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

By

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B.Sc., University of Oklahoma, 1973

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY in THE FACULTY OF GRADUATE STUDIES (Department of Botany)

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

October, 1978

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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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ACKNOWLEDGEMENTS

"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* Schröeder, known as strawberry begonia, strawberry geranium, or mother-of-thousands.

Although several early botanists contributed greatly to the knowledge of the genus (Linnaeus 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 serpens*—*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. *Integrifoliæ* of Engler and Irmscher 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 Berkeley (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>
<thead>
<tr>
<th>Taxon</th>
<th>Collection Code Number</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. rufidula</td>
<td>616</td>
<td>Viento, rest area on Interstate 8, 0.9 mi w. of Viento St. Pk., Hood River Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>608</td>
<td>Troutdale, 1.3 mi s. of Sandy R. Bridge, Multnomah Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>610</td>
<td>Yeon Pk., ca. 1.5 mi along trail to McCord Falls, Multnomah Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>612A</td>
<td>Mayer Pk., 0.8 mi n. of Mayer St.Pk., Wasco Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>613A</td>
<td>The Dalles, 2.0 mi w. of Chynoweth Cr. on Old U.S. Hwy. 30, Wasco Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>637</td>
<td>Mosier, 1.0 mi e. of Mosier on Old Columbia R. Hwy., Wasco Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>673</td>
<td>Lake Crescent, 8.5 mi e. of Fairholm on U.S. Hwy. 101, Clallam Co., Wash.</td>
</tr>
<tr>
<td></td>
<td>675A</td>
<td>Mt. Pleasant, 1.9 mi e. of the Clark-Skamania Co. bdry. on St. Hwy. 14, Clark Co., Wash.</td>
</tr>
<tr>
<td></td>
<td>647A</td>
<td>Washougal, 1.0 mi w. of Clark-Skamania Co. bdry. on St. Hwy. 14, Clark Co., Wash.</td>
</tr>
<tr>
<td></td>
<td>76-1</td>
<td>Marmot Pass, ca. 5 mi s. of Camp Mystery, s.e. of Marmot Pass, Jefferson Co., Wash.</td>
</tr>
<tr>
<td></td>
<td>617A</td>
<td>Bingen, 5.6 mi e. of Bingen, on St. Hwy 14, Klickitat Co., Wash.</td>
</tr>
<tr>
<td></td>
<td>669A</td>
<td>Bingen Lk., 7.4 mi e. of w. bdry. of Klickitat Co. on St. Hwy. 14, Wash.</td>
</tr>
<tr>
<td></td>
<td>672</td>
<td>Cock, 9.8 mi w. of e. bdry. of Skamania Co. on St. Hwy. 14, Wash.</td>
</tr>
<tr>
<td></td>
<td>618A</td>
<td>Skamania Co., 3.5 mi e. of Clark-Skamania Co. bdry. on St. Hwy. 14, Wash.</td>
</tr>
<tr>
<td></td>
<td>645A</td>
<td>Collins, 0.9 mi e. of Collins Depot Rd. on St. Hwy. 14, Skamania Co., Wash.</td>
