UNIVERSAL
LIBRARY

OU_162712

UNIVERSAL
LIBRARY

OUP—552—7-7-66—10,000

OSMANIA UNIVERSITY LIBRARY

Call No. 590/B11A Accession No. 2207

Author

Title

This book should be returned on or before the date last marked below.

THE AMERICAN SPECIES OF CREPIS

THEIR INTERRELATIONSHIPS AND DISTRIBUTION AS AFFECTED BY POLYPLOIDY AND APOMIXIS

E. B. BABCOCK
G. L. STEBBINS, JR.

PUBLISHED BY CARNEGIE INSTITUTION OF WASHINGTON
WASHINGTON, D. C.
1938

CARNEGIE INSTITUTION OF WASHINGTON PUBLICATION NO. 504

[*This book first issued December 6, 1938*]

PRESS OF W. F. ROBERTS COMPANY
LANMAN ENGRAVING COMPANY
WASHINGTON, D. C.

CONTENTS

	PAGE
Introduction	1
Taxonomic History of the Indigenous Species	3
Present Distribution of the Species	4
Cytology of the Species	5
Genetic Interrelationships of the Species	11
Factors Affecting the Distribution of the Species	13
Origin and Development of the Species	27
The Effect of Polyploidy and Apomixis on Evolution	44
The Systematic Treatment of the Agamic Complex	63
Summary of the Preceding Sections	69
Material and Methods	73
Acknowledgments	74
Literature Cited	75
Generic Description	79
Key to the Western American Species of *Crepis*	79
Descriptions of Species	
1. *Crepis nana*	84
2. *Crepis elegans*	85
3. *Crepis nicæensis*	85
4. *Crepis capillaris*	86
4*a*. *Crepis tectorum*	87
5. *Crepis rubra*	87
6. *Crepis bursifolia*	88
7. *Crepis setosa* subsp. *typica*	89
8. *Crepis vesicaria* subsp. *taraxacifolia*	90
9. *Crepis runcinata*	90
10. *Crepis pleurocarpa*	107
11. *Crepis monticola*	114
12. *Crepis occidentalis*	118
13. *Crepis Bakeri*	138
14. *Crepis modocensis*	141
15. *Crepis barbigera*	154
16. *Crepis exilis*	159
17. *Crepis acuminata*	169
18. *Crepis intermedia*	179
Index to Species, Subspecies, and Synonyms	188
Index to Exsiccatæ	189

THE AMERICAN SPECIES OF CREPIS

THEIR INTERRELATIONSHIPS AND DISTRIBUTION AS AFFECTED BY POLYPLOIDY AND APOMIXIS

INTRODUCTION

The present contribution is an outgrowth of the senior author's monographic studies of the genus *Crepis*. In the early stages of this work it was realized that the native American species of *Crepis* present especially difficult problems for the taxonomist. These problems, it was found, consist not only in the extreme variability which is so characteristic of these species, but also in certain difficulties that were encountered when attempting to introduce them into cultivation and to apply experimental research methods. All of these species are perennials and in most of them there is a very long, slender, woody root, which develops rapidly in the young seedling, and by means of which the plants persist for several years, oftentimes on steep, semiarid mountain sides. Because of this peculiarity the transplantation of wild plants is laborious and the results uncertain. The culture of seedlings is also more difficult than in most *Crepis* species and two or three years are required for a seedling to mature. Furthermore, apogamy is of frequent occurrence in most of the species that have a wide distribution; and it is now realized that such species consist of numerous local and often apomictic races.

For these reasons the final treatment of this portion of the genus was postponed until field trips and cytological studies could be made and special methods devised by which our data on chromosome numbers could be adapted for the study of herbarium material. The application of these special methods, the studies of geographical distribution based on the data accompanying herbarium specimens, supplemented by field studies in certain critical areas, and the theoretical basis for the taxonomic treatment are the work of the junior author.

The present treatment is an attempt to apply directly some of the best-established principles of modern cytogenetics to the species problem. Those who are not familiar with this field can find a general discussion of these principles, with references to the original papers on which they are based, in almost any modern book on cytology or genetics (see in particular Anderson, 1936*a*, 1937; Dobzhansky, 1937, chap. VII). These principles are: first, that by

means of doubling their chromosome number, many hybrids, originally sterile, can become fertile and self-perpetuating; second, that this fertility is further assured in the polyploids of *Crepis* and other genera by the presence of apomixis, or reproduction without fertilization. Since the reversion from polyploidy to diploidy is very rare, the assumption is safely made that the diploid forms represent the original ones, from which the polyploids have been derived by means of two processes: multiplication of the chromosome number and hybridization. For this reason, the basis for the delimitation of species in the group containing the polyploids has been the characteristics of these seven diploid forms (diploid *C. pleurocarpa, C. monticola, C. occidentalis, C. Bakeri, C. modocensis, C. exilis,* and *C. acuminata*). For reasons discussed on pages 66–68, all the species within this group contain, in addition to the diploid form, polyploids both of non-hybrid and of hybrid origin, i.e., both auto- and allopolyploids. Two species, *C. barbigera* and *C. intermedia*, contain only polyploids. The method used in building up this systematic treatment is described on pages 63–69. The recognition of *formæ apomicticæ* under each species as described entities with no taxonomic status (see p. 69) is an innovation in a systematic treatment such as this, but it is not entirely without precedent (see Turesson, 1926) and after careful consideration has seemed to the writers the most satisfactory method of handling these entities. Perhaps the most cogent reason for this is the fact that their description as species, subspecies, or any other recognized category would require the monographer to describe all of them known to him. This would be an endless task, and would result in confusion rather than clarification; the student "would not be able to see the forest for the trees." A glance at the systematic literature on the European *Hieracium* and *Taraxacum* is enough to emphasize this point. On the other hand, the usefulness of these *formæ apomicticæ* in an attack on problems of distribution (see pp. 39–44) makes imperative the description of some of them.

The taxonomic treatment finally adopted is the result of our joint efforts, except that the division of the species into *formæ apomicticæ* is entirely the work of the junior author. It is presented here in the conviction that it is the only sort of treatment which can adequately describe this ramarkable group of species. All but one of the earlier treatments have necessarily been brief and inadequate since they are merely small portions of general or local floras. It is the purpose of this contribution to provide a systematic classification which shall be not only scientific in respect to the concepts and principles on which it is based, but also of practical use to botanists, foresters, students, and others.

The twelve indigenous New World species of *Crepis* are all found in the western half of North America, except one (*C. nana*) which also occurs on the coasts of Labrador and Newfoundland. The others are, for the most part, restricted to the region extending from the Rocky Mountains to the Pacific Coast and from southwestern Canada to northern Mexico. In addition to these native species there are several species, mostly common European weeds, which have been introduced at various points in the United States, Canada, Mexico, and South America, mostly in coastal districts or localities. Seven of these adventive species have been reported in western North America. These will be very briefly treated in the present work, since their complete descriptions will appear in the general monograph which is now in preparation.

TAXONOMIC HISTORY OF THE INDIGENOUS SPECIES

The first record of the occurrence of *Crepis* in North America (outside of the arctic regions) was made by Hooker in his "Flora Boreali-Americani" (1834, vol. 1, p. 297), in which he identified as the European *C. biennis* James's *Hieracium runcinatum.* In the same year Nuttall published his *C. occidentalis,* and seven years later (1841), in describing the plants collected on a tour to the Pacific, added another species, *C. acuminata.* In this publication he created a new genus, *Psilochenia,* for *C. occidentalis,* and another, *Crepidium,* for *Hieracium runcinatum* (Hooker's "*C. biennis*" of America), and placed *Crepis acuminata* in a new subgenus, *Leptotheca.* Two new species, *Crepidium glaucum* and *C. caulescens,* were also described. Two years later Torrey and Gray (1843) reduced Nuttall's two genera to *Crepis,* and recognized, in addition to the arctic-alpine *C. nana* Richards., and *C. elegans* Hook., four species, *C. runcinata, C. glauca, C. occidentalis,* and *C. acuminata.* For the next fifty-three years the group received little attention, although a few species and varieties were described by Gray and others. In his "Synoptical Flora of North America" (1876) Gray recognized, in addition to the six species included in his earlier work, two more, *C. Andersonii* Gray and *C. intermedia* Gray, and listed two varieties under the latter and three under *C. occidentalis.* With the heading of the section including *C. occidentalis, intermedia,* and *acuminata* he made the terse comment "species difficult," an opinion with which all later workers on the group, including the present writers, are inclined to agree.

Coville (1896) was the first to make a monographic study of any of the American species. Omitting the arctic-alpine species and

the group of *C. runcinata*, as well as *C. acuminata* and *C. intermedia*, which latter he considered to be not well enough understood, he included seven species, four of which, *C. monticola, C. scopulorum, C. rostrata*, and *C. barbigera*, were described as new. His treatment, although well worked out according to the knowledge then available, was based on a relatively meager series of specimens, and included little information on the interrelationships of the species, while their distribution could be stated only in relatively broad terms.

Since the work of Coville, no particular attention has been paid to the genus in North America, except for the description of numerous new "species," mostly of the group of *C. runcinata*, by Greene, Rydberg, and others. These were published without consideration of the group as a whole, were based on fickle characters such as leaf shape and pubescence, and none of them are considered valid by the present writers. Meanwhile in the affinity of *C. occidentalis* and *C. acuminata* the species were variously interpreted by the writers of the different floras, the keys to them varied considerably, while the identification of the ever increasing number of collections by various students of the western flora bore out Gray's opinion, "species difficult."

PRESENT DISTRIBUTION OF THE SPECIES

The three groups of native American species of *Crepis* differ markedly from one another. *C. nana* and *C. elegans* are arctic-alpine plants, coming south only on the highest crests of the western cordillera. The former is a circumpolar species, whose affinity is with a group of species of central Asia, where it undoubtedly had its origin, while *C. elegans* is a specialized form derived from it. Hence these two species may be considered among the Old World element of the circumpolar flora, and need not be discussed further in connection with the endemic American groups.

These latter groups are confined largely to the western and northwestern United States, occurring primarily in the Transition life zone of Merriam (1892), although they enter both the upper Sonoran and the Canadian zones, and occasionally even the Hudsonian zone. Of the two groups one, consisting of the polymorphic *C. runcinata*, has its center in the central Rocky Mountains, extending eastward nearly to the eastern border of the Great Plains in Minnesota and Manitoba, and westward to the western edge of the Great Basin in California (fig. 6). This species is primarily one of moist meadows. While in the center of its range it occupies meadows of all degrees of acidity or alkalinity, toward the peri-

phery, particularly in the western part, it shows a decided preference for alkaline situations.

The other group of species, which consists of the nine remaining, is more western in distribution, being best developed in the Columbia Plateau province and the northern Great Basin province of Fenneman (1931) (fig. 1). These species are typical of arid, well-drained hill and mountain slopes, in the lower edge of the *Pinus ponderosa* belt, and in the adjoining bunch-grass and sagebrush areas. With the exception of *C. acuminata*, *C. modocensis*, and some forms of *C. intermedia*, they prefer a relatively deep, rich soil, and hence are more predominant in the bunch-grass than in the sagebrush areas (see Peck, 1925). The underlying rock throughout most of their range consists of basaltic lava flows and eruptive rocks of Tertiary age. The soil reaction is uniformly circumneutral (pH 6.4–7.2).

Of the seven species characteristic of this area, two, *C. exilis* and *C. barbigera*, are essentially northern in distribution, occurring primarily in central Washington; three, *C. occidentalis*, *C. intermedia*, and *C. Bakeri*, are essentially southern, being best developed in northern California and southern Oregon; while the other two, *C. acuminata* and *C. modocensis*, occur about equally throughout the area, though the latter is more or less local in distribution, and is most abundant eastward. All these species, with the exception of *C. barbigera*, extend eastward into the Rocky Mountains, but occur in the Plains province only where there are outliers of the cordillera in the form of hills or ridges.

Two species, *C. monticola* and *C. pleurocarpa*, have somewhat different distributions from the others. These species occur primarily in the Klamath Mountain province of northern California and southern Oregon, where they enter the Humid Transition life zone. The underlying rocks here are a metamorphic complex of Paleozoic and Mesozoic age. The *Crepis* species occur primarily on the more basic rocks of this complex, being rare or absent from the areas underlain by granitic rocks.

CYTOLOGY OF THE SPECIES

The chromosome numbers of the species were first reported by Hollingshead and the senior author (1930), who established $x = 11$ as the basic haploid number for all the endemic species. This is in striking contrast to the Old World species of *Crepis*, whose basic haploid numbers range from $x = 3$ to $x = 7$, 4 and 5 being much the most common. These authors found also that while *C. runcinata* (including, as here revised, *C. glauca* and *C. Andersonii*) is

exclusively diploid, with the somatic number $2n = 22$, the other species all include within themselves an ascending series of polyploid numbers from $2n$ (i.e., $3x$) $= 33$ up to 44, 55, and 88. (The present usage of the symbols n and x is that now adopted by most cytologists; see Darlington, 1937, p. 62). These counts have more recently been supplemented by many others, made chiefly by Dr. J. A. Jenkins (unpublished), which have borne out and extended the results reported in the earlier paper. A summary of all the numbers now recorded for the group is presented in table 1. The large size of the chromosomes in relation to that of the nucleus makes the exact counting of the higher numbers difficult, so that these must still be considered as only approximate. There is some evidence that aneuploid numbers occur, i.e., 45, 76, and 86, but these are in every case very nearly multiples of 11, and are grouped with the nearest euploid number in table 1.

TABLE 1. SUMMARY OF THE KNOWN CHROMOSOME NUMBERS OF AMERICAN SPECIES OF *Crepis* (EXCLUDING *C. nana, elegans,* AND *runcinata*)

(Names in parentheses and quotation marks are those used in previous publications for some of the forms of the species or subspecies after whose name they are given. The numbers in the table indicate the number of collections examined.)

Species	Somatic chromosome number					
	22	33	44	55	77	88
C. pleurocarpa ("*C. acuminata,* form")	1	...	...	1	...	...
C. monticola	1	...	1	1	...	...
C. occidentalis						
subsp. *typica*	3	6	2	...	...	...
subsp. *costata*	...	...	1	...	...	...
subsp. *pumila*	...	1	...	...	1	...
subsp. *conjuncta*	..	...	1	...	...	...
C. Bakeri						
subsp. *typica*	...	...	1	...	...	...
subsp. *Cusickii* ("*C. occidentalis,* form")	2	...	...	...	...	...
C. modocensis ("*C. scopulorum*")						
subsp. *typica*	..	...	1	...	...	...
subsp. *subacaulis*	...	...	2	...	...	...
C. exilis ("*C. gracilis*")						
subsp. *originalis*	1	...	1	1	...	...
C. acuminata	2	2	1	...	...	...
C. intermedia ("*C. acuminata,* form") (inc. "*C. atribarba*")	..	3	2	2	...	1
C. barbigera	...	...	1	...	...	4

In addition, the degree of polyploidy of most of the other forms has been estimated by measuring the length of the guard cells of the stomata of the basal leaves. This method of detecting poly-

ploid races has long been known to cytologists, and has been applied to the study of herbarium specimens in a previous publication of the present authors (Babcock and Stebbins, 1937), as well as by Sax and Sax (1937). In *Crepis* the size of the stomata is a more reliable criterion than their distribution over the surface of the leaf, since the latter varies considerably from species to species of the diploid group, depending upon the structure of the epidermis. The stomatal size characteristic of each chromosome number was determined by obtaining the average length of the guard cells of 20 stomata, obtained from a median, lateral segment of a fully developed basal leaf, in herbarium specimens of plants whose number was obtained from actual counts. Table 2 shows the results obtained. It will be seen that there is some variation among the different diploid forms, which must be taken into account in estimating the number of polyploids of hybrid origin.

TABLE 2. LENGTH OF THE STOMATA IN FORMS OF *Crepis* OF WHICH THE CHROMOSOME NUMBER HAS BEEN COUNTED

Species	Length of guard cells of basal leaves (in μ)	
	Range	Average
Diploid ($2x=22$)		
C. pleurocarpa	31–36	33.9±0.3
C. monticola	34–41	37.0±0.4
C. occidentalis subsp. *typica*	31–40	35.8±0.5
C. Bakeri subsp. *Cusickii*	35–42	38.1±0.4
C. exilis subsp. *originalis*	33–42	37.0±0.3
C. acuminata	32–41	36.3±0.5
Triploid ($3x=33$)		
C. occidentalis	38–47	43.3±0.6
C. acuminata	38–47	43.3±0.51
Tetraploid ($4x=44$)		
C. monticola	43–54	48.2±0.6
C. occidentalis subsp. *costata*	45–57	51.1±0.5
C. Bakeri subsp. *typica*	43–54	48.6±0.6
C. modocensis subsp. *subacaulis*	46–55	49.6±0.5
C. exilis subsp. *originalis*	40–52	45.5±0.7
C. intermedia	41–47	44.9±0.4
Pentaploid ($5x=55$)		
C. monticola	45–58	51.3±0.8
C. exilis subsp. *originalis*	47–59	51.1±0.6
C. intermedia	42–54	48.7±0.7
Heptaploid ($7x=77$)		
C. occidentalis subsp. *pumila*	43–57	51.1±0.9
Octoploid ($8x=88$)		
C. barbigera	49–60	55.0±0.7

In addition, studies of the pollen grain morphology were in many cases a valuable aid in estimating the numbers. Diploid forms

all have pollen grains nearly or quite uniform in size, and all are 3-pored. Tetraploid forms, with 44 somatic chromosomes, also have in most cases nearly or quite regular pollen (unless it is absent altogether). In some species—*C. exilis, C. modocensis* subspp. *typica* and *rostrata,* and *C. barbigera*—the grains of tetraploids are predominantly 3-pored, as in the diploids, while in others—*C. occidentalis, C. Bakeri, C. intermedia, C. modocensis* subsp. *subacaulis* and occasionally subsp. *typica,* and *C. monticola*—the grains are predominantly 4-pored. In the 33- and 55-chromosome forms the pollen is markedly irregular, and at least a small percentage of 4-pored grains occurs. The differentiation between adjacent chromosome numbers, for example between 22 and 33 or 44 and 55, may therefore be made by examination of the pollen, while the distinction between 22 and 44 or 33 and 55 is obvious from the size of the stomata. Numbers higher than 55 are more difficult to estimate. The number 66 has not yet been counted, although there is no reason to believe that it does not exist, and hence the estimation of this number from stomatal measurements has been purely arbitrary, based on a size intermediate between that of 55- and 88-chromosome forms.

By this method, the chromosome number has been estimated of nearly every collection of *Crepis* available to the writers, and the geographic distribution of the diploid and polyploid forms has been mapped (see figs. 14, 16, 18, 23, 24, 27, 29, 31, 33). The diploid forms of all the species have a more restricted range than the related polyploids, and, with the exception of *C. acuminata,* are confined to small areas along the western edge of the range of the group. They are concentrated in two centers, one chiefly in northern California and adjacent Oregon, the other in central Washington (fig. 1). The first center is the largest both in extent and in the number of diploid forms present, but even within this area the diploid forms are decidedly local. The area is very diverse in both its climatic and its edaphic characteristics, and each of the diploid forms occupies a particular habitat within the area that is different not only from that occupied by the other diploid forms, but also from many habitats occupied only by polyploid derivatives. The northern center is smaller in extent and contains only two diploid forms, those of *C. exilis* and of *C. modocensis* subsp. *rostrata.* This area has been relatively little studied, having been visited only once by the senior author in 1926, before the cytological situation in this group was known. Judging from herbarium specimens, the diploid forms occurring there are less local in their distribution. The significance of this localized distribution of the diploid forms will be

discussed more fully below. It is closely paralleled by the situation in *Tradescantia* (Anderson, 1937), in which genus the distribution of the diploids also permits the establishment of centers of distribution.

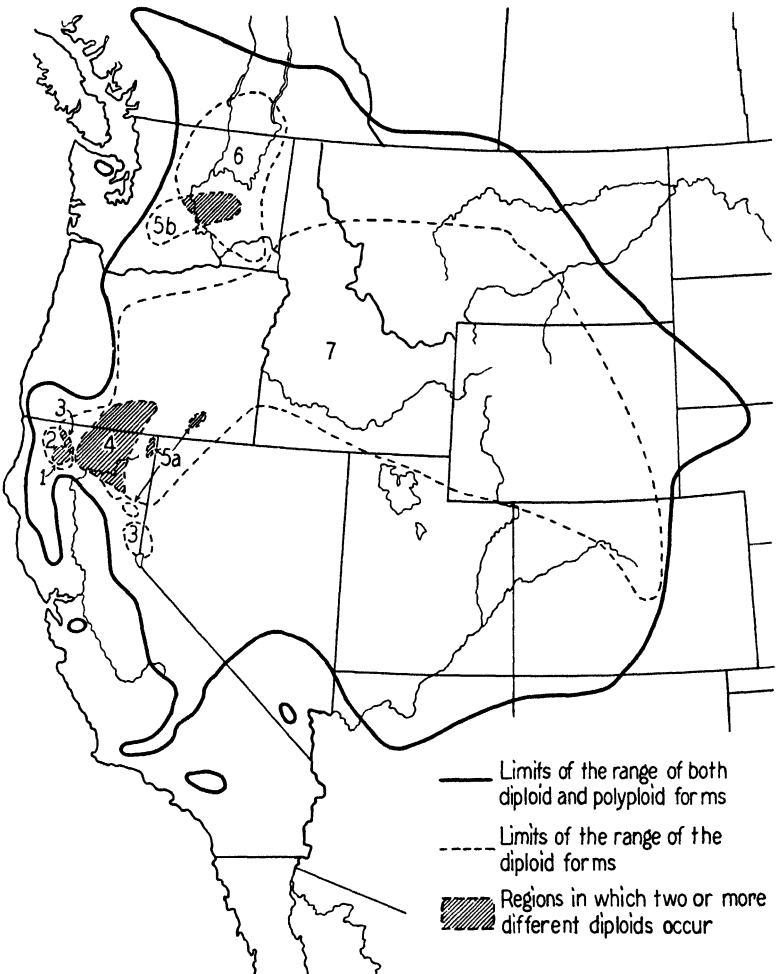


FIG. 1. The relative areas of distribution of diploid and polyploid forms of *Crepis* species in North America (excluding *C. nana, C. elegans,* and *C. runcinata*). Compiled from figures 14, 16, 18, 23, 24, 29, 31, and 33, which should be consulted to obtain the range of individual species. The numbers refer to the various diploid forms, as follows: 1, *C. pleurocarpa*; 2, *C. monticola*; 3, *C. occidentalis*; 4, *C. Bakeri* subsp. *Cusickii*; 5*a*, *C. modocensis* subsp. *typica*; 5*b*, *C. modocensis* subsp. *rostrata*; 6, *C. exilis*; 7, *C. acuminata*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

The distribution of the higher numbers does not follow any definite plan either geographically or in relation to interspecific differences. The number 33 is found in all the species except *C. barbigera,* although it is rare in *C. monticola.* The number 44 is the most widespread, since there is evidence of its occurrence in all the species, and in the more widespread species, such as *C. occidentalis, C. acuminata, C. exilis,* and *C. modocensis,* forms with either 33 or 44 chromosomes are found practically throughout their range. The number 55 is common in *C. intermedia, C. pleurocarpa, C. monticola,* and *C. occidentalis* subsp. *pumila,* and occurs fairly frequently in *C. exilis.* It is rare, however, in *C. acuminata,* occurring only in forms obviously derived from hybridization with *C. pleurocarpa* and perhaps other species. It is also rare in *C. modocensis,* and there is no clear evidence for its occurrence in *C. Bakeri* or *C. barbigera.* The number 66 has not been counted, so that no sure inferences on its distribution based on the stomatal method can be made; while the number 77, although known to occur in *C. occidentalis* subsp. *pumila,* is too difficult to distinguish from 55 by the stomatal method for its distribution to be inferred. The number 88 is common in *C. barbigera,* and has been counted also in *C. intermedia.* In addition, either 77 or 88 apparently occurs in *C. exilis,* C. *occidentalis* subspp. *costata* and *conjuncta, C. pleurocarpa,* and *C. modocensis* subsp. *subacaulis.* Geographically, the higher numbers are less widespread and tend to be more abundant near the centers of distribution, although this is not exclusively the case. The outlying stations for *Crepis* in the coast ranges of Santa Barbara County, southern California, on Mount Hamilton in central California, and in the Olympic Mountains of western Washington are occupied by forms with 55, 77, or 88 chromosomes, while a few such types occur in the mountains of central Nevada and in the Rocky Mountain region.

The frequent presence of "unbalanced" chromosome numbers, i.e., 33, 55, and 77, is in itself strong evidence that these numbers are maintained by some form of asexual reproduction. Furthermore, heads of *C. occidentalis* and *C. intermedia* were castrated and bagged during the season of 1936. Those of diploid *C. occidentalis* yielded no achenes whatever, while those of the triploid and tetraploid forms developed viable seeds. Although no reliable statistical evidence could be obtained, owing to the destruction of some of the achenes in nearly every head by insect larvæ, a common occurrence in natural populations of *Crepis,* there is a strong indication that facultative as well as obligate apomixis is present. The yield from some of the triploid forms of *C. occidentalis* ap-

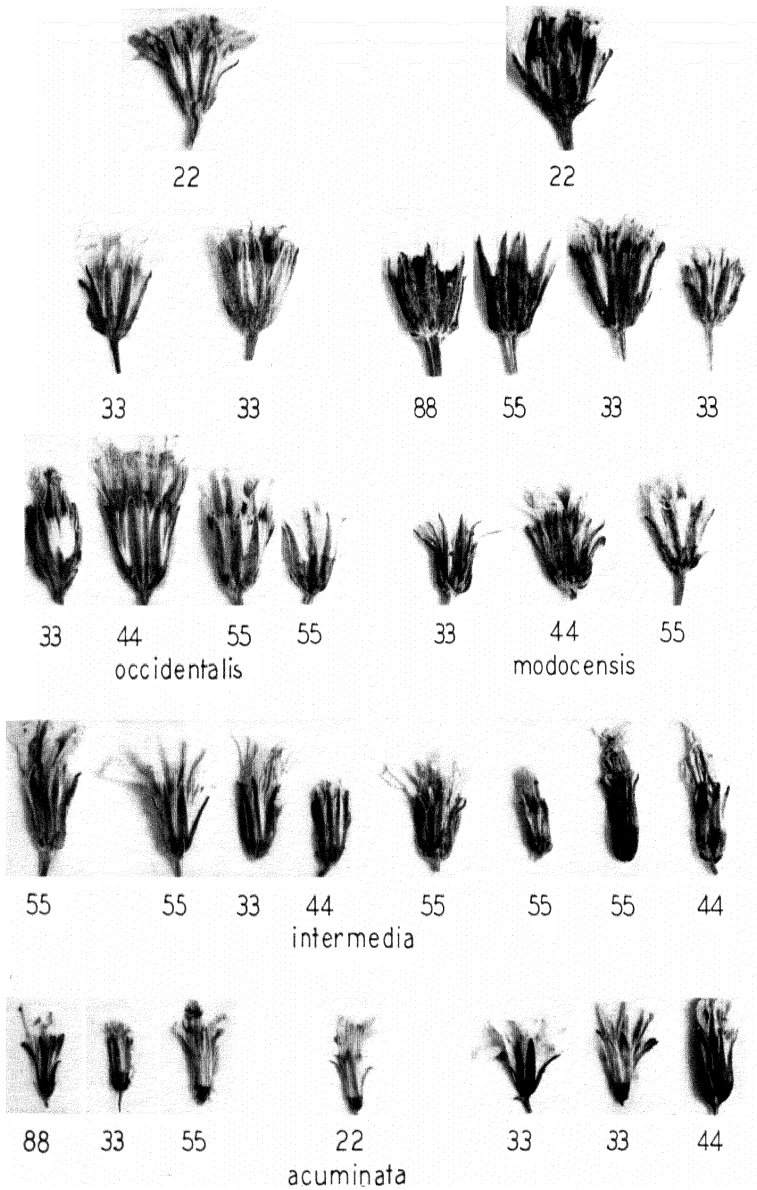
peared to be definitely less than that from *C. intermedia,* indicating that in the former some of the florets are normally pollinated, since these plants with open pollination set a high proportion of seed. A cytological study of apomixis in these species will be discussed in a later publication (Stebbins and Jenkins, in press). The results to date indicate that the type of apomixis is apospory, through the replacement of the megaspore mother cell during the prophases of meiosis by a cell from the nucellus or from one of the integuments. The situation in both the pollen and ovule development is essentially similar to that found in *Hieracium* by Rosenberg (1906, 1930). Apomixis is mostly facultative, although in the majority of the forms very few seeds are produced by the sexual method.

GENETIC INTERRELATIONSHIPS OF THE SPECIES

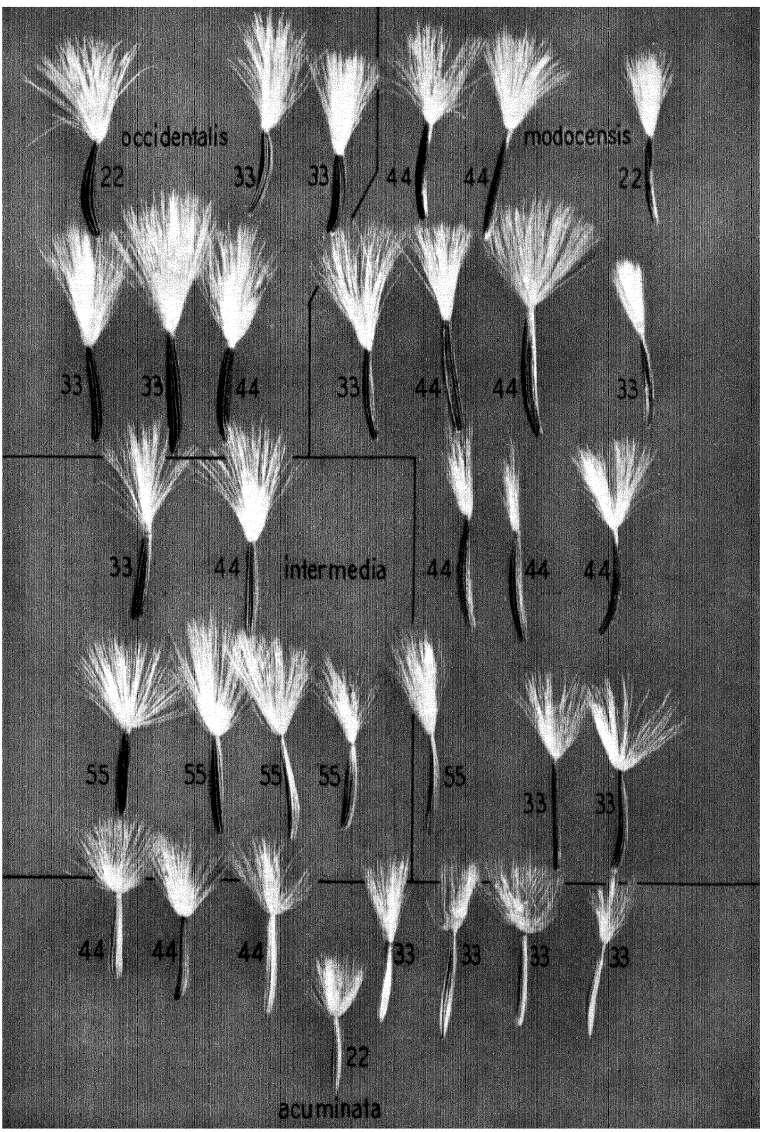
Unfortunately, the specialized soil and climatic requirements of these species, as well as their slow rate of development, have made it impossible to grow them at Berkeley readily enough so that their interrelations could be tested by hybridization. Nevertheless, some inferences concerning their genetic behavior can be drawn from a study of natural populations and herbarium specimens, and of the plants as raised in the greenhouse and compared with the same forms in the field.

Based on these studies, the group of *C. runcinata* is interpreted as a *Rassenkreis* (Rensch, 1929). There is no evidence that it has been able to cross with any of the other species, and its subdivisions are so similar in habit, in the majority of their floral characteristics, and in their climatic and edaphic preferences that there is little doubt of their relatively recent common origin. The various subdivisions of this species are, however, probably ecotypes rather than ecospecies (Turesson, 1929), since there is no evidence of genetic isolation among them. They all intergrade morphologically with one another in the areas in which they overlap or approach one another, and, judging from the character of their pollen and the abundance of their seed setting, the intermediate forms are sexually reproducing and fully fertile, or nearly so. In the case of the most extreme unit, *C. runcinata* subsp. *Andersonii,* two of the subspecies intermediate between it and subsp. *typica* occupy definite geographical ranges, although they intergrade at either end of their range with other forms. The subdivisions of *C. runcinata* most clearly understood by the authors have been designated as subspecies. There are many other forms in existence, but since the species has not been studied in the field from this point of view, only those have been described which can be easily recognized from a series of

Herbarium specimens of diploid *C. occidentalis* (upper left), *C. modocensis* (upper right), *C. acuminata* (lower right), and of selected polyploid derivatives of them (including *C. intermedia*). The numbers indicate the probable chromosome numbers of each form. About 1/7 natural size.



Involucres of forms corresponding to those in plate 1. Slightly reduced.



Achenes of forms corresponding to those in plates 1 and 2. About twice natural size.

forms in one or more characteristics are spoken of as allopolyploids. Many of the allopolyploid forms are much nearer to one diploid species than to the others, and are therefore included in the taxonomic treatment under that species. Although the parentage of each of the forms cannot be determined from its morphological characteristics alone, the resemblance to the various diploid forms of each of the *formæ apomicticæ* described in the taxonomic section is recorded in tables 5 to 12 (pp. 196–200) as an aid in the determination of their affinities. From these tables the fact is evident that many of them are secondary derivatives combining the characteristics of three or more of the diploid forms.

In these tables are listed the various characteristics in which each apomict resembles the diploid form of some species other than that under which that apomict has been placed in the systematic treatment. Each number and letter refers to a particular characteristic, and corresponds to those used in table 4. A symbol in parentheses indicates a very slight resemblance; a symbol in italics indicates as great or a greater resemblance to the species under which the symbol occurs than to the species under which the apomict has been placed in the systematic treatment. For instance, in table 5, under *C. pleurocarpa* apm. *Grayi* the symbols indicate that this apomict slightly resembles diploid *C. monticola* in the shape of the cauline leaves (4c), and diploid *C. occidentalis* in lobing of leaves (2b) and in length of corolla (7a); is definitely transitional from diploid *C. pleurocarpa* toward diploid *C. occidentalis* in its indumentum (1), length and width of its basal leaves (2a), stature (3), and length of its anthers and style branches (7b and 7c), although nearest diploid *C. pleurocarpa* in all these respects; also it strongly resembles diploid *C. occidentalis* in the ribbing of its achenes (8d) and the length of the pappus (8f). In all other characteristics apm. *Grayi* is typical of *C. pleurocarpa*.

FACTORS AFFECTING THE DISTRIBUTION OF THE SPECIES

CLIMATIC FACTORS

Perhaps the most important factor affecting the distribution of the American species of *Crepis* is the climatic one. The climatic diversity of the area in which they occur is reflected in the diversity of the species and varieties of this genus, and particular species, subspecies, and apomictic forms show in their distribution a striking correlation with the distribution of the climatic provinces into which this area is divided. This fact is emphasized by a comparison of the distribution of the seven diploid forms, as outlined in figure 1, with the distribution of the climatic provinces as classified by

Thornthwaite (1931). If we compare figure 1 of this publication with Thornthwaite's map, we find that each of the diploid forms of *Crepis* occurs in only one or a part of one of Thornthwaite's provinces. In particular, the most widespread diploid, that of *C. acuminata*, occupies a climatic province which is also the most widespread, i.e., one which is microthermal as to temperature and has a moisture deficiency at all seasons. On the other hand, those diploids which are most restricted in distribution are found in a series of climatic provinces whose distribution is also relatively limited, i.e., those with winter precipitation and a deficiency of moisture during the summer. These are found near the Pacific Coast.

A second fact, which is evident from a study of figure 1 alone, but which is emphasized by comparison with Thornthwaite's map is that the five diploids found in the provinces characterized by summer moisture deficiency may be arranged in a progressive series in regard to their tolerance of cold and dryness. Diploid *C. pleurocarpa* and *C. monticola* are found in the mildest, most humid climate of all, i.e., mostly at low and medium altitudes (800–1500 m) in the Klamath Mountains of northern California. Diploid *C. occidentalis* occurs chiefly in a drier and slightly cooler climate, i.e., at elevations of 1200–1600 m on the arid east side of the Sierra Nevada, while *C. Bakeri* subsp. *Cusickii* occurs in the same climatic province as diploid *C. occidentalis*, but farther north. The fifth diploid, or pair of closely related diploids, those of *C. modocensis* subspp. *typica* and *rostrata*, occurs in regions as dry as or drier than that occupied by the diploid forms of *C. occidentalis* and *C. Bakeri* subsp. *Cusickii*, but considerably farther north than either of these two, or, in the case of *C. modocensis* subsp. *typica*, chiefly at higher altitudes, above 2200 m. This arrangement of the diploids, furthermore, forms a series characterized by a progressively increasing geographical range. Diploid *C. pleurocarpa* has the most restricted range, and diploid *C. modocensis* (including both subspecies) is the most widespread of the five. In the opinion of the writers, this correlation has a considerable bearing on the problem of the origin and history of the various diploids, as is brought out in the next section.

Finally, the distribution of the polyploid apomicts shows an interesting correlation with their morphological resemblances to the different diploids. Those which resemble closely only one of the diploids, and are therefore probably of non-hybrid (autopolyploid) origin, occur for the most part only within the same climatic province as that which contains their diploid progenitor. Where

these autopolyploids are much more widespread than the diploids, as in the case of *C. pleurocarpa,* the diploid occupies only a small part of its climatic province. The chief exception to this rule is that of *C. acuminata.* Autopolyploids of this species are common along the eastern side of the Sierra Nevada, in a climate characterized by summer precipitation deficiency, while the diploid occurs chiefly in regions with a uniform deficiency of precipitation.

The polyploids of hybrid origin (allopolyploids) combine in a striking manner the climatic requirements of the diploids from which, judging by their morphological characteristics, they are probably derived. This fact is best illustrated by analyzing in relation to their morphological resemblances the distribution of the various allopolyploid apomicts which have been grouped in the systematic treatment under the four subspecies of *C. occidentalis.* All of these show definite morphological resemblances to the diploid form of this species, and hence would be expected to possess some of the climatic preferences of this form. The basis of the following analysis is the description of the apomictic forms found on pages 122–138, as well as tables 4 and 7 (end of volume). These should be consulted for reference.

The wide range of *C. occidentalis,* as recognized in the systematic treatment (see fig. 18), which is in such striking contrast with the restricted distribution of its diploid form, is apparently due chiefly to the fact that the polyploid apomicts have combined certain of the climatic requirements, as well as the morphological characteristics, of various other species with those of diploid *C. occidentalis.* Those of subsp. *typica* that are identical with the diploid form do not occur outside the climatic province of the latter. Apm. *Nuttallii* (see p. 123), which occurs in a climate with moisture deficiency at all seasons, is in its reduced number of involucral bracts and florets somewhat transitional toward *C. acuminata,* which occurs characteristically within this province. The apomicts grouped under subsp. *costata,* which are in several characteristics transitional toward *C. intermedia* and therefore toward *C. acuminata* (see p. 126), occur almost entirely within the provinces occupied by the latter species. Their greater extension southward in these areas, as compared with diploid *C. acuminata,* is correlated with the relatively southerly range and the consequently greater tolerance of heat of diploid *C. occidentalis.*

Crepis occidentalis subsp. *pumila,* most of the apomicts of which are transitional toward *C. pleurocarpa,* extends the range of *C. occidentalis* chiefly into the humid province occupied by diploid *C. pleurocarpa,* although it also occurs sparingly in other provinces

with uniform deficiency. The apomicts which occur in these latter provinces are somewhat transitional in leaf shape toward *C. modocensis* (apm. *Rydbergii,* p. 130) or toward *C. acuminata* (apm. *longifolia,* p. 131). Subsp. *conjuncta,* which like subsp. *pumila* is somewhat transitional toward *C. pleurocarpa,* also occurs in the humid province, though at higher elevations than subsp. *pumila,* and extends, in dry situations, into the wet climatic province of the Sierra Nevada. Its tolerance of a colder climate than the diploid forms of either *C. occidentalis* subsp. *typica* or *C. pleurocarpa* is correlated with its resemblance in habit and leaf shape to *C. Bakeri* and *C. modocensis.*

This tendency for the polyploids to combine the climatic preferences of different diploids is illustrated also by the characteristics of two apomicts occupying one of the isolated outposts of the range of the group as a whole, i.e., the Mount Hamilton range in west central California. The climate in this area is different from that found in any of the regions occupied by diploids. It is as mild as that in which diploid *C. pleurocarpa* and *C. monticola* are found, and therefore milder than that occupied by any other diploid. On the other hand, it is drier than the climate required by these two diploids, and approaches in dryness that occupied by diploid *C. occidentalis.* Of the two apomicts of *Crepis* found in this area, one combines the morphological characteristics of diploid *C. occidentalis* and diploid *C. pleurocarpa* (*C. occidentalis* subsp. *pumila* apm. *hamiltonensis,* see p. 132), while the other is intermediate between the diploids of *C. occidentalis* and *C. monticola* (*C. monticola* apm. *australis,* see p. 117). This suggests that these two apomicts have combined the preference for a mild climate of *C. pleurocarpa* and *C. monticola* with the tolerance of aridity of diploid *C. occidentalis,* and that this favorable combination of the different climatic preferences of their two diploid ancestors has been largely responsible for the ability of these allopolyploids to spread into a region not inhabited by any diploid.

These comparisons suggest that the wider distribution of the polyploid forms of *Crepis* can be largely explained on the basis of their origin by hybridization, with previous or subsequent doubling of the chromosome number, if one assumes that the physiological characteristics which control their climatic requirement combine and segregate in the same manner as do their morphological characteristics. The mere presence of polyploidy appears to have had less effect on their climatic tolerance, although in several cases it undoubtedly has increased their tolerance for extremes of temperature. This is evident from the fact that the forms occuring in the mesothermic areas of central and southern California, as well as

those on the higher mountains of the Sierra Nevada and the Olympics, are apparently high polyploids, while within the area occupied by the diploids of some species, such as *C. monticola* and *C. pleurocarpa*, these original forms are outnumbered by their polyploid relatives.

EDAPHIC FACTORS

Crepis runcinata differs so radically in its habitat from the other endemic species that the edaphic factors controlling its distribution must be considered separately. *C. runcinata*, being a plant of wet meadows, is governed by the distribution of such sites within its range, and hence tends to follow the various watercourses. For this reason, the chief mountain ranges are more important in controlling its distribution than is the case in the other group. The Continental Divide is, in general, the western boundary of the range of subsp. *typica*, although its range extends slightly westward into Utah, opposite the region of southern Wyoming in which the Rockies break down as a continuous range. This subspecies has developed forms, probably ecotypes, fitted to varying altitudes and degrees of soil acidity and alkalinity, so that it is prevalent throughout its range, being replaced only in the most alkaline localities by subsp. *glauca*. Subsp. *glauca*, as well as subspp. *hispidulosa, imbricata*, and *Andersonii*, the latter three occurring predominantly or entirely on the west side of the Rockies, are more restricted in their requirements, having a decided preference for alkalinity. They occur mostly in the major valleys of the Great Basin area, where the drainage is relatively poor, and the alkali tends to accumulate. The absence of montane forms of *C. runcinata* from the mountains of Oregon, Washington, and most of Idaho, which otherwise have a large representation of Rocky Mountain types, and possess many situations similar to those in Colorado, Wyoming, and Montana that are regularly occupied by *C. runcinata*, may be attributed to this cause. Furthermore, the relative aridity of the Great Basin and Columbia Plateau areas reduces the number of moist habitats favorable to *C. runcinata*, and causes the subspecies inhabiting this region to be more local and discontinuous in their ranges. This is particularly true of the western portion of the Great Basin, i.e., the area occupied by subspp. *Andersonii, imbricata*, and *Hallii*.

In the case of the other species, which occur primarily on semiarid, well-drained hillsides, the principal edaphic factors governing their distribution are first the degree of exposure, the amount of available moisture, etc., and second the character of the soil. In

regard to the former characteristics the regions in which they occur are so variable that almost any ecological niche permitted by the gross climatic factors can be found. For instance, diploid *C. occidentalis* adjusts itself to the very different ecological conditions on either side of Long Valley, south of Honey Lake, California, by changing its habitat. On the western side of this valley, as in Sierra Valley, where the precipitation is relatively high and the temperatures are lower, *C. occidentalis* occurs on sunny, south-facing slopes, in the driest spots available. On the east side of the valley, as in the arid mountains back of Constantia (Red Rock), it is confined to north- or northwest-facing slopes, often among low shrubs which partially shade it. Hence these edaphic factors are of minor significance as compared with climate in controlling the geographic distribution of the forms.

Diploid *C. pleurocarpa*, however, differs strikingly from the other species in its moisture requirements. Not only does it occur exclusively in the humid climatic belt, but within this area it has been collected only along streams, in dense forests of *Pinus ponderosa, Libocedrus decurrens*, and *Pseudotsuga mucronata*. Although *C. pleurocarpa* is found chiefly in well-drained sites, one colony was seen along the headwaters of the Trinity River in a moist, boggy spot, growing with such species as *Carex mendocinensis* Olney, *Helenium Bigelovii* Gray, and *Rudbeckia californica* var. *glauca* Blake.

The other major factor, the soil requirement, is of primary importance. The best evidence for this is the fact that the distribution of the various diploids, in the regions in which they have been studied by the writers, is strikingly correlated with the distribution of certain geological formations. Diploid *C. pleurocarpa* and *C. monticola* are confined to the Mesozoic and Paleozoic rocks of the Klamath Mountains, but both are rare in or absent from the regions underlain by granodiorite. Diploid *C. pleurocarpa*, moreover, has been found only on serpentine and similar formations. A third species, *C. occidentalis*, occurs chiefly on the softer volcanic rocks of Miocene age or on formations derived from them, although it has been collected once on granodiorite, and once (at Montague) on unconsolidated sediments derived from the Mesozoic complex of the Klamath area. The great gap in its range (see fig. 18) from south of Honey Lake Valley to the north end of Shasta Valley, a distance of 170 miles (272 km), is correlated with the presence in the intervening area of a nearly continuous sheet of basalt of Pliocene age, i.e., younger than the Miocene volcanics on which diploid *C. occidentalis* grows, and much less strongly weathered. Previous to 1937 about twelve collections of *C. occidentalis* were known from

this intervening area, all of them polyploid. During the summer of 1937 the junior author, with Dr. J. A. Jenkins, made a careful survey of this area to see whether diploid *C. occidentalis* could be found in it. On the Pliocene basalt itself, all forms of *C. occidentalis* were found to be rare, and confined either to alluvial deposits along dry watercourses or to sunny hillsides within the pine forest. All the forms collected in this area were judged, either from the size of their stomata or by actual count, to be polyploids. *C. occidentalis* was found more abundantly in and near the valley of the Pit River, where there are many valley flats and alluvial terraces, and where several basaltic ridges of Miocene age rise above the Pliocene basaltic flow. In a cross section of this area, from Burney nearly to Alturas, nine large colonies of *Crepis* were found, all but two of them consisting of hundreds of plants. Examination of all the variant forms in each of these colonies revealed that all had the stomatal size of polyploids. Since diploid forms have been found in nearly half of the colonies of *C. occidentalis* known south of Honey Lake Valley, there is good evidence that the gap in the range of this diploid is actual, and is correlated with the unsuitable character of most of the soils in the intervening area.

Diploid *C. modocensis* occurs on the strongly weathered basalts of Miocene age (or on sediments derived from them), while in northeastern California and adjacent Oregon diploid *C. acuminata* is confined to the hard, Pliocene basalt, except for one known station on a hard outcrop of Miocene basalt.

In order to obtain more accurate information on the types of soil produced by the various geological formations on which *Crepis* occurs, a rough analysis of soil samples collected at typical stations for the various species was made. This is presented in table 3, along with the underlying geological formation and the species of *Crepis* found at each station.

Although the number of samples analyzed is small, many more were taken, and a rough comparison between them indicates strongly that, as expected, the general type of soil found on a particular type of geological formation and in similar situations is fairly constant, and that the differences between the different formations are valid. The geological formations were obtained chiefly from the geologic map of the Northern Sierra Nevada prepared by Dr. Olaf P. Jenkins of the California State Division of Mines, and from a similar unpublished map of the Siskiyou region, for the loan of which the writers express their thanks. These were supplemented by field observations of the junior author. The pH determinations of the soils were made in the field by Dr. J. A. Jenkins and the junior author by means of a Lamotte-Kenny field

TABLE 3. SOIL CHARACTERISTICS OF SELECTED LOCALITIES FOR *Crepis* SPECIES IN NORTHEASTERN CALIFORNIA AND WESTERN NEVADA

Locality	Species found	Geological formation	Soil pH		Soil texture
			6 in.	12 in.	
Park's Creek, Siskiyou Co.	*C. pleurocarpa* 2*x* and 3*x*	Ultrabasic intrusives	6 8	6.8	Light clay
West of Mt. Shasta, Siskiyou Co	*C. pleurocarpa* 3*x* and 5*x*				
	C. monticola 2*x* and 4*x*	Serpentine	6.8	7.2	Light clay
Reno, Nevada	*C. occidentalis* 2*x*	Alluvial terrace	7	7.2	Light clay
Sierra Valley, Sierra Co.	*C. occidentalis* 2*x*, 3*x*, 4*x*				
	C. modocensis subacaulis 3*x*	Miocene volcanics	6.6	6.8	Light clay
Head of Ball's Creek, Sierra Co	*C. occidentalis pumila* 3*x*				
	C. Bakeri 4*x*	Miocene volcanics	6 6	6.8	Sandy clay
	C. modocensis subacaulis 4*x*				
Summit of Diamond Mtn., Lassen Co.	*C. modocensis* 2*x*, 3*x*, 4*x*	Miocene volcanics	6.8		Clay loam (almost sandy clay loam)
Susanville, Lassen Co.	*C. monticola* 5*x*				
	C. occidentalis pumila 5*x*	Pliocene basalt	6 6	6 8	Heavy clay loam
	C. intermedia 4*x*				
	C. acuminata 3*x*				
Southwest of Horse Lake, Lassen Co.	*C. acuminata* 2*x* and 3*x*	Pliocene basalt	6.4		Light clay loam
	C. intermedia 3*x*				
Along Ball's Creek, Sierra Co	*C. acuminata* 3*x*	Acidic intrusives (granodiorite ?)	6.6	6.8	Sandy loam
	C. intermedia 3*x*				
	C. modocensis subacaulis 4*x*				

indicator set. The mechanical analyses of their texture were made by Mr. C. Cleary from single samples collected by the junior author. For his services and for much advice on this section of the work the writers are indebted to Dr. G. B. Bodman.

The similarity in pH reaction of all these different soils, derived from very different geological formations, is very striking. Other measurements of the junior author have shown that in these dry regions soils derived even from acidic intrusive rocks (granite, diorite, etc.) are almost neutral, so that a preference for circumneutral or slightly alkaline soils is characteristic of all plants inhabiting them. *C. pleurocarpa,* which exists in more humid regions, shows its preference for neutral or slightly alkaline soils by usually avoiding granitic areas. The same is true of *C. monticola, C. Bakeri,* and most forms of *C. occidentalis,* whereas *C. acuminata* appears to be more acid tolerant than the other species. This, perhaps, explains the fact that polyploid derivatives of this species are the only forms of *Crepis* which are frequent in the granitic areas of the Sierra Nevada.

In the texture of the soils inhabited by *Crepis* there are more definite differences. Diploid *C. pleurocarpa, C. monticola, C. occidentalis,* and probably *C. Bakeri* prefer light clays, while diploid *C. modocensis, C. acuminata,* and probably *C. exilis* occur in more loamy soils. The stony, light clays on which *Crepis* species are found appear to be formed by intensive disintegration and weathering on well-drained hill slopes; *Crepis* is never found on the heavier valley clays. The harder basalts and the granitic rocks do not produce the lighter clay soils. This seems to be the best explanation for the fact that diploid *C. acuminata* and *C. modocensis* have been found in northeastern California and adjacent Oregon only in basaltic areas, while diploid *C. occidentalis* occurs chiefly on the softer volcanics or, as at Reno, on river terraces.

The polyploid apomicts tend to combine the soil preferences of different diploids just as they combine their climatic preferences. In general, they are most frequent in soils similar to those occupied by the diploids which they resemble most closely morphologically. Thus polyploid *C. acuminata* and *C. intermedia* are the only polyploids which are frequent in basaltic or granitic areas in northeastern California, although apomicts of *C. occidentalis* subsp. *pumila* which show definite resemblances to *C. acuminata,* as well as those of *C. monticola* which are transitional toward *C. acuminata* and *C. modocensis,* are also found. Polyploid apomicts of *C. acuminata* occur also in areas underlain by the softer volcanics, but here they have a different ecological distribution. In basaltic and granitic areas different apomicts of *C. acuminata* occur both

in wooded and in open sagebrush areas, but are more frequent in open country; whereas, in areas underlain by the softer volcanics they are largely confined to pine woods or to sheltered north-facing slopes. The open, exposed spots in these areas are occupied mostly by forms of *C. occidentalis* that show little or no resemblance to *C. acuminata*. There is, therefore, reason to believe that the tolerance for different types of soil is inherited in these allopolyploids of *Crepis* much as are their morphological characteristics.

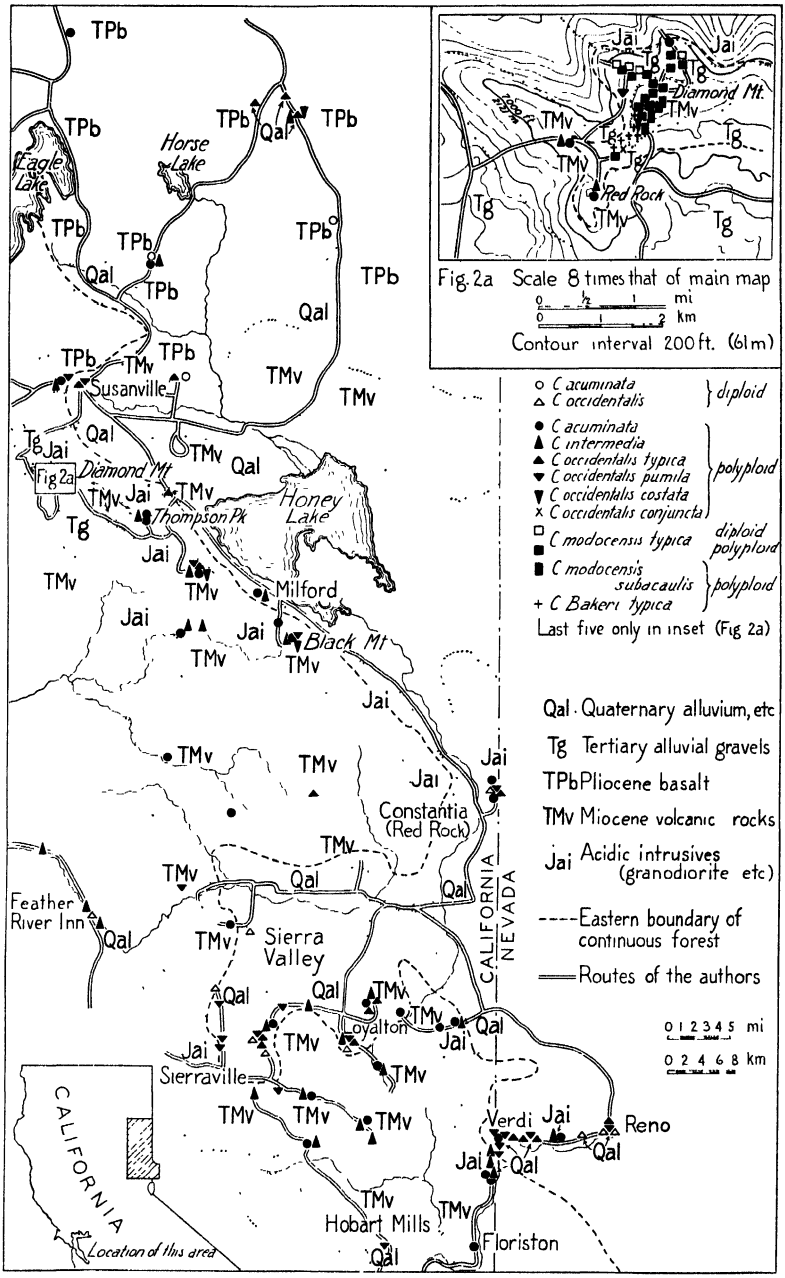
The effect of climatic and soil conditions on the distribution of the various forms can best be illustrated by describing a critical region in which two of the most widely differing diploids, those of *C. acuminata* and *C. occidentalis*, occur in adjoining areas. This is a part of northeastern California and adjacent Nevada illustrated in figure 2. The principal topographic and climatic features of this region may be summarized as follows: The eastern escarpment of the Sierra Nevada cuts across the center of it, running from the Truckee River west of Verdi north to the southern end of Honey Lake Valley, and thence northwestward to Diamond Mountain, where it ends. This escarpment varies in height from about 800 to 1000 m, the altitude of its base above sea level being 1200 to 1500 m, and of its crests about 2000 to 2450 m. It is the principal factor determining the climate of the region, since on its upper slopes, crests, and everywhere westward there is abundant precipitation. This region, therefore, is well forested except on the more exposed crests and in the larger valleys; whereas to the eastward lies the desert area of the Great Basin, in which the *Artemisia* ("sagebrush") association predominates. The approximate eastern boundary of the forest is marked on the map by a broken line. The Sierran escarpment breaks down in one place, i.e., opposite Sierra Valley.

Here a large bay of the *Artemisia* association projects into the forest area. This association forms a fringe all around the edge of the valley, and completely replaces the pine forest on its eastern side. There are other smaller valleys occupied by this association

---

FIG. 2. Map of a portion of northeastern California and adjacent Nevada, showing the distribution in that region of diploid ***Crepis occidentalis*** and ***C. acuminata*** and of their polyploid derivatives. Many stations for ***C. occidentalis*** subsp. ***conjuncta***, ***C. Bakeri*** subsp. ***typica***, and ***C. modocensis*** subspp. ***typica*** and ***subacaulis*** exist in this region, but have been omitted from the main map for the sake of simplicity. In the inset, figure 2*a*, all known stations for ***Crepis*** are shown. Diploid forms of a species are indicated by symbols in outline; solid symbols indicate polyploids.

(Base map adapted from U. S. Forest Service maps of Tahoe and Plumas National Forests, and from U. S. Geological Survey map, Honey Lake Quadrangle. Geological formations obtained chiefly from map prepared by Olaf P. Jenkins, geologist, California State Division of Mines, supplemented by observations of the junior author.)



(For description see opposite page.)

scattered throughout the area west of the escarpment. East of the escarpment, there are irregular mountain peaks and ranges of varying altitudes whose slopes are treeless or support low trees of *Juniperus occidentalis* and *Cercocarpus ledifolius*. North of the Honey Lake Valley is an undulating plateau with an altitude of about 1500 m, from which rise mountains, mostly of gentle contours, whose summits are 2000-2350 m high. The part of this plateau figured in the map supports a sparse growth of *Juniperus occidentalis*, along with a typical *Artemisia* association.

Three of the geological formations found in this area are significant in determining the ranges of *Crepis occidentalis* and *C. acuminata*. These are acidic intrusives ("granitic" rocks, mostly granodiorite) of Jurassic age; Miocene volcanics, including the harder basalts, rhyolites, etc., as well as the softer tuffs, agglomerates, and the like; and the Pliocene basaltic flow. The two former alternate with each other in the region south and west of Honey Lake. North of this lake begins the extensive basaltic plateau which extends from here northward through eastern Oregon to Washington (see Fenneman, 1931).

As can be seen on the map, diploid *C. occidentalis* occurs only south of Honey Lake, and east of the forest boundary (except in one open valley along the Feather River). There is one station for it on the granitic formation, but all the others are either on the Miocene volcanics or (as at Reno) on river terraces. Diploid *C. acuminata*, on the other hand, is found only on the basaltic plateau. Although only three stations for this diploid are shown, many others undoubtedly exist within the area, and several are known farther north. In Oregon it is common on the basaltic plateau (see Peck, 1925). The polyploid apomicts of both species, as well as of their allopolyploid derivative, *C. intermedia*, occur throughout the area, although all are most abundant in the regions underlain by Miocene volcanics. In the granitic regions, all forms of *Crepis* are rare or absent within the limits of continuous forest, while the open country is populated chiefly by polyploid *C. acuminata* and *C. intermedia*. In the region underlain by Miocene volcanics, these two species are more common in wooded areas, while diploid and polyploid *C. occidentalis* occur on the open slopes. In the basaltic area, polyploid *C. occidentalis* occurs only along dry watercourses and alluvial flats that are not too alkaline, and is therefore very local.

The detailed study of almost any small area inhabited by several different forms of *Crepis* shows that, like many other forms closely related to each other, they are sensitive even to relatively slight local changes in the environment. A good illustration of this point

is the *Crepis* population on two mountain summits of northeastern California, i.e., Diamond Mountain and Red Rock (see inset, fig. 2*a*). These are two nearly parallel ridges, about 1.6 km (1 mile) apart, running approximately west-northwest and east-southeast. The ridge of Diamond Mountain varies from about 2180 to 2340 m (7200 to 7700 feet) above sea level; that of Red Rock does not become higher than 2240 m (7400 feet), while the lowest point of the connecting ridge is about 2200 m. Both crests are of highly weathered Miocene volcanic rock, but the connecting ridge consists partly of an alluvial formation derived from these volcanics and from the granitic rock adjoining them. Terraces of the same alluvium extend to the northward and eastward of Diamond Mountain. The ridges are all arid and treeless. Diamond Mountain, facing the dry Honey Lake Valley and the deserts to the eastward, is exposed to strong, desiccating winds, and is relatively cold, the snowdrifts lying about it in sheltered spots through July. Red Rock is less exposed, somewhat lower, and warmer, while the intervening ridge provides an intermediate habitat, although at its inner end it is more sheltered than is either of the main ridges.

On the most exposed, driest part of this area, i.e., the alluvial terraces north and east of Diamond Mountain, occurs diploid *C. modocensis* subsp. *typica* along with its autopolyploid derivatives. This diploid is known elsewhere only from two other mountain ranges on the northeast side of the Great Basin (see figs. 1, 24), whereas polyploid apomicts of subsp. *typica* are characteristic Great Basin–Rocky Mountain forms. The other vegetation here is a dwarf form of *Artemisia tridentata, Leptodactylon pungens,* and a series of herbs most characteristic of the Great Basin ranges and the dry eastern slope of the Sierra Nevada. Among such characteristic species as *Sitanion hystrix* (Nutt.) J. G. Sm., *Allium parvum* Kell., *Eriogonum Douglasii* Benth., *Parrya cheiranthoides* (Nutt.) Jepson, *Astragalus Hookerianus* Gray, and *Scutellaria nana* Gray, there occur two rarities, *Pentstemon miser* Gray, and *Cryptantha humilis* (Gray) Payson (= *Oreocarya humilis* Greene). (For the determination of the former the authors express their thanks to Dr. D. D. Keck, for the latter, to Dr. I. M. Johnston). Both of these, which also are known from only two or three other stations in California, occur, like diploid *C. modocensis,* exclusively on the northeast slope of the ridge, and predominantly or entirely on the alluvial formation.

About the summit of Diamond Mountain, and at the beginning of the connecting ridge, polyploid *C. modocensis* is the most common form of *Crepis,* and several different apomicts occur. Those found on the most exposed west- and northwest-facing slopes are

mostly autopolyploid, but on the southeast- and south-facing slopes and in the saddles they give way to subsp. *subacaulis* apm. *diamondica* (see p. 150) and other apomicts transitional toward *C. Bakeri* and *C. occidentalis*. *C. Bakeri* subsp. *typica* is found all along the connecting ridge in more sheltered spots and at lower altitudes, while one small colony each of *C. occidentalis* subsp. *costata* and of subsp. *conjuncta* was found. *C. Bakeri* and *C. occidentalis* subsp. *conjuncta* are characteristic of middle altitudes and relatively sheltered, not extremely arid spots in the northern Sierra Nevada; subsp. *costata* occurs at low altitudes chiefly in the Columbia Plateau and Rocky Mountain regions. The other vegetation found about the summit of Diamond Mountain and the beginning of the connecting ridge, i.e., in the area in which autopolyploid *C. modocensis* is dominant, shows a predominance of species characteristic of the northern Great Basin, the Columbia Plateau region, and the Rocky Mountains, which are here at or near the southwestern or western limit of their range. These include *Eriogonum Douglasii* Benth., *Arenaria aculeata* Wats., *Beckwithia Andersonii* (Gray) Jepson, *Lesquerella diversifolia* Greene, *Gilia congesta* Hook. f. (typical), *Erigeron linearis* (Hook. f.) Piper, *E. Eatonii* Gray, and Aplopappus acaulis (Nutt.) Gray. As the ridge becomes lower and less exposed, *C. modocensis* subsp. *typica* becomes less common and subsp. *subacaulis* and *C. Bakeri* more so, while most of the Great Basin species disappear, being replaced by species characteristic of the northern Sierra Nevada, such as *Allium platycaule* Wats., *Trifolium Kingii* Wats., *Viola purpurea* Kell., and *Wyethia mollis* Gray.

Finally, on the ridge of Red Rock, there occur apomicts of *Crepis* typical of middle and higher altitudes in the Sierra Nevada. On the crests are a form of *C. intermedia* close to apm. *sierræ*, (see p. 185) and one of *C. acuminata* near apm. *depauperata* (see p. 175), while other larger apomicts of the same two species occur on the southwest slope of this ridge. The other species on this ridge are also more typically Sierran. Although the Great Basin–Columbia Plateau element is still represented by *Eriogonum proliferum* T. & G., *E. Douglasii* Benth., *Pentstemon lætus* Gray subsp. *Roezlii* (Regel) Keck, and *Aplopappus acaulis*, there is a definitely larger number of typical Sierran species, e.g., *Calochortus Leichtlinii* Hook f., *Eriogonum ursinum* Wats., and *E. marifolium* T. & G., *Polygonum Davisiæ* Brew., *Pentstemon gracilentus* Gray, *Galium multiflorum* Kell. var. *hirsutum* Gray, *Orthocarpus pachystachyus* Gray var. *cuspidatus* (Greene) Jepson, and *Erigeron ursinus* Eat. Within this small area, then, the distribution of *Crepis* apomicts is closely correlated both with the climatic and

edaphic features of the environment, and with the other elements of the vegetation.

This illustrates the fact that the apomicts of *Crepis* and other genera, with their narrowly restricted requirements, are ideally suited to serve as "indicators" of the vegetation of a particular area. This point has already been brought out by Gustafsson (1935*b*) in connection with *Taraxacum* and *Rubus* apomicts. An added advantage of the use for this purpose of apomictic and other polyploid groups is that polyploids in general are younger than their diploid relatives. Furthermore, the origin of a particular polyploid from one or more diploids can often, as in *Crepis,* be inferred from morphological resemblances or in some cases can be verified by hybridization experiments. Hence a study of several of these groups within the same floras should provide valuable information concerning the interrelationships and derivations of the floras themselves. A case which suggests the possibilities of this method is provided by the relationship between the *Crepis* species found in two of the "endemic areas" of Jepson (1925, pp. 12–13), i.e., the Klamath and the Tehaman areas. *Crepis pleurocarpa* and *C. monticola* occur in both these areas, but are rare outside them. In both cases the original diploid, sexual form is confined to the Klamath area, while the Tehaman is occupied only by polyploid apomicts. The only other form of *Crepis* frequent in the Tehaman area is *C. occidentalis* subsp. *conjuncta,* a series of polyploid apomicts of complex origin, three of whose putative parents, diploid *C. occidentalis, C. pleurocarpa,* and *C. Bakeri* subsp. *Cusickii,* occur in the Klamath area. This indicates that the *Crepis* flora of the Tehaman area is derived from that of the Klamath, and suggests the possibility of a similar origin for other elements of the former.

ORIGIN AND DEVELOPMENT OF THE SPECIES

The present distribution of the species, as well as our knowledge of their cytology and their relationships to the Old World species of *Crepis,* gives a good foundation on which we can form a plausible theory concerning their origin and development. The occurrence of the following sequence of events is strongly supported by the cytological and morphological evidence.

The American group, with $x = 11$ as their basic chromosome number, was probably derived in the first place from hybridization between 4-paired and 7-paired species of the Old World, followed by doubling of the chromosome number, to produce fertile allopolyploids (see Hollingshead and Babcock, 1930). The numbers 4 and

7 rather than 5 and 6 are selected because of the obvious affinities between the American group and several 4-paired Asiatic species (see below, p. 30). Judging from the great diversity of the 11-paired species, they probably differ from each other in their origin, and several different 4- and 7-paired species were involved in their parentage. Very likely the various allopolyploids appeared at different times. After their appearance these original 11-paired species became more and more isolated from one another, and, with the exception of *C. runcinata* and *C. acuminata*, each became more and more uniform in its morphological characteristics and ecological requirements, so that their ranges became more and more restricted. Then the development of polyploidy, probably accompanied by a reversal in climatic conditions, enabled the species to come together again, and the complex series of allopolyploid, apomictic forms, which are now the dominant representatives of the group, was built up. In *Crepis*, the evidence as to whether chromosome doubling preceded hybridization or whether diploid hybrids were formed first is conflicting. In favor of the hypothesis that the original polyploids were autopolyploids, formed directly by the doubling of the chromosome set of the diploid forms, are the following facts. The 11-paired species are now so well isolated from one another geographically that they rarely grow together and diploid, F_1 hybrids between them have not been found in spite of diligent search. Secondly, the autopolyploid, i.e., the non-hybrid polyploid forms of different species, do occasionally grow together, or the autopolyploid of one species may grow with the diploid of another. Hence, since experimental and cytological evidence indicates that these autopolyploids have retained some ability for sexual reproduction, both tetraploid and triploid hybrids could be produced at present from these contacts. These hybrids could at once develop apomixis, and so perpetuate themselves.

A fact that is difficult to reconcile with this hypothesis, however, is the failure of *C. runcinata* to develop autopolyploid forms. This species has chromosomes very similar to those of the other species, its habit of growth is not radically different, and it has been subjected to very similar changes in environmental conditions. If hybridization has preceded polyploidy in *Crepis*, the exclusively diploid condition of *C. runcinata* can be explained. It has a very different geographical and ecological distribution from that of the other diploids, which makes hybridization between it and them very unlikely. Furthermore, sterility barriers have apparently not developed within *C. runcinata* itself. Sterile hybrids, from which allopolyploids usually arise, could not, therefore, be formed involving *C. runcinata*.

An alternative hypothesis must therefore be considered as possible, i.e., that the diploid forms of *pleurocarpa, occidentalis, acuminata*, etc. had wider geographical and ecological ranges in the past, and that these ranges once overlapped. On this basis, polyploidy could have developed first in sterile, diploid hybrids which were formed before the diploids became isolated from one another, and which have long been extinct.

The situation in *Crepis*, nevertheless, does not favor Ernst's (1918) theory, that hybridization is the cause of apomixis, but rather that of more recent workers (Winkler, 1920; Gustafsson, 1932; Darlington, 1937), that it is an accompanying phenomenon. In *Crepis* many of the autopolyploids are just as completely apomictic as are the allopolyploids.

The production of these polyploid derivatives must have taken place over a considerable period of time, during which a large series of them were produced. There are several lines of evidence for this fact. In the first place, the high numbers and complex affinities of many of them indicate that they most certainly are secondary and tertiary derivatives of the original allopolyploid, 33- and 44-chromosome forms. Secondly, many of them are considerably isolated from their nearest relatives. In some cases the gap between them is not favorable for the growth of *Crepis*. Such is the case of the isolated outposts of the genus on Mount Hamilton and the San Bernardino Mountains of California, the Charleston Mountains of Nevada, and the Olympic Mountains of Washington. In others, however, the intervening territory is occupied by other forms of *Crepis*, as is true of the isolation of *C. pleurocarpa* on the east side of the Cascade Mountains, Washington (fig. 14), of *C. Bakeri* subsp. *idahoensis* (fig. 23), of *C. occidentalis* subsp. *conjuncta* in the Teton Mountains of Wyoming (fig. 18), and of *C. occidentalis* subsp. *costata* along the Fraser River in British Columbia (fig. 18). Finally, a few of the allopolyploids combine the characteristics of species whose diploid forms are now widely separated from each other. The most notable of these is *C. intermedia* apm. *cupressensis*, which is intermediate between *C. occidentalis* and *C. exilis* (see p. 187). This form must have originated a long time ago, before the parental types became so completely separated from each other. Significantly, the unusual forms of this type occur at the periphery of the range of the group.

