (COLO, DAO).

comparing tetraploids and 12-ploids found that seed diameter in the former was 0.7-0.8 mm, while in the latter it ranged from 1.1 to 1.4 mm, but the sample size was small. Seed diameter in the 12-ploid plants from Banff referred to in Table 1 ranged from 0.7 to 1.1 mm.

Yet another feature of the genus considered here, and one that has contributed to the creation of many names of dubious value, is the wide ecological diversity of the wild populations. This diversity is evident from the habitat descriptions in various floras and from first-hand field observations. Wild populations occur in montane meadows, sage deserts, prairies, and seashores, and often along roads as weeds.

TAXONOMY

Among the many species names currently in use for the American populations of *Sisyrinchium,* the most widely employed are perhaps *S. angustifolium* Mill. and *S. montanum* Greene. The former is applied to eastern North American populations from eastern Canada to Florida and Texas (Fernald, 1950; Shinners, 1963); the latter most often to western populations from the Northwest Territories and British Columbia south to Colorado, but also eastward to New York, eastern Canada, and Greenland (Fernald, 1950; Böcher, 1966). The most important character by which these two species are purported to differ is branching, *S. angustifolium* being branched and *S. montanum* unbranched. It is very common, however, to find both branched and unbranched plants in many populations, although one type is usually much more frequent than the other. It would be much more useful, therefore, to consider these two species to be conspecific, as Rydberg (1932) thought. Another widely used name is *S. idahoense* Bicknell. Yet plants of this species from Idaho, Oregon, and California do not differ in any single trait or combination of traits from the *S. montanum*—*S. angustifolium* populations considered above. Similarly some other names which are currently used in floras appear to apply to populations which have morphological traits well within the range of variability of the populations considered above. Thus species like *S. campestre* Bicknell, *S. albidum* Raf., *S. graminoides* Bicknell (see Shinners, 1962, for discussion of this name), *S. langloisii* Greene, *S. sagittiferum* Bicknell, *S. littorale* Greene, *S. sarmentosum* Suksdorf, and *S. halophilum* Greene, as far as I can judge from descriptions in floras and also from comparisons of herbarium specimens, are very likely best treated within a single widespread species. The correct name for this widespread species appears to be *S. bermudiana* L. (Shinners, 1962).

Several additional species have been described which, in contrast to those mentioned above, are, at least in their morphological characteristics, modally distinct from *S. bermudiana*. These are *S. atlanticum* Bicknell, *S. mucronatum* Greene, *S. arenicola* Bicknell, *S. capillare* Bicknell, and in the west perhaps *S. bellum* Wats., although many populations of the last species, particularly from the Sierra Nevada of California, would readily pass for collections from the eastern United States (see Munz, 1959, for brief discussion of *S. bellum*.)

Correlations and Discussion

Correlations between morphological characters on the one hand and ecology, chromosome number, distribution, and breeding habit on the other provide the basis for contemplating the details of a classification that not only would be readily usable but would closely reflect our present knowledge of genetic relationship. Perhaps the most important correlation between these characteristics in *Sisyrinchium*, and one that is of vital significance to the classification of this genus, is a negative one, namely, morphological differentiation is, for the most part, not associated with chromosomal differentiation. Hence chromosome numbers will not play an important role in helping to construct a useful classification for this genus.

Another fact is that ecological similarities or differences very frequently are not accompanied by corresponding morphological patterns. For example, a population from a marshy habitat in sage desert near

Virginia City, Nevada (*Gillett & Moulds 12700,* DAO), is virtually identical in all features of external morphology with plants collected on dry grassy stream banks in montane yellow pine forest of the Sierra Nevada (*Mosquin & Gillett 5307,* DAO). In this example the former colony is tetraploid while the latter is 12-ploid. In yet another case, the octoploid populations of Montana do not appear to differ ecologically from the geographically adjacent 12-ploid colonies. Neither do these two chromosome races in Montana differ morphologically in any perceivable way. As a last example, plants of Greenland (Böcher, 1966) are essentially identical with many populations in the western United States; the Greenland plants are tetraploid, while at least three chromosome races (tetraploid, octoploid, and 12-ploid) are found in the western United States. Other examples could be cited. That such relationships may also occur in other species of *Sisyrinchium* is suggested from reports of the numbers **n = 8, 16,** and **48** and **2n = 96** from *S. atlanticum* Bicknell (Löve and Löve, 1958; Oliver and Lewis, 1962; Oliver, 1966).

The geographical distribution of the chromosome races of *S. bermudiana* is of interest. The tetraploids occur in southern portions of the United States, in the Great Plains, in western Alberta, in California, and, surprisingly, in Greenland. Octoploids are known only from Texas and Montana, while 12-ploid populations are very widespread in the northern regions and also occur in the Queen Charlotte Islands, British Columbia (Taylor and Mulligan, 1968). Figure 1 gives the distribution of the chromsome races. Evolution by aneuploid decrease from **2n = 96** is clearly occurring in the eastern United States, with numbers as low as **2n = 82** recorded (Ingram, 1967). The count of **2n = 90** (Bowden, 1945; and present paper) from the Sierra Nevada suggests that an aneuploid reduction series from **2n = 96** may also be present in the western United States.

The geographical origin of the Greenland tetraploids poses a special problem. It would be useful to determine the chromosome number of populations in Newfoundland and particularly in the vicinity of Goose Bay, Labrador, since presumably the Greenland tetraploids originated from some locality in northeastern North America.

Some additional reports of chromosome numbers in *S. bermudiana* have been published by Löve and Löve (1958) under different species names. These are given in their paper as having been determined from "many plants from the southern and eastern parts of the province of Quebec" and from "northern Virginia" (**2n = 96** as *S. angustifolium*), from "the Canadian prairies" and from "a few places in Ontario and Quebec" (**2n = 32** as *S. montanum*), and from "a couple of localities in southern Wisconsin and Ontario" (**2n = 32** as *S. albidum*). These report could not be included in Fig. 1 because the exact localities and voucher information were not given in the paper. Löve and Löve also report having determined the number **2n = 96** from plants of

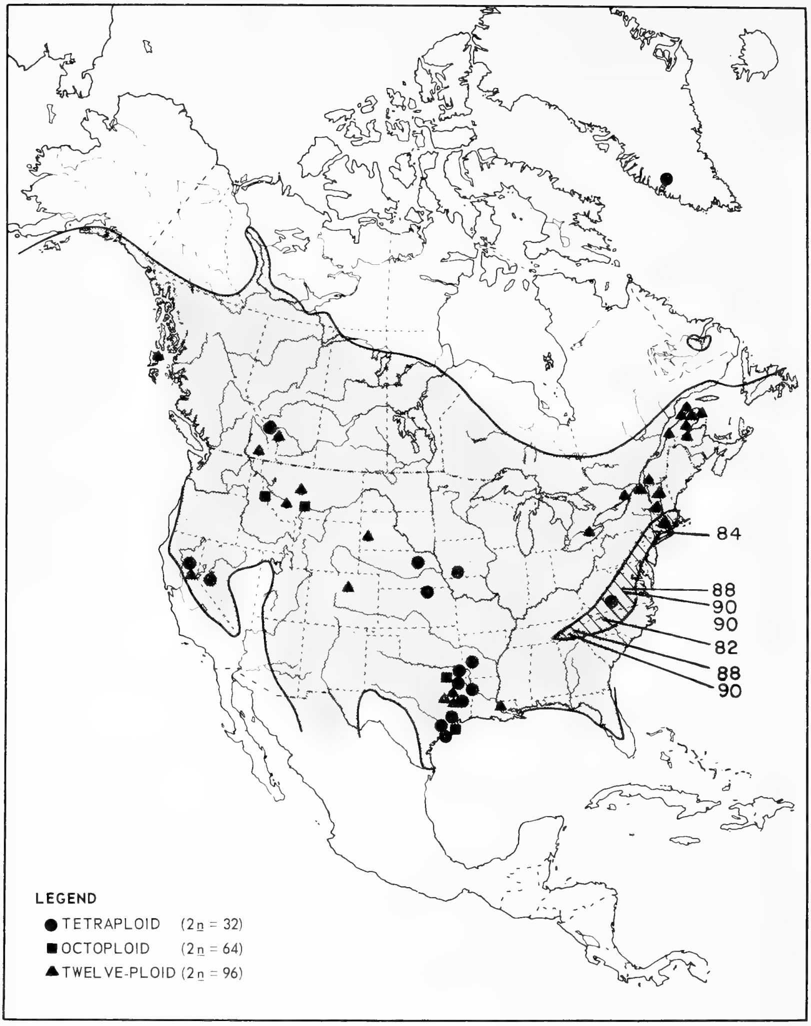

FIG. 1. Distribution of *Sisyrinchium bermudiana* (dotted area) showing locations of populations with chromosome counts. Chromosome counts previously reported under the names *S. albidum* (Bowden, 1945; Oliver and Lewis, 1962), *S. angustifolium* (Bowden, 1945), *S. campestre* (Oliver and Lewis, 1962; Oliver, 1966), *S. groenlandicum* (Böcher, 1966), *S. langloisii* (Oliver and Lewis, 1962), and *S. montanum* (Ingram, 1967) are included. The counts for *S. bermudiana* given by Ingram (1967) are also included.

S. bermudiana from "several localities in Britain and Scandinavia," as well as the number **2n = 64** from one Irish population which they describe as a new species (Löve and Löve, 1961). The correct number of the Irish population has now been shown to be **2n = 88** (Ingram, 1967). The morphology and chromosome number of the Irish plants fall well into the range of variability of *S. bermudiana* even when grown under similar conditions in the greenhouse (Ingram, 1967). In a detailed study of the Ireland plants Ingram concluded that they should be most usefully treated as *S. bermudiana*. There seems little doubt that adopting a wide species concept for the North American Sisyrinchiums would provide biologists with a maximally useful classification.

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Plant Research Institute, Canada Department of Agriculture, Ottawa

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COMPARATIVE NATURAL HISTORY OF TWO SYMPATRIC POPULATIONS OF PHOLISTOMA (HYDROPHYLLACEAE)

KAREN B. SEARCY

The generalization that similar species are allopatric has stood the test of numerous systematic studies. It is usually assumed that it is competition which makes the ranges of these species mutually exclusive. Occasionally populations of two similar species can be found growing together at the same site. Such sympatric occurrences provide an ideal opportunity to test the assumption and to look for influences of one population on another. In addition, sympatric occurrences may help us recognize features of each population which provide for their continued reproductive independence.

The object of the study was to investigate a site where two closely related species of *Pholistoma* were found growing together. Constance (1939) has shown by careful morphological study that *P. racemosum* (Nutt.) Constance and *P. auritum* (Lindl.) Lilja. are far more similar to each other than to any other taxa, and has segregated the two out of the genus *Nemophila* and placed them in *Pholistoma*. The other taxa in *Pholistoma, P. membranaceum* (Benth.) segregated out of the genus *Ellisia*, and *P. auritum* var. *arizonicum* (M. E. Jones) were not considered in this study.

Pholistoma auritum var. *auritum* and *P. racemosum* are allopatric throughout most of their range. *Pholistoma auritum,* which has larger purple flowers, is found in the coast ranges of California from San Diego north to Lake Co., in the Sierra Nevada foothills from Calaveras Co., to Kern Co., and on Santa Catalina, San Clemente, and Santa Cruz islands. *Pholistoma racemosum,* with small white flowers, is found in northern Baja California, San Diego Co., and on the off-shore islands of Baja California and California. The one know site where they do occur together (Raven, 1963) is at the base of a large rock outcrop in Little Sycamore Canyon near the west end of the Santa Monica Mountains, Ventura Co. The site is moist, and is characterized by morning and evening fog tending to make a more equable climate than other such woodlands in the Santa Monica Mountains.

The two species differ greatly in their breeding systems. Greenhouse culture showed *P. racemosum* to be autogamous while *P. auritum* is self-compatible but does not set any seed unless artificially self-pollinated. *Pholistoma auritum* is kept from self-pollinating by two mechanisms: protandry, and the fact that the inflorescence rarely has more than one flower shedding pollen at a time. The next flower on the inflorescence usually does not open until 1–3 days after the previous flower has opened. Although the flowers of *P. auritum* have no perceptible odor, they have 5 yellow nectaries which were conspicuous when the flower first opened but faded within one day.

Field studies confirmed that *P. auritum* was predominantly outcrossed and *P. racemosum* inbred. *Pholistoma auritum* was regularly visited by pollinators, usually between 0900 and 1100, which was shortly after the flowers opened and while pollen was being shed. The bees removed almost all of the pollen before noon, at which time the stigmas elongated and became receptive. Observation of pollinators was made during the time of maximum flowering from 0700 to 1400 on 16 April 1966 and from 1630 to 1800 on 13 April 1966. No pollinators were observed visiting *P. racemosum* during the time of maximum flowering. Observations were made between 1300 and 1900 on 30 March 1966 and 0530 to 1300 on 2 April 1966. In addition, *P. racemosum* lacked any regular time of opening, although it tended to open in the late afternoon.

No hybrids were found between *P. auritum* and *P. racemosum* although individuals of the two species were growing just a few feet from each other. The absence of hybrids may be partly due to a difference in flowering time. *Pholistoma racemosum* bloomed earlier than *P. auritum* during 1966. The first flower of *P. racemosum* opened about 15 March 1966; maximum flowering was two weeks later, capsules were formed and the plants were beginning to dry about 16 April 1966. *Pholistoma auritum* opened for the first time on 2 April 1966; maximum flowering occurred two weeks later, the capsules matured and the plants were dying by 11 May 1966.

The two species also differed in microhabitat. *Pholistoma racemosum* occupied areas receiving much less direct sunlight than the areas in which *P. auritum* was found. The densest clusters of *P. racemosum* occurred on the N slope of the rock outcrop where it received direct light for only about 20 minutes each day. The next densest clusters were on the N sides of rocks and trees on the NW slope of the rock outcrop, and received about 2 hours of sunlight during each day. In contrast, *P. auritum* was found on the SW slopes leading away from the rock outcrop, and received direct sun most of the day. Early in the year, *P. auritum* also occurred on the NW slopes, but almost all of these plants died before flowering. In addition, the sites occupied by *P. racemosum* were characterized by shallow soil, little leaf litter and few other plants, whereas sites occupied by *P. auritum* were characterized by deep soil, considerable litter, and much other vegetation.

An examination of herbarium specimens of *P. racemosum* and *P. auritum* var. *auritum* showed that the plants in the study area do not differ morphologically from those in other parts of the ranges. Flowering dates also seem to be the same and the populations do not differ chromosomally. Cave and Constance (1942;1957;1959) have reported both species to be $\mathbf{n} = \mathbf{9}$. The chromosome numbers of plants from both species from the study site are also $\mathbf{n} = \mathbf{9}$. (*P. auritum, Bartholomew 023,* LA; *P. racemosum, Bartholomew 015,* LA).

A study of the two sympatric populations of *Pholistoma* has led me to the following conclusions. The two species growing together in Little Sycamore Canyon occupy sufficiently different microhabitats so that they are not in direct competition. Their breeding systems are sufficiently different so that they do not even compete for the same pollinator. The two sympatric populations show no differences from other populations of their species, so that neither character displacement nor introgression have occurred. Thus, the normally allopatric distribution cannot be attributed to competitive exclusion, rather the populations must be though of as ecologically quite different, and it is this difference which causes their difference in geographical distribution.

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A PRELIMINARY REPORT OF THE MYXOMYCETES OF CRATER LAKE NATIONAL PARK, OREGON

Dwayne H. Curtis

Crater Lake National Park is located in southeastern Oregon where volcanic activity and glaciers shaped the surrounding mountains and valleys. During the winter months the park is noted for an abundance of snow accumulation, often exceeding 50 feet of measured depth from November to May. The average annual precipitation is about 70 inches. In contrast, the summer is quite dry since very little rain falls during the months of July and August. The flora in the park must withstand the extreme weather conditions in order to survive. It is common to observe living trees bent from the shifting snow. In many places the forest floor is covered with broken limbs and fallen trees.

Slime molds or Myxomycetes are characteristically associated with moist areas on decaying organic matter such as duff, wood, bark, and fallen twigs. An ideal habitat for slime molds is formed on the fallen logs and forest litter dampened by the large amount of water from the melting snow.

The collections for this report were obtained during the summers of 1966 and 1967. The 43 species, listed here, were collected in the field on some form of decaying wood or duff at altitudes from 4,000 to 7,500 feet. At least one collection of each species has been deposited in the University of Iowa Herbarium, Iowa City, Iowa and where possible, duplicate specimens have been given to the Crater Lake National Park Herbarium, Crater Lake, Oregon. The numbers given for the collections are my own and they indicate only those specimens given to the University of Iowa Herbarium.

CERATIOMYXACEAE

Ceratiomyxa fructiculosa (Müll.) Macbr. On decayed wood, Kerr Valley, 6,500 feet, *48,* July 28, 1966.

LICEACEAE

Lisea minima Fries. One collection on decayed wood, Sleepy Hollow Creek area, 6,500 feet, *16,* June 18, 1966.

L. pusilla Schrad. One collection on decayed coniferous wood, 0.2 miles north of Park Headquarters, 6,500 feet, *6,* June 15, 1966. This exceedingly tiny species was recently reported by Kowalski (1966) from California. Previously, it had only been found as far west as Iowa, and is considered rare.

RETICULARIACEAE

Lycogala epidendrum (L.) Fries. On decayed wood, Grouse Hill, 7,000 feet, *832,* June 29, 1967.

L. flavofuscum (Ehrenb.) Rost. I obtained only one aethalium on the side of a dead, barkless stump about 4 feet above the ground on the east side of Kerr Valley, 6,500 feet, *52,* July 28, 1966.

Enteridium olivaceum Ehrenb. On decayed wood, Vidae Falls area, 6,500 feet, *859,* July 2, 1967.

CRIBRARIACEAE

Cribraria argillacea (Pers.) Pers. Inside a decaying log, 2 miles south of Park Headquarters, 6,400 feet, *1007,* July 8, 1967.

C. rufa (Roth) Rost. On decayed wood, Kerr Valley, 6,800 feet, *1130,* July 29, 1967.

Lindbladia effusa (Ehrenb.) Rost. One large collection on the side of a decaying log, 0.5 miles west of Rim Village, 6,800 feet, *1083*, July 16, 1967.

DIANEMACEAE

Dianema andersoni Morgan. One collection on decayed wood, about 2 miles north of Park Headquarters, 6,800 feet, *1067,* July 14, 1967. This Myxomycete has been reported from Washington, British Columbia, and more recently from California (Kowalski and Curtis, 1968). It is considered rare.

D. corticatum Lister. On decayed wood buried in duff, 2 miles north of Park Headquarters, 6,800 feet, *1052,* July 14, 1967. Numerous collections of this slime mold were obtained at elevations from 5,000 to 7,000 feet.

Prototrichia metallica (Berk.) Massee. On decayed wood, Grouse Hill, 7,000 feet, *829,* June 29, 1967. This Myxomycete is very common throughout the park.

TRICHIACEAE

Arcyria versicolor Phill. On bark, 0.5 miles west of Rim Village, 6,800 feet, *1114,* July 18, 1967. Several specimens were collected at elevations from 6,000 to 7,000 feet.

Hemitrichia karstenii (Rost.) Lister. On the bark of a small fallen twig, 4 miles north of the south park boundry, 5,000 feet, *779,* June 17, 1967.

H. montana (Morgan) Macbr. On decayed wood, 2 miles south of Park Headquarters on Munson Ridge, 6,500 feet, *67,* August 4, 1966. This Myxomycete is very common in the park at elevations from 6,000 to 7,000 feet.

Oligonema schweinitzii (Berk.) G. W. Martin. On decayed wood, Goodbye Creek area, 6,000 feet, *748,* June 14, 1967.

Trichia affinis De Bary. On decayed wood, 1 mile northeast of Park Headquarters, 6,650 feet, *45,* July 18, 1966.

T. contorta (Ditmar) Rost. On fallen twigs, 0.5 miles west of Rim Village, 6,800 feet, *1077,* July 16, 1967.

T. favoginea (Batsch) Pers. On decayed wood, Lightning Springs area, 6,800 feet, *71,* August 16, 1966.

T. lutescens Lister. One collection on duff, Sleepy Hollow Springs area, 6,600 feet, *794,* June 25, 1967.

T. pusilla (Hedw.) G. W. Martin. On decayed wood, Sleepy Hollow Springs area, 6,500 feet, *810,* June 28, 1967.

T. varia (Pers.) Pers. One collection on decayed wood, Annie Creek near park boundary, 4,400 feet, *20,* June 18, 1966.

STEMONITACEAE

Barbeyella minutissima Meylan. One collection of three sporangia on decayed wood, 0.5 miles south of Park Headquarters on Munson Ridge, 6,600 feet, *782,* June 22, 1967. I (Curtis, 1968) recently reported the occurrence of this exceedingly rare Myxomycete from the park. Previously, it had only been reported from Switzerland, Poland, and Japan.

C. fusiforme Kowalski. On decayed wood, 1 mile south of Vidae Falls, 6,700 feet, *883,* July 3, 1967. This Myxomycete is very common in the park at elevations from 5,000 to 7,000 feet.

C. nigra (Pers.) Schroet. On decayed wood, Grouse Hill, 7,000 feet, *830,* June 29, 1967.

C. pacifica (Macbr.) Peck & Gilbert. On bark and twigs, 0.3 miles kest of Goodbye Creek and the Park Road, 6,000 feet, *897,* June 15, 1967.

C. suksdorfii Ellis & Ev. On bark, Munson Point, 7,000 feet, *757,* July 4, 1967. Numerous collections were obtained throughout the park at elevations from 5,700 to 7,100 feet.

C. typhoides (Bull.) Rost. One collection on decayed wood, Goodbye Springs area, 6,300 feet, *73,* September 7, 1966.

Enerthenema melanospermum Macbr. & Mart. On decayed wood, Grouse Hill, 7,000 feet, *848,* June 29, 1967.

Lamproderma arcyrioides (Sommerf.) Rost. On decayed twigs, Sleepy Holly Springs area, 6,600 feet, *1015,* July 9, 1967. A slime mold commonly found throughout the park.

L. biasperosporum Kowalski. One collection on the side of a decaying log, 0.5 miles west of Rim Village, 6,800 feet, *1068,* July 14, 1967. This rare Myxomycete was recently described by Kowalski (1968). It has only been reported from California, Kentucky, and Oregon.

L. carestiae (Ces. & De-Not.) Meylan. On decayed twigs, Grouse Hill, 7,000 feet, *842,* June 29, 1967.

L. sauteri Rost. On bark, Sleepy Hollow Springs area, 6,600 feet, *804,* June 25, 1967.

PHYSARACEAE

Fuligo septica (L.) Webber. On a decaying log, White Horse Creek area, 5,700 feet, *58,* August 3, 1966.

Physarum albescens Macbr. On decayed twigs, 1.5 miles southeast of Park Headquarters, 6,600 feet, *940,* July 6, 1967. Numerous specimens of this Myxomycete were collected in the park.

P. auripigmentum G. W. Martin. Beneath layers of decayed wood on a fallen log, 2 miles south of Park Headquarters, 6,400 feet, *1006,* July 8, 1967.

P. decipiens Curt. On decayed twigs, Sleepy Hollow Springs area, 6,600 feet, *1012,* July 9, 1967.

DIDYMIACEAE

Diderma deplanatum Fries. On decayed wood, 0.5 miles west of Goodbye Bridge, 6,000 feet, *762,* June 17, 1967.

D. nigrum Kowalski. One collection on coniferous twigs, 2 miles south of Park Headquarters, 6,200 feet, *1041,* July 10, 1967. This rare Myxomycete was recently described by Kowalski (1968).

D. niveum (Rost.) Macbr. On bark and fallen twigs, 2 miles west of Annie Creek Entrance Station, 6,100 feet, *812,* June 28, 1967. This slime mold occurs throughout the park at elevations from 5,000 to 7,000 feet.

D. subcaeruleum Kowalski. On coniferous twigs, 2 miles south of Park Headquarters, 6,400 feet, *986,* July 8, 1967. Kowalski (1968) recently described this Myxomycete from the park.

Lepidoderma carestianum (Rab.) Rost. One collection on a decayed twig, 0.5 miles west of Rim Village, 6,800 feet, *1109,* July 18, 1967.

L. chailletii Rost. On fallen twigs, Grouse Hill, 7,000 feet, *846,* June 29, 1967.

ACKNOWLEDGEMENTS

I am indebted to Donald T. Kowalski for verifying the determinations and for his assistance throughout the course of this investigation.

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A NEW VARARIA FROM WESTERN NORTH AMERICA

Robert L. Gilbertson

Collecting in Alberta in 1964 and 1966 and in Arizona in 1967 has yielded a number of interesting wood-rotting fungi not previously reported from western North America. One of these is a striking species of *Vararia* P. Karst. (Basidiomycetes-Thelephoraceae s.l.) described as new in this paper.

Vararia athabascensis Gilbertson, sp. nov. Fructification effusa, ochracea vel incarnata, 30–350 μ crassa; hyphae nodoso-septatae, 2–3.5 μ diam; dichohyphidia abundanta, 1–3 μ diam, tunicus densus, dextrinoideus; gloeocystidia abundanta, tenitunicata, sinuoso-constricta vel cylindracea, 3–10 μ diam; basidia cylindracea-clavata, 30–40 × 6–6.5 μ, 4-sterigmatibus; basidiosporae tenuitunicatae, laeves, hyalinae, subclavatae, subarcutatae, non-amyloideae, 11–16 × 3–5 μ.

Type. Canada, Alberta. Along Athabasca River, Jasper National Park, on *Pinus contorta* Dougl., *Gilbertson 4752,* July 21, 1964 (BPI-holotype).

Basidiocarps annual, effused in small patches up to 10 cm long, 30–350 μ thick, not readily separable; margin not differentiated, abrupt to thinning out; hymenial surface Pale Ochraceous-Buff to Pinkish-Buff when fresh and on drying, cracking on drying, finely tomentose under a 30x lens; subiculum concolorous with hymenial surface, soft, easily sectioned, uniform in color and consistency.

Sections not darkening in KOH solution, darkening in Melzer's reagent; generative hyphae of subiculum difficult to discern, thin-walled, nodose-septate, 2–3.5 μ in diam (fig. 1a) giving rise to the dichohyphidia and gloeocystidia which are the conspicuous elements of the subiculum; gloeocystidia abundant, imbedded in subiculum and projecting from hymenial region, staining deeply in phloxine and also strongly positive in sulfobenzaldehyde reagent, spherical to elongated, up to 10 μ in diam,

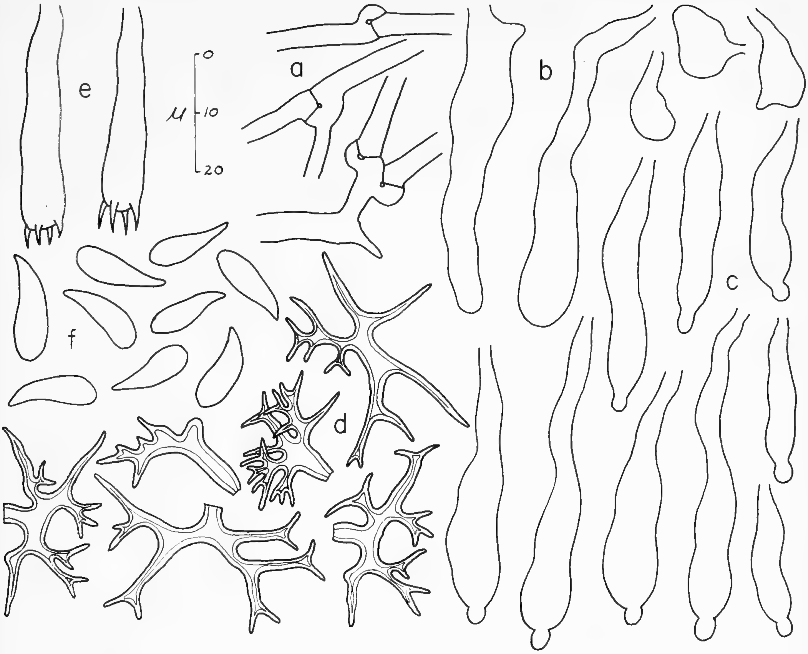

FIG. 1. Microscopic characters of basidiocarps of *V. athabascensis:* a, thin-walled, nodose-septate subicular hyphae; b, irregularly shaped, imbedded gloeocystidia; c, elongated, mammillate gloeocystidia from hymenial region; d, dichohyphidia; e, basidia; f, basidiospores (type).

but usually 3–5 μ in diam, often mammillate (fig. 1b, c); dichohyphidia abundant, strongly dextrinoid in Melzer's reagent, especially in the hymenial region, thick-walled, aseptate, main branches up to 3 μ in diam, some branches long, slender, and unbranched (fig. 1d); hymenial structures forming a typical catahymenium, with basidia developing in the mass of dichohyphidia, apparently from spherical probasidia, becoming elongated, cylindric to narrowly clavate with slight constrictions, swollen at the base, 4-sterigmate, 6–6.5 μ in diam, 30–40 μ long (fig. 1e); basidiospores hyaline, smooth, nonamyloid, attenuated at the basal end and appearing tear-shaped, 11–16 μ long, 3–5 μ wide at the distal end (fig. 1f).

Specimens examined. ALBERTA: Grizzly Creek, near Athabasca River, on *P. contorta, Gilbertson 6504, 6515,* July 30, 1966. ARIZONA: Mt. Lemmon, Santa Catalina Mtns., Coronado Nat. Forest, Pima Co., on *Populus tremuloides* Michx. (quaking aspen), *Gilbertson 7135,* Aug. 16, 1967.

Other species of *Vararia* known from the Rocky Mountains are *V. investiens* (Schw.) Karst., *V. racemosa* (Burt) Rogers and Jackson, and *V. granulosa* (Fries) M. Laur. The growth habit of *V. athabascensis* is similar to that of *V. investiens,* both fruiting on small twigs and branches in the litter as well as on larger branches and logs on the ground. *Vararia investiens* differs in having more slender and abundant dichohyphidia, spores that taper toward both ends, and lacks the sulfobenzaldehyde-positive gloeocystidia. *Vararia granulosa* differs in its amyloid spores, less conspicuous gloeocystidia, and larger dichohyphidia. *Vararia racemosa* has small clusters of densely branched dichohyphidia, cylindric spores, and broad, mucronate gloeocystidia that are not positive in sulfobenzaldaldehyde reagent. Welden (1965) and Gilbertson (1965) give complete descriptions and illustrations of these three species. Another species, *Scytinostroma praestans* (Jacks.) Donk, has spores and cystidia very similar to those of *V. athabascensis,* but has dendrohyphidia typical of the genus *Scytinostroma* (Jackson, 1948). *Scytinostroma praestans* also is present in the lodgepole pine stands along the Athabasca River *(Gilbertson 6511)* and resembles *V. athabascensis* very closely macroscopically. The presence of *V. athabascensis* in widely separated stations in Alberta and Arizona indicates its probable occurrence in the Rocky Mountains between those areas.

The decay associated with basidiocarps of *V. athabascensis* is of the white rot type with a pale orange discoloration in the early stages. The positive oxidase reaction of cultures on gallic and tannic acid media and with gum guaiac support of the field observations of a white rot.

Cultures were obtained from freshly collected basidiocarps by suspending small pieces over the slant surface of 2% Difco malt extract agar medium in a culture tube. Spore prints were transferred to sterile tubes as soon as they become discernible. Cultures from which descriptive data were taken were grown on 2% Difco malt extract agar medium in the dark at 25 C. Gallic and tannic acid media (Davidson, et al, 1938) and gum guaiac solution (Nobles, 1958) were used to test for the presence of extracellular oxidases. Cultures examined: *Gilbertson 6504* and *6515* previously listed.

Growth characters: Growth slow, radial growth 40–50 mm in 17 days; mat white, appressed, with short, radially appressed fibrils, rather uniform over entire surface in 17 days, with some faint radial zones of sparser aerial mycelium; margin not differentiated, even to slightly bayed; cottony aerial mycelium developing around and over original inoculum after 17 days, this mycelium with a faint pinkish tint; no distinctive odor; no reverse discoloration on malt agar medium; oxidase reactions strongly positive with gum guaiac solution and on both gallic and tannic acid media within 48 hours, no growth on either acid medium.

Microscopic characters: hyphae of advancing zone staining with phloxine, thin-walled, with conspicuous clamp connections, 2.5–6 μ in diam (fig. 2a), giving rise to branches which may become contorted or much-branched (fig. 2b), frequently branching just behind the transverse septum of the clamp, commonly with constrictions, these non-staining (fig.

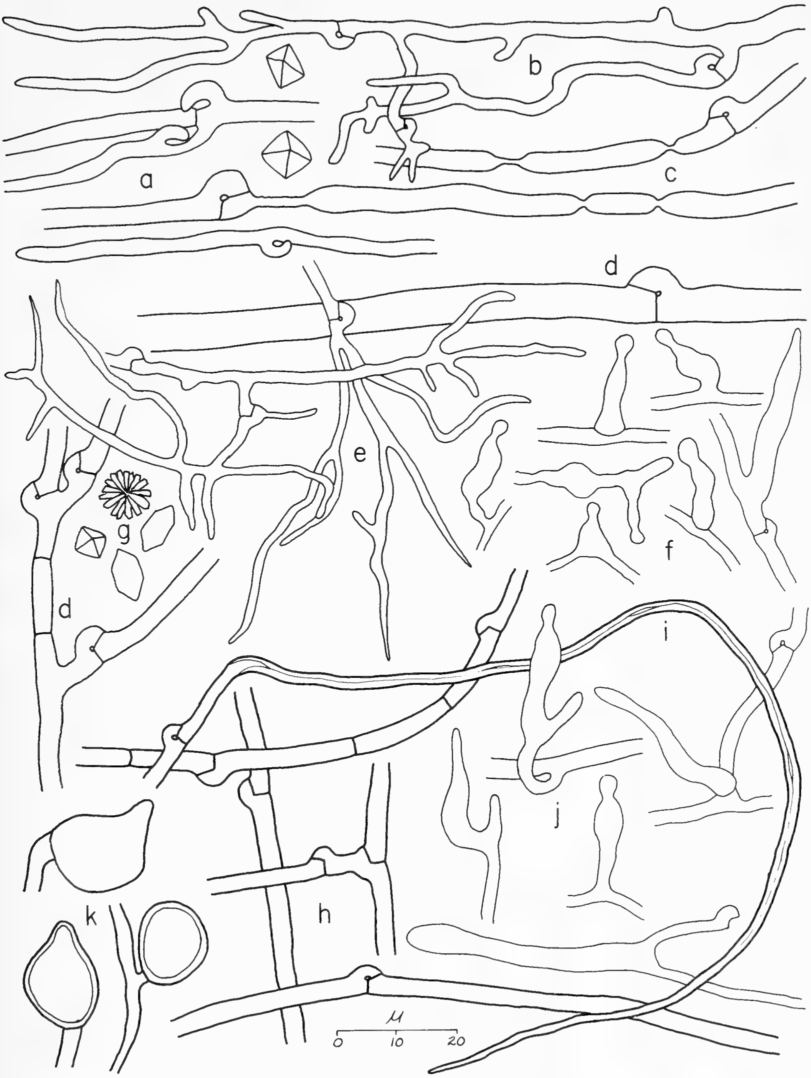

FIG. 2. Microscopic characters of cultures of *V. athabascensis:* a, hyphae from advancing zone; b, much-branched hypha from advancing zone; c, hyphae from advancing zone with constrictions; d, large, unbranched hyphae from submerged mycelium; e, much-branched, slender hypha from submerged mycelium; f, gloeocystidia from submerged mycelium; g, crystals associated with submerged mycelium; h, thin-walled hyphae from aerial mycelium; i, slender, thick-walled fiber hypha from aerial mycelium; j, gloeocystidia from aerial mycelium; k, vesicular bodies found in submerged and aerial mycelium after 6 weeks *(Gilbertson 6504).*

2c); cordons formed from several intertwined hyphae also frequent; hyphae of submerged mycelium thin-walled, staining, with conspicuous clamp connections and also some secondary septa, some extending long distances with little or no branching, 2.5–6 μ in diam (fig. 2d), others branching frequently, often just behind the transverse septum of a clamp, eventually giving rise to profusely branched complexes of very slender and flexuous hyphae tapering down to less than 1 mm in diam (fig. 2e); some hyphae giving rise to gloeocystidia similar to those seen in the basidiocarp, these often mammillate, highly refractive and varying greatly in size (fig. 2f); crystals small plate-like hexagons, rhomboids, or druse-like clusters (fig. 2g); aerial mycelium with thin-walled hyphae, these with conspicuous clamp connections and some secondary septa (fig. 2h), giving rise to fiber hyphae not seen in submerged mycelium or advancing zone, these hyaline, thick-walled, non-staining in phloxine, aseptate, 1–2 μ in diam, tapering to a very slender tip (fig. 2i), generative hyphae also giving rise to gloeocystidial hyphae and gloeocystidia as seen in submerged mycelium, these highly refractive in KOH and phloxine and positive in sulfobenzaldehyde reagent (fig. 2j), generative hyphae also giving rise to much-branched hyphae as in other areas; after 6 weeks large, globose or elongated, thin-walled to moderately thick-walled, hyaline vesicular bodies develop in submerged and aerial mycelium, these up to 15 μ in diam (fig. 2k).

According to the key system proposed by Nobles (1965) the key pattern for cultures of *V. athabascensis* would be 2.3.8.15.36.38.44.55. Using the system proposed by Davidson, et al. (1942), one finds the key pattern to be E-P-S-1-11-16.

Cultures of *V. athabascensis* in petri plates eventually develop areas of brownish mycelium around the periphery of the plates. This brownish mycelium contains abundant slender fiber hyphae as described above in addition to other types of hyphae typical of the aerial mycelium. No dichohyphidia were found in this brownish mycelium and no dextrinoid reactions were observed. No fruiting structures developed in any of the plates or tubes under study. Older cultures also showed secondary septa to be frequent in thin-walled aerial hyphae. The distinguishing characters of *V. athabascensis* in culture are the cottony pinkish aerial mycelium and the conspicuous gloeocystidia.

Duplicates from all collections cited have been deposited in the National Fungus Collections, Beltsville, Md., and the Canadian National Herbarium, Ottawa. Capitalized color names are based on Ridgway (1912).

ACKNOWLEDGMENTS

The Alberta collections of *V. athabascensis* cited in this paper were made on field trips with the mycology class of the University of Montana Biological Station, while the author was serving as visiting Associate Professor of Botany there during the summers of 1964 and 1966.

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REVIEW

Plants of the Oregon Coastal Dunes. By Alfred M. Wiedemann, La Rea J. Dennis, and Frank H. Smith. 117 pp., illus. O.S.U. Book Stores, Inc., Corvallis, Oregon, 1969. $1.95.

In recent years there has been an increasing variety of inexpensive popular books that deal with the plants in various regions or habitats of the Pacific coast states. The present book is concerned with plants of the Oregon coastal sand dunes and with some of the climatic and geological features of these dunes. It is directed at "the visitor to the sand dunes, regardless of his background." The coastal sand dunes of Oregon are perhaps the best developed of those of any of the Pacific coast states and support an interesting flora that attracts the attention of ordinary vacationers as well as more experienced natural historians. The first portion of this attractive little book is concerned with the physical setting of coastal dunes and their vegetational history. Subsequent chapters deal with plant communities and succession and the use of plants for stabilizing dunes. The final chapters present a key to about 90 characteristic dune plants and descriptions and black and white photographic illustrations of half of these plants. The quality of the photographs generally is good, although some of them—such as those of *Rumex maritima* var. *fueginus, Cakile edentula* var. *californica,* and *Lonicera involucrata*—are not as informative as they might be. The level of accuracy is high and the format is a pleasing one, although I suspect that the level of presentation is somewhat too high for the average citizen.

This book might be considered superfluous to P. A. Munz's *Shore Wildflowers of California, Oregon and Washington* issued by the University of California Press in 1964. However, I think that because of its extensive discussion of the ecology of coastal dunes and its low price, the Wiedemann, Dennis, and Smith volume should be considered as a complementary volume—if not a replacement in Oregon—for the Munz book.—Robert Ornduff, University of California, Berkeley.

Grass Systematics. By FRANK W. GOULD. xi + 382 pp., illustrated. McGraw-Hill Book Co., New York. 1968. $14.50.

This well designed book brings grass taxonomy up to date. In a systematic and careful approach Professor Gould has covered all of the classical aspects of grass taxonomy, and has superimposed upon them the more recent developments in the field. Thus the introductory three chapters, and part of the fourth, cover microscopic characters such as epidermal and cytological studies, data from biochemical studies, physiological, ecological and genetic aspects in addition to the expected discussion of gross vegetative and spikelet morphology. A good balance between coverage and depth has been achieved; the reader is given basic information on a topic and liberal references to individual papers should he wish further information. The illustrations in this section are well chosen and well executed.

The discussion of characters is concluded in chapter four with the presentation of a classification system, essentially following that of Stebbins and Crampton (Rec. Adv. Bot. 1: 133–145. 1961). To those systematists raised on the manuals and revisions of Hitchcock and Chase this system is radically different, both in the number of subfamilies as well as their generic content. Essentially many genera formerly included in the Festucoideae have been shifted to new subfamilies which reflect more accurately the correlation of new characters with the old. Especially clever are the maps showing relative geographic representation of these subfamilies.

Chapter five includes keys to and descriptions of the genera of grasses in the United States. The generic key is basically artificial. While I have not had the opportunity to use the key at length, a few chosen genera keyed out with no difficulty.

Most of the genera treated will be familiar but a few unfamiliar names appear, mostly following usage now common in other countries, especially European, or as the result of relatively recent monographs and revisions. Among the "new" names not often seen previously in American agrostological literature are the following examples. The annual species of *Festuca,* often treated in U.S. manuals as the section *Vulpia* of that genus, are given generic status. *Elymus caput-medusae* becomes *Taeniatherum caput-medusae. Trichachne* is placed in *Digitaria. Paspalidium* is recognized, containing two U.S. species placed in *Panicum* by Hitchcock. The four U.S. species in *Panicum* subgen. *Paurochaetium* are in *Setaria,* following a recent monograph of the latter. *Andropogon, Bothriochloa* and *Schizachrium* are recognized instead of the single genus *Andropogon* following current thinking of workers in that group. *Neeragrostis* is recognized, containing the former *Eragrostis reptans* as its single species. *Erioneuron,* contains five species, all placed in *Tridens* by Hitchcock. *Allolepis* contains one of the species formerly included in *Distichlis, D. texana. Uniola* has lost some of its species to *Chasmanthium,* again reflecting a recent monograph. *Ventenata dubia,* reported for the U.S. since Hitchcock's Manual is included. No new combinations are made. Representative species of many genera are illustrated. Most of the drawings are good, some are excellent, some over-shaded or over-reduced. The placement of some drawings leaves as much as one-half of the page blank contributing to a "clean" appearance, but wasting space.

The final chapter is devoted to a discussion of grassland associations in North America, with the recognition of seven associations: true prairie, coastal prairie, mixed prairie, fescue prairie, palouse prairie, pacific prairie and desert plains grassland.

A short appendix on the preparation of specimens concludes the basic part of the book.

Considering its size, but not its value, the book is overpriced, but perhaps we have been spoiled by the past availability of Hitchcock's *Manual* at such a low price.—DENNIS ANDERSON, Division of Biological Sciences, Humboldt State College, Arcata, California.