</tr>
<tr>
<td>NMO-B</td>
<td></td>
<td>Nanaimo, ca. 5 mi s. of Nanaimo on White Rapids Rd., V.I., B.C.</td>
</tr>
<tr>
<td>Taxon</td>
<td>Collection Code</td>
<td>Location</td>
</tr>
<tr>
<td>--------------------------</td>
<td>-----------------</td>
<td>-------------------------------------------------------------------------</td>
</tr>
<tr>
<td><em>S. occidentalis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>var. <em>denata</em></td>
<td>629A</td>
<td>Saddle Mt., on trail to summit near westernmost peak, Clatsop Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>606</td>
<td>Delena, Beaver Creek Falls, 2.8 mi w. of Delena, Columbia Co., Ore.</td>
</tr>
<tr>
<td></td>
<td>630</td>
<td>Tillamook Co., 2.0 mi w. of e. bdry. of Tillamock Co. cn St. Hwy. 6, Ore.</td>
</tr>
<tr>
<td></td>
<td>607</td>
<td>Kalama R., 3 mi e. of Interstate 5 on Kalama R. Rd., Cowlitz Co., Wash.</td>
</tr>
<tr>
<td>var. <em>latipetiolata</em></td>
<td>629C</td>
<td>Saddle Mt., on trail to summit near top, Clatsop Co., Ore.</td>
</tr>
<tr>
<td><em>S. occidentalis</em></td>
<td>605</td>
<td>Chehalis R. (hybrid), 3.3 mi w. of Littel, Lewis Co., Wash.</td>
</tr>
<tr>
<td></td>
<td>626</td>
<td>Yale, ca. 1.5 mi e. and n. of Yale below Can. Hwy. 1, B.C.</td>
</tr>
<tr>
<td></td>
<td>666</td>
<td>Liumchen Ridge, s. of Sardis, B.C.</td>
</tr>
<tr>
<td></td>
<td>CORN</td>
<td>Cornwall Lookout, se. of Hat Creek, B.C.</td>
</tr>
<tr>
<td></td>
<td>687</td>
<td>Boctanie Valley, Skwaha Mt. area n. of Lytton, B.C.</td>
</tr>
<tr>
<td><em>S. integrifolia</em></td>
<td>641</td>
<td>Giliam Co., 1.7 mi e. of w. bdry. Giliam Co. on Interstate 80 n., Ore.</td>
</tr>
<tr>
<td>Collection Code Number</td>
<td>Location</td>
<td></td>
</tr>
<tr>
<td>------------------------</td>
<td>----------</td>
<td></td>
</tr>
<tr>
<td>609</td>
<td>Troutdale, 1.3 mi s. of Sandy R. Bridge, Multnomah Co., Ore.</td>
<td></td>
</tr>
<tr>
<td>611</td>
<td>Rowena, 2.4 mi w. of Rowena overpass on Interstate 80-N., Wasco co., Ore.</td>
<td></td>
</tr>
<tr>
<td>612B</td>
<td>Mayer Pk., 0.8mi n. of Mayer St. Pk., Wasco Co., Ore.</td>
<td></td>
</tr>
<tr>
<td>613B</td>
<td>The Dalles, 2.0 mi w. of Chynoweth Cr. on Old U.S. Hwy. 30, Wasco Co. Ore.</td>
<td></td>
</tr>
<tr>
<td>667</td>
<td>Biggs, 1.25 mi e. of jct. with U.S Hwy. 97 on U.S. Hwy. 30, Sherman Co., Ore.</td>
<td></td>
</tr>
<tr>
<td>675B</td>
<td>Mt. Pleasant, 1.9 mi e. of the Clark-Skamania Co. bdry. on St.Hwy. 14, Clark Co., Wash.</td>
<td></td>
</tr>
<tr>
<td>668</td>
<td>Lyle, 1.6 mi n. of jct. with St. Hwy. 142, Klickitat Co., Wash.</td>
<td></td>
</tr>
<tr>
<td>669B</td>
<td>Bingen Lk., 7.4 mi e. of w. bdry. of Klickitat Co. on St. Hwy. 14, Wash.</td>
<td></td>
</tr>
<tr>
<td>617B</td>
<td>Bingen, 5.6 mi e. of Bingen, on St. Hwy 14, Klickitat Co., Wash.</td>
<td></td>
</tr>
<tr>
<td>619</td>
<td>Clark Co. line, bdry. with Skamania Co. on St. Hwy. 14, Wash.</td>
<td></td>
</tr>
</tbody>
</table>

