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NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* DR. K. E. DENFORD

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THE UNIVERSITY OF ALBERTA

A SYSTEMATIC STUDY OF HERBACEOUS *CORNUS* L. IN NORTHWESTERN NORTH AMERICA

by

© JOHN F. BAIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF BOTANY

EDMONTON, ALBERTA

FALL, 1977

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "A SYSTEMATIC STUDY OF HERBACEOUS *CORNUS* L. IN NORTHWESTERN NORTH AMERICA" submitted by John F. Bain in partial fulfilment of the requirements for the degree of Master of Science.

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Supervisor

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DATE 20th May 1977

ABSTRACT

Structural, cytological and chemical data are used to establish synonymy, taxonomic relationships and a classification of the herbaceous taxa of *Cornus* L. The two species, *Cornus canadensis* L. and *Cornus suecica* L., are structurally distinct and diploid (2n=22). A chemical difference (the presence or absence of quercetin 3-O gentiobioside) further separates these species. The populations which are structurally intermediate between the two species are separated into two taxa; a diploid (2n=22) hybrid, *Cornus canadensis* X *suecica* (2n=22) and an amphidiploid species *Cornus unalaschkensis* Ledeb. (2n=44). The chemical compound that separates *Cornus canadensis* from *Cornus suecica* also separates the two intermediate taxa. The diploid intermediate exhibits pollen inviability. A hybrid origin of the diploid intermediate is proposed based on the results presented. The formation of the amphidiploid through allopolyploidy is also proposed. The disjunct distribution of the amphidiploid with respect to *C. suecica* is discussed in relation to the effect glaciation and climatic changes had on the spread and distribution of the two species.

ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. K.E. Denford for his faith, support, and guidance throughout the course of this investigation, and to Dr. J.G. Packer, Dr. D.H. Vitt, and Dr. G.E. Ball for their assistance and critical review of this manuscript. I would also like to thank the various people who accompanied me in the field and assisted me in the laboratory, and to Mrs. E. Ford for typing the manuscript. Thanks also to the curators of the various herbaria who have given me access to specimens through loans for examination. This research was supported by National Research Council of Canada Grant No. (NRC-A-6663) to Dr. K.E. Denford and by a Grant-in-aid from the Boreal Institute for Northern Studies.

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CHAPTER I

INTRODUCTION

The status of taxa within the family Cornaceae has been the source of much discussion in the past. The high degree of heterogeneity within the family has led to difficulties in establishing taxonomic boundaries. As a result, several generic classifications have been proposed (Wangerin, 1910; Hutchinson, 1948; Core, 1955; Gleason and Cronquist, 1963). The relationship of the family to that of the Umbelliferae, Rosaceae, Alanginaceae and Nyssaceae has been periodically examined, changed and reproposed by various workers (Dermen, 1932; Rickett, 1945; Eyde, 1967). The opinion currently expressed by many taxonomists is that the Cornaceae are a family, separate from, although closely related to, the Nyssaceae, Alanginaceae and Araliaceae (Takhtagan, 1959; Gunderson, 1950; Rodriquez, 1957; Philipson, 1967).

The Cornaceae are represented in North America by one genus, *Cornus* Linnaeus (1753), which originally included five species: *Cornus mas* L., *C. sanguinea* L., *C. suecica* L., *C. canadensis* L., and *C. florida* L.. *Cornus mas* was designated by Dumortier (see Ferguson, 1966) as the type species for the genus. A number of infrageneric classification systems have been proposed in an effort to satisfactorily deal with the diversity in both gross habit and floral structure that the genus *Cornus* embodies (Nakai, 1909; Hutchinson, 1942: Hara, 1942). A review of the various classifications of the genus *Cornus* has been presented by Ferguson (1966).

In most of the classifications which have been proposed, the

taxon. The rank of this taxon varies, depending upon the classification. A list of the various taxa described containing the herbaceous members of *Cornus* is given in Table 1.

One of the proposed changes is the segregation of herbaceous *Cornus* into the genus *Chamaepericlymenum* Hill.. In my opinion the correct authority name for *Chamaepericlymenum* is Hill not Graebner, as is often given in the literature (*e.g.* Löve and Löve, 1975; Hutchinson, 1942). The reason for this apparent error of citation is that Hill's description of *Chamaepericlymenum* appeared in a volume which did not use the Linnaean system of binary nomenclature consistently. His generic name is therefore very commonly considered not to have been validly published. However, according to Article 23 of the International Code of Botanical Nomenclature (1972), only specific epithets published in such works are considered to be invalidly published. Therefore, Hill's name, since it is a generic name, is validly published. This is the position of Dandy (1972) in his consideration of the question. Further, Hill's indirect, yet unmistakable reference to the Linnaean species *Cornus suecica* as being contained in *Chamaepericlymenum* served to typify the genus. The publication of the name *Chamaepericlymenum* by Graebner (Ascherson and Graebner, 1898) is superceded by Hill's name.

Although the separation of the herbaceous members of the genus *Cornus* into the segregate genus *Chamaepericlymenum* has been supported by a number of authors, retention of these taxa within the genus *Cornus* is the most common method of classification in North America at this time (Rickett, 1945; Fernald, 1950; Hultén, 1968). For this reason, the herbaceous taxa will be treated as members of the

TABLE 1

A list of the proposed taxa containing the herbaceous species of *Cornus* L. (after Ferguson, 1966)

Chamaepericlymenum Hill (1756)

Cornus a. *Arctocrania* Endl. (1839)

Cornus sect. *Cornion* Spach (1839)

Cornus subg. *Arctocrania* Reich. (1841)

Cornus sect. *Arctocrania* (Reich.) Lede. (1844)

Cornella Rydberg (1909)

Arctocrania (Reich.) Nakai (1909)

Mesomera [Rudbeck] Niewland and Lunell (1916)

genus *Cornus* subgenus *Arctocrania* Endl. *ex* Reich. in this study. Only the herbaceous taxa of *Cornus* are contained in the subgenus *Arctocrania*.

Research involving the genus *Cornus* has been carried out in the cytotaxonomic, chemosystematic, and developmental fields of botany. These studies have served to augment the data available for classificatory purposes.

Eyde (1967) related *Nyssa* L. and *Alangium* Lam. to *Cornus*, based on evidence derived from gynoecial vasculature. Chopra and Kauer (1965), after studying the embryo development of *Cornus*, suggested that *Alangium* (Alanginaceae) should be included in the Cornaceae. Wilkinson (1944) studied the floral vasculature of a number of species of *Cornus*, but did not propose any new taxonomic groups. However, *C. florida* was considered to be the least specialized, based upon the extensive vasculature in the sepals and ovule, and a vestigial vascular trace in the receptacle (this occurrence suggests a reduction in sepal size and ovule number which has not been accompanied by vascular reduction). Conversely, *C. alternifolia* L., *C. stolonifera*, and *C. suecica* were considered the most advanced.

Cytological studies of the genus revealed basic chromosome numbers of x=9, 10, 11 with x=11 the most common (Dermen, 1932). *Cornus mas* (n=9) has two pairs of long chromosomes with median or sub-median constrictions. The fragmentation of these chromosomes could result in the x=10 and x=11 chromosome numbers observed. *Cornus mas* could then be considered to have given rise to other members of the genus with higher chromosome numbers. One polyploid taxon was found; *Cornus canadensis* (n=22). (*Nyssa sylvatica* Marsh

also has a chromosome number of n=22 and this is cited as evidence for its affiliation to the Cornaceae [Dermen, 1932].) Clay and Nath (1971) found some specimens of *C. rugosa* Lam. to contain an extra chromosome. This further suggests the possiblity of chromosome addition to the basic x=9 number. All but one species examined in this study contained one pair of chromosomes longer than all others. *Cornus canadensis* had two longer pairs. Polyploidy was not considered an important method of speciation within the genus, since only one tetraploid species was found.

Definitive phytochemical research within the family started with a serological study of the Cornaceae and the related family Nyssaceae (Fairbrothers and Johnson, 1966). Antisera were produced against four species of *Cornus* (*C. amomum* Mill., *C. canadensis*, *C. florida*, and *C. racemosa* Lam.), two species of *Nyssa* (*N. sylvatica* Marsh. and *N. aquatica* L.) and *Davidia involucrata* Baill.. The results supported the inclusion of all the *Cornus* species in the same genus as well as supporting Rickett's (1945) exclusion of *Nyssa* and *Davidia* from *Cornus*. The serological evidence also supported the separation of the herbaceous taxa into a distinct group, which was not considered by the authors to be of generic rank.

A chemical survey of the genus *Cornus* using nonflavonoid glycosides has also been carried out (Jensen *et al.*, 1975a). The classification, based upon chemical data, which resulted from this survey was very similar to other proposed classifications, most closely resembling the classification proposed by Nakai (1909). Again, as in the study carried out by Fairbrothers and Johnson (1966), it was found that the herbaceous species could be separated from the rest of the

genus *Cornus* (in this case by their possession of monotropein and geneposide).

The relationship of the herbaceous species of *Cornus* to the rest of the genus has been outlined (see Table 1; also Ferguson, 1966). Although considerable work has been done relating the herbaceous taxa to other *Cornus*, very little research aimed at uncovering the relationships within the subgenus *Arctocrania* has been carried out. Results of these studies indicate that further study is necessary to answer certain questions which can be raised concerning the classification of the herbaceous taxa of *Cornus*.

Three herbaceous species of *Cornus* have been recognized, *Cornus canadensis*, *Cornus suecica*, and *Cornus unalaschkensis* Ledeb. and hence are the concern of the present work. *Cornus canadensis* is found mainly in North America, but also in northwestern Asia and at higher altitudes in Japan (see Map 1). It has been distinguished from *C. suecica* by the presence of a whorl of 4-6 leaves at the apex of the shoot and only one pair of leaves (usually reduced) on the lower stem. *Cornus suecica* has 3-6 pairs of approximately equal-sized leaves along the stem. Sometimes they resemble a whorl at the shoot apex. The inflorescence of *C. canadensis* is similar to that of *C. suecica* but lacks the purple pigmentation on the perianth which is characteristic of *C. suecica*. The distribution of *C. suecica* is circumpolar. It has been collected on both the northwestern and northeastern coasts of North America as well as Greenland, Great Britain, Scandinavia, and Siberia (see Map 2).

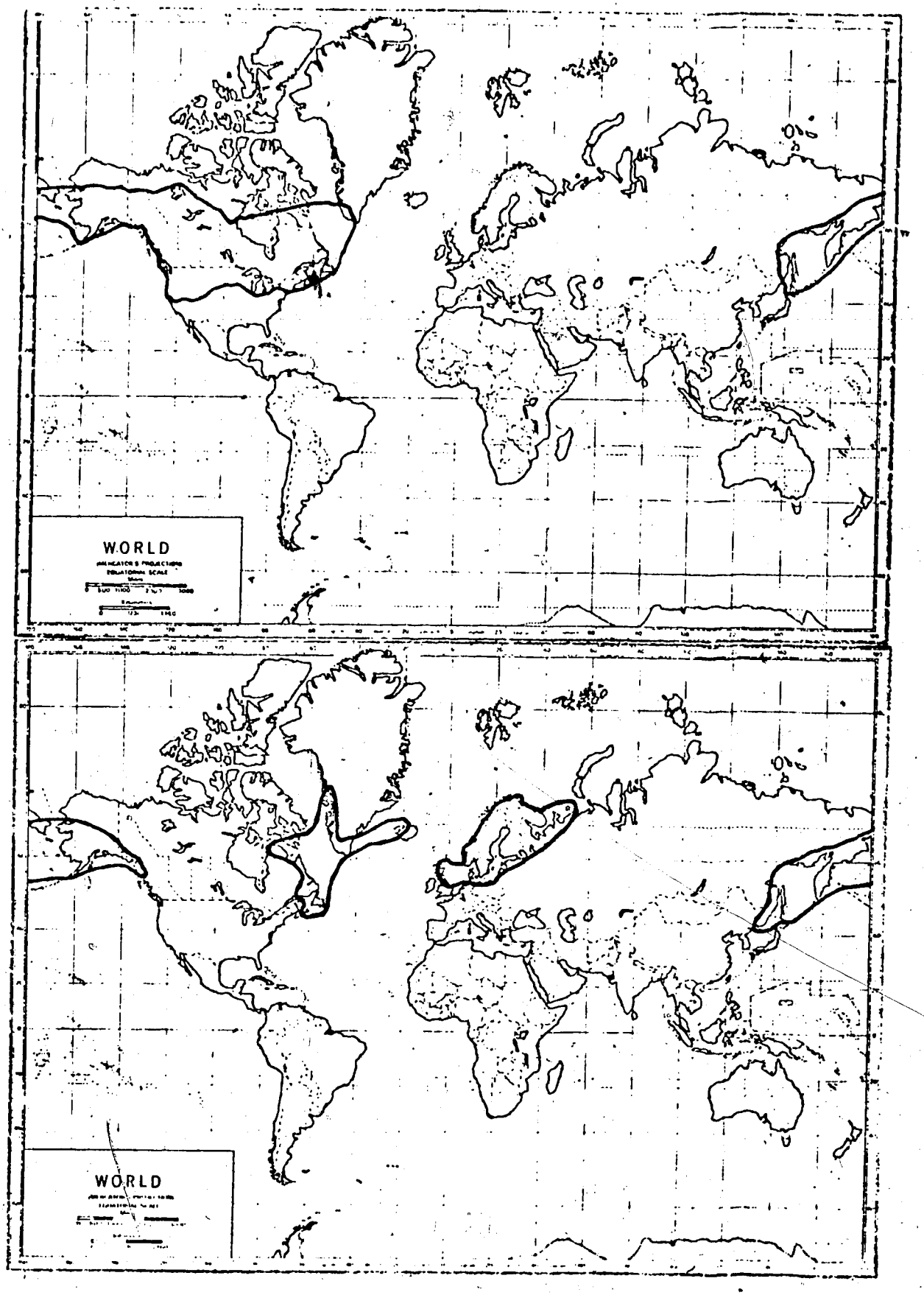
A taxon intermediate between these two species was first described by Ledebour (1841-1846) as *Cornus unalaschkensis* Ledeb., then

MAP 1

Geographical Distribution of *Cornus canadensis* L. (based on data from Rickett, 1945; Hultén, 1968; and herbarium specimens examined).

MAP 2

Geographical Distribution of *Cornus suecica* L. (based on data from Hultén, 1958; Hultén, 1968; and herbarium specimens examined).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as *Cornus canadensis* var. *intermedia* Farr (1904) and eventually as *Cornus canadensis* X *suecica* Hultén (1937a). It was considered by Hultén to be a hybrid. Farr (1904) stated that the whorl of upper leaves and the pale colour of the flower are constant characters which relate the taxon more closely to *C. canadensis*, and therefore it should be considered a variety of *C. canadensis*.

A major obstacle to the acceptance of a hybrid origin of this taxon by certain workers is outlined by Porsild (1939). Collections have been reported over one thousand miles from the nearest *C. suecica* location. Such a disjunct distribution is explained by Hultén (1968) as a range extension of both *C. suecica* and the intermediate prior to glaciation, followed by the survival of only the more continentally adapted intermediate. The distribution of the intermediate taxon is shown in Map 3.

Photographs of the type specimens of *Cornus canadensis*, *C. suecica*, and *C. unalaschkensis* are shown in Figures 1-3.

The chromosome numbers that have been reported for the herbaceous taxa of *Cornus* are summarized in Table 2. The table has been taken largely from Löve and Löve (1975) and serves to illustrate another problem related to the classification of these herbaceous *Cornus*. The chromosome number of 2n=22 reported by Löve as *Chamaepericlymenum unalaschkense* (Ledeb.) Rydb. (*Cornus unalaschkensis* Ledeb.) and attributed to Packer (1964) was in fact reported by Packer (1964) as *Chamaepericlymenum canadense* (L.) Graeb.. The count attributed to Mulligan and Cody (Löve, 1971) under *Chamaepericlymenum unalaschkense* was also initially reported as *Cornus canadensis*. The actual specific status of these specimens is apparently a subject of controversy.

MAP 3

Geographical Distribution of the intermediate taxon of herbaceous *Cornus* (based on data from Hultén, 1958; and herbarium specimens examined).

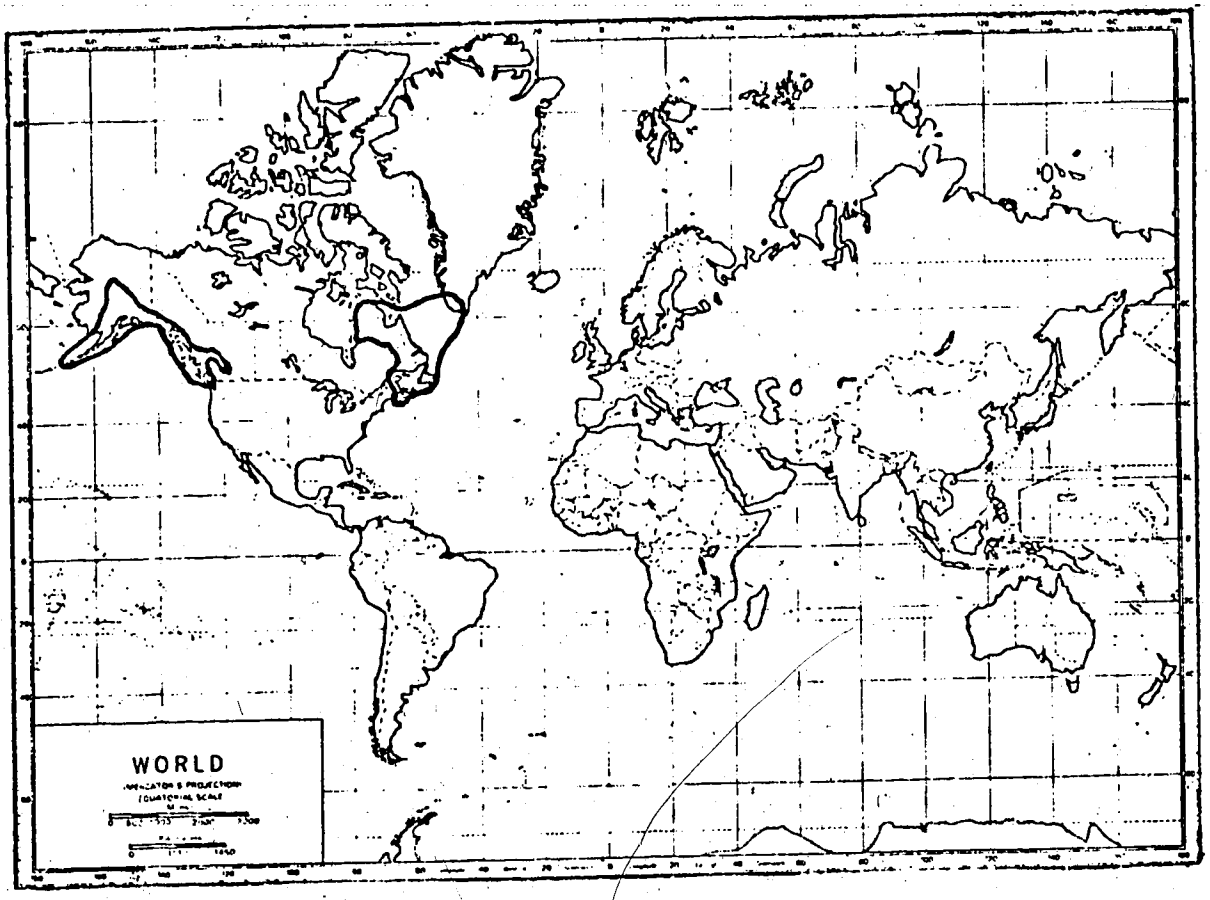
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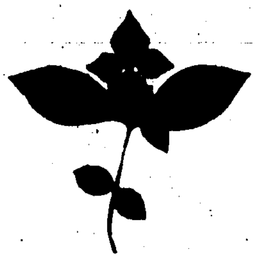
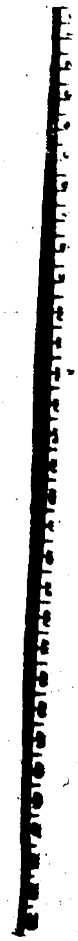
FIGURE 1.

Type Specimen of *Cornus canadensis* L.





HERBARIUM LINNAEANUM

Form of Savage Catalogue entries:

Some of the specific epithets and numbers are printed in solid type, *but solely as a help to the eye in tracing named specimens.* When these are not followed by the writer's name in square brackets they are written on the sheets by Linnaeus. Apart from everything enclosed in square brackets, all inscriptions in roman type are written by Linnaeus. The inscriptions by all other writers are printed *in italics.*

Where the same writer is responsible for the inscriptions both before and after his name, two colons are used to show this,—e. g. [:m.Sm:].

Inscriptions at the top of a sheet are *followed* by the sign /; those on the verso are *preceded* by the sign //.

The sign □ is used for "Label"; and a + sign before a writer's name means that the ensuing inscription is an addition to the one that precedes it.

