

SYSTEMATICS OF SAXIFRAGA RUFIDULA AND RELATED  
SPECIES FROM THE COLUMBIA RIVER GORGE  
TO SOUTHWESTERN BRITISH COLUMBIA

By

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# ABSTRACT

In the Pacific Northwest, hybridization and polyploid variation have produced confusion in the relationships among Saxifraga rufidula (Small) James Macoun and its relatives. The entities from the Columbia River Gorge are particularly difficult to separate taxonomically. Some authors have recognized several species from that area while others recognize one highly variable, widely distributed species with varietal components. The present study approached the systematic treatment of S. rufidula and related subspecific taxa of S. occidentalis Wats. with data from numerical studies, studies of meiosis, observations of artificial and natural hybrid individuals and populations, breeding system experiments, observations of pollinators, and ecological observations. Polyploid intermediates and plants with introgressant characteristics are shown to occur, many of which appear to be the result of hybridization with the S. integrifolia species complex. Sufficient correlations of morphological, ecological and geographic discontinuities exist to substantiate the treatment of S. rufidula, S. occidentalis var. latipetiolata, S. occidentalis var. dentata, and S. occidentalis var. occidentalis as a species. According to the rules of nomenclature S. rufidula becomes S. aequidentata, S. occidentalis var. latipetiolata becomes S. latipetiolata, S. occidentalis var. dentata becomes S. gormanii, and S. occidentalis var. occidentalis becomes S. occidentalis.

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"The journey need not be alone at all moments.  
We can and do spark one another, and carry each other on."  
Paulus Berensohn

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whose spirits live on where the wild things grow.

A Sort of a Song

Let the snake wait under  
his weed  
and the writing  
be of words, slow and quick, sharp  
to strike, quiet to wait,  
sleepless.

Through metaphor to reconcile  
the people and the stones.  
Compose. (No ideas  
but in things) Invent!  
Saxifrage is my flower that splits  
the rocks.

-William Carlos Williams

(1883-1963)

## INTRODUCTION

The genus Saxifraga L. is composed of herbaceous, mostly perennial, plants which are found in arctic, alpine and rocky places in temperate regions. The genus is circumboreal and restricted mostly to the Northern Hemisphere. The name, Saxifraga, comes from the Latin words, saxi-meaning rock and fragere meaning to break or fragment, and is probably a reference to the habitats which many members occupy. A less likely derivation could be attributed to the folk use of some members of the genus for the treatment of kidney stones (Spongberg 1972). Ethnobotanical uses of Saxifraga species are as a leaf exudate for treatment of superficial wounds and boils (Hunan 1974), as a root extract used for the treatment of a wide range of disorders from a child's teething pains to relief of dysentery (Watt 1972), as alpine rock garden plants, and as the hanging basket houseplant, S. sarmentosa Schreder, known as strawberry begonia, strawberry geranium, or mother-of-thousands.

Although several early botanists contributed greatly to the knowledge of the genus (Linneaus 1753, Don 1822, Hooker 1833), the comprehensive monograph of Engler and Irmscher (1916) brought together the earlier taxonomic information and today constitutes the standard reference for this group of plants.

In North America the section Boraphila of Engler and Irmscher (1916) has two temperate centers of species diversity, one in the Eastern Appalachian Region and the other in the Rocky Mountain Region of the Pacific Northwest (Spongberg 1972). Both areas were strongly influenced by recent Pleistocene glaciations

and the evolutionary history of the plants in those areas is, in many respects, closely linked with the history of glacial advance and retreat. This is especially evident in the rapidly evolving species complexes of those areas. In such complexes single morphological characteristics which separate one entity from its close relatives are often difficult to find.

The name, rufidula, was first used to describe a species of the genus Micranthes by Small and Rydberg (1905). It was subsequently treated as a part of the genus Saxifraga by James Macoun (1906) whose father, John, collected the type material from Mt. Finlayson on Vancouver Island, British Columbia in 1887. Persistent confusion has surrounded the relationships among Saxifraga rufidula (Small) James Macoun and its close Pacific Northwest relatives in the section Boraphila subsection Nivali-virginiensis (Engler and Irmscher, 1916) up to the present time. Early monographic treatments dealt with the variability extant within this closely related group by recognizing a large number of specific entities (Small and Rydberg 1905, Johnson 1923). More recently, these have been reduced to two or three broadly defined species complexes with subspecific or varietal components (Bacigalupi 1944, Hitchcock et al. 1961, Hitchcock and Cronquist 1973, Krause and Beamish 1972, 1973).

The channeling of the Columbia River through its gorge has permitted a zone of contact between drier interior floristic elements and more mesic coastal species. The intimate contact of otherwise generally ecologically and geographically isolated plants in situations where environmentally intermediate or

perhaps unique microhabitats are available apparently has led to complicated patterns of variability and evolution within several groups of plants, including the Claytonia perfoliata polyploid complex (Miller 1976), and the Sisyrinchium sarmentosum-idahoense-littorale duodecaploid species group (Henderson 1976).

Several authors have commented on the extent of morphological intermediacy between S. rufidula and S. occidentalis S. Wats. Bacigalupi, in Abram's flora (1944), tentatively divided S. occidentalis into two subspecific taxa; subspecies occidentalis and rufidula. Hitchcock et al. (1961), and Hitchcock and Cronquist (1973) treated S. rufidula as a variety of S. occidentalis and considered variety rufidula transitional to variety dentata (Engl. and Irmsch.) C.L. Hitchcock and variety allenii (Small) C.L. Hitchcock in the Columbia River Gorge and adjacent Oregon. Hitchcock also included variety idahoensis (Piper) C.L. Hitchcock in S. occidentalis and described a new variety, latipetiolata C.L. Hitchcock. Saxifraga rufidula was confirmed by Krause and Beamish (1973) as a species and S. occidentalis was considered as an extremely variable entity without subspecific taxa. They noted that the extent of intergradation between S. rufidula and S. occidentalis in the Columbia River Gorge was largely unexplored. The entity idahoensis had been treated by Krause and Beamish (1972) as a subspecies of S. marshallii but they recognized that S. marshallii subsp. idahoensis has some introgressant characteristics of S. occidentalis. Elvander (1975) confirmed the classification by Hitchcock et al. (1961),



and Hitchcock and Cronquist (1973) of S. occidentalis varieties idahoensis, rufidula, and latipetiolata. He considered the varieties dentata and allenii to lack morphological distinctions and vary continuously with variety occidentalis and consequently, he treated them as synonyms of variety occidentalis.

None of these previous systematic investigations have addressed the problem of the confusion that exists among the relatives of S. rufidula in the Columbia River Gorge. Beamish (1961, 1967) and Krause and Beamish (1972, 1973) focused their studies on relationships mainly in British Columbia although they reported several chromosome counts of the material from the Columbia River Gorge and other areas of Oregon and Washington. Elvander (1975) based his study on numerical, cytological, and chromatographic evidence in plants largely from Idaho and Montana. He briefly discussed S. rufidula, S. occidentalis var. dentata, and S. occidentalis var. latipetiolata but did not include data from populations of those entities in his basic study.

The relationships among S. rufidula, S. occidentalis var. occidentalis, S. occidentalis var. dentata and S. occidentalis var. latipetiolata in the Columbia River Gorge and other areas extending northward into Southwestern B.C. are dealt with in the present paper. Correlations of hybridization studies and ecological observations with cytological studies and morphological analyses based on three different numerical approaches are presented in an effort to provide a more natural classification. Since S. rufidula and its close relatives are

often found growing sympatrically with members of S. integrifolia (sect. Integrifoliae of Engler and Irmischer 1916), the varieties integrifolia, claytoniifolia, and leptopetala are also included as potential sources of hybridization and character introgression in the studies presented here.

Several taxa peripheral to the main thrust of this study may have some close relationships with the taxa discussed in this paper. Evidence that S. oregana has close ties to S. occidentalis var. latipetiolata is brought forth and as a result it is included in the key to species. A systematic study of S. integrifolia and S. oregana sensu lato is currently in progress at the University of Washington (Elvander, PhD dissertation, in preparation). Saxifraga occidentalis var. dentata may introgress to S. marshallii subsp. marshallii. Other taxa mentioned here include S. marshallii subsp. idahoensis, S. reflexa, S. nivalis, S. californica, S. integrifolia var. columbiana, S. rhomboidea, S. ferruginea and a group of Eastern North American species. Saxifraga integrifolia var. columbiana is treated here as equivalent to S. integrifolia var. leptopetala. The present paper uses the terminology of Hitchcock for S. occidentalis but S. rufidula and S. marshallii subsp. idahoensis are treated as recognized by Krause and Beamish (1972, 1973), and S. occidentalis var. allenii as synonymous with var. occidentalis.

Proposed changes in the classification and revised nomenclature of the taxa studied appear in the Taxonomy and Conclusions sections of this paper.

## MATERIALS AND METHODS

Live plants, pressed specimens, flower buds and several soil samples were collected from populations from the mouth of the Columbia River east to beyond the Columbia River Gorge. Some collections were also made in areas extending north and south in the lower Columbia River area and adjacent Coast Range. Populations from the Olympic Mountains, Southeastern Vancouver Island, and Cascades in Washington and the Southern Mainland of British Columbia (Fig. 1, Table I) were also sampled. Many collections came from localities with two sympatric taxa. Fifteen to twenty rosettes from a large number of the populations sampled were transplanted to coldframes filled with a peat-vermiculite bedding mixture which were located at the University of British Columbia. Mass collections of buds in meiosis were sampled. Buds from individual plants were collected and a large number of plants were pressed as voucher material. Specimens are on deposit at the University of British Columbia.

Specimens studied for morphological comparison, classification, annotation, and geographic distribution included a total of 1,507 herbarium sheets representing about 5,000 plants from the following herbaria: Brigham Young University (BRY), University of Minnesota (MIN), U.S. National Herbarium (NA), University of Oregon (ORE), Oregon State University (OSC), University of British Columbia (UBC), University of California at Berkely (UC), British Columbia Provincial Museum (V), Washington State University (WS), and University of Washington (WTU). Several hundred additional herbarium sheets were also

Figure 1: Collection sites in the Pacific Northwest for the present study. One collection from Berthoud Pass, Colorado, is not shown.

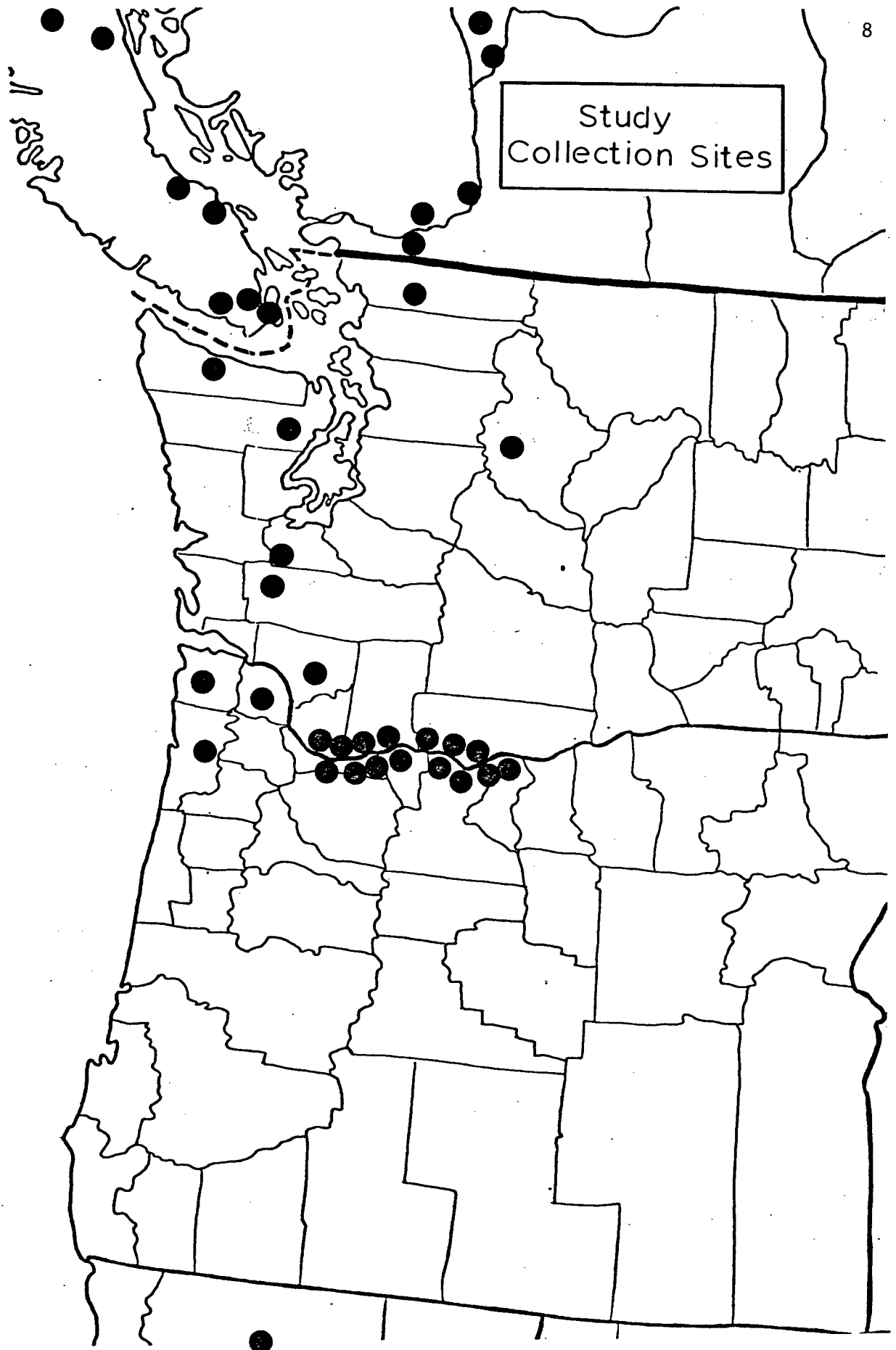


Table I.  
Collections for Study.

<u>Taxon</u>	<u>Collection Code Number</u>	<u>Location</u>
<u>S. rufidula</u>	616	Viento, rest area on Interstate 8, 0.9 mi w. of Viento St. Pk., Hood River Co., Ore.
	608	Troutdale, 1.3 mi s. of Sandy R. Bridge, Multnomah Co., Ore.
	610	Yeon Pk., ca. 1.5 mi along trail to McCord Falls, Multnomah Co. Ore.
	612A	Mayer Pk., 0.8 mi n. of Mayer St. Pk., Wasco Co., Ore.
	613A	The Dalles, 2.0 mi w. of Chynoweth Cr. on Old U.S. Hwy. 30, Wasco Co., Ore.
	637	Mosier, 1.0 mi e. of Mosier on Old Columbia R. Hwy., Wasco Co., Ore.
	673	Lake Crescent, 8.5 mi e. of Fairholm on U.S. Hwy. 101, Clallam Co., Wash.
	675A	Mt. Pleasant, 1.9 mi e. of the Clark-Skamania Co. bdry. on St. Hwy. 14, Clark Co., Wash.
	647A	Washougal, 1.0 mi w. of Clark- Skamania Co. bdry. on St. Hwy. 14, Clark Co., Wash.
	76-1	Marmot Pass, ca. 5 mi s. of Camp Mystery, s.e. of Marmot Pass, Jefferson Co., Wash.
	617A	Bingen, 5.6 mi e. of Bingen, on St. Hwy 14, Klickitat Co., Wash.
	669A	Bingen Lk., 7.4 mi e. of w. bdry. of Klickitat Co. on St. Hwy. 14, Wash.
	672	Cock, 9.8 mi w. of e. bdry. of Skamania Co. on St. Hwy. 14, Wash.
	618A	Skamania Co., 3.5 mi e. of Clark- Skamania Co. bdry. on St. Hwy. 1 Wash.
	645A	Collins, 0.9 mi e. of Collins Depot Rd. on St. Hwy. 14, Skamania Co., Wash.
	NMO-R	Nanaimo, ca. 5 mi s. of Nanaimo on White Rapids Rd., V.I., B.C.

Table I. (cont)

<u>Taxon</u>	<u>Collection Code Number</u>	<u>Location</u>
	NOOS-R	Nanoose Hill, ca. 15 mi n. of Nanaimo on Nanoose Hill, V.I., B.C.
	UCL-R	Upper Campbell Lk., 7.4 mi w. of Campbell Lake Bridge, V.I., B.C.
	623A	Sooke, s. side of Sooke R. at Sooke Potholes Pk., V.I., B.C.
	624B	Mill Hill, Capital Distr. Pk., Victoria, V.I., B.C.
	627A	Mt. Finlayson, Goldstream Prov. Pk., V.I., B.C.
<u>S. occidentalis</u> <u>var. denata</u>	629A	Saddle Mt., on trail to summit near westernmost Peak, Clatsop Co., Ore.
	606	Delena, Beaver Creek Falls, 2.8 mi w. of Delena, Columbia Co., Ore.
	630	Tillamook Co., 2.0 mi w. of e. bdry. of Tillamook Co. on St. Hwy. 6, Ore.
	607	Kalama R., 3 mi e. of Interstate 5 on Kalama R. Rd., Cowlitz Co., Wash.
<u>S. occidentalis</u> <u>var. latipetiolata</u>	629C	Saddle Mt., on trail to summit near top, Clatsop Co., Ore.
<u>S. occidentalis</u> <u>var. occidentalis</u>	605	Chehalis R. (hybrid), 3.3 mi w. of Littel, Lewis Co., Wash.
	BAKR	Mt. Baker Natl. forest, Yellow Aster Meadows, Whatcom Co., Wash.
	626	Yale, ca. 1.5 mi e. and n. of Yale below Can. Hwy. 1, B.C.
	666	Liumchen Ridge, s. of Sardis, B.C.
	CORN	Cornwall Lookout, se. of Hat Creek, B.C.
	687	Bootanie Valley, Skwaha Mt. area n. of Lytton, B.C.
<u>S. integrifolia</u> <u>var. claytoniifolia</u>	641	Giliam Co., 1.7 mi e. of w. bdry. Giliam Co. on Interstate 80 n., Ore.

Table I. (con't)

<u>Taxon</u>	<u>Collection Code Number</u>	<u>Location</u>
	609	Troutdale, 1.3 mi s. of Sandy R. Bridge, Multnomah Co., Ore.
	611	Rowena, 2.4 mi w. of Rowena overpass on Interstate 80-N., Wasco co., Ore.
	612B	Mayer Pk., 0.8mi n. of Mayer St. Pk., Wasco Co., Ore.
	613B	The Dalles, 2.0 mi w. of Chynoweth Cr. on Old U.S. Hwy. 30, Wasco Co. Ore.
	667	Biggs, 1.25 mi e. of jct. with U.S Hwy. 97 on U.S. Hwy. 30, Sherman Co., Ore.
	692	Stephen's Pass, 11 mi e. of Stephen's Pass Ski Lodge on U.S. Hwy. 2, Chelan Co., Wash.
	675B	Mt. Pleasant, 1.9 mi e. of the Clark-Skamania Co. bdry. on St. Hwy. 14, Clark Co., Wash.
	668	Lyle, 1.6 mi n. of jct. with St. Hwy. 142, Klickitat Co., Wash.
	669B	Bingen Lk., 7.4 mi e. of w. bdry. of Klickitat Co. on St. Hwy. 14, Wash.
	642	Benchmark, U.S.G.S. V425, 1968, 5.2 mi e. of The Dalles bridge, Klickitat Co., Wash.
	617B	Bingen, 5.6 mi e. of Bingen, on St. Hwy 14, Klickitat Co., Wash.
	619	Clark Co. line, bdry. with Skamania Co. on St. Hwy. 14, Wash.
<u>S. integrifolia</u>	671	Grizzly Lk., about 0.5 mi downstream from Grizzly Lk. Siskiyou Co., California
<u>var. integrifolia</u>	MIMA	Mima Mounds, w. of Little Rock on Rd. to Mima, Thurston Co., Wash.
	623B	Sooke, s. side of Sooke R. at Potholes Pk., V.I., B.C.
	624B	Mill Hill, Mill Hill Capital Distr. Pk., Victoria, V.I., B.C.
	627B	Mt. Finlayson, Goldstream Prov. Pk., V.I., B.C.



Table I. (con't)

<u>Taxon</u>	<u>Collection Code Number</u>	<u>Location</u>
	NMO-B	Nanaimo, ca. 5 mi s. of Nanaimo on White Rapids Rd., V.I., E.C.
	NOOS-B	Nanoose Hill, ca. 15 mi n. of Nanaimo on Nanoose Hill, V.I., B.C.
	625	Yale, ca. 1.5 mi e. and n. of Yale below Can. Hwy 1, B.C.
	617B	Bingen, 5.6 mi e. of Bingen on St. Hwy. 14, Klickitat Co., Wash.
	78-1	Harrison Lk., 1.5 mi w. of Harrison, Hot Springs, B.C.
	682	Elk Falls, below Campbell Lk. Dam, V.I., B.C.
<u>S. integrifolia</u> <u>var. leptopetala</u>	648	Princeton, off Hwy. e. of Princeton, road to golf course, B.C.
<u>S. oregana</u>	BERH	Berthoud Pass, Bdry. of Grand Co. Colorado

inspected from material on loan to the University of Washington.

### Chromosomal Studies

Squashes of anther tissue were made by first fixing bud material in Carnoy's 3:1, absolute ethanol:glacial acetic acid fluid. Buds were then stained using Snow's (1963) bulk method and warmed in a 40 C oven for about 24 hours. Slide preparations were preserved in Hoyer's permanent medium (Alexopoulos and Beneke 1952).

Pollen stainability of live, preserved and dried flowers was measured by counting up to 200 pollen grains which had been stained and mounted in lactophenol-aniline blue stain (Sass 1958). Large, dark-staining grains were considered fertile. Preliminary investigations of pollen grain size confirmed Sokolovskaya's (1958) reports that pollen size does not appear to be correlated with chromosome number and further investigation was discontinued.

### Hybridization Studies

Plants used as female parents were emasculated, bagged with water-resistant parchment bags prior to flowering and artificially cross-pollinated under a dissecting microscope. Only crosses involving simultaneously blooming plants were successful. Stigmatic receptivity was estimated from the onset of a slight watery appearance and papillate condition of the stigmatic surface. Increased stainability using lactophenol-aniline blue stain (Sass 1958) also indicated stigmatic receptivity. Whole anthers were used to transfer pollen masses to the stigmas.

Samples of hybrid and outcrossed seed were planted in a well-drained sandy soil mixture in early December in rows beneath about 1-2mm of sand and a 1cm layer of pea-sized gravel in large-mouthed pots set in a shallow pan of water. Plantings were placed outside under ambient temperature and light conditions and misted periodically to maintain a moist environment. By April seedlings of nearly every cross had germinated and later were transplanted to sandy propagation beds where they were allowed to grow for one season. In the spring of the second season seedlings were transplanted into pots. As they flowered, samples were examined for their morphology and behaviour in meiosis, then preserved as pressed specimens.

## Numerical Studies

Forty-three quantitative characters or character combinations (Table II) were measured on 263 live, flowering plants (from natural populations and artificially produced hybrids) for numerical taxonomic treatments. Periodic infestations of rust, aphids, mildews, slugs and root weevils not only increased plant mortality but occasionally altered the developmental morphology of some growing plants. Such individuals were avoided wherever possible in the study but a certain amount of spurious variation may be the result of responses to minor infestation or subsequent pesticide treatment. Population samples consisted of 8-10 plants chosen at random from well-established transplantations grown in cold frames. Leaf measurements were taken of a mature leaf of each plant after it was carefully removed from the outer rosette whorl and pressed. Flower measurements were standardized by choosing flowers as close as possible to the sequential midpoint of anther dehiscence and by trying to obtain flowers from equivalent positions in the inflorescence. Linear variables were converted to metric values, counted variables were transformed using the square root transformation and the resultant data matrix was subjected to three different available computer programs. The hierarchical clustering analysis program which was used is called UBC-CGROUP, available at the University of British Columbia Computing Center. The algorithm used is that of Ward (1963) and the coding is modified from Veldman (1967). A Principal Components Analysis (PCA) program called PRINCOMPS

Table II.  
Characters used in Numerical Studies

<u>No.</u>	<u>Character</u>	<u>No.</u>	<u>Character</u>
1.	petal ln.	2.	petal ln./wd. ratio
3.	sepal ln.	4.	sepal ln./wd. ratio
5.	gland wd.	6.	gland ln./wd. ratio
7.	style ht.	8.	filament wd. at middle/wd. at bottom ratio
9.	perianth wd.	10.	gynoecium ht.
11.	filament wd. at bottom	12.	pedicel ln.
13.	hair no. at leaf tip	14.	hair ln. leaf tip
15.	hair no. on pedicel	16.	angle of lowest inflorescence branch
17.	angle of lowest bract to stem	18.	hair ln. at lowest branch
19.	hair no. at lowest branch	20.	hair no. at scape bottom
21.	hair no. on petiole	22.	lowest bract ln.
23.	lowest bract ln./wd. ratio	24.	teeth no. on lowest branch
25.	scape diam. at lowest branch	26.	inflorescence angle
27.	plant ht.	28.	filament ln.
29.	inflorescence ln./wd. ratio	30.	plant ln./ln. to lowest branch ratio
31.	inflorescence ln. from widest part to top	32.	leaf ln.
33.	leaf ln./wd. ratio	34.	teeth no. on leaf
35.	hair ln. petiole	36.	angle of leaf tip
37.	angle leaf shoulder	38.	petiole wd.
39.	petiole ln./wd. ratio	40.	ln. of tooth at leaf tip
41.	style ln. + gland ht./ gynoecium ln.	42.	gland wd. squared + filament ln. squared/ (style ln. + gland ln.) squared.
43.	leaf ln./petiole ln. ratio		

Abbreviations: ht.=height, ln.=length, no.=number, wd.=width

(available from Bradfield, University of British Columbia, Department of Botany) was used to obtain a standardized correlation matrix which was then operated upon to form an eigenvector matrix. First vs. second, first vs. third, and second vs. third eigenvector plots were also produced. Ten groups including hybrid and intermediate groups were assigned and analysed using a stepwise discriminate function analysis program (BMD07M, Dixon 1970) to determine categorizing functions, important discriminating variables and group hyperspace relationships.

### Breeding Systems

Tests for autogamous pollination were carried out by; 1) bagging flower buds for the flowering season and 2) hand pollinating emasculated, bagged flowers with pollen from other flowers on the same plant. Tests for asexual seed production which also served as procedural controls for hand pollination experiments were conducted by allowing emasculated, bagged buds to mature within the pollination bags. Undehisced seed and unfertilized ovules were recorded in a subsample of each inflorescence. Seed number was estimated where high numbers of seeds were produced.

The number of seeds in immature carpels was counted from several plants of each taxon. Repeated counts on a single inflorescence were grouped according to the determinate order and position of the flowers on the inflorescence branches.

### Habitat And Pollination Studies

Observations of insect behavior on Saxifraga flowers were taken over a period of 21 hours on 5 days at 3 locations. The locations included two on Vancouver Island where S. rufidula and S. integrifolia are sympatric and a S. occidentalis population at Yale, British Columbia. Observations of behaviour included the time spent foraging (for nectar and/or pollen) or resting, the numbers of and distances between flowers and inflorescences visited, and if possible, the visitors' preferences for flowers in various stages of anthesis. Insects observed visiting Saxifraga flowers were collected and identified to assist in identification of similar uncaptured visitors. Pollen was washed or scraped from the collected insects to determine the amount of Saxifraga pollen present.

Soil depth to rock substrate (or in rare cases to a maximum depth of 30 cm) was measured from beneath 15 to 30 plants chosen at random and representing populations on Vancouver Island, the Lower Mainland of British Columbia, and a transect of stations along the Columbia River Gorge. About 20 cc samples of soil were taken from beneath 15 plants chosen at random from 7 populations (6 on Vancouver Island, 1 at Yale, British Columbia). Three locations received repeated sampling over the course of one flowering season. The samples from each population were homogenized, weighed and dried in a 60 C vacuum oven for 24 hours before dry weight measurements were taken.

## RESULTS AND DISCUSSION

### Morphology

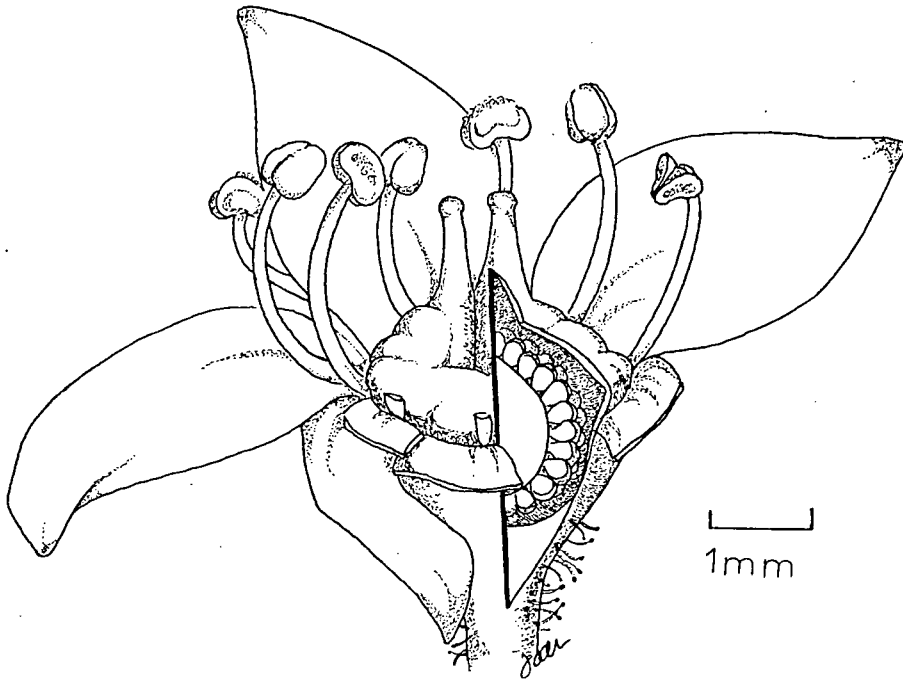
Morphological features which distinguish between the taxa include both floral and vegetative characteristics in most taxonomic treatments. The position of the ovary has been used as an important key characteristic. A developmental feature which has created problems for taxonomists is the disparity between the degree of ovary inferiority at early anthesis (judged by midpoint of anther dehiscence) and later at maturity of the fruit. For instance, in S. occidentalis var. latipetiolata development proceeds from a greater than half inferior ovary as in S. integrifolia and S. oregana to an almost completely superior ovary in fruit (Fig.2A,B). Evidently the difference between flowering and fruiting conditions is difficult to detect on pressed specimens and has led to some ambiguities in previous taxonomic treatments if an early fruiting condition where petals are persistent is interpreted as anthesis.

Pressing and drying processes may distort precise ovary relationships. Even in live material that is standardized by using midpoint of anther dehiscence as a precise event in anthesis, variability in stylar elongation, receptacle width and gland positioning create difficulties in quantitative measurement. Nonetheless, as a characteristic which separates the major species complexes, ovary position is useful provided that anthesis is clearly defined by discrete events such as anther

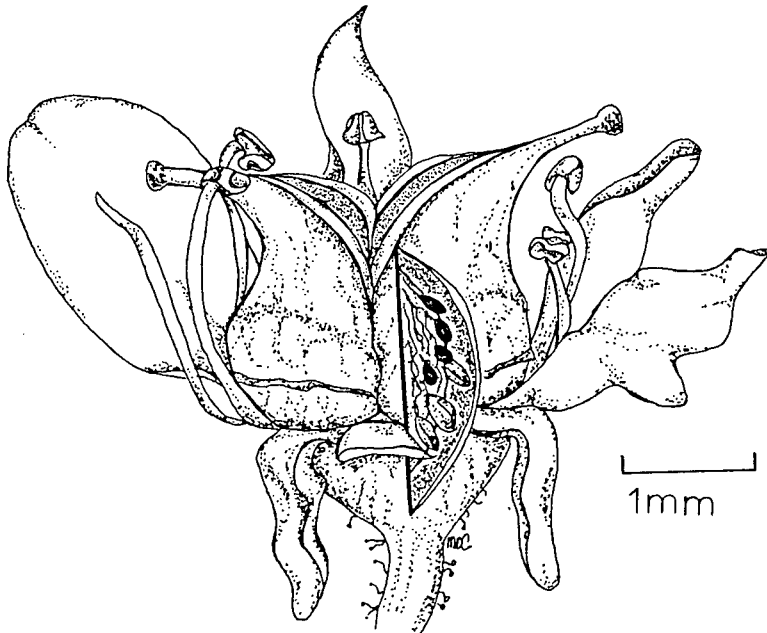


Figure 2: Drawing of S. occidentalis var. latipetiolata flower (A) and fruit (B). Flower is at midpoint of anther dehiscence. Sepals, nearest petals, filaments and a pie-shaped segment of ovary are removed to show the position of the ovary. Note the differences in ovary position and gland structure between flower and fruit.

A.



B.

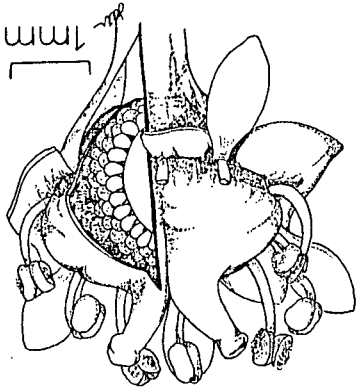


dehiscence. On herbarium material it is often possible to interpret flowers which are past anther dehiscence as being those from which pollen has been removed by pollinators.