Using these postulates as a basis, a plausible account of the origin and development of the species can be built up. In the first place, the nature of the 4- and 7-paired ancestors of the American species can be inferred from their affinity to present-day species of northern Asia. These affinities are:

Crepis runcinata is closely similar in habit and general floral characteristics to two 4-paired species, *C. præmorsa* Tausch., and *C. gymnopus* Koidz. The former occurs throughout northern Eurasia, extending eastward to the upper Lena basin of eastern Siberia, while the latter is endemic to the island of Hokkaido, northern Japan. The former is a species of rich woodlands, the latter of alpine meadows. The two undoubtedly had a common ancestor, and that ancestor figured also in the ancestry of *C. runcinata.*

Crepis pleurocarpa does not have a recognizable affinity to any Old World species. Since it is essentially endemic in northern California and adjacent Oregon, and its diploid form is narrowly restricted to a geologically and floristically ancient region, i.e., the Klamath area (see p. 110, also Jepson, 1925, p. 12), it may represent an older type than the other species, and may either have progressed since its appearance along a divergent path of evolution or be descended from a form that has no living relatives.

The nearest relatives of *C. monticola* are *C. kashmirica* Babc. (Univ. Calif. Publ. Bot. 14: 328, 1928) and *Dubyæa hispida* (Don) DC., which is also known as *Crepis Dubyæa* (C. B. Clarke) Marq. et Shaw, and as *C. bhotanica* Hutchinson. Both these species are found in the Himalayan region. *C. monticola* differs considerably from *C. kashmirica* in habit, but resembles it in the long hirsute involucres and peduncles, the attenuate involucral bracts, and the shape and ribbing of the achenes. The resemblance in habit between *C. monticola* and *Dubyæa hispida* is, on the other hand, rather close, and both are strikingly characterized by their hirsute indumentum and very narrow attenuate outer involucral bracts. The differences between them are chiefly those that separate *Dubyæa* from *Crepis*, i.e., *D. hispida* has more flattened style-branches, a coarser pappus, and somewhat obcompressed, unequally ribbed achenes. Since *Dubyæa* is considered by the authors to represent a primitive type related to the ancestors of *Crepis*, the Old World ancestors of *C. monticola* may have been among the oldest, most primitive members of the genus. The chromosome numbers of *C. kashmirica* and *D. hispida*, i.e., $n = 6$ and $n = 8$ respectively (Babcock and Cameron, 1934), indicate that they are not the direct ancestors of *C. monticola*, but the past existence of a relative of these three species with $n = 7$ is not unlikely.

Crepis occidentalis has as its closest relative *C. oreades* Schrenk., a rare, 4-paired species of the mountains of Soongaria, on the western edge of the Tibetan plateau. This species closely resembles *C. occidentalis* in its grayish tomentum and particularly in the

size, shape, tomentum, and glandulosity of its involucres, and in the relative length of their inner and outer bracts. As contrasted with *C. oreades, C. occidentalis* is stouter and larger and has a more strongly branched inflorescence. The latter characteristic suggests the 7-paired species to be mentioned below.

Crepis Bakeri is strikingly similar in floral characteristics to *C. Bungei* Ledeb. of the Altai region, another 4-paired species. Furthermore, *C. Bakeri* subsp. *Cusickii*, which includes the diploid form, is sometimes found in moist meadows or valley flats, recalling the habitat of *C. Bungei.*

Crepis modocensis shows an equally close resemblance to *C. burejensis* Fr. Schmidt, another 4-paired species of the northern islands of Japan. Both these species have long, whitish-tipped glandless trichomes on their involucres, and slender, black achenes which in *C. burejensis* and *C. modocensis* subsp. *rostrata* are shortly beaked. The leaves of *C. burejensis* are, however, much less strongly pinnatifid, while the ribs of its achenes are slenderer and more numerous. *C. chrysantha* Froel., a relative of *C. burejensis* which occurs even farther northeast, in Kamchatka, is less close to *C. modocensis.*

Crepis exilis resembles *C. modocensis* and therefore *C. burejensis* in its achenes, but in its much-branched, dichotomous inflorescence it approaches *C. flexuosa* (DC.) Benth. et Hook. f., a 7-paired species of the Tibetan region. In habit, *C. exilis* suggests *Youngia tenuifolia* (Willd.) Babc. et Stebbins, also of the Altai-Tibetan region, but the latter species is quite different in its achenes and other critical characteristics (see Babcock and Stebbins, 1937). Furthermore, its diploid form has presumably 5 pairs of chromosomes (ibid., p. 47). Hence it could not have figured in the ancestry of the American species, although, since it partly bridges the gap between *Youngia* and *Crepis*, it may have had once a 7-paired relative in *Crepis*, which could have figured also in the ancestry of *C. exilis.*

Crepis acuminata also resembles *C. flexuosa* in its inflorescence, as well as its glabrous, markedly calyculate involucres, and in the shape and color of its achenes.

The Old World species mentioned above include the majority of the *Crepis* flora or northeastern Asia. This theory, therefore, leads to the inference that at the time when the younger of the American species originated, the genus was nearly as well developed in northeastern Asia as it is today, and that nearly all the 4- and 7-paired species present entered into the formation of the polyploids. An alternative explanation, that the resemblance between the American species and the Asiatic ones mentioned above is due to parallel

evolution, is made unlikely by the fact that in southwestern Asia and the Mediterranean region the very much larger number of *Crepis* species present does not include any which resemble the American group as closely as those mentioned above.

The place of origin of the 11-paired species was most probably somewhere between their present locality and the present centers of their Old World relatives, i.e., the secondary centers in the Altai region and northeastern Asia (see Babcock, 1936). If the 7- and 4-paired species had crossed to this continent, we should expect to find at least some of their descendants still here, particularly in Alaska, most of which has been open to plant habitation throughout the Cenozoic, and which among its diverse climatic habitats includes some that are closely similar to those inhabited by such Old World species as *C. chrysantha* and *C. burejensis*. On the other hand, if the 11-paired species had originated in central Asia, they certainly would have established themselves in that region, which is so similar ecologically to their present habitat. A more likely hypothesis is that they originated in eastern Siberia at a time when a subhumid to semiarid, cool temperate rather than an arctic climate prevailed there, at least in the lowlands.

Strong evidence that Asia and America have been connected by a belt of semiarid, temperate climate at some time since the advent of modern floras is provided by the distribution of certain plants in the two regions. Fernald (1925, p. 258) has mentioned the case of *Aster angustus*, a species of saline habitats found on the dry, northwestern portion of the Great Plains of North America, and recurring in Tibet and Afghanistan. A similar distribution is shown by *Artemisia Dracunculus* L. (*sensu latior*), while *Lactuca pulchella* DC., which in America has nearly the same range as *Crepis*, has been considered by Lindberg (1936) to be identical with *L. tatarica* (L.) C. A. Meyer, another species of the steppes of central Asia. The writers have not seen enough specimens of *L. tatarica* to judge as to its identity with *L. pulchella*, but at least the two species are very closely related to each other, and are much less close to any other species of *Lactuca*, either of the Old World or the New. Two genera which support this affinity are *Chamærhodos* and *Stipa*. The former consists of three or four species in central Asia, one of which, *C. erecta* (L.) Bunge, is very close to the single American species, *C. Nuttallii* Pick., of the northwestern Great Plains, whose range in this region coincides almost exactly with the eastern portion of the range of *Crepis runcinata*. *Stipa* is one of the most highly developed of all genera of grasses on the semiarid plains and open forests occupied by *Crepis* in America, and has a similarly strong representation in central Asia. It is rare or absent in the

boreal and arctic regions intervening. These species and genera are all steppe rather than boreal forest or tundra types, and they certainly could not have crossed the Siberian-Alaskan land bridge under the conditions that prevail at present. The necessary climatic change, however, would need only to be one of temperature. The precipitation recorded for central and northern Alaska varies from about 5 to 15 inches (117–351 mm), and is therefore less than that now required by *Crepis*, while Abbe (in Brooks, 1906) says of the interior of this peninsula, "It is characterized by great extremes of temperature and a very moderate rainfall, such as prevail in eastern Oregon and Washington" (p. 141). Furthermore, a few of the steppe types, such as *Chamærhodos Nuttallii* and *Stipa comata*, still persist in the upper Yukon region. Direct evidence of a temperate, though humid, climate along the coast of Alaska in early Tertiary time is clearly shown by the abundant series of plant fossils found there (Hollick, 1936). And through the distribution of animal fossils, indirect evidence exists for the presence in late Tertiary time of a climatic connection through this region of the semiarid, temperate type required by most of the American species of *Crepis*. During the early Pliocene, certain primitive New World types of horse suddenly appeared on the plains of Eurasia (Osborn, 1910, p. 264); while this period saw also the first arrival of camels in the Old World from the New (Mathew, 1915, p. 243) and of the Old World antelopes in North America (ibid., p. 247). This connection was undoubtedly broken in late Pliocene time with the onset of the glacial climate, but the presence of Pleistocene fossil horses in northern Siberia and in Alaska (Hay, 1913) suggests that a semiarid, temperate climate may have been temporarily reestablished there during one of the earlier interglacial periods (Sangamon, Aftonian) of the Pleistocene. There was, therefore, a considerable period of time during which the majority of the 11-paired species of *Crepis* could have been formed in this region. Preceding the period of semiarid climate was one in which an extensive mesophytic forest stretched from Siberia through Alaska to the rest of North America (see Hollick, 1936), and which probably supplied conditions like those now required by *C. pleurocarpa*.

One great difficulty with this or any other hypothesis to explain the origin of the 11-paired American species is the complete absence at present of members of this group in the Old World, and the corresponding absence of 4- and 7-paired species (except for *C. nana* and *C. elegans*, which are obviously not closely related to the 11-paired species) in the New World. A possible explanation of this puzzling situation is as follows.

The region in which the 11-paired species were formed was probably on the Siberian side of the land bridge rather than in Alaska. The newly formed allopolyploids must have migrated extensively throughout the semiarid parts of North America, but made little or no headway to the westward for the following reasons: (1) The prevailing westerly winds would make migration of the wind-borne achenes of *Crepis* more rapid to the eastward than to the west. (2) In migrating westward, these newly formed species would come into direct competition with the parental types, while their eastward migration would carry them into a territory not yet occupied by *Crepis*. A parallel case is presented by the present distribution of *C. acuminata*, the polyploid forms of which have migrated extensively to the southward, but have not competed successfully with the diploid form in the central, northern, and eastern parts of its range. (3) The principal mountain ranges of Siberia run generally east and west, rather than north and south, as do those of North America. As the climate became cooler in late Pliocene time, therefore, even these relatively low mountains might stand as a barrier to the southward migration of plants. Hence there was a greater chance that the newly formed species would become exterminated in the Old World than in the New. Their 4- and 7-paired ancestors, which must previously have ranged continuously from central Asia to eastern Siberia, were preserved only south of these mountains.

Although both present and fossil evidence concerning the migration of the species of *Crepis* from Alaska to the western United States is lacking, some idea of the time of migration of the various species can be obtained from the nature of the flora during the Tertiary in the regions which they now occupy. In Miocene time, central Oregon was a region of relatively low relief, and the dominant vegetation, at least in the valleys, is represented by the Mascall flora (Chaney, 1925). This contained *Sequoia*, and consisted chiefly of *Lithocarpus,* black oaks, and other broad-leaved types. This forest vegetation, indicating a relatively mild and humid climate, would not be favorable to *Crepis*. However, a similar type of forest existing today in northwestern California is bounded on the east by a region having a slightly cooler but hardly drier climate, and covered with a forest of *Pinus ponderosa*, *Pseudotsuga mucronata*, and *Libocedrus decurrens*. This is the habitat of diploid *Crepis pleurocarpa* and *C. monticola*. Since *Pseudotsuga* and *Libocedrus* both occur sporadically in the Mascall flora, such a forest may have occupied upland habitats during the Miocene, and have been the first available habitat for *Crepis*, i.e., for *C. pleurocarpa* and *C. monticola*. By Pliocene time the climate of

California was as dry and as diversified as it is at present, though slightly warmer (Dorf, 1933), while in central Oregon there existed along stream banks the Deschutes flora (Chaney, 1938), which consisted of the prototypes of *Populus trichocarpa, P. tremuloides,* and other species which occupy stream banks today in the regions inhabited by *Crepis occidentalis, C. Bakeri, C. acuminata,* and *C. modocensis.* The period during which the 11-paired species could have been formed and have migrated to the region that they now occupy is thus limited to late Miocene, Pliocene, and early Pleistocene time. If each of these species is considered separately, the evidence points strongly to the fact that they appeared at different times during this period.

Crepis pleurocarpa and *C. monticola* show the greatest morphological divergence from the Old World species, and therefore must be judged the oldest from the taxonomic point of view; that is, they must either have progressed farther along their own lines of evolution than the other species, or have evolved from more ancient, extinct 4- and 7-paired types. Furthermore, the range of their diploid forms is narrowly restricted to a geologically ancient area and is the most remote of all from the Old World. Hence they are to be considered relics from the phytogeographic viewpoint. Thirdly, the climatic province that they occupy was more widespread at an earlier date than that occupied by the other species. Finally, their preference is for the highly weathered soils produced by igneous and the metamorphic rocks long exposed to weathering, while diploid *C. pleurocarpa* is now restricted to serpentine. Neither of the diploid forms of these species would be adapted to life on the great lava flows of the Columbia Plateau, even if the climate there were suitable for them. Hence every line of evidence points to the concept that these two species are older than the others, and that their origin and spread was at the beginning of the time alloted for the group as a whole, i.e., during the Miocene epoch. This was the period when the outpouring of lava flows in this region was taking place (Fenneman, 1931, p. 229), and when considerable areas of the underlying rock must have been still exposed. The restriction of their ranges probably took place during the Pliocene, and was apparently determined by two factors: the drying of the climate, and the further outpouring of lava, particularly in southern Oregon and northern California.

Crepis occidentalis and *C. Bakeri* show in all these respects a younger age than *C. pleurocarpa* and *C. monticola.* They have more definite relationships among the Old World species, although the nearest relative of *C. occidentalis, C. oreades,* is the rarest and, next to the Himalayan relatives of *C. monticola,* the most remote

from its New World relatives of any of the species involved. In their ranges, the diploid forms of *C. occidentalis* and *C. Bakeri* are less restricted than those of *C. pleurocarpa* and *C. monticola*, but more so than are *C. modocensis* (including subspp. *rostrata* and *glaucosa*), *C. exilis*, *C. acuminata*, and *C. runcinata*. The climatic province that they occupy is drier than that occupied by *C. pleurocarpa* and *C. monticola*, but warmer than those in which the four other diploids are found. Furthermore, along with the two oldest species, they are adapted to the type of climate with winter precipitation and summer drought, which is not found in Asia (Thornthwaite, 1933). Hence, they have acquired a climatic specialization not possessed by their Old World ancestors. Finally, they are best adapted to light clay soils, which are rare on the more recent lavas, and even today the northward distribution of diploid *C. occidentalis* is partly limited by the Pliocene basalt flows of northeastern California. Hence the same four lines of evidence point to their establishment during the middle of the period mentioned.

A relatively recent origin, on the basis of all these criteria, is indicated for the four remaining diploids, *C. modocensis*, *C. exilis*, *C. acuminata*, and *C. runcinata*. All of them show definite affinities to widespread Old World species (see p. 31). They are all more widespread in their total range than the four preceding (although the range of *C. modocensis* has become broken up, probably in recent time), and occupy for the most part territory that is geologically young. Their preference is for a cool, dry climate and, except for *C. modocensis*, for one with uniform precipitation deficiency, such as exists in Central Asia (Thornthwaite, 1933). Finally, their preference is for less highly weathered soils, and they are well adapted to life on the great lava flows, except, of course, *C. runcinata*. These four species, therefore, were most probably formed during the end of the period allotted for the group, i.e., during mid-Pliocene or early Pleistocene time.

The history of *C. runcinata* must have been quite different from that of the other three species of similar age. Since it is adapted to moist stream banks, it tends to follow the valleys rather than the mountain ranges. Hence it could migrate more easily along the east side of the Rockies than the west, because the drainage basins there are more continuous. This would explain the different center of distribution which this species has at present, even though it probably originated in the same region as the others.

The final stage in its history was also somewhat different. Since it was isolated from all the others ecologically and from most of them in its geographic distribution as well, it did not form allopoly-

ploids with them. Its own origin was relatively homogeneous, and apparently its geographic segregates are not far enough apart so that hybrids between them have a tendency toward the formation of unreduced gametes and therefore allopolyploidy. Autopolyploidy, also, does not occur, for reasons not understood.

It has established a "gene center" in the Rocky Mountains of Colorado and southern Wyoming, where many different climatic and ecological conditions are concentrated into a relatively small area, and the more widespread subspecies appear to have radiated from this center. In the northern and eastern part of its range, where no important geographic or climatic barriers exist, no distinct subspecies have been differentiated, but in the Great Basin region and the mountains of New Mexico and northern Mexico, with their complex drainage systems and isolated valleys, several geographical segregates have developed. The formation of these segregates must have been strongly favored by the drying up of the great glacial lakes of the Great Basin (see Wright, 1914), so that some of them, such as subspp. *imbricata* and *Hallii*, may be of recent origin.

For the second phase of the evolution of the other 11-paired species, i.e., their isolation from each other and their segregation into climatological and ecological provinces, the action of two factors is now clear. In the first place, they differ both in their ancestry and in the time of their origin. Secondly, they arrived in their present habitats at a time when extensive physiographic changes were taking place in the form of mountain building and volcanic activity (Fenneman, 1931, p. 229), which naturally produced great changes in climate and a great diversification within this area. This would tend to emphasize their original diversity.

The final stage in the evolution of this species complex, the formation of the polyploid apomictic derivatives, could have begun as soon as the 11-paired forms were established, and probably took place over a long period of time. The oldest of these apomicts, however, since they had little ability to vary, were undoubtedly exterminated by the great climatic and physiographic changes that have taken place more recently, so that the greater part of those now extant are of Pleistocene or recent origin. A great impetus to their formation was the onset of the glacial climate, which produced moister conditions throughout the region in question (see Dorf, 1933; Wright, 1914, pp. 195–196). This enabled diploid and autopolyploid forms previously isolated from one another by desert conditions surrounding their montane habitats to come together, and thus promoted the production of allopolyploids. In addition it favored the spread of these forms when they appeared, in par-

ticular the ones that were adapted to cooler, moister conditions. The only center which could have existed at that time was the southern one, that is, northern California and adjacent Oregon (see below), so that the Pleistocene routes of migration must have radiated chiefly from that center. The distribution of the species forming this center was undoubtedly different from what it is now, but the area is at present so diverse, and is bounded on all sides by climates so different from those found within it, that the amount of this shifting need not have been very great. For instance, in the region about Honey Lake, diploid *C. occidentalis* and *C. modocensis* could, by migrating 40 km (25 miles) to the eastward, reach a region with only one-half the precipitation of that which they now occupy, and there is no reason to suppose that they would have had to migrate farther to compensate for the greater humidity of the Pleistocene climate.

The northern center of distribution must have developed much more recently than the southern one. Its location, in the coulee region of central Washington, was right at the edge of the last ice sheet, and therefore must have had a tundra or boreal climate until post-Pleistocene time; much of it was submerged at this time (Fenneman, 1931, p. 263). The ancestors of the two diploid species which occur there, *C. exilis* subsp. *originalis* and *C. modocensis* subspp. *rostrata* and *glareosa*, must have existed farther south during the Pleistocene, probably on the basaltic plains of central Oregon and southern Idaho. This would have brought them into contact with *C. modocensis* subsp. *typica* and *C. acuminata*, and have made possible the formation of allopolyploids involving these three species. Such allopolyploids, a group of which constitute *C. exilis* subsp. *typica*, are among the most characteristic *Crepis* apomicts in the Rocky Mountain region. The differentiation of the various diploid subspecies of *C. modocensis* probably came with the warming of the climate at the end of the Pleistocene. Those forms of the species which migrated northward became subspp. *rostrata* and *glareosa*, while those which were left as relics on the higher crests in southern Oregon and northeastern California were differentiated into subsp. *typica*. When, after the retreat of the ice and the subsidence of the postglacial streams, *Crepis* became established in central Washington, the formation of a new series of allopolyploids began. These, chiefly *C. barbigera*, show the variability and "aggressiveness" characteristic of youthful types, and have become common in suitable places. Moreover, they appear to have completely wiped out by competition the *occidentals* subsp. *costata* apomicts which must have migrated through this region in postglacial time to reach British Columbia (see below, p. 41). *C.*

barbigera, therefore, is definitely the most recent of all of the species. It has high chromosome numbers, a continuous range in which it is common and within which all its parental types are found, and a large number of apomicts concentrated within a small area. There is no doubt that many new apomicts of this species are still being formed.

The distribution of certain of the apomictic forms shows several interesting irregularities and discontinuities, the explanation of which should give interesting evidence concerning the history of the floras of which they form a part. For an understanding of the following discussions, the reader should refer when necessary to the descriptions in the systematic section of the apomicts mentioned, while further information concerning their relationships can be obtained from the tables on pages 195–200. The regions in which these interesting anomalies of distribution have been noted are as follows:

Southern California. The *Crepis* flora of the southern Sierra Nevada, as well as that of the Tehachapi Mountains, the San Bernardino range, and the higher summits of the South Coast Ranges, shows a definite break from that of the central Sierra Nevada. None of the apomicts found in the Sierra Nevada between Lake Tahoe and northern Inyo and Fresno Counties is known farther south than this region, while conversely the forms found farther south have few relatives nearer to them than the Truckee-Reno region. The following are the apomicts or groups of apomicts found in southern California and their affinities.

Crepis acuminata apm. *bernardina* and apm. *longiloba* (see pp. 176–177): This group of closely related apomicts, characterized by the unusual combination of lightly tomentulose involucral bracts and 5-flowered involucres, is the most general one throughout the southern Sierra Nevada and the southern California mountains. Related forms are known at relatively high elevations in the Klamath Mountain area of Trinity and Siskiyou Counties and adjacent Oregon, and in the northern Sierra Nevada of Alpine and Plumas Counties. Hence the distribution of this group follows that indicated by Jepson (1925, p. 11) for *Pinus Balfouriana* and several other species. Compared with the group mentioned by Jepson, however, the *Crepis* apomicts are characteristic of lower altitudes and a more arid climate, and are correspondingly more abundant in the southern part of this range.

Crepis occidentalis subsp. *pumila*, apm. *tehachapensis* and relatives of apm. *Rydbergii* (see p. 131): These forms are not known from the southern Sierra Nevada or the San Bernardino Mountains, but are characteristic of the Tehachapi range and the southernmost

peaks of the Coast Ranges (Mount Pinos, Mount Frazier, etc.). The form of subsp. *pumila* in the Charleston Mountains of Nevada is also of this affinity. The nearest relatives of these forms occur in Siskiyou and Plumas Counties, although apm. *longifolia,* which has been found as far southward as Mono Lake, is not very different from the larger forms of subsp. *pumila* from the Tehachapan area.

Crepis occidentalis subsp. *typica* apm. *humilior* (p. 123): This form, or one closely related to it, occurs in the San Bernardino Mountains and the Mount Pinos region, but has not been seen from the Tehachapi Mountains or the southern Sierra Nevada. It recurs along the east side of the Sierra Nevada, from the Truckee River northward, and in this region is connected with the other apomicts of subsp. *typica* by a large series of intergrading forms.

Crepis modocensis subsp. *subacaulis* apm. *bernardina* (p. 150): This form displays the most striking isolation of all. It is represented by two separate collections from Bear Valley, in the San Bernardino Mountains, but since this valley has been converted into a reservoir, is perhaps extinct in the region. The nearest locality to this at which any form of *C. modocensis* has been found is 640 km (400 miles) north, in the region of Reno and of Donner Summit in the northern Sierra Nevada. Nevertheless, one of the numerous apomicts of *C. modocensis* subsp. *subacaulis* in this latter region is identical with that from southern California. There are a few other species which have exactly the same gap in their ranges, the most notable of which are *Draba Douglasii* Gray and *Lewisia minor* Rydb. An explanation of these remarkable isolations should be easier to give after more of the intervening country is explored, to determine the actual extent of the gap.

The Coast Ranges of California. All the forms in this region, i.e., in Mendocino and Lake Counties and on Mount Hamilton, are closely related to or identical with apomicts of the Klamath region, and are derived from *C. pleurocarpa, C. monticola,* and *C. occidentalis.* They are probably young (the high chromosome number of *C. occidentalis* apm. *hamiltonensis* is further evidence of this), and attained their present distribution in late Pleistocene time, coincidentally with the final advance of the ice. The sharp distinction between the apomicts of the Mount Hamilton region and those found on Mount Pinos indicates that the arid transition flora did not extend all the way down the Coast Ranges to the latter region during the Pleistocene.

Southern British Columbia. The two apomicts in this region of which the distribution is particularly interesting are those belonging to *C. occidentalis,* i.e., subsp. *typica* apm. *columbiana* (see p. 124) and the form of subsp. *costata* found at Spence's Bridge

(see p. 127, fig. 18). Both of these forms are known only from the valley of the Fraser River, which was thoroughly glaciated in Wisconsin time, and they must therefore have migrated into this region in postglacial time. Apm. *columbiana* is so little known and of such obscure affinity that little can be said concerning it, except that it appears to represent the result of crossing between facultatively apomictic forms of *C. occidentalis* and *C. modocensis* subsp. *rostrata*. The British Columbia form of *C. occidentalis* subsp. *costata*, however, is closely related to other forms of this subspecies common in central Oregon, and occurring north as far as Klickitat County, southern Washington. But this latter locality and Spence's Bridge are separated by a distance of 512 km (320 miles) and within that gap no *C. occidentalis* is known. This intervening area contains many sites suitable for *Crepis*, and much of it, particularly the plains of central Washington, has been thoroughly explored botanically. This is, in fact, the site of the northern center of distribution of *Crepis* diploids (see p. 8), and in it *C. modocensis* subsp. *rostrata*, *C. exilis*, and *C. barbigera* are common. There is apparently no radical change in the geological formations which could serve as an explanation, nor are the climates of Klickitat County and Spence's Bridge more similar to each other than to that of the intervening area. A possible explanation is as follows: *C. occidentalis* subsp. *costata* probably migrated from Oregon through Washington to the Fraser Valley early in postglacial times, but was represented north of Oregon by relatively few apomicts. At about the same time the diploid, sexual forms of *C. modocensis* subsp. *rostrata* and of *C. exilis* established themselves in central Washington, and began to give rise to a large series of young, aggressive apomicts which by selection became perfectly adapted to their environment. These new apomicts, perhaps aided by a changing climate, competed successfully with the few, relatively constant apomicts of *C. occidentalis* subsp. *costata*, and exterminated them except in localities relatively remote from the center of distribution of the new forms. The disruption of the ranges of some forms as a result of competition with their close relatives is a hypothesis which deserves consideration by plant geographers. When forms occur in very similar habitats, keen competition of this sort is inevitable.

The Wenatchee and Blue Mountains of Washington and Oregon. The most interesting apomicts found in these regions are *C. pleurocarpa* apm. *breviramea* (see p. 113, fig. 14) and two forms of *C. occidentalis* subsp. *conjuncta* (fig. 18). Apm. *breviramea*, known from one locality in the Wenatchee Mountains, is the only form of *C. pleurocarpa* known north of the Klamath Mountains of

northern California and adjacent Oregon, while apomicts of subsp. *conjuncta*, which occur in both the Wenatchee and the Blue Mountains, are closely related to forms of this subspecies frequent in northern California, and were probably derived also from this center of distribution. The recurrence of species in these widely separated areas, i.e., the Wenatchee (Mount Stuart region), Blue, and Klamath Mountains, was first noted by Piper (1906, pp. 69–71), who gave a long list of species with this distribution (some of which, however, have been found more recently in the intervening areas). He ascribed it to the facts, first that the Wenatchee, Klamath, and parts of the Blue Mountains "are alike in being composed wholly or largely of granitic rocks; second, the intervening portion of the Cascades is wholly made up of volcanic rocks." This hypothesis agrees with the distribution of *C. pleurocarpa* in California in that this species avoids the volcanic areas. In the Klamath region, however, it is rare in granitic areas, and occurs chiefly on serpentine and other ultrabasic intrusives. Furthermore, an examination of U. S. Geological Survey folio no. 106 (Mount Stuart) has shown that an extensive area of the latter type of rock exists in the Wenatchee Mountains and includes Iron Mountain, the only known locality for *C. pleurocarpa* in Washington (see p. 108). Hence the principle of Piper's explanation applies very well to *C. pleurocarpa*, since the distribution of ultrabasic intrusive rocks in Washington and Oregon parallels that of the granitic areas.

This striking isolation of *C. pleurocarpa* in the Wenatchee Mountains, along with the evidence presented above that the diploid form of *C. pleurocarpa* is one of the oldest of the 11-paired *Crepis* species, suggests that the Wenatchee form of this species, apm. *breviramea*, is a relic whose ancestors were widespread in Tertiary time and were isolated by the outpourings of volcanic rock in the Cascades. Its recent introduction is made unlikely by the fact that it is quite different from any of the apomicts of *C. pleurocarpa* occurring in northern California or southern Oregon, and that it shows the results of hybridization with *C. intermedia*, a species which also occurs in the serpentine area of the Wenatchees. Furthermore, both the diploid form and the polyploid apomicts of *C. pleurocarpa* found in California and southern Oregon are confined to the Transition and Canadian zones, while apm. *breviramea* occurs on grassy slopes at an elevation of 2000 m (6500 feet), in the Hudsonian zone. If its ancestor was a form of *C. pleurocarpa* which was introduced from the south in postglacial times, and which became well enough established to hybridize with *C. intermedia*, this ancestor should still occur in the Wenatchee Mountains. In that case it would probably be known, since this region, as a result of the enthusiastic

and thorough collecting of Mr. J. W. Thompson, is relatively well known botanically. On the other hand, if apm. *breviramea* is a preglacial relic, the absence of its *pleurocarpa* ancestors could be explained by the fact that this species (except for apm. *breviramea*) does not tolerate an extremely cold climate. Although there were no large glaciers in this part of the Cascades, the main ice sheet was only eighty miles away, and so the climate must have been considerably more severe than that which now prevails in this region, which in turn is a good deal colder than that of the region in which *C. pleurocarpa* occurs in California and Oregon. Hence the absence of typical *C. pleurocarpa* would be expected on this basis, and the preservation of apm. *breviramea* could be ascribed to its acquisition of hardiness from *C. acuminata* (through *C. intermedia*). The suggestion of Piper (*op. cit.*, p. 69) that many of the species isolated in the Mount Stuart region are Tertiary relics is therefore well supported by the case of *C. pleurocarpa*. Since serpentine areas occur in the Blue Mountains of Oregon, and forms of both *C. acuminata* and *C. intermedia* which are transitional toward *C. pleurocarpa* are known from this same region, *C. pleurocarpa* itself should also be sought there.

In the case of the distribution of the two apomicts of *C. occidentalis* subsp. *conjuncta* this explanation does not hold. In the northern Sierra Nevada subsp. *conjuncta* is found primarily on volcanic rocks, while the nothern Blue Mountains of Washington, where subsp. *conjuncta* apm. *crassa* occurs (see p. 137) are also volcanic (Piper, 1906, p. 71). An alternative explanation would have to take into account the fact that these apomicts are polyploids of complex derivation, as well as the fact that, in contrast with *C. pleurocarpa* apm. *breviramea*, they are nearly or quite identical with apomicts occurring in California. Furthermore, the evidence presented above indicates that diploid *C. occidentalis* and *C. Bakeri* subsp. *Cusickii*, the probable ancestors of subsp. *conjuncta*, are younger than *C. pleurocarpa*; and *C. Bakeri* subsp. *Cusickii* occurs chiefly in the volcanic areas. For these reasons, the writers are inclined to believe that the apomicts of *C. occidentalis* subsp. *conjuncta* attained their present distribution during Pleistocene or recent times. Their complete absence from the Cascade Mountains in Oregon cannot be considered proved as yet. Since the eastern slope of these mountains is relatively steep, there is a relatively narrow belt that is climatically suited to them, much of which is still unexplored botanically. Hence any new hypothesis to explain these isolations would be premature.

The Olympic Mountains of western Washington. Only two closely related apomicts, referred to *C. occidentalis subsp. pumila*,

have been found here (chiefly apm. *olympica*, see p. 134). These are transitional between subsp. *pumila* and subsp. *typica*. One *Crepis* species of the Olympic Mountains is listed by Jones (1936, p. 26, "*C. intermedia*") with a group of arid transition species occurring in the grassland climax in the Hudsonian zone. He considers these as "the remnant of a former vegetation, of a flora which once occupied the lowlands, and that on account of suitable ecological conditions they have been able to persist in the mountains." On page 260 he correctly distinguishes this form from *C. occidentalis* of the "Upper Sonoran and Arid Transition zones of eastern Washington," i.e., subspp. *typica* and *costata*, but erroneously identifies it with *C. intermedia*. The characters mentioned are exactly those of *C. occidentalis* subsp. *pumila* as defined in this work. This subspecies has not been seen from the Yakima or Wenatchee regions, so that the nearest relatives of apm. *olympica* are in the Blue Mountains and the Snake River region of southeastern Washington. From this evidence the following conclusions can be drawn concerning the origin of apm. *olympica*, and perhaps, therefore, of other arid transition plants in the Olympic Mountains: (1) It is probably not a recent introduction, through bird migration etc., since in that case representatives of the much nearer *Crepis* flora of the eastern side of the Cascades should also have been established here by the same agency. (2) It is a complex, secondary polyploid derivative, and is probably not of preglacial (i.e., Pliocene) origin.

Hence the best explanation is that its ancestors arrived during some hot, dry period, either interglacial or early postglacial. Then a change of climatic conditions exterminated the forms that lived in the lowland and connected it with other forms. Only apm. *olympica* was adapted to life in the semiarid Hudsonian zone, and thus able to survive.

THE EFFECT OF POLYPLOIDY AND APOMIXIS ON EVOLUTION

The American species of *Crepis* can be divided into two groups on the basis of the type of evolution that has taken place within them. In *C. runcinata* (and also *C. nana* and *C. elegans*) there have been no changes in chromosome number, other than the initial polyploid derivation of *C. runcinata* from its 7- and 4-paired ancestors, and reproduction has remained entirely sexual. Evolution in this group has apparently proceeded by means of genetic change through mutation and perhaps other agencies, with selection in response to climatic and edaphic influences. There has thus

been developed a typical *Rassenkreis* (Rensch, 1929), in which morphological variation is more or less directly correlated with climatic and edaphic differences, and the most extreme habitats are occupied by extreme morphological types. Since there is a complete series of intergradations between these extreme forms, and there is no evidence that the intermediate types are sterile hybrids, *C. runcinata* can be considered a single species.

On the other hand, the nine other species, *C. pleurocarpa, occidentalis, acuminata*, etc., have had a very different evolutionary history, owing to the prevalence of three processes; polyploidy, hybridization, and apomixis. As has already been pointed out, the sexual forms of these species, except that of *C. acuminata*, are very restricted in their distribution and in the degree of their morphological variation. Furthermore, if the polyploid derivatives are excluded, these diploids are completely distinct from one another in their morphological characteristics, and are completely isolated from one another genetically. No evidence whatever of diploid hybrids between any two of these species has been found, in spite of diligent search, and the behavior of their allopolyploid derivatives indicates that such hybrids, if they existed, would be highly sterile.

The vast majority of the representatives of these species are the polyploids, and it is these which exhibit the enormous amount of intergradation between the various species, as represented by their original, diploid forms. Since these polyploid apomicts must have been descended from the diploid, sexual forms, their course of evolution since the beginning of their formation is clearly outlined, and the three factors which have been at work are definitely known. Hence a comparison of the polyploids with the diploid members of the same complex, and a comparison of the whole complex with the polymorphic species *C. runcinata* (which is homoploid), should shed considerable light on the influence of polyploidy, hybridization, and apomixis on evolution.

The point which should be emphasized in this connection, and which has already been mentioned, is that, while most of the diploids possess characteristics not found in any other diploid of this complex, all the polyploids *are either identical with one or other of the diploid forms except for size differences and different ecological preferences, or else combine the characteristics of these forms.*

From this fact we may conclude that divergent evolution has been at a standstill in these polyploids, and that all evolutionary changes within them have been through the activity of the three processes mentioned above. These changes have involved both the

morphological characteristics of the plant and its ecological preferences.

Morphological change has been of three types:

1. The production of *gigas* characteristics.
2. The recombination of the various characteristics of the diploids in many different ways.
3. The breaking up of the polyploid complex into "microspecies," the individuals of which are identical with each other, and separated from the nearest related "microspecies" by minute differences.

The first part of our task, therefore, is to find out what rôle each of the three processes—polyploidy, hybridization, and apomixis—has played in the production of these three types of change.

Increased size is known to be the result of both polyploidy and hybridization. *Gigas* characteristics have been found in many autopolyploids, notably those of *Solanum* (Winkler, 1916), in which the effect of hybridism is ruled out, and a good account of them is given by Müntzing (1936). On the other hand, increased size due to hybrid vigor is a phenomenon familiar to all geneticists, and its preservation by means of allopolyploidy is an established fact (see Sansome and Philp, 1932, p. 212). In *Crepis*, both these factors have been active. Some (though by no means all) of the autopolyploids possess distinct *gigas* characteristics; these are most marked in *C. Bakeri*, *C. monticola*, and *C. acuminata*, but they are practically absent in *C. occidentalis* and *C. exilis*. *Gigas* allopolyploids which are unusual in the size and luxuriance of their vegetative parts include several apomicts of *C. intermedia* (see apm. *grandis*, p. 184) and most of those of *C. barbigera*, while unusually large heads, florets, and achenes are found in derivatives of *C. occidentalis* and *C. modocensis* (see *C. modocensis* subsp. *subacaulis* apm. *grandiceps*, p. 149). The effects of polyploidy and hybridization on size and vigor are so closely interrelated that no separate analysis of their rôles can be made.

The recombination of the characteristics of the diploids has been primarily the result of hybridization. Polyploidy has assisted this process by making possible the hybridization of species whose diploid representatives could not grow together because of their very different ecological preferences. Apomixis has greatly increased the number of recombinations possible, since it has made possible the perpetuation of forms with unbalanced chromosome numbers (i.e., 33, 55, etc.), and of other types which, if sexual, would be sterile because of difficulties in chromosome pairing at meiosis (see Darlington, 1937, p. 194).

The establishment of "microspecies" has, of course, been primarily the result of apomixis, although some of the sterility barriers which exist between closely related members of this complex are due also to polyploidy. The existence of "microspecies" has been observed by all students of apomictic groups, and is the chief basis of their taxonomic difficulties. The phenomenon can best be seen by observing populations of such a group in the field. By comparing individuals of such populations, the observer can quickly see that two or three characters "go together," that is, there is a definite correlation in the variation of several characteristics, and a definite discontinuity in some of them, i.e., certain intermediate types are rare or absent from the population. This was studied in an apomictic population found on Black Mountain, Lassen County, in northeastern California. All the plants of *C. acuminata* in this colony were without pollen, so that they are practically obligate apomicts. There were two easily recognizable apomictic forms, one (*C. acuminata* apm. *longiceps*, see p. 174) coarser, with broader lobes on its leaves, relatively long involucres, few inner bracts and florets, short outer bracts, and longer pappus; the other (apm. *sierræ*, see p. 175) more slender, with narrower leaf-lobes, shorter involucres, relatively numerous inner bracts and florets, longer outer bracts, and shorter pappus. In addition there were several individuals which did not correspond to either form, some of which could be "matched" with each other, so that they appeared to form additional, less common apomicts. In figure 3A,B,C, the type of variation found within fifty-five plants of this colony is plotted in respect to three characteristics: length of the longest outer bract, average number of florets per head, and average length of the pappus. Those individuals which in their other characteristics agree with one of the two chief apomictic forms are represented on the graphs by simple dots; those which are more or less aberrant in the dimensions of their involucres, achenes, etc. are indicated by open circles. When the length of the outer bracts is plotted against the length of the pappus or the number of florets, the individuals fall very distinctly into two groups, representing the two chief apomictic forms. Ten of the fifty-five plants counted are aberrant, and these can be grouped into five classes. They represent five additional apomicts, of which only 3, 2, or 1 individuals were obtained. When number of florets is plotted against pappus length, the distinction is less clear, but can still be recognized. The distinction between the two main apomicts is emphasized by the fact that one of them (apm. *sierræ*) has the stomatal size of a triploid, and the other (apm. *longiceps*) that of a tetraploid or pentaploid (a fact which was not realized when the study was

made), but equally definite differences could be found between apomicts having the same chromosome number.

As a contrast to this situation, the variation in respect to the same three characteristics within the same number of plants of a purely sexual, diploid colony of the same species is plotted in figure 3D,E,F. This colony was found on the north side of Mount Shasta, Siskiyou County. Actual counts of $2n = 22$ were made on two individuals of this colony, while the stomatal size and the character of the pollen of sixteen more, including the most extreme variants, indicated that all of these were also diploid. The figures show that, although the degree of variation is greater than that in the entire Black Mountain population, no segregation into groups exists. The variation within this population is extreme for *C. acuminata*; in fact the entire series of specimens from the eastern part of the range of the diploid form, i.e., Idaho, Montana, Wyoming, and Colorado, shows much less variation than that found in this single colony.

Although one might expect the presence of apomixis to limit strongly the number of biotypes present in a species as a whole, this does not seem to be the case, at least in regions close to or within the range of a diploid ancestor of the apomicts. Although the number of biotypes within a single population is definitely limited, different populations, even within the same small area, differ considerably from one another. For instance, along the escarpment southwest of Honey Lake (fig. 2) there have been found, in an area 45 km (30 miles) long by 13 km broad, ten different colonies of apomictic *C. acuminata*. Of these, only two possessed an apomictic form in common, namely, the two on Black Mountain, which are only about 1 km apart. The total number of apomicts of *C. acuminata* now known from this area is thirteen, and doubtless many more exist, since much of it is still unexplored. Of this number, two, apm. *longiceps* and apm. *sierræ*, have been found outside the area, and the latter extends north and south along the Sierra Nevada for a distance of at least 130 km (80 miles). Nevertheless, the majority of the apomicts of *C. acuminata* in the Sierra Nevada are very restricted in their distribution, and their number is very large. This is true of most of the other species in northernmost California, although the apomicts of *C. intermedia* and to some extent *C. occidentalis* tend to be more widespread.

On the other hand, the situation in localities more remote from the centers of distribution is very different. On the Mount Hamilton range in central California only two apomicts of *Crepis* are found: *C. occidentalis* apm. *hamiltonensis* (p. 132) and *C. monticola* apm. *australis* (p. 117). Both of these recur 250 km. (160

miles) to the northward in the north Coast Ranges of Mendocino and Lake Counties. The majority of the *Crepis* apomicts in southern California have been found in more than one locality, while two of them, *C. occidentalis* apm. *humilior* (p. 123) and *C. modocensis* apm. *bernardina* (p. 150), are identical with forms found 600 km to the northward. The situation in the Rocky Mountain region is apparently somewhat similar, although the apomicts of this area have not been so carefully studied. For instance, one very distinctive apomict, *C. exilis* apm. *Osterhoutii* (p. 167), is found in the Rocky Mountains from the Canadian border at Glacier National Park south to northern Colorado, a distance of 1200 km (750 miles.) The agamic complex of *Crepis*, therefore, and probably other such complexes as well, shows very marked concentrations of variability at or near the centers of distribution of the diploid sexual forms, and a progressive "thinning out" of the biotypes at greater and greater distances from these centers, so that the number of forms in any one locality becomes fewer and fewer, and they become more and more distinct from one another. The same phenomenon is found to a much less extent in sexual species, i.e., "gene centers" have been described in them by Vavilov and others. The accentuation of this characteristic in an agamic complex is due to the following causes:

1. The sexual forms are able to keep on producing polyploids, which then tend to become apomictic, so that within the distributional center new apomicts are constantly being produced.

2. Evidence from both the cytology and the morphological variability of the populations points to the fact that the facultative apomixis often precedes the obligate type in the history of a group of forms. Although the phenomena of pollen development do not always parallel those in the ovule, there is a definite trend in the former case which is probably similar in the latter. Within the range of the diploid forms of *C. acuminata* and *C. modocensis*, the autopolyploid derivatives form pollen which is nearly or quite normal, but in more distant localities (as well as along the edge of the range of *C. acuminata*) more and more apomicts are found in which no pollen at all is formed. Since the facultative apomicts can produce many new forms in each generation, there is considerable variability within populations containing these types. This was found by Ostenfeld (1910) in *Hieracium* subg. *Pilosella*. Although Gustafsson (1935*a*, p. 61) and Ernst (1918) believe that the presence of total apomicts in *Taraxacum* and *Archieracium* indicates that "parthenogenesis has evidently arisen all at once" in these groups, this need not be so, and probably is not so in *Crepis acuminata*. The *Taraxacum* and *Archieracium* apomicts studied

are apparently far removed from their sexual ancestors, at least from regions in which these ancestors are of general occurrence. If regions could be found in which these sexual forms are abundant (perhaps they no longer exist), facultative apomicts might, in the opinion of the writers, be found there. In *Antennaria Parlinii* Fernald there is a suggestive analogy. This species throughout New York, New England, and elsewhere in the northern part of its range consists entirely of total apomicts, and staminate plants of it are in this region practically unknown. In Virginia and West Virginia, and elsewhere in the southern part of its range, occur forms of which the staminate plants are as common as the pistillate, and produce good pollen. In the intervening areas, as about Washington, D. C., true staminate plants with good pollen are absent, but staminate intersexual plants are occasional. These form a few good achenes and, judging from megaspore development, are facultatively apomictic (Stebbins, 1932). The evidence from both *Crepis* and *Antennaria*, therefore, points to the hypothesis that the onset of total apomixis is a gradual process.

3. In localities remote from the center of distribution, the apomicts found will be mostly those which have been selected as particularly well adapted to a certain type of environment, and have been able to migrate long distances. Near the centers of distribution, the apomict population includes many "beginners," most of which are destined to failure and oblivion; at remote distances the dominant forms are "veterans," which have been tried by the rigors of the environment. That these total apomicts have not completely lost their ability for variation was shown by Ostenfeld's (1921) discovery of "apogamic mutation" in *Hieracium* sect. *vulgata*.

There remains to be considered the effect of polyploidy, hybridization, and apomixis on the ecological and distributional history of a group. The effect of these three processes together can best be judged by comparing the complex of apomictic forms first with their sexual ancestors, and second with their exclusively diploid, sexual relative, *C. runcinata*. The first comparison has already been made (p. 8), and it demonstrates clearly that the effect of these processes is similar to that produced by polyploidy alone; that is, the range of the species is greatly increased. A similar increase of range due to polyploidy has been found by Manton (1934, 1937) in *Biscutella*, Anderson and Sax (1936) in *Tradescantia*, Fagerlind (1937) in *Galium*, and in several other genera (see Müntzing, 1936). The second comparison, i.e., that of the whole complex of apomicts and their sexual ancestors with a purely sexual, diploid species (*C. runcinata*), raises doubt that this in-

crease in distribution is beyond what can be achieved by a related, homoploid species in which neither polyploidy nor apomixis occurs.

As has been brought out in the previous section, the origin of *C. runcinata* was much the same as that of the diploid ancestors of the apomicts. On comparison of the present ranges of the two groups (figs. 1 and 6), the fact is evident that *C. runcinata,* in spite of its lack of polyploidy, has acquired a greater geographic range than have all the nine species of the apomictic group put together. Moreover, the range of habitat of *C. runcinata* is equally great. It occurs in the Subalpine zone in Colorado at 3300 m, and in the Sonoran zone in southern Utah and Nevada; in the humid, forested region of the northern Rocky Mountains and in the desert valleys of Nevada; beside cool mountain streams and about hot springs; in granitic regions, where the soil reaction is presumably acid, and on alkaline flats. Moreover, it is as common and "aggressive" in the center of its range as are any of the polyploid derivatives of the agamic complex. Such a comparison is perhaps not fully justified, because at least some of the ancestors of *runcinata* must have been different species from those which produced *pleurocarpa, acuminata, occidentalis,* etc. In other words, if *runcinata* should develop polyploidy and apomixis, it might extend its distributional area even farther than it has. Nevertheless, since all the present-day species of *Crepis* are more or less closely related to one another (see Babcock and Emsweller, 1936), the ancestors of *runcinata* were in all likelihood closely related to those of the apomictic complex. Moreover, several different 4- and 7-paired species must have figured in the origin of the apomictic group, whereas only two or three were involved in the origin of *runcinata.* Hence the potentialities in the whole group of apomictic species would be expected to be greater than those in *C. runcinata* alone.

Furthermore, the most extreme in its habitats of all the New World species of *Crepis* is the arctic-alpine *C. nana,* which has only 7 pairs of chromosomes. Since several of the 4-paired Asiatic relatives of the American species are also alpine or subalpine in their habitats, the genus *Crepis* is another exception to the principle of Tischler (1935), that polyploids are more characteristic of colder climates. Finally, the tolerance of aridity characteristic of the American species occurs also in their 7-paired Asiatic relative, *C. flexuosa.*

A similar situation can be found in other genera in which polyploid complexes are highly developed. The European *Antennaria dioica* (L.) Gaertn. though strictly diploid, has as wide a geographic and ecological range as the (ecologically though not systematically or phylogenetically) comparable American species,

A. neodioica, in which polyploidy is highly developed. In *Potentilla* the most common and widespread species in California is *P. glandulosa* Lindl., which has an almost unbelievable range of ecological habitats, from sea level up to 3300 m, and from the rain-forest belt along the coast to the semiarid interior; yet this species is strictly diploid. On the other hand, the high polyploid *P. gracilis*, though almost equally polymorphic and common in many regions, is more restricted in the climatic zones which it occupies than *P. glandulosa*. Hence many species which have remained diploid have acquired as great ranges of distribution and climatic tolerance as have other members of the same genus which have developed high polyploidy.

There are at least two factors which serve to exaggerate the difference in distribution between polyploid forms and their diploid ancestors. In the first place, the polyploid forms come into direct competition with their progenitors, so that the slightest increase in vigor will cause the polyploid to spread at the expense of the diploid, and therefore to reduce the range of the latter. This has been noted by Huskins (1931) in *Spartina Townsendii*, and appears to be one cause of the rarity of some of the diploid forms of *Crepis*, particularly those of *C. pleurocarpa*, *C. monticola*, and *C. modocensis*. Secondly, the production of new forms through polyploidy is much more rapid than by the ordinary genetical processes. The vigor due directly to chromosome doubling as well as the hybrid vigor perpetuated by allopolyploidy is manifest immediately, while the newly acquired chromosome number protects any favorable combination of characters from being "swamped" by hybridization. Hence under rapidly changing environmental conditions, the production and perpetuation of polyploids will be strongly favored, while many diploid forms will not be able to produce new ecotypes quickly enough, and will disappear.

There is every reason to believe that one of the principal causes of the great abundance of polyploid types among Angiosperms at present is the great variation in climate that accompanied the last glaciation. In other words, polyploidy is largely a "short cut" by which a species or genus may adapt itself easily to a rapidly changing environment. In the case of *Crepis*, the diploid forms within the agamic complex have undoubtedly been subjected to greater climatic changes than has *C. runcinata*. The region which the former now occupy is climatically very diversified (Thornthwaite, 1931), and has been subjected not only to considerable changes in humidity and to glaciation in its northernmost part, but also to extensive mountain-building activity by faulting and volcanism in Pleistocene and recent times. While similar changes have taken

place in the Rocky Mountains, they have in general been less pronounced, and have had less effect on the climate. In this inland region, the mountains do not influence the climate as directly as they do in the region near the Pacific Coast, where they act as barriers to moisture-laden winds from the ocean.

The writers do not mean to underestimate the important rôle that polyploidy has played in extending the range of many groups of Angiosperms. But we believe that its importance has been due largely to the rapid changes that have taken place on the earth recently, and that other, slower methods might be equally effective in the long run in dispersing the species or genus.

In analyzing the effects of the three processes individually, that of apomixis must first be separated from those of polyploidy and hybridization. For this purpose, the most significant fact is the close parallelism between apomictic complexes and sexual polyploid groups in the relative distribution of their diploid and polyploid members. In both types polyploidy with or without hybridization has greatly increased the range of the species involved, and the presence of apomixis appears to have had little effect on this increase. For this reason, the relative importance of the other two processes, polyploidy and hybridization, can be analyzed equally well in complexes with apomixis as in purely sexual ones. This analysis involves a comparison between the two types of polyploids, i.e., the non-hybrid ones (autopolyploids), and those of hybrid origin (allopolyploids).

Since both auto- and allopolyploid types exist in *Crepis*, these species are good objects for such an analysis. With respect to the evolution of morphological differences, the evidence in this group indicates that mere doubling of the chromosomes has produced no changes except of the purely quantitative type: increase in size and thickness of leaves and floral parts, delay and prolongation of blooming season, etc.; and in most cases even these are not marked, i.e., there is definite overlapping between diploids and polyploids. Müntzing (1936), in an extensive and very able review of this subject, has come to a similar conclusion (p. 269), but lists five cases in which supposed autopolyploids are said to differ qualitatively from their diploid progenitors. The five species thus listed, however, all belong to complex genera (*Draba, Festuca, Ægilops, Opuntia*) and have many close relatives. Hence careful examination of them with this point in mind may reveal that the qualitative differences are due to an admixture of characters of another species, i.e., to partial allopolyploidy. At present, therefore, there is little definite evidence that polyploidy in itself can produce any evolutionary changes except those that result directly from the increased cell size

and the slower growth rate that are usually characteristic of polyploids (see Müntzing, op. cit.). Hence the great majority of the new or divergent morphological types which arise in a polyploid complex are allo- rather than strictly autopolyploids.

In contrast with its relatively slight morphological effect, autopolyploidy has been said to be much more significant in its effect on geographic distribution (see Müntzing, 1936; Anderson and Sax, 1936; Fagerlind, 1937). In *Crepis*, however, as described above (pp. 14–15), the strict autopolyploids are much less widespread than the partially or wholly allopolyploid types, and the extent of their range as compared with that of the diploids is not nearly so great as it is in *Tradescantia* or *Galium*. This is due to the fact that the two factors, i.e., greater vigor and a longer growing season, which make the autopolyploids of *Tradescantia, Galium,* and probably other genera so much more successful than the diploids, are not so valuable to the *Crepis* species in question. Most of them grow in regions of moisture deficiency, in which great vigor might cause a plant to demand more water than that available. Furthermore, in regions of summer drought an abnormally long blooming season is a disadvantage, since the plant must be adjusted to a definite moisture cycle. The only species of which autopolyploid derivatives have extended the range appreciably is *C. acuminata.* Its autopolyploids are common in the northern Sierra Nevada, where their greater vigor has enabled them to compete successfully with a more luxuriant vegetation than is generally found in the habitats of the diploid.

The increased tolerance of aridity observed by Hagerup (1928) in presumably autopolyploid forms of *Eragrostis* is not found in these xerophytic species of *Crepis.* The most arid habitats in which the writers have seen *Crepis,* i.e., at Reno and on the basaltic plateau north of Susanville, have been occupied by diploid forms of *C. occidentalis* and *C. acuminata.*

In *Crepis,* therefore, the importance of polyploidy in extending the range of the species has been chiefly due to the new combinations of characters found in the allopolyploids, which have as a result been able to invade many new habitats.

In addition to these positive effects on evolution, the principal negative effect, i.e., the failure of new characters to appear, must be considered in relation to the three processes under discussion. Apomixis, through its "fixing" of morphological types, is most important in this failure, but polyploidy alone may also play a significant rôle. As Manton, after a study of sexual polyploid groups in the Cruciferæ, has expressed it, "high polyploidy, however much it may figure in the elaboration of specific forms, *is a barrier to true*

progress" (i.e., divergent evolution). A genetical basis of this fact has been suggested, namely, the relative difficulty with which the effects of recessive and incompletely dominant mutations are expressed in polyploids, owing to the duplication of gene pairs (see Dobzhansky, 1937, pp. 226–227).

Whether this is of general occurrence will not be certain until more agamic polyploid complexes are understood *in toto*. The opinion of most workers on the polymorphic complexes of *Taraxacum* and *Hieracium* (Gustafsson, 1932; Ostenfeld, 1910) is that mutation has been effective in them after the onset of apomixis, and that "the evolution of new species goes on coincidentally with the existence of apogamy" (Ostenfeld, 1910, p. 275). These complexes, however, are only partly known cytogenetically, and are best known in Scandinavia, which has a very recent flora and probably is remote from their center of distribution. Until all the sexual species of these genera are recognized and compared morphologically, no conclusions can be drawn as to the presence or absence of "new" characteristics in the apomicts. It may be said here that the "species" referred to by Ostenfeld and Gustafsson are comparable to the *formæ apomicticæ* of the present study (see p. 69) and that the species of *Crepis* as here recognized have a wider range of morphological variability than have many of the "sections" of *Hieracium* and *Taraxacum* as recognized by European specialists.

There are undoubtedly many species groups in the plant kingdom in which polyploidy and hybridization with or without apomixis have produced a large amount of recombination of the characteristics of species originally quite distinct from one another, along with the acquisition of *gigas* characteristics and a change of ecological tolerance and geographic distribution. Since these groups have played a large rôle in the evolution of the higher plants, a full understanding of them will be of tremendous value in clarifying both the present interrelationships of plant species and the past histories of floras. Their phylogenetic importance has already been emphasized by Anderson (1931, 1936*a*). Hence they should be recognized by both cytogeneticists and systematic botanists. For this reason, the writers propose to name them and to distinguish between their different types. Any group of this sort may aptly be termed a *heteroploid complex*. A heteroploid complex may be defined as: *a group of species, containing forms with different chromosome numbers, of which those with the lowest number (i.e., the diploids) are more or less distinct from one another morphologically, and are usually isolated from one another by sterility barriers, but in which some of the aneuploid or poly-*

ploid types are intermediate between the diploids or show different recombinations of their characteristics. In other words a heteroploid complex consists of three cytological and morphological types, diploids, autopolyploids, and allopolyploids, the latter passing into each other by a series of intergrades.

Cytologically, heteroploid complexes are of two types, euploid or polyploid, and aneuploid. In the former the chromosome numbers are all direct multiples of one basic number; in the latter, aneuploid numbers occur. Polyploid complexes are much more

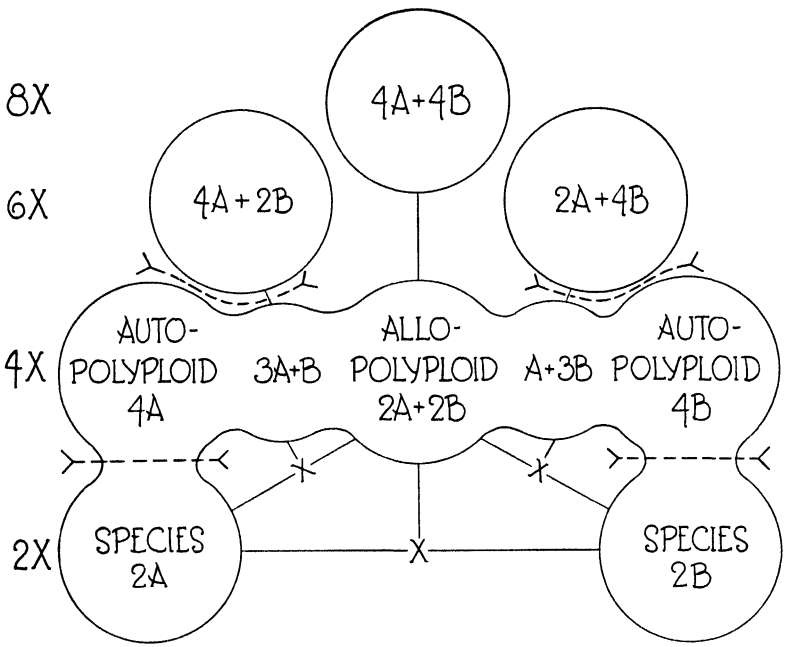


FIG. 4. Hypothetical diagram illustrating a sexual polyploid complex. Explanation on page 58.

common; of the aneuploid types there are only two definite and two imperfectly known examples. The first two are *Viola,* sect. *Melanium,* and *V. canina* and its relatives (J. Clausen, 1931); and the other two, *Poa alpina* and *P. pratensis* (Müntzing, 1933). Because of the infrequency of aneuploid complexes the term polyploid complex is more generally useful than the more inclusive term heteroploid complex.

Genetically and morphologically, polyploid complexes are of two types: (*a*) sexual polyploid complexes; (*b*) agamic heteroploid (i.e., polyploid or aneuploid) complexes.

Sexual polyploid complexes are the most general among plants and are probably of widespread occurrence. Examples are:

Phleum nodosum-pratense-alpinum (Gregor and Sansome, 1930; Nordenskiöld, 1937)
Pæonia triternata, Broteri, corallina, etc. (Stebbins, 1939)
Biscutella, sect. *lævigatæ* (Manton, 1934, 1937)
Zauschneria (Clausen, Keck, and Heusi, 1932)
Crepis vesicaria-taraxacifolia-taraxacoides-stellata (Babcock and Cameron, 1934)

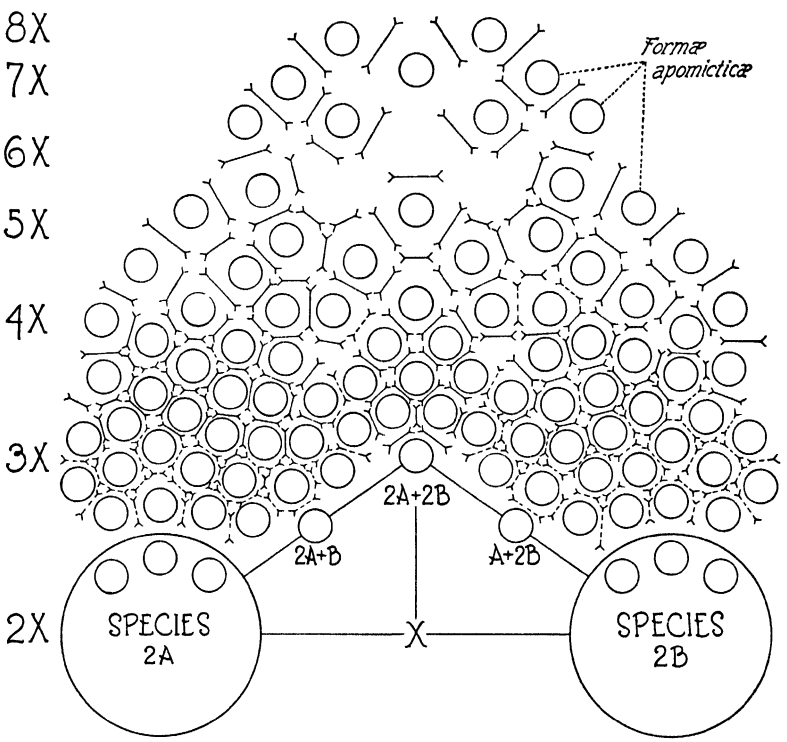


FIG. 5. Hypothetical diagram illustrating an agamic complex.
Explanation on page 59.

Species groups such as *Galeopsis* (Müntzing, 1931) and the *Nicotiana tomentosiformis—Tabacum—sylvestris* series (Goodspeed and Clausen, 1928; Goodspeed, 1934) are distinguished from polyploid complexes in that the genetic isolation between the diploids and the allopolyploids is nearly or quite complete, and autopolyploid types are not known in nature. Hence there are sharply defined morphological differences between the diploids and

the polyploids. On the other hand, such groups as *Dactylis* (Müntzing, 1937) differ in that only one diploid species is known, and allopolyploids are therefore absent. However, there are probably no sharp boundaries between the polyploid complex and either of the two simpler types of species groups represented by *Nicotiana* and *Dactylis*.

Agamic heteroploid complexes (or, more briefly, *agamic complexes*) are those in which the normal sexual reproduction of the polyploid derivatives (or rarely some diploid forms, see *Potentilla*, Müntzing, 1928) is partially or wholly replaced by some sort of a sexual propagation for dispersal, e.g., formation of bulbils, nucellar embryony, apogamy, apospory, parthenogenesis, pseudogamy, etc. Reproduction by rhizomes or stolons is not included in this category, since the clone is not naturally dispersed over a wide geographic range by these methods.

The following agamic complexes are known in addition to that of *Crepis* described in the present study (in some of them, not all the component types have been recognized):

Festuca ovina et aff. (Turesson, 1926)
Potentilla spp. (Müntzing, 1928, 1931)
Alchemilla (Murbeck, 1901)
Rubus, sect. *Eubatus* (Focke, 1914; Gustafsson, 1930)
Rosa, sect. *Canina* (Täckholm, 1922)
Antennaria (Stebbins, 1932; Bergman, 1935)
Taraxacum (Gustafsson, 1932, 1935, 1937, etc.)
Chondrilla (Poddubnaja-Arnoldi, 1933)
Hieracium, subg. *Archieracium* and subg. *Pilosella* (Ostenfeld, 1910, 1921; Rosenberg, 1907, 1930, etc.)

In addition, the presence of polyploidy coupled with known or probable cases of apomixis suggests that such complexes may exist in the following genera: *Poa, Calamagrostis, Buchloe, Allium, Burmannia, Nigritella, Balanophora, Rafflesia, Elatostemma, Cratægus, Malus, Sorbus, Ochna, Orobanche, Eupatorium, Erigeron, Artemisia, Arnica, Youngia*, and *Ixeris*. This list indicates that agamic complexes are by no means rare in the plant kingdom, and that they are particularly frequent in the Gramineæ, Rosaceæ, and Compositæ, families notorious for their taxonomic complexity.

Figures 4 and 5 are a series of hypothetical diagrams illustrating the three types of polyploid complexes. In each case, the degree of variation due to polyploidy is represented vertically, while that due to genic differences is indicated by the horizontal dimensions. Solid lines between two circles indicate more or less complete genetic isolation; broken lines incomplete isolation. In the sexual com-

plex, the circles representing the polyploids are all merged together. Barriers of incompatibility may separate portions of these complexes, particularly those with different chromosome numbers. However, the morphological distinction between these groups is in many cases, including most *Crepis* species, not absolute; that is, individuals with a lower chromosome number may be in all their quantitative characteristics as large as or larger than those with a higher one. The simplest case is that illustrated in figure 4, in which only two diploid species are included. When, as in *Crepis*, several diploids exist, the complex would have to be illustrated by a three-dimensional diagram, in which the diploid species formed the pillars supporting a complex network of passageways which represented the polyploid group. Such a diagram is best left to the imagination—no artist could do it justice. Hence the evolutionary pattern of such a group as the agamic complex of *Crepis* is much too complex to be illustrated, and is therefore omitted.

The agamic complex must be illustrated by a different type of diagram. Here the polyploids (or aneuploids) are a series of discrete entities, separated from one another by partial or complete barriers, depending on the degree of completeness of the apomixis. Furthermore, since "unbalanced" as well as "balanced" chromosome numbers can exist, the variation due to chromosomal differences is much more continuous. Figure 5 gives the writers' concept of such a complex.

The painstaking and penetrating analysis of the genus *Rubus* subg. *Eubatus* made by Focke (1914) demonstrated the presence of a complex with all the characteristics of the agamic complex as defined here, even though its author could not, at a time when these phenomena were relatively little known, have realized the significance of the presence of polyploidy and apomixis in this subgenus. Focke pointed out the existence among the European blackberries of certain species with normal pollen, and of others with very irregular pollen. The latter are the common and widespread species of Europe, while the fertile types are confined to southern and eastern Europe, and to Madeira, the Azores, and the Canary Islands; while certain American types with normal pollen are closely related to the common European species. Focke (1914, pp. 11–12) has stated that nearly all the blackberries of Europe either resemble closely one or another of the species with normal pollen, or show combinations of the characteristics of these species, thus indicating that *Rubus* subg. *Eubatus* is an agamic complex quite comparable to that of *Crepis*, except that it is much larger. The presence of apomixis and polyploidy in this group has more recently been demonstrated with certainty (Gustafsson, 1930).

When heteroploid complexes in general are compared as to their phenotypic aspect with the homoploid ecospecies or *Rassenkreis*, the following differences may be noted:

1. While only one member of a given *Rassenkreis* may occur in a particular region (or ecological habitat) (Rensch, 1929, p. 11), two or more members of a heteroploid complex may occur together, since the presence of different chromosome numbers and, in agamic complexes, of apomixis constitutes a barrier to the mingling of some of the forms.

2. While the variations within a *Rassenkreis* are more or less closely correlated with adaptation to the environment, those of the heteroploid complex may or may not be so correlated. In heteroploid complexes variation in the morphology and structure of the floral parts, i.e., the "fundamental characters" of the taxonomist, is much greater than it is in the *Rassenkreis*. A comparison between the type of variation found within the *Rassenkreis* of *C. runcinata* and that of the agamic complex comprising the other nine species will emphasize this point. The variations within *C. runcinata* involve chiefly the shape of the leaves, the stature of the plant, the degree of glandulosity, etc., while such characteristics as the nature of the inflorescence, the number of florets per involucre, and the color, shape, and ribbing of the achenes are relatively constant. The agamic complex, on the other hand, shows, in addition to the type of variation characteristic of *C. runcinata*, extreme polymorphism in the characters of flowers and fruits just mentioned. As is clear from the discussion given in the previous section, this is due to the very different ancestry of its various diploid members.

3. It follows from the two previous points that polymorphism is greater in the heteroploid complex than in the *Rassenkreis*.

4. If the sexual homoploid *Rassenkreis* and the agamic polyploid complex of *Crepis* are compared, a very different distribution of the extremes of variation is found. In *C. runcinata* the extremes of morphological variation, since they are produced directly through the selective action of the environment, are near the periphery of the geographical and ecological range of the species (see subspp. *Barberi*, *Andersonii*, and *imbricata*, pp. 100–104). In the agamic complex, on the other hand, the extreme morphological types are represented by the diploids (see p. 12), most of which occur at or near the center of distribution of the species (see pp. 12, 45). The extreme environments (for the complex) are occupied by forms which have become adapted to them through the processes of polyploidy and hybridization, with consequent selection of favorable types from the numerous derivative forms (see p. 15). These

highly selected inhabitants of the edges and the isolated outposts of the total range of the complex are morphological blends. It would be interesting to examine other heteroploid complexes from this point of view, to see how far this generalization can be extended. From the junior author's familiarity with the complex series of agamic complexes in the genus *Antennaria*, he is of the opinion that the distribution of morphological extremes here is much as it is in *Crepis*.

The principal effects of polyploidy, therefore, are to increase the polymorphism of a group, and to spread intermediate, "hybrid" types, as well as *"gigas"* types morphologically similar to the diploids, over a wide geographic territory, and into a large number of diverse habitats. A heteroploid complex must be thought of as a group in which the ordinarily rare hybrid types have become among its most common, dominant representatives. Viewed in this light, the taxonomic diversity of these complexes become comprehensible, even though their classification according to the accepted methods still presents great difficulties.

The most important way in which apomixis accompanied by hybridization and polyploidy influences the evolutionary history of a group of species is through its rapid production and "fixing" of new variants in certain parts of the range of the group, and its limitation of variability in other parts. By means of the former process, the agamic complex is, in localities adjacent to its distributional centers, even better suited to take rapid advantage of changing conditions than are sexual heteroploid complexes. This is strikingly manifest in the "weedy" tendency of many apomicts of *Taraxacum*, *Hieracium*, and *Antennaria*. On the other hand, the limitation of variation near the periphery of their range reduces the ability of these complexes to cope with further changes in their environment. An agamic complex is a "closed system," whose ultimate fate is bound up in the fate of its sexual members. It can give rise to nothing new, and can keep abreast of changing conditions only through the activity of the latter forms. If, as in the case of *C. acuminata*, the sexual forms retain an extensive range and a great amount of variability, new apomicts can be constantly produced, some of which will be adapted to new environments, and the complex can therefore maintain its "youth" and "aggressiveness." If, on the other hand, the sexual forms become much restricted geographically and ecologically, as are those of *C. pleurocarpa* and *C. monticola*, the plasticity of the species is lost, and they are destined to become "senescent." This is definitely true in the case of the species mentioned. *C. acuminata* and *C. intermedia* are dominant, "aggressive" species in most parts of their range; the

former has withstood in many localities the radical changes in vegetation that have accompanied heavy grazing by sheep, while the latter (apm. *sicrræ*, p. 185) has ascended higher into the glaciated valleys of the central Sierra Nevada than has any other species of *Crepis*. On the other hand, *C. pleurocarpa* and *C. monticola* are typically conservative. For instance, the latter is on Mount Hamilton one of the rarest of species (*fide* H. K. Sharsmith, oral communication), yet the locality at which it has been found is by no means unusual. It occurs in the *Pinus Sabiniana* association at an elevation of about 825 m (2700 feet). Such sites occur by the thousand in the inner Coast Ranges of California, yet *C. monticola* occupies only a very few of them. The only region in which these two species are abundant is within or near the range of the diploid forms, i.e., the Klamath-Siskiyou Mountain area. Here they are able to maintain themselves successfully, and actually show signs of "aggressiveness," as on the stream terraces south of Yreka.