No. 151.13

CORNUS

13 canadensis 5 Kalm

FIGURE 2

Type specimen of *Cornus suecica* L.

HERBARIUM LINNAEANUM

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The sign ▭ is used for "Label"; and a + sign before a writer's name means that the ensuing inscription is an addition to the one that precedes it.

No. 151.12

CORNUS

12 suecica 4 [v. A.spec.] 3 [to next spec.] 4.

151.12

FIGURE 3.

Type Specimen of *Cornus unalaschkensis* Ledeb.

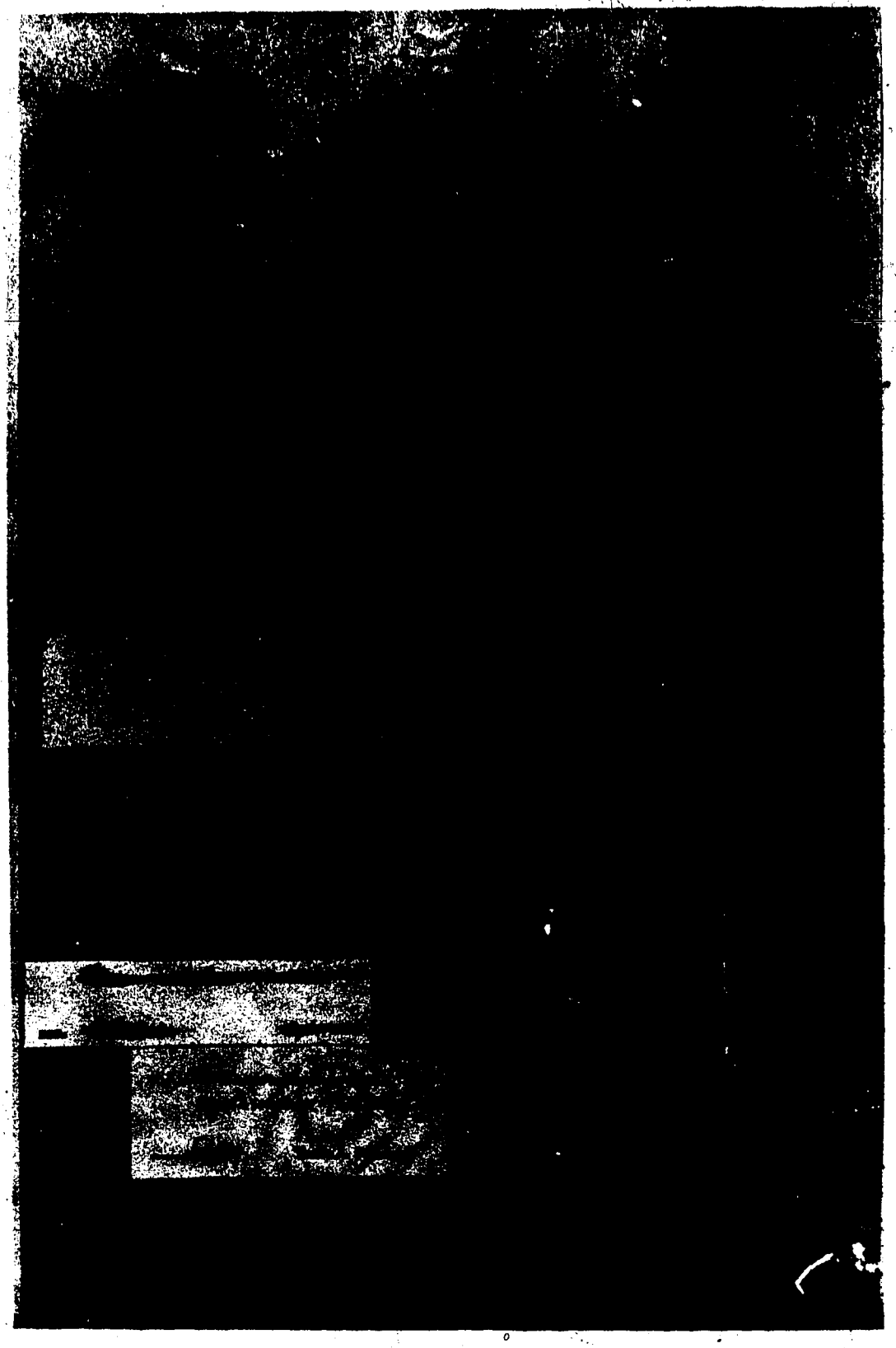


TABLE 2

Chromosome numbers reported for *Cornus* subg. *Arctocrania* (after Löve and Löve, 1975)

Cornus suecica

22 Wulff, H.D. 1939c

22 Löve, A. 1954b.

22 Löve, A. and Löve, D. 1956b

22 Jörgensen, C.A., Sörensen, T. & Westergaard, M. 1958

22 Sorsa, V. 1963c

22 Lovkvist, B. (In Welmarck, 1963)

Cornus canadensis

44 Dermen, H. 1932

44 Löve, A. 1954b

44 Sokolovskaya, A.P. 1960a

44 Löve, A. and Löve, D. 1966b

44 Sokolovskaya, A.P. 1966

44 Clay, S.N. and Nath, J. 1971

Cornus unalaschkensis

*22 Packer, J.G. 1964

22 Löve A. and Löve D. 1966b

22 Hedberg, O. 1967

*22 Mulligan, G.A. and Cody, W.J. (In Love, 1971c)

**22 Taylor, R.L. and Brockman, R.P. 1966

**44 Taylor, R.L. and Mulligan, G.A. 1968

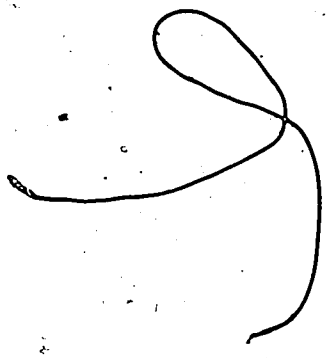
*Reported as *Cornus canadensis* (*Chamaepericlymenum canadense*) by original authors.

**Not contained in Löve and Löve (1975).

The relationship of the intermediate taxon to *Cornus canadensis* and *C. suecica* is considered at present to be unclear. The morphological, phytogeographical, and cytotaxonomic information so far reported is inadequate and in part contradictory.

A study of various populations of the herbaceous *Cornus* species collected throughout northwestern North America has been carried out using the following approaches: phytochemical data accumulated through the study of population flavonoid profiles; cytological data compiled from chromosome counts of the populations; and morphological data based on comparative population studies and hybrid indices.

A correlative interpretation of these data have also been attempted to assess the mode of speciation and distribution of the *Cornus canadensis-suecica* complex in northwestern North America.



CHAPTER II

MATERIALS AND METHODS

Collections were made throughout Alberta, although primarily in the Rocky Mountain region, as well as north-central British Columbia, Queen Charlotte Islands, Yukon Territory and Alaska. Living and dried material, as well as pressed specimens were obtained from most sites. The living specimens were used for cytological study while the dried material was necessary for phytochemical work. In addition to the pressed material collected, herbarium specimens were examined to obtain morphological and distributional data. Loans of herbarium material came from the National Museum of Canada, the Canada Department of Agriculture, the Komorov Botanical Institute, Leningrad. The University of Alberta specimens were also examined. The abbreviations in the citation of specimens examined (appendix) are those adopted in Index Herbariorum (Holmgren and Keuken, 1974). Morphological variation was studied at both an infraspecific and an interspecific level.

Chromosome counts were made from actively growing root tips (in mitotic phases). The source of the root tips was living material transplanted from the field into 4-inch pots and grown in the greenhouse. Some root-tips were collected in the field and preserved in a solution of acetic acid and 95% ethanol (1:3).

Root tips to be examined were prepared using the method of Tijo and Levan (1950). The tissue was fixed in 0.004 M 8-hydroxyquinoline for 2 -3 hours at 13-16°C, then washed in distilled water for five minutes and transferred to a watch glass containing 1% acetic orcein

solution mixed with 1 N HCl (9:1). The solution containing the root tips was heated over a bunsen for a few minutes and stained for thirty minutes. Slides were prepared by placing the root tip in a drop of 45% acetic acid and squashing it under a coverslip. Voucher slides were made semipermanent by ringing the coverslip with a mixture (1:1) of Mastic gum and paraffin. A voucher specimen for each collection is deposited in the herbarium at the University of Alberta.

Guard cell length measurements were taken as another method of examining differences between organisms belonging to a polyploid series. Various workers have found a correlation between cell size and ploidy level (Stebbins, 1971; Sax and Sax, 1937). The most reliable method for recording these differences is thought to be measure of guard cell length (Sax, 1938; Kliphius, 1973).

Preparations were made from living material by peeling the epidermis from the lower side of the leaf with a razor blade, then mounting the peel in water on a microscope slide. Length of guard cells was measured with an eyepiece micrometer at 400 X using an AO microscope.

A phytochemical study of the flavonoids of various populations was carried out, using the methods of Mabry *et al.* (1969), Harborne (1973), and Ribéreau-Gayon (1972).

Whole plants used in flavonoid extraction were collected in the field and dried in paper bags. Prior to extraction, collections were sorted to ensure only leaves and stems were used for extraction. Approximately 20 gm dry weight of plant material was used in the analysis. The material was eluted in approximately 300 ml of 80%

ethanol and ground up in a Oster blender for 15 minutes. Separation of the extract was accomplished by filtration through cheesecloth and a Buchner funnel, then Whatmann #1 or #2 filter paper and a Buchner funnel.

The solution was evaporated *in vacuo* using a Buchler roto-evaporator until reduced to approximately 50 ml. Ten drops of the extract were spotted on each of the 32 sheets of Whatmann #3MM chromatography paper. These were run using descending chromatography in two dimensions with two different solvents. The first dimension was run using 1-butanol:acetic acid:H_2O (BAW 4:1:5, upper phase) and the second was run using 15% acetic acid. The resulting spots were examined using u/v light (3660 Å) on untreated sheets and on sheets fumed with ammonia. Spots were also examined under visible light after they had been treated with ferric chloride - Ferrous cyanide stain* or Benedict's reagent (sprayed). Ferric chloride-ferrous cyanide stains phenolic compounds. Benedict's reagent stains flavonoids.

Spots that overlapped on the initial chromatograph could, in most cases, be separated by eluting the spots together and streaking the mixture on full-size sheets of Whatmann #1 paper then chromatographing in one dimension, using BAW (4:1:5 BAW; upper phase) as the solvent.

Compounds exhibiting a positive reaction with both ferric chloride-ferrous cyanide (blue) and Benedict's reagent (yellow) were cut out and eluted from unstained chromatograms in a minimum amount of spectral grade methanol. They were then analyzed using ultra-violet

---

*3% $FeCl_3$ in H_2O)
3% $K_3Fe(CN)_6$ in H_2O) equal volumes/dilute X 10.
Dip chromatogram in solution then in 10% HCl then in H_2O.

spectrophotometry, so that an identification of the compound could be obtained. The analysis was carried out on a Unicam SP 1800 ultra-violet spectrophotometer. Scans were recorded for the methanol solution, followed by scans of the solution after the addition of sodium methoxide, anhydrous aluminum trichloride, aluminum trichloride and hydrochloric acid (N), sodium acetate, and sodium acetate and boric acid (Mabry *et al.*, 1969, pp. 35-61).

To further aid identification, all pure compounds were chromatographed in one-dimension using four different solvent systems on half-sheets (23 x 57 cm) of Whatmann #1 paper. The solvent systems were:

(a) 1-butanol:acetic acid:H_2O (4:1:5, upper phase);

(b) saturated phenol (80% phenol:H_2O);

(c) 15% acetic acid;

(d) water.

The glycosides were then hydrolyzed to aglycone and sugar constituents by refluxing in 5-7 ml of 2N HCl. Variation in the amount of HCl added occurred because of a variation in concentration of the methanol-glycoside mixture as indicated by the colour of the solution. Refluxing was carried out for fifteen minutes in a reflux condenser at 100°C. After hydrolysis the solution was cooled and partitioned against three to five ml of ethyl ether. The lower aqueous layer containing the sugars and the upper ether layer containing the aglycones were separated. After drying the aglycone and redissolving it in spectral grade methanol, part of the extract was analyzed spectrophotometrically as outlined above and the remaining solution chromatographed in one dimension using 4:1:5 BAW. Identification in all cases

was made from spectral scans and supported by Rf data. The aqueous fraction, containing the sugars, was concentrated, then spotted on half-sheets of Whatmann #1 paper. In each case two spots of the unknown sugars were made. To one spot was added 30 µl of 0.005 Molar standard solution of glucose. The chromatographs were run using 80% iso-propanol as the solvent. The sugars were stained using aniline hydrogen pthalate solution. Unknown sugars were identified by their Rg (distance from origin/ distance of glucose from origin x 100) and by their colour after staining.

Identification of the compounds was confirmed for three separate populations (Collecton # 75033, 75029, 75070), then the reamining populations were analyzed chromatographically in two dimensions in a manner similar to that previously described, using a reduced amount of material. Three grams of plant material were eluted in 50 ml of 80% ethanol for each of the populations. Seven drops of extract were spotted on only two sheets of Whatmann #3MM chromatography paper. No attempt was made to condense the extract by roto-evaporation. The two sheets were run chromatographically in two dimensions in the manner previously described and the chromatographic profiles were compared with no attempt to elute the spots. A series of flavonoid profiles was obtained. Spots with the same Rf values were identified by comparison with the original major populations.

Pollen grain viability can be useful as an indicator of sterility, a trait which can be used in distinguishing suspected hybrid organisms from non-hybrids (see Lawrence, 1951). The pollen grains of hybrids may be non-viable, shrunken and may lack turgidity. Using fresh pollen gathered from specimens grown in the greenhouse, slides were made by placing the pollen in a drop of

lacto-phenol cotton blue stain and waiting five minutes. The slides were then examined at X200 magnification of an AO microscope. Pollen grains were considered viable if they took up stain and appeared a deep blue in colour. The taking up of the stain indicates the presence of living cytoplasm.

CHAPTER III

RESULTS

Analysis of the results of this study has enabled the delimitation of four taxa: two diploid species *Cornus canadensis* (2n=22) and *Cornus suecica* (2n=22), an amphidiploid species, *Cornus unalaschkensis* (2n=44) and a diploid hybrid, *Cornus canadensis* X *suecica* (2n=22). In the reporting of the results the taxa will be referred to by these four names. A discussion of this classification is given later in the text.

Morphology

Eleven key or critical characters by which *C. canadensis* and *C. suecica* specimens could be separated were chosen. They are given in Table 3.

Initial examination of the intermediate specimens collected indicated that they exhibited many combinations of the eleven character traits of the two other species. In addition, many intermediates exhibited character states somewhere in between the variation defined by the character states of the other two species. This problem was dealt with in the following manner.

The eleven characters previously mentioned were used in the examination of all collections. For each of the eleven characters a numerical value was given to each of the two contrasting character states; zero for the character state extreme associated with *C. suecica*, and one for the character state extreme associated with *C. canadensis*. For character states between these two extremes, a numerical value between zero and one was given, which reflected

TABLE 3

Comparative Characters Used in the Morphological Analysis of the *Cornus canadensis-Cornus suecica* complex.

Character	Character State *C. canadensis* (numerical value = 1)*	Character State *C. suecica* (numerical value = 0)*
1. Leaf length/width ratio	>1.50	<1.25
2. Leaf arrangement	whorl in 4-6 leaves at summit	3-6 subequal pairs of leaves
3. Leaf shape	ovate to elliptic	lanceolate to ovate
4. Leaf tip	acute to shortly acuminate	broadly acute to obtuse
5. Leaf base	narrowed at base with distinct petiole	clasping at base
6. Leaf venation	2-3 veins on either side of midrib	5-7 veins arising from base of leaf
7. Flower number	>25 flowers	<15 flowers
8. Primary branches in cyme	4 primary branches discernible	primary branches not discernible
9. Sepal and hypanthium colour and pubescence	cream to green coloured usually ciliate	blue or purplish coloured ciliate with white trichomes only at base
10. Petal colour	yellowish	blue or purple
11. Stamen length	not longer than style	longer than style

*Character states which fell between the two extreme states shown were given an appropriate numerical value between 0 and 1.

which extreme this character state most closely resembled, and to what degree. This technique was reviewed by Gay (1960). Consequently, each collection was given a numberical value expressed as a percentage of the total. A 'pure' *C. canadensis* specimen would have a numerical morphological index value of 100% while a 'pure' *C. suecica* specimen would have a value of 0%. The results are given in Table 4. In no instance was a collection of 'pure' (0%) *C. suecica* found, but two populations (75060, 75063) were, after a more complete analysis, identified as *C. suecica*.

Morphological analysis resulted in the recognition of a key or critical character, petal colour. Plants whose petals showed any purple pigmentation did not correspond to the more complete *C. canadensis* description afforded by examining the other characters. Hence this character could be used as a quick method of separating *C. canadensis* from *C. suecica* and the intermediate form. Unfortunately, the separation of *C. suecica* from the intermediate was not accomplished so easily. Incorporation of cytological and phytochemical data is necessary to separate the two entities; a point discussed in a later section.

Chromosome Numbers

Somatic chromosome counts were determined for 48 populations as outlined in Tables 5 and 6. Chromosome studies of cells undergoing meiotic division were attempted but were not successful. Two chromosome races were present among these collections: the diploid (2n=22) and tetraploid (2n=44) races (Fig. 4) described in previous publications.

Map 4 (pg. 36) shows the distribution of these two chromosome

TABLE 4

Morphological Index Values (%) for Collections of Herbaceous* *Cornus*

Collection # and Name		Morphological Index Value (%)
75007	*C. canadensis*	100
75037	*C. canadensis*	100
75043	*C. canadensis*	100
75046W	*C. canadensis*	100
75058	*C. canadensis*	100
75059	*C. canadensis*	100
75003	*C. canadensis*	99
75005	*C. canadensis*	99
75009	*C. canadensis*	99
75004	*C. canadensis*	98
75011	*C. canadensis*	98
75036	*C. canadensis*	98
75008	*C. canadensis*	96
75010	*C. canadensis*	95
75014	*C. canadensis*	95
76101	*C. canadensis*	95
75073	*C. canadensis*	94
76102	*C. canadensis*	92
75035	*C. unalaschkensis*	89
75026	*C. unalaschkensis*	88
75031	*C. unalaschkensis*	86
75019	*C. unalaschkensis*	85
75032	*C. unalaschkensis*	84
75016	*C. unalaschkensis*	82
75033	*C. unalaschkensis*	82
75038	*C. unalaschkensis*	82
75018	*C. unalaschkensis*	81
75028	*C. unalaschkensis*	80
75024	*C. unalaschkensis*	79

TABLE 4. Continued.

Collection # and Name		Morphological Index Value (%)
75052	*C. canadensis* X *suecica*	79
75053	*C. canadensis* X *suecica*	79
75055	*C. canadensis* X *suecica*	78
76104	*C. unalaschkensis*	77
76107	*C. unalaschkensis*	72
76110	*C. unalaschkensis*	71
75048	*C. canadensis* X *suecica*	70
75046P	*C. canadensis*	70
75067	*C. canadensis* X *suecica*	70
76108	*C. unalaschkensis*	67
75054	*C. canadensis* X *suecica*	64
76111	*C. unalaschkensis*	57
76109	*C. unalaschkensis*	46
76106	*C. unalaschkensis*	40
76105	*C. unalaschkensis*	37
76103	*C. unalaschkensis*	31
75063	*C. suecica*	28
75060	*C. suecica*	21

*The morphological index value in each case represents the average value from 5-7 specimens.

TABLE 5

List of Diploid Specimens used in Cytological Study*

CANADA

Alberta: Pembina River, 75001, June 15/75; Nojack campsite, 75002, June 15/75; Mulhurst, 75003, June 18/75; 20 mi E. of Rocky Mountain House, 75004, June 18/75; 35 mi W. of Rocky Mountain House, 75005, June 18/75; Herbert Lake, 75006, June 19/75; Lake Louise, 75007, June 19/75; Mt. Norquay, 75008, June 19/75; Finn Creek, 75009, June 19/75; 26 mi E. of Radium, 75011, June 20/75; Altitude Creek, 75012, June 20/75; Sunshine Village, 75013, June 20/75; Lake Minnewanka, 75014, June 21/75; Sulphur Mtn., 75015, June 21/75; Reesor Lake, 76101, June 23/76; Spruce Coulee, 76102, June 23/76.

British Columbia: 20 mi S of Smithers, 75036, July 6/75; 55 mi W. of McBride, 75040, July 7/75; 75 mi W. of Jasper, 75041, July 7/75; Summit Lake, Alaska Hwy., 75073, July 27/75; 90 mi N. of Ft. St. John, 75074, July 27/75.

Yukon: Mi. 46, Dempster Hwy., 75070, July 24/75.

U.S.A.