*S. integrifolia* var. *integrifolia*

<table>
<thead>
<tr>
<th>Collection Code Number</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>671</td>
<td>Grizzly Lk., about 0.5 mi downstream from Grizzly Lk. Siskiyou Co., California</td>
</tr>
<tr>
<td>MIMA</td>
<td>Mima Mounds, w. of Little Rock on Rd. to Mima, Thurston Co., Wash.</td>
</tr>
<tr>
<td>623B</td>
<td>Sooke, s. side of Sooke R. at Potholes Pk., V.I., B.C.</td>
</tr>
<tr>
<td>624B</td>
<td>Mill Hill, Mill Hill Capital Dist. Pk., Victoria, V.I.,B.C.</td>
</tr>
<tr>
<td>627B</td>
<td>Mt. Finlayson, Goldstream Prcv. Pk., V.I., B.C.</td>
</tr>
<tr>
<td>Taxon</td>
<td>Collection Code Number</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td><strong>NJ30-B</strong></td>
<td>Nanaimo, ca. 5 mi s. of Nanaimo on White Rapids Rd., V.I., E.C.</td>
</tr>
<tr>
<td><strong>NOOS-B</strong></td>
<td>Nanoose Hill, ca. 15 mi n. of Nanaimo on Nanoose Hill, V.I., B.C.</td>
</tr>
<tr>
<td><strong>625</strong></td>
<td>Yale, ca. 1.5 mi e. and n. of Yale below Can. Hwy 1, B.C.</td>
</tr>
<tr>
<td><strong>617B</strong></td>
<td>Bingen, 5.6 mi e. of Bingen on St. Hwy. 14, Klickitat Co., Wash.</td>
</tr>
<tr>
<td><strong>78-1</strong></td>
<td>Harrison Lk., 1.5 mi w. of Harrison, Hot Springs, B.C.</td>
</tr>
<tr>
<td><strong>682</strong></td>
<td>Elk Falls, below Campbell Lk. Dam, V.I., B.C.</td>
</tr>
<tr>
<td><strong>S. integrifolia</strong></td>
<td>648</td>
</tr>
<tr>
<td><strong>var. leptopetala</strong></td>
<td></td>
</tr>
<tr>
<td><strong>S. oregana</strong></td>
<td>BERH</td>
</tr>
</tbody>
</table>
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 (Alexopoulcos 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

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

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. *latipetioloata* 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. *latipeticlata* 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.
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. 3A,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. 3C), *S. occidentalis* var. *latipeticlata* (Fig. 2A), and members of the *S. integrifolia – oregana* complex (Fig. 3D-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. 3A-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.
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. *integri folia*. 
*Saxifraga occidentalis* var. *latipeti olata* 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. *latipeti olata*, 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. 9A-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 papilloscity 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 \((n=29, \text{Fig. 13C, D})\). 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.

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

*Numbers in parentheses indicate the number of plants with the particular chromosome number.
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<tr>
<th>Taxa, locations (collection no.)</th>
<th>No. Plants</th>
<th>No. Cells</th>
<th>Meiotic Chromosome No (II or IIII)*</th>
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<tr>
<td>occidentalis x integrifolia pop. Chehalis R., Wash. (605)</td>
<td>4</td>
<td>11</td>
<td>28,29(3)</td>
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<tr>
<td>latipetiolata Saddle Mt., Ore. (629C)</td>
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<td>23</td>
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<td>3</td>
<td>19</td>
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<td>2</td>
<td>19</td>
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<td>Elk Falls, V.I., B.C. (682)</td>
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<td>Harrison Lake, B.C. (78-1)</td>
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<td>3</td>
<td>19</td>
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<td>Yale, B.C. (625)</td>
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<td>2</td>
<td>19</td>
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<td>19</td>
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<tr>
<td>Bingen, Wash. (617)</td>
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<td>1</td>
<td>19</td>
</tr>
<tr>
<td>Mima Mounds, Wash. (MIMA)</td>
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<tr>
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<td>16</td>
<td>10(4),19</td>
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<td>12</td>
<td>10,8+11(4)</td>
</tr>
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<td>27</td>
<td>10(3),9+5</td>
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<td>The Dalles, Ore. (613)</td>
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<td>6</td>
<td>10</td>
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<tr>
<td>Biggs, Ore. (640)</td>
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<td>55</td>
<td>10</td>
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<tr>
<td>Clark-Skamania Co. line 3 Wash. (619)</td>
<td>3</td>
<td>20</td>
<td>10</td>
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<td>Gilliam Co., Ore. (641)</td>
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<td>10</td>
</tr>
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<td>Cape Horn, Wash. (646)</td>
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<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Lyle, Wash. (617)</td>
<td>1</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td>Bingen, Wash. (617)</td>
<td>6</td>
<td>30</td>
<td>10(2),14+10, ca.14+13, ca.18+9, ca.23+10</td>
</tr>
<tr>
<td>oregana Berthoud Pass, Colo. (BER)</td>
<td>1</td>
<td>3</td>
<td>ca.36</td>
</tr>
</tbody>
</table>
n=ca. 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.
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
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
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
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, or 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. *claytoniiifolia* 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. *latipetiola* and *S. integrifolia* plants.

