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**CYTOTAXONOMY AND CYTOGEOGRAPHY OF SELECTED**  
**ARCTIC AND BOREAL ALASKAN VASCULAR PLANT**  
**TAXA.**

**UNIVERSITY OF ALASKA, M.S., 1979**

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CYTOTAXONOMY AND CYTOGEOGRAPHY OF SELECTED  
ARCTIC AND BOREAL ALASKAN VASCULAR PLANT TAXA

A  
THESIS

Presented to the Faculty of the  
University of Alaska in partial fulfillment  
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for the Degree of

MASTER OF SCIENCE

By  
Janice C. Dawe, B.A.  
Fairbanks, Alaska  
December, 1979

CYTOTAXONOMY AND CYTOGEOGRAPHY OF SELECTED  
ARCTIC AND BOREAL ALASKAN VASCULAR PLANT TAXA

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## ABSTRACT

Chromosome numbers of 141 Alaskan plant taxa were determined from seedling root tips and apical meristems, yielding 17 first chromosome counts, 17 new ploidy levels, and 47 first reports for Alaskan material. These data were then applied to problems of systematics and plant geography. Oceanic and circumboreal taxa show more numerous cytotypes and morphotypes than continental taxa, perhaps due to the greater number of refugia from which they have radiated. Extreme environment may account for the chromosomal conservatism seen in high arctic circumpolar as opposed to low arctic circumboreal taxa. An analysis of the polyploid age spectra represented by these elements should help resolve problems concerning Alaska's floristic history.

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## INTRODUCTION

Within systematics, chromosome botany provides a powerful tool for phylogeographic and taxonomic investigations. In phylogeography, chromosome number patterns within both whole floras and species complexes often help elucidate their histories. In taxonomy, chromosome numbers and morphologies may serve as diagnostic features for the definition of species, but some controversy surrounds the proper emphasis of karyology in that activity. Three contrasting viewpoints should be reviewed. Each is championed by different botanists who have worked directly with the chromosome botany of the northern flora, which is the subject of this thesis.

Throughout his monumental treatment of the Alaskan flora, Hultén (1937, 1968) attached little taxonomic importance to chromosome number variation. He routinely maintained morphologically similar though chromosomally distinct taxa as subspecies or varieties of a single species.

At the opposite extreme, Löve and Löve purport that chromosome number differences between plants nearly always signal the existence of reproductive discontinuities that should be given recognition in formal classification schemes. The following statement (Löve and Löve, 1966, p. 2) clearly outlines the philosophy upon which the authors have based their taxonomic decisions on the arctic flora (Löve and Löve, 1975a):

Critical taxa can be more exactly defined if the number and morphology of their chromosomes is known so this character can be compared to that of closely related taxa which may have been confused with them; this kind of work is based on the fact that a

biologically well-defined species can have but a single chromosome number and a limited variation in chromosome morphology...Even a single chromosome count has proven of greater value for recognizing the distinctness of a species than do hours of morphological comparisons....

Most other workers (Mosquin, 1966a; Mosquin and Hayley, 1966; Small, 1968), and I include myself among them, adopt a cytotaxonomic philosophy midway between the two opposing views mentioned above. As stated by Mosquin (1966a, p. 213):

Mechanisms of evolution differ from group to group and there are many bases for, and kinds and degrees of, discontinuities in nature. Taxa, since they after all represent only our legally formalized concepts of how natural variation should be grouped, therefore represent many sorts of things. It follows that no strictly imposed criterion (e.g., that of chromosome number or reproductive isolation) can serve as the most useful basis for biological classification...a taxonomy based on reproductive isolation would reflect only reproductive isolation...In contrast, a classification based on many features, since it reflects accurately the complex interacting genetics of organisms will reflect a greater number of biological facts.

Morphological and chromosomal evolution often proceed at different rates, and the discontinuities they produce in diverging taxa are not likely to be equivalent. Therefore, rigid adherence to either criterion alone can produce an arbitrary and unsatisfactory classification scheme. Like all other phenotypic variables, chromosome number and morphology have unequal taxonomic value, and should only be evaluated on a taxon by taxon basis.

In Alaska, noteworthy cytotaxonomic studies have been conducted in the Interior (Hämet-Ahti and Virrankoski, 1971; Knaben, 1968) and north of the Brooks Range (Hedberg, 1967; Holmen, 1962, 1964; Johnson and Packer, 1968; Packer and McPherson, 1974). Papers dealing with cytologic

aspects of individual Alaskan taxa are too numerous to list here, but are included whenever appropriate in the Results section.

My research comprised a cytologic survey of 141 selected arctic and boreal Alaskan vascular plant taxa. Once this critical mass of chromosome information had been gathered it became possible to ask: do chromosome numbers accurately reflect relatedness within and between taxa? The answer to this question should be evident from the foregoing discussion: chromosome numbers do not always reflect relatedness. Some taxa, including those recognized as species, genera, and even entire families, are chromosomally conservative, i.e. they do maintain constant chromosome number. In these cases, morphologic evolution proceeds at a faster rate than gross chromosomal evolution, and the morphologic discontinuities produced have traditionally been heavily weighted in classification schemes. In contrast with such cytologically stable taxa, others are cytologically labile and variable, so that even a single population may include members at several chromosome levels. Here, chromosomal evolution and the discontinuities produced outstrip morphologic evolution. Experimental taxonomic techniques employ chromosome discontinuities as important characters for use in constructing classification systems.

As so often happens, answering one question only raises a host of new ones. In this case: If chromosome numbers for a taxon do not show constancy, are they more often geographically delimited, i.e. do they show areal specificity? This question lies within the realm of phytogeographic investigation. Historically, chromosome botany has been applied to this field through computation of the polyploid frequencies of entire floras.

The pioneering work of Hagerup (1928, 1931), Tischler (1935), and Muntzing (1936) dominated cytogeographic thought for thirty years. Findings from those initial studies suggested that the polyploid frequency of angiosperm floras increased with 1) latitude, 2) altitude, and 3) "severity" of environment. However, these early studies were all conducted in Europe, and while some of the trends recorded can be correlated with historic events peculiar to that region, those same trends were not found in other parts of the world (Favarger, 1954; Gustaffson, 1948; Johnson and Packer, 1967; Knaben, 1950; Pignatti, 1960; Reese, 1957). As a result of this, Löve and Löve (1957) suggested that the original correlation noted between high ploidy and extreme environment applied only to arctic and subarctic regions. Their hypothesis was then already at odds with the finding of a lower than expected polyploid frequency in the Kolguev Island, U.S.S.R. flora (Sokolovskaya and Strelkova, 1941). As long ago as 1948, Gustaffson suggested that polyploidy in the north is correlated not with extreme environments but with the prevalent herbaceous perennial growth habit, and that it is this growth habit, not polyploidy per se, that is selected for by the arctic environment. Gustaffson's hypothesis is the most satisfying one offered to date, because it directly relates chromosome adaptations to the taxa involved, instead of stressing the indirect relationship of chromosomes to environment. It has subsequently been supported by much work (cf. Johnson, Packer, and Reese, 1965).

Alaska has long been recognized as the meeting ground of four distinct floras: 1) the high latitude, circumboreal flora, which is believed to have evolved in situ since the late Tertiary period, 2) the floristically rich, biogeographically young, endemic Beringian flora,

3) the northeastern Asian alpine complex, and 4) the North American Cordillera alpine complex. Thus because of their position, these different sectors of the Alaskan flora show their closest affinities with taxa in the Canadian arctic, Siberia, and the Rocky Mountains. Furthermore, Alaskan Pleistocene glacial history has left a mosaic pattern of glaciated and unglaciated areas. This complex history makes Alaska an exceptional outdoor laboratory for studying the phyto- and cytogeography of the northern flora.

Several critical studies have already been conducted in the state: 1) Hultén's classical ones of the historic biogeography and taxonomy of the Alaskan flora (Hultén, 1937, 1968), 2) Johnson and Packer's (1968) synthetic study of the flora of Ogotoruk Creek, and 3) Young's (1971) floristic zonation of the widespread circumboreal element of the Alaskan flora. The cytogeographic implications of each of these studies were examined and compared with findings from my own work. From this synthesis a framework for the study of the chromosome evolution of the Alaskan flora presented itself. Is chromosome number, specifically ploidy level, correlated with the geographic affinities of the Alaskan flora? Does each floristic element, the 1) late Tertiary, 2) endemic Beringian, 3) northeast Asian alpine, and 4) Cordilleran alpine, display cytological cohesiveness? If so, are these coincidentally similar patterns the result of common histories and do the shared patterns denote common evolutionary mode?

Full answers to these and other questions of similar magnitude will be a long time in coming, if in fact they are answerable at all.

This thesis presents one attempt to recognize and understand the issues involved and their implications for evolutionary biology.

## MATERIALS AND METHODS

### Geographic Provenance of Cytologic Material

The seven major collection areas for plant material examined during the course of this study are shown in Fig. 1. Area (a) in northeastern Alaska comprises the Yukon River-Prudhoe Bay Haul Road and the Arctic National Wildlife Range. It is bounded on the west by the Haul Road, on the north by the Arctic Ocean, and on the south by the Yukon River. Area (b) includes portions of the western Brooks Range, primarily National Petroleum Reserve-Alaska, while (c) shows the Koyuk area of southeastern Seward Peninsula. Section (d) includes the Shumigan and Sutwik island groups, and (e) presents an area of southcentral Alaska from which a miscellany of taxa was collected, ranging from the Copper River delta in the west through Yakutat and Haines in the east. Areas (f) and (g) are the regions from which the material for the bulk of my chromosome counts was taken, with (f) representing a triangle made between Delta Junction to the north, Tok to the east, and Tangle Lakes to the southwest, and (g) comprising the Forty-Mile River drainage in Alaska and that portion of the Yukon River between Eagle and Kathul Mt. (113 km downriver between Eagle and Circle). Chromosome counts were made for 23 taxa in area (a), 11 in (b), 19 in (c), 9 in (d), 8 in (e), 62 in (f), and 32 taxa in area (g).

### Preparation and Documentation of Chromosome Spreads

Mature seeds collected for each taxon provided the material for subsequent germination and chromosome study in the laboratory. Each

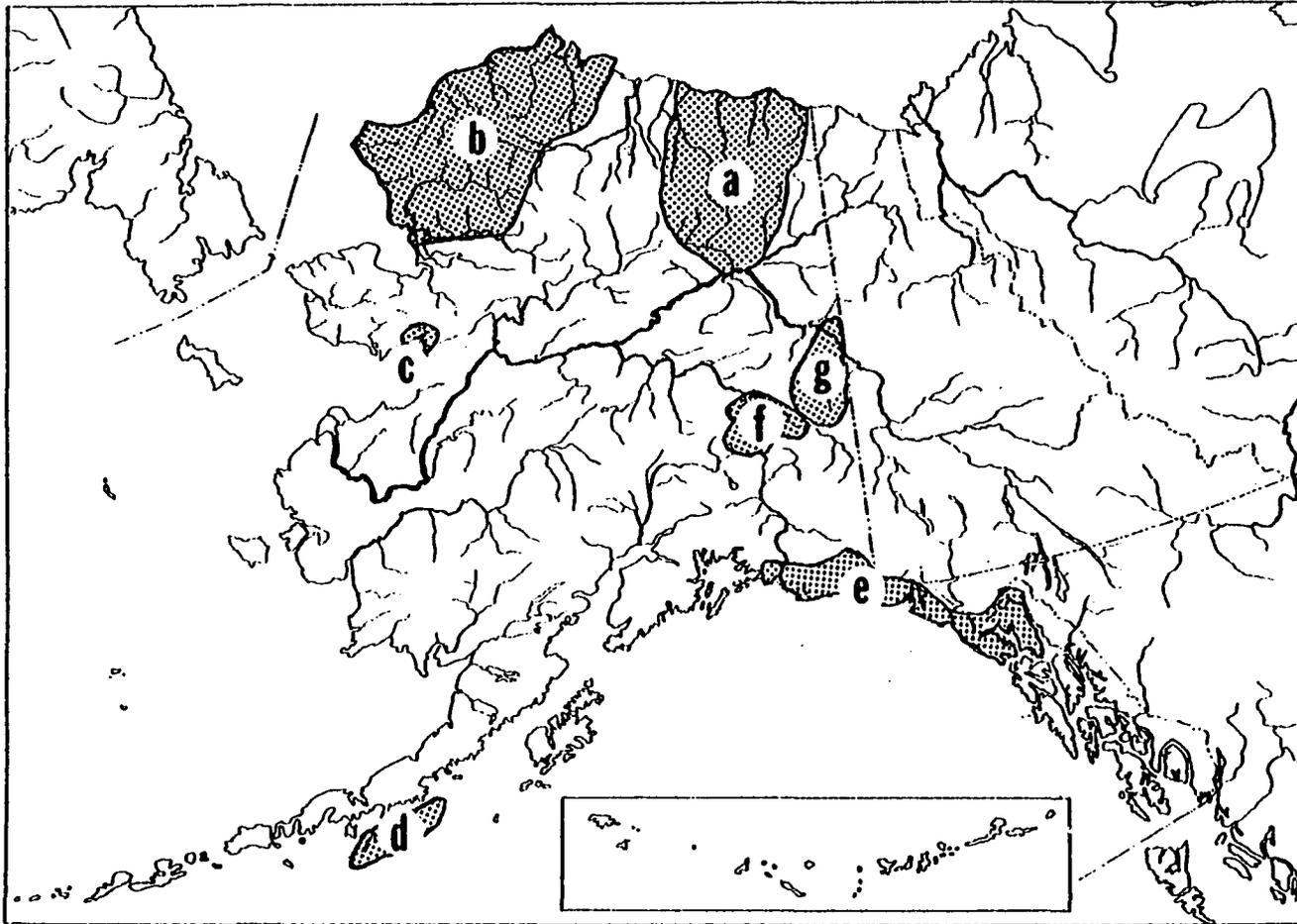


Fig. 1. Seven major collection areas for cytologic material [see text for explanation of areas (a) - (g)].

seed collection was accompanied by a permanent plant voucher specimen. These vouchers are deposited in the University of Alaska Herbarium in Fairbanks, Alaska (ALA).

Chromosome number determinations were made according to methods presented in Darlington and La Cour (1975). Seeds were stratified on moist paper for two to four weeks at 4°C. Seedlings were harvested when their root tips reached 1-3 mm in length. They were first pretreated with 8-hydroxyquinoline for two hours, then fixed in 1:3 acetic alcohol and processed according to the standard Feulgen staining procedure: 1) eight minute hydrolysis in 1N HCl maintained at 60°C, followed by 2) two hours immersion in leucobasic fuchsin, 3) several rinses in sulfur water, and 4) storage at 4°C.

All material was examined within two days of processing. The most darkly stained, mitotically active portion of a root tip or apical meristem was squashed on a slide in a drop of 50% acetic acid. No permanent slides were made but instead the chromosome counts were documented by camera lucida drawings at c. 1500x. A voucher drawing for each count is presented in the Appendix section.

Chromosome counts for the taxa surveyed are discussed under the subheading Annotated Species List in the Results section. Species are arranged phylogenetically by family and alphabetically within families. Nomenclature follows Hultén (1968) or the most recent monographer's treatment, and synonyms under which chromosome counts for any taxon have been published are cited. Specimen voucher information includes collector and collection number(s), place name within the appropriate U.S. Geological Survey 1:250,000 topographic map quadrangle, and

latitude and longitude of the collection site. Other chromosome number reports for each taxon (if any) are presented and the taxonomic and evolutionary implications suggested by these findings are discussed. Nomenclatural changes supported by other plant chromosome workers are mentioned but are not accepted unless indicated as a synonym under the taxon name at the beginning of each entry.

Finally, compilations of the cytotaxonomic and cytogeographic findings of this study are presented under Results: Summary.

RESULTS.

Annotated Species List

Poaceae (Gramineae)

AGROPYRON MACROURUM (Turcz.) Drobov

A. sericeum Hitch.

2n=28: Batten and Dawe 78-416. Eagle Quad.: jct. of Walker and South forks of the Forty-Mile River, 64°06'N, 141°46'W.

This number has been reported three times previously in northwest North America for this amphi-Beringian taxon, including a count made by Hodgson (1964) from Palmer in southcentral Alaska. No chromosome numbers have been reported for it in Siberia.

ELYMUS MOLLIS Trin.

2n=28: Troy S-15. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

This count agrees with all 25 other reports for the taxon throughout its range along the shorelines of Japan, North America, Greenland, and Iceland. It has been counted from three localities in southcentral Alaska by Bowden (1957), Anchorage by Hedberg (1967), Ogotoruk Creek by Johnson and Packer (1968), and Barrow by Packer and McPherson (1974).

FESTUCA ALTAICA Trin.

2n=28: Dawe 703. Mt. Hayes Quad.: Tangle Lakes, 63°02'N, 146°01'W.

Festuca altaica has been counted exclusively at the tetraploid level,  $2n=28$ , in Alaska (Bowden, 1960a; Holmen, 1964; Johnson and Packer, 1968; Knaben, 1968), Canada, and the U.S.S.R.

HIEROCHLOË ALPINA (Sw.) Roem. & Shult. ssp. ALPINA

H. alpina (Sw.) Roem. & Schult.

$2n=56$ : Dawe 699. Mt. Hayes Quad.: Tangle Lakes,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

Hierochloë alpina is a circumpolar, arctic-montane perennial grass with two morphologically distinct subspecies, ssp. alpina and ssp. orthantha (Sørensen) G. Weim., both of which occur in Alaska. The Tangle Lakes population reported here is referable to typical ssp. alpina and agrees with 17 other octoploid reports,  $2n=56$ , for the taxon from Spitzbergen, Norway, Asiatic U.S.S.R., Japan, Alaska, Canada, and Greenland (cf. Weimarck, 1970a, for summary). Subspecies orthantha, with a much more restricted range in south Greenland, adjacent parts of eastern North America, Alaska, and possibly eastern Soviet Union, has been counted six times at  $2n=63$  (Weimarck, 1970a), with deviant counts of  $2n=58$  from New Hampshire (Weimarck, 1970a) and  $2n=56$  from New York (Bowden, 1960b).

Gunnar Weimarck's extensive work with the H. alpina complex (Weimarck, 1967, 1970a, 1970b, 1971a, 1971b, 1973, 1975, 1976) has brought to light several interesting patterns. Morphological, cytological, and chromatographical evidence indicates that ssp. orthantha is an aneuploid derivative of ssp. alpina. Both ssp. alpina and ssp. orthantha show badly disturbed or completely abortive male meiosis,

and the majority of embryo sacs examined in each were unreduced. This led Weimarck to the conclusion that H. alpina is a facultative, but not absolute, apomict (since some viable seed is set in each subspecies), and that the subspecies are separated by the same reproductive barriers that cause reduced sexual reproduction between individuals in various populations.

Observations from two parts of the range of ssp. alpina run counter to this generalization. In northern Scandinavia aneuploids,  $2n=66,72,75,76,77,78$  are the rule, with  $2n=75$  and  $2n=77$  most often counted (Weimarck, 1976). While any individual plant gave only one chromosome number, up to four different chromosome numbers could be found in a population. Chromosome morphology varied within populations as well as numbers, exhibiting a range from continuous variation and no individually recognizable chromosomes, to karyotypes with several marker chromosomes, presumably the result of chromosomal rearrangements.

This demonstrated variability in chromosome number, karyotype, and chromatographic spot phenotypes (cf. Weimarck, 1976) indicates that some mechanism in addition to somatic recombination and segregation is operating to maintain the population structure of ssp. alpina in northern Scandinavia. According to Weimarck (1976), the population structure is probably controlled by competition between reduced and unreduced embryo sacs. Given this, the increase from the normal euploid number,  $2n=56$ , could be accomplished by fertilization between one reduced and one unreduced gamete, with a subsequent loss of chromosomes due to chromosome and cell imbalances.

Plants of the Bering Strait district of Alaska also present anomalies to the usual pattern of variation seen in the H. alpina complex. Populations that fit both subspecies occur there and morphologic intermediates between the two subspecies are found on St. Lawrence Island and at Point Barrow (Weimarck, 1971a). One count of  $2n=56$  has been reported for H. alpina from Barrow (Packer and McPherson, 1974) but this account did not include comments about the morphologic subspecies to which the count applied. Cytologic and complementary data are needed for the morphologically intermediate specimens and for the plants of the mega-Beringian region in general.

HORDEUM BRACHYANTHERUM Nevski

$2n=28$ : Hatch 197. Sutwik I. Quad.: Chowiet I.,  $56^{\circ}02'N$ ,  $156^{\circ}42'W$ .

This report is based on material from the northern limit of the taxon's primary distribution; along the Pacific coastal arc from eastern Asia through the Aleutian Islands and Alaska panhandle south to California, and it agrees with seven previous counts for the taxon.

Hordeum brachyantherum shows a propensity for hybridization with H. jubatum L.,  $2n=28$ . Where the two meet on disturbed soils in southcentral Alaska the hybrid taxon, H. caespitosum Scribn., results (Mitchell and Wilton, 1964; Mitchell, 1967). In this area, however, the hybrid is short lived with markedly disturbed meiosis and low fertility. It regains a measure of fertility in regions where H. brachyantherum is rare or absent (such as the Midwest of the United States) where it may preserve its identity as a separate taxon.

Considerable taxonomic debate has been waged over whether or not these three taxa, H. brachyantherum, H. jubatum, and H. caespitosum, should be reduced to one taxon, H. jubatum (Bowden, 1962; Mitchell and Wilton, 1964). The absence of introgression of morphologic characters from one parental type into the other and the maintenance of these taxa as separate morphologic and breeding units in many areas of sympatry argue against allocation to one genetic unit.

Löve and Löve (1975a) contend that these perennial members of the genus are so different from their annual congeners in morphology and cytogenetics that they should be separated into another genus, Critesion Rafin. Thus, they refer H. brachyantherum to C. jubatum (L.) Nevski ssp. breviaristatum (Bowden) Löve and Löve. However, Baum (1978) maintained Critesion, which he characterized as perennial, and Hordeum, characterized as both annual and perennial, at a congeneric level. In fact he made the demonstrated coupling relationship of these two taxa (OTUs) the test for admissible classifications in his numerical taxonomic evaluation of the tribe Triticeae.

#### Cyperaceae

CAREX OBTUSATA Liljeb1.

2n=52: Batten and Dawe 78-346. Charley R. Quad.: Kathul Mt., 65°21'N,  
141°18'W.

This is the first count for the taxon in Alaska and it agrees with the report from Wrangel Island (Zhukova and Petrovsky, 1971).

ERIOPHORUM SCHEUCHZERI Hoppe

2n=58: Dawe 775. Mt. Hayes Quad.: Mi 31 Denali Hwy, 63°04'N, 146°15'W.

Eriophorum scheuchzeri has been documented to have 2n=58 chromosomes 13 times from locations throughout its circumpolar range, including one report from Ogotoruk Creek on the northwest coast of Alaska (Johnson and Packer, 1968). Mosquin and Hayley (1966) reported 2n=58 ± 2 from Melville Island.

#### Juncaceae

LUZULA ARCUATA (Wahlenb.) Sw. ssp. UNALASCHKENSIS (Buchenau) Hult.

L. beringensis Tolm.

2n=36: Dawe 681. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

In order to gain perspective on the cytology of Luzula arcuata we need to delve into its taxonomy, best described by Hämet-Ahti (1973). She discussed two subspecies of L. arcuata: ssp. unalaschkensis and ssp. arcuata. Hultén (1968) reported both for the flora of Alaska but Hämet-Ahti, after examining Hultén's specimens of ssp. arcuata, concluded that most of the Bering Strait material is referable to ssp. unalaschkensis. The rest, together with the Interior collections, are apparent hybrids between ssp. unalaschkensis and L. confusa Lindeb. Hultén (1968) placed L. beringensis Tolm. from the Anadyr region in synonymy with L. arcuata ssp. arcuata and Hämet-Ahti included beringensis within ssp. unalaschkensis because of its close resemblance to the latter taxon from Kamchatka.

According to Hämet-Ahti's taxonomy, ssp. unalaschkensis is a "southern Beringian radiant", found in the mountains of western North America from northernmost Washington through Alaska, including the Aleutian Islands, and in northeast Asia from the Bering Strait to Kamchatka, the Komandorsky and Kuril islands, Hokkaido, Honshu, northern Korea, and isolated spots in the mountains near the Sea of Okhotsk. There is no zone of overlap between this taxon and ssp. arcuata which occurs in the mountains of Fennoscandia, northernmost European Russia, Spitzbergen, Scotland, the Faeroe Islands, Iceland, and Greenland.

If we accept these biogeographic circumscriptions, and use them to assign published chromosome counts for L. arcuata s.lat. to subspecific rank, an interesting pattern emerges. Luzula arcuata ssp. unalaschkensis has been counted without exception at the hexaploid level,  $2n=36$ , twice from Russia (Sokolovskaya, 1968; Zhukova, 1967) and once from Jasper National Park, Alberta (Packer, 1964). This first Alaskan report, from the south slope of the Alaska Range, is consistent with other reports for the subspecies. In contrast, ssp. arcuata presents a confusing array of hexaploids ( $2n=36$ ), septaploids ( $2n=42$ ), and octoploids ( $2n=48$ ), frequently with plants of different ploidy levels growing side by side, as found by Knaben (1950) with  $2n=36$  and  $2n=42$  plants mixed at Knutshø, central Norway, by Nordenskiöld (1951) with plants of  $2n=36$  and  $2n=42$  in Lapland (see also Nordenskiöld, 1949, 1953), and by Jörgensen, Sørensen, and Westergaard (1958) for meiotic material ranging between  $n=18$  and  $n=24$  from Claverling Island, northeast Greenland.

This cytologic diversity is ignored by Löve and Löve (1975a) who purport one taxon-one chromosome number:  $2n=36$  for L. beringensis

(L. arcuata ssp. unalaschkensis) and  $2n=48$  for L. arcuata (= L. arcuata ssp. arcuata). They omit all divergent counts for L. arcuata (Löve and Löve, 1975a), including counts made from the same populations as those reported (cf. Knaben, 1950; Jörgensen, Sörensen, and Westergaard, 1958). By oversimplifying the cytotaxonomy of L. arcuata in the arctic flora, Löve and Löve (1975a) present a distorted picture of the chromosome data for the taxon which, taken at face value, masks the more potentially interesting facets of its cytogeography and evolution.

#### LUZULA GROENLANDICA Böcher

$2n=24$ : Troy S-44. Norton Bay Quad.: Koyuk,  $64^{\circ}50'N$ ,  $160^{\circ}54'W$ .

According to Löve and Löve (1975a), L. groenlandica is synonymous with L. tundricola auct. and L. kjellmaniana auct., non Miyabe & Kudo. They do not provide documentation to justify their contention, nor does the literature support their interpretation. L. groenlandica is instead most certainly a member of the L. multiflora (Retz.) Lej. complex although its taxonomic rank cannot be clarified until the complex is monographed (Böcher, 1950; Hämet-Ahti and Virrankoski, 1971; Hultén, 1973). The taxon's closest affinities in Alaska are with L. multiflora ssp. frigida (Buch.) Krecz. from which it differs by its distinctly shorter perianth, seeds, and stomata (Böcher, 1950). According to Böcher the two forms, L. multiflora ssp. frigida and L. groenlandica, are well separated ecologically and edaphic conditions probably control their distribution patterns to a great extent. The former taxon, studied by Böcher (1950) in Scandinavia and northwest Newfoundland, is widely

distributed in oligotrophic mountain habitats while the latter, in Greenland, occurs on neutral to basic, nutrient rich, moist soils of valley floors up to 350 m altitude.

L. groenlandica is the only tetraploid ( $2n=24$ ) member of the L. multiflora complex and it has been reported at this number six times. A seventh count of  $2n=24$ , made by Zhukova (1967) from Wrangel Island, is cited as L. multiflora ssp. kjellmaniana (Miyabe & Kudo) Tolm. and, according to Hämet-Ahti and Virrankoski (1971), "may relate to L. groenlandica or to some other member of the L. multiflora complex". A count of an aberrant number,  $2n=36$ , is attributed to L. groenlandica by Lambert and Giesi (1967) and it may belong to this taxon.

LUZULA MULTIFLORA (Retz.) Lej. ssp. FRIGIDA (Buchenau) Krecz.

L. frigida (Buch.) Sam., L. multiflora ssp. multiflora var. frigida (Buch.) Sam.

$2n=36$ : Dawe 737. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

Luzula multiflora ssp. frigida presents a model of a taxon with variable phenotype but constant chromosome number. Böcher (1950) stated that while L. multiflora ssp. multiflora and ssp. frigida show no clear morphological distinctions and share chromosome number (all populations are hexaploid,  $2n=36$ ) their very different ecological and distributional requirements warrant treatment of frigida as a separate taxon. L. multiflora ssp. frigida has been reported in ten accounts from across its circumpolar range, including three alpine stations in Alaska (Livengood Quad.: Cache Mt. in Knaben, 1968; Circle

Quad.: Twelvemile Summit and Mt. Hayes Quad.: Fielding Lake in Hämet-Ahti and Virrankoski, 1971).

#### Liliaceae

ALLIUM SCHOENOPRASUM L. ssp. SIBIRICUM (L.) Hartm.

2n=16: Batten and Dawe 78-414. Eagle Quad.: jct. of the Walker and South forks of the Forty-Mile River, 64°06'N, 141°46'W.  
Troy S-11. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

This number is reported from Ogotoruk Creek (Johnson and Packer, 1968), and 37 citations document diploids (2n=16) for circumpolar A. schoenoprasum. Five of these references (Levan, 1931, 1935, 1936; Turesson, 1931; Rohweder, 1937) also record tetraploids (2n=32), and one (Levan, 1936) reports a triploid (2n=24).

ZYGADENUS ELEGANS Pursh

2n=32: Dawe GR 2. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

This North American endemic has been counted at the same tetraploid level five times before, including a count made by Johnson and Packer (1968) from Ogotoruk Creek.

#### Iridaceae

IRIS SETOSA Pall. ssp. SETOSA

2n=38: Troy S-10. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

Iris is a genus marked by several aneuploid-euploid cycles both

between and within taxa (cf. Federov, 1969, for summary table). Given this characteristic, the chromosome numbers of Iris setosa may represent a hypoploid reduction series from  $x=20$ , with six counts from North America at  $2n=38$  [including a count made by Hedberg (1967) on material from Anchorage], and two counts from Siberia,  $2n=36$  (Sokolovskaya, 1960) and  $2n=34-36$  (Sokolovskaya, 1963). The mechanism of chromosome loss has not been postulated, to my knowledge.