The effect of the prolonged separation of a group of apomicts from their sexual ancestors is shown by the *Antennarias* of Newfoundland (see Fernald, 1933). These apomicts have completely lost the power of sexual reproduction, as is evident from the absence of staminate plants. They are relic types, many of them highly localized in distribution, and show no tendency toward "aggressiveness." On the other hand, their close relatives in the west, where sexual forms still occur, are quite the reverse. In the Sierra Nevada, *A. media* and its relatives are dominant species of alpine meadows and gravelly flats in both unglaciated and glaciated districts; while both sexual and apomictic forms are common. Judging from the specimens available, the same is true of other western relatives of the Newfoundland *Antennarias*, such as *A. reflexa* Nels., and *A. umbrinella* Rydb. There is abundant evidence (see Dobzhansky, 1937, pp. 134–137; Anderson, 1936*a*, p. 496) that isolation of a small part of a sexual population tends to produce constancy and therefore conservatism. This phenomenon is obviously much accentuated by apomixis.

The ultimate fate of an agamic complex of which the sexual ancestors have become restricted or extinct can be predicted; it will flourish as long as the conditions that existed during its formation prevail, but it will be unable to meet any new changes of environment, and will therefore in time become more and more restricted, and will finally die out. The great prevalence of apomixis in the Gramineæ, Rosaceæ, and Compositæ is not, in the opinion of the writers, due to an unusual quality of the germ plasm of these families. They are groups which have been evolving rapidly in comparatively recent times; hence they possess many agamic

complexes which are still young and vigorous. In one obviously ancient family, the Saururaceæ, is a good example of an agamic complex in its decadence. *Houttuynia cordata* Thunb., although it is a monotype and has no close relatives in any other genus, is a high polyploid and is apomictic (Okabe, 1930). On the basis of our present knowledge of apomictic groups, there is only one good explanation of this fact, i.e., that diploid species of *Houttuynia* once existed, but are now extinct. *H. cordata* is the last relic of a once polymorphic agamic complex, and perhaps owes its survival to its adaptation to "weedy" habitats about human habitations. The other members of the Saururaceæ, i.e., *Saururus*, with one species in eastern America and one in eastern Asia, and the anomalous monotypic *Anemopsis californica* of western America, are all three relics. The entire family must have been larger and more widespread in the past. In the opinion of the writers, the eventual fate of the agamic complexes of *Taraxacum, Hieracium, Antennaria*, and *Crepis* will be that of *Houttuynia*.

THE SYSTEMATIC TREATMENT OF THE AGAMIC COMPLEX

The complexes in which apomixis is prevalent are notorious for their taxonomic complexity, and their treatment by different systematists has varied tremendously. In the opinion of the writers, the only basis for the satisfactory treatment of these complexes is obtained through an understanding of the rôle that the three important processes, polyploidy, hybridization, and apomixis, have played in their formation. From the present study it is very evident that species as they are ordinarly conceived, and as they originally existed within the same genus before apomixis was developed, have been profoundly modified by the three processes mentioned above. In fact, the following analysis will demonstrate that in an agamic complex no entities exist which are homologous to the species as found in homoploid, sexual groups.

The writers feel that in distinguishing between species three criteria must, wherever possible, be taken into consideration, namely, morphological likeness or distinctiveness, the degree of genetical isolation, and the degree of similarity in the evolutionary history of the components of the species. Morphological considerations are of primary significance, since species have always been conceived and described primarily in morphological terms, but a consideration of the other two criteria is essential to a true understanding of interspecific relationships. On the basis of these three criteria, the following facts about a species may be considered fundamental principles:

1. The individuals composing it are all interfertile, or at least there are no sterility barriers which are correlated with morphological differences. Intraspecific variation is in general continuous, and no morphological discontinuity determined by barriers of genetic isolation is present (see Rensch, 1929; Du Rietz, 1930; Turesson, 1929).

2. All the individuals possessing the morphological characteristics of a species fall within its limits.

3. The subdivisions of a species have had a common or at least a very similar origin (Rensch, 1929; Turesson, 1929).

When the agamic complex is analyzed according to these criteria, the following facts are evident:

1. Genetically determined differences that are discontinuous, as well as genetic isolation, may occur between forms, all of which fall within the range of variation of other fully interfertile populations. This is true of the autopolyploid apomicts of *C. acuminata*, when compared with sexual populations of the same species (see fig. 3).

2. Forms which are obviously of very different origin, see both genetically and phylogenetically, are connected with each other by a nearly continuous series of intergrades. If the polyploid apomicts are included in the series, no gaps of morphological discontinuity can be found between such very different forms as diploid *C. occidentalis* and *C. acuminata* that are greater than the gaps between two autopolyploid apomicts of the latter species.

Hence the processes which form an agamic complex actually obliterate the differences between well-established and even distantly related species, so that in these complexes there are no entities that are homologous to species as they exist in sexual groups. The species, in the case of a sexual group, is an actuality as well as a human concept; in an agamic complex it ceases to be an actuality. The same conclusion about apomictic groups has been reached by Dobzhansky (1937, pp. 320–321).

Nevertheless, it is obvious that these complexes cannot be understood unless they are treated systematically in a manner similar to that used for sexual groups, i.e., by the recognition of species and subspecies or varieties. Therefore, these entities must be delimited more or less arbitrarily, in such a manner as to express as clearly as possible the phylogenetic interrelationships of the complex.

The two extreme treatments of this group would be, on the one hand, to disregard the discontinuity between the different apomicts and, where it exists, between them and the sexual forms, as inconsequential, and on the basis of a continuous series of intergradations to regard the entire complex as a single species. This has not been done with any agamic complex, so far as the present

writers are aware, although its possibility is suggested by the statement of Müntzing, Tedin, and Turesson (1931) that ". . . in some cases the only natural group above the apomictic forms may be so extensive that it corresponds to a taxonomical section or even to a genus. . . ." This treatment, however, would have obvious disadvantages. In the first place, such "species" would be enormous, unwieldy taxonomic units, of no practical value. Secondly, such a treatment would obscure rather than clarify the actual interrelationships and phylogenetic history of the group, and would do violence to the principle that the members of a species have had a common or at least a similar origin.

The other extreme, that of recognizing each apomict as a distinct species, has been applied by European specialists to *Hieracium* and *Taraxacum*, and is defended theoretically by Du Rietz (1930). Du Rietz's opinion on this point has been justly criticized by Müntzing, Tedin, and Turesson (1931). Practically, this method is satisfactory only when applied to groups of obligate apomicts which are relatively few in number and are separated by relatively clear differences, as is true of the Newfoundland *Antennarias* mentioned previously (p. 62); its impracticability in most cases is clearly demonstrated by the astronomical number of described "species" that has resulted from its application to *Hieracium* and *Taraxacum*. Furthermore, its theoretical unsoundness is clear from a study of *Crepis acuminata*. Apomicts of this species, such as those found on Black Mountain, are just as distinct from each other as are the "species" proposed by the *Hieracium* specialists, yet in other populations of *C. acuminata*, found only a few miles away, these same "species" can be exactly matched by different individuals of a fully interfertile population, and by applying the same criteria of "species" differentiation as those applied to the apomicts, each individual would be made into a different "species." As Fernald (1933, p. 383) has expressed it: "Genetically they [the apomicts] are not species or anything but trivial variations which, under normal sexual reproduction, would quickly be lost in a common blend."

Clearly, the only satisfactory treatment of an agamic complex is one which is intermediate between these two extremes. The morphological distinctness of and the genetic isolation between the different diploid sexual forms indicates that these were originally distinct species. The known phylogenetic history of the group, therefore, is best expressed by retaining them as specifically distinct. The correct disposition of the apomicts in relation to the sexual forms can be determined by comparing the agamic with the sexual polyploid complex, since the

fundamental nature of the variation in the two types of complexes is found to be essentially the same (see figs. 4 and 5), so that in both of them there are no real specific boundaries among the polyploids, at least between those with the same chromosome number. In the sexual polyploid complex, however, genetic incompatibility exists only between the polyploids and their diploid ancestors, and in some cases this is accompanied by morphological discontinuity. For this reason, Müntzing (1936) and Fagerlind (1937) have suggested that such polyploids be recognized wherever possible as distinct species. On this basis the entire group of polyploids of a complex, whether sexual or agamic, might be recognized as a single species, and separated from each one of its diploid ancestors by quantitative characteristics. This treatment, however, would be impracticable, particularly in those complexes containing many diploid species. It would, furthermore, be inconsistent with the morphological criteria of specific distinctness in cases such as these American species of *Crepis*, in which autopolyploids fall within the range of variation of the diploids. Furthermore, it would be inconsistent with both the morphological and the phylogenetic criteria of species differentiation to group together forms which both genetically and phylogenetically have had very different origins, i.e., the autopolyploid derivatives of two different species, and at the same time to keep these autopolyploids distinct from their diploid ancestors, from which they have arisen by means of the single process of doubling the chromosome set.

The autopolyploids of both sexual and agamic continuous polyploid complexes should therefore be included within the same species as their diploid ancestors, at least if there is no definite morphological difference between the two. The species which contain the diploid forms and their autopolyploid derivatives may be termed the *original species* of the complex.

The correct placing of the partial and complete allopolyploids presents more difficulties. Ideally, the best system of treatment would be to include within the original species only the diploids and their strictly autopolyploid derivatives, and to group the allopolyploids into a series of *agamospecies* (cf. Turesson, 1929), each of which would contain all the allopolyploid apomicts of common parentage. There are practical difficulties, however, connected with this method. In the first place, the exact limits of variation of the diploid species are difficult to determine, and therefore the exact distinction between the morphological auto- and the allopolyploids is equally difficult. For instance, on the basis of the amount of variation within the specimens of diploid *C. acuminata* available to the authors before the collecting season of 1936, many apomicts

of *C. acuminata* were interpreted as partial allopolyploids. Then the discovery of a single highly variable population of the diploid form, i.e., that on Mount Shasta, showed that these supposed partial allopolyploids fall within the limits of variation of diploid *C. acuminata*. Hence if specific lines were based on these criteria, each new colony discovered of the sexual species might necessitate a complete realignment of interspecific distinctions within the genus. Furthermore, Anderson (1936*b*) proved conclusively in the case of *Apocynum* that extreme variants of a good diploid species may be hybrid derivatives; hence it is altogether possible for partial allopolyploids to fall within the range of variation of the diploid form of the species. In fact, the writers suspect that this is true of *Crepis acuminata*, i.e., that the extreme variants of its diploid form that occur in California, the only place in which it comes in close contact with other diploids, are of the same partially hybrid origin, just as are the variants of *Apocynum* (Anderson 1936*b*), so that the apomicts which resemble these variants are actually partial allopolyploids. The only safe procedure, therefore, is to recognize at least some of the partial allopolyploids as belonging to one or other of the original species.

The delimiting of the agamospecies is difficult because the exact parentage of many of the apomicts is difficult to determine. The errors which may result from trying to infer the ancestry of a hybrid or hybrid derivatives from its morphological appearance alone have been clearly demonstrated by Heribert Nilsson (1918) in *Salix*. In *Crepis* there are many characteristics that are so similar in otherwise very different diploid species, such as the achenes of *C. occidentalis*, *C. monticola*, and *C. pleurocarpa*, that many of the apomicts could have acquired their distinguishing characteristics from one of several sources. Tables 4 to 12 are the nearest approximation that can be made toward determining the ancestry of the various apomicts, without a long series of hybridization experiments which would be totally impracticable in this group. Furthermore, many of the apomicts are secondary and tertiary derivatives, combining the characteristics of three or more different sexual species. Hence the most practical course within the present complex has been to recognize relatively few agamospecies, and to include within them only those forms which are strikingly different from any of the diploids and which show their common or at least similar origin by the possession of certain well-marked characteristics in common.

The procedure which to the writers seems both the soundest theoretically and the most practical is therefore as follows:

1. All the diploid forms (and the sexual polyploids, if present) are identified by means of cytological studies, supplemented by a survey of the stomatal size and the character of the pollen, when significant, in all available herbarium specimens.

2. The morphological characteristics of the diploids are carefully tabulated, and the important differences between them are noted. Each of these represents the morphological (though not necessarily the nomenclatural) type of a species. Then those apomicts which fall (except for quantitative differences) within the range of variation of the diploids, as well as those partial allopolyploids which, by the possession of certain well-marked characteristics, show their undoubted affinity to one or other of the diploids, are assigned to the original species which they resemble. The other allopolyploid apomicts are grouped into agamospecies, each of which has approximately the same degree of variation as the original species, and contains apomicts which appear to have originated from the same or similar hybridization. The species thus formed are naturally rather polymorphic, and are distinguished from one another by more or less artificial differences, but this is inevitable when, as already pointed out, natural species do not exist.

3. Within the species, the diploid form is carefully described and distinguished from the polyploids, and in addition the species is divided into subspecies or varieties on the same basis as are sexual species; that is, those forms which resemble each other closely and have a common or similar range are grouped together, while groups of apomicts which deviate from the rest in both their morphological characteristics and their geographic distribution are recognized as distinct subspecies or geographic varieties. The writers have found that conservatism in this respect has been the wisest course; at best the subspecies have proved very difficult to define.

4. The delimiting of species and subspecies has been done more or less independently of the nomenclatural history of the forms involved, though not, of course, of the morphological distinctions used by previous students of the group. After these subdivisions were defined morphologically the correct names for them were determined according to the International Rules of Nomenclature. In some cases, as in *C. exilis* and *C. Bakeri*, the nomenclatural type is in a different subspecies from that containing the diploid form. In this case the term "subsp. *typica*" is applied, following general usage, to that containing the nomenclatural type. That containing the morphological or phylogenetic type, i.e., the diploid form, is designated, if no other name for it exists, by the term "subsp. *originalis*."

5. The apomictic forms are purposely left out of consideration as taxonomic entities, since they are not comparable to any of the subdivisions of a sexual species. Following the precedent of Turesson (1926), they are given Latin names preceded by the abbreviation "apm." (for *forma apomictica*), and short English descriptions. Since neither the category nor the English descriptions are recognized by the rules, these apomicts have no taxonomic status. Only a small proportion of their total number has been described; these have been selected so as to illustrate the extent of variation within the species, and to emphasize the more interesting facts about their distribution; that is for the most part those apomicts occurring at outlying or isolated localities have been described. In order to give a more complete picture of the range of the species, additional specimens of undescribed apomicts have been cited; the relationship of these as suggested by morphological resemblances to described apomicts has been indicated. The distinction made by Turesson (op. cit.) in the viviparous *Festuca* between facultative and obligate apomicts (*"formæ amphi-apomicticæ"* and *"formæ apomicticæ"*) was not practicable in *Crepis*, since there was no way of determining which type of development was present except in the few plants subjected to castration experiments and cytological study. Hence the abbreviation "apm." is used in this study to cover both types.

The most likely parentage of each allopolyploid derivative, based on the sum total of its characteristics as given in tables 4–12, is given in parentheses after the name of the apomict. The species whose diploid form it most resembles is given first, while those to which the affinity is doubtful are followed by a question mark.

Emphasis must be placed on the necessity of studying the *whole* of an agamic complex before a satisfactory treatment of it can be made. This is relatively easy in the case of *Crepis*, in which the complex has a relatively small and unified range, but would present more difficulties in such widespread complexes as those of *Taraxacum* and *Antennaria*. Nevertheless, the writers feel that a method based on the principles mentioned above or on similar ones would provide a treatment that would give us a much better understanding of all agamic complexes than we now have.

SUMMARY OF THE PRECEDING SECTIONS

Present distribution of the species. *C. nana* and *C. elegans* are arctic-alpine, the former circumpolar. The other indigenous species occur primarily in the Arid Transition zone of the western United States, although they are found also in the upper Sonoran, Cana-

dian, and occasionally the Hudsonian zone. *C. runcinata* has its center of distribution in the central Rocky Mountains; the other nine species are best developed in the Columbia Plateau province and the northern part of the Great Basin.

Cytology of the species. The American species (excluding *C. nana* and *C. elegans*) all have chromosome numbers based on the haploid number $x = 11$. *C. runcinata* is exclusively diploid ($2n = 22$), while the other species contain polyploid series, with numbers ranging from 22 through $2n$ (i.e., $3x$) $= 33$ to $2n = 44$, 55, 77, and 88. The polyploids are not always distinguishable from the diploids in morphological characteristics, but can nearly always be recognized by the size of their stomata, and in many cases by the morphology of their pollen grains. With the exception of *C. acuminata*, the diploid forms of each species are very restricted in distribution, being confined to two regions, northeastern California and adjacent Oregon, and central Washington. The general presence of apomixis in the polyploids has been demonstrated, and will be discussed further in another publication.

Genetic interrelationships of the species. Crepis runcinata is a typical *Rassenkreis*, consisting of seven probably interfertile subspecies which occupy different geographical ranges and ecological habitats. There is no evidence of hybridization between it and any other of the species recognized.

Included in the nine other species are seven different diploid forms, which, when taken by themselves, are entirely distinct from one another. These are, however, connected by a continuous and complex series of intergrading forms, all of which are polyploid and wholly or partly apomictic. The polyploids are of two sorts, morphological autopolyploids, which are identical with the diploids except for possessing *gigas* characteristics; and allopolyploids, which combine the characteristics of two or more diploids, and are evidently the result of hybridization as well as polyploidy. The latter are much more numerous than the former.

Factors affecting the distribution of the species. When the distribution of *Crepis* is compared with that of climatic zones as classified by Thornthwaite, a striking correspondence is found. Except for *C. runcinata*, which occupies almost the whole of two provinces, each diploid is confined to a single province or a part of one. They can be arranged in a progressive series as to their tolerance of drought and cold, from diploid *C. pleurocarpa* to diploid *C. modocensis*, *exilis*, and *acuminata*. The latter two differ from the others in preferring regions with a uniform rather than a summer precipitation deficiency. The autopolyploids of each species, except that of *C. acuminata*, do not occur outside the

climatic province which contains their diploid ancestors. The allopolyploids show by their distribution the combination through hybridization of the physiological characteristics that determine this distribution, just as their appearance shows the combination of the morphological characteristics of their diploid ancestors.

Edaphically, *C. runcinata* is set off from the other species by its preference for moist situations. All the subspecies except *typica* prefer alkaline situations, and are confined to, or are more common in, the western part of the range of the species.

The principal edaphic factor governing the distribution of the other species is the character of the soil, which is largely determined by the underlying geological formations. Although all are alike in preferring soils circumneutral as to pH reaction, some of them prefer light clays, while others prefer more loamy soils. For this reason the latter are abundant in basaltic areas and often occur in granitic areas, while the former occur chiefly in regions underlain either by ultrabasic intrusive rocks or by the softer volcanics. The relationship of the topographic features and the underlying geological formations to the distribution of *Crepis* is brought out by a detailed study of a portion of northeastern California, where several different types of habitats adjoin one another. The distribution of the *Crepis* apomicts on two mountain peaks of this area shows a close correlation with that of the rest of the herbaceous vegetation. These apomicts, therefore, are good indicators of the vegetation of a particular area. Much information can be obtained from them on the origin and interrelationships of the various floras of which they form a part.

Origin and development of the species. The American group with $x = 11$ as their basic number probably was originally derived by allopolyploidy from hybrids between 4- and 7-paired species of the Old World. They may have originated in eastern Siberia in middle or late Tertiary times, when the climate was milder there than at present. Definite similarities to all the American species can be found among various 4- and 7-paired species of eastern Asia. The different 11-paired species probably arose at different times. Their migration to North America very likely was coincident with that of many other species of both plants and animals that are characteristic prairie or steppe types. Soon after the original 11-paired species were formed, they began to produce the higher, apomictic polyploids, and the formation of these has continued up to recent times. Stimulated largely by the great climatic and physiographic changes that took place during the Pleistocene, the polyploids have spread at the expense of the diploids, while the latter have become restricted to two centers of distribu-

tion. The largest and oldest of these centers is the Klamath Mountain region of northern California and the mountain ranges to the east of it. The distribution of apomicts whose sexual, diploid ancestors occur in this center gives information concerning certain elements of the flora of the southern Sierra Nevada, the Tehachapi, San Bernardino, and Mount Hamilton ranges in California, the Blue Mountains of Oregon and Washington, the Olympic and Wenatchee Mountains of Washington, and the Teton Mountains of Wyoming. The second center, in central Washington, could not have been occupied by *Crepis* until postglacial times, and the apomicts derived from it have spread only a short way beyond its boundaries. There is good evidence that these apomicts of recent origin have by competition exterminated from this region the older apomicts of *C. occidentalis*, and have caused a disruption in the range of the latter species.

The effect of polyploidy and apomixis on evolution. In the species under discussion (except *C. runcinata*), evolution, since their formation, has involved primarily three processes: polyploidy, hybridization, and apomixis. The fact that each diploid is relatively uniform morphologically and that all the polyploids are either identical with one or other of the diploids except for the effects of polyploidy, or else combine their characteristics, indicates that divergent evolution has been virtually at a standstill in the group. Morphologically, polyploidy and hybridization have produced *gigas* phenomena, recombination, and segregation of forms. Apomixis has produced slight morphological discontinuities, which are statistically demonstrated, and the breaking up of the species into numerous apomictic forms. These are much more numerous near the centers of distribution, and relatively few in areas remote from these centers. Conversely the apomicts occupying these remote areas have in general wider ranges than those occurring near the center. The extension of the range of the polyploids over that of the diploids is the result of both polyploidy and hybridization, but is not greater than that which has been achieved by related, homoploid species (*C. nana*, *C. runcinata*), in which these two processes have been absent. In extending the range of the group, polyploidy with hybridization (allopolyploidy) has been much more important than the former process alone (autopolyploidy).

To aid the study of polyploidy in plants, certain groups containing interrelated diploid and heteroploid (chiefly polyploid) forms are defined as heteroploid (chiefly *polyploid*) *complexes*. Cytologically these are either polyploid or aneuploid. Genetically they can be classified as sexual or agamic complexes. These complexes are compared with homoploid groups.

The systematic treatment of the agamic complex. The application to agamic complexes of the usual criteria on which the species concept is based indicates that there are in these complexes no entities that are homologous to species as they exist in homoploid, sexual groups. Considering this, the best systematic treatment of this type of complex is, in the opinion of the writers, that outlined on pages 68 to 69.

MATERIAL AND METHODS

This contribution is based largely on herbarium specimens, of which a large series has been studied. The method of citation followed is described elsewhere (Babcock and Stebbins, 1937, p. 23). The following herbaria are represented; their names are preceded by the abbreviations used in citation.

Blake—Private herbarium, Dr. S. F. Blake, Washington, D. C.
CA—California Academy of Sciences, San Francisco, California
CFE—California Forest Experiment Station, Berkeley, California
Clo—Private herbarium, Dr. Ira W. Clokey, South Pasadena, California
DS—Dudley Herbarium, Stanford University, California
FM—Field Museum, Chicago, Illinois
G—Gray Herbarium, Harvard University, Cambridge, Massachusetts
Minn—University of Minnesota, Minneapolis, Minnesota
Mo—Missouri Botanical Garden, St. Louis, Missouri
ND—University of Notre Dame, Notre Dame, Ind.
Nev—University of Nevada, Reno, Nevada
NY—New York Botanical Garden, New York
Or—University of Oregon, Eugene, Oregon
PA—Philadelphia Academy of Sciences, Philadelphia, Pennsylvania
Po—Pomona College, Claremont, California
RM–Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming
SB—Museum of Natural History, Santa Barbara, California
UC—University of California, Berkeley, California
US—National Herbarium, Smithsonian Institution, Washington, D. C.
Wn—University of Washington, Seattle, Washington
WSC—Washington State College, Pullman, Washington
Will—Willamette University, Salem, Oregon
Ya—Yale University, New Haven, Connecticut

The field studies have been carried on during eight seasons. In 1925, the senior author with Dr. H. M. Hall collected roots and seeds for cultures in northern Nevada, southeastern Oregon, and northern California. The following year, he, with Dr. J. L. Collins, collected specimens, roots, and seeds in northern California, central and eastern Washington, northeastern Oregon, and adjacent Idaho.

In 1927, with Dr. D. R. Goddard, he visited for the same purposes Arizona, New Mexico, Colorado, Wyoming, Yellowstone National Park, northern Utah, and northern and western Nevada. During 1928, 1932, and 1934, with Dr. M. Navashin and others, he collected in various parts of northern and eastern California. In 1936, the authors made a joint trip to northeastern California and adjacent Oregon, during which cytological material of buds was collected, castration experiments were made, and comparative studies of the sexual and apomictic populations were undertaken for the first time. This work was continued in 1937 by the junior author and Dr. J. A. Jenkins, in two trips to the same region. In the citation of the numerous specimens collected by the authors and their associates, their names are abbreviated as follows: *B*=the senior author, *B & C*=Babcock and Collins, *B & N*=Babcock and Navashin, *B & S*=the two authors, *S & J*=Stebbins and Jenkins.

ACKNOWLEDGMENTS

The charts and most of the drawings were prepared by Mrs. Katherine D. Jenkins (figs. 9–13 by Miss Anna Hamilton), using the methods already described (Babcock and Stebbins, 1937, pp. 22–23). The photographs were made by Mr. W. C. Matthews. The maps were made by the junior author, assisted by Mrs. Jenkins, using as base maps tracings from Rand McNally's "Premier Atlas of the World," pages 12 and 13, through permission of the publishers, except figure 2 which is based on a tracing from the Honey Lake sheet of the U. S. Geological Survey.

The authors are indebted to the directors and curators of all botanic gardens and herbaria from which specimens have been borrowed. We are particularly grateful to the following persons for assistance in obtaining living material: Mr. Leland S. Smith, Range Examiner of the U. S. Forest Service; Dr. J. L. Collins, University of Hawaii; the late Dr. H. M. Hall, Carnegie Institution of Washington; Dr. Jens Clausen and Dr. D. D. Keck, Carnegie Institution of Washington; Dr. Helen Mar Wheeler, Department of Botany, University of California; Mr. O. A. Garrett, Salt Lake City, Utah; the late Mrs. Ynes Mexia, Berkeley, California; Dr. D. R. Goddard, Department of Botany, University of Rochester; Mr. G. W. Gasser, Agriculture College, Fairbanks, Alaska; Professor W. P. Frazer, University of Saskatchewan; Mrs. Clara Bishop Swift, Berkeley, California; Mr. W. W. Jones, Salt Lake City, Utah; Dr. C. W. T. Penland, Colorado College, Colorado Springs; Dr. Paul C. Standley, Field Museum of Natural History; the late Mr. Wilhelm Suksdorf, Bingen, Washington. To the U. S. Forest Service we are indebted

for maps and information which have been of much assistance in our distributional studies. We also acknowledge with many thanks the help, advice, and criticism of the following on various features of the work: Dr. G. B. Bodman, Dr. R. W. Chaney, Dr. C. L. Camp, Dr. J. B. Leighly, Dr. Lillian Hill née Hollingshead, and Dr. J. A. Jenkins, of the University of California; Dr. Olaf P. Jenkins, California State Bureau of Mines. For technical assistance in the growing of cultures and the preparation of cytological material we acknowledge the services of Mr. C. W. Haney and Mr. E. G. Jund. We are especially indebted to Dr. Jens Clausen and Dr. D. D. Keck for their critical reading of the manuscript and for many helpful suggestions.

Grateful acknowledgment is also made for the partial support of these investigations by special grants from the following institutions: Rockefeller Foundation; Carnegie Institution of Washington; University of California, Board of Research. Most of the stenographic and clerical assistance has been provided by the Works Progress Administration under Official Project 465-03-3-631, unit 822.

LITERATURE CITED

ANDERSON, E. 1931. Internal factors affecting discontinuity between species. Am. Nat. 65:144–148.

——— 1936*a*. The species problem in *Iris*. Ann Mo. Bot. Gard. 23:457–509.

——— 1936*b*. An experimental study of hybridization in the genus *Apocynum*. Ann. Mo. Bot. Gard. 23:159–167.

——— 1937. Cytology in its relation to taxonomy. Bot. Rev. 3:335–363.

——— and K. SAX. 1936 A cytological monograph of the American species of *Tradescantia*. Bot. Gaz. 97:433–476.

BABCOCK, E. B. 1936. The origin of *Crepis* and related genera with particular reference to distribution and chromosome relationships. Univ. Calif. Publ. Bot., Essays in Geobotany in Honor of William Albert Setchell. pp. 9–53.

——— and D. R. CAMERON. 1934. Chromosomes and phylogeny in *Crepis* II. The relationships of one hundred eight species. Univ. Calif. Publ. Agr. Sci. 6:287–324.

——— and S. L. EMSWELLER. 1936. Meiosis in certain interspecific hybrids in *Crepis* and its bearing on taxonomic relationship. Univ. Calif Publ. Agr. Sci. 6:325–368.

——— and G. L. STEBBINS, JR. 1937. The genus *Youngia*. Carnegie Inst. Wash. Pub. No. 484. 106 pp.

BROOKS, A. H. 1906 The geography and geology of Alaska. U. S. Geol. Surv. Prof. Paper No. 45.

CHANEY, RALPH W. 1925. The Mascall flora, its distribution and climatic relation. Carnegie Inst. Wash Pub. No 349, pp. 23–48.

——— 1938 The Deschutes flora of eastern Oregon. Carnegie Inst. Wash. Pub. No. 476, pp. 185–216.

CLAUSEN, J. 1931*a*. *Viola canina* L.—A cytologically irregular species. Hereditas 15:67–88.

——— 1931*b*. Cytogenetic and taxonomic investigations on Melanium violets. Hereditas 15:219–308.

CLAUSEN, J., D. D. KECK, and W M. HEUSI. 1932. Experimental taxonomy. Carnegie Inst. Wash. Year Book No. 31, pp. 201–205.

COVILLE, F. V. 1896. *Crepis occidentalis* Nutt. and its allies. Contr. U. S. Nat. Herb. 3:559–565

DARLINGTON, C. D. 1937. Recent advances in cytology, 2d ed. 671 pp. London: J. & A. Churchill, Ltd.

DOBZHANSKY, TH. 1937 Genetics and the origin of species. 364 pp. New York: Columbia University Press.

DORF, E.1933. Studies of Phocene palæobotany of California. Carnegie Inst Wash. Pub No. 412, pp. 1–112.

DU RIETZ, G. E 1930. The fundamental units of biological taxonomy. Svensk. Bot. Tidskr. 24:333.

ERNST, A. 1918. Bastardierung als Ursache der Apogamie im Pflanzenreich. 665 pp. Jena: G. Fischer.

FAGERLIND, F 1937. Embryologische, zytologische, und bestäubungsexperimentelle Studien in der familien Rubiaceæ, nebst Bemerkungen über einige Polyploiditätsprobleme Acta Horti Bergiani 11:195–470.

FENNEMAN, N. M 1931. Physiography of the western United States. 534 pp. New York: McGraw-Hill Book Co.

FERNALD, M. L. 1925 The persistence of plants in unglaciated areas of boreal America Mem. Am. Acad Sci. 15.295–317.

——— 1933. Recent discoveries in the Newfoundland flora. Rhodora 35:327–347; 369–386.

FLINT, R F 1937. The Pleistocene drift border in eastern Washington. Bull. Geol Soc. Am. 48:203–232

FOCKE, W. O. 1914 Species Ruborum, pt. III. Bibl Bot. 80. 274 pp.

GOODSPEED, T. H. 1934 *Nicotiana* phylesis in the light of chromosome number, morphology, and behavior Univ. Calif. Publ. Bot 17:369–398.

——— and R. E. CLAUSEN. 1928. Interspecific hybridization in *Nicotiana* VIII. The *sylvestris—tomentosa—Tabacum* triangle and its bearing on the origin of *Tabacum*. Univ. Calif. Publ. Bot. 11:245–256.

GRAY, A. 1876 *Crepis*, L., *in* Synoptical flora of North America 2 (pt. 2): 430–432.

GREGOR, J. W., and F W. SANSOME. 1930 Experiments on the genetics of wild populations II. *Phleum pratense* L., and the hybrid *P. pratense* × *P. alpinum* L. Jour. Genetics 22.373–389

GUSTAFSSON, A. 1930. Castrierung und Pseudogamie in der Gattung *Rubus*. Bot. Notiser (Lund) 1930:477–494.

——— 1932 Zytologische und experimentelle Studien in der Gattung *Taraxacum*. Hereditas 16:41–62

——— 1935*a*. Studies on the mechanism of parthenogenesis. Hereditas 21:1–112

——— 1935*b*. The importance of apomicts for plant geography. Bot Notiser: 325–330.

——— 1937. The occurrence of a sexual poplation within the apomictic *Taraxacum vulgare* group. Bot. Notiser. 332–336.

HAGERUP, O 1932 Über Polyploidie in Beziehung zur Klima, Ökologie, und Phylogenie. Hereditas 16:19–40.

HAY, O. P. 1913 Description of the skull of an extinct horse found in central Alaska. Misc Coll. Smithsonian Inst. 61, No. 2. 18 pp.

HERIBERT-NILSSON, N. 1918. Experimentelle Untersuchungen über Variabilität, Spaltung, Artbildung, und Evolution der Gattung *Salix*. Lunds Univ. Lunds Univ. Årsskrift N. F. 14, Avd. 2, no. 28. 145 pp.

HOLLICK, A. H. 1936. The Tertiary floras of Alaska. U. S. Geol. Surv. Prof. Paper No. 182.

HOLLINGSHEAD, L., and E. B. BABCOCK. 1930. Chromosomes and phylogeny in *Crepis*. Univ. Calif. Publ Agr. Sci 6:1–53.

HOOKER, J. D. 1834. *Crepis*, L., *in* Flora Boreali-Americani 1:297.

HUSKINS, C. L 1931. The origin of *Spartina Townsendii*. Genetica 12:531–538.

JEPSON, W. L. 1925. A manual of the flowering plants of California. 1238 pp. Berkeley: Univ. of California.

JONES, G. N. 1936. A botanical survey of the Olympic Peninsula. Univ. Wash. Publ. Biology 5:1–286.

LINDBERG, H. 1936. *Lactuca tatarica* (L.) C. A. Meyer i Norden. Svensk Bot. Tidskr. 30:652–660.

MANTON, I. 1932. Introduction to the general cytology of the Cruciferæ. Ann Bot. 46:509–556.

——— 1934 The problem of *Biscutella lævigata*. Zeitschr. Ind. Abst. u. Vererbungsl. 67:41-57.

——— 1937. The problem of *Biscutella lævigata* L II. The evidence from meiosis. Ann. Bot. n. s. 1:439–462.

MATHEW, W. D. 1915 Climate and evolution. Ann New York Acad. Sci. 24:171–318.

MERRIAM, C. H. 1892. The geographic distribution of life in North America with special reference to the Mammalia Proc Biol. Soc. Wash. 7:1–64.

MÜNTZING, A. 1930. Über Chromosomenvermehrung in *Galeopsis*—Kreuzungen und ihre phylogenetische Bedeutung. Hereditas 14:153–172.

——— 1932. Apomictic and sexual seed formation in *Poa*. Hereditas 17:131–154.

——— 1936 The evolutionary significance of autopolyploidy. Hereditas 21:263–378.

——— 1937. The effects of chromosomal variation in *Dactylis*. Hereditas 23:113–235.

——— O. TEDIN, and G. TURESSON 1931. Field studies and experimental methods in taxonomy. Hereditas 15:1–12.

MURBECK, S 1901. Parthenogenetische Embryobildung in der Gattung *Alchemilla*. Lunds Univ. Årsskrift 36, Afd. 2, No. 7. 41 pp.

NORDENSKIÖLD, H. 1937 Intra and interspecific hybrids of *Phleum pratense* and *P. alpinum* Hereditas 23:304–317.

NUTTALL, T. 1841. *Crepidium, Crepis*, and *Psilochenia, in* Descriptions of new species and genera of plants, etc. Trans. Am Phil. Soc. n. s. 7:435–437.

OKABE, S 1930. Über Parthenogenesis bei *Houttuynia cordata*. Jap. Jour. Genet. 6:14–19 (Japanese, German summary).

OSBORN, H. F. 1910. The age of mammals in Europe, Asia, and North America. 635 pp New York: The MacMillan Co.

OSTENFELD, C. H. 1910. Further studies on the apogamy and hybridization of the *Hieracia*. Zeitschr. Ind. Abst. u. Vererbungsl. 3:241–285.

——— 1921. Some experiments on the origin of new forms in the genus *Hieracium* sub-genus *Archieracium*. Jour. Genet. 11:117–122.

PECK, M. E. 1925. A preliminary sketch of the plant regions of Oregon. Am. Jour. Bot. 12:33–49; 69–81.

PIPER, C. V. 1906. Flora of the State of Washington. Contr. U. S. Nat. Herb. 11. 637 pp.

PODDUBNAJA-ARNOLDI, W. A. 1933. Geschlechtliche und ungeschlechtliche Fortpflanzung bei einigen *Chondrilla*-Arten. Planta 19:46–86.

RENSCH, B. 1929. Das Prinzip geographischer Rassenkreise und das Problem der Artbildung. 206 pp. Berlin: Gebr. Borntraeger.

ROSENBERG, O. 1907. Cytological studies on the apogamy in *Hieracium*. Bot. Tidsskr. 28:143–170.

——— 1930 Apogamie und Parthenogenesis bei Pflanzen. Handbuch der Vererbungswiss. 2. 66 pp.

SANSOME, F. W., and J. PHILP. 1932. Recent advances in plant genetics. 414 pp. London: J. & A. Churchill, Ltd.

SAX, K, and H. J. SAX 1937 Stomata size and distribution in diploid and polyploid plants. Jour. Arn. Arb. 18:164–172.

STEBBINS, G. L., JR. 1932. Cytology of *Antennaria* II. Parthenogenetic species. Bot. Gaz. 94:322–345.

——— 1939. Notes on the systematic relationships of the Old World species and of some horticultural forms of *Pæonia*. Univ. Calif. Publ Bot. 19 (7) · (in press).

TÄCKHOLM, G. 1922. Zytologische Studien über die Gattung *Rosa*. Acta Horti Bergiani 7:97–381.

THORNTHWAITE, C. W. 1931. The climates of North America, according to a new classification. Geogr. Rev. 21:633–655

——— 1933. The climates of the earth. Geogr. Rev. 23:433–440.

TISCHLER, G. 1935. Die Bedeutung der Polyploidie für die Verbreitung der Angiospermen, erläutert an den Arten Schleswig-Holsteins mit Ausblicken auf andere Florengebiete. Bot. Jahrb. 67:1–36.

TORREY, J., and A. GRAY. 1843. *Crepis*, L., *in* Flora of North America II:487–489.

TURESSON, G. 1926. Studien über *Festuca ovina* L. I. Normalgeschlechtliche, halb- und ganz-vivipäre Typen nordischer Herkunft. Hereditas 8:161–206.

——— 1929. Zur Natur und Begrenzung der Arteinheiten. Hereditas 12:323–333.

WINKLER, H 1916. Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. Zeitschr. für Bot. 8:417–531.

——— 1920. Verbreitung und Ursache der Parthenogenesis im Pflanzen- und Tierreiche. Jena.

WRIGHT, W. B 1914. The Quaternary Ice Age. 464 pp. London: MacMillan & Co

GENERIC DESCRIPTION

Crepis (Vaill.) Linn., Sp. Pl. ed. 1, 805, 1753

Annual, biennial or perennial herbs and, in the last, the caudex woody with a strong root and leafy at crown; caudical leaves entire, dentate or pinnatifid, glabrous, pubescent, or tomentose; cauline leaves mostly reduced, the uppermost bractlike; stem or stems elongate or very short in tufted species, paniculately or cymosely branched with few or many heads; heads small to large, few– to many-flowered, florets all ligulate; involucre cylindric or campanulate, calyculate, the outer bracts shorter, few or many, linear to ovate and then sometimes imbricate, the inner bracts in 1 or 2 series, ± scarious-margined; receptacle naked or ciliate (never paleaceous in the American species); ligules yellow, sometimes reddish on outer face (in a few Old World species pink or white), anther-tubes yellow, with oblong or lanceolate appendages; style-branches yellow or green, semicylindric, linear; achenes terete or subterete, fusiform, attenuate upward, or prolonged into a short or long, coarse or fine beak, 10–20-ribbed, ribs coarse or fine; pappus white or dusky, usually exceeding the involucre, of 1 to several series of barbellulate capillary bristles.

KEY TO THE WESTERN AMERICAN SPECIES OF CREPIS

A. Plants of arctic-alpine climates, wholly glabrous; leaves small, spatulate to elliptic, entire or few-toothed or lyrate with few lateral lobes.
  B. Plant small, tufted, 2–7 cm high or, in elongate forms, 8–18 cm high; caudex slender, often stoloniferous; achenes columnar, slightly or definitely attenuate or very shortly beaked, the ribs broad, rounded, smooth or rugulose . . . . . 1. *C. nana* (p. 84)
  B. Plant larger, not tufted, 15–25 cm high and as broad or broader; caudex thicker, never stoloniferous; achenes fusiform, attenuate into a delicate beak about ¼ as long as the body, the ribs narrow, spiculate . . . . . 2. *C. elegans* (p. 85)

A. Plants of cold-temperate or temperate climates, never completely glabrous; leaves larger, oblanceolate, mostly pinnatifid, lobed, or strongly dentate.
  C. Flowers pink or white; heads nodding before anthesis; achenes 9–20 mm long,[1] with a coarse or slender but not filiform beak 1–2 times as long as the body of the achene; occasionally escaped from gardens . . . . . 5. *C. rubra* (p. 87)
  C. Flowers yellow; heads erect before anthesis; achenes 1.5–11 mm long, either not beaked or, if beaked, the beak either filiform or not longer than the body of the achene; introduced weeds and native forage plants.

[1] Achene lengths always include the beak, when present.

D. Stems several, decumbent; achenes beaked, the beak filiform; ligules greenish on outer face; introduced perennial weed..... 6. *C. bursifolia* (p 88)

D. Stem erect or, if stems several and rarely decumbent, the achenes beakless or the beak not filiform; ligules yellow or reddish on outer face.

E. Heads mostly smaller; involucre 5–10 (–12) mm high; achenes beaked or, if beakless, less than 4 mm long; introduced annuals or biennials of fields, lawns, or waste places.

F. Achenes beakless, 1.5–4 mm long

G. Inner involucral bracts glabrous on inner face; mature achenes tawny or pale brown, slightly attenuate at the summit

H. Involucres 5–8 mm long, 3–4 mm wide at middle; receptacle glabrous; achenes brownish yellow, pale brown, or dark brown, 1.5–2.5 mm long, narrowly ribbed... 4. *C. capillaris* (p. 86)

H. Involucres 8–10 mm long, 4–6 mm wide at middle; receptacle ciliate; achenes golden brown, 2.5–3.8 mm long, broadly ribbed. 3 *C. nicæensis* (p 85)

G. Inner involucral bracts pubescent on inner face; mature achenes dark purplish brown, strongly attenuate at the summit..... 4*a C. tectorum* (p 87)

F. Achenes finely beaked, 3–9 mm long.

I. Involucre and stems strongly setose with stiff yellow bristles; achenes 3–5 mm long.. 7. *C. setosa* subsp. *typica* (p 89)

I. Involucre and stems tomentulose, pubescent, or setulose with short black setules; achenes 5–9 mm long..... 8 *C. vesicaria* subsp. *taraxacifolia* (p 90)

E. Heads mostly larger; involucre (7–) 9–22 mm long; achenes beakless or very shortly and coarsely beaked, 4–11 mm long; native perennials with strong roots, mostly montane or desert species

J. Stem and leaves glabrous or glaucous or sometimes hispidulous; cauline leaves generally all reduced, narrow, inconspicuous, or rarely the lowest one similar to caudical leaves; involucre turbinate-campanulate; plants of moist situations ..... 9 *C. runcinata* (p 90)

J. Leaves and stems at least slightly tomentose with a fine, appressed tomentum, and often hirsute, setose, or glandular-pubescent as well; 1–3 cauline leaves generally well developed (except in *C. pleurocarpa*); involucres

narrowly or broadly cylindric; plants of dry situations.

K. Herbage and involucres slightly tomentulose and shaggy-hirsute with long (1–3 mm) gland-tipped hairs; inner involucral bracts long attenuate, their tips not folded over the florets in the buds; outer bracts linear-lanceolate ..... 11 *C. monticola* (p. 114)

K Herbage and involucres sometimes setose or glandular-pubescent, but the hairs, if glandular, short; inner bracts acute, acuminate, or somewhat attenuate at the apex, folded over the florets in the buds; outer bracts mostly lanceolate or ovate-lanceolate.

L. Involucral bracts densely beset with blackish, whitish, or yellowish, curved or crisped glandless setæ or, if with few or no setæ on the involucres, the basal part of the stem and petioles conspicuously setose; achenes blackish, or greenish, or less commonly yellowish or brownish, slightly costate or generally merely striate, distinctly attenuate at the apex.

M. Stems 0.6–3.5 dm high; inflorescence of 1–9 heads; involucres with 8–15 inner bracts and 10–60 florets; longest of the outer bracts generally 2/5–2/3 the length of the inner ..... 14 *C. modocensis* (p. 141)

M. Stems 2.5–6 dm high; inflorescence of 6-70 heads; involucres with 5–10 inner bracts and 6–20 florets; longest of the outer bracts 1/4–2/5 the length of the inner..... 15. *C. barbigera* (p 154)

L Involucral bracts glabrous, tomentose, glandular-pubescent, or, if with a few straight black setæ, the stems and petioles not setose; achenes various.

N. Largest heads of the inflorescence with 5–7 inner involucral bracts; 5–10-flowered.

O. Involucral bracts glabrous or sparingly and evenly tomentulose, the inner yellowish green, shading indistinctly into the scarious margins; achenes yellow or buff colored, with slender ribs, equaling or exceeding the pappus; 1–3

well - developed cauline leaves present; inflorescence confined to the upper half of the stem with 15–200, generally 30–100 heads in well-developed plants ..... 17. *C. acuminata* (p. 169)

O. Involucral bracts with a glabrate central portion, conspicuously white-tomentose on the scarious margins; achenes reddish or brownish, strongly costate, shorter than the pappus; cauline leaves generally much reduced or absent; inflorescence usually branching from the middle of the stem or below, with 7–40, generally 15–30 heads in well-developed plants ..... 10. *C. pleurocarpa* (p. 107)

N. Largest heads of the inflorescence with 8–13 inner bracts; 9–40 flowered.

P. Achenes deep or pale green, strongly attenuate or subrostrate at the apex; lobes of leaves linear or narrowly lanceolate, 0.5–2.5 mm broad, falcate, mostly entire ..... 16. *C. exilis* (p. 159)

P. Achenes yellowish or brownish; lobes of leaves broadly lanceolate or deltoid or, if narrower, generally toothed or lobed.

Q. Plants mostly 1–3 dm tall, bearing a cymose inflorescence of 2–25 heads; involucres broadly cylindric, 5–9 mm broad at anthesis, 9–40-, averaging 12–25-flowered; longest outer bracts (except in 2 subspp.) 5–9 mm long, 1/3–2/3 the length of the inner.

R. Leaves grayish - tomentose, but not glandular pubescent; peduncles not expanded toward the apex ..... 12. *C. occidentalis* (p. 118)

R. Leaves green and glandular pubescent, in fresh specimens with a conspicuous

reddish midrib and petiole; peduncles expanded toward the apex ..... 13. *C. Bakeri* (p. 138)

Q. Plants mostly 2.5–6 dm tall, bearing an ample cymose panicle of 20–60 heads; involucres narrowly cylindric, 3–5.5 mm broad at anthesis, 7–15-, averaging 8–10-flowered; longest outer bracts mostly 3–5 mm long, 1/5–1/3 the length of the inner.

S. Involucres glabrous.. 17. *C. acuminata* subsp. *pluriflora* (p. 178)

S. Involucres tomentulose or tomentose.

T. Basal leaves glabrate; involucral bracts glabrate on the central portion, strongly tomentose on the scarious margin. 10. *C. pleurocarpa* (apm *plumaënsis*) (p. 113)

T. Basal leaves grayish - tomentose; involucral bracts evenly tomentose or tomentulose.. 18. *C. intermedia* (p. 179)

DESCRIPTIONS OF SPECIES

1. Crepis nana Richards., Bot. Append. of Franklin, 1st Jour. ed. 1, 746 (p. 18 in repr.), 1823; ed. 2, 757 (p. 29 in repr.), 1823

Plant perennial, glabrous, with slender rootstock, only 0.2–0.7 dm high, tufted, with the heads borne among the leaves, or 0.8–1.8 dm high, with leafy stems and the heads borne well above the basal leaves; leaves up to 8.5 cm long, 2.5 cm wide, spatulate, orbicular, elliptic, or ovate, obtuse or acute, long- or short-petioled, glaucous, often purplish; heads erect, narrow, 9–12-flowered; involucre cylindric, 8–13 mm long, 2–3 mm wide at middle; outer bracts 5–8, unequal, very short or the innermost nearly 1/3 as long as the inner bracts, ovate or lanceolate, acute; inner bracts about 10, oblong, narrowed near the obtuse purplish ciliate tip, becoming carinately thickened near the base; receptacle glabrous; corolla 7–9 mm long, the ligules yellow or purplish; corolla-tube 2.5–5 mm long, glabrous; anther-tube about 2.5 mm long, yellow; style-branches about 1 mm long, yellow; achenes golden brown, subterete, columnar, slightly constricted or definitely attenuate at the summit or with a very short beak, 10–13-ribbed, ribs rounded, smooth or rugulose; pappus white, 4–6 mm long, the bristles fine, soft, deciduous. (*Barkhausia nana* DC., Prod. 7:156, 1838; *Hieraciodes nanum* O. Ktze., Rev. Gen. 346, 1891; *Youngia nana* Rydb., Fl. Rocky Mts. 1021, 1917.) *Note*: The synonyms listed under this and the following species include only those which appear in other works dealing with North American species.

Boreal and alpine, this is the most widely distributed species in the genus. In Asia from Altai to Kamchatka. In North American arctic regions from Alaska to Newfoundland and at high elevations in the Rocky Mountains and on higher ranges of Utah, Nevada, and the Pacific Coast states.

Usually sporadic on gravel or loose rocks, often near melting snow or glaciers, sometimes on sand bars along high mountain streams, this plant is adapted to most rigorous conditions. Specimens from arctic locations are very uniform in habit, closely resembling the type of the species. Yet they show notable variations in leaf shape and especially in shape of the achenes, particularly in the degree of attenuateness at the summit. From the alpine and subalpine stations of more southerly latitudes, the specimens show a general trend toward larger size, especially in the leaves and heads, and occasionally they have more elongate stems and branches. No doubt some of these variations are merely ecological. Even among the arctic plants a few cases of this sort occur. But the more extreme variations in size and habit found in certain of the more southern forms, particularly those of the Olympic Mountains of western Washington, very probably are genetic in nature. The chromosome number of this taller, ramose form is not known. Typical plants from Alaska had 14 chromosomes in root-tip cells.

2. **Crepis elegans** Hook., Fl. Bor. Am. 1:297, 1834

Plant perennial, glabrous, 1.5–2.5 dm high and as broad or broader; caudex 4–6 mm wide, cylindric or conical, tapering into a strong woody taproot; stems several or numerous, stiffly erect or semi-erect, dichotomously branched from the base upward, in older plants excessively branched, forming a dense obconical clump topped by a mass of flowerheads; caudical leaves numerous, up to 6 cm long, 1.5 cm wide, spatulate, elliptic or ovate, acute, entire or coarsely dentate, with petiole equal to or longer than the blade, glaucous and purplish; cauline leaves linear, acuminate, petiolate or sessile; heads erect, small, 9–10-flowered; involucre cylindric, 8–10 mm long, 2–3 mm wide at middle; outer bracts 7–8, very short, ovate or oblong, acute; inner bracts 8–10, oblong, acute or obtuse, purple at tip, becoming carinately thickened near base; receptacle glabrous; corolla about 8 mm long, the ligules yellow; corolla-tube about 4 mm long, glabrous; anther-tube about 2.75 mm long, yellow; style-branches 0.5 mm long, yellow; achenes golden brown, about 5 mm long, very slender, subterete or definitely flattened on one side, fusiform, attenuate into a delicate beak about ¼ as long as the body, 10-ribbed, the ribs narrow, spiculate; pappus white, about 4 mm long, very fine, soft, caducous. (*Barkhausia elegans* Nutt., Trans. Am. Philos. Soc. 7:485, 1841; *Youngia elegans* Rydb., Fl. Rocky Mts., 1021, 1917; *Hieraciodes elegans* O. Ktze., Rev. Gen. 345, 1891.)

Northwestern North America, from central Alaska south to Alberta, Saskatchewan, Montana, and Wyoming; along river banks, on sand bars, occasionally on dry plains and bluffs, from 600 to 1500 m altitude.

Although closely related to *C. nana,* and probably descended from it, *C. elegans* is very distinct in habit, floral characters, and achenes. Also its distribution in a warmer life zone sets it off sharply from *C. nana;* and apparently it is much less variable. It also has 14 chromosomes in its somatic cells.

3. **Crepis nicæensis** Balb., ex Pers., Syn. Pl. 2:376, 1807; Mem. Acad. Sci. Turin, 16:226, 1809

Plant biennial or annual, 2.5–11 dm high; caudical leaves up to 19 cm long, 4 cm wide, usually much smaller, oblanceolate, obtuse, runcinate-pinnatifid, dentate or finely denticulate, with a short petiole, hispidulous; lowest cauline leaves similar or longer petioled, the others mostly lanceolate, sessile, usually with acuminate pendant auricles; stem erect, densely hispidulous below, branched near summit or lower, the aggregate inflorescence corymbiform; peduncles rather slender, like branches and involucres pubescent with long and short glandulose or eglandulose hairs and like involucres more or less canescent-tomentose; heads erect, many-flowered; involucre campanulate, 8–10 mm long, 4–6 mm wide at receptacle; outer bracts about 8, linear, acute, 1/3–1/2 (2/3) as long as the inner, becoming lax; inner bracts 10–15, lanceolate, strongly attenuate, obtuse at the ciliate tip, glabrous on inner face, becoming strongly carinate in fruit; receptacle alveolate, finely ciliate; corolla about 11 mm

long, the ligule yellow or sometimes red at the summit; corolla-tube about 3 mm long, sparsely pubescent; anther-tube about 3.8 mm long, yellow; style-branches about 1.7 mm long, dark green; achenes golden brown, 2.5–3.8 mm long, about 0.6 mm wide at middle and 0.3 mm wide at summit, fusiform, 10–ribbed, ribs broad, rounded, smooth or finely spiculate; pappus white, 4–5 mm long, 2-seriate, more or less united at base, deciduous.

Southern Europe. Introduced into central and western Europe and into eastern and western North America along with cultivated forage plants. Although it has been reported from only one locality in the west (Marysville, Washington), it is likely to appear elsewhere.

Superficially, this species resembles the well-known *Crepis biennis* L., of southern Europe, from which it is easily distinguished by the smaller heads with linear outer involucral bracts and the inner bracts glabrous within, as well as by the shorter achenes, always with 10 broader ribs. Furthermore, this species has only 8 chromosomes in the somatic cells, whereas *biennis* has about 40.

4. **Crepis capillaris** (L.) Wallr., Linnæa, 14:657, 1840

Plant annual or occasionally biennial, 0.2–9 dm high; caudical leaves 3–30 cm long, 0.5–4.5 cm wide, lanceolate or oblanceolate, obtuse or acute, denticuate, dentate, runcinate-pinnatifid, or lyrately pinnately or bipinnately parted with remote oblanceolate or linear lobes, long or shortly petiolate, glabrous or hispidulous on midrib beneath or hispidulous on both sides with short yellow eglandulose hairs; lower cauline leaves similar, the others lanceolate, acute, sessile, amplexicaul, acutely auriculate; stem erect, branched above, or profusely branched from base upward, or the central axis short with numerous semi-erect nearly equal stems, or stems diffuse, semi-procumbent, arcuate, hispidulous near base or throughout; aggregate inflorescence corymbiform or paniculate-corymbiform; peduncles 0.5–6.5 mm long, slender, canescent-tomentose like base of involucre or glabrous, sometimes with a few black gland-hairs; heads erect, small, 20-60-flowered; involucre cylindric to turbinate, 5–8 mm long; outer bracts about 8, linear, 1/3–1/2 as long as the inner, green or somewhat scarious, glabrous, tomentose, or with a few gland-hairs, becoming lax; inner bracts 8–16, lanceolate, acute, tomentose, often with a double row of short black glandular bristles, becoming spongy-thickened dorsally, confluent with the much swollen base of the head in fruit, ventrally glabrous; receptacle glabrous; corolla 7.5–12 mm long, the ligule deep yellow, reddish on outer face; corolla-tube 2–3 mm long, pubescent; anther-tube 3–3.5 mm long, yellow; style-branches 1–1.5 mm long, yellow, greenish, or green; achenes tawny, pale brown, or dark brown, 1.5–2.5 mm long, fusiform or oblong, abruptly narrowed at both ends, about 10-ribbed, ribs narrow, rounded, smooth or finely spiculate; pappus white, 3–4 mm long, 2-seriate, fine, soft, caducous. (*Lapsana capillaris* L., Sp. Pl. ed. 1, 2:812, 1753; *Crepis virens* L., Sp. Pl. ed. 2, 1:1134, 1763; *Malacothrix crepoides* Gray, ex J. G.

Cooper, Pac. R. R. Rept. 12:53, 1860; *Crepis Cooperi* Gray, Proc. Am. Acad. 9:214, 1874.)

Southern and middle Europe. Frequently adventive along coasts in many parts of the world. Naturalized in western North America from British Columbia to middle California and eastward in the Cascades and the Sierra Nevada in meadows, pastures, lawns, and waste places.

Although the type is a low, diffuse, small-headed form, and although similar forms occur occasionally throughout the range of the species, yet the more typical, i.e., usual forms of this very polymorphic species are taller and more robust, with erect or nearly erect stems and larger heads. All the uncultivated forms thus far examined cytologically have 6 chromosomes as the diploid number; but it is possible that certain "*gigas*" forms are polyploids.

4*a*. **Crepis tectorum** L., Sp. Pl. 2:807, 1753

Plant annual, 3–97 cm high; caudical leaves up to 15 cm long, 4 cm wide, lanceolate or oblanceolate, acute, denticulate to pinnately parted, petiolate, glabrous or puberulent; cauline leaves mostly linear, sessile, auriculate; stem erect, simple and few-headed or branched above or from the base; peduncles 0.3–7 cm long, slender, tomentulose or sometimes hispidulose; heads erect, 30–70-flowered; involucre cylindric-campanulate, up to 9 mm long, 7 mm wide in fruiting heads; outer bracts 12, about 1/3 as long as the inner, subulate; inner bracts 12–15, lanceolate, acuminate, becoming carinate and thickened near base, pubescent on inner face; receptacle very finely ciliate; corolla up to 13 mm long; corolla-tube 3–4 mm long, shortly pubescent; anther-tube 2–3 mm long; style-branches 1–1.5 mm long, dark green; achenes 2.5–4.5 mm long, dark purplish brown, fusiform, rather strongly attenuate, scarcely beaked, 10-ribbed, ribs finely spiculate; pappus 4–5 mm long, white, fine, 1-seriate, deciduous.

Most of Europe and the greater part of Siberia. It has become naturalized in other continents, notably in North America and Australia. The only records of this species known to us from our area are the collection of McCabe in 1934 near Marguerite, on the Fraser River between Soda Creek and Quesnel, British Columbia, and Brinkman no. 2534 at Bashaw, Stettler District, Alberta.

This widespread species of the lowlands occurs in Europe under a great variety of ecological conditions with a consequent diversity of forms. But the slender, erect, few-headed type is most frequent. The diploid chromosome number is 8.

5. **Crepis rubra** L., Sp. Pl. 2:806, 1753

Plant annual, 0.4–3.8 dm high; caudical leaves 2–16 cm long, 0.5–3 cm wide, oblanceolate, acute or obtuse, denticulate, dentate, runcinate-pinnatifid, or pinnately parted with acute denticulate or dentate lateral lobes, sometimes lyrate, petiolate, finely pubescent with short pale eglandulose hairs; cauline leaves few, much reduced; stems 1–12, usually scapiform, arcuate or semi-decumbent, sometimes with a short central

axis, 1–5-branched near base, the branches pedunculate, strict or arcuate, puberulent; peduncles somewhat thickened, sulcate and setulose near base of head; heads medium to large, many-flowered, nodding before anthesis; involucre cylindric-campanulate, 10–15 mm long, 5–8 mm wide at middle in fruiting heads; outer bracts numerous, imbricate, the longest about ½ as long as the inner, lanceolate, acuminate, pale, glabrous or tomentulose; inner bracts 8–16, oblong-lanceolate, acute, densely pubescent or setulose with long and short gland-hairs, becoming navicular, enclosing marginal achenes, ventrally appressed-pubescent; receptacle densely ciliate; corolla 13–17 mm long, the ligule pink or white; corolla-tubes about 5 mm long, sparsely pubescent; anther-tube about 3.5 mm long, pink or white; style-branches 1.75 mm long, yellow; achenes dark reddish brown below, stramineous above, 9–19 mm long, dimorphic, the marginal curved, constricted at base, gradually attenuate to summit, laterally compressed, obscurely 4-angled, with oblique dorsal basal scar, the inner slender, with narrowly fusiform body, gradually attenuate into a rather coarse beak 1 1/2–2 1/2 times as long, subterete or obscurely angular, all achenes about 16-striate, striæ narrow, close, strongly spiculate; pappus cream white, 5–8 mm long, 3-seriate, rather fine, soft, persistent.

Italy and the Balkans. Long since introduced into Old World gardens and occasionally escaping from cultivation in America. Although reported only once from our region (Belvedere, Marin County, California) it is likely to appear again.

The garden forms are usually more robust and larger flowered, at least under cultivation, than the indigenous plants, although the latter exhibit great variation in size, apparently in response to differences in exposure and moisture. The diploid chromosome number is 10.

6. **Crepis bursifolia** L., Sp. Pl. 2:805, 1753

Plant perennial, 1–3 dm high; caudex woody, prolonged into a strong root, simple or divided at the crown; caudical leaves 5–25 cm long, 1.5–5 cm wide, oblanceolate, obtuse, lyrately pinnately divided with large or small denticulate or dentate terminal segment and oblong or lanceolate acute dentate lateral segments, gradually reduced into a short or long petiole, pubescent especially along midrib beneath with short white hairs; cauline leaves usually much reduced or bracteiform, in robust specimens sometimes large, similar to the caudical leaves; stems several or numerous, slender, terete, tomentulose, becoming stramineous in fruit, semi-decumbent or arcuate, branched above or from near base, 2–14-headed; peduncles 0.5–6 cm long, slender, farinose, slightly thickened near the head; heads erect, small, many-flowered; involucre cylindric, 9–11 mm long, 3–4 mm wide at middle, canescent-farinose; outer bracts 8–10, unequal, 1/4–1/3 as long as the inner, linear, acuminate, green with blunt white tip; inner bracts 8–10, lanceolate, obtuse, dark green near margin, pale in mid region, with or without a few yellow eglandulose setules, sparsely pubescent on inner face near tip, becoming strongly carinate and thickened near base; receptacle alveolate, shortly ciliate; corolla about 10 mm

long, the ligule yellow on inner face, dull green on outer face; corolla-tube 2–3 mm long, pubescent; anther-tube about 3 mm long, yellow; style-branches 1–1.5 mm long, green; achenes light brown, 6–7.5 mm long, 0.3–0.5 mm wide, dorsoventrally subcompressed, the body fusiform, abruptly constricted into the pale filamentous beak once or twice as long, 10-ribbed, ribs narrow, rounded, strongly spiculate; pappus white or cream, 3–4 mm long, 2- or 3-seriate, very fine, soft, deciduous.

Southern France and Italy in lawns and waste places. Introduced here and there in the Mediterranean region. Introduced and well established on the campus of the University of California at Berkeley.

This is one of the few perennial species of subg. *Barkhausia*. It has no very close relatives. The somatic chromosome number is 8.

7. **Crepis setosa** Hall. f., Roem. Arch. Bot. 1(2):1, 1797; subsp. **typica** nom. nov.

Plant annual, 1.8–8 dm high; caudical leaves few or many, 6–30 cm long, 1.5–8 cm wide, oblanceolate, obtuse or acute, denticulate, dentate, runcinate-pinnatifid, or pinnately parted, terminal segment large or sometimes small, lateral segments triangular to lanceolate, acute and dentate, finely hispid, petiolate, petiole narrow or broadly winged; cauline leaves mostly lanceolate, acuminate, dentate to deeply laciniate near base, amplexicaul-auriculate, auricles acuminate; stem erect, short and branched from near the base, or elongate and remotely branched from base to summit, hispid, the branches long, spreading or strict, few-headed; peduncles slender, erect, hispid or like the involucre setose, the setæ yellow, eglandulose; heads small to medium, many-flowered; involucre cylindric-campanulate, somewhat turbinate in fruit, 8–10 mm long, 4–8 mm wide; outer bracts 10–14, the longest 1/2 as long as the inner, linear, acuminate, carinate, lax; inner bracts 12–16, lanceolate, acuminate, becoming strongly carinate, thickened at base, ventrally pubescent; receptacle areolate, shortly ciliate; corolla yellow, 10–13 mm long, the ligule red on outer face; corolla-tube 3.5–4.5 mm long, pubescent; anther-tube 3.5 mm long, yellow; style-branches 1.75–2.5 mm long, dark green; achenes pale brown, 3.25–5 mm long, 0.3–0.6 mm wide, fusiform, abruptly or gradually attenuate into a usually fine beak 1–2.5 mm long, 10-ribbed, the ribs rather prominent, narrow, rounded, strongly spiculate near base of beak; pappus white, 1-seriate, 2.5–5 mm long, fine, soft, deciduous.

Southeastern Europe, in fields and waste places at lower altitudes. Introduced with forage crops throughout Europe and in North and South America and New Zealand. The only record of this species from our area is a very robust form which was collected at Silverton, Oregon, in 1919.

This species of subg. *Barkhausia* also has no very close relatives, although it superficially resembles *C. aspera* L., a species of the eastern Mediterranean littoral. Its diploid chromosome number is 8, and in the morphology of its chromosomes it stands apart from all species of *Barkhausia* thus far studied cytologically.

8. **Crepis vesicaria** L., Sp. Pl. 2:805, 1753; subsp. **taraxacifolia** (Thuill.) Thell., ex Schinz et Keller, Fl. Schweiz ed. 3, 1:594, 1909

Plant annual, biennial, or sometimes perennial, 0.3–8 dm high; root vertical, often woody, sometimes thickened below the simple or divided caudex; caudical leaves narrowly oblanceolate to ovate or spatulate, obtuse or acute, denticulate, dentate, runcinate-pinnatifid, or lyrately pinnately parted with a larger terminal lobe, or pectinately parted with a small terminal lobe and close narrow lateral segments, petiolate, finely pubescent on both sides with short pale eglandulose hairs; cauline leaves similar or sessile, acute or acuminate, nearly entire to pinnately parted, the middle ones amplexicaul-auriculate; stem erect, more or less tomentose, hispid and purple near the base, branched above or from near the base upward, the lower branches elongate, few-headed, or stems several, sometimes strictly ascending, usually divaricate; peduncles 1–13 cm long; heads erect, small to medium, many-flowered; involucre cylindric-campanulate, 8–12 mm long, 3–7 mm wide at middle; outer bracts 5–12, lanceolate or ovate-lanceolate, not imbricate, scarious at margin; inner bracts 9–13, lanceolate, obtuse, tomentose, often gland-pubescent, sometimes setulose with black eglandulose setules near the tip, becoming carinate and thickened in fruit, appressed-pubescent on inner face; receptacle alveolate, shortly ciliate; corolla 9–12 mm long, yellow, the ligues red, purple, or brown on outer face; corolla-tube about 3.5 mm long, pubescent; anther-tube about 3.5 mm long, yellow; style-branches 1.5–2 mm long, green; achenes pale brown, 4.5–9 mm long, monomorphic, subterete, fusiform, gradually attenuate into a fine beak equal to or slightly longer than the body, 10-ribbed, ribs narrow, rounded, finely spiculate, muriculate or nearly smooth; pappus white, 4–6 mm long, 1–2-seriate, fine, soft, deciduous. (*C. taraxacifolia* Thuill., Fl. Par. 409, 1799.)

Western Europe and northwestern Africa. Introduced on the east and west coasts of North America, in New Zealand and Australia. Fields, waste places, and borders of woods. Adventive near Los Angeles; naturalized along the coast of Mendocino County, and at Berkeley, California.

This is an extremely polymorphic subspecies of a very large, inclusive species. It includes an extensive series of forms, many of which are evidently due to rather simple genetic variations, resulting from intercrossing and recombination of characters. At the same time, it crosses readily with several other subspecies, producing highly fertile hybrids, and numerous intergrading forms occur where these subspecies overlap in their indigenous areas. However, the only forms thus far reported in our region are fully typical of this subspecies. Such typical forms as have been examined have 8 chromosomes in their somatic cells.

9. **Crepis runcinata** Torr. et Gray, Fl. N. Am. 2:487, 1843 (Figs. 7–13)

Plant perennial, 10–80 (usually 25–50) cm high, with 1–3 stems from each caudex, corymbosely branching above or from near the middle, or sometimes simple, completely glabrous to more or less glandular or hispidulous especially on the peduncles and involucres; basal leaves 3–30

(usually 7–15) cm long, 0.5–8 cm wide, elliptic or obovate to oblanceolate, lanceolate, or linear, obtuse or acute, sessile or tapering into a short or long more or less winged petiole, pinnatifid, runcinately toothed, denticulate, or entire; cauline leaves much reduced, usually lanceolate or linear and bractlike; inflorescence of 1–30 heads; involucres campanulate or turbinate, calyculate or less commonly imbricate, 8–21 mm long, the

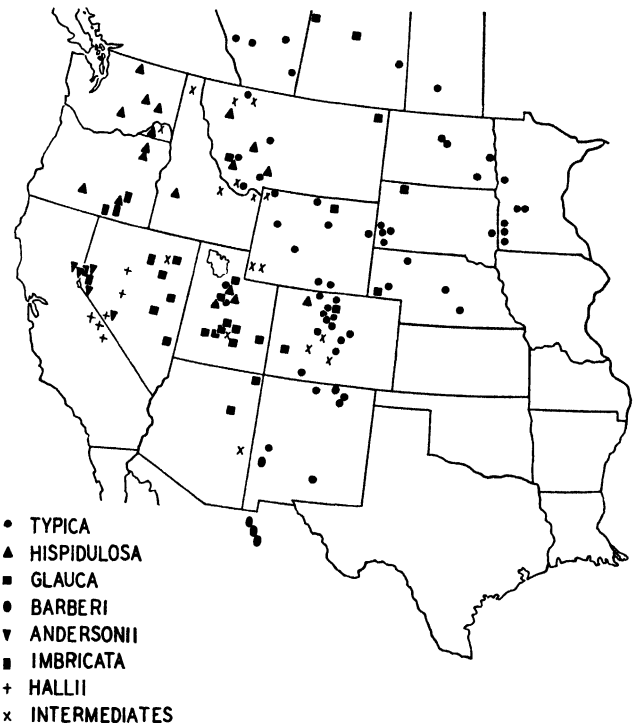


FIG. 6. Distribution of the various subspecies of *Crepis runcinata*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

longest outer bracts 1/4–2/3 as long as the inner, deltoid or linear to broadly lanceolate, or oblong, appressed; inner bracts 10–15, linear-lanceolate to broadly lanceolate, obtuse to acute or acuminate, glabrous within, somewhat thickened at base in fruiting heads; florets 20–50, the corollas 9–18 mm long, ligules golden yellow; achenes from light to very dark brown in color, fusiform, moderately attenuate to definitely but shortly beaked, 3.5–7.5 mm long, 10–13-ribbed, ribs smooth or minutely scabridulous; pappus white, 4–8 mm long, exceeding the involucre.

