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Systematics of the *Vic[illegible]ttallii* Complex

by

D. M. Fabijan

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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Supervisor

.....

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Date December 12, 1983

Abstract

Morphological, cytological and phytochemical data were incorporated into numerical and statistical analyses resulting in a revision of *Viola* subsection Nuttallianae. Five species, with three subspecies, were recognized. A basic chromosome number of x = 6 was confirmed in this polyploid complex which includes *V. vallicola*, 2N = 12; *V. tomentosa*, 2N = 12; *V. nuttallii*, 2N = 24; *V. praemorsa*, 2N = 36 and 48; and, *V. bakeri*, 2N = 48. A total of twenty-nine flavonoid compounds were found in leaf tissue extracts from these eight taxa. Identified flavones and flavonols included the arabinose, galactose, glucose, rhamnose, and rutin glycosides of apigenin, kaempferol, luteolin and quercetin. The number of different flavonoid compounds per taxon increased with ploidy level within this complex.

V. vallicola subspecies *vallicola* possessed primarily apigenin glycosides and occurred in Alberta and Saskatchewan. Subspecies *major*, on the other hand, was found to possess predominently kaempferol glycosides and occurred only in the interior of British Columbia. A number of specimens of *V. vallicola* from the Great Basin regions of Idaho and Nevada displayed intermediate flavonoid profiles. The derivation of the subspecies is hypothesized to be a result of isolation on either side of the continental divide during post-glacial northward migration.

V. nuttallii possessed apigenin, kaempferol and quercetin flavonoids suggesting that it is an allotetraploid of *V. vallicola* subspecies *vallicola* and and *V. tomentosa* which also possessed apigenin, kaempferol and quercetin derivatives. *V. tomentosa* has since become restricted in range to the Sierra Nevada mountains and *V. nuttallii* is found only on the east side of the Rocky Mountains. *V. vallicola* has the widest distribution of any of the Nuttallianae, ranging from southern British Columbia to Manitoba and south to Arkansas and Nevada.

V. bakeri and *V. praemorsa* possessed the most diverse flavonoid profiles, up to twenty per taxon, including luteolin aglycone and glycosidic derivatives. Presence or absence of different flavonoid aglycones appeared to be random in the specimens in these taxa. The three subspecies of *V. praemorsa*: *praemorsa*, *linguaefolia*, and *flavovirens*, were recognized by their morphological characteristics, though they appear to represent extremes in a continuous range of variation. The existence of hybrids

supports the hypothesis that other previously recognized subspecific taxa, subspecies *arida* and *oregona*, are the result of hybrid crosses of *V. praemorsa* and *V. bakeri* or with members of closely related subsections.

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Sincere thanks are due to Ian J. Dymock who acted as mentor throughout the course of my studies and as editor in the final analysis.

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I. INTRODUCTION

A. General Introduction

The *Viola nuttallii* complex of the family Violaceae has been identified as a polyploid series; the taxa in this group contain meiotic chromosome complements of 6, 12, 18, and 24. Due to their morphological similarities, they have been difficult to distinguish, resulting in the description of twenty different taxa since *Viola nuttallii* was described in 1814. The *Viola nuttallii* complex thus provided a challenging taxonomic problem.

1. The Family Violaceae

The family Violaceae consists of 16 genera and approximately 800 species of worldwide distribution (Cronquist, 1981). Fourteen of the sixteen genera in the family are restricted to the southern hemisphere and particularly to South America.

Melchior (1925) divided the family into two subfamilies based primarily on floral characters. Leonideae have terminally opening stamens and nut-like fruit, while the Violoideae have introse stamens and capsular fruit. The subfamily Violoideae was further divided into two tribes; the Violeae Gingins was distinquished from the Rinoreae Reiche and Taubert by the possession of zygomorphic flowers in which the lower petal was saccate or spurred. The tribe Violeae was further divided into the subtribes Hybanthinae with two genera, and the Violinae with five genera including *Viola* L. The Violinae are distinguished by a relatively long spurred anterior petal and distinct stamens with appendages extending into the spur.

2. The Genus *Viola* L.

The nearly 400 species of the family Violaceae belong to the genus *Viola*, which is composed primarily of annual and perennial herbs, although shrubby and arboresent species are found in South America (Camp, 1947). Whereas actinomorphous flowers predominate in other genera of the Violaceae, those of the genus *Viola* L. are strongly irregular (Clausen, 1929; Cronquist, 1981).

Camp (1947) proposed Central and South America to be the area of origin of the Violaceae and of the genus *Viola*. He based this hypothesis on the southern distributions of many of the genera in the family, particularly the *Rinorea* which were considered primitive within the family (Cronquist, 1981).

The only genus within the family which is best developed in north temperate regions and in tropical mountains is *Viola* (Figure 1). Its South American members have been shown to possess the greatest number of primitive character states that are most closely related to other members of the Violaceae (Clausen, 1929). Camp (1947) contended that *Viola* was "evolutionarly preconditioned" at high elevations in the Andes for its dispersal via Mexico and North America, into the northern hemisphere.

The approximately 400 species in the genus *Viola* were divided into 14 sections by Becker (1925). Six sections occur in the northern hemisphere, and of these, three are found in North America (Valentine, 1962). The sections Chamaemelanium Ging. (Figure 1) and Viola are distributed in both Asia and North America, while Melanium Ging. is primarily European with one species occuring in North America.

3. The section Chamaemelanium

The section Chamaemelanium contains the greatest number of western North American *Viola* species (Baker, 1949c). Violets of the Chamaemelanium section are distinguished from those of other northern sections by their small stipules, yellow or yellowish flowers with capitate styles, and the presence of cleistogamous flowers on aerial stems (Becker, 1925; Baker, 1935 and 1949c).

Two classifications of the subsections in the Chamaemelanium are shown in Table 1.

Clausen (1964) recognized three Chaemaemelanium subsections: the Pedunculatae the Purpureae, and the Nuttallianae whereas Becker (1925) had grouped all of the species into one subsection, Nuttallianae. The Nuttallianae and Purpureae, which were both composed of large species complexes, had previously been grouped into one subsection, Nuttallianae (Baker, 1949c), which was otherwise identical to Clausen (1964).

The Nuttallianae are distinguished by the presence of glabrous capsules as compared to the appressed, puberulent capsules of the Purpureae; by generally lacking

Figure 1. The worldwide distribution of *Viola* and the section Chamaemelanium Ging. (Clausen, 1929; Camp, 1947). (adapted from)

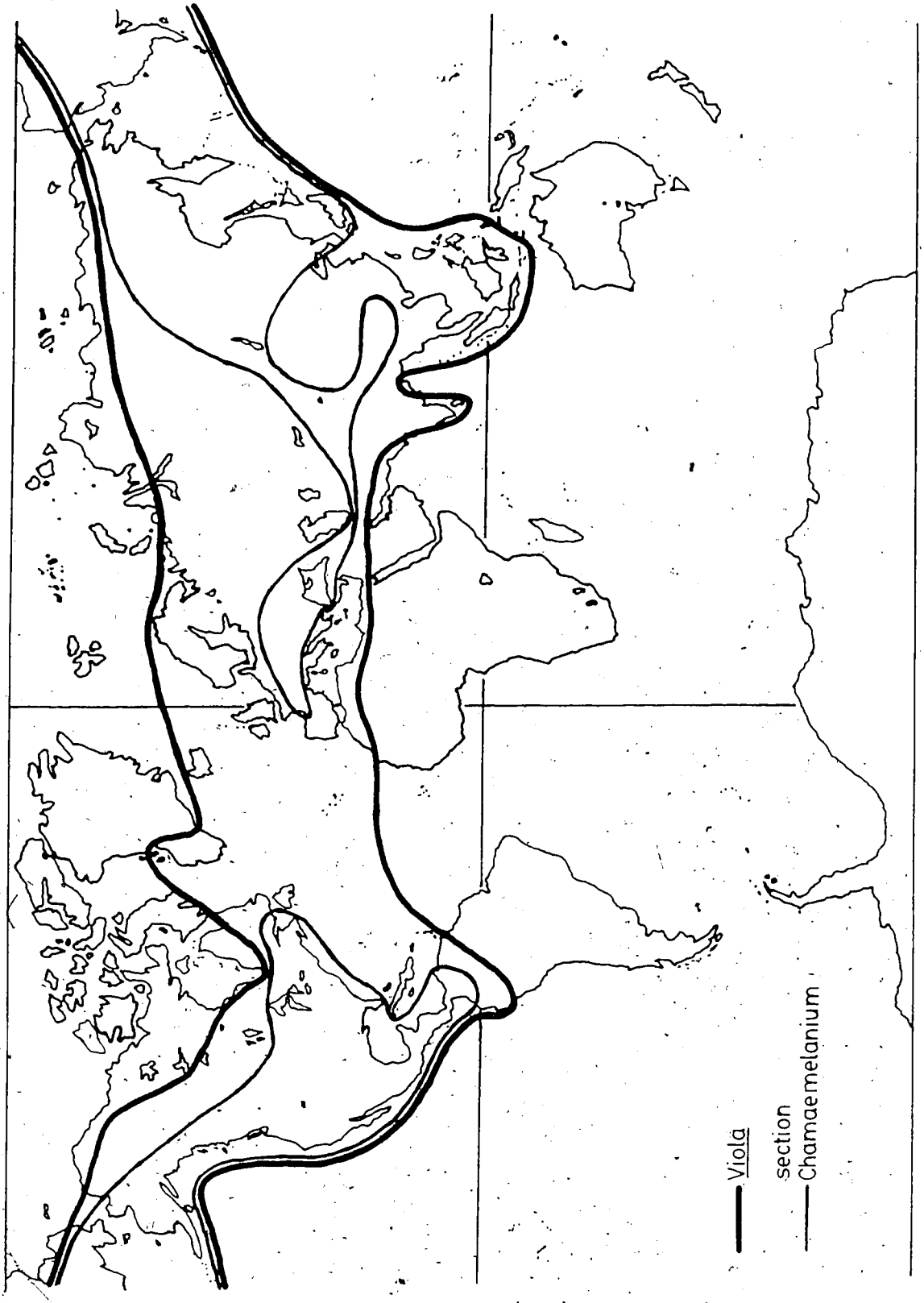


Table 1. The subsections of the Chamaemelanium Ging. (Becker, 1925; Clausen, 1964).

Becker	Clausen
Barroetanae Bckr.	
Nuttallianae Bckr.	Nuttallianae (Bckr.) Cl. Purpureae Cl. Pedunculatae Cl.
Chrysanthae Bckr.	Chrysanthae Bckr.
Erectae - Monophyllos Bckr. - Nudicaulis Bckr. - Canadensis Bckr.	Nudicaulis Bckr. Canadensis Bckr.
Flagelliformes Bckr.	
Section Dischidium Ging.	Biflorae Cl.

elongated aerial stems; and, by size and shape differences in the basal leaves (Baker, 1957; Clausen, 1951; 1964). Further, in contrast to the Purpureae (n = 6), the Nuttallianae constituted a polyploid species complex with chromosome numbers of n = 6, 12, 18 and 24.

Members of the Chamaemelanium section found in western North America and Mexico may represent the prototypes of the temperate *Viola*, constituting a link between South American tropical members and the other northern temperate violets (Clausen, 1929; 1964). The species of the Chamaemelanium were judged to be the most primitive of the *Viola* on the basis of their low chromosome number of n = 6, and the presence of variations in style shape, stigma form, and leaf form found in other sections (Clausen, 1929). Cytological and morphological data coupled with geographic distribution led to a p[illegible]hetic proposal for the northern violets by Clausen (1929), in which the [illegible]elanium section was thought to be the central group from amounst whose members the ancestors of the other northern subsections and sections might have been found.

B. The *Viola nuttallii* Pursh Complex

1. Historical Introduction

Viola nuttallii Pursh was first collected by Thomas Nuttall in 1811 while he was on the Astor Expedition on the Missouri River. Pursh's (1814) publication described a pubescent unbranched plant having ovate-oblong, nearly entire leaves with long gradually tapering petioles.

In 1829, Lindley published the description of a new species by D. Douglas, *Viola praemorsa* Dougl. ex Lindl. It was named for its truncate rootstock, and was distinguished from *V. nuttallii* by possessing denticulate, ovate-oblong leaves covered by hirsute hairs. *V. praemorsa* was found to be abundant on the dry plains of the Columbia River and especially along the Pacific Coast. It was only one year later that Hooker (1930) included in this species a rare form from the Columbia River area, *V. nuttallii* Pursh variety *major* Hook. with wide leaves and large flowers and growing in the shade of pines. He stated that this taxon was related to the collections of Nuttall from the

Missouri River. Hooker also synonymized *V. glareosa* Dougl. with variety *major*, though it was never published.

The Flora of North America by Torrey and Gray (1843) included yet another species description by Nuttall of a plant which he collected in 1834 while accompanying the Wyeth Expedition. *V. linguaefolia* Nutt. ex T. & G. possessed pubescent, oblong-lanciolate and somewhat serrate leaves, being intermediate between those of *V. nuttallii* and *V. praemorsa*.

Based on collections of Heller in Idaho in 1896, Pollard (1897) described *V. flavovirens* Poll. as a tall yellowish-green plant covered with fine hirsute pubescence.

In 1898, *V. bakeri* Greene was described as a pubescent form with entire, ciliate margined leaves intermediate between *V. nuttallii* and *V. praemorsa* from California.

V. vallicola A. Nels. was not described until Nelson (1899) distinguished it from *V. praemorsa* by its finely puberulent or glabrous character and peduncles which did not elevate the flowers above the height of the leaf blades. In 1900 Nelson described another related species from subalpine habitats in Wyoming and Idaho. This species, *V. erectifolia* A. Nels., was distiguished from *V. nuttallii* by its erect leaves being somewhat wider and with a single vertical taproot. Otherwise, *V. erectifolia* appeared to be very similar to the *V. nuttallii* represented by the drawing in Hooker (1830).

Other species continued to be described as related to *V. nuttallii*, for example: *V. gomphopetala* Greene and *V. physalodes* Greene (Greene, 1901), *V. subsagittifolia* Suks. and *V. xylorrhiza* Suks. (Suksdorf, 1927), and *V. russellii* Boivin (Boivin, 1951). New combinations also began to appear for previously described taxa: *V. nuttallii praemorsa* (Piper, 1906), *V. nuttallii linguaefolia* Piper (Piper and Beattie, 1914), *V. nuttallii* var. *vallicola* (St. John, 1937), *V. praemorsa* var. *linguaefolia* (Peck, 1941), to mention but a few.

2. Cytological Investigations

With the advent of cytological methods, new emphasis was placed on chromosome numbers in taxonomic work. Amongst the first plants investigated were members of the genus *Viola* (Miyaji, 1913, in German translation, 1930). Miyaji, in a study of Japanese violets, found meiotic chromosome numbers of 6, 12, 18, 24 and 36–

present in the genus. The cytology of North American violets was first investigated in conjunction with the hybridization studies occuring in the early years of this century (Brainerd, 1904; Gershoy, 1928; 1934).

It was also at this time that Milo Baker, in collaboration with Jens Clausen, began a revision of western North American violets using cytological techniques. Their determinations, which were included in numerous publications between 1935 and 1960, were subsequently summerized with documentation by Clausen (1964). As a result, a number of new combinations were made and new taxa described. *V. tomentosa* Baker (1949a), n = 6, a rare endemic of the Sierra Nevada was similar to *V. bakeri*, n = 24, and *V. nuttallii*, n = 12, but with densely tomentose leaves and capsules. *V. bakeri* subspecies *grandis* Baker (1949a), was described as a larger leaved form of *V. bakeri*. *V. praemorsa* subsp. *linguaefolia* (Nutt.) Baker and Clausen (Baker, 1957), n = 18, and *V. praemorsa* subsp. *major* (Hook.) Baker and Clausen (Baker, 1957), n = 24, represent two new combinations. *V. praemorsa* subsp. *arida* Baker (1957), n = 24, was very similar to subsp. *praemorsa* except for its short and sparse pubescence on leaves and capsules. *V. praemorsa* subsp. *oregona* Baker (1957), n = 24, was found in a few isolated areas in southern Oregon and northern California; it differed from *arida* by having spreading instead of erect foliage, and minutely puberulent capsules.

To this point each taxon was represented by only one or very few chromosome counts. Davidse (1976), in the most recent work on this group, undertook an extensive cytological investigation of the members of the Chamaemelanium section, including some Nuttallianae, in the Intermountain Region between the coastal Sierra Nevada mountains and the Rocky mountains. He confirmed all of the above reports except for *linguaefolia* for which he acquired nine counts of n = 24 (Table 2).

3. Classification of the Nuttallianae

As a basis for discussion, and by way of a summ[illegible]e most extensive work done to date, the classificatioh of Clausen (1964) wil[illegible]e r[illegible] This classification included *V. tomentosa* Baker, *V. bakeri* Greene, *V. nuttall[illegible]* *vallicola* A. Nels., *V. linguaefolia* Nutt. ex T. & G., and *V. praemorsa* Dougl. ex L[illegible] three subspecies *praemorsa*, *major* (Hook.) Baker and Clausen, and *oregona* Baker [illegible]ause

Table 2. Cytology of the Nuttallianae and reported hybrids.

Taxa	N	Reference
Viola tomentosa	6	Baker, 1949a and b
V. bakeri	24	Baker, 1949b
V. vallicola	6	Baker, 1949b; Davidse, 1976
V. nuttallii	12	Baker, 1949b
V. linguaefolia	18	Baker, 1949b
	24	Gershoy, 1934; Davidse, 1976
V. praemorsa		
subspecies *praemorsa*	15	Gershoy, 1928
	18	Gershoy, 1934; Baker, 1949b
subspecies *major*	24	Baker, 1949b; Davidse, 1976
subspecies *oregona*	24	Baker, 1949b
Reported Natural Hybrids		
V. praemorsa		
subspecies *major X V. utahensis* (Purpureae)	18	Davidse, 1976
subspecies *major X V. douglasii* (Chrysanthae)	24	Clausen, 1964
V. tomentosa X V. purpurea (Purpureae)		
subspecies *purpurea*	-	Baker, 1949a; Clausen, 1964
subspecies *integrifolia*	-	Baker, 1949a; Clausen, 1964
V. tomentosa X V. sheltonii (Chrysanthae)	-	Baker, 1949a; Clausen, 1964

The classification of the Nuttallianae by Clausen (1964) has not, however, been accepted universally. Several authors have chosen to designate all taxa uniformly as varieties (Hitchcock and Cronquist, 1961; Scoggan, 1978) or subspecies (Peck, 1961) of *V. nuttallii* due to the lack of sufficient cytological data and the absence of reliable morphological or geographical differences in the cases of some taxa.

In his synopsis of the western North American violets, Clausen (1964) concluded that the 33 taxa within the Chamaemelanium section belonged to at least seven polyploid lines which represented distinct evolutionary sequences. The subsection Nuttallianae comprised two of these polyploid lines, based on two geographically separated diploid species.

The first polyploid line was based on *V. tomentosa*, n = 6, a rare endemic of the Sierra Nevada (Baker, 1949a). This line was thought to be more closely related to the subsection Purpureae (*V. purpurea*, *V. quercetorum*, and *V. utahensis*) than to other members of the Nuttallianae. *V. tomentosa* was presumed most closely related to *V. bakeri*, n = 24, based on morphological characters, although no hexaploid species was known with which it could have hybridized to produce *V. bakeri*.

The second series included *V. vallicola*, *V. nuttallii*, *V. praemorsa*, and *V. linguaefolia*. Clausen suggested that this line arose from *V. vallicola*.

V. nuttallii, n = 12, is a prairie species that remains east of the continental divide in a range extending from the Canadian prairie provinces as far south as Arizona and as far east as Nebraska. It is distinguished by its lanceolate leaves which are attenuated to a long petiole and minutely puberulent throughout, and by arising from a deep-seated rootstock with renewal buds below the soil surface.

V. vallicola, n = 6, has the widest distribution of any taxon in the complex. It is sympatric with *V. nuttallii*, but also ranges into central British Columbia, Washington and Oregon. It has a truncated, vertical rootstock and ovate of oblong leaves which tend to have truncate or subcordate bases (Baker, 1957).

Baker (1957) suggested that *V. nuttallii* was an autotetraploid of *V. vallicola*, although Clausen (1964) questioned this conclusion based on their morphological distinctiveness. He suggested that an undiscovered diploid *V. nuttallii* might exist from which the known tetraploid arose via autopolyploidy. No such diploid has been

discovered and its existence was considered to be unlikely by Davidse (1976).

V. praemorsa subspecies *praemorsa*, n = 18, occurs in the humid regions of the Pacific coast from California to southwestern British Columbia. It was named for the praemorse habit of its roots and is distinguished by its dense, hirsute pubescence throughout, its oblong-ovate leaves with truncate bases, and flowers on peduncles which surpass the leaves in height.

V. linguaefolia is a montane to subalpine violet of the Great Basin Ranges and Rocky mountains, extending northward into Alberta, geogrphically separated from subspecies *praemorsa*. It possesses ovate leaves with cuneate bases that are between *V. vallicola* and *V. nuttallii* in form. This suggested to Clausen (1964) that *linguaefolia* may be a natural amphiploid of these two species.

V. praemorsa subspecies *major*, n = 24, was morphologically very difficult to distinguish from *V. linguaefolia*, n = 18, the only reliable means being cytological. Clausen found it to differ from subspecies *praemorsa* by its erect ovate or oblong leaves which equal or surpass the flowers in height. Subspecies *major* is found from Washington to central California through the Cascade and Sierra Nevada mountains.

Baker (1949b) reported *V. linguaefolia* to be a hexaploid, n = 18, like *V. praemorsa* subspecies *praemorsa*. He postulated that *praemorsa* probably differentiated from *linguaefolia* as a result of westward dispersal through the Columbia Gap to the coast (Baker, 1957). Clausen (1964), on the other hand, suggested that the rise of the Cascade mountains lead to the present geographic separation of these two hexaploids which were once connected across the low plains.

Davidse (1976) could not corrobarate early reports of n = 18 for *linguaefolia* from nine populations in Utah, Nevada, and Idaho. Each population had a count of n = 24 with regular meiosis and high pollen fertility. As no reliable morphological or geographical differences could be found, he considered *V. linguaefolia* to be synonymous with *V. praemorsa* subspecies *major*. Davidse further suggested that the previous count of n = 18 from Utah may have been based on a hybrid between *major* and *V. utahensis* Baker and Clausen (subsection Purpureae), similar to the one reported by him (Table 2).

V. praemorsa subspecies *oregona* has a chromosome complement of n = 24 and reportedly occurs in limited areas of southern Oregon and northern California. Leaves of this taxon are grayish in colour due to a continuous coat of pubescence and similar in form to the ovate- or oblong-lanceolate leaves of *V. bakeri*. Baker (1957) referred to *oregona* as a subspecies in the making and that as such, it was probably the youngest taxon of the *V. praemorsa*.

C. Objectives

The major objective of this study was to attempt to construct a revised classification of the *Viola nuttallii* complex. Related to this was the need to investigate the relationship between *V. vallicola* and *V. nuttallii*, and between these taxa and the remainder of the group.

In order to achieve this, a cytological survey of the members of this complex was undertaken, particularly of those members which occur in Canada. Detailed morphological investigations of the characteristics of this group were also carried out in order to establish a usable classification based on readily observable features which are statistically significant in distinguishing between taxa. Flavonoids present in the leaf tissue of the members of the *V. nuttallii* complex were also examined in order to supplement and corroborate the morphological data.

Numerical techniques provide a powerful tool by which to analyze complex phenetic relationships among groups of organisms (Sokal and Sneath, 1978). Although the resultant classification would be based on data not ordinarily used in routine field identification, it must be correlated with readily observable morphological characters to be of general use. Numerical techniques have the ability not only to supply a classification but also to statistically determine which characters are "good" in the taxonomic sense. These objectives were based on the need to use a holistic approach, that is, to investigate as many aspects of the problem as was practical.

The operational species concept applied in this study was a practical one, following that of Cronquist (1978): "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." This concept incorporates the working assumptions of many plant taxonomists. The smallest groups

are those which cannot be further subdivided and still conform to the definition. Consistent features exhibited by an individual must fit into the range of variation within the group, and, group variation must have a discontinuity with the variation exhibited by other groups. These group variations must be reasonably persistent between generations and must be distinguishable by means ordinarily used by a botanist, that is, using a hand lens. Reproductive isolation is implied by the definition, since phenetic discontinuity cannot be maintained in the absence of some barrier to interbreeding.

For the remainder of this discussion, the taxa in question will be refered to by their specific epithets only, to avoid any confusion as to their taxonomic status.

II. Materials and Methods

A. Herbarium Loans

Specimens from the following herbaria were examined: Arnold Arboretum of Harvard University (A); University of Alberta (ALTA); British Museum, London, England (BM); National Museums of Canada (CAN); Dudley Herbarium (DS) and California Academy of Sciences (CAS), Stanford University; Agriculture Canada (DAO), Gray Herbarium of Harvard University (G); University of Idaho (ID); Jepson Herbarium, University of California (JEPS); KEW Botanical Gardens, England (KEW); Missouri Botanical Garden (MO); University of Pennsylvania (PENN); Academy of Natural Sciences of Philadelphia (PH); Rocky Mountain Herbarium, University of Wyoming (RM); W.P. Fraser Herbarium, University of Saskatchewan (SASK); University of Calgary (UAC); University of British Columbia (UBC); University of California (UC); Smithsonian Institute, U.S. National Herbarium (US); University of Regina (USAS); University of Victoria (UVIC); British Columbia Provincial Museum (V); Willamette Herbarium (WILLU) of Oregon State University (OSU); and, Marion Ownbey Herbarium, Washington State University (WS).

Abbreviations follow those used by Holmgren and Keuben (1974).

B. Collections

1. Field Studies

Field collections were made throughout as much of the reported range of the *V. nuttallii* complex as was possible during the spring and summer of 1981 and 1982. This included the Canadian range, extending from Vancouver Island through southern British Columbia, Alberta, and Saskatchewan; and selected sites in the United States Pacific Northwest including Washington, Oregon, California, Idaho, and Montana. At each collection site, representative members of the population were sampled and pressed for voucher specimens. Others were collected in bulk and air dried for chemical analysis. Pollen and flower buds were sampled and preserved. At least two live plants were potted for transplantation. All materials were subsequently transported to the University of Alberta for cultivation in the greenhouses, deposition of voucher specimens, and/or

detailed chemical and morphological analysis.

2. Greenhouse Cultivation of Live Material

Plants in the greenhouse were maintained under a 16 hour photoperiod throughout the year, supplemented with high intensity discard (HID) lamps which provided a minimum intensity of 80 uE.m^{-2}s^{-1}. Temperature was maintained at 18° C during the day and 15° C during the night. Relative humidity was held constant at 60%.

Some plants were overwintered naturally outside while others were induced into dormancy and stored in a freezer (McPherson, 1972). The dormancy induction schedule covered nine days during which the plants were brought from 18° to -2° C: three days at 12°, two days at 8°, three days at 2 to 4° in darkness, then watered well, placed in sealed plastic bags and stored at -1° to -4° in the dark. After five weeks, the plants were removed from the freezer and returned directly to the greenhouse growing regime. The survival of plants subjected to both natural and artificial overwintering conditions was about 35% for *V. vallicola* and *V. nuttallii*. *V. praemorsa* specimens, which grew well under greenhouse conditions, die back to the roots and regenerated repeatedly throughout the year, and were not subjected to overwintering procedures. *V. nuttallii* and *V. vallicola* also underwent a period of dormancy naturally in the greenhouse but did not regenerate until the following March.

The overall survival of collected specimens following transplantation and cultivation was about 80%. Difficulty of cultivation of these taxa over long periods was reported by Baker (Clausen, 1964).

Seeds were collected from cultivated plants by bagging the expanding capsules in muslin, allowing for retention of the seeds after the dehiscence of the capsule.

3. Cytological Studies

Mitotic chromosome counts were made on root tip squashes prepared from actively growing roots using a modification of the method of Tijo and Levan (1950). Root tips were treated in a 0.002M solution a 8-hydroxyquinoline for 2 to 2.5 hours at 14 to 17° C. Tips were washed in distilled water for 10 minutes, transfered to a watch glass containing aceto-orcein and 1N hydrochloric acid (9:1 by volume) for 30 minutes.

The solution was warmed over an alcohol flame briefly 3 to 5 times in 30 minutes. Tips were then placed on a microscope slide in 45% acetic acid. All but the apical 1mm of the root tip was removed, a cover slip applied, and the preparation was squashed by tapping the coverslip several times. Semi-permanent slides were made by ringing the coverslip with a melted mixture of gum mastic and parafin wax (2:1 by volume). Chromosomes were examined under oil emersion with a green filter using an Olympus BHA,PM-10-M photomicrographic system and photographed with an Olympus C-35 camera.

Cytological examination of pollen mother cells was carried out using the iron-aceto-carmine method (Clausen, 1929; Radford et al., 1974; Sharman and Sharma, 1980). Flower buds were collected in the field and fixed in Carnoy's solution (chloroform:ethanol:acetic acid, 4:3:1 by volume) then transferred to 70% ethanol and stored at -4° C until slide preparation and examination.

4. Pollen Viability Tests

Pollen was collected in the field by dissecting anthers from chasmogamous flowers and placing them directly into small vials containing lacto-phenol cotton blue stain (Radford et al, 1974). Vials were stored under refrigeration for up to four months prior to examination. Pollen stored in this manner showed no significant difference in viability or size from that stained and examined fresh. Pollen was examined at 400X magnification; the diameter was measured using a calibrated occular micrometer.

Viability was estimated as the percentage of pollen grains that were stained dark blue in the 100 grains examined. The diameter of 100 viable pollen grains was measured in up to five pollen samples collected at random from each flowering population. Significance of means was tested using the t-test (Campbell, 1974).

5. Morphological Measurements

Characters were selected on the basis of previous authors' treatments of the *nuttallii* complex (Baker, 1935, 1949b; Clausen, 1964); those used in other descriptions of the taxa; and, through the examination of a wide range of living and herbarium material. As a result, 19 morphological characters were selected for scoring the specimens. Each quantitative character was measured a minimum of ten times. Characters were

scored at the same relative position and developemental stage on each plant.

Measurements of leaf characters (length, width, and basal angle), flower size (length of lower petal including the spur in chasmogamous flowers), length of cleistogamous sepals, length of leaf pubescence, and presence or absence of pubescence on sepals and capsules were made from voucher specimens. Seeds produced by cleistogamous and chasmogamous flowers showed no significant differences in morphological characteristics (length, width, weight, colour, and caruncle size); therefore, no distinction was made between them. Data represent means of from 2 to 100 seeds, the total being dependent on the number of seeds produced by each plant cultivated in the greenhouse facilities.

6. Scanning Electron Microscopy

A Cambridge Spectroscan 250 was used to make detailed examinations of pubescence and surface characteristics of both seeds and pollen. Samples were glued to the specimen stud using two-sided adhesive tape. The material was treated for four minutes in plasma mode in a sputter coater, shadowing it with approximately 15 nm of gold prior to examination.

C. Flavonoid Chemistry

1. Paper Chromatography

A survey of flavonoids from all field collections and selected herbarium specimens was carried out by extracting 25 mg of dry, powdered leaf tissue in 2 ml of 80% methanol overnight on a shaker. One ml of this extract was spotted dropwise on 46 by 57 cm Whatman 3MM chromatography paper. Each chromatograph was subjected to two dimensional descending liquid chromatography. The first solvent was butanol:acetic acid:water, BAW (4:1:5 by volume, upper phase), and the second was 15% acetic acid. Each chromatogram was dried and rotated 90° between the two solvent runs. The resulting chromatograms were examined for colour under ultra-violet light (3660 A); in the presence of ammonia vapor and UV light; and, after spraying with NA reagent (diphenylboric acid-2-amino ethyl ester in methanol).

Tissue from five representative populations (D.F. collections 478, 507, 532, 537, and 648) was extracted for identification of constituent flavonoids. Five grams of dried, powdered leaf tissue from each sample were extracted with shaking in 100 ml of 50% methanol overnight, filtered *in vacuo* and re-extracted in the same manner in 80% methanol. The two filtrates from each sample were bulked, and the aqueous phase reduced to a minimum, at 55° C *in vacuo* using a Buchi rotary evaporator.

At least 36 replicates of each extract were spotted and chromatographed in BAW and Acetic acid as previously described. For each extract, only those compounds from the resultant chromatograms which showed a positive colour reaction to NA reagent during the preliminary survey were investigated further.

For each sample, each compound was coded, the spots on the chromatographic paper cut out, and extracted overnight with shaking in 100% methanol. The extracts were filtered *in vacuo* and evaporated to near dryness at 55° *in vacuo* on a rotary evaporator.

Each compound was checked for purity by subjecting it to one-dimensional descending paper chromatography on 23 by 57 cm Whatman 1MM paper in each of four solvent systems: BAW (A); distilled water (B); 15% acetic acid (C); and, 80% phenol in water (by volume)(D) as described in Harborne (1967). Rf values for each compound in each of these four solvent systems were then determined in comparison to Rutin which was run concurrently on each chromatograph. Any further necessary purification was carried out on Whatman 1MM paper using the solvent system which gave the best separation.

Thin layer chromatography (TLC) was also employed on the purified extracts using four different systems. Polyamid-6 (MN Polygram, 0.1 mm thick) plastic TLC plates were run in two separate systems. System E was an aqueous solvent consisting of water: ethanol:methylethyl ketone (70:20:10 by volume) which took about 90 minutes to run 10 cm. The organic solvent (System F), 1,2-dichloroethane: methylethyl ketone:water (50:25:21:4 by volume) took about 65 minutes to run 10 cm. Cellulose plates (DC-fertigplatten PEI-Cellulose) were run in 15% acetic acid for 10 cm, taking about 50 minutes (System G). Silica gel G plates on glass (System H) were run in a solvent system of methylethyl ketone:acetic acid:water (85:12:3, by volume) for 10 cm which took about 45 minutes.

Thus, each extracted and purified compound was run in eight different paper and thin layer chromatographic systems.

2. Spectral Analysis

Flavonoids exhibit characteristic absorbance peaks when examined in UV and visible light. The two major absorption peaks occur in the 300-400 nm (Band I) and 240-280 nm (Band II) range and are associated with substitutions on the B- and A- rings, respectively, of the flavonoid structure. A flavonoid compound may be characterized by first determining its absorption spectrum in absolute methanol, and secondly, by the addition of five diagnostic reagents: powdered sodium methoxide (NaOMe), to saturation; 6 drops of methanol saturated with anhydrous aluminum chloride ($AlCl_3$); 3 drops of 30% hydrochloric acid (HCl); powdered sodium acetate (NaOAc); and, boric acid (H_3BO_3) as described by Mabry et al., (1970). These spectra were obtained from paper chromatographically purified compounds on a Unicam SP1800 spectraphotometer. Compounds were identified by comparison to published spectral and chromatographic data (Mabry et al., 1970; Jay et al., 1975)

3. Hydrolysis of Flavonoid Glycosides

Hydrolysis of the sugar component of the flavonoid glycosides was carried out under acidic conditions. A portion of the purified extract was transfered to a test tube in methanol. A maximum of 5 ml of 10% hydrochloric acid was added, the test tubes were covered with aluminum foil, and heated at 100° C in a water bath for 90 minutes. On cooling, this mixture was partitioned three times with 2 mls of amyl alcohol, and both fractions were then evaporated to dryness. The alcohol fractions , which contained the aglycones, were redissolved in absolute methanol and subjected to the same spectral analysis described previously.

The acidic aqueous fractions containing the sugar residues were then chromatographed, with standards, on silica gel (DC Fertiplatten S.1 G-25) thin layer chromatography plates. These were chromatographed twice in the same solvent system: ethyl-acetate:isopropanol:water (65:22:11 by volume); then, air dried, sprayed with aniline phthalate reagent (aniline, 4.6 g; Phthalic acid, 8.0 g; n-butanol; 245 ml; ether,

245 ml; and, water, 10 ml), and developed by heating at 100° C for 15 to 30 minutes.

Identification of sugars was accomplished by comparison of Rf values to known standards which were chromatographed at the same time. The most common flavonoid sugar residues, glucose, galactose, rhamnose, xylose and arabinose, were used as standards.

D. Numerical Analysis

Fifty chemical and morphological characters were employed in the statistical and numerical analyses (Table 3) including 48 continuous and two classed characters.

Flavonoid characters were scored as quantitative characters on a continuous scale of 0 to 3 where 0 was absent, and 3 indicated a relatively dark spot was present on the given chromatographic paper. All flavonoids reacting positively to NA reagent were included whether or not they were successfully identified.

Chromosome number and seed colour were included as unordered classed characters though it could be argued that they were continuous. By recording these attributes as unordered classes one avoided the problems of *a priori* designations of linear relationships between the character states and of unequal spacing or unequal size of the classes (Sneath and Sokal, 1973).

The Operational Taxonomic Unit (OTU) was defined here as the sum of all individuals observed from an isolated population of plants, including the voucher specimen, living material, and dried material used in chemical analysis. The major criteria for including OTUs in the numerical analysis was the availability of cytological data, though this requirement was waived in the case of type specimens.

The numerical analysis was performed at two levels: on the individual OTUs to investigate the validity of the taxa, and on the taxa for evaluating phenetic and chemical interrelationships. The individual OTU analysis included cytologically known specimens for which flavonoid analysis was available and selected type specimens for which only limited morphological data could be acquired.

The classification program used to aid in establishing taxa was TAXMAP, a program developed by Dr. J. W. Carmichael of the University of Alberta. TAXMAP was employed in preference to the other available classification programs for a number of

Table 3. Characters used for numerical analysis.

No.	Type[1]	Character name and states	95% CL
1	2	K[2] 3-O rut (0,1,2,3: absent to very dark)	2.00
2	2	A 7-O rut	2.00
3	2	A -	2.00
4	2	K 6-Me,3-O rut	2.00
5	2	-	2.00
6	2	Q 3-O rut	2.00
7	2	Q 3,7-O digly	2.00
8	2	Q 3-O monoglu	2.00
9	2	K 3,7-O rhagal	2.00
10	2	-	2.00
11	2	L 7-O monogal	2.00
12	2	-	2.00
13	2	L aglycone	2.00
14	2	A 7-O monoglu	2.00
15	2	L 7-O monoglu	2.00
16	2	A 6-Me, 7-O ara,glu	2.00
17	2	L 7-O triglu	2.00
18	2	-	2.00
19	2	-	2.00
20	2	-	2.00
21	2	-	2.00
22	2	-	2.00
23	2	-	2.00
24	2	-	2.00
25	2	-	2.00
26	2	-	2.00
27	2	Q 3-O digly	2.00
28	2	-	2.00
29	2	-	2.00
30	5	2N Chromosome number (1,2,3,4: 12,24,36,48)	0.10
31	2	Cauline leaf length (mm)	4.00
32	2	Cauline leaf width (mm)	2.00
33	2	Cauline leaf length / width ratio	0.42
34	2	Cauline leaf basal angle (°)	16.00
35	2	Pubescence length (mm)	0.05
36	2	Margin serration (0,1,2,3: entire to serrate)	0.80
37	2	Margin ciliation (0,1: absent, present)	0.80
38	5	Sepal pubescence (0,1,2,3: absent, auricles, ciliate, all)	0.80
39	2	Petal length (mm)	0.86
40	2	Cleistogamous sepal length (mm)	0.42
41	2	Capsule pubescence (0,1: absent, present)	0.80
42	2	Seed length (mm)	0.09
43	2	Seed width (mm)	0.70
44	2	Seed length / width ratio	0.12
45	2	Seed weight (mg)	0.28
46	2	Caruncle length (mm)	0.10
47	2	Caruncle length / seed length ratio	0.05
48	2	Caruncle covering seed apex(0,1: absent, present)	0.10
49	6	Seed colour (1,2,3,4,5,6: tan, light brown, brown, dark brown, red brown, white)	0.10
50	2	Pollen diameter (um)	0.72

[1]Weighting: 2 = log 2 of number of confidence interval classes in range. Includes continuous state and ordered classes
3 to N - unordered classes; match weight = log 2 N, no-match weight = 1.0

[2]Compounds: A = Apigenin, K = Kaempferol, L = Luteolin, Q = Quercetin, gly = glycoside, glu = glucose, rha = rhamnose, gal = galactose, rut = rutin, - = unidentified.

reasons related to the nature of the data used in this study. TAXMAP is versatile in its requirements for data types, it can handle continuous or real number data, ordered classes and unordered classes simultaneously. Distance calculations can incorporate inherent information content provided by the confidence intervals. A very important feature is the ability to handle missing data.

TAXMAP calculates the ranges of the attribute values, normalizes the raw data as fractions of the range, and then calculates a relative distance between each pair of OTUs. TAXMAP also allows for distance calculations to be made by the weighting of attributes according to their relative information content as given by 95% confidence limits. Both equally weighted and weighted analyses were used. The clustering procedure as outlined by Carmichael (1980), was illustrated by means of a taxometric map (Carmichael and Sneath, 1969). Taxometric maps were drawn with the aid of the Calcomp plotter at the University of Alberta Computing Services or by hand based on the information provided by TAXMAP. The map represents a two-dimensional display of the multi-dimensional hyperspace in which the clusters exist.

Three TAXMAP analyses were performed. Firstly, weighted and equally weighted analyses based on all 50 attributes were made of the 59 OTUs representing the author's collections. It was felt that this represented the most reliable analysis based on the greatest available information. A second analysis making use of morphological data only (21 attributes) was compared to the first analysis. The third analysis was run to include a number of herbarium specimens for which cytological data were available and flavonoid analysis was possible, and a number of type specimens for which only limited morphological data were attainable. This brought the total number of OTUs to 95 (Table 4).

Table 4. Specimens used in TAXMAP analysis.

