AN ABSTRACT OF THE THESIS OF

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Species relationships were investigated in a western North American polyploid complex in the genus Aster (Asteraceae). A combination of cytological, genetical, chemical, morphological and numerical approaches was employed. Fifteen presently recognized species were included in the study, and populations were sampled throughout most of the range of the group. Living plants from these populations were maintained in greenhouse and garden culture for studies of reproductive behavior, crossability, and flavonoid chemistry.

A total of 232 chromosome counts were made from the sampled populations. Chromosomes were observed at meiosis in flower buds and in mitotic divisions in root-tip cells. The principal base chromosome number in the group is x = 8; six ploidy levels occur, ranging from n = 8 to n = 48. A few aneuploid numbers based on x = 9 were also recorded, and one species was found to have a base number of x = 13.

Measurements of 35 morphological characters on 78 diploid specimens, followed by cluster analysis and discriminant analysis of the clusters, resolved seven phenotypic groups at the diploid

level. These correspond to seven currently recognized taxa in six species. Three other taxa in which a diploid chromosome number was found failed to separate from these clusters; this may reflect the choice of characters used in the analysis, or an incorrect placement of these species by contemporary taxonomists. Morphological variation among the polyploids was greater than at the diploid level, and this variability included intermediates between certain diploid groups as well as forms not found among the extant diploids.

Crossing experiments between diploids showed that in most cases the species are only partially interfertile. An exception was Aster greatai, a morphologically distinctive endemic taxon of southern California, which crosses readily with most of the other taxa. Several of the crosses yielded hybrid progeny; these had normal chromosome pairing at meiosis but lowered pollen viability.

A preliminary investigation of flavonoid chemistry in 30 populations (representing seven taxa) was carried out using two-dimensional thin-layer chromatograms. Considerable chemical variation was found, which was not closely correlated with variation in external morphology. Detailed analysis of a clone of Aster eatonii revealed 11 flavones and flavonols, which were characterized and identified.

A new finding was the common occurrence of diploid and tetraploid chromosome numbers based on x = 13 in the widespread species Aster ascendens. The karyotype of A. ascendens is distinctly asymmetrical, in contrast to the symmetrical karyotypes of the species based on x = 8. In view of the asymmetrical karyotype reported earlier for the related species A. ericoides (with n = 5), it seems likely that

the genome of A. ascendens evolved from hybridization between a taxon with n = 5 and one (perhaps A. occidentalis) with n = 8.

The complex is considered to contain approximately 14 species, of which nine contain some diploid populations. The present study extends the known morphological and geographical ranges of the diploid taxa, and improves understanding of species relationships and probable evolutionary lines within the group.

Biosystematics of a Western North American Polyploid Complex in the Genus *Aster*

by

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I. INTRODUCTION AND LITERATURE REVIEW

The genus *Aster* is a large, predominantly North American genus of perhaps 250 species. It is well known for its taxonomic complexity at all levels. Although it contains some species that are clearly marked, others grade into one another and can be delimited only with difficulty. Species relationships in the genus can best be understood by accumulating as many different kinds of information as possible about the plants and their variation in natural populations. A combination of cytological, morphological, numerical and chemical approaches is used here to investigate one group of *Aster* species. The purposes of the study are to improve present knowledge of the relationships and evolutionary history of these species, and to establish a basis for a more natural and useful taxonomy of the group.

The species complex investigated here is a North American group of approximately 15 species which extends throughout the western part of the continent, from Alaska to Mexico and from the Rocky Mountains to the Pacific Coast. Most of the taxa are widely distributed; a few are regional endemics. The group forms a fairly distinct natural assemblage, differing from related groups in a combination of growth habit, pubescence type, leaf shape, and structure of flowers and involucre. Certain of the species (*Aster laevis*, *A. hesperius*, *A. foliaceus* and *A. ascendens*) have ranges extending east of the

Rocky Mountains; the complex may be related through some of these taxa to other groups of species in eastern North America.

The plants of this group are perennial rhizomatous herbs with fibrous roots and leafy stems, and often with showy inflorescences. They occur on mesic to damp sites over a wide range of elevations, occupying habitats such as forest edges, meadows and stream banks. Within the group there is considerable variation in leaf morphology and arrangement, branching pattern, color and number of disk and ray flowers, size and number of flower heads, size and shape of phyllaries, and pubescence.

Table 1 gives a summary of the taxonomic history of this group of asters over the last 140 years. The first formal taxonomic treatment of the group was that of Torrey and Gray (1841), who recognized 13 species (omitting some still undiscovered endemics). This was followed by the 1884 treatment of Gray, much of which still stands. Later work by Greene (1891-1909) and Rydberg (1917), reflecting a narrower species concept, resulted in a great proliferation of names many of which were later placed in synonymy. Jepson (1925) adopted a more conservative approach, but placed emphasis on variation in the California taxa with which he was most familiar.

The first study focusing specifically on relationships in this group, rather than on general floristic aspects, was that of Cronquist (1943). He examined morphological variation in detail, reduced all

Table 1. Published taxonomic treatments of the group and their comparison with the treatment of Dean (1966).

Dean (1966)	Torrey and Gray (1841)	Gray (1884)
A. laevis L.	A. laevis L.	A. laevis var. geyeri Gray
A. subspicatus Nees	A. subspicatus Nees A. douglasii Lindl. A. amplus Lindl.	A. douglasii Lindl. A. amplus Lindl.
A. chilensis Nees	A. chilensis Nees A. menziesii Lindl.	A. chamissonis Gray A. menziesii Lindl.
A. lentus Greene		
A. hallii Gray		A. hallii Gray
A. adscendens Lindl.	A. nuttallii T. & G. A. ascendens Lindl. var. denudatus T. & G. var. ciliatifolius T. & G.	A. adscendens Lindl. var. denudatus T. & G.

Table 1. (continued)

Greene (1891-1909)	Rydberg (1917)	Jepson (1925)
--	A. laevis L. A. geyeri Howell A. brevibracteatus Rydb. A. scribneri Rydb. A. subsalignus Rydb.	--
--	A. douglasii Lindl. A. amplus Lindl. A. butleri Rydb. A. subcaudatus Rydb. A. umbachii Rydb.	A. douglasii Lindl.
A. chilensis Nees A. invenustus Greene A. militaris Greene A. menziesii Lindl.		A. chilensis Nees var. invenustus Jeps. var. medius Jeps.
A. lentus Greene A. sonomensis Greene		var. lentus Jeps. var. sonomensis Jeps.
	A. hallii Gray	
A. ascendens Lindl. A. armeriaefolius Greene A. denudatus Nutt. A. distichophyllus Greene A. griseus Greene A. halophilus Greene A. leucopsis Greene A. limoniifolius Greene	A. adscendens Lindl. A. armeriaefolius Greene A. denudatus Nutt. A. griseolus Rydb. A. halophilus Greene A. leucopsis Greene A. nelsonii Greene A. nuttallii T. & G.	A. adscendens Lindl. (var. adscendens)

Table 1. (continued)

Cronquist (1943)	Cronquist (1955)	Ferris (1959)
--	A. laevis L. var. geyeri Gray	A. laevis L. var. geyeri Gray
A. douglasii Lindl.	A. subspicatus Nees var. grayi (Suksd.) Cronq.	A. subspicatus Nees
A. chilensis Nees ssp. typicus Cronq.	A. chilensis Nees ssp. chilensis	A. chilensis Nees var. invenustus Jeps. var. medius Jeps.
		var. lentus Jeps. var. sonomensis Jeps.
ssp. hallii (Gray) Cronq.	ssp. hallii (Gray) Cronq.	A. hallii Gray
ssp. adscendens (Lindl. ex DC.) Cronq. var. euadscendens Cronq.	ssp. adscendens (Lindl.) Cronq.	A. adscendens Lindl.

Table 1. (continued)

Dean (1966)	Torrey and Gray (1841)	Gray (1884)
A. ascendens (cont.)		
A. bernardinus Hall		
A. occidentalis (Nutt.) T. & G. ssp. occidentalis	A. ascendens Lindl. var. fremontii T. & G. A. occidentalis (Nutt.) T. & G.	A. adscendens Lindl. var. yosemitanus Gray A. fremontii Gray var. parishii Gray A. occidentalis (Nutt.) T. & G. var. intermedius Gray A. andinus Nutt.
ssp. intermedius (Gray) Piper	A. andinus Nutt.	
A. eatonii (Gray) Howell	A. oregonus (Nutt.) T. & G. A. bracteolatus Nutt.	A. oreganus (Nutt.) T. & G. A. foliaceus Lindl. var. eatonii Gray

Table 1. (continued)

Greene (1891-1909)	Rydberg (1917)	Jepson (1925)
A. nelsonii Greene	A. subgriseus Rydb.	
A. orthophyllus Greene	A. subracemosus Rydb.	
A. oxylepis Greene	A. underwoodii Rydb.	
A. pratincola Greene	A. violaceus Greene	
A. spithameus Greene		
A. violaceus Greene		
A. yosemitanus Greene	A. occidentalis Nutt.	A. adscendens Lindl.
A. copelandii Greene	A. corymbiformis Rydb.	var. fremontii Gray
	A. fremontii Gray	var. yosemitanus Gray
A. vallicola Greene	A. williamsii Rydb.	var. delectabilis Jeps.
	A. andinus Nutt.	
	A. subspathulatus Rydb.	
A. oreganus (Nutt.) T. & G.	A. eatonii (Gray) Howell	A. foliaceus Lindl.
A. exsul Greene	A. fulcratus Greene	var. eatonii Gray
A. fulcratus Greene	A. lonchophyllus Greene	
A. lonchophyllus Greene	A. proximus Greene	
A. proximus Greene	A. mearnsii Rydb.	
A. microlonchus Greene	A. microlonchus Greene	
	A. roseolus Rydb.	

Table 1. (continued)

Cronquist (1943)	Cronquist (1955)	Ferris (1959)
var. bernardinus (Hall) Cronq.		A. bernardinus Hall
A. occidentalis (Nutt.) T. & G. var. typicus Cronq. var. yosemitanus (Gray) Cronq. var. intermedius Gray	A. occidentalis (Nutt.) T. & G. var. occidentalis var. intermedius Gray	A. paludicola Piper A. occidentalis (Nutt.) T. & G. var. yosemitanus (Gray) Cronq. var. parishii (Gray) Ferris var. delectabilis (Hall) Ferris var. intermedius Gray
A. oregonus (Nutt.) T. & G.	A. eatonii (Gray) Howell	A. eatonii (Gray) Howell

Table 1. (continued)

Dean (1966)	Torrey and Gray (1841)	Gray (1884)
A. foliaceus Lindl. ssp. foliaceus ssp. parryi (D.C. Eaton) Dean ssp. apricus (Gray) Piper	A. foliaceus Lindl.	A. foliaceus Lindl. var. frondeus Gray var. parryi Gray var. burkei Gray var. canbyi Gray var. apricus Gray
A. cusickii Gray		A. cusickii Gray var. lyallii Gray
A. hesperius Gray		A. hesperius Gray
A. jessicae Piper		
A. greatai Parish		
A. "idahoensis" Dean (unpubl.)		

Table 1. (continued)

Greene (1891-1909)	Rydberg (1917)	Jepson (1925)
A. foliaceus Lindl. A. amplissimus Greene A. frondeus Greene A. majusculus Greene A. glastifolius Greene	A. frondeus Greene A. canbyi Vasey A. burkei Howell A. ciliomarginatus Rydb. A. diabolicus Piper A. tweedyi Rydb. A. apricus Rydb.	A. foliaceus Lindl. var. foliaceus var. frondeus Gray var. apricus Gray
	A. cusickii Gray A. eriocaulis Rydb. A. hendersonii Fernald A. kootenayi Nels. & McBr.	
A. hesperius Gray A. ensatus Greene A. laetevirens Greene A. limosus Greene A. wootonii Greene Brachyactis hybrida Greene	A. hesperius Gray A. laetevirens Greene A. osterhoutii Rydb.	var. hesperius Jeps.
	A. jessicae Piper	
		A. greatai Parish

Table 1. (continued)

Cronquist (1943)	Cronquist (1955)	Ferris (1959)
A. foliaceus Lindl. var. typicus Onno var. frondeus Gray var. canbyi Gray var. apricus Gray	A. foliaceus Lindl. var. foliaceus var. canbyi Gray var. parryi (D.C. Eaton) Gray var. apricus Gray	A. foliaceus Lindl. ex DC. var. foliaceus var. canbyi Gray var. apricus Gray
var. cusickii (Gray) Cronq. var. lyallii (Gray) Cronq.	var. cusickii (Gray) Cronq. var. lyallii (Gray) Cronq.	var. cusickii (Gray) Cronq. var. lyallii (Gray) Cronq.
A. coerulescens DC. var. typicus Cronq. var. laetevirens (Greene) Cronq.	A. hesperius Gray var. laetevirens (Greene) Cronq.	A. hesperius Gray
A. jessicae Piper	A. jessicae Piper	A. jessicae Piper
A. greatai Parish		A. greatai Parish

existing names to synonymy within eight species, and proposed a phylogeny of the group. Later floristic treatments (Hitchcock et al. 1955, Abrams and Ferris 1959) reflect his work.

The group was most recently studied by Dean (1966), who improved on the classical morphological approach by investigating chromosome numbers and crossing relationships. He showed that the group is a polyploid complex with up to six ploidy levels, and that many of the species cross readily, especially at the polyploid levels. Most of the plants he examined had a chromosome base number of eight. His study contributed a wealth of new cytological information and an improved taxonomic treatment. Table 2 lists the taxa included in this group by Dean, which are used as the starting point for this study.

Many questions remain unanswered in this group. In particular, relatively little information exists concerning patterns of variation at the diploid level, interfertility between diploid taxa, and the origin of some of the aneuploid chromosome numbers that have been found. The diploid progenitors of such variable and widespread taxa as Aster foliaceus and A. occidentalis are poorly known, as are the status and relationships of regional endemics such as A. lentus, A. greatai and the as yet unpublished "A. idahoensis" proposed by Dean (1966). The origin of chromosome numbers based on x = 13 in A. ascendens is of particular interest. These numbers could have resulted from alloploidy, combining an n = 8 with an n = 5 genome (an

Table 2. *Aster* species included in the study by Dean (1966).

A. ascendens Lindley

A. bernardinus Hall

A. chilensis Nees

A. cusickii A. Gray

A. eatonii (A. Gray) Howell

A. foliaceus Lindley

A. greatai Parish

A. hallii A. Gray

A. hesperius A. Gray

A. "idahoensis" Dean, ined.

A. jessicae Piper

A. laevis Linnaeus

A. lentus Greene

A. occidentalis (Nuttall) Torrey & Gray

A. subspicatus Nees

attractive hypothesis since both base numbers exist in the genus), or from aneuploid increase or decrease from a number based on n = 8 (the prevailing base number in this group). Apart from miscellaneous chromosome counts, little has actually been published on the cytology of the group, though other work has been done in related sections of the genus (Jones 1977).

Recent studies in Aster have been mainly on the generic level. Both Jones (1980a) and Semple and Brouillet (1980a) have proposed reorganizations of the genus along lines suggested by the various chromosome base numbers (which include 5, 8 and 9). However, much remains to be learned about individual species and species groups.

II. METHODS

Plant material was collected at approximately 200 localities scattered over the range of the group. Whenever possible, all the material collected under a given number was obtained from a single clone. At each site I obtained (1) pressed herbarium specimens, (2) live rhizomes or whole plants (transferred in the field into plastic bags or directly into pots), and (3) buds for cytological analysis (where available). Additionally, at sites with abundant plant material, whole flowering stems were collected and dried for later chemical analysis. The asters of this group transplant readily and will propagate from a relatively small fragment of rhizome. Live material was maintained either in the greenhouse or in a field plot. The live plants were used for crossing experiments, and also served as a source of any additional material needed for cytological or chemical analysis.

Since this group is a polyploid complex, determination of chromosome numbers was of primary importance. Only plants of known chromosome number were used in studies of the morphology, flavonoid chemistry and reproductive biology.

Most chromosome numbers were determined from meiotic material. Buds of different sizes were collected directly into Carnoy's fixative (chloroform, acetic acid and ethanol, 6:1:3). After three to five days they were transferred to 70% ethanol. The buds were stored at $0^{o}C$, at which temperature they remained usable indefinitely. Before

dissection the buds were bulk-stained in Snow's alcoholic HCl-carmine stain (Snow 1963) at 60°C for 24 to 36 hours. They were then returned to 70% ethanol, and the anthers dissected out from the individual florets and squashed in 45% acetic acid.

Rhizomes collected during field expeditions were initially planted in pots in the greenhouse; many specimens grew rapidly under these conditions and were later moved outdoors into the field plot. Mitotic chromosome counts from root tips were made for specimens for which buds were not collected, and also for those of particular interest for which karyotypes were needed.

Root tips were collected from potted plants into small vials of cold distilled water. They were given a pre-fixation treatment with α-bromonaphthalene (one drop per vial) for three to four hours at 4°C, then were transferred to ethanol-acetic acid (3:1). Storage in the fixative for up to several months produced no noticeable deterioration. Root tip material to be examined was hydrolyzed for 15 minutes in 1 N HCl at 60°C, then stained in leuco-basic fuchsin for one to several hours, and squashed on a slide in 45% acetic acid (Darlington & La Cour 1960).

Chromosomes were photographed, for documentation and karyotype analysis, using a Pentax camera body mounted on a trinocular Zeiss phase-contrast microscope. Film used was Kodak Panatomic-X (ASA 32). Microscope slides were made permanent by freezing in liquid N_2 to

facilitate removal of the coverslip, dehydrating in absolute ethanol, and mounting in Euparal.

Specimens of known chromosome number were grouped by ploidy level for morphological study. An array of 35 morphological characters, obtained from both pressed and fresh plant material, was measured on a total of 243 specimens. Characters were selected to represent all parts of the plant and included features considered by previous workers to be of taxonomic importance. The characters used, and the coding states or units of measurement, are given in Table 3. All characters were converted to some form of quantitative multistate (Sneath & Sokal 1973). Characters 1 to 10 and 14 to 30 were measured on pressed specimens, and the remaining characters on fresh flowering material. Of the 243 specimens measured, only 167 had values for all 35 characters. The remainder were herbarium sheets on which characters 11 to 13 and 31 to 35 could not be measured. The data matrix thus had a large block of missing values. Each analysis performed was run three times: (1) on the subset of specimens for which all 35 character measurements were available, (2) on the full set of specimens with a subset of 27 characters, and (3) on the reduced subset of specimens as in (1) but with 27 characters. The runs were then compared.

Two approaches were taken to the statistical analysis of these data: (1) a cluster analysis followed by canonical analysis of discriminance to assess the distinctness of the clusters, and (2) principal components analysis to arrange the individual specimens along axes of maximum

Table 3. Morphological characters used for numerical analysis.

	Character	Abbreviation	Coding states or units of measurement
1.	Plant height	PLANTHT	cm
2.	Number of internodes (along main stem)	NOINTNOD	
3.	Number of flower heads	NOFLHDS	
4.	Inflorescence length (from attachment of lowest branch to top of plant)	INFLLEN	cm
5.	Inflorescence side branch length (at midpoint of inflorescence)	INFLSIBR	cm
6.	Order of branching	ORBRAN	0 = no side branches (single flower head) 1 = one level of branching 2 = two levels of branching 3 = three levels of branching
7.	Length of inflorescence bract (at midpoint of inflorescence)	BRACLEN	mm
8.	Cauline leaf length (using leaf nearest midpoint of stem, excluding inflorescence)	CLFLEN	mm
9.	Cauline leaf length/width ratio	CLFLW	
10.	Cauline leaf base shape	CLFBAS	1 = narrow 2 = rounded 3 = clasping
11.	Basal leaf length	BLFLEN	mm
12.	Basal leaf length/width ratio	BLFLW	

	Character	Abbreviation	Coding states or units of measurement
13.	Basal leaf base shape	BLFBAS	1 = tapered to base, no obvious petiole 2 = tapered to base, petiolate 3 = abruptly narrowed to base, petiolate
14.	Shape of leaf margin	LFMAR	1 = entire 2 = minutely toothed 3 = dentate 4 = deeply or conspicuously dentate
15.	Stem color	STCOL	1 = green 2 = with reddish tinge 3 = dark reddish
16.	Achene pubescence	ACHPUB	1 = glabrous 2 = sparsely to moderately pubescent 3 = densely pubescent
17.	Pubescence of involucre	INVPUB	1 = glabrous 2 = ciliate along phyllary edges 3 = ciliate along edges and on surface of phyllaries
18.	Stem pubescence at top	STPUBT	1 = glabrous 2 = pubescent in thin lines 3 = pubescent in heavy lines with scattered hairs between 4 = densely pubescent
19.	Stem pubescence at midpoint	STPUBM	(as for character 18)
20.	Pubescence of leaf margin	LMARPUB	Number/mm
21.	Length of outer phyllary	OPHYLEN	mm

	Character	Abbreviation	Coding states or units of measurement
22.	Length/width ratio of outer phyllary	OPHYLW	
23.	Shape of outer phyllary tip	OPHYTIP	1 = narrowly acute (angle less than 45^{o}) 2 = acute (angle between 45^{o} and 90^{o}) 3 = obtuse (angle greater than 90^{o}) 4 = rounded
24.	Ratio of scarious edge length to total length for outer phyllary	OPHYMAR	
25.	Length of inner phyllary	IPHYLEN	mm
26.	Length/width ratio of inner phyllary	IPHYLW	
27.	Shape of inner phyllary tip	IPHYTIP	(as for character 23)
28.	Ratio of scarious edge length to total length for inner phyllary	IPHYMAR	
29.	Number of ray flowers per head	NORAYS	
30.	Number of disk flowers per head	NODISKS	
31.	Color of rays	RAYCOL	1 = white 2 = very pale purple to pink 3 = pale purple 4 = darker purple
32.	Ray length (from tip to top of achene)	RAYLEN	mm
33.	Length of style branches on disk flowers	STYBRLEN	mm
34.	Ratio of style appendage to style branch length on disk flowers	STYLAPP	

Character	Abbreviation	Coding states or units of measurement
35. Disk corolla color in age	CORCOL	1 = yellow 2 = slightly reddish 3 = dark red

variation. All analyses were performed on standardized data (the original measurement for each character being modified by subtracting the mean for that character and dividing by the standard deviation). Standardization equalizes the relative importance of the characters, eliminating the weighting effect of different units of measurement and different variances.

The program used for the cluster analysis, CLUSB (obtained from Dr. C. D. McIntire, Department of Botany, Oregon State University), is a nonhierarchical divisive clustering program which divides a set of specimens into successively larger numbers of clusters, minimizing total within-group variance at each stage. The clusters produced by this program were then ordinated using the discriminant analysis subprogram of SPSS (produced by Northwestern University) in order to see how they were related. The program used for the principal components analysis (PCA) was ORDIFLEX (produced by Cornell University) which performs several ordination procedures useful for ecological and taxonomic applications. The groups produced by CLUSB were plotted on the PCA ordinations of the same data in order to compare the two approaches.

A program of crossing experiments involving selected diploid individuals from different morphological groups was carried out in order to examine reproductive relationships between groups at the diploid level. According to Dean (1966), asters of this group are obligate outcrossers. This was checked for most of the clones used in the crossing experiments by bagging inflorescences, and collecting seed from heads

from which foreign pollen had been excluded. The resulting seeds were counted and then germinated on a standard potting soil mix in small pots, and percent germination recorded.

Since collections of plant material were continued over three field seasons, parent clones used in the crossing experiments were those obtained early in the study and did not represent all of the variation encountered at the diploid level. However, a reasonable sample of morphological types and geographical locations was obtained. Crosses were made between different plants by rubbing pairs of heads together, then labelling each head to indicate the pollen parent. Flower heads to be used in crossing experiments were enclosed in fine-mesh nylon bags before the flowers opened, and remained enclosed until after anthesis. Most of the plants used were grown outdoors in a field plot; those growing in pots were kept in the greenhouse or in a pollinator exclusion cage consisting of fine-mesh nylon fabric on a wooden frame. Seeds resulting from the crosses were collected when ripe, stored at $4^{o}C$ for several months, then planted in seed flats in standard potting soil. Seedlings were transferred to individual pots and then to the field plot, where (time permitting) they were raised to flowering size. They were then examined for morphological similarity to their respective parents, and buds were collected for examination of chromosome behavior at meiosis.

Pollen samples were collected from all specimens which flowered in cultivation in order to determine (1) whether pollen viability is

related to ploidy level, (2) whether morphological discontinuities among diploids are associated with decreased pollen fertility, and (3) what the levels of fertility are in hybrid progeny. Pollen samples were gathered from flowers which were allowed to open in the laboratory; these were stained in lactophenol - aniline blue (which stains cytoplasm dark blue) for one to several hours. At least 1000 grains were counted for each collection, and the number of dark-staining grains recorded.

A detailed analysis of flavonoid compounds was made on a large collection from a single clone of Aster eatonii, using the methods of Guppy & Bohm (1976). Approximately 200 g of fresh leaves and flower heads were extracted in three changes of hot methanol. The crude extract was reduced to a small volume, dissolved in boiling water, treated with Celite (diatomaceous earth) and filtered. The filtrate was then extracted with 1-butanol in a separatory funnel, and the 1-butanol extract removed and evaporated to dryness. This extract was initially separated by column chromatography on Sephadex LH-20 and on Polyamide DC-6.6, using a gradient from water to methanol. Further purification was done by thin layer chromatography on Avicel (microcrystalline cellulose) using 15% acetic acid, and on Polyamide DC-6.6 using the following solvents:

1. benzene, 2-butanone, methanol, water (55:22:20:3)
2. water, 1-butanol, acetone, dioxane (70:15:10:5)
3. chloroform, 2-butanone, methanol (70:15:15)

Purified compounds were identified by inspection of Rf values, analysis of the UV spectrum using diagnostic reagents (Mabry et al. 1973), and identification of hydrolysis products. Hydrolysis was performed by addition of trifluoroacetic acid, in a hot water bath at 80°C for 20 to 40 minutes. The aglycone was extracted from the hydrolysate using ethyl acetate, and the aqueous residue containing the sugar was passed through a small polyamide column to remove any remaining phenolics; it was then taken to dryness twice on a rotary evaporator to remove the trifluoroacetic acid. Aglycones were identified by co-chromatography with standard compounds in two solvents. Sugars were chromatographed together with standards on cellulose layers in ethyl acetate- pyridine-water (10:3:2), and visualized by spraying with p-anisidine phthalate followed by heating at 110°C.

Thirty other collections were also examined to determine the range of flavonoid variation present in the group. The crude extraction procedure was followed as described above, substituting ethyl acetate for 1-butanol (this solvent extracts flavonoids less efficiently, but takes up fewer non-phenolic substances to interfere with thin-layer chromatography). The ethyl acetate extract was spotted on a prepared polyamide thin layer on plastic backing. This was then run in two directions using solvents 1 and 2 above, and the flavonoid spots visualized by spraying with 0.25% diphenyl boric acid-ethanolamine in 50% methanol. The plates were permanently recorded by tracing, and also by photographing under UV light (366 nm) with Kodachrome 25 film and a Kodak Wratten 2E ultraviolet-blocking filter.

III. RESULTS

Variation in Chromosome Numbers

The wide range of chromosome numbers in this group of asters was first documented by Dean (1966). In the present study, 232 chromosome counts from 208 localities were made; these are listed in Appendix I. Combining these with the counts made by Dean and by others (Clausen et al. 1940, Huziwara 1958 and 1965, Raven et al. 1960, Solbrig et al. 1969, Kovanda 1972, Strother 1972, Anderson et al. 1974, Jones 1980b) gives a total of more than 400 counts, distributed over the whole geographical range of the group (Figure 1).

Chromosome numbers in this complex are for the most part multiples of eight, and range from diploid (n = 8) to duodecaploid (n = 48). Other numbers found, which may be the result of aneuploidy or of combinations between different base numbers, include multiples of nine and thirteen. Figure 2 shows the distribution of chromosome numbers over the different ploidy levels in the group, based on all counts made thus far. The different ploidy levels occur at roughly similar frequencies, although the highest numbers (n = 40 and 48) are somewhat rarer.

Accessory or B chromosomes are also common in the group. These chromosomes are small and heterochromatic, often lag at cell division, and vary widely in number (Muntzing 1958).

Figure 1. Localities for all known chromosome numbers in the group under study.

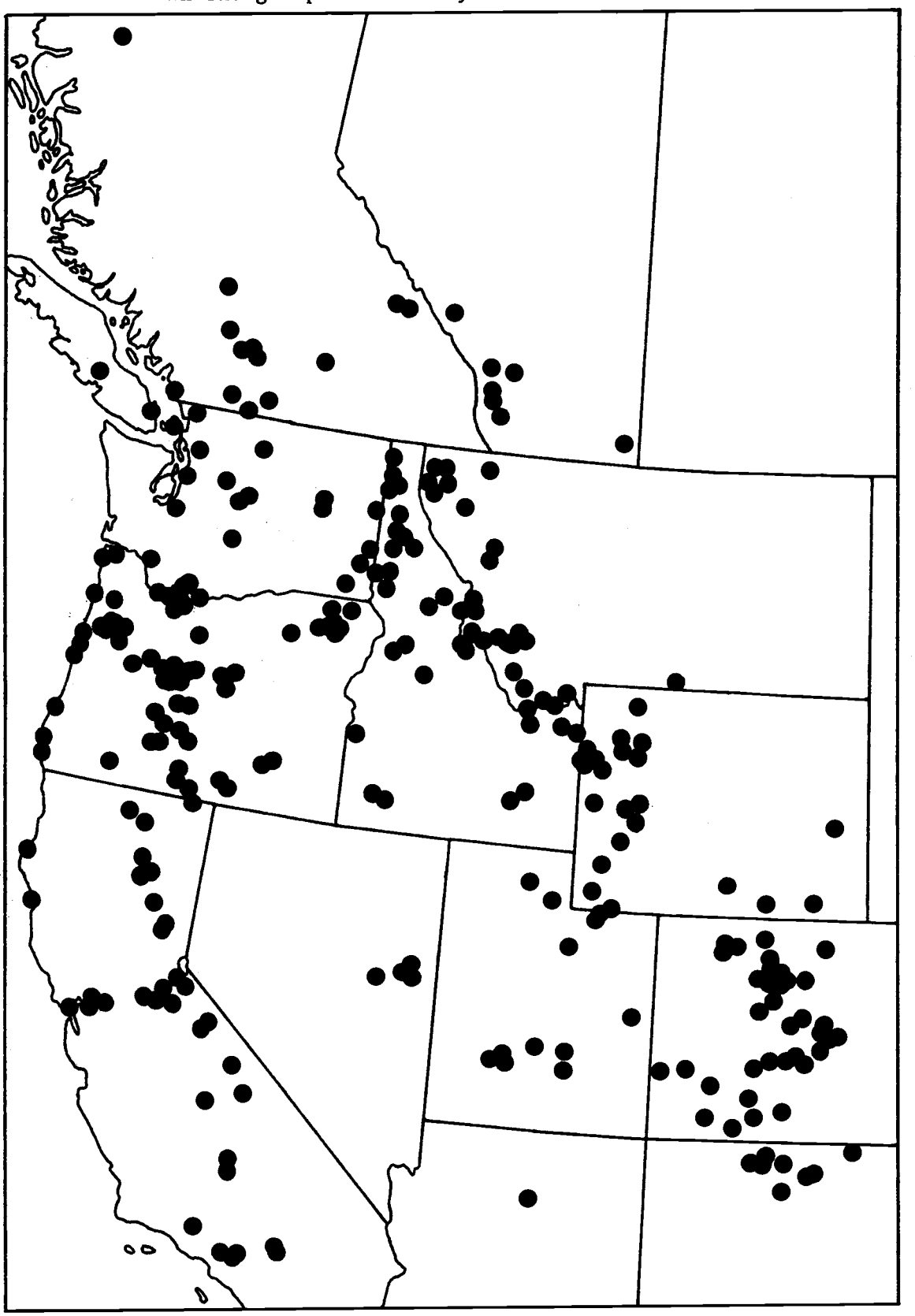
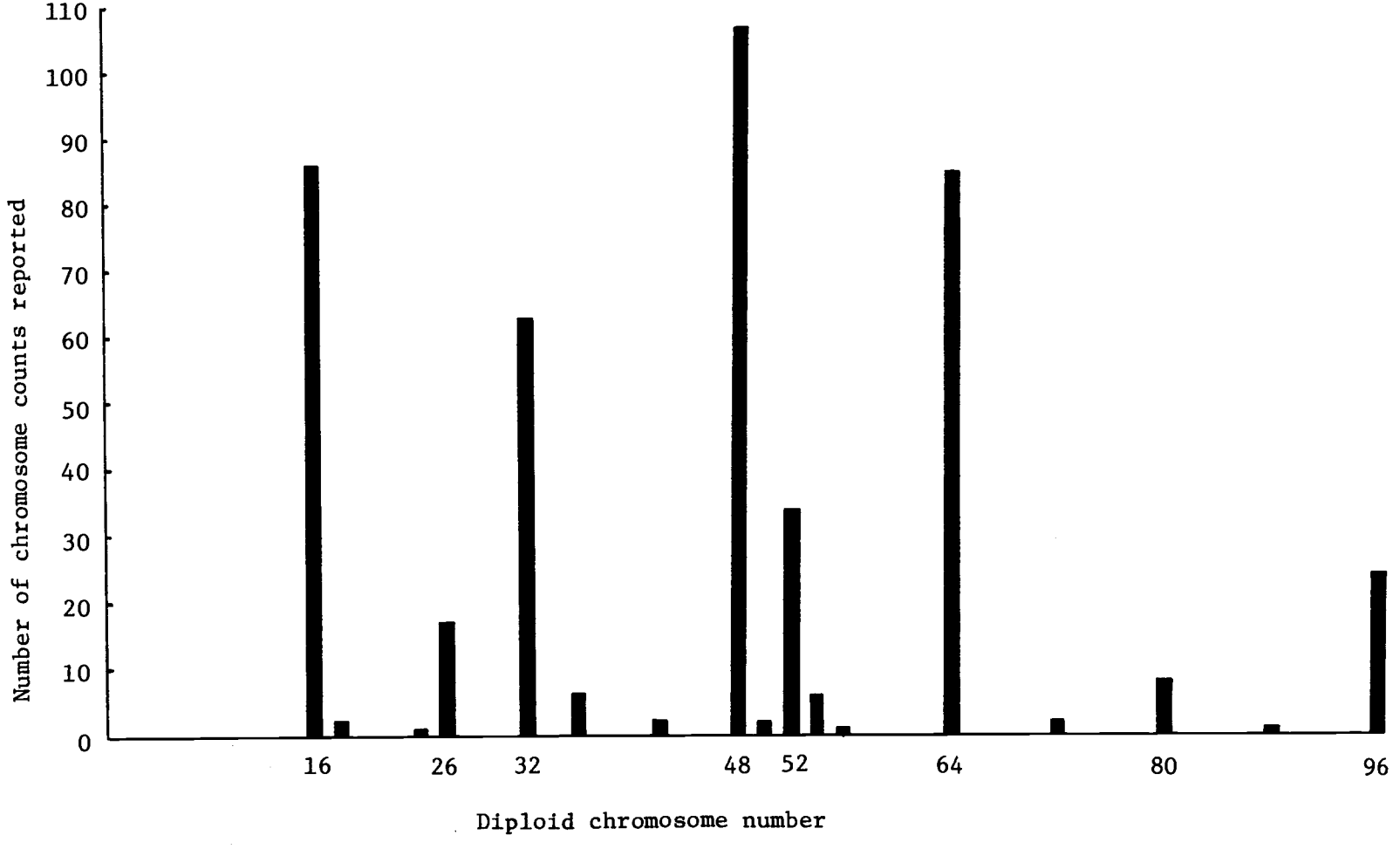


Figure 2. Frequencies of different chromosome numbers in the group under study.



