

AN ABSTRACT OF THE THESIS OF

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Section Aster, in Western North America

Abstract approved \_\_\_\_\_

A biosystematic investigation was undertaken in 15 species and three subspecies of the genus Aster, in western North America. Previous studies had been based entirely on external morphological features, and it was believed that much could be learned about the natural affinities of the taxa by exploring their cytological and genetical characteristics.

More than 160 accessions were made during the course of the study. In the majority of cases, living rhizomes were transplanted in the greenhouse to provide material for making chromosome counts and hybridization experiments.

Whenever possible, chromosomes were observed during meiotic divisions in microsporogenesis. One or more chromosome counts were made in 17 of the 18 taxa studied, 12 of which had not previously been examined cytologically. Ten taxa were found to include plants at two or more chromosome levels. The entire assemblage of species

contains chromosome numbers on the basis of  $X = 8$ , with counts ranging from  $n = 8$  to  $n = 48$ . Examples of aneuploidy, B-chromosomes, and meiotic irregularities were also discovered.

A total of 383 artificial hybridizations was made among the species studied, resulting in the production of at least one fruit from 198 crosses. Most of the attempted crosses were interspecific, with the results indicating a striking lack of genetic incompatibility between the species at all polyploid levels. However, nearly all crosses involving diploid plants produced no fruits. First-generation hybrids of most species combinations were grown to maturity, and their potential fertility was estimated by observing the stainability of their pollen. The percent of pollen stainability in most of the hybrids was high enough to be judged partly or fully fertile.

The polyploid complex composed of the species of Aster included in this study is comparable to certain other known complexes. Such complexes are similar in that the diploids are rather distinct morphologically and genetically, but they have contributed to the formation of a vast array of potentially interbreeding polyploids which lack sharp morphological definition. Most of the polyploids can be assigned to morphological categories that are more similar to related diploids than to other polyploids.

Consequently, certain of the species have been delineated along vertical lines of relationship which may include several chromosome levels. In addition, some entities are retained as species which are known only as polyploids, but which are relatively distinct and cannot be definitely connected to a diploid species. This method is believed to be more indicative of relationship than would a system of grouping the entire polyploid assemblage in one highly polymorphic species.

A phylogenetic chart of putative relationships among the taxa is presented, based largely on chromosome counts and morphology. The diploid entities are judged to be ancestral to, and thus more primitive than the polyploids. It was not possible to establish particular morphological traits as being more primitive or more advanced. Rather, it appears that evolution of morphological features has occurred at the diploid level, with subsequent polyploidy serving primarily to recombine the distinctive diploid features into various combinations. The information gained from the hybridization experiments contributed relatively little to an understanding of natural affinities among these species, owing to the free crossability between the polyploids. Too few crosses were made involving diploids to determine accurately the degree of genetic incompatibility.

Over 8000 herbarium specimens were examined in the process of delimiting species. The taxonomy section includes a key to the species, plus lists of synonyms, technical descriptions, citation of representative specimens, distribution maps, and brief discussions of the species. One new species, Aster idahoensis, is described in the thesis.

A BIOSYSTEMATIC STUDY IN THE GENUS ASTER, SECTION ASTER,  
IN WESTERN NORTH AMERICA

by

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A BIOSYSTEMATIC STUDY IN THE GENUS ASTER, SECTION ASTER,  
IN WESTERN NORTH AMERICA

INTRODUCTION

The species of the genus Aster in North America number well over 150 and are widely distributed and common in most parts. They form a colorful part of the late summer and fall flora in open woods, mountain meadows and on stream banks, but perhaps they are noticed most often as semi-weedy plants growing along roadsides, ditchbanks, and other waste places. Many species have showy flowers and are used as ornamental border plants. The single outer series of ray flowers in each head ranges in color from purple, reddish-purple or blue, to pink or white, with the central disk flowers a bright yellow to sometimes reddish.

The geographic area encompassed by this study extends from the Rocky Mountains to the Pacific Ocean, and from the border of Mexico to Alaska. The Rocky Mountains form a rather natural dividing line between the eastern and western members of the section Aster. This section, by far the largest of the genus, includes between 125 and 150 species. Of this number, only about 10 species have any appreciable distribution on both sides of the Rockies. Within western North America, as defined above, present-day authors of regional floras list approximately 25 species in the section Aster, excluding those species which barely extend to the

Rockies from the east. The present study deals primarily with 15 of these 25 species. Chromosome counts indicate the 15 included species are all part of a monobasic series of  $X = 8$ . Morphologically they have many similarities, the distinction between species usually being based upon a combination of characteristics. Most of the 10 or 11 species of the section Aster which are not included in this study have rather distinctive characteristics, such as glandularness, leaves that are thick, rough or serrate, or phyllaries that are spine-tipped, etc.; and they are consequently not difficult to identify and define taxonomically. In addition, chromosome counts of some of the excluded species showed base numbers of  $X = 5$  and  $X = 9$ , but none with  $X = 8$ . Thus the 15 species included in this study appear to be a distinctly natural group.

That great taxonomic difficulties exist within the genus has long been recognized. In 1884, Dr. Asa Gray stated, "Aster is far the most difficult of our genera, both for the settlement of the names of the species and for their limitation" (24, p. 72).

Much of the confusion abounding in the section Aster in the West was resolved by Arthur Cronquist in his fine revision of a part of the section, including most of the species treated here (14). He brought the nomenclatural chaos into functional order by reducing over 100 published names to eight species, three subspecies, and 12 varieties. In the

course of his study he noted what appeared to be many intermediate or hybrid types both in the field and on herbarium sheets. However, his taxonomic treatment was based strictly on external morphological features, and it did not include studies of the cytology or genetic relationships of the taxa. The present study was undertaken because it was felt that much could be learned in this apparently freely hybridizing and rapidly evolving group by applying these newer tools of taxonomy. The principal goals have been to discover the extent of biological distinctness, or intergradation between species, and to gain a better understanding of the pattern of speciation within this group.

## METHODS

### Transplants

In a biosystematic study of a group whose members are so widely distributed geographically, the plants must be brought together in a common garden or greenhouse. For this purpose, over 160 accessions were made from parts of Washington, Oregon, California, Idaho, Utah, Wyoming, and Colorado. Most of the material from Washington, Oregon, and Idaho was collected by the author and constitutes the majority of the plants used in hybridizations. The other collections were made by the people listed in Table I: I am extremely grateful to all these persons for their assistance.

Transplants were made by digging up the rhizomes of the plant, separating them from the stem, and enclosing them in polyethylene (plastic) bags. After transport to the greenhouse at O.S.U., they were planted in a soil mixture of loam, peat, and inorganic fertilizer in 6 inch clay or plastic pots. Asters make very good material for this kind of treatment, because the rhizomes are hardy and vigorous and survive well in the plastic bags for several days or even weeks. After being planted, they begin to send up shoots almost immediately and may come into flower in three or four months.

The stems of the transplants were pressed as voucher

specimens, along with other samples from each locality. In addition, notes were made of particular characteristics of the plants, and of the nature of their habitat.

All of the transplants were grown in the greenhouse for the first two years of the study. During this time all of the hybridizations were performed. Then parent plants and hybrids were transplanted again into an open plot at the Botany Farm near Corvallis, where they were exposed to the natural environment. Here the plants were observed for two growing seasons, and pressed vouchers were made of all the hybrid types.

### Cytology

As many chromosome counts were made in each species as possible. Because nearly all the counts were made from pollen mother cells during stages of meiosis, the pairing behavior of the chromosomes was observed in most cases as well. When possible, the young buds were placed in the killing and fixing solution in the field. If buds with the right stages were not available at collection time, they were obtained later from transplants in the greenhouse. The killing solution used is that of Newcomer (49): it was found that buds could be stored up to two years in this fluid without appreciable loss of chromosome stainability. Before staining, the buds were transferred to 70 percent alcohol for a short time.

Staining of the chromosomes was accomplished by either of two methods: direct staining on the slide or bulk staining before making the slide. In the former, a drop of aceto-carmin, aceto-orcin, or lacto-propionic-orcin was applied directly on the anthers after they had been removed from the floret. The cover slip was then placed on the anthers and stain, the cells were tapped out of the anthers, and pressure was applied to the slide in order to flatten the cells. In the second method, the whole heads were placed in alcoholic-hydrochloric-carmin stain of Snow (57) for several days at room temperature, or 24 hours at 50-60° C. The anthers were then dissected from the floret in a drop of 45 percent acetic acid, a drop of Hoyer's mounting medium added, cover slip applied, and the cells tapped out and flattened as discussed above. This latter method proved to be much more satisfactory, both for better staining and for making the slides permanent. Because the mounting medium is added before applying the cover slip, the slide is effectively permanent immediately after flattening of the cells. In the first method, removal of the cover slip in order to add the mounting medium (diaphane), often resulted in loss of some cells.

### Hybridizations

Artificial hybridizations within and between species were performed during the two years that the plants were

growing in the greenhouse. Although Aster species are mostly self-incompatible, they will occasionally set some seed from self-pollination. For controlled pollination, emasculation of the maternal parent was necessary before each attempted cross. This was accomplished by cutting out all the perfect disk flowers before they had opened, leaving only the pistillate ray flowers. Because the latter were usually not yet mature at the time of emasculation, a small wax paper bag was placed over the head for a few days. Then the bag was removed, pollen from a mature head of another species was dusted onto the receptive stigmas, and a label with the appropriate crossing information was tied to the head.

Some possible sources of error are inherent in this method of testing genetic compatibility. 1. The ray flowers may not be pollinated at the peak of their receptivity. However, observations of the length of time the stigmas are open indicate that the receptive period may last for two or more days. Also, records which were kept on the time of day that pollinations were made showed no significant difference in success between morning and afternoon. 2. An obvious possibility is that cutting out the disk flowers may damage the ray flowers. Certainly this occurred in some cases and accounted for low or no fruit production. But in many crosses nearly every ray flower in the head set good fruit, and it is felt that if proper care was taken

the ray flowers need not have been damaged. 3. Another possibility is that the stigmas could have been damaged during actual pollination, as they were touched by the pollinating flower; but the same answer might be given for this as for the second possibility. 4. The greenhouse environment may be somewhat less than ideal for the successful completion of the reproductive processes. This is especially true for the "potato greenhouse", in which nearly all crossing attempts failed. The potato greenhouse, which was used for only part of one summer, lacked adequate ventilation and temperature control and thus became very hot and humid in the daytime. This resulted in abnormally luxuriant vegetative growth by the plants, and was apparently detrimental to some aspect of reproduction. In contrast, the large quantity of fruit produced by hybrid plants following open pollination at the Botany Farm indicates the more favorable conditions of the natural environment.

Although the methods used may have led to artificially reduced estimates of crossability, they have the advantage of guaranteeing that any fruits obtained were the products of cross- rather than self-pollination. Growth of many  $F_1$  plants has verified their hybrid nature.

Following harvest of the fruits, a certain number of them from selected crosses were sown, germination percentages were recorded, and some of the  $F_1$  plants were raised

to maturity. Crosses were then carried out between some of these F<sub>1</sub> plants. These results and additional information concerning hybridization are discussed in the hybridization section.

#### Herbarium study

Making a biosystematic study in a group of plants does not eliminate the study of herbarium specimens; in fact this is still a major part of the work involved. Specimens were borrowed from 10 different herbaria and were of invaluable assistance in formulating species boundaries, as well as in providing the basis for distributional maps and specimen citations found elsewhere in the thesis.

## TAXONOMIC HISTORY

The genus Aster was established by Joseph Tournefort in 1710 and maintained in 1753 by Carolus Linnaeus in his Species Plantarum. Of the group here considered, only one species, Aster laevis, was listed by Linnaeus. The first notable monographer of the genus was Nees von Esenbeck, whose Genera et Species Asterearum was published in 1832. In it he named two species of the present group, A. subspicatus and A. chilensis. Nees subdivided the genus into three sections, placing the two above mentioned species, along with A. laevis, in the section Genuini. Contemporary with Nees was the English botanist, John Lindley, who named and described most of the new Aster species appearing in W. J. Hooker's Flora Boreali-Americana in 1834, and in A. P. De Candolle's Prodromus in 1836. In both of these works Nees' treatment of the genus was followed, except that in the Flora the three major subdivisions were called "sections", and in the Prodromus they were called "series". Lindley added five species in the Flora, placing two of them in the section Amelli and three in the section Genuini. Only one additional species was added in the Prodromus, this being placed in the section Alpigeni. In 1840, Thomas Nuttall (50) described four additional species, two being listed in the separate genus Tripolium. In 1841, Torrey and Gray (62) recognized 13 species and 3

varieties in the present group, yet had them scattered over 50 pages of text and in three different sections.

The difficulty of assigning species relationships can readily be appreciated when knowledge of the plants was based on rather scanty or incomplete material, as must have been the case with Torrey and Gray and the previous workers. By contrast, 43 years later in the Synoptical Flora of North America, Asa Gray recognized 15 species and 12 varieties, all of which were placed in the same section, Euaster or Aster proper, and even in the same subsection. It was during the next 40 years that the extreme multiplication of species' names occurred, thus making taxonomic determinations so difficult. This nomenclatural splitting was occasioned particularly by the very narrow species concepts of P. A. Rydberg and E. L. Greene. As stated in the introduction, it was with this background of increasing taxonomic confusion that Cronquist made his valuable contribution in 1943.

One significant point of nomenclatural history remains to be discussed. Since Linnaeus did not designate a type species for the genus, a lectotype was chosen in 1913 by Britton and Brown (9, p. 406). They chose A. amellus, a species of central Europe. According to the International Code of Botanical Nomenclature, article 32 (37, p. 22), the subgenus or section containing the type species must bear the genus name unaltered. Nees (48) placed A. amellus in

his section Amelli. In 1880, Gray (23) proposed 12 sections (or subgenera) for the genus, including Euaster, containing the majority of the species, and Amellastrum, containing only A. amellus and A. alpinus, an arctic-alpine, circumboreal species. Cronquist (29, p. 74) followed Gray in the use of Euaster and Amellastrum. Thus if the rules are applied correctly to the classification of Gray, his section Amellastrum must take the name of the genus and become section Aster, and the original section Genuini of Nees must be supplied to replace the sectional name of Euaster.

However, not all workers agree with Gray. In treating the Compositae for Die Natürlichen Pflanzenfamilien, Hoffman did not recognize the section Amellastrum, but included A. amellus in Euaster (30, p. 163). Hegi (28, p. 417) repeated Hoffman's treatment. Thus in this scheme, the section name Aster can remain in its broad and widespread usage because it includes the type species, A. amellus. For the present, I will choose to follow Hoffman for two major reasons. First, A. amellus and A. alpinus are rhizomatous asters and in general habit are not unlike some members of the group here studied, esp. A. foliaceus ssp. apricus. The primary technical difference, that of achene shape and venation, does not seem great enough by itself to warrant sectional separation. Secondly, the present concept of the section Aster, which includes the majority of the rhizomatous asters, is so widespread that I am not inclined to change it without

more careful study.

## MORPHOLOGY

Plants in the section Aster incorporate the following characteristics which distinguish them from plants in the other sections of the genus. They are fibrous-rooted rhizomatous perennials, with the basal and often lower cauline leaves usually petiolate and larger than the sessile upper ones. The stems are usually erect, and vary from simple and monocephalous to much-branched and many-headed. The phyllaries of the involucre vary from completely herbaceous and green, to green only at the tip and whitened-chartaceous below with a scarious margin. They also vary from being markedly graduated in size with the outer much shorter than the inner, to being nearly equal or the outer ones enlarged and foliaceous. The phyllaries are never keeled on the back. The number of ray flowers may be as low as 12, but is usually more than 20. The pappus is a single series of usually soft capillary bristles.

Within the homogeneous group of species comprising this study, the following features of gross morphology have been most often used by taxonomists to recognize or define the species.

Leaves. In many of the species, the basal and lower cauline leaves are deciduous before flowering time, and the middle and upper leaves are the ones usually referred

to. Absolute size is quite variable, but the ratio of length to width is fairly reliable. Leaf shape is relatively stable in most species, perhaps providing the best leaf characteristic. Only two species, A. subspicatus and A. laevis, consistently have serrate leaves, but this trait shows up sporadically in the other species. Auriculate or clasping leaf bases are quite constant for those species in which they occur. Veination and size and shape of areolae have been relied upon by some previous workers, but they were not used to any extent in this study.

Pubescence. The amount of pubescence is quite variable. Some of the species vary from nearly glabrous to densely pubescent. Even A. cusickii, which is characteristically long pilose to nearly woolly in extreme forms, may be nearly glabrous in other forms. However, the distribution and type of pubescence is quite constant. Aster hesperius is unique in having pubescence in lines under the heads as well as on the stem. Those species that are most consistent in their pubescence characteristics are A. bernardinus, A. eatonii, A. greatai, and A. jessicae; in addition, A. laevis is consistently glabrous.

Inflorescence. Except for the monocephalous, or nearly so, subalpine subspecies of A. foliaceus, most species attain enough secondary branching to produce a paniculate arrangement of the heads. Infrequently, single heads terminate the unbranched primary branches, resulting

in a racemose inflorescence. The two taxonomically most important aspects of the inflorescence are the shape of the inflorescence and the type and quantity of leaflike bracts along the branches. Shape refers to whether the panicle is long and narrow, or broad and open, or somewhat flat topped or corymbiform, etc. These characteristic habit patterns are determined by the angle of primary branching, length of the branches, and amount of secondary branching. In the majority of specimens these patterns provide a reliable clue to species identity.

The leaflike bracts on the inflorescence branches will subsequently be called bracts, and they will be distinguished from the upper stem leaves which subtend primary branches, and from the bracts of the involucre which will be called phyllaries. The bracts vary from large and leafy to very small and scalelike and from spreading to appressed. They also vary in shape and in quantity. In their respective features they are diagnostic for a majority of the species.

Involucre. More emphasis has been placed on characteristics of the involucre than on any other morphological feature. The major taxonomic characteristics are the size and shape of the phyllaries, and the relative proportion of herbaceous to chartaceous portion composing the phyllaries. The presence or absence of a scarious margin on the phyllaries has some value. Also, the total involucre or head

size may be important in a few cases.

The apex of the outer phyllaries is designated as either obtuse to rounded, or acute to acuminate. This is probably the most constant trait of the phyllaries. The inner phyllaries of most species are acute to acuminate or nearly attenuate. Also valuable but not quite as reliable as apex shape is the relative length of the phyllaries. The outer ones are either much shorter, forming an imbricate or strongly graduated involucre, or the outer ones are nearly equal in length to the inner ones. The inconsistencies in this trait usually occur in those species with characteristically imbricate phyllaries; occasional specimens may have subequal, or at least not strongly graduated ones. In connection with the aspect of phyllary length, only mature, non-terminal heads should be used for keying, if possible. The terminal heads of the main stem or primary branches often have somewhat enlarged phyllaries, and young heads are often not reliable for determining length or shape of the phyllaries. The difference between green-herbaceous and whitened-chartaceous portions of the phyllaries is often more easily distinguishable in dry, pressed specimens than in living ones. The amount of chartaceous portion is rather variable in those species, such as A. occidentalis and A. foliaceus, which have predominantly herbaceous phyllaries; occasional specimens may

have a sizeable amount of chartaceous portion on the lower half. In other species, such as A. adscendens, A. hallii and A. laevis, which characteristically have a green tip and up to half or more of the lower portion chartaceous, the proportion is less variable.

In a few species with normally imbricate involucre, occasionally specimens will have enlarged foliaceous phyllaries. This is particularly true in plants of A. chilensis and A. subspicatus from coastal or near coastal environments.

Ray flowers. Color is the only feature of the rays or ligules used taxonomically. The predominant ray color of the majority of the species is some shade of violet or purple, but a few species exhibit distinctive variations from this. Plants of A. hallii are nearly always white-rayed, rarely lavender or light purple. Aster eatonii is also white-rayed, but is unique in having many pink-rayed plants or even plants with slightly flesh-colored rays. In less contrast with the majority of species, yet often evident, are the usually bluer rays of A. laevis and the redder rays of A. foliaceus ssp. foliaceus and ssp. apricus.

Effects of greenhouse and garden culture on key characteristics. The modifying effect of the greenhouse environment on key characteristics was quite striking in many instances. The general tendency was for an overall increase in size of most plant parts, although not

necessarily in the height of the plant. Unfortunately the phyllaries were one of the most drastically affected structures. The modifications usually resulted in graduated phyllaries becoming equal or subequal, appressed phyllaries becoming loose and spreading, and normally subequal or even sometimes imbricate phyllaries becoming large and foliaceous. Phyllaries also tended to be more herbaceous and thus less chartaceous than usual.

The typical size of leaves and inflorescence bracts was also usually increased, but the shape remained fairly constant. Surprisingly, the size and shape of the inflorescence was not much altered, or if anything, it was reduced in size.

Growth of the plants in the uniform garden at the Botany Farm resulted in a nearly opposite pattern from that in the greenhouse. In the garden the plants showed an overall increase in height and plant size, yet not so much modification of individual parts. The phyllaries particularly were more representative of their species. The size of the leaves and inflorescence bracts was not excessive, but was proportional to the increase in plant size. In some plants of A. foliaceus ssp. parryi, the leaves even became narrower than when they were collected in nature. The inflorescence, however, was usually somewhat larger and more branched, thus changing the typical appearance of the species in this characteristic. The expression of

pubescence in both greenhouse and garden was close to being consistent with its expression in nature. The expression of ray flower color was not altered in either environment.

Modifications similar to those of the plants in the garden were also noted by Anderson for plants of Aster anomalus (2). He concluded from his transplant experiments that the characteristics of the individual structures, such as size and shape of phyllaries, bracts, and leaves, etc., are more rigidly controlled by the germ plasm than are the features of total plant size, amount of branching, and number of heads. Anderson did not grow his plants in the greenhouse, and so may not have realized the modifying effect of the greenhouse environment on the supposedly more stable characteristics. In another study, Clausen, Keck and Hiesey (13, p. 386-393) found that some aster plants remained phenotypically rather constant for most traits, including height and amount of branching, in three different environments while other plants varied considerably from one environment to another.

From the above observations it is evident that the genotypes of most Aster species allow considerable variation of phenotypic expression. This is not surprising in light of the polyploidy and natural hybridization which is so prevalent in this group, and which contributes substantially to genetic heterogeneity. Because of these factors of polyploidy, hybridization, and environmental modification

taxonomically reliable characteristics are difficult to ascribe to each species. Usually taxonomic determinations must be made by considering a combination of several traits which are found most consistently throughout the geographic range of the species. In this study, a comparison of the cultivated plants with those growing in nature, showed that the "key characteristics" remained more similar to those in nature in the garden-grown plants than in the greenhouse-grown plants.

## CYTOLOGY

Chromosome counts

Chromosome counts in the genus Aster have been gradually accumulating for a number of years, with a marked increase in the last ten years. However, chromosome numbers in only five of the species in the present study, A. adscendens, A. chilensis, A. laevis, A. occidentalis, and A. subspicatus, have been previously reported; and in each of these species only a single chromosome level had been discovered. Consequently, new counts are reported here for every species except A. laevis. This species is so far known only at the hexaploid level.

All plant collections from which chromosome counts were obtained are listed in Table I. The results of the counts reveal that these plants belong to an extremely complex polyploid group. The base number is  $X = 8$ , with counts of  $n = 8, 16, 24, 32, 40$ , and  $48$  (Fig. 1, 2, 3) having been determined. This information in itself gives a solid clue to the reason for taxonomic difficulty. It is not at all possible to segregate species on the basis of ploidy level because as many as four levels are represented in one species with only slight variation in external morphology. This tends to indicate that autopolyploidy has been involved in the chromosome increase. In some species I feel that this has been the case, even though

Table I. Chromosome numbers and collection data for the species of Aster studied

Taxon	Chromosome* number	Accession number	Locality and collector**
<u>A. adscendens</u>	2n = 8II, 5B	322	Oregon: Lake Co., 1-2 mi. N of Silver Lake town along road to Fort Rock.
	2n = 16, 4B	425	Idaho: Owyhee Co., near Big Springs Ranch.
	2n = 13II	313	Oregon: Klamath Co., U.S. Hwy. 97 at Scott Cr.
		353	Oregon: Deschutes Co., 0.5 mi. E of Metolius R. road on U.S. Hwy. 20.
		354b	Oregon: Deschutes Co., 1 mi. E of #353.
	2n = 32	426	Idaho: Owyhee Co., 20-25 mi. SW of Grandview on Fairylawn road.
	2n = 18II	340	Idaho: Fremont Co., N of Ashton, <u>Hyslop s.n.</u>
	2n = 24II	421	Oregon: Crook Co., 10 mi. N of Paulina.
	2n = 26II, 2 or 3B 27II, 1 or 2B	339a,b,c	Wyoming: Park Co., E entrance to Yellowstone N.P. <u>Hyslop s.n.</u>
		476	Utah: Wasatch Co., Lodgepole campground, Daniels Canyon. <u>Chambers s.n.</u>

Table I. Continued

<u>A. adscendens</u>	2n = 26II, 2 or 3B	479	Colorado: Summit Co., near Dillon.
	27II, 1 or 2B		<u>Chambers s.n.</u>
		481b,c,d	Colorado: Eagle Co., N Side of Vail Pass. <u>Chambers s.n.</u>
<u>A. bernardinus</u>	2n = 18II	389	California: San Bernardino Co., Mohave R. just E of Victorville. <u>Raven 16742.</u>
		399	California: Los Angeles Co., Rancho Santa Ana Botanic Garden, Claremont. <u>Raven 16864.</u>
<u>A. chilensis</u>	2n = 24II	297	Oregon: Lincoln Co., 1 mi. S of Yachats.
		299	Oregon: Curry Co., Battle Rock State Park.
		300	Oregon: Curry Co., Rogue R. at Gold Beach.
		342	Oregon: Lincoln Co., 1 mi. S of Yachats.
		343	Oregon: Lincoln Co., 2 mi. N of Yachats.
		344	Oregon: Lincoln Co., Bay Front Street in Waldport.
		361	Oregon: Clatsop Co., 1-2 mi. N of Gearhart.

Table I. Continued

<u>A. chilensis</u>	2n = 24II	397	California: Humboldt Co., 4 mi. N of Loleta. <u>Wolfe 9355</u> .
		---	California: San Francisco Bay region. <u>Raven 16564</u> .
	2n = 32II	298	Oregon: Coos Co., Sunset Bay State Park.
<u>A. cusickii</u>	2n = 8II	440	Oregon: Union Co., Frye Meadows. <u>Carlson s.n.</u>
		467	Idaho: Shoshone Co., 1 mi. S of Clarkia.
	2n = 16II	438	Oregon: Union Co., ca. 12 mi. N of La Grande on Mt. Emily Lookout road.
	2n = 16II, 1B	462	Idaho: Bonner Co., State Hwy. 57 near road to Outlet Bay on Priest Lake.
<u>A. eatonii</u>	2n = 8II, 1B	315	Oregon: Klamath Co., Williamson R. at Chiloquin.
	2n = 8II	320	Oregon: Lake Co., 8.6 mi. N of Adel.
		324	Oregon: Deschutes Co., banks of Deschutes R. at Sawyer State Park.
		403	Oregon: Deschutes Co., in Sisters.

Table I. Continued

<u>A. eatonii</u>	2n = 8II	452	Washington: Lincoln Co., 3 mi. E of Creston.
		471	Washington: Skamania Co., 2-3 mi. W of Underwood.
	2n = 16II	319	Oregon: Lake Co., 8 mi. N of Adel.
		345, 346	Oregon: Jackson Co., Applegate R. 1 mi. W of Ruch.
		380	Oregon: Wallowa Co., 2-3 mi. W of Enterprise.
		468, 469	Washington: Columbia Co., Tucannon R. at Zumwalt.
<u>A. foliaceus</u> ssp. <u>foliaceus</u>	2n = 24II	360	Oregon: Clatsop Co., 1 mi. S of Svenson.
	2n = 32II	445	Washington: Chelan Co., Stevens Pass, S side of road.
<u>A. foliaceus</u> ssp. <u>parryi</u>	2n = 8II, 1B	330a	Idaho: Idaho Co., near Lloyd Lake.
		330b	Idaho: Idaho Co., near Lloyd Lake.
	2n = 16II	436	Oregon: Union Co., ca 10 mi. N of La Grande on Mt. Emily Lookout road.

Table I. Continued

A. foliaceus  
ssp. parryi

2n = 32II

- |        |   |
|--------|---|
| 316    | Oregon: Lake Co., 0.5 mi. E of Quartz Mt. summit.                     |
| 328a,b | Oregon: Linn Co., N side of Lost Lake.                                |
| 335    | Idaho: Valley Co., So. Fk. Salmon R., ca. 13 mi. N of Knox.           |
| 354a   | Oregon: Deschutes Co., 1.5 mi. E of Metolius R. road on U.S. Hwy. 20. |
| 355    | Oregon: Deschutes Co., 2.5 mi. E of #354a.                            |
| 409    | Oregon: Wheeler Co., ca. 32 mi. E of Prineville on U.S. Hwy. 26.      |
| 412    | Oregon: Wheeler Co., ca. 10 mi. W of Mitchell on U.S. Hwy. 26.        |
| 420    | Oregon: Crook Co., Cold Spring Guard Station.                         |
| 423    | Oregon: Jefferson Co., 2 mi. E of Santiam Pass.                       |
| 475    | Oregon: Hood River Co., 3 mi. S of Parkdale.                          |

Table I. Continued

<u>A. foliaceus</u> ssp. <u>parryi</u>	2n = ca.64	488	Washington: Klickitat Co., Falcon Valley at Laurel.
	2n = 40II	481a	Colorado: Eagle Co., N side of Vail Pass. <u>Chambers s.n.</u>
		449	Washington: Chelan Co., Wenatchee R. 7 mi. N of Leavenworth.
<u>A. greatai</u>	2n = 8II	396	California: Los Angeles Co., Upper Arroyo Seco, 200 yards above Switzer Camp, San Gabriel Mts. <u>Raven &amp; Griesel 16842.</u>
<u>A. hallii</u>	2n = 8II	367	Oregon: Hood River Co., ca. 8 mi. W of Mosier on old road to Hood River.
	2n = 8II, 1B	401	Oregon: Benton Co., 2-3 mi. N of Corvallis on Highland Way.
	2n = 16II	348	Oregon: Linn Co., 3 mi. S of Albany on U.S. Hwy. 99E.
		349	Oregon: Linn Co., 4 mi. S of Albany, 0.5 mi. E of Interstate Hwy. 5.
	2n = 24II	398	Oregon: Benton Co., 1 mi. N of Corvallis on Kings Road.
<u>A. hesperius</u>	2n = ca.32II	433, 434	Idaho: Canyon Co., 3 mi. S of Nampa.

Table I. Continued

<u>A. hesperius</u>	2n = ca.32II	435	Idaho: Canyon Co., 6 mi. SW of Nampa.
		453	Washington: Spokane Co., Little Spokane R. at Chatteroy.
		---	Colorado: Boulder Co., 28th and Arapahoe Sts. in Boulder. <u>Weber 12054</u> .
<u>A. idahoensis</u>	2n = 8II	466	Idaho: Shoshone Co., 2 mi. S of Clarkia.
		464	Idaho: Benewah Co., S edge of Santa.
		465	Idaho: Benewah Co., 5 mi. SE of Santa.
<u>A. jessicae</u>	2n = 16II	463	Idaho: Kootenai Co., 15 mi. N of Harrison.
		430	Idaho: Latah Co., 10 mi. E of Moscow. <u>Aller s.n.</u>
		375	Idaho: Latah Co., 4.5 mi. S of Potlatch on Moscow Mt. road.
<u>A. laevis</u>	2n = 24II	392	Connecticut: New Haven Co., near Branford. <u>Ebinger 3925</u> .
		454	Washington: Pend Oreille Co., Pend Oreille R. at Usk.

Table I. Continued

<u>A. lentus</u>	2n = 8II	442b	California: Solano Co., Suisun-Rio Vista road, 0.7 mi. E of railroad crossing on Suisun-Fairfield road at Suisun. <u>Chambers 2059</u> .
<u>A. occidentalis</u>	2n = 8II	317	Oregon: Lake Co., 0.5 mi. E of Quartz Mt. summit.
<u>ssp. intermedius</u>		395	California: Eldorado Co., head of Fallen Leaf Lake. <u>Stebbins s.n.</u>
		474	Oregon: Hood River Co., 6 mi. S of Odell on State Hwy. 35.
	2n = 16II	374	Idaho: Latah Co., 6.5 mi. S of Potlatch on Moscow Mt. road.
	2n = 32	487	Washington: Klickitat Co., Falcon Valley 0.5 mi. S of Laurel.
		489	Washington: Klickitat Co., Falcon Valley 1 mi. E of Laurel.
	2n = 16II, 1 or 2B	368	Washington: Whitman Co., N edge of Colfax on Palouse R.
	2n = 24II	369, 370	Washington: Whitman Co., 0.5 mi. S of Colfax on U.S. Hwy. 195.
<u>A. occidentalis</u>	2n = 24II	427	Oregon: Union Co., Grande Ronde R. at Hilgard Jct. State Park.
<u>ssp. intermedius</u>			

Table I. Continued

<u>A. occidentalis</u>	2n = 24II	451	Washington: Lincoln Co., 3 mi. E of Creston.
<u>ssp. intermedius</u>			
<u>A. occidentalis</u>	2n = 16II	309	Oregon: Lane Co., 4 mi. W of Klamath Co. line on State Hwy. 58.
<u>ssp. occidentalis</u>			
	2n = 16II, 1B	310	Oregon: Lane Co., 0.7 mi. E of #309.
	2n = 16II	312	Oregon: Klamath Co., Little Deschutes R. at State Hwy. 58.
		326	Oregon: Jefferson Co., 0.5 mi. N of Lake Cr. Lodge on Metolius R. road.
		352	Oregon: Linn-Jefferson Co. line on Santiam Pass, S side of road.
		357	California: Mono Co., Mono Cr. near junction with the creek from fourth recess, Mt. Abbott quadrangle. <u>Snow s.n.</u>
		387	California: Alpine Co., 1 mi. N of State Hwy. 88, above Carson Pass summit. <u>Stebbins s.n.</u>
		390	California: San Bernardino Co., creek above Metcalfe Bay, Big Bear Valley, San Bernardino Mts. <u>Raven 16775.</u>

Table I. Continued

<u>A. occidentalis</u>	2n = 16II	424	Oregon: Linn Co., 8-10 mi. W of Santiam Pass.
<u>ssp. occidentalis</u>		439, 441	Oregon: Union Co., Frye Meadows. <u>Carl bom s.n.</u>
	2n = 24II	458	Idaho: Bonner Co., 2-3 mi. W of Coolin on Priest R.
<u>A. subspicatus</u>	2n = 24II	485	Washington: San Juan Co., Friday Harbor. <u>Chambers s.n.</u>
	2n = 32II	432	Washington: King Co., near Seattle. <u>Beckman s.n.</u>
	2n = ca.48II	301	Oregon: Tillamook Co., 0.2 mi. S of Cloverdale Grade School on U.S. Hwy. 101.
		304	Oregon: Benton Co., 1.1 mi. W of 43rd St. on Oak Cr. road W of Corvallis.
		305	Oregon: Benton Co., along Mary's R. S of Corvallis on So. 43rd St.
		306, 307	Oregon: Benton Co., 0.2 mi. S of #305.
		341	Oregon: Multnomah Co., along Latourelle Falls trail. <u>Chambers s.n.</u>

Table I. Continued

<u>A. subspicatus</u>	2n = ca.48II	350	Oregon: Benton Co., 4-5 mi. W of Philomath on Woods Cr. road.
		351	Oregon: Linn Co., on O.S.U. Botany Farm.
		358	Oregon: Clatsop Co., along trail to summit of Saddle Mt.
		364, 365	Oregon: Multnomah Co., 1.5-2 mi. W of Bonneville Dam entrance road on U.S. Hwy. 30.
		366	Oregon: Hood River Co., entrance to Starvation Cr. State Park.
		443	Washington: Cowlitz Co., 1-2 mi. N of Kalama.
		444	Washington: Pierce Co., Nisqually R., 3 mi. from U.S. Hwy. 99.
		472	Oregon: Wasco Co., Mayer State Park, 6 mi. W of The Dalles. <u>Estes 62.</u>

Table I. Continued

\*The designation "II" indicates counts were made from meiotic divisions in microsporogenesis; those counts lacking such a symbol were made from mitotic divisions in root tip cells. Small chromosome fragments or B-chromosomes are indicated by the capital letter B.

