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THE TAXONOMY OF *MINUARTIA ROSSII* (R. BR. *ex* RICHARDS.) GRAEBN. *SENSU LATO* (CARYOPHYLLACEAE)

by

© STEVEN J. WOLF

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 "The Taxonomy of *Minuartia rossii* (R.Br. ex Richards.)Graebn. *sensu lato* (Carvophyllaceae) submitted by Steven J. Wolf in partial fulfillment of the requirements for the degree of Master of Science.

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(Supervisor)

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Dated.....June 15, 1977.....

ABSTRACT

The *Minuartia rossii* (R. Br. *ex* Richards.) Graebn. complex is composed of three morphologically distinct taxa which, for the most part, correspond to the three subspecies recognized previously as ssp. *rossii*, *elegans* and *columbiana*. Cytological, chemical, breeding system and phytogeographical evidence also support the recognition of three taxa. The basic chromosome number of the complex, x=15, has been confirmed, with spp. *rossii* having 2n=60, ssp. *columbiana* 2n=30 and ssp. *elegans* both 2n=30 and 2n=60. With the exception of guard cell size, no differences were observed between the diploid and tetraploid races of ssp. *elegans*. The tetraploid of this taxon has probably been derived from the diploid by autopolyploidy. The flavonoid Apigenin 6-C-arabinosylglucosyl-7-0 glucoside was found to be taxon specific, being present in ssp. *rossii* and *elegans* and absent in ssp. *columbiana*. The complex as a whole exhibits pronounced protandry and is gynodioecious, however ssp. *rossii* rarely flowers and relies almost exclusively on vegetative reproduction via bulbils. The three taxa have distinct geographical distributions; ssp. *rossii* occupies high arctic North America and Greenland, ssp. *elegans* is restricted to Alaska, the Yukon and north-eastern British Columbia and ssp. *columbiana* is confined to the front ranges of the northern and central Rocky Mountains. This distribution pattern is probably the result of the Pleistocene isolation of the taxa in three major areas: Beringia, the Canadian Arctic Archipelago and south of the ice. The three taxa are recognized at the specific level and ssp. *rossii* and *elegans* are treated as *Minuartia rossii* (R. Br. *ex* Richards.) Graebn. and *Minuartia elegans* (Cham. and

Schlecht.)Schischk. respectively. Examination of the type specimen has revealed that the epithet *columbiana* is synonymous with *elegans* and the name *Minuartia austromontana* is proposed for this taxon.

ACKNOWLEDGEMENTS

I would like to thank Dr. J. G. Packer for suggesting this project and for his support and guidance throughout the course of the investigation. I would also like to express my gratitude to Dr. K. E. Denford for his patience, time and invaluable advice. I am also indebted to Dr. G. E. Ball for his critical review of the manuscript I would especially like to thank my fellow students for their help: J. Bain, W. Elisens, W. Peterson, M. See and J. Tande. Lastly, thanks are extended to the curators of the various herbaria who have given me access to and the loan of specimens for examination. This research was supported by National Research Council of Canada Grant No. A-2582 to Dr. J. G. Packer.

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CHAPTER I

INTRODUCTION

The genus *Minuartia*[1] is a member of the sub-family *Alsinoideae* Pax and Hoffman (1934) of the Caryophyllaceae. The members of the Alsinoideae are distinguished from the Paronychioideae by their possession of true petals (not petaloid staminoides) and exstipulate leaves, and from the Silenoideae by their free sepals. Within the Alsinoideae, the largest group, in both numbers of species and generic diversity, is the *Arenaria sensu latissimo* complex (McNeill, 1962). Generic delimitation within the *Arenaria* complex has always been a matter of considerable dispute between North American and European taxonomists. European taxonomists have long recognized three main genera: *Minuartia* L., *Arenaria* L., and *Moehringia* L. (plus a number of smaller genera including: *Hohkenya* Ehrh., *Wilhelmsia* Reichb., *Cherlia* L. and *Queria* Loefl.), distinguished by the presence or absence of a seed strophiole and the number of capsule valves. *Moehringia* species possess a seed strophiole while *Arenaria* and *Minuartia* do not. The chief distinction between *Minuartia* and *Arenaria* is the dehiscence of the capsule of the former by three valves and of the latter by six valves. North American taxonomists, largely influenced by Fernald (1919), have considered this character too trivial to delimit the two genera and hence treat *Minuartia* as section *Alsine* Benth. and Hook. of *Arenaria*.

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[1] named for Minuart, professor at Madrid (1693-1768).

In his "Genera Plantarum", Linnaeus (1737) recognized only *Arenaria sensu lato*, but by 1753 he recognized five genera: *Minuartia, Arenaria, Moehringia, Queria* and *Cherleria*. Gaertner (1791) was the first to emphasize the importance of capsule dehiscence in the classification of *Arenaria sensu lato* and placed the 3-valved members in the genus *Alsine* L. Schischkin (1936) and McNeill (1962) have discussed the displacement of the name *Alsine* with the coming of the type concept. According to Schischkin (l.c.) a ruling of the Brussels International Congress of 1905 stipulated the retention of the name *Alsine* for *Minuartia* as a *nomen conservandum*. However, the two species referred to the genus *Alsine* by Linnaeus (1753), 272, namely *A. media* L. and *A. segetalis* L., are *Stellaria media* (L.) Cyrill. and *Delia segetalis* Dum. respectively. Since Linnaeus also described five species of *Stellaria* L. and *Delia segetalis* does not fit into the concept of *Stellaria*, Schischkin (1936) retained the name *Alsine* for the monotypic *Delia* and referred *Alsine media* to *Stellaria*. Linnaeus (1753), 89, referred three species to the genus *Minuartia*: namely *M. dichotoma* L., *M. campestris* L. and *M. montana* L.; all of which have 3-valved capsular dehiscence. According to Schischkin (1936) and McNeill (1962) the correct name according to the rules of priority should therefore be *Minuartia*.

With the exception of Bentham and Hooker (1862), most European taxonomists have accepted Fenzl's (1833, 1841, 1842) separation of *Minuartia* (as *Alsine*) from *Arenaria*. The name *Minuartia* became firmly established in Europe with the publication of Mattfeldt's (1922) monograph of this genus. Mattfeldt (l.c.) has shown that the lines of dehiscence of the capsule are determined at an early stage of development by the distribution of vascular tissue in the ovary wall. He concluded

that this is a fundamental difference between the loculicidal capsule of *Minuartia* and the loculicidal *and* septicidal capsule of *Arenaria* and justifies recognition of the two genera.

North American taxonomists have objected to the splitting of the genus *Arenaria* because when this is done, plants of similar habitats are generically separated (Fernald, 1919; Maguire, 1951). McNeill (1962) notes several examples of generic separations within the Caryophyllaceae which ignore similar habitat parallels. Most notable is the separation of *Stellaria* L. and *Cerastium* L. In addition to capsule dehiscence, McNeill (l.c.) maintains that *Minuartia* and *Arenaria* can be distinguished by characters of the sepals and seeds. *Minuartia* species have very prominent sepal nerves and brown seeds while *Arenaria* species have indistinct sepal nerves and either red or black seeds. In addition to morphological characters, cytological evidence further strengthens the case for maintaining two genera. It has been shown that the predominant basic chromosome numbers of *Arenaria* are x=10 and 11 (Favarger, 1962; Baad, 1969). McNeill (1962) has noted that *Minuartia* has a very heterogeneous assemblage of basic chromosome numbers with x=12 and 13 being the most common, but also including x=10 and 11.

McNeill (1962), who has done the most recent monographic work on these two genera, has suggested that the view taken by North American taxonomists is a result of the relative paucity of the *Arenaria sensu lato* flora of North America. There are 30-35 species of *Arenaria* in North America while there are about 200 world wide. McNeill (l.c.) maintains that when the group is studied on a world wide basis, two distinct "natural" groups can be recognized, these being the 3-valved and 6-valved taxa. More recently, North American taxonomists have begun

to adopt a narrower generic concept within this group and have begun to recognize *Minuartia* as a separate genus. Most notable are McNeill (1962), Johnson and Packer (1968) and Porsild (1975). This view is not only more practical (it recognizes more natural groups (Davis and Heywood, 1963)), but it also provides for much needed worldwide uniformity. Based upon cytological data, Löve and Löve (1975), have split the genus *Minuartia* into six smaller genera including *Alsinanthe* (Fenzl) Rchb., *Lidia* Löve and Löve and *Wierzbickia* Rchb. This philosophical difference between the generic concepts of North American and European taxonomists is evident generally.

MINUARTIA L.[2]

Minuartia Linnaeus Sp. pl. (1753) 89; Hiern. Journ. of Bot. XXXVII (1899) 321.

Alsine Gaertner. De Fruct. II (1791) 223; non L.
Arenaria L. Sp. pl. (1753) 432, ex parte.
Sagina Duce. Proc. Linn. Soc. (1907) 77, non L.
Alsinopsis Small. Fl. S.E. U.S. (1903) 419.

Annual to perennial herbs with opposite, sessile, linear to broad (sometimes fleshy), exstipulate leaves; flowers usually in open and diffuse to contracted or capitate many to few flowered cymes, occasionally single and terminal, small, usually complete or apetalous, sometimes functionally imperfect; sepals free or connate only at the base, 1-3 nerved; petals 5, white, from 2 or 3 times as long as the calyx to greatly reduced or wanting, entire to slightly emarginate; stamens usually 10, inserted with the petals at the edge of a very slightly developed to fairly prominent, glandular, perigynous disc surrounding the ovary, often alternate with small glandlike protuberances; styles usually 3; capsule 1 celled, few to several seeded, dehiscing by 3 valves, membranous to firm or moderately indurate; seeds reniform, unappendaged, buff or dark brown (Schischkin, 1936; Fernald, 1950; Hitchcock *et al.*, 1964).

A genus of about 130 species distributed throughout the Northern Hemisphere (McNeill, 1962) with about 20 species in North America (Maguire, 1951).

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[2]Synonymy based on Schischkin (1936), 482.

Biosystematic work within the genus *Minuartia* has been confined largely to reports of chromosome numbers. Basic numbers of x=8,9,10,11, 12,15 and 23 have been found with x=12 and 13 being the most common (Löve and Löve, 1975; McNeill, 1962). Löve and Löve (1.c.) have carried out the most recent review of the genus. Based on chromosome number, karyomorphology and pollen and seed coat morphology they split the genus into several smaller genera. McNeill and Bassett (1974) studied pollen morphology and its use in the infrageneric classification of the genus and concluded that differences in pollen size and pore number are of greatest systematic value at the species level.

Within the genus *Minuartia* no studies of flavonoids and their glycosides have been made, however two studies have been conducted within the closely related genus *Arenaria*. Of considerable interest is the reported absence of Quercetin and Kaempferol, the two most widely distributed of the flavonols (Harborne, 1967), in the two species of *Arenaria* investigated by Bate-Smith (1962). Baad (1969) compared phenolic spot patterns of the North American species of *Arenaria* subgenus *Eremogone* Fenzl but found them of little taxonomic value. Hartman (1974) found leaf flavonoids to be especially useful in solving taxonomic problems at the specific and subspecific levels in *Paronychia* L. Also of particular interest is the occurrence of C-glycoflavones in several members of the Caryophyllaceae (Hegnauer, 1964), since these flavonoids have been referred to as being indicators of primitive taxa (Harborne, 1972).

This investigation is concerned with three taxa of the *Alsinanthe sensu* Löve and Löve (1975) which possess a basic chromosome number of x=15 and which have been referred to as *Minuartia rossii*

(Richards.) Graebn. by Mattfeldt (1922). *Minuartia rossii* is restricted primarily to arctic and alpine North America. More specifically it is confined to calcareous regions of the central and northern Rocky Mountains (principally in the front ranges); throughout arctic and alpine Alaska, the Yukon; and throughout the Canadian Arctic Archipelago. A few locations have also been recorded from extreme eastern Siberia, Greenland and Spitzbergen. The species forms small dense tufts in the arctic and in high alpine habitats in the Rocky Mountains, and loose tufted to large mats throughout Alaska and the Yukon.

Minuartia rossii (R. Br. *ex* Richards.) Graebn.[3]

Arenaria rossii R. Br. *ex* Richards. App. Frankl. Journ. 738. 1823.
Arenaria elegans Cham. and Schlecht. Linnaea. 1: 57. 1826.
Alsine rossii (Richards.) Fenzl. Verbreit. Alsin. 18. 1833.
Alsine elegans (Richards.) Fenzl. Verbreit. Alsin. 18. 1833.
Alsinopsis rossii (Richards.) Rydb. Bull. Tor. Bot. Club. 33: 140. 1906.
Minuartia rossii (Richards.) Graebn. in Asch. and Graebn. Syn. Mitteleur. Fl. 5: 772. 1918.
Arenaria rossii Richards var. *columbiana* Raup. Contr. Arnold Arb. 6: 157. 1934.
Minuartia elegans (Cham. and Schlecht.) Schischk. Fl. U.R.S.S. 6: 508. 1936.
Minuartia orthotrichoides Schischk. Fl. U.R.S.S. 6: 507. 1936.[4]
Arenaria rossii Richards var. *daethiana* Polunin. Bot. Can. E. Arct. 201. 1940.[5]
Arenaria rossii Richards var. *apetala* Maguire. Am. Md. Nat. 46(2): 510. 1951.
Minuartia rolfii Nann. Nytt. Mag. Bot. 3: 161. 1954.
Arenaria rossii Richards. ssp. *elegans* (Cham. and Schlecht.) Maguire. Rhodora. 60(710): 47. 1958.
Arenaria rossii Richards. ssp. *columbiana* (Raup) Maguire. Rhodora. 60 (710): 48. 1958.
Minuartia rossii (Richards.) Graebn. var. *elegans* (Cham and Schlecht.) Hult. Ark. Bot. 7: 52. 1968.