Morphological Variation in Diploids and Polyploids

An effort was made to examine morphological variation as objectively as possible, by selecting an array of characters reflecting all features of the plants and measuring these in a standard fashion for each specimen. A non-hierarchical clustering program was then used to get objective and homogeneous groupings, which could be compared with the more subjective taxonomic groups recognized by Dean and others in earlier studies of this complex. For the numerical analyses, each operational taxonomic unit (OTU) was a single specimen.

Measurements were made only on plants of known chromosome number. Initial emphasis was placed on the diploids since they should yield the most information on evolutionary trends in the group.

1. Diploids

Morphological measurements were obtained for a total of 78 diploid specimens. Some of the characteristics were measured on dried herbarium materials and others directly on live plants.

The clustering program, CLUSB, tended to arrange the specimens (OTUs) into two to three relatively distinct clusters and a number of more diffuse and overlapping groups. Although this program minimizes within-group variance at each stage, the groups become closer and closer together in hyperspace at higher clustering levels, so the data may become "over-divided" and yield clusters that are scarcely distinct.

With the data set used here, the tendency at the highest clustering levels was for individual outlying OTUs to be separated into single-membered clusters. Eventually the program began to divide relatively cohesive clusters into increasingly arbitrary subgroups; this could to some extent be seen by comparing runs using different numbers of OTUs or characters to see which clusters were the least stable. Even rearrangement of the data deck caused alterations in the groups in some cases, due to rounding error accumulated during repeated calculations.

The number of OTUs dropped from 78 to 52 when all 35 of the characters measured were included in the analysis. This altered the clusters somewhat, since the specimens omitted were not a representative sample of all the diploids used. Using only those 27 characters that could be measured on pressed specimens also had a definite effect on the groupings, since this gave much less emphasis on flower characters (most of which were measured on live material). However, certain groups of specimens consistently clustered together in all runs. These outlying groups were removed and the clustering was then repeated, in order to make clearer the patterns formed by the remaining less discretely clustered OTUs.

The number of morphologically defined groups at the diploid level was determined partly by comparison of different clustering runs, and partly by visual inspection of grouped specimens. The OTUs were considered to be too finely divided if the clusters were not readily

separable by a fairly consistent suite of characters visible on a pressed specimen. Seven groups were distinguished; others may exist at the diploid level, but either these did not cluster separately with the characters used or they were not represented in this data set. The specimens used in this analysis, arranged in the seven groups, are listed in Table 4. The discreteness of the groups was examined by using discriminant analysis. In a reclassification of the members assigned to each group, based on the same 27 characters mainly used in forming the groups, 100% of the OTUs were reassigned to the group to which they actually belonged. This indicates that the clusters were reasonably distinct. Reclassification runs using all 35 characters on the same clusters did result in some misclassifications, indicating that different groups of characters show different variation patterns.

A canonical analysis of discriminance was used to arrange the groups along axes maximizing between-group distances, as shown in Figures 3 and 4. In Figure 3 the axes were calculated using the OTUs in all seven of the diploid groups obtained by the clustering program, above. This resulted in good separation of the second group (A. foliaceus var. canbyi), while the other six groups remain clumped. In Figure 4, only these latter six groups were used in calculating the directions of the axes, although all 78 OTUs are plotted. This gave minimal overlap for these groups, although Group 2 overlaps with Groups 5, 6 and 7 in these dimensions. Thus all of the seven groups are distinct in at least one direction, although some are slightly more

Table 4. Diploid specimens used in the numerical analysis.[1]

Group	Collection numbers of specimens[2]	
1. *A. ascendens*	502	845
	504	849
	512	Dean 313
	688	Dean 353
	689	Dean 354
	844	
2. *A. foliaceus* var. *canbyi*	BFL-18	BFL-21
	BFL-19	BFL-22
	BFL-20	BFL-23
3. *A. foliaceus* var. *foliaceus* and var. *parryi*	715	806
	739	816
	740	830
	766	865
	798	Dean 467
	801	
4. *A. idahoensis*	641	
	Dean 466	
5. *A. occidentalis*	555	685
	556	722
	557	725
	558	726
	561	731
	582	Dean 317
	586	Dean 322
	590	Dean 395
	609	Dean 474
6. *A. eatonii*	513	856
	514	860
	542	861
	553	BFL-29
	560	Chambers 4414
	575	Dean 315
	622	Dean 320
	736	Dean 324
	756	Dean 452
	775	Jones 3941
		Jones 3979

[1]Vouchers for all collections are deposited in OSC.

[2]Collection numbers are mine unless otherwise indicated.

Table 4. (continued)

Group	Collection numbers of specimens	
7. A. hallii	852	
	CW-1	BFL-4
	CW-2	Dean 367
	BFL-3	

Figure 3. Discriminant analysis of diploid groups, based on 27 morphological variables.

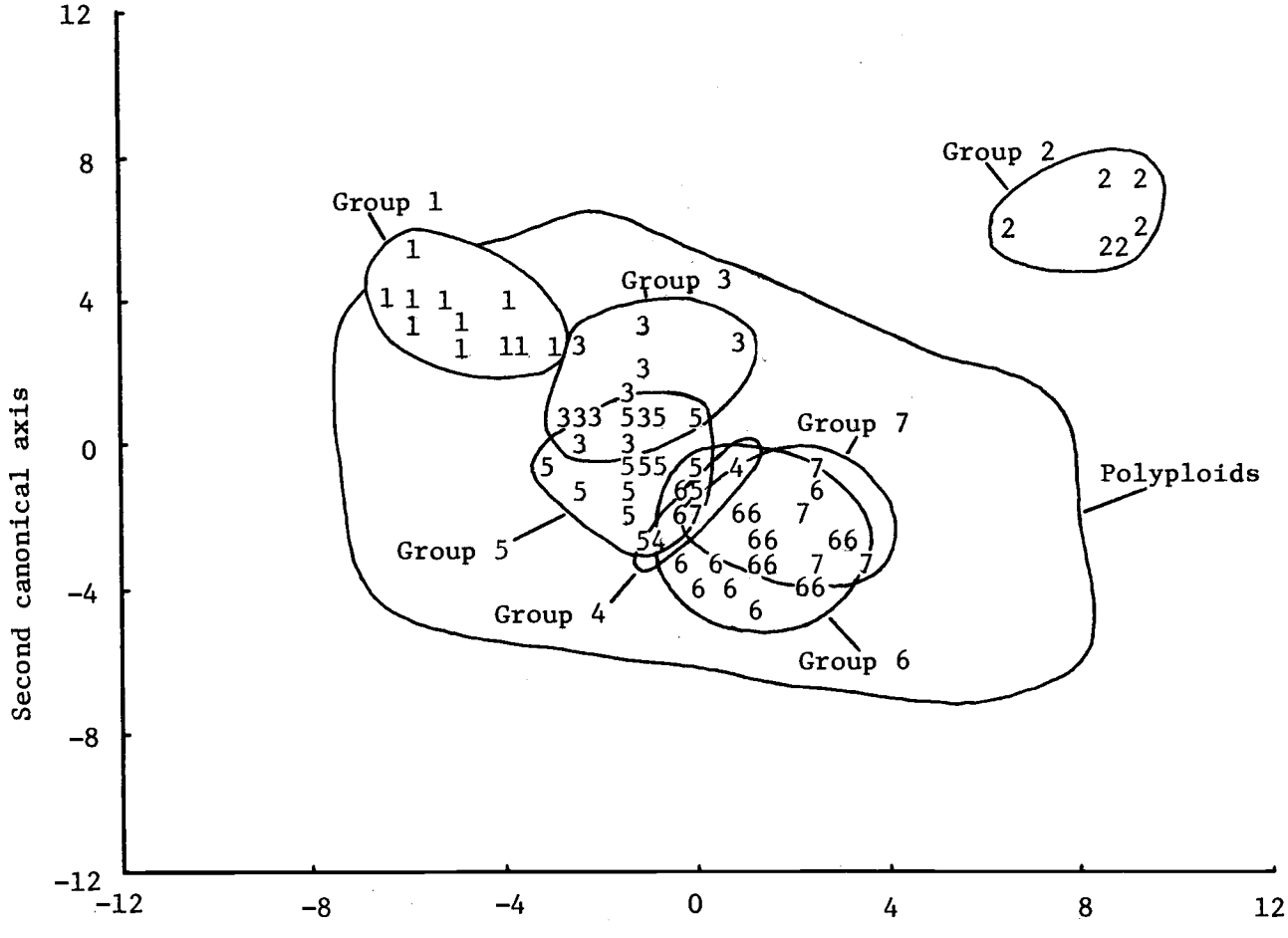
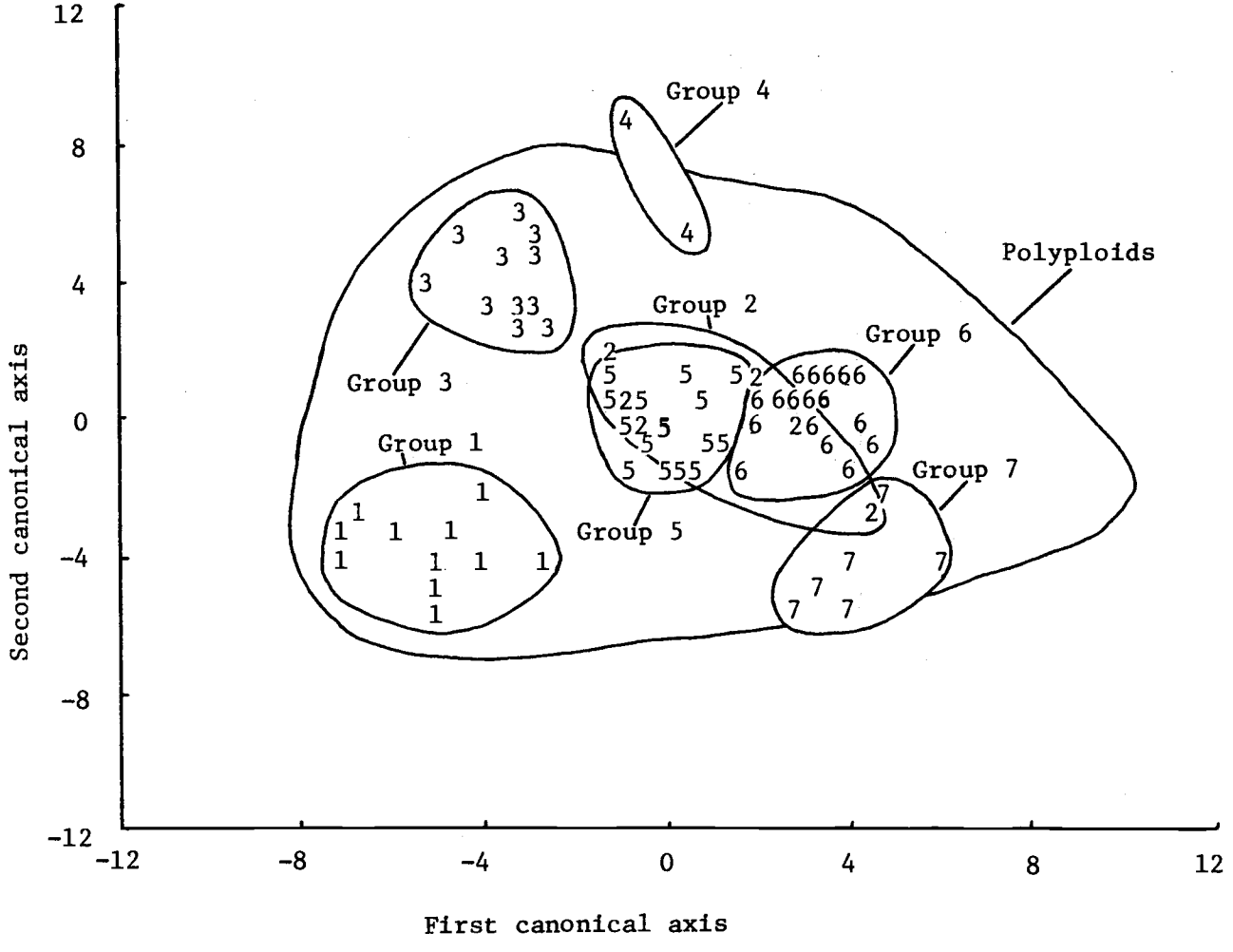


Figure 4. Discriminant analysis of diploid groups, with Group 2 (Aster foliaceus var. canbyi) excluded from the calculation of the axes.



isolated and distinct than others.

Principal components analysis, an ordination method which arranges a "cloud" of OTUs along orthogonal axes of maximum variance, was also performed on the same data matrix for comparison. The individual diploid OTUs plotted along the first two component axes are shown in Figure 5, and the boundaries of the seven diploid groups defined by the clustering program were superimposed. Separation is reasonably good except for Groups 4 and 5. Group 4 (A. "idahoensis") is lacking in coherence; this group was based on only two specimens, and should be examined further before being accepted as a distinct cluster. Group 5 (A. occidentalis) overlaps with Group 1 (A. ascendens) and Group 6 (A. eatonii). However, it may be separated along other axes, since the amount of the total variation expressed along the axes shown (as obtained by summing the first two eigenvalues and dividing by the eigenvalue total) is only 33%.

The principal components analysis, in addition to showing relationships among OTUs, also yielded some information about character association. Examination of the character correlation matrices for various runs showed that the characters used fall into several highly correlated groups. Figure 6 shows significant correlations among all 35 characters, based on 52 diploid specimens. (Symbols used are those given in Table 3). There are two main groups, one consisting of plant habit characters (plant height, inflorescence length, number of flower heads, etc.) and the other including mainly characters of the flowers

Figure 5. Principal components analysis of diploid specimens, using 27 morphological variables.

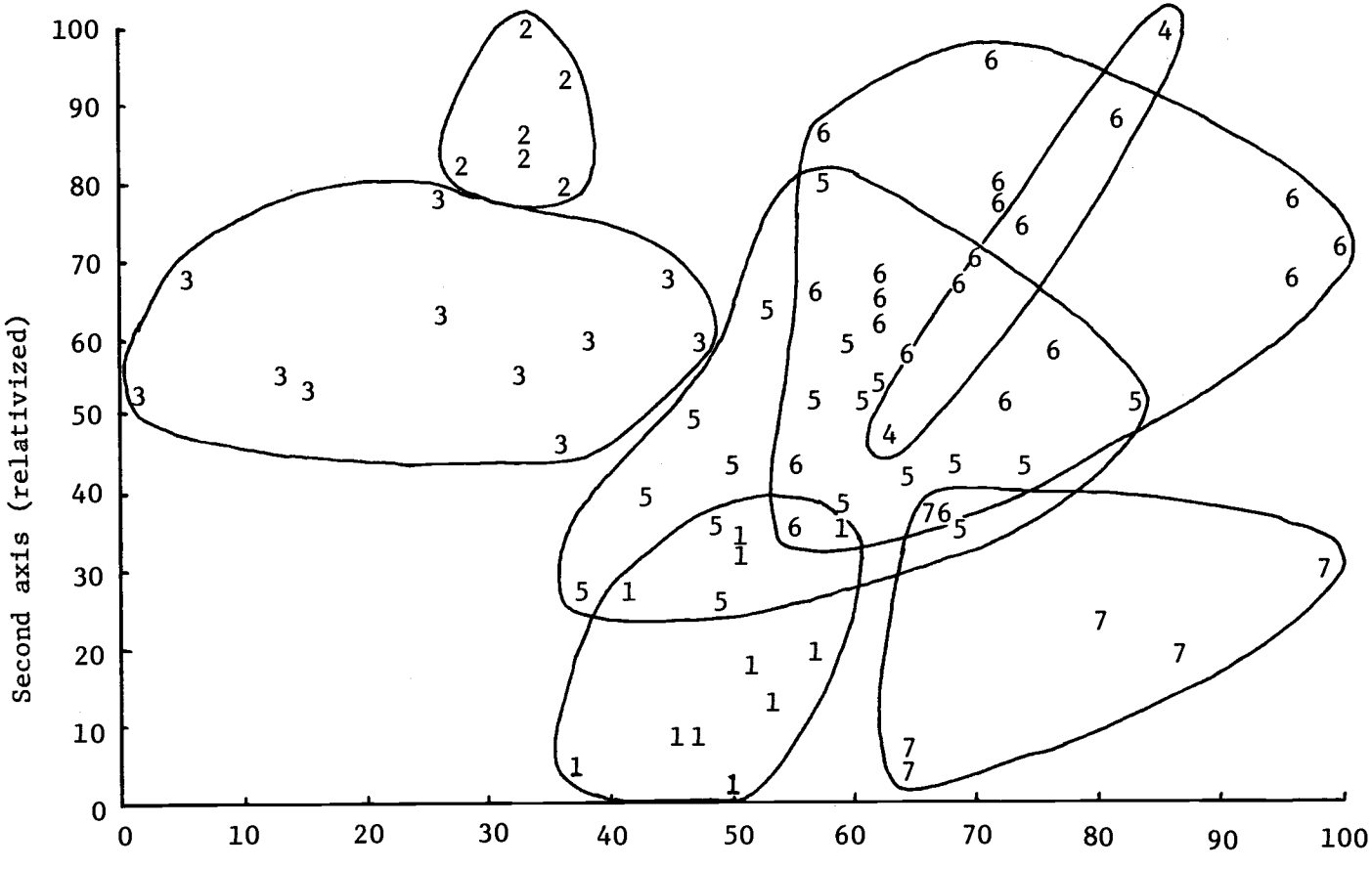
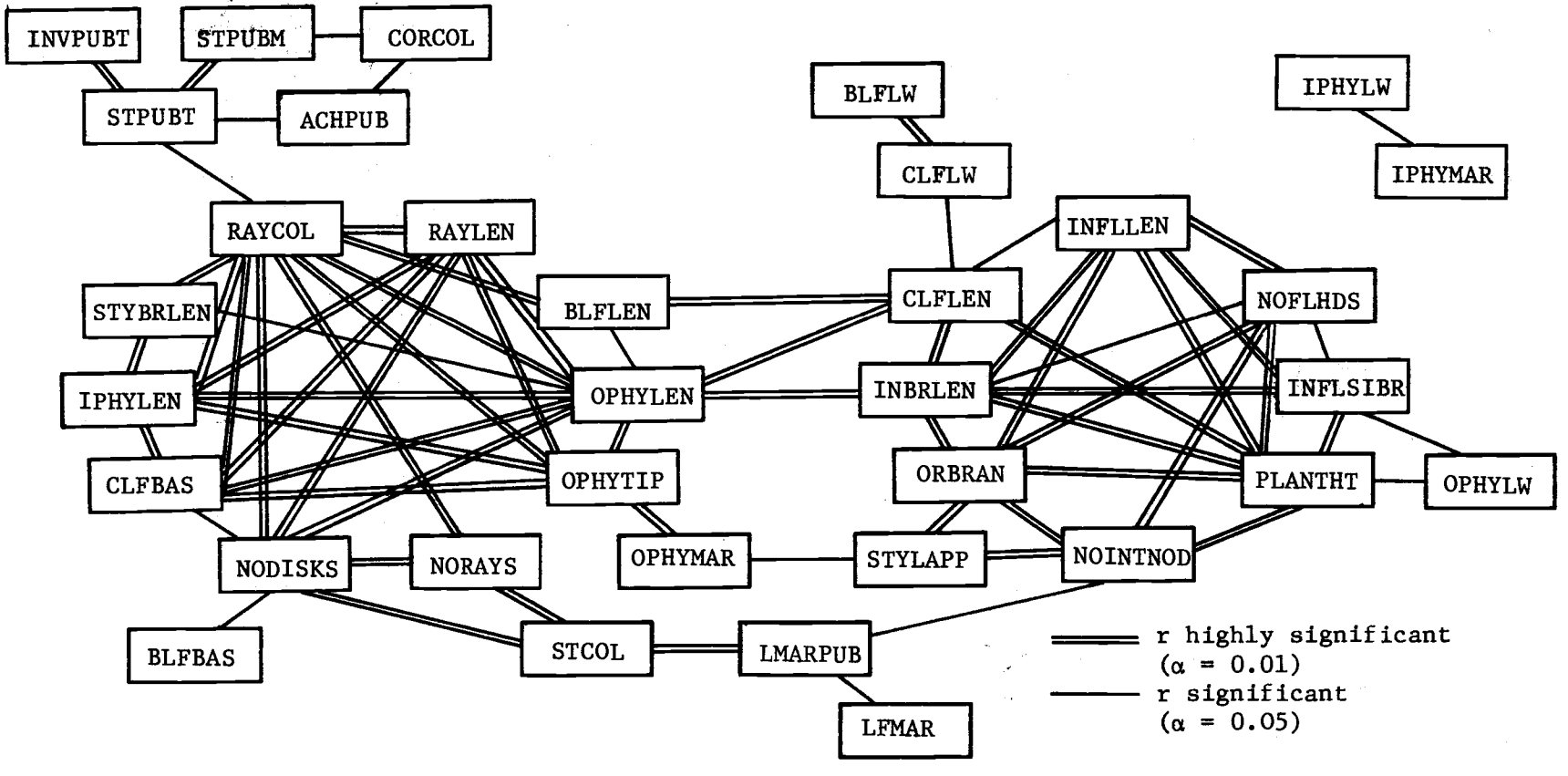


Figure 6. Constellation diagram showing correlations between morphological characters.



and flower heads. There is also a small group of characters dealing with pubescence. Some of these groups may well reflect environmental parameters acting simultaneously on several characters, rather than actual genetic correlation.

For both the clustering and principal components analysis, results were less affected by removing characters than by reducing the number of specimens examined. The groups finally arrived at were based mainly on the characters for which all OTUs had values, in order to make use of as many diploid specimens as possible.

Morphological features of the seven main groups are briefly outlined below, and the mean character values for each group are given in Table 5. For convenience each group is referred to by the name of the taxon (Dean 1966) which it most closely resembles. The groups are:

(1) A. ascendens -- plants of short to moderate height, with narrow, grayish-green, slightly leathery leaves; flower heads variable in number; phyllaries imbricate, the inner acute, the outer ones obtuse; rays violet; plants moderately pubescent throughout.

(2) A. foliaceus var. canbyi -- plants of medium height with long internodes, leaves large and reduced up the stem, cauline leaves often clasping; flower heads few, large; phyllaries very foliaceous, outer ones obtuse to spatulate; rays violet.

(3) A. foliaceus vars. foliaceus, parryi -- plants short to medium height, with long internodes; leaves reduced up the stem; flower heads large, few; phyllaries foliaceous to imbricate, outer ones

Table 5. Means and standard deviations of character values for each diploid group.

Character	Diploid groups						
	1	2	3	4	5	6	7
PLANTHT	28.3 ± 8.2	48.0 ± 8.9	29.9 ± 19.0	96.0 ± 38.3	49.7 ± 20.0	77.1 ± 22.5	44.4 ± 15.0
NOINTNOD	19.3 ± 5.4	11.8 ± 1.2	9.5 ± 3.7	25.5 ± 3.6	21.6 ± 9.9	30.8 ± 7.9	44.8 ± 7.3
NOFLHDS	20.9 ± 19.9	11.0 ± 3.0	8.0 ± 7.3	46.0 ± 4.2	33.2 ± 29.6	66.0 ± 50.3	78.4 ± 69.0
INFLLEN	22.6 ± 25.9	27.7 ± 5.9	14.0 ± 9.9	52.0 ± 25.5	20.7 ± 10.5	34.6 ± 13.5	18.8 ± 10.8
INFLSIBR	5.9 ± 3.0	11.4 ± 2.5	4.7 ± 3.3	25.5 ± 17.7	7.3 ± 4.1	8.4 ± 3.7	6.5 ± 4.7
ORBRAN	1.75 ± .58	1.85 ± .27	1.00 ± .53	2.50 ± .71	1.97 ± .46	2.24 ± .41	2.24 ± .51
BRACLEN	2.0 ± 1.2	4.9 ± 0.5	3.0 ± 1.3	4.1 ± .8	3.2 ± 1.7	5.5 ± 1.8	1.6 ± .3
CLFLEN	47.1 ± 12.2	91.7 ± 10.5	64.0 ± 16.0	48.5 ± 9.2	77.8 ± 19.0	92.2 ± 27.0	35.8 ± 15.9
CLFLW	92.8 ± 12.0	139.0 ± 47.8	68.8 ± 23.6	36.0 ± 8.5	144.5 ± 96.0	129.6 ± 54.6	132.8 ± 87.8
CLFBAS	1.07 ± .79	1.83 ± .41	1.29 ± .80	1.00 ± 1.41	1.16 ± .75	0.82 ± .65	1.00 ± .71
LFMAR	1.05 ± .15	1.18 ± .33	1.19 ± .36	1.00 ± 0	1.24 ± .34	1.24 ± .37	1.30 ± .45
STCOL	1.41 ± .40	1.45 ± .41	1.98 ± .71	1.75 ± .35	1.52 ± .55	1.75 ± .52	1.00 ± 0
ACHPUB	2.70 ± .34	1.00 ± 0	2.00 ± .13	2.50 ± .71	2.12 ± .27	2.00 ± .29	2.16 ± .36
INVPUB	2.64 ± .46	1.83 ± .29	2.00 ± .51	1.25 ± .35	2.00 ± .47	1.55 ± .29	1.40 ± .55

Table 5. (continued)

Character	Diploid groups 1	2	3	4	5	6	7
STPUBT	3.41 ± .51	2.72 ± .34	3.25 ± .49	2.75 ± .35	3.10 ± .60	2.98 ± .37	2.30 ± .45
STPUBM	2.03 ± .46	1.88 ± .29	1.98 ± .57	1.50 ± .71	1.63 ± .68	1.83 ± .62	1.62 ± .79
LMARPUB	4.8 ± .8	5.7 ± 1.1	6.8 ± 3.0	8.3 ± 4.6	6.6 ± 2.4	6.8 ± 1.5	8.0 ± 1.9
OPHYLEN	2.92 ± .53	7.20 ± .54	5.41 ± 1.72	3.05 ± .07	3.65 ± .84	4.70 ± 1.34	2.70 ± .12
OPHYLW	4.2 ± .8	2.2 ± .2	5.2 ± 1.2	7.8 ± 2.1	4.9 ± 1.0	4.7 ± 1.0	3.5 ± .5
OPHYTIP	2.7 ± .5	3.8 ± .3	1.9 ± .5	1.8 ± .4	1.9 ± .3	1.9 ± .6	2.3 ± .6
OPHYMAR	.50 ± .08	.47 ± .03	.10 ± .10	0 ± 0	.31 ± .12	.28 ± .11	.58 ± .06
IPHYLEN	4.76 ± .54	9.63 ± 1.00	6.37 ± 1.41	4.60 ± .42	4.61 ± .47	4.78 ± .54	4.20 ± .32
IPHYLW	7.4 ± 1.3	8.0 ± 2.6	7.0 ± 1.9	10.4 ± .9	7.7 ± 1.1	7.3 ± 1.6	7.1 ± 1.4
IPHYTIP	1.6 ± .4	1.6 ± .6	1.3 ± .5	1.0 ± 0	1.6 ± .5	1.7 ± .3	1.6 ± .4
IPHYMAR	.65 ± .07	.66 ± .07	.52 ± .19	.50 ± .06	.61 ± .16	.63 ± .16	.68 ± .01
NORAYS	27.9 ± 6.0	30.8 ± 2.1	37.7 ± 7.0	35.0 ± 5.6	25.2 ± 5.8	27.3 ± 5.8	16.8 ± 2.9
NODISKS	44.4 ± 9.9	100.7 ± 19.8	107.9 ± 34.5	74.5 ± 6.4	58.3 ± 21.0	51.8 ± 11.4	22.6 ± 4.8

mostly acute to slightly obtuse; rays violet.

(4) A. idahoensis -- plants moderately tall, leaves somewhat reduced upward; inflorescence with long side branches; flower heads moderately numerous; phyllaries imbricate, acute and extremely narrow; rays violet.

(5) A. occidentalis -- plants short to moderately tall; leaves variable in shape, reduced upwards; flower heads moderately numerous; phyllaries imbricate to somewhat foliaceous, acute; rays violet.

(6) A. eatonii -- plants moderately to very tall; leaves broad, scarcely reduced upward, basal leaves usually absent by anthesis; inflorescence often long and slender, leafy, with very numerous flower heads; phyllaries foliaceous (especially in terminal heads), often somewhat reflexed, acute; rays pink to white.

(7) A. hallii -- plants of moderate height, with many short internodes; leaves small, not reduced upwards, basal leaves absent by anthesis; inflorescence elongate to corymbose, with short side branches; flower heads very numerous, small, with few rays and disks; phyllaries imbricate, mostly acute; rays pinkish-white to white.