Manitoba, western Minnesota, Iowa, and Nebraska, southwest in the mountains to northern Mexico, and west to eastern California, Oregon, and Washington (fig. 6). The most widespread and, along with *C. occi-*

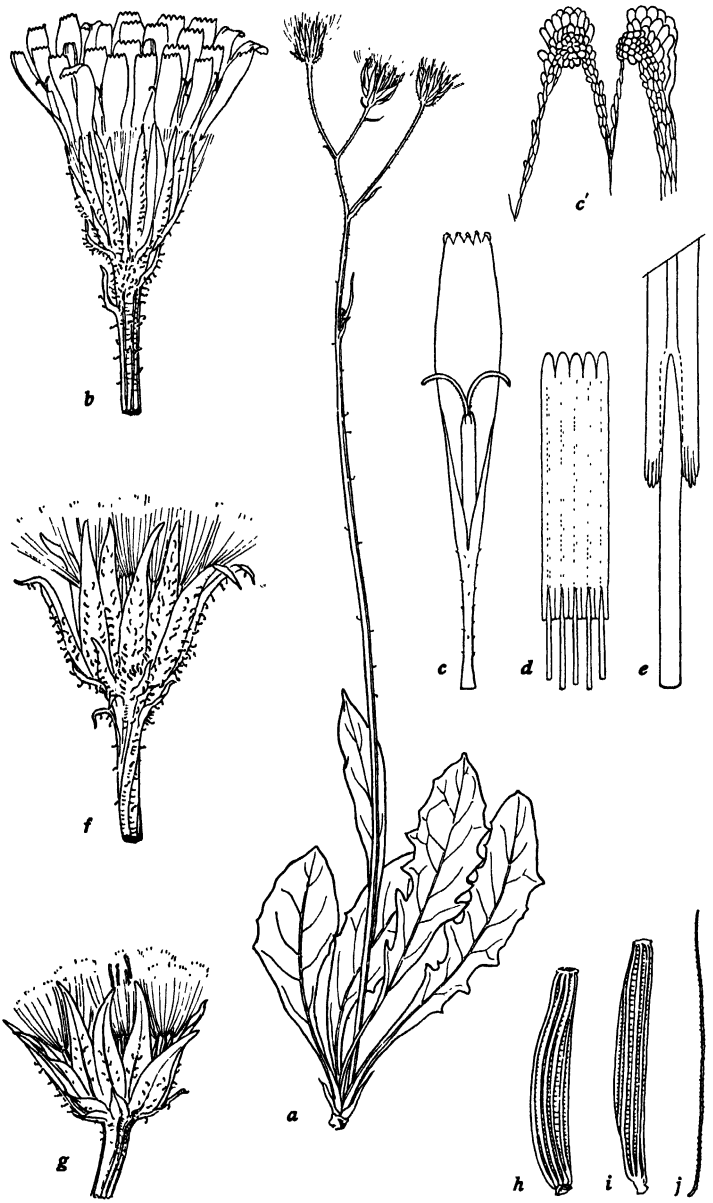


FIG. 7. *Crepis runcinata* subsp. *typica*. *a*, from *Rydberg 840*, plant, × ½. *b–e*, from *Moodie* in 1913: *b*, flower-head, × 2; *c*, corolla, × 4; *c'*, detail of ligule-teeth, × 50; *d*, anther-tube, × 16; *e*, detail of appendages, × 32. *f*, from *Moodie 921*, fruiting head, ×2. *g–j*, from *Rydberg 217*; fruiting head, ×2; *h–j*, achenes and pappus-bristle. × 8.

though a collection from the type locality made by the author of this "species" (*Nelson* no. 8693) is indistinguishable from typical *C. runcinata* in both the size of its heads and the character of its leaves. *C. denticulata* represents forms transitional toward subsp. *hispidulosa*, while the other five "species" listed in the synonymy given above are said to differ from typical *C. runcinata* in such characteristics as the pubescence of the leaves, the length of the petioles, and the dentation of the leaf margins. All of these are most fickle characters, in which extreme variants occur sporadically throughout the range of the species. As an example of the unreliability of Rydberg's descriptions in this genus may be cited *C. tomentulosa*. In both the original description and the key in the "Rocky Mountain Flora" this "species" is distinguished from *C. runcinata* by the lack of glandulosity on its involucres. However, on all specimens seen of the type collection, as well as of several other collections from the type locality, glandular hairs are more or less abundant on the involucre, and the plants are otherwise indistinguishable from typical *C. runcinata*. The following are typical: WITHOUT DEFINITE LOCALITY: plains of the Platte, *Nuttall* in 1834 (type, PA). MANITOBA: Oak River at Lothair, *Macoun & Herriot* 42863 (NY, Mo, Po, FM). MINNESOTA: Moorehead, Clay County, *Ballard 2824* (Minn); Montevideo, Chippewa County, *Moyer* in 1896 and in 1897 (US, Minn); Idlewild, Lincoln County, *Wickersheim* in 1891 (Minn); Rock County, *Huntington* in 1890 (Minn). SASKATCHEWAN: without locality, *Bourgeau* in 1858 (G, NY); Yorkton, *Herriot 42864* (G, NY, FM). NORTH DAKOTA: without definite locality, *Nicollet Exped.* in 1839 (NY); Grand Forks, Grand Forks County, *Brannon* in 1896 (Mo); Valley City, Barnes County, *Stevens* in 1934 (UC); Leeds, Benson County, *Lunell* in 1899 (US, G, DS); Butte, Benson County, *Lunell* in 1912 (type of *C. dakotana*, US, Minn). SOUTH DAKOTA: Brookings, Brookings County, *Thornber* in 1894 (UC, Mo); Elder Creek, Lawrence County, *Over 16305* (US); Rochford, Pennington County, *Rydberg* in 1892 (US, G, NY). NEBRASKA: Callaway, Custer County, *Bates* in 1899 (G); Minden, Kearney County, *Hapeman* in 1932 (UC); Sheridan County, *Clements 152* (Mo); Platte Bottom, Cheyenne County, *Rydberg 217* (US, NY). ALBERTA: near Banff, *Macoun* in 1891 (NY, Mo); Bow River near Calgary, *Moodie* in 1913 (US); Medicine Hat, *Macoun* in 1894 (Minn). MONTANA: Deer Lodge, Powell County, *Scheuber* in 1901 part, (US, NY); near Lake McDermott, Glacier National Park, *Standley 16892* (US); Little Belt Mtns., Cascade or Meagher County, alt. 2200 m, *Flodman* in 1896 (type of *C. runcinata alpicola*, NY, US); Bracket Creek, Gallatin County, *Jones* in 1902 (UC); Monida, Beaverhead County, *Jones* in 1908 (Po). WYOMING: Boyd, Weston County, *Nelson 9437* (UC); Centennial, Albany County, *Nelson 8693* (UC, US, Po); Encampment, Carbon County, *Tweedy 4081* (type of *C. perplexans*, NY); Bill's Flat, Bighorn County, *Goodding 522* (UC, US, G, Mo, Clo); north fork Powder River, Johnson County, alt. 2730 m, *Williams 3129* (WSC); Pacific Creek, Teton Forest Reserve, Lincoln County, alt. 2420 m, *Tweedy 603* (type of *C. glaucella*, NY); near Mammoth Hot Springs, Yellowstone National Park,

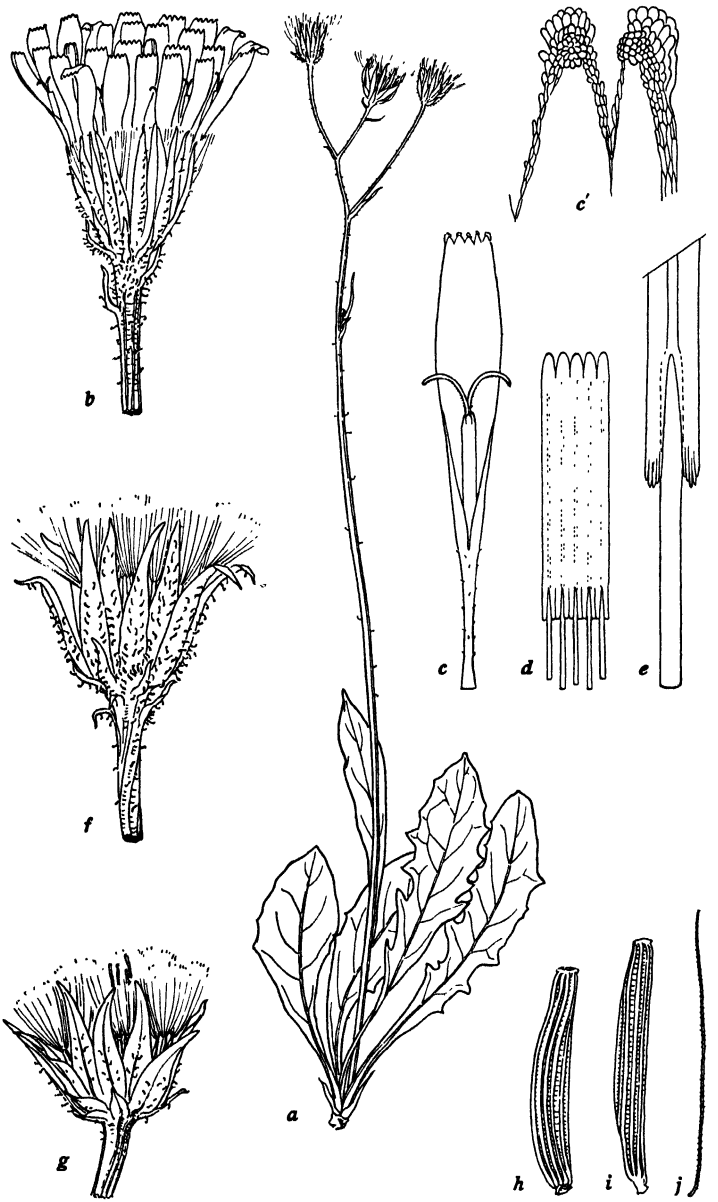


FIG. 7. *Crepis runcinata* subsp. *typica*. *a*, from *Rydberg 840*, plant, × ½. *b–e*, from *Moodie* in 1913: *b*, flower-head, × 2; *c*, corolla, × 4; *c'*, detail of ligule-teeth, × 50; *d*, anther-tube, × 16; *e*, detail of appendages, × 32. *f*, from *Moodie 921*, fruiting head, ×2. *g–j*, from *Rydberg 217*; fruiting head, ×2; *h–j*, achenes and pappus-bristle. × 8.

though a collection from the type locality made by the author of this "species" (*Nelson* no. 8693) is indistinguishable from typical *C. runcinata* in both the size of its heads and the character of its leaves. *C. denticulata* represents forms transitional toward subsp. *hispidulosa*, while the other five "species" listed in the synonymy given above are said to differ from typical *C. runcinata* in such characteristics as the pubescence of the leaves, the length of the petioles, and the dentation of the leaf margins. All of these are most fickle characters, in which extreme variants occur sporadically throughout the range of the species. As an example of the unreliability of Rydberg's descriptions in this genus may be cited *C. tomentulosa*. In both the original description and the key in the "Rocky Mountain Flora" this "species" is distinguished from *C. runcinata* by the lack of glandulosity on its involucres. However, on all specimens seen of the type collection, as well as of several other collections from the type locality, glandular hairs are more or less abundant on the involucre, and the plants are otherwise indistinguishable from typical *C. runcinata*. The following are typical: WITHOUT DEFINITE LOCALITY: plains of the Platte, *Nuttall* in 1834 (type, PA). MANITOBA: Oak River at Lothair, *Macoun & Herriot* 42863 (NY, Mo, Po, FM). MINNESOTA: Moorehead, Clay County, *Ballard 2824* (Minn); Montevideo, Chippewa County, *Moyer* in 1896 and in 1897 (US, Minn); Idlewild, Lincoln County, *Wickersheim* in 1891 (Minn); Rock County, *Huntington* in 1890 (Minn). SASKATCHEWAN: without locality, *Bourgeau* in 1858 (G, NY); Yorkton, *Herriot 42864* (G, NY, FM). NORTH DAKOTA: without definite locality, *Nicollet Exped.* in 1839 (NY); Grand Forks, Grand Forks County, *Brannon* in 1896 (Mo); Valley City, Barnes County, *Stevens* in 1934 (UC); Leeds, Benson County, *Lunell* in 1899 (US, G, DS); Butte, Benson County, *Lunell* in 1912 (type of *C. dakotana*, US, Minn). SOUTH DAKOTA: Brookings, Brookings County, *Thornber* in 1894 (UC, Mo); Elder Creek, Lawrence County, *Over 16305* (US); Rochford, Pennington County, *Rydberg* in 1892 (US, G, NY). NEBRASKA: Callaway, Custer County, *Bates* in 1899 (G); Minden, Kearney County, *Hapeman* in 1932 (UC); Sheridan County, *Clements 152* (Mo); Platte Bottom, Cheyenne County, *Rydberg 217* (US, NY). ALBERTA: near Banff, *Macoun* in 1891 (NY, Mo); Bow River near Calgary, *Moodie* in 1913 (US); Medicine Hat, *Macoun* in 1894 (Minn). MONTANA: Deer Lodge, Powell County, *Scheuber* in 1901 part, (US, NY); near Lake McDermott, Glacier National Park, *Standley 16892* (US); Little Belt Mtns., Cascade or Meagher County, alt. 2200 m, *Flodman* in 1896 (type of *C. runcinata alpicola*, NY, US); Bracket Creek, Gallatin County, *Jones* in 1902 (UC); Monida, Beaverhead County, *Jones* in 1908 (Po). WYOMING: Boyd, Weston County, *Nelson 9437* (UC); Centennial, Albany County, *Nelson 8693* (UC, US, Po); Encampment, Carbon County, *Tweedy 4081* (type of *C. perplexans*, NY); Bill's Flat, Bighorn County, *Goodding 522* (UC, US, G, Mo, Clo); north fork Powder River, Johnson County, alt. 2730 m, *Williams 3129* (WSC); Pacific Creek, Teton Forest Reserve, Lincoln County, alt. 2420 m, *Tweedy 603* (type of *C. glaucella*, NY); near Mammoth Hot Springs, Yellowstone National Park,

alt. 1800–2100 m, *Burglehaus* in 1894 (Minn); Pinedale, Sublette County, *Payson 2914* (NY, Mo, Po). COLORADO: Fort Collins, Larimer County, distributed by N. Y. Bot. Gard., *3327* (US, RM); Long's Peak, Larimer County, alt. 3330 m, *Cooper 218* (RM); Sterling, Logan County, *Osterhout* in 1897 (G, NY); Lakewood, Boulder County, alt. 2720 m, *Hanson C45* (Mo); Tolland, Gilpin County, alt. 2700 m, *Clokey 3973* (DS, G, US, NY, CA, Clo, Pa, RM, FM); Georgetown, Clear Creek County, alt. 2570 m, *Patterson 86*, part (UC, US, Minn); divide between Colorado Springs and Denver, El Paso County, *Jones 159* (Po); Ruxton Dell, near Pike's Peak, alt. 2950 m, *Clements 342* (type collection of *C. tomentulosa*, DS, G, US, NY, RM, Mo); North Park, Jackson County, *Shear & Bessey 4004* (type of *C. denticulata*, NY); without definite locality, Fremont County, *Brandegee 754* (UC); Twin Lakes, Lake County, alt. 2650 m, *Clokey 3429*, part (DS, Po); Pagosa Springs, Archuleta County, alt. 2150 m, *Baker 737* (US, G, NY, Po). NEW MEXICO: Ute Park, Colfax County, alt. 2200 m, *Standley 13326* (US); Costilla Valley, Taos County, alt. 3000 m, *Wooton* in 1913 (US); vicinity of Chama, Rio Arriba County, alt. 2380–2850 m, *Standley 6636* (US); Datil Forest, Catron County, *Forest Service 23916* (US); Tularosa Creek, Otero County, *Wooton* in 1906 (type of *C. neomexicana*, US). UTAH: Juab, Juab County, *Goodding 1087* (UC, US, G, NY, Mo); Salt Lake City, alt. 1300 m, *Jones 1758*, part (Po).

9*b* (2). **Crepis runcinata** subsp. **hispidulosa** (Howell), comb. nov. (Fig. 8.)—Leaves broader and more rounded at the apex than in the typical form, 6–25 cm long, 2.5–8 cm broad, mostly 2–3.5 times longer than broad; stems glabrous or occasionally glandular-hispid; inflorescence an ample cyme of 10–30 heads; involucres strongly or minutely glandular-hispid, averaging slightly smaller than in subsp. *typica*, 8–12 mm high; achenes 3.5–5 mm long. (*C. platyphylla* Greene, Pittonia 3:27, 1896; *C. runcinata* var. *hispidulosa* Howell, Mem. N. Y. Bot. Gard. 1:461, 1900; *C. petiolata* Rydb., Bull. Torr. Bot. Club 32:134, 1905, part; *C. aculeolata* Greene and *C. pallens* Greene, Leaflets Bot. Obs. 2:86, 1910; *C. obtusissima* Greene, op. cit., 87.)

In the northwestern portion of the range of *C. runcinata*, east to western Montana, eastern Idaho, and northwestern Colorado, where it intergrades with subsp. *typica*, south to southern Oregon and northern Utah, where it intergrades with subsp. *glauca*.

The following are typical: MONTANA: Central Park, *Brandegee* in 1898 (UC); Helena, *Kelsey* in 1890 (Minn); Ronan, alt. 900 m, *Jones* in 1909 (Po); Deer Lodge Valley, alt. 1500 m, *Jones* in 1905 (Po). COLORADO: Steamboat Springs, Routt County, *Goodding 1657* (US, UC, DS, G, Mo, NY, PA, RM). IDAHO: Emmett, Canyon County, alt. 900 m, *Macbride 884* (as *C. riparia, fide* Nelson, DS, Minn). UTAH: Rabbit Valley, alt. 2000 m, *Ward 606* (US; another sheet of this collection, US 47205, without locality, is the type of *C. aculeolata*); Heber Valley, alt. 1800 m, *Watson 712* (US; other sheets of this same collection number from Jordan Valley, NY, Ya); Springville, *Jones* in 1897 (Po); Kimball's, Parley's Park, *Clemens* in 1909 (Po, Clo); Salt Lake City, *Jones*

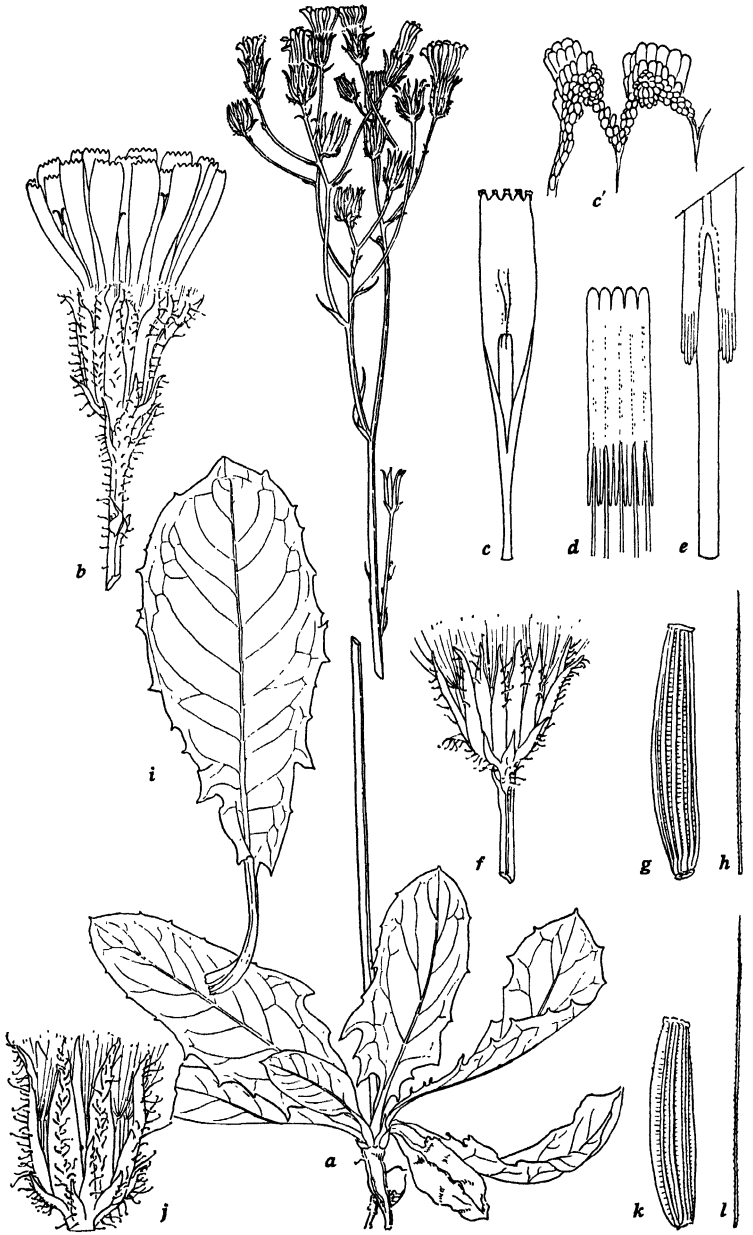


FIG. 8. *Crepis runcinata* subsp. *hispidulosa*. *a–h*, from *Cusick 1713*: *a*, plant, × ½; *b*, flower-head, × 2; *c*, corolla, × 4; *c'*, detail of ligule-teeth, × 50; *d*, anther-tube, × 8; *e*, detail of appendages, × 32; *f*, fruiting head, × 2; *g*, *h*, achene and pappus-bristle, × 8. *i–k*, from *Goodding 1657*: *i*, leaf, × ½; *j*, fruiting head, × ½; *k*, *l*, achene and pappus-bristle, × 8.

758, part (Po). WASHINGTON: without locality, *Vasey 564* (US); Walla Walla region, *Brandegee* in 1883 (UC); Toppenish, Yakima County, alt. 235 m. *Keck & Clausen 3502* (UC, WSC); Sprague, Lincoln County, alt. 550 m, *Sandberg & Leiberg 208* (UC, Pa); Coulee City, Grant or Douglas County, *B. & C. 53–55* (UC); Loomis, Okanogan County, *Jones* in 1911 (Po). OREGON: Stein's Mtns., Harney County, *Howell* in 1885 (type, US, DS, G, NY, PA, Or); eastern part without locality, *Cusick 1713* (UC, DS, Mo, Minn); Summer Lake, Lake County, alt. 1280 m, *Keck & Clausen 3698* (UC); Baker, Baker County, *Peck 10796* (Will); Hot Lake, Union County, *Peck 4975* (Will).

Transitional toward *typica*.–At various places within the range of this subspecies plants occur which have fewer and somewhat larger heads and leaves which are generally intermediate between the two subspecies. Outstanding among these is the collection cited below from Idaho. These robust plants have long lanceolate leaves and only 5 or 6 large heads. The pollen is irregular and large (35–44μ) and 5-pored grains occur. It seems probable that these are triploid forms of *typica*. MONTANA: Midvale, Glacier County, *Umbach 295* (US, FM); Monida, Beaverhead County, *Jones* in 1922 (Po); Deer Lodge, Powell County, *Scheuber* in 1901 part, (US, Minn); Kennedy Creek, *Weller* in 1901 (US); Bigfork, Lake or Flathead County, *Jones* in 1908 (Po, DS). WYOMING: Fort Bridger, Uinta County, *Porter* in 1873 (US); Evanston, Uinta County, *Williams* in 1897 (US). IDAHO: Santianne Creek, Coeur d'Alene Mtns., alt. 950 m, *Leiberg 1039*, part (UC, DS, Po, RM, G). UTAH: Fish Lake, Sevier County, alt. 2727 m, *Jones 5743, 5790* (US, Po). WASHINGTON: Endicott, Whitman County, *Elmer 1031* (Minn). OREGON: Otis Creek, alt. 1100 m, *Leiberg 2323* (UC, Po).

9*c* (3). **Crepis runcinata** subsp. **glauca** (Nutt.) comb. nov. (Fig. 9.)—Leaves glaucous, variable in size and lobing, mostly oblanceolate in shape, and in general like those of subsp. *typica*, but with the petioles more strongly wing-margined; stems as in subsp. *typica*; heads 3–15 in an inflorescence; involucres 7–12 mm high, averaging somewhat smaller than in subsp. *typica*; both the inner and outer bracts completely glabrous; outer bracts deltoid, less than 1/4 the length of the inner, often pale or whitish, achenes somewhat smaller than in subsp. *typica*, 3.5–5.5 mm long. (*Crepidium glaucum* Nutt., Trans. Am. Phil. Soc. n. s. 7:436, 1841; *C. caulescens* Nutt., ibid.; *Crepis glauca* Torr. et Gray, Fl. N. Am. 2:488, 1843; *Hieraciodes caulescens* O. Ktze., Rev. Gen. 345, 1891; *C. chamæphylla* Wooton et Standley, Contr. U.S. Nat. Herb. 16:175, 1913.)

Saskatchewan to Idaho, south to New Mexico and Arizona. Found sparingly in the northeastern part of the range of *C. runcinata*, becoming common in Utah and Nevada. Grows in more alkaline situations than subspp. *typica* and *hispidulosa*.

The following are typical: WITHOUT DEFINITE LOCALITY: plains of the Platte, *Nuttall* in 1834 (type of *Crepidium glaucum* in herb. British Museum, London; photo and fragments in UC). SASKATCHEWAN: Little Manitou Lake, *Macoun & Herriot 42866* (NY, Po, FM); near Saska-

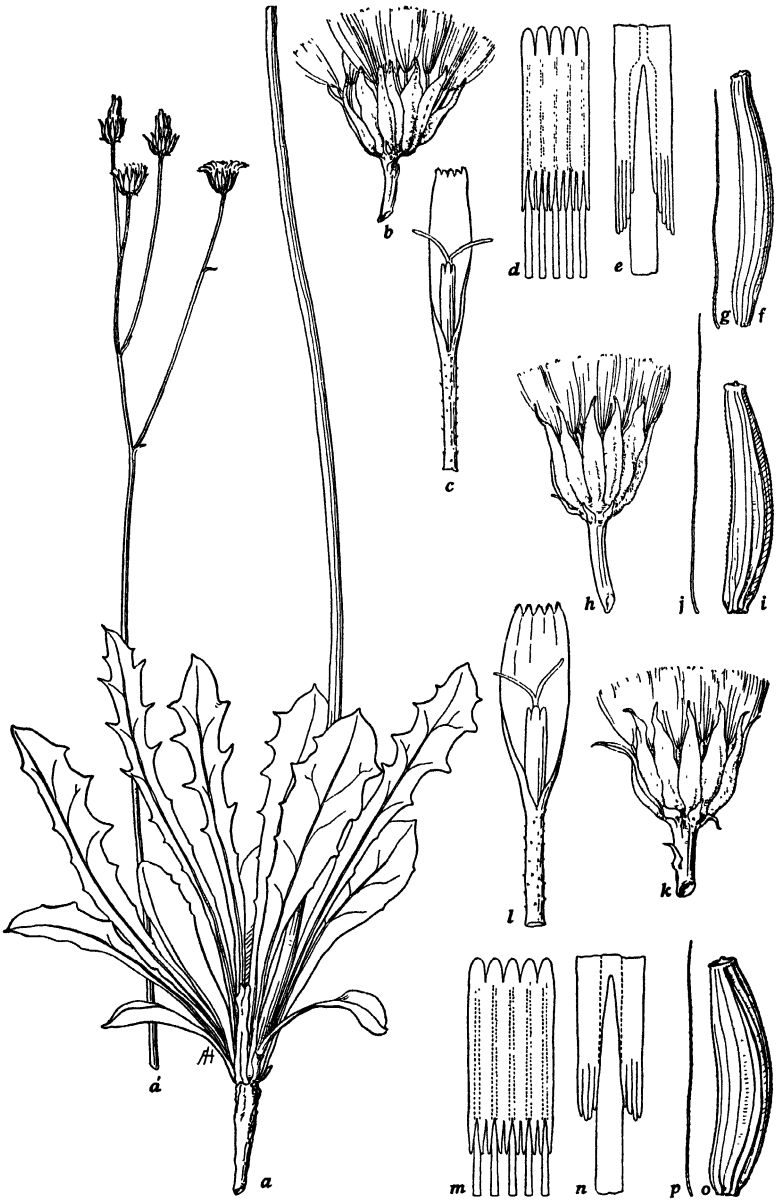


FIG. 9. *Crepis runcinata* subsp. *glauca*. *a–g*, from *Greene* in 1896: *a*, plant, × ½; *b*, head, × 2; *c*, corolla, × 4; *d*, anther-tube, × 8; *e*, detail of appendages, × 32; *f*, *g*, achene and pappus-bristle, × 8. *h–j*, from *Garrett 1497*: *h*, head, × 2; *i*, *j*, achene and pappus-bristle, × 8. *k–n*, from *UC Gen 27.2079* (grown from roots collected at type locality of *C. chamæphylla* Woot. et Stand.): *k*, head, × 2; *l*, corolla, × 4; *m*, anther-tube, × 8; *n*, detail of appendages, × 32; *o*, *p*, achene and pappus-bristle, × 8.

toon, *Fraser* in 1925 (UC). SOUTH DAKOTA: Cave Hills, Harding County, *Visher 402* (G, RM). MONTANA: Westby, Sheridan County, *Larsen 108* (Mo); Deer Lodge, Powell County, *Jones* in 1905 (US, Po). WYOMING: northwestern Wyoming, *Rose 458* (US); near Flockert's Ranch, *Merrill & Wilcox 721* (G, NY); Buffalo, Johnson County, *Nelson 2513* (Minn); Meadow Creek, *Nelson 787* (US). COLORADO: near Delta, Delta County, *Osterhout 6580* (Po); Fort Collins, *Osterhout* in 1896 (Minn). IDAHO: Thousand Springs Valley, alt. 2030 m, *Henderson 3668, 3669* (US). UTAH: Rabbit Valley, alt. 2020 m, *Ward 533* (US, G); Becks Hot Springs, Salt Lake County, alt. 1360 m, *Garrett 1497* (US, G, DS, PA); Juab, Juab County, *Goodding 1089* (US, Po); Gunnison, San Pete County, alt. 1670 m, *Jones* in 1910 (Po); near Emery, Emery County, *Jones* in 1894 (Po); Monroe, Sevier County, *Jones* in 1894 (US); Milford, Beaver County, *Jones* in 1880 (Po); above Marysvale, Piute County, *Rydberg & Carlton 6923* (US, G, NY, RM, Nev); near Teasdale, Wayne County, alt. 1700 m, *Jones* in 1894 (Po); Moab, Grand County, *Jones* in 1913 (Po). NEVADA: north of Wells, Elko County, *Jones* in 1901 (Po); Ruby Valley, Elko County, *Heller 9474* (US, NY, Mo, PA); near Ely, White Pine County, *Hitchcock 1349* (US); Panaca, Lincoln County, *Jones* in 1912 (Po); near Currant, Nye County, *Bentley* in 1916 (DS, Po). ARIZONA; Holbrook, Navajo County, *Zuck* in 1896 (US); north end Carrizo Mtns., *Standley 7419* (type of *C. chamæphylla*, US).

Subsp, *glauca*, although strikingly different in its most typical form from typical *runcinata*, yet passes into subsp. *typica* through such a gradual series of intermediate forms that it cannot be considered specifically distinct. Forms of subsp. *typica* occur with only a trace of glandulosity at the base of the involucres, and with the leaves more or less glaucous, while others agree with subsp. *glauca* in their glabrous involucres, but have relatively long, narrow outer bracts as in subsp. *typica*, and less glaucous leaves. Subsp. *glauca* occurs, though rarely, throughout most of the range of subsp. *typica*, but prefers alkaline situations, and is most characteristic of the southern Great Basin area, i.e., central Utah and eastern Nevada, where it is the only subspecies of *C. runcinata* found.

Transitional from subsp. *typica* to subsp. *glauca* (cf. *Crepis lancifolia* Greene, Pittonia 3:108, 1896).—IDAHO: Clyde, Blaine County, *Macbride & Payson 3173* (US, G, NY, RM, Mo, DS, CA); Henry Lake, Fremont County, *Payson 2007* (NY, CA, Mo). WYOMING: Elk Park, Yellowstone National Park, *Nelson 6147* (US, G, NY, DS, Po, Mo, Minn); between Norris Junction and Cascades, Yellowstone National Park, *B. 118* (UC). COLORADO: Weston's Pass, *Coulter* in 1873 (US); San Luis Valley, *Wolf 664* (US); Twin Lakes, Lake County, *Clokey 3429*, part (DS, NY, RM, Po, Clo, CA); Doyle's, Gunnison County, *Baker 644* (UC, US, G, NY, Po, Mo, Minn); Marshall Pass, *Greene* in 1896 (type of *C. lancifolia*, ND).

9*d* (4). **Crepis runcinata** subsp. **Barberi** (Greenm.) comb. nov. (Fig. 10.)—Stems 3.5–6.5 dm high; basal leaves glabrous and more or less glaucous, narrowly oblanceolate, 10–20 cm long, 0.5–2cm broad, retrorsely

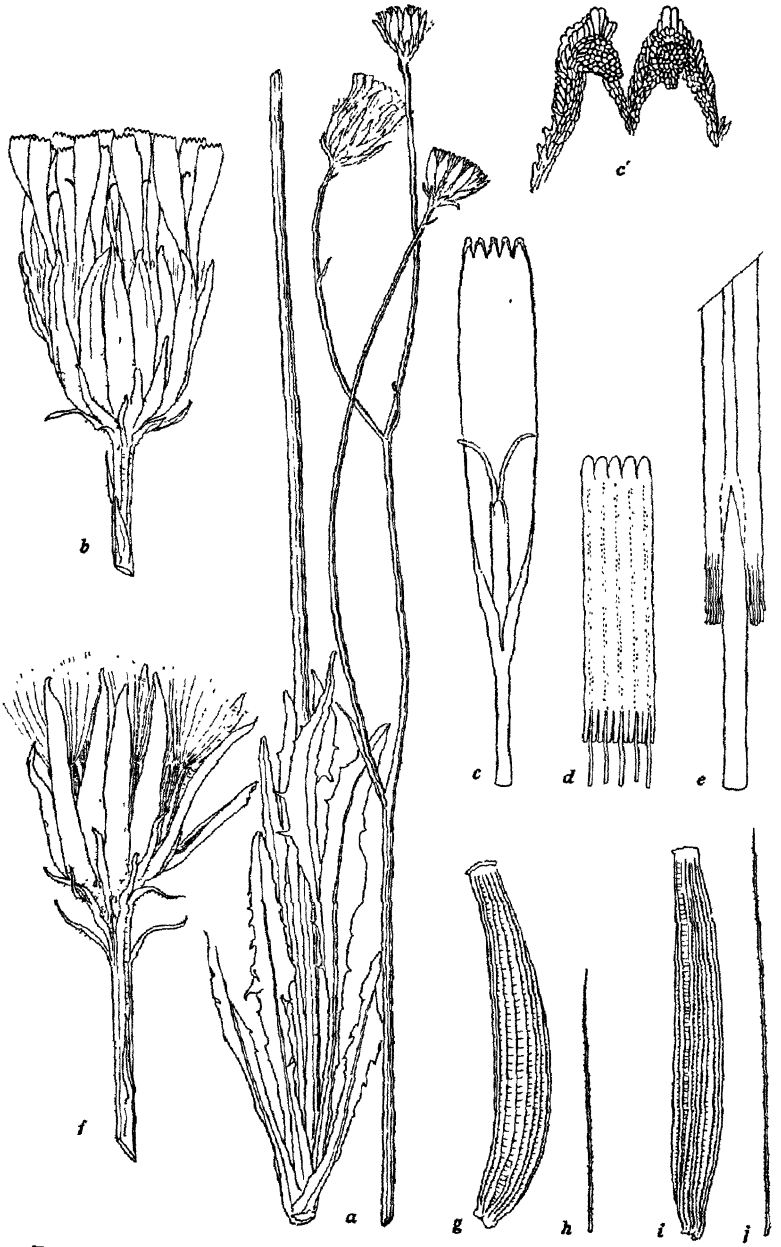


FIG. 10. *Crepis runcinata* subsp. *Barberi*. *a–e*, from type collection of *C. Barberi*: *a*, plant, × ½; *b*, flower-head, × 2; *c*, corolla, ×4; *c'*, detail of ligule-teeth, × 50; *d*, anther-tube, × 16; *e*, detail of appendages, × 32. *f–i*, from *Jones* in 1903; *f*, fruiting head, × 2; *g–i*, achenes and pappus-bristle, × 8.

dentate or pinnatifid with lanceolate lobes; heads 3–7 in an inflorescence; involucres 11–17 mm high, completely glabrous; inner bracts conspicuously scarious-margined; outer bracts narrowly lanceolate, the longest about ½ the length of the inner; achenes 5.5–7 mm long, dark brown in color; pappus 7–8 mm. (*Crepis Barberi* Greenm., Proc. Am. Acad. 40:52, 1904; *C. mogollonica* Greene, Contr. U. S. Nat. Herb. 16:176, 1913.)

In the Mogollon Mtns., western New Mexico, and the Sierra Madre, province of Chihuahua, Mexico. The following have been seen: MEXICO: near Colonia Garcia, Sierra Madre Mtns., alt. 2285 m, *Townsend & Barber 206* (type of *C. Barberi*, G, US, Mo, Po); Sierra Madre, *Nelson 6107* (G, US); Mound Valley, Sierra Madre Mtns., alt. 2120 m, *Jones* in 1903 (Po). NEW MEXICO: west fork of Gila River, Mogollon Mtns., Catron ("Socorro") County, alt. 2420 m, *Metcalfe 576* (type of *C. mogollonica*, US, Minn).

This subspecies, though extreme in the narrow shape of its leaves, does not possess any other characteristics which set it off sharply from the others. The involucres are glabrous as in subsp. *glauca*, but the outer bracts are elongate, as in forms of subsp. *typica*. In these respects the involucre resembles that of specimens from Colorado listed as intermediate between subspp. *typica* and *glauca*. The involucres and achenes of the Mexican specimens are unusually large for *C. runcinata*, although they are equaled by those of some forms from Colorado, but the collection from New Mexico is intermediate in this respect.

Transitional from subsp. *glauca* to subsp. *Barberi*.—ARIZONA: White Mtns., *Griffiths 5354* (US). This specimen has the narrow leaves of subsp. *Barberi*, but the size of the involucres and the shape of the bracts is as in subsp. *glauca*.

9*e* (5). **Crepis runcinata** subsp. **imbricata** subsp. nov. (Fig. 11.)—Folia 5–11 cm longa, oblanceolata vel elliptica, valde dentata, dentibus albido-mucronatis; capitula 10–12 mm alta; phylla imbricata, obtusa vel acuta, minute glandulosa; achenia 4.5–5 mm longa, ad apicem contracta vel attenuata nec rostrata.

Leaves 5–11 cm long, 1.5–3 cm broad, oblanceolate or elliptic; strongly and closely dentate, the teeth tipped with conspicuous white corneous mucros; stems 1.5–3 dm high; heads 3–7 in an inflorescence; involucres 10–12 mm high, inner bracts broad, mostly obtuse; outer bracts similar, elliptic, 2–3 mm broad, the longest about 2/3 the length of the inner; achenes 4.5–5 mm long, reddish brown, somewhat tapering at the apex but not at all rostrate; pappus 5–7 mm long.

Southern Oregon to northern and western Nevada, in alkaline meadows. The following have been seen: OREGON: Alvord Valley, Harney County, *Cusick 2014* (type UC no. 31293, G, Minn; all identified as *C. Andersonii* Gray); near Alvord Lake, alt. 1300 m, *Leiberg 2529* (UC, G); near Alberson, Harney County, *Peck 14019* (Will); north of Adel, Lake County, *Peck 19487* (UC, Will). NEVADA: Steamboat Springs, Washoe County, *Eastwood 14853* (CA); Lemmon Valley, Washoe County, *Kennedy 2061*, part (UC); east of Elko, Elko County, *Eastwood & Howell 276* (CA).

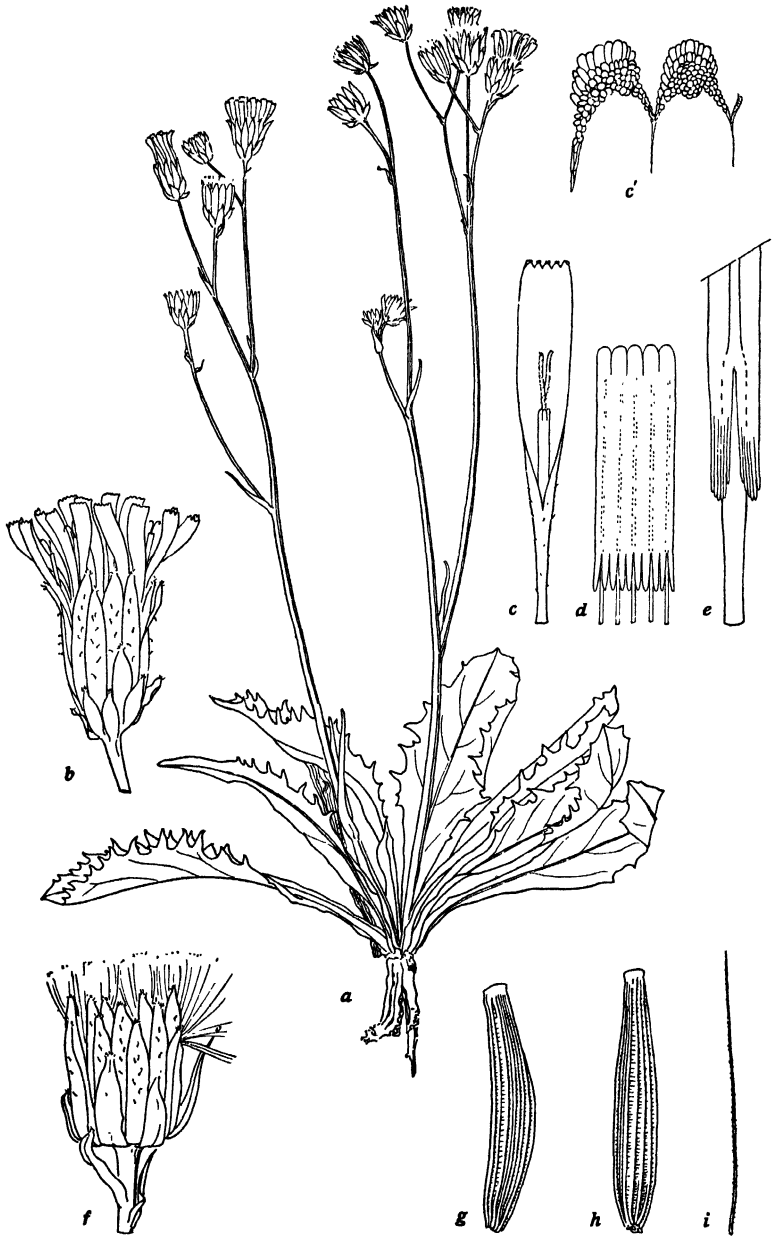


FIG. 11. *Crepis runcinata* subsp. *imbricata*. *a–e*, from the type, *Cusick 2014*: *a*, plant, × ½; *b*, flower-head; × 2; *c*, corolla, × 4; *c'*, detail of ligule-teeth, × 50; *d*, anther-tube, × 8; *e*, detail of appendages, × 32. *f–i*, from *Eastwood 14853*: *f*, fruiting head, × 2; *g–i*, achenes and pappus-bristle, × 8.

This subspecies resembles subsp. *Andersonii* in its leaves and in the broad, strongly imbricated bracts of its involucre, but the heads are the same size as those of subsp. *typica*, while the achenes are not at all beaked.

9*f* (6). **Crepis runcinata** subsp. **Andersonii** (Gray) comb. nov. (Fig. 12.)—Leaves as in subsp. *imbricata*, but often larger, up to 2 cm long and 5 cm broad; stems mostly robust, 2.5–5 dm high; inflorescence generally with 6–20 heads; involucres 13–21 mm high, glandular-pubescent; inner bracts more or less strongly attenuate at the apex; outer bracts similar, 2–3 mm broad, the longest about 2/3 the length of the inner; achenes 6–8 mm long, pale yellow to reddish brown, more or less strongly rostrate at the apex; pappus 6–9 mm. (*Crepis Andersonii* Gray, Proc. Am. Acad. 6:553, 1865.)

Western Nevada and adjacent California, in damp, alkaline meadows. The following have been seen: NEVADA: near Carson City, Ormsby County, *Anderson* in 1865 (type G, US); about Carson City, alt. 1446 m, *Baker 1062* (UC, G); Reno, Washoe County, *Brandegee* in 1883 (UC); Washoe Lake, *Bryant* (UC); Soda Springs, Esmeralda County, *Shockley 266* (UC, G, DS). CALIFORNIA: Sierra County, *Lemmon* in 1874 (G); Loyalton, Sierra County, *Eastwood 7792* (CA); Purdy, Sierra County, *Heller & Kennedy 8666* (UC, G, DS, Nev). The specimens from Sierra Valley differ strikingly from typical *C. Andersonii* in their deeply pinnatifid leaves, which, along with the stems, are strongly hispidulose.

Subsp. *Andersonii* is by far the most marked variant of *C. runcinata*, but the specimens now available indicate that it intergrades with the other subspecies at the limits of its range. Although the beaked achenes have been generally used to keep it distinct from all its relatives, there is every transition from truly beaked achenes to those merely attenuate at the apex, even in plants otherwise typical of subsp. *Andersonii*, while well-developed beaks occur on some plants cited below which have involucres typical of *C. runcinata*. The large involucres and attenuate bracts are also in their most typical form strikingly different from those of *C. runcinata*, but the specimens from Purdy and from Washoe County show all degrees of transition in these characteristics. The following may be considered transitional forms (cf. *C. subcarnosa* Greene, Pittonia 3:107, 1896; *C. runcinata ciliosa* Greene, ibid. ? ex descr.): NEVADA: Lemmon Valley, Washoe County, *Kennedy 2061*, part (UC), involucres transitional from subsp. *Andersonii* to subsp. *imbricata*; Humboldt Wells, *Greene* in 1893 (type of *C. subcarnosa* Greene, UC), leaves and achenes as in subsp. *Andersonii*, involucres more as in subsp. *typica*, whole plant densely hispidulose.

9*g* (7). **Crepis runcinata** subsp. **Hallii** subsp. nov. (Fig. 13)—Folia glauca, 6.5–27 cm longa, 1.5–3 cm lata, oblanceolata vel anguste obovata, in petiolum latum alatum angustata, dentata vel subpinnatifida; capitula 4–14 pro inflorescentia; involucra 9–13 mm longa, minute glandulosa; phylla exteriora brevia, anguste deltoidea; phylla interiora angusta, apice acuta nec acuminata vel attenuata; achenia 4.5–6.5 mm longa, ad apicem longe attenuata vel rostrata.

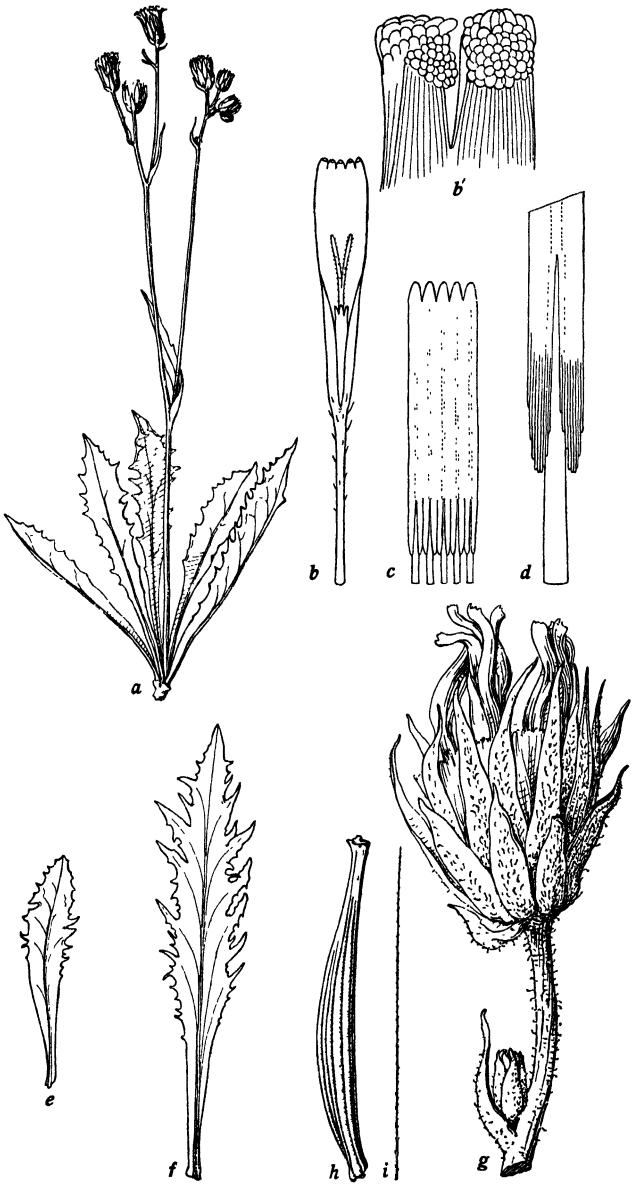


FIG. 12. *Crepis runcinata* subsp. *Andersonii*. *a–d*, from *Baker 1062*: *a*, plant, × ¼; *b*, corolla, × 4; *b'*, detail of ligule-teeth, × 50; *c*, anther-tube, × 8; *d*, detail of appendages, × 32. *e–i*, from type collection: *e*, *f*, basal leaves, × ½; *g*, flowering head, ×2; *h*, *i*, achene and pappus-bristle, × 8.

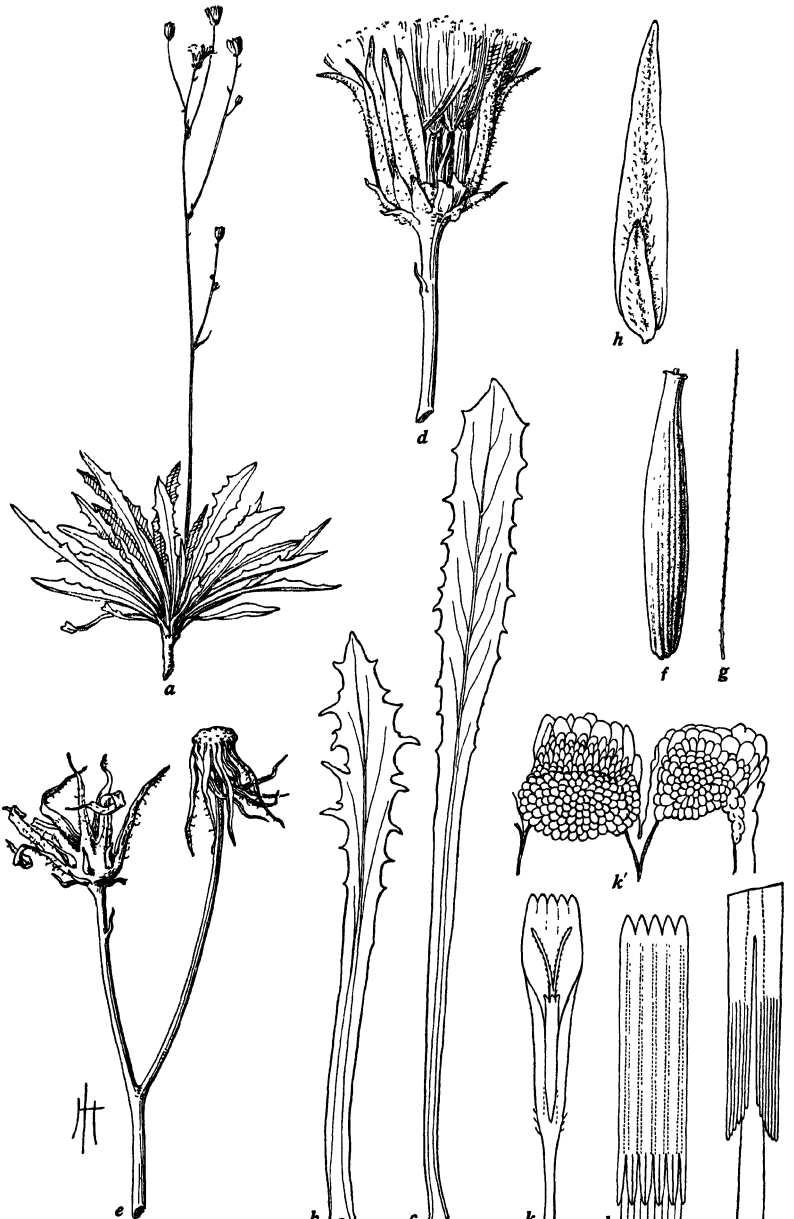


FIG. 13. *Crepis runcinata* subsp. *Hallii*. *a*, from *Hall 11824*, plant, × ¼. *b–h*, from the type *Hall 12281*: *b*, *c*, basal leaves, × ⅛; *d*, fruiting head, × 2; *e*, old heads and peduncles, × 2; *f*, *g*, achene and pappus-bristle, × 8; *h*, outer and inner involucral bract, outer face, × 4. *k–m*, from *Linsdale 624*: *k*, corolla, × 4; *k′*, detail of ligule-teeth, × 50; *l*, anther-tube, × 8; *m*, detail of appendages, × 32.

Leaves glaucous, 6.5-27 cm long, 1.5–3 cm broad, oblanceolate or narrowly obovate, gradually narrowed to a short, broadly winged petiolar base; closely and coarsely dentate or subpinnatifid, the teeth slightly whitish-tipped; stems 20–62 cm high; inflorescence of 5–14 heads on elongate ascending peduncles; involucres 9–13 mm high, minutely glandular, outer bracts narrowly deltoid, the longest about ½ the length of the inner; inner bracts 1.2–1.8 mm broad, acute but not acuminate or attenuate; achenes 4.5–6.5 mm long, chestnut brown, short-rostrate or at least strongly tapering toward the apex.

Eastern California to central Nevada. The following have been seen: CALIFORNIA: in *Distichlis* sod, Benton, Mono County, *Hall 12281* (type, UC no. 313486); Adobe Valley, north of Benton, *Hall 11824* (UC); Bishop, Inyo County, *Davidson 2570* (UC); near Bishop, *Jones* in 1927 (Po); Bridgeport, Mono County, *Blake 11837* (UC). NEVADA: between Battle Mtn. and Austin, alt. 1950 m, Lander County, *Hitchcock 698* (US); southeast of Millet, Nye County, alt. 1660 m, *Linsdale 613, 624* (UC); Trail Creek, White Mtns., Esmeralda County, alt. 2530 m,*Duran 2501* (UC).

This subspecies occurs south of the range of subsp. *Andersonii* and west of that of subsp. *glauca*. Both in morphological characteristics and in geographic distribution it is intermediate between these two subspecies. Although most specimens have the achenes definitely beaked as in subsp. *Andersonii*, the involucres are much smaller and the bracts are narrower and not attenuate. Occasional specimens, like those of Blake from Bridgeport, have the achenes hardly at all beaked, and these are very difficult to distinguish from subsp. *typica*. However, the more closely dentate, broader-based, glaucous leaves are quite distinct from most of subsp. *typica*, while the big gap in the range of the two subspecies, and the very different ecological habitats that they occupy, are further reasons for keeping them separate.

10. **Crepis pleurocarpa** Gray, Proc. Am. Acad. 17:221, 1882 (Fig. 15)

Root slenderer than in other species of this group; leaves and stem usually greenish rather than grayish, tomentulose or glabrate, sometimes glandular-pubescent; basal leaves 7–28 cm long, usually runcinate-pinnatifid with deltoid or lanceolate, acute or acuminate, entire or dentate lobes, the lobes generally separated by shallow U-shaped sinuses, the terminal segment rather short, 1–5 (–7) cm long, acute or acuminate, but rarely attenuate; stems 1.5–6 dm (mostly 2–4 dm) high, mostly divaricately branching near the base; cauline leaves few and all but the lowest much reduced in size; heads 7–40, generally 15–30 in an inflorescence, mostly on elongate peduncles; involucres 8.5–17 mm high; inner bracts generally 5, in a few forms 6–8, rather broad (2–4 mm), acute, or somewhat obtuse at the apex; deep green or blackish in drying, with conspicuous scarious margins, these densely floccose-tomentulose, the central portion glabrate; florets 5–8, in the larger heads of some forms 10–12; outer bracts broadly deltoid, small, the longest 1.5–4 mm long,

1/6–1/3 the length of the inner; corollas 15–20 mm long; achenes 5–8 mm long, deep chestnut brown, thick and 10-ribbed, slightly or sometimes more strongly contracted at the apex; pappus setæ equaling or usually exceeding the achene, 6–12 mm long. (*C. intermedia* var. *pleurocarpa* Gray, Syn. Fl. 1 (2):432, 1884; *C. acuminata* var. *pleurocarpa* Jepson, Man. Fl. Pl. Calif. 1012, 1925.)

Northern California and southwestern Oregon, south in the Coast Ranges to Lake County and in the Sierra Nevada to Eldorado County, north in Oregon to Curry and Douglas Counties, and in the Wenatchee Mtns. of central Washington (see fig. 14).

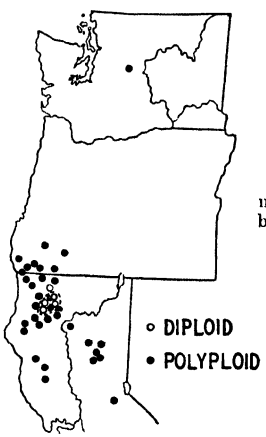


FIG. 14. Distribution of *Crepis pleurocarpa*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

Two years after Gray described this species, he reduced it to a variety of *C. intermedia*, based on the additional collections of Pringle in 1882, of which he said that (apparently in contrast with Pringle's collections of 1881) it "accords both as to leaves and achenes with *C. intermedia*." A careful examination of the specimens of both collections, kindly loaned by the Gray Herbarium, indicates that, while the achenes in those of the 1882 collection are somewhat more attenuate at the apex than in the specimens of 1881, they are in both definitely costate, and similar to those of *C. occidentalis* rather than to those of typical *C. intermedia*. Furthermore, *C. intermedia* differs from *C. pleurocarpa* in its basal leaves, which have generally narrower and more closely spaced segments, its usually taller stems with more numerous, well-developed cauline leaves, and its involucres, which have more numerous though usually narrower inner bracts, and more florets. The inner bracts of *C. pleurocarpa* are very distinct from those of *C. intermedia* in their conspicuous white-tomentose margin and glabrate central portion, those of *C. intermedia* being uniformly tomentose. *C. acuminata*, which also has few-flowered heads like those of *C. pleurocarpa*, has basal leaves and stems similar to those of *C. intermedia*, and in addition more numerous, generally smaller heads, with narrower, glabrous or only slightly tomentulose involucral bracts, and very different achenes, which are longer than the pappus.

There are remarkably few intermediates between *C. acuminata* and *C. pleurocarpa*, although both pass gradually into *C. intermedia*, and through it to *C. occidentalis*.

C. pleurocarpa, moreover, occupies an ecological habitat and a geographical range quite different from that of either *C. intermedia* and *C. acuminata*, and in the former respect differs from all the American species of *Crepis*, as described above (p. 18).

Key to the apomictic forms of C. pleurocarpa

(For a discussion of the taxonomic status of these forms, see p. 69)

A. Heads with 5 inner bracts and 5 florets (rarely 4 or 6 in a few heads of the inflorescence).
  B. Stems 2.5–4 dm high; basal leaves 9–27 cm long.
    C. Involucres 8.5–12.5 mm long; stems slender and elongate; heads on slender flexuous peduncles; cauline leaves narrowly elliptic or lanceolate, broadest near the middle..... diploid form
    C. Involucres 12–16 mm long; stems stouter and stiffer.
      D. Leaves and stems glabrate or slightly tomentulose; pappus 8.5–10 mm long.
        E. Cauline leaves lanceolate or elliptic, broadest near the middle.
          F. Larger basal leaves 10–17 cm long, the largest lobes deltoid or lanceolate, 0.7–1.8 cm long; peduncles slender and more or less flexuous; pappus 8.5–9.5 mm long..... 1. apm. *Pringlei*
          F. Larger basal leaves 17–25 cm long, the largest lobes lanceolate, 2.2–3.5 cm. long; peduncles straight and stiff; pappus 9–10 mm.
            G. Inner involucral bracts 2–2.8 mm broad, broadest near the base and tapering gradually upward.. 2. apm. *rigida*
            G. Inner involucral bracts 2.5–4 mm broad, broadest near the middle and rather abruptly narrowed to the acute apex..... 3. apm. *latibractea*
        E. Cauline leaves ovate or ovate-lanceolate, broadest near the base; basal leaves 12–17 mm long, elliptic, the lobes close together; pappus 9.5–10 mm 4. apm. *Grayi*
      D. Leaves and stems minutely glandular-hirsute; pappus 7–7.5 mm..... 6. apm. *glandulosa*
  B. Stems 1.5–3 dm high; basal leaves 7–14 cm long; involucres 10–12 mm high..... 5. apm. *humilis*
A. Larger heads of the inflorescence with 6–8 involucral bracts and 6–12 florets.
    H. Stem and leaves glandular-hirsute ..... 7. apm. *monticoloides*
    H. Stem and leaves tomentulose or glabrate.
      I. Largest heads of the inflorescence with 6–7 inner bracts and 7–10 florets.

J. Involucres 12–15 mm high, their bracts not strongly attenuate; pappus 8–9 mm long.
K. Inflorescence branching from near the base of the stem; largest heads with 10 florets ..... 8. apm *pluriflora*
K. Inflorescence branching from the middle of the stem or above; largest heads with 7 florets..... 10 apm *breviamea*
J Involucres 14–17 mm high, their bracts strongly attenuate; pappus 11–12 mm long..... 9. apm *attenuata*
I Largest heads of the inflorescence with 8 inner bracts and 12 florets ..... 11. apm *plumacensis*

Diploid form (fig. 15*a–f*).—This is characterized chiefly by its slender stems and peduncles and its relatively small involucres, along with a tall habit of growth. Apm. *humilis* has involucres as short as those of the diploid, but the plants are much smaller in that form, and the cauline leaves are much reduced.

There is some variation in pubescence within the diploid form. The specimens from near Mount Shasta and from Stewart's Springs are glandular-hirsute on the leaves and stems, while the others are glabrate. Only the following collections have been seen: CALIFORNIA: Sulloway Creek, near Mt. Shasta, Siskiyou County, *Smith 474* (G, CA, Clo); Mt. Eddy, Siskiyou County, alt. 1818 m, *Copeland 3755*, part (G); Sisson's (Mt. Shasta), Siskiyou County, *Brandegee* in 1887, part (UC); Parks Creek, below Stewart's Springs, T. 41 N., R. 5 W., Siskiyou County, alt. 1125 m, *S. & J. 2434* (UC); along Trinity River, north of Carrville, Trinity County, alt. 910–1060 m, *S. & J. 2462, 2463, 2471* (UC); Tangle Blue Creek, Scott Mtns., Trinity County, alt. 1515 m, *Howell 12804* (CA).

1. apm. *Pringlei* (fig. 15*g–i*).—Habit of the diploid form, but the involucres longer (12–14 mm long); basal leaves deeply pinnatifid; leaves of the inflorescence entire or remotely toothed, lanceolate, elongate; achenes 6.5 mm long, pappus 8.5–9.5 mm; ($2n = 33$?). CALIFORNIA: headwaters of the Sacramento River, alt. 1520–2420 m, *Pringle* in 1882, part (G, WSC, RM); Dorleska, Trinity County, alt. 2000 m, *Hall 8597*, part (UC, DS, G, RM); Shackleford Creek, Siskiyou County, alt. 1360 m, *Butler 1758* (UC, DS, RM); south fork Salmon River, near Big Flat, Siskiyou County, *Howell 13192* (CA). OREGON: Red Blanket Creek, southwest corner of Crater Lake National Park, Klamath County, alt. 1200 m, *Applegate 11305* (DS).

Related to apm. *Pringlei*.—CALIFORNIA: Camp Sacramento, Eldorado County, alt. 1900–2400 m, *Vortriede* in 1931 (CA).

2. apm. *rigida* (*pleurocarpa-occidentalis?*).—Similar to the preceding, but the leaves larger, more glabrate, and the lobes more remote; stems stout, striate; involucres and achenes similar to apm. *Pringlei*; pappus 9–10 mm long; (2*n*–55?). CALIFORNIA: upper Sacramento River, Shasta County, alt. 450 m, *Hall & Babcock 4024* (UC, DS, US, RM, Po); Weaverville, Trinity County, *Kildale 10815* (DS); north side of Scott Mtn., alt. 1210 m, *S. & J. 2446* (UC).

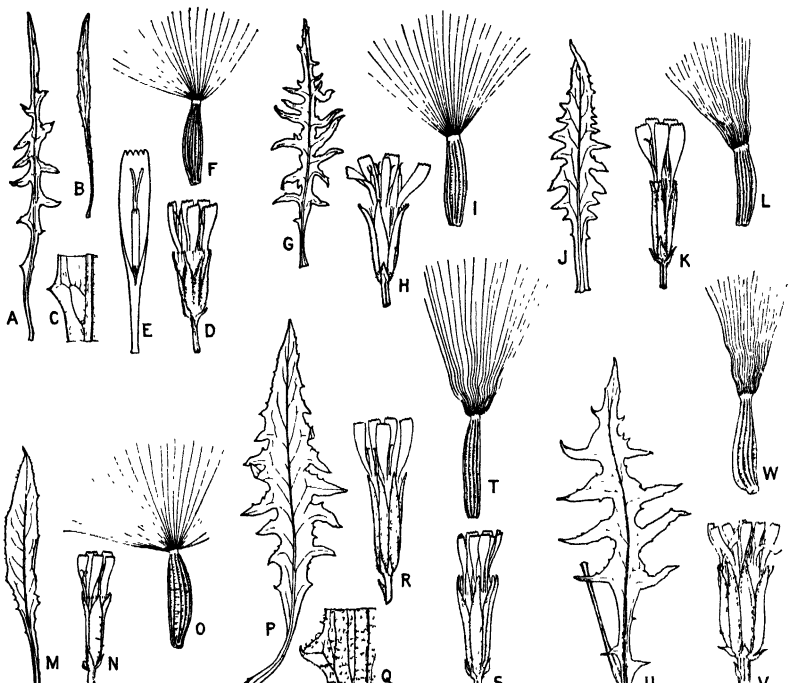


FIG. 15. *Crepis pleurocarpa*. *a–f*, diploid form—*a*, *b*, *d*, *e*, from *S. & J. 2463*; *c*, *f*, from *S. & J. 2471*: *a*, *b*, leaves, × ¼; *c*, detail of surface, × 1; *d*, involucre, × 1, *e*, corolla, × 2; *f*, achene, × 2 *g–i*, apm. *Pringlei*, from *Pringle* in 1882: *g*, leaf, × ¼; *h*, involucre, ×1; *i*, achene, × 2. *j–l*, apm. *Grayi*—*j*, from *Heller 12104*; *k*, *l*, from *Pringle* in 1881: *j*, leaf, × ¼; *k*, involucre, × 1; *l*, achene, × 2. *m–o*, apm. *humilis*, from *S. & J. 2436*: *m*, leaf, × ¼; *n*, involucre, × 1; *o*, achene, × 2. *p–r*, apm. *monticoloides*, from *Eastwood 11925a*: *p*, leaf, × ¼; *q*, detail of surface, × 1; *r*, involucre, × 1. *s*, *t*, apm. *attenuata*, from *Tracy 2794*: *s*, involucre, × 1; *t*, achene, × 2. *u–w*, apm. *plumaensis*, from *Hall and Babcock 4438*: *u*, leaf, × ¼; *v*, involucre, × 1; *w*, achene, × 2.

Related to apm. *rigida*.—CALIFORNIA: Elk Mtn., Lake County, alt. 1210–1500 m, *Tracy 2276* (UC); Mt. Sanhedrin, Lake County, alt. 1600 m, *Hall 9504* (UC, G). OREGON: Umpqua Valley, Douglas County, *Howell* in 1887 (Minn).

3. apm. *latibractea* (*pleurocarpa-occidentalis?*).—Stems 2.5–3.5 dm high; basal leaves 17–22 cm long, rather strongly tomentose, deeply pin-

natifid with elongate, narrowly lanceolate entire lobes; cauline leaves much reduced, all but the uppermost pinnatifid with linear, falcate, ascending lobes; involucres 13–14 mm high; inner bracts lanceolate-elliptic, 2.5–4 mm broad; achenes 6.5–7 mm long, strongly ribbed; pappus 9.5–10 mm; ($2n = 33$?). CALIFORNIA: east of Meadow Valley, Plumas County, alt. 1150 m, *B. 161* (UC); same locality, *S. & J. 2209* (UC).

4. apm. *Grayi* (*pleurocarpa-occidentalis*) (fig. 15*j–l*).—Stems shorter than in the last two, and rather stout; leaves floccose-tomentulose below, the basal 12–17 mm long, elliptic, dentate or pinnatifid with narrowly deltoid lobes; cauline leaves ovate-lanceolate, entire or remotely dentate; achenes 5.5–6.5 mm; pappus 9.5–10 mm; ($2n = 55$?). CALIFORNIA: headwaters of the Sacramento River, *Pringle* in 1881 (type of *C. pleurocarpa*, G); Mt. Eddy, Siskiyou County, alt. 1360 m, *Heller 12104* (DS, G, CA); Dorleska, Trinity County, alt. 2000 m, *Hall 8597*, part (UC, DS, G, Po).

Related to apm. *Grayi*.—CALIFORNIA: Horse Mtn., Humboldt County, alt. 1500 m, *Tracy 7621*, part (UC); Gordon Mtn., Del Norte County, alt. 1212 m, *Gillespie 9884* (DS); Preston Peak, Siskiyou County, alt. 2120 m, *Kildale 8845* (DS).

5. apm. *humilis* (*pleurocarpa-occidentalis*) (fig. 15*m–o*).—Stems 1.5–2 dm high; leaves floccose-tomentulose at least toward the base 7–14 cm long; entire or pinnatifid with lanceolate, spreading or reflexed lobes; leaves of the inflorescence much reduced, lance-linear, 2–3 cm long; involucres 10–12 mm high; achenes 5.5–6.5 mm long; pappus 9–10 mm long; ($2n = 44$ or 55 ?).—CALIFORNIA: headwaters of the Sacramento River, *Pringle* in 1882, part (G, WSC); Castle Lake, Siskiyou County, *Eastwood 10780*, part (CA); Shaft-Rock Mtn., near Hilt, Siskiyou County, *Rixford* (CA); north side of Scott Mtn., Siskiyou County, alt. 1210 m, *S. & J. 2446A* (UC). OREGON: west of Waldo, Josephine County, *Peck 8425* (G, Will).

6. apm. *glandulosa* (*pleurocarpa-occidentalis* or *monticola*?).—Stems and leaves minutely glandular-hirsute; stems 3.5–4 dm high; basal leaves lanceolate, 19–27 cm long, with remote, narrowly deltoid lobes, or merely dentate; cauline leaves lanceolate, the lowermost well developed; cyme large and open; involucre 12–14 cm long; achenes 6.5–7.5 mm long; pappus 7–7.5 mm; ($2n = 33$?). CALIFORNIA: near Mt. Shasta, Siskiyou County, alt. 1180 m, *S. & J. 2423* (UC); Forest House Mtn., near Yreka, Siskiyou County, alt. 1200 m, *B. & S. 1896* (UC); north side of Scott Mtn., Siskiyou County, alt. 1210 m. *S. & J. 2447* (UC).

7. apm. *monticoloides* (*pleurocarpa-monticola*) (fig. 15 *p–r*).—Stems, leaves, and peduncles conspicuously glandular-pubescent; stems rather stout, about 3 dm tall; basal leaves elliptic, 18–22 cm long, pinnatifid with deltoid, acuminate lobes; cauline leaves elliptic, dentate with coarse, acuminate teeth; involucres 15–16 mm high; inner bracts 5–7; florets 6–8; achenes 7.5–8 mm long, distinctly attenuate toward the apex; pappus setæ 10 mm long; ($2n = 44$?). CALIFORNIA: Cantara, Siskiyou County *Eastwood 11925a* (CA); Forest House Mtn., southwest of Yreka, alt. 1363 m, Siskiyou County, *B. & S. 1897* (UC).

In its pubescence, the shape of its cauline leaves, and its achenes, this form is distinctly transitional toward *C. monticola.*

8. apm. *pluriflora* (*pleurocarpa-occidentalis-monticola?*).—Similar in habit, leaves, etc. to apm. *rigida*; involucres 12–15 mm high; inner bracts 5–7; florets 6–10; achenes 7–7.5 mm long; pappus setæ 8 mm long; ($2n =$ 77 or 88 ?). CALIFORNIA: Hawkins Bar, Trinity County, alt. 180 m, *Kildale 10701* (DS); near Mt. Shasta, Siskiyou County, *B. & S. 1977* (UC).

Related to apm. *pluriflora.*—CALIFORNIA: near Covelo, Mendocino County, *Eastwood 15180* (CA). OREGON: Snow Camp, Curry County, alt. 1210–1280 m, *Thompson 32* ($2n = 55$?) (DS); Stein's Butte, Jackson County, *Peck 16431* ($2n = 44$?) (Will).

9. apm. *attenuata* (*pleurocarpa-occidentalis-monticola*) (fig. 15*s*, *t*).—Stems rather tall and slender, 3–4.5 dm high; leaves grayish-tomentulose, the basal 17–28 cm long, merely dentate, or pinnatifid with very short, acuminate lobes; cauline leaves entire or dentate with acuminate teeth; involucres 14–17 mm high; inner bracts 5–7, attenuate at the apex; florets 6–8; achenes 7–8 mm long, distinctly contracted at the apex; pappus 12 mm long; ($2n = 44$?). CALIFORNIA: between Van Duzen and Mad Rivers, Trinity and Humboldt Counties, alt. 909 m, *Tracy 2794* (UC, G); Hay Fork Mtn., Trinity County, *Tracy 6455* (UC).