#### Betulaceae

BETULA GLANDULOSA Michx.

$2n=28$ : Dawe 670. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

This count, the first for Betula glandulosa in Alaska, agrees with five other reports for the taxon in North America and Greenland. The systematic relationship between B. glandulosa, closely related Alaskan B. nana L. ssp. exilis (Sukatch.) Hult.,  $2n=28$  (Löve and Löve, 1966), and their hybrids, is not clear, and chromosome number does not appear to be a discriminating character in this complex.

#### Polygonaceae

BISTORTA VIVIPARA (L.) S. F. Gray

Polygonum viviparum L.

$2n=c. 100$  ( $2n=96,106$  on same plant): Dawe 728. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

Bistorta vivipara is a distinctive and widespread arctic-alpine circumpolar taxon. The viviparous bulblets along its flower spike

release B. vivipara from normal meiotic constraints such as homologous chromosome pairing, bivalency, and equal segregation. The taxon therefore shows a wide range of high ploidy levels (based on  $x=11$ ) with no chromosome counts at less than the hexaploid,  $2n=66$ , level and a maintenance of odd-ploidy levels,  $2n=7x=77$  (with one divergent count of  $2n=80$ ) in Iceland,  $2n=9x=99$  in Greenland, the Dolomite Mts. of Italy, and Tatra Mts. of Poland (Engell, 1972). Material from eastern arctic Yakutia (U.S.S.R.) was counted at  $2n=80$  by Zhukova, Korobkov, and Tikhonova (1977). The count reported here, which represents the mean ploidy level for the taxon, has been recorded twelve other times, including counts based on material from two locations in Alaska (Johnson and Packer, 1968; Packer and McPherson, 1974). Higher ploidy levels,  $2n=120$  (Löve and Löve, 1966; Löve and Ritchie, 1966) and  $2n=132$  (with one count at  $2n=130$ ) (Welslo, 1967), have been found in North America and the Tatra Mts., respectively. Although the taxon shows considerable morphologic amplitude over its large distribution range, no correlation between morphotype and cytotype is apparent.

OXYRIA DIGYNA (L.) Hill

$2n=14$ : Dawe 689. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

This common, arctic-alpine plant has been counted at the same diploid number,  $2n=14$ , 40 times throughout its circumpolar range, including counts made on material from Ogotoruk Creek (Johnson and Packer, 1968) and Barrow (Packer and McPherson, 1974). Only three deviant counts, all made on specimens from the U.S.S.R., have ever been

recorded:  $2n=14,28$  (Menshikova, 1964) and  $2n=42$  (Belaeva and Siplivinsky, 1975; Sokolovskaya and Strelkova, 1948). While the taxon's circumpolar distribution (with great latitudinal span) and stable morphology establish its antiquity, its monotypic position within the Polygonaceae and uniform diploid chromosome number make it an excellent candidate for Favarger's oldest relative age class, "ancient diploid" (Favarger, 1961).

POLYGONUM ALASKANUM (Small) Wight

$2n=20$ : Dawe 778. Mt. Hayes Quad.: Mi 21 Denali Hwy.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

The diploid number,  $2n=20$ , has been counted twice before, including a count made by Zhukova (in Yurtsev et al., 1975), which extends the range of the species, from western North America (Hult en, 1968) to the Chukchi Peninsula across the Bering Strait from Seward Peninsula.

RUMEX ARCTICUS Trautv.

$2n=40$ : Dawe 140. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$  (gametic material:  $n=20$ ).

Dawe 674. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

$2n=c.80$  Troy S-39. Norton Bay Quad.: Koyuk,  $64^{\circ}50'N$ ,  $160^{\circ}54'W$ .

This arctic-alpine species, widespread in northwestern North America and arctic U.S.S.R., presents a puzzling array of cytotypes across its range. When Mulligan and Frankton (1972) reviewed the chromosome races of Rumex arcticus, the situation appeared much more

simple than it does today. All North American counts except one ( $2n=c.170$ ) made at Ogotoruk Creek on Alaska's northwest coast, were tetraploid,  $2n=40$ , while all Siberian counts were dodecaploid,  $2n=120$ , or higher (Mulligan and Frankton, 1972). The two cytotypes differed appreciably: the tetraploids were larger than the dodecaploids, with more congested inflorescences, and smaller pollen grains. Had this comprised the total range of variation for the taxon, it would have seemed a clear cut case of two cytotypes correlated with different morphologies and geographies. Although its chromosome number(s) was not then known, another taxon recognized in northeastern Siberia, Rumex kamtschadalus Kom., was presumed to be tetraploid on the basis of its morphology which is similar to tetraploid North American R. arcticus, including large stature and compacted inflorescence. Most authors considered these synonyms (Mulligan and Frankton, 1972), but Löve and Löve (1975a), presumably on the basis of determining a count of  $2n=40$  from Kamchatka (Löve and Löve, 1975a) to which they assigned the name R. kamtschadalus, have treated all  $2n=40$  reports as R. kamtschadalus, and reserved the name R. arcticus Trautv., s.str., for all counts of  $2n=120$ .

This segregation of cytotypes and named taxa is an oversimplification of the complexities of the problem, as shown by Sokolovskaya (1968) who counted R. arcticus var. kamtschadalus (Kom) Rech. f. from Kamchatka at  $2n=c.200$ , not  $2n=40$ . Moreover, an herbarium specimen, identified as R. kamtschadalus and housed in Leningrad, showed flowers with large pollen grains typical of dodecaploid R. arcticus (Mulligan and Frankton, 1972).

Additional chromosome counts, made after Mulligan and Frankton's review (1972), complicate matters more (Fig. 2). Octoploid Rumex

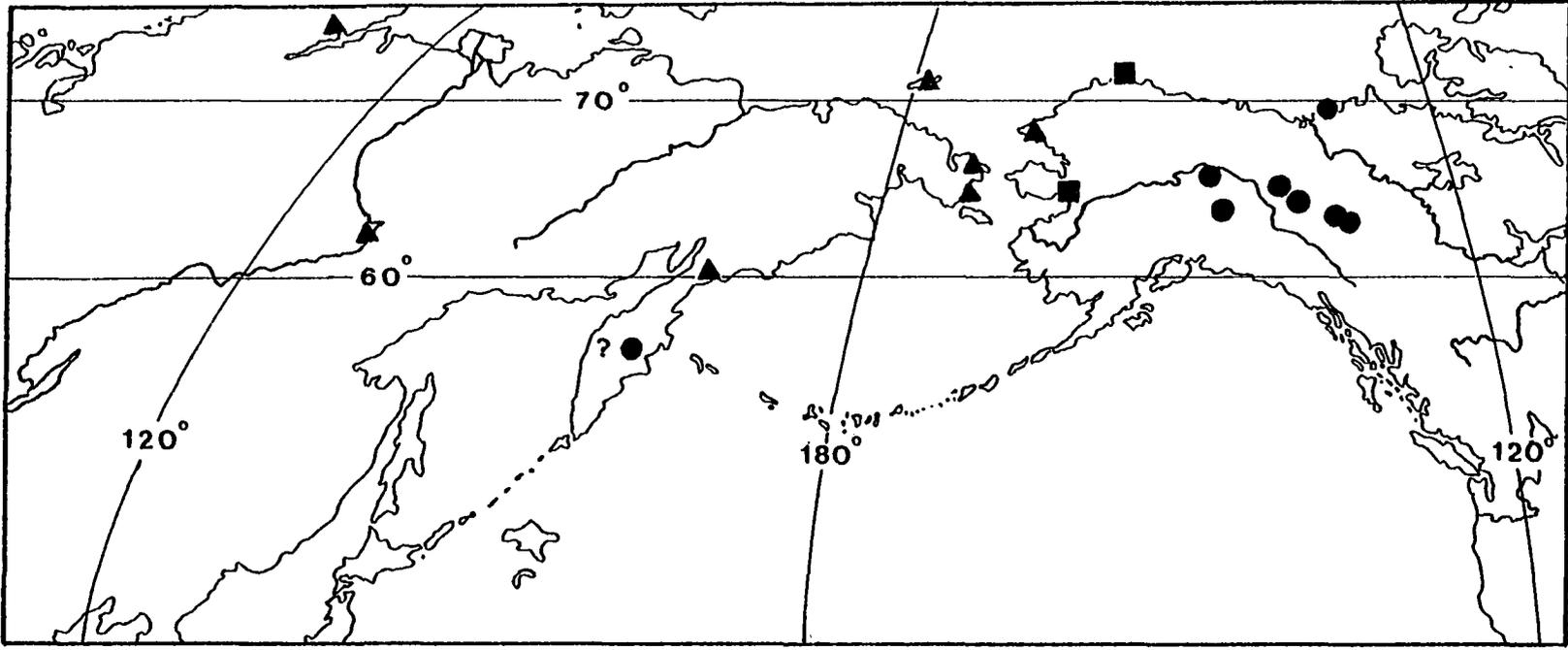


Fig. 2. Distribution of chromosome numbers in Rumex arcticus Trautv. - Rumex kantschadalis Komarov. 2n=40 (●), 2n=80 (■), 2n=120,150,170,200 (▲).

arcticus,  $2n=80$ , has been counted from Barrow by Packer and McPherson (1974) and by me from Koyuk on southeasternmost Seward Peninsula ( $2n=c.80$ ). R. kamtschadalus has been counted at  $2n=40$  from Kamchatka (Löve and Löve, 1975a), extending the range of tetraploids from North America into eastern Siberia. There must be clear segregation of morphotype and cytotype if both names, R. kamtschadalus and R. arcticus, are to be used. Today, the likelihood of recognizing the chromosome races of Rumex arcticus taxonomically is more remote than ever, and we need much additional cytologic and morphologic information for the taxon throughout its range.

RUMEX SIBIRICUS Hult.

$2n=20$ : Batten and Dawe 78-263. Charley R. Quad.: upstream of Montauk Bluff,  $65^{\circ}06'N$ ,  $141^{\circ}29'W$ .

This amphi-Beringian species has been counted twice before at the diploid level ( $2n=20$ ). One of these counts, made by Askeell Löve (1967), is from Alaska, but specific locality data are not available.

Portulacaceae

CLAYTONIA ARCTICA Adams

$2n=c.40(42)$ : Dawe and Lipkin 77-552. Howard Pass Quad.: Feniak L.,  $68^{\circ}15'N$ ,  $158^{\circ}20'W$ .

This is the first report of an octoploid for this rare amphi-Beringian taxon, which has been counted twice before at the diploid level,

2n=10, from the Ogilvie Mts., Yukon Territory (Mulligan and Porsild, 1969) and northeast Siberia (Zhukova, 1966).

The Feniak Lake population initially described by Young (1974) as a possibly undescribed Claytonia, shows clear morphologic affinities with C. arctica sensu Porsild and C. scammaniana, and is notable for several reasons besides its unusual chromosome number. Feniak Lake is the sixth location where the taxon has been collected in the state (inspection of ALA specimens), disjunct 160 miles to the west from the next collection site at Anaktuvuk Pass (Porsild, 1975). While the Anaktuvuk Pass population has white flowers typical of the taxon (Hultén, 1968), the Feniak Lake plants have deep purple-red flowers, as do plants collected east of Galbraith Lake, 60 miles northeast of Anaktuvuk Pass. Clearly, the taxon is too poorly understood to state the normal range of color variation and its causes (genetic vs. environmental).

The Feniak Lake plants may differ from typical C. arctica because of the unusual microhabitat conditions under which they are growing (which approach those of rockslide C. scammaniana). Hultén (1968) described typical habitat for the taxon as alpine tundra, and most specimens at ALA were collected from moist tundra sites. The Feniak Lake plants, however, were growing in shattered serpentine bedrock and scree, as well as alluvial outwash, with little organic soil development, and few or no species associates. In this otherwise "biological desert" microhabitat, the Feniak claytonias were abundant and robust, caespitose, consistently purple flowered, with thick, deeply reddish tinged leaves. These last two characteristics may be influenced by the heavy metal ion content of the serpentine substrate.

Since this report represents a new ploidy level for the taxon, and especially because it was determined on only one mitotic spread from one seedling root tip, it should be viewed with caution unless confirmation comes from additional counts made on plants from the Feniak Lake population. All preliminary information; morphologic, cytologic, ecologic, points to the Feniak Lake population as an unusual and important one, and further study of it is needed. Additionally, more information for the taxon throughout Alaska must be gathered.

CLAYTONIA SIBIRICA L.

Montia sibirica (L.) Howell

2n=12: Batten and Murphy 77-401. Cordova Quad.: Softuk Lagoon, 60°13'N, 144°40'W.

Heffner s.n., July 13, 1978. Seward Quad.: Eagle Bay, 60°54'N, 147°10'W.

Hatch 300. Sutwik I. Quad.: Chowiet I., 56°02'N, 156°42'W.

Moe 33. Stepovak Bay Quad.: Big Koniuji I., 55°06'N, 159°33'W.

Diploid (2n=12) members of Claytonia sibirica have previously been counted from Medny Island (the eastern Komandorsky Island, located east of Kamchatka Peninsula) and Queen Charlotte City, Queen Charlotte Island (tetraploids were counted one mile away from the diploid material) (Sokolovskaya, 1968; Taylor and Mulligan, 1968, respectively). The four diploid populations reported here fill a gap in our knowledge of the species' cytology in Alaska. The only other Alaskan count, a tetraploid, 2n=24, comes from Kuiu Island in the Alexander Archipelago, southeastern Alaska.

In his synopsis of relationships between members of the subfamily Montioideae (Portulacaceae), Swanson (1966) proposed that the distribution and habitat requirements of Claytonia, together with morphologic patterns, suggests derivation of lowland annuals (restricted to the United States south of Canada) from montane perennials. Moreover, Swanson (1966) stated that the evidence points to the unglaciated refugia of Alaska and Kamchatka as the centers of distribution for most primitive members of the subfamily. The unusual distribution of Claytonia sibirica, from Kamchatka Peninsula through the Aleutian Islands, coastal Alaska, British Columbia, and south through California (Fig. 3), when superimposed on its cytogeography (diploids in the north, tetraploids in the central, and tetra-, hexa-, and octoploids in the southern part of its range), is consistent with Swanson's hypothesis of north to south migration, speciation, and evolution within Montioideae. These characteristics, together with evidence from chromosome morphologies (Lewis and Suda, 1968), and the behavior of Claytonia sibirica as a facultative-annual, suggest it is the intermediate link between primitive and advanced members of the subfamily (Swanson, 1966). The morphology, cytology, and biogeography of Claytonia sibirica provide a clear circumscription of the northern and southern complexes.

#### Caryophyllaceae

##### CERASTIUM MAXIMUM L.

2n=28: Batten and Dawe 78-350. Charley R. Quad.: Kathul Mt., 65<sup>0</sup>21'N,  
142<sup>0</sup>20'W.

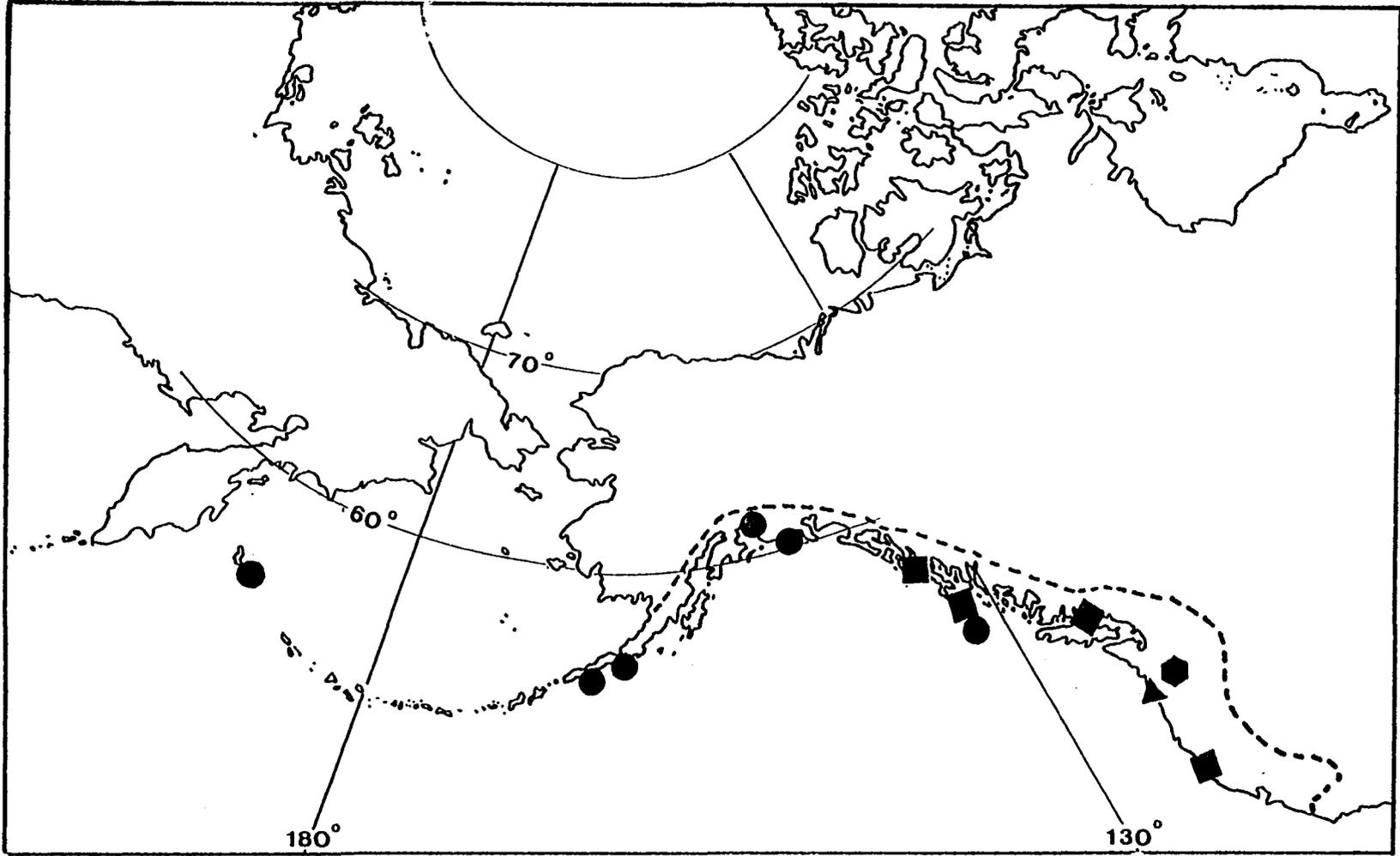


Fig. 3. Distribution of chromosome numbers in *Claytonia sibirica* L. (dashed line = limits of its geographic distribution). 2n=12 (●), 2n=24 (■), 2n=36 (▲), 2n=48 (⬡).

This count, first for the taxon in Alaska, agrees with nine previous counts from the Canadian arctic and Siberia. Löve and Löve (1975a) proposed to treat this as Dichodon maximum (L.) Löve and Löve, segregating as members of Dichodon all sections of Cerastium "characterized by the same rare chromosome number  $x=19$ , as contrasted to  $x=9$  of Cerastium proper" (Löve and Löve, 1975a).

SAGINA MAXIMA A. Gray ssp. CRASSICAULIS (Wats.) Crow

S. crassicaulis S. Wats.

$2n=66$ : Batten and Murphy 77-168. Yakutat Quad.: between Lost and Situk river mouths,  $59^{\circ}27'N$ ,  $139^{\circ}35'W$ .

This hexaploid count, based on  $x=11$ , is the first for the taxon in Alaska, and agrees with a count made on material of S. maxima from the Queen Charlotte Islands (Taylor and Mulligan, 1968). However, no subspecies designation was given the Queen Charlotte specimen, and it could apply to either ssp. crassicaulis or ssp. maxima, since both occur on the islands and introgression between them is common there (Crow, 1978). Crow's meiotic count,  $2n=46$ , for material from the type locality of ssp. crassicaulis is not surprising, because aneuploidy is the rule, not the exception, in Sagina (Crow, 1978). One other count,  $2n=44$ , based on material from Hokkaido, Japan, was attributed to ssp. crassicaulis by Taylor (1967). Crow (1978), however, examined the chromosome voucher and annotated it as a glabrous form of S. maxima, S. maxima ssp. maxima. Neither Crow (letter dated 4 January 1979 from Garrett E. Crow, Curator of the Hodgdon Herbarium, University of New Hampshire, Durham, New

Hampshire) nor Mizushima (1960) feel that ssp. crassicaulis occurs in Japan. Instead, its distribution is restricted to northwestern North America.

SILENE ACAULIS L. ssp. ACAULIS

S. acaulis ssp. arctica Löve and Löve

2n=24: Dawe 693. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

The same number has been reported for the taxon 32 times across its nearly circumpolar range.

SILENE REPENS Patrin. ssp. PURPURATA (Greene) Hitchc. & Maguire

2n=24: Batten and Dawe 78-303. Charley R. Quad.: Kathul Mt., 65°20'N, 142°18'W.

This is the first count for the Alaska-Yukon S. repens ssp. purpurata. Both diploids (2n=24) and tetraploids (2n=48) have been found in the Eurasiatic S. repens ssp. typica Hitchc. & Maguire (Löve and Löve, 1975b; Sokolovskaya, 1963; Zhukova and Petrovsky, 1972) and western North American S. repens ssp. australis Maguire & Hitchc. (Sokolovskaya, 1963). It is important to know whether or not tetraploids also exist in ssp. purpurata.

WILHELMSIA PHYSODES (Fisch.) McNeill

Merckia physodes (Fisch.) Fisch.

2n=66: Batten and Dawe 78-389. Eagle Quad.: S Fork Forty-Mile R., 64°04'N, 141°50'W.

Packer and McPherson (1974) reported  $2n=50-60$  for Wilhelmsia physodes from Meade River, while Johnson and Packer (1968) counted  $2n=100-110$  for the Ogotoruk Creek population 300 km (260 mi) to the southwest. Material from northeast Siberia has been counted at  $2n=66$  (Zhukova, 1966),  $2n=68$  (Zhukova, Korobkov, and Tikhonova, 1977), and  $2n=72$  (Zhukova, 1966).

#### Ranunculaceae

AQUILEGIA BREVISTYLA Hook.

$2n=16$ : Batten and Dawe 78-365. Eagle Quad.: Eagle Bluff,  $64^{\circ}48'N$ ,  $141^{\circ}12'W$ .

Surprisingly, this appears to be the first chromosome count made for this common North American endemic. It represents one of only seven aneuploid counts found to date in the genus Aquilegia, for which  $2n=14$  has been determined in 56 out of 58 taxa (cf. Federov, 1969).

PULSATILLA PATENS (L.) Mill. ssp. MULTIFIDA (Pritzel) Zamels

$2n=16$ : Batten and Dawe 78-175. Tanacross Quad.: W Fork Dennison Fork campground,  $63^{\circ}54'N$ ,  $142^{\circ}24'W$ .

This taxon was also counted at the same number from Umiat Mt. (Bormann and Beatty, 1955). It appears to be uniformly diploid throughout its range in Siberia and North America, except for one report,  $2n=16,32$  (Baumberger, 1970).

## Papaveraceae

PAPAVER ALBOROSEUM Hult.

2n=28: Welsh and Moore 8146. Seward Quad.: Portage Glacier, 60°46'N,  
148°48'W.

The same number was reported from Kamchatka (Knaben, 1959a, 1959b).  
Papaver alboroseum var. elongatum Hult. was recorded from Japan at 2n=42  
(Kawatani and Ohno, 1965).

PAPAVER LAPPONICUM (Tolm.) Nordh.

P. radicatum Rottb. ssp. lapponicum Tolm.

2n=56: Dawe 476. Mi 77 Denali Hwy (Susitna R. Lodge), 63°05'N, 147°29'W.

This first Alaskan count for P. lapponicum extends the range of octoploids for the circumpolar species complex from northern Scandinavia, Greenland, and Canada to interior Alaska. Tetraploids, hexaploids, and octoploids all occur in northeastern Siberia (Sokolovskaya and Strelkova, 1960; Zhukova, 1968; Zhukova, Korobkov, and Tikhonova, 1977; Zhukova and Petrovsky, 1971, 1975, 1976).

PAPAVER NUDICAULE L.

2n=28: Batten and Dawe 78-382. Eagle Quad.: Mi 72.2 Taylor Hwy, vic.  
Chicken, 64°04'N, 141°50'W.

This is the first population of Papaver nudicaule examined cytologically in Alaska, and it presents both an unusual cytotype and morphotype for the taxon. The same chromosome number has been found in Scandinavia

(Horn, 1938), Kashmir (Koul and Gohil, 1973), the Baikal region in the U.S.S.R. (Belaeva and Siplivinsky, 1975), and, reported under ssp. tamirensis Henelt, in Mongolia (Henelt, 1973). Apart from these counts, natural populations are uniformly diploid ( $2n=14$ ). In addition to this cytologic anomaly, a population of the Alaskan taxon found at Kathul Mountain on the Yukon River differs from P. nudicaule in pubescence and flower color. With the exception of one small stand of all white flowered plants upstream of Kathul Mountain, the plants of this morphotype along the upper Yukon and Forty-Mile rivers were all yellow, not multicolored as is usual. Hult n (1944) noted a fragmentary white flowered specimen collected on the Yukon River between Rampart and Tanana (Palmer 54), which he considered either a white-flowered variety of P. nudicaule or a new species. A preliminary review of herbarium specimens at ALA supports the hypothesis that there is a Forty-Mile morphotype markedly different from that found to the southwest along the Richardson, Denali, and Parks highways. The very real possibility exists that we are dealing with an undescribed Papaver in Alaska, related to, but distinct from the introduced P. nudicaule. Further collections and study of the Forty-Mile populations could prove only fruitful in understanding this problem.

#### Brassicaceae (Cruciferae)

ALYSSUM AMERICANUM Greene

A. biovulatum N. Busch

$2n=32$ : Batten and Dawe 78-392. Eagle Quad.: Chicken, S Fork Forty-Mile R.,  $64^{\circ}05'N$ ,  $141^{\circ}46'W$ .

This first count for Alyssum americanum in North America agrees with the count made by Zhukova and Petrovsky (1975) on material from western Chukotka Peninsula.

ARABIS HOLBOELLII Hornem.

2n=14: Batten and Dawe 78-192. Eagle Quad.: Eagle Bluff, 64°48'N,  
141°13'W.

This number has been reported once before from Alaska (Böcher and Larsen, 1950) but accurate locality data are not available. Böcher and Larsen (1950) also reported 2n=21,28,42 from west Greenland. The taxon's reproductive behavior ranges from that of a completely sexual plant in Alaska, to a facultative apomict in Canada and Greenland, where triploids and B-chromosomes are commonly seen (Böcher, 1947, 1951, 1954, 1960; Mulligan, 1964; Packer, 1964; Rollins, 1941; Rollins and Ruedenberg, 1971). This complex has the most extensive distribution of any North American Arabis species, and is difficult to classify because of its extremely variable morphology (Mulligan, 1964).

ARABIS LYRATA L. ssp. KAMCHATICA (Fisch.) Hult.

2n=16: Dawe s.n., August 29, 1976. Mt. Hayes Quad.: Paxson, 63°02'N,  
145°29'W.

This North American taxon is represented in Alaska by both diploids, 2n=16, and tetraploids, 2n=32 (Johnson and Packer, 1968; Knaben, 1968; Rollins, 1966). Diploids have been found in Saskatchewan (Mulligan,

1964) but all other counts from Canada are tetraploid (Mulligan, 1964; Mulligan and Porsild, 1969, 1970; Taylor and Mulligan, 1968). No chromosome counts have been reported for the taxon from Siberia. Eastern North American ssp. lyrata has been counted from Wisconsin (Smith, 1938) and Connecticut (Rollins, 1941) at  $2n=16$ .

BARBAREA ORTHOCERAS Ledeb.

$2n=16$ : Hatch 79. Sutwik I. Quad.: Chowiet I.,  $63^{\circ}04'N$ ,  $147^{\circ}28'W$ .

This species is diploid throughout its range. One of the counts was made on a plant from Summit Lake on the north side of the Alaska Range (Knaben, 1968).

BRAYA BARTLETTIANA Jordal

$2n=56$ : Batten 75-503. Fort Yukon Quad.: Sheenjek R.,  $68^{\circ}41'N$ ,  $143^{\circ}35'W$ .

This is the first count reported for this Beringian taxon and comes from the easternmost population known for it.

BRAYA PILOSA Hook.

$2n=28$ : Young 7523. Utukok Quad.: Archimedes Ridge,  $69^{\circ}10'N$ ,  $161^{\circ}16'W$ .

$2n=56$ : Murray 3383. Beechey Point Quad.: Prudhoe Bay,  $70^{\circ}22'N$ ,  $148^{\circ}22'W$ .

$2n=64$ : Walker 546. Beechey Point Quad.: Prudhoe Bay,  $70^{\circ}22'N$ ,  $148^{\circ}22'W$ .

These three counts are the first for Braya pilosa in the state and possibly do not represent all the chromosome numbers to be found in the taxon in Alaska. The three different numbers are remarkable because

1) the populations they come from are relatively close together, 2) they indicate a high polyploid series for the taxon, and 3) they present evidence that B. pilosa is dibasic:  $x=7$  ( $2n=4x=28$  and  $2n=8x=56$ ) and  $x=8$  ( $2n=8x=64$ ). A parallel situation is found in the Braya humilis (C. A. Mey.) Robins. complex with  $2n=40,42,56,64,70$  (cf. Böcher, 1956). The situation in B. pilosa, however, is especially notable because dibasic specimens ( $2n=56$  and  $2n=64$ ) have been found in the same population (Prudhoe Bay). Obviously, these findings are only preliminary, and they must be substantiated by a more intensive cytologic investigation before too much weight is placed on them. If the alleged difference in basic chromosome number is supported by this further work, then a taxonomic review of Braya pilosa will be in order, because, as Böcher stated in reference to B. humilis (Böcher, 1956, p. 6):

Whereas a polyploid series within a species is not always accompanied by appreciable morphological differences which justify a division into independent species, two different series of numbers will no doubt rarely occur without it proving to be justifiable to subdivide the species.