\*\*All collections were by the author and the collection number is identical to the accession number, except those collections which are otherwise designated.

Figure 1. Camera lucida drawings of meiotic chromosome complements in Aster, X 2400. A. Aster eatonii, 324, first prometaphase;  $2n = 8II$ . B. Aster hallii, 401, first metaphase;  $2n = 8II$ , 1B. C. Aster adscendens, 322, first anaphase;  $2n = 8II$ , 5B. D. Aster adscendens, 354b, second anaphase;  $n = 13$ . E. Aster cusickii, 462, first metaphase;  $2n = 16II$ , 1B (one pair has separated). F. Aster chilensis, 299, first prometaphase;  $2n = 24II$ . G. Aster bernardinus, 389, diakinesis;  $2n = 18II$ .



A



B



C



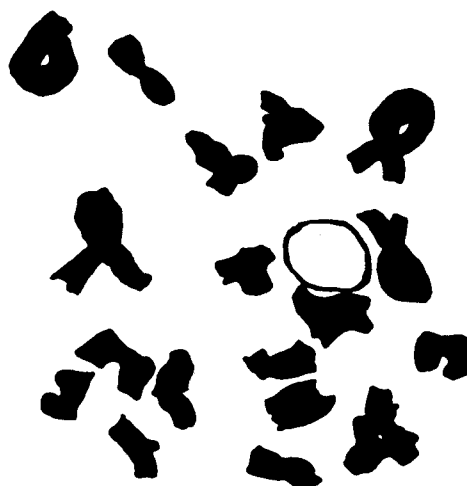
D



E

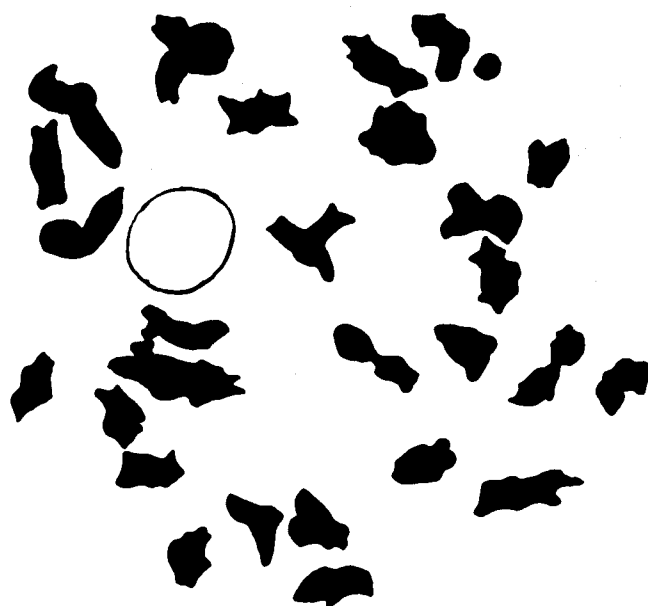


F



G

Figure 2. Camera lucida drawings of meiotic chromosome complements in Aster, X 2400. A. Aster adscendens, 339a, late diakinesis;  $2n = 27\text{II}$ , 1B. B. Aster hesperius, 453, first prometaphase;  $2n = 32\text{II}$ .

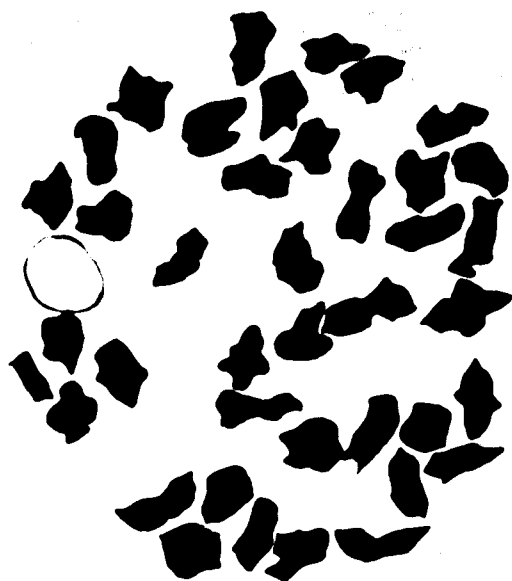


A

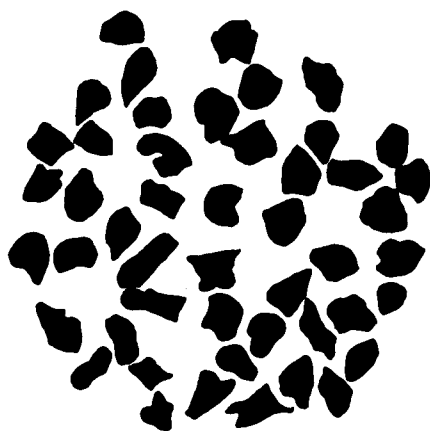


B

Figure 3. Camera lucida drawings of meiotic chromosome complements in Aster, X 2400. A. Aster foliaceus ssp. parryi, 449, first prometaphase;  $2n = 40\text{II}$ . B. Aster subspicatus, 350, first metaphase;  $2n = 48\text{II}$ .



A



B

expected trivalent or quadrivalent associations have not been observed in meiosis. In most cases, however, the nearly regular chromosome pairing at all polyploid levels suggests an allopolyploid origin.

In addition to polyploidy, some aneuploidy has occurred in the group. Two collections of A. bernardinus and one of A. adscendens revealed chromosome numbers of  $2n = 18II$  (Fig. 1G). Other counts in A. adscendens include  $2n = 13$ , 26, and  $27II$  (Fig. 2A). The count of 13 is particularly unusual and may actually be a triploid. However, it did not show the usual meiotic irregularities expected in a triploid. Thirteen pairs of chromosomes were seen at diakinesis and metaphase I, although they were rather sticky and hard to distinguish, and four sets of 13 singles were clearly seen at anaphase II (Fig. 1D). Occasional chromosome lagging was also seen at anaphase I.

In fertile triploid hybrids obtained from crossing heterophyllous Aster species, Avers (5) observed that the unpaired univalents divided at both divisions of meiosis, thus causing the number of chromosomes in each microspore to be higher than expected. Subsequent backcrosses with the tetraploid parent resulted in offspring with chromosome numbers closer to the tetraploid than to the triploid level. If the same type of phenomenon occurs in the asters of this study, the plants with 13 chromosome pairs might have arisen from a triploid by the chance combination in

the zygote of 26 chromosomes which were able to form pairs at meiosis, and which subsequently became stabilized.

The numbers of  $2n = 26$  or  $27II$  appear to be widespread in A. adscendens in the Rocky Mountains. As noted in Table I, the two numbers may be intermixed even in the same population. However, the presence of chromosome fragments makes accurate counting difficult, and more counts may establish a definite number of pairs with varying numbers of fragments. The obvious correlation of 13 and 26 allows further speculation that those plants with 26 pairs of chromosomes may be polyploid derivatives from the 13-paired plants. Striking morphological similarities indicate such a relationship is possible, although the known populations with the two chromosome levels are widely separated geographically. Further collecting and chromosome counting may narrow the distance between their known distributions, as well as uncover other aneuploid numbers, such as  $n = 14$ . The latter, combined with  $n = 13$ , would provide a basis for obtaining the polyploid number of  $2n = 27II$ .

Other workers have also noted some aneuploidy in Aster. Raven, et al. (53) reported  $n = 25$  for A. subspicatus. Huziwara (35) reported aneuploidy in at least four taxa of the genus in eastern United States.

Many aster specimens had small chromosome fragments or B-chromosomes in addition to the normal chromosome

complement or A-chromosomes (Fig. 1B, 1C, 1E, 2A). These small fragments have also been called supernumeraries and accessory chromosomes. In a recent review of the subject, Müntzing (46) stated that the terms accessory and B-chromosomes were preferable to the term supernumeraries, although he gave no technical difference. Other authorities seem to use the terms interchangeable.

The B-chromosomes in Aster are much smaller than the A-chromosomes, but they stain normally and they divide, indicating they have a centromere. They do not divide with the bivalents, however, but are usually seen dividing when the A-chromosomes have nearly reached the poles in first meiotic anaphase (Fig. 1B). In all of these features the B-chromosomes in Aster are similar to those in Secale, described by Müntzing (45) as "standard fragments". Knowledge of their behavior at second meiotic metaphase and anaphase is uncertain, but their presence at second anaphase was observed in some cases.

The function of B-chromosomes is not known, but Darlington (16, p. 25) has pointed out that they are more common in diploids than in polyploids, and he postulates that they provide such diploids with a greater genetic heterogeneity, such as genomic duplication confers on polyploids; this in turn allows such plants to invade more rigorous or severe environments. The present study has no bearing on Darlington's theory, but it does show

that the B-chromosomes are more commonly found in diploid and tetraploid asters than in the higher polyploids.

Clausen, Keck and Hiesey (13, p. 393) also noted a single B-chromosome in a diploid plant of A. adscendens.

#### Meiotic irregularities.

Many microspore mother cells in a great number of specimens showed slight meiotic irregularities of some sort. These consisted mostly of stickiness between pairs in diakinesis and metaphase I; late division and lagging chromosomes in early anaphase I; and chromosome bridges in late anaphase I and in anaphase II. These irregularities were particularly prevalent in those plants with aneuploidy or with B-chromosomes, but chromosome lagging and bridges were occasionally seen in plants without extra chromosomes or fragments, and which appeared to have good pairing in diakinesis and metaphase.

A careful cytological analysis of meiosis was not included as a part of this study, so the reasons for the observed meiotic disturbances are not yet clear. However, it is believed that the stickiness, or tendency of the bivalents sometimes to clump together may be due to close chromosomal homology resulting from autopolyploidy or at least segmental allopolyploidy as described by Stebbins (58). Stebbins feels that pure autopolyploidy is quite rare, yet on an external morphological basis, it seems to

be the most likely explanation of tetraploidy in at least two taxa, A. hallii and A. idahoensis. As stated earlier, however, the chromosomes do not form multivalents characteristic of autopolyploids.

Usually a chromosome bridge at anaphase is associated with an acentric fragment, and together the bridge-fragment configuration is indicative of a paracentric inversion. However, the presence of an acentric fragment could not be determined with certainty in most of the cells seen. The fragments usually present were late-dividing B-chromosomes which were also present at diakinesis or metaphase. Nevertheless, no explanation other than that of chromosomal inversions is postulated for the presence of bridges at anaphase I and II.

In order to determine if the meiotic irregularities affected pollen fertility (as indicated by stainability), as well as to determine if pollen infertility might be a factor in reducing crossability, pollen samples from all the parent plants used in the hybridization experiments were stained. The stain used was aceto-carmin, and the results are listed in Table II as percent stainability. The staining technique involved tapping out the pollen from several flowers in a drop of aceto-carmin. The stain was allowed to penetrate and darken for several minutes, then a drop of Hoyer's mounting medium was added and mixed with the stain, and the cover slip was applied.

Table II. Pollen Stainability of Plants Used in Hybridizations

Taxon	Accession number	Number of grains counted	Percent of stainable pollen
<u>adscendens</u>	313	452	77.4
	314	425	58.8
	322	392	89.3
	339c	412	97.1
	353	396	63.1
	354b	403	74.4
<u>bernardinus</u>	399	424	94.3
<u>chilensis</u>	297	402	99.5
	298	387	77.5
	299	403	99.3
	300	400	100.0
	343	401	99.8
	344	443	90.3
	361	405	98.8
	397	468	85.5
<u>eatonii</u>	315	450	52.7
	320	416	96.1
	324	412	97.1
	345	411	53.0
	346	454	88.1
<u>foliaceus</u> ssp. <u>parryi</u>	316	409	97.6
	330a	421	48.4

Table II. Continued

Taxon	Accession number	Number of grains counted	Percent of stainable pollen
<u>foliaceus</u>	330b	459	87.1
<u>ssp. parryi</u>	335	409	97.6
	354a	450	88.9
	355	409	97.6
<u>greatai</u>	396	414	96.6
<u>hallii</u>	348	480	16.7
	367	419	59.7
	398	408	98.0
	401	427	82.0
<u>laevis</u>	375	445	90.0
<u>occidentalis</u>	368	450	66.7
<u>ssp. intermedius</u>	369	404	99.0
	370	424	94.3
	374	402	99.5
<u>occidentalis</u>	309	414	96.6
<u>ssp. occidentalis</u>	310	420	95.0
	312	409	97.8
	326	411	85.1
	328a	416	96.1
	352	438	62.8
	357	440	43.2
<u>subspicatus</u>	301	415	96.4

Table II. Continued

Taxon	Accession number	Number of grains counted	Percent of stainable pollen
<u>subspicatus</u>	304	386	84.2
	305	401	99.8
	306	436	91.7
	307	401	99.8
	341	400	100.0
	350	402	99.5
	351	400	100.0
	358	402	99.5

Aceto-carmin was used in preference to aniline blue dissolved in lactophenol (cotton blue) because the former stains the nuclei as well as the cytoplasm. In mature pollen grains of *asters*, the two mature male gametes are present and they stain much darker than the cytoplasm. Thus I used their relative development, as well as cytoplasm stainability, as an indicator of pollen viability. In addition to making the slides permanent, Hoyer's mounting medium clears the thick wall of the pollen grain and stops the action of the stain, thus rendering the slides usable for years.

The results of the pollen staining were found to correlate quite closely to the cytological situation found in meiosis. Some exceptions can be noted, such as

the high percentage of stainable pollen (97.1) for collection 339c of A. adscendens, which had several irregularities at meiosis. It is interesting to note that a greater percentage of plants at the diploid and tetraploid levels had reduced pollen stainability than did plants at the higher levels. This is not particularly correlated with a greater amount of meiotic disturbance in plants at the lower ploidy levels, but is likely associated with the extensive duplication of genetic material in the higher polyploids which acts as a buffer against genic or chromosomal deviations that would be destructive in diploids or tetraploids.

#### Pollen size as an indication of polyploidy

An attempt was made to establish a correlation between pollen size and the various ploidy levels. The pollen used was all from dried, pressed specimens. Anthers were taken from several flowers on each plant and the pollen was tapped out in a drop of cotton blue. Only those grains were measured in which the cytoplasm was well stained. Aster pollen is spiny and is mostly round or sometimes slightly ovoid. In the latter case the grains were measured across the narrower diameter. Measurements were made from outside wall to outside wall at the base of the spines, i.e. spines were not included in the

measurements. The information obtained is given in Table III.

Table III. Comparative Pollen Grain Size in Microns

Taxon	Accession number	Number of grains measured	Size Range	Mean
		<u>Diploids</u>		
<u>lentus</u>	Heller 7547	25	18.2 - 22.8	20.5
<u>occidentalis</u> ssp. <u>interm.</u>	395	25	18.8 - 23.4	21.4
"	317	27	21.1 - 25.1	22.6
<u>greatai</u>	396	25	19.9 - 24.5	22.7
<u>adscendens</u>	322	25	21.1 - 25.6	23.0
<u>foliaceus</u> ssp. <u>parryi</u>	330a	50	21.1 - 27.4	23.9
<u>hallii</u>	401	25	21.7 - 26.2	24.1
<u>eatonii</u>	320	25	21.7 - 27.4	24.6
<u>cusickii</u>	Cronquist 6048	45	22.2 - 27.4	24.9
<u>hallii</u>	367	26	21.7 - 31.3	26.6
		<u>Tetraploids</u>		
<u>eatonii</u>	346	26	22.2 - 26.2	24.3
<u>occidentalis</u> ssp. <u>occid.</u>	312	26	22.2 - 26.8	24.6
"	390	25	22.8 - 28.5	25.0
<u>hallii</u>	349	26	23.9 - 26.8	25.2
<u>eatonii</u>	319	25	23.4 - 28.5	25.5

Table III. Continued

Taxon	Accession number	Number of grains measured	Size Range	Mean
<u>Tetraploids</u>				
<u>occidentalis</u> ssp. <u>occid.</u>	309	25	23.9 - 27.9	25.5
"	310	25	23.9 - 27.4	26.0
<u>hallii</u>	348	25	24.5 - 27.9	26.0
<u>foliaceus</u> ssp. <u>parryi</u>	330b	25	23.9 - 29.1	26.5
<u>occidentalis</u> ssp. <u>interm.</u>	374	25	24.5 - 31.9	26.6
"	368	26	23.9 - 29.6	27.1
<u>occidentalis</u> ssp. <u>occid.</u>	352	25	25.1 - 29.6	27.4
<u>Hexaploids</u>				
<u>occidentalis</u> ssp. <u>interm.</u>	370	25	22.8 - 27.4	24.4
<u>eatonii</u>	360	25	23.9 - 27.4	25.5
<u>laevis</u>	375	25	23.4 - 29.6	25.8
<u>occidentalis</u> ssp. <u>interm.</u>	369	25	25.1 - 28.5	26.6
<u>chilensis</u>	Raven 16564	20	24.5 - 29.6	26.7
<u>adscendens</u>	339c	25	25.1 - 29.1	26.9
<u>chilensis</u>	397	25	25.1 - 30.8	27.0
<u>hallii</u>	398	25	26.2 - 30.2	28.0
<u>chilensis</u>	342	25	26.8 - 30.2	28.8
"	300	25	26.8 - 32.5	29.5

Table III. Continued

Taxon	Accession number	Number of grains measured	Size Range	Mean
<u>Hexaploids</u>				
<u>chilensis</u>	297	25	28.5 - 31.9	29.9
<u>Octoploids</u>				
<u>hesperius</u>	433	25	23.9 - 27.9	25.4
<u>foliaceus</u>				
ssp. <u>parryi</u>	316	25	23.9 - 28.5	26.3
"	354a	25	25.1 - 28.5	26.3
"	335	25	27.4 - 32.5	29.9
<u>chilensis</u>	298	25	30.2 - 38.8	32.9
<u>Duodecaploids</u>				
<u>subspicatus</u> (Fd)*	305	25	26.2 - 30.8	29.2
" (GH)*	305	25	27.9 - 33.6	30.8
"	350	25	28.5 - 33.1	30.9

\*Fd designates field collection; GH designates greenhouse collection.

As was true in some other studies (7, p. 8; 8, 27), a definitive correlation could not be made, due to the overlap of size range between the various ploidy levels. However, the information derived from measuring pollen was helpful in locating populations of diploid plants. If pollen from a plant of unknown chromosome number measured less than 25.0 $\mu$ , the plant was estimated to be either diploid or tetraploid. If the pollen was less than 23.0 $\mu$ ,

the plant was strongly suspected of being a diploid. By using this method, at least two species, A. cusickii and A. lentus, were first suspected of being diploids. The suspicions were subsequently confirmed by chromosome counts.

If pollen measures larger than 25.0 $\mu$ , it is not at all possible to tell at what ploidy level the plant is, but only that it is a high polyploid. In addition to the 40 collections listed in Table III, pollen samples from about 115 different herbarium specimens, representing most of the taxa studied, were measured. The results of these measurements will not be formally listed but comments about particularly interesting ones will be made in the individual species discussions.

## HYBRIDIZATION

Artificial Hybridizations

A total of 383 artificial hybridizations were made in the greenhouse at Oregon State University during 1961 and 1962. The majority of the crosses were interspecific, while a few were intraspecific, with the complete results listed in Table IV. Each head used as a pistillate parent was considered as part of a separate hybridization, i.e. if several heads on one plant were pollinated by a plant of another species, the results from each head were recorded separately. Of the total number of crosses, 198 resulted in the production of at least one normal fruit, and 185 failed to produce any fruits.

In the following comments on some of the more prominent aspects of the hybridization results, it is well realized that much of the data is scanty and inconclusive. In a species group of this size, it would take well over a thousand crosses to get a complete and accurate picture of breeding trends and interspecific relationships. Seven taxa were not even included in the hybridizations because living material was obtained too late in the study. Other taxa were only sparingly involved. Nevertheless, enough crosses were made, and hybrids obtained, to reveal some aspects of reproductive intercompatibility in the genus Aster.

Table IV. Crossing Relationships Among Aster Species

Pistillate parent		Staminate parent	Number of heads	Number of flowers pollinated	Percent flowers setting normal fruit
<u>adscendens</u>	X	<u>chilensis</u>	2	69	0.0
<u>bernardinus</u>	X	<u>adscendens</u>	2	78	0.0
<u>chilensis</u>	X	<u>adscendens</u>	13	352	3.4
"	X	<u>bernardinus</u>	17	426	40.5
"	X	<u>chilensis</u>	14	446	32.5
"	X	<u>eatonii</u>	4	121	0.0
"	X	<u>foliaceus</u> <u>ssp. parryi</u>	15	404	18.8
"	X	<u>greatai</u>	8	209	0.0
"	X	<u>hallii</u>	15	422	41.5
"	X	<u>occidentalis</u> <u>ssp. interm.</u>	10	284	79.9
"	X	<u>occidentalis</u> <u>ssp. occid.</u>	10	306	34.6
"	X	<u>subspicatus</u>	14	502	8.2
<u>eatonii</u>	X	<u>chilensis</u>	7	222	1.3
"	X	<u>foliaceus</u> <u>ssp. parryi</u>	1	39	2.6
"	X	<u>hallii</u>	1	28	42.9
"	X	<u>occidentalis</u> <u>ssp. occid.</u>	4	142	38.0
"	X	<u>subspicatus</u>	9	333	0.3
<u>foliaceus</u> <u>ssp. parryi</u>	X	<u>bernardinus</u>	4	135	11.8

Table IV. Continued

Pistillate parent		Staminate parent	Number of heads	Number of flowers pollin- ated	Percent flowers setting normal fruit
<u>foliaceus</u> <u>ssp. parryi</u>	X	<u>chilensis</u>	6	181	5.5
"	X	<u>foliaceus</u> <u>ssp. parryi</u>	3	74	43.2
"	X	<u>hallii</u>	1	35	0.0
"	X	<u>laevis</u>	1	29	93.1
"	X	<u>occidentalis</u> <u>ssp. interm.</u>	1	35	74.3
"	X	<u>occidentalis</u> <u>ssp. occid.</u>	3	82	0.0
"	X	<u>subspicatus</u>	10	313	27.8
<u>greatai</u>	X	<u>occidentalis</u> <u>ssp. occid.</u>	2	80	0.0
"	X	<u>subspicatus</u>	4	158	0.0
<u>hallii</u>	X	<u>chilensis</u>	3	89	80.0
"	X	<u>occidentalis</u> <u>ssp. occid.</u>	2	50	26.0
<u>laevis</u>	X	<u>chilensis</u>	3	99	51.5
"	X	<u>foliaceus</u> <u>ssp. parryi</u>	2	61	68.8
"	X	<u>hallii</u>	3	71	0.0
"	X	<u>laevis</u>	2	67	52.2
"	X	<u>subspicatus</u>	7	236	16.9
<u>occidentalis</u> <u>ssp. interm.</u>	X	<u>chilensis</u>	4	144	43.7

Table IV. Continued

Pistillate parent	Staminate parent	Number of heads	Number of flowers pollin- ated	Percent flowers setting normal fruit
<u>occidentalis</u> <u>ssp. interm.</u>	X <u>foliaceus</u> <u>ssp. parryi</u>	4	148	0.0
"	X <u>occidentalis</u> <u>ssp. interm.</u>	1	47	21.3
"	X <u>occidentalis</u> <u>ssp. occid.</u>	5	222	24.3
"	X <u>subspicatus</u>	4	162	19.7
<u>occidentalis</u> <u>ssp. occid.</u>	X <u>adscendens</u>	10	320	9.4
"	X <u>chilensis</u>	7	214	20.1
"	X <u>eatonii</u>	2	55	0.0
"	X <u>foliaceus</u> <u>ssp. parryi</u>	6	200	25.5
"	X <u>greatai</u>	8	235	0.0
"	X <u>hallii</u>	4	132	37.9
"	X <u>laevis</u>	8	244	14.3
"	X <u>occidentalis</u> <u>ssp. interm.</u>	2	55	43.6
"	X <u>subspicatus</u>	10	312	2.2
<u>subspicatus</u>	X <u>adscendens</u>	16	460	0.0
"	X <u>chilensis</u>	11	355	36.6
"	X <u>eatonii</u>	10	306	0.0
"	X <u>foliaceus</u> <u>ssp. parryi</u>	13	393	59.0

Table IV. Continued

Pistillate parent		Staminate parent	Number of heads	Number of flowers pollinated	Percent flowers setting normal fruit
<u>subspicatus</u>	X	<u>greatai</u>	3	101	0.0
"	X	<u>hallii</u>	7	255	36.5
"	X	<u>laevis</u>	9	303	73.6
"	X	<u>occidentalis</u> <u>ssp. interm.</u>	21	636	0.3
"	X	<u>occidentalis</u> <u>ssp. occid.</u>	8	230	16.9
"	X	<u>subspicatus</u>	7	180	24.4

The most striking result of the hybridization experiments was the discovery of a lack of genetic barriers between many of the species. A notable example of this was the series of crosses involving A. laevis. This species is widespread in eastern United States, but is not very common west of the Rocky Mountains. This fact, together with its morphological distinctness, would tend to indicate biological isolation from the more western members of this study. However, successful crosses with plants from the coast, the Willamette Valley, and the Cascade Mountains emphasize that close genomic homologies probably characterize this entire group of plants.

In some cases interspecific crosses were more successful than were intraspecific crosses. However, this

ease of crossability was true only at the various polyploid levels. In nearly all crosses between polyploids and diploids, fruit-set was very low or lacking. All diploids used in hybridizations are included in the species A. adscendens, A. eatonii, A. greatai, and A. hallii. Of the successful crosses listed in Table IV which involve these species, most were those in which polyploids were used. Unfortunately, no crosses were made between two diploid species, thus no information is available on relative crossability at that homoploid level.

The fact that polyploid plants of different chromosome levels were rather freely crossable is also a noteworthy feature. This can be seen in Table V, which summarizes information on F<sub>1</sub>'s from selected homoploid and heteroploid crosses. However, the wider the gap between chromosome levels, the lower the percentage of fruit-set. Crosses involving duodecaploid A. subspicatus are particularly illustrative of this point.

Another interesting aspect is the tendency for the fruit-set in reciprocal crosses to be higher when the staminate parent has a smaller chromosome number than the pistillate parent. This is likewise best seen in reciprocal crosses involving duodecaploid A. subspicatus, especially accession numbers 301 and 304 cited in Table V. Stebbins (60) has reviewed a number of studies which all showed a similar trend. Obvious exceptions in the crosses reported

Table V. Relative Success of Selected Homoploid and Heteroploid Crosses as Indicated  
By Fruit-set, Seed Germination and Stainable Pollen of the Hybrids

HOMOPLOID CROSSES			Number of heads	Number of flowers polli- nated	Percent flowers setting normal fruit	Number of fruits sown	Percent germi- nation	Percent stainable pollen of F <sub>1</sub>
A. Tetraploid:								
<u>hallii</u>	348 X 309	<u>occid.</u> <u>ssp. occid.</u>	2	50	26.0	13	7.7	52.4
<u>occid.</u> <u>ssp. occid.</u>	309 X 348	<u>hallii</u>	1	33	78.8	26	15.4	97.0
B. Hexaploid:								
<u>chilensis</u>	300 X 370	<u>occid.</u> <u>ssp. interm.</u>	1	38	60.5	23	39.1	97.5
"	397 X 370	"	4	94	77.7	15	73.0	95.1
"	344 X 339c	<u>adscendens</u>	1	22	54.5	12	16.7	80.2
<u>hallii</u>	398 X 397	<u>chilensis</u>	3	89	80.0	23	73.9	99.0
<u>occid.</u> <u>ssp. interm.</u>	369 X 397	"	4	144	43.7	16	93.7	98.8
<u>laevis</u>	375 X 300	"	3	99	51.5	17	88.2	90.7

Table V. Continued

HOMOPLOID CROSSES			Number of heads	Number of flowers polli- nated	Percent flowers setting normal fruit	Number of fruits sown	Percent germi- nation	Percent stainable pollen of F <sub>1</sub>
C. Octoploid:								
<u>foliaceus</u> ssp. <u>parryi</u>	316 X 328a	<u>foliaceus</u> ssp. <u>parryi</u>	1	22	36.4	8	25.0	99.0
D. Duodecaploid:								
<u>subspicatus</u>	304 X 358	<u>subspicatus</u>	3	100	17.0	13	76.9	99.0
"	307 X 341	"	2	37	59.5	12	75.0	100.0
HETEROPLOID CROSSES								
A. Diploid X tetraploid:								
<u>eatonii</u>	324 X 312	<u>occid.</u> ssp. <u>occid.</u>	4	142	38.0	18	0.0	
B. Diploid X hexaploid:								
<u>eatonii</u>	324 X 297	<u>chilensis</u>	2	60	5.0	3	33.3	21.2
C. Tetraploid X triploid?:								
<u>occid.</u> ssp. <u>occid.</u>	352 X 354b	<u>adscendens</u>	2	77	37.7	16	6.2	

Table V. Continued

HETEROPOID CROSSES			Number of heads	Number of flowers polli- nated	Percent flowers setting normal fruit	Number of fruits sown	Percent germi- nation	Percent stainable pollen of F <sub>1</sub>
D. Tetraploid X hexaploid:								
<u>eatonii</u>	346 X 398	<u>hallii</u>	1	28	42.9	12	91.7	86.1
<u>occid.</u> ssp. <u>occid.</u>	312 X 398	"	2	67	23.9	13	15.4	78.2
"	326 X 370	<u>occid.</u> ssp. <u>interm.</u>	2	55	43.6	12	50.0	31.2
"	357 X 299	<u>chilensis</u>	2	58	29.3	7	71.4	64.1
"	357 X 397	"	1	37	56.7	21	42.8	64.7
"	357 X 375	<u>laevis</u>	8	244	14.3	13	38.5	74.2
E. Tetraploid X octoploid:								
<u>occid.</u> ssp. <u>occid.</u>	312 X 316	<u>foliaceus</u> ssp. <u>parryi</u>	1	36	66.7	24	4.2	98.4
F. Tetraploid X duodecaploid:								
<u>occid.</u> ssp. <u>occid.</u>	309 X 301	<u>subspicatus</u>	2	69	5.8	4	50.0	65.8

Table V. Continued

HETEROPLOID CROSSES			Number of heads	Number of flowers polli- nated	Percent flowers setting normal fruit	Number of fruits sown	Percent germi- nation	Percent stainable pollen of F <sub>1</sub>
G. Hexaploid X tetraploid:								
<u>chilensis</u>	300 X 399	<u>bernardinus</u>	7	172	32.6	19	68.4	81.9
"	397 X 399	"	5	125	50.4	16	87.5	93.9
<u>occid.</u> <u>ssp. interm.</u>	369 X 368	<u>occid.</u> <u>ssp. interm.</u>	1	47	21.3	10	80.0	87.2
"	369 X 352	<u>occid.</u> <u>ssp. occid.</u>	2	82	26.8	12	50.0	76.7
"	370 X 326	"	1	60	50.0	15	40.0	81.2
H. Hexaploid X octoploid:								
<u>chilensis</u>	300 X 298	<u>chilensis</u>	2	78	32.0	24	91.7	0.0
"	397 X 328a	<u>foliaceus</u> <u>ssp. parryi</u>	1	28	67.9	10	90.0	94.4
<u>laevis</u>	375 X 355	"	2	61	68.8	13	69.2	97.2
I. Hexaploid X duodecaploid:								
<u>chilensis</u>	300 X 304	<u>subspicatus</u>	2	78	2.5	2	100.0	90.2

Table V. Continued

HETEROPOLOID CROSSES				Number of heads	Number of flowers polli- nated	Percent flowers setting normal fruit	Number of fruits sown	Percent germi- nation	Percent stainable pollen of F <sub>1</sub>
<u>occid.</u> <u>ssp. interm.</u>	369 X 301	<u>subspicatus</u>		2	71	28.2	12	75.0	96.8
"	369 X 350	"		2	91	13.2	12	25.0	96.8
J. Octoploid X tetraploid:									
<u>foliaceus</u> <u>ssp. parryi</u>	354aX 399	<u>bernardinus</u>		1	30	6.7	2	100.0	64.6
K. Octoploid X hexaploid:									
<u>chilensis</u>	298 X 369	<u>occid.</u> <u>ssp. interm.</u>		1	24	95.8	23	52.2	90.5
"	298 X 398	<u>hallii</u>		3	73	84.9	20	65.0	91.3
<u>foliaceus</u> <u>ssp. parryi</u>	355 X 369	<u>occid.</u> <u>ssp. interm.</u>		1	35	74.3	15	66.7	94.4
"	316 X 299	<u>chilensis</u>		2	54	18.5	10	80.0	95.1
L. Octoploid X duodecaploid:									
<u>chilensis</u>	298 X 305	<u>subspicatus</u>		1	31	77.4	23	91.3	97.1

Table V. Continued

HETEROPOLOID CROSSES			Number of heads	Number of flowers polli- nated	Percent flowers setting normal fruit	Number of fruits sown	Percent germi- nation	Percent stainable pollen of F <sub>1</sub>
<u>foliaceus</u> <u>ssp. parryi</u>	316 X 341	<u>subspicatus</u>	3	91	12.1	11	36.4	94.9
M. Duodecaploid X hexaploid:								
<u>subspicatus</u>	301 X 397	<u>chilensis</u>	3	140	80.7	28	60.7	92.8
"	304 X 375	<u>laevis</u>	8	251	78.9	27	29.6	98.6
"	351 X 369	<u>occid.</u> <u>ssp. interm.</u>	2	68	2.9	2	100.0	97.9
N. Duodecaploid X octoploid:								
<u>subspicatus</u>	301 X 316	<u>foliaceus</u> <u>ssp. parryi</u>	2	59	72.9	22	27.3	96.7
"	306 X 316	"	2	44	54.5	15	13.3	99.5
"	304 X 355	"	4	134	97.0	29	13.8	94.6

here are those of A. subspicatus X A. occidentalis ssp. intermedius (Table IV). Only two fruits were produced from 636 flowers in 21 heads. The reciprocal crosses, in which the higher polyploid plant was the staminate parent, resulted in 32 fruits from 162 flowers. However, nearly all of the former crosses were attempted in the "potato greenhouse", which, as indicated earlier, may account for the failures.