A=PMC at diplctene-diakinesis; *S. occidentalis* var. *latipetiola* (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. *latipetiola* (E0629C) n=38
D=PMC at diakinesis; *S. integrifolia* var. *integrifolia* (EPMIMA) n=ca. 47
E=PMC at diakinesis; *S. integrifolia* var. *integrifolia* (EPMNO-I) n=19
Figure 17: Camera lucida drawings of PMC's. Plants from Berthoud Pass, The Dalles, Lyle, Bingen, Troutdale, and Bowena populations. The upper scale is for cells A-C, the lower scale is for cells D-F.

A=PMC at anaphase I; *S. oregana* (EPBBER) 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 Beamish
1973) where diploids, tetraploids, and hexaploids were found in
eone 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.
taylori, 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 = \textit{S. occidentalis} var. \textit{dentata}
- I = \textit{S. integrifolia} var. \textit{integriofilia}
- L = \textit{S. occidentalis} var. \textit{latipetiolata}
- o = \textit{S. occidentalis}
- R = \textit{S. rufidula} (from Vancouver Island and the Olympic Mountains)

where:

1 = \textit{S. rufidula} (R) x \textit{S. integrifolia} (I)
2 = \textit{S. rufidula} (R) x \textit{S. occidentalis} (o)
3 = \textit{S. occidentalis} (o) x \textit{S. occidentalis} var. \textit{dentata} (D)
4 = \textit{S. rufidula} (R) x \textit{S. occidentalis} var. \textit{dentata} (D)
5 = \textit{S. rufidula} (R) x \textit{S. occidentalis} var. \textit{dentata} (D)
6 = \textit{S. rufidula} (R) x \textit{S. occidentalis} var. \textit{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 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.
Table IV.
Hybrid Pollen Fertility.

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<th>Cross Between:</th>
<th>No. Individuals</th>
<th>Average % Fertility</th>
<th>Range % Fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>ruf. (10) x occ. (19)</td>
<td>4</td>
<td>9.9</td>
<td>(0.6-24.0)</td>
</tr>
<tr>
<td>ruf. (19) x occ. (19)</td>
<td>4</td>
<td>19.9</td>
<td>(4.1-33.1)</td>
</tr>
<tr>
<td>ruf. (10) x dent. (19)</td>
<td>3</td>
<td>37.1</td>
<td>(0.7-73.4)</td>
</tr>
<tr>
<td>ruf. (19) x dent. (19)</td>
<td>1</td>
<td>1.0</td>
<td>(1.0)</td>
</tr>
<tr>
<td>occ. (19) x dent. (19)</td>
<td>3</td>
<td>3.0</td>
<td>(0.0-8.2)</td>
</tr>
<tr>
<td>lati. (ca. 38) x ruf. (19)</td>
<td>3</td>
<td>31.0</td>
<td>(2.3-78.5)</td>
</tr>
<tr>
<td>int. (19) x ruf. (10)*</td>
<td>4</td>
<td>2.4</td>
<td>(0.0-4.6)</td>
</tr>
<tr>
<td>int. (19) x lept. (19)*</td>
<td>2</td>
<td>1.8</td>
<td>(1.7-1.9)</td>
</tr>
</tbody>
</table>

* 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 Irmscher'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 Irmscher 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.
Gland Wd. (mm)
- □ ≥ 6
- ○ 4.59
- ◊ ≤ .39

Plant Ht. (cm)

Petal Ln. (mm)
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 \textit{S. occidentalis} var. \textit{occidentalis} (squares, EP626, Yale, B.C.) and Columbia River Gorge \textit{S. rufidula} plants (circles). Triangles represent presumably non-introgressant diploid \textit{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. *claytoniiifolia* (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. *latipetala* 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 characterisitics. 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.
Eigenvector 3

Eigenvector 1
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.
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* 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), gynoecium 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. *latipetiola* and *S. integrifolia* var. *leptopetala* from the other groups while gland height/width ratio (Variable 6) discriminates diploid *S. rufidula*, *S. occidentalis* var. *latipetiola*, and *S. occidentalis* var. *dentata* groups. Petiole length/width ratio (Variable 39) distinguishes *S. integrifolia* var. *claytoniifolia* and *S. integrifolia* var. *leptopetala* and gynoecium 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. *latipetiola* (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 (FP605) 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. claytoniiifolia
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. *claytoniiifolia* 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 points 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. aeguidentata, 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.