Apparently, Braya pilosa is Beringian in distribution, with its westernmost boundary near the Taimyr Peninsula in arctic U.S.S.R. and its easternmost limit in the Canadian archipelago north of Hudson Bay. Material both from Wrangel Island and eastern Siberia has been reported to have  $2n=28$  chromosomes (Zhukova and Petrovsky, 1972; Zhukova, Petrovsky, and Plieva, 1973, respectively), but at this time it is not known if North American and Soviet taxonomists are addressing the same taxon.

## BRAYA PURPURASCENS (R. Br.) Bunge

2n=56: Murray 3518. Flaxman I. Quad.: delta of Canning R., 70°04'N,  
145°30'W.

Dawe and Lipkin 77-845. Teshekpuk Quad.: Inigok R. drill site,  
70°00'N, 153°05'W.

Octoploids, 2n=56, have been reported eleven times for Braya purpurascens throughout its circumpolar range including Alaskan counts from Donnelly, north of the Alaska Range (Mulligan, 1965) and Ogotoruk Creek on the coast of the Chukchi Sea (Johnson and Packer, 1968). The only divergent count, 2n=64, attributed to the unpublished findings of Sørensen and Westergaard by Löve and Löve (1948), was later retracted by Jørgensen, Sørensen, and Westergaard (1958) who reexamined the same material from Claverling Island, NE Greenland.

## CARDAMINE BELLIDIFOLIA L.

2n=16: Murray and Johnson 6242. Philip Smith Mts. Quad.: Atigun Pass,  
68°08'N, 149°50'W.

The same number has been reported 18 times from locations throughout the circumpolar distribution of this taxon, including counts in Alaska from Ogotoruk Creek (Johnson and Packer, 1968) and Barrow (Packer and McPherson, 1974).

## COCHLEARIA ARCTICA Schlecht.

C. officinalis L. ssp. arctica (Schlecht.) Hult.

2n=14: Schamel s.n., 1975. Beechey Point Quad.: Prudhoe Bay, 70°22'N,  
148°22'W.

Cochlearia arctica, the most widespread member of the taxonomically complicated, circumpolar C. officinalis complex, is uniformly diploid across Siberia, Alaska (Packer and McPherson, 1974), Canada, Greenland, and Scandinavia, whereas C. officinalis has been counted four times in northern Europe to have  $2n=24$  (+ 0-4 B-) chromosomes, and once to have  $2n=36$  chromosomes.

DRABA ADAMSII Ledeb.

D. micropetala auct., D. oblongata auct.

$2n=48$ : Lipkin 78-13. Barrow Quad.: c. 5 km W of Elson Lagoon,  $71^{\circ}14'N$ ,  $156^{\circ}17'W$ .

Draba adamsii, found in Spitzbergen, the northern parts of Alaska and Greenland, and on high arctic islands in the U.S.S.R. and Canadian Archipelago, has been counted at  $2n=32$  from Barrow (Packer and McPherson, 1974) and from northeast Siberia (Zhukova, Petrovsky, and Plieva, 1973). Intraspecific polyploidy, based on  $x=8$ , is not uncommon in Draba (cf. Federov, 1969), and if, as appears to be the case, both tetraploids ( $2n=4x=32$ ) and hexaploids ( $2n=6x=48$ ) occur in the vicinity of Barrow, it would be important to determine chromosome numbers for the taxon from other parts of its range.

DRABA LACTEA Adams

$2n=16$ : Batten, Dawe, and Murray 78-67. Mt. Hayes Quad.: Mi 222 Richardson Hwy.,  $63^{\circ}28'N$ ,  $145^{\circ}49'W$ .

This is the first diploid report for Draba lactea, which is

hexaploid,  $2n=48$ , at Barrow (Packer and McPherson, 1974), Gaedtuk (St. Lawrence Island) and the upper White River valley (Mulligan, 1974). A tetraploid population ( $2n=32$ ) has been reported from Siberia (Zhukova, Petrovsky, and Plieva, 1973), and hexaploids have been reported eight times from localities throughout the Soviet Union, Canada, and Greenland.

DRABA MURRAYI Mulligan in sched.

$2n=48$ : Batten and Dawe 78-291. Charley R. Quad.: Kathul Mt.,  $65^{\circ}20'N$ ,  $142^{\circ}15'W$ .

This is the first count for this previously undescribed taxon. Few taxa, i.e. six out of 53 in Draba, have been counted at  $2n=48$  (Löve and Löve, 1975a; Moore, 1973). These include D. lactea Adams, D. cinerea Adams, D. norvegica Gunn., D. arctogena E. Ekman, D. juvenalis (Pohl.) Kom., and D. pseudopilosa Pohl. A seventh taxon, D. adamsii Ledeb., is reported at this number for the first time in this report.

DRABA PALANDERIANA Kjellman

$2n=16$ : Dawe and Lipkin 77-134. Misheguk Mt. Quad.: Meat Mt.,  $68^{\circ}56'N$ ,  $160^{\circ}45'W$ .

This plant is the subject of a taxonomic dispute which has not yet been resolved. G. A. Mulligan has counted the chromosomes of the taxon from Lake Peters at  $2n=16$  (letter from G. A. Mulligan, Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Canada to D. F. Murray, University of Alaska, Fairbanks, Alaska). He maintained that Draba palanderiana, a species of the mountains

of Alaska, Yukon Territory, and the Mackenzie District, is distinct from Asian D. caesia Adams. The Soviets believe that the two taxa are synonymous, and call their taxon, which has been counted twice from northeastern Siberia at  $2n=32$  (Zhukova, 1968; Zhukova and Tikhonova, 1971), D. palanderiana. I am uncertain about the morphologic units to which the Soviet chromosome counts apply.

ERYSIMUM ANGUSTATUM Rydb.

$2n=36$ : Batten and Dawe 78-220. Eagle Quad.: Eagle Bluff,  $64^{\circ}48'N$ ,  
 $141^{\circ}13'W$ .

This, the first chromosome count for E. angustatum, fits within the pattern of aneuploid base numbers shown by members of Erysimum, where  $x=6,7,8,9$ . It is not possible at this time to state whether the plant whose chromosomes I counted is a tetraploid of base number  $x=9$  or a hexaploid of  $x=6$ . Attention to chromosome morphologies, pairing at meiosis, and differential chromosome banding techniques could solve this problem, which has bearing on the origin and ancestry of this Alaska-Yukon endemic.

HALIMOLOBUS MOLLIS (Hook.) Rollins

$2n=16$ : Batten and Dawe 78-384. Eagle Quad.: Mi 72.2 Taylor Hwy., vic. Chicken,  $64^{\circ}05'N$ ,  $141^{\circ}16'W$ .

This is the first count for H. mollis from Alaska, and agrees with reports from the Yukon Territory (Mulligan, 1964) and Greenland (Jørgensen, Sørensen, and Westergaard, 1958).

LESQUERELLA ARCTICA (Wormsk.) S. Wats.

L. arctica var. scammanae Rollins

2n=60: Murray 6727. Chandalar Quad.: Sukakpak Mt., 67°36'N, 149°45'W.  
Batten and Dawe 78-440. Mt. Hayes Quad.: Gunnysack Creek,  
 63°32'N, 145°51'W.

This taxon is uniform in chromosome number throughout its range, from Wrangel Island (Zhukova, 1965b) and Magadon (Berkutenko and Gurzenkov, 1976), to the White Mts. of central Alaska (Knaben, 1968), northwestern Canada (Mulligan and Porsild, 1969), and Greenland (Böcher and Larsen, 1950; Holmen, 1952; Jørgensen, Sørensen, and Westergaard, 1958).

RORIPPA BARBARAEFOLIA (DC.) Kitagawa

2n=16: Murray and Johnson 6310. Bettles Quad.: No Name Ck., 66°07'N,  
 150°10'W.

This Beringian taxon has been counted at the same number from Bettles, Alaska (Jonsell, 1968), the Klondike River near Dawson (Mulligan and Porsild, 1968), and Ogilvie Mts., Yukon Territory (Mulligan and Porsild, 1970).

RORIPPA PALUSTRIS (L.) Besser ssp. HISPIDA (Desv.) Jonsell

2n=32: Murray and Johnson 6309. Bettles Quad.: No Name Ck., 66°07'N,  
 150°10'W.

In this discussion, I follow the taxonomic treatment of B. Jonsell (1968), monographer of Rorippa in northwestern Europe. According to

Jonsell's circumscription, R. palustris (L.) Besser is the only tetraploid member of the R. islandica (Oeder) Borbas group, from which it was derived (Jonsell, 1968). It is circumpolar in distribution, and reaches its greatest morphologic variability in North America (Jonsell, 1968). All four subspecies of R. palustris occur and intergrade with one another in Alaska and adjacent parts of Canada, and it has probably only recently been introduced on the Alaskan Arctic Slope (Jonsell, 1968). The chromosomes of the species have been counted five times in Alaska at the same tetraploid level,  $2n=32$  (Jonsell, 1968), and all the chromosome vouchers fall within the range of the highly variable ssp. palustris (Jonsell, 1968). Counts from fifteen localities in Canada (Jonsell, 1968; Mulligan, 1964), include members, with one exception, of all the subspecies of R. palustris.

R. palustris ssp. hispidula is the subspecies most clearly recognizable as a separate taxon within the palustris group, because it forms a cohesive morphologic unit with a limited geographic range (Asian-American) (Jonsell, 1968). Since it is widespread, it is surprising that it has only been counted once before in Quebec, also at  $2n=32$  (Mulligan, 1964 as R. islandica).

SMELOWSKIA BOREALIS (Greene) Drury & Rollins

var. JORDALII Drury & Rollins:

$2n=12$ : Batten 75-455. Table Mt. Quad.: Sheenjek R., vic. of Lost Lake,  
 $67^{\circ}39'N$ ,  $143^{\circ}52'W$ .

var. KOLIANA Drury & Rollins:

$2n=12$ : Rice s.n., August 15, 1977. Healy Quad.: Sable Mt.,  $63^{\circ}34'N$ ,  
 $149^{\circ}42'W$ .

Smelowskia borealis is found in Alaska, the Northwest Territories, and Yukon Territory. The species has been divided into four varieties on the basis of silique type and pubescence of leaves, stems, and pedicels. The varieties show considerable uniformity in flower and vegetative characteristics and this argues for their conservative treatment as members of a single species (Drury and Rollins, 1952). Each morphotype occurs in relatively local, homogeneous populations, usually at high altitudes in mountainous areas that were not covered by Pleistocene ice.

The chromosomes of three of the four subspecies have each been counted once; two of these counts are reported here for the first time. Variety jordalii, with caducous calyx, short style, and long membranaceous fruits, is found in the Brooks Range and Romanzof Mountains of northern and northeastern Alaska. Variety kohliana, with persistent calyx, long style, and long, membranaceous, inflated siliques, is known only from Mount McKinley National Park. Variety villosa Drury & Rollins, found only on Sable Mt., Mount McKinley National Park, gave a chromosome count of  $2n=12$  (Drury and Rollins, 1952). This taxon differs from the other varieties mentioned by its long, oblong siliques and pubescence of dense, white-villous trichomes. The fourth race, var. borealis, has short, ovate or obovate siliques and is found in the Mackenzie Mts. of the Northwest Territories, Yukon Territory, and Alaska-Yukon border (Drury and Rollins, 1952). The fact remains that this geographic pattern and these varieties may only be apparent, not real, since two of the taxa (var. kohliana and var. villosa) were named on the basis of one or two specimens and may exist solely because of scant collections.

SMELOWSKIA CALYCINA (Steph.) C. A. Mey.

ssp. INTEGRIFOLIA (Seem.) Hult. var. PORSILDII (Drury & Rollins) Hult.:

2n=22: Young 7519, 7520. Utukok Quad.: Archimedes Ridge, 69°10'N, 161°16'W.

ssp. MEDIA Drury & Rollins:

2n=12: Murray 6901. Mt. Michelson Quad.: Ignek Ck., 69°35'N, 145°55'W.

Murray 6903. Mt. Michelson Quad.: Ignek Mesa, 69°33'N, 145°20'W.

Smelowskia calycina, as described by Drury and Rollins (1952), is the most variable and wide-ranging species in the genus. It shows an amphi-Beringian distribution, with three of its five races restricted to North America. Although the data are scant, cytologic findings seem to concur with the morphologic conclusions of Drury and Rollins (1952) (Table 1). Subspecies media, found in northern Yukon and northeast Alaska, is the connecting link between var. calycina of northeast and central Siberia, and var. americana of the North American Cordillera. With the exception of the counts for var. americana from Alberta at 2n=22 (Packer in Johnson and Packer, 1968; Packer, 1968), these three closely related taxa are all diploid, 2n=12 (the count reported in this paper for ssp. media is the first for the taxon). Subspecies integrifolia, the clearly marked taxon of northwestern Alaska, and the variety subsumed by it, var. porsildii, found in mountainous regions of western Alaska and the Chukchi Peninsula, are differentiated from the other three races morphologically and cytologically, with 2n=22,24. The reason for the discrepancy between the chromosome counts made for var. porsildii in the Soviet Union (2n=24) and those made for ssp. integrifolia and var. porsildii in Alaska (2n=22) cannot be suggested at this time, but certainly deserves further study.

Table 1. Chromosome numbers in the Smelowskia calycina (Steph.) C. A. Mey. complex.

Taxon	2n	Locality	Source
ssp. <u>media</u> Drury & Rollins	12	Ignek Creek and Mesa, Alaska	this paper
var. <u>americana</u> (Rege1 & Herder)	12	Wyoming, Colorado, Utah	Drury and Rollins, 1952
Drury & Rollins	12	Colorado	Johnson and Packer, 1968
	22	Mt. Park, Alberta	Packer, 1968
	22	Alberta	Johnson and Packer, 1968
var. <u>calycina</u> (Steph.)	12	middle Asia	Zakharyeva and Astanova, 1968
C. A. Mey	12	northeast Asia	Yurtsev and Zhukova, 1972
ssp. <u>integrifolia</u> (Seem.) Hult.	22	Ogotoruk Creek, Alaska	Johnson and Packer, 1968
var. <u>porsildii</u> (Drury &	22	Archimedes Ridge, Alaska	this paper
Rollins) Hult.	24	Chukchi Peninsula, U.S.S.R.	Zhukova, 1969
	24	northeast Asia	Yurtsev and Zhukova, 1972

## THLASPI ARCTICUM Pors.

2n=14: Murray 6199. Beechey Point Quad.: Prudhoe Bay, 70<sup>0</sup>22'N, 148<sup>0</sup>22'W.

This is the first chromosome count for this rare species found along the arctic coasts of Alaska, British Columbia, and Yukon Territory, and in the St. Elias Mts. of Yukon Territory.

## Crassulaceae

## SEDUM DIVERGENS Wats.

2n=16: Weeden s.n., May 26, 1976. Skagway Quad.: Mi 10 Haines Hwy., 59<sup>0</sup>18'N, 135<sup>0</sup>40'W.

This chromosome count agrees with the ones made for the taxon from the Queen Charlotte Islands (Taylor and Mulligan, 1968), and extends the range of Sedum divergens from northwestern United States and adjacent parts of Canada to southeastern Alaska. An earlier count of 2n=28 (Baldwin, 1935) was applied to incorrectly identified material, according to Taylor and Mulligan (1968), and should be disregarded.

## SEDUM INTEGRIFOLIUM (Ruf.) Nels.

2n=36: Hatch 160. Sutwik I. Quad.: Chowiet I., 56<sup>0</sup>02'N, 156<sup>0</sup>42'W.

This taxon has been previously counted at the tetraploid level (2n=36) four times (Löve and Kapoor, 1968; Uhl, 1952, 1963; Zhukova and Tikhonova, 1973). Another count, 2n=18 [Sokolovskaya and Strelkova, 1960 as S. roseum (L.) Scop.] may in fact belong to this taxon. More data are needed to assess the relationship of S. integrifolium to

various Asiatic species, including S. atropurpureum Turcz., which may be a subspecies of S. integrifolium or a synonym of it (Clausen, 1975).

### Saxifragaceae

SAXIFRAGA HIRCULUS L.

2n=16: Dawe 729. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

Löve, Löve, and Kapoor (1971) split this American-Asiatic arctic-alpine species into two subspecies, diploid American ssp. propinqua, and tetraploid Asiatic ssp. alpina; these taxa were maintained by Löve and Löve (1975a). According to Hult n (1973), however, the morphotypes do not correlate with their proposed geographic circumscriptions, and should be retained under the name S. hirculus. The taxon has been counted at the diploid level, 2n=16, from nine locations (four of the counts were 2n=c.16) in Alaska (Hedberg, 1967; Johnson and Packer, 1968; Packer and McPherson, 1974); from Canada (Hedberg, 1967; Mosquin and Hayley, 1966); from Colorado (L ve, L ve, and Kapoor, 1971); and from Pamir, U.S.S.R. (Sokolovskaya in L ve and L ve, 1961; Sokolovskaya and Strelkova, 1939). A triploid, 2n=24, was found at Resolute, Cornwallis Island (Hedberg, 1967), and 2n=28 has been counted twice from the Pamir and Altai regions in central Asia (Sokolovskaya and Strelkova, 1938, 1948). Tetraploids have been counted in eleven reports from the U.S.S.R., Spitzbergen, Iceland, Greenland, and western Canada.

### Rosaceae

ACOMASTYLIS ROSSII (R. Br.) Greene

Geum Rossii (R. Br.) Ser.

2n=70: Dawe GR 40. Mt. Hayes Quad.; Gerstle R., 63°46'N, 145°02'W.

Chromosome counts of 2n=56 and 2n=70 have each been reported seven times for this amphi-Beringian taxon from locations throughout its range.

CHAMAERHODOS ERECTA (L.) Bunge ssp. NUTTALLII (Torr. & Gray) Hult.

C. nuttallii (Torr. & Gray) Pickering

2n=14: Batten and Dawe 78-353. Charley R. Quad.: Kathul Mt., 65°21'N, 142°20'W.

The material from which this first Alaskan chromosome count was made represents a northwest range extension for the taxon in North America. Its chromosomes have been counted at the diploid level, 2n=14, four times before, in Canada (Mulligan and Porsild, 1969; Taylor, 1967), eastern U.S.S.R. (Zhukova, Petrovsky, and Plieva, 1973), and Mongolia (Mesicek and Sojak, 1969).

DRYAS DRUMMONDII Richards.

2n=18: Dawe GR 64. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

The same chromosome number has been counted for this gravel bar species from the Gulkana Glacier, Alaska Range (Knaben, 1968) and from three areas in Canada (Mulligan and Porsild, 1969, 1970; Packer, 1964). Its present day distribution is interrupted between the Gulf of St. Lawrence in eastern North America and the Rocky Mt. Cordillera in western North America (with an isolated population at Lake Superior), and

is probably much contracted from the area it occupied during the Tertiary, which included an area in eastern Asia (Hultén, 1959).

DRYAS INTEGRIFOLIA M. Vahl ssp. SYLVATICA (Hult.) Hult.

2n=18: Dawe GR 10. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

Dryas integrifolia is a primarily Nearctic taxon which previously extended farther south into the Rocky Mts. and westward in eastern Siberia to Lake Baikal (Hultén, 1959). It probably survived Pleistocene glacial events in locations south of the ice sheet and in unglaciated portions of Alaska and Yukon, and since then has reoccupied much of its former range in northern North America (Porsild, 1947). The local race, ssp. sylvatica, may have developed in ice-free portions of Alaska and Yukon during the Pleistocene (Hultén, 1959) and maintained, though not expanded, its initial range in sympatry with ssp. integrifolia. Apparently this is the first chromosome count for ssp. sylvatica. Material of D. integrifolia (no ssp. designation given) has been counted from Barrow (Packer and McPherson, 1974), Canada, and northeastern Siberia.

GEUM MACROPHYLLUM Willd. ssp. MACROPHYLLUM

2n=42: Hatch 81. Sutwik I. Quad.: Chowiet I., 56°02'N, 156°42'W.

The same chromosome number has been reported from nine previous counts for Geum macrophyllum from Eurasia and Canada.

PENTAPHYLLOIDES FRUTICOSA (L.) Rydb.

2n=14: Dawe 654, 701. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

The recent transfer of this taxon from the genus Potentilla (cf. Löve, 1954a) is a satisfactory one from the standpoint of gross morphology, however, judgement concerning Löve's taxonomic interpretation of the Pentaphylloides fruticosa complex (Löve, 1954a) within the genus must be deferred until the critical literature is in hand (Elkington, 1969; Kupfer, 1971; Pursh, 1814; Sokolovskaya and Strelkova, 1948; Tureson, 1938). A brief summary of the controversy is given below.

In his cytotaxonomic investigation of some American representatives of circumpolar taxa, Löve (1954a) proposed that a diploid,  $2n=14$ , American taxon, which he named Pentaphylloides floribunda (Pursh) Löve, is distinct at the species level from characteristically tetraploid,  $2n=28$ , European P. fruticosa, and that the two could be distinguished by the morphologic traits listed in Table 2.

According to Hultén (1971), however, these criteria were not reliable when he examined more extensive series of material from North America and Eurasia. Leaflet form was highly variable, although narrow leaflets were commonly found in China and the Himalayas, and broad leaflets in coastal areas of Newfoundland and Japan. Leaf pubescence was similarly variable, but he found no overall difference in the vein network spacing, and the leaf margins were usually reflexed throughout the taxon's entire distribution range.

Löve (1954b) proposed that the presumed dichotomy between European P. fruticosa,  $2n=28$ , and North American P. floribunda,  $2n=14$ , was an example of substitution species: false vicariads, or taxa that differentiate first (here, presumably by chromosome number change) and then occupy distinct territories. But in a paper that he wrote earlier

Table 2. Morphologic differences between European and American members of the Pentaphylloides fruticosa (L.) Rydb. complex (nomenclature follows Löve, 1954a).

Morphologic Characteristic	European <u>P. fruticosa</u> (L.) Rydb.	American <u>P. floribunda</u> (Pursh) Löve
leaf pubescence	soft-hairy	subglabrous to silky
leaf venation	thin, colorless, in wide mesh network	thick, closely meshed network
leaf margin	flat	more or less revolute
leaflets	short, oblong-lanceolate	narrower and longer

that year (Löve, 1954a), Löve stressed that "the general distribution of P. fruticosa in its strict sense is not known with certainty, nor is the Asiatic distribution of P. floribunda." In effect, he defined the type of speciation operating in the P. fruticosa group on the basis of geography, and had to admit that he didn't know the geographic limits of the taxa with which he was dealing.

Over time, Löve's taxonomic concepts of P. floribunda and P. fruticosa appear to have changed. In his most recent paper dealing with the taxon (Löve, Löve, and Kapoor, 1971), he stated that P. floribunda is an "old and plastic taxon" found in North America, eastern Asia, and (rarely) in southern Europe, which is diploid throughout its entire circumpolar range, while P. fruticosa has a much more restricted Eurasiatic distribution and is tetraploid. Monographers of European and Asian floras, however (cf. Hultén, 1971), believe that the American species is synonymous with the Eurasiatic one, and occurs as far south as central Asia and Manchuria.

This latter interpretation is taken by most workers who have presented chromosome counts for members of the complex. Kupfer (1974) reported diploid Dasiphora fruticosa from the Alps and Pyrenees. These fall outside the range of diploids sensu Löve (1954a). A hexaploid representative of the taxon was reported for material found inside the diploid's normal distribution range (sensu Löve) in eastern Asia (Sokolovskaya and Strelkova, 1948). The diploid number was found in specimens from Alaska once before (Johnson and Packer, 1968, at Ogotoruk Creek), and the complex is nearly equally represented by

diploid and tetraploid chromosome count reports (11;9 respectively) throughout the rest of its circumpolar range.

POTENTILLA BIPINNATIFIDA Hook.

2n=56: Murray 6975. Mt. Michelson Quad.: Okpilak R. valley,  
69°25'N, 144°03'W.

Octoploid (2n=8x=56) P. binnatifida is the highest ploidy member of the P. pensylvanica species complex (Kohli and Packer, 1976). Its distribution, along the North American Cordillera and across the prairies and boreal forests of Canada and the United States, parallels that of tetraploid (2n=28) P. pensylvanica L. The third species in the complex, diploid (2n=14) P. finitima Kohli and Packer, is restricted to the prairie provinces in Canada, and to northern portions of North Dakota and Minnesota in the United States (Kohli and Packer, 1976).

POTENTILLA EGEDII Wormsk.

2n=28: Troy S-45. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

Specimens of Potentilla egedii from Ogotoruk Creek (Johnson and Packer, 1968), Canada, Greenland, Europe, and the U.S.S.R. have all proven to be tetraploid, 2n=28, while Scandinavian plants, though usually tetraploid, have also yielded a few counts of 2n=35 and 2n=42 (Erlandsson, 1942).

POTENTILLA HYPARCTICA Malte

P. emarginata Pursh., P. robbinsiana ssp. hyparctica (Malte) Löve

2n=42: Dawe s.n., August 29, 1976. Mt. Hayes Quad., Paxson, 63°02'N, 145°29'W.

Dawe 712. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

Potentilla hyparctica has been reported to have 2n=42 (or. c.42) chromosomes twelve times before, including counts based on material from Ogotoruk Creek (Johnson and Packer, 1968) and Barrow (Dansereau and Steiner, 1956; Packer and McPherson, 1974). Dansereau and Steiner (1956) reported 2n=49 for the taxon from central Baffin Island. The same number has been found in material from Mount Washington, New Hampshire, by Löve and Löve (1966) who called the taxon P. robbinsiana ssp. hyparctica.

POTENTILLA MULTIFIDA L.

2n=28: Dawe GR 44. Mt. Hayes Quad.; Gerstle R., 63°46'N, 145°02'W.

Potentilla multifida forms numerous geographic races throughout its arctic-montane distribution in Eurasia and northern North America (Hultén, 1971). The tetraploid report, 2n=28, cited here, is the first chromosome count made for the taxon in North America. The same number has been counted seven times before for the taxon in Scandinavia, central Europe, and the U.S.S.R., while a diploid specimen, 2n=14, was counted by Tischler (1929), and hexaploids were reported by Popov (1939) and Shimotamai (1930).

POTENTILLA PENNSYLVANICA L.

2n=28: Batten and Dawe 78-331. Charley R. Quad.: Kathul Mt., 65°21'N, 142°13'W.

According to Kohli and Packer (1975), the P. pensylvanica complex is represented in North America by three morphologically and cytologically distinct species, diploid ( $2n=14$ ) P. finitima Kohli and Packer, tetraploid ( $2n=28$ ) P. pensylvanica L., and octoploid ( $2n=56$ ) P. bipinnatifida Hook. P. pensylvanica has been counted at the tetraploid level from the U.S.S.R. and Japan, while two reports of pentaploids ( $2n=35$ ) are known [one from the U.S.S.R. (Christoff and Papasova, 1943), the other from the Prague Botanical Garden (Popoff, 1939)]. Popoff (1939) also reported a dodecaploid,  $2n=84$ , for specimens from botanical gardens in Ottawa and Edinburgh.

POTENTILLA VILLOSA Pall.

$2n=14$ : Hatch 87. Sutwik I. Quad.: Chowiet I.,  $56^{\circ}02'N$ ,  $156^{\circ}42'W$ .

The diploid chromosome level,  $2n=14$ , was determined for this Beringian species by Taylor and Mulligan (1968), Tischler (1929), and Zhukova (1965a), and a hexaploid,  $2n=42$ , was reported by Popoff (1939). The counts,  $2n=42$ , 49, made by Muntzing (1931) on material from Sweden were incorrectly attributed to P. villosa Pall. Muntzing's specimens, Eurasiatic P. crantzii Beck., are synonymous with P. villosa Zimm., but not with the taxon discussed here (Taylor and Mulligan, 1968).

SANGUISORBA OFFICINALIS L.

$2n=28$ : Dawe GR 4. Mt. Hayes Quad.: Gerstle R.,  $63^{\circ}46'N$ ,  $145^{\circ}02'W$ .

A tetraploid was determined from Ogotoruk Creek by Johnson and Packer (1968). Elsewhere throughout its circumpolar range, Sanguisorba

officinalis has been counted at  $2n=28,42,56,c.70$ . Löve and Löve (1975a) maintained that all S. officinalis L., s.str, is  $2n=28$ , and that reports of  $2n=56$  belong to S. polygama Nyl, s.str. Nordborg, who had worked extensively with S. officinalis (Nordborg, 1958, 1963), reported tetraploids,  $2n=28$ , from seven Eurasian countries, and octoploids,  $2n=56$ , from eleven. According to her (Nordborg, 1963), tetraploids predominate slightly in the western part of central Europe, while octoploids are somewhat better represented in the eastern part. Although she could sometimes detect ecological differences between specimens at the two ploidy levels, there were no consistent distinguishing morphologic characteristics, except in pollen grain sculpturing. Nordborg's attempts to cross the two cytotypes were unsuccessful, but in the absence of morphologic markers, the sterility barrier was considered insufficient grounds for elevating the cytotypes to formal taxonomic rank. Nordborg commented (1963) that although Polya (1951) counted  $2n=42$  chromosomes from Polish plants, she could only find  $2n=56$  from nearby locations. She also found  $2n=56$  in plants east of Reykjavik, Iceland (1953), not  $2n=42$  as reported by Löve and Löve (1956) from Iceland. In a letter to Nordborg (cf. Nordborg, 1963), Löve and Löve reported that they published the last-mentioned count with hesitation because the slides were not very good, and Nordborg (1963) implied that it may therefore not be an accurate chromosome count. Finally, a dodecaploid,  $2n=c.70$ , was counted by Sokolovskaya (1963) from Kamchatka.

SANGUISORBA STIPULATA Raf.

S. canadensis L. ssp. latifolia (Hook.) Calder and Taylor; S. sitchensis  
C. A. Mey.

2n=28: Hatch 277. Sutwik I. Quad.: Chowiet I., 56°02'N, 156°42'W.

The same tetraploid chromosome number has been reported four times previously, including counts made on Alaskan material from the Black Rapids Glacier (Knaben, 1968) and Susitna (Hedberg, 1967), and from the Queen Charlotte Islands (Taylor and Mulligan, 1968) and U.S.S.R. (Sokolovskaya, 1960).