2. Polyploids

To determine overall patterns of variation in the group, polyploid specimens were added to the diploids to bring the total to 200 specimens (the maximum capacity of the clustering program used), and the entire data set was analyzed by the same methods as for the diploids alone. Cluster analysis using CLUSB with 27 characters showed that for the most part, the diploids grouped into the same clusters as before,

especially the more distinct groups such as A. foliaceus var. canbyi. The polyploids, as might be expected, tended to clump with the diploids that they resembled, but many more intermediate forms were apparent. Thus the clusters were considerably less distinct when the polyploids were included. Treatments of this group by previous authors recognize a number of taxa which contain only polyploid chromosome numbers. Specimens belonging to these taxa tended not to form their own groups but clustered with various groups of diploids. Only specimens referable to A. cusickii (a taxon closely allied to A. foliaceus) formed a separate group.

When discriminant analysis is used to superimpose the polyploid OTUs on a plot displaying the diploid groups (see Figures 3 and 4), it is apparent that the polyploids encompass the whole range of variability of the diploids (with the exception of group 1) and extend beyond this range, evidently including combinations of characters not found at the diploid level. Principal components analysis also showed that variation at the polyploid level eclipsed that at the diploid level (Figure 7).

Variation among polyploids was distributed somewhat differently at each ploidy level. Figures 8 and 9 show how the arrangements of the various ploidy levels in discriminant space relate to those of the diploid groups and to the total polyploid distribution. Figure 8 views the groups from the same perspective as in Figure 3, and Figure 9 axes correspond to those of Figure 4. Tetraploid (n = 16) and hexaploid (n = 24) levels showed the greatest variability. Some polyploids showed

Figure 7. Principal components analysis of 200 diploid and polyploid specimens, using 27 morphological variables.

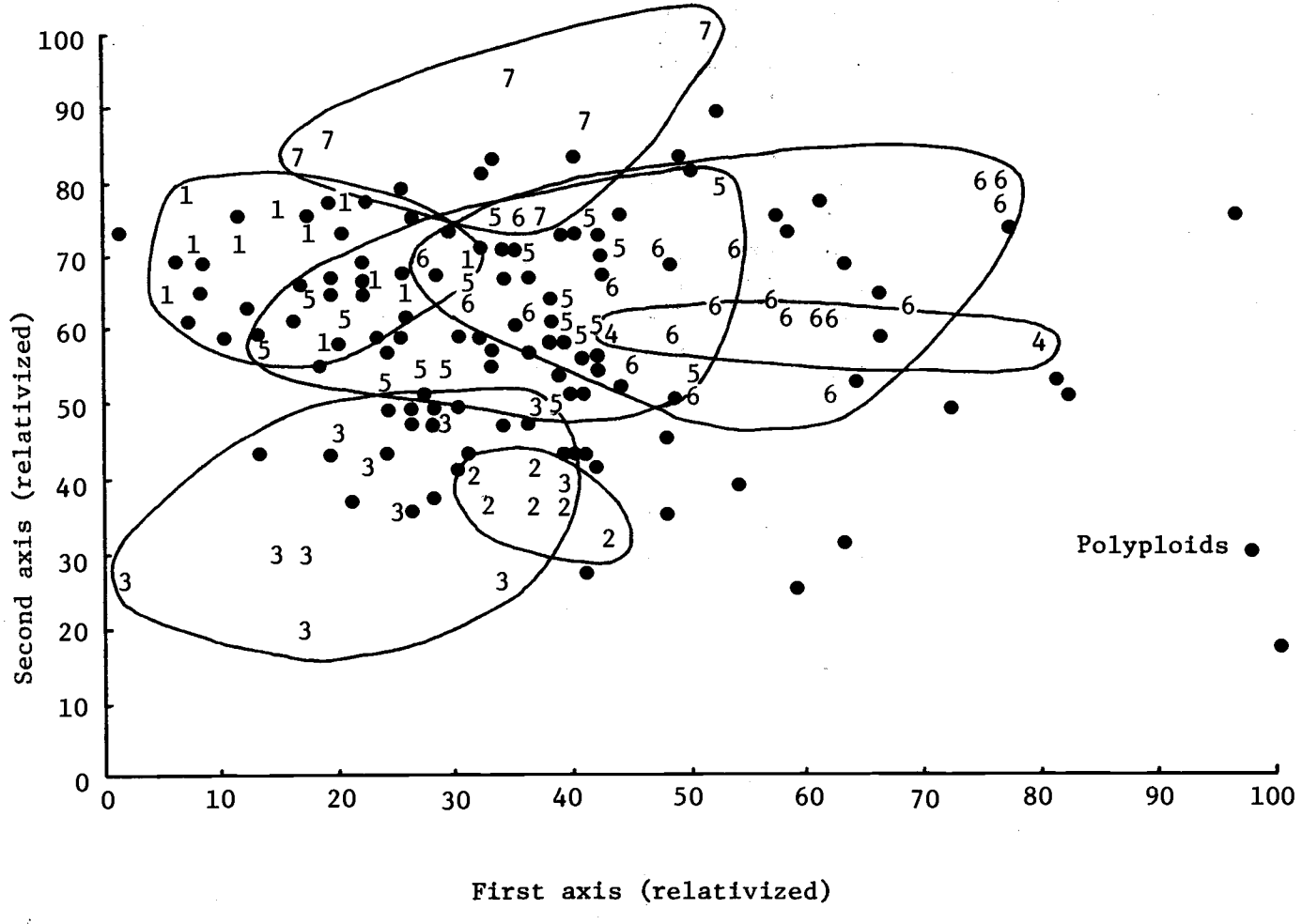


Figure 8. Discriminant analysis of different polyploid levels, superimposed on the axes calculated from seven diploid groups.

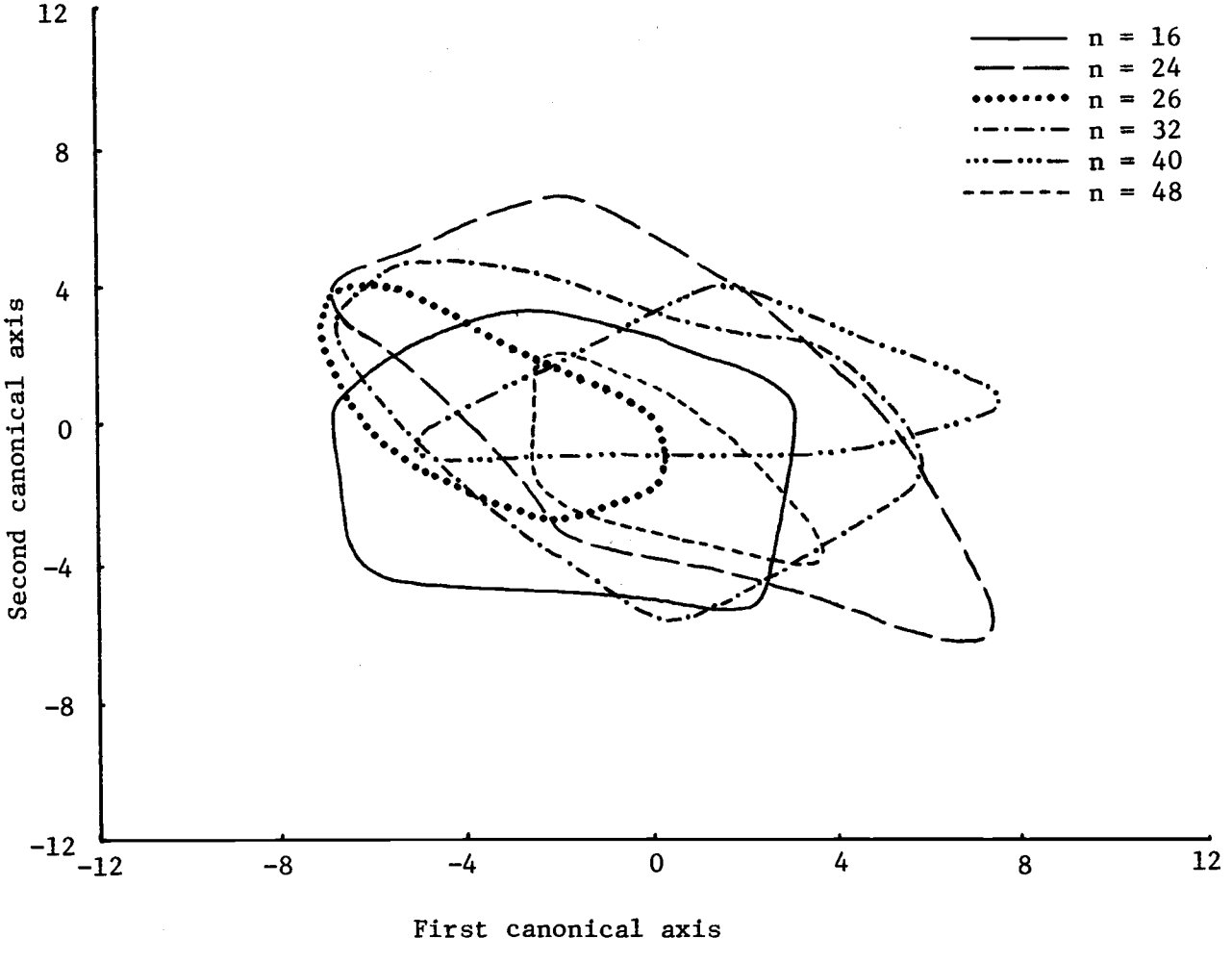
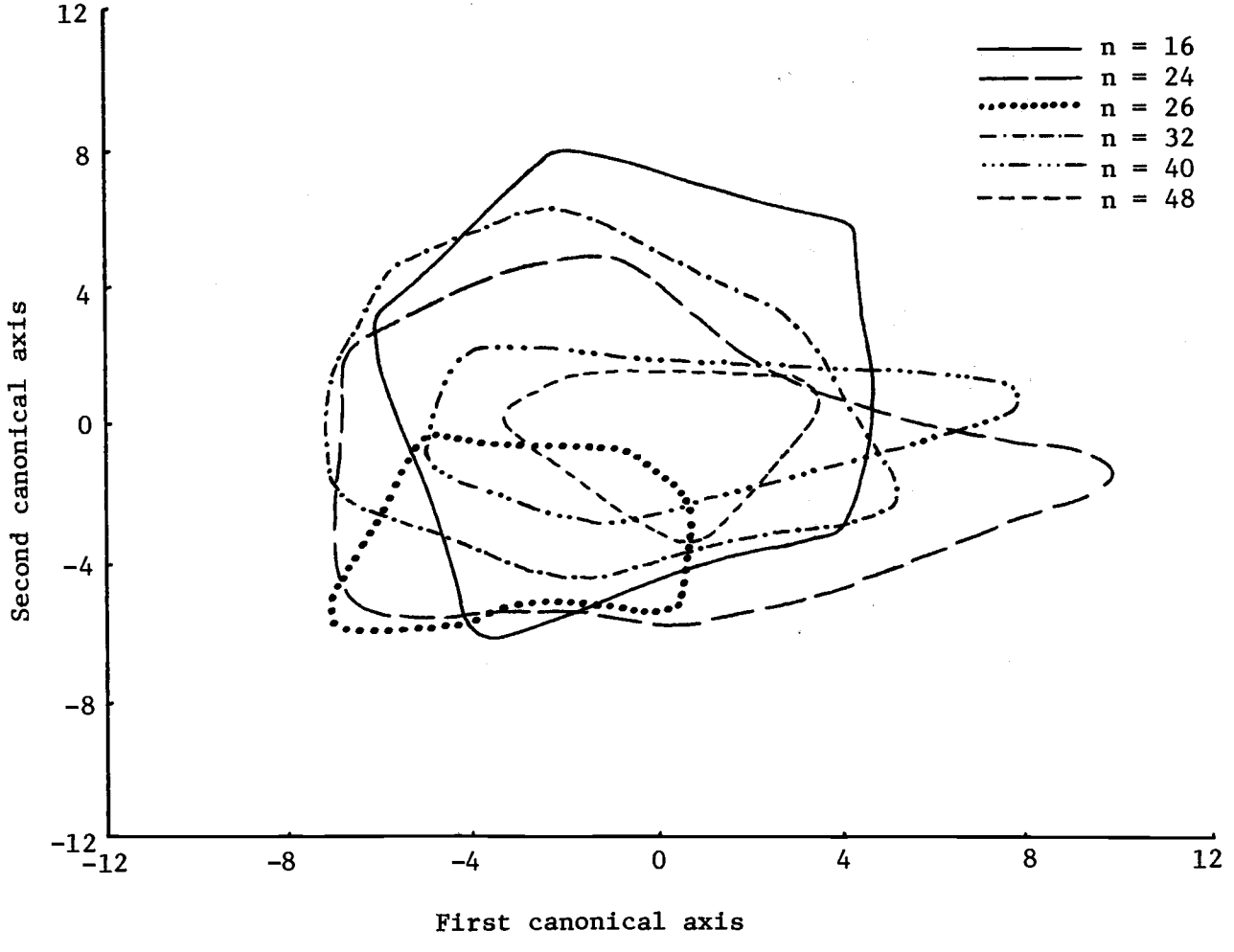


Figure 9. Discriminant analysis of different polyploid levels, superimposed on the axes calculated from six diploid groups.



a close relationship to a particular diploid group; for example, the polyploids with n = 26 corresponded closely with the diploid group 1, which has n = 13. However, most polyploid levels bridged several diploid groups.

Chromosome Behavior and Karyotype Analysis

1. Chromosome Behavior

Pairing of chromosomes was normal in most of the meiotic preparations examined. Figures 10 to 13 show Metaphase I in four plants of various ploidy levels. In general, polyploids showed no multivalent formation or other evidence of autoploidy. The exceptions to this were polyploids with a chromosome number of n = 26. In many of these the chromosomes were "sticky" and not readily separated at Metaphase I (Figures 14 and 15). A single diploid specimen of A. occidentalis from northern California showed 6 chromosome pairs and a ring of 4 chromosomes (Figure 16). Other plants from the same population showed normal pairing.

In many of the plants examined, especially diploids, B chromosomes were present. They were very small and sometimes lagged on the metaphase plate during cell division. The largest number found was in a specimen of the endemic California taxon A. greatai, which had 6 accessory chromosomes (Figure 17). Although not closely associated with any particular morphological type, B chromosomes occurred most commonly in A. eatonii, A. occidentalis and A. foliaceus.

Figure 10. Meiosis in Aster foliaceus (#806).

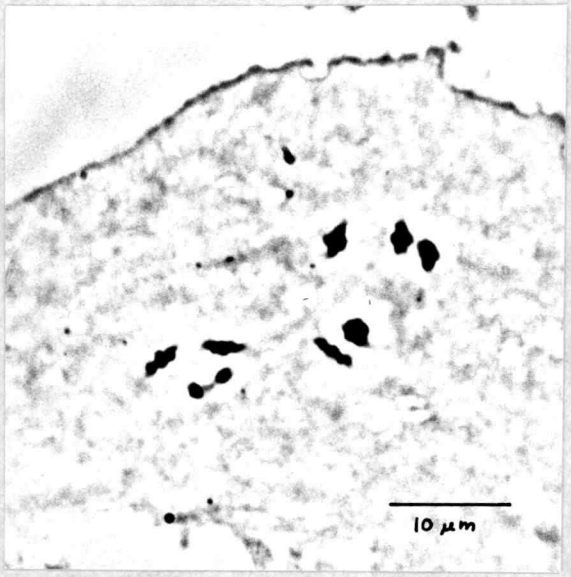


Figure 11. Meiosis in Aster occidentalis (#634).

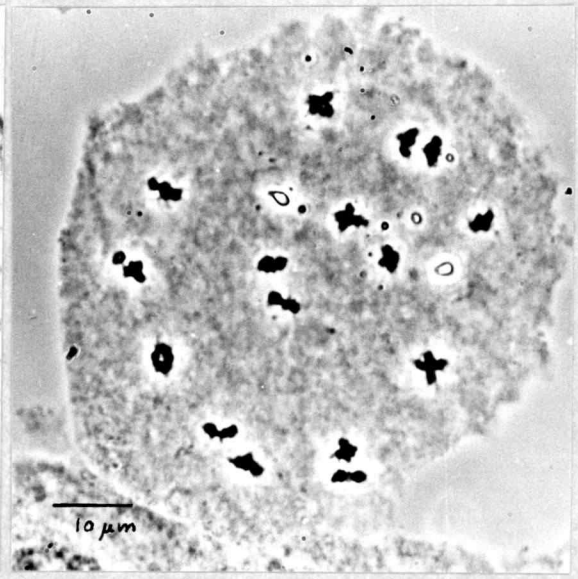


Figure 12. Meiosis in Aster eatonii (#622).

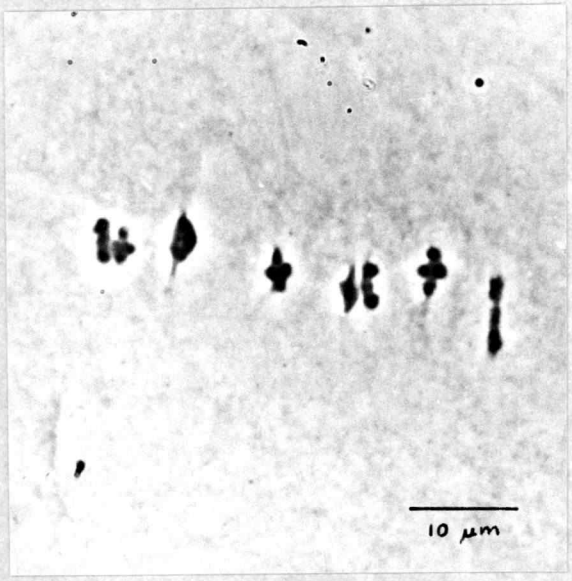


Figure 13. Meiosis in Aster subspicatus (#522).

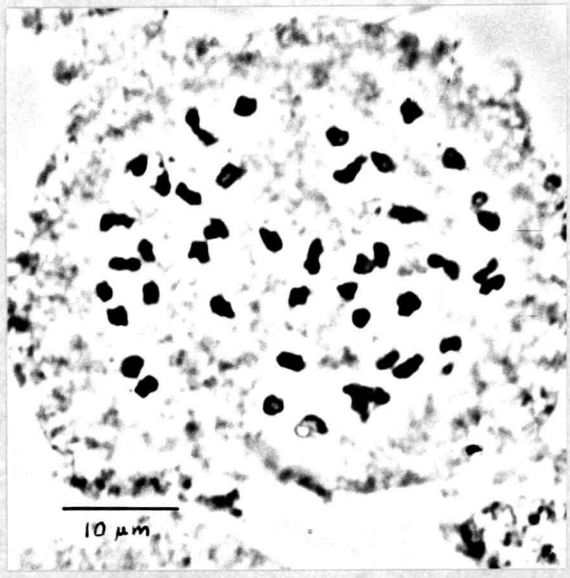


Figure 14. Meiosis in Aster ascendens tetraploid, showing "sticky" chromosomes.

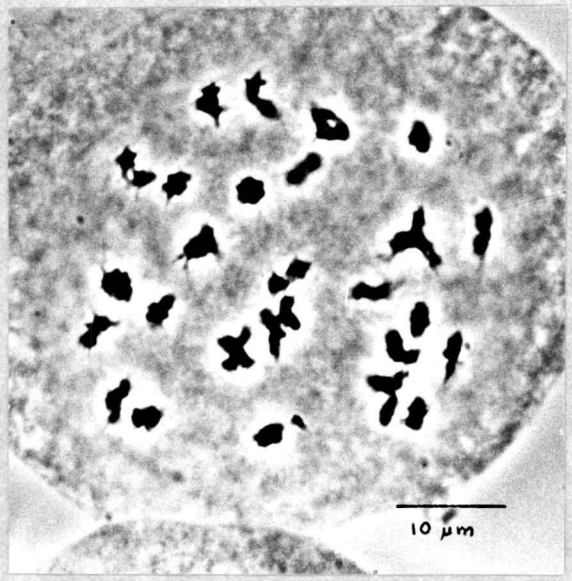


Figure 15. Meiosis in Aster ascendens tetraploid, showing "sticky" chromosomes.

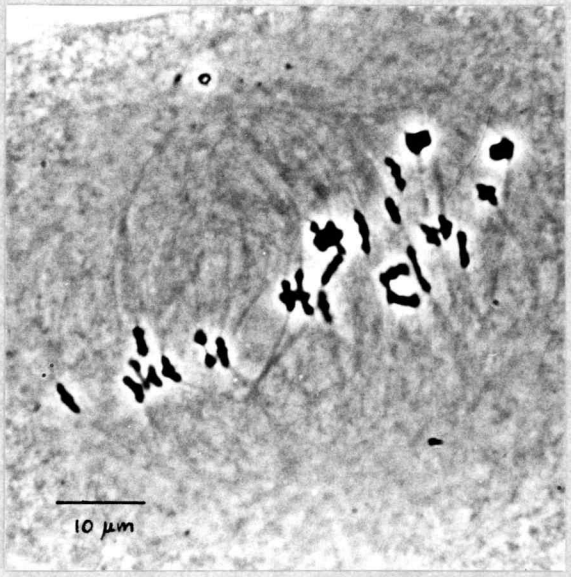


Figure 16. Meiosis in Aster occidentalis (#558) showing six pairs and a ring of four.

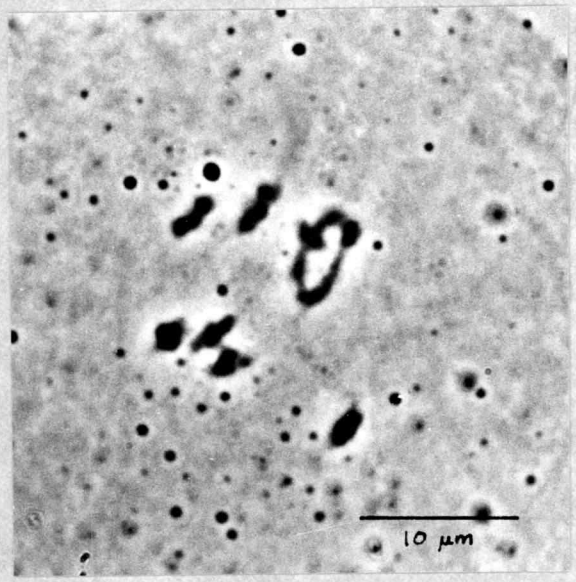
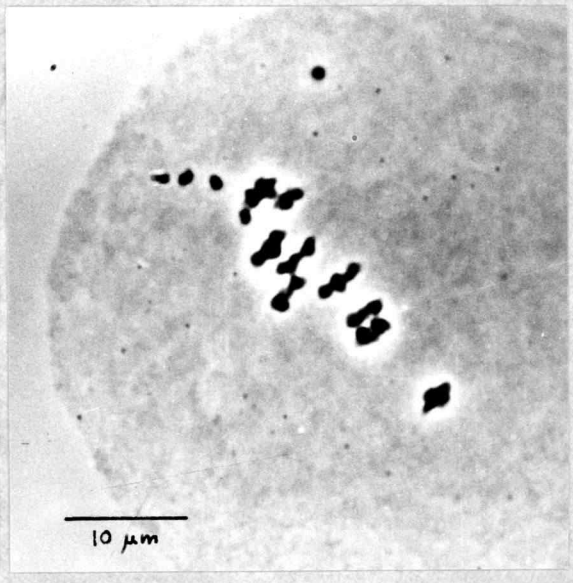


Figure 17. Meiosis in Aster greatai (#605) showing B chromosomes.



2. Karyotype Analysis

Root tip preparations of various morphological types and ploidy levels were made for karyotype analysis. Specimens from the following morphological groups were examined: A. eatonii (n = 8), A. occidentalis (n = 8, n = 16), A. foliaceus (n = 8, n = 9, n = 18, n = 32) and A. ascendens (n = 13, n = 21, n = 26). The karyotypes of these and related asters have been little investigated by previous workers, since most of the chromosome numbers that have been published were determined from buds. The literature contains a single report by Huziwara (1958) on the karyotype of A. occidentalis and other North American species, and a report by Semple (1976) on the karyotype of a distantly related species, A. ericoides.

The karyotypes of the specimens examined here fell into two groups. The first of these was a relatively symmetrical karyotype (the ratio of the longest to shortest chromosomes in well-condensed chromosome preparations ranged from 1.6 to 2.0) and included all specimens with chromosome base numbers of 8 or 9. Within this group there was little variation among specimens (see Figures 18 to 22). Centromeres varied from median to submedian, and in several specimens (Figures 20, 21 and 22) a secondary constriction was visible on one pair of chromosomes, forming a large satellite.

The second group consisted of specimens having the morphology of A. ascendens, with chromosome numbers of n = 13, 21 or 26. These had a much more asymmetrical karyotype, with the ratio of the longest to

Figure 18. Karyotype of Aster foliaceus (#801).

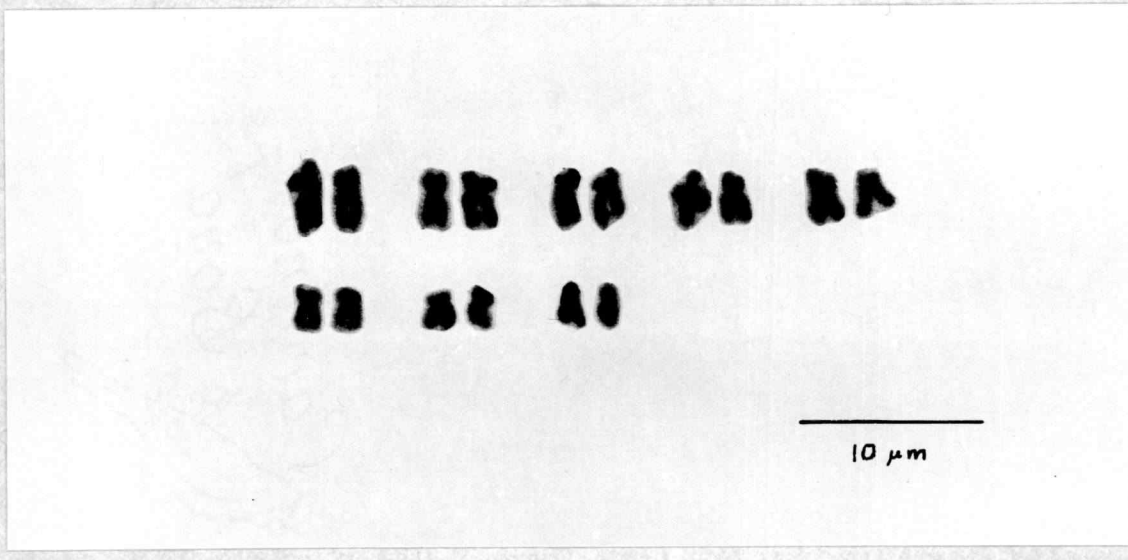


Figure 19. Karyotype of Aster foliaceus (#715).

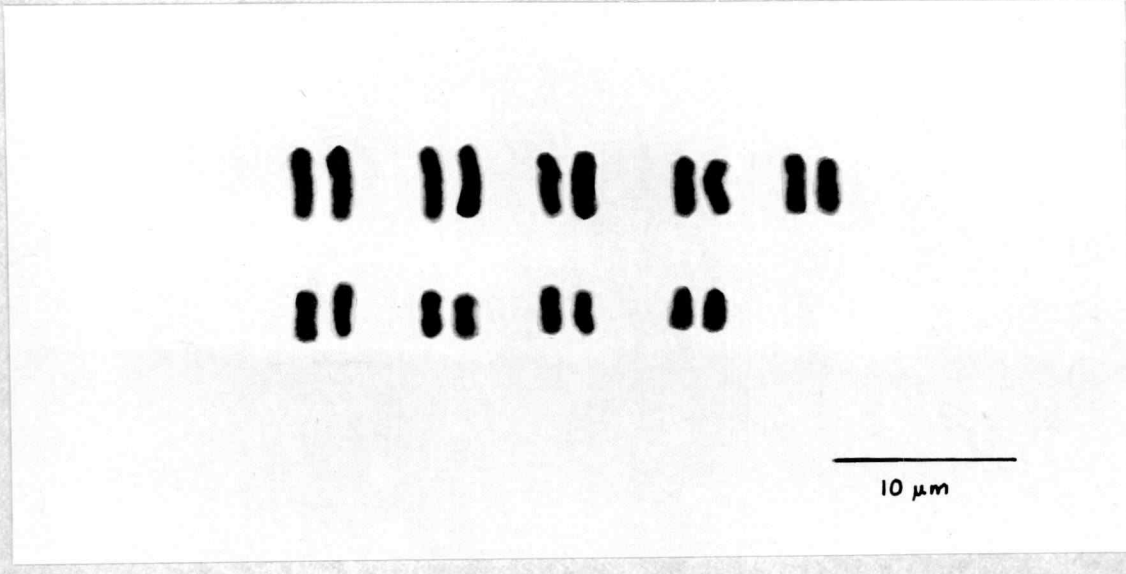


Figure 20. Karyotype of Aster occidentalis (#556).

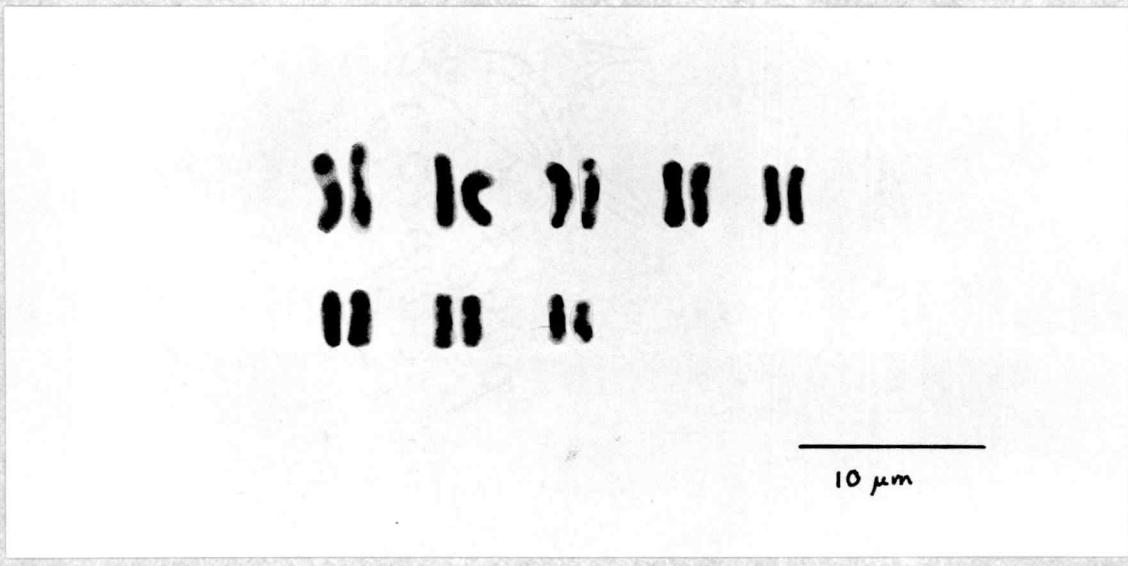


Figure 21. Karyotype of Aster occidentalis (#585).

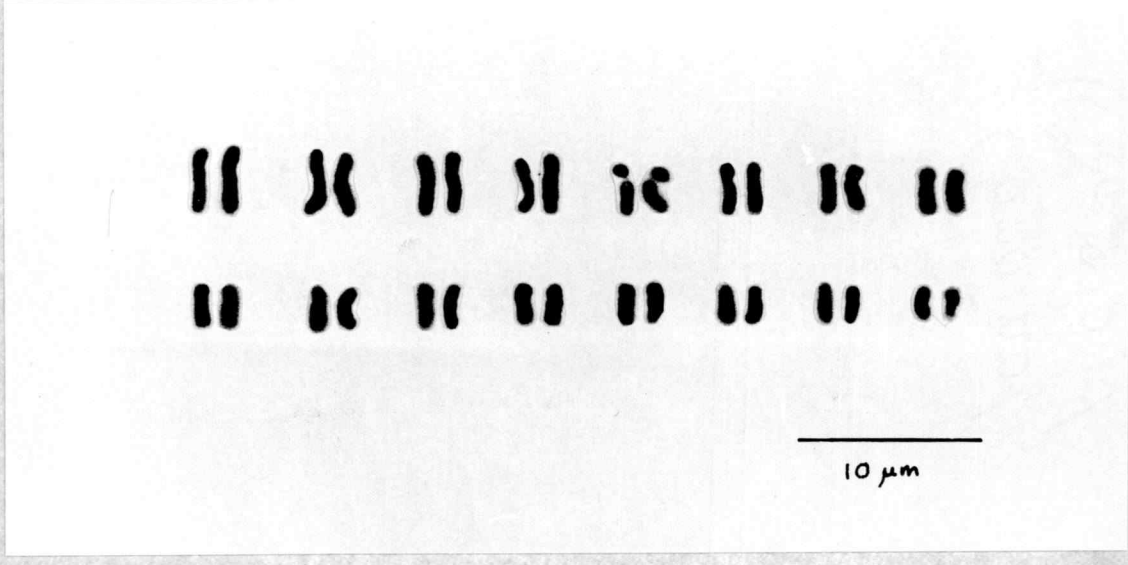


Figure 22. Karyotype of Aster eatonii (#860).

