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Title: TAXONOMIC STUDIES OF THE EUCEPHALUS COMPLEX OF ASTER IN THE PACIFIC NORTHWEST

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The Pacific Northwest Eucephalus complex is a poorly defined series of Aster taxa occupying montane habitats from the Cascade and Rocky Mountains of southern British Columbia south through the mountain ranges of Washington and Oregon into the Trinity Alps and other ranges of northern California. Several of the taxa have extremely limited distribution, while others extend through more than half geographic range. In several cases, two or more of these taxa are existing sympatrically. Similarity among members of the has been discussed in taxonomic literature since classification of the group began in the mid 1800's. The present work seeks to define taxonomic relationships using native population studies, garden trials, experimental crosses, and herbarium collections. This study does not propose a complete taxonomic solution for the group, but it does advance hypotheses on primary relationships and does propose nomenclatural simplifications.

Taxonomic Studies of the *Eucephalus* Complex of *Aster* in the Pacific Northwest

by

Dennis Dean Thompson

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APPROVED:

Redacted for privacy

Professor of Botany
in charge of major

Redacted for privacy

Chairman of the Department of Botany and Plant Pathology

Redacted for privacy

Dean of Graduate School

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

TAXONOMIC STUDIES OF THE *EUCEPHALUS* COMPLEX OF *ASTER* IN THE PACIFIC NORTHWEST

I. INTRODUCTION

The *Eucephalus* complex of *Aster* has occupied several taxonomic niches in its 135 year history. In 1840 Nuttall proposed a new genus Eucephalus and described its members as follows:

> Capitulum radiate, styliferous rays fertile; liguli of one series (seven to fifteen); hermaphrodite florets of the disk fertile. Stigma slender, filiform, acuminate, nearly smooth. Involucrum ovate, imbricate, of three or four series of nearly similar ovate, carinated scales. Receptacle flat, alveolate, fimbrillate. Achenia angular, pubescent (or smooth). Pappus about two series, scabrous, simple and clavellate. Herbaceous perennials with nearly simple stems, the sumit, or the fastigiate branches, corymbose. Leaves entire, the radical rarely serrulate. Disk yellow. Liguli pale purple or white. Plants with the habit of *Galatella*, and the pappus of *Sericocarpus*. (Nuttall, 1841, p. 298).

Torrey and Gray submerged *Eucephalus*, along with two other genera proposed by Nuttall, into the genus *Aster* as subgenus *Orthomeris* (Torrey and Gray, 1841, p. 156; 1880, p. 98; 1884, p. 198). Greene chose to resurrect "Nuttall's long suppressed genus" in 1896, and, to reinforce his interpretation, he described a new species, *Eucephalus serrulatus*, "distributed for real *E. engelmannii*, from which it is most distinct, although doubtless confused with it by Dr. Gray" (Greene, 1896, p. 55). Greene recognized nineteen species, ten which he proposed. Acceptance of full generic status held for several years, but with *Eucephalus* as with *Biotia*, *Ionactis*, and many others

allied to Aster, the distinguishing characteristics for defining the genus are very tenuous. A large genus Aster with several such small satellite genera is no more practical than single inclusive genus (Cronquist and Keck, 1957). Therefore, modern taxonomic systems most often include the members of the Eucephalus complex as a section of the genus Aster.

In most modern treatments the Eucephalus complex include the following species: Aster engelmannii (D. C. Eaton) A. Gray, a species common through the Rocky Mountains and other mountain ranges of the Northwestern United States and Southwestern Canada; Aster perelegans Nels. & Macbr., which is widely distributed over the interior Northwestern United States; Aster ledophyllus (A. Gray) A. Gray, a species extending through the mountain ranges of the Pacific Northwest; and several relatively localized species including Aster paucicapitatus (Robinson) Robinson, Aster glaucescens (A. Gray) Blake, Aster gormanii (Piper) Blake, Aster vialis (Bradshaw) Blake, Aster brickellioides Greene, and Aster siskiyouensis Nels. & Macbr., distributed along the Olympic, Cascade, and Siskiyou Mountain Ranges.

The present study begun in 1971 encompasses the distribution, morphology, and taxonomy of those members of the Eucephalus complex that occur in the Pacific Northwest region. The work includes field observations, greenhouse studies, and herbarium research with special attention given to collections made at sites where species grow sympatrically. The study area comprised the western mountain regions

from British Columbia south into Northern California. The eastern limits of the Cascade and Siskiyou Mountain Ranges form the inland boundary. This area was chosen because species east of the Cascades and Siskiyou Ranges are either very widely distributed or are geographically disjunct from the taxa of the Pacific Northwest. Species incorporated in the study were A. ledophyllus, A. paucicapitatus, A. glaucescens, A. gormanii, A. vialis, A. brickellioides, A. siskiyouensis, and the Pacific Northwestern representative of A. engelmannii.

The purpose of the study was to examine this section of Aster which has drawn numerous comments in floras and journals about the relationships of member species. Although many of these taxa are not rare, few collections of six of the eight species were made in the past forty years and no information was available on culture, growth, or habitat. This study was initiated to fill these unknowns.

II. LITERATURE REVIEW

Taxonomy

Nuttall (1841) defined the genus Eucephalus to include E. elegans Nutt., E. albus (Nutt.) Nutt., E. glaucus Nutt., and E. ericoides (Torr.) Nutt. Torrey and Gray in 1841 combined Eucephalus with two other Nuttallian genera into Aster subgenus Orthomeris. In 1896 E. L. Greene challenged Gray's generic views and reinstated Eucephalus

to include ten species. Piper, in his Flora of the State of Washington (1906), chose to use Greene's interpretation, whereas, Frye and Rigg in their 1912 edition of Northwest Flora utilized Gray's more inclusive Aster classification. Bradshaw, when describing Eucephalus vialis in 1921, elected to follow Nuttall's and Greene's generic concept. In 1928, however, Blake transferred E. vialis to Aster. As late as 1931, Eucephalus was still recognized as a genus by some taxonomists, (Eastwood, 1931). By 1941, however, when M. E. Peck published his Manual of the Higher Plants of Oregon, it was generally accepted that Aster was an inclusive genus containing, as subgenera or sections, peripheral groups-Eucephalus, Amellastrum, Biotia, Doellingeria, Ionactis, Machaeranthera, and others. In separating Machaeranthera from Aster in 1957, Cronquist and Keck pointed out that all of these taxa varied from the original Aster in one or more respects. Their conclusion was that most of these groups could be retained within the genus Aster without disrupting the concepts of the genus, whereas removing them into individual genera still left a large core genus with an unwieldy number of small satellite genera.

The first species proposed by Nuttall (1841) was Eucephalus elegans later renamed Aster perelegans Nels. & Macbr., a plant with numerous small heads, whose distribution ranges from the low dry lands of eastern Oregon and Washington, eastward to Montana and Utah. In the same publication, Nuttall named Eucephalus glaucus (now known as Aster glaucodes Blake) of the Rocky Mountains.

The first member of this group to be described from the area under study was Aster engelmannii (D. C. Eaton) Gray, first published as Aster elegans (Nutt.) T. & G. var. engelmannii D. C. Eaton (1871). In 1880, Gray raised the taxon to the rank of species, where it remained until Greene (1896) devised the combination Eucephalus engelmannii (D. C. Eaton) Greene. Nearly all modern references use the name Aster engelmannii.

In 1871 Gray published the description of another member of the section, Aster engelmannii var. ledophyllus. Gray raised the variety to a species in 1880, as Aster ledophyllus (Gray) Gray, although in 1884, he returned the taxon to the varietal level under A. engelmannii. Greene changed the name to Eucephalus ledophyllus (Gray) Greene, in 1896. Greene described a related species based on a Coville collection from near Crater Lake, calling it Eucephalus covillei Greene. In 1941, Peck published for this taxa the name Aster covillei (Greene) Blake ex Peck. Cronquist (Hitchcock et al., 1955) reduced the taxon to varietal status as Aster ledophyllus var. covillei (Greene) Cronquist.

Aster glaucescens (Gray) Blake was first described by Gray (1884) as Aster engelmannii var. glaucescens, based on a Suksdorf collection on Mt. Adams. Greene elevated the taxon to Eucephalus glaucescens in 1896 and cited Suksdorf 118 as the type. In 1906, Piper proposed a new name, Eucephalus glaucophyllus Piper, for this species, and this epithet, although illegitimate under the modern rules of nomenclature, was transferred to Aster by Frye and Rigg in 1912. Blake (1912) pointed

out that the name Aster glaucescens was not preoccupied as Piper had believed, and he named the taxon Aster glaucescens (Gray) Blake. In Greene's 1896 publication, he named Eucephalus serrulatus as a new species from another Suksdorf collection from Mt. Adams. Frye and Rigg made the combination Aster serrulatus (Greene) Frye & Rigg (1912). More through disuse than positive action, this taxon has been submerged in A. glaucescens (Hitchcock et al., 1955).

Robinson (1891) proposed the name Aster engelmannii var. paucicapitatus from a collection by Piper in the Olympic Mountains. In 1894 he revised his classification, raising it to Aster paucicapitatus (Robins.) Robinson. Greene included the plant in his 1896 work as Eucephalus paucicapitatus (Robins.) Greene. As with the other members of the section, it has reverted to Aster in recent publications (Hitchcock et al., 1955).