As stated above, a number of intraspecific crosses were less fertile than were interspecific crosses (see Table IV). Most of these cases are probably a matter of too few crosses having been attempted. Certainly this is true for A. foliaceus ssp. parryi, A. laevis, and A. occidentalis ssp. intermedius, within none of which were more than three crosses made. On the other hand, the number of crosses made within A. chilensis and A. subspicatus, 14 and seven respectively, appears to be sufficient for making a reliable estimate of fertility. The most likely explanation of their reduced intrafertility stems from the time of year some of the crosses were made. Because of their proximity to Corvallis these two species were the first ones collected and started in the greenhouse. The plants did not bloom until late fall or winter, at which time flower development may not have been as normal as at their usual summer blooming time. Also, the first hybridization attempts of the study, which may have

lacked later finesse, involved these plants. In any case, some of these early hybridization attempts failed, whereas later ones succeeded.

#### Description of the F<sub>1</sub> Hybrids

The hybrid fruits were sown on vermiculite in flats in the greenhouse. Because of space limitations, not all of the seedlings were raised to maturity. Six seedlings of each hybrid type were selected and transplanted to clay or plastic pots, if that many seedlings were available. Later, when the plants were transplanted to the Botany Farm, only four plants of each type were chosen. The plants of each hybrid type were usually all quite similar and more or less intermediate morphologically between the parents, with little evidence of genetic segregation. As yet F<sub>2</sub> plants have not been obtained.

The hybrid vigor of most of the F<sub>1</sub>'s was readily apparent as early as the seedling stage. They grew rapidly and often attained a larger size than either parent, and in some cases they flowered sooner. On the other hand, some hybrid fruits were slow to germinate and the seedlings were weak and slow to develop. A few of these died, but if the plants survived the seedling stage, they usually attained normal size and later flowered. Heterosis was especially apparent after the hybrids were transplanted to the Botany Farm. The hybrids were planted in three rows

at the Farm, and the parent plants were in three different rows. A casual observer could readily distinguish the different rows by the vigor of the plants.

No examination of meiosis has yet been done on any of the F<sub>1</sub> plants. This is certain to prove a very fascinating aspect of the study, and is badly needed to aid in determination of phylogenetic relationships among the species. Some indication of fertility has been gained by the method of pollen stainability with aceto-carmin, as outlined in the cytology section. From this evidence, given in the last column in Table V, it would appear that meiosis has not been too greatly upset in most cases; or at least that it allowed enough chromosomes to get into each microspore so that normal appearing pollen grains and male gametes were formed. Of the 44 crosses summarized in Table V which resulted in the growth of hybrid plants, 28 of the hybrids had pollen stainability of 90.0 percent or better. Fourteen of the 16 hybrids which had less than 90 percent stainable pollen were from crosses which involved diploids or tetraploids. These figures are more or less consistent with the fertilities indicated for the parent plants by pollen stainability (Table II), and they again illustrate the inability of plants at the lower ploidy levels to tolerate genetic imbalance as well as do plants at the higher levels.

The reciprocal crosses 348 X 309, 309 X 348 and 326 X

370, 370 X 326 illustrate the point that a degree of infertility in one parent has a greater effect on the offspring when that parent is maternal than when it is paternal. This is likely a reflection of the endosperm development, or of embryo, endosperm, and maternal tissue interaction. The lack of pollen production in the intraspecific A. chilensis cross, 300 X 298, is certainly surprising in light of other results, but no explanation is now available.

Perhaps the most convincing evidence of the fertility of the hybrid plants is the abundant amount of fruit that was produced following open pollination at the Botany Farm. The plants were simply allowed to grow in the open plot, where they were visited by numerous bees. Nearly every hybrid plant produced some fruit, and most of them had several to many full heads of fruit. Even one plant of the 300 X 298 cross had several heads with normal looking fruits. The hybrid plant 324 X 297 had a number of well-fruited heads.

A remarkable thing regarding the production of fruit by these hybrid plants is that the source of pollen in any one pollination is unknown, and the resulting seed may contain several different genomes other than the ones already contributed by the maternal parent. The only plants from which fruits were not collected were those of the crosses 357 X 299, 357 X 375, and 344 X 339c. In addition, only

one plant of cross 357 X 397 produced normal looking fruit. The two plants of the 344 X 339c cross were very slow to develop and did not flower until late fall when the rains had started and bees were not active.

The only successful hybridization which involved a diploid parent, 324 X 297, resulted in a very interesting hybrid plant. The pistillate parent is typical of A. eatonii in being tall and erect, with linear leaves, subequal phyllaries, pink ray flowers, and numerous heads in a long, narrow, leafy panicle. The staminate parent was collected on a bluff overlooking the ocean where it grew in a low prostrate manner; it retained this habit under cultivation in the greenhouse. Its other features of a loosely branching inflorescence with many heads, crenate to serrate, ovate to oblong-lanceolate leaves, graduated phyllaries, and purple rays are characteristic of A. chilensis.

The hybrid plant is mostly prostrate with a few erect stems. The several main branches are quite divergent, but secondary branches are short and close together. The inflorescence is not as leafy as in 324; the leaves are narrowly oblong-lanceolate and irregularly incised. The phyllaries are nearly equal and the ray flowers are a rich pink. The hybrid approaches 297 in habit and leaf serration; it is intermediate in leaf shape and in branching pattern; and it is closer to 324 in both phyllary size and

ray color. An interesting point to note is that the prostrate habit of 297 is not only genetically determined, but is dominant over the erectness of 324, at least in this cross. It was also surprising to find that purple ray color, by far the most common ray color in the genus Aster, was recessive to pink in this case.

Additional hybrid plants will not be described, but comments on some specific characteristics may be worthwhile. At least one plant of each of the hybrid combinations was analyzed on the basis of the five key characteristics discussed in the morphology section. The leaf shape of most hybrid plants was intermediate between that of the parents. Exceptions include dominance of linear leaves in some crosses involving A. bernardinus, A. eatonii and A. hallii; and dominance of clasping leaf bases in crosses involving A. laevis. Crenate or serrate leaves appeared on most hybrids with A. laevis or A. subspicatus as one parent.

In most cases the pubescence of both parents was too similar to provide a detectable marker in the hybrids. The few notable exceptions include accessions 399, 397 and 369. The former one is normal A. bernardinus, but the latter two are exceptionally pubescent forms of A. chilensis and A. occidentalis ssp. intermedius respectively. In all crosses involving these plants the presence of abundant pubescence was definitely dominant. Consistent

with this observation is the fact that all hybrids having the glabrous species A. laevis (375) as a parent are pubescent to some degree, although such hybrids are nearly always recognizable owing to their distinctively shaped inflorescence bracts which also characterize A. laevis.

The only type of inflorescence pattern that was consistently dominant genetically in the hybrids was the crowded, many-headed type of A. hallii, especially accession 348, and accession 339c of A. adscendens. Otherwise, most hybrids were intermediate in this feature.

In crosses between plants with graduated phyllaries and those with subequal phyllaries, the latter type quite consistently was dominant. Likewise, acute outer phyllaries usually prevailed over obtuse outer phyllaries in the hybrid phenotypes. It should be pointed out, however, that these results may not be due entirely to genetic factors, since environmental modifications of the transplanted parents with graduated, obtuse phyllaries tended towards more equal, acute phyllaries. Such easily dominated or modified features contribute to taxonomic confusion and error by simulating the phenotypes of other species. On the other hand, their consistent expression in certain species indicates the plants must be homozygous, or nearly so, for genes determining such a phenotype. The traits are therefore markers for the homozygous recessive condition and as such give a more accurate assessment of the

lack of hybridity of a genotype than would traits determined by dominant genes.

Ray flower color of the parents differed markedly only when A. hallii (348, 398), A. eatonii (324, 346), and accession 300 of A. chilensis were used as one parent. The color of 324 has been described; the others had either white or pale lavender flowers. In all crosses of these plants with violet- or purple-rayed plants, the hybrids were either an intermediate lavender or were closer in color to the darker parent. Thus incomplete dominance or quantitative inheritance involving a few genes is suggested for inheritance of flower color in these plants.

#### Natural Hybridization

Judging from results of the artificial hybridizations, one might expect to find many interspecific hybrids in nature. Also, from the number of herbarium specimens which could be designated as putative hybrids, the same conclusion would be reached, at least for some areas. Actually, very few examples of natural hybridization were encountered in the course of several field trips through parts of Oregon, Washington, and Idaho. The most apparent reason for this was that seldom were two or more species found in the same population or even in the same locality. In most of the situations where two species were growing together, one of them was a diploid, or probably so, and

the other was a high polyploid. In none of these places was there evidence of hybridization.

The only observed examples of apparent natural hybridization are the following. Accession numbers 330a and 330b represent diploid and tetraploid plants respectively of A. foliaceus ssp. parryi. These plants were growing in a mixed population in a meadow near Lloyd Lake, Idaho County, Idaho. About  $\frac{1}{2}$  mile away, also in a meadow, was growing a large population of A. cusickii. The recognizable differences of 330b from 330a are all in the direction of A. cusickii, although not decidedly enough to place the plants in that species. Consequently, the hybrid origin of 330b is strongly suspected. Some plants of A. cusickii were collected, but they later died and no chromosome counts were obtained.

Accessions 439, 440, and 441 were all made in Frye Meadows, Union County, Oregon by Mr. Curt Carlhom. Collection 439 is typical tetraploid A. occidentalis ssp. occidentalis, and was growing in a meadow. Accession 440 is a typical diploid A. cusickii, and was growing near 439 in openings in a grove of trees. Voucher specimens of collection 441 represent a series of intermediate types between 439 and 440. Only two plants from the 441 population were obtained for cultivation and these were both morphologically closer to A. occidentalis than to A. cusickii; their chromosome number was  $2n = 16II$ . However, the vouchers

indicate probable hybridization.

The final example also involves A. cusickii and strikingly illustrates alloploidy. Accessions 466 and 467, A. idahoensis and A. cusickii respectively, were growing together along the road about one mile south of Clarkia, Shoshone County, Idaho. Plants of both species are diploid at this locality, and are very distinct phenotypically. One plant, however, was noticed to be intermediate; subsequent chromosome counting revealed it to have the tetraploid number. Hence this plant may well be a recently derived natural allotetraploid. In appearance it resembles A. cusickii in the features of pubescence and somewhat enlarged leaves with auriculate-clasping bases; it approaches A. idahoensis in the traits of a branching, many-headed inflorescence and narrow, equal phyllaries. Meiosis appeared to be nearly normal, with 16 bivalents at diakinesis and metaphase, but some lagging chromosomes at both anaphase I and II.

## DISCUSSION

Polyploidy

Polyploidy in itself can no longer be considered a surprising or novel feature in the plant kingdom. At least one-third, and perhaps closer to one-half, of all cytologically studied angiosperms are estimated to be of polyploid origin (18, p. 213). The various mechanisms allowing genomic increase are now well known. The primary problem in regard to polyploids in many plant groups concerns their systematic placement or taxonomic status. Theoretically, polyploidy would not cause any taxonomic problems if all the polyploids were allopolyploids of quite distinct species, and thus were morphologically intermediate between, and reproductively isolated from, their parents. Such is not the case, however, since all degrees of intermediate conditions of polyploidy exist between extreme allopoloidy on one hand and strict autopoloidy on the other.

Although Stebbins (59, p. 316) and others feel that strict autopoloidy is very rare, Darlington (16, p. 15) states that it commonly occurs in true-breeding or non-hybrid diploids. Apart from this controversy, both are agreed along with many biosystematists (18, p. 215-221), that hybridization between ecological races, varieties, or

subspecies of one species, with subsequent chromosome doubling, is an important contribution to polyploid complexity. Löve (43) calls such polyploids "hemiallopolyploids" and states that their evolution is the most common kind of abrupt speciation. Although this is technically autopolyploidy, since it is intraspecific, enough genic differentiation may have occurred in the two contributing entities that chromosome pairing may not be too drastically upset by multivalent attraction in the tetraploid. Perhaps equally as common as this latter "autopolyploidy" is the type of segmental allopolyploidy first discussed by Stebbins (58). This situation involves hybridization of entities which have diverged sufficiently to be called different species, but which still have much chromosome homology. Thus the diploid hybrid may have good chromosome pairing, while being sterile, but the derived tetraploid may have some meiotic irregularity due to multivalent associations.

Since the contributing diploids are quite similar in appearance in the types of polyploidy mentioned above, the tetraploid may be difficult to distinguish from its parents. However, even when definite allopolyploidy is involved the polyploid may not be intermediate. Stebbins (59, p. 309) cites examples from the genera Nasturtium and Madia, in which the allopolyploids derived from two distinct species with widely different chromosomes resembled one parent so closely that the investigators classed them as autopolyploids.

Stebbins also postulates (59, p. 312) that following allotetraploidy and subsequent segregation within the tetraploid, or following backcrossing with either diploid progenitor, natural selection would tend to choose those segregants which are morphologically and physiologically most like the well adapted diploid species. Thus he believes that many apparent autopolyploids actually have an allopolyploid origin.

From the foregoing considerations of polyploidy it is evident that both autopolyploidy and allopolyploidy might contribute to what Larsen (39) called "cryptospecies" in Lathyrus pratensis and Kohlrauschia prolifera, and what Davis and Heywood (18, p. 217-221) discuss as "cryptic polyploids". The latter authors explain that the term may be applied to those cases where morphological markers are absent or virtually so, and the exact nature of the polyploidy is not known. They cite a number of examples.

The taxonomic problems involved in the disposition of such cryptic polyploids are obvious, and general agreement among taxonomists regarding the solutions has not been reached. This is in fact one of the most controversial subjects of modern taxonomy. At one extreme is the opinion of Löve (42), who states that the members of each level of a polyploid series should be given specific rank regardless of closeness of similarity. He feels that no matter how similar, they can be found to have some distinguishing

characteristics upon careful study. Valentine and Löve (64) modify this extreme view somewhat, admitting that there are some cases where specific distinction is impractical.

Basic to Löve's original thesis and reiterated again in 1960 (43, p. 120) is the opinion that polyploidy "always imposes a strong and effective barrier of sterility, or even incompatibility, between parent and progeny". That this is usually true at the diploid-tetraploid level is verified by the sterile condition of most triploids. But even at this level, triploids have had some significance in introgression, as noted by Stebbins (59, p. 269) in Tradescantia. Avers (5) obtained three fertile triploid plants from a cross between Aster shortii ( $n = 18$ ) and Aster cordifolius ( $n = 9$ ). Although some univalents and trivalents were seen at meiosis, all three hybrids had 90-95 percent stainable pollen. From backcrosses of the hybrids with the tetraploid parent, nine plants were obtained. These had 80-90 percent stainable pollen. Avers was also able to locate a natural triploid similar to her artificially produced ones. This plant had 80 percent stainable pollen. Jones (36) states the opinion that triploids and other uneven polyploids need not form the highly effective barrier to gene exchange that is commonly believed. Rather, he postulates that hybrid sterility at the diploid level may form a greater barrier to gene

exchange, and when polyploidy does occur the capacity for gene exchange may be enhanced rather than lessened. In addition to potential fertility, the triploid has a greater proneness to produce unreduced gametes and thus contribute to further variation in chromosome number. Reasonable evidence for these conclusions is cited from studies in Anthoxanthum, Carduus, Dactylis, and Gladiolus.

Above the diploid-tetraploid level, however, increasing numbers of studies have revealed that fertile hybrids are produced much more readily between polyploid races or species, even those at different chromosome levels, than between diploid species. This situation, determined both by intensive field studies and garden experimentation, represents a further contradiction to Löve's position. It has also intensified the taxonomic perplexity for the workers in these groups. The treatments accorded some of these polyploid complexes represent the opposite point of view from that of Löve, and they will be discussed in the next subsection.

#### Aster as a Polyploid Complex

The term polyploid complex was proposed by Babcock and Stebbins (7, p. 56) to apply to sexually reproducing plant groups, usually genera or subdivisions thereof, which contain rather distinct well-characterized diploids, and less well-defined intergrading polyploids. Davis and Heywood

(18, p. 227-231) have since discussed this condition as a "polyploid pillar complex". The implication of this latter term is that the diploids are the pillars or basic taxonomic units--the relatively stable and mostly reproductively isolated species which support the complex and sometimes massive superstructure of the polyploids.

Several different kinds of polyploid complexes may be noted, based primarily on the degree of distinctness of the diploid and polyploid units, and the extent of gene flow between chromosome levels. The genus Clarkia (40) typifies the situation in which gene flow is rather limited between any level, and the taxonomic units are reasonably distinct. Three chromosome levels are represented, along with a considerable amount of aneuploidy, and structural hybridity accounts for much of the sterility between homoploid species. This latter aspect is characteristic of many groups of annual plants.

A second type of polyploid complex is exemplified by the genera Dodecatheon (61) and Vaccinium, subgenus Cyanococcus (11). In these two groups gene exchange is restricted between different chromosome levels, but is rather free between different species at the same level. Although in both genera some of the tetraploids are considered to be autopolyploids and are very similar to their diploid progenitors, Camp, in Vaccinium, gives each unit a species name, while Thompson, in Dodecatheon, retains the diploids

and tetraploids and sometimes even hexaploids in the same species.

In Phacelia (27) very few artificial hybrids were obtained, but extensive field collections indicated considerable hybridization at the tetraploid level and also apparent introgression with the diploids. The diploids, however, were found to be rather distinct and appeared to be reproductively isolated. Heckard placed diploids and the most closely associated tetraploids in the same taxon, and gave species recognition to other tetraploid types which were seen as forming somewhat distinct, though interconnected, morphological plateaus.

Achillea (21), Cardamine (44) and Danthonia (10) characterize a fourth type of complex. In these groups, polyploid series are continuous from tetraploid to octoploid or decaploid. Within this framework, hybrids can be freely obtained in homoploid and heteroploid crosses above the tetraploid level. Crosses involving tetraploids with the higher levels are usually much less productive, and the gene exchange between any of the polyploids and the diploids is almost completely restricted. In the Achillea millefolium complex, Ehrendorfer retains specific names for plants at each chromosome level, including several distinct diploids, two tetraploids and three hexaploids. The tetraploids are still somewhat ecologically isolated, but the hexaploids hybridize so freely that Ehrendorfer states they

may have to be merged into a single species. In the Cardamine pratensis complex, Lövkvist included the diploid, tetraploid, and hexaploid plants in one species, C. pratensis, and the octoploids and decaploids in another, C. palustris. This decision was based on the relative restriction of gene exchange between the two groups. In Danthonia gene exchange was even more freely possible between all chromosome levels, with viable hybrids being obtained from several diploid-tetraploid crosses and one diploid-hexaploid cross. Among the many species studied, Brock and Brown recognized two species which included plants of three chromosome levels and several taxa which included two levels.

The plants of the genus Aster, section Aster, included in this study are certainly part of a polyploid complex. Cytological and experimental investigation indicates that the variation pattern in this group is probably most similar to the examples of the fourth type listed above. In addition, it is felt that some introgression with the diploids has occurred as in Phacelia of the third type. Aster adscendens, A. eatonii, A. hallii, and A. idahoensis all have diploid and tetraploid populations so similar that autopoloidy, or the "hemiallopoloidy" of Löve, is suspected for the tetraploid origin. At least they qualify as cryptospecies in the sense of Larsen. In A. adscendens this designation can be extended to include

plants at the hexaploid level as well. Similarly, in taxa which are predominantly polyploid at two or more chromosome levels, such as A. chilensis, A. foliaceus ssp. parryi and A. subspicatus, very little distinction can be made between plants of various levels. Selected populations of diploid, tetraploid, and hexaploid plants of A. occidentalis ssp. intermedius can be morphologically distinguished but the intergradation is so complete over the whole range of the subspecies that taxonomic separation would be impractical.

The diploids of the various taxa in Aster are morphologically sharply distinct, just as in the other polyploid complexes listed above. As stated earlier, no hybridizations were made between diploids, so it is not known to what degree sterility barriers have been developed at this basic level. However, since the same basic genomes are present in various combinations in the polyploids, the degree of interfertility between the polyploid units suggests that a considerable amount of homology still exists between the genomes. On the other hand, if the attainment of polyploid status allows a greater degree of intercrossability than is possible at the diploid level, this in itself would tend to break down genic or chromosomal crossing barriers and favor convergence of the entities both genetically and morphologically. At the same time, the diploids, whose breeding is primarily intraspecific, could be gradually diverging by means of genic or chromosomal changes

which might restrict or only rarely allow hybridization. Thus the interfertility of the polyploids may not at all be an accurate indicator of the breeding potential among the diploids. That the diploids in Aster are not as reproductively isolated as this latter argument suggests is indicated by the few collections mentioned in the hybridization section, by herbarium specimens which appear to be introgressants in areas where diploids are known to occur together, and by other studies in the genus. Avers (3) was able to obtain a large number of moderately to highly fertile diploid hybrids from a series of crosses among the heterophyllous asters of eastern United States. Wetmore and Delisle (66) described the complete interfertility between very different appearing A. novae-angliae and A. multiflorus (ericoides), the hybrids of which fit the description of a named species, A. amethystinus.

The intriguing question of why polyploidy occurs so much more commonly in some genera than in others has not been answered. However, Gustafsson (26), Stebbins (59, p. 355-356), and others have pointed out that perenniality, particularly by strong spreading rhizomes, and self-incompatibility are two features which favor the establishment of polyploids. The perennial nature will allow a rather sterile polyploid plant to survive for several years, during which time chance genetic recombination may result in some viable gametes. The somewhat sterile

condition is also thought to stimulate the production of unreduced gametes, which, also by chance, may reach some other polyploids in the area. The production of unreduced gametes in Aster species was reported in the two studies mentioned in the preceding paragraph. In three different crosses Avers used diploid plants as pistillate parents and tetraploid plants as the staminate parents. In each case the resulting hybrids were tetraploid, indicating the formation of unreduced eggs. During the course of their study, Wetmore and Delisle found one plant of A. novae-angliae possessing tetraploid pollen mother cells in association with diploid PMC in the same microsporangium. Assuming normal meiosis occurred in all PMC, both diploid and haploid microspores would result. Thus species of Aster may have a propensity for producing unreduced gametes, but much more study is necessary before any general conclusions on this point can be reached.

#### Summary of Taxonomic Concepts

If the definition of species submitted by Dobzhansky is applied to the plants in this study, considerable lumping would have to be done. He states: "Species are formed when a once actually or potentially interbreeding array of mendelian populations becomes segregated into two or more reproductively isolated groups" (20, p. 262). At the other extreme, if the wishes of those desiring species status for

every recognizably different polyploid were followed, many new names would have to be proposed.

As is characteristic for most of the polyploid complexes discussed above, the diploid members of Aster have the attributes of good species. They are relatively isolated reproductively and are morphologically distinct. However, if the criterion of genetic incompatibility is used to differentiate species among the vast assemblage of polyploids, the entire group would have to be included in one taxon. This very artificial treatment would bring together morphological extremes nearly as great as those among the diploids, and would fail to show evolutionary relationships.

Actually, the polyploid members of a species resemble their diploid counterparts much more closely than they resemble polyploids of other species. This similarity is usually so close that it would be illogical to follow any other course than to include them in the same species. Other polyploids, which have no diploid counterparts and which constitute a fairly well defined aggregation, warrant species recognition.

Thus a species in the genus Aster may include several chromosome levels. It may be genetically compatible with other species and hybridize at points of contact. It may not have the morphological distinction that is desired in

good species. Yet in considering the genus there are definite plateaus of morphological similarity, as Heckard stated for plants in Phacelia (27). For the reasons stated above and elsewhere in the thesis, it seems more advisable to designate each plateau as a species rather than as a subspecies, despite the potentiality for gene exchange among the polyploids. Epling and Catlin (22) and Lewis (41) concur in pointing out that evolution has not placed a premium on complete reproductive isolation, but in many species variation for subsequent evolution is obtained through gene exchange between sympatric species. Lewis further states that species are of many different sorts; they are as varied as the factors that contribute to evolutionary change and therefore only a flexible concept of their nature will suffice.

#### Tentative Phylogeny

The evidence is as yet inadequate to provide anything more than tentative conclusions on the phylogenetic relationships among the species treated here. The evidence available includes that provided by morphology, cytology, ecology, distribution, and to a lesser extent artificial hybridizations. The information gained from this latter source emphasizes that the whole group consists of closely related species which are freely crossable, but it does not clarify particular relationships.

The question of evolutionary trends in morphology is also one to which cytological data can contribute. Suggestions as to possibly primitive morphological features in Aster were made by Cronquist (14, p. 432), who listed the following traits as being the least specialized ones:

1. few heads; 2. large heads; 3. foliaceous involucre, as opposed to more chartaceous imbricated involucre;
4. few leaves; 5. large leaves.

Because diploids give rise to, and are thus ancestral to polyploids, one might expect that plants showing a combination of the above features would be found among the diploids in section Aster. However, the taxon most resembling the primitive type, A. foliaceus ssp. foliaceus, is known only as a high polyploid. Certain primitive traits occur in diploids of A. foliaceus ssp. parryi and A. cusickii, but many other diploids have most of the characteristics which Cronquist considered more advanced. Examples of the latter are A. eatonii, A. hallii, A. lentus, A. idahoensis, and A. greatai. At higher levels in three of these same species there is little change in number of heads or leaves, but there is some increase in size of these parts. In species known only as polyploids, such as A. chilensis, A. hesperius, A. laevis, and A. subspicatus, most have a combination of primitive and advanced traits including large leaves, many heads, and imbricate chartaceous phyllaries. One can conclude that polyploidy was not necessary to the evolution

of specialized morphology in this group of asters, and that it may be a relatively recent phenomenon whose effect has been to recombine morphological types that had already differentiated at the diploid level.

The chromosomal relationships among the species in this study and their phylogenetic implications are depicted in figure 4. Solid lines are used to indicate relationships based on the most positive evidence. In most cases these are straight line connections within a species, such as A. eatonii and A. hallii, in which the diploids certainly are involved in the formation of the higher polyploid levels. However, it is usually not known whether evolution has occurred in these species principally by allopolyploidy or autopolyploidy. A few solid line connections are also made between one taxon and another, in which the taxon at the lower level is believed to be a direct progenitor of the taxon at the higher level. In some cases only one progenitor can now be named, as in the A. adscendens to A. bernardinus connection, but in other examples the evidence indicates that allopolyploidy has been involved, as in the origin of A. jessicae and duodecaploid A. subspicatus.

Dashed lines are used to indicate the less certain affinities. These include relationships in which the superficial similarity between the taxa may be due either to an allopolyploid origin of one from the other or merely to an introgression of genes from one into the other, but

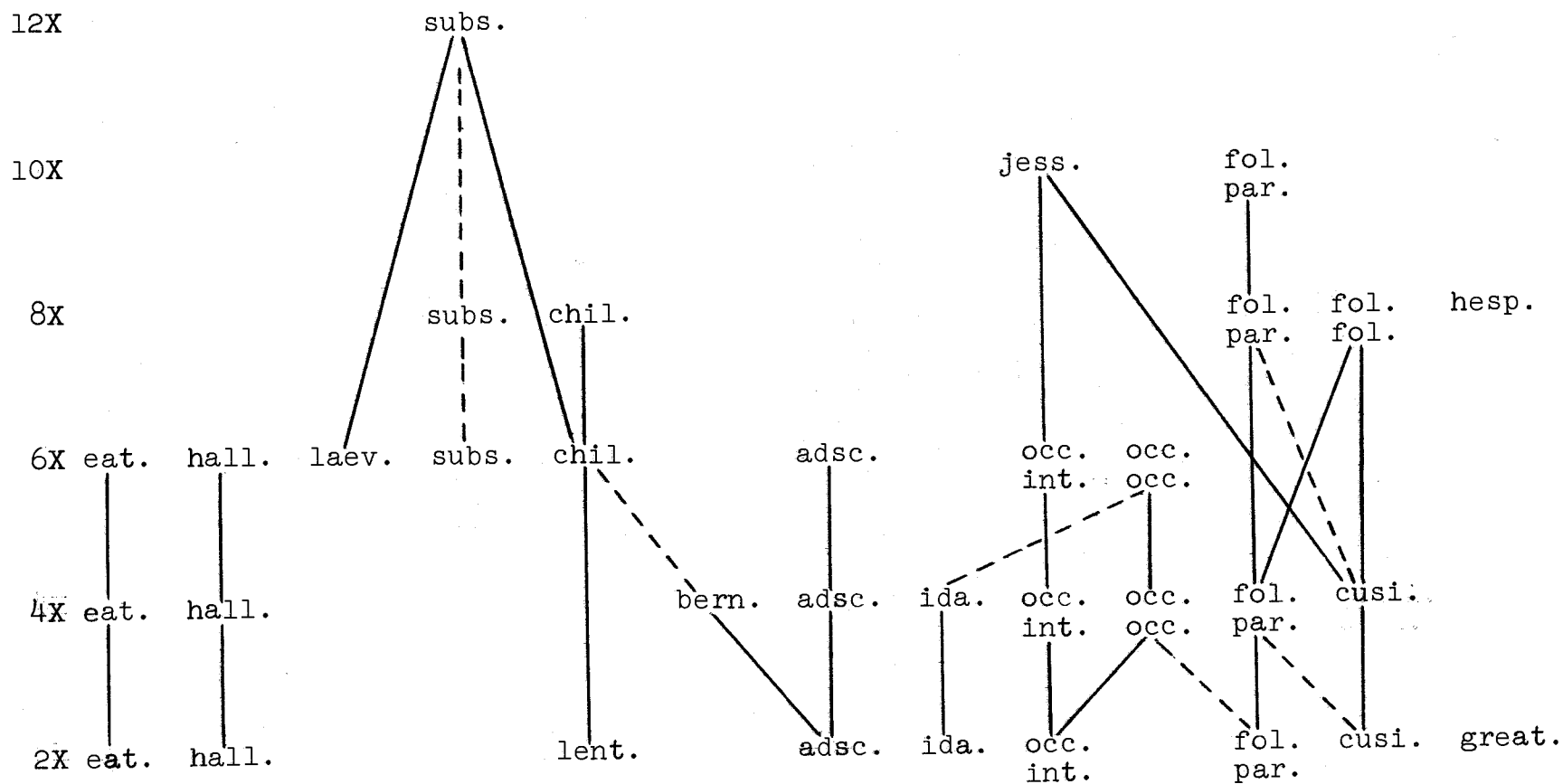


Figure 4. Tentative phylogenetic relationships among the species of Aster comprising this study.

conclusive evidence is not available. No attempt is made in figure 4 to show the amount of intergradation between taxa at the same chromosome level. Further discussion of the phylogenetic chart will be made in the next section, where each relationship will be discussed under the individual species involved.

## TAXONOMY

The following classification represents a conservative treatment of the species studied, since it does not differ greatly from many recent treatments found in regional floras (1, 29, 47, 51). However, taxonomic changes were made where it was believed the available evidence justified them. As noted a number of times, the species of Aster are not well marked by clear differences, but rather, are characterized by various combinations of traits which together comprise subtle species differences. For this reason the key to species is largely artificial, in order to facilitate identification, and it may not show natural relationships. The vast majority of specimens can be correctly identified, but allowance was not made for all the variations or anomalies that might occur within each species. Mention has been made of the way some characteristics may be environmentally altered, so that habitat and distribution must be considered in the identification of many specimens.

Over 8000 specimens from 10 different herbaria were examined during the study. Only a representative sample is cited for each taxon, but all of the specimens are spotted on the distribution maps. Each of the type specimens is cited in the list of synonyms and in most cases is not then cited again among the representative specimens.

If the holotype or an isotype was seen, an exclamation mark (!) follows the citation. Special thanks are due to the various herbarium curators for making these specimens available. The herbarium abbreviations in the citation of specimens are according to the fifth edition of Index Herbariorum (38) by Lanjouw and Stafleu.

#### Artificial Key to the Species and Subspecies

1. Involucres strongly graduated, the outer phyllaries markedly shorter than the inner, not foliaceous, usually with an herbaceous green tip and chartaceous base.
2. Outer phyllaries obtuse or rounded, with green tip and chartaceous base.
3. Plants mostly glabrous, sometimes appearing glaucescent or succulent; inflorescence bracts subclasping, lanceolate to linear or subulate, strictly ascending or appressed; in or near marshes of the San Francisco Bay region.

#### 4. A. lentus

3. Plants more or less pubescent; inflorescence bracts usually not clasping, more spreading.
4. Ray flowers mostly white to sometimes lavender; heads small, the involucre 4-9 mm. broad; inflorescence crowded, conspicuously divaricate-bracteate. 1. A. hallii

4. Ray flowers mostly violet to purple, rarely white; heads larger; inflorescence variable.
5. Plants uniformly and rather densely spreading cinereous pubescent; cauline leaves spreading to often reflexed, most often with a tuft of leaves in the axil; plants of southern California.

3. A. bernardinus

5. Plants not with the above combination of characters.
6. Innermost phyllaries obtuse to acutish; primary inflorescence branches often long and spreading, 10-25 cm. long, usually with many spreading bracts.

5. A. chilensis

6. Innermost phyllaries acute to acuminate or attenuate; inflorescence usually rather narrow, the primary branches mostly ascending, 5-15 cm. long, bracts usually few.

2. A. adscendens

2. Outer phyllaries acute, or if obtuse, then wholly green without chartaceous base.
7. Achenes glabrous; plants mostly glabrous and often glaucous; leaves and inflorescence bracts

somewhat auriculate-clasping.

6. A. laevis

7. Achenes pubescent; plants variously pubescent; leaves and inflorescence bracts usually not auriculate-clasping.

8. Plants rather densely and uniformly cinereous pubescent, this usually soft and strigose or spreading with curled hairs; cauline leaves often somewhat auriculate-clasping and slightly constricted above the base; plants of southeast Washington and adjacent Idaho.

12. A. jessicae

8. Plants not with the above combination of characters.
9. Pubescence in lines decurrent from the leaf bases, neither uniform under the heads nor confined to the inflorescence; middle stem leaves lanceolate to linear; inflorescence a rather narrow, many-headed panicle.

10. A. hesperius

9. Pubescence usually uniform under the heads and uniform or in lines on the stem, or occasionally in lines only and confined to the inflorescence; middle

stem leaves ovate to oblanceolate; inflorescence usually an open spreading panicle, or if narrow, then few-headed.