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[3]named for Lieutenant James C. Ross, a member of the first Parry voyage in search of a northwest passage.

[4]type specimen not seen.

[5]only photograph of type seen.

Minuartia rossii (Richards.) Graebn. var. *orthotrichoides* (Schischk.) Hult. Ark. Bot. 7: 52. 1968.
Arenaria rossii Richards. var. *elegans* (Cham. and Schlecht.) Welsh. Great Basin Natur. 28: 148. 1968.
Minuartia rossii (Richards.) Graebn. ssp. *elegans* (Cham. and Schlecht.) Rebr. Flora Arctica U.R.S.S. 6: 64. 1971.
Alsinanthe rossii (Richards.) Löve and Löve. Bot. Not. 128: 509. 1975.
Alsinanthe elegans (Cham. and Schlecht.) Löve and Löve. Bot. Not. 128: 509. 1975.

Description of *Minuartia rossii*

> Densely pulvinate to loosely tufted perennial, forming cushions 5-20 cm broad; glabrous throughout; stems profusely branched at base, densely leafy; leaves 2-10 mm long, linear to trigonous, fleshy, obtuse, 1 nerved, with small leaved fascicles in the axils; flowers solitary at the ends of stems; pedicels filiform, 2-50 mm long, ebracteate; sepals ovate to lanceolate, 1.5-3.5 mm long, actue to obtuse, 3(1) nerved, sometimes scarious margined; petals white, from twice as long as sepals to rudimentary or lacking, oblong to obovate, obtuse or emarginate; capsule ovoid-globular, about as long as the calyx; seeds dark brown, reniform, 0.5-1 mm long, rugose (Schischkin, 1936; Maguire, 1958; Hitchcock *et al.*, 1964).

Minuartia rossii was first described as *Arenaria rossii* from Melville Island in 1823 by Dr. Richardson, a naturalist on the Parry voyages of 1819-22 in search of a northwest passage. Both Richardson and Robert Brown (1824) had collected the plant and published a description of it attributing the specific epithet to the other. However, since Richardson's report was published first, his name prevails as the authority for the description and type specimen (Article 11, International Botanical Code) while Brown is given credit for the epithet *rossii* (Article 46C).

Chamisso and Schlechtendal (1826) described *Arenaria elegans* from the Chukchi peninsula of Siberia. Fenzl (1840) recognized that *Arenaria elegans* and *Arenaria rossii* were closely related and placed them in the same section, *Alsinanthe*, of the genus *Alsine*. Fenzl (1842)

also recognized that *Arenaria rossii sensu lato* possessed both petalous and apetalous forms, he designated these as formas *corollina* and *apetala* respectively. Mattfeldt (1922) was the first to suggest that the Rocky Mountain members of *Minuartia rossii* were different from the arctic and Alaskan plants, however lack of material did not permit any firm conclusions to be drawn. Raup (1934) described a Rocky Mountain variety from northern British Columbia as variety *columbiana* of *Arenaria rossii*. Nannfeldt (1954) reported that the epithet *rossii* was illegitimate because Richardson's description was based on a dwarf form of *Minuartia stricta* (S.W.) Hiern. which lacked vegetative propagules. However, Porsild (1955) has shown that the type sheet contains six specimens all of which possess vegetative propagules and are referrable to the species *Minuartia rossii*. This has been confirmed in the present study.

Maguire, in his 1958 monograph of this complex, recognized that these three taxa were very closely related and he treated them as subspecies *rossii*, *elegans* and *columbiana* of *Arenaria rossii*. Today this is the most widely accepted treatment of this complex. Maguire (l.c.) recognized that these three subspecies have very distinct allopatric distributions: ssp. *rossii* is restricted to Arctic North America east of the Richardson Mountains, N.W.T., ssp. *elegans* is restricted to the Alaska-Yukon region and ssp. *columbiana* is found in the northern and central Rocky Mountains. The type specimens of these three taxa are shown in Figures 1, 2 and 3.

Mattfeldt (1922) suggested that *Minuartia rossii sensu lato* was part of a group of plants from northeast Asia that migrated to North America during the Tertiary. He hypothesized that *Minuartia elegans* and *Minuartia* became differentiated as they spread out to the arctic

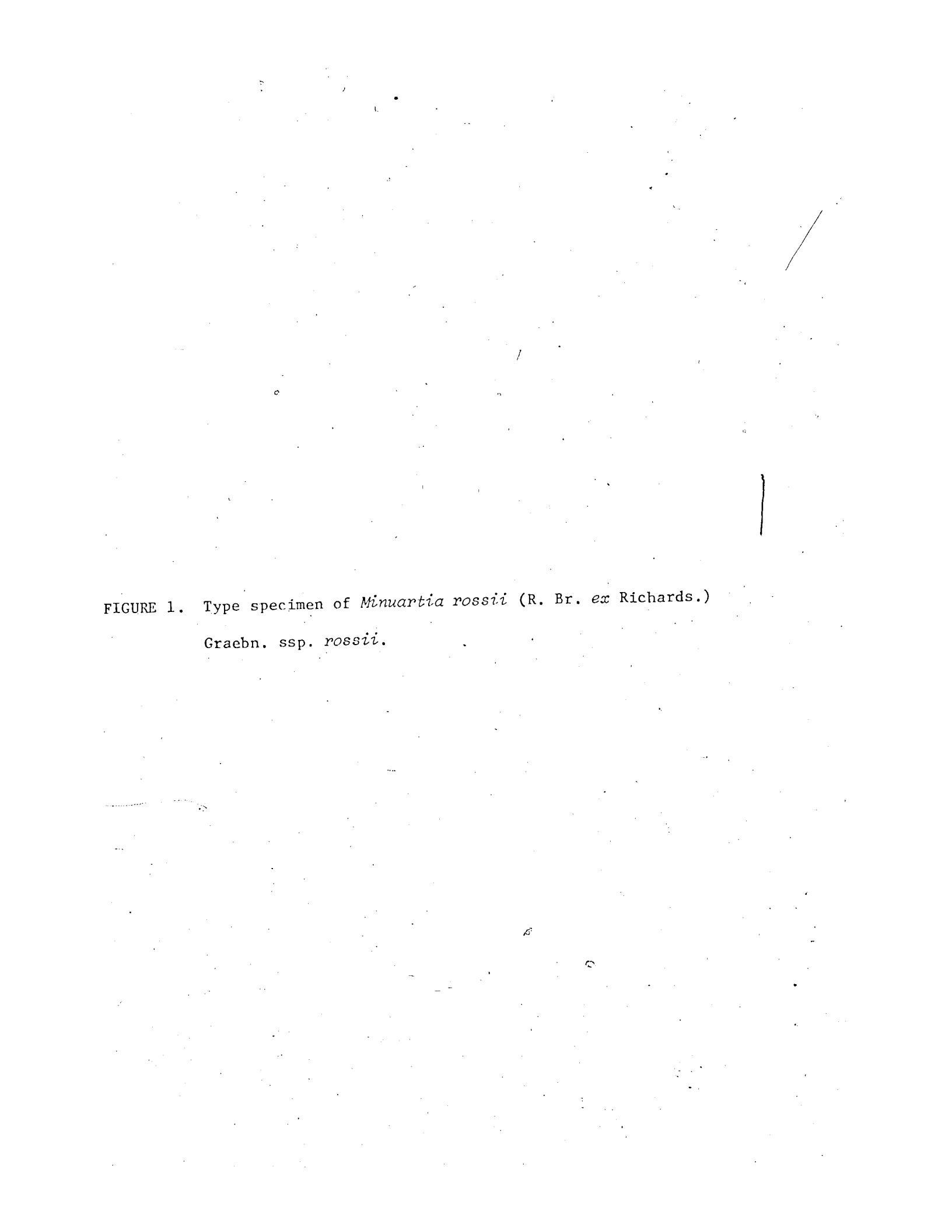


FIGURE 1. Type specimen of *Minuartia rossii* (R. Br. *ex* Richards.) Graebn. ssp. *rossii*.

Lecidea

BRITISH NORTH AMERICA.
Dr. RICHARDSON 1819 - 22.

1/100.

Arctomia
Rocky Mts.

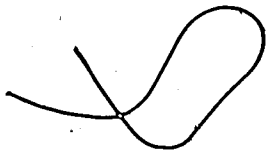
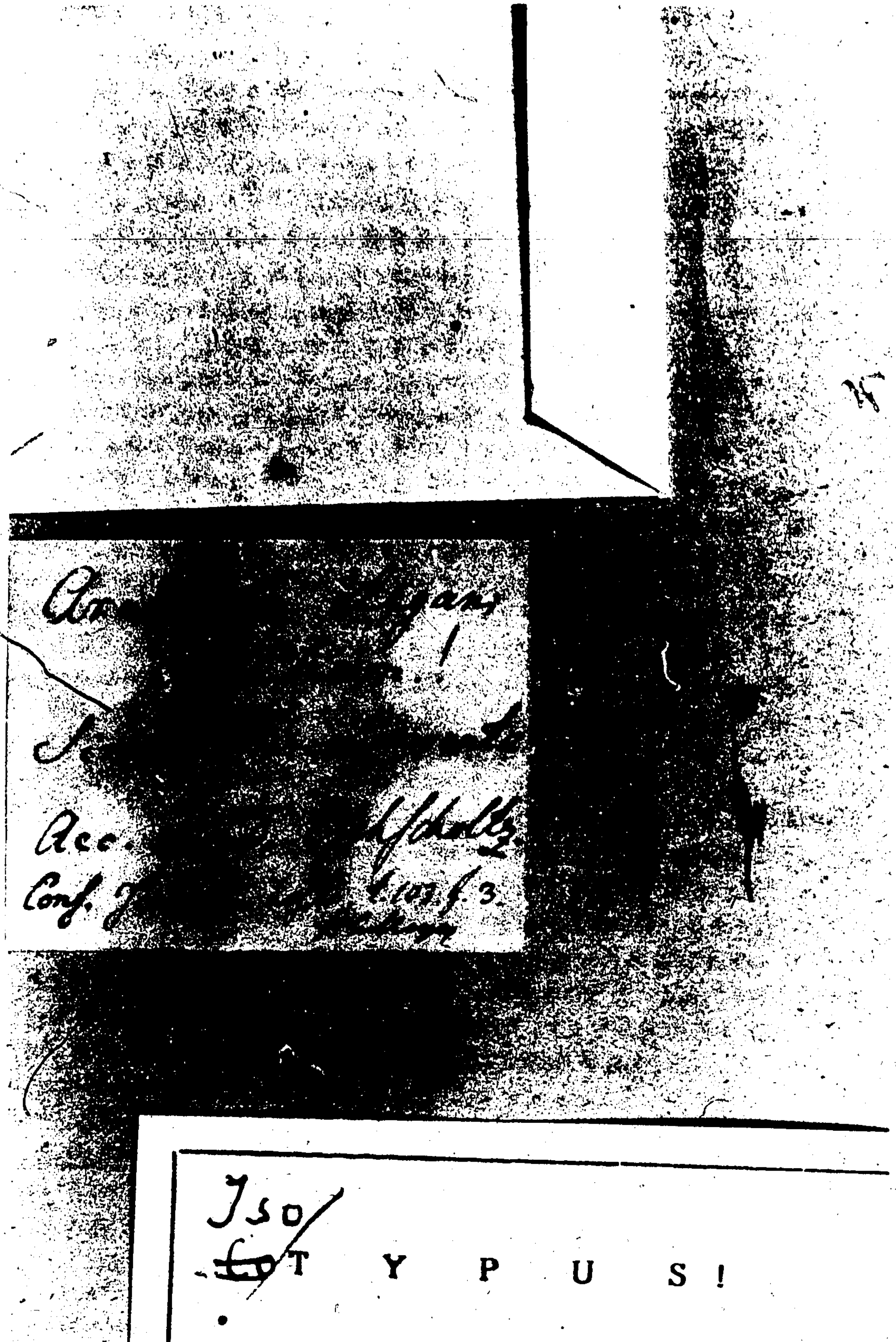


FIGURE 2. Type specimen of *Minuartia rossii* (R. Br. *ex* Richards.) Graebn. ssp. *elegans* (Cham. and Schlecht.) Rebr.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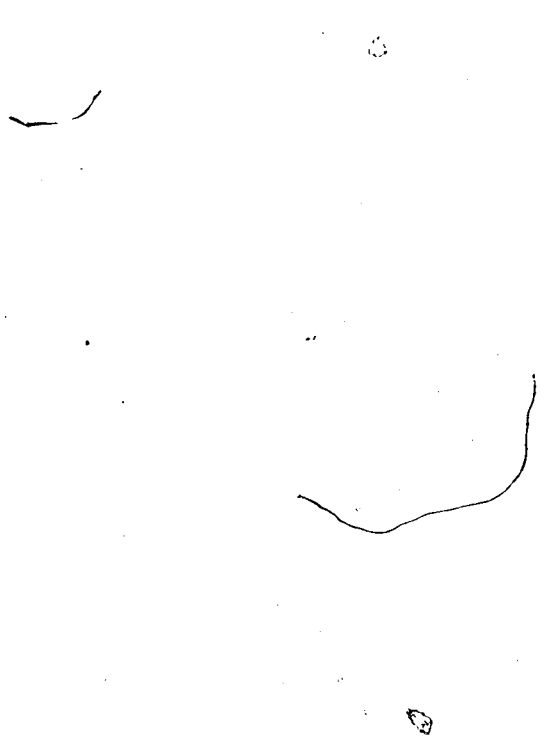


FIGURE 3. Type specimen of *Arenaria rossii* (R. Br. *ex* Richards.) ssp. *columbiana* (Raup) Maguire.