<table>
<thead>
<tr>
<th>Selfed by Hand</th>
<th>Bagged Untreated</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. Fruits (Plants)</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Abbreviated Taxa</td>
<td></td>
</tr>
<tr>
<td>ruf. (dipl.)</td>
<td>57 (6)</td>
</tr>
<tr>
<td>ruf. (poly.)</td>
<td>33 (5)</td>
</tr>
<tr>
<td>dent. (dipl.)</td>
<td>82 (4)</td>
</tr>
<tr>
<td>dent. (tetr.)</td>
<td>35 (3)</td>
</tr>
<tr>
<td>occ. (tetr.)</td>
<td>40 (3)</td>
</tr>
<tr>
<td>lati. (n=38)</td>
<td>112 (3)</td>
</tr>
<tr>
<td>int. (tetr.)</td>
<td>13 (2)</td>
</tr>
<tr>
<td>clay. (dipl.)</td>
<td>67 (3)</td>
</tr>
<tr>
<td>lept. (tetr.)</td>
<td>8 (1)</td>
</tr>
</tbody>
</table>

* "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.

<table>
<thead>
<tr>
<th>Abbreviated Taxa</th>
<th>Outcrossed by Hand</th>
<th>Outcrossing Control Untreated</th>
<th>Emasculated Bagged</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>Total</td>
<td>% Good*</td>
</tr>
<tr>
<td>Fruits</td>
<td>Seed</td>
<td>(Plants)</td>
<td>Fruits</td>
</tr>
</tbody>
</table>

- **ruf.**
  - (dipl.): 10(2) 505 59.6 315(8) 7698 66.3 10(2) 608 0.0
  - (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
  - (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. *claytoniiifolia*, 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 \textit{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 \textit{S. occidentalis} var. \textit{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 vernaly 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. virginiciensis*, 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. integripolia* 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. *claytoniiifolia* 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. *claytoniiifolia* 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.

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

* A subsample of *integrifolia* var. *integrifolia* (n=20) from this locality had an average depth of 14.9 cm. Other Columbia River Gorge plants are var. *claytoniiifolia* 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. H₂O (g. dry weight)⁻¹ under plants at five sympatric localities.

<table>
<thead>
<tr>
<th>Site</th>
<th>Date</th>
<th><em>rufidula</em></th>
<th><em>integrifolia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Nanoose</td>
<td>March</td>
<td>1.039*</td>
<td>.565</td>
</tr>
<tr>
<td></td>
<td>April</td>
<td>.801</td>
<td>.675*</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>.514</td>
<td>.216</td>
</tr>
<tr>
<td>Nanaimo</td>
<td>March</td>
<td>1.117</td>
<td>.487</td>
</tr>
<tr>
<td></td>
<td>May</td>
<td>1.014*</td>
<td>.517*</td>
</tr>
<tr>
<td>Mt. Finlayson</td>
<td>March</td>
<td>.995*</td>
<td>.638</td>
</tr>
<tr>
<td>Socke</td>
<td>March</td>
<td>.752*</td>
<td>.725</td>
</tr>
<tr>
<td>Yale</td>
<td>April</td>
<td>occidentalis</td>
<td>integrifolia</td>
</tr>
<tr>
<td></td>
<td></td>
<td>.614*</td>
<td>.426</td>
</tr>
</tbody>
</table>