In 1889 Greene published the description of a new species collected near Waldo, Oregon, which he called Sericocarpus tomentellus Greene. Later the same year he revised its generic placement calling the taxon Aster brickellioides Greene. He qualified his new diagnosis, "Although rayless, it must be rather closely connected with Aster ledophyllus, a plant which Dr. Gray at length placed in the rank of a variety of A. engelmannii." He continued, describing a second specimen, "I have this year collected a plant which, in the face of a good deal of dissimilarity as regards form and texture and even the venation and pubescence of the leaves, I nevertheless place provisionally under

A. brickellioides, as a variety glabratus." When he revived the genus Eucephalus in 1896, he returned to the specific epithet tomentellus. Eucephalus tomentellus Greene was accompanied in Greene's work by the companion species Eucephalus glabratus Greene. In 1913 Nelson and MacBride published Aster siskiyouensis Nels. & MacBr. as an alternative to the latter name, because Aster glabratus was already occupied by a Kuntze species. In 1931 Alice Eastwood proposed two new species closely related to A. brickellioides (E. tomentellus) and A. siskiyouensis (E. glabratus). She wrote that Eucephalus bycolor Eastw."... differs from E. tomentellus Greene in the rayed heads and the densely white pubescence of the lower leaf surface." Eucephalus glandulosus Eastw. "... is related to E. glabratus Greene, differing in the glandular-scabrous pubescence which extends to the upper leaf surface and the involucres." Neither of Eastwood's species was considered sufficiently different from the two earlier ones to be maintained in later publications such as those of Abrams (1960) or Munz and Keck (1959).

M. V. Gorman's collection 2851 was the type for Piper's Eucephalus gormanii. In his 1916 publication of this as a new species, Piper pointed out that this collection from the Mt. Jefferson area was "Most nearly allied to E. paucicapitatus (Rob.) Greene." Blake retrieved the species from Eucephalus and in 1928 published the name Aster gormanii (Piper) Blake.

The final recognized species of this area was described from the vicinity of Eugene, Oregon. Eucephalus vialis Brads. was collected in 1918 and published in 1921. It occurs at lower elevations than any of the other species. In the original publication, Bradshaw stated "I have come to the conclusion that it belongs to the genus, Eucephalus and that it is very closely related to E. Engelmannii." Blake made the combination Aster vialis (Brads.) Blake in 1928. In 1933, L. F. Henderson proposed the name Sericocarpus sipei for a plant of this species collected by F. B. Sipe, being unaware of Bradshaw's earlier name.

III. METHODS AND MATERIALS

Transplanting Technique

Collection sites were usually within a few hours hiking distance of road access, thus the time between removal and final potting of the plants was rarely more than twenty-four hours. Often these sites were close enough to a roadway to allow immediate potting, reducing plant losses due to drying and mechanically damaged root systems. Small plastic bags were used to cover the rootballs when populations were more distant. The plants were then placed in tall, narrow cardboard boxes or large plastic pots inside of a backpack to help prevent crushing.

Plants were dug with a rootball at least six inches in diameter whenever possible. The rootball was more often eight inches and up

to twelve inches in diameter on some occasions. Aster gormanii and A. paucicapitatus, which grow in talus areas, were impossible to collect with rootballs. These plants were carefully dug and the roots wrapped in moist soil from neighboring areas.

The plants were watered with a 500 ppm solution of Transplantone (American Chemical Corporation) when they were potted. This solution was then applied every second day for their first two weeks in the greenhouse at Oregon State University. Because of the peculiar edaphic conditions associated with many of the collection sites, at least one member of each population was potted in its native soil. In the case of A. gormanii and A. paucicapitatus, special mixtures of talus and soil from the area were used.

General Cultural Technique

At the end of the second week in the greenhouse, a program of light fertilization was instigated. Scope (Chemgro Corporation) a liquid insecticide, was applied periodically to control insect populations. The most frequent pest was whitefly.

Flower Forcing Technique

Greenhouse plants were subjected to a reduced annual cycle during their first year. After the plants completed their normal bloom cycle in late November, pots were moved into a cold frame for two months.

They were then returned to the greenhouse at minimum 15°C day and 10°C night temperatures. Artificial lights were used with the late season plants in an attempt to encourage earlier bud set. The second year of greenhouse culture dropped both the cold cycle and additional light period. Available light at various latitudes compiled from weather recording station data (Legge, 1971) was used in the original attempt to simulate various day lengths for the more southerly collections.

Pollination Technique

Heads were selected at random to be used for test and control. At least two heads for each clone were labelled as controls. Rayed heads were selected as the female parent since the ray florets are fertile and pistillate. Since A. brickellioides and A. siskiyouensis are generally rayless, they served as pollen sources. The one exception was an A. siskiyouensis which occasionally produced one to two rays per head. Crosses were made using a single head as the pollen source crossed to a single head as the female parent.

One or more fertile anthers were removed with forceps and brushed lightly against the stigma of the test head. The ray florets are receptive at least half a day before any of the disc flowers of a head open. Hence, no attempt was made to remove disc flowers in test heads since the mechanical disturbance could cause

abortion. Controls were handled similarly except pollination was delayed until anthers within the disc florets of the same head began to shed pollen.

Several variations of bagging and isolating were attempted. Glassine bags were slipped over the heads and clipped to the stem; glassine bags were gathered into loose caps and slipped over the head so that none of the flowers could rub against the bag; and onion skin paper diapers were folded around the pollinated heads.

A follow-up to the controlled pollination was conducted. Instead of using the pistillate rays, pollen was brushed against the stigmas in disc florets before the anthers in these florets began shedding pollen. No controls were designated since the purpose was not to record the mature seeds of known parentage, but to try to produce seeds that would yield plants with intermediate characteristics.

See Table I for attempted crosses.

IV. OBSERVATIONS AND RESULTS

Collected Material

The first collected plants were A. ledophyllus from Mt. Jefferson in October 1970. Collected plants in 1971 included A. ledophyllus from Mt. Hood; A. gormanii from Mt. Jefferson; A. brickellioides from Flycatcher Spring, Pyramid Rock, and near Patrick Creek in the Siskiyou; and A. siskiyouensis from Pyramid Rock. In 1972, specimens

Table I. Attempted Crosses.

Female Parent		Male Parent		Year
Aster ledophyllus	(A 1)	Aster ledophyllus	(A 3)	1971
A. ledophyllus	(A 2)	A. gormanii	(A 6)	1972
A. ledophyllus	(A 3)	A. gormanii	(A 6)	1972
A. ledophyllus	(A 3)	A. gormanii	(A 6)	1972
A. ledophyllus	(A 2)	A. brickellioides	(A 5)	1971
A. ledophyllus	(A 3)	A. brickellioides	(A 5)	1971
A. ledophyllus	(A 3)	A. brickellioides	(A 5)	1971
A. ledophyllus	(A 2)	A. siskiyouensis	(A 4)	1971
A. ledophyllus	(A 1)	A. paucicapitatus	(A 7)	1972
A. gormanii	(A 6)	A. ledophyllus	(A 2)	1972
A. gormanii	(A 6)	A. ledophyllus	(A 3)	1972
A. gormanii	(A 6)	A. ledophyllus	(A 3)	1972
A. gormanii	(A 6)	A. paucicapitatus	(A 7)	1972
A. ledophyllus	(A 10)	A. siskiyouensis	(A 4)	1972
A. siskiyouensis	(A 4)	A. brickellioides	(A 5)	1971
A. paucicapitatus	(A 7)	A. gormanii	(A 6)	1972
A. paucicapitatus	(A 7)	A. gormanii	(A 6)	1972
A. paucicapitatus	(A 7)	A. ledophyllus	(A 3)	1972
A. ledophyllus	(A 1)	Selfed		1971
A. ledophyllus	(A 2)	Selfed		1971

Table I. Continued.

Female Parent		Male Parent	year
A. ledophyllus	(A 3)	Selfed	1971
A. ledophyllus	(A 3)	Selfed	1972
A. siskiyouensis	(A 4)	Selfed	1971
A. gormanii	(A 6)	Selfed	1972
A. paucicapitatus	(A 7)	Selfed	1972

of A. gormanii from Mt. Jefferson; A. paucicapitatus from Hurricane Ridge and Mt. Constance; A. ledophyllus from Mt. Adams and Crater Lake; and A. brickellioides from Gasquet Flats were added to the collection. See Figure I and Table II for more information.