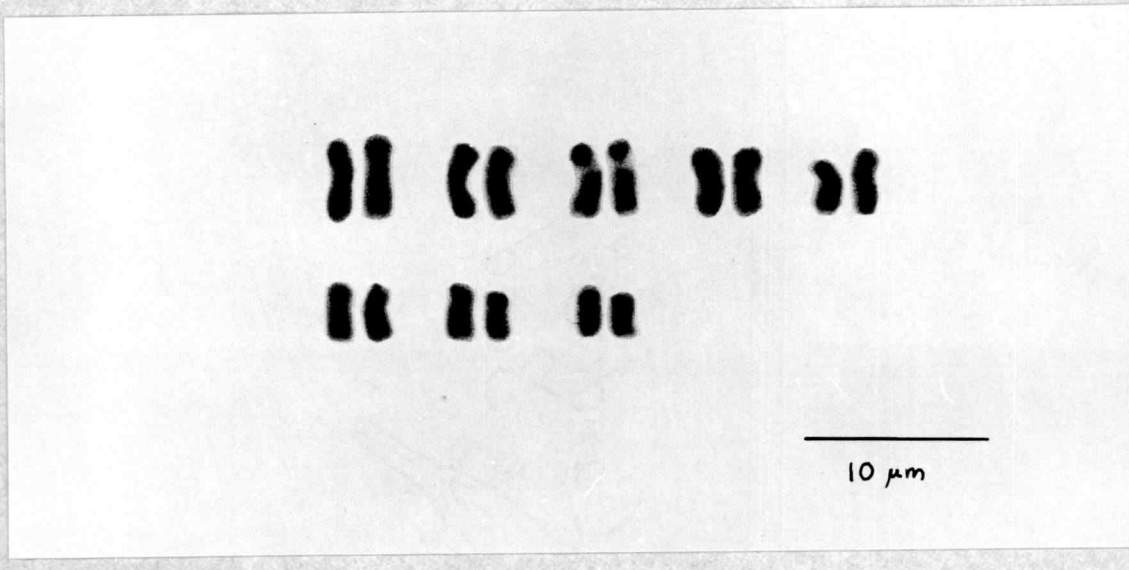
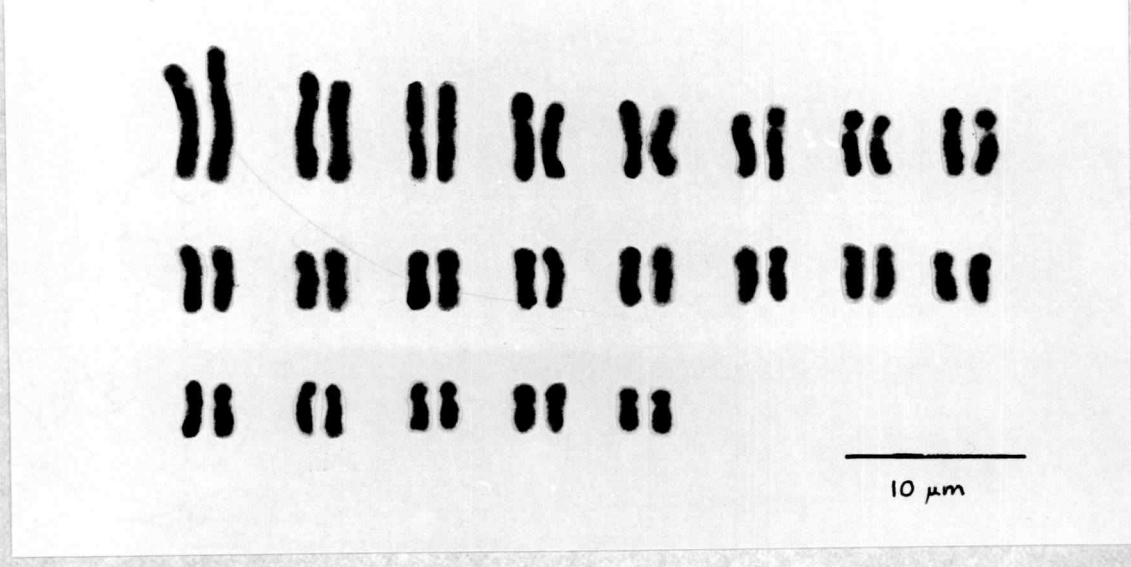


Figure 23. Karyotype of Aster bernardinus (#603).



the shortest chromosomes falling into the range 2.6 to 3.2 (Figures 23 to 25). In this group the karyotype shows three to six pairs of large chromosomes that are individually recognizable and are readily distinguished from the more uniformly sized smaller chromosomes. The positions of centromeres varied from median to subterminal. Secondary constrictions like those present in the previous group were also visible in some cases (Figures 23 and 25).

Reproductive Biology and Hybridization Experiments

1. Breeding System

To determine if the Aster species studied are obligate outcrossers, germination rates of seed obtained from selfing were examined in a number of specimens used for the crossing experiments. The results are given in Table 6. Only a few plants produced any viable offspring at all. Seed set rates for crosses made in the greenhouse by Dean (1966), between different plants of the same species, varied from 21.3% to 74.3%. Dean's results may be an underestimate of seed set under natural conditions, since plants grown in a field plot generally had much better seed set when outcrossed than plants grown in the greenhouse.

2. Interfertility at the Diploid Level

Crosses involving both diploid and polyploid specimens representing a variety of morphological types were performed during three field seasons. Table 7 summarizes the crosses made. Of these, the few that yielded progeny are listed in Table 8. Figure 26 gives the attempted

Figure 24. Karyotype of Aster ascendens (#502).

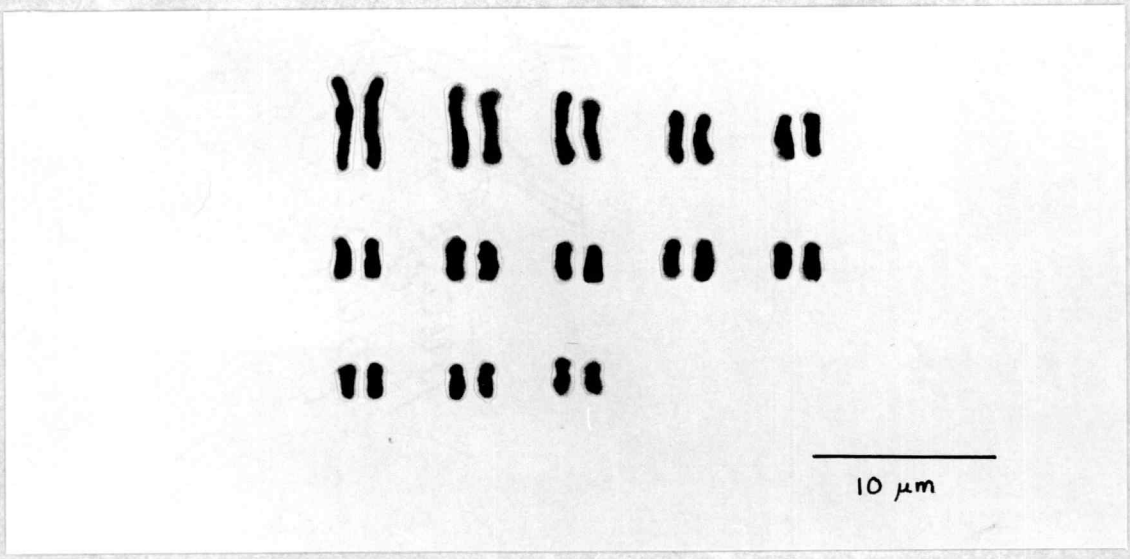


Figure 25. Karyotype of Aster ascendens (#758).

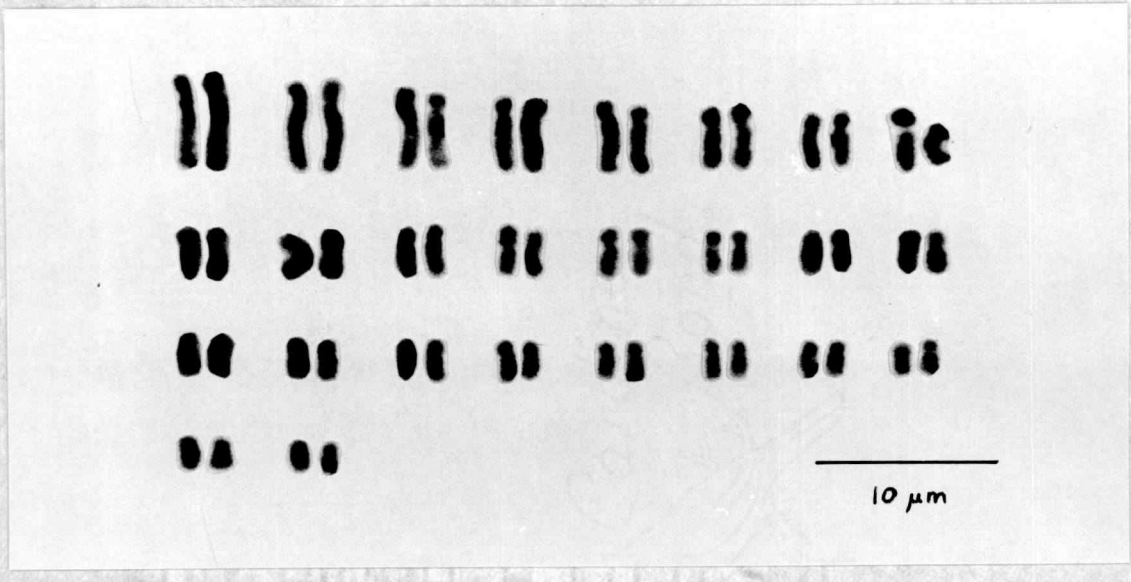


Table 6. Germination rates for self-pollinated seed.

Species	Collection Number	Number of seeds	Percent Germination
A. ascendens	501	250	0
	502	250	0
	512	85	0
	688	150	0.7
A. eatonii	553	90	0
	653	60	0
	B-7	100	0
	B-9	35	3.0
	B-29	250	0
A. foliaceus	B-19	250	0
	B-20	250	0
	B-22	250	0
	B-23	250	1.6
A. idahoensis	641	250	0
A. occidentalis	561	150	0
	582	100	0
	609	100	0
	666	100	3.3

Table 7. Plants used for crosses involving diploids.[1]

Seed Parent	Pollen Parent: A. ascendens	A. eatonii	A. foliaceus var. canbyi
A. ascendens		504 x 553	
A. eatonii	553 x 504	(KLC 4414 x 653) (653 x KLC 4414)	
A. foliaceus var. canbyi		BFL-19 x BFL-7 BFL-19 x BFL-29	
A. foliaceus var. foliaceus			
A. foliaceus var. parryi		830 x 860	
A. greatai		605 x 553	605 x BFL-19
A. hallii	CW-1 x 504	CW-1 x 553 BFL-4 x 856	BFL-3 x BFL-19
A. idahoensis	641 x 688 641 x 512	641 x KLC 4414 (641 x 653) 641 x BFL-7	641 x BFL-23
A. lentus			
A. occidentalis	582 x 688	(711 x 653) 561 x BFL-9	557 x BFL-19 582 x BFL-19 609 x BFL-23

[1]If crosses are in parentheses, only one parent was diploid.

Table 7. (continued)

Seed Parent	Pollen Parent: A. foliaceus var. foliaceus	A. foliaceus var. parryi	A. greatai
A. ascendens			
A. eatonii	BFL-7 x BFL-19	860 x 830	553 x 605
A. foliaceus var. canbyi			BFL-19 x 605
A. foliaceus var. foliaceus			
A. foliaceus var. parryi			
A. greatai			
A. hallii	(CW-2 x 661)	BFL-3 x 806	CW-2 x 605 BFL-3 x 605
A. idahoensis			641 x 605
A. lentus	(578 x 661)		(579 x 605) (578 x 605)
A. occidentalis	(666 x 661)		625 x 605 (666 x 605) 609 x 605

Table 7. (continued)

Seed Parent	Pollen Parent		
	A. hallii	*A. idahoensis*	*A. lentus*
A. ascendens	504 x CW-1	688 x 641 512 x 641	
A. eatonii	553 x CW-1 856 x BFL-4	KLC 4414 x 641 (653 x 641) BFL-7 x 641	
A. foliaceus var. *canbyi*	BFL-19 x BFL-3	BFL-23 x 641	
A. foliaceus var. *foliaceus*	(661 x CW-2)		(661 x 578)
A. foliaceus var. *parryi*	806 x BFL-3		
A. greatai	605 x CW-2 605 x BFL-3	605 x 641	(605 x 578) (605 x 579)
A. hallii		CW-1 x 641 BFL-3 x 641	(CW-3 x 578)
A. idahoensis	641 x CW-1 641 x BFL-3		
A. lentus	(578 x CW-3)		
A. occidentalis	625 x CW-1 555 x BFL-4	582 x 641 722 x 641 556 x 641	(665 x 578) (666 x 578)

Table 7. (continued)

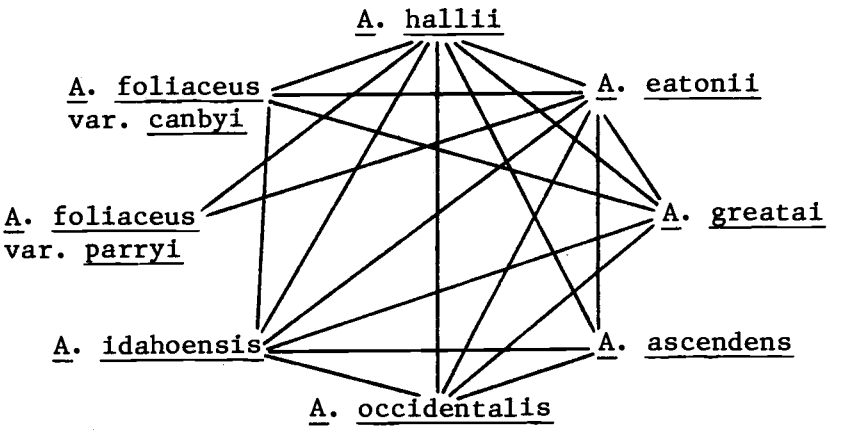
Seed Parent	Pollen Parent A. occidentalis
A. ascendens	688 x 625 504 x 625
A. eatonii	(553 x 666) (653 x 711) BFL-9 x 556
A. foliaceus var. canbyi	BFL-19 x 557 BFL-19 x 582 BFL-23 x 609
A. foliaceus var. foliaceus	(661 x 666)
A. foliaceus var. parryi	
A. greatai	605 x 625 (605 x 666) 605 x 609 605 x 725
A. hallii	CW-1 x 625 (CW-1 x 666) BFL-4 x 555
A. idahoensis	641 x 582 641 x 625 641 x 722 641 x 556
A. lentus	(578 x 665) (578 x 666)
A. occidentalis	(625 x 666) (666 x 625) 609 x 722 722 x 609

Table 8. Successful crosses involving diploids.

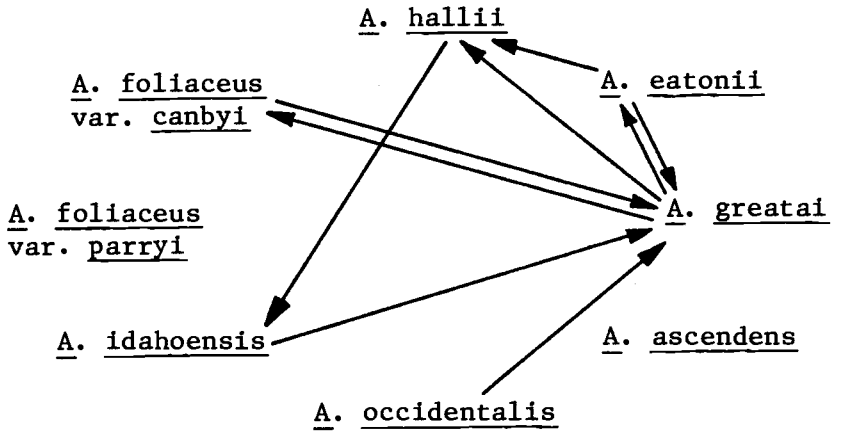
A. hallii (CW-2)	x	A. greatai (605)
A. eatonii (553)	x	A. greatai (605)
A. greatai (605)	x	A. eatonii (553)
A. greatai (605)	x	A. lentus (579)
A. greatai (605)	x	A. occidentalis (625)
A. greatai (605)	x	A. occidentalis (666)
A. greatai (605)	x	A. idahoensis (641)
A. idahoensis (641)	x	A. hallii (CW-1)
A. foliaceus var. canbyi (BFL-19)	x	A. greatai (605)
A. greatai (605)	x	A. foliaceus var. canbyi (BFL-19)
A. eatonii (653)	x	A. occidentalis (711)
A. lentus (578)	x	A. foliaceus var. foliaceus (661)
A. hallii (CW-1)	x	A. eatonii (553)

Figure 26. Attempted and successful crosses at the diploid level.

ATTEMPTED



SUCCESSFUL
(arrow indicates direction of pollen flow)



and successful crosses between diploid taxa. One species, A. greatai, crossed readily with all of the taxa with which it was hybridized. This species has a very restricted distribution and is ecologically and geographically well separated from other taxa in the group. The only taxa which did not yield at least some progeny from artificial hybridizations were A. ascendens, which (as already shown) is cytologically and in general morphologically distinct from the other groups, and A. foliaceus var. foliaceus and parryi (for which only two crosses were made).

Offspring from several of the interspecific crosses reached flowering size. Their morphology was compared to that of their respective parent species, and pollen viability and pairing at meiosis were also examined. Hybrid progeny that flowered were as follows (female parent is listed first):

(1) A. greatai (# 605) x A. eatonii (# 553) and reciprocal cross -- plants were very tall (1 m), with leafy stems (leaves reduced upward) and a well-developed inflorescence with long side branches; flower heads were very numerous; leaves were large and wide, toothed and coarsely pubescent over the surface as in A. greatai; phyllaries were foliaceous, acute, somewhat recurved as in A. eatonii, and rays were pink to white. The reciprocal crosses showed no morphological differences from one another. Pollen viability (from 3 plants) varied from 41.2% to 68.0%.

(2) A. greatai (# 605) x A. occidentalis (# 625) -- the plant was of medium height with well-developed inflorescence; cauline leaves

were narrow, basal leaves wider, all with somewhat toothed margins and scabrous-hairy surface as in A. greatai; phyllaries were long and narrow, acute, with chartaceous edges, the outer ones somewhat foliaceous as in A. occidentalis; flower heads were numerous, with rays very pale violet to white. Pollen viability was 52.4%.

(3) A. idahoensis (# 641) x A. hallii (# CW-1) -- the plant was tall with large leafy-bracted inflorescence; leaves were fairly narrow, reduced upwards; phyllaries were narrow and foliaceous; flower heads were small, with rays white. Pollen viability was 65.2%.

Meiosis was examined in the first two of these crosses. Chromosome pairing was completely regular in both cases (see Figure 27), indicating a close resemblance between the genomes of the respective parents. Pollen viabilities were low in comparison with plants collected in the wild (see next section below).

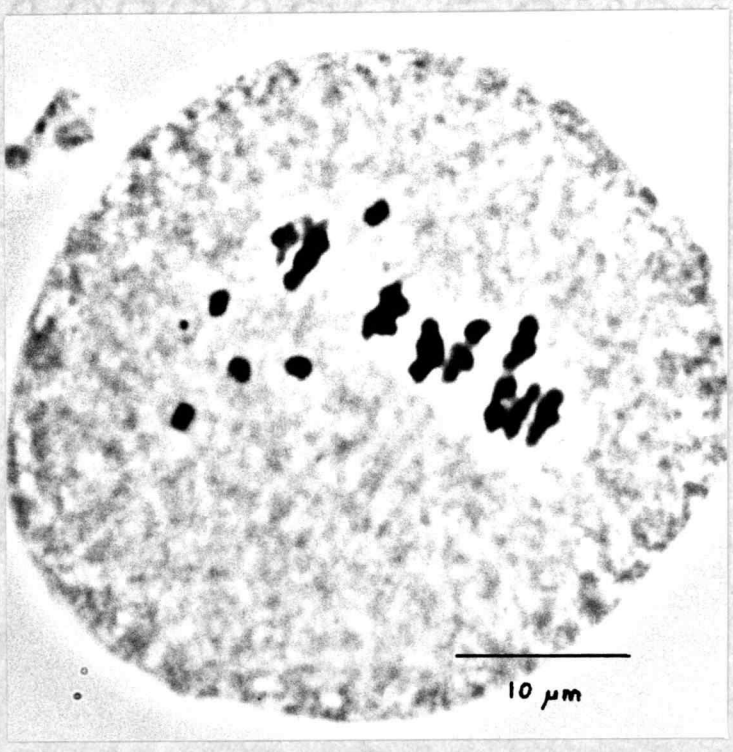
All of the above crosses were between diploids. Two other putative hybrid offspring were also raised to flowering size. These were:

A. greatai (# 605, n = 8) x A. lentus (# 579, n = 32)

A. greatai (# 605, n = 8) x A. occidentalis (# 666, n = 16).

Both plants were morphologically similar to the seed parent; examination of meiosis showed both parents to be diploid (n = 8) with normal pairing. This suggests both were the result of self-pollination in A. greatai. This species, like the others already tested, produces very little normal-appearing seed when prevented from outcrossing, but may have a low rate of self-pollination. The first plant above produced no pollen, and the second had pollen viability of 41.6%; this

Figure 27. Meiosis in an artificial hybrid between A. greatai and A. eatonii, showing regularity of pairing. (B chromosomes are also present.)



is consistent with the "inbreeding depression" that might be expected to result from self-pollination in a normally outcrossing group.

3. Pollen Viability

Pollen viability (as estimated by stainability of samples of 1000 pollen grains) was examined in a large number of specimens collected over the range of the group, in order to investigate the following: (a) the relationship (if any) between pollen viability and ploidy level, and (b) the relationship between pollen viability in diploids and morphological discontinuities between diploid groups.

Pollen stainability counts for all specimens examined are given in Table 9. Figure 28 shows the range of pollen stainabilities at different ploidy levels. There was no difference between the different ploidy levels, except that diploids tended to show more very low counts than the polyploids. This might be expected if the higher ploidy levels were mostly of alloploid origin, since the existence of many similar or duplicate loci derived from different parents should have a buffering effect against deleterious alleles.

No obvious relationship was apparent between low pollen viability of diploids and the pattern of morphological variation. If non-modal morphological types were the result of crossing between diploid species, these might (if the parents were sufficiently different) show a decrease in pollen viability. However, of the nine specimens I examined which had pollen counts below 80% (the normal range was 90 - 100%), most were

Table 9. Pollen viability counts.

Haploid Chromosome Number	Collection Number	Number of viable grains per 1000	Percent Stainability[1]
8	542	932, 892	91.2
8	553	976	97.6
8	555	931	93.1
8	556	924, 981	95.3
8	557	981, 987	98.4
8	560	938	93.8
8	561	925, 629	77.7
8	582	662	66.2
8	586	854	85.4
8	590	844	84.4
8	605	767, 809	78.8
8	609	491, 986	73.9
8	622	968	96.8
8	641	488	48.8
8	722	956	95.6
8	725	838	83.8
8	726	no pollen produced	
8	734	940	94.0
8	736	988	98.8
8	739	705	70.5
8	740	935	93.5

[1]averaged if more than one sample was taken

Table 9. (continued)

Haploid Chromosome Number	Collection Number	Number of viable grains per 1000	Percent Stainability
13	501	852	85.2
13	502	964	96.4
13	504	786, 571, 445	60.1
13	512	945	94.5
13	689	664	66.4
13	845	861	86.1
16	633	888, 930	90.9
16	634	965, 998	98.2
16	648	983	98.3
16	650	981	98.1
16	653	947, 991	96.9
16	665	733, 747	74.0
16	666	765	76.5
16	712	890	89.1
16	BFL-6	775, 789, 852	80.5
24	517	974	97.4
24	702	987	98.7
24	BFL-8	816	81.6
24	BFL-12	907	90.7
24	BFL-14	969	96.9
24	BFL-27	948	94.8
24	BFL-28	958	95.8
24	BFL-32	998	99.8

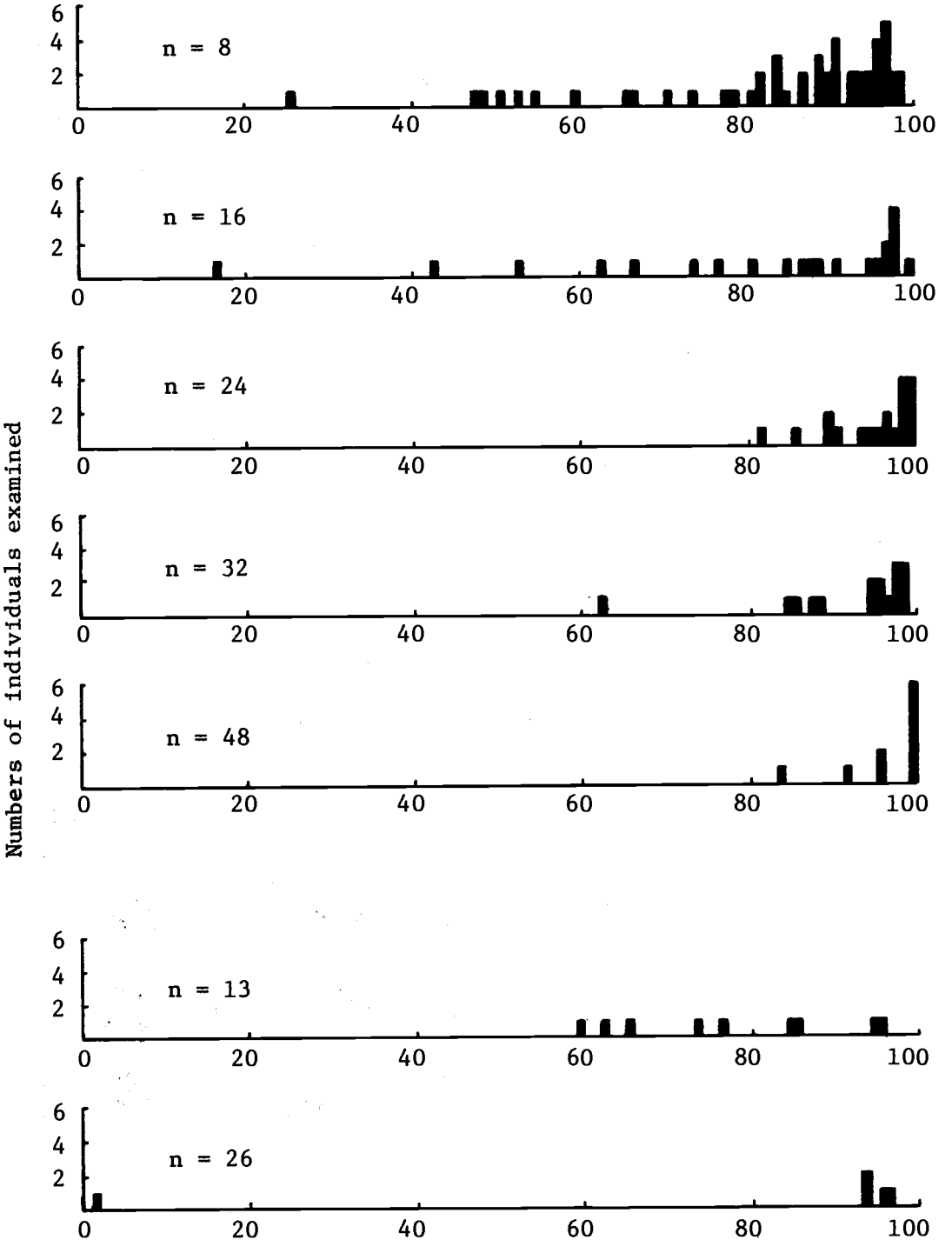
Table 9. (continued)

Haploid Chromosome Number	Collection Number	Number of viable grains per 1000	Percent Stainability
8	766	925	92.5
8	798	no pollen produced	
8	801	914	91.4
8	806	965	96.5
8	809	913	91.3
8	816	891	89.1
8	830	987	98.7
8	852	950	95.0
8	856	906	90.6
8	860	317, 192	25.5
8	861	843	84.3
8	BFL-3	594, 432	51.3
8	BFL-4	805, 926	86.6
8	BFL-7	545	54.5
8	BFL-9	953	95.3
8	BFL-18	674	67.4
8	BFL-19	872	87.2
8	BFL-20	903, 954	92.9
8	BFL-21	960	96.0
8	BFL-22	887, 758	82.3
8	BFL-23	956	95.6
8	BFL-29	971	97.1
8	CW-1	516 (out of 640)	80.6

Table 9. (continued)

Haploid Chromosome Number	Collection Number	Number of viable grains per 1000	Percent Stainability
26	753	943	94.3
26	794	957	95.7
26	802	13, 33	2.3
26	841	943	94.3
32	578	993	99.3
32	707	877	87.7
32	713	846	84.6
32	714	963	96.3
32	727	947	94.7
32	738	986	98.6
32	817	985	98.5
32	BFL-15	623, 634	62.9
32	BFL-16	863	86.3
32	BFL-24	959	95.9
32	BFL-25	951	95.1
32	BFL-26	981, 966	97.4
48	522	960	96.0

Figure 28. Pollen viabilities at different ploidy levels.



not at all morphologically unusual and were readily assignable to a diploid group. Two specimens with low pollen viability counts (# 605 and # 641) belonged to rare taxa (A. greatai and A. idahoensis, respectively). However, pollen viability may be strongly influenced by environmental factors, since a given plant sometimes gave widely differing pollen viability counts at different times.

Flavonoid Chemistry

Flavonoids are among the most easily identified secondary metabolites and have often been found to be taxonomically useful (e.g. McClure and Alston 1966, Bohm et al. 1974). In this study, variation in flavonoid composition was surveyed in a variety of morphological types, mostly at the diploid level. One sample was analyzed in detail and the flavonoids isolated and identified. Collections that were made for flavonoid analysis are listed in Table 10.