N. of Robb L., B.C., Mrs. J. Norman Henry, no. 262, July 25, 1932.

58p. col'd m
B.

GRAY HERBARIUM
Plants of British Columbia

No. 262 Arenaria Rossii Richards.
var. columbiana Rand.
(Fragment of type)

Wet stones in pan, alt. 5,000 ft.
Pass N. of Robb L., B.C.
Mrs. J. Norman Henry July 25, 1932

and Rocky Mountains. Hultén (1937) proposed two hypotheses to explain the principally North American distribution of *Minuartia rossii*. He proposed that either it was once widespread over the arctic and northern mountains, including the alpine of eastern Asia and then had its range much reduced by the Pleistocene glaciations, or that it never had a very wide distribution at all. Hultén (l.c.) concluded that because of a lack of evidence to support either hypothesis, the question would have to remain unresolved. Gelting (1934) considered *Minuartia rossii* a pre-Pleistocene relict which had survived *in situ* in small unglaciated areas of Greenland.

Hultén (1969) considered *Minuartia rossii* a key indicator of the Kodiak Island refugium because of its widely disjunct distribution between the island and continental Alaska. Yurtsev (1972) considered the species' presence on the Wrangel Islands of Siberia as an indicator of floristic migrations between eastern Asia and Alaska via the Bering land bridge during the Pleistocene.

Biosystematic studies of *Minuartia rossii* have been confined to cytological examinations by a few workers, their published chromosome counts are summarized in Table 1. The basic chromosome number of the species was shown by Packer (1964) to be x=15. Subspecies *columbiana* has 2n=30 (Packer, 1968), ssp. *rossii* 2n=60 (A. Löve, 1975) and ssp. *elegans* has both 2n=30 (Packer, 1964) and 2n=60 (Johnson and Packer, 1968). Zukhova (1966) has reported 2n=58 for ssp. *rossii* from Wrangel Island. However, Johnson and Packer (l.c.) noted that ssp. *rossii* is restricted to the eastern North American Arctic and Zukhova's report requires further investigation.

The presence of two chromosome races in *Minuartia rossii*, its

TABLE 1. Published chromosome counts of the subspecies of *Minuartia rossii* (R. Br. *ex* Richards.) Graebn.

Subspecies	2n=	Locality	Reference
columbiana	30	Waterton Park, Alberta	Packer (1968)
elegans	30	Richardson Mts., Y.T.	Packer (1964)
elegans	60	Ogotoruk Creek, Alaska	Johnson and Packer (1968)
elegans	60	Pt. Barrow, Alaska	Löve and Löve (1975)
rossii	58	Wrangel Island, U.S.S.R.	Zhukova (1966)
rossii	58	Wrangel Island, U.S.S.R.	Zhukova and Petrovsky (1972)
rossii	58	Wrangel Island, U.S.S.R.	Zhukova *et al.* (1973)
rossii	60	Melville Island, N.W.T.	Löve and Löve (1975)

principally North American distribution and the possibility that it is composed of three morphologically and geographically distinct taxa suggests that further investigation is required in order to clarify its taxonomy. The present study was initiated to investigate the morphological, cytological, chemical and phytogeographical aspects of *Minuartia rossii* as they relate to the Pleistocene history of the complex and its infra-specific classification as proposed by Maguire (1958).

Since no previous investigations of flavonoids within the genus *Minuartia* have been conducted, the present investigation could serve as a starting point for comparative flavonoid studies within the genus. Denford (1973) has suggested that biochemical markers could be of use in establishing the existance of glacial refugia. Identification of the flavonoid constituents of *Minuartia rossii* would not only provide much needed chemical data for this genus, but may also be of use in interpreting the history of the species complex.

CHAPTER 2

MATERIALS AND METHODS

Collections

Collections of *Minuartia rossii* were made throughout as much of its range as possible. This included most of its continental North American distribution. In addition, material was collected by Mr. P.A. Addison from Cornwallis Island, N.W.T.. Collections from each locality included, where possible, pressed specimens, a quantity of air dried, unpressed material for use in chemical studies and live plants. The latter were transplanted into 4 inch pots and brought back to the greenhouse facilities of the University of Alberta.

Herbarium Studies

Morphological and distributional studies were based on living material and herbarium specimens from the following herbaria: University of Alaska (ALA); University of Alberta (ALTA); Brigham Young University (BRY); National Museum of Canada, Ottawa (CAN); University of Colorado (COLO); The Gray Herbarium of Harvard University (GH); Herbarium of the Komarov Botanical Institute, Leningrad (LE); University of Montana (MONTU); The New York Botanical Garden (NY); Botanical Museum, Oslo (O); Oregon State University (OSC); Rocky Mountain Herbarium at the University of Wyoming (RM); Swedish Museum of Natural History, Stockholm (S); University of British Columbia (UBC); University of California at Berkeley (UC). (Abbreviations as used in Index Herbariorum 1974).

Cultivation

Plants in the greenhouse were maintained under a diurnal temperature range of 10-16°C with a relative humidity of 60%. During the summer only natural lighting was used, however, at other times of the year this was supplemented with artificial lighting to produce a 16 hour photoperiod.

In an attempt to induce flowering in arctic specimens, several plants were placed in a growth chamber which was "programmed to simulate" diurnal fluctuations in temperature and light intensities of the arctic. Temperatures ranged from 0-10°C and light intensities were lowered with temperature to simulate arctic summer conditions.

Inducement of flowering in both arctic and alpine specimens was attempted by freezing plants for three weeks at -5°C. Prior to freezing, dormancy was induced by keeping the plants in the dark at 5°C for one week.

Bulbil Germinations

Porsild (1955) and Nannfeldt (1954) have noted that arctic populations of *Minuartia rossii* rarely flower and reproduce largely vegetatively by the production of bulbils in the axils of the primary leaves. Bulbil germination experiments were conducted to test the effectiveness of this type of reproduction in both arctic and alpine plants of this species.

Fifty to one hundred bulbils per plant were detached from healthy plants and tossed (this was to simulate their dispersal in nature) into flower pots containing a standard mixture of greenhouse soil. These cultures were maintained at the greenhouse temperature and

light conditions previously outlined for plant cultivation. Time of establishment, *i.e.* rooting, and percent establishment were then noted over a six week period.

Cytology

Mitotic chromosome counts were made from actively dividing root tips using the procedures of Tijo and Levan (1950) with slight modifications. Root tips were treated with a 0.002 molar solution of 8-hydroxyquinoline (0.116 gm in 400 ml of water) for 2-2½ hours at 13-16°C. The tips were then washed in distilled water for 5 minutes, transferred to a watch glass and stained for 30 minutes in a solution of acetic orcein and 1N HCl (12:1). This solution was warmed over a bunsen burner 8-10 times during a thirty minute period. The tips were then placed on a slide in a drop of 45% acetic acid and a coverslip applied. The tips were then squashed and made semi-permanent by ringing the coverlsip with a mixture of gum mastic and paraffin wax (4:1). Chromosome counts were made under the oil immersion objective of an American Optical microscope with a green filter.

Guard Cells

It has long been noted (Sax and Sax, 1937; Muntzing, 1936) that polyploidy is often accompanied by an increase in cell volume. In an effort to distinguish diploid and tetraploid races of *Minuartia rossii* by cell size, measurements of epidermal guard cells were made. Leaves were soaked in boiling water for 5 minutes, the lower epidermis was then peeled off and placed on a microscope slide in a drop of water. Measurements were made using a micrometer eyepiece on an American Optical microscope.

Chemistry

Identification of the flavonoids of eight populations of *Minuartia rossii* was carried out. In addition to the identification of compounds in these eight populations, chromatographic profiles of sixteen populations were compared.

Prior to chemical analysis the plants to be used were sorted to remove any contaminants. Flavonoids were extracted using a blender, 20 gm (dry weight) of plant material being ground for 15 minutes in 250 ml of 80% ethanol. The extract was filtered through cheesecloth followed by Whatman #1 filter paper. The extract was then reduced in a roto-evaporator under vacuum to 20 ml. Chlorophyll and other photosynthetic pigments were removed by partitioning with an equal volume of petroleum ether (B.P. 60-64°C). This extract will hereafter be referred to as the *stock solution*.

To identify the flavonoid aglycones, 10 ml of the stock solution was combined with an equal volume of 2N HCl and refluxed at 110°C for 4 hours. The aglycones were then partitioned against ether, allowed to evaporate to dryness, and then redissolved in a minimum volume of spectrograde methanol. Subsequently they were spotted in varying concentrations on half sheets of Whatman 1 MM chromatography paper. Descending chromatography was carried out using two solvent systems: BAW (n-butanol-acetic acid-water, 4:1:5 upper phase) and Forestal (acetic acid-water-HCl, 30:10:3). Identifications were made by comparison of R_f's with those reported by Harborne (1967) and Ribéreau-Gayon (1972).

Seikel *et al.* (1966) have reported that C-glycoflavones remain in the aqueous sugar layer after acid hydrolysis and ether extraction of

the aglycones. To check for possible C-glycoflavones in the stock solution the sugar layer was evaporated to dryness, redissolved in minimum methanol and spotted on half sheets of Whatman 1 MM paper. Descending chromatography of these sheets was then carried out in BAW as well as 15% acetic acid. R_f's were then compared with those reported by Harborne (1967).

Separation of the flavonoids of the stock solution was carried out on Whatman 3 MM chromatography paper. To determine the optimum concentration for separation, varying volumes of the stock solution were spotted on 3 MM paper and chromatographed descendingly in BAW for 16-19 hours. The sheets were then air dried, rotated 90° and then run in 15% acetic acid for 6-8 hours. The chromatograms were then viewed under uv light (3660Å) to determine efficiency of separation. The concentration which yielded the best separation was then used in the further isolation procedures.

Five to nine drops of the stock solution were spotted on thirty two sheets of Whatman 3 MM paper and chromatographed in BAW and 15% acetic acid according to the procedures outlined above. The chromatograms were then viewed under uv light (3660Å) in the presence and absence of fuming NH_3. Spots resolved under either of these conditions were then circled and their colours noted. To test for the presence of flavonoids, one sheet was sprayed with Benedict's reagent (positive yellow reaction). Another sheet, used for the detection of phenolics, was treated with a 3% aqueous solution of ferric chloride-ferricyanide (positive blue reaction)[6]. Spots which gave both of the above reactions

[6]Chromatograms were dipped in a solution containing equal amounts of ferric chloride and ferricyanide stains diluted 1:10 with water, then dipped in a 10% solution of HCl and washed with water.

were cut out from the remaining sheets and eluted in 80% ethanol. These solutions were then evaporated to dryness.

To ensure that the isolated flavonoids were pure, they were redissolved in minimum methanol and spotted on full sheets of Whatman 1 MM paper. The sheets were then run in the usual manner in BAW and 15% acetic acid. Those solutions which were found to consist of more than one compound as indicated by this technique were then streaked on Whatman 3 MM paper in the solvent system which gave the best separation.

The isolated flavonoids were identified using the procedures of Mabry *et al.* (1969). The compounds were redissolved in minimum absolute methanol and spotted on half sheets of Whatman 1 MM paper until a yellow colour was visible. Approximately 10 µl of a 10^{-3} m solution of Rutin (Quercetin 3-O-rhamnoglucoside) in methanolic solution was spotted on each sheet to serve as a reference. Descending chromatography of these sheets was carried out in four solvent systems: BAW, 15% acetic acid, water and saturated phenol (phenol-water, 4:1). R_f's in each of the four solvent systems were then calculated for each of the unknowns and compared with those reported in Harborne (1967) and Ribereau-Gayon (1972).

Ultra-violet spectral analysis using a Unicam SP1800 spectrophotometer was carried out on each unknown using the procedures of Mabry *et al.* (1969). These procedures include the comparison of methanol scans with those obtained after the addition of several diagnostic agents. Solutions used include sodium methoxide, aluminum trichloride, aluminum trichloride plus hydrochloric acid, sodium acetate and sodium acetate plus boric acid.

Aglycones of the unknowns were separated by ether extraction

after refluxing methanolic solutions with an equal amount of 2N HCl at 100°C f[illegible] minutes to 2 hours depending upon the nature of the glycoside linkage (Ribéreau-Gayon, 1972, p. 124). The ether fraction was then evaporated to dryness, redissolved in minimum methanol and chromatographed on Whatman 1 MM paper in both BAW and Forestal. The aglycones were also chromatographed in 15% acetic acid to insure that the sugar had been liberated (aglycones have a yellow colour in UV light and very low mobility in this solvent).

Identification of flavonoid sugars was carried out using the procedures of Ribéreau-Gayon (1972). After refluxing and separation of the aglycone by ether extraction, the sugars remain in the acidic aqueous fraction. Neutralization of this solution was carried out using a 10% solution of di-n-octylmethylamine v/v in chloroform. Twenty-five ml of this solution was shaken in a separatory funnel for two minutes and the aqueous phase containing the sugars was evaporated to dryness. The sugars were then redissolved in a minimum amount of water and spotted (two spots side by side) on half sheets of Whatman 1 MM paper with the lower edge serrated. Five µl of a 0.5% solution of D-glucose in 10% isopropanol was added to one of these spots. The sheets were then descendingly run in 80% isopropanol for 36 hours, air dried, dipped in aniline hydrogen-phthalate reagent and heated in an oven at 55°C for 20 minutes. R_g's were calculated for each sugar by dividing the distance the sugar moved by the distance the glucose marker moved. Identification of the sugar was then made by comparison of its R_g and colour with those reported by Zweig and Sherma (1972).