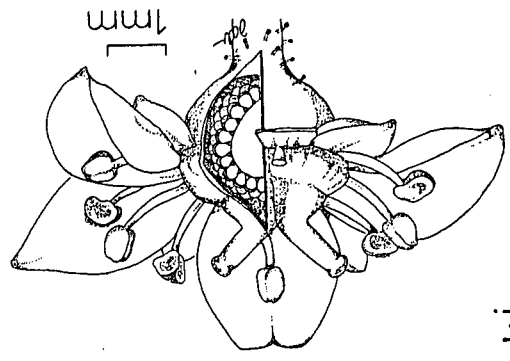
The breadth and shape of the nectar gland are useful characteristics in separating some species and species complexes. In S. rufidula and many populations of S. occidentalis var. occidentalis it is a small ringlike band encircling the lower portion of the ovary (Fig. 3,A,B). The gland and its secretions are hidden at the base of the appressed petals and filaments in many of these plants. In S. occidentalis var. dentata (Fig. 3,C), S. occidentalis var. latipetiolata (Fig. 2A), and members of the S. integrifolia - oregana complex (Fig. 3,D-F) the gland at anthesis is an obconic disc which covers a considerable portion of the top of the ovary and exudes nectar in diffuse, glistening droplets.

Filament shape varies widely among relatives of S. occidentalis var. occidentalis (Fig. 3,A-C). In S. rufidula and S. occidentalis var. dentata filaments are linear or subulate. A few plants from high mountain populations of S. rufidula on Vancouver Island and the Olympic Mountains have slightly clavate filaments. In S. occidentalis var. occidentalis the filaments are usually at least somewhat clavate but on some pressed specimens shrinkage in drying produces apparently linear filaments. All members of the S. integrifolia - oregana complex have linear or subulate filaments (Fig. 3D-F). It is interesting that in other relatives of S. occidentalis such as S. marshallii, which have yellow or green petal spots the filaments are broadly clavate and may have

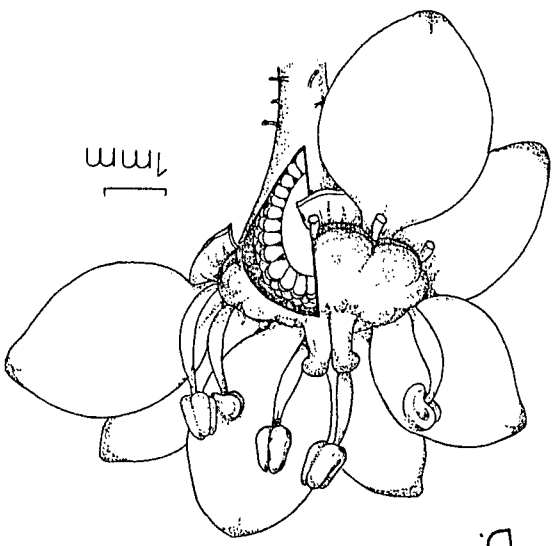
Figure 3: Drawing of S. occidentalis var. occidentalis (A), S. rufidula (B), S. occidentalis var. dentata (C), S. integrifolia var. claytoniifolia (D), S. integrifolia var. integrifolia (E), S. integrifolia var. leptopetala (F), flowers at midpoint of anther dehiscence. Nearest sepals, petals, filaments and a pie-shaped segment of the ovary wall are removed to show the position of the ovary. Note differences in nectar gland features, ovary position, filament structure and petal shape in the flowers. The gland is the swollen structure immediately above the bases of the filaments.



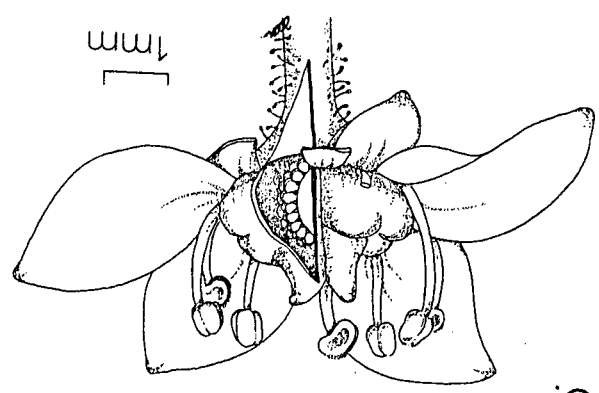
F.



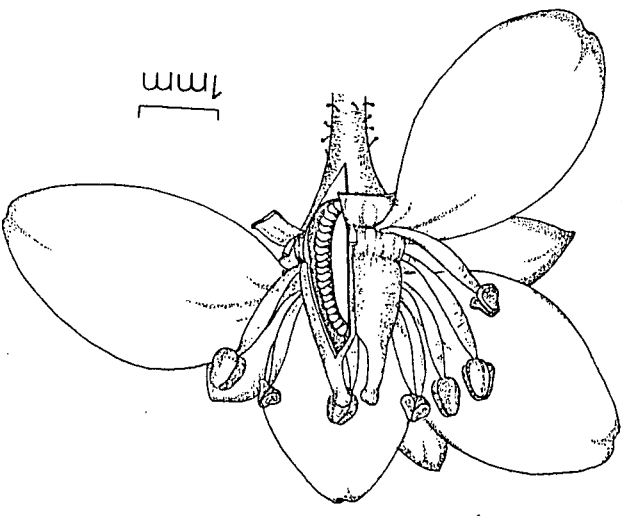
E.



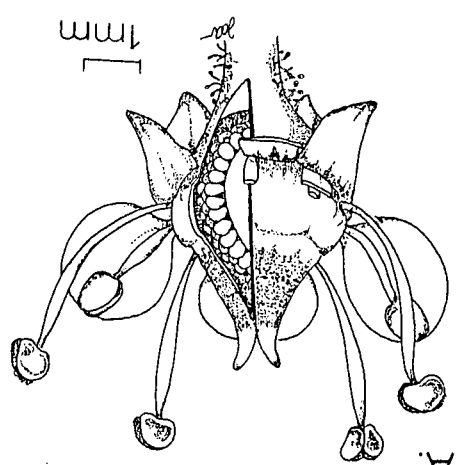
D.



C.



B.



A.

a special function in pollinator attraction. Correlations of these features as well as gland characters with diverse pollination strategies could perhaps provide an interesting evolutionary story.

Petal size, color, and shape vary considerably among the taxa (Fig. 2,3). Saxifraga occidentalis var. occidentalis differs from its relatives in this study by having usually elliptic petals which often are somewhat narrowed into a clawlike base. Certain dwarfed alpine forms of S. occidentalis var. occidentalis as well as S. rufidula may be nearly apetalous with darkly anthocyanic inflorescences and flower parts. Saxifraga rufidula, S. occidentalis var. dentata and S. occidentalis var. latipetiolata usually have ovate petals with broad bases. Varieties of S. integrifolia range from apetalous or with small greenish-petaled forms to large, white-petaled forms.

Saxifraga rufidula has a flat-topped or broadly convex, diffuse-flowered inflorescence (Fig. 4, A, 5, B). Some Columbia River Gorge plants have broadly obconic inflorescences. In contrast, S. occidentalis var. occidentalis (Fig. 4, B), S. occidentalis var. latipetiolata (Fig. 7, A), S. occidentalis var. dentata (Fig. 5, A) and most varieties of S. integrifolia (Fig. 6, B) usually have conic or interrupted-conic inflorescences which range in flower density from open to congested. Montane forms of S. occidentalis var. occidentalis as well as S. integrifolia var. apetala are usually few-flowered, dense, capitate panicles. Flower number ranges per inflorescence from few (4-42) in S. rufidula, especially those

on Vancouver Island and the Olympic Mountains, to several (13-81) in S. occidentalis var. occidentalis, S. occidentalis var. dentata and S. integrifolia var. integrifolia. Saxifraga occidentalis var. latipetiolata and S. integrifolia var. claytoniifolia have a large number of flowers, usually exceeding 75.

Saxifraga occidentalis var. dentata and S. integrifolia var. claytoniifolia have fine, brittle, vertically penetrating networks of rhizomes. Such networks may also be present in S. marshallii subsp. marshallii and S. integrifolia var. leptopetala. The other taxa have short, stout, horizontal rhizomes which do not form deep networks, although rosette replacement from short branches and branchlike basal bulblets appears to be a common means of vegetative growth in this group of plants.

Many features of the leaves in most taxa vary within a rosette. The terminal leaves are usually more pubescent with fewer teeth and are much smaller in size than the leaves from the outer whorl of the rosette. The leaves may also demonstrate a plastic response to shaded conditions in which they become elongate and have a greater surface area.

Some leaf characteristics are of taxonomic significance. S. occidentalis var. latipetiolata, as the name implies, has broad, short, rather indistinct petioles (Fig. 9D). In that feature it resembles S. oregana and differs from the other taxa which have distinctly narrowed, evident petioles (Fig. 9,A-C,E). The transition from blade to petiole is most abrupt in S. integrifolia var. claytoniifolia and S. occidentalis var.

Figure 4: Habit sketch of artificial hybrids and representative parental plants. Tetraploid S. rufidula (A), tetraploid S. occidentalis var. occidentalis (B), and an artificially produced S. rufidula x S. occidentalis var. occidentalis F1 hybrid plant (C). Magnification x 2/3.



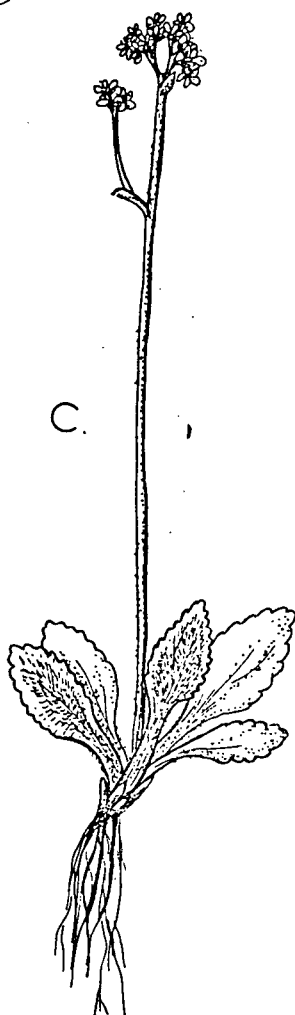
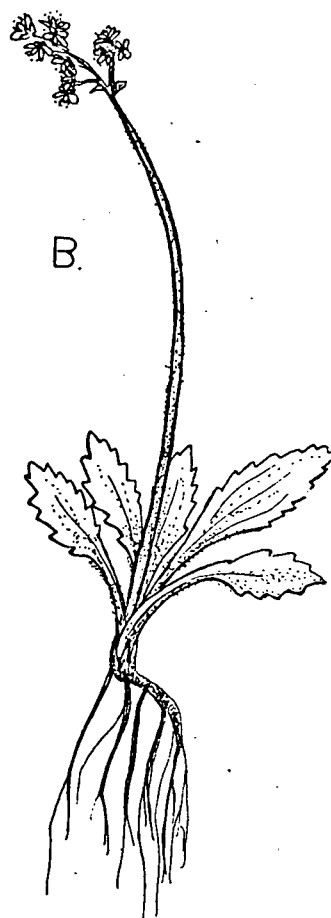
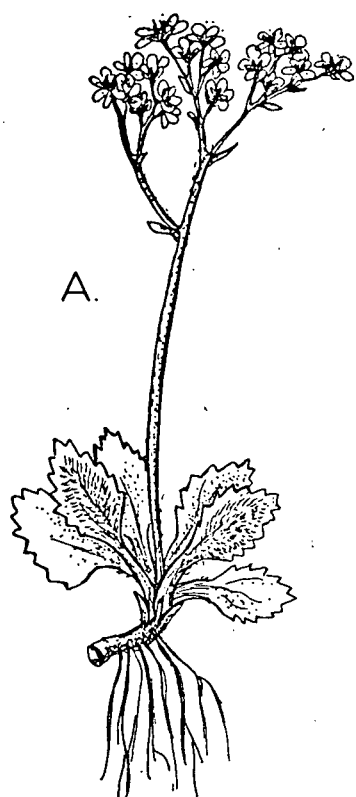


Figure 5: Habit sketch of artificial hybrids and representative parental plants. Tetraploid S. occidentalis var. dentata (A), diploid S. rufidula (B), and an artificially produced S. rufidula x S. occidentalis var. dentata F1 hybrid plant (C). Magnification x 2/3.



Figure 6: Habit sketch of artificial hybrids and representative parental plants. Diploid S. rufidula (A), tetraploid S. integrifolia (B), and an artificially produced S. rufidula x S. integrifolia F1 hybrid plant (C). Magnification x 2/3.

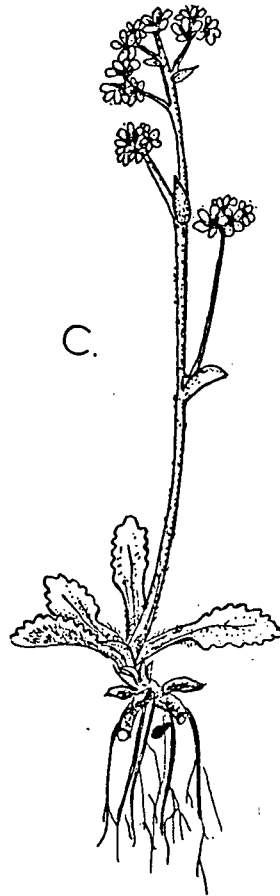
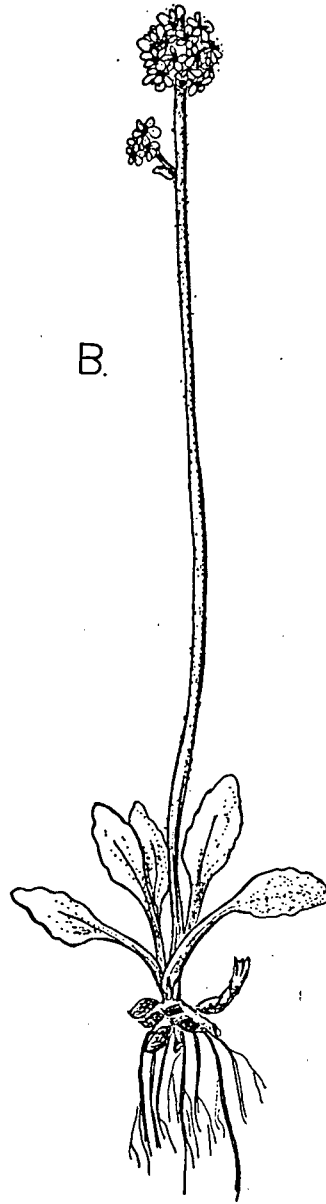
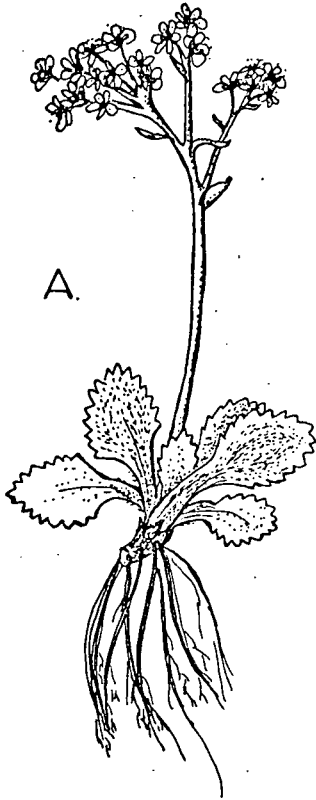


Figure 7: Habit sketch of artificial hybrids and representative parental plants. N=38 S. occidentalis var. latipetiolata (A), tetraploid S. rufidula (B), and an artificially produced S. rufidula x S. occidentalis var. latipetiolata F1 hybrid plant (C). Magnification x 2/3.



Figure 8: Habit sketch of artificial hybrids and representative parental plants. Tetraploid S. occidentalis var. dentata (A), tetraploid S. occidentalis (B), and an artificially produced S. occidentalis x S. occidentalis var. dentata F1 hybrid plant (C). Magnification x 2/3.





dentata (Fig. 10) and usually more gradual for members of the other groups (Fig. 9). The rather distinct rounded or somewhat squared teeth of S. rufidula and S. occidentalis make the blade-petiole transition evident but the actual angle of the blade base is usually rather obtuse in these taxa (Fig. 10). Marginal teeth of S. rufidula tend to be deeply rounded and acute whereas S. occidentalis var. occidentalis teeth are usually right-angled or obtuse. However, S. rufidula plants from the Columbia River Gorge are apparently introgressant for this character (Fig. 9, A-C). Leaves of S. rufidula are usually reddish tinged on the lower surfaces while those of S. occidentalis var. occidentalis and S. occidentalis var. dentata vary from green to reddish. Saxifraga occidentalis var. latipetiolata leaves are usually light green on both surfaces, a feature resembling members of the S. integrifolia-oregana group.

Some morphological features which require a broader survey and further attention include: leaf thickness in cross section, stomate characteristics, fine structural differences in seed coat sculpturing, and papillosity of petals, filaments, and nectar glands. Although variation was observed in these features, definite correlations with most groups were not possible on the basis of limited material and data concerning the extent of variability in other members of Saxifraga. These characteristics may be of considerable usefulness in definition of subsections within the genus. It was noted that S. integrifolia var. leptopetala apparently is unique among the observed taxa in that its petals are without adaxial

Figure 9: Leaf outline drawing showing variability in shape and margin characteristics in samples of diploid S. rufidula (A), tetraploid S. occidentalis var. occidentalis (B), tetraploid and hexaploid S. rufidula in the Columbia River Gorge (C), n=38 S. occidentalis var. latipetiolata (D), and tetraploid S. integrifolia var. integrifolia (E) leaves. Each sample is from one population. Each leaf is taken from the lower whorl of leaves from a separate plant. Line is 5 cm long. Note differences in petiole length and width, petiole-blade transition and dentition. Increased variability of Columbia River Gorge polyploid S. rufidula plants and resemblance to S. occidentalis is also apparent.

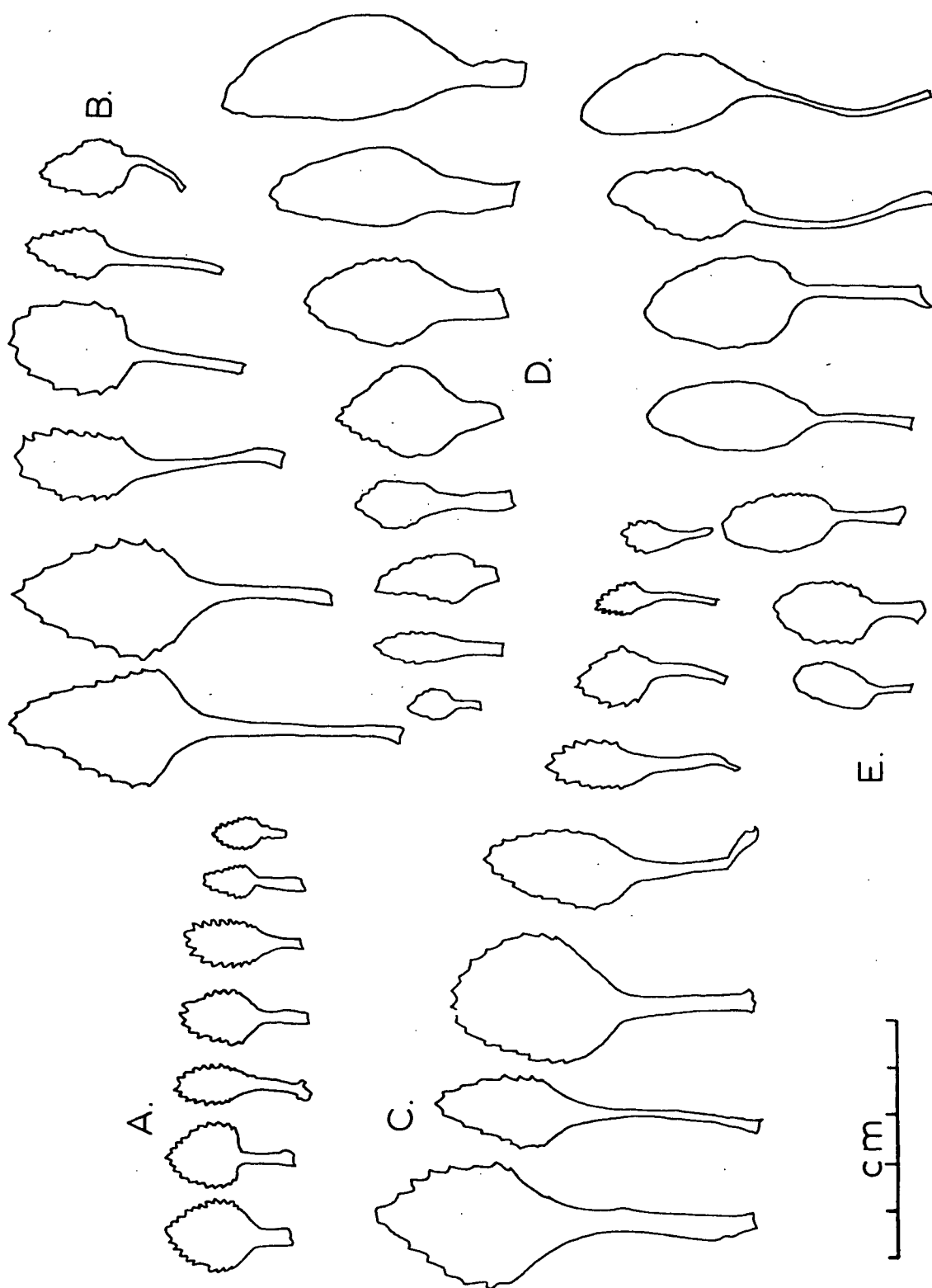
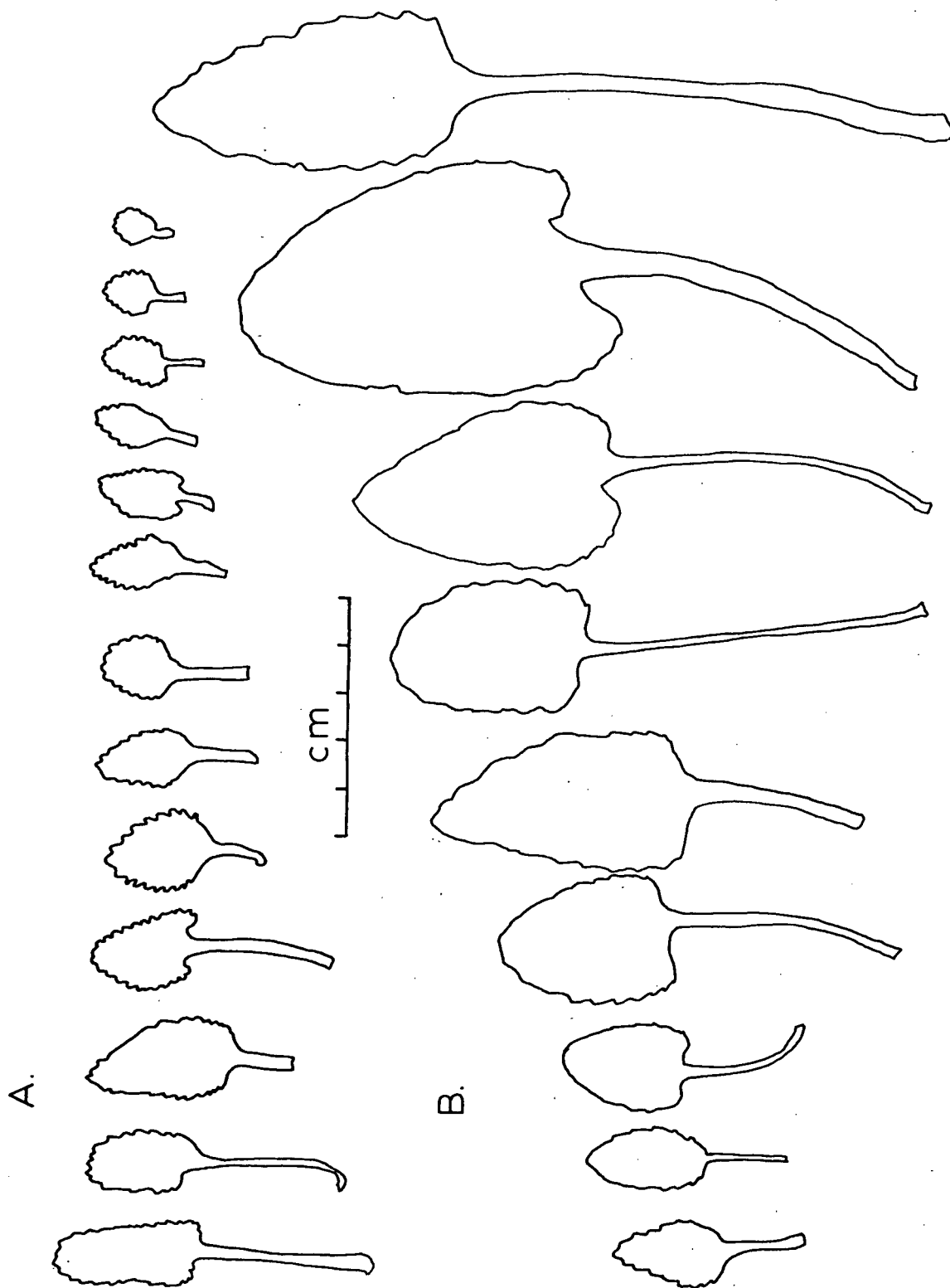


Figure 10: Leaf outline drawing showing variability in shape and dentition in samples of diploid (A) and tetraploid (B) S. occidentalis var. dentata. Samples are from four different populations. Each leaf is taken from the lower whorl of leaves from a separate plant. Line is 5 cm long. Note the variation in leaf size and extent of dentition.



papillae and the fine structure of seed coat surfaces is without ridges or projections. It would be of interest to study differences in floral ultra-violet reflectance patterns for this taxon and its relatives. Use of these characteristics may prove especially helpful in studies of Eastern and Western North American species-pairs.

### Chromosomal Studies

Polyploid-aneuploid series are common for many groups of plants (Tobgy 1943, Lewis and Raven 1958, Jackson 1962, Kyhos 1965, Carr 1975, Subhasi 1975) including Saxifraga (Dambolt and Podlech 1965, Dambolt 1968, Elvander 1975) and are confirmed in the present study as well.

Diploids with 10 pairs, tetraploids with 19 pairs and hexaploids with 29 or 28 pairs have been reported for S. occidentalis var. occidentalis and S. rufidula (Krause and Beamish 1972, 1973). It is interesting that in S. ferruginea a 10-paired diploid and 19-paired reduced tetraploid situation (Randhawa and Beamish 1972) has evolved in an apparently parallel polyploid-aneuploid pattern to the one seen in S. rufidula and its relatives. The same situation may also be the case in S. integrifolia var. integrifolia where 19-paired populations are common.

Chromosome counts for Saxifraga populations are summarized in Table III. Populations of S. rufidula from Vancouver Island, the Olympic Peninsula and the Upper Willamette River drainage are, with one exception, composed of diploid individuals with 10

pairs of chromosomes (see Fig. 14C). Krause and Beamish (1973) have reported a hexaploid population ( $n=29$ ) at Elk Falls on Vancouver Island. Attempts to relocate that population were unsuccessful, possibly because of local extinction resulting from hydroelectric water diversion.

Saxifraga rufidula populations from the Columbia River Gorge are more complex and variable in their chromosome numbers. Diploid individuals ( $n=10$ ) occur in some mixed populations with the more common tetraploid ( $n=19$ ) (Fig. 11). Other populations had only tetraploid or hexaploid representatives (Fig. 12), but the possibility of rare diploid individuals cannot be ruled out considering the small number of counts made. Some of the S. rufidula plants from most populations along the Columbia River Gorge undergo an abnormal meiosis typical of hybrids between plants of different levels of polyploidy (Fig. 13A,B). Diploid, tetraploid and hexaploid plants and their putative natural hybrids are morphologically almost identical.

A population from along the Chehalis River in Southwestern Washington previously referred to S. occidentalis (Krause and Maze No. 690001 in Krause and Beamish 1972) is morphologically intermediate between S. occidentalis and S. integrifolia. Individuals sampled were uniformly hexaploid ( $n=29$ , Fig. 13C,D). This population probably represents a rare, stabilized allopolyploid hybrid entity. Attempts to locate similar populations elsewhere in the area were unsuccessful, although there are resemblances to certain S. integrifolia specimens of the Fort Lewis and Olympia, Washington regions. One specimen from near Mima, Washington had an uncertain chromosome count of



Table III.  
Summary of Chromosome Numbers.

Taxa, locations (collection no.)	No. Plants	No. Cells	Meiotic Chromosome No. (II or II+I) *
<u>occidentalis</u>			
Yale, B.C. (626)	2	6	19
Cornwall Lookout, B.C. (CORN)	3	10	19
Mt. Baker, Wash. (BAK)	2	5	19
<u>dentata</u>			
Saddle Mt., Oregon (629A)	3	8	10
Tillamook, Oregon (630)	11	44	10
Kalama River, Wash. (607)	2	7	20
Delena, Oregon (606)	8	23	20 (6), 19+2 (2)
<u>rufidula</u>			
Mt. Finlayson, V.I., E.C. (627A)	3	20	10
Nanoose Hill, V.I., E.C. (NOOS-R)	4	7	10
Nanaimo, V.I., B.C. (NMO-R)	4	31	10
Upper Campbell Lake, V.I., B.C. (UCL-R)	3	5	10
Lake Crescent, Wash. (673)	4	16	10
Bingen Lake, Wash. (669A)	2	10	29
Mt. Pleasant, Wash. (675A)	1	3	10
Yeon Park, Ore. (610)	6	21	10 (2), 19 (3), ca. 20
Viento, Ore. (616)	5	13	19 (4), ca. 19
Troutdale, Ore. (608)	5	7	ca. 20+1, ca. 27+2, 29, 19+12, 19+13
Mayer Park, Ore. (612A)	4	11	ca. 19, ca. 16+8, ca. 29, ca. 20+5
The Dalles, Ore. Skamania Co., Wash. (618A)	4 4	16 26	ca. 29 (3), ca. 26+6 19 (3), ca. 14+8

\*Numbers in parentheses indicate the number of plants with the particular chromosome number.

Table III. (con't)

Taxa, locations (collection no.)	No. Plants	No. Cells	Meiotic Chromosome No (II or II+I)*
<u>occidentalis</u> x <u>integrifolia</u> pop.			
Chehalis R., Wash. (605)	4	11	28,29 (3)
<u>latipetiolata</u>			
Saddle Mt., Ore. (629C)	5	23	ca.36,38 (3), ca.40
<u>integrifolia</u>			
Mt. Finlayson, V.I., B.C. (627)	3	3	19
Nanaimo, V.I., B.C., (NMO-I)	1	2	19
Elk Falls, V.I., B.C., (682)	1	3	19
Harrison Lake, B.C., (78-1)	1	3	19
Yale, B.C. (625)	1	2	19
Mayer Park, Ore. (612B)	4	20	19, ca.17+5 (3)
Grizzly Lake, Ca. (671)	1	4	19
Bingen, Wash. (617)	1	1	19
Mima Mounds, Wash. (MIMA)	1	4	ca.47
<u>claytoniifolia</u>			
Troutdale, Ore. (609)	5	16	10 (4), 19
Rowena, Ore. (611)	5	12	10, 8+11 (4)
Mayer Pk., Ore. (612)	4	27	10 (3), 9+5
The Dalles, Ore. (613)	2	6	10
Biggs, Ore. (640)	10	55	10
Clark-Skamania Co. line Wash. (619)	3	20	10
Gilliam Co., Ore. (641)	1	2	10
Cape Horn, Wash. (646)	1	10	10
Lyle, Wash.	1	1	10
Bingen, Wash. (617)	6	30	10 (2), 14+10, ca.14+13, ca.18+9, ca.23+10
<u>oregana</u>			
Berthoud Pass, Colo. (BER)	1	3	ca.36

$n \approx 47$  (see Fig. 16D) and may be related to the Chehalis hybrid population or to S. oregana (Elvander, personal communication).

The chromosome counts for S. occidentalis var. occidentalis agree with the majority of earlier counts (Beamish 1961, Krause and Beamish 1972) of  $n=19$  for all populations sampled in the present study (Fig. 14A,B,D). Packer (1968) has reported a diploid  $n=10$  population from Blakeston Mt., Alberta and Elvander (1975) records two mixed diploid and tetraploid populations from Trapper Peak in the Bitterroot Mts., Montana and from the Storm Lake Pass in the Anaconda Range, Montana, where individuals apparently are intermediate between S. marshallii subsp. idahoensis and S. occidentalis var. occidentalis. Krause (Krause and Beamish 1972) has recorded higher numbers of  $n=28$  or ca. 29 for populations in Northern British Columbia and the mountains of Idaho.

Plants identified as S. occidentalis var. dentata (Hitchcock et al, 1973) were collected from four locations west of the Columbia River Gorge and toward the mouth of the Columbia River. Plants of the Coast Range of Oregon, including those from Saddle Mountain, Clatsop County, are diploid ( $n=10$ ) (Fig. 15C-E). Plants from Columbia County (EP606), Oregon, and Cowlitz Co., Washington (EP607), have 20 or sometimes 19 pairs of chromosomes (Fig. 15A,B). These tetraploids as well as other plants from the Willamette River Valley probably represent allotetraploid hybridizations between S. integrifolia var. claytoniifolia and diploid S. occidentalis var. dentata as judged by their morphological resemblance and the proximity of

Figure 11: Camera lucida drawing of pollen mother cells (PMC's). Nucleolar organizers are grey circles. Drawings here are from four plants in one population along the Columbia River Gorge. Parts D and E are from the same plant.