A preliminary investigation was done to determine how these compounds were distributed through the plant, using a hexaploid collection of A. chilensis (# 516). The specimen was separated into six categories of parts: ray flowers, disk flowers, involucre (including receptacle), leaves, stems, and roots. Equal amounts (approximately 1 g) of each tissue were separately extracted, and the extracts compared. Figure 29 shows that the majority of flavonoid material present was found in the flower heads (rays, disks and involucres). Relatively little pigment, representing only one or two

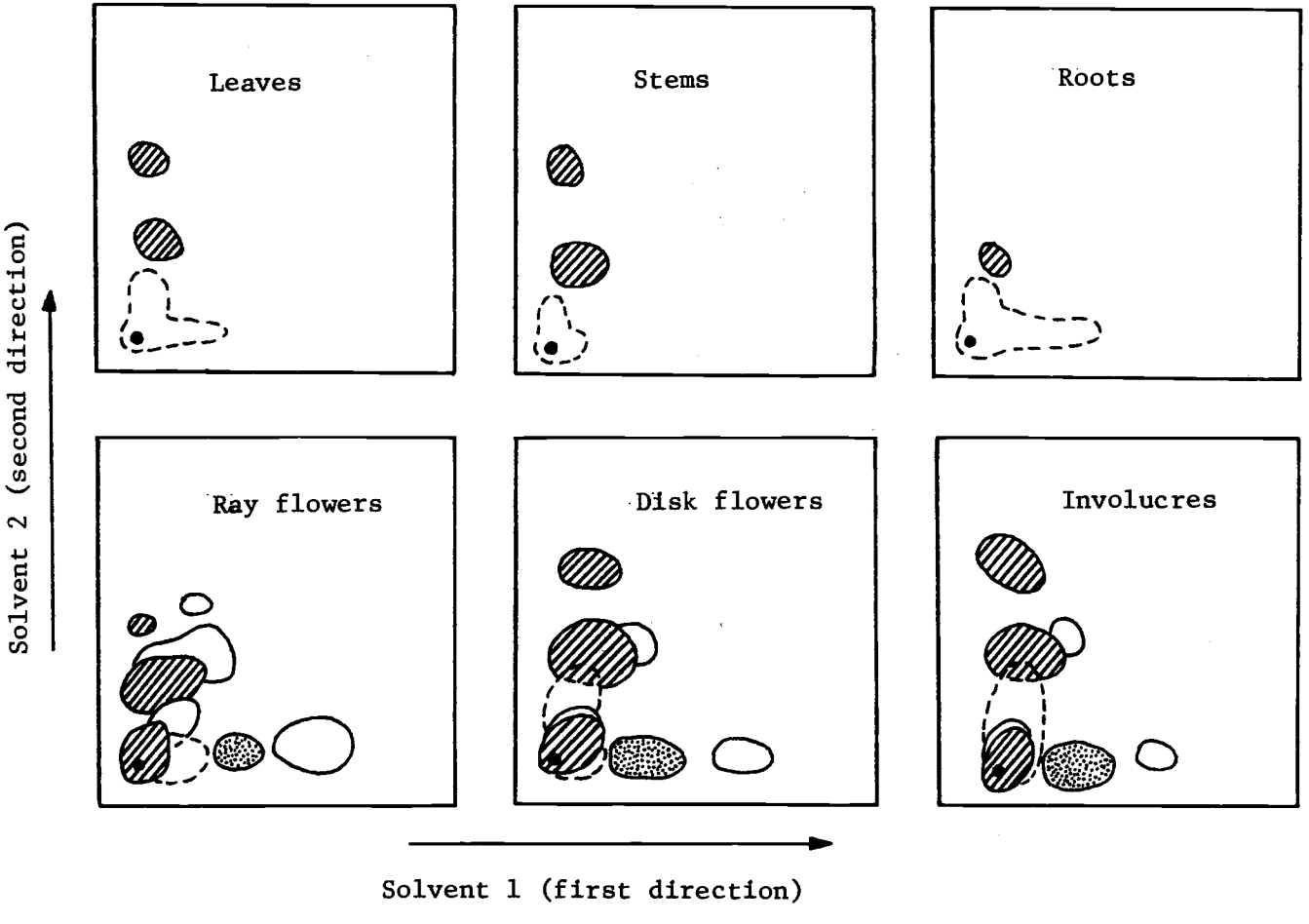
Table 10. Plant Collections used for chemical analysis.

Taxon	Haploid Chromosome Number	Collection Number
A. ascendens	13	501
	13	849
	26	786
A. eatonii	8	542
	8	553
	8	560
	8	736
	8	856
	8	BFL-7
	8	BFL-29
A. foliaceus var. canbyi	8	BFL-19
	8	BFL-20
	8	BFL-22
A. foliaceus var. parryi	8	806
	8	816
	8	830
A. greatai	8	605
A. hallii	8	BFL-3
	8	852
	16	BFL-16
A. occidentalis	8	555
	8	556
	8	557

Table 10. (continued)

Taxon	Haploid Chromosome Number	Collection Number
A. occidentalis (cont.)	8	561
	8	586
	8	609
	8	722
	8	725
	8	734

Figure 29. Two-dimensional chromatograms showing flavonoids in different parts of Aster chilensis.



compounds, was present in the remainder of the plant. The rays, disk flowers and involucres had approximately equal amounts of flavonoid, but the rays had the greatest proportion of green-fluorescing compounds and the involucres the greatest amounts of orange- and yellow-fluorescing compounds. (Colors in UV light are indicated in the same manner as in Figure 30.)

A detailed analysis of compounds present was performed on a collection of A. eatonii from Hood River, Oregon. Thirteen compounds were isolated and their component fragments identified. These are listed in Table 11 together with Rf values and color reactions. Ten of the compounds were completely characterized. In the remaining three, although the sugars present were identified, the order of sugar attachment was not determined due to lack of material for partial hydrolysis. Figure 30 shows a two-dimensional thin layer chromatogram of the whole plant extract of A. eatonii (# 553), displaying the positions of the various compounds that were identified. The major compound present in this plant was quercetin 3-O-galactoside, a common and widespread flavonol. Both flavone and flavonol glycosides were found, but the flavonols were present in the largest diversity and the highest yield. This was of interest since the bulk of the aglycone was made up of flavones, as is clear from the two-dimensional chromatogram. Flavonols may be more readily glycosylated than flavones in this plant.

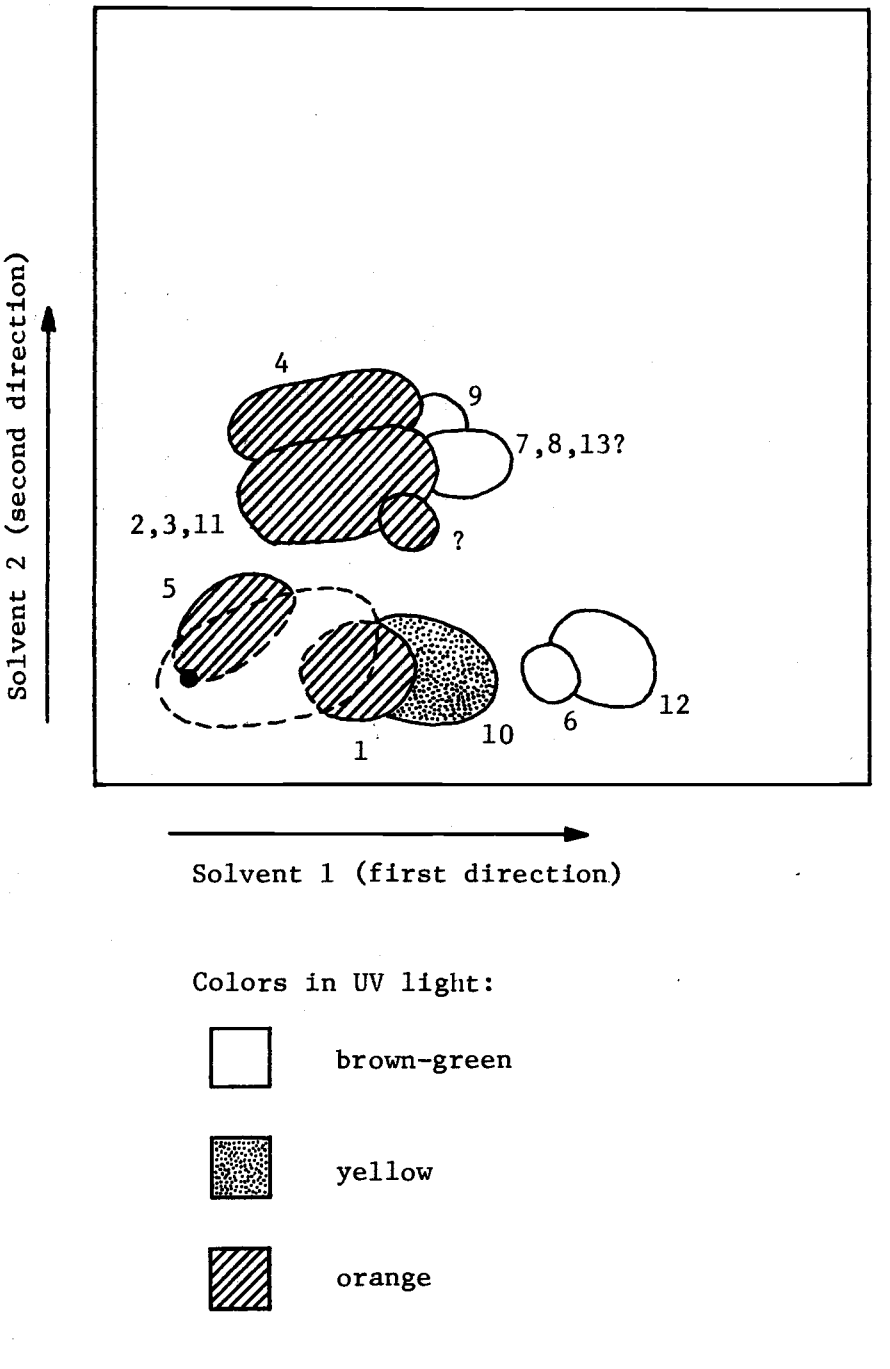
To estimate the variation in flavonoid constitunts in this group, whole plant extracts were made from a total of 30 additional plant

Table 11. Flavonoid compounds found in Aster eatonii (#553).

Compound	Rf X 100 Solvent 1	Rf X 100 Solvent 2	Color in UV light (366 nm) unsprayed	Color in UV light (366 nm) sprayed with diphenyl borate
1. quercetin	32	3	orange-yellow	orange
2. quercetin 3-0-glucoside	15	28	purple-brown	orange
3. quercetin 3-0-galactoside	15	28	purple-brown	orange
4. quercetin 3-0-(rhamnose, galactose)[1]	11	55	purple-brown	orange
5. quercetin 3-0-(xylose, glucuronic acid)[1]	2	3	purple-brown	orange
6. kaempferol	45	4	dull yellow	green
7. kaempferol 3-0-glucoside	23	30	purple	brown-green
8. kaempferol 3-0-galactoside	23	30	purple	brown-green
9. kaempferol 3-0-(rhamnose, galactose)[1]	19	60	purple	brown-green
10. luteolin	42	5	purple-brown	yellow
11. luteolin 7-0-galactoside	16	33	purple-brown	orange
12. apigenin	63	7	purple	brown-green
13. apigenin 7-0-galactoside	32	36	purple	brown-green

[1]Order of sugar attachment was not determined.

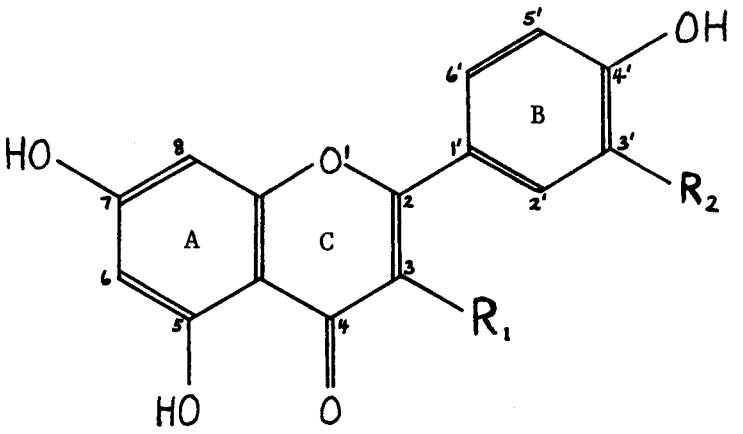
Figure 30. Two-dimensional chromatogram of Aster eatonii (#553), showing locations of known compounds.



collections of known morphology and chromosome number (Table 10). Of these 27 were diploids, two were tetraploid and one was duodecaploid. Two-dimensional chromatograms of each extract were made. Conclusions were then drawn about the kinds of flavonoids present in each collection, based on comparisons with the compounds of known structure in Figure 30 and with other standard compounds also run on a chromatogram. Individual flavone and flavonol aglycones are readily separable by color and by position along the horizontal axis. Glycoside groups can be distinguished as follows: (a) biosides (flavonoids carrying two sugar molecules) are more polar than monosides (carrying one sugar) and therefore run higher in solvent 2 and lower in solvent 1; (b) compounds having only one hydroxyl group on the B-ring (see Figure 31 for structure and numbering system of the flavonoid skeleton) are more nonpolar than compounds having two hydroxyls on the B-ring; and (c) glycosides containing uronic acid residues have very low Rf values in both solvents.

Considerable variation was observed both within and between taxa. Four main kinds of variation were observed: (a) presence or absence of flavonol aglycones, (b) presence or absence of biosides, (c) presence or absence of compounds with a single B-ring hydroxyl group, and (4) presence or absence of glucuronides. In addition many of the chromatograms showed extra orange-fluorescing spots in the lower right corner; these could be still other aglycone types, or they could be acylated glycosides. Further investigation would be required to determine their structure.

Figure 31. The basic structure of flavones and flavonols.



Flavones:

Apigenin	R_1 = H	R_2 = H
Luteolin	R_1 = H	R_2 = OH

Flavonols:

Kaempferol	R_1 = OH	R_2 = H
Quercetin	R_1 = OH	R_2 = OH

Table 12 reports the variation found in the diploid collections examined. The 27 diploid individuals fell into 7 taxa. Of the five taxa for which more than one collection was available, four showed intraspecific variation. Some of this variation may reflect the detection limits of the methods used rather than the actual biosysnthetic capabilities of the plants, but differences evidently exist.

Flavones were present in essentially all cases. Flavonols appeared to be sometimes absent in A. ascendens, A. eatonii and A. occidentalis. Glucuronides were consistently present in A. occidentalis and A. foliaceus, absent in A. greatai, absent except for traces in A. hallii and A. ascendens, and sometimes absent in A. eatonii. Aster greatai and some specimens of A. eatonii lacked compounds with a single hydroxyl group on the B-ring, and A. foliaceus var. canbyi was unique in lacking all but a trace of biosides. Within some of the species there appeared to be trends related to geographical distribution. Only two specimens of A. ascendens were examined, one from central Oregon and one from eastern Nevada; they showed considerable differences. In A. eatonii, three specimens which lacked or had only traces of (1) flavonols and (2) glucuronides all came from west of the Cascade-Sierra crest; the remaining specimens, which had these compounds, were collected farther east. Although a similar variation in flavonols was apparent in A. occidentalis, there was no obvious connection with habitat or geographical range.

Figures 32 to 43 are drawings of some of the two-dimensional

Table 12. Flavonoids found in diploid Aster collections, based on two-dimensional chromatograms.

	A. ascendens		A. eatonii							A. foliaceus var. canbyi		A. hallii	
	501	849	542	553	560	736	856	BFL-7	BFL-29	BFL-19	BFL-22	BFL-3	852
flavones	+	+	+	+	+	+	+	(+)	+	+	+	+	+
flavonols		+	(+)			+	+	+	+	+	+	+	+
biosides		+	+	+	+	+	+	+	+	(+)		+	+
3'-H, 4'-OH	+	+		+	+	+	+	+	+	+	+	+	+
glucuronides		(+)		(+)		+	+	+	(+)	(+)	+		(+)

	A. foliaceus var. parryi			A. greatai	A. occidentalis								
	806	816	830	605	555	556	557	561	586	609	722	725	734
flavones	+	+	+	(+)	+	+	+	+	+	+	+	+	+
flavonols	+	+	+	+	+		+	+		+		+	+
biosides	+	+	+	+	+	+	+	+	+	+	+	+	+
3'-H, 4'-OH	+	+	+		+	+	+	+	+	+	+	+	+
glucuronides	+	+	+		+	+	+	(+)	(+)	+	+	(+)	+

Figure 32. Two-dimensional chromatogram of Aster ascendens (#501).

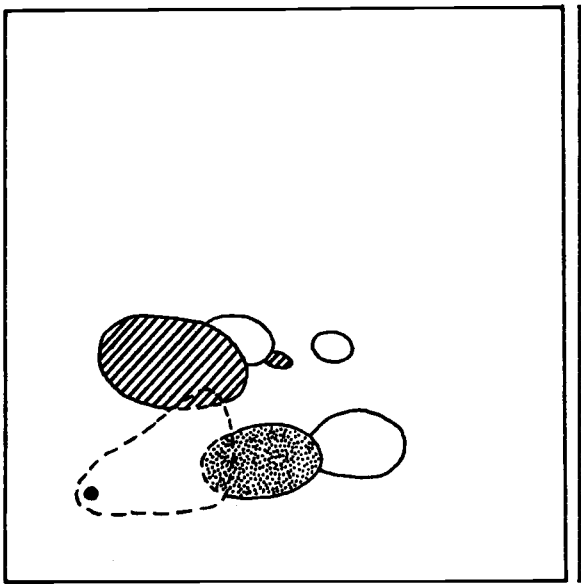


Figure 33. Two-dimensional chromatogram of Aster ascendens (#849).

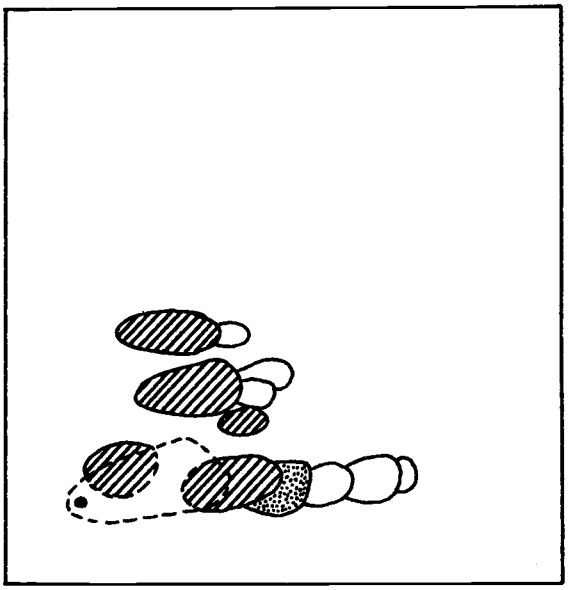


Figure 34. Two-dimensional chromatogram of Aster foliaceus var. parryi (#806).

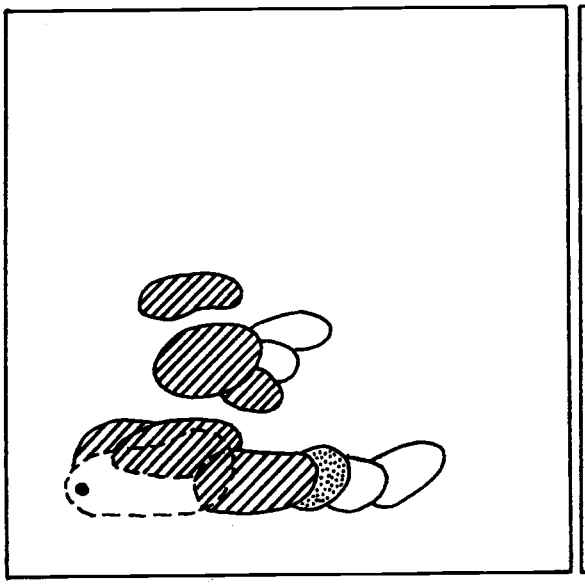


Figure 35. Two-dimensional chromatogram of Aster foliaceus var. canbyi (#BFL-19).

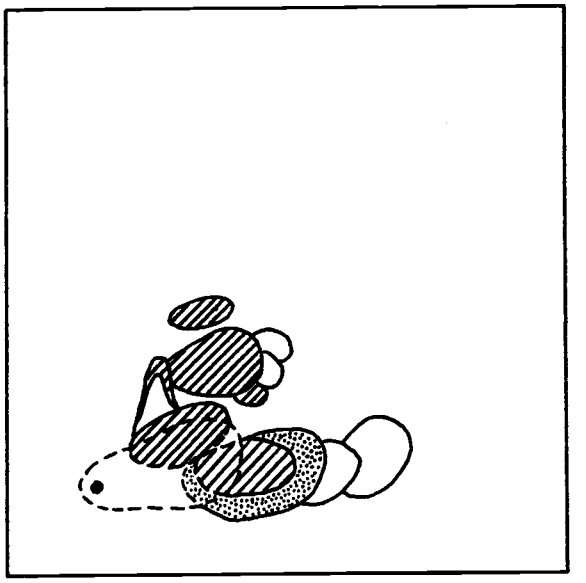


Figure 36. Two-dimensional Chromatogram of Aster eatonii (#BFL-29).

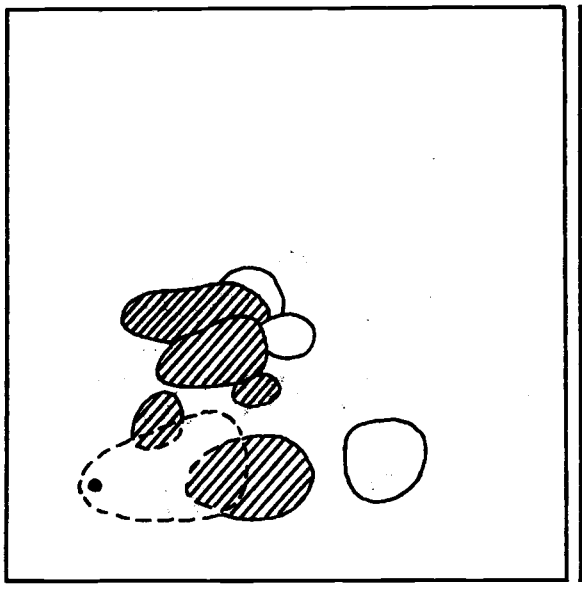


Figure 37. Two-dimensional chromatogram of Aster eatonii (#856).

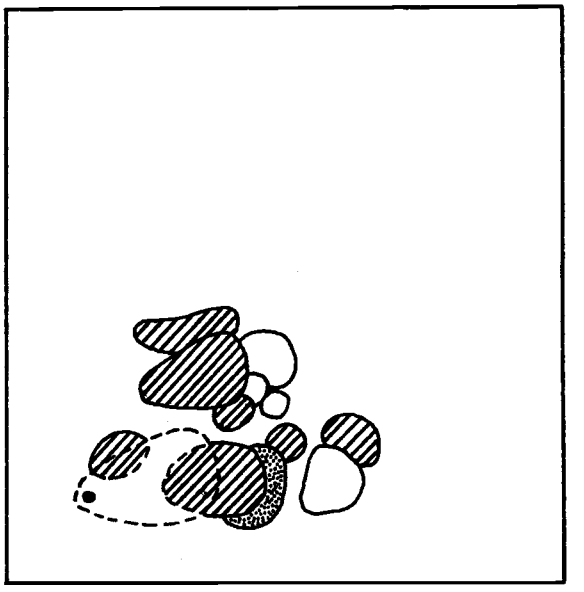


Figure 38. Two-dimensional chromatogram of Aster eatonii (#560).

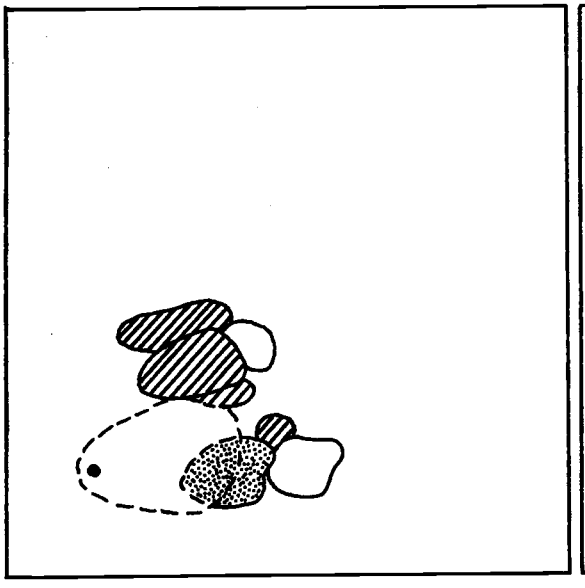


Figure 39. Two-dimensional chromatogram of Aster greatai (#605).

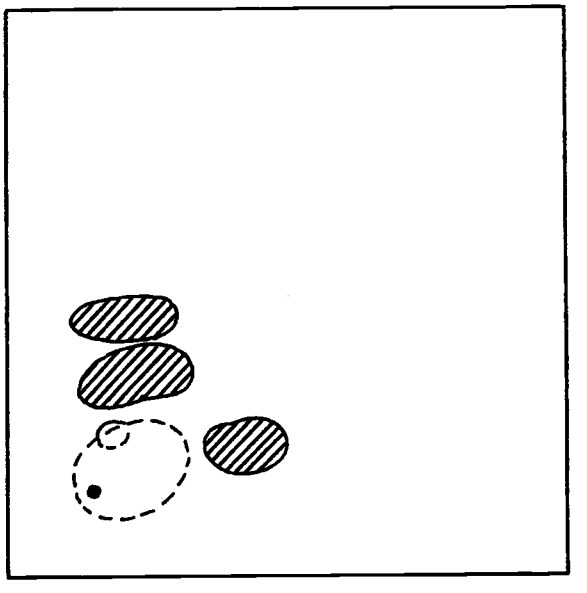


Figure 40. Two-dimensional chromatogram of Aster hallii (#BFL-3).

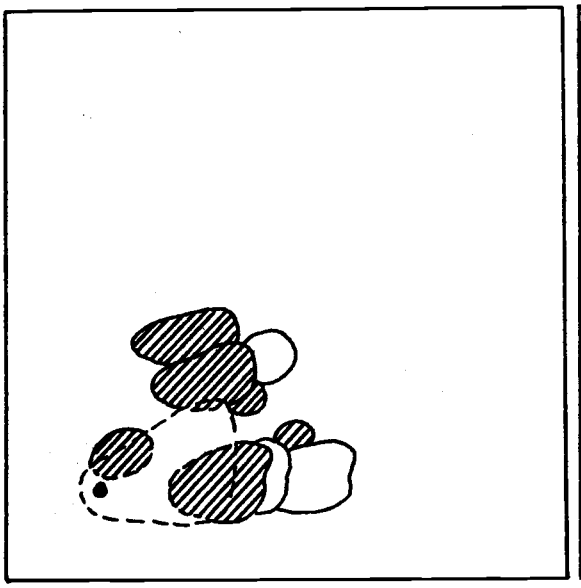


Figure 41. Two-dimensional chromatogram of Aster occidentalis (#557).

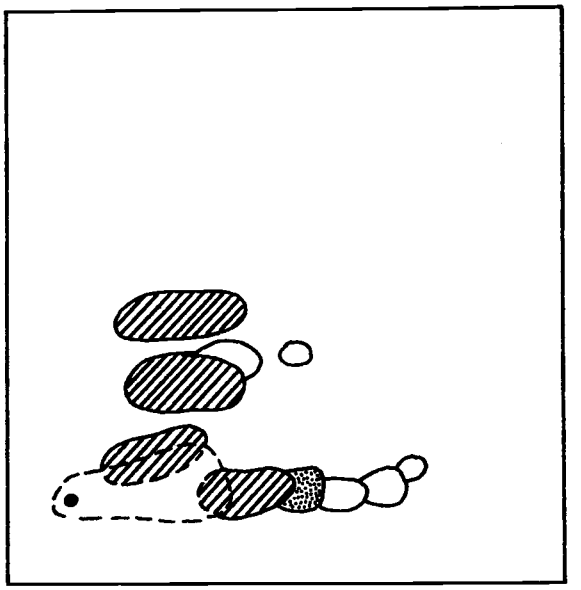


Figure 42. Two-dimensional chromatogram of Aster occidentalis (#586).

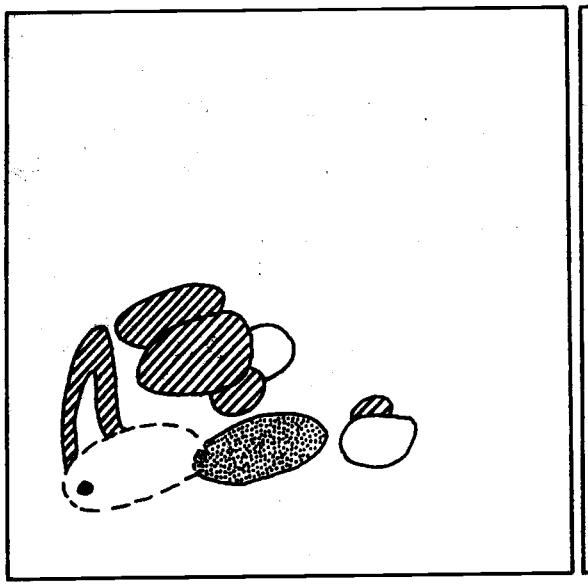
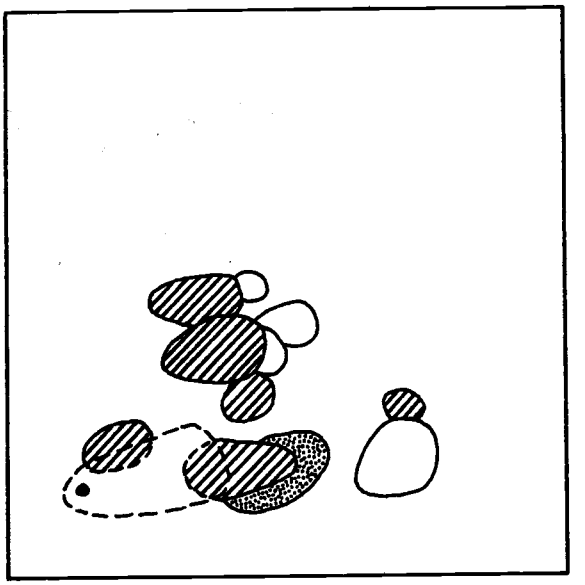


Figure 43. Two-dimensional chromatogram of Aster occidentalis (#725).



chromatograms used as the source of the data in Table 12. (Colors of the spots are indicated as in Figure 30.)

IV. DISCUSSION

A polyploid complex is best understood by examining the diploids, since in the evolution of such complexes diploid individuals can produce unreduced gametes or undergo chromosome doubling to form hybrid polyploid populations, while the reverse process (polyhaploidy) only rarely occurs (Stebbins 1971). The diploids probably best approximate, genetically and morphologically, the ancestral populations from which the group has originated. They are not always a close approximation, firstly because some of the diploid progenitors of a group may be so closely related that they give fertile hybrid offspring at the diploid as well as at the polyploid level, and secondly because some of the ancestral diploids may be rare or extinct. Nevertheless the major genetic discontinuities that exist between taxa should be most apparent at the diploid level, where the least hybridization has occurred.

In the present study, emphasis was placed on variation among diploids. Analysis of morphological variation by numerical methods, using 78 specimens, yielded seven reasonably distinct groups (Figures 3, 4 and 6). Although discriminant analysis of clusters showed these to be fairly well separated, the specimens in each group showed considerable variability for the traits characterizing that group.

Group 1 (A. ascendens) is set apart from the remaining groups by its unique chromosome number based on x = 13, and by its asymmetrical karyotype. However, it sometimes shows a morphological resemblance to

A. occidentalis where their ranges overlap, although phyllary shape and plant habit usually distinguish them.

Group 2 (A. foliaceus var. canbyi) is morphologically the most distinct and uniform of the seven groups. It might well merit specific status. However, its distinctness in the present study may be an artifact of sampling, since the six plants that were examined all came from approximately the same locality in northern Arizona, and the next nearest locality sampled in this study was 250 miles away.

Group 3 includes A. folicaceus var. foliaceus and var. parryi. Both this group and Group 2 are characterized by few but large flower heads and long internodes. In Group 3 these traits are rather variable, however, and the involucre also varies from foliaceous to imbricate. The plants with imbricate involucral bracts and narrower leaves grade into Group 5, A. occidentalis.

Group 7 (A. hallii) was also fairly well defined. This group has numerous small white flower heads, relatively small leaves closely crowded on the stem, and basal leaves that disappear by flowering time. In the cluster analysis it tended to cluster with specimens of Group 6, but was distinguishable by plant habit and flower characters.

The fourth group, A. "idahoensis" (a taxon proposed by Dean, 1966, but as yet unpublished) is distinguished by extremely narrow phyllaries. Otherwise the plants of this cluster closely resemble some

forms of A. occidentalis. Only two specimens were examined; one of these was consistently split into a group by itself in the cluster analysis, while the other tended to cluster with Group 5. The divergence between the two specimens may be due to environmentally induced individual variation rather than genetic distinctness. Further investigation of this group is needed in order to determine how closely it resembles A. occidentalis.

Group 6 (A. eatonii) shows relatively little variation. The plants of this group are pink- or white-flowered, with characteristic short, stout rhizomes and tall leafy stems.