Survival

Losses of materials in transplanting amounted to less than 25% of the total collections. In no case were all of the examples of any population lost. There appeared to be no significant difference in the mortality of those planted in native soil under greenhouse conditions. Under garden conditions at Corvallis, however, A. brickellioides (A 4) and A. siskiyouensis (A 5) were lost the first year (1971-1972). Aster paucicapitatus (A 8), A. ledophyllus (A 1), and A. gormanii (A 6) declined. Other collections showed no noticeable response. Aster ledophyllus (A 3) and A. paucicapitatus (A 8) died soon after moving the plants to the second garden in Seattle. To date, A. gormanii has survived and appears to be progressing in the lighter soil. Aster ledophyllus from the lower elevations in the Cascades (A 10) and A. engelmannii (A 12) also appear to survive at lower elevations under garden conditions. Whether the original losses were due to the extremely heavy clay soil of the first site, or to the temperature-life cycle variations, or to a combination of factors is not certain. Likewise, moving the plants to a new site during the active growing season, when temperatures were in the high 80-90^{o}F

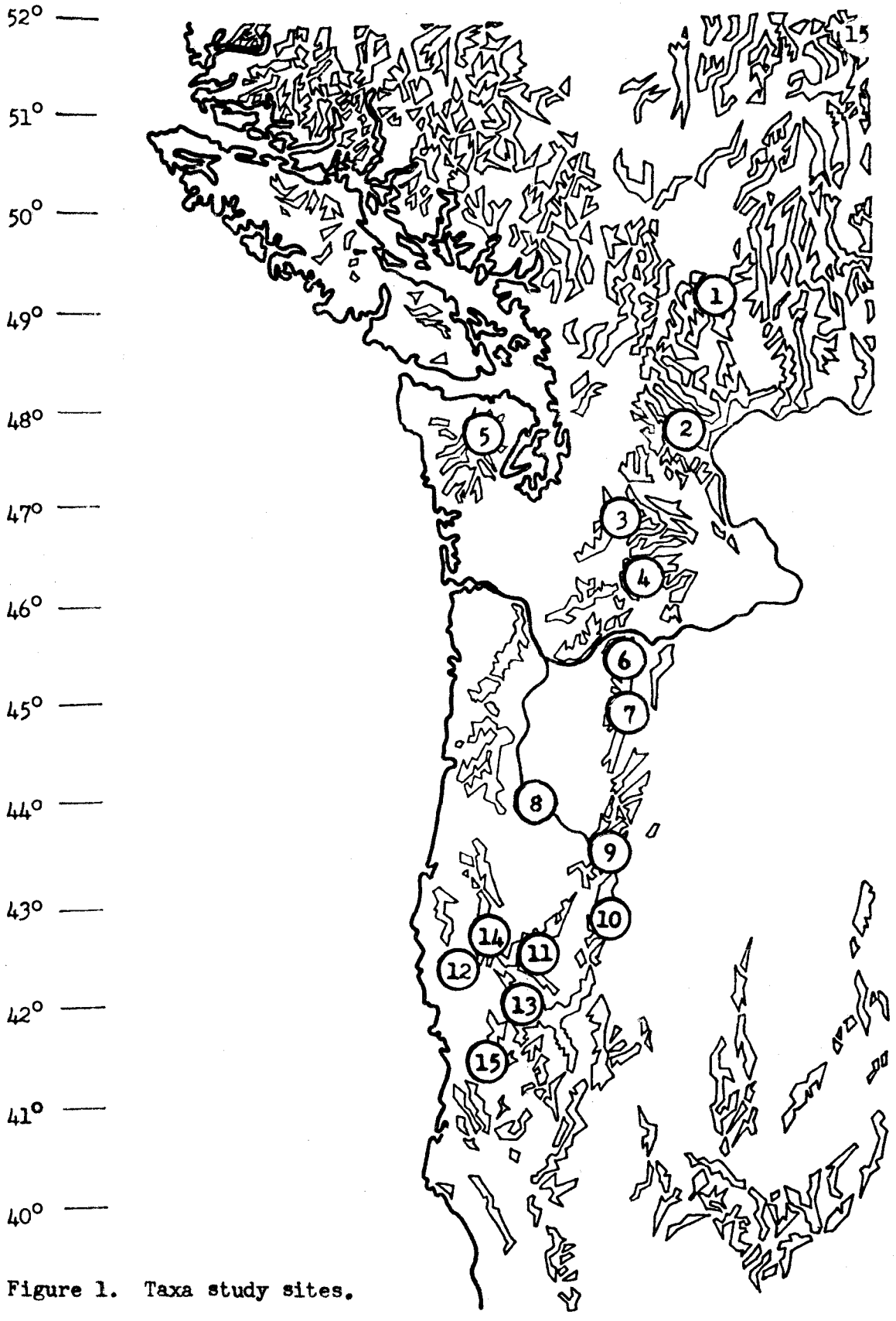


Figure 1. Taxa study sites.

Table II. Site and collection data.

H - Herbarium collection number
A - Garden accession number
S - Seeds gathered in native habitat

Study Area	Number of Fieldtrips and Garden Plants	Collections H	A	S
1 Manning Provincial Park, British Columbia, Canada; 40 miles south of Hope on Trans-Canada Hwy. 3; open woodland; el. 5000 ft.	One trip.			
2 Eagle Creek, Cascade and Wenachee Mountains, Washington; 8 miles northeast of Leavenworth on Eagle Creek Rd. via State Hwy. 209; open woodland; el. 3800 ft.	Five trips; one plant, 1973.	892, 898 & 899	12	
3 Mount Rainier, Cascade Mountains, Washington;				
Sunrise Ridge, 4 miles from State Hwy. 410 on road to ranger station; open woodland; el. 4800 ft.	One trip.			
Chinook Pass, summit on State Hwy. 410; open southern slopes; el. 5500 ft.	Two trips.			
4 Mount Adams, Cascade Mountains, Washington; 39 miles on Signal Peak Rd. from U. S. Hwy. 12; open grassy slope; el. 5000 ft.	Data and plants supplied by Allan Legge, 1971.		9	*
5 Olympic Mountains, Washington				

Table II. Continued.

Study Area	Number of Fieldtrips and Garden Plants	Collections H	A	S
5 Continued				
Hurricane Ridge, 15 miles up Hurricane Ridge Rd. from Port Angeles and along Park Rd. at Deer Park trailhead and at Obstruction Point; open woodland on southern slopes; el. 4500 ft.	Four trips; two plants, 1971.		7	*
Mount Constance, Marmot Pass summit on U. S. Hwy. 101; open woodland and slopes; el. 4400 ft.	One trip; one plant, 1971.		8	
6 Mount Hood, Cascade Mountains, Oregon;				
Timberline Lodge, off U. S. Hwy. 26; open woodland and open slopes at timberline; el. 4200 ft.	Three trips; one plant, 1971.		2	
Cloudcap Inn, off State Hwy. 35; open woodland; el. 4000 ft.	Two trips; two plants, 1971.		3	
7 Mount Jefferson, Cascade Mountains, Oregon;				
Breitenbush Lake Rd., 1.5 miles east of Breitenbush Lake on S 42; open woodland and meadows; el. 5200 ft.	Three trips; two plants, 1970.	243	1	*

Table II. Continued.

Study Area	Number of Fieldtrips and Garden Plants	Collections H	A	S
7 Continued				
Breitenbush lake trail to Park Ridge, 2.1 miles to saddle before final ascent and 0.3 to 1.0 miles along southeast slope; open talus slopes; el. 6000 ft.	Three trips; three plants, 1971 and fifteen plants, 1975.	275, 276 & 286	6 17	
Whitewater Creek trail (3429), 5.0 miles into Jefferson Park; open talus slopes and edges of new trails; el. 5500 ft.	Two trips; two plants, 1974.		16	
8 Eugene, Spencer and Skinner Buttes, Willamette Valley, Oregon; el. 2100.	Two trips.			
9 Oakridge, Cascade Mountains, Oregon; State Hwy. 58 and Service Rd. 2108 from Dexter Reservoir to Hills Creek Dam, el. 3500 to 4000 ft.	One trip; no plants, lowest reported elevation for typical Aster ledophyllus.			
10 Crater Lake, Cascade Mountains, Oregon; 4 miles south of South Shore Picnic Area and Rim Rd. at Cloudcap and Applegate Peak; open areas, particularly in talus; el. 5500 to 7000 ft.	One trip; one plant, 1972.		10	*
11 Eight Dollar Mountain, Siskiyou Mountains, Oregon; 3 miles west of Selma on road to Store Gulch; open woodland and slopes; el. 2000 ft.	One trip; one plant, 1973.	901	13	

Table II. Continued

Study Area	Number of Fieldtrips and Garden Plants	Collections H	A	S
12 Siskiyou Mountains, Oregon;				
Flycatcher Springs, south of Gold Beach on Hunter Creek Rd. to Service Rd. 3503 via Service Rd. 368, 28 miles; serpentine woodland, shade; el. 1400 ft.	One trip; one plant, 1971.	497	4	*
Pyramid Rock, 3/4 mile northeast of Flycatcher Springs off Service Rd. 3503; serpentine open woodland; el. 1600 ft.	One trip; three plants, 1971.	498	4	*
13 O'Brien, Siskiyou Mountains, Oregon;				
Takilma Road, 3.5 miles east of O'Brien; open woodland; el. 2000 ft.	One trip; one plant, 1973.		14	
Rough and Ready Desert, 3 miles north of O'Brien on U. S. Hwy. 199; open, flat serpentine prairie; el. 1800 ft.	Two trips.			
14 Rogue River Canyon, Siskiyou Mountains, Oregon; 5 miles southeast to 6.5 miles north of Agness on the Gold Beach to Illahe Rd.; open woodland slopes; el. 1000 ft.	Four trips, various sites along road; two plants, 1973.		15	

Table II. Continued.

Study Area	Number of Fieldtrips and Garden Plants	Collections H	A	S
15 Siskiyou Mountains, California;				
Patrick's Creek, near Patrick's Creek Lodge, U. S. Hwy. 199; open woodland; el. 2000 ft.	One trip; one plant, 1971.		5	
Gasquet Flats, Gasquet, U. S. Hwy. 199; open, dry floodplain; el. 1200 ft.	Two trips; one plant, 1973.		11	

range and the humidity was low, possibly contributed more to their demise than the garden site. It is notable, however, that A. gormanii survived all of the transitions (1971-1975).

Greenhouse Culture

The variations in day lengths provided by the supplemental lighting were inadequate environmental variation to force concurrent blooming among the various collections. They were sufficient, however, to provide a second blooming period each year. With the exception of A. ledophyllus (A 3) all field material performed well under greenhouse conditions. The Mt. Hood collection remained in a rosetted condition during the entire trial period, blooming each period as much as 40 days after the final flowering of any other collection.