OTU Number	OTU Name[1]	Location	2N
1	1-572	Chin Lake, 23km S Taber, Alberta. 3000'.	12
2	4-524	Nose Hill, Calgary, Alberta. 3700'.	12
3	9-550	Little Fish Lake, Alberta. 3600'.	12
4	15-567	Spruce Coulee, Cypress Hills, Alberta. 3600'.	12
5	34-516	Leitch Collieries, Crowsnest Pass, Alberta. 4500'.	12
6	35-517	1km S of Bow Crow Forest Entrance, S of Hillcrest, Alberta. 5500'.	12
7	36-519	Lynx Creek, 19km S of Hillcrest, Alberta. 4500'.	12
8	37-520	Castle River, S of Hillcrest, Alberta. 4500'.	12
9	38-523	Beauvais Lake, Alberta. 4500'.	12
10	54d-533	Nose Hill, Calgary, Alberta. 3700'.	12
11	56-551	Hand Hills, N of Little Fish Lake, Alberta. 3000'.	12
12	57-579	1.8km SW of Cypress Hills Park, Saskatchewan. 4100'.	12
13	58-590	3.7km S of Moose Jaw, Saskatchewan.	12
15	10-556	3.0km E of Cereal, Alberta. 2600'.	12
16	25-545	0.5km W of Turner Valley, Alberta. 4000'.	12
17	22-489	3.6km E of Cawston, British Columbia. 3000'.	12
18	23-487	Courtney Lake, B.C. 3500'.	12
19	24-488	Princeton, B.C. 2500'.	12
20	50-471	57.7km S of Washington state border, Oregon hwy#3.	
21	52-486	11.4km S of Kamloops toward Lac La Jeune, B.C.	12
22	53-507	13,3km E of Grand Forks, B.C. 2000'.	12
23	21-499	Johnston Creek Park, B.C. 3000'.	12
24	6a-570	N bank of Bow River, Scandia, Alberta. 2400'.	24
25	8-538	Cochrane Hill, Cochrane, Alberta. 4000'.	24
26	13-571	N bank of Old Man River, Taber, Alberta. 2500'.	24
27	16a-573	Etzikom Coulee, 38.6km S of Taber, Alberta. 3100'.	24
28	17-576	Writting-on-Stone, Alberta. 3000'.	24
29	54a-537	Nose Hill, Calgary, Alberta. 3700'.	24
30	59-596	3.5km S and 2.3km W of Wood Mountain Park, Saskatchewan.	24
31	26-253	Fabyan, Alberta. 2100'.	24
32	27-531	18km N of Wainwright, Alberta. 2000'.	24
33	62-622	Red Rock Pass, Idaho. 7000'. **Type site - *erectifolia***	48
34	63-631	McDonald Pass, Montana. 6325'.	48
35	64-648	Carthew Summit, Waterton, Alberta. 7500'.	48
36	65-654	Boivin Lake, Alberta. 6800'.	48
37	51-478	1.5km S and 9.6km E of Anatone, Washington.	36
38	40-375	Klickitat Valley, N of Maryhill, Washington.	48
39	41-394	2.7km N and 4.3km W of Lyle, Washington.	36
40	42-396	Trout Lake, Washington. 12,325'.	48
41	43-398	5.8km E of Husum, Washington. **Type site - *xylorrhiza***	36
42	44-414	Tacoma, Washington. **Lectotype site - *typica***	36
43	45-442	Greensprings Mountain, E of Ashland, Oregon. 4550'.	36
44	46-443	Klamath River, E of Klamath Falls, Oregon. **Type site - *oregona***	36
45	47-458	Klamath Falls, Oregon. **Type site - *arida***	48
46	48-459	Kneeland, California..	36
47	49b-463	Howard's Gulch, 4km NW of hwy#229 on hwy# 139, California.	36

48	5b-548	5.7km E of Cluny, Alberta. 2800'.	12
49	7-568	Whitla Coulee, 0.3km E of Etzikom turnoff on hwy#3, Alberta. 2700'.	12
50	12-565	4.6km N of Golden Prairie turnoff on hwy#41, Alberta. 2700'.	12
51	14-566	Medicine Hat, Alberta. 2300'.	12
52	30-547	Bow Crow Forest entrance, 10km W of Turner Valley, Alberta.4800'.	12
53	31-276	Waterton, Alberta. 4400'.	12
54	29-268	8.0km W of Longview, Alberta. 4300'.	
55	16b-194	Etzikom Coulee, 38.6km S of Taber, Alberta. 3100'.	12
56	28-256	Porcupine Hills, 8.7km E of hwy#22 towards Nanton, Alberta. 4500'.	12
57	5a-549	5.7km E of Cluny, Alberta. 2800'.	24
58	55-546	Turner Valley, Alberta. 4100'.	24
59	2-112	Expanse Coulee above Old Man River, Alberta. 2500'.	
60	B9634	(MO) Tacoma, Washington. April, 1940. **Lectotype** - *praemorsa* Baker	36
61	B8059	(CAS) Humbolt County., California. April, 1935.	36
62	D1738	(MO) Elko Co., Nevada. May, 1969.	48
63	B8385	(DS) Sierra Co., California. June, 1936	48
64	B8403	(DS) Placer Co., California. June, 1936.	48
65	B7354	(CAS, MO) Siskiyou Co., California. April, 1933.	48
66	B8388	(DS) Sierra Co., California. 6770'. June, 1936.	48
67	B5215	(DS) Placer Co., California. May, 1936.	48
68	B8406	(DS) Nevada Co., California. 6000'. June, 1936.	48
69	B8377	(DS) Tehama Co., California. 6000'. June, 1936.	48
70	D1746	(CAS, MO) Owyhee Co., Idaho. May, 1969.	48
71	GD1640	(CAS, MO) Humbolt Co., Nevada. 6960'. June, 1967.	48
72	B8052	(DS) Mount Lassen, California. 5800'. June, 1935.	48
73	B11462	(DS, MO) Klamath River, Oregon. May, 1946. **Isotype** - *oregona* B. & Cl.	48
74	B12086	(DS, CAS) Klamath Falls, Oregon. April, 1949. **Isotype** - *arida* B, & Cl.	48
75	B7408	(CAS, MO) Kamiah, Idaho. 1500'. April, 1933.	48
76	A8317	(DS) Klamath Co., Oregon.	48
77	B9359	(CAS, MO) Ruby Mountains, Nevada. June, 1939.	12
78	D1754	(MO) Blaine Co., Idaho. May, 1969.	12
79	D1732	(MO) Elko Co., Nevada. May, 1969.	12
80	D1753	(MO) Camas Co., Idaho. May, 1969.	12
81	D1736	(MO) Elko Co., Nevada. May, 1969.	12
82	D1745	(MO) Owyhee Co., Idaho. May, 1969.	12
83	B8699	(DS) Sierra Co., California. 5400'. July, 1937.	12
84	HOOK/K	(KEW)Camas Prairie near source of Columbia, 1834. **Type** - *major* Hook.	
85	AN4340	(PH) Pole Creek, Wyoming. May, 1894. **Co-type** - *vallicola* Nels.	
86	S10200	(PH) Husum, Washington. June, 1920. **Type** - *xylorrhiza* Suks.	
87	S8530	(PH) Spangle, Washington. May, 1916. **Type** - *subsagittifolia* Suks.	
88	CFB67	(DS) Amarron, Colorado. 6900'. 1901. **Type** - *physalodes* Greene	
89	RS-BS	(DAO) Duval, Saskatchewan. May, 1942. **Type** - *russellii* Boivin	
90	ANSIPH	(PH) Missouri. **Type** - *nuttallii* Pursh	
91	B8662	(MO) 20.5 mi. W of Klamath Falls, Oregon. May, 1937. **Type** - *oregona* B. & Cl.	48

92	AN5481	(WS) Continental Divide near Henry's Lake, Idaho. **Type** - *erectifolia* Nels.
93	CFB225	(WS, RM) Grand Mesa, Colorado. 9000'. June, 1902. **Type** - *gomphopetala* Greene
94	H3156	(WS, DAO, MO, US) Lake Waha, Nez Perce Co., Idaho. 3500-4000'. June, 1896. **Type** - *flavovirens* Poll.
95	SMH222	(US, UC, GH) Craig Mountains, Nez Perce Co., Idaho. 900m. May, 1892. **Co-type** - *flavovirens* Poll.

[1] Unless otherwise specified, all collection numbers are the author's and consist of a site number-collection number designation. A = E. Applegate, B = M. S. Baker, D = G. Davidse, GD = J. Gentry and G. Davidse, S = W. Suksdorf, AN = A. Nelson, RS-BB = R. S. Russell and B. S. Sallons, HOOK = W. Hooker, CFB = C. F. Baker, H = Heller.

[2] Herbaria from which leaf tissue was obtained for chemical extraction, or where type specimens are located.

III. Results

A. Cytology and Palynology

In his 1964 review, Clausen expressed the need for an extensive cytological investigation of the Chamaemelanium in order to provide a more firm basis for the classification of this section. In this study 59 new chromosome counts; were made 57 for the Nuttallianae subsection, one in the Purpureae subsection, and one possible hybrid (Table 5). Voucher specimens are deposited at the University of Alberta (ALTA).

Somatic chromosome numbers of 2N = 12, 24, 36, and 48 were found. That these counts are all multiples of six supports the hypothesis that the base chromosome number for the Nuttallianae subsection is x = 6. When compared to reports of other chromosome numbers in the Chamaemelanium the base number for the entire section is likely to be 6 (Davidse, 1976; Clausen, 1964), contrary to the earlier work of Clausen (1927, 1929), which was based on very few counts.

Measurements of pollen size and estimates of pollen viability were made on cytologically known specimens (Figure 2). A t-test indicated no significant difference (P = 0.01%) in pollen diameter or viability estimates for pollen from cleistogamous versus chasmogamous flowers on the same plant (data not shown). All measurements reported here were subsequently made using only pollen from chasmogamous flowers.

The results from stored and fresh pollen measurements were compared for selected samples using the paired sample t-test (Campbell, 1974). At the P = 0.1% level, no significant difference was evident in either size or viability, though pollen grains stored in stain tended to be slightly larger than those examined within a few hours of staining (data not shown).

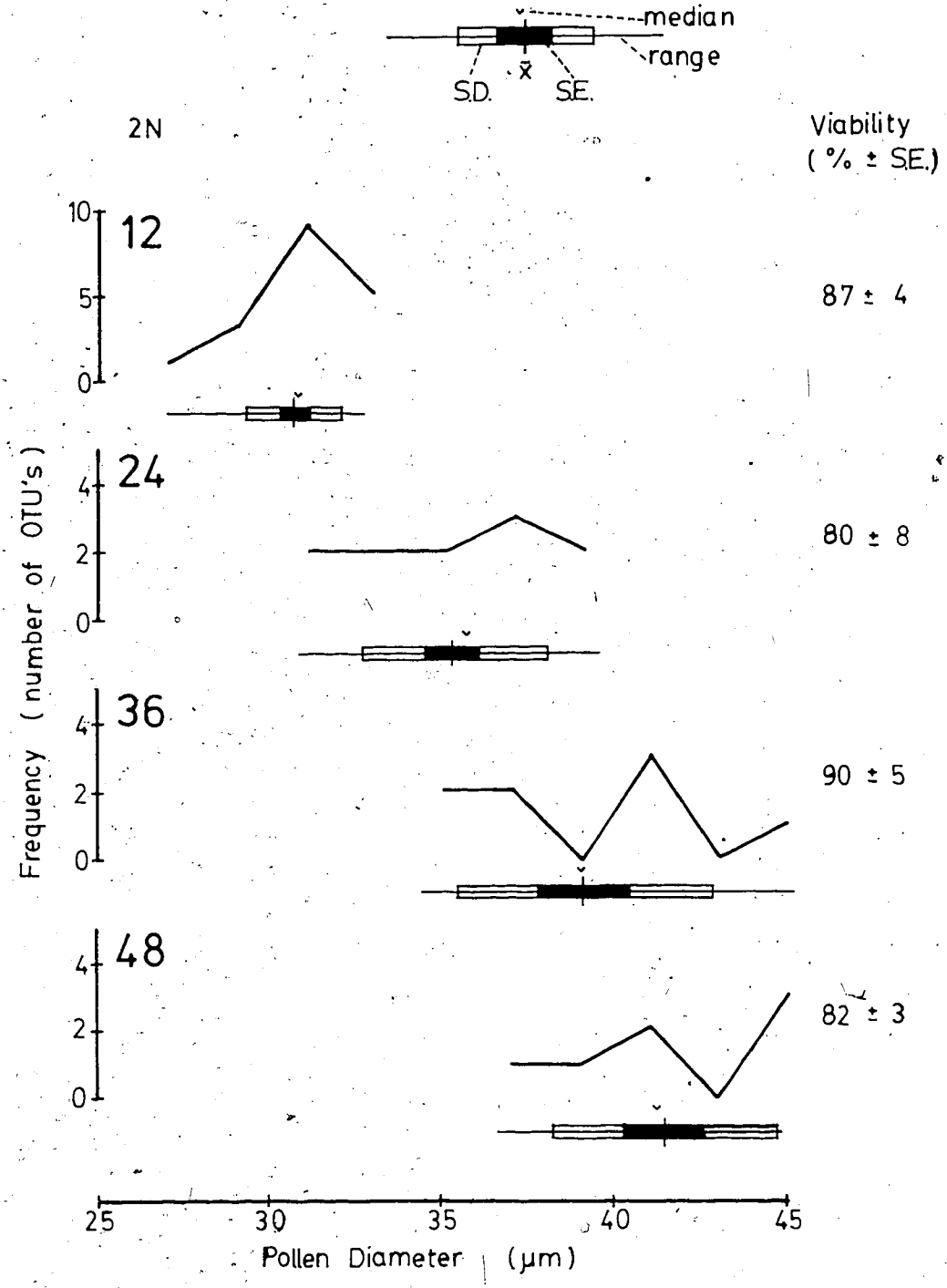
For within-population viability, 2 to 7 measurements from selected populations were examined (data not shown). Standard deviation, SD, for any given measurement was about 9% and the standard error, SE, 2%. Standard deviation, however, could range from 0 to 41% within a population. Within a given sample, pollen size varied about 2.5 um SD (0.5 um SE) and within-population variation was only slightly higher (data not shown).

Table 5. New chromosome counts in the *Viola nuttallii* complex and other Chamaemelanium. All collections were made by the author.

2N	Location	Site Number	Collection Numbers
Subsection Nuttallianae			
Viola vallicola			
12	ALBERTA		
	West bank of Chin Lake	1	105,572
	Nose Hill, Calgary	4	126,524
	Cluny	5b	134,548
	Whitla Coulee	7	148,568
	Little Fish Lake	9	150,550
	Cereal	10	155,556
	Golden Prairie	12	165,565
	Medicine Hat	14	178,566
	Spruce Coulee, Cypress Hills	15	181,567
	Etzikom Coulee	16	194,574
	Turner Valley	25	233,545
	Porcupine Hills	28	256,244
	Bow Crow Forest	30	270,547
	Crownest Pass, Leitch Collieries	34	295,516
	Hillcrest	35	296,517
	Lynx Creek Campground	36	297,519
	Castle River near bridge	37	300,520
	Beavais Lake Park	38	311,523
	Nose Hill, Calgary	54d	532
	Hand Hills NE of Little Fish Lake	56	551
12	BRITISH COLUMBIA		
	Kettle River	20	224
	Johnston Creek Park	21	499
	Cawston Road to Oliver	33	229,489
	Courtney Lake	23	230,487
	West of Princeton	24	232,488
	Lac La Jeune	52	486
	E of Grand Forks	53	507
12	SASKATCHEWAN		
	W of Cypress Hills	57	579
	S of Wood Mountain	58	590
	S of Moose Jaw	60	604
Viola nuttallii			
24	ALBERTA		
	Cluny	5a	128,549
	Scandia	6	145,570
	Cochrane Hill, Cochrane	8	149,538
	Empress	11	161,561
	Taber	13	170,571
	Etzikom Coulee	17	193,573
	Writting-on-Stone Park,	17	198,576
	Fabyan	26	253,530
	Wainwright	27	531
	Nose Hill, Calgary	54a	537
	Turner Valley	55	546

24	SASKATCHEWAN		
	Wood Mountain	59	596
Viola praemorsa			
36	WASHINGTON		
	Lyle	41	394
	Husum	43	397,398,399
	Tacoma	44	414
	Anatone	51	478
36	OREGON		
	Green Springs Mountain	45	442
	Klamath River	46	443,444
36	CALIFORNIA		
	Kneeland	48	459
	Howard's Gulch	49B	463
48	WASHINGTON		
	Klickitat Valley north of Maryshill	40	375
48	OREGON		
	Klamath Falls	47	458
48	IDAHO		
	Red Rock Pass	62	622
48	MONTANA		
	McDonald Pass	63	631
48	ALBERTA		
	Carthew Summit, Waterton	64	648
	Bovin Lake	65	654
Viola Bakeri			
48	WASHINGTON		
	Trout Lake	42	395
Subsection Purpureae			
Viola purpurea			
12	CALIFORNIA		
	Howard's Gulch	49A	462
V. purpurea X V. praemorsa			
28	CALIFORNIA		
	Howard's Gulch	49C	462a

Figure 2. Pollen grain diameter and viability estimates for the chromosome races in the *Viola nuttallii* complex.



Pollen viability estimates were generally over 80% for each chromosome class (Figure 2). Very low viability measurements obtained in some cases were likely due to adverse environmental conditions in the field. Where viability estimates were low for pollen samples collected in the field, pollen from the same plant under cultivated conditions typically showed viability greater than 80%. Investigators, therefore, should be wary of basing conclusions regarding hybridization solely on low pollen viability without testing interpopulation measurements and insuring that these measurements are made under "ideal" conditions.

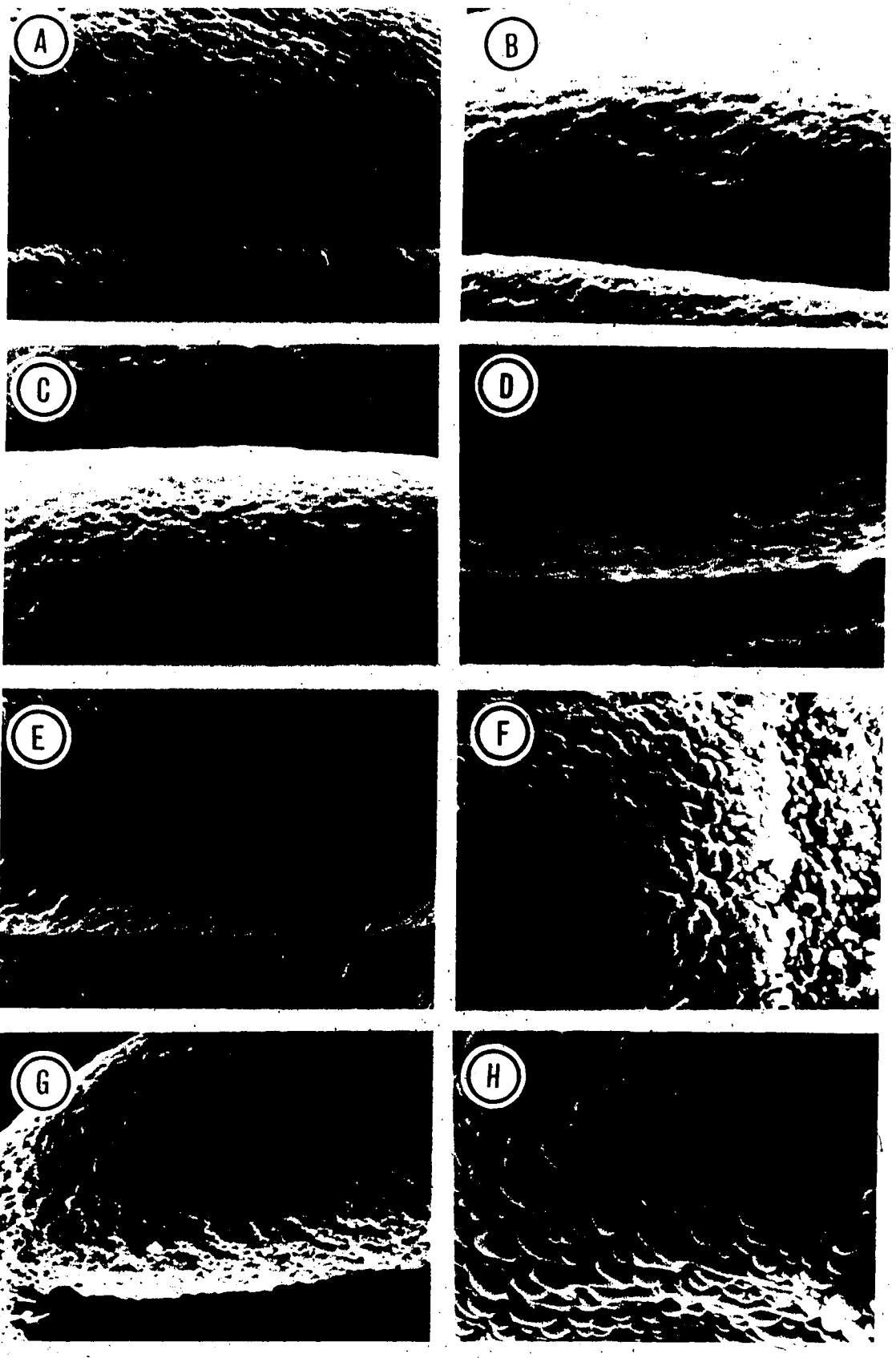
Pollen diameter increased with ploidy level (Figure 2). Pollen size for the two ploidy levels 2N = 12 and 24 were found to be significantly different (P = 1%) from each other and from the other ploidy levels using the Kruskal-Wallis analysis of variance of ranks (Campbell, 1976). No significant difference (P = 1%) was found between the size of pollen grains in the 2N = 36 and 48 ploidy levels. Their ranges overlapped significantly. When comparing the frequency graphs, each may be composed of two or three size classes. Conversely, a given pollen size class may represent two ploidy levels.

Scanning Electron Microscopy (SEM) of selected pollen samples confirmed light microscope observations that these medium sized grains were tricolpate with granulate aperture membranes (Figure 3). In the light microscope observations, pollen in polar view appeared to be triangular to circular in shape. SEM observations of untreated pollen grains from voucher specimens revealed elliptic pollen grains as seen in equatorial view, indicating that dry pollen shrinks to a fusiform appearance. The foveolate or pitted surfaces vary in the density and size of pits and in the presence of scabration or rugulation.

Pollen from cleistogamous and chasmogamous flowers of 15 specimens were examined. In some specimens, some minor differences in pollen grain surface sculpturing were observed between cleistogamous versus chasmogamous flowers (data not shown). No consistant variation was detectable in this limited study due to the small sample size, though there may be a trend toward an increase in the size of scabrae and rugulation with increased chromosome number.

Figure 3. Scanning Electron Microscopy of *Viola nuttallii* complex pollen grains. Specimens for each photo are indicated by the site number and collection number; all collections were made by the author.

A. *V. vallicola*, 2N = 12. (DF 50-471)
B. *V. vallicola*, 2N = 12. (DF 52-486)
C. *V. nuttallii*, 2N = 24. (DF 8-538)
D. *V. bakeri*, 2N = 48. (DF 42-396)
E. *V. praemorsa* supspecies *praemorsa*, 2N = 36. (DF 44-414)
F. *V. flavovirens*, 2N = 36. (DF 51-478)
G. *V. praemorsa* subspecies *arida*, 2N = 48. (DF 47-458)
H. *V. linguaefolia*, 2N = 48. (DF 64-648)


A
B
C
D
E
F
G
H

In summary, pollen grain size provided a reliable means of distinguishing two of the ploidy levels and was therefore incorporated into the numerical analysis. Details of pollen surface features were not included in the subsequent numerical analysis. More extensive sampling would be required in order to do this.

B. Morphology

1. Floral Characteristics

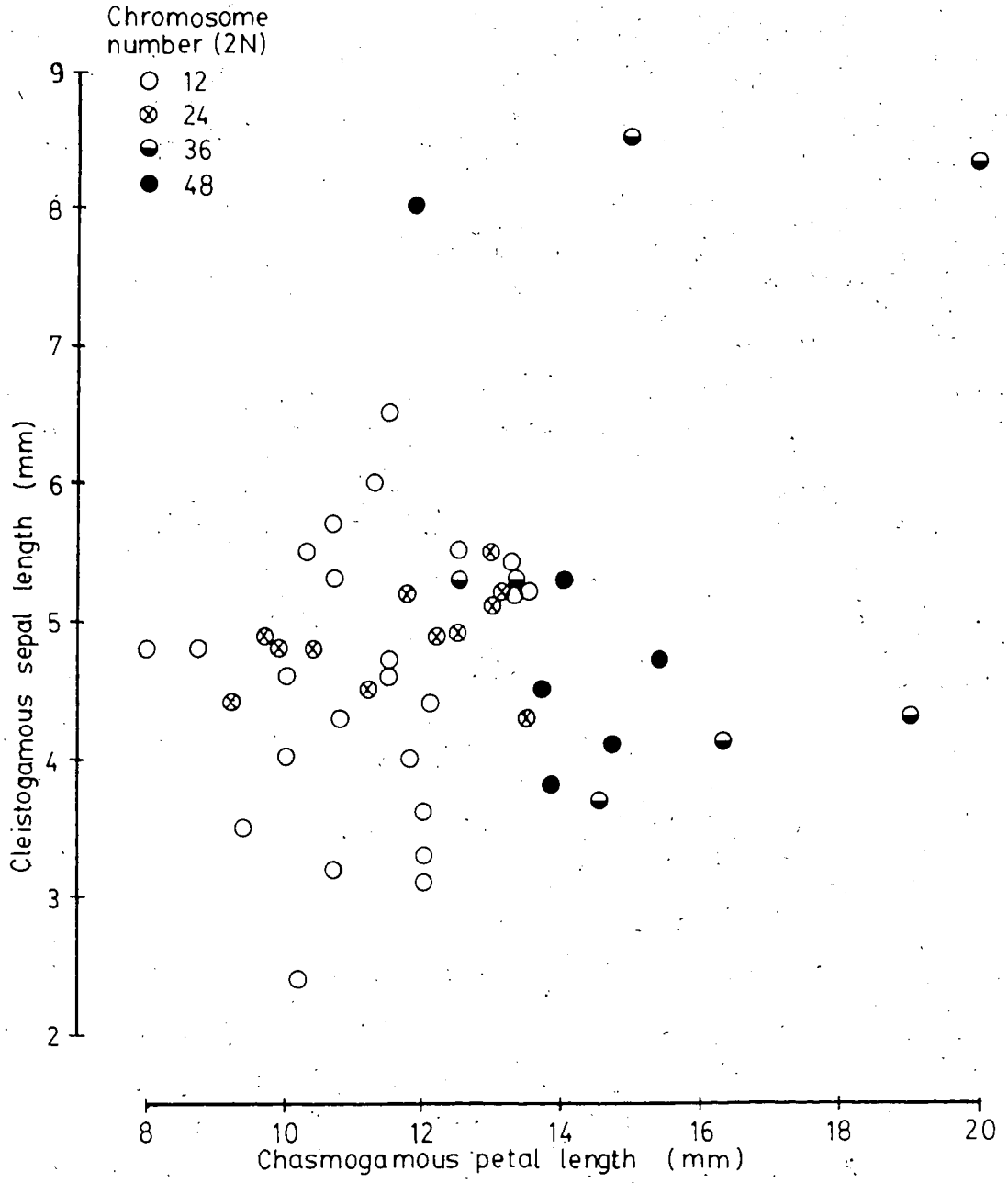
Measurements of flower size were carried out on well pressed herbarium specimens and compared to those of fresh flowers. Significant shrinkage occured in even the best pressed specimens; thus only measurements of live material were included here. Using the total length of the lower, spurred petal as an indicator of chasmogamous flower size (Figure 4), it was evident that, although there was some overlap, there were two distinct classes of petal size. The chasmogamous petal length of the 2N = 12 and 24 chromosome groups was about 11.5 mm, while those of the 36 and 48 chromosome levels ranged much larger, from 13.5 to 20 mm long. Thus, this attribute may be useful in distinguishing these two chromosome groups.

No such reliable separation was evident in the measurement of cleistogamous flower size as measured by the length of sepals (Figure 4). Though little variation occured within the 12 and 24 chromosome groups, the sepal length means were not significantly different. A great deal of variation occured in those specimens with 36 and 48 chromosome numbers. This attribute was therefore considered to be of limited importance in distinguishing between chromosome groups. It did however, separate out three OTUs which had cleistogamous flowers much longer than the others. This attribute was also included in the numerical analyses.

2. Leaf Characteristics

The attributes most commonly enlisted to differentiate among members of the *nuttallii* complex were the characteristics of leaf size and shape: length, width, basal shape of the leaf blade, margin serration, and pubescence. With the exception of serration, these characters were easily quantified. Serration was included in the

Figure 4 Chasmogamous petal length and Cleistogamous sepal length in the *Viola nuttallii* complex.



numerical analyses as an attribute with ordered character states from entire (0) to serrate (3).

Diploid OTUs had generally narrower leaf blades, though their length was not vastly different from those of other OTUs (Figure 5). Tetraploid OTUs, on the other hand, had wider and somewhat shorter leaf blades. As for the octoploids and hexaploids, their leaf blades were wider still and some were much longer than those of the diploids and tetraploids. These two characters, although of obvious value in separating the diploids and tetraploids, were of limited utility in distinguishing between octoploids and hexaploids.

The shape of the leaf blade was described by the two attributes of basal blade angle and the length to width ratio (Figure 6). Diploid OTUs possessed leaves with truncate bases (angles approaching 180°) and blades generally twice as long as wide. Tetraploid OTUs displayed leaf blades up to five times as long as wide with attenuate bases (angles of less than 60°). Again, these two characters alone did not discriminate between the 2N = 36 and 48 chromosome levels. These OTUs commonly had leaf blades two to three times as long as broad, with cuneate (angles of 50° to 80 °) or truncate leaf bases.

The length of leaf pubescence was measured on trichomes which appeared on the leaf midrib near its base, where even near-glabrous plants often displayed some pubescence. Both groups 2N = 12 and 24 had short trichomes averaging 0.14 mm long (Figure 7). The 2N = 36 chromosome group exhibited the widest range of variability, from entirely glabrous to those with trichomes 1 mm long. The octoploids had trichomes generally 0.3 mm long, but this fell within the range of hexaploid variability.

Using the Student's t-test (Campbell, 1974), trichome length was not found to be significantly different between diploids and tetraploids, nor between hexaploids and octoploids. There were significant differences (P = 1.0%) between all pairs of combinations between the above two groups.

Because of the ability of this attribute to distinguish between at least two groups of OTUs, it was included in the numerical analysis, even though trichome length alone was not a dependable method of determining ploidy level.

Figure 5 Cauline leaf length and width in the *Viola nuttallii* complex

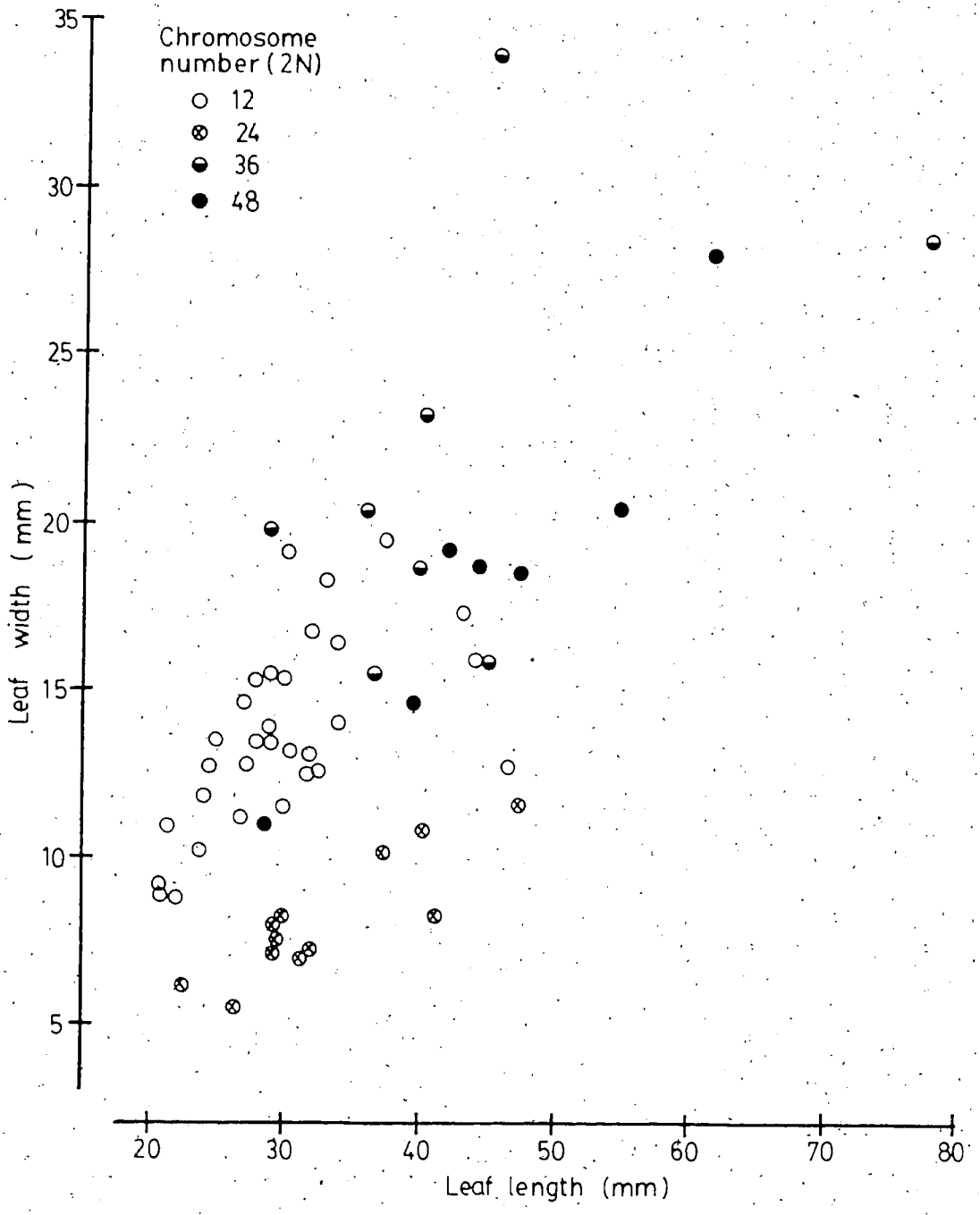


Figure 6. Cauline leaf length to width ratio and blade basal angle in the *Viola nuttallii* complex.

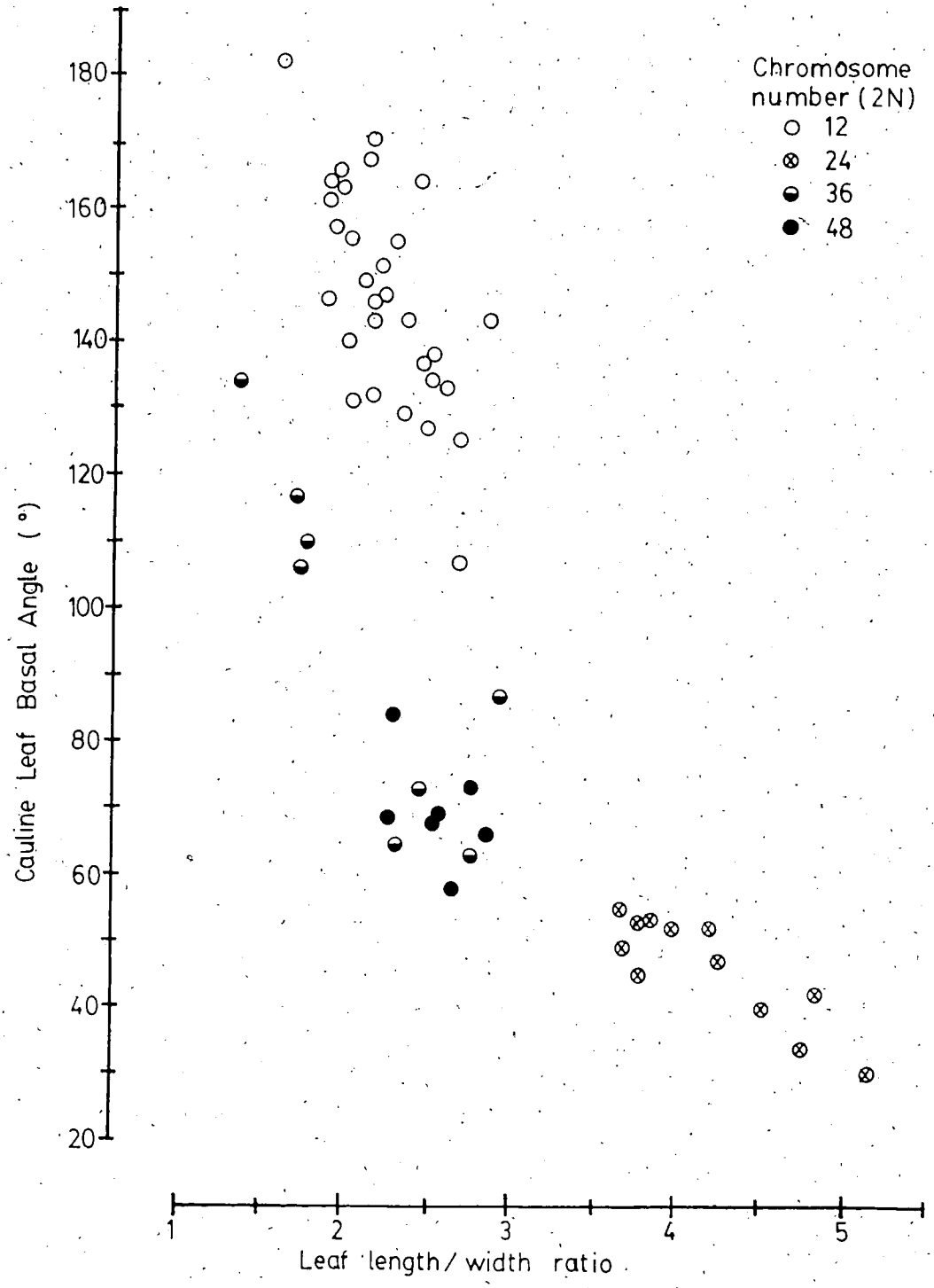
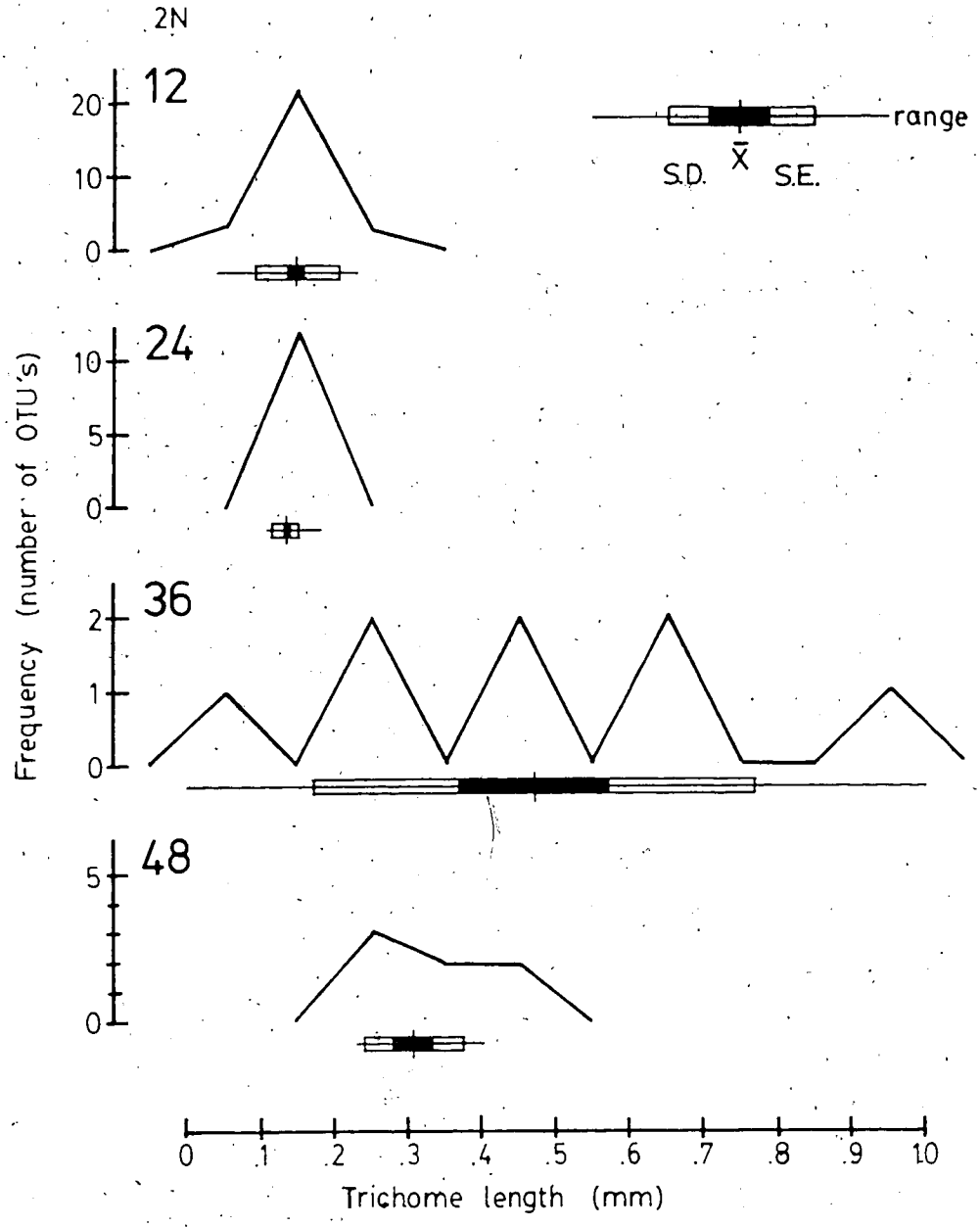


Figure 7 Leaf trichome length in chromosome races of the *Viola nuttallii* complex.



3. Seed Characteristics

Size, shape, colour, weight, and caruncle forms of seeds have been described for some taxa in the Nuttallianae (Baker, 1957, 1949b) but have not been used in distinguishing among taxa or groups of taxa.

Seeds were collected from the chasmogamous and cleistogamous fruit of living specimens as described previously. Using the paired sample t-test, no significant differences at the 0.1% level were evident between chasmogamous and cleistogamous seeds for the above attributes. No distinction was made, therefore, between the sources of seeds.

Seed length and width measurements are illustrated in Figure 8 for 58 OTUs, 55 of which were cytologically known. Diploid OTUs possessed tan coloured seeds 1.9 to 2.3 mm long and 1.1 to 1.4 mm wide. Three notable exceptions should be mentioned. All three appeared to be longer than the others and one was also wider (DF 489, 488 and 612). Two of these anomalous OTUs also displayed darker seed colouring than seen in other diploids.

Tetraploid OTUs possessed brown seeds that were both wider and longer than those of the diploids.

Hexaploid OTUs displayed a variety of seed coat colours including white, light brown, dark brown, and red-brown. Hexaploid seeds were normally longer and wider than those of the diploids and generally wider than those of the tetraploids. There appeared to be no clear distinction between hexaploids and octoploids in colour and size of seeds. Figure 8 indicates that diploids and tetraploids can be readily distinguished from each other and from the octoploids and hexaploids.

Seed length-to-width ratio ranges for all cytological types overlap, though tetraploid OTUs have slightly longer seeds and octoploids and hexaploids have generally wider seeds (Figure 9). These differences in form are complemented by differences in weight: seed weight tended to increase with chromosome number.

It was notable that two diploid OTUs (DF 488, 489) displayed characters similar to the tetraploids. These were the same OTUs which showed anomalous character states in seed length and width (Figure 8).