10. apm. *breviramea* (*pleurocarpa-occidentalis-acuminata*).–Stems 2.2–2.7 dm high; basal leaves 11–16 cm long, pinnatifid with deltoid, reflexed, dentate lobes; inflorescence of 10–20 heads on short, ascending peduncles, the branches arising from the middle of the stem or above; involucres 12–14 mm high; outer bracts narrowly deltoid, the longest 4–5 mm long; inner bracts 5–6; florets 5–7; achenes 5–5.8 mm long, not strongly ribbed; pappus 9 mm; ($2n = 44$?) (see p. 41). WASHINGTON: Iron Mtn., Mt. Stuart region, Kittitas County, alt. 1970 m, *Thompson 7659*, part (UC, Mo).

This collection consists of two different forms. The one described is represented by two plants in UC, and one in Mo, while those seen from G and the second plant on the sheet from Mo differ in their broader, more deeply pinnatifid leaves, their larger inflorescences, and longer (13–15 mm) involucres. The latter more nearly suggests *C. pleurocarpa* in habit, but both are very definitely transitional toward *C. intermedia.*

11. apm. *plumaënsis* (*pleurocarpa-occidentalis*) (fig. 15 *u–w*).—Stems 4–6 dm high; basal leaves deeply pinnatifid, the lobes remote, acute or acuminate, remotely dentate; inflorescence cymose; involucres 11–13 mm high; inner bracts 7–8, tomentulose, glabrate above the middle, yellowish green, the apex obtuse; florets 8–12; achenes 6.5–7.5 mm long; pappus 8–9 mm; ($2n = 55$?). CALIFORNIA: Genesee Valley, Plumas County, alt. 1100 m, *Hall & Babcock 4438* (UC, DS); west of Blairsden, Plumas County, *B. & N. 180* (UC); Battle Creek Meadows, Lassen Butte region, *Eastwood 1902* (CA); west of Susanville, Lassen County, *B & C. 89* (UC).

Related to apm. *plumaënsis.*—CALIFORNIA: Goose Valley, Shasta County, *Eastwood 827* (G, CA); near Cantara, Siskiyou County, *Eastwood 11925* (CA).

This form is transitional to *C. intermedia* in the number of bracts and florets per head, but is characteristic of *C. pleurocarpa* in its habit, the tomentum on the involucres, and the achenes. It is the common form of *Crepis* in the well-watered forests of central and western Plumas County, California, where the same apomict has been collected in several different localities, and is usually the only one to be found there.

11. **Crepis monticola** Coville, Contr. U. S. Nat. Herb. 3:562, 1896 (Fig. 17)

Stems, leaves, and involucres sparingly tomentulose and (except in apm. *calva*) densely hirsute with long gland-tipped trichomes; basal leaves 10–20 cm long, elliptic in outline, generally pinnatifid with deltoid or lanceolate, angular, dentate lobes, the teeth acuminate or apiculate; stems 1.3–3.5 dm high, stout or sometimes slender; cauline leaves elliptic,

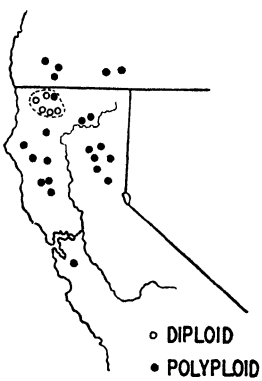


FIG. 16. Distribution of *Crepis monticola*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

mostly rather broad-based, and often more or less clasping, pinnatifid like the basal leaves or merely toothed; inflorescence of 4–20 heads; peduncles expanded toward the apex; involucres large, 14–24 mm, usually over 18 mm high; inner bracts 7–12; lanceolate and (except in apm. *plumaënsis*) strongly attenuate toward the apex, generally erect and not folded over the florets in bud; outer bracts narrowly lanceolate or linear, the longest 1/2–3/4 the length of the inner; florets large, corolla 16–21 mm long; anther tube 5–6 mm long; style-branches 1.5–3 mm long; achenes 5.5–9 mm long, fusiform, tapering toward the apex, more or less strongly costate, reddish brown; pappus setæ distinctly exceeding the achene, 9–13 mm long. (*C. occidentalis* var. *crinita* Gray, Bot. Cal. 1:435, 1876; Syn. Fl. 1(2):432, 1884, as to California plants.)

Southern Oregon and northern California, south in the Sierra Nevada to Sierra County, and in the Coast Ranges to Lake County and Mt. Hamilton (cf. fig. 16).

C. monticola is strikingly distinct from all others of the American species of *Crepis* in its indumentum of dense, shaggy, glandular tri-

chomes, and particularly in its attenuate inner bracts, which do not cover the florets in the buds. In the latter respect it resembles the species of the American genera *Agoseris* and *Microseris* subg. *Scorzonella*. It is the most restricted in range of all of the species considered. The original diploid form occurs only in the valley flats and lower foothills of central Siskiyou County, California, where it is, however, rather abundant. Polyploid forms essentially similar to, and probably directly derived from, this original diploid form occur with it and for some distance to the north and south. Other polyploid races, more or less transitional either to *C. occidentalis*, *C. pleurocarpa*, or *C. modocensis*, extend the range southward and eastward, into the Tehaman area of Jepson as well as the western edge of the Great Basin.

The following is a key to such forms as have been distinguished (for a discussion of their taxonomic status, see p. 69):

A. Longest of the outer bracts 10–15 mm long, 2/3–3/4 the length of the inner.
  B. Stems rather slender; leaves cordate-clasping at the base, involucres at anthesis 16–20 mm high; broadest of the inner bracts 1.8–2 mm broad near the base ..... diploid form
  B. Stems very stout; involucres at anthesis 19–24 mm high; broadest of the inner bracts 2.8–4 mm broad.
    C. Largest heads of the inflorescence with 11–13 inner bracts and 17–25 florets.
      D. Cauline leaves broadly ovate, cordate-clasping at the base..... 1. apm. *simulans*
      D. Cauline leaves narrowly ovate, tapering rather abruptly to a sessile base..... 2. apm. *triploidea*
    C. Largest heads of the inflorescence with 15 inner bracts and 35 florets..... 3. apm. *pluriflora*

A. Longest of the outer bracts 7.5–10 mm long, 1/2–2/3 the length of the inner; leaves mostly tapering toward the base.
  E. Leaves and involucres sparingly tomentulose and copiously beset with long glandular setæ.
    F. Involucres in fruit 15–22 mm high, the inner bracts distinctly attenuate at the apex; longest outer bracts 6.5–10 mm long
      G. Involucres of largest heads with 10–12 inner bracts.
        H. Glandular trichomes rather soft and slender, somewhat crisped, and more or less greenish or blackish.
          I. Largest heads with 10 inner bracts and 15–18 florets; plants 2–3.5 dm tall; achenes chocolate brown or blackish ..... 4 apm. *angustata*
          I. Largest heads with 11–12 inner bracts and 20–25 florets; plants 1.6–2 dm

high; achenes chestnut brown ..... 5. apm. *australis*
H. Glandular trichomes stiff and straight, rather broad-based, pale yellow and hyaline; achenes deep brown or blackish ..... 6. apm *setosa*
G. Involucres of largest heads with 8–9 inner bracts; plants 1.3–1.8 dm tall.
J. Basal leaves dentate or pinnatifid with broadly deltoid lobes; involucres 15–19 mm high; achenes 6–7 mm long.. 7. apm. *sanhedrensis*
J. Basal leaves deeply pinnatifid with lanceolate lobes; involucres 17–22 mm high; achenes 7.5–8.5 mm long..... 8. apm. *lassenensis*
F. Involucres in fruit 14–16 mm high; the inner bracts not at all or only slightly attenuate at the apex; longest of the outer bracts 5–6 mm long. 9. apm. *plumaënsis*
E. Leaves and involucres distinctly grayish-tomentose, and with relatively short glandular setæ; plants 3.5 dm high.... 10. apm. *calva*

Diploid form ($2n = 22$?) (fig. 17*a–e*).—This form is characterized by its broad-based, more or less clasping cauline leaves, and its extremely slender, attenuate involucral bracts. The achenes vary from merely attenuate at the apex to subrostrate. They are somewhat narrower than those of typical *C. occidentalis* and are less strongly costate, but are similar in color. CALIFORNIA: near Yreka, Siskiyou County, *Butler 750* (UC, DS); south of Yreka, alt. 810 m, *B. & S. 1887, 1888, 1928* (UC); northeast side of Scott Valley; alt. 900 m, *S. & J. 2442* (UC); Etna, Siskiyou County, *Eastwood & Howell 5032* (CA); near Mt. Shasta, Siskiyou County, *B. & S. 1973, 1974* (UC); summit of Scott Mtns., north of Carrville, Trinity County, *Howell 13689* (UC, CA).

1. apm. *simulans* (fig. 17*f*).—Similar to the diploid but larger and stouter; stems 2–3 dm tall; basal leaves 11–15 cm long; inner bracts 2–4 mm broad at the base; ($2n = 55$?). CALIFORNIA: near Yreka, Siskiyou County, *Greene 810* (from type collection of *C. monticola*, G); French Gulch, Shasta County, *Blasdale* in 1896 (UC); Hettien Chow Valley, Trinity County, *Blankinship* in 1893 (UC). OREGON: Grant's Pass, Josephine County, *Prescott* in 1912 (Will).

2. apm. *triploidea* (*monticola-occidentalis*?).—Similar to apm. *simulans*, but with the leaves narrower; achenes 7–7.5 mm, slightly contracted at the apex and rather strongly ribbed; ($2n = 33$?). OREGON: Woodville, Jackson County, *Peck 3978* (Will); Grant's Pass, Josephine County, *Gibbons* in 1896 (UC).

3. apm. *pluriflora* (*monticola-Bakeri* or *modocensis*).—Similar to apm. *simulans*, but with broader involucres which have more numerous inner bracts and up to 35 florets. OREGON: Dog Mtn., west of Lakeview, *Peck 15538* (Will).

4. apm. *angustata* (*monticola-pleurocarpa-occidentalis?*) (fig. 17*g*, *h*).—Stems 2–3.5 dm tall; basal leaves 13–20 cm long; cauline leaves cuneate at the base; involucres 15–20 mm high; inner bracts 8–10; florets 12–15; longest of the outer bracts 7–9 mm long; ($2n = 55$?). CALIFORNIA: Big Valley, near Bieber, Lassen County, *Baker* in 1894 (UC); Big Valley Mtns., alt. 1200 m, *S. & J. 2360* (UC).

FIG. 17. *Crepis monticola*. *a–e*, diploid form—*a–d*, from *B & S. 1973, 1974*; *e*, from *B. & S. 1888*: *a*, leaf, × ¼; *b*, detail of surface, × 1; *c*, involucre, × 1; *d*, corolla, × 2; *e*, achene, × 2. *f*, apm. *simulans*, from *Greene 810* (type of *C. monticola*), involucre, × 1. *g*, *h*, apm. *angustata*—*g*, leaf, × ¼, from *S. & J. 2360*; *h*, involucre, × 1, from *Baker and Nutting* in 1894. *i*, apm. *australis*, from *Swabey* in 1923, involucre, × 1. *j–l*, apm. *setosa*, from Sierra Valley, *Lemmon*: *j*, leaf, × ¼; *k*, involucre, × 1; *l*, achene, × 2. *m–p*, apm. *sanhedrensis*—*m*, from *Heller* in 1902; *n–p*, from *Hall 9468*: *m*, leaf, × ¼; *n*, involucre, × 1; *o*, corolla, × 2; *p*, achene, × 2.

5. apm. *australis* (*monticola-occidentalis*) (fig. 17*i*).—Stems 1.6–2 dm high; basal leaves tapering toward the base; involucres 16–22 mm high; inner bracts 9–12; florets 12–25; longest of the outer bracts about 10 mm long, 1/2–2/3 the length of the inner; achenes 7.5–9 mm long, strongly costate and only slightly tapering toward the apex; ($2n = 44$!) (cf. pp. 16, 48). CALIFORNIA: Mt. Hull, Lake County, alt. 1750 m, *Hall 9532* (UC); Seeboy Ridge, east of Mt. Hamilton, Santa Clara County, alt. 825 m, *Sharsmith 3059* (UC); pine woods near Mt. Hamilton, *Swabey* in 1923 (DS).

Related to apm. *australis*.—CALIFORNIA: near Yreka, Siskiyou County, alt. 810 m, *B. & S. 1930* (UC). OREGON: Crane Creek Mtn., Lake County, alt. 2120–2270 m, *Ferris & Duthie 281* (DS).

6. apm. *setosa* (*monticola-modocensis-acuminata*) (fig. 17*j–l*).—Stems low, 1.5–2 dm. high; basal leaves deeply pinnatifid with reflexed lobes, the cauline narrowly elliptic or lanceolate; glandular trichomes on leaves and stem stiff, broad-based and pale yellow, somewhat resembling the glandless setæ of *C. modocensis;* involucres similar to apm. *australis;* achenes 8.5–9 mm long, chocolate brown, distinctly tapering toward the apex; ($2n = 44$?). CALIFORNIA: Sierra Valley, Sierra County, *Lemmon* in 1874, part (UC, G).

Related to apm. *setosa*.—CALIFORNIA: Susanville, Lassen County, *Brandegee* in 1892 (UC).

7. apm. *sanhedrensis* (*monticola-pleurocarpa*) (fig. 17*m–p*).—Similar in habit to apm. *australis*; involucres with only 7–9 inner bracts and 8–18 florets; longest of the outer bracts 7.5–8 mm long; achenes 6–7 mm long; pappus 9–9.5 mm long; ($2n = 77$ or 88 ?). CALIFORNIA: Mt. Sanhedrin, Lake County, alt. 1600 m, *Hall 9468* (UC); same locality, *Heller* in 1902 (DS).

Related to apm. *sanhedrensis*.—CALIFORNIA: Buck Mtn., Humboldt County, alt. 1210 m, *Tracy 2915* ($2n = 77$ or 88 ?) (UC).

8. apm. *lassenensis* (*monticola-Bakeri-pleurocarpa*).—Similar to the preceding, but the leaves more deeply pinnatifid; involucres longer, 17–22 mm high; longest of the outer bracts 8–10 mm long; achenes 7.5–8.5 mm long; pappus 9.5–10 mm long; ($2n = 55$?). CALIFORNIA: Plumas County, *Ames* in 1878 (G); Drakes, Lassen County, *Austin* in 1897 (US); Lassen National Park, *Pearson 6829* (Po).

9. apm. *plumaëensis* (*monticola-pleurocarpa-acuminata*).—Similar to the last two; leaves not deeply pinnatifid; involucres 14–16 mm high; inner involucral bracts slightly or not at all attenuate; achenes 5.5–6.5 mm long; pappus 9–9.5 mm long; ($2n = 55$!). CALIFORNIA: Meadow Valley, Plumas County, *B. & N. 183* (UC)

10. apm. *calva* (*monticola-occidentalis-pleurocarpa?*).—Stems 3.5 dm tall; leaves and involucres grayish-tomentose and with less copious, shorter, glandular trichomes than in typical *C. monticola*; involucres 14–17 mm high; inner bracts 8–11, attenuate at the apex; outer bracts lance-linear, the longest 7.5 mm long; achenes 7 mm long, chocolate brown, strongly costate and slightly tapering at the apex; pappus 9.5 mm long; ($2n = 44$?). CALIFORNIA: near Yreka, alt. 810 m, *B. & S. 1937* (UC).

This form is almost exactly intermediate between *C. monticola* and *C. occidentalis.*

12. Crepis occidentalis Nutt., Jour. Acad. Phila. 7:29, 1834 (Figs. 19–22*e*)

Plant perennial, 0.8–4 (usually 1.5–2.5) dm high, with 1–3 stout stems from each caudex, corymbosely branching above or from near the base, bearing, like the leaves and flower-heads, a close gray tomentum (this

often thin and with a tendency to fall in age), often glandular-hirsute above especially on the peduncles, sometimes with black glandular bristles especially on the involucre; leaves sessile or with winged amplexicaul petioles, thickish, runcinately toothed to deeply pinnatifid with lanceolate or linear toothed lobes, the apical portion entire, acute or acuminate, the uppermost cauline leaves linear, entire; involucres 9–40-flowered, 11–19 mm high, cylindric or campanulate, calyculate, the longest outer bracts 1/3–2/3 as long as the inner and usually triangular or ovate-acuminate, appressed, rarely linear, and more or less spreading, the 7–18 inner bracts lanceolate, acute or acuminate, with membranous margins; achenes from light to very dark brown in color, fusiform, 6–10 mm long, 10–18-costate, only slightly attenuate at the apex or tapering to 1/2 the width of the body of the achene; pappus copious, soft, white of yellowish white, exceeding the involucre at maturity.

Saskatchewan and Montana west to British Columbia, south to New Mexico, Arizona, and southern California (see fig. 18). One of the most widespread and perhaps the most polymorphic of the American species of *Crepis*, although *C. runcinata* is a close competitor in regard to polymorphism. The many local apomicts of *C. occidentalis* fall into four morphologically distinct groups which differ in their geographic ranges. These groups of apomicts are recognized as subspecies.

Subspecies

Key to the Subspecies of *C. occidentalis*

A. Involucres with at least some glandular pubescence.
  B. Involucres, peduncles, and upper cauline leaves slightly or strongly glandular; largest heads of the inflorescence with 10–13 inner bracts, 18–30-flowered ..... *a. typica*
  B Involucres, peduncles, and generally the upper cauline leaves covered with conspicuous dark, gland-tipped trichomes; largest heads of the inflorescence with 8 inner bracts, 12–14-flowered.. *b. costata*
A. Involucres completely devoid of glandular pubescence; if with a few glandular trichomes, the involucres with 8 inner bracts and less than 15 florets.
  C. Stems well developed, 1–4 dm high, with a well-defined primary axis; longest outer bracts of the involucre generally 1/3–1/2 the length of the inner; leaves, if pinnatifid, with closely spaced, strongly toothed or pinnatifid lobes; heads mostly with 8 inner bracts and 10–20-florets ..... *c. pumila*
  C. Stems low, 0.5–2 dm high; inflorescence branching from near the base of the stem and bearing heads mostly on the end of long, divergent peduncles; longest outer bracts (5–) 7–9 mm long, 1/2–2/3 as long as the inner; leaves deeply pinnatifid, with remotely spaced, lanceolate, acute or acuminate, entire or coarsely few-toothed lobes..... *d. conjuncta*

12*a*. **Crepis occidentalis** subsp. **typica** nom. nov. (Figs. 19, 20*a*, *b*.)—Habit and leaves various; inflorescence bearing about 10–30 heads; peduncles usually glandular-pubescent; involucres broadly cylindrical or cyathiform, their bracts densely or sparsely glandular; inner bracts 8–13, always at least 10 on the largest heads; florets 12–30 per involucre, 18

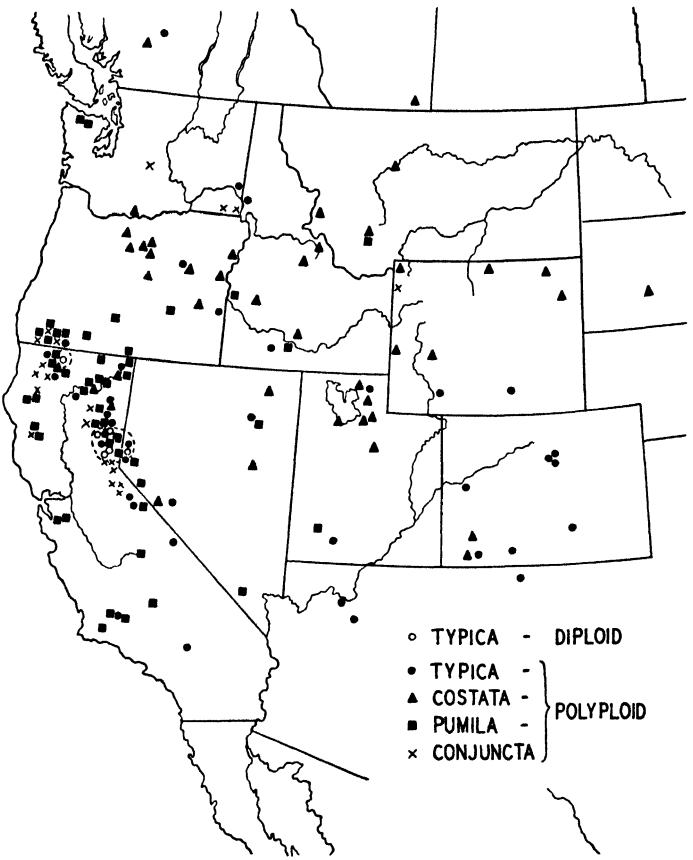


FIG. 18. Distribution of *Crepis occidentalis*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

or more in the larger ones. (*C. occidentalis* Nutt., loc. cit.; *Psilochœnia occidentalis* Nutt., Trans. Am. Phil. Soc. n. s. 7:436, 1840, in part; *Hieraciodes occidentale* O. Ktze., Rev. Gen. 346. 1891.)

Common through most of the western and southern portion of the range of *C. occidentalis*; becoming rare in central, northern, and eastern Oregon, and in southeastern Washington; occasional in Idaho, western Wyoming, Utah, Colorado, and New Mexico, but not seen from Montana, eastern Wyoming, or the Great Plains area.

This subspecies contains the diploid forms which represent the original stock of *C. occidentalis*. These forms are confined to northern and eastern California and adjacent Nevada. Within this range, and extending outward from it in different directions, are many polyploid forms; most

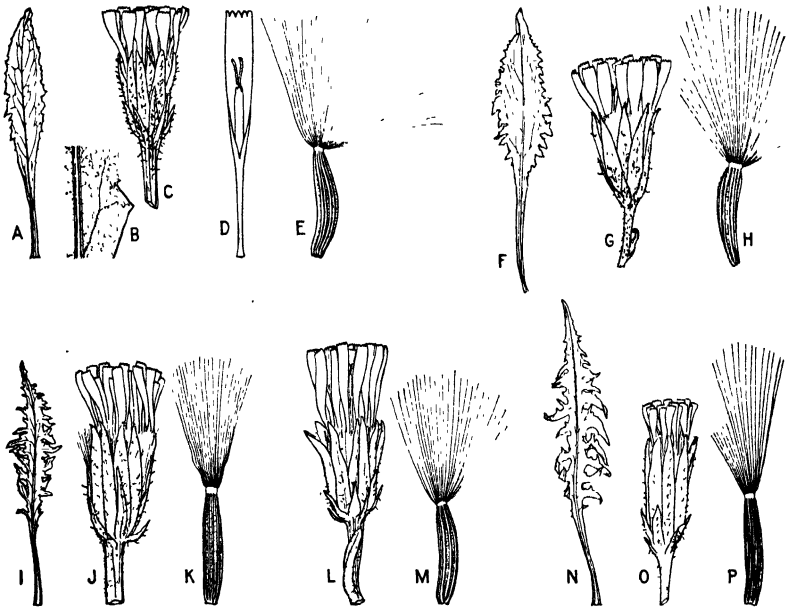


FIG. 19. *Crepis occidentalis* subsp. *typica*. *a–e*, diploid form—*a*, *b*, *e*. from *S. & J. 2185*; *c*, *d*, from *B. & N. 168*: *a*, leaf, × ¼; *b*, detail of surface, × 1; *c*, involucre, × 1; *d*, corolla, × 2; *e*, achene, × 2. *f–h*, autopolyploid form (near apm. *simulans*), from *B. & S. 1685*: *f*, leaf, × ¼; *g*, involucre, × 1; *h*, achene, × 2. *i–k*, apm. *humilior*, from *Elmer 3892*: *i*, leaf, × ¼; *j*, involucre, × 1; *k*, achene, × 2. *l*, *m*, apm. *inyoënsis*: *l*, involucre, × 1, from *Hall and Chandler 7156*; *m*, achene, × 2, from *B. 408*. *n–p*, apm. *Nuttallii*, from *Elmer 747*: *n*, leaf, × ¼; *o*, involucre × 1; *p*, achene, ×2.

or all of them partially or wholly apomictic. A few of these are morphologically identical with the diploid forms, except for the larger size of all their parts, but most of them show slight variations toward one or other of the different subspecies of *C. occidentalis*, or toward other species of *Crepis*.

C. occidentalis typica—key to apomictic forms (see p. 69)

A. Largest heads of the inflorescence with 11–14 inner bracts and 21–30 florets.
  B. Leaves merely toothed, or with short, deltoid lobes; involucral bracts broad, merely acute at the apex ..... { diploid form / 1. apm. *simulans*

B. Leaves deeply pinnatifid with narrowly deltoid or lanceolate lobes; involucral bracts more or less attenuate toward the apex.
C. Longest of the outer bracts about 1/2 the length of the inner; achenes 7–9 mm long.
D. Stems 2–3 dm tall; achenes 7–7.5 mm long.. 2. apm. *pinnatisecta*
D. Stems 1.5–2 dm tall; achenes 8–9 mm long.. 3. apm. *humilior*
C. Longest of the outer bracts about 1/3 the length of the inner; achenes 6.5–7.5 mm long.
D. Leaf segments and teeth acuminate, strongly mucronate; achenes blackish brown, slender, not strongly ribbed..... 7. apm. *columbiana*
D. Leaf segments obtuse or acute; achenes light or dark brown, thick, and strongly costate.
E. Plants sparsely glandular; pappus 8–9 mm long..... 4. apm. *inyoënsis*
E. Plants densely glandular; pappus 9.5–10.5 mm long..... 6. apm. *calyculata*
A. Largest heads of the inflorescence with 10 inner bracts and 18–20 florets..... 5. apm. *Nuttallii*

Diploid form (fig. 19*a–e*).—Stems 1.7–3.5 dm high; leaves broadly or narrowly elliptic, irregularly dentate or with short, deltoid lobes, never truly pinnatifid; involucres, peduncles, and upper cauline leaves covered with a fine, yellow glandular pubescence or the latter merely tomentose; involucre 12–16 mm high; inner bracts 8–13; florets 15–30; longest of the outer bracts about 1/2 the length of the inner; corollas 16–19 mm long; achenes 6.5–8 mm long; pappus 7–11 mm long; ($2n = 22$!). Castration experiments on plants of this form indicate complete absence of apomixis. CALIFORNIA: northwest of Sierraville, Sierra County, alt. 1600 m, *B. & N. 168* (UC); Feather River Inn, Plumas County, *B. 157* (UC); ridge east of Red Rock (Constantia), Lassen County, *B. & S. 1748* (UC); Montague, Siskiyou County, *Smith 696* (G, CA). NEVADA: Reno, Washoe County, *Kennedy* in 1901 (UC); same locality, *S. & J. 2170* (UC); west of Reno, *S. & J. 2185* (UC).

1. apm. *simulans*.—Morphologically similar to the diploid form, but with the pollen and stomata of triploids; involucres 14–17.5 mm high; corollas 19–22 mm long; achenes 7.5–8.5; pappus 11.5 mm; ($2n = 33$!). NEVADA: east of Verdi, Washoe County, alt. 1480 m, *S. & J. 2182* (UC); Lemmon Valley, Washoe County, *Kennedy 2094* (UC).

Related to apm. *simulans* (fig. 19*f–h*).—CALIFORNIA: northeast of Sierraville, Sierra County, alt. 1600 m, *B. & S. 1630, 1685, 1691* (UC); south of Loyalton, Sierra County, alt. 1600 m. *B. & S. 1724* (UC).

2. apm. *pinnatisecta* (*occidentalis-modocensis*).—Leaves narrowly elliptic or lanceolate in outline, strongly runcinate-pinnatifid, the lobes narrowly deltoid, strongly toothed or again lobed; stem and peduncles more slender than in the preceding forms, without glandular pubescence; involucre bearing a few dark glandular trichomes, 12.5–16 mm high; inner bracts strongly attenuate at the apex, somewhat spreading after anthesis; achenes 7–7.5 mm long; pappus 9.5–10 mm long; ($2n =$ about

33!). CALIFORNIA: Sierra Valley, northeast of Sierraville, Sierra County, alt. 1600 m, *B. & S. 1687, 1693* (UC).

Similar to apm. *pinnatisecta.*—CALIFORNIA: Sierra Valley, northeast of Sierraville, alt. 1600 m, *Smith* in 1927 (UC); Yreka, Siskiyou County, *Collins* in 1927 ($2n = 33$?); near Mogul, Alpine County, alt. 2400 m, *Yates 5305* ($2n = 44$?), part (CFE). NEVADA: King's Canyon, Ormsby County, alt. 1700–2000 m, *Baker 1070* ($2n = 33$?) (UC, CA, G).

3. apm. *humilior* (*occidentalis-Bakeri* or *modocensis*) (fig. 19*i–k*).—Dwarf, 1.2–2 dm high; heads 3–12 in an inflorescence; leaves narrowly elliptic or lanceolate, more or less pinnatifid, the lobes acute and strongly toothed; involucre and peduncles with a few large black glandular trichomes; involucre 13.5–17 mm high; inner bracts 8–12, attenuate at the apex; outer bracts lanceolate-attenuate, the longest about 1/2 the length of the inner; achenes 8–9 mm long, dark brown; pappus 9–10 mm long; ($2n = 33$?) (see pp. 39–40). CALIFORNIA: Sisson (Mt. Shasta), Siskiyou County, alt. 1075 m, *Brown 382,* part (UC); south of Ravendale, Lassen County, *Keck & Clausen 3752* (UC); Griffins, Ventura County, *Elmer 3892* (UC, DS, Minn, G); Bear Valley, San Bernardino County, *Parish 3720,* part (UC, G).

Related to apm. *humilior.*—NEVADA: Reno, alt. 1250 m, *S. & J. 2169* (UC). CALIFORNIA: Burney, Shasta County, alt. 1060 m, *S. & J. 2401* (UC). OREGON: Sucker Creek Canyon, Malheur County, *Henderson 8525* (CA).

4. apm. *inyoënsis* (*occidentalis-acuminata*) (fig. 19*l, m*).—Stems 1.5–2.5 dm high; leaves as in the preceding; involucre with a few small glandular trichomes, 13–16 mm high; inner bracts 8–12, narrow and attenuate at the apex; florets 15–25; outer bracts lance-deltoid, attenuate, *the longest about 1/3 the length of the inner*; achenes 6.5–7.5 mm; pappus 8–9 mm; ($2n = 33$?). CALIFORNIA: Hunter's Ranch Mtns., Inyo County, *Hall & Chandler 7156* (UC); Argus Mtns., Inyo County, alt. 1360–1500 m, *Purpus 5423* (UC); Mono Lake, Mono County, *B. 408A* (UC). NEVADA: Gold Mtn., Esmeralda County, alt. 2400 m, *Keck 564* (UC).

Related to apm. *inyoënsis.*—COLORADO: near Canyon City, Fremont County, *Brandegee 924* (UC). WYOMING: Fort Steele, Carbon County, *Nelson 7243,* part (NY, Minn, CA). (Both probably $2n = 44$.)

5. apm. *Nuttallii* (*occidentalis-acuminata-modocensis*) (fig. 19*n–p*).—Stems 1.7–2.5 dm high; leaves narrowly elliptic, strongly pinnatifid with acute sharply dentate lobes; involucres and peduncles with conspicuous but scattered glandular trichomes; involucres 14–19 mm high; inner bracts 8–10; florets 12–20; outer bracts lance-deltoid, strongly acute or somewhat attenuate, the longest 2/5–1/2 the length of the inner; achenes 8–8.5 mm, dark brown, rather strongly tapering at the apex; pappus 11 mm long; ($2n = 33$?) (see pp. 15–16). WASHINGTON: on the borders and in the vicinity of the Columbia River, *Wyeth* (type of *C. occidentalis,* G); Wawawai, Whitman County, *Elmer 747* (UC, Minn).

Related to apm. *Nuttallii.*—UTAH: Blacksmith Fork Canyon, Cache County, *Maguire 3911* (UC). COLORADO: Grand Junction, *Eastwood* in

1916 (CA). IDAHO: Hot Hole, East Fork Bruneau, Owyhee County, *Nelson & Macbride 1885* (Minn, G); Lewiston Hill, Lewiston, alt. 400 m, *Hitchcock & Samuel 2534* (CA, WSC). CALIFORNIA: south of Yreka, Siskiyou County, *B. & S. 1886* (UC); Davis Creek, Modoc County, *B. & S. 1844* (UC); Burney, Shasta County, *S. & J. 2400* (UC); Dixey Mtns., Lassen County, *Baker & Nutting* in 1894 (UC); near highway from Tioga Lodge to Bridgeport, Mono County, *B. 411* ($2n = 33$!) (UC). OREGON: near Siskiyou, Jackson County, *Sherwood 610* (Will). NEVADA: Cave Creek, Elko County, *Mason 4721* (UC).

6. apm. *calyculata* (*occidentalis-Bakeri-acuminata*) (fig. 20*a*, *b*).—Stems, leaves, and involucres densely glandular; stems 1.8–2.8 dm high; leaves narrowly elliptic or lanceolate in outline, deeply pinnatifid with slightly reflexed, strongly toothed lobes; involucres 13–16 mm high; inner bracts 8–11, florets 15–24; achenes 6.5–7.5 mm, pappus 9.5–10.5 mm long; ($2n = 44$?). COLORADO: Golden, Jefferson County, alt. 1730 m, *Bethel & Clokey 4413* (DS, CA, Minn, RM, Clo); Morrison, Jefferson County, *Clokey 4414* (Clo); Boulder, Boulder County, *Vestal* in 1913 (DS).

Similar to apm. *calyculata*.—COLORADO: Durango, *Eastwood 5285* (CA); north side of Pagosa Springs, *Schmoll 1225* (RM). UTAH: southern, without definite locality, *Palmer 291* (NY); Bryce's Canyon, *Jones* in 1922 (NY). NEW MEXICO: Tierra Amarilla, Rio Arriba County, alt. 2320 m, *Eggleston 6596* (US). ARIZONA: Grand Canyon, *Eastwood 5725* (CA); near Flagstaff, alt. 2100 m, *Purpus 7088* (UC). IDAHO: Garden Creek, near Challis, Custer County, alt. 1630 m, *MacBride & Payson 3352* ($2n = 33$?) (G). CALIFORNIA: Goose Lake, Modoc County, *Bruce 2181* ($2n = 33$?), part (UC).

7. apm. *columbiana* (*occidentalis-modocensis*).—Stems about 2 dm high; leaves deeply pinnatifid, the lobes acuminate, strongly dentate or again pinnatifid; inflorescence of 4–10 heads on rather slender peduncles; involucres 15–16 mm high in fruit, 14–20-flowered; outer bracts lanceolate, acuminate, the longest about 1/3 the length of the inner; inner bracts lanceolate or linear, somewhat attenuate; achenes dark brown or black, 8.5–9 mm long, rather slender (1.2 mm thick); pappus 9.5 mm; ($2n = 55$?). BRITISH COLUMBIA: Kamloops, *Macoun* in 1889 (G).

This is a most anamalous form, resembling *C. modocensis* subsp. *rostrata* in the shape of its leaves, *C. exilis* in the slender peduncles and the shape of the involucral bracts, and approaching both these species in the shape and color of its achenes. With further material available, it might be considered a distinct subspecies.

12*b*. **Crepis occidentalis** subsp. **costata** (Gray) comb. nov. (Fig. 20*c–k*.)—Involucres, peduncles, and often the upper cauline leaves covered with coarse dark glandular trichomes; leaves mostly pinnatifid with elliptic, variously toothed or cleft segments; inflorescence mostly with 15–30 heads; involucres narrower than in subsp. *typica*, with 8 inner bracts and 10–14 florets; achenes often darker and more conspicuously costate than in subsp. *typica*. (*Crepis occidentalis* var. *costata* Gray,

Bot. Calif. 1:435, 1876; *Psilochenia occidentalis* Nutt., loc. cit., in part; *Crepis grandifolia* Greene, Pittonia 3:107, 1897.)

With the habit of subsp. *typica*; the involucres, peduncles, and upper cauline leaves densely beset with dark, gland-tipped trichomes; inner involucral bracts 7–8; outer bracts as in subsp. *typica* or shorter; florets 9–14 per involucre; achenes and pappus as in subsp. *typica*. In some forms, including that to which the type belongs, the achenes are as described by Gray, *i.e.*, more strongly ribbed (as well as darker in color) than in typical *C. occidentalis*, but this characteristic is inconstant, and it occurs also in forms of subspp. *typica* and *pumila*.

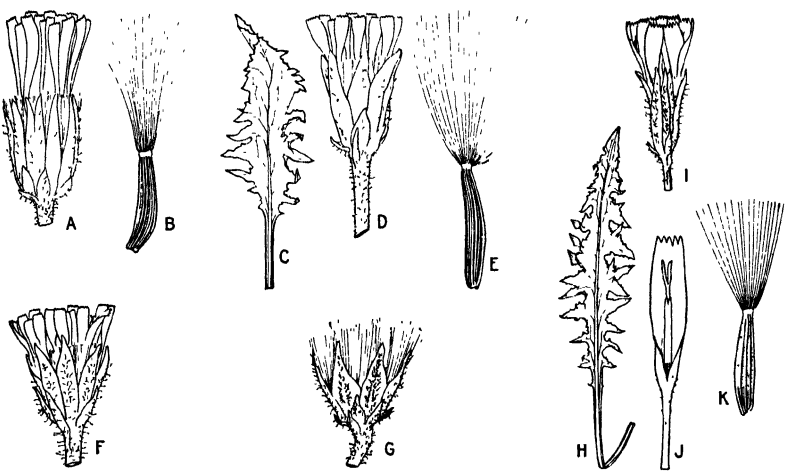


FIG. 20. *Crepis occidentalis* *a*, *b*, subsp *typica* apm. *calyculata*, from *Clokey 4413*: *a*, involucre, × 1; *b*, achene, × 2.
c–k, subsp. *costata*; *c–e*, apm. *Grayi*—*c*, *d*, from Palmer 140; *e*, from *UC Gen 1921*: *c*, leaf, × ¼; *d*, involucre, ×1, *e*, achene, × 2. *f*, apm. *elliptica*, involucre, × 1, from *B & S. 1934*. *g*, apm. *deltoidea*, involucre, × 1, from *Macoun 11709*. *h–k*, near apm. *montanensis*, from *Burglehaus in 1893*: *h*, leaf, × ¼; *i*, involucre, × 1; *j*, corolla, × 2; *k*, achene, × 2.

Although the specimen (Howell no. 140, from eastern Oregon) considered by Coville (Contr. U. S. Nat. Herb. 3:560, 1896) to be identical with the type of *C. occidentalis* has the heavily glandular involucral bracts and inflorescences as well as the relatively few-flowered involucres of this subspecies, it differs in this respect from the specimen collected by Wyeth upon which Nuttall based his description. The latter has only a very few glands near the apex of the peduncles, and a few more on the involucres, but the upper leaves and bracts are devoid of glands. Furthermore, in the only head of this specimen that is sufficiently expanded for this purpose, 16 florets can be counted. Coville's selection, therefore, of the Howell specimen as an exact match for the type was not correct, and in the opinion of the present writers the two

specimens belong to different subspecies. The type has already been cited under subsp. *typica,* apm. *Nuttallii.*

Throughout the northern half of the range of the species, and in this area the most common type; south to Colorado, Utah, and northern California. This subspecies, as here recognized, is a series of polyploid, presumably apomictic races which in their few flowered heads, and the frequent reduction in size of their outer involucral bracts are definitely transitional toward *C. intermedia.* They show a definite affinity toward *C. Bakeri* in their strong glandular pubescence, and most forms also in their deeply pinnatifid and toothed leaves, although other races of subsp. *costata* are in this respect nearer to subsp. *typica.* The following forms represent the degree of variation to be found here:

C. occidentalis costata—key to apomictic forms *(see p. 69)*

A. Longest of the outer bracts 2/5–1/2 the length of the inner.
  B. Inner bracts lanceolate or linear, 2–4 mm broad.
    C. Involucres 14–18 mm high.
      D. Leaves of the inflorescence toothed or pinnatifid, narrow and tapering toward the base; outer involucral bracts deltoid.
        E. Achenes 8–9 mm long; pappus 9–10 mm long ..... 8. apm. *Grayi*
        E. Achenes 6.5–8 mm long; pappus 11–12 mm long ..... 9. apm *ampla*
      D. Leaves of the inflorescence entire, broad and somewhat cordate-clasping at the base; outer involucral bracts lanceolate or linear, long attenuate at the apex..... 10. apm *elliptica*
    C. Involucres 11–13 mm high..... 11 apm *parviceps*
  B. Inner bracts broadly lanceolate or deltoid, with conspicuous scarious margins, 3.5–5 mm broad... 12. apm *deltoidea*
A. Longest of the outer bracts 1/3–2/5 the length of the inner ..... 13. apm. *montanensis*

8. apm. *Grayi* (*occidentalis-acuminata-Bakeri*) (fig. 20c–e).—Stems 2–3 dm high; leaves narrowly or broadly elliptic, the basal pinnatifid with broad, coarsely and irregularly toothed, mostly overlapping lobes; involucres 14–17 mm high; achenes dark brown, 8–9 mm long, strongly scabrous and prominently ribbed; pappus 9–9.5 mm long; ($2n = 44$!). UTAH: Stansbury Island, Great Salt Lake, alt. 1300 m. *Watson 715* (*type* of *C. occidentalis* var. *costata,* G); Salt Lake City, *Garrett 1829* (DS); same locality and collector, UC Gen 1921 ($2n = 44$!) (UC). IDAHO: Shoshone, *Palmer 140* (DS, G, Clo).

Related to apm. *Grayi.*—UTAH: Newton to Hyde Park, Cache County, *Jones 498* ($2n = 88$?) (G). COLORADO: Thompson's Park, east of Mancos, alt. 2270 m, *Baker, Earle, & Tracy 461* ($2n = 33$?) (Minn). WYOMING: east of Afton, Lincoln County, alt. 2000 m, *Payson & Armstrong 3323* ($2n = 44$?) (G, RM); Green River, *Nelson 4719,* part (NY, G, RM). IDAHO: Salmon, Lemhi County, alt. 1360 m, *Payson 1752* ($2n = 44$?) (G, RM). NEVADA: near Moore's Station, Elko County, *Greene* in 1895

($2n = 44$?) (type of *C. grandifolia*, ND); Emigrant Pass, on Victory Highway, *Eastwood & Howell* in 1933 ($2n = 55$?) (CA); Trail Creek, White Mtns., Esmeralda County, alt. 2500 m, *Duran 3257* (UC). CALIFORNIA: Stony Ridge, T. 27 N., R. 13 E, alt. 1940 m, Lassen County, *S. & J. 2305* (UC). BRITISH COLUMBIA: Spence's Bridge, Fletcher in 1885 (G).

9. apm. *ampla* (*occidentalis-Bakeri-acuminata*).—Stems rather stout, 2.3–3.3 dm high; leaves about as in the preceding; involucres 15–18 mm high; outer bracts narrowly deltoid to lanceolate, the longest 7–9 mm long; achenes 6.5–8 mm long, deep brown or blackish when mature; pappus 11–12 mm long; ($2n = 33$?). OREGON: near Beulah, Malheur ("Mathew") County, alt. 1200 m, *Leiberg 2294* (US, G). CALIFORNIA: Fall River Mills, Shasta County, alt. 1000 m, *S. & J. 2382* (UC); Burney, Shasta County, alt. 1060 m, *S. & J. 2402* (UC).

Related to apm. *ampla*.—CALIFORNIA: south of Ravendale, Lassen County, *S. & J.* 2221 (UC). OREGON: Grizzly Butte, Crook County, alt. 1300 m, *Leiberg 233*, part (UC, US, G); Gateway, Jefferson County, *Peck 13802* (Will); without locality, *Howell* in 1880 (US); Pine Creek, Baker County, *Cusick 2540* (UC, G, RM, Mo, Minn); Fossil, Wheeler County, *Henderson 5266* ($2n = 44$?) (DS, G, CA). WASHINGTON: near Rockland, Klickitat County, *Suksdorf 5085* (Minn, DS, G,). IDAHO: Boise City, Boise County, *Coville & Kearney 209* (G). WYOMING: Ewing, Crook County, *Seig 20* (RM). UTAH: near Salem, Utah County, *Eastwood & Howell 565* (CA).

10. apm. *elliptica* (*occidentalis-acuminata* or *pleurocarpa-monticola*).—Stems 2.5–3 dm high; leaves *merely dentate*, not truly pinnatifid, those on the stem, and particularly on the inflorescence, nearly *entire and with broad, partly clasping bases;* glandular trichomes paler, longer, and slenderer than in other forms of this subspecies; *outer involucral bracts narrowly deltoid to lanceolate or linear;* involucres 14–16 mm high; pappus 9–11 mm long at flowering time; mature achenes not seen; ($2n = 33$?). CALIFORNIA: Grenada, Siskiyou County, *Heller 8065* (UC, DS, G, Minn); near Yreka, Siskiyou County, *Butler 754* (UC); same locality, *B. & S. 1934* (UC).

An anomalous form, in its cauline leaves, glandulosity, and outer involucral bracts transitional toward *C. monticola*.

11. apm. *parviceps* (*occidentalis-acuminata-Bakeri*).—About 2 dm high; leaves elliptic-lanceolate, with narrowly lanceolate, remote, toothed lobes; heads 11-13 mm high; outer bracts as in apm. *Grayi*; corolla about 15 mm long; achenes 6–6.5 mm; pappus 7–7.5 mm long; ($2n = 33$?). OREGON: Dixie Pass, Grant County, alt. 1280 m, *Keck & Clausen 3665* (UC). CALIFORNIA: north of Weed, Siskiyou County, alt. 810 m, *B. & S. 1884* (UC).

Sharply distinguished from the last three forms in its very small heads, florets, and achenes.

12. apm. *deltoidea* (*occidentalis-Bakeri-acuminata*) (fig. 20*g*).—Stems 1.5–2 dm high; basal leaves elliptic, very thick and with broadly deltoid, obtuse lobes; heads 12–15 mm high; outer bracts broadly deltoid, 1/3

the length of the inner, or less; inner bracts *deltoid, obtuse, up to 4.5 mm broad at the base, the innermost with broad scarious margins*; achenes 6–8 mm long; ($2n = 44$?). ALBERTA or SASKATCHEWAN: Cypress Hills, *Macoun 11709* (US, Minn).

Related to apm. *deltoidea*.—NEVADA: Currant Summit, White Pine County, alt. 2225 m, *Keck 613* ($2n = 77$ or 88 ?) (UC).

13. apm. *montanensis (occidentalis-acuminata-Bakeri* or *modocensis)*.—Stems 2–3 dm high; basal leaves narrowly elliptic, with narrowly deltoid, strongly toothed lobes; branches of the inflorescence strongly ascending; heads 13–16 mm high; *outer bracts broadly deltoid, the longest less than 1/3 the length of the inner;* corollas about 20 mm long; achenes 8.5–9 mm; pappus 9.5–10 mm long; ($2n = 33$?). MONTANA: Midvale, *Umbach 139, 424a* (DS); Great Falls, *Williams 242* (Minn.); Bridger Mtns., alt. 2120 m, *Rydberg & Bessey 5306*, part (UC).

Related to apm. *montanensis* (fig. 20*h–k*).—ROCKY MTNS.: *Nuttall* without date (G). MONTANA: Hamilton, *Blankinship 560a* (UC, DS, Po, RM). WYOMING: Newcastle, *Bates* in 1896 ($2n = 44$?) (G, Minn); Big Piney, Sublette County, *Payson 2607* ($2n = 44$?) (UC, G, RM); Mammoth Hot Springs, *Burglehaus* in 1893 ($2n = 33$?) (Minn); east of Sheridan, Sheridan County, alt. 1150 m, *Sharp 119* (RM). UTAH: Bear River, Summit County, alt. 2400 m, *Payson 4869* ($2n = 33$?) (UC, G, RM, Mo). COLORADO: Ridgway, Ouray County, *Payson 3839* ($2n = 44$?) (G). SOUTH DAKOTA: near Wall, Pennington County, *Palmer 37310* ($2n = 44$?) (G).

This series of forms shows an increasing similarity to *C. intermedia* and *C. acuminata* in the reduction in number of the inner bracts and florets, and in the shape of the outer bracts. Apm. *montanensis*, in particular, is as near to *C. intermedia* as to *C. occidentalis* in all floral characteristics except the achenes, and some related forms (e.g., the Burglehaus collection) are very near to *C. intermedia* in habit. The strong glandular pubescence of this subspecies, as well as the tendency toward much dissected leaves, indicates a stronger affinity to *C. Bakeri* than to typical *C. occidentalis*.

12c. **Crepis occidentalis** subsp. **pumila** (Rydb.) comb. nov. (Fig. 21.)—Plants completely devoid of glandular pubescence (except in apm. *olympica*); more variable in habit than subsp. *typica;* leaves variously pinnatifid; involucres narrower than in subsp. *typica*, with mostly 8 inner bracts and 12–20 florets; achenes and pappus as in subsp. *typica*. (*Crepis pumila* Rydb., Mem. N. Y. Bot. Gard. 1:462, 1900.)

Common in the range of the species in California, western Nevada, and southern Oregon, and with isolated occurrences in the mountains of Montana, Idaho, and Washington.

This group of forms is in general transitional from subsp. *typica* toward *C. intermedia*, i.e., they are *C. occidentalis* with an admixture of *C. acuminata* or *C. pleurocarpa*. Some of them are practically identical with the taller forms of subsp. *typica*, from which they differ only in their complete lack of glandular pubescence and their tendency toward fewer bracts and florets, but these pass through a gradual series of inter-

mediate forms into such as apm. *multiceps*, which in both habit and floral characteristics is closely similar to the larger-headed forms of *C. intermedia*. The dwarf forms of this subspecies, including that represented by the type and those found in Southern California, show in their leaf shape, habit, and sometimes their involucral bracts a decided admixture of *C. Bakeri* or *C. modocensis*, but no clear dividing line,

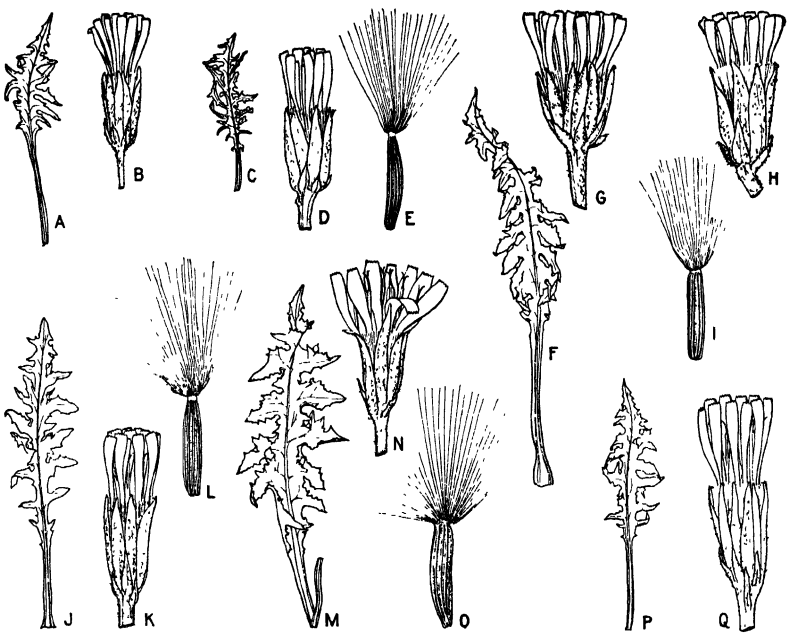


FIG. 21. *Crepis occidentalis* subsp. *pumila*. *a*, *b*, apm. ***Rydbergii***, from ***Rydberg 5305***: *a*, leaf, × ¼; *b*, involucre, × 1. *c–e*, apm. ***tehachapensis***, from ***Hasse and Davidson*** in ***1907***: *c*, leaf, × ¼; *d*, involucre, × 1; *e*, achene, × 2. *f*, *g*, apm. ***longifolia***, from ***B. & S. 1846***: *f*, leaf, × ¼; *g*, involucre, × 1. *h*, *i*, apm. ***hamiltonensis***, from ***Elmer 4872***: *h*, involucre, × 1; *i*, achene, × 2. *j–l*, apm. ***media***—*j*, *k*, from ***B. & S. 1632***; *l*, from ***S. & J. 2318***: *j*, leaf, × ¼; *k*, involucre, × 1; *l*, achene, × 2. *m–o*, apm. ***glabrescens***, from ***B & S. 1932***: *m*, leaf, × ¼; *n*, involucre, × 1, *o*, achene, × 2. *p*, *q*, apm. ***olympica***, from ***Elmer 2621***: *p*, leaf, × ¼; *q*, involucre, × 1.

either morphologically or geographically, can be drawn between these and the tall, robust forms most common in northern California. Although Rydberg, in the "Rocky Mountain Flora," gave a rather broad range for *C. pumila* in that region, careful examination of the specimens in the herbarium of the New York Botanical Garden identified by him as that species revealed that one of them is *C. modocensis*, one is *C. pleurocarpa*, and of the remaining six, representing localities in all the states mentioned by him except Nevada, only one besides the type sheet has the involucral bracts completely glandless. That one, *Tweedy 917*,

is transitional from subsp. *pumila* to subsp. *conjuncta*, and owing to the length of the outer bracts, has been included in the latter subspecies. Hence subsp. *pumila* is much rarer in the Rocky Mountain region than is indicated by the statement concerning its range in Rydberg's flora.

C. occidentalis pumila—key to apomictic forms *(see p. 69)*

A Largest heads of the inflorescence with 10–13 inner bracts and 17–25 florets.
  B. Involucres 15–18 mm high; longest of the outer bracts about 1/2 the length of the inner..... 16. apm. *elatior*
  B Involucres 13–16 mm high; longest of the outer bracts 1/3–1/2 times the length of the inner... 17. apm. *longifolia*
A Largest heads of the inflorescence with 8–9 inner bracts and 12–20 florets.
  C. Involucral bracts completely glandless.
    D. Stems 1–2 dm high; basal leaves deeply pinnatifid with strongly toothed, acute, lanceolate lobes; heads 3–16 in an inflorescence.
      E. Stems 1.5–2 dm high; heads 12–16 in an inflorescence ..... 14. apm. *Rydbergii*
      E. Stems very dwarf, 1–1.5 dm high; heads 3–15, mostly 10 or less in an inflorescence. 16. apm. *tchachapensis*
    D. Stems 1.5–3.8 dm high; basal leaves merely dentate or with deltoid lobes; heads 7–30 in an inflorescence
      F. Stems very stout; involucres 15–18 mm high; longest of the outer bracts 2/5–1/2 the length of the inner; achenes 5.5–7 mm long, slightly contracted at the apex..... 18. apm. *hamiltonensis*
      F. Stems more slender; involucres 12–16 mm high.
        G. Longest of the outer bracts about 1/2 the length of the inner; inflorescence with 10–20 heads; involucres 13–15 mm high ..... 19 apm. *media*
        G. Longest of the outer bracts 1/3–2/5 the length of the inner.
          H. Stems 1.7–2 dm high; basal leaves broadly elliptic, 8–12 cm long, dentate or with obtuse lobes; heads 7–15 in an inflorescence..... 20 apm. *brevis*
          H. Stems 2.6–3.8 dm high; basal leaves 15–25 cm long, the lobes acute; heads 15–30 in an inflorescence.
            I. Inflorescence with 15–20 heads; involucre 13–15 mm high; achenes 7–7.5 mm long..... 21. apm. *glabrescens*
            I. Inflorescence with 15–30 heads; involucre 12–14 mm high; achenes 5.5–6.5 mm long..... 22. apm. *multiceps*
  C. Involucral bracts with a few scattered glandular trichomes ..... 23. apm. *olympica*

14. apm. *Rydbergii* (*occidentalis-acuminata-modocensis*) (fig. 21*a*, *b*). —Stems 1.8–2 dm tall; leaves narrowly elliptic, deeply pinnatifid with strongly toothed lobes; heads 12–16 per inflorescence; involucres

13–14 mm high; inner bracts 8; florets 7–12; longest outer bracts 4.5–5.5 mm long; pappus at flowering time 9 mm long; achenes not seen; ($2n = 55$?) (see p. 16). MONTANA: Bridger Mtns., alt. 2100 m, *Rydberg & Bessey 5305* (type of *Crepis pumila*, NY).

Related to apm. *Rydbergii*.—CALIFORNIA: near Sheep Rock, Mt. Shasta, Siskiyou County, alt. 1500 m, *Hall & Babcock 4116* ($2n = 33$?) (UC, DS); Round Lake, Plumas County, alt. 2000 m, *Head* in 1921 ($2n = 44$?) (CA); Frazier Mtn., Ventura County, *Hall 6595* ($2n = 33$?) (UC, DS, RM). NEVADA: Kyle Canyon, Charleston Mtns., alt. 2570 m, *Jaeger* in 1926 ($2n = 44$?) (UC).

These forms are somewhat transitional toward subsp. *conjuncta*.

15. apm. *tehachapensis* (*occidentalis-acuminata-modocensis*) (fig. 21*c–e*).—Stems 1–1.5 dm high; leaves with remote, strongly toothed segments; inflorescence with 3–15 heads; involucres 13–15 mm high; inner bracts 8; florets 8–13; outer bracts deltoid, the longest 4.5–5 mm long, 1/3 the length of the inner; achenes dark brown, 7–8 mm long, attenuate toward the apex; pappus 9–10 mm long; ($2n = 66$–88 ?) (see p. 39). CALIFORNIA: Tehachapi Mtns., Kern County, alt. 1500 m, *Hasse & Davidson* in 1907 (UC); Mt. Pinos, Kern County, alt. 1520 m, *Hall 6388* (UC); Big Pine Mtn., San Rafael Mtns., Santa Barbara County, alt. 1820 m, *Hoffmann* in 1929 (SB).

16. apm. *elatior* (*occidentalis-acuminata*).—Stems 3–4 dm high; leaves elliptic, with short, broadly deltoid, toothed lobes; involucres 15–18 mm high; *inner bracts 8–11*, acute or obtuse at the apex; florets 10–20; outer bracts lance-deltoid, the longest 1/2 the length of the inner or more; achenes pale brown, 8.5–9.5 mm; pappus 10 mm long; ($2n = 33$?). CALIFORNIA: south of Loyalton, Sierra County, alt. 1500 m, *B. & S. 1727* (UC); Alturas, Modoc County, alt. 1360 m, *B. & S. 1795* (UC). OREGON: Lakeview, Lake County, alt. 1400 m, *B. & S. 1858* (UC).

Related to apm. *elatior*.—CALIFORNIA: Sierra Valley, northeast of Sattley, Sierra County, alt. 1600 m, *B. & S. 1749* ($2n = 33$?); Big Valley Mtns., Lassen County, alt. 1130 m, *S. & J. 2351* (UC); Davis Creek, Modoc County, alt. 1400 m, *B. & S. 1845* ($2n = 55$?); Burney, Shasta County, alt. 1060 m, *S. & J. 2407* (UC); near Bridgeville, Humboldt County, *B. 2402* ($2n = 88$?) (UC). NEVADA: near Carson City, *Anderson* in 1865 ($2n = 33$?) (G); near Tim Smith's, Douglas County, alt. 1930 m, *Thomas* in 1935 ($2n = 33$?) (CFE).

17. apm. *longifolia* (*occidentalis-acuminata*) (fig. 21*f, g*).—Habit, leaves, and pubescence similar to the last; involucre 13–16 mm high; *inner bracts 8–13*, acute and somewhat attenuate at the apex; florets 10–25 *outer bracts narrowly deltoid, 1/3–2/5 the length of the inner;* achenes 7.5–9.5 mm long; ($2n = 33$!) (see p. 16). CALIFORNIA: Sierra Valley, northeast of Sierraville, Sierra County, alt. 1600 m, *B. & S. 1689* (UC); Susanville, Lassen County, alt. 1340 m, *Keck & Clausen 3759* (UC); near Davis Creek, Modoc County, alt. 1400 m, *B. & S. 1846* (UC); Mono Lake, Mono County, *B. 408B* (UC). NEVADA: Cave Creek, Elko County, *Mason 4804* (UC).

Related to apm. *longifolia*.—CALIFORNIA: near Shaver, Fresno County, alt. 1820 m, *Smiley 571* (G); east of Red Rock, Lassen County, alt. 1600 m, *B. & S. 1750* (UC) ($2n = 33$?); Yreka, Siskiyou County, alt. 810 m, *Collins* in 1927 (UC) ($2n = 44$?); near Hawkinsville, Siskiyou County, *Butler 748* (UC) ($2n = 55$?). OREGON: Ashland, Jackson County, *Peck 14990* (Will) ($2n = 55$?); Grant's Pass, Jackson County, *Howell 172* (G). UTAH: Milford, Beaver County, *Goodding* in 1902 (RM).

18. apm. *hamiltonensis* (*occidentalis-pleurocarpa*) (fig. 21*h*, *i*).—*Stems very stout*, 2.3–3.5 dm tall; leaves elliptic, pinnatifid with deltoid, obtuse, toothed lobes; involucres 15–18 mm high; inner bracts 8–9, very broad and obtuse at the apex; florets 12–20; outer bracts narrowly deltoid, the longest 6.5–8 mm long, 2/5–1/2 the length of the inner; achenes 5.5–7 mm long, pale brown, sharply truncate at the apex; pappus 9–10 mm long; ($2n = 77$!) (see pp. 16, 48). CALIFORNIA: Humboldt County, *Rattan* in 1867 (DS); Elk Ridge, Mendocino County, *Bolander 6498* (UC, US); Mt. Hamilton, Santa Clara County, alt. 1200 m, *Elmer 4872* (UC, DS, CA, Minn); head of Colorado Creek, Red Mtns., Stanislaus County, alt. 900 m, *Sharsmith 3185* (UC).

Related to apm. *hamiltonensis*.—OREGEN: Lakeview, Lake County, alt. 1400 m, *B. & S. 1856* ($2n = 55$?) (UC).

19. apm. *media* (*occidentalis-acuminata-modocensis*) (fig. 21*j–l*).—Intermediate in habit between apm. *hamiltonensis* and *Rydbergii;* stems 2–3 dm high; basal leaves narrowly elliptic-lanceolate, pinnatifid with deltoid, obtuse lobes; involucres 13–15 mm high; inner bracts strictly 8, somewhat acute at the apex; florets 12–16; outer bracts narrowly deltoid, the longest about 1/2 the length of the inner; achenes 6.8–7.5 mm long, somewhat contracted at the apex; pappus 10–11 mm long; ($2n = 33$?). CALIFORNIA: Lake City, Modoc County, alt. 1515 m, *B. & S. 1796* (UC); Black Mtn., Lassen County, alt. 1935 m, *S. & J. 2318* (UC); Last Chance Creek, Plumas County, *Swift* in 1931 (UC); northeast of Sattley, Sierra County, alt. 1600 m, *B. & S. 1632, 1648* (UC).

Related to apm. *media*.—OREGON: between Fort Klamath and Summit, Klamath County, *Furlong et al.* in 1901 ($2n = 44$ or 55 ?) (UC); Lakeview, Lake County, alt. 1400 m, *B. & S. 1857* ($2n = 55$?) (UC). CALIFORNIA: Big Valley Mtns., Lassen County, alt. 1120–1300 m, *S. & J. 2352, 2359* ($2n = 77$ of 88 ?) (UC).

20. apm. *brevis* (*occidentalis-pleurocarpa-monticola*).—Stems 1.7–2 dm high; basal leaves broadly elliptic, 8–12 cm long, 3–4 cm broad, merely dentate or with short, deltoid lobes; heads 7–15 in an inflorescence; involucre 12.5–14 mm high; outer bracts narrowly deltoid, acute to acuminate, the longest 4.5–5 mm long; florets 12–15; achenes 6–7 mm long, more or less contracted at the apex, deep brown or chocolate colored; pappus 9–10 mm long; ($2n = 55$?). CALIFORNIA: Forest House Mtn., near Yreka, Siskiyou County, alt. 1363 m, *B. & S. 1901* (UC); Saddle Mtn., near Fall River Mills, Shasta County, alt. 1300–1500 m, *S. & J. 2387* (UC); Burney, Shasta County, alt. 1060 m, *S. & J. 2403* (UC); head of Stony Ridge, alt. 1930 m, Lassen County, *S. & J. 2304* (UC).

This form is in habit and achenes typical of *C. occidentalis*, but the rather short outer bracts and fewer-flowered involucres suggest a transition to *C. pleurocarpa*.

Related to apm. *brevis*.—CALIFORNIA: Big Valley, Lassen County, alt. 1050 m, *S. & J. 2362* (UC); Castella, Siskiyou County, *Piper 6386* (G). OREGON: Summer Lake, Lake County, *Peck 15680a* (Will); Burns, Harney County, *Peck 3980, 4144* (Will). IDAHO: Falk's Store, Canyon County, alt. 670 m, *Macbride 61* ($2n = 44$?) (UC, DS, G, Minn).

This specimen bears a few glands on the involucre, and hence is somewhat transitional toward subsp. *costata*.

21. apm. *glabrescens* (*occidentalis-pleurocarpa-monticola*).—Stems 2.5–3.5 dm high; basal leaves 15–25 cm long, elliptic in outline, pinnatifid with angular, acute, irregularly dentate or incised lobes; inflorescence with 16–20 heads; involucre 13–16 mm high; inner bracts strictly 8, pale green, acute at the apex; florets 8–15; outer bracts narrowly deltoid, the longest 1/3–2/5 the length of the inner; achenes pale brown, 7–7.5 mm long, somewhat contracted at the apex; pappus 9.5–10.5 mm long; ($2n = 55$?). CALIFORNIA: south of Yreka, Siskiyou County, alt. 810 m, *B. & S. 1932, 1938* (UC); near Fort Bidwell, Modoc County, *Manning 181* (UC); Susanville, Lassen County, alt. 1250 m, *S. & J. 2196* (UC); Burney, Shasta County, alt. 1060 m, *S. & J. 2409* (UC); Campbell's Hot Springs, Plumas County, *Head* in 1921 (CA); Mt. Hull, Lake County, alt. 2050 m, *Hall 9533* (UC, US, G).

Related to apm. *glabrescens*.—CALIFORNIA: Big Valley, Lassen County, alt. 1050 m, *S. & J. 2362A* (UC); Champ's, Lassen County, alt. 1720 m, *S. & J. 2339* (UC); Dinsmore's Ranch, between Van Duzen and Mad Rivers, alt. 1060 m, Humboldt County, *Tracy 4256* (UC, US). OREGON: Ashland, Jackson County, *Peck 3981, 4140* (Will). NEVADA: Verdi, Washoe County, alt. 1360 m, *S. & J. 2175* (UC). IDAHO: Twin Falls, Twin Falls County, *Bennett 74* (RM).

22. apm. *multiceps* (*occidentalis-pleurocarpa-monticola?*).—Basal leaves 16–23 cm long, elliptic, pinnatifid with short, broadly or narrowly deltoid, acute, dentate lobes; stems 2.5–3.8 dm high; heads mostly numerous, 15–30 in an inflorescence; involucres 12–14 mm high; inner bracts 8; florets 10–14; outer bracts deltoid, the longest about 2/5 the length of the inner; *achenes 5.5–6.5 mm long;* pappus 9–10 mm; ($2n = 44$?) CALIFORNIA: Yreka, Siskiyou County, alt. 810 m, *Butler 1365* (UC, DS, CA, US, Po, RM). OREGON: Takilma, Josephine County, *Peck 8015* (G. Will).

This form is very close to both *C. intermedia* and *C. pleurocarpa*. Some of the specimens of related forms cited below could just as easily be classified with the latter species, which they resemble considerably in habit.

Related to apm. *multiceps*.—CALIFORNIA: Goose Valley, Shasta County, *Eastwood 827a* ($2n = 33$?) (CA); Sisson (Mt. Shasta), Siskiyou County, *Eastwood 1188* ($2n = 55$?) (CA); Forest House Mtn., alt. 1210 m, Siskiyou County, *B. & S. 1898, 1900, 1903, 1904* ($2n = 33$ and 44 ?) (UC). OREGON: Dead Indian Road, Jackson County, *Peck 16734* (Will).

23. apm. *olympica* (*occidentalis-acuminata-modocensis*) (fig. 21*p*, *q*).—Stems 1–2.6 dm high; leaves narrowly elliptic, deeply pinnatifid, the lobes rather remote, acute, sharply and irregularly dentate; branches of the inflorescence strongly ascending; involucres 13–17 mm high, inner bracts 7–8, *bearing a few glandular trichomes;* florets 10–14; outer bracts narrowly deltoid, the longest 4.5–6 mm long, 1/3–2/5 the length of the inner; achenes 8–9 mm long, very slightly contracted and truncate at the apex; pappus 9–10 mm; ($2n = 55$?) (see p. 44). WASHINGTON: Olympic Mtns., Clallam County, *Elmer 2621* (DS, Minn); Mt. Angeles, Olympic Peninsula, alt. 1670 m, *Jones 3168, 3330* (Wn); Hurricane Ridge, Olympic Peninsula, alt. 1360 m, *Jones 3215* (Wn).

This form, endemic to the Olympic Peninsula, is in habit nearest to apm. *Rydbergii* and its allies, but differs from it in possessing a few glandular trichomes on the involucres, and may be considered transitional to subsp. *typica*, apm. *Nuttallii*, which it also resembles in habit.

12*d*. **Crepis occidentalis** subsp. **conjuncta** (Jepson) comb. nov. (Fig 22*a–c*).—Humilis; folia 10–18 cm longa, pinnatifida, segmenta remota, lanceolata, ad apicem adscendentia, acuta vel acuminata, integra vel remote et acute dentata; caules 0.5–1.8 dm alti, ad basim ramosi; rami divergentes; capitula 2–9 pro inflorescentia, saepe longe pedunculata, tomentulosa sed non setosa vel glandulosa, 12–18 mm longa; involucri phylla interiores 8–13, exteriores anguste deltoidea, longiora, (6–)7–9 mm longa; achænia ut in præcedentibus.

Low; stems 0.5–2 dm high; leaves 10–18 cm long, pinnatifid, segments remote, lanceolate, curved upwards toward the apex, acute or acuminate (rarely obtuse), entire or remotely and acutely dentate; stems 0.5–1.8 dm tall, branching from near the base, the branches divergent but erect toward the apex; heads 2–9 in an inflorescence, mostly on long peduncles; involucres tomentulose but not at all glandular or setose; inner bracts 8–12; outer bracts narrowly deltoid (or sometimes elliptic deltoid), the longest 6–9 mm long, 1/2–2/3 the length of the inner; achenes and pappus as in the preceding subspecies. (*C. occidentalis* var. *conjuncta* Jepson, in herb., *C. occidentalis* var. *nevadensis* Kellogg, Proc. Cal. Acad. Sci. 5:50, 1873 in part (?); Gray, Syn. Fl. 1 (2):432, 1884.

Sierra Nevada, and the mountains of northern California and southwestern Oregon, where it passes into subsp. *pumila*, also the mountains of central and southeastern Washington, and of northwestern Wyoming.

This is a most striking subspecies, combining, as its name implies, the habit and elongate outer involucral bracts of *C. Bakeri* or of *C. modocensis* with a leaf shape most characteristic of *C. modocensis*, but with the pubescence and achene characters just as in *C. occidentalis* subsp. *pumila*. Through apm. *Jepsonii* it passes into the smaller forms of subsp. *pumila*, while through apm. *pluriflora* it passes into *C. modocensis* subsp. *subacaulis*.

This was probably included by Kellogg in his description of *C. occidentalis* var. *nevadensis*, and certainly was considered to be this variety by both Gray and Coville, since a duplicate of it in the U. S. National

Herbarium was so identified by Coville, and another identical collection from the same locality (Bolander and Kellogg in 1872) in the Gray Herbarium was similarly identified by Gray. However, the specimens of both of these collections are just coming into bloom, and no achenes, mature or immature, are available on them. Kellogg's description of the achenes of his var. *nevadensis* must have been based on some specimen now lost, but similar to one collected by him July 10, 1870, on the "Summit of the Sierra Nevada." The latter specimen was considered by Coville to be identical with the type of var. *nevadensis*, although it was not mentioned in Kellogg's description. Its achenes are ribbed or merely striate, and definitely exceed the pappus in length. This is in accordance with Kellogg's description of var. *nevadensis*, but they are not similar to those of subsp. *conjuncta*, which are well shown by Jones' collection from Soda Springs, some plants of which are undoubtedly the same form as those of the Kellogg collection (see fig. 22c). They are reddish brown, strongly ribbed, and definitely shorter than the pappus, i.e., just like those of typical *C. occidentalis*.

In its habitat subsp. *conjuncta* differs considerably from the other subspecies of *C. occidentalis*. It prefers forested areas with a relatively high precipitation, and in the Sierra Nevada is locally frequent on the west slope at middle altitudes, where it is often the only form of *Crepis* found, since the other subspecies occur mostly in the open valleys and brush-covered hills on the east side of these mountains.

The name was suggested by Dr. W. L. Jepson, who recognized the distinctness of this form as represented by Chandler's collection from Marble Mountain, although he never described it. The Chandler collection, although it was designated by Jepson as the type of *C. occidentalis* var. *conjuncta*, has not been retained as such by the present authors, because it is not absolutely characteristic of the subspecies as conceived by us, being more or less transitional in its more numerous heads and relatively shorter involucral bracts to subsp. *pumila*. Of the considerable number of specimens from the Sierra Nevada which we consider to be typical of subsp. *conjuncta*, we have selected that of Kellogg as being the oldest and the best known.