SIBBALDIA PROCUMBENS L.

2n=14: Dawe 683. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

This wide ranging arctic-alpine species has been reported at the diploid level, 2n=14, from locations throughout its entire distribution range, including a count (2n=c.14) made on a population growing at Susitna, central Alaska, by Hedberg (1967). The only divergent count, 2n=28, was determined by Böcher (1969), working with plants from the Shensi Mts., China, which were cultivated in a botanical garden.

## Fabaceae (Leguminosae)

ASTRAGALUS ABORIGINORUM Richards.

A. richardsonii Sheldon, A. lepagei Hult.

2n=16: Batten and Dawe 78-243. Eagle Quad.: Eagle Bluff, 64°48'N, 141°12'W.

This is the first diploid documented in the state. Löve and Löve (1975a) incorrectly cited that Johnson and Packer (1968) recorded A. lepagei from Ogotoruk Creek at 2n=16. Only A. australis was (mistakenly) listed in the paper by Johnson and Packer, and no chromosome number corresponded to that entry. Tetraploid (2n=32) populations have been reported from Umiat (Hedberg, 1967) and Liberator Lake (Holmen, 1962), as well as the Soviet Union (Yurtsev and Zhukova, 1968; Zhukova and Petrovsky, 1971; Zhukova, Petrovsky, and Plieva, 1973), while hexaploids (2n=48) have been found in Southwest Asia (Ledingham and Rever, 1963) and in the Soviet Union (Chouxanova, 1967). Two morphotypes may be included (A. lepagei as distinct from A. richardsonii) at each of these ploidy levels. American populations may actually represent nearctic A. australis (letter from R. Barneby, New York Botanical Garden, Bronx, to D. F. Murray, University of Alaska, Fairbanks, Alaska).

ASTRAGALUS EUCOSMUS Robins. ssp. EUCOSMUS

2n=32: Batten and Dawe 78-217, 78-374. Eagle Quad.: Eagle Bluff,  
64°48'N, 141°14'W.

This first chromosome count from Alaska agrees with other reports for the taxon from Canada and the continental United States.

ASTRAGALUS NUTZOTINENSIS Rousseau

2n=22: Murray 3347. Mt. Michelson Quad.: Cache Creek, 69°25'N, 146°00'W.

Astragalus nutzotinensis, an Alaskan arctic-alpine endemic, has been counted once before at the same number on material from McKinley River (Ledingham, 1960).

ASTRAGALUS ROBBINSII (Oakes) Gray

2n=32: Batten and Dawe 78-312. Charley R. Quad.: Kathul Mt., 65°20'N, 142°19'W.

The same number has been reported from northern Ontario by Ledingham (1960).

ASTRAGALUS SEALEI Lepage

A. eucosmus Robins. ssp. sealei (Lepage) Hult.

2n=16: Murray 6943. Demarcation Pt. Quad.: Jago R. valley, 69°24'N, 143°41'W.

Astragalus sealei, which is largely restricted to floodplains of arctic rivers, has been counted once before at 2n=16 (Ledingham, 1960) from "Nabesna Rd., Mi 91, Alaska" (letter dated 21 March 1979 from G. F. Ledingham, Department of Biology, University of Regina, Regina, Saskatchewan, Canada).

HEDYSARUM ALPINUM L. ssp. AMERICANUM (Michx.) Fedtsch.

2n=14: Troy S-37. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.  
Dawe GR 5. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

This taxon has been reported at the same diploid chromosome number ten times previously, including counts made on material from Lake Peters (Holmen, 1962) and Ogotoruk Creek (Johnson and Packer, 1968). The latter population is especially interesting because tetraploid plants,  $2n=28$ , were also found to occur there, and, in fact, were more widespread than the diploids (Johnson and Packer, 1968). Johnson and Packer found that the two cytotypes were ecologically and morphologically distinct (diploid plants, with normal leaflets, growing on well drained upland soils vs. tetraploids, with emarginate leaflets, growing abundantly on gravel bars, benches, and frost scars), but seemed to be only a local occurrence. No other population examined throughout the taxon's North American distribution showed emarginate leaflets (Johnson and Packer, 1968). The other count diverging from the diploid standard for this taxon was made by Hedberg (1967), who counted plants with  $2n=16$  chromosomes from Bettles, Alaska.

LATHYRUS PILOSUS Cham.

L. palustris L. ssp. pilosus (Cham.) Hult.

$2n=14$ : Troy S-33. Norton Bay Quad.: Koyuk,  $64^{\circ}50'N$ ,  $160^{\circ}54'W$ .

Five diploid chromosome number reports have been made for arctic-montane Lathyrus pilosus from its distribution range in Eastern Asia and the North American Pacific coast. It is a member of the circumboreal (excluding Greenland) L. palustris L. complex, and differs cytologically from European L. palustris s.str., whose chromosomes have been counted consistently at the hexaploid level,  $2n=42$  (cf. Löve and Löve, 1975a).

LUPINUS ARCTICUS S. Wats.

2n=48: Dawe 157. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

Lupinus arcticus, a North American endemic, is widespread in Alaska, Northwest Territories, and the Canadian Rocky Mt. Cordillera. Two cytotypes, a hexaploid (2n=48) and dodecaploid (2n=96) occur and may be present in the same population as was found at Umiat, where Holmen (1962) made a chromosome count of 2n=48 and Packer and McPherson (1974) subsequently reported 2n=c.96. Tetraploid plants have also been found at Anchorage (Hedberg, 1967, as 2n=c.48) and Ogotoruk Creek (Johnson and Packer, 1968). A determination of 2n=c.96 was made on freshly germinated seeds, purportedly of Pleistocene age, which were found in Canada (Porsild, Harington, and Mulligan, 1967).

Oxytropis campestris (L.) DC. complex

Oxytropis campestris s.lat. comprises an ancient, circumpolar constellation of 20 to 33 morphologically and sometimes also chromosomally diverse taxa with centers of distribution in northwestern North America, western Siberia, and north-central Europe (Table 3). Published chromosome counts indicate that it represents a mature polyploid complex (sensu Stebbins, 1971) with extant euploid members ranging between diploid, 2n=16 (x=8), and dodecaploid, 2n=96, levels. Fifteen named taxa have been counted to date but eight of these counts were made on only one population each. Given the complicated chromosome patterns already shown by some of these taxa it seems likely that even more variability will be found with additional counts. Keeping all these limitations in

Table 3. Number of taxa in the three major distribution centers for the Oxytropis campestris (L.) DC. complex.

Geographic Area	Number of taxa
North America	12
Siberia	6-13
Europe	5

mind, the following picture emerges (Fig. 4). Figure 4 shows that some taxa were counted at more than one ploidy level. Of the 15 taxa represented, eleven are hexaploid, six are tetraploid, and two are octoploid. Three taxa are diploid, and three are dodecaploid.

When geographic setting is superimposed on the chromosome data, a striking pattern is revealed (Fig. 4). Four European counts, representing two taxa, all show the modal, hexaploid level of the species complex,  $2n=48$ , while the four Siberian taxa indicate that only high ploidy levels, from  $6x$  to  $12x$ , exist there. The eleven taxa counted across southern Canada and south to the Great Plains and western Cordillera are tightly clustered around the intermediate ploidy levels of  $4x$  and  $6x$ . Only in Alaska are there representatives at each ploidy level,  $2x$  through  $12x$ .

Four taxa included in the *O. campestris* line: *O. campestris* ssp. *varians* (Rydb.) Barneby, *O. jordalii* Pors., *O. viscida* Nutt., and *O. borealis* DC., are found in Alaska. Table 4 summarizes the cytogeography of the Alaskan members of the complex, as known from previous chromosome counts, and may be easily contrasted with the new chromosome counts I am reporting (Table 5).

As stated earlier, Alaska is the only place where all euploid levels found across the complex are represented. *O. campestris* ssp. *varians* is the only member of the complex to exhibit all ploidy levels, and this fact, together with its widespread distribution and morphologic allegiance with many members of the complex, makes it the most likely candidate for the "proto-campestris" stock proposed by Elisens (1978).

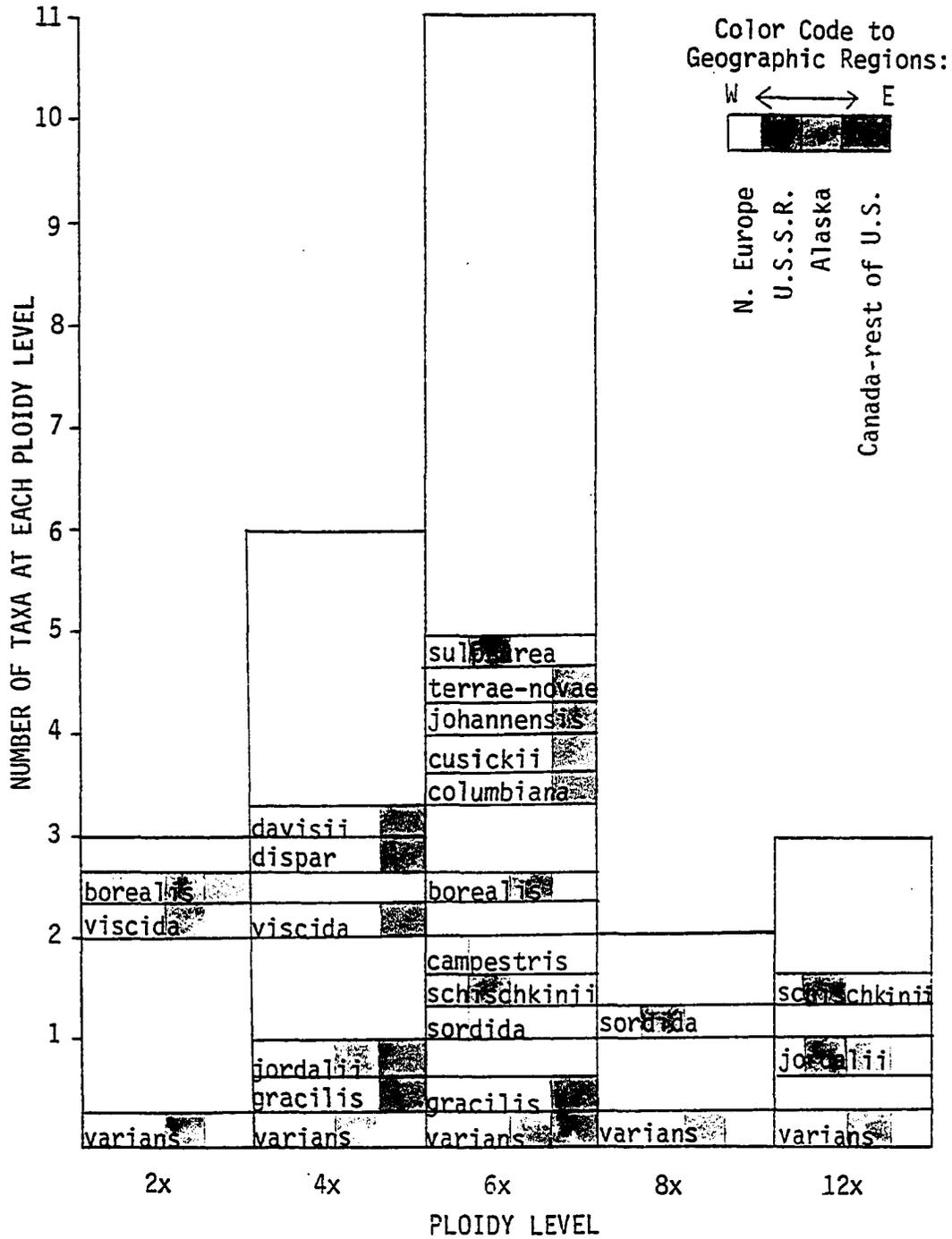


Fig. 4. Geographic provenance and number of taxa at each ploidy level in the *Oxytropis campestris* (L.) DC. species complex.

Table 4. Previous chromosome counts made on North American representatives of the Oxytropis campestris (L.) DC. complex.

<u>Taxon</u> Chrom. No.	Alaska	Canada/NW U.S.A.	U.S.S.R.
<u>varians</u>			
2n=36	Knaben, 1968		
2n=48	Elisens, 1978	Elisens, 1978	
2n=60+	Johnson and Packer, 1968		
2n=96	Elisens, 1978		
<u>jordalii</u>			
2n=32	Knaben, 1968	Elisens, 1978	
2n=96			Zhukova and Petrovsky, 1972
<u>viscida</u>			
2n=32		Ledingham, 1958	
<u>borealis</u>			
2n=32		Mulligan and Porsild, 1970	
2n=48	Holmen, 1962 Johnson and Packer, 1968 (as 2n=c.48)		Zhukova, Korobkov, and Tikhonova, 1977
2n=96			Zhukova, Korobkov, and Tikhonova, 1977

Table 5. Original chromosome counts for Alaskan representatives of the Oxytropis campestris (L.) DC. complex.

Taxon	2n	Quad. Place Name	Latitude/Longitude	Collector(s) and Coll. No.(s)
<u>varians</u>	16	Eagle: Calico Bluff	64°55'N 141°11'W	Batten and Dawe 78-260
	16	Mt. Hayes: Gunnysack Cr.	63°32'N 145°51'W	Batten and Dawe 78-439
	32	Eagle: Eagle Bluff	64°48'N 141°12'W	Batten and Dawe 78-361, -369
	96	Mt. Michelson: Jago R.	69°25'N 144°03'W	Murray 6956
	96	Mt. Hayes: Donnelly Cr. campgrd.	63°40'N 145°52'W	Dawe GR 66
<u>jordalii</u>	36	Sagavanirktok: Franklin Bluff	69°48'N 148°40'W	Kubanis s.n., August 1977
<u>viscida</u>	16	Eagle: Chicken	64°03'N 141°46'W	Batten and Dawe 78-390
	16	Tanacross: Northway Jct.	63°01'N 141°48'W	Bourdo 33244
<u>borealis</u>	48	Sagavanirktok: Franklin Bluff	69°48'N 148°40'W	Kubanis s.n., August 1977
	48	Mt. Hayes: Donnelly Cr. campgrd.	63°40'N 145°52'W	Batten and Dawe 78-433

Moreover, the clustering of all diploid members found in the complex (*O. campestris* ssp. *varians*, *O. borealis*, and *O. viscida*) in unglaciated eastern Alaska and adjacent Yukon Territory, and the unparalleled species diversity for the group which is found there (cf. Barneby, 1952; Elisens, 1978; Hultén, 1968), present strong evidence that that area may be the center of origin and diversification for the *O. campestris* complex. Clearly, further study of the relationships between members of the complex found in Alaska is needed.

The following taxa will be discussed as members of the *O. campestris* complex:

*O. borealis* DC.

*O. campestris* (L.) DC. ssp. *varians* (Rydb.) Barneby

*O. jordalii* Porsild

*O. viscida* Nutt.

OXYTROPIS BOREALIS DC.

*O. glutinosa* Pors.

2n=48: Kubanis s.n. Sagavanirktok Quad.: Franklin Bluff, 69°48'N,  
148°40'W.

Batten and Dawe 78-433. Mt. Hayes Quad.: Donnelly Creek  
Campground, 63°40'N, 145°52'W.

The northern range of *Oxytropis borealis* stretches in a narrow band from Kamchatka Peninsula across the Brooks Range to the coastline of the Northwest Territories, while its southern distribution lies primarily in the Alaska Range. Its chromosomes have been counted in Alaska at 2n=48 from Lake Peters [Holmen, 1962, as *O. leucantha* (Pall.)

Bunge] and  $2n=c.48$  from Ogotoruk Creek (Johnson and Packer, 1968, as *O. glutinosa* Pors.). In eastern Siberia, separate seeds from one specimen of *O. leucantha* (Pall.) Bunge emend. Welsh = *O. borealis* DC. = *O. schischkinii* auct. were found to have  $2n=48$  and  $2n=96$  (Zhukova, Korobkov, and Tikhonova, 1977). Mulligan and Porsild (1970) counted the chromosomes of closely related *O. glutinosa* Pors. at  $2n=16$  from the Ogilvie Mts., Yukon Territory.

This taxon has been treated differently by various workers. Welsh (1963) adopted too broad a species concept when he included this species as a synonym of *O. viscida* Nutt. Barneby's treatment (1952) of the taxon as var. *subsucculenta* (Hook.) Barneby of *O. viscida* is decidedly preferable, because it emphasizes the different distribution ranges (cf. discussion under *O. viscida*), flower colors (purple *borealis* vs. yellow *viscida*), viscosity, and ecological requirements of *O. borealis* and *O. viscida*.

My treatment of the *O. viscida* complex, including *O. borealis*, as a member of the larger *O. campestris* complex (Fig. 4, Tables 4 and 5 in general discussion of *O. campestris* complex; discussion under *O. viscida*) is supported by the presence of a putative hybrid swarm between *O. borealis* and *O. campestris* at Franklin Bluff. There, *O. borealis* type specimens, which probably include parental stock, have so far given chromosome counts of  $2n=48$  and  $2n=c.56$  (although the exact number could not be determined from this last plant, it definitely had an elevated chromosome number). According to Barneby (1952), this situation is not unusual. Hybrids between forms of *O. campestris* and *O. viscida* are to be expected wherever the two occur sympatrically (Barneby, 1952).

OXYTROPIS CAMPESTRIS (L.) DC. ssp. VARIANS (Rydb.) Barneby

O. varians (Rydb.) Hult.

2n=16: Batten and Dawe 78-260. Eagle Quad.: Calico Bluff, 64°55'N,  
141°11'W.

Batten and Dawe 78-439. Mt. Hayes Quad.: Gunnysack Creek,  
63°32'N, 145°51'W.

2n=32: Batten and Dawe 78-361, 78-369. Eagle Quad.: Eagle Bluff,  
64°48'N, 141°12'W.

2n=96: Murray 6956. Mt. Michelson Quad.: Jago R., 69°25'N, 144°03'W.  
Dawe GR 66. Mt. Hayes Quad.: Donnelly Ck. campground, 63°40'N,  
145°52'W.

The Calico Bluff and Gunnysack Creek plants are the first diploids (2n=16) reported for the circumpolar Oxytropis campestris species complex, while the Eagle Bluff plants, thirteen miles (9 km) upstream from Calico Bluff, are tetraploids at 2n=32 (Fig. 5). Both the Yukon River populations belong to the same morphotype, O. campestris ssp. variens (Rydb.) Barneby, but have several anomalous though weakly expressed features, i.e. viscid calyx lobes and black seeds, that are associated with O. viscida Nutt. Elsewhere in the state, ssp. variens has been counted at 2n=36 (Knaben, 1968), 2n=60+ (Johnson and Packer, 1968), but most commonly, 2n=96 [Elisens, 1978, as var. variens (Rydb.) Barneby]. Tetraploids predominate in the rest of North America (Ledingham, 1957, 1960; Ledingham and Fahselt, 1964), and hexaploids (2n=48) are reported for O. campestris in Scandinavia (Jalas, 1950; Sorsa, 1963) and Europe (Kupfer, 1974; Majovsky et al., 1974). An unpublished count of 2n=36 from an

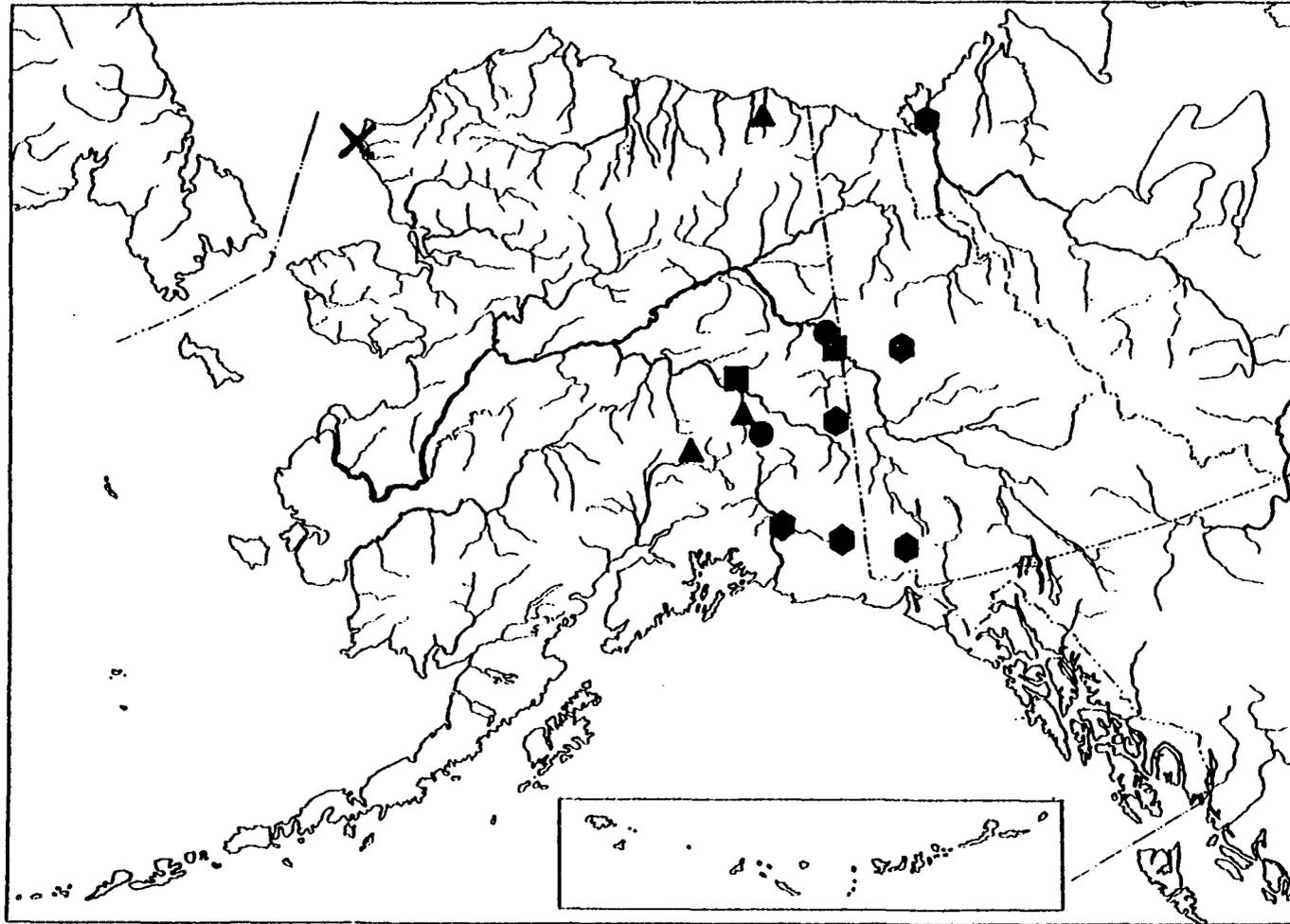


Fig. 5. Distribution of chromosome numbers in *Oxytropis campestris* (L.) DC. ssp. *varians* (Rydb.) Barneby in Alaska, Yukon, and Northwest Territories. 2n=16 (●), 2n=c.32 (■), 2n=48 (◼), 2n=c.64 (X), 2n=96 (▲).

unknown locality for O. campestris is attributed to Jalas in Löve and Löve (1948); however Jalas never published or referred to this count in any of his publications. The cytology, morphology, and biogeography of the Yukon River bluff plants and their position in the species complex of O. campestris warrant intensive study.

OXYTROPIS cf. JORDALII

O. campestris (L.) DC. ssp. jordalii (Pors.) Hult.

2n=36: Kubanis s.n. Sagavanirktok Quad.: Franklin Bluff, 69°48'N, 148°40'W. This is probably a hybrid plant close to O. jordalii, or possibly O. campestris ssp. varians.

Oxytropis jordalii has a spotty, restricted alpine distribution in Alaska, Yukon and Northwest Territories, British Columbia, and perhaps, Kamchatka and Wrangel Island. Its chromosomes have previously been counted at 2n=32 by Knaben (1968) from the White Mts., central Alaska, and by Elisens (1978) from Alberta and Northwest Territories, and at 2n=96 by Zhukova and Petrovsky (1972) from Wrangel Island (cf. Table 4). The identity of the Wrangel Island plants with the Alaskan and western Canadian populations is questionable, so that the Soviet chromosome count should be regarded as tentative at this time.

OXYTROPIS VISCIDA Nutt.

2n=16: Batten and Dawe 78-390. Eagle Quad.: Chicken, 64°04'N, 141°58'W. Bourdo 33244. Tanacross Quad.: Northway Junction, 63°01'N, 141°48'W.

This taxon has been counted once before, at  $2n=32$ , from Alberta (Ledingham, 1958).

The primary distribution of O. viscida lies along the Rocky Mt. Cordillera. The taxon is a member of a complex which includes Oxytropis borealis DC. and O. hudsonica (Greene) Fern. (Barneby, 1952), and, as stated by Barneby (1952), the members of this complex are the only glandular representatives of Oxytropis in North America. The close relationship of the O. viscida complex to the eglandular O. campestris species group, however, is shown by the occasional plant of O. viscida with paired leaflets, the easy hybridization between the two complexes, and in general, the parallel trends in morphologic variation exhibited by them (Barneby, 1952). With regard to the relationship between the viscida and campestris series, Barneby (1952, p. 184) stated:

visciduity and its absence and both paired and solitary leaflets occur in each of the four possible combinations in species alike as to floral and carpological structures, and segregation of each series as a section tends to obscure rather than clarify the relationship between them.

I take Barneby's taxonomic concept to its natural conclusion, to include members of the O. viscida group within the O. campestris species complex. Supportive evidence for this comes from:

1) Cytology

the three taxa included within the O. viscida complex show the same chromosome number pattern as the rest of the campestris constellation (Tables 4 and 5), which differs from the chromosome behavior shown by other members of Oxytropis,

2) Biogeography

the distribution range of this complex follows that of the

campestris group, again distinct from other oxytropes, and

### 3) Morphology

the presence of fasciculated leaves and varying viscosity makes it appear closely allied to gracilis-varians (Barneby, 1952).

Furthermore, the low chromosome number,  $2n=16$ , retained by at least two of the three members of the viscida line (O. viscida and O. borealis) may argue for their position as relatively primitive members of the mature polyploid O. campestris complex.

OXYTROPIS DEFLEXA (Pall.) DC. var. FOLIOLOSA (Hook.) Barneby

O. foliolosa Hook.

$2n=16$ : Murray 6994. Mt. Michelson Quad.: Lake Peters,  $63^{\circ}19'N$ ,  $145^{\circ}03'W$ .  
Batten and Dawe 78-421. Mt. Hayes Quad.: Donnelly Ck. campground,  $63^{\circ}40'N$ ,  $145^{\circ}52'W$ .

The chromosomes of Oxytropis deflexa have been counted four times before from Siberia and North America, all at  $2n=16$ .

OXYTROPIS HUDELSONII Pors.

$2n=16$ : Murray 516. Kluane Lake Quad.: Observation Mt.,  $60^{\circ}48'N$ ,  $138^{\circ}43'W$ .  
Murray 2168. McCarthy Quad.: vic. Russell Glacier terminus, upper White R. valley,  $61^{\circ}42'N$ ,  $141^{\circ}45'W$ .

Mulligan and Porsild (1969) reported the same number from the unglaciated Yukon plateau for this narrowly restricted, Alaska-western Canadian endemic taxon.

## OXYTROPIS KOBUKENSIS Welsh

2n=80: Lewis M-4. Ambler R. Quad.: Great Kobuk Sand Dunes, 67°04'N,  
158°54'W.

This is the first chromosome count for this rare taxon which is found only along the Kobuk River, Brooks Range, and represents the decaploid ploidy level (with  $x=8$ ).

## OXYTROPIS KOYUKUKENSIS Pors.

2n=48: Parker s.n. Chandalar Quad.: 5-10 mi N. of Wiseman, 67°29'N,  
149°53'W.

Oxytropis koyukukensis is another rare Alaskan endemic species, which has been counted at the same hexaploid level from Umiat (Holmen, 1962).

## OXYTROPIS SCAMMANIANA Hult.

2n=16: Murray 2260. McCarthy Quad.: vic. Sheep Glacier terminus, upper White R. valley, 61°42'N, 141°39'W.

Oxytropis scammaniana is restricted to alpine heaths in Alaska, Yukon Territory and British Columbia. This is the first diploid chromosome count for the species, which was counted once before by Knaben (1968), at 2n=32, from the Sourdough Mts., central Alaska.

## Linaceae

## LINUM LEWISII Pursh

L. perenne L. ssp. lewisii (Pursh) Hult.

2n=18: Batten and Dawe 78-373. Eagle Quad.: Eagle Bluff, 64°48'N,  
141°11'W.

This first count in Alaska gives the same number as seven reports for the taxon in continental North America.

#### Elaeagnaceae

ELAEAGNUS COMMUTATA Bernh.

2n=28: Dawe GR 49. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

This first chromosome count for North American endemic Elaeagnus commutata agrees with the chromosome number reported in four out of the five members of the genus cited in Federov (1969).

SHEPHERDIA CANADENSIS (L.) Nutt.

2n=22: Dawe s.n., August 29, 1976. Mt. Hayes Quad.: Paxson, 63°02'N,  
145°29'W.

The same chromosome number has been reported twice before for this species which is widespread in, but restricted to, North America.

#### Geraniaceae

GERANIUM ERIANTHUM DC.

2n=28: Hatch 85. Sutwik I. Quad.: Chowiet I., 56°02'N, 156°42'W.

The chromosomes of this Asian-American Pacific coastal taxon have previously been counted in Japan at 2n=28 + 1-2B (Shimizu, 1971) and

2n=30 (Sakai, 1935). Sokolovskaya (1960) reported 2n=28 for plants from southeastern Siberia. Until more chromosome counts are available it will be impossible to assess how widespread B chromosomes or aneuploidy are in Geranium erianthum.

#### Onagraceae

EPILOBIUM ANGUSTIFOLIUM L. ssp. ANGUSTIFOLIUM

Chamerion angustifolium (L.) Holub., s.str., C. angustifolium (L.) Scop.

Epilobium spicatum Lam.