No plant displayed an apparent need for a dormant cold period. There was neither a decrease of growth vigor or of flowering after two consecutive bloom periods without a cold cycle. Plants from the Siskiyou Mountains began active new growth before the Mt. Hood collection had completed blooming. In the cases of A. paucicapitatus (A 7 and A 8) and A. gormanii (A 6), it was possible to observe living material from the same plants grown one season in the native habitat against new material grown the second season in the greenhouse. There was only a slight variation in vegetative characteristics in the A. paucicapitatus, but A. gormanii exhibited noticeable variations in plant size, leaf shape and pubescence.

Attempted Hybridizations

Pollination attempts with both the cross-pollinated heads and control heads aborted the first year. Heat build-up inside the glassine bags or possibly mechanical damage caused by rubbing against the sides of the bags are suspected causes since unbagged heads produced viable seeds.

Germination

Of seeds from A. brickellioides (A 4, A 13, and A 15) and A. siskiyouensis (A 4 and A 5) in their native habitat, less than three percent germinated over three years' trials. Aster gormanii (A 6 and A 16) produced about four percent germination, although no young seedlings were seen in the field. These taxa included A. ledophyllus (A 1) which gave about eight percent germination and A. engelmannii (A 12) which gave almost nine percent germination. In most cases, the seedlings were very weak and died within the first year after germination.

Herbarium Studies and Patterns of Distribution

Aster engelmannii has been collected rather commonly across southern British Columbia as far north as Mt. Taseko, latitude 51° 10′N and longitude 123° 45′W (Beamish & Pinder-Moss 690103), and Kinbasket Mountain, latitude 52° 00′N and longitude 118° 01′W (Taylor & Ferguson 3668) in the Canadian Rocky Mountains. There are also good collections

of material from the Selkirk Mountains near Banff (Hunnewell 6405; Ulke 305; Turner 3860; Macoun, unnumbered collections of the Herb. Geol. & Nat. Hist. Survey of Canada; Shaw 592, 1181). These collections and those of A. engelmannii from the North Cascade and Wenachee Mountain ranges of Washington have been variously described as having ray corollas that are pink, pale lilac, and magenta. Unlike the typical A. engelmannii of the Colorado and Wyoming mountain areas, white forms are rare. The range of this species in my study area is shown in Figure 2.

Further south in the Cle Elum and Mt. Rainier areas of Washington, intergradation occurs between A. engelmannii and A. ledophyllus. Intermediate plants from this region become extremely difficult to separate from the parent species, and intermediates are more common than plants clearly related to either A. engelmannii or A. ledophyllus (Piper 499, 2117; Heller 14765; Suksdorf 2409; Tarleton 2; Allen 284; Eastham 19, 4313; Warren 1538; Smith 2181, 2244; Grant 8900; McCalla 5230; Skully 543; Schwartze 6; Thompson 11076, 12501, 14997, 15117; Coville 793; Franklin 460; Thayer 7316; Jones 9697; St. John, Davison, English & Jones 7403). This area of intergradation is shown in Figures 2 and 3. Plants usually have the sparsely villose and glandular hairs of A. engelmannii along the stem, but there is frequently a light tomentum on the undersides of the leaves, as in A. ledophyllus. The leaves have the typical thin texture of A. engelmannii. Ray corollas are often an intense purple, much like A. ledophyllus in color.

Aster engelmannii var. engelmannii

Aster ledophyllus

Aster paucicapitatus var. paucicapitatus

Aster glaucescens

Aster gormanii (Aster paucicapitatus var. paucicapitatus)

Aster vialis (Aster engelmannii var. vialis)

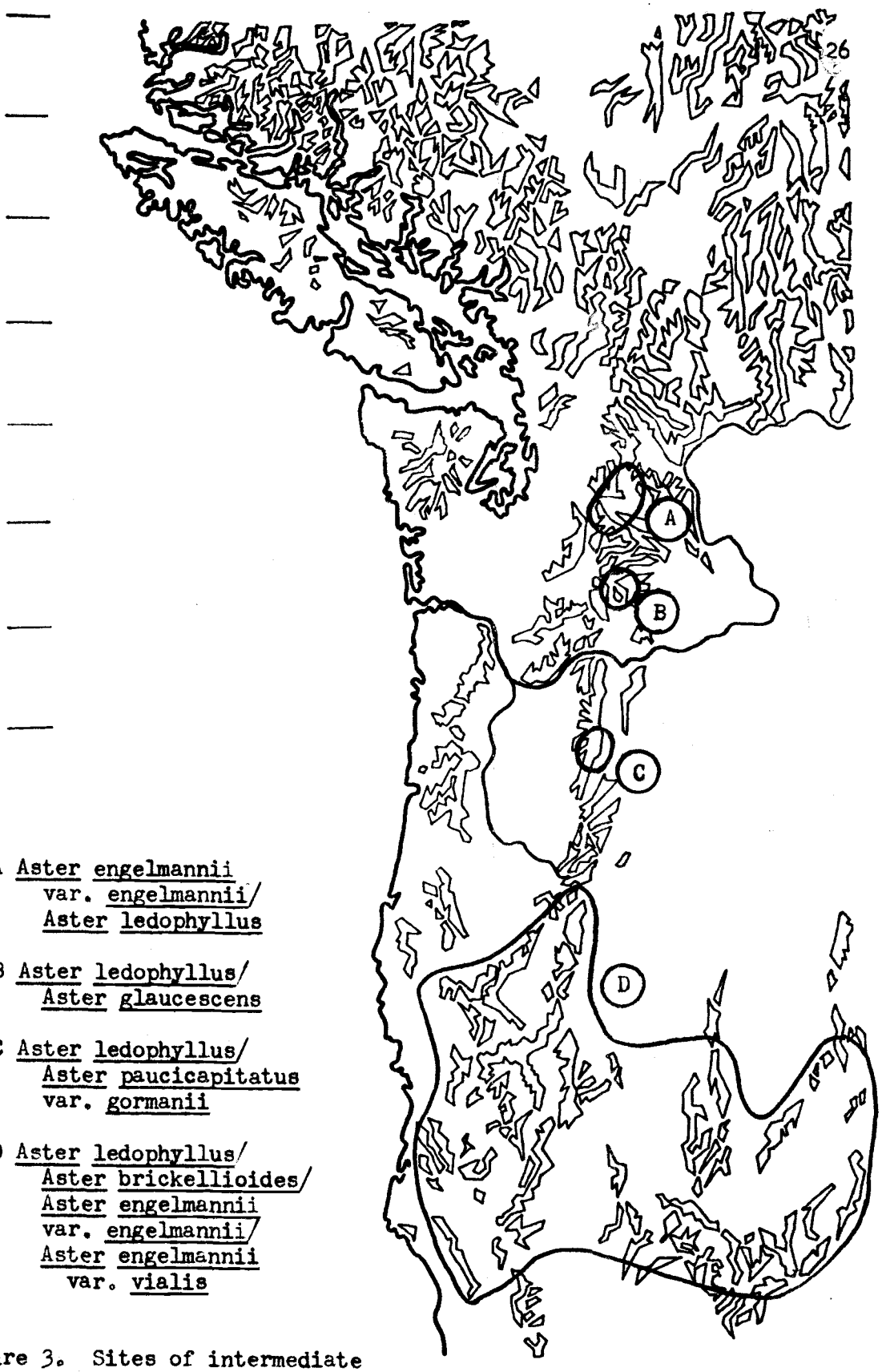
Aster brickellioides

Aster siskiyouensis (Aster brickellioides)

Figure 2. Distribution of section Eucephalus in the Pacific Northwest.

In the Cascade Mountains of southern Washington, plants of A. engelmannii are extremely rare, although populations still bear some traits of this species. Leaves are somewhat smaller and thicker than in the more northerly populations. Tomentum appears more often on the leaves, frequently accompanied by a few long pilose hairs on the veins.

In Skamania and Yakima counties, A. ledophyllus (Figures 2 and 3) enters the range of A. glaucescens. Aster glaucescens occupies areas of Mt. Adams, Strawberry Mountain, Mt. Margaret, and Satus Peak (Figure 2). Leaves of this species are usually glaucous and glabrous, and their shape is strap-like. The tips of the involucral bracts are green although there is anthocyanic coloring along the margins. Major collections of the Mt. Adams area were made by Wilhelm N. Suksdorf, Thomas Howell, and Lewis F. Henderson. Each of these collectors obtained specimens of both Aster glaucescens (Suksdorf 31, 118, 651, 5842, 6074, 6353, 7172, 7331, 9470, 9471, 9478, 9483; Howell 20, 401, unnumbered collections in 1882; Henderson 462, unnumbered collections in 1882, 1884, 1892) and A. ledophyllus (Suksdorf 359, 4319, 6341, 9496, unnumbered collection in 1884; Howell 38, unnumbered collection in 1882; Henderson 461, unnumbered collections in 1882, 1892). Aster glaucescens was collected near Satus Peak (Cotton 1562), and supposedly once as far north as the Mt. Rainier area (Flett, in 1899). Two of Suksdorf's collections labeled A. glaucescens (Suksdorf 6340, 9118) appear to be intermediate between the two species. Leaves of the plants are typical in size, shape, and color to A. glaucescens, but the specimens have pubescent leaf undersurfaces and purple-tipped involucral bracts.