Alaska: S. Delta Jctn., 75043, July 12/75; Paxon, 75046, July 13/75; Mi 27, Denali Hwy., 75047, July 13/75; Mi. 42, Denali Hwy., 75048, July 13/75; Mi. 42, Denali Hwy., 75050, July 13/75; Mt. Eliason, McKinley Pk., 75052, 75053, July 14/75; 30 mi E. of Fairbanks, 75056, July 16/75; Glen Hwy, near Tazlina, 75059, July 19/75; Mirror Lake, near Anchorage, 75060, July 19/75; Seward, 75062, July 20/75; 37 mi N. of Seward, 75063, July 20/75; 12 mi N. of Houston, 75065, July 21/75;

TABLE 5. Continued.

Mi. 102, Hwy. 3., 75066, July 21/75.

*All collections were made by the author.

TABLE 6

List of Tetraploid Specimens used in Cytological Study*

Canada

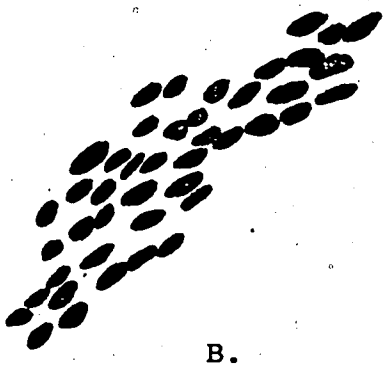
British olumbia: Moresby Lake, Queen Charlotte Is., 75016, 75017, 75019, June 29/75; Upper Victoria Lake, Queen Charlotte Is., 75024, 75026, July 1/75; Tow Hill, Queen Charlotte Is., 75030, 75031, July 3/75; Tlell River, Queen Charlotte Is., 75032, July 4/75; Olive Lake, 75033, July 6/75; Seely Lake Prov. Pk., 75035, July 6/75; Purden Lake Prov. Pk., 75038, July 7/75.

U.S.A,

Alaska: Petersburg, 76105, July 12/76.

*All collections were made by the author.

A.



B.

Figure 4. Somatic Chromosomes of Herbaceous Cornus.

A. 2n=22

B. 2n=44

MAP 4

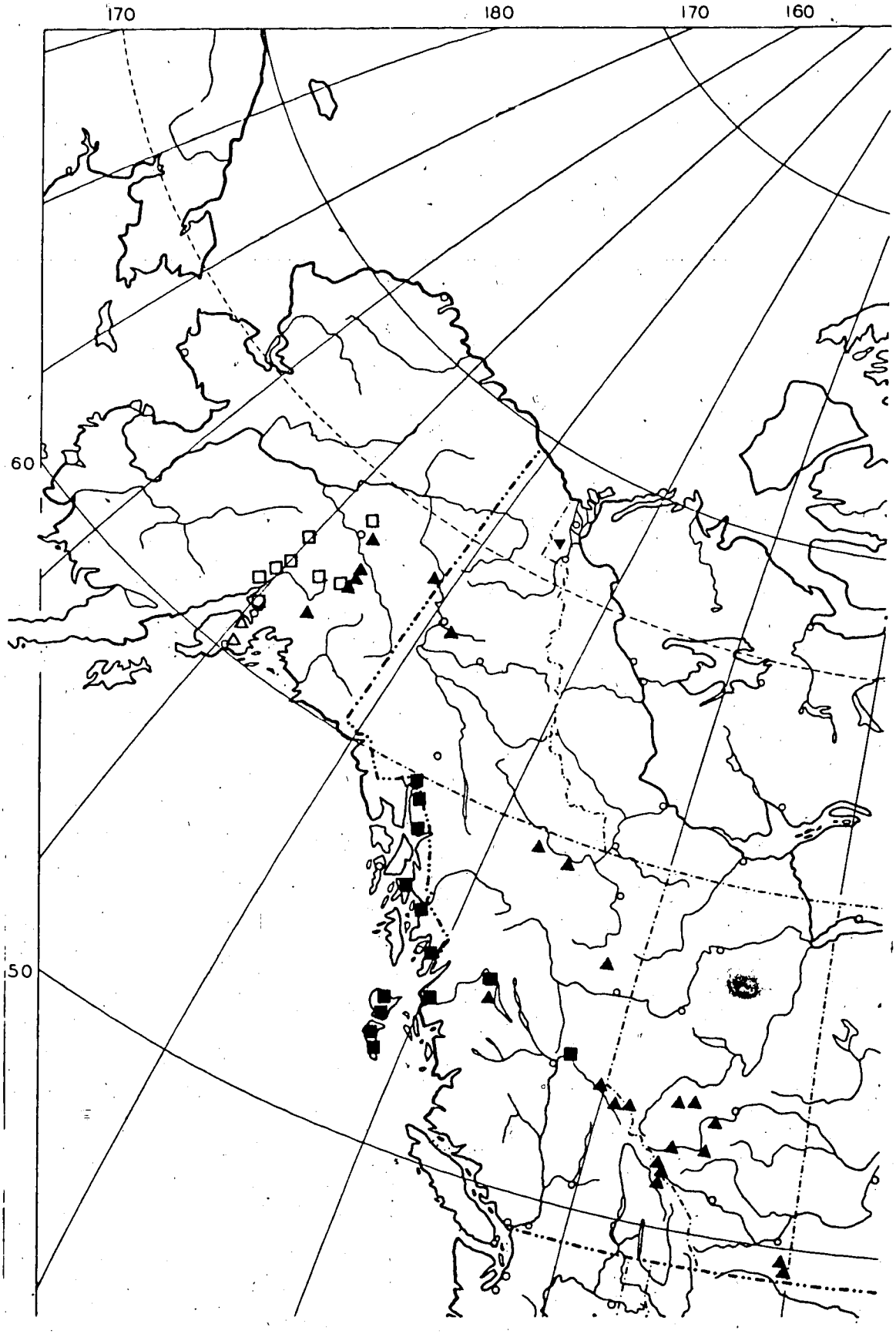
Chromosome numbers of herbaceous *Cornus* in northwestern North America.

▲- diploid *Cornus canadensis* (2n=22)

□- diploid *Cornus canadensis* X *suecica* (2n=22)

△- diploid *Cornus suecica* (2n=22)

■- tetraploid *Cornus unalaschkensis* (2n=44)


170
180
170
160
60
50

races, based upon the collections cited in Tables 5 and 6. For some of the locations indicated on the map, chromosome number was inferred from guard cell size because plant material necessary for obtaining a chromosome count was unavailable. Information concerning guard cell size is contained in a later section.

To verify the identification of some of the previous chromosome counts reported, voucher specimens for the counts reported by Packer (1964) and Taylor and Brockman (1966) were examined. The former specimen was *Chamaepericlymenum canadense* (*Cornus canadensis*) as the author reported. It was not *Cornus unalaschkensis* (*Chamaepericlymenum unalaschkense*) as reported by Löve and Löve (1975) (see Table 2). The latter specimen was *Cornus canadensis* and not *Cornus intermedia* (Farr.) Calder & Taylor (*Cornus unalaschkensis*) as was reported by the authors (see Table 2).

Pollen Viability

A test to determine pollen viability, as previously outlined, was carried out on those specimens which flowered under greenhouse conditions. The results of this test were:

Collection # and Name	X-some #	% viable pollen grains
75005 *C. canadensis*	22	99
75008 *C. canadensis*	22	99
75024 *C. unalaschkensis*	44	98
75035 *C. unalaschkensis*	44	96
75053 *C. canadensis* X *suecica*	22	54
75054 *C. canadensis* X *suecica*	22	52

Collection # and Name	X-some #	% viable pollen grains
75063 *C. suecica*	22	98

Viable pollen grains are defined, in this instance, as those pollen grains which took up the stain and so appeared a dark blue colour under the microscope. Although the results of this test cannot always be considered to be definitive, in this case the difference in colour of staining was great enough to eliminate any difficulty in discerning a positive from a negative reaction. The results reported in each case were from a single plant.

Guard Cells

Guard cell length was positively correlated with ploidy level. Diploid specimens possessed guard cells of a smaller length than tetraploid specimens. There was a significant difference between the mean guard cell sizes of the diploid ($\bar{x}$ = 25.20; 1008 cells) and tetraploid ($\bar{x}$ = 32.05; 904 cells) species as demonstrated by a two sample Student's t test (s = 1.48, t = 4.64). Guard cell length of the diploids ranged from 17.9 to 38.3 µ while the guard cell length of the tetraploids ranged from 23.0 to 43.4 µ. A graph illustrating the range of guard cell lengths found of the two chromosome races is shown in Fig. 5. This relationship was established by measuring guard cell lengths in specimens of known chromosome number, but the results were applicable when predicting the ploidy level of specimens for which chromosome number of the specimen was not available. The graph illustrates a relationship of ploidy level to guard cell size only. No evidence of a difference in guard cell size between different species of the same chromosome number was found.

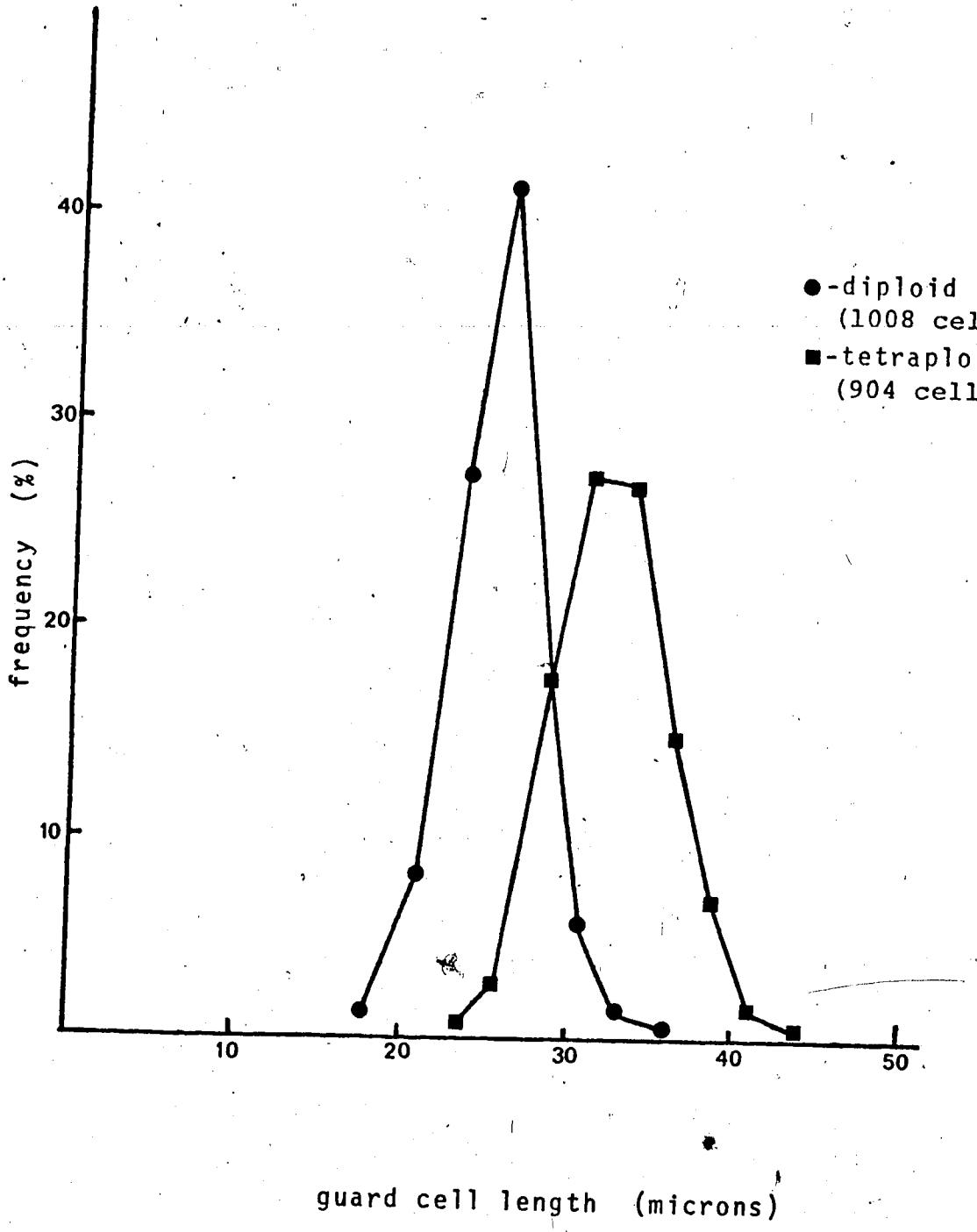


Figure 5. Guard Cell Length Frequencies in Herbaceous Cornus taxa.

Observations of Floral Development and Reproduction

No experiments were carried out to ascertain the type of breeding system found in the herbaceous *Cornus* species. However, some observations were made of the floral development of plants in the greenhouse.

At the tip of each flower bud, attached to one of the four petals is an awn-like projection which stands erect from the bud. The bud itself is similar to a small tent in structure, with the stamen bent and completely enclosed by the four petals (see Fig. 6). The whole bud springs open when the awn-like projection is touched. Simultaneously, the anthers dehisce, sending a cloud of pollen into the air. Much of the pollen lands on the flower's own stigma. Fruit very seldom developed in the greenhouse. Protandry is suspected as the means to prevent obligate selfing. The most likely means of triggering the bud opening and pollen release is the touching of the awn-like projection by an insect. The insect could act as a pollen carrier, effecting cross-pollination. Vegetative reproduction by means of underground rhizomes is very commonly observed in the field.

Phytochemistry

The phytochemical results reported are based upon separate extracts, prepared from dried plant material from the collections listed in Table 7 (pg. 62).

A diagram of hypothetical master chromatogram which shows the total number of flavonoid compounds identified is shown in Figure 7. Rf and spectral data for these compounds (identified as flavonoids by their colour reaction with Ferric chloride/ferrous cyanide (blue) and Benedict's reagent (yellow) are given in Figures 8 through 14.

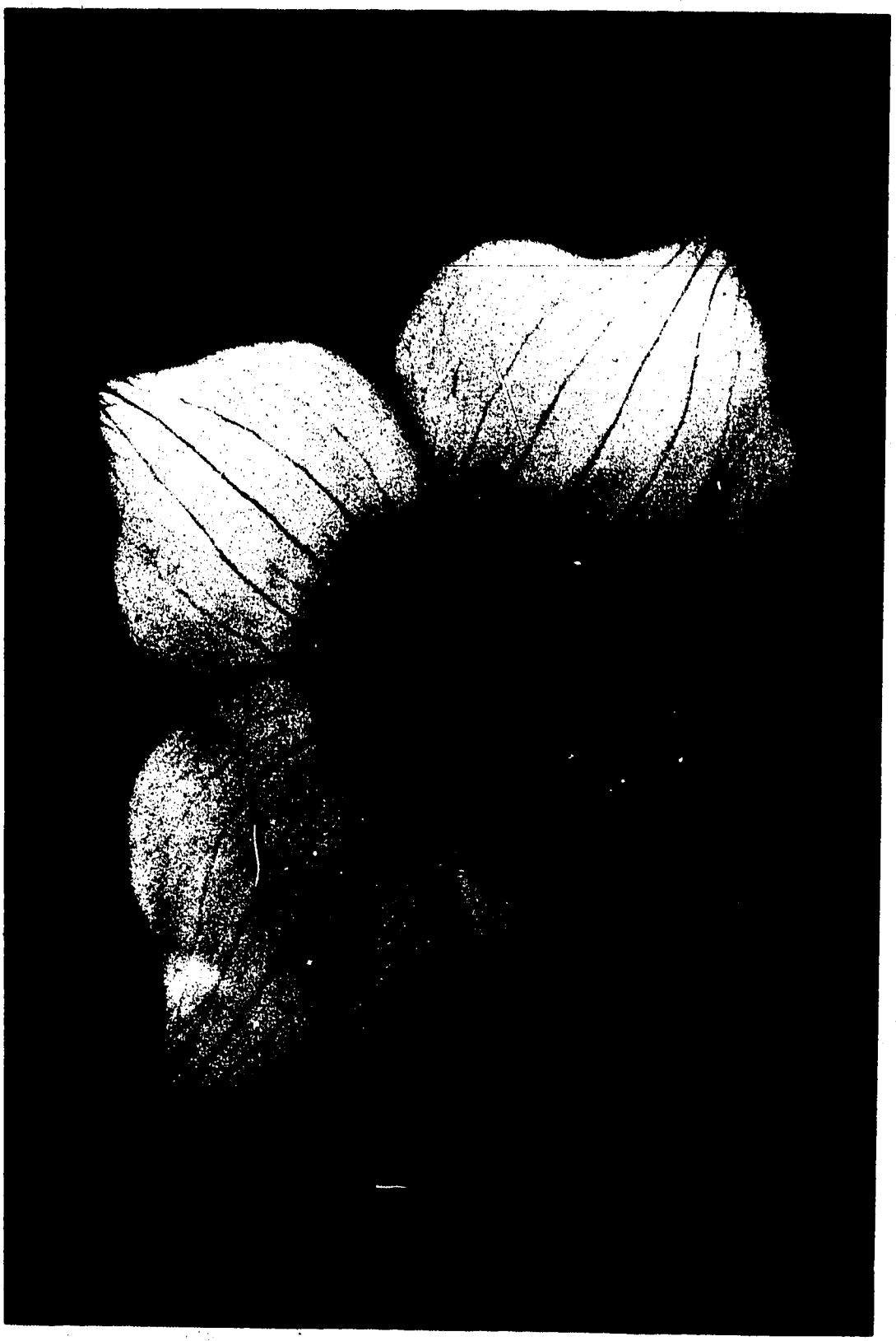
FIGURE 6

Inflorescence of Herbaceous *Cornus*

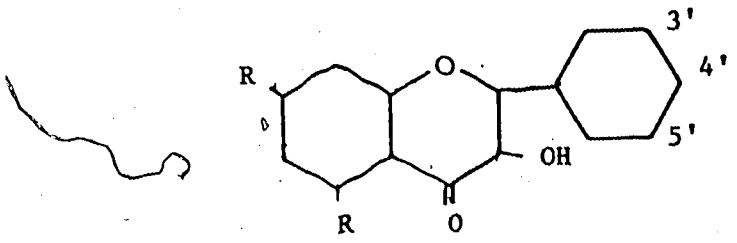
(#75024, *C. unalaschkensis*)

A. - flexed filament of stamen enclosed in flower bud.

B. - petal of closed flower bud.



Of the eight flavonoids identified, all were of the flavonol variety. The basic structure of a flavonol is:



A-ring B-ring

The three most common types of flavonols are kaempferol, quercetin, and myricetin. They differ from one another in their b-ring hydroxylation pattern. Kaempferol has a single OH group at the 4' position, while quercetin has two OH groups at the 3' and 4' positions respectively and myricetin has three OH groups at the 3', 4', and 5' positions on the molecule.

No glycosides of the myricetin type were found in any collections examined. However, glycosides of both kaempferol and quercetin were isolated from all collections examined (see Fig. 7). The kaempferol glycosides were visible on the chromatogram as one spot but further chromatography separated the spot into two separate entities with a possible third compound visible. After identification of the two easily discernible spots as kaempferol 3-O glucoside and kaempferol 3-O arabinoside, the original large spot was hydrolyzed. The only aglycone present in the large spot was kaempferol; however, three sugars, glucose, arabinose, and galactose were isolated. This result shows that a third very similar compound is present in the original large spot - kaempferol 3-O galactoside. No figure showing Rf and spectral data is present for this compound because not enough material was available for analysis.

Seven of the eight flavonols identified were present in all the collections examined. The eighth compound was present only in some of the collections examined as outlined in Table 8. Map 5 outlines the distribution of the collections which contain quercetin 3-O gentiobioside compared with the distribution of collections which do not contain quercetin 3-O gentiobioside.