Figure 8. Seed length, width and coat colour in the *Viola nuttallii* complex

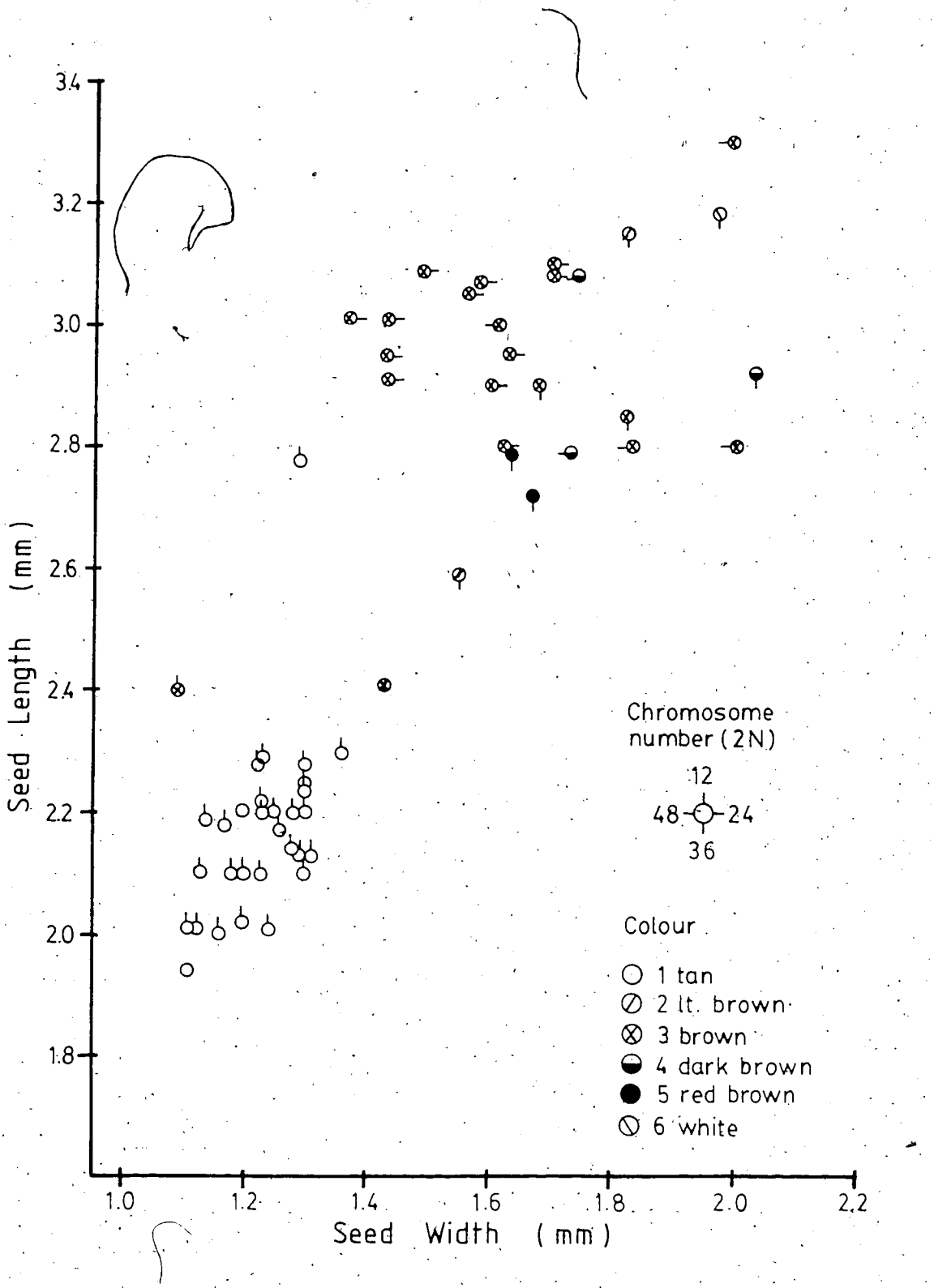
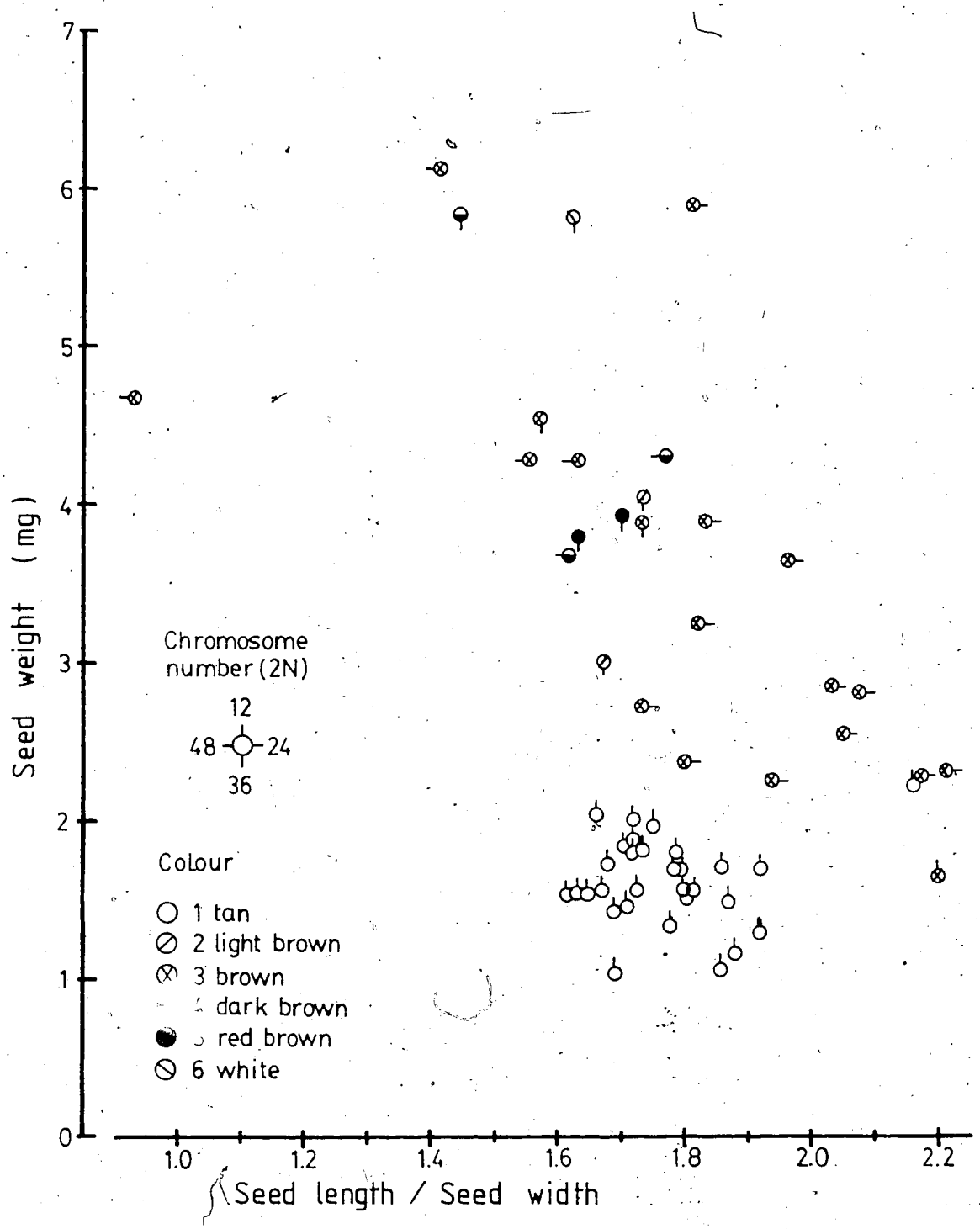


Figure 9. Seed length to width ratio, weight and coat colour in the *Viola nuttallii* -complex.



Due to the clear distinction of at least three groups of OTUs by seed length to width ratio, seed weight and seed coat colour, these attributes were incorporated into the numerical analyses.

Baker (1949b) noted that the caruncle of *Viola* seeds was large enough to almost cover the entire funiculus. Through observation, four features of the caruncle seemed to be possible distinguishing features. The form of the caruncle was recorded as unordered state characters, either absent (0) or present (1). The caruncle typically was either dorsally flattened (1) or of amorphous form (0); it either extended to cover the tip of the seed (1) or was attached in a limited area and did not cover the tip (0). These two features and the total length of the caruncle and the percent of the length of the seed which it covered are illustrated in Figure 10.

Diploids possessed caruncles of 0.7 to 0.9 mm in length that extended over 29 to 40% of the seed length. Tetraploids displayed significantly (at P = 0.1) longer caruncles which extended over the same proportion of the seed length and often beyond the seed tip. Tetraploid seed caruncle length was not significantly different from either the hexaploid or octoploid seeds, though the relative length of the caruncle was significantly (P = 0.1) different from that of hexaploids.

The form of the caruncle correlated well with two cytological groups. The 2N = 12 and 24 OTUs possessed seeds with caruncles which were dorsally flattened and covered the tip of the seed, while the 2N = 36 and 48 OTUs had globular caruncles which did not extend over the tip of the seed. One notable exception was an octoploid (DF 395) with a dorsally flattened caruncle which did not extend over the tip of the seed.

C. Flavonoid Chemistry

Twenty-nine flavonoid compounds were detected in the leaf tissue of members of the *Viola nuttallii* complex including flavone glycosides, flavonol glycosides and aglycones. A composite two-dimensional paper chromatographic profile of all compounds is given in Figure 11. All available chromatographic and spectral data for these compounds is presented in Table 6. Compound numbers in Figure 11 and Table 6 correspond to attribute numbers in the numerical analysis. Equivalence of compounds was judged by colour reactions, Rf values and co-chromatography.

Figure 10. Seed caruncle length and form in the *Viola nuttallii* complex.

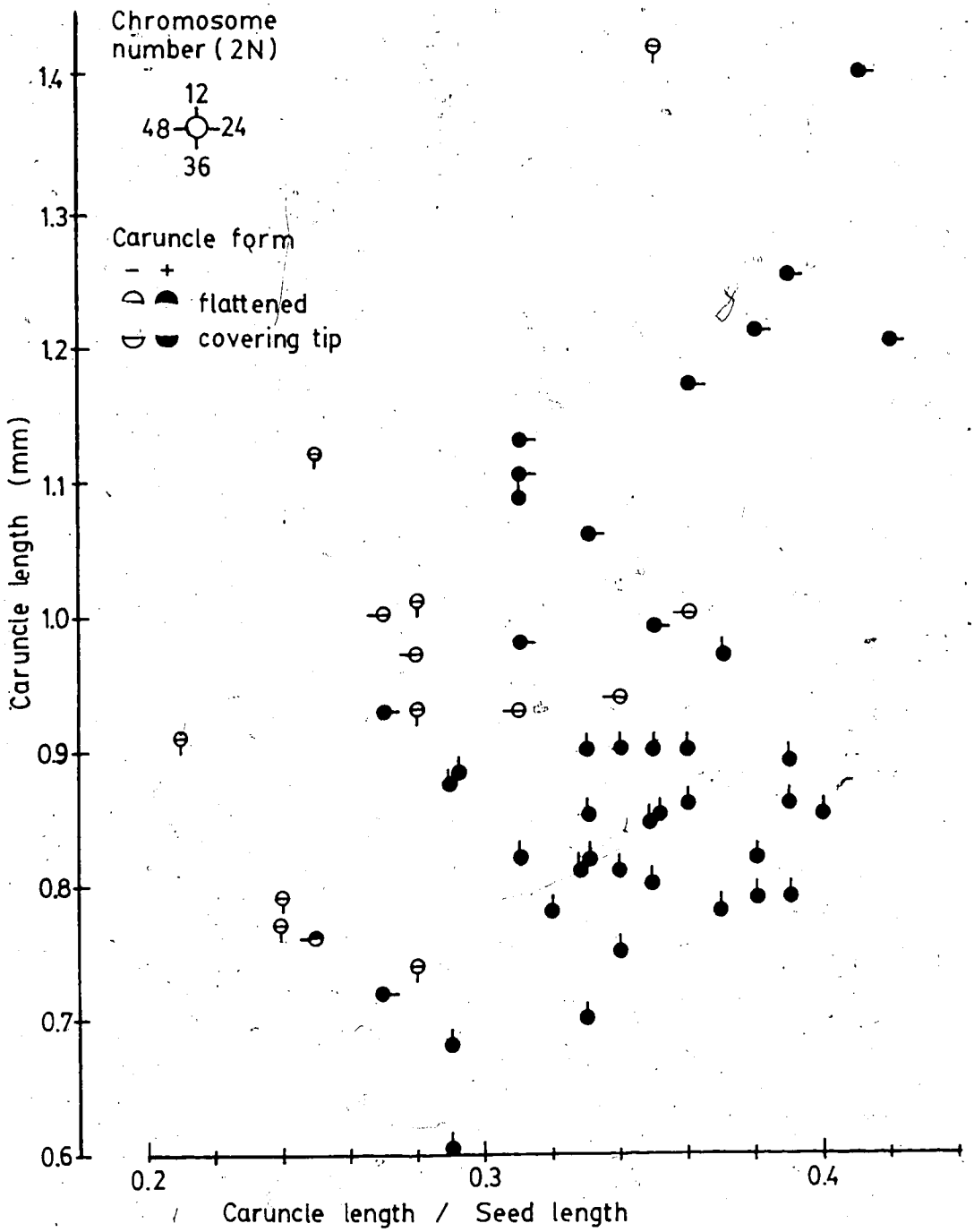


Figure 11. Composite chromatograph of the flavonoid glycosides of the *Viola nuttallii* complex. Numbers correspond to attribute numbers in the numerical analyses.

1. Kaempferol 3-O rut
2. Apigenin 7-O rut
3. Apigenin ?
4. Kaempferol 6-Me, 3-O rhm,glu
6. Quercetin 3-O rut
7. Quercetin 3,7-O diglu
8. Quercetin 3-O glu
9. Kaempferol 3,7-O rhm,gal
11. Luteolin 7-O gal
13. Luteolin ?
14. Apigenin 7-O glu
15. Luteolin 6-Me, 7-O glu,ara
16. Apigenin 7-O glu
17. Luteolin 7-O triglu
27. Quercetin 3-O digly

Compounds: A= apigenin, K= kaempferol, L= luteolin, Q= quercetin, ara= arabinose, gal= galactose, glu= glucose, gly= glycoside, rhm= rhamnose, rut= rhamnosylglucoside, xyl= xylose.

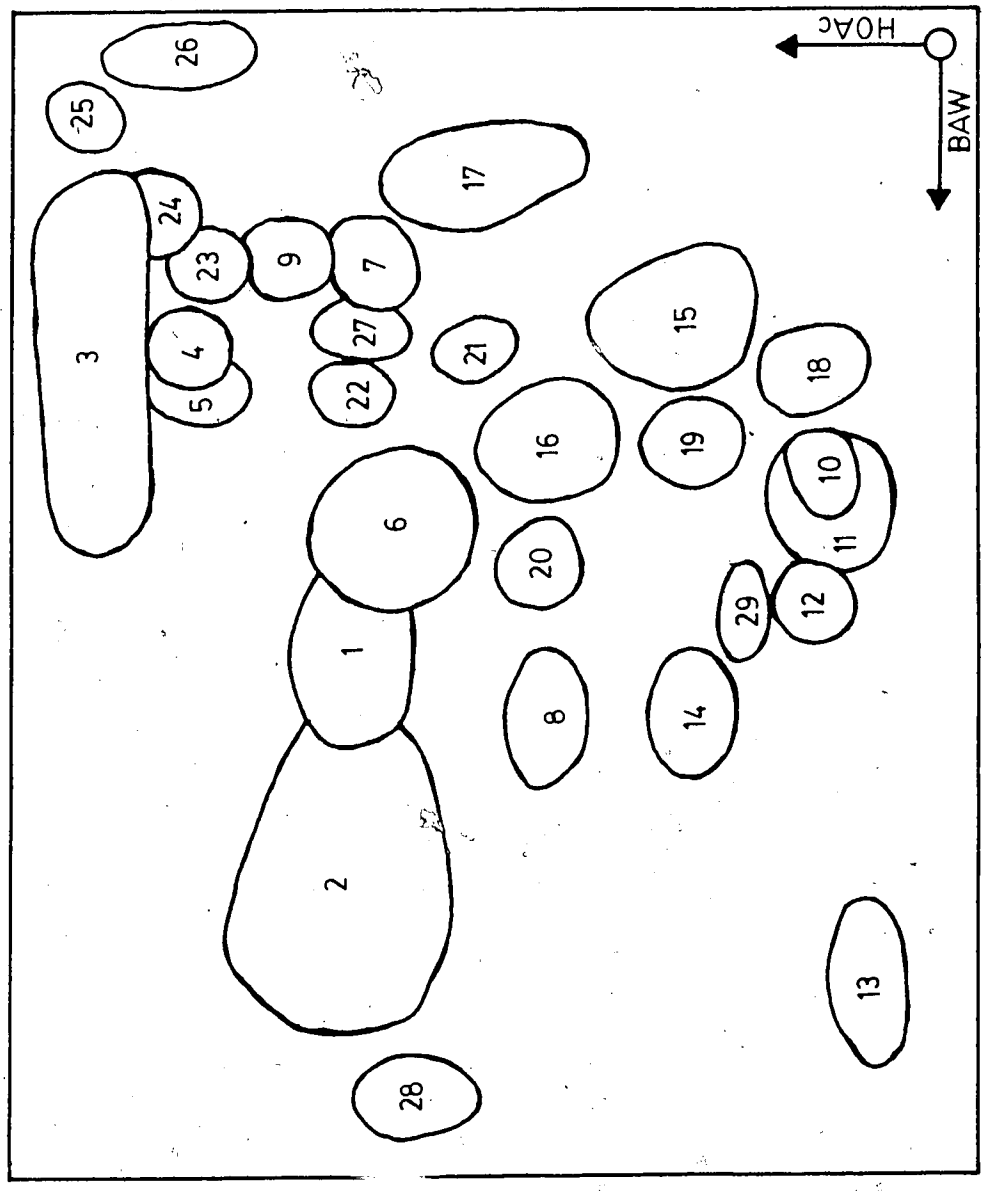

HOAc
BAW
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

Table 6. Chromatographic and spectral data for flavonoid compounds isolated from the leaf tissue of members of the *Viola nuttallii* complex.

		Chromatography (Rf X 100)								Spectral Data[4]								
		Paper[2]				Thin Layer[3]				MeOH		NaM	$AlCl_3$	+HCl	NaA	H_3BO_3		
NO	Colour[1]	A	B	C	D	E	F	G	H	II	I	I	I	I	I	II	I	Compound
1	p-bk-y	58	27	55	64	18	31	60	4	267	349	405	354,402	350 400	405	267	356	K 3-O rut
2	p-y-yg	71	36	72	70	18	31	60	4	267	349	383	347,402	343,399	382	266	345	A 3-O rut
3	p-g-yg	33	57	72	55	72	6	89	18	268	335	400	350	347	360	268	345	A ?
4	p-bk-bk	35	25	61	59					269	328	410	350	348.	399	268	350	K 6-C,3-O rut
5	p-g-0	36		61														
6	p-yg-yo	46	23	53	47	25	24	53	55	260	360	428	435	368,400	405	256	373	Q 3-O rut
7	p-y-o	24	38	61	40	61	6	69	15	258	360	416	440	366 406	410	262	382	Q 3,7-O diglu
8	p-y-o	62	5	52	53	6	22	23	82	256	360	430	414	366,400	425	262	382	Q 3-O monoglu
9	p-g-yg	28	44	69	53	66	6	77	12	266	350	400	352	350	400	266	350	K 3,7-O rhm,gal
10	o-y-y	32	9	44														
11	p-y-o	43	1	16	67	11	32	11	81	256	350	398	430	360,390	404	260	374	L 7-O gal
12	o-o-y	58		15														
13	p-g-y	80	0	4	59	0	29	4	97	254	348	403	420	358,386	400	252	370	L
14	p-g-og	58	5	23	67	11	31	16	83	269	329	394	383	344,380	389	269	331	A 7-O monoglu
15	p-y-yo	29	6	31	51	35	16	27	23	257	351	397	432	366,390	406	260	373	L 7-O monoglu
16	p-g-yg	37	8	39	65	34	31	35	23	270	330	392	349	344	402	269	334	A 6-C,7-O glu,ara
17	p-y-yo	26	10	38	39	45	5	35	9	258	351	401	433	366 390	403	260	373	L 7-O triglu
18	p-y-y	33		25														
19	p-y-y	38		36														
20	p-g-g	49		47														
21	p-y-bk	34		58														
22	p-yg-g	34		69														
23	p-o-o	24		77														
24	p-o-o	21		83														
25	p-o-o	11		88														
26	p-bl-blo	6		77														
27	p-yo-o	31	29	60	44	45	10	59	20	258	357	431	406	362 398	410	262	380	Q 3-O digly
28	p-bl-bl	95		63														
29	o-w-y	51		15														

[1] Colours UV - UV+NH_3 - UV+NA. bk= black, bl= blue, g= green, o= orange, p= purple, w= white, y= yellow.
[2] Paper Chromatography A= BAW, B= H_2O, C= 15% Acetic acid, D= Phenol.
[3] TLC E= Polyamide-aqueous, F= Polyamide-organic, G= Cellulose H= Silica
[4] Spectra 100% MeOH, NaOMe (NaM), $AlCl_3$, $AlCl_3$ + HCl NaOAc (NaA), H_3BO_3, I = Band I, II = Band II.
[5] Compounds A= Apigenin, K= Kaempferol, L= Luteolin, Q= Quercetin, ara= arabinose gal= galactose, glu= glucose rhm= rhamnose, rut= rutin, gly= glycoside ? = glycosylation unknown

Of the 83 OTUs extracted for flavonoid analysis, 79 were cytologically known, 24 of these were specimens taken from herbarium sheets on loan from DS, CAS, UC and MO (Table 4).

Three flavonoid patterns were discovered within the diploid (2N = 12) chromosome level (Table 7). Groups 1, 2 and 3, though not morphologically distinct, were distinguished by different chromatographic patterns. In group 1, the major flavonoids 2 and 3 were both apigenin glycosides. Group 3 OTUs contained 1, 9, 10 and 11, kaempferol and luteolin glycosides. Though not consistently separable by means of any of the morphological features examined previously, groups 1 and 3 were found to be geographically separated, occuring east and west of the Rocky Mountains, respectively. Group 2 consisted of six specimens from the Great Basin region, that had intermediate flavonoid profiles. They contained compounds in common with group 1 (1, 2 and 3) and group 2 (1, 5 and 10), and the unique compound, 29.

Group 4, also 2N = 12, consisted of one specimen of *V. tomentosa* (*M. S. Baker 8699*, OTU 83) which possessed attributes 1, 2, 3, 6, 7, and 8, apigenin, kaempferol and quercetin glycosides.

The OTUs containing 24 somatic chromosomes (group 5) bore some similarity to groups 1, 2, 3 and 4 in possessing attributes 1, 3, 4, 6, and 7. These compounds correspond to an apigenin glycoside, kaempferol 3-0 diglycosides and quercetin 3-0 and 3,7-0 diglycosides.

The eight compounds mentioned thus far were found consistently in over 50% of the OTUs in a given group. The groups contained from 4 to 8 different flavonoid compounds each.

A much greater variety of flavonoid compounds was found in the remaining groups, those with chromosome complements of 36 and 48. These were segregated in Table 7 according to preliminary taxonomic groupings based on identifications made by Baker and Clausen: 6, *praemorsa*; 7, *oregona*; 8, *major*; 9, *arida*; 10, *bakeri*; and, 11, *linguaefolia*.

Group 11 was the only group with a distinct flavonoid profile. Like groups 1 to 5, it possessed compounds 1 and 10; like groups 5 to 10 it contained compounds 6, 7, 8 and 9; and unique to this group was compound 27. Group 11 contained a variety of

Table 7. Distribution of flavonoid compounds in the *Viola nuttallii* complex.

	Frequency (X100)										
Taxon[1] Attribute[2]	1	2	3	4	5	6	7	8	9	10	11
2 A 7-O digly	96	17		100							
3 A -	100	100		100	100						
14 A 7-O monogly						100	50	64	40	100	
16 A 6-C,7-O gly						100	100	73	80	86	
13 L						100	50	55	80	86	
11 L 7-O monogly			17			100	100	100	80	100	
15 L 7-O gly						100	100	91	100	100	
17 L 7-O trigly						100	100	73	100	100	
1 K 3-O digly	4	100	100	100	55						100
4 K 3-O digly	13				73						
9 K 3,7-O gly		100				66	100	55	80	86	75
6 Q 3-O digly	4		100	100	100		100	73	100	43	100
8 Q 3-O monogly				100	27	33	50	45		14	50
7 Q 3,7-O gly	9			100	82	66	50	27	80	43	100
27 Q 3-O trigly											75
5 -		100									
10 -		50	17		9						25
12 -					9						
18 -								9			
19 -						33		9	40		
20 -								18	20		
21 -							18			29	
22 -						33	100	18	40	14	
23 -								18		29	
24 -				100				18	40	14	
25 -								45	20	43	
26 -						33	50	9		14	
28 -									60	43	
29 -			16					18			
Total flavonoid attributes / taxon	5	6	4	7	8	13	12	20	15	17	7
Chromosome No.	12	12	12	12	24	36	36,48	36,48	48	48	48
Total populations surveyed	23	6	6	1	11	3	2	11	5	7	4

[1] Taxa: 1 = *vallicola*, 2 = *vallicola*, 3 = *vallicola*, 4 = *tomentosa*, 5 = *nuttallii* 6 = *praemorsa*, 7 = *oregona*, 8 = *major*, 9 = *arida*, 10 = *bakeri*, 11 = *linguaefolia*.
[2] Compounds: A = Apigenin, K = Kaempferol, L = Luteolin, Q = Quercetin, gly = glycoside.

flavonols, but no identified flavones: kaempferol 3-0 and 3,7-0 diglycosides, quercetin 3-0 and 3,7-0 diglycosides and a quercetin 3-0 triglycoside.

Compounds 6, 7, 9, 11, 13, 14, 15, 16 and 17 were commonly found in many of the OTUs in most all of the above groups. These major compounds were apigenin, kaempferol, quercetin and luteolin derivatives. None of the groups, even group 10, *bakeri*, which was morphologically distinct from the others displayed obvious, unique profiles. With increasing chromosome number, OTUs possessed increased numbers of more complex flavonols and flavones.

All raw data presented above and used in the numerical analyses are presented in Appendix. 1.

D. Numerical Analysis

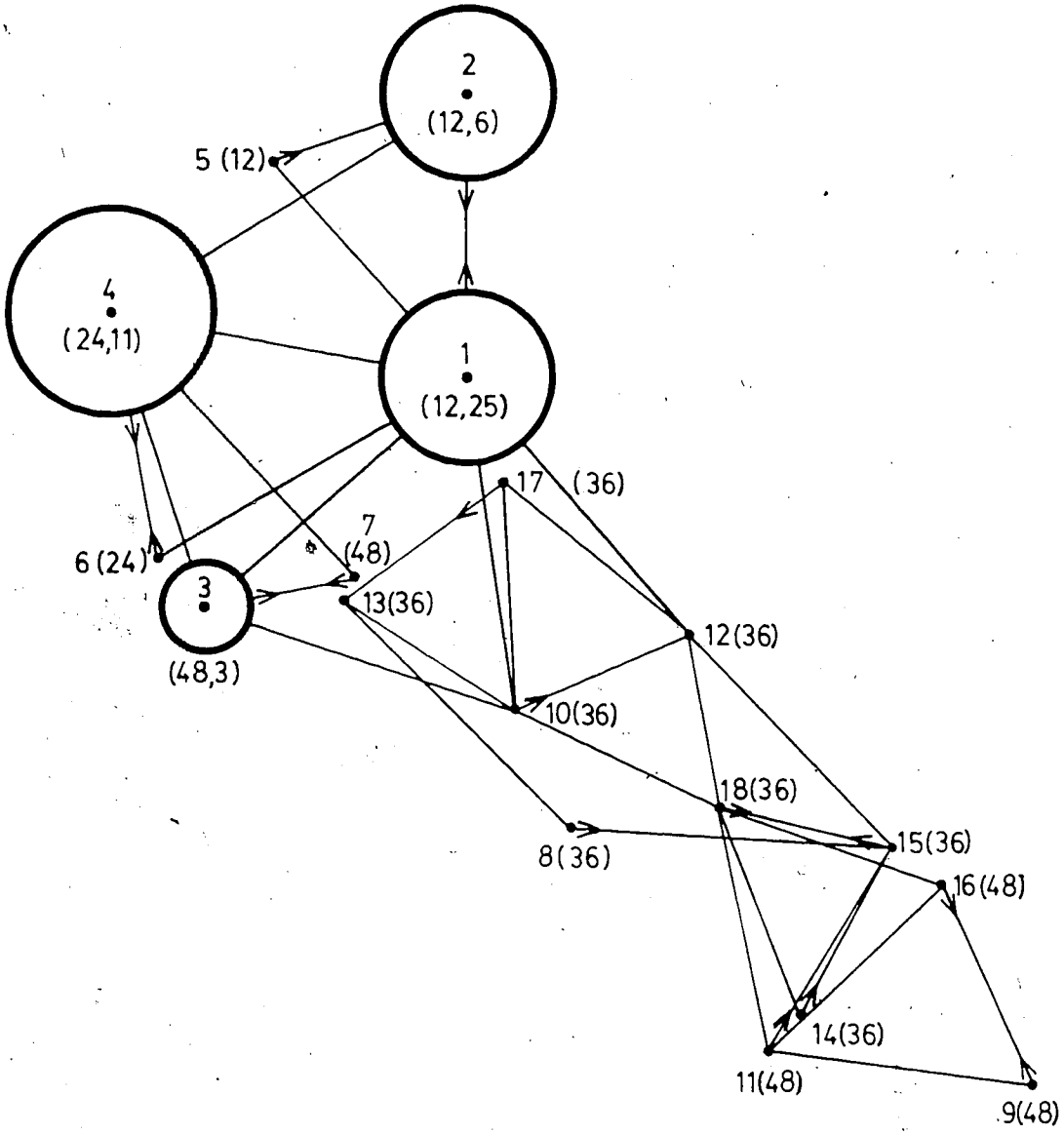
1. TAXMAP analysis one

The initial TAXMAP analysis was performed using the author's collections, which totaled 59 OTUs scored for 50 attributes, both structural and chemical in nature. Due to the maximum information content of this analysis, it was presumed to be the most accurate. The resulting clusters from the equally weighted analysis are illustrated in the CALCOMP plot of cluster configurations (Figure 12, see Appendix 2 for the complete TAXMAP printout). This analysis provided 4 multi-membered clusters and 14 single membered clusters.

Cluster 1 included 25 OTUs, all of which were found to have somatic chromosome numbers of 12. All members were located in Alberta and Saskatchewan, east of the Rocky Mountains. The flavonoids present in members of this group were attribute numbers 2 and 3 (apigenin derivatives). These were plants with small (30 mm) ovate or ovate-oblong, nearly entire leaves with truncate bases, covered with very short puberulence, possessing small flowers, and with pollen 31 um in diameter.

Closely linked to Cluster 1 was Cluster 2 which contained morphologically similar OTUs but which had additional flavonoids: attributes 1 and 9 (kaempferol 3-O diglycoside and kaempferol 3,7-O glycoside, respectively). All six members of Cluster 2 were collected in British Columbia or Oregon, west of the Rocky Mountains.

Figure 12. TAXMAP cluster analysis of 59 OTUs for 50 attributes, equally weighted analysis. Dots indicate cluster centers, circles indicate multi-membered cluster diameters, arrows indicate nearest neighbours, and lines indicate intercluster distances. Each cluster is defined by its cluster number and the chromosome number of its members in parenthesis. For multimembered clusters, the number of OTUs is also indicated in parenthesis.



Cluster 3 consisted of three OTUs possessing flavonoids 1, 6, 7, 8, and 9 (kaempferol and quercetin derivatives). These OTUs had a chromosome count of 48. Their leaves were generally twice as long as wide and about as wide as those in cluster 1 and 2; leaves had more cuneate bases; and, leaf pubescence tended to be slightly longer, about 0.15 mm. Seed morphology also differentiated this group. Cluster 7 (OTU 35) was the mutual nearest neighbour of cluster 3.

Cluster 4 contained 11 OTUs, all having chromosome complements of 24. These OTUs were characterized by their narrow cauline leaves which were more than three times longer than wide and had attenuate bases. Seeds of this group were the largest found in the complex and had brown seed coats. OTUs in cluster 4 commonly possessed flavonoid attributes 3, 4, 6, and 7 (apigenin, kaempferol and quercetin derivatives). Cluster 6 (OTU 29) was a single-membered cluster whose nearest neighbours were all in Cluster 4, and thus it could be considered part of it.

Clusters 8 to 18 were single-membered clusters. None of their nearest neighbours were closer than 0.15 units, unlike the distance relationships within other clusters. A more extensive analysis of these OTUs (analysis three), which included more OTUs in an attempt to overcome the problem of restricted sample size, was performed.

2. TAXMAP Analysis Two

Analysis two contained 72 OTUs and is presented in Appendix 3. The additional 13 OTUs represented type specimens (holotypes, paratypes, and isotypes) on loan from other herbaria. Due to the nature of these specimens, limited information could be obtained from them. None of these OTUs were sampled for flavonoid analysis, only three were cytologically known, and none possessed mature seeds for measurement. It must also be recognized when comparing the results of analyses one and two that since distance calculations in TAXMAP represent relative distances, cluster membership was expected to deviate somewhat from that in analysis one.

Whereas analysis one had split violets with 2N = 12 into two clusters, analysis two created nine clusters (1, 2, 4, 5, 7, 8, 9, 10, 11, and 26). which were linked or had each other as their eight closest neighbours and very small intervening distances. Membership in some of these clusters was made up of members of both cluster 1 and 2 of analysis

one. For these reasons it seemed most reliable to consider all of these OTUs as one cluster.

The group with 2N = 12 now contained four type OTUs: AN4340 (*vallicola* A. Nels.); S8530 (*subsagittifolia* Suks.); RS-BB (*russellii* B. Boivin); and CFB67 (*physalodes* Greene). Single-membered cluster HOOK/K (type specimen of *major* Hooker) had four of its nearest neighbours in this group and was therefore included.

Although the type *major* Hook. clustered here and is the oldest published name associated with this large group, it was not adopted as it has no priority outside the varietal level. Nuttall collected this specimen on the banks of the Columbia River, west of the Rocky Mountains. It was appropriate to apply this name to the chemical form (cluster 2, analysis one) found there. The flavonoid form most common east of the continental divide will be designated *vallicola*, the most elligible and applicable specific name.

Cluster 6 contained OTUs with 2N = 24 chromosomes and the same OTUs as cluster 4 of analysis one. Although not a member of it, OTU ANSPH (the type specimen of *nuttallii* Pursh), single member cluster 27, was associated with this cluster by virtue of its nearest neigbour list and its intercluster distances. This specimen is more closely aligned with members of cluster 6 than with any other cluster or OTU. The members of this group shall, therefore, be refered to as *nuttallii*. As no other specimen could be associated with this group, the name is confidently applied.

Cluster 3 of analysis 2 corresponded exactly to cluster 3 of analysis one, containing OTUs of chromosome number 48. It also contained two type OTUs: CFB225, *gomphopetala* Greene and AN5481, *erectifolia* A. Nels. No type specimen of *linguaefolia* Nutt. was available for numerical analysis, but the description and distribution of this taxon indicate that it may be refered here. Close examination of the photographs of the type specimen (PH and G) indicate that based on leaf shape and pubescence as well as its location near the sources of the Oregon [River], it should be included with this cluster. Cluster 3 was assigned the oldest applicable name, *linguaefolia*.

As in analysis one, several OTUs represented single-member clusters.

3. TAXMAP Analysis Three

In an attempt to clarify the relationship between the single-membered clusters, a number of additional OTUs from herbarium loans were added to the analysis. These were chosen by virtue of the availability of chromosome counts. Permission was obtained to remove one leaf from each of these specimens for flavonoid extraction. All specimens from clusters 1, 2 and 4 of analysis one, their associated single membered clusters, and associated type specimens were removed from this analysis. Cluster three members were retained for analysis because a number of morphological attributes and chromosome counts of 2N = 48 indicated that its members were more similar to the remaining OTUs eventhough their flavonoid profiles were distinctly different. Analysis three thus contained 39 OTUs, 17 were from the author's collection, 16 from herbarium loans, and eight were type specimens.

The weighted cluster analysis is illustrated in Figure 13 (see Appendix 4 for a complete listing of the TAXMAP analysis). Analysis three produced 10 multi-membered clusters and 9 single-membered clusters.

Cluster one contained the same OTUs as were found in cluster three of analysis two: *linguaefolia* , 2N = 48.

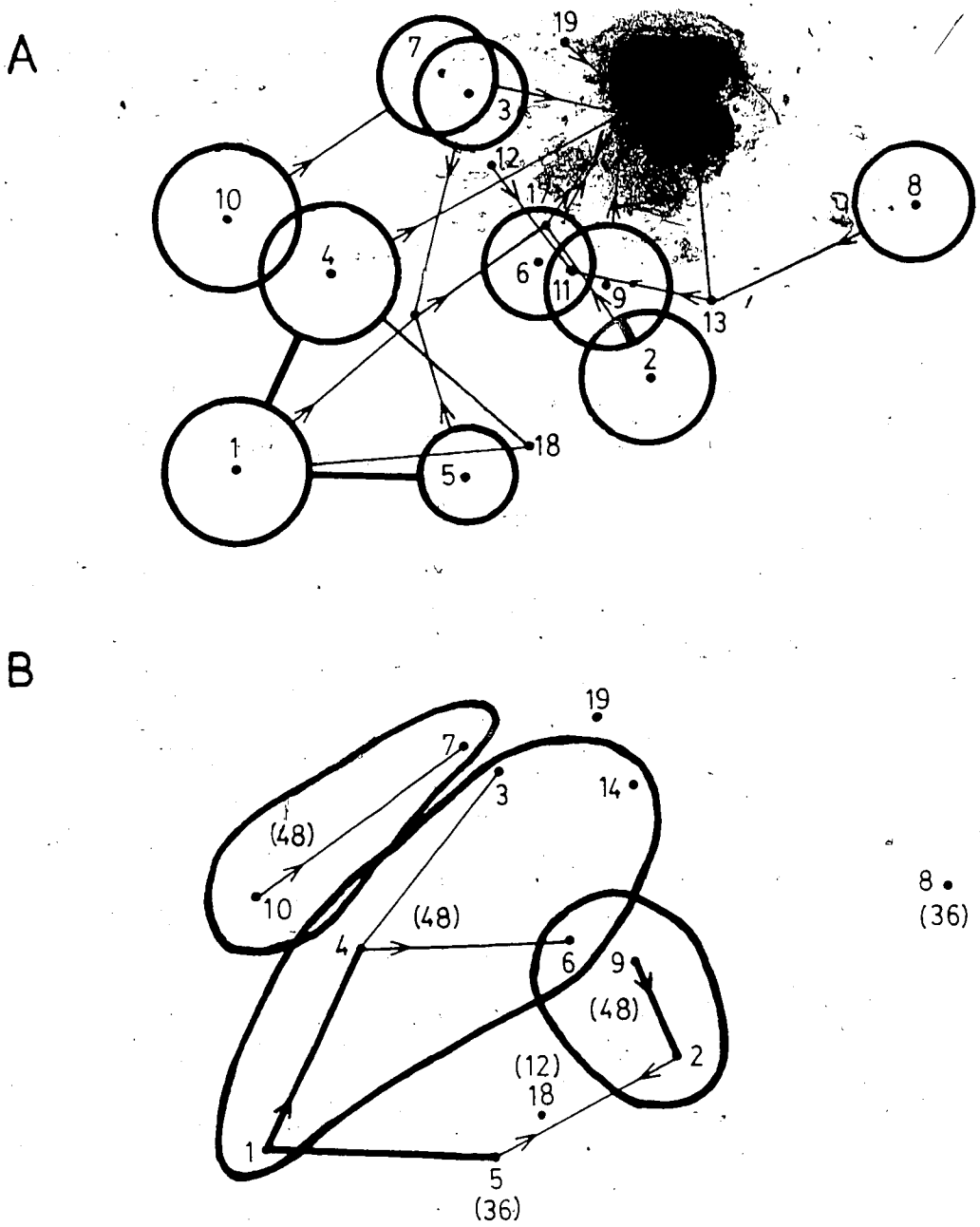
Linked to 1 was cluster 4, 2N = 48, containing the type specimen *oregona* Baker. Cluster 4 differed from one in its lack of flavonoid 1 and the presence of flavonoids 6, 7, 8, 11, 13, 14, 15, 16, 17, and 24 (quercetin, luteolin and apigenin glycosides). These OTUs had shorter leaves only 2.2 times longer than wide, with a basal angle larger than 90°, slightly longer leaf pubescence and some sepal pubescence.

Cluster 5 was also linked to cluster 1, though its members' chromosome complement was 2N = 36. Cluster 5 had no associated type specimen. It differed from clusters 1 and 4 in not containing flavonoids 7, 8 or 24 (quercetin 3-O and 3,7-O glycosides) but otherwise containing all of those found in *oregona*. Leaves in cluster 5 OTUs were slightly longer than wide (ratio of 2.5), had a smaller basal angle than *oregona*, entire margins, no sepal pubescence, seed caruncles were shorter than in *linguaefolia* with red-brown seed coats. In keeping with its chromosome complement of 36, pollen diameter in cluster 5 was smaller than that of *linguaefolia*.

Figure 13. TAXMAP cluster analysis 3, of 79 OTUs for 50 attributes in a weighted analysis.

A. Calcomp plot of cluster analysis.

B. Nearest neighbour analysis with clusters (dots) joined to nearest neighbours (arrows) or linked cluster (heavy lines) and grouped according to TAXMAP analysis using only morphological characters (heavy circles). Cluster numbers correspond to A, chromosome numbers are included in parenthesis.



Cluster 2 members contained flavonoids 7, 9, 11, 13, 14, 15, 16, 17, and 26 (quercetin 3,7-O and kaempferol 3,7-O glycosides), and a variety of luteolin and apigenin 7-O derivatives). These OTUs had small leaves with a length to width ratio of 2.3, a basal angle of 85°, entire margins, chasmogamous flower petals 10 mm long, glabrous capsules, and a chromosome complement of 2N = 48. These OTUs were identified as *Viola bakeri* Greene by M. S. Baker and J. Clausen on annotation labels.

Cluster 9 was linked to cluster 2 in containing basically the same flavonoids and the same chromosome number, but had slightly smaller leaves and larger cleistogamous and chasmogamous flowers. These specimens were also identified as *bakeri*.

Cluster 6 contained two OTUs with chromosome numbers of 2N = 48 and with similar flavonoid profiles to clusters 2 and 9. Morphologically similar to clusters 2 and 9, cluster 6 had only slightly larger chasmogamous petals to distinguish it from the others.

Cluster 3 contained the two isotype specimens for *arida* Baker, which have mosome numbers of 2N =48. These specimens contained flavonoids 6, 7, 9, 11, 16, 17, and 28 (quercetin, kaempferol, luteolin and apigenin derivatives). Their leaves were 2.0 times as long as wide, 42 mm by 22 mm on the average, a relatively wide basal angle of 110°, very short pubescence, serrulate leaf margins, and sepals with pubescent auricles.

Cluster 7 contained only two OTUs with chromosome numbers of 2N=48 and flavonoids 6, 14, 15, 16, 17, and 24 (Quercetin, Apigenin, and Luteolin derivatives). Their ovate-oblong leaves were large, 66 by 30 mm, had cuneate bases, were pubescent, serrate, and had large chasmogamous flowers.

Cluster 7 was the nearest neighbour of cluster 10 which contained the two type specimens of *flavovirens* Pollard and one OTU with a chromosome count of 36. Most morphological features were very similar though the size of leaves in cluster 10 OTUs were slightly larger. The OTUs in this cluster will be refered to as *flavovirens*.

Part B of Figure 13 presents a simplification of Part A with most single-membered clusters removed, except those which were type specimens. Clusters were represented only by their centers, linkages between clusters were represented by thick lines, and nearest neighbours were represented by lines with directional arrows. Interpretation of the nearest neighbour indexis is cautioned as the intercluster distances

represented here were relatively large (greater than .250) and do not vary much at all from intracluster OTU distances.

When TAXMAP analysis three was run using only morphological attributes (30 to 50), the clusters of analysis three were reduced in number (Appendix 4). Figure 13 Part B illustrates the new clusters by circling and linkages between these new clusters was indicated by overlapping the circles. Clusters 1, 3, 4, 6 and 14 were grouped togeather (*linguaefolia, arida, oregona, bakeri*, and *arida*, respectively). Clusters 2 and 9 (*bakeri*) were also closely linked to the new larger cluster. Cluster 8 (*praemorsa*) and cluster 5 (triploid) remained intact. Two members of clusters 7 and 10 were clustered together while the other OTUs previously in these clusters were found in single-membered clusters (*flavovirens*).

Cluster 19 (type *xylorrhiza*) was noteworthy by remaining as a single-membered cluster and not in close association with any other cluster. Cluster 18 (*tomentosa*) also remained as a single-membered cluster, though this was not as surprising considering its distinctive features of chromosome number (2N = 12) and very dense tomentose pubescence. This OTU contained the flavonoid constituents 1, 2, 3, 6, 7, 8 and 23 (apigenin, kaempferol, and quercetin derivatives), a range of compounds intermediate to those found in *nuttallii* and *linguaefolia*.

4. Kruskal-Wallis Test

The Kruskal-Wallis test is a nonparametric analysis of rank which does not require the assumptions of normality and equal variances in randomly sampled populations having continuous distributions. This test was employed to test the null hypothesis that the distribution of an attribute was the same in all strata, or clusters, against the alternate hypothesis that at least one population differed from the others.

Table 8 lists all 50 attributes and their significance level based on the Kruskal-Wallis test on eight TAXMAP clusters designated in analysis one and three. The characters were divided into three significance levels. Seventeen attributes including one structual attribute, were not significant at the 5 percent level and were therefore considered invalid for separating taxa. Of the remaining thirty-three attributes, twenty-eight were significant at less than or equal to the 1 percent level. It was attributes in this latter

Table 8. Kruskal-Wallis test for significance of flavonoid and morphological attributes.

Not significant at .05 level	Significant at .05 level	Significant at .01 level
Flavonoid Attributes[1]		
5 -	14 A 7-O monoglu	1 K 3-O rut
8 Q 3-O glu	16 A 6-C,7-O glu,ara	2 A 7-O rut
10 -		3 A
12 -		4 K 6-C,3-O rut
18 -		6 Q 3-O rut
19 -		7 Q 3,7-O diglu
20 -		9 K 3,7-O rha,glu
21 -		11 L 7-O monogal
22 -		13 L
23 -		15 L 7-O monoglu
24 -		17 L 7-O triglu
25		
26		
27 Q 3-O digly		
28		
29		
Cytological and Morphological Attributes[2]		
37 leaf margin ciliation	38 CH sepal pubescence	30 Ploidy level
	40 CL sepal length	31 Cauline leaf length
	41 capsule pubescence	32 Cauline leaf width
		33 Leaf length / width
		34 Leaf basal angle
		35 Pubescence length
		36 Leaf margin serration
		39 CH petal length
		42 Seed length
		43 Seed width
		44 Seed length / width
		45 Seed weight
		46 Caruncle length
		47 Caruncle / seed length
		48 Caruncle covering tip
		49 Seed colour
		50 Pollen diameter

[1] Compounds: A = Apigenin, K = Kaempferol, L = Luteolin, Q = Quercetin, gly = glycoside, ara = arabinose, gal = galactose, glu = glucose, rha = rhamnose, rut = rutin.
[2] CH = chasmogamous, CL = cleistogamous.

group which were considered the most reliable for separating taxa, and were used in making the taxonomic keys.

E. Taxonomy

Viola L. (Sp. Plant. Ed. I:933. 1753.)