A WEST AMERICAN JOURNAL OF BOTANY

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Abbreviations of botanical journals should follow those in *Botanico-Periodicum-Huntianum* (Hunt Botanical Library, Carnegie-Mellon University, Pittsburgh, Pennsylvania, 1968).

Footnotes should be avoided whenever possible.

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THE FLORA AND PLANT COMMUNITIES OF BODEGA HEAD, CALIFORNIA

M. G. Barbour

The distribution, time of flowering, habit (annual-biennial-perennial), and history (native or introduced) of 215 vascular plant species in a 2.5 mi^2 coastal peninsula are noted. The flora is divided into six communities: dune, grassland, ocean-facing bluff, saline-wet, fresh-wet, and disturbed. Those species which occur in two or more very different communities are discussed. Recent history of Bodega Head is summarized, and aspects of the climate and soil are presented.

Introduction

Bodega Head, California (38°20′N, 123°04′W) is a coastal peninsula which lies about 65 miles north of San Francisco. The 2.5 mi^2 area of this study (fig. 1) is limited by State Highway 1 on the northeast, Salmon Creek on the north, Bodega Harbor on the southeast, and Pacific Ocean on the west and south. The Bodega Marine Laboratory and Refuge, owned by the Regents of the University of California, occupies 326 acres near the middle of the peninsula. The facility is used for teaching and research by faculty and students of the Berkeley, Davis, San Francisco, and Santa Cruz campuses.

According to the Geologic Map of California (1963), the southern fourth of the peninsula is of Mesozoic granitic rock (tonalite and diorite), the central half is dune sand, and the northern fourth is of Pleistocene marine and marine terrace deposits. The southern fourth (to which the term "head" is often restricted) is hilly and edged with steep cliffs leading to a rocky shoreline. The highest hill reaches 266 feet. The central dunes are low except for a pronounced foredune (39 feet or less) and hinddune (145 feet or less). Beachgrass (*Ammophila arenaria*) has been planted on the dunes at several times over the past 45 years, and in addition native plants such as *Lupinus arboreus* are common on the hinddune; but sand movement is still considerable and land accretion along the harbor has resulted under prevailing winds from the northwest. The *Ammophila* plants were brought from Golden Gate Park in San Francisco, and originally came from European stock collected by Adolf Sutro. About 45 acres of this central section (along the harbor side) are in a low, fresh-water marsh. The northeastern fourth consists of gentle hills cut by several gulleys running roughly east-west.

Climatic information for the peninsula itself is extremely sketchy but is perhaps sufficient to distinguish it from the climate at the nearest official Weather Bureua station at Fort Ross, 17 miles north. Weather instruments at the Marine Laboratory include a recording anemometer

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Madroño, Vol. 20, No. 6, pp. 289–336. October 29, 1970.

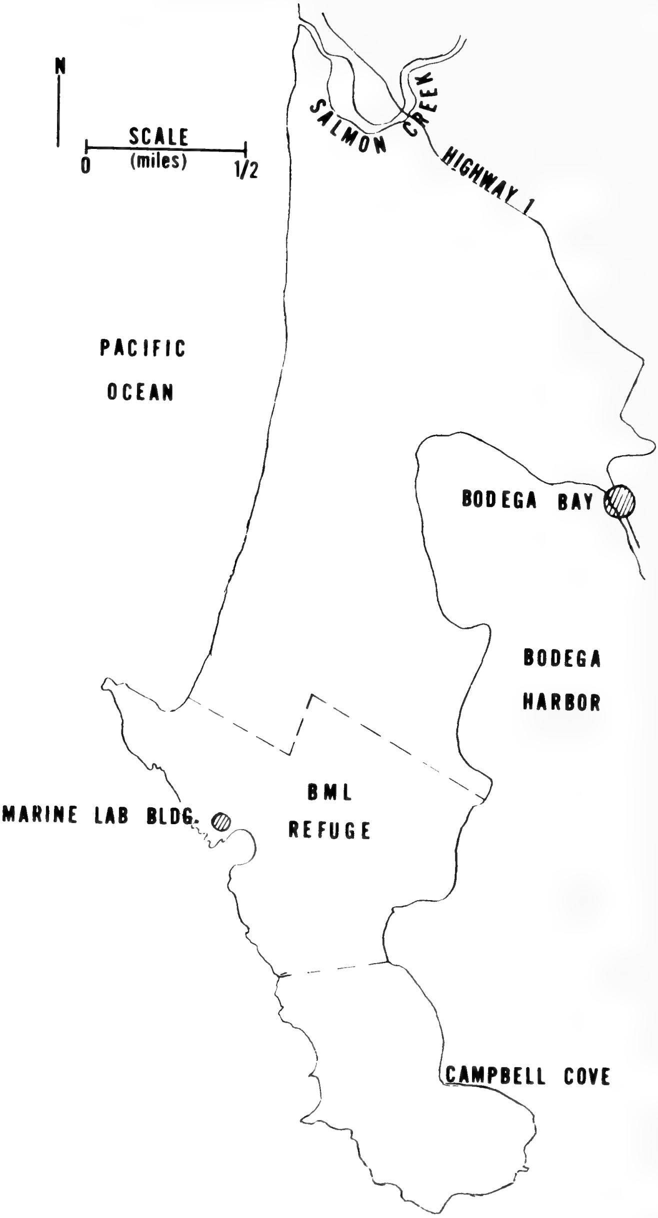

Fig. 1. Map of Bodega Head, boundary of the 326 acre Bodega Marine Laboratory (BML) Refuge is shown by dashed lines.

30 feet above the ground, a thermograph in a standard shelter 4.5 feet above the ground, a pyrheliometer, a standard rain gauge, and a max-min thermometer (Taylor type) hung vertically on a shaded stake such that the bottom of the U-tube is 2cm above the ground. These instruments are all located in grassland on the hilly, granitic southern part of the peninsula. The max-min thermometers are read daily. Rainfall records have also been collected since July, 1958 by Otto Henninger in the town of Bodega Bay, less than a mile across the harbor from the center of the peninsula. A summary of the wind records, from Deceember, 1966 to October, 1968 was kindly provided by J. W. Johnson, Professor of Hydraulic Engineering at Berkeley.

As at Fort Ross, the warmest month seems to be August or September. Mean daily maximum (4.5 feet) for August, 1968 was 70°F, mean daily minimum was 60°; mean daily maximum for January, 1968 was 51°, mean daily minimum was 37°. Mean max-mins at Fort Ross (over a period of years) are 68–61° in September and 56–42° in January. Mean max-mins 2 cm above the ground were 73–53 in August, 1968 and 60–43 in January. Annual rainfall is extremely erratic, ranging from 18 inches in July, 1958–June, 1959 to 49 inches in July, 1966–June, 1967. Average rainfall for the 10-year period was 30 inches, and all but 1 inch falls in the period October-April. In contrast, average annual rainfall at Fort Ross is 40 inches. Wind is very predominantly out of the northwest. Of 49 equal-length data collecting periods, the prevailing wind was out of the northwest 63% of the time, out of the southwest 20%, and out of the southeast 17%. Wind speed is approximately equal throughout the year, with average wind speed at 10-12 mph. Storms are most frequent in November, January, and February and during storms billows of foam may be blown across the dunes and grassland. Fog is especially common during late spring and early summer. Insolation ranges from 0.15 kcal/cm^2/day in winter to 0.50 kcal/cm^2/day in spring.

As an indication of temperatures just above and below the soil in contrast to air temperature, Table 1 lists air, leaf, and soil temperature (taken with thermistor leads and a telethermometer) on the south- and north-facing sides of a small sand hummock in the dune area. The plant was *Ambrosia chamissonis* and its leaves were 1 cm from the sand surface.

Soils are predominantly sandy, ranging from pure sand in the central dunes to sandy loam in the northeast and southern parts of the peninsula. Marked gradients of topsoil salinity exist in the dunes and grassland as one moves inland (east) from the shore. At selected points, about 500 g of soil from the top six inches were collected, dried, put through a 2 mm sieve, and a 1:1 (soil:water) extract made. Conductivity of the extract was measured and converted to ppm total salt (Jackson, 1958). Samples were collected in grassland from the lip of an ocean-facing bluff and at 10-m intervals inland to a distance of 50 m. Table 2 presents the

TABLE 1. AIR AND SOIL TEMPERATURES ON NORTH- AND SOUTH-FACING SLOPES OF A SAND DUNE. OCTOBER 26, 1968, 2 P.M., CLEAR DAY. THE LEAF IS OF AMBROSIA CHAMISSONIS AT ½ INCH ABOVE THE DUNE SURFACE.

Position (inches)	Temperature (°F) South-facing	Temperature (°F) North-facing
+48	65	65
+ 2	76	67
—¼	107	81
— 3	105	69
— 6	66	66
leaf	72	72

TABLE 2. TOPSOIL SALINITY IN GRASSLAND AS A FUNCTION OF DISTANCE FROM THE LIP.

Distance from lip (meters)	Soluble salts (ppm)
0	1,920
10	960
20	621
30	634
40	454
50	314

results. Samples were collected in dunes from the strand where *Cakile maritima* was growing and at 50-m intervals to a distance of 750 m, where *Lupinus arboreus* was established on the hinddune. Table 3 presents the results.

In addition, the salinity of soil at the base of ocean-facing bluffs (which supported dense stands of *Scirpus koilolepis, Distichlis spicata* var. *stolonifera,* and *Jaumia carnosa*) and of sandy flats at the harbor edge (which supported *Salicornia virginica, Distichlis spicata* var. *stolonifera* and *Scirpus americanus*) was determined by the same method. Average of two bluff bottom samples was 1,600 ppm; average of five sand flat samples was 4,100 ppm.

The pH of the 1:1 extract was measured with a Beckman portable pH meter. Soil pH did not fluctuate with distance from shore, but did differ between dune (average = 8.3) ad grassland (average = 7.2). Bluff bottom and sand flat pH were similar and equal to that of grassland.

RECENT HISTORY

This short summary is taken principally from Kinnard (1966), Hoover and Rensch (1948), Hunt and Sanchez (1929), and personal communications from Cadet Hand.

The Spanish explorer Jaun Francisco de la Bodega y Cuadra discovered Bodega Bay and Bodega Harbor on October 3rd, 1775, but the Russians were the first white men to settle the immediate area. Ivan Kuskov, in 1809, built a settlement at the southeast side of Bodega

Table 3. Topsoil Salinity in Dunes as a Function of Distance from the Strand.

Distance from strand (meters)	Soluble salts (ppm)	Comments
0	460	strand with *Cakile*
50	185	foredune
100	122	foredune
150	45	low dunes
200	51	"
250	32	"
300	38	"
350	40	"
400	42	"
450	36	"
500	45	"
550	38	"
600	32	"
650	45	hinddune with *Lupinus*
700	83	hinddune with *Lupinus*
750	33	hinddune with *Lupinus*

Head, near the inlet, at a place now known as Campbell Cove. Kuskov noted it was a wind-blown site and lacked trees, but did have a spring. A larger settlement was built at Fort Ross in 1811. Although the area between Modega Head and Fort Ross was devoid of timber, the Russians found it adequate for grazing and vegetable growing. Cattle, sheep, horses, and pigs, bought from the Spanish nearby, heavily grazed the area, and potatoes became the favorite crop. By 1830, Fort Ross had become established as a shipyard, and the settlement on the Head became the principal import-export port for food, bricks, and general supplies. A brickyard, built near the Head, exported 10,000 bricks in 1830. The Bay became known to Americans as a good place for ships to take on water.

Within another decade, however, the Russians came to look at their California settlements as a liability because the agriculture was no longer sufficient to sustain the colony without imports, the otter and seal had been hunted nearly to extinction, and it seemed impossible to negotiate with Mexico for more land. The Emperor of Russia gave permission to move to Sitka, and a sale for all movable property was concluded with Captain John A. Sutter. Heavily in debt, Sutter never made payment, and the discouraged Russians left in 1841. Voznesenski's 1841 collection of the flora near Bodega Head has been discussed by Howell (1937).

The Mexican government claimed the land and divided it into large ranchros. Rancho Bodega, some 35,000 acres which ran from the Russian River south to Estero Americano River (present boundary of Marin and Sonoma Counties), was granted to an American named Stephen Smith in 1844. He set up a sawmill in a redwood area to the northeast of Salmon Creek.

TABLE 4. COMPARISON OF COMMUNITY NAMES IN THIS STUDY WITH THOSE DESCRIBED BY MUNZ (1959).

Bodega Head	Munz
dune	coastal strand
grassland	coastal prairie
ocean-facing bluff	coastal strand + northern coastal scrub
saline-wet	coastal salt marsh
fresh-wet	freshwater marsh + northern coastal scrub
disturbed	no equivalent

The goldrush and statehood swelled the population. Rancho Bodega became broken up into several holdings on the peninsula alone, and the Gaffney family came to own over 400 acres in the center. Mrs. Rose Gaffney, who came to Bodega Head in 1913, still lives in Salmon Creek. She recalls that much of the present dune area was pasture in the early 1900's, but that sand continually encroached from the west. Raising potatoes and grazing dairy herds continued to be prime land uses until the 1930's, when many marginal dairy herds were exchanged for sheep. Mrs. Gaffney claims that sheep were grazed on her property for only two months in 1942, but that cattle and horses were regularly present. She remarked that the show of early-summer flowers now (since the property has been a preserve) is much more spectacular than at any previous time.

In 1959, a Chancellor's Committee (Berkeley) For The Selection of a Marine Station Site recommended Bodega Head, and in 1962 the University of California acquired most of the Gaffney property and established it as a reserve. Over 200 acres at the tip of Bodega Head was purchased by Pacific Gas and Electric Company in 1960, with an eye to establishing an atomic-powered steam generator for production of electricity. Proximity of the site of the San Andreas fault, however, led to abandonment of the idea and the land is currently being leased to Sonoma Co. as a recreation area. Most of the dune area was purchased by the State of California in 1962 and incorporated into Sonoma Coast State Beach. The Laboratory was constructed in 1966 with the help of a National Science Foundation grant, and the facility is currently funded by the University of California.

PLANT COMMUNITIES

The flora and community descriptions were compiled in the course of monthly visits to the area over a period of more than 2 years. Undoubtedly there are species and varieties which I have missed, and undoubtedly my choice of communities could be refined with further field work. However, at this point in time, there appear to be six communities on the peninsula: dune, grassland, ocean-facing bluff, saline-wet, fresh-wet, and disturbed. In comparing my species lists for these communities to similar communities described by Munz (1959), it became

TABLE 5. COVER ALONG A 500-M × ⅓-M STRIP TRANSECT OF DUNE (RUNNING FROM STRAND TO HINDDUNE) IN JUNE, 1968.

Species	Cover (%)
bare	49
Ammophila arenaria	30
dead herbage (mostly of *Ammophila* and *Mesembryanthemum*)	18
Mesembryanthemum chilense	1
Lupinus arboreus	1
others	1

apparent that the two lists of communities were not quite the same. Table 4 summarizes the relationships between my choice of communities and their closest equivalents in Munz.

Dune. This community covers the largest area (39% of the peninsula). It is characterized by only a few common species, and a change in species with increasing distance from shore. On the strand itself is only one species, *Cakile maritima,* and it occurs in scattered clumps. *Ammophila arenaria,* planted in rows parallel to the shore, dominates the ground from the foredune back. It is especially dense on the foredune. Behind the foredune, *Mesembryanthemum chilense, Lotus heermannii,* and *Camissonia cheiranthifolia* are occasional; *Cakile* is absent. Finally, about 700 m from the strand, the hinddune is reached and *Lupinus arboreus* becomes common. On dunes dominated by *Lupinus,* and presumably older, many other species are common: *Abronia latifolia, Agoseris apargioides, Baccharis pilularis* ssp *consanguinea, Aplopappus ericoides, Elymus vancouverensis, Ambrosia chamissonis,* and *Poa douglasii.*

In June, 1968, I noted plant cover along a 500-m × ⅓-m strip transect which ran from strand to hinddune. Table 5 summarizes plant cover along the transect.

Grassland. Grassland covers almost as large an area (36% of the peninsula) as dune. In contrast, it is marked by a great diversity of species and a changing seasonal aspect. Very generally, the grassland is dominated by annual and perennial herbs and annual grasses. *Lupinus arboreus* dominates patches of grassland, but is nearly absent over much of it (but small seedlings are occasional to common). Many *Lupinus* shrubs—sometimes singly, sometimes in clusters, sometimes large, sometimes small—exhibit wilted foliage. With time the leaves turn gray and then fall, leaving a skeleton of apparently dead branches. If recently afflicted plants are uprooted, it is seen that the roots are nearly hollowed out by the burrowing activity of a small larva, identified as *Hepialus behrensi* Stretch by W. H. Lange, Professor of Entomology at Davis. An additional pest of *Lupinus,* prevalent in summer, is the caterpillar of the salt marsh moth, *Estigmene acraea,* identified by Paul Hurd, Professor of Entomology at Berkeley.

TABLE 6. COVER ALONG A 200-M × ⅓-M STRIP TRANSECT OF GRASSLAND (RUNNING FROM LIP OF OCEAN-FACING BLUFF INLAND) IN JUNE, 1968.

Species	Cover (%)
dead herbage (mostly of *Lupinus* and scattered litter)	33
annual grasses (many dying)	32
perennial and annual herbs	30
perennial grasses (mainly *Bromus carinatus*)	2
bare	2
Lupinus arboreus	1

The spring grassland is a wet green color, dominated by *Montia perfoliata, Stachys rigida, Luzula subsessilis,* with occasional color from *Arabis blepharophylla, Amsinckia menziesii, Iris douglasiana, Nemophila menziesii,* and *Ranunculus californicus.*

The early summer grassland is a carpet of yellow petals, principally of *Lasthenia chrysostoma, Eschscholzia californica, Layia platyglossa,* and *Platystemon californicus.* Less abundant herbs includes *Marah fabaceus, Phacelia distans, Silybum marianum, Sisyrinchium bellum,* and *Sonchus* spp. By June and July the grasses dominate the community. The most common species are *Aira caryophylla, Bromus arvensis, B. diandrus,* and *Lolium multiflorum,* all introduced. The most common native grass, the perennial *Bromus carinatus,* is much less common than the others.

In June, 1968, I noted plant cover along a 200-m × ⅓-m strip transect which ran across typical grassland from the lip of an ocean-facing bluff inland. Table 6 shows annual and perennial cover along the transect.

The late summer grassland is dull brown in color from dead annual grasses. *Eschscholzia californica* and *Lupinus arboreus* continue to flower, and *Achillea borealis* ssp. *arenicola* and *Cirsium vulgare* are common. *Holcus lanatus* forms dense stands in low spots, and its purple-tinged florets add a little more color.

Throughout the year, several species are restricted to the rocky crests of grassland hills: *Arabis blepharophylla, Brodiaea pulchella, Chlorogalum pomeridianum, Iris douglasiana, Luzula subsessilis,* and *Rhus diversiloba.*

Ocean-facing bluff. Only 7% of the area is dominated by this community, which occurs at the lip and rocky shelf at the base of ocean-facing bluffs. When the bluff is cut with a gulley so that the face is no longer vertical, the same community occurs down the face. Characteristic species include the low shrubs *Artemisia pycnocephala* and *Eriophyllum staechadifolium,* and the perennial herbs *Armeria maritima* var. *californica, Mesembryanthemum chilense, Plantago maritima* var. *californica,* and *Spergularia macrotheca.* The annual bulrush, *Scirpus koilolepis,* is restricted to the basal shelf and often occurs with *Distichlis spicata* and *Jaumia carnosa.* If a seep runs down to the shelf, species of grassland or disturbed communities may be present: *Anagallis arvensis, Polypogon monspeliensis, Sonchus* spp.

Saline-wet. This community dominates the saline, sandy flats at the edge of Bodega Harbor—about 1% of the area of this study. The species are principally low, rhizomatous perennials: *Distichlis spicata, Frankesia grandifolia, Jaumia carnosa, Salicornia virginica, Scirpus americanus.* Further from shore, and less common, are *Atriplex patula* ssp. *hastata* and *Holcus lanatus.*

The water table (brackish water) lies 15 cm or less beneath the surface. Algal mats often coat the ground surface. In October the upper shoots of *Salicornia* turn bright red and make this ordinarily dull-colored, monotonous community more lively.

A prominent species found here but not along saline cliff basis is *Scirpus americanus,* and species common to the cliff bases but not found here are *Mesembryanthemum chilense, Scirpus koilolepis,* and *Spergularia macrotheca.*

Fresh-wet. Members of this community range in habitat from fresh-water marshes to soil near seeps to moist, shaded hillsides and gulleys to depressions which exhibit standing water only during the wet season. Fresh-water marshes are dominated by *Scripus microcarpus* and *Sparganium eurycarpum* in the center, *Juncus balticus, Juncus leseurii, Oenanthe sarmentosa,* and *Potentilla egedii* var. *grandis* near the edge. Surprisingly, *Oenanthe* and *Potentilla* also occur at the edge of some saline flats.

Depressions which are seasonally wet support *Cotula coronopifolia, Scripus microcarpus* and *Typha angustifolia. Cotula* does also occur in the center of fresh-water marshes, but is not very prevalent there.

Shaded banks, gulleys, and seeps support a great variety of species, principally *Anaphalis margaritacea, Calamogrostis nutkaensis, Castilleja wrightii, Conium maculatum, Equisetum telmateia* var. *braunii, Heracleum lanatum, Mimulus guttatus* ssp. *litoralis, Nasturtium officinale, Polystichum munitum, Rubus procerus, Salix laevigata, Salix lasiolepis, Stellaria media,* and *Vicia gigantea.* There are also a great number of uncommon species, which will not be listed here, except for the rarest: *Fritillaria recurva,* only one specimen seen during the entire two years.

This diverse fresh-wet community occupies about 5% of the study area.

Disturbed. "Disturbed" must be a relative term here, for the entire area has been severely disturbed by grazing, farming, and human activity over the past 150 years. However, plants which are placed in this community occupy sites continuously being traveled over such as roadsides and footpaths. In this light, the disturbed community occupies 12% of the total area.

Table 7. Species with Long Flowering Periods.

Species	Flower ing period
Abronia latifolia	April-October
Brassica campestris	March-October
Cakile maritima	March-October
Castilleja wrightii	April-October
Cotula coronopifolia	March-October
Erodium cicutarium	March-October
Eschsholzia californica	March-October
Hypochoeris radicata	April-October
Mimulus guttatus ssp. *litoralis*	April-October
Nemophila menziesii	March-October
Mesembryanthemum chilense	March-September
Camissonia cheiranthifolia	April-October
Sonchus spp.	April-September

Along grassland paths are *Lasthenia minor, Calandrinia ciliata, Cardionema ramosissimum, Hypochoeris radicata, Orthocarpus erianthus* (in patches), *Plantago lanceolata, Phacelia distans,* and *Spergularia rubra.*

Roadsides show tremendous fluctuations in seasonal aspect. In spring, *Brassica campestris* and *Raphanus sativus* dominate; in early summer, *Brassica nigra, Cotula coronpifolia, Lotus corniculatus,* and *Polypogon monspeliensis* dominate; and in late summer and fall *Baccharis pilularis* ssp. *consanguinea, Conyza canadensis, Epilobium adenocaulon* var. *occidentale, Foeniculum vulgare, Melitotus albus, Rumex crispus,* and *Rubus vitifolius* dominate.

Miscellaneous Notes

The flora of Bodega Head consists of at least 215 species, representing 157 genera and 56 families. Introduced species make up 36%. Seven introduced species were probably only noted where planted and should not technically be included in the flora: *Acacia longifolia, Ceanothus thyrsiflorus* var. *repens, Cupressus macrocarpa, Eucalyptus globulus, Myoporum laetum, Pinus muricata* and *P. radiata.*

Some 14 species exhibited very erratic flowering times and were almost equally in flower for a period of 7-8 months. Table 7 lists these species and their flowering period. Only three of these species showed a major peak in flowering within that long period: *Abronia latifolia* (July-August), *Brassica campestris* (March-April), and *Nemophila menziesii* (March-April). *Cakile, Cotula, Mesembryanthemum,* and *Sonchus* had a few flowers even in December.

Another 11 species were found in two or more quite different habitats; their distributions are summarized in Table 8.

Voucher specimens of all species included in the check list have been deposited in the herbarium of the University of California, Davis (DAV).

TABLE 8. SPECIES WITH UNUSUAL DISTRIBUTIONS.

Species	Distribution
Anagallis arvensis	roadsides, base of ocean bluff in seep
Cotula coronopifolia	roadsides, wet ditches, fresht-water marsh
Dudleya farinosa	lip of ocean-facing bluff and lip of gulley
Grindelia stricta ssp. *venulosa*	roadsides, ocean-facing bluff
Holcuslanatus	edge of saline flat, wet area of grassland
Mesembryanthemum chilense	dunes, lip of ocean-facing bluff
Oenanthe sarmentosa	edge of fresh-water and salt-water marshes
Potentialla egedii var. *grandis*	edge of fresh-water and salt-water marshes
Polypogon monspeliensis	roadside, base of ocean-facing bluff (in seep), wet, shaded stream bank
Sonchus spp.	grassland, base of ocean-facing bluff in seep
Solanum nodiflorum	stabilized dunes, wet, shaded stream bank

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CHECK LIST

Calamophyta

Equisetaceae

Equisetum arvense L. Common horsetail. Perennial, native. Occasional to common in seasonally wet, but disturbed areas along roads and on steep, wet hillsides. Only vegetative shoots seen.

Equisetum telmateia Ehr. var. *braunii* Milde. Giant horsetail. Perennial, native. Common to abundant on steep, wet hillsxides. Fertile shoots produced in March.

Pterophyta

Aspidiaceae

Athyrium felix-femina (L.) Roth var. *sitchense* Rupr. Lady fern. Perennial, native. Rare to occasional in shaded gulley near stream.

Polystichum munitum (Kaulf.) Presl. Sword fern. Perennial, native. Common in large clumps on steep, wet hillsxides.

Polypodiaceae

Polypodium scouleri Hook. & Gray. Polybody. Perennial, native. Occasional on grassland hill-tops next to rocks.

Pteridiaceae

Pteridium .aquilinum (L.) Kuhn var. *lanuginosum* (Bong.) Fern Bracken. Perennial, native. Occasional in grassland, more common when *Lupinus arboreus* is present.

Coniferophyta

Cupressaceae

Cupressus macrocarpa Hartw. ex Gordon. Monterey cypress. Perennial, planted or escaped. Rare along roads, in dunes, near Marine Laboratory.

Pinaceae

Pinus muricata D. Don. Bishop pine. Perennial, probably planted. Rare along road near Salmon Creek.

P. radiata D. Don. Monterey pine. Perennial, probably planted. Occasional along roads.

Anthophyta—Dicotyledoneae

Aizoaceae

Mesembryanthemum chilense Mol. Sea-fig. Perennial, introduced. Common along ocean-facing cliffs (especially at the lip) and on dunes. Flowering sporadic, March-September.

M. edule L. Hottentot-fig. Perennial, Introduced. Common in dunes, planted along roadbanks. Flowering March-July.

Anacardiaceae

Rhus diversiloba T. & G. Poison oak. Perennial, native. Occasional in grassland and along shaded streambank. Only vegetative shoots seen.

Apocynaceae

Vinca major L. Periwinkle. Perennial, introduced. Possibly planted in dense strips along one road and at edge of a fresh-water marsh; otherwise rare. Flowering in March and October, possibly in months between.

Berberidaceae

Berberis pinnata Lag. Barberry. Perennial, native. Common on one grassland hill, otherwise rare. Only vegetative shoots seen.

Boraginaceae

Amsinckia menziesii (Lehm.) Nels. & Macbr. Fiddleneck. Annual, native. Common in grassland; variable in size and leaf shape. Flowering April-June.

A. spectabilis F. & M. Fiddleneck. Annual, native. Common on established dunes (with *Lupinus arboreus*); prostrate and sparsely hispid. Flowering June-July.

Cryptantha leiocarpa (F. & M.) Greene. Annual, native. Occasional in dunes. Flowering June.

Plagiobothrys tenellus (Nutt.) Gray. Annual, native. Occasional to common in disturbed areas. Flowering April-May.

Caryophyllaceae

Cardionema ramosissimum (Weinm.) Nels. & Macbr. Perennial, native. Occasional to common as prostrate mats in grassland footpaths. June-July.

Silene gallica L. Windmill pink. Annual, introduced. Occasional in grassland. May-June.

Spergula arvensis L. Spurrey. Annual, introduced. Occasional in disturbed areas. March-July.

Spergularia macrotheca (Hornem.) Heynh. Sand-spurrey. Perennial, native. Occasional to comon on shelf at base of ocean-facing cliff, also occasional along path in grassland; prosetrate. May-August.

S. rubra (L.) J. & C. Presl. Sand-spurrey. Annual, native. Common in disturbed areas along roads. March-July.

Stellaria media (L.) Cyr. Chickweed. Annual, introduced. Common in grassland, abundant along shaded stream. March-April.

Chenopodiaceae

Atriplex patula L. ssp. *hastata* (L.) Hall & Clem. Annual, introduced. Occasional at outer edge of saline flats near shore. August.

A. patula L. ssp. *obtusa* (Cham.) Hall & Clem. Annual, introduced. Occasional to rare on saline flat near ocean. October.

Chenopodium album L. Pigweed. Perennial, introduced. Rare in seasonally wet area along road. July.

C. ambrosoides L. var. *vagans* (Standl.) Howell. Mexican tea. Annual-perennial, native. Rare in disturbed areas. August-September.

C. californicum (Wats.) Wats. Pigweed. Perennial, native. Occasional in grassland, more common in disturbed areas. April-June.

Salicornia virginica L. Pickleweed. Perennial, native. Abundant in saline flats near shore, common along shelf at base of ocean-facing cliff. October; inflorescences and upper stems becoming reddish at that time.

Compositae

Achillea borealis Bong. ssp. *arenicola* (Hel.) Keck. Yarrow. Perennial, native. Common in grassland, established dunes (with *Lupinus arboreus*), and occasional in disturbed areas along roads. May-October.

Agoseris apargioides (Less.) Greene ssp. *maritima* (Sheld.) Jones. Beach dandelion. Common on established dunes. Flowering sporadic, April-October. Perennial, native.

Anaphalis margaritacea (L.) B. & H. Pearly everlasting. Perennial, native. Common to occasional on steep, shaded, wet hillsides. July-October.

Haplopappus ericoides (Less.) H. & A. Perennial, native. Occasional on established dunes (with *Lupinus arboreus*). August-October.

Artemisia douglasiana Bess. in Hook. Sagebrush. Perennial, native. Semi-prostrate; occurs in dense clusters on established dunes, in grassland, and along roads; generally rare. August-October.

A. pycnocephala DC. Sagebrush. Perennial, native. Occasional along lip of ocean-facing bluff. July-September.

Aster chilensis Nees. Perennial, native. Occasional in grassland. September.

Baccharis pilularis DC. ssp. *consanguinea* (DC). Wolf. Coyote bush. Perennial, native. Rare in dunes, occasional in disturbed areas along roads. September-October.

Carduus pycnocephalus L. Italian thistle. Annual, introduced. Occasional in disturbed areas. May-June.

Centaurea solstitialis L. Star thistle. Annual, introduced. Rare along roads. September.

Chrysanthemum segetum L. Corn chrysanthemum. Annual, introduced. Rare in disturbed areas along roads. June-July.

Cichorium intybus L. Chicory. Perennial, introduced. Rare in disturbed areas along roads. August.

Cirsium andrewsii (Gray) Jeps. Thistle. Perennial, native. Flowering stalk short (hardly higher than basal leaves); occasional in grassland. May-July.

C. occidentale (Nutt.) Jeps. Thistle. Perennial, native. Tall (to 2 m) and clumped, herbage covered with dense arachnoid pubescence; occasional on established dunes. May-July.

C. vulgare (Savi) Ten. Bull thistle. The most common of the three thistles; common in grassland and in shaded, wet hillside. July-October.

Conyza canadensis (L.) Cronq. Horseweed. Annual, introduced. Common to abundant in disturbed areas along roads. September-October.

Cotula coronopifolia L. Brass buttons. Perennial, introduced. Common in fresh-water marshes and near roads. Flowering sporadic. March-October.

Erechtites arguta (A. Rich.) DC. Fireweed. Annual, introduced. Occasional along roads. July-August.

E. prenanthoides (A. Rich.) DC. Fireweed. Annual, introduced. Occasional at edge of fresh-water marsh, common along steep, wet hillsides, sometimes near roads. July-September.

Erigeron glaucus Ker. Seaside daisy. Perennial, native. Occasional on established dunes and cliff edges, rare in grassland. June-September.

Eriophyllum lanatum (Pursh) Forbes var. *arachnoideum* (Fisch. & Ave-Lall.) Jeps. Perennial, native. Rare to occasional in dunes. May.

E. staechadifolium Lag. Perennial, native. Common along lip of ocean-facing bluff. July-September.

Ambrosia chamissonis (Less.) Greene. Perennial, native. Common on dunes. Two forms occur intermixed: one form with broadly lobed leaves, the other with smaller, pinnate to bipinnate lobes. The two leaf forms do not occur on the same plant, but the two plants may grow side-by-side. July-August.

Gnaphalium chilense Spreng. Cud-weed. Annual-biennial, native. Occasional in grassland and along roads. May-October.

G. chilense Spreng. var. *confertifolium* Greene. Cud-weed. Annual-biennial, native. Less common than the species; grassland and along roads; June.

G. purpureum Locc. Cud-weed. Annual-biennial, native. Rare along road. May.

Grindelia stricta DC. ssp. *venulosa* (Jeps.) Keck. Gum-weed. Perennial, native. Occasional along road and ocean-facing bluff. May-September.

Hypochoeris radicata L. Hairy cat's ear. Perennial, introduced. The most common member of Compositae; variable in flower size and color (yellow to gold-orange); sometimes with swollen stems. Common in disturbed areas, especially along grassland footpaths. Sporadic flowering, April to October.

Jaumia carnosa (Less.) Gray. Perennial, native. Occasional to common in saline flats near coast and at base of ocean-facing bluff on shelf. September-October.

Lasthenia chrysostoma (F. & M.) Greene. Goldfields. Annual, native. Common to abundant in grassland and in paths through it. May-June.

L. minor (DC.) Ferris. Annual, native. Common in footpaths, less common in grassland. March-April.

Layia platyglossa (F. & M.) Gray. Tidy tips. Occasional to common in grassland and along footpaths through it. May-July.

Madia sativa Mol. Coast tarweed. Annual, native. Common in grassland, occasional in disturbed areas along roads. May-October.

Silybum marianum (L.) Gaertn. Milk-thistle. Annual-biennial, introduced. Occasional in grassland. April-June.

Solidago californica Nutt. California goldenrod. Perennial, native. Rare along shaded stream bank. September.

Sonchus asper L. Sow-thistle. Annual, introduced. Common to abundant in grassland, occasional along roads and on shelf at base of ocean-facing cliff. Flowering sporadic. April-September.

S. oleraceus L. Sow-thistle. Annual, introduced. Distribution and flowering as with *S. asper*.

Wyethia angustifolia (DC.) Nutt. Perennial, native. Rare along roads. April.

Convolvulaceae

Convolvulus occidentalis Gray var. *saxicola* (Eastw.) Howell. Morning glory. Perennial, native. Occasional in grassland. April-May.

Crassulaceae

Dudleya farinosa (Lindl.) Britt. & Rose. Live-forever. Perennial, native. Occasional on ocean-facing bluff, on rocky hill tops, and at lip of wet, shaded gulley. July-August.

Cruciferae

Arabis blepharophylla H. & A. Rock-cress. Perennial, native. Common near summits of grassland hills. March-April.

Barbarea orthoceras Ledeb. Winter-cress. Biennial-perennial, native. Rare in disturbed part of grassland. March-April.

Brassica campestris L. Field mustard. Annual, introduced. Common along roads, occasional in seasonally wet sites. Principal flowering time March-April, a few plants in flower in October, possibly some flowered during intervening months.

B. nigra (L.) Koch. Black mustard. Annual, introduced. Common along roads. Principal flowering time May-August, some through October.

Cakile maritima Scop. Sea rocket. Annual, introduced. Common facing ocean on outer-most dunes or on strand, once seen inland near road in seasonally wet area; occurs in clumps which seem to build mounds of sand. Although *C. edentula* var. *californica* has been reported for the area, I have yet to see it. Flowering sporadic, March-October.

Cardamine oligosperma Nutt. Bitter-cress. Annual-biennial, native. Common in grassland in patches, the siliques popping open and spraying out seeds as one walks through in April. Flowering in March.

Nasturtium officinale R. Br. Water-cress. Perennial, introduced. Common to abundant on very wet shaded streambank and in the stream itself. June-August.

Raphanus sativus L. Wild radish. Annual-biennial, introduced. Common along roads, occasional in grassland; leaves may be smooth or hispid; petals white, yellow, or blue. Principal flowering time March-July, a few in flower in September-October.

Rorippa curvisiliqua (Hook.) Bessey. Yellow-cress. Annual-biennial, native. Rare in disturbed area of grassland. June.

Cucurbitaceae

Marah fabaceus (Naud.) Dunn. Manroot. Perennial, native. Common in grassland dominated by *Lupinus arboreus*. March-June.

Cuscutaceae

Cuscuta salina Engelm. Dodder. Perennial, native. Occasional on *Salicornia* in salt marsh. June.

C. subinclusa Dur. & Hilg. Dodder. Perennial, native. Occasional on *Jaumia* in salt marsh. June.

Frankeniaceae

Frankenia grandifolia C. & S. Perennial, native. Occasional to common at edge of salt flats near ocean. August.

Geraniaceae

Erodium cicutarium (L.) L'Her. Red-stem filaree. Annual, introduced.

Common in disturbed areas of grassland. Flowering sporadic, March-October.

E. moschatum (L.) L'Her. White-stem filaree. Annual, introduced. Also in disturbed areas, but less common than *E. cicutarium*. March-May.

Hydrophyllaceae

Nemophila menziesii H. & A. Baby-blue-eyes. Annual, native. Common in grassland; variable in petal color (white to dark blue). Principal flowering time March, some flowering to August.

Phacelia californica Cham. Perennial, native. Occasional along lip of ocean-facing bluffs. Not seen flowering.

P. distans Benth. Wild heliotrope. Annual, native. Common in disturbed areas of grassland, less common in grassland. April-August.

Labiatae

Mentha pulegium L. Pennyroyal. Perennial, introduced. Occasional on established dunes. September.

Stachys rigida Nutt. ex Benth. ssp. *quercetorum* (Heller) Epl. Hedge-nettle. Perennial, native. Common to abundant in grassland, less noticeable in late summer and fall. Principal flowering in April-May, some flowering to October.

Leguminosae

Acacia longifolia Willd. Perennial, introduced. Probably planted, rare along seasonally wet roadside. April.

Cytisus monspessulanus L. French broom. Perennial, introduced. Rare along roadsi des. September.

Lotus corniculatus L. Bird's foot trefoil. Perennial, introduced. Common to abundant along roadsides, creating solid strips of yellow when in flower. June-August.

L. heermanii (Dur. & Hilg.) Greene var. *eriophorus* (Greene) Ottley. Bird's foot trefoil. Perennial, native. Occasional in dunes; petals red to yellow. May-June.

L. subpinnatus Lag. Bird's foot trefoil. Annual, native. The least attractive and least common on the three trefoils; rare along roads. August.

Lupinus arboreus Sims. Lupine. Perennial, native. Common in grassland (abundant in patches), on stabilized dunes at some distance from shore, and occasional on ocean-facing bluffs. April-August; flowers variable in color even on same shrub (white, yellow, blue).

L. bicolor Lindl. ssp. *umbellatus* (Greene) Dunn. Lupine. Annual, native. Occasional along roads. April-July.

Medicago polymorpha L. var. *vulgaris* (Benth.) Shinners. Bur-medick. Annual, introduced. Occasional to common along roads. April.

Melitotus albus Desr. White sweet-clover. Annual-biennial, introduced. Occasional to common along roads. August-September.

M. indicus (L.) All. Yellow sweet-clover. Annual-biennial, introduced. Occasional along roads. April-July.

Trifolium barbigerum Torr. Clover. Annual, native. Occasional in disturbed areas. April.

T. fucatum Lindl. Clover. Annual, native. Rare along lip of ocean-facing bluff. May.

T. repens L. White clover. Perennial, introduced. Occasional to common along roads. June.

T. wormskioldii Lehm. Clover. Perennial, native. Rare to occasional in disturbed areas of grassland. May-July.

Vicia americana Muhl. ssp. *oregana* (Nutt.) Abrams. Vetch. Perennial, native. Occasional to rare in grassland and disturbed areas of grassland. April.

V. californica Greene. Vetch. Perenial, native. Occasional to common in grassland and disturbed areas of grassland. May.

V. gigantea Hook. Vetch. Perennial, native. Common on steep, wet hillsides. March-July.

Malvaceae

Lavatera arborea L. Tree-mallow. Perennial, introduced. Rare along roadsides. July.

Sidalcea malviflora (DC.) Gray ex Benth. ssp. *laciniata* Hitchck. Checker. Perennial, native. Rare along roadsides. April.

Myoporaceae

Myoporum laetum Forst. Perennial, introduced. Planted near Marine Laboratory. Flowering sporadic, March-July.

Myricaceae

Myrica californica C. & S. Wax myrtle. Perennial, native. Rare on steep, wet hillsides. February.

Myrtaceae

Eucalyptus globulus Labil. Tasmanian blue-gum. Perennial, introduced. Planted or possibly escaped in wet, shaded gulley. April-August.

Nyctaginaceae

Abronia latifolia Esch. Sand verbena. Perennial, native. Common on established dunes (with *Lupinus arboreus*), occasional along roads in grassland. Flowering sporadic, April-October.

Onagraceae

Epilobium adenocaulon Hausskn. var. *occidentale* Trel. Willow-herb. Perennial, native. Occasional along roads. August-September.

E. watsonii Barbey var. *franciscanum* (Barbey) Jeps. Willow-herb. Perennial, native. Rare along roads. August-September.

Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann. Evening primrose. Common on established and shifting dunes. Flowering sporadic, April-October.

Oxalidaceae

Oxalis corniculata L. Wood-sorrel. Pearennial, introduced. Occasional in grassland. September.

O. pes-caprae L. Wood-sorrel. Perennial, introduced. Rare in seasonally wet area near road. March.

Papaveraceae

Eschscholzia californica Cham. California poppy. Perennial, native. One of the most comon species in grassland and on established dunes (with *Lupinus arboreus*). Flowering sporadic, March-October.

Platystemon californicus Benth. Cream cups. Annual, native. Common to abundant in grassland; some petals all white, others with yellow tpis; variable in size of plant; together with *Lasthenia chrysostoma* and *Eschscholzia californica,* forms much of the spring color show. April-July.

Plantaginaceae

Plantago lanceolata L. Plantain. Perennial, introduced. Occasional to common in disturbed areas. April-July.

P. maritima L. var. *californica* (Fern.) Pilg. Plantain. Perennial, native. Common at base of ocean-facing bluffs. May-July.

Plumbaginaceae

Armeria maritima (Mill.) Willd. var. *californica* (Boiss.) Lawr. Thrift. Perennial, native. Abundant along lip of ocean-facing bluffs, common at their base. April-July.