The least well defined of the seven groups produced by the clustering was Group 5, A. occidentalis. This species is wide-ranging, variable, and commonly encountered. It showed overlap with Groups 3, 4 and 6, and to some extent with Group 1.

There are a number of drawbacks to the analytical approach used in this study. A severe constraint was imposed on sample size by the necessity of obtaining chromosome numbers for all specimens collected, in order to identify the diploids. Consequently, the sample size was small enough that the variation seen may not be representative of all the variation present at the diploid level. The species comprising this study are very common and widely distributed, so even in relatively well-sampled regions the sampling rate was very low.

The specimens on which morphological measurements were made were largely vouchers collected in the wild, thus the variation actually seen was the result of both genotypic and environmental influences. This could obscure genetic differentiation between groups, due to random environmental effects; it could also create spurious correlations between characters that are responding to the same environmental stimulus, or accentuate existing correlations (as may have happened in this study). Such effects could only be tested by reexamining vouchers from the same clones grown under uniform conditions.

The results of any numerical taxonomic analysis are very sensitive to character selection and weighting. If characters of different types (for example leaf traits, flower traits) show different patterns of variation in a given species group, comparisons between species will be influenced by the numbers of each kind of character that are selected. Different groups of characters might give completely different classifications, as has been found in a number of other numerical taxonomic studies (Ornduff & Crovello 1968, Gilmartin 1976). In this study, removing some of the flower characters from the analysis had some impact, though not a large one.

Ideally each unit character should reflect the same amount of information about the specimen (for example, the same number of genetic loci), but in practice this is impossible to attain. Characters are selected in part for practical reasons, and those that may be rapid and practical to measure are often not unit characters, but a composite of

several traits that (theoretically at least) are individually measurable. If one assumes that all the characters being used are unit characters, it is defensible to give them all equal weight. However, some characters are much more sensitive to environmental variation than others. In order to detect genetically based patterns of variation in spite of the blurring effect of random environmental influences it might be justifiable to weight such characters less heavily. Also many taxa are identified in practice by combinations of relatively few characters that consistently occur together, while their other characters may not covary in any consistent way. However, deciding how to weight such characters and how much emphasis to place on the weighting may be very difficult, since different decisions could have very different results.

The numerical analysis failed to give separation of some taxa that have been considered distinct. One of these is the endemic, A. greatai, which clustered with Group 6. This taxon is known only from a few localities in the San Gabriel Mountains of southern California, and only one specimen was examined in this study. The species is readily recognizable in the field, and it is morphologically and ecologically so distinct from other species that its failure to cluster separately may well be the result of the characters selected. A second taxon not separated by the CLUSB program was the putatively diploid A. lentus (reported by Dean, 1966, as n = 8). It is found in marshes around the San Francisco Bay area of California. The analysis included it (on the basis of similarities in overall habit) with Group 6 (A. eatonii).

The more recently obtained chromosome numbers of A. lentus have all been n = 32. This plant may not be separable from the coastal polyploid species A. chilensis, with which it is allied.

Variation observed in the polyploids reflected that at the diploid level in general, with a greater number of intermediate forms. A given morphological type thus usually contained at least two ploidy levels, and in some forms (e.g., A. foliaceus var. foliaceus) as many as six levels. Exceptions to this were the diploids A. greatai and A. foliaceus var. canbyi, both of which were examined from only one locality. Some recognizable polyploid entities exist which have character combinations not found at the diploid level; these are discussed further under the individual species.

The Taxa and Their Interrelationships

In a polyploid complex such as this, overall morphological discontinuities are few. Thus the group is most logically divided on the basis of discontinuities in the diploids, which best reflect the evolutionary origins of the group.

Aster laevis

Aster laevis was tentatively included in this group by Dean (1966), but is considered by Jones (1977) to be more closely related to eastern species of Aster section Heterophylli. In the present study it was commonly encountered in the Rocky Mountains, and it has been

found as far west as Idaho. It is recognizable by the narrow, closely imbricate phyllaries, the glaucous foliage, and the basal leaves narrowing abruptly to the petiole. The species is commonly found along roadsides and on other disturbed sites. The 25 chromosome counts obtained for this species (see Appendix I) show that it is mainly hexaploid (n = 24) but occasionally octoploid (n = 32). It was distinct wherever encountered; no indications were found that it hybridized or intergraded with any of the other species considered here.

The remaining species fall into several related groups. These are as follows:

(1) A. ascendens and A. bernardinus -- These two species form a Great Basin and desert group extending from southern Montana and Idaho to California and New Mexico.

(2) A. occidentalis, A. foliaceus, A. "idahoensis" and A. jessicae -- This is a very large, variable and complex group. Both A. occidentalis and A. foliaceus are very common and widespread, the former at middle to lower elevations and the latter at higher elevations. Aster idahoensis and A. jessicae are regional endemics, and are related to A. occidentalis and A. foliaceus respectively.

(3) A. greatai -- This distinctive diploid species has a very local distribution, and has probably been isolated from other members of the complex for some time.

(4) A. hallii -- This is another relatively distinct species that occurs in western Oregon and adjacent Washington.

(5) A. eatonii and A. hesperius -- These two species form a widespread but morphologically rather uniform group. They occur on wet sites; A. eatonii is mainly diploid and may well be a progenitor of the octoploid A. hesperius.

(6) A. chilensis, A. lentus and A. subspicatus -- These species form a mainly coastal group. Aster chilensis intergrades with A. lentus in the San Francisco Bay area. Aster subspicatus is high polyploid, and is probably the result of hybridization involving several species.

The individual species are discussed in more detail below.

Aster ascendens

This species is distinguished by its imbricate involucre with obtuse outer phyllaries, and narrow gray-green leaves. The plant is generally pubescent (more so on the upper parts) with strigose hairs. The cauline leaves are reduced upwards on the stem, and the inflorescence is a narrow or sometimes flat-topped panicle.

Aster ascendens is a species of the Great Basin and Intermountain Region. It occupies the driest habitats of any species in this group, and is often found in sagebrush desert, tending to occur on the damper sites along creek beds and road shoulders.

This species is unique in having a chromosome base number of x = 13. This number was reported by Dean (1966) from two counties in Oregon; seven additional localities are documented here. A number of

reports of n = ca. 25, 26 or 27 (mainly from specimens collected in the Rockies) have appeared in the literature (Solbrig et al. 1969, Anderson et al. 1974); these are probably all derived from doubling of n = 13.

Dean postulated that the base number of 13 might be due to aneuploid reduction (perhaps from n = 16) or to triploidy. He found no evidence of irregular pairing, however. Pollen viabilities of n = 13 plants examined in this study were comparable with those of plants having 8 pairs of chromosomes. Evidence presented here suggests a hybrid origin from species of different base numbers. A number of Aster species, notably those in the subgenera Heleastrum, Oxytripolium and Virgulus of Jones (1980a), which have been segregated into the genus Lasallea by Semple and Brouillet (1980a), have a chromosome base number of 5. Asters of this group that occur in western North America include A. falcatus Lindley, A. ericoides L. (= A. pansus (Blake) Cronq.) and A. campestris Nuttall. The former species is polyploid, while both A. ericoides and A. campestris have chromosome numbers of n = 5. Both of these are also species of dryland habitats.

This study shows that A. ascendens has a much more asymmetrical karyotype than do members of the group with the base number x = 8. A recent paper by Semple (1976) on the karyotype of A. ericoides shows that it also is asymmetrical, with a ratio of largest to smallest chromosomes in the range of 2.6. Addition of the five chromosomes of A. ericoides to the chromosomes of a species with eight pairs might well

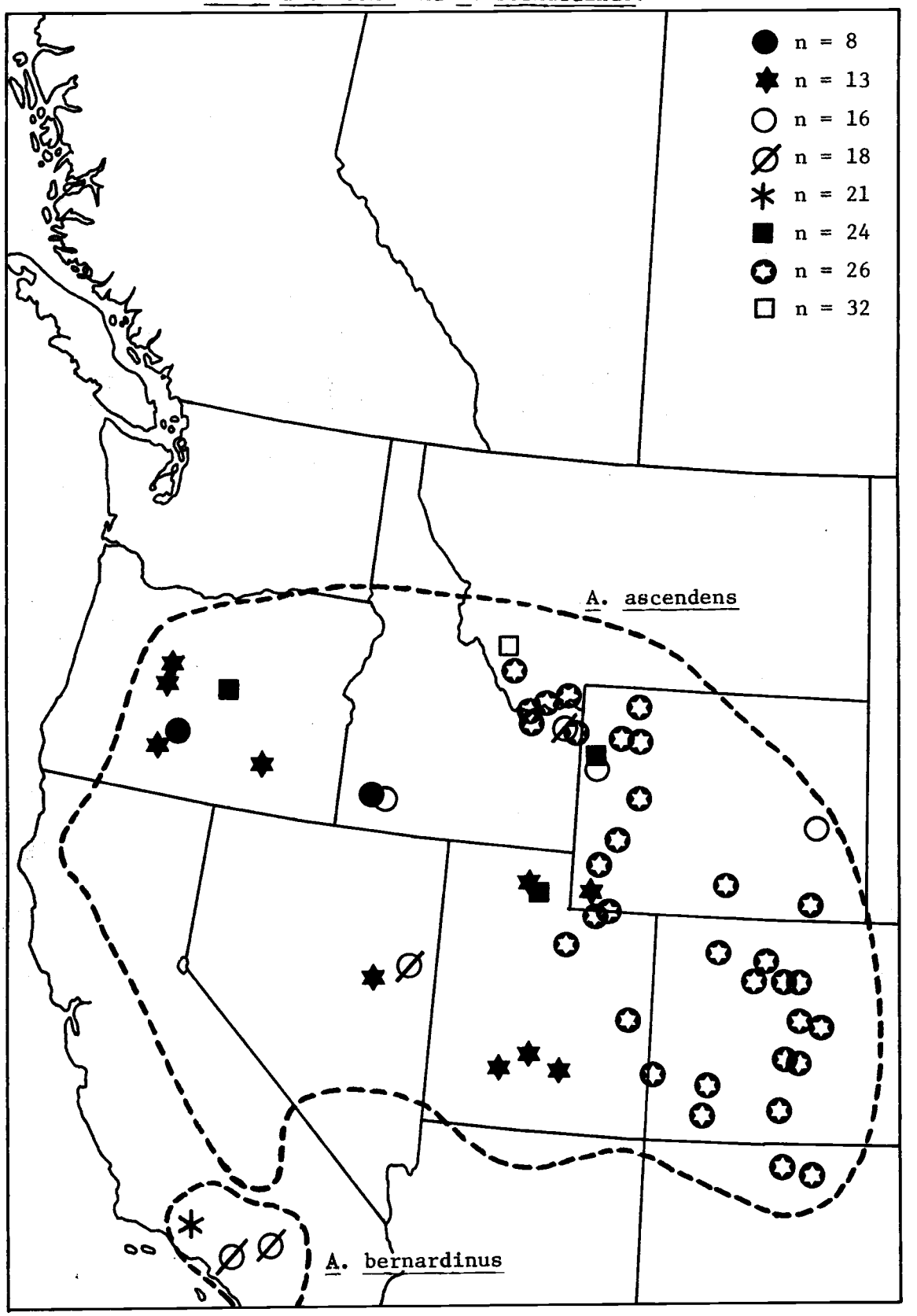
yield a plant whose karyotype resembles that of A. ascendens. A likely candidate for the n = 8 parent, based on morphological similarity and range overlap, is A. occidentalis.

The tetraploid populations of A. ascendens that are encountered in the Rocky Mountains are probably autoploids resulting from chromosome doubling in specimens with n = 13. This hypothesis is supported by the close morphological similarity between the two ploidy levels in this species, and by the fact that the tetraploids often show "sticky" chromosomes and/or fragments at meiosis. Such imperfections in pairing make chromosome counting at meiosis in these plants difficult and could easily result in reports of n = 25 or n = 27.

The geographical distribution of the chromosome numbers reported for this species is shown in Figure 44. The diploids are all found in the western part of the range, and the tetraploids to the east. The latter appear at present to be more common; however, this species has not been thoroughly sampled in the range of the diploids, and further diploid localities will undoubtedly be found. Counts for this species based on n = 8 have also been reported; however, the identity of the specimens is not clear, and some of the counts may derive from incorrectly identified material.

The genetic distinctness of A. ascendens is supported by its apparent lack of interfertility with the other species considered here. Crosses were attempted with four other species, including

Figure 44. Distributions of chromosome numbers in Aster ascendens and A. bernardinus.



A. occidentalis. However, the number of heads involved was relatively few. If A. ascendens originated as suggested, it may share a part of its genome with A. occidentalis and might well be interfertile with it. Chemically these two species resemble one another somewhat, but the chemical variability within each taxon is so great (even in the few specimens examined) and the results so preliminary that no firm conclusions can be drawn.

Cronquist (1943) considered A. ascendens to be a subspecies of the more coastal species A. chilensis. The main point of resemblance between the two taxa seems to be the obtuse outer phyllaries. A number of other species in this and related groups (including A. ericoides) also have outer phyllaries of this shape. Aster chilensis and A. ascendens otherwise are quite different morphologically and ecologically. They are also allopatric, A. chilensis occurring only west of the Cascade-Sierra crest (mainly along the coast).

Aster bernardinus

This species is relatively uncommon and has a restricted range in southern California. It is morphologically very similar to A. ascendens, differing mainly in the denser pubescence on the herbage and the taller and leafier stems.

A chromosome number of n = 18 was reported for this species by Dean (1966). The single collection obtained in this study was counted from both bud and root tip material, and was found to have a haploid

number of 21. The karyotype of this plant (see Figure 23) closely resembles that of A. ascendens, with two to three large pairs of chromosomes and numerous rather similar smaller pairs. Both the karyotype and the chromosome number strongly suggest that it may have originated from a backcross between diploid A. ascendens and a plant with a chromosome number of n = 8. The latter could well be A. occidentalis, which is commonly found in the diploid form in the Sierra Nevada and other mountains of California. Dean's counts of n = 18, if accurate, may reflect another backcross between A. ascendens and its putative ancestor with n = 5. This could be determined by examining karyotypes in the plants having n = 18. The localities of the few chromosome counts that have been made in A. bernardinus are shown in Figure 44.

Dean considered A. bernardinus to be to some extent intergradient with A. chilensis. The former may be one of the progenitors of the latter species, although its anomalous chromosome numbers do not give support to this idea. Cronquist (1943) relegated A. bernardinus to varietal status under A. ascendens, and this may well be the most appropriate treatment of it.

Aster occidentalis

This is perhaps the least sharply defined taxon in this complex. Although it is a recognizable morphological type, it intergrades in various parts of its range with at least four of the other taxa with which it is sympatric.

Aster occidentalis occurs at middle to low elevations from the Sierra Nevada and Cascade Mountains east to the Rockies, and from southern British Columbia to southern California. It commonly occupies meadows, forest openings and other mesic sites, and in the Great Basin portion of its range it occurs in relatively damper midmontane habitats.

The plants are of moderate height with oblanceolate leaves that are reduced upward on the stem. The involucre varies from imbricate to somewhat foliaceous, with acute outer and inner phyllaries. It is separable from A. ascendens by outer phyllary shape and also differs somewhat in habit, tending to be a taller and longer-leaved plant. At higher elevations A. occidentalis intergrades with A. foliaceus var. parryi; the latter generally has fewer and larger flower heads and smaller stature, but there are no clear morphological discontinuities even at the diploid level. These two species are evidently very closely related.

One new finding of this study was the convergence of A. occidentalis towards A. eatonii in the more easterly portions of its range. In the west, the common phase of A. occidentalis has relatively well-developed basal leaves and progressively smaller cauline leaves; the inflorescence has numerous lavender-rayed flower heads and relatively long primary branches. In the northern Rocky Mountains, diploid plants were encountered which had leafy stems, narrow to corymbiform inflorescences and often paler rays. These were distinct from the tall, white-rayed A. eatonii also found in this region, but nevertheless shared some of

the same traits. Aster occidentalis appears to form a consistent race in the northeastern part of its range, which may well merit varietal status. The apparent intergradation of the two species that was shown in the numerical analysis was due to these plants.

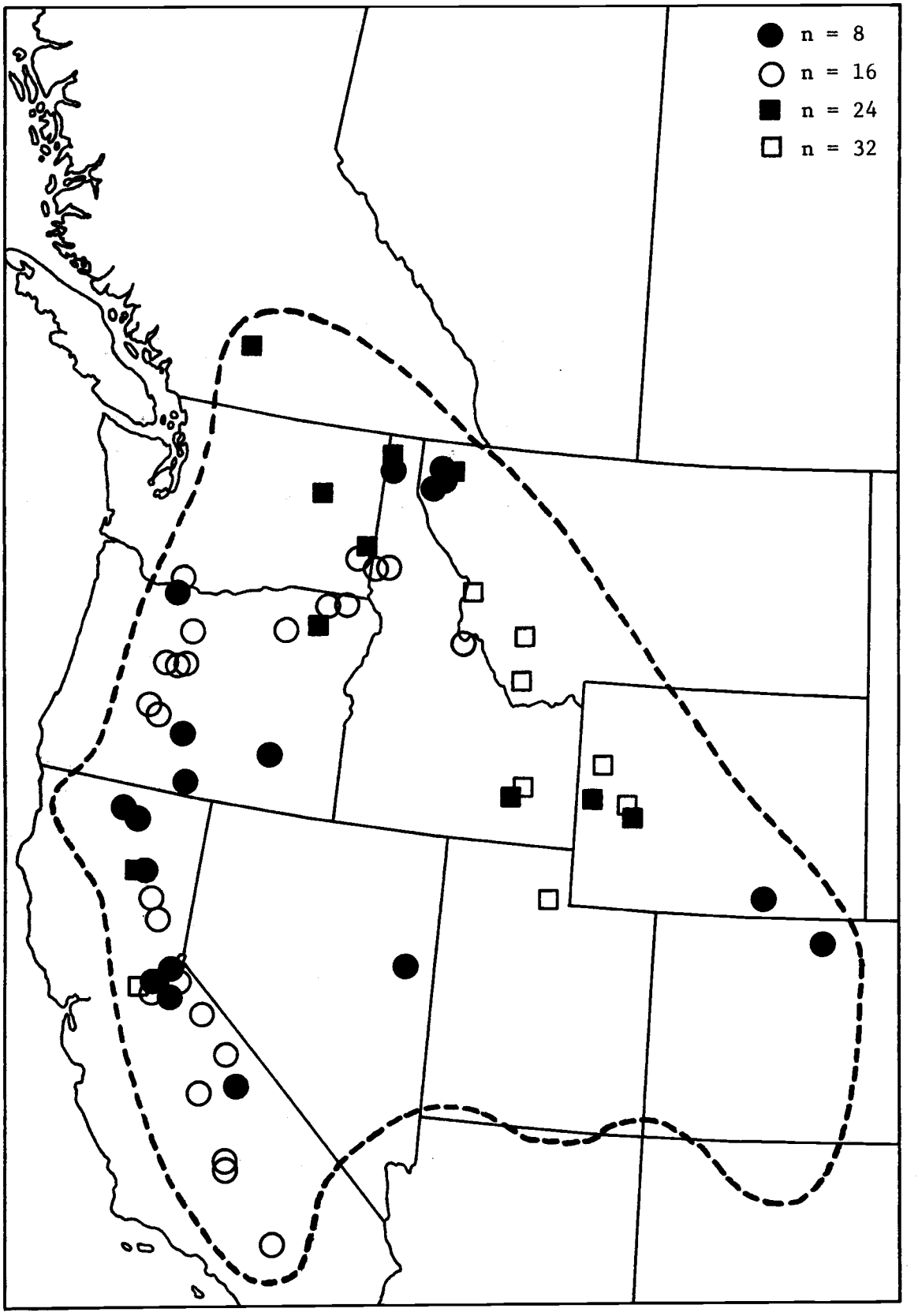
Aster occidentalis includes four ploidy levels, from diploid to octoploid (Figure 45). The diploids are distributed fairly widely over the range of the species; they occur somewhat disjunctly, though this may be an artifact of sampling. The tetraploids are concentrated in the northern and western parts of the range, the hexaploids to the north, and the octoploids to the east. This may indicate that the group originated in the west and spread eastward. In any case, the wide distribution of diploids suggests a long-established species.

Two varieties, occidentalis and intermedius, have been recognized in this species. The former variety intergrades with A. foliaceus var. parryi, as indicated above, and is scarcely distinct from it. Aster occidentalis var. intermedius is the more common and typical phase of the species.

Aster "idahoensis"

This is an endemic species of northern Idaho and adjacent Washington, proposed by Dean (1966) but not yet formally published. It contains both diploids and tetraploids, and is distinguished from A. occidentalis by the extremely narrow and acute involucral bracts. It otherwise closely resembles the latter species. Intermediate forms

Figure 45. Distribution of chromosome numbers in Aster occidentalis.



are also common. Only one typical, diploid specimen was collected in this study; further work is needed to see how this taxon varies and the extent to which it intergrades with A. occidentalis. It may be best to treat this entity as a variety of A. occidentalis. Geographical locations for chromosome counts in A. idahoensis are shown in Figure 46.

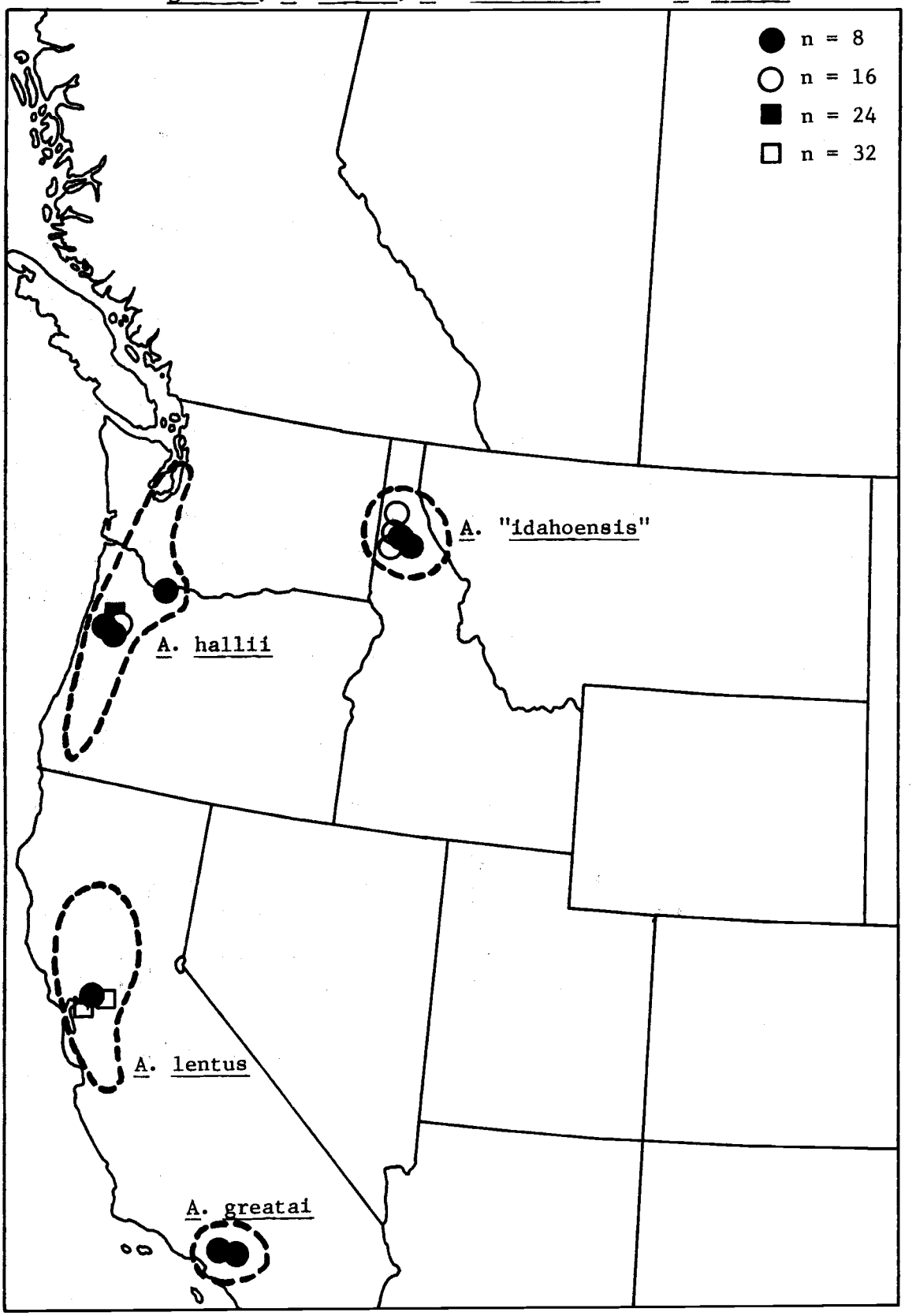
Aster foliaceus

This species occupies the highest-elevation habitats of any taxon in the group. It has a very large geographic range, covering the mountainous regions of the western United States as far south as California and New Mexico and extending north through British Columbia to Alaska. The species is extremely variable, containing at least four well-defined varieties (as many as six, according to some authors). This variability may be related to the distribution of the habitats it occupies. It often occurs on widely separated mountain tops, thus its range may be relatively discontinuous and the species fragmented into numerous small populations. This should decrease gene flow, allow random genetic drift and accentuate divergence between populations (Wright 1931).

All varieties of the species tend to have few, large flower heads. The involucre varies from imbricate to very leafy, and leaves vary in overall size, width and degree of clasping of the stem.

Aster foliaceus occurs over the whole range of ploidy levels that are found in the group, from diploid to duodecaploid. Aneuploids have

Figure 46. Distributions of chromosome numbers in Aster greatai, A. hallii, A. "idahoensis" and A. lentus.



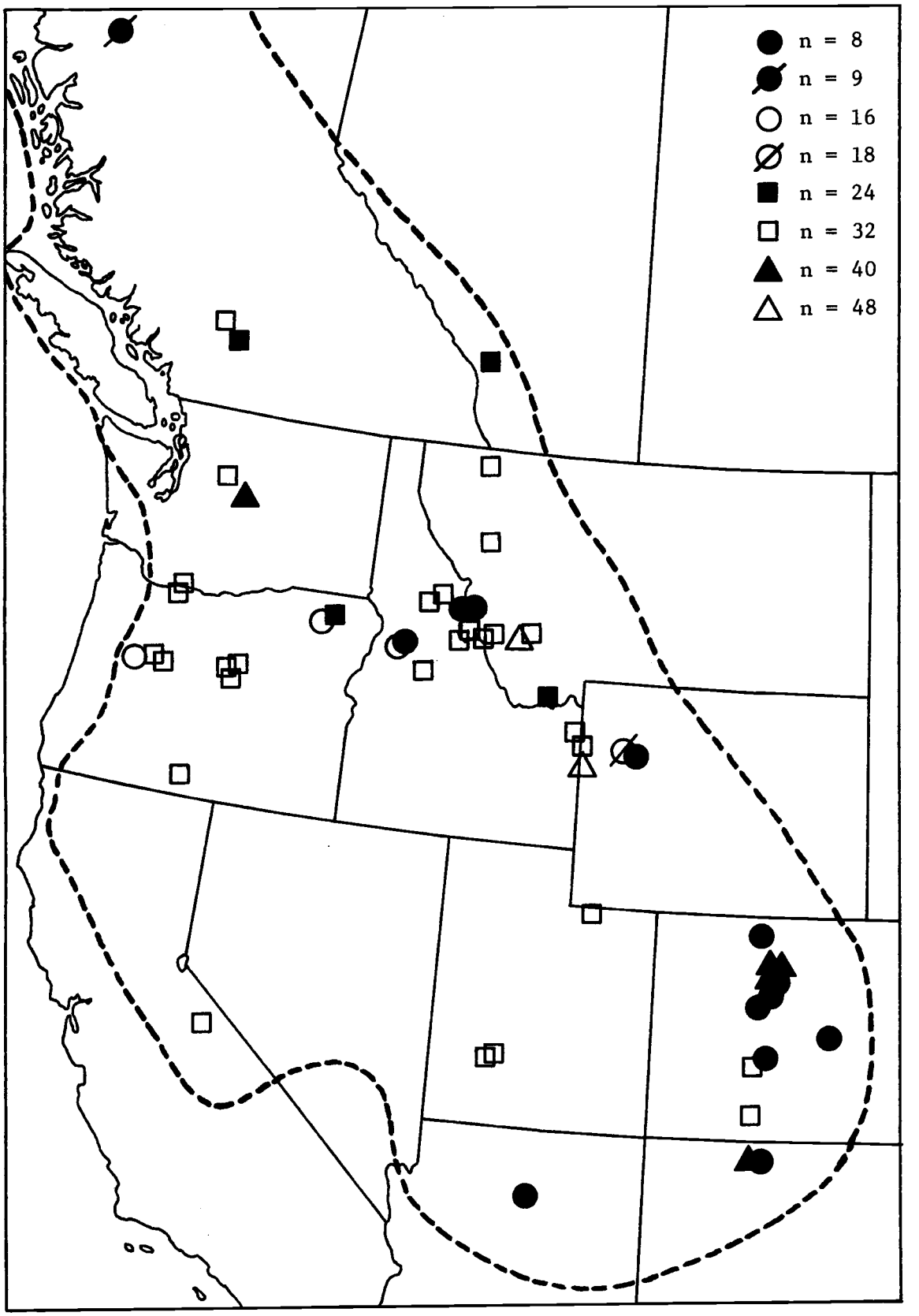
also been found. The commonest chromosome numbers encountered in the present study were n = 8 and n = 32 (see Figure 47). The diploids are scattered throughout the range of the species but were more commonly encountered to the south, while polyploids were more abundant to the north. Four Canadian populations were sampled, only one of which turned out to be diploid. This species was the only taxon in which multiples of a base number of 9 were found. This is a common base number in other parts of the genus, but is scarcely known in this group. Two collections with a base number of nine were found in the present study, one a diploid and one a tetraploid. The karyotype of the diploid proved to closely resemble that of similar specimens with n = 8 (Figure 19). The karyotype was relatively symmetrical. The extra chromosome might have originated by duplication of one of those already present (this might be tested by examining pairing at meiosis). No evidence of chromosomal rearrangement was seen, though it does occasionally occur in this group of asters, as indicated by a specimen of A. occidentalis which had six pairs and a ring of four (Figure 16).

Four recognizable varieties occur in A. foliaceus at the diploid level. These are:

(a) var. canbyi -- seen only from one area, but quite distinct. The plants are fairly tall, with large heads and very leafy phyllaries; outer phyllary tips are enlarged and spatulate.

(b) var. foliaceus -- widespread over the range of the species. The flower heads are few and large; involucres are very leafy, with obtuse to acute outer phyllaries; leaves are often wide and plants

Figure 47. Distribution of chromosome numbers in Aster foliaceus.



often of short stature.

(c) var. cusickii -- localized in northern Idaho and adjacent Washington and Oregon. Flower heads are large and phyllaries leafy; leaves are large, the cauline leaves wide and with an extremely clasping base; herbage is often pubescent.

(d) var. parryi -- a widespread variety. Flower heads are relatively few and large, but tend to be smaller than in the other varieties; the involucre is imbricate to somewhat foliaceous, the phyllaries acute; the leaves are variable, often narrow. This variety intergrades with A. occidentalis var. occidentalis.

Aster jessicae

This species is a rare and local endemic of northern Idaho. Only one specimen was collected during this study. The plants occupy low to middle elevation habitats, and are characterized by wide leaves, large flower heads with a foliaceous to imbricate involucre, and densely hairy foliage. The species resembles A. foliaceus var. cusickii, though it lacks the clasping cauline leaves of that taxon. Dean (1966) suggested that this species originated by hybridization between A. foliaceus var. cusickii and A. occidentalis var. intermedius. This remains speculative; the species has rarely been collected, and only two chromosome counts have been made (n = 40 and n = 18). The latter count, if it actually reflects a base number of 9 rather than the presence of B chromosomes, may indicate an affinity with A. foliaceus, since this is the only other taxon in the group in which similar chromosome numbers have been found. Localities for the chromosome

counts made in A. jessicae are shown in Figure 48.