2n=36: Troy S-4. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

Epilobium angustifolium is "one of the most completely circumpolar of all plants" (Hultén, 1971, p. 88). Both its morphology and cytology indicate that it is comprised of two subspecies; widespread, diploid, arctic-montane ssp. angustifolium and [partially mapped as ssp. macrophyllum (Hausk.) Hult. in Hultén, 1968] the more southerly, tetraploid-hexaploid ssp. circumvagum Mosquin (Mosquin, 1966c). Mosquin, from a detailed study of the entire species complex (1966a, 1966b, 1966c), has demonstrated that repeated autopolyploidization within the northern diploid chromosome race most probably led to the origin of the geographically variable but taxonomically cohesive tetraploid populations found in the south. A general trend was established, with increased ploidy to the hexaploid level, toward successful heat tolerant, lowland plants. This explanation of the origin and distribution of the chromosomal and taxonomic races of Epilobium angustifolium seems consistent with all available data and it is therefore preferable to the opposite interpretation

given by Hultén (1971, p. 88) that the southern race is older and the northern one derived.

Epilobium angustifolium ssp. angustifolium has been reported at the diploid level,  $2n=36$ , from Ogotoruk Creek (Johnson and Packer, 1968) and 29 other times throughout its range in Europe, Asia, and North America. The chromosome count reported here is interesting because it comes from a zone of contact (cf. maps for the species in Hultén, 1968) between ssp. angustifolium and ssp. circumvagum. Morphologically and cytologically the chromosome voucher belongs to northern ssp. angustifolium.

#### EPILOBIUM LATIFOLIUM L.

$2n=72$ : Dawe 652. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

According to Small (1968) the two major chromosome races of Epilobium latifolium (diploid,  $2n=36$ , and tetraploid,  $2n=72$ ) are segregated geographically in North America, with diploid plants in Alaska (based on one chromosome count made on material from Ogotoruk Creek reported in Johnson and Packer, 1968) and the western Cordillera, and tetraploids in southeastern Quebec, western Greenland, and Iceland. Of all morphologic characters tested only the frequency of three- vs. four-pored pollen grains were useful in predicting the actual ploidy level of a given plant. By extrapolating from the pollen morphologies he found in 400 herbarium specimens, Small mapped the probable distribution of diploids and tetraploids in the western hemisphere (cf. Figs. 4 and 5, pp. 174-5 in Small, 1968). Following these maps and Small's reasoning, it can be

seen that all Alaskan populations should be diploid. The tetraploid count reported in this paper from the south side of the Alaska Range is therefore particularly interesting because all populations that were examined close to Tangle Lakes consistently showed diploid type, three pored pollen. This chromosome count should be treated with caution however. Many more counts need to be made from the Tangle Lakes region before we can decide whether or not tetraploids are the norm there.

The situation in eastern Siberia is even less clear-cut than in North America (Small, 1968). Pollen grain morph types are mixed in narrowly circumscribed geographic regions and the same trend is beginning to be seen in chromosome counts as more data are accumulated. A count of  $2n=36$  was reported by Sokolovskaya (1968) from northeast Kamchatka where the three closest populations showed 0-10%, 31-50%, and 11-30% four pored pollen grains, respectively, while  $2n=72$  was reported from Wrangel Island (Zhukova and Petrovsky, 1971). The two populations from the Chukchi Peninsula (which are the populations closest to Wrangel Island) gave 0-10% and 71-100% four pored pollen.

Given the complex nature of morphologic and cytologic variation in this widespread taxon, Small's conclusion (1968) that infraspecific recognition should not be given to its chromosome races seems amply justified.

#### Apiaceae (Umbelliferae)

BUPLEURUM TRIRADIATUM Adams ssp. ARCTICUM (Regel) Hult.

B. americanum Coult. & Rose

$2n=28$ : Murray 6977. Mt. Michelson Quad.: Okpilak R. valley,  $69^{\circ}25'N$ ,  
 $144^{\circ}03'W$ .

Bupleurum triradiatum ssp. arcticum is a Beringian taxon with a disjunct population in the southern Rocky Mts. and it is most certainly a pre-Pleistocene relic (Hultén, 1944). Johnson and Packer (1968) found diploid plants,  $2n=14$ , at Ogotoruk Creek while Bell and Constance (1966) reported a tetraploid,  $2n=28$ , from material collected north of Whitehorse, Yukon Territory. Two reports in the Soviet literature,  $2n=12$  (Gurzenkov and Gorovoy, 1971) and  $2n=16$  (Belaeva and Siplivinsky, 1977) have shown that aneuploidy exists in B. triradiatum but these reports did not indicate to which subspecies the counts belong, ssp. triradiatum (found at Lake Baikal and west) or ssp. arcticum (Lake Baikal and east).

Although based on scanty data the pattern of increasing ploidy level from eastern Asia across North America, when coupled with morphologic considerations, suggests that the taxon originated in Asia and migrated across the Bering Strait to occupy its present distribution range in North America.

CNIDIUM CNIDIIFOLIUM (Turcz.) Schischk.

$2n=22$ : Dawe GR 11. Mt. Hayes Quad.; Gerstle R.,  $63^{\circ}46'N$ ,  $145^{\circ}02'W$ .

Asian-American Cnidium cnidiifolium has been reported to have the same diploid chromosome number (based on  $x=11$ ) four times before, including counts made on plants from Ogotoruk Creek (Johnson and Packer, 1968), Chicken, Alaska and Mayo Highway, Yukon Territory (Bell and Constance, 1966), Wrangel Island (Zhukova and Petrovsky, 1972) and mainland eastern Siberia (Gurzenkov and Gorovoy, 1971).

## Diapensiaceae

DIAPENSIA LAPPONICA L. ssp. OBOVATA (F. Schm.) Hult.

2n=12: Dawe 692. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

Diapensia lapponica ssp. obovata, the Pacific race of the D. lapponica complex, has shown the same chromosome number in six other reports, including one from Ogotoruk Creek (Johnson and Packer, 1968). Hultén (1958, p. 222) made a typographical error when he stated that ssp. obovata, instead of ssp. lapponica, is the amphi-Atlantic member of the species.

## Primulaceae

ANDROSACE SEPTENTRIONALIS L.

2n=20: Batten and Dawe 78-280. Charley R. Quad.: Kathul Mt., 65°20'N, 142°15'W.

Dawe 746. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

The same number has been reported 22 times from all parts of the nearly circumpolar range of this species complex, including four counts from Alaska [Johnson and Packer, 1968; Knaben, 1968; Packer and McPherson, 1974 (who report the taxon at 2n=c.20)].

DODECATHEON FRIGIDUM Cham. & Schlecht.

2n=44: Dawe 741. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

This is the only member of the genus whose range extends beyond North America into northeastern Siberia (Thompson, 1953). Its distrib-

ution is continental (Thompson, 1953). Determination of  $2n=44$  has been made from three locations in Alaska (Beamish, 1955; Johnson and Packer, 1968; Thompson, 1953) and three locations in northeastern U.S.S.R. (Zhukova, 1969; Zhukova and Tikhonova, 1971, 1973).

DODECATHEON PULCHELLUM (Raf.) Merr. ssp. PAUCIFLORUM (Greene) Hult.

D. radicum Greene ssp. radicum

$2n=44$ : Batten and Dawe 78-293. Charley R. Quad.: Kathul Mt.,  $65^{\circ}20'N$ ,  $142^{\circ}15'W$ .

Pertinent chromosome counts are difficult to trace in the literature because of the nomenclatural confusion attending this taxon. Hultén (1968), whose taxonomy I follow for historic as well as morphologic reasons, adopted a more conservative taxonomic concept than other workers studying Dodecatheon. He divided D. pulchellum into three related but morphologically distinct subspecies: 1) ssp. superbum (Pennell and Stair) Hult. extending east along the Pacific coast from northeastern Alaska Peninsula to Oregon and including Vancouver and Queen Charlotte islands, 2) morphologically similar but small statured ssp. alaskanum (Hult.) Hult. found on Kodiak Island and at Glacier Bay, and 3) inland ssp. pauciflorum (Greene) Hult. Hultén's first two subspecies were combined under D. radicum Greene ssp. macrocarpum (Gray) Beamish although, as Hultén (1967) said, Beamish probably never saw any authentic ssp. alaskanum before she merged it with D. radicum ssp. macrocarpum. The third subspecies recognized by Hultén (1967, 1968)

as D. pulchellum ssp. pauciflorum is synonymous with D. radicum ssp. radicum.

Cytologically, the inland subspecies (D. pulchellum ssp. pauciflorum), to which the Kathul Mt. population belongs, appears characteristically diploid ( $x=22$  for the genus), while the coastal races (D. pulchellum ssp. alaskanum and ssp. superbum) are polyploid ( $4x$  and higher). Chromosomes of D. pulchellum ssp. pauciflorum have been counted by Beamish (1955) as D. radicum ssp. radicum at  $2n=44$  from Mortlach, Saskatchewan, and  $2n=c.44$  from Fairmont and Dutch Creek, British Columbia. A third report of D. pulchellum,  $2n=44$ , was made by Reveal and Styer (1974), but I have not been able to determine the geographic origin of the plant counted by them. Beamish (1955) reported D. radicum ssp. macrocarpum at  $2n=c.88$  from two locations, Lulu Island and Anchorage, Alaska, and  $2n=c.132$  from Victoria, Vancouver Island, while Taylor and Mulligan (1968) reported a chromosome count of  $2n=c.88$  for plants from the Queen Charlotte Islands.

DOUGLASIA ARCTICA Hook.

D. ochotensis (Willd.) Hult. ssp. arctica (Cham. & Schlecht.) Löve and Löve  
 $2n=38$ : Batten and Dawe 78-318. Charley R. Quad.: Kathul Mt.,  $65^{\circ}21'N$ ,  
 $142^{\circ}18'W$ .

The chromosomes of this taxon have been counted once before in western Canada by Packer (1964), also at  $2n=38$ .

#### Gentianaceae

GENTIANA GLAUCA Pa11.

2n=24: Dawe 680. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

The chromosomes of this Beringian taxon have been reported at the same tetraploid level (based on x=6) six times in the Soviet Union, and twice from North America, including a count made by Johnson and Packer (1968) at Ogotoruk Creek, Alaska.

SWERTIA PERENNIS L.

2n=28: Dawe 738. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

The same chromosome number has been reported for this taxon five times before this. One deviant count, 2n=24, was cited by Woycicki (1937), which Taylor and Mulligan (1968) caution to ignore, unless subsequently confirmed by other workers.

#### Polemoniaceae

POLEMONIUM ACUTIFLORUM Willd.

P. pacificum V. Vass.

2n=18: Troy S-42. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

Dawe 665. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

This species has been recorded at the diploid level (2n=18) eighteen times throughout its range in North America and Eurasia, including counts made on material from Ogotoruk Creek (Johnson and Packer, 1968) and Lake Peters (Knaben, 1968).

POLEMONIUM BOREALE Adams ssp. BOREALE var. VILLOSISSIMUM Hult.

2n=18: Murray 6329. Healy Quad.: Cathedral Mt., 63°34'N, 149°36'W.

Polemonium boreale ssp. boreale var. villosissimum, found in the alpine tundra of the Alaska Range, and morphologically distinct from typical ssp. boreale by its small stature and densely capitate, long white villous inflorescence (Hultén, 1967), nevertheless gives the same chromosome number ( $2n=28$ ) as ssp. boreale. Typical ssp. boreale has been counted at  $2n=18$  ten times before in North America, Siberia, and Europe, including a count made on an Ogotoruk Creek population by Johnson and Packer (1968).

The genus Polemonium is characterized by extremely long and morphologically variable chromosomes that, to some extent, show "natural bands", i.e., alternating light and dark bands which appear chromosome specific when stained with basic fuchsin. These characteristics, and the ease of obtaining ample, flat mitotic spreads, make P. boreale an excellent candidate for C-, and perhaps, G-banding. In this case, chromosome morphology, as a character with finer resolution than chromosome number alone, may be useful in distinguishing taxa of infraspecific rank.

POLEMONIUM PULCHERRIMUM Hook.

$2n=18$ : Batten and Dawe 78-170. Tanacross Quad.: W Fork Dennison R. campground, Mi 48.9 Taylor Hwy.,  $63^{\circ}54'N$ ,  $143^{\circ}24'W$ .

Hedberg (1967) reported one diploid ( $2n=18$ ) count for this taxon from Anchorage, while Knaben (1968) counted both a diploid from Copper Center and a tetraploid ( $2n=36$ ) from Rainbow Mt. in the Alaska Range. Only diploids are known so far from other parts of the range of this western North American taxon.

## Hydrophyllaceae

PHACELIA MOLLIS Macbr.

2n=22: Batten and Dawe 78-418. Eagle Quad.: Mi 70.3 Taylor Hwy.,  
vic. Chicken, 64°04'N, 141°58'W.

Phacelia mollis, narrowly restricted to unglaciated portions of eastern interior Alaska and Yukon Territory, has been counted at the same number three times before.

PHACELIA SERICEA (Graham) A. Gray

2n=22: Batten and Dawe 78-371. Eagle Quad.: Eagle Bluff, 64°48'N,  
141°11'W.

This count, the first for Phacelia sericea in Alaska, agrees with four previous reports for the taxon. The haploid complement,  $x=11$ , from which this number was derived, is by far the most common base number in Phacelia, with 75 out of 145 species at  $2n=22$  (Constance, 1963).

## Boraginaceae

CRYPTANTHA SHACKLETTEANA Higgins

2n=24: Batten and Dawe 78-206. Eagle Quad.: Eagle Bluff, 64°04'N,  
141°13'W.

This is the first report for the taxon, and unfortunately, little cytological information exists for Cryptantha. Eight of the 57 species in Oreocarya, the subgenus to which our taxon belongs, have each been counted one time. Seven of these taxa, at  $2n=24$ , indicate a base number

of  $x=12$ , while the eighth taxon, C. macounii Eastw. [=C. celosioides (Eastw.) Payson],  $2n=18$  ( $x=9$ ), which is closely related to C. shackletteana, suggests presence of an aneuploid base number series. Any statement of the cytotaxonomic trends within Cryptantha would be premature at this time, but the narrow endemism and remarkable specializations shown by many members of the genus make it especially interesting evolutionarily.

MERTENSIA DRUMMONDII (Lehm.) G. Don

$2n=24$ : Komarkova, Hansell, and Seabert 170. Meade R. Quad.: near Atkasook,  $70^{\circ}28'N$ ,  $157^{\circ}24'W$ .

This is the first chromosome count reported for this very rare arctic species which has been collected only from Meade River, Alaska, and Victoria Island in the Canadian arctic archipelago. Mertensia drummondii was suggested as a far northern disjunct of M. viridis A. Nels., found in mountains of southeastern Wyoming, Colorado, and Utah by Williams (1940).

MERTENSIA MARITIMA (L.) S. F. Gray

$2n=24$ : Lipkin 78-82. Demarcation Point Quad.: Demarcation Point,  $69^{\circ}41'N$ ,  $141^{\circ}19'W$ .

Mertensia maritima is an amphi-Atlantic seashore species which is found along the entire coastline of Alaska (except the southern southeastern portion of the state), and west to the Chukchi and Kamchatka peninsulas. Its chromosomes have been counted at the tetraploid level,

$2n=24$ , eight times before, including counts made on Alaskan specimens from Barrow (Packer and McPherson, 1974) and Ogotoruk Creek (Johnson and Packer, 1968).

MERTENSIA PANICULATA (Ait.) G. Don

$2n=72$ : Troy S-5. Norton Bay Quad.: Koyuk  $64^{\circ}50'N$ ,  $160^{\circ}54'W$ .

This chromosome count, made on material from Koyuk, represents a new ploidy level (dodecaploid, based on  $x=6$ ) for the taxon, and is the highest ploidy level found to date in the genus Mertensia (cf. Federov, 1969). Chromosomes of M. paniculata have been counted previously at  $2n=24$  from Grassy Narrows, Manitoba (Löve and Löve, 1975c) and near Boulder, Colorado (Wiens and Halleck, 1962).

Scrophulariaceae

CASTILLEJA CAUDATA (Pennell) Rebr.

$2n=24$ : Troy S-27. Norton Bay Quad.: Koyuk  $64^{\circ}50'N$ ,  $160^{\circ}54'W$ .

$2n=72$ : Dawe 756. Mt. Hayes Quad.: Mi 34.5 Denali Hwy.,  $63^{\circ}04'N$ ,  $146^{\circ}15'W$ .

Castilleja caudata is amphi-Beringian in distribution. To date, its chromosomes have been counted only from Alaskan material. It is represented here by various ploidy levels (based on  $x=6$ ):  $2n=4x=24$  at Koyuk,  $2n=12x=72$  at Mi 34.5 Denali Hwy., and  $2n=16x=96$  at Ogotoruk Creek (Johnson and Packer, 1968) (Fig. 6). To discover the limits of this taxon's cytologic variability, many more chromosome counts are needed from throughout its range.

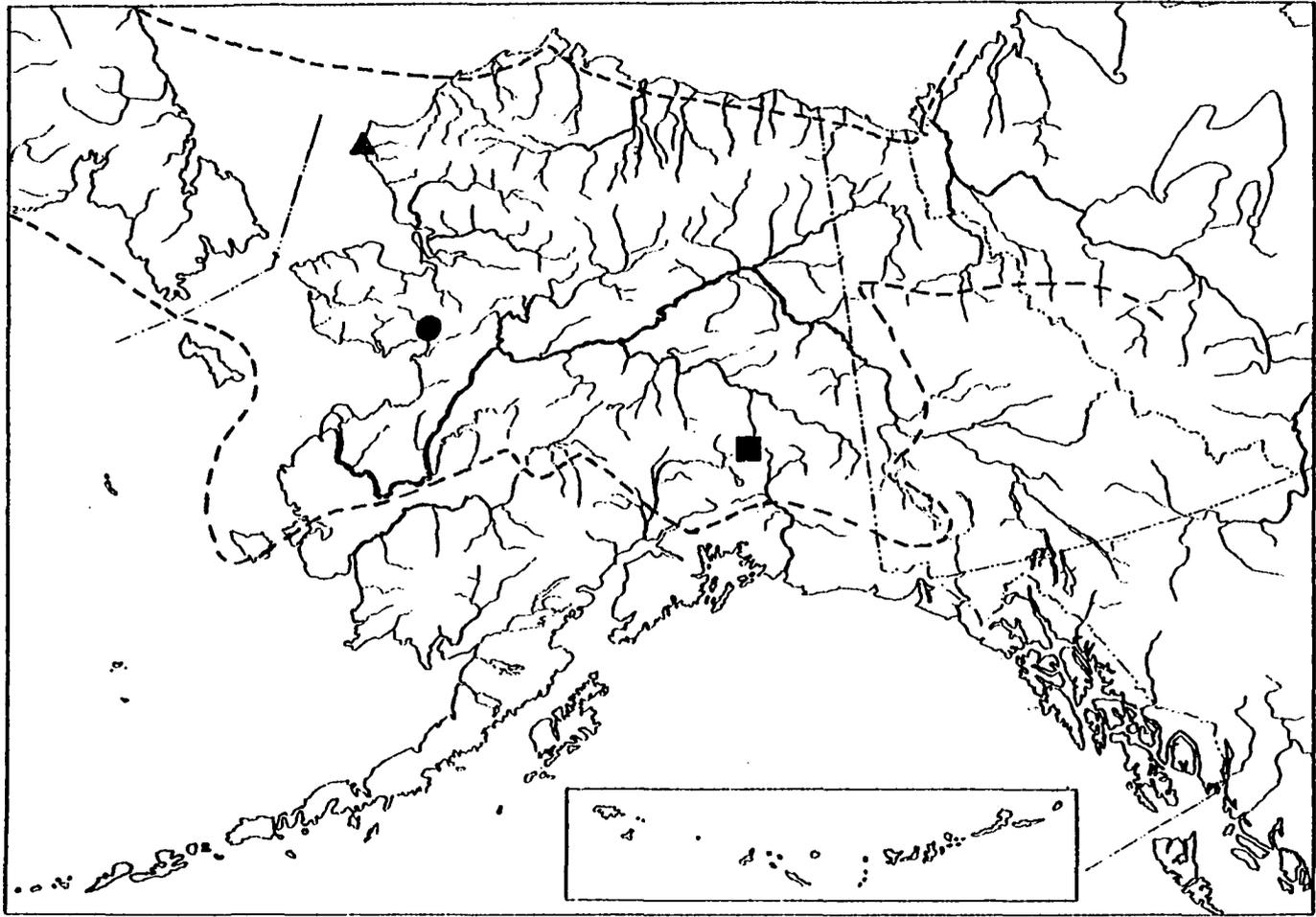


Fig. 6. Distribution of chromosome numbers in *Castilleja caudata* (Pennell) Rupr. in Alaska (dashed lines = limits of its geographic range). 2n=24 (●), 2n=72 (■), 2n=96 (▲).

## CASTILLEJA ELEGANS Maite

2n=24: Batten and Dawe 78-381. Eagle Quad.: Mi 72.2 Taylor Hwy.,  
vic. Chicken, 64°04'N, 141°50'W.

Castilleja elegans has been reported to have the same chromosome number from Ogotoruk Creek, Alaska (Johnson and Packer, 1968) and across the Bering Strait, in northeastern Siberia (Zhukova, 1966).

## PEDICULARIS LANATA Cham. &amp; Schlecht.

2n=16: Troy S-18. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

The chromosome number of Pedicularis lanata has been counted at 2n=16 from five locations throughout its range in northeastern Siberia, northern North America, and western Greenland. Chromosome reports have been made on Alaskan material from Barrow (Packer and McPherson, 1974) and Ogotoruk Creek (Johnson and Packer, 1968).

## PEDICULARIS SUDETICA Willd.

2n=16 + 10B (10 dets./1 root tip), 2n=16 + 8B (1 det./1 root tip):

Troy S-40. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

Pedicularis sudetica includes at least eight taxonomically accepted races (Hultén, 1971), all of which have been reported (in 19 sources) to have 2n=16. In Alaska, chromosome counts are available only for ssp. albolabiata. It has been counted from Barrow (Mulligan, 1969; Packer and McPherson, 1974) and Ogotoruk Creek (Johnson and Packer, 1968).

The chromosome count reported here for the Koyuk specimen is

especially interesting because it presents the first documented case of microchromosomes in Pedicularis. Microchromosomes rarely occur in the Scrophulariaceae, and only five of its 75 genera included in Federov (1969) show fragments or B chromosomes.

PEDICULARIS VERTICILLATA L.

$2n=12 + 0-2f$ :

Batten and Dawe 78-121. Mt. Hayes Quad.: Donnelly Ck. bluff, Delta R. floodplain,  $63^{\circ}40'N$ ,  $145^{\circ}52'W$ .

Pedicularis verticillata is the only member of the genus with a base number other than  $x=8$ . Its chromosomes have been counted at least seven times throughout Europe, Asia, and North America at  $2n=12$ , indicating that for this taxon  $x=6$ . This new chromosome count, based on a specimen from the Delta River floodplain, Alaska Range, presents the second case of microchromosomes in Pedicularis (cf. discussion under P. sudetica).

PENSTEMON GORMANII Greene

$2n=16 + 0-5B$ :

Batten and Dawe 78-302. Charley R. Quad.: Kathul Mt.,  $65^{\circ}20'N$ ,  $142^{\circ}18'W$ .

This first Alaskan report is intriguing because B chromosomes were present in many of the seedlings counted. Mulligan and Porsild (1969) have counted the chromosomes of this northwest North American endemic from the unglaciated central Yukon plateau in Canada at  $2n=16$ .

## Valerianaceae

VALERIANA CAPITATA Pall.

2n=64: Dawe 707. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

Valeriana capitata is found in the northern parts of Europe and the U.S.S.R., and throughout most of Alaska and western Canada. It demonstrates considerable aneuploidy, and the chromosome counts, found in sixteen sources, range between 2n=52 and 2n=120, with a mode of 2n=60. Obviously, no base number or base number series can be established for the taxon until the extremes of cytologic variability within it have been delimited. Knowledge of meiotic behavior could contribute greatly to our understanding of the cytogenetics of the taxon. Johnson and Packer (1968) recorded 2n=c.60 for Ogotoruk Creek plants, and Packer and McPherson (1974) found that Meade River plants had between 2n=52 and 2n=58 chromosomes.

## Campanulaceae

CAMPANULA AURITA Greene

2n=34: Batten and Dawe 78-368. Eagle Quad.: Eagle Bluff, 64°48'N, 141°12'W.

The same number, 2n=34, has been reported for this North America endemic from the White Mts. of Alaska by Knaben (1968).

## Asteraceae (Compositae)

ARTEMISIA ALASKANA Rydb.

2n=18: Dawe GR 43. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

Artemisia alaskana, endemic to Alaska, Yukon, and British Columbia, has been reported once before from Shaw Creek in interior Alaska (Knaben, 1968) to have  $2n=18$  chromosomes. Löve and Löve (1975a) considered the Soviet taxon, A. kruhsiana auct., to be synonymous with North American A. alaskana, and listed two Siberian chromosome counts (A. kruhsiana Bess.,  $2n=18$ , in Korobkov, 1972, and A. kruhsiana Krasch.,  $2n=18$ , in Zhukova, 1966). At the present time, too few data are available to determine the exact relationship between A. kruhsiana and A. alaskana, but Hultén (1973) considered them to be distinct.

According to Porsild (1951), A. Tyrrellii Rydb. is synonymous with and antedates A. alaskana Rydb., but is based on scanty material. For this reason, the name A. alaskana Rydb. has been conserved.

#### ARTEMISIA ARCTICA Less. ssp. ARCTICA

$2n=18$ : Dawe 657. Mt. Hayes Quad.: Tangle L.,  $63^{\circ}02'N$ ,  $146^{\circ}01'W$ .

The Artemisia arctica complex is primarily Beringian in distribution, and reaches into southwestern United States and the mountains south of the Sea of Okhotsk in the Soviet Union. Taxonomic treatment of the complex has varied considerably, but Hultén (1954), whose taxonomy I follow, divides it into ten distinct subspecific groups, three of which occur in Alaska. Its chromosomes have been reported at the diploid level,  $2n=18$ , nine times before, and at the tetraploid level,  $2n=36$ , five times (including a count made on material from Ogotoruk Creek and cited as ssp. comata Hult. in Johnson and Packer, 1968). Many more chromosome counts are needed before an assessment of the correlation (or

lack thereof) between cytotypes and morphotypes can be made. The species is closely related to Asiatic Artemisia norvegica Fr. (Hultén, 1967).

ARTEMISIA BOREALIS Pall.

2n=36: Batten and Dawe 78-255. Eagle Quad.: Calico Bluff, 64°55'N, 141°11'W.

Dawe GR 23. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

These counts agree with the report based on material from Ogotoruk Creek on the northwest coast of Alaska (Johnson and Packer, 1968). Elsewhere tetraploid counts (2n=36) are in the minority. They are found with diploids (2n=18) in Japan, but to date, diploids predominate in the U.S.S.R., and are found exclusively in the Canadian arctic, Greenland, and the Rocky Mts. Löve and Löve (1975a) maintained that only 2n=36 plants belong to Oligosporus borealis (Pall.) Polyak, s.str. (=A. borealis Pall., s.str.). They refer all 2n=18 counts to Oligosporus groenlandicus (Hornem.) Löve and Löve (=A. borealis var. purshii Bess.). Hultén (1968) felt there was no morphologic discontinuity between A. borealis and var. purshii, and would therefore presumably accept both 2n=18 and 2n=36 as widespread A. borealis.

ARTEMISIA FRIGIDA Willd.

2n=18: Dawe GR 61. Mt. Hayes Quad.: Gerstle R., 63°46'N, 145°02'W.

Artemisia frigida shows a conspicuous Beringian gap in its bilobed Asian-American distribution range (cf. map in Hultén, 1968, p. 904). Its chromosomes have been reported at 2n=18 in North America [from Shaw

Creek in interior Alaska (Knaben, 1968), as well as from western Canada, the Great Plains, and southwest United States]. One other chromosome count of  $2n=18$  has been made (Kawatani and Ohno, 1964), but I do not have that paper in hand, and so do not know its geographic provenance. Belaeva and Siplivinsky (1977) reported  $2n=54$  chromosomes for the taxon from Lake Baikal.

ARTEMISIA FURCATA Bieb., s.str.

A. trifurcata Steph.

$2n=18$ : Young 7506. Misheguk Mt. Quad.: Driftwood,  $68^{\circ}51'N$ ,  $161^{\circ}07'W$ .

$2n=18 + 0-3B$ : Young 7510. Utukok Quad.: Archimedes Ridge,  $69^{\circ}10'N$ ,  $161^{\circ}16'W$ .

Artemisia furcata shows a spotty distribution along south facing slopes and open ground in western U.S.S.R., Japan, and northwest North America. It has been treated quite differently by Soviet and American workers (cf. Hult en, 1973, p. 506). Korobkov (1972) has extensively studied the taxon in the Soviet Union, and found that the two chromosome races present (diploid  $2n=18$  and tetraploid  $2n=36$ ) are fairly well separated geographically with nine diploid representatives from the Taimyr region, arctic Yakutia, and western Chukchi Peninsula, and 42 tetraploid counts from Wrangel I., eastern Chukchi Peninsula, and north of Magadan. Both ploidy levels were found in a population near Chaun (Korobkov, 1972). In Japan, Kawatani and Ohno (1964) reported three ploidy levels,  $2n=18,36,54$ ; in North America, the only previous count, a decaploid,  $2n=90$ , was made on the population at Ogotoruk Creek (Johnson and Packer,

1968 as A. trifurcata). The counts reported here from the western Brooks Range are interesting because of the presence of microchromosomes, which had not yet been reported for the taxon.

ARTEMISIA TILESII Ledeb.

2n=18: Troy S-49. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

2n=36: Dawe s.n., August 29, 1976. Mt. Hayes Quad.: Paxson, 63°02'N, 145°29'W.

ssp. ELATIOR (Torr. & Gray) Hult.:

2n=36: Dawe 777. Mt. Hayes Quad.: Mi 21 Denali Hwy., 63°02'N, 146°01'W.

ssp. GORMANI (Rydb.) Hult.:

2n=36: Dawe 659. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

ssp. UNALASCHCENSIS (Bess.) Hult.:

2n=36: Hatch 190. Sutwik I. Quad.: Chowiet I., 56°02'N, 156°42'W.