Polemonicaceae

Gilia capitata Sims. var. *chamissonis* (Greene) Grant. Annual, native. Rare on established dunes (with *Lupinus arboreus*). May.

Navarretia squarrosa (Eschs.) H. & A. Skunkweed. Annual, native. Occasional on established dunes (with *Lupinus arboreus*); giving off a strong skunklike odor easily detected when walking near the plants. June-July.

Polygonaceae

Chorizanthe cuspidata Wats. var. *villosa* (Eastw.) Munz. Annual, native. Occasional along footpath in grassland. June.

Eriogonum latifolium Sm. Wild buckwheat. Perennial, native. Occasional in grassland at some distance from shore, and along lip of ocean-facing bluffs. July-September.

Polygonum patulum Biebst. Knotweed. Annual, introduced. Rare along roads. May.

Pterostegia drymarioides F. & M. Annual, native. Rare in grassland. April.

Rumex acetosella L. Sheep sorrel. Perennial, introduced. Common in grassland and disturbed areas of grassland. March-July.

R. crispus L. Curly dock. Annual, introduced. Occasional along roads. May-July.

R. pulcher L. Fiddle dock. Perennial, introduced. Occasional along roads. June-July.

Portulacaceae

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr. Red maids. Annual, native. Common in disturbed areas; variable in morphology. March-April.

Montia perfoliata (Donn) Howell. Miner's lettuce. Annual, native. Common to abundant in grassland; together with *Stachys rigida* ssp. *quercetorum,* forming much of forb growth in grassland in very early spring. March-April.

Primulaceae

Anagallis arvensis L. Scarlet pimpernel. Annual, introduced. Occasional to common in grassland, in disturbed areas, and rare at base of ocean-facing bluff. Flowering sporadic, March-September.

Ranunculaceae

Ranunculus californicus Benth. var. *cuneatus* Greene. Buttercup. Perennial, antive. Common in grassland and in paths of grassland; petals all yellow or white-tipped. March-April.

Rhamnaceae

Ceanothus thyrsiflorus Eschs. var. *repens* McMinn. Blue-blossom. Perennial, native. Probably planted, near Marine Laboratory; only vegetative shoots seen (young plants).

Rhamnus californica Eschs. ssp. *tomentella* (Benth.) Wolf. Buckthorn. Perennial, native. Rare to occasional on steep, wet hillsides. Only vegetative shoots seen.

Rosaceae

Fragaria chiloensis (L.) Duchn. Beach strawberry. Perennial, introduced. Despite the name, only seen in grassland; rare. March.

Horkelia marinensis (Elmer) Crum ex Keck. Perennial, native. Rare about rocks in grassland.

Potentilla egedii Wormsk. var. *grandis* (Rydb.) Howell. Cinquefoil. Perennial, native. Abundant in seasonally wet (fresh water) swale through grassland, also in narrow strip at edge of saline flat near ocean. Flowering April-July principally, a few flowering to September.

Rosa eglanteria L. Eglantine. Perennial, introduced. Occasional in grassland away from coast; viciously armed. Only vegetative shoots seen.

Rubus procerus P. J. Muell. Himalaya berry. Perennial, introduced. Forming tall thickets along shaded stream banks, also as a climber over shrubs in grassland away from the coast. Occasional. June.

R. spectabilis Pursh. var. *franciscanus* (Rydb.) Howell. Salmon berry. Perennial, native. Rare to occasional on steep, wet hillsides. March.

R. ursinus C. & S. California blackberry. Perennial, native. Rare as climber over shrubs away from coast. April.

R. vitifolius C. & S. California blackberry. Occasional in grassland away from coast and along roads. Perennial, native.

Rubiaceae

Galium asperrimum Gray. Perennial, native, April.

Salicaceae

Salix laevigata Bebb. Willow. Perennial, native. Common in wet, shaded gulleys. Only vegetative shoots seen.

S. lasiolepis Benth. Arroyo willow. Perennial, native. Common in wet, shaded gulleys. Only vegetative shoots seen.

S. lasiolepis Benth. var. *bigelovii* (Torr.) Bebb. Willow. Perennial, native. Rare on established dunes. Only vegetative shoots seen.

Scrophulariaceae

Castilleja wrightii Elmer. Paintbrush. Perennial, native. Occasional to common in seasonally wet (but disturbed) areas, also on steep, wet hillsides; once seen on ocean-facing bluff; bracts and calyx variable in color (yellow, dull red, bright red). Flowering sporadic, April-October.

Cordylanthus maritimus Nutt. ex Benth. Annual, native. Common in the higher part of coastal salt marsh.

Mimulus aurantiacus Curt. Bush monkey-flower. Perennial, native. Common in grassland and along roads away from coast. April-July.

M. guttatus Fisch. ex DC. ssp. *litoralis* Penn. Monkey-flower. Perennial, native. Occasional in seasonally wet areas along roads. Flowering sporadic, April-October.

Orthocarpus erianthus Bench. var. *roseus* Gray. Johnny-tuck. Annual, native. Abundant in rare patches in disturbed parts of grassland. April-May.

Scrophularia californica C. & S. Figwort. Perennial, native. Rare along roads. May.

Veronica americana Schwein. Speedwell. Perennial, native. Occcasional near center of fresh-water marsh (with *Sparganium eurycarpum*). July.

Solanaceae

Solanum nodiflorum Jacq. Nightshade. Annual-perennial, native. Occasional herb with flowering shoot over 2 m tall, along roads and in wet, shaded gulley. June-July.

Umbelliferae

Angelica hendersonii Coult. and Rose. Perennial, native. Occasional along ocean-facing bluffs. August-September.

Conium maculatum L. Poison hemlock. Occasional along roads and in seasonally wet areas.

Daucus carota L. Queen Anne's lace. Biennial, introduced. Occasional along roads. July-September.

D. pusillus Michx. Ratlesnake weed. Annual native. Rare in dunes. April.

Foeniculum vulgare Mill. Sweet fennel. Biennial-perennial, introduced. Occasional along roads; odor of licorice. July-September.

Heracleum lanatum Michx. Cow parsnip. Perennial, native. Common on steep, wet hillsides. April.

Oenanthe sarmentosa Presl. Perennial, native. Abundant in narrow strip at edge of saline flats near ocean, also in fresh-water marsh. May-September.

Sanicula arctopoides H. & A. Yellow mats. Perennial, native. Occasional in grassland very close to shore. March.

Monocotyledoneae

Amaryllidaceae

Allium dichlamydeum Greene. Wild onion. Perennial, native. Rare on grassland hilltops. June.

A. triquetrum L. Wild onion. Perennial, introduced. Rare in seasonally wet area near road. March.

Brodiaea pulchella (Salisb.) Greene. Blue dicks. Perennial, native. Occasional near crests of grassland hills. June-July.

Cyperaceae

Carex barbarae Dewey. Sedge. Perennial, native. Occasional along road. June-July.

Cyperus eragrostis Lam. Umbrella sedge. Perennial, native. Occasional in seasonally wet areas near roads, abundant in center of fresh-water marshes. August-September.

Scirpus americanus Pers. Bulrush. Perennial, native. Common in saline flats near ocean and in standing brackish water. April-June.

S. cernuus Vahl. var. *californicus* (Torr.) Beetle. Bulrush. Annual, natve. Rare in dunes. July.

S. koilolepis (Steud.) Gleason. Bulrush. Annual, native. Common in clumps at base of ocean-facing bluffs. August.

S. microcarpus Presl. Bulrush. Perennial, native. Largest of the Cyperaceae; common in fresh-water marshes. July.

Gramineae

Aira caryophylla L. Hairgrass. Annual, introduced. Common to abundant in grassland and in disturbed parts of grassland; contribution to standing biomass often overlooked because of short size. April-June.

Agrostis exarata Trin. Bent grass. Perennial, native. Rare along shaded streambank. July.

Ammophila arenaria (L.) Link. Beachgrass. Perennial, introduced. Widely planted on dunes, probably escaped in other areas; abundant. Flowering sporadic, along the outer dune in July, variable further inland.

Avena barbata Brot. Wild oat. Annual, introduced. Common along roads. May.

Briza maxima L. Quaking grass. Annual, introduced. Rare along roads. June.

B. minor L. Quaking grass. Annual, introduced. Rare along roads. June.

Bromus carinatus H. & M. California brome. Perennial, native. Occasional to common in grassland. May-June.

B. mollis L. Soft chess. Annual, introduced. Rare in disturbed areas. June.

B. diandrus Roth. Ripgut. Annual, introduced. Abundant in grassland, occasional in disturbed areas. April.

Calamagrostis nutkaensis (Presl) Steud. Reedgrass. Perennial, native. Occasional to common on steep, wet hillsides. November.

Cortaderia selloana (Schult.) Arch. & Graebn. Pampas grass. Perennial, introduced. Possibly planted; near Marine Laboratory; rare. September.

Dactylis glomerata L. Orchard grass. Perennial, introduced. Rare along roads. June.

Distichlis spicata (L.) Greene var. *stolonifera* Beetle. Perennial, native. Salt grass. Common in saline flats near ocean and at base of ocean-facing cliffs. Only vegetative shoots seen.

Elymus glaucus Buckl. Rye grass. Perennial, native. Rare in wet, shaded gulley. July.

E. vancouverensis Vasey. Rye grass. Perennial, native. Occasional in stabilized dunes (with *Lupinus arboreus*), along roads, and near lip of ocean-facing bluff. August.

Festuca dertonensis (All.) Arch. & Graebn. Fescue. Annual, introduced. Occasional at edge of saline flat near ocean, with *Holcus lanatus*. May.

Holcus lanatus L. Velvet grass. Perennial, introduced. Abundant in low area of grassland (near *Potentilla egedii* var. *grandis*) and on saline flat near ocean; occasional in disturbed areas of grassland. June-August.

Hordeum brachyantherum Nevski. Perennial, native. Occasional in grassland. April.

H. depressum (Scribn. & Sm.) Rydb. Wild barley. Annual, native. Common in grassland, occasional along roads. May.

H. leporinum Link. Farmer's foxtail. Annual, introduced. Occasional in disturbed areas. March-June.

Lolium multiflorum Lam. Italian ryegrass. Annual, introduced. Together with *Aira caryophylla, Bromus arvensis, Bromus rigidus,* makes up most of the grass cover in grassland. Abundant. May-June.

Poa douglasii Nees. Sand bluegrass. Perennial, native. Occasional on established dunes. March-April.

P. scabrella (Thurb.) Benth. Blue grass. Perennial, native. Occasional in grassland. April.

Polypogon monspeliensis (L.) Desf. Rabbit-foot grass. Annual, introduced. Occasional in disturbed areas and along base of ocean-facing bluff, rare along shaded streambank. June-September. Variable morphology.

Iridaceae

Iris douglasiana Herb. Wild iris. Perennial, native. Occasional in grassland close to and away from the shore. March-April.

Sisyrinchium bellum Wats. Blue-eyed grass. Perennial, native. Occasional in low areas of grassland. April-July.

Juncaceae

Juncus balticus Willd. Rush. Perennial, native. Abundant in occasional patches in wet, low parts of grassland. March.

J. bolanderi Engelm. Rush. Perennial, native. Rare in wet areas along roads. August.

J. bufonius L. Toad rush. Annual, native. Smallest of the rushes at the Head; rare in seasonally wet area near road (with *Cyperus eragrostis*. August.

J. effusus L. var. *brunneus* Engelm. Rush. Perennial, native. Occasional along road. May-October.

J. leseurii Bol. Rush. Perennial, native. The most wide-spread and common of the rushes at the Head; common in dunes near a pond, abundant in fresh-water marsh, occasional along roads. May-October.

Luzula subsessilis (Wats.) Buch. Wood rush. Perennial, native. Common in grassland, especially near crests of hills. March.

Juncaginaceae

Triglochin maritima L. Arrow grass. Perennial, native. Common in salt marsh. May-June.

Liliaceae

Chlorogalum pomeridianum (DC.) Kunth. Soap plant. Perennial, native. Common in grassland; only vegetative shoots seen.

Fritillaria recurva Benth. Fritillary. Perennial, native. Rare, at lip of steep hillside, in grassland. March.

Potamogetonaceae

Potamogeton crispus L. Perennial, introduced. Occasional in fresh water ponds. Leaves broad. Only vegetative material seen.

P. pectinatus L. Perennial, native. Common in fresh water ponds. Leaves linear. Only vegetative material seen.

Sparganiaceae

Sparganium eurycarpum Engelm. Bur-reed. Perennial, native. Occasional in center of fresh-water marshes. July-September.

Typhaceae

Typha angustifolia L. Cat-tail. Perrenial, introduced. Occasional in seasonally wet areas near road (often with *Cyperus eragrostis*). August-September.

Zosteraceae

Phyllospadix torreyi Wats. Surf-grass. Occasionally thrown up on beach from near the low-tide level. Perennial, native.

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THE CONSPECIFICITY OF HETEROSIPHONIA ASYMMETRIA AND H. DENSIUSCULA AND THEIR LIFE HISTORIES IN CULTURE

JOHN A. WEST

INTRODUCTION

The marine red algal genus *Heterosiphonia* (Ceramiales, Dasyaceae) includes about 40 species which are widely distributed in temperate, tropical and cold waters. The genus is characterized as having polysiphonous and corticated main axes which branch in a sympodial manner. The lateral branches are alternate, distichous and either monosiphonous or polysiphonous. Spermatangia and tetrasporangia are borne in specialized conical reproductive structures called stichidia (Kylin, 1956).

On the Pacific coast of North America five species are known. *Heterosiphonia densiuscula* and *H. laxa* were described from Friday Harbor, Washington by Kylin (1925). Both species are known only from northern Washington and southern British Columbia (Scagel, 1957). *Heterosiphonia asymmetria,* described by Hollenberg (1945), has a range extending from Santa Catalina Island to the Monterey Peninsula in California (Hollenberg and Abbott, 1966). Gardner (1927) described *H. erecta* which ranges from southern California to Baja, California (Dawson, 1963). *Heterosiphonia wurdemannii* Børgesen is broadly distributed in tropical waters and is present in the Gulf of California (Dawson, 1963).

Heterosiphonia erecta and *H. wurdemannii* are described as having four pericentral cells, *H. asymmetria* as having five, and *H. laxa* and *H. densiuscula* as having six to nine. The first two species appear to be morphologically distinct taxa, but *H. asymmetria, H. densiuscula* and possibly *H. laxa* appear very closely related, if not identical, for reasons which will be brought out in the observations and discussion section of this paper. Because of the apparent taxonomic problems involving these three species, I considered it necessary to re-investigate various aspects of their morphology and life histories.

MATERIALS AND METHODS

For the culture of *H. densiuscula,* specimens were dredged from about 15 m depth at Partridge Bank, west of Whidbey I., Washington, on July 6, 1965. This clone has been maintained for over four year in unialgal culture with Provasoli's enriched seawater medium (Provasoli, 1966) in 10 C, 16 hr daily photoperiod and 20–40 ft-c cool white fluorescent lighting. The clone of *H. asymmetria* was isolated from material collected in the drift at the south end of Carmel Beach, Monterey Peninsula, California, April 19, 1967. It has been cultured for more than two years in 15 C, 15—150 ft-c cool white lighting and 16 hr daily photoperiod with Provasoli's medium.

All seawater for these culture studies was obtained from the Bodega Marine Laboratory, Bodega Bay, California. It was aged at least 30 days in the dark at 20–22 C before use. The salinity was adjusted to 30–31% by adding glass distilled water. The seawater was then steam sterilized for 30 mintues and stored until use. The enrichment medium was added to the sterile seawater just prior to use.

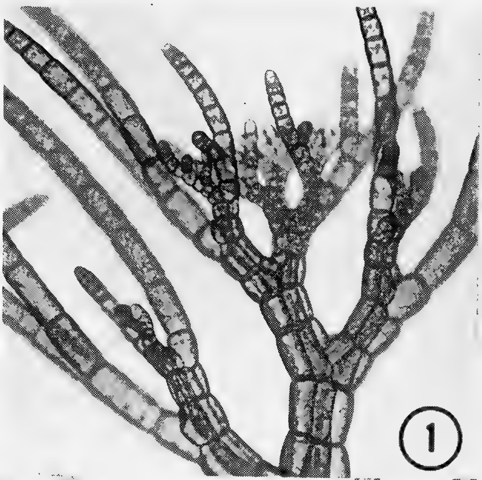
All cultures were maintained in either Pyrex (No. 3250) 100 x 80 deep storage dishes with 150–200 ml of the medium or in Pyrex 90 x 50 mm crystallizing dishes with 100 ml of the medium.

Tetraspores were allowed to attach to coverslips which were transferred to fresh medium every 14–30 days.

OBSERVATIONS AND DISCUSSION

Culture studies. Heterosiphonia densiuscula grows well in culture without significant deviation from the morphology observed in field-collected specimens. The initially tetrasporophytes produced tetraspores which gave rise to tetrasporangia-bearing plants after 3 months at about 30 ft-c illumination. The plants in culture are 3.0 to 5.0 cm long when reproductive, in contrast to plants from nature which often reach 10 to 15 cm in length when reproductive. Neither carpogonia nor spermatangia were observed on any of more than 500 plants from four successive generations. The tetrasporangia are normal in morphology and release 4 spores. Each fertile segment of the stichidium bears 4 to 6 sporangia in a whorl (fig. 2). Spore germination is similar to that described for most of the Ceramiales. The spore first divides into two unequal cells. The smaller cell is the initial of the basal system. It forms either an elongate multicellular rhizoid or a multicellular lobed at-

FIGS. 1–5. 1–4, *Heterosiphonia densiuscula;* 5, *H. asymmetria;* 1, 2, same scale; 1, apex of cultured plant, sympodial, alternate, distichous branching of main polysiphonous branch is evident; 2, cultured tetrasporophyte with pedicellate stichidium borne on polysiphonous basal portion of lateral branch; 3, squashed preparation of type specimen showing branch bearing five pericentral cells enclosing axial cell (ac); 4, young germling in monosiphonous stage, new apical meristem developing from intercalary cell and multicellular lobed attachment organs are evident; 5, habit photograph of typical specimen collected from same location at same date as cultured specimen.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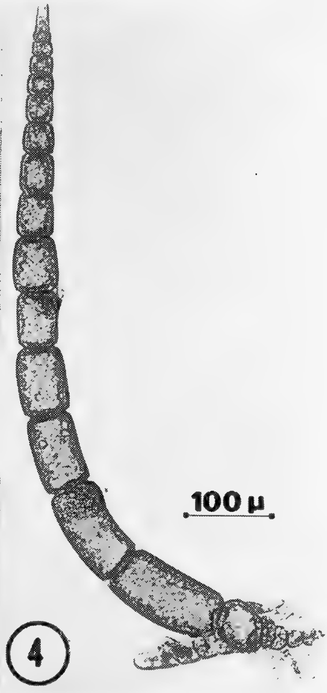
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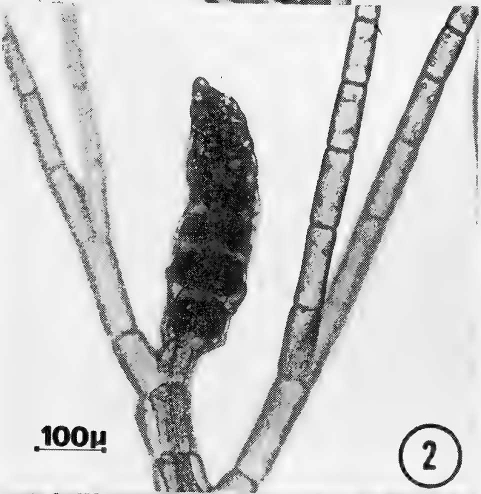
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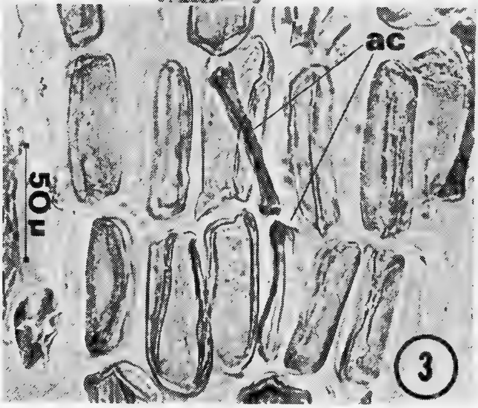
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FIG. 6. *Heterosiphonia densiuscula,* habit photograph of typical specimen dredged from Hein Bank, south of San Juan I., Washington.

tachment disk (fig. 4). The larger of the two cells derived from spore division is the precursor of the erect system. When the primary erect monosiphonous filament becomes about 1 mm in length, the apical meristem begins to branch sympodially. Additional meristems may be established from intercalary cells by an oblique lateral division which produces a new initial (fig. 4). The meristems give rise to the polysiphonous sympodially branched axes of the developing plant (fig. 1).

Heterosiphonia asymmetria cultures also were started from a field-collected tetrasporophyte and the tetraspores also gave rise to tetrasporangia-bearing plants for two successive generations. The cultured plants were much smaller than plants from nature, rarely exceeding

1.0 cm in length. The third generation is morphologically aberrant and does not grow well but it is being maintained for further study. It grows primarily by proliferation of the uniseriately filamentous basal system from which occasionally arise erect polysiphonous branches that bear tetrasporangia.

Heterosiphonia densiuscula cannot tolerate light intensities above 50 ft.-c. Above 75 ft-c the germlings bleach and die within a week. On the other hand, *H. asymmetria* grows and reproduces in intensities from 15 to 150 ft-c.

Morphological studies on field-collected specimens. The types of *H. densiuscula* and *H. laxa* were re-examined and found to have only 5 pericentral cells per segment instead of 6–9 as recorded in the original description (Kylin, 1925). Kylin's own figure (fig. 44, p. 68) shows only three pericentral cells on one side which is indicative of five or, at the most, six. Re-examination of *H. asymmetria* type specimen reveals 5 pericentral cells per segment as indicated in the original description (Hollenberg, 1945). The pericentral cells of all three species are characteristically arranged so that three are evident in face view on one side of the branch and two are seen on the opposite side when the branch is turned over.

Although all three species are similar, an insufficient number of *H. laxa* specimens are available for a thorough re-examination of its morphology. A comparison of the major morphological characteristics of *H. densiuscula* and *H. asymmetria* (table 1) indicates that clear similarities exist.

The reproductive patterns of life histories of these two species also appear similar. A survey of *H. densiuscula* from several herbaria shows that of approximately 110 specimens, 95% bear tetrasporangia and the remaining 5% are sterile. The original description likewise refers only to tetrasporangiate plants. Recently, however, male and female gametophytes were collected by Michael Wynne from Puget Sound in Washington. Mature cystocarps were present on the female plants indicating that both sexes possess functional sexual structures. The presence of gametophytes, even though they are extremely scarce, suggests that this species exhibits two types of life histories in the same locality. It is possible that two distinct genetic races have developed, one exhibiting the typical sexual red algal life history and the other exhibiting a non-sexual type. Gametophytes are not yet available for a culture study.

A survey of *H. asymmetria* herbarium specimens from the Monterey Peninsula reveals that 44 of 45 plants examined are tetrasporophytes. The remaining plant is sterile. To the best of my knowledge gametophytes have been collected only twice. The type specimen is a male collected February 12, 1938 from Corona Del Mar, Orange Co., California. Two cystocarpic female specimens were collected by E. Yale Dawson from White's Cove on Santa Catalina Island, California, October 31, 1948. It is apparent in this case that on the Monterey Peninsula a type

TABLE 1. MORPHOLOGICAL COMPARISON OF HETEROSIPHONIA ASYMMETRIA AND H. DENSIUSCULA.

	H. asymmetria	H. densiuscula
Main branches sympodial, distichous and alternate	+	+
Main branches (1st & 2nd orders) lacking pubescence of monosiphonous branchlets	+	+
Number of segments between branch	2–3	2
Ratio of dimensions of segments	0.5 to 1.5 x as long as broad	0.5 to 1.5 x as long as broad
Number of pericentral cells	5	5
Arrangement of pericentral cells (in side view)	transverse to slightly asymmetric	transverse to slightly asymmetric
Arrangement of pericentral cells (in cross section)	3 + 2	3 + 2
Cortication by longitudinal filaments derived from pericentral cells	+	+
Stichida on monosiphonous & poysiphonous branchlets	+	+
Stichidia pedicellate or sessile	+	+
Pedicels monosiphonous or	+	+
polysiphonous	3–5	4–6
Number of sporangia/fertile segment in stichidium	up to 800 μ	up to 800 μ
Maximum diameter of main axis	up to 15 cm	up to 15 cm
Total height of plants	intertidal & subtidal	subtidal
Habitat		

of life history similar to that observed for *H. densiuscula* occurs. Male and female plants are reported only from the southern limits of its range in California which suggests that only certain populations may exhibit a life history characteristic for the higher Florideophyceae. However, tetrasporophytes are not known to occur in the same locality.

The tetrasporangia from field-collected specimens of both species appear normal morphologically and form tetrads of spores but evidently are mitotic, in most instances, rather than meiotic, because in the cultured clones tetrasporophytes develop repeatedly.

Although the non-sexual type of life history is not common among the higher Florideophyceae, there is good evidence that some species are represented only by the tetrasporophytes in nature. Svedelius (1937) demonstrated that tetrasporangia of *Lomentaria rosea* are apomeiotic. Sparling (1961) noted that *Halosaccion glandiforme* (Gmelin) Ruprecht and *Rhodymenia palmata* f. *mollis* Setchell and Gardner never or very rarely have been found to bear spermatia, carpogonia or cystocarps. She maintained tetraspore germlings of both species in culture for about 2 years, but was not able to observe any reproduction. This suggests, at least, that heteromorphic gametophytes and tetrasporophytes do not occur in these species and that mitotic tetraspores are the only means of reproduction.

On the basis of their morphological similarities and the evident similarities in their life histories *H. asymmetria* Hollenberg should be considered a synonym of *H. densiuscula* Kylin. *Heterosiphonia laxa* and *H. densiuscula* also appear closely related. In addition, as *H. laxa* is separated from *H. densiuscula* only by the comparative sparsity of branching in the former, it cannot be concluded at this time that it is conspecific. Insufficient material is available for morphological comparison and no living plants are available for culture. Moreover, all three phases of *H. laxa* frequently occur in nature, indicating that it may have a typical sexual life history.

ACKNOWLEDGEMENTS

I am grateful to George Hollenberg for the loan of the type specimen of *Heterosiphonia asymmetria* and to G. F. Papenfuss for obtaining the type specimens of *H. densiuscula* and *H. laxa* from Almborn of the Botanical Museum of Lund University in Sweden. R. E. Norris, Michael Wynne, R. F. Scagel, and J. S. Garth made specimens available. Michael Wynne provided liquid preserved and living male and female specimens of *H. densiuscula*. G. F. Papenfuss also offered many helpful comments on this manuscript.

SUMMARY

Similarities in the morphology and life histories of H. *asymmetria* and *H. densiuscula* indicate that they are conspecific. The two clones studied in cultures formed successive generations of tetrasporophytes. This correlates well with information on the field collected plants, 95% or more of which are also tetrasporophytes.

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A NEW PROSTRATE VARIETY OF ERIOGONUM APRICUM (POLYGONACEAE)

Rodney Myatt

The Ione Buckwheat, *Eriogonum apricum* Howell, is a narrow endemic restricted to acidic, kaolinitic, clay soils of the Ione Formation (Allen, 1929) near Ione, Amador Co., California. The original population, discovered by Howell in 1954, is located on an exposed red clay hill about four miles south of Ione. A second population is located along California Highway 88, about two miles south of Ione (Roderick, 1964). Recently a third population was discovered by Gankin and Hildreth in February 1967 about five miles north of Ione, which differs from the previously known populations in having prostrate stems.

Eriogonum apricum Howell var. **prostratum** Myatt, var. nov. A var. *apico* differt caulibus prostratis, foliis minoribus. Similar to var. *apricum* except that the basal rosette is 3–7 cm across, with glabrous prostrate stems; leaves orbicular to ovate, truncate to slightly cordate, woolly-tomentose beneath, glabrous above, (3–) 5–6 (–9) mm long (fig. 1).

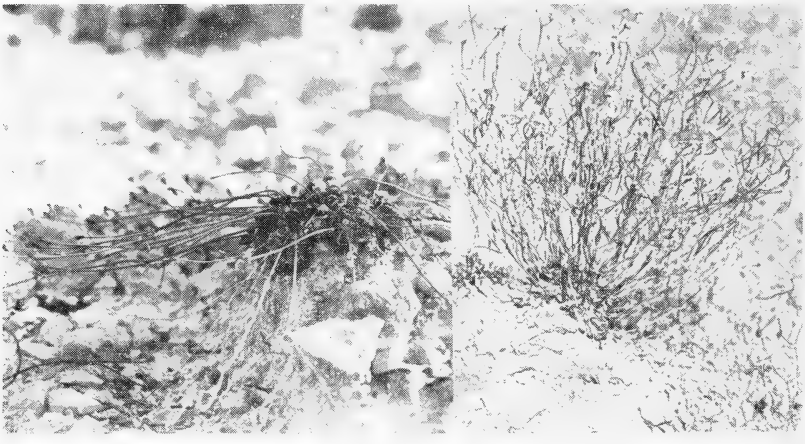

Fig. 1. *Eriogonum apricum:* left, var. *prostratum;* right, var. *apricum.*

Type. Open areas among *Arctostaphylos myrtifolia* Parry on red clay soil, near the Irish Hill Road about 3 miles from the junction with Highway 104, about 5 miles north of Ione, Amador Co., California, elevation ca. 300 ft., June 20, 1967, *Myatt s.n.* (DAV–holotype).

All three known populations of *E. apricum* are located within exposed areas of *Arctostaphylos myrtifolia* Parry vegetation, which is apparently an azonal vegetation type (Gankin & Major, 1964).

The new variety differs from *E. apricum* var. *apricum* in several subtle but consistent ways. The var. *prostratum* flowers from mid-June to early

July, with the seeds being shed by mid July. The two populations of var. *apricum,* however, flower from mid July through September and seeds are shed from August through late October. The leaves of var. *prostratum* are generally smaller than those of var. *apricum,* the former averaging 5–6 mm and are often 10–11 mm long. The only anatomical difference evident is that the cortex cells in the flowering stems of var. *prostratum* are of a longer, palisade type, being 2–3 times the length of those in var. *apricum.* Greenhouse studies have shown that plants grown from seeds of var. *prostratum* retain these distinctive characteristics under uniform conditions.

I would like to thank Grady Webster for the Latin diagnosis and his advice in preparing this article, and also John M. Tucker for his help with the description.

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CLARKIA JOLONENSIS (ONAGRACEAE), A NEW SPECIES FROM THE INNER COAST RANGES OF CALIFORNIA

DENNIS R. PARNELL

In the most recent taxonomic discussion of *Clarkia deflexa,* Lewis and Lewis (1955) pointed out that this endemic California species "shows considerable variation, particularly from population to population and to some extent regionally." A further study of this species (Parnell, 1968) has clarified that, in fact, what has been included under the name *C. deflexa* are two morphologically distinct population groups effectively separated from each other by both geographical and internal barriers to gene exchange.

The first group of populations is found in the outer Coast Ranges of California from Orange Co. north to San Luis Obispo Co. Although there is a high degree of morphological variation between these populations, hybrids between them are highly fertile (Lewis, 1953; Parnell, 1968).

The second group of populations is known only from the inner Coast Ranges of Monterey Co. As in the case of the first group, interpopulational hybrids are fully fertile.

Except for two individuals from populations in the outer Coast Ranges who were heterozygous for a single translocation, all individuals including the hybrid progeny regularly formed nine pairs of chromosomes at meiotic metaphase I.

Intergroup hybrids have been obtained only seven times (four of the individuals came from the seeds of a single capsule) and only after numerous pollinations had been attempted. The difficulty in obtaining these hybrids stems from embryo inviability caused by genetic and possibly cytoplasmic differences between the two groups. The seeds of the plants belonging to the two groups are markedly different and provide the only consistent way of telling them apart. In the Monterey Co. plants the seeds are heavily covered with scales and appear dark gray. Seeds from other populations are covered primarily by small papiliform projections and appear black or brown in color.

In view of these morphological differences and the well developed barriers to hybridization, it seems appropriate to recognize the Monterey County populations as a distinct species.

Clarkia jolonensis Parnell, sp. nov. Herba erecta, altitudine ad 6 dm; caulibus simplicibus vel ramosis; foliis 2–6 cm longis, 2–5 mm lato; calycis limbo 9–15 mm longo, 2–3 lato; petalis 11–19 mm longis, 9–14 mm latop stylo 9–14 mm longo, quam staminibus longiore vel longitudine aequa; semina cinera propter squamas.

Type. California, Monterey Co., 9 mi. N.W. of Bradley along Jolon Road, June 3, 1963, *R. F. Thorne & P. Everett 32186.* (DS, LA-holotype).

Specimens examined. Monterey Co: Road to Pleyto, 0.4 mi. south of Bradley-Jolon Road, *Lewis & Epling 192* (LA); 3.1 mi. north of San Antonio Road, Lockwood-San Lucas Road, *Hardham 4318* (LA); Shale Hills, w. side Hames Valley, Jolon-Bradley Road, *Hardham 1299* (LA); Mill Creek, road to Adler Creek, *Hardham 6049* (LA); foot of grade to King City, *Dudley* (DS).

Most populations of *C. jolonensis* are uniform in appearance except for one population located 9.1 mile east of the San Lucas Road turnoff in Lockwood. When compared with other populations, the seedlings and adult plants of this population tend to be smaller. The petals are 3–8 mm shorter in length and 3–5 mm narrower in width as well as being a much more pale pink. The style is shorter than the stamens and very seldom has it been observed to fall clear of them. Since pollen is being shed at the time the stigma becomes receptive some degree of self-pollination undoubtedly occurs. This is indicated by the full seed set that is obtained when plants from this population are left unattended in the greenhouse. Although this does not exclude a certain amount of outcrossing, it does indicate that self-pollination is probably the norm for the population in contrast to all other populations which ordinarily set no seed under similar conditions and show no sign of fertilization (e.g., swelling of the ovary accomplished by abscission of the flower.)

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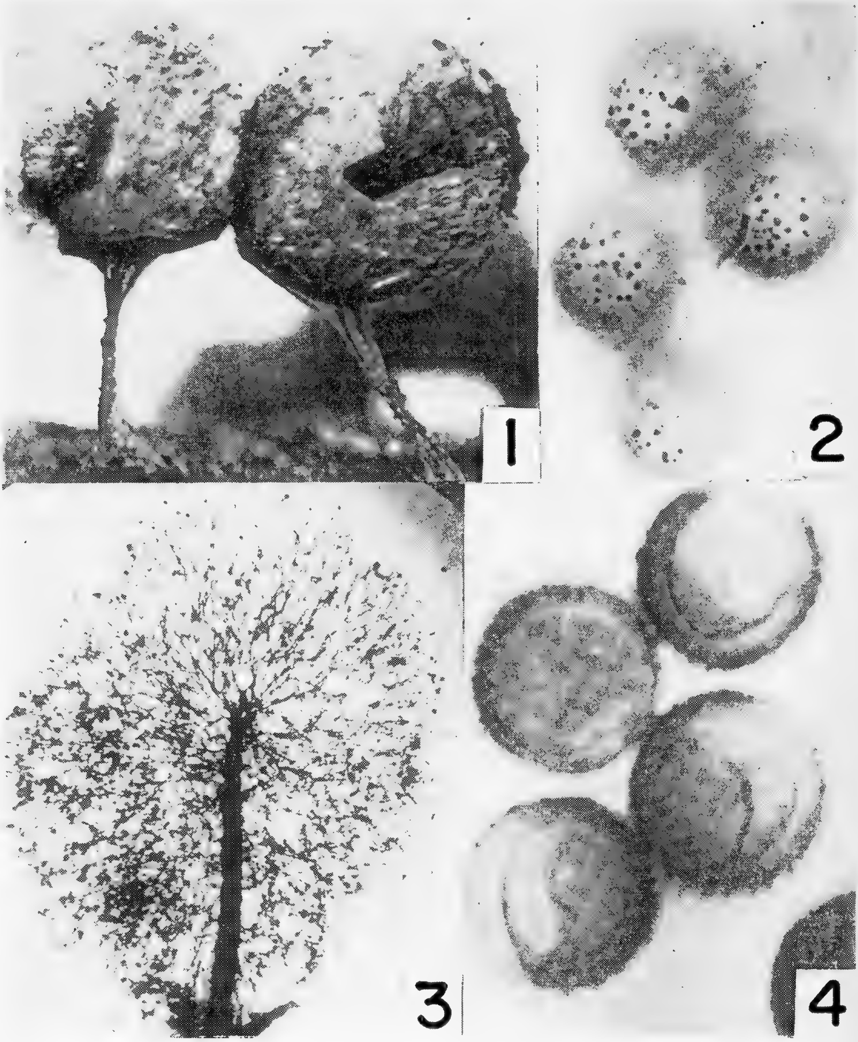
CONCERNING THE VALIDITY OF LAMPRODERMA ECHINOSPORUM

DONALD T. KOWALSKI

In 1924 Meylan described *Lamproderma echinosporum* on the basis of several collections from the Jura Mountains of Switzeralnd. This species was a typical snowline Myxomycete, i.e., found only at high elevations near the melting snow. Lister (1925) did not mention this taxon in her monograph, probably because it was described too late to be included in her work. In 1924 Macbride and Martin recognized the species as valid, but apparently did not have any material for observation. Dennison (1945), however, placed *L. echinosporum* under the heading of doubtful species. She had no material for study and on the basis of the description, she thought it was very close to *L. echinulatum* (Berk.) Rost. Hagelstein (1944) and Martin (1949) did not include it in their monographs because it was not reported from North America. During my work in the western United States, I have made five collections of a species which does not fit any of the generally recognized taxa, but which match perfectly with five of Meylan's collections of *L. echinosporum*. These five collections were obtained on loan from the Musée de Botanique, Lausanne, Switzeralnd. I believe that *L. echinosporum* is a good species and my collections (*3601, 3668, 6240, 8284, 8286*) apparently represent the first time that this taxon has been reported from the Western Hemisphere. All of my collections are from northern California and *8284* has been deposited in the University of Iowa Herbarium.

Meylan did not specifically designate a type collection and his species diagnosis was, in my opinion, incomplete. Thus, I am designating his April, 1923 collection from Prise as the lectotype and including a detailed English description with accompanying paragraphs dealing with the majoror characteristics and relationships of this taxon.

LAMPRODERMA ECHINOSPORUM Meylan. Sporangia (fig. 1) scattered to loosely clustered in small groups of 3–6, sessile or briefly stipitate, broadly ovoid to occasionally globose, 1.0–1.5 mm in diameter, color variable, dark brown to blue, dull, occasionally slightly iridescent; stipes, when present, short, averaging about 1.0 mm in length, shiny brownish-black; peridium membranous, thin, usually long persistent,



Figs. 1–4. *Lamproderma echinosporum*. 1, sporangia, × 30; 2, spores, × 1130; 3, columella and capillitium × 50; 4, spores, × 1740.

splitting irregularly, covered with numerous depressed, dark brownish-black areas, giving it a mottled appearance, depressed areas circular to slightly elongated, few near the base of the sporangium, becoming plentiful in the upper half; hypothallus poorly developed, discoid, thin, transparent, often merging at the margins into adjacent hypothalli, reddish-brown; columella (fig. 3) black, tapering only slightly towards the truncate or bluntly pointed apex, usually attaining two-thirds the height of the sporangium, often branching at the apex where it forms the primary branch of the capillitium; capillitium (fig. 3) forming a distinct, dense net, with abundant free ends, dark brown throughout, becoming hyaline only at the extreme tips, arising predominantly from the apex of the columella, threads of predominantly uniform thickness, 2–4 μ in diameter, usually not expanded in the axils, often covered with numerous nodules, averaging 5–10 μ in diameter; spores (figs. 2, 4) globose, dark brown in mass, dusky brown by transmitted light, covered with large irregularly distributed spines, often reaching 1.0 μ in length, including ornamentation, 13–16 μ in diameter; plasmodium unknown.

This species is known only from Switzerland and California. All of the Switzerland collections examined appear to be on herbaceous plant debris while the California collections are all on fallen coniferous twigs.

There is no characteristic that can be used to identify this species in the field. Typically, it forms small fruitings, consisting of only 20–30 sporangia. Small fruitings, however, can be found in several other species of *Lamproderma*. There is, however, one distinctive feature which makes *L. echinosporum* very easy to identify under the stereoscopic microscope, and that is the presence of the dark depressed areas on the peridium. It is interesting that Meylan did not mention the presence of this characteristic in his diagnosis and as far as I can determine, it has not been mentioned by anyone in the literature. In 1919, five years before describing *L. echinosporum,* Meylan described *L. gulielmae* from the mountains of Switzerland. This is the only other species in the genus that also has the dark depressed areas on the peridium. I do not believe, however, that these taxa are closely related. There are many differnces which distinguish them. In *L. gulielmae* the sporangia are small, 0.3–0.5 mm in diameter, the peridium is silvery-blue, the stipe, in relation to the size of the sporangium, is long, about four times the diameter of the sporangium, and the capillitium forms a lax net which is distinctly hyaline or pallid. In *L. echinosporum* the sporangia are large, 1.0–1.5 mm in diameter, the peridium is dark brown or blue, the stalk, in relation to the size of the sporangium, is short, about equal to, or less than, the diameter of the sporangium, and the capillitium forms a dense net which is dark brown.

Although Meylan (1924) thought *L. echinosporum* was related to as *L. atrosporum* Meylan, and Dennison (1945) believed it was near *L. echinulatum,* I believe *L. echinosporum* is probably most closely related to *L. sauteri* Rost. These taxa share many characteristics in common. Both have large sporangia, 1–2 mm in diameter; short stalks, 1.0 mm or less in length; peridia that are dull, rarely iridescent; capillitia which form dense dark brown nets; and spore sizes which overlap, 13–16 μ in *L. echinosporum* and 12–15 μ in *L. sauteri*. There are, however, significant differences between these two species. In *L. echinosporum* the peridium is covered with dark depressed areas while *L. sauteri* lacks this feature entirely. The spores of *L. echinosporum* are uniformly dusky in color and covered with irregularly distributed spines which may reach 1.0 μ in length, while in *L. sauteri* the spores are dark violet brown and distinctly lighter on one side, and regularly and densely spinulose, the spines attaining only 0.5 μ in length.

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PERENNATION IN ASTRAGALUS LENTIGINOSUS AND TRIDENS PULCHELLUS IN RELATION TO RAINFALL

JANICE C. BEATLEY

In late winter-early spring (March 15–April 12) of 1965, at a season when precipitation is not predictable, rains of extraordinary frequency and magnitude fell over most parts of south-central Nevada. Rainfall during this period on the Nevada Test Site, Nye Co., was from 2.5 to more than 5 inches at elevations below 5,000 feet, where the communities and flora belong to the Mojave Desert (Beatley, 1969). Late autumn rains the same year were even more extraordinary, and for the 1965 calendar year precipitation totalled 8 to more than 15 inches over the Test Site, with many areas receiving in excess of 10 inches.

A number of biological phenomena following the spring rains, and in the 1966 spring season following the autumn rains, were as exceptional as the rainfall which preceded them. Among these was the appearance in certain areas of conspicuous numbers of seedlings of *Astragalus lentiginosus* Dougl. var. *fremontii* (Gray) Wats. (Leguminosae) and *Tridens pulchellus* (HBK.) Hitchc. (Gramineae) in the spring of 1965, and spectacular flowering populations of the *Astragalus* in the spring of 1966. On permanent study sites located in these areas, year-round environmental measurements and plant data collections in the spring of each year enabled a history of the populations to be quantitatively documented in relation to certain environmental variables.