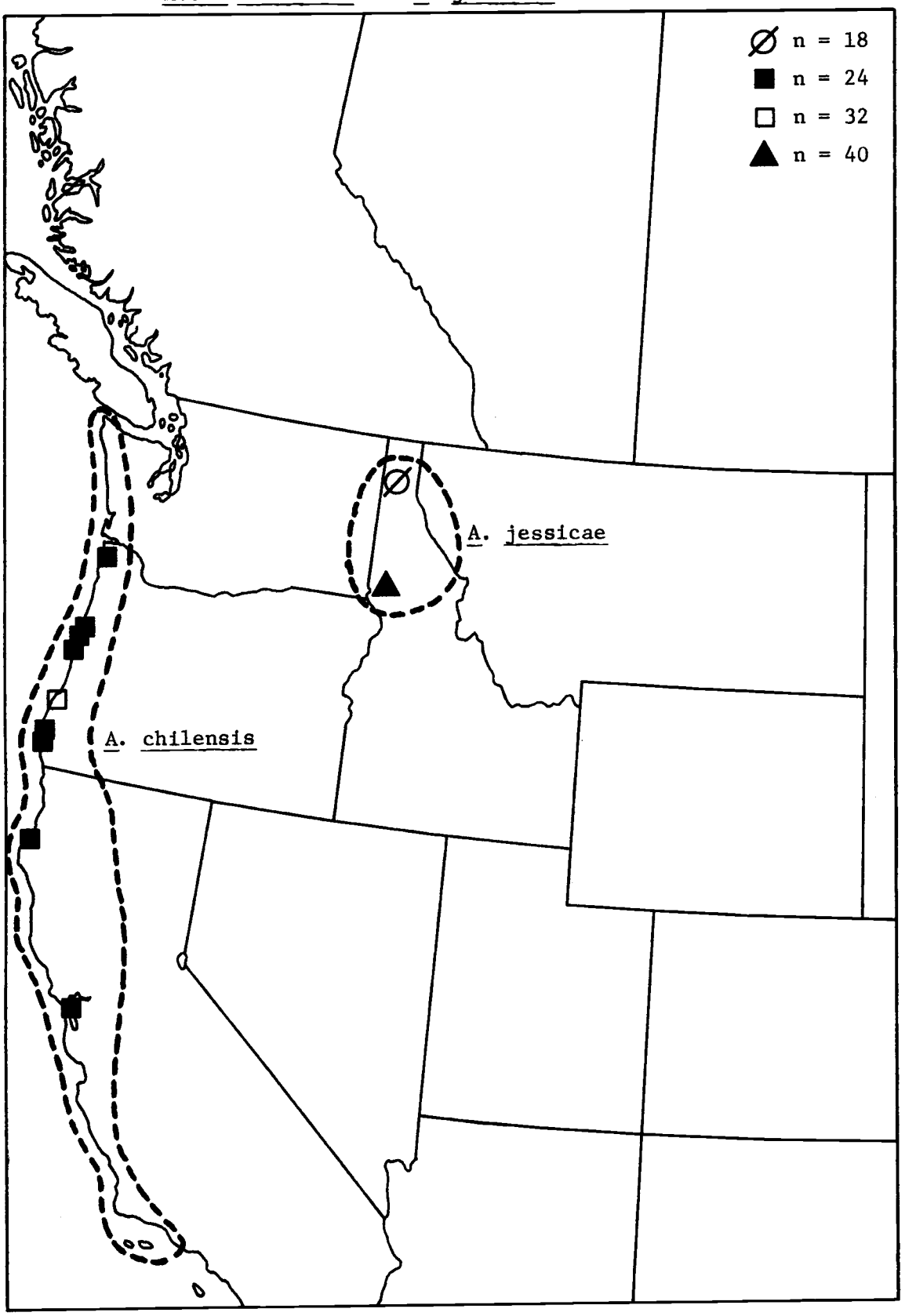
Aster greatai

This species is perhaps the most distinct in the group; it is the only species for which no polyploid chromosome counts are known. It occurs in a few damp canyons in the San Gabriel Mountains of southern California, and is isolated both geographically and ecologically. It is tall and leafy-stemmed; the wide, often toothed leaves are covered with short, stiff hairs, making them characteristically scabrous to the touch. The inflorescence is often markedly divaricate, and the flower heads are pale pink to white with numerous narrow rays. This species, though morphologically well marked, proved to be interfertile with every other diploid taxon with which it was hybridized. Such high crossability was unique among the diploids, most of which yielded few progeny from crosses. Possibly A. greatai has been so well isolated that insufficient contact has occurred with any of the other species to allow selection for formation of reproductive barriers.

Aster hallii

This species is an endemic of the Willamette Valley of western Oregon and adjacent areas, where it occupies grassland habitats. It has slender stems of medium height, with small leaves and short internodes. The flowers are white-rayed, small and numerous. The involucre resembles that of A. chilensis, with obtuse outer and acute inner phyllaries. The basal leaves are absent by flowering time.

Figure 48. Distributions of chromosome numbers in Aster chilensis and A. jessicae.



Aster hallii is largely diploid, with some tetraploids and an occasional hexaploid (Dean 1966). Localities for the chromosome counts are shown in Figure 46. The cluster analysis showed that this species is distinct from the other diploid taxa, though at higher ploidy levels it shows a tendency to intergrade with the only species with which it is sympatric, A. subspicatus. This species is probably related to A. eatonii, which it resembles in some flower and habit features.

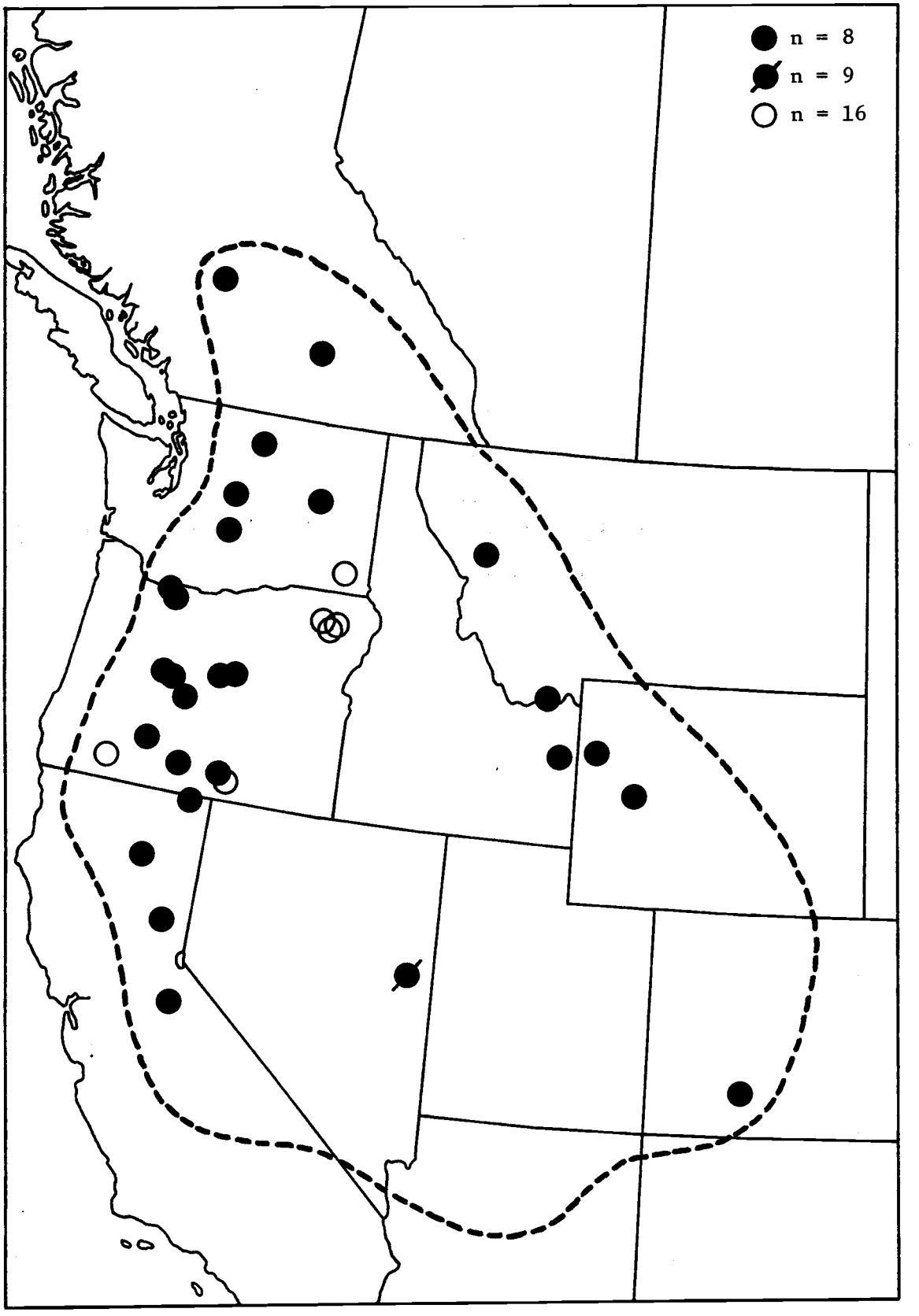
Aster eatonii

This species, though widespread and common, is morphologically rather uniform. It is a species of wet sites, characteristically found in marshes and along ditches and watercourses. It occurs in scattered localities throughout the mountainous regions of the western U.S.

Aster eatonii is a tall and leafy-stemmed plant with a long slender inflorescence and white-rayed flowers. The basal leaves are soon deciduous, and the cauline leaves are scarcely reduced upward. The phyllaries are acute, foliaceous and slightly recurved. The plants often bear short reddish rhizomes at the base of the stem, and may grow in dense clumps.

Figure 49 shows that this species is mainly diploid throughout its range. A few tetraploids have also been found. In the northern Rockies some introgression may have occurred between this species and A. occidentalis, although these two taxa are quite distinct in the western parts of their ranges. They may occupy more similar and over-

Figure 49. Distribution of chromosome numbers in Aster eatonii.



lapping habitats in the Rocky Mountains, offering greater opportunities for gene exchange and allowing intermediate forms to arise. At the polyploid level, A. eatonii has affinities with A. hesperius and probably with A. subspicatus and A. chilensis.

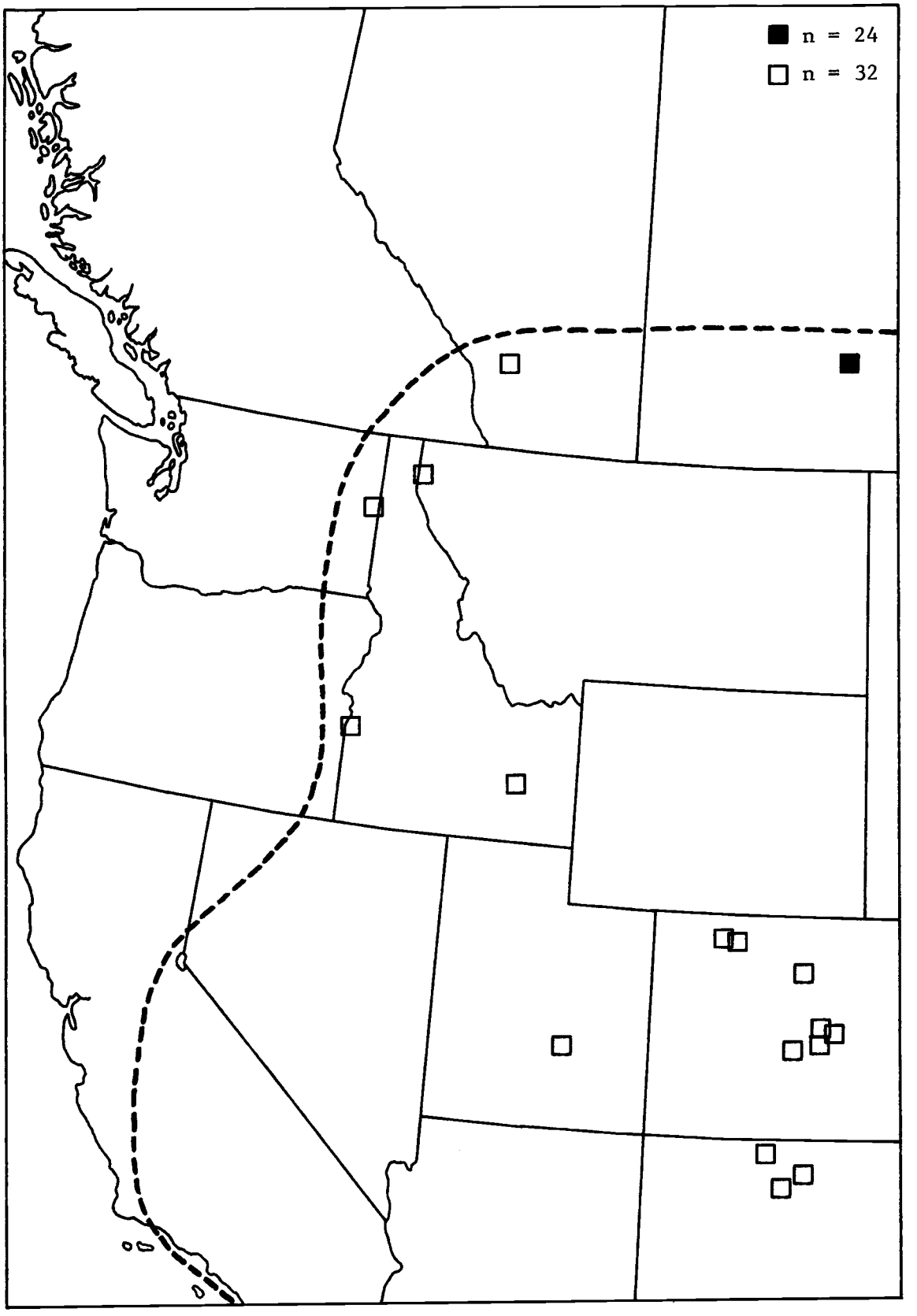
Aster hesperius

This species was not extensively investigated in the present study. Its range extends from the Rocky Mountains eastward to Texas and Saskatchewan; only specimens encountered in the Rockies were examined. This species resembles A. eatonii, differing in the more imbricate involucre, violet rays, narrower leaves and pubescence in lines on the stem. Lines of pubescence occur in many species (e.g. A. foliaceus) but are particularly marked in A. hesperius. All of the specimens examined (with the exception of one septaploid individual, with 2n = 56) had 32 pairs of chromosomes. This species probably originated in part from A. eatonii; other possible contributing species are unknown. Localities of specimens counted are shown in Figure 50.

Aster chilensis

This coastal species was also given relatively little attention in this study. It is a vigorous and often weedy species, with ascending to erect stems, well-developed cauline leaves, and an imbricate involucre with obtuse outer phyllaries. Its range extends from southern British Columbia to southern California. All specimens that have been examined are hexaploid; these are shown in Figure 48. Although the chromosome numbers are so far very constant, counts have not been

Figure 50. Distribution of chromosome numbers in Aster hesperius.



obtained from the extremes of the range. Aster chilensis is sympatric with two other species of this group: A. lentus in the San Francisco Bay area, and A. subspicatus to the north. It intergrades with both of these, and also possibly with A. bernardinus in the south.

Aster lentus

This species is endemic to the marshy regions of the Sacramento delta and San Francisco Bay. It is a very tall, slender, much-branched species with numerous flower heads, imbricate involucre and narrow leaves. It intergrades with A. chilensis, and Jepson (1925) and Ferris (1959) both considered it a variety of this species.

Chromosome counts from two localities are available for this species. At one locality an octoploid was found, with n = 32; at the other, Dean (1966) found a diploid, but later resampling from the same site by the present author yielded only octoploids. Further chromosome numbers are needed for this taxon before speculation is possible on whether A. lentus is a progenitor or a derivative of A. chilensis. If the latter, it might well be best recognized as a variety.

Aster subspicatus

This weedy species is extremely variable. Its range extends from Oregon and Idaho to Alaska, where it grows in a variety of disturbed habitats from salt marshes to road shoulders. The species includes a variety of entities combining characteristics of A. chilensis, A. eatonii, A. foliaceus and A. occidentalis. Its progenitors probably include all

of these, though its closest affinities are with the first two species. Chromosome numbers in A. subspicatus range from n = 24 to n = 48; these are shown in Figure 51.

The overall relationships in this polyploid complex are summarized in Figure 52. The group contains a mixture of distinct, sharply defined taxa and variable, intergradient taxa; these are indicated by the degree of confluence of circles on the diagram. The lack of sharp boundaries between some of the species in this group is due in part to allopolyploidy (as in the following subgroups: A. lentus - A. chilensis - A. subspicatus, A. eatonii - A. hesperius, A. foliaceus - A. jessicae) and in part to direct hybridization between species at the diploid level (as in the A. foliaceus - A. occidentalis - A. idahoensis subgroup). Autoploidy has apparently occurred also in some species (e.g. A. ascendens, A. eatonii, A. hallii); this may contribute to the breakdown of species boundaries by allowing interfertile crosses between taxa at the same polyploid level.

It is of interest to consider how the diploids in this group might have evolved. Those that now intergrade may be hybridizing, or they may never have completely diverged from one another. The preliminary results obtained from crossing experiments indicate some degree of interfertility between diploid species, perhaps enough to allow introgression to blur morphological differences. However, the species that hybridizes most readily, A. greatai, is also one of the most distinct and well-defined. Hybridization experiments, followed by examination

Figure 51. Distribution of chromosome numbers in Aster subspicatus.

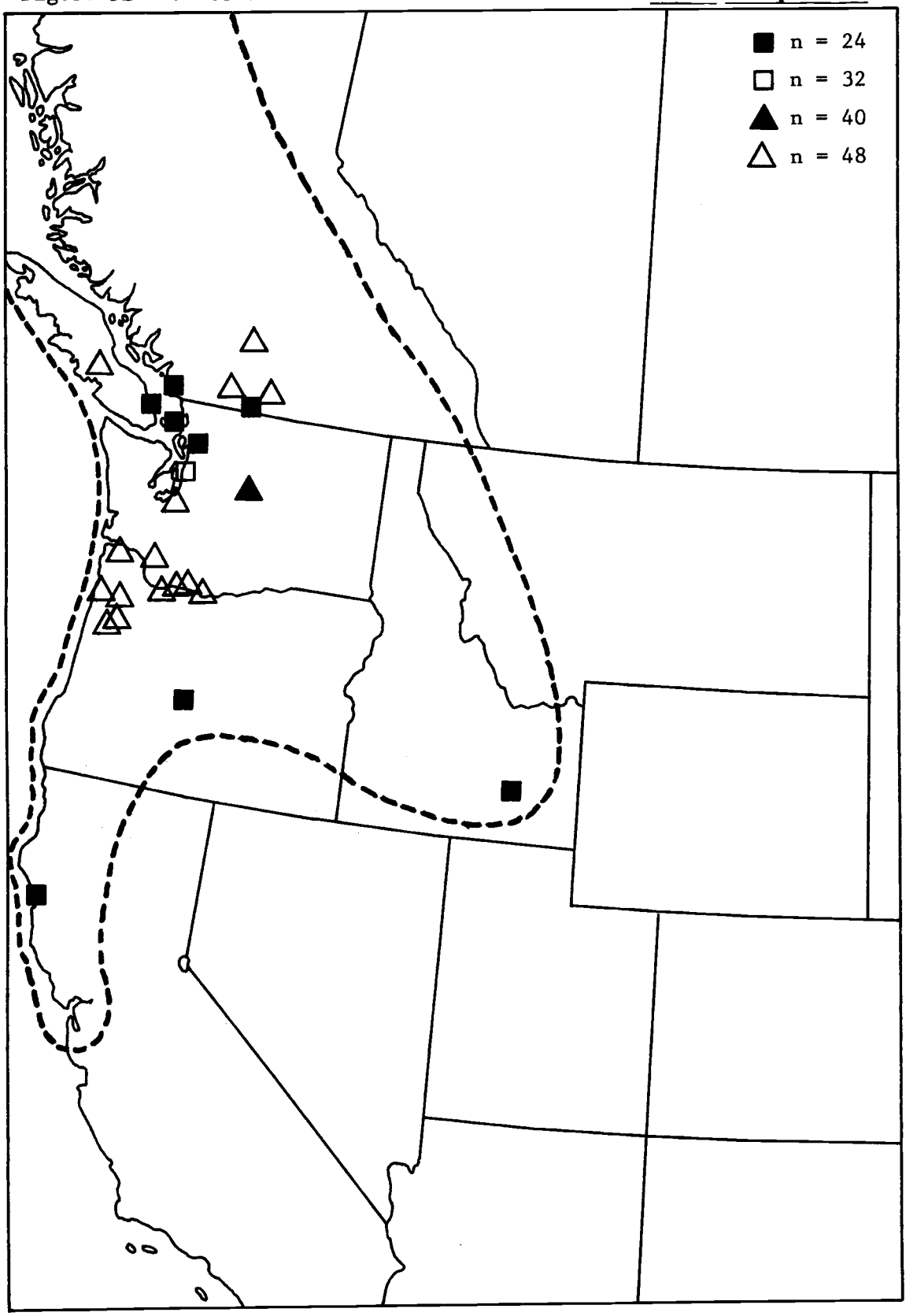
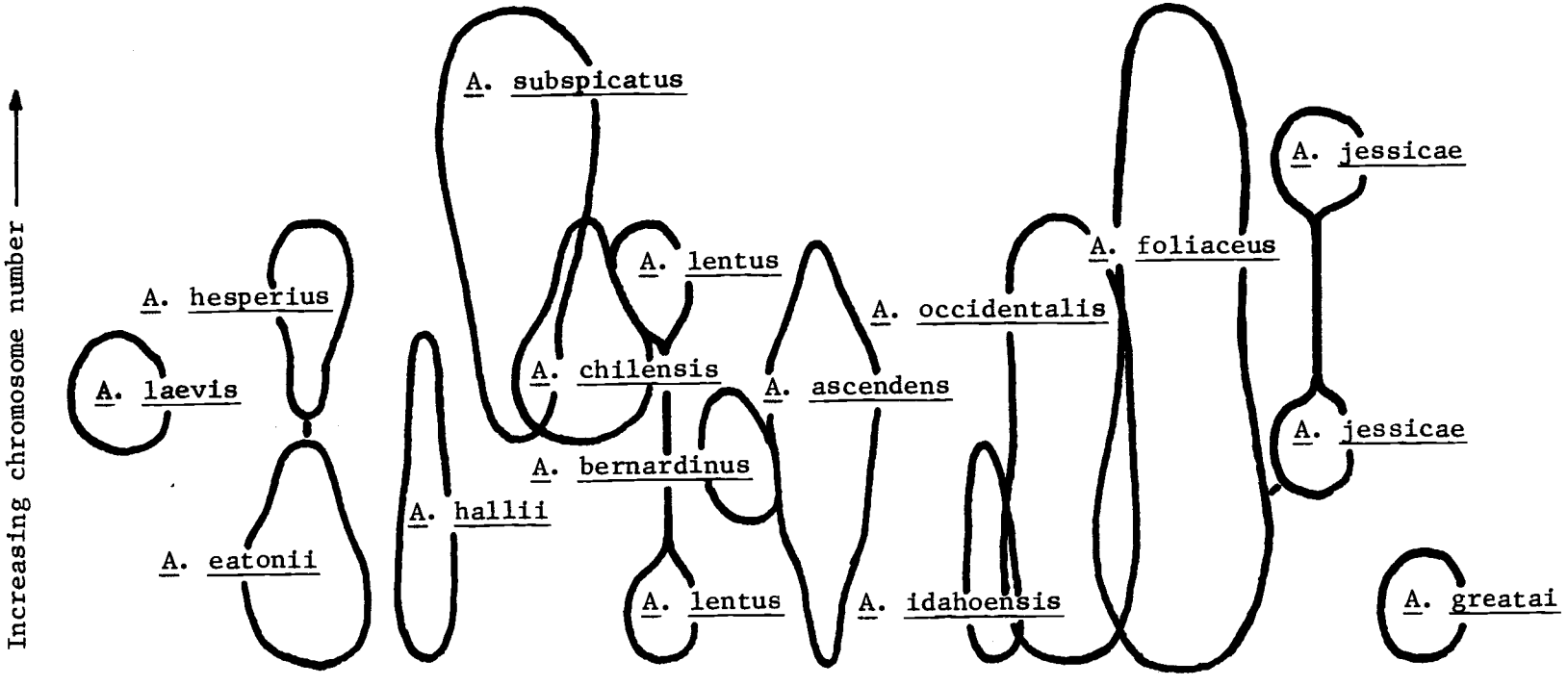


Figure 52. A tentative phylogenetic arrangement of the group studied.



of the fertility of any resulting offspring, have been a standard approach to the study of species relationships (Davis & Heywood 1963). However, the geographical isolation of A. greatai may have allowed it to diverge morphologically while failing to evolve reproductive barriers against gene exchange. It crosses with some taxa to which it has no particularly close resemblance. Evidently species do not diverge in all characteristics at the same rate.

A number of taxa in this group are of restricted distribution. These are more or less concentrated in two general regions: (1) northern Idaho and (2) southern California. The former region contains three taxa: A. "idahoensis", A. foliaceus var. cusickii, and A. jessicae. Endemics of southern California include A. greatai and A. bernardinus. Centers of endemism are possible areas of origin for a group, and the endemic species may most closely resemble the ancestral taxa. However, the endemics of this group include both diploids (patroendemics) and polyploids (apoendemics)(Stebbins 1971) and they could well be relicts which once were more widely distributed. It is not clear what diploid entity may have given rise to this complex, if indeed it is of monophyletic origin. Aster occidentalis var. intermedius perhaps comes nearest to being morphologically "typical" for the group.

This group has not been considered by all authors to form a natural assemblage. Jones (1980a), basing her classification on morphology and on chromosome base number, distributes these taxa through two different sections of the genus; Semple and Brouillet

(1980a) place them in two subsections of a single section. However, the coherence of the group as treated in this study is supported by the morphological intergradation between species, by the existence of at least some degree of interfertility among the diploids, and by the freely occurring hybridization between polyploids (Dean 1966).

LITERATURE CITED

Abrams, L. and R. S. Ferris. 1960. Illustrated Flora of the Pacific States. Vol. IV. Bignoniaceae to Compositae. Stanford Univ. Press, Stanford.

Anderson, L. C., D. W. Kyhos, T. Mosquin, A. M. Powell and P. H. Raven. 1974. Chromosome numbers in Compositae. IX. Haplopappus and other Astereae. Amer. J. Bot. 61:665-671.

Bohm, B. A., N. A. M. Saleh and R. Ornduff. 1974. The flavonoids of Lasthenia (Compositae). Amer. J. Bot. 61:551-561.

Clausen, J., D. D. Keck and W. M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Wash. Publ. No. 520:386-393.

Cronquist, A. 1943. Revision of the western North American species of Aster centering about Aster foliaceus Lindl. Amer. Midl. Nat. 29:429-468.

Darlington, C. D. and L. F. LaCour. 1960. The Handling of Chromosomes. MacMillan Co., New York.

Davis, P. H. and V. H. Heywood. 1963. Principles of Angiosperm Taxonomy. Robert E. Krieger Publishing Co., New York (reprinted 1973).

Dean, M. L. 1966. A biosystematic study in the genus Aster, section Aster, in western North America. Ph. D. dissertation, Oregon State University, Corvallis, Oregon.

Gilmartin, A. J. 1976. Effect of changes in character-sets upon within-group phenetic distance. Syst. Zool. 25:129-136.

Gray, A. 1884. Synoptical Flora of North America. Vol. 1, Pt. 2. Ivison, Blakeman and Taylor, New York.

Greene, E. L. 1891. Flora Franciscana. Cubery and Company, San Francisco.

Greene, E. L. 1894. Manual of the botany of the region of San Francisco Bay. Cubery and Company, San Francisco.

Greene, E. L. 1900. Some Rocky Mountain Asters. Pittonia 4:212-224.

Greene, E. L. 1905. New plants from southwestern mountains. Leafl. Bot. Obs. 1:145-154.

Greene, E. L. 1909. New western Asteraceae. Leafl. Bot. Obs. 2:8-13.

Guppy, G. A. and B. A. Bohm. 1976. Flavonoids of five Hieracium species of British Columbia. Biochem. Syst. and Ecol. 4:231-234.

Hitchcock, C. L., A. Cronquist, M. Ownbey and J. W. Thompson. 1955. Vascular plants of the Pacific Northwest. Vol. 5. Compositae. Univ. Washington Publ. Bot. 17. Seattle.

Huziwara, Y. 1958. Karyotype analysis in some genera of Compositae. V. The chromosomes of American Aster species. Japan. J. Genet. 33:129-137.

Huziwara, Y. 1965. Chromosome analysis in the tribe Astereae. Japan. J. Genet. 40:63-72.

Jepson, W.L. 1925. Manual of the flowering plants of California. Assoc. Students Store, Univ. California, Berkeley.

Jones, A. G. 1977. New data on chromosome numbers in Aster section Heterophylli and their phylogenetic implications. Syst. Bot. 2:334-347.

Jones, A. G. 1980a. A classification of the new world species of Aster (Asteraceae). Brittonia 32:230-239.

Jones, A. G. 1980b. Data on chromosome numbers in Aster (Asteraceae), with comments on the status and relationships of certain North American species. Brittonia 32:240-261.

Kovanda, M. 1972. Somatic chromosome numbers for some Asteraceae. Rhodora 74:102-116.

Mabry, T. J., K. B. Markham and M. B. Thomas. 1970. The Systematic Identification of Flavonoids. Springer-Verlag, New York.

McClure, J. W. and R. C. Alston. 1966. A chemotaxonomic study of Lemnaceae. Amer. J. Bot. 53:849-859.

Muntzing, A. 1959. A new category of chromosomes. IN: Proc. 10th Int. Congress of Genetics, McGill University, Montreal, 1958. U. of Toronto Press, Toronto.

Ornduff, R. and T. J. Crovello. 1968. Numerical taxonomy of Limnanthaceae. Am. J. Bot. 55:173-182.

Raven, P. H., O. T. Solbrig, D. W. Kyhos and R. Snow. 1960. Chromosome numbers in Compositae. I. Astereae. Amer. J. Bot. 47:124-132.

Rydberg, P. A. 1917. Flora of the Rocky Mountains and adjacent plains. Rydberg, New York.

Semple, J. C. 1976. The karyotype of Aster ericoides (Asteraceae): some Canadian populations. Can. J. Genet. Cytol. 18:661-664.

Semple, J. C. and L. Brouillet. 1980a. A synopsis of North American asters: the subgenera, sections and subsections of Aster and Lasallea. Am. J. Bot. 67:1010-1026.

Semple, J. C. and L. Brouillet. 1980b. Chromosome numbers and satellite chromosome morphology in Aster and Lasallea. Am. J. Bot. 67:1027-1039.

Sneath, P. H. A. and R. R. Sokal. 1973. Numerical Taxonomy. W. H. Freeman and Company, San Francisco.

Snow, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. Stain Technol. 38:9-13.

Solbrig, O. T., L. C. Anderson, D. W. Kyhos and P. H. Raven. 1969. Chromosome numbers in Compositae VII: Astereae III. Amer. J. Bot. 56:348-353.

Stebbins, G. L. 1971. Chromosomal Evolution in Higher Plants. Edward Arnold (Publishers) Ltd., London.

Strother, J. L. 1972. Chromosome studies in western North American Compositae. Amer. J. Bot. 59:242-247.

Torrey, J. and A. Gray. 1841. Flora of North America. Part 2. Wiley and Putnam, New York.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16: 97-159.

APPENDIX

Appendix 1. Chromosome numbers and collection localities.

Taxon	Diploid Chromosome Number[1]	Collection Number[2]	Locality
A. ascendens	13 II	501	OREGON: Deschutes Co., along Hwy. 20 near Black Butte, 0.25 mi. east of jct. with Camp Sherman Road.
	13 II	502	OREGON: Deschutes Co., along Hwy. 20 near Black Butte, 0.25 mi. east of jct. with Camp Sherman Road.
	13 II	503	OREGON: Deschutes Co., along Hwy. 20 near Black Butte, 0.25 mi. east of jct. with Camp Sherman Road.
	13 II	504	OREGON: Deschutes Co., along Hwy. 20 near Black Butte, 0.25 mi. east of jct. with Camp Sherman Road.
	13 II	512	OREGON: Deschutes Co., along Hwy. 97 at jct. with Paulina Creek Road, on gravel road shoulder.
	13 II	687	OREGON: Harney Co., along Steens Mountain Road, 2.4 mi. east of Frenchglen, 50 ft. southwest of large pond.