The Eurasian-American Artemisia tilesii complex is comprised of four more or less distinct subspecific taxa that are sympatric (in part) in Alaska, and appear to intergrade. This could be because 1) the morphologic characters used to separate them are variable, or 2) they hybridize as suggested by Hultén (1968). Previous counts made in Alaska include 2n=36 for A. tilesii (no subspecies given) from Umiat (Packer and McPherson, 1974), 2n=18 for ssp. elator from Ogotoruk Creek (Johnson and Packer, 1968), and 2n=54 for ssp. unalaschcensis from Unalaska (Babcock and Stebbins, 1938). Both diploids (2n=18) and tetraploids (2n=36) have been recorded for the complex in Canada and the U.S.S.R.

Löve and Löve (1975a) divided the complex strictly along cytologic lines, when they reported that all representatives of A. tilesii s.str. must be diploid, and all ssp. elator Torr. & Gray, s.str., tetraploid. In fact, they shifted Johnson and Packer's chromosome count of  $2n=18$  for ssp. elator (Johnson and Packer, 1968) to A. tilesii s.str., presumably to have that chromosome count conform with the pattern they perceived. Granted that the morphotypes do overlap and that the nomenclature is somewhat tentative, Löve and Löve (1975a) were nevertheless taking a great liberty in the case just mentioned. Their conclusion that a good correlation existed between morphotypes and cytotypes, based on a small sample, was consequently premature. Many more data are needed before the complex can be effectively analyzed in terms of its cytologic characteristics.

#### ASTER SIBIRICUS L.

$2n=18$ : Dawe s.n., August 29, 1976. Mt. Hayes Quad.: Paxson,  $63^{\circ}02'N$ ,  $145^{\circ}29'W$ .

The same chromosome number has been reported sixteen times for the taxon throughout North America, Asia, and Europe. Its chromosomes have been counted in Alaska on plants from Ogotoruk Creek (Johnson and Packer, 1968) and Wild Lake (Hedberg, 1967).

Hultén (1967) reviewed the Soviets' amended treatment of A. sibiricus as three morphologically and geographically separated species. He found (1967) that the two aggregate taxa were only later synonyms of the third (A. sibiricus), and that the transition between what the Soviet

workers considered a morphologically distinct taxon and typical A. sibiricus was complete here in Alaska. For these reasons, Hultén (1967) retained A. sibiricus as the name for the western North American taxon.

CHRYSANTHEMUM ARCTICUM L.

Leucanthemum hultenii Löve and Löve, Dendranthema arcticum (L.) Tzvelev.

Chrysanthemum arcticum has been reported to have  $2n=18$  chromosomes from Ogotoruk Creek (Johnson and Packer, 1968 as Leucanthemum hultenii) and northwest Siberia (six records). Dowrick (1952) and Natarajan (1964) have reported octoploids ( $2n=72$ ) and Tahara (1915a, 1915b, 1921) decaploids ( $2n=90$ ). Löve and Löve (1975a) reported all  $2n=72$  counts as Dendranthema arcticum s.str. and treated all plants with  $2n=18$  chromosomes as D. hultenii (Löve and Löve) Tzvelev.

CREPIS ELEGANS Hook.

$2n=14$ : Dawe GR 26. Mt. Hayes Quad.: Gerstle R.,  $63^{\circ}46'N$ ,  $145^{\circ}02'W$ .

The same number was recorded in Alaska for this North American Cordilleran species by Legge (1971) from Bettles, Eagle Summit, and Riley Creek, by Babcock and Stebbins (1938) from Mt. McKinley National Park, by Hedberg (1967) from Umiat, and by Johnson and Packer (1968) from Ogotoruk Creek. Elsewhere it has been counted at  $2n=14$  by Hollingshead and Babcock (1930).

CREPIS NANA Richards. ssp. NANA

2n=14: Dawe 611. Mt. Hayes Quad.: Paxson, 63°02'N, 145°29'W.

Crepis nana is the most widely distributed member of the genus Crepis and is found in the mountainous areas of central Asia, Siberia, Alaska, and Canada, including the entire length of the North American Cordillera (Legge, 1971). In North America it is comprised of three morphologically and ecotypically well marked subspecies. Tap rooted, gravel bar inhabiting ssp. nana, and rhizomatous, talus slope ssp. clivicola Legge, both occur in Alaska, while ssp. ramosa Babco. is found in the mountains of British Columbia south to Colorado (Legge, 1971).

Despite the well marked morphotypes and ecotypes that are presented in the complex, it retains a uniform chromosome number of 2n=14. In Alaska, the chromosomes of ssp. nana have been counted from six locales by Legge (1971) and from Umiat by Hedberg (1967). Legge (1971) reported a count for ssp. clivicola from Sable Mt., Mt. McKinley National Park, and also referred the count made by Johnson and Packer (1968) on plants from Ogotoruk Creek to this same subspecies. Babcock (1947) listed a chromosome count for C. nana [no subspecies designation given, which Legge (1971) tentatively placed under ssp. nana] from "Alaska". No better locality data are available for Babcock's count. In addition to those, chromosome counts for C. nana have been published in nine reports for locations throughout Canada, the western United States, and Soviet Union.

In his detailed study of the genealogy of Crepis nana in arctic and alpine North America, Legge (1971) did not complete any karyotypic

analyses, but wrote that morphological differences do exist that could be helpful in future studies of the complex. Although the chromosomes are relatively small, they show definite morphologic differences in size and placement of centromere. Abundant, flat mitotic spreads are easy to obtain; thus the C. nana complex is an attractive candidate for chromosome banding, a technique that may have sufficient resolution to detect any existing infraspecific karyotypic differences.

ERIGERON ACRIS L. ssp. POLITUS (E. Fries) Schinz and Keller

2n=18: Dawe 602. Mt. Hayes Quad.: Paxson, 63°02'N, 145°29'W.

Dawe 776. Mt. Hayes Quad.: Mi 21 Denali Hwy., 63°02'N, 146°01'W.

Erigeron acris includes a number of very closely related taxa that readily intergrade with each other. All chromosome counts reported for the species to date have been diploid, 2n=18, including a count based on material from Beaver Creek in the White Mts. of central Alaska (Knaben, 1968). The chromosome vouchers from the Alaska Range, reported here, belong to ssp. politus, the circumpolar, arctic-montane race of the acris complex.

ERIGERON CAESPITOSUS Nutt.

2n=18: Murray and Johnson 6262. Chandalar Quad.: Sukakpak Mt., 67°36'N, 149°45'W.

This diploid report for Erigeron caespitosus, a western North American endemic, represents a new ploidy level for the species. Its chromosomes have been counted only once before, at the tetraploid level

( $2n=36$ ), from material collected near Fort MacLeod, Alberta (Taylor and Brockman, 1966).

ERIGERON GRANDIFLORUS Hook.

$2n=36$ : Murray and Johnson 6491. Philip Smith Mts. Quad.: Galbraith Lake,  $68^{\circ}30'N$ ,  $149^{\circ}25'W$ .

The distribution of Erigeron grandiflorus is narrowly restricted to the mouth of the Mackenzie River, the Alaska Range, and Rocky Mt. Cordillera. In the southern part of its range, it is comprised of apomictic triploids,  $2n=27$  (Spongberg, 1973). This first Alaskan count, for a tetraploid, sexually reproducing plant, runs counter to Spongberg's prediction (1973) that the Alaskan population would also be apomictic and triploid. The only other published chromosome count,  $2n=18$  [based on material purported to be E. grandiflorus by Chouksanova, Sveshnikova, and Alexandrova (1968)], may have been made on material from outside the distribution range accepted for the taxon by American workers.

ERIGERON MUIRII Gray

E. grandiflorus Hook. ssp. muirii (Gray) Hult.

$2n=18$ : Roseneau s.n., August 25, 1977. Point Hope Quad.: Cape Thompson,  $68^{\circ}09'N$ ,  $165^{\circ}59'W$ .

This is the first chromosome number reported for this rare Alaska-Yukon endemic, which differs from closely related E. grandiflorus by its dense, lanate pubescence. According to D. F. Murray (oral comm. on 1

March 1979 by D. F. Murray, Curator of the University of Alaska Herbarium, Fairbanks, Alaska), who reviewed all the specimens assigned to this taxon at National Herbarium of Canada (CAN) and Swedish Museum of Natural History (S), the dot from Herschel Island should be removed from Hulten's distribution map for E. muirii (1968, p. 866).

ERIGERON PURPURATUS Greene

2n=18: Murray and Johnson 6976. Mt. Michelson Quad.: Okpilak R. valley, 69°25'N, 144°03'W.

Batten, Dawe, and Murray 78-72. Mt. Hayes Quad.: Falls Creek, Mi 226 Richardson Hwy., 63°31'N, 145°51'W.

The same number has been reported from Livengood (Knaben, 1968) and Umiat (Hedberg, 1967; Packer and McPherson, 1974) in Alaska. Mulligan and Porsild (1970) reported it from the Ogilvie Mts., Yukon Territory.

SAUSSUREA NUDA Ledeb.

2n=26: Troy S-3. Norton Bay Quad.: Koyuk, 64°50'N, 160°54'W.

Saussurea nuda has been counted once before at 2n=26 by Zhukova (1966).

SENECIO OGOTORUKENSIS Packer

2n=46: Dawe 744. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

The same chromosome number has been reported for this rare Alaska-Yukon endemic based on material from Ogotoruk Creek (Johnson and Packer,

1968) and Kluane Lake, Yukon Territory (Packer, 1972). Senecio ogotorukensis has received widely different treatment by various authors. Packer's review (1972) seems the most taxonomically and cytologically satisfying, in that he distinguished glabrous Alaska-Yukon material, S. ogotorukensis (2n=46) from glabrous Rocky Mt. (Alberta and Montana) S. conterminus Greenman (2n=160+), and restricted S. hyperborealis Greenman (2n=46) to northern material showing hirtellous achenes (Packer, 1972). Barkley (in Cronquist et al., 1978) appears to have adopted too broad a taxonomic concept by including S. ogotorukensis in S. hyperborealis, and Löve and Löve (1975a) presented too narrow a generic concept by transferring S. ogotorukensis, S. resedifolius, and S. hyperborealis to a separate genus, Packera.

SOLIDAGO MULTIRADIATA Ait.

var. MULTIRADIATA:

2n=36: Dawe s.n., August 29, 1976. Mt. Hayes Quad.: Paxson, 63°02'N,  
146°29'W.

Dawe 715. Mt. Hayes Quad.: Tangle L., 63°02'N, 146°01'W.

var. ARCTICA (DC.) Fern.:

2n=36 + 2-4B: Hatch 193. Sutwik I. Quad.: Chowiet I., 56°02'N, 156°42'W.

According to Hultén (1947, 1971), Solidago multiradiata is represented by three minor geographic and morphologic races in Alaskan and neighboring territories, which need monographic treatment before their interrelationships can be appreciated. As would be expected, Löve and Löve (1975a) tolerated much less infraspecific variation in their species

concept than Hultén did, and split the taxon into two species on the basis of cytology. All  $2n=18$  chromosome counts were maintained as S. multiradiata s.str.; those plants with  $2n=36$  chromosomes were transferred to S. compacta Turcz. This division runs counter to Hultén's circumscriptions, both in the morphology exhibited by the specimens and the geographic range occupied. Following Hultén's taxonomy, all the varieties are known to exist at the diploid and tetraploid ( $2n=36$ ) levels. Obviously, more data are needed before good cytologic analyses of the complex can be made, but generally, diploid populations are found in the southern and eastern parts of the complex's range, and tetraploids in the northwestern region.

The chromosomes of S. multiradiata have been counted once before in Alaska from Ogotoruk Creek on the northwest coast (Johnson and Packer, 1968). Note that in the chromosome counts reported here for the first time, the Chowiet Island plants show microchromosomes, while the specimens from the Alaska Range do not.

TRIPLEUROSPERMUM PHAEOCEPHALUM (Rupr.) Pobed.

Matricaria ambigua (Ledeb.) Kryl., M. maritima var. phaeocephala (Rupr.) Hyl.

$2n=18$ : Troy S-31. Norton Bay Quad.: Koyuk,  $64^{\circ}50'N$ ,  $160^{\circ}54'W$ .

The chromosome number of Tripleurospermum phaeocephalum has been found to be  $2n=18$  six times before, including counts on material from northeast Greenland, Scandinavia, and Chukchi Peninsula. I have not been able to locate papers by Ishikawa (1916, 1921) to determine where that material came from.

## Summary

### Cytotaxonomy

The Alaskan vascular plant taxa which have been examined cytologically during the course of this study are shown in Table 6. First chromosome counts are reported for 17 taxa and the same number of taxa are reported at new ploidy levels. Forty-seven chromosome counts are first reports for Alaskan material.

Many of these taxa may be placed along a continuum of cytologic-morphologic-biogeographic variability (Table 7). At one extreme of this continuum [Table 7(a),(b)] are taxa having within-species morphologic differences that are too small or inconsistent for formal taxonomic recognition. The variability seen in taxa occupying the middle portion of the continuum [Table 7(c)-(e)] is marked in at least some criteria and allows segregation of new morphological and/or geographic types. At the continuum's other extreme are those taxa that are determined discontinuous by criteria of cytology, morphology, and geography [Table 7(f)].

My interest and emphasis lie in using chromosome information to clarify problems of taxonomic importance. The resolution given by functional diploid chromosome number alone is often highly limited, a problem manifested by taxa at any level of the taxonomic hierarchy. For example, eight species of the genus Dryas are well-marked morphologically, and the fundamental differences between these species presume their reproductive isolation from one another. Importantly, this isolation has developed in the absence of cytological differences in functional diploid chromosome number. In every species,  $2n=18$  (cf. Federov, 1969). More

Table 6. Original chromosome counts from selected Alaskan vascular plant taxa.

Taxon	2n	1st count for taxon	new ploidy level	1st Ak. count	previously counted-Ak.
Poaceae (Gramineae)					
<i>Agropyron macrourum</i>	28				x
<i>Elymus mollis</i>	28				x
<i>Festuca altaica</i>	28				x
<i>Hierochloë alpina alpina</i>	56				x
<i>Hordeum brachyantherum</i>	28			x	
Cyperaceae					
<i>Carex obtusata</i>	52			x	
<i>Eriophorum scheuchzeri</i>	58				x
Juncaceae					
<i>Luzula arcuata unalaschkensis</i>	36			x	
<i>Luzula groenlandica</i>	24			x	
<i>Luzula multiflora frigida</i>	36				x
Liliaceae					
<i>Allium schoenoprasum sibiricum</i>	16				x
<i>Zygadenus elegans</i>					x
Iridaceae					
<i>Iris setosa setosa</i>	38				x
Betulaceae					
<i>Betula glandulosa</i>	28			x	
Polygonaceae					
<i>Bistorta vivipara</i>	c.100				x
<i>Oxyria digyna</i>	14				x
<i>Polygonum alaskanum</i>	20			x	
<i>Rumex arcticus</i>	40				x
	c.80				x
<i>Rumex sibiricus</i>	20				x
Portulacaceae					
<i>Claytonia arctica</i>	c.40		x		x
<i>Claytonia sibirica</i>	12				x
Caryophyllaceae					
<i>Cerastium maximum</i>	38			x	
<i>Sagina maxima crassicaulis</i>	66			x	
<i>Silene acaulis acaulis</i>	24				x
<i>Silene reprens purpurata</i>	24	x			
<i>Wilhelmsia physodes</i>	66				x
Ranunculaceae					
<i>Aquilegia brevistyla</i>	16	x			
<i>Pulsatilla patens multifida</i>	16				x

Table 6. (Continued)

Taxon	2n	1st count for taxon	new ploidy level	1st Ak. count	previously counted-Ak.
Papaveraceae					
<i>Papaver alboroseum</i>	28			x	
<i>Papaver lapponicum</i>	56			x	
<i>Papaver nudicaule</i>	28			x	
Brassicaceae (Cruciferae)					
<i>Alyssum americanum</i>	32			x	
<i>Arabis holboellii</i>	14				x
<i>Arabis lyrata kamchatica</i>	16				x
<i>Barbarea orthoceras</i>	16				x
<i>Braya bartlettiana</i>	56	x			
<i>Braya pilosa</i>	28			x	
	56		x		
	64		x		
<i>Braya purpurascens</i>	56				x
<i>Cardamine bellidifolia</i>	16				x
<i>Cochlearia arctica</i>	14				x
<i>Draba adamsii</i>	48		x		x
<i>Draba lactea</i>	16		x		x
<i>Draba murrayi</i>	48	x			
<i>Draba palanderiana</i>	16				x
<i>Draba stenoloba</i>	16		x	x	
<i>Erysimum angustatum</i>	36	x			
<i>Halimolobus mollis</i>	16			x	
<i>Lesquerella arctica</i>	60				x
<i>Rorippa barbaraefolia</i>	16				x
<i>Rorippa palustris hispida</i>	32			x	
<i>Smelowskia borealis jordalii</i>	12	x			
<i>Smelowskia borealis kohliana</i>	12	x			
<i>Smelowskia calycina integ-</i> <i>rifolia porsildii</i>	22		x	x	
<i>Smelowskia calycina media</i>	12	x			
<i>Thlaspi arcticum</i>	14	x			
Crassulaceae					
<i>Sedum divergens</i>	16			x	
<i>Sedum integrifolium</i>	36			x	
Saxifragaceae					
<i>Saxifraga hirculus</i>	16				x
Rosaceae					
<i>Acomastylis rossii</i>	70			x	
<i>Chamaerhodos erecta nuttallii</i>	14			x	
<i>Dryas drummondii</i>	18				x
<i>Dryas integrifolia sylvatica</i>	18	x			
<i>Geum macrophyllum macrophyllum</i>	42			x	
<i>Pentaphylloides fruticosa</i>	14				x

Table 6. (Continued)

Taxon	2n	1st count for taxon	new ploidy level	1st Ak. count	previously counted-Ak.
<i>Potentilla bipinnatifida</i>	56			x	
<i>Potentilla egedii</i>	28			x	
<i>Potentilla hyparctica</i>	42				x
<i>Potentilla multifida</i>	28			x	
<i>Potentilla pennsylvanica</i>	28			x	
<i>Potentilla villosa</i>	14			x	
<i>Sanguisorba officinalis</i>	28				x
<i>Sanguisorba stipulata</i>	28				x
<i>Sibbaldia procumbens</i>	14				x
Fabaceae (Leguminosae)					
<i>Astragalus aboriginorum</i>	16		x		x
<i>Astragalus eucosmus eucosmus</i>	32			x	
<i>Astragalus nutzotinensis</i>	22				x
<i>Astragalus robbinsii</i>	32			x	
<i>Astragalus sealei</i>	16				x
<i>Hedysarum alpinum americanum</i>	14				x
<i>Lathyrus pilosus</i>	14			x	
<i>Lupinus arcticus</i>	48				x
<i>Oxytropis borealis</i>	48				x
<i>Oxytropis campestris varians</i>	16		x		x
	32		x		
	96				x
<i>Oxytropis jordalii</i>	36				x
<i>Oxytropis viscida</i>	16		x	x	
<i>Oxytropis deflexa foliolosa</i>	16			x	
<i>Oxytropis huddelsonii</i>	16			x	
<i>Oxytropis kobukensis</i>	80	x			
<i>Oxytropis koyukukensis</i>	48				x
<i>Oxytropis scammaniana</i>	16		x		x
Linaceae					
<i>Linum lewisii</i>	18			x	
Elaeagnaceae					
<i>Elaeagnus commutata</i>	28	x			
<i>Shepherdia canadensis</i>	22			x	
Geraniaceae					
<i>Geranium erianthum</i>	28			x	
Onagraceae					
<i>Epilobium angustifolium</i>					
<i>angustifolium</i>	36				x
<i>Epilobium latifolium</i>	72				x
Apiaceae (Umbelliferae)					
<i>Bupleurum triradiatum arcticum</i>	28				x
<i>Cnidium cnidiifolium</i>	22				x

Table 6. (Continued)

Taxon	2n	1st count for taxon	new ploidy level	1st Ak. count	previously counted-Ak.
Diapensiaceae					
<i>Diapensia lapponica obovata</i>	12				x
Primulaceae					
<i>Androsace septentrionalis</i>	20				x
<i>Dodecatheon frigidum</i>	44				x
<i>Dodecatheon pulchellum</i> pauciflorum	44			x	
<i>Douglasia arctica</i>	38			x	
Gentianaceae					
<i>Gentiana glauca</i>	24				x
<i>Swertia perennis</i>	28			x	
Polemoniaceae					
<i>Polemonium acutiflorum</i>	18				x
<i>Polemonium boreale boreale</i> villosissimum	18	x			
<i>Polemonium pulcherrimum</i>	18				x
Hydrophyllaceae					
<i>Phacelia mollis</i>	22			x	
<i>Phacelia sericea</i>	22			x	
Boraginaceae					
<i>Cryptantha shackletteana</i>	24	x			
<i>Mertensia drummondii</i>	24	x			
<i>Mertensia maritima</i>	24				x
<i>Mertensia paniculata</i>	72		x	x	
Scrophulariaceae					
<i>Castilleja caudata</i>	24		x		x
	72		x		
<i>Castilleja elegans</i>	24				x
<i>Pedicularis lanata</i>	16				x
<i>Pedicularis sudetica</i>	16 + 8-10B				x
<i>Pedicularis verticillata</i>	12 + 0-2f				x
<i>Penstemon gormanii</i>	16 + 0-5B			x	
Valerianaceae					
<i>Valeriana capitata</i>	64				x
Campanulaceae					
<i>Campanula aurita</i>	34				x

Table 6. (Continued)

Taxon	2n	1st count for taxon	new ploidy level	1st Ak. count	previously counted-Ak.
Asteraceae (Compositae)					
<i>Artemisia alaskana</i>	18				x
<i>Artemisia arctica arctica</i>	18				x
<i>Artemisia borealis</i>	36				x
<i>Artemisia frigida</i>	18				x
<i>Artemisia furcata</i>	18 + 0-3f				x
<i>Artemisia tilesii</i>	18				x
	36				
<i>Aster sibiricus</i>	18				x
<i>Chrysanthemum arcticum</i>	18				x
<i>Crepis elegans</i>	14				x
<i>Crepis nana nana</i>	14				x
<i>Erigeron acris politus</i>	18				x
<i>Erigeron caespitosus</i>	18		x	x	
<i>Erigeron grandiflorus</i>	36		x	x	
<i>Erigeron muirii</i>	18	x			
<i>Erigeron purpuratus</i>	18				x
<i>Saussurea nuda</i>	26			x	
<i>Senecio ogotorukensis</i>	46				x
<i>Solidago multiradiata arctica</i>	36 + 2-4f				x
<i>Solidago multiradiata multiradiata</i>	36				x
<i>Tripleurospermum phaeocephalum</i>	18			x	

Table 7. Continuum of cytologic-morphologic-biogeographic variability seen in selected Alaskan vascular plant taxa.

← a	b	c	d	e →
one morphotype/two to several cytotypes:	morphotypes and cytotypes not correlated with each other:	cytotypes geographically segregated but no morphologic distinctions:	cytotypes and morphotypes correlated with geography or ecology but taxa not morphologically recognized:	taxa distinct morphologically, chromosomally, and ecologically:
<u>Hierochloë alpina</u> <u>ssp. alpina</u> <u>Iris setosa</u> <u>ssp. setosa</u> <u>Sagina maxima</u> <u>Wilhelmsia physodes</u> <u>Papaver lapponicum</u> <u>Papaver nudicaule</u> <u>Arabis lyrata</u> <u>ssp. kamchatica</u> <u>Draba adamsii</u> <u>Draba lactea</u> <u>Pentaphylloides</u> <u>fruticosa</u> <u>Potentilla egedii</u> <u>Potentilla hyparctica</u> <u>Potentilla multifida</u> <u>Potentilla pensylvanica</u> <u>Sanguisorba officinalis</u> <u>Lupinus arcticus</u> <u>Oxytropis borealis</u> <u>Polemonium pulcherrimum</u> <u>Castilleja caudata</u> <u>Valeriana capitata</u> <u>Artemisia borealis</u> <u>Artemisia furcata</u> <u>Aster sibiricus</u> <u>Chrysanthemum arcticum</u>	<u>Bistorta vivipara</u> <u>Rumex arcticus</u> <u>Saxifraga hirculus</u> <u>Astragalus aboriginorum</u> <u>Oxytropis campestris</u> <u>ssp. varians</u> <u>Epilobium latifolium</u> <u>Artemisia arctica</u> <u>Artemisia tilesii</u> <u>Solidago multiradiata</u>	<u>Draba palanderiana-</u> <u>D. caesia</u> <u>Smetowskia calycina</u> <u>ssp. integrifolia</u> <u>var. porsildii</u> <u>Oxytropis jordalii</u> <u>Bupleurum triradiatum</u> <u>ssp. arcticum</u> <u>Artemisia frigida</u>	<u>Claytonia sibirica</u> <u>Arabis holboellii</u> <u>Hedysarum alpinum</u> <u>ssp. americanum</u> <u>Erigeron grandiflorus</u>	<u>Papaver alboroseum-</u> <u>var. elongatum</u> <u>Hierochloë alpina</u> ssp. <u>alpina-ssp. orthantha</u> <u>Lathyrus pilosus-</u> <u>L. palustris</u> <u>Epilobium angustifolium</u> <u>ssp. angustifolium</u> <u>ssp. macrophyllum</u> <u>Dodecatheon pulchellum</u> <u>ssp. pauciflorum-</u> <u>ssp. alaskanum-</u> <u>ssp. macrocarpum</u>

sophisticated cytologic techniques may demonstrate differential chromosome banding types between Dryas species and provide cytologic evidence for reproductive isolation and differentiation.

The same problem of resolution occurs with taxa at infraspecific levels. Five pairs of taxa included in this study show ecological and morphological discontinuities in the absence of corresponding cytological differences in functional diploid chromosome number. These taxa include Betula nana-B. glandulosa, Dryas integrifolia ssp. integrifolia-ssp. sylvatica, Polemonium boreale ssp. boreale var. boreale-ssp. boreale var. villosissimum, Crepis nana ssp. nana-ssp. clivicola, and Smelowskia borealis var. kohliana-var. villosa. (Smelowskia borealis is only tentatively placed here because the taxonomic differences perceived between the two named varieties may simply have resulted from having scant material available for describing the varieties). In each example (excluding Betula) the races which are treated as subspecies or varieties formed without any obvious change in karyotype. Yet each pair occurs sympatrically, which separates these taxa both from the true vicariads, corresponding taxa that come to occupy different regions prior to their differentiation, and false vicariads, taxa which first differentiate and then enter new territories (Löve, 1953, 1955). Once again the fundamental differences between the two taxa in each pair presumes their reproductive isolation.

Despite the limitations mentioned above, chromosome numbers often signal fundamental changes within morphologically defined taxa. Each of the 24 taxa included under (a) in Table 7 possesses one morphotype but two to several cytotypes. Several patterns may be seen within these

cytologically variable, but morphologically constant taxa:

(1) Eight of the taxa are cytologically uniform throughout most of their geographic ranges, but have local populations whose members show divergent chromosome numbers. Three of these, Papaver lapponicum, Iris setosa ssp. setosa, and (in part) Draba lactea, have different chromosome numbers on either side of the Bering Strait, while a fourth taxon, Artemisia borealis, appears to behave differently in Japan and Alaska than throughout the U.S.S.R., Canadian arctic, Greenland, and Rocky Mountains. Two of the eight taxa show divergent chromosome numbers in parts of North America: Arabis lyrata ssp. kamchatica is cytologically variable in Alaska, but, with one exception, uniform in Canada, whereas Potentilla hyparctica is uniformly hexaploid throughout its circumboreal range, except east of Hudson Bay, where it is also septaploid. Finally, two taxa, Potentilla egedii and Hierochloë alpina ssp. alpina, have constant chromosome numbers everywhere except in Scandinavia, where both taxa show proliferation of higher aneuploid populations.

(2) Three taxa show divergent chromosome numbers both within specific populations and throughout their entire range: Lupinus arcticus, Oxytropis borealis, and Draba adamsii.

(3) Five taxa: Papaver nudicaule, Wilhelmsia physodes, Pentaphylloides fruticosa, Sanguisorba officinalis, and Valeriana capitata, have been found to have different chromosome numbers throughout their ranges, but so far, only constant chromosome numbers within any one population.

(4) Seven taxa show variable cytotypes and uniform morphology, but in each case there are too few data to determine any geographic trends.

These taxa are Sagina maxima, Potentilla multifida, P. pensylvanica, Polemonium pulcherrimum, Castilleja caudata, Artemisia furcata, and Chrysanthemum arcticum.

Located further along the continuum, towards taxa that are morphologically variable, are nine species or species complexes [Table 7(b)] in which the various cytotypes show no correlation with the different morphotypes present.

Next a group of five taxa shows geographically segregated cytotypes with no apparent morphologic distinctions between them [Table 7(c)]. With regard to this type of problem, Soviet workers appear to reverse their usual "splitter" stance by treating Asian Draba caesia,  $2n=32$ , and American D. palanderiana,  $2n=16$ , as one taxon, D. palanderiana. A problem of similar magnitude may be presented by so-called Oxytropis jordalii,  $2n=96$ , from Wrangel Island, U.S.S.R., and O. jordalii,  $2n=32$ , Alaska, Alberta, and Northwest Territories. Three other taxa show clear geographic and cytologic differences. One of these, Smelowskia calycina ssp. integrifolia var. porsildii is cytologically distinct on either side of the Bering Strait. (A parallel situation in conspecific North American S. calycina var. americana has been found, in that its northern population exhibits a different chromosome number than its southern one). Lastly, Bupleurum triradiatum ssp. arcticum, and tentatively, Artemisia frigida, show Eurasiatic vs. American population segregates.

Four taxa show at least local correspondence between morphotype and cytotype [Table 7(d)]. In part of its range, Hedysarum alpinum ssp. americanum shows parallel cytotypes and morphotypes with distinct

ecological requirements, but elsewhere in its range, Hedysarum alpinum shows no evidence of two independently evolving populations. The three other taxa included in Table 7(d): Claytonia sibirica, Arabis holboellii, and Erigeron grandiflorus, show local cytotypes and correlated morphotypes. In each of these taxa, however, the infraspecific differences have not generally been considered distinct enough to warrant taxonomic recognition.