A=PMC at diplotene-diakinesis; S. rufidula (EP610) n=20

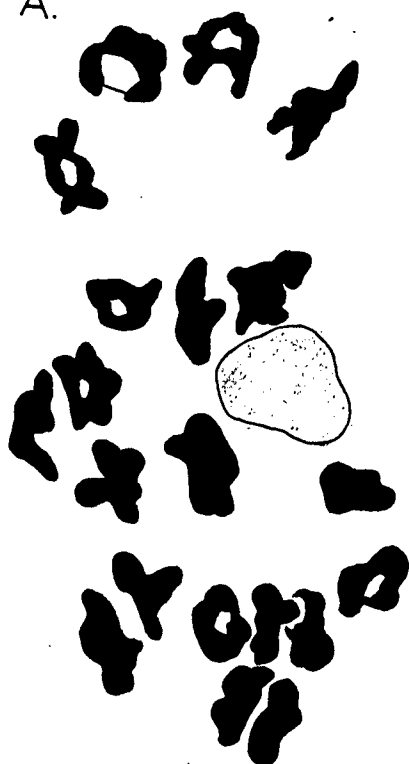
B=PMC at diplotene-diakinesis; S. rufidula (EP610) n=19

C=PMC at diakinesis; S. rufidula (EP610) n=19

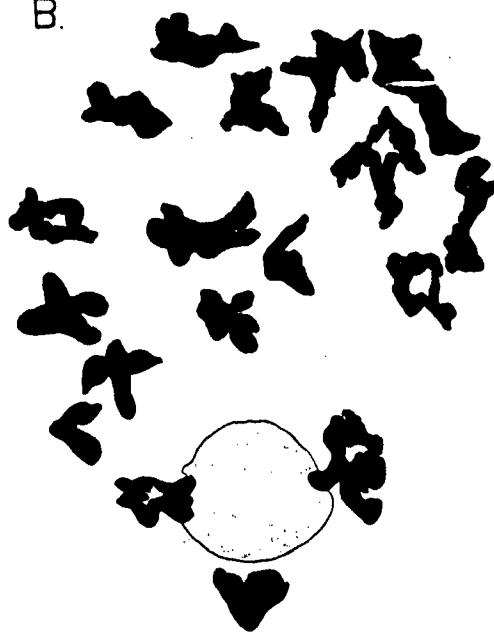
D=PMC at diplotene-diakinesis; S. rufidula (EP610) n=10

E=PMC at metaphase II; S. rufidula (EP610) n=10, each daughter cell.

A.



B.



C.



10μ

A horizontal scale bar with vertical end caps, labeled "10μ".

D.



E.



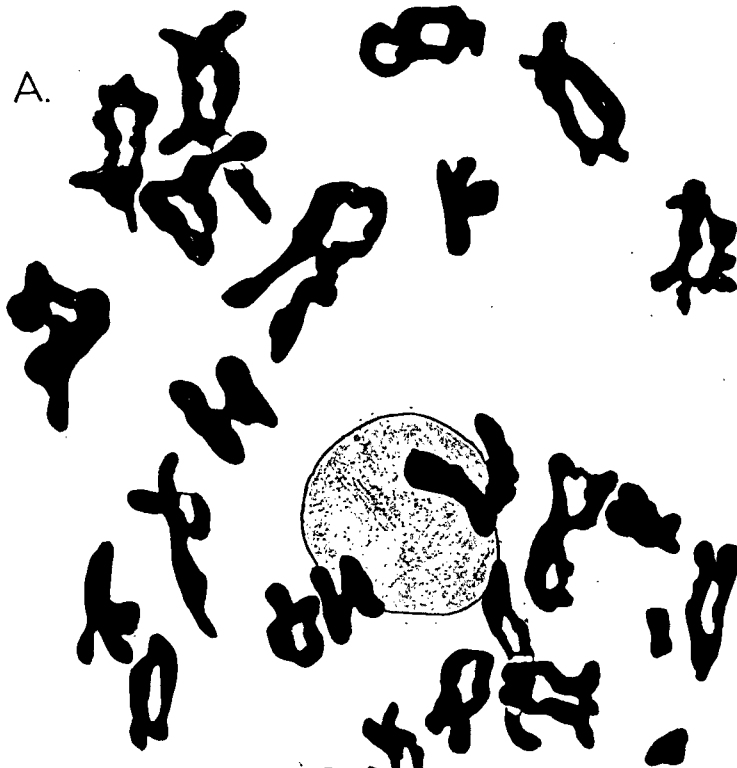
Figure 12: Camera lucida drawings of PMC's. Saxifraga rufidula plants from the Troutdale population.

A=PMC at diplotene-diakinesis; S. rufidula (EP608-16) n=ca. 27 bivalents + 2 univalents in the lower left

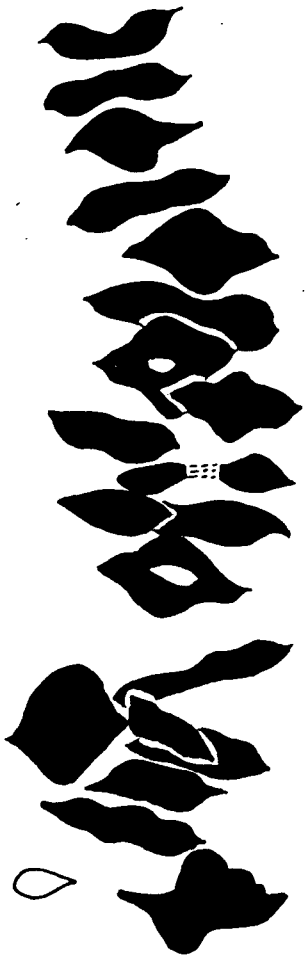
B=PMC at metaphase I; S. rufidula (EP608-24) n=ca. 20 bivalents + 1 univalent

C=PMC at diplotene; S. rufidula (EP608-26) n=29

A.



B.



C.

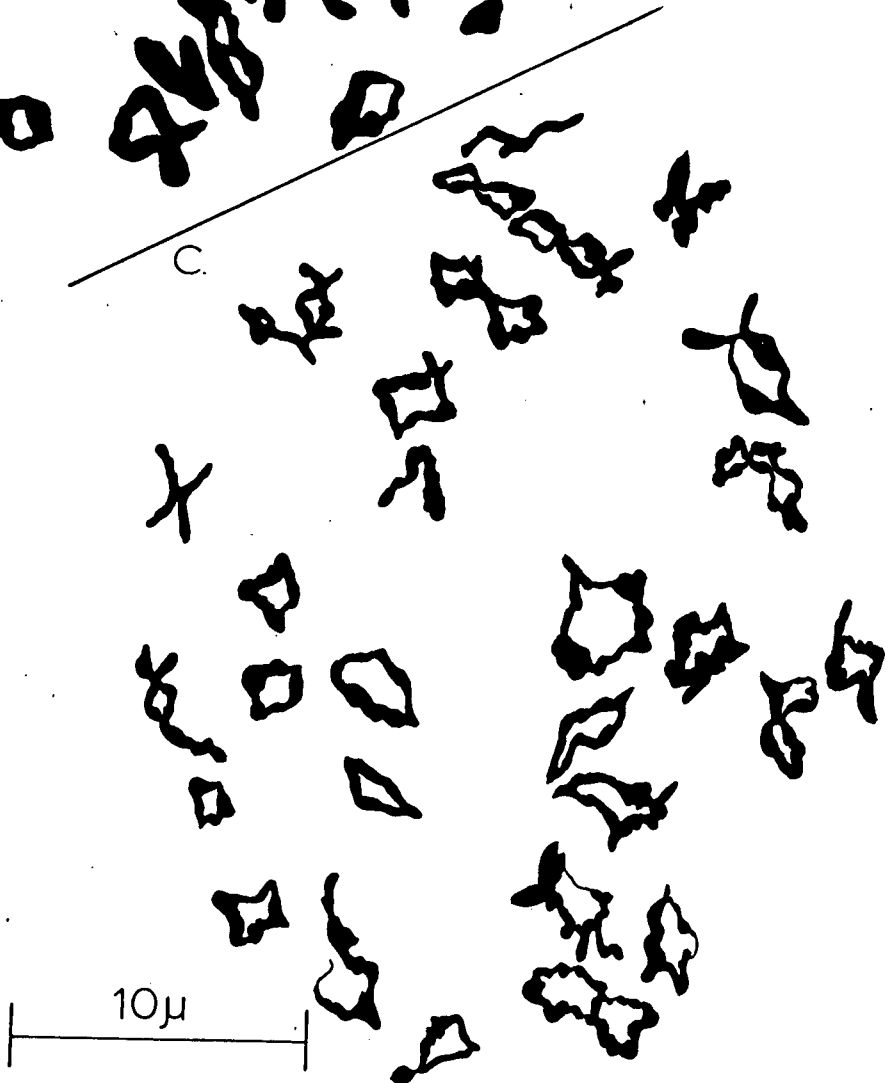


Figure 13: Camera lucida drawings of PMC's. Cryptic hybrid plants from Troutdale (A,B) and Chehalis River (C,D).

A=PMC at late metaphase I; S. rufidula-cryptic hybrid (EP608-14) n=ca.19 bivalents + 13 univalents (2 bivalents in upper right possibly multivalents?)

B=PMC at late metaphase I; S. rufidula cryptic hybrid (EP608-5) n=ca.19 bivalents + 12 univalents

C=PMC at diplotene-diakinesis; S. occidentalis- var. occidentalis hexaploid hybrid (EP605-12) n=29

D=pollen grain mitosis; metaphase; S. occidentalis- var. occidentalis hexaploid hybrid (EP605-26) n=29





Figure 14: Camera lucida drawings of PMC's. Plants from Yale, Mt. Baker and Cornwall populations of S. occidentalis var. occidentalis and Mt. Finlayson population of S. rufidula. Upper scale is for cells A-C, lower scale is for cells D and E.

A=PMC at diplotene-diakinesis; S. occidentalis var. occidentalis (EP626) n=19

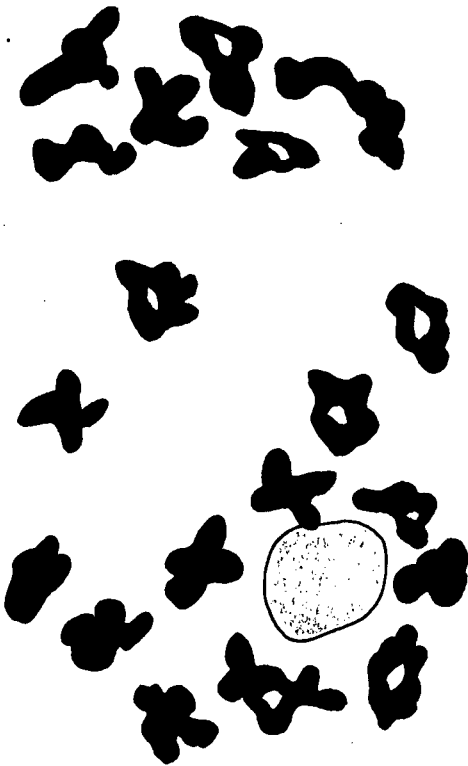
B=PMC at metaphase I; S. occidentalis var. occidentalis (BAKER) n=19

C=PMC at diplotene-diakinesis; S. rufidula (EP627) n=10

D=PMC at metaphase I; S. occidentalis var. occidentalis (EPCORN) n=19

E=PMC at metaphase I; S. rufidula (EP618-17) n=19

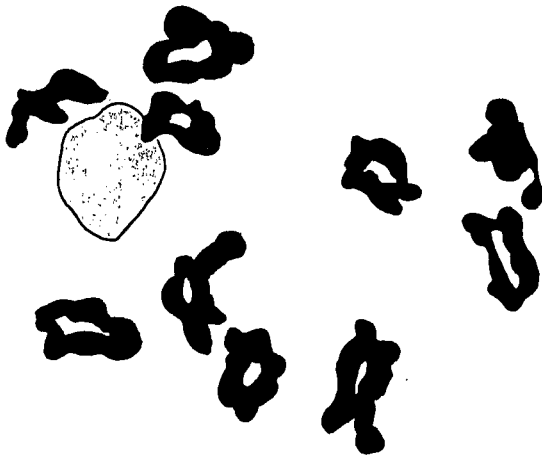
A.



B.



C.



10μ

D.



10μ

E.



Figure 15: Camera lucida drawings of PMC's. S. occidentalis var. dentata plants from Kalama River, Delena, Tilamook, and Saddle Mountain.

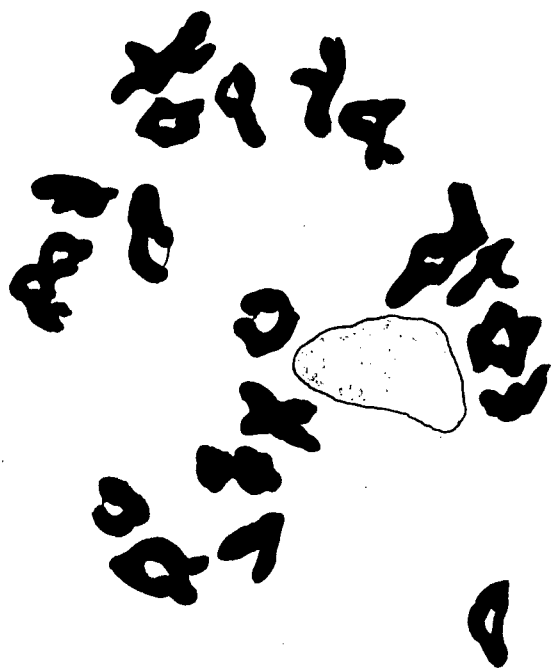
A=PMC at diplotene-diakinesis; S. occidentalis var. dentata tetraploid (EP607) n=19

B=PMC at diplotene-diakinesis; S. occidentalis var. dentata tetraploid (EP606-24) n=20

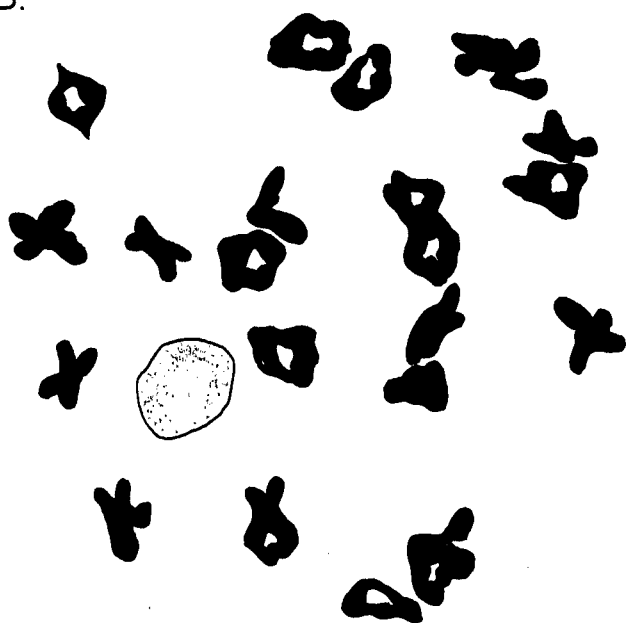
C=PMC at diplotene-diakinesis; S. occidentalis var. dentata diploid (EP630-25) n=10

D,E=PMC at diakinesis and diplotene-diakinesis; S. occidentalis var. dentata-diploid (EP629A-25) n=10

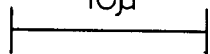
A.



B.



10μ



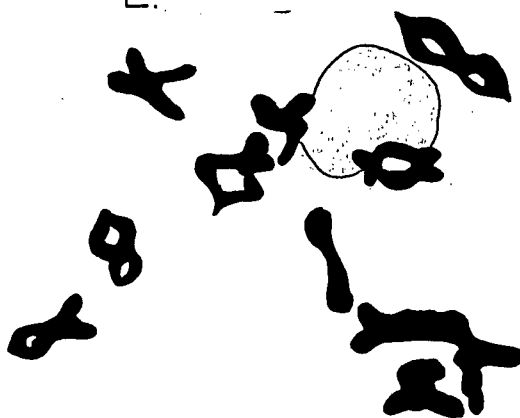
C.



D.



E.



S. integrifolia var. claytoniifolia plants. However, some of the S. occidentalis var. dentata plants from the Willamette River intergrade in features such as clavate filaments to S. marshallii subsp. marshallii but the filaments are less expanded and petal-like than those of S. marshallii subsp. marshallii.

Plants known as S. occidentalis var. latipetiolata (Hitchcock et al, 1973) from isolated peaks of the Northern Oregon Coast Range (Chambers 1974), were found to have a high number of chromosomes. Counts varied somewhat, with most being around 38 or 39 pairs (Fig. 16A,C). This corresponds with counts of S. oregana from Mt. Hood, Oregon ( $n=ca. 38$ , Elvander, personal communication) and from Berthoud Pass, Colorado ( $n=ca. 36$ ) (Fig. 17,A).

Saxifraga integrifolia has 19 chromosome pairs on the Lower Mainland of British Columbia, on Vancouver Island ( Fig. 16,B,E) and southward into Washington. Plants from the Columbia River Gorge and Upper Willamette River are more variable and further cytological studies are necessary to detect correlated chromosomal differences. At least some of the plants from the Columbia River Gorge have the 19-paired complement. Populations from the prairies south of Tacoma and Olympia Washington may be related to S. oregana and one individual had a high number of chromosomes ( $2n=ca. 47,51$ ) (my counts, Fig. 16,D and Elvander, personal communication).

Saxifraga integrifolia var. claytoniifolia populations have been repeatedly counted as diploids with 10 chromosome pairs (Fig. 17,B-F). One 19-paired individual was recovered from

the otherwise 10-paired population at Troutdale, Oregon. Plants from near Bingen, Washington were mostly sterile hybrid forms with abnormal meiosis although a few 10-paired individuals were found. Further cytological and morphological analyses of the Eastern Columbia River Gorge populations are necessary to unravel the complicated relationships between these plants and the closely related S. integrifolia var. integrifolia and S. integrifolia var. leptopetala which also occur there. Northward in its range S. integrifolia var. leptopetala has 19 pairs of chromosomes but populations from the Eastern Columbia River Gorge may be more complex chromosomally where they intergrade with S. integrifolia var. claytoniifolia and S. integrifolia var. integrifolia.

In Saxifraga close diploid relatives with 9 chromosome pairs are notably absent from literature reports and from the present study. The lack of such entities in nature argues against the production of 19-paired plants directly from chromosome doubling of a hybrid between 10 and 9-paired parental plants. A more plausible hypothesis for the 10,19,20,28,29,38 polyploid-aneuploid sequence based on the available evidence is that 10-paired progenitors gave rise to polyploid offspring with 20 pairs of chromosomes followed by subsequent loss of a chromosome pair. Some pairing instability is apparent in one 20-paired population of S. occidentalis var. dentata which may be an indication that it is of recent origin and may eventually conform to the 19-paired polyploid-aneuploid pattern found in many populations of the other taxa. Contact and crossing between 19 and 10-paired plants followed by doubling of chromosome

Figure 16: Camera lucida drawings of PMC's of S. occidentalis var. latipetiolata and S. integrifolia plants.

A=PMC at diplotene-diakinesis; S. occidentalis var. latipetiolata (EP629C) n=ca. 38

B=PMC at metaphase I; S. integrifolia var. integrifolia (EP617B) n=19

C=PMC at early metaphase I; S. occidentalis var. latipetiolata (EP629C) n=38

D=PMC at diakinesis; S. integrifolia-S. oregana? (EPMIMA) n=ca. 47

E=PMC at diakinesis; S. integrifolia var. integrifolia (EPNMO-I) n=19



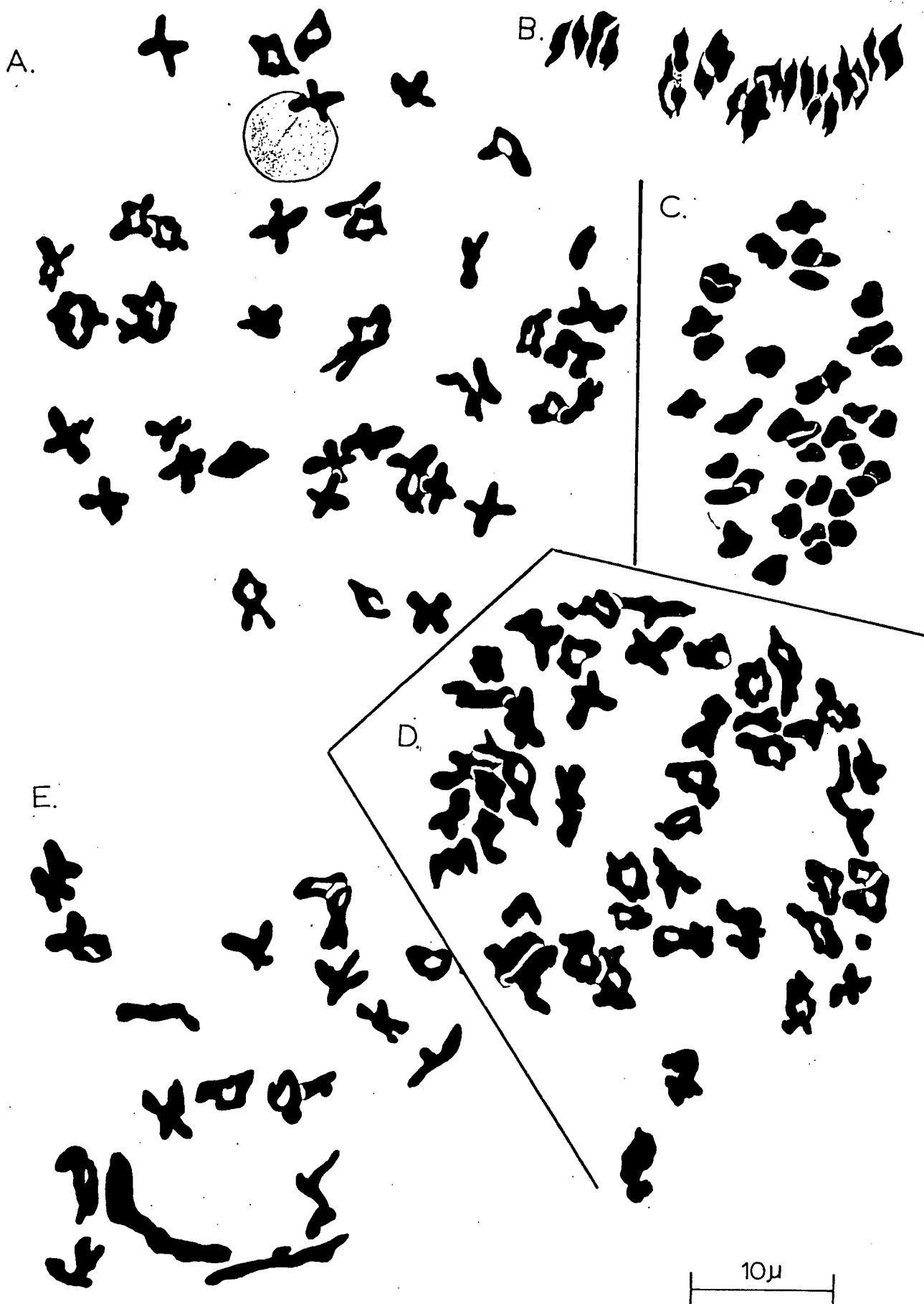


Figure 17: Camera lucida drawings of PMC's. Plants from Berthoud Pass, The Dalles, Lyle, Bingen, Troutdale, and Rowena populations. The upper scale is for cells A-C, the lower scale is for cells D-F.

A=PMC at anaphase I; S. oregana (EPBER) n=ca. 36

Upper pole shows 34 bodies of which at least 2 are overlapping.

lower pole shows 35 bodies of which at least 2 are overlapping.

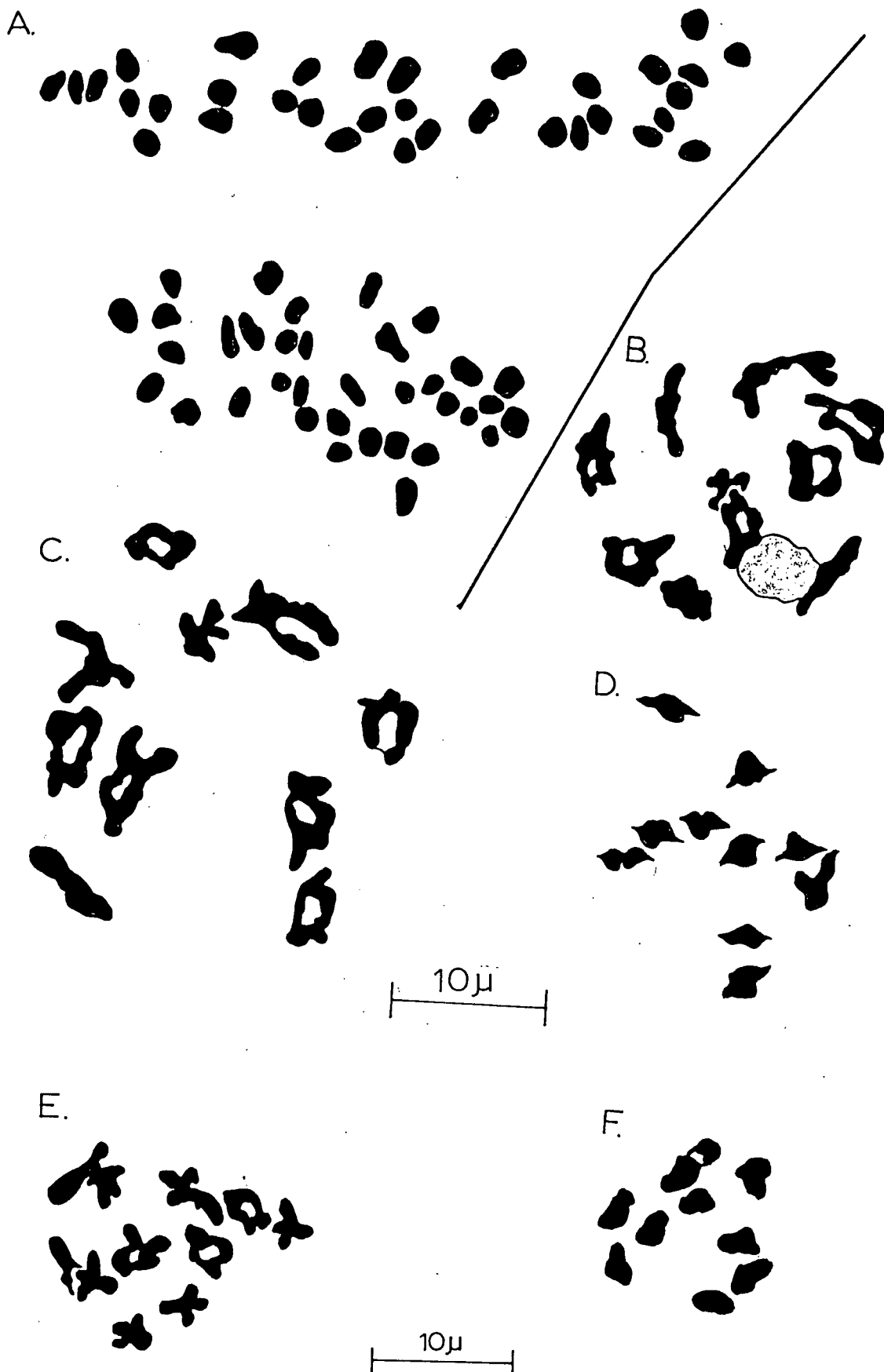
B=PMC at diplotene-diakinesis; S. integrifolia var. claytoniifolia (EP613-34) n=10

C=PMC at diakinesis; S. integrifolia var. claytoniifolia (EP668-14) n=10

D=PMC at metaphase I; S. integrifolia var. claytoniifolia (EP617-21) n=10

E=PMC at diakinesis; S. integrifolia var. claytoniifolia (EP609-310) n=10

F=PMC at late diakinesis; S. integrifolia var. claytoniifolia (EP611) n=10



number produced 29-paired populations, and the  $n=28$  counts may be further aneuploid reductions. Probably counts of 38 pairs represent hybrid combinations of two 19-paired entities or combinations involving diploid and hexaploid components.

Although the polyploid processes in this group appear to involve mostly allopolyploidy, the possibility of autopolyploidy cannot be eliminated. Reports in S. reflexa (Krause and Eamish 1973) where diploids, tetraploids, and hexaploids were found in one population seem to indicate that autopolyploidy occurs in related taxa. Moore (1959) and Taylor and Mulligan (1968) report an apparently autopolyploid derivation for populations of S. taylora, an endemic to the Queen Charlotte Islands and the Brooks Peninsula on Vancouver Island, British Columbia.

#### Hybridization

Most artificial F1 hybrids among S. rufidula, S. occidentalis var. occidentalis, S. occidentalis var. dentata, and S. integrifolia, are generally morphologically intermediate between the two parental entities (Fig. 4-8). However, the multivariate computer analyses placed certain hybrids closer to their polyploid parents than to their diploid parents, especially S. integrifolia and S. occidentalis (Fig. 19-21). Pollen fertility of hybrids is summarized in Table IV.

Artificial hybridizations were successful among all combinations of taxa which were attempted (Fig. 22). Differences in seed set per attempt possibly reflects variations brought about by inefficient crossing techniques as well as small sample

sizes. Similar variation in seed germination rates (.18-.90) may be the result of difficulties in assessment of seed maturity, improper germination conditions, or small sample sizes. Apparently it is possible to obtain F1 hybrids from crosses among most plants in this related group without difficulty.

The artificial F1 hybrids which survived to maturity demonstrated various meiotic behaviours. Bivalent formation was restricted to a fraction of the genome and multivalents were absent in nearly all crosses (Fig. 18). A possible exception is the cross between S. rufidula (n=19) and S. occidentalis var. latipetiolata (n=38) where larger figures, possibly multivalent associations, could be seen in some cells. Bivalent formation was high (15-19 pairs), possibly indicating that S. occidentalis var. latipetiolata had a hybrid origin involving tetraploid S. rufidula. The morphological affinities and ploidy level (n=ca. 38) of S. occidentalis var. latipetiolata suggest that S. oregana (n=19?, ca. 36, ca. 38) was probably the other parent.

Analysis of meiosis in artificial intervarietal and interspecific crosses indicates that there has been considerable genomic divergence among the taxa. When diploid S. rufidula is crossed to tetraploid S. occidentalis, the resultant hybrid has 10 or fewer bivalents. Hybrids between S. rufidula (n=19) and S. occidentalis var. occidentalis (n=19) produced about 9 bivalents indicating that they have only a partial chromosome complement in common (Fig. 18,C). In contrast, the cross between S. occidentalis var. occidentalis and S. occidentalis var. dentata (n=20) produced F1 individuals which were almost completely sterile and failed to undergo meiotic division. When

S. rufidula (n=10) is crossed with S. integrifolia (n=19) usually 10 or fewer bivalents are formed (Fig. 18). The resultant hybrids closely resemble the sterile intermediates found in many field situations (see Fig. 6). The cross between S. occidentalis var. latipetiolata and polyploid S. rufidula produced several vigorous F1 hybrids which had a higher pollen fertility than other artificial hybrids (Table IV). Occasionally an artificial F1 hybrid deviated entirely from either parental or intermediate morphologies (Fig. 19-21, plant no. 3\*). Crosses between S. integrifolia and S. integrifolia var. leptopetala resembled S. integrifolia in petal characteristics and had from 6 to nearly 19 bivalents but even in the higher pairing individuals anaphase abnormalities produce highly sterile pollen. S. rufidula x S. occidentalis F1 hybrids resembled S. occidentalis in inflorescence shape and size (see Fig. 4). Although biological relationships and affinities may be elucidated by hybridization experiments, taxonomic decisions in this group probably should be based on the more pragmatic similarities and discontinuities of morphological and morphometric data.

Since all possible crosses were not completed (Fig. 22), many aspects of the hybrid relationships are as yet unclear. Even if all hybrids were available for analysis considerable caution in interpretation would be necessary in light of literature reports that in wheat, oats, rye, and others, homeologous pairing is under genetic control (Riley 1960, Riley and Law 1965, Rajhathy and Thomas 1972, Hossain 1977) and that bivalent or multivalent formation may be a function of the

Figure 18: Camera lucida drawings of PMC's from artificial hybrids. The upper scale is for cells A-B, the lower scale is for cells C-D.