10. Leaves oblanceolate to linear, mostly 1 cm. wide or less, usually entire; inflorescence bracts narrowly lanceolate or linear, usually ascending. 14b. A. occidentalis  
ssp. intermedius

10. Leaves obovate to lanceolate, usually 1-4 cm. wide, often serrate; inflorescence bracts ovate to lanceolate, spreading.

11. Leaves scabrous on both surfaces; stems somewhat uniformly spreading hairy; outer phyllaries mostly green with small chartaceous portion below; plants of southern California. 8. A. greatai

11. Leaves scabrous only on the margins; stem pubescence mostly in lines; outer phyllaries chartaceous up to half their length, this often

darkened in dried specimens.

7. A. subspicatus

1. Involucres not markedly graduated, the phyllaries nearly equal or the outer sometimes enlarged and foliaceous, often wholly herbaceous varying to chartaceous at the base.
12. Ray flowers mostly white to pink, sometimes violet; stems rather uniformly puberulent; inflorescence usually a long, narrow, leafy panicle.

9. A. eatonii

12. Ray flowers mostly violet to purple; stem pubescence various, not as above; inflorescence usually more open and terminal or few-headed.
13. Plants monocephalous or few-headed (4-6); heads large, the involucre 12-25 (30) mm. broad; phyllaries mostly green and foliaceous, glabrous; leaves mostly glabrous to sparingly pubescent; rays rose-purple to deep violet; plants of alpine to subalpine localities or northern latitudes.
14. Stems usually stout and erect, 2-6 dm. high; basal leaves petiolate, up to 25 cm. long and 2-4 cm. wide; Cascades of northern Washington to Alaska.

15a. A. foliaceus  
ssp. foliaceus

14. Stems cespitose and decumbent at base,  
1-2 (3) dm. high; basal leaves sub-  
petiolate, up to 15 cm. long and 5-15 mm.  
wide; widespread in mountains of Western  
U. S.

15b. A. foliaceus  
ssp. apricus

13. Plants usually several- to many-headed; heads  
small to large, phyllaries and pubescence  
various; rays violet to purple.
15. Plants rather densely and uniformly soft  
pubescent throughout, rarely nearly gla-  
brous; cauline leaves more or less auric-  
ulate-clasping; basal leaf blades abrupt-  
ly contracted to the petiole.
16. Pubescence usually white and spread-  
ing; cauline leaves conspicuously  
auriculate-clasping and constricted  
above the base; some outer phyl-  
laries nearly always enlarged and  
surpassing the inner; achenes often  
glabrous.
11. A. cusickii
16. Pubescence usually cinereous and  
strigose or spreading; cauline  
leaves slightly or not auriculate-  
clasping and constricted above the  
base; occasional outer phyllaries

may surpass the inner; achenes

pubescent. 12. A. jessicae

15. Plants not densely pubescent, uniformly pubescent only under the heads; cauline leaves auriculate-clasping or not; basal leaf blades tapering to the petiole.
17. Inflorescence usually an elongate, many-headed leafy panicle, the primary branches ascending, 10-40 cm. long; phyllaries very narrow, mostly 0.5 mm. wide or less, attenuate, the outer wholly green.

13. A. idahoensis

17. Inflorescence usually shorter, terminal, not conspicuously leafy, the primary branches mostly less than 20 cm. long, ascending or spreading; phyllaries usually 0.5 mm. wide or wider with some chartaceous portion below.
18. Lower and middle cauline leaves mostly less than 1 cm. wide, 7-20 times longer than wide; phyllaries mostly narrow, acute to acuminate, slightly imbricate to subequal.

14a. A. occidentalis  
       ssp. occidentalis

18. Lower and middle cauline  
       leaves over 1 cm. wide, mostly  
       less than 7 times longer than  
       wide; phyllaries narrow and  
       acute or acuminate, to broadly  
       oblanceolate or spatulate and  
       obtuse or rounded, usually sub-  
       equal or often some of the out-  
       er enlarged and foliaceous.

15c. A. foliaceus  
       ssp. parryi

1. Aster hallii Gray

Aster hallii Gray, Proc. Am. Acad. 8:368. 1872, nomen  
 nudum. A. hallii Gray, Syn. Fl. N. Am. 1<sup>2</sup>:191. 1884.  
A. chilensis Nees ssp. hallii Cronq. Am. Midl. Nat.  
 29:462. 1943. (Type: E. Hall 243, dry ground, Oregon,  
 1871, GH! isotype NY!). Hall's 243 was the first of  
 three different collections listed by Gray. However,  
 Cronquist, loc. cit., selected the third collection,  
Henderson 14, 1883, as the lectotype. Later, Cronquist  
 reversed himself and reinstated Hall 243 as the type  
 (29, p. 78).

Stems slender, rather strict and erect, simple and  
 rather naked until near the top, then paniculately branched,

brownish, glabrate below to rather densely hirsutulose above; basal leaves long-petiolate, mostly less than 10 cm. long and about 1 cm. wide, obovate, early deciduous; cauline leaves also often deciduous before flowering, linear, up to 7 cm. long and 5 mm. wide, glabrous to scabrous above, margins scabrous, entire; inflorescence usually a narrow crowded panicle, branches mostly short but some up to 20 cm. long, rather stiffly ascending, with abundant divaricate-spreading lanceolate bracts, these mostly less than 2 cm. long and 5 mm. wide; heads small, involucre mostly 4-9 mm. broad and 4-7 mm. high; phyllaries strongly graduated in 5-6 series, green-tipped and ribbed, with chartaceous base and rather prominent scarious margin, the outer ones obtuse to nearly rounded, often mucronate, the green tip less than half the phyllary length, the inner ones obtusish to acute, almost entirely chartaceous with the scarious margin extending to the tip, glabrous to minutely scaberulous abaxially, faintly pubescent adaxially, scarcely ciliate marginally; ray flowers 20-35, ligules 1-2 mm. wide, 7-12 mm. long, mostly white, to lavender or light purple; pappus white; achenes pubescent.

Roadsides, fields, and ditch banks. Umpqua and Willamette R. valleys to Hood R., Oregon, and possibly Seattle and Okanogan Co., Washington.

Representative specimens. OREGON: Douglas Co., Riddle, Ward 65, Sept. 22, 1899 (NY, CAS). Lane Co.,

Eugene, Henderson 16624, Sept. 17, 1934 (DS, UC). Marion Co., 1 mi. N of Salem, Nelson 2436, Aug. 20, 1918 (WS).

Aster hallii is a relatively distinct species even though it includes some polyploids. Probably the majority of the plants are diploid, but both tetraploids and hexaploids are known. An unusual fact about this species is that all three chromosome levels have been found within 10 miles of each other near Corvallis, Oregon. Two lines of evidence suggest that evolution has been in part by autopoloidy. Because the only other species of Aster in the middle Willamette Valley is the duodecaploid A. subspicatus, there is no available species with which allopoloidy could be reasonably postulated. Also, the close morphological similarity between the diploids and the tetraploids suggests the autopoloid origin of the latter. However, the regular pairing of chromosomes in meiosis of the tetraploids is not typical of autopoloidy. The hexaploid population which is referred to A. hallii differs enough from plants of the other two chromosome levels so that autopoloidy does not appear to be involved. Its appearance suggests characteristics of A. chilensis or A. subspicatus to some degree.

Throughout much of the Willamette Valley, A. hallii and A. subspicatus are sympatric and often grow side by side in fields or waste places. Very few collections show evidence of hybridation. This apparent genetic isolation

is probably due both to the difference in chromosome number mentioned above, and also the difference in flowering time. Plants of A. subspicatus often begin flowering in middle or late July and continue through September and perhaps into October. Plants of A. hallii, on the other hand, do not begin flowering until late August or early September and continue through October and into November. Although there is some overlap of flowering time, if plants of both species are present in the same field, there is usually at least a month difference in the beginning of their flowering times.

The extent of the range of A. hallii in Washington is very uncertain. Two or three collections from near Seattle had been so named by previous workers, as had one collection from both Kittitas and Okanogan Counties east of the Cascades. However, none of these collections were good representatives of A. hallii, and those east of the Cascades were particularly unlikely to be members of the species. Pollen from two of the collections from near Seattle, Thompson 5121 and Thompson 8107, was measured. Collection 1521 averaged  $26.2\mu$  and 8107 averaged  $28.5\mu$ . The size of the former falls well within the tetraploid, or even diploid range (see Table III), and this collection comes the closest to A. hallii of any of the Seattle plants. The pollen size of 8107 indicates the likelihood of a hexaploid or higher chromosome level, and the plants

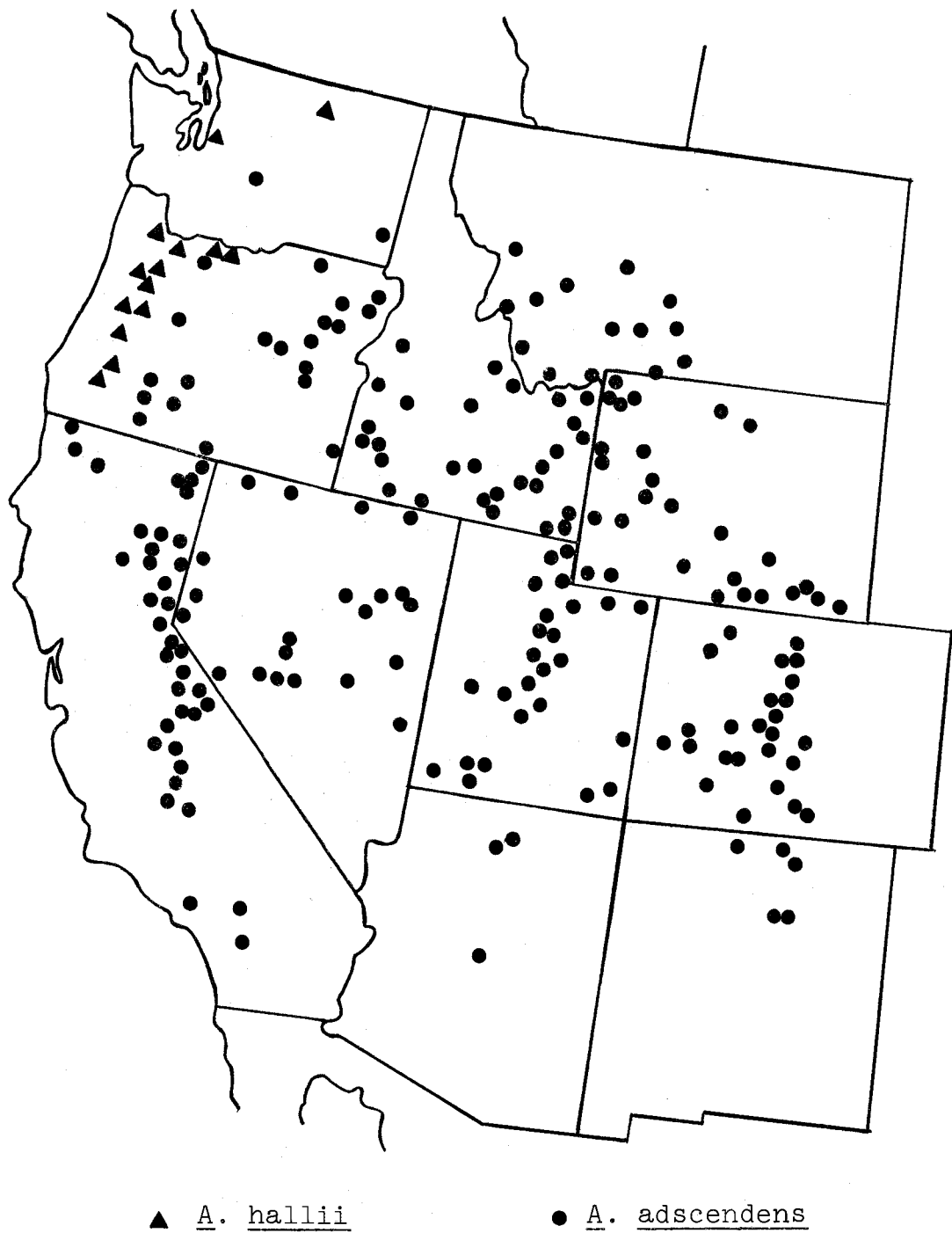


Figure 5. Distribution of *Aster hallii* and *A. adscendens*

were closer in appearance to A. subspicatus. Thus A. hallii may extend to Seattle or even farther north, but the evidence as yet is meager.

2. Aster adscendens Lindl. in Hook.

Aster adscendens Lindl. in Hook. Fl. Bor. Am. 2:8. 1834, (as "ascendens"). A. chilensis Nees ssp. adscendens Cronq. Am. Midl. Nat. 29:458. 1943. A. chilensis Nees ssp. adscendens var. euadscendens Cronq. op. cit. p. 460. (Type: Drummond s.n., banks of the Saskatchewan).

Aster denudatus Nutt. Trans. Am. Phil. Soc. II.7:292. 1840. A. adscendens var. denudatus T. & G. Fl. N. Am. 2:111. 1841. (Type: Nuttall s.n., Rocky Mts., near Lewis' (Snake) R., lat. 42 degrees, PH; isotype: GH!).

Aster denudatus Nutt. var. ciliatifolius Nutt. op. cit. p. 293. A. adscendens var. ciliatifolius T. & G. loc. cit. (Type: with A. denudatus).

Aster nuttallii T. & G. Fl. N. Am. 2:126. 1841. (Type: Nuttall s.n., plains of Lewis' R., lat. 42 degrees).

Aster subracemosus Rydb. Mem. N.Y. Bot. Gard. 1:394. 1900. (Type: Kelsey s.n., Helena, Lewis and Clark Co., Mont., Sept. 8, 1890, NY!).

Aster distichophyllus Greene, Pitt. 4:213. 1900. (Type: Greene s.n., below Marshall Pass, southern Colorado, Sept. 4, 1896, ND!).

Aster violaceus Greene, loc. cit. (Type: Greene s.n., base of Little Ouray Mt. east of Marshall Pass, Colo., Sept. 4, 1896, ND!).

Aster armeriaefolius Greene, op. cit. p. 214. A. adscendens var. armeriaefolius A. Nels. N. Man. Rocky Mt. Bot. 517. 1909. (Type: Greene s.n., below Marshall Pass, Colo., Sept. 4, 1896, ND!).

Aster pratincola Greene, op. cit. p. 215. (Type: Greene s.n., Gunnison R. at Gunnison, Gunnison Co., Colo. Sept. 1, 1896, ND!).

Aster spithameus Greene, op. cit. p. 217. (Type: Greene s.n., above Gunnison, Gunnison Co., Colo., Sept. 10, 1890, ND!).

Aster nelsonii Greene, op. cit. p. 219. (Type: Nelson 5326, Fisher's Ranch, Albany Co., Wyoming, Sept. 13, 1898, ND).

Aster limoniifolius Greene, op. cit. p. 222. (Type: Greene s.n., Pine Valley above Palisade, Nevada, July 25, 1896, ND!).

Aster oxylepis Greene, op. cit. p. 223. (Type: Greene s.n., Humboldt R. below Palisade, Eureka Co., Nevada, Aug. 24, 1896, ND!).

Aster griseolus Rydb. Bull. Torrey Club 31:653. 1904. (Type: Clements 37, Mt. Harvard, Gunnison Co., Colo. 1896, NY!).

Aster underwoodii Rydb. loc. cit. (Type: Underwood & Selby 318, Iron-ton Park, Ouray Co., Colo., Sept. 11, 1901, NY!).

Aster orthophyllus Greene, Leaf1. Bot. Obs. 1:146. 1905.  
(Type: Baker 570, along river at Gunnison, Gunnison Co., Colo., July 23, 1900, ND!).

Aster griseus Greene, op. cit. p. 147. Aster subgriseus Rydb. Fl. Rocky Mts. 884. 1917. (Type: Greene s.n., Rocky Mts. W of Denver, 9000 feet, 1875, ND; syntype: Baker 632, Doyle's, Gunnison Co., Colo., July 28, 1901. UC! NY! POM! WS!). Not A. griseus Kuntze, Rev. Gen. 316. 1891.

Aster halophyllus Greene, Leaf1. Bot. Obs. 2:8. 1910.  
(Type: Garrett s.n., Beck's Hot Springs, Salt Lake Co., Utah, Sept. 6, 1906, ND!).

Aster leucopsis Greene, loc. cit. (Type: Garrett s.n., near Salt Lake City, Salt Lake Co., Utah, Sept. 5, 1905, ND!).

Aster delectus Piper, Contr. U.S. Nat. Herb. 16:210. 1913.  
(Type: Cusick 2761, Cygan R., Klamath Co., Oregon, Aug. 15, 1901, US; isotypes: UC! GH! NY! WS!).  
Probably represents a hybrid between A. adscendens and A. occidentalis ssp. intermedius.

Stems usually slender, ascending to erect, 2-6 dm. high, sparsely to densely pubescent; pubescence usually

rather uniform and increasing in density upward, mostly strigose below, strigose and spreading above; lower leaves oblanceolate or spatulate, the blade tapering to the narrowly winged petiole, up to 20 (25) cm. long, and 20 (25) mm. wide, usually deciduous except in smaller plants; middle and upper leaves gradually reduced and sessile, usually ascending, oblanceolate to lanceolate, obtuse to acutish, usually somewhat strigose at least on the upper surface, margin usually entire, scabrous; inflorescence often beginning well down the plant and forming over one-half the total height, the primary branches axillary and ascending, 5-15 cm. long, forming a narrow raceme or cymose panicle, not conspicuously bracteate; heads few to numerous, small to medium-sized; involucre 8-15 mm. wide, 5-7 mm. high; phyllaries usually strongly graduated in about 4 series, mostly erect to sometimes spreading, the outer oblanceolate and obtuse, the inner acute to acuminate, all with herbaceous green tip and midrib and chartaceous lower part with a narrow scarious margin, the chartaceous portion up to half the total length, usually ciliate marginally and strigose adaxially, glabrous to strigose abaxially; flowers mostly 25-35, the ligules light lavender to bluish-violet or purple, 1-1.5 mm. wide and 8-15 mm. long; pappus white to tawny or seldom reddish; achenes pubescent.

Roadsides and other waste places, or along streams, ditches, and on open hillsides. Southeastern Washington

southward through eastern Oregon and California east of the Cascades and Sierras to San Bernardino and possibly Riverside Co., east to Saskatchewan and northern New Mexico.

Representative specimens. CANADA: Alberta, near Olds on Calgary-Edmonton Hwy., Nelson 4763, Aug. 22, 1941 (UC). Saskatchewan, Cypress Hills, Breitung 5713, Aug. 21, 1947 (RM). ARIZONA: Coconino Co., near Flagstaff, Lemmon s.n., Aug., 1884 (UC). CALIFORNIA: Fresno Co., Mono Hot Springs, 7000 ft., Kruckeberg 3573, July 19, 1954 (RM, DS, WTU, WS, NY). Lassen Co., Janesville, Hoover 4654, Oct. 1, 1940 (UC). Los Angeles Co., N side San Gabriel Mts., M.E. Jones s.n., Sept. 10, 1924 (POM). Modoc Co., Jack Swamp, NW of Alturas, Grant & Schneider 8335, Aug. 28, 1947 (UC). Mono Co., Hot Cr. Fish Hatchery, Ferris & Lorraine 11060, Aug. 24, 1945 (UC, CAS, DS, WTU). Nevada Co., Truckee R., 1 mi. above Truckee, Heller 7106, Aug. 7, 1903 (UC, WTU, POM, DS, NY). San Bernardino Co., Barton Flats, San Bernardino Mts., 6500 ft., Munz 6318, Aug. 27, 1922 (UC, POM). Trinity Co., Derr Creek, Kruckeberg 3755, Aug. 11, 1954 (RM, DS, WTU, WS, NY). COLORADO: Archuleta Co., Pagosa Springs, 7100 ft., Baker 641, Aug. 31, 1899 (RM, POM, UC, GH). Garfield Co., Glenwood Springs, Osterhout 5834, Aug. 21, 1918 (RM). Park Co., Fairplay, 9900 ft., Weber 7915, Aug. 14, 1952 (RM, WS, RSA, WTU). Weld Co., Windsor, Osterhout s.n., Aug. 28, 1925 (POM). IDAHO: Bonneville Co., 1 mi. S pine Cr. summit, Christ 16319,

Aug. 11, 1946 (WS, NY). Cassia Co., Raft River Valley, Biggers s.n., 1929 (NY). Gem Co., 12 mi. W of Emmett, Christ 8542, Aug. 7, 1937 (NY). Owyhee Co., open meadow, Reynolds Creek, Baker 8326, July 29, 1951 (ID, NY).

MONTANA: Madison Co., 30 mi. S Varney, 6100 ft., Parker 7029, Aug. 18, 1949 (CAS, RSA, UC). Missoula Co., Miller Cr. road, Missoula, Kirkwood 2435, Aug. 27, 1927 (RM, UC). Wheatland Co., Careless Cr., 16 mi. E of Judith Gap, Wright s.n., Aug. 16, 1952 (WTU). NEVADA: Elko Co., Maggie Cr., Kennedy 653, Aug. 14, 1902 (RM). Lincoln Co., near Ryan St. Park, 4 mi. S of Caliente, Train 2449, Sept. 2, 1938 (UC). Washoe Co., near Indian Agency, Pyramid, Hudson s.n., Oct. 22, 1909 (UC). NEW MEXICO: Rio Arriba Co., Chama, 7850 ft., Baker 642, Sept. 1, 1899 (RM, NY, POM). OREGON: Lake Co., Cyscan Marsh, Cusick 2746, Aug. 12, 1901 (NY, WS). Malheur Co., Owyhee R. at Three Forks, Dean 180, Aug. 20, 1957 (NY, OSC). Umatilla Co., Bingham Springs R.R. station, Cusick 3327, Oct. 10, 1908 (UC, GH, WS, NY, DS, RSA, WTU). Union Co., Grand Ronde Valley, 3000 ft., Cusick 3397, Aug. 14, 1909 (RM, WS, NY, RSA, DS, WTU).

UTAH: Cache Co., Elk Valley, 7200 ft., Cottam, et al. 15955, Aug. 5, 1959 (DS, RSA). Iron Co., Cedar Breaks Lodge, Maguire 15732, Aug. 29, 1934 (RM, UC). San Juan Co., Armstrong & White Canyons, Rydberg & Garrett 9445, Aug. 4-6, 1911 (RM, NY). WASHINGTON: Kittitas Co., near Ellensburg, Jones s.n., Sept. 19, 1937 (DS). Whitman Co.,

3 mi. N of Colfax, Cronquist 6132, Sept. 24, 1949 (UC, CAS, RSA, WTU, WS, ID, NY). WYOMING: Albany Co., Laramie, 7200 ft., Clokey 2915, Aug. 17, 1917 (CAS, NY, DS, UC). Johnson Co., Buffalo, 4000-5000 ft., Tweedy 3111, Sept., 1900 (RM, NY, WS). Uinta Co., Evanston, Nelson s.n., Aug. 28, 1900 (RM). Yellowstone National Park, Snake River, Nelson 6567, Aug. 20, 1899 (RM, DS, UC, WTU, WS, NY).

Aster adscendens is primarily a species of the lower and middle elevations in the Great Basin and Intermountain area, although it may reach higher elevations in a number of places. The most typical plants are centered in an area that includes much of Nevada, Utah, western Colorado and Wyoming, and southern Idaho. Away from this center the species is increasingly difficult to distinguish from other species with which it appears to hybridize. Some notable areas of difficulty include the following.

In the valleys of northeast Oregon and southeast Washington A. adscendens comes into contact with A. occidentalis ssp. intermedius, and many specimens appear to incorporate characteristics of both species. Cronquist's collections 6132 - 6136 from three miles north of Colfax, Whitman County, Washington, are examples of an intergrading series between these two entities. Similar contact is made at various points along the eastern base of the Cascades in Oregon and the eastern slope of the Sierras in California. The type of A. delectus Piper,

from Cygan Marsh, Lake County, Oregon, is somewhat intermediate between A. adscendens and A. occidentalis ssp. intermedius and is only provisionally placed under A. adscendens at the present time. This form is more densely pubescent with smaller, more crowded heads than typical A. adscendens. It is found from northern Klamath County, Oregon, to Siskiyou County, California. My collections which most closely approach the type of A. delectus in appearance include numbers 313, 353, and 354b, all of which have the unusual chromosome number of  $2n = 13II$ .

Two of my collections from Lake County, Oregon, illustrate the difficulty of determining taxonomic affinities. Collections 317 and 322 are both diploids and are somewhat similar in appearance. However, 317, from a higher and more moist elevation, was nearly identical with another diploid, collection 474 from Hood River County. Both 317 and 474 had eight pairs of chromosomes with no B-chromosomes and both were identified morphologically as A. occidentalis ssp. intermedius (Table I). On the other hand, 322, from a lower and dryer elevation, had enough characteristics of A. adscendens to be classified in the latter species. Cytologically, plants of collection 322 were found to have five B-chromosomes in addition to the eight pairs. This karyotype was nearly duplicated by another diploid plant, collection 425 from Owyhee County, Idaho. This plant had 16 normal or A-chromosomes plus

four B-chromosomes in root tip cells. Since only fruits were obtained from the plant and no voucher was made, its morphology could not be compared with 322. However, notes made at the time of seed collection indicate the plant was of the adscendens type. Herbarium specimens of A. adscendens from nearby localities in Owhyee County are nearly all typical of the species. Thus it appears from these limited observations that A. adscendens and A. occidentalis ssp. intermedius are ecologically and cytologically distinct entities, although morphologically similar, particularly in adjacent localities.

The traits which separate these two taxa include the following: leaves and outer phyllaries apically obtuse in A. adscendens and acute in A. occidentalis ssp. intermedius; branches usually ascending in adscendens and spreading in ssp. intermedius; bracts numerous and ascending to erect in ssp. intermedius and few and spreading to ascending in adscendens.

Many asters from the Sierras in California are especially difficult to classify. In general, "good" A. adscendens occurs at lower elevations on the east slope and "good" A. occidentalis ssp. occidentalis occurs at quite high elevations, but plants from the intervening area provide the majority of the taxonomic problems. Aster occidentalis ssp. intermedius is again involved in the complex at middle elevations on both sides of the mountains.

In the Rocky Mountains A. adscendens is taxonomically confused primarily with A. occidentalis ssp. occidentalis, and to a lesser extent with that part of A. foliaceus ssp. parryi which has previously been designated A. f. var. canbyi. This latter entity usually has quite obtuse or rounded, subequal phyllaries and large clasping leaves. However, many plants with smaller leaves and more graduated phyllaries may be difficult to distinguish from A. adscendens.

### 3. Aster bernardinus Hall

Aster bernardinus Hall, U. Cal. Pub. Bot. 3:79. 1907. A. menziesii Lindl. in Hook. var. bernardinus Jeps. Man. Pl. Calif. 1046. 1925. A. chilensis Nees ssp. adscendens (Lindl. in Hook.) Cronq. var. bernardinus Cronq. Am. Midl. Nat. 29:461. 1943. (Type: Parish 5543, vicinity of San Bernardino, San Bernardino Co., Calif., Sept. 5, 1905, UC! isotypes: GH! NY! RM! POM! US).

Aster deserticola Macbr. Contr. Gray Herb. 55:36. 1918. (Type: Spencer 629, Mohave Desert, San Bernardino Co., Calif., Oct. 3, 1917. GH; isotypes NY! POM!).

Stems mostly 0.5-1.5 m. high, rather strict and erect, usually densely and uniformly spreading-pubescent, this usually soft and cinereous, denser above; radical and lower cauline leaves early deciduous, oblanceolate to lanceolate,

up to 15 (20) cm. long, 10-15 mm. wide; middle and upper cauline leaves numerous, gradually reduced upward, lanceolate to linear, usually with a fascicle of leaves in the axils, ascending to often lax and spreading or reflexed, strigose or somewhat spreading-pubescent throughout, margins scabrous, entire; branches erect to spreading, short and simple with terminal heads, or longer and paniculately branched, invested with numerous erect or spreading linear bracts; heads few to numerous, small to medium-sized, the involucre 9-15 mm. wide, 5-7 mm. high; phyllaries usually strongly graduated in 4-6 series, erect or often somewhat spreading, the outer ones obtuse or rounded, mucronate, the inner ones obtusish to acute, all with green tip and midrib and white chartaceous base, the green tip composing two-thirds the length of the outer phyllaries and decreasing amounts of the inner ones, usually pubescent to nearly glabrate on the back, ciliate on the margins; ray flowers 25-35, ligules nearly white to purple, spreading to often reflexed, 1-2 mm. wide, 8-15 mm. long; pappus sordid; achenes pubescent.

Along streams and in meadows. Confined to Southern California in San Bernardino, Riverside, San Diego, Orange and Los Angeles Counties.

Representative specimens. CALIFORNIA: Los Angeles Co., Compton, McClatchie s.n., Oct. 20, 1897 (NY). Orange Co., Bryant Ranch, Wolf 3851, July 7, 1932 (UC, RSA, WTU, DS).

Riverside Co., El Casco, San Trimoteo Canyon, Roos 5323, Oct. 19, 1951 (RSA). San Bernardino Co., near Chino, I.M. Johnston 2156, Oct. 5, 1918 (POM, UC, DS). San Diego Co., Boulder Cr. near Cuyamaca Lake, Wiggins 2128, Oct. 16, 1926 (WTU, DS, UC).

Aster bernardinus is a fairly well characterized species, having dense cinereous pubescence, often spreading or reflexed leaves, and apically obtuse or rounded outer phyllaries. However, its close affinity to A. adscendens is readily apparent from a few collections of intermediate types from southern California. Cytologically, A. bernardinus also shows close relationship to A. adscendens. The unusual chromosome number, for this group, of  $2n = 18II$  was found for two collections of A. bernardinus and one collection of A. adscendens. Although the plants from which these numbers were determined were collected many hundred miles apart, they represent the only counts of 18 pairs found in this group. Cronquist (14) catalogued A. bernardinus as a variety of A. adscendens. However, I feel that the morphological distinctness and relative geographical isolation of A. bernardinus from A. adscendens are sufficient to warrant specific recognition for A. bernardinus.

Along the coast from Santa Barbara to San Diego County and inland to Tejon Pass and the Greenhorn Mountains, a form commonly occurs which has dense cinereous pubescence,

but which in most other features belongs to A. chilensis. This form, previously called A. menziesii Lindl., appears to represent introgression of A. bernardinus genes into A. chilensis in the southern portion of its range.

A few other collections, which are more closely intermediate between A. bernardinus and A. chilensis, suggest that the former, a tetraploid, may be involved in the allopolyploid origin of the latter, a hexaploid. More study is necessary before this speculation can be substantiated.

#### 4. Aster lentus Greene

Aster lentus Greene, Man. Bay Reg. Bot. 180. 1894. A.

chilensis Nees var. lentus Jeps. Fl. W. Middle Calif.

566. 1901. (Type: Greene s.n., Suisun marshes, Solano Co., Calif., ND; cultivar of type collection, UC!).

Aster sonomensis Greene, loc. cit. A. chilensis Nees var.

sonomensis Jeps. loc. cit. (Type: Greene s.n., open plains of Sonoma Valley, Sonoma Co., Calif., ND).

Aster chilensis Nees var. medius Jeps. Man. Pl. Calif.

1047. 1925. (Type: Jepson s.n., lower Sacramento R. Valley, UC).

Stems 0.3-2 m. high, often diffusely branching above, glabrous and sometimes glaucescent or with a few light lines of pubescence above; lower leaves linear to narrowly lanceolate, 10-15 cm. long, mostly less than 1 cm. wide, glabrous to sparingly short pubescent, margins entire and usually

lightly scabrous, early deciduous; upper leaves markedly reduced, the inflorescence branches rather densely clothed with lance-linear or subulate, ascending to appressed bracts, these mostly less than 15 mm. long (2-18 mm.) and 4 mm. wide (0.2-5 mm.); inflorescence often racemose with single heads terminating the branches, to paniculate with the branches abundant and widely spreading; heads medium-sized, the involucre 8-15 mm. wide, 5-8 mm. high; phyllaries narrowly oblanceolate, strongly imbricate in 4-5 series, glabrous and somewhat succulent, the outer obtuse to slightly acute, the inner acute to acuminate or often not much different in shape than the outer, most with a green tip and white chartaceous base, the latter mostly less than half the length in the outer phyllaries, margins somewhat scarious; ray flowers 25-40, ligules violet to purple, 1-2 mm. wide, 10-15 mm. long; pappus white; achenes pubescent.

Open ground or more commonly in marshy ground or in sloughs around San Francisco Bay.

Representative specimens. CALIFORNIA: Alameda Co., Alameda, Tidestrom s.n., Oct., 1894 (UC, POM). Colusa Co., Colusa Gun Club, Baker 11618, Sept. 4, 1946 (RSA, UC). Santa Clara Co., Agnews, Abrams 3088, Sept. 19, 1902 (RM, DS, POM). Santa Clara Co., Alviso, Baker 1828, Oct. 20, 1902 (NY, POM, UC). Solano Co., branch of Suisun Slough, Alexander & Kellogg 2649, Oct. 27, 1941 (RM, WTU, WS, DS,

UC, NY). Sonoma Co., Petaluma marshes, Davy 4030, Sept. 19, 1897 (UC, POM). Sutter Co., Garden Hwy. along Feather R., 15 mi. from Sacramento, Ferris 6934, Nov. 5, 1927 (DS, NY, POM).

Aster lentus is being recognized as a species in this treatment because plants collected near the type locality, Suisun Marsh, were found to be diploid. The species was suspected of being diploid after pollen grains were measured from representative collections, selected because the plants were recognizably distinct from the more common A. chilensis of the California coast. Two such collections and their measurements are those of Heller 9547, 20.5 $\mu$ , and Davy s.n., 20.9 $\mu$ . However, another collection from Suisun Marsh, Peirson 6441, showed an average pollen size of 27.7 $\mu$ , indicating either that A. lentus occurs at a higher ploidy level or that A. chilensis also occurs in the marsh. The plants of this latter collection were not typical of either species, but tended more toward A. lentus.

Aster lentus is definitely considered to be one progenitor of A. chilensis. The degree of intergradation and the differences between these two species are discussed under A. chilensis.