It is the objective of this report to record the fate of the *Astragalus* seedlings on five sites, and *Tridens* on one site, as a contribution to understanding of the annual-biennial-perennial habit in these, and perhaps other desert species, in relation to precipitation.

METHODS

Four of the sites (Plots 16, 17, 66 and 67) were located on the upper bajada of eastern Jackass Flats, a major drainage basin in the southwestern part of the Test Site and at the northern edge of the Mojave Desert. Vegetation was *Larrea-Lycium andersonii-Grayia,* which characterizes the high Mojave Desert vegetation of the region (Beatley, 1969). Soils were predominantly sand and essentially without desert pavement. The sites had an altitudinal range of around 500 feet. Plot 16 was about three miles downslope from Plots 66 and 67, with Plot 17 about half-way between. Plots 66 and 67 were at the divide between Jackass Flats and Frenchman Flat on the undisturbed remnant of a townsite (Wahmonie) laid out in the 1920's; the former was in undisturbed shrub vegetation, and on the latter, in an adjacent clearing for a street of the townsite, there were occasional scattered shrubs of the same species.

On a fifth site (Plot 42), in Mid Valley to the north of Jackass Flats, the *Coleogyne* shrub cover had been destroyed by fire in 1959, and the site was essentially without shrub vegetation during the period of this study. Elevation was over 400 feet higher than that of the Wahmonie sites, and nearly 1000 feet higher than the lowest of the Jackass Flats plots. Desert pavement of the soil surface was in a disturbed condition.

The sixth site (Plot 36) was on the bajada below the Ranger Mountains in southeastern Frenchman Flat, where the vegetation was *Larrea-Atriplex-Lycium shockleyi,* and the well developed desert pavement was typical of that below limestone mountain ranges of the region.

In May 1965, seedlings of *Astragalus* were counted in 50 0.1 m^2 quadrats, and the number/m^2 calculated. Data for *Astragalus* or *Tridens* plants intercepting 11 permanent parallel transect lines, 100 feet long × inch wide and 10 feet apart, were recorded in late May or early June of consecutive years. For each intercepting plant were recorded: 1, the locations of the beginning and ending intercept (to tenths of feet) along each of the 100-foot lines; 2, height, measured to the nearest inch; 3, whether living or dead; and 4, if living, whether flowering, fruiting, or vegetative only. From interception values for the total 1,100 feet of transect percentage cover of the soil surface was calculated for the species.

Rainfall was recorded year-round on each site, using an 8-inch funnel feeding into a two-liter bottle buried below the soil surface. Bottles were emptied weekly, and the measured milliliters converted to inches of precipitation.

Table 1. Number of Plants of Astragalus lentiginosus var. fremontii Intercepting 1,100 Feet of Line (May–June), Percentage Cover, and Precipitation on Five Sites in Eastern Jackass Flats and Northern Mid Valley, Nevada Test Site, Nye Co., Nevada (3,800–4,750 feet elevation). 1965–1967.

	Jackass Flats								Mid Valley	
	Plot 16 (3800 ft.)		Plot 17 (465 ft.)		Plot 66 (4330 ft.)		Plot 67 (4325 ft.)		Plot 42 (4750 ft.)	
	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967
Number of plants	236	112	253	153	278	135	236	131	123	136
% living	100.0	0.9	100.0	4.6	100.0	34.8	100.0	41.2	100.0	95.6
% apparently dead	0.0	99.1	0.0	95.4	0.0	65.2	0.0	58.8	0.0	4.4
% flowering/fruiting	100.0	0.0	99.7	2.0	100.0	34.8	100.0	38.9	96.7	95.6
%vegetative only	0.0	0.9	0.3	2.6	0.0	0.0	0.0	2.3	3.3	0.0
Percentage cover	12.0	3.3	11.1	4.7	13.4	5.4	10.3	4.0	6.0	10.4
Precipitation (inches										
Mar.–Apr. 1965 (germination)	2.64		3.25		3.99		4.02		4.04	
May–Oct. 1965 (seedling stage)	1.13		1.06		1.70		1.90		2.78	
Nov. 1965–May 1966 (seeding through flowering/fruiting	5.28		5.45		7.31		7.26		10.36*	
June 1966–May 1967	4.38		4.96		5.63		6.00		8.39**	

* Incomplete; rain gauge overflowed three times.

** Incomplete; rain gauge overflowed once.

ASTRAGALUS LENTIGINOSUS

Astragalus lentiginosus var. *fremontii* is the common *Astragalus* of the region, where it is usually associated with sandy soils derived from volcanic rocks. In extreme western Jackass Flats, at 3,000-3,300 feet elevation, it is entirely replaced by var. *variabilis* Barneby on deep sands of the bajada below the volcanic Calico Hills. Where soils are derived from limestones and dolomites, the common perennial *Astragalus* is *A. tidestromii* (Rydb.) Clokey.

Seedlings of var. *fremontii* were conspicuous, though scattered, and rather uniformly spaced in the spring of 1965; density was 3–7/m^2 on the five sites under consideration. On all of the plots there was an occasional plant that was not a seedling, but none intercepted the lines at time of the 1965 spring data collections. Apparently all, or nearly all, of the seedlings survived the relatively dry summer and autumn, and following the heavy late autumn rains grew uniformly and rapidly, especially during late winter. By mid-April 1966 nearly all plants were flowering profusely, and by early May were in abundant fruit; plants were commonly a foot or more in diameter, and averaged 7–8 inches high. Over several square miles of eastern Jackass Flats and the larger "burn" of northern Mid Valley, flowering and fruiting populations were the highly colorful landscape feature noted by Barneby (1964) to be characteristic of this variety of *A. lentiginosus*.

In Table 1 are the quantitative data for the populations on each of the five sites, for the 1966 and following spring season. It is apparent from the data that numbers (and size) of plants, and total cover of the soil surface in 1966 were remarkably similar on the Jackass Flats plots. The Mid Valley population was about half the size of the populations in Jackass Flats.

Percentage survival of individuals from 1966 to 1967 in Jackass Flats was in a gradient upslope, and was directly correlated with a precipitation gradient from the lower to the higher elevations. Essentially none survived at the lowest elevation, where there was the least rainfall during all periods. Nearly all survived on the Mid Valley site, at the highest elevation and where rainfall was consistently the greatest from time of germination (and plants in 1967 were commonly two feet or more in diameter). There were somewhat fewer and smaller plants (average 6.6 inches high) in 1966 on the disturbed Plot 67, as compared with the undisturbed Plot 66 (average height 7.8 inches), but the percentage surviving until the next year was somewhat higher on the disturbed site.

The large majority of plants, which germinated in the spring of one season and flowered and fruited the next spring season, and also died the second season, were distinctly biennials; the annual, biennial, and short-lived perennial habit are all ascribed to this variety of *A. lentiginosus* by Barneby (1964). Whether populations or individual plants are biennial or perennial appears from the data to be under the control of soil moisture. The large flowering populations, which appear in the spring on the basin floors of southern Nevada and then vanish for a period of years, apparently are associated with the occurrence the year before of an exceptionally heavy rain, at a time when temperatures were not limiting to germination, and most of the plants were destined from time of germination to be biennials; the number surviving on a given site until the next season is related to the local (and probably microvariations in) soil moisture regimes. The predominantly perennial populations are those of the higher elevations (4,500-7,500 feet on the Test Site), where there is more frequent and greater rainfall, and greater precipitation effectiveness at the lower prevailing temperatures; even these are usually short-lived, though occasional plants may persist for several years.

It is possible that the rain "triggering" mass germination may also be autumn precipitation, when at least one heavy rain is predictable in this region. Mass germination of this species in the autumn, however, has not been observed at the Test Site, although occasional seedlings commonly occur with the winter annual seedlings after autumn germination. In those flowering the next spring but not surviving to the following year, the life cycle is identical to that of the winter annuals.

Variety *variabilis,* the representative of the species in western Jackass Flats, also apparently germinated following the early spring rains of 1965, but flowered and fruited into mid-summer of the same season, and died during the summer. Perennial plants are scattered in this area, but the largest flowering populations, at least in this case, exhibited an annual growth habit. The variety is described by Barneby (1964) as a perennial of short duration or monocarpic.

TRIDENS PULCHELLUS

This low, tufted perennial grass, of usually calcareous soils, germinated in large numbers in Frenchman Flat following the 1965 spring rains. In Table 2 are the data for this species on one site for four years along the same 1,100 feet of transect. The seedlings matured, though most of the plants at maturity were less than an inch in diameter, and flowered and fruited abundantly through the late spring of 1965. In the spring of 1966, three-fourths of the plants yet present were dead; apparently 15–20 percent of the 1965 plants survived as perennials through 1966 and 1967. In the 1965 population, around 80 percent behaved as annuals, with a life cycle of several weeks only.

On another site (Plot 33, on the east slope of Frenchman Flat), there were 427 plants in 1967 along the 1,100 feet of transect (where there had been only 13 plants in 1966). The plants germinated following a mid-September rain, 1966, which was locally 1.5 inches on the east slope of Frenchman Flat, and only 0.5 inch or less on Plot 36 and elsewhere on the Test Site. Seeds of this species, therefore, may germinate either in early spring or early autumn. Data were not collected again in 1968,

TABLE 2. NUMBER OF PLANTS OF TRIDENS PULCHELLUS INTERCEPTING 1,100 FEET OF LINE, PERCENT COVER, AND PRECIPITATION, PLOT 36, SOUTHEASTERN FRENCHMAN FLAT, NEVADA TEST SITE, NYE CO., NEVADA (3,085 feet elevation). 1964–1967.

	1964	1965	1966	1967
Number of plants	28	218	125	42
% apparently dead	....	0.0	74.4	0.0
% flowering/fruiting	....	99.1	25.6	81.0
Percentage cover	0.5	2.3	1.4	0.7
Precipitation (inches)				
Mar.–June 1965 (germination through flowering/fruiting)				2.64
July 1965–June 1966				6.64
July 1966–June 1967				5.65

but observation indicated that living plants were rare in the spring of 1968 here and elsewhere on this slope of Frenchman Flat, and for the most part the plants had exhibited a winter annual growth regime.

DISCUSSION

In *Astragalus lentiginosus* and *Tidens pulchellus* it appears the large and importantly reproducing populations in the northern Mojave Desert are biennials or annuals, which germinate following unusually heavy rainfall in the spring or autumn. Only a limited number successfully perennate where precipitation is irregular and variable from season to season. In these environments, those that do become perennial plants flower and fruit during the years between large germinations and give continuity to the presence of the species in the community (of potential significance especially to any dependent consumers in the community). The large perennial populations of *Astragalus* are confined to the higher valley floors and mountains, where there is relative constancy of precipitation above a minimum necessary for the perennial habit. *Tridens* does not occur at the higher elevations in this region, and the perennial populations are those which survive the vagaries of precipitation at the lower elevations.

A potential in higher-elevation perennials for the biennial or annual life cycle at lower elevations could be expected to enable such species to occur over a greater altitudinal range, and hence belong to a greater diversity of plant communities in desert regions, if variables other than rainfall are not limiting at the lower elevations. *Astragalus lentiginosus* var. *fremontii,* in fact, is nearly unique in the herbaceous perennial flora of the Test Site region for its altitudinal range from the lowest to the highest elevations (3,000–7,500 feet), and its occurrence to a greater or lesser degree in nearly all kinds of plant communities, except where soils are highly calcareous. The diversity of communities in which it occurs—from *Larrea – Franseria* to *Artemisia – Pinyon – Juniper* — is matched only by that of *Oryzopsis hymenoides* (R. & S.) Ricker.

The facultative life cycle may characterize a number of other desert herbaceous species usually considered perennial, but which perhaps may in fact flourish intermittently as biennials or annuals during periods following extremes in amount or timing of rainfall. Other perennials in the Test Site flora suspect of having a facultative life cycle are especially the species of *Sphaeralcea, Mirabilis pudica* Barneby, and *Eriogonum inflatum* T. & F., in which large and conscpicuous populations one year are often absent the following season.

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REVIEWS

Principles and Methods of Plant Biosystematics. By Otto T. Solbrig. xii + 226 pp. MacMillan Company, New York. 1970. $9.95.

Solbrig states that his objective has been "to present the theoretical and technical aspects of systematics that are not adequately covered in most of the presently available text-books." Within his self-imposed limits and the limitations of space (possibly imposed by the publisher) he has succeeded remarkably well. As reflected in the title and the quoted excerpt from the preface, the book provides a synopis of current principles and methods used by practicing biosystematists. The book is in two parts. The first summarizes the current rationale behind biosystematic research; the second briefly reviews various "modern" data-gathering techniques employed by biosystematists. The latter section is well suited to development of a series of laboratory exercises to complement the discussions in the former section.

Organization of material, format, illustrations, etc. are very good and the breadth of treatment of particular topics is generally uniform and adequate for elementary students. For advanced classes the discussions form a sound base from which more thorough analyses of particular principles or methods may be developed. The following list of chapter headings indicates the scope of the text: Part I—Introduction and Historical Background, Synthetic Theory of Evolution, Patterns of Phenetic Variability, Breeding Systems, Speciation, Hybridization, and The Species Problem and Classification; Part II—Genetics, Cytology, Chemistry, Mathematics and Statistics, and Conclusion.

Most of the discussions of theoretical points are clear, concise, and well supported through reference to published work. There are, however, several distressing syntactical monstrosities which should never have reached the printed page.

"Under such conditions the plants in each population that are most dissimilar in their requirements can grow where a minimum number of plants of the other population can grow." p. 85.

"Biological phenomena are never undimensional." p. 109.

"The important thing is not to make biosystematic or chemical conclusions inconsistent with the data at hand." p. 162.

". . . what constitutes a 'character' is therefore somewhat irrelevant to the problem at hand. What is important is to be sure when establishing relationships that comparable characters are considered." p. 183.

Further, there is an alarming number of spelling errors and minor errors of fact, e.g., "*annus*" for *annuus* (pp. 7 & 8), "$6^{(10^4)} = 6^{40}$" (?) (p. 21), "subtrite for subtribe (p. 38), "Macmillan" for McMillan (pp. 41–43—the work of the publisher?), "*chrysosthoma*" for *chrysostoma* (p. 112), herbaceous Baptisias are said to be shrubby (p. 164), "betalins" for betalains (p. 164 and glossary). It is hoped that such errors will be corrected in future printings.

It is unfortunate that in such a small book several pages are wasted in duplicating material. An adequate page of Contents is followed by four pages of Detailed Contents. "Genetic system" is defined in the text on p. 49 and again in a footnote on p. 157. The glossary of some twelve pages could easily have been left out and needed definitions made parenthetically. "Chromatin" is defined both in the glossary *and* parenthetically in the text (p. 143). Additionally, many of the glossary entries are more misleading than informative: An "achaene" (sic) is described as dehiscent while no mention of dehiscence is made in the entry for "capsule". "Chiasma" is said to be "an exchange of partners . . .". "Relationship. A statement about two or more objects that is either true or false."

While the general coverage of topics germane to biosystematics is quite good, there are a few conspicuous omissions. There is no discussion of apomixis even though this phenomenon is of major importance in the biosystematics of many genera of flowering plants. Ecotypic variation is very well treated but there is no mention of clinal variation. Finally, perhaps a minor point, there is no mention of the importance of voucher specimens for documenting biosystematic research.

Apart from the points raised above, I feel that the author has realized his objective. No other textbook approximates to such a neat synopsis of current thought and method in today's biosystematics. Solbrig is to be congratulated for recognizing an empty niche and capably filling it. It will be interesting to see whether his text will succeed or be displaced by competitors, which are sure to come.—JOHN L. STROTHER, Herbarium, University of California, Berkeley.

The Native Cacti of California. By LYMAN BENSON. xii + 243 pp., illus. Stanford University Press. 1969. $7.95.

Lyman Benson, leading specialist in the taxonomy of the cacti of the United States and Canada, has produced a well-organized and thoroughly illustrated book on the more than 50 different taxa of this family that occur naturally within California. This compact publication will appeal to a broad range of readers.

A two and one-half page key introduces the nine genera that are covered. Each genus is treated in detail with a description and, where needed, a key to the species and varieties. The individual taxa are described and their distribution within the state is mapped; nearly all are also illustrated, often more than once.

Four color plates by L. C. C. Krieger are superb; the colors, shading, detail, and accuracy may well be the best that have been employed to illustrate cacti. Also very good are the black and white photographs by David Griffiths and the line drawings by Lucretia B. Hamilton. Some of the color photographs taken in the field are less inspiring but are nearly always helpful for identification. Most of the legends are informative; but a few would have been more useful if the taxonomic significance of the flower parts had been commented on, rather than the names of these parts merely pointed out. In one unfortunate instance there are eight pages of color plates inserted between a photographic figure and its legend.

Some of the distributional information is, of necessity, incomplete. The author has constructed distribution maps primarily on the basis of herbarium specimens examined; however, as cacti are seldom collected by most botanists and only rarely collected in large duplicate sets, the herbarium record often leaves a part of the distribution undocumented. For example, the distribution of *Opuntia prolifera* actually includes four other Southern California off-shore islands in addition to the three indicated. Further, *O. oricola* and *O. littoralis* var. *littoralis* occur on all the islands of this group; and the distribution of *O. phaecantha* var. *major,* as it is designated in this publication, extends into the southernmost portion of Santa Barbara County rather than merely along its northern fringe as shown. It should also be noted that this latter taxon is the only native flat-jointed *Opuntia* known from San Luis Obispo County. The mapping of *O. l.* var. *littoralis* in this county is in error.

With the anticipated publication of his more technical and comprehensive *Cacti of the United States and Canada,* the present book is, in many ways, intentionally popular. In deference to the layman, the descriptions have been written in non-metric terms; but many readers will find fractions of an inch, such as 1/128, more awkward than decimal equivalents in millimeters.

In addition to the features already mentioned, this book contains the following special sections: a taxonomic summary inside the front and back covers, a long general introduction, a historical section, and a pertinent biographical list. The taxonomic summary serves as a convenient index and outline of general classification and distribution; it is surprising to note that within California nearly as many kinds of cacti occur in the chapparal as in the Mojave Desert. Also of interest is the large number of plant communities in which one can expect to find the beaver-tail cactus, *Opuntia basilaris* var. *basilaris.*

The first 60 or so pages form a relatively elementary introduction that is conspicuously different from the rest of the text. This introductory portion contains general botanical information on structure, identification, classification, nomenclature, distribution, climate, paleobotany, and vegetation types. Such material will be an aid primarily to the beginning student or amateur cactus enthusiast, but everyone will appreciate the characteristically handsome photographs with which these concepts are illustrated.

The historical section was contributed by David L. Walkington and is extremely interesting and pertinent in a plant group where man has played such a significant role in altering recent evolution. This chronological account of cacti in California should, however, have begun with Portola's observation of *Opuntia* along the California coast in 1769, a date which is 24 years earlier than the first event considered here.

The taxonomic portion of the book brings together a number of relatively recent name combinations at the generic, specific, and subspecific level. A few readers, especially those who are familiar with the author's conservative point of view, may be surprised at the recognition of three genera, *Sclerocactus* and *Neolloydia* (segregates of *Echinocactus*) and *Coryphantha* (a segregate of *Mammillaria*).

On the whole, this book is an admirable combination of convenience, attractiveness, and completeness—a book that will be used by cactus enthusiasts, students, and amateur and professional botanists.—Ralph N. Philbrick, Santa Barbara Botanic Garden.

Modern Methods in Plant Taxonomy. Edited by V. H. Heywood. xvi + 312 pp. Academic Press, London and New York. 1968. 84s.

This collection of papers is one of the best surveys of current trends in plant taxonomy published to date. The papers were presented at the conference on Modern Methods in Plant Taxonomy which was held at the University of Liverpool in September of 1967. Included in this volume, in addition to the introduction by V. H. Heywood, are 16 papers grouped somewhat arbitrarily under the following four headings: The Continuing Role of the Modern Herbarium in Taxonomic Research; The Role of Experimental Data; Biochemistry, Computers, and Taxonomy; and Geography and Ecology.

In general, the various authors reviewed recent developments, discussed particular problems, and presented original work in areas of interest to the plant systematist. However, not only do these papers form a comprehensive discussion of Modern Methods in Plant Taxonomy, but when viewed collectively they also emphasize the various philosophical differences which exist within the field. One has only to read, for example, the papers by Cronquist, Solbrig, and Johnson and Holm, to detect that the meaning or value assigned to such concepts as "phylogenetic classification" and "biological species," are quite different, if not diametrically opposed. Nevertheless, this dimension of the book should not obscure its basic importance, an excellent review and analysis of modern plant taxonomy as well as an indication of its future directions.—Dennis R. Parnell, Department of Biological Science, California State College, Hayward.

Pacific Northwest Ferns and Their Allies. By Thomas M. C. Taylor. x + 248 pp., illustrated. Univ. of Toronto Press, Toronto and Buffalo. 1970. $15.00.

Renewed interest in pteridoyphytes during the past two decades has resulted in an eminently more natural classification system. A consequence of this research is the outdating of older floristic treatments. Taylor's book on the Pacific Northwest ferns and their allies helps fill this gap by bringing together our present knowledge of these plants in a well-documented but aesthetically pleasing format.

By the author's estimate, about one-quarter of the known species of pteridophytes occurring on the North American continent north of Mexico are to be found in the area treated (Oregon, Washington, British Columbia, and Yukon Territory, and Alaska excluding the Aleutian Islands). Not surprisingly, 45% of the 97 species Taylor records for the area are circumboreal.

Keys and concise descriptions are provided for families, genera, and species. Synonymy, although not complete, is adequate for the purposes of a flora. References are given to earlier floristic treatments and illustrations. Habitat and range are given for all species. Brief comments include mention of diagostic features, cytological data, and taxonomic problems requiring additional study. Full page original line drawings, showing both habit and details, are provided for each species; although somewhat stylized, these are entirely adequate in most cases for identification. Chromosome numbers (with references) and lists of species grouped by distributional patterns are listed in appendices. That the pteridophtes of the area are exceptionally well studied cytologically is evident from the fact that only 18 taxa remain uncounted.

The author wisely relies on the judgments of monographers in treating many of the critical genera, including *Pellaea, Woodsia, Cystopteris, Botrychium,* and *Equisetum,* while incorporating the most recent biosystematic data available in the treatment of such genera as *Polystichum, Dryopteris,* and *Polypodium.* He recognizes such "splinter" genera as *Mecodium* (*Hymenophyllum*) and *Aspidotis* (*Cheilantes*), but maintains *Thelypteris* and *Lycopodium* in a broad sense.

The book is written both for the professional botanist and for the amateur fern enthusiast. The latter will find the brief introduction and glossary helpful. However, common names are not given, nor is reference made to the culture of these ferns, many of which would make attractive additions to a garden of native plants.

The book is nearly free of both typographical and factual errors, and those that were found do not detract from the usefulness of the flora. One possible source of confusion is the placement of unlabeled distribution maps of some species on pages where another taxon is treated.

Pacific Northwest Ferns and Their Allies will doubtless be a useful reference for identification and a source of information for many years to come. One suspects that only its price might preclude its reaching a wider audience.—ALAN R. SMITH, Department of Botany, University of California, Berkeley.

NOTES AND NEWS

NEW PUBLICATIONS

Vascular Plants of Wells Gray Provincial Park and Its Vicinity, in Eastern British Columbia. By LEENA HÄMET-AHTI. Annales Botanici Fennici 2:138–164. 1965. This paper will be of interest to anyone concerned with the flora and plant geography of British Columbia.

Flora of Montana. Part II. By W. E. BOOTH and J. C. WRIGHT. 305 pp. Department of Botany, Montana State University, Bozeman. 1966. This part of the *Flora of Montana* contains the Dicotyledons and is a corrected and amended version of the first edition of 1959.

The Redwood Trail. By P. H. BRYDON. 24 pp., illustrated. Strybing Arboretum Society, Golden Gate Park, San Francisco. 1963. This is a guide to the redwood trail of the Arboretum.

A Monograph of Lemnaceae. By EDWIN HORACE DAUBS. Illinois Biological Monographs 34: vii + 1–118. University of Illinois Press, Urbana. 1965.

Ecology of Soil-Borne Plant Pathogens. Edited by KENNETH F. BAKER and WILLIAM C. SNYDER. xiii + 571 pp. University of California Press, Berkeley and Los Angeles. 1965.

Plants in Perspective, A Laboratory Manual of Modern Biology. By ELDON H. NEWCOMB, GERALD C. GERLOFF, and WILLIAM F. WHITTINGHAM. 218 pp. W. H. Freeman and Company, San Francisco. 1964.

Dictionary of Word Roots and Combining Forms. By DONALD J. BORROR. vi + 134 pp. National Press, Palo Alto, California. 1960.

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EMBRYOLOGY OF CHRYSOTHAMNUS (ASTEREAE, COMPOSITAE)

Loran C. Anderson

Embryological information is scanty on the wide-spread *Chrysothamnus* of western America. "Embryology" is used here in its broad sense, following Davis (1966) and others. Snow (1945) reported details of gametogenesis for a population referrable to *C. nauseosus* (Pallas) Britt. ssp. *albicaulis* (Nutt.) H. & C. Although gametogenesis is similar in some other subspecies of *C. nauseosus,* it certainly is not homogeneous throughout the genus. Embryological data on all species of *Chrysothamnus* are recorded here as part of an intensive study (Anderson, 1970) on the floral anatomy of the genus. Those features of embryology that characterize the genus or the entire family are treated only briefly.

Methods and Materials

Over 90 populations were studied. Most materials were preserved in FPA in conjunction with general anatomic studies. That fixative was acceptable but caused considerable shrinkage in the embryo sacs. Killing heads in Craf V (Sass, 1958) resulted in much better preservation. Fixed tissues were dehydrated in a graded TBA series, embedded in paraplast, and cut at 9–12μ, depending on age of the flowers. Sectioned tissues used in general studies were stained in safranin-fast green with tannic acid-ferric chloride mordanting. Tissues prepared specifically for this study were stained in Harris hematoxylin followed by fast green and mounted in permount. Many of the slides were prepared by Kent Fish.

Embryology

Growth of flowers in one head is closely synchronized. Although individual flowers develop acropetally on the receptacle (Snow, 1945), they usually undergo either microsporogenesis or megasporogenesis simultaneously regardless of differences in individual flower size. The least synchronous species is *C. linifolius* Greene. In it, older flowers of the head have mature embryo sacs when the youngest flower undergoes meiosis in the ovule.

Anthers in *Chrysothamnus* are tetrasporangiate. Method of wall formation is the dicotyledonous type (Davis, 1966) with a glandular tapetum. Many aspects of microsporogenesis have been considered earlier (Anderson, 1966).

The ovules are anatropus, unitegmic, and tenuinucellar. Four cellular megaspores result from meiosis. The chalazal megaspore usually pro-

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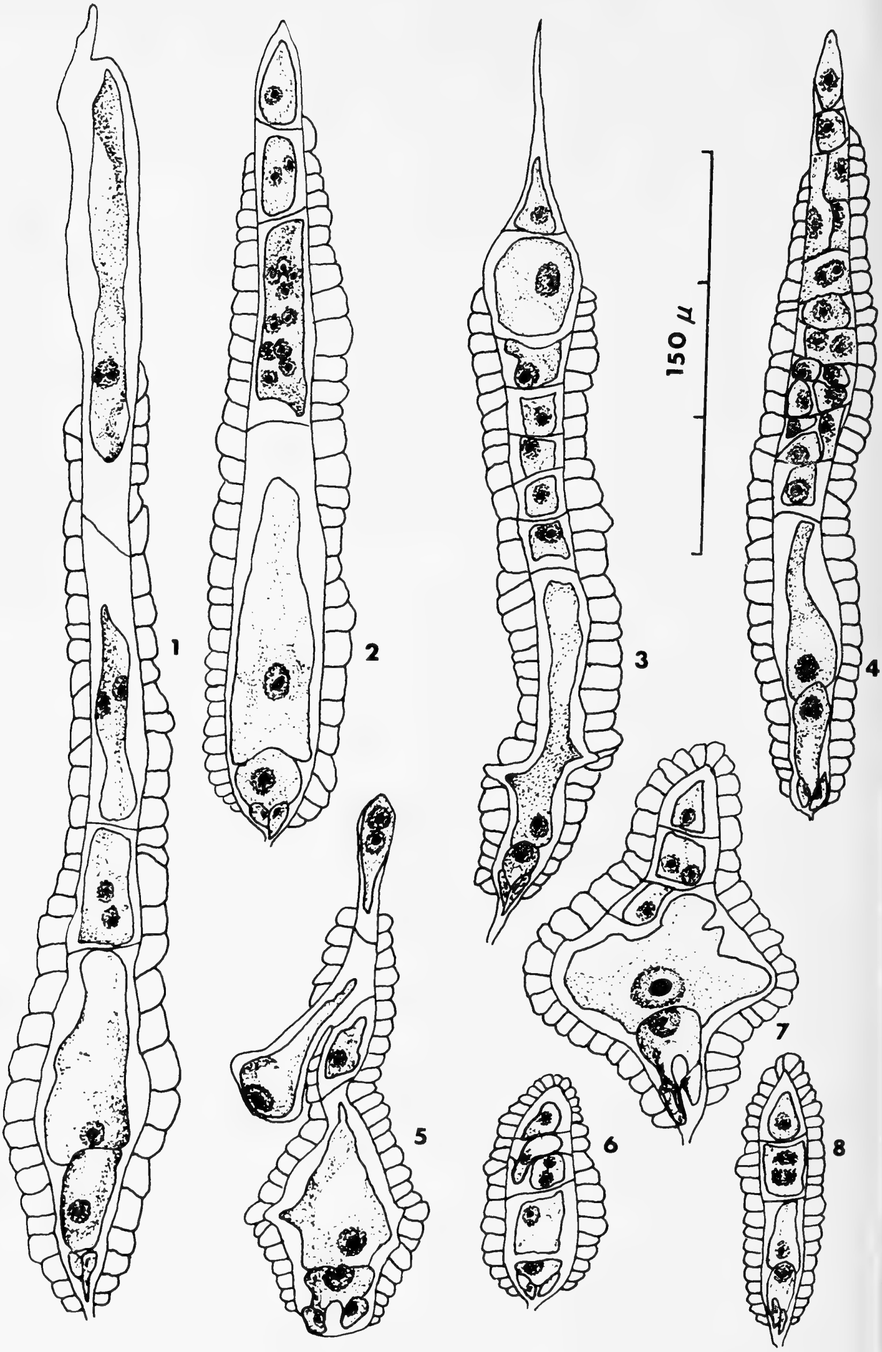
Madroño, Vol. 20, No. 7, pp. 337–384. March 17, 1971.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duces the embryo sac; however, a functional micropylar megaspore was observed in one sample of *C. linifolius* (*Anderson 2738,* KSC). The nucellus is intact at the tetrad stage but breaks down concurrently with three megaspores before the enlarged functional megaspore divides. On disintegration of the nucellus, an endothelium (integumentary tapetum) develops; its cells are often binucleate.

Taxa of *Chrysothamnus* develop a Polygonum type embryo sac. Mature embryo sacs (figs. 1–8) are typically long and narrow. The longest observed (fig. 1) was 495μ (44% of total ovule length at that age). In most samples embryo sacs range from 150–300μ (15–20% of total ovule length). The wider embryo sac shown in fig. 7 probably is a post-fertilization condition.

The synergids are somewhat vacuolated and usually extend into the micropyle, especially in *C. nauseosus* (fig. 7). The egg is characteristically overarched by the central cell (figs. 2, 7) in which the polar nuclei fuse prior to fertilization. Average antipodal size is 20–30μ. The largest is usually the chalazal antipodal, over 200μ in *C. viscidiflorus* (Hook.) Nutt. ssp. *lanceolatus* (Nutt.) Piper (fig. 1) and *C. viscidiflorus* ssp. *puberulus* (D.C.Eat.) H. & C. The largest basal antipodal observed was 80μ (fig. 2). Occasionally, one of the interstitial antipodals is the largest, but never over 50μ long.

The antipodal apparatus in the megagametophyte varies widely. Three trends were observed: 1, antipodal cells reduced to two, one with two nuclei (fig. 8); 2, nuclei multiplied so that one or more of the three antipodals are multinucleate (fig. 2), and some individual nuclei may be multinucleolate; 3, divisions continued to more than three antipodals (fig. 3). The last two trends are interrelated; several antipodals may be present with one or more multinucleate (fig. 4). Antipodal cell number and frequency for all species are listed in Table 1.

In the Compositae, antipodal multiplaction often results in persistent, haustorial cells (Davis, 1966). In *Chrysothamnus,* truly haustorial antipodals are infrequent. A strong lateral haustorium was observed only in *C. viscidiflorus* ssp. *humilis* (Greene) H. & C. (fig. 5). An indication of a weak lateral haustorium was seen in *C. linifolius* (fig. 6). The production of an haustorium by elongation of the chalazal antipodal (figs. 1–5) is more frequent than lateral haustoria. If the chalazal antipodal surpasses the endothelium, it is considered haustorial. Nonetheless, haustorial activity is not prolonged in *Chrysothamnus* because the antipodals usually become inactive and disintegrate shortly after fertilization or

---

FIGS. 1–8. Mature embryo sacs and endothelium in *Chrysothamnus:* 1, *C. viscidiflorus* ssp. *lanceolatus (Anderson 2717,* KSC); 2, *C. nauseosus* ssp. *leiospermus* (*Anderson 1995,* KSC); 3, *C. pulchellus* (*Anderson 3213,* KSC); 4, *C. parryi* affin. ssp. *nevadensis* (*Anderson 2966,* KSC); 5, *C. viscidiflorus* ssp. *humilis* (*Anderson 2950,* KSC); 6, *C. linifolius* (*Anderson 2500,* KSC); 7, *C. nauseosus* ssp. *nauseosus* (*Anderson 2707,* KSC); 8, *C. viscidiflorus* ssp. *viscidiflorus* (*Anderson 2900,* KSC).

TABLE 1. NUMBER OF ANTIPODALS AND THEIR OBSERVED FREQUENCY IN EMBRYO SACS IN CHRYSOTHAMNUS.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
NAUSEOSI															
C. parryi		2	8	7	7	4	3	1	1	1	2	1		1	
C. nauseosus		6	5	8	5	3	3	2	2		2				
CHRYSOTHAMNUS															
C. linifolius		3	1	1	1										
C. spathulatus		1	1												
C. albidus	1	2	1		1										
C. greenei		2	4		2	1									
C. viscidiflorus	3	11	7	6	4	3									
PULCHELLI															
C. vaseyi		2	2	1											
C. molestus			4	1											
C. depressus		1	1	1	1										
C. pulchellus				1	1	1									
PUNCTATI															
C. paniculatus		1	3	1	1								1		1
C. teretifolius			2	1											

occasionally prior to fertilization as in *Anderson 2927* (KSC, *C. nauseosus* ssp. *albicaulis*). Relatively persistent chalazal haustoria were found in *C. albidus* (Jones) Greene and *C. greenei* (Gray) Greene.

Shortly after fertilization the embryo sac becomes laterally distended in all taxa (as in fig. 7). Embryogeny is the asterad type. Endosperm formation is nuclear at first. Further growth precipiates wall formation that progresses to form a cellular endosperm.

DISCUSSION

Size of embryo sacs in *Chrysothamnus* varys widely. Extremes (figs. 1, 8) are found in C. *viscidiflorus,* the only species known to contain polyploids (Anderson, 1966). Polyploidy evidently has no significant bearing on embryo sac size; the largest as well as the smallest come from diploids.

Howe (1959) found lateral haustoria in species of *Grindelia, Gutierrezia,* and *Haplopappus.* He used that phenomenon (less frequent than chalazal haustoria in Astereae) to suggest interrelationship of the taxa. Nevertheless, the presence of a lateral haustorium in *C. viscidiflorus* ssp. *humilis* does not suggest that it is related to those taxa also. It does, however, point to the distinctness of that taxon. In fact, unique features in its floral anatomy reinforced my decision to recognize it as a separate species (Anderson, 1970).

Species are listed in table 1 in a phylogenetic sequence (assumed from gross morphology). Patterns in antipodal numbers are fairly well in accord within sections, except for the unusual bimodal pattern in *C. paniculatus* (Gray) Hall. In section *Chrysothamnus,* and particularly in the *Pulchelli,* the average number reflects the assumed phylogeny.

Antipodal apparatus in *Nauseosi* is especially interesting as both species of that section are considered primitive and have numerous subspecies. In a statistical study of floral features (Anderson and Fisher, in press) *C. parryi* (Gray) Greene ssp. *parryi* was determined the most primitive taxon in the genus. If the postulate that an antipodal number of three is primitive, it is noteworthy that embryo sacs in *C. parryi* ssp. *parryi* usually have five to seven antipodals. The more primitive taxa of *C. nauseosus* have megagametophytes with three to five antipodals. In both species the higher numbers of antipodals are found in taxa adapted to xeric environments. If that is a trend, it is not universal; in section *Chrysothamnus, C. albidus* and *C. viscidiflorus* with two to three antipodals are fairly well adapted to xerism.

Hall (Hall and Clements, 1932) stated *C. paniculatus* was the most stable and primitive species in the genus. Its uniformity in external morphology is not seen in its embryology. Contrary to Hall's view, that species is very specialized (table 1). I had considered it less so than *C. teretifolius* (Dur. & Hilg.) Hall; however, embryological information reinforces a more recent determination (Anderson and Fisher, in press) that it is more specialized.

The close similarity of the *Punctati to Haplopappus,* section *Ericameria* (Anderson, 1966), now includes their embryology. *Haplopappus propinquus* Blake (*Raven 16802*, RSA) has four antipodals in the megagametophyte, and *H. trianthus* Blake (*Anderson 3032,* KSC) has five. Similarly, the *Nauseosi* are close to *Haplopappus,* section *Macronema* (Anderson and Reveal, 1966); *H. macronema* Gray from California (*Anderson 2922,* KSC) has five to seven antipodals, and another population from Colorado (*Anderson 2540,* KSC) has 10 antipodals.

In the Astereae, a multinucleate antipodal apparatus is known for several genera related to *Chrysothamnus; i.e., Haplopappus* (Harling, 1951), *Petradoria* (Anderson, 1963), and *Solidago* (Beaudry, 1958). In none, with the possible exception of *Haplopappus,* is the latitude of variability in the megagametophyte so great as it is in *Chrysothamnus.*

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Division of Biology, Kansas State University, Manhattan

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TWO NEW SPECIES OF LAMOUROUXIA (SCROPHULARIACEAE) IN MEXICO

WALLACE R. ERNST and MICHAEL F. BAAD

The genus *Lamourouxia* H. B. K., nom. cons. (Taxon 18: 479–480. 1969), allied to the Rhinanthoideae of Scrophulariaceae, is distributed from northern Mexico through Central America to South America about as far south as Lima, Peru. Of the approximately 26 species, the following two have been studied jointly. They are placed in section *Hemispadon* Bentham, having long tubular, red corollas with a pair of large anthers and a pair of sterile staminal filaments. Search through the literature and at least 25 herbaria, including the major ones of Europe, has failed to disclose other names or collections for these two species. They are being described here to make the names available before a taxonomic revision and a discussion of their morphological relationships to avoid a longer author citation.

Lamourouxia colimae Ernst & Baad, sp. nov. Herba suffruticosa, erecta. Folia glabriuscula, elliptica vel ovata, pauce dentata, attenuata basin versus, nervatura supra impressa. Calyx glaber, limbis patulis, late triangulatis. Corolla coccinea, cylindrica, labio superiore bifido, lobis rotundatis parum cuspidatis, non vel minime reflexis, labio inferiore

FIG. 1. Holotype, *Lamourouxia colimae*.

brevissime trifido. Stamina inferiora fertilia, superiora breviora, parva, sterilia. Affinis sectionis *Hemispadon,* verosimiliter *L. gracilis* vel *L. lanceolata.*

Type: Colima: mountain summits near pass ca. 11 miles south-southwest of Colima on Manzanillo road, elevation 500 m, *Rogers McVaugh 18077* (& *H. F. Loveland, R. W. Pippen*) (MICH-holotype), Sept. 21, 1958 (fig. 1).

Stems erect to 1 m tall. Leaves glabrous or with very few hairs, elliptical or ovate, 18–26 mm long, 6–10 mm broad, attenuate basally, mostly with a very short or indistinct petiole, margins revolute with 3–6 teeth on a side, veining standing out below, the midrib and 3–6 laterals recessed above. Inflorescence erect; pedicels 3–4 mm long. Calyx glabrous or microscopically papillate and possibly glandular, 6–7 mm long, 4 mm broad, the lobes 4–6 mm long, broadly triangular, spreading. Corolla scarlet, 30–35 mm long, 6–7 mm broad, the upper lip 12–13 mm long, the lobes shallow, rounded, slightly cuspidate, little or not rereflexed; the lobes of the lower lip about 1 mm long. Upper pair of stamens ½ or less the length of the corolla, their anthers vestigial and glabrous; lower pair of stamens as long as the corolla, the filaments slightly expanded distally, the anthers shaggy pubescent, their lobes short acuminate at base. Style with a few short hairs.

This species is known only from the type collection, thus the discussion cannot reflect a sense of variation. The new species seems somewhat similar to *L. gracilis* Robinson & Greenman, a rare species in Guerrero and Morelos, having proportionately broader corollas and narrower, basally more attenuate leaves. The flowers recall those of *L. lanceolata* Bentham in DC. in Oaxaca and Central America but in that species the inflorescences are dependent, the flowers resupinate, and the serrate leaves are longer and narrower. The flowers also resemble those of *L. gutierrezii* Oersted in Bentham & Oersted in Central America but that species has scabrous leaves and calyx.

Lamourouxia jaliscana Ernst & Baad, sp. nov. Herba suffruticosa, erecta. Folia pubescentia, anguste lanceolata, grosse dentata, attenuata basin versus. Calyx glandulo-pubescens, limbis subulatis. Corolla rubra, cylindrica, labio superiore bifido, lobis late attenuatis, reflexis, labio inferiore anguste trifido. Stamina inferiora fertilia, superiora breviora, parva, sterilia. Affinia sectionis *Hemispadon,* specie proxima dubia.

Type. Jalisco: Sierra de Caule, southwest of Talpa de Allende, southwest of Piedra Rajada, elevation 1800-2250 m, *Rogers McVaugh 14250* (& *J. Sooby, Jr.*) (MICH-holotype, and duplicate), Nov. 19-21, 1952, (fig. 2).

Other material examined. Jalisco: 11-12 miles south of Talpa de Allende, headwaters of west branch of Rio de Talpa, elevation 1200-1700 m, *McVaugh 21325* (& *C. Feddema, R. Pippen*) (MICH) Nov. 23-25, 1960.

FIG. 2. Holotype, *Lamourouxia jaliscana*.