A Aster engelmannii var. engelmannii/ Aster ledophyllus

B Aster ledophyllus/ Aster glaucescens

C Aster ledophyllus/ Aster paucicapitatus var. gormanii

D Aster ledophyllus/ Aster brickellioides/ Aster engelmannii var. engelmannii/ Aster engelmannii var. vialis

Figure 3. Sites of intermediate populations.

The final species of section Eucephalus in Washington is A. paucicapitatus of the Olympic Peninsula (Figure 2). Like the taxa just mentioned, it is a sub-alpine species. Its heads are large and showy, but are few to occasionally solitary on each plant. The rays at anthesis are pink, opening white, and finally aging pink. Discs are bright yellow with the labella aging red. Distribution of A. paucicapitatus var. paucicapitatus is geographically limited to the Olympic Mountains of Washington, and Mt. Arrowsmith on Vancouver Island, Canada (Lohbrunner 9391; Calder & MacKay 32521). A depauperate form was collected by Macoun (82776, 82776a) and given an unpublished nomen nudum, Eucephalus confinis, by Greene.

Aster ledophyllus continues south in the Cascade Range of Oregon through the Mt. Jefferson area, occupying mostly open, dry areas, often in rock outcrops. The leaves are notably thicker and smaller than in plants of this species from farther north and the number of rays per head decreases. There is a heavy tomentum on the leaf undersides.

On south-facing talus slopes of the Jefferson Park area are found occasional populations of A. gormanii, a taxon that appears to be restricted to this region Aster gormanii was described from the Martin Gorman collection 285, a specimen with about 10 ray flowers which are white in color. Most collections of A. gormanii over succeeding years were made by Morton E. Peck, who collected the plant in the many ray-colored forms that I found to exist within the populations. In Peck's Manual of the Higher Plants of Oregon (1941) this species is described

as having white or sometimes pink rays. In existing populations, there are numerous shades of white, pink, and purple. In the same area, but on more stable ground, is A. ledophyllus. Whether there has been recent introgression of genes from A. ledophyllus, which is now beginning to create a heterogeneous population in A. gormanii, or whether the plants have been morphologically variable for an extended period is impossible to determine. Many variations appear within a small population (D. Thompson 275, 276 and 281, 921, and A2, A16 and A17) which is possibly a hybrid swarm existing in the A. gormanii parental habitat. Marked similarity occurs between A. gormanii and A. paucicapitatus, the former being almost identical to the depauperate form of the latter found on Vancouver Island. The range of this is shown in Figure 2.

In the Crater Lake area, the leaves of A. ledophyllus are often finely and sparsely tomentose below and glandular above. Pubescence on the peduncles is more pronounced than in other places in the Cascade Range of Oregon. Ray flowers frequently range in number from 6-10, and the leaves are much reduced in size. These particular populations have been variously called Eucephalus covillei Greene, Aster covillei (Greene) Peck, and Aster ledophyllus var. covillei (Greene) Cronquist.

The Siskiyou Mountain Range of southern Oregon and the Siskiyou, Klamath, Scott, Trinity, Marble and Yolla Bolla Mountain ranges of Northern California contain the most numerous variations within and among species in the Eucephalus section. Scattered through the ranges are the few-headed species, A. ledophyllus and A. engelmannii, and the

many-headed A. brickellioides and A. siskiyouensis (Figure 2).

Aster perelegans, although not directly covered in this study, does have potential genetic influence on the other species that are under consideration. Like A. brickellioides and A. siskiyouensis, A. perelegans is a member of the Eucephalus group having numerous small heads. The heads have usually 10 or fewer purple ray florets. It comes closest to the range of the other species in Eastern Oregon, Northwestern Nevada, and Northeastern California.

Aster engelmannii is present in the mountain ranges of California (Figure 2), but it appears to be much reduced in size when compared with the plants of its northern range. Rays are 3-12 in number and vary from pale pink to lavender. The heads are large and few or solitary on each plant. Herbarium specimens of A. engelmannii are rare from this area, tending to be collected mostly from higher elevations (Alexander & Kellog 5854; Kildare 6577; Emmel 93; Butler 295).

Aster brickellioides is an endemic species of the Siskiyou Mountains. Its sister taxon, A. siskiyouensis, has been separated taxonomically from the former chiefly by the reduced pubescence on its leaves. Both are essentially rayless (one to five rays occasionally are found). Based on their similarities, they are here considered conspecific. Aster ledophyllus in the Siskiyou area has five to eight ray flowers and occasionally has as many as seven heads in an inflorescence. Populations of the species just mentioned are frequently found intermingled in nature, with two or all three co-existing within a few feet

of one another. This complex extends south beyond the bounds of the Siskiyous, there being collections from as far south as Black Butte, Glenn County (Howell 19245; Baker 10679), the Trinity-Tehama County Line (Munz 16613) and the northern Sierra Nevada Mountains at Gold Lake, Sierra County (Eggleston 6267) and the Red Mountain, Nevada County (Eggleston 21671). The A. brickellioides complex ranges north into the low hills just south of Eugene, Oregon. Collections from Bristow Prairie, Lane County (D. C. Ingram) seem to mark the northern boundary. Southern collections are at elevations of 5900-7000 feet while the more northerly collections are often below 3000 feet. Lines of distinction are so tentative and intermediates are so common, that a simple species delineation does not exist (Figures 2 and 3).

In the southern Willamette Valley the species A. vialis is or was present (the most recent collection was made in 1933). It is similar in habit and vegetative characters to A. engelmannii of the Canadian area. The heads are large but rayless. It has been collected on Spencer Butte, Eugene (Brown 230; Henderson 15708, 15896; Bradshaw 1914) and southwest of Eugene toward Lorane (Constance 951). It has also been collected in the foothills south of Eugene (Bradshaw, unnumbered collection) and in the foothills east of Eugene along the upper Willamette River (Bradshaw, unnumbered collection. Other specimens are somewhat reduced in size, with a tendency towards more numerous heads, and these are somewhat intermediate between A. vialis and A. brickellioides

(Ingram 1077). This entity, here called A. engelmannii var. vialis, is mapped in Figure 2.

Field Observations of Selected Taxa of Section Eucephalus

The section Eucephalus has features that can be used to separate it in the field rather quickly from other sections of Aster. It comprises herbaceous perennials having a woody, often creeping root-stock, with stems very leafy their entire length. Leaves at the base of the stem are reduced occasionally to the point of being scale-like, and they are also reduced below the flower heads, although not so noticeably as at the base of the stem. Leaves are sessile. Stems and peduncles are often pubescent with pilose or glandular hairs. The involucre consists of several series of imbricated, keeled bracts, the outermost of which are normally herbaceous and green. The inner bracts are more or less chartaceous or scabrous at their bases, with acute herbaceous tips; pigmentation is anthocyanic, often lightly along the margin or on the bract tips.

Plants in the northern distribution of our area exist mainly in the Hudsonian zone. They have large and few heads, 6-12 in number or occasionally solitary. Populations are most often found on dry slopes with extremely sunny exposure. Southern members of the group include plants that have much-branched upper stems with many (15-30) small heads. These plants often occur at lower elevations and may grow in more heavily wooded areas.

Manning Provincial Park

Aster engelmannii in the northern Cascade area was morphologically relatively consistent within populations. In the population observed in southern British Columbia plants were 10-15 dm tall. The larger leaves on the plants were 5.5-8.5 cm long and 1.6-3.2 cm wide. The thin lanceolate leaves were more or less rounded at the base. The blades were generally glabrous above with occasional small hairs large, often 10-12 per plant. The bracts were in about six series and strongly graduated. Inner bracts were somewhat oblong, chartaceous at the base with a herbaceous, purple tinged tip. Heads contained 14-16 ray flowers with lavendar purple corollas. The population included nine plants in an open woodland area near Highway 3 (Table II).

Eagle Creek

The second population of A. engelmannii contained several hundred plants, much larger than the Canadian population. Most plants were 8-10 dm tall. Larger leaves on the plants averaged 5.5-8.0 cm long and 1.8-2.0 cm wide. The leaves were thin like those in the Canadian population, but there was more pubescence present. Occasionally there were glandular hairs on the upper side of the leaves, and often pilose and glandular hairs occured along the veins on the underside of the leaves. The heads and the bracts were similar to the Canadian specimens, but the ray color was more intense orchid purple (Table II). In both cases plants were in rocky soil of igneous origin.

Mt. Rainier

The Sunrise Ridge and Chinook pass of Mt. Rainier is a favorite botanical collecting area, and botanists have taken many pressed specimens of A. engelmannii and A. ledophyllus, as well as many intermediate forms, from this location (Figures 2 and 3). The area was chosen as a central Cascade study point for this reason. Plants were about 5.0-8.0 dm in height, with leaves that appeared to be thicker than in the more northerly study sites. The larger leaves were lanceolate and entire, measuring 5.5-7.0 cm long and 1.7-2.00 cm wide. Bracts were chartaceous toward the base, having herbaceous tips with strong purple coloring. There were a few pilose hairs on the central vein of the younger leaf surface, and rather dense pilose hairs on the dorsal veins of the young leaves. Older leaves often showed this dense pubescence, as well. Ray flowers ranged from 15 to 20 and had intense purple pigmentation (Table III).

Several of the plants on Sunrise Ridge were intermediate between A. engelmannii and A. ledophyllus, having the ciliated bracts of A. engelmannii and light tomentum on the underside of the leaves, or they possessed very few hairs on the bract margins or leaves. A number of specimens could easily be classified as A. ledophyllus, but there were no plants that entirely fitted the description of the A. engelmannii (Figure 3). Although sters of the Eucephalus section seem to grow almost exclusively in dry areas, three plants were found growing on the margins of bodies of water in the Sunrise Ridge locality.