* 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. Bees</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. rufidula</em></td>
<td></td>
</tr>
<tr>
<td>(NOOS-B)</td>
<td>14</td>
</tr>
<tr>
<td>(NMO-B)</td>
<td>10</td>
</tr>
<tr>
<td>10.5 hrs.; 4, 5 April</td>
<td></td>
</tr>
<tr>
<td>5.25 hrs.; 21, 22 April</td>
<td></td>
</tr>
<tr>
<td><em>S. occidentalis</em></td>
<td></td>
</tr>
<tr>
<td>(Yale-626)</td>
<td>13</td>
</tr>
<tr>
<td>2 hrs.; 19 April</td>
<td></td>
</tr>
<tr>
<td><em>S. integrifolia</em></td>
<td></td>
</tr>
<tr>
<td>(NMO-I)</td>
<td>2</td>
</tr>
<tr>
<td>4 hrs.; 10, 11 May</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>% Bees</th>
<th>No. Wasps</th>
</tr>
</thead>
<tbody>
<tr>
<td>32.5%</td>
<td>29</td>
</tr>
<tr>
<td>19.0%</td>
<td>43</td>
</tr>
<tr>
<td>54.2%</td>
<td>11</td>
</tr>
<tr>
<td>5.8%</td>
<td>32</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Total Visitors</th>
</tr>
</thead>
<tbody>
<tr>
<td>43</td>
</tr>
<tr>
<td>53</td>
</tr>
<tr>
<td>24</td>
</tr>
<tr>
<td>34</td>
</tr>
</tbody>
</table>
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 Antovonics 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).
**TAXONOMY**

**Species 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 gormaniai 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 *Torreya* 23:106. 1923. (M.W. Gorman 4081, Elk Rock, Multnomah Co., Oregon, June 2, 1917 WS!)


Perennial, rosette-forming herb with dark, reddish, delicate, deeply-growing and branching rhizomes. Leaves simple, extstipulate; 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 cliffsides in vernally 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.E. Dotting 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).


Micranthes occidentalis Small, N. Am. Fl. 22(2):144. 1905.
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. Stylar 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, P. 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, P. 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, Ashncla Dist., 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.B. 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, Pioneer Range, 24 July 1946, C.L. Hitchcock and C.Y. Muhlick 14925 (WS); Deerlodge Co.: ca. 18 mi s.w. of Anaconda 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.:


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


Perennial rosette-forming herb with short, stout, few
branching, horizontal rhizomes. Leaves simple, extipulate; 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 stylar 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 cliff sides in vernally 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.Y. Mulick 21501 (WS); Lane Co.: steep, gravelly, wet soil, O'Leary Mtn., 2800', 28 June 1938, L.F. Detling 3082 (ORE); Linn Co.: moss mats on e. facing cliff, Santiam R., 20 mi e. of Sweethome, 7 April 1951, A. Cronquist 6928 (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 Bcb, 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).


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. Letting 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.F. Henderson 5945 (ORE); Douglas Co.: rocky hillside, thin soil, 10 mi Reston Rd., 24 Feb. 1973, M. Williams s.n. (ORE).


Perennial, rosette-forming herb with short, stout, seldom branching rhizome. Leaves simple, extipulate 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 Irmscher 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. aeguidentata, 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. aeguidentata*, 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. aeguidentata* 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. latipetirolata*, formerly *S. occidentalis* var. *latipetirolata*, than to *S. occidentalis* or *S. aeguidentata*. 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. *claytoniiifolia*. 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. aeguidentata, 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-aeguidentata species group, they are less useful as a taxonomic tool.

The post-glacial history of the group is complex and apparently varied. Bandhawa 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. Bandhawa and Beamish (1972) used the
Figure 36: Speculative polyploid formations within the *S. occidentalis* and *S. aeguidentata* (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.
integrifolia ca 55

occurrentis 29→ 28

occidentalis 29→ 28

rufidula 29→ 28

oregana 38

latipetiola 38

occidentalis 19

claytoniifolia 10

occurrentis 20→ 19

gormanii 20→ 19

rufidula 20→ 19

reflexa 20

marshallii 10

idahoensis 10

reflexa 10

Proto integrifolia (10)

Proto occidentalis (10)
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. gormarii* and *S. latipetioluta*. 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 sympoty 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. latipetioluta*.

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. virginiensis*,
*S. oregana*- *S. pensylvanica*, *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.
LITERATURE CITED


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APPENDIX

Insect Specimens

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

HYMENOPTERA: 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: Anthomyiidae (3): *Scatophaga* spp. P(6); Tachinidae P(8); Bombyliidae: *Bombylius major* P(2); Empidiae 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. gormani*. The single square is the hexaploid intermediate population (*S. occidentalis* × *S. integrifolia*).
Figure 38: Map of the distribution of *S. aeguidentata* (the synonym, *S. rufidula* is used in the figure) and *S. latipetiolata*. Dotted line indicates the western limit of *S. oregana* and morphologically related lint.
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*