Stems erect to 1.5 m tall. Leaves very pubescent, possibly scabrous above, soft below, narrowly lanceolate, 50-80 mm long, 6-10 mm broad, attenuate apically and basally, revolute, dentate with 12-22 coarse teeth on a side. Inflorescence erect; the pedicels 5-8 mm long. Calyx glandular pubescent, 14-16 mm long, 5 mm broad, the lobes narrowly subulate, 10-12 mm long. Corolla red, cylindrical, 56-63 mm long, 9-10 mm broad, the upper lip 16-25 mm long, the lobes broadly attenuate, 5-7 mm long, reflexed; the lobes of the prominent lower lip narrow, 5-8 mm long. Upper pair of stamens half as long as corolla, the anthers vestigial and glabrous; lower pair of stamens nearly as long as corolla, the filaments slightly dilated distally, the anthers shaggy pubescent, the lobes acuminate at base. Style with spreading hairs. Fruits ovoid, 12-13 mm long, 7-8 mm broad.

This species, known from only two collections, is distinguished by its large, long, narrow, coarsely-toothed and very pubescent leaves, the long narrow, glandular calyx lobes, and the large size of the corolla. The size of the leaves and flowers somewhat recalls *L. longiflora* Bentham of section Lamourouxia, which has entire leaves. The texture of the leaves somewhat recalls *L. viscosa* H. B. K., but the new species does not seem to be closely allied to any other species.

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A NEW TETRAGASTRIS (BURSERACEAE) FROM PANAMA

Duncan M. Porter

The following new species of *Tetragastris* was discovered during a survey of the Burseraceae for the *Flora of Panama*. It is apparently endemic to the Republic of Panama.

Tetragastris tomentosa D. M. Porter, sp. nov. A *T. panamensis* (Engl.) O. Ktze. quadrimerus floribus et foliolis costa infernis conspicuis luteis-tomentosis statim diagnoscenda.

A tree ca. 8 m high; branchlets densely yellowish-tomentose. Leaves once-pinnate, 37 cm long or longer and to 24.5 cm wide; petioles striate, densely yellowish-tomentose, canaliculate above, 84 mm long; leaflets 7(?), membranaceous, elliptic to ovate, abruptly acuminate apically, slightly oblique basally, the main vein densely yellowish-tomentose below, minutely puberulent above, the secondary veins and blade with scattered trichomes on both surfaces, to 18.5 cm long and 9 cm wide, the laterals largest, the lowermost smallest and reflexed; petiolules densely yellowish-tomentose, canaliculate above, swollen apically, the laterals 15-24 mm long, the terminals 48-59 mm long. Staminate inflorescences axillary panicles, branched from the base, spreading, densely yellowish-tomentose, to 19 cm long. Staminate flowers cream-yellow, 4-merous; pedicels sparsely yellowish-tomentose, 1.5-3 mm long; calyx broadly cupular, sparsely yellowish-tomentose, ca. 1 mm high and 2.5 mm wide, the lobes 4, acute, spreading; corolla yellowish, tubular, densely yellowish-tomentose without, pubescent within, ca. 3 mm long, the lobes 4, thick, acute, 1-1.5 mm long and ca. 1 mm wide, with an incurved apical process adaxially; stamens 8, ca. as high as the corolla tube, the filaments subulate, inserted at the base of the disc between the lobes, the 4 opposite the sepals adnate basally to the corolla below the clefts, the anthers sagittate, basifixed; disc sulcate, 8-lobed, glabrous, half as high as the ovary; ovary tomentose, ovoid, ca. 1 mm in diameter. half immersed in the disc, the style columnar. Fruits unknown.

Type. Panama: Bocas del Toro Province, Fish Creek Hills, *H. von Wedel 2398* (GH, MO-holotype, US) May 7, 1941. Known only from the type collection.

Tetragastris tomentosa is easily separated from *T. panamensis* (Engl.) O. Ktze., the only other species of the genus known from Panama, by a number of characters, the most obvious being its 4-merous flowers and the conspicuous yellow tomentum on the midribs of the leaflets. *Tetragastris panamensis* has 5-merous flowers and sparingly pubescent to glabrate lower leaflet midribs. A flower will be illustrated in the forthcoming treatment of the Burseraceae for the *Flora of Panama.*

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NOTES ON SOME MEXICAN SPECIES OF GOSSYPIUM (MALVACEAE)

Paul A. Fryxell

Gossypium aridum (Rose & Standley) Skovsted was originally described as *Erioxylum aridum* Rose & Standley and based on material from the state of Sinaloa (Culiacan, *Rose, Standley* & *Russell 14199,* US). Rose and Standley regarded this species as distinct from *Erioxylum palermi* (Rose) Rose & Standley based on a collection from Colima (*Palmer* 1316, GH, MEXU, US). Prokhanov accepted this view and transferred the latter species, then known only from the type, to *Gossypium* as *G. rosei* Prokh. Consequently, *G. aridum* has long been regarded as endemic to Sinaloa.

The distinctions between these two taxa are slight. Indeed, more recently collected material shows that they are conspecific. Moreover, this species ranges southeastward far beyond the states of Sinaloa and Colima, covering at least 1000 miles of the west coast of Mexico, and extending to beyond Tehuantepec. The following is a list of specimens of *G. aridum* excluding numerous collections from Sinaloa.

COLIMA: Tecomán, *Miranda 9108* (MEXU); Tecolapa, *McVaugh 15543* (MEXU, US). JALISCO: Navidad, *McVaugh 11882* (MEXU). MICHOACAN: Infiernillo, *Bratz s.n.*, 28.xi.1964 (MEXU). GUERRERO: 95 miles NW of Acapulco, *Fryxell 625* (TAES); 57 miles NW of Acapulco, *Anderson & Laskowski 4489* (MICH-n.v.), *Fryxell 624* (GH, MICH, TAES, UT); Acapulco, *Miranda 4350* (MEXU). OAXACA: 5 miles W of Tehuantepec, *Fryxell 753* (F, MEXU, MO, NA, TAES, U, UC, US), *Smith 3221* (n.v.: MEXU, PH, US); 7 miles W of Nilotepec, *Fryxell & Bates 908* (BH, TAES).

Two recent articles (Fryxell, 1965; Fryxell and Parks, 1967) have dealt with the distribution of *Gossypium trilobum* (Moc. & Sess. ex DC). Skov. An additional specimen has come to my attention from Polotitlán (*Miranda 27172*, MEXU) that extends our knowledge of the distribution of this species. Polotitlán is in the northern extremity of the state of México at an elevation of 2400 m. Previous collections have all been made between 800 and 1800 m elevation.

This record notably extends not only the geographical and altitudinal ranges of *G. trilobum* but also those of the entire subgenus, composed of the American diploid species of *Gossypium*, of which *G. trilobum* is the type species. These plants are distributed solely on the Pacific (western)slopes of the New World, except in the Isthmus of Tehuantepec, where *G. gossypioides* (Ulbr.) Standley also crosses a short distance to the east of the continental divide north of Oaxaca. The present specimen was collected very near the continental divide and, in fact, from an area that drains to the east. This additional trivial exception emphasizes the distinctive western distribution of the group. No collections have previously been reported, to my knowledge, from elevations this high.

The basionym of *Gossypium gossypioides* (Ulbr.) Standley is *Selera gossypioides* Ulbr., and was based on a specimen from Oaxaca (San Bartolo Yautepec, *C.* & *E. Seler 1700*, Jan. 6, 1896). The holotype was at the Berlin herbarium but is now lost. Since no isotypes are known to exist, and Ulbrich cited no other material, it becomes necessary to designate a neotype.

Such a designation raises no significant problems, since the species shows relatively little variability and is quite distinctive, both in morphology and in distribution. Ulbrich indeed chose to place it in a monotypic genus. The specimen chosen as neotype was collected within approximately 10 km of the type locality, at what appears to be the lower elevational limit of the species, these limits being approximately 800–1400 m.

Neotype of *Selera gossypioides* Ulbr.: OAXACA: 39 km W of Tequisistlán, on Hwy. 190 at K 706½, in rocky hills. Elev. 2900 feet. Tree to 15 feet tall. *Fryxell 757* (F, MEXU, MO, NA, US-neotype, TAES), Sept. 9, 1968.

Note added in proof: The distribution of *G. aridum* may also be extended inland to the state of Puebla on the basis of the following specimens. PUEBLA: Tecomatlán, C. Pollatzin, *Miranda 2609* (MEXU); Tecuatitlán San Martín, near Tecomatlán, 3000 ft. alt., *Fryxell 759* (ARIX, MEXU, MICH, NA, NY, US), *Fryxell* & *Bates 918* (BH, MEXU, NA, US).

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NOTES AND NEWS

RECORDS AND OBSERVATIONS ON A RARE PLANT, OXALIS LAXA IN CALIFORNIA. — *Oxalis laxa* H. & A. has previously been reported as sparingly naturalized at Stinson Beach, Marin Co. and near San Andreas, Calaveras Co., California where it has been introduced from Chile (Munz, A California flora, 1959). Recent field collections and subsequent investigation of previously undetermined specimens in the Fresno State College Herbarium have revealed several additional populations, some very extensive, outside the range reported in Munz. The new populations are documented by herbarium vouchers filed at Fresno State College Herbarium. My collections have been widely distributed to other institutions.

The sites reported below are centered in an area less than ten miles wide on either side of the San Joaquin River extending both upstream and downstream from the former site of Fort Millerton. All collections were made between 300 and 700 feet elevation. Those sites some distance removed from the river are found in drainage basins of creeks where the plants usually grow on high, dry soil away from streamside. Soil is thin, of decomposed granite, and usually supports sparse vegetation. *Oxalis* at these sites may grow fully exposed to sun or occasionally in dense shade provided by boulders or scattered shrubs of *Ceanothus cuneatus* or *Lupinus albifrons* and trees of *Quercus douglasii.*

Plants grown from seeds taken at the Madera Co. site yielded chromosome counts of **n = 10** from pollen mother cells squashed in aceto-carmine and proved to be self-compatable, setting abundant seeds when cultivated individually in pots. In this respect the plants are illustrative of the idea proposed by Baker (Evolution 9:347–348, 1955) that establishment after long distance dispersal is greatly enhanced if the organism is self compatable. It remains to be seen whether this group of populations is to be regarded as resulting from a separate introduction or whether it is part of a much broader undetected distribution in the sierran foothills ranging southward from the San Andreas site.

Fresno Co.: along the San Joaquin River near Fort Millerton, *Quibell 1158,* April 4, 1929; Temperance Flat east of Friant, *B. Brock 415,* March 19, 1959; along the San Joaquin River 2 miles downstream from Friant Dam, *Field & Munger,* May 1, 1960; along Little Dry Creek near its crossing with Millerton Road 2 miles east of Auberry Road junction, *Weiler 65024,* April 13, 1965.

Madera Co.: near Cottonwood Creek 5 miles north of the San Joaquin River between Friant and North Fork, *Weiler 65007,* March 5, 1965.—JOHN WEILER, Department of Biology, Fresno State College, Fresno.

OENOTHERA BRANDEGEEI FROM BAJA CALIFORNIA, MEXICO, AND A REVIEW OF SUBGENUS PACHYLOPHUS (ONAGRACEAE)

Peter H. Raven

In December 1887, while collecting for the Smithsonian Institution, Edward Palmer made two collections of an interesting annual *Oenothera* on stony ridges near Bahía de los Angeles on the east coast of Baja California (*542,* GH, and *582,* US). These collections, each of a single plant, were determined by Sereno Watson as *O. caespitosa* Nutt. They remained under this name until 1930, when they were studied by P. A. Munz (1931) for his revision of *Oenothera* subg. *Pachylophus.* Munz considered them a distinctive unnamed variety of *O. caespitosa* which he named var. *brandegeei* Munz (1931), selecting no. *542* as the holotype. Munz assumed this plant to be the same as the one mentioned by T. S. Brandegee (1889) as "*Oenothera caespitosa* Nutt. var. Leaves finely divided and villous.—El Campo Aleman"; but Brandegee's specimen (El Pozo Alemán, 23 April 1889, UC) had long since been determined by Katherine Brandegee as *O. primiveris* Gray, and Munz himself concurred when he examined the specimen in 1932. In 1965, treating the Onagraceae for the North American Flora Munz raised this rare and local endemic to the rank of subspecies as *O. caespitosa* Nutt. ssp. *brandegeei* (Munz) Munz. Until 1966, Palmer's two plants remained the only known representatives of *O. caespitosa* var. *brandegeei.*

Recently, Reid Moran very kindly sent me a collection he had obtained 22 April 1966 on Isla Angel de la Guarda in the Gulf of California. The plants grew among volcanic rocks on the north slope of the peak southwest of Pond Island, ca. 350 m elevation, near 29°01′N, 113°10′W, *12983* (DS, RSA, SD). Moran found occasional woody dead plants from earlier years' growth with the capsules adhering, and also a few dozen living ones with leaves mostly 3–4 cm long and one capsule per plant (Palmer's had leaves respectively ca. 8 and ca. 15 cm long). In these depauperate plants, the terminal lobes of the leaves are less prominent than in Palmer's collections, and the flowers are smaller: hypanthium 5 mm. long, sepals 5 × 0.7 mm, petals about 8 × 4.5 mm, filaments 5 mm long, anthers about 3 mm long in Moran's material, and respectively 38 mm, 12 × 3 mm, 16 × 15 mm, 7 mm. and 5 mm in Palmer's *582.* In every other way, however, Moran's plants are identical with Palmer's, and there is no doubt that all three represent the same entity. The dead plants of earlier years that Moran collected were much more robust, with about 30 capsules per plant.

When I examined Moran's material, it became clear to me that these slender annuals of Baja California should not be considered conspecific with *O. caespitosa* Nutt., itself an exceedingly polymorphic species, but a robust, tufted perennial with much larger flowers. *O. caespitosa* is basically a species of the Great Basin of the western United States, extending south to the San Bernardino Mts. of southern California and the Huachuca Mts. of southeastern Arizona, but not known from Mexico. *Oenothera caespitosa* is, as far as is known, always self-incompatible (Gregory, 1963; Klein, pers. comm.) whereas "var. *brandegeei*," with its small flowers and stigma surrounded by the shedding anthers at anthesis, is highly autogamous as shown by three plants grown at Stanford from Moran's collection. The change from self-incompatibility to autogamy is known often to accompany a change from the perennial to the annual habit in angiosperms.

This discussion to this point establishes the desirability of separating "var. *brandegeei*" from *O. caespitosa* at the specific level. There is, however, another basically annual species with small white flowers which is closely related to *O. caespitosa,* namely *O. cavernae* Munz (1941). *Oenothera cavernae* is so similar to "var. *brandegeei*" that Munz annotated a specimen of the former ("Utah, Capt. Bishop, 1872," US) as follows: "*Oenothera caespitosa* var. *brandegeei* . . . This is a plant from Lower California. The data on the label certainly incorrect. PAM—1930." This was, of course, before Munz was aware of the existence of *O. cavernae* as a distinct entity. Despite their overall similarity, there are a few differences which clearly distinguish *O. cavernae* from "var. *brandegeei*." As pointed out by Munz, the leaves of "var. *brandegeei*" are distinctive in the *O. casespitosa* alliance in being deeply divided into narrow, acuminate, lobes which are directed forward, toward the apex of the leaf. These lobes are much reduced, and the treminal lobe is very prominent in well-developed individuals. In *O. cavernae,* on the other hand, as is usually the case in *O. caespitosa,* the lateral lobes are acute or obtuse and stand out at right angles to the rachis. The terminal lobe of the leaf is much less prominent than in "var. *brandegeei*." The capsules of the two entities likewise differ modally, those of var. *brandegeei*" being short and stout, 14–18 mm. long, with very prominent, well separated tubercles along the lines of dehiscence; whereas those of *O. cavernae* are often longer, 15–38 mm long, with an acuminate apex and less prominent or distinct tubercles.

In summary, their morphological distinctiveness and wide geographical separation suggests that these two white-flowered, autogamous annual species were derived independently from *O. caespitosa* as the deserts of western North America expanded and the available habitats became progressively less favorable for their perennial ancestor. The distinctive leaves of "var. *brandegeei*" suggest that it may have been the earlier derivative, an hypothesis consistent with its present geographical separation from *O. caespitosa*. *Oenothera cavernae* occurs on the desert slopes of southern Nevada (Clark Co.) and southeastward to Toroweap and

Havasu Canyon on the Colorado River in northwestern Arizona. *O. caespitosa* occurs at higher elevations and presumably in more mesic sites, often associated with juniper woodland and sometimes with pinyons, in the same region. In view of these considerations, a new combination seems appropriate.

OENOTHERA **brandegeei** (Munz) Raven, comb. nov. *O. caespitosa* Nutt. var. *brandegeei* Munz, Amer. J. Bot. 18:732. 1931; *O. caespitosa* ssp. *brandegeei* (Munz) Munz, N. Amer. Fl. II. 5:101. 1965.

As I have earlier pointed out the importance of a modern and comprehensive reevaluation of sectional and subgeneric alignments in *Oenothera* (Raven, 1964), it may be appropriate at this point to offer a few comments concerning the relationships of the six species currently referred to subg. (sec.) *Pachylophus* and the overall constitution of the group. First, it is clear that *O. caespitosa, O. cavernae,* and *O. brandegeei* form a close-knit alliance. In the protologue of *O. cavernae,* Munz compared it with the yellow-flowered desert annual *O. primiveris* Gray, but these two species do not appear to be closely related. On the other hand, the annual *O. primiveris* does appear to be related to the yellow-flowered perennial *O. xylocarpa* Cov., a narrow endemic found along the east flank of the southern Sierra Nevada in California and Nevada. Unlike *O. caespitosa, O. xylocarpa* has swollen, fleshy underground parts. In this, as in the morphology of the capsule, it closely resembles the sixth species of the group, the white-flowered (not yellow, contrary to the prediction of Munz (1931; 1965), *O. tubifera* Sessé & Mocino ex Ser. of central Mexico.

Oenothera tubifera in turn is obviously closely related to another white-flowered perennial Mexican species currently referred to subg. *Raimannia*: *O. muelleri* Munz. Although the flowers of *O. muelleri* are much larger, these two species can be crossed easily in cultivation, and the seeds germinate readily to produce healthy F_1 individuals. These two species are identical in capsule morphology and in habit, the plants producing a series of decumbent flowering branches from a central rosette.

Another Mexican species currently referred to subg. *Raimannia, O. macrosceles* Gray, is similar in habit, but has yellow flowers and much more slender capsules. It is clearly not as closely related to *O. muelleri* and *O. tubifera* as they are to one another. *Oenothera macrosceles* can easily be hybridized with *O. muelleri* and *O. tubifera* in cultivation, however, but we have not yet succeeded in germinating the seeds. On the other hand, Cleland (1968) has recently shown that *O. macrosceles* does not hybridize readily with any species of *Raimannia*. On the balance, it would seem that *O. macrosceles* should be placed in subg. *Pachylophus*.

Although the yellow-flowered *O. maysillesii* Munz of Durango, Mexico, is similar in habit and has been compared with *O. muelleri* and *O. macrosceles,* its status is currently being investigated, and it is best retained at least for the time being, in subg. *Raimannia,* as originally placed.

Oenothera subg. *Raimannia* (revised by Munz, 1935) is a relatively homogeneous group in South America, but has been made to include a much more diverse assemblage of North American species. *Oenothera macrosceles* and *O. muelleri,* as suggested above, seem best referred to subg. *Pachylophus,* and *O. albicaulis* Pursh and *O. coronopifolia* T. & G. are best romoved to a ditypic group of their own—sect. *Kleinia* Munz (1965), perhaps best thought of as intermediate between subg. *Raimannia* and subg. *Anogra. Oenothera organensis* is now regarded as belonging to a monotypic sect. *Emersonia* (Munz, 1965) perhaps intermediate to subg. *Oenothera* (*Euoenothera*). With these subtractions, subg. (sect.) *Raimannia* appears to be a reasonably natural group, although rich in species. Interestingly, all of the remaining species would have yellow flowers.

These rearrangements would leave *Oenothera* subg. *Pachylophus* with a total of eight species, with *O. macrosceles* and *O. xylocarpa* yellow-flowered perennials, *O. primiveris* a yellow-flowered annual, *O. tubifera, O. muelleri,* and *O. caespitosa* white-flowered perennials, and *O. brandegeei* and *O. cavernae* white-flowered annuals. Relationships within this group need further clarification by biosystematic studies, but it appears at present that *O. caespitosa, O. cavernae,* and *O. brandegeei*; *O. xylocarpa* and *O. primiveris* (which have been hybridized experimentally, although the seeds could not be germinated; Klein, pers. comm.); *O. macrosceles*; and *O. muelleri* and *O. tubifera* constitute four distinct subgroups. Three species, *O. caespitosa, O. xylocarpa,* and *O. primiveris,* are self-incompatible (Klein, pers. comm.); two, *O. muelleri* and *O. macrosceles,* are self-compatible but modally outcrossing; and two, *O. brandegeei* and *O. cavernae,* are autogamous. In *Oenothera tubifera,* self-pollination is frequent but since a relatively small load of pollen is deposited on the stigma, full seed set does not normally result.

Oenothera subg. *Pachylophus* as constituted here appears to include an assemblage of relatively closely related species, and to embody a useful taxonomic concept. The four groups mentioned above might reasonably be regarded as distinct sectioins, but further studies of the entire genus will be necessary to determine the best systematic treatment for the group as a whole. It might be noted in closing that *O. caespitosa* and *O. primiveris* include several distinct races best recognized at the subspecific level, but the other species appear relatively homogeneous.

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POLLEN APERTURE VARIATION AND PHYLOGENY IN DICENTRA (FUMARIACEAE)

Kingsley R. Stern

Dicentra Bernh., comprising some 20 species of perennial and biennial herbs and climbers of North American and East Asian distribution, was monographed by Hutchinson (1921) as part of a larger treatment. Fedde (1936) largely followed Hutchinson's treatment in his discussion of the Papaveraceae, although both earlier works were incomplete. In my revision of the genus (1961; 1967), phylogenetic trends, based primarily on morphological and anatomical features, were discussed. Berg (1964), studying seed dispersal ecology in *Dicentra* independently, reached essentially similar conclusions about the intrageneric phylogeny, as did Fahselt and Ownbey (1968) while investigating the flavonoid components. Cytological evidence obtained by Ryberg (1960), Ernst (1965), Stern (1968) and others suggests the development of a polyploid series accompanying morphological and chemical advancement, but further extensive study is needed before the role of polyploidy in the evolution of the genus, and cytotaxonomic interrelationships in general can be clearly portrayed.

After brief mention of pollen morphology in my 1961 monograph, I studied *Dicentra* pollen grains in more detail (Stern, 1962), and found the interspecific variation not only extensive, but specifically constant enough to permit distinguishing between all except two of the species on the basis of pollen morphology alone. Such interspecific variation is exceptional, although not wholly unique, as the representative studies of Dahl (1952), Fasbender (1959), Helmich (1963) and Lewis (1965) suggest. My 1962 study included descriptions and dimensions of the pollen grains and mention of phylogenetic trends. This study amplifies and details the extensive aperture variation found, indicates correlations between pollen morphology and other features, and, on the basis of new evidence, revises some phylogenetic concepts.

Pollen grains for this study were mounted in lactic acid (ca. 85%), after removal from herbarium specimens, and slides were made semi-permanent by the addition of ringing cement and cover glasses. Additional mounts in Dahl's medium (Stern, 1961), Calberla's solution, silicone oil (Anderson, 1960) and glycerine jelly, following acetolysis, (Erdtman, 1960) were made for comparison, although it was found that the latter preparations were of more value in exine studies than in aperture studies. A duplicate set of acetolyzed pollen slides has been deposited in the collections of the Palynologiska Laboratoriet, Stockholm-Solna, Sweden.

D. burmanica Stern: *Kaulback 267* (BM, E).

D. canadensis (Goldie) Walp.: *Hone 179* (MIN); *Shafer 130* (UC); *Stern 190* (UC); *Stern 192* (UC); *Umbach 1570* (S).

D. chrysantha (H. & A.) Walp.: *Bacigalupi & Holmgren 3179* (UC); *Meyer 745* (UC); *Sharsmith 4277* (S); *Sowder 431* (UC); *Stern 157* (MIN); *Van Dyke s.n.* (CAS, F, POM).

D. cucullaria (L.) Bernh.: *Anderson 661* (UC); *Bush 13228* (S); *Nielsen 2399* (MIN); *Stern 191* (UC); *Stern 193* (UC); *Umbach s.n.* (F, MICH, UC, US, WIS).

D. eximia (Ker) Torr.: *McVaugh 5714* (UC); *Stern 2021* (UC); *Stern 197* (UC); *Stern 202* (UC).

D. formosa (Haw.) Walp.: *Brown s.n.* (MIN); *Everett & Balls 9458* (S); *Henry s.n.* (DS); *Kruckeberg 4990* (UC); *Leach & Leach 1360* (ORE)); *Stern 775* (UC).

D. grandifoliolata (Merrill) Stern: *Ward 143 (Vernay-Cutting Expdn.)* (GH, NY).

D. lichiagensis Fedde: *Handel-Mazzetti 4329* (GH, US); *Maire 3265B* (UC); *Schneider 2004* (B, US); *Tsai 56060* (AAH).

D. macrantha Oliv.: *Forrest 26601* (E, NY, W, US); *Smith 2098* (UPS).

D. macrocapnos Prain: *E.I.C. Kew Distr. No. 119* (GH, K, L, LE, M, S); *Stainton, Sykes & Williams 4254* (BM); *Stainton, Sykes & Williams 5009* (BM).

D. nevadensis Eastw.: *Cronquist 2148* (MO); *Darland s.n.* (UC); *Stern 166* (MIN).

D. ochroleuca Engelm.: *Clokey & Templeton 4615* (UC); *French 332* (UC); *Gifford 195* (UC); *Howell 4079* (CAS); *Pollard s.n.* (S); *Stern 158* (MIN).

D. pauciflora Wats.: *Brown 418* (UC); *Haddock 14* (DS, UC); *Purpus 3140* (UC); *Rowntree s.n.* (CAS).

D. paucinervia Stern: *Ludlow & Sheriff 15838* (BM).

D. peregrina (Rudolph) Makino: *Hiroe 7054* (UC); *Jochelson 228* (NY, S).

D. roylei Hook. f. & Th.: *Lace 1516* (E); *Ten 1367* (B).

D. scandens (D. Don) Walp.: *Ownbey, s.n.* (WS); *Schneider 3244* (B); *Tsai 52955* (GH).

D. spectabilis (L.) Lem.: *Bazilevski s.n.* (LE); *Maire 2714* (UC); *Umbach s.n.* (WIS, UC, F).

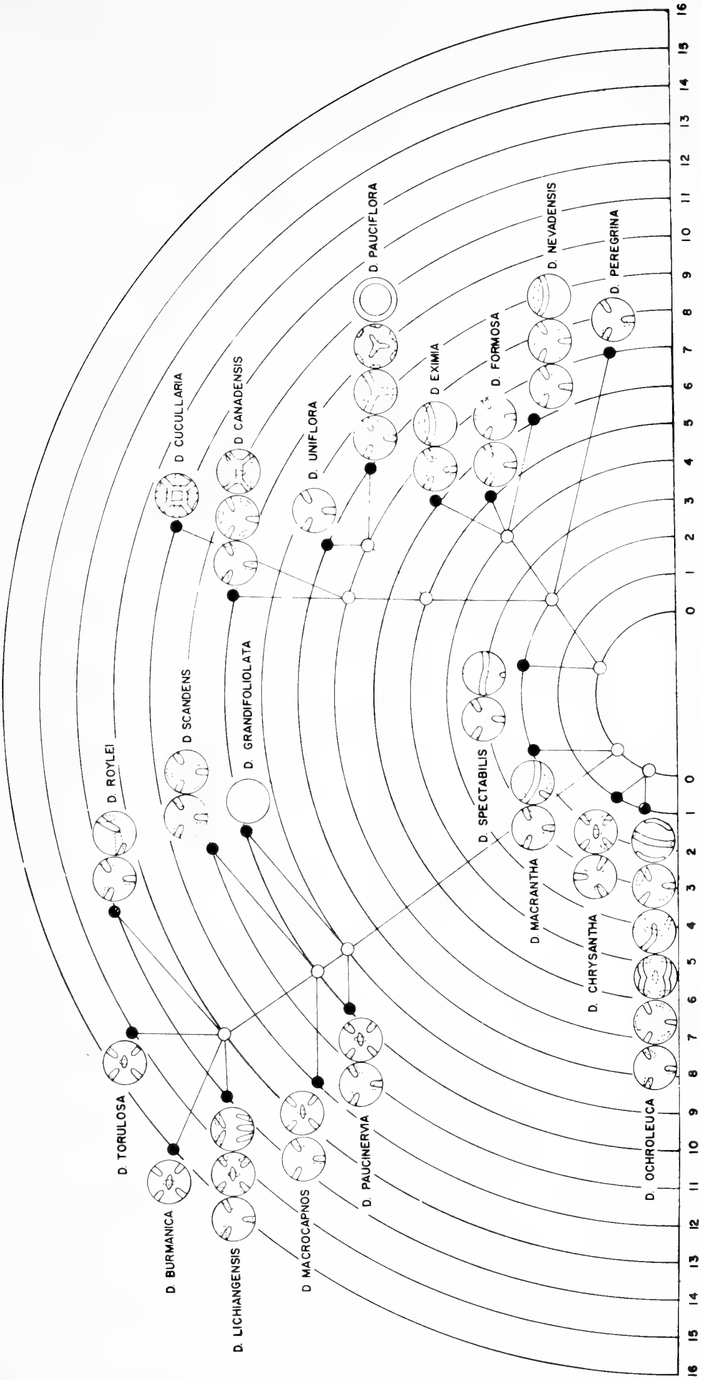
D. torulosa Hook f. & Th.: *Cooper 3129* (E); *Ducloux 948* (E); *Maire 725* (BM, E); *Tsiang 8866* (UC).

D. uniflora Kell.: *G. N. Jones 9935* (GH); *M. E. Jones s.n.* (POM, UC); *Steward & Gilkey* (OSC).

Figure 1 illustrates, via diagrams, the various aperture arrangements occurring in pollen grains of *Dicentra* species. The pollen diagrams themselves are superimposed on a diagram revised and adapted from Stern (1961), which indicates presumed relationships between species, based on advancement indices derived primarily from morphology and anatomy. As observed by Alston and Turner (1963), such base diagrams do not indicate the factor of time for the assumed branching, since the angles of divergence, etc., are strictly diagrammatic, and are not intended to signify constant rates of evolution. Nevertheless, in the absence of extensive genetic and experimental evidence. they do serve a useful purpose as a framework for future investigation. As indicated earlier, since the base diagram appeared in its original form, support for many of the phylogenetic positions indicated has been derived from seed dispersal ecology studies and chemotaxonomy. An exception to this is the position of *D. spectabilis,* which was originally included in the subgenus *Chrysocapnos* Engelm. A reconsideration of the pollen exine morphology suggests its affinities lie closer to members of the subgenus *Dicentra,* and the chemical evidence presented by Fahselt and Ownbey (1968) tends to substantiate this. The morphology and anatomy of the species, however, is sufficiently distinctive to warrant its relegation to a monotypic subgeneric ranking of its own. *Dicentra macrantha* also is here accorded subgeneric ranking, since its floral morphology differs so markedly from that of other members of the subgenus *Chrysocapnos;* further, although it is not scandent, it does appear, vegetatively, to be more closely related to members of the subgenus *Dactylicapnos* (Wall.) Stern.

Subgenus **Hedycapnos** (Planch.) Stern, stat. nov. *Capnorchis* subg. *Hedycapnos* Planch. Fl. Serres 8:193. 1853. *Eucapnos* Sieb. & Zucc. Abh. Math.-Phys. Cl. Konigl. Bayer. Akad. Wiss. 3:721. 1840, non Bernh. Linnaea 8:468. 1833. *Dicentra* subg. *Chrysocapnos* sect. *Hedycapnos* (Planch.) Stern, Brittonia 13:21. 1961. Type species: *Dicentra spectabilis* (L.) Lem. Fl. Serres I. 3:pl. 258. 1847.

FIG. 1. Diagram indicating presumed phylogenetic relationships and correlations of pollen aperture types in *Dicentra*.


D. PAUCIFLORA
D. NEVADENSIS
D. PEREGRINA
D. CUCULLARIA
D. CANADENSIS
D. UNIFLORA
D. EXIMIA
D. FORMOSA
D. ROYLEI
D. SCANDENS
D. GRANDIFOLIOLATA
D. SPECTABILIS
D. MACRANTHA
D. CHRYSANTHA
D. OCHROLEUCA
D. TORULOSA
D. BURMANICA
D. LICHIANGENSIS
D. MACROCAPNOS
D. PAUCINERVIA
16
15
14
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3
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Subgenus **Macranthos** (Stern) Stern, stat. nov. *Dicentra* subg. *Chrysocarpnos* sect. *Macranthos* Stern, Brittonia 13:24. 1961. Type species: *Dicentra macrantha* Oliv. For further discussion and species synonymy see Stern (1961).

When the pollen aperture diagrams are added to the presumed phylogeny base diagram, (fig. 1), certain correlations between gross morphology and pollen morphology become apparent. The more primitive species possess numerically constant (3 or 6) apertures, which are also distinct. *Dicentra ochroleuca,* and occasionally *D. macrantha,* do, in addition to the basic 3 or 6 apertures, exhibit anomotreme pollen grains, often with bizarre aperture configurations, which are, however, always distinct. The proportion of aperture to non-aperture surface area in these and other *Dicentra* pollen grains appears to be more or less constant, regardless of the particular configurations or numbers of apertures. To demonstrate this mathematically in prolate spheroids with so many grain-to-grain variables would, however, be a most challenging task.

The more advanced species, in the subgenera *Dicentra* and *Dactylicapnos,* in general, have numerically inconstant apertures, and, in the latter subgenus in particular, the apertures become less distinct. Also, in the subgenus *Dicentra,* there is a trend toward more numerous apertures, and eventual fusion of the apertures. Although an occasional anomotreme pollen grain will appear in the four most primitive species (*D. formosa, D. nevadensis, D. eximia* and *D. peregrina*), fusion of apertures has not been observed. In *D. pauciflora,* however, some pollen grains are 8-aperturate, the apertures consisting of 6 separate rugae or colpi, plus 6 more rugae coalesced into 2 triradiate apertures. In *D. canadensis,* some basically 12-aperturate pollen grains become synaperturate, and in *D. cucullaria,* various configurations, but all synperturate, are typical. If increase in numbers of apertures, and fusion of apertures, as well as decreases in the distinctness of aperture margins in the pollen grains of *Dicentra* may be considered advancement, such advancement appears to have accompanied morphological and anatomical advancement in the genus.

This was part of a larger study, for which partial support from the National Science Foundation, under grant GB-4498, is gratefully acknowledged. The author is also grateful to G. Erdtman for the use of the facilities of the Palynologiska Laboratoriet, in Stockholm-Solna, Sweden.

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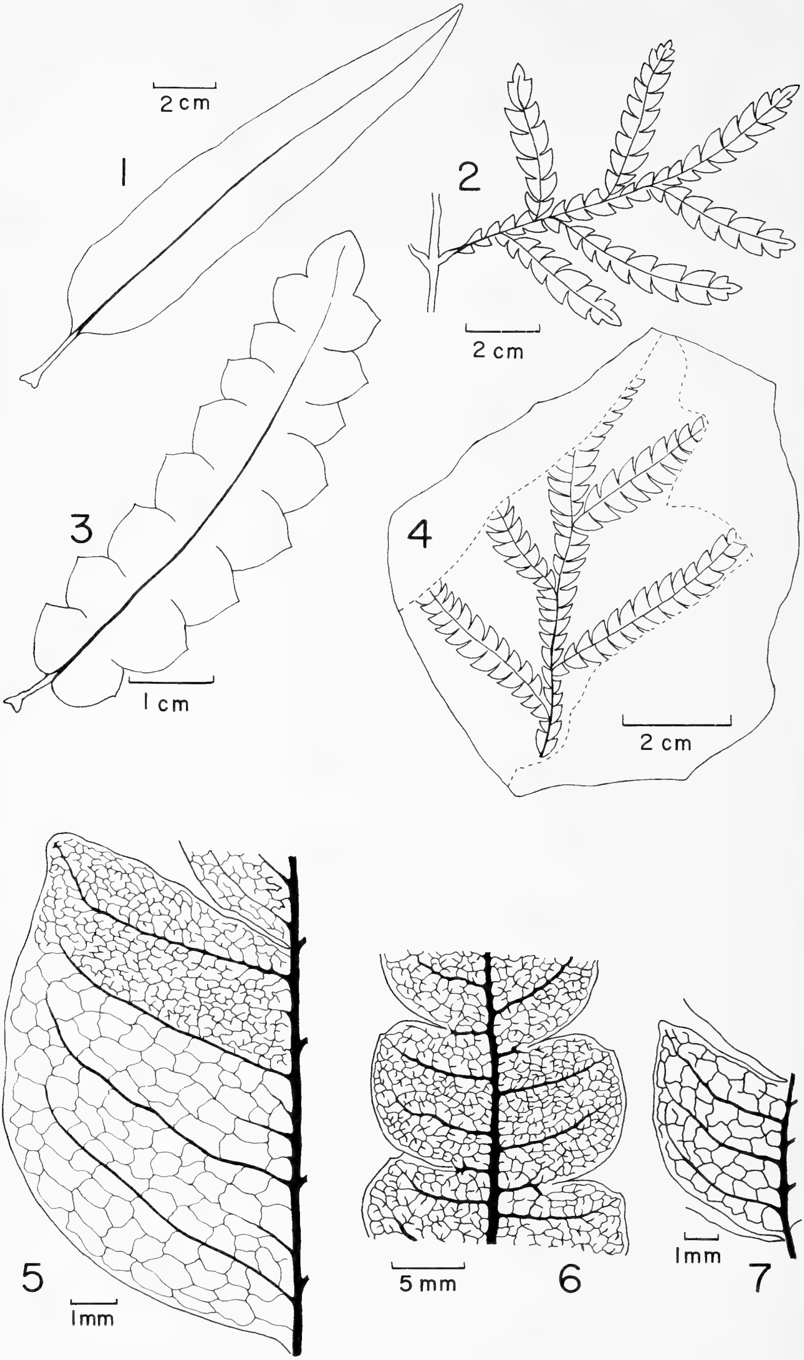
FOSSIL LEAVES OF LYONOTHAMNUS

SATISH C. BANWAR

Leaves of the extant genera *Lyonothamnus,* belonging to the family Rosaceae, and *Comptonia,* belonging to the family Myricaceae, are very similar in external appearance. Many paleobotanists who have examined fossil leaves of *Lyonothamnus* were at times led to identify them as *Comptonia.* This study was conducted to examine and compare leaves of *Lyonothamnus,* both extinct and extant, and those of *Comptonia,* so that differences and similarities in shape, nature, and venation could be established, which would then help to distinguish them.

Fossil leaves, identified as those of *Lyonothamnus,* have been collected in various localities in the western United States from Washington to Oregon, California, and Nevada. The ages of all these fossil leaves range from Miocene to Pliocene. All the specimens collected so far are comparable to leaves of the extant *L. floribundus* Gray ssp. *asplenifolius* (Greene) Raven. The leaves of subspecies *asplenifolius* are so distinctive that similarities with the fossil forms are easily recognized (figs. 2, 4). So far, to my knowledge, no one has reported the presence of fossil leaves which may be comparable to foliage of subspecies *floribundus* (fig. 1).

The first fossil specimens to be identified as *Lyonothamnus* were collected by Axelrod in 1939 from the Tehachapi area of California; he


2 cm
1
2
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7

described and named these specimens as *L. mohavensis* (Axelrod, 1939). The age of these specimens was determined as Middle Miocene; they were in small fragments and only portions of leaflets were present, but the general appearance, shape, and venation were similar to those of leaves of living *L. floribundus* ssp. *apslenifolius*. Since then Axelrod has reported the occurence of *L. mohavensis* from many other localities in California and Nevada. The sites and their ages are as follows: Furnace Creek Flora, California (Mio-pliocene), Mint Canyon Flora, California (Upper Miocene), Upper Modella Flora, California (Upper Miocene), Coal Valley Flora, Nevada (Upper Miocene), Mulholland Flora, California (Middle Pliocene) (Axelrod, 1940). In 1956, while examining the Mio-pliocene floras from west-central Nevada, the same author described many fossil specimens as *C. parvifolia,* because to him they resembled the leaves of members of the extant genus *Comptonia* (Axelrod, 1958). These leaf specimens reported as *Comptonia* were much larger and better preserved than those reported earlier as *Lyonothamnus*.

Wolfe, while investigating the Miocene floras from Fingerrock Wash, Nevada, reassigned *C. parvifolia* to *L. parvifolia* (Axelrod) Wolfe. He justified his reassignment on the basis of venation pattern (Wolfe, 1964). Wolfe also believed he could distinguish two forms of fossil *Lyonothamnus:* one form having seven to nine leaflets or pinnae and the other fewer than seven leaflets. The former represents *L. parvifolia,* the latter *L. mohavensis*. He was of the opinion that these two forms should be regarded as two different species, and that *L. mohavensis* is closer to the extant forms.

Page (1964) has recently described as *Lyonothamnoxylon nevadensis,* fossil wood from the lower Pliocene of Nevada. The wood of *L. nevadensis* most closely resembles that of *Lyonothamnus*.

The genus *Lyonothamnus* comprises a single living species with two subspecies (Raven, 1963), namely *L. floribundus* Gray ssp. *floribundus* and *L. floribundus* ssp. *asplenifolius* (Greene) Raven. The genus is endemic to the islands off the shores of southern California; no natural population exists on the mainland. The distribution of the subspecies on the islands is also very interesting. Subspecies *floribundus* is confined to Santa Catalina I., while ssp. *asplenifolius* is restricted to Santa Rosa, Santa Cruz, and San Clemente islands. The two subspecies are distinguished from each other by the nature and form of the leaves they bear. The leaves of ssp. *floribundus* are simple, lanceolate, and have an entire margin (fig. 1), while those of ssp. *asplenifolius* are pinnately compound

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FIGS. 1–7. *Lyonothamnus* and *Comptonia:* 1, leaf of *L. floribundus* ssp. *floribundus;* 2, leaf of *L. floribundus* ssp. *asplenifolius;* 3, leaf of *C. peregrina* showing the lobes (Transylvania Co., North Carolina, *Fox 704,* UC); 4 fossil specimen of *L. parvifolia,* collected by the author at Stewart Springs area, Mineral Co., Nevada; 5, a leaf lobe of *L. floribundus* ssp. *asplenifolius,* showing venation pattern; 6, portion of leaf *C. peregrina,* showing venation of lobes; and 7, a leaf lobe of *L. parvifolia,* showing venation pattern.

and have a dissected lamina (fig. 2).

The members of the genus *Comptonia* are confined in their distribution to the eastern United States. The leaves of *C. peregrina* (L.) Coult. (fig. 3) are simple, and the laminae are dissected somewhat like those of *L. floribundus* ssp. *asplenifolius*.

MATERIALS AND METHODS

Fossil specimens were examined in the excellent collections of the Museum of Paleontology, University of California, Berkeley. Some specimens were collected personally from Stewart Springs, Mineral Co., Nevada. They [fossil leaves] were examined under a dissecting microscope, and the venation patterns were observed by wetting the specimens with clove oil.

Leaves of living plants of *Lyonothamnus* were obtained from the Rancho Santa Ana Botanical Gardens at Claremont and from the University of California Campus at Berkeley. At both of these places the trees are cultivated. Leaves of *C. peregrina* were obtained from herbarium specimens housed in the University of California Herbarium, Berkeley.