FIGURE 7

aster Chromatogram of Flavonoids found in the Herbaceous Taxa of *Cornus*

1 Quercetin 3-0 glucoside

2 Quercetin 3-0 arabinoside

3 Quercetin 3-0 gentiobioside

4 Quercetin 3-0 galactoside

5 Quercetin 3-0 sophoroside

6 Kaempferol 3-0 glucoside

7 Kaempferol 3-0 arabinoside

8 Kaempferol 3-0 galactoside

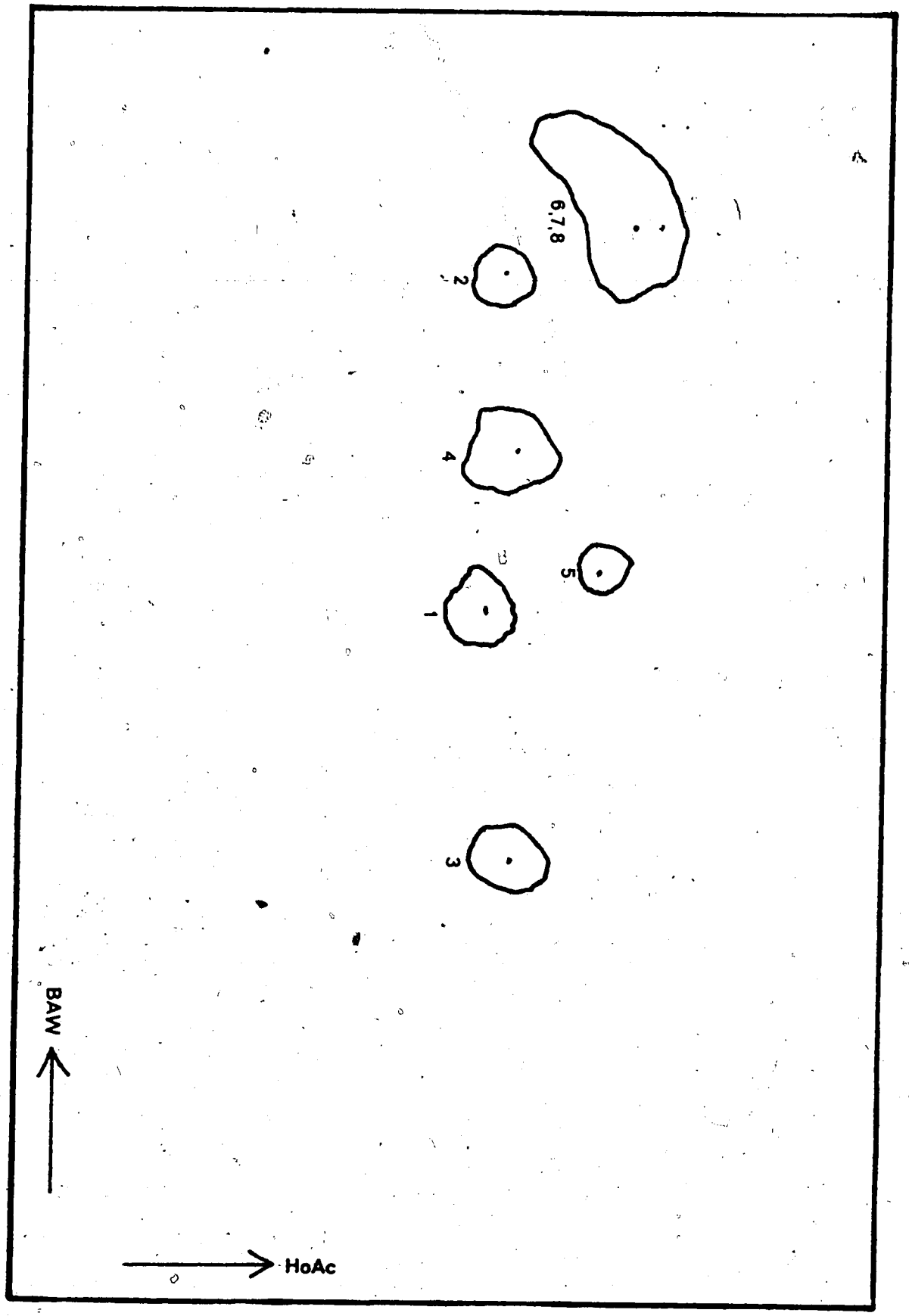
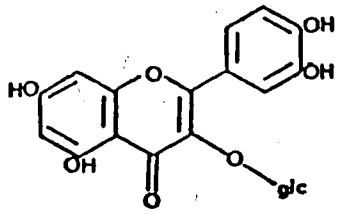

6,7,8
2
4
5
1
3
BAW
HoAc

FIGURE 8

Rf and Spectral Data for Quercetin 3-O Glucoside

Quercetin 3-O-glucoside

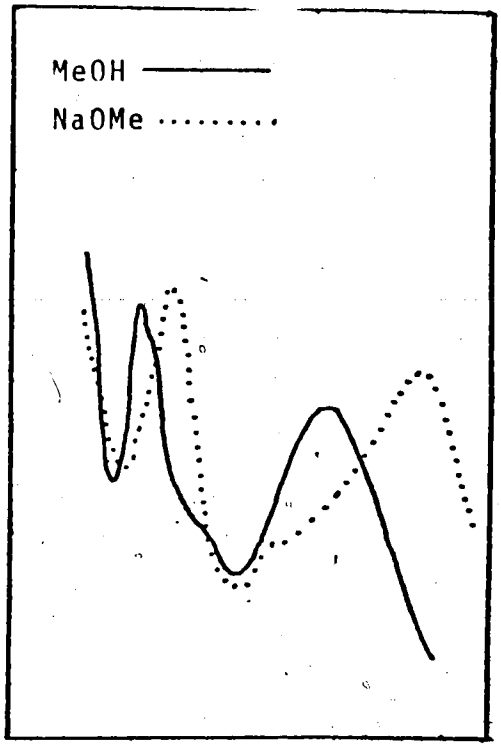


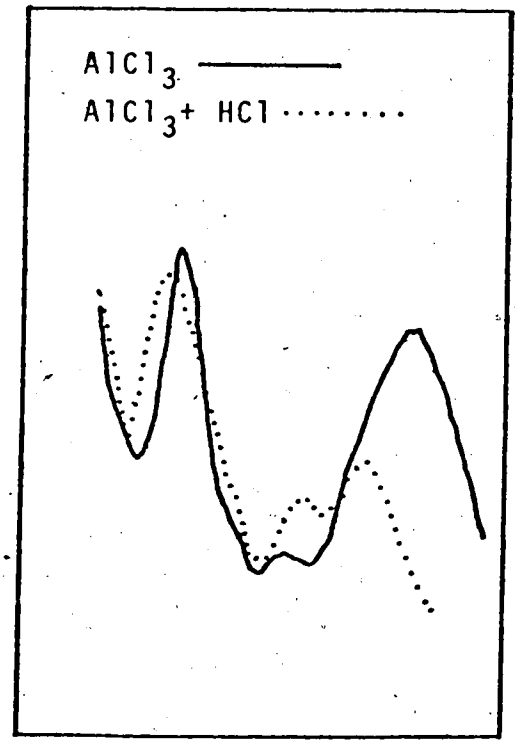
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	Ph	UV	UV/NH_3
60	11	29	40	ppl	ylw

UV Spectral Data

MeOH	259, 266sh, 298sh, 361
NaOMe	279, 331, 411
$AlCl_3$	275, 308sh, 330, 402
$AlCl_3$/ HCl	270, 305sh, 341, 373
NaOAc	268, 310sh, 362
H_3BO_3	264, 299sh, 380





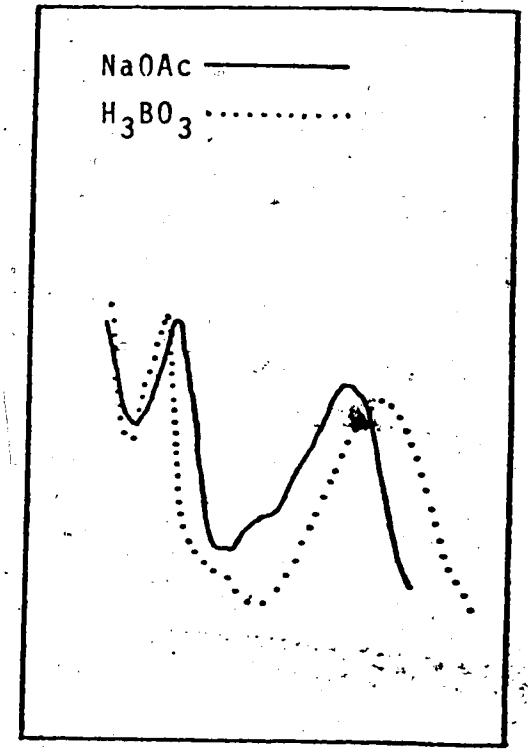
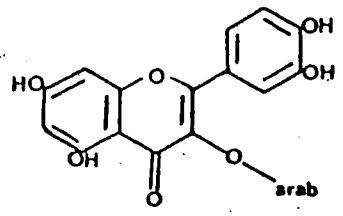


FIGURE 9

Rf and Spectral Data for Quercetin 3-O Arabinoside

Quercetin 3-O-arabinoside

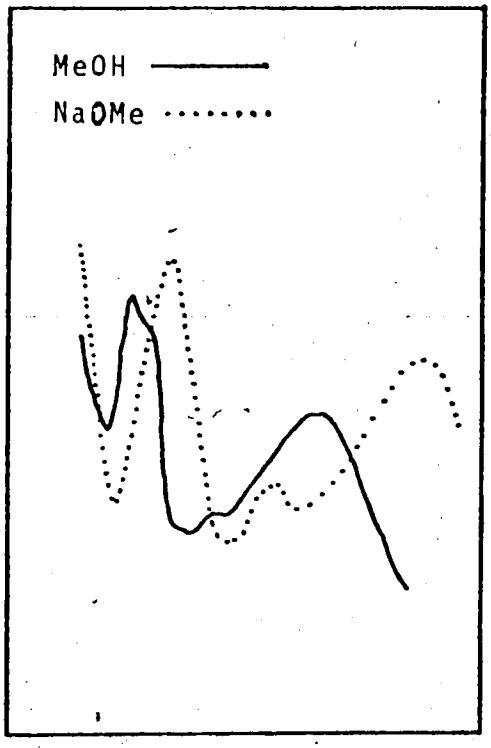


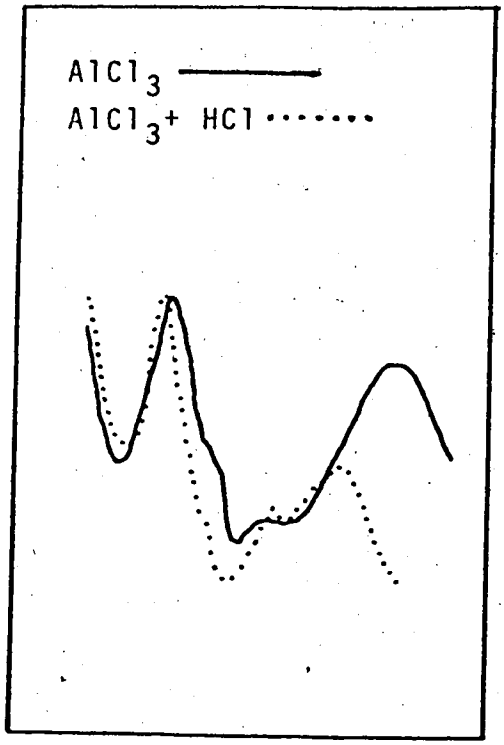
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	Ph	UV	UV/NH_3
80	09	29	66	ppl	ylw

UV Spectral Data

MeOH	258, 268sh, 298sh, 356
NaOMe	281, 334sh, 418
$AlCl_3$	275, 301sh, 321sh, 400
$AlCl_3$/ HCl	271, 295sh, 331sh, 369
NaOAc	266, 318sh, 372
H_3BO_3	261, 295sh, 370





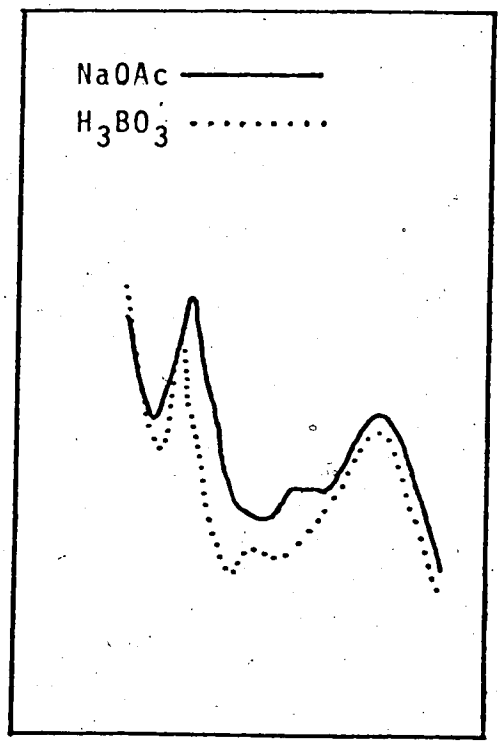
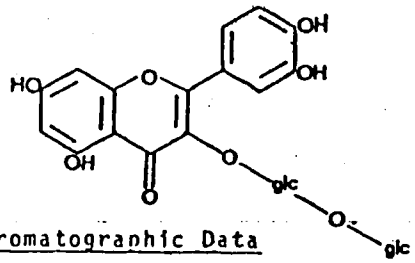


FIGURE 10

Rf and Spectral Data for Quercetin 3-O Gentiobioside

Quercetin 3-O-gentiobioside

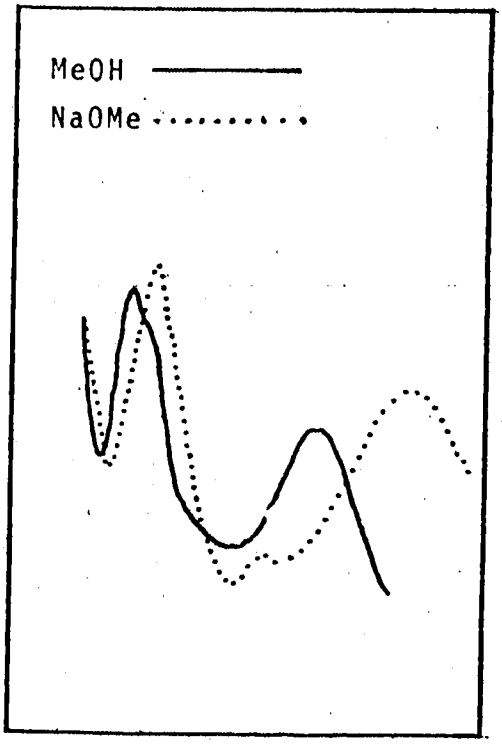


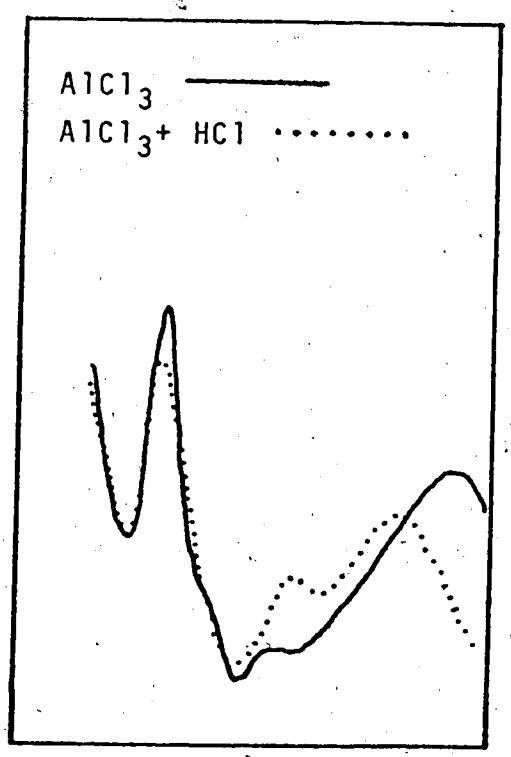
Chromatographic Data

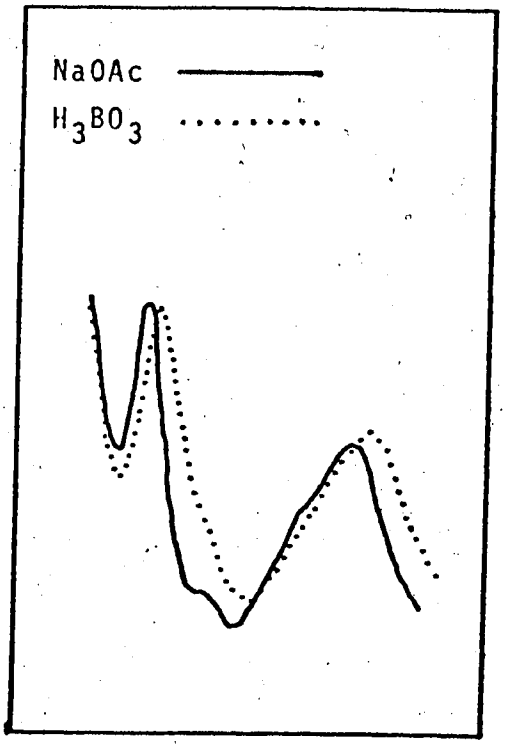
Rf Values				Spot Colour	
BAW	H_2O	HoAc	Ph	UV	UV/NH_3
35	17	28	40	ppl	ylw

UV Spectral Data

MeOH	258, 270sh, 359
NaoMe	270, 330sh, 409
$AlCl_3$	272, 301sh, 325sh, 431
$AlCl_3$/ HCl	270, 302sh, 342sh, 403
NaOAc	269, 306sh, 384
H_3BO_3	263, 304sh, 375







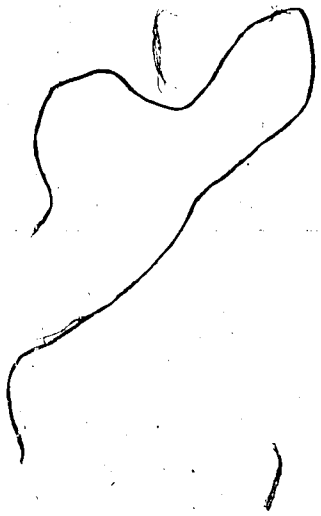
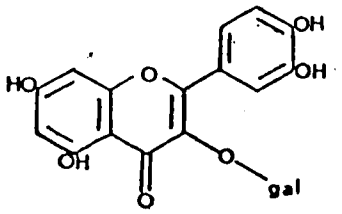


FIGURE 11

Rf and Spectral Data for Quercetin 3-O Galactoside

Quercetin 3-O-galactoside

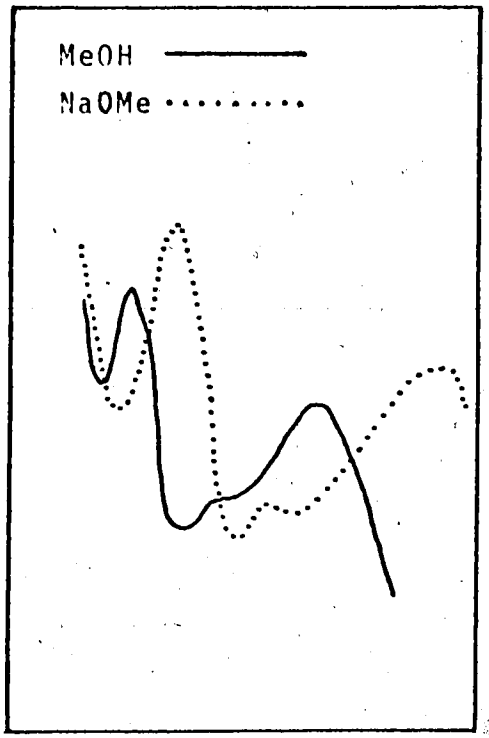


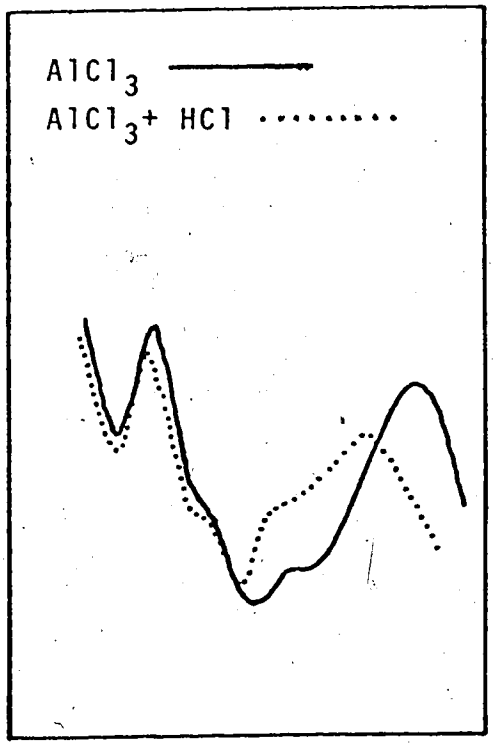
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	Ph	UV	UV/NH_3
68	14	37	61	ppl	ylw

UV Spectral Data

MeOH	258, 268sh, 302sh, 361
NaOMe	284, 330sh, 426
$AlCl_3$	270, 308sh, 345sh, 411
$AlCl_3$/ HCl	268, 300sh, 333sh, 381
NaOAc	266, 313sh, 378
H_3BO_3	263, 308sh, 381





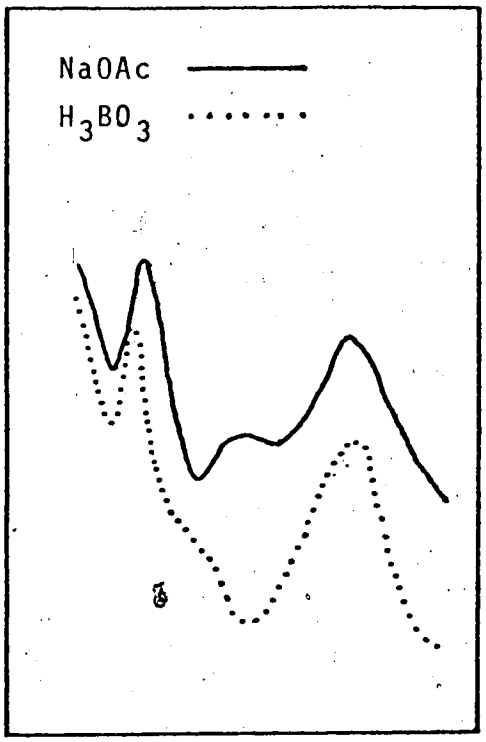
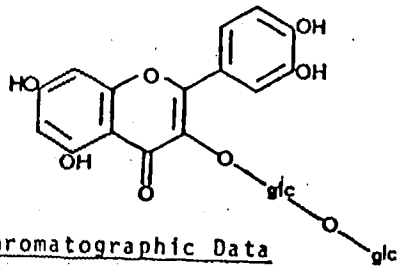