Small trees, shrubs or herbs, the latter annual or perennial; leaves simple, alternate or basal with foliaceous stipules; flowers perfect, zygomorphic, on axillary, one-flowered peduncles, often inverted; chasmogamous flowers, petaliferous, pentamerous and irregular as to calyx, corolla, and stamens; sepals 5, auricled, persistant; petals 5, lowest spurred or saccate, others in two pairs, the laterals usually bearded within, imbricate on the bud; stamens closely surrounding the ovary, distinct but more or less coherent, two lower with nectar bearing appendages projecting into the spur, filaments short and broad or lacking; ovary hypogynous, pistil solitary, style one, with usually oblique stigma unilocular with three parietal placentae; fruit a loculicidal capsule, ovoid to cylindric, cartilaginous, valves three, seminiferous in middle, contracting when open and ejecting seeds; seeds ovoid, anatropous with a crustaceous coat, caruncúlate; embryo straight in copious endosperm, cotyledons flat, cleistogamous flowers, if present, with petals rudimentary or lacking, self-fertilizing within the closed calyx, occasionally subterraneous.

Type species of the genus: *Viola odorata* L.

Key to the species of the *Viola nuttallii* complex:

1. a. Leaves entire or nearly so, minutely puberulent, hairs 0.01 to 0.15 mm long, or glabrous; seeds tan or medium brown; caruncle flattened, extending beyond and covering the funiculus.
    2. a. Leaves more than 3.5 times longer than wide, 6 to 13 mm wide, base attenuate (angle 30 to 55°); seeds medium brown, 3mm long and 1.5 mm wide; pollen 35.2 um in diameter; found only east of the Rocky Mountains

at elevations of 700 to 2400 m; 2N=24 . . . . . *V. nuttallii*

2. b. Leaves 2.0 times longer than wide, base truncate (angle 120 to 180°), some later cauline leaves becoming cuneate; seeds mostly tan, 2.2 mm long and 1.2 mm wide; pollen 31 um in diameter; found from Great Basin to mid-western plains at elevations of 400 to 2800 m; 2N = 12 . . . . . *V. vallicola*

1. b. Leaves entire, serrulate or serrate; pubescent throughout, hairs greater than 0.5 mm long, or occasionaly glabrous; seeds silvery-purple to glossy reddish-brown; the caruncle globular, not extending beyond or covering the funiculus.

3. a. Cauline leaves 13.5 mm wide and more 2.3 to 2.5 times longer than wide, margins entire; chasmogamous flowers 8 to 15 mm long; seeds 1.7 to 1.8 mm wide, reddish brown 2N = 12 or 48

4. a. Densely tomentose throughout, hair length 1.4 mm or longer; seeds 2.7 mm long and 2.0 mm wide, 1.4 times longer than wide, caruncle small, 0.5 mm; 2N = 12 . . . . . *V. tomentosa*

4. b. Densely pubescent throughout, hair length 0.3 to 0.4 mm; seeds 3.1 mm long and 1.8 mm wide , 1.7 times longer than wide, caruncle 0.9 mm long; 2N = 48 . . . . . *V. bakeri*

3. b. Cauline leaves 14 to 30 mm wide and 1.6 to 2.6 times longer than wide, margins crenate or serrate; chasmogamous flowers 12 to 20 mm long; seeds 1.7 to 2.0 mm wide, medium to dark brown; 2N = 36 or 48 . . . . . *V. praemorsa*

Viola nuttallii Pursh. Fl. Am. Sept., 1: 74. 1814.

Type: "On the banks of the Missouri. June. v.s. Herb. Nuttall." PH! (holotype).

Crocien nuttallii (Pursh) Nieuwland and Lunell. Am. Midl. Nat. 4(11): 478. 1916.

A herbaceous perennial, 5 to 20 cm tall, from an erect, woody rootstock; glabrous or with puberulence throughout or only on leaf veins; stem appearing acaulescent

or becoming greatly elongated especially in late season growth; radical leaves ovate to oblong-lanceolate, acute, cuneate to attenuate ; cauline leaves mostly lanceolate, 26 to 40 mm long, 6 to 10 mm wide, 3.5 to 4.5 times as long as broad, some late season exceptions are shorter, base attenuate (angle 40 to 50°); laminal margins entire to distantly subserrulate, minutely ciliate; pubescence about 0.1 mm long; sepals linear, acute, auricles with or without pubescence; corolla yellow, tinted brown outside, lateral petals bearded within , lower and lateral petals marked with brown lines within, lower petal 10 to 13 mm long including short (1 mm) spur; stigma short tubular, style capitate, head retrosely bearded at sides; ovary glabrous or sparsely, minutely puberulent; cleistogamous flowers minute, sepals 5 mm long, common throughout growing season; fruit a valvular capsule producing about 10 seeds per capsule; seeds brown, 3 mm long and 1.5 mm wide, weighing 3 mg each; caruncle distally flattened, 1.1 mm long, extending beyond and completely covering the funiculus; pollen 35.2 um in diameter; 2N = 24.

V. nuttallii is widespread east of the Rocky Mountains in the southern regions of Alberta, Saskatchewan and Manitoba, Canada, and in the mid-western United States of Montana, North Dakota, South Dakota, Wyoming, Colorado, Nebraska, and Kansas. It occurs at elevations of 700 to 2400 meters above sea level (Figure 14).

Leaf tissue of specimens from this species was commonly found to contain apigenin, kaempferol, and quercetin flavonoid derivatives.

The specimen designated as the type (Figure 15), "on the sandy plains of the Missouri", appears to be Nuttall's type collection. The plate published in Hooker's *Flora* (1830) has been refered to as the standard drawing of this species (Baker, 1957).

V. nuttallii has been found in association with *Phlox hoodii, Lithospermum incisum, Opuntia polyacantha, Bouteloua gracilis, Zygadenus elegans, Artemisia frigida, Allium textile, Rhus aromatica, Sisyrinchium montanum, Cornus alba*, and, *Rosa aciculari*s . All of these species are indicative of the xeric conditions to which *V. nuttallii* appears to be adapted. Field observations indicated that, relative to the other members of the Nuttallianae, *V. nuttallii* occurs in the driest conditions.

Viola nuttallii has been shown to possess a chromosome number of 2N = 24 and shows no evidence of hybridization anywhere within its range. A barrier to gene exchange can reliably be assumed to exist. This taxon is certainly a "good" species

Figure 14. Distribution of *Viola nuttallii* Pursh.

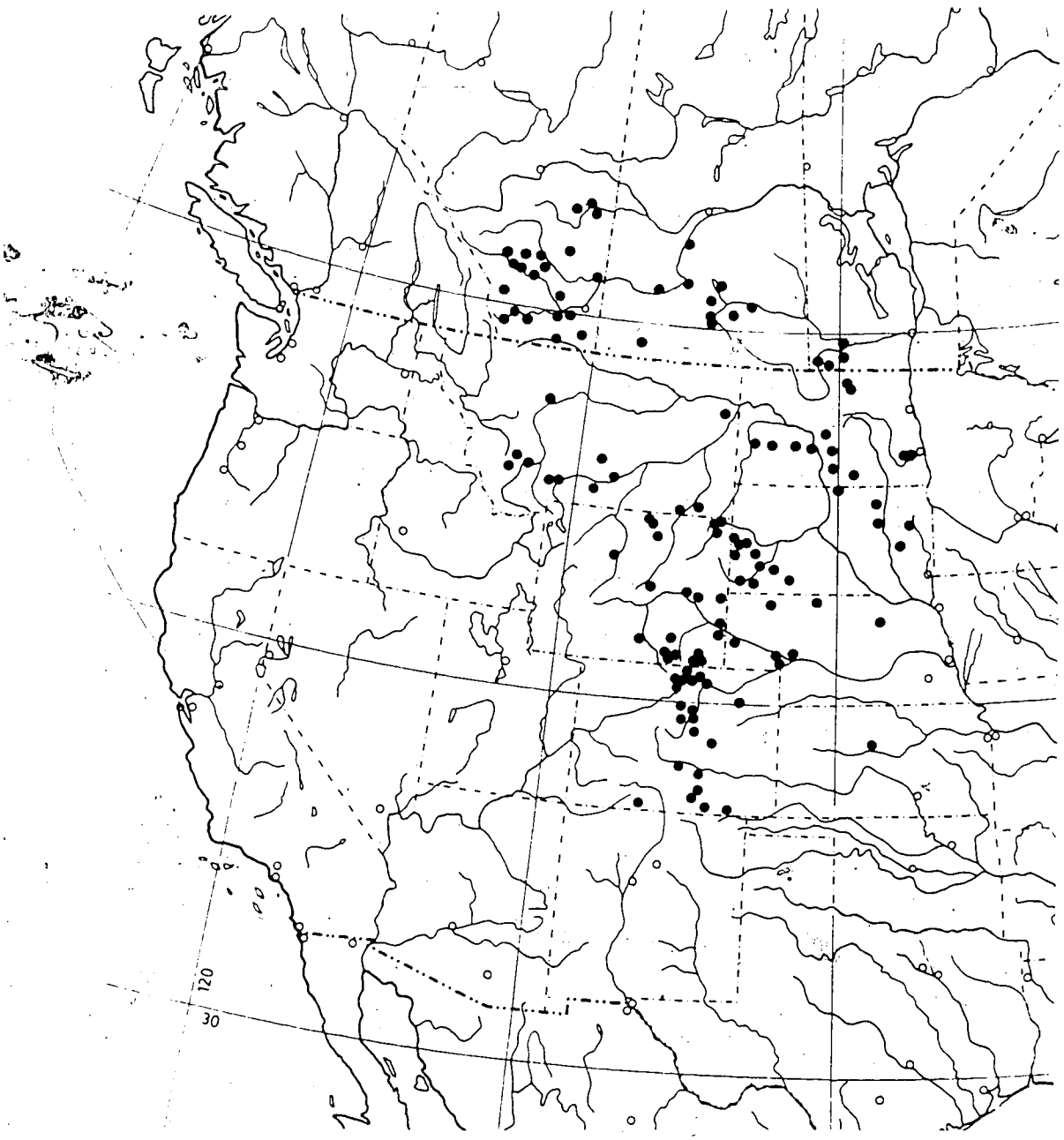


Figure 15. Holotype of *Viola nuttallii* Pursh.

TYPE COLLECTION

Viola Nuttallii - Pursh
(Nutt.)

Annotation Label
CENOSPECIES VIOLA NUTTALLII
Viola Nuttallii Pursh
Type-collection!
Det. by M. S. Baker and J. Clausen 1936
ACADEMY OF NATURAL SCIENCES, PHILADELPHIA.

Viola Nuttallii Pursh

according to the definition adopted for this study. Though some variation in leaf shape can be observed, particularily in late season growth, *V. nuttallii* can be reliably distinguished from all other members of the complex by it's leaf shape, short puberulence, and large, brown seeds.

Viola vallicola A. Nels. Bull. Torrey Bot. Club 26: 122-134. 1899.

Type: "Collected in several places in the state, the following numbers well representing it: 43, 4340, 4345, 4525." *A. Nelson 4340*, Pine Ridge, Wyoming. June 7, 1898. RM! (holotype).

Viola glareosa Dougl. MSS, never published.

Viola physolodes Greene. Pl. Baker. 3: 12. 1901.

Type: "In thickets along the Cimarrom River, 7 June, 1901." *C. F. Baker 67*. RM! (isotype).

Crocien vallicola (A. Nels.) Nwd. and Gunnell. Am. Midl. Nat. 4(1,1): 467-487. 1916.

Viola subsagittifolia Suks. Werdenda 1: 25-26. 1927.

Type: *W. Suksdorf 8530*, 10 km southeast of Spangle, Spokane County, [Washington,] 26 April and 15 May, 1916. WS! (holotype); PH!, UC!, MO! (isotypes).

Viola nuttallii Pursh variety *vallicola* (A. Nels.) St. John. *Fl. S.E. Washington and adjacent Idaho.* 1937.

Viola Russellii Boivin. Can. Field Nat. 65(1): 22. 1951.

Type: "Saskatchewan: R. C. Russell and B. J. Sallons, Duval, Last Mountain, small draw on hillside. May 13, 1940. DAO! (holotype).

Viola nuttallii Pursh subspecies *vallicola* (A. Nels.) Taylor and MacBryde. Can. J. Bot. 56(2): 190. 1978.

Perennial from relatively shallow-seated rootstock; habit decumbent, subcaulescent, stems elongating and erect late in season; leaves ovate to oblong-ovate, 19 to 43 mm long and 9 to 11 mm wide, blades about 2.2 times as long as broad, truncate to subcordate at base (angle 170 to 185°); glabrous to minutely puberulent throughout; margins entire to subentire, ciliate; chasmogamous flower lower petal 9 to 14 mm long,

sepals glabrous or puberulent on auricles only; cleistogamous flower sepals 4.5 mm long; ovary or expanding capsule glabrous or sparsely, minutely puberulent; seeds 2.2 mm long and 1.2 mm broad, weighing about 1.6 mg each; caruncle distally flattened, 0.8 mm long, extending beyond the funiculus and covering it, extending along up to 40% the length of the seed; seed coat tan with dark brown edges around caruncle; pollen 31.4 um in diameter; 2N = 12.

Viola vallicola has the widest distribution of any taxon within the Nuttallianae, ranging from south-central British Columbia to southwestern Manitoba and the Dakotas, south to Nevada, Utah, Colorado, and Arkansas (Figure 16). It occurs at elevations of 400 to 2800 m. The distribution appears to be continuous across mountain ranges, particularily through the intermountain region of Nevada and Utah. Flowering time was common throughout May though they were not uncommonly observed anytime from late March to early July.

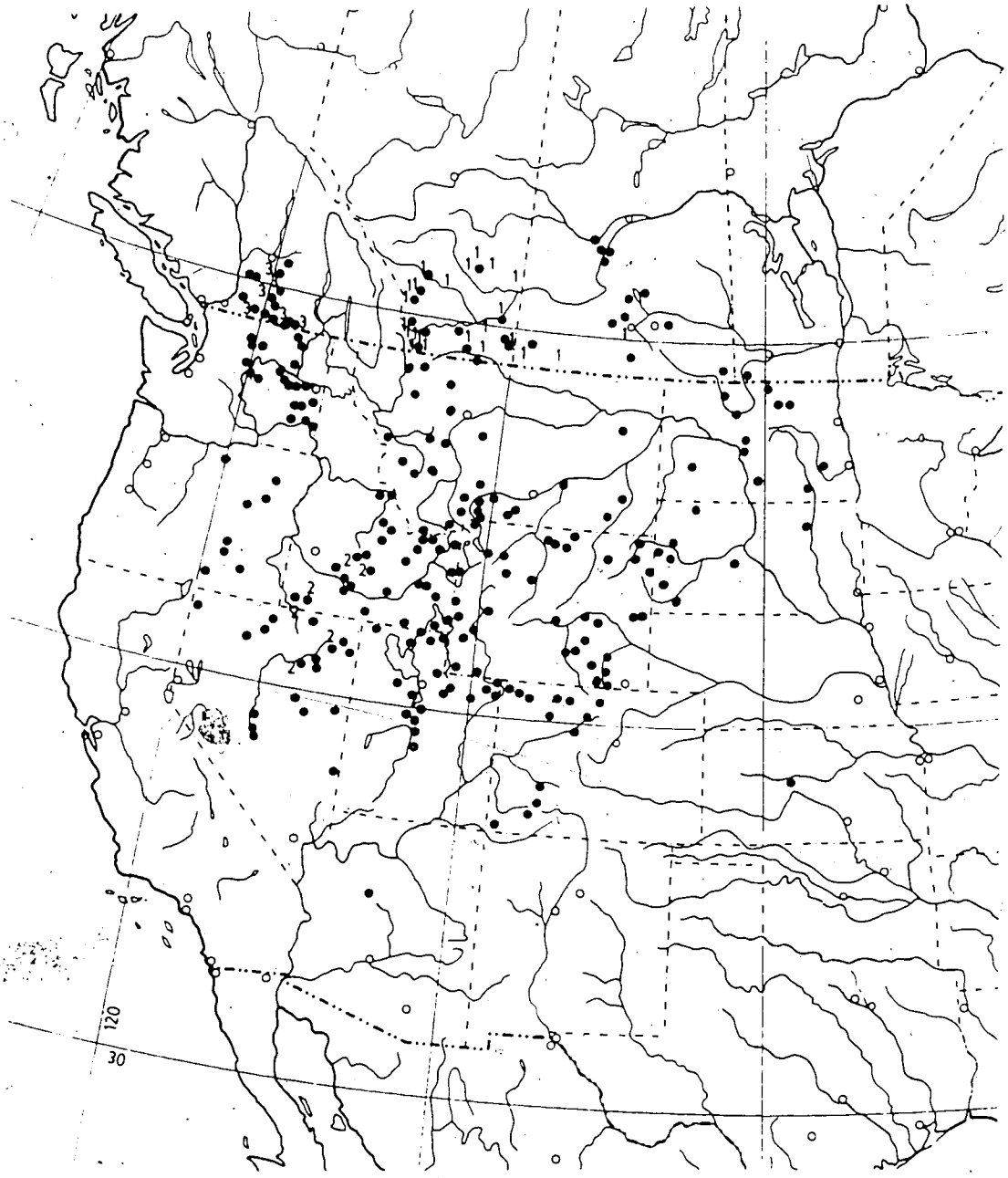
V. subsagittifolia Suksdorf from Washington certainly represents *V. vallicola* and must be included here. The new combinations published by St. John (1937) and Taylor and MacBryde (1978) were meant to refer to the taxon located in Washington and British Columbia, respectively. As no specimens were available from which to obtain flavonoid profiles, it was considered more logical to refer these combinations to the specific level. The C. F. Baker specimen from eastern Colorado also must be the eastern chemical form. Though no chemical extractions could be made, it is possible that this collection may be closer to the intermountain intermediate than to the eastern form.

Crocien vallicola Nwd. and Lll. was recombined as a result of a desire to subdivide the genus *Viola* into several genera based on plant caulescence and type of cleistogamous flowers, if present (Niewland and Kaczmarel, 1914). This division into seven new genera and three subgenera was never widely adopted. The study was based on the examination of very few species, and in fact did not include any members of the *nuttallii* complex. The section and subsection notation as used in this study was much more widely accepted and used since it was thought to reflect *Viola* as a natural group.

Boivin's description of *V. russellii* (1951) represents a species whose attributes match those of *vallicola* and whose type was located in the range of the eastern subspecies, *vallicola*. The publication gives no explanation for segregating *russellii*

Figure 16. Distribution of *Viola vallicola* Nels.

Black dots represent specimens of *V. vallicola*, 1= subspecies *vallicola*, 2= flavonoid intermediates, and 3= subspecies *major*



and *vallicola* though in a reply to an inquiry from M. Bowerman (1952, see DAO 288885) Boivin makes it apparent that no type specimens were examined and that he found it "difficult . . . to state the differences between these two species." Listed paratypes were from British Columbia, Alberta, and Montana, and the type was from Saskatchewan. This taxon was considered as synonymous with *V. vallicola*.

V. vallicola does display some variability in the size of leaves, degree of basal truncation, stem elongation, and chasmogamous flower size. Despite these minor variations, specimens of this species can easily be distinguished from *nuttallii* by leaf shape, and from other Nuttallianae by their near glabrous leaves.

Two chemotypes were observed within this species which likely represent two extremes in a range of variability.

Key to the subspecies of *Viola vallicola* A. Nels.

1. a. Leaf flavonoids primarily kaempferol derivatives; found west of the continental divide . . . . . subspecies *major*

1. b. Leaf flavonoids all apigenin derivatives; found east of the Rocky Mountains . . . . . .subspecies *vallicola*

Viola vallicola A. Nels. subspecies **major** (Hook.) Fabijan comb. nov.

Viola nuttallii variety *major* Hook. Fl. Bor. Am. 70. 1830.

Type: "Abundant under to shade of pines on the dry sandy p of the Columbia." KEW.! (holotype), UC! (photo of holotype).

Viola nuttallii major (Hook.) Piper. Contr. U. S. Nat. Herb. 11: 393. 1906.

Viola praemorsa variety *major* (Hook.) Peck. Madrono 6: 135. 1941.

Viola praemorsa Dougl. subspecies *major* (Hook.) Baker. Madrono 10: 128. 1949.

Leaf flavonoids primarily kaempferol derivatives; occurring west of the continental divide.

Subspecies *major* occurs west of the Rocky Mountains in British Columbia and Oregon (number 3 in Figure 16).

William Hooker (1830) described *major* as having wider leaves and larger flowers than *V. nuttallii*. The only specimen referred to was a Douglas collection which he had described in manuscript as a new species, *V. glareosa*. This specimen (H 1526/82) was from Herbariorum Hookeriana, was designated as the type at KEW (Figure 17). The label reads "*Viola glareosa* abundant under shade of solitary pines on dry sandy soil of Columbia." There can be little doubt of its application to the epithet "*major*", and thus, its connection to the western flavonoid form of *V. vallicola*.

Viola vallicola A. Nels. subspecies **vallicola**

Viola vallicola A. Nelson. Bull. Torrey Bot. Club 26: 122-134. 1899.

Type: "Collected in several places in the state, the following numbers well representing it: 43, 4340, 4345, 4525." *A. Nelson 4340*, Pine Ridge, Wyoming. June 7, 1898. RM! (holotype).

Leaf flavonoids all only apigenin flavones; occurs east of the continental divide in Alberta and Saskatchewan.

Though there was a tendency to shorter, wider cauline leaves, the range of variation was too great to be significant. The only reliable means by which to make identifications being geographical, it was thought that distinction at subspecies level was acceptable between *major* and *vallicola*.

The specimens cited by Nelson (1899) were all collected in Wyoming. Though number 43 was the first number refered to in publication, number 4340 was designated as the type specimen in the Rocky Mountain Herbarium. Pine Ridge is in the Black Hills in Crook County, northeastern Wyoming and logically may be refered to the eastern flavonoid form.

The two chemical forms, *major* and *vallicola*, could not be reliably distinguished on the basis of any morphological character examined in this study. Although there was a tendency for *major* specimens to display slightly smaller leaf length-to-width ratios, and

Figure 17. Holotype of *Viola vallicola* A. Nels. subspecies *major* (Hook.) Fabijan.

subentire, ciliate leaf margins as compared to *vallicola*. As noted in the morphological results, two specimens of *major* showed longer or darker seeds. None of these attributes were consistent or significant.

The only reliable means of identifying the subspecies appeared to be flavonoid chemistry, with apigenins commonly found in *vallicola* and kaempferols in *major*. These two taxa are not geographically isolated except in the northern extreme of the range. Genetic isolation cannot be assumed between the subspecies which likely intermingle, particularily in the intermountain regions of Idaho and Nevada. Examination of the leaf flavonoids from specimens in that area (OTUs 77, 78, 79, 80, 81: B9354, D1754, D1732, D1753, and D1736, respectively) contained apigenin and kaempferol derivatives.

Viola tomentosa Baker and Clausen. Leafl. West. Bot. 5: 141-147. 1949.

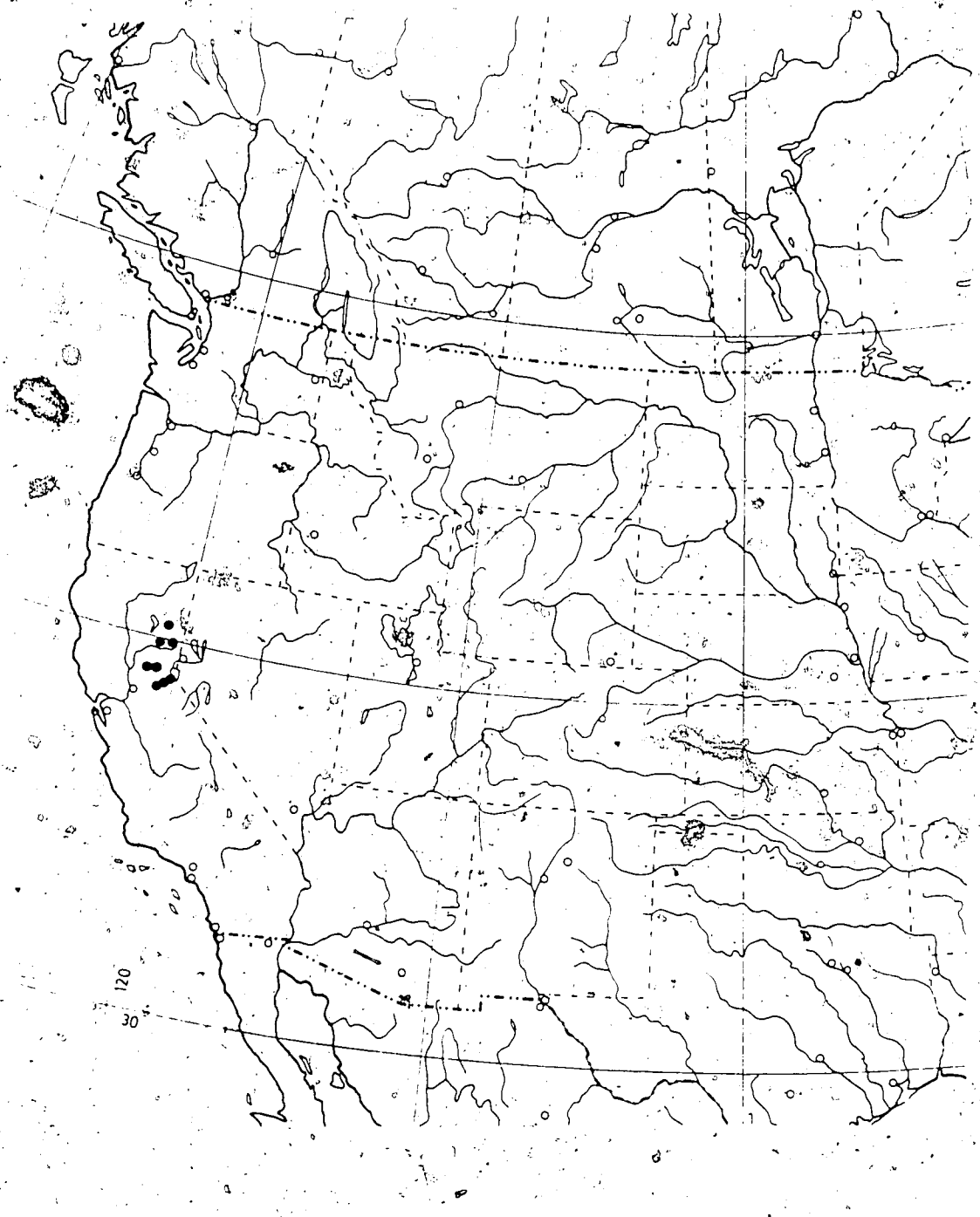
> Type: *M. S. Baker 8722A*, "July 9, 1937 (early growth), . . . collected along California highway 20, about 13 miles westerly from Cisco, Nevada Co., California, at about 5000 ft. elevation in forests of *Pinus ponderosa, Quercus Kelloggii*, and *Libocedrus decurrens*." CAS (holotype), UC!, OSU, MO, NY, US, and G (isotypes).

Plant densely woolly tomentose throughout; leaves 15 to 50 mm long, 9 to 25 mm ide, ovate to elliptic, margins entire; chasmogamous flowers small, lower petal about 9 mm long; cleistogamous flowers unknown; 2N = 12.

In terms of leaf flavonoids, *tomentosa* contained kaempferol, apigenin, and quercetin as had *nuttallii*. This was intermediate between *major*, and *praemorsa* and *bakeri*. *V. tomentosa* appears to be rare and restricted to the Sierra Nevada of California at elevations of 1500 to 2000 m (Figure 18). It has been found in dry gravelly soil of open coniferous forests. *V. tomentosa* has an extended flowering season from June to August.

V. tomentosa was without a doubt distinctive both in terms of its morphology and its diploid chromosome complement.

Figure 18. Distribution of *Viola tomentosa* Baker & Clausen.



Viola bakeri Greene. ia 3: 307. 1898.

Type: Bear Valley mountains, Siskiyou County, California., June, 1896. UC (holotype), DS! (isotype).

Viola bakeri Greene subspecies *grandis* Baker. Madrono 10: 117. 1949d. (Nom. Nud.)

Viola bakeri Greene subspecies *shastensis* Baker. Madrono 15: 203-204. 1960.

Type: *Baker 13045.* "Postpile Camp, altitude 8000 ft., western Tehama County, California." July 1, 1955. UC! (holotype).

Viola nuttallii A. Nelson variety *bakeri* (Greene) Hitchcock. *Vascular plants of the Pacific Northwest* 3: 447. 1961.

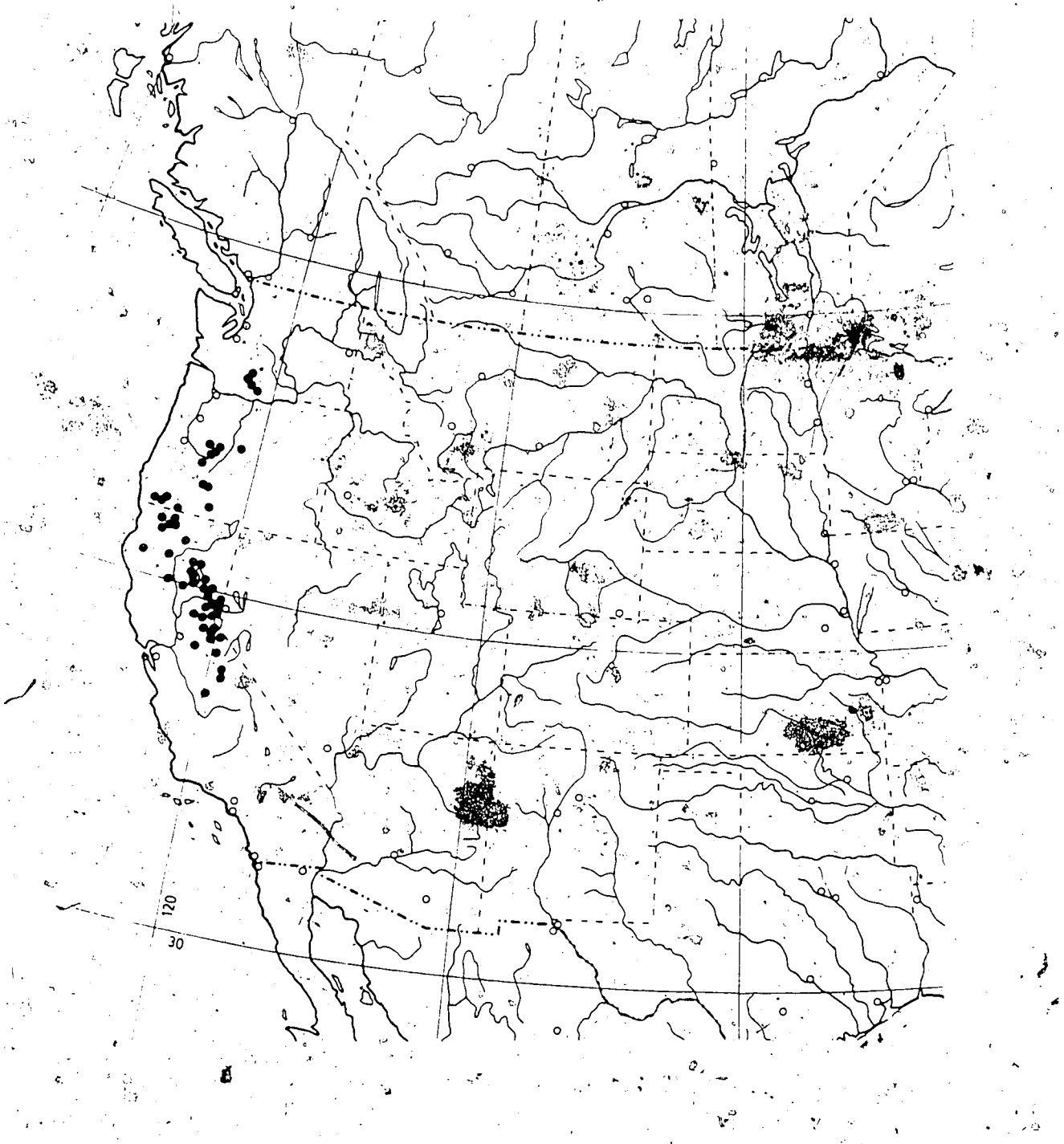
Viola bakeri Greene subspecies *puberulenta* Baker (mss., not published).

Subcaulecent early in the season and displaying elongated stems in later growth; radical and cauline leaves 20 to 40 mm long and 10 to 15 mm wide, ovate-lanceolate to ovate or elliptical, 2.1 to 2.7 times as long as wide, bases cuneate (55 to 80°), margins always entire and ciliate; more or less pubescent throughout, hairs 0.3 to 0.4 mm long, occasionally hirsute; lower chasmogamous flower petal 10 to 15 mm long; style capitate and retrosely bearded on sides as in all Nuttallianae; cleistogamous flowers 3.5 to 8.0 mm long; seeds dark red-brown, 1.8 mm wide and 3.1 mm long, 1.7 times longer than wide, weight 4.2 mg; caruncle 29% the length of the seed but not extending beyond the tip of the seed and covering the funiculus; pollen 44 um in diameter; 2N = 48.

Viola bakeri was distributed from the Cascades of southern Washington to the Sierra Nevada of California (Figure 19). It occurs at elevations from 900 to 3800 m, most commonly above 1700 m. Flowering time peaked from mid June to mid July, but sometimes occurred as early as May and as late as August.

Bakeri may be easily distinguished from *tomentosa* by the shorted length and lower density of its pubescence, by its chromosome number and by its more diverse flavonoid profile. Leaves of *bakeri* contained luteolin derivatives, as well as apigenin, kaempferol and quercetin derivatives.

Figure 19. Distribution of *Viola bakeri* Greene.



Viola bakeri may be distinguished from *nuttallii* primarily by its entire leaf margins and by its distribution east of the Rocky Mountains. The true distinction would be chromosome number, *bakeri* is an octoploid and *nuttallii* is a tetraploid. The characters of ovary pubescence and margin ciliation were not always consistent within the taxa and were, therefore, not applicable in distinguishing them (Table 8).

Baker (1949c) mentioned two subspecies, *typica* and *grandis* without descriptions or explanations. The invalid subspecies *typica* should properly have been referred to as *bakeri*, priority being given to the oldest published applicable epithet. Subspecies *grandis* was not validly published in receiving no latin description or designated type specimen. Baker (1960) maintained *grandis* as "nomen nudum". He deferred properly describing it due to a lack of continuity in its range.

The subspecies *shastensis* (Baker, 1960) was described as differing from *bakeri* by the presence of short appressed hairs on the sepals and capsules. These features (Table 8) were not consistently reliable in distinguishing between taxa. Creating a new subspecies based on inconsistent character states could not be justified by this study and the name was considered synonymous with *bakeri*.

Viola praemorsa Dougl. ex Lindl. Edward's Bot. Reg. 15: pl. 1254. 1829.

For synonymy and typification see subspecies headings.

An herbaceous perennial from a short, occasionally praemorse rootstock; appearing acaulescent but stem elongating during the growing season; 6 to 20 cm high; glabrous or conspicuously hirsute throughout; radical leaves various but mostly broadly ovate to obovate; cauline leaves ovate to oblong-lanceolate, base cuneate to truncate or subcordate; margins sub-entire to serrate; corolla of chasmogamous flowers yellow, lower petal up to 20 mm long including the spur; style 2.5 mm long, capitate head retrosely bearded on sides; capsule glabrous to puberulent; cleistogamous flower sepals 3.5 to 8.3 mm long; seeds of various colours from medium to dark brown; mostly 1.6 times longer than wide; caruncle short, globose, not extending beyond the seed apex or covering the funiculus; pollen diameter 41 to 45 um; 2N = 36, 48.

V. praemorsa occurs in the western half of the Nuttallianae range from southwestern Alberta and the Intermountain regions of Utah west through the Great Basin to Vancouver Island and central California.

Viola praemorsa is broadly defined here, in the tradition of Baker (1957), based on morphological variations in leaf shape, pubescence, and seed morphology. *V. praemorsa* specimens can be easily recognized by their hirsute pubescence, if present, larger leaf size, and the distinct caruncle form of the seeds. A wide array of structural variation exists in this species throughout its range. The three subspecies recognized in this study exhibited gradual intergradation whose intermediates are difficult to identify and classify. The influences of physical and environmental factors, along with hybridization and introgressive influences contribute to the multifarious nature of the structural forms observed. These subspecies represent variants defined primarily on extremes in leaf form, whose character states tend to overlap. The relationships of these taxa are discussed in more detail later.

Key to the subspecies of *Viola praemorsa*

1. a. Cauline leaves mostly short, 23 to 40 mm long; ovate to broadly ovate, length to width ratio of 1.6; blade base approaching truncate (106 to 172°), margins serrate; seeds dark brown, widely ovate, length to width ratio 1.4, 5.8 mg each, caruncle relatively short, 0.7 mm long; 2N = 36. . . . . subspecies *praemorsa*

1. b. Cauline leaves mostly longer, 33 to 80 mm; ovate to elliptical, length to width ratio of 1.8 to 3.2; basal angle 63 to 112°, margins subserrate to serrate; seeds medium brown, ovate, 1.5 to 1.7 times longer than wide, 3.9 to 5.1 mg; caruncle 0.8 to 1.0 mm long; 2N = 36, 48.

2. a. Cauline leaves 33 to 62 mm long; 15 to 23 mm wide, ovate to broadly ovate; 2N = 36, 48 . . . . . subspecies *linguaefolia*

2. b. Cauline leaves large, 60 to 80 mm long, 23 to 31 mm wide, elliptic; 2N = 36, 48 . . . . . subspecies *flavovirens*

Viola praemorsa Dougl. ex Lindl. subspecies **praemorsa**

Viola praemorsa Dougl. ex Lindl. Edward's Botanical Register 15: plate 1254. 1829. Type: "According to Mr. Douglas, in dry upland soils, under the shade of solitary Pine trees on the banks of the Columbia, and the plains above the river Aguilar, in California. Our drawing was made in the Garden of the Horticultural Society in 1828." CGE (holotype), DS! (photograph of holotype). Lectotype: *M. S. Baker 9634*, South Tacoma, Washington. UC! (lectotype); WS!, RM!, MO!, DAO! (isolectotypes). Lectotypification redundant.

Viola nuttallii variety *praemorsa* (Dougl. ex Lindl.) S. Wats. *Botany, Clarence King Expedition; U.S. Geological Exploration of the Fortieth Parallel* 5: 35. 1871.

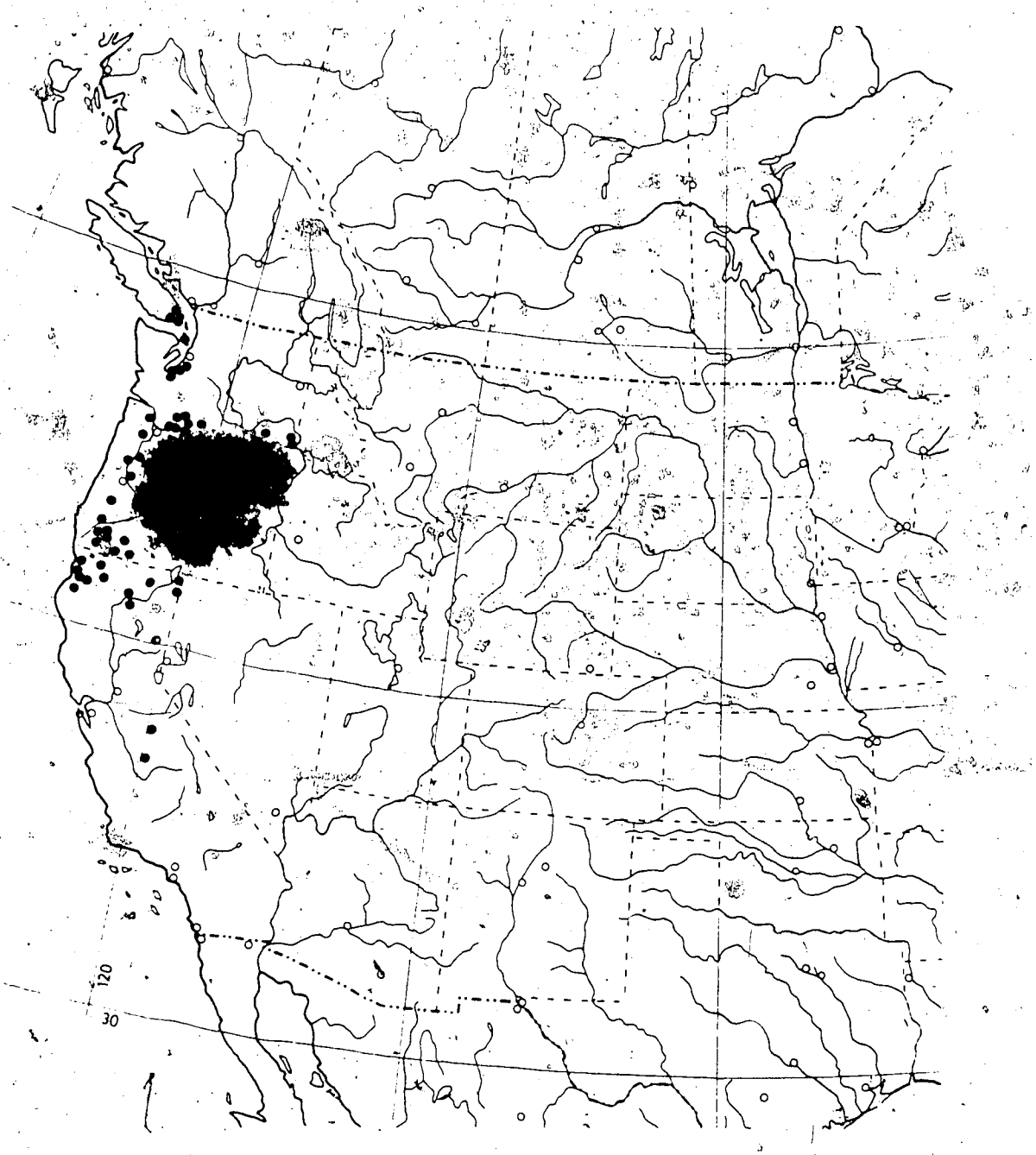
Viola nuttallii praemorsa (Dougl. ex Lindl.) Piper. Contr. U.S. Nat. Herb. 11: 393. 1906.

A herbaceous perennial, with short leaves, 20 to 40 mm long, length to width ratio of 1.6; leaf bases approaching truncate; pubescence densely hirsute at least on petioles and young leaves; seeds widely ovate, length to width ratio only 1.4, and weighing 5.8 mg, caruncle relatively short, 0.7 mm long, seed coat dark brown; 2N = 36.

This taxon occurs from the Saanich Peninsula of Vancouver Island south along the Coastal Ranges to northern California (Figure 20). Invaginations inland were evident along the Columbia River in Washington and toward the Sierra Nevada in California. Subspecies *praemorsa* was commonly found at elevations of 100 to 2500 m, though a few inland collections were found at elevations up to 7000 m. Flowering times were generally middle of April to early May but have been observed from March to June.

This taxon was first collected by D. Douglas near the mouth of the Columbia River. The published drawing was made from transplanted specimens at the Botanic Garden, but the original specimens appeared to have been lost. Most workers accepted the drawing in lieu of a holotype (Brainerd, 1921). From a photograph (DS 558332), it appears that a collection purchased from Lindley's herbarium had found its way to Cambridge and may well be the original type specimen. The label reads: "North West America, Douglas."

Figure 20. Distribution of *Viola praemorsa* Dougl. ex Lindl. subspecies *praemorsa*.



Cambridge Botanical Museum." Herb. J. Lindley, PhD. Purchased 1866." Baker (1899) lectotypified this taxon with a collection from Tacoma, Washington which is considered to be redundant.

Viola praemorsa Dougl. ex Lindl. subspecies **linguaefolia** (Nutt. ex T. & G.) Baker. Brittonia 9: 226. 1957.

Viola linguaefolia Nutt. ex T. & G. *A Flora of North America* 1: 141. 1838.

Type: "Kamas prairie, near the sources of the Oregon, Mr. Wyeth."

PH! (holotype); GH! (photograph of holotype), WS! (photograph of holotype); BM! (isotype); GH! (photograph of isotype),

Viola erectifolia A. Nels. Botanical Gazette 29: 143. 1900.

Type: *A. Nelson 5481*, Henry's Lake, Idaho, June 22, 1899. RM! (holotype); PH!, MO!, RM!, UC!, US!, and GH! (isotypes); ALTA (topotype, DF 622).

Viola gomphopetala Greene. Plantae Bakerianae 3: 11. 1903.

Type: *C. F. Baker 225*, on open hillsides of Grand Mesa [Colorado], June 23, 1902. RM! (holotype); RM!, WS!, UC!, GH! (isotypes).

Viola nuttallii linguaefolia (Nutt. ex T. & G.) Piper. Flora of Southeast Washington. 1914.

Viola nuttallii Pursh variety *lingulaefolia* (Nutt. ex T. & G.) Jeps. *A Man. Fl. Plants of Calif.*, 645. 1925.