The species complexes listed under Table 7(e) present cases in which the taxa have become distinct from one another chromosomally, morphologically, and ecologically; however, the degree of separation is not considered great enough to raise any of the infraspecific taxa to the rank of species. In each of these examples, chromosome number differences have provided part of the basis for making the original taxonomic distinctions, or have added support for reinstating older nomenclatural combinations for taxa that had more recently been subsumed under one name.

### Cytogeography

The preceding summary emphasizes inferences about the genetic and evolutionary histories of individual taxa based on chromosome number analyses. Knowledge of the presence or absence, degree, and type of polyploidy within taxa can be paramount to understanding their evolutionary divergences but the subsequent characterization of these taxa and their placement along a continuum of cytologic, morphologic, and biogeographic variability is not meant to imply an on-going process of differentiation and speciation. In a broad sense, however, it appears

that speciation may occur with the ecologic or geographic segregation of polyploid derivatives of morphologically defined taxa.

In the same way that evolutionary histories of individual taxa may be clarified by their chromosome number patterns, so too may the history of an entire flora be elucidated by determining the characteristic chromosome number variability or stability shown by its floristic components. Historically, this has been quantified as the percentage of polyploidy within a given flora. As pointed out in the introduction, classical hypotheses that proposed absolute latitudinal gradients of polyploidy, or correlations between polyploidy and "severity" of environment, have been dismissed as overly simplistic and misleading. Instead, polyploidy appears to become important when taxa are stressed beyond the limits of their ecologic tolerances, established by adaptations to the environment(s) in which they evolved. These ecological parameters, in turn, are largely determined by the geographic and climatic conditions under which the flora developed.

Cytogeographic trends with Hultén's equiformal distribution areas.

In order to determine the relationship between polyploidy and the history of the portion of the Alaskan flora I studied, I separated my taxa into 10 of the 39 progressive equiformal distribution areas defined by Hultén (1937). In his analysis of the floras of northern northwest America and northeast Siberia, Hultén (1937) found that taxa could be grouped into distribution patterns characterized by sets of Pleistocene refugia from which the taxa dispersed in a pattern of ever widening lobes or circles. Hultén assumed that most present day taxa already occupied their current distribution areas by the Great Interglacial, i.e. the relatively long,

warm, dry period preceding the maximum, or Wisconsin, glaciation 35,000 years ago (Hopkins, 1967). Given this assumption, Hultén (1937) proposed that the current distribution patterns of the species in the floras he studied reflect historic pulses of migration-expansion and extermination-contraction, largely controlled by Pleistocene glacial related phenomena. Hultén's units are clearly historically, not taxonomically, based, although relatively recently derived groups of taxa may show their common origin and dispersal patterns by aggregating into one or several distribution types (Draba and Braya/Northern Beringian, Mertensia and Oxytropis/Continental West American, and Artemisia/Arctic-Montane).

Using Hultén's geographic distribution classification scheme (Hultén, 1937), I divided 105 taxa from which I obtained chromosome counts into the following groups:

(a) continental:

- (1) Continental Eurasiatic
- (2) Continental West American

(b) Beringian:

- (3) North Beringian
- (4) South Beringian
- (5) Bilateral Radiants of North Beringia
- (6) Arctic-Pacific
- (7) Atlantic-Pacific
- (8) West American Coastal Radiants

(c) circumboreal:

- (9) Arctic-Montane
- (10) Boreal Circumboreal

Only one taxon fell within the Continental Eurasiatic group; it was therefore seldom used in subsequent analyses. The rest of the taxa were grouped in four inclusive categories: Beringian, Continental West American, Arctic-Montane, and Boreal Circumboreal. Later, subelements of three of these groups (all except Continental West American) were defined and tested for divergent within-group chromosome behavior.

Appropriate cytologic and biogeographic characteristics were noted for each taxon in Table 8. These include the taxon's chromosome behavior throughout its distribution range; whether it demonstrates constant chromosome number, a euploid series of chromosome numbers, a euploid-aneuploid series, or an aneuploid series alone. Next, a geographic descriptor was applied to each taxon which signified whether its main distribution is continental, strictly coastal (oceanic), mainly coastal but extending somewhat into continental areas along rivers or montane routes, or circumboreal (often including both continental and oceanic populations for a given taxon).

When the percentage of taxa showing constant chromosome number (as opposed to a lumped class of taxa showing various types of multiple chromosome numbers; euploid, aneuploid, euploid-aneuploid) was calculated for each geographic class, a definite trend became apparent (Table 9). Narrowly restricted continental groups, i.e. Beringian Continental (a subelement common to several of the six Beringian distribution types) and Continental West American taxa, showed the most conservative chromosome behavior, with 73% and 67% constant chromosome numbers, respectively. Circumboreal groups, Arctic-Montane and Boreal Circumboreal, showed intermediate levels of constant chromosome number (60%

Table 8. Placement of 104 taxa analyzed in this study in historic-geographic categories (after Hultén, 1937). S=constant chromosome number throughout range, E=euploid series, D=euploid/aneuploid series, A=aneuploid series; N=continental distribution, O=oceanic, T=tending towards oceanic, C=circumboreal.

BERINGIAN:		CONTINENTAL EUROPEAN:		ARCTIC-MONTANE continued:		
<u>North Beringian Radiants</u>			Rorippa barbaraefolia	S N	Smelowskia calycina	B N
Agropyron macrourum	S N				Sedum integrifolium	S N
Rumex sibiricus	S N	CONTINENTAL WEST AMERICAN RADIANTS:			Potentilla hyperctica	S C
Claytonia arctica	E N	Luzula arcuata unalaschensis	S N	Sibbaldia procumbens	S C	
Oxytropis jordalii	S N	Zygadenus elegans	S N	Astragalus aboriginorum	E N	
Cnidium cndiifolium	S N	Betula glandulosa	S N	Astragalus eucosmus eucosmus	S N	
		Arabis holboellii	E N	Oxytropis borealis	E N	
<u>South Beringian Radiants</u>		Barbarea orthoceras	S N	Oxytropis deflexa	S N	
Solidago multiradiata arctica	E O	Smelowskia borealis	S N	Epilobium latifolium	E C	
		Sedum divergens	S N	Diapensia lapponica obovata	S N	
<u>Bilateral Radiants of N. Beringia</u>		Acomastylis rossii	E N	Polemonium acutiflorum	S N	
Wilhelmsia physodes	B N	Chamaerhodos erecta nuttallii	S N	Pedicularis sudetica	S N	
Braya pilosa	B O	Dryas drummondii	S N	Pedicularis verticillata	S N	
Braya purpurascens	S T	Potentilla pensylvanica	E N	Valeriana capitata	B N	
Cochlearia officinalis arctica	S O	Hedysarum alpinum americanum	E N	Artemisia arctica	E N	
Draba adamsii	E O	Oxytropis campestris varians	B N	Artemisia borealis	E N	
Lesquerella arctica	S N	Oxytropis huddelsonii	S N	Artemisia frigida	S N	
Polemonium boreale boreale	S T	Oxytropis viscida	E N	Artemisia furcata	E N	
Castilleja caudata	E N	Bupleurum trifidatum arcticum	B N	Artemisia tilesii	E N	
Tripleurospermum phaeocephalum	S O	Dodecatheon pulchellum pauciflorum	S N	Crepis nana nana	S N	
Papaver lapponicum	E N	Dodecatheon frigidum	S N	Erigeron grandiflorus	E N	
		Gentiana glauca	S N			
<u>Arctic-Pacific Plants</u>		Polemonium pulcherrimum	E N	BOREAL CIRCUMBOREAL:		
Rumex arcticus	E T	Phacelia mollis	S N	Luzula groenlandica	S N	
Chrysanthemum arcticum	E O	Phacelia sericea	S N	Luzula multiflora frigida	S C	
		Hertensia paniculata	E N	Allium schoenoprasum	E C	
<u>Atlantic-Pacific Plants</u>		Crepis nana	S N	Arabis lyrata kamchatica	E C	
Elymus mollis	S O	Erigeron purpuratus	S N	Saxifraga hirculus	E C	
Halimolobus mollis	S N	Senecio ogotorukensis	S N	Potentilla multifida	E C	
Potentilla egedii	B O	Linum lewisii	S N	Pentaphragmoides fruticosa	E C	
Hertensia maritima	S O			Sanguisorba officinalis	E C	
Solidago multiradiata multiradiata	E N	ARCTIC-MONTANE:		Lathyrus pilosus	S C	
		Festuca altaica	S C	Shepherdia canadensis	S N	
<u>West American Coastal Radiants</u>		Hierochloë alpina alpina	S C	Epilobium angustifolium	S C	
Hordeum brachyantherum	S N	Eriophorum scheuchzeri	S C	Androsace septentrionalis	S C	
Iris setosa	A O	Polygonum viviparum	B C	Aster sibiricus	S N	
Claytonia sibirica	E O	Oxyria digyna	S C	Erigeron acris politus	S C	
Sagina maxima crassicaulis	B O	Cerastium maximum	S N			
Geum macrophyllum macrophyllum	S T	Silene acaulis acaulis	S N			
Potentilla villosa	E O	Cardamine bellidifolia	S C			
Sanguisorba stipulata	S N	Draba lactea	E C			
Geranium erianthum	S N					
Swertia perennis	S N					

Table 9. Percent taxa showing constant chromosome number in each geographic distribution class or subelement.

Distribution group	No. taxa showing constant chrom. no. Total no. taxa in group	Percent taxa showing constant chrom. no.
Beringian Continental	11/15	73
Continental West American	18/27	67
Arctic-Montane	18/30	60
Boreal Circumboreal	8/14	57
Beringian Oceanic	7/17	47

and 57%, respectively), while the one oceanic element, Beringian Oceanic (the second subelement of the Beringian distribution types), demonstrated less conservative chromosome behavior (47% constant chromosome number).

Although the trend discussed above may represent the chromosome behavior operating throughout the various geographic-floristic elements, the differences between them were not found to be statistically significant (Table 10) in a binomial probability distribution, in which the chromosome number(s) for each taxon was scored as either "constant" or "variable", such that:

$$\frac{p_1 - p_2}{\sqrt{\frac{p_1 q_1}{n_1} - \frac{p_2 q_2}{n_2}}} = \alpha$$

where:

p = probability that taxa in distribution class have constant chromosome number

q = probability that taxa in distribution class have variable chromosome number

n = total number of taxa in distribution class

$\alpha$  = critical value in Student's t distribution

Although the differences between the classes were not statistically significant, the trend suggests that with larger sample size and more

Table 10. Critical values (student's t-test,  $\alpha$ ) found by comparing the proportions of taxa showing constant chromosome number in various geographic elements. Results are considered statistically significant if  $\alpha \geq 1.96$  ( $n \geq 30$ ) for  $p=0.05$ , 2-tailed test.

Geographic Element	Geographic Element	Beringian oceanic	Continental West Amer	Arctic-Montane	circumboreal	continental	Boreal Circumboreal	circumboreal	continental	Circumboreal combined	Not circumboreal Arctic-Montane and Boreal Circumboreal	Continental combined	Not Circumboreal combined
constant chrom. no. taxa all taxa in distrib. class		$\frac{8}{17}$	$\frac{18}{27}$	$\frac{18}{30}$	$\frac{7}{10}$	$\frac{11}{20}$	$\frac{8}{14}$	$\frac{5}{11}$	$\frac{3}{3}$	$\frac{12}{21}$	$\frac{14}{23}$	$\frac{44}{67}$	$\frac{52}{81}$
Beringian	$\frac{19}{33}$	1.29	0.73	0.20	0.74	0.18	0.03	0.70	4.93	0.03	0.25	0.78	0.43
continental	$\frac{11}{19}$	1.29	0.14	0.60	0.07	0.86	0.66	1.23	2.70	0.73	0.51	0.24	0.53
oceanic	$\frac{8}{17}$	--	1.30	0.86	1.22	0.48	0.56	0.08	4.37	0.62	0.87	1.39	1.39
Continental W. Amer.	$\frac{18}{27}$		--	0.52	0.19	0.81	0.59	1.21	3.67	0.68	0.42	0.92	0.43
Arctic-Montane	$\frac{18}{30}$			--	0.59	0.35	0.18	0.83	4.47	0.20	0.06	0.53	0.18
circumboreal	$\frac{7}{10}$				--	0.82	0.66	1.18	2.07	0.71	0.52	0.28	0.53
continental	$\frac{11}{20}$					--	0.12	0.51	4.05	0.14	0.39	0.85	0.56
Boreal Circumboreal	$\frac{8}{14}$						--	--	--	0.00	0.22	0.59	0.33
circumboreal	$\frac{5}{11}$							--	3.63	0.63	0.85	1.26	1.03
continental	$\frac{3}{3}$								--	3.97	3.85	5.92	7.19
Circumboreal combined	$\frac{12}{21}$									--	0.25	0.70	0.40
Not circumboreal Arctic-Montane and Boreal Circumboreal	$\frac{14}{23}$										--	0.41	0.09
Continental combined	$\frac{44}{67}$											--	0.48
Not circumboreal combined	$\frac{52}{81}$												--

narrow resolution given by a multinomial, rather than binomial test, significant differences may be found.

Floristic zonation by Young. A different evaluation of the mechanisms governing present-day distribution patterns in the arctic flora was made by Young (1971), and it should be considered for its implications regarding the chromosome behavior of Alaskan floristic components. Young studied the vascular floras of several arctic Alaskan locations and compared them with floras from similar sites throughout the arctic. He found that while the ranges of non-circumpolar taxa largely reflected historic events, the distribution patterns of circumboreal taxa were mainly controlled by climatic factors, specifically, the amount of available summer warmth. Young's interpretation of distribution patterns therefore differs from that of Hultén (1937), who argued that gaps in the range of a circumboreal taxon represent contractions of its former, pre-Pleistocene range. Instead, Young stated that such gaps represent ecologically unsuitable areas for the otherwise circumboreal taxon, and that its present distribution expresses its total range, not a contraction of a pre-glacial one.

Young (1971) divided the circumboreal arctic flora into four zones, with boundaries defined by the northernmost limits of distribution of particular sets of taxa. While these floristically defined boundaries vary with the taxa chosen to define them, the concentricity of floristic zonation from the low arctic (zone 1) through the high arctic (zones 3 and 4) remains constant. Once established, the zones were found to be predictive for both the flora and the climatic regime when applied to a new area.

Only 19 of my taxa were included among the common circumboreal taxa found in each zone (Young, 1971); therefore, to increase sample size I added literature reports for 106 taxa whose chromosomes have been counted from Alaskan populations (Dawe and Murray, in prep.)(Table 11). Once again, each taxon was scored as either "constant" or "variable". The results of the various binomial distribution tests are shown in Table 12.

When all taxa included in each zone were tested against each other [Table 12(a)], only zones 1 and 4 showed statistically significant differences from each other (t-test,  $p < 0.05$ ). Dicots alone [Table 12(b)] showed a significant trend in increasing constancy of chromosome number from low arctic to high arctic (t-test,  $p < 0.10$  for zones 1 and 2, and zones 3 and 4;  $p < 0.05$  for zones 1 and 3, zones 1 and 4, and zones 2 and 4; zones 2 and 3 not statistically different). Monocots [Table 12(c)] show a general, but not statistically significant, trend of increasing constancy of chromosome number from the high arctic to the low arctic (t-test,  $p < 0.05$  between zones 1 and 4, and zones 2 and 4). These results should be viewed with caution because of the small sample sizes involved; four to 16 taxa in each zone. Grasses alone [Table 12(d)] appeared uniform in chromosome behavior throughout the zones, but again, sample sizes are too small to attach much confidence to the results. The sedge classes were too small to test, so a comparison of the chromosome behavior of grasses and sedges could not be performed. Finally, a comparison of the chromosome number patterns of monocots as opposed to dicots in each zone showed a general trend of increasingly divergent chromosome number

Table 11. Taxa used in chromosome number analysis of arctic floristic zones (after Young, 1971).

<u>Zone 1</u>	<u>Zone 2</u>	<u>Zone 3</u>	<u>Zone 4</u>
<i>Alopecurus alpina</i>	<i>Equisetum arvense</i>	<i>Calamagrostis purpurascens</i>	<i>Calamagrostis canadensis</i>
<i>Arctagrostis latifolia</i>	<i>Lycopodium selago</i>	<i>Elymus arenarius</i> s.l.	<i>Calamagrostis lapponica</i>
<i>Deschampsia caespitosa</i> s.l.	<i>Hierochloa alpina</i>	<i>Festuca rubra</i>	<i>Luzula parviflora</i>
<i>Dupontia fischeri</i> s.l.	<i>Hierochloa pauciflora</i>	<i>Poa alpina</i>	<i>Betula glandulosa</i> s.l.
<i>Phippsia algida</i>	<i>Puccinellia phryganodes</i>	<i>Poa glauca</i>	<i>Stellaria calycantha</i> s.l.
<i>Poa alpigena</i>	<i>Trisetum spicatum</i> s.l.	<i>Carex bigelowii</i>	<i>Rorippa islandica</i>
<i>Poa arctica</i> s.l.	<i>Carex aquatilis</i>	<i>Carex capillaris</i>	<i>Potentilla egedii</i>
<i>Carex ursina</i>	<i>Carex misandra</i>	<i>Carex glareosa</i>	<i>Rubus arcticus</i>
<i>Juncus biglumis</i>	<i>Carex rupestris</i>	<i>Carex sclerpoidea</i>	<i>Viola epipsila</i> s.l.
<i>Luzula arctica</i>	<i>Carex saxatilis</i>	<i>Carex subspathacea</i>	<i>Epilobium angustifolium</i>
<i>Luzula confusa</i>	<i>Eriophorum angustifolium</i> s.l.	<i>Eriophorum russeolum</i>	<i>Epilobium palustre</i>
<i>Salix arctica</i>	<i>Eriophorum scheuchzeri</i>	<i>Eriophorum vaginatum</i>	<i>Orthilia secunda</i>
<i>Oxyria digyna</i>	<i>Kobresia myosuroides</i>	<i>Kobresia simpliciuscula</i>	<i>Andromeda polifolia</i>
<i>Minuartia rubella</i>	<i>Polygonum viviparum</i>	<i>Luzula wahlenbergii</i>	<i>Pedicularis labradorica</i>
<i>Ranunculus sulphureus</i>	<i>Melandrium affine</i>	<i>Tofieldia coccinea</i>	
<i>Papaver radicans</i> s.l.	<i>Melandrium apetalum</i>	<i>Tofieldia pusilla</i>	
<i>Cardamine bellidifolia</i>	<i>Sagina intermedia</i>	<i>Salix glauca</i>	
<i>Draba alpina</i>	<i>Stellaria humifusa</i>	<i>Salix reticulata</i>	
<i>Saxifraga cernua</i>	<i>Ranunculus hyperboreus</i>	<i>Betula nana</i> s.l.	
<i>Saxifraga flagellaris</i>	<i>Ranunculus nivalis</i>	<i>Koenigia islandica</i>	
<i>Saxifraga hirculus</i>	<i>Ranunculus pedatifidus</i>	<i>Honckenya peplodes</i>	
<i>Saxifraga nivalis</i>	<i>Ranunculus pygmaeus</i>	<i>Draba hirta</i>	
<i>Saxifraga oppositifolia</i>	<i>Braya purpurascens</i>	<i>Ranunculus lapponicus</i>	
<i>Saxifraga rivularis</i>	<i>Cardamine pratensis</i>	<i>Hippuris vulgaris</i>	
<i>Potentilla hyperarctica</i> s.l.	<i>Cochlearia officinalis</i>	<i>Empetrum nigrum</i>	
	<i>Draba lactea</i>	<i>Pyrola grandiflora</i>	
	<i>Eutrema edwardsii</i>	<i>Ledum decumbens</i>	
	<i>Saxifraga foliolosa</i>	<i>Arctostaphylos alpina</i>	
	<i>Saxifraga hieracifolia</i>	<i>Vaccinium vitis-idaea</i>	
	<i>Astragalus alpinus</i>	<i>Diapensia lapponica</i>	
	<i>Epilobium latifolium</i>	<i>Arnica alpina</i>	
	<i>Cassiope tetragona</i>	<i>Artemisia borealis</i>	
	<i>Pedicularis capitata</i>		
	<i>Armeria maritima</i>		
	<i>Senecio congestus</i>		
	<i>Taraxacum</i> spp.		

Table 12. (facing page). Critical values (student's t-test,  $\alpha$ ) found by comparing proportions of taxa showing constant chromosome number in the four arctic floristic zones defined by Young (1971), where  $x$ =number of taxa in floristic zone with constant chromosome number, and  $n$ =total number of taxa in that zone. Floristic elements analyzed include (a) all plants, (b) dicots alone, (c) monocots alone, (d) grasses, and (e) monocots (horizontal axis) vs. dicots (vertical axis). Results are considered statistically significant for two-tailed student's t-distribution when test statistic,  $\alpha \geq 1.96$  ( $n \geq 30$ ) for  $p < 0.05$  (\*), or  $\alpha \geq 2.58$  ( $n \geq 30$ ) for  $p < 0.01$  (\*\*).

Floristic Zone					
	1	2	3	4	
	$\frac{x}{n}$	$\frac{21}{25}$	$\frac{23}{34}$	$\frac{24}{32}$	$\frac{8}{15}$
1	$\frac{21}{25}$	--	1.51	0.85	2.05*
2	$\frac{23}{34}$		--	0.66	0.94
3	$\frac{24}{32}$			--	1.45
4	$\frac{8}{15}$				--

Floristic Zone					
	1	2	3	4	
	$\frac{x}{n}$	$\frac{13}{14}$	$\frac{15}{21}$	$\frac{10}{16}$	$\frac{4}{11}$
1	$\frac{13}{14}$	--	1.78	2.18*	3.52**
2	$\frac{15}{21}$		--	0.57	2.00*
3	$\frac{10}{16}$			--	1.38
4	$\frac{4}{11}$				--

Floristic Zone					
	1	2	3	4	
	$\frac{x}{n}$	$\frac{8}{11}$	$\frac{8}{13}$	$\frac{14}{16}$	$\frac{4}{4}$
1	$\frac{8}{11}$	--	0.59	0.94	2.03*
2	$\frac{8}{13}$		--	1.64	2.05*
3	$\frac{14}{16}$			--	1.51
4	$\frac{4}{4}$				--

Floristic Zone					
	1	2	3	4	
	$\frac{x}{n}$	$\frac{6}{7}$	$\frac{3}{4}$	$\frac{4}{5}$	$\frac{2}{2}$
1	$\frac{6}{7}$	--	0.42	0.26	1.08
2	$\frac{3}{4}$		--	0.18	1.16
3	$\frac{4}{5}$			--	1.12
4	$\frac{2}{2}$				--

Floristic Zone					
	1	2	3	4	
	$\frac{x}{n}$	$\frac{8}{11}$	$\frac{8}{13}$	$\frac{14}{16}$	$\frac{4}{4}$
1	$\frac{13}{14}$	1.33			
2	$\frac{15}{21}$		0.59		
3	$\frac{10}{16}$			1.71	
4	$\frac{4}{11}$				4.39**

patterns from high arctic to low arctic. Their patterns were most similar in zones 1 and 2, the two zones under the most rigid ecological, and possibly, reproductive constraints, and most dissimilar in floristically rich and variable zone 4 (t-test,  $p < 0.05$ ). Larger sample sizes need to be tested before any conclusions can be stated with certainty.

## DISCUSSION

When the taxa whose chromosomes I counted were analyzed on the basis of shared distribution patterns, I noted a trend between each group's geographic provenance and the percentage of its taxa showing constant chromosome number (Table 9). Generally, narrowly restricted continental groups displayed the highest percentages of constant chromosome number, while circumboreal and wide ranging oceanic groups demonstrated the lowest percentages of constant chromosome number.

Several sources of error may influence this apparent trend. First, sample size within each distribution class was small, ranging between 14 and 30 taxa. Moreover, the taxa included in each geographic group represent a nonrandom sample of it, because I determined chromosome numbers only for those taxa that I was initially interested in for taxonomic or cytogenetic reasons. Even then, serendipity played a role in determining which seeds germinated and provided healthy root tips for mitotic chromosome preparations. Second, imperfectly known distribution ranges for some taxa made assigning them to a geographic group risky, especially for those taxa that are poorly defined or rare. Third, few chromosome counts were available for many of these taxa. Each taxon included in the analysis is represented by a minimum of three chromosome counts throughout its range, but these may not show the total variability of its chromosome numbers and behavior (i.e. euploid vs. euploid-aneuploid vs. aneuploid). Finally, the trend may simply reflect relative distribution sizes and the rule of thumb that taxa with narrow ranges show fewer different chromosome numbers than taxa with wide ranges.

Given all these qualifications, the observation remains that continental taxa appear more chromosomally conservative than circumboreal or oceanic ones. This trend is not surprising, but agrees with the pattern of infraspecific morphologic variation seen in taxa exemplifying the various historic-geographic patterns. Hultén (1937) reasoned that circumboreal taxa show a larger number of infraspecific races than continental ones because they radiate from a larger number of refugia, in which long periods of spatial isolation could lead to the proliferation of numerous population isolates and morphotypes. By comparison, continental taxa radiate from fewer refugia and generally show fewer morphotypes.

If proliferation of population isolates, followed by conservation of newly derived morphotypes, does in fact foster chromosome number divergence, this may account for the different chromosome behavior exhibited by circumboreal, as opposed to continental, taxa. The chromosome behavior of oceanic taxa appears to parallel that of circumboreal species, but for somewhat different historic and biogeographic causes. While circumboreal taxa often migrate along a broad front and in so doing encounter numerous specialized habitats, oceanic taxa usually exhibit a linear range along the coastlines they occupy (their continental extensions also follow essentially linear river or montane routes). This makes them, as a group, more vulnerable to glacial related climatic changes than either circumboreal or continental taxa, since they are more likely than the other two elements to suffer severely reduced biotypes by becoming trapped by glaciers that reach tidewater. Numerous population isolates are then created, and, if the same reasoning

applied to circumboreal taxa may be used here, this may account for the preponderance of divergent chromosome numbers shown within many oceanic taxa.

The weaknesses evident in my analysis were overcome in the study conducted by Johnson and Packer (1967, 1968) on the total vascular plant flora at Ogotoruk Creek on the northwest coast of Alaska. Before comparing the results from Johnson's and Packer's study and my own, the differences between them should be considered. First, the studies were conducted on historically and floristically different parts of the Alaskan flora. Johnson and Packer (1967, 1968) analyzed the total flora of a single area, an unglaciated portion of mega-Beringia. My analysis, on the other hand, constituted a more heterogeneous mixture of species from both glaciated and unglaciated stations throughout the state. Second, we derived somewhat different geographic elements from Hultén's (1937) geographic patterns, so that our results are not entirely comparable. Johnson and Packer found that the 266 taxa they analyzed fit into 22 of Hultén's distribution classes, which they redistributed into four more inclusive ones: oceanic (mostly strand species), arctic (species which occur only in the arctic), montane (those with at least one alpine lobe), and boreal taxa (species mainly associated with the boreal forest, but reaching at least the low arctic). In effect, these four geographic elements emphasize present-day distributions, while the ones I use, Beringian, Continental North American, Arctic-Montane, and Boreal Circumboreal, more closely parallel Hultén's treatment (1937) of the historic derivations of present-day patterns. To illustrate the

difference between these two approaches: Hultén (1937) never considered that taxa restricted to the arctic could arise de novo, but only as disjuncts or continuations of other distribution patterns (usually Beringian or Arctic-Montane). Neither treatment necessarily presents a more accurate interpretation of the events leading to the evolution of the present flora. It would be interesting, at a later date, to re-analyze my data in light of Johnson's and Packer's treatment.

Another difference between the two studies comes from Johnson's and Packer's classification of the taxa within each geographic element according to Favarger's polyploid age spectrum; ancient diploid, paleopolyploid, mesopolyploid, neopolyploid-chromosome races. Statistically significant differences between the four geographic classes were pronounced when a single age element was considered at a time [Table 13(a)-(d)]. However, these differences were lost when the age classes were lumped in each geographic class, and the data treated as they had been in my analysis, with all taxa scored as either "constant" or "variable"[Table 13(e)]. If I may extrapolate from Johnson's and Packer's study to my own, polyploid age differences may contribute significantly to the within-group variability of my distribution categories. Although analysis of my data in terms of Favarger's polyploid age spectrum is beyond the scope of the present study, it should be performed subsequently.

The results from analogous geographic elements in our two studies were not significantly different (Table 14) except in the case of oceanic taxa (t-test,  $p < 0.10$ ), where the difference is probably accounted for

Table 13. (facing page). Critical values (student's t-test,  $\alpha$ ) obtained by comparing proportions of taxa with constant chromosome number in the four geographic elements of the Ogotoruk Creek flora (from Johnson and Packer, 1967), where  $x$ =number of taxa in distribution element with constant chromosome number, and  $n$ =total number of taxa in that distribution element. Each polyploid age class (cf. Favarger, 1961) is analyzed separately: (a) ancient diploids, (b) paleopolyploids, (c) mesopolyploids, (d) neopolyploids and chromosome races combined, and (e) all plants in flora (no age differentiations). Results are considered statistically significant for two-tailed student's t-distribution when test-statistic,  $\alpha \geq 1.96$  ( $n \geq 30$ ) for  $p < 0.05$  (\*), or  $\alpha \geq 2.58$  ( $n \geq 30$ ) for  $p < 0.01$  (\*\*).