FIGURE 12

Rf and Spectral Data for Quercetin 3-O Sophoroside

Quercetin 3-O-sophoroside

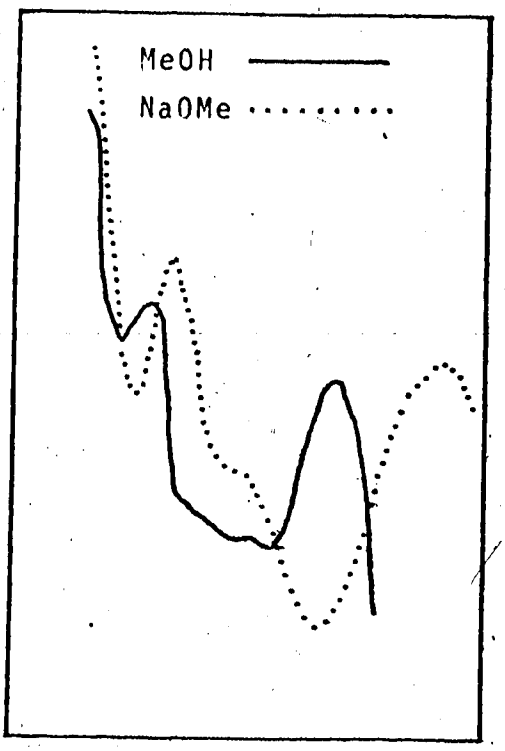


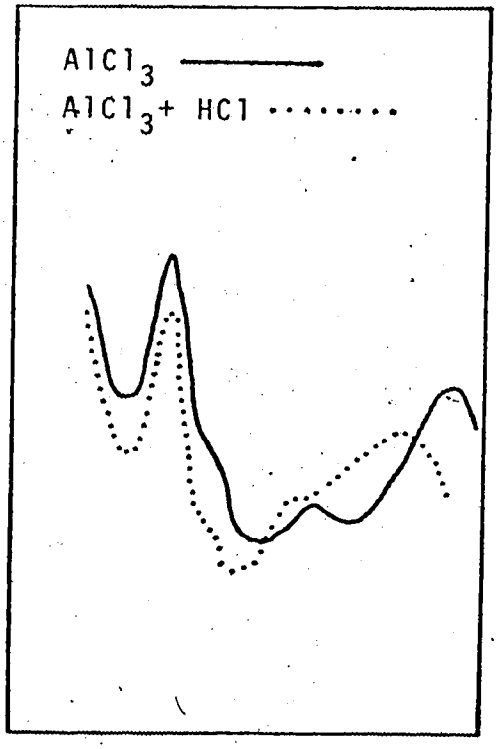
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	Ph	UV	UV/NH_3
46	28	47	37	ppl	ylw

UV Spectral Data

M [illegible]70, 300sh, 358
[illegible], 322sh, 431
[illegible]306sh, 352sh,428
[illegible]302sh, 342, 403
[illegible]306sh, 376
[illegible]301sh, 390





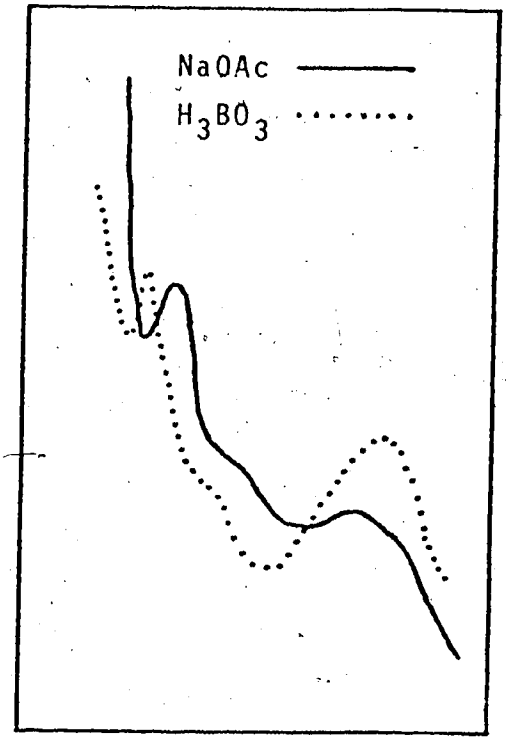
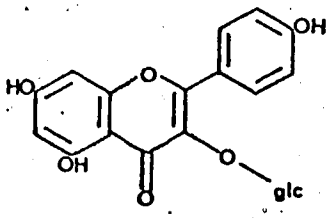


FIGURE 13

Rf and Spectral Data for Kaempferol 3-O Glucoside

Kaempferol 3-O-glucoside

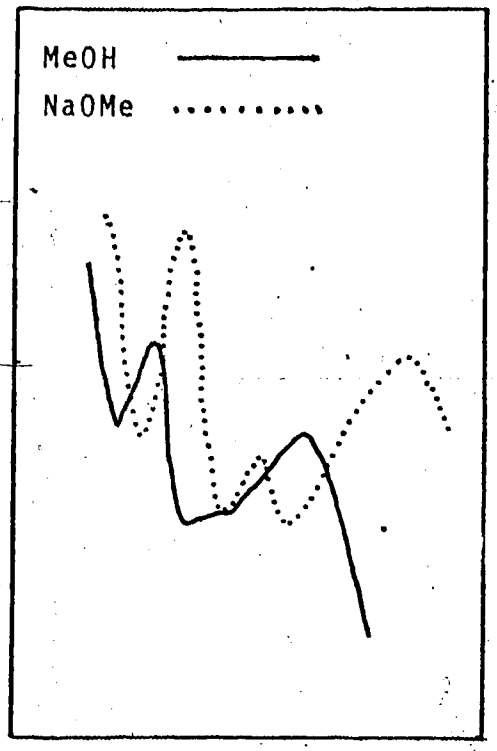


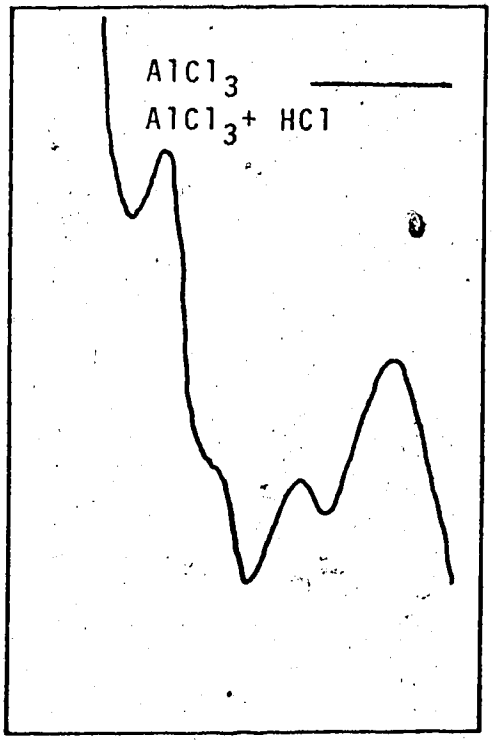
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	Ph	UV	UV/NH_3
72	18	42	70	ppl	ylw

UV Spectral Data

MeOH	268, 300sh, 358
NaOMe	284, 329sh, 408
$AlCl_3$	274, 306sh, 350, 400
$AlCl_3$/ HCl	274, 306sh, 350, 400
NaOAc	273, 302sh, 362
H_3BO_3	268, 359





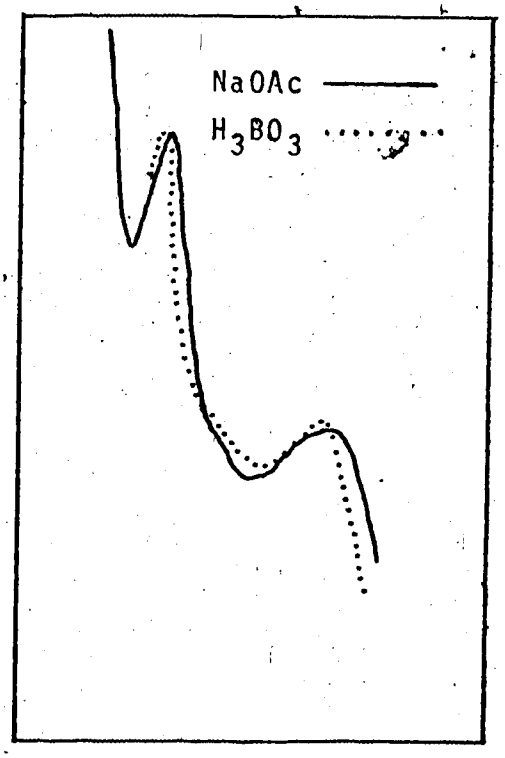
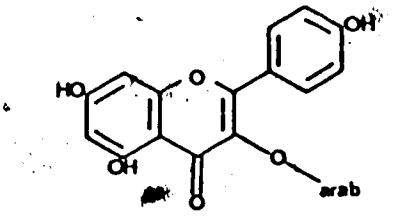


FIGURE 14

Rf and Spectral Data for Kaempferol 3-O Arabinoside

Kaempferol 3-O-arabinoside

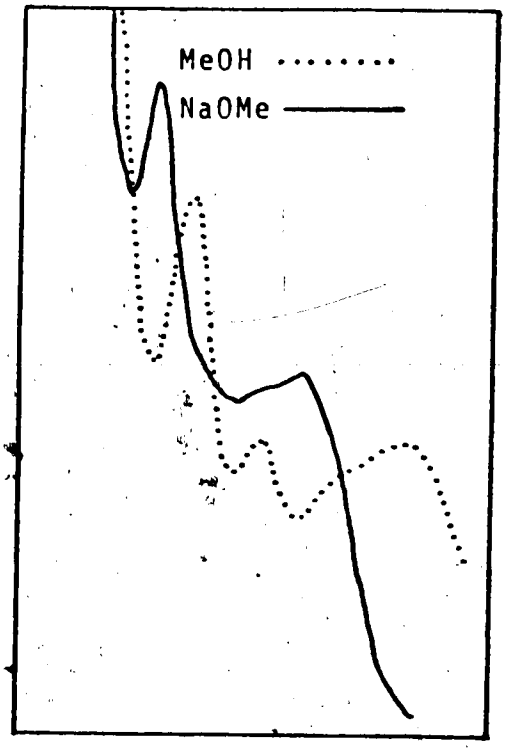


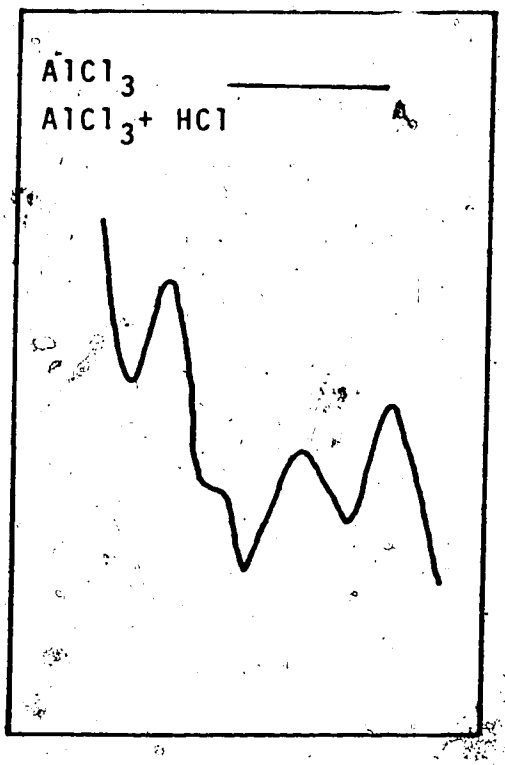
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	Ph	UV	UV/NH_3
84	08	27	34	ppl	ylw

UV Spectral Data

MeOH	268, 332sh, 351
NaOMe	284, 327sh, 366, 406
$AlCl_3$	275, 306sh, 352sh, 398
$AlCl_3$/ HCl	275, 306sh, 353sh, 396
NaOAc	273, 304sh, 360
H_3BO_3	268, 302sh, 351





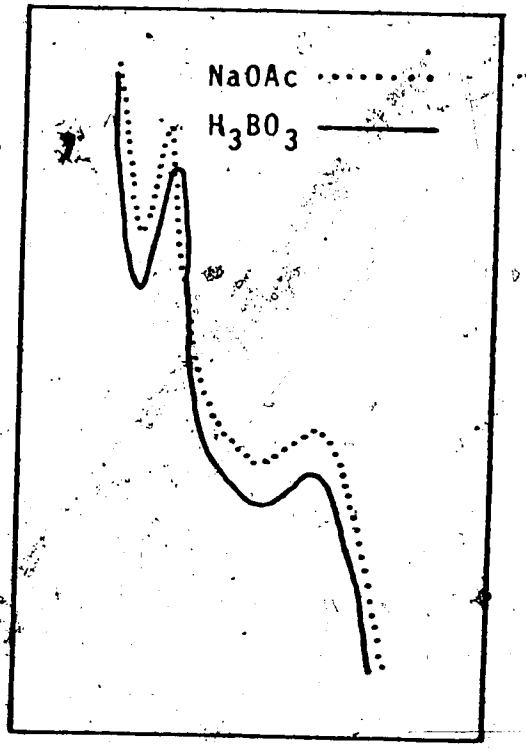


TABLE 7

List of Specimens used for Phytochemical Study*

CANADA

Alberta: Nojack Campsite, 75002, June 15/75; Mulhurst, 75003, June 18/75; 20 mi. E. of Rocky Mtn. House, 75004, June 18/75; 35 mi. W. of Rocky Mtn. House, 75005, June 18/75; Herbert Lake, 75006, June 19/75; Finn Creek, 75009, June 19/75; Olive Lake 75010, June 20/75; E. of Radium, 75011, June 20/75; Lake Minnewanka, 75014, June 21/75; Sulphur Mtn., 75015, June 21/75; Reesor Lake, 76101, June 23/76; Spruce Coulee, 76102, June 23/76.

British Columbia: Moresby Lake, Queen Charlotte Is., 75016, 75017, 75018, 75019, June 29, 30/75; Upper Victoria Lake, Queen Charlotte,Is., 75024, 75026, 75028, July 1/75; Pt. Clements, Queen Charlotte Is., 75029, July 3/75; Tow Hill, Queen Charlotte Is., 75030, 75031, July 3/75; Tlell River, Queen Charlotte Is., 75032, July 4/75; Oliver Lake, 75033, July 6/75; Terrace, 75034, July 6/75; Seely Lake Prov. Pk., 75035, July 6/75; 20 mi. S. of Smithers, 75036, July 6/75; S. of Burns Lake, 75037, July 6/75; Purden Lake Prov. Pk., 75038, July 7/75; 15 mi. E. of Purden Lake, 75039, July 7/75; 75 mi. W. of Jasper, 75041, July 7/75; 25 mi. W. of Jasper, 75042, July 7/75; 90 mi. N. of Ft. St. John, 75074, July 27/75.

Yukon: Mi. 46, Dempster Hwy., 75070, July 24/75; Mi. 757, Alaska Hwy., 75071, July 26/75; Coal River Crossing, 75072, July 26/75.

U.S.A.

Alaska: S. of Delta Jctn., 75043, July 12/75; 30 mi. N. of Paxon,

TABLE 7. Continued.

75044, July 13/75; Paxon, 75045, 75046, July 13/75; Mi. 27, Denali Hwy., 75047, July 13/75; Mi. 42, Denali Hwy., 75048, 75049, 75050, July 13/75; Mi. 115, Denali Hwy., 75051, July 14/75; Mt. Eliason, McKinley Pk., 75052, 75053, July 14/75; Broad Pass, 75054, July 15/75; Mi. 84, Steese Hwy., 75055, July 15/75; E. of Fairbanks, 75056, July 16/75; 19 mi. W. of Delta Jctn., 75057, July 16/75; S. of Eagle, 75058, July 17/75; Tazlina, 75059, July 18/75; Mirror Lake, near Anchorage, 75060, July 18/75; 40 mi. N. of Seward, 75063, July 20/75; 12 mi. S. of Anchorage, 75064, July 20/75; 12 mi. N. of Houston, 75066, July 21/75; Little Coal Creek, 75067, July 21/75; Mi. 138, Hwy. 3, 75068, July 21/75; Glenallen, 75069, July 22/75; Perseverence Lake, Ketchikan, 76103, July 7/76; Pat's Creek, 76104, July 10/76; Petersburg, 76105, July 12/76; Ohmer Creek, 76106, 76107, July 13, 15/76; W. Glacier Trail, Juneau, 76108, July 18/76; Spaulding Trail, Auke Bay, 76109, July 20/76; Chilkat Lake, Haines, 76110, July 22/76; Haines, 76111, July 23/76.

*All collections were made by the author.

TABLE 8

List of Specimens which contain Quercetin 3-O Gentiobioside*

CANADA

British Columbia: Moresby Lake, Queen Charlotte Is., 75016, 75017, 75018, 75019, June 29/75; Upper Victoria Lake, Queen Charlotte Is., 75024, 75026, 75028, July 1, 2/75; Pt. Clements, Queen Charlotte Is., 75029, July 3/75; Tow Hill, Queen Charlotte Is., 75030, 75031, July 3/75; Tlell River, Queen Charlotte Is., 75032, July 4/75; Oliver Lake, 75033, July 6/75; Terrace, 75034, July 6/75; Seely Lake Prov. Pk., 75035, July 6/75; Purden Lake Prov. Pk., 75038, July 7/75; 15 mi. E. of Purden Lake, 75039, July 7/75.

U.S.A.

Alaska: Mirror Lake, Anchorage, 75060, July 19/75; 41 mi. N. of Seward, 75063, July 20/75; Perseverence Lake, Ketchikan, 76103, July 7/76; Pat's Creek, 76104, July 10/76; Petersburg, 76105, July 12/76; Ohmer Creek, 76106, 76107, July 13, 15/76; W. Glacier Trail, Juneau, 76108, July 18/76; Spaulding Trail, Auke Bay, 76109, July 20/76; Chilkat Lake, Haines, 76110, July 22/76; Haines, 76111, July 23/76.

*All collections were made by the author.

MAP 5

Geographical Distribution of the Herbaceous *Cornus* taxa which contain Quercetin 3-0 gentiobioside*

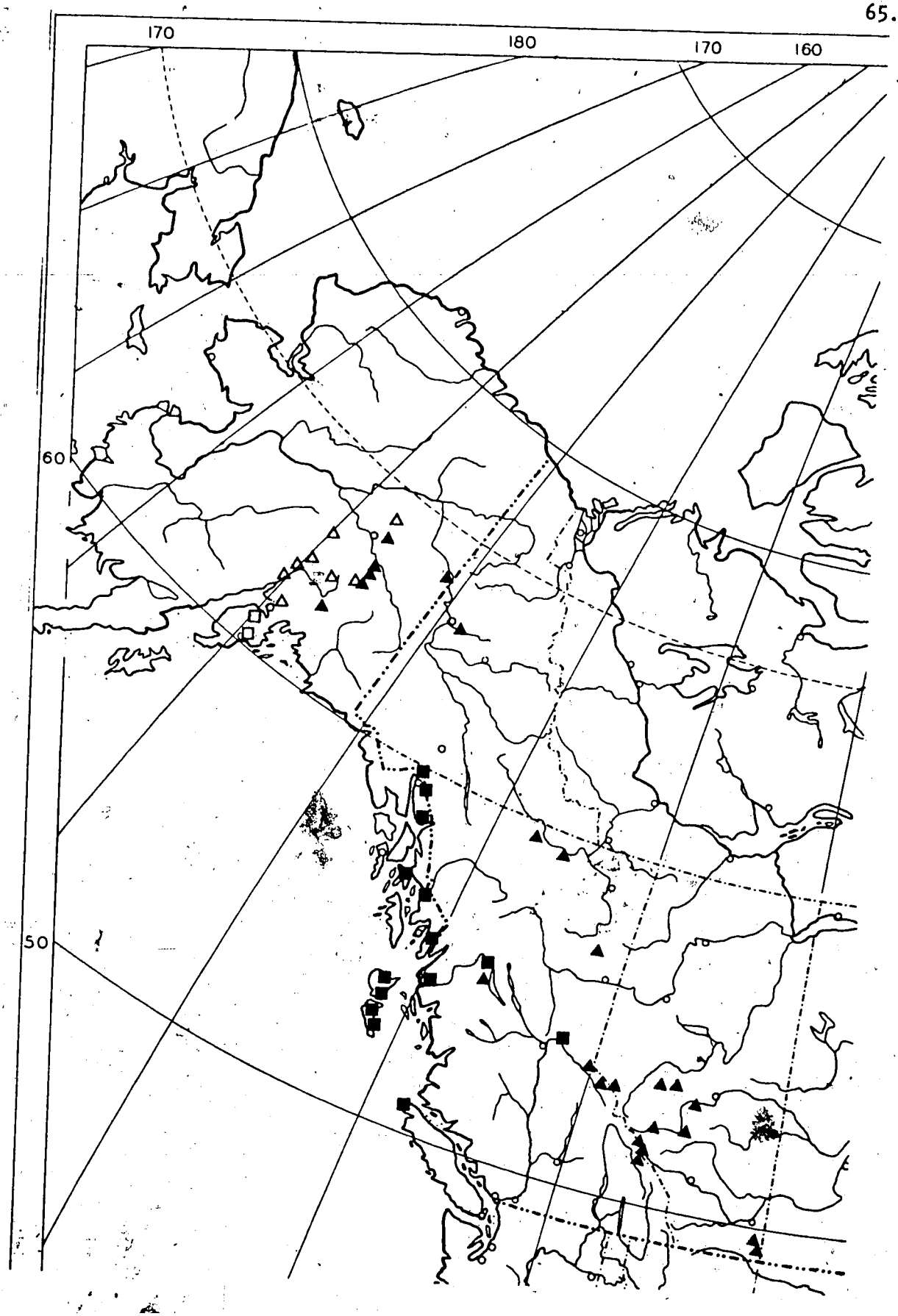
□- *Cornus suecica* - quercetin 3-0 gentiobioside present

■- *Cornus unalaschkensis* - quercetin 3-0 gentiobioside present

Δ- *Cornus canadensis* X *suecica* - quercetin 3-0 gentiobioside absent

▲- *Cornus canadensis* - quercetin 3-0 gentiobioside absent

*Based on collections cited in Tables 7 and 8.