Viola xylorrhiza Suks. Werdenda 1: 25, 1927.

Type: *W. Suksdorf 10200*, east of Husum, Klickitat County, Washington, 10 May, 30 June, 1919 and 1 June, 1920. WS! (holotype); UC!, MO!, CAS!, and DAO! (isotypes); ALTA (topotype, DF 397).

Viola praemorsa variety *oregana* (Baker and Clausen) Peck. *Man. High. Plants of Oregon*, 486. 1941.

Viola praemorsa variety *linguaefolia* (Nutt. ex T. & G.) Peck. Madrono 6: 135. 1941.

Viola praemorsa Dougl. ex Lindl. subspecies *arida* Baker. Brittonia 9: 227-228. 1957.

Type: *M. S. Baker 11462* in fruit, outskirts Klamath Falls, Oregon. UC! (holotype); RM!, DS!, MO!; and DAO! (isotypes).

Paratype: M. S. Baker 12086 in flower, from same colony. UC! (holotype); MO!, RM!, DAO! (isotypes); GH! (photograph of holotype).

Viola praemorsa Dougl. ex Lindl. subspecies *oregona* Baker. Brittonia 9: 228-229. 1957.

Type: *M. S. Baker 8862*. "The type locality is about half mile west of Klamath River Bridge on the Klamath Falls to Medford hwy c. 20 miles from Klamath Falls." DS! (holotype); RM!, MO!, and DAO! (isotypes); GH! (photograph of holotype). ALTA (topotype. DF 443).

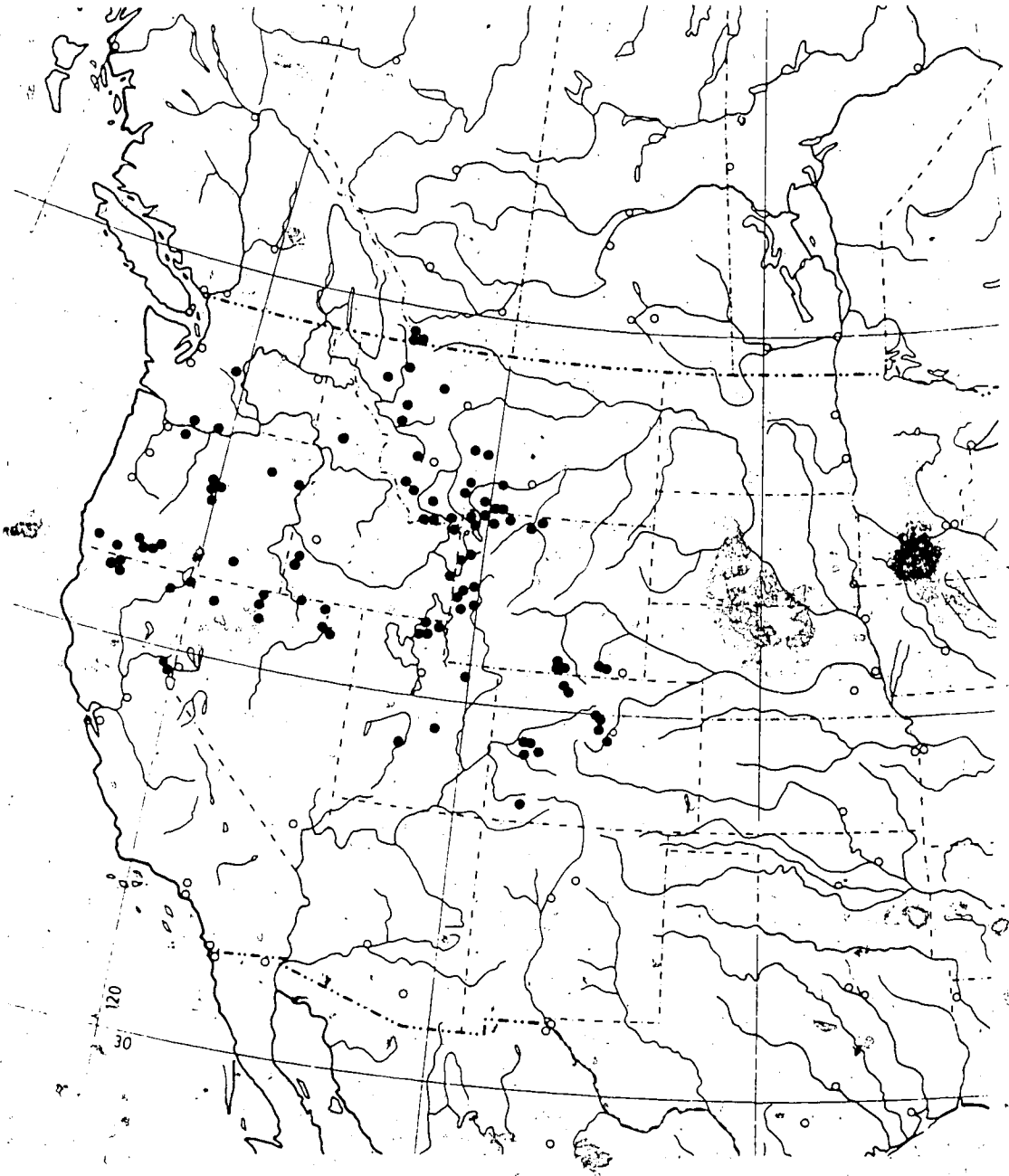
Leaves tongue-shaped, 33 to 62 mm long and 15 to 23 mm wide, ovate to narrowly ovate; blades cuneate (63 to 112°), margins subserrulate to serrulate; seeds brown to red-brown, 1.5 times longer than wide, weighing up to 5.1 mg with caruncles less than 1 mm in length; pollen large, 37 to 45 um in diameter; 2N = 36, 48.

Occurs from the Rocky Mountains of southwestern Alberta through Wyoming, Colorado and Utah, through the Intermountain region into the Great Basin ranges in northern Nevada and California, Oregon and Washington (Figure 21) at elevations of 1300 to 3500 meters above sea level. The peak flowering times were from mid-June to early August, but some flowers appeared as early as the first week of May. This distribution range overlapped significantly with *bakeri* in central Washington, Oregon, and California; with subspecies *praemorsa* along the Columbia River and in the Sierra Nevada; with subspecies *flavovirens* in Idaho, Washington and Wyoming, and, with *tomentosa* in the Sierra Nevada. The many morphological variants which were observed in this study may be symptomatic of these sympatric distributions which lead to the possibilities of hybridization and/or introgression.

The confusion in this taxon arises from the range of variation which exists in leaf shape and pubescence, and the presence of two different chromosome complements. The confusion in the relationships of the subspecies of *praemorsa* can be illustrated by the number of combinations which have been published by various authors.

A specimen at PH was annotated as the type specimen of *Viola linguaefolia*. It's label read "*V. nuttallii* / *linguifolia* / HK... *Hookeri. Kamas Prairie near the source of the Columbia (Nutt. from Wyeth)." This label matches the information given in

Figure 21. Distribution of *Viola praemorsa* Dougl. ex Lindl. subspecies *linguaefolia* (Nutt. ex T. &G.) Baker.



the publication (Nutt. ex T. & G.). The handwritting on this specimen also matches that of a specimen located in the British Museum (photographs!) dated June 20. The BM specimen was surely an isotype of the original collection on the Columbia, formerly known as the Oregon River. Nuttall was in Philadelphia from 1836 to 1841 (Brainerd, 1921), during the time when Torrey and Gray published their *Flora* (1838), and it seems most likely that the PH specimen is the holotype.

As shown in the numerical analysis *erectifolia* A. Nels. and *gomphopetala* Greene were both consistently associated with *linguaefolia*. Both were collected in mountainous regions within the range of *linguaefolia*.

Another source of confusion arises from the discovered misapplication of the epithet "*major*" to this taxon. Piper (1906) listed four specimens as representative of *V. nuttallii major*. Three of these specimens were examined and found to be referable here rather than with *major sensu* Hook. in both appearance and location. In listing *major* here, a confusion as to its correct application began which has been perpetuated to this day. It was apparent that Piper did not see the original specimen; if he had seen the specimen there would have been no need to cite Hooker's authority for the synonomy of *glareosa* Dougl. and *major*.

The description and distribution of Jepson's combination (1925) matched perfectly that of *linguaefolia*, though he cited no representative specimens.

It was almost one hundred years after Douglas published *praemorsa* (1829) that workers began to recognize *linguaefolia* as being more closely affiliated with *praemorsa* than with *nuttallii*. Morton Peck (1941) was the first to combine *linguaefolia* and *major* as varieties of *praemorsa*, though no explanations were given. Baker (1949c) listed both of these taxa as subspecies of *praemorsa*. It was not apparent whether type specimens had been examined, but detailed descriptions, distributions, and lists of representative specimens included at the time of publication permited these combinations to be equated here. Baker offered several methods by which to distinguish *major* and *linguaefolia* as he understood them, including leaf and capsule pubescence, leaf width and basal angle, and chromosome complements of 2N = 48 and 36, respectively. As already mentioned, relative puberulence of capsules and density of leaf pubescence have been shown to be inconsistent (Table 8), and therefore, unreliable as distinguishing

characters. The extremes of leaf shape used to define these two conceptual subspecies have been shown to represent the ends of a continuum between which no lines could be drawn based on present knowledge.

It is curious to mention at this point that Peck (1941) had published a new combination of *oregana*, apparently a spelling mistake, before the subspecies was actually described (Baker, 1957). Since no explanation was given, one can only assume that he had prior communication with Baker and Clausen before the 1957 publication.

Baker's subspecies *oregona* and *arida* (1957) were shown, in the numerical analysis (Figure 13, Appendix 4), to be morphologically indistinguishable within the continuum of attributes representing subspecies *linguaefolia*. Subspecies *arida* was distinguished because it was octoploid and had puberulent cleistogamous capsules in comparison to the glabrate ones in *major sensu* Baker and *praemorsa*. Subspecies *arida* had been found in a few scattered locations in eastern and southern Oregon and northern California. This range overlaps those of *linguaefolia* and *praemorsa*. I agree with Clausen (1964) who believed that the creation of a new subspecies based on tenuous characters within the range of a taxon from which it could not be reliably distinguished was unjustifiable.

Subspecies *oregona* is restricted to four sites in southern Oregon. It is distinguished by shorter than normal pubescence for the *praemorsa* group, with a leaf shape approaching that of *bakeri* but with serrate margins. The numerical analysis included this taxon morphologically with *linguaefolia* but chemically as intermediate between *linguaefolia* and *bakeri* (Appendix 4). This evidence supports the suggestion of possible hybridization between the two (Baker, 1957) due to their cytological, morphological and flavonoid similarities in conjunction with their overlapping distributions.

The broadly defined subspecies *linguaefolia* was observed to display at least two different flavonoid patterns. In one group, 12 to 20 different flavones and flavonols (apigenin, luteolin, kaempferol, and quercetin derivatives) were present in each specimen extracted. The types of flavonoids and their patterns resembled those found in *bakeri* and *flavovirens*. The second group was found to contain only flavonols, derivatives of quercetin and kaempferol. The profiles of these variants represents a decrease in the diversity of flavonoids to only seven compounds in total. No correlation with

morphology, cytology or geographic distribution could be made for these two chemical variants except that all of the reduced profile specimens had a chromosome count of 48.

Viola praemorsa Dougl. ex Lindl. subspecies **flavovirens** (Pollard) Fabijan stat. et comb. nov.

Viola flavovirens Pollard. Bull. Torrey Bot. Club 24: 405. 1897.

Type: *A. A. Heller 3156* "at Lake Waha, Nez Perces Co., Idaho, June 3 and 4, 1896". PH! (holotype); DAO!, MO!, WS!, UC!, and US! (isotypes).

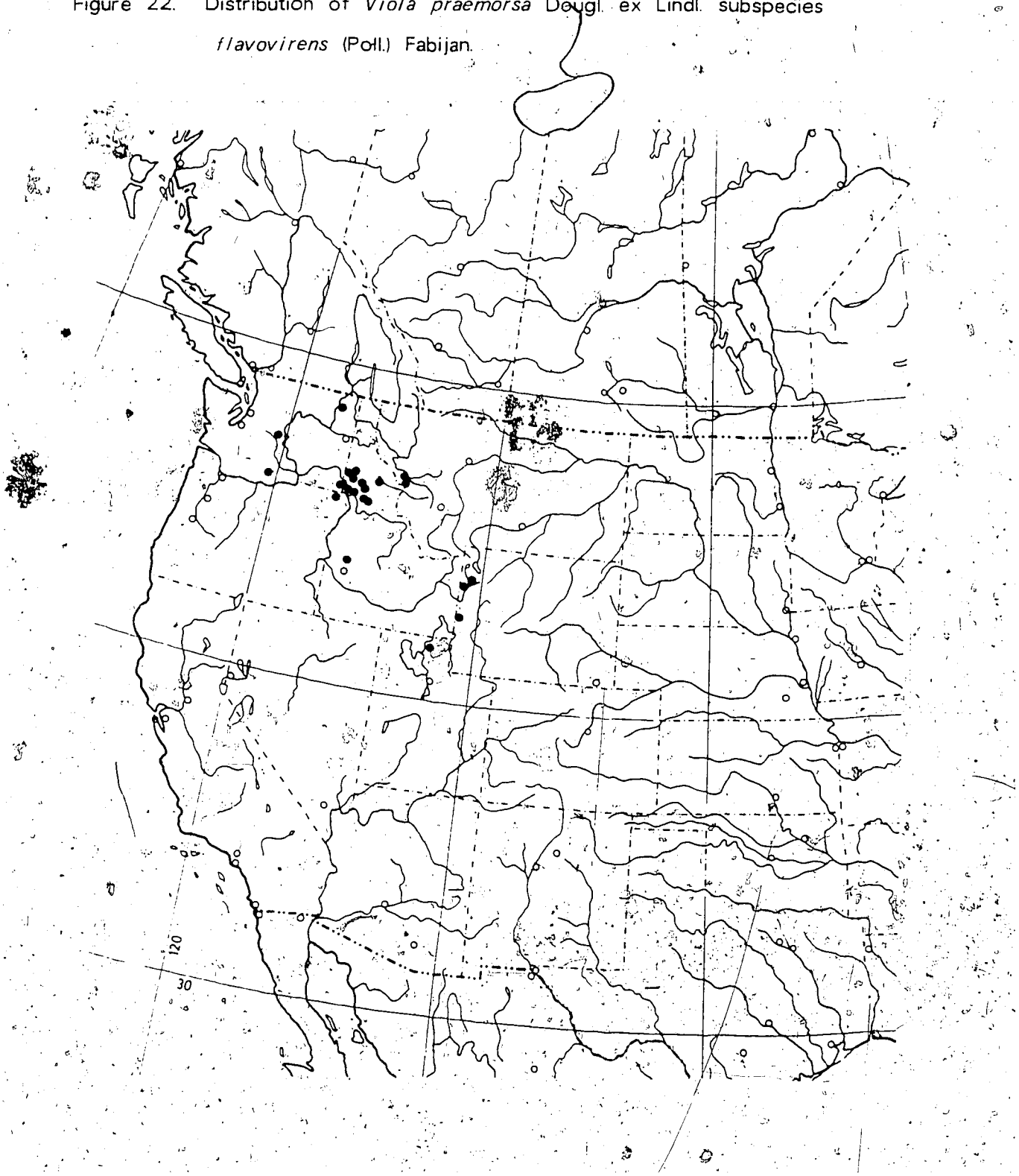
Leaves 60 to 80 mm long and 23 to 21 mm wide, when fully matured, margins regularly serrate-crenate; pubescence generally over 0.5 mm long, seeds about 4.1 mg; caruncle less than 30% of its length; pollen 34 to 37 um in diameter; 2N = 36, 48.

Occurs in the Rocky Mountains of the Idaho panhandle and adjacent Washington and Montana, with a few distant populations in western Wyoming and northern Utah (Figure 22). Found at lower elevations of 900 to 1200 m. The flowering period was from late April to early or mid June.

The collection number of the type specimens appears to have been misprinted at the time of publication as 3106 instead of the 3156 indicated on the type specimen which was from the correct location and on the correct date. The specimen at UC of the same collection without a collection number must be referred to here as well since it was collected at the same time and place.

Beginning with Piper and Beattie (1914), *flavovirens* has been treated as synonymous with *V. praemorsa* subspecies *major* by all authors. Annotations on herbarium sheets by M. S. Baker and J. Clausen indicated they may have considered reassigning it to variety or subspecies level. No such combination was ever published.

Figure 22. Distribution of *Viola praemorsa* Dougl. ex Lindl. subspecies *flavovirens* (Poll.) Fabijan.



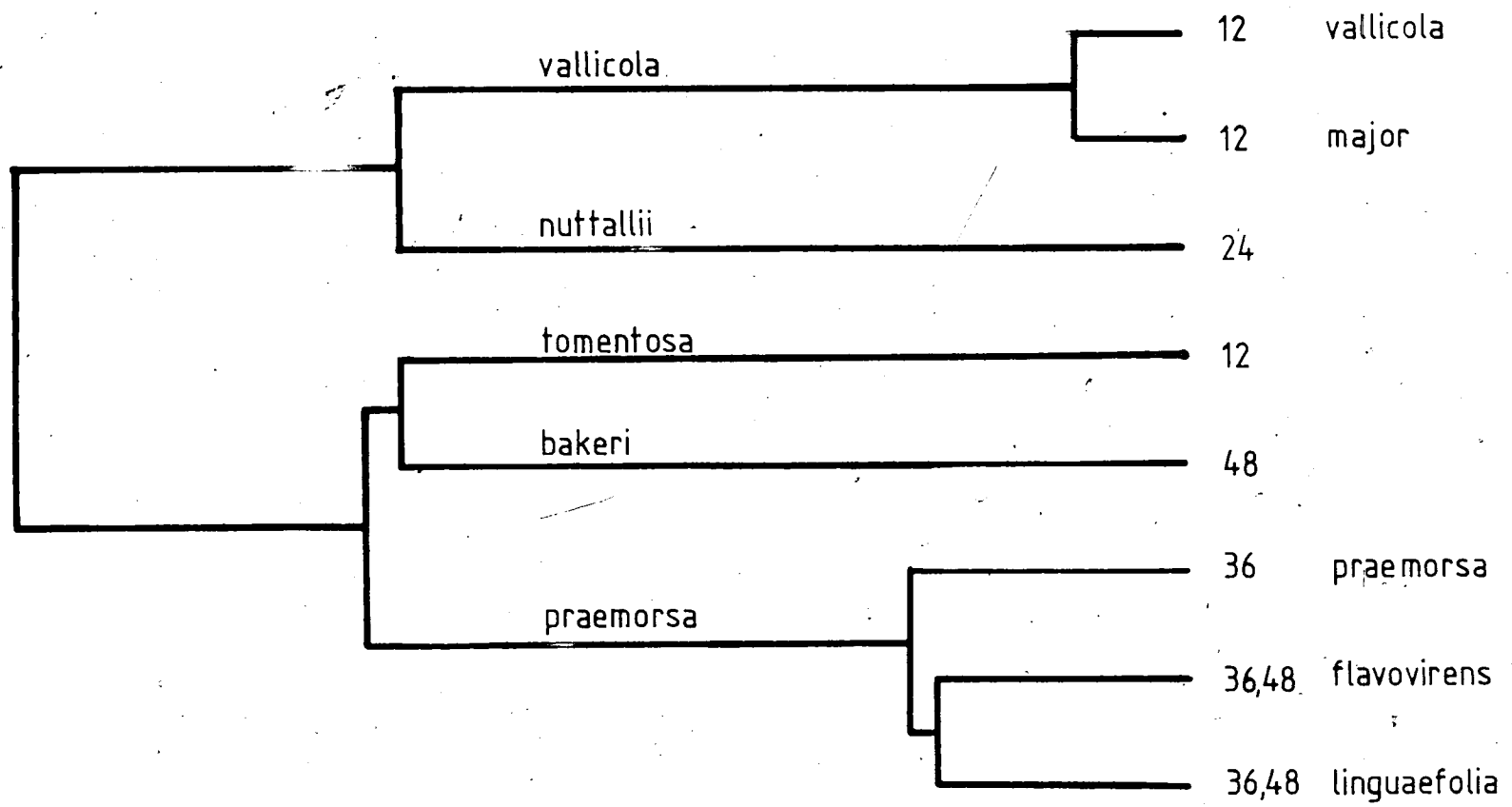
IV. DISCUSSION

This investigation of the *Viola nuttallii* complex resulted in the recognition of eight taxa (five species and three subspecies) based on their differences in ploidy level, morphological attributes and flavonoid chemistry: *V. vallicola*, 2N = 12; *V. nuttallii*, 2N = 24; *V. praemorsa*, 2N = 36, 48; *V. bakeri*, 2N = 48; and *V. tomentosa*, 2N = 12. Departures from the most recent, detailed analysis (Clausen, 1964) include the recognition of two subspecies of *V. vallicola*: *vallicola and major*; *V. praemorsa* is envisaged as embracing a wide range of morphological and chemical diversity the extremes of which are recognized as the subspecies *praemorsa*, *flavovirens*, and *linguaefolia*. In the absence of morphological or geographical differences between *V. linguaefolia* and *V. praemorsa* subspecies *major* and *oregona*, taxa recognized by Clausen (1964), these are included in subspecies *linguaefolia*. This treatment is supported by cytological and chemical evidence. A diagramatic representation of the taxonomic relationships among the members of the Nuttallianae is given in (Figure 23).

The *V. nuttallii* complex has long been recognized as a polyploid series with a basic chromosome number of x = 6. Chromosome counts of 2N = 12, 24, 36 and 48 obtained in this study confirm all previous counts reported for this complex (Table 5). It is known that in related species, cell sizes increase with increased ploidy level (Sax and Sax, 1937). This principle was confirmed for the *V. nuttallii* complex, in which pollen grain diameter is correlated with an increase in chromosome number (Figure 2). Pollen size can, therefore be employed in determining ploidy level in this complex, and may be of considerable utility in any future investigation of these taxa.

Hybrids had been reported in the literature by both Clausen (1964) and Davidse (1976). These included hybrids between subspecies *linguaefolia* and *V. utahensis* (Purpureae) which produced an n = 18 individual; and between *linguaefolia* and *V. douglasii* (Chrysanthae). This latter hybridization was believed by Clausen (1964) to have given rise to what Baker (1949c) considered to be *V. praemorsa* subspecies *arvensis*. Hybridizations between *V. tomentosa* and various members of the Purpureae and Chrysanthae subsections have also been found (Table 2). The presence of these reported hybrids indicates a close relationship between the *praemorsa*, *tomentosa*

Figure 23. Taxonomic relationship of the members of the *Viola nuttallii* complex.



species and other subsections in the Chamaemelanium.

A new hybrid (Table 5) was discovered between subspecies *linguaefolia* (2N = 36) and *V. purpurea* (2N = 12), subsection Purpurea, which grew intermixed at a location in California. The hybrid had a mitotic chromosome complement of 2N = 28 and pollen viability was estimated at only 7%, indicating that it was probably sterile.

No hybrids involving *V. vallicola* or *V. nuttallii* were observed nor have any been reported.

Prior to this investigation, very little was known about the flavonoid chemistry of *Viola*. The genus had been reported to contain the following flavones and flavonols: quercetin, kaempferol, luteolin, apigenin, violanthin, vitexin, saponaretin, orientin, and isoorientin (Bate-Smith, 1962; Wagner *et al.*, 1972; Gibbs, 1974; and Harborne, 1975). The only taxonomic work within the genus involving flavonoids, used only flavonoid profile analysis (Stebbins *et al.*, 1963 and McPherson, 1972).

The present study identified luteolin aglycone, oxygenated glycosides of apigenin, luteolin, kaempferol, and quercetin; a 6-methyl apigenin glycoside; and, a 6-methyl kaempferol glycoside. The most common glycosides were rutinose, glucose, galactose, rhamnose and arabinose (Figure 11 and Table 6). Further identification of the unknown compounds is expected to reveal the presence of some of the other previously reported flavonoids. Their presence is suspected from the comparison of Rf values with those reported in the literature (Harborne, 1967; Mabry *et al.*, 1970; and Jay *et al.*, 1975).

Despite the incomplete identification of all extracted flavonoids, careful examination of flavonoid spot patterns on two-dimensional paper chromatography and comparison of the major types of aglycones proved to be helpful in evaluating taxonomic boundaries and relationships among taxa. Flavonoid profiles have proven useful in related work in *Viola* subsection Purpurea (Stebbins *et al.*, 1963) where the ancestry of amphiploids and introgressants were investigated.

In the *V. nuttallii* complex, it was possible to correlate flavonoid pattern with ploidy level, morphological features, and distributions. The phytogeographic and phylogenetic implications of flavonoid analysis will be discussed for each taxon. The

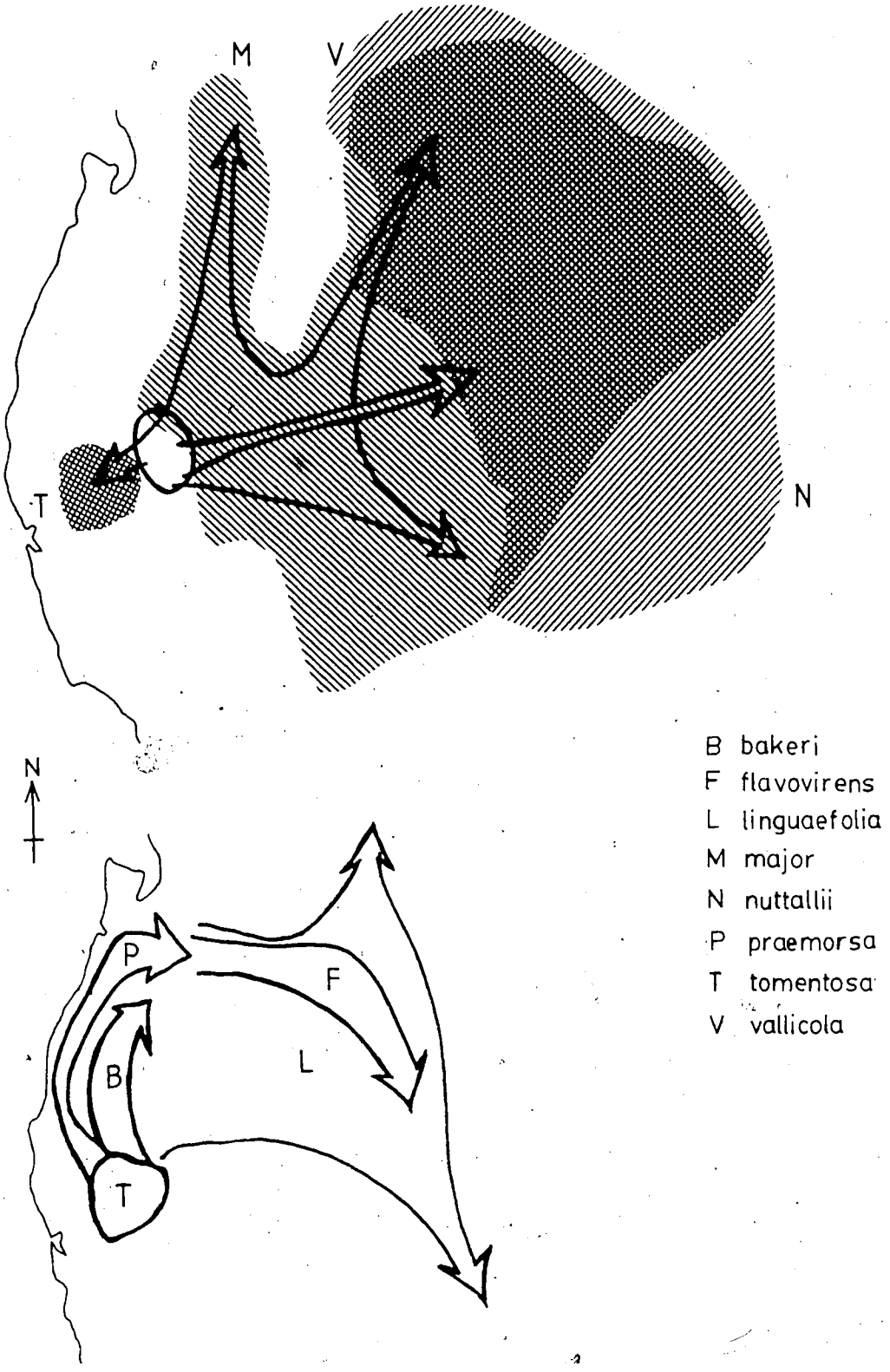
proposals for the evolutionary history of the members of the Nuttallianae are summarized in Figure 24.

The chromosome number of 2N = 12 for *V. vallicola* for 30 populations from British Columbia, Alberta and Saskatchewan (Table 5) supplements 19 previous counts (Davidse, 1976) from Idaho, Nevada, and Utah. Together, these reports cover a large portion of the range of this taxon. Only the easternmost populations in the range remain to be examined.

Viola vallicola specimens contained a total of eleven different flavonoid compounds: attributes 1, 2, 3, 4, 5, 6, 7, 9, 10, 11 and 29 (Table 7). Examination of chromatographic profiles revealed the presence of two distinct flavonoid races in this species plus a third pattern which appeared to be intermediate. None of these patterns could be correlated with any morphological feature examined in this study (Appendix 3), they could, however, be correlated with geographic occurrence (Figure 16). Subspecies *vallicola* contained primarily (frequency of 50% or greater) apigenin derivatives, compounds 2 and 3 (Table 7), and was found in Alberta and Saskatchewan. Subspecies *major* was found to contain predominantly kaempferol glycosides, compounds 1 and 9, and occurred in the interior of British Columbia and Oregon. A number of specimens from the Great Basin regions of Idaho and Nevada were found to be intermediate; they lacked compounds 2 and 9, but possessed compounds 1 and 3, and also contained two novel compounds, 5 and 10.

The recent elucidation of the general biosynthetic pathways of flavonoids in a number of higher plant taxa (Giannasi, 1978) indicate that the flavone apigenin represents one biosynthetic step from the precursor flavanone while kaempferol represents two biosynthetic steps: from flavanone to flavanonol to flavonol. Subspecies *major*, which possessed flavonols, may be considered further removed from the ancestor than subspecies *vallicola* because of its possession of these more complex flavonoid characters. The intermediates could be considered as either ancestral to one, or both subspecies, or as introgressive hybrids between two ancestral chemical forms. It would be impossible to prove which of these possibilities was true until specimens from the entire range of *V. vallicola* were examined for their flavonoid profiles and all compounds

Figure 24. A proposal for the evolutionary history of the *Viola nuttallii* complex.



were positively identified.

The Great Basin region, lying in the area of continuous distribution across the continental divide, could represent the point where one subspecies migrated across giving rise to the other; the area of dispersal of the species resulting in two chemical variants; or the area of overlap of two ancestral chemical forms with the opportunity for introgression. The hypothesis of genetic flow across this region is supported by the apparent filtering of biosynthetic capabilities across it (Table 7). Compound 2, found at 96% frequency in subspecies *vallicola*, was present in 17% of the intermediates and 0% of subspecies *major*. Compound 1, present in 100% of the *major* specimens and intermediate specimens, was found in one specimen of subspecies *vallicola*. Compound 10 was present in only 50% of the intermediates, and was present in 17% of the subspecies *major* specimens. The only unique compound present in the intermediate was compound 5. Until all compounds are identified, this interpretation remains speculative.

Alston and Turner (1962) used flavonoid patterns to investigate introgression in natural hybrids and concluded that progeny resulting from introgressive hybridization rarely contain unique compounds. More recent work (Levy and Levin, 1971) indicates that novel compounds are produced in hybrids. The novel compounds were the probable result of repression or suppression of glycosylation in the hybrid, which would result in less highly glycosylated flavonoids than those found in either of the parents. The situation for *V. vallicola* could be clarified simply by examining the flavonoids present in artificial hybrids between the two subspecies.

Three phylogenetic senarios are proposed. With the gradual, continuous uplift of the Rocky Mountains during the Quaternary, *V. vallicola* or its ancestral form became split into eastern and western populations. The Oligocene cooling trend also resulted in gradual migration of vegetation to lowland areas (Tidwell *et al.*, 1972). The three major glaciations of the Pleistocene covered the eastern Sierra Nevadas, Cascades, northeastern Utah, the Uinta Mountains, and parts of the Great Basin, as well as the Rocky Mountains and most of western Canada (Tidwell *et al.*, 1972). The Intermountain region however, was semiarid during these maximum advances perhaps allowing for the meeting of the two subspecies. The consequence was introgressive hybridization with disruption of

flavonoid biosynthesis at the genetic or regulatory levels (Levy and Levin, 1971)

If before the Pleistocene glaciations *V. vallicola* or its ancestor was found on only one side of the Rocky Mountains, migration south to the Great Basin area during glacial maxima, may have afforded it an opportunity to migrate across the continental divide and expand its range concomitent with an evolutionary change in flavonoid biosynthesis.

The third proposal, favored by the author, suggests that isolation during post-glacial migration northward on either side of the mountains could account for the differentiation of two subspecies. The loss of flavonoid synthesizing capability for flavonols in subspecies *vallicola* is incomplete because some specimens appeared to accumulate kaempferol and quercetin derivatives. Genetic isolation, therefore, cannot be absolute even in the northern most portion of the range. Further flavonoid surveys would help to establish whether the subspecies were a purely northern phenomenon or represent an east-west differentiation.

Twelve populations of *V. nuttallii* from Alberta and Saskatchewan were found to possess somatic chromosome counts of 2N = 24 (Table 5), confirming the two previous counts for this taxon (Baker, 1949c; Clausen, 1964). One of these counts was from a transplant of nursery stock from Colorado; the other from buds fixed by W. C. McCalla (*7355*, ALTA) from a population in Calgary, Alberta.

Viola nuttallii contains one flavone (3, an apigenin derivative), several flavonols (1 and 4, kaempferol 3-O diglycosides; and 6, 7, 8, quercetin 3-O and 3,7-O diglycosides) and other flavonoids (8, 10, 12, at low frequencies; see Table 7). Morphologically, *V. nuttallii* is most similar to *V. vallicola*, differing principally in leaf shape, and seed size and colour (Figure 12, Appendices 2 and 3). Chemically, *nuttallii* is most similar to *V. vallicola* subspecies *vallicola*, with 56% of their flavonoids in common and *V. tomentosa*, with 50% of their flavonoids common (Table 7) and which it approaches in leaf basal angle and seed colour.

V. vallicola and *V. nuttallii* are sympatric east of the Rocky Mountains (Figures 14 and 16) and some populations in Alberta and Saskatchewan were observed to grow in close proximity. No hybrids were observed and none have been reported in the literature.

V. nuttallii was thought to be an autotetraploid of *V. vallicola* by Baker (1957), while Clausen (1964) speculated that it might have originated from an as yet undiscovered diploid race of *V. nuttallii*. No such diploid has been discovered. Morphological and chemical evidence presented in this study suggest the possibility that *V. nuttallii* is an allotetraploid of *V. vallicola* and *V. tomentosa* (Table 7).

Levy (1976) found that colchicine-induced autotetraploids of *Phlox* exhibited novel glycoflavonoids, loss of diploid glycoflavonoids and deregulation of glycoflavonoid biosynthesis. All of these features can be observed in the differences in leaf flavonoids between *V. nuttallii* and *V. vallicola* subspecies *vallicola*. *V. nuttallii* did not possess apigenin 7-O diglycoside (2) but did possess novel flavonoids 8 (quercetin 3-O monoglycoside), 10, and 12. Deregulation of flavonoid biosynthesis was found for compounds 1, 4, 6 and 7, both in terms of frequency and in relative intensity of spot patterns on paper chromatographs (Appendix 1).

The same comparison of lost and novel compounds, and the deregulation of flavonoid production was observed between *V. tomentosa* and *V. vallicola*. They are not sympatric at the present time, but their ranges may have overlapped at some time in the past. With the increasing Pleistocene aridity in the Great Basin and California, *nuttallii* (and *vallicola*) is proposed to have become adapted to more xeric conditions than *tomentosa*, and moved into the lowland and prairie environments (Figure 24A). *V. nuttallii* is not known west of the Rocky Mountains, it's range overlaps only with *V. vallicola* subspecies *vallicola*. The ecological requirements of *V. nuttallii* are very similar to those of *V. vallicola* and may lead one to expect them to have the same distributions. However, *V. nuttallii* has a maximum elevational range of 2400 m, not as high as *V. vallicola*, and may have been unable to migrate westward over the mountains.

Viola tomentosa, a diploid, possessed apigenin (2 and 3), kaempferol (1) and quercetin (6, 7, 8) derivatives, and flavonoid 24 (Table 7). It had 38% of its flavonoids in common with the diploid *V. vallicola*, and 50% in common with the tetraploid *V. nuttallii*. This suggests that these taxa are related in some way. The distributions of *V. vallicola* and *V. nuttallii* do not overlap with *V. tomentosa*, which occurs in upland forest areas in the Sierra Nevada. Their ranges may have diminished in recent times due to the Pliocene

uplift of the Sierra Nevada and Cascade Ranges (Jardin and McKenzie, 1972) in conjunction with the increasing aridity and summer drought conditions on the west coast (Chaney, 1947).

A chromosome count of 2n = 48 (Table 5) for *V. bakeri* from Trout Lake, Washington, is the first for this taxon outside of California (Baker, 1949a). *V. bakeri* was most similar to *V. tomentosa*, whose range it overlaps in the Sierra Nevada (Figure 19). No tetraploid intermediate is known in that range, nor does there appear to be a suitable hexaploid with which it could have hybridized.

V. bakeri and *V. tomentosa* have only four (24%) of their flavonoids in common; three of these are quercetin derivatives (Table 7). The unique feature of *bakeri* (and *praemorsa*) specimens is the presence of a diverse array of different flavonoids and the presence of luteolin derivatives (11, 13, 15, and 17). The biosynthetic capability to produce these new flavonoids may be due to the effects of past (unknown) polyploidy or may have been introduced through hybridization with species in the closely related subsections Purpureae and Chrysanthae (Table 2).

V. bakeri occurs in the Sierra Nevada and Coastal ranges and occupies areas which also overlap with the subspecies of *V. praemorsa*. That *V. bakeri* possesses no compounds not found in *V. praemorsa* is a strong indication of a close phylogenetic relationship, perhaps through a common ancestor. The ancestral flavonoid pattern must then have included compounds 6, 7, 8, 11, 13, 14, 15, 16, 17, and 22, apigenin, luteolin, kaempferol and quercetin derivatives. It is also possible that hybridizations may occur between *bakeri* and octoploid *linguaefolia* and *flavovirens* in their regions of overlap in central Washington and southern Oregon and northern California. These regions contain a number of examples of possible hybrids such as subspecies *oregona* Baker (1957) in southern Oregon. TAXMAP analysis three (Figure 13, Appendix 4) revealed that though specimens of *oregona* were morphologically clustered with *linguaefolia*, they occupied a position intermediate between *bakeri* and *linguaefolia*.

V. praemorsa is composed of three subspecies which represent recognizable extremes in the range of morphological variation present in the species. As outlined in

the results these variations existed in cytological, morphological, and chemical attributes. These taxa were found to contain a vast array of different flavonoids, up to 20 in one taxon, in comparison to diploid and tetraploid taxa (Table 7). One strikingly unique feature of this flavonoid profile was the presence of a new aglycone base, luteolin. The four identified luteolin derivatives (11, 13, 15, and 17) were prominent in the profiles of most specimens of *V. praemorsa* and *V. bakeri*.

Chromosome counts of 2N = 36 from two populations of *V. praemorsa* subspecies *praemorsa* in Washington and California, including a topolectotype (*DF 414*), of subspecies *praemorsa* (Table 5) confirm previous reports (Gershoy, 1934; Baker, 1949c and 1957, and Clausen, 1964). Subspecies *praemorsa* is a Pacific coast entity whose range extends inland in the region of the Columbia River and again along the Oregon California boundaries (Figure 20). In both of these inland areas it overlaps the ranges of *V. vallicola* subspecies *vallicola*, *V. bakeri*, subspecies *flavovirens*, and subspecies *linguaefolia*.

Subspecies *flavovirens* represents a morphologically distinct taxon which occurs in isolated pockets in the Rocky Mountains within the range of subspecies *linguaefolia* (Figure 22). Counts of 2N = 36 and 48 are the first reported chromosome numbers for this taxon (Table 5).

The previous reports of chromosome counts for *linguaefolia* of n = 18 (Clausen, 1964) and n = 24 (Davidse, 1976) were both confirmed for ten populations in Washington, Oregon, California, Idaho, Montana, and Alberta (Table 5). In all cases pollen viability estimates were high (80 to 95%, Figure 2). Clausen and Baker (Baker, 1949c) first reported a chromosome count of 2N =36 for two populations of *linguaefolia* from Idaho and Utah (Clausen, 1964), and 2N = 48 for four populations of *major sensu* Baker. Even though "the morphological characters are not highly distinct," Clausen retained *linguaefolia* at species level, because of his belief of its unique chromosome number. Davidse (1976), finding only counts of 2N = 48, preferred to consider *linguaefolia* in synonymy with *V. praemorsa* subspecies *major sensu* Baker. In nine populations from

Utah, Nevada, and Idaho, all plants had n = 24 with regular meiosis and high pollen fertility. No reliable morphological characteristics or geographic distributions could be correlated with ploidy level (Figure 13, Appendix 4), so it was not considered justifiable to recognize other infraspecific taxa.

Subspecies *linguaefolia* is certainly the most morphologically heterogenous taxon in the species. Considering the areas of sympatry, and chromosome complement similarities, assumptions of genetic isolation between the three *praemorsa* subspecies are not justified. In fact, the possibility of hybridization between these taxa and species of other sections or subsections (Table 2, Table 5) have been reported.

Subspecies *linguaefolia* appears to contain two flavonoid forms (Table 7). The first, and apparently most widespread, resembles the general diverse pattern as defined above. The second is a much reduced profile containing primarily kaempferol (1 and 9) and quercetin (6, 7, 8, and 27) derivatives. The ubiquitous luteolin and apigenin derivatives of *bakeri* and *praemorsa* were completely absent in these specimens, which contained only seven flavonoids including three novel compounds (1, 10 and 27), but did not display any unique morphological features (Figure 13). The possibility exists that these individuals represent ecologically isolated populations which subsequently underwent a reduction of flavonoid profile (Wolf and Denford, 1983). More complete flavonoid surveys may reveal geographic isolation at high elevations or high latitudes at the northeastern edge of the range of *praemorsa*. Certainly it was impossible to establish any correlations based on the meager sampling of only four populations, though these were all collected on or near the continental divide (Table 4).

The diversity of flavonoids present in the leaves of *V. bakeri* and *V. praemorsa*, the extent of morphological variation and the existence of hybrids lead to the hypothesis that these taxa are the most recent in the *V. nuttallii* complex. In only a few scattered populations of *linguaefolia* was it possible to observe flavonoid reduction (Wolf and Denford, 1983) in the elimination of all flavone biosynthesis.

Glaciation events during the Pleistocene likely had an effect on speciation in the Nuttallianae by drastically effecting the the climatic conditions on the west coast. At some point in the evolutionary history of these taxa, two lineages arose. *V. vallicola*

and *V. nuttallii*, probably the oldest taxa in the Nuttallianae, differentiated and became established in the more xeric habitats of the valley bottoms in the rainshadows of the Cascade and Rocky Mountains. They can be differentiated from the other Nuttallianae by their minute puberulence, nearly entire leaf margins, seeds with flattened caruncles which cover the funiculus and exceed it in length, and reduced flavonoid profiles consisting of apigenin , kaempferol and quercetin derivatives.

V. tomentosa, *V. bakeri*, and *V. praemorsa* became adapted to the more mesic forest habitats of the coastal and montane forests. These taxa, though of diverse morphology, generally possess long pubescence, seeds with globose caruncles which do not cover or exceed the funiculus in length, and diverse flavonoid profiles consisting of apigenin, kaempferol and luteolin compounds. Hybridization between these taxa and taxa of the subsections Chrysanthae and Purpurea indicated that the phylogenetic relationship of the Nuttallianae to other subsections is through these species, as proposed by Clausen (1929). Diploids, tetraploids, hexaploids and octoploids alike have expanded into previously glaciated areas.

Ploidy level in the Nuttallianae has been correlated with morphology, flavonoid chemistry, and phytogeographic data. A classification has been formulated based on these data, which proposes that the *nuttallii* complex be split into eight taxa - five species and three subspecies. This classification, which takes into account the polyploid nature of the complex, attempts to incorporate events of genetic isolation, hybridization, and introgression into the evolutionary history of the group. Correlation of some morphological characters and the presence of different flavonoid profiles support the speculation that two groups of species differentiated from a single ancestral complex. The first group includes *V. vallicola* and *V. nuttallii*, two of the oldest members of the Nuttallianae, which represent homogenous species of wide-ranging distribution. The second group comprises the remaining three species in the Nuttallianae. *V. tomentosa* and *V. bakeri*, also of homogenous morphology, display much more restricted distributions. *V. praemorsa* surely represents the most difficult systematic problem remaining in the complex due to its heterogenous nature and widespread distribution. Hypothetical relationships advanced in this discussion await more in depth analysis into the

morphological, biochemical, and cytological aspects of *V. praemorsa* as well as breeding experiments for confirmation.