A=PMC at metaphase I; S. occidentalis var. latipetiolata x S. rufidula tetraploid n=ca.18 bivalents + 14 univalents

B=PMC at late metaphase I; S. rufidula diploid x S. integrifolia var. integrifolia n=ca.7 bivalents + 14 univalents

C=PMC at metaphase I; S. rufidula tetraploid x S. occidentalis var. occidentalis n=ca.9 bivalents + ca.19 univalents

D=PMC at metaphase I; S. occidentalis var. dentata tetraploid x S. rufidula diploid n=ca.10 bivalents + 10 univalents

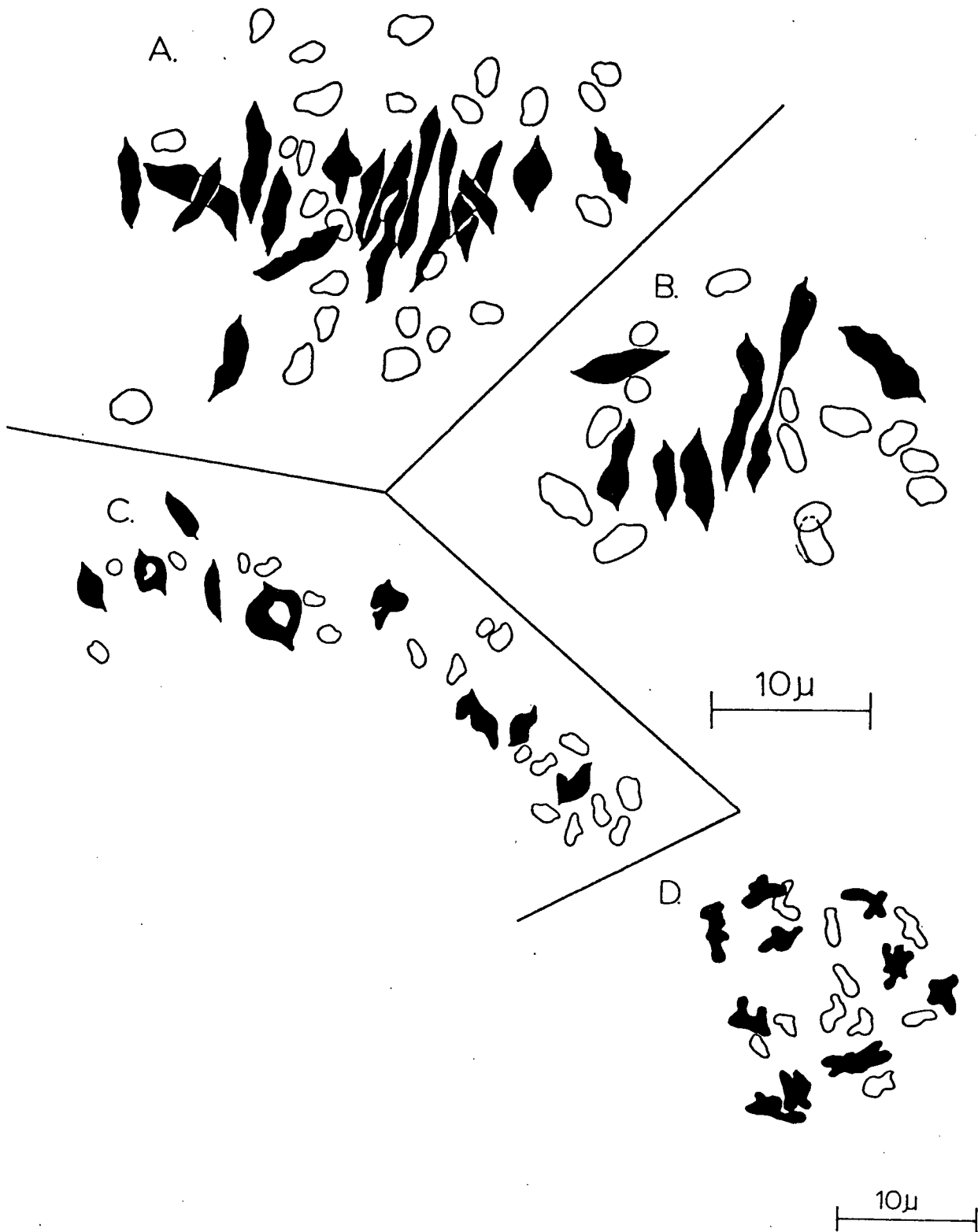




Figure 19: Principal components analysis graph of axis one vs. two showing artificially produced hybrid individuals and representative parental populations.

Symbols are as follows:

- D= S. occidentalis var. dentata
- I= S. integrifolia var. integrifolia
- L= S. occidentalis var. latipetiolata
- o= S. occidentalis
- R= S. rufidula (from Vancouver Island and the Olympic Mountains)
- r= S. rufidula (from the Columbia River Gorge)
- 1= S. rufidula (R) x S. integrifolia (I)
- 2= S. rufidula (R) x S. occidentalis (o)
- 3= S. occidentalis (o) x S. occidentalis var. dentata (D)
- 4= S. rufidula (R) x S. occidentalis var. dentata (D)
- 5= S. rufidula (r) x S. occidentalis var. dentata (D)
- 6= S. rufidula (R) x S. occidentalis var. latipetiolata (L)

3\* occupies a point to the right of its placement within the plot. It is probably an aberrant individual. The percentage of the total variance accounted for by the first three axes is 21.36, 11.73, and 7.87 percent respectively.

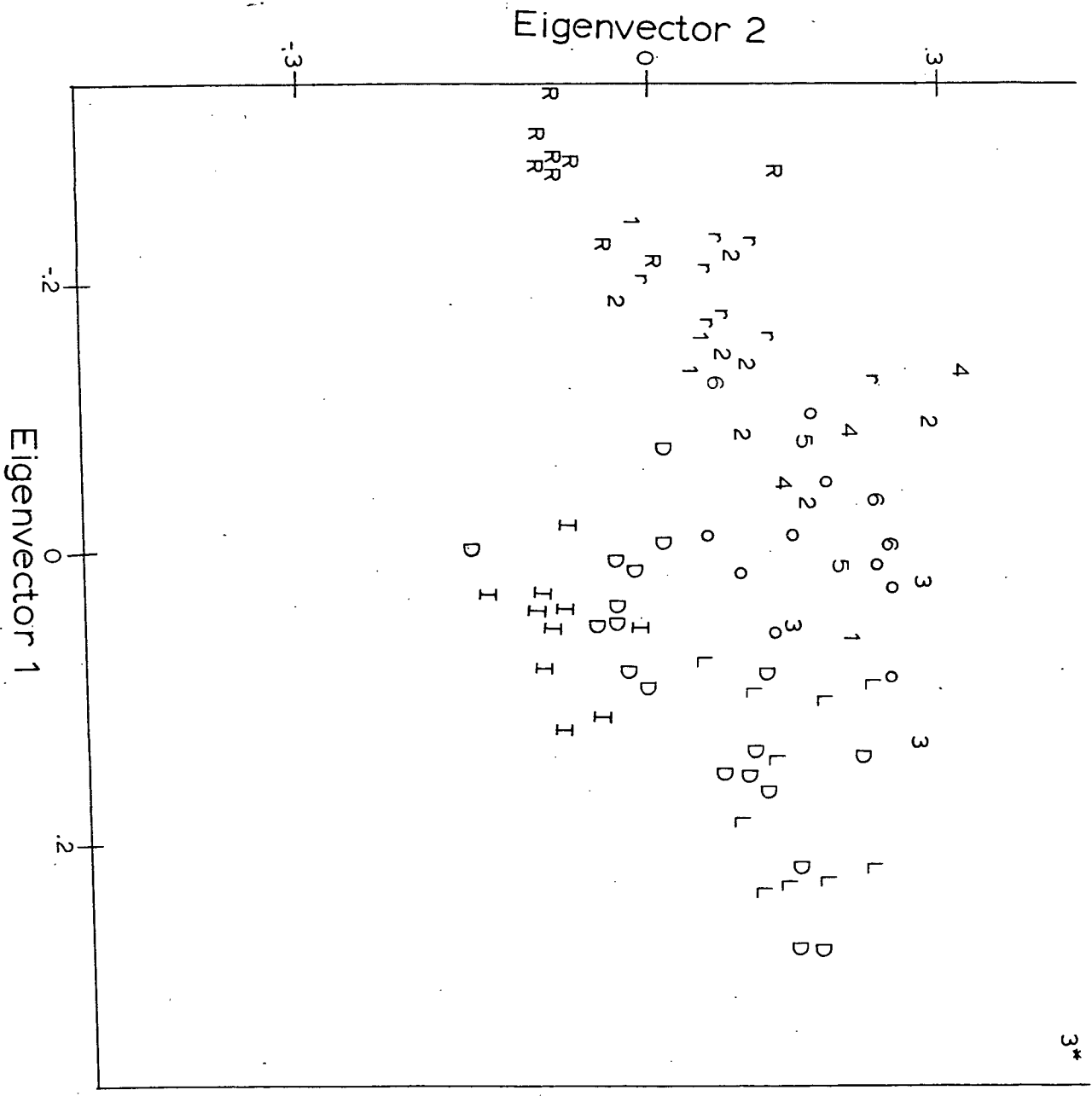


Figure 20: Principal components analysis graph of axis one vs. three showing artificially produced hybrid individuals and representative parental populations. Symbols and total variance figures are as in Figure 19.

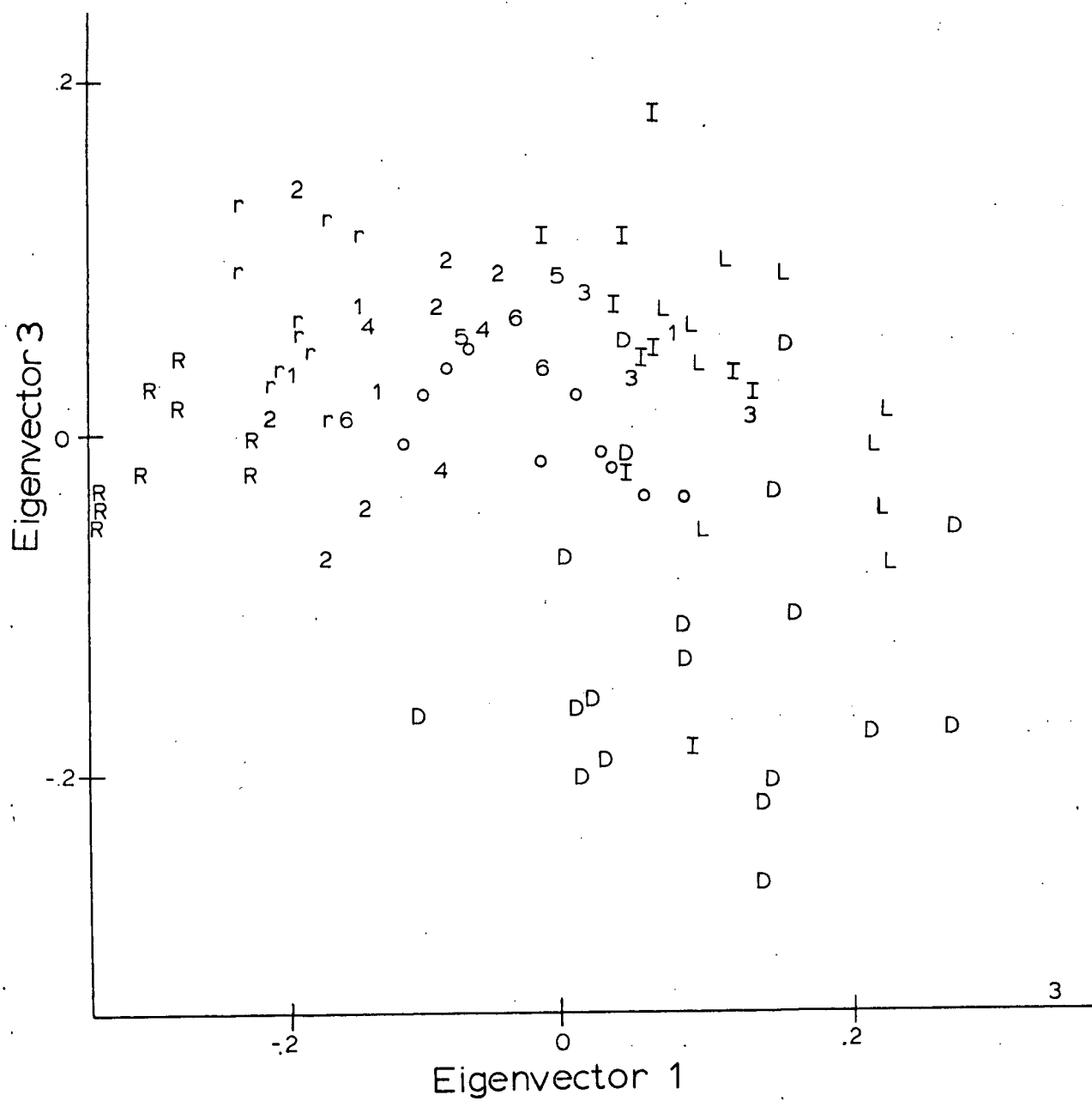


Figure 21: Principal components analysis graph of axis two vs. three showing artificially produced hybrid individuals and representative parental populations. Symbols and total variance figures are as in as in Figure 19. The actual point for hybrid plant 3\* lies further to the lower right corner than drawn here.

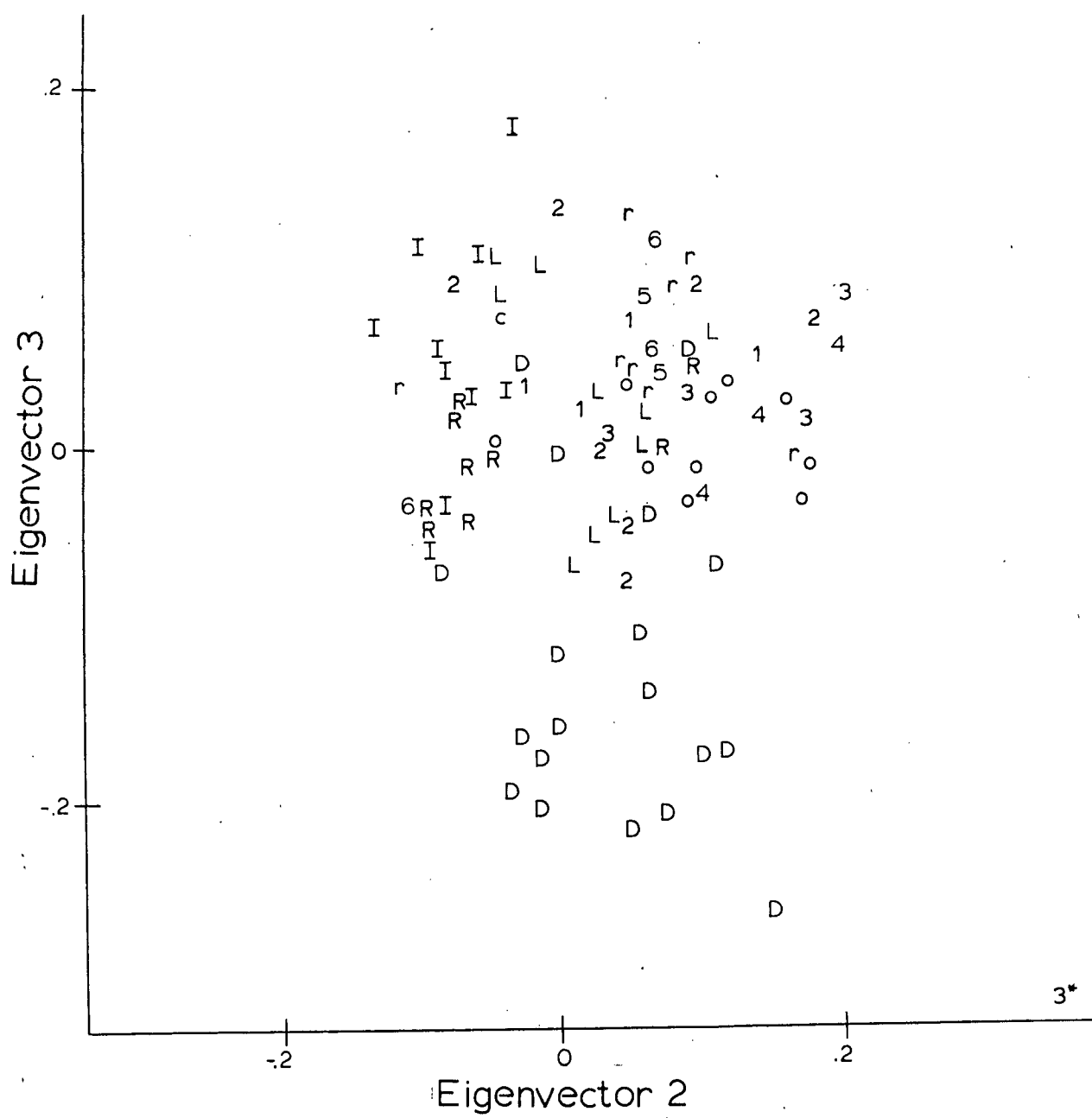


Figure 22: Crossing success chart for the taxa considered in the present study. Line number and thickness indicates relative success of seed set. Numbers outside the hexagons are the haploid chromosome number. Numbers adjacent to the lines are the average number of seeds set per attempt. Numbers inside parentheses are total seed set followed by number of crossing attempts. Letters represent as follows: D=S. occidentalis var. dentata, L=S. occidentalis var. latipetiolata, O=S. occidentalis var. occidentalis, and B=S. rufidula. The absence of connecting lines indicates that those crosses were not attempted.

# Crossing Ability

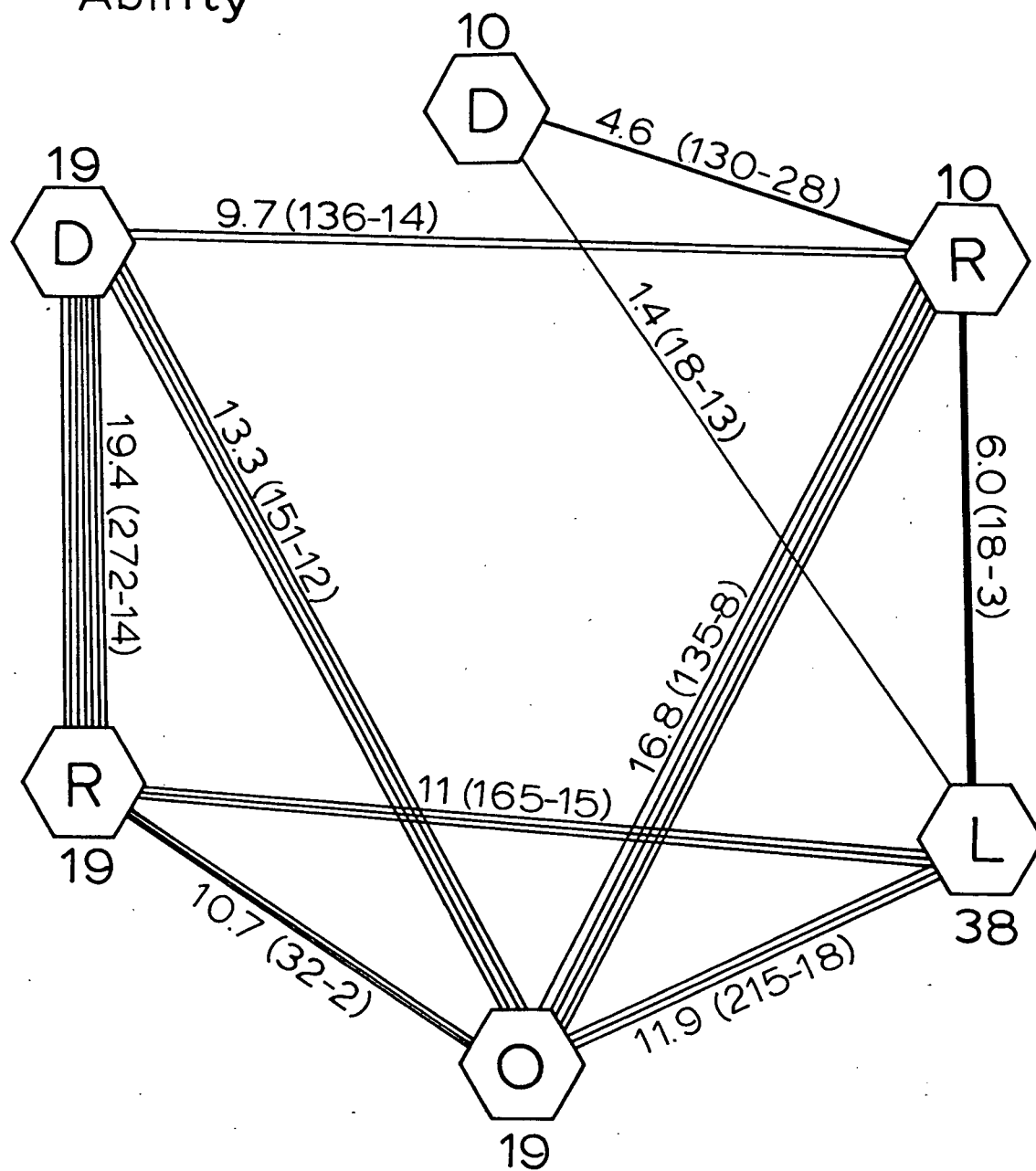




Table IV.  
Hybrid Pollen Fertility.

<u>Cross Between:</u>	<u>No.</u> <u>Individuals</u>	<u>Average</u> <u>% Fertility</u>	<u>Range</u> <u>% Fertility</u>
ruf. (10) x occ. (19)	4	9.9	(0.8-24.0)
ruf. (19) x occ. (19)	4	19.9	(4.1-33.1)
ruf. (10) x dent. (19)	3	37.1	(0.7-73.4)
ruf. (19) x dent. (19)	1	1.0	(1.0)
occ. (19) x dent. (19)	3	3.0	(0.0-8.2)
lati. (ca. 38) x ruf. (19)	3	31.0	(2.3-78.5)
int. (19) x ruf. (10) *	4	2.4	(0.0-4.6)
int. (19) x lept. (19) *	2	1.8	(1.7-1.9)

\* These crosses were made earlier by K.I. Beamish and are included here for comparison. Varietal names are abbreviated to the first three or four letters. Numbers in parenthesis indicate haploid number.

presence of certain genes or gene combinations. Furthermore, numerous authors have shown that meiotic events in anther tissue can be environmentally modified (Skovsted 1934, Sax 1937, Singh 1975, Beamish 1961). Ornduff (1969) has presented several cases which argue against rigid species definitions based on crossability and/or interfertility in plant hybridization studies.

Naturally occurring hybrids between locally sympatric S. rufidula and S. integrifolia var. integrifolia on Vancouver Island and in places along the Columbia River Gorge can be tentatively recognized by their intermediate morphology which resembles the artificially produced hybrid (Fig. 6), abnormal meiosis, and their high degree of pollen sterility.

Hybrid intermediates consistently fail to set good seed but are vegetatively vigorous and may exist in nature for many years. Artificial F1 hybrids between S. rufidula and S. integrifolia have flourished under cultivation in the cold frames at the University of British Columbia for 12 years. Judging from a large population south of Nanaimo, B.C., sterile intermediate individuals are, in nature, usually rare in comparison to their parental entities. Only about 30 putative hybrids were seen compared to about 3,000 S. rufidula plants and considerably more S. integrifolia var. integrifolia individuals. In other populations, somewhat aberrant individuals resembling S. rufidula in habitat and morphology are perhaps more common.

The exact nature of hybrid relationships is much more difficult to determine in the Columbia River Gorge area where

S. rufidula and up to three varieties of S. integrifolia may occur in close proximity. Variability in levels of ploidy within populations of S. rufidula as well as S. integrifolia var. claytoniifolia also confound precise determinations of hybrid origins. Individuals which are morphologically close to one or the other of the parental entities may prove to be meiotically irregular and pollen sterile. Samples for certain Columbia River Gorge locations, notably the S. integrifolia population near Bingen, Washington, contain a large proportion of these cryptic hybrids.

Judging from herbarium material, hybrid swarms are common in several areas. Wilhelm Suksdorf in 1916 made a mass collection of one such area of Eastern Washington near Spokane and Spangle where putative S. occidentalis (or S. marshallii subsp. idahoensis) x S. integrifolia var. leptopetala (or var. columbiana?) hybrids were found. Parental plants were either rare or inadequately collected. Many of the putative hybrid plants had reduced pollen fertility as well as being somewhat intermediate in appearance. Another area with high numbers of putative hybrid individuals between S. occidentalis var. occidentalis and S. integrifolia var. leptopetala is the Petes Point area of the Wallowa Mountains of northeastern Oregon. Hybrid swarms probably involving S. integrifolia var. claytoniifolia and S. marshallii subsp. marshallii have been recorded for the Mary's Peak area of the Coast Range and Upper Willamette region of western and central Oregon. In these areas short-term hybrid fitness, longevity, vegetative reproduction, and large areas of possibly intermediate habitat may explain the

apparent abundance of hybrid forms and scarcity of parental forms.

Fertile polyploid populations of probable hybrid origin are common in several locations in the Lower Columbia River area. Two tetraploid populations of S. occidentalis var. dentata which conform to Engler and Irmischer's (1916) description and which are near the type locality for S. occidentalis var. dentata, are morphologically intermediate between diploid Coast Range S. occidentalis var. dentata and S. integrifolia var. claytoniifolia (Fig. 23). These resemble the type specimens of S. occidentalis var. dentata from Elk Rock, near Oswego, Clackamas County, Oregon (the first specimen cited in Engler and Irmischer 1916, is Heller 10059). Krause and Beamish (1972) have previously referred the Clatsop Co. Plants to S. occidentalis but synonymized S. occidentalis var. dentata with S. marshallii subsp. marshallii.

Introgression of S. integrifolia var. claytoniifolia characteristics into S. rufidula in the Columbia River Gorge can be seen by comparing S. rufidula plants from sympatric and non-sympatric sites (Fig. 24). Since the introgressant S. rufidula plants are also completely introgressant to S. occidentalis (Fig. 25) it is unclear whether intermediacy resulted from past hybridization between S. rufidula and S. occidentalis followed by the local extinction of S. occidentalis from the Columbia River Gorge area or is the result of the leakage of S. integrifolia genes, especially those of S. integrifolia var. claytoniifolia, into S. rufidula. The hybrid origin of S. rufidula in the Columbia River Gorge may

Figure 23: Scatter diagram showing introgression of certain characteristics between S. integrifolia var. claytoniifolia (squares) and tetraploid S. occidentalis var. dentata plants (circles). Diploid S. occidentalis var. dentata plants are triangles.

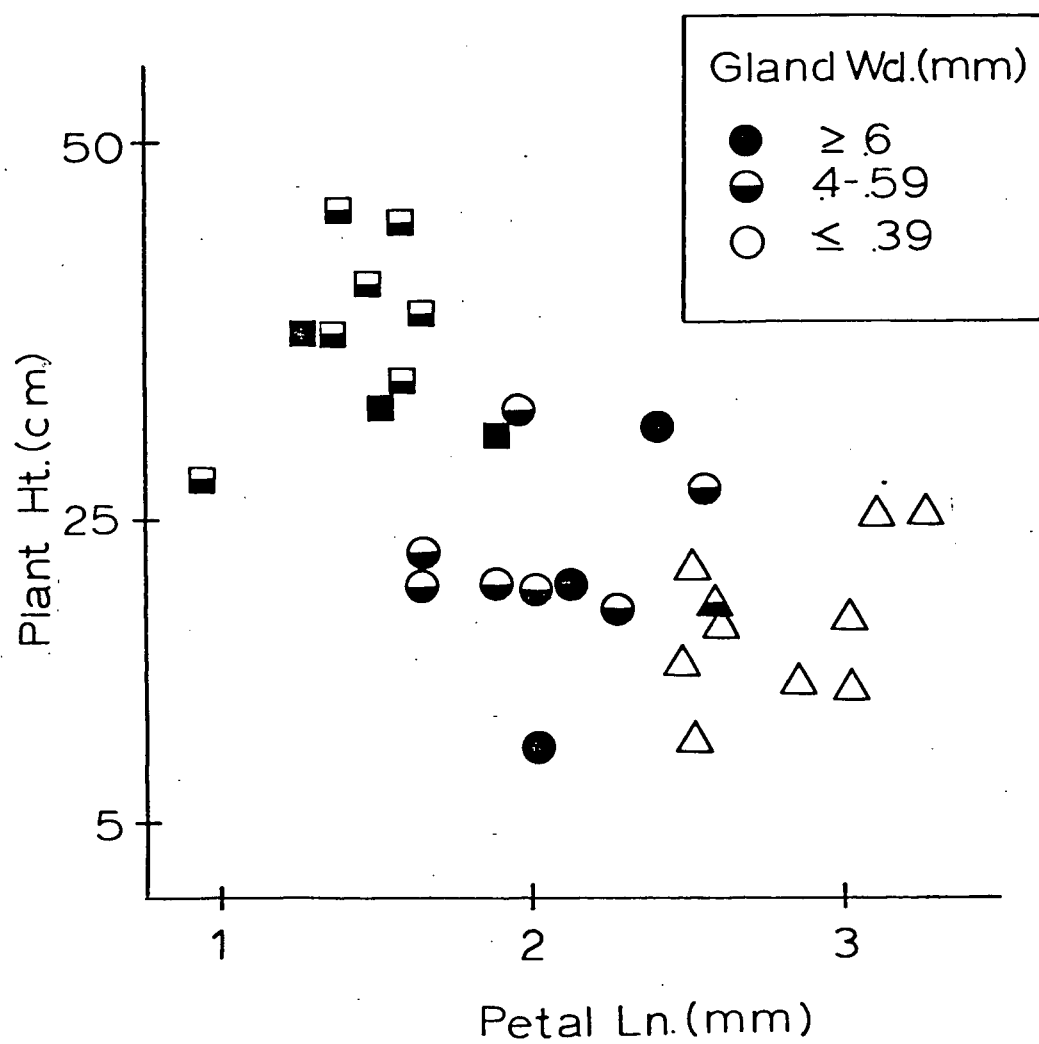


Figure 24: Scatter diagram showing introgression of characteristics between S. integrifolia var. claytoniifolia (squares) and sympatric S. rufidula (circles) individuals. Plants in lower right are S. rufidula plants from a nearby population which is not locally sympatric with S. integrifolia var. claytoniifolia (triangles) (EP608,609,610).