170
180
170
160
60
50

Taxonomy

The results already reported under separate headings are strongly interrelated. Because of this, these results may also be reported with respect to the information they give when combined.

Collections of the tetraploid populations were made mainly along the northwestern coast of North America. In addition, two collections from continental B.C. were made - Purden Lake (75038) and New Hazelton (75035). All collections of the tetraploid populations were made from a *Picea sitchensis* (Bong.) Carv., *Tsuga heterophylla* (Raf.) Sarg. dominated coastal forest habitat, or from the peat bogs which intersperse the coastal forest, where *Pinus contorta* Dougl. is the dominant tree species. Map 4 shows the distribution of diploid and tetraploid taxa.

The diploid populations have been collected from a wider range of habitats than those populated by the tetraploids. Most commonly the diploid taxa are found in a habitat receiving less rainfall than the coastal forest, in association with such tree species as *Populus tremuloides* Michx., *Picea glauca* (Moench) Voss or *Pinus contorta*.

Separation of two cytotypes is not in exact agreement with separation of structural types. All those specimens which are morphologically identified as *Cornus canadensis* belong to the diploid cytotype. Other identifications based on morphology cannot be made with as much assurance as can the identification of *C. canadensis*, so cytological and chemical evidence must be used to help form the groups.

Those collections which are structurally intermediate are in two groups cytologically and phytochemically. These intermediate forms are either diploid or tetraploid (see Map 4) and they either possess

quercetin 3-O gentiobioside or they do not. All the tetraploid specimens examined possess quercetin 3-O gentiobioside. All of the diploid specimens examined do not contain quercetin 3-O gentiobioside. In contrast, *Cornus suecica* is diploid (2n=22) and possesses quercetin 3-O gentiobioside. The combination of these latter two characters easily separates it from the intermediate populations. A comparison, based only on structure does not permit such a reliable classification.

Table 9 shows summary of the data collected for the four taxa.

TABLE 9

A summary of the data given for herbaceous *Cornus*

	Cornus canadensis	*Cornus canadensis* X *suecica*	*Cornus unalaschkensis*	*Cornus suecica*
Chromosome Number	2n = 22	2n = 22	2n = 44	2n = 22
Quercetin 3-O gentiobioside	-	-	+	+
Pollen viability	≈98%	≈52%	≈98%	≈98%
Morphological Index Values	92%-100%	64%-79%	31%-89%	21%-28%

CHAPTER 4

DISCUSSION

The delimitation of taxa within any group of plants requires a certain amount of subjectivity. Strict adherence to either the biological or the morphological species definition does not inevitably result in the most useful classification. In delineating 'species' in this study, three major factors were taken into account: structural differences, distributional differences and genetic isolation. Differences in structure were considered to be important for two reasons. First, these differences are traits most commonly used in existing classifications to delimit species, and second, these differences very often reflect genetic discontinuities between the taxa being compared. The final classification, however, incorporated all available information.

Previous attempts to classify the taxa within the subgenus *Arctocrania* have also relied heavily upon structural characters and some confusing results have been obtained. For example, petal colour was considered by Calder and Taylor (1968) to be the diagnostic character by which the three species they recognized (*C. canadensis, C. suecica, C. unalaschkensis*) could be separated. Although, as has been previously mentioned (pg. 28), petal colour is useful in quickly separating *C. canadensis* from the rest of the complex, it has not been found useful in separating *C. suecica* from either *Cornus unalaschkensis* or *Cornus canadensis* X *suecica*. The petals of *C. suecica* were thought by Calder and Taylor (1968), to be completely purple, and conversely, the petals

of the intermediates were considered to be only partially purple. I found this not so.

Another classification based strictly upon structural characters was proposed by Lepage (1946, 1950, 1955) who described various forms (Figures 15-18). These forms of *C. canadensis* were separated, mainly on leaf and bract abnormalities. The results of this study indicate that the forms are rare and are most often contained in populations of otherwise normal *C. canadensis*. The form names are, therefore, considered synonyms of *C. canadensis*.

The structural variation within the *C. canadensis-suecica* complex as outlined on pages 26 to 30, is most accurately represented through the delimitation of the three groups; *C. canadensis*, *C suecica*, and an intermediate group. (The intermediate group is further subdivided into the two taxa *Cornus unalaschkensis* and *Cornus canadensis X suecica* but this segregation is not based on structural differences.) The use of all eleven morphological characters (pg. 27) does, in most cases, give an accurate breakdown of the complex into these three groups, but the incorporation of the other data generated by this study into the classification allows a more confident separation of the taxa as well as more clearly indicating the evolutionary relationships present.

The previous reports of two chromosome numbers within the complex (see Table 2) were confirmed by this study. *Cornus canadensis* and *Cornus suecica* were both found to be diploid while the intermediates were found to be composed of both a diploid and a tetraploid chromosome race. As previously mentioned (pg. 66) the latter is confined to a wet, primarily coastal environment. *C. suecica*, one of the diploid members of the complex, is also restricted to a primarily coastal environment,

FIGURE 15

A. *Cornus canadensis* L. forma *secunda* Lepage.

B. *Cornus canadensis* L. forma *infraverticillata* Lepage.

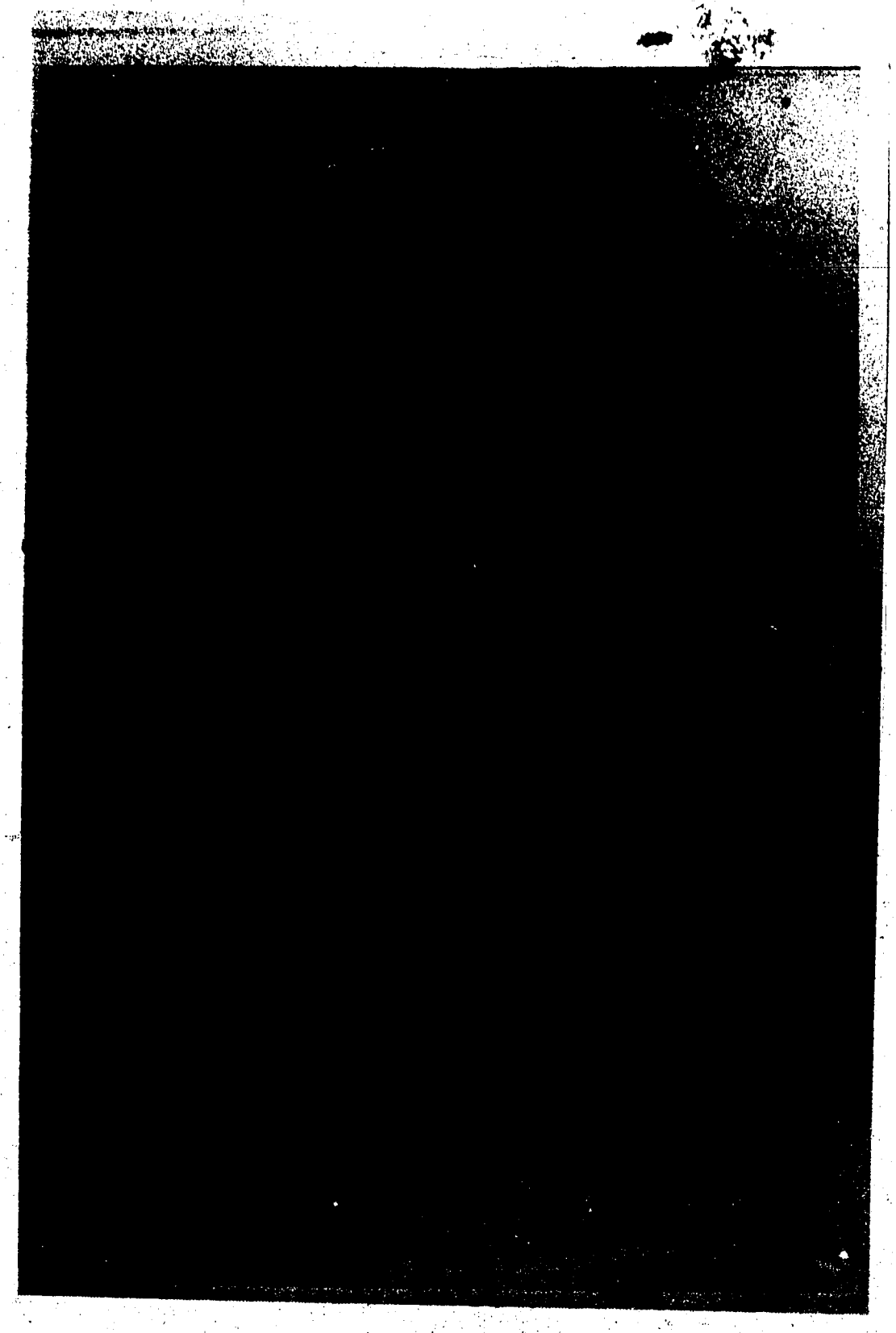


FIGURE 16

A. *Cornus canadensis* L. forma *aphylla* Lepage.

B. *Cornus canadensis* L. forma *foliolosa* Lepage.

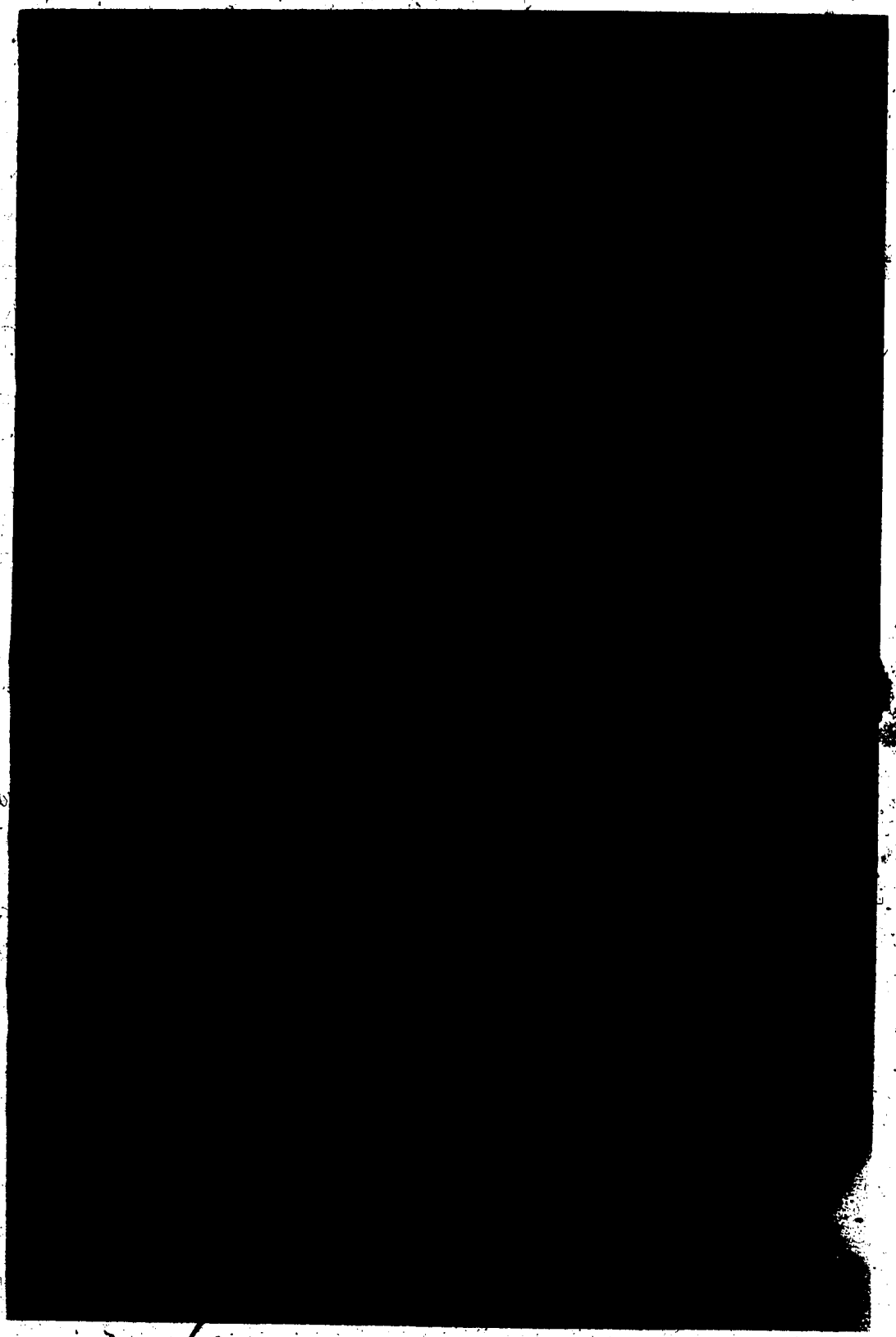
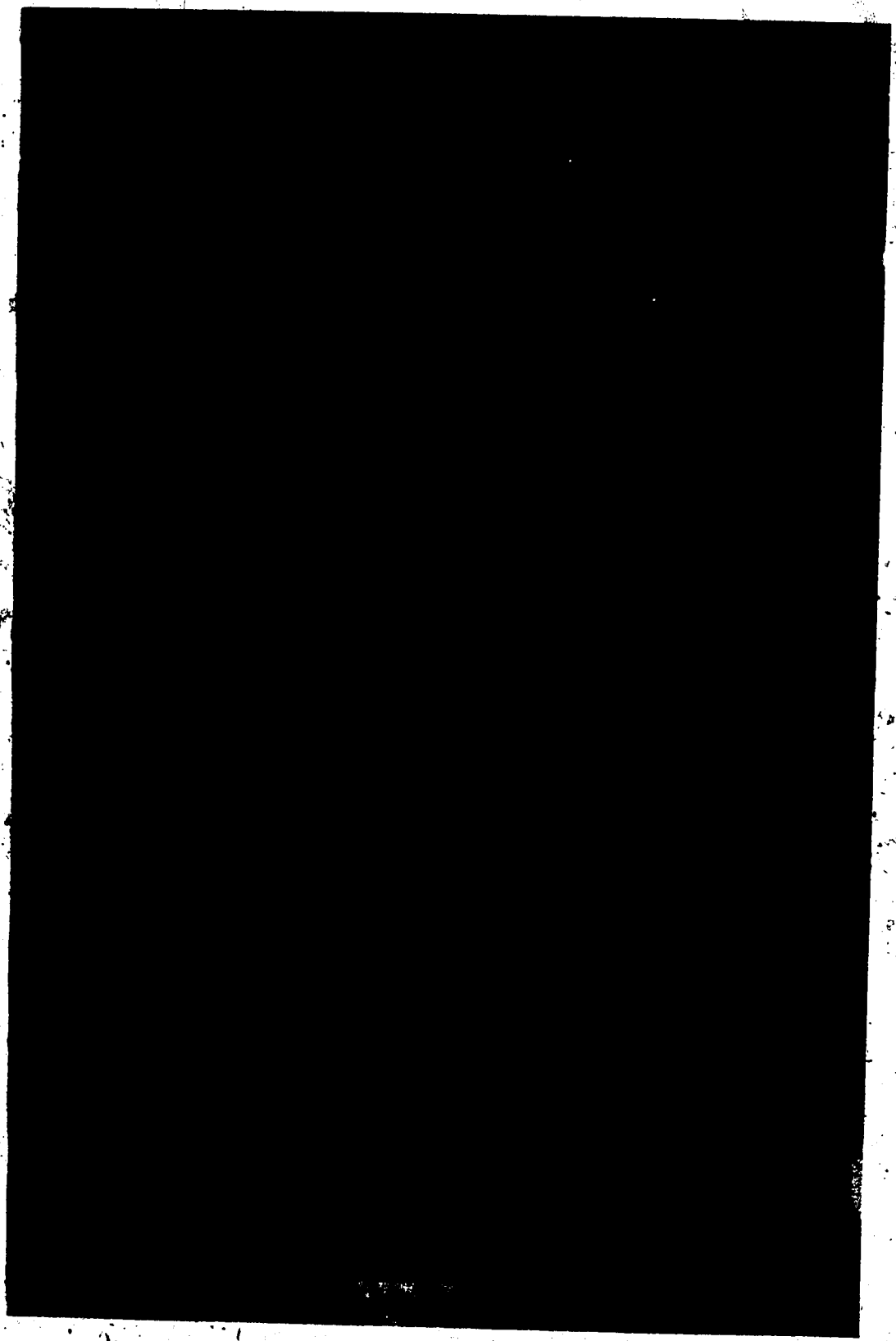