C. occidentalis conjuncta—key to apomictic forms *(see p. 69)*

A. Leaves not unusually thick in texture, their lobes mostly acute; involucral bracts lance-linear, gradually attenuate to the apex, the broadest 2.5–3 mm broad.
  B. Largest heads of the inflorescence with 9–13 inner bracts; flowering stems equaling or barely exceeding the leaves in length..... 24 apm. *pluriflora*
  B. Largest heads of the inflorescence with 8 inner bracts; flowering stems definitely longer than, mostly about 1 1/2 times as long as, the leaves.
    C. Heads on elongate peduncles; involucres 14–16 mm high; longest outer bracts 1/2–2/3 the length of the inner..... 25. apm. *tenuis*

C. At least some of the heads on short, divaricate peduncles; involucres 12–14 mm high; longest outer bracts 2/5–1/2 the length of the inner.. 26. apm. *Jepsonii*

A. Leaves thick in texture, their lobes obtuse; involucral bracts elliptic-lanceolate, sharply contracted to the acute apex, the broadest 3.5–4 mm broad..... 27. apm. *crassa*

24. apm. *pluriflora* (*occidentalis-modocensis-Bakeri-pleurocarpa?*) (fig. 22*a–c*).—Leaves typical of the species; flowering stems 0.8–1.5 dm high, about equaling the leaves in length; heads on peduncles 1–4 cm long; involucres 14–16 mm high; larger heads with 10–13 inner bracts and 20–30 florets; achenes 7–8.5 mm long, definitely contracted at the apex; pappus 9–10 mm; ($2n = 44$?). CALIFORNIA: Camp Yuba, Cisco, Placer County, *Kellogg*, June 18, 1870 (type of subsp. *conjuncta*, UC no. 31318, US, G, DS); Soda Springs, Nevada County, alt. 2120 m, *Jones* in 1881, part (Po); Dardanelles Mtn., Alpine County, alt. 2200 m, *Eggleston 9943* (US); Deer Park, Placer County, *Geis 33* (UC); Tahoe City, Placer County, *Eastwood 460* (Ca, Clo); Truckee, Nevada County, *Sonne* in 1884 (UC); Hobart Mills, Nevada County, *Drew* in 1925 (DS); Gray Eagle resort, Plumas County, *B. 153, 154* (UC). WASHINGTON: Beverly Creek, Kittitas County, *Thompson 6635* (G, Mo).

Related to apm. *pluriflora*.—CALIFORNIA: Black Mtn., south of Milford, Lassen County, alt. 1940 m, *S. & J. 2319* (UC); Mt. Sanhedrin, Mendocino County, *Blankinship* in 1893 ($2n = 44$?) (US).

25. apm. *tenuis* (*occidentalis-Bakeri* or *modocensis-pleurocarpa*).—Leaves about as in the last, but the lobes somewhat broader, and more or less reflexed; flowering stems definitely exceeding the leaves, slender and flexuous; peduncles up to 6 or 7 cm long; involucres 14–16 mm high; inner bracts 7–8 or rarely 9; achenes 8.5–9.5 mm long; pappus 10.5–11.5 mm; ($2n = 44$?). CALIFORNIA: Clark's Fork Ranger Station, Alpine County, alt. 1660 m, *Eggleston 9542* (US); Lake Valley, Eldorado County, *Baker* in 1904 (UC); near Cisco, Placer County, alt. 1880 m, *Hall 8743* (UC); near Butte Creek Meadows, Butte County, *Copeland 1532* (UC).

Near apm. *tenuis*.—CALIFORNIA: near Camp Baxter, Tuolumne County, alt. 1670–1730 m, *Stanford 1063* (US); Avery, Calaveras County, alt. 1000 m, *Eggleston 9278* (US); Lassen's Peak, alt. 1820 m, *Jones* in 1897 (Po); Humboldt County, *Rattan* in 1878 (DS). WYOMING: Cement Creek, alt. 2420 m, Teton Forest Reserve, Lincoln County, *Tweedy 602* (NY).

The last-named specimen shows a strikingly close resemblance to those from California. It is the only one of this subspecies seen from the Rocky Mtn. region, so that further records of its occurrence there would be of great interest (see p. 000).

26. apm. *Jepsonii* (*occidentalis-pleurocarpa-Bakeri*).—Similar to apm. *tenuis* except that the peduncles are shorter, involucres are smaller (12–14 mm high), and the longest outer bracts are only 1/3–2/5 the length of the inner; achenes brown, 6–7 mm long; pappus 9 mm long; ($2n = 44$?). CALIFORNIA: Marble Mtn., Siskiyou County, alt. 2500 m, *Chand-*

ler 1644 (DS, US, G, Minn, Mo); Salmon Summit, Siskiyou County, *Kildale 5374* (DS). OREGON: Near Siskiyou, Jackson County, *Sherwood 602* (Will); west of Waldo, Josephine County, *Peck 8267* (Will).

This form is transitional toward subsp. *pumila*, and some of the plants of the Chandler collection approach that subspecies in their relatively tall stems and more numerous heads.

Related to apm. *Jepsonii*.—CALIFORNIA: Dorleska, Trinity County, *Hall 8597* ($2n = 77$ or 88 ?), part (DS); near summit of ridge south of Milford, Lassen County, alt. 1700 m, *S. & J. 2230* (UC).

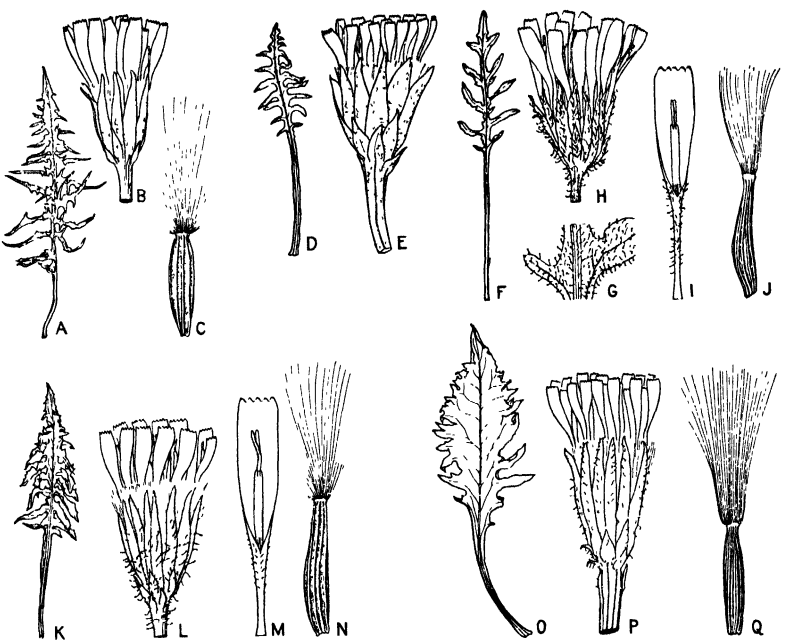


FIG. 22. *a–e, Crepis occidentalis* subsp. *conjuncta*. *a–c*, apm. *pluriflora—a, b,* from *B. 154*; *c*, from *Geis 33*: *a*, leaf, × ¼; *b*, involucre, × 1, *c*, achene, × 2. *d, e,* apm. *crassa*, from *St. John and Smith 8372*: *d*, leaf, × ¼; *e*, involucre, × 1. *f–g, Crepis Bakeri*. *f–j*, subsp. *Cusickii*, diploid form, from *Smith 699*: *f*, leaf, × ¼; *g*, detail of surface, ×1; *h*, involucre, × 1; *i*, corolla, × 2; *j*, achene, × 2. *k–n*, subsp. *typica*, from *Kennedy 1634*: k, leaf, × ¼; *l*, involucre, × 1; *m*, corolla, × 2, *n*, achene, × 2. *o–q*, subsp. *idahoensis*, from type: *o, leaf*, × ¼; *p*, involucre, × 1; *q*, achene, × 2.

27. apm. *crassa* (*occidentalis-Bakeri-pleurocarpa*) (fig. 22*d, e*).—Similar to apm. *multiflora;* stems 0.7–1 dm high; leaves thick, the lobes obtuse; peduncles somewhat swollen at the apex; involucres 14–18 mm high, the bracts dark lead color; outer bracts elliptic, acute, the longest 7–8 mm long; inner bracts 8–10 or 12, elliptic-lanceolate, the broadest 3.5–4 mm broad; florets 12–20 per head; achenes 8–8.5 mm long; pappus 9.5–10 mm; ($2n = 77$ or 88 ?) (see p. 43). WASHINGTON: Stayawhile

Springs, Columbia County, alt. 1670 m, *St. John & Smith 8372* (UC, WSC); Blue Mtns., Asotin County, *Jones 1926* (WSC).

Near apm. *crassa*.—CALIFORNIA: Goose Valley, Shasta County, *Eastwood 769* (CA).

This apomict is near apm. *pluriflora*, but has certain distinctive characteristics. Some, such as the thickness of the leaves and the stoutness of the stems and peduncles, are due to its high polyploid condition, but others, such as the shape of the leaves and involucral bracts, the swollen peduncles, and the apparent presence of reddish pigment, are strongly suggestive of *C. Bakeri*. This fact, along with its close resemblance to California forms of the subspecies, is strong evidence that this outlier of subsp. *conjuncta* is derived from the Klamath region (see p. 000).

13. **Crepis Bakeri** Greene, Erythea 3:73, 1895 (Fig. 22*f–g*)

Plant perennial, 8–30 cm high, with 1–3 stout stems from each caudex, divaricately branching from near the base, glabrate or glandular-hispid; leaves green, sparingly tomentulose, covered with short, glandular trichomes, mostly deeply pinnatifid with obtuse or acute, lanceolate or narrowly elliptic coarsely dentate segments, the midrib conspicuously reddish in living specimens; heads 1–22 in an inflorescence, on stout peduncles which are expanded toward the apex; involucres 11–20 mm high, the bracts numerous, dark green, lightly tomentulose and conspicuously glandular-hispid; outer bracts lanceolate or deltoid, acute or acuminate, the longest generally 1/2–2/3 the length of the inner; inner bracts 10–14, acuminate or somewhat attenuate at the apex; slightly or not at all thickened at maturity; florets 11–40 or more; corollas, anthers, and style branches as in *C. occidentalis;* achenes chocolate brown or paler, sometimes yellowish, 5–10 mm long, 1.2–1.8 mm thick, the apex more or less contracted or subrostrate, costæ medium or strong; pappus setæ 7.5–13 mm long.

Central Washington and eastern Idaho locally south through central Oregon to northern California (see fig. 23).

This species is, on the basis of its achenes, closest to *C. occidentalis*, but it differs not only in its green, sparingly tomentose leaves with conspicuous reddish midribs, but also in its fewer-headed inflorescence, broader involucres, and in particular the swollen apices of the peduncles and the lack of thickening of the mature involucral bracts. In leaf shape, the character of its inflorescence, and the shape of its involucres it suggests *C. modocensis*, while in its glandular-hispid indumentum and the swollen apices of its peduncles it approaches *C. monticola*. Its ecological requirements are intermediate between those of *C. monticola* and *C. modocensis*. Like them it is distinctly a montane species, as opposed to *C. occidentalis*, which occurs more often on the lower slopes and valley terraces. It is found in more arid, less heavily wooded areas than is *C. monticola*, but usually not in as exposed situations as *C. modocensis*, although it often grows together with the latter in the region about Sierra Valley and southwest of Honey Lake.

Three subspecies can be recognized as follows:

A. Involucres broadly cylindric or cyathiform; outer bracts lanceolate, the longest 1/2–2/3 the length of the inner; inner bracts lanceolate, acute, their midribs not thickened at maturity; pappus about equaling or shorter than the achenes.
  B. Involucres in flower 14–17 mm. in fruit 16–20 mm high; pappus at flowering time 9–12 mm long; achenes slightly contracted at the apex.. *a. typica*
  B. Involucres in flower 10–15 mm, in fruit 13–17 mm high; pappus 6–9 mm long; mature achenes strongly attenuate or subrostrate at the apex... *b. Cusickii*
A. Involucres narrowly cylindric or turbinate, 18–21 mm high in fruit; outer bracts deltoid, the longest 1/3–2/5 the length of the inner; inner bracts lanceolate or linear, attenuate at the apex, their midribs thickened at maturity; pappus 12–13 mm long, much exceeding the achenes..... *c. idahoensis*

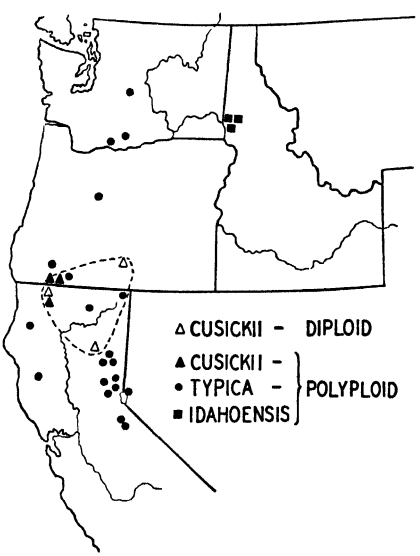


FIG. 23. Distribution of *Crepis Bakeri*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

13*a* (1). **Crepis Bakeri** subsp. **typica** nom. nov. (Fig. 22*k–n.*)—Habit, leaves, etc. as described above for the species; heads 1–12 in an inflorescence; involucres broadly cylindric or cyathiform; bracts lanceolate, rather evenly imbricate, the longest 1/2–2/3 the length of the inner; inner bracts more or less unequal, lanceolate, acute, their midribs not thickened at maturity; pappus about equaling or shorter than the achenes. (*Crepis Bakeri*, Greene, loc. cit.).

Range of the species, except in Idaho.

This subspecies contains only polyploid forms, most of which are apparently tetraploid. No distinct *formæ apomicticæ* could be recognized, perhaps because the degree of variation within the subspecies is relatively slight, perhaps because the collections are from too widely scattered localities, and possibly because apomixis is less strongly developed in this species.

The type specimen of *C. Bakeri*, although originally cited as in the University of California Herbarium, was apparently removed by Greene when he left that institution, and is now in the Greene Herbarium at Notre Dame. An excellent photograph of this type was sent to the writers by Dr. Th. Just, curator of this herbarium, and its identity with the specimens cited is unquestionable. The following specimens have been seen: CALIFORNIA: Egg Lake, Modoc County, *Baker & Nutting* in 1893 (type of *C. Bakeri*, photo in UC); Bald Peak, Alpine County, alt. 2700 m, *Hoover 1423* (UC); Wheats Meadow Ranger Station, Tuolumne County, alt. 2000 m, *Eggleston 9353* (US); Summit, Placer County, *Eastwood* in 1898 (CA); Sardine Peak, Sierra County, *B. 141, 142, 143* (UC); Beckwith Peak, Plumas County, alt. 1700 m, *S. & J. 2149* (UC); between Diamond Mtn. and Red Rock, Plumas and Lassen Counties, alt. 2150–2270 m, *S. & J. 2260* (UC); Fort Bidwell, Modoc County, alt. 1510 m, *Manning 471* (UC, US); Goosenest foothills, Siskiyou County, alt. 1500 m, *Butler 1328* (UC, DS, G, RM); South Fork Mtn., Trinity County, alt. 1060 m, *Tracy 6513* (UC); east of Round Valley, Mendocino County, *Rattan* in 1884, part (DS, G). The last three transitional toward subsp. *Cusickii*. NEVADA: Dinsmore Camp, Hunter Creek, alt. 1820 m, *Kennedy 1634* (UC, DS, US). OREGON: near head of Kean Creek, Jackson County, alt. 1550 m, *Applegate 2300* (DS, US); Rogue River, Jackson or Josephine County, *Austin* in 1893 (UC); Grizzly Butte, Crook County, alt. 1250 m, *Leiberg 219* (UC, US). WASHINGTON: without locality, *Vasey 548* (US); hillsides near Lyle, Klickitat County, *Suksdorf 875* (UC, US); north of Ellensburg, Kittitas County, alt. 550 m, *Keck & Clausen 3530* ($2n = 45$!) (UC).

13*b*(2). **Crepis Bakeri** subsp. **Cusickii** (Eastw.) comb. nov. (Fig. 22*f–j*.)—Similar to subsp. *typica*, but smaller throughout; involucres in flower 10–15 mm, in fruit 13–17 mm high; pappus 6–9 mm long; mature achenes strongly attenuate or subrostrate at the apex. (*Crepis Cusickii* Eastwood, Bull. Torr. Bot. Club 30:503, 1903.)

Northern California and southern Oregon.

This subspecies contains the diploid form, as well as forms apparently triploid but morphologically indistinguishable from the former. It is distinguished from *C. Bakeri* by very few characteristics except for the smaller size of both its vegetative and floral parts, but since these differences are associated with a definite, relatively restricted geographic range, its recognition as a subspecies seems advisable. The following specimens have been seen:

Diploid form.—CALIFORNIA: north of Hornbrook, Siskiyou County, *Collins 2220* ($2n = 22$!) (UC); Yreka, Siskiyou County, *Smith 699* (US, CA); between Bogard Ranger Station and Harvey Valley, T. 32 N.,

R. 8 E., alt. 1630 m, Lassen County, *S. & J. 2331* ($2n = 22$!) (UC). OREGON: south of Bulls Prairie, Lake County, *Loveless 146* (UC).

Triploid forms.—CALIFORNIA: Hilt, Siskiyou County, *Smith* in 1915 (US, CA); north of Susanville, Lassen County, *Gillespie 9337* (DS). OREGON: 15 miles east of Ashland, alt. 1200 m, *Cusick 2872* (type collection of *C. Cusickii*, UC, DS, G, Po, Minn); top and south slope of Siskiyou Mtns., along Pacific Highway, Jackson County, *Henderson 12910* (UC).

13*c*(3). **Crepis Bakeri** subsp. **idahoensis** subsp. nov. (Fig. 22*o–q*).—Planta 2.5–3 dm alta; folia elliptica, pinnatifida, lobis brevibus acuminatis mucronatis, dentatis; capitula 11–17 pro inflorescentia; involucra anguste cylindrica vel turbinata, phyllis exterioribus deltoideis, interioribus lanceolatis vel linearibus, attenuatis; pappi setæ achæniis valde longioris.

Stems 2.5–3 dm high; basal leaves 15–18 cm long, 5–5.5 cm broad, elliptic, shallowly pinnatifid with short deltoid acuminate mucronate dentate lobes, sparingly tomentulose and sparsely and minutely glandular-hirsute; cauline leaves similar, the lobes more strongly mucronate; inflorescence of 11–22 heads, the peduncles conspicuously expanded toward the apex; involucres at flowering time 16–18 mm, in fruit 18–21 mm high; florets 18–25; outer bracts deltoid, acute or acuminate, the longest 1/3–2/5 the length of the inner; inner bracts 8–13, lanceolate or linear, attenuate at the apex, grayish-tomentulose at the base and conspicuously glandular-hispid throughout, the midrib becoming thickened at maturity near the base; achenes chestnut brown, 7.5–8 mm long, rather strongly contracted toward the apex; pappus setæ 12–13 mm long; ($2n = 55$?). IDAHO: valley of Clearwater River, Nez Perces County, *Sandberg, MacDougal, & Heller 268* (type G, Minn, RM); near Culdesac, Nez Perces County, *Warren* in 1932 (WSC); Lake Waha, Nez Perces County, *Henderson* in 1894 (RM); Lewiston, alt. 400 m, *Hitchcock & Samuel 2533* (RM, CA).

This subspecies, although represented by collections from only a restricted region, is so strikingly different from any other form of either *C. Bakeri* or *C. occidentalis* that it deserves recognition. In its leaf shape and the thickening of its inner bracts it approaches *C. occidentalis*, but the lack of tomentum, the glandulosity, and the swollen peduncles are characteristic of *C. Bakeri*. Furthermore, it differs from the only forms of *C. occidentalis* occurring in the vicinity in its much more numerous inner bracts and florets. In the shape of its involucres, inner bracts, and achenes it suggests *C. monticola*. It is apparently an allopolyploid derivative of complex origin, involving *C. Bakeri*, *C. occidentalis*, and probably also *C. monticola*. The specimens from Lake Waha and Culdesac belong to the same *forma apomictica* as the type, while that from Lewiston differs in its less attenuate inner bracts, and is therefore transitional toward *C. occidentalis* subsp. *costata*.

14. **Crepis modocensis** Greene, Erythea 3:48, 1895 (Figs. 25, 26)

Stems 0.5–4.5 dm high, stout, glabrate or tomentose, the basal part or occasionally the entire stem covered with spreading glandless setæ or

trichomes; basal leaves 7–25 cm long, glabrate or tomentose and generally setose along the petioles and midribs, deeply pinnatifid with lanceolate, toothed, or again pinnatifid segments, the ultimate segments or teeth acute or acuminate, tipped with a hard, corneous mucro; heads 1–10 in an inflorescence; involucres 11–21 mm high; inner bracts 8–18, glabrate or tomentulose and (except in a few forms of subsp. *subacaulis*) bearing blackish or whitish glandless trichomes along the midrib; outer bracts lanceolate or narrowly deltoid, the longest mostly 1/2–2/3 the length of the inner; florets 10–60; corollas 13–22 mm long; style-branches 2.5–3.5 mm long; achenes 7–12 mm long, blackish, greenish, or (chiefly in forms of subsp. *subacaulis*) brownish or reddish, distinctly attenuate or rostrate at the apex, with about 10 low and relatively indistinct ribs; pappus setæ 5–13.5 mm long, mostly shorter than or equaling the achene.

Montana to southern British Columbia and central Washington, south to Colorado, Utah, Nevada, and in the mountains to southern California (see fig. 24).

Four subspecies may be recognized:

A. Trichomes on the stem and petioles stiff, yellowish, those on the involucres blackish, all straight or slightly curved, not conspicuously crisped (in some forms of subsp. *subacaulis* whitish and crisped, but these have brownish achenes).
  B Stems low or tall, rather slender and generally branching from 1/3 of the way up or higher; largest involucres of the inflorescence 13–16 mm high in fruit; pappus setæ 5–10 mm long..... *a. typica*
  B Stems low and rather stout, generally branching from near the base; largest involucres of the inflorescence 15–21 mm high in fruit; pappus setæ 9–13.5 mm long..... *b. subacaulis*
A Trichomes all or nearly all whitish, elongate, and conspicuously curled or crisped; those on the involucres generally very dense; achenes always greenish or blackish.
  C Stems 1.5–3 dm tall; involucre 14–17 mm high; corollas 18–22 mm long; achenes more or less beaked, 7–10 mm long; pappus setæ 7–10 mm long ..... *c. rostrata*
  C Stems 0.6–1.3 dm tall; involucre 11–13 mm high; corollas 14–16 mm long; achenes merely attenuate at the apex, 6–7 mm long; pappus setæ 5.5–6.5 mm long..... *d. glareosa*

14*a*. **Crepis modocensis** subsp. **typica** nom. nov. (Fig. 25.)—Plants variable in size and habit, but always with a well-developed primary axis; involucres 11–16 mm high, their bracts always setose throughout their length; achenes 7–12 mm long, weakly striate or nearly smooth, varying from greenish black to deep reddish brown, distinctly exceeding the pappus; pappus 5–10 mm long. (*Crepis modocensis* Greene, loc. cit., 1895; *C. scopulorum* Coville, Contr. U. S. Nat. Herb. 3:563, pl. XXIV, 1896.)

Range of the species, except that it is replaced by subsp. *subacaulis* in central and southern California, and by subspp. *rostrata* and *glareosa* in central Washington.

The type collection of *C. modocensis*, i.e., lava beds, Modoc County, California, Mrs. R. M. Austin in 1894, includes two different forms. One, a relatively tall plant with very few setæ on the base of the stem and petioles, and with an inflorescence of rather numerous heads for this

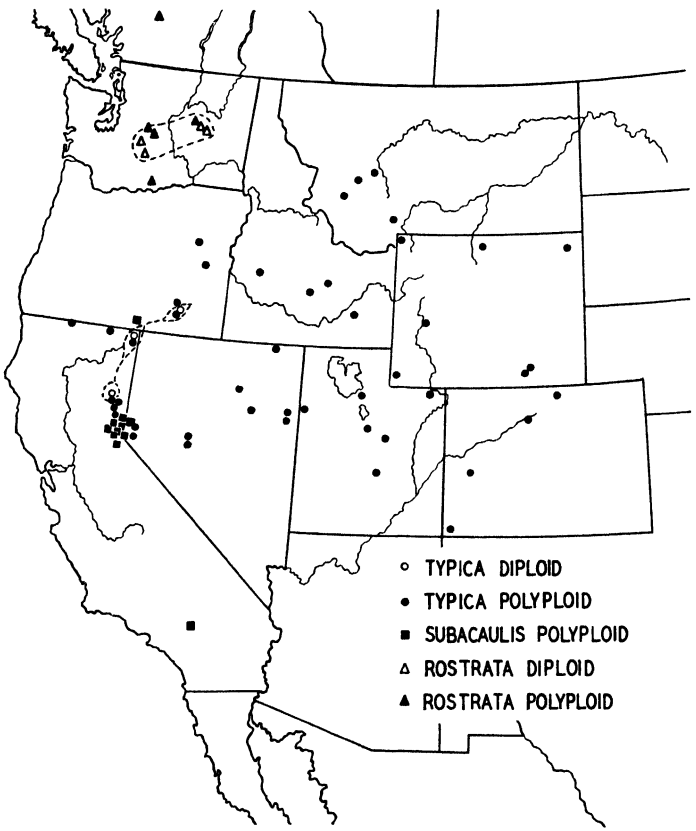


FIG. 24. Distribution of *Crepis modocensis*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

species, fits best Greene's description, and may be taken as the type. It is listed below as a relative of apm. *pauciflora*. In habit it is more or less transitional from the most characteristic forms of *C. modocensis*, i.e. the diploid form, to *C. intermedia*, although it has the relatively numerous bracts and florets found in other forms of *C. modocensis*. No achenes are present on the specimens of this taller plant. The other form in the type collection, described below as apm. *Austinæ*, is lower

and with fewer heads, and is more densely setose on the petioles and the lower part of the stem. It is rather close to the type of *C. scopulorum* Coville, from which it differs chiefly in its heavier tomentum. It is in the latter respect, and to some extent in leaf shape, transitional toward *C. occidentalis* subsp. *pumila*. Its immature achenes are typical of *C. modocensis* in shape, but are slightly more costate and more reddish, although they might be more typical of the species in color when mature.

Coville (Contr. U. S. Nat. Herb. 3:562, 1896) referred *C. modocensis* doubtfully to his *C. subacaulis* "on account of its pubescence, achenia, and the form of its leaves." He then suggested that a fuller series of specimens than that available to him might show intergradation between the latter species and his *C. scopulorum*. In the opinion of the writers, this intergradation has been found to such an extent that the two species must be merged. Furthermore, the characters of leaf shape and pubescence mentioned by him have not proved to hold at all as valid criteria for separating the two forms, and the taller race of the type collection of *C. modocensis* has leaf segments as narrow as those in plants referred by Coville to *C. scopulorum*. Furthermore, the types of *C. scopulorum* and *C. modocensis* are in habit, in the size of the involucres and florets, and in the length of the pappus setæ much more nearly alike than either is to typical material of *C. subacaulis*. Hence *C. modocensis* is, in the opinion of the writers, best regarded as synonymous with *C. scopulorum* rather than with *C. subacaulis*. In any case, Greene's name antedates both of Coville's specific names by a year, and must therefore be retained.

The original, diploid form of *C. modocensis* subsp. *typica* is a low plant, with slightly tomentulose but densely setose stems and leaves, an inflorescence of 1–4 heads, which are many-bracted and many-flowered. The achenes are blackish, slender, obtusely and indistinctly costate, and markedly tapering toward the pale apex. This form is known only from three separate mountain ranges, the ridge southwest of Honey Lake, California, the Warner Mountains of northeastern California, and Stein's Mountains of southern Oregon, but forms morphologically similar that have the stomata and pollen of polyploids occur in neighboring regions. In addition there are polyploid forms transitional toward *C. acuminata*, to one of which the larger plants of the type collection belong, and others passing toward subsp. *subacaulis* and therefore toward *C. occidentalis*. The following is a key to such apomicts of subsp. *typica* as have been recognized. Since the writers have not studied most of them in the field, only a small number of them is included.

C. modocensis typica—key to apomictic forms *(see p. 69)*

A. All of the heads with a least 10–12 inner involucral bracts and 16 or more florets.
  B. Stems 6–16 cm (rarely up to 24 cm) tall, bearing 1–4 heads; involucres 11–14 mm high at anthesis; anther tube well developed and bearing pollen ..... { diploid forms / 1. apm. *simulans*

B. Stems 15–30 cm tall, bearing 3–8 heads.
  C. Anthers rudimentary and without pollen.
    D. Plants 15–23 cm high; involucres 11–14 mm high ..... 2. apm. *parviceps*
    D. Plants 30–40 cm high; involucres 13–15 mm high ..... 4. apm. *tenuifolia*
  C. Anthers well developed and bearing pollen.
    E. Leaves and involucres lightly tomentulose; longest outer bract 6.5–8 mm long 3 apm. *elatior*
    E. Leaves and involucres grayish-tomentulose; longest outer bracts 5–6.5 mm long ..... 5 apm. *Austinæ*
A. At least some of the involucres with only 8–10 inner bracts and 10–14 florets..... 6. apm. *pauciflora*

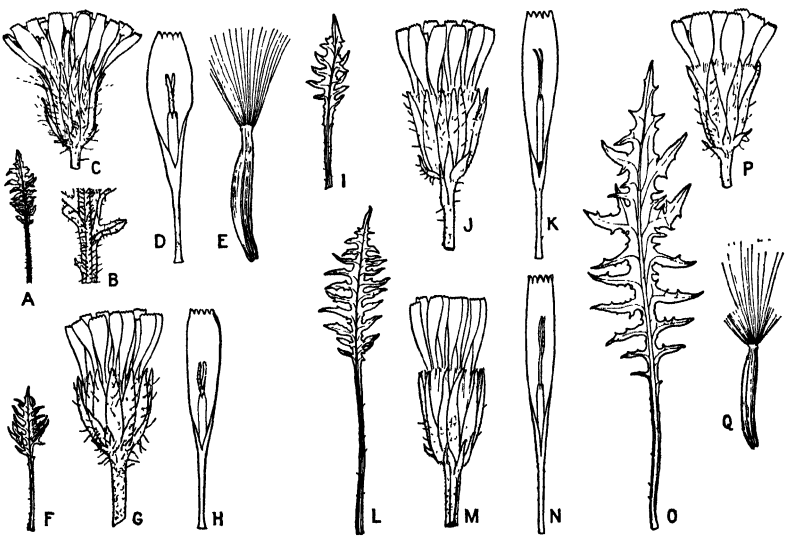


FIG. 25. *Crepis modocensis* subsp. *typica*. *a–e*, diploid form—*a–d*, from ***Bruce 2164***; *e*, from ***Cusick 1988***: *a*, leaf, × ¼; *b*, detail of surface, × 1; *c*, involucre, × 1; *d*, corolla, × 2; *e*, achene, × 2. *f–h*, apm. ***parviceps***, from ***Osterhout 3531***: *f*, leaf, × ¼; *g*, involucre, × 1; *h*, corolla, × 2. *i–k*, apm. ***Austinæ***, from ***Austin*** in 1894: *i*, leaf, × ¼; *j*, involucre, × 1; *k*, corrolla, × 2. *l–n*, near apm. ***pauciflora***, from ***Austin*** in 1894: *l*, *leaf*, × ¼; *m*, involucre, × 1; *n*, corolla, × 2. *o–q*, near apm. ***pauciflora***, from ***B. & S. 1806***: *o*, leaf, × ¼; *p*, involucre, × 1; *q*, achene, × 2.

Diploid form (fig. 25*a–e*).—This is characterized by its low stature, rather slightly tomentulose leaves, few heads on a plant, numerous inner bracts an florets, and deep greensh or blackish (not at all brownish or reddish) achenes. Only four collections of it are known: OREGON: Stein's Mtns., Harney County, *Cusick 1988*, part (UC). CALIFORNIA: Lake City Mtn., Modoc County, *Bruce 2164*, part (UC, DS); west of Cedarville, alt. 1515–1666 m, *B. & S. 1808A* (UC); Diamond Mtn., near Susanville, Lassen County, alt. 2200 m, *S. & J. 2276* (UC).

1. apm. *simulans*.—Similar to the diploid form, but with the stomata and pollen of triploids; ($2n = 33$?). OREGON: Stein's Mtns., *Cusick 1988*, part (UC, G, Po, Minn, RM). CALIFORNIA: Lake City Mtn., *Bruce 2164*, part (UC, DS); Diamond Mtn., near Susanville, Lassen County, alt. 2200 m, *Jones* in 1897 (Po); same locality, *S. & J. 2277* (UC). NEVADA: Jarbidge, Elko County, alt. 2120 m, *Nelson & MacBride 1932* (G, NY, Minn).

Related to apm. *simulans*.—CALIFORNIA: west of Cedarville, Modoc County, alt. 1515–1606 m, *B. & S. 1807A, 1808B* ($2n = 44$?), *1803, 1807B* ($2n = 33$?) (UC). NEVADA: Big Creek, Toiyabe Range, Lander County, alt. 2270 m, *Kennedy 4109* (UC).

2. apm. *parviceps* (*modocensis-acuminata?*) (fig. 25*f–h*).—Similar to the diploid form, but somewhat taller and with more numerous heads per plant; involucral bracts slightly broader and more abruptly contracted toward the apex; anther-tube rudimentary and without pollen; ($2n = 33$?). MONTANA: Mt. Ascension, *Brandegee* in 1898 (UC); St. Joe Creek, *Jones* in 1899, part (UC). WYOMING: Evanston, *Nelson 4548* (G, Minn); COLORADO: Sulphur Springs, Grand County, *Osterhout 3531* (DS, Minn).

Related to apm. *parviceps*.—MONTANA: Bozeman, Gallatin County, *Moore* in 1910 (UC); Yellowstone National Park, *Rose 680* (type of *C. scopulorum*, US); Mt. Helena, Lewis and Clark County, *Anderson* in 1887 (UC); Deer Lodge Valley, Deer Lodge County, *Jones* in 1905 (Po); east of Drummond, Granite County, *Hitchcock 2308* (CA). WYOMING: Indian Creek, Carbon County, *Goodding 95* (DS, Po, RM, Clo); west of Big Piney, Sublette County, *Payson 2609A* (RM); Big Horn County, *Worthley 16* (RM). IDAHO: Mackay, Custer County, alt. 1770 m, *Nelson & MacBride 1488* (G, Minn); Ketchum, Blaine County, *Nelson & MacBride 1233* (G, DS, Minn); Beaver Canyon, *Rydberg* in 1895 (NY, as *C. pumila*). UTAH: Scofield, Carbon County, *Jones* in 1904 (Po). OREGON: Juntura, Malheur County, *Henderson 8532* (CA). CALIFORNIA: near Lost Lake, Warner Mtns., Modoc County, alt. 2420 m, *Howell 12144*, part (CA); Stony Ridge, south of Milford, Lassen County, alt. 1930 m, *S. & J. 2298, 2299* (UC); Beckwith Peak, south of Beckwith, Plumas County, alt. 1670–1820 m, *S. & J. 2151* ($2n = 44$?) (UC). NEVADA: Spencemont, *Jones* in 1891 (Po).

3. apm. *elatior* (*modocensis-acuminata* or *exilis*).—Stems considerably taller than in the last, 18–30 cm tall; basal leaves 15–18 cm long, the lobes linear-lanceolate, acuminate; heads 4–7 on well-developed plants; involucre at anthesis 14–15 mm high; corollas 17–20 mm long; anther-tube well developed and bearing pollen; achenes 9–10 mm long; pappus setæ 8–9 mm long; ($2n = 44$?). IDAHO: Boise, alt. 870 m, *Clark 29* (UC, DS, G, NY, Po, RM, Minn).

Related to apm. *elatior*.—WYOMING: northwest of Hulett, Crook County, alt. 1150 m, *Ownbey 657* (WSC). UTAH: near Salina Experiment Station, Sevier County, *Keck 671* (UC, DS); Flaming Gorge, Daggett County, *Williams 524* (CA). OREGON: south of Burns, Harney County, *Henderson 8531* (CA). CALIFORNIA: Lost Lake, Warner Mtns.,

Modoc County, alt. 2420 m, *Howell 12144*, part (CA); Ager, Siskiyou County, *Brandegee* in 1887 (UC); near Sierraville, Sierra County, alt. 1800 m, *B. 130* (UC); along Truckee River, Nevada or Placer County, *Sonne* in 1885 (UC).

4. apm. *tenuifolia* (*modocensis-exilis*).—Stems 30–40 cm high; petioles and stems with few and small setæ; basal leaves sparsely tomentulose, the lobes narrowly lanceolate, falcate-ascending, entire or remotely toothed; heads 5–8 in an inflorescence; involucres at anthesis 13–15 mm high; longest outer bracts 5–6.5 mm long, 2/5–1/2 the length of the inner; anther-tube rudimentary and without pollen; mature achenes not seen; ($2n = 44$?). OREGON: Ochoco Forest, Peck *17091* (Will).

Related to apm. *tenuifolia*.—COLORADO: Sapinero, Gunnison County, *Wheeler 474* (RM). IDAHO: Pocatello, *Soth P242* (RM). OREGON: Fish Lake, Stein's Mtns., Harney County, *Henderson 8527* (CA).

5. apm. *Austinæ* (*modocensis-occidentalis-acuminata*) (fig. 25*i–k*).—Stems 15–25 cm tall; leaves densely grayish-tomentose, and setose on the midrib and petioles as well; lobes of leaves broadly lanceolate, obtuse, entire or nearly so; heads 3–7 in an inflorescence; involucre at anthesis 12–14 mm high, the bracts densely tomentose as well as setose; anthers well developed and bearing pollen; immature achenes 8 mm long, brownish, conspicuously striate; ($2n = 55$?). CALIFORNIA: lava beds, Modoc County, *Austin* in 1894, part (UC, US, type collection of *C. modocensis*).

Related to apm. *Austinæ*.—OREGON: Stein's Mtns., alt. 2350 m, *Leiberg 2493* (US).

6. apm. *pauciflora* (*modocensis-acuminata*).—Stems 25–35 cm high; basal leaves 15–20 cm long, loosely tomentose and conspicuously setose on the midrib and the principal veins below; lobes of leaves lanceolate, acute or acuminate, strongly toothed or again pinnatifid; heads 5–10 in an inflorescence; involucres 13–15 mm high, the larger (central) with 11–12 inner bracts and 20–27 florets; the smaller (lateral) with 8–10 inner bracts and 10–14 florets; longest outer bract 6–8 mm, 2/5–1/2 the length of the inner; anther-tube rudimentary and without pollen; achenes 9–10.5 mm long, reddish when immature, but becoming more or less blackish at maturity; pappus setæ 8–9 mm long; ($2n = 44$?). UTAH: Clifton, *Jones* in 1891 (Po); Dutch Mtn., Tooele County, alt. 1600 m, *Jones* in 1891 (Po). NEVADA: Palisade, Eureka County, *Jones* in 1882 (Po); Cave Creek, Elko County, *Mason 4752* (UC).

Related to apm. *pauciflora*.—MONTANA: Mammoth Hot Springs, Yellowstone National Park, *Nelson 5646* (G, NY, Minn). WYOMING: Fort Steele, Carbon County, *Nelson 7239*, part (RM, Po). COLORADO: near Livermore, Larimer County, *Osterhout* in 1897 (US, Minn, Po); Cerro Summit, alt. 2424 m, *Baker 148* (UC, DS, G, RM, Minn, Po); Park Point, Mesa Verde Park, alt. 2580 m, *Schmoll & Nusbaum 1589* (RM). UTAH: City Creek Canyon, Salt Lake City, *Garrett* in 1927 (UC); Mt. Nebo, eastern Juab County, alt. 2720 m, *Jones* in 1910 (Po). NEVADA: Aurum, White Pine County, alt. 2200 m, *Jones* in 1893 (Po); Reno, Washoe County, *Hillman* in 1894 (US, Po); near Carson City, Ormsby County, *Jones* in 1897 (Po). CALIFORNIA: lava beds, Modoc County,

Austin in 1894, part (type collection of *C. modocensis*, UC, US); west of Cedarville, Modoc County, alt. 1520 m, *B. & S. 1806* (UC) (see fig. 25*o–q*).

14*b*. **Crepis modocensis** subsp. **subacaulis** (Kellogg) comb. nov. (Fig. 26*a–m*.)—Plant 6–20 cm (rarely 25–30 cm) high; basal leaves somewhat broader than in subsp. *typica*, the lobes generally conspicuously toothed or again pinnatifid; stems mostly branching from near the base, bearing 1–5 heads; involucres 13–21 mm high, the bracts usually less setose than in subsp. *typica*, and sometimes completely devoid of setæ; achenes varying from blackish to brownish or reddish, more strongly striate than in subsp. *typica* or even costate; pappus setæ 9–13.5 mm long, equaling or exceeding the achene. (*C. occidentalis* var. *subacaulis* Kellogg, Proc. Cal. Acad. 5:50, 1873; *C. occidentalis* var. *nevadensis* Kellogg, ibid.; *C. subacaulis* Coville, Contr. U. S. Nat. Herb. 3:562, 1896.)

Northern Sierra Nevada, and San Bernardino Mountains, California, and in the Warner Mountains, southern Oregon. The only specimen of the type collection of this subspecies known to us is the small plant in the Gray Herbarium cited and illustrated by Coville (loc. cit.). It does not bear achenes, but in its habit, setæ, the shape of its basal leaves, and the character of its involucral bracts is certainly closer to *C. modocensis* than to *C. occidentalis*. A later collection from near the same locality (summit, Sierra Nevada, *Bolander & Keller* in 1872), contains some specimens quite similar to the type, which bear nearly mature achenes. These are, as Kellogg stated, 9–10-ribbed and about equal to the pappus, and approach in color those of *C. occidentalis*, but they are much less strongly costate than in that species, are slenderer, and taper toward the apex as in *C. modocensis*, i.e., they are exactly intermediate between those of typical *C. occidentalis* and typical (diploid) *C. modocensis*. Other plants similar in habit to, and generally found in company with, the preceding have the typical black, weakly ribbed achenes of *C. modocensis*. These fit the original description of *C. occidentalis* var. *nevadensis* Kellogg, and one of them, (Summit, Sierra Nevada Mountains, *Kellogg*, July 10, 1870, CA), was designated by Coville as identical with that variety. Since *subacaulis* and *nevadensis* were considered synonymous by Coville, his statement that "the achenium character appears to constitute the crucial distinction" between *C. subacaulis* and his *C. scopulorum* is inconsistent with the presence of *scopulorum*-like achenes found on the plant which he designated as typical of var. *nevadensis*. Hence there is every reason for uniting *C. scopulorum* and *C. subacaulis* as one species, as well as for regarding the latter as a series of forms transitional chiefly between typical (diploid) *C. modocensis* and *C. occidentalis*. Some of the forms (apm. *turbinata* and *setosissima*), furthermore, approach *C. monticola*, which has achenes essentially similar to those of *C. occidentalis*. In the forms inhabiting the region between Honey Lake and Sierra Valley, where the ranges of *C. modocensis typica* and *subacaulis* overlap, every intergradation between them in the habit of the plant and the size of the involu-

cre occurs, a fact which makes the recognition of *C. subacaulis* as a distinct species impracticable.

The *formæ apomicticæ* of this subspecies have been more completely described than those of most other subspecies, since nearly all of them have been observed in the field by the authors. Furthermore, they are easily distinguished in the field, have definite ecological preferences, and among them is apparently included nearly every chromosome number from 33 up to 88.

The following apomictic forms of this subspecies may be recognized:

A. Involucre devoid of setæ; these present, but inconspicuous, on the stems and petioles.
  B. Involucres at anthesis 13–15, in fruit 14–17 mm high; achenes 8–9 mm long, brownish, conspicuously striate ..... 7. apm. *Kelloggii*
  B. Involucres at anthesis 13–17, in fruit 17–19 mm high; achenes 10–11.5 mm long, black, weakly striate ..... 8. apm. *grandiceps*
A. Involucre setose; achenes brownish or reddish.
  C. Achenes about equaling the pappus.
    D. Achenes obscurely striate; lobes of leaves obtuse or acute, entire or sparingly dentate ..... 9. apm. *diamondica*
    D. Achenes definitely striate or ribbed; lobes of leaves acuminate, strongly dentate..... 10. apm. *bernardina*
  C. Achenes definitely shorter than the pappus.
    E. Peduncles not expanded at the apex; involucral bracts not attenuate.
      F. Peduncles sparsely or not at all setose.
        G. Basal leaves 10–13 cm long, 4–6 cm broad; largest heads of the inflorescence 16–18 mm high. .... 11. apm. *multiflora*
        G. Basal leaves when well developed 14–17 cm long, 7–8 cm broad; largest heads 19–21 mm high... 12. apm. *robusta*
      F. Peduncles strongly setose; plant densely setose-hispid throughout.. 13. apm. *setosissima*
    E. Peduncles expanded at the apex; involucral bracts attenuate..... 14. apm. *turbinata*

7. apm. *Kelloggii* (*modocensis-occidentalis*) (fig. 26*a–c*).—Dwarf, stems 0.6–1.5 dm high, rather inconspicuously setose near the base; lobes of leaves strongly toothed or pinnatifid; achenes 8–9 mm long, brownish, conspicuously striate, distinctly attenuate toward the apex; pappus setæ 8–9 mm long; ($2n = 44$?). CALIFORNIA: Cisco, Placer County, *Kellogg & Brannan* in 1870 (type collection of *C. occidentalis* var. *subacaulis*, G); Summit, Sierra Nevada, *Kellogg* in 1870, part (G); same locality, *Bolander & Keller* in 1872 (G, CA); vicinity of Truckee, alt. 2100–2600 m, *Hitchcock 388* (US). NEVADA: Peavine Mtn., Washoe County, *Heller 9715*, part (DS).

Related to apm. *Kelloggii*.—CALIFORNIA: Lake Lucile, Eldorado County, *Baker* in 1904 ($2n = 88$?) (UC).

8. apm. *grandiceps* (*modocensis-occidentalis-Bakeri*?) (fig. 26*d, e*).—In habit similar to the last, but the involucres much larger (17–19 mm

long in fruit); achenes blackish, weakly striate, 10–11.5 mm long; ($2n =$ 66 or 88 ?) (CALIFORNIA: Lake Independence, Plumas County, alt. 2120 m, *Head* in 1921 (CA); Castle Peak, Nevada County, *Heller 7086*, part (UC, DS, US, G, Po, RM); Summit, Sierra Nevada, *Kellogg* in 1870, part (CA).

Related to apm. *grandiceps*.—CALIFORNIA: north of Truckee, Nevada County, alt. 1750 m, *B. & N. 121* ($2n = 44$!) (UC).

9. apm. *diamondica* (*modocensis-Bakeri*) (fig. 26*f–h*).—Stems 11–15 cm high, sparingly setose below; basal leaves 10–12 cm long, on slender petioles, the lobes entire or sparingly dentate; inflorescence of 2–4 heads; involucres in fruit 14–17 mm high, the bracts rather sparingly setose, blackish; inner bracts 10–12; florets 20–30; achenes 9–10 mm long, dark reddish or chocolate brown, obscurely ribbed; pappus 9–9.5 mm; ($2n =$ 33 ?) (see p. 26). CALIFORNIA: Diamond Mtn., south of Susanville, alt. 2250 m, *S. & J. 2278* (UC).

10. apm. *bernardina* (*modocensis-Bakeri-occidentalis*?).—Lower part of stems and petioles sparingly to densely setose; stems 10–13 cm high, bearing 1–3 heads; basal leaves 7–10 cm long, densely tomentose, lobes rather broad, irregularly toothed or pinnatifid; involucre 14–17 mm high in fruit; longest outer bracts 8–10 mm long, about 3/5–2/3 the length of the inner; inner bracts 11–14, 2–4 mm broad, rather abruptly contracted to the acute apex, setose with scattered black trichomes, or some of them merely tomentulose, florets about 25–35; achenes 8–10 mm long, rather strongly contracted at the apex, brick red, the ribs fairly prominent; pappus 9.5–10.5 mm; ($2n = 44$?). CALIFORNIA: Bear Valley, San Bernardino County, alt. 1820 m, *Parish* in 1886 (G); Metcalf's, Bear Valley, alt. 1970 m, *Parish 10967* (DS); Castle Peak, Nevada County, *Heller 7086*, part (UC, US); Diamond Mtn., south of Susanville, Lassen County, *S. & J. 2257* (UC). NEVADA: Peavine Mtn., Washoe County, *Heller 9715*, part (DS).

The recurrence of this form in such widely separated localities as southern California and the northern Sierra Nevada is very remarkable. In the latter locality it grows among its close relatives, both polyploid and, as on Diamond Mountain, diploid, while in southern California it is isolated by 400 miles from any other known locality for *C. modocensis*. It apparently migrated to the latter locality by some route as yet unknown, without changing its genetic constitution. "Way stations" may occur for it along the eastern crests of the Sierra Nevada, since this region is relatively little known floristically, particularly as regards early blooming species such as *C. modocensis* (see pp. 40, 49).

11. apm. *multiflora* (*modocensis-occidentalis*) (fig. 26*i–k*).—Plant more densely setose than the last; stems 13–18 cm tall, bearing 3–7 heads; basal leaves 10–13 cm long, 4–6 cm broad, doubly pinnatifid with acute lobes; involucres 15–17 mm high; longest outer bracts 10–12.5 mm long, 2/3–3/4 the length of the inner; inner bracts 12–16, 1.5–2.5 mm broad, tapering gradually toward the apex, sparsely setose with long, black trichomes; florets 25–40; achenes 7–8 mm, brick red, somewhat contracted at the apex, the ribs fairly prominent; pappus 11–12 mm; ($2n = 33$?).

CALIFORNIA: along Lemmon Canyon Road, east of Sierraville, Sierra County, *B. and N. 137, 172* (UC); near Dark Canyon, between Loyalton and Purdy, Sierra County, alt. 1900 m, *S. & J. 2158* (UC); between

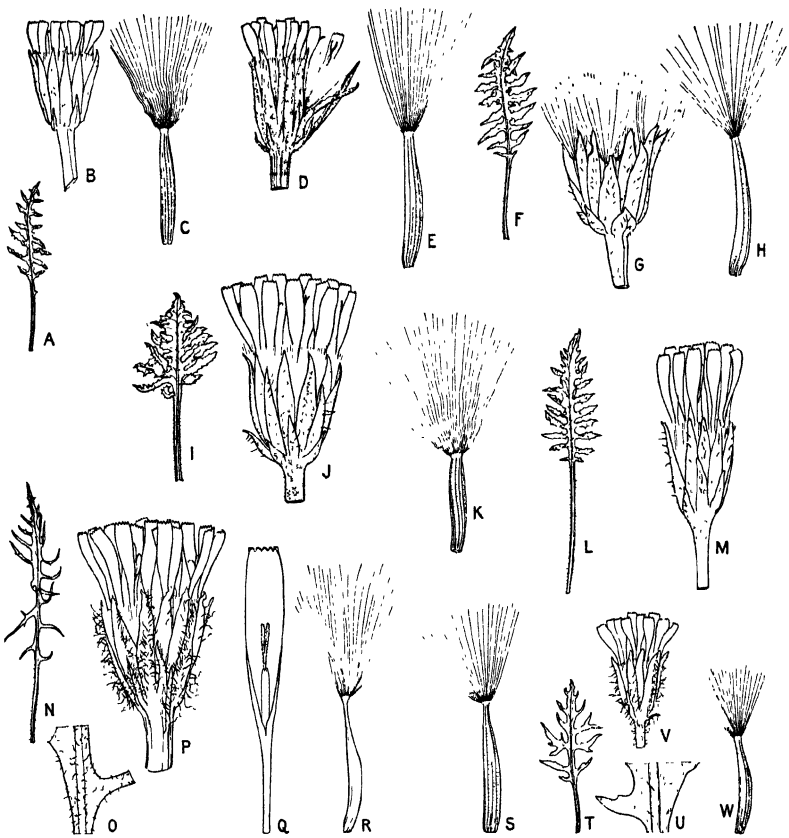


FIG. 26. *Crepis modocensis.* *a–m*, subsp. *subacaulis*; *a–c*, apm. *Kelloggii*, from *Bolander and Keller* in 1872: *a*, leaf, × ¼; *b*, involucre, × 1; *c*, achene, × 2. *d, e*, apm. *grandiceps* et aff.: *d*, involucre, × 1, from *B. & N. 121*; *e*, achene, × 2, from *Heller 7086*. *f–h*, apm. *diamondica*, from *S. & J. 2278*: *f*, leaf, × ¼; *g*, fruiting involucre, × 1; *h*, achene, × 2. *i–k*, apm. multiflora, from *B. 137*: *i*, leaf, × ¼; *j*, involucre, × 1; *k*, achene, × 2. *l, m*, apm. *turbinata*, from *S. & J. 2152*: *l*, leaf, × ¼; *m*, involucre, × 1. *n–s*, subsp. *rostrata*, diploid form—*n, o, r*, from cotype; *p, q*, from *Warren 1807*: *n*, leaf, × ¼; *o*, detail of surface, × 1; *p*, involucre, × 1; *q*, corolla, × 2; *r*, achene, × 2; *s*, achene, from *Grant* in 1930, showing transition to subsp. *glareosa*. *t–w*, subsp. *glareosa*, diploid form, from type: *t*, leaf, × ¼; *u*, detail of surface, × 1; *v*, involucre, × 1; *w*, achene, × 2.

Truckee and Hobart Mills, Nevada County, *B. & S. 1606* (UC); Five Lakes, west of Tahoe City, Placer County, *Smith* in 1927 (UC).

12. apm. *robusta* (*modocensis-occidentalis*).—Habit, pubescence, and leaves similar to the last; stems 17–27 cm high; larger basal leaves 14–17

mm long and 7–8 mm broad; involucres 17–21 mm high; outer and inner bracts as in the last; achenes 6.5–7.5 mm; pappus 12–13.5 mm long; ($2n = 55$?). CALIFORNIA: Sierra Valley, *Lemmon* in 1875 (G); between Truckee and Hobart Mills, Nevada County, *B. & S. 1598* (UC).

This form is closely similar to apm. *multiflora*, except for its larger size and shorter achenes, which are less contracted at the apex, and its higher chromosome number. Near Hobart Mills, where the two are found growing together, they are easily told apart, and no intermediate forms were seen.

Related to apm. *robusta*.—OREGON: Lakeview, Lake County, *Peck 15255* (DS), *19608* (Will, UC).

13. apm. *setosissima* (*modocensis-monticola*).—Entire plant densely setose with elongate, crisped trichomes, and grayish-tomentose as well; stems 10–16 cm tall; basal leaves 9–14 cm long, 4–5 cm broad, the lobes broad and strongly toothed; heads 4–9; involucres 15–18 mm high, the bracts densely setose with elongate trichomes which are black at the base but whitish and crisped at the apex; longest outer bracts 8–10 mm long; inner bracts 12–16, 2–3 mm broad, tapering gradually toward the apex; achenes 7.8–8.5 mm long, chestnut brown, shape and ribbing as in apm. *multiflora*; pappus 11–12.5 mm long; ($2n = 44$!). CALIFORNIA: Hobart Mills, Nevada County, *Drew* in 1925 (DS); Balls Creek, between Loyalton and Purdy, Sierra County, alt. 1780–1820 m, *S. & J. 2159, 2166* (UC).

This race and the next approach *C. monticola* in the character of their trichomes, as well as in the shape and color of their achenes. They are found more frequently in woods or shady places, while apm. *multiflora* and *robusta* occur on open hillsides among sagebrush.

14. apm. *turbinata* (*modocensis-monticola*) (fig. 26*l*, *m*).—Pubescence of stems and leaves as in the last; stems 12–19 cm high; basal leaves 10–15 cm long, 3–4 cm broad, the lobes relatively remote, remotely dentate or nearly entire; heads 2–5; involucre 15–19 mm high, attenuate at the base to the swollen apex of the peduncle, the bracts densely setose as in the last; longest outer bracts 7–10 mm long; inner bracts 11–15, 2–3 mm broad, both the inner and the outer strongly attenuate at the apex; heads 20–30-flowered, achenes 8.5–9.5 mm long, brownish to reddish, slightly contracted at the apex and rather strongly costate; pappus 9–11 mm long; ($2n = 55$?). CALIFORNIA: Sierra Valley, Sierra County, *Lemmon* in 1880, part (UC, G); northeast of Sattley, Sierra Valley, Sierra County, alt. 1550 m, *B. & S. 1641* (UC); Portola, Plumas County, alt. 1515 m, *S. & J. 2152* (UC).

This form is almost exactly intermediate between *C. modocensis* and *C. monticola*.

14*c* (15). **Crepis modocensis** subsp. **rostrata** (Coville) comb. nov. (Fig. 26*n–s*.)—Stems 1.5–3 dm high, rather stout, striate, densely hirsute with whitish, crisped trichomes or merely tomentulose; basal leaves 10–15 cm long, the blades glabrate or tomentulose, the midribs and usually the petioles hirsute, deeply (rarely shallowly) pinnatifid with lanceolate, toothed lobes, these acute or acuminate and with whitish, calloused

tips; inflorescence of 1–6 heads on mostly elongate, stout peduncles; involucres 14–17 mm high; inner bracts tomentulose and hirsute with long, whitish, crisped trichomes; florets 18–60; outer bracts lanceolate, the longest about 1/2 the length of the inner; corollas 14–22 mm long; style-branches 1.8–3 mm long; achenes 7–10 mm long, the body greenish black to somewhat yellowish, 10-ribbed with five low but pale and rather conspicuous ribs and five more or less obscure ones between them, tapering to a pale, thick beak 0.5–2.5 mm long; pappus setæ 7–10 mm long, shorter than or equaling the achene. (*Crepis rostrata* Coville, Contr. U. S. Nat. Herb. 3:564, pl. XXV, 1896; *C. occidentalis* var. *crinita* Gray, Bot. Cal. 1:435, 1876, as to material from Washington.)

Central Washington and southern British Columbia.

The only consistent difference between this subspecies and subsp. *typica* is in the nature of the trichomes on the involucre and on the stems and leaves. Since, furthermore, at least one form of subsp. *subacaulis* has trichomes resembling those of the present form, the reduction of *C. rostrata* to a subspecies of *C. modocensis* seems well justified, even though the ranges of the two do not overlap. The achenes of subsp. *rostrata* are considerably more beaked than those of any other subspecies of *C. modocensis*, and there is more of a tendency toward unequal ribbing. Furthermore, the leaves are in general longer and narrower than those of *C. modocensis*. However, intergrading forms occur in both of these characteristics.

Gray's original description of his *C. occidentalis* var. *crinita* in the "Botany of California" (loc. cit.) undoubtedly referred to the collection of the present subspecies made by the Wilkes Expedition (although this was not specifically cited), but he referred also to "somewhat similar Californian specimens" with glandular bristles. In the "Synoptical Flora" (1(2):432, 1884) he made the latter the basis of his description of the same variety, and cited them. They are both good *C. monticola* Cov., with which species the description in the "Synoptical Flora" agrees. In this later publication the Wilkes specimen "from Washington Territory, or pehaps rather N. California" is cited after the others, and obviously was not the basis of his description, although it agrees with the earlier diagnosis in the "Botany of California." Hence in both descriptions Gray made reference to *C. monticola* as well as to *C. modocensis* subsp. *rostrata*. Therefore var. *crinita* may be regarded as a *nomen confusum*, and given up in favor of the well-characterized *C. rostrata*.

This subspecies includes both diploid and polyploid forms. The latter are mostly stouter, and have somewhat larger heads and corollas, and their achenes are often less strongly beaked. They occur most frequently in the same localities as the diploid forms, and in some cases both types have been included within the same collection. No division into apomictic races is possible with the material at hand. Specimens examined: WASHINGTON: near Crab Creek, Grant County, alt. 720 m, *Sandberg & Leiberg 225* ($2n = 22$?) (type, UC, G, Ore); Wilson Creek, Grant County, *Sandberg & Leiberg* in 1893 ($2n = 22$?) (Minn); near Coulee City, Grant County, *Thompson 6174* ($2n = 22$? and $2n = 44$?) (DS, G, Blake); north

of Ellensburg, Kittitas County, *Thompson 8252* ($2n = 33$? and $2n = 44$?) (UC, DS, RM, CA, Blake); near Liberty, Kittitas County, alt. 1060 m, *Thompson 11543* ($2n = 44$?) (CA, WSC, Blake); upper Naches River, Yakima County, *Grant* in 1930 ($2n = 22$?) (UC, Blake); south of Tieton River, Yakima County, *Warren 1807* ($2n = 22$? and $2n = 44$?) (Blake); between the Naches (Spipen) and Wenatchee (north branch Columbia) Rivers, *Wilkes Exped.* in 1841 ($2n = 44$?) (G, NY); Goldendale, Klickitat County, *Howell* in 1879 (Ore). BRITISH COLUMBIA: Spence's Bridge, Thompson River, *Fletcher* in 1885 (G).

14*d* (16). **Crepis modocensis** subsp. **glareosa** (Piper) comb. nov. (Fig. 26*t–w*.)—The type of *C. glareosa*, as described by Piper, is very different from that of *C. rostrata*. In addition to the characters included in the key, may be mentioned the shorter anther-tubes (4–4.5 mm long) and style-branches (1.8–2 mm) and the leaf-segments with very conspicuous white calloused tips. Although Piper described them as without hirsute pubescence, there are many trichomes on the midribs of the leaves of some plants in the type collection, and some plants of subsp. *rostrata* agree with subsp. *glareosa* in the absence of hirsute pubescence on the stems. The most conspicuous difference between these two subspecies is in the achenes, but one collection of diploid plants, that of Grant from the Naches River, contains a complete series of achenes passing from those nearly as in subsp. *rostrata* to those typical of subsp. *glareosa* (fig. 26*s*). Furthermore, the collection of Thompson (no. 8252) from near the type locality of *C. glareosa* contains several plants which approach it in habit, as well as others which are much like subsp. *rostrata*. Hence, since *C. glareosa* in its typical form has been collected only once, and that within the range of subsp. *rostrata*, the former seems best considered as a (genetically) dwarf extreme of subsp. *rostrata*. (*Crepis glareosa* Piper, Bull. Torr. Bot. Club 28:42, 1901.)

Known only from the type; Ellensburg, Washington, *Piper 2704* (US, G).

15. **Crepis barbigera** Leiberg ex Coville, Contr. U. S. Nat. Herb. 3:565, 1896 (Fig. 28)

Perennial, with rather slender tapering taproot bearing a single or double caudex, or occasionally 2–3-divided, each division with a single caudex; basal leaves erect, up to 40 cm long, 7 cm wide, lanceolate, caudate-acute or -acuminate, pinnately or bi-pinnately toothed or (sometimes deeply) parted, segments lanceolate, acuminate or acute, ± salient, tapering into a long stout narrowly winged petiole, sparsely canescent-tomentulose or glabrate; cauline leaves sometimes more deeply segmented, sometimes entire; stems 1 or 2 to a caudex, stout, up to 65 cm high, 6 mm wide near base, branched above or near the middle, branches stiffly ascending, bearing a few short secondary branches near top, secondary and ultimate branches mostly arcuate, pedunculate, the aggregate inflorescence rather closely corymbiform, upper stem and branches

often sparsely scabrid with stout yellow eglandulose bristles; heads few or many, with 8–25 florets; involucre cylindrical, ± densely beset with long stout recurved eglandulose yellow or greenish bristles, canescent- or somewhat fuscous-tomentose; outer bracts 5–7, lanceolate, acute, 2–5 mm long; inner bracts 7–10, lanceolate, acute, 9–17 mm long; corolla about 18 mm long; ligule about 11 mm long, 3 mm wide; style-branches 1.5–2.3 mm long; anther-tube 5–6 mm long; achenes olive green or yellowish, 6.5–10 mm long, fusiform, gradually attenuate to the rather broad pale summit and slightly narrowed to the yellow calloused base, 10–12 ribbed, ribs strong, rounded, finely spiculate near summit; pappus yellowish white, rather copious and stiff, 5–10 mm long.

Northwestern Idaho, throughout eastern Washington to the Cascade Mountains, and eastern Oregon as far south as northern Harney County (see fig. 27).

This is an agamospecies, consisting of a series of apomicts which combine the characteristics of *C. exilis*, *C. modocensis* subspp. *rostrata* and *glareosa*, and *C. acuminata*. Although restricted in range, it is very abundant in the regions in which it does occur, and is correspondingly variable. There is no evidence as to whether apomixis is facultative or complete in this species, but some of the very large number of apomictic forms seem to have a definite range. The eight selected for description indicate the amount of variation within the species, but many of them are represented by only one collection. The following is a key to these forms (see p. 69).

A. Involucres definitely tomentose, with 7–11 inner bracts and 11–25 florets.
  B Stems and leaves not setose.
    C Stems 3–6.5 dm high; inflorescence of 8–30 heads; largest heads of the inflorescence with 8–10 inner bracts and 14–21 florets.
      D. Involucral bracts setose only on the upper ½ ..... 2. apm. *semibarbata*
      D. Involucral bracts setose throughout.
        E. Involucres 13–17 mm high; achenes 9–10.5 mm long; pappus 8.5–10 mm..... 1. apm. *Leibergii*
        E. Involucres 10–14 mm high; achenes 6.5–9 mm long; pappus 5.5–8.5 mm.
          F. Central portion of basal leaves linear-lanceolate, 0.5–2 cm broad, narrower than the length of the lobes. 3. apm. *dentata*
          F. Central portion of basal leaves elliptic, 2.5–4 cm broad, definitely broader than the length of the lobes.
            G. Inflorescence of 8–11 heads; achenes greenish; pappus 8–8.5 mm long ..... 6. apm. *falcata*
            G. Inflorescence of 19–30 heads; achenes dull brown; pappus 6.5 mm long ..... 7. apm. *breviloba*
    C. Stems 2.5 dm high; inflorescence of 7–8 heads; largest heads of the inflorescence with 10–11 inner bracts and 25 florets..... 5. apm. *laticeps*

B. Stems, margins and midribs of leaves strongly setose ..... 4. apm. *setosissima*
A. Involucres glabrate, with 6–8 inner bracts and 8–10 florets ..... 8 apm. *pauciflora*

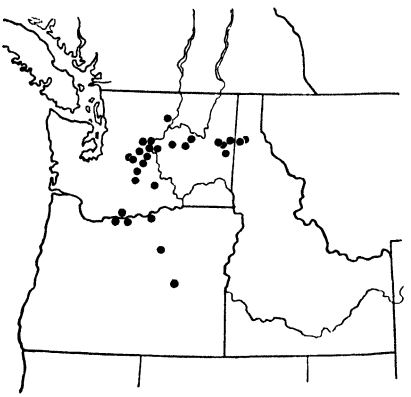


FIG. 27. Distribution of *Crepis barbigera*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

1. apm. *Leibergii* (*exilis-acuminata-mod. rostrata*) (fig. 28*a–c*).—Stems 4.5 dm high; basal leaves 28–35 cm long, lanceolate in outline, the lobes remote, lanceolate, entire; inflorescence of 15–17 heads; involucres 13–17 mm high; inner bracts 8, their trichomes elongate, yellow; florets 11–14; achenes 9.5 mm long, dull grayish green, only slightly contracted at the apex; pappus 8.5–10 mm. WASHINGTON: near Alkali Lake, Douglas County, alt. 400 m, *Sandberg & Leiberg 313* (type of *C. barbigera*, US no. 413938, G, CA).

Related to apm. *Leibergii*.—WASHINGTON: Wilson Creek, Grant County, alt. 600–900 m, *Sandberg & Leiberg* in 1893 ($2n = 88$?) (Minn); between Cle Elum and Easton, Kittitas County, *Thompson 6689* ($2n = 44$ or 55 ?) (DS, US); west of Spokane, *B. & C. 61* ($2n = 88$?) (UC).

2. apm. *semibarbata* (*exilis-acuminata-mod. rostrata*) (fig. 28*d, e*).—Stems 6 dm high, leaves as in apm. *Leibergii;* inflorescence of 15–20 heads on stout, elongate peduncles; involucres 13.5–16 mm high; inner bracts 8–10, somewhat glabrate along the midrib; *setæ crowded near the apex of the bracts;* florets 12–16; achenes 10.5 mm long, yellowish green at maturity, somewhat contracted at the apex; pappus 8–8.5 mm long; ($2n = 44$?). WASHINGTON: near Easton, Kittitas County, *Thompson 9013* (UC).

Related to apm. *semibarbata*.—OREGON: between Mosier and The Dalles, Wasco County, *Thompson 4314* (US); eastern Oregon, *Howell* in 1881 (US).

This form approaches *C. intermedia* in the lack of setæ on the lower part of the involucral bracts, as well as in their shape, but the setæ present are characteristic of *C. barbigera*, as are also the achenes.

3. apm. *dentata* (*exilis-acuminata-mod. rostrata*).—Stems 3–4.5 dm high; basal leaves 18–25 cm long, the central portion lanceolate, the lobes lanceolate, 2–3.5 cm long, mostly toothed or pinnatifid; heads 15–25 in an inflorescence, on short, divaricate peduncles; involucres 10–12 mm high; inner bracts 8, very densely setose, the setæ somewhat greenish; florets 13–18; achenes 6.5–7.5 mm long; pappus 5.5–6.5 mm; ($2n = 88$?). WASHINGTON: Rattlesnake Mtns., Yakima region, Yakima County, alt. 1060 m, *Cotton 705* (G, US); 15 miles north of Ellensburg, Kittitas

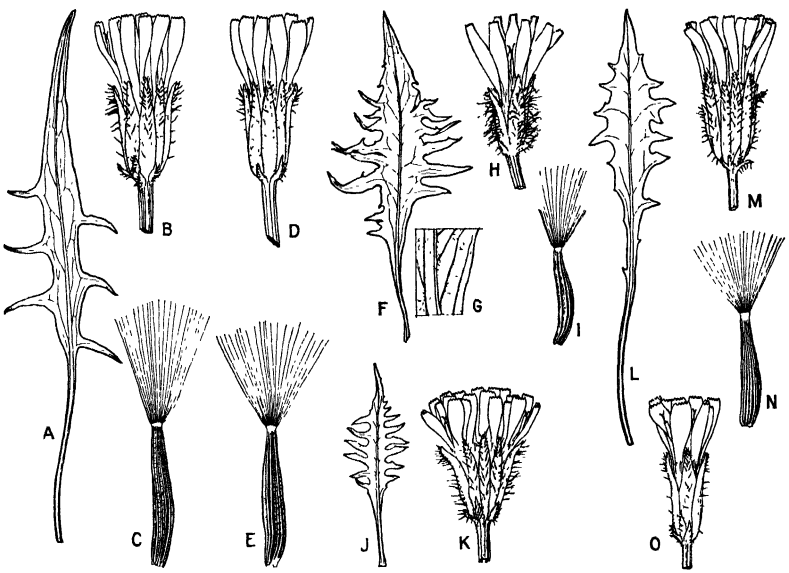


FIG. 28. *Crepis barbigera*. *a–c*, apm. *Leibergii*, from cotype of *C. barbigera*: *a*, leaf, × ¼; *b*, involucre, × 1; *c*, achene, ×2. *d*, *e*, apm. *semibarbata*, from *Thompson 9013*: *d*, involucre, × 1; *e*, achene, × 2. *f–i*, near apm. *dentata*, from *Suksdorf 378*: *f*, leaf, × ¼; *g*, detail of surface, × 1; *h*, involucre, × 1; *i*, achene, × 2. *j*, *k*, apm. laticeps, from *Thompson 8352*: *j*, leaf, × ¼; *k*, involucre, × 1. *l–n*, apm. *breviloba—l*, *m*, from *Henderson 5268*; *n*, from *Peck 9925*: *l*, leaf, × ¼; *m*, involucre, ×1; *n*, achene, × 2. *o*, apm. *pauciflora*, involucre, × 1, from *Leiberg 2361*.

County, *Keck & Clausen 3529*, part (UC, WSC); west of Ellensburg, *B. & C. 35, 38* (UC); "Columbia River," western Klickitat County, *Suksdorf* in 1885 (US).

Related to apm. *dentata* (fig. 28*f–i*).—OREGON: Hood River, *Peck 2973* ($2n = 55$?) and *2972* ($2n = 88$?) (Will). WASHINGTON: northwest of Wenatchee, *Whited 1267* (US); Spokane County, *Suksdorf 378* (G); Spokane, *Piper 2265* (G). IDAHO: Post Falls, Kootenai County, *Rust 332* (US); shores of Lake Pend Oreille, *Leiberg* in 1891 (US).