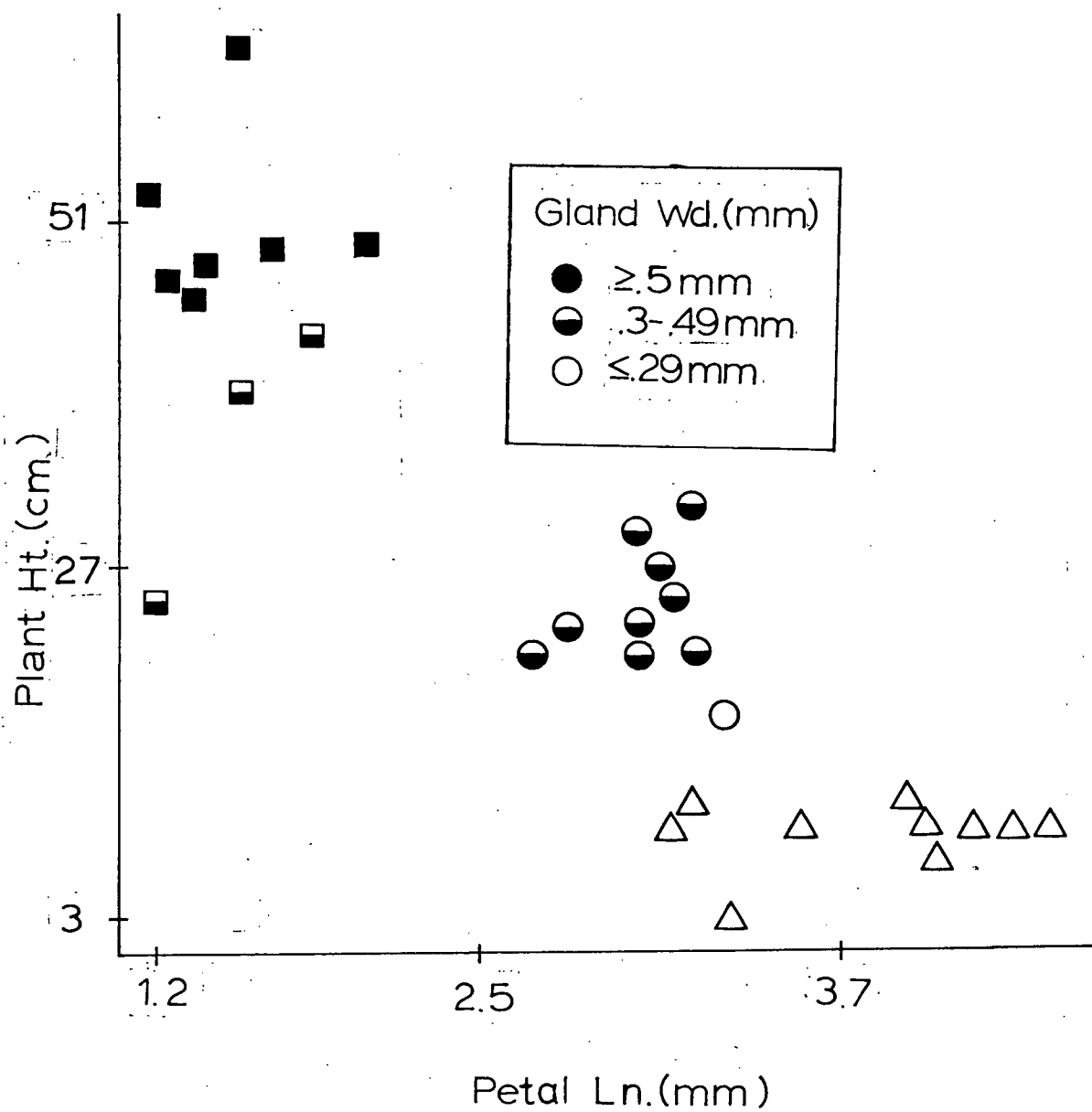
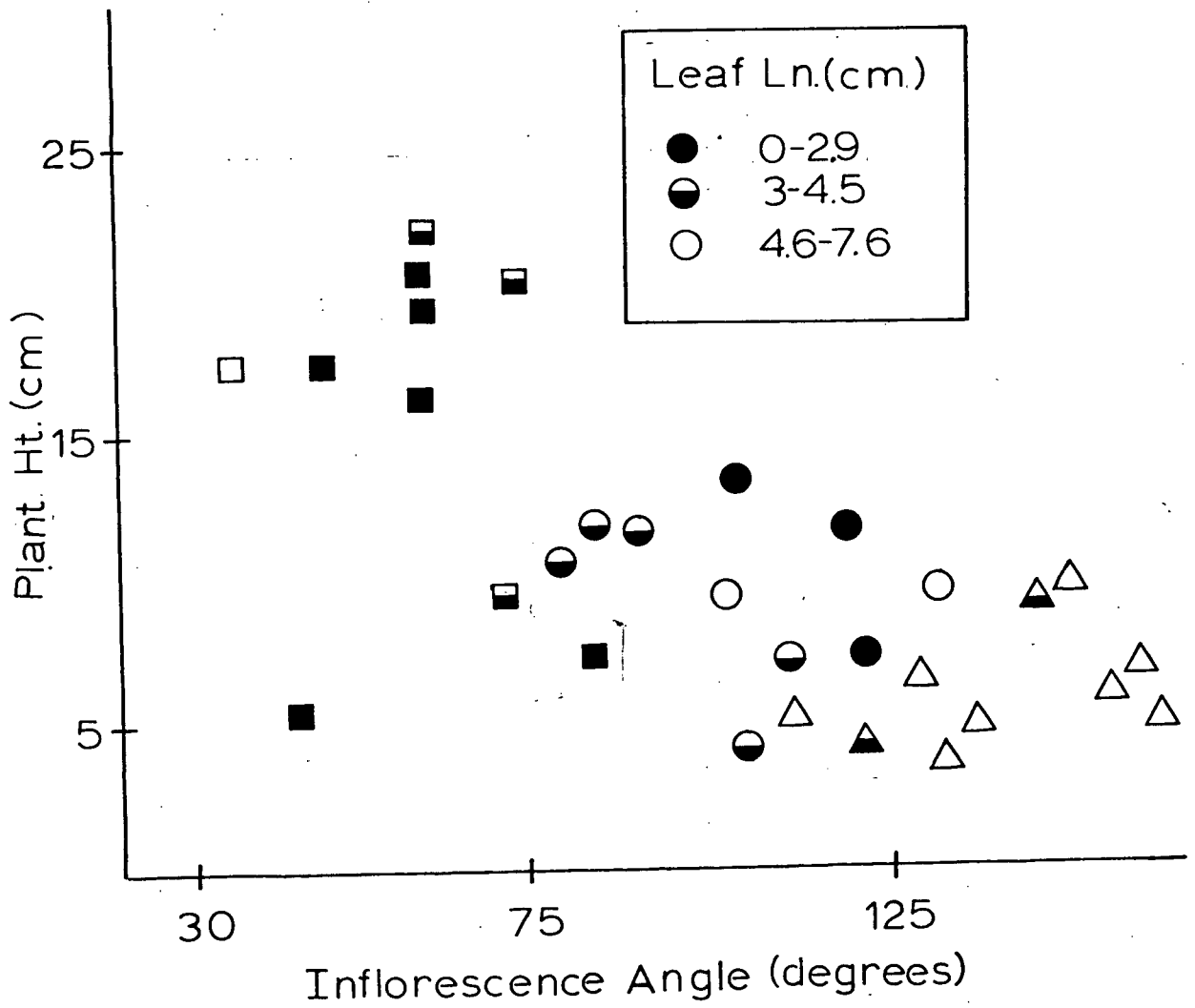




Figure 25: Scatter diagram showing intermediacy of certain characteristics between S. occidentalis var. occidentalis (squares, EP626, Yale, B.C.) and Columbia River Gorge S. rufidula plants (circles). Triangles represent presumably non-introgressant diploid S. rufidula plants from Vancouver Island.



have led to a secondary resemblance between S. rufidula and S. occidentalis. The more variable introgressant morphs of S. rufidula are mostly those of higher ploidy levels and thus have probably arisen via doubling of the chromosome complements of sterile hybrid individuals.

Variability within S. occidentalis var. dentata can be demonstrated to correlate with a higher ploidy level which probably reflects a hybrid origin. Tetraploids appear to be completely introgressant with S. integrifolia var. claytoniifolia (Fig. 23). Scatter diagrams in this group are perhaps less useful than multivariate analyses as tools to document introgression since they utilize a rather small number of characteristics.

Further evidence of introgression is provided by both Principle Components Analysis and Stepwise Discriminant Function programs. The programs show that the Columbia River Gorge S. rufidula plants are more variable than diploid S. rufidula populations from Vancouver Island and the Olympic Mountains. The Columbia River plants also form intermediate spatial relationships between the S. occidentalis or S. integrifolia groups and the Vancouver Island S. rufidula groups (see Fig. 27, 28, 30-35). The latter are apparently not introgressant with either sympatric S. integrifolia var. integrifolia or allopatric S. occidentalis var. occidentalis.

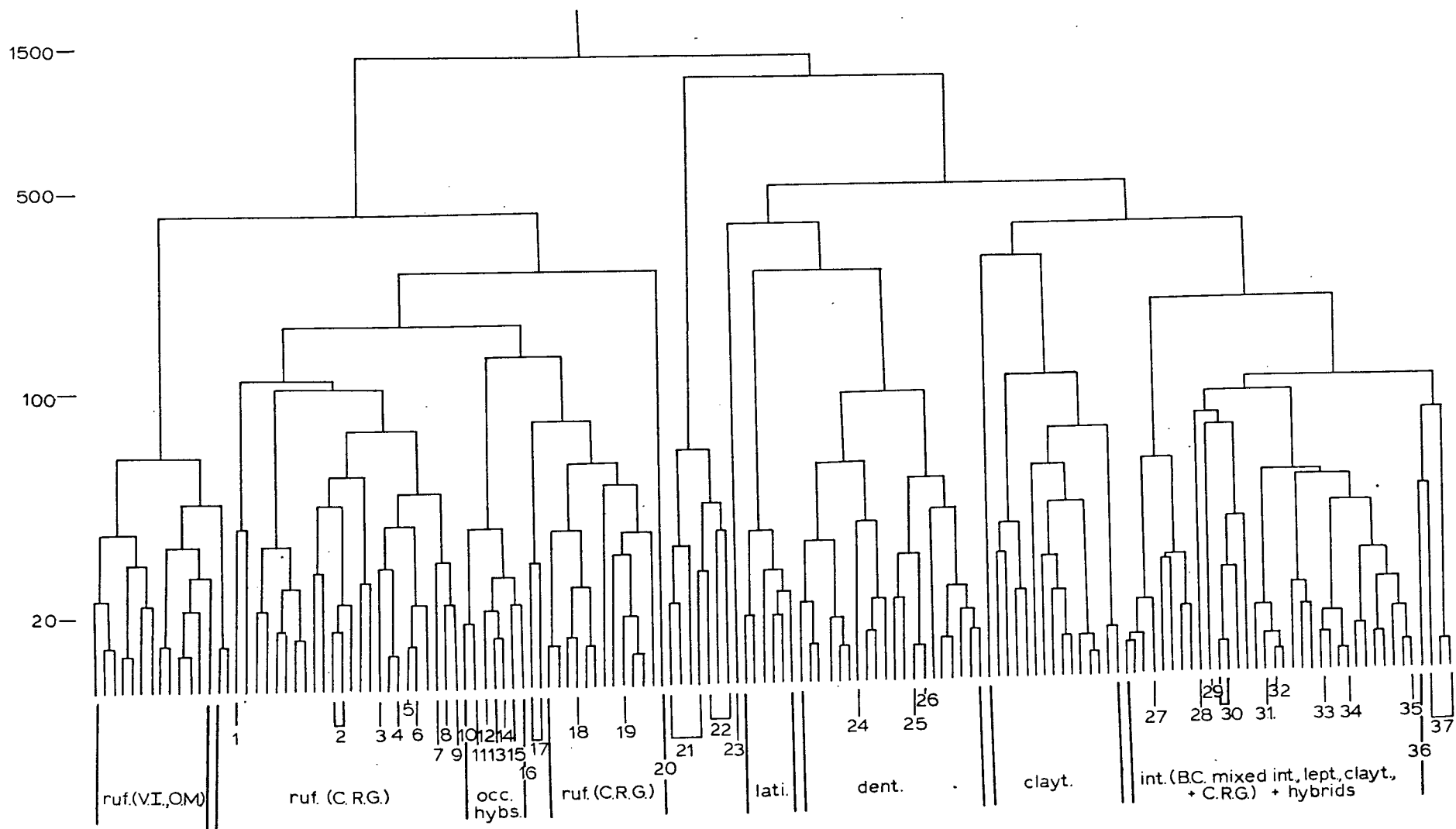
## Numerical Studies

Identification of major groups and populations was possible using the hierarchical clustering program called UBC-CGROUP. Relationships among larger groups in the phenogram (Fig. 26) were similar regardless of whether artificial hybrids are included or excluded from the analysis with the exception that all S. integrifolia plants group together at greater levels of similarity in the absence of hybrids. Artificial hybrids were usually clustered within one parental group although a few clustered independently or with a nonparental group. S. rufidula separated into northern and Columbia River Gorge populations while S. occidentalis grouped with the larger body of S. rufidula plants for the Columbia River Gorge. Diploid S. rufidula populations clustered together as a group with phenetic similarity to their Columbia River Gorge counterparts. It is interesting that S. occidentalis var. dentata and S. occidentalis var. latipetiolata show closer affinities to each other and to varieties of S. integrifolia than to the S. rufidula and S. occidentalis var. occidentalis group. Perhaps this is because of the several characteristics which S. occidentalis var. latipetiolata and S. occidentalis var. dentata have in common with S. integrifolia such as gland features and inflorescence shape. Alternatively it may be a distortion of the relationships between phenetically dissimilar groups of OTU's (Crovello 1970). More precise measurement of ovary position could perhaps have increased the phenetic similarity between S. occidentalis var. dentata and the

Figure 26: Dendrogram using UBC-CGROUP clustering program. Forty-three standardized variables from 262 individuals were used. Plot is the log of the error value at a given clustering step. Individuals are clustered under one line below an error value of 15. Reference to the numbers is given in the accompanying key. Varietal names are abbreviated to the first 3 or 4 letters. B.C.=British Columbia, O.M.=Olympic Mountains, C.R.G.=Columbia River Gorge, V.I.=Vancouver Island, Hybs.=hybrids.

Key to line numbers:

1. rufidula x occidentalis
2. latipetiolata x rufidula
3. rufidula x dentata
4. integrifolia x rufidula
5. rufidula x 605 occidentalis (Chehalis R.)
6. integrifolia x rufidula
7. rufidula (618); dentata (629)
8. dentata (630D)
9. 2 rufidula : integrifolia x rufidula;
- dentata x rufidula
10. occidentalis x dentata
11. rufidula x occidentalis
12. occidentalis x dentata
13. rufidula x occidentalis
14. 2 rufidula x occidentalis
15. rufidula x occidentalis
16. dentata x rufidula; rufidula x occidentalis
17. occidentalis; rufidula
18. occidentalis
19. 3 rufidula; claytoniifolia
20. EP605 (Chehalis R.)
21. integrifolia; leptopetala
22. integrifolia
23. occidentalis x dentata
24. rufidula
25. rufidula
26. rufidula
27. rufidula : integrifolia
28. rufidula
29. occidentalis x dentata
30. 2 dentata
31. integrifolia x leptopetala
32. integrifolia x leptopetala;
- leptopetala x dentata
33. rufidula x (EP605) Chehalis R.
34. rufidula
35. dentata
36. rufidula x dentata
37. (EP605) Chehalis R., S. occidentalis x
- S. integrifolia hexaploid population



S. rufidula and S. occidentalis groups. Results of the hierarchical grouping analysis of S. occidentalis var. dentata and S. occidentalis var. latipetiolata clearly indicate that these two groups deserve specific status.

Saxifraga integrifolia var. leptopetala failed to separate from S. integrifolia var. integrifolia, probably because of the extensive numbers of intermediate Columbia River Gorge plants in the sample. In contrast, S. integrifolia var. claytoniifolia populations form a fairly distinct group from S. integrifolia in spite of close contacts in the Columbia River Gorge (Fig. 26).

The population from Chehalis, Washington (EP605) clustered independently with some affinities for the group of mixed S. integrifolia, S. integrifolia var. leptopetala, S. integrifolia var. claytoniifolia, and hybrids. Its morphology and chromosome number ( $n=29$ ) suggest an allohexaploid origin between S. occidentalis and S. integrifolia.

The relationships of groups in the hierarchical clustering analysis compare only roughly with present taxonomic treatments (Krause and Beamish 1972, 1973, Hitchcock et al. 1961, Hitchcock and Cronquist 1973, Elvander 1975). Saxifraga occidentalis var. latipetiolata and S. occidentalis var. dentata do not appear to cluster as good subspecific entities of S. occidentalis var. occidentalis. The allohexaploid population from near Chehalis, Washington does not group with the S. occidentalis or S. rufidula individuals although it is considered within S. occidentalis by Krause and Beamish (1972) and is probably a hybrid involving S. occidentalis. The clustering of this

population as well as that of a number of artificial hybrid individuals is similar to the clustering pattern described by Smith (1969) in Vaccinium where natural hybrids formed clusters that were distinct from clusters of their presumed parents.

The usefulness of a clustering technique in the present study appears limited to the definition of larger natural groups on the basis of multiple characteristics. Determination of biological relationships, phenetic distance among the groups, hybrid affinities, and correlations to chromosome number are all questionable using this technique. However, the surprisingly high grouping error level between S. occidentalis var. dentata and S. occidentalis var. latipetiolata strongly suggests that they are morphologically distinct from S. occidentalis var. occidentalis and S. rufidula.

The present study confirmed reports by others (Eyles and Blackith 1965, Rising 1968, Whitehouse 1969, Schilling and Heiser 1976) that Principal Components Analysis (PCA) treats hybrid relationships and other factors including correlations with cytological data in a more precise manner than standard hierarchical clustering methods. The recognized taxonomic groups present spatial overlaps with intermediate individuals among several groups (Fig. 27-29). In contrast to a repeated multivariate study of introgression which involves crossovers in hybrids and backcrossing to one parent at the diploid level (Bloom 1976) the introgression within the present group appears to involve processes of polyploidization and consequently increased variability within the parental entities. Considering the probable hybrid origins of such polyploid taxa as



S. occidentalis, S. integrifolia, S. occidentalis var. latipetiolata, and certain populations of S. rufidula and S. occidentalis var. dentata, intermediacies represent reasonable assessments of the complex relationships involved.

Saxifraga rufidula populations separated into two clouds with northern diploids grading into a mixed group of diploid, tetraploid, and hexaploid individuals from the Columbia River Gorge (Fig. 27,28). Tetraploid S. occidentalis var. dentata populations showed greater variability and tended to group in intermediate hyperspaces close to S. occidentalis, and S. occidentalis var. latipetiolata, S. integrifolia and the allohexaploid plants from Chehalis, Washington.

When artificial hybrids are included in the PCA, their intermediacy and variability is clearly represented (see Fig. 19-21). Occasional segregates (Fig. 19-21, plant 3\*) appear different and are probably extremely unbalanced monstrosities which would not survive in nature. Most hybrid individuals show closer affinities to the Columbia River Gorge S. rufidula, S. occidentalis or S. integrifolia parent than to the other parental group. The raw principal component (eigenvector) solutions (Table V, hybrids excluded) are similar whether or not artificial hybrids are included in the analysis.

Ten parental and hybrid groups defined by hierarchical grouping and principal components analyses and standard taxonomic treatments were recognized for use in the stepwise discriminant function (SDF) analysis (Fig. 30-35). The six discriminating variables and F values for inclusion (critical F probability 0.05), in the order used, were: plant height (51.9),

Figure 27: Principal components graph of axis one vs. two showing individuals from several natural taxa and populations. Artificial hybrids are not included. Symbols are as follows:

R=diploid Vancouver Island and Olympic Mountains  
S. rufidula  
 r=polyploid Columbia River Gorge S. rufidula  
 D= S. occidentalis var. dentata  
 O= S. occidentalis var. occidentalis  
 L= S. occidentalis var. latipetiolata  
 X=hexaploid hybrid population from Chehalis River  
 EP605  
 I= S. integrifolia var. integrifolia  
 C= S. integrifolia var. claytoniifolia  
 M= S. integrifolia var. leptopetala

The percentage of the total variance accounted for by the first three axes is 19.95, 12.17, and 6.87 percent respectively.

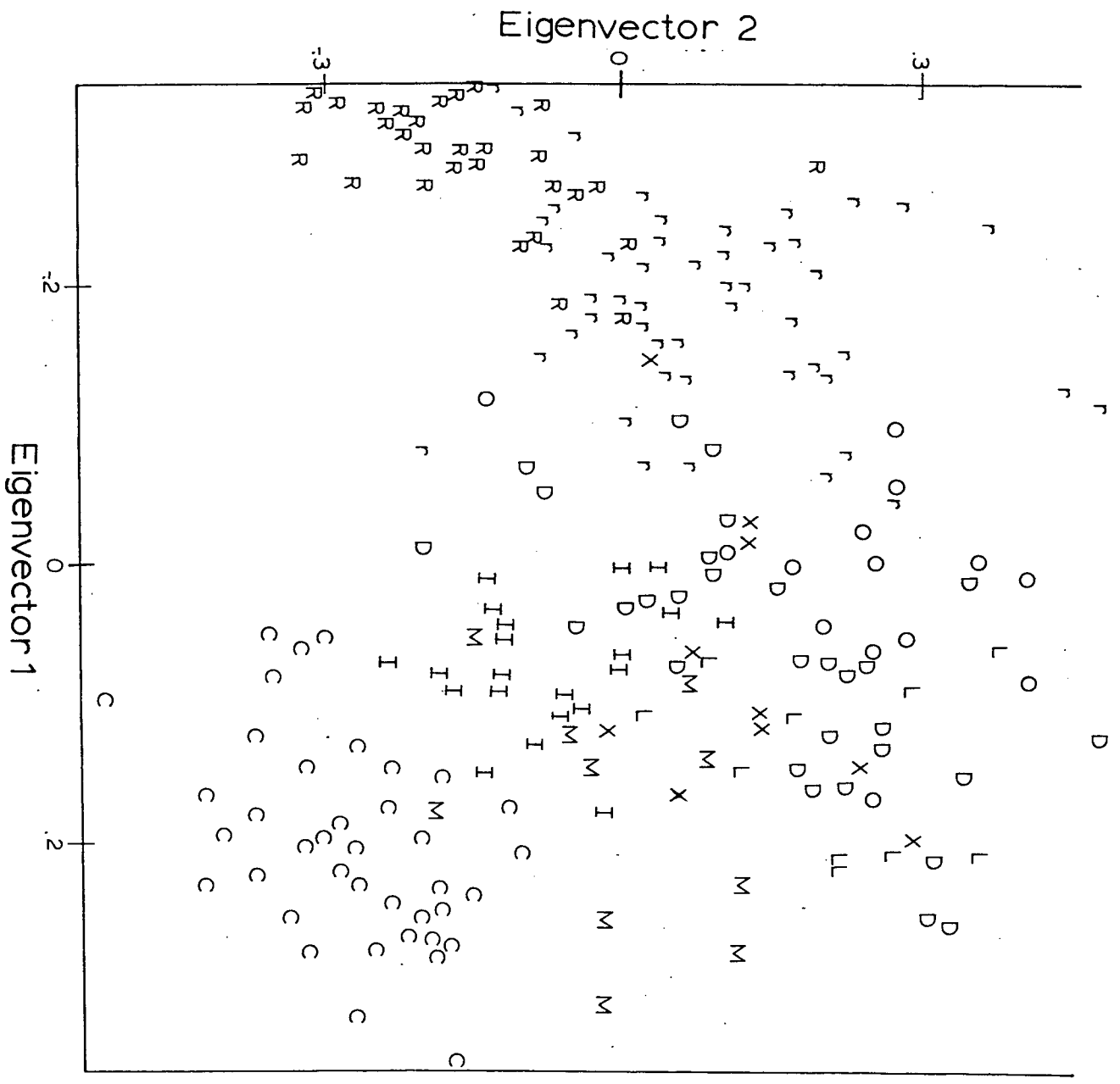


Figure 28: Principal components graph of axis one vs. three showing individuals from several natural taxa and populations. Artificial hybrids are not included. Symbols are as in Figure 26.

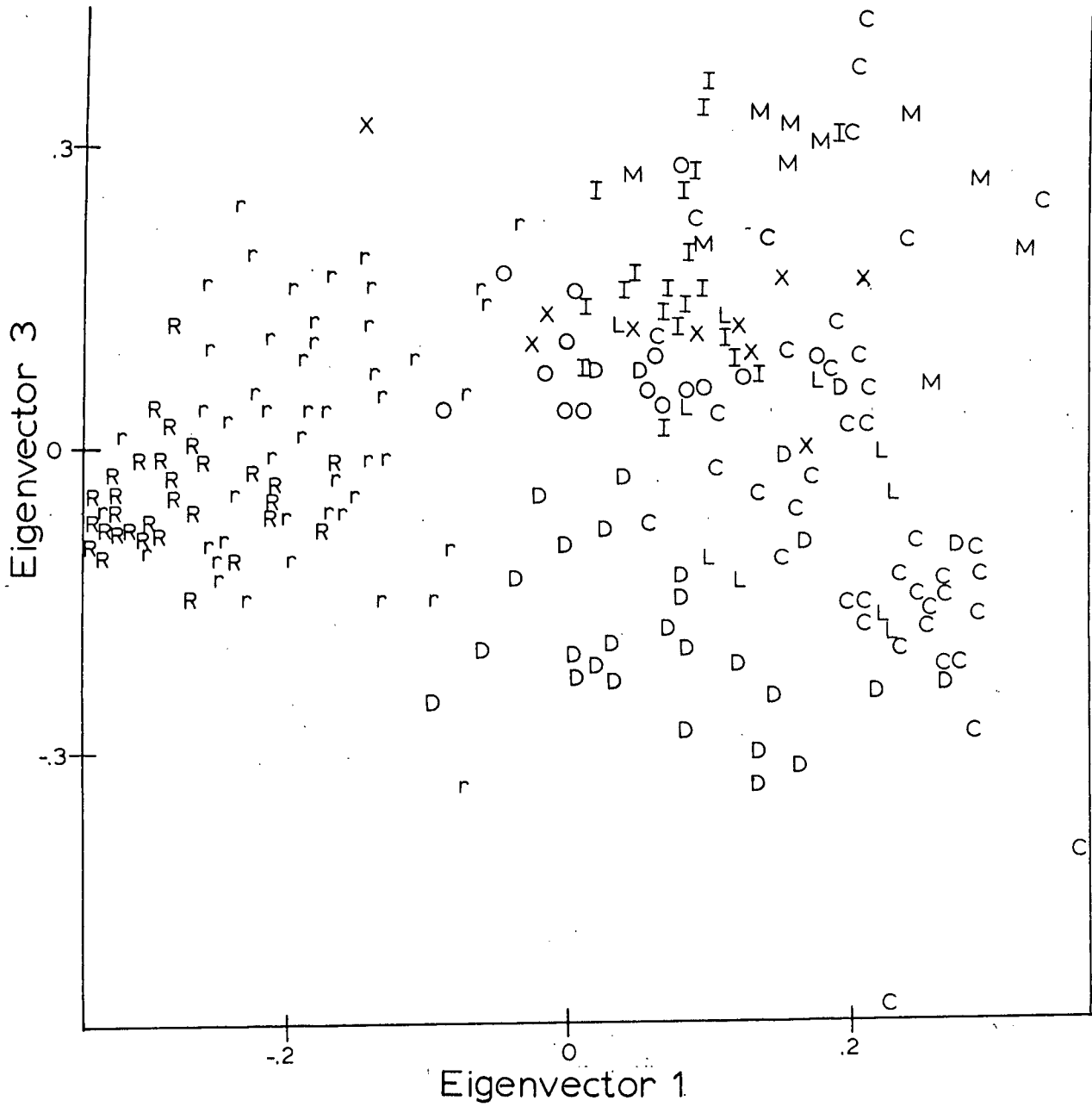


Figure 29: Principal components graph of axis two vs. three showing individuals from several natural taxa and populations. Artificial hybrids are not included. Symbols are as in Figure 26. Plant \*C is displaced slightly to the right in this representation.

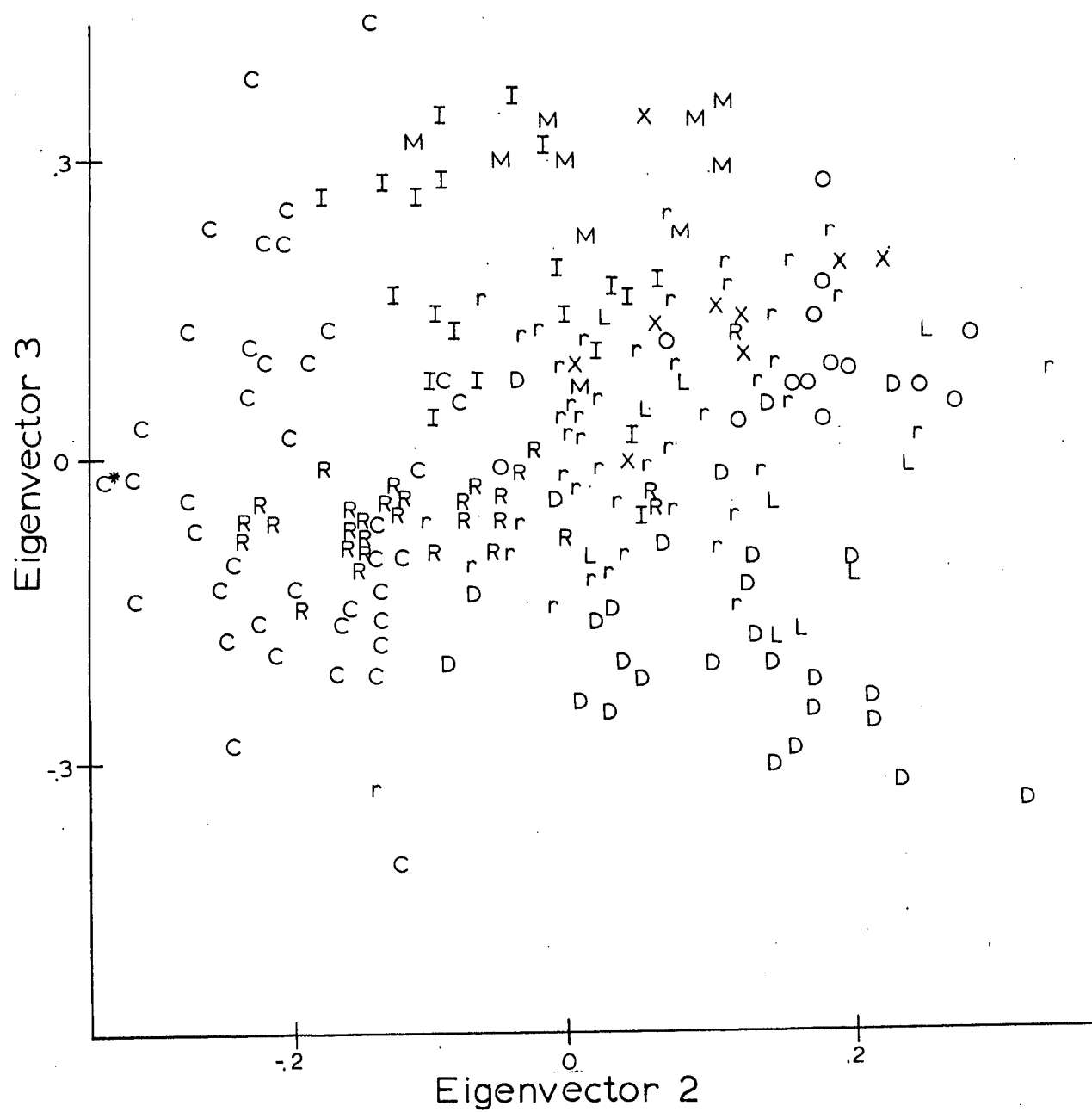


Table V.  
The raw principal component solution.\*

<u>Variable No.**</u>	<u>1st</u>	<u>2nd</u>	<u>3rd</u>	<u>4th</u>
1.	-0.1174	0.2560	0.0362	0.0733
2.	0.0941	0.1533	0.0639	0.0938
3.	-0.0110	0.1943	0.1528	0.0401
4.	0.1087	0.1238	-0.0270	-0.2052
5.	0.2609	-0.0537	0.1897	-0.0963
6.	-0.0485	-0.0380	-0.0228	-0.1423
7.	-0.1232	0.2034	0.0256	0.2571
8.	0.1223	-0.0767	-0.0233	0.0258
9.	0.1798	-0.0644	0.3628	-0.0733
10.	-0.0812	0.2692	-0.0656	0.1438
11.	-0.0397	0.0204	0.1641	-0.2045
12.	0.0768	0.1146	-0.3414	0.1300
13.	0.0114	0.3009	0.0120	-0.0150
14.	-0.0368	0.1845	0.0738	0.0048
15.	0.1485	0.2158	0.1051	-0.0034
16.	0.1247	0.1240	0.1093	0.0663
17.	-0.0268	0.0197	-0.0664	-0.0991
18.	0.0922	0.1000	0.0863	-0.1326
19.	0.1828	0.1409	0.1536	0.1225
20.	0.1451	0.1982	0.1312	-0.0790
21.	-0.1307	0.2130	0.0324	-0.1724
22.	0.1143	0.0221	-0.2373	-0.1960
23.	0.0214	-0.0568	-0.1147	-0.0713
24.	0.1383	0.1932	-0.2079	-0.0001
25.	0.2367	0.0714	-0.1214	-0.2404
26.	-0.2871	0.0182	-0.0938	-0.1099
27.	0.2956	-0.0747	-0.0520	-0.0546
28.	-0.0455	0.2652	0.1701	0.1720
29.	0.0639	0.1619	-0.1869	-0.0798
30.	0.2615	-0.0067	-0.2043	-0.0916
31.	0.2743	-0.0533	-0.1184	0.1539
32.	0.1939	-0.0791	0.0717	0.3015
33.	0.1864	0.2205	-0.1632	-0.0470
34.	-0.1018	0.2619	0.0607	-0.0926
35.	0.0595	0.0153	-0.2388	0.1640
36.	0.2190	-0.0025	0.2913	0.0396
37.	0.0748	0.1716	0.1181	-0.3577
38.	0.1621	-0.1472	-0.1351	0.3517
39.	-0.1733	0.2272	-0.2316	0.0896
40.	0.2593	0.0451	-0.1651	-0.1821
41.	0.1418	0.0209	0.1137	0.0500
42.	-0.0074	0.0292	0.0793	0.2037
43.	0.0821	0.1830	-0.0541	-0.1629
44.	0.0821	0.1830	-0.0541	-0.1629

\* These expressed as eigenvectors; results of the principle components without artificial hybrids are similar to those with hybrids (above).

\*\* Variables are as coded in Table II.



leaf blade angle at petiole (23.16), gland height/width (21.09), petiole length/width (17.81), gynoeceum height (15.52), and leaf length (12.76).

Group classification functions show that plant height (Variable 27) effectively discriminates S. occidentalis and diploid, polyploid, and hybrid S. rufidula individuals from the remaining taxa and S. integrifolia var. claytoniifolia from all the others. Leaf shoulder angle (Variable 37) separates S. occidentalis var. latipetiolata and S. integrifolia var. leptopetala from the other groups while gland height/width ratio (Variable 6) discriminates diploid S. rufidula, S. occidentalis var. latipetiolata, and S. occidentalis var. dentata groups. Petiole length/width ratio (Variable 39) distinguishes S. integrifolia var. claytoniifolia and S. integrifolia var. leptopetala and gynoeceum height (Variable 10) separates S. occidentalis and the S. occidentalis hexaploid hybrid population. Leaf length (Variable 32) separates both groups of S. rufidula from the remaining group. Of the total cases, 65.79% were correctly classified by SDF analysis including over 65% of S. integrifolia var. integrifolia, S. occidentalis var. occidentalis, S. occidentalis var. latipetiolata (Fig. 31), S. integrifolia var. claytoniifolia, and Vancouver Island and Olympic Mountains S. rufidula individuals. Some 63.7% of the S. integrifolia var. leptopetala plants were grouped with S. integrifolia (Fig. 31,B), while individuals of the allohexaploid population (EP605) were scattered among S. occidentalis (20%), tetraploid or hybrid S. rufidula (30%), and diploid S. rufidula (20%) groups (Fig.

Figure 30: Stepwise discriminant functions plot of the first three canonical variables. The first two canonical variables are stratified on the third variable to produce a stratified three-dimensional plot which clarifies hyperspatial relationships. This representation depicts relationships of group means as spheres on supporting lines.