FIGURE 17

A. *Cornus canadensis* L. forma *ornata* Lepage.

B. *Cornus canadensis* L. forma *bifoliata* Lepage.



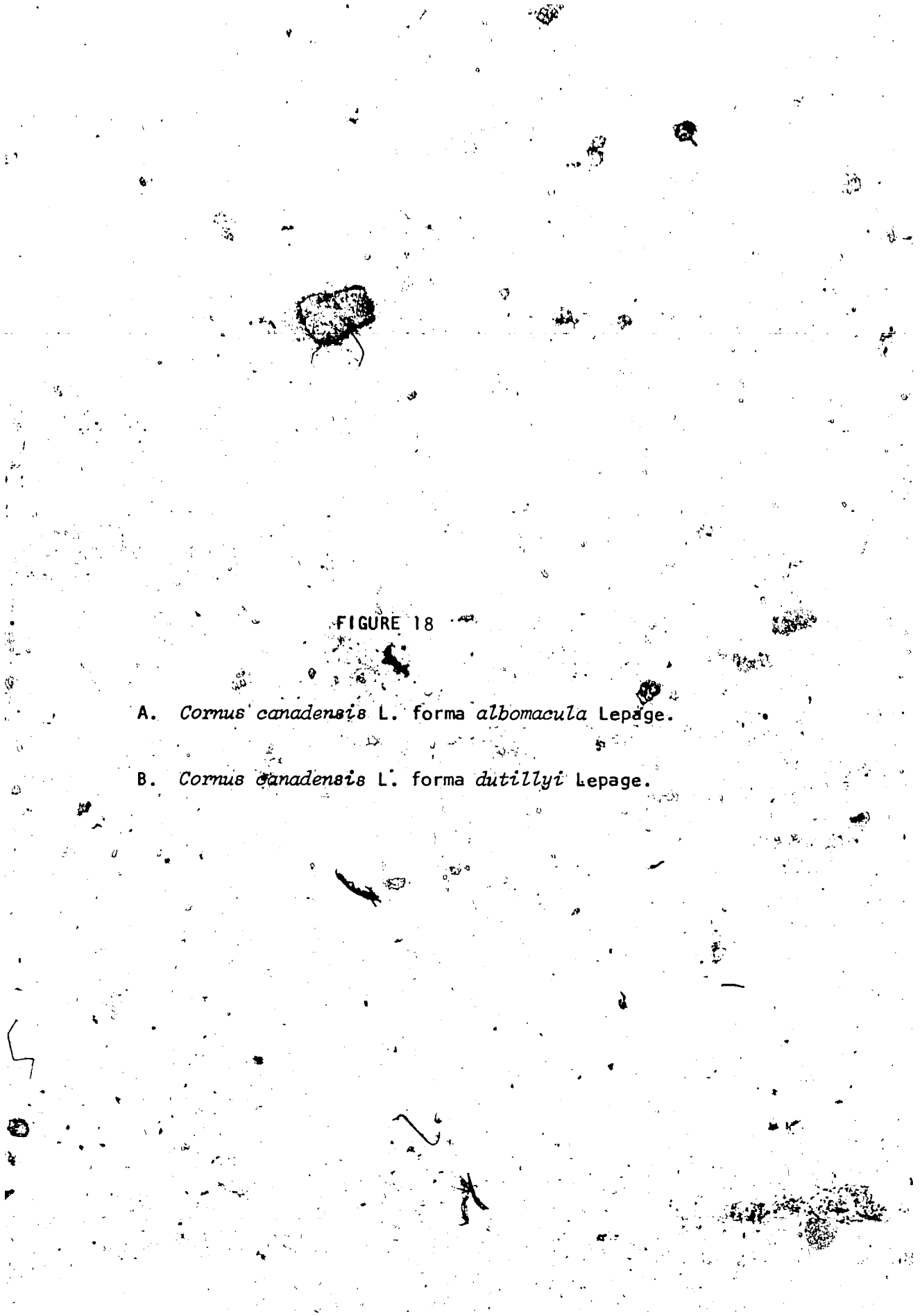
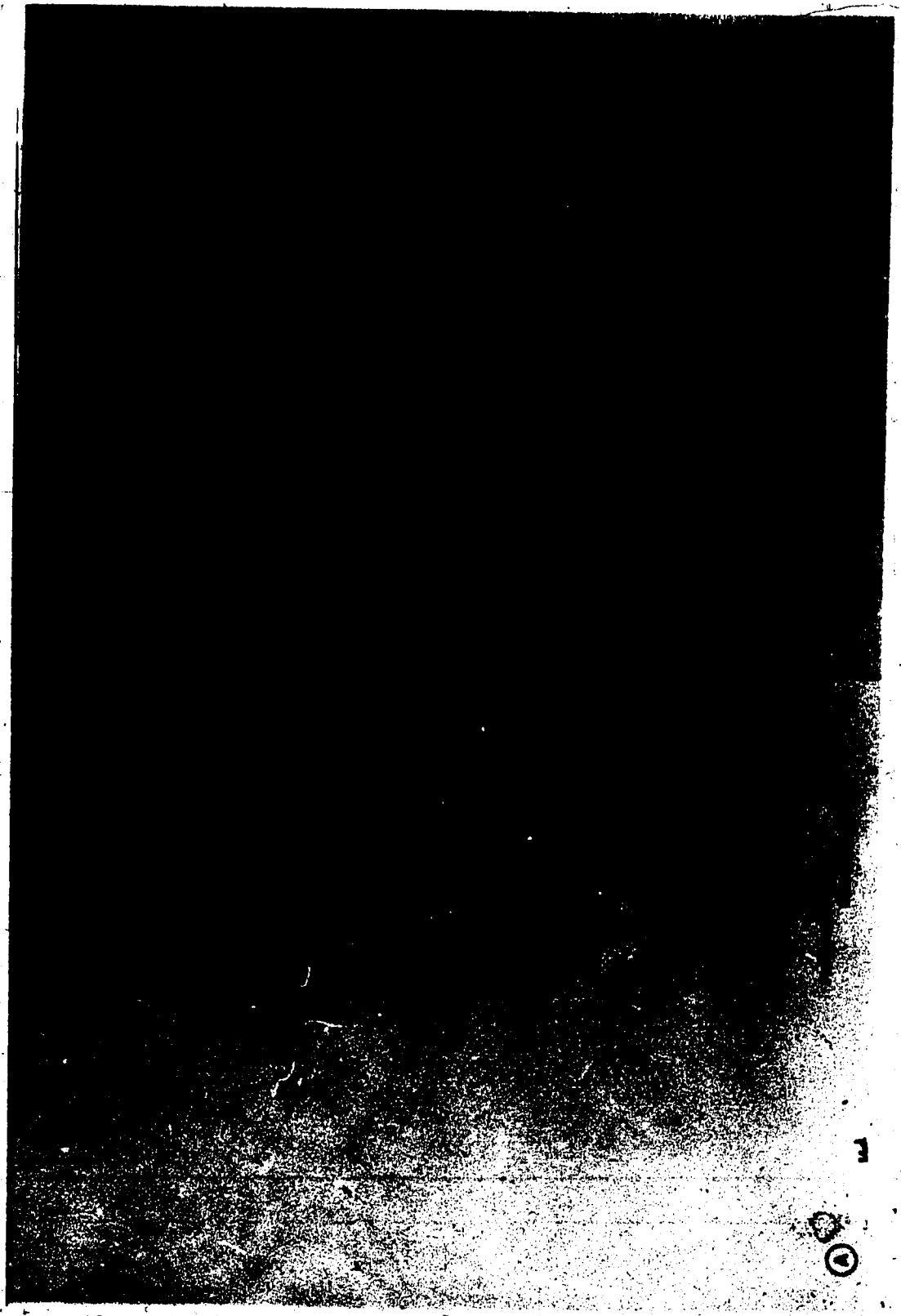


FIGURE 18

A. *Cornus canadensis* L. forma *albomacula* Lepage.

B. *Cornus canadensis* L. forma *dutillyi* Lepage.



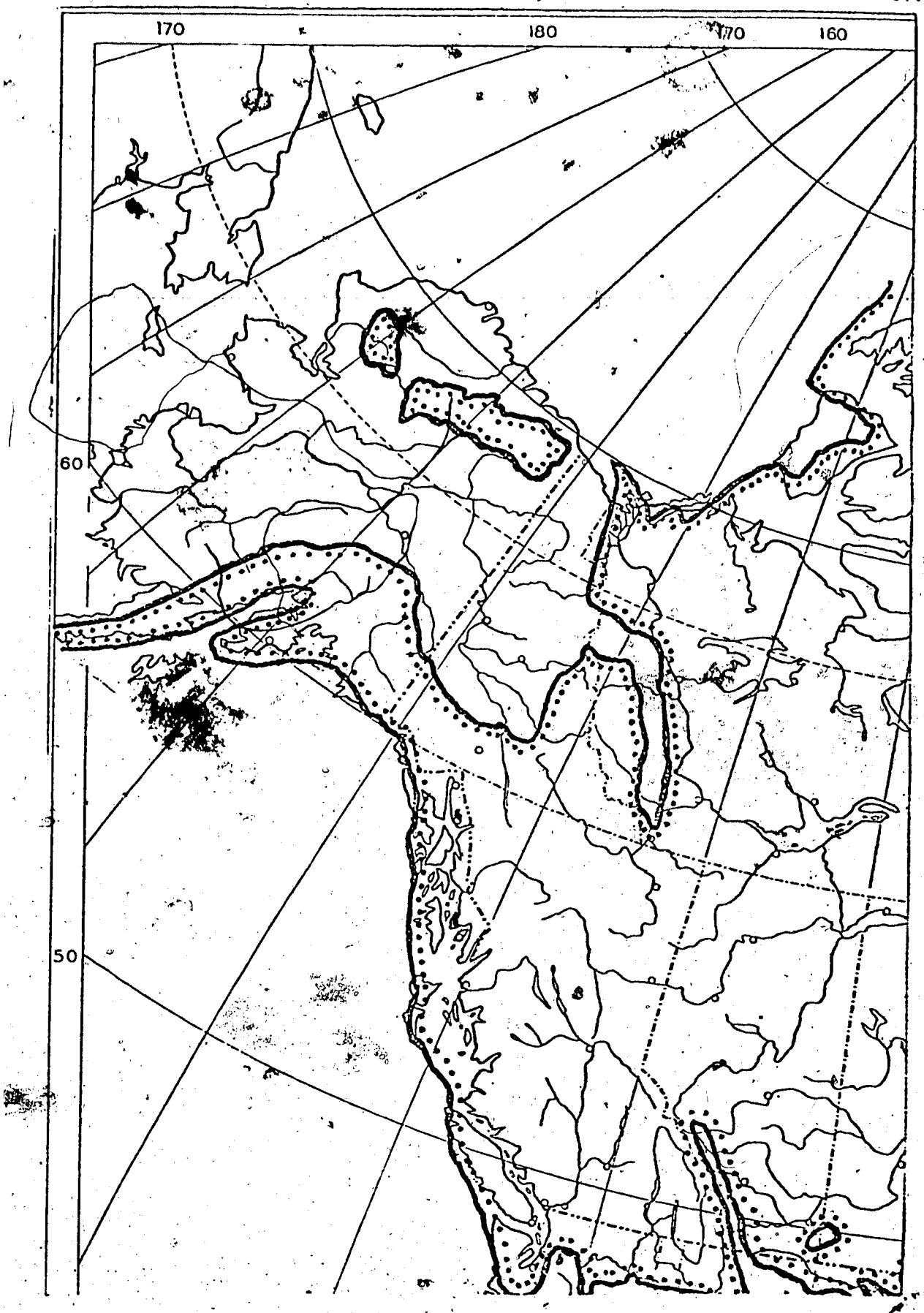
suggesting a close relationship between *C. suecica* and the tetraploid populations with respect to their environmental tolerances. The distribution patterns of these two groups do differ, as *C. suecica* is found on more northerly coasts than the tetraploid. Although there is no evidence in this survey that the distributions of the two overlap in any area, no significant difference in habitat was found, so sympatry is considered likely.

Differences in distribution of the diploid and tetraploid taxa do not support the theory that frequency of polyploidy increases with latitude since the diploids are more northern than are the tetraploids. A possible reason for the increase in frequency of polyploidy in northern floras is that polyploids are perhaps better able to invade new areas left open after the recession of glacial ice than are diploids. (A review of this theory is found in Johnson *et al.* [1965].) In this study, the distribution pattern could be explained as resulting from glaciation. The coastal areas, now occupied by the tetraploid, were all glaciated during the last advance of the ice, although various coastal refugia or unglaciated areas may have existed along the coast. (Heusseur, 1965; Savile, 1968; Randhawa and Beamish, 1972). As the ice receded the areas were reinvaded by the tetraploid. The more northern areas, although also unglaciated in many parts, do not show evidence of invasion by the tetraploid, perhaps because the tetraploid race may not have existed so far north in pre-glacial times and so was not present to invade these areas. Perhaps also the tetraploid race is not well adapted to survive in more northern latitudes. Map 7 shows approximate extent of glaciation during the Wisconsin.

Results of pollen viability tests conducted tie in very closely

MAP 6

Approximate extent of the Wisconsin glaciation in northwestern North America. (Based on Geological Survey Map No. 1257A, 1969.)


170
180
170
160
60
50

with information pertaining to chromosome number. The few results indicate partial sterility of the diploid intermediate. In this context they substantiate field observations made by other researchers (Hultén, 1937a; Olsen, 1914) concerning sterility of the intermediate. The problem of sterility within the complex is overcome partially, by vegetative reproduction of these plants. From the information generated by this study, it is not possible to predict what percentage of the diploid intermediates are sterile or semi-sterile. If diploid intermediate populations were completely fertile, a high degree of backcrossing with both the diploid parents could be expected. Observation in the field of diploid intermediates growing beside *C. canadensis*, with no evidence of interbreeding, (Coll #75052, 75048, 75046) suggests that backcrossing in these cases at least does not occur. However, 50% of the pollen in those specimens examined (75053, 75054) was viable indicating that backcrossing is at least possible and hence would be expected to introduce variability into the two parent species, so that they would resemble the intermediates. It would also tend to reduce gaps in variation between the two species and the intermediates. Table 4 (pg. 29) shows that the *C. suecica* populations analyzed have a morphological index value much higher (21% and 28%) than the postulated 0%. The gaps in variation between the two species (*C. canadensis* and *C. suecica*) and the intermediate taxa are also small (*C. canadensis* = 92%+; intermediates = 31%-89%; *C. suecica* = 21%-28%). A certain degree of backcrossing therefore occurs.

The chemical profile of the *C. canadensis-C. suecica* complex is relatively simple. The presence of only flavonol glycosides in the complex indicates only a modest chemical diversity. The presence of

only flavonol glycosides within a plant group has been previously reported by Harborne and Williams (1971) and Rosler *et al.* (1966), for *Opuntia*. The pattern is considered common. The evolutionary significance of this specific profile is not clear. A major evolutionary step within the plant kingdom which has been shown to affect the flavonoid content of plants is the step from the woody habit to the more advanced herbaceous habit (Swain, 1975). The change produces three typical changes in leaf flavonoids: loss of protoanthocyanidins, loss of b-ring trihydroxylation, and replacement of flavonols by flavones. Only the last two changes were examined in this study. Because members of the *C. canadensis-C. suecica* complex are the only herbaceous members of an otherwise woody genus, it is therefore not surprising that they only exhibit one of the chemical changes usually associated with the morphological change from a woody to herbaceous habit. The loss of b-hydroxylation is shown by the lack of myricetin, but there is no evidence of flavones replacing flavonols. The uniformity of flavonoid glycosides probably extends throughout the genus and is perhaps the reason Jensen *et al.* (1975a) turned to nonflavonoid glycosides in their attempt to establish phytochemical relationships within the genus.

The only division within the *C. canadensis-C. suecica* complex which could be drawn using exclusively chemical data was based upon presence or absence of quercetin 3-O gentiobioside. This division is strongly correlated with a division based upon chromosome number. Because these character systems are concordant there are not intermediate forms which must be categorized subjectively. Correlation of chromosome number and chemical constituents enables one to postulate the possible

inheritance pattern for quercetin 3-0 gentiobioside. Some diploids (*C. suecica*) and tetraploids have quercetin 3-0 gentiobioside while only some diploids (*C. canadensis* and *C. canadensis* X *suecica*) lack the compound. If one assumes that the diploid *C. suecica* gave rise directly, through simple chromosome doubling, to the tetraploid populations, then the pattern evident in the chemistry is easy to explain. However, morphological diversity of the tetraploid indicates that it was not directly derived from *C. suecica*. The presence of a diploid taxon, intermediate in structure between *C. suecica* and *C. canadensis* and therefore morphologically very similar to the tetraploid species, strongly indicates that the tetraploid probably arose from this intermediate through doubling of the chromosome number. The diploid intermediate, like *C. canadensis*, does not possess quercetin 3-0 gentiobioside. If the diploid is of a hybrid origin, then the most plausible explanation for inheritance of quercetin 3-0 gentiobioside is the following. If one considers the production of the compound to be controlled by a homozygous condition 'AA' and that this 'double' dosage of the 'A' allele is required for the production of the compound, then 'Aa' does not produce the compound. The doubling of the 'Aa' found in the diploid intermediate produces 'AaAa' in the tetraploid intermediate and thus the double 'A' dosage necessary for the production of gentiobioside is once again present. An alternative explanation would be that quercetin 3-0 gentiobioside is controlled by two recessive alleles. *C. suecica* would be recessive homozygous 'aa' while *C. canadensis* would be homozygous for the dominant allele 'AA'. The diploid intermediate would be heterozygous 'Aa' and thus not produce quercetin 3-0 gentiobioside. The production of the compound again in the tetraploid could only be explained through

the re-arrangement of recessive alleles, so that one of the now two gene loci controlling the inheritance of gentiobioside, was homozygous recessive. The chance of this occurring, coupled with the possibility of a recessive allele actively producing a compound, or coding for the production of a compound, is considered small. This theory is consequently considered improbable. Although the former theory best fits the information available at present, much more information would be required to conclusively prove this mode of inheritance.

The data presented in this study have been gathered to obtain a further understanding regarding the origin (of the intermediates) and relationships within the *Cornus canadensis-suecica* complex in North America.

The intermediate taxa in this complex, *Cornus canadensis* X *suecica* and *Cornus unalaschkensis* are considered by this author to both be of hybrid origin for the following reasons, all of which are based on the results of this study:

- Although their phenotypes exhibit a high degree of variation in expression, the diploid hybrid and the tetraploid are structurally 'in between' the two parent species.

- The tetraploids contain the full complement of flavonoids produced by the two parent species and a relationship between the diploid hybrid and the tetraploid can be postulated, based on chemical data (see previous page).

- The diploid hybrid is restricted in distribution to the overlap areas of the two species. It also exhibits pollen inviability (pg. 37) which suggests a degree of meiotic failure, probably resulting from the hybrid origin of the genome.

The tetraploid, although it was not found in the overlap areas of the two species, lives in a habitat which is very similar to the coastal overlap areas occupied by the diploid hybrid. Its survival in these outlying areas is not difficult to envision since it is fully fertile.

Based upon the evidence presented here, it is suggested that the intermediates, both diploid and tetraploid, are the results of hybridization originally and that the tetraploid has been derived from the diploid intermediate through chromosome doubling. The tetraploid, because it is fully fertile, and is wider ranging than the diploid intermediate, is thought to represent an older group of plants than the diploid hybrids examined.

The putative parent species can be separated from one another quite easily. Morphologically they are distinguishable from one another (pg. 28). They differ by having or lacking quercetin 3-O gentiobioside (Table 8) and by having different distribution patterns. *Cornus canadensis* is mostly continental in its distribution, while *C. suecica* is mainly coastal (Maps 1 and 2). Their areas of distribution overlap, but it is only at the periphery. Although the two species do have the same chromosome number, there is some degree of isolation in breeding, as shown by the semi-sterility evident in the diploid hybrid (pg. 37). For these reasons no change in the taxonomic status of these two species is proposed. Although it can be argued that the two species are very closely related because of the morphological variation present in the hybrid, which tends to make the complex look like one group, the evidence of hybridization and subsequent evolution within the group is there and is best shown in retaining the specific status of the two

parental taxa. Also, because of the circumboreal distribution of *C. suecica*, there are other distinct areas of distribution where *C. canadensis* is not present, as in northern Europe. Here the specific status of *C. suecica* may not be in question, since there has been no opportunity for backcrossing to introduce variation into the species. Retention of the specific status of *C. canadensis* and *C. suecica* is conservative and until a more complete geographic study is made I believe this classification is the most reasonable.

Classification of the intermediates represents another problem, the history of which has previously been dealt with (see pg. 6). Ledebour (1841-1846) described the species *Cornus unalaschkensis* (see Fig. 3) with no knowledge of floral characters, and described the leaf venation pattern of *C. unalaschkensis* as being similar to *C. suecica*. The latter description of leaf venation does not fit the type specimen. This incorrect description, coupled with the lack of information about the flowers, makes the description of *C. unalaschkensis* unclear. It does however definitely describe a species intermediate between *Cornus canadensis* and *Cornus suecica*.

Farr's description of *C. canadensis* var. *intermedia* (Pg. 9) does not comply with the morphological variation found within the intermediates. It describes only a small sector of the group.

Because Hultén's description of *Cornus canadensis* X *suecica* Hult. (Pg. 8) complies with the results obtained from this study, it is proposed that this hybrid formula be retained and used to designate the diploid hybrid taxon. The formula gives information about the origin and evolution of the group it names and is in accordance with the articles and recommendations set out in the International Code of

Botanical Nomenclature (Stafleau *et al.*, 1972) for naming hybrids.

The allotetraploid or amphidiploid intermediate, because it is fully fertile and reproductively isolated is considered to be a distinct species, *Cornus unalaschkensis* Ledeb. Examination of guard cells from specimens collected from the type location suggests that the type specimen is tetraploid. Examination of guard cells of the type specimen produced inconclusive results. Although morphology does not allow the easy distinction of *Cornus unalaschkensis* from *Cornus canadensis* X *suecica*, they can be separated on the basis of their different chromosome numbers, guard cell sizes, pollen viability, geographical distribution and possession of quercetin 3-O gentiobioside. The formula *Cornus canadensis* X *suecica* has been chosen to delimit the hybrid rather than using the name *Cornus* X *unalaschkensis* because it is felt that the simultaneous use of the epithets *unalaschkensis* and X *unalaschkensis* would result in confusion. Article 50 of the Nomenclature Code (1972) intimates through example that the two epithets are mutually exclusive, but more important is the fact that in the past the two have been used interchangably, and such a similarity in name would encourage the practice to continue.