The leaves of *Lyonothamnus* and *Comptonia* were found to be very rich in tannin and thus the clearing technique had to be modified slightly. Both dried and fresh leaves were boiled in water and then in alcohol to remove the chloroplasts. The leaves were then washed in running tap water for some time and soaked in My-pro Bleach (manufactured by Crown Products, San Francisco), which removed all the tannin and made the leaves white. The timing in this bleach had to be adjusted for each leaf because a prolonged treatment in bleach macerated all the tissues. After this the leaves were washed again in tap water for several hours and then soaked in a saturated solution of chloral hydrate. They were then washed in water and stained in the usual way with 1 percent alcoholic safranin. It was found that dried plant materials yielded better results than did similarly treated living materials. The leaves were mounted in Picolyte on large glass plates.

OBSERVATIONS

Most of the fossil specimens examined are only fragments of large leaves. Some of these fragments are fairly large while others are small, but even from the latter it was evident that the original laminae were pinnately compound and that each pinna had several dissected lobes. The definite number of pinnae present on each leaf could not be determined because of the small size of the fragments or their arrangement. Some of them have as few as three pinnae, while others have as many as nine. The lobes are not exactly opposite each other on a pinna but are "staggered" or arranged alternately. Each lobe is somewhat triangular in shape with an acute pointed apex. The lobes are sessile and attached by one complete side to the axis of the pinna (fig. 4).

In each lobe, several secondary veins are given off from the axis of the pinna. These extend nearly to the margin of the lobe. Each secondary vein produces several tertiary veins, which also divide further and form a fine network of veins. The finer details and the details of the vein endings could not be examined as they were not well preserved in the fossils. Among th secondary veins, it is the uppermost (or first) secondary vein which terminates in the apex of the lobe, while the other secondary veins form a loop at the distal margin and join with the secondary vein above (fig. 7).

In the genus *Lyonothamnus,* only leaves of ssp. *asplenifolius* were examined in detail because it is in this subspecies that similarities have been noted with the various fossil leaves mentioned and with leaves of *Comptonia.*

Leaves of *L. floribundus* ssp. *asplenifolius* are opposite (although members of the Rosaceae are usually considered to have alternate leaves) and pinnately compound with several pinnae (fig. 2). The number of pinnae varies between three and seven on different trees and even on different branches of the same tree. No leaf was observed to have as many as nine pinnae. Each pinna is divided into several lobes, the sinuses extending clear into the axis of the pinna. These are slightly staggered or alternate to each other on the axis of the pinna, and are sessile and triangular in outline. Each lobe has an acute apex and one complete side is attached to the axis of the pinna (fig. 2). In each lobe, several secondary veins are given off from the axis of the pinna and extend nearly to the margin of the lobe. Each secondary vein produces several branches which divide further and produce a fine network of veins with free vein endings. It is the uppermost (first) secondary vein which terminates in the apex of each lobe (fig. 5), while the other secondary veins form loops near the distal margin and join with the adjacent secondary vein towards the apex.

Leaves of *C. peregrina* are alternate and simple. The lamina is dissected into nearly opposite lobes, but the sinuses do not extend all the way to the midrib (figs. 3, 6). The size of the leaves varies and so also does the number of the lobes. But it is evident that the lobes are very different from those of *Lyonothamnus.* Each lobe has an obtuse apex. Generally three secondary veins develop in each lobe, the first extending only to the sinus, and (in contrast to the situation in *Lyonothamnus*) the second or central secondary vein terminating in the apex of the lobe (fig. 6). Each secondary vein produces several tertiary veins which divide further and produce a fine net-work of veins with free vein endings.

DISCUSSION

From the external morphology of the leaves studied, it is very clear that the fossil leaves of *Lyonothamnus* are very similar to those of the extant ssp. *asplenifolius.* The similarity with leaves of *Comptonia* is very superficial. The leaves of *Comptonia* are simple, the incisions of the lamina are shallow, and the lobes are opposite or nearly so, while those of *Lyonothamnus* are compound with a number of pinnae and the incisions of the lamina are deep, extending right up to the axis of the pinna. The shape, position, and nature of the lobes and their apices are also very different.

The venation patterns are also distinct. The venation of both extant and fossil leaves of *Lyonothamnus* examined were very similar. In both it is the first, or uppermost, secondary vein which terminates in the apex of the lobe. In *Comptonia* it is the second, or the central, secondary vein which does so. Thus on the basis of venation pattern also the fossil leaves show a greater similarity with those of the extant ssp. *asplenifolius*. The similarity with those of *Comptonia* is very superficial.

This study agrees with the views of Wolfe in reassigning all the fossil leaves described as *C. parvifolia* Axelrod to *Lyonothamnus parvifolia* (Axelrod) Wolfe, although the creation of two species among the fossil leaves is debatable.

The author wishes to thank Lincoln Constance, A. S. Foster, and W. L. Fry, of the University of California, Berkeley, for guiding and helping me in this study. This study was a part of the doctoral thesis submitted at the University of California, Berkeley. The author is also very thankful to the directors of the Paleontological Museum and Herbarium of the University of California, Berkeley, for allowing the use of their collections.

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NOTES AND NEWS

EDITORSHIP OF MADROÑO.—Some time during the summer of 1971, Dr. Robert Ornduff, Department of Botany, University of California, Berkeley, will become the Editor of Madroño. At the same time, Dr. John Strother, also at Berkeley, will become Managing Editor. In preparation for the change of Editors, it is requested that all new manuscripts intended for publication in Madroño be sent to Berkeley rather than Stanford.

CHROMOSOME STUDIES IN MELAMPODIUM (COMPOSITAE, HELIANTHEAE)

Tod F. Stuessy

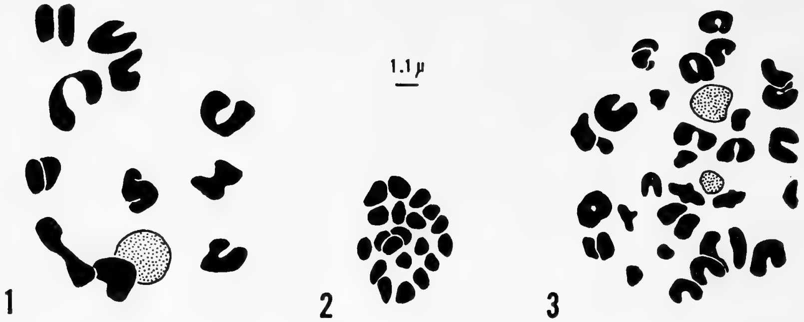
A number of chromosome counts for the genus *Melampodium* already have been reported (Negodi, 1938; Jackson, 1957; Turner, Beaman, and Rock, 1961; Turner and Johnston, 1961; Turner and King, 1962; 1964; Turner and Flyr, 1966). These studies surveyed 21 of the 35 presently recognized in the genus (Stuessy, 1968) and indicated the presence of intraspecific polyploidy in several taxa (Turner and King, 1962). In addition, base numbers for the genus have been tentatively proposed as **x** = **9** (Negodi, 1938) and **x** = **10** (Turner and King, 1962). The present studies significantly add to previous work by 1, most importantly, putting the old counts into the framework of the recent taxonomic concepts and nomenclature (Stuessy, 1968), 2, adding new counts for two species, 3, surveying intra- and inter-populational chromosome variability throughout the ranges of many species which more clearly indicates the significance of polyploidy in each species and in the whole genus, and 4, clarifying certain problems mentioned in earlier chromsome treatments.

Methods and Materials. Buds for meiotic counts were collected in the field in modified Carnoy's fixative, 4 parts chloroform, 3 parts absolute alcohol, and 1 part glacial acetic acid, and refrigerated in the laboratory (Walters, 1952), until subsequently counted by acetocarmine squash techniques. Material stored in this manner lasted as long as one year and still produced clear meiotic figures, although some hardening of the cells was noticed.

Seeds for the few mitotic counts were treated as in Speese and Baldwin (1952), first being germinated on filter paper in petri dishes, pretreated for an hour in a saturated aqueous solution of PDB, then fixed in 3:1:1 (3 absolute alcohol: 1 chloroform: 1 glacial acetic acid) and finally squashed under acetocarmine stain.

Results and Discussion. Table 1 lists the various chromosome counts known for the genus *Melampodium*. Due to problematical nomenclature, many previous counts were reported under names now regarded as synonyms (Stuessy, 1968). In addition, the recognition of new varieties in *M. cinereum, M. leucanthum* and *M. montanum* (Stuessy, 1968) has required putting old counts referred to these species into the proposed respective varietal categories.

Two species, *M. glabrum* and *M. hispidum,* are here reported for the first time as **n** = **11** (fig. 1) and **n** = **20** (fig. 2), respectively. *Melampodium glabrum* thus coincides cytologically with the morphologically similar species, M. perfoliatum (**n** = **11, 12**), which strengthens the

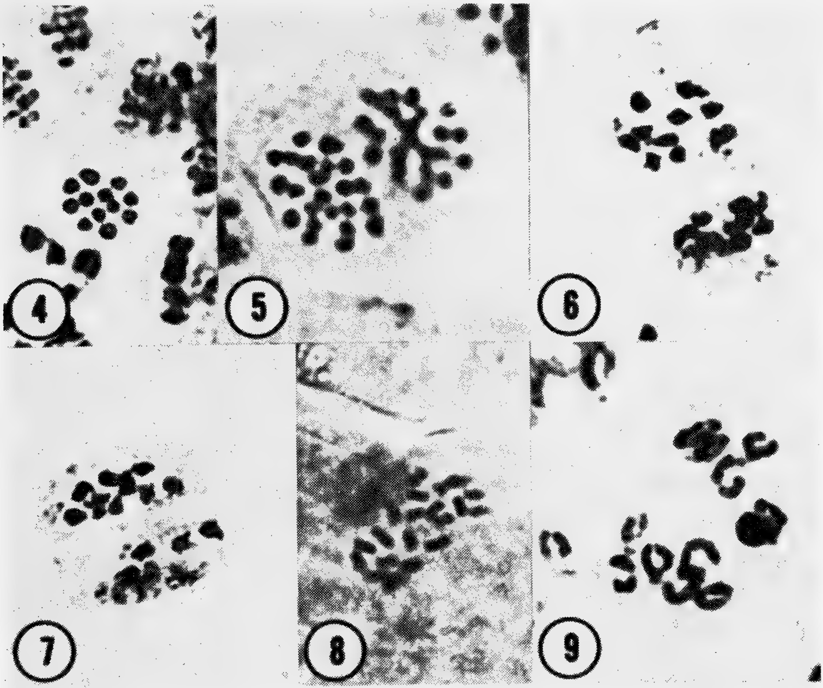


FIGS. 1–3. Camera lucida drawings of chromosomes of species of *Melampodium:* 1, *M. glabrum,* diakinesis, **n = 11**, *Stuessy 708;* 2, *M. hispidum,* metaphase II (½ of cell drawn, **n = 20**, *Stuessy 1038;* and 3, *M. sericeum,* diakinesis, **n = 30**, *Stuessy 364.*

inferred close phyletic relationship of these two taxa. *Melampodium hispidum* is a mountainous species very similar morphologically to *M. sericeum* (**n = 30**; 20 large and 10 small bivalents, fig. 3). It may be that an ancestor of *M. hispidum* was involved in the evolution of this hexaploid species, perhaps contributing the 20 larger bivalents. The close morphological similarity of *M. sericeum* to another species, *M.* sp. nov. (*P. Goldsmith 133;* chromosomally unknown but placed in the **x = 10** section of the genus), suggests that an ancestor of the latter may have donated the smaller set of 10 bivalents. This speculative origin of *M. sericeum* contrasts markedly with that indicated by Turner and King (1962). While they noted the close relationship to *M. hispidum* (first perceived by Robinson, 1901), they suggested the possible involvement of an ancestor of *M. camphoratum* (**n = 16**) by the incorporation of some of its small chromosomes into the genome of the incipient *M. sericeum* through amphiploidy. But since *M. camphoratum,* in my opinion, belongs to the rather distantly related genus *Unxia* (closely related to *Polymia*), the likelihood of such an origin seems remote.

Extensive surveying of many populations of species previously counted (118 new population reports) has shown that all but three species are apparently uniformly diploid throughout most of their ranges. The diploid-tetraploid races in *M. cinereum* and *M. leucanthum* noted by Turner and King (1962) have been verified in the present study (table 1) and will be discussed at length elsewhere. *Melampodium dicoelocarpum* is the only other species that has been found to possess polyploid races, being diploid at **n = 12** (new report, fig. 4) and aneuploid (at the tetraploid level) with **n = 23** (fig. 5). Although quantitative morphological differences are present between the latter two races, too few counts have been made and too few herbarium records are available to comment on significant geographical or ecological differences.

Melampodium longipilum has been counted previously only once



FIGS. 4–9. Photographs of chromosomes of species of *Melampodium:* 4, 5, *M. dicoelocarpum,* metaphase II; 4, **n = 12**, *Stuessy 693;* 5, **n = 23**, *Stuessy 716;* 6–8, *M. longipilum;* 6, 7, anaphase I, **n = 10**, *Stuessy 373;* 8, metaphase, **2n = 20**, *Stuessy 634;* and 9, *M. perfoliatum,* diakinesis, **n = 11**, *Stuessy 379.* All approximately × 1800.

(Turner and King, 1962), the authors commenting that, "This collection is interesting in that its habit and floral features are similar to *M. divaricatum,* but the achenes bear well-developed hoods such as are characteristic of the section *Melampodium.* Its chromosome number, **n = 11**, however, would be exceptional for the latter section." Although on close examination this species is quite distinct within the genus, it seems morphologically closest to *M. diffusum* (**n = 10**) and on this basis would be expected to fall into the section *Melampodium.* Since meiotic (and one mitotic) counts have been made from six populations of this species in the present study (table 1) and all have yielded unequivocal counts of **n = 10** (figs. 6–8), it is probable that the normal chromosome number of this species is **n = 10**.

The reported counts of *M. perfoliatum* (Turner and King, 1962; 1964) have been both **n = 11** and **n = 12**. Although the present study recorded only counts of **n = 11** for this species (fig. 9), more survey work is needed to discover the factors involved in the establishment and maintenance of these two chromosomal levels, if two indeed exist. The chromosomal voucher specimens of the two races cannot be distinguished morphologically.

The early counts of $\mathbf{n} = \mathbf{10}$ for both *M. divaricatum* and *M. perfoliatum* reported by Negodi (1938) accompanied by descriptions and photographs of the plants, contrast with the consistent subsequent counts of other workers of $\mathbf{n} = \mathbf{12}$ and $\mathbf{n} = \mathbf{11}$ and $\mathbf{12}$, respectively. It is likely that these unusual $\mathbf{n} = \mathbf{10}$ counts represent either very anomalous conditions or perhaps erroneous observations.

Negodi (1938) was the first to discuss the taxonomy of *Melampodium* in a phyletic sense. Based on counts of $\mathbf{n} = \mathbf{9}$ and $\mathbf{n} = \mathbf{10}$ for three species, he felt that $\mathbf{n} = \mathbf{9}$ was the ancestral base, followed by an aneuploid gain to $\mathbf{n} = \mathbf{10}$. Turner and King (1962) however, comment that, "It is obviously impossible to know what the ancestral basic chromosome number for the genus might have been, but it does seem significant that the number, $\mathbf{n} = \mathbf{10}$, is found in a wider range of morphological types than is any other number." The fact that a large number of morphologically diverse species within a genus has a certain characteristic (e.g., $\mathbf{x} = \mathbf{10}$) by no means designates this unequivocally as a primitive trait. But it may be suggestive, especially in recently evolved groups such as the Compositae. Nevertheless, phylogenetic speculations including base number hypotheses must be based on all available evidence, not numerology or one or two characters alone. Further insight into aneuploid trends in *Melampodium* must wait for a compilation of evidence that is accumulating on other aspects of the genus.

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Note added in proof: *M. hispidum* has been counted recently as $\mathbf{n} = \mathbf{20}$ by Powell and Sikes (1970).

TABLE 1. CHROMOSOME COUNTS IN MELAMPODIUM

All voucher specimens cited in this study are deposited in the University of Texas Herbarium, Austin.

All citations are meiotic counts showing clear bivalents unless otherwise indicated at the end of each voucher citation.

Superscripts after voucher specimens refer to counts not made by the author but found in the following references:

[a] Negodi (1938)
[b] Jackson (1957)
[c] Turner, Beaman and Rock (1961)

[d] Turner and Johnston (1961)
[e] Turner and King (1962)
[f] Turner and King (1964)
[g] Turner and Flyr (1966)
[h] Powell, A. M., and B. L. Turner (unpublished)
[k] Raven, P. H. (unpublished)
[m] Turner, B. L. (unpublished)
[n] Turner, B. L., W. L. Ellison, and R. M. King (unpublished)

Different voucher numbers from the same locality refer to counts from buds from an individual plant (listed first) and from a populational sample. Irving, Stuessy and Turner collections of *M. cinereum* and *M. leucanthum,* however, are all individual plants.

M. americanum L. **n = 10**. GUATEMALA. Baja Verapaz: near Salamá, *King 3260* (reported as *M. americanum* var.)[e]; Progreso: 35 mi NE of Guatemala, *Stuessy 602*. MEXICO. Chiapas: Santa Isabel, *Stuessy 632;* Colima: Alzada, *Stuessy 727;* Guerrero: 9 mi NW of Taxco, *King 4168* (reported as *M. kunthianum*)[e]; 25 mi NE of Acapulco, *King 4178* (reported as *M. kunthianum*)[e]; Michoacán: 7 mi S of Ario de Rosales, *Stuessy 688,689;* Nayarit: 25 mi N of Tepic, *King 3699*[n]; Vera Cruz: 20 mi. E of Cuitlahuac, *King 2679*[e]; 26 mi E of Cuitlahuac, *King 2682*[e]; 9 mi NW of Alvarado, *King 2709*[e]; 9 mi SE of Alvarado, *King 2718*[e]; 24 mi E of Cuitlahuac, *Stuessy 314, 315;* 27 mi S of jct rtes 110 & 105; *Stuessy 469, 470* (ca **10**); 19 mi S of Diamante, *Stuessy 481;* 34 mi NW of José Cardel, *Stuessy 484, 485;* 14 mi E of La Tinaja, *Stuessy 516;* Salinas, *Stuessy 518, 519;* near Catemaco, *Stuessy 522*.

M. aureum Brandg. **n = 33**. MEXICO. Michoacán: 20 mi W of Ciudad Hidalgo, *King 3617*[e]; 21 mi NW of Ciudad Hidalgo, *Stuessy 683, 684;* Oaxaca: 7 mi NE of Nochistlán, *Stuessy 663* (& frag.).

M. cinereum DC. var. *cinereum*. **n = 10**. MEXICO. Tamaulipas: 59 N of Sabinas Hidalgo, *Stuessy 857a*. TEXAS. Hidalgo Co.: 6 mi E of Sullivan City, *Turner 4490* (reported as *M. cinereum*)[e]; Webb Co.: ca 22 mi NW of jct rtes 83 & 81 (35), *Stuessy 869;* 37 mi N of Zapata, *Thompson 174* (reported as *M. cinereum*[e]; Zapata Co.: 14.6 mi N of San Ygnacio, *Strother 556;* 27 mi N of Zapata, *Thompson 175* (reported as *M. cinereum*)[e]; Zavala Co.: 11 mi SE of Batesville, *Sullivan & Turner 22* (reported as *M. cinereum*)[e]; 6 mi S of Batesville, *Turner 5006* (reported as *M. cinereum*)[g].

M. cinereum DC. var. *cinereum*. **n = 20**. TEXAS. Duval Co.: 25 mi N of Hebbronville, *Stuessy 429;* Jim Hogg Co.: 10 mi E of Hebbronville, *Stuessy 423* (ca **20**); near Hebbronville, *Stuessy 425;* Hebbronville, *Stuessy 426;* near Hebbronville, *Stuessy 428;* Hebbronville, *Thompson 177* (reported as *M. cinereum*)[e]; Jim Wells Co.: near Orange Grove, *Strother 565;* Live Oak Ca.: ca 32 mi S of Whitsett, *Stuessy 772, 773;* 14 mi S of George West, *Thompson 180* (reported as *M. cinereum*)[e]; Zapata Co.: 17 mi NE of Zapata, *Thompson 176* (reported as *M. cinereum*).[e]

M. cinereum DC. var. nov. **n = 10**. MEXICO. Coahuila: near Nueva Rosita, *Stuessy 902a;* 21 mi S of Monclova, *Stuessy 912;* Nuevo León: 15 mi N of Sabinas Hidalgo, *Stuessy 854;* 26 mi N of Sabinas Hidalgo, *Stuessy 855a;* 38 mi N of Sabinas Hidalgo, *Stuessy 856a*.

M. cinereum DC. var. *ramosissimum* (DC.) A. Gray. **n = 10**. MEXICO. Tamaulipas: San Fernando, *Stuessy 450, 541;* Reynosa, *Stuessy 778, 779;* 27 mi S of Reynosa, *Stuessy 787*.

M. cupulatum A. Gray. MEXICO. Sinaloa: near Culiacán, *Flyr 112* (reported as *M. rosei*)[g].

M. dicoelocarpum Rob. **n = 12**. MEXICO. Michoacán: 25 mi S of Ario de

Rosales, *Stuessy 693* (fig. 4).

M. dicoelocarpum Rob. **n = 23**. MEXICO. Michoacán: near Cotija, *King & Soderstrom 4646* (reported as *M. microcephalum*)[e]; 15 mi S of jct & rtes 15 & rd to Cotija, *Stuessy 715, 716* (fig. 5).

M. diffusum Cass. **n = 10**. MEXICO. Guerrero: 26 mi S of Acapulco, *Powell 758*[e]; Acapulco, *Stuessy 366*.

M. divaricatum (Rich. in Pers.) DC. **n = 10**. Plants obtained from bot. gard. Göteborg[a].

M. divaricatum (Rich. in Pers.) DC. **n = 12**. EL SALVADOR. Santa Ana: near Santa Ana, *Stuessy 609*. GUATEMALA. Alta Verapaz: 28 mi E of San Miguel Uspantán, *Stuessy 588; Jutiapa:* 25 mi E of Cuilapa, *Stuessy 605*. MEXICO. Campeche: Champotón, *Stuessy 532;* Chiapas: Tapachula, *Stuessy 626;* Morelos: 6 mi NW of Cuautla, *Stuessy 351;* 10 mi S of Cuernavaca, *Stuessy 358, 359;* Oaxaca: Huajuapan de León, *Stuessy 341;* Zimatlán, *Stuessy 655;* Tabasco: near Villa Hermosa, *Stuessy 547;* Vera Cruz: 23.2 mi SE of Alvarado, *Stuessy 319;* 12 mi S of Tantoyuca, *Stuessy 473* (& 2–3 frag.), *474;* 23 mi S of Tecolutla, *Stuessy 480;* Jalapa, *Stuessy 486;* 34 mi NW of Tehuacán, *Stuessy 506;* Fortin, *Stuessy 507;* 20 mi S of Alvarado, *Stuessy 520* (& 3–5 frag.); 49 mi SE of Catemaco, *Stuessy 526* (& 2 frag.); many Mexican states: 29 different population counts[e]. NICARAGUA. Granada: Granada, *Stuessy 620;* Managua: Managua, *Stuessy 616;* Matagalpa: Sebaco, *Stuessy 614, 615*.

M. sp. nov. **n = 25 ± 1**. COSTA RICA. Cartago: Turrialba, *King 5348* (reported as *M.* cf. *flaccidum*)[f].

M. glabrum Wats. **n = 11**. MEXICO. Jalisco: near La Barca, *Stuessy 707, 708* (fig. 1); Michoacán: 9 mi S of jct rte 15 & rd to Cotija, *Stuessy 714*.

M. gracile Less. **n = 9**. MEXICO. Campeche: Champotón, *Stuessy 530, 531;* 16 mi N of Champotón, *Stuessy 533;* Chiapas: 28 mi SE of Comitán, *King 3042* (reported as *M.* cf. *brachyglossum*)[g]; 17 mi S of Tuxtla Gutierrez, *King 3096* (reported as *M.* cf. *brachyglossum*)[e]; 32 mi SE of Comitán, *Stuessy 573;* Michoacán: near Jiquilpan, *King 3636* (reported as *M.* cf. *brachyglossum*)[g]; 3 mi NW of Zamora, *Stuessy 393;* 25 mi S of Ario de Rosales, *Stuessy 694;* Morelos: 7 mi NW of Cuautla, *Stuessy 354, 356;* San Luis Potosí: El Salto, *King 3887* (reported as *M. microcarpum*)[e]; Tamaulipas: 6 mi N of Antiguo Morelos, *Stuessy 454, 455;* 8 mi E of Antiguo Morelos, *Stuessy 458, 459;* 33 mi N of Ciudad Valles, *Stuessy 464;* 18 mi S of jct rtes 110 & 105, *Stuessy 466;* Yucatán: 13 km N of Mérida, *Stuessy 536, 537;* Vera Cruz: 13 mi W of Orizaba, *Graham & Johnston 4777*[d]; 13 mi W of Orizaba, *Johnston 4777* (reported as *M. microcarpum*)[e]; 7 mi SW of Morelos, *Powell 646* (reported as *M.* cf. *brachyglossum*)[e].

M. hispidum H. B. K. **n = 20**. MEXICO. Chihuahua: Cuauhtémoc, *Stuessy 1038* (fig. 2).

M. leucanthum Torr. & A. Gray var. *leucanthum*. **n = 10**. ARIZONA. Coconino Co.: near Sedona, *Turner 5738*[m]; Gila Co.: 16 mi NW of Globe, *Turner 5736;* Pima Co.: near Greaterville, *Turner 5735*[m]. COLORADO. Fremont Co.: near Portland, *Irving 823–1, 823–2, 823–3;* near Canon City, *Turner 5638;* Prowers Co.: 31 mi S of Lamar, *Irving 825*. MEXICO Chihuahua: 59 mi N of Villa Ahumada, *Stuessy 1122*. NEW MEXICO. Bernalillo Co.: *Jackson 2082* (reported as *M. leucanthum*)[b]; DeBaca Co.: 6 mi E of Yeso, *Turner 5673*[m]; Dona Ana Co.: Organ Mts, San Augustin Pass, *Turner 5748;* Eddy Co.: near Whites City, *Turner 5653;* Hidalgo Co.: 7 mi S of Road Forks, *Turner 5719;* Santa Fe Co.: 22 mi SW of Santa Fe, *Turner 5676*[m]; Torrance Co.: 3 mi NE of Duran, *Raven 19130*[k]. OKLAHOMA. Cimarron Co.: 6.8 mi N of Cimarron River on rte 287, *Irving 824-A, 824-B*. TEXAS. Blanco Co.: near Johnson City, *Thompson & Graham 17* (reported as *M. leucanthum*)[e]; Brewster Co.: Marathon, *Stuessy 230, 231;* near Brewster-Pecos Co. line on rte 90, *Stuessy 235* (ca **10**); Culberson Co.: 6 mi S of Van Horn, *Turner 4738*[m]; El Paso Co.: 28 mi SE of El Paso, *Stuessy 1126;* Loving

Co.: Mentone, *Stuessy 182;* Oldham Co.: 16 mi N of Vega, *Turner 5632, 5632b;* Presidio Co.: near Marfa, *Stuessy 201, 202, 203, 204 (& frag.), 206, 207* (ca **10**), *213;* Redford, *Stuessy 227, 228;* Travis Co.: near Austin, *Thompson & Graham 87* (reported as *M. leucanthum*)[e]; Mt. Bonnell, Austin, *Stuessy 138;* Winkler Co.: 1 mi N into Winkler Co. on rte 18, *Stuessy 152, 153, 154;* Kermit, *Stuessy 167, 168, 169.*

M. leucanthum Torr. & Gray var. *leucanthum.* **n = 20**. TEXAS. Blanco Co.: 10 mi N of Johnson City, *Thompson & Graham 18* (reported as *M. leucanthum*)[e]; Hays Co.: Dripping Springs, *Thompson & Graham 16* (reported as *M. leucanthum*)[e]; Travis Co.: near Austin, *Thompson & Graham 15* (reported as *M. leucanthum*)[e]; near jct Balcones Rd & 2222, *Stuessy 418;* Mansfield Dam, *Stuessy 420* (ca **20**) ; 7 mi SW of Zilker Pk, Austin, *Stuessy 752* (**2n = 40**). *755-3, 755-4.*

M. linearilobum DC. **n = 10**. EL SALVADOR. San Salvador: 24 mi E of turnoff to San Vicente, *Stuessy 612, 613.* GUATEMALA. Jutiapa: 8 mi NE of Jutiapa, *Stuessy 606, 607.* MEXICO. Michoacán: Apatzingán, *Stuessy 697;* Oaxaca: 40 mi W of Tehuantepec, *King 2891*[e]; 11 mi E of Zanatepec, *King 3449*[e]; 37 mi W of Tehuantepec, *King 3454*[e]. NICARAGUA. Granada: Granada, *Stuessy 618, 619.*

M. longifolium Cerv. ex Cav. **n = 9**. MEXICO. Oaxaca: Las Sedas, *Stuessy 659*; San Luis Potosí: 22 mi E of San Luis Potosí, *Powell 551*[g]. Plants obtained from bot. gard. Copenhagen[a].

M. longipes (A. Gray) Rob. **n = 10**. MEXICO. Jalisco: Tequila, *King 3662*[e]; Tequila, *Stuessy 396, 737, 738.*

M. longipilum Rob. **n = 10**. MEXICO. Guerrero: 19 mi N of Chilpancingo, *Stuessy 373* (figs. 6, 7), *374;* Oaxaca: 13 mi NW of Tehuantepec, *Stuessy 328, 329*; 3.8 mi NW of Huajuapan de León, *Stuessy 343*; 10 mi NW of Tehuantepec, *Stuessy 633, 634* (**n = 10** & **2n = 20**, fig. 8) ; near Huajuapan de León, *Stuessy 666*; Puebla: Tehuitzingo, *Stuessy 667.*

M. longipilum Rob. **n = 11**. MEXICO. Oaxaca: 64 mi SE of Oaxaca, *King 3461* (reported as *M.* sp. nov.)[e].

M. microcephalum Less. **n = 9**. GUATEMALA. Huehuetenango: 6 mi S of Huehuetenango, *King 3425* (reported as *M. oblongifolium*)[e]. MEXICO. Chiapas: 10 mi SE of Tonalá, *Stuessy 627, 628;* Michoacán: near Ciudad Hidalgo, *King 3607*[e] (reported as *M. oblongifolium*)[e]; 6 mi NW of Tuxpan, *Stuessy 383, 384;* near Ciudad Hidalgo, *Stuessy 680, 681;* Oaxaca: Monte Albán, *Stuessy 638.*

M. montanum Benth. var. *montanum.* **n = 11**. MEXICO. Oaxaca: 10 mi N of jct rtes 190 & 175, *King 3492* (ca **11**; reported as *M.* cf. *montanum*)[e].

M. montanum Benth. var. nov. **n = 11**. GUATEMALA. Huehuetenango: between Chemal & San Juan Ixcoy, *Beaman 3043* (reported as *M. montanum*)[c]. MEXICO. Chiapas: 17 mi W of San Cristóbal de Las Casas, *King 2796* (reported as *M. montanum*)[e]; 5 mi E of San Cristóbal de Las Casas, *King 2801* (reported as *M. montanum*)[e]; Teopisca, *King 2843* (reported as *M. montanum*)[e]; 34 mi S of Ishuatán, *Stuessy 559, 560;* 20 mi W of San Cristóbal de Las Casas, *Stuessy 566.*

M. paniculatum Gardn. **n = 18**. GUATEMALA. Alta Verapaz: near San Pedro Carchá, *King 3329* (reported as *M. mimulifolium*)[e]; San Pedro Carchá, *Stuessy 594;* Huehuetenango: near Huehuetenango, *King 3417* (reported as *M. dicoelocarpum*)[e]; Huehuetenango, *Stuessy 578;* 12 mi E of Huehuetenango, *Stuessy 582;* Sololá: near Panajachel, *King 3242* (reported as *M.* cf. *mimulifolium*)[e].

M. perfoliatum (Cav.) H. B. K. **n = 10**. Plants obtained from bot. gard. Göteborg[a].

M. perfoliatum (Cav.) H. B. K. **n = 11**. COSTA RICA. Cartago: Turrialba, *King 5350*[f]; near Cartago, *King 5407*[f]. *GUATEMALA.* Guatemala: Guatemala, *King 3248* (reported as *M.* cf. *perfoliatum*)[e]; Huehuetenango: Huehuetenango, *King 3410* (reported as *M.* cf. *perfoliatum*)[e]; Huehuetenango, *Stuessy 576.* MEXICO. Michoacán: 45 mi W of Morelia, *King 3635* (reported as *M.* cf. *perfoliatum*)[e]; 8 km S of Uruapán, *King & Soderstrom 4707*[f]*;* Ciudad Hidalgo, *Powell & Edmondson 816* (reported as *M.* cf. *perfoliatum*)[e]; Zitacuaro, *Stuessy 379* (fig. 9), *380;* Oaxaca: Zimatlán, *Stuessy 654.*

M. perfoliatum (Cav.) H. B. K. **n** = **12**. MEXICO. Michoacán: 11 mi W of Michoacán-Mexico state border, rte 15, *King 3600*[e]; Puebla: near Puebla, *King 3560*[f].

M. rosei Rob. **n** = **10**. MEXICO. Simaloa: Mazatlán, *Flyr 138*[g]; 13 mi N of Rosario, *King 3710*[e]; 21 mi N of Rosario, *King 3712*[e]; near Mazatlán, *King 3715*[e]; 10 mi NE of jct rtes 40 & 15, *King 3716*[n]; Isla Piedra, *Stuessy 747, 748;* near Mazatlán, *Stuessy 749, 750.*

M. sericeum Lag. **n** = **30**. MEXICO. Guerrero: Petaquillas, *Stuessy 364* (fig. 3); Michoacán: Zitacuaro, *Stuessy 377* (ca **30**); 7 mi S of Ario de Rosales, *Stuessy 690 (& frag.) 691;* Oaxaca: 53 mi S of Tehuacán, *Powell 660* (reported as *M. sericeum* var. *sericeum*)[e]; Las Sedas, *Stuessy 660* (ca **30**); Querétaro: 6 mi W of Querétaro, *Powell & Edmondson 579* (ca **30**, reported as *M. sericeum* var. *exappendiculatum*)[e]; near Querétaro, *Rock M-442* (reported as *M. sericeum* var. *exappendiculatum*)[e].

M. tenellum Hook. & Arn. **n** = **10**. MEXICO. Nayarit: 38 mi S of Sinaloa-Nayarit border, *King 3703* (reported as *M. cupulatum*)[e]; 28 mi S of Sinaloa-Nayarit border, *King 3704* (reported as *M. cupulatum*)[e]; ca 21 mi S of Sinaloa-Nayarit border, *King 3705*[n]; Sinaloa-Nayarit border, *King 3706* (reported as *M. cupulatum*)[e]; 27.9 mi SE of Nayarit-Sinaloa border, *Stuessy 401;* 10 mi NW of jct rte 15 & rd to Tuxpán, *Stuessy 744* (ca **10**), *745.*

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HAROLD ERNEST PARKS

Lee Bonar

Harold Ernest Parks was born at Albany, Oregon, August 5, 1880. Some of his early years were spent in Tacoma, Washington. Following the death of his father the family moved to California in 1890, living in various localities in the San Francisco Bay area while young Harold attended public school.

He became a member of the California National Guard in San Rafael, and his unit was mustered into federal service as part of "K" Company, First California U.S. Volunteer Division, April 27, 1898, and sailed on the transport, City of Pekin, May 28, 1898. "K" Company participated in the capture of Guam, June 1898, and arrived in the Philippines, June 30, 1898, taking part in the battles around Manila and the capture of the city, August 13, 1898. The company continued service in that area during the Philippine Insurrection and Parks was wounded in action, February 28, 1899. He served later that year on Negros Island and was discharged from the Army, September 21, 1899, at San Francisco.

He moved to Tacoma, and worked as a salesman for H. J. Henry and the National Biscuit Company from 1900 through 1910.

While in Tacoma he married Bessie A. Reynolds. Three sons were born to this marriage: Robert Wayne, Wendell King, and Laurance Dale. The family moved to Santa Cruz, California, where Parks worked as mill worker and salesman until 1914, when he went to San Jose, California, as a special clerk in the Post Office. Mr. and Mrs. Parks were divorced in 1924.

During these years in California Parks took a number of courses in language and business training from the International Correspondence School of Scranton, Pennsylvania. Also during this period he developed an interest in the study of plants, especially certain groups of fleshy fungi. He wrote letters of inquiry seeking advice from professional men and finally settled on a program of research in fungi with W. A. Setchell as advisor and authority to whom he submitted collections for identification. Parks soon developed an especial interest in the collection and study of the hypogeous fungi of his area.

During the period 1916 to 1921 he collected, traveling by bicycle, in the hill areas west of San Jose. All his free time was devoted to collecting, compiling notes, and sending out collections. A file shows 30 letters written him by Setchell during the calendar year 1918 giving answers to questions and identifications for specimens. Some letters gave up to 25 identifications.

With the encouragement of W. A. Murrill and Setchell, Parks wrote two papers on fungi during this time: Notes on California Fungi (Mycologia 9:10-21. 1919), and California Hypogeous Fungi—Tuberaceae (Mycologia 13:301-314. 1921).

He also wrote, with suggestions and advice from certain zoologists, a paper relating to the habits of the wood rats and their use of hypogeous fungi as food: The genus *Neotoma* in the Santa Cruz Mountains (J. Mammology 3:241-253. 1922).

Setchell once said that this man Parks bombarded him with so much work that he decided that he had better try to get him to come to Berkeley and work for the Botany Department. On August 23, 1921, Setchell offered Parks a position as helper and general handy man at a salary of $150 per month; Parks served as technical assistant from September 1, 1921 through June 30, 1922.

He was appointed Collector for the Department of Botany, University of California, July 1, 1922, and continued in this position until he resigned June 30, 1928. He was Associate Curator of the University of California Herbarium, without salary, July 1, 1928, to June 30, 1950, and held the title of Honorary Curator until his death.

His extensive general knowledge of field botany made Parks a very valuable employee of the department. His main duties were collecting class and research material for staff and graduate students. He also had charge of the departmental storeroom and was general handy man for the department. During this time he combined his interest in fungi and obtaining specimens of them with collecting class material.

Parks became known as an outstanding student and collector of hypogeous Gasteromycetes and contributed very extensive amounts of material to S. M. Zeller and C. W. Dodge for some twenty years, starting in 1918. His collections are repeatedly cited in their monographic studies published in the Annals of the Missouri Botanical Garden.

Parks had extensive experience in collecting during several summer trips to certain Pacific Islands. He went as assistant to W. A. Setchell on the University of California-Carnegie Institution Expedition to Tahiti, May 16-July 19, 1922. With W. A. Setchell, C. B. Setchell, J. E. Hofmeister, and J. M. Ostergard on an Expedition to the Tonga Islands under the auspices of the Bernice P. Bishop Museum, May 31-August 23, 1926. Parks spent most of his time in a botanical survey of Eua Island. During the summer of 1927 he made a collecting trip to Fiji as Research Associate of the Bishop Museum.

He was married to Susan Priscilla Thew in October 1927. They made a trip, on their own, May to July 1930, to Raratonga and the Cook Islands.

Parks made general collections on these expeditions but gave special care to the collection of fungi and distribution of specimens following the return of the expedition. He sent material to various specialists over the world and compiled publications on some of it. James R. Weir, C. L. Shear, and other members of the staff in charge of the Pathological Collections of the United States Department of Agriculture were most helpful with this work. Duplicates deposited in the University of Cali-

H.E. Parks At 77

fornia Herbarium have greatly enriched our collections. Published records on some of these collections are as follows: Lichenes a W. A. Setchell et H. E. Parks in insula Tahiti a 1922 collecti, by E. A. Vainio (Univ. Calif. Publ. Bot. 12:1-16. 1922); Report on a collection of ferns from Tahiti, by W. R. Maxon (Univ. Calif. Publ. Bot. 12:17-44. 1924); Tahitian mosses collected by W. A. Setchell and H. E. Parks, determined by V. F. Brotherus (Univ. Calif. Publ. Bot. 12:45-48. 1924); Tahitian fungi collected by W. A. Setchell and H. E. Parks, by H. E. Parks (Univ. Calif. Publ. Bot. 12:49-59. 1926); Tahitian algae collected by W. A. Setchell, C. B. Setchell, and H. E. Parks, by W. A. Setchell (Univ. Calif. Publ. Bot. 12:61-142. 1926); Tahitian spermatophytes collected by W. A. Setchell, C. B. Setchell, and H. E. Parks, by W. A. Setchell (Univ. Calif. Publ. Bot. 12:143-230, 1926); The Tonga expedition of 1926, by W. A. Setchell (Science 64:440-442. 1926); Ferns of Fiji, by E. B. Copeland (Bernice P. Bishop Mus. Bull. 59:1-106. 1929); Raratonga ferns, collected by Harold E. and Susan Thew Parks, and miscellaneous oriental pteridophytes, by E. B. Copeland (Univ. Calif. Publ. Bot. 12:395-381. 1931); and New Plants from Fiji—I, by J. W. Gillespie (Bernice P. Bishop Mus. Bull. 74:1-99. 1930).

During 1931 the Parkses became established in a home overlooking the Pacific at Trinidad, Humboldt Co., California. This was an area little known mycologically, and Parks continued his botanical work in this area for twenty-two years. He formed a close working relationship with another enthusiastic botanical student, Joseph P. Tracy (UC '03) of Eureka, California, and the two very often collected together to advantage, since Tracy was well-known for his studies on the higher plants of that region. Parks collected fungi generally, but his emphasis was on parasitic fungi and all sorts of micro-fungi. His series of collection numbers of California fungi reached approximately 9000; these were almost all sent to the University of California Herbarium. This material came with a goodly portion of it already identified, and was collected, when possible, in sufficient quantity to make distribution sets of 25-30 duplicates. The fact that Parks collected 696 of the first 1225 sets of Fungi of California distributed by the University of California Herbarium exemplifies the extent of his contributions.

Parks frequently received requests from specialists for collections of particular fungi in which they were interested and had correspondence with many mycologists. He collected *Discomycetes* for Edith K. Cash and *Thelephoraceae* for H. S. Jackson.

The following thirty of Parks' collections, including one new genus, were named in his honor; these represent widely different types of plants from different parts of the Pacific Basin: *Parksia libocedri* Cash, California; *Asplenium parksii* Copel., Raratonga; *Belonidium parksii* Cash, California; *Cyathea parksiae* Copel., Raratonga; *Cyrtandra parksii* Setch., Tahiti; *Dennstedtia parksii* Copel., Tongatabu; *Ectocarpus* *parksii* Setch. & Gardn., California; *Eryrotrichia parksii* Setch. & Gardn., California; *Freycinetia parksii* Mart., Fiji; *Fucus parksii* Setch. & Gardn., California; *Gautieria parksiana* Zell. & Dodge, California; *Hydnangium parksii* Zell. & Dodge, California; *Hymenogaster parksii* Zell. & Dodge, California; *Hypoxylon parksii* Lloyd, Tahiti; *Iridophycus parksii* Setch. & Gardn., California; *Languas parksii* Gill., Fiji; *Loxogramme parksii* Copel., Fiji; *Lycopodium parksii* Copel., Fiji; *Maesa parksii* Gill., Fiji; *Melanogaster parksii* Zell. & Dodge, California; *Oleandra parksii* Copel., Fiji; *Pandanus odoratissimus* L. var. *parksii* Mart., Tonga; *Peridermium parksianum* Faull, California; *Polypodium parksii* Copel., Fiji; *Poria parksii* Murr., California; *Puccinia parksiana* Cumm., Fiji; *Salix parksii* Ball, California; *Spireanthemum parksii* Gill., Fiji; *Strigula (Melanothele) parksii* Ras. ex Sbarb., Cook Islands; and *Aglaia parksii* A. C. Smith, Fiji.