Group means symbols are as follows:

A= S. rufidula plants from the Columbia River Gorge and hybrids

B= S. integrifolia var. integrifolia plants from the Columbia River Gorge

C= S. integrifolia var. claytoniifolia

D= S. occidentalis var. dentata

L= S. occidentalis var. latipetiolata

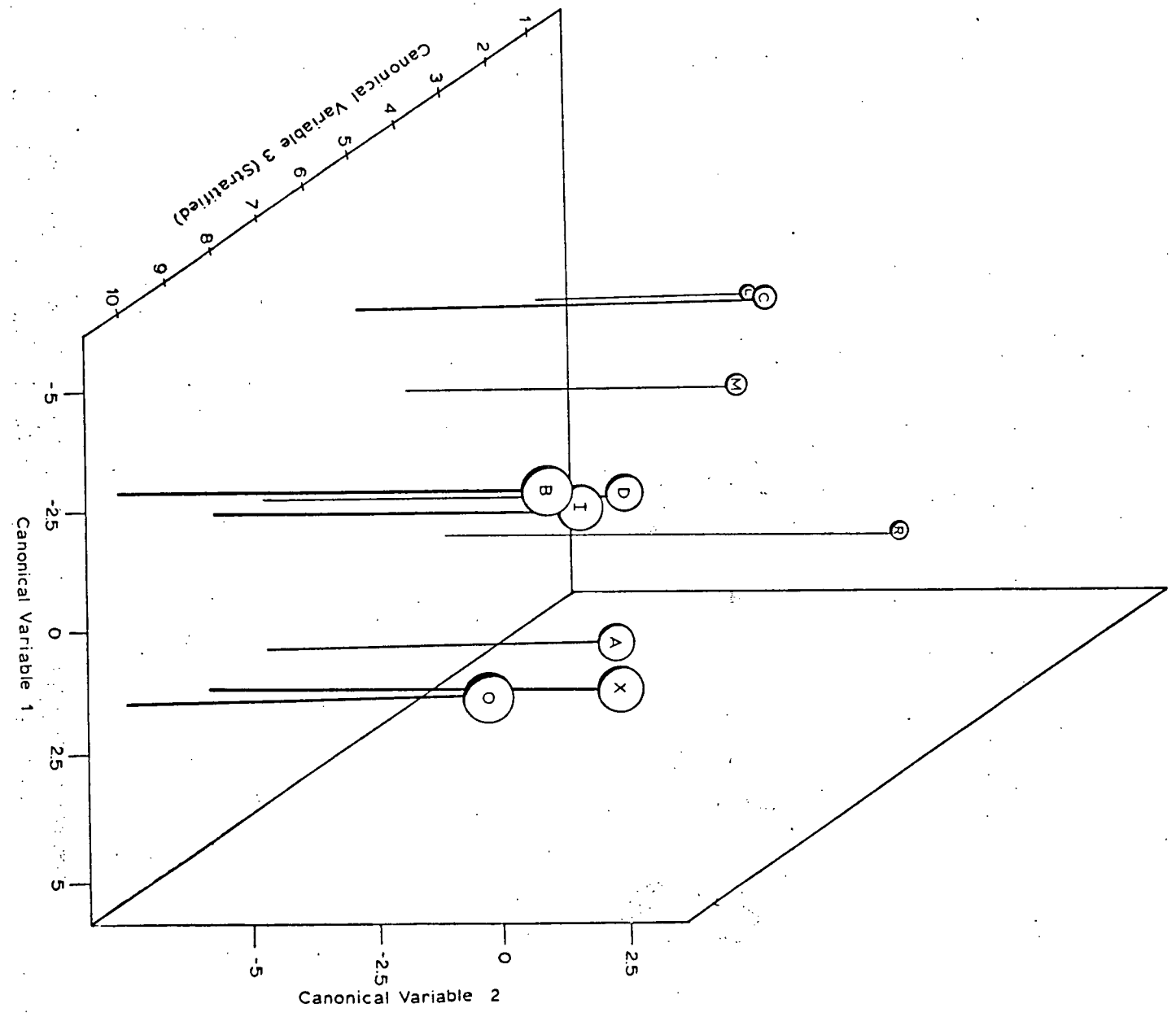
M= S. integrifolia var. leptopetala

O= S. occidentalis var. occidentalis

R= S. rufidula plants from Vancouver Island and the Olympic Mountains

I= S. integrifolia var. integrifolia plants from Vancouver Island

X= Hexaploid S. occidentalis x S. integrifolia plants from Chehalis, Wash.



32,A). Of S. occidentalis var. dentata-individuals, 28% were placed into the S. integrifolia group (Fig. 33,A). Columbia River Gorge S. integrifolia plants (Fig. 34,A) demonstrate intermediacies with S. integrifolia var. claytoniifolia (19%) (Fig. 34,B) but probably they have insignificant differences from the Vancouver Island S. integrifolia var. integrifolia group with which 12% are classified. Several Columbia River Gorge S. rufidula individuals including artificial hybrids (Fig. 35,B) are intermediate between S. integrifolia var. integrifolia (5%), S. occidentalis (12.5%), S. rufidula (10%) and S. occidentalis var. dentata (5%). Such intermediacies and increased variability in SDF analysis relationships have been used as evidence for the occurrence of introgression in natural populations (Schueler and Rising 1976). It has been suggested that SDF analysis is a preferred method for separation of parental species groups, especially where they are difficult to separate by other means (Danick and Burns 1975, Namkoong 1966). The probable hybrid nature of the tetraploid S. occidentalis var. dentata plants, Columbia River Gorge S. rufidula groups (Fig. 35,B), and a hexaploid population from Chehalis, Washington is documented by SDF analysis as is the uniqueness of the S. occidentalis var. latipetiolata morphology. Taken in conjunction with results of the hierarchical clustering analysis program, the SDF program results agree favorably with a treatment which classifies S. rufidula, S. occidentalis var. latipetiolata, and S. occidentalis var. dentata as distinct species from S. occidentalis.

According to the rules of botanical nomenclature

Figure 31: Stepwise discriminant functions plots of the first three canonical variables. The first two canonical variables are stratified on the third variable to produce a stratified three-dimensional plot which clarifies hyperspatial relationships. Group means are shown as in the Figure 29. Part A shows individual plant points for the S. integrifolia var. claytoniifolia cloud as triangular symbols and Part B shows similar hyperspace points for the S. integrifolia var. leptopetala cloud. Symbols are as in Figure 29.

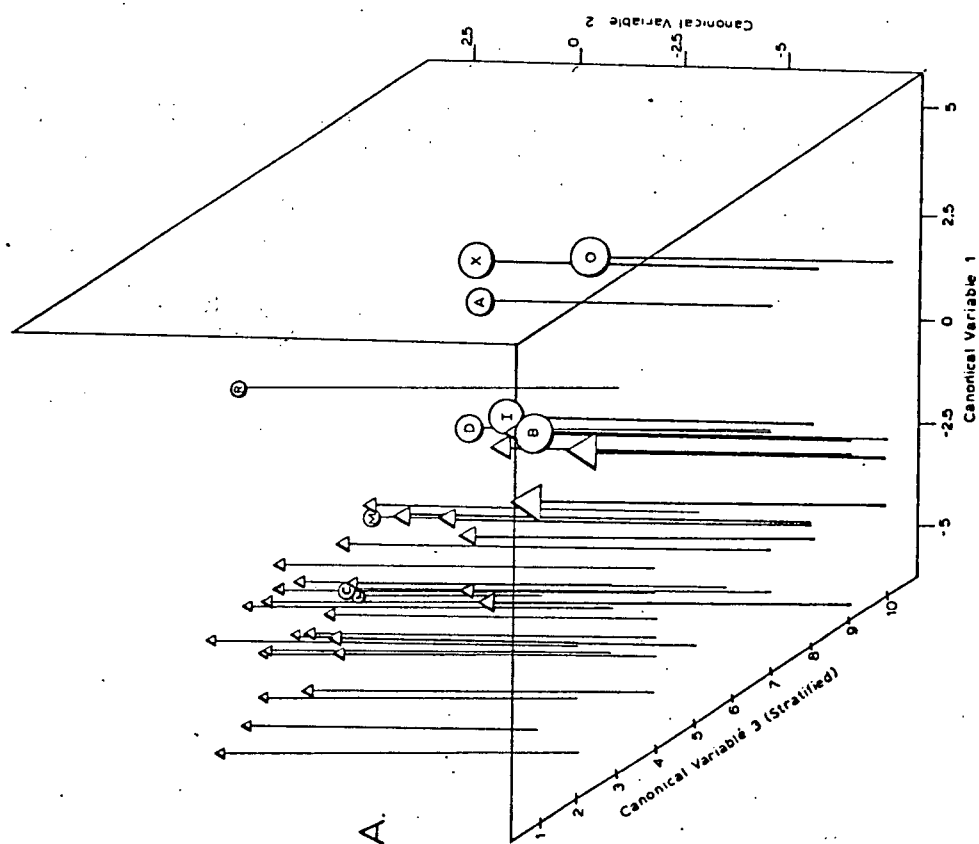
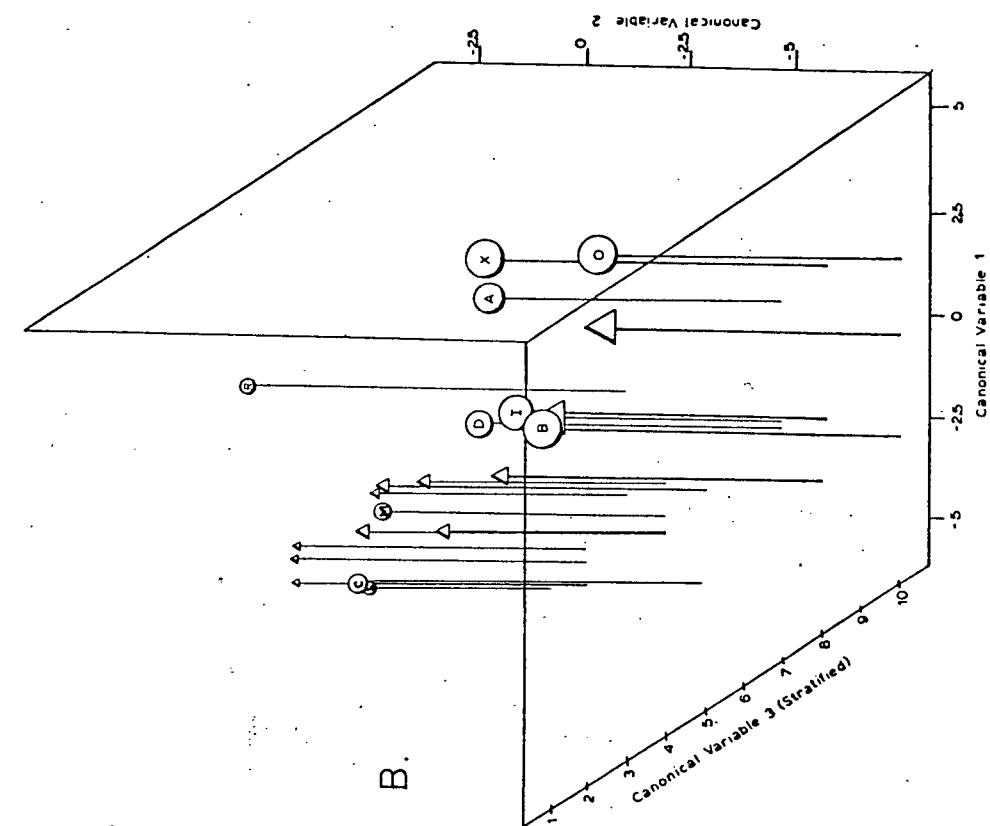


Figure 32: Stepwise discriminant functions plots of the first three canonical variables. The first two canonical variables are stratified on the third variable to produce a stratified three-dimensional plot which clarifies hyperspatial relationships. Group means are shown as in the Figure 29. Part A shows individual plant points for the S. occidentalis hexaploid hybrid (Chehalis River, EP605) cloud as triangular symbols and Part B shows similar hyperspace points for the S. occidentalis var. latipetiolata cloud. Symbols are as in Figure 29.

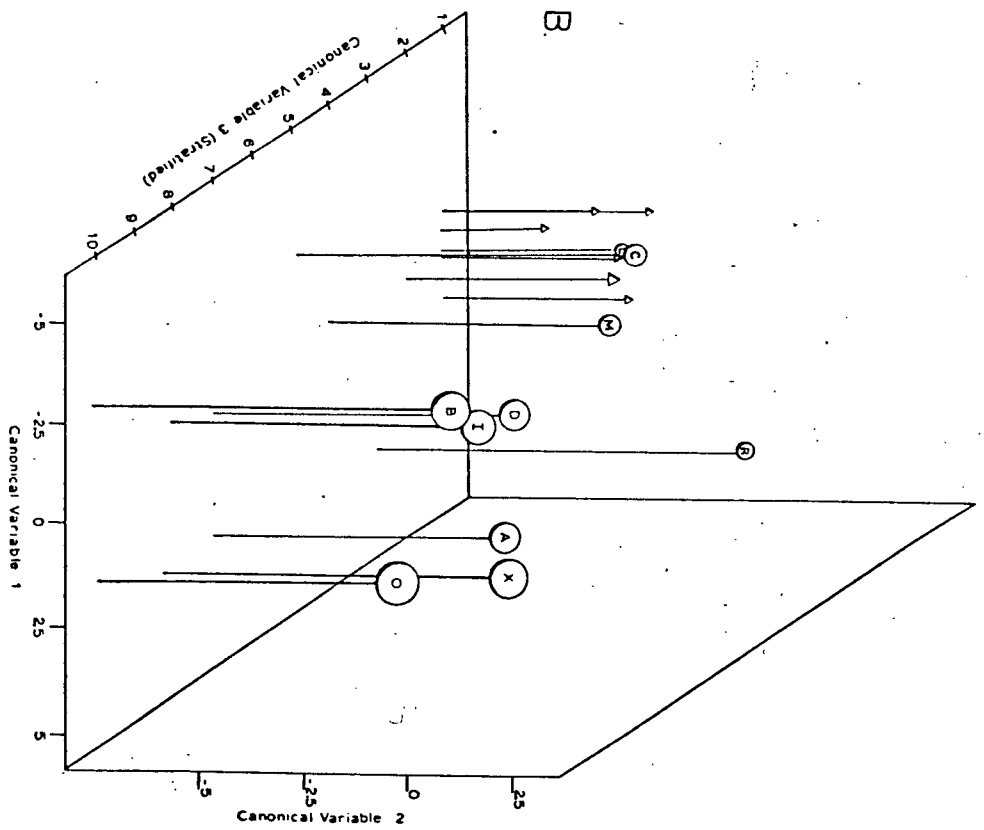
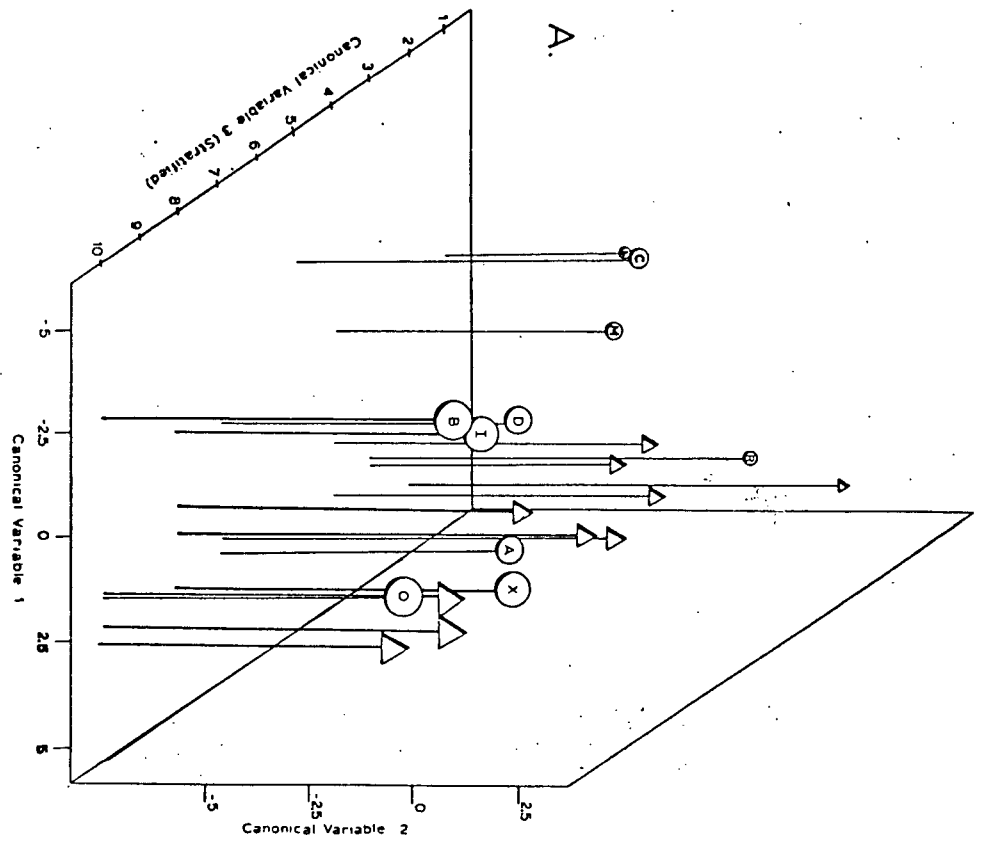




Figure 33: Stepwise discriminant functions plots of the first three canonical variables. The first two canonical variables are stratified on the third variable to produce a stratified three-dimensional plot which clarifies hyperspatial relationships. Group means are shown as in the Figure 29. Part A shows individual plant points for the S. occidentalis var. dentata cloud as triangular symbols and Part B shows similar hyperspace points for the S. occidentalis var. occidentalis cloud. Symbols are as in Figure 29.

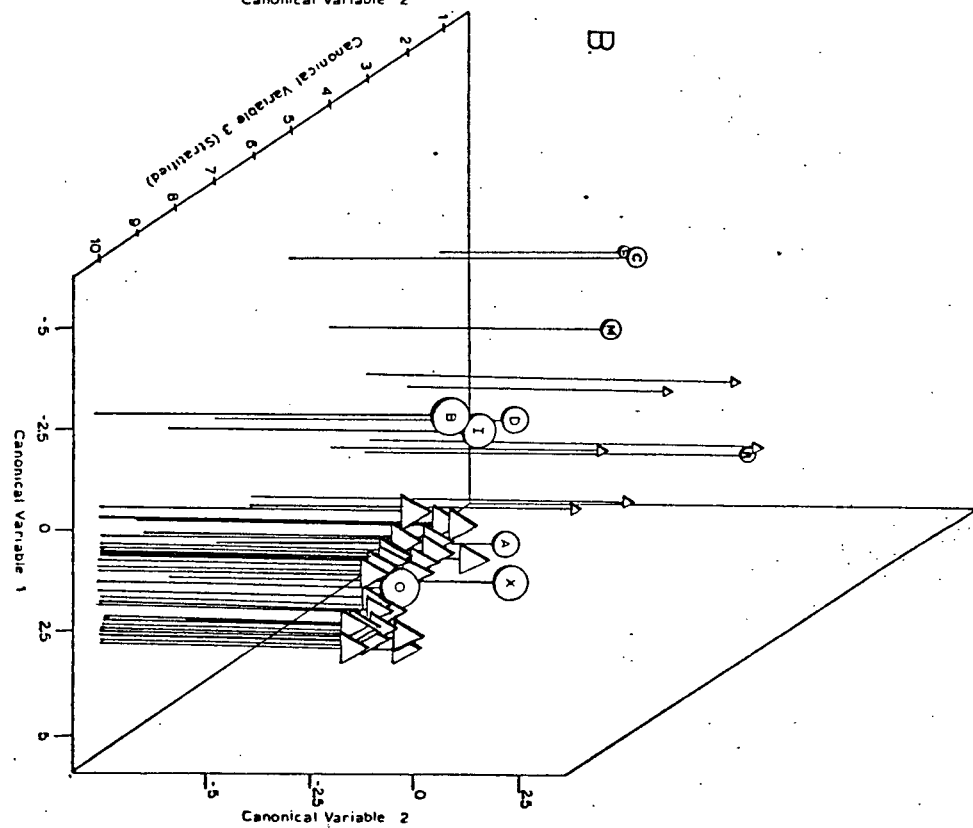
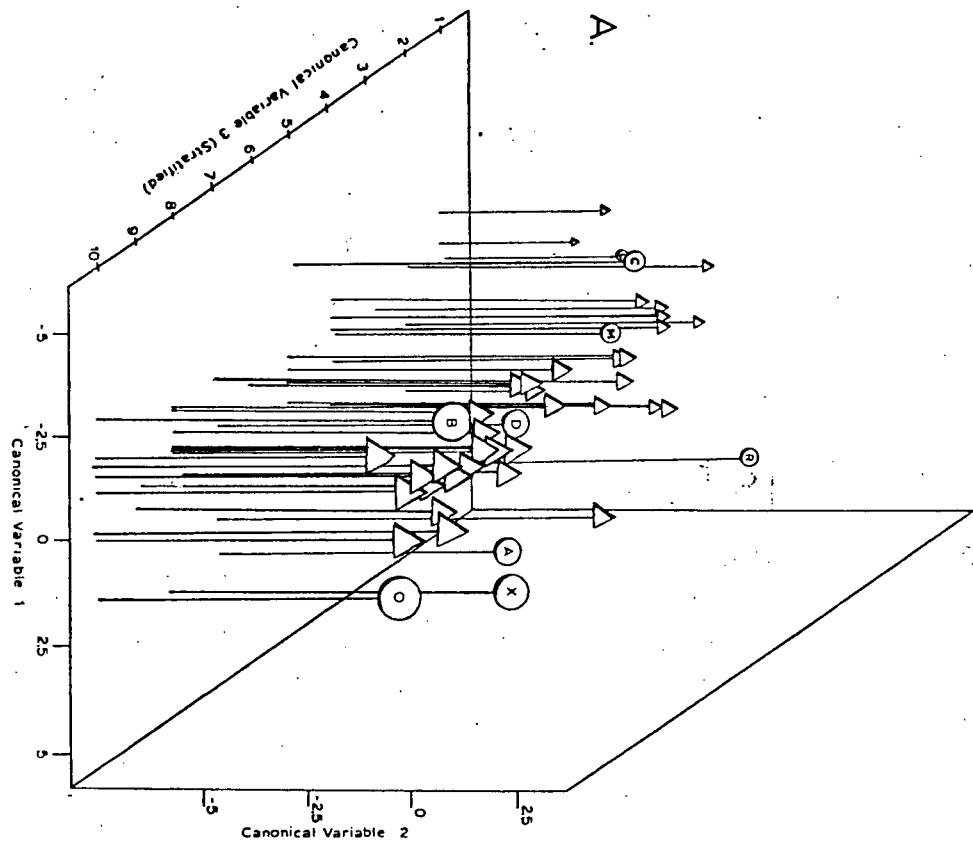


Figure 34: Stepwise discriminant functions plots of the first three canonical variables. The first two canonical variables are stratified on the third variable to produce a stratified three-dimensional plot which clarifies hyperspatial relationships. Group means are shown as in the Figure 29. Part A shows individual plant points for the S. integrifolia var. integrifolia cloud from the Columbia River Gorge as triangular symbols and Part B shows similar hyperspace points for the S. integrifolia var. integrifolia cloud from Vancouver Island and the B.C. Mainland. Symbols are as in Figure 29.

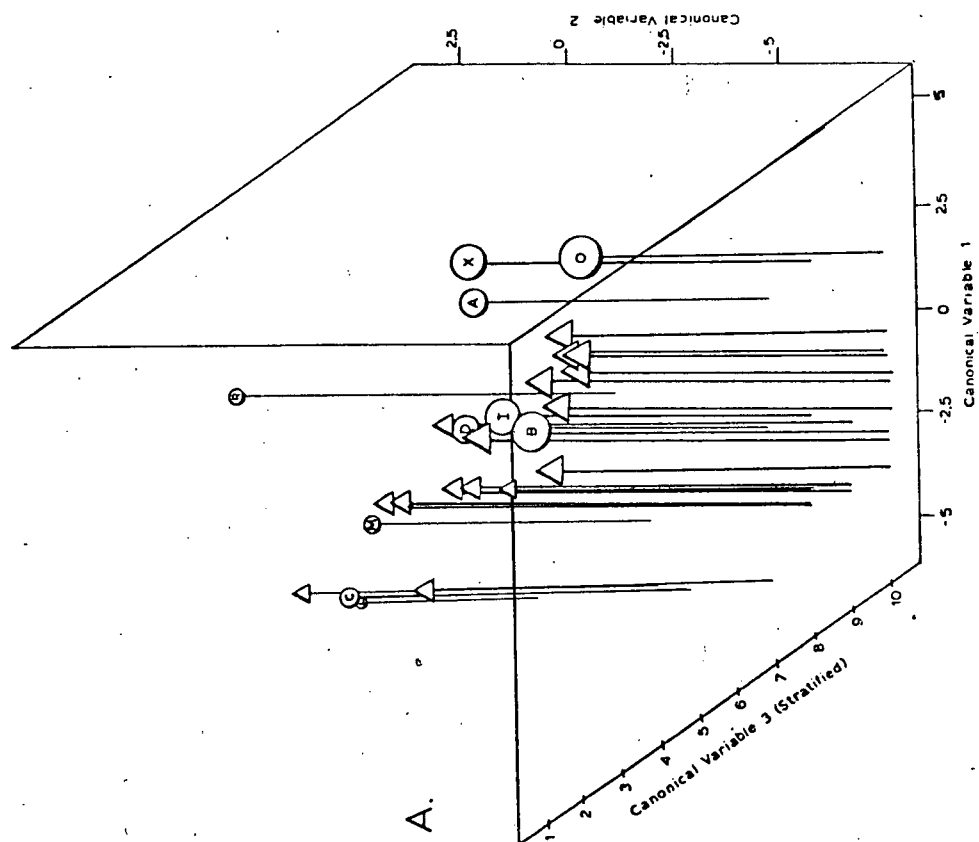
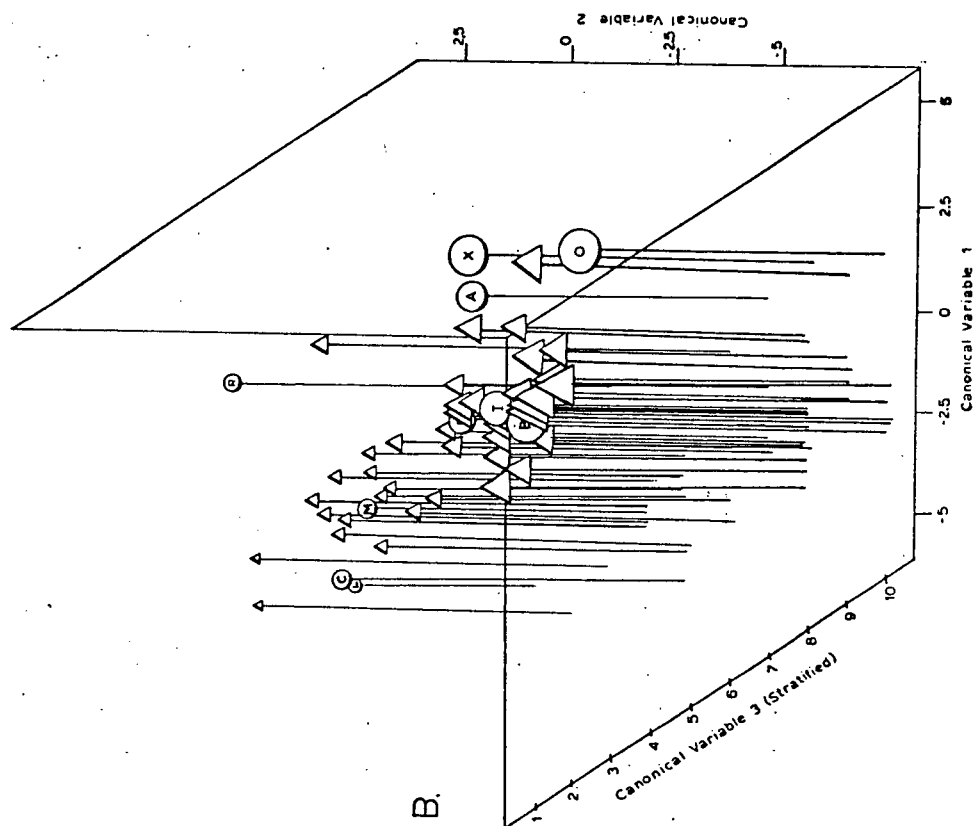
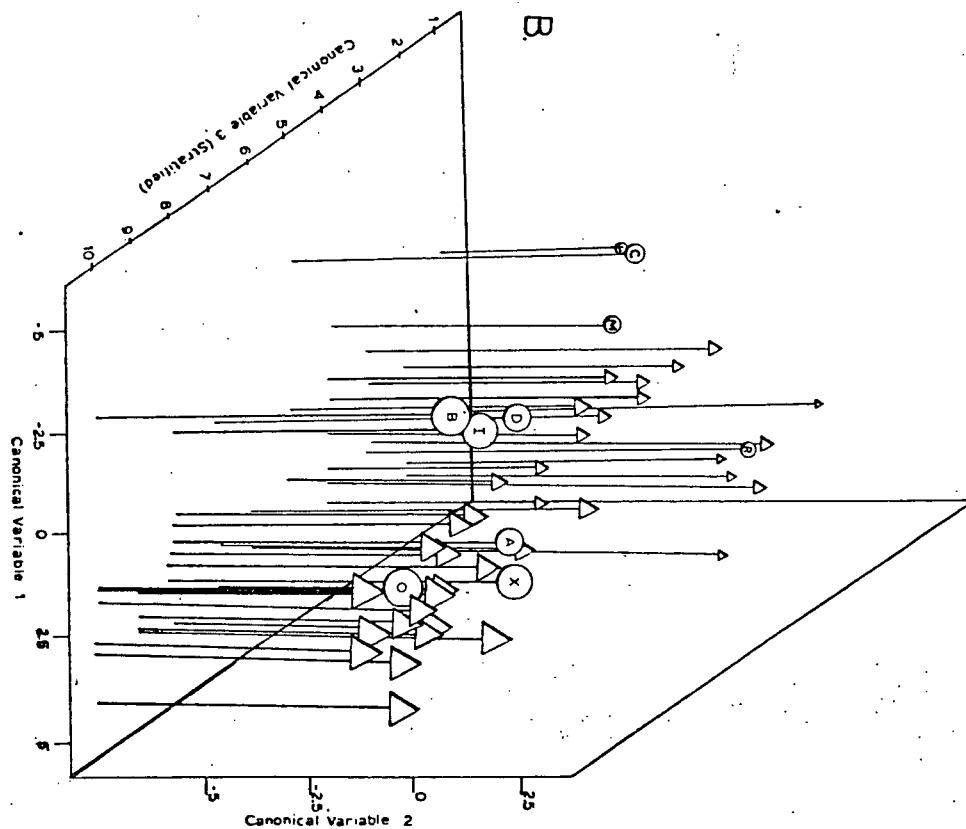
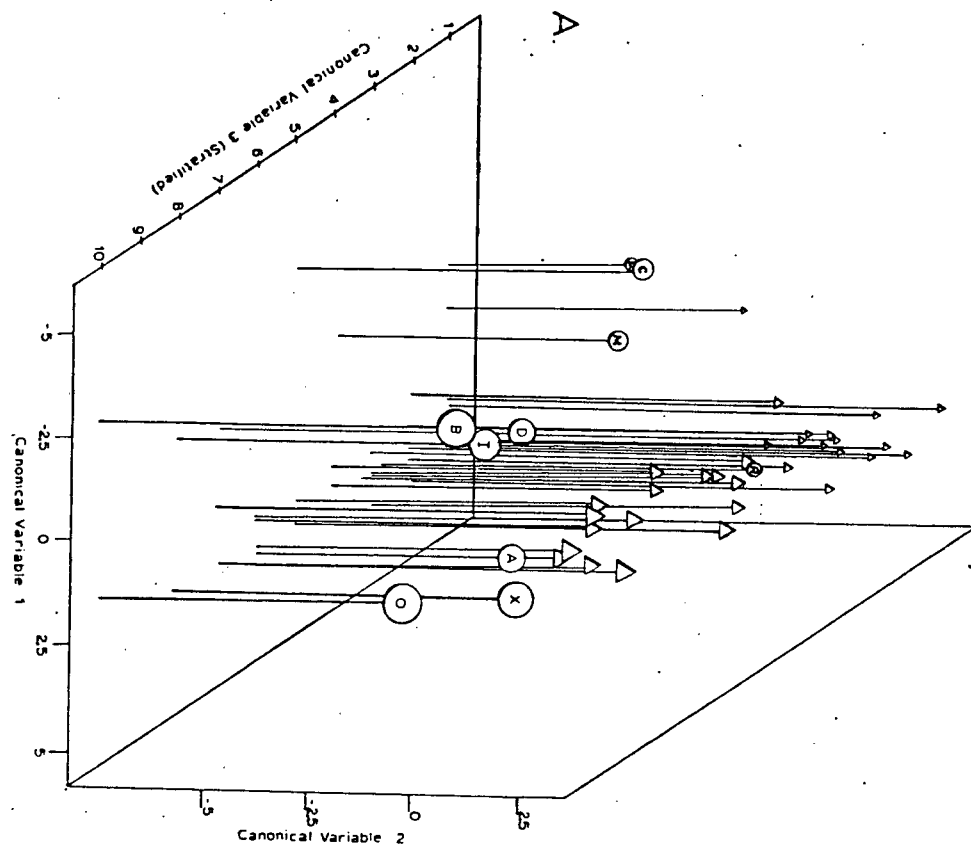


Figure 35: Stepwise discriminant functions plots of the first three canonical variables. The first two canonical variables are stratified on the third variable to produce a stratified three-dimensional plot which clarifies hyperspatial relationships. Group means are shown as in the Figure 29. Part A shows individual plant points for the S. rufidula cloud from Vancouver Island and the Olympic Mountains as triangular symbols and Part B shows similar hyperspace pcints for the S. rufidula-cloud from the Columbia River Gorge and the S. rufidula-hybrid cloud. Symbols are as in Figure 29.