4. apm. *setosissima* (*exilis-acuminata-mod. rostrata*).—Similar in habit and inflorescence to the last; stems, midribs, and borders of the leaves strongly setose; involucres 10–12 mm high; inner bracts 8, very strongly

setose; florets 12–20; achenes 6.5–8 mm long, green, somewhat contracted at the apex; pappus 5–6.5 mm long; ($2n = 44$?). WASHINGTON: north of Ellensburg, Kittitas County, alt. 550 m, *Keck & Clausen 3529*, part (UC); west of Ellensburg, *B. & C. 33* (UC); "Columbia River," western Klickitat County, *Suksdorf* in 1885, part (DS).

Related to apm. *setosissima*.—Wenatchee, Douglas County, *Whited 2632* (US).

5. apm. *laticeps* (*exilis-mod. rostrata-acuminata*) (fig. 28*j*, *k*).—Stems low, 2.5 dm high; basal leaves 10–14 cm long, the lobes entire or remotely dentate, the terminal portion narrowly deltoid; inflorescence of 7–8 heads; involucres 11–13 mm high; inner bracts 8–11; densely setose with coarse, greenish setæ, outer bracts short as in typical *C. barbigera;* florets 12–25; pappus 7.5 mm long; achenes not seen; ($2n = 44$?). WASHINGTON: north of Ellensburg, Kittitas County, *Thompson 8352* (NY, DS).

6. apm. *falcata* (*acuminata-exilis-mod. rostrata*).—Stems 4.5–6.5 dm high; basal leaves 25–35 cm long, the central portion narrowly elliptic, 2.5–3.5 cm broad, the lobes short, lanceolate, falcate, entire; leaves of the inflorescence well developed, mostly entire; inflorescence of 8–11 heads; involucres 13–14 mm high; inner bracts 8, rather thickly beset with yellowish bristles; florets 16–21; achenes 8–9 mm long, distinctly contracted or subrostrate at the apex; pappus 8–8.5 mm long; ($2n = ca.$ 88 !). WASHINGTON: Swauk Creek Canyon, between Ellensburg and Wenatchee, Kittitas County, *B. & C. 49* UC Gen 1840 (UC); east Wenatchee, Douglas County, alt. 200 m, *Keck & Clausen 3555* (UC).

7. apm. *breviloba* (*acuminata-exilis-mod. rostrata*) (fig. 28*l–n*).—Stems 3.5–6 dm high; basal leaves elliptic, 22–28 cm long, the central portion 3–4 cm broad, the lobes lanceolate, short, mostly entire, the terminal portion short, deltoid; leaves of the inflorescence large, the lower pinnatifid, inflorescence of 19–30 heads, involucres 11–14 mm high; inner bracts 7–8, their setæ abundant, yellowish; florets 12–18; achenes 7.5–9 mm long, dull brown, somewhat contracted at the apex; pappus 6.5 mm long; ($2n = 88$?). OREGON: west of The Dalles, Wasco County, *Peck 9925* (DS, Will); near mouth of John Day River, Sherman County, *Henderson 5268* (DS, G, CA).

8. apm. *pauciflora* (*acuminata-exilis-mod. rostrata*) (fig. 28*o*).—Stems 5.5–6 dm high; basal leaves 20–25 cm long, elliptic in outline, the central portion 2.5–4 cm broad, the lobes elongate, entire; leaves of the inflorescence large, the lowest pinnatifid; inflorescence branching from below the middle of the stem, bearing 60–70 heads; involucres narrow, 11–14 mm high; inner bracts 6–8, glabrate, with scattered yellowish bristles; florets 8–10; anther-tube short and without pollen; pappus 9 mm long; achenes not seen; ($2n = 88$?). OREGON: near Stinking Water, Harney County, *Leiberg 2361* (UC, G, Po).

Related to apm. *pauciflora*.—WASHINGTON: Spokane, *Piper 2264* ($2n =$ 44 ?) (UC). OREGON: Fossil, Wheeler County, *Lawrence 452* (US).

This form approaches *C. acuminata* in its glabrate, few-flowered involucres, as well as in the character of its inflorescence and leaves. Furthermore, it is the only form of *C. barbigera* in which the anthers are

reduced and without pollen, a characteristic common in polyploid *C. acuminata*.

The distribution of the various forms of *C. barbigera* accords well with the supposition that they are derived from intercrossing of the three species, *C. modocensis* subsp. *rostrata*, *C. exilis*, and *C. acuminata*. Apm. *dentata*, which approaches most nearly *C. exilis*, is within the range of the diploid form of that species; *setosissima* and *laticeps*, which are nearest to *C. modocensis* subsp. *rostrata*, are within the range of that local subspecies; *breviloba* and *pauciflora*, which occur within the range of diploid *C. acuminata*, approach most nearly that species.

16. **Crepis exilis** Osterhout, Muhlenbergia 1:142, 1906 (fig. 30)

Plants perennial, 1.5–6 dm tall, stems 1 or 2 from each caudex, below the inflorescence straight, erect, tomentulose or glabrate; longest basal leaves 1–3.5 dm long, lanceolate to linear, pinnately or bipinnately divided into linear or lanceolate segments or rarely entire, the tips of the leaves elongate, linear or lanceolate, grayish-tomentulose or more often glabrate; inflorescence dichotomous, or the stem more or less branched, forming a corymbiform cyme with 3–30 or 40 heads; involucres 8–15 mm long, cylindrical, grayish-tomentose, glabrate, or rarely glabrous, with or without black glandless setæ on the inner and sometimes the outer bracts; outer bracts 5–10, deltoid, acute, the longest 1/4–1/3 as long as the inner ones; inner bracts 6–10, lanceolate, acute or obtuse; florets 6–35 per involucre; anther-tube 3.5–6 mm long, or in some forms abortive, with no pollen; style-branches 1.5–3 mm long; achenes 3–10 mm long, slender, of various shades of green or rarely brownish, weakly or strongly ribbed, usually attenuate at the apex or subrostrate; pappus 5.5–10 mm long.

Montana west to British Columbia, south to Colorado, Utah, Nevada, and central Oregon (see fig. 29).

Unfortunately, the well-known and oldest name for this species, *C. gracilis* (D. C. Eaton) Rydb., must be given up, as it was applied earlier to a species of the Himalayas (see below for synonymy). *C. angustata* Rydb., the next specific name chronologically which should be considered for it, includes, according to Rydberg's description in the "Rocky Mountain Flora," forms referred by the present authors to *C. exilis*, but Rydberg's type of the former species has few-flowered, nearly glabrous involucres, achenes in shape and color like those of *C. acuminata*, and leaves which also approach those of *C. acuminata*. Hence *C. angustata* is best considered as a form of *C. acuminata*, and the next available name, *C. exilis* Osterhout, must be taken up in place of the untenable *C. gracilis*.

The nomenclatural type of *C. exilis* belongs to one of a series of *formæ apomicticæ* which resemble *C. modocensis* in their low stature and the relatively few and large heads of their inflorescence, as well as in the setæ on their involucral bracts. These are widespread throughout the Rocky Mountain region, extending westward to eastern Washington and

northeastern Oregon, where they occur chiefly in the mountains. In the latter regions there is a complete series of forms connecting typical *C. exilis* with the form most characteristic of lower altitudes in the northwestern states. The latter plants are taller and have a larger inflorescence with smaller heads, and their involucral bracts are nearly or quite devoid of setæ. These tall forms comprise a number of *formæ apomicticæ,* and in addition the diploid sexual form of *C. exilis,* which occurs from southern British Columbia to central Washington.

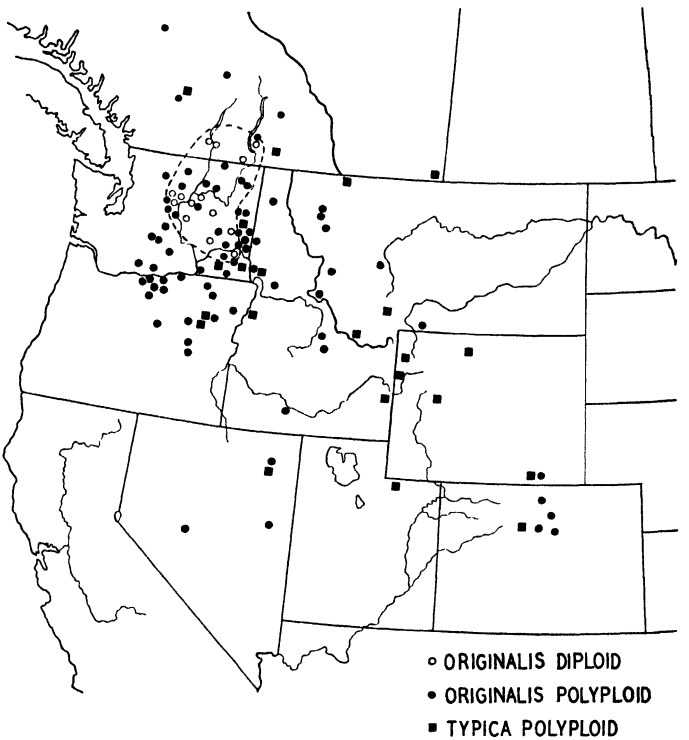


FIG. 29. Distribution of *Crepis exilis.* (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

Since these two series possess different geographic ranges and occupy different habitats, they constitute different subspecies. They may be differentiated as follows:

Stems 3–7 dm. averaging 3.5–5 dm tall; heads 10–30 or more in an inflorescence; involucral bracts without setæ, or the setæ few and confined to the tips of the bracts ..... *a. originalis*

Stems 1.5–3.5 dm tall; heads 3–18 in an inflorescence; involucral bracts bearing black glandless setæ throughout their length..... *b. typica*

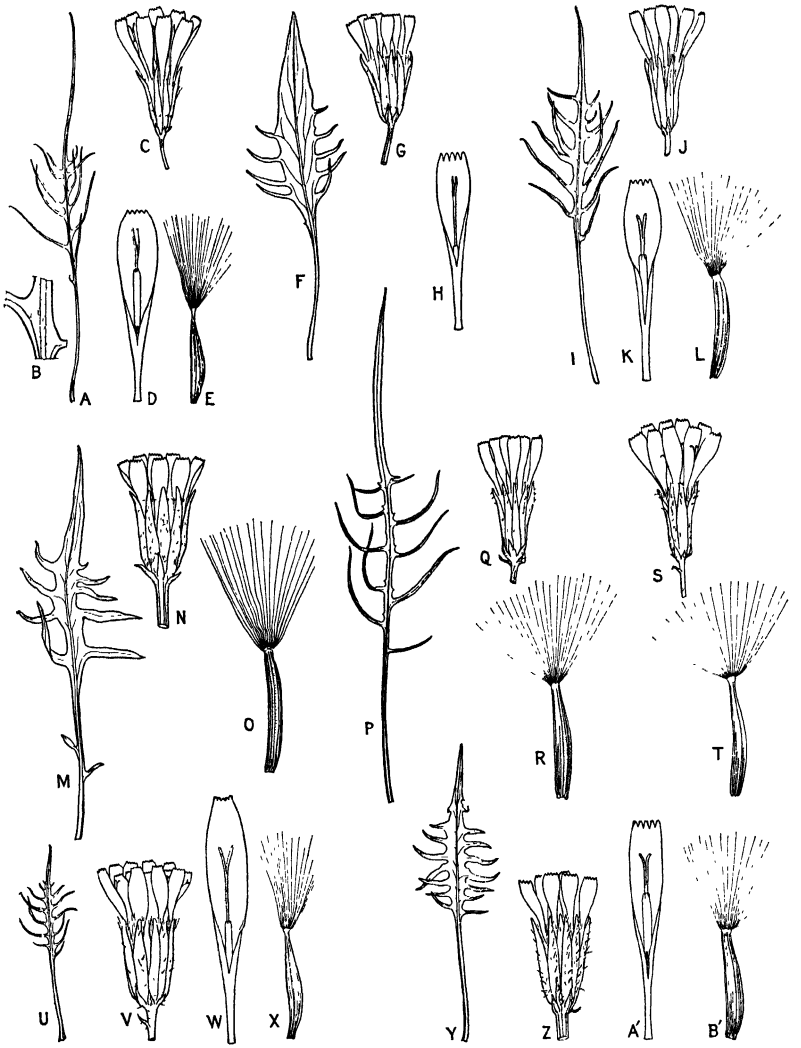


FIG. 30. *Crepis exilis*. *a–t*, subsp. *originalis*. *a–e*, diploid form—*a–d*, from type of subsp. *originalis*; *e*, from *Jones* in 1911: *a*, leaf, × ¼; *b*, detail of pubescence, × 1; *c*, involucre, × 1; *d*, corolla, × 2; *e*, achene, × 2. *f–h*, apm. *breviloba*, from *Fiker 710*: *f*, leaf, × ¼; *g*, involucre, × 1; *h*, corolla, × 2. *i–l*, apm. *longiloba*—*i*, *l*, from Elmer 102; *j*, *k*, from *Piper* in 1894: *i*, leaf, × ¼; *j*, involucre, × 1; *k*, *corolla*, × 2, *l*, achene, × 2. *m–o*, apm. *coloradensis*, from *Baker* in 1895: *m*, leaf, × ¼; *n*, involucre, × 1; *o*, achene, × 2. *p–r*, apm. *paucibarba*, from *Keck and s*, achene, × 2. *y–a'*, apm. *Helleri*, from *Heller 3302*: *y*, leaf, × ¼; *z*, involucre, × 1; *Clausen 3569*: *p*, leaf, × ¼; *q*, involucre, × 1; *r*, achene, × 2. *s*, *t*, apm. *sterilis*, from *Jones* in 1878: *s*, involucre, × 1; *t*, achene, × 2. *u–b'*, subsp. *typica*. *u–x*, apm. *Osterhoutii*, from *Nelson 1393*: *u*, leaf, × ¼; *v*, involucre, × 1; *w*, corolla, × 2; *a'*, corolla, × 2; *b'*, near apm. *Helleri*, achene, × 2, from *Henderson 5559*.

16*a*. **Crepis exilis** subsp. **originalis** subsp. nov. (Fig. 30*a–t*.)—Planta 3–7 dm alta; folia elongata, sæpissime glabrescentia; inflorescentia cymosa, capitulis 10–40 pro inflorescentia; involucri phylla asetosa vel ad apicem parce setosa.

Stems 3–7 dm tall; leaves mostly elongate, various in outline, but most often with linear, falcate-ascending, entire lobes, usually glabrate; inflorescence cymose, freely branching, strictly dichotomous or with a well-defined primary axis, bearing 10–40 heads; involucres variable as to height, number of bracts and florets, but mostly narrower than in subsp. *typica*, the inner bracts without setæ, or bearing a few glandless setæ at the apex; outer bracts usually short, the longest about 1/4 the length of the inner; florets, achenes, and pappus with more variation than in subsp. *typica*, but not materially different. (*C. occidentalis* var. *gracilis* D. C. Eaton, Rep. U. S. Geol. Expl. 40th Par. 5:203, 1871, in part; *C. acuminata* var. *gracilis* Torr., ex Eaton, ibid.; *C. intermedia* var. *gracilis* Gray, Syn. Fl. 1(2):432, 1884, in part; *C. gracilis* Rydb., Mem. N. Y. Bot. Gard. 1:461, 1900, *non* Hook, f. et Thoms. ex C. B. Clarke, Comp. Ind. 254, 1876; *C. angustata* Rydb., Bull. Torr. Bot. Club 32:135, 1905, in part.)

Subsp. *originalis* is considered to be the original form of this species, since it includes the diploid, sexual form. The two specimens on which Eaton based his description (loc. cit.) of *C. occidentalis* var. *gracilis*, i.e., that of Parry from Middle Park, Colorado, and Watson no. 716 from Nevada, differ in just those characteristics that separate subsp. *originalis* as here recognized from typical *C. exilis*. The Parry specimen resembles the diploid form in its relatively numerous, slender heads and short outer bracts, and the setæ are restricted to the apices of the inner bracts; that of Watson has only three heads that are considerably broader and have relatively long outer bracts, while the setæ are scattered over the upper half of the inner bracts. The original description, which calls for "3–6 narrow 9–14-flowered heads," partly covers both specimens (although that of Parry actually has 10 heads and 3 undeveloped buds in its inflorescence) and therefore, when applied to the segregation of *C. exilis* into two subspecies as outlined above, does not fit either one of them. Consequently, var. *gracilis* is best regarded as an ambiguous name, and is not applied to either of the two subspecies here recognized.

Almost throughout the range of the species, but rare in the Rocky Mountains, and not occurring at higher altitudes.

The following is a key to the apomicts which have been selected as representing the amount of variability to be found within the species. Many other forms exist, but they are more or less similar to those described. For a discussion of their taxonomic status, see p. 69.

A. Inflorescence strictly dichotomous, i.e., without a straight central axis..... { diploid forms / 1. apm. *simulans*

A. Inflorescence corymbose, i.e., with a more or less straight central axis which is stronger than the side branches.

B. Involucral bracts devoid of setæ.
  C. Lobes of leaves absent or short, shorter than the width of the lanceolate or narrowly elliptic central portion; involucre 8–10 mm high 2. apm. *breviloba*
  C. Lobes of leaves elongate, much longer than the lanceolate or linear central portion.
    D. Achenes 7–10 mm long, strongly attenuate or subrostrate toward the apex; leaves green and sparsely tomentose or glabrate.
      E. Involucres definitely tomentose.
        F. Pappus setæ 6.5–8 mm long.
          G. Lobes of leaves linear, entire; stems and peduncles slender, ascending; achenes yellowish green .... 3. apm. *longiloba*
          G. Lobes of leaves lanceolate, with a few, prominent teeth; stems and peduncles stout, the latter divaricate; achenes at maturity deep blackish green..... 4. apm. *yakimensis*
        F. Pappus setæ 9–10 mm long; lobes of leaves lanceolate, entire; achenes brownish green at maturity..... 5. apm. *coloradensis*
      E. Involucres glabrate; pappus 8–9 mm long 6. apm. *glabrescens*
    D. Achenes 5–7.5 mm long, thick and slightly contracted at the apex; leaves and stems conspicuously tomentose ..... 7. apm. *brevicarpa*
B. Inner (and rarely the outer) involucral bracts bearing a few glandless setæ at the apex.
      H. Anthers well developed and pollen-bearing.
        I. Lobes of basal leaves elongate; involucres 12–13 mm high; longest outer bracts 4.5–5 mm long..... 8. apm. *paucibarba*
        I. Lobes of basal leaves very short, barely exceeding the narrowly lanceolate central portion; involucres 11 mm high; longest outer bracts about 3 mm long.. 9. apm. *graminifolia*
      H. Anthers abortive, 3.5–4 mm long, and without pollen..... 10. apm. *sterilis*

Diploid form (fig. 30*a–e*).—Stems 3.5–6.5 dm high; basal leaves glabrate, 19–33 cm long, 0.5–10 cm broad, pinnatifid with linear lobes; *inflorescence strictly dichotomous*, without a well-defined central axis; bearing 10–30 heads on well-developed plants; involucral bracts 7–10, not setose; florets 22–35 per involucre; achenes deep green or greenish black, (3–)5.5–8 mm long, contracted at the apex or subrostrate; pappus 6–8 mm long. BRITISH COLUMBIA: near Similkameen River, near Hedley, alt. about 525 m, *Wheeler* in 1928 ($2n = 22$!) (type of subsp. *originalis*, UC no. 346445); Deer Park, Lower Arrow Lake, *Macoun* in 1890 (US); Cascade, near international boundary, *Macoun 65028* (G, NY, DS). WASHINGTON: junction of Crab and Wilson Creeks, Grant ("Douglas")

County, alt. 475 m, *Sandberg & Leiberg 256*, part (UC); north of Blewett, Chelan County, alt. 500 m, *Keck & Clausen 3554* (UC); Garfield County, *Darlington* in 1913 (WSC); shore of Omak Lake, Okanogan County, *Fiker 1258, 1259* (WSC); north of Kahlotus, Franklin County, *Constance & McMurray 1159* (WSC); east of Winona, Whitman County, *Eastwood & St. John 13217* (WSC); Hartline, Grant County, alt. 580 m, *Eggleston 12869* (US); Chelan, Chelan County, *Jones* in 1911 (Po).

The Eggleston collection is an anomalous form with small heads and exceptionally short achenes, 3–4.5 mm long. Since, however, this form is not known to have a definite geographic distribution, and is approached in the size of the involucres and achenes by the three specimens cited previously to it, as well as by some of the plants of Miss Wheeler's collection from British Columbia, the treatment of it as a taxonomic segregate does not seem advisable at present.

1. apm. *simulans*.—Similar morphologically to the diploid form, but with the stomatal size of tetraploids; ($2n = 44$?). BRITISH COLUMBIA: Lake Osoyoos, *Macoun 76, 992* (NY); south of Lytton, junction of Fraser and Thompson Rivers, *McCabe 200* (UC). WASHINGTON: Wilson Creek, Douglas County, *Sandberg & Leiberg* in 1893 (Po); near Bickleton, Klickitat County, *Suksdorf 1997* (WSC); Deep Creek Canyon, Spokane County, *Large 42* (WSC). OREGON: near Kent, Sherman County, *Peck 9978* (DS, Will); Meacham, Umatilla County, *Peck 4143* (Will).

Related to apm. *simulans*.—WASHINGTON: Waitsburg, Walla Walla County, *Horner 167* ($2n = 33$?) (WSC). OREGON: east of Mitchell, Wheeler County, *Keck & Clausen 3672* ($2n = 33$?) (UC).

2. apm. *breviloba* (*exilis-acuminata*) (fig. 30*f–h*).—Stems 4–4.5 dm high; basal leaves narrowly elliptic, with a broad (1–3 cm) central portion and short, strongly falcate and ascending lobes; inflorescence with a zigzag, but well-defined central axis, bearing 25–35 heads; involucres 8.5–9 mm high; inner bracts 6–8; florets 7–10; pappus 6.5 mm long; achenes 6–6.5 mm long, pale green; ($2n = 44$?). WASHINGTON: Wawawai, Whitman County, *Elmer 761* (NY, Po, Minn, WSC); Conconully, Okanogan County, *Fiker 710, 770* (WSC); Coleville Reservation, Okanogan County, *Griffiths & Cotton 421* (NY, WSC). OREGON: East of Pendleton, Umatilla County, *Thompson 4755* (DS); Deep Creek, Wallowa County, *Sheldon 8316*, part (NY).

Related to apm. *breviloba*.—OREGON: Wallowa Mtns., trail to Ice Lake, Wallowa County, alt. 1970 m, *B. & C. 79* ($2n = 55$!) (UC). IDAHO: Greer, Clearwater County, *Stillinger* in 1923 (WSC).

3. apm. *longiloba* (*exilis-acuminata*) (fig. 30*i–l*).—Stems 3.5–5.5 dm high; basal leaves with lance-linear central portion, and linear, ascending lobes; inflorescence with slender, ascending branches, bearing 17–25 heads; involucres 11–13 mm high; inner bracts 6–9; florets 8–11; achenes pale yellowish green, 7.5–8.5 mm long; pappus 7–8 mm; ($2n = 55$?). WASHINGTON: Pullman, Whitman County, *Elmer 102* (UC, Minn, Po, RM); Almota, Whitman County, *Piper* in 1894 (WSC). IDAHO: near Lake Coeur d'Alene, Kootenai County, *Aiton* in 1892 (Minn); Bear Creek

below Parker Mountain, Custer County, alt. 1750 m, *Macbride & Payson 3293*, part (UC, DS, Po, RM); Lake Waha, Nez Perces County, *Henderson* in 1894 (RM). MONTANA: Alta, Ravalli County, alt. 1515 m, *Jones* in 1909 (Po); Jack Creek Canyon, alt. 2120 m, *Rydberg & Bessey 5304*, part (G, UC, NY, RM).

Related to apm. *longiloba*.—BRITISH COLUMBIA: Deer Park, Lower Arrow Lake, *Macoun* in 1890 (NY); above Lardo, alt. 850 m, *Shaw 683* (NY); east of Kamloops, *McCabe 2358* (UC); Chilcotin, *Newcombe* in 1915 (G). WASHINGTON: Kettle Falls, Stevens County, *Beattie & Chapman* in 1903 (WSC, Clo). OREGON: near Blue Mtn. Hot Springs, Grant County, *Ferris & Duthie 842* (DS, RM); Mitchell, Wheeler County, *Peck 10100* (Will); near Blalock, Gilliam County, *Sherwood 340* (Will); Kamela, Union County, *Peck 4142* (Will); Ice Lake trail, Wallowa Mtns., *Eastwood & Howell 3303* (CA). MONTANA: Bigfork, Flathead County, alt. 909 m, *Jones* in 1908 (DS, Po); Helena, Lewis and Clark County, *Kelsey* in 1898 (UC); between Hamilton and Darby, Ravalli County, *Kirkwood 1763* (CA, RM, FM). WYOMING: Yellowstone River near Junction Butte, Yellowstone National Park, *Nelson 5755*, part (NY, G, RM, Minn).

4. apm. *yakimensis* (*exilis-acuminata*).—Stems rather stout, 3.5–4 dm high; basal leaves with a lanceolate-linear central portion and lanceolate, toothed lobes; inflorescence with rather stout, divaricate branches; involucres 12–14 mm high; inner bracts 8–9; florets 13–15; achenes deep green, 7–9 mm long; pappus 7–8 mm long; ($2n = 88$?). WASHINGTON: Natchez Valley near N. Yakima, Yakima County, *Piper 2737* (G, NY).

Related to apm. *yakimensis*.—WASHINGTON: Ellensburg, Kittitas County, *Whited 455* (WSC); Wenatchee, Chelan County, *Whited 1112* (US, WSC); south of Omak, Okanogan County, *Fiker 1596* (WSC); Stehekin, Chelan County, *Griffiths & Cotton 214* (US).

This form with its relatives is similar in habit to *C. barbigera* but is distinguished from that species by the complete absence of bristles from the involucres.

5. apm. *coloradensis* (*exilis-acuminata*) (fig. 30*m–o*).—Stems about 5 dm tall; basal leaves with lanceolate central portion and lanceolate, entire lobes; branches of the inflorescence ascending; involucres 12–15 mm high; inner bracts 8; florets 12–16; achenes 9–10 mm long, brownish when young, but becoming distinctly greenish at maturity; pappus setæ 9–10 mm long; ($2n = 55$?). COLORADO: Larimer County, alt. 1660 m, *Baker* in 1895 (Po, Minn); Boulder Canyon, Jefferson County, *Ramaley 7014* (RM). Transitional to *C. intermedia*.

6. apm. *glabrescens* (*exilis-acuminata*).—Stems stout, 6–7 dm tall; basal leaves with a lanceolate central portion and linear-lanceolate, entire, ascending lobes; inflorescence with very numerous heads, as in *C. acuminata;* involucres 12–13 mm high; inner bracts 6–8, *nearly glabrous*; florets 7–10; achenes 7–8 mm long, deep blackish green at maturity; pappus setæ 8–9 mm long; ($2n = 55$?). WASHINGTON: Ellensburg Kittitas County, *Elmer 383* (Minn, Mo); near Wilson Creek, Douglas County, alt. 680 m, *Sandberg & Leiberg 232* (UC, Minn, WSC).

This form resembles *C. acuminata* in habit and in the glabrate involucres, but the achenes resemble those of *C. exilis* in shape and color.

Related to apm. *glabrescens*.—WASHINGTON: Oroville, Okanogan County, *Jones* in 1911 (UC, Po).

7. apm. *brevicarpa* (*exilis-acuminata-modocensis?*).—Stems 5 dm tall, rather stout; basal leaves with lanceolate-linear central portion and linear, spreading or reflexed lobes; both the stems and leaves rather strongly tomentose; branches of the inflorescence short and stout; involucres 8.5–10 mm high; inner bracts 8, obtuse; florets 10–12; achenes 5–7.5 mm long, thick and only slightly attenuate at the apex; pappus 5.5–6 mm long; ($2n = 44$?). WASHINGTON: Sawtooth Ridge, valley of War Creek, Okanogan County, alt. 1210 m, *St. John, Courtney, & Parker 3712* (WSC).

8. apm. *paucibarba* (*exilis-acuminata-modocensis?*) (fig. 30*p–r*).—Stems 5–6 dm tall; basal leaves with a linear central portion and elongate, linear lobes; inflorescence ample, many-headed; involucres 10–14 mm high; inner bracts 8–10, somewhat glabrate, with a few black setæ near the apex; florets 10–15; outer bracts narrowly deltoid or lanceolate, the longest 4–5 mm long; anthers well developed and pollen-bearing; achenes deep green, 7.5–9 mm long; pappus 7.5–8 mm long; ($2n = 44$?). WASHINGTON: Snipe's Mtn., Yakima County, *Cotton 383* (G, RM, WSC); west of Ritzville, Adams County, alt. 550 m, *Keck & Clausen 3569* (UC); Wallula, Walla Walla County, *Cotton 1068* (NY, US, WSC); above Palouse Falls, Whitman County, *St. John & Pickett 6167* (WSC). OREGON: Grant's, Wasco County, *Suksdorf 195* (G, WSC); Arlington Hills, Gilliam County, *Henderson 14479* (UC); near Moro, Sherman County, *Lawrence & Powell 2913* (DS).

Related to apm. *paucibarba*.—WASHINGTON: Status Creek south of Toppenish, Yakima County, alt. 235 m, *Keck & Clausen 3503* ($2n = 44$!) (UC); Bridge Creek, near Lake Chelan, Chelan County, alt. 900 m, *Jones* in 1911 (Po); west of Spokane, *B. & C. 58* ($2n =$ ca. 88!) (UC); southeast of Salmon Meadows, Okanogan County, *Fiker 251* (WSC). OREGON: Paterson Ferry, Morrow County, *Eastwood & Howell 3527* (CA). IDAHO: Moscow Mtn., Latah County, *Piper 1611* (G. NY, Minn).

9. apm. *graminifolia* (*exilis-modocensis-acuminata*).—Stems 3.5–4 dm high; basal leaves with linear-lanceolate central portion and short, strongly falcate, linear lobes; inflorescence of 5–10 heads; involucres 10–11 mm high; inner bracts 8, with a few black setæ near the apex; florets 10–12; outer bracts lance-deltoid, the longest 2.5–3 mm long; pappus setæ 8 mm long; achenes not seen; ($2n = 33$?). OREGON: Silvies River, Harney County, *Peck 4139* (Will); mouth of Emigrant Creek, Harney County, *Peck 3977* (Will).

10. apm. *sterilis* (*exilis-acuminata-modocensis*) (fig. 30*s, t*)—Stems 3–5 dm tall, slender; basal leaves with linear-lanceolate central portion and linear, spreading or slightly ascending lobes; branches of the inflorescence conspicuously divaricate; involucres 11–13 mm high, inner bracts 7–9, with a few black setæ near the apex; florets 7–12; outer bracts narrowly deltoid, the longest 2.5–3 mm long; anthers abortive and without

pollen; achenes 8–9.5 mm long, grayish green at maturity; pappus 7–8 mm long; ($2n = 44$ or 55 ?). COLORADO: Middle Park, *Parry* in 1864 (G); near Golden, Jefferson County, *Jones* in 1878 (Po).

Related to apm. *sterilis*.—MONTANA: Ravalli, Lake County, alt. 900 m, *Jones* in 1909 (Po); Spanish Basin, Gallatin County, *Flodman 922* (Minn); Hamilton, Ravalli County, *Blankinship 1906* (Po). WASHINGTON: near Trout Lake, Klickitat County, *Suksdorf 2693* (G, DS, Minn, WSC); near Spangle, Spokane County, *Suksdorf 1642, 12710* (WSC). COLORADO: Sulphur Springs, Grand County, *Osterhout 3315* (G, NY, RM, Nev). IDAHO: Shoshone Falls, Twin Falls County, alt. 1120 m, *Nelson & Macbride 1727* (RM, Minn); Nez Perces County, *Sandberg* in 1892 (Minn). NEVADA: Bunker Hill, Toiyabe Range, Lander County, alt. 2420 m, *Kennedy 4120* Nev); Clover Mtns., Elko County, *Greene* in 1893 (UC); Duck Creek, Schell Creek Mtns., White Pine County, *Jones* in 1924 (Po).

16*b*. **Crepis exilis** subsp. **typica** nom. nov. (Fig. 30*u–b'*.)—Stems stouter than in subsp. *originalis*, 1.5–3.5 dm tall; heads 3–18, mostly 5–10 in an inflorescence; involucres rather broad and many-flowered, longest outer bracts mostly about 1/3 the length of the inner; inner bracts bearing black setæ throughout their length. (*Crepis exilis* Osterhout, loc. cit., *C. occidentalis* var. *gracilis* Gray, loc. cit., and *C. gracilis* Rydb., loc. cit., all in part; *C. atribarba* Heller, Bull. Torr. Bot. Club 26:314, 1899.)

British Columbia to Alberta, south to the Blue Mountains of Oregon, and in the Rockies to Colorado, at higher elevations than subsp. *originalis*.

The following apomicts may be recognized (see p. 69):

A. Lobes of leaves linear; anthers abortive and without pollen.
  B. Longest of the outer involucral bracts 3.5–5.5 mm long ..... 11. apm. *Osterhoutii*
  B. Longest of the outer involucral bracts 2–3.5 mm long ..... 12. apm. *ambigua*
A. Lobes of basal leaves lanceolate; anthers well developed and bearing pollen..... 13. apm. *Helleri*

11. apm. *Osterhoutii* (*exilis-modocensis*) (fig. 30*u–x*). Stems 2–3 dm high; basal leaves with lance-linear central portion and short, linear spreading or ascending lobes; heads 3–8 in an inflorescence; involucre 11–13 mm high and rather broad; longest of the outer bracts 3.5–5.5 mm long; inner bracts 8–10, setose throughout most of their length; florets 12–20; anthers abortive and without pollen; achenes 8–8.5 mm long, brownish when immature but becoming greenish at least in the lower half at maturity; pappus 7.5–8 mm long; ($2n = 44$ or 55 ?) (see p. 49). MONTANA: Lima, Beaverhead County, *Jones* in 1908 (Po); Glacier National Park, *Van Dyke* in 1930 (CA). WYOMING: Jackson Lodge, Grand Teton National Park, *Van Dyke* in 1930 (CA); Pole Creek, *Nelson 1393* (G, Minn, RM); Green Top, *Nelson 3251* (RM); Mountain Home, Albany County, alt. 2600 m, *Keck 902* (DS); Big Horn County,

Worthley 57 (RM). COLORADO: Sulphur Springs, Grand County, *Osterhout 2979* (type collection of *C. exilis,* NY). IDAHO: Caribou Mtns., Bonneville County, *Payson & Armstrong 3558* (G, Po, RM).

Although this apomict includes the nomenclatural type of *C. exilis,* it is morphologically intermediate between the original, diploid form of the species and *C. modocensis.* It agrees with the latter species in its few-headed inflorescence, and broad, many-flowered involucres, and in the glandless setæ on the involucral bracts, but differs in the narrower leaves with linear lobes, and in the absence of yellow setæ on the stems and leaves.

Related to apm. *Osterhoutii.*—MONTANA: Spanish Basin, Gallatin County, alt. 1970 m, *Rydberg & Bessey 5308* (G, US, Minn, RM). WYOMING: Teton Pass, Lincoln County, alt, 2575 m. *Hall 11468,* part (UC); Green River Lakes, Sublette County, alt. 2575 m, *Payson 4584* (WSC, RM). COLORADO: Larimer County, *Osterhout* in 1894 (Minn). NEVADA: East Humboldt Mtns., Elko County, *Watson 716* (G).

12. apm. *ambigua* (*exilis-acuminata-modocensis*).—Stems slender, 2.5–3.5 dm high; basal leaves with linear central portion and linear, ascending lobes; branches of the inflorescence short and divaricate; involucres 8–11 mm high; outer bracts lance-deltoid, the longest 2–3.5 mm long; inner bracts 7–9, bearing greenish or blackish setæ through most of their length; florets 10–18; anthers without pollen; achenes bright green, 7–7.5 mm long; pappus 6.5–7 mm long; ($2n = 33$?). UTAH: near Mill Creek, Uintah Mtns., Summit County, alt. 2500 m, *Payson 4892* (UC, Minn, Po, WSC).

Related to apm. *ambigua.*—ALBERTA: Cypress Hills, *Macoun* in 1884 (G). BRITISH COLUMBIA: Spence's Bridge, *collector unnamed 1098,* in 1875 (G). IDAHO: Seven Devil Mtns., Washington County, alt. 1820 m, *Jones* in 1899 (Po). WASHINGTON: Blue Mtns., Walla Walla County, *Piper 2437* (G, WSC); southeast of Spangle, Spokane County, *Suksdorf 12704* (WSC). OREGON: South of Baker, Dooley Mtn. Grade, Baker County, alt. 1400 m, *Keck & Clausen 3634* (UC). NEVADA: Star Peak, alt 2420 m, *Jones* in 1901 (Po).

13. apm. *Helleri* (*exilis-acuminata-modocensis*) (fig. 30*y–á*).—Stems 2.2–3.5 dm high; basal leaves 15–18 cm long and 5–7 cm broad, their lobes lanceolate; heads 5–14 in an inflorescence, involucres 13–15 mm high; outer bracts narrowly deltoid, the longest 4.5–5 mm long; inner bracts 8–11; florets 15–20; anthers well developed and bearing pollen; achenes not seen; ($2n = 44$?). IDAHO: Lake Waha, Nez Perces County, *Heller 3302* (type collection of *C. atribarba,* UC, US, Minn). WASHINGTON: Blue Mtns., Asotin County, *Jones 979* (Wn).

Related to apm. *Helleri* (fig. 30*b'*).—BRITISH COLUMBIA: Kootenay Valley, *Dawson* in 1883 (G). OREGON: Dixie Mtn., Grant County, alt. 2120 m, *Henderson 5559* (DS, CA).

This form closely resembles apm. *Osterhoutii* in the character of its involucres, differing from it chiefly in its greater stature and larger, broader leaves. The achenes present on the Henderson specimens from Oregon,

which differ from apm. *Helleri* only in their slightly narrower leaf-segments and smaller involucres, are brownish green, as in apm. *Osterhoutii*, but thicker and less contracted at the apex than in the latter form.

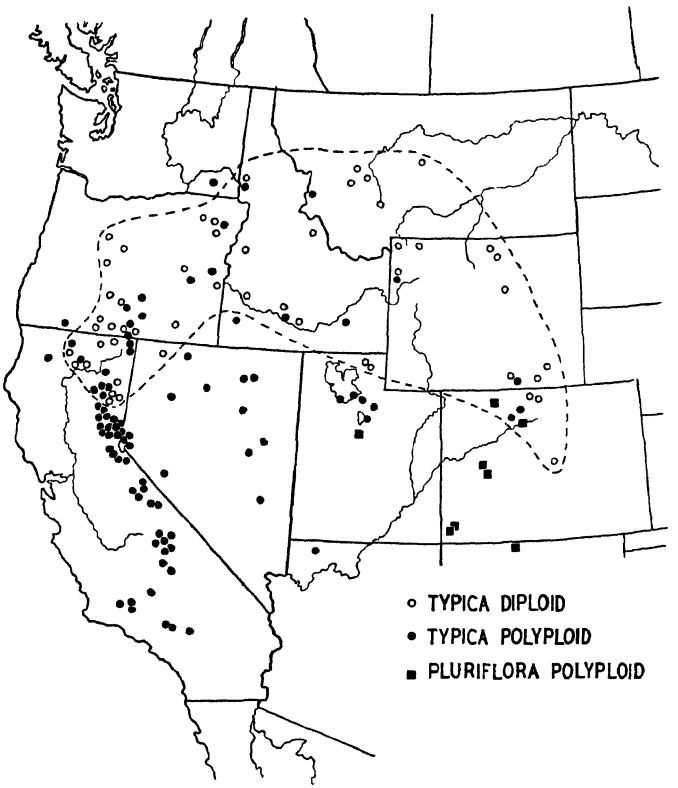


FIG. 31. Distribution of *Crepis acuminata*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

17. **Crepis acuminata** Nutt., Trans. Am. Phil. Soc. n. s. 7:437, 1841 (Fig. 32)

Stems 1–2 from the end of a taproot 2–4 mm in diameter, surrounded by 2–7 basal leaves; basal leaves 12–40 cm long, blade lanceolate-elliptic, 0.5–11 cm wide, lobes 5–10 on each side, lance-deltoid, 0.7–3 cm long, 0.2–1.2 cm in width, entire or toothed, apical portion (beyond the lobes) 3–8 cm long, the whole leaf sparsely or more usually densely grayish-tomentose with appressed, crinkled hairs; stem 2–6.5 dm high, stout, 3–5 mm wide, striate; principal cauline leaves 1–3, 6–30 cm long; inflorescence corymbiform, with 15–240, usually 30–100 heads; peduncles 0.2–2 cm long; involucre 8.5–16 mm high, 5–12-flowered; outer bracts

lance-deltoid, 1–3 mm (rarely up to 6 mm) long, acute, conspicuously ciliate on margin; inner bracts 5–8, glabrous or tomentulose, yellowish or olive green, 1.5–2.5 mm broad, their apex obtuse, ciliate, ventrally glabrous, at maturity bearing a fleshy dorsal thickening 1/4–2/5 their length; corollas 10–18 mm long, the tube 3.5–5.5 mm, scabrous or glabrous, the ligule 6.5–13 mm long, 2.2–3.5 mm broad; anther-tube yellow, 3–7 mm long; style-branches yellow, 1.5–3 mm long; achenes 5.5–9 mm long, average length 6.5–8 mm, fusiform, slightly or strongly tapering at the apex, about 12-ribbed, pale yellow or brownish, smooth or spiculate toward the apex, 1–1.2 mm wide; pappus 5–10 mm long, white or cream colored.

Montana to Washington, south to northern New Mexico, Northern Arizona, central Nevada, and the mountains of Southern California (see fig. 31).

The following two subspecies can be recognized:

Involucres with 5–8 inner bracts and 5–10 florets..... *a. typica*
Involucres with strictly 8 inner bracts and 9–12 florets.. *b. pluriflora*

17*a*. **Crepis acuminata** subsp. **typica** nom. nov. (Fig. 32*a–t*.)—Characters of the species except that at least the majority of the involucres of the inflorescence have only 5–7 inner bracts and 5–10 florets. (*Crepis acuminata* Nutt., loc. cit.; *C. angustata* Rydb., Bull. Torr. Bot. Club 32:135, 1905, in part; *C. sesclifolia* Rydb., op. cit. 38:14, 1911; *Hieraciodes acuminatum* O. Ktze., Rev. Gen. 345, 1891.

Range of the species except in southwestern Colorado and adjacent New Mexico. This subspecies includes the diploid form, as well as a large series of polyploid, apomictic derivatives.

C. acuminata differs from all the other species of its group in that the diploid, sexual form is the most widespread. It is consequently more variable than the corresponding forms of the other species. Throughout most of its range, the diploid is relatively easily recognized by its small involucres, 9–12 mm high, which are strictly 5- or rarely 6-flowered. In southwestern Oregon and northern California, however, where diploid *C. acuminata* occurs together with the polyploid forms of both it and *C. intermedia*, there is much more variation, and diploid forms exist with as many as 8-12 florets, and with involucres up to 15 mm high. These can be distinguished from the polyploid forms only by their smaller stomata and by their regular pollen, consisting entirely of 3-pored grains. The majority of the polyploid apomicts of *C. acuminata* produce no pollen whatever, and when present, the pollen is very irregular. Morphologically, these forms include a most gradual intergradation from those indistinguishable from sexual *C. acuminata* to forms differing almost imperceptibly from small-headed, lightly tomentose extremes of *C. intermedia*. Although some of the forms of this subspecies are very distinct from the diploid form, all attempts to group them into separate subspecies, distinguished by recognizable characters and possessing definite ranges, have failed

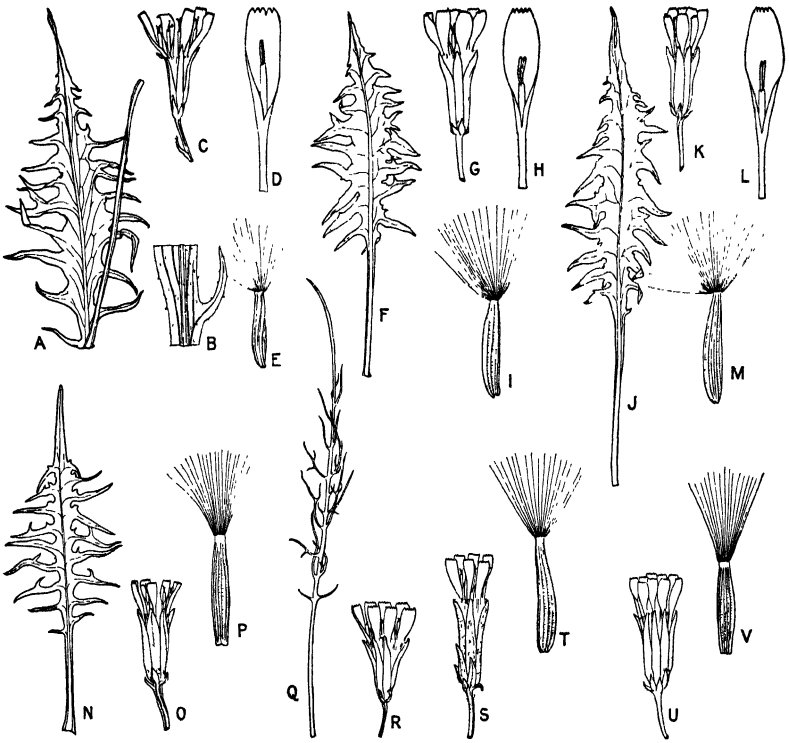


FIG. 32. *Crepis acuminata*. *a–t*, subsp. *typica*. *a–e*, diploid form—*a–d*, from *B. & S. 1864*; *e*, from *Hall 11439*: *a*, leaf, × ¼; *b*, detail of surface, × 1; *c*, involucre, × 1; *d*, corolla, × 2; *e*, achene, × 2. *f–i*, apm. *longiceps*, from *S. & J. 2313*; *f*, leaf, × ¼; *g*, involucre, × 1; *h*, corolla, × 2; *i*, achene, × 2. *j–m*, apm. *sierrae*, from *S. & J. 2314*: *j*, leaf, × ¼; *k*, involucre, × 1; *l*, corolla, × 2; *m*, achene, × 2. *n–p*, apm. *longiloba*—*n*, *p*, from *Hall 6702*; *o*, from *Hall 6384*: *n*, leaf, × ¼; *o*, involucre, × 1; *p*, achene, × 2. *q*, *r*, apm. *Rydbergii*, from *Sandberg, MacDougal, & Heller 326*: *q*, leaf, × ¼; *r*, involucre, × 1. *s*, *t*, apm. *tetoncnsis*, from *Hall 11468*: *s*, involucre, × 1; *t*, achene, × 2. *u*, *v*, subsp. *pluriflora*, from *Baker, Earle, and Tracy 66*: *u*, involucre, × 1; *v*, achene, × 2.

The following is a key to the apomictic forms recognized (see p. 69):

A. Involucral bracts completely glabrous.
  B. Anthers well developed, 4.5–7 mm long, bearing pollen.
    C. Basal leaves grayish-tomentose.
      D. Lobes of leaves lanceolate or broader; inflorescence bearing 35–200 heads, except in dwarfed specimens.
        E. Pollen regular, the grains all 3-pored; involucres mostly 9–12 mm high..... diploid form
        E. Pollen-grains irregular in size, some of them 4-pored; involucres 12–14 mm high ..... 1. apm. *simulans*

D. Lobes of leaves linear; inflorescence of 7–20 heads on slender peduncles.
E. Segments of basal leaves entire; involucres 11–11.5 mm high..... 3. apm. *tenuis*
E. Segments of basal leaves with 1–2 lobes; involucres 9–11 mm high..... 14. apm. *Rydbergii*
C. Basal leaves green and glabrate..... 15. apm. *viridis*
B Anthers rudimentary, 3–4.5 mm long, without pollen.
F. Largest heads of the inflorescence with 5–6 inner bracts and 6–7 florets.
G. Terminal portion of leaves narrowly deltoid, not attenuate; inner involucral bracts without setæ or emergences at the apex.. 2. apm. *utahensis*
G. Terminal portion of leaves lance-linear, attenuate; inner involucral bracts with a few minute setæ or emergences at the apex (these often obscure in herbarium material).
H. Stems low or dwarfed, 1.8–3.5 dm high.
I. Involucres 10–12 mm high; pappus 6.8–7 2 mm long.. 5. apm. *depauperata*
I. Involucres 11.5–13.5 mm high; pappus 8 5-9 mm long ..... 6 apm. *patens*
H. Stems tall, 4–6 dm high; involucres 12–14.5 mm high; pappus 6.8–7.5 mm long.... 4. apm. *longiceps*
F. Largest heads of the inflorescence with 7–8 inner bracts and 7–10 florets
J. Inflorescence of 40–65 heads; involucres 10–13 mm high; pappus 5.8–6.8 mm long..... 7. apm. *sierræ*
J Inflorescence of 15–30 heads; involucres 11 5–13 5 mm high; pappus 8–8 5 mm long..... 8. apm. *yosemitana*
A. Involucral bracts tomentulose or tomentose.
K. Basal leaves densely grayish-tomentose, their lobes lanceolate or deltoid; involucral bracts mostly without setæ at the apex.
L. Involucral bracts lightly tomentulose.
M. Largest heads of the inflorescence with 5–6 inner bracts and 5–6 florets.
N. Lobes of basal leaves 1–2.5 cm long; pappus 7–7.5 mm long 9. apm. *bernardina*
N. Lobes of well-developed basal leaves 2.5–4 cm long; pappus 6.5–7 mm long.. 10 apm. *longiloba*

M. Largest heads of the inflorescence with 7 inner bracts and 7–9 florets 11. apm. *nevadensis*

L. Inner bracts densely tomentose.

O. Outer bracts short, the longest about 3.5 mm long; pappus 9.5–10 mm long, about equalling the achenes..... 12. apm. *wallowensis*

O. Outer bracts elongate, the longest 5–6 mm long; pappus 7 mm long, distinctly shorter than the achenes ..... 13. apm. *tetonensis*

K. Basal leaves green and glabrate, their lobes lance-linear; involucral bracts with distinct blackish setæ at the apex.. 16. apm. *exiloides*

Diploid form (fig. 32*a–e*).—This is the common form of *C. acuminata* except in the southern part of its range in Utah, Nevada, and California. The following are typical: WITHOUT DEFINITE LOCALITY: plains of the Platte, *Nuttall* (type of *C. acuminata*, G, Po). MONTANA: Old Hollowtop, near Pony, alt. 2720 m, *Rydberg & Bessey 5302* (UC, Minn); Deer Lodge, *Scheuber* in 1901 (Minn); near Jefferson City, *Scribner 126a* (G); Spanish Basin, Gallatin County, alt. 1800 m, *Rydberg & Bessey 5301* (G, RM). WYOMING: head of Middle Fork of Powder River, Bighorn County, *Goodding 323* (UC, DS, Po, RM, Clo); Laramie Hills, *Nelson 356* (Minn); 12 miles west of Saratoga, alt. 2420 m, *Babcock & Goddard 1012* (UC); Yellowstone National Park, near Camp Roosevelt, *B. 116* (UC); Coal Gulch, Teton Mtns., alt. 2270 m, *Hall 11439* (UC). COLORADO: mountains of Larimer County, *Osterhout* in 1894 (Minn); Ute Pass, near Manitou, *Letterman* in 1884 (G). IDAHO: Lemhi Range, alt. 2575 m, east slope, *Hall 11510* (UC); Twin Falls and Shoshone Falls, alt. 1100 m, *Nelson & MacBride 1339* (UC, RM, Minn); Shoshone, Lincoln County, *Nelson & MacBride 1176* (UC, RM, Minn). UTAH: Pine Canyon, Wellsville Mtns., Cache County, *Maguire 3169* (RM). OREGON: eastern Oregon, *Cusick 2511* (UC, RM); near Desert Well, south of Button Springs, alt. 1440 m, *Leiberg 391* (UC); southwest of Kamela, Union County, alt. about 1035 m, *Keck & Clausen 3614* (UC); Redmond, Deschutes County, *Whited 1916* (DS); Drake Peak, Warner Mtns., Lake County, *Applegate 1936* (DS); Keno, Klamath County, *Peck 9366* (DS); north of Seneca, Grant County, *Thompson 11949* (CA). NEVADA: Pine Forest Mtns., Humboldt County, alt. 1500 m, *Taylor & Richardson 13* (UC). CALIFORNIA: lava beds, Modoc County, *Baker* in 1893 (UC, Minn, RM); southeast of Sheep Rock, on north side of Mt. Shasta, alt. 1500 m, *B. & S. 1964–1972, S. & J. 2432* (UC); Saddle Mtn., near Fall River Mills, Shasta County, alt. 1480 m, *S. & J. 2390* (UC); Secret Valley, south of Ravendale, Lassen County, alt. 1363 m, *B. & S. 1776* (UC).

1. apm. *simulans*.—Stems 6–7 dm high; basal leaves 23–28 cm long, pinnatifid with lanceolate, entire segments, the terminal narrowly deltoid, not attenuate, leaves of the inflorescence mostly entire, broadest at the base, attenuate at the apex; inflorescence of 70–80 heads; involucres 12–14 mm high; inner bracts 5–6, the apex without setæ; florets 5–6; anther-tube 6–6.5 mm long, bearing abundant pollen; achenes 8–8.5 mm, not contracted at the apex; pappus 7–7.5 mm; ($2n = 33$?). IDAHO: Silver City, Owyhee County, alt. 2120 m, *Macbride 378* (UC, G, Minn, RM). UTAH: City Creek Canyon, alt. 1360 m, *Stokes* in 1901 (UC, DS, Minn).

Related to apm. *simulans*.—OREGON: Brogan, Malheur County, Cooper *1174* (Will). WYOMING: Chug Creek, Albany County, *Nelson 7331* (Minn, RM). NEVADA: Ward Mtn., south of Ely, White Pine County, alt. 2000 m, *Keck 622* (UC). CALIFORNIA: near Hope Valley, alt. 2270 m, *Evans* in 1918 (UC).

2. apm. *utahensis*.—Stems 4–4.5 dm high; basal leaves 18–25 cm long, with a broad central portion and narrowly deltoid or lanceolate entire lobes, the terminal portion deltoid, acute; inflorescence of 25–45 heads, its branches short and crowded; involucres 9–11 mm high; inner bracts 5, without setæ; florets 5–6; anther-tube short and without pollen; achenes 6.5–7 mm long, slightly contracted at the apex; pappus 6.5–7.5 mm; ($2n = 33$!). UTAH: City Creek Canyon, Salt Lake City, *Garrett*, UC Gen 1922 (UC); same locality, *Jones* in 1886 (Po, RM); Snyderville, Summit County, alt. 2000 m, *Keck 753* (UC).

Related to apm. *utahensis*.—COLORADO: Coulter, Grand County, *Osterhout 3003* (RM). OREGON: Hart Mtn., Lake County, *Applegate 7680* (DS). NEVADA: Duck Creek, Schell Creek Mtns., White Pine County, *Jones* in 1924 (Po); Little Lakes Canyon, near Stampede, Elko County, *Kennedy 539* (RM); near Pioche, Lincoln County, alt. 1970 m, *Minthorn 99* (UC).

3. apm. *tenuis* (*acuminata-pleurocarpa?*).—Stems slender, 4–4.5 dm high; basal leaves 20–25 cm long, lanceolate in outline, the lobes and terminal portion linear-lanceolate, entire; inflorescence of 7–20 heads on slender, elongate peduncles; involucres 11–11.5 mm high, inner bracts 5, without bristles; florets 5–6; anther-tube 5.2–5.5 mm long, bearing pollen; achenes 7.5–8 mm long, pale brown, somewhat contracted at the apex; pappus 7–7.5 mm long; ($2n = 33$?). CALIFORNIA: Goosenest foothills, Siskiyou County, alt. 1210 m, *Butler 1639* (UC).

This form is most distinctive in its narrow leaves and slender peduncles, suggesting *C. exilis* in these respects, but otherwise it is typical of *C. acuminata*.

4. apm. *longiceps* (fig. 32*f–i*).—Stems 4–6 dm high; basal leaves 22–35 cm long, the lobes entire or remotely dentate, the terminal portion linear-lanceolate, attenuate; inflorescence of 35–70 heads; involucres 12–14.5 mm high; inner bracts 5–6, with one or two minute blackish setæ at the apex; florets 5–7; anther-tube small and without pollen; achenes 7–7.8 mm long; pappus 6.8–7.5 mm; ($2n = 55$?) (see p. 47). CALIFORNIA: Black Mtn., near Milford, Lassen County, alt. 1930 m, *S. & J. 2313* (UC); Fall River Mills, Shasta County, *S. & J. 2380* (UC).

Related to apm. *longiceps*.—UTAH: Antelope Island, alt. 1510 m, *Watson 717* ($2n = 44$?) (G). IDAHO: Pocatello, Bannock County, *Soth P76* (RM). OREGON: near Beulah, Malheur County, alt. 1080 m, *Leiberg 2313* ($2n = 44$?) (G). NEVADA: Verdi, Washoe County, alt. 1480 m, *S. & J. 2177A* (UC).

5. apm. *depauperata*.—Stems 1.8–3.5 dm high; basal leaves 12–19 cm long, conspicuously grayish-tomentose, the lobes lanceolate, reflexed, coarsely toothed, the terminal portion linear-lanceolate, attenuate; heads 20–35 in an inflorescence; involucres 10–12 mm high; inner bracts 5–6, with a few short black setæ at the apex; florets 5–6; anther-tube short and without pollen; achenes 7.5–8 mm long; pappus 6.8–7.2 mm; ($2n = 33$?). CALIFORNIA: Echo Peak, Eldorado County, alt. 2700 m, *B. 432* (UC); near Glen Alpine, Eldorado County, alt. 2000 m, *Pendleton & Reed 1227* (UC); east cone of Dardanelles, Alpine County, alt. 2575 m, *Howden* in 1935, part (CFE); Bishop Creek, Inyo County, *Davidson 2599* (UC); above Glacier Point, Yosemite National Park, alt. 2420 m, *Michaels* in 1921 (CA); east of Twin Lakes, Mammoth Lakes district, Mono County, alt. 2670 m, *Stebbins 2549* (UC).

Related to apm. *depauperata*.—CALIFORNIA: Red Rock, north of Engelmine, Plumas County, alt. 2120 m, *S. & J. 2250* (UC); Parker Creek, Warner Mountains, Modoc County, *Ferris & Duthie 183* ($2n = 33$?) (DS, RM).

6. apm. *patens*.—Similar in habit to the last; involucres 11.5–13.5 mm high; achenes 7–7.5 mm long; pappus 8.5–9 mm; ($2n = 55$?). CALIFORNIA: Carson Spur, Amador County, alt. 2460 m, *B. 446* (UC); Last Chance Creek, Plumas County, *Swift* in 1931 (UC).

7. apm. *sierræ* (fig. 32*j–m*).—Stems 4–6 dm high; basal leaves 22–28 cm long, the lobes lanceolate, mostly entire; inflorescence of 40–65 heads; involucres 10–13 mm high; inner bracts 5–8, some conspicuously narrower than the others, mostly with a few minute setæ at the apex; florets 6–10; anther-tube reduced and without pollen; achenes 7–8 mm long; pappus 5.8–6.8 mm; (*2n = 33 ?*) (see p. 47). CALIFORNIA: Black Mtn., south of Milford, Lassen County, alt. 1930 m, *S. & J. 2314* (UC); east of Sierraville, Sierra County, *B. 148* (UC); road to Glen Alpine Springs, Eldorado County, *Lathrop* in 1909 (DS).

Related to apm. *sierræ*.—UTAH: Miller Creek, alt. 1820 m, *Jones* in 1910 (Po); Thistle, Utah County, alt. 1600 m, *Jones 5528* (UC, RM). NEVADA: Virgin Valley, Humboldt County, *Kellogg* in 1909 (UC); east of Elko, Elko County, *Eastwood & Howell 259* (CA); between Lovelock and Imlay, Pershing County, *Eastwood & Howell 148* (CA). OREGON: Lakeview, Lake County, alt. 1500 m, *B. & S. 1848* (UC). CALIFORNIA: Cedar Creek Canyon, west of Cedarville, Modoc County, alt. 1600 m, *B. & S. 1810* (UC); above Round Lake, Feather River region, Plumas County, alt. 1900 m, *Head* in 1921 (CA); Castle Peak, Nevada County, alt. 2727 m, *Heller 7087* (DS); between Tioga Lodge and Bridgeport, Mono County, *B. 410* (UC).

Many other specimens related to this form have been seen, most of which differ from each other very slightly, but are not enough alike so

that they can be identified as the same biotype. All of them are apparently triploid and completely without pollen.

8. apm. *yosemitana* (*acuminata-occidentalis*).—Stems 6–6.5 dm high; basal leaves 23–30 cm long, the lobes and terminal portion lance-deltoid, the former remotely and coarsely dentate; inflorescence an open panicle of 15–30 heads; involucres 11.5–13.5 mm high; inner bracts 5–8, with a few minute setæ at the apex; anther-tube rudimentary and without pollen; achenes 7.5–8.5 mm long, distinctly contracted at the apex; pappus 8–8.5 mm; ($2n = 33$?). CALIFORNIA: Yosemite Valley, Yosemite National Park, alt. 1210–1360 m, *Abrams 4497* (UC, DS, G, Minn, Po); Little Yosemite, Yosemite National Park, alt. 1870 m, *Hall 9065* (UC).

Related to apm. *yosemitana*.—UTAH: Stansbury Island, Salt Lake, *Capt. Stansbury* (G). NEVADA: Spence, *Jones* in 1891 (UC); Verdi, Washoe County, alt. 1515 m. *S. & J. 2177* (UC). CALIFORNIA: near Champs, T.33 N., R.10 E., Lassen County, alt. 1720 m, *S. & J. 2338* (UC); east of Constantia (Red Rock), Lassen County, alt. 1600 m, *B. & S. 1751* (UC).

This approaches, in its open, few-headed panicle and large many-flowered heads, subsp. *pluriflora* and hence *C. intermedia*.

9. apm. *bernardina* (*acuminata-pleurocarpa* or *occidentalis* ?).—Stems 2.5–5 dm high; basal leaves 13–18 cm long, lanceolate in outline, the lobes short, 1–2.5 mm long, reflexed, entire or remotely dentate; inflorescence of 25–35 heads; involucres 10–11 mm high; inner bracts 5–6, lightly tomentulose, without setæ; florets 5–6; anther-tube rudimentary and without pollen; achenes 7–8 mm long; pappus 7–7.5 mm; ($2n = 33$?) (see p. 39). CALIFORNIA: Sugarloaf Mtn., San Bernardino Mtns., alt. 2185 m, *Hall 7534* (UC); Pine Mtn. Ridge, San Antonio Mtns., San Bernardino County, alt. 2500 m, *Johnston 1650* (UC, DS).

Related to apm. *bernardina*.—CALIFORNIA: Summit, Sierra Nevada, alt. 2500 m, *Jones* in 1900 (Po); Bullion Flat, region of Mt. Whitney, Tulare County, *Dudley 2540* (DS). NEVADA: Hawthorne, Mineral County, alt. 1500 m, *Jones* in 1897 (Po). OREGON: Dutchman's Peak, Siskiyou Mtns., Jackson County, alt. 2270 m, *Thompson 12406* (Wn).

10. apm. *longiloba* (*acuminata-pleurocarpa* or *occidentalis* ?) (fig. 32*n–p*).—Stems 4.5–5.5 dm high, stout; basal leaves 18–25 cm long, the lobes elongate, 2.5–4 cm long, strongly dentate or again pinnatifid, the terminal portion linear-lanceolate, attenuate; inflorescence with 35–60 heads; involucres 10.5–12 mm high; inner bracts and florets 5 or rarely 6, closely resembling those of the preceding; achenes 7–7.5 mm; pappus 6.5–7 mm; ($2n = 44$?) (cf. p. 39). CALIFORNIA: Sawmill Peak, Mt. Pinos, Kern County, alt. 1820 m, *Hall 6384* (UC, DS); Alamos Mtn., Ventura County, alt. 1970 m, *Hall 6702* (UC); Erskine Creek, Kern County, alt. 1220–1500 m, *Purpus 5295* (G).

Related to apm. *longiloba*.—CALIFORNIA: near Big Flat, Siskiyou County, alt. 1600 m, *Howell 13331* (CA); Honey Lake, Lassen County, *Brandegee* in 1892 (UC); Gold Lake region, Plumas County, alt. 1400 m, *Bacigalupi 1700* (DS, CA); Lake Tahoe, *Evans* in 1891 (Minn); Highland Lakes, Alpine County, alt. 2650 m, *Howden* in 1935 (CFE); Mineral

King, Tulare County, alt. 2400 m, *Larkins* in 1904 (UC); Farewell Gap, Tulare County, *Culbertson 4560* (UC, DS, G, Po); near Tehachapi Peak, Tehachapi Mtns., Kern County, *Dudley 328* (UC, DS); Mt. Frazier, Ventura County, *Elmer 3884* (UC, DS, G, Minn, Po); Bear Valley San Bernardino Mtns., *Parish 1460* (UC, DS, G).

11. apm. *nevadensis* (*acuminata-occidentalis*).—Stems 3.5–4 dm high, basal leaves 20–25 cm long, elliptic-lanceolate in outline, the lobes lanceolate, acuminate, coarsely dentate, the terminal portion somewhat attenuate; lobes of cauline leaves linear-lanceolate, strongly attenuate, inflorescence crowded, of 20–40 heads; involucres 10–12.5 mm high; inner bracts 5–7, tomentulose; florets 5–9; pollen 0; achenes 7–8 mm long, definitely contracted at the apex; pappus 7.5 mm long; ($2n = 44$?). CALIFORNIA: east of Constantia (Red Rock), Lassen County, alt. 1818 m, *B. & S. 1763A* (UC). NEVADA: Lawton Springs, west of Reno, Washoe County, alt. 1450 m, *S. & J. 2186* (UC).

Related to apm. *nevadensis*.—CALIFORNIA: junction of East and Bubbs Creeks, Fresno County, alt, 2575 m, *Ferris & Bacigalupi 3814* (DS); Hockett trail to Little Kern River, Tulare County, alt. 2120–2420 m, *Dudley 1073* (DS). ARIZONA: Jacob's Pool, Kaibab Forest, *Jaeger* in 1926 (UC).

12. apm. *wallowensis* (*acuminata-pleurocarpa-occidentalis*).—Stems 3–3.5 dm high; basal leaves 18–20 cm long, broadly elliptic in outline, densely tomentose, the lobes narrowly deltoid; cauline leaves well developed, extending up into the inflorescence; inflorescence branching from the middle of the stem or below, bearing about 25 heads; involucre 13–15 mm high; inner bracts 5, densely tomentose, rather broad and obtuse, without setæ; florets 5-6; anther-tube 7 mm long, bearing pollen; achenes 9–10 mm long, brown, rather strongly ribbed; pappus 9.5–10 mm; ($2n = 88$?). OREGON: trail to Ice Lake, Wallowa Mtns., Wallowa County, alt. 2270 m, *B. & C. 80* (UC).

Related to apm. *wallowensis*.—CALIFORNIA: Thompson Peak, south of Janesville, Lassen County, alt. 2120 m, *S. & J. 2294* (UC).

These two collections are among the few forms transitional from *C. acuminata* to *C. pleurocarpa*.

13. apm. *tetonensis* (*acuminata-occidentalis-pleurocarpa*) (fig. 32*s*, *t*).—Height, shape of leaves, and character of the inflorescence similar to the last; lobes of leaves strongly dentate or again pinnatifid; involucres 11–13 mm high; inner bracts 5, similar to those of apm. *wallowensis*; outer bracts elongate, the longest 5–6 mm long; florets 5–6; anther-tube rudimentary and without pollen; achenes 8.5–9 mm long, distinctly contracted at the apex; pappus 7 mm; ($2n = 88$?). WYOMING: Teton Pass, Lincoln County, alt. 2575 m, *Hall 11468*, part (UC).

This form strongly resembles the last in habit, but is very distinctive in its elongate outer bracts.

14. apm. *Rydbergii* (*acuminata-exilis*) (fig. 32*q*, *r*).—Stems 6 dm high; basal leaves with linear central portion and linear, entire or pinnatifid lobes; inflorescence of 15–20 heads on slender, long or short peduncles; involucre 9–11 mm high; inner bracts 5–7, glabrous, without

setæ at the apex; florets 6–8; anther-tube well developed, 5 mm long, bearing pollen; pappus 5 mm long; achenes not seen; ($2n = 33$?). IDAHO: valley of Big Potlach River, Nez Perces County, *Sandberg, MacDougal, & Heller 326* (type of *C. seselifolia*, NY).

This form has leaves much like those of *C. exilis*, but its glabrous, few-flowered involucres are typical of *C. acuminata*. The only specimen seen is in very early flowering condition, and hence there is no evidence as to the nature of its achenes; with better material it may be characterized as a distinct subspecies.

15. apm. *viridis* (*acuminata-exilis*).—Stems 6.5–7 dm high; basal leaves green and glabrate, lanceolate in outline, the lobes short, lance-linear, entire; inflorescence more or less dichotomously branched, of 45–50 heads; involucre 13–15 mm high; inner bracts 5–8, glabrous, without setæ at the apex; florets 6–9; anther-tube 7 mm long, bearing pollen; pappus 9 mm long; achenes not seen; ($2n = 44$?). IDAHO: Nez Perces County, *Sandberg* in 1892 (Minn).

This form also approaches *C. exilis* in its leaves and inflorescence.

16. apm. *exiloides* (*acuminata-exilis*).—Stems 3.5 dm high; basal leaves green and glabrate, elliptic-lanceolate in outline, the lobes linear-lanceolate, attenuate, entire; inflorescence of 20–40 heads on short, erect peduncles; involucres 10–12 mm high; inner bracts 5–6, tomentulose, with rather conspicuous greenish-black setæ at the apex; florets 5–9; anther-tube 4.5 mm long, bearing pollen; achenes 6.5–7 mm long, brown, finely ribbed, slightly contracted at the apex; papus 5.5–6.5 mm; ($2n = 44$?). WASHINGTON: Clarkston-Pomeroy grade, Garfield County, *Pickett 1496* (WSC). OREGON: "Clear Water," *Spalding* (G).

Related to apm. *exiloides*.—COLORADO: North Park, alt. 2424 m, *Baker* in 1896 (type collection of *C. angustata*, NY). WYOMING: Bridger's Pass, Rocky Mtns., *Engelmann 185f* (G).

This form approaches still more closely to *C. exilis*, but its few-flowered heads and brown achenes place it in *C. acuminata*.

17*b* (17). **Crepis acuminata** subsp. **pluriflora** subsp. nov. (Fig. 32*u*, *v*.) —A subsp. *typica* differt capitulis cum 9–12 floribus; phyllis involucri interioribus 8, glabris vel ad basim minute tomentulosis; antheris 3.5–4 mm longis, sterilibus; styli ramis 2.8–3 mm longis; achæniis pallidis vel castaneis, valde costatis.

Differs from a subsp. *typica* in its larger involucres, which have consistently 8 inner bracts and 9–12 florets. The bracts, however, are glabrous or nearly so. The anthers are reduced and without pollen, while the style-branches are longer than those of diploid *C. acuminata*, although these are equaled by some of the polyploid forms of subsp. *typica*. The achenes are rather strongly costate, but not more so than those of some forms of subsp. *typica*.

Western and southwestern Colorado to northern New Mexico, where it is the only form of *C. acuminata* known, west to central Utah.

Although all the specimens of this subspecies seen bear no pollen whatever, and hence are almost wholly or completely apomictic, there is apparently quite a number of different apomicts present. Owing to lack of

sufficient material, these could not be adequately characterized. The chromosome numbers are probably $2n = 33$ and $2n = 44$. The following collections of this subspecies have been examined: COLORADO: Cedar Edge, Delta County, alt. 2120 m, *Baker 243* (type, UC no. 91870, Po, Minn, but some specimens of this collection are *C. intermedia*, see p. 185); Williams Fork, Routt County, *Sturgis* in 1903 (G); above Cimarron, Montrose County, alt. 2575 m, *Baker 386* (UC, DS, Po, RM, Minn); Sulphur Springs, Grand County, *Osterhout 3314* (Minn); Mancos, Montezuma County, *Baker, Earle, & Tracy 66*, part (UC, Clo); entrance to Mesa Verde National Park, 2120 m, *Goodman & Hitchcock 1358* (UC, DS). NEW MEXICO: without locality, *Palmer* in 1869 (US). UTAH: Mt. Nebo, Juab County, *Rydberg & Carlton 7702* (RM).

This subspecies might well be placed in *C. intermedia*, but since its glabrous involucres are so characteristic of *C. acuminata*, it is retained in the latter species.