The Parkses became well-known and active members of the community in the Trinidad and Eureka area and many visitors enjoyed the hospitality of their pleasant home. With advancing age and increasing health problems they disposed of their home in 1953 and spent the remainder of their time in traveling, living in guest hotels and health resorts. Parks died after protracted illness at Calistoga, California, March 5, 1967. His wife, Susan Thew Parks, followed him in death on January 29, 1968. They are buried at Visalia, California. The University of California Herbarium owes much to the numerous contributions of Harold Ernest Parks.

Department of Botany, University of California, Berkeley

NEW RECORDS OF MYXOMYCETES FROM CALIFORNIA IV.

Donald T. Kowalski and Dwayne H. Curtis

The new records of slime molds listed in our last paper (Kowalski and Curtis, 1968) brought the total number of Myxomycetes recorded in print for California to 190. Since then, seven new species and two new records have been reported from the state (Kowalski, 1968a; 1968b; 1969a; 1969b; 1970). Ten new records are reported in this paper. This brings the total number of slime molds found in California to 209 species. All collections cited here have been deposited in the Herbarium of the University of California at Berkeley. Unless otherwise stated, the numbers are those of the authors, labeled K and C respectively. With the exception of *Diderma umbilicatum* Pers., the names of the organisms are those accepted by Martin (1949). This investigation was supported by National Science Foundation Grant GB-5799.

Liceaceae

Licea parasitica (Zukal) Martin. Four collections, three on oak bark from Lower Bidwell Park, Chico, Butte Co., *K 2342,* Jan. 8, 1966, *K 9648,* Dec. 22, 1966, *K 9739,* March 13, 1967, and one on decayed wood, Sutter Buttes, 700 ft. elev., Sutter Co., *K 5739,* Feb. 18, 1967. All four collections were made accidentally, i.e., they were not found in the field. In each case, the substrate upon which *L. parasitica* was growing was originally collected because it had another, larger myxomycetous species upon it. The minute sporangia of *L. parasitica* were discovered later in the laboratory while the substrate was being scanned with a stereoscopic microscope. There are only two species in the genus *Licea* that are sessile and dehisce in a circumscissile manner by a preformed lid, namely, *L. parasitica* and *L. kleistobolus Martin.* The sporangia of both species are similar in shape and size, being subglobose to discoid and 0.05–0.2 mm in diameter. They differ, however, in color and texture. The sporangia of *L. parasitica* are dark brown or black and have a thick horny wall at maturity, while those of *L. kleistobolus* are bright coppery-brown and have a membranous wall. *Licea parasitica* has been found as far west as Iowa and Texas and is considered rare. This, however, may be due to its small size and it probably occurs throughout the United States.

Tubifera ferruginosa (Batsch) Gmel. Two collections, both on decayed wood, MacKerricher Beach State Park, Mendocino Co., *C 428,* Jan. 26, 1967 and *C 1138,* Jan. 25, 1968. Although the pseudoaethalia in these collections are smaller than normal, measuring less than 1.0 cm in diameter, their identity is easily established. There are four known species in the genus and *T. ferruginosa* is separated from the other three by the lack of a pseudocapillitium, the sessile fruiting bodies and by having spores 6–8 μ in diameter. This is a common taxon, being known throughout the United States.

CRIBRARIACEAE

Cribraria microcarpa (Schrad.) Pers. Two collections, one developing in a damp chamber from wood collected in Muir Woods, Marin Co., by Victor Duran on Feb. 8, 1965, and one on decayed wood, 3 miles west of Paul Dimmick State Park, Mendocino Co., *K 8164,* April 10, 1968. The lack of a distinct basal cup, stalks more than six times the diameter of the sporangia, and the small sporangial size, less than 0.3 mm in diameter, separate this taxon from other members of the genus. The sporangia in these collections are, in fact, much smaller. The majority are about 0.1 mm in diameter. This is a common species, known from many collections throughout the United States. It has probably been overlooked in California until now because of its minute size.

Cribraria minutissima Schw. On decayed wood, Juniper Lake, Lassen Volcanic National Park, 6,700 ft. elev., Lassen Co., *K 3874,* July 22, 1966. This is another tiny species, the sporangia being 0.1–0.2 mm in diameter. It can be distinguished from *C. microcarpa* by the presence of a distinct basal cup which is often constricted at the apex and by the shorter stalks. As mentioned above, in *C. microcarpa* the stalks are usually more than six times the diameter of the sporangia while in *C. minutissima* they are usually less than four times the diameter of the sporangia. This species is also widely distributed in the United States, but because of its small size, is not often collected.

ECHINOSTELIACEAE

Echinostelium minutum De Bary. Three collections, two on decayed wood, *K 5949,* Covered Bridge, Honeyrun Road, Butte Co., April 15, 1967, *K 7562,* 5 miles east of Mineral, 5,800 ft. elev., Tehama Co., May 15, 1966, and one on bark, Lower Bidwell Park, Chico, Butte Co., *K 9732,* Dec. 27, 1966. As was the case with the *Licea parasitica* collections mentioned above, these specimens were also found by accident in the laboratory while viewing the substrate under a stereoscopic microscope. Because of its small size, the sporangia being about 50 μ in diameter, most of the known collections of this species were made from moist chamber culture. Thus, these collections are valuable since they represent natural fruitings which are rarely made. Of the four known species in the genus, only *E. minutum* and *E. cribrarioides* Alex. have a capillitium. *Echinostelium minutum* can be separated from *E. cribrarioides* by the fact that it has a scanty capillitium with free, hooked ends and spores 7–8 μ in diameter, while *E. cribrarioides* has a well-developed capillitium which forms a complete net and spores 9–10 μ in diameter. Previously, the furthest known western locality of *E. minutum* in the United States was Texas. However, this taxon can probably be found in every state of the union, since any diligent damp chamber work will usually turn up this tiny species.

STEMONITACEAE

Stemonitis webberi Rex. Two collections, both on decayed wood, *K 1679,* Patrick's Point State Park, Humboldt Co., July 3, 1965, and *K 4381,* Lower Bidwell Park, Chico, Butte Co., Dec. 22, 1966. This taxon and *S. splendens* Rost. are very closely related. In general, the sporangial and spore characteristics are identical. The two taxa are separated on capillitial differences. The capillitium of *S. splendens* is purplish-brown and the meshes of the surface net are 20–50 μ in diameter. The capillitium of *S. webberi* has red metallic reflections and the meshes of the surface net are mainly 30–100 μ in diameter. As can be seen, these differences are slight and it is possible that both of these taxa simply represent different forms of the same species. *Stemonitis webberi* is known throughout the United States and its exclusion from the published reports from California may be due to some workers just considering it as a form of *S. splendens.*

Comatricha lurida Lister. On decaying leaves, Lower Bidwell Park, Chico, Butte Co., *C 578,* Feb. 16, 1967. The sporangia in this collection have a total height of 1.0–1.5 mm, a capillitium that arises mainly from the apex of the columella and coarsely warted spores 8–10 μ in diameter. These features all fit the published descriptions for this taxon. There is one characteristic, however, which is atypical, and that is, several of the sporangia have pieces of the peridium remaining attached to the ends of the capillitium. In one sporangium the peridium is almost completely persistent, being fugacious only at the apex. This unusual feature is not found in any of the published descriptions for this taxon. It is simply stated that the peridium is fugacious or evanescent. Because this species can have a partially persistent peridium, but, more importantly, since most of the capillitium arises from the apex of the columella, perhaps this species and *C. elegans* (Racib.) Lister, which is similar to *C. lurida,* should be transferred to *Lamproderma.* This is the genus in the Stemonitaceae which contains species that have persistent peridia and a capillitium radiating from the apex of the columella. We believe these species are more closely related to *Lamproderma arcyrionema Rost.* and *L. biasperosporum* Kowalski than to any other species of *Comatricha.* However, since we do not have adequate material of either species, we do not plan to make the transfers at this time. According to Martin (1949), *C. lurida* is a rare species. In the United States it has only been reported from Iowa and New York.

PHYSARACEAE

Physarum leucopus Link. Five collections, all from Lower Bidwell Park, Chico, Butte Co., *C 562,* Feb. 3, 1967, *K 4145,* Dec. 10, 1966, and *K 5227,* Feb. 4, 1967 on decaying bark and *C 128,* Dec. 7, 1966, and *K 2145,* Nov. 21, 1965 on decayed wood. The sporangia in these collections all have small patches of white lime on the peridium and stalks that are white and distinctly calcareous. In general, these collections fit the published descriptions perfectly. While throughout the United States this is not a particularly common species, it is extremely abundant in the Sacramento Valley. We have made numerous collections of this taxon, but for the sake of brevity, we only list five here.

Physarum luteolum Peck. Two collections, both made on decaying bark, 2 miles west of Child's Meadows, 4,400 ft. elev., Tehama Co., April 16, 1966, *K 2724* and *2748.* The sporangia in these collections are sessile, crowded, brilliant yellow in color and have a single-layered peridium. This species is not common. Except for a listing by Hagelstein (1944) from Colorado, this species is only known from lower elevations east of the Mississippi River. It is thus surprising that the only known California collections are from the mountains. Our work has shown that, with few exceptions, species of Myxomycetes found in the mountains are not found in the lowland areas and vice-versa. Perhaps the montane California collections represent a different ecotype from the eastern lowland collections. On a morphological basis, however, there is no question that they represent the same species.

DIDYMIACEAE

Diderma umbilicatum Pers. Five collections, three on decayed wood, Butte Creek and Skyway, Butte Co., *K 4469* and *4492,* Dec. 27, 1966, *K 5822,* March 18, 1967, one on decaying *Eucalyptus* bark, Point Reyes Ranger Station, Marin Co., *K 5148,* Jan. 29, 1967, and one on decayed leaves, Sutter Buttes, 700 ft. elev., Sutter Co., *K 7891,* March 2, 1968. This species is also very common in the lowland areas of California. We have found it approximately 40 times, but only list five specimens here to conserve space. The exact taxonomic standing of this taxon varies with different authors. Both Lister (1925) and Hagelstein (1944) treat it as a variety of *Diderma radiatum* (L.) Mrogan. Martin (1949) simply placed it in synonymy with *D. radiatum*. We believe, however, that the differences which it exhibits from *D. radiatum* are distinct and consistent enough to warrant its retention as a separate species. The major differences between the two species are as follows: In *D. radiatum* the sporangia are gray to, more commonly, brownish or red-brown, the stalks are ochraceous to reddish brown and the sporangial wall is distinctly cartilaginous and dehisces in a stellate fashion. In *D. umbilicatum* the sporangia are usually white but may be cream-colored, but are never brown or red, the stalks are white or cream-colored and the cartilaginous nature of the sporangial wall can only barely be observed and it never dehisces in a stellate manner. In fact, except for a few cracks in the wall at the apex of the sporangium, dehiscence must be by external breakage. *Diderma umbilicatum* is apparently a rare taxon.

Although Lister (1925) states that it has been found in many of the United States, we do not have knowledge of any collections other than our own.

Department of Biology, Chico State College, Chico, California.

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NOTES AND NEWS

Fasciation of Coastal Redwoods.—Fasciation involves a flattening of the normally cylindrical stem. A fasciated stem is usually much heavier than a normal shoot. The flattened growth is due to the formation of a row of linked meristems, instead of a single one at the apex. It occurs both on conifers and on hardwoods as well as on many other plants. Fasciation has not yet been reported on coastal redwood. Its cause is unknown, and according to my experience of seven years of redwood research I have seen only two cases of this curious phenomenon.

Fig. 1. Fasciation in *Sequoia sempervirens*.

Fasciation is sometimes only of annual duration, some of the terminal buds resume normal shoot growth again the following growing season, but it may continue for longer periods. Fasciation can be due to wound stimulation, possibly as a result of insect attack, or to overnutrition or a disbalance of growth hormones. There is no evidence to support this in the two cases observed in fasciation of coastal redwood. In some cases, it is considered to be genetically controlled by a mutation, which can be propagated vegetatively and which may come true from seed. However, the above two reported cases indicate that only one or two leaders developed such fasciation out of a young growth redwood tree. Another possibility may be to rank it as a pathological curiosity, probably caused by virus infection. It is very rare which is the reason to report it here. The photographs illustrate (fig. 1) this phenomenon on a young growth redwood tree collected January 5, 1966, by Robert J. Wright, Utility Tree Service, Inc., Eureka, California on the

Fickle Hill Road above Arcata, California. The specimen has not been preserved to my knowledge. It is known that the Utility Tree Service, Inc. crews have used herbicides in their program of brush control on power line right-of-ways.

The author is interested in receiving information about any extraordinary or abnormal growth features on coastal redwoods. Any such information should include details about the observed abnormality and should possibly be accompanied with the abnormal specimen itself or a photograph.—RUDOLF W. BECKING, School of Natural Resources, Humboldt State College, Arcata, California.

BACK ISSUES OF MADROÑO.—Back issues of most numbers of Madroño are still available. Some numbers are in short supply. Any surplus copies of any issue of Madroño will be gratefully received by the Corresponding Secretary, Department of Botany, University of California, Berkeley, California 94720.

REVIEWS

Marin Flora. Manual of the Flowering Plants and Ferns of Marin County, California. Second edition with supplement. By JOHN THOMAS HOWELL. University of California Press, Berkeley and Los Angeles, California, vii + 366 pp. 1970. $10.00.

Since 1949, when the first edition of this book appeared, the population of the ten counties making up the immediate San Francisco Bay Area has approximately tripled to its present level of about five million people. Within the next decade, if present trends continue, there will be about as many people in this single metropolitan area as there were in the entire world at the time of Christ. In view of this, it is extremely fortunate that more than a fifth of the 529 square miles of the lovely Marin County peninsula have been set aside for public enjoyment, the largest segment being the Point Reyes National Seashore of about 53,000 acres which was authorized in 1962. It is likewise fortunate that the University of California Press has added to their extensive publication list of local natural history guides a new version of this delightfully written and scientifically critical flora.

For the most part, the 1970 printing exactly duplicates that of 1949, but with several improvements. The quality of the paper and the binding have been improved greatly and the size of the pages increased slightly, making the type much easier to read. In addition, a 43-page supplement has been added, demonstrating that four genera and 26 species have been added to the indigenous flora of the County, together with 37 genera and 99 species of adventive plants. There are at present 1023 indigenous species and 408 introduced species recorded from the region. Among the attractive features of the original work that have been retained are the 25 black-and-white photographs of Charles H. Townsend, perhaps a third of which (those not on public lands) could not be duplicated today. The maps of localities in Marin County and of trails and localities on Mt. Tamalpais, being larger, are clearer than in the original. The price continues to be reasonable, and there is every reason to expect that *Marin Flora* will continue to enjoy as much popularity in the years to come as it has in the past.—PETER H. RAVEN, Department of Biological Sciences, Stanford University.

Nightshades, The Paradoxical Plants, by Charles B. Heiser, Jr., 200 pp. W. H. Freeman and Company, San Francisco. 1969. $5.95.

Charles Heiser has written an entertaining and informative book about those members of the Nightshade Family (Solonaceae) that have been important in human history. The orientation of the book is neither too technical for the layman nor too popular for the professional biologist.

The prologue, written in Heiser's very personal style, sets the tone for the entire volume. In it he briefly sketches the pertinent information about the taxonomy, morphology, and cytology of the Solonaceae. Although the organization of a few of the chapters suggests that there was some difficulty in integrating material from diverse sources, the accounts of the various species make for enjoyable reading. One chapter ("Some Like It Hot") discusses the uses and economic history of the chili pepper, *Capsicum,* while another chapter ("Love Apples") chronicles the tomato in European culture. Among the other nightshades discussed in the book are those of medicinal, horticultural, magical and narcotic value. The most interesting chapter, however, describes the controversy between Luther Burbank and *The Rural New Yorker* concerning Burbank's "Wonderberry." *The Rural New Yorker* claimed Burbank's creation was a fraud. They believed "Wonderberry" to be nothing more than the common nightshade *Solanum nigrum,* rather than a hybrid between *S. guineense* and *S. villosum.* Heiser's own investigation into the matter provides a satisfying conclusion to the chapter.

One would hope that more books in this vain and of this quality will soon appear. *Nightshades, The Paradoxical Plants,* will make an important addition to any botanical library.—Dennis R. Parnell, Department of Biological Science, California State College, Hayward.

Flowers of the Point Reyes National Seashore. By Roxana S. Ferris. xi + 119 pp., illustrated. University of California Press, Berkeley. 1970. $2.65, paper, $7.95 cloth.

The majority of books about the plants of different areas fall into one of two categories: 1, they are intensely technical and hence difficult for the interested amateur, or 2, they are too sketchy, too abbreviated and hence satisfy no one, neither the amateur nor the professional. This very nice book about the plants of the Point Reyes National Seashore in Marin County, California, strikes a good balance between the two extremes. The text is accurate, interesting to read, and is accompanied by nearly 200 line drawings by Jeanne R. Janish. Keys are not used, but the plants are grouped by flower color. The introductory material contains a map of the Point Reyes area, some 53,000 acres, and a description of the plant associations found within the Seashore. An index of both botanical and popular names is included as well as a bibliography.

We should have many more books like this for different areas so that the public can gain a better understanding of the world around us.—John H. Thomas, Department of Biological Sciences, Stanford University.

A WEST AMERICAN JOURNAL OF BOTANY

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

Abbreviations of botanical journals should follow those in *Botanico-Periodicum-Huntianum* (Hunt Botanical Library, Carnegie-Mellon University, Pittsburgh, Pennsylvania, 1968).

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I certify that the statements made by me above are correct and complete.

JOHN H. THOMAS, Editor

Nov. 1, 1970.

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AN ECOLOGICAL CONTRIBUTION TO THE TAXONOMY OF ARTEMISIA

A. A. Beetle

Beetle (1960) recognized three species of *Artemisia (A. arbuscula, A. nova,* and *A. longiloba)* as distinct because they were "distinguishable on the basis of morphology, distribution, and ecology in addition to being reasonably disjunct." Holmgren and Reveal (1966) in a checklist recognized only one species, *Artemisia arbuscula.* This they divided into ssp. *arbuscula* (with *A. longiloba* as a synonym) and ssp. *nova* implying that these taxa are not as distinct as maintained by Beetle.

In recent years the woody species of *Artemisia* have been studied intensively both in the field and in the herbarium. Most of the field work has resulted from the emergence of a new field of science, range management. Woody species of sagebrush are unproductive in terms of domestic animal carrying capacity, and because various taxa respond differently to chemical spraying, to protection, to burning, to various degrees of ungulate grazing and to mechanical treatments they have received much attention.

Range managers have been able to describe differences in phenology, and in edaphic distributions. This remarkably productive area of field observation, carried out in at least five different states and by independent workers representing different institutions and using varying research techniques, has resulted in a western concensus about the number of species and the degree of subspecific variation.

Passey and Hugie (1962) recognized *A. arbuscula* (low sagebrush), *A. nova* (black sagebrush) and *A. longiloba* (alkali sagebrush) as species. They described the different soils on which each occurs "on the foothills and plains of the Great Basin."

Robertson, et al. (1966) found that "in North Park, Colorado, the alkali sagebrush *(A. longiloba)* plant community stands out in sharp contrast from adjacent sagebrush range." In a similar study of sites in Wyoming, Thatcher (1959) found *A. nova* equally distinct on its own site. In Nevada Zamora (1968) found *A. arbuscula, A. longiloba* and *A. nova* distinct.

In Oregon, Gates (1964) recognized leaf defoliating moths as occurring on both *A. nova* and *A. arbuscula.*

Young, et al. (1963) studied chemically the three species in question as they occurred in Wyoming and recognized all three as distinct. A similar study in Nevada (Holbo and Mozingo, 1965) achieved similar results. More recently, in Idaho, Winward and Tisdale (1969) have agreed with both Young and Holbo.

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There may be an explanation for the fact that floral lists usually disagree with the conclusions of field workers. Often field identification of sagebrush is definitive, but the same plant on a pressed specimen in the herbarium may be quite confusing. Field students are largely concerned with mapable units of vegetation and study pure stands. Collectors who contribute to herbaria are more likely to be concerned with variation. Variation is easy to find since all species hybridize when given the opportunity. These hybrids have a longer survival value in the herbarium than they do in the field. Herbarium material of the woody species of *Artemisia* does not reflect accurately the field situation. In the herbarium the percentage of sheets representing hybrid variants is much higher and relatively more significance is placed on them because of the taxonomic difficulty of pidgonholing such specimens.

While most of the species in this section of *Artemisia* are old, conservative, and derived from diploid populations (e.g., *A. nova* and *A. longiloba*), some of the entities (e.g., *A. arbuscula*) are synthetic. Unless these differences are understood the taxonomic treatment may fail to reflect the true situation.

Eventually the two groups (field ecologists and herbarium taxonomists) will find a common meeting ground but for the present, it may be expected that a difference in taxonomic treatment of the same group of plants will continue.

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C. LEO HITCHCOCK

A TRIBUTE FROM THE CALIFORNIA BOTANICAL SOCIETY

To friends, colleagues and students he is known simply as "Hitchy." This informal nickname epitomizes Dr. C. Leo Hitchcock the man, and conjures up warm memories for the many who have known him over the years. He who tries to classify Hitchy encounters a tough taxonomic problem. The attributes of the taxon run the gamut from thorough monographer of several genera of flowering plants, writer of floristics, and peerless teacher, to long-distance backpacker, keen horticulturalist, avid 'birder,' terrific bridge-player, and formidable touch-footballer.

C. Leo Hitchcock was born (April 23, 1902) and grew up in California and so came to know that flora intimately under the tutelage and companionship of such eminent California botanists as Philip Munz, Edmund Jaeger, and Marcus E. Jones, and as well as through his frequent field trips with fellow students David Keck, George Goodman and others. Hitchy's undergraduate training was at Pomona College where he stayed on to do a Master's thesis with Dr. Munz on *Clarkia* (then, *Godetia*). He allows that he was ultimately scooped years later by Harlan Lewis.

During the time Hitchy was in college he worked in the nearby oil fields. We suspect that his earthy camaraderie may have been nurtured by association there with fellow crewmen. From Pomona, Hitchy went on to Washington University and the Missouri Botanical Garden, to study with J. M. Greenman; Edgar Anderson's influence on Hitchcock must be acknowledged too. His Ph.D. thesis (1931) was on the solanaceous genus *Lycium;* he is still called on to arbitrate problems in the group.

Hitchy's long and colorful teaching career started at Pomona College (1931-32); he soon moved to the University of Montana where he taught general botany and taxonomy. We still encounter former students (many now in forestry and range management) who vividly remember the demanding pace (pedagogical and physical) that Hitchy set for them, yet always generously laced with fun and games. It was at Montana that he produced a field manual on grasses and grass-like plants which showed early in his career his dual skills—as a meticulous taxonomist and as a consummate artist-draftsman. The Montana epoch also saw the beginning of the unique Summer Field Courses which Hitchy continued to run when he came to Seattle in 1937. Beginning then in the Department of Botany at the University of Washington where he soon became chairman, the legend of the man continued to grow. The remarkable 'espirit' that has made the department such a friendly, livable habitat for botanists is surely traceable to the Hitch-

Dr. C. Leo Hitchcock

cock inoculum both while he was chairman and in more recent years when he returned to full-time teaching and research. For the many graduate students in taxonomy who began their professional careers with Hitchy, the frequent gay soirees hosted at their home by Evelyn and her man make memorable embellishments on the fabric of an educational experience with Hitchcock.

For "years and years and years," Hitchy has taught general botany to foresters, elementary taxonomy (local flora, a course open to and eagerly sought by all), as well as ornamental plants and advanced taxonomy. Not only have generations of young students benefited from the experience of the local flora course from Hitchy, but repeatedly through the years have adults in the continuing education program come to count on his evening and weekend offerings. And, of course, the famous Summer Field Trips continued for many years. Who could forget a typical day for the field party, camped out miles away from the nearest town? Up at 5:00 a.m. to the din of kitchen-pot cymbals and a hearty breakfast of Hitchcock pancakes or biscuits. Then with hardly a breather, off into the field they would go, students trying hard to keep up with the master who fired off binomial salvos and sundry anecdotal items about the plants in the area. All the while, his assistants were 'making hay,' putting up herbarium material in substantial replicate for the UW Herbarium and for exchange. To finish the day in camp, some violent sport, like touch football took over with Hitchy sparking the play. The years that *Draba* was being monographed, each Summer Field Class literally ran up and down most of the high peaks in the West.

During the war years when there was little demand for classes in taxonomy, Hitchy and his close friend and field companion, Clarence V. Muhlick used their rationed gas to put up thousands of plants from the most inaccessible places throughout the Pacific Northwest. These collections have formed the solid nucleus for floristic study of the region. Nearly every major herbarium in the U. S. and elsewhere surely have "Hitchcock and Muhlick" sheets—always skillfully prepared (including pressed mosquitos) and amply documented.

In the early 1950's, Hitchcock joined his taxonomic talents with those of Arthur Cronquist, Marion Ownbey, and J. W. Thompson to begin the projected five-volume illustrated flora of the Pacific Northwest. One by one the volumes have appeared, beginning with Volume 5 (the Compositae by Cronquist), and culminating in 1969 with Volume 1. Modesty would get in the way of Hitchy's accounts of his contribution to this monumental work, but we all well know that he has been the chief and most persistent organizer-catalyst-editor-caretaker of the project as well as author of many substantial families in the flora. The botanical public will be pleased to know that a one-volume abridgement is nearing completion; Hitchy, again in collaboration with Cronquist, has devoted his energies to all phases of this long-awaited condensation.

So we salute you, C. Leo Hitchcock. We wish you many more years of productive taxonomic output, and hope the years ahead also give you ample time for gardening, for responding to the seasonal call of the game birds, and for the perpetual rejuvenation that you may deservedly derive from continued contact with your many, many friends—students, fellow botanists, neighbors, and all others who have drawn from your well of friendship. — A. R. K.

IRIS PSEUDACORUS IN WESTERN NORTH AMERICA

Peter H. Raven and John H. Thomas

Iris pseudacorus L. has been well established in swamps and other wet habitats in eastern North America for nearly a century (Cody, 1961). In western North America this showy, yellow-flowered *Iris* is of more recent introduction, and as in the east seems destined to spread even farther.

Preece (1964) has reported it from several localities in western Montana and it has since become increasingly more common in glacial potholes, along ditches, and marshy areas in the Mission Valley in Lake Co. (*Thomas 11020,* DS, US; *Woodland 319,* DS). In British Columbia it is known from Lulu I., near Vancouver (*Beamish* & *Vrugtman 60540,* OSC). In Oregon it has been found in Columbia Co. (*Wolrod* s. n., OSC) and in Benton Co. (*Merkle* & *Merkle* s. n., OSC).

Hitchcock, et al. (1969), in summary, recorded this species in this Pacific Northwest as "well established in our area in many lakes and ponds and along rocky stream banks."

In California the first record was probably that of Mason (1957), who reported *I. pseudacorus* from Merced Co. Subsequently Rubtzoff (1959) recorded it from Forestville, Sonoma Co. (*Rubtzoff 1836,* CAS, RSA; *1258,* CAS; *1813,* CAS; *1549,* CAS; *1946,* CAS). Other California localities are: Searsville, San Mateo Co. (Rubtzoff, 1959; Thomas, 1961) (*Thomas 7165,* CAS, DS; *9221,* DS); Mettlers Station, Kern Co. (Munz, 1969; Twisselmann, 1963; 1967) (*Twisselmann 8028,* CAS); near Yountville, Napa Co. (*Thomas 15027,* DS); Santa Cruz, Santa Cruz Co. (Rubtzoff, 1959; Thomas, 1961) (*Hesse 2764,* DS) near Montague, Siskiyou Co. (Rubtzoff, 1959) (*Howell 28360,* CAS); and Lyons Springs, Ventura Co. (Rubtzoff, 1959) (*Pollard* s. n., CAS).

Mason (1959) remarked that *I. pseudacorus* "is apparently moving down the watercourses." This prediction has been fulfilled. T. C. Fuller, of the California Department of Agriculture, has told us that there are dense colonies of this species all along the Merced River in Merced Co. Along Dana Slough west of Snelling, Fuller noted that this *Iris* was the most common species of marsh plants, growing to the complete exclusion of *Typha* and other characteristic California marsh plants.

In the Delta Region, *I. pseudacorus* still grows as relatively small isolated clumps and local populations. During April 27–28, 1969, one of us (PHR) observed it at the following points near and just east of the Franks Tract in the delta of the San Joaquin River, Contra Costa Co.: Sand Mound Slough, about 1.3 miles southwest of Franks Tract; Rock Slough, about 1.2 miles east of junction with Sand Mound Slough; southwest corner of Quimby I.; and two clumps about 0.4 miles apart at the southeast end of Mandeville I. It is probably much more widely distributed in the Delta Region than these sight observations would indicate.

It seems worthwhile to record these occurrences as there is every indication that this *Iris* will spread and displace many native plants. It is, of course, regrettable to see the populations of native species declining in the face of this new alien, which apparently spread from moist gardens, but one can at least be grateful that they are losing ground to such an attractive plant.

Kenton L. Chambers, Reid V. Moran, and Robert R. Thorne have kindly supplied information about specimens of *I. pseudacorus*.

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NOTES AND NEWS

MADROÑO.—Please send all manuscripts intended for publication in Madroño to Dr. Robert Ornduff, Department of Botany, University of California, Berkeley, California 94720.

The titlepage and index for Volume 20 of Madroño will be mailed with an early number of Volume 21.

Numbers 1, 2, and 3 of Volume 21, will appear very shortly and publication will then be on schedule.

A NEW SPECIES OF PROBOSCIDEA (MARTYNIACEAE) FROM BAJA CALIFORNIA, MEXICO

Richard H. Hevly

Annetta Carter recently asked me to annotate some specimens of *Proboscidea* which she had collected in Baja California. Besides *P. altheifolia* (Benth.) Decne., a yellow-flowered, tuberous-rooted perennial, these included a purple-flowered annual superficially resembling *P. parviflora* (Woot.) Woot. & Standl. Careful study, including comparison with the type specimens of all described species of the genus, convinced me that the latter specimens represent a new species endemic to the Sierra de la Giganta of Baja California. This new species is described below and compared with the other annual species from the Sonoran Desert (fig. 1).

Proboscidea gracillima Hevly, sp. nov. Herba annua, glandulosa ad viscido-pubescens, ramosissma, ad circa 3 dm lata et 4.5 dm alta; folia opposita vel alterna, ovata vel deltoida, basibus cordatis, marginibus integeris vel inaequaliter dentatis, petiolis 5–10 cm longis; racemi terminales, 3–5—floribus, pedicellis per anthesin tenuissimis, circa 2.5–3.5 cm longis, sed maturitate crescentibus ad circa 4 cm longitudine; calyx 0.9–1.4 cm longus, 5—lobatus, ad basim ventraliter fissus, basi bracteolis duabus, ovatis vel oblongis; corolla oblique infundibularis, 2.4–3.5 cm longa, limbo 5 lobato, 1.6-3.0 cm lato, luteo-violaceo; stamina fertilia 4, didynama, quinto rudimentario; stylus stamina superans; stigmata duo; fructus ovatus, circa 9 cm longus.

Viscid to glandular pubescent annual herb arising from a well-developed tap root with fibrous secondaries; stems 30–45 cm in height, the branches and leaves opposite or subopposite; petioles 5–10 cm long, glandular-pubescent on the nerves below; basal leaves 3.75–6.75 cm long and 3.25–6.50 cm wide, broadly ovate to deltoid, entire or with a very shallowly undulate (sinuate) margin; inflorescence racemose, 10–18 cm long, only one- or two-flowered at any one time but ultimately producing about 20 flowers, pedicels in anthesis erect to ascending, 2.5–3.5 cm long, 1 mm thick but becoming reflexed, thicker (2–3) mm, and longer (up to 4 cm) in fruit; bracts 2, broadly ovate, oblong or falcate, 4–5 mm long and 2–3 mm broad; calyx thin, papery 0.9 to 1.4 cm long and 1.0 cm broad, 5 lobed, the terminal lobe extended, the lateral lobes 3–5 mm wide, the intermediate and basal lobes 9 to 1.3 mm long, the sinus ½ to ⅓ the length of the calyx; corolla 2.4–3.5 cm long, strongly ventricose, (dorsal and ventral measurements differing by as much as 1 cm), the narrow portion of the tube 0.5–1.0 cm long, the flaring portion 1.5–2.5 cm long and 1.1 to 2.0 wide at the mouth, reddish purple

FIG. 1. Holotype of *P. gracillima*. A young specimen with immature fruit.

externally. Yellowish purple within, with conspicuous purple dots, a pronounced yellow band extending somewhat over the lower lobe, the limb 1.6–3.0 cm broad, reddish purple, the upper lobes maroon, the lobes 0.5–1.0 cm long and 0.7–1.2 cm broad; stamens 4, didynamous; ovary 1 celled with two parietal placentae, style exceeding the stamens, stigmas 2, ovate and sensitive; fruit an ovate to elliptical ligneous drupe 4–5 cm long with a prominent dorsal crest and horns 4–5 cm long; seeds numerous (fig. 1).

Table 1. A Comparison of P. gracillima, P. parviflora, and P. sinaloensis.

	P. gracillima	*P. parviflora*	*P. sinaloensis*
Geographic Distribution	Sierra de la Giganta, Baja California, Sur	Arizona, New Mexico, Trans-Pecos Texas and adjoining Mexico	Coastal plains of Sinaloa and S. Sonora, Mexico
Leaves	Generally less than 7 cm long and wide, entire	Generally more than 12 cm long and wide, shallowly lobed and frequently dentate	Generally more than 12 cm long and wide, with 3-5(-7) palmate lobes
Inflorescence	Surpassing the foliage	Equalling or surpassed by the foilage	Surpassing the foliage
Corolla Length	2.4 – 3.5 cm	2.0 – 4.0 cm	3.75 – 7.00 cm
Corolla Color	Reddish purple, upper lobes maroon	Reddish purple to pinkish lavender or rarely ivory; purple blotches may be present on upper lobes	Pinkish lavender, large maroon blotch may be present in upper lobes
Corolla Throat Ornamentation (internal)	Conspicuous reddish purple blotches extending the length of the tube and across the base of the tube, but not across the base of the dorsal lobes, not forming distinct rows	Conspicuous reddish purple blotches absent.	Conspicuous reddish purple blotches extending the length of tube and across the base of the tube but not across the base of the dorsal lobes, more or less forming two rows
Filaments	Glabrous or sparsely villous at and below their point of attachment; the arcuately curved portion glutinous and conspicuously glandular	Glandular at and below their point of attachment, the arcuately curved portion glabrous	Pilose-villous at, below, and occasionally above their point of attachment, the arcuately curved portion not noticeably glutinous and essentially eglandular

Type. Mexico: Baja California, Mesa del Potrero de San Javier (northeast of Mission San Javier), *Carter 4993* (MEX, UC-holotype), Sept. 20, 1965.

Other collections. Sierra de la Giganta, *Carter 3137* (UC), *Carter 4478* (UC), *Carter 5289* (UC). These and the type came from elevations between 500 and 700 m. North of Comondu, *Hammerly 179* (DS, UC).

Proboscidea gracillima belongs to section *Proboscidea* (=Sect. *Euproboscidea* Stapf) (Stapf, 1895), characterized by annual habit and purplish, reddish, pinkish, or whitish flowers. It is most similar to *P. parviflora* vegetatively and keys to that species in the most recent revision of the genus (Van Eseltine, 1929). In internal throat ornamentation and in infloresence, however, it shows some affinity to *P. sinaloensis* Van Eselt. All three species have small calyces and may be distinguished by leaf shape, infloresence characteristics, corolla size and color, and filament pubescence, as well as by geographical distribution (table 1).

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A NEW ASTRAGALUS (FABACEAE) FROM NEVADA

R. C. BARNEBY

Astragalus phoenix Barneby, sp. nov., in sect. *Argophyllis* juxta *A. newberryi* Gray a quo habitu multicipiti late pulviniformi nec simplicius caespitoso, pube crasse tomentoso-pilosa candidissima, racemisque brevissime pedunculatis 1—2 (nec 3—8)-floris absimilis inserenda.

Diu perennis subacaulescens e radice perpendiculari valida, caudicis iteratim ramosi ramulis superne stipulis petiolisque marcidis crebre obsitis columnaribus, demum pulvinos hemisphaericos vel depresse-convexos ad 4—5 dm usque latos efformantibus, tota pilis patulis rigidiusculis (minime gossypinis) ad 0.8—1.3 mm longis piloso-tomentosa cana; stipulae crebre imbricatae ovatae acutae vel breviter acuminatae 2—3 mm longae, extus tomentosae, intus glabrae venosae; foliorum 1.5—3.5(4) cm longorum petiolus rigidus marcescens, foliola 1—4-, saepissime 2 vel 3-juga ovata vel obovata (2)3—6(7) mm longa secus rachin 2—10(15) mm longum conferta, mox decidua; pedunculus utriusque ramuli unicus erectus brevissime 1—2-florus 2—5 mm longus stipulis fulcrantibus ad maximum duplo longiribus; calycis laxe pilosuli 12.5—

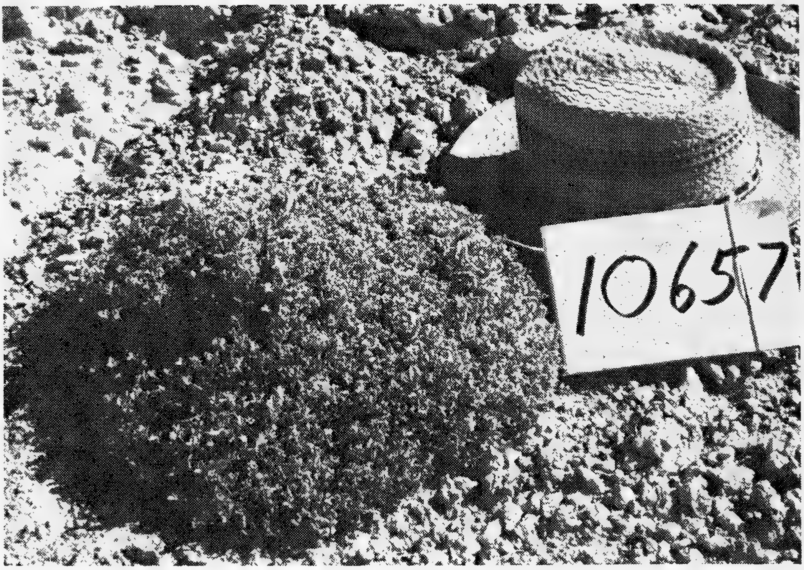

FIG. 1. A mature plant of *Astragalus phoenix,* which furnished the type specimen. The cushion of foliage is approximately 3.2 dm in diameter. Photograph by A. Cronquist.

15 mm longi tubus cylindricus subtumescens 9.5—11 mm longus, 4—4.6 mm diametro, dentes subulati 3—4 mm longi; petala pallide lilacina, vexillo pallidori, omnia sicca straminea, quoad formam illis *A. newberryi* simillima; vexillum 24—25 mm longum, 9.5—11 mm latum; alae ± 20.5 mm longae; carinae 19—21 mm longae unguiculi ± 11.5 mm, laminae lunatim semi-ellipticae 8—8.5 mm longae obtusae; antherae 0.7—0.8 mm longae; legumen eum *A. newberryi* exacte simulans, ovoideo-acuminatum ultra medium incurvum ± 1.8 cm longum, 1 cm diametro, valvulis coriaceis simul tomentulosis ac pilosis, pilis brevioribus densis longioribus patulis nitidis ad 2 mm usque longis; ovula ± 32.

Type. Nevada: Nye Co., on barren, alkaline, white clay slopes overlooking a dry wash at the east end of Ash Meadows, elevation 2300 feet, Township 18 S, Range 50 E, section 1 or 12, *Cronquist 10657* (BRY, NY-holotype, RSA, UTC), April 21, 1966.

Additional specimens. Nevada: Nye Co., with *Enceliopsis nudicaulis* and *Distichlis stricta,* on dry, hard, alkaline flats, Ash Meadows between Big Spring and Point of Rocks, elevation 2280 feet, *Roos & Roos 6143* (NY), June 13, 1954; Ash Meadows, *Purpus 6034* (POM). The three localities are probably all close together, possibly all the same, lying in the southern angle of Nye Co. close to the California boundary.

The Ash Meadows Milk-vetch, *A. phoenix,* was first collected, in fragmentary specimens, as long ago as the summer of 1898 by Carl

Anton Purpus, who crossed Pahrump Valley on his adventurous journey across the then pathless Mohave Desert into the botanically unknown mountains of southern Nevada. More complete material was gathered by Roos and Roos in 1954, but again too late in the year (mid-June) to show more than withered flowers and dehiscent pods. I have already referred to theses two collections (Barneby, 1964) as representing a species related to *A. newberryi* Gray but probably undescribed. The fine flowering specimens now before me, complemented by field-notes and the photograph reproduced herewith, confirm this conjecture.

Detached from the plant, the individual flower and pod of *A. phoenix* (born of ashes) cannot be distinguished from those of typical large-flowered *A. newberryi*. The average mature plant of the latter consists of some one to five, exceptionally a dozen scarcely elongating rosettes of leaves gathered into a tuft sessile or nearly so on the root-crown; if caudex-branches develop, they remain short, always shorter than the longest leaves, and are simple or little ramified. The pubescence of the foliage is variable in quality and orientation, but the young, newly expanded leaves are always silvery-silky with shining hairs. The flowers are only exceptionally less than three to the raceme and are elevated on a scapelike peduncle seldom less than 1 cm long. As the flowers fade the peduncle bends outward, and the pods ripen in contact with the ground. By contrast the mature plant of *A. phoenix* forms a dense hemisphere or depressed mound of foliage that reaches a diameter of 4—5 dm and is composed of several score, perhaps over 100 rosettes of leaves. The caudex is repeatedly branched, becoming several times longer than the longest leaf. Deep within the cushion, impacted with white clay, the older branches are brown and woody, clothed in a flaking bark, but distally become columnar from the thatch of tomentose stipules and stout persistent leaf-stalks. Already at early anthesis the pubescence is composed of relatively coarse, spreading hairs, the general effect of which is white-tomentose rather than silky. The flowers, pink-purple with a paler banner, followed by the pods, sit apparently stemless, one or two together, among the leaves. The permanently erect peduncle is at most 5 mm long and often scarcely surpasses the subtending stipules.