S. rufidula becomes S. aequidentata, S. occidentalis var. latipetiolata becomes S. latipetiolata, S. occidentalis var. dentata becomes S. gormanii, and S. occidentalis becomes S. occidentalis (see descriptions in Taxonomy section).

#### Breeding System Observations

##### Bagging Tests

The results of tests for automatic selfing and self incompatibility are presented in Table VI. Seed set from automatic selfing tests in the bagged, untreated condition is frequently higher than seed set in the hand-selfed condition. This probably resulted from damage in handling especially during emasculation and difficulty in timing pollinations to coincide with stigmatic receptivity. All taxa are clearly self-compatible and the relatives of S. rufidula, e.g. S. occidentalis var. dentata and S. occidentalis as well as S. integrifolia var. leptopetala may have a higher degree of potential self-fertilization than S. integrifolia var. integrifolia, S. integrifolia var. claytoniifolia, or S. occidentalis var. latipetiolata. Elvander (personal communication) reports that he obtained no seed set for members of the S. integrifolia-S. oregana complex in bagged, untreated conditions but similar seed set in bagged hand-selfed tests to those reported here for S. integrifolia and its relatives. Differences in the results cited here are possibly due to the bagging method used in this

Table VI.  
Bagging tests for selfing.

Abbreviated Taxa	Selfed by Hand			Bagged Untreated		
	No. Fruits (Plants)	Total Seed	% Good* Seed	No. Fruits (Plants)	Total Seed	% Good Seed
ruf. (dipl.)	57 (6)	1402	55.2	19 (3)	990	48.
ruf. (poly.)	33 (5)	646	25.1	4 (1)	230	7.8
dent. (dipl.)	82 (4)	1313	55.9	7 (1)	228	0.0
dent. (tetr.)	35 (3)	1312	59.1	11 (1)	254	76.4
occ. (tetr.)	40 (3)	1719	27.9	27 (3)	1516	48.9
lati. (n=38)	112 (3)	1087	6.3	59 (2)	530	5.8
int. (tetr.)	13 (2)	646	13.9	5 (2)	407	0.4
clay. (dipl.)	67 (3)	603	16.9	20 (1)	179	15.1
lept. (tetr.)	8 (1)	37	21.6	37 (3)	470	35.5

\* "Good" seed defined as large, swollen seed versus small, shriveled seed which was considered unfertilized potential seed.



Table VII.  
Bagging tests for outcrossing and apomixis.

Abbreviated Taxa	Outcrossed by Hand			Outcrossing <u>Control, Untreated</u>			Emasculated <u>Bagged</u>		
	No. Fruits (Plants)	Total Seed	% Good* Seed	No. Fruits (Plants)	Total Seed	% Good* Seed	No. Fruits (Plants)	Total Seed	% Good Seed
ruf. (dipl.)	10 (2)	505	59.6	315 (8)	7698	66.3	10 (2)	608	0.0
ruf. (poly.)	20 (3)	932	56.1	103 (5)	4054	38.9	21 (4)	621	0.5
dent. (dipl.)	17 (1)	206	33.5	355 (5)	3304	69.4	6 (1)	149	0.0
dent. (tetr.)	17 (1)	675	71.0	61 (4)	2253	63.3	-----	---	--
occ. (tetr.)	21 (2)	1210	62.5	41 (3)	2767	45.5	47 (7)	2554	0.2
lati. (n=38)	52 (2)	707	39.6	6 (1)	348	0.0	15 (2)	676	0.0
int. (tetr.)	-----	---	----	35 (5)	1852	75.1	30 (6)	1691	0.0
clay. (dipl.)	22 (2)	1271	74.3	41 (1)	401	0.0	32 (2)	410	0.0
lept. (tetr.)	8 (4)	681	82.5	12 (1)	544	1.3	44 (6)	1175	0.3

\* Good seed defined in Table VI.

study which may have allowed autodeposition as a result of mechanical jarring of the bagged, untreated inflorescences.

Seed set in outcrossing experiments (Table VII) was usually higher in S. integrifolia relatives, or nearly equal in S. occidentalis relatives, to seed set in the selfing tests. In a few cases the outcrossed seed set was lower than in selfing tests. Ter-Avanesian (1978) has reported that in several different flowering plant groups, low numbers of pollen grains deposited on receptive stigmas result in a general failure of fertilization. This may account for failure of some individuals to set seed where efforts to deposit large amounts of pollen were unsuccessful. Single individuals of S. occidentalis var. latipetiolata, S. integrifolia var. claytoniifolia, and S. integrifolia var. leptopetala failed to set large amounts of seed when exposed to pollinators, perhaps as a result of premature harvesting or infertility in those particular individuals.

In all cases seed set was absent or at low background levels (less than 1.0%) in emasculated, bagged inflorescences (Table VII). Although apomixis which requires pollination is possible, the wide range of variability of offspring from individual plants and the fact that hybridizations produce offspring which differ markedly from the female parent argues against its occurrence at least as a major means of seed production.

### Floral Observations

Nectar production begins with anther dehiscence and continues for several days until the apparently receptive, papillate, stigmatic surface loses its characteristic wetness. Some UV-absorbing and re-emitting substances are present in Saxifraga nectar which may be visual stimuli to foraging bees or flies. Saxifraga flowers are characteristically protandrous but there is an overlap in final anther dehiscence and onset of stigmatic receptivity. Although some spatial separation exists between dehisced anthers and stigmas (Fig. 2,3), filament and style elongation and curvature may bring the anthers and stigmas into close proximity so that auto-deposition is possible provided that pollen has not been previously removed by foraging insects and that slight external forces bring the anther and stigma into contact. There is also the possibility that pollen may float across a film of water from anther to stigma, as observed for other plants by Hagerup (1950, 1951) or be blown about by wind (Hyde 1950, 1969, Hyde and Williams 1961, Proctor and Yeo 1973), especially since pollen was observed to lose its self-adherent properties after prolonged contact with air. No tests for wind-pollination or repeated tests for water-mediated selfing were carried out in the present study. However, casual observations demonstrate that fresh Saxifraga pollen is hydrophobic and droplets from a light misting can accumulate in Saxifraga flowers producing a continuous water surface between anthers and stigma on which rafts of pollen were observed to float and apparently contact the stigma. Also a reduction was

noted in the adherence of pollen grains to each other and to the tapetal wall after prolonged exposure to the atmosphere. Such a reduction in oily adherence may enhance the chances of limited anemophily for these open, dish-type flowers in the absence of animal pollen vectors.

Temporal separation of flowering times is evident between sympatric taxa. However, in most cases there is a short period of phenological overlap during which interspecific pollinations are possible. No such pollinations were recorded during periods of insect observation but the presence of hybrid individuals testifies to the occasional occurrence of hybridizing events. Whether there are phenological differences correlated with different levels of polyploidy within populations as Lewis and Suda (1976) have described for Claytonia virginica is unclear from the present samples. Determination of such differences would require more extensive and temporally separated sampling of individual populations which exhibit two or more levels of polyploidy. It is interesting to note that where different diploid and polyploid taxa occur sympatrically, the polyploids tend to flower later in the season than the diploids. Seasonal isolation also appears to occur to some extent within taxa over broad geographic or topographic ranges. Southern lowland populations tend to bloom earlier than those at higher latitudes or altitudes, even under uniform transplant conditions.

The number of ovules per carpel varies considerably within an inflorescence. The earlier-maturing flowers which occupy positions closer to the central branches produce more ovules than the later maturing ones which are at progressively more

terminal positions on the inflorescence branches. Some differences in ovule/carpel number among taxa exist. When the earliest, most central flowers are compared, S. occidentalis var. dentata, S. rufidula, S. integrifolia var. integrifolia and S. occidentalis var. latipetiolata plants form a series from lowest to higher numbers of ovules per carpel with the highest numbers appearing in S. integrifolia var. leptopetala, S. integrifolia var. claytoniifolia and S. occidentalis plants in that order. These trends do not seem to be correlated with inflorescence size, extent of branching, or flower number. Although detailed observations are lacking, other floral features do not seem to show such a marked reduction in numbers or size with position in the inflorescence. Further studies are needed to determine the systematic and biological significance of these observed differences in ovule/carpel number.

Elvander (1978) has observed that some populations of S. integrifolia var. integrifolia are gynodioecious, an observation which is supported by the finding of male-sterile plants, apparently seed-fertile on Vancouver Island. He has noted a positive correlation between the degree of compaction of the inflorescence and the degree of flowering synchrony among varieties of S. integrifolia. He concluded that inflorescence compaction and associated flowering synchrony promotes outcrossing in populations with compacted or congested inflorescences. Evidently S. integrifolia var. integrifolia populations with less compacted inflorescences are the ones which are gynodioecious. Evidence of male-sterile individuals and evidence for similar correlations involving degree of

compaction and gynodioecy in the taxa other than S. integrifolia is lacking from the present study.

The reasons for complete seed and pollen sterility in some individuals are unclear, but one possibility is that they represent vegetatively vigorous segregant hybrid or mutant forms which closely resemble one or the other parent in morphology and habitat preference. Another explanation may involve the degree of instability inherent in a polyploid genome with geologically recent origins. In certain sterile individuals what appear to be mycelial fragments may be seen among the abortive pollen or pollen mother cells. Fungus-induced sterility may indeed be a common feature of certain populations. Whatever the explanation, such vegetatively vigorous, sterile individuals may compose a large portion of certain populations (Beamish 1961).

Although the bagging tests and floral observations reveal interesting biological and evolutionary tendencies, they are not useful in uncovering characteristics to separate the closely related taxonomic entities involved in this study.

#### Geography, Habitat And Pollination Ecology Observations

Geographically S. occidentalis var. occidentalis is a widespread entity which is found on mountaintops and cliffsides in the Rocky Mountains and Cascades from southern Alaska and the Yukon to Montana and Idaho. It grows on exposed mossy or bare ground in rock crevices and on rocky peaks in vernal mesic habitats which become rapidly xeric as the season progresses. It is not found on Vancouver Island, the Olympic Mountains or in

the Columbia River Gorge. Saxifraga rufidula grows commonly on lowland cliffs and other sites where early spring runoff is abundant. It is found from Lane County in Oregon north into the Columbia River Gorge and then in the Olympic Mountains and northward on the east side of Vancouver Island. It occurs on mountaintop areas in the Olympic Mountains and on Vancouver Island as well as at lower elevations. Local population extinction caused by increased grazing pressure with the recent introduction of mountain goats may explain failure to find S. rufidula plants which have been reported on Hurricane Ridge and in the Obstruction Pass Area of the Olympic Mountains. Verbal reports that S. rufidula occurs on the British Columbia mainland were also investigated but only one occurrence has been documented. Literature reports (Welsh 1974) of S. rufidula in Alaska may be the result of confusion with S. occidentalis var. occidentalis or S. nivalis since there are no specimens of S. rufidula or S. occidentalis var. rufidula in the collections at the University of Alaska, the State Museum at Juneau, in the Anderson collection at Ames, Iowa, or among Welsh's specimens from BYU. The specimen reported for southern Alaska by Engler and Irmscher (1916) is also probably a small S. occidentalis var. occidentalis plant since it was first labeled as S. virginiensis, although it was not seen during the present study.

The habitats of S. occidentalis var. dentata are similar to those of S. rufidula but S. occidentalis var. dentata is found west of the Columbia River Gorge in the Columbia River and Willamette River lowlands and higher into the Coast Range of

Oregon. It is commonly found on shallow soil of volcanic rock faces in open or partly shaded seepage areas where early spring moisture is abundant. Its extensive rhizome system apparently allows it to obtain footholds on loose or crumbling substrate and propagate by vegetative means. It is interesting that Chambers (personal communication) has collected material from a sunny location on Saddle Mountain which closely resembles S. rufidula while other plants in shady areas from the same locality are nearer to S. occidentalis var. dentata. Examination of plants from open, sunny areas at the same locality in the present study indicates that the smaller, heliophilic forms are diploid S. occidentalis var. dentata plants but further cytological studies might reveal tetraploid or hexaploid S. rufidula plants in the vicinity.

Saxifraga occidentalis var. latipetiolata is endemic to a few isolated volcanic plugs and mountaintop balds of Clatsop and Tillamook Counties, Oregon. It grows in open, rather grassy areas in somewhat deeper and perhaps drier soil. It blooms later in the season than S. occidentalis var. dentata which is sympatric with it on Saddle Mountain and probably at other sites as well.

The varieties of S. integrifolia are geographically segregated over much of their range, but in the Columbia River Gorge they often are found growing together in mixed populations. Seasonal differences in flowering times and possible microhabitat differences apparently isolate the varieties which are sympatric although there is evidence that hybridization and introgression are common in the Columbia River



Gorge. Saxifraga integrifolia var. integrifolia occurs on open grassy soil pockets and ledges of rocky headlands and outcrops from the Upper Fraser Valley and Central Vancouver Island south through the Puget Sound and then east into the Columbia River Gorge and southward as far as south central Oregon. S. integrifolia var. leptopetala is commonly found in open rocky places or grassy savannah beneath Pinus ponderosa in the British Columbia interior southward to Montana, Idaho, and Oregon and west as far as the eastern portion of the Columbia River Gorge. S. integrifolia var. claytoniifolia occurs in shallow and often gravelly or disturbed soil along roadcuts and streambanks as well as on ledges of rocky outcrops and cliffsides from the Washington Cascades south to the Columbia River Gorge and from northeast Oregon and western Idaho west and south to Northern California.

Observations on soil depth indicate a significant difference between the S. rufidula or S. occidentalis plants and the locally sympatric varieties of S. integrifolia (Table VIII). Differences in soil depth preferences for one larger sample of sympatric S. integrifolia var. claytoniifolia and S. integrifolia var. integrifolia plants from the Columbia River Gorge were less obvious. Similarly no clear differences in depth of soil to rocky substrate emerge between northern and southern S. rufidula populations. S. occidentalis var. occidentalis may have a deeper soil depth preference than does S. rufidula but further observations are necessary. Naturally occurring hybrids between S. rufidula and S. integrifolia were sampled at one locality and average soil depth is intermediate

Table VIII.

Average soil depth (cm) beneath plants representing two sympatric taxa from localities in the Columbia River Gorge and British Columbia.

<u>Localities</u>	<u>rufidula</u>		<u>integrifolia</u>	
	No. Plants	Ave. Depth	No. Plants	Ave. Depth
Columbia River Gorge				
Troutdale	10	4.3	10	4.9
Mt. Pleasant	9	3.6	9	6.7
Clark Co. Line	9	3.3	10	9.6
Mosier	10	4.4	10	8.6
Mayer Park	10	4.9	10	14.0
The Dalles	10	4.5	20	11.6*
British Columbia				
Mt. Finlayson	15	6.2	15	10.7
Sooke	15	3.3	15	6.5
Nanaimo**	15	3.6	15	6.5
Nanoose	15	3.1	15	5.7

\* A subsample of integrifolia var. integrifolia (n=20) from this locality had an average depth of 14.9cm. Other Columbia River Gorge plants are var. claytoniifolia and B.C. plants are var. integrifolia.

\*\* An intermediate hybrid subsample (n=15) from this site had an average soil depth of 5.5 cm.

Table IX.

Soil moisture in g. H<sub>2</sub>O (g. dry weight)<sup>-1</sup> under plants at five sympatric localities.

<u>Site</u>	<u>Date</u>	<u>rufidula</u>	<u>integrifolia</u>
Nanoose	March	1.039*	.565
	April	.801	.675*
	May	.514	.216
Nanaimo	March	1.117	.487
	May	1.014*	.517*
Mt. Finlayson	March	.995*	.638
Sooke	March	.752*	.725
Yale	April	<u>occidentalis</u>	<u>integrifolia</u>
		.614*	.426

\* These dates closest to height of bloom for that plant taxon at each locality.

for the hybrid plants.

A few sympatric locations were sampled for soil moisture to document differences in water relations between S. rufidula and S. integrifolia and between S. occidentalis and S. integrifolia (Table IX). Especially during peak flowering times the soil beneath S. rufidula plants contains more moisture than soil beneath S. integrifolia plants. If field germination occurs in about April or May, as it does for seedlings in cultivation under natural temperature and light conditions, similar differences in soil moisture levels may be important factors in habitat selection at the seedling establishment phase. Such differences in water relations help to explain higher observed mortality rates in transplanted S. rufidula specimens, assuming that the artificial watering regime duplicated S. integrifolia soil moisture parameters but failed to maintain adequate or sustained soil water levels for S. rufidula.

Insect spectra are summarized in Table X. Flowers of all taxa studied were visited predominantly by nectar-loving flies although bees and occasionally wasps are also attracted to the flowers and collect both pollen and nectar. The flies are divisible by their behavior into motile and more sedentary categories with the larger anthophilous Syrphids, Bombylids, and deerflies much more likely to effect cross-pollination than their smaller, ground-loving cohorts.

One possible pollinator difference among the taxa observed could be the greater dependence of S. integrifolia var. integrifolia upon flies as pollinating agents (Table X). Numerous authors have suggested that bees in particular show

Table X.

Summary of major groups of insect visitors  
observed in 4 populations. Numbers indicate the  
total number of insect visitors recorded.

	No. Bees, <u>Wasps</u>	% Bees, <u>Wasps</u>	No. <u>Diptera</u>	Total <u>Visitors</u>
<u>S. rufidula</u> (NOOS-R) 10.5 hrs.; 4, 5 April	14	32.5%	29	43
<u>S. rufidula</u> (NMO-R) 5.25 hrs.; 21, 22 April	10	19.0%	43	53
<u>S. occidentalis</u> (Yale-626) 2 hrs.; 19 April	13	54.2%	11	24
<u>S. integrifolia</u> (NMO-I) 4 hrs.; 10, 11 May	2	5.8%	32	34

less interest and constancy in a species as its frequency in the immediate flora declines (Brittain and Newton 1933, Stephens 1956, Simpson and Duncan 1956, Lewis 1961, Free 1963, 1968, Levin and Anderson 1970). Competition for Hymenopteran pollinators in the later flowering S. integrifolia var. integrifolia could be more intense judging from the greater variety and abundance of concurrently flowering species which are perhaps more attractive to bees than Saxifraga flowers. Slight selection pressure due to competition for pollinators may favor more pronounced seasonal differences in flowering time (McNeilly and Antonovics 1967, Paterniani 1969) and greater self-compatibility within sympatric S. rufidula populations (Antonovics 1968). A shift in visitor spectra between sympatric S. integrifolia and S. rufidula type plants, if further, more detailed observations confirm this speculation, may have been an important evolutionary influence in the development of such possibly fly-adapted structures as the enlarged nectar gland which presents diffuse, glistening, ultra-violet absorbing nectar (Percival 1965) as well as reduced petal size, papillae, and showiness in S. integrifolia var. leptopetala. The evolution of gynodioecy in S. integrifolia may also be correlated to such a pollinator shift if selection favors proportionately more outcrossing events to compensate for irregular and unreliable fly visitors (Percival 1965, Faegri and van der Pijl 1966).

TAXONOMYSpecies Definition In This Complex

The definition of a species in this complex group of taxa must allow for overlaps in variability and the morphological intermediacy of many specimens. Hence, it must focus on the clusters of variability which exist around certain morphological characteristics. Isolating mechanisms which restrict gene flow are considered of secondary importance to morphological trends in arriving at a workable classification in this particular group. If the presence of intermediates and evidence of gene flow are used as main criteria for treating the taxa at a subspecific level, the resulting species are extremely large and variable with unmanageable ranges in morphology, ecology, cytology, etc. When these entities are included in regional floras, perhaps a functional approach would be to treat them as species aggregates in the main key with a separate, more precise key to the aggregate taxa.

## Key To The Species

The following key does not discriminate varietal or subspecific taxa within S. integrifolia or S. oregana sensu Hitchcock and Cronquist (1973) or the taxa peripherally related to S. occidentalis such as subspecies of S. marshallii, S. reflexa, or the S. nivalis-tenuis complex sensu Krause and Beamish (1972, 1973). Saxifraga integrifolia and S. oregana are not included in the following descriptions. A shorter, simplified key is presented in the Appendix. It is designed for identification of the majority of specimens, but many intermediate or hybrid specimens will not identify easily using that key.

A. Ovary less than half inferior at anther dehiscence and scapes .5m or less tall (nearly to about half inferior in some hybrid entities of S. occidentalis and S. gormanii; petiole distinct, usually more than 2x as long as wide; leaf margins from shallowly sinuate-dentate to, more commonly, rounded or square-dentate (if teeth markedly reduced or near absent see lead AA); petals usually 2.5mm or greater (sometimes small, greenish, reddish or lacking in alpine forms of S. occidentalis, C and S. aequidentata, CC).

B. Nectar gland at anthesis a swollen, cylindric or doughnut-shaped ring that almost covers the ovary; rhizomes forming a fine network rarely present or as a few small reddish-brown fragments in pressed material; leaves tapering abruptly into an elongate petiole; ovary usually



from 1/3 to about 1/2 inferior at anther dehiscence.

..... Saxifraga gormanii -1.

BB. Nectar gland reduced to a narrow band, ringing the ovary wall; rhizomes short, stout, with few branches, horizontal; leaves tapering more or less gradually from the blade into a petiole; ovary 1/3 or less inferior at anther dehiscence.

C. Inflorescence usually from conical to a tightly clustered headlike panicle; filaments usually clavate to sometimes narrowly oblanceolate; teeth on leaf margins square-dentate; petals usually tapered into a somewhat narrowed base; gland from inconspicuous to a somewhat broadened band.

..... S. occidentalis 2.

CC. Inflorescence usually flat topped to obtuse conical, not tightly clustered into a dense headlike panicle; filaments linear or subulate, rarely slightly clavate or oblanceolate in montane forms; teeth on leaf margins sinuate-dentate to squarish-dentate; petals with a rather broad base; gland an inconspicuous, narrow band.

..... S. aequidentata -3.

AA. Ovary half or more inferior at anther dehiscence (becoming superior in fruit in some cases) or, if less than half inferior, then scapes exceeding .5 meters; petiole from almost lacking, to elongate and narrow; leaf margins entire or minutely denticulate to shallowly or unevenly sinuate-dentate; petals about 2.5mm or less (greater in

S. integrifolia, see DD and S. latipetiolata, E).

D. Petioles almost lacking, short and broad usually less than 2x as broad as long; leaf blades tapering gradually into petiolar region; margins uneven undulate dentate to shallowly and unevenly sinuate dentate; vestiture in inflorescence often with long, clear or merely pinkish glandular hairs.

E. Scapes usually less than 0.5m; plants in moist grassy soil of Northwest Oregon Coastal Range mountaintop "balds".

..... S. latipetiolata 4.

EE. Scapes often 0.5m or greater; plants in boggy or swampy places from the Sierra Nevada north to the Cascades of central Washington and west throughout the Rockies Mountains.

..... S. oregana.

DD. Petioles elongate even if reduced in length, distinctly narrowed and evident; leaf blades tapering gradually or abruptly into petiolar region; margins various, commonly nearly entire; vestiture in inflorescence usually with dark reddish-tipped glands.

..... S. integrifolia.

1. Saxifraga gormanii Suksdorf Torrey 23:106. 1923. (M.W. Gorman 4081, Elk Rock, Multnomah Co., Oregon, June 2, 1917 WS!)

S. marshallii f. dentata Engl. & Irmsch. Pflanzenr. IV, 117, 1:36. 1916. (Heller 10059, Elk Rock, near Oswego, Clackamas Co., Oregon)

S. occidentalis Wats. var. dentata (Engl. & Irmsch.) C.L. Hitchc., Vasc. Pl. Pac. Northw., Univ. Wash. Press, Hitchcock et al. III:149. 1961.

Perennial, rosette-forming herb with dark, reddish, delicate, deeply-growing and branching rhizomes. Leaves simple, exstipulate; blades elliptic to ovate, tapering abruptly or somewhat gradually into a distinct petiole usually more than 2x as long as broad, glabrous above, from near glabrous to sparsely rusty villous below; margins from subentire (in some tetraploid introgressants with S. integrifolia var. claytoniifolia) to sinuate dentate; teeth nearest apex about 0.5 mm long. Inflorescence several-flowered (20-81), open, conical paniculate; rachis indefinite or evident. Flowers perfect, regular 5-merous; sepals spreading or ascending; petals about 2.5 mm long or longer, white, tapering gradually to a broad base, mostly deciduous in fruit; anthers orange to yellow; filaments linear to subulate (rarely clavate in intermediates with S. marshallii subsp. marshallii; carpels broadly pyriform at anthesis; gland swollen, doughnut-shaped, surrounding the upper portion of the ovary; ovary usually less than 1/2 inferior at anther dehiscence; gland remnant often a linear ridge encircling the fruit. (n=10,19,20) March to April. Rocky cliff-sides in vernal wet seeps or moist places from Clatsop

County, Oregon east to Cowlitz Co, Washington and south to Lincoln and Marion Counties in Oregon.

### Representative Specimens

OREGON: Clatsop Co.: exposed bare slope of main westernmost summit peak, Saddle Mt. State Park, on Saddle Mt., ca. 3225', 3 June 1973, K.L. Chambers 3752 (WTU, UBC); rock crevices and bluffs, near Astoria, 6 May 1933, G.P. Baker s.n. (ORE); Lincoln Co.: Otter Crest, 26 March 1930, anonymous s.n. (ORE); Tillamook Co.: exposed knobs, ridges above burned forest, gravelly slopes, Tillamook Burn area, N. Wilson River Hwy., exactly 3 mi se. of Blue Lake, 3000', 6 June 1975, K.L. Chambers 4065 (OSC).

The following specimens tend to resemble S. integrifolia var. claytoniifolia in their greater plant size (ca. 20 cm), more nearly half inferior ovaries, and reduced teeth: OREGON: Columbia Co.: damp rocky bluffs, about waterfalls, s. fork of Clatskanie Creek, 10 mi above Clatskanie, 15 May 1927, J.W. Thompson 2447 (WTU); Lane Co.: Hill's Creek, 300', 29 May 1938, L.F. Detling 2783 (ORE).

This specimen is probably a hybrid between S. gormanii and S. integrifolia var. claytoniifolia (pollen is 100% sterile): OREGON: Clackamas Co.: near Milwaukee, Elk Rock, 28 March 1885, anonymous 239 (ORE).

2. Saxifraga occidentalis S. Wats. Proc. Am. Acad. 23:264, 1888.

S. saximontana E. Nels. Erythea 7:168. 1899.

Micranthes occidentalis Small, N. Am. Fl. 22(2):144. 1905.

(J. Macoun. N.C. Yale Mt., B.C. May 17, 1875. CAN)

Micranthes saximontana Small, N. Am. Fl. 22(2):145. 1905. (A. & E. Nelson, 5917, Yancey's, Yellowstone Natl. Park July 17, 1889 MINN!)

Micranthes lata Small, N. Am. Fl. 22(2):145. 1905. (John Macoun, Lytton, B.C. April 16, 1889)

Micranthes allenii Small, N. Am. Fl. 22(2):144. 1905. (O.D. Allen 242, Goat Mountains, Wash. June 27, 1896)

S. lata Fedde, Just Bot. Jahresb. 31(1):613. 1906.

S. allenii Fedde, Just Bot. Jahresb. 31(1):613. 1906.

S. microcarpa Johnson, Minn. St. Pl. Sci. 4:25. 1923. (M.F. Elrod 98a, Missoula, Mont. MINN!)

S. occidentalis var. wallowensis Peck, Leaflet West. Bot. 5:60. 1947. (Peck 18542, above Ice Lake, Wallowa Mts., Wallowa Co., Oregon July 4, 1894)

S. occidentalis var. allenii C.L. Hitchc., Vasc. Pl. Pac. Northw., Univ. Wash. Press, Hitchc. et al., III:49. 1961.

Perennial, rosette-forming herb with short, stout, seldom-branching rhizome. Leaves simple, exstipulate; blades ovate to obovate tapering gradually or sometimes abruptly into a distinct petiole, usually glabrous above, or rarely puberulent, sparsely to distinctly rusty villous below; margins usually square dentate; teeth nearest apex usually ca. 5mm long or longer. Inflorescence several-flowered (13-50), paniculate to densely clustered headlike paniculate, conical to spherical in more headlike individuals; rachis indefinite or distinct. Flowers perfect, regular, 5-merous; sepals spreading to somewhat reflexed; petals about 2.5 mm long, white, usually tapering

abruptly or gradually to a narrow, clawlike base; anthers orange to yellow; filaments usually at least slightly clavate to definitely clavate (although not petaloid); carpels elongate, bottle shaped at anthesis; gland a band-like ring encircling the ovary wall; ovary  $1/3$  or less (sometimes almost  $1/2$ ) inferior at anther dehiscence. Styler beaks recurved in fruit; gland remnants usually inconspicuous. (n=10,19,28,29) April to August. Rocky outcrops, cliffsides and mountaintops adjacent to vernal streamlets, seeps, wet rock faces or moist areas in shallow soil (about 7 cm deep), widespread in the Rocky Mountain region and north Cascades from Washington, Idaho, and Montana north to Southwestern Alaska and adjacent Yukon.

#### Representative Specimens

ALBERTA: rocky slope above Bertha Lake, Waterton Lakes Natl. Park, 21 June 1930, W.C. McCalla 3618 (MIN); BRITISH COLUMBIA: among rocks, Atlin Hot Springs, 2250', 5 July 1914, E.M. Anderson 2420 (V); Lillooet, 13 May 1916, E.M. Anderson 2419 (V); rock outcrops, Manning Park, Blackwall, 14 July 1960, K.I. Beamish, F. Vrugtman 60805 (V, UBC); calcareous foot of glacier, Cougar Valley, Selkirk Mts., 1600', 18 July 1908, F.K. Butters and E.W.D. Holway 340 (MIN); meadow, Mt. Robson Park, Snowbird Pass, 9 Aug. 1975, C.C. Chuang 751399 (V); glacial moraines, Sphinx Glacier foreland, Garibaldi Park, 5000', 26 Aug. 1965, B. Fraser s.n. (UBC); rockslide above river on e. wall, Alexandria Bridge, 3500', 18 April 1934, E.T. McCabe 758 (UC, WTU); Cronin Mt., 10 mi s. of Smithers, 1 July 1967, G.

Mendel 127 (V); wet crevices, Cathedral Lakes, Mt. Bcmford, Ashnola Distr., 7000', 12 July 1951, T.M.C. Taylor 1346 (WS,UC); Marble Mts., Lake Bootahnie, 5000', 20,25 June 1938, J.W. and E.M. Thompson 70 (UC,WS,MIN); McComal Creek Quadrangle, ca. 2 mi w. of sw. corner of Thutade, Stikine Mt., 4500', 14 June 1969, S.L. Welsh, K. Rigby 9109 (BRY). IDAHO: Kootenai Co.: June 1892, J.E. Hieberg s.n. (ORE); Custer Co.: among rocks in seepage from snowbank, common, Mt. ssw. of Alturus Lake, Stanley, n=10, 11 Aug. 1969, D.L. Krause 68 (UEC). MONTANA: Beaver Head Co.: top of Odell Peak, Picneer Range, 24 July 1946, C.L. Hitchcock and C.V. Muhlick 14925 (WS); Deerlodge Co.: ca. 18 mi s.w. of Anacnda on e. slope above trail between Storm Lake Pass and Goat Flat just on Goat Flat side of a large limestone outcropping, 9100', 7 July 1974, P. Elvander 443 (WTU). Glacier Co.: grassland on well drained soil, 2.6 mi n. of St. Mary, 4 July 1950, D. Lynch 6284 (WS); NEVADA: Elko Co.: infrequent in crevices of rocks along stream bank, 1/2 mi above Thomas Canyon Campgrounds, La Moille Canyon, 15 June 1941, A.H. Holmgren 1122 (UC). OREGON: Grant Co.: rocky slope, ne. of summit of Strawberry Mt., 8900', 1 Aug. 1953, A. Cronquist 7703 (WS,WTU); Wallowa Co.: steep exposed slopes of Pete's Point, 19 July 1962, G. Mason 5478 (OSC). WASHINGTON: Snohomish Co.: under dripping cliffs, Mt. Dickerson, Cascade Mts., 5000', 17 July 1932, J.W. Thompson 8853 (WTU); Okanagan Co.: rocky outcrops, below Slate Peak at the head of the Slate Fork of the Paysatan River, 28 July 1940, M. Ownby, F.G. Meyer 2299 (WS,ORE,OSC,MIN,UC); Pierce Co.: rocky slope, Mt. Rainier Natl. Park, Crystal Mt. Indian Henry's, 2 July 1928, F.A. Warren 785 (WS); Skamania Co.:

shallow rocky soil, Sisters Rock, Columbia Natl. Forest, 4000',  
 7 June 1945, D.C. Ingraham 1877 (WS, OSC); Spokane Co.: damp rocky  
 hillside, near Latah Creek, se. of Spangle, 12 May, 27 June  
 1916, W.S. Suksdorf 8616 (WS); Whatcom Co.: shallow soil on  
 rocky slopes at timberline, Mt. Baker, 6200', 11 July 1922, H.L.  
 Mason 3871 (UC). WYOMING: Grand Teton Natl. Park: moist mossy  
 hillside, Cascade Canyon, 7500', 19 June 1933, L. Williams 1135  
 (OSC).