The above procedures were found to be sufficient for the identification of the more common types of flavonoids in the populations

surveyed. However, the presence of two less common types of flavonoids, acylated flavonoids and C-glycoflavones, required additional procedures for their identification. Acylated flavonoids were identified using the procedures of Harborne (1964). The compound to be identifed was dissolved in minimum methanol and refluxed in 2N HCl for 20 minutes at 100°C. The aglycones and sugars were identified using the procedures already outlined. In order to identify the acylated sugar, a portion of the sugar layer was chromatographed on Whatman 1 MM paper in BAW and saturated phenol. R_f's and colours in UV light in the presence and absence of NH_3 were then compared with those reported by Harborne (1964).

Beacuse of the very similar structures and low mobilities in BAW of the several C-glycoflavones, they showed little separation using standard chromatographic procedures and required slight modifications in chromatographic techniques. Sheets of Whatman 3 MM paper were spotted with stock solution in the usual manner but the chromatograms were run in BAW for 40 hours in the "short" direction of the sheet with the lower edge serrated. The sheets were then run in the "long" direction for 9-10 hours. In most cases this procedure yielded fairly distinct spots which were then cut out, eluted and streaked on 3 MM paper in both BAW and 15% acetic acid.

C-glycoflavones are isomerized via pyran ring openings in acid medium and yield two compounds upon acid hydrolysis (Seikel *et al.*, 1966). Identification of the C-glycoflavones was carried out on both of the isomers extracted in the sugar layer after 2-4 hours of refluxing in 2N HCl. In addition to the identification of sugars by normal procedures, a large amount of the sugar layer was streaked on Whatman 3 MM paper and chromatographed in 15% acetic acid. The resulting two

"aglycones" were then identified using normal chromatographic and spectral procedures. Once the basic C-glycoflavone "aglycone" was identified, it was used as a standard in co-chromatography of the remaining C-glycoflavones and their "Aglycones".

After the identification of the compounds of the eight selected populations was completed, a chromatographic analysis of the spot patterns of the sixteen populations was conducted. Populations used in flavonoid analysis are listed in Table 6 (page 70). About 10 gm dry weight of material was ground up in 50 ml of 80% ethanol. As little as 2 gm was found to be sufficient when the amount of material was limited. Each of these solutions were chromatographed on Whatman 3 MM paper in two ways. Solutions were chromatographed using the standard procedures for flavonoids and also in the manner previously outlined for C-glycoflavones. Spot patterns and colour reactions in NH_3 were then compared with those of the master chromatograms from populations in which compounds were identified.

CHAPTER 3

RESULTS

Morphology

Structural analysis revealed three morphologically and geographically distinct taxa which, to a large extent, correspond to the three subspecies of Maguire (1958). For purposes of discussion, the three taxa shall therefore be referred to as subspecies *rossii*, *elegans* and *columbiana* as treated by Maguire (l.c.). The three taxa were found to differ in general habit, habitat and several characters of the leaves, sepals and petals. These differences are summarized in Table 2. Distribution of the three subspecies are given in Maps 1, 2 and 3.

Maguire (1958) recognized both apetalous and petalous varieties of ssp. *columbiana* which, he noted, formed distinct populations throughout the Rocky Mountains. Results of this investigation indicate that ssp. *columbiana* is predominately apetalous, but that individual plants within the same population and even individual flowers on the same plant can be either petalous or apetalous. Petal development in this subspecies is probably affected by environmental factors. One specimen collected at Beartooth Pass, Montana by the author, which had well developed petals in the field, flowered twice in the greenhouse and both times the flowers were apetalous.

Cytology

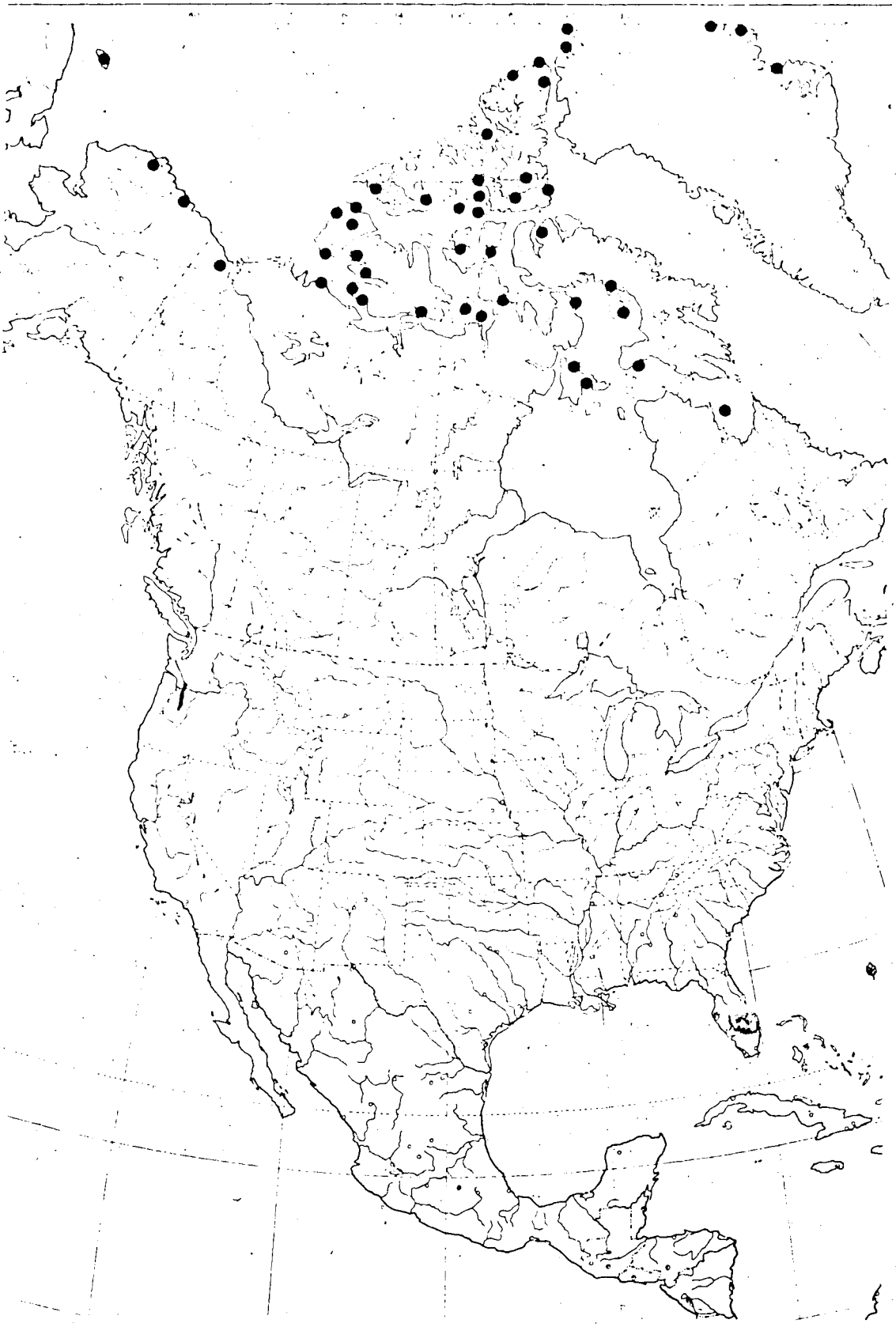
Cytological investigation confirmed Packer's (1964) observation that the basic chromosome number of *Minuartia rossii* is x=15. Mitotic

TABLE 2. Comparative morphological characters of the three subspecies of *Minuartia rossii* (R. Br. *ex* Richards.) Graebn.

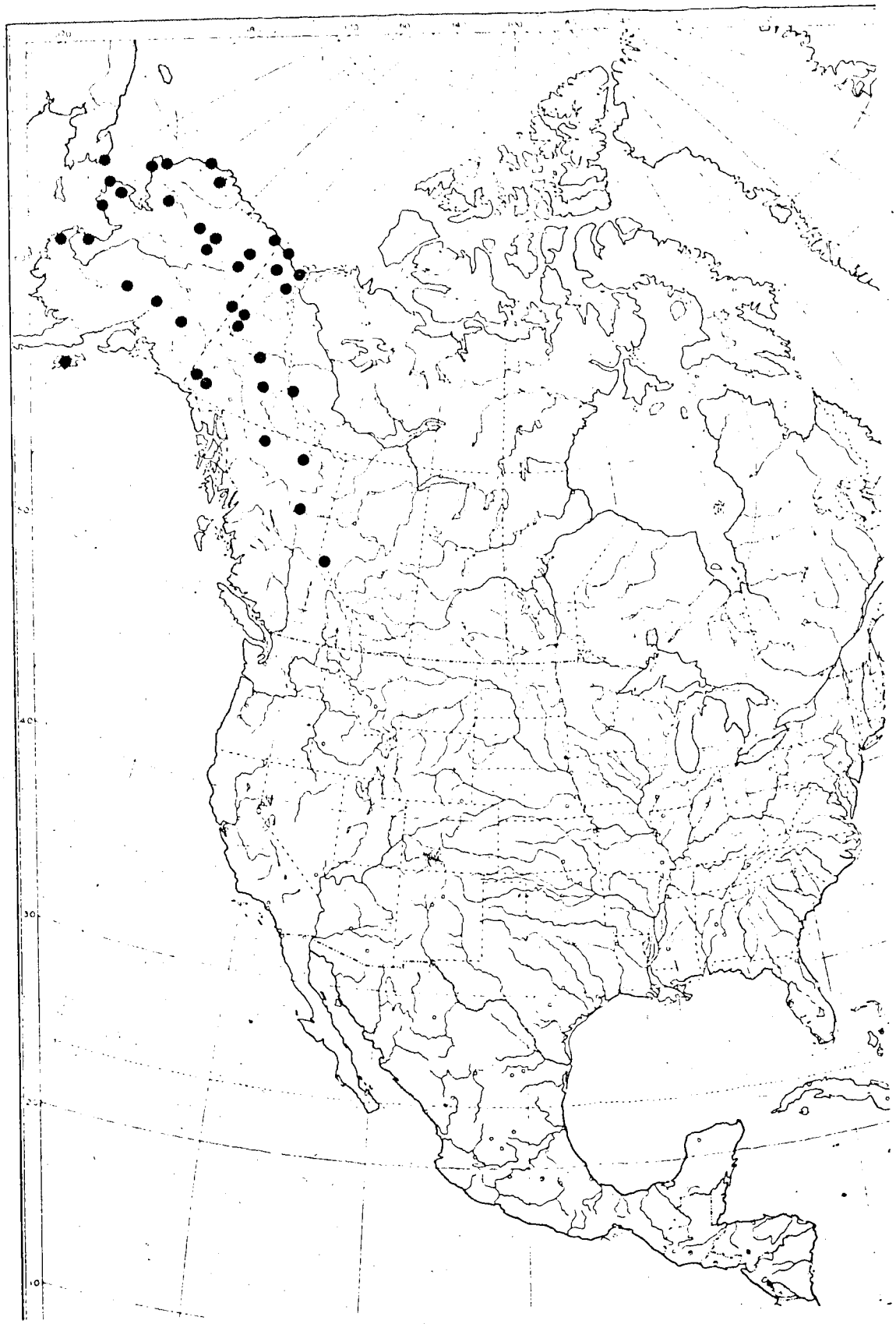
	rossii	*elegans*	*columbiana*
Habit	pulvinate	loosely tufted	caespitose
Size (cm)	3-8(10)	5-20(30)	3-15
Sepals - colour	purple	purple	green
length (mm)	1.5-2.5	2-4	2-3
shape	oblong-ovate	ovate-lanceolate	linear to lanceolate
apex	obtuse to acuminate	acute	acute
venation	1-nerved	weakly 3-nerved	strongly 3-nerved
Petals - shape	obovate to spatulate	oblong to obovate	linear to oblong
size	1.5-2X calyx length	equal to calyx (sometimes lacking)	usually lacking (shorter than calyx)
Pedicel length (mm)	5-20	10-40	5-15
length (mm)	2-4	3-10	3-6
Leaves - shape	trigonous, subulate	linear, plane	subulate
position	imbricate	ascending	spreading to ascending
Flowers	rare	abundant	abundant

MAP 1. Distribution of *Minuartia rossii* (R. Br. *ex* Richards.) Graebn. ssp. *rossii* [7] based on the author's collections and selected herbarium material.