The inclusion of A. sonomensis Greene and A. chilensis var. medius Jeps. as synonyms under A. lentus is not entirely satisfactory, and is only temporary pending further

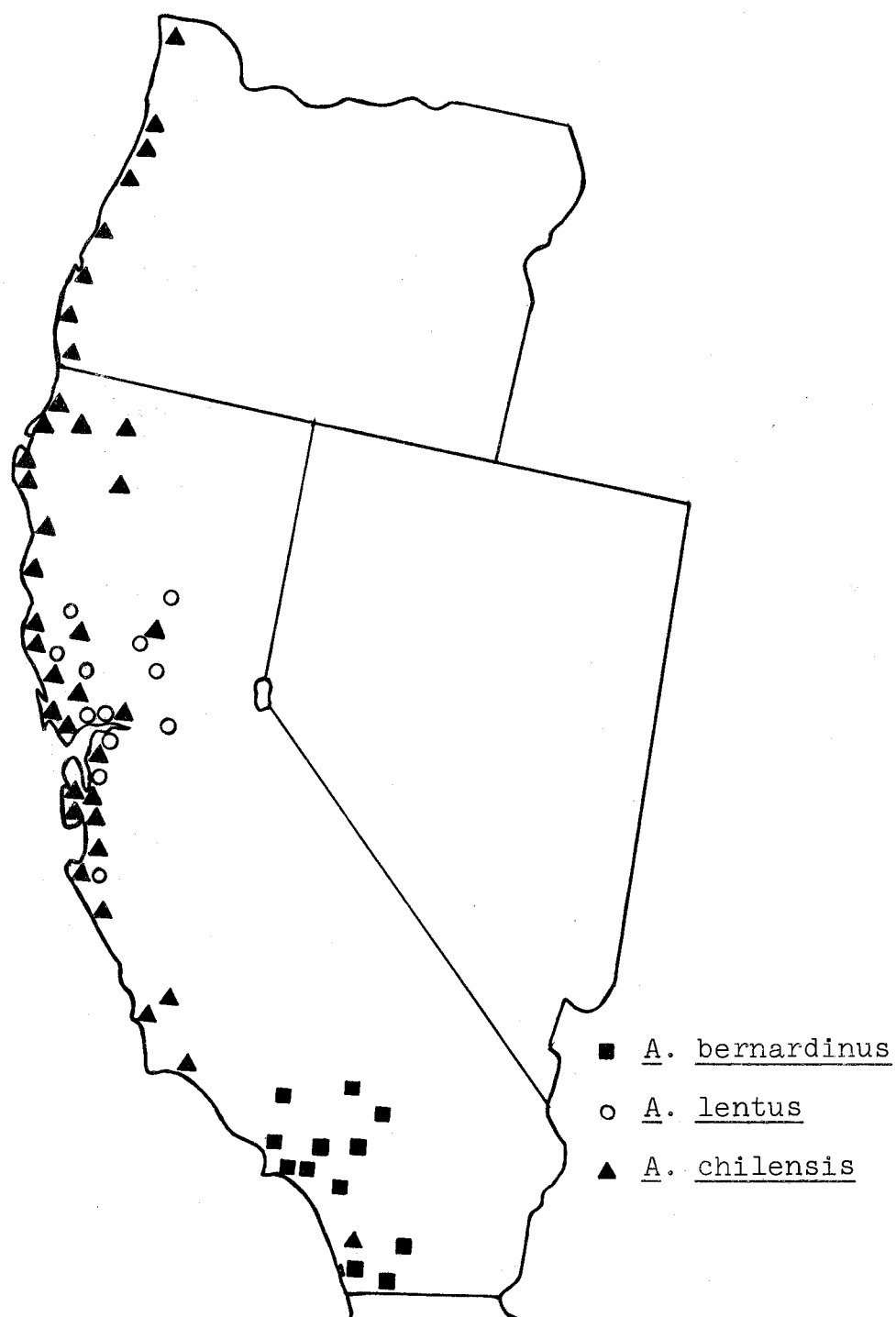


Figure 6. Distribution of Aster bernardinus, A. lentus and A. chilensis

study. They are so treated because of general agreement of bract and phyllary characteristics and of glabrousness. Also, pollen measurements indicate a correspondingly low chromosome number. Two collections which were originally called A. sonomensis, and their measurements, are Howell 11679, 21.4 $\mu$ , and Mason 12708, 23.4 $\mu$ . One collection originally designated as A. chilensis var. medius, and its pollen measurement, is Ferris 6934, 20.7 $\mu$ .

There are some morphological and perhaps distributional differences between the various entities discussed above, but since their habitats were not visited and no living plants of the sonomensis type or medius type were obtained, the significance of such differences is difficult to evaluate. For the present, their similarities rather than differences are being emphasized, and only one species is being recognized.

#### 5. Aster chilensis Nees

Aster chilensis Nees, Gen. et Sp. Aster. 123. 1832. (Type: Haenke s.n., Calif., incorrectly thought by Nees to have come from Chile).

Aster menziesii Lindl. in Hook. Fl. Bor. Am. 2:12. 1834.  
(Type: Menzies s.n., N. W. coast of Am., K?).

Aster chamissonis Gray ex Torr. in Bot. Wilkes Exp. 341.  
1874. (Type: Chamisso s.n., Calif., LE?).

Aster invenustus Greene, Man. Bay Reg. Bot. 179. 1894. A.

chilensis var. invenustus Jeps. Fl. W. Middle Calif.

556. 1901. (Type: Greene s.n., near Calistoga, Napa Co., Calif., Aug. 1888, ND; isotype: UC!).

Aster militaris Greene, Proc. Acad. Phila. 1895:550. 1896.

(Howell s.n., Grants Pass, Josephine Co., Oregon, Sept., 1892, ND; isotype UC!).

Stems usually stout, from vigorous creeping rhizomes, erect to ascending or nearly prostrate, green to reddish, 3-10 (12) dm. high, paniculately branched above; stem pubescence varying from densely cinereous to white hirsute and from sparse but uniform to pubescent mainly in lines; basal leaves broadly petiolate, oblanceolate, up to 20 cm. long and 4 cm. wide, petiole 3-12 mm. wide and half-clasping, often deciduous; middle and upper stem leaves gradually reduced, mostly less than 10 cm. long and 2 (3) cm. wide, sessile, usually not clasping, these as well as lower leaves often crenate or serrate, often scabrous as well as strigose on upper surface; branches ascending to spreading, up to 24 cm. long, with many linear-lanceolate spreading bracts, these 0.5-3 cm. long, often with a fascicle of leaves in the axil; heads usually numerous, clustered at the tips of the branches, medium-sized; involucre mostly 10-15 mm. wide, 5-8 mm. high; phyllaries typically quite imbricated in 4-5 series although sometimes enlarged and subequal, glabrous to sparsely pubescent, erect to

spreading, the outer obtuse to nearly rounded, mucronulate, the inner narrowly obtuse to acutish, all with herbaceous green tip and midrib, and contrasting chartaceous base with a conspicuous scarious margin, the chartaceous portion extending half way up the outer phyllaries and nearly to the tip on the inner; ray flowers mostly 25-40, the ligules bluish-violet to deep purple, rarely white, 1.5-2.5 mm. wide, 9-15 mm. long; pappus white to sordid; achenes pubescent.

Fields, waste places, and marshes. Abundant along the coast from Santa Barbara to central or northern Oregon, perhaps reaching San Diego Co. to the south and Washington to the north, extending into the coast ranges and scattered in the Central Valley of California and possibly in the lower Sierra Nevadas of California and valleys of western Oregon.

Representative specimens. CALIFORNIA: Del Norte Co., Crescent City, Parks 24071, Sept., 1937 (UC, NY). San Diego Co., Palomar Mt., 5500 ft., Spencer 1992, 1993, (UC, POM) Sept. 14, 1922. Santa Barbara Co., Carpinteria, Hall 3166, May, 1902 (DS, UC). Santa Clara Co., Palo Alto, Abrams 2235, 2234, (RM, DS, POM) Sept. 12, 1904. Siskiyou Co., Hwy. 96 along Klamath R., 1.8 mi. N of Somesbar, Everett & Balls 20296, Oct. 14, 1954 (RM, UC, RSA, NY). OREGON: Curry Co., Brookings, Thompson 12543, Aug. 7, 1935 (WTU, NY). Lane Co., Heceta Head, Cronquist 6115, Aug. 29,

1949 (WS, WTU). Lincoln Co., near Seal Rock, Peck 10544, Aug. 15, 1921 (DS).

Aster chilensis is the predominant species along the coasts of California and Oregon. It is best recognized by the distinctly graduated involucre with obtuse to rounded outer phyllaries and obtuse to acutish inner phyllaries, all of which have a scarious margin. In the southern part of this species' range, many otherwise typical specimens have a dense, cinereous to black pubescence which indicates introgression from A. bernardinus.

In the marshy areas of the lower Sacramento River and San Francisco Bay regions, intergradation between A. chilensis and A. lentus is obvious from the many intermediate specimens. It is postulated that the diploid A. lentus is one progenitor of the polyploid A. chilensis. Thus the intermediate forms may represent segregants of A. chilensis which in the marshy habitat are genetically selected or environmentally modified to simulate the phenotype of A. lentus. On higher ground or in drier habitats in the Bay region, most specimens are typical of A. chilensis, but characteristics of A. lentus appeared on a number of herbarium specimens both from around the bay and less frequently some distance from the bay. The major characteristics upon which A. chilensis may be distinguished from A. lentus include wider and more obtuse phyllaries; lower and middle stem leaves mostly over one cm. in width,

versus mostly less than one cm. wide in A. lentus; pubescence present, sometimes densely so, versus mostly glabrous or lightly pubescent in lines in A. lentus; absence of the fleshiness of phyllaries and leaves which typifies A. lentus. The latter's bracts typically have a flared, clasping base tapering to the pointed tip.

A few other troublesome forms, which have previously been given separate names, occur in the San Francisco Bay area. Until further study can be done with living plants, these forms have mostly been placed in synonymy with A. lentus. Only one such form, A. invenustus Greene, has been placed with A. chilensis. It apparently occurs on the drier hills around the bay, and is classed with A. chilensis because of its dense pubescence.

Along the Oregon coast A. chilensis comes into contact with A. subspicatus, and many plants in this area are difficult to assign with certainty to either of the species. The diagnostic features of each species were established from morphologically and cytologically typical plants of each. For A. chilensis, such plants center in California and are predominantly hexaploid with 24 pairs of chromosomes. Aster subspicatus is the common species in the Willamette Valley and along the Columbia River, where it has been found to be entirely duodecaploid with 48 pairs of chromosomes. On a chromosome basis the predominant species along the Oregon coast is judged to be A. chilensis, since

the majority of the plants collected were hexaploid. The morphological distinction is much less clear cut, but it also favors such a decision. The genic influence of A. subspicatus is unmistakable, but it is not overwhelming. Thus, it seems more valid to interpret the coastal assemblage as a northward extension of A. chilensis, with intrusions by a generally more inland species, A. subspicatus.

Since no collections were made along the southern Washington coast, the limits of northward distribution for A. chilensis are not known. The few collections from the Puget Sound area were all referred to A. subspicatus, even though the chromosome levels were hexaploid and octoploid. These collections are discussed further under the latter species.

#### 6. Aster laevis L.

Aster laevis L. Sp. Pl. 876. 1753. (Kalm s.n., North America).

Aster laevis var. geyeri Gray, Syn Fl. N. Am. 1<sup>2</sup>:183.

1884. A. geyeri Howell, Fl. N. W. Am. 1:308. 1900.

A. laevis ssp. geyeri Piper, Contr. U.S. Nat. Herb.

11:573. 1906. (Type: Geyer 638, meadows, Spokane and Columbia R. valleys, Wash., K?).

Aster brevibracteatus Rydb. Mem. N.Y. Bot. Gard. 1:392.

1900. (Type: Suksdorf 928, Spokane Co., Wash., 1889, WS!).

Aster scribneri Rydb. op. cit. p. 393. (Type: Scribner 91, Bird Tail Creek, Montana, 1883, NY?).

Aster subsalignus Rydb. Bull. Torrey Club 37:140. 1910.

(Type: Osterhout 3397, Glenwood Springs, Garfield Co., Colo., Aug. 18, 1906, NY).

Aster pickettianus Suksd. Werdenda 1:42. 1927. (Type:

Suksdorf 8984, near Spangle, Spokane Co., Wash., Aug. 3, 1916, WS! isotypes: DS! WTU!).

Stems erect, moderately stout, mostly 3-12 dm. high, usually red or reddish-brown, freely branching near the summit, plants usually glabrous throughout to rarely some light lines of pubescence in the inflorescence, often glaucous; basal leaves early deciduous, similar to the usually persistent lower cauline leaves, these ovate or broadly lanceolate, 10-20 cm. long and 2-4 cm. wide, acute to acuminate, narrowed to a winged clasping petiole half the total length or less, often somewhat reddish, often sharply serrate; upper cauline leaves gradually reduced to the inflorescence, then markedly so, ovate to linear-lanceolate, sessile by a cordate-clasping base, usually entire, glabrous but scabrous margined; inflorescence often widely branching, paniculate, the branches strictly ascending to slightly arcuate-spreading, up to 20 (25) cm. long, with numerous cordate-clasping to lanceolate or subulate, attenuate bracts, these mostly 2-30 mm. long and 0.5-5 mm. wide or wider at the base; heads usually numerous, small to

medium-sized, the involucre 6-12 mm. broad and 4-8 mm. high; phyllaries strongly graduated in 4-5 series, usually rather stiff and erect, broadest at the base and tapering to the acute or acuminate apex, mostly white chartaceous below with a shorter rhombic or lance-rhombic green tip, the scarious margin inconspicuous to rather prominent and extending nearly to the apex, glabrous throughout except the sparsely ciliate margin; ray flowers 25-40, the ligules blue to violet, 1.5-2.5 mm. wide and 12-30 mm. long; pappus straw-colored to usually reddish; achenes mostly glabrous to faintly pubescent.

Roadsides, stream banks and open woods. Widespread in eastern United States, extending from Alberta questionably to Vancouver, B.C., south in the Rocky Mts. to New Mexico, northcentral Idaho and the northern part of Washington, possibly west to the Cascades. Also possibly relict in the mountains of northern California.

Representative specimens. CANADA: Alberta, Waterton Lakes, Nelson 3106, Sept. 1, 1938 (RM, UC). British Columbia, New Westminster (Cumberland St.-possibly cultivated), J. K. Henry s.n. or J. R. Anderson s.n., Sept. 15, 1915 (DS). CALIFORNIA: Trinity Co., Saddle between Red Mts. and Granite Pk., 7200 ft., Baker 230b-26, Aug. 8, 1926 (UC). COLORADO: Archuleta Co., 2 mi. SE of Pagosa Springs (road to Chama), 8500 ft., Bacigalupi 7495, Sept. 6, 1960 (UC). Chaffee Co., Buena Vista, Clokey 3509,

Aug. 9, 1919 (RM, DS, CAS, WS). Larimer Co., Loveland, Johnston 274, Aug. 8, 1917 (RM). IDAHO: Bonner Co., near Hope, Sandberg et al. 953, Aug. 25, 1892 (DS, CAS). Kootenai Co., Indian Cr., near Coeur de'Alene Mission, Henderson 2801, Aug. 12, 1894 (RM, DS). MONTANA: Lewis & Clark Co., West Fk. Sun River, Kirkwood 2347, Sept. 2, 1925 (RM, UC). NEW MEXICO: Otero Co., Mescalero, Blake 33308, Sept. 8, 1939 (WTU). San Miguel Co., Las Vegas, Porvenir, Bro. Arsene 17805, Sept. 6, 1926 (UC). UTAH: Grand Co., Mill Canyon, LaSal Mts., Maguire & Richards 15733, Aug. 17, 1934 (RM). WASHINGTON: Ferry Co., Nancy Cr., Boner & Weldert 254, July 31, 1939 (RM, DS, WTU, UC, WS). WYOMING: Crook Co., 5 mi. NW of Hulett, 4000 ft., Williams 2524, Aug. 31, 1935 (UC, RM, WS). Sweetwater Co., Three Forks, Nelson 354a, Sept. 22, 1932 (RM).

Aster laevis has the largest distribution of any of the species of this study, as indicated earlier in the description. It is so far known to have only the hexaploid chromosome number of  $2n = 24II$ , based on my counts and those of Van Faasen (63). It is a remarkably distinct species in its pure form, but it may also participate in considerable hybridization in some areas. Some specific areas include eastern Washington, northern Idaho, western Montana, and southern British Columbia and Alberta. Sympatric species with which A. laevis intergrades include the two subspecies of A. occidentalis, and to a lesser degree A. foliaceus ssp.

parryi and A. adscendens. The unusually high success in obtaining vigorous  $F_1$  hybrids from artificial crosses involving A. laevis was pointed out in the hybridization section.

A number of synonyms are usually listed under A. laevis in its treatment in floras of the eastern United States. Likewise, five synonyms are listed above for the western range of the species. In most or perhaps all cases, the synonyms probably represent genetic segregants resulting from hybridization. Many authors have treated the eastern portion of the species as A. laevis var. laevis and the western portion as A. l. var. geyeri. This was not followed here for the reason that geographic separation is not at all complete between the forms. Although the type specimen of A. l. var. geyeri was not seen, the original description, along with many labeled specimens, indicates an introgression of genes from some form of A. occidentalis. In addition, the type specimens of A. brevibracteatus Rydb. and A. pickettianus Suksd. were both collected from the same area of Washington and suggest a similar origin as that of A. laevis var. geyeri. The geyeri type of plant is common in eastern Washington, but it is not the only form present. Very typical examples of the species as it occurs in the east are also present in the west. My collection from Idaho, Dean 375, keys easily to the eastern form, A. l. var. laevis. Similarly, the geyeri type of morphology can

be seen in a number of collections from eastern United States.

Another particularly interesting problem is the possible occurrence of A. subspicatus with A. laevis in northern Idaho and surrounding regions. These two species share at least two traits which are lacking in most of the other species: serrate leaves and a reddish pappus. They differ mainly in the shape of the phyllaries and in degree of pubescence. Typical plants of A. laevis, when combined with some other entity, such as A. foliaceus ssp. parryi, may be modified enough to simulate A. subspicatus. This phenomenon was observed in hybrids artificially produced in the greenhouse. Thus many of the herbarium specimens labelled A. subspicatus from the area occupied by A. laevis may have been derived in the manner suggested above. It is not yet known whether plants of A. subspicatus occurring east of the Cascade Mountains in Washington have the typical duodecaploid condition. However, A. laevis, in combination with A. chilensis, is believed to be one of the original progenitors of A. subspicatus, and it may be immaterial that the chromosome number has not reached the duodecaploid level as long as the plants are so morphologically similar to A. subspicatus that they cannot be referred to either of its parents. I am therefore still acknowledging the presence of A. subspicatus in northern Idaho and even in western Montana, but with the reservation

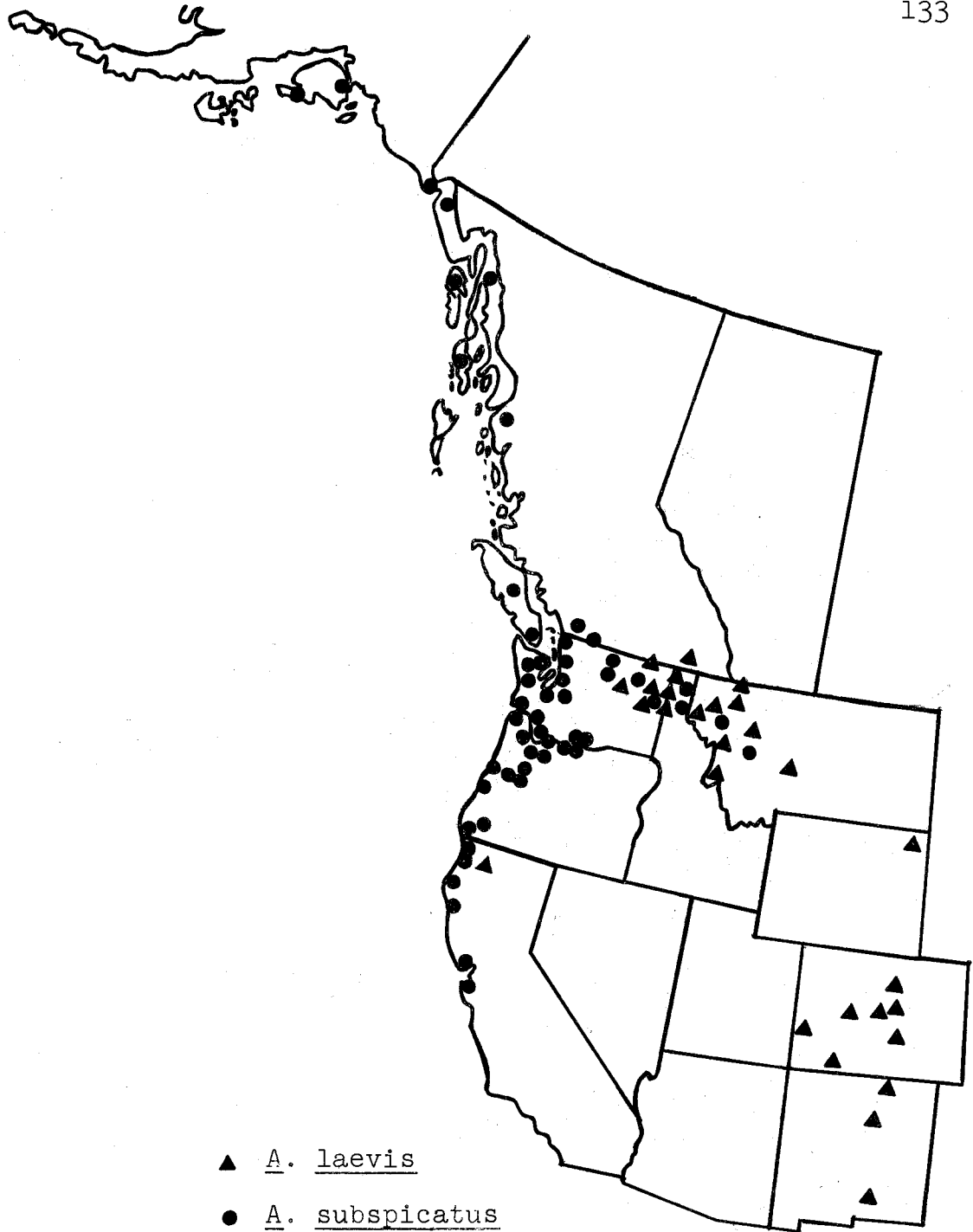


Figure 7. Distribution of Aster laevis and A. subspicatus

that it is probably not of the same origin in this area as in areas west of the Cascades. Whenever possible, questionable herbarium specimens were referred to either A. laevis or the other species which appeared to be the most likely parent.

The discovery of a collection of A. laevis from California was unexpected and constitutes a new record for that state. It also indicates the possibility of a previously wider distribution of the species. Even more interesting is the speculation that the mountains of northern California are a refuge for a number of species which were formerly more widespread. Asters that provide some evidence for this hypothesis include plants of A. laevis, A. cusickii, and one collection from Trinity Summit, Humboldt County, Kildale 1215, which appears to have genes of A. idahoensis. All three of these taxa are now largely confined to areas including, and northeast of, the Wallowa Mountains of Oregon.

#### 7. Aster subspicatus Nees

Aster subspicatus Nees, Gen. et Sp. Aster. 74. 1832. (Type: Haenke s.n., Fort Mulgrave, Yakutat Bay, Alaska).

Aster douglasii Lindl. in Hook. Fl. Bor. Am. 2:11. 1834.

(Type: Douglas s.n., on the N. W. Coast, near the confluence of the Columbia, K).

Aster amplus Lindl. in Hook. op. cit. p. 10. (Type:

Drummond s.n., Rocky Mts., K; isotype?: NY!).

Tripolium oregonum Nutt. Trans. Am. Phil. Soc. II. 7:296.

1840. Aster oregonus T. & G. Fl. N. Am. 2:163. 1841.

(Type: Nuttall s.n., banks of the Wahlamet (Willamette R., Oregon), BM).

Aster elmeri Piper, Bull. Torrey Club 29:645. 1902. A.

okanoganus Piper, Proc. Biol. Soc. Wash. 29:101.

1916. (Type: Elmer 571 Sinlahekin Basin, Okanogan Co., Wash., Aug., 1897, US; isotype: WS!). Not A.

elmeri Greene, Pitt. 2:170. 1891.

Aster wattii Piper, loc. cit. (Type: Watt s.n., North

Yakima, Yakima Co., Wash., Aug., 1895, US; isotype:

WS!). Not A. wattii Clarke, Journ. Linn. Soc. 25:36. 1889.

Aster umbraticus Sheldon, Bull. Torrey Club 30:130. 1903.

(Type: Sheldon 11310, University Park, Multnomah Co., Oregon, Sept. 14, 1902, NY! isotypes: DS! POM! WS! US).

Aster butleri Rydb. Bull. Torrey Club 37:139. 1910. (Type:

Butler 443, Gateway, Gallatin Co., Montana, Aug. 16, 1908, NY!).

Aster subcaudatus Rydb. op. cit. p. 143. (Type: Rosendahl

1089, Laggan, Lake Louise region, Alberta, Canada,

Aug. 23, 1902, NY!).

Aster umbachii Rydb. op. cit. p. 144. (Type; Umbach 275,

Lake MacDonald, Flathead Co., Montana, Aug. 20, 1901,

NY!).

Aster carterianus Henry, Ottawa Nat. 31:57. 1917. (Type: Carter 225, Cameron Lake, Vancouver Island, British Columbia, Canada, Sept., 1916, CAN; isotype: WS!).

Stems stout, from strong creeping rhizomes, green to brown or often reddish, erect and usually freely branching above, mostly 4-12 dm. high, glabrous below or sometimes throughout, more commonly pubescent in lines above and moderately or lightly uniform-pubescent under the heads, or rarely rather densely hirsute to pilose; basal and lowermost cauline leaves usually deciduous to sometimes persistent, petioled, usually not much larger and often smaller than the persistent cauline leaves just above; cauline leaves sessile, scarcely or not clasping, obovate to lanceolate, acute to acuminate, entire to usually serrate, the largest up to 20 cm. long and 4 cm. wide but usually less, gradually reduced upward, glabrous to sparingly strigose or rarely densely pilose, margin scabrous; inflorescence usually ample, paniculate, often more than half the total height of the plant, the branches ascending to spreading, with few to numerous leafy bracts, these erect to spreading, lanceolate, occasionally serrate, 2-30 mm. long and 0.5-8 mm. wide; heads few to numerous, solitary to crowded at the tips of the branches, small to medium-sized, the involucre 6-15 mm. wide and 5-10 mm. high; phyllaries usually strongly graduated in 4-6 series, erect to

spreading, the outer obtusish to acute, mucronate, with chartaceous lower half and green tip, the inner acute to attenuate with increasingly more chartaceous portion, the chartaceous portion of all the phyllaries commonly brown or darkened in dried specimens, the scarious margin usually conspicuous and long ciliate, extending nearly to the tip of the inner phyllaries, usually glabrous abaxially, pubescent adaxially; occasionally the outer phyllaries are loose and spreading, nearly wholly green and as long as the inner; ray flowers 15-45, the ligules lavender to violet or purple, 1.5-2.5 mm. wide and 10-20 mm. long; pappus white to tawny or reddish; achenes pubescent.

Roadsides, stream banks and open woods. Coastal Alaska and British Columbia, inland to northern Idaho and possible northwest Montana, south commonly through western Washington and infrequently central Washington, Willamette Valley and coastal Oregon, possibly to coastal California.

Representative specimens. ALASKA: Prince of Wales Island, Klawak Lake, E. P. Walker, 1007, Sept. 12, 1915 (RM, DS, NY, WS). Yes Bay, T. Howell 1632, Aug. 17, 1895 (UC, WS, DS, NY). CANADA: British Columbia, Skeena, J. P. Anderson s.n., Sept. 9, 1910 (WS). CALIFORNIA: Del Norte Co., Crescent City, Eastwood 2269, Sept. 19, 1912 (CAS, DS, POM). IDAHO: Bonner Co., Hope, near Lake Pend'Oreille, Sandberg et al. 957, Aug. 25, 1892 (NY, DS. POM). MONTANA: Lake Co., Flathead Lake at Polson, Muenschner 11367, Sept. 2,

1937 (WTU). OREGON: Clatsop Co., Youngs Bay, Astoria, Henderson 11397, Aug. 2, 1929 (UC). Hood River Co., Hood River, Suksdorf 3390, July 8, 1927 (WS). Lane Co., Willamette R. at Eugene, Constance 1445, Aug. 28, 1935 (WS, DS). Marion Co. low ground near Salem, Nelson 799, July 20, 1916 (DS, WS). Multnomah Co., Troutdale, Abrams 9304, July 25, 1922 (RM, POM, DS). WASHINGTON: Grays Harbor Co., Lake Quinalt, Meyer 995, Aug. 6, 1937, (WS, WTU). Okanogan Co., Okanogan R. S of Omak, Fiker 1136, Aug. 21, 1932 (DS, WTU). Stevens Co., Columbia R., 1 mi. S of Kettle Falls, Boner & Weldert 250, July 30, 1939 (CAS, UC, WTU, DS, NY). Whatcom Co., Bellingham, Piper s.n., Sept. 12, 1914 (WS, UC).

Plants of A. subspicatus are primarily duodecaploids and are found abundantly from Seattle south through the Puget Trough of Washington and the Willamette Valley of Oregon, and east up the Columbia River to at least The Dalles. Throughout this area the species is reasonably uniform, except for the appearance of genes of A. eatonii in some plants of the Puget Trough, and occasional segregants which resemble the putative parents of A. subspicatus.

As was pointed out in the discussion of A. laevis, that species and A. chilensis are postulated as the progenitors of A. subspicatus. This hypothesis is based on cytology, morphology, and distribution. Both of the former species are primarily hexaploid and a doubling of the chromosomes of their hybrid would yield a duodecaploid.

Morphologically, A. subspicatus combines many of the traits of both putative parents and is thus largely intermediate. Artificial crosses were made in the greenhouse between A. laevis, collection 375, and A. chilensis, collection 300, and hybrids were obtained. These hybrids closely simulated typical A. subspicatus. In addition, some naturally occurring plants of this latter species approach either A. chilensis or A. laevis. Collection 351 from near Corvallis and 366 from near Hood River, Oregon, both resembled A. chilensis in having numerous, spreading bracts and obtuse outer phyllaries. Collection 363 from along the Molalla River near Canby, Oregon, clearly resembled A. laevis in having phyllaries broadest at the base with a rhombic green tip, bracts slightly clasping, and plants nearly glabrous. No chromosome counts were obtained from plants of this collection but they are assumed to be duodecaploid.

Although A. chilensis and A. laevis are probably entirely allopatric today, they may have been sympatric during some period in their history. It is not difficult to imagine that climatic conditions during a Pleistocene ice age forced A. laevis to the south and to the west, where it came into contact with A. chilensis. The fact that a collection of A. laevis was seen from the Siskiyou Mountains of northern California indicates that this species did have a greater southward distribution at one time.

The occurrence of chromosome numbers lower than the duodecaploid level in plants keying to A. subspicatus is puzzling. Both hexaploid and octoploid levels have been found in plants from the Puget Sound area. The hexaploids may represent a northward extension of plants of A. chilensis which have completely lost their identity through introgression with A. subspicatus. Another possibility is that they were derived from hybridization between A. chilensis and A. laevis in the manner suggested above, but without a subsequent chromosome doubling. The only evidence which bears on these hypotheses is that from the artificial hybridizations. The hybrids from A. chilensis X A. subspicatus crosses did resemble A. subspicatus more closely in the key characteristics. The cross between A. chilensis and A. laevis shows only that an A. subspicatus-like offspring is produced, but no examination has yet been made of the chromosome number or homology in the hybrid. The octoploid chromosome number is even harder to explain and no speculation is proposed here.

It appears that three major problems exist in the taxonomy and distribution of A. subspicatus. First is the northward extension of this species into Alaska and its interaction there with A. foliaceus ssp. foliaceus. Second is the degree of intergradation with A. chilensis along the Oregon coast and the extent to which this intergradation extends into Washington on the north and

California on the south. Third is the question of whether A. subspicatus actually occurs east of the Cascades in northern Washington and into Idaho, and if so to what extent. The uncertainty of this last point is caused by the hybridization of A. laevis with perhaps several different species, resulting in hybrids simulating A. subspicatus. Many of the names in synonymy under A. subspicatus were proposed for confusing segregants from such a hybrid origin.

Each of the three problems listed above is discussed more completely under the respective species with which A. subspicatus is involved. It is obvious that little more than defining some of the problems has as yet been accomplished in this species. Only a great deal of careful field observations and extensive chromosome counting will begin to elucidate the solutions to these problems.

#### 8. Aster greatai Parish

Aster greatai Parish, Bull. So. Calif. Acad. 1:15. 1902.

(Type: Greata s.n., Eaton Canyon, Los Angeles Co., Calif., Sept. 30, 1900; isotypes: UC! NY! US).

Stems stout, ascending to erect, often with a flexuous pattern above, 0.5-1.5 (2) m. high, few- to many-branched above, green to reddish, glabrous below, increasingly hispidulous above; basal leaves early deciduous, up to 30 cm. long and 5 cm. wide, broadly oblanceolate or

obovate, tapering to a winged, clasping petiole; cauline leaves gradually reduced to the inflorescence, then markedly so, subpetiolate to sessile, clasping and often auriculate, obovate to broadly lanceolate, apex acute to acuminate and mucronate, 2-15 cm. long, 1-4 cm. wide, nearly entire to more commonly sharply serrate, both leaf surfaces usually scabrous; inflorescence usually a many-headed panicle, the divergent branches up to 25 cm. long with numerous oblanceolate or lanceolate, divaricately spreading bracts, these mostly less than 2 cm. long and 8 mm. wide; heads small to medium-sized, the involucre 8-13 mm. broad, 5-8 mm. high; phyllaries strongly to scarcely graduated in 4-6 series, often spreading or squarrose, narrowly oblanceolate to linear, acute to acuminate, outer mostly green with small chartaceous portion below, inner increasingly chartaceous with narrow scarious margin, glabrate to puberulent abaxially, puberulent adaxially, ciliate marginally; ray flowers 30-50, ligules pink to light purple, 1-2 mm. wide, 10-15 mm. long; pappus white to tawny; achenes pubescent.

Stream banks and canyons of the San Gabriel Mts. and possibly San Bernardino Mts. of Los Angeles Co., California.

Representative specimens. CALIFORNIA: Los Angeles Co., Negro Canyon, San Gabriel Mts. near Pasadena, Grinnell s.n., Sept. 23, 1917 (RM, POM, DS).