3. Saxifraga aequidentata (Small) Rosend. In Engl. Bot. Jahrb.  
 37, Beibl. 83:70, 1905.

Saxifraga rufidula (Small) James Macoun Ottawa Nat. 20:162.  
 1906.

Micranthes rufidula Small, N. Am. Fl. 22(2):140. 1905. (John  
 Macoun, Mt. Finlayson, Vancouver Island May 17, 1887 NY)

Micranthes aequidentata Small, N. Am. Fl. 22(2):145. 1905.  
 (Suksdorf 967, Lower Cascades, Skamania Co., Wash. WS)

S. rufidula f. major Engl. & Irmsch. Pflanzenr. IV, 117, 1:39.  
 1916.

S. rufidula f. minor Engl. & Irmsch. Pflanzenr. IV, 117, 1:39.  
 1916.

S. klickitatensis Johnson, Minn. Stud. Pl. Sci. 4:25. 1923.  
 (Suksdorf, Klickitat Co., Wash. April 9 and May 1883 WS!)

S. occidentalis Wats. subsp. rufidula Bacigalupi in Abrams,  
 Ill. Fl. Pac. St. 2:366. 1944.

S. occidentalis var. rufidula Hitchc., Vasc. Pl. Pac.  
 Northw., Univ. Wash. Press, Hitchc. Et al., III:49. 1961.

Perennial rosette-forming herb with short, stout, few



branching, horizontal rhizomes. Leaves simple, exstipulate; blades elliptic to ovate, tapering somewhat gradually to abruptly into a distinct petiole, glabrous above, rusty tomentose to rusty villous below; margins deeply sinuate dentate to somewhat shallowly sinuate dentate; teeth nearest apex usually greater than .5mm long. Inflorescence few-(4-42) to several-flowered (as high as 74), open, spreading, flat-topped, convex or obtusely conical; rachis usually indefinite. Flowers perfect, regular, 5-merous; sepals spreading or ascending; petals 2.5 mm long or longer, white, tapering gradually to a usually broad base, mostly deciduous in fruit; anthers from dark red to yellow; filaments linear or oblanceolate to slightly clavate in some montane forms; carpels narrow, bottle-shaped at anthesis; gland a narrow, inconspicuous band-like ring encircling the ovary wall; ovary 1/3 or less inferior at anther dehiscence. Fruiting styler beaks recurved; gland remnant inconspicuous in fruit. (n=10,19,28 ca. 28,29) Mid February to July. On shallow soil (ca. 3-4 cm) of rocky outcrops and cliffsides in vernal moist, often dripping seeps, washes or rivulets from the Upper Willamette River Area north and east into the Columbia River Gorge, then found from the Olympic Mountains to east central Vancouver Island.

#### Representative Specimens

BRITISH COLUMBIA: Alberni, Vancouver Island, April 1914, W.R. Carter C159 (V); rocky bluffs, Cowichan Lake, Bald Mt., Vancouver Island, 24 March 1940, I.M. Cowan s.n. (V); in

crevices of rocks, soil damp, n. end of Shawnigan Lake, Vancouver Island, (n=10), 20 Feb. 1971, D.L. Krause 1-71 (UBC); mossy wet rocks, Mill Hill, Vancouver Island, 17 March 1895, J.R. Anderson 84 (V). OREGON: Clackamas Co.: Elk Rock Cliffs 2 mi n. of Oswego Lk., (n=10), 17 March 1971, D.L. Krause 9-71 (UBC,UBC); Hood River Co.: open basaltic knolls with Selaginella wallacii, 12.5 mi w. of Hood River along portion Old Columbia River Hwy., 11 April 1958, C.L. Hitchcock and C.V. Mulick 21501 (WS); Lane Co.: steep, gravelly, wet soil, O'Leary Mtn., 2800', 28 June 1938, L.E. Detling 3082 (ORE); Linn Co.: moss mats on e. facing cliff, Santiam R., 20 mi e. of Sweethome, 7 April 1951, A. Cronquist 6828 (WS); Marion Co.: cliff, Silver Creek Falls, 9 April 1940, M. Wright s.n. (OSC); Multnomah Co.: on rocks and rocky cliffs near Elk Rock, 12 April 1903, M.W. Gorman s.n. (herbarium no. 22637) (WTU); along Sandy River at junction of e. Starke Rd. and e. Columbia Hwy., 22 March 1926, M.E. Peck 14521 (OSC); moist slopes, near Multnomah Falls, 18 April 1935, J.W. Thompson 17370 (WS); Wasco Co.: wet cliffs, 6 mi w. of The Dalles on Columbia River Hwy., (pollen fertility, sterile-14, fertile-190, E. Perkins), 27 March 1946, W.H. Baker 274 (OSC). WASHINGTON: Clark Co.: on wet rocks beside road, 1 mi w. of Clark-Skamania Co. line, St. Hwy. 14, n=10, 14 March 1971, D.L. Krause 2-71 (UBC); Greys Harbor Co.: wet cliffs of Mt. Colonel Bob, 3500', 12 July 1930, J.W. Thompson 9404 (UC); Jefferson Co.: rocky crest of Constance Ridge, 5500', 30 May 1931, J.W. Thompson 6583 (OSC); Klickitat Co.: 3 mi e. of Bingen, 300', 26 April 1950, L.S. Rose 50073 (UC); Mason Co.: rock outcrops where protected in narrow canyons, near summit of

Mt. Elinor, 11 June 1940, F.G. Meyer 1783 (WS); Skamania Co.: wet cliffs, Cape Horn, 10 April, 27 May 1920, W. Suksdorf 10365 (WS, UC).

The following specimens, usually of higher mountain areas, show slight resemblances in clavate filaments and clustered paniculate inflorescences to S. occidentalis: BRITISH COLUMBIA: Strathcona Park, Mt. Rooster Comb, Vancouver Island, July 1937, N.C. Stewart 10481 (V). WASHINGTON: Jefferson Co.: ridge, head of Dosewallips R., 6000', 29 July 1921, W.P. Taylor s.n. (UC); Clallam Co.: moist rocky banks, Mt. Angeles, 5000', 16 July 1931, J.W. Thompson 7399 (UC, OSC).

These specimens approach S. marshallii in their clavate filaments, longer pedicels and often reflexed sepals: OREGON: Linn Co.: e. facing cliff along Santiam R., 20 mi e. of Sweethome, 7 April 1951, A. Cronquist 6828 (UC); Lane Co.: steep n. slope, moist, Mt. O'Leary, 4800', 28 June 1938, L.E. Detling 3082 (UC); Marion Co.: cliff, top of House Mt., 31 May 1926, M.E. Peck 14638 (OSC).

These specimens are tentatively classified here as S. howellii Greene but this taxon is doubtfully distinct from S. rufidula. Further work is necessary on this problem. OREGON: Josephine Co.: dried up but lately moist bluffs, Eight Dollar Mt. near Selma, 26 March 1926, L.E. Henderson 5845 (ORE); Douglas Co.: rocky hillside, thin soil, 10 mi Reston Rd., 24 Feb. 1973, M. Williams s.n. (ORE).

4. Saxifraga latipetiolata (C.L. Hitchcock) Perkins and Elvander.

S. occidentalis var. latipetiolata C.L. Hitchc., Vasc. Pl. Pac. Northw., Univ. Wash. Press, Hitchc. et al., III:49. 1961. (M.W. Gorman 3561, Saddle Mt., Clatsop Co., Oregon, June 20, 1915. WTU!)

Perennial, rosette-forming herb with short, stout, seldom branching rhizome. Leaves simple, exstipulate blades ciliate above, sparsely long villous below, widely ovate, tapering gradually to a short, broad, ciliate, petiolar region, puberulent above and below to faintly rusty sericeous below; margins dentate to undulate erose. Inflorescence usually many-flowered (46-231), congested, conic panicle, to a somewhat congested, paniculate (occasionally corymbiform) head; central rachis evident to indistinct. Flowers perfect, regular, 5-merous; sepals reflexed; petals about 2.5 mm long or longer, white, tapering gradually to a broad base, persistent into fruit; anthers yellow; filaments linear; carpels obconic or umbonate obconic; gland a flattened disc covering the top of the ovary at anther dehiscence, grading into the stylar tissue; ovary 1/2 or more inferior at anther dehiscence, becoming superior in fruit. Fruiting stylar beak reflexed; gland remnant a linear ridge encircling the fruit. (n=ca. 38) Late May to early July. Shallow soil of higher volcanic plugs and mountaintop "balds" in moist, grassy areas of Clatsop and northern Tillamook Counties, Oregon.

#### Representative Specimens

OREGON: Clatsop Co.; rocky slopes, Saddle Mt., 2800-3300',

20 June 1915, M.W. Gorman 3561 ISOTYPE (WS); moist open slopes, Saddle Mt., 28 June 1952, J.T. Howell s.n. (UC); Douglas fir-spruce forest, rock crevices nw. exposure, moderate shade, Saddle Mt., 2200', 19 June 1932, L.E. Detling 7906 (ORE).

The following are classified as S. integrifolia but resemble S. latipetiolata in leaf shape, broad short petioles, and white pubescence on the upper leaf surface: OREGON: Polk Co.: very wet places, Monmouth, 20 May 1893, W.J. Spillman 78 (WS); Marion Co.: gravelly soil, common, Salem, Brooks Pasture, 5 April 1919, M.W. Gorman 4415 (WS); WASHINGTON: Thurston Co.: Rock Prairie, 12 May 1934, I.C. Otis 1893 (WS).

## CONCLUSIONS

The present studies indicate that a reassessment of the S. occidentalis species complex is necessary. The varietal taxa which Hitchcock et al. (1961) and Hitchcock and Cronquist (1973) list for S. occidentalis, namely rufidula, dentata, and latipetiolata, are not merely entities which represent distinct evolutionary trends within S. occidentalis. They are morphologically, geographically, and cytologically separated over much of their ranges. Although character intergradation does occur among some taxa in certain areas, especially in polyploid individuals and populations, the distinctions based on certain combinations of characters are sufficient to maintain each of these. Many of the taxonomic difficulties among these taxa can be attributed to hybridization and allopolyploidy involving various members of the S. integrifolia species complex. Autopolyploid evolution in this group appears to be of less importance but it is possible that nearly identical diploid and tetraploid or tetraploid and hexaploid S. aequidentata plants from the same location have arisen directly and without hybridization with other taxa.

Saxifraga aequidentata is confirmed as a cytologically and morphologically variable species in agreement with several previous taxonomic treatments (Small and Rydberg 1905, Macoun 1906, Engler and Irmischer 1916, Krause and Beamish 1973). Some individuals from the Columbia River Gorge area resemble S. occidentalis morphologically but the resemblance may be the result of complex hybridization and polyploidization probably

involving S. integrifolia var. claytoniifolia or its relatives in that area. There is evidence that some introgression between S. integrifolia var. claytoniifolia and S. aequidentata is occurring in sympatric populations along the Columbia River Gorge. The tetraploid S. occidentalis genome is also probably the result of ancient hybridizations and polyploidy perhaps between S. occidentalis and sympatric S. integrifolia progenitors similar to S. integrifolia var. leptopetala. Even if resemblance is the result of past contact and introgression with S. occidentalis it appears that S. aequidentata is presently geographically isolated and genetically distinct with several characteristic morphological features. Artificial hybrids between S. aequidentata and S. occidentalis are pollen and seed sterile and show no greater cytological similarities than crosses involving presumably more distantly related entities. Numerical treatments also tend to distinguish a S. aequidentata group. Columbia River Gorge S. aequidentata populations show closer similarities to S. occidentalis and other polyploid or hybrid individuals than do S. aequidentata plants from Vancouver Island and the Olympic Mountains. The relationship between S. aequidentata and the morphologically similar and cytologically unknown entity, S. howellii, of southwestern Oregon and northwest California deserves further study.

Saxifraga occidentalis is defined as a variable, montane taxon which shows evidence of hybridization in several areas of its range. Detailed examination of its relationships with S. nivalis and S. tenuis as well as with S. marshallii subsp.

marshallii and subsp. idahoensis is necessary. Further work using artificial hybridizations among diploid S. occidentalis, S. reflexa, S. nivalis, subspecies of S. marshallii, diploid S. aequidentata, and S. gormanii would be a useful addition to the present study. A major problem with such studies would be the strong seasonal separation in flowering times among these plants which are adapted to flowering regimes in diverse altitudes and latitudes.

Saxifraga gormanii Suksdorf, formerly S. occidentalis var. dentata, is treated here as a separate species from S. occidentalis and S. aequidentata, formerly S. rufidula, with a distinguishable morphology and a geographical distribution in the Coast Range and Lower Willamette River of Oregon extending north to Clark County, Washington. The type location is Elk Rock, Oregon and specimens from that site closely resemble nearby tetraploid plants ( $n=20,19$ ). Tetraploids group with diploid populations in the numerical studies. Artificial hybrids between tetraploid S. occidentalis and tetraploid S. gormanii are sterile and consistently fail to undergo meiotic divisions in anther tissue, in contrast to crosses involving S. gormanii and S. aequidentata where meiosis in the F1 hybrid does occur but is irregular and pollen fertility is low. As a group, S. gormanii shows closer phenetic affinities to varieties of S. integrifolia and S. latipetiolata, formerly S. occidentalis var. latipetiolata, than to S. occidentalis or S. aequidentata. Some specimens tend toward S. marshallii subsp. marshallii and further studies, especially in the Willamette River area are needed to clarify this problem.



Evidence is presented that S. latipetiolata (C.L. Hitchcock) Perkins and Elvander is also a separate species from S. occidentalis. Saxifraga latipetiolata has several similarities to S. oregana and the S. integrifolia-complex. Morphological, cytological ( $n=ca.38$ ), and numerical analysis all indicate a hybrid origin and affinities with S. oregana ( $n=38$ ). Other systematic evidence from studies of the S. integrifolia group, S. rhomboidea, and Californian relatives of S. integrifolia (Elvander, personal communication, 1978) confirm that it is probably more closely related to S. oregana. However it is ecologically and geographically isolated from S. oregana and has a number of distinctive morphological features. Therefore it is treated here as a separate species.

Sterile intermediates occur in intermediate habitats in most areas where S. aequidentata comes in close sympatric contact with S. integrifolia or S. integrifolia var. claytoniifolia. These can be recognized morphologically and cytologically or by studies of pollen fertility. Hybrid swarms occur in several areas, some of which may involve S. aequidentata and S. integrifolia var. integrifolia as parental entities but others are more likely the result of previous contact between S. occidentalis or S. marshallii subsp. idahoensis and S. integrifolia var. leptopetala.

Cryptic natural hybrids which resemble one parental entity and undergo abnormal meiosis or exhibit reduced fertility are not uncommon, especially in the Columbia River Gorge area among populations of mixed diploid and tetraploid or tetraploid and hexaploid S. aequidentata plants, but also in other areas and

for other taxa such as S. integrifolia var. claytoniifolia. It is difficult to tell whether these individuals, especially in the Columbia River Gorge, are the result of crosses between two sibling entities with different ploidy levels or segregates of interspecific crosses which closely resemble the parent in morphology and habitat preferences.

One population west of Chehalis, Washington (EP605), (n=29) is apparently an intermediate between S. occidentalis and S. integrifolia. The most reasonable treatment of this problematical population appears to be to classify it with S. occidentalis and further document its unique background. The possibility cannot be excluded that it is a relictual population of a once more widespread entity. Its apparent close relationship to S. integrifolia plants from the Mima and Ft. Lewis, Washington, region needs further investigation. It is treated here as belonging to S. occidentalis.

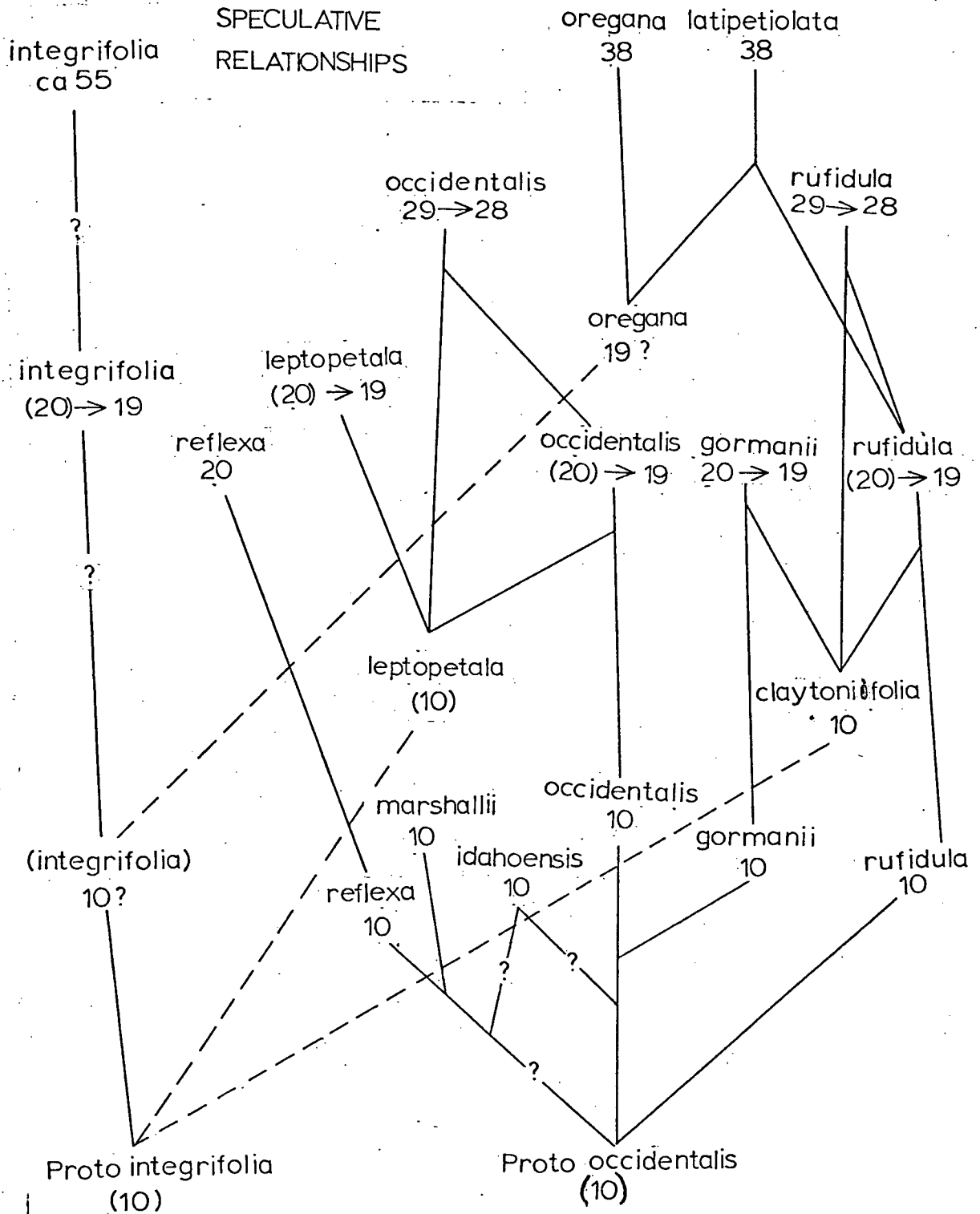
The general pattern of polyploid evolution in the group has most likely been one of several probably independent diploid hybridizations followed by chromosome doubling and coupled with aneuploid reduction (in the absence of an available nine-paired parental species). This cycle has apparently repeated itself in several areas to give rise to higher ploidy levels and introgressant forms. In S. aequidentata populations which exhibit mixed ploidy levels, higher levels of polyploidy may have occurred through the combination of rare unreduced gametes from the same population but hybridization with other taxa, followed by chromosome doubling is more likely. A speculative chart of the relationships involving S. aequidentata and its

allies is presented in Figure 36. The combined difficulties of limited artificial hybrid combinations, possible differences in genetic control of synapsis, and the possibility of extinct parental entities limits the precision of any such speculation.

Bagging tests demonstrate that the plants investigated are most likely facultative sexual outcrossers. There is little evidence in favor of apomictic seed production. The somewhat earlier flowering members of the *occidentalis* group (*S. occidentalis*, *S. aequidentata*, and *S. gormanii*) are capable of setting more autogamous seed and may be frequented by relatively higher numbers of Hymenopteran versus Dipteran pollinators than the *integrifolia* relatives (*S. integrifolia* var. *integrifolia*, *S. integrifolia* var. *claytoniifolia*, *S. integrifolia* var. *leptopetala*, and *S. latipetiolata*). These observations may be correlated with the general differences in floral morphology between the two groups as well as the occurrence of gynodioecy in certain populations of *S. integrifolia* var. *integrifolia*. Although the results of bagging tests and pollination studies show interesting differences between the major species complexes studied, within the morphologically similar *S. occidentalis*-*aequidentata* species group, they are less useful as a taxonomic tool.

The post-glacial history of the group is complex and apparently varied. Randhawa and Beamish (1972) reviewed the evidence for glacial refugia in northwestern North America. The refugial areas apparently contain relictual diploid populations in contrast to widespread polyploid colonizers of surrounding glaciated areas. Randhawa and Beamish (1972) used the

Figure 36: Speculative polyploid formations within the S. occidentalis and S. aequidentata (the synonym rufidula is used in the figure) lineage with emphasis on the Columbia River Gorge relationships. Several other constructions are also logically possible. Numbers in parenthesis are not supported in the literature. Joining lines indicate possible allopolyploid relationships but in certain instances autopolyploidy is probable (CF. S. reflexa). For most others, allopolyploid origins are possible but less likely.

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distribution of 10 and 19 paired populations of S. ferruginea as an example of such a pattern. The narrow southern and western distribution of diploids and widespread ranges of polyploids within S. occidentalis and some members of S. integrifolia conform well to the pattern exhibited by S. ferruginea. Although diploid S. aequidentata populations have recolonized formerly glaciated areas of the Olympic Mountains and Vancouver Island, polyploids and introgressants are abundant in areas south of the glacial boundary presumably resulting from contacts between coastal and interior floristic elements in the Columbia River Gorge. Similar complex hybridization and polyploidization processes are also evident in the history of S. gormanii and S. latipetiolata. Zones of complex hybrid activity such as the Columbia River Gorge may provide the raw materials in the form of more variable gene pools upon which selection can operate in future glacial or interglacial epochs (Stebbins 1971).

Hexaploid and octoploid populations in restricted areas may represent the remnants of a once more widespread distribution or such restriction may be the result of narrow ecogeographic sympatry between two tetraploid or tetraploid-diploid progenitors which have since become locally extinct. The absence of S. oregana from the Coast Range of Oregon appears to be in the latter category with respect to its probable parental relationship to S. latipetiolata.

A thorough examination is necessary of S. integrifolia and its relatives including S. oregana, S. rhomboidea, and S. californica, the latter two perhaps having rather closer ties with S. occidentalis and S. marshallii respectively. There is a

strong need for a systematic study of the relationships between disjunct Western and Eastern North American species pairs (Spongberg 1972) such as S. occidentalis-S. virginianensis, S. oregana-S. pennsylvanica, S. ferruginea-S. michauxii, S. reflexa-S. micranthidifolia and S. marshallii-S. caroliniana. Chromosome counts are incomplete for many taxa, especially those where the field season conflicts with institutional schedules and those which are less accessible. Attention should be given to further systematic investigation of hybrid swarms and areas of introgression in the Upper Willamette River area, the Wallowa Mountains of northeastern Oregon, the Spokane area of eastern Washington, and the higher mountain areas of northern California and southern Oregon.

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APPENDIXInsect Specimens

List of insects captured while visiting Saxifraga flowers: P=with Saxifraga pollen on body or legs; (No.)=number of visitors collected.

HYMENTOPTERA: Vespidae P(2): Polistes fuscatus (1); Formicidae (1); Apidae: Apis mellifera P(3); Bombidae: Bombus spp. P(2); Diprionidae (1); Andrenidae P(11).

COLEOPTERA: Elateridae (1).

DIPTERA: Anthomyidae (3): Scatophaga spp. P(6); Tachinidae P(8); Bombyliidae: Bombylius major P(2); Empidae P(7); Calliphoridae (1); Muscidae: Musca domestica (1); Ceratopogonidae (2); Mycetophilidae P(2); Chironomidae (4); Syrphidae (3): Metasyrphus spp. (5); Dasysyrphus sp. (1); Sphaerophoria sp. (1); Agromyzidae (1).

Figure 37: Map of distributions of S. occidentalis (in Oregon, Washington, and southwestern British Columbia only) and S. gormanii. The single square is the hexaploid intermediate population (S. occidentalis x S. integrifolia).

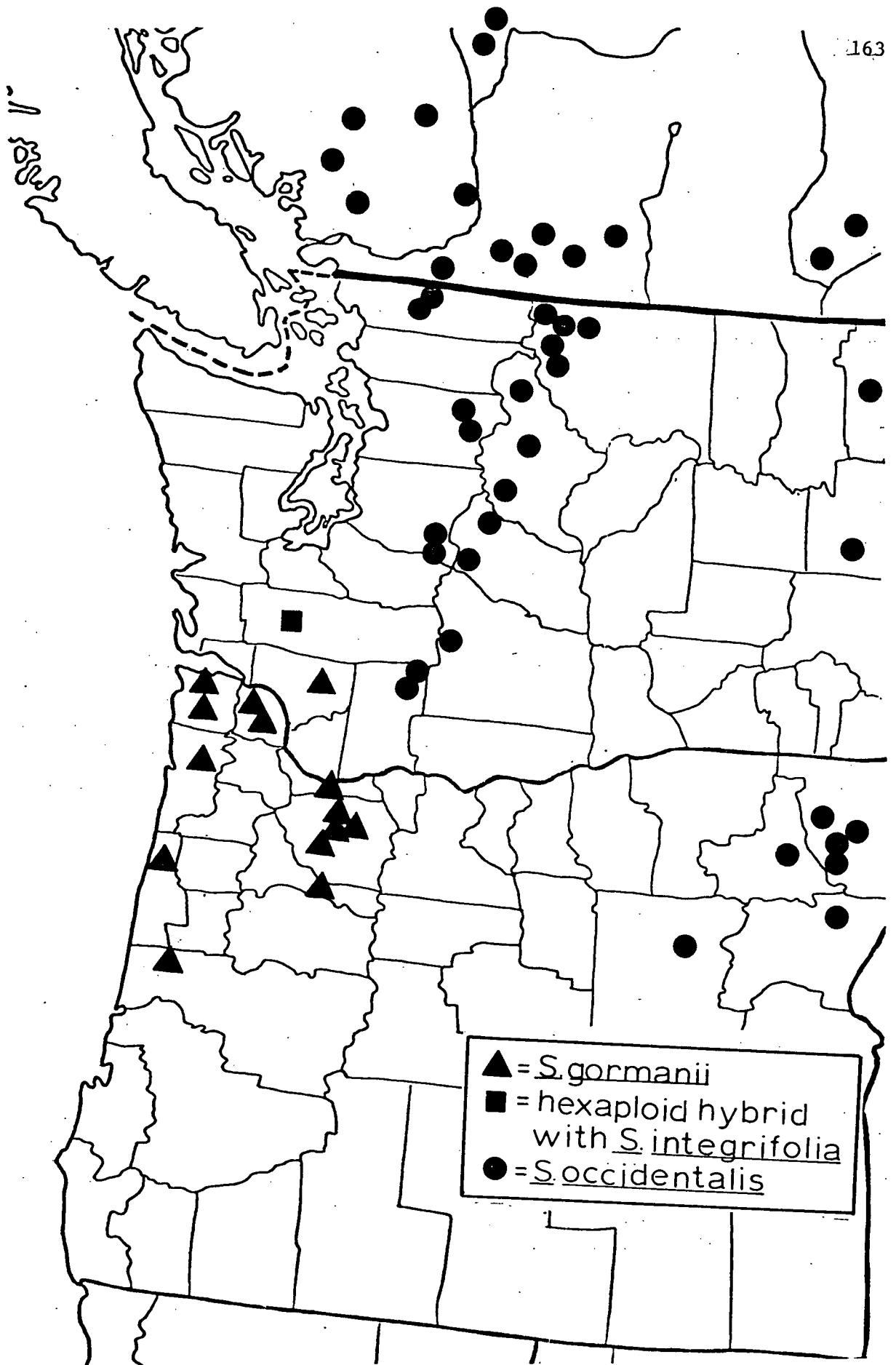
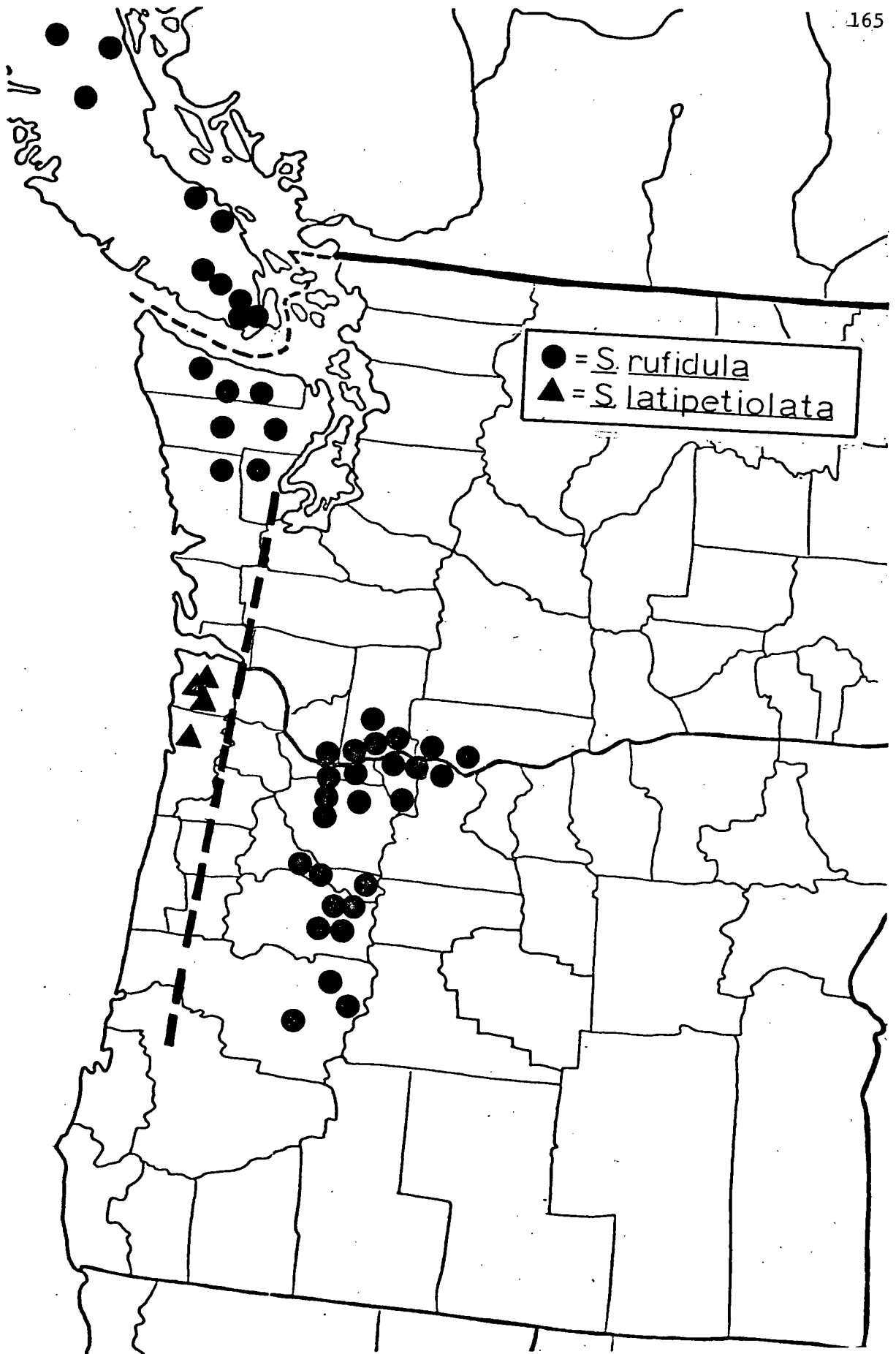




Figure 38: Map of the distribution of S. aequidentata (the synonym, S. rufidula is used in the figure) and S. latipetiolata. Dotted line indicates the western limit of S. oregana and morphologically related !int.



ABBREVIATED KEY

A. Ovary less than half inferior at anthesis; leaf margins shallowly sinuate-dentate to evenly dentate

B. Nectar gland a doughnut-shaped ring at anthesis;  
rhizomes, when present, a fine, reddish brown network

.....S. gormanii

BB. Nectar gland reduced to a narrow band; rhizomes short,  
stout, horizontal

C. Inflorescence flat-topped or obtuse-conical,  
filaments subulate.....S. aequidentata

CC. Inflorescence not flat-topped, usually a  
clustered, headlike to narrowly conical panicle,  
filaments clavate.....S. occidentalis

AA. Ovary half or more inferior at anthesis; leaf margins entire to  
unevenly sinuate-dentate (distantly serrate in S. oregana)

D. Petioles almost lacking, grading into blades; vestiture  
in inflorescence with long, clear or pinkish-glandular hairs

E. Scapes usually 0.5m or less  
.....S. latipetiolata

EE. Scapes usually more than 0.5m

.....S. oregana

DD. Petioles elongate, broadening more or less abruptly  
into blades; vestiture in inflorescence with reddish  
glands.....S. integrifolia