[1] If numbers of pairs are indicated, counts are from buds; otherwise they are from root tips.

[2] All collection numbers are mine unless otherwise indicated. Vouchers for all collections have been deposited in OSC.

Taxon	Diploid Chromosome Number[1]	Collection Number[2]	Locality
A. ascendens (cont.)	26	688	OREGON: Harney Co., along Steens Mountain Road, 2.4 mi. east of Frenchglen, 50 ft. southwest of large pond.
	13 II + 2-3 B	842	UTAH: Wayne Co., 2.1 mi. east of Capitol Reef National Park, along Hwy. 24 on banks of Fremont River. Open sandy flats near water.
	26	844	UTAH: Wayne Co., on Hwy. 24 approx. 3 mi. west of Loa, in grassy strip along road shoulder.
	13 II	845	UTAH: Piute Co., 12 mi. west of Junction on Hwy. 153, at jct. with Kents Road. Heavily grazed meadow in aspen-spruce parkland.
	13 II	849	NEVADA: White Pine Co., 21 mi. east of Pancake Summit on Hwy. 50, along edge of seasonal stream.
	24 II?	763	WYOMING: Teton Co., 2 mi. west of Wilson on Hwy. 22. Gravel road shoulder.
	26 II	749	MONTANA: Beaverhead Co., 9.5 mi. south of Medicine Lodge Creek, in Kissick Canyon along edges of Cochran Creek.
	26 II	751	IDAHO: Clark Co., along I-15, 3.3 mi. south of Montana state line.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. ascendens (cont.)	26 II	753	IDAHO: Clark Co., campground at Stoddard Cr., 12 mi. south of Montana state line; open grassy areas under aspen.
	26 II	757	MONTANA: Beaverhead Co., east of upper Red Rock Lake near small seasonal creek leading into lake.
	52	758	MONTANA: Beaverhead Co., in grassy meadow at Red Rock Pass.
	26 II	759	IDAHO: Fremont Co., east of Ashton on road to Cave Falls, 7 mi. east of crossing of Porcupine Creek.
	26 II	765	WYOMING: Teton Co., 0.8 mi. east of Togwotee Pass, on road shoulder at turnoff to Wind River Lake picnic area.
	26 II	770	WYOMING: Teton Co., at Black Rock Creek, 9 mi. east of Moran jct. on Hwy. 26/287.
	26 II	772	WYOMING: Sublette Co., north of Pinedale on road to Elkhart Park, 2 mi. from end of road (elev. 8500 ft.). Old clearing in lodgepole pine forest.
	26 II	777	WYOMING: Lincoln Co., 0.5 mi. north of La Barge along banks of Green River.
	26 II	778	WYOMING: Lincoln Co., 0.5 mi. north of La Barge along banks of Green River.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. ascendens (cont.)	26 II	779	WYOMING: Lincoln Co., south of Kemmerer at jct. of Hwys. 30 and 189, on gravel road shoulder.
	26 II	781	UTAH: Summit Co., at Trailhead campground on east Fork Smithsfork Creek; sagebrush hillside above creek.
	26 II	785	WYOMING: Uinta Co., county road #294, 2 mi. south of Lone Tree on grassy road shoulder.
	26 II	786	WYOMING: Carbon Co., on Hwy. 789, 14 mi. south of Divide, in dry creek bed.
	26 II	789	COLORADO: Routt Co., 2 mi. west of Hayden on Hwy. 40, along sandy banks of Yampa River.
	26 II	794	COLORADO: Grand Co., 11 mi. north of Kremmling on Hwy. 40, in grassy meadow beside creek.
	26 II	799	COLORADO: Clear Creek Co., 2.5 mi. east of Loveland Pass on Hwy. 6, on hillside above creek (elev. 11,500 ft.)
	26 II	802	COLORADO: Park Co., 6 mi. south of Fairplay on Hwy. 9 near crossing of Middle Fork South Platte River.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. ascendens (cont.)	26 II	807	COLORADO: Teller Co., south of Divide, on USFS #383, 0.5 mi. from Hwy. 67; grassy meadow near stream.
	26 II	814	COLORADO: Fremont Co., Hayden Creek campground, in Sangre de Cristo Mts. southwest of Coaldale. Roadside near creek.
	26 II	818	COLORADO: Saguache Co., 4 mi. south of Poncha Pass on Hwy. 285, at Clover Creek.
	26 II	819	COLORADO: Rio Grande Co., Hwy. 285 at crossing of Rio Grande. Grassy area under cottonwoods near river.
	26 II	823	NEW MEXICO: Taos Co., south of Taos, on Rio Chiquito road 3.3 mi. from Hwy. 3, on banks of creek.
	26 II	828	NEW MEXICO: Rio Arriba Co., 4 mi. south of Cebolla on Hwy. 84; gravel road shoulder on edge of juniper forest.
	26 II	836	COLORADO: La Plata Co., on Hwy. 550 north of Durango at turnoff to Rockwood.
	52	838	COLORADO: Ouray Co., 3 mi. north of Red Mountain Pass on Hwy. 550; disturbed site on edge of aspen grove in loop of road.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. ascendens (cont.)	26 II	841	COLORADO: San Miguel Co., on Hwy. 141 near Slick Rock. Sandy banks of Dolores River.
	32 II	747	MONTANA: Beaverhead Co., 10 mi. north of Wisdom on Hwy. 43; damp area near roadside and in adjacent meadow.
A. bernardinus	ca. 21 II	602	CALIFORNIA: Kern Co., Mt. Piños road, 0.5 mi. west of jct. with Frazier Park road, on small dirt side road. Dry creek bed.
	42	603	CALIFORNIA: Kern Co., Mt. Piños road, 0.5 mi. west of jct. with Frazier Park road, on small dirt side road. Dry creek bed.
A. chilensis	48	870	OREGON: Lincoln Co., sand dunes south of Newport Bay, at South Beach. Deflation plain behind foredune.
	24 II + 3-4 B	515	OREGON: Lincoln Co., Waldport. Gravel roadside next to high school.
	24 II	516	OREGON: Lincoln Co., Hwy. 101, 0.2 mi. south of Driftwood Beach State Park. Road shoulder.
	24 II	BFL-13 (Chambers s.n.)	OREGON: Lincoln Co., Heceta Head north of Florence.
	24 II	BFL-14 (Chambers s.n.)	OREGON: Lincoln Co., Heceta Head north of Florence.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. eatonii	16	542	BRITISH COLUMBIA: north of Moha (near Lillooet), 5-10 mi. from Bridge River on Yalakom River road. Gravelly edge of river.
	8 II	553	OREGON: Hood River Co., 6 mi. north of Parkdale on road to Odell. Bank with seepage, at forest edge.
	8 II	560	CALIFORNIA: Shasta Co., approx. 3 mi. south of Hat Creek general store on Hwy. 89. Edges of ditch along road.
	8 II	575	CALIFORNIA: Sierra Co., on Hwy. 49 at Big Springs, 3 mi. east of Sierra City. Edge of stream.
	8 II	590	CALIFORNIA: Tuolumne Co., in Stanislaus National Forest, east of Tuolumne City at Hacienda campground. Damp hollow near stream, under black oak.
	8 II	622	CALIFORNIA: Modoc Co., 4.5 mi. south of New Pine Creek, on Hwy. 395 near Goose Lake. Roadside ditch.
	16	692	BRITISH COLUMBIA: Hwy. 97 north of Vernon, 2.4 mi. south of jct. with Hwy. 97A. Wet area along roadside.
	8 II + 1B	736	MONTANA: Lake Co., 8.6 mi. north of Arlee on Hwy. 93, along edge of Jocko River.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. eatonii (cont.)	8 II	756	MONTANA: Beaverhead Co., Red Rock Lakes region, along edge of stream in Lakeview township.
	8 II + 1B	775	WYOMING: Sublette Co., in campground on east side of Fremont Lake. Damp area in forest near small creek.
	8 II + 1B	856	WASHINGTON: Okanogan Co., on North Cascades Hwy., 3 mi. west of Winthrop. Sand bar in Methow River.
	16	860	WASHINGTON: Kittitas Co., 7.5 mi. south of Swauk Pass along Hwy. 97, on forested road shoulder near Swauk Creek.
	8 II + 3B	861	WASHINGTON: Kittitas Co., on Hwy. 821 in Yakima Canyon, 6 mi. north of Yakima County line, along banks of Yakima River.
	8 II	514	OREGON: Deschutes Co., on road to Paulina Lakes, along banks of Paulina Creek at McKay Crossing.
	8 II	513	OREGON: Deschutes Co., on road to Paulina Lakes, along banks of Paulina Creek at McKay Crossing.
	8 II	BFL-29 (Chambers s.n.)	OREGON: Jefferson Co., on banks of Metolius River, at Camp Sherman.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. eatonii (cont.)	16	Chambers 4414	OREGON: Deschutes Co., Tumalo State Park northwest of Bend, on side road South of Hwy. 20 along banks of Deschutes River.
	16 II	653	OREGON: Wallowa Co., 4 mi. north of Enterprise on Hwy. 3, in shallow ditch along edge of plowed field.
	ca. 16 II	655	OREGON: Wallowa Co., 2 mi. east of Minam on Hwy. 82 (just west of state park). Road cut with seep water, above highway.
A. foliaceus var. canbyi	8 II	BFL-18 (Rominger s.n.)	ARIZONA: Coconino Co., San Francisco Mt., north of Flagstaff.
	8 II	BFL-19 (Rominger s.n.)	ARIZONA: Coconino Co., San Francisco Mt., north of Flagstaff.
	8 II	BFL-20 (Rominger s.n.)	ARIZONA: Coconino Co., San Francisco Mt., north of Flagstaff.
	8 II	BFL-21 (Rominger s.n.)	ARIZONA: Coconino Co., San Francisco Mt., north of Flagstaff.
	8 II	BFL-22 (Rominger s.n.)	ARIZONA: Coconino Co., San Francisco Mt., north of Flagstaff.
	8 II	BFL-23 (Rominger s.n.)	ARIZONA: Coconino Co., San Francisco Mt., north of Flagstaff.
A. foliaceus var. foliaceus	16	798	COLORADO: Clear Creek Co., 2.5 mi. east of Loveland Pass on Hwy. 6 (elev. 11,500 ft.). Seep on hillside above creek.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. foliaceus var. foliaceus (cont.)	16	801	COLORADO: Summit Co., on Boreas Pass Road east of Breckenridge, at Baker's Tank picnic ground. Road shoulder at meadow edge near stream.
	16	865 (Geber s.n.)	COLORADO: Park Co., Pennsylvania Mt., in alpine meadows.
	18	715 (Pojar s.n.)	BRITISH COLUMBIA: North of Smithers at ski area on Hudson Bay Mt.; meadow in subalpine parkland.
	36	767	WYOMING: Teton Co., Togwotee Pass on Hwy. 26/287; meadow in hollow immediately west of pass.
	24 II	534	BRITISH COLUMBIA: North of Lytton, subalpine meadow on Morgan Mt. above Botanie Valley.
	24 II	535	BRITISH COLUMBIA: North of Lytton, subalpine meadow on Morgan Mt. above Botanie Valley.
	24 II	702	ALBERTA: Kananaskis Rd. 54 mi. north of Coleman. Rocky banks of creek in small steep ravine.
	64	545	BRITISH COLUMBIA: 32.5 mi. north of Moka (near Lillooet) on road to Poison Mt.; meadow in lodgepole pine forest, Stern Creek drainage.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. foliaceus var. foliaceus (cont.)	32 II	707	MONTANA: Glacier National Park, along Going-to-the-Sun Road, on wet cliffs along roadside at Haystack Creek.
	32 II	743	MONTANA: Beaverhead Co., 0.5 mi. east of Chief Joseph Pass on Hwy. 43, at edge of small creek in lodgepole pine forest.
	64	822	COLORADO: Conejas Co., Rio Grande National Forest, on USFS #250, 1 mi. north of Stunner Pass.
	64	848	UTAH: Beaver Co., 10-15 mi. east of Beaver on Hwy. 153. Edge of stream bank in spruce-aspen grove.
	64	858	WASHINGTON: Chelan Co., 1.4 mi. east of Stevens Pass on Hwy. 2; small opening near creek.
	40 II	793	COLORADO: Grand Co., 11 mi. north of Kremmling on Hwy. 40. Grassy meadow beside creek.
	40 II	797	COLORADO: Summit Co., west side of Green Mt. Reservoir 1.5 mi. north of Heeney at BLM campground. Banks of small creek.
	40 II	800	COLORADO: Summit Co., 3.3 mi. west of Loveland Pass on Hwy. 6, on road shoulder in subalpine forest.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. foliaceus var. foliaceus (cont.)	ca. 44 II	762	WYOMING: Teton Co., Teton Pass on Hwy. 22. Lush subalpine meadow.
A. foliaceus var. parryi	8 II + 1B	739	MONTANA: Ravalli Co., Bitterroot Mts., on grassy banks of Lost Horse Creek 8 mi. west of turnoff to Lost Horse Observation Point.
	8 II	740	MONTANA: Ravalli Co., Bitterroot Mts., in grassy meadow near Twin Lakes at head of Lost Horse Creek.
	16	766	WYOMING: Fremont Co., 6.7 mi. east of Togwotee Pass on side road north of Falls campground.
	8 II	806	COLORADO: Teller Co., south of Divide, on USFS #383, 0.5 mi. from Hwy. 67. Grassy meadow.
	16	816	COLORADO: Chaffee Co., 2 mi. east of Monarch Pass on Hwy. 50, at edge of seep in subalpine forest.
	8 II	830	NEW MEXICO: Rio Arriba Co., 4 mi. west of road to Hopewell Lake on Hwy. 64. Openings in subalpine parkland.
	24	847	UTAH: Beaver Co., 0.8 mi. west of Big Flat Ranger Station on Hwy. 153, in subalpine meadow.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. foliaceus var. parryi (cont.)	32	661	OREGON: Union Co., on road from La Grande to Mt. Emily; hillside at 6000 ft.
	32	851	OREGON: Linn Co., west of Tombstone Pass on Hwy. 20, 0.6 mi. east of Snow Creek. Disturbed area along road edge.
	24 II	662	OREGON: Union Co., on north edge of La Grande, along edge of field.
	24 II	755	MONTANA: Beaverhead Co., along shores of Lower Red Rock Lake.
	64	713	IDAHO: Idaho Co., Powell campground on Hwy. 12, along banks of Lochsa River.
	32 II	714	IDAHO: Idaho Co., 33.5 mi. east of Lowell on Hwy. 12, along Lochsa River.
	32 II	741	MONTANA: Ravalli Co., near Painted Rocks Lake at Slate Creek.
	32 II	742	IDAHO: Lemhi Co., Bitterroot Mts., along Woods Fork Horse Creek (off USFS #065) at Horse Hot Springs campground.
	32 II	745	MONTANA: Beaverhead Co., 4.5 mi. east of Chief Joseph Pass on Hwy. 43; grassy meadow along Joseph Creek.
	32 II	760	IDAHO: Fremont Co., east of Ashton on road to Cave Falls, 7 mi. east of Porcupine Creek crossing.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. foliaceus var. parryi (cont.)	32 II	761	WYOMING: Teton Co., road up South Leigh Creek, 0.8 mi. east of Idaho state line. Dry creek bed.
	64	780	UTAH: Summit Co., Trailhead campground on east Fork Smithsfork Creek, in willow scrub.
	32 II	817	COLORADO: Chaffee Co., 2 mi. east of Monarch Pass on Hwy. 50. Edge of seep in subalpine forest.
	32 II	846	UTAH: Beaver Co., near Big Flat Ranger Station on Hwy. 153, in subalpine meadow.
	40 II	831	NEW MEXICO: Rio Arriba Co., 18 mi. east of Tierra Amarilla on Hwy. 64.
	48 II	764	WYOMING: Teton Co., 2 mi. west of Wilson on Hwy. 22. Gravel road shoulder.
A. greatai	8 II + 7-8 B	605	CALIFORNIA: Los Angeles Co., upper Arroyo Seco, approx. 0.5 mi. downstream from Switzer's picnic ground. Damp places along creek and on canyon wall.
A. hallii	16	852 (Schofield s.n.)	OREGON: Polk Co., 12 mi. west of Monmouth, near Falls City.
	8 II	BFL-3 (Chambers s.n.)	OREGON: Benton Co., grasslands near Corvallis.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. hallii (cont.)	8 II	BFL-4 (Chambers s.n.)	OREGON: Benton Co., grasslands near Corvallis.
	8 II + 1B	CW-1 (Chambers s.n.)	OREGON: Benton Co., meadow near Canterbury Circle off Hwy. 99W, north of Corvallis.
	16	CW-2 (Chambers s.n.)	OREGON: Benton Co., meadow near Canterbury Circle off Hwy. 99W, north of Corvallis.
	16 II	BFL-6 (Chambers s.n.)	OREGON: Benton Co., grasslands near Corvallis.
A. hesperius	ca. 56	840	COLORADO: San Miguel Co., 6 mi. east of Norwood on Hwy. 145, along banks of San Miguel River.
	64	727	MONTANA: Lincoln Co., rocky shoreline of Bull Lake along Hwy. 56 (202).
	32 II	787	COLORADO: Moffat Co., Hwy. 789 just north of Craig. Edge of swampy creek.
	32 II	788	COLORADO: Routt Co., 2 mi. west of Hayden on Hwy. 40, along sandy banks of Yampa River.
	32 II	803	COLORADO: Park Co., 1.5 mi. south of Lake George on Eleven Mile Canyon road, along gravel edge of South Platte River.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. hesperius (cont.)	32 II	804	COLORADO: Park Co., 10 mi. south of Lake George on Eleven Mile Canyon road, along gravel edge of South Platte River.
	32 II	808	COLORADO: El Paso Co., along Hwy. 24 at Cascade, on banks of Crystola Creek.
	32 II + 3B	811	COLORADO: Fremont Co., 0.5 mi. west of Canon City. Gravel edge of irrigation ditch near Arkansas River.
	32 II	812	COLORADO: Fremont Co., 0.5 mi. west of Canon City. Gravel edge of irrigation ditch near Arkansas River.
	32 II + 6B	815	COLORADO: Fremont Co., 3 mi. east of Swissvale on Hwy. 50; willow scrub near Arkansas River.
	32 II	825	NEW MEXICO: Taos Co., 1 mi. from Hwy. 3 south of Taos on Rio Chiquito Road, in willow scrub along creek.
	32 II + 2B	827	NEW MEXICO: Rio Arriba Co., Espanola, near Rio Grande north of Hwy. 84; banks of muddy pond.
	32 II	832	NEW MEXICO: Rio Arriba Co., on Hwy. 84 at Chama, along road shoulder.
	ca. 32 II	843	UTAH: Wayne Co., 2 mi. east of Capitol Reef National Park on Hwy. 24. Edge of Fremont River.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. hesperius (cont.)	32 II	BFL-16 (Chambers 3822)	COLORADO: Boulder Co., Baseline Road east of Boulder (0.9 mi. west of 76th St.); edge of creek.
	32 II	BFL-17 (Chambers 3822)	COLORADO: Boulder Co., Baseline Road east of Boulder (0.9 mi. west of 76th St.); edge of creek.
	32 II	BFL-24 (Chambers 3591)	IDAHO: Bannock Co., 10 mi. west of Ft. Hall on road to historic Ft. Hall site. Sedgy meadows.
A. idahoensis	8 II + 3B	641	IDAHO: Shoshone Co., 3 mi. north of Clarkia turnoff on Hwy. 3, at crossing of St. Maries River.
A. jessicae	18 II	721	IDAHO: Bonner Co., 9 mi. north of Priest River, on Quartz Mt. road 1 mi. from highway. Gravel road shoulder.
A. laevis	48	694	BRITISH COLUMBIA: 11 mi. north of Golden on Hwy. 1, along banks of small creek near Columbia River.
	48	695	BRITISH COLUMBIA: 11 mi. north of Golden on Hwy. 1, along banks of small creek near Columbia River.
	48	697	ALBERTA: 6 mi. north of Coleman on Kananaskis Road, along creek bank in lodgepole pine forest.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. laevis (cont.)	24 II	698	ALBERTA: 36 mi. north of Coleman on Kananaskis Road; creek edge.
	24 II	699	ALBERTA: 37 mi. north of Coleman on Kananaskis Road; banks of Speers Creek.
	48	703	ALBERTA: 46 mi. north of Coleman on Kananaskis Road; banks of Northtwin Creek.
	24 II	704	ALBERTA: 28 mi. north of Coleman on Kananaskis Road; seep above Oldman River.
	48	705	ALBERTA: 28 mi. north of Coleman on Kananaskis Road; seep above Oldman River.
	ca. 48	708	MONTANA: Lake Co., 2-3 mi. south of Big Fork on east side of Flathead Lake. Road shoulder.
	24 II + 1B	723	IDAHO: Bonner Co., 1 mi. east of Priest River on Hwy. 2; forest edge.
	24 II	728	MONTANA: Lincoln Co., 12 mi. west of Libby on Hwy. 2; forest edge.
	24 II	729	MONTANA: Lincoln Co., 6.5 mi. west of Libby on banks of Kootenai River.
	24 II	733	MONTANA: Flathead Co., 38 mi. west of Kalispell on Hwy. 2; road shoulder.
	48	752	IDAHO: Clark Co., 3 mi. south of Montana state line on I-15; grass along road.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. laevis (cont.)	24 II	810	COLORADO: El Paso Co., 2.4 mi. west of Manitou Springs on Hwy. 24 (eastbound lane). Road shoulder and edges of creek.
	24 II	833	COLORADO: Archuleta Co., northwest of Pagosa Springs on USFS #629, 9 mi. from Hwy. 160.
	24 II	835	COLORADO: Archuleta Co., on Hwy. 160 at crossing of Piedra River, on sand bar along river.
	24 II	839	COLORADO: San Miguel Co., 6 mi. east of Norwood on Hwy. 145. Edge of San Miguel River.
	24 II	BFL-11 (Chambers s.n.)	MONTANA: Carbon Co., south of Red Lodge, near aspen grove in floodplain of Rock Creek.
	24 II	BFL-12 (Chambers s.n.)	MONTANA: Carbon Co., south of Red Lodge, near aspen grove in floodplain of Rock Creek.
	32 II	754	MONTANA: Beaverhead Co., 11 mi. east of Monida on Red Rock Lakes road, along edge of irrigation ditch near Price Creek.
	32 II	783	UTAH: Summit Co., ridge 0.5 mi. west of China Meadows near Trailhead campground.
	ca. 32 II	826	NEW MEXICO: Taos Co., south of Taos on Hwy. 3 (5 mi. north of jct. with Hwy. 75). Road shoulder.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. lentus	32 II	578	CALIFORNIA: Solano Co., near Suisun City on road to Rio Vista (Hwy. 12), 0.7 mi. east of railroad crossing. Edge of canal.
	64	579	CALIFORNIA: Solano Co., near Suisun City on road to Rio Vista (Hwy. 12), 0.7 mi. east of railroad crossing. Edge of canal.
	32 II	Knight + Heckard 3293	CALIFORNIA: Contra Costa Co., Browns Island.
A. occidentalis var. intermedius	8 II	555	CALIFORNIA: Siskiyou Co., near Panther Meadows campground on Mt. Shasta. Edge of snowmelt stream.
	8 II + 1B	556	CALIFORNIA: Siskiyou Co., 15 mi. east of I-5 on Hwy. 89 at Elk Creek.
	8 II	557	CALIFORNIA: Shasta Co., Hwy. 89 at Cayton Creek, north of Britton Lake. Damp meadow along creek.
	6 II + 1 IV (=16)	558	CALIFORNIA: Shasta Co., Hwy. 89 at Cayton Creek, north of Britton Lake. Damp meadow along creek.
	16	561	CALIFORNIA: Shasta Co., Lassen National Park at Lost Creek in mudslide zone.
	8 II	582	CALIFORNIA: El Dorado Co., 2 mi. north of Hwy. 88 on road from Corral Flat to Pollock Pines; meadow at Leek Springs.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. occidentalis var. intermedius (cont.)	8 II	609	CALIFORNIA: Inyo Co., 17 mi. west of Bishop on Hwy. 168, at Aspendell. Sedgy meadow.
	16 + 2B	625	OREGON: Lake Co., 2-3 mi. north of Silver Lake on road to Fort Rock. Damp pasture edge.
	8 II	685	OREGON: Harney Co., 2 mi. east of Hwy. 205 on Krumbo Lake road, along edge of ditch.
	8 II	722	IDAHO: Bonner Co., 3 mi. north of Priest River on Hwy. 57. Road cut at forest edge.
	8 II	731	MONTANA: Lincoln Co., 6.5 mi. west of Libby along banks of Kootenai River.
	16 II	567	CALIFORNIA: Plumas Co., 0.5 mi. south of Crescent Mills on Hwy. 89. Grassy hollow between road and railroad.
	16 II	568	CALIFORNIA: Plumas Co., 0.5 mi. south of Crescent Mills on Hwy. 89. Grassy hollow between road and railroad.
	16 II	571	CALIFORNIA: Plumas Co., road to Gold Lake, on side road to Lakes Basin campground. Dry creek bed.
	32	592	CALIFORNIA: Fresno Co., Hwy. 168 just north of Shaver Lake. Woodland near town.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. occidentalis var. intermedius (cont.)	16 II	593	CALIFORNIA: Fresno Co., Hwy. 168 just north of Shaver Lake. Woodland near town.
	16 II	598	CALIFORNIA: Tulare Co., 0.5 mi. east of Quaking Aspen campground on Hwy. 190, in meadow.
	16 II	610	CALIFORNIA: Mono Co., 3 mi. south of Crowley Lake exit on Hwy. 395 (north of Tom's Place). Wet meadow on east side of road.
	32	617	CALIFORNIA: Alpine Co., 1.3 mi. south of Luther Pass on Hwy. 89 south of Lake Tahoe.
	16 II	648	IDAHO: Latah Co., 4 mi. south of Moscow on Hwy. 95. Road cut along wheatfield.
	16 II	666 (Chambers s.n.)	OREGON: Deschutes Co., Metolius Meadows.
	24 II	656	OREGON: Union Co., 7 mi. east of Elgin on Hwy. 82, on high plateau. Edge of ditch along road.
	24 II	718	IDAHO: Bonner Co., 9 mi. north of Priest River on Quartz Mt. road, 2 mi. from highway.
	24 II	719	IDAHO: Bonner Co., 9 mi. north of Priest River on Quartz Mt. road, 2 mi. from highway.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. occidentalis var. intermedius (cont.)	48	730	MONTANA: Lincoln Co., 6.5 mi. west of Libby on rocky and grassy banks of Kootenai River.
	24 II	BFL-27 (Chambers 3809)	IDAHO: Bannock Co., 10 mi. west of Ft. Hall on road to historic Ft. Hall site. Grassy meadow.
	24 II	BFL-32 (Chambers 3809)	IDAHO: Bannock Co., 10 mi. west of Ft. Hall on road to historic Ft. Hall site. Grassy meadow.
	64	584	CALIFORNIA: Amador Co., Hwy. 88 at Corral Flat. Ditch along road.
	32 II	737	MONTANA: Ravalli Co., along sandy banks of Bitterroot River just west of Stevensville.
	32 II	748	MONTANA: Silver Bow Co., along banks of Big Hole River just west of Melrose.
	32 II	750	MONTANA: Beaverhead Co., Horse Prairie Creek just west of Clark Canyon Reservoir.
	32 II	776	WYOMING: Sublette Co., on edge of Fremont Lake 2 mi. north of turnoff to Elkhart Park.
	32 II	BFL-25 (Chambers 3809)	IDAHO: Bannock Co., 10 mi. west of Ft. Hall on road to historic Ft. Hall site. Grassy meadow.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. occidentalis var. occidentalis	8 II	586	CALIFORNIA: Tuolomne Co., off Hwy. 108 near Pinecrest. Damp stream bank.
	8 II	725	MONTANA: Sanders Co., Hwy. 200 at crossing of Bull River, grassy edge of river.
	16	726	MONTANA: Sanders Co., 2.5 mi. south of Hwy. 56 on Snake Creek Pass road, gravel banks of Bull River.
	16 II	585	CALIFORNIA: Amador Co., Hwy. 88 at Corral Flat. Ditch along road.
	16 II	599	CALIFORNIA: Tulare Co., 0.5 mi. east of Quaking Aspen campground on Hwy. 190, in meadow.
	32	601	CALIFORNIA: Tulare Co., Sequoia National Forest, near Redwood Meadows campground.
	16 II + 4B	633	IDAHO: Latah Co., 8 mi. south of Deary on Hwy. 3, on high plateau. Shallow ditches along road.
	16 II	634	IDAHO: Latah Co., 8 mi. south of Deary on Hwy. 3, on high plateau. Shallow ditches along road.
	16 II	635	IDAHO: Latah Co., 8 mi. south of Deary on Hwy. 3, on high plateau. Shallow ditches along road.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. occidentalis var. occidentalis (cont.)	16 II	650	OREGON: Wallowa Co., 5 mi. south of Washington state line on Hwy. 3, in small meadow.
	16 II	665 (Chambers s.n.)	OREGON: Deschutes Co., Metolius Meadows.
	16 II	710	IDAHO: Idaho Co., Packer Meadows 1.5 mi. south of Lolo Pass.
	32	711	IDAHO: Idaho Co., Packer Meadows 1.5 mi. south of Lolo Pass.
	16 II	712	IDAHO: Idaho Co., Packer Meadows 1.5 mi. south of Lolo Pass.
	24 II	548	BRITISH COLUMBIA: 7 mi. south of Merritt on Hwy. 5. Damp grassy area on south side of small reedy lake.
	24 II	566	CALIFORNIA: Tehama Co., Lassen National Park, at edge of road below Diamond Peak.
	24 II + 8 B	771	WYOMING: Sublette Co., 2 mi. east of Granite Creek turnoff on Hwy. 187/189, along banks of Hoback River.
	32 II	738	MONTANA: Ravalli Co., sandy banks of Bitterroot River just west of Stevensville.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. porteri	8 II	809	COLORADO: El Paso Co., 2.4 mi. west of Manitou Springs on Hwy. 24 (eastbound lane). Gravel road shoulder.
A. subspicatus	48	517	BRITISH COLUMBIA: Vancouver Island, Patricia Bay on west side of Saanich Peninsula.
	48	521	BRITISH COLUMBIA: North Vancouver, Maplewood mud flats east of Second Narrows bridge.
	24 II	682	WASHINGTON: Snohomish Co., 23 mi. north of Everett On I-5. Road shoulder.
	24 II	684	WASHINGTON: Snohomish Co., 23 mi. north of Everett on I-5. Road shoulder.
	48	690	BRITISH COLUMBIA: Hwy. 3 (Hope-Princeton Hwy.) just east of Sunday Summit. Small creek bed.
	24 II	511	OREGON: Deschutes Co., Hwy. 97 at turnoff to Paulina Lakes. Gravel road shoulder.
	24 II	BFL-28 (Chambers 3591)	IDAHO: Bannock Co., 10 mi. west of Ft. Hall on road to historic Ft. Hall site.
	ca. 80	859	WASHINGTON: Chelan Co., Hwy. 209 at Leavenworth. Disturbed area at edge of ponderosa pine forest.

Taxon	Diploid Chromosome Number	Collection Number	Locality
A. subspicatus (cont.)	48 II	519	BRITISH COLUMBIA: Vancouver Island, along Port Alberni to Tofino road, west of Sutton Pass on Kennedy River. Gravel bar.
	48 II	522	BRITISH COLUMBIA: 0.5 mi. east of Yale along edge of Fraser River.
	48 II	523	BRITISH COLUMBIA: 0.5 mi. east of Yale along edge of Fraser River.
	48 II	547	BRITISH COLUMBIA: Hwy. 8 between Spences Bridge and Merritt, just east of Canfield, along old riverbed near Nicola River.
	ca. 96	691	BRITISH COLUMBIA: Hwy. 3 east of Princeton, on side road near bridge west of Stemwinder campground. Gravel banks of Similkameen River.
	ca. 96	853	OREGON: Polk Co., 12 mi. west of Monmouth near Falls City.