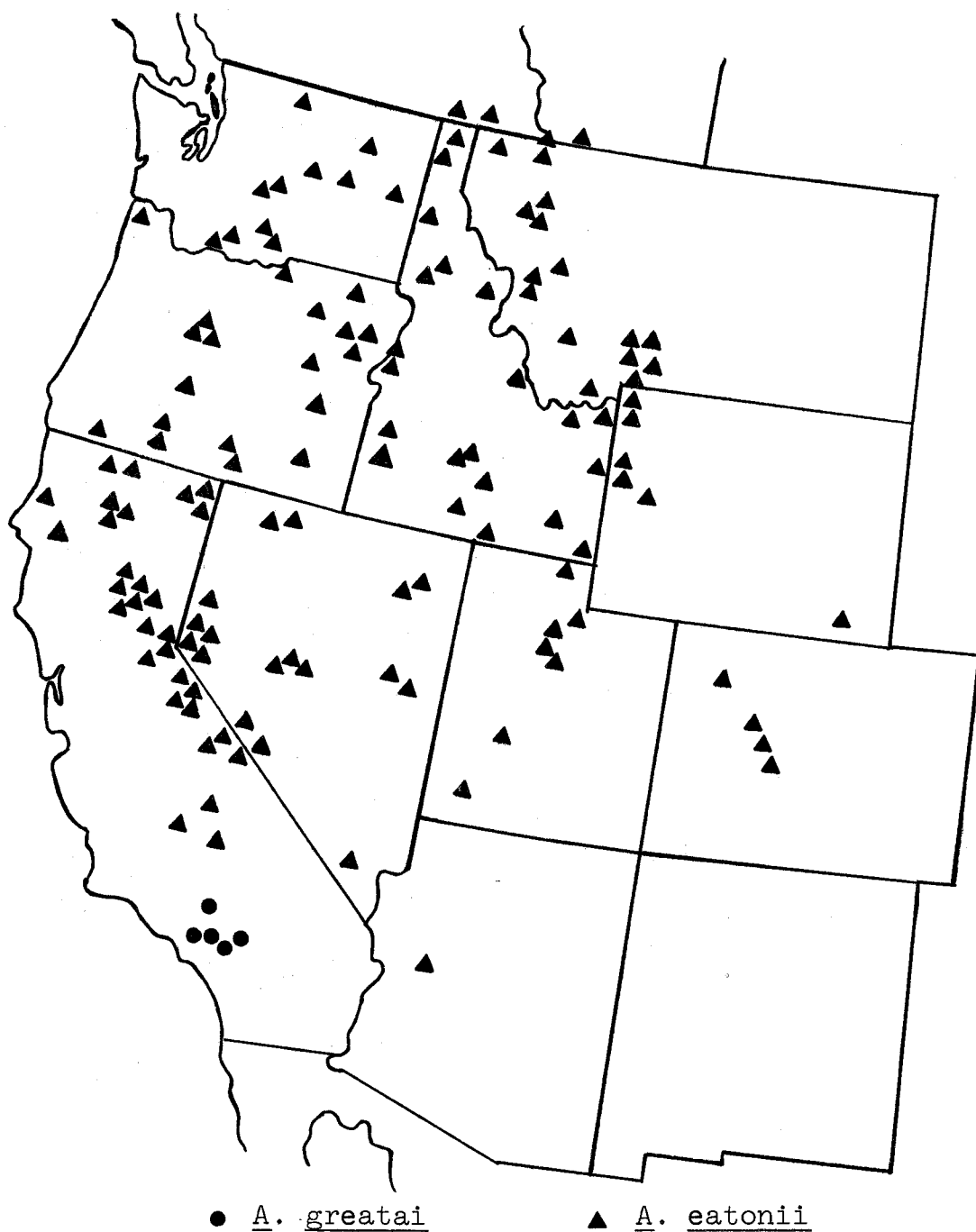


Figure 8. Distribution of *Aster greatai* and *A. eatonii*

Aster greatai is one of the few species of this study which is distinctive and not difficult to classify. It also has one of the most restricted distributions of any of the species. These conditions may be due to the fact that A. greatai is a diploid species, and as such, it has not been able successfully to hybridize and intergrade with other species, nor has it been able to invade new ecological territory. In hybridization experiments, 14 attempted crosses involving A. greatai all resulted in failure to set any fruit, giving some indication of its genetic incompatibility at the diploid level. Since the species is rather distinctive, no affinities with any other species are readily apparent.

#### 9. Aster eatonii (Gray) Howell

Aster oregonus or oreganus of authors, not Nutt.

Aster occidentalis (Nutt.) T. & G. var. scabriusculus Gray, Syn Fl. N. Am. 1<sup>2</sup>:192. 1884. (Type: Watson 506, northern Nevada, 1868, GH! isotype: NY!).

Aster foliaceus Lindl. in DC. var. eatonii Gray, Syn. Fl. N. Am. 1<sup>2</sup>:194. 1884. A. eatonii Howell, Fl. N. W. Am. 310. 1900. (Type: Watson 505, Virginia Mts., Elko Co., Nevada, August, 1867. GH!).

Aster fulcratus Greene, Pitt. 4:217. 1900. (Type: Baker 638, near Pagosa Peak, Mineral Co., Colo., Aug. 12, 1899, ND! isotypes: UC! GH! RM! US).

Aster proximus Greene, op. cit. p. 220. (Type: Nelson 6788, Madison R., Yellowstone Nat'l. Park, Wyoming, ND!).

Aster exsul Greene, op. cit. p. 221. (Type: Greene s.n., Humboldt R. at Deeth, Elko Co., Nevada, Aug. 5, 1895, ND!).

Aster microlonchus Greene, Ottawa Nat. 15:278. 1902.

(Type: Macoun 26384 and 26385, Chilliwack Valley, British Columbia, CAN; isotype: GH!).

Aster mucronatus Sheld. Bull. Torrey Club 30:309. 1903.

(Type: Sheldon 11171, Mt. Scott, Multnomah Co., Oregon, GH! isotypes: NY! WS! US). Appears most likely to be a hybrid between A. eatonii and A. subspicatus.

Aster lonchophyllus Greene, Leafl. Bot. Obs. 1:146. 1905.

(Type: Baker 805, Crested Butte, Gunnison Co., Colo., Aug. 13, 1901, ND; isotypes; GH! RM! WS! US).

Aster roseolus Rydb. Bull. Torrey Club 37:141. 1910.

(Type: Rydberg 2817, Melrose, Silverbow Co., Mont., 1895, NY!).

Aster mearnsii Rydb. op. cit. p. 144. (Type: Mearns 4806, Mammoth Hot Springs, Yellowstone Nat'l. Park, Wyoming, Oct. 11, 1902, NY!).

Stems from strong rhizomes with usually a conspicuous whorl of reddish branches just below the soil line, rather stout, 0.5-1.5 m. high, usually strict and erect, though often characterized by a flexuous growth pattern above, mostly red or reddish-brown to greenish, sparsely (below)

to often rather densely and uniformly puberulent above, this appressed or usually spreading; leaves all lanceolate or linear, more or less sessile and slightly auriculate, only gradually reduced upward, the lower up to 20 cm. long and 20 mm. wide, though usually narrower, deciduous, the upper subtending a branch, scabrous above, scabrous or glabrate below, margins usually entire and scabrous; inflorescence an elongated narrow panicle, one-half to two-thirds the total height, the branches relatively short (to 15 cm.), ascending, many-headed, with numerous leafy bracts; heads small to medium-sized, the involucre 7-14 mm. wide, 5-8 mm. high; phyllaries in 3-4 series, narrowly oblanceolate, obtuse to acute, graduated to usually subequal, erect to usually spreading, wholly green to often partly chartaceous below with a scarious margin, usually glabrous abaxially, strigose adaxially; ray flowers 20-35, the ligules white to pink or violet, 1-2 mm. wide, 7-15 mm. long; pappus usually white; achenes strigose.

Stream banks, ditchbanks, marshes and other wet places. Widespread east of the Cascade-Sierra mountain chain from southern British Columbia to Alberta, southward to central California and northern New Mexico; also lower Columbia R., lower Klamath R., Rogue R. Valley, and Mts. of northern California.

Representative specimens. CANADA: Alberta, North Saskatchewan R., 13 mi. N of Saskatchewan R. Trading Post,

Weber 2484, July 15, 1941 (NY). British Columbia, Clinton,  
Anderson 775, Aug. 23, 1918 (WS). ARIZONA: Yavapai Co.,  
 Mts. near Prescott, Kusche s.n., Sept. 1-5, 1929 (CAS).  
 CALIFORNIA: Butte Co., Butte Meadows, 4000 ft., Heller  
11655, Aug. 7, 1914 (WTU, UC, DS, CAS, NY). Humboldt Co.,  
 Trinity R. near mouth of Willow Cr., 500 ft., Tracy 5209,  
 Sept. 7, 1931 (UC). Inyo Co., Wyman Cr., Roberts Ranch,  
 8000 ft., Duran 3141, July 22, 1931 (RM, UC, DS, POM, RSA,  
 WTU, WS, CAS, NY). Trinity Co., Forest Glen, S. Fk. Trin-  
 ity R., Munz 14368, Aug. 11, 1936 (UC, POM, DS). Tulare  
 Co., Giant Forest, Sequoia National Park, Abrams 7736,  
 Sept. 27, 1920 (DS, NY). COLORADO: Pitkin Co., 2 mi.  
 below Capitol Lake, Penland 3446, Aug. 11, 1946 (WS).  
 Rio Blanco Co., North Elk Canyon, Sturgis s.n., July 31,  
 1902 (CAS). IDAHO: Boundary Co., Bonners Ferry, Christ  
2028, Aug. 2, 1932 (ID, NY). Custer Co., Red Fish Lake,  
Worley & Mann 270, July 29, 1936 (WS, ID). Fremont Co.,  
 Henry's Lake, Nelson & Nelson 6798, Sept. 1, 1899 (RM).  
 Owyhee Co., Flint Creek, 4200 ft., Macbride 491, July 30,  
 1910 (RM, WS, WTU, UC, NY). MONTANA: Cascade Co., Great  
 Falls, Anderson 93, Aug. 1, 1885 (UC). Granite Co., Rock  
 Creek, Hitchcock & Muhlick 13695, Aug. 19, 1945 (RM, WTU,  
 UC, DS, CAS, NY, WS). NEVADA: Clark Co., Charleston Park,  
 7600 ft., Clokey 8164, Sept. 3, 1938 (DS, WS, POM, WTU).  
 Lander Co., Kingston Canyon, Toiyabe Range, 9000 ft.,  
Train 3388, Aug. 21, 1939 (WTU, RSA, NY). Ormsby Co.,

Eagle Valley, 4770 ft., Baker 1399, July 31, 1902 (RM, POM, CAS, NY, UC). OREGON: Douglas Co., S end of Diamond Lake, Applegate 4565, Sept. 14, 1925 (DS). Malheur Co., Owyhee R. at Three Forks, 3900 ft., Dean 189, Aug. 20, 1957 (NY, OSC). Umatilla Co., Bingham Springs, 2500 ft., Cusick 3328, Oct. 10, 1908 (NY, DS, UC, WTU, WS). Union Co., Starkey-Granite Road, 6 mi. S of Starkey, Hitchcock 19756, July 17, 1952 (RM, UC, RSA, WTU, WS). UTAH: Piute Co., Marysvale, Tate Mine, 9000 ft., M. E. Jones 5863h, Aug. 2, 1894 (POM). Salt Lake Co., Lambs Cr., Wasatch Mts., 6300 ft., Vickery 2458, Aug. 14, 1959 (UC, RSA, DS). WASHINGTON: Chelan Co., Chiwaukum, 1800 ft., Otis 1095, Aug. 12, 1921 (WS, WTU). Okanogan Co., Johnson Cr., SW of Omak, Fiker 1156, Sept. 1, 1932 (WS, WTU, DS). Spokane Co., near Spokane, Turesson 8, 1912 (RM, WS). WYOMING: Big Horn Co., Lower Canon Creek, Goodding 491, Aug. 6, 1901 (RM). Carbon Co., Pass Cr., Nelson 2478, July 21, 1896 (RM).

Aster eatonii is one of the widespread species in this study, yet it is reasonably uniform throughout its range. This is due to at least two factors. The limited number of chromosome counts which have been made indicate that the plants are largely diploid. Also the species is one of the most aquatic of this group, preferring marshes, ditchbanks and riverbanks where the rhizomes are often in the water. If this ecological condition is a requirement for growth of

plants of this species, seedlings of hybrid derivative would probably be eliminated, or only those hybrid seedlings which are physiologically similar to A. eatonii could survive in such a habitat.

Despite the two factors mentioned above, plants of A. eatonii probably are involved in some natural hybridization. The most taxonomic confusion comes from its intergradation with A. hesperius. The habitat preference of the latter species is quite similar to that of A. eatonii, so that the plants are frequently in contact. The only chromosome number so far determined for A. hesperius is  $2n = 32II$ , which would be likely to prevent any hybridization with diploid plants of A. eatonii. However, some tetraploids and a rare hexaploid have been found in A. eatonii, and plants with these chromosome complements could hybridize with the octoploid A. hesperius. Taxonomically confusing or intermediate specimens were seen from every state in which both A. eatonii and A. hesperius occur, but not in great numbers from any one area.

The only other species with which A. eatonii appears to hybridize to any extent is A. subspicatus where the two meet in the Columbia River gorge near Hood River, Oregon, and westward on both sides of the river. Here again the high number of chromosomes in plants of A. subspicatus should make them incompatable with diploid plants of A. eatonii, but this may not prevent their successful

hybridization with tetraploid and hexaploid plants. No tetraploid A. eatonii has yet been found in this area, but the only hexaploid thus far counted in the species was located near the town of Svenson, Oregon, not far from the mouth of the Columbia River.

A number of W. Suksdorf's collections around Bingen, Washington, showed evidence of possible hybridization. Pollen measurements were made from a series of specimens; it was found that the smallest and largest pollen came from the most clearly recognizable specimens of A. eatonii and A. subspicatus respectively, and intermediate sizes represented taxonomically more difficult specimens. The collection numbers (all Suksdorf's) and mean pollen grain sizes are as follows: 9148-23.8 $\mu$ ; 9451-26.4 $\mu$ ; 2397-28.5 $\mu$ ; 5882-28.7 $\mu$ ; 5120-31.0 $\mu$ . Closer to Portland, Oregon, the type collection of A. mucronatus, collected and described by Sheldon, may possibly be a hybrid. The mean pollen measurement of 27.4 $\mu$  indicates a tetraploid or higher chromosome number. In addition to these examples mentioned above, an occasional specimen from north of the Columbia River towards Seattle, Washington, showed characteristics of A. eatonii, yet no "good" representatives of the species were seen. Considerably more field work and chromosome counts may establish western Washington as part of the range of A. eatonii.

10. Aster hesperius Gray

Aster coerulescens of authors, not A. coerulescens DC.

Prod. 5:235. 1836.

Aster hesperius Gray, Syn. Fl. N. Am. 1<sup>2</sup>:192. 1884. A. foliaceus Lindl. in DC. var. hesperius Jeps. Man. Pl. Calif. 1047. 1925. (Lectotype: Wright 1158, Rio Grande R. valley, Hudspeth Co., Texas, Sept., 1849, GH!) Lectotype chosen by Rydberg, Bull. Torrey Club 37:140. 1910.

Aster hesperius var. wootonii Greene, Bull. Torrey Club 25:119. 1898. A. wootonii Greene, Leaflet. Bot. Obs. 1:146. 1905. A. coerulescens DC. var. wootonii Wiegand, Rhodora 35:28. 1933. (Type: Wooton 329, White Mts., Lincoln Co., New Mexico, Aug. 12, 1897, ND; isotype: NY! UC! POM!).

Aster laetevirens Greene, Pitt. 4:219. 1900. A. coerulescens DC. var. laetevirens Cronq. Am. Midl. Nat. 29:437. 1943. A. hesperius var. laetevirens Cronq. Leaflet. W. Bot. 6:44. 1950. (Lectotype: Nelson 5293, Huttons Lake, Albany Co., Wyo. Sept. 7, 1898, ND! isotypes; RM! NY! US). Very close to A. eatonii.

Aster limosus Greene, op. cit. p. 222. (Type: Greene s.n., Palisade, Eureka Co., Nevada, Aug. 24, 1896, ND!).

Aster ensatus Greene, op. cit. p. 223. 1900. (Type: Parish 3818, near San Bernardino, San Bernardino Co., Calif., Oct. 15, 1895, ND! isotype: UC!).

Aster osterhoutii Rydb. Bull. Torrey Club 31:654. 1904.  
(Type: Osterhout 2506, New Windsor, Weld Co., Colo., Sept. 29, 1899, NY! isotype: RM!).

Brachyactis hybrida Greene, Leaflet Bot. Obs. 1:147. 1905.  
(Type: Baker 937, Gunnison, Gunnison Co., Colo., Aug. 27, 1901, ND; isotypes: WS! US).

Aster fluvialis Osterh. Bull. Torrey Club 32:611. 1905.  
(Type: Osterhout 2941. Cache La Poudre R. at New Windsor, Weld Co., Colo., Sept. 11, 1904).

Stems stout, erect, generally quite tall, 0.5-2 m. high, often diffusely branched above, green or reddish, usually glabrous below, pubescent in lines decurrent from leaf bases above, pubescence not uniform under the heads although denser there due to the concentration of leafy bracts; junction of stem and rhizome often swollen; leaves all narrowly oblanceolate to linear, glabrous or sparingly scabrous on the upper surface, margins entire to sometimes conspicuously low serrate, scabrous, the midrib on the lower surface often whitish and rather conspicuous; lower leaves up to 20 cm. long and 20 (25) mm. wide, sessile or the petiole broadly winged, subclasping, usually early deciduous; cauline leaves well spaced, gradually reduced upward, sessile and subclasping, apex acuminate;

inflorescence moderately open to usually crowded, forming a corymbose panicle, the branches rather strictly ascending, longest in the mid-part of the inflorescence, up to 15 (18) cm. long, moderately to densely leafy-bracted, the bracts lanceolate, 1-25 mm. long and 0.5-5 mm. wide; heads small to medium-sized, the involucre 7-13 mm. broad, 4.5-8 mm. high; phyllaries usually graduated in 4-5 (6) series, or nearly subequal, narrowly oblanceolate to linear, acute to acuminate, spreading, seldom wholly green, mostly with an elongate green tip and chartaceous base, the chartaceous portion forming a white border nearly half way up the outer phyllaries and much farther on the inner ones, glabrous on the back, strigose within, margins scarcely to evidently scarious, sparingly ciliate; ray flowers 20-40, ligules white to violet, 1-1.5 mm. wide, 8-14 mm. long; pappus white; achenes pubescent.

Ditchbanks, moist fields, and marshes in the valleys and plains. Saskatchewan to Texas, west to eastern Washington and southern California.

Representative specimens. CANADA: Alberta, 13 mi. S of Calgary, Howell 7854, Aug. 20, 1931 (CAS). Saskatchewan, Cypress Hills, Battle Creek Ranger Station, Breitung 5437, Aug. 5, 1947 (RM). ARIZONA: Coconino Co., Flagstaff, Hanson 79, Aug. 29, 1922 (NY). CALIFORNIA: Inyo Co., Bishop, Larson s.n., July 3, 1925 (CAS). Orange Co., Wintersburg, sea level, Peirson 5241, Oct. 19, 1924

(CAS, POM, RSA). San Diego Co., 10 mi. N of Santa Ysabel, M. E. Jones s.n., Oct. 3, 1926 (POM). COLORADO: Custer Co., Westcliffe, Shear 3819, Aug. 13, 1896 (NY). Gunnison Co., Gunnison, 7680 ft., Baker 817, Aug. 16, 1901 (RM, NY, UC, GH, POM). Montezuma Co., Mancos, 7000 ft., Munz 13116, Aug. 14, 1934 (UC, POM). IDAHO: Ada Co., Eagle, ditch-bank, Christ & Ward 8801, Aug. 27, 1937 (NY). Cassia Co., Raft R., 6 mi. E of Almo, Baker 8788, Aug. 29, 1951 (ID, NY). MONTANA: Lewis & Clark Co., Helena, Kelsey s.n., Aug. 16, 1892 (NY). NEVADA: Lincoln Co., 4 mi. S of Caliente, Train 2451, Sept. 3, 1938 (UC, DS). Washoe Co., Wadsworth, Palmer 179, Aug., 1876 (NY, UC). NEW MEXICO: Dona Ana Co., Mesilla Valley, Wootton 1490, Sept. 22, 1899 (NY, UC, POM, DS). San Miguel Co., near Pecos, 6700 ft., Standley 5132, Aug. 20, 1908 (NY). UTAH: Cache Co., U.S.A. C. Campus, Logan, Cronquist 1100, Sept. 2, 1938 (UC, WTU). Washington Co., Springdale, 4000 ft., Jones 6080h, Sept. 25, 1894 (POM). WYOMING: Albany Co., Laramie, Nelson 8668, Aug. 20, 1901 (RM). Sheridan Co., Big Horn Mts., 7500 ft., Tweedy 2024, Aug. 15, 1899 (NY).

Aster hesperius is a wide-ranging species on both sides of the Rocky Mountains, reaching the Pacific coast in southern California but barely reaching Washington and Oregon. Thus, access to living populations was limited to two areas on the edge of the species range, eastern Washington

and southwestern Idaho. More study of living populations over the entire range is needed before the biological relationships of this species are well known.

Judging from the literature (67) and from herbarium specimens, A. hesperius is morphologically more closely allied to some species of eastern and midwestern United States, such as A. lateriflorus (L.) Britt. and A. simplex Willd., than to the other species of the present study. Recent chromosome counts by Van Faasen in Michigan (63) have revealed that both of the above mentioned species have chromosome numbers based on  $X = 8$ . Thus, A. hesperius may well be derived from the eastern segment of the genus rather than the western. These eastern species are not known to me, and I can draw no conclusions about this tentative hypothesis.

In its western distribution A. hesperius is variable but usually recognizable. It appears to intergrade to some degree with other species. These include A. eatonii, A. foliaceus ssp. parryi, A. o. ssp. occidentalis, and perhaps A. adscendens. The worst problem of confusion, that with A. eatonii, is discussed under that species. The distribution of A. hesperius into Montana and Wyoming is quite questionable. Most herbarium specimens which have been determined as this species from that area seem to be closer to other species, especially to A. foliaceus ssp. parryi. One collection from Albany County, Wyoming,

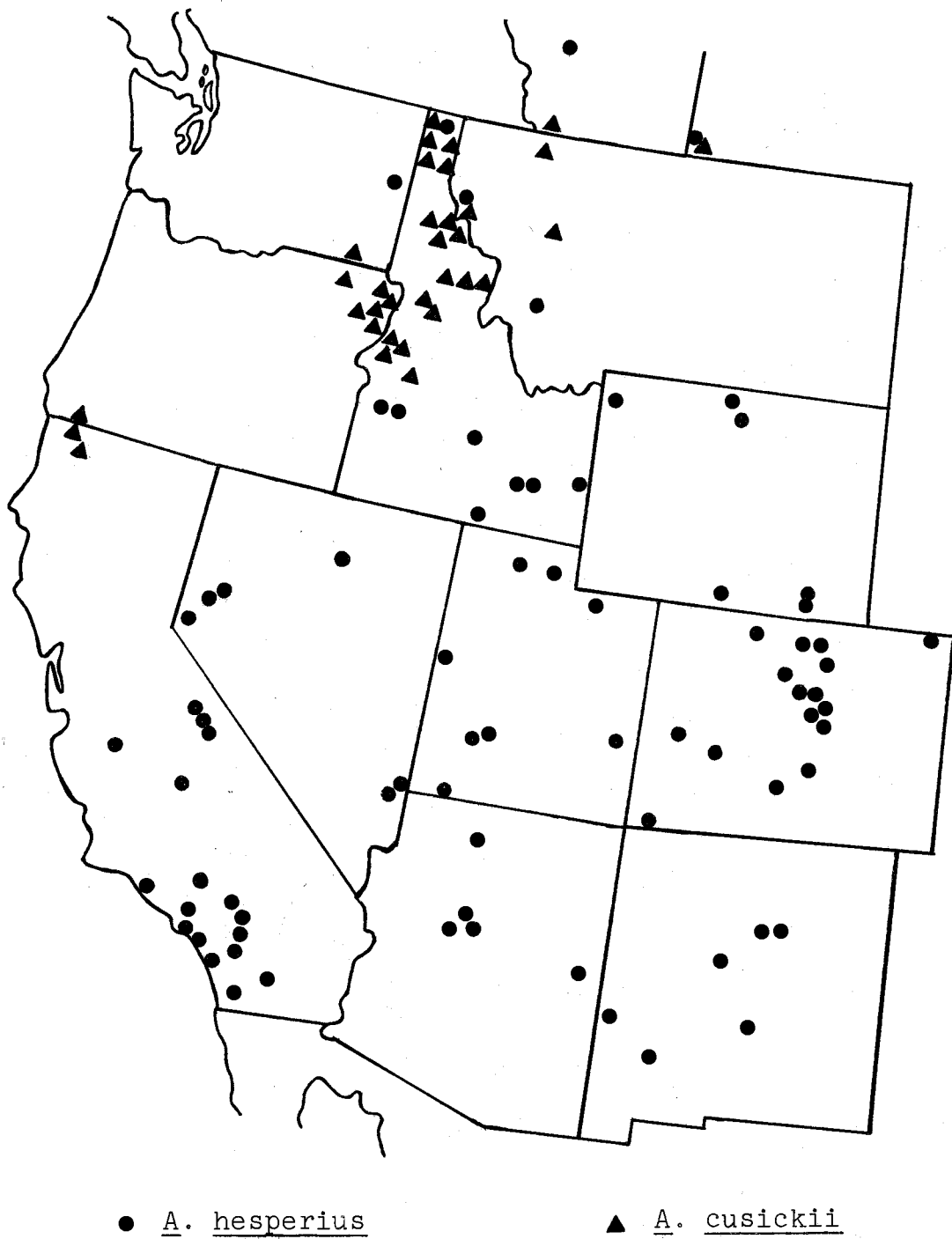


Figure 9. Distribution of Aster hesperius and A. cusickii

Nelson 1118, chosen by E. L. Greene as a cotype for A. laetevirens Greene, fits into A. o. ssp. occidentalis better than into A. hesperius.

The past treatment of variability in A. hesperius includes the recognition by Cronquist (14) of two varieties in the species. However, the distribution of each variety covers much of the same area, and the cited specimens in some cases are from the same locality and even the same population. It seems unlikely that rather freely interbreeding polyploids of the same species could maintain morphological distinctness in the same habitat. Rather, the recognizable differences are probably due to genetic segregation and recombination of a gene pool which has become enlarged by occasional interchanges with related species. Therefore, no varieties or subspecies were delimited for A. hesperius in this study.

The plants of this species had long been treated as part of A. coerulescens. However, Shinnars (56) has pointed out that the type of the latter taxon was actually a form of A. praealtus in eastern Texas, a part of Texas where plants of the present species do not occur. Thus, A. hesperius became the earliest valid name for this species.

11. Aster cusickii Gray

Aster cusickii Gray, Proc. Am. Acad. 16:99. 1881. A.

foliaceus Lindl. in DC. var. cusickii Cronq. Am. Midl.

Nat. 29:443. 1943. (Type: Cusick s.n., subalpine streams, Union Co., Oregon, July-August, 1878, GH! isotype: WS!).

Aster cusickii var. lyallii Gray, Syn. Fl. N. Am. 1<sup>2</sup>:195.

1884. A. kootenayi Nels. & Macbr. Bot. Gaz. 56:477.

1913. A. foliaceus var. lyallii Cronq. loc. cit.

(Type: Lyall s.n., between the Kootenay and Pend Oreille, Idaho, Aug., 1861, K).

Aster hendersonii Fernald, Bull. Torrey Club 22:273. 1895.

(Type: Henderson 2798, St. Maries R., Kootenai Co., Idaho. Aug. 5, 1894, GH! isotype: RM!)

Aster eriocalis Rydb. Bull. Torrey Club 37:143. 1910.

(Sandberg, MacDougal & Heller 877, valley of Traill R., Kootenai Co., Aug. 9, 1892, NY! isotypes: GH! CAS!).

Stems erect to ascending or sometimes lax and leaning, simple or branching above, sparsely to densely soft white tomentose, 5-10 dm. high; lower leaves up to 20 cm. long, the elliptic to oval blade abruptly contracted to the narrow, 5-10 cm. long clasping petiole, usually deciduous; cauline leaves hardly reduced upward, 1-4 cm. wide, few to numerous, sessile, ovate- to oblong-lanceolate, usually conspicuously constricted above the auriculate-clasping

base, densely soft puberulent to nearly glabrate, rather thin, margins scabrous, entire to sometimes distantly serrate; inflorescence from monocephalous to a many-headed, widely branching panicle; heads large, the involucre 1.5-3 cm. wide, 8-12 (15) mm. high, often closely subtended by a large leafy bract which surpasses the head; phyllaries linear to broadly lanceolate, subequal in 3-4 series or the outer elongated, acute to acuminate, usually spreading, mostly green and herbaceous with lower portion chartaceous, glabrate to densely pubescent; ray flowers 30-50, ligules violet to deep purple, 1-2 mm. wide and 15-20 mm. long; pappus white; achenes sparsely strigose to usually glabrous.

Along streams and in mountain meadows and woodlands. Blue and Wallowa Mts. of Oregon and Washington, to western Montana and southern Canada; also Siskiyou Mts. of southern Oregon and northern California.

Representative specimens. CANADA: Alberta, Cameron Lake, Waterton Lakes National Park, 5450 ft., Breitung 17320, Aug. 8, 1953 (NY, UC). CALIFORNIA: Siskiyou Co., Sky High Valley, Marble Mts., 6000 ft., Howell 15134, Aug. 7, 1939 (CAS). IDAHO: Adams Co., Black Lake, Weiser N.F., Christ 8704, 8645, Aug. 8, 1937 (NY). Bonner Co., Hughes Mdw., Kaniksu N.F. Christ 11571, Aug. 4, 1940 (NY, ID). Shoshone Co., 2 mi. S of Clarkia, Cronquist 6048, Aug. 7, 1949 (WTU, WS, ID, RSA, DS, NY, CAS, UC). MONTANA:

Glacier Co., Blackfoot Glacier, Glacier National Park, M. E. Jones s.n., Aug. 30, 1909 (POM, DS). Mineral Co., St. Regis R., 6 mi. W of Saltese, Cronquist 6726, July 21, 1950, (WS, WTU, NY). OREGON: Josephine Co., Mt. Elijah, Siskiyou Mts., 6100 ft., Whittaker SS 318-E, Aug. 9, 1949 (WS). Wallowa Co., 1 mi. W of Hat Point, Maguire & Holmgren 27023, Aug. 15, 1946 (DS, WS, POM, UC, WTU, NY).

Aster cusickii is one of the most distinctive of the aster species in its typical diploid form. However, the effects of polyploidy and hybridization often alter the distinctive features. This is particularly true of the characteristically abundant pubescence; many plants which fit the species in all other respects are nearly glabrous or only lightly pubescent.

The center of distribution of typical plants extends from the Wallowa Mountains of northeast Oregon into the mountains of central Idaho and north into the mountains and lower elevations of northern Idaho. A few collections from Montana, Canada and southeastern Washington are perhaps less typical but belong to this species. A remarkable discovery during the course of the study was three collections from the Siskiyou Mountains of southern Oregon and northern California which must be assigned to this species. This greatly enlarges the known distribution of the species and raises questions about its former distribution.

The asters from the Olympic and Cascade Mountains of northern Washington have traditionally been treated as A. foliaceus ssp. foliaceus, yet many specimens have striking similarities to plants of A. cusickii. This similarity, together with finding A. cusickii in the Siskiyou, supports the hypothesis that A. cusickii was once much more widespread than it is today. Its distribution appears to have included possibly all of the Cascade range from Washington to California and perhaps farther south in the Sierras. Therefore the asters of the mountains of western Washington appear to be closely allied to A. cusickii, from which they are now isolated by the prairies of eastern Washington. More collecting and chromosome counting is needed to establish the degree of relationship.

Some natural hybridization involving A. cusickii was discussed in the hybridization section. It appears to account for the plants upon which at least some of the names in synonymy under A. cusickii are based. Type specimens of A. hendersonii and A. eriocaulis are judged to be hybrids or hybrid derivatives from crosses between A. cusickii and A. idahoensis. They are here placed under A. cusickii because of a slightly stronger affinity to that species, although they possess recognizable traits of both.

The type specimen of A. cusickii var. lyallii was not seen, but the original description by Asa Gray indicates a strong similarity of this entity to A. cusickii. Cronquist

placed both lyallii and cusickii as separate varieties of A. foliaceus, but the traits by which lyallii is supposed to differ from cusickii are all in the direction of A. idahoensis, so that the type specimen of lyallii is also presumed to be a hybrid derivative of A. cusickii crossed with A. idahoensis. Even though these hybridizations do occur naturally, resulting in recognizably intermediate offspring, it seems best in this case to refer such offspring to the parent species with which they are most similar rather than maintaining a separate category to include them.

12. Aster jessicae Piper

Aster jessicae Piper, Erythea 6:30. 1898. (Type: Piper 1604, Palouse R. at Pullman, Whitman Co., Wash., Aug. 1893, WS! isotypes: DS! GH! NY! WTU!). Piper 2663, also from Pullman, is marked as the type in Piper's own hand at the U. S. National Herbarium, but is not cited in the original description.

Aster latahensis Henders. Contr. U. S. Nat. Herb. 5:201. 1899. (Type: Henderson 2987, American Ridge, Latah Co., Idaho, US; isotypes: GH! WS!).

Stems stout, erect to ascending, arising singly or in clusters up to 1.5 m. high, simple to usually branched above, the whole plant rather densely and uniformly cinereous pubescent, this strigose or spreading with curved or

curled hairs, soft to rather harsh and stiff; plants leafy throughout, the basal and lower leaves oblong-ovate, tapering or usually abruptly contracted to the winged petiole, up to 15 cm. long and 4 cm. wide, mostly early deciduous; middle and upper stem leaves short-petioled to sessile by a clasping, often somewhat auriculate base, obovate to lanceolate, often slightly constricted above the base, apex acute to acuminate, the larger leaves up to 15 cm. long and 3 (3.5) cm. wide, considerably reduced above, margins mostly entire but sometimes wavy; inflorescence narrowly racemose to more open and paniculate, branches mostly short or some up to 20 cm. long, quite leafy-bracteate with oblong-lanceolate bracts 5-30 mm. long and 1-10 mm. wide; heads usually numerous, medium-sized, the involucre 1-2 cm. broad and 6-10 mm. high; phyllaries usually strongly graduated to subequal in about 4 series, acute to acuminate or sometimes the outer obtusish, oblanceolate to linear, mostly with some chartaceous portion below or the outer sometimes wholly green, slight or no scarious margin, occasionally the outer enlarged and foliaceous and surpassing the inner, sparsely to densely pubescent on both surfaces; ray flowers 20-40, the ligules 1.5-2.5 mm. wide and 12-20 mm. long; pappus white to tawny; achenes pubescent.

Stream banks and fields. In the vicinity of Pullman, Washington, and Moscow, Idaho.

Representative specimens. IDAHO: Latah Co., 1 mi. S of Troy, Constance 1811, Sept. 7, 1936 (DS, UC, WS, WTU). American Ridge, common along roads, in fields and pastures, Henderson 2987, Sept. 5, 1897 (GH, WS). WASHINGTON: Same as type.