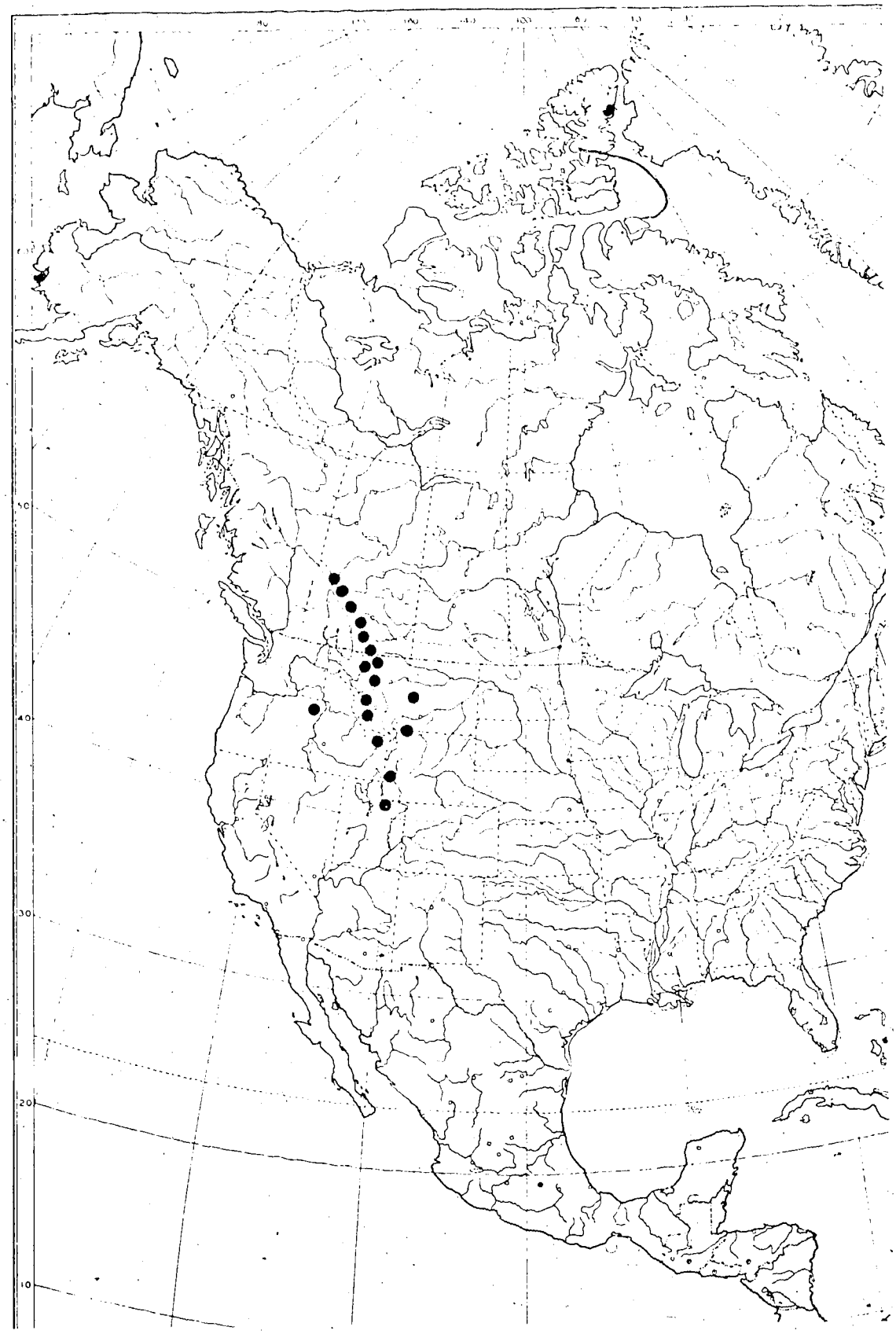
[7]Range also includes Spitzbergen.



MAP 2. Distribution of *Minuartia rossii* (R. Br. *ex* Richards.) Graebn. ssp. *elegans* (Cham. and Schlecht.) Rebr. based on the author's collections and selected herbarium material.



MAP 3. Distribution of *Arenaria rossii* (R. Br. *ex* Richards.) ssp. *columbiana* (Raup) Maguire based on the author's collections and selected herbarium material.


50
40
30
20
10

chromosome counts revealed ssp. *rossii* has a chromosome number of 2n=60, ssp. *columbiana* has 2n=30, and ssp. *elegans* has both 2n=30 and 2n=60. Specimens from which chromosome counts were made are listed in Tables 3 and 4. A map showing the distribution of the two chromosome races of ssp. *elegans* is presented in Map 4. This map includes published chromosome counts (Table 4, page 37), the author's chromosome counts and also chromosome numbers inferred by guard cell measurements. Information on guard cell measurements will be discussed in the next section.

Because of the small size of the chromosomes after treatment with 8-hydroxyquinoline, no karyotype analysis was conducted. A photograph of a diploid cell and a camera lucida drawing of a tetraploid cell are presented in Figures 4 and 5 respectively.

Attempts at obtaining meiotic chromosome counts by fixing immature flower buds in acetic alcohol (acetic acid-absolute ethanol, 1:3) yielded no satisfactory results for two reasons. *Minuartia rossii* is gynodioecious and determination of the sex of the immature flower buds proved difficult. It was also found that anthers and pollen matured very early in the development of the buds. This was evident in many cases in which fully developed anthers protruded out from small immature buds.

Guard Cells

Guard cell measurements showed a positive correlation between guard cell length and ploidy level in subspecies *elegans*. The mean cell length for the diploid (2n=30) was 23.2 microns (N=872) while the mean for the tetraploid (2n=60) was 27.9 microns (N=686). A student's t test (s=0.84, t=7.61) showed a significant difference between the two means

TABLE 3. Collections on which Diploid (2n=30) chromosome counts are based.

Alaska: *SJW* #139, 146, 147, 151 McKinley Park, July 14/75; *SJW* #243, 244, 245 Mi. 12.5, Denali Highway, June 25/76; *SJW* #254, 255, 257A Mi. 108, Steese Highway, June 29/76; *SJW* #279, 280 Atigun Pass, Brooks Range, July 4/76.

Alberta: *W.J. Elisens* #77 Hailstone Butte, Kananaskis Forestry Rd., July 16/75; *SJW* #117A, 117B Grave Flats, Mt. Park, June 21/75; *SJW* #119, 127, 128, 129 Cardinal River Divide, Mt. Park, June 23/75; *SJW* #223, 224 Carthew Mt., Waterton Park, Aug. 16/75; *SJW* #232, 233, 234 Highwood Pass, Kananaskis Forestry Rd., Aug. 18/75; *SJW* #237 Sunshine Village, Banff Park, Aug. 20/75; *SJW* #241 Signal Mt., Jasper Park, Aug. 28/75.

Montana: *SJW* #197, 198, 199, 200, 203, 207 Beartooth Pass, Aug. 12/75; *SJW* #216, 217 Goat Flats, Deerlodge Cty., Aug. 14/75; *SJW* #219 Choteau Mt., Teton Cty., Aug. 15/75.

Yukon: *SJW* #156, 165, 169, 170, 171 Southern Ogilvie Mts., 64°18'N, 137°20'W, July 19-20/75.

TABLE 4. Collections on which tetraploid (2n=60) chromosome counts are based.

Alaska: *SJW* #260, 262 Mi. 307 TAPS Highway, J[illegible]3/76; *SJW* #266 Prudhoe Bay, July 4/76.

Alberta: *J. Tande*, Adam's Creek, Willmore, Wilderness Park.

British Columbia: *SJW* #194, 195 Summit Lake, July 27/75.

Northwest Territories: *P.A. Addison* #R5, R8 Resolute Bay, Cornwallis Island, July 5/75.

Yukon: *SJW* #183, 185, 186, 187, 188, 189 Mi. 95.6, Dempster Highway, July 25/75; *SJW* #285 Mi. 57, Dempster Highway.

MAP 4. Distribution of the chromosome races of ssp. *elegans* based on the author's collections, published chomosome counts and quard cell measurements of herbarium material.

▲ - diploid (2n=30)

■ - tetraploid (2n=60)

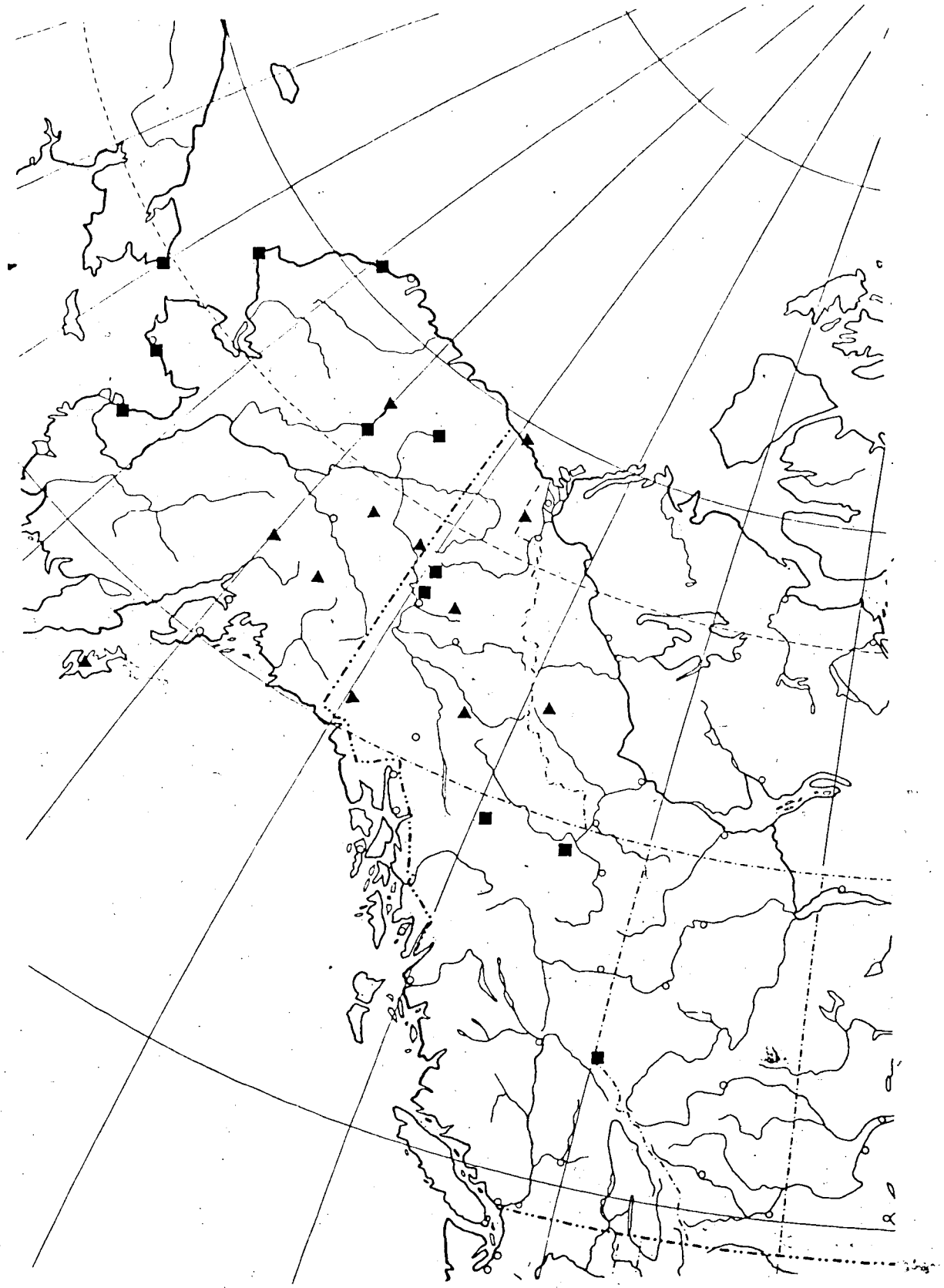


FIGURE 4. Photograph of a diploid (2n=30) cell of ssp. *columbiana*.

FIGURE 5. Camera lucida drawing of a tetraploid (2n=60) cell of ssp. *rossii*.

at the 1% level. A graph showing the range of variation between the two ploidy levels is presented in Figure 6. The significant difference between the mean cell lengths made possible the determination of ploidy levels from herbarium sheets. Only those specimens in which the average cell length was within 1.5 microns of the predicted mean were used. Herbarium specimens examined are listed in Table 5 and their distribution is included in Map 4 (page 39). Tetraploids were found to occur primarily in coastal Alaska, the Brooks Range and Northeastern British Columbia, while diploids were found to be restricted to the central Alaska-Yukon region.

Mean guard cell length for the tetraploid ssp. *rossii* and diploid ssp. *columbiana* were found to be 28.4 microns and 25 microns respectively.

Reproductive Biology

Both subspecies *elegans* and subspecies *columbiana* were found to be gynodioecious. Female flowers of these subspecies have very short undeveloped stamens (Figure 7). Insufficient flowering material of ssp. *rossii* prevented any direct observation of its sexual condition, however it is also probably gynodioecious judging from Kurtz's (1894) observation of *staminibus longioribus* and *staminibus brevioribus* flowers on separate plants of this taxon.

Several plants flowered abundantly in the greenhouse, however no seed was set. Outbreeding in *Minuartia rossii* is reinforced by pronounced protandry (Figure 8). Baad (1969) found that all of the North American species of *Arenaria* subgenus *Eremogone* exhibited protandry. Baad (l.c.) also noted that the unspecialized flowers of *Eremogone arenaris* attracted indiscriminate insect pollinators. This