These two taxa are associated, in that an earlier *Cornus canadensis* X *suecica* presumably gave rise to *Cornus unalaschkensis*. So they are both originally of hybrid origin. The difference in geographic distribution between diploids and tetraploids is perhaps the result of reinvasion after glaciation. Hultén (1968) suggested that *C. suecica* in a previous time had a more southerly distribution which has been reduced due to a change in climate. The tetraploid has apparently not suffered the same reduction in distribution. The existence of the

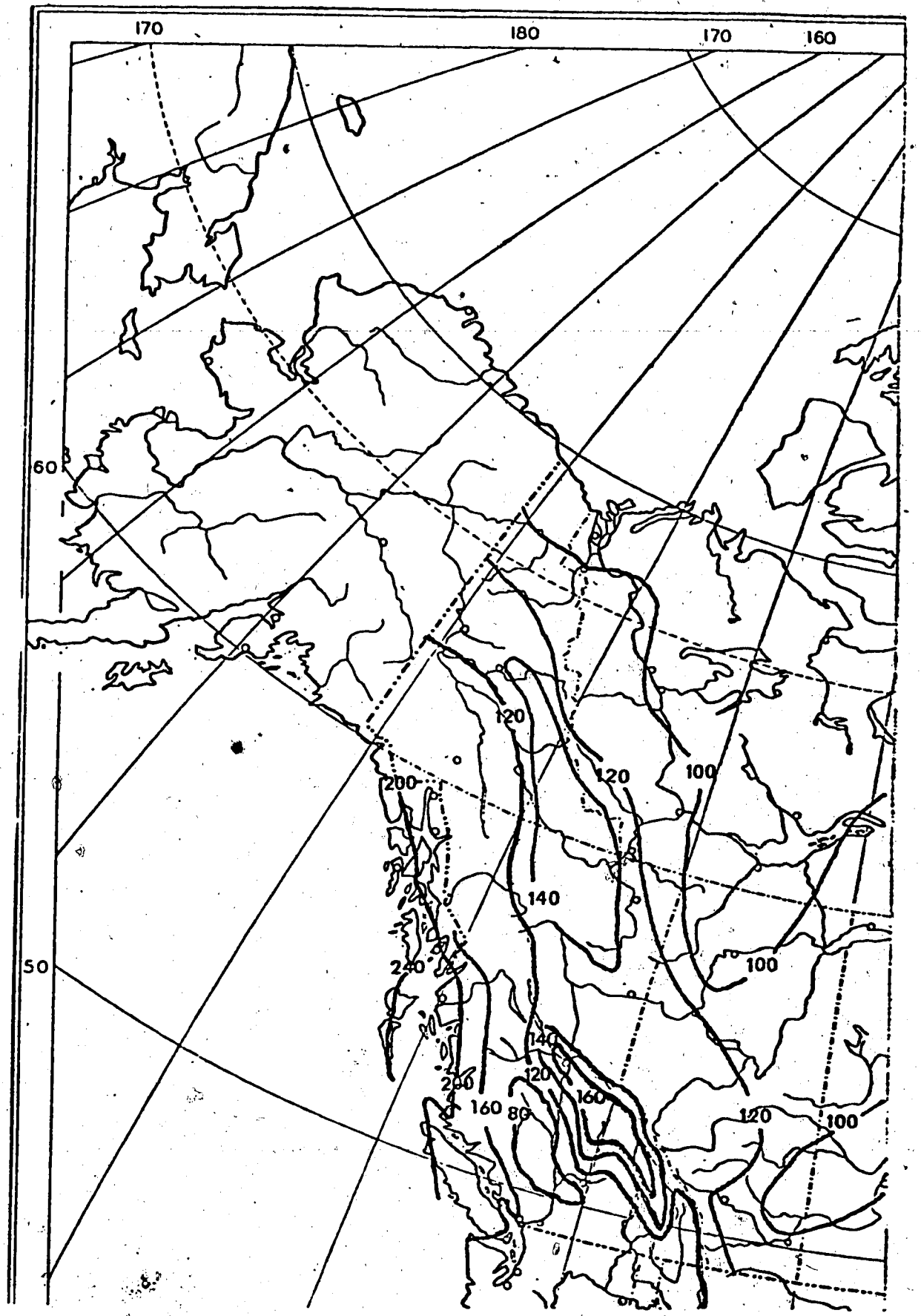
tetraploid chromosome race, as well as extant members of the ancestral diploid race, is unusual and has possibly resulted from the change in geographical distribution of *C. suecica*. The climatic changes which Hultén (1968) has suggested account for the restricted distribution of *C. suecica* in relation to *C. unalaschkensis* may also have changed the distribution of *C. suecica* enough to create a new 'overlap area' with *C. canadensis* and allow the process of hybridization to begin again in a new, more northern area. The different distributions of *C. unalaschkensis* and *C. suecica* could also be explained as the result of the invasion of new, more southern habitats by *C. unalaschkensis*. The presence of *C. unalaschkensis* in central British Columbia (Purden Lake 75038) is evidence that the spread of this species is possible and is, in fact, occurring. The variation within *C. unalaschkensis* suggests that the doubling of the diploid chromosome number has occurred on more than one occasion and it can be considered to be a continuing event. Therefore, although a breeding barrier does exist, it may not in fact be a barrier to gene flow from the diploid to the tetraploid. Gene exchange in the other direction, however, is limited by this breeding barrier. An alternative explanation for the variation found within *C. unalaschkensis* would be that numerous populations were isolated in coastal refugia during the Wisconsin glaciation and were subject to evolutionary divergence. In view of the present day distribution and the previous glacial history of the area, this explanation appears valid.

The genomes of the two parental species, *Cornus canadensis* and *Cornus suecica* have presumably been combined in the amphidiploid *Cornus unalaschkensis*. If this combination has conferred upon it the combined environmental tolerances of these two parents, this could

explain the wider distribution of the amphidiploid in relation to *C. suecica*. It appears that lack of moisture is a limiting factor in the distribution of the tetraploid for although it was found in the mesic forests near Prince George, B.C. (Coll #75038) it was replaced by the diploid *C. canadensis* in the drier region between the coast and Prince George. The distribution matches closely the areas of high annual precipitation as outlined by Map 8. It can be envisioned that further evolution of the tetraploid may allow it to extend its range to other habitats. The presence of tetraploids in eastern North America (Dermen, 1932) indicates that the tetraploid genome is not as restricted to habitat as is suggested bythis study. Specific information concerning the collection sites in eastern North America is lacking, however, so one can only generally infer the conditions present, as different from the western coastal rain forest. The tetraploid in northwestern North America appears to be a vigorous entity capable though its own fertility of adapting, through gene exchange, to various environments. If it has in fact combined the ecological tolerances of the two parents its gradual spread is highly likely, perhaps at the expense of the diploid parents.

MAP 7

Annual number of days with precipitation in Western Canada. (Based on National Atlas of Canada, 1974.)


170
180
170
160
60
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120
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200
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240
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160
80
120
100

CHAPTER 5

CONCLUSIONS

The conclusions of this study, briefly stated, are as follows. Hybridization has occurred between the two diploid species, *Cornus canadensis* and *Cornus suecica*. In the earliest of the two known instances a chromosome doubling produced a fully fertile allotetraploid. This tetraploid survived the Pleistocene glaciations and climatic changes in areas where *Cornus suecica* failed to survive, so the present southern extremities of the distribution of the tetraploid and that of *Cornus suecica* are widely separate. The second instance of hybridization has occurred in more recent times resulting in formation of a diploid entity in the present overlap areas of the two species. The eventual production of the tetraploid in these overlap areas is certainly possible and would represent an example of polytopic speciation. Both existing diploid and tetraploid entities are considered also to have had a polytopic and polychronistic origin.

Synopsis of *Cornus* subg. *Arctocrania*

in northwestern North America

Flowers greenish-white; stamens mostly shorter than the style; hypantheum hoary.

Cornus canadensis

Flowers purple or partly purple; stamens mostly longer than the style; hypantheum sparsely strigillose to hoary.

Leaves mostly arranged in a whorl of 4-6 at the shoot apex, often with 1-2 pairs of stem leaves 4-6 cm below the whorl; leaves mostly petiolate, sometimes sessile; leaf veins arising from a distinct midrib, seldom from the leaf base.

Distribution restricted to continental Alaska; Chromosome number 2n=22; pollen sometimes partially inviable; Quercetin 3-O gentiobioside absent.

Cornus canadensis X *suecica*

Distribution restricted to coastal northwestern North America (including the Aleutian Is.) and the western side of the Rocky Mountains; Chromosome number 2n=44; pollen mostly all viable; Quercetin 3-O gentiobioside present.

Cornus unalaschkensis

Leaves mostly arranged in 3-6 sub-equal pairs, sometimes simulating a whorl at the shoot apex; leaves sessile to subsessile; leaf veins arising from the base or if from the midrib, from the basal 1/4 to 1/3 of the leaf.

Cornus suecica

Cornus canadensis L. Sp. Pl. 118. 1753.*

Chamaepericlymenum canadense (L.) Asch. & Graebn. Fl. Nordostd. Flachl. 799. 1898.

Cornella canadensis (L.) Rydb. Bull. Torrey Club 33: 147. 1906.

Arctocrania canadensis (L.) Nakai Bot. Mag. Tokyo 23: 40. 1909.

Cynoxylon canadense (L.) J.H. Schafn. Cat. Ohio Pl. 22. 1914. (taken from Rickett, 1945).

Mesomera canadensis (L.) Nieuwl. & Lunell Am. Midl. Nat. 4: 87. 1916. (taken from Rickett, 1945).

Cornus canadensis L. forma *dutillyi* Lepage Nat. Can. 73: 10. 1946.

Cornus canadensis L. forma *infraverticillata* Lepage Nat. Can. 73: 7 1946.

Cornus canadensis L. forma *bifoliata* Lepage Nat. Can. 78: 342. 1951.

Cornus canadensis L. forma *secunda* Lepage Nat. Can. 78: 343. 1951.

Cornus canadensis L. forma *albomacula* Lepage Nat. Can. 82: 99. 1955.

Cornus canadensis L. forma *aphylla* Lepage Nat. Can. 82: 99. 1955.

Cornus canadensis L. forma *foliolosa* Lepage Nat. Can. 82: 101. 1955.

Cornus canadensis L. forma *ornata* Lepage Nat. Can. 82: 100. 1955.

*A number of varieties and forms of *Cornus canadensis* have been described which have not been included in this study.

Plants herbaceous annuals with subterranean, perennial rhizomes; simple stems 4-20 cm high, exlcusive of peduncle. Leaves 4-6 in a terminal whorl consisting of one terminal pair of leaves, each leaf subtended by one or two leaves from an undeveloped axillary branch, with a pair of scale-like prophylls 2-8 cm below, these often approaching the size of the terminal leaves; all leaves having a short but distinct petiole, the blades 2-9 cm long, 1-6 cm broad, obovate to elliptic, entire, acute to acuminate, obtuse at base, sparsely strigillose above, underside glabrous; veins 2-3 on either side of the midrib arising from the basal 1/4 to 1/3 of the midrib. Inflorescence a cyme containing 15-30 flowers; peduncle terminal and erect, 1-3 cm long, the four primary branches of the inflorescence each bearing a white bract, sometimes purple tipped; bract 7-25 mm long, 5-18 mm broad; hypantheum 1-1.5 mm long, green, hoary; sepals 0.4-0.5 mm long, broadly triangular, greenish; petals 1-2 mm long, yellowish or cream-coloured; style 1,

1-2 mm long, purplish; drupe red, 8 mm in diameter, one seeded. Chromosome number 2n=22.

Cornus suecica L. Sp. Pl. 118. 1753.

Cornus borealis Krash. Gort. Fl. Ingr. 24. 1761)) (Taken
Cornus herbacea Pall. Fl. Ross. 1: 121. 1784.)) from
Cornus biramis Stokes Bot. Mat. Med. 1: 221. 1812.) Rickett, 1945)
Chamaepericlymenum suecicum (L.) Asch. & Graebn. Fl. Nordostd. Flachl. 539. 1898.

Cornella suecica (L.) Rydb. Bull. Torrey Club 33: 147. 1906.
Arctocrania suecica (L.) Nakai Bot. Mag. Tokyo 23: 39. 1909.

Plants herbaceous annuals with subterranean, perennial rhizomes; stems 2-15 cm high, exclusive of peduncle, often with some branching. Leaves opposite, in 3-6 sub-equal pairs, sometimes simulating a whorl at the summit; leaves sessile, the blades commonly 2-3 cm long, 1.5-2.0 cm broad, ovate to elliptic, entire, acute to acuminate or apiculate, cuneate and clasping at the base, sparsely strigillose above, glabrous below; veins 5-7, arising from or near the base, or if midrib is present veins 4-6 arising from the basal 1/4 to 1/3 of the midrib. Inflorescence an umbelliform cyme (primary branches not discernible) containing 10-20 flowers; peduncle 1-2.5 cm long, commonly sparsely strigillose, four bracts 8-12 mm long, 5-10 mm broad; hypantheum 1-2 mm long, purplish, sparsely strigillose to strigillose especially at the base; sepals 0.3-0.6 mm long, triangular, purplish; petals 1-1.5 mm long, purplish; style 1, 1-2 mm long, purplish; drupe red, 8 mm in diameter, one-seeded. Chromosome number 2n=22.

Cornus unalaschkensis Ledebour Fl. Ross. 2: 378. 1844.

Cornus canadensis var. *intermedia* Farr Contr. Bot. Lab. Univ. Pa. 2: 423. 1904. (Type specimen not seen)
Cornella unalaschkensis (Ledeb.) Rydb. Bull. Torrey Club 33: 147. 1906.
Arctocrania unalaschkensis (Ledeb.) Nakai Bt. Mag. Tokyo 23: 39. 1909.
Svida unalaschkensis (Ledeb.) Heller Cat. N. Am. Pl. ed. 3. 273. 1914. (Taken from Rickett, 1945)
Chamaepericlymenum unalaschense (Ledeb.) Rydb. Fl. Rocky Mts. 635. 1917.
Cornus intermedia (Farr) Calder & Taylor Can. J. Bot. 43: 1396. 1965.

Plants herbaceous annuals with subterranean perennial rhizomes; stems 5-25 cm high, exclusive of the peduncle, occasionally with some axillary branching. Leaves either arranged in a terminal whorl of 4-6 leaves with one pair of large cauline leaves subtending the whorl, or arranged in 3-6 sub-equal pairs; leaves often petiolate, the blades often 3-7 cm long, 2-4 cm broad, entire, acute to acuminate or apiculate, obtuse or clasping at the base, sparsely strigillose above, glabrous below; veins most commonly 4-6 arising from the basal 1/4 of the midrib or if midrib is absent arising from the base.

Inflorescence a closed cyme or umbelliform cyme, peduncle 1-3.5 cm long, sparsely strigillose to glabrous, terminal and erect, four white bracts 7-25 mm long, 5-20 mm broad, arising from the apex of the peduncle or from the four primary branches of the inflorescence (when present); hypantheum 1-2 mm long, greenish, or partly or wholly purplish, sparsely strigillose to hoary; sepals 0.3-0.6 mm long, triangular, greenish or purplish; petals 1.0-2.0 mm long, purplish or partly purplish; style 1, 1-2 mm long, purplish; drupe red. 8 mm in diameter, one seeded; Chromosome number 2n=44.

Cornus canadensis X *suecica* Hultén Fl. Aleut. 253. 1937.

- as above but exhibiting some pollen inviability. Chromosome number 2n=22.

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APPENDIX

Representative Specimens

Cornus canadensis L.

Type Locality: Canada, Linnaeus.

(LINN; holotype. DAO 029014 [photograph of holotype]).

Alberta: CAN 85847, Mt. Norquay; CAN 85848, Lake Louise; CAN 85859, Amethyst Lake; CAN 85860, Tonquin Valley; CAN 85871, Mt. Rundle; CAN 267967, Wood Buffalo Pk.; CAN 85858, Red Deer; DAO 118516, Kananaskis; DAO 118510, Banff; DAO 118417, Elk Is. Pk.; DAO 118415, Waterton Lakes Pk.; DAO 118412, Maligne Lake; DAO 118408, Beaverlodge; DAO 118406, Lake Athabasca; DAO 118401, Ft. Saskatchewan; DAO 118395, 20 mi. N. of Vermilion; DAO 627760, Mildred Lake; DAO 640032, Pigeon Lake; ALTA 13540, Edmonton; ALTA 64416, Ma-Me-O Beach; ALTA 62865, Athabasca; ALTA 46467, Cypress Hills; ALTA 30521, Fox Creek; ALTA 39339, Beaverlodge; ALTA 24024, Dutch Creek.

British Columbia: CAN 341617, Florence Bay; CAN 343423, Mt. Arrowsmith-Vancouver Is.; CAN 363141, Glacier Nat'l Pk.; CAN 342214, Revelstoke Pk.; CAN 264080, Laird Hot Spring; CAN 85888, Yale; CAN 85884, Trail; CAN 85877, Prince George; DAO 118466, Mt. Robson Prov. Pk.; DAO 118464, Galloway; DAO 118453, Rolla; DAO 118450, S. of Ft. Nelson; DAO 118446, Grand Forks; DAO 118436, Dawson Creek; DAO 118426, Kootenay Nat'l Pk.; DAO 118422, Quesnel; ALTA 53652, Ft. St. John.

Yukon: CAN 303687, Keno Hill; CAN 293691, Dezadeash; CAN 270029, Mackintosh; CAN 208721, Carcross; CAN 127187, McQueston; CAN 85908, Whitehorse; CAN 85905, Dawson; CAN 85899, Mayo; CAN 85894, Canol Rd.;

DAO 118016, Watson Lake; DAO 118010, McIntyre Creek; DAO 118006, Cassiar Mtn.; DAO 118005, 60 mi. Rd.-W. of Dawson; ALTA 27322, Mi. 22-Dempster Hwy.

N.W.T.: CAN 370054, Wood Buffalo Pk.; CAN 359820, Hay River; CAN 279895, Ft. Smith; CAN 85341, Great Bear R.; CAN 268871, Brintnell Lake; CAN 268872, Ft. Simpson; DAO 118002, Charleton Is.-Keewatin; DAO 117999, Great Slave Lake; DAO 117998, Yellowknife; DAO 117994, E. of Ft. Smith; DAO 117991, Hay River; DAO 117985, Ft. Simpson; DAO 117976, Ft. Laird; ALTA 13550, Great Slave Lake; ALTA 30790, Wood Buffalo Pk.; ALTA 13551, Ft. Smith.

Alaska: CAN 362399, Mt. Hayes; CAN 362400, Big Delta Jctn.; CAN 363571, 20 mi. N. of Cordova; CAN 298891, Circle Hot Springs; CAN 281057, Tanana River; CAN 258492, Cathedral Bluffs; CAN 253646, Prince William Sound; CAN 85920, Gakona; CAN 85915, Unalaska Is.; CAN 85912, Seward; CAN 85911, Matanuska; CAN 85910, Hope; DAO 118037, Cooper's Landing; DAO 118036, Mi. 187-Richardson Hwy.; DAO 118031, Mi. 140-Steese Hwy.; DAO 118027, Glacier Bay Nt'l Monument; DAO 118022, Palmer.

Cornus suecica L.

Type Locality: "Suecia, Norvegia, Russia", Linnaeus.

(LINN; holotype. DAO 140742 [photograph of holotype])

Alaska: CAN 274322, Kotzebue; CAN 253643, Unalaska; CAN 248098, Middleton Is.; CAN 238242, Kodiak Is.; CAN 86214, Buckland River; CAN 86213, Akutan Is.; CAN 86201, Seward; DAO 626396, Adak Is.; DAO 117917, Attu Is.; DAO 117918, Resurrection Bay (Seward); DAO 117920, Hope; DAO 117924, Kenai; DAO 117927, Sterling Hwy.; ALTA 20539, Kotzebue.

Quebec: CAN 86197, Bradore Bay; CAN 86194, Seven Is.; CAN 86175, Blanc Sablon River; CAN 86192, Ile du Bic; CAN 86191, Magdalen Is.; CAN 86190, Coffin Is.; CAN 300329, Harrington Harbour; DAO 643166, Ile aux Basques; DAO 117946, Lake Tashwak; DAO 117954, Kamouraska; DAO 117958, Port Harrison.

Nova Scotia: CAN 251079, Scatari Is.; CAN 227764, Scatari Is.; CAN 86181, Canso; CAN 86182, Trinity Cove; DAO 117941, St. Paul Is.

Newfoundland: DAO 117931, Indian Harbour; DAO 117935, St. Anthony Is.; DAO 117934, Seal Is.; DAO 117937, St. Anthony Is.

Cornus unalaschkensis Ledebour.

Type Locality: Unalaska, Ledebour.

(LE; holotype. *Cornus unalaschkensis* Ledeb. 440.2)

British Columbia: CAN 85924, Vancouver Is.; CAN 152161, Triangle Is.; DAO 118439, Lake Azonzetta.

Yukon: CAN 85932, Canol Rd., Mi. 240.

Alaska: CAN 326919, Amchitka Is.; CAN 85943, Unalaska Is.; DAO 149331, Queen Charlotte Is.; DAO 149351, Queen Charlotte Is.; DAO 149359, Queen Charlotte Isl; DAO 149364, Queen Charlotte Is.; DAO 149368, Hope Island; DAO 149375, Glacier Nat'l Pk.; DAO 118446, Grand Forks; DAO 149400, Skeena Crossing; DAO 149398, Smithers; DAO 149396, Prince Rupert.

Oregon: DAO 149403, Lincoln Beach.

Cornus canadensis X *suecica* Hultén

(typical specimen: BAIN #75053).

Alaska: CAN 85938, Talkeetna; CAN 85937, Matanuska.