Aster jessicae is an unusual species in that it is a local endemic with a high chromosome number. It apparently has the smallest distribution of any species in this study, and it is the only species with the single chromosome number of 40II. The reasons for its limited range can only be speculated upon: it may be only recently derived; the particular combination of chromosomes does not allow more than a very narrow range of ecological tolerance; some other unknown factors are operating to limit its spread. No evidence is yet available to bear on any of these speculations.

The origin of A. jessicae is also open to speculation, but certain morphological features give clues to its progenitors. The dense soft pubescence is usually not as long nor as white as that of A. cusickii, but it is suggestive of this species, as are the often auriculate-clasping leaves, the occasional enlarged outer phyllary, and lower leaves with blades abruptly contracted to the petiole. On the other hand, the shape and branching of the inflorescence, number of inflorescence bracts, and usually imbricate phyllaries suggest features of A. occidentalis ssp.

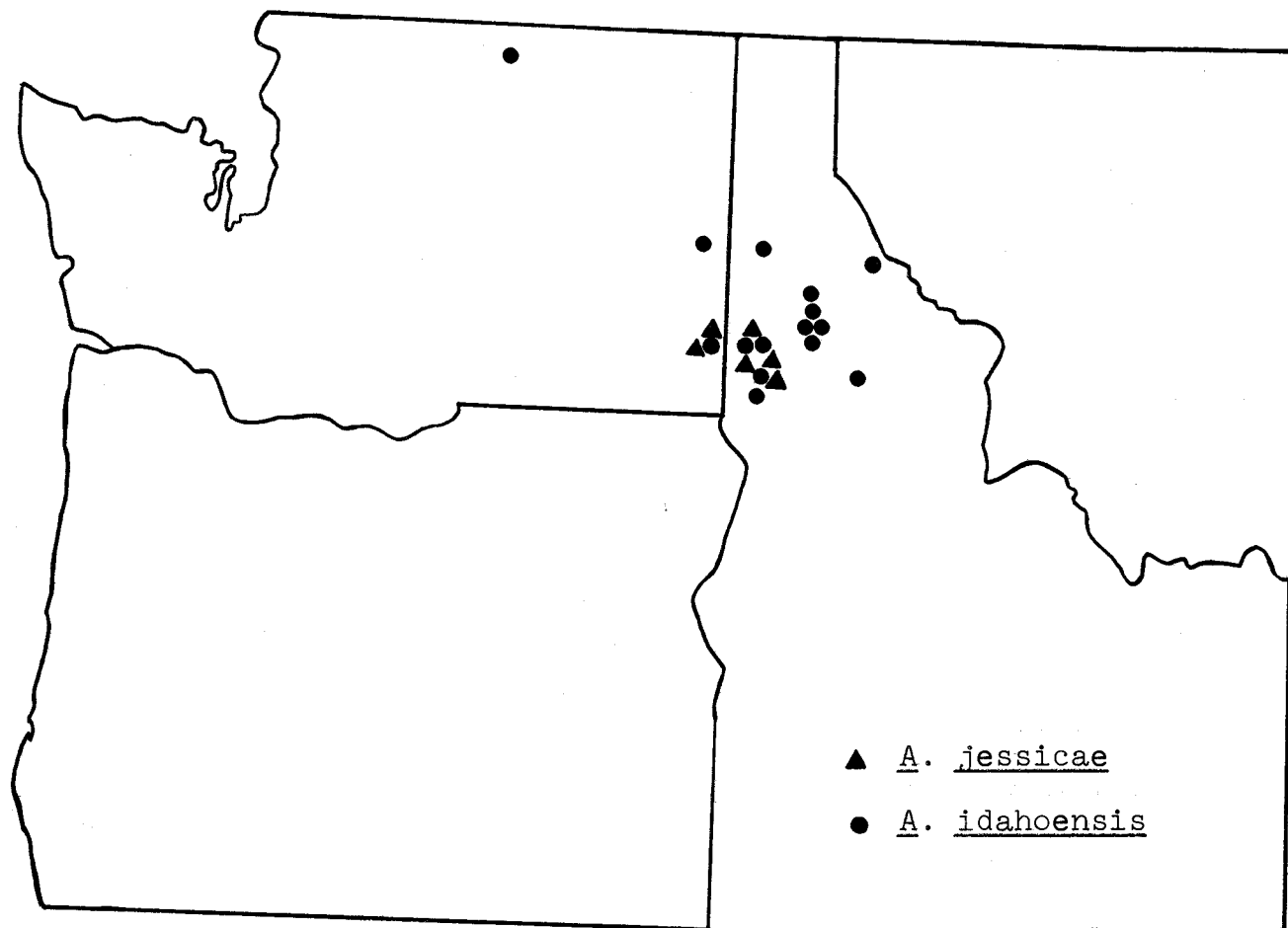


Figure 10. Distribution of Aster jessicae and A. idahoensis.

intermedius.

Aster occidentalis ssp. intermedius is the common aster in the Pullman-Moscow area. No collections of A. cusickii were seen from this immediate area, but the nearest collection, from Shoshone County, Idaho, is not more than 30 miles away. Closer populations may occur even today, but they may have been much closer in the past. If it is assumed that a tetraploid ( $n = 16$ ) A. cusickii crossed with a hexaploid ( $n = 24$ ) A. occidentalis ssp. intermedius, a doubling of their zygotic chromosome number would have resulted in 40 pairs of chromosomes. No experimental hybridizations have yet been carried out between these two taxa, but the morphological evidence strongly indicates them to be the progenitors of A. jessicae.

13. Aster idahoensis Dean, sp. nov.

Type: Dean 466, 2 mi. S of Clarkia along West Fork of St. Maries R., Shoshone Co., Idaho, Sept. 19, 1964, OSC!

Herbae perennes caudicibus apud basem lignosis. Rami floriferi foliosi. Capitula numerosa involucris squamis numerosis linearis angustissimis subaequalibus extimis ex toto viridibus extentis.

Rhizomes and usually several erect stems arising from a persistent woody crown; stems mostly brown, simple below and freely-branched above, up to 1.5 m. high, with low

longitudinal ridges giving a striate or angled appearance, glabrate below, gradually puberulent in lines above to rather uniformly so under the heads; basal and lower cauline leaves usually early deciduous, the lanceolate blade tapering to an acuminate apex and narrowly winged petiole, up to 15 cm. long and 1-2 cm. wide; middle and upper cauline leaves narrowly ovate to lanceolate, sometimes wider than the basal ones, up to 10 (12) cm. long and 2.5 cm. wide, gradually reduced above, sessile by a subclasping auriculate base, glabrous on both surfaces to lightly scabrous above, margins entire and scabrous; inflorescence an abundantly leafy, many-headed, often flat-topped panicle, the branches ascending, up to 40 cm. long, with many linear bracts; heads small to medium-sized, the involucre 8-20 mm. wide, 5-10 mm. high; phyllaries in 4-5 series, somewhat graduated to usually subequal or the outer occasionally longer, spreading to sometimes recurved, linear, mostly 0.5 mm. wide or less, acute to attenuate, outer ones wholly green or with only a small portion of the base chartaceous, inner ones usually not chartaceous more than half their length, margins slightly scarious below, mostly glabrous abaxially, lightly pubescent adaxially, ciliate on the lower margins; ray flowers 25-45, ligules violet to purple, 1-2 mm. wide, 9-15 mm. long; pappus white; achenes pubescent.

Roadside ditches and stream banks. Valleys of north-central Idaho to eastern Washington and western Montana.

Representative specimens. IDAHO: Kootenai Co., wet meadows, Collins, Piper 2910, July, 1898 (WS, NY). Clearwater Co., 6 mi. E of Bovill, Cronquist & Jones 5998, July 24, 1949 (ID, WS, DS, RSA, UC, NY, WTU). Idaho Co., Bimrick Meadows, Daubenmire 46276, July 23, 1946 (WS). Latah Co., 6 mi. N of Bovill, 3000 ft., Cronquist 6029, Aug. 6, 1949 (ID, WS, DS, UC, NY, RSA, WTU). Lewis Co., 2 mi. W of Winchester, Christ & Ward 8778, Aug. 25, 1937 (ID, NY). Nez Perce Co., Forest, Brown 13, Aug., 1896 (UC, DS, NY). Shoshone Co., 2 mi. S of Clarkia, 2900 ft., Cronquist & Jones 6049, Aug. 7, 1949 (ID, WS, DS, WTU, UC, NY, RSA). MONTANA: Ravalli Co., 7 mi. NE Lolo Hot Springs, Baker 14620, Aug. 17, 1956 (ID). WASHINGTON: Okanogan Co., Sinlahekin Cr., Fiker 2320, Aug. 8, 1936 (WS). Spokane Co., Hangsmans Creek, Suksdorf 9123, July 11, 1889 (WS). Whitman Co., low ground, Pullman, Piper 1605, Aug. 5, 1893 (DS), Aug. 12, 1893 (DS, NY, WTU, WS).

Like A. lentus and A. cusickii, A. idahoensis is being recognized as a species not only because of morphological uniqueness, but because it occurs at the diploid chromosome level. Although not previously named, plants of A. idahoensis were noted by Cronquist as being distinctive and possibly deserving of taxonomic recognition (29, p. 90).

Aster occidentalis ssp. intermedius appears to be the taxon most closely related to A. idahoensis, and taxonomically confusing variations occur where these two entities meet. Intergradation appears to be most striking in plants collected near Moscow, Idaho, of which representative collections include Gail s.n., Baker 14446, and Dean 374. Most of these plants have the strongly imbricate phyllaries and reduced branching characteristic of A. occidentalis ssp. intermedius and probably should be thus classified.

Hybridization of A. idahoensis with A. cusickii is discussed under the latter species. Aster idahoensis probably also hybridizes with A. occidentalis ssp. occidentalis, but the evidence is very meager. The only plants of A. o. ssp. occidentalis which were hexaploid, Dean 458, appeared questionably to contain genes of A. idahoensis.

#### 14. Aster occidentalis (Nutt.) T. and G.

##### 14a. Aster occidentalis ssp. occidentalis

Aster spathulatus Lindl. in Hook. Fl. Bor. Am. 2:8. 1834.

A. subspathulatus Rydb. Mem. N. Y. Bot. Gard. 1:395.

1900. (Type: Richardson s.n., Bear Lake and Fort Franklin on Mackenzie R., Northwest Territory, Canada, K; isotype: GH!). Not A. spathulatus Lag. ex Nees, Aster. 283. 1832.

Tripolium occidentale Nutt. Trans. Am. Phil. Soc. II. 7:296.

1840. A. occidentalis T. & G. Fl. N. Am. 2:164. 1841.

A. occidentalis var. typicus Cronq. Am. Midl. Nat.

29:463. 1943. (Type: Lewis s.n., muddy streams, Rocky Mts., PH; isotype: GH!).

Aster andinus Nutt. Trans. Am. Phil. Soc. II. 7:290. 1840.

(Type: Nuttall s.n., Thornberg's Ridge (Wyo.), Rocky Mts., lat. 42 degrees, PH; isotype: GH! NY!).

Aster adscendens Lindl. in Hook. var. fremontii T. & G. Fl.

N. Am. 2:503. 1841. A. fremontii Gray, Syn. Fl. N. Am.

1<sup>2</sup>:191. 1884. (Type: Fremont s.n., Wind River chain of the Rocky Mts., above 7000 feet, GH! isotype: NY!).

Aster fremontii var. parishii Gray, Syn. Fl. N. Am. 1<sup>2</sup>:192.

1884. A. occidentalis var. parishii Ferris, Madrono

15:128. 1959. (Type: Parish & Parish 180, Bear

Valley, San Bernardino Co., Calif., Aug., 1882, GH! isotype: NY!).

Aster adscendens var. yosemitanus Gray, Syn. Fl. N. Am.

1<sup>2</sup>:191. 1884. A. yosemitanus Greene, Fl. Franciscana.

383. 1897. A. occidentalis var. yosemitanus Cronq. Am.

Midl. Nat. 29:467. 1943. (Type: Hooker & Gray s.n., near Vernal Fall, Yosemite Nat'l. Park, Calif., 1877, GH!).

Aster durbrowii Eastwood, Proc. Cal. Acad. ser 3, Bot.

2:292, 1902. (Type: Eastwood s.n., Horse Corral Meadows, Fresno or Tulare Co., Calif., July 11, 1899, CAS!).

Aster corymbiformis Rydb. Bull. Torrey Club 31:655. 1904.

(Type: Shear 3460, Westcliffe, Custer Co., Colo., NY).

Aster copelandii Greene, Leaflet Bot. Obs. 1:200. 1906.

(Type: Copeland 3867, 6000 feet on Mt. Eddy, northern Calif. (Siskiyou Co.), Sept. 7, 1903, ND; isotypes: UC! GH! POM! WS! US).

Aster delectabilis Hall, U. Cal. Pub. Bot. 3:82. 1907. A.

adscendens var. delectabilis Jeps. Man. Pl. Calif.

1047. 1925. A. occidentalis var. delectabilis Ferris, Madrono 15:128. 1959. (Type: Smith 76, Mill Creek, San Bernardino Mts., San Bernardino Co., Calif., Aug. 30, 1904, UC!).

Aster williamsii Rydb. Bull. Torrey Club 37:136. 1910.

(Type: Williams s.n., North Fork Clear Cr., Johnson or Sheridan Co., Wyo., Aug. 12, 1898, NY!).

Aster paludicola Piper, Contr. U. S. Nat. Herb. 16:210.

1913. (Type: Piper s.n., Darlingtonia swamps, Eight Dollar Mt., Josephine Co., Oregon, Aug. 15, 1907, US).

Aster misellus Piper, Proc. Biol. Soc. Wash. 33:105. 1920.

(Type: Cusick 3636, Strawberry Lake, Grant Co., Oregon, Sept. 9, 1910; syntype: Cusick 3625, same locality and date, WS! WTU!).

Stems slender, erect to ascending from a slender rhizome or small woody crown, green to tawny or often reddish, mostly 2-10 dm. high, usually glabrous below, pubescent in lines above and uniformly under the heads, to

nearly glabrate throughout; basal and lower stem leaves often persistent to deciduous, mostly narrowly oblanceolate, acuminate, tapered to a narrowly winged petiole, up to 15 cm. long and 15 mm. wide, glabrous except for the scabrous and sometimes faintly toothed margin; middle and upper cauline leaves gradually reduced above, oblanceolate to linear, acuminate, sessile by a clasping to non-clasping base, mostly less than 15 cm. long and 15 mm. wide, mostly 7-20 times longer than wide, glabrous, margins entire and scabrous; inflorescence usually a terminal, relatively few-branched cymose panicle, the branches ascending to spreading, up to 15 cm. long, with usually few spreading linear bracts; heads 1-15 or 20 but mostly less than 10, medium-sized, the involucre 10-18 mm. wide and 6-10 mm. high; phyllaries somewhat imbricate to usually subequal in 3-4 series, mostly loose and spreading, acute to acuminate or attenuate, sometimes purple-tipped, the outer often wholly green or usually with at least a small chartaceous portion at base, the inner increasingly chartaceous, margins scarcely to evidently scarious, ciliate, glabrous on both surfaces to sparingly pubescent; ray flowers 20-40, lavender to violet or purple, 1-2 mm. wide and 10-18 mm. long; pappus white to tawny or reddish; achenes pubescent.

Roadsides, stream banks and meadows, mostly at higher elevations. Cascades and Sierras from northern Washington to southern California and possibly to Lower California,

east to Alberta, Colorado and possibly New Mexico.

Representative specimens. CALIFORNIA: Humboldt Co., Horse Mt., 4600 ft., Tracy 16402, Aug. 16, 1939 (UC). Inyo Co., N Fk. of Bishop Cr., Peirson 2518, Aug. 7, 1921 (RSA). Mono Co., Conway Summit, 5 mi. N of Mono Lake, Rose 50168, July 25, 1950 (CAS, NY). Nevada Co., Donner Lake, Heller 7146, Aug. 11, 1903 (RM, WTU, UC, NY, POM). San Bernardino Co., S of Bear Lake, 7260 ft., Clokey 7011, Sept. 13, 1936 (RM, NY, POM, WTU, RSA, UC). Siskiyou Co., outlet of Castle Lake, Heller 15760, July 24, 1940 (WTU, UC, WS, NY, DS). Trinity Co., Black Rock Lake, North Yolla Bolly Mts. 6500 ft., Munz 16729, July 20, 1951 (DS, CAS, RSA). Tulare Co., near Mineral King P.O. and Cold Spring Public Camp, 7900 ft., Ferris & Lorraine 11217, Aug. 23, 1946 (RM, CAS, RSA, WTU, DS). COLORADO: Lake Co., Twin Lakes, 9400 ft., Clokey 3492, Aug. 15, 1919 (POM, CAS, UC, NY, WSU). Larimer Co., Estes Park, Osterhout 529, Aug., 1895 (RM). Teller Co., Catamount Cr., Penland 3929, July 31, 1959 (NY). IDAHO: Caribou Co., 1.5 mi. N of Soda Springs, Bear River, Christ 8999, Sept. 6, 1937 (NY). Custer Co., Stanley Lake, 6500 ft., Thompson 13946, July 25, 1937 (NY, WTU, UC, CAS). Kootenai Co., Lakeview, Sandberg, McDougal & Heller 868, Aug. 6, 1892 (CAS, POM, NY). MONTANA: Beaverhead Co., Pintlar Cr., 14 mi. N of Wisdom, Hitchcock & Muhlick 12606, July 21, 1945 (DS, CAS, WS, WTU, UC, NY). Flathead Co., Bigfork, near Flathead Lake, Jones s.n., July 28, 1908

(POM). Madison Co., Beaver Cr., Hitchcock & Muhlick 15116, July 30, 1946, (WS, WTU, NY). NEVADA: Nye Co., 1 mi. S of Potts R. S., Monitor Valley, Maguire & Holmgren 25762, July 14, 1945 (WS, WTU, NY, UC, CAS). Washoe Co., 7 mi. NE of Incline Beach Jct., Lake Tahoe, 8300 ft., Mason 12355, Aug. 1, 1940 (RM, POM, WTU, UC, WS, NY, CAS, RSA). NEW MEXICO: Taos Co., Carson Forest, Rio Fernandez de Taos Canyon, Eggleston 19289, Aug. 24, 1923 (NY). OREGON: Crook Co., Big Summit Mdns., Ochoco Mts. between Pine & Mitchell, 5000 ft., Cronquist 7760, Aug. 7, 1953 (WS, UC, NY, WTU). Lane Co., 8 mi. W of McKenzie Pass, Cronquist 6119, Aug. 29, 1949 (WS, NY, UC, RSA, ID, WTU). Wallowa Co., Wallowa Mts., 8000 ft., Cusick 2495, Aug. 30, 1900 (RM, WS, POM, UC, NY). UTAH: Kane Co., Duck Cr. Lake, Dixie National Forest, 8500 ft., Maguire 19657, July 16, 1940 (WS, NY). Uinta Co., Long Park Dam site, Uinta Mts., Maguire 17691, Aug. 21, 1939 (NY, UC). WASHINGTON: Kittitas Co., Table Mt., 6200 ft., Thompson 9807, Aug. 9, 1933 (WTU). Okanogan Co., bog near Wauconda summit, 3500 ft., Thompson 10943, July 4, 1934 (WTU, NY, POM, CAS). WYOMING: Sheridan Co., Dome Lake, Nelson 2396, July, 1896 (RM, CAS). Sublette Co., Green River Lakes, 8000 ft., Payson & Payson 4524, Aug. 4, 1925 (WS). Uinta Co., Evanston, Williams s.n., July 10-12, 1897 (NY).

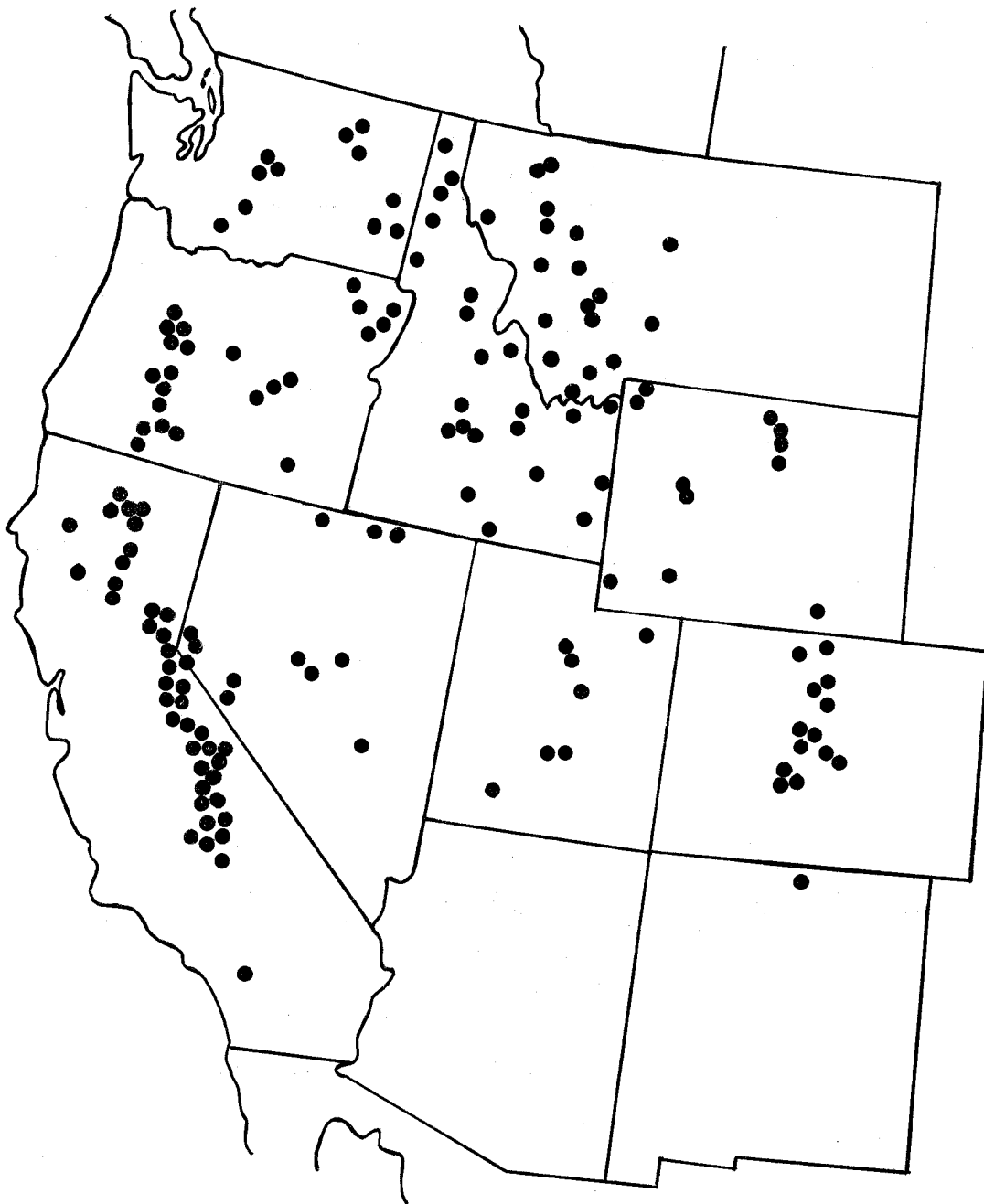


Figure 11. Distribution of Aster occidentalis  
ssp. occidentalis.

Aster occidentalis ssp. occidentalis is a widespread entity usually found at higher elevations throughout the mountains of the west. As presently defined it includes a considerable amount of local variation. The large number of synonyms indicates the heterogeneous assemblage which this subspecies now embraces. Because of this diversity and lack of sharp definition, this taxon is probably the least satisfactory of all those in the study. Yet the recognition of each vocal variant is unjustified in view of the complete intergradation of one form into another.

One reason for the morphological heterogeneity of this subspecies is that it is largely, or perhaps entirely, polyploid. Thus far it is known mostly at the tetraploid level, with no diploid and only one hexaploid count having been made. More important to diversity than polyploidy is the fact that in adjacent geographical areas different taxa are involved in contributing to the genetic composition of A. o. ssp. occidentalis. Thus A. o. ssp. occidentalis illustrates, perhaps better than any other of the polyploid species, a nomenclatural category consisting simply of plants with a similar combination of characteristics. The category includes those plants which are relatively simple and few-branched, with usually less than 10 heads, narrow, acute leaves (usually less than 1 cm. wide), and narrow, acute, subequal to equal phyllaries. The phyllaries may sometimes be slightly imbricate and sometimes obtusish, but

then they are usually wholly green. Since plants having this complement of traits may have rather diverse genetic backgrounds, this category is quite artificial compared with a diploid species whose members all have a somewhat similar origin.

In the Cascade Mountains of southern Washington and Oregon, this subspecies is common in high mountain meadows, but comes into contact with both A. foliaceus ssp. parryi and A. occidentalis ssp. intermedius at slightly lower elevations. This latter subspecies occurs in part as a diploid in this area and is definitely postulated as a progenitor of A. o. ssp. occidentalis. In fact, subspecies occidentalis has probably diverged from subspecies intermedius as a subalpine ecotype. Farther south in the Sierra Nevada Mountains of California, A. adscendens apparently competes directly with A. o. ssp. intermedius on the eastern slope and is able to reach fairly high elevations. Where this occurs, contact with A. o. ssp. occidentalis results in considerable intergradation.

The complexity of the A. o. ssp. occidentalis - A. foliaceus ssp. parryi relationship in the Cascades of Oregon is discussed under the latter species. However, the situation between these two taxa in the northern Rocky Mountains, particularly in Montana, appears to be even more confusing. Their artificial separation primarily on the basis of leaf size is admittedly weak and often quite

unsatisfactory; yet a lumping of taxa at this point may be no more justified than the same treatment of other intergrading taxa and may not result in a more natural classification. Unfortunately, no field work was done in this area and no chromosome counts were obtained. Further study may well indicate the advisability of recognizing fewer taxa at the species level, but more infraspecific categories.

Farther south in the Rockies, as in the Sierras of California, A. adscendens is the species most commonly confused with A. o. ssp. occidentalis. This point is illustrated by part of the type collection of the latter. The holotype was not seen, but an isotype sheet from the Gray Herbarium, consisting of two plants, was studied. One of the plants approaches A. adscendens in having obtusish outer phyllaries which are only half as long as the inner. However, they are characteristic of A. o. ssp. occidentalis in being wholly herbaceous. The other plant on the sheet shows this latter taxon's traits in having acute, subequal phyllaries.

Concerning other type specimens, those of A. andinus, A. spathulatus, and A. fremontii are all reasonably typical of A. o. ssp. occidentalis. Aster parishii and A. delectabilis are similar to each other in features of the involucre, but differ in size and number of leaves. The phyllaries are not typical of A. o. ssp. occidentalis in that the outer ones are often scarious-margined and much shorter

than the inner, although they are quite acute. These features indicate possible introgression from A. hesperius, but the combination of traits, including habitat and tetraploid chromosome number (Table I, accession 390), is closer to A. o. ssp. occidentalis.

The taxon called A. occidentalis var. yosemitanus by Cronquist (14) is at best only an anomalous variant from A. o. ssp. occidentalis and apparently has always lacked certain definition. The determination of many herbarium specimens illustrates this latter statement. Contrasting characteristics of different specimens which have been called A. o. var. yosemitanus include long linear leaves and short lanceolate leaves; clasping and non-clasping leaf bases; imbricated and equal phyllaries; widely spreading branches and ascending to strict branches. Cronquist characterized the variety by saying "it is of rather sporadic occurrence, and is distinguishable only with difficulty from the typical form of the species" (14, p. 468). Therefore, owing to this lack of distinction and definition, this entity is here also reduced to synonymy.

14b. Aster occidentalis ssp. intermedius (Gray) Piper

Aster occidentalis (Nutt.) T. & G. var. intermedius Gray,

Syn. Fl. N. Am. 1<sup>2</sup>:192. 1884. A. occidentalis ssp.

intermedius Piper, Cont. U. S. Nat. Herb. 11:574.

1906. (Type: Suksdorf 62, Falcon Valley (near

Laurel), Klickitat Co., Wash., Sept. 5, 1882, GH!

isotypes: UC! WS!).

Aster vallicola Greene, Pitt. 4:219. 1900. (Type: Greene  
s.n., Pine Valley above Palisade, Nevada, July 25,  
1896, ND!).

Stems slender, ascending to erect, often several from a small woody crown, 2-10 dm. high, few to many branches above, usually lightly pubescent, the pubescence uniform under the heads and often in lines down to the glabrous lower stem, or occasionally the whole plant densely pubescent with spreading and strigose hairs intermixed; lower leaves usually long-petioled and lanceolate or narrowly oblong, persistent to often deciduous, up to 20 cm. long and 1.5 (2) cm. wide, the petiole up to half the length, glabrous and entire; middle stem leaves subpetiolate to sessile, linear to oblanceolate, apex acute to acuminate, mostly glabrous with scabrous and entire margins or occasionally a few low teeth, mostly less than 15 cm. long and 1 cm. wide; upper stem leaves rather markedly reduced, linear and bractlike in the inflorescence; inflorescence a few- to many-headed panicle, the branches spreading to ascending, up to 20 cm. long, with often numerous, ascending linear bracts, these 0.5-5 mm. wide and 0.5-3 cm. long; heads small to medium-sized, the involucre 8-15 mm. broad and 5-8 mm. high; phyllaries moderately to usually strongly graduated in 4-5 series, narrow and linear, the outer

sometimes wholly green but usually with a chartaceous base and narrow scarious margin, obtusish to mostly acute and mucronate, the inner acute to acuminate or attenuate, glabrous abaxially, sparsely pubescent adaxially and ciliate marginally; ray flowers 30-50, the ligules mostly violet or purple, 1-2 mm. wide and 10-15 mm. long; pappus white to tawny or sordid; achenes pubescent.

Roadsides, ditch banks and meadows at low to medium elevations. Eastern edge of the Cascades in Washington east to western Idaho, south to Grande Ronde R. valley in Oregon and south along the east slope of the Cascades to the Sierras of north and central California, and mountains of northern Nevada.

Representative specimens. CALIFORNIA: Fresno Co., Blaney Mdws., Hot Springs, 7800 ft., Raven 4893, Aug. 2, 1952 (CAS). Modoc Co., W of Hwy. 395, S of Alturas, Grant & Schneider 8093, July 20, 1947 (UC, WTU). Mono Co., Crooked Creek, 6750 ft., Howell 14327, Aug. 7, 1938 (WTU, UC, CAS). Plumas Co., 5 mi. SE of Graeagle, Sulphur Cr., Hwy. 89, Balls 15872, Sept. 16, 1950 (RSA). Siskiyou Co., Mt. Eddy, Copeland 3856, Sept. 8, 1903 (UC, NY, POM). IDAHO: Latah Co., 6.5 mi. SW of Potlatch on Moscow Mt. road, Dean 374, Sept. 19, 1961 (OSC). NEVADA: Douglas Co., E side of Lake Tahoe, 6300 ft., Nichols & Lund 687, Aug. 24, 1937 (NY). OREGON: Baker Co., Powder R. Mts., Piper 2517, Aug., 1896 (WS). Hood River Co., Baldwins, near Mt. Hood, Henderson

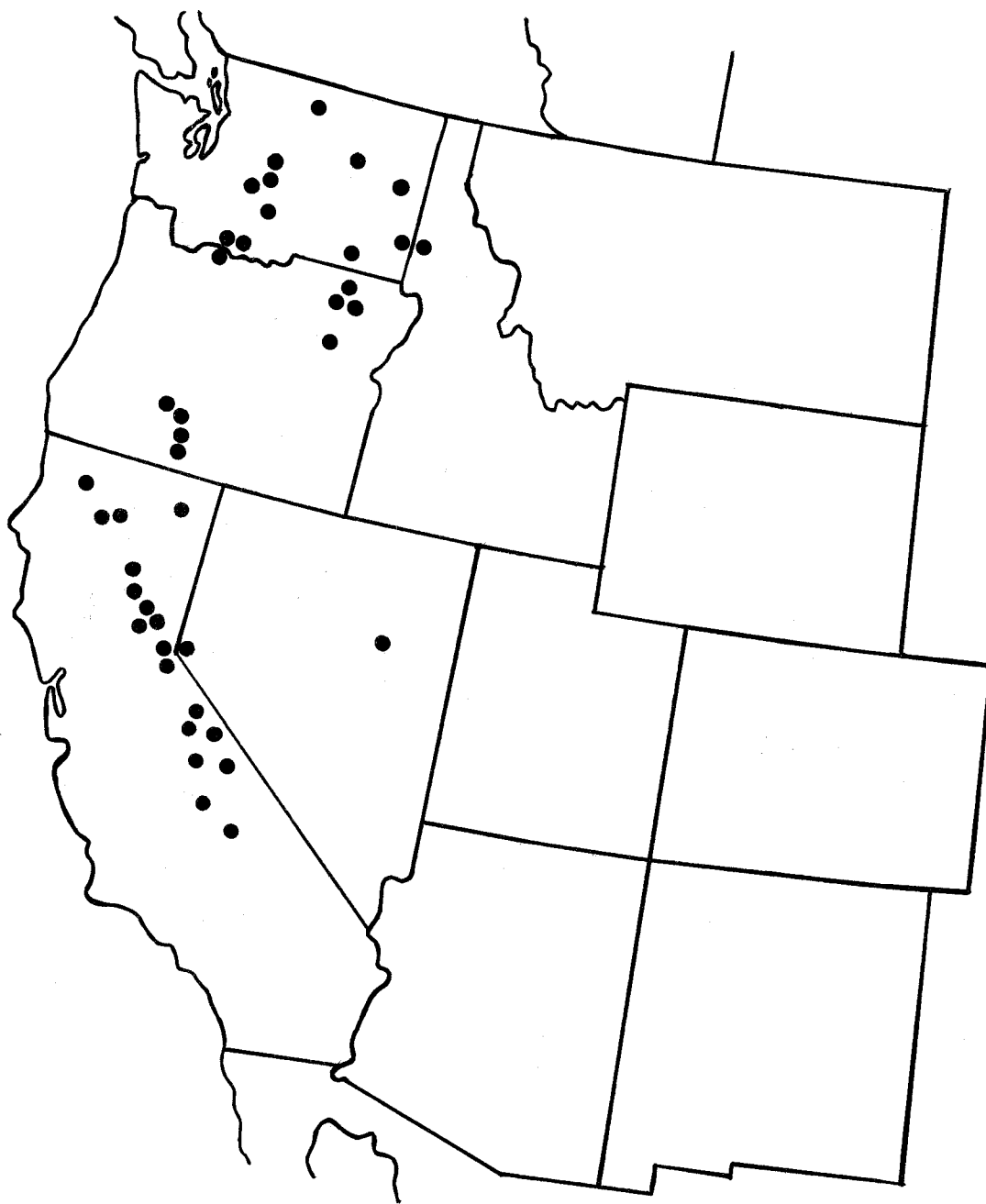


Figure 12. Distribution of *Aster occidentalis* ssp. intermedius.

s.n., Aug. 24, 1882 (NY). Wallowa Co., Little Minam R., 3500 ft., Cusick 3407, Aug. 17, 1909 (WS, WTU, RSA, NY, UC). WASHINGTON: Chelan Co., Nigger Cr., 2500 ft., Thompson 12608, Aug. 19, 1935 (WTU, CAS, NY). Klickitat Co., Western Klickitat Co., Suksdorf 768, Sept. 16, 1885 (WS, NY, UC, DS). Spokane Co., Spangle, Suksdorf 9129, Aug. 2, 1889 (WS). Whitman Co., 3 mi. N of Colfax, Cronquist 6133, Sept. 24, 1949 (WS, WTU). Yakima Co., upper Naches R., 3500-4000 ft., Thompson 12599, Aug. 17, 1935 (WTU, UC, DS, NY, CAS).