It seems probable that *A. phoenix* is derived by specialization from *A. newberryi*. The species is adapted and very likely confined to a peculiar habitat of calcareous flats and knolls on the valley floor, a habitat that provides a home for some other pulvinate species of the Nevadan deserts such as *Lepidium nanum* Wats., *Eriogonum shockleyi* Wats., as well as for some pulvinate ecotypes of ordinarily cespitose *Astragalus calycosus* Torr. ex Wats. and *Oxytropis oreophila* Gray. The elevation of Ash Meadows is near 2280 ft (685 m). In the mountains of the eastern Mohave Desert and the Death Valley region *A. newberryi* is not uncommon on limestone formations in the pinyon-belt, but has not been collected and cannot be expected below an elevation of about 5000 ft

(1500 m). Three other densely pubescent *Argophylli* occur near *A. phoenix*: *A. coccineus* Brandg., *A. funereus* Jones, and *A. purshii* var. *tinctus* Jones. The first of these has in common with *A. phoenix* persistent petioles and coarse pubescence, but has more numerous and longer red flowers elevated on long peduncles. The other two have finer, cottony pubescence, soft petioles, and three or more flowers borne together, again on developed scapes. The pod of the nearly sympatric *A. funerus* is much larger, 3—5 not 2 cm long; that of *A. purshii* var. *tinctus* is in the same size-range as that of *A. phoenix,* but the whole appearance of the plant is quite different.

New York Botanical Garden, New York

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NOTES ON LOEFLINGIA (CAROPHYLLACEAE)

R. C. Barneby and Ernest C. Twisselmann

Introduction

The small caryophyllaceous genus *Loeflingia* is of interest to plant geographers because of its bicentric dispersal. In the Old World its center of abundance coincides with the western end of the Mediterranean basin, with greatest concentration of variability and of numbers in the southern and eastern quarters of the Iberian Peninsula and in northern Morocco and Algeria. In Africa it extends south into the Sahara, but from the Mediterranean coast eastward from the longitude of Malta there are only a few scattered records of the common species, *L. hispanica* L. In the Old World, *Loeflingia* is clearly a west-Mediterranean type. The range of the genus in North America is less extensive but more discontinuous. Representatives occupy four well defined floristic provinces, one east and three west of the Continental Divide: 1, east-central Texas north, interruptedly, to western Nebraska; 2) floor of the Sonoran Desert in southern Arizona and northern Sonora; 3, the Basin and Range sagebrush deserts of northeastern California, southeastern Oregon, and southwestern Wyoming; and 4, cismontane California southward from Santa Cruz and Stanislaus counties into northern Baja California. Wherever they occur, the loeflingias are associated with light, often disturbed or wind-modified, commonly sandy soils, and show marked tolerance or even preference for genuine dune habitats. They appear intolerant of competition and tend to occupy microhabitats in which most plants have difficulty in taking foothold.

It was early suggested by Hooker (1840) and by Brandegee (1890) that *Loeflingia* might not be native to America, but this view is untenable. Variation in our plants is plainly correlated with familiar dispersal patterns, a situation that could not be expected of immigrant weeds. Furthermore the Old World loeflingias differ from ours in having at once smaller capsules, larger petals, and longer styles; and although the mode of branching is alike everywhere in basic design there are differences in ratio of the main internodes to length (and density) of the monochasial cymes beyond the initial dichotomies of the stem that give the North American and Mediterranean plants a subtly different aspect. However, as Hooker remarked (1840), when he described *L. texana,* the species are so similar in general organization that a case could be made for treating all as races of the original *L. hispanica.*

While the generic range of *Leoflingia* is probably now well worked out in broad outline (if not yet in fine detail), the taxonomy remains in a fluid state. Comparison of two recent accounts of the Old World species (Maire, 1963; Heywood, 1964) and of the modern floras covering the Intermountain United States and Sonoran Desert in America make this very clear. Our interest in the Mediterranean species is aroused by the similarity of the problems presented by *Leoflingia* in its two main areas of dispersal, but we lack the material to pursue it. The objectives of this study are to determine: a, the nature, and the relationship to *L. squarrosa* Nutt., of the long known but mysteriously local *L. pusilla* Curran, reported only from Kern Co., California; and b) the identity of the loeflingias found in the Sonoran Desert, and of similar plants encountered in widely scattered stations in the Intermountain region northward. Along the way we have been obliged to reexamine all the North American species.

History of Loeflingia in America

The *Loeflingia* first described from America was *L. squarrosa* (Torrey and Gray, 1838–1840), based on a plant collected by Nuttall near San Diego, California, in 1836. The genus had actually been discovered slightly earlier, in 1833 or 1834, by Drummond in Texas. Hooker (1840) described and figured Drummond's plant as *L. texana,* a proposition promptly reduced by Torrey and Gray (1838–1840) to *L. squarrosa.* Matters rested there until Mary K. Curran (Katharine Brandegee) (1885) described *L. pusilla* from plants collected the previous summer along the railroad west of Tehachapi. This was said to differ from *L. squarrosa* in being "much more delicate" and inferentially in its short, straight, entire sepals; it was further noted as pentandrous and apetalous. The only other described American species, *L. verna* Nelson, is *Arenaria pusilla* Wats. (*Loeflingia verna* Nelson, Bot. Gaz. (Crawfordsville) 54:138. 1912, "Secured by Macbride . . . near New Plymouth, [Idaho], April 24, 1911, no. 773.", DS!, RM!—hototype).

Systematic literature dealing with the genus in America is meager. It appeared in Gray's *Genera* (1849) where *L. texana* is illustrated under the name *L. squarrosa*. Robinson (1893) furnished a key to the three described species, distinguishing *L. pusilla* from the rest by its toothless outer sepals and separating *L. squarrosa* from *L. texana* by supposedly smaller stature, less secund branching, recurving sepals, and oblong-elliptic rather than obovate seeds. According to Robinson all *Loeflingia* in the New World should be triandrous, in contradiction to the protologues of *L. squarrosa* and *L. pusilla* and to Gray's account of the genus just mentioned. This point has long been in dispute. Brandegee (1890) had already remarked that the flower of *L. pusilla* was triandrous, although this is untrue of the one individual plant known to survive out of the type-collection. We now know of apparently constant pentandrous populations, of pentandrous individuals in largely triandrous populations, and of individual flowers varying in number of stamens on a single plant.

During the present century it has been customary to follow Robinson in maintaining *L. squarrosa* and *L. texana* as distinct species, but their ranges are so well separated that no occasion has arisen to compare them critically. With the few exceptions mentioned directly, *L. squarrosa* has been treated as endemic to cismontane Califorina or at least to the California floristic province. Peck (1941) extended the range of *L. squarrosa* to interior Oregon in Harney Co. Its presence in Arizona was confirmed by Kearney and Peebles (1942). However, Shreve and Wiggins (1964) subsequently referred the Arizona plant to *L. texana,* a species not recorded otherwise from west of the Divide. In floras that cover all of California, Jepson (1914), Abrams (1944), and Munz (1959) agree that *L. pusilla* is known only from Tehachapi, and all published accounts of this species, up to a recent report by Twisselmann (1967) from the western Mojave Desert in Kern Co., go back to the type collection, for which no exact match has ever been encountered. Before presenting our views on the taxonomy, we propose to discuss briefly the comparatively few phenotypic characters that have been used or promise to prove useful in delimiting taxa.

HABIT AND MODE OF BRANCHING

Branching in *Loeflingia* is of two types, one preceding the other: strictly dichotomous, when the primary axis divides into two branches of equal vigor, usually containing a sessile flower in the fork; and monochasial, as one branch of the dichotomy becomes reduced or obsolete at several successive nodes. Dichotomy may start directly from the axils of the cotyledons, or beyond several internodes of a simple axis, and distally gives way, either abruptly or gradually, to a more or less pronounced monochasial mode. When the distal monochasia are well developed, they form fan-shaped sprays; when poorly developed, each may be reduced to a single flower and the inflorescence comes to simulate a spike. The position of the first dichotomy and the relative size of the monochasia together determine the aspect of the plant, an aspect which is often characteristic of all members of a population and also tends to be dominant over large areas. We have developed no objective formula for describing the permutations of branching, but believe that the intangible quality of habit permits intuitive sorting of material into categories that coincide with comprehensible dispersal patterns. Stature of the individual plant is governed to some extent by variations in rainfall from year to year, as observed at several stations in Kern Co. On the other hand maximum or potential stature is to some degree genetically controlled, for none of the desert loeflingias, however favorable the season, seem ever to surpass three centimeters in height.

FLOWERS

The flowers of *Loeflingia,* at least in America, are cleistogamous. The five sepals, the two outermost of which are often leaflike in form and are perceived as sepals through their position and (occasionally) by being accompanied by an opposed stamen, connive over the ovary throughout anthesis. The three, four, or five filaments are closely contained between the sepals and the ovary and the filaments are exactly long enough to elevate the minute anthers to the level of the (in America subsessile) stigmas. Pollination is automatic, and ordinarily (disregarding some terminal buds which never reach maturity) is 100% effective, for it is rare indeed to find on any plant a single infertile flower. Obligate autogamy gives rise to internal homogeneous populations which, immune to the leveling effects of outcrossing, hand on intact an indefinitely reduplicated genetic structure. The resulting phenetic uniformity of populations has tended to elevate the apparent taxonomic value of minor characters and permits the elaborate but, we suspect, artificial heirarchy of subspecies and formae worked out by Maire (1963) for *L. hispanica* sens. lat. in North Africa. In America few such characters find uniform expression over any considerable land area, and there is only limited correlation between any pair of them. The reduced flower of *Leoflingia,* commonly apetalous in the American forms or with petals represented by vestigial and somewhat amorphous scales, presents few taxonomic features: length and curvature of sepals; presence of lateral teeth on 2 or more sepals; and stamen number.

Within populations as represented by herbarium specimens we have seen little variation in length of the outer sepals, which are, however, normally longer than the three inner ones. The variation between populations is marked. In cismontane California the longest sepal of *L. squarrosa* sens. str. varies from approximately 3 to 6 mm in length, that is from a trifle longer to twice as long as the capsule. The curvature of the sepal seems largely a function of its length, modified by age. Sepals nearly straight in bud become squarrose as the fruit ripens, but curvature occurs mainly in the part projecting beyond the capsule. It follows that the longer the sepal the greater the curvature. Length and curvature of the sepals seem to bear some relation to geographic dispersal but are poorly linked with other morphological characters and we believe that they have been overestimated as taxonomic criteria.

A filamentous or setiform tooth or spur arising on each side of at least the two outermost sepals is a generic character of *Loeflingia*. The tooth appears homologous with what is generally interpreted, in the cauline leaves, as the free tip of a partially adnate stipule. Rare individuals that lack all such appendages become technically indistinguishable from *Minuartia*. The sepal teeth vary considerably in length and stoutness, and the stipules vary with them, suggesting that they are under the control of the same gene or genes. In America the outer sepals are nearly always appendaged, the three inner ones very rarely so. Usually the toothed outer pair do not subtend a functional stamen and then, because they are not only longer than the three inner but also entirely leaflike in shape and texture, they simulate bracts enclosing a trimerous flower. Occasionally, however, the presence of an opposed stamen reveals the sepaloid nature of the outer pair. In those rare instances where the sepal teeth are obsolete, and the outer pair of sepals become obviously sepaloid and unleaflike, the flower becomes pentandrous. Thus the passage from true leaf into segment of the perianth is not marked by the usual discontinuity. We have learned to regard the presence of teeth on 2, 3, or 5 sepals and the occasional absence of teeth from all sepals as in the nature of individual variation, linked neither with geography nor with other characters. On the other hand the longer and stiffer setae on both leaves and sepals of the Texan loeflingias contribute materially toward the distinct facies of the populations east of the Continental Divide.

We have noted the correlation between a pentandrous flower and sepaloid sepals and between a triandrous flower and a pair of foliaceous, toothed exterior sepals. The latter combination is far the commoner everywhere in America, universal (so far as we have observed) east of the Divide. In cismontane California we find only sporadic instances of more than three stamens, and these sometimes occur on the same plant with triandrous flowers, for example, Los Angeles Co., Newhall, *Pringle,* NY; San Diego, *Orcutt,* NY; the condition described by Torrey and Gray for the original *L. squarrosa* though since denied. In the Intermountain region there are populations fully pentandrous (*Ripley & Barneby 7938,* CAS, NY), partly triandrous and partly pentandrous (Honey Lake, *Brandegee,* UC), and wholly, so far as sampled, triandrous, but no correlation with other phenetic characters has been discovered. Probably all loeflngias are primarily triandrous but retain a latent potentiality for return to what is presumably the primitive pentandrous condition.

CAPSULE AND SEED

West of the Sierra crest in California the capsule of *Loeflingia* is narrowly ovate to lanceolate in profile, with width-length ratio of approximately 1:3–4. All capsules of drought-inhibited individuals and late capsules of vigorous plants tend to be smaller than average but no wider proportionately. On the deserts and east of the Divide the capsule is ovate in profile, with width-length ratio of 1:2–2.5. In both areas some capsules lie inconveniently in the ratio of 1:2.5–3, but these are generally longer absolutely if from west of the Sierra, absolutely shorter if from the east. There is no abrupt discontinuity, but nevertheless we have found the capsule-outline more helpful than any other character in delimiting typical *L. squarrosa*. As shown below, it was crucial in our disposition of the litigious *L. pusilla*.

Robinson (1893) was the first to notice differences in size and outline of the seeds of *L. texana* and *L. squarrosa,* the former being shorter and plumper. Within a given capsule the seeds are virtually uniform in size, and within the population the difference, if any, is barely perceptible. Seeds of cismontane California *Loeflingia* are 0.4–0.5 mm, rarely up to 0.55 mm long; of *L. texana* 0.3–0.4 mm long. In the Sonoran Desert the seeds fall within the size-range of *L. texana;* in the Intermountain region within that of *L. squarrosa*. In conjunction, the capsule and seeds, as so often in Caryophyllaceae, furnish useful, even though not infallible taxonomic criteria.

CONCLUSIONS

When Robinson contrasted a Californian *L. squarrosa* characterized by long, recurved sepals and relatively long seeds with a Texan *L. texana* differing in its relatively straight sepals and short, plump seeds, he had for comparison no material at all from intervening territories and only a few specimens even from California. Plants collected since his day, especially on the deserts, have effectively blurred the supposed morphological discontinuity between the loeflingias of the Pacific and Atlantic slopes. The Arizona plants, which have been referred because of their recurving sepals to *L. squarrosa* and alternatively because of their small seeds to *L. texana,* are neatly intermediate in terms of Robinson's criteria. They lean somewhat to *L. texana* in their relatively stiff and long sepal teeth, but differ greatly in their diminutive stature and their habit of dense dichotomous branching which starts from the cotyledons or from the first node. This growth habit is equally alien to *L. squarrosa* and *L. texana,* but is nearly duplicated in the loeflingias found in the Intermountain region to the north. The latter, now known from five mutually remote areas of small extent, three in transmontane California, one in southeastern Oregon, and one in southwestern Wyoming, have characteristically short, straight sepals combined with the seeds of

L. squarrosa in the capsule of *L. texana.* Because of overlapping and recombination of the available criteria in these four geographic provinces we believe the American loeflingias are reasonably interpreted as a single species, *L. squarrosa,* composed of four subspecies.

KEY TO THE SUBSPECIES OF L. SQUARROSA NUTT. IN TORR. & GRAY

Capsule narrowly ovate to lanceolate in profile, (2.5)2.7–3.7 mm long, 0.8–1 mm in diameter, the width-length ratio mostly 1:3–4; stems usually 3–10 cm long, shorter only in depauperate individuals or in populations dwarfed by drought; primary stem axis usually simple through 2–3 internodes, the first flower borne at a point 5 mm or more distant from the cotyledons (this character fallible especially in drought inhibited plants); distal monochasia mostly 1-flowered; stipules and sepal teeth weak, short, filamentous, usually less than 1 mm long; sepals variable in length, the longest 3–6 mm long, slightly longer to twice as long as the capsule, when long becoming squarrose in age; cismontane California southward from Stanislaus and Santa Cruz counties to northern Baja California, and one locality on the western Mojave Desert in Kern Co., where sympatric but not intergrading with ssp. *artemisiarum*. . . . ssp. *squarrosa*

Capsule ovate in profile, (1.5)1.8–2.5(2.7) mm long, (0.7)0.8–1.2 mm in diameter, the width-length ratio mostly 1:2–2.7(3); east of the crests of the Sierra Nevada in California, to Wyoming, Nebraska, Texas, and Sonora.

  Diminutive plants, stems to 3 cm long, often less, mostly dichotomous from the cotyledons or from the first succeeding node, the first flower borne at a point only 1–4(5) mm distant from the cotyledons; monochasia distal to the dichotomies all reduced to one flower; seeds, sepals, and stipular setae various; Intermountain states and Sonoran Desert.

    Seeds 0.4–0.5 mm long; sepals always short, 1.8–4 mm long, not or little recurved at tip; stipular setae and sepal teeth weak, filamentous, less than 1 mm long (as in ssp. *squarrosa*); Intermountain United States, southwestern Wyoming to southeastern Oregon and northeastern California, and on the western Mojave Desert in Kern and Inyo counties, California . . . . ssp. *artemisiarum*

    Seeds 0.3–0.4 mm long; sepals mostly to 3.5–5 mm long, squarrose; stipular setae and sepal teeth intermediate in length and rigidity between those of ssp. *squarrosa* and ssp. *texana;* Sonoran Desert, from south central Arizona to northern Sonora. . . . . ssp. *cactorum*

  Taller plants, the stems, unless depauperate, 4–15 cm long, bearing the first flower at points at least 5 mm from the cotyledons, following several simple internodes; monochasia distal to the dichotomies more than 1-flowered, tending to form scorpioid cymes; seeds small, 0.3–0.4 cm long; stipular setae and sepal teeth stiff, subspinose, 1–1.5 mm long; east central Texas northward interruptedly to western Nebraska . . . . ssp. *texana*

LOEFLINGA SQUARROSA Nutt. in Torr. & Gray ssp. SQUARROSA, Fl. N. Amer. 1:174. 1838, "Sandy plains, St. Diego, California . . . *Nuttall.*", NY!—isotype. *L. pusilla* Curran, Bull. Calif. Acad. Sci. 1:152. 1885, "Tehachapi, Alt. 4,000 feet, May.", UC!—isotype labelled: "Bet. Tehachapi and Girard Station (now Marcel), along the railway, May, 1884. Pt of type, K.B." The holotype collected in 1884 by M. K. Curran was not found at CAS and was probably destroyed.

Thin sandy and gravelly soils, mostly below 2000 ft, sometimes in dry stream-beds, in abandoned fields, waysides, and dunes, South Coast

Ranges of California inland from the ocean from Santa Cruz to Santa Barbara Co.; margins of San Joaquin Valley and Sierra foothills from Stanislaus to Kern Co., there ascending through the Digger Pine belt to about 3900 ft; thence south through coastal and interior southern California to San Bernardino Valley and western San Diego Co.; and reportedly (Brandegee, 1890) to lat N. 28° in Baja California; and in Kern Co. at 2450 ft on stabilized dunes around Buckhorn Dry Lake in the western Mojave Desert, there sympatric with ssp. *artemisiarum.*

Representative specimens. California: *Hoover 5130,* NY, UC; *Keck & Stockwell 3354,* DS; *Twisselmann 2008, 2856, 8489, 13016,* all CAS; *Brandegee,* in 1909, CAS, DS, UC; *Howell 5814, 29243,* all CAS; *Howell & Barneby 29424,* CAS; *Parish 4158,* NY, UC; *Brandegee,* in 1898, NY, UC.

DISPOSITION OF L. PUSILLA

We have already noted that until 1967 all records in the literature of *L. pusilla* are based on the type collection, which to date has never been precisely matched. The holotype was presumably part of the California Academy collection lost in the San Francisco fire in 1906. A single individual that survived labelled as authentic by K. Brandegee (UC) and agrees perfectly with the protologue, up to the last detail of toothless sepals and pentandrous flowers. We surmise that this specimen and *T. S. Brandegee* s. n., 23 June 1892 (UC), from Honey Lake, California furnished the model for Abrams's Fig. 1718 (1944), of which the only fault is that the capsule is enlarged twice as much as that of *L. squarrosa* in Fig. 1717, thereby giving a false impression of the proportionate differences. Repeated search around Tehachapi has yielded nothing quite like *L. pusilla,* although ssp. *squarrosa* was collected as early as 1909 by Brandegee at Keene, close to the type locality. Because the type of *L. pusilla* was collected along the railroad we cannot discount the possibility that it was a waif: but if waif it was, its origin will remain obscure until it can be matched with some naturally occurring population. We can affirm, in any case, that *L. pusilla* is not an introduced form or race of *L. hispanica.* It can be accommodated without severe strain in our concept of *L. squarrosa* because, although it possesses a unique combination of characters, some of them uncommon in the species, it has no character unique to itself. The only outstanding question is whether to refer it to the cismontane or transmontane Californian subspecies of *L. squarrosa.*

The unique character combinations in *L. pusilla* are: a, small stature, to 5 cm; b, dichotomies and flowers starting only 2 mm from the cotyledons; c, distal monochasia more than 1-flowered; d, obsolete or vestigial stipule tips and sepal teeth; e, sepals all short, 3–3.5 mm; f, 5 stamens; g, slenderly ovoid capsule (± 3 X 1 mm), and h, relatively large seeds, between 0.5 and 0.55 mm. Of these characters a is easily matched in cismontane ssp. *squarrosa,* especially in dry years; the plant is not "much more delicate" than many modern collections from the Coast Ranges, but is taller than any known individual of ssp. *artemisiarum.* Characters c and g are normal for ssp. *squarrosa,* alien to ssp. *artemisiarum,* and g (slender capsule) is in our opinion one of the best diagnostic features of the former. Characters b, e, and f, are all known to occur in ssp. *squarrosa,* but only exceptionally, and elsewhere not together; only b and e are characteristic of ssp. *artemisiarum;* f is sporadic in both. Character h, common to ssp. *artemisiarum* and ssp. *squarrosa* serves only to exclude *L. pusilla* decisively from the more eastern races of the species (either of which *could* have been adventive at Tehachapi). Character d has been seen in only one other *Loeflingia,* Brandegee's collection of ssp. *artemisiarum* from Honey Lake. We have already suggested that loss of setae is an individual variation of no systematic importance. Thus we are led to believe that the type of *L. pusilla* was an unusual variant of ssp. *squarrosa* in which several rare features are combined. The plants cited as *L. pusilla* by Twisselmann (1967) from the western Mojave Desert in Kern Co. are now interpreted as *L. squarrosa* ssp. *artemisiarum.* The dunes around Buckhorn Lake are the only station in which two subspecies of *L. squarrosa* are known to grow together. Twisselmann (1967) has already observed that in this locality the two seem to have slightly different ecological preferences, the ssp. *artemisiarum* favoring the stiffer, more alkaline soils.

LOEFLINGIA SQUARROSA Nutt. in Torr. & Gray ssp. **artemisiarum** Barneby & Twisselmann, ssp. nov. Habitu pumilo ssp. *cactorum* simulans sed imprimis seminibus majusculis (0.4–0.5 mm longis) iis ssp. *squarrosae* aequimagnis sepalis sesmper abbreviatis rectis capsulam paullo superantibus absimilis, a ssp. *squarrosa* fere toto allopatrica praeertim statura semper minima atque capsula latius ovoidea breviori recedens.

Type. Oregon: Harney Co., sandy flats 3 miles south of Wright's Point, June 24, 1942, *Morton E. Peck 21370,* NY!, CAS!—holotype.

Dunes and sandy flats, often among sagebrush, mostly between 4000 and 7000 feet, northeastern California (Lassen and Plumas counties) and southeastern Oregon (Harney Co.), to be sought in northern Nevada; southwestern Wyoming (upper Green River Valley in Sweetwater Co.); also in Owens Valley in Inyo Co. and at approximately 2450 ft. around Buckhorn, Rogers, and Rosamond dry lakes on the western Mojave Desert in southeastern Kern and adjacent Los Angeles counties, California (there sometimes associated with ssp. *squarrosa*).

Specimens examined. Wyoming: Sweetwater Co., 26 miles east of Farson, *Ripley & Barneby 7938,* CAS, NY. Oregon: Harney Co., French Glen, *Peck 21419,* CAS; 8 miles north of Narrows, *Ripley & Barneby 6086,* CAS. California: Lassen Co., Honey Lake, *Brandegee,* UC; Plumas

Co., 5.8 miles east of Beckwourth, *Howell,* CAS; Inyo Co., near Bigpine, *Twisselmann 15537,* CAS, NY, RSA; Kern Co., Buckhorn Dry Lake, *Twisselmann 10777, 10838,* both CAS; between Old Pancho Barnes place and Buckhorn Dry Lake, *Twisselmann, McMillan, & Smith 14227,* CAS, NY; south end of Rogers Dry Lake, *Twisselmann 10714,* CAS; Los Angeles Co., 5 miles north of Lancaster, *Hoffmann,* SBM.

LOEFLINGIA SQUARROSA Nutt. in Torr. & Gray ssp. **cactorum** Barneby & Twisselmann, ssp. nov. Habitu deminuto, caulibus ex ipso basi simul dichotomis ac florigeris ssp. *artemisiarum* proxima sed sepalis elongatis demum recurvis et praesertim seminibus minoribus 0.3–0.4 mm longis iis ssp. *texanae* aequimagnis absimilis. A ssp. *squarrosa* necnon ssp. *texana* statura minima, habitu, monochasiis superioribus 1-floris, ulterius ab illa seminibus parvis recedens, ab omnibus affinibus deserto Sonorensi incola allopatrica.

Type. Arizona: Pima Co., Sabino Canyon, Santa Catalina Mountains, *J. J. Thornber 5340,* Mar. 26, 1905, CAS!, DS!, NY!—holotype.

Sandy and gravelly desert flats, sometimes in hard-packed soil of ridges and adobe flood plains, below 3300 ft; south central Arizona in Pima Co., and in Pinal and Maricopa counties according to Kearney and Peebles (1951); and in the districts of Altar, Magdalena, and Hermosillo in Sonora.

Specimens examined. Arizona: Pima Co., 16 miles north of Tucson, *Abrams 13100,* DS. Sonora: 15 miles north of Magdalena, *Fosberg 7468,* DS; 7 miles south of Sasabe, *Keck 3970,* DS; 10 km northeast of San Pedro, east of Hermosillo, *Ripley 14333,* CAS, NY; north of Cumerol, *Abrams 13170,* DS.

LOEFLINGIA SQUARROSA Nutt. in Torr. & Gray ssp. **texana** (Hook.) Barneby & Twisselmann, comb. nov. *L. texana* Hook., Icones plantarum 3: tab. 275. 1840, "Interior of Texas. Drummond (3d Coll. n. 464)", presumed isotype, *Drummond 464* (but "Coll. II"), NY!

Sandy soils below 2000 ft; east central Texas, the lower Colorado and Brazos valleys in Travis, Waller, and Colorado counties, and around Dallas and Fort Worth, Dallas and Tarrant counties; north central Oklahoma, the Cimarron Valley in Payne Co.; and greatly disjunct at about 3400 ft near the headwaters of the Niobrara River in Dawes Co., Nebraska.

Representative specimens. Texas: *Hall 480,* NY; *Wright 25,* NY; Reverchon distrib. *Curtiss 346,* NY; *Lundell 14031;* UC; *Shinners 14650,* CAS. Oklahoma: *Waterfall 13170,* CAS. Nebraska: *Webber,* in 1889, NY.

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UNUSUAL FACTORS CONTRIBUTING TO THE DESTRUCTION OF YOUNG GIANT SEQUOIAS

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During the summer of 1966, a stand of dead and dying 10- and 11-year-old giant sequoias, *Sequoiadendron giganteum,* was discovered in the Abbot Creek drainage of the Cherry Gap Grove of Sequoias in Sequoia National Forest. This grove is located immediately south of Converse Basin at 36°46′5″ N lat., and 118°56′49″W long.

This area was originally logged along with Converse Basin during the latter part of the last century. Although evidence is lacking, it is felt that the parent trees of the young sequoias in question were seeded at the time of logging. In 1955, this entire area was consumed by an intensely hot fire known locally as the "McGee Burn." The parent trees were killed by the fire, but disseminated the seeds which had apparently remained viable in the green cones after the fire.

FIG. 1. Stump of a 10 year old giant sequoia showing the base girdled by rodents and the fruiting bodies of *Hyphloma* sp.

Approximately 150 saplings were examined along a tributary of Abbot Creek where soil moisture conditions were suitable for germination and rapid seedling growth. With almost full sunlight, the young trees had grown to heights varying from 5 to 15 feet.

Of the 150 saplings, 54 had been damaged by small rodents. Of these, 27 had been completely girdled and were dead, and the remainding 17 were partially chewed and displayed varying degrees of browning foliage. There was no apparent selectivity for trees of any size class or crown condition.

Judging from the tooth marks on the xylem, the rodents were small, probably meadow mice, *Microtus* sp, or possibly gophers, *Thomomys* sp. Bark from two of the trees was removed to a height of about 1½ feet above the ground, indicating that the feeding may have occurred during the winter on the surface of the snow. Similar microtine damage has been observed by the authors on *Abies concolor* nearby in Kings Canyon National Park,, but it has not been previously recorded for the giant sequoia.

Nearly all of the dead saplings were being attacked by a fungus whose bright yellow fruiting bodies clustered densely at the base of each tree (fig. 1). Robert Bega of the Pacific Southwest Forest and Range Experiment Station, and Lee Bonar of the University of California identified the fungus as *Hyphloma,* possibly *H. fasciculare,* a known saprophyte. This genus is previously unrecorded in association with sequoia. It seems noteworthy that a species of tree whose remnants have lain undecayed for as long as 2,000 years is here found in a state of decay within two or three years after death. The wood of these stems was, however, largely sapwood which lacked heavy deposition of tannin characteristic of old heartwood.

Several of the dead trunks which were examined for insect activity showed considerable working of Cerambycid beetles, *Semanotus ligneus amplus,* to a depth of 3 or 4 inches in the xylem tissue. These activities occurred after the death of the trees as far as could be ascertained.

These unique interrelationships are probably due in part to the usually wet soil habitat and lack of over story vegetation in which these trees are now growing. Such conditions are conducive both to microtine populations and to the growth of the fungus. Within the range of the giant sequoias, these conditions are uncommon at this early stage of plant succession. It is felt that an unusually high population density of rodents developed and, under winter conditions, they resorted to the sequoia saplings which provided the most abundant source of food. The damage inflicted by the rodents was followed by fungus and beetle attacks upon the weakened or killed trees.

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LINEAR MICROSPORE TETRADS IN THE GRASS STIPA ICHU

Frank W. Gould

Microspores of angiosperms commonly are in tetrahedal, isobilateral, or decussate tetrads. T-shaped tetrads have been reported for *Aristolochia* (Samuelsson, 1914) and *Butomopsis* (Johri, 1936), and linear tetrads are known to occur in *Halophila* of the Hydrocharitaceae (Kausik and Rao, 1942) *Zostera* of the Zosteraceae (Rosenberg, 1901), and some genera of the Asclepidaceae (Gager, 1902). Two or three types of microspore tetrads have been reported for a number of genera including the monocots *Musa, Agave,* and *Habeneria* (Maheshwari, 1950).

In the Gramineae, division of the microspore mother cells is of the successive type. A cell plate is laid down immediately after the first meiotic division (Maheshwari, 1950). Characteristically and with great regularity the microspore tetrads are isobilateral. Davis (1966) noted that grass microspore tetrads are "occasionally T-shaped or linear" but cited no specific references. It is to be assumed that the extensive literature citation of Davis does include reports of T-shaped and linear grass microspore tetrads but such types certainly are rare.

The purpose of the present paper is to report the occurrence of linear and T-shaped microspore tetrads (figs. 1, 2) in addition to the usual isobilateral tetrads (fig. 3) in *Stipa ichu* (Ruiz & Pav.) Kunth and also the occasional development of linear groups of five microspores (fig. 4) in the same species. Linear and T-shaped microspore tetrads were observed in bud material of *S. ichu* from two widely separated localities in Mexico. One collection *(Gould 11622,* TAES*)* was from 20 miles east of Mexico City and the other *(Gould 11681,* TAES) was from near San Cristóbal de las Casas, near the Guatemalan border. Chromosome numbers were determined to be **2n = 40** in both collections. Pollen mother cell divisions in the San Cristóbal material, however, were not entirely regular and the count was reported as ca. **2n = 40** (Gould, 1966). Of possible significance was the collection of *Stipa virescens* H. B. K. at the same locality with a chromosome number of **2n = 60** and very irregular meiotic divisions.

About 70% of the microspore tetrads of the San Cristóbal *Stipa ichu* plant were linear and the remainder were T-shaped and isobilateral in about equal proportions. A few linear groups of five microspores (fig. 4) were also present. The percentage of linear tetrads in the Mexico City collection was somewhat less than in the San Cristóbal material but linear and T-shaped tetrads were numerous.

Maheshwari (1950) noted that the formation of groups of more than four microspores usually results from lagging chromosomes which organize into micronuclei. He further stated that in general such abnormal-

Figs. 1–4. Microspores of *Stipa ichu*: 1, linear tetrad; 2 linear tetrad and T-shaped tetrad; 3, isobilateral tetrad; 4, linear group of five microspores. Magnifications not uniform.

ities are found only in hybrids characterized by a high degree of sterility. As can be observed in Fig. 4, the five spores of the *Stipa ichu* "pentad" are fairly uniform in size and all but the apical cell have well-developed, apparently functional nuclei. It is possible that the fifth cell has been organized about a micronucleus, but in that case the terminal position of the extra cell is difficult to explain.

This paper is technical article no. TA 7470, Texas Agricultural Experiment Station.

Department of Range Science, Texas A & M University

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EXTENSION OF THE RANGE OF ABIES LASIOCARPA INTO CALIFORNIA

J. O. SAWYER, D. A. THORNBURGH, and W. F. BOWMAN

Abies lasiocarpa (Hook.) Nutt. has been located in two drainages near Russian Peak in the Salmon Mountains of Siskiyou Co. During the summer of 1968, while making a vegetational reconnaissance of this area, *A. lasiocarpa* was first located in forests surrounding the meadows west of Little Duck Lake (Etna quadrangle, T. 40N. R. 9W. Sec. 19, elev. 6400 ft). Here it forms a forest with *Tsuga mertensiana* (Bong.) Carr., *Pinus monticola* Dougl., and *Abies magnifica* A. Murr. var. *shastensis* Lemmon. The trees are healthy; reproduction is plentiful with some advancing into the wet meadows.

Later a more extensive forest was found along South Sugar Creek (T. 40N. R. 9W. Sec. 30, 31). In this area the trees not only occur around the wet meadows near South Sugar Lake at 6800 ft, but descend along the creek terraces to 5800 ft. Below 6400 ft *A. lasiocarpa* is mixed with *Picea engelmannii* Parry ex Engelm. Both species are vigorous, and are reproducing well.

It is surprising that this species has not been reported previously. Munz (1959) reports *P. engelmannii* along Sugar Creek, tributary of the Scott River. South Sugar Creek is a branch of this stream. Only a rough and apparently recent trail has been constructed by fishermen to South Sugar Lake, so accessibility is recent. An established Forest Service trail parallels Sugar Creek through stands of *P. engelmannii.* This might explain the oversight.

Some older literature incorrectly reports the occurrence of *A. lasiocarpa* in the "Salmon Mountains." The references are traceable to specimens of *Abies amabilis* (Dougl.) Forbes collected by Gillespie in 1928 near Hancock Lake in the Marble Mountain Wilderness Area (Gillespie, 1931). Haddock (1961) discusses the history of the confusion noting that *A. amabilis* was first correctly recognized in that location in 1932 by Crebbin, a forester on the staff of the Klamath National Forest.

These new records do not greatly extend the range of *A. lasiocarpa.* Fowells (1965) follows earlier general references in showing the southern range of *A. lasiocarpa* to be in the Cascades in the vicinity of Crater Lake. The first discovery of *A. lasiocarpa* in the Klamath Region was made by Dennis (1959) on the slopes of Mt. Ashland, Jackson Co., thus extending the range further south. He found one small group, possibly a single clone due to layering. Our findings continue the range about 50 miles south of the Mt. Ashland location, and into a more central part of the Klamath Region.

Its presence, here, accentuates the region's central refugial nature as discussed by Whittaker (1960; 1961). What is more noteworthy is that *A. lasiocarpa* and *P. engelmannii* are only two of 17 conifers found above 5000 ft in the Sugar Creek drainage. These are as follows: *Abies concolor* (Gord. & Glend.) Lindl., *A. lasiocarpa* (Hook.) Nutt., *A. magnifica* A.Murr. var. *shastensis* Lemmon, *Juniperus communis* L. var. *saxatilis* Pall., *Libocedrus decurrens* Torr., *P. breweriana* Wats., *P. engelmannii* Parry ex Engelm., *Pinus albicaulis* Engelm., *P. balfouriana* Grev. & Balf., *P. contorta* Dougl. var. *murrayana* (Grev. & Balf.) Engelm., *P. jeffreyi* Grev. & Balf., *P. lambertiana* Dougl., *P. monticola* Dougl., *P. ponderosa* Dougl. ex P. & C. Lawson, *Pseudotsuga menziesii* (Mirb.) Franco, *Taxus brevifolia* Nutt., and *Tsuga mertensiana* (Bong) Carr.

A notable species is *Pinus balfouriana* Grev. & Balf. on a ridge overlooking Little Duck Lake and Sugar Lake stands of *A. lasiocarpa* and *P. engelmannii.* Possibly nowhere else in California is such a complete representation of northwestern and Serrian conifers present in a single square mile. We also doubt that any region can match the number of conifers found in one small area.

Initial studies have begun in this area on the other plant groups. The flowering plants are now incompletely collected due to time limitations. The collected material, though, shows a similar pattern of mixing of northwestern and Serrain floras. For example, the northwestern *Phyllodoce empetriformis* (Sm.) D. Don is present rather than *Phyllodoce breweri* (Gray) Hell. Other northwestern shrubs which are rather common in the area include *Vaccinium membranaceum* Dougl., *Vaccinium* *scoparium* Leib., and the sub-shrub *Leutkea pectinata* (Pursh) Kuntze. Mixed with the *Vaccinium* is the Serrian *Leucothoe davisiae* Torr. The rare to California *Gaultheria humifusa* (Graham) Rydb. was found near the Little Duck Lake stand of *A. lasiocarpa*. Interesting herbs include the "uncommon" *Mitella pentandra* Hook. and *Cypripedium fasciculatum* Kell. A complete study of the vascular plant flora of this area is planned by us for the 1969 field season.

Specimens of *A. lasiocarpa* are in the following herbaria: HSC, JEPS, and the Klamath National Forest Herbarium, Yreka.

This study is in cooperation wtih and partially financed by the Pacific Southwest Forest and Range Experiment Station, Berkeley.

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REVIEWS

The Plant Hunters. By Tyler Whittle. xii + 283 pp., illustrated. Chilton Book Co., 401 Walnut St., Philadelphia, Penn. 19106. 1970. $8.95.

The subtitle of this book sums up its contents very well: "being an examination of collecting with an account of the careers & the methods of a number of those who have searched the world for wild plants." Starting with Queen Hatshepsut and continuing into the 20th Century the author of this very interesting and eminently readable book has detailed the story of the men and women who went around the world looking for plants, sometimes for medical reasons, sometimes in search of ornamentals, sometimes to find spices, and sometimes to advance the knowledge of the kinds of plants. The whole world is covered, hence no one geographical area has received exhaustive treatment: nor in a book of this kind would one want it.

The vistas and unspoiled plant communities of the past are often no longer with us. It makes one rather depressed to realize what man has done and is continuing to do to his surroundings, especially in decreasing the diversity of living things. Perhaps one of the great services of this book, especially to young readers, will be to install in them a sense of curiosity about and interest in plants, for after-all, there is little motivation to preserve that about which one knows nothing or in which one has no interest.—John H. Thomas, Department of Biological Sciences, Stanford University.

Plant Variation and Evolution. By D. Briggs and S. M. Walters. 256 pp., illustrated. McGraw-Hill Book Company, New York, 1969. $2.45

This book is an introduction to plant biosystematics. The initial chapters sketch briefly the historical context in which modern plant systematics developed. The remainder and major portion of the book is written essentially as a discussion of speciation and includes the following topis: changes in population, breeding systems, hybridization, polyploidy, and patterns of evolution. The many well illustrated examples which accompany the text are drawn primarily from studies of the European Flora.

Many sections within the various chapters are exceptionally well written. Of particular note is the treatment of apomixis and hybridization. Although considerable space is devoted to the factors involved in species formation, the discussion of the "species problem" is most unsatisfactory. Rather than questioning if a single species definition is possible or desirable the authors state that "the 'ideal' 'biological', or 'evolutionary species' of the experamentalist is the *hologamodeme,* defined as composed of individuals which 'are believed to interbreed with a high level of freedom under a specified set of conditions, and separated from other hologamodemes by at least partial sterility' ". Such a definition is clearly non-operational for most plant groups and therefore cannot be used as an absolute guideline by plant systematists.

The recently published *Plant Biosystematics* by Otto T. Solbrig is the only book comparable in its scope to *Plant Variation and Evolution.* However, in contrast, the Solbrig book appears to offer a more complete and accurate treatment of many topics.

Plant Variation and Evolution should best be regarded as a reference work for students.—Dennis R. Parnell, Department of Biological Science, California State College, Hayward, California.

NOTES AND NEWS

Ribes malvaceum in the Foothills of Calaveras County, California.—In March, 1967, I observed a small population of *Ribes malvaceum* Sm. in the foothills of the Sierra Nevada near Valley Springs along the access road to the south arm of New Hogan Reservoir. Subsequent search revealed a considerable number of stations scattered a few miles apart in the chaparral at elevations ranging from 450 to 1000 feet. One large group of about 200 shrubs is located at the junction of the Southern Pacific Railroad with State Highway 12, 2 miles west of Valley Springs (*Taylor 11,* CAS, Fresno State College Herbarium, GH, MO). The plants at this locality are well spaced on a northwest exposure in association with a number of chaparral species including *Quercus wislizenii, Arctostaphylos mariposa, Baccharis pilularis* var. *consanguinea, Adenostoma fasciculatum,* and *Fremontodendron californicum.* Other localities in the area include the spillway at New Hogan Reservoir and along the south arm of the Reservoir (*Taylor 12,* Fresno State College Herbarium). All localities show uniformity as to slope, soil, and composition of the vegetation. This population extends the range southward in the Sierra Nevada from El Dorado Co.—Dean William Taylor, Biology Department, Fresno State College, Fresno, California.

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Classified entries: authors; book reviews; botanical names (excluding taxa in floristic lists); major subject headings; new combinations and taxa (in **boldface**); and titles.

To you "Bill," WILLIAM MCKINLEY HIESEY, the California Botanical Society takes sincere pride and pleasure in dedicating Volume Twenty of Madroño. Your sound and constructive guidance during a long and active membership; as Business Manager, President, and Member of the Board of Directors has set a standard that has, and will benefit the society for years in the future.

As the plant physiologist and "anchor-man" on the Carnegie Institution of Washington's Experimental Taxonomy team of Clausen, Keck and Hiesey, your imaginative transplant studies have fused the diverse disciplines of genetics, cytology, taxonomy and environmental distribution with basic physiology, giving a lucid picture of the genecological nature of plant species and an insight into the processes of natural selection which have molded these entities. As a pioneer in physiological ecology your careful, precise research has established a firm foundation which will endure in all future studies.

Quiet and modest, your primary energy is devoted to research and post-doctoral teaching; however, students of biology at all levels of training throughout the world seek your council and all receive generously of your enthusiastic guidance and warm friendship. In sincere appreciation we thank you and look forward to many future years of your warm human guidance.

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