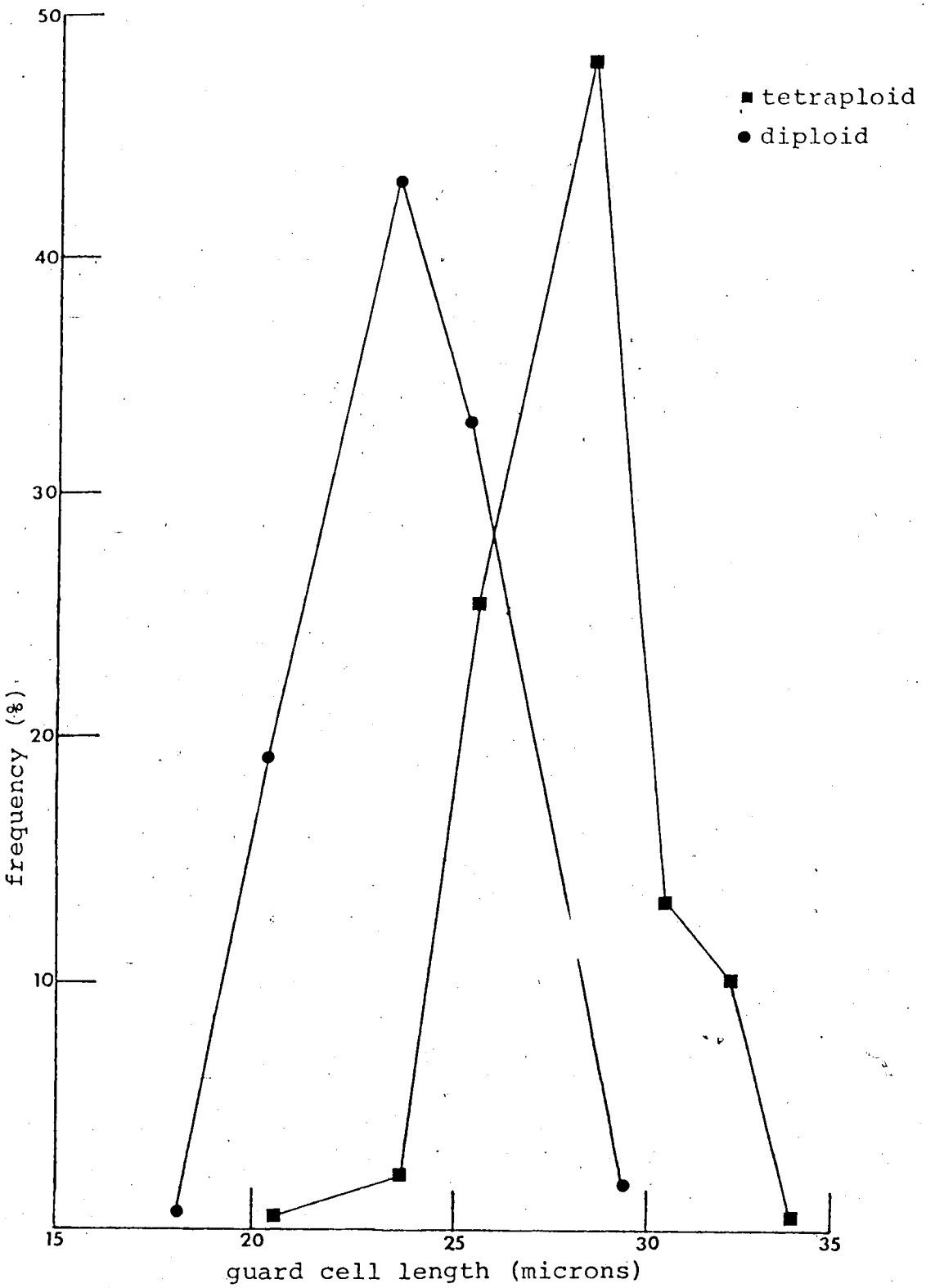


Figure 6. Guard cell length frequencies in ssp. elegans

TABLE 5. Herbarium specimens from which chromosome number has been determined by guard cell measurement.

2n=	Locality	Collector(s)	Herbarium
30	Mackenzie Mts., N.W.T.	H.M. Raup and J.H. Soper 9416	GH
30	Herschel Island, Y.T.	R. Wood 146	CAN
30	Eagle, Alas[illegible]	G. Smith 4213	CAN
30	Kodiak Island, Alaska	E. Hultén	S
30	Kluane Lake, Y.T.	H.M. and L.C. Raup and S.K. Harris 12344	GH
30	Canol Rd., Y.T.	A.E. Porsild and A.J. Breitung 10891	CAN
60	Chukchi Peninsula, U.S.S.R.	B. B. Petrovsky	LE
60	Nome, Alaska	A.E. and R.T. Porsild 1336	GH
60	Arctic Village, Alaska	L. Hettinger 824	CAN
60	Norton Sound, Alaska	A.E. and R.T. Porsild 984	CAN
60	North of Cassiar, B.C.	K. Beamish *et al.* 730376	CAN

FIGURE 7. Female flower of ssp. *columbiana*.

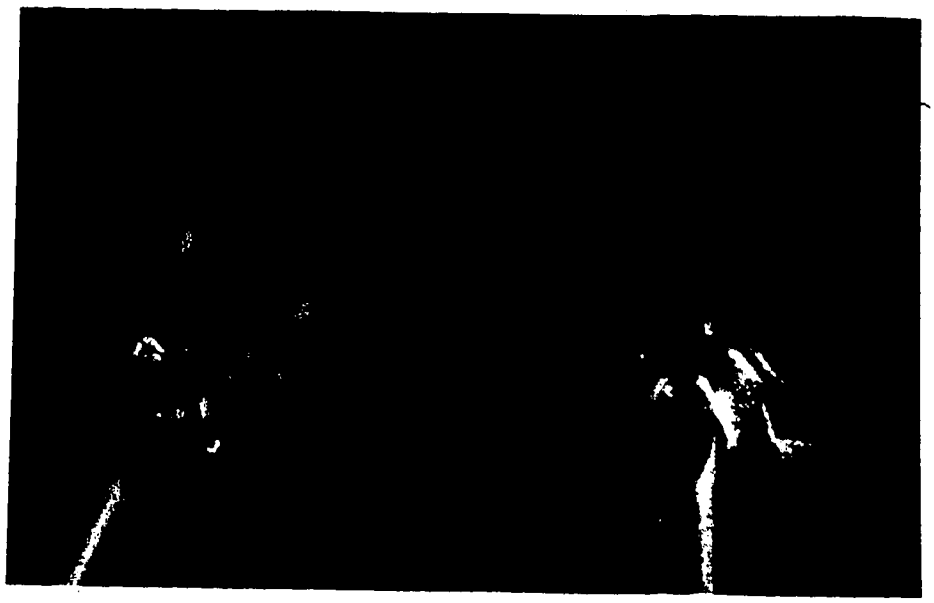


FIGURE 8. Protandry in ssp. *columbiana*.

was also found to be the case in *Minuartia rossii*, numerous types of insects were observed visiting the flowers. All three subspecies possess a pair of nectar glands at the base of each stamen which secrete large amounts of nectar. This is undoubtably the major insect attractant since insects showed no preferences for petalous flowers over apetalous ones and the petals showed no UV patterns under either short or long wave UV light.

It has long been noted that ssp. *rossii* rarely flowers but reproduces vegetatively by bulbils (Sorensen, 1933). These bulbils are small [redacted] of leaves produced in the axils of the primary leaves and are found in all three subspecies. Bulbil germination tests for each of the subspecies yielded 98% establishment for ssp. *rossii* in three weeks, 10% establishment for ssp. *elegans* in six weeks, and 14% establishment for ssp. *columbiana* in six weeks. Bulbils from ssp. *rossii* were easily detached (in the field wi would probably be sufficient) while those from ssp. *elegans* and *columbiana* had to be forcibly detached. Establishment times for ssp. *elegans* and *columbiana* were twice that of ssp. *rossii* and the bulbils required very moist conditions for germination. However, these moist conditions would rarely be available in the relatively dry habitats of ssp. *elegans* and *columbiana*. It appears that ssp. *rossii* is well adapted for and relies primarily upon vegetative reproduction while this type of reproduction probably plays a very insignificant role, if any, in ssp. *columbiana* and *elegans*.

Chemistry

A master chromatogram showing the flavonoid profile of *Minuartia rossii* is presented in Figure 9. R_f values, UV spectral data and colour reactions of the nine compounds identified are presented in

FIGURE 9. Master chromatogram of flavonoids in *Minuartia rossii sensu lato*.

1. Kaempferol 3-p-Courmaroylglucoside
2. Apigenin 6-C-glucoside
3. Quercetin 3-O-glucoside
4. Kaempferol 3-O-sophoroside
5. Quercetin 3-O-sophoroside
6. Apigenin 6-C-arabinosylglucosyl-7-O-glucoside
7. Apigenin 6-C-arabinosyldiglucoside
8. Apigenin 6-C-triglucoside
9. Quercetin 3-O-glucosylgalactoside

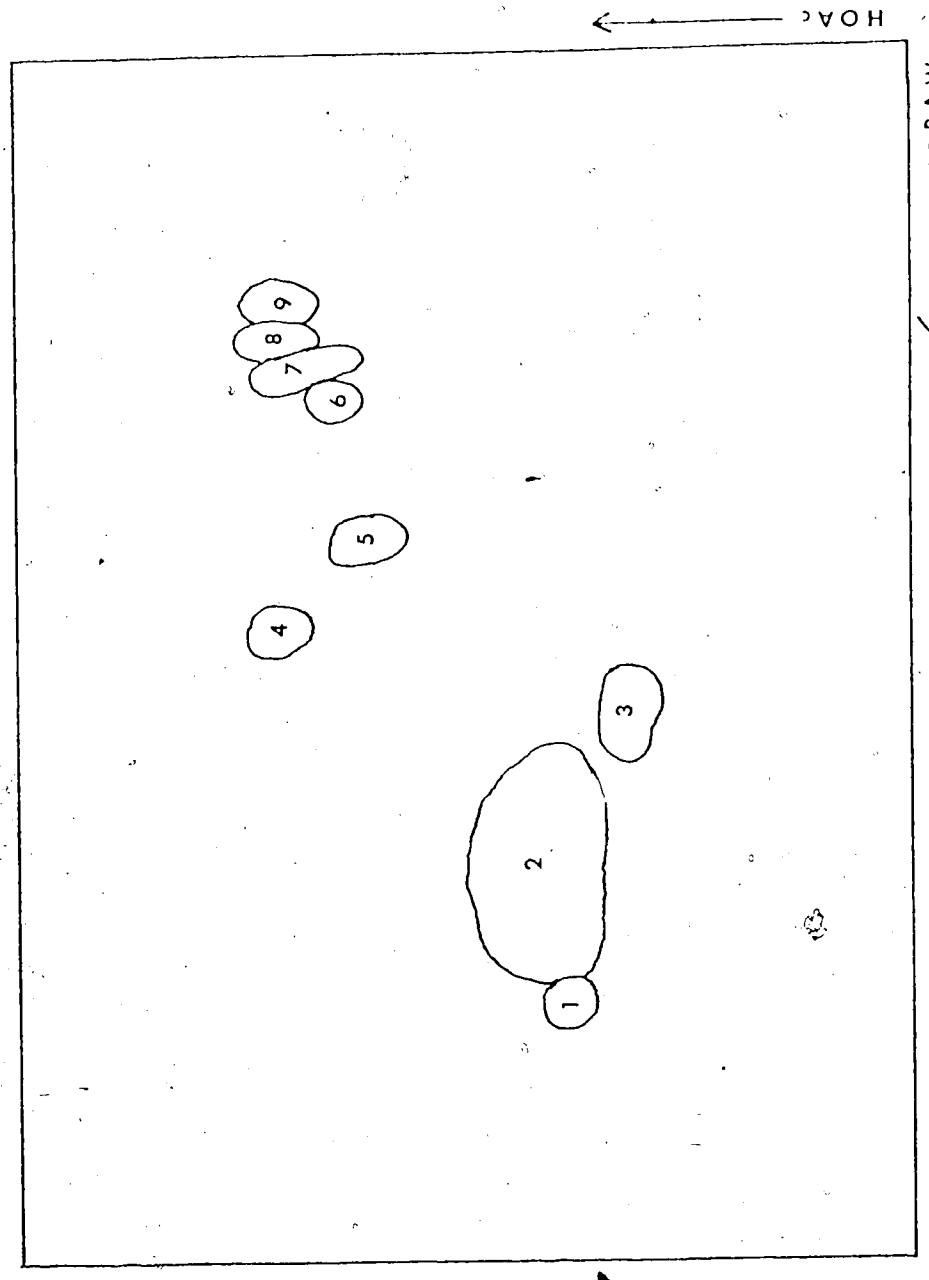
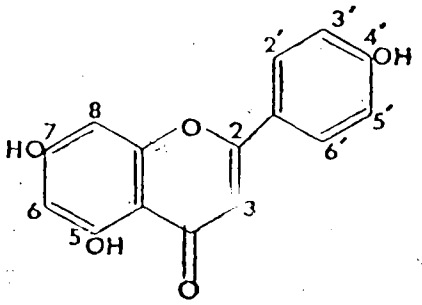


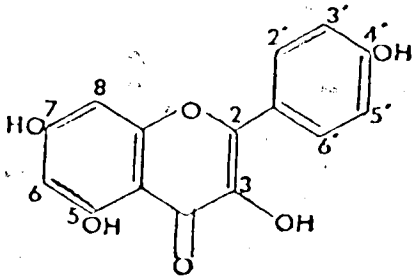
Figure 9. Master chromatogram of flavonoids in Minuartia rossii sensu lato.

Figures 10-18. A total of twenty-four populations were surveyed. Collections used in chromatographic analysis are listed in Table 6.

Minuartia rossii was found to possess both flavonols and flavones. Flavones are distinguished from flavonols by the absence of a hydroxyl group or glycoside at the 3 position.



FLAVONE



FLAVONOL

Five flavonol glycosides were found to be present in all populations of *Minuartia rossii*: kaempferol 3-O-sophoroside, kaempferol 3-p-Coumaroylglucoside, quercetin 3-O-glucoside, quercetin 3-O-sophoroside and quercetin 3-O-glucosylgalactoside. Acid hydrolysis of kaempferol 3-p-Coumaroylglucoside yielded kaempferol and p-Coumaroylglucose (R_f 57 in BAW, 77 in saturated phenol, colour blue in UV+NH_3). Acid hydrolysis of the remaining glycosides yielded the aglycones quercetin or kaempferol plus the glycoside residue.

A total of four flavones were found in the populations surveyed. The four flavones were all of the C-glycoflavone type, *i.e.* with the sugar molecule attached to the flavonoid molecule via a direct carbon to carbon bond. Three of the flavones were found to be present in all populations surveyed: apigenin 6-C-glucoside (isovitexin), apigenin 6-C-triglucoside and apigenin 6-C-arabinosyldiglucoside. The fourth flavone, apigenin 6-C-arabinosylglucosyl-7-O-glucoside, was found to be of limited

distribution, being present in ssp. *elegans* and ssp. *rossii* and absent in ssp. *columbiana*. Acid hydrolysis of the C-glycosylavones yielded apigenin 6-C-glucoside (isovitexin), its 8 carbon isomer apigenin 8-C-glucoside (vitexin) and the oxygen bound sugar molecules.