V. BIBLIOGRAPHY

Alston, R.E. and B.L. Turner. 1962. New techniques in analysis of complex natural hybridization. Proc. Nat. Acad. Sci. U.S. 48(2): 130-137.

Baker, M.S. 1935. Studies in western violets. I. Sections Chamaemelanium and Nomimium. Madrono 3: 51-57.

----- 1949a. Studies in western violets - IV. Leafl. West. Bot. 5: 141-147.

-----1949b. Studies in western violets - V. Leafl. West. Bot. 5: 173-177.

-----1949c. Studies in western violets VI. Madrono 10. 110-128.

----- 1957. Studies in western violets. VIII. The Nuttallianae continued. Brittonia 9: 217-230.

----- 1960. Studies in western violets. IX. Miscellaneous species in the sections Nomimium and Chamaemelanium. Madrono 15: 199-204.

Bate-Smith, E.C. 1962. The phenolic constituents of plants and their taxonomic significance. I. Dicotyledons. J. Linn. Soc. (Bot.) 58: 95-175.

Becker, W. 1925. *Viola*. In Engler, A. and K. Prantl. *Die naturlichen Pflanzenfamilien* 21: 363-376.

Blankinship, J.W. 1905. A century of botanical exploration in Montana, 1805-1905 Collectors, herbaria and bibliography. Mont. Agr. Coll. Sci. Studies. Botany. 1(1): 82-83.

Boivin, B. 1951. Centurie de plantes Canadiennes. II. Can. Field Nat. 65: 1-22.

Bold, H.C. and A. Gershoy. 1934. Studies in North American violets. IV. Chromosome relations and fertility in diploid and tetraploid [illegible]ies hybrids. Vt. Agr. Exp. Stat. Bull. 378.

Brainerd, E. 1904. Hybridism in the genus *Viola*. Rhodora 6 213-22[illegible].

----- 1906a. Hybridism in the genus *Viola*. II. Rhodora 8: 6-[illegible]

----- 1906b. Hybridism in the genus *Viola*. III. Rhodora 8: 49-61.

----- 1921. Violets of North America. Vt. Agr. Exp. Stat. Bull. 224.

----- 1924. Some natural violet hybrids of North America. Vt. Agr. Exp. Stat. Bull. 239.

Camp, W.H. 1947. Distribution patterns in modern plants and the problems of ancient dispersals. Ecol. Mono. 17: 159-183.

Campbell, R.C. 1974. *Statistics for Biologists*, 2nd edition. Cambridge University Press, London, U.K.

Carmichael, J.W., George, J.A., and J.S. Julius. 1968. Finding natural clusters. Syst. Zool. 17(2): 144-150.

----- and P.H.A. Sneath. 1969. Taxometric maps. Syst. Zool. 18(4): 402-415.

Chaney, R.W. 1947. Tertiary centers and migration routes. Ecol. Monogr. 17: 139-148.

Clausen, J. 1927. Chromosome number and the relationship of species in the genus *Viola*. Ann. Bot. 41: 677-714.

----- 1929. Chromosome number and relationship of North American species of *Viola*. Ann. Bot. 43: 741-764.

----- 1951. *Stages in the Evolution of Plant Species*. Ithaca, Cornell University Press, New York.

----- 1964. Cytotaxonomy and distributional ecology of western North American violets. Madrono 17: 173-204.

Cronquist, A. 1978. Once again, what is a species? Beltsville Symp. Agric. Res. No. 2. Allanheld, Osmum and Co., Montclair, N.J.

----- 1981. *An Integrated System of Classification of Flowering Plants*. Columbia University Press, New York.

Davidse, G. 1976. A study of some intermountain violets (*Viola* sect. Chamaemelanium). Madrono 23: 274-283.

Douglas, D. 1829. *Viola praemorsa*. In J. Lindley. Edwards's Bot. Reg. 15: pl. 1254.

Fernald, M.L. 1950. *Gray's Manual of Botany*, 8th edition. American Book Co., New York.

Gershoy, A. 1928. Studies in North American violets. I. General considerations. Vt. Agr. Exp. Stat. Bull. 279.

----- 1934. Studies in North American violets. III. Chromosome numbers and species characters. Vt. Agr. Exp. Stat. Bull. 367.

Giannasi, D.E. 1978. Systematic aspects of flavonoid biosynthesis and evolution. Bot. Rev. 44: 339-429.

Gibbs, R.D. 1974. *Chemotaxonomy of Flowering Plants*. Vols. 1-4. McGill-Queens University Press, Montreal.

Gleason, H.A. 1952. *The new Britton and Brown Illustrated flora of the Northeastern United States and Adjacent Canada. Vol. 2 The Choripetalous Dicotyledoneae*. New York Bot. Gard., New York.

Greene, E.L. 1898. *V. bakeri*. Pittonia 3: 307.

----- 1901. *Plantae Bakerianae*. Vol. 3: 11-12.

Hallem, A. 1970. Continental drift and the fossil record. Sci. Am. 223(4): 56-66.

Harborne, J.B. 1967. *Comparative Biochemistry of the Flavonoids*. Academic Press, London, U.K.

----- 1975. Flavonoid bisulphates and their co-occurences with ellagic acid in the Bivaceae, Frankiniaceae and related families. Phytochem. 14: 1331-1337.

Hitchcock, C.L., and A. Cronquist. 1961. *Vascular Plants of the Pacific Northwest. Part III. Saxifragaceae to Ericaceae*. University of Washington Press, Seattle.

----- 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, U.S.A.

Holmgren, P.K. and W. Keuben. 1974. *Index Herbariorum Part I. The Herbaria of the World*. Ossthock, Scheltema and Holkema, Utrecht, Netherlands.

Hooker, W.J. 1830. *Flora Boreali-Americana. Vol. I*. Henry G. Bohn, London, U.K.

Jardine, N. and D. McKenzie. 1972. Continental drift and the dispersal and evolution of organisms. Nature 235: 20-24.

Jay, M., Gonnet, J., Wollenweber, E., and B. Voirin. 1975. Sur l'analyse qualitative des aglycones flavoniques dans une optique chimiotaxinomique. Phytochem. 14: 1605-1612.

Jepson, W.L. 1925. *A Manual of the Flowering Plants of California*. Assoc. Students Store, University of California, Berkeley, California, U.S.A.

Levy, M. 1976. Altered glycoflavone expression in induced autotetraploids of *Phlox drummondii*. Biochem. Syst. Ecol. 4: 249-254.

----- and D.A. Levin. 1971. The origin of novel flavonoids in *Phlox* allotetraploids.

Proc. Nat. Acad. Sci. USA 68(7): 1627-1630.

Lewis, W.H. (edit.) 1980. *Polyploidy, biological relevance.* Basic Life Sciences, Vol. 13. Plenum Press, New York, U.S.A.

Lord, E.M. 1981. Cleistogamy: a tool for the study of floral morphogenesis, function and evolution. Bot. Rev. 47: 421-449.

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

McPherson, G.D. 1972. *The taxonomy of* Viola adunca *J.E. Smith.* M.Sc. thesis, Botany Department, University of Alberta, Edmonton, Alberta, Canada.

Melchior, H. 1925. Violaceae. In Engler, A., and K. Prantl. *Die Naturlichen Pflanzenfamilien.* Vol. 21: 329-376.

Miyaji, Y. 1930. Betrachtungen uber die chromosomenzahlen von *Viola*, Violaceen und verwandlen Familien. Planta 11: 630-649.

Nelson, A. 1899. New plants from Wyoming VI. Bull. Torrey Bot. Club 26: 122-134.

----- 1900. A new violet. Bot. Gaz. 29: 143.

Nieuwland, J.A. and R.M. Kaczamarel. 1914. Studies in *Viola*. - I. Proposed segregates of *Viola*. Am. Midl. Natl. 3(8): 207-217.

Nuttall, T. 1838. *Viola linguaefolia.* In Torrey, J. and A. Gray. *A Flora of North America* I: 141. Hafner Publ. Co., New York, U.S.A.

Peck, M.E. 1941. Combinations proposed in *"The Higher plants of Oregon."* Madrono 6:133-137.

----- 1961. *A Manual of the Higher Plants of Oregon,* Second edition. Oregon State University Press, Portland, U.S.A.

Piper, C.V. 1906. *Flora of the State of Washington.* Washington Government Printing House, U.S.A.

----- and R.K. Beattie. 1914. *Flora of Southeast Washington.* New Era Printing Co., Lancaster, Pa., U.S.A.

Pollard, C.L. 1897. Two new violets. Bull. Torrey Bot. Club 24: 404-405.

Pursh, F. 1814. *Flora Americae Septentrionalis.* J. Cramer, Germany.

Radford, A.E., Dickison, W.C., Massey, J.R., and C.R. Bell. 1974. *Vascular Plant Systematics.* Harper and Row, New York, U.S.A.

Russell, N.H. 1965. Violets (*Viola*) of central and eastern United States and introductory survey. Sida 2: 1-113.

Sax, K. and H.J. Sax. 1937. Stomata size and distribution in diploid plants. J. Arnold Arb. 18: 164-172.

Scoggan, H.J. 1978. *Flora of Canada*. National Museum of Natural Sciences Publications in Botany No. 7(1-4). National Museums of Canada, Ottawa.

Sharma, A.K., and A. Sharma. 1980. *Chromosome Techniques: Theory and Practice*, 3rd edition. Butterworth and Co., London, U.K.

St. John, H. 1937. *Flora of Southeastern Washington and adjacent Idaho.* Students Book Corp., Pullman, Wash., USA.

Stebbins, G.L., Harvey, B.L., Cox, E.L., Rutger, J.N., Jelencovic, G., and E. Yagil. 1963. ·tification of the ancestry of an amphidiploid *Viola* with the aid of paper ·matography. Am. J. Bot. 50: 830-839.

Suksdorf, W.N. 1927. Werdenda 1: 25-26.

Taylor, R.L. and B. MacBryde. 1978. New taxa and nomenclatural changes with respect to *The Vascular Plants of British Columbia: A Descriptive Resource Inventory*. Can. J. Bot. 56(2):

Tidwell, W.D., Rushforth, S.R., and D. Simper. 1972. In Cronquist, A., Holmgren, A.H., Holmgren, N.H., and J.L. Reveal (edits.) *Intermountain Flora* I: 19-39. Hafner Publ. Inc., New York, USA.

Tijo, H.J. and A. Levan. 1950. The use of oxyquinoline in chromosome analysis. An. Estac. Exp. Aula Die 2: 21-64.

Torrey, J. and A. Gray. 1843. *A Flora of North America.* Vol. 1: 135-144.

Valentine, D.H. 1962. Variation and evolution in the genus *Viola*. Preslia 34: 190-206.

Wagner, H., Resprim, L., and P. Dull. 1972. Die flavon-c-glykoside von *Viola tricolor* L. Z. Naturforsch. 27b: 954-958.

Watson, S. 1871. Clarence King Expedition. Botany. Volume 5 of U.S. Geological Exploration of the Fortieth Parallel. Government Printing Office, Washington, USA.

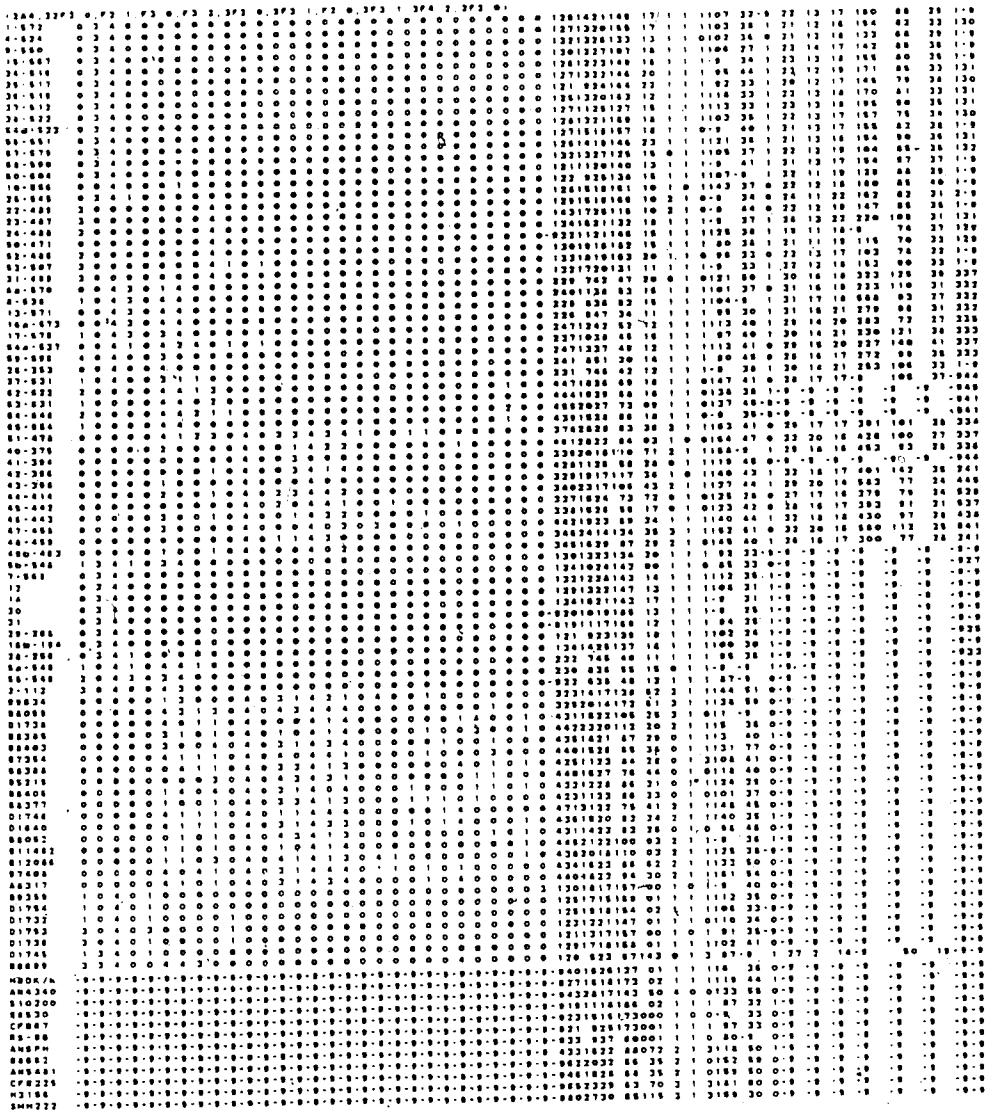
Wolf, S.J. and K.E. Denford. 1983. Flavonoid variation in *Arnica cordifolia*: an

apomictic polyploid complex. Biochem. Syst. Ecol. 11(2): 111-114.

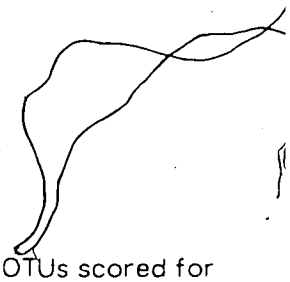
Wolfe, J.A. 1978. A paleobotanical interpretation of tertiary climates in the northern hemisphere. Am. Sci. 66: 694-703.

VI. APPENDIX 1. Data for TAXMAP analyses.

The raw data for all 95 OTUs (Table 4) and 50 attributes (Table 3), is listed as arranged for the TAXMAP data file. The first line represents the FORTRAN format statement.



VII. APPENDIX 2. TAXMAP Analysis 1.



This analysis was performed using the author's collection of 59 OTUs scored for 50 attributes including flavonoid chemistry, cytological and morphological characteristics. TAXMAP was ran using an equally weighted analysis which does not take into account the relative information content of each attribute.

The TAXMAP print out includes the complete proximity table of the relative distance of each OTU from every other OTU. The nearest neighbour table lists the eight closest neighbours of each OTU in order with their distances. The table summarizing the cluster anaysis lists the clusters, cluster members, and and single-membered clusters. The Mapping Aids includes the intercluster distances as center-to-center distances and minimum intercluster discontinuities.

PROXIMITIES (AS DISTANCE * 1000), COMPUTED FOR ATTRIBUTES 1 TO 50

1	2	31	3	61	4	47	5	30	6	33	7	43	8	25	9	39	10	28	11	54	12	30	13	60	14	39	15	81	16	79
1	17	217	18	200	19	166	20	132	21	165	22	162	23	140	24	291	25	265	26	271	27	269	28	269	29	277	30	255	31	211
1	32	214	33	383	34	337	35	411	36	279	37	536	38	470	39	314	40	364	41	340	42	468	43	379	44	426	45	374	46	404
1	47	330	48	107	49	69	50	41	51	24	52	24	53	30	54	26	55	23	56	49	57	271	58	292	59	213	3	88	4	47
2	5	27	6	28	7	24	8	27	9	42	10	21	11	51	12	25	13	54	14	37	15	85	16	99	17	240	18	221	19	168
2	20	123	21	138	22	191	23	134	24	287	25	290	26	275	27	266	28	274	29	272	30	282	31	236	32	221	33	420	34	350
2	35	435	36	301	37	562	38	493	39	323	40	405	41	348	42	471	43	400	44	431	45	383	46	433	47	351	48	104	49	97
2	50	41	51	20	52	43	53	36	54	24	55	41	56	42	57	278	58	289	59	235	4	99	5	83	6	87	7	96	8	87
3	9	91	10	90	11	66	12	98	13	93	14	95	15	121	16	106	17	194	18	155	19	219	20	181	21	200	22	147	23	181
3	24	281	25	275	26	308	27	304	28	294	29	311	30	268	31	229	32	258	33	364	34	351	35	380	36	248	37	545	38	433
3	39	374	40	393	41	403	42	519	43	341	44	416	45	417	46	433	47	331	48	157	49	50	50	78	51	78	52	100	53	98
3	54	105	55	96	56	85	57	310	58	338	59	230	5	31	6	36	7	49	8	46	9	22	10	35	11	69	12	40	13	39
4	14	39	15	87	16	110	17	266	18	206	19	178	20	141	21	177	22	210	23	146	24	260	25	270	26	254	27	253	28	249
4	29	243	30	244	31	205	32	185	33	397	34	317	35	415	36	281	37	549	38	487	39	310	40	359	41	328	42	443	43	389
4	44	408	45	361	46	417	47	324	48	112	49	95	50	46	51	39	52	46	53	63	54	56	55	43	56	51	57	254	58	264
4	59	226	6	19	7	30	8	21	9	20	10	19	11	49	12	29	13	41	14	30	15	74	16	92	17	241	18	204	19	159
5	20	119	21	151	22	192	23	131	24	264	25	270	26	255	27	248	28	253	29	248	30	260	31	218	32	201	33	416	34	341
5	35	431	36	295	37	551	38	489	39	321	40	391	41	336	42	468	43	393	44	420	45	365	46	432	47	338	48	102	49	84
5	50	45	51	20	52	37	53	35	54	28	55	29	56	35	57	260	58	271	59	234	7	39	8	26	9	22	10	24	11	64
6	12	35	13	34	14	43	15	67	16	93	17	233	18	201	19	154	20	126	21	147	22	196	23	130	24	276	25	270	26	260
6	27	250	28	254	29	253	30	258	31	227	32	196	33	420	34	350	35	435	36	301	37	554	38	494	39	320	40	389	41	343
6	42	466	43	396	44	421	45	365	46	427	47	345	48	105	49	88	50	41	51	25	52	46	53	41	54	36	55	39	56	40
6	57	267	58	282	59	238	8	35	9	46	10	28	11	49	12	31	13	60	14	36	15	88	16	101	17	254	18	227	19	183
7	20	115	21	148	22	196	23	149	24	284	25	306	26	287	27	275	28	288	29	274	30	287	31	243	32	231	33	439	34	359
7	35	454	36	310	37	566	38	509	39	342	40	420	41	355	42	491	43	419	44	450	45	396	46	444	47	359	48	97	49	102
7	50	45	51	23	52	40	53	30	54	19	55	33	56	43	57	290	58	287	59	234	9	30	10	22	11	51	12	26	13	48
8	14	32	15	77	16	87	17	224	18	212	19	161	20	113	21	148	22	177	23	126	24	283	25	277	26	261	27	257	28	257
8	29	259	30	267	31	229	32	207	33	415	34	344	35	429	36	300	37	551	38	489	39	320	40	399	41	338	42	471	43	400
8	44	425	45	371	46	434	47	338	48	100	49	83	50	44	51	21	52	34	53	22	54	19	55	39	56	39	57	269	58	279
8	59	242	10	31	11	68	12	35	13	35	14	33	15	72	16	97	17	249	18	202	19	158	20	126	21	166	22	204	23	132
9	24	262	25	262	26	245	27	244	28	250	29	240	30	248	31	207	32	188	33	411	34	336	35	424	36	298	37	546	38	485
9	39	315	40	375	41	334	42	463	43	393	44	411	45	359	46	423	47	340	48	109	49	80	50	43	51	31	52	41	53	44
9	54	42	55	38	56	43	57	255	58	263	59	227	11	51	12	31	13	49	14	37	15	84	16	95	17	240	18	218	19	167
10	20	124	21	143	22	184	23	138	24	282	25	285	26	269	27	265	28	263	29	265	30	270	31	227	32	211	33	423	34	350
10	35	438	36	306	37	558	38	496	39	323	40	395	41	343	42	466	43	396	44	423	45	375	46	431	47	344	48	104	49	89
10	50	36	51	21	52	41	53	36	54	28	55	44	56	45	57	275	58	287	59	243	12	48	13	83	14	52	15	119	16	115
11	17	216	18	192	19	197	20	148	21	177	22	158	23	163	24	249	25	318	26	303	27	291	28	299	29	285	30	295	31	257
11	32	246	33	391	34	313	35	409	36	254	37	577	38	469	39	346	40	429	41	358	42	497	43	376	44	401	45	404	46	459
11	47	314	48	123	49	77	50	80	51	46	52	48	53	63	54	56	55	64	56	70	57	304	58	306	59	279	13	53	14	22
12	15	85	16	95	17	245	18	217	19	166	20	119	21	160	22	185	23	134	24	282	25	284	26	269	27	269	28	273	29	259
1	30	270	31	227	32	219	33	409	34	332	35	425	36	297	37	548	38	485	39	308	40	396	41	327	42	463	43	394	44	424
12	5	372	46	420	47	341	48	97	49	91	50	49	51	24	52	26	53	41	54	32	55	40	56	41	57	280	58	281	59	247
13	4	48	15	69	16	100	17	251	18	196	19	173	20	137	21	166	22	208	23	139	24	269	25	273	26	261	27	264	28	253
13	29	251	30	252	31	227	32	204	33	422	34	349	35	434	36	298	37	556	38	498	39	329	40	385	41	349	42	475	43	389
13	44	405	45	372	46	439	47	347	48	117	49	98	50	48	51	44	52	55	53	58	54	65	55	58	56	45	57	277	58	267
13	59	248	15	74	16	92	17	250	18	210	19	167	20	116	21	167	22	198	23	135	24	272	25	275	26	259	27	256	28	262
14	29	246	30	254	31	215	32	206	33	414	34	334	35	424	36	300	37	547	38	481	39	316	40	394	41	327	42	471	43	402
14	44	419	45	368	46	424	47	344	48	103	49	84	50	48	51	27	52	30	53	31	54	28	55	33	56	46	57	267	58	271
14	59	237	16	136	17	221	18	189	19	149	20	107	21	143	22	192	23	123	24	253	25	236	26	212	27	219	28	215	29	223
15	30	248	31	214	32	170	33	385	34	320	35	404	36	254	37	515	38	471	39	303	40	376	41	335	42	454	43	384	44	400
15	45	345	46	412	47	325	48	134	49	120	50	76	51	82	52	93	53	78	54	89	55	79	56	77	57	236	58	249	59	185
16	17	240	18	210	19	231	20	185	21	215	22	203	23	189	24	322	25	276	26	306	27	312	28	305	29	299	30	261	31	240
16	32	275	33	431	34	405	35	440	36	348	37	567	38	447	39	383	40	415	41	346	42	530	43	413	44	483	45	429	46	439
16	47	408	48	151	49	95	50	109	51	92	52	93	53	99	54	116	55	128	56	87	57	322	58	321	59	264	18	82	19	132
17	20	168	21	137	22	76	23	131	24	369	25	331	26	388	27	372	28	355	29	375	30	283	31	314	32	333	33	299	34	317
17	35	351	36	251	37	503	38	457	39	372	40	412	41	387	42	508	43	372	44	428	45	443	46	436	47	297	48	289	49	195
17	50	249	51	241	52	246	53	265	54	242	55	252	56	245	57	383	58	383	59	265	19	122	20	153	21	123	22	63	23	90

18	24	335	25	309	26	373	27	367	28	328	29	355	30	241	31	274	32	288	33	266	34	276	35	309	36	230	37	475	38	422
18	39	351	40	386	41	389	42	479	43	341	44	393	45	405	46	409	47	296	48	266	49	160	50	220	51	207	52	214	53	249
18	54	278	55	257	56	208	57	357	58	361	59	259	20	106	21	70	22	111	23	46	24	324	25	289	26	310	27	287	28	281
19	29	281	30	243	31	277	32	217	33	317	34	283	35	374	36	263	37	483	38	475	39	295	40	385	41	315	42	437	43	401
19	44	398	45	354	46	410	47	324	48	226	49	223	50	178	51	169	52	162	53	190	54	180	55	170	56	170	57	290	58	286
19	59	246	21	76	22	126	23	72	24	300	25	305	26	269	27	287	28	281	29	277	30	290	31	250	32	236	33	333	34	270
20	35	379	36	240	37	481	38	470	39	288	40	357	41	306	42	421	43	375	44	384	45	343	46	404	47	293	48	175	49	177
20	50	125	51	111	52	122	53	119	54	126	55	134	56	121	57	293	58	296	59	272	22	96	23	43	24	359	25	337	26	346
21	27	332	28	314	29	337	30	295	31	313	32	267	33	359	34	322	35	404	36	291	37	527	38	514	39	343	40	416	41	361
21	42	469	43	426	44	435	45	393	46	450	47	352	48	208	49	219	50	161	51	149	52	167	53	160	54	170	55	193	56	157
21	57	332	58	324	59	255	23	83	24	349	25	320	26	376	27	380	28	353	29	374	30	281	31	289	32	312	33	270	34	286
22	35	325	36	235	37	490	38	434	39	359	40	388	41	384	42	492	43	342	44	404	45	419	46	423	47	310	48	238	49	155
22	50	201	51	192	52	184	53	216	54	239	55	241	56	201	57	369	58	368	59	260	24	329	25	304	26	308	27	305	28	290
23	29	303	30	260	31	273	32	234	33	320	34	285	35	365	36	268	37	490	38	474	39	308	40	378	41	330	42	445	43	393
23	44	396	45	357	46	421	47	320	48	190	49	190	50	147	51	131	52	134	53	158	54	177	55	171	56	134	57	294	58	296
23	59	243	25	136	26	116	27	101	28	134	29	138	30	206	31	177	32	185	33	317	34	244	35	339	36	216	37	539	38	417
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24	54	234	55	242	56	272	57	119	58	86	59	195	26	79	27	80	28	72	29	108	30	118	31	104	32	154	33	268	34	258
25	35	293	36	199	37	448	38	426	39	370	40	394	41	393	42	511	43	416	44	422	45	360	46	441	47	394	48	219	49	277
25	50	278	51	288	52	281	53	294	54	260	55	271	56	264	57	97	58	82	59	91	27	63	28	69	29	114	30	192	31	141
26	32	161	33	295	34	243	35	309	36	221	37	465	38	435	39	319	40	403	41	360	42	447	43	426	44	383	45	317	46	411
26	47	369	48	222	49	305	50	258	51	271	52	270	53	249	54	215	55	225	56	253	57	83	58	86	59	130	28	62	29	90
27	30	176	31	122	32	114	33	329	34	269	35	350	36	234	37	494	38	468	39	360	40	426	41	383	42	504	43	458	44	414
27	45	354	46	493	47	387	48	224	49	310	50	269	51	264	52	272	53	264	54	215	55	226	56	255	57	73	58	86	59	125
28	29	104	30	146	31	142	32	129	33	301	34	244	35	320	36	203	37	479	38	455	39	346	40	432	41	395	42	473	43	434
28	44	393	45	343	46	477	47	358	48	201	49	311	50	247	51	263	52	269	53	265	54	236	55	247	56	247	57	95	58	89
28	59	135	30	148	31	139	32	116	33	318	34	262	35	321	36	223	37	464	38	480	39	367	40	444	41	376	42	509	43	464
29	44	419	45	363	46	493	47	393	48	209	49	308	50	267	51	263	52	251	53	261	54	226	55	235	56	243	57	89	58	107
29	59	146	31	90	32	142	33	286	34	280	35	299	36	219	37	454	38	411	39	357	40	388	41	358	42	492	43	404	44	405
30	45	349	46	423	47	376	48	270	49	263	50	271	51	266	52	258	53	258	54	283	55	239	56	271	57	160	58	137	59	73
31	32	124	33	286	34	260	35	298	36	230	37	413	38	379	39	315	40	344	41	345	42	456	43	358	44	363	45	318	46	399
31	47	337	48	247	49	225	50	229	51	224	52	224	53	234	54	200	55	208	56	233	57	126	58	155	59	112	33	325	34	276
32	35	342	36	211	37	486	38	473	39	362	40	397	41	349	42	469	43	433	44	386	45	326	46	456	47	358	48	205	49	257
32	50	214	51	204	52	218	53	202	54	189	55	205	56	218	57	90	58	153	59	120	34	89	35	78	36	77	37	365	38	309
33	39	330	40	336	41	363	42	426	43	355	44	353	45	315	46	391	47	306	48	367	49	370	50	422	51	407	52	407	53	427
33	54	370	55	383	56	420	57	264	58	303	59	216	35	132	36	60	37	390	38	308	39	270	40	331	41	293	42	375	43	331
34	44	289	45	254	46	395	47	244	48	287	49	349	50	358	51	329	52	327	53	341	54	278	55	299	56	348	57	220	58	240
34	59	219	36	91	37	402	38	317	39	356	40	373	41	389	42	430	43	375	44	374	45	342	46	404	47	332	48	385	19	379
35	50	437	51	425	52	424	53	447	54	381	55	393	56	435	57	286	58	328	59	225	37	495	38	340	39	320	40	355	41	391
36	42	426	43	334	44	317	45	271	46	408	47	252	48	214	49	281	50	294	51	284	52	283	53	280	54	272	55	289	56	293
36	57	193	58	215	59	163	38	305	39	313	40	299	41	374	42	264	43	303	44	257	45	324	46	301	47	316	48	552	49	557
37	50	549	51	561	52	542	53	598	54	583	55	568	56	585	57	459	58	519	59	526	39	326	40	259	41	281	42	326	43	270
38	44	271	45	189	46	279	47	273	48	531	49	434	50	491	51	493	52	484	53	520	54	466	55	465	56	497	57	442	58	503
38	59	467	40	251	41	186	42	199	43	252	44	297	45	250	46	222	47	221	48	394	49	380	50	324	51	324	52	309	53	302
39	54	251	55	260	56	330	57	338	58	371	59	384	41	276	42	249	43	212	44	230	45	209	46	251	47	241	48	471	49	399
40	50	393	51	390	52	402	53	415	54	354	55	368	56	407	57	401	58	439	59	362	42	263	43	276	44	285	45	209	46	235
41	47	173	48	391	49	397	50	358	51	329	52	330	53	315	54	254	55	280	56	350	57	346	58	371	59	373	43	253	44	246
42	45	249	46	192	47	235	48	509	49	530	50	466	51	463	52	469	53	463	54	412	55	435	56	478	57	474	58	511	59	481
43	44	162	45	279	46	217	47	196	48	469	49	356	50	393	51	401	52	397	53	428	54	379	55	377	56	402	57	437	58	475
43	59	415	45	234	46	300	47	170	48	446	49	423	50	416	51	426	52	417	53	446	54	407	55	406	56	426	57	395	58	425
44	59	432	46	293	47	202	48	396	49	421	50	373	51	376	52	369	53	384	54	326	55	331	56	374	57	326	58	384	59	360
46	47	274	48	508	49	436	50	432	51	432	52	427	53	431	54	363	55	384	56	441	57	454	58	514	59	421	48	386	49	350
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51	57	265	58	277	59	236	53	37	54	36	55	34	56	42	57	278	58	274	59	249	54	13	55	21	56	56	57	259	58	266
53	59	244	55	29	56	55	57	215	58	239	59	236	56	49	57	230	58	254	59	223	57	261	58	272	59	254	58	91	59	111
58	59	111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

NEAREST NEIGHBOURS (DISTANCE *1000)

1	1-572	v-a	1	55	23	1	51	24	1	52	24	1	8	25	1	54	26	1	10	28	1	5	30	1	53	30
2	4-524	v-a	2	51	20	2	10	21	2	7	24	2	54	24	2	12	25	2	5	27	2	8	27	2	6	28
3	9-550	v-a	3	49	50	1	3	61	3	11	66	3	51	78	3	50	78	3	5	83	3	56	85	3	8	87
4	15-567	v-a	4	9	22	4	5	31	4	10	35	4	6	36	4	51	39	4	14	39	4	13	39	4	12	40
5	34-516	v-a	5	6	19	5	10	19	5	51	20	5	9	20	5	8	21	2	5	27	5	54	28	5	12	29
6	35-517	v-a	5	6	19	6	9	22	6	10	24	6	51	25	6	8	26	2	6	28	1	6	33	6	13	34
7	36-519	v-a	7	54	19	7	51	23	2	7	24	7	10	28	5	7	30	7	53	30	7	12	31	7	55	33
8	37-520	v-a	8	54	19	5	8	21	8	51	21	8	53	22	8	10	22	1	8	25	8	12	26	6	8	26
9	38-523	v-a	5	9	20	4	9	22	6	9	22	8	8	30	9	51	31	9	10	31	9	14	33	9	13	35
10	540-533	v-a	5	10	19	2	10	21	10	51	21	8	10	22	6	10	24	1	10	28	10	54	28	7	10	28
11	56-551	v-a	11	51	46	11	12	48	11	52	48	7	11	49	5	11	49	8	11	51	2	11	51	10	11	51
12	57-579	v-s	12	14	22	12	51	24	2	12	25	8	12	26	12	52	26	5	12	29	1	12	30	7	12	31
13	58-590	v-s	6	13	34	9	13	35	4	13	39	5	13	41	13	51	44	13	56	45	13	50	48	8	13	48
14	60-604	v-s	12	14	22	14	51	27	14	54	28	5	14	30	14	52	30	14	53	31	8	14	32	14	55	33
15	10-556	v-a	6	15	67	13	15	69	9	15	72	14	15	74	5	15	74	15	50	76	15	56	77	8	15	77
16	25-545	v-a	1	16	79	16	56	87	8	16	87	14	16	92	16	51	92	5	16	92	16	52	93	6	16	93
17	22-489	v-bc	17	22	76	17	18	82	17	23	131	17	19	132	17	21	137	17	20	168	3	17	194	17	49	195
18	23-487	v-bc	18	22	63	17	18	82	18	23	90	18	19	122	18	21	123	18	20	153	3	18	155	18	49	160
19	24-488	v-bc	19	23	46	19	21	70	19	20	106	19	22	111	18	19	122	17	19	132	15	19	149	6	19	154
20	50-471	v-o	20	23	72	20	21	76	19	20	106	15	20	107	20	51	111	8	20	113	7	20	115	14	20	116
21	52-486	v-bc	21	23	43	19	21	70	20	21	76	21	22	96	18	21	123	17	21	137	2	21	138	10	21	143
22	53-507	v-bc	18	22	63	17	22	76	22	23	83	21	22	96	19	22	111	20	22	126	3	22	147	22	49	155
23	21-499	v-bc	21	23	43	19	23	46	20	23	72	22	23	83	18	23	90	15	23	123	8	23	126	6	23	130
24	6a-570	n-a	24	58	86	24	27	101	24	26	116	24	57	119	24	28	134	24	25	136	24	29	138	24	31	177
25	8-538	n-a	25	28	72	25	26	79	25	27	80	25	58	82	25	59	91	25	57	97	25	31	104	25	29	108
26	13-571	n-a	26	27	63	26	28	69	25	26	79	26	57	83	26	58	86	26	29	114	24	26	116	26	59	130
27	16a-573	n-a	27	28	62	26	27	63	27	57	73	25	27	80	27	58	86	27	29	90	24	27	101	27	32	114
28	17-576	n-a	27	28	62	26	28	69	25	28	72	28	58	89	28	57	95	28	29	104	28	32	129	24	28	134
29	54a-537	n-a	29	57	89	27	29	90	28	29	104	29	58	107	25	29	108	26	29	114	29	32	116	24	29	138
30	59-596	n-s	30	59	73	30	31	90	25	30	118	30	58	137	30	32	142	28	30	146	29	30	148	30	57	160
31	26-253	n-a	30	31	90	25	31	104	31	59	112	27	31	122	31	32	124	31	57	126	29	31	139	26	31	141
32	27-531	n-a	32	57	90	27	32	114	29	32	116	32	59	120	31	32	124	28	32	129	30	32	142	32	58	153
33	62-622	l-l	33	36	77	33	35	78	33	34	89	33	59	216	33	57	264	18	33	266	25	33	268	22	33	270
34	63-631	l-m	34	36	60	33	34	89	34	35	132	34	59	219	34	57	220	34	58	240	26	34	243	28	34	244
35	64-648	l-a	33	35	78	35	36	91	34	35	132	35	59	225	35	57	286	25	35	293	31	35	298	30	35	299
36	65-654	l-a	34	36	60	33	36	77	35	36	91	36	59	163	36	57	193	25	36	199	28	36	203	32	36	211
37	51-478	m-w	37	44	257	37	42	264	37	40	299	37	46	301	37	43	303	37	38	305	37	39	313	37	47	316
38	40-375	m-w	38	45	189	38	40	259	38	43	270	38	44	271	38	47	273	38	46	279	38	41	281	37	38	305
39	41-394	m-w	39	41	186	39	42	199	39	47	221	39	46	222	39	45	250	39	54	251	39	40	251	39	43	252
40	42-396	b-w	40	45	209	40	43	212	40	44	230	40	47	241	40	42	249	40	46	251	39	40	251	38	40	259
41	43-398	m-w	41	47	173	39	41	186	41	45	209	41	46	235	41	54	254	41	42	263	40	41	276	41	43	276
42	44-414	p-w	42	46	192	39	42	199	42	47	235	42	44	246	40	42	249	42	45	249	42	43	253	41	42	263
43	45-442	m-o	43	44	162	43	47	196	40	43	212	43	46	217	39	43	252	42	43	253	38	43	270	41	43	276
44	46-443	o-o	43	44	162	44	47	170	40	44	230	44	45	234	42	44	246	37	44	257	38	44	271	41	44	285
45	47-458	a-o	38	45	189	45	47	202	40	45	209	41	45	209	44	45	234	42	45	249	39	45	250	34	45	254
46	48-459	m-c	42	46	192	43	46	217	39	46	222	41	46	235	40	46	251	46	47	274	38	46	279	45	46	293
47	496-463	m-c	44	47	170	41	47	173	43	47	196	45	47	202	39	47	221	42	47	235	40	47	241	34	47	244
48	5b-548	v-a	48	56	79	48	51	90	48	52	95	12	48	97	7	48	97	8	48	100	5	48	102	14	48	103
49	7-568	v-a	3	49	50	1	49	69	11	49	77	9	49	80	8	49	83	5	49	84	14	49	84	49	51	87
50	12-565	v-a	50	51	32	10	50	36	2	50	41	1	50	41	6	50	41	9	50	43	50	56	43	8	50	44
51	14-566	v-a	2	51	20	5	51	20	10	51	21	8	51	21	7	51	23	1	51	24	12	51	24	6	51	25
52	30-547	v-a	1	52	24	12	52	26	51	52	27	14	52	30	52	55	34	8	52	34	52	54	36	52	53	37
53	31-276	v-a	53	54	13	53	55	21	8	53	22	1	53	30	7	53	30	14	53	31	51	53	32	5	53	35
54	29-268	v-a	53	54	13	8	54	19	7	54	19	2	54	24	1	54	26	51	54	26	10	54	28	14	54	28
55	16b-194	v-a	53	55	21	1	55	23	51	55	28	5	55	29	54	55	29	7	55	33	14	55	33	52	55	34
56	28-256	v-a	51	56	33	5	56	35	8	56	39	6	56	40	12	56	41	52	56	42	2	56	42	9	56	43
57	5a-549	n-a	27	57	73	26	57	83	29	57	89	32	57	90	57	58	91	28	57	95	25	57	97	57	59	104
58	55-546	n-a	25	58	82	26	58	86	27	58	86	24	58	86	28	58	89	57	58	91	29	58	107	58	59	111
59	2-112	n-a	30	59	73	25	59	91	57	59	104	58	59	111	31	59	112	32	59	120	27	59	125	26	59	130

MAP CLUSTER ANALYSIS:-NUTTALLIANAE, SEPTEMBER, 1983; PLUS HERBARIUM SPECIMENS

(MINIMUM NUCLEUS 0.080, MAXIMUM DROP 0.0439 BOTH ARE 100% OF NORMAL)
EQUALLY WEIGHTED ATTRIBUTES

CLUSTER NO	OTU NOS	DIST BEST LINK	OTU BEST LINK	AVGOF NEW LINKS	DROP IN AVG.	FAR DIST OTU	FLAG	NAME OF OTU	
1	53							31-276	v-a
	54	0.01						29-268	v-a
	8	0.02	54	0.021 0.007	53	0.02		37-520	v-a
	7	0.02	54	0.029 0.008	8	0.04		36-519	v-a
	5	0.02	8	0.029 0.000	53	0.04		34-516	v-a
	6	0.02	5	0.033 0.004	53	0.04		35-517	v-a
	10	0.02	5	0.027-0.006	53	0.04		54d-533	v-a
	51	0.02	5	0.025-0.002	53	0.03		14-566	v-a
	2	0.02	51	0.026 0.002	53	0.04		4-524	v-a
	9	0.02	5	0.035 0.009	7	0.05		38-523	v-a
	55	0.02	53	0.034-0.000	10	0.04		16b-194	v-a
	4	0.02	9	0.043 0.008	53	0.06		15-567	v-a
	1	0.02	55	0.032-0.011	4	0.05		1-572	v-a
	12	0.02	51	0.033 0.000	53	0.04		57-579	v-s
	14	0.02	12	0.034 0.001	6	0.04		60-604	v-s
	52	0.02	1	0.037 0.003	4	0.05		30-547	v-a
	50	0.03	51	0.045 0.008	52	0.05		12-565	v-a
	56	0.03	51	0.045 0.000	53	0.06		28-256	v-a
	13	0.03	6	0.050 0.006	54	0.07		58-590	v-s
	11	0.05	51	0.059 0.009	13	0.08		56-551	v-a
	3	0.06	1	0.089 0.030	54	0.11		9-550	v-a
	49	0.05	3	0.091 0.002	55	0.12		7-568	v-a
	15	0.07	6	0.086-0.005	3	0.12		10-556	v-a
	48	0.08	56	0.112 0.027	49	0.17		5b-548	v-a
	16	0.08	1	0.103-0.009	48	0.15		25-545	v-a
	20	0.11	15	0.133 0.030	16	0.19	200	50-471	v-o
2	21							52-486	v-bc
	23	0.04						21-499	v-bc
	19	0.05	23	0.059 0.015	21	0.07		24-488	v-bc
	20	0.07	23	0.085 0.026	19	0.11		50-471	v-o
	22	0.08	23	0.105 0.020	20	0.13		53-507	v-bc
	18	0.06	22	0.111 0.006	20	0.15		23-487	v-bc
	17	0.08	22	0.121 0.011	20	0.17		22-489	v-bc
	15	0.11	20	0.161 0.040	17	0.22	204	10-556	v-a
3	34							63-631	l-m
	36	0.06						65-654	l-a
	33	0.08	36	0.083 0.023	34	0.09		62-622	l-l
	35	0.08	33	0.101 0.017	34	0.13		64-648	l-a
	59	0.16	36	0.206 0.105	35	0.23	1200	2-112	n-a
4	27							16a-573	n-a
	28	0.06						17-576	n-a
	26	0.06	27	0.067 0.004	28	0.07		13-571	n-a
	25	0.07	28	0.078 0.011	27	0.08		8-538	n-a
	57	0.07	27	0.078 0.010	25	0.10		5a-549	n-a
	58	0.08	25	0.087-0.000	57	0.09		55-546	n-a
	24	0.09	58	0.116 0.029	25	0.14		6a-570	n-a
	29	0.09	57	0.108-0.008	24	0.14		54a-537	n-a
	32	0.09	57	0.138 0.031	24	0.19		27-531	n-a
	59	0.09	25	0.129-0.009	24	0.20		2-112	n-a
	30	0.07	59	0.150 0.021	24	0.21		59-596	n-s
	31	0.09	30	0.131-0.020	24	0.18		26-253	n-a
	36	0.16	59	0.211 0.080	27	0.23	1204	65-654	l-a

ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER	OTU	LABEL	
5	37	51-478	m-w
6	38	40-375	m-w
7	39	41-394	m-w
8	40	42-396	b-w
9	41	43-398	m-w
10	42	44-414	p-w
11	43	45-442	m-o
12	44	46-443	o-o
13	45	47-458	a-o
14	46	48-459	m-c
15	47	49b-463	m-c

CLUSTER MEMBERSHIP INDEX

1	1	11	1	21	2	31	4	41	9	51
2	1	12	1	22	2	32	4	42	10	52
3	1	13	1	23	2	33	3	43	11	53
4	1	14	1	24	4	34	3	44	12	54
5	1	15	1	25	4	35	3	45	13	55
6	1	16	1	26	4	36	3	46	14	56
7	1	17	2	27	4	37	5	47	15	57
8	1	18	2	28	4	38	6	48	1	58
9	1	19	2	29		39	7	49	1	59
10	1	20	2	30		40	8	50		

MAPPING AIDS

CENTRALITY-PERIPHERALITY ORDER

OTU'S	39	41	34	47	33	45	35	31	26	40	57	43	28	18	20	19	44	32	23	30	22	36	27	17	29
CLUSTERS	7	9	3	15	3	13	3	4	4	8	4	11	4	2	2	2	12	4	2	4	2	3	4	2	4
OTU'S	25	46	15	58	59	21	42	38	1	24	52	3	9	14	12	4	50	8	5	48	6	56	13	49	10
CLUSTERS	4	14	1	4	4	2	10	6	1	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
OTU'S	51	2	7	16	55	11	54	53	37																
CLUSTERS	1	1	1	1	1	1	1	1	5																

CLUSTER DISTANCES (*1000)

MAIN DIAGONAL = CLUSTER RADII (I.E. 1/2 THE DISTANCE BETWEEN THE TWO MOST DISTANT OTUS IN THE CLUSTER)

LOWER TRIANGLE = CENTER TO CENTER DISTANCES OF CLUSTER CIRCLES (I.E. RADIUS 'A' + RADIUS 'B' + DISTANCE BETWEEN NEAREST NEIGHBORS IN A AND B)

UPPER TRIANGLE = MINIMUM INTER-CLUSTER DISCONTINUITIES

CLUSTER	1	2	3	4	5	6	7	8	9	10
1	84	107	214	168	515	433	251	354	254	412
2	276	84	230	217	475	422	288	357	306	421
3	365	381	66	163	365	308	270	331	293	375
4	357	404	332	103	413	379	315	344	345	447
5	600	560	431	517	0	305	313	299	374	264
6	518	506	374	483	305	0	326	259	281	326
7	336	372	336	419	313	326	0	251	186	199
8	439	441	397	447	299	259	251	0	276	249
9	339	390	359	448	374	281	186	276	0	263
10	497	506	441	550	264	326	199	249	263	0
11	426	425	401	461	303	270	252	212	276	253
12	485	469	355	467	257	271	297	230	285	246
13	411	427	320	420	324	189	250	209	209	249
14	448	488	457	502	301	279	222	251	235	192
15	389	377	310	441	316	273	221	241	173	235

CLUSTER	11	12	13	14	15
1	341	400	326	363	304
2	341	384	343	404	293
3	334	289	254	391	244
4	358	363	317	399	337
5	303	257	324	301	316
6	270	271	189	279	273
7	252	297	250	222	221
8	212	230	209	251	241
9	276	285	209	235	173
10	253	246	249	192	235
11	0	162	279	217	196
12	162	0	234	300	170
13	279	234	0	293	202
14	217	300	293	0	274
15	196	170	202	274	0

VIII. APPENDIX 3. TAXMAP Analysis 2.

TAXMAP analysis 2 contained 72 OTUs including a 13 OTUs representing typespecimens (holotypes, isotypes, and paratypes) along with the 59 OTUs used for TAXMAP analysis 1 (Appendix 2). A weighted analysis employed the relative information content of the attributes to calculate the relative inter-OTU distances.