Table III. Comparison of morphological characteristics of the section Eucephalus in the Pacific Northwest. Column headings are as follows:

A Plant height
B Stem pubescence
C Stem habit
D Caudex and roots
E Involucre shape
F Series of bracts
G Involucral bract shape and texture
H Involucral bract pubescence
I Involucral bract size
J Number of heads
K Inflorescence type
L Number of ray flowers
M Head size
N Ray flower color
O Length of ray flower
P Leaf margin
Q Upper leaf surface
R Lower leaf surface
S Leaf texture
T Leaf shape
U Leaf length
V Leaf base shape
W Leaf width
X Leaf apex shape
Y Achene characteristics

Table III.

Taxon	A	B	C	D	E
Aster ledophyllus	2.0 - 9.0 dm	Loosely pilose to densely tomentose	Several; erect to ascending	Woody caudex, fibrous roots	Broadly campanulate
Aster engelmannii var. *engelmannii*	1.0 - 25.0 dm	Sparsely pilose, rarely glandular, to glabrous beneath	Several; erect	Woody caudex or rhizome, fibrous roots	Broadly campanulate
Aster engelmannii var. *vialis*	6.0 - 15.0 dm	As above, with minute stipitate glands	Several; erect	Woody caudex, fibrous roots	Turbinate - narrowly campanulate
Aster paucicapitatus var. *paucicapitatus*	2.0 - 5.0 dm	Thinly pilose with some stipitate glands	Several; erect to ascending	Woody caudex, sometimes with taproot	Hemispheric - broadly campanulate
Aster paucicapitatus var. *gormanii*	1.0 - 1.5 dm	As above, often less pilose and more glandular	Several; ascending	Woody caudex with stout root(s)	Hemispheric - broadly campanulate
Aster glaucescens	4.0 - 15.0 dm	Striate, glabrous and varyingly glaucous	Several; erect	Woody caudex, fibrous roots	Broadly campanulate
Aster brickellioides	3.0 - 10.0 dm	Glabrous to arachnoid-tomentose with minute glands, red below	Often single or few; erect or ascending	Woody caudex, rhizome or taproot	Turbinate - narrowly campanulate
Aster perelegans	3.0 - 10.0 dm	Striate and finely puberulent	Often single; erect	Woody caudex, fibrous roots	Narrowly campanulate

Table III. Continued

Taxon	F	G	H	I
Aster ledophyllus	4 - 5	Subulate to lanceolate; attenuate herbaceous tip; short indurate base	Finely glandular; usually purple edged	0.7 - 1.1 cm
As Aster engelmannii var. engelmannii	5 - 6	Linear to subulate or lanceolate; other as above	Glabrous or pubescent, often pilose-ciliate; frequently purple edged	0.7 - 1.1 cm
Aster engelmannii var. vialis	5 - 6	Linear to linear-lanceolate; other as above	Stipitate-glandular, sparsely pilose-ciliate; frequently purple edged	0.7 - 1.0 cm
Aster paucicapitatus var. paucicapitatus	3 - 4 scarcely graduate	Linear-lanceolate; acuminate herbaceous tip: other as above	Obscurely glandular, sometimes pilose-ciliate; sometimes purple edged	0.7 - 1.0 cm
Aster paucicapitatus var. gormanii	3 - 4 slightly graduate	Lanceolate to ovate or oblong; subacuminate or acute herbaceous tip; other as above	Nearly glabrous, pilose-ciliate (mainly dorsal); frequently purple edged	0.6 - 0.9 cm
Aster glaucescens	4 - 5	Ovate to oblanceolate; attenuate herbaceous tip; other as above	Glandular-puberulous to subglabrous, obscurely lacerate-ciliate; rarely purple edged	0.6 - 0.9 cm
Aster brickellioides	4 - 6	Linear or lanceolate to ovate; obtuse to acute herbaceous tip; large indurate base	Tomentose or sometimes glabrous, pilose-ciliate; frequently purple edged	0.6 - 0.9 cm
Aster perelegans	5 - 7	Ovate to linear-oblong; other as above; inner bracts sometimes deciduous	Subglabrous or puberulous, densely villous-ciliate; strongly purple edged	0.6 - 0.9 cm

Table III. Continued.

Taxon	J	K	L	M	N	O
Aster ledophyllus	Several to few or solitary	Corymbose to corymbiform panicle	5 - 21	2.0 - 4.0 cm	Violet, purple, or lavendar pink	1.0 - 2.5 cm
Aster engelmannii var. engelmannii	Several to solitary	Short round cyme or cymose panicle	8 - 13	2.0 - 4.5 cm	Lavendar, purple or, rarely, whitish	1.0 - 1.7 cm
Aster engelmannii var. vialis	Several to few	Narrowed cymose panicle	0	1.0 - 1.5 cm		
Aster paucicapitatus var. paucicapitatus	Solitary to few		8 - 21	2.5 - 4.0 cm	White aging pink; disk lobes aging red	0.8 - 1.4 cm
Aster paucicapitatus var. gormanii	Solitary; rarely, two		3 - 21	2.0 - 3.0 cm	White aging pink; disk lobes rarely aging red	0.6 - 0.8 cm
Aster glaucescens	Few to many or solitary	Cymose panicle	8 - 13	2.5 - 3.5 cm	Violet or purple	1.0 - 2.2 cm
Aster brickellioides	Several to very many	Elongated cymose panicle	0 - 5	0.6 - 1.0 cm	Purple or lavendar	0.6 - 0.8 cm
Aster perelegans	Solitary to many	Corymbiform or short rounded cymose panicle	6 - 11	2.0 - 2.8 cm	Violet or purple	0.8 - 1.3 cm

Table III. Continued.

Taxon	P	Q	R	S
Aster ledophyllus	Entire or nearly so with irregular teeth	Glabrous or lightly pilulose	Griseous tomentose to cinereous tomentose	Thin to subcoriaceous
Aster engelmannii var. engelmannii	Entire or rarely with few teeth	Glabrous except near costa	Sparsely pilulose or pilose (costa), sometimes glandular	Thin
Aster engelmannii var. vialis	Entire or rarely with few teeth	Glabrous or obscurely glandular	Sparsely pilose and often stipitate glandular	Thin
Aster paucicapitatus var. paucicapitatus	Entire or nearly so	Obscurely glandular, rarely pilulose, on costa or glabrous	Stipitate glandular, thinly pilose and ciliolate	Thin to firm
Aster paucicapitatus var. paucicapitatus	Entire	Glabrous or obscurely glandular	Stipitate glandular, hispidulous-ciliolate	Firm
Aster glaucescens	Entire or serrulate	Glabrous and glaucous	Glabrous and glaucous, rarely sparsely pilose	Thin to firm
Aster brickellioides	Entire or nearly so; sometimes revolute	Finely rough hispidulous	Cinereous tomentose, glandular puberulent, pilose or glabrous	Thin to coriaceous
Aster perelegans	Entire		Finely rough hispidulous to hispidulose ciliolate	Thin to firm

Table III. Continued

Taxon	T	U	V	W	X	Y
Aster ledophyllus	Lance-elliptic to oblong-lanceolate	1.5 - 6.5 cm	Rounded; broad	0.4 - 2.0 cm	Acute to obtuse, sometimes acuminate	2 - 5 nerved: thinly pilose, especially near summit
Aster engelmannii var. engelmannii	Elliptic to oval or cuniform	3.0 - 11.0 cm	Rounded or narrowed	1.0 - 3.5 cm	Acute to acuminate	2 - 5 nerved: appressed pilose
Aster engelmannii var. vialis	Elliptic to elliptic-oblong	3.5 - 9.0 cm	Rounded	0.8 - 3.0 cm	Acute to subacuminate	2 - 5 nerved; compressed; pilose
Aster paucicapitatus var. paucicapitatus	Elliptic to elliptic-oblong	1.5 - 4.0 cm	Narrowed	0.4 - 1.3 cm	Acute to apiculate	Often 4 nerved; compressed; appressed pilose
Aster paucicapitatus var. gormanii	Elliptic to lance-elliptic	1.5 - 3.0 cm	Often narrowed	0.3 - 1.0 cm	Obtuse, acute, or apiculate	3 - 4 nerved: somewhat compressed; thinly pilose
Aster glaucescens	Lanceolate to linear-lanceolate	3.5 - 9.5 cm	Narrowed	0.4 - 1.5 cm	Acuminate to acute	2 - 5 nerved; appressed pilose
Aster brickellioides	Oval to linear-oblong	3.0 - 6.0 cm	Rounded; broad	0.8 - 2.0 cm	Acute, obtuse, or apiculate	As above to villose, glandular or glabrous
Aster perelegans	Elliptic to lance-linear	2.5 - 6.0 cm	Rounded	0.3 - 1.1 cm	Acute or rarely obtuse	Mostly 5 nerved; compressed; appressed pilose

Mt. Adams

Although Mt. Adams is the type location for A. glaucescens, only a single plant was located. Its growth appeared somewhat stunted, 1.2 dm high, and there was but a single flowering head. The foliage bore a distinct blue cast and was glabrous except for a few minute hairs along the veins on the underside of the leaves. Ray flowers were dark purple and there were 11 in the existing head. The inner bracts were herbaceous-tipped, graduated, scarious or chartaceous margined, with only slight anthocyanic coloring along the upper margins. The bracts had scattered glandular hairs (Table III). Three populations of A. ledophyllus were growing in the general vicinity and appeared similar to many of the specimens on Mt. Rainier, (Figure 3).