18. **Crepis intermedia** Gray, Syn. Fl. 1, (2): 432, 1884 (Fig. 34)

Stems 3–7 dm tall (1.5–3 dm in one dwarf form), rather stout, striate, tomentose; basal leaves 1.5–4 dm long, narrowly elliptic in outline, long-petioled, pinnatifid with lanceolate, acute, ascending or reflexed, entire or dentate segments, the tips of the leaves mostly elongate and tapering, sparsely or strongly grayish-tomentose throughout; inflorescence an ample cymose panicle of 10–60 heads; involucres narrowly cylindrical, their bracts grayish-tomentose, less often glabrate or completely glabrous, occasionally glandular-pubescent or with a few black, glandless setae near the tips of the inner bracts; inner bracts 7–8 (rarely 10–12), lanceolate, obtuse; outer bracts deltoid, the longest 1/5–1/3 the length of the inner; florets 7–12 (–16) per involucre; corollas 14–30 mm long; anther-tube when well developed 5–6 mm long, or in some forms only 3–4 mm long, and abortive, with no pollen; style-branches 2.5–3.5 mm long; achenes 5.5–9 mm long, buff color or yellowish to brown, weakly to strongly costate, shorter than or exceeding the pappus. (*Hieraciodes intermedium* O. Ktze., Rev. Gen. 345, 1891; *Crepis acuminata* var. *intermedia Jepson*, Man. Fl. Pl. Calif. 1012, 1925.)

Sierra Nevada, California, north to Washington, east to Arizona, Utah, New Mexico, Colorado, southwestern Wyoming, and Alberta. Common in the western part of its range, infrequent and local eastward (see fig. 33).

This is an agamospecies, i.e., a group of polyploid apomicts which combine the characters of *C. occidentalis* and of either *C. acuminata* or *C. pleurocarpa*, or of all three of these species, while some of them possess characteristics of *C. modocensis* and *C. exilis*. The closest resemblance in habit is in most cases to *C. acuminata*, and for this reason, as well as the fact that the two species are connected by a continuous series of intergrades, Jepson's reduction of *C. intermedia* to a variety of *C. acuminata* is to some extent justified. Nevertheless, since there is an equally gradual transition from *C. intermedia* to *C. occidentalis* subsp. *pumila*, and so

to typical *C. occidentalis*, the only logical conclusion based on the existence of intergrading forms would be to include the whole group under a single species. This would make a very unwieldy systematic unit, and would obscure the real nature of the connections between the various forms.

FIG. 33. Distribution of *Crepis intermedia*. (Base map copyrighted by Rand McNally Company; reproduced by special permission.)

With the original description of *C. intermedia*, Gray did not cite any specimens; hence there is no type specimen for the species. Most of the specimens in the Gray Herbarium identified by Gray as *C. intermedia* are more or less fragmentary, but one of the best preserved, which shows both florets and achenes like those described by him, is a collection of Bolander from Yosemite Valley (no. 4930). This may therefore, for practical purposes, be considered as the type of *C. intermedia*. It is very much like apm. *Grayi* as described below, but the heads are somewhat

larger, the involucre being 15–16 mm long, and the achenes are longer, 9–10 mm long.

Of the large number of apomicts included in this species, the following are representative (see p. 69):

A. Largest heads of the inflorescence with 8 inner bracts and 10–15 florets.
  B. Plants not glandular.
    C. Achenes equaling or exceeding the pappus, contracted at the apex, the ribs mostly thin and not prominent.
      D. Involucral bracts devoid of setæ.
        E. Anther-tube well developed and bearing pollen.
          F. Stems 4–5 dm high; longest outer bracts 3.5 mm long; pappus 7.5–8.5 mm long ..... 1. apm. *Grayi*
          F. Stems 2.2–3.2 dm high; longest outer bracts 4.5–5.5 mm long; pappus 8.5–9 mm ..... 2. apm. *montana*
        E. Anther-tube rudimentary and without pollen ..... 3. apm. *sterilis*
      D. Involucral bracts bearing black, glandless setæ.
        G. Setæ present throughout the length of the inner and sometimes on the outer bracts ..... 13. apm. *setosa*
        G. Inner bracts bearing a few setæ near the apex.
          H. Anther-tube well developed and bearing pollen, 5–6 mm long.
            I. Leaf-segments entire or sparingly dentate; larger involucres of the inflorescence 13–14 mm long... 4. apm. *longifolia*
            I. Leaf-segments conspicuously dentate or again pinnatifid; larger involucres 16–17 mm long..... 5. apm. *arizonica*
          H. Anther-tube 3.5–4.5 mm long, rudimentary and without pollen.
            J. Stems 3–6 dm high; achenes 8–9.5 mm long.
              K. Stems very stout and tall; central part of leaves (excluding lobes) 2–4.5 cm broad; involucres 12–15 mm high; achenes yellowish ..... 6. apm. *grandis*
              K. Stems shorter; central part of leaves (excluding lobes) 0.7–1.8 cm broad ; involucres 10–13 mm high; achenes deep reddish brown ..... 7. apm. *washingtonensis*
            J. Stems 1.6–3 dm high; basal leaves with acuminate, strongly toothed or pinnatifid lobes; involucre 10–12 mm high; achenes 6–7.5 mm; pappus 6–7 mm long..... 8. apm. *sierræ*

C. Achenes shorter than the pappus, mostly rather thick and slightly contracted at the apex, strongly ribbed.
L. Involucral bracts without black setæ.
M. Larger lobes of well-developed basal leaves 2.5–4 cm long, dentate or pinnatifid; inflorescence ample, bearing 15–30 heads in well-developed plants, and branching from below the middle of the stem.
N. Involucres 11–13 mm high; pappus 7.5–8.5 mm long; achenes thick.... 9. apm. *plumaënsis*
N. Involucres 13–16 mm high; pappus 9–10 mm long; achenes slender.... 9*a*. apm. *lacustrensis*
M. Larger lobes of basal leaves 1–2 cm long, entire or somewhat dentate; inflorescence of 5–15 heads, mostly branching from above the middle of the stem.... 10. apm. *angustifolia*
L. Inner involucral bracts with a few black, glandless setæ at the apex; involucres 15–17 mm high; pappus 9–10 mm..... 11. apm. *longiceps*
B. Peduncles and involucres densely glandular-setose. 12. apm. *glandulosa*
A. Largest heads of the inflorescence with 10–11 inner bracts and about 20 florets..... 14. apm. *cupressensis*

1. apm. *Grayi* (*acuminata-occidentalis*) (fig. 34a-d).—Stems 4–5 dm high; basal leaves 2–2.5 dm long, with lanceolate, somewhat reflexed segments; leaves (bracts) of the inflorescence mostly entire; involucres 12–15 mm high; inner bracts 7–8, without trichomes or glandular pubescence; florets 8–10; longest outer bracts 3.5 mm long; anther-tube 5–5.5 mm long, bearing pollen; achenes 7.5–9 mm long; pappus 7.5–8.5 mm; ($2n = 55$?). CALIFORNIA: Collins Meadow, Fresno County, alt. 2120 m, *Hall & Chandler 540* (UC, DS, Minn); Buck Camp, Mariposa County, *Congdon* in 1895 (UC, DS, G); Sunnyside, Eldorado County, *Eastwood 57* (CA); Summit, Sierra Nevada, (Placer County ?), alt. 2500 m, *Jones 12253* (Po); west of Loyalton, Sierra County, alt. 1600 m, *B. & S. 1711* (UC). NEVADA: Verdi, Washoe County, alt. 1550 m, *S. & J. 2178* (UC).

Related to apm. *Grayi*.—CALIFORNIA: Yosemite Valley, *Bolander 4930* (G); "Sierras," alt. 2120 m, *Bolander* in 1872 (G). UTAH: City Creek Canyon, alt. 1970 m, *Jones* in 1880, part (Po).

2. apm *montana* (*occidentalis-acuminata*).—Stems 2.3–3.2 dm high; basal leaves 14–18 cm long, with narrowly deltoid, reflexed, entire or coarsely dentate lobes; heads 11–20 in an inflorescence; involucres 13–15 mm high, loosely whitish-tomentose near the base, more or less glabrate toward the apex of the inner bracts; outer bracts narrowly lance-deltoid, the longest 4.5–5.5 mm long; inner bracts 7–8; florets 8–12; anther-tube 6.5 mm long, well developed and bearing pollen; achenes 8.5–9.5 mm long, brown at maturity, somewhat attenuate and rather strongly ribbed; pappus 8.5-9 mm long; ($2n = 33$?). CALIFORNIA: Red Rock, north of Engelmine, Plumas County, alt. 2150 m, *S. & J. 2233* (UC); north of Mill Creek Meadows, Warner Mtns., Modoc County, *Applegate 8002*

(DS). OREGON: Lake County, alt. 1670–1970 m, *Ferris & Duthie 202* (DS).

Related to apm. *montana*.—CALIFORNIA: upper Relief Valley, Tuolumne County, *Peterson 447* ($2n = 55$?) (CFE). WASHINGTON: between Ellensburg and Wenatchee, Kittitas County, alt. 1350 m, *B. & C. 51* ($2n = 33$?) (UC); Liberty, Kittitas County, alt. 650 m, *Keck & Clausen 3538* ($2n = 33$?) (UC); Blue Mtns., Walla Walla County, *Piper 2438* (G). IDAHO: Teton Pass Mtns., east of Victor, Teton County, *Payson 2149*, part (CA).

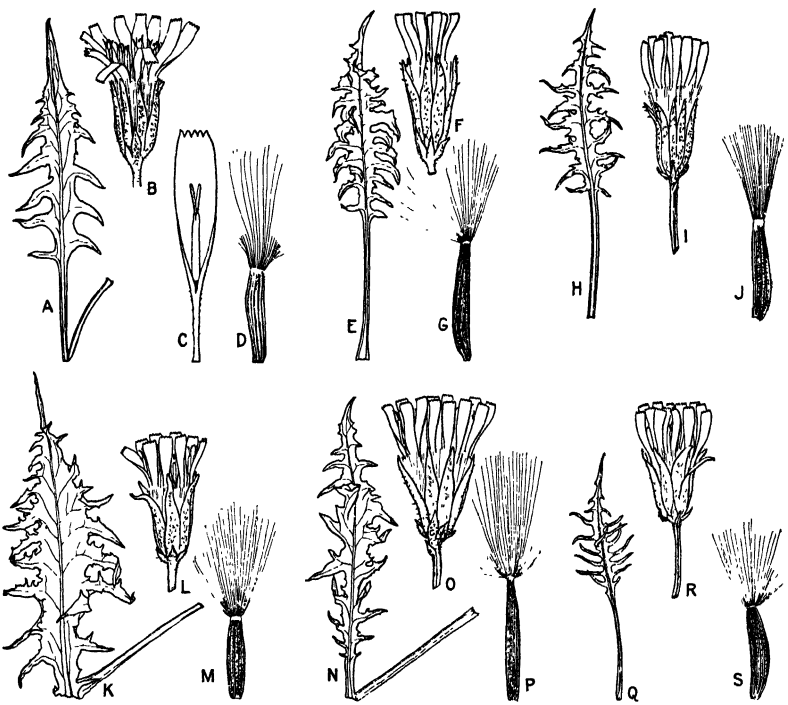


FIG. 34. *Crepis intermedia*. *a–d*, apm. *Grayi*, from *B & S. 1711*: *a*, leaf, × ¼; *b*, involucre, × 1; *c*, corolla, × 2; *d*, achene, × 2. *e–g*, apm. *arizonica*—*e*, *f*, from *Ferris and Duncan 2246*; *g*, from *Babcock and Goddard 534*: *e*, leaf, × ¼; *f*, involucre, × 1; *g*, achene, × 2. *h–j*, apm. *sierræ*, from *Heller 7087*: *h*, leaf, × ¼; *i*, involucre, × 1; *j*, achene, × 2. *k–m*, apm. *plumaënsis*, from *B. 156*: *k*, leaf, × ¼; *l*, involucre, × 1; *m*, achene, × 2. *n–p*, apm. *setosa*, from Harrison, Nebr., *Bates*: *n*, leaf, × ¼; *o*, involucre, × 1; *p*, achene, × 2. *q–s*, apm. *cupressensis*, from *Macoun 5080*: *q*, leaf, × ¼; *r*, involucre, × 1; *s*, achene, × 2.

3. apm. *sterilis*.—Similar to apm. *Grayi*, but with the lobes of the basal leaves narrower and mostly remotely dentate; involucres 12–14 mm high; *anther-tube rudimentary, 3–4 mm long, and without pollen*; achenes 8–9 mm long; pappus about the same length; ($2n = 55$?). NEVADA: Chiatovitch Creek, White Mtns., Esmeralda County, alt. 2450 m, *Duran 3077* (UC, RM); Big Indian Canyon, Hawthorne, Mineral County, alt. 1520

m, *Jones* in 1897 (Po); below Webber Wells, Charleston Mtns., Clark County, *Clokey 7404* (Clo).

Related to apm. *sterilis*.—CALIFORNIA: Convict Lake, Mono County, alt. 2300 m, *Lundh 322* ($2n = 44$?) (CFE); east of Mogul, Alpine County, alt. 2400 m, *Yates 5307* (CFE). NEVADA: Lawton Springs, west of Reno, Washoe County, alt. 1450 m, *S. & J. 2187* (UC). UTAH: Pine Valley Mtns., Washington County, *Purpus 6221* (US).

4. apm. *longifolia* (*acuminata-occidentalis-modocensis?*).—Stems 4–5 dm high; basal leaves 2.5–3 dm long, lobes lanceolate, reflexed, entire or coarsely toothed; involucre greenish and glabrate, 12–14 mm high; inner bracts 7–8, *with a few coarse, black, glandless setæ near the apex*; anther-tube 5.5 mm long, bearing pollen; achenes not seen; pappus about 8 mm; ($2n = 55$?). CALIFORNIA: near Loyalton, Sierra County, alt. 1600 m, *B. & S. 1720, 1730* (UC); Sardine Peak, Sierra County, *B. 139* (UC). NEVADA: Verdi, Washoe County, alt. 1515 m, *S. & J. 2174A* (UC). COLORADO: Mancos, Montezuma County, alt. 2120 m, *Baker, Earle, & Tracy 66*, part (Po, Minn).

No difference whatever could be found between the Colorado specimens and those from California, a remarkable fact in view of the great distance separating them.

5. apm. *arizonica* (*acuminata-occidentalis-modocensis?*) (fig. 34*e–g*).—Stems 3–4.5 dm high; basal leaves 15–20 cm long, the segments strongly and acutely dentate or again pinnatifid; heads 8–25 in an inflorescence; involucres 14–17 mm high; florets 9–13; anthers bearing some pollen; achenes 8.5–9.5 mm long, yellowish to dark brown when mature, rather strongly costate; pappus 8.5–9.5 mm; ($2n = 55$?). ARIZONA: Grand Canyon, Coconino County, alt. 1970–2050 m, *Babcock & Goddard 534* (UC); same locality, *Ferris & Duncan 2246* (DS, CA); *Toumey 664* (G). NEVADA: Charleston Park Camp Grounds, Charleston Mtns., Clark County, alt. 2270 m, *Clokey 7460*, part (Clo).

Like the last, this apomict is represented by forms practically indistinguishable from each other occuring at widely separated localities. Although *C. intermedia* was found by the senior author to be abundant at the Grand Canyon, only one apomict of it was found, which is identical with that found by the other two collectors whose specimens have been seen. In contrast to this, an equal area along the eastern side of the Sierra Nevada contains dozens of them. In the Charleston Mountains, as might be expected from their location, the situation is more nearly like that in the Sierras, since the two collections of *C. intermedia* seen from this region include three different apomicts.

6. apm. *grandis* (*acuminata-occidentalis-modocensis?*).—Stems 5–6 dm high, very stout; leaves 2.5–3 dm long, 7–11 cm broad, lobes irregularly reflexed, mostly entire; involucres 12.5–14.5 mm high; inner bracts densely grayish-tomentose, rather broad and obtuse at the apex, with a few black, glandless setæ near the apex; *anther-tube 4.5 mm long, with little or no pollen*; achenes 8.5–9.5 mm long, yellowish; pappus 8–8.5 mm; ($2n = 44$ or 55?). NEVADA: King's Canyon, Ormsby County, alt. 1700–2000 m, *Baker 1101*, part (UC, Po, G, RM); near Carson City, *Anderson* in 1865,

part (G,); Verdi, Washoe County, *S. & J. 2173A* (UC). CALIFORNIA: Bishop Creek, Inyo County, alt. 1880 m, *Hall and Chandler 7235* (UC).

Related to apm. *grandis*.—CALIFORNIA: Sierra Valley, northeast of Sierraville, Sierra County, alt. 1600 m, *B. 124, 125* (UC); Fallen Leaf Lodge, Lake Tahoe region, Eldorado County, alt. 2090 m, *Abrams 4867* (DS, G, Po); southwest of Horse Lake, Lassen County, alt. 1850 m, *S. & J. 2216* (UC). UTAH: Marysvale, Piute County, alt. 1820 m, *Jones 5388 i*, part (Po). COLORADO: Cedar Edge, Delta County, alt. 2120 m, *Baker 243*, part (G, Po).

7. apm. *washingtonensis* (*acuminata-exilis-modocensis-occidentalis?*). —Stems 3–5 dm high; basal leaves pinnatifid with linear-lanceolate, falcate, mostly strongly toothed lobes; lobes of the cauline leaves strongly ascending; *heads 10–13 mm high;* inner bracts 7–8, rather narrow, somewhat glabrate, with a few glandless trichomes near the apex; florets 8–12; anther-tube redimentary and without pollen; achenes 8–9 mm long, rather slender, *deep brown*, finely striate, slightly tapering toward the apex; pappus 8–8.5 mm; ($2n = 44$ or 55?). WASHINGTON: upper Naches region, Yakima County, *Grant 8351* (US); North Fork Ahtanum Creek, alt. 1060 m, Yakima County, *Bernath 1060* (WSC); between Cle-Elum and Easton, Kittitas County, *Thompson 6689*, part (US); western Klickitat County, *Suksdorf* in 1881 (US).

Related to apm. *washingtonenesis*.—WASHINGTON: between Asotin and Anatone, Asotin County, *Eastwood & Howell 3213* (CA). OREGON: Barnhard, Umatilla County, *Henderson* in 1886 (DS); The Dalles, Wasco County, *Heller 10083* (DS, US, G).

8. apm. *sierræ* (*acuminata-modocensis-occidentalis*) (fig. 34*h–j*).— *Dwarf;* stems 1.6–3 dm high; basal leaves 1–2 dm long, the lobes acuminate, callous-tipped, strongly toothed or again pinnatifid into linear lobes; involucre 10–12 mm high; inner bracts 6–8, tomentulose to glabrate, with a few black, glandless trichomes near the apex; florets 8–11; anther-tube about 4.5 mm, bearing some pollen; achenes 6–7.5 mm long, yellowish; pappus 6–7 mm; ($2n = 44$?) (see p. 62). CALIFORNIA: Castle Peak, Nevada County, alt. 2730 m, *Heller 7087*, part (UC, DS, RM); Middle Fork of San Joaquin River, Madera County, alt. 2570 m, *Ferris 8838* (DS); Gaylor Lakes, Yosemite National Park, alt. 3180 m, *Mason 11395* (UC); Red Rock, north of Engelmine, Plumas County, alt. 2150 m, *S. & J. 2251* (UC); east of Twin Lakes, Mammoth Lakes district, Mono County, alt. 2670 m, *Stebbins 2548* (UC).

Related to apm. *sierræ*.—CALIFORNIA: Kaiser Peak, Fresno County, alt. 3100 m, *Grant 1119* (DS); San Joaquin Park, Mono County, alt. 2800–3300 m, *Wright* in 1930 (SB); Hunter's Ranch Mtns., Inyo County, *Hall & Chandler 7117* (UC). UTAH: La Sal Mtns., *Jones* in 1913 (Po). WYOMING: Green River, Sweetwater County, *Nelson 4730* (Po, RM); Carter, Uinta County, *Nelson* in 1902 (RM).

9. apm. *plumaënsis* (*acuminata-pleurocarpa-occidentalis*) (fig. 34*k–m*). —Plants 5–6 dm tall; basal leaves more densely tomentose than in the last, less deeply pinnatifid, but the lobes very sharply dentate or again lobed; inflorescence more nearly like that of subsp. *typica*, with generally more numerous heads; involucres 11–13 mm high; inner bracts 8;

florets 8–12; anthers 5.5 mm long, bearing pollen; achenes 6–7.5 mm long; pappus 7.5–8.5 mm; ($2n = 55$?). CALIFORNIA: below Sloat, Plumas County, *B. 159* (UC); below Blairsden, Plumas County, *B. 155* (UC); Feather River Inn, Plumas County, *B. 156* (UC); Susanville, Lassen County, alt. 1280 m, *S. & J. 2203* (UC); Burgess Springs, T. 33 N., R. 8 E., Lassen County, alt. 1700 m, *S. & J. 2335* (UC).

Related to apm. *plumaënsis*.—CALIFORNIA: head of Lemmon Canyon, east of Sierraville, Sierra County, alt. 2060 m, *B. 146* (UC). WASHINGTON: Earl Ridge, Kittitas County, alt. 1360 m, *Thompson 9543* (Mo).

9*a*. apm. *lacustrensis* (*acuminata-occidentalis-pleurocarpa*).—Similar in habit and leaf shape to apm. *plumaënsis*; involucres 13–16 mm high; inner bracts 8, conspicuously white tomentose on the margins; florets 9–13; anthers 5.5 mm long, bearing pollen; achenes 7.5–8 mm long, slender and contracted at the apex; pappus 9–10 mm long; ($2n =$ about 55!). CALIFORNIA: near Clear Lake, Lake County, *Torrey 267a* (G); 9 miles southeast of Lower Lake, Lake County, *Stebbins 2499* (UC); 2 miles southeast of Lower Lake, *Stebbins 2500* (UC); near Cache Creek, east of Clear Lake, Lake County, *Stebbins 2501* (UC).

Related to apm. *lacustrensis*.—CALIFORNIA: near Auburn but in Eldorado County, *Brandegee* in 1908 (UC).

10. apm. *angustifolia* (*acuminata-occidentalis-pleurocarpa*).—Stems 4–6 dm high; leaves about as in the last, but somewhat narrower; inflorescence as in the last, with 18–32 heads; involucres 13–16 mm high; outer bracts narrowly deltoid, the longest 3–3.6 mm long; inner bracts 6–8, florets 6–10; achenes 7–8 mm; pappus 8–9 mm long; ($2n = 55$?). CALIFORNIA: Black Mtn., near Milford, Lassen County, alt. 1930 m, *S. & J. 2315* (UC); Milford, Lassen County, *Brandegee* in 1892 (UC); east of Champ's, Lassen County, alt. 1720 m, *S. & J. 2340* (UC).

Related to apm. *angustifolia*.—CALIFORNIA: between Fallen Leaf and Cascade Lakes, Eldorado County, *Baker* in 1904 (UC); near Loyalton, Sierra County, alt. 1600 m, *B. & S. 1712, 1713, 1728, 1729* (UC); north of Davis Creek, Modoc County, alt. 1525 m, *Keck & Clausen 3721* (UC); Saddle Mtn., near Fall River Mills, Shasta County, alt. 1450 m, *S. & J. 2388* (UC). OREGON: west side of Summer Lake, Lake County, *Applegate* 7377 (DS); trail to Wenaha River, Wallowa County, *Darlington 293* (WSC). WASHINGTON: Godman Springs, Blue Mtns., Columbia County, *Constance et al. 1202* (WSC).

11. apm. *longiceps* (*acuminata-occidentalis-modocensis*).—Stems 5–6.5 dm high; basal leaves pinnatifid with narrowly deltoid or lanceolate strongly toothed lobes; involucre 16–17 mm high, outer bracts narrowly deltoid or lanceolate, the longest 4.2–5.8 mm long; inner bracts 6–8, *bearing a few black setæ near the apex*; florets 8–12; anther-tube well developed, 6 mm long; achenes 8–10 mm long; pappus 9–10 mm; ($2n =$ 44?). CALIFORNIA: Black Mtn., near Milford, Lassen County, alt. 1880–1950 m, *S. & J. 2316, 2328* (UC).

Related to apm. *longiceps*.—CALIFORNIA: Red Rock, north of Engelmine, Plumas County, *S. & J. 2232* (UC); Willow Creek, southeast of Adin, alt. 1750 m, *S. & J. 2347* (UC); Fall River Mills, Shasta County, alt. 1000 m, *S. & J. 2381* (UC).

12. apm. *glandulosa* (*acuminoto-occidentalis-Bakeri*).—Stems 2.7–3 dm high; basal leaves about 15 cm long, with lanceolate, coarsely toothed lobes; inflorescence a dense cyme of 15–25 heads on short, divaricate peduncles, these and the involucres densely beset with coarse, gland-tipped setæ; involucres 10–12 mm high; outer bracts deltoid, the longest 4.5–5 mm long; inner bracts 7–8; florets 10–12; achenes 6.5–7.5 mm long, slender, attenuate toward the apex, the ribs rather prominent, dark brown at maturity; pappus 6.5–7.5 long; ($2n = 33$?). WYOMING: Fort Steele, Carbon County, *Nelson 7239*, part (G, Minn).

Related to apm. *glandulosa*.—CALIFORNIA: north of Sierraville, Sierra County, alt. 1515 m, *B. 126, 127* (UC).

13. apm. *setosa* (*acuminata-modocensis-occidentalis*) (fig. 34*n–p*).—Stems 3–3.5 dm high; basal leaves elongate, 15–25 cm long, the lobes narrowly deltoid, strongly dentate; inflorescence of 5–8 heads; involucres 13–14 mm high; outer bracts deltoid, the longest 4–4.5 mm long; inner bracts 7–8, conspicuously setose throughout; florets about 12; anthers well developed and bearing pollen; achenes 9–9.5 mm long, slender, deep reddish brown; pappus 9 mm; ($2n = 44$?). WYOMING: Newcastle, Weston County, *Bates* in 1896 (Minn). NEBRASKA: Harrison, Sioux County, *Bates* in 1896 (G).

This form is transitional from *C. acuminata* to *C. modocensis* but probably has some admixture of *C. occidentalis* also.

14. apm. *cupressensis* (*occidentalis-exilis*) (fig. 34 *q–s*).—Stems 2.2–3 dm high; basal leaves 9–13 cm long, with lance-linear central portion and elongate, lance-linear, entire lobes; inflorescence of 4–8 heads in a flat-topped cyme; involucres 10–11 mm high; inner bracts 8–11, narrow, without setæ; outer bracts lance-deltoid, the longest 3–4 mm long, about 1/3 the length of the inner; florets 15–20; corollas 11–12 mm long; anther-tube rudimentary and without pollen; achenes chestnut brown, 6.5–7 mm long, thick and strongly costate, slightly contracted at the apex; pappus 5.5–6 mm; ($2n = 33$ or 44?).—ALBERTA or SASKATCHEWAN ("Assiniboia"): Cypress Hills, *Macoun 5080* (Minn, Mo).

This form is placed very tentatively in *C. intermedia* on the basis of its narrow heads, brown achenes, and short pappus. In habit, particularly the shape of the leaves and involucral bracts, it strongly suggests *C. exilis*, but the brown, strongly costate achenes are those of *C. occidentalis* or *C. intermedia*. In the key to the species presented above, the few-headed inflorescences and many-flowered involucres of this form would place it in *C. occidentalis*, but in its other characteristics it would go into *C. intermedia*. It apparently represents an allopolyploid derivative of *C. occidentalis* and *C. exilis*, and as such could be treated as a distinct species if more material of it were available.

C. intermedia, affinity not certain.–ALBERTA: Crow's Nest Lake, *Macoun 23095* ($2n = 88$?) (Po). In its thick, strongly ribbed achenes, which are greenish at the base, this race is unique, and it appears to be a derivative from crossing of all three species, *C. acuminata, C. occidentalis*, and *C. exilis*. However, the one specimen at hand is in too poor a condition for an adequate description to be made.

INDEX TO SPECIES, SUBSPECIES, AND SYNONYMS

(Valid species are printed in roman; synonyms are italicized.)

Barkhausia elegans, 85
nana, 84

Crepidium caulescens, 98
glaucum, 98
runcinatum, 93

Crepis aculeolata, 96
acuminata, 169, 170
acuminata gracilis, 162
acuminata intermedia, 179
acuminata pleurocarpa, 108
acuminata pluriflora, 178
acuminata typica, 170
alpicola, 93
Andersonii, 104
angustata, 162, 170
atribarba, 167
Bakeri, 138, 139
Bakeri Cusickii, 140
Bakeri idahoensis, 141
Bakeri typica, 139
Barberi, 102
barbigera, 154
biennis, 93
biennis var. *americana*, 93
bursifolia, 88
capillaris, 86
chamæphylla, 98
Cooperi, 87
Cusickii, 140
dakotana, 93
denticulata, 93
elegans, 85
exilis, 159, 167
exilis originalis, 162
exilis typica, 167
glareosa, 154
glauca, 98
glaucella, 93
gracilis, 162, 167
grandifolia, 125
intermedia, 179
intermedia gracilis, 162
intermedia pleurocarpa, 108
lancifolia, 100
modocensis, 141, 142
modocensis glareosa, 154
modocensis rostrata, 152
modocensis subacaulis, 148
modocensis typica, 142
mogollonica, 102
monticola, 114
nana, 84
neomexicana, 93
nicæensis, 85
obtusissima, 96
occidentalis, 118
occidentalis conjuncta, 134
occidentalis, costata, 124
occidentalis crinita, 114, 153
occidentalis gracilis, 162, 167
occidentalis nevadensis, 134, 148
occidentalis pumila, 128
occidentalis subacaulis, 148
occidentalis typica, 120
pallens, 96
perplexans, 93
petiolata, 96
platyphylla, 96
pleurocarpa, 107
pumila, 128
riparia, 93
riparia parva, 93
rostrata, 153
rubra, 87
runcinata, 90
runcinata alpicola, 93
runcinata Andersonii, 104
runcinata Barberi, 100
runcinata ciliosa, 104
runcinata glauca, 98
runcinata Hallii, 104
runcinata hispidulosa, 96
runcinata imbricata, 102
runcinata typica, 93
scopulorum, 142
sesilifolia, 170
setosa typica, 89
subacaulis, 148
subcarnosa, 104
taraxacifolia, 90
tectorum, 87
tomentulosa, 93
vesicaria taraxacifolia, 90
virens, 86

Hieraciodes acuminatum, 170
caulescens, 98
elegans, 85
intermedium, 179
nanum, 84
occidentale, 120
runcinatum, 93

Hieracium runcinatum, 93

Lapsana capillaris, 86

Malacothrix crepoides, 86

Psilochaenia occidentalis, 120, 125

Youngia elegans, 85
nana, 84

INDEX TO EXSICCATÆ CITED

The specimens are cited by the collector's number in italics, when present, otherwise by the year of collection. Within the parentheses are given the number of the species (preceding the colon, in bold-face type), and of the subspecies or apomictic form (following the colon) with which the specimen is identified. The letter D indicates that the specimen belongs to the diploid form of the species in question.

Abrams, LeRoy, *4497* (**17**:8); *4867* (**18**:6)
Aiton, G. B., in 1892 (**16**:3)
Ames, Mrs. Pulsifer, in 1878 (**11**:8)
Anderson, C. L., in 1865 (**9**:6; **12**:16; **18**:6)
Anderson, F. W., in 1887 (**14**:2)
Applegate, E., *1936* (**17**:D); *2300* (**13**:1); *7377* (**18**:10); *7680* (**17**:2); *8002* (**18**:2); *11305* (**10**:1)
Austin, Mrs. R. M., in 1893 (**13**:1); in 1894 (**14**:5,6); in 1897 (**11**:8)
Babcock, E. B. (B.), *116* (**17**:D); *118* (**9**:1–3); *124, 125* (**18**:6); *126, 127* (**18**:12); *130* (**14**:3); *139* (**18**:4); *141, 142, 143* (**13**:1); *146, 155, 156, 159* (**18**:9); *148, 410* (**17**:7); *153, 154,* (**12**:24); *157* (**12**:D); *161* (**10**:3); *408A* (**12**:4); *408B* (**12**:17); *411* (**12**:5); *432* (**17**:5); *446* (**17**:6); *2402* (**12**:16)
Babcock, E. B., and Collins, J. L. (B. & C.), *33* (**15**:4); *35, 38* (**15**:3) *49* (**15**:6); *51* (**18**:2); *53, 54, 55* (**9**:2); *58* (**16**:8); *61* (**15**:1); *79* (**16**:2); *80* (**17**:12); *89* (**10**:11)
Babcock, E. B., and Goddard, D., *534* (**18**:5); *1012* (**17**:D)
Babcock, E. B., and Navashin, M. (B. & N.), *121* (**14**:8); *137, 172* (**14**:11); *168* (**12**:D); *180* (**10**:11); *183* (**11**: 9)
Babcock, E. B., and Stebbins, G. L. Jr. (B. & S.), *1598* (**14**:12); *1606* (**14**:11); *1630, 1685, 1691* (**12**:1); *1632, 1648, 1796, 1857* (**12**:19); *1641* (**14**:14); *1687, 1693* (**12**:2); *1689, 1750, 1846* (**12**:17); *1711* (**18**:1); *1712, 1713, 1728, 1729* (**18**:10); *1720, 1730* (**18**:4); *1724* (**12**:1); *1727, 1749, 1795, 1845, 1858* (**12**:16); *1748* (**12**:-D); *1751* (**17**:8); *1763A* (**17**:11); *1776, 1964–1972* (**17**:D); *1803, 1807, 1808B* (**14**:1); *1806* (**14**:6); *1808A* (**14**:D); *1810, 1848* (**17**:7);, *1844, 1886* (**12**:5); *1856* (**12**:18); *1884* (**12**:11); *1887, 1888, 1928, 1973* (**11**:D); *1896* (**10**:6); *1897* (**10**:7); *1898, 1900, 1903, 1904* (**12**:22); *1901* (**12**:20); *1930* **11**:5); *1932, 1938* (**12**:21); *1934* (**12**:10); *1937* (**11**:10); *1973* (**11**:D); *1977* (**10**:8)
Bacigalupi, R., *1700* (**17**:10)
Baker, C. F., in 1895 (**16**:5); in 1896 (**17**:16); *148* (**14**:6); *243* (**17**:17; **18**:6); *386* (**17**:17); *644* (**9**:1–3); *737* (**9**:1); *1062* (**9**:6); *1070* (**12**:2); *1101* (**18**:6)
Baker, C. F., Earle, F. S., and Tracy, C. M., *66* (**17**:17; **18**:4); *461* (**12**:8)
Baker, M. S., in 1893 (**17**:D); in 1894 (**11**:4); in 1904 (**12**:25; **14**:7; **18**:10)
Baker, M. S., and Nutting, F., in 1893 (**13**:1); in 1894 (**12**:5)
Ballard, C. A., *2824* (**9**:1)
Bates, J. M., in 1896 (**12**:13; **18**:13); in 1899 (**9**:1)
Beattie, R. K., and Chapman, R., in 1903 (**16**:3)
Bennett, D., *74* (**12**:21)
Bentley, G. H., in 1916 (**9**:3)
Bernath, F. E., *1060* (**18**:7)
Bethel, E., and Clokey, I. W., *4413* (**12**:6)
Blake, S F., *11837* (**9**:7)
Blankinship, J. W., in 1893 (**11**:1, **12**:24); *560a* (**12**:13); *1906* (**16**:10)
Blasdale, W. C., in 1896 (**11**:1)
Bolander, H. N., in 1872, *4930* (**18**:1); *6498* (**12**:18)
Bolander, H. N. and Keller in 1872 (**14**:7)
Bourgeau, E., in 1858 (**9**:1)
Brandegee, E. N., in 1898 (**9**:2; **14**:2)
Brandegee, K., in 1908 (**18**:*9a*)
Brandegee, T. S., in 1883 (**9**:2, 6); in 1887 (**10**:D; **14**:3); in 1892 (**11**:6; **17**:10; **18**:10); *754* (**9**:1); *924* (**12**:4)
Brannon, M. A., in 1896 (**9**:1)

Brown, H. E., *382* (12:3)
Bruce, Mrs. C. C., *2164* (14:D, 1); *2181* (12:6)
Burglehaus, F. H., in 1893 (12:13); in 1894 (9:1)
Butler, D. C., *748* (12:17); *750* (11:D); *754* (12:10); *1328* (13:1); *1365* (12:22); *1639* (17:3); *1758* (10:1)
Chandler, H. P., *1644* (12:26)
Clark, J. A., *29* (14:3)
Clemens, Mrs. J., in 1909 (9:2)
Clements, F. E., *152, 342* (9:1)
Clokey, I. W., *3429* (9:1, 1–3); *3973* (9:1); *4414* (12:6); *7404* (18:3); *7460* (18:5)
Collins, J. L., in 1927 (12:2, 17); *2220* (13:2)
Congdon, J. W., in 1895 (18:1)
Constance, L., and McMurray *1159* (16:D)
Constance, L., et al. *1202* (18:10)
Cooper, Mrs. R. D., *1174* (17:1)
Cooper, W. S., *218* (9:1)
Copeland, E. B., *1532* (12:25); *3755* (10:D)
Cotton, J. S, *383* (16:8); *705* (15:3); *1068* (16:8)
Coulter, J. M., in 1873 (9:1–3)
Coville, F. V., and Kearney, T. H., *209* (12:9)
Cowgill, T. W., in 1901 (12:17)
Culbertson *4560* (17:10)
Cusick, W. C., *1713* (9:2); *1988* (14:D, 1); *2014* (9:5); *2511* (17:D); *2540* (12:9); *2872* (13:2)
Darlington, H. T., in 1913 (16:D); *293* (18:10)
Davidson, A., *2570* (9:7); *2599* (17:5)
Dawson, G., in 1883 (16:13)
Drew, E. R., in 1925 (12:24, 14:13)
Dudley, W. R., *328* (17:10); *1073* (17:11); *2540* (17:9)
Duran, V., *2501* (9:7); *3077* (18:3); *3257* (12:8)
Eastwood, A., in 1898 (13:1); in 1916 (12:5); *57* (18:1); *460* (12:24); *769* (12:27); *827* (10:11); *827a, 1188* (12:22); *1902* (10:11); *5285, 5725* (12:6); *7792* (9:6); *10780* (10:5); *11925* (10:11); *11925a* (10:7); *14853* (9:5); *15180* (10:9)
Eastwood, A., and Howell, J. T., in 1933 (12:8); *148, 259* (17:7) *276* (9:5); *565* (12:9); *3213* (18:7); *3303* (16:3); *3527* (16:8); *5032* (11:D)
Eastwood, A., and St. John, H., 13217 (16:D)
Eggleston, W. W., *6596* (12:6); *9278, 9542* (12:25); *9353* (13:1); *9943* (12:24); *12869* (16:D)
Elmer, A. D. E., *102* (16:3); *383* (16:6); *747* (12:5); *761* (16:2); *1031* (9:1, 2); *2621* (12:23); *3884* (17:10); *3892* (12:3); *4872* (12:18)
Engelmann, W. H., *185f* (17:16)
Evans, H. M., in 1918 (17:1)
Evans, W. H., in 1891 (17:10)
Ferris, R. S., *8838* (18:8)
Ferris, R. S., and Bacigalupi, R., *3814* (17:11)
Ferris, R. S., and Duncan, C., *2246* (18:5)
Ferris, R. S., and Duthie, R., *183* (17:5); *202* (18:2); *281* (11:5); *842* (16:3)
Fiker, C. B., *251* (16:8); *710, 770* (16:2); *1258, 1259* (16:D); *1596* (16:4)
Fletcher, J., in 1885 (12:8; 14:15)
Flodman, J. H., in 1896 (9:1); *922* (16:10)
Forest Service 23916 (9:1)
Fraser, W. P., in 1925 (9:3)
Furlong, H. W., et al. in 1901 (12:19)
Garrett, A. O., in 1927 (14:6); *1497* (9:3); *1829* (12:8)
Geis, H., *33* (12:24)
Gibbons, W. P., in 1896 (11:2)
Gillespie, D. K. (see Kildale)

Goodding, L. N., in 1902 (12:17); *95* (14:2); *323* (17:D); *522, 1087* (9:1); *1089* (9:3); *1657* (9:2)
Goodman, G., and Hitchcock, C. L., *1358* (17:17)
Grant, A. L., *1119* (18:8)
Grant, J. M., in 1930 (14:15); *8351* (18:7)
Greene, E. L., in 1893 (9:1–6; 16:10); in 1895 (12:8); in 1896 (9:1–3); *810* (11:1)
Griffiths, D., *5354* (9:3, 4)
Griffiths, D., and Cotton, J. S., *214* (16:4); *421* (16:2)
Hall, H. M., *6384, 6702* (17:10); *6388* (12:15); *6595* (12:14); *7534* (17:9); *8597* (10:1, 4; 12:26); *8743* (12:25); *9065* (17:8); *9468* (11:7); *9504* (10:2); *9532* (11:5); *9533* (12:21); *11439* (17:D); *11468* (16:11; 17:13); *11510* (17:D); *11824, 11281* (9:71)
Hall, H. M., and Babcock, E. B., *4024* (10:2); *4116* (12:14); *4438* (10:11)
Hall, H. M., and Chandler, H. P., *540* (18:1); *7117* (18:8); *7156* (12:4); *7235* (18:6)
Hanson, H., *C 45* (9:1)
Hapeman, H., in 1932 (9:1)
Hasse and Davidson in 1907 (12:15)
Head, A., in 1921 (12:14, 21; 14:8; 17:7)
Heller, A. A., in 1902 (11:7); *3302* (16:13); *7086* (14:8, 10); *7087* (17:7; 18:8); *8065* (12:10); *9474* (9:3); *9715* (14:7, 10); *10083* (18:7); *12104* (10:4)
Heller, A. A., and Kennedy, P. B., *8802* (18:1); *8666* (9:6)
Henderson, L. F., in 1886 (18:7); in 1894 (13:3; 16:3); *3668, 3669* (9:3); *5266* (12:9); *5268* (15:7); *5559* (16:13); *8525* (12:3); *8527* (14:4); *8531* (14:3); *8532* (14:2); *12910* (13:2); *14479* (16:8)
Herriot, W., *42864* (9:1)
Hillman, F. H., in 1894 (14:6)
Hitchcock, A. E., *388* (14:7); *698* (9:7); *1349* (9:3)
Hitchcock, C. L., *2308* (14:2)
Hitchcock, C. L., and Samuel, E., *2533* (13:3); *2534* (12:5)
Hoffman, R., in 1929 (12:15)
Hoover, R. F., *1423* (18:1)
Horner, R. M., *167* (16:1)
Howden, W. R., in 1935 (17:5, 10)
Howell, J. T., *12144* (14:2, 3); *12804* (10:D); *13192* (10:1); *13331* (17:10); *13689* 11:D)
Howell, Thomas, in 1879 (14:15); in 1880 (12:9); in 1881 (15:2); in 1885 (9:2); in 1887 (10:2); *172* (12:17)
Huntington, A. E., in 1890 (9:1)
Jaeger, E. C., in 1926 (12:14; 17:11)
Johnston, I. M., *1650* (17:9)
Jones, G. N., *979* (16:13); *1926* (12:27); *3168, 3215, 3330* (12:23)
Jones, M. E., in 1878 (16:10); in 1880 (9:3; 18:1); in 1881 (12:24); in 1882 (14:6); in 1886 (17:2); in 1891 (14:2, 6; 17:8); in 1893 (14:6); in 1894 (9:3); in 1897 (9:2; 12:25; 14:1, 6; 17:9; 18:3); in 1899 (16:12); in 1900 (17:9); in 1901 (9:3; 16:12); in 1903 (9:4); in 1904 (14:2); in 1905 (9:2; 14:2); in 1908 (9:1; 16:3, 11); in 1909 (9:2; 16:3, 10); in 1910 (9:3; 14:6; 17:7); in 1911 (9:2; 16:D, 6, 8); in 1912 (9:3); in 1913 (9:3; 18:8); in 1922 (9:1, 2; 12:6); in 1924 (16:10; 17:2); in 1927 (9:7); *159, 1758* (9:1); *758* (9:2); *5388i* (18:6); *5528* (17:7); *5743, 5790* (9:1, 2); *12253* (18:1)
Jones, W. W., in 1899 (14:2); in 1902 (9:1); *498* (12:8)
Keck, D. D., *564* (12:4); *613* (12:12); *622* (17:1); *671* (14:3); *753* (17:2); *902* (16:11)
Keck, D. D., and Clausen, J., *3502* (9:2); *3503* (16:8); *3529* (15:3, 4); *3530* (13:1); *3538* (18:2); *3554* (16:D); *3555* (15:6); *3569* (16:8); *3614* (17:D); *3634* (16:12); *3665* (12:11); *3672* (16:1); *3698* (9:2); *3721* (18:10); *3752* (12:3); *3759* (12:17)
Kellogg, A., in 1870 (12:24; 14:7, 8)

Kellogg, A., and Brannan in 1870 (**14**:7)
Kellogg, L., in 1909 (**17**:7)
Kelsey, F. D., in 1890 (**9**:2); in 1898 (**16**:3)
Kennedy, P. B., in 1901 (**12**:D); *539* (**17**:2); *1634* (**13**:1); *2061* (**9**:5); *2094* (**12**:1); *4109* (**14**:1); *4120* (**16**:10)
Kildale, D., *5374* (**12**:26); *8845* (**10**:4); *9337* (**13**:2); *9884* (**10**:5); *10701* (**10**:8); *10815* (**10**:2)
Kirkwood, J. E., *1763* (**16**:3)
Large, T., *42* (**16**:1)
Larkins, Mrs. C. L., in 1904 (**17**:10)
Larsen, E. L., *108* (**9**:3)
Lathrop, L. M., in 1909 (**17**:7)
Lawrence, W. E., *452* (**15**:8)
Lawrence, W. E., and Powell, G. M., *2913* (**16**:8)
Leiberg, J. B., in 1891 (**15**:3); *219* (**13**:1); *233, 2294* (**12**:9); *391* (**17**:D); *1039, 2323* (**9**.1, 2); *2313* (**17**:4); *2361* (**15**:8); *2493* (**14**:5); *2529* (**9**:5)
Lemmon, J. G., in 1874 (**9**:6; **11**:6); in 1875 (**14**:12); in 1880 (**14**:14)
Letterman, G. W., in 1884 (**17**:D)
Linsdale *613, 624* (**9**·7)
Loveless, M., *146* (**13**·2)
Lundh, R. W., *322* (**18**:3)
Lunell, J., in 1899, 1912 (**9**:1)
MacBride, J. F., *61* (**12**:20); *378* (**17**:1); *884* (**9**:2)
MacBride, J. F., and Payson, E. B., *3173* (**9**:1–3); *3283* (**16**:3; *3352* (**12**:6)
McCabe, T. T., *200* (**16**:1); *2358* (**16**:3)
Macoun, J., in 1884 (**16**:12); in 1889 (**12**:7); in 1890 (**16**:D, 3); in 1891, 1894 (**9**:1); *5080* (**18**:14); *11709* (**12**:12); *23095* (**18**:?); *65028* (**16**:D); *76992* (**16**:1)
Macoun, J., and Herriot, W., *42863* (**9**:1); *42866* (**9**:3)
Maguire, B., *3169* (**17**:D); *3911* (**12**:5)
Manning, Mrs. M. H., *181* (**12**:21); *471* (**13**:1)
Mason, H. L., *4721* (**12**:5); *4752* (**14**:6); *4804* (**12**:17); *11395* (**18**:8)
Merrill, E. D., and Wilcox *721* (**9**:3)
Metcalfe, O. B., *576* (**9**:4)
Michaels, E., in 1921 (**17**:5)
Minthorn, M., *99* (**17**:2)
Moodie, M. E., in 1913 (**9**:1)
Moore, E. J., in 1910 (**14**:2)
Moyer, L. R., in 1896, 1897 (**9**:1)
Nelson, A., in 1902 (**18**:8); *356* (**17**:D); *787, 2513* (**9**:3); *1393, 3251* (**16**:11); *4548* **14**:2); *4719* (**12**:8); *4730* (**18**:8); *5646* (**14**:6); *6147* (**9**:1–3); *7239* (**14**:6; **18**:12); *7243* (**12**:4); *7331* (**17**:1); *8693, 9437* (**9**:1)
Nelson, A. and E., *5755* (**16**:3)
Nelson, A., and MacBride, J. F., *1176, 1339* (**17**:D); *1233* (**14**:2); *1488* (**14**:2); *1727* (**16**:10); *1885* (**12**:5); *1932* (**14**:1)
Nelson, E. W., *6107* (**9**:14)
New York Botanical Garden *3327* (**9**:1)
Newcombe, W. A., in 1915 (**16**:3)
Nicollet Expedition in 1839 (**9**:1)
Nuttall, T., *s. n.* (**12**:13, **17**:D); in 1834 (**9**:13)
Osterhout, G. E., in 1894 (**16**:11, **17**:D); in 1896 (**9**:3); in 1897 (**9**:1, **14**:6); *2979* (**16**:11); *3003* (**17**:2); *3314* (**17**:17); *3315* (**16**:10); *3531* (**14**:2); *6580* (**9**:3)
Over, W. H., *16305* (**9**:1)
Ownbey, M., *657* (**14**:3)
Palmer, Edward, in 1869 (**17**:17); *140* (**12**:8); *291* (**12**:6)
Palmer, Ernest J., *37310* (**12**:13)
Parish, S. B., in 1886 (**14**:10); *3720* (**12**:3); *10967* (**14**:10)
Parish, S. B. and W. F., *1460* (**17**:10)

Parry, C. C., in 1864 (16:10)
Patterson, H. N., *86* (9:1)
Payson, E. B. and L. B., *1752* (12:8); *2007* (9:1–3); *2149* (18:2); *2607* (12:13); *2609A* (14:2); *2914* (9:1); *3839* (12:13); *4584* (16:11); *4869* (12:13); *4892* (16:12)
Payson, E. B., and Armstrong *3323* (12:8); *3558* (16:11)
Peck, M. E. *2972, 2973* (15:3); *3977* (16:9); *3978* (11:2); *3980, 4144, 15680a* (12:20); *3981, 4140* (12:21); *4139* (16:9); *4142* (16:3); *4143* (16:1); *4975, 10796* (9:2); *8015, 16734* (12:22); *8267* (12:26); *8425* (10:5); *9366* (17:D); *9925* (15:7); *9978* (16:1); *10100* (16:3); *13802* (12:9); *14019, 19487* (9:5); *14990* (12:17); *15255* (14:12); *15538* (11:3); *16431* (10:8); *17091* (14:4); *19608* (14:12)
Peirson, F. W., *6829* (11:8)
Pendleton, T., and Reed, F. M., *1227* (17:5)
Peterson, W. A., *447* (18:2)
Pickett, F. L., *1496* (17:16)
Piper, C. V., in 1894 (16:3); *1611* (16:8); *2264* (15:8); *2265* (15:3); *2437* (16:12); *2438* (18:2); *2509* (18:4); *2704* (14:16); *2737* (16:4); *6386* (12:20)
Porter, T. C., in 1873 (9:1, 2)
Prescott, H. S., in 1912 (11:1)
Pringle, C. G., in 1881 (10:4); in 1882 (10:1, 5)
Purpus, C. A., *5295* (17:10); *5423* (12:4); *6221* (18:3); *7088* (12:6)
Ramaley, F., *7014* (16:5)
Rattan, V., in 1867 (12:18); in 1878 (12:25); in 1884 (13:1)
Rixford, G., *s. n.* (10:5)
Rose, J. N., *458* (9:3); *680* (14:2)
Rust, H. J., *332* (15:3)
Rydberg, P. A., in 1892 (9:1); in 1895 (14:2); *217* (9:1)
Rydberg, P. A., and Bessey *5301, 5302* (17:D); *5304* (16:3); *5305* (12:14); *5306* (12:13); *5308* (16:11)
Rydberg, R. A., and Carlton *6923* (9:3); *7702* (17:17)
St. John, H., Courtney, and Parker *3712* (16:7)
St. John, H., and Pickett, F. L., *6167* (16:8)
St. John, H., and Smith, C. P., *8372* (12:27)
Sandberg, J. H., in 1892 (16:10; 17:15)
Sandberg, J. H., and Leiberg, J. B., in 1893 (14:15; 15:1; 16:1); *208* (9:2); *225* (14:15); *232* (16:6); *256* (16:D); *313* (15:1)
Sandberg, J. H., MacDougal, D. T., and Heller, A. A., *268* (18:3); *326* (17:14)
Scheuber, E. W., in 1901 (9:1, 2; 17:D)
Schmoll, H., *1225* (12:6)
Schmoll, H., and Nusbaum, D., *1589* (14:6)
Scribner, F. L., *126a* (17:D)
Seig, S., *20* (12:9)
Sharp, S. S., *119* (12:13)
Sharsmith, H. K., *3059* (11:5); *3185* (12:18)
Shaw, C. H., *683* (16:3)
Shear and Bessey *4004* (9:1)
Sheldon, R. P., *8316* (16:2)
Sherwood, W., *340* (16:3); *602* (12:26); *610* (12:5)
Shockley, W. N., *266* (9:6)
Smiley, F. J., *571* (12:17)
Smith, L. E., in 1915 (13:2); in 1927 (12:2; 14:11); *474* (10:D); *696* (12:D); *699* (13:2)
Sonne, C. F., in 1884 (12:24); in 1885 (14:3)
Soth, Mrs. M. E., *P26* (17:4); *P242* (14:4)
Spalding, *s.n.* (17:16)
Standley, P. C., *6636, 13326, 16892* (9:1); *7419* (9:3)
Stanford, E. E., *1063* (12:25)
Stansbury, Capt., *s. n.* (17:8)

Stebbins, G. L., *2499, 2500, 2501* (18:9a); *2548* (18:8); *2549* (17:5)
Stebbins, G. L., and Jenkins, J. A. (S. and J.), *2149, 2260* (13:1); *2151* (14:2); *2152* (14:14); *2158* (14:11); *2159, 2166* (14:13); *2169* (12:3); *2170, 2185* (12:D); *2173A* (18:6); *2174A* (18:4); *2175, 2196, 2339, 2362A, 2409* (12:21); *2177, 2338* (17:8); *2177A, 2313, 2380* (17:4); *2178* (18:1); *2182* (12:1); *2186* (17:11); *2187* (18:3); *2203, 2335* (18:9); *2209* (10:3); *2216* (18:6); *2221, 2382, 2402* (12:9); *2230* (12:26); *2232, 2316, 2328, 2347, 2381* (18:11); *2233* (18:2); *2250* (17:5); *2251* (18:8); *2257* (14:10); *2276* (14D); *2277* (14:1); *2278* (14:9); *2294* (17:12); *2298, 2299* (14:2), *2304, 2362, 2387, 2403* (12:20); *2305* (12:8); *2314* (17:7); *2315, 2340, 2388* (18:10); *2318, 2352, 2359* (12:19); *2319* (12:24); *2331* (13:2); *2351, 2407* (12:16); *2360* (11:4); *2390, 2432* (17:D); *2401* (12:3); *2423, 2447* (10:6); *2434, 2462, 2463, 2471* (10:D); *2446* (10:2); *2446A* (10:5)
Stevens, O. A., in 1934 (9:1)
Stillinger, C. R., in 1923 (16:2)
Stokes, S. G., in 1901 (17:1)
Sturgis, W. C., in 1903 (17:17)
Suksdorf, W. N., in 1881 (18:7); in 1885 (15:3, 4); *195* (16:8); *378* (15:3); *875* (13:1); *997* (16:1); *1642, 2693, 12710* (16:10); *5085* (12:9); *12704* (16:12)
Swabey, M., in 1923 (11:5)
Swift, Mrs. L. W., in 1931 (12:19; 17:6)
Taylor, W. R., and Richardson, C. H., *13* (17:D)
Thomas, W. D., in 1935 (12:16)
Thompson *32* (10:8)
Thompson, J. W., *4314* (15:2); *4755* (16:2); *6174, 8252, 11543* (14:15); *6635* (12:24); *6689* (15:1; 18:7); *7659* (10:10); *8352* (15:5); *9013* (15:2); *9543* (18:9); *11949* (17:D); *12406* (17:9)
Thornber, J. J., in 1894 (9:1)
Torrey, J., *267a* (18:9a)
Toumey, J. W., *664* (18:5)
Townsend, C. H., and Barber *206* (9:4)
Tracy, J. P., *2276* (10:2); *2794* (10:9); *2915* (11:7); *4256* (12:21); *6455* (10:9); *6513* (13:1); *7621* (10:4)
Tweedy, F., *602* (12:25); *603, 4081* (9:1)
Umbach, L. M., *139, 424a* (12:13); *295* (9:1, 2)
Van Dyke, Mrs. E. C., in 1930 (16:11)
Vasey, G. R., *548* (13:1); *564* (9:2);
Vestal, A. G., in 1913 (12·6)
Visher, S. S., *402* (9:3)
Vortriede, W., in 1931 (10:1)
Ward, L. F., *533* (9:3); *606* (9:2)
Warren, F. A., in 1932 (13:3); *1807* (14:15)
Watson, S., *712* (9:2); *715* (12:8); *716* (16:11); *717* (17:4)
Weller, S., in 1901 (9:1, 2)
Wheeler, H. M., in 1928 (16:D)
Wheeler, H. N., *474* (14:4)
Whited, K., *455, 1112* (16:4); *1267* (15:3); *1916* (17:D); *2632* (15:4)
Wickersheim, W. J., in 1891 (9:1)
Wilkes Expedition in 1841 (14:15)
Williams, L. O., *524* (14:3); *3129* (9:1)
Williams, R. S., *242* (12:13)
Williams, T. A., in 1897 (9:1, 2)
Wolf, J., *664* (9:1–3)
Wooton, E. O., in 1906, 1913 (9:1)
Worthley, I. T., *16* (14:2); *57* (16:11)
Wright in 1930 (18:8)
Wyeth, N., *s. n.* (12:5)
Yates, H. S., *5305* (12:2); *5307* (18:3)
Zuck, M., in 1896 (9:3)

TABLE 5. *Crepis pleurocarpa:* RESEMBLANCES OF APOMICTIC FORMS
(Numbers and letters correspond to those for each characteristic in the first column of table 4; see page 13)

Form	*monticola*	*occidentalis*	*acuminata*
apm. *Pringlei*		(8d), (8f)	
apm. *rigida*		(7a–b), (8d), (8f)	
apm. *latibractea*		1, *8d*, 8f	(2b)
apm. *Grayi*	(4c)	1, 2a, (2b), 3, (7a), 7b–c, *8d*, *8f*	
apm. *humilis*		1, *2a*, 2b, *3*, 8d, 8f	
apm. *glandulosa*	(1)	(2a–b), 7b–c, (8a), 8d	
apm. *monticoloides*	1, 2a–b, 4b, *4c*, *7a–b*, 8f	7c	
apm. *pluriflora*	(3), (4b), 8e	1, 2a, (3), (5b), (6b), (6c), (6g), (6h), 8a–b, 8d, 8f	
apm. *attenuata*	(6a), (6c), (6e), 6f, (6h), *8e*, 8f	1, 2b, 4c, *7a–b*, *8a–b*, 8d	
apm. *breviramea*		1, 2a, *3*, 4a, *5a*, 6b, (6d), (6e), 6g, (6h), (7c), *8f*	1, 2b, 4a, 4c, *5b*
apm. *plumaënsis*		(2b), (4b), (6b), 6e, 6g–h, 7a–b, 8a, 8d, 8f	8e

TABLE 6. *Crepis monticola:* RESEMBLANCES OF APOMICTIC FORMS
(Explanation on page 13)

Form	*pleurocarpa*	*occidentalis*	*Bakeri* subsp. *Cusickii*	*modocensis*	*acuminata*
apm. *simulans*		(6f)			
apm. *triploidea*		(6f), 6g, 8b, 8d			
apm. *pluriflora*		5a	(6c), 6e–f, 6h	(4c), (6c), 6e–f, 6h	
apm. *angustata*	2a, 3, 5a, 5b, 5c, (6a), 6b, (6c), 6d g	(1), 8b, 8d			
apm. *australis*		1, (2b), 4c, *5a–b*, 5c, (6b), 6c–d, *6f–g*, *8b–e*			
apm. *setosa*		(6b), (6d), (6g), (8d)		1, (2a – b), (4c), *5b*, (5c), (6b), 6f	(6d–e), (6g–h)
apm. *sanhedrensis*	1, (4c), 5b–c, (6a–d), 6e–f, *6g*, (6h), (7a), *8a*, 8c				
apm. *lassenensis*	(6b), 6e, *6g*, 6h		1, 2a, *2b*, (4c), 5a, 5c, 6b–d, 6f, (8e)		
apm. *plumaënsis*	1, (2b), (4c), 5c, 6a, 6c–f, 6h, *8a*				(2b), 5b, 6a, 6b–f, *6g*, 6h
apm. *calva*	(5a–b), (6e), (6h), *7a–b*	*1*, 2a–b, *3*, 4c, *5a*, *5c*, *6a*, 6b, 8d			

TABLE 8. *Crepis modocensis:* RESEMBLANCES OF APOMICTIC FORMS
(Explanation on page 13)

Form	*monticola*	*occidentalis*	*Bakeri* subsp. *Cusickii*	*exilis*	*acuminata*
subsp. *typica*:					
apm. *simulans* ..					
apm. *parviceps* .	.....	.....	.....	.....	(5b), (6a), (6d)
apm. *elatior*	.....	.....	.....	(2a), (2b), 3, 4a, (4c), 5a, (5b)	3, (4c), (5a–b), (6b), (8e)
apm. *tenuifolia* .	.....	.....	.....	1, 2a–b, 3, 4a, 4c, 5a–b, (6b), 6c–d, 6f	
apm. *Austinæ* ..	.....	1, (2b), (4b), 6b, 8d	2b, 4b	.....	(6c), 6d, (6e), (6h), 8d
apm. *pauciflora* .	.....	.....	.....	.....	(1), 2a, (2b), 3, 5a–b, (6b), 6e, 6g–h, 8e
subsp. *subacaulis*:					
apm. *Kelloggii* ..	.....	1, *6b*, 8d–f	(8d–f)		
apm. *grandiceps* .	.....	1, 5b, 6b, 6d, (6g), (8b), (8d), 8f)	5b, (8d), (8f)		
apm. *diamondica*	.....	.....	(1), *2b*, *4c*, 5b, *8c*, 8f		
apm. *bernardina*.	.....	(1), (8d–f)	5b, 8d, *8e*, 8f		
apm. *multiflora* .	.....	5b, 6b, (6g), (8b), *8c*, 8d–e, *8f*			
apm. *robusta* ...		cf. apm. *multiflora*			
apm. *setosissima*.	(1), 2b, 4c, (5b), (6c), *8d–e*, *8f*				
apm. *turbinata*..	(1), 2b, 4c, *5b*, 6a, 6c, 6f, *8d–f*	(1), (8c)			

TABLE 9 *Crepis barbigera:* RESEMBLANCES OF APOMICTIC FORMS
(Explanation on page 13)

Form	*modocensis* subsp. *rostrata*	*exilis*	*acuminata*
apm. *Leibergii*	4a, 5c, *6a, 6b*, 6f, 7b–c, 8a–b, 8d–e, *8f*	*1*, 2a–b, 3, *4b, 4c, 5a*, 5b–c, (6b), 6c–h, 7a–c, 8a–e	2a–b, 3, 4a, (4b), (4c), 5b–c, 6c–d, 6f–g, 7a–c, 8a–d
apm. *semibarbata*	4a, 5b–c, 6a, (6b), 6f, *7a*, 7b–c, 8a–f	*1*, 2a–b, 3, 4b–c, *5a*, 5b–c, *6b*, 6c–h, 7b–c, 8a–f	2a–b, 3, 4a–c, 6c–d, 6f–g, 7b, 8a–d, (8e), 8f
apm. *dentata*	(2a–b), (4b–c), 5a, (5c), *6b*, 6f, 8a–f	*1*, 2a–b, *3*, *4a*, 4b–c, *5a–b*, (5c), 6a–d, *6e*, 6f–h, 8a–f	2a–b, 4b–c, *5c*, 6a, 6c–d, 6f–g, 8a–d, 8f
apm. *setosissima*	*1*, (2b), 4a, *6b*, 7b, 8a–f	1, *2a–b*, *3*, *4b–c*, 5a–b, 6a–d, *6e*, 6f–g, *6h*, 7b, 8a–f	4a, (5a), 5b, *5c*, 6a, 6c–d, 6f–g, *7a*, 7b, *7c*, 8a–d, 8f
apm. *laticeps*	*2a*, 3, 4a, *5a*, 5c, *6b*, 6e, 6f, 6h, 7b	1, 2b–c, 3, 4a–c, 5a, *5b*, 5c, *6a*, 6c–h, 7b	*1*, 2b–c, 4b–c, 6c–d, 6f–g, *7a*, *7b*, *7c*
apm. *falcata*	6b, 6f, 6h, 7b, 8a–f	1, 2a–b, 3, 4a–c, *5a–b*, *6a*, 6b–d, *6e*, 6f–h, 7b, 8a–f	*2a–b*, 3, *4a–c*, 5b, *5c*, 6c–d, 6f, 6g, *7a*, 7b, *7c*, 8a–d, 8f
apm. *breviloba*	4a, 6b, 6f, 7b–c, 8a–c, (8d), (8e), 8f	*1*, (2b), 3, 4a, (4c), 5b, 6a–g, *6h*, 7b–c, 8a–d, (8e), 8f	*2a–b*, *3*, 4a, *4b–c*, *5a*, 5b, *5c*, 6a, 6c–d, (6e), 6f–g, *7a*, 7b–c, 8a–d, *8e*, 8f
apm. *pauciflora*	5b, 6a, 6f, 7c	3, 6a, 6c–h, 7c	*1*, *2a–b*, *3*, *4a*, *4b–e*, *5a–c*, 6a–h, *7a–b*, 7c

TABLE 10. *Crepis exilis:* RESEMBLANCES OF APOMICTIC FORMS
(Explanation on page 13)

Form	*modocensis*	*acuminata*
subsp. *originalis*:		
apm. *simulans*		
apm. *breviloba*		2a–b, 4b–c, 5b, 6a, 6e, 6h, 8c
apm. *longiloba*		(5a), 5b, 6b, (6h), 8e
apm. *yakimensis*		1, (2b), (5a), *5b*
apm. *coloradensis*		(1), 2a, *2b*, 4c, 5a, *5b*, 8e
apm. *glabrescens*		1, *2a–b*, 3, 4b, *4c*, *5a–c*, 6b, 6e, 6h, 8b–c
apm. *brevicarpa*	(8a)	1, 5b, 6a
apm. *paucibarba*	(6b), (6c), (6d)	1, (5a), 5b, (6h)
apm. *graminifolia*	4a, 5a, (6b)	6h
apm. *sterilis*	6b	(2b), 5b, 6h, (8e)
subsp. *typica*:		
apm. *ambigua*	(5a), 6b	1, (2b), (4c), 5b, (6h), (8e)
apm. *Osterhoutii*	2a, 3, 4a, 5a, 5b, 6a, *6b*, (6c–d), 6e, 6g	
apm. *Helleri*	2a, 4c, 6a, *6b*, (6c–d)	1, 2a, 2b, 4c–d, 5b, 8c, 8e

TABLE 11. *Crepis acuminata:* RESEMBLANCES OF APOMICTIC FORMS
(Explanation on page 13)

Form	*pleurocarpa*	*occidentalis*	*modocensis*	*exilis*
subsp. *typica*:				
apm. *simulans*, apm. *utahensis*, apm. *longiceps*, apm. *depauperata*, apm. *patens*				
apm. *tenuis*	2b, 4a, 5a–b			2b
apm. *sierræ*		(6c–d), (6e), (6g)		
apm. *yosemitana*		5a, (6e), (6g)		
apm. *bernardina*, apm. *longiloba*	(6b), (8e)	(6b), (8e)		
apm. *nevadensis*		6b, (6e), (6h), 8e	(2b), (4c)	
apm. *wallowensis*	3, 4b, 5a–b, 6f, (6g), 8f	(2a), (3), 4a, (4b), 5a, *6b*, 8f		
apm. *tetonensis*	5b, 6f	*6b–d*, 8e		
apm. *Rydbergii*				*2b*, *4c*, *5a–b*, (6e), (6h)
apm. *viridis*				*1*, 2b, (4c), 5b, 6e, 6h
apm. *exiloides*				*1*, 2b, 4c, (6b), (6h), 8c
subsp. *pluriflora*		(5a), 6e, 6h, 8d		

TABLE 12. *Crepis intermedia:* RESEMBLANCES OF APOMICTIC FORMS
(Explanation on page 13)

Form	*pleurocarpa*	*occidentalis*	*Bakeri*	*modocensis*	*exilis*	*acuminata*
apm. *Grayi*		1, 2a, (3), ***4a***, 4b, ***5a***, 5b, 6a, ***6b***, 6e–h, ***7a***, ***7b***, 7c, 8a, 8c, (8f)				1, 2a, ***2b***, 3, 4b, ***4c***, 5b, ***5c***, 6a, ***6c–d***, 6e–h, 7c, 8a, ***8b***, 8c, ***8d–e***, 8f
apm. *montana*		1, 2b, 3, 4a, ***4b***, ***5a***, 6a, ***6b–d***, 6e–h, ***7b***, ***7c***, 8a–e, ***8f***				1, ***2a***, 2b, 3, 4a, ***4c***, ***5b–c***, (6a), 6e–h, ***7a***, 8a–e
apm. *sterilis*		1, 4a–b, 5a–b, 6a–h, ***7a***, 7c, 8a, 8c				1, 2a, ***2b***, ***3***, 4a–b, ***4c***, 5a–b, 5c, 6a–b, (6c–d), 6e–h, ***7b***, 7c, 8a, ***8b***, 8c, ***8d–f***
apm. *longifolia*		1, 5a–b, ***6b***, (6c), (6d), 6e–h, 7b, ***7c***		(6b–d)		1, 2a, ***2b***, ***3***, ***4a–c***, 5a–b, ***5c***, ***6a***, 6c–h, 7a–b
apm. *grandis*		1, 4a, ***6b***, (6c), (6d), 6e–h, 7c, 8a, 8c–f		(6b–d)		1, ***2a–b***, ***3***, 4a, ***4b–c***, ***5a–c***, ***6a***, 6c–h, ***7a–b***, 7c, 8a, ***8b***, 8c–f
apm. *washingtonensis*		(1), (4a), (6b), (6e–g), (6h), 7c		(2b), (3), (4a–c), (6b), 8a–b, 8d–f	(6b), (6e–h), 7c, 8a–b, 8d–f	1, ***2a***, 2b, 3, 4a–c, ***5a***, 5b–c, (6b), 6c–h, ***7a–b***, 8a–b, ***8c***, 8d–f
apm. *sierræ*		1, 6b, 6f–g, 8a–f		2a–b, 3, 4a–c, 5a, 5c, (6b), 6e, 6h		1, 2a–b, 3, 4a–c, 5a–c, ***6a***, 6b, ***6c–d***, 6e–h, ***7a–c***, 8a–f
apm. *plumaënsis*	4a, ***4b***, 5b, 6a–f, 6h, 7a–c, 8a–f	1, 6b, 6e–h, 7b, 8a–f		(2b), (4c)		1, ***2a***, 2b, ***3***, 4a, 4c, ***5a***, 5b, 6a–h, 7a–c, 8a, 8c, 8e–f
apm. *angustifolia*	(2a), 5a–b, 6b–f, 6h, 7a–c, 8b–f	1. 2b, 3, 4a–c, 5a, 6a–b, 6e–f, 6h, 7a–b, 8a–f				1, 2a–b, 3, 4a, ***4b***, 4c, 5a–b, ***5c***, 6a–h, 7a–c, 8a–c, 8e
apm. *longiceps*		1, ***6a***, 6b, (6c–d), 6e–h, 7a–b, ***7c***, 8a, 8c–e, ***8f***		6a, (6b), 6c–f, 6h, 7a–b, 8a–d, (8e)		1, ***2a–b***, ***3***, ***4a–c***, ***5a–c***, 6b–h, 7a, 8a–e
apm. *cupressensis*		1, ***5a***, 5b, (6b), 6e–h, 8a–b, ***8c***, 8d, ***8e***			1, ***2a–b***, ***3***, ***4a–c***, 5b, ***6a–d***, (6e–f), 6g, (6h), ***7a–b***, 7c, 8a–b, 8d–f	5b
apm. *glandulosa*		1, 2a, 3, 5a, (6c–d), 6e–h, 7b–c, 8a, 8c–e	1, ***6b***, (6c–d), 6e, 6h, 7b–c, 8a–f	(1), (6b), (8e)	4a–b, (4c)	1, ***2b***, 3, 4a–b, ***4c***, 5a, ***5b–c***, ***6a***, 6b–h, ***7a***, 7b–c, 8a–c, 8f
apm. *setosa*		1, 4a, 5a, 5c, 6a, (6b), (6c), 6d–h, 7a, 7b, 7c, 8c, 8e		2b, 4a–c, 5a, 5c, 6a, ***6b***, 6d–f, 6h, 7a–c, 8a–f		1, ***2a***, 2b, ***3***, 4a–c, 5a, ***5b***, 5c, 6c–e, 6g–h, 7a–c, 8a–d, 8f