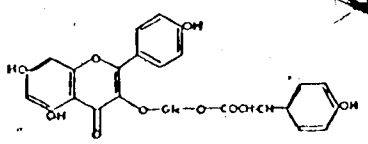
In their study of isovitexin (apigenin 6-C-glucoside) glycosides in *Melandrium album* Garcke, van Brederode and van Nigtevecht (1972) found petal development to be correlated with 7 position glycosylation. They found plants which possessed an isovitexin 7-glycoside had well developed petals while those that lacked a 7 position sugar had poorly developed narrower petals. The presence of an isovitexin 7-O-glycoside (apigenin 6-C-arabinosylglucosyl-7-O-glucoside) in the predominately petalous ssp. *elegans* and its absence in the apetalous ssp. *columbiana* suggests that this compound may also be correlated with petal development in *Minuartia rossii*. To test whether this compound was subspecies specific or confined only to apetalous individuals, the flavonoids of a known apetalous plant of ssp. *elegans* (SJW #243, Denali Highway, Alaska) were isolated and identified. It was found to possess the isovitexin 7-O-glucoside and it can therefore be concluded, that this compound is subspecies specific, being found in ssp. *rossii* and ssp. *elegans* and lacking in ssp. *columbiana*.

No differences in flavonoid profiles of diploid and tetraploid populations of ssp. *elegans* were noted.

The chemical and spectral characteristics of the flavonoid glycosides of the *Minuartia rossii* complex are summarized in Table 8 (page 107).

FIGURE 10. Chromatographic and spectral data for Kaempferol 3-p-Courmaroylglucoside.

Kaempferol 3-p-Courmaroylglucoside



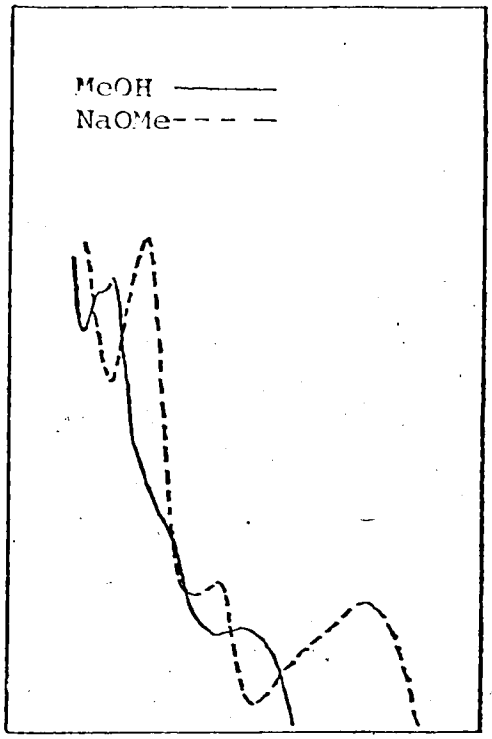
CHROMATOGRAPHIC DATA

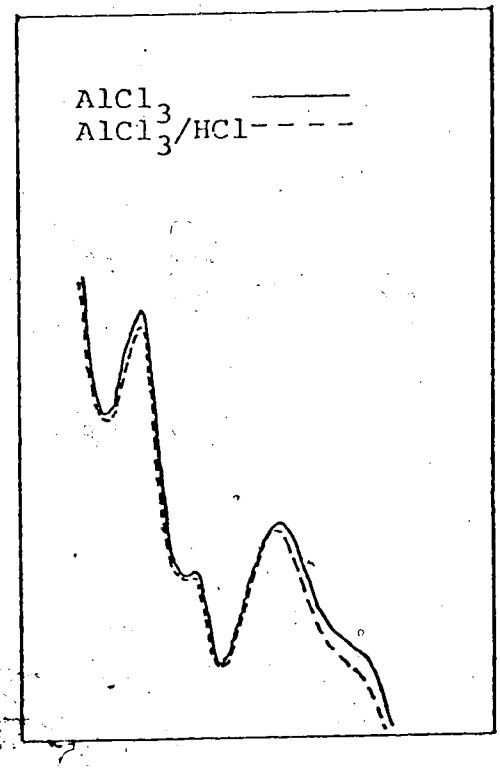
Spot Appearance: (uv) deep purple
(UV/NH_3) yellow-green

R_f Values: 0.80(BAW) 0.10(H_2O) 0.39(HoAc) 0.75(PhOH)

UV SPECTRAL DATA (nm)

MeoH	260s, 277, 301s, 338
NaOMe	286, 326, 375s, 408
$AlCl_3$	276, 306, 353, 408s
$AlCl_3$/HCl	276, 306, 351, 408s
NaOAc	276, 306s, 378
NaOAc/H_3BO_3	269, 282s, 352





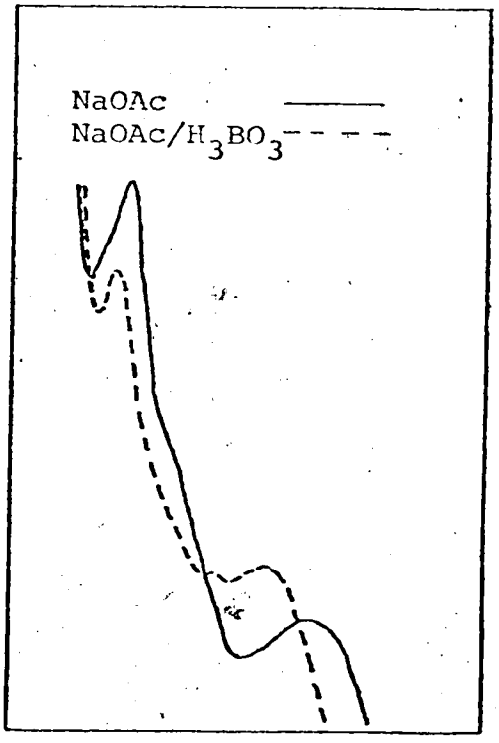
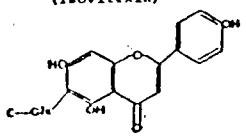


FIGURE 11. Chromatographic and spectral data for Apigenin 6-C-glucoside.

Apigenin 6-C-glucoside
(Isovitexin)



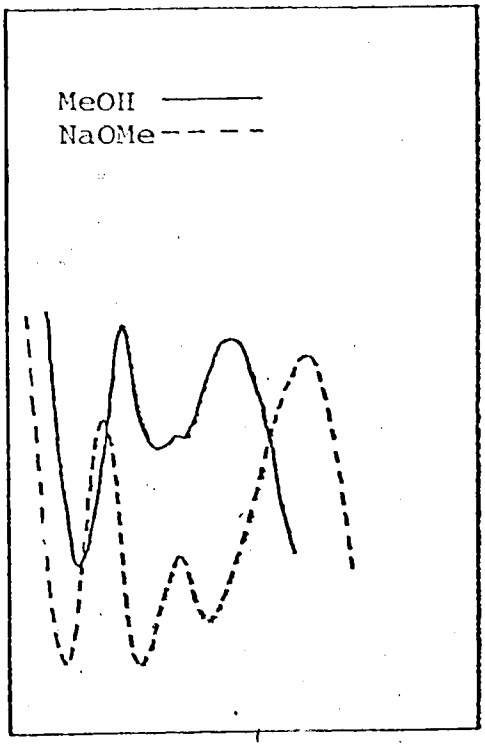
CHROMATOGRAPHIC DATA

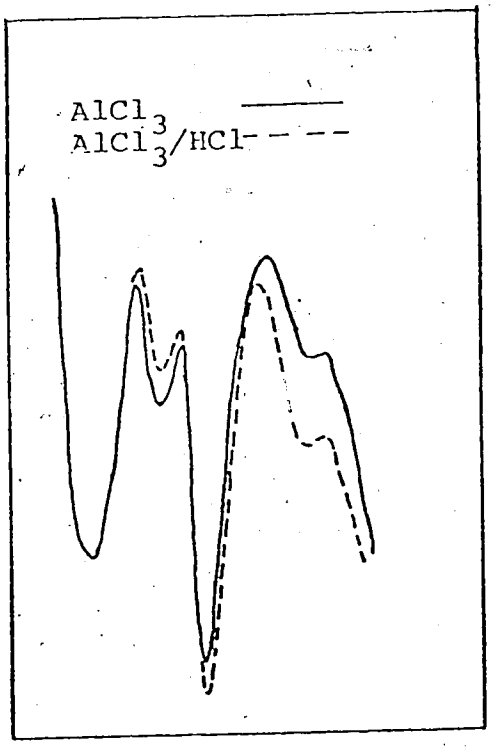
Spot Appearance: (UV) deep purple
(UV/NH_3) yellow-green

R_f Values: 0.61(BAW) 0.15(H_2O) 0.42(HoAc) 0.77(PhOH)

UV SPECTRAL DATA(nm)

MeOH	274, 306s, 334
NaOMe	284, 326, 399
$AlCl_3$	262s, 281, 305, 354, 385
$AlCl_3$/HCl	262s, 282, 304, 349, 384
NaOAc	281, 312s, 394
NaOAc/H_3BO_3	275, 310, 348





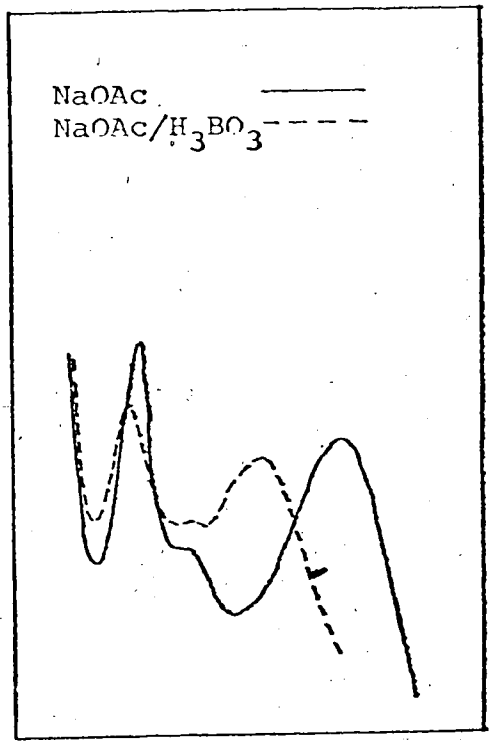
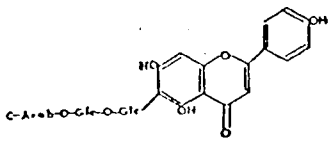


FIGURE 12. Chromatographic and spectral data for Apigenin 6-C-arabinosyldiglucoside.

Apigenin 6-C-arabinosyldiglucoside



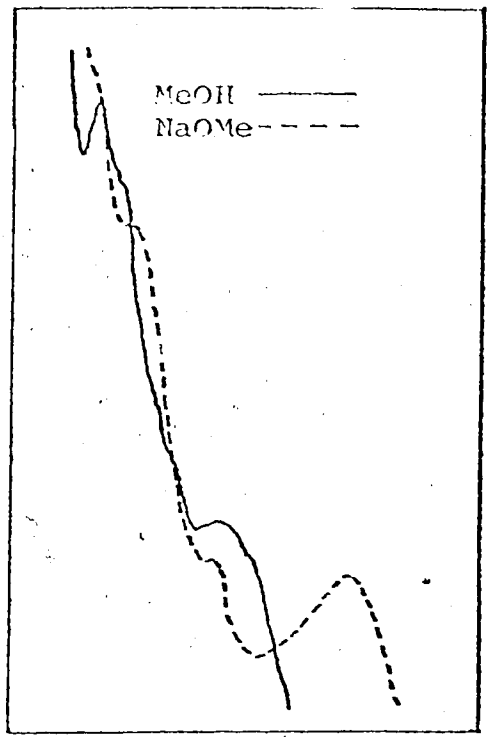
CHROMATOGRAPHIC DATA

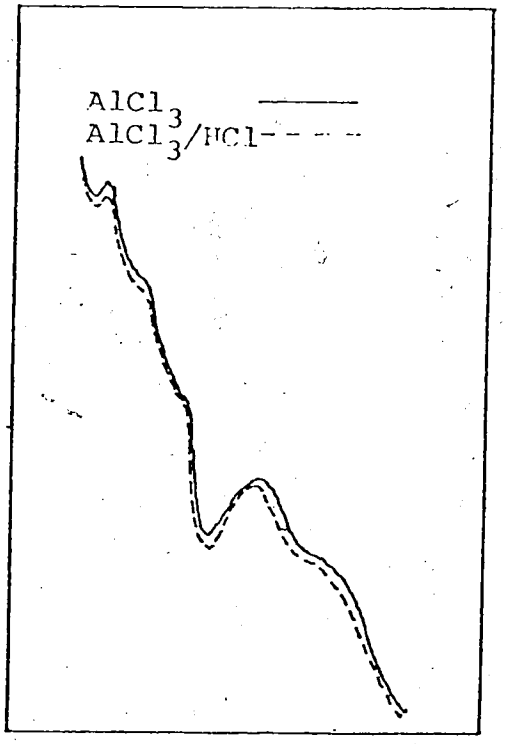
Spot Appearance: (UV) deep purple
(UV/NH_3) yellow-green

R_f Values: 0.26(BAW) 0.46(H_2O) 0.66(HOAc) 0.62(PhOH)

UV SPECTRAL DATA (nm)

MeOH	274, 312s, 334
NaOMe	286, 328, 402
$AlCl_3$	279, 305, 350
$AlCl_3$/HCl	278, 305, 346, 394s
NaOAc	282, 303s, 380
NaOAc/H_3BO_3	274, 306s, 346





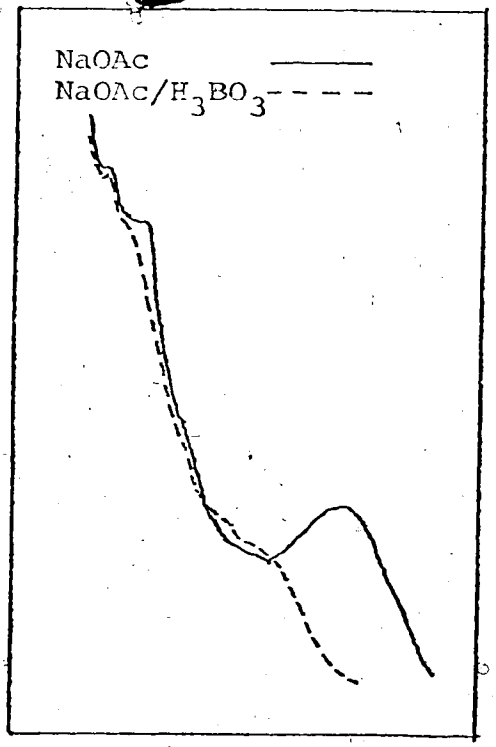
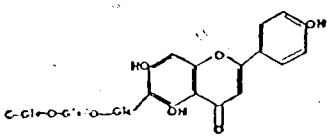


FIGURE 13. Chromatographic and spectral data for Apigenin 6-C-triglucoside.