The diploid members of this subspecies have thus far been found only along the eastern slope of the Cascade Mountains in Oregon and at middle to upper elevations near the east side of the Sierra Nevadas in California. From these locations, polyploid derivatives appear to have diverged in two directions. Those moving to higher elevations have differentiated to form the basis of A. o. ssp. occidentalis. Those moving to lower elevations or more arid habitats have also become visibly different, but still form an intergrading series with the diploids. The decision to place the diploids of A. occidentalis with ssp. intermedius rather than ssp. occidentalis was somewhat arbitrary, since they are nearly intermediate and provide a definite connecting link between the two. However, the imbricate phyllaries, number of heads, and branching pattern are a bit more characteristic of ssp. intermedius.

The preponderance of herbarium specimens, and those most like the type specimen of this subspecies, were collected in the semiarid regions of Washington. Here the majority of the plants are polyploids, as shown by the chromosome counts obtained in this study. Both tetraploids and hexaploids occur without marked differences between them. Two collections from the locality of the type collection, Dean 487 and 489, indicate that the type was probably tetraploid (see Table I).

Wherever this subspecies comes into contact with closely related taxa, intergradation is usually evident. The areas and species involved include A. idahoensis in the vicinity of Moscow, Idaho; A. adscendens in the valleys of northeast Oregon and southwest Washington, and also along the eastern base of the Cascades and Sierras in Oregon and California respectively; and A. o. ssp. occidentalis at higher elevations in the Cascades and Sierras. Each of these hybridization problems is discussed more completely under each of the three taxa listed.

15. Aster foliaceus Lindl. in DC.

15a. Aster foliaceus ssp. foliaceus.

Aster foliaceus Lindl. in DC. Prodr. 5:228. 1836. A. foliaceus var. typicus Onno, Bibl. Botanica 106:7. 1932.

(Type: Fischer s.n., Unalaschka.).

Aster amplissimus Greene, Proc. Acad. Phila. 1895:551. 1896.

(Type: Greene s.n., wet subalpine meadows near timberline on Mt. Rainier, Washington, Aug. 21, 1889, ND!).

Stems erect to ascending, 2-6 dm. high, often reddish, simple and monocephalous to few-branched with 4-6 heads, nearly glabrous to densely tomentose under the heads and less so below, or in lines from the leaf bases; lower leaves usually persistent, or deciduous in Alaska material, up to 25 cm. long and 4 cm. wide, the oblanceolate to obovate blade tapering into a winged, scarcely clasping petiole; cauline leaves only gradually reduced upwards, usually few and well spaced to sometimes more numerous, broadly lanceolate or oblanceolate, sessile by a clasping base, usually not much auriculate, leaves rather thin and glabrous, margins scabrous, entire to faintly serrate; heads large, the involucre 1.5-2.5 (3) cm. broad, 10-15 mm. high; phyllaries mostly green and herbaceous in 3-4 equal series or some of the outer enlarged and foliaceous, broadly oblanceolate to lanceolate, obtuse to acute, glabrous abaxially but strigose adaxially, ciliate, the outer often with crisped or curled margins, chartaceous at the base in more numerous-headed plants; ray flowers 20-40, the ligules reddish-purple to violet or purple, 2-3 mm. wide, 12-20 mm. long; pappus white to tawny; achenes strigose.

Moist places in mountains, to the seacoast. Northern Washington to Alaska and the Aleutian Islands at 60 degrees

north latitude; also possibly in the mountains of northern Idaho and Montana.

Representative specimens. CANADA: British Columbia, 3 mi. N Takla Landing, McCabe 7904, July 18, 1940 (UC). British Columbia, Chipuin Mt. in Marble Mts., 6000 ft., Thompson & Thompson 548, July 21, 1938 (UC, NY, CAS, WTU, ID). ALASKA: Aleutian Islands, Unalaska, Sommer Bay, Hultén 7617, Aug. 15, 1932 (NY, CAS); Eyerdam 2255, Aug. 22, 1932, (NY, CAS). Evans Island, Eyerdam 7110, Aug. 25, 1948 (WS); Eyerdam 7212, Aug. 25, 1948 (ID). IDAHO: Shoshone Co., Stevens peak, 6500 ft., Leiberg 1443, Aug. 3, 1895 (POM, NY, DS). MONTANA: Flathead Co., 6 mi. NE of Echo Lake, 6500 ft., Rogers & Rogers 1283, 1284, Aug. 28, 1942 (WS, NY). WASHINGTON: Clallam Co., Seven Lakes Basin, G. N. Jones 8216, 8283, 8306, Aug. 24, 1935 (WTU). Kittitas Co., base of Iron Pk., upper N Fk. Teanaway R., Kruckeberg 2590, Aug. 7, 1950 (WS, UC, RSA, NY, WTU). Okanogan Co., 2 mi. W of Gilbert, 5000 ft., Hitchcock 8068, Aug. 4, 1942 (UC, WTU, WS, DS). Snohomish Co., Mt. Pugh, 7000 ft., Thompson 14331, Aug. 18, 1938 (CAS, WTU, NY, WS, UC, RSA, DS).

Aster foliaceus ssp. foliaceus is the predominant aster in the Olympic and Cascade Mountains of northwestern Washington. Its distribution extends north through the mountains of British Columbia to Alaska, where it comes down to sea level and extends out along the Aleutian Island

chain. The similarity of the plants of this subspecies in Washington to the plants of A. cusickii was noted in the discussion of the latter species, where the speculation was also made that A. cusickii is one progenitor of A. f. ssp. foliaceus. The only chromosome counts so far available show counts of 8II and 16II for A. cusickii and 32II for A. f. ssp. foliaceus. Thus the latter may be a polyploid derivative of the former.

Along the Alaska coast A. foliaceus appears to intergrade freely with A. subspicatus, so that taxonomic separation of the two species is quite difficult. In fact Hultén, in his Flora of Alaska and Yukon (33, p. 1497), stated that the two taxa are conspecific in Alaska and the Yukon, and he placed A. foliaceus in synonymy under A. subspicatus. Cronquist later argued for retention of both taxa (15), and cited a personal communication with Hultén in which Hultén agreed there were some morphological differences between the two. Hultén agreed that plants most typical of A. foliaceus are found on the Aleutian Islands and are usually lower in stature and monocephalous, and have entire leaves and more completely herbaceous phyllaries. Conversely, plants most typical of A. subspicatus are found on the Alaska mainland and are taller with several to many heads, and have serrate leaves and scarious margins on the outer phyllaries. In accordance with this later viewpoint, as stated by Cronquist, Hultén recognized

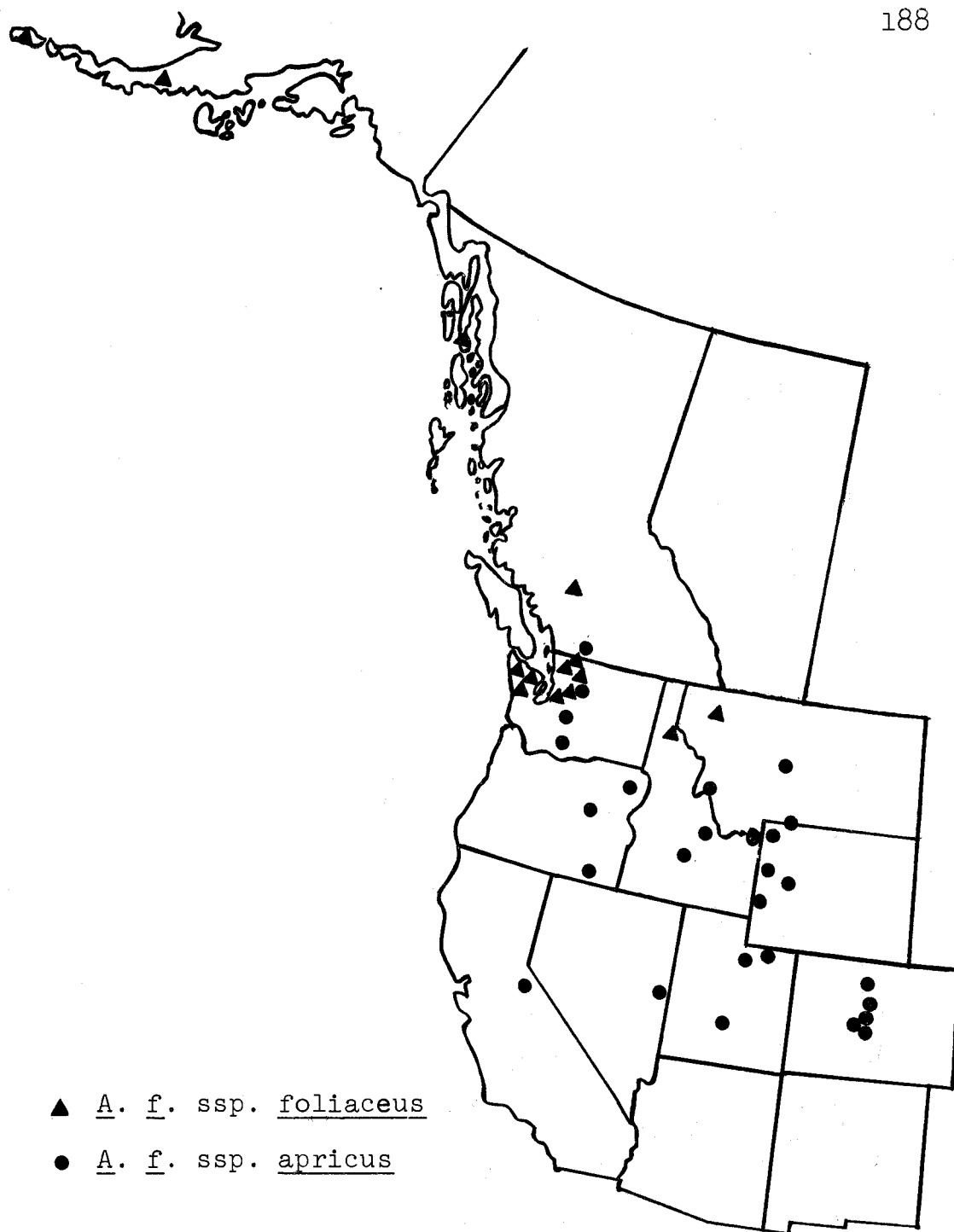


Figure 13. Distribution of *Aster foliaceus* ssp. *foliaceus* ssp. *foliaceus* and *A. f. ssp. apricus*

A. foliaceus as a species in his more recent second edition of Flora of the Aleutian Islands (34, p. 341).

In spite of the differences listed above, which generally separate A. foliaceus from A. subspicatus in Alaska, the delineation appears to be very tenuous. I am inclined to agree with Hult  n's earlier opinion that the two are conspecific in the far north. However, since I was unable to visit Alaska during the study and no living plants were obtained, I will remain conservative for the present time and treat the assemblage as two species. Further reason for being conservative is that considerable name changing would be necessary if the two were merged. Aster subspicatus is the older name of the two. Therefore A. foliaceus would no longer be available, and a new name would have to be applied to all of the plants presently known by that name in North America south of Alaska.

15b. Aster foliaceus ssp. apricus (Gray) Piper

Aster foliaceus var. apricus Gray, Syn. Fl. N. Am. 1<sup>2</sup>:193.

1884. A. apricus Rydb. Mem. N. Y. Bot. Gard. 1:396.

1900. A. foliaceus ssp. apricus Piper, Contr. U. S. Nat. Herb. 11:573. 1906. (Type: Wolf & Rothrock 521, Union Pass, Colo., 1873, GH! isotype: NY!).

Aster incertus A. Nels. Bot. Gaz. 37:269. 1904. (Type: Nelson 7924, Telephone Mines, Albany Co., Wyoming, Aug. 2, 1900, RM! isotypes: UC! GH! US).

Stems usually cespitose and decumbent, 1-2 (3) dm. high, rather glabrous below to more or less densely pubescent under the heads; basal leaves usually persistent, subpetiolate, oblanceolate, 5-15 cm. long, 5-15 mm. wide, glabrous or lightly pubescent on the upper surface, margins scabrous and entire; cauline leaves similar to the basal, sessile, not much reduced; inflorescence terminal, usually monocephalous to few-headed; heads medium-sized to large, the involucre 12-20 mm. wide, 7-12 mm. high; phyllaries mostly wholly green, broadly linear or lanceolate, loose and spreading in 2-4 series, the outer mostly obtuse, equaling or sometimes surpassing the more acute inner ones, usually glabrous abaxially and soft-pubescent adaxially, ciliate marginally; ray flowers 20-40, the ligules rose-purple to deep violet, 1.5-2.5 mm. wide, 10-20 mm. long; pappus white to tawny; achenes pubescent.

Alpine or subalpine meadows. Mountains of southern British Columbia to northern California, east to Montana and Colorado.

Representative specimens. CANADA: British Columbia, Mts. near Skagit R., Macoun 76849, June 23, 1905 (NY). CALIFORNIA: Alpine Co., Sonora Pk., Albertus 360, Sept. 8, 1936 (UC). COLORADO: Summit Co., Climax, Clokey 3504, Aug. 7, 1919 (NY, CAS, WTU, UC, DS, POM, RM). IDAHO: Fremont Co., Targhee Pk., 14 mi. N of Macks Inn. Christ 19062, July 16, 1949 (NY, ID). MONTANA: Carbon Co., 23 mi.

SW of Red Lodge, Beartooth Mts., Cronquist 8071, Aug. 5, 1955 (NY, WTU, UC, WS, RSA). Park Co., 3 mi. E Cooke City, 8000 ft., Witt 1400, Aug. 27, 1948 (NY, WTU, WS, RSA, CAS). NEVADA: White Pine Co., Johnson Lake, Snake Cr. Canyon, Snake Cr. Range, Holmgren & Tillett 10761, Aug. 4, 1954 (NY, UC). OREGON: Harney Co., head of Kiger Cr., Steens Mt., Cronquist 8804, July 29, 1959 (RSA, UC, WTU). Wallowa Co., Aneroid Lake, Peck 18020, July 29, 1933 (DS, NY). UTAH: Summit Co., above Henry's Fork Lake, 10,850 ft., Maguire, et al. 14389, Aug. 4, 1936 (UC, NY). WYOMING: Albany Co., Medicine Bow Range, Libby Flats, 10,500 ft., Finzel 143, Aug. 15, 1958 (RM). Park Co., Wyoming Cr., Beartooth Range, Johnson 254b, Aug. 19, 1959 (RM). Sublette Co., Green River Lakes, 10,000 ft., Payson & Payson 4671, Aug. 11, 1925 (RM).

Aster foliaceus ssp. apricus is only provisionally retained as a recognized entity until more information can be learned about it. No living material was obtained for this study and consequently no chromosome counts or reproductive data were acquired. Herbarium specimens constituted the primary source of information, and upon this basis the taxon can be fairly well delimited using distribution, size of the plants, and type of involucre as criteria. Even so, there is marked similarity with and intergradation into the two other subspecies of A. foliaceus.

15c. Aster foliaceus ssp. parryi (D.C. Eat.) Dean, comb.  
nov.

Aster adscendens Lindl. in Hook. var. parryi D.C. Eat. Bot.  
King Exp. 139. 1871. A. foliaceus var. parryi Gray,  
Syn. Fl. N. Am. 1<sup>2</sup>:193. 1884. A. foliaceus var.  
frondeus Gray, loc. cit., (based on A. adscendens var.  
parryi, and thus is an illegitimate superfluous name).  
A. frondeus Greene, Proc. Acad, Phila. 1895:551. 1896,  
(based on A. foliaceus var. frondeus in part, but as  
no lectotype was given, this is also an illegitimate  
name). A. foliaceus ssp. frondeus Piper, Contr. U.S.  
Nat. Herb. 11:573. 1906, (illegitimate name).  
(Lectotype, by Cronquist (29, p. 82): Parry 417,  
latitude 39-40 degrees, Colo., 1862, GH! isotype: NY!).

Aster foliaceus var. canbyi Gray, Syn. Fl. N. Am. 1<sup>2</sup>:193.  
1884. A. canbyi Vasey ex Rydb. Fl. Colo. 354, 356.  
1906. (Type: Vasey 262, White River, Colo., Oct.,  
1868, GH! isotype: NY!). Not A. canbyi Kuntze, Rev.  
Gen. 315. 1891.

Aster foliaceus var. burkei Gray, Syn. Fl. N. Am. 1<sup>2</sup>:193.  
1884. A. burkei Howell, Fl. N. W. Am. 1:310. 1900.  
(Type: Burke s.n., Rocky Mts., GH!).

Aster majusculus Greene, Pitt. 4:215. 1900. (Type: Greene  
s.n., above Cimarron, Montrose Co., Colo., Sept.,  
1896, ND; isotype: NY!).

Aster glastifolius Greene, op. cit. p. 218. (Type: Nelson 3555, North Vermillion Creek, Sweetwater Co., Wyo., July 17, 1897, ND!).

Aster ciliomarginatus Rydb. Mem. N. Y. Bot. Gard. 1:392. 1900. (Type: Rydberg & Bessey 5128, Electric Peak, Park Co., Mont., Aug. 20, 1897, NY! isotype: US).

Aster diabolicus Piper, Bull. Torrey Club 29:645. 1902. A. foliaceus var. diabolicus Onno, Bibl. Botanica 106:10. 1932. (Type: Cusick 2670, Squaw Cr., Crook Co., (now Deschutes Co.), Oregon, July 17, 1901. US; isotypes: UC! GH! NY! POM! RM! WS!).

Aster vaccinus Piper, op. cit. p. 646. (Type: Cusick 2782, Cow Valley, Malheur Co., Oregon, Sept. 4, 1901, US; isotypes: UC! GH! NY! POM! RM! WS!).

Aster tweedyi Rydb. Bull. Torrey Club 31:655. 1904. (Type: Tweedy 4096, Copperton, Carbon Co., Wyoming, Aug. 6, 1901 NY!).

Aster grayi Suksd. Werdenda 1:41. 1927. A. subspicatus var. grayi Cronq. Vasc. Pl. Pac. N. W. 5:97. 1955. (Type: Suksdorf 12062 Holmes Cr. near Laurel, Klickitat Co. Wash., Aug. 22, 1926, WS! isotypes: DS! UC! WTU!).

Stems erect to ascending or sometimes decumbent at the base, mostly 3-10 dm. high, simple to several-branched, greenish to straw-colored or reddish, rarely glabrous throughout to usually with some pubescence in lines from the leaf bases and uniformly distributed under the heads

and on peduncles; basal leaves usually deciduous, up to 30 cm. long, 2-4 cm. wide, the long, winged petiole gradually to somewhat abruptly enlarging into the oblanceolate to obovate blade, usually glabrous, finely scabrous marginally; cauline leaves gradually reduced up to the inflorescence, then often rather markedly reduced, obovate to broadly lanceolate, usually sessile by a more or less clasping, sometimes auriculate base; middle stem leaves usually over 1 cm. wide and less than 7 times as long as wide, glabrous to finely strigose on the upper surface, scabrous, mostly entire; inflorescence usually few-headed and racemose, to many-headed and paniculate, the branches ascending, usually less than 20 cm. long, not conspicuously leafy-bracteate; heads medium-sized to large, the involucre 10-20 (25) mm. wide, 5-10 mm. high; phyllaries variable in 3-4 series, graduated to usually subequal or the outer occasionally enlarged, wholly green to usually with a chartaceous base and narrow scarious margin below, broadly spatulate to more often oblanceolate to lanceolate or linear, obtuse or rounded to acute, sometimes mucronulate, usually loose and spreading, glabrous to sparsely strigose abaxially, strigose adaxially and ciliate marginally; ray flowers 20-40, ligules 1.5-2.5 mm. wide, 10-15 mm. long, bluish-violet to purple; pappus white to tawny or faintly reddish; achenes pubescent.

Mountain meadows, stream banks, copses. Cascade Mts. of Washington and Oregon, and Sierra Nevada of north and central California, east to southern Alberta and New Mexico.

Representative specimens. CANADA: Alberta, near Lake Louise, Eggleston 21800, Sept. 12, 1927 (NY). Alberta, Cameron Lake, Waterton Lakes Park, Moss 1261, Aug. 19, 1941 (NY). ARIZONA: Apache Co., Phelps Botanical Area, White Mts., 9500 ft., Phillips 3351, Sept. 4, 1949 (RSA, CAS). Coconino Co., S of Flagstaff, Clark 12159, Aug. 26, 1944 (RM). Yuma Co., DeMotte Park, Buckskin Mts., Jones 6956, Sept. 19, 1894 (POM). CALIFORNIA: Butte Co., Butte Cr. near Jonesville, 5000 ft., Copeland s.n., Aug. 16, 1932 (UC). Humboldt Co., Murphy Meadow, Bald Mt., 3500 ft., Tracy 4836, Sept. 1, 1917 (DS, CAS, POM, UC). Modoc Co., Mt. Bidwell, Manning 272, Aug. 25, 1903 (UC). Siskiyou Co., Spirit Lake, 6000 ft., Howell 14877, Aug. 2, 1939 (POM, CAS). COLORADO: Archuleta Co., near Pagasa Peak, 9000 ft., Baker 639, Aug., 1899 (POM, NY). Boulder Co., Lake Eldora, 9280 ft., Clokey 3180, Aug. 8, 1918 (CAS, NY, DS, UC, WTU). Routt Co., Steamboat Springs, Shear 3967, July 31, 1898 (NY). IDAHO: Blaine Co., Wood R. at Easley Forest Camp, Thompson 14098, Aug. 2, 1937 (UC, DS, CAS, WTU, NY). Bonner Co., Priest Lake, Nelson 3038, Aug. 21, 1938 (RM, UC, NY, WTU). Owyhee Co., Jordan Cr. 1.5 mi. S of Silver City, Baker 8582, Aug. 13, 1951 (NY, ID). Teton Co., 4 mi. SE of Victor, Baker 9729, Aug. 11, 1952 (ID, NY).

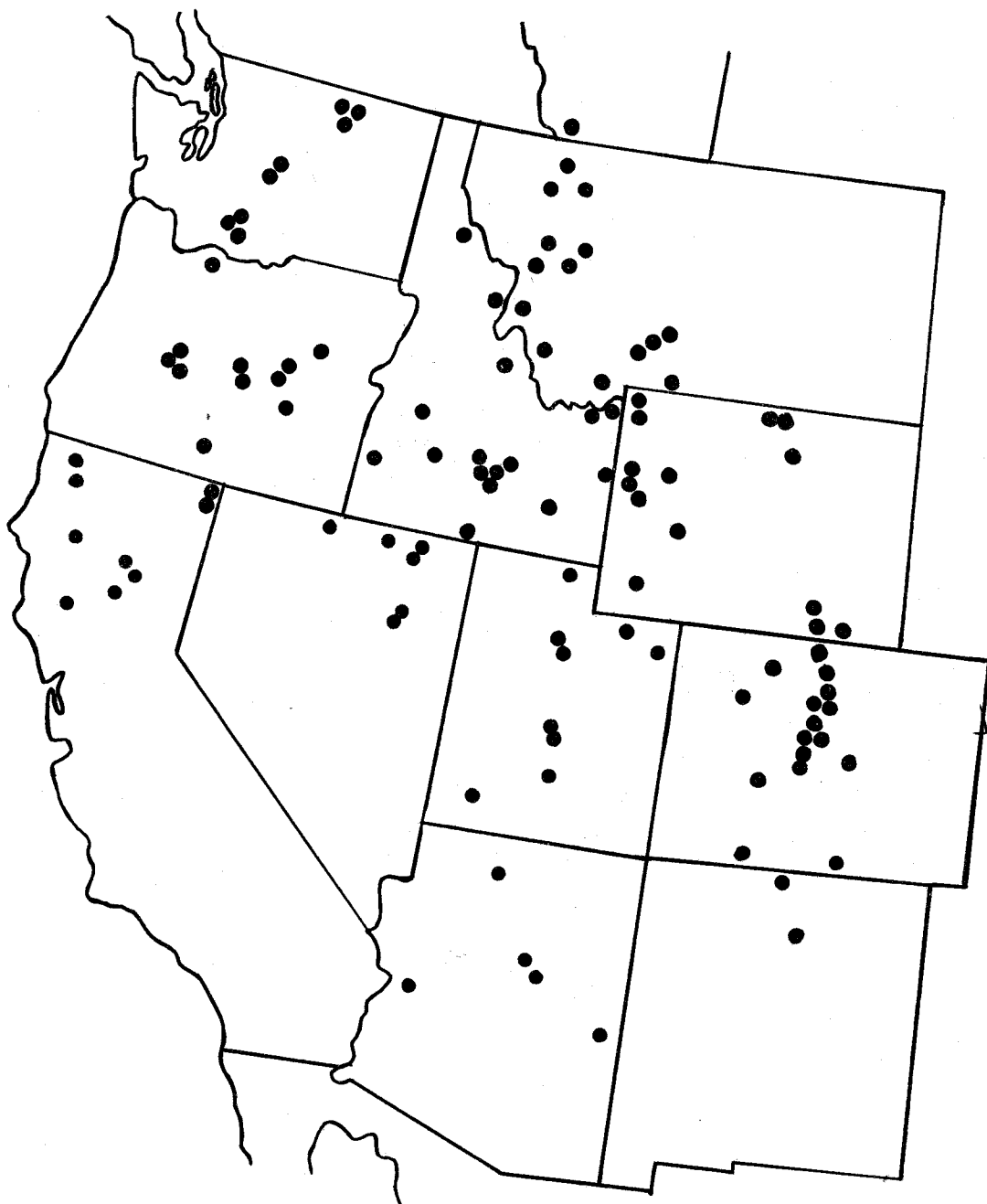


Figure 14. Distribution of *Aster foliaceus* ssp. *parryi*.

MONTANA: Flathead Co., 6 mi. NE of Echo Lake, Rogers & Rogers 1284, Aug. 28, 1942 (NY). Park Co., near Cooke City, Witt 1340, 1341, Aug. 5, 1948; Witt 1897, Aug. 27, 1949 (WTU, WS, RSA, NY, CAS). Stillwater Co., Independence, head of Boulder Cr., 8000 ft., Hitchcock & Muhlick 13344, Aug. 7, 1945 (NY, RM, DS, CAS, WS, UC, WTU). NEVADA: Elko Co., Lamoille Canyon, Heller 9322, Aug. 6, 1908 (NY, UC). Humboldt Co., Martin Cr., Santa Rosa Mts., 7000 ft., Munz 16130, July 25, 1940 (UC). NEW MEXICO: San Miguel Co., Pouchuelo Cr., 8400 ft., Standley 4583, July 30, 1908 (RM, NY). OREGON: Baker Co., Anthony Lakes, Thompson 13462, July 24, 1936 (RSA, NY, WTU, WS, CAS). Grant Co., Beech Cr. N of Mt. Vernon, 4900 ft., Cronquist 7733, Aug. 4, 1953 (NY, WS, UC, WTU). Lane Co., 5 mi. N of McKenzie Pass, 4600 ft., Campbell 17491, Aug. 28, 1952 (RSA, WTU, NY). UTAH: Salt Lake Co., Alta, 8500 ft., M. E. Jones 1226, Aug. 8, 1879 (NY, POM). Sevier Co., Fish Lake, 8900 ft., Maguire 16159, Aug. 24, 1938 (POM, NY). Summit Co., 2 mi. N of Henry's Fk. Lake, 10,500 ft., Maguire 14650, Aug. 16, 1936 (UC, NY). WASHINGTON: Kittitas Co., Table Mt., 5000 ft., Thompson 9764, Aug. 9, 1933 (NY, WTU). Pierce Co., Upper Valley of Nisqually, Allen 283, Aug. 20, 1897 (UC, WS, CAS, DS, NY). WYOMING: Albany Co., Centennial, Nelson 8790, Aug. 7, 1902 (UC, POM, RM). Lincoln Co., Jackson Hole, 6700 ft., Payson & Payson 2273, Aug. 11, 1920 (NY, CAS). Sheridan Co., N Fk. Tongue River, 8000 ft.,

Ownbey 990, Aug. 29, 1935 (RM, WS).

Aster foliaceus ssp. parryi, as here defined, includes the two varieties designated by Cronquist (14) as A. f. var. parryi Gray and A. f. var. canbyi Gray. The characteristics used by Cronquist to separate the two varieties are those of the phyllaries: narrower and acute in parryi and broader and obtuse to rounded in canbyi; and those of the leaves: more strongly and abruptly reduced in size above and thinner in parryi. The decision to combine the two varieties into one subspecies is based on the following facts. Much of their range overlaps; often plants of one type are found very close to or even in the same population as plants of the other type; the morphologically distinguishing traits completely intergrade within the overlapping range; the whole group is a polyploid complex; the type specimens of the two varieties are both from Colorado and are definitely part of the same polyploid complex.

The plants comprising this widespread subspecies are found primarily in mountains, often at quite high elevations, and are located in a variety of habitats including roadside, stream bank, open woods, and meadows. Within the range of this widespread subspecies there is a distributional trend of each of the morphological types discussed above. The parryi type predominates in the north and west and the canbyi type predominates in the south and east. At the extremes of the range, the parryi type is perhaps the

only one to be found in the northern parts of Washington and Idaho and in most of Montana, while the canbyi type is perhaps the sole representative in Arizona and New Mexico. Thus the extremes are relatively distinct, but the great majority of the material forms an intergrading complex. The fact that this majority is a polyploid complex, which increases the ease of hybridization and multiplies subsequent random segregation, is the primary reason for combining the erstwhile varieties into one subspecies.

Several diploids may contribute to the formation of this A. f. ssp. parryi complex. One of these is A. cusickii. The presence of genes of A. cusickii was particularly seen in plants with auriculate-clasping leaves, or with leaves constricted above the base, or with excess soft pubescence on the stems, or with large foliaceous outer phyllaries which exceed the inner phyllaries in length. Even though a plant had one of these features, the plant was classified as A. f. ssp. parryi if the aggregate of traits were more typical of the latter taxon. Such plants are found sympatrically with A. cusickii in the mountains of northeast Oregon and central Idaho, and allopatrically to the southeast in the Yellowstone Park area, Wyoming, Utah and Colorado.

Another contributing diploid, Dean 330, was collected in the mountains of central Idaho. The collection turned out to be a mixture of diploid and tetraploid plants, with

the tetraploids showing some characteristics of A. cusickii. The diploids are quite simple plants, many being monocephalous, with only slightly clasping medium-sized leaves (1-2 cm. wide) which are gradually reduced in size upwards. The base of the involucre is essentially glabrous. The phyllaries are nearly equal in 2-3 series and are almost entirely herbaceous with acute apices. This diploid thus fits the parryi type more than the canbyi type. Actually, it is close to the A. occidentalis ssp. occidentalis category, being separated largely on the basis of leaf size and number of heads.

The third contributing "diploid" is only tentatively diploid and is perhaps more likely tetraploid. The population is represented by two collections of W. S. and T. K. Phillips, 3316 and 3351, in the Phelps Botanical Area, White Mountains, Apache County, Arizona. The available information is not from chromosome counts but from pollen measurements of the 3316 collection, which averaged 24.7 $\mu$ . As seen in Table III, this measurement is in the range of both diploids and tetraploids. The plants definitely fall within Cronquist's concept of A. f. var. canbyi. The phyllaries are broadly spatulate, 2-4 mm. wide, with rounded green tip, chartaceous base and scarious margin. The leaves are lanceolate, 1-2 cm. wide and only slightly reduced upwards, with clasping base (the petioled lower leaves are deciduous). The pubescence is short and rather

dense on the upper stem, but reduced to lines below. As thus characterized, the plants compare most closely with the type specimen of an entity called A. f. var. burkei Gray. Cronquist reduced this to synonymy under A. f. var. canbyi. However, if further study shows this entity to be a diploid and possibly worthy of species recognition, it would assume the name of A. burkei (Gray) Howell, since T. Howell recognized it at the species level in his Flora of Northwest America (32, p. 310). All of the specimens seen from Arizona and New Mexico would likewise be referred to the burkei type on a morphological basis, although no other pollen measurements were as low as that of the Phillips collection.

The influence of genes from introgression by the two subspecies of A. occidentalis is evident in the northern and western part of the range of A. foliaceus ssp. parryi. The problem is particularly acute in some areas. One such area includes much of the higher elevations of the Cascade Mountains in Oregon. Four collections were made along the Santiam Highway (U. S. 20) from two miles east of Santiam pass summit to 10 miles west of the summit. Two of the collections were from more moist or shaded habitats, had slightly larger leaves, and had 32 pairs of chromosomes. These were designated as A. f. ssp. parryi. The other two collections were from more open and drier habitats, had narrower leaves, and had 16 pairs of chromosomes. These

plants were designated as A. occidentalis ssp. occidentalis. Actually, all the plants were quite similar in appearance and thus difficult to classify. Without knowledge of the chromosome number, one might judge the populations to be ecological variants of the same species. With knowledge of the chromosome number, one is tempted to conclude that the chromosome number is correlated with ecological preference, and therefore the two chromosome levels represent two species which are ecologically isolated.

About 50 miles to the south, another set of four collections was made along a similar length of the Willamette Pass Highway (Oregon 58). Here, two collections were also made from wet or shady habitats and two from drier, open habitats. As described above for the Santiam Pass plants, the morphological features also varied in the same way for the Willamette Pass plants. However, the chromosome number for all of the latter plants was  $2n = 16II$ , and they were all classified as A. o. ssp. occidentalis.

It should be evident from the above observations that no good criteria have been found to separate A. foliaceus ssp. parryi from A. occidentalis ssp. occidentalis in this area. In fact, the traits used in the key to separate these two taxa are admittedly very artificial. If only the Northwest plants were to be considered, merging of the two taxa under one species name might be justified. Despite these difficulties, the majority of plants which have been

keyed out to A. f. ssp. parryi on the artificial morphological basis, have proven to be high polyploids with 32 or 40 pairs of chromosomes. Conversely, most plants determined as A. o. ssp. occidentalis have been tetraploids with 16 pairs of chromosomes. Therefore, separate maintenance of the taxa appears to be reasonable even though such treatment seems morphologically artificial. The relatively greater distinctness between plants of the two taxa in the Rocky Mountain and Great Basin regions would further warrant maintaining separate taxa.

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