Only the TAXMAP cluster analysis is listed here.

MAP CLUSTER ANALYSIS:-NUTTALLIANAE, 1983: 72 OTUS, ATT 1-50, weighted

(MINIMUM NUCLEUS 0.102, MAXIMUM DROP 0.0400 BOTH ARE 100% OF NORMAL)

CLUSTER NO.	OTU NOS	DIST BEST LINK	OTU BEST LINK	AVGOF NEW LINKS	DROP IN AVG.	FAR OTU	DIST FAR OTU	FLAG	NAME OF OTU	
1	53								31-276	v-a
	54	0.03							29-268	v-a
	7	0.03	54	0.042	0.017	53	0.05		36-519	v-a
	2	0.03	7	0.045	0.003	53	0.06		4-524	v-a
	51	0.03	2	0.042	-0.004	53	0.05		14-566	v-a
	10	0.03	2	0.044	0.002	53	0.06		54d-533	v-a
	5	0.03	10	0.043	-0.000	53	0.06		34-516	v-a
	6	0.03	5	0.048	0.004	53	0.07		35-517	v-a
	9	0.03	5	0.055	0.007	54	0.08		38-523	v-a
	8	0.03	5	0.039	-0.016	7	0.05		37-520	v-a
	1	0.03	51	0.046	0.007	7	0.06		1-572	v-a
	52	0.03	1	0.057	0.011	6	0.07		30-547	v-a
	4	0.03	9	0.067	0.011	53	0.10		15-567	v-a
	12	0.03	8	0.047	-0.021	53	0.07		57-579	v-s
	14	0.03	12	0.052	0.005	4	0.07		60-604	v-s
	55	0.04	53	0.064	0.012	4	0.09		16b-194	v-a
	64	0.04	54	0.115	0.051	4	0.21	1000	S8530	type-s
2	13								58-590	v-s
	56	0.05							28-256	v-a
	52	0.05	56	0.064	0.012	13	0.07	4	30-547	v-a
	LINK TO CLUSTER -1									
3	34								63-631	l-m
	36	0.06							65-654	l-a
	33	0.07	34	0.071	0.010	36	0.07		62-622	l-i
	70	0.08	33	0.107	0.036	34	0.14		CFB225	type-g
	69	0.08	70	0.146	0.039	36	0.19		AN5481	type-e
	35	0.09	33	0.108	-0.038	69	0.12		64-648	l-a
	47	0.10	70	0.180	0.071	35	0.25	1000	49b-463	m-c
4	3								9-550	v-a
	50	0.06							12-565	v-a
	7	0.06	50	0.077	0.014	3	0.09	4	36-519	v-a
	LINK TO CLUSTER -1									
5	21								52-486	v-bc
	23	0.07							21-499	v-bc
	19	0.07	23	0.087	0.021	21	0.11		24-488	v-bc
	62	0.07	23	0.082	-0.006	21	0.09		AN4340	type-v
	10	0.07	62	0.113	0.031	19	0.15	4	54d-533	v-a
	LINK TO CLUSTER -1									
6	24								6a-570	n-a
	58	0.07							55-546	n-a
	25	0.08	58	0.100	0.031	24	0.12		8-538	n-a
	28	0.08	25	0.111	0.010	24	0.14		17-576	n-a
	27	0.08	28	0.092	-0.018	58	0.10		16a-573	n-a
	57	0.08	27	0.098	0.006	28	0.12		5a-549	n-a
	32	0.08	57	0.118	0.020	24	0.14		27-531	n-a
	26	0.09	25	0.111	-0.007	32	0.16		13-571	n-a
	59	0.09	57	0.111	-0.000	24	0.15		2-112	n-a
	29	0.10	25	0.120	0.009	59	0.15		54a-537	n-a
	30	0.10	59	0.136	0.016	26	0.19		59-596	n-s
	31	0.10	25	0.120	-0.016	24	0.14		26-253	n-a
	67	0.11	59	0.167	0.046	28	0.21	1000	ANSPH	type-n

```
          7   16                                              25-545  v-a
              49 0.08                                         7-568   v-a

** NEEDED .GT. FOUND FOR NEXT OTU **

              12 0.08   49 0.355 0 273   72 0 63 1004 57-579  v-s
        ------------------------------------------------------------------
          8   64                                              S8530   type-s
              66 0.09                                         RS-BB   type-r

** NEEDED .GT. FOUND FOR NEXT OTU **

              54 0.09   66 0.359 0.273   72 0 63 1004 29-268  v-a
        ------------------------------------------------------------------
          9   17                                              22-489  v-bc
              22 0.09                                         53-507  v-bc
              18 0.10   17 0.099 0.008   22 0.10             23-487  v-bc

              65 0.10   17 0.152 0 053   18 0.23 1000 CFB67  type-ph
        ------------------------------------------------------------------
         10   11                                              56-551  v-a
              48 0.10                                         5b-548  v-a

** NEEDED .GT. FOUND FOR NEXT OTU **

               9 0.10   48 0.364 0.268   72 0.63 1004 38-523  v-a
        ------------------------------------------------------------------
         11   15                                              10-556  v-a
              20 0.10                                         50-471  v-o

              64 0.10   20 0.135 0.033   15 0.17    4 S8530   type-s
               LINK TO CLUSTER  -8
        ------------------------------------------------------------------

        ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

        CLUSTER OTU LABEL
             12  37 51-478  f-w
             13  38 40-375  m-w
             14  39 41-394  m-w
             15  40 42-396  b-w
             16  41 43-398  m-w
             17  42 44-414  p-w
             18  43 45-442  m-o
             19  44 46-443  o-o
             20  45 47-458  a-o
             21  46 48-459  m-c
             22  47 49b-463 m-c
             23  60 B9634   ltype-p
             24  61 HOOK/k  type-m
             25  63 S10200  type-x
             26  65 CFB67   type-ph
             27  67 ANSPH   type-n
             28  68 B8662   type-o
             29  71 H3156   type-f
             30  72 SMH222  ctype-f

        CLUSTER MEMBERSHIP INDEX

          1   1    11  10    21   5    31   6    41  16    51   1    61  24    71  29
          2   1    12   1    22   9    32   6    42  17    52   1    62   5    72  30
          3   4    13   2    23   5    33   3    43  18    53   1    63  25
          4   1    14   1    24   6    34   3    44  19    54   1    64   8
          5   1    15  11    25   6    35   3    45  20    55   1    65  26
          6   1    16   7    26   6    36   3    46  21    56   2    66   8
          7   1    17   9    27   6    37  12    47  22    57   6    67  27
          8   1    18   9    28   6    38  13    48  10    58   6    68  28
          9   1    19   5    29   6    39  14    49   7    59   6    69   3
         10   1    20  11    30   6    40  15    50   4    60  23    70   3
```

IX. APPENDIX 4. TAXMAP Analysis 3.

TAXMAP analysis 3 contained 39 OTUs 17 OTUs from the author's collection, 8 OTUs from cytologically known herbarium specimens which were extracted for flavonoid profile analysis, and 8 type specimens. In an attempt to clarify the relationships between *V. praemorsa, bakeri* and *linguaefolia*, all specimens of *V. vallicola* and *V. nuttallii* were removed from this analysis.

A weighted analysis was performed using attributes 1 to 50. The resulting output is given in the form of a cluster analysis table. A second TAXMAP analysis was performed using only the morphological attributes, 30 to 50. The resulting output from the morphological analysis is also given as a cluster analysis table.

MAP CLUSTER ANALYSIS:-NUTTALLIANAE, PRAEMORSA: 39 OTUS, ATT 1-50, WEIGHTED

(MINIMUM NUCLEUS 0.180, MAXIMUM DROP 0.0318 BOTH ARE 100% OF NORMAL)

CLUSTER NO	OTU NOS	DIST BEST LINK	OTU BEST LINK	AVGOF NEW LINKS	DROP IN AVG.	FAR OTU	DIST FAR OTU	FLAG	NAME OF OTU	
1	2								63-631	l-m
	4	0.07							65-654	l-a
	1	0.08	4	0.084	0.012	2	0.09		62-622	l-l
	37	0.09	1	0.115	0.031	2	0.15		CFB225	type-g
	36	0.09	37	0.162	0.047	4	0.20		AN5481	type-e
	3	0.10	4	0.124	-0.038	2	0.15		64-648	l-a
	15	0.10	37	0.212	0.088	3	0.32	1000	49b-463	m-c
2	22								B8388	b-c
	28	0.09							B8052	b-c
	25	0.10	28	0.120	0.031	22	0.14		B8377	b-c
	23	0.12	28	0.150	0.030	22	0.18		B5215	bg-c
	37	0.13	23	0.206	0.056	22	0.26	1004	CFB225	type-g
3	19								B8385	a-c
	29	0.10							B11462	ltype-a
	30	0.10	29	0.126	0.031	19	0.15		B12086	ltype-a
	15	0.13	29	0.185	0.058	30	0.22	1000	49b-463	m-c
4	31								B7408	m-l
	35	0.10							B8662	type-o
	32	0.11	31	0.150	0.053	35	0.19		A8317	a-o
	27	0.11	32	0.141	-0.008	31	0.16		GD1640	m-n
	37	0.11	32	0.175	0.033	35	0.22	4	CFB225	type-g
	LINK TO CLUSTER -1									
5	11								45-442	m-o
	12	0.14							46-443	o-o typesite
	37	0.16	11	0.159	0.022	12	0.16	4	CFB225	type-g
	LINK TO CLUSTER -1									
6	20								B8403	b-c
	24	0.16							B8406	b-c
	13	0.16	20	0.199	0.042	24	0.24	1000	47-458	a-o typesite
7	6								40-375	m-w
	26	0.16							D1756	m-l
	5	0.17	26	0.218	0.055	6	0.26	1000	51-478	m-w
8	16								B9634	ltype-p
	17	0.17							B8059	p-c
	31	0.19	16	0.203	0.036	17	0.22	1004	B7408	m-l
9	8								42-396	b-w
	21	0.18							B7354	o-c
	23	0.18	21	0.183	0.007	8	0.18	4	B5215	bg-c
	LINK TO CLUSTER -2									
10	38								H3156	type-f
	39	0.18							SMH222	co-type-f
	5	0.19	39	0.197	0.020	38	0.21		51-478	m-w
	37	0.19	5	0.244	0.047	39	0.33	1004	CFB225	type-g

ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER	OTU	LABEL	
11	7	41-394	m-w
12	9	43-398	m-w
13	10	44-414	p-w ltypesite
14	13	47-458	a-o typesite
15	14	48-459	m-c
16	15	49b-463	m-c
17	18	D1738	m-n
18	33	B8699	t-c
19	34	S10200	type-x

CLUSTER MEMBERSHIP INDEX

1	1	11	5	21	9	31	4
2	1	12	5	22	2	32	4
3	1	13	14	23	2	33	18
4	1	14	15	24	6	34	19
5	10	15	16	25	2	35	4
6	7	16	8	26	7	36	1
7	11	17	8	27	4	37	1
8	9	18	17	28	2	38	10
9	12	19	3	29	3	39	10
10	13	20	6	30	3		

MAP CLUSTER ANALYSIS:-NUTTALLIANAE, PRAEMORSA: 39 OTUS, ATT 30-50, WEIGHTED

(MINIMUM NUCLEUS 0.148, MAXIMUM DROP 0.0350 BOTH ARE 100% OF NORMAL)

CLUSTER NO	OTU NOS	DIST BEST LINK	OTU BEST LINK	AVGOF NEW LINKS	DROP IN AVG.	FAR DIST OTU	FLAG	NAME OF OTU	
1	29							B11462	ltype-a
	30	0.05						B12086	ltype-a
	19	0.08	30	0.083	-0.032	29 0.09		B8385	a-c
	27	0.08	29	0.087	0.004	19 0.10		GD1640	m-n
	20	0.08	27	0.121	0.034	19 0.14		B8403	b-c
	13	0.09	27	0.131	0.010	19 0.17		47-458	a-o typesite
	32	0.10	13	0.123	-0.008	29 0.14		A8317	a-o
	31	0.09	32	0.146	0.023	29 0.20		B7408	m-l
	35	0.10	31	0.180	0.034	19 0.25		B8662	type-o
	37	0.11	32	0.198	0.017	30 0.25		CFB225	type-g
	1	0.09	37	0.175	-0.023	35 0.25		62-622	l-l
	4	0.08	1	0.168	-0.006	35 0.22		65-654	l-a
	23	0.08	4	0.175	0.006	29 0.25		B5215	bg-c
	2	0.09	4	0.153	-0.021	31 0.21		63-631	l-m
	3	0.09	4	0.183	0.030	13 0.28		64-648	l-a
	24	0.09	23	0.169	-0.014	29 0.22		B8406	b-c
	22	0.09	24	0.204	0.035	29 0.27	1000	B8388	b-c
2	22							B8388	b-c
	25	0.06						B8377	b-c
	28	0.06	25	0.072	0.017	22 0.08		B8052	b-c
	24	0.09	22	0.103	0.031	28 0.11	4	B8406	b-c
	LINK TO CLUSTER -1								
3	8							42-396	b-w
	21	0.07						B7354	o-c
	24	0.13	8	0.134	0.062	21 0.14	4	B8406	b-c
	LINK TO CLUSTER -1								
4	16							B9634	ltype-p
	17	0.11						B8059	p-c
	31	0.14	16	0.173	0.067	17 0.21	1004	B7408	m-l
5	5							51-478	m-w
	26	0.12						D1756	m-l
	19	0.16	26	0.198	0.080	5 0.23	1204	B8385	a-c
6	11							45-442	m-o
	12	0.12						46-443	o-o typesite
	31	0.15	11	0.191	0.070	12 0.24	1004	B7408	m-l

ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER	OTU	LABEL	
7	6	40-375	m-w
8	7	41-394	m-w
9	9	43-398	m-w
10	10	44-414	p-w ltypesite
11	14	48-459	m-c
12	15	49b-463	m-c
13	18	D1738	m-n
14	33	B8699	t-c
15	34	S10200	type-x
16	36	AN5481	type-e
17	38	H3156	type-f
18	39	SMH222	co-type-f

CLUSTER MEMBERSHIP INDEX

1	1	11	6	21	3	31	1
2	1	12	6	22	2	32	1
3	1	13	1	23	1	33	14
4	1	14	11	24	1	34	15
5	5	15	12	25	2	35	1
6	7	16	4	26	5	36	16
7	8	17	4	27	1	37	1
8	3	18	13	28	2	38	17
9	9	19	1	29	1	39	18
10	10	20	1	30	1		

X. APPENDIX 5. Representative Specimens

Viola nuttallii

CANADA, Alberta: *D Fabijan 570* (ALTA), N bank of Bow River, Scandia, 2400'; *538* (ALTA), Cochrane Hill, Cochrane, 4000'; *571* (ALTA), N bank Old Man River, Taber, 2500'; *573* (ALTA), Etzikom Coulee 38.6 km S of Taber on hwy 36, 3100'; *576* (ALTA), Writting-On-Stone, 3000'; *537* (ALTA), Nose Hill, Calgary, 3700'; *253* (ALTA), Fabyan, 2100'; *531* (ALTA), 18 km N of Wainwright on hwy 41, 2000'; *549* (ALTA), 5.7 km E Cluny on hwy 1, 2800'; *546* (ALTA), Turner Valley, 4100'; *C Strand 18* (ALTA, DAO), 2 mi S of Pearce, Old Man River Valley; *EH Moss 1107* (ALTA, DAO, G), S of Lethbridge; *MG Dumais 6054* (ALTA), W of Wainwright at Battle River Campsite, hwy 14; *6514* (ALTA), Drumheller, W side of River; *WC McCalla 11071* (ALTA), W of MacLeod; *7355* (ALTA), Calgary; *4594* (ALTA, UBC), North Hill, Calgary; *8554* (ALTA, UBC), Riley Park, Calgary; *8557* (G, UBC), N of Riley Park, Calgary; *8576* (G), N of Riley Park, Calgary; *8601* (ALTA, UBC), N of Riley Park, Calgary; *9382* (ALTA, DAO, G, UBC), N of Riley Park, Calgary; *10313* (ALTA, UBC), N of Riley Park, Calgary; *12850* (ALTA, UBC), N of Riley Park, Calgary; *HW Pinel and C.A. Wallis V-77* (CAN), 4 mi ENE of Rosebud, 2600'; *V-12* (DAO), 1/4 mi W of Gatine, 2350'; *HJ Scoggan 16607* (CAN), Pincher Creek; *ME Moodie 821* (G, MO, US), Black Birch Coulee, Rosedale, 2200-2500'.

Saskatchewan: *D Fabijan 596* (ALTA), 3.5 km S and 2.3 km W of Wood Mountain Park; *B deVries 468* (DAO), E of Lebret, Qu'Appellee Valley; *B Boivin 13450* (DAO), R. Tete-a-la-Biche, 3 mi S of Carievale; *RJ Ledingham and R.C. Russell S4910* (DAO), Moose Jaw; *S4916* (DAO), Elbow, Sask. R. Valley; *S5036* (DAO), Outlook, towards river; *B.J. Sallans and R.C. Russell* (DAO), Fort Qu'Appelle; *L.T. Carmichael R-14* (DAO), Qu'Appelle Valley; *R.C. Russell and W.P. Fraser* (DAO), Sutherland; *B.J. Sallans and R.C. Russell* (DAO), Buffalo Pound Lk., Chamberlain; *N.A. Skoglund 26* (DAO,CAN,G), 35 km SE of Kyle; *R.C. Russell S4736* (DAO), Katepwe, Qu'Appelle Valley; *2828* (DAO), Katepwa; *G.F. Ledingham 49-13* (DAO), N of Wascana Pond, Regina; *J.H. Hudson 1937* (DAO), Mortlach, Moose Jaw district; *G.J. Jones 634* (DAO), Lake Marguerite, 12 mi S of

Indian Head; *W.H. Cameron* (DAO), Sutherland: *W.P. Fraser* (DAO), Saskatoon.

Manitoba: *B. Boivin 13427* (DAO), 1 mi SE of Goodlands; *G. Stevenson 431* (DAO), Brandon; *H.H. Marshall 34* (DAO), Brandon: *T.J.W. Burgess* (DAO), first crossing, Souris River; *G.M. Dawson 198* (DAO), E crossing, Souris River; *H.J. Scoggan 7183* (CAN), Souris River, 8 mi N of Minto; *G.A. Stevenson 766* (CAN), Brandon; *J. Macoun 12446* (CAN), entrance to Exp. Farm, Brandon; *R.D. Bird* (ALTA), Little Saskatchewan River, Brandon; *B Boivin 13429* (DAO,G), W of Dalny, Souris River.

UNITED STATES: Montana: *WW Jones* (RM,DS,G,UC,US), Gallatin Co., Bozeman; *EJ Moore* (RM,DS,US,G), Gallatin Co., Bozeman; *JW Blankinship 552* (RM,PH,DS,US,UC,MO), Bozeman; (UC,G), Broadwater Co.,Lombard; *Hoag and Mayer 1* (RM), Decker Quadrangle, Big Horn Co., 3430-3800'; *WE Booth* (RM), 2 mi N of Ryegate, Golden Valley Co.; *LC Ellison 3301* (RM), Custer Co,, 2800'; *AW Collotzi and G Davidse 647* (CAS,DS,PH,G,US,WS), S of Billings airport, Yellowstone Co.; *HR Flint 46* (RM), Long Pines Div., Custer Forest, 3800'; *TN Traphagen* (PH), Deer Lodge; *HT and JM Rogers 1334* (WS), Lambert, Richland Co.; *PH Hawkins* (UC), Absarokee; *ED Wooton* (US), Vicinity of Helena, Clark Co; *J Roseneau* (DAO), coulee near Giant Sprints Rocky area, Great Falls, Cascade Co; *E. Starz* (MO), Helena.

North Dakota: *J. Lunnel* (DS,RM,PH,MO,US), Leeds, Benson Co; (G), Butte, Benson Co; *W.F. Bergman 1370* (DS), Enderlin; *E.T. Wherry* (PH), Stark Co., 3.5 mi W Dickinson; *C.L. and M.W. Porter 10,368a* (RM), Billings Co., Medora and T. Roosevelt Nat. Mem. Park, 2500'; *W.F. Bergman 1434* (PH), Kathyrn; *L.F. Lautenschlager 206* (CAN), Ward Co.; *J.T. Sarvis 39* (US), Mandan, Morton Co.; *O.A. Stevens 2587* (CAN, UC, US), Morton Co., Glen Ullin; (US), Steele; *W. Harken* (US), prairies; *W.N. Suksdorf (WS), Sedalia; J.F. Brenkle* (MO), Kulm; *J.F. Bergman 1370* (MO), Enderlin; *R.P. Williams 880* (MO), Shell Butte, 13.5 mi S, 3 mi W of Napolean.

South Dakota: *W.F. Forwood 38* (US,CAN), Meade Co., Black Hills near Ft. Meade; *F.L. Bennett 72* (MO), N Black Hills, N Spearfish; *D. Griffiths (GH, US), Brown Co., Aberdeen; J.J. Thornber* (GH, UC, MO), Iroquis; *J.F. Brenckle 41-06* (GH, MO), Northville; *L.A. Hanna 141* (MO), Quashnick farm, Artas; *W. Larwence* (WS), Lake Kampesky; *W.H. Over 2097* (US), Bear Creek, Washabaugh Co.; *P.A. Rydberg 550* (GH), Hot Springs, 3500'; *J. Murdock 4060* (GH), Rocky Ridge, Bald Hills, 5200'; *E.T. Wherry* (PH), Fall

R. Co., 8 mi E Smithwick, *C.A. Barr 1059* (PH), 8 mi SE Smithwick; *R.R. Krebs 62* (RM); Jackson Co., Buffalo Gap Nat. Grassland, 2500'; *H.E. Hayword 655* (RM), Badlands Cedar Canyon; *985* (RM), Boulder Cr. Park, 6 mi E Deadwood; *938* (RM), Kermosa; *H. Lee 532* (RM), Rapid City; *G.M. Dodge 21* (RM), Custer Forest, Eagle's Nest Ranger Station; *L.W. Shevling 34.5* (RM), Custer Forest.

Nebraska: *E.S. Nixon 4* (RM), Sheridan Co., 13 mi N Hay Springs; *J.M. Bates* (RM), Valentine; *R.L. McGregor 19869* (DS), Garden Co., 4 mi S Lewellen; *F.V. Hagen* (MO), Willow Creek; *W.L. Todstead 12* (GH), Holt Co., Niobrara R. valley N of O'Neill; *41* (GH), a mi W of Ohadron; *S. Stephens 38080* (GH), Deuel Co., 2 mi N, .5 W Big Springs; *S. Stephens and R. Brooks 11587* (GH), Scotts Bluff Co., 2 mi W of Gering; *S. Stephens 38062* (GH), Keith Co., 13 mi W Lamoyne.

Kansas: *L. Watson* (GH), Ellis.

Wyoming: *Hayden* (GH), Cheyenne, Wyoming Terr.; *M. Cary 315* (US), W of Isley; *L. Williams 2185* (UC, US, WS), 1 mi E of Laramie, Albany Co., *C.L. and M.W. Porter 7747* (DAO, UC, CAS), near Rock River, Albany Co.; *7734* (RM), Sybille Cr., Platte Co.; *H. Symons 51* (CAN), near Laramie; *A. Brebner 5* (CAN), N or Laramie; *K. Roach* (CAN), Laramie plains; *A. Nelson 6826* (CAN, PH, DS, CAS, UC, MO, RM, US, WS, GH), Laramie hills, Albany Co.; *226* (GH, RM), Laramie hills; *6956* (GH, MO, US, RM), Sand Cr., Albany Co.; *209* (UC), Laramie; *37* (GH, US, PH, RM), Laramie hills; *1229* (RM), Laramie; *M. Ownbey 544a* (UC, WS, RM, DS), 5 mi NW Hulett, Crook Co., 4300'; *544b* (UC, RM, DS), 7 mi NW Hulett, Crook Co., 4500'; *583* (MO, UC, WS, DS), 8 mi NW Hulett, Crook Co., 4500'; *F. Tweedy 4627* (US), Fort Steele, Carbon Co.; *A.A. Beetle 10359* (UC), Boulton Creek Expt. Area, Natrona Co.; *J.F. Macbride 2271* (RM), Albany Co., Centennial; *B.C. Buffum* (RM), Laramie hills; *W.G. Solhiem 418* (RM), Laramie hills; *B.E. and L. Barsum 1206* (RM), Albany Co., Sheep Mtn, #11 1.9 mi SW of #130, 7800'; *J. Finzell 171* (RM), Laramie Co., 7 mi W Cheyenne, 6000'; *F.B. Current 242* (RM), Laramie Co., 5 mi NW Cheyenne, 6100'; *A. Nelson* (RM), Moorcroft; *9614* (RM), Bird's Eye; *B. Dickson 273* (RM), Sheridan Co., Big Horn For., 4500'; *D.G. Reardon and L.M. Mayor 136* (RM), Sheridan Co., Big Horn coal site; *B.E. Nelson 1586* (RM), Niobrara Co., 22.5 mi NW Lusk, 5200'; *1535* (RM), Platte Co., 21 mi N Guernsey, 5350'; *C.L. Turner 63* (RM), Converse Co., W of Douglas; *E.B. Snell* (DS), Buffalo; *B. Luce 2* (RM), Goshen Co., Table Mtn Wildlife Unit; *D.L. Martin*

1520 (RM), Hot Springs Co., Eagles Nest Ranch, 6770'; *1145* (RM), Kirby, Little Sand Draw oilfield; *G.R. Kleeberger* (CAS), Wyo.; *J.F. Macbride 2720* (RM), Rock River, 7000'; *Cox, Dunn, F. Leak 1764* (RM), Goshen Co., 1.5 mi N Lingle.

Arizona: *L.M. Newlon 783* (JEPS), Yarapai Co., Ash Fork, 20 mi SW.; *H.H. Rusby* (US), Ash Fork.

Colorado: *E.L. Johnston 8746* (US), Lyons, Boulder Co.; *837* (GH), Trinidad; *886* (GH), Morley; *R.F. Daubenmire* (WS),Boulder Co., Redrocks, Boulder; *Ramely and Richards 15950* (UC, WS, DS, PH, CAS, RM), Black shales N of Boulder; *C.T. Robbins 355* (UC), Flagstaff Mtn, ca .5 mi W of Boulder; *514* (UC), Las Aminas Co., E of Delagua; *K.M. and M.C. Wiegand 1485* (GH), Crouse, Larimer Co.; *C.S. Crandell 469* (US), Howes Gulch; (US), Dixon Canon; (US, CAN, UC, GH, RM, DS), Horsetooth Gulch; (GH, CAN, US, RM), Bluffs N of La Porte; *J.H. Cowan* (US, RM), Horsetooth Gulch; *59*, (MO), Fort Collins; *J.H. Ehlers 6914* (GH), Lookout Mtn, Golden, Jefferson Co., 5600'; *7961* (GH), Golden; *6788* (GH), Walsenberg, Huerfana Co.; *6774* (GH), Morley, Las Animas Co.; *L.J. Dorr 209* (MO), Golden, Jefferson Co.; *I.W. Clokey 4209* (WS, US, PH, CAS, RM), Clear Creek, Jefferson Co.; *2676* (CAN, UC), Prairie, Denver; *2767* (PH, RM), Denver; *R. Duthie and I.W. Clokey 3819* (CAS, DS, CAN, DAO, GH, PH, MO, US, UC, WS, RM), Wolhurst, Douglas Co.; *J. Wolf 76(56)* (US), Denver; *M. Lamm 19393* (CAN, RM, PH), Ramah, El Paso Co.; *W.W. Eggleston 20171* (GH, RM), Branson, Las Animas Co.; *C.M. Rogers 5656* (US), W end Mesa de Maya; *R.C. Rollins 2061* (GH, UC, DS), Pueblo Co., 11 mi S of Pueblo, 4700'; *A. Nelson 11526a* (UC, RM), Walsenburg-Pueblo; *R.A. Rydberg and F.K. Vreeland 5883* (CAN, WS), Cuchara valley, near La Veta, 2100m; *5884* (RM), near Denver; *T.J. Bandergee* (GH), Canon City, 5400'; *42* (MO, UC, PH), Canon City, Colorada Terr.; *H.L. Zobel and C.W. Penland 1205* (PH, CAS), Deer Creek Canyon, Canyon City Road, 5800'; *J.A. Ewan 12985* (CAS), Las Animas Co., Berwind Canyon; *11165* (CAS), Boulder Co., Gregory Creek above Boulder; *R.K. Gierisch 1351* (RM), Clear Creek Co., Rio Grande Forest; *B.H. Smith 7* (PH), Pagosa Springs; *K.E. Phelps* (CAS), Broomfield; *R.K. Gierisch 869* (RM), 9 mi N Denver; *C.S. Williamson* (PH), Denver Co.; *J.M. Coulter* (PH), Denver; *E.L. Berthand* (RM), Golden, Jefferson Co.; *A. Eastwood 5392* (CAS), Clear Creek Valley, 1587m; *G.E. Osterhaut 680* (RM), 2-3 mi E Spring Canon; *5238* (RM), Gulch E of Horsetooth Mtn; (RM), Weld Co., New Windsor; (RM), Dale Creek; *B. Hammel 208* (RM), 3 mi N Livermore

hwy 287, 5600'; *G.S. Dodds 1979* (RM), Valley-Fossil Creek; *C.F. Baker 801* (RM, US, MO), Larimer Co.; *W.S. Cooper 74* (RM), Estes Park, Forks of Big Thompson, 6000'; *F. Tweedy 5565* (RM), near Boulder; *F. Ramaley 1530* (RM), near Boulder; *40* (RM), near Boulder; *A.G. Vestal 343* (DS), Boulder; *A.L. Bacon* (PH), Greeley; *M.E. Newlin* (PH), Colorado; *W.A. Henry 165* (PH, MO), Boulder Canon; *E. Hall and J.P. Harbour 55* (US, GH), Lat 41°; *H.L. Shantz 1359* (US), Akron; *E. Palmer* (US), Colo. Terr.; *H.C. Hanson c482* (MO), Boulder; *F. Nislizenus 1169* (MO), Denver.

Viola vallicola A. Nels.

CANADA, British Columbia: *H. Groh* (DAO), Bridesville; (DAO), Summerland; *J. Bostock* (DAO), Keremeos; (DAO), Summerland; *Hitchins 1-003* (UBC), Hat Creek, 3300'; *Beamish, Luetiens, Krause 680015* (CAN), Old Cawston Road, Oliver, 2800'; *Beamish and Vrugthon 60298* (UBC), Oliver; *W.B. Johnston* (UBC), Newgate; *E. Jacobs 56* (UBC), Midway; *Spreadborough 70,877* (CAN), Midway; *D. Morrison* (UBC), Flatiron Mtn; *D.L. Krause* (UBC), 10 mi SW Princeton; *J. Grant* (UBC), Vernon, 1200'; *E.W. Warren* (UBC), Vernon; *E. Wilson 5274* (UBC), Armstrong, Okanogan; *J.W. Eastman* (UBC), Penticton; *J.A. Calder and D.B.O. Saville 8125* (DAO), 8 mi SW Okanogan Falls, 3800'; *Calder, J.A. Parmelee and R.L. Taylor 16793* (DAO), 14 mi N Merritt; *167474* (DAO, UC, US), Stump Lake 25 mi NE Merritt; *W.C. McCalla 6874* (UBC, ALTA), Cranbrook; *E. Wilson 15* (WS), Armstrong; *J.R. Anderson 69* (WS), Grand Forks; *T.T. McCabe 1975* (UC), 20.5 mi E Kamloops; *1978* (UC), 10.2 mi from Pritchard to Princeton; *5955* (UC), Anarchist Mtn, Osoyoos.
Alberta: *W.C. McCalla 8667* (ALTA), N of Calgary; *11353* (ALTA), Nose Hill, Calgary; *11382* (ALTA), Nose Hill, Calgary; *10383* (ALTA, GH), Nose Hille, Calgary; *8600* (ALTA, CAN), Normal School, Calgary; *3642* (ALTA), Normal School, Calgary; *8573* (ALTA, CAN, DAO), NW of Calgary; *8587* (ALTA, DAO), NW of Calgary; *8587* (ALTA, GH), NW of Calgary; *8567* (ALTA, DAO), King George School, Calgary; *8572* (ALTA), King George School, Calgary; *12210* (ALTA, GH), Highwood River; 6 mi W Longview; *6817* (ALTA, DAO), between Pincher Creek and Cowley; *9386* (ALTA, GH), east of Cowley; *9617* (GH), Nose Hill, Calgary; *J. Macoun 18201* (CAN), Calgary; *V.C. Brink* (UBC), Scotfield, SE of Hanna;

D. Hancock 33 (ALTA), 3 mi S of Aden; *E.H. Moss 5075* (ALTA), near DeWinton, S of Okotoks; *9777* (ALTA, CAN, DAO), near Elkwater, Cypress Hills; *McCormack* (ALTA), Cypress Hills; *Lewis and Kulyk 77-5* (CAN), Cypress Hills Prov. Park; *Spreadborough 3095* (CAN), Medicine Hat; *H.E. Groh 64* (ALTA), E of Lethbridge; *Dawson 246* (CAN), N of Milk River; *J.J. Sexsmith 513* (DAO), Brocket; *F.J. Jenkins 102703* (CAN), Porcupine Hills; *J.G. Packer 5064* (ALTA), Maskinonge Lake, Waterton; *R.C. Russell S5190* (DAO), Elkwater; *R. Kuchar 2366* (ALTA), Waterton, Blakiston Cr., 4300'; *J. Kuijt 9* (CAN), Waterton, Bellevue Ridge.

Saskatchewan: *R.J. Ledingham and R.C. Russell 4934* (DAO), Cypress Hills, 20 mi S of Maple Creek; *S4920* (DAO), Keeler; *R.C. Russell and B.J. Sallons* (DAO), Duval, Last Mountain; *B. Rawlinson and G. Ledingham 49-162* (DAO), Pilot Butte, 10 mi E of Regina; *B. Boivin 13466* (DAO), R. Plumee, 7 mi S of Carnduff; *L. Jenkins* (DAO), Hoosier; *J.H. Hudson 1933* (DAO), Trewdale; *C. Frankton 1131* (DAO), 8 mi S, 1 mi W of Saskatoon near Beaver Creek; *R.C. Russell S4129* (DAO), Aylesbury, valley of Arm River; *D.S.E. Clark* (DAO), Cypress Hills; *R.C. Russell* (DAO), Saskatoon; *W.P. Fraser* (ALTA, DAO), Saskatoon; *J. Looman* (DAO), Mortlach; *G.H. Argus 3811* (DAO, GH), nwy 5 E Borden on N Saskatchewan R.; *A.W. Anderson* (CAN), Pike Lake; *G.H. Turner 5597* (ALTA), S of Karen; *J.M. Macoun 3095* (US), Cypress Hills, NWT; (US, GH), Crane Lake, Assa.; *I.W. Clokey* (UC), Sefton.

Manitoba: *B. Boivin 13429* (ALTA), l'ouest de Dalney, Riviere Souris.

UNITED STATES, Montana: *J. Grove* (DAO), 8 mi N of Kalispel; *J.W. Blankinship 8* (US); (UC, RM), Bozeman; *77* (CAN, DS, PH, MO), Bozeman; *78* (CAN, PH, US), Bozeman; (GH), Custer; *E.O. Wooton* (US), vicinity of Helena; *F.H. Rose 27* (WS), between Drummond and Garrison; *40* (GH, MO, PH, DS, CAS, UC, WS), Miller Creel valley near Missoula; *55* (DAO, WS), Missoula Co, Send Higgins ave Paddy Cr, Missoula; *C.H. Moore* (MO), near Butte, 5500-6000'; *R.A. Coster 2* (RM), Beartooth Forest, 6000'; *C.H. Hurst 285* (RM), Absaroka Forest, 6300'; P.F. Stickney 426 (RM), Missoula Co, Mt Jumbo, Lolo Forest, .25 mi E Missoula, 3500'; *J.E. Kirkwood 1363* (GH, PH, UC), Sentinal MT, S of U, Missoula, 3300'; *P. Cantoú* (CAS), Rattlesnake Cr, Bonner; *Dietter and Barkley 2347* (RM, UC, MO), N slope Mt, Sentinel, 3300'; *B.B. Irwin 99* (RM), plains about Missoula; *G.E. Osterhaut 3233a* (RM),

Grand Co, Sulphur springs; *H.N. Wheeler 595* (RM), Saprinerd; *A. Nelson 5438* (GH, UC, WS, MO, DS, RM), Madison Co, 10 mi E of Monida;(RM), La Plata Mtns; *C.W. Griffins* (RM), Hodge, Wilbur Co; *W.W. Eggleston* (RM), Grey cliff, Sweet Grass Co, 1190m; *W.E. Booth 8551* (RM), Big Timber, Sweet Grass Co; *56202* (DAO), Conrad, Pondera Co, 15 mi S; *A. Roemer 718* (RM), Park Co, Absaroka Forest, Eagle Creek, 5000'; *W.W. Jones* (CAS, US, WS), Bozeman; *J. Williams 3* (DS), Bozeman, near flour mill; *E.J. Moore* (DS, GH, US), Bozeman; *B.J. Jones* (DS, MO, US), Bozeman; (GH, US), Sedan; *E.P. White 581* (RM), Gallatin Forest, 6500'; *R.L. Grabhover 7* (RM), Jefferson Forest, Carrless Creek, 6500'; *E.J. Woolfolk W-12* (RM), Custer Co, US range livestock expt stat, 2400'; *W.M. Laybourn D8-6* (RM), Jefferson Forest; *E.W. Hartwell 324* (RM), Custer Forest, La Porte School sect.; *529* (RM), Custer Forest, White tail R.-St. Powder R. Co, 3600'; *323* (RM), White tail Ranger Station; *A.W. Vogelsang D2-16* (RM), Beaverhead Forest; *H.H. Hendron D4-85* (RM), Lewis and Clark Forest, 4500'; *J.E. Schmartz JES-311* (RM), Powell Co, Deerlodge, 6450'; *J.H. Thomas 2623* (RM), Mt Helen, Helena; *H.D. Cook* (GH), Bozeman; *J. Kinney* (US), Bozeman; *J.S. Flaherty* (US), Bozeman; *C.H. Draper* (US), NW of Redlodge, Carbon Co; *G. Davidse and A.W. Collotzi 644* (GH, UC, US), 10 mi E Bozeman; *W.N. Suksdorf 256* (WS), Jackrabbit Gulch, 10 mi Wilsall; (WS), Bozeman; *Nawrocki and Neff 8* (UC), Missoula River; *W.E. Booth 56269* (DAO), 12 mi S Choteau, Teton Co; *56202* (DAO), 15 mi S Conrad, Pondera Co; *A. Naasz 1055* (DAO), Watkins, Prairie Co; *J.M. Gilbert and R.M. Taylor 10927* (DAO), Lower St Mary Lake, 7 mi N of St Mary, Glacier Co; *E.W. Scheuber* (US); Yellowstone Park; (UC), Livingston; *R.S. Williams 116* (US), Columbia Falls; *P.A. Rydberg and E.A. Bessey 4541* (US), Briger Mtns, 7000'.

North Dakota: *J. Murdock 3507* (GH), Spearfish Red Beds at mouth of Beaver Cr, 3700'; *W.P. Taylor 351* (WS), Washburn; *J. Lunnell* (US, UC, GH, DS, RM), Butte, Benson Co; (PH, MO), Minot; (PH), Leeds; *R.P. Williams 866* (MO), Emmons Co, 4 mi W of Temil; *W.C. Whitman* (US), Stark Co, Dickson; *J.F. Bergman 1495* (GH), Church's Ferry; *O.A. Stevens 131* (DAO, UC, RM), Berlin; *2388* (US), Kenmare, Ward Co; *2579* (UC, US), Dunseith, Rolette Co; *Fieldstad* (RM), Valley City.