Hurricane Ridge

The general habitat and plant populations on Hurricane Ridge and Marmot Pass were much alike. The only member of section Eucephalus which was present in the Olympic Mountains was A. paucicapitatus. This species had very large heads; the ray corollas were pink at anthesis, white at maturity, and orchid-pink as they faded. One of the most striking features of the plant was the aging of the lobes of the disk flowers to a dark red. Heads were borne a few on a stem or occasionally were solitary; their peduncles were often stipitate-glandular and somewhat pilose. The leaves were 2.3 to 4.0 cm

long and 1.0 to 1.3 cm wide; their blades were somewhat narrowed at the base and mostly entire, with the margins often ciliated. There frequently were stipitate-glandular or glandular-puberulent hairs along the veins on the undersides of the leaves. Bracts were scarious margined, mostly green above and narrowly edged with purple. The outer bracts often were wholly herbaceous. The A. paucicapitatus was common on open dry, talus or rocky slopes and was a major inhabitant of the rocky road shoulder on Hurricane Ridge.

Mt. Hood

Populations of A. ledophyllus were observed over a three year period in the vicinity of Timberline Lodge and Cloud Cap Inn (Table II). In the forest around Timberline Lodge, populations of A. ledophyllus were common where there were openings in the tree cover. Asters in this area, as well as Government Camp and Barlow Pass, were generally 2.0-5.0 dm in height. The leaves were somewhat smaller than in the Washington specimens, 4.0-6.7 cm long and 1.3-2.0 cm wide. Peduncles were frequently pale with short pilose hairs. The undersides of the leaves were softly tomentose, but there was rarely any pronounced hair on the upper surface of the leaves. The leaves occasionally had irregularly dentate margins. Heads were relatively large, and their purple ray florets ranged from 14 to 22 per head. The inner involucral bracts were imbricated and green toward the tips, with varying amounts of purple. A few clumps of A. ledophyllus were located above timberline

not far from the lodge. These plants were less than 2.0 dm in height and tended to be later blooming and less floriferous.

On the other side of Mt. Hood, at Cloud Cap Inn, plants of A. ledophyllus were growing in the road banks where few other plants had yet established. There were also plants growing around the old lodge building in areas of deeper shade than is normal for the species' habitat. There was no noticeable difference in these plants from those in the Timberline Lodge area. Blooming season was from early-mid July to the first major freeze, usually September.

Mt. Jefferson

Over a five year observation period two major populations of A. gormanii were located and observed. The first population studied was sighted a few thousand feet northeast of the last saddle before reaching Park View Ridge from Breitenbush Lake. The plants occupied dry, open, rocky south-facing slopes above the summer snow banks. A very slight exposure variation marked the edge of the population in each case. The plants were among few inhabitants of the loose rock slopes and had well-developed creeping rootstocks often reaching three or four feet up the slope. They grew in low, multistemmed mats 3.0-18.0 dm across and 1.0-2.0 dm tall. The flowers were in solitary heads, or in rare cases there were two or three to a stem. Although vegetative characteristics appeared relatively uniform here, floral variations were extreme. Ray flowers varied from 3-22 and were almost any shade of

white, pink, or purple. White forms opened from pink buds. Among the white-flowered forms were plants whose disk flower tips aged red like those of A. paucicapitatus. This red aging did not appear to be present in the pink and purple forms. The ligules ranged from long and narrowly spathulate to broadly elliptical. Leaves were strongly reduced, ranging from 1.2-3.0 cm long and 0.3-1.0 cm wide. There was little pubescence on the leaves,with the exception of occasional glandular hairs and scattered marginal cilia.

Aster gormanii was found along Whitewater Creek Trail into Jefferson Park, occupying a small area about three miles above the parking lot at the trailhead. The habitat was an extremely hot south-facing scree slope below a series of rock shelves. The species appeared most aggressive on the slopes of the newly built trail. It was also present on the upper side of the trail, where it did not appear to be competing as successfully. On the rocky ledges themselves were a wide variety of rock plants and at least two plants of A. ledophyllus. The A. gormanii here was mostly white-rayed, with an occasional pink (pale) flowered plant. Plant height ranged to about 3.0 dm, and vegetative characteristics were similar to those of the Park View Ridge site. Rays numbers ranged from 10 to 16.

Aster ledophyllus did not grow in the scree of loose rock, although it was present within a few feet of the A. gormanii populations. It was a much more common species in this area; large populations of it growing along the Breitenbush Lake Road, at lower elevations. Aster ledophyllus

grew from 2.5 to 5.0 dm tall in the Mt. Jefferson area. The peduncles were usually pilose and the leaves were often cottony tomentose below. Ray flowers were purple and ranged in number from 8-20. All the specimens were in general similar to those collected on Mt. Hood.

Eugene and Oakridge

Trips were made into the Eugene area to try to locate A. vialis at one of its former collection sites or in similar areas. Each trip ended without that species being sighted. A trip to Oakridge to examine the lowest elevation population of A. ledophyllus north of the Siskiyou Mountains ended without finding any of these plants.

Crater Lake

The A. ledophyllus of the Crater Lake area was extremely different from that of the Mt. Rainier area. Stems of the plants were typically more highly branched, and there was rather sparse tomentum or pilose hairs along the peduncles. The leaves were smaller than in other populations, varying from 1.8 to 3.5 cm wide. The inflorescence tended to be a corymbiform cluster, very reminiscent of A. perelegans. The inner bracts were very scarious except for the tip, and were heavily sprinkled with glandular hairs; the very tip of each bract was tinted purple. Ray flowers were purple and usually numbered 6-10. Populations around the rim of the lake were first viewed in 1971. In 1972 the snow was so slow leaving the area that no flowering plants were

observed. In 1973 my observations were similar to those in 1971; no major dieback seemed to have resulted from the previous year.

Siskiyou Mountains

The Eucephalus section of Aster was not among the conspicuous plants of the ranges comprising Siskiyou Mountains, although populations were frequently encountered. Plants were present at a variety of elevations through the area, often in mixed populations. They were usually restricted to areas of serpentine-derived soils, often growing in thin layers of soil only a few inches above ultrabasic parent material, as well as in other igneously derived soils such as ash and pumice.

The most common taxa were A. brickellioides and A. siskiyouensis. Unlike the northern taxa these plants were commonly many-branched from a solitary stem. There were as many as 16-30 small heads on vigorous individuals. The plants usually had corymbiform clusters of heads that were rayless, or occasionally had one to three pink or purple ray corollas. Within A. brickellioides leaves ranged from rather thin and ovate-lanceolate to very leathery and broadly elliptical with pale tomentum beneath. In A. siskiyouensis the leaves ranged from ovate-lanceolate to narrowly elliptical, and varied in texture from rather thin to (more often) stiff and leathery. Leaves of this taxon were not tomentose below, although they occasionally had glandular hairs. Inner bracts of both taxa were barely herbaceous at the tip and frequently had very little anthocyanic pigment. The bracts of A.

brickellioides often were somewhat tomentose, while the bracts of A. siskiyouensis were almost glabrous. Except in rare cases, A. brickellioides was more vigorous than A. siskiyouensis, averaging 4.0-10.0 dm in height while the latter species was 3.0-6.0 dm tall.

At Flycatcher Springs and on the road to Pyramid Rock (see Table I for locality data) the two taxa were found growing within a meter of each other. Root squashes made from each of the species at Pyramid Rock revealed 2n - 18 in both. Specimens of both also were observed on a slope about one mile from Store Gulch (Table I). Few of the study populations consisted of plants that strictly fitted the taxonomic descriptions of the two taxa. Intermediate individuals were more prevalent than those representing the defined species.

In the three years that the above areas were studied, no A. ledophyllus was located. However, in Gasquet Flats (Table II), in 1972, a plant of A. brickellioides with only nine heads, arranged in a raceme-like cluster, was discovered. Three of the heads had purple rays; two heads had one ray floret each and one had three rays. The heads were relatively small and their bracts had some glandular hairs, suggesting an intermediate condition between A. brickellioides and A. ledophyllus.

Search of the Patricks Creek area of California, as well as the Illinois River basin near O'Brien and the Rough and Ready Desert in Josephine County, Oregon, did not lead to the discovery of any of the populations that were reported by earlier collectors.

Evolutionary Speciation

Interbreeding between biological species is limited by three major isolating barriers. Geographical isolation exists between allopatric species whose respective areas are separated by gaps greater than the normal radius of their pollen and seed dispersal. Ecological isolation is due to variation in environmental requirements. Species may share the same geographical area while occupying discretely different habitats. "Intermediate" habitats are not rare in nature, but habitats that are sufficiently hybridized to allow free reproduction of hybrids are less common (Anderson, 1948). Such habitats are produced mainly by human activities (e.g. farming, logging, and road building), although they are also created by various natural processes throughout geological time. Reproductive isolation (Grant, 1971), third mode of isolation, refers to dissimilarities in reproductive organs, reproductive habit, or fertility relationships. These blocks may be internal (e.g. incompatibility, hybrid inviability, hybrid sterility, or hybrid breakdown) or external (e.g. bloom period or pollinator).