Geographic Element	Geographic Element				
	$\frac{x}{n}$	Oceanic	Arctic	Montane	Boreal
	$\frac{0}{0}$	0	$\frac{3}{70}$	$\frac{23}{103}$	$\frac{11}{27}$
Oceanic	$\frac{0}{0}$	--	--	--	--
Arctic	$\frac{3}{70}$		--	** 3.79	** 3.74
Montane	$\frac{23}{103}$			--	1.79
Boreal	$\frac{11}{27}$				--

Geographic Element	Geographic Element				
	$\frac{x}{n}$	Oceanic	Arctic	Montane	Boreal
	$\frac{1}{14}$	$\frac{1}{14}$	$\frac{4}{67}$	$\frac{2}{80}$	$\frac{5}{16}$
Oceanic	$\frac{1}{14}$	--	0.16	0.65	1.79
Arctic	$\frac{4}{67}$		--	1.55	1.83
Montane	$\frac{2}{80}$			--	** 2.45
Boreal	$\frac{5}{16}$				--

Geographic Element	Geographic Element				
	$\frac{x}{n}$	Oceanic	Arctic	Montane	Boreal
	$\frac{10}{14}$	$\frac{10}{14}$	$\frac{26}{67}$	$\frac{44}{80}$	$\frac{6}{11}$
Oceanic	$\frac{10}{14}$	--	2.42*	1.24	0.88
Arctic	$\frac{26}{67}$		--	* 1.99	0.97
Montane	$\frac{44}{80}$			--	0.28
Boreal	$\frac{6}{11}$				--

Geographic Element	Geographic Element				
	$\frac{x}{n}$	Oceanic	Arctic	Montane	Boreal
	$\frac{3}{14}$	$\frac{3}{14}$	$\frac{37}{67}$	$\frac{33}{80}$	$\frac{4}{16}$
Oceanic	$\frac{3}{14}$	--	* 2.70	1.62	0.23
Arctic	$\frac{37}{67}$		--	1.71	* 2.44
Montane	$\frac{33}{80}$			--	1.34
Boreal	$\frac{4}{16}$				--

Geographic Element	Geographic Element				
	$\frac{x}{n}$	Oceanic	Arctic	Montane	Boreal
	$\frac{11}{14}$	$\frac{11}{14}$	$\frac{30}{67}$	$\frac{46}{80}$	$\frac{11}{16}$
Oceanic	$\frac{11}{14}$	--	* 2.70	1.72	0.62
Arctic	$\frac{30}{67}$		--	1.55	1.83
Montane	$\frac{46}{80}$			--	0.88
Boreal	$\frac{11}{16}$				--

Table 14. Critical values (student's t-test,  $\alpha$ ) obtained by comparing proportions of taxa with constant chromosome number in geographic elements of the Ogotoruk Creek flora (horizontal axis) with those from the present study (vertical axis).  $x$ =number of taxa in distribution element with constant chromosome number, and  $n$ =total number of taxa in that distribution element. None of the results are statistically significant at the  $p < 0.05$  level.

		Ogotoruk Creek			
		Geographic Element	Oceanic	Montane	Boreal
		$\frac{x}{n}$	$\frac{11}{14}$	$\frac{46}{80}$	$\frac{11}{16}$
Present study	Oceanic	$\frac{8}{17}$	1.93		
	Montane	$\frac{18}{30}$		0.24	
	Boreal	$\frac{8}{14}$			0.66

by nonrandom sampling and small sample size. Johnson's and Packer's oceanic class is comprised primarily of strand species, which as a group are believed to be ancient, and both morphologically and cytologically conservative (Johnson and Packer, 1967). In contrast to this, my oceanic category is heavily weighted by non-strand species, including species with continental extensions along riparian and montane routes. These non-strand oceanic taxa appear less conservative in morphology and chromosome number than strand species.

## CONCLUSIONS

Historically, the fundamental application of chromosome botany to plant systematics has been found in delimiting taxa. Karyotypes may serve as a diagnostic feature in much the same way as other morphologic characters and on a case by case basis help resolve taxonomic difficulties. But chromosome number, size, and shape divulge only a portion of a taxon's characteristics at a specific point along the continuum of its evolution in time and space.

With regard to taxonomy and the process of classification chromosome information can be valuable in constructing classification schemes, but only when employed against a background of morphologic, biochemical, ecologic, and geographic data. When any one of these criteria is stressed to the exclusion of the others, an untenable taxonomic picture is likely to result. Therefore, I reject all classifications that rigidly adhere to chromosome discontinuities and purport one species:one chromosome number. Diverse chromosome behavior between and within plant populations quickly denigrates absolute cytotaxonomic systems to artificial and impractical status. Besides presenting a grossly simplified version of evolution, these classification schemes overlook some of the most interesting problems in systematics; the origin and diversification of chromosome races and their potential emergence as recognizable taxa. Karyotypic information must be evaluated in concert with other data appropriate to systematics. Only then may phylogenetic classification ever remotely approach its double-edged goal to present a practical scheme and reflect natural plant groupings.

The fact that chromosome data have been distorted beyond their inherent properties in constructing taxonomic hierarchies by some does not diminish their importance to plant systematics, but only demands that proper emphasis be placed on the type of information that chromosomes yield. Because they bear the physical unit of evolutionary change (DNA), chromosomes may more directly show the origins and nature of genetic variation in plants than other morphologic features. Karyotypic analyses are therefore more appropriately used in biosystematic studies, that part of taxonomy concerned with the variation and evolution of taxa, than in the process of classification itself. Where sufficient, accurate information about chromosome numbers exists karyotypic trends among closely related taxa may be observed, especially by constructing base number indices at generic and familial levels. The role of polyploidy, both as a mode of speciation and a product of that process, is paramount to understanding the genetic basis of evolutionary change in plants.

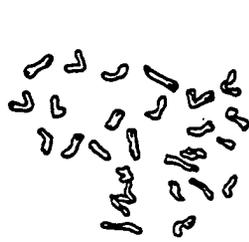
When chromosome information is superimposed on the geographic ranges of taxa patterns between characteristic chromosome behavior and phytogeography may be revealed that would otherwise pass unnoticed. Polyploidy may correlate with geographic features such as landform and substrate. Conversely, taxa conforming to any of Favarger's age categories of ancient diploids, mesopolyploids, or chromosome races (Favarger, 1961) may correspond in their speciation and distribution patterns. Clearly, from these and other problems similar in scope, the exceptional value of chromosome botany to plant systematics lies in elucidating the evolutionary patterns of plants.

## APPENDIX

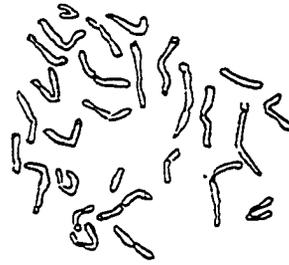
## DOCUMENTATION OF CHROMOSOME COUNTS

(camera lucida drawings at c.1500x unless otherwise noted)

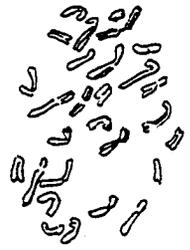
Fig. 1. Agropyron macrourum, Batten and Dawe 78-416;  $2n=28$ . Fig. 2. Elymus mollis, Troy S-15;  $2n=28$ . Fig. 3. Festuca altaica, Dawe 703;  $2n=28$ . Fig. 4. Hierochloë alpina, Dawe 699;  $2n=56$ . Fig. 5. Hordeum brachyantherum, Hatch 197;  $2n=28$ . Fig. 6. Carex obtusata, Batten and Dawe 78-346;  $2n=52$ . Fig. 7. Eriophorum scheuchzeri, Dawe 775;  $2n=58$ . Fig. 8. Luzula arcuata unalaschkensis, Dawe 681;  $2n=36$ . Fig. 9. Luzula groenlandica, Troy S-44;  $2n=24$ . Fig. 10. Luzula multiflora frigida, Dawe 737;  $2n=36$ . Fig. 11. Allium schoenoprasum sibiricum, Batten and Dawe 78-414;  $2n=16$ . Fig. 12. Allium schoenoprasum sibiricum, Troy S-11;  $2n=16$ . Fig. 13. Zygadenus elegans, Dawe GR 2;  $2n=32$ .



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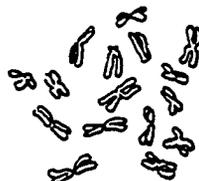
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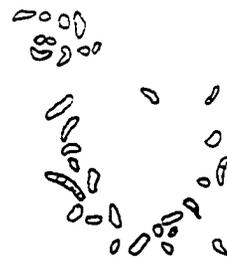
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Fig. 14. Iris setosa setosa, Troy S-10; 2n=38. Fig. 15. Betula glandu-  
losa, Dawe 670; 2n=28. Fig. 16. Bistorta vivipara, Dawe 728; 2n=c.100.  
Fig. 17. Oxyria digyna, Dawe 689; 2n=14. Fig. 18. Polygonum alaskanum,  
Dawe 778; 2n=20. Fig. 19. Rumex arcticus, Dawe 674; 2n=40. Fig. 20.  
Rumex sibiricus; Batten and Dawe 78-263; 2n=20. Fig. 21. Claytonia  
arctica, Dawe and Lipkin 77-552; 2n=c.40(42). Fig. 22. Claytonia  
sibirica, Batten and Murphy 77-401; 2n=12. Fig. 23. Claytonia sibirica,  
Heffner s.n.; 2n=12 (c.4500x). Fig. 24. Claytonia sibirica, Hatch 300;  
2n=12. Fig. 25. Claytonia sibirica, Moe 33; 2n=12.

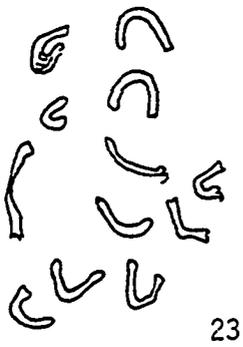
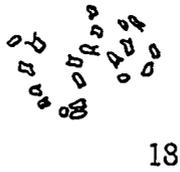
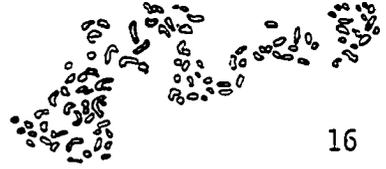


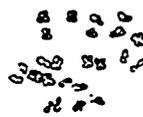
Fig. 26. Cerastium maximum, Batten and Dawe 78-350; 2n=28. Fig. 27. Sagina maxima crassicaulis, Batten and Murphy 77-168; 2n=66. Fig. 28. Silene acaulis acaulis, Dawe 693; 2n=24. Fig. 29. Silene repens purpurata, Batten and Dawe 78-303; 2n=24. Fig. 30. Wilhelmsia physodes, Batten and Dawe 78-389; 2n=66. Fig. 31. Aquilegia brevistyla, Batten and Dawe 78-365; 2n=16. Fig. 32. Pulsatilla patens multifida, Batten and Dawe 78-175; 2n=16. Fig. 33. Papaver alboroseum, Welsh and Moore 8146; 2n=28. Fig. 34. Papaver lapponicum, Dawe 476; 2n=56. Fig. 35. Papaver nudicaule, Batten and Dawe 78-382; 2n=28. Fig. 36. Alyssum americanum, Batten and Dawe 78-392; 2n=32. Fig. 37. Arabis holboellii, Batten and Dawe 78-192; 2n=14. Fig. 38. Arabis lyrata kamchatica, Dawe s.n., 2n=16. Fig. 39. Barbarea orthoceras, Hatch 79; 2n=16. Fig. 40. Braya bartlettiana, Batten 75-503; 2n=56.



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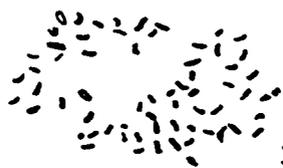
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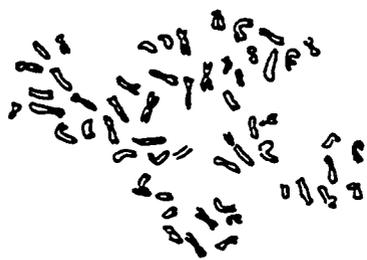
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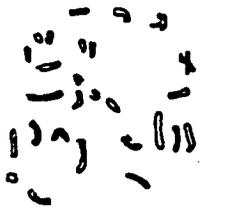


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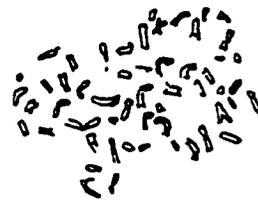


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Fig. 41. Braya pilosa, Young 7523; 2n=28. Fig. 42. Braya pilosa, Murray 3383; 2n=56. Fig. 43. Braya pilosa, Walker 546; 2n=64. Fig. 44. Braya purpurascens, Murray 3518; 2n=56. Fig. 45. Braya purpurascens, Dawe and Lipkin 77-845; 2n=56. Fig. 46. Cardamine bellidifolia, Murray and Johnson 6242; 2n=16. Fig. 47. Cochlearia arctica, SchamI s.n.; 2n=14. Fig. 48. Draba adamsii, Lipkin 78-13; 2n=48 (c.4500x). Fig. 49. Draba lactea, Batten, Dawe, and Murray 78-67; 2n=16.



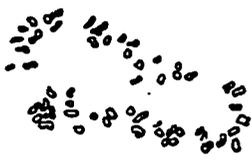
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Fig. 50. Draba murrayi, Batten and Dawe 78-391; 2n=48. Fig. 51. Draba palanderiana, Dawe and Lipkin 77-134; 2n=16. Fig. 52. Erysimum angustatum, Batten and Dawe 78-220; 2n=36. Fig. 53. Halimolobus mollis, Batten and Dawe 78-384; 2n=16. Fig. 54. Lesquerella arctica, Murray 6727; 2n=60. Fig. 55. Lesquerella arctica, Batten and Dawe 78-440; 2n=60. Fig. 56. Rorippa barbaraefolia, Murray and Johnson 6310; 2n=16. Fig. 57. Rorippa palustris hispida, Murray and Johnson 6309; 2n=32. Fig. 58. Smelowskia borealis jordalii, Batten 75-455; 2n=12. Fig. 59. Smelowskia borealis koliana, Rice s.n.; 2n=12. Fig. 60. Smelowskia calycina integrifolia porsildii, Young 7520; 2n=22. Fig. 61. Smelowskia calycina integrifolia porsildii, Young 7520; 2n=22. Fig. 62. Smelowskia calycina media, Murray 6901; 2n=12. Fig. 63. Smelowskia calycina media, Murray 6903; 2n=12.

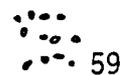
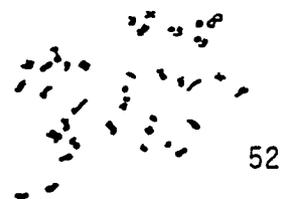
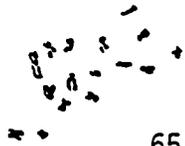


Fig. 64. Thlaspi arcticum, Murray 6199; 2n=14. Fig. 65. Sedum divergens, Weeden s.n.; 2n=16. Fig. 66. Sedum integrifolium, Hatch 160; 2n=36. Fig. 67. Saxifraga hirculus, Dawe 729; 2n=16. Fig. 68. Acomastylis rossii, Dawe GR 40; 2n=70. Fig. 69. Chamaerhodos erecta nuttallii, Batten and Dawe 78-353; 2n=14. Fig. 70. Dryas drummondii, Dawe GR 64, 2n=18. Fig. 71. Dryas integrifolia sylvatica, Dawe GR 10, 2n=18. Fig. 72. Geum macrophyllum macrophyllum, Hatch 81; 2n=42. Fig. 73. Pentaphylloides fruticosa, Dawe 654; 2n=14. Fig. 74. Pentaphylloides fruticosa, Dawe 701; 2n=14. Fig. 75. Potentilla bipinnatifida, Murray 6975; 2n=56. Fig. 76. Potentilla egedii, Troy S-45; 2n=28. Fig. 77. Potentilla hyparctica, Dawe s.n., 2n=42. Fig. 78. Potentilla hyparctica, Dawe 712; 2n=42.



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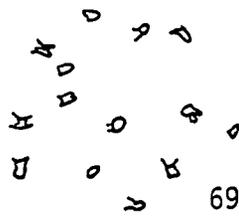
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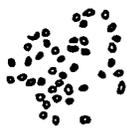
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Fig. 79. Potentilla multifida, Dawe GR 44; 2n=28. Fig. 80. Potentilla  
pennsylvanica, Batten and Dawe 78-331; 2n=28 (c.4500x). Fig. 81.  
Potentilla villosa, Hatch 87; 2n=14. Fig. 82. Sanguisorba officinalis,  
Dawe GR 4; 2n=28. Fig. 83. Sanguisorba stipulata, Hatch 277; 2n=28.  
Fig. 84. Sibbaldia procumbens, Dawe 683; 2n=14. Fig. 85. Astragalus  
aboriginorum, Batten and Dawe 78-243; 2n=16. Fig. 86. Astragalus eucos-  
mus eucosmus, Batten and Dawe 78-217; 2n=32. Fig. 87. Astragalus eucos-  
mus eucosmus, Batten and Dawe 78-374; 2n=32. Fig. 88. Astragalus  
nutzotinensis, Murray 3347; 2n=22.



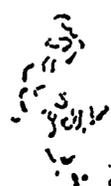
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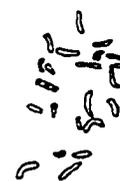
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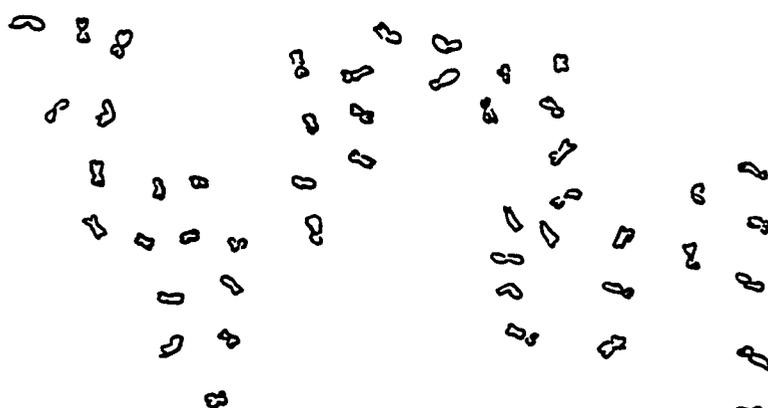
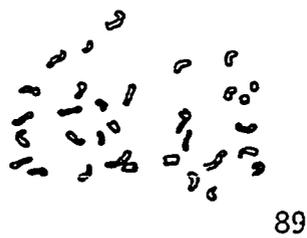


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Fig. 89. Astragalus robbinsii, Batten and Dawe 78-312;  $2n=32$ . Fig. 90. Astragalus sealei, Murray 6943;  $2n=16$ . Fig. 91. Hedysarum alpinum americanum, Troy S-37;  $2n=14$ . Fig. 92. Hedysarum alpinum americanum, Dawe GR 5;  $2n=14$ . Fig. 93. Lathyrus pilosus, Troy S-33;  $2n=14$ . Fig. 94. Lupinus arcticus, Dawe 157;  $2n=48$ . Fig. 95. Oxytropis borealis, Kubanis s.n.,  $2n=48$ . Fig. 96. Oxytropis borealis, Batten and Dawe 78-433;  $2n=48$  (c.4500x).



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Fig. 97. Oxytropis campestris varians, Batten and Dawe 78-260; 2n=16.  
Fig. 98. Oxytropis campestris varians, Batten and Dawe 78-439; 2n=16.  
Fig. 99. Oxytropis campestris varians, Batten and Dawe 78-361; 2n=32.  
Fig. 100. Oxytropis campestris varians, Batten and Dawe 78-369; 2n=32.  
Fig. 101. Oxytropis campestris varians, Murray 6956; 2n=96. Fig. 102.  
Oxytropis campestris varians, Dawe GR 66; 2n=96. Fig. 103. Oxytropis  
cf. jordalii, Kubanis s.n.; 2n=36. Fig. 104. Oxytropis viscida, Batten  
and Dawe 78-390; 2n=16. Fig. 105. Oxytropis viscida, Bourdo 33244; 2n=16.



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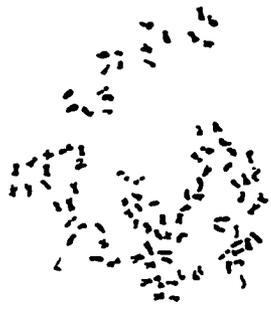
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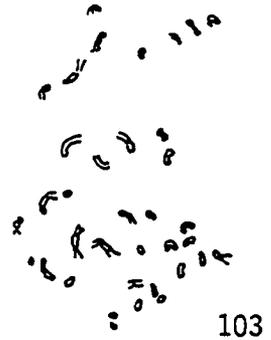
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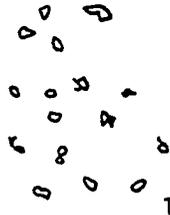


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Fig. 106. Oxytropis deflexa foliolosa, Murray and Johnson 6994; 2n=16.  
Fig. 107. Oxytropis deflexa foliolosa, Batten and Dawe 78-421; 2n=16.  
Fig. 108. Oxytropis huddelsonii, Murray 516; 2n=16. Fig. 109. Oxytropis huddelsonii, Murray 2168; 2n=16 (c.4500x). Fig. 110. Oxytropis kobukensis, Lewis M-4; 2n=80. Fig. 111. Oxytropis koyukukensis, Parker s.n.; 2n=48.  
Fig. 112. Oxytropis scammaniana, Dawe 78-373; 2n=18. Fig. 114. Elaeagnus commutata, Dawe GR 49; 2n=28. Fig. 115. Shepherdia canadensis, Dawe s.n., 2n=22.



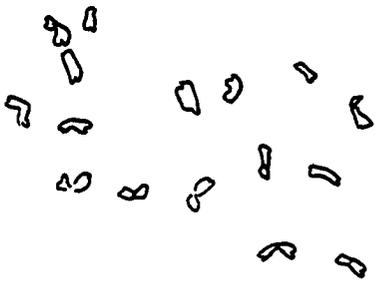
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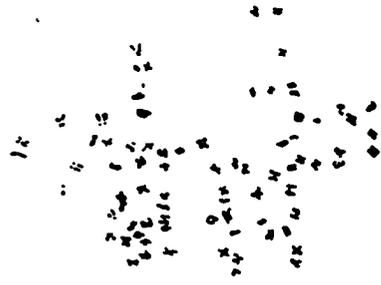
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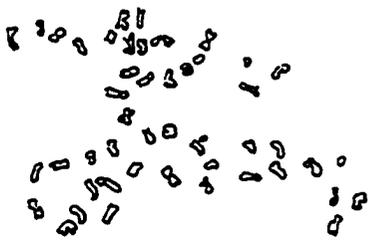
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Fig. 116. Geranium erianthum, Hatch 85; 2n=28. Fig. 117. Epilobium angustifolium angustifolium, Troy S-4; 2n=36. Fig. 118. Epilobium latifolium, Dawe 652; 2n=72. Fig. 119. Bupleurum triradiatum arcticum, Murray 6977; 2n=28. Fig. 120. Cnidium cnidiifolium, Dawe GR 11; 2n=22. Fig. 121. Diapensia lapponica obovata, Dawe 692; 2n=12. Fig. 122. Androsace septentrionalis, Batten and Dawe 78-280; 2n=20. Fig. 123. Androsace septentrionalis, Dawe 746; 2n=20. Fig. 124. Dodecatheon frigidum, Dawe 741; 2n=44. Fig. 125. Dodecatheon pulchellum pauciflorum, Batten and Dawe 78-293; 2n=44. Fig. 126. Douglasia arctica, Batten and Dawe 78-318; 2n=38.



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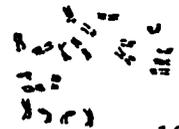
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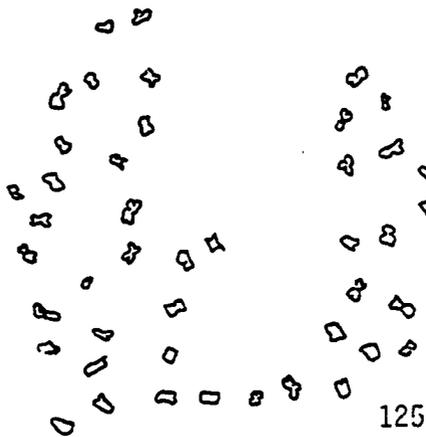
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Fig. 127. Gentiana glauca, Dawe 680; 2n=22. Fig. 128. Swertia perennis, Dawe 738; 2n=28. Fig. 129. Polemonium acutiflorum, Troy S-42; 2n=18. Fig. 130. Polemonium acutiflorum, Dawe 665; 2n=18. Fig. 131. Polemonium boreale boreale villosissimum, Murray 6329; 2n=18 (c.1000x). Fig. 132. Polemonium pulcherrimum, Batten and Dawe 78-170; 2n=18. Fig. 133. Phacelia mollis, Batten and Dawe 78-418; 2n=22. Fig. 134. Phacelia sericea, Batten and Dawe 78-371; 2n=22. Fig. 135. Cryptantha shackletteana, Batten and Dawe 78-206; 2n=24. Fig. 136. Mertensia drummondii, Komarkova, Hansell, and Seabert 170; 2n=24. Fig. 137. Mertensia maritima, Lipkin 78-82; 2n=24 (c.4500x). Fig. 138. Mertensia paniculata, Troy S-5; 2n=72. Fig. 139. Castilleja caudata, Troy S-27; 2n=24. Fig. 140. Castilleja caudata, Dawe 756; 2n=72.



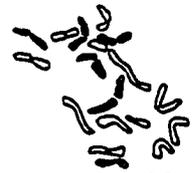
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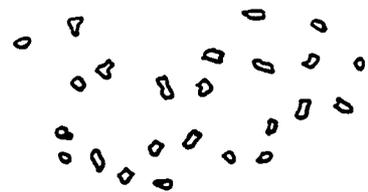
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Fig. 141. Castilleja elegans, Batten and Dawe 78-381;  $2n=24$  (c.4500x).  
Fig. 142. Pedicularis lanata, Troy S-18;  $2n=16$ . Fig. 143. Pedicularis  
sudetica, Troy S-40;  $2n=16 + 10B$ . Fig. 144. Pedicularis verticillata,  
Batten and Dawe 78-121;  $2n=16 + 2f$ . Fig. 145. Penstemon gormanii,  
Batten and Dawe 78-302;  $2n=16 + 5B$ . Fig. 146. Valeriana capitata, Dawe  
707;  $2n=53$ . Fig. 147. Campanula aurita, Batten and Dawe 78-368;  $2n=34$ .  
Fig. 148. Artemisia alaskana, Dawe GR 43;  $2n=18$ . Fig. 149. Artemisia  
arctica arctica, Dawe 657;  $2n=18$ . Fig. 150. Artemisia borealis,  
Batten and Dawe 78-255;  $2n=36$ . Fig. 151. Artemisia borealis; Dawe GR 23;  
 $2n=36$ . Fig. 152. Artemisia frigida, Dawe GR 61;  $2n=18$ .

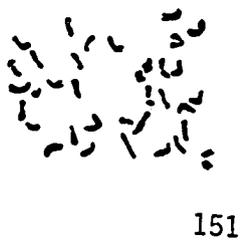
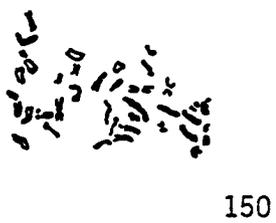
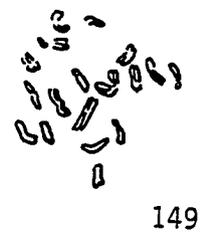
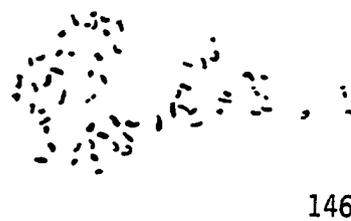
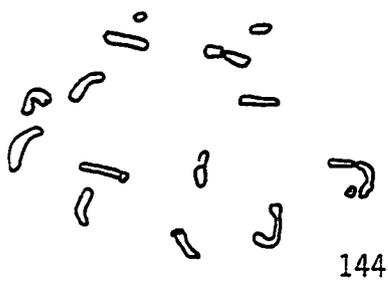
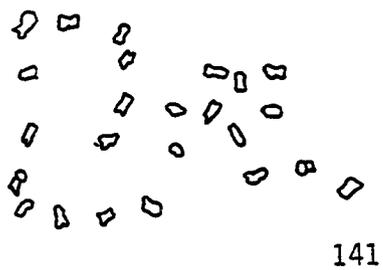
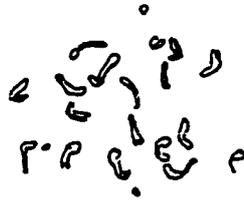


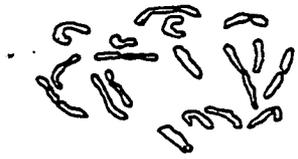
Fig. 153. Artemisia furcata, Young 7506; 2n=18. Fig. 154. Artemisia furcata, Young 7510; 2n=18 + 3B. Fig. 155. Artemisia tilesii, Troy S-49; 2n=18. Fig. 156. Artemisia tilesii, Dawe s.n.; 2n=36. Fig. 157. Artemisia tilesii elatior, Dawe 777; 2n=36. Fig. 158. Artemisia tilesii gormani, Dawe 659; 2n=36. Fig. 159. Artemisia tilesii unalaschcensis, Hatch 190; 2n=36. Fig. 160. Aster sibiricus, Dawe s.n.; 2n=18. Fig. 161. Chrysanthemum arcticum, Troy S-19; 2n=18. Fig. 162. Crepis elegans, Dawe GR 26; 2n=14. Fig. 163. Crepis nana nana, Dawe 611; 2n=14. Fig. 164. Erigeron acris politus, Dawe 602; 2n=18. Fig. 165. Erigeron acris politus, Dawe 776; 2n=18.



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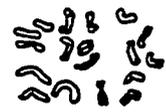
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Fig. 166. Erigeron caespitosus, Murray and Johnson 6262;  $2n=18$ .  
Fig. 167. Erigeron grandiflorus, Murray and Johnson 6491;  $2n=36$ . Fig.  
168. Erigeron muirii, Roseneau s.n.;  $2n=18$ . Fig. 169. Erigeron  
purpuratus, Murray and Johnson 6976;  $2n=18$ . Fig. 170. Erigeron  
purpuratus, Batten, Dawe, and Murray 78-72;  $2n=18$ . Fig. 171. Saussurea  
nuda, Troy S-3;  $2n=26$ . Fig. 172. Senecio ogotorukensis, Dawe 744;  $2n=46$ .  
Fig. 173. Solidago multiradiata multiradiata, Dawe s.n.;  $2n=36$ . Fig. 174.  
Solidago multiradiata multiradiata, Dawe 715;  $2n=36$ . Fig. 175. Solidago  
multiradiata arctica, Hatch 193;  $2n=36 + 4B$ . Fig. 176. Tripleurospermum  
phaeocephalum, Troy S-31;  $2n=18$ .



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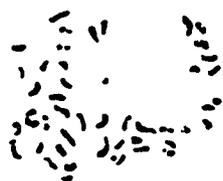
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