South Dakota: *W.H. Forwood 39* (US), Black Hills, Ft. Meade; *W.P. Carr 9* (CAN, GH, MO, US), Newell; *S.S. Visher 559* (RM), Date, Perkins Co; *A.C. McIntosh 62* (RM), Tilford-Elk Creek, Peidmont; *P.L. Ginter 36* (RM), Harney Forest, head of Wolf Canon, 6250';

E.T. Wherry (PH), Custer Co, 3 mi S of Custer St. Park; *C.A. Barr 1063* (PH), Custer C., 11 mi NW of Custer in Black Hills; *1064* (PH), 11 mi NW of Custer; *1061* (PH), 3 mi W Smithwick; *1060* (PH), 3 mi W Smithwick; *1062* (PH), cultivated, originally from S Custer Co 18 mi N Hot Springs; *J.F. Brenckle* (CAS), Northville; *E. Bondy 376* (CAS), Ellis Co, near Cean Hill N of Hays.

Colorado: *H.D. Ripley 5475* (CAS), 25 mi N Loma, W Garfield Creek, 6000'; *G.R. Hall 348* (RM), Whte River Forest; *R.W. Pohl 1949* (PH), Grand Co, S of Sulphur Springs; *C.R. Towne T-85* (RM), Oray Co, Uncompahgre, 8500'; *G. Van Buren GVB-22* (RM), Routte Co, Yampa, White R Forest, 7800'; *E.H. Graham 9113* (DS), Moffati, near Price Creek, 6400'; *9129* (DS), Moffat, 10 mi W Youghall, 7700'; *G.E. Osterhaut 2617* (RM), between Mecker and Craig; *2555a* (RM), Minturn, Eagle Co; *2555* (RM), Minturn, Eagle Co; *C.F. Baker 67* (UC, MO, WS), Gunnison Water Shed, Camarron, 6900'; *I. Tidestrom 3420* (US), Mt Caribou; *C.S. Crandell 469* (US), Howes Gulch; *L. Crawford* (GH, US), Routt Co, Steamboat Springs.

Wyoming: *A. Nelson 7038* (RM, GH), Sand Creek, Albany Co; *4375* (GH, MO), Plambago Canon; *8235* (GH, MO, UC, US, DS, RM), Tie City; *8943* (GH, UC, US, PH, CAS), Laramie Hills; *19* (CAN, GH, MO, UC, US), Head of Pole Creek; *1215* (US, RM), head of Pole Creek; *43* (GH, US), head of Pole Creek; (RM), Moorcroft; *9612* (RM), Birds Eye; *4525* (US), Evanston; *K. Roach* (CAN), Tie City; *C.L. Porter 3050* (GH, UC, US, DS, RM), Fox Creek, Albany Co; *8567* (DS, RM, GH, DAO, UC), Natrono Co, Casper Mtn, 8000'; *4886* (RM, DAO), N Platt R valley near Big Creek; *F.X. Jozwik 64* (GH, RM), Casper Mtn, Garden Creek Falls, 6400'; *N.H. and P.K. Holmgren 5017* (US), Lincoln Co, Twin Creek valley, old US hwy 30 N, 6750'; *L.M. Shultz 2537* (MO), Lincoln Co, Salt Creel Pass, Bridger Nat Forest; *M. Ownbey 553* (US, WS, MO, RM, DS), 7 mi NW Hulett, 4500'; *R.C. Rollins 568* (WS), Johnson Co, Upper Johnson Creek, 4000'; *S. Stephens 39523* (UC), Weston Co, 10.5 mi NE Four Corners; *R. Adams* (US), Upper Falls of the Yellowstone; *E.A. Mearns 989* (US), Mommoth Hot Springs; *F. Tweedy 408* (US), Mommoth Hot Springs; *F.H. Burgleshaus* (US), Mommoth Hot Springs; *M.S. Baker* (ALTA), Yellowstone Nat Park; *B. Maguire 13596* (GH), Yellowstone Park, 10 mi N Yellowstone Falls; *D. Mason* (US), Ft. McKinney; *E. Stevenson 73* (US), Uinta Co, La Barge; *I.J. Worthley 137* (US), Big Horn Co.; *OMurie 257* (US), Jackson; *F.V. Hayden* (MO), Wind Rain valley, 5000-8000'; *C.W.T. Penland*

1827 (CAS), Summitt Co, 8500'; *C.R. Clark 10* (RM), Albany Co, 6900'; *J.F. Macvride 2720a* (RM), Rock River, 7000'; *G.I. Sellon 72* (RM), hills E of Laramie; *B.E. and L. Nelson 398* (RM), Woods landing, S of Sheep Mt, 7800'; *1554* (RM), 20.5 mi WNW Lusk, 12.5 mi WNW Manville, 5200'; *R. O'Brien 1029* (RM), 21 mi SW Wheatland; *J. Weatherell 19* (DS), Pole Mt region, Happy Jack Rec Area, 8300'; *13* (DS, RM), Laramie Co, Laramie range, Happy Jack Road, 7500'; *W.J. Cockran C-150* (RM), Bighorn Co, Shell Ranger Station, 7750'; *R.L. Hartman 2946* (RM), Carbon Co, 2 mi NNW Elk Mtn to Hanna, 7400'; *R.B. Current 288* (RM), Shirley Basin 35 mi SSE Casper, 7110'; *309* (RM), Pathfinder Mtn, 34 mi SSE Casper, 7110'; *R. Schreibeis and K. Roman 667* (RM), Fremont Co, Gas Hills NE Jeffery City; *Olson, Gerhart, Rizer, Jones 17* (RM), above Goose Lake, 11.5 mi NE Dubois, 7280'; *H.G. Fisser 368* (RM), SW Thermopolis, Wind R Canyon, 5800'; *R.M. Hurd 329* (RM), Bighorn For, road to Cull Watt Park, 7200'; *O.C. Harrison 123* (RM), Star valley, Greys R., Afton area, 6000'; *R.E. Pfadt 156* (RM), Niobrara Co, Manville; *E&D Pearson 57* (RM), on Little Rocky, Clark's Fork valley, 5000'; *A Aldrich 26* (RM), Sweetwater Co, NE Cedar Mt, 8120'; *V Willits 12(406)* (RM), Little Goose Valley; *406* (RM), Hanna Creek; *529* (RM), Hanna Creek; *R Lichvar 92* (RM), Teton Co, Gros Ventre River; *RH Ohl 24* (RM), Teton For, Buffalo Ranger Station; 6500'; *PW Danwiddie 14* (RM), E Fork River near Boulder, 7000'; *JA Moore, LM Mayer, GG Reardon 506>* (RM), Uinta Co, 6880-7140'; *BL Coulter 67* (RM), Teton Forest, Horsetail Ranger Station, 7300'; *LA Well 66* (RM), between Fish and middle Piney Creek, 7500'; *EJ Williams F-17* (RM), Medicine Bow For, E Beaver Cr, 9000'; *FE McGrew 175* (RM), Shoshone For, 6000'.

Utah: *BF Harrison 7237* (MO), Toole Co, 10 mi S of Lolgreen; *8712* (DS), Wasatch Co, near East Portal, 8000'; *8313* (DS), Deer Cr Canyon, Utah Co, 7000'; *ME Jones (DS, CAS, PH, UC, US, MO), Echo; HM Christensen G-28* (RM), Sevier Co, Fish Lake For, Mud Flat, 7500'; *WB Miller 2-24* (RM), Fish Lake For, Birch Cr Canyon, 7500'; *EH Graham 8815* (DS, GH, US), Uintah Co, above Dry Fork, 6700'; *8084* (DS, MO), Diamond Mt plateau, 6500'; *8016* (DS, GH, UC), Duschne Co, Uinta R, 7200'; *8096* (DS, MO), Daggett Co, Grouse (summitt) Cr Canyon, 7000'; *9257* (MO), Wasatch Co, Horse Cr SW of Strawberry Resevoir, 7700'; *G Davidse 343* (DAO, GH, UC, CAS, DS), Cache Co, 11 mi up Hyrum Canyon, 5400'; *1018* (PH), Wellsville Canyon, 5000'; *356* (GH, UC, US), 1 mi up left Fork Blacksmith Fork Canyon, 5700'; *364* (UC, US), .5 mi W Herd Hollow, 6000'; *375* (UC),

20.5 mi up Logan Canyon near Twin Cr Rd, 6200'; *417* (UC), 3 mi N of Hardware Ranch, 6000'; *1045* (US), Rich Co, 1 mi W Garden City, 6100'; *993* (UC), Box Elder Co, .5 mi E Deweyville, 4600'; *1011* (UC, US), Raft R Mtns, Sawtooth Natl For, 6200'; *316* (UC, US), Juab Co, Mt Nebo, 2 mi SE Mona; *330* (GH, UC), Utah Co, 3 mi SE Nestle, Manti-LaSat Nat For, 5400'; *WC Muenscher, B Maguire 2384* (RM, GH, UC), 1 mi W Smithfield Sugar Factory; *2383* (UC), Spring Hollow, Logan Canyon; *B Maguire 3576* (UC, RM, DS, PH), 3 mi E Logan; *3566* (MO, UC, RM), Boy Scout Camp, Logan Canyon, 5400'; *CP Smith 2370* (DS, RM), Lewiston, Webster Spur; *E Tucker 1171* (DS), Boy Scout Camp, Logan Canyon; *1136* (DS), hwy at Preston Camp, Logan Canyon; *R Foster 7817* (RM), Duschne Co, Uinta River, 7200'; *L Williams 559* (CAS, GH, MO), Daggett Co, Summitt Springs Ranger Station, 9000'; *RT Best 18* (DS), Elko Co, Boy Scout Camp, 7200'; *AR Standing 112* (RM), Uinta For, Lower Pole Canyon, 6700'; *AE Aldous 3847* (RM), Manti Nat For, 6700'; *C DeMoisy 9* (RM), Ashley Forest, Whiterocks, 6000'; *M Burke 3567* (UC), Cache Co, Green Canyon, 5400'; *AH Holmgren, RJ Shaw 7642* (US), San Pete Co, Manti Nat For; *WC Clos 11* (US), Wasatch Mtns, Ephraim Canon, 2100m; *I Tidestrom 1019* (US), Wasatch Mts, Ephraim Canyon, 7500'.

Nevada: *HL Mason 4713* (UC), Cave Cr Post Office, Ruby Valley; *4760* (DS, GH, UC), 1 mi SW Cave Cr Post Office; *AH Holmgren 812* (UC), Elko Co, Mt S of Railroad Canyon; *986* (UC), 18 mi NE San Jacinto; *G Davidse and JL Gentry 1503* (GH, UC, WS, DS, RM, PH, DAO, MO), Pequop Mts, 5 mi W of hwy 40 and 30, 6790'; *1099* (UC, US), Humbolt Co, NE Winnemucca, 6100'; *1639* (GH, UC, US), Humbolt Nat For, 6100'; *H Engelmann 122* (MO), W slope Seftor valley, 6600'; *AE Hitchcock 891* (US), Kingston canyon and Birch Cr, 2250-2800m; *FS Goodner and WH Henning 131* (UC), Lander Co, Birch cr S of Austin; *P Train 2757* (UC), Kingston Co, E Toiyabe Range, 5500'; *GE Moore M-311* (RM), White Pine Co, Nevada For, 8000'; *M-610* (RM), New For, Rock Sprint near Hamilton, 8000'; *C McMillan and KH Knight 59* (RM), 40 mi E Ely; *MA King* (CAS), Warm Springs, White Pine Co; *JH and YM Robertson 49* (CAS, RM), Elko Co, Humbolt Nat For, Clover Cr, 5900'; *SL Glowenke 11023* (PH), Lincoln Co, Spring valley 5 mi W Ursine; *JM & MAR Linsdale 38M* (CAS), Kingston Cr, Landon Co, 7500'; *893* (CAS), Nye Co, S Twin River, 7300'; *HD Ripley & RC Barneby 6020* (CAS), N Wachre Co, 7 mi SW Vyr, 6000'.

Arizona: *HH Rusby 523* (UC, MO), Ash Fork, AT.

Kansas: *E Bondy 515* (MO, US), Hays.

Washington: *ZP Tammer 8* (WS), Lincoln Co, Creston Site Inventory; *TH Scheffer* (WS), Grant Co, E side upper Grand Coulee; *RG Jeffery* (WS), Adams Co, 2 mi N of Macall; *GR Vasey* (US), Washington Territory; *V Batie* (WS, RM), Okanogan Co, Twisp; *V Duthie* (DS), Spokane Co, near Spangle; *Sandberg & Leiberg 47* (DS, CAS, US, MO, UC, GH), Hangman Cr, Spokane Co; *HT Rogers 350* (CAS, DS, PH, ALTA, US, UC, MO, WS, GH), Ferry Co, Columbia River, 10 mi N Hunters Ferry, 1290'; *CS Williamson* (PH), Almota; *CV Piper 1715* (RM, GH, US, WS), Pullman; *A Radigan 91* (RM), Colville For, 3300'; *ME Jones* (DS), Davenport; *WN Suksdorf 8530* (MO, WS, UC), SE Spangle; *1895* (GH, WS), Spokane Co, Spangle; *9584* (WS), Klickitat Co, Binden; *10200* (DAO), E of Husum; *J Gleason 245* (WS), W of 7 Mile and N Reardon; *M Whicker* (WS), Williams Lake; *Hull & LF Anderson 2499* (GH), Campus, Pullman; *WR Hull 418* (WS), Pullman; *FL Moore* (MO), Pullman; *GH Jones 1500* (WS), Whitman Co, .5 mi N Pullman; *A Eastwood & H St John 13220* (WS), Whitman Co, Winona; *H St John, Cary, FL Pickett, FA Warren 6262* (WS), Rock Cr, W Winona; *6274* (WS), Rock Cr, W of Winona; *6887* (WS), Rock Lake; *6931* (WS), Palouse R, 2 mi E Hooper; *FG Meyer 174* (MO), near Wawawai; *1436* (GH, MO, US), S end Rock Lake; *K Whited 1216* (US, WS), Douglas Co, Waterville; (WS), Ellensburg; *279* (US), Kittitas Co, 6 mi S Ellensburg; *CB Fiker 588* (WS), Okanagan Co, Lime Belt; *649* (WS), Blue Lake, in Lime Belt, W of Omak; *OT Edwards 213* (WS), Patterson Lake, W of Winthrop; *FL Pickett 473* (WS), Grant Co, Coulee City; *E Zaring 79* (WS), Grant Co, Mtn E of Steamboat Rock, Grand Coulee; *UH Zuberbahler* (WS), Buttercaves, 2 mi W Trout Lake; *GH Ward 293* (US), Chelan Co, St Louis Ranch, N of Chelan; *JA Calder, RC Taylor & JA Parmelee 16116* (DAO), Lincoln Co, 6 mi SE Creston, hwy 2; *R Daubenmire 59174* (WS), Lincoln Co, 9 mi N Davenport.

Oregon: *WC Cusick* (WS), E Oregon; *1608* (DS, GH, UC, US), E Oregon; *1653* (DS, GH, MO, UC, US), prairies of S Blue Mts; *3156* (GH, MO, US), eastern Oregon; *1849* (DAO, GH, UC, US, WS), eastern Oregon; *3760* (WS), Union Co, Hog Mt, 4000'; *AW Sampson 233* (RM), Wallowa Nat For; *DC Ingram 1589* (RM), Ololla Ranger Station, Cascade For, 5000'; *T Howell 353* (PH, CAN, GH, US), Harney valley; *LF Henderson 9244* (CAS), Harney Co, Burns; *9245* (DS, CAS), Malhuer Co, N Malhuer River, Scotts; *5194* (CAS, DS, MO), Grant Co, Prairie City; *EH Reid and LF Henderson* (RM), Grant Co, PNW Whitman For, 6000';

NP Gale 142 (DS), Gilliam Co, near Condon; *JB Leiberg 2172* (GH, UC, US), Owyhee, Malheur Divide, 1250m; *RD Cooper* (WS), Riley; *ME Peck 20707* (UC), 18 mi W Burns, Harney Co; *25209* (UC), 3 mi S Frenchglen; *26133* (DAO), N of Burns; *JH Bartholf* (MO), Camp Harney; *OV Deming 27* (GH), Guard Cr at the Post, Hart Mtn Nat Antelope Refuge. **Idaho**: *G Davidse 1036* (UC, US), Bear Lake Co, 1.3 mi W Ovid; *1757* (MO), Butte Co, W Atomic City; *JF MacBride & EB Payson 3055* (GH, RM), Martin, Blaine Co; *A Cronquist 2432* (GH, MO), Blaine Co, 9 mi N Ketchum; *2275* (GH, MO), Bannock Co, 3 mi S Pocatello, 4500'; *CL Hitchcock & CV Muhlick 8810* (CAN, GH, UC, WS, MO, DS, RM), Custer Co, 20 mi N Sun Valley; *CL Hitchcock 23633* (WS, UC, DS, RM), between Challis and Mackay; *A Nelson & JF Macbride 1812* (GH), Owyhee Co, House Creek; *EB & LB Payson 1803* (GH, MO, CAS, RM), Lemhi Co, Salmon; *DA Saunders 4425* (US), Lincoln Co, Shoshone; *A Nelson 10057* (GH, MO, UC, RM), Victor; *RL Lingenfelter 605* (DAO, GH, WS, UC), Mink Cr Canyon, 5 mi S Pocatello; *532* (WS), Clark Co, 1947 burn area, US sheep expl station; *RJ Davis 1895* (UC, WS), Pocatello; *E Palmer 40* (US), Pocatello; *B Maguire 2386* (GH), Franklin Co, 6 mi N Preston; *W Trelease 4424* (US), Shoshone Falls; *CD Marsh* (US), Soda Springs; *JH & CD Christ 19618* (WS), Cassia Co, 13 mi SW Oakley; *CC Parry 34* (GH), Snake Co; *EH Quayle 13* (DS, RM, UC), Juniper Hills, 10 mi W St Anthony; *JF Macbride 11* (RM, GH, MO), Montpelier; *FA Barkley & R Blondeau 4004* (UC, PH), Clark Co, S of Humphrey; *Olson & Bergstien* (DS), Bannock Co, City Creek; *ME Soth P-8* (RM), Pocatello; *R Foster 6081* (RM), Caddy canyon; *J Pechaea &GD Pickford 33-8* (RM), Dubois, 5600'; *HH Van Winkle VW-5* (RM), Lemhi For, Warm Springs Ranger Station; *GA Miller M-63* (RM), Lemhi For; *AH Wheeler 4* (RM), Salmon For, Boyle Cr Basin; *FW Godden 13* (RM), Salmon For; *DE Romano 13* (RM), Salmon For; *CF Cusick 13* (RM), Lemhi For, Mohogany Cr R Stat, 7600'; *OW Mink 66* (RM), Lemhi For, Warm Spring R Stat, 6800'; *JG Koock JK-54* (RM), Targhee For, Table Rock, 5800'; *M Anderson 4* (RM), Caribou For, Maple Hollow, 4900'; *JO Stewart c-23* (RM), Cache For, Maple Hollow; *S Welsh 16655* (RM), Oneide Co, 8 mi W Holbrook; *D Bennitt 9* (RM), Twin Falls; *JF Pechance 35-37* (RM), Fremont Co, burning project; *H Work 528* (RM), Custer Co, Challis For; *562* (RM), Custer Co, Challis For, Morgan Cr, 5800'; *CB Kock 37* (RM), Challis For, Big Hill near divide, 9000'; *NH & PK Holmgren 4781* (CAS), Bear R Co, 2.2 mi W Bloomington, 6100'; *EE Stock 162* (RM), Minidoka For, Nooning Place, 6000'.

Viola vallicola subspecies *vallicola*

CANADA, Alberta: *D Fabijan 572* (ALTA), Chin Lake 23 km S Taber, 3000'; *524* (ALTA), Nose Hill, Calgary, 3700'; *550* (ALTA), Little Fish Lake, 3600'; *567* (ALTA), Spruce Coulee, Cypress Hills, 3600'; *516* (ALTA), Leitch Collieries, Crowsnest Pass, 4500'; *517* (ALTA), 1 km S of Bow Crow Forest Entrance, S of Hillcrest, 5500'; *519* (ALTA), Lynx Creel, 19 km S of Hillcrest, 4500'; *520* (ALTA), Castle River, S of Hillcrest, 4500'; *523* (ALTA), Beauvais Lake, 4500'; *533* (ALTA), Nose Hill, Calgary, 3700'; *551* (ALTA), Hand Hills, N of Little Fish Lake, 3000'; *556* (ALTA), 3 km E Cereal on hwy 9, 2600'; *545* (ALTA), .5 km W Turner Valley, 4000'; *548* (ALTA), 5.7 km E of Cluny on hwy 1, 2800'; *568* (ALTA), Whitla Coulee, .3 km E of Etzikom turnoff on hwy 3, 2700'; *565* (ALTA), 4.6 km N of Golden Prairie turnoffon hwy 41, 2700'; *566* (ALTA), Medicine Hat, 2300'; *547* (ALTA), Bow Crow For entrance 10 km W Turner Valley on hwy 546, 4800'; *276* (ALTA), Waterton, 4400'; *268* (ALTA), 8 km W Longview on hwy 541, 4300'; *194* (ALTA), Etzikom Coulee, 38.6 km S Taber on hwy 36, 3100'; *256* (ALTA), Porcupine Hills, 8.7 km E of hwy 22 towards Nanton, 4500'.

Saskatchewan: *D Fabijan 579* (ALTA), 1.8 km SW of Cypress Hills Park, 4100'; *590* (ALTA), 3.7 km S of Moose Jaw.

Viola vallicola subspecies *major*

CANADA, British Columbia: *D Fabijan 489* (ALTA), 3.6 km E Cawston, 3000'; *487* (ALTA), Courtney Lake, 3500'; *488* (ALTA), Princeton, 2500'; *486* (ALTA), 11.4 km S of Kamloops toward Lac La Jeune; *499* (ALTA), 13.3 km E of Grand Forks, 2000'; *507* (ALTA), Johnston Creek Park, 3000';

UNITED STATES, Oregon: *D Fabijan 471* (ALTA), 57.7 km S of Washington State border on hwy 3.

Viola praemorsa subspecies *praemorsa*

CANADA, British Columbia: *JR Anderson 198.5* (DAO), Thetis Lake, Vancouver Island; *AJ Pineo* (UC), Victoria; *J Hett & W Armstong 12* (UBC), above Royal Oak peat bog, VI; *JK Henry* (UBC), Victoria; *9110* (CAS), Victoria; *AJ Hill 204* (DAO), Victoria; *GM Dawson 33940*, (CAN), Vancouver Island; *J Macoun 2421* (CAN, GH), vicinity of Victoria; *2467* (CAN), Cedar Hill, near Victoria; *87046* (CAN), Beacon Hill, near Victoria; *78,459* (US), vicinity of Victoria, VI; *Dr Lyall* (GH), near Nanimo, VI; *JA Calder & A Szczawinski 28523* (DAO), small park in Victoria; *PP Henson* (DAO), Uplands, Victoria; *MC Melburn* (DAO), westside Uplands Park, Victoria; *CF Newcombe*F (GH), Observatory Hill, VI.

UNITED STATES, Washington: *D Fabijan 414* (ALTA), Tacoma; *394* (ALTA), Lyle; *JW Thompson 14278* (GH), Klickitat Co, near Centerville; *11373* (GH), near Lyle; *5137* (GH, MO, US), Pierce Co, near Tacoma; *8238* (CAN, DS), near Roy; *W Suksdorf 22* (CAN, WS), Mt Bingen, Bingen; *5552* (WS), Bingen; *5563* (DAO, WS), near Bingen; *9565* (WS), Klickitat Mt near Rockland; *9579* (WS), Bingen; *100* (GH), Klicitat Co, woods; *10828* (WS), Skamania Co, Hood; *10829* (WS), Skamania Co, Hood; *UH Zuberbuhler* (UC), Buttercaves, 2 mi W Trout Lake; *WJ Eyerdam* (MO, UC), Pierce Co, Niqually Prairie; *JM Grant* (UC), Lakeview; *L Benson 1204* (DS, MO), Pierce Co, south Tacoma, 300'; *Brandell* (MO), prairies, Tacoma; *AJ Leroas* (DS, UC), South Tacoma, W end 66 St; *JB Flett* (UC), Tacoma; *MS Baker 9634* (DAO, MO, WS), South Tacoma, near old Municiple Auto Court; *OD Allen 101* (GH), Roy; *RM Horner 58* (WS), Waitsburg; *R59B83* (GH, US), Waitsburg; *NL Gardner 30* (WS, UC), Whidbey Is.

Oregon: *LF Henderson 86* (DS, UC), College Campus, Forest Grove; *5872* (DS, CAS, MO), near Selma; *JW Thompson 2140* (DS), Jackson Co, E of Brownsboro; *527* (DS), Washington Co, Forest Grove; *567* (MO), summitt David's Hill, Forest Grove; *2030* (DS), Roseburg; *4124* (DS, GH, MO, US), Salem; *MS Baker* (DS), Kirby; *5442* (DS, UC, US), Josephine Co, Grant's Pass; *5441* (UC), near Medford; *EI Applegate 4061* (DS), Ashland Co, Keene Creek Ridge Ashland-Klamath Falls hwy; *MW Gorman 4416* (DS, WS), Salem; *JC*

Nelson 23 (DS), Polk Co. *L Dale* (DS), Gilbert Creek near Grants Pass; *L Constance* (CAS, UC), Lane Co. Coburg, N of Eugene; (UC), vicinity of Eugene; (UC), Spencer Butte, S of Eugene; *EW Hammond 27* (GH, US), Jackson Co, near Wimer; *JO Steward 16* (US), Horsefly valley, Klamath Co, 4800'; *WJ Spillman 21* (WS), Monmouth; *Watkins & Dunn 448* (MO), Umatilla Co, S hwy 395 Camas Cr and N Fork John Day River; *W Cusick 3956* (WS), Douglas Co, Looking Glass; *Drake & Dickson* (MO), Scappouse.

California: *WA Weber 12294* (DAO), Humbolt Co, Van Duzen River, W of Dinsmore, 2400'; *MS Baker 8059* (GH, MO, UC, CAS, DS), Humbolt Co, headwaters of Yager Cr, 2 mi W Bridgeville on Kneeland hwy; *JP Tracey 4159* (UC), near summit Buck Mt, *6067* (UC), head of south Yager Creek; *6609* (UC), Lawrence Creek, Kneeland pasture, 2500'; *8730* (DS, JEPS, UC), Kneeland pasture, 2500'; *12566* (UC), Hoopa Mt, near summit, W of Hoopa, 3500'; *18607* (UC), Van Duzen R, opposite Buck Mt, 2500'; *AM Alexander & M Kellogg 4662* (DS, UC), Modoc Co, Warner Mts S of Eagleville, 7000'; *MPE Ames* (US, GH), Plumas Co; *A Eastwood 899* (MO), Shasta Co, Goose valley; *R VanDeventer 335* (JEPS), Del Norte Co, Beer s Rd at Flume crossing; *LE Smith 88* (US), Siskiyou Co, Sisson; *GD Butler 1325* (DS, UC, US), Siskiyou Co, Bulls meadows, Goosenest Mt; *S & CH Quibell 2852* (UC), Fresno Co, Ball Diamond meadow, off 168 between Shaver L and Rock Haven; *HP Chandler 1288* (CAS, DS, UC, US), Hupa Indian Res, 3600'; *JG Lemmon 48* (GH, UC), Sierra valley; *DK Kildale 5185* (DS), Humbolt Co, Chalk Mt; *5975* (DS), Horse Mt, *A Eastwood & T Howell 5410* (CAS), Madera Co, Bass Lake; *E Beltell* (CAS), Burney, Shasta Co.

Viola praemorsa subspecies *linguaefolia*

CANADA, Alberta; *D Fabijan 648* (ALTA), Carthew Summit, Waterton, 7500'; *654* (ALTA), Boivin Lake, 6800'; *AJ Breitung 16670* (DAO, UC), Waterton, Carthew Pass, 8000'; *13935* (ALTA), Mt Carthew; *16999* (DAO), Crypt Lake, S facing slope; *17275* (ALTA), Avion Ridge, S facing cirque; *FW Hunnewell 15560* (GH), Waterton, Crypt Lake, 6800'; *EH Moss 3335* (ALTA), Waterton, Cameron Lake; *JG Packer 3716* (ALTA), Waterton, bank of Bertha Creek, by bridge; *4175* (ALTA), above Goat Lake, 6500'; *J*

Kuijt, J Nagy, M Gadd 3662 (CAN), Carthew summit, scree slope; *4043* (CAN), W of Lost Lake, E facing scree slope, 7000'.

UNITED STATES, Washington: *D Fabijan 398* (ALTA), 5.8 km E Husum.

Oregon: *EI Applegate 46* (US), Swan Lake Valley; *2281* (US), Jackson Co, head of Kear Creek; *JP Rose* 1692 (MO), Pine ridge, Klamath Co; *LF Henderson 640, 1924* (MO), Hood R Co, open pine woods; *CL Hitchcock 20531* (CAN, DAO, WS), Wheeler Co, 15 mi N Spray on hwy 207; *20524* (CAN), 5 mi SW Lonerock; *GW & GD Douglas 3366* (DAO), 1.2 mi W Mitchell, 4500'; *A Cronquist 6340* (WS), 15 mi NE Spray; *G Davidse & AW Collotzi 506* (GH), Harney Co, 8 mi SE Frenchglen to Fish Lake, 6000'; *WC Cusick 1987* (GH, US, WS), Harney Co, higher Steins Mtns; *3165* (MO, WS, US), Union Co, Bank of East Eagle Cr, Wallowa Mt, 1330m; *1876* (GH), eastern Oregon; *FH Whittaker SS237* (WS), Josephine Co, Lake Mt, Grayback area, Siskiyou Mts, 6500'; *ME Peck 25985* (WS), Baker Co, 4 mi SE Halfway.

Idaho: *D Fabijan 622* (ALTA), Red Rock Pass, 7000'; *EB & LB Payson 1973* (GH), Summit to base of Mt NE Henry Lake; *JF Macbride 952* (GH, US, WS), Silver City, Owyhee Co, 7000'; *CL Hitchcock, RV Rethke, R VanRaadshooven 3852* (WS), Yellowstone NP, 1 mi below Flat Rock Camp, S of Wentrona, 6500'; *NH Holmgren 5578* (CAS), Bonneville Co, Big Elk Mt, S of Palisade Dam, 8800'.

Montana: *D Fabijan 631* (ALTA), McDonald Pass, 6325'; *DT MacDougall 819* (US), MacDougall Peak, 6800'; *O Thompson* (US), Glacier Park Station; *A Cronquist 7934* (GH), Missoula Co, Holland Lake, 7500'; *CL Hitchcock 16378* (GH, UC, WS, DS), Park Co, Silver Pass, 10 mi W Four Mile Ranger Stat; *16651* (DS, GH, DAO, WS, US), Park Co, near Lookout Stat, 3 mi W Veartooth Lake; *16510* (CAN, WS), Sweergrass Co, 2 mi below Rainbow lake; *16828* (CAN, UC, WS), Madison Co, S side Black Butte, 10,000'; *16919* (CAN, GH, US, WS), Red Hill, Gravelly Range, 9500'; *JG Witt 1188* (WS), Cooke Co, 3 mi E Cooke City, 8000'; *1665* (DAO, GH, WS), 2 mi E Cooke City, 8000'; *1705* (DAO, GH, WS), 4 mi N Cooke City; *DW Swingle* (DAO), Gallatin Co, Bozeman, Monument Mt, 9500'; *EJ Moore* (GH, WS, US), Bridger Mts; *PA Rydberg & EA Bessey 4539* (US), Bridger Mts; *4540* (GH), Madison Co, Old Hollowtop, Pony Mts, 8500'; *CL Hitchcock & CB Muhlick 12755* (DS, CAS, WS), Beaverhead Co, W Oreamnos Lake, Anaconda Range; *12953* (CAS, GH, MO, UC), Pioneer Range, between Sheep and Black Lim Mts, 9000'; *12114* (WS), Meagher

Co, Checkerboard Cr, Castle Mts; *12343* (DS, CAS, MO, WS). .5 mi S Yogo Peak, Little Belt Mts; *LM Umbach 81* (DS, GH, US). Coulees, Midvale; *106* (DS, US). Tavines, Midvale *JF Morton &JM Venn NA4839* (CAN). Cookes City at edge of Yellostone; *W Sundell 2* (CAS). Missoula Co.

Colorado: *CF Baker 225* (GH, MO, UC, WS), Grand Mesa, Gunnison Watershed, 9000'; *GE Osterhout 2694* (GH); Mts E of Steamboat Springs; *LN Gooding 1572* (DS, GF, MO, UC, US), Rabbit Ear Range; *SA Spongberg 62-34* (US); Gunnison Co, N of Mtn Biol Lab, Gothic; *WW Eggleston 90* (GH, MO, US), Kebler Pass, 3050m; *J Langenheim 591-48* (UC), Trail to Virginia Basin, 105000'; , *F Ramaley 10537* (UC), East Fores Lake near Tolland; *Lethel, Willey & Clokey 4205* (CAN, MO, UC, US, WS), Boulder Co, Lake Wldora, 2850m; *GN Jones 34155* (UC), Yankee Doodle Lake, 10700'; *TS Bandegee 13234* (MO), Mt Carbon, Elk Mts; *E Payson 370* (GH), Tabeguache Basin, 8000'; *IW Clokey 4209* (UC), Hefferson Co Clear Cr, 1578m; *I Tidestrom 3420* (UC), Mt Caribou; *NH Russell 59-72* (DS), Gunnison Co, Gothic; *59-74* (CAS), Emerald Lake, Gothic.

Wyoming: *EA Mearns 638* (US), Melvin Gulch, Mammoth Hot Springs; *AE Porsild 16956* (CAN), Park Co, Mt Washburn, Yellowstone NP, 10000'; *G Davidse & AW Collotzi 676* (GH, UC, US), 32 mi S Red Lodge on hwy 212; *670* (UC), Lincoln Co, summit hwy 89 S of Afton; *B Venrick 173* (MO), Dunraven Pass, Yellowstone NP, 8600'; *RG Stolze 871* (GH), Beartooth Mts, Clay Butte, 2800m; *EB Payson & GM Armstrong 3352* (GH), 5 mi E Afton; *3647* (GH), Redmount, NE Smoot, 9600'; *RA & A Nelson 84* (DS, MO, WS), U of W summer camp, Medicine Bow Mts, 10,000'; *A Nelson 7914* (GH), Medicine Bow Mts, *110005* (WS), Medicine Bow Mts; *GT Goodman 627* (MO), Medicine Bow Mts; *LC Anderson 252* (UC), Teton Co, Treasure Mt scout camp, 11 mi E Driggs; *R Williams 24* (MO, WS), STS Ranch, Moose, 6700'; *2174* (UC, WS), Double Diamoun Ranch, Moose, 7000'; *EB & LB Payson 2713* (GH, UC), Sublette Co, Piney Mt, 25 mi W Big Piney; *2783* (GH, MO, UC, US), 15 mi E Merna; *JH Beaman & KJ Stone 1402* (DAO), Carbon Co, near Bridger Peak, Sierra Madre Range, 10,700'; *M Ownbey 844* (DS, WS), Big Horn Co, near Medicine Mt, 9500'; *107* (DS), Albany Co, U of W summer camp, Medicine Bow Mts, 9500'; *LO & R Williams 3077* (GH, MO, WS), 10-15 mi E Kane, 8500'.

Utah: *EH Graham 8147* (GH, MO, US, DS), Dushesne Co, E slope Wolf Creek Pass, Uinta Basin, 9000'; *ME Jones 6175* (DS, MO, UC, US), Crystal Mine, Marysvale, 9000'; *E Tucker*

1203 (DS), Cache Co, Brush Canyon, Wellsville Mts; *S Clark & K Taylor 2435* (DS), Emery Co, E of Cleveland Reservoir, 8500'; *CP Smith 2370* (CAS), Cache Co, Lewiston-Webster spur; *G Davidse 1726* (CAS), Bear R Mts, Twin Creek.

Nevada: *NH & PK Holmgren 4898* (CAS), Humbolt Co, Independence Mts, 29 mi NNW Elko, 6400'; *A Nelson & JF Macbride 1942* (GH, MO, US), Jarbidge, 8500'; *2040* (GH), Jarbidge, upper corral Creek, 7000'; *AA Heller 10547* (GH, US), Ruby Mts, Star canyon near Deeth, 8500'; *M & GB Ownbey 2808* (DAO, WS), Humbolt Co, Buckskin Mtn, 12 mi S & 14 mi E McDermitt; *JL Gentry & G Davidse 1640* (DAO), Santa Rosa Range, 33.5 mi NE US 95 and Nev 83, 6960'; *Holmgren, JJ Fay & BL Bethers 4327* (UBC), Black Rock Range, Mahogany Cr Canyon E of Summit Lake, 7200'.

California: *L Whitney 1739* (UC), Modoc Co, Happy Camp, 15 mi W Canby, 4800'; *1738* (UC), Crowder Flat, 5000'; *RM Austin 453* (US), Goose Lake valley; *LE Smith 690* (GH, US), Sisson; *A Eastwood 361* (GH, US), Deer Park, Lake Tahoe region.

Viola praemorsa subspecies *flavovirens*

UNITED STATES, Washington: *D Fabijan 478* (ALTA), 1.5 km S and 4.5 km E Anatone; *375* (ALTA), Klickitat Valley, N of Maryhill on hwy 97; *WC McCalla 5413* (ALTA), Kittitas Co, Lake Cle Elum.

Oregon: *Gillet & Taylor 11013* (CAN, DAO), Wallowa Co, 8 mi S of Washington border on hwy 3; *NP Gale 52* (MO, GH), S of Myrtle Cr, Douglas Co.

Idaho: *E McKay* (WS), Vollmer; *M Ownbey 2043* (DS, DAO, CAN, UC, US, ALTA), Idaho Co, 1 mi E Kooskia; *MS Baker 7408* (CAS, DS, DAO, MO, WS), Clearwater River, Kamiah, 1500'; *HA & EG Heller 3156* (CAS, DAO, DS, MO, RM, UC, WS), Lake Waha, Nez Perce Co, 2000-3500'; *Sandberg, MacDougall, Heller 222* (DS, MO, UC, US), Lake Waha; *Sharsmith 3534* (UC, WS), Lake Waha; *M Ownbey 2043* (MO), 1 mi E Kooskia, Idaho Co; *JF Mcbride 860* (DS), Boise Co, Squaw Cr, 3500'; *W Burns 52* (WS), Latah Co, Potlatch Canyon Kendrick; *JH Christ 18268* (WS), Idaho Co, Lower slopes Mt Idaho; *J Gleason 449* (WS), Idaho Co, near Grangeville; *CL Hitchcock & CV Muhlick 8422* (DS, GH), Clearwater Co, 2 mi N of Cavendish; *LF Henderson* (DS, US), bluff above Juliaetta.

Montana: *W Sundell 2* (DAO, GH), Missoula Co; *Burdick 5* (DAO), Missoula Co, 10 mi S Missoula on Bitterroot R.

Wyoming: *EB Payson & GM Armstrong 3288* (MO), E of Afton, 7500'; *L Williams 1091* (MO), Double Diamond Ranch, Teton Co, 7000'; *663* (UC), Grand Teton NP, Jenny Lake Canyon, 7500'.

Viola bakeri

UNITED STATES, Washington: *D Fabijan 396* (ALTA), Trout Lake, 12,325'; *WC McCalla 5358* (ALTA), Klickitat Co, N of Husum, on White Salmon River; *6222* (ALTA), Calaveras Co, Big Meadow, valley floor, 6800'; *6324* (ALTA), near Summit Lake, Lassen NP, 6700'; *W Suksdorf 1894* (WS), Klickitat Co, Falcon valley.

Oregon: *EI Applegate 10532* (DS), Union Rock, Crater Lake NP; *8317* (DS), Klamath Co, Grizzly Hill, Swan Lake Valley; *6164* (DS), Josephine Co, Grayback Mt; *10424* (DS), Josephine Co, Lake Mtn Trail; *5764* (DS), Warner Valley, E Mt Lassen; *GE Kelly* (CAS), Crater Lake; *VL Crosby 589* (DS), Josephine Co, 15 mi E Cave Junction; *EP Sheldon 12580* (DS), Lane Co, Lake Valley; *CL Hitchcock and JS Martin 5245* (DS), Josephine Co, Lake Mt Trail, 4 mi E Oregon Caves, 6400'; *4863* (DS), Deschutes Co, 4 mi N North Sister Mts, MacKenzie Pass, 6800'; *4855* (DS), Deschutes Co, 6 mi W MacKensie Pass, 4800'; *JW Thompson 13040* (CAS), Jackson Co, Huckleberry Mt, Rogue Range Nat For, 3000'; *A Cronquist 7851* (CAS), 9 mi N Sisters, Trout Cr, 4500'; *RS Ferry & R Duthie 462* (DS), Crook Co, Tumalo Ranger Station, 6700'; *JT Howell 7156* (CAS), Deschutes Co, Sparks Lakes.

California: *MS Baker 5215* (CAS, DS, UC, US), Placer Co, hwy 40, 1.5 mi W Big Bend Ranger Station; *8406* (DS, UC), Nevada Co, 5 mi W Bowman Lake, 6000'; *8403* (DS), Placer Co, Squaw Cr near hwy to Taho; *8388* (DS), Sierra Co, Webber Lake; *8377* (DS), Tehama Co, hwy 89 [illegible]000'; *8052* (DS, CAS), Mt Lassen hwy (89) near checking station, 5800'; *8556* (UC), Amador Co, S end Silver Lake, 7290'; *10232* (CAS), Glenn Co, Black Butte, 6700'; *ER Drew* (DS), Sierra Co, Independence Lake; *EB Babock & GL Stebbins 1576* (DS), Yuba Pass, 1818m; *BJ Jorgensen 477* (DS), Little Truckee Rd between

Independence and Webber Lakes; *HK Wagnon 1684* (DS), Webber Lake; *A Head* (DS), Gold Lake, 6700'; (CAS) Plumas Co, Gold Lake, Feather R region, 6300'; (CAS) Plumas Co, Lake Center camp, Feather R region, 6300'; *CC Bruce 1276* (DS), Shasta Co, Mt Lassen; *JT Howell 36558* (CAS), Dusch Meadows, 6500'; *36574* (CAS), Tehama Co, Sulphur works station, Lassen P, 6600'; *27610* (CAS), Jamison Cr, 6200-6400'; *35675* (CAS), Drakesbad, 5300-6000'; *35900* (CAS), Drakesbad, 5300-6000'; *H Leschke* (CAS), Cold Boiling Lake, Lassen NP, 7550'; *A Eastwood 870* (CAS), Shasta Co, Mt Lassen; *7001* (CAS), Portola; *BF Jackson* (CAS), Yuba Pass; *Kelloge* (DS, G), Placer Co, Cisco; *ME Jones* (DS), Emigrant Gap; (DS), Plumas Co, 13 mi W Prattville, 4500'; *AA Heller 9859* (DS), Placer Co, Summit, 7000'; *BJ Jorgenson 515* (CAS, DS), Nevada Co, Soda Springs; *MS Baker & HK Wagnon 13012* (DS), Theama Co, 6.1 m3 NW Cohillack Camp; *CR Quick 50-25* (CAS), Mill Cr Meadows W of Gurnsey Camp, Lassen N For; *HC Cantelow* (CAS), S of Bucks Lake; *RJ Weatherby 1438* (CAS), Lake Almanor, 4650'; *R Baergabipi 1733* (DS), Plumas Co, Little Grey Eagle Cr, Gold Lake region, 6700'; *FN Bennett* (CAS), Butte Co, Jonesville; *WL Atkinson 1900* (DS), Edorado Co, Pyramid Peak; *GT Robbins 2019* (CAS), Eldorado Co, 4 mi S of Wrights Lake, 6700'; *L Beane 1842* (DS), Fresno Co, Huntington Lake, 7000'; *E Carter 64* (DS), Fresno Co, Huntington Lake, 7000'; *MS Jussel* (G, CAS), Camp Baxter, 20 mi from Darringtons; *LS Rose 40438* (CAS, UC), Nevada Co, Soda Springs, 6700'; *54053* (CAS), 3 mi W Soda Springs; *FA MacFadden* (CAS), Donner Lake; *DD Keck 4363* (DS), Mariposa Co, Yosemite NP, 2375m; *A Eastwood & JT Howell 4999* (CAS), Trinity Co, Scott Mts N of Carrville; *JP Tracey 10596* (DS), Humbolt Co, Trinity summit, 6000'; *AM Vollner & L Beane 9* (DS), Siskiyou Co, Scott Mtn; *RS Ferris & L Lorraine 11712b* (DS), Siskiyou Co, Plowman's (Noyes) valley, E fork Scott R; *HP Chandler 1688* (DS), Marble Mt, 8000'; *DE Breedlow 3366* (DS, CAS), hwy 89, 8 mi E McCloud, 3700'; *L Rowntree* (CAS), 40 mi E of McCloud, 4000'; *A Eastwood 1107* (CAS), McCloud; *ED Cantelow 1454* (CAS), Scott Mtn, 5000'.