During early evolution of species divergence, populations are related as geographical or ecological races. They occupy adjacent territories, interbreed, and intergrade freely. As divergence progresses, more generic differences arise that affect morphological and physiological traits. Populations develop that are neither races nor

species, but rather are referred to as semispecies. Such evolutionary divergence is subject to reversal, however, reduction or removal of some isolating barriers between two semispecies may not only deter the development of well isolated biological species, but also may lead to large numbers of natural hybrids which develop as introgressive populations or hybrid swarms. An introgressive population arises through repeated backcrosses of the hybrids to one parental species. The population resembles the recurrent parent species but varies in the direction of the opposite parent (Anderson, 1949).

The hybrid swarm is a mixture of parental forms, F_1 hybrids, backcrosses, and segregation products. The reproduction of natural hybrids with an outcrossing breeding system commonly follows the pathway of backcrossing and introgression (Grant, 1971).

Where interspecific hybridization occurs in nature, the most inclusive breeding group is the syngameon. Limited gene exchange is occurring between otherwise isolated species or semispecies, and the unit of interbreeding is a community of species. Thus, the syngameon is "the sum total of species or semispecies linked by frequent or occasional hybridization in nature; a hybridizing group of species..." (Grant, 1963). The merging of species may proceed to completion or remain in an intermediate phase for an indefinite time. In the same complex of plants, it is possible to illustrate both extremes as well as intermediate stages of the hybridizing structure. The original biological species in a syngameon may either persist as discrete species

within the complex or, through the hybridizing process, come to occupy a subordinate position (Grant, 1971). One of the best known examples of this process is the Pacific Coast irises (Lenz, 1959).

Aster section Eucephalus as a Syngameon

The Compositae have become well known for their plasticity and failure to fit into neat patterns (Stebbins, 1950). The section Eucephalus is a classic example. Analysis of distribution, floral characters, vegetative characters, collection data, field notes, and experimental observations suggest that the group is closely interrelated and interfertile. Some cases of gradual variation suggest that the later generations may also have a high degree of fertility, while other variational features suggest that there are probably barriers which limit but do not prevent further hybridization.

Aster engelmannii in the Pacific Northwest most often has orchid or purple ray flowers rather than the white of its Rocky Mountain congeners. There is no clear separation of range or habitat between A. engelmannii and A. ledophyllus. Aster engelmannii is a species of the Canadian Rocky Mountains and the North Cascade Mountains, with disjunct populations in northern California. Aster ledophyllus is a species of the South Cascade Mountains and the Siskiyou Mountain complexes. At points where the ranges meet, plants of intermediate morphology dominate, and few if any distinct specimens of typical A. engelmannii or A. ledophyllus exist.

Gradual variation from A. engelmannii to A. ledophyllus var. covillei and even to Aster brickellioides or Aster perelegans may be simple clinal variation of a single species. Following G. F. Ferris's advice, "the proper aim is not to name species but to know them," I make no attempt at major alterations in nomenclature. Proposed changes below are intended only to indicate close relationships in specific groups.

Observing the white forms of A. gormanii growing along the Whitewater Creek Trail and near the Breitenbush Trail into Jefferson Park, and comparing them with populations of A. paucicapitatus in the Olympic Mountains of Washington and Vancouver Island, B. C., it is evident to me that the relationship between these taxa is quite close. The similarity has been noted by taxonomists ever since A. gormanii was described by Piper. This relationship is even more noticeable when the depauperate forms of A. paucicapitatus collected by Macoun (82776, 82776a) are examined. The taxonomy proposed here places A. gormanii as a variety of A. paucicapitatus. The present disjunction between these plants leads to some suppositions about the original distribution of A. paucicapitatus. Since Aster paucicapitatus appears to be restricted to the mountains of the Olympic peninsula area, it is suggested that the material in the Mt. Jefferson area might be a relic of a typically more southerly occurrence in preglacial or interglacial times. The time of the northerly advance would appear not to have been recent, but the refugial plant, A. gormanii appears to hybridize readily with A. ledophyllus to produce a myriad of

corolla variations. These putative introgressants happily occupy the A. gormanii parent's pioneer-type habitat but have not deposed the original white-rayed form. With this distribution of taxa in the Cascade Range and the Olympic Range, it is also interesting to note that there is neither A. engelmanii nor A. ledophyllus in any portion of the Olympics or on Vancouver Island.

Aster glaucescens, although appearing to hybridize with A. ledophyllus, is sufficiently isolated geographically and is enough outside of the clinal variation tendencies of A. ledophyllus to be at least an ecospecies.

The southern Oregon and northern California mountains contain a great mixed association from the Eucephalus section. This complex includes a number of the species which are normally found at higher elevations (A. ledophyllus and A. engelmannii) and endemic taxa (A. brickellioides and A. siskiyouensis) which seem to adapt well to lower altitudes. The two latter taxa are small, multi-headed plants apparently more or less restricted to serpentine soils. (Far less frequent populations are occasionally found slightly north of the serpentine areas in Oregon and south of the serpentine areas in California.) Aster perelegans is slightly east of the range of this report, but the southern endemic taxa bear some strong resemblances to this species.

The A. engelmannii present in California tends to form the southern limit of the Eucephalus distribution and exists generally at higher elevations. It is vegetatively much reduced from the northerly form and often

bears only one or two large heads per plant. Eucephalus bicolor Eastw., now classified as a form of A. brickellioides, is probably the most distinct taxon in the area. The extremely leathery, convex leaf with its heavy tomentum below, and the few flowered heads probably characterize the purest form of the species. Other Siskiyou populations resemble more a mixture of segregating hybrids than a series of species. It is questionable whether a group of plants which share a common habitat, common geography, common flowering time, and a multitude of intermediate characters should be classified taxonomically as separate species. However, since A. engelmannii appears somewhat distinct in its extension to the south, and since A. ledophyllus has been retained as a species, it is simplest to maintain a species designation for the small, multiple-headed plants of the Siskiyou Mountains.

Aster vialis represents a slightly different situation. Unlike the Asters in the Siskiyou Mountains area, it is isolated in the Willamette Valley at a low elevation. As in many of the forms of A. brickellioides, its heads are rayless and numerous; however, they are also large with bracts resembling the Canadian, Wyoming, and Montana forms of A. engelmannii. It is quite probably a member of the Siskiyou complex that adapted to lower elevation woodlands. Species-level classification overemphasizes its distinctness, I believe. Its geographical and ecological isolation do merit recognition from A. engelmannii or A. brickellioides, and it is probably best considered a rayless variety of A. engelmannii.

The following names are proposed for the accepted taxa of Aster section Eucephalus in the Pacific Northwest:

ASTER LEDOPHYLLUS (Gray) Gray

ASTER ENGELMANNII (D. C. Eaton) Gray var. ENGELMANNII

ASTER ENGELMANNII (D. C. Eaton) Gray var. VIALIS (Brads.) D.D.Thompson

ASTER PAUCICAPITATUS (Robins.) Robins. var. PAUCICAPITATUS

ASTER PAUCICAPITATUS (Robins.) Robins. var. GORMANII (Piper)D.D.Thompson

ASTER GLAUCESCENS (Gray) Blake

ASTER PERELEGANS Nels. & MacBr.

ASTER BRICKELLIOIDES Greene

Key to Species and Varieties

A. Heads solitary, rarely 3-4 per stem; ray flowers pink at anthesis, white at maturity, often aging pink. *Aster paucicapitatus*

B. Leaves with sparse short pubescence beneath; plants 1.5-5.0 dm; disk flowers aging red; Olympic Peninsula, Washington and Vancouver Island, British Columbia. var. *paucicapitatus*

BB. Leaves without short pubescence beneath; plants 1.0-1.5 dm; disk flowers rarely aging red; Mt. Jefferson, Oregon. var. *gormanii*

AA. Heads several to numerous; ray flowers lavendar, purple, or absent.

C. Leaves 3.5-9.5 cm long, 8-12 times as long as wide, glabrous; rays 8-18; Mt. Adams region, Washington. *Aster glaucescens*

CC. Leaves less than 8 times as long as wide, or leaves pubescent, or rays fewer than 8.

D. Leaves tomentose below, especially when young.

E. Heads small (often under 0.5 cm in diameter, not including occasional ray flowers); peduncles much branched; leaves sometimes coriaceous; Siskiyou Mountains, Oregon and California. *Aster brickellioides*

EE. Heads larger (0.5 cm and over excluding ray flowers); peduncles not much branched; leaves not coriaceous; Cascade Mountains Oregon and Washington. *Aster ledophyllus*

DD. Leaves glabrous to pilose below.

F. Heads large (0.5 cm or over excluding ray flowers). *Aster engelmannii*

G. Ray flowers pale lavendar to violet; leaves bright green below. var. *engelmannii*

GG. Ray flowers absent; leaves often dull below; vicinity of Eugene, Oregon. var. *vialis*

FF. Heads smaller (less than 0.5 cm in diameter excluding ray flowers); Siskiyou Mountains, Oregon and California. *Aster brickellioides*

Many intermediates between species are found in areas where members of the Eucephalus complex come into contact. Intermediates between A. ledophyllus and A. glaucescens occur in Mt. Adams region. Aster ledophyllus x A. engelmannii hybrids are found in the Cascade Mountains of Washington. Aster ledophyllus x A. paucicapitatus var. gormanii hybrids are more common in the Mt. Jefferson region than is the parent A. paucicapitatus var. gormanii (the type sheet of A. gormanii includes one of these hybrids). Aster engelmannii var. vialis is an intermediate between A. engelmannii and A. brickellioides which successfully established on the igneous buttes around Eugene, Oregon, well out of the range of either parent. Intermediates among A. ledophyllus x A. brickellioides are frequent in the Siskiyou Mountains of Oregon and California. In many cases designation of a species name is extremely difficult in these populations.

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