Apigenin 6-C-triglucoside



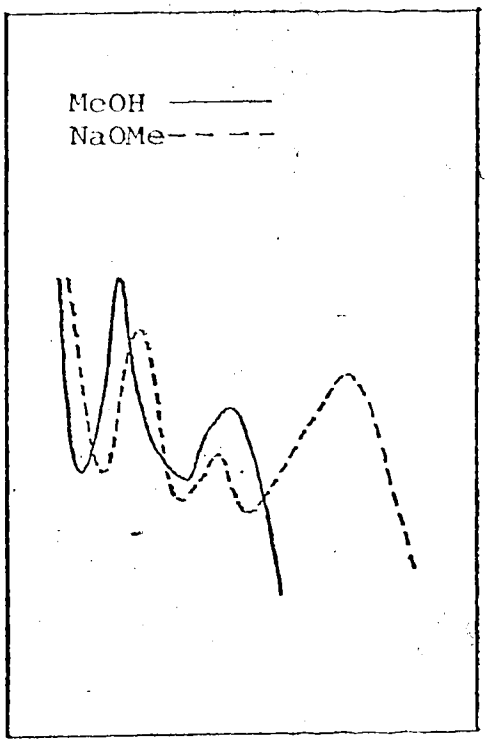
CHROMATOGRAPHIC DATA

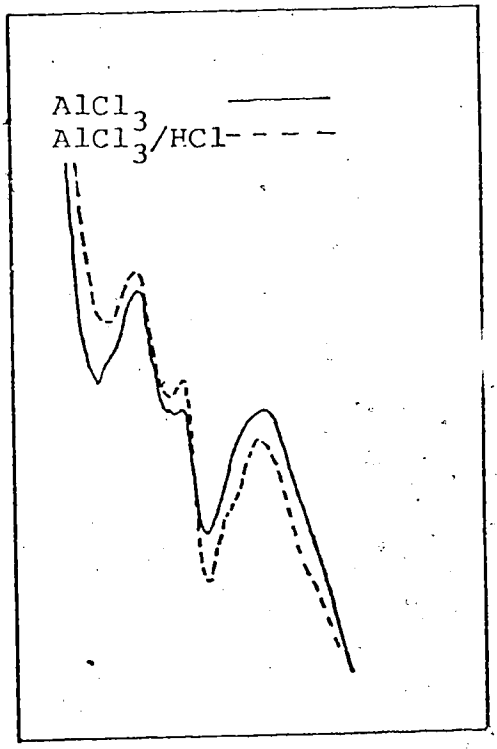
Spot Appearance: (UV) deep purple
(UV/NH_3) yellow-green

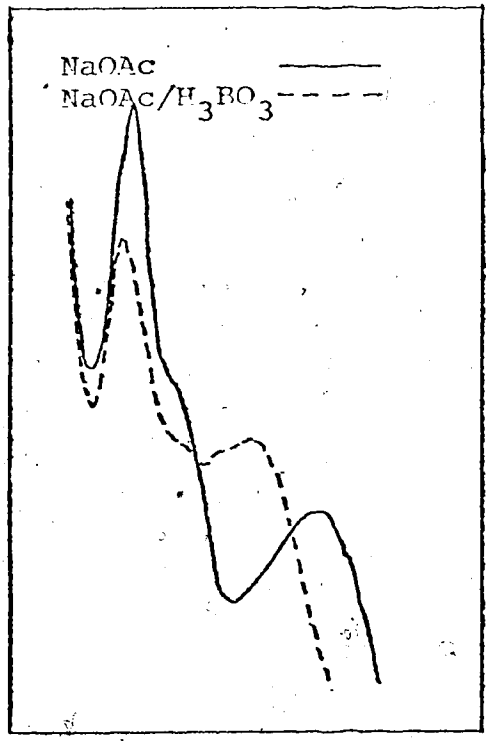
R_f Values: 0.24(BAW) 0.51(H_2O) 0.6[illegible]Ac) 0.53(PhOH)

UV SPECTRAL DATA (nm)

MeOH	259, 274,330
NaOMe	259s, 280, 328, 402
$AlCl_3$	259, 283s, 304s, 346, 390s
$AlCl_3$/HCl	260, 283s, 304s, 344, 390s
NaOAc	260, 282, 396
NaOAc/H_3BO_3	258, 274s, 358s







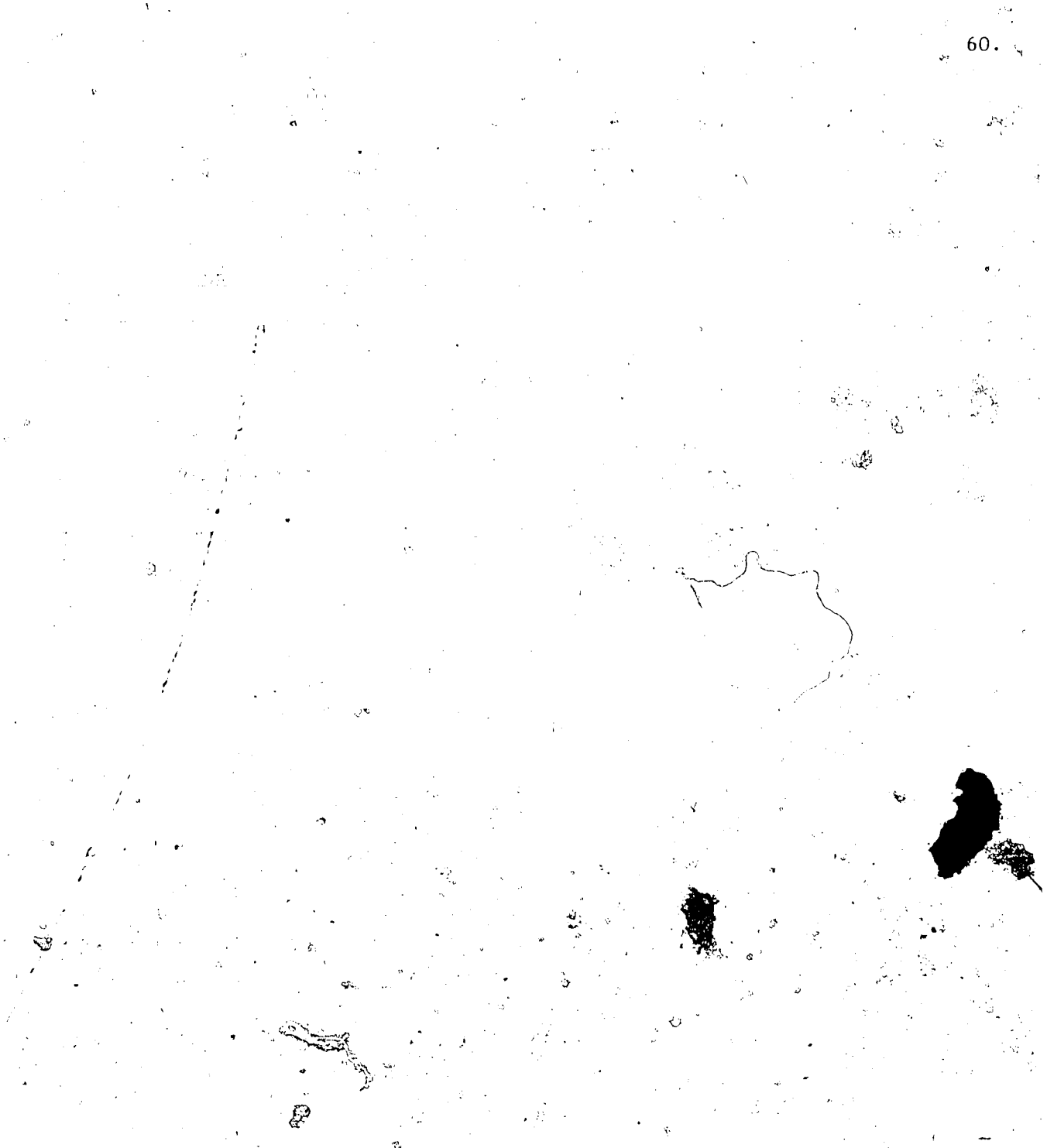
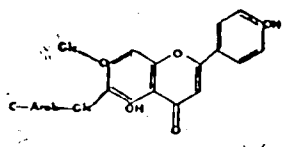


FIGURE 14. Chromatographic and spectral data for Apigenin 6-C-arabinosylglucosyl-7-O-glucoside.

Apigenin 6-C-arabinosylglucosyl-7-O-glucoside



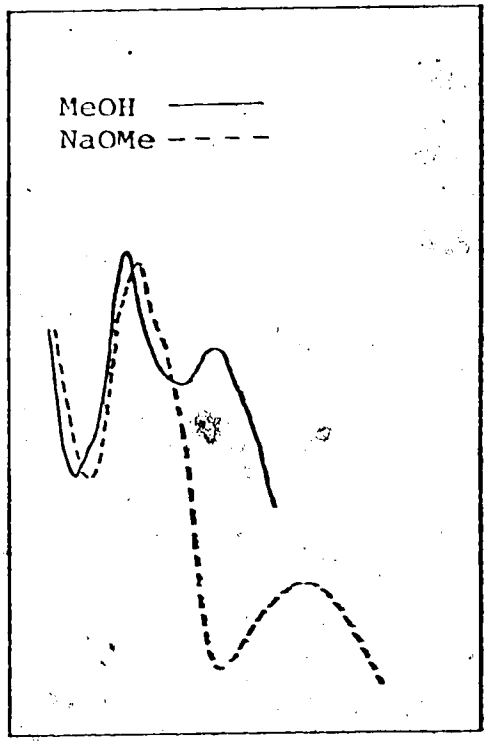
CHROMATOGRAPHIC DATA

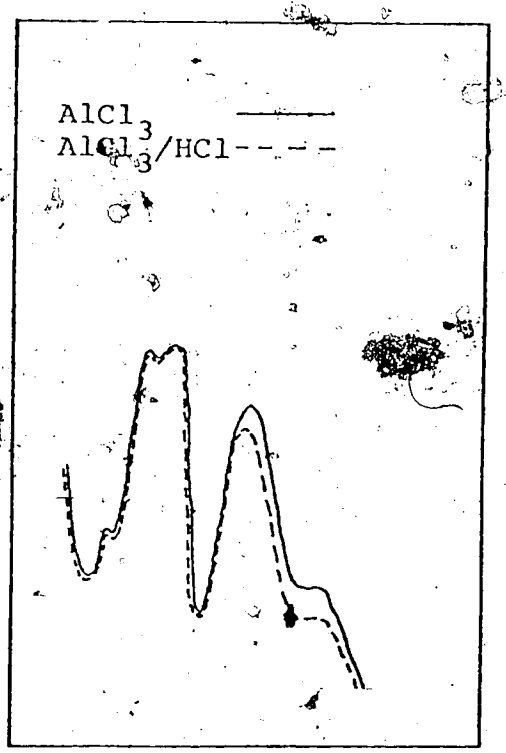
Spot Appearance: (UV) deep purple
(UV/NH_3) yellow-green

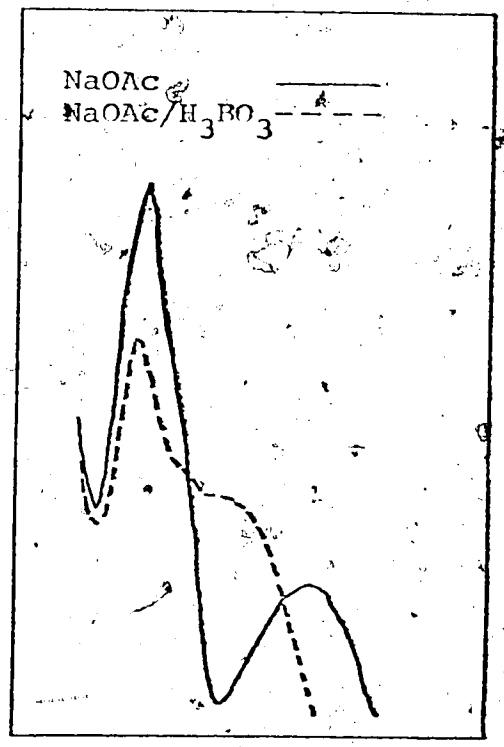
R_f Values: 0.29(BAW) 0.42(H_2O) 0.66(HoAc) 0.68(PhOH)

UV SPECTRAL DATA (nm)

MeOH	276, 326
NaOMe	282, 294s, 378
$AlCl_3$	262, 2[illegible], 300, 343, 348s
$AlCl_3$/HCl	262, 2[illegible], 300, 340, 282s
NaOAc	282 299s, 376
NaOAc/H_3BO_3	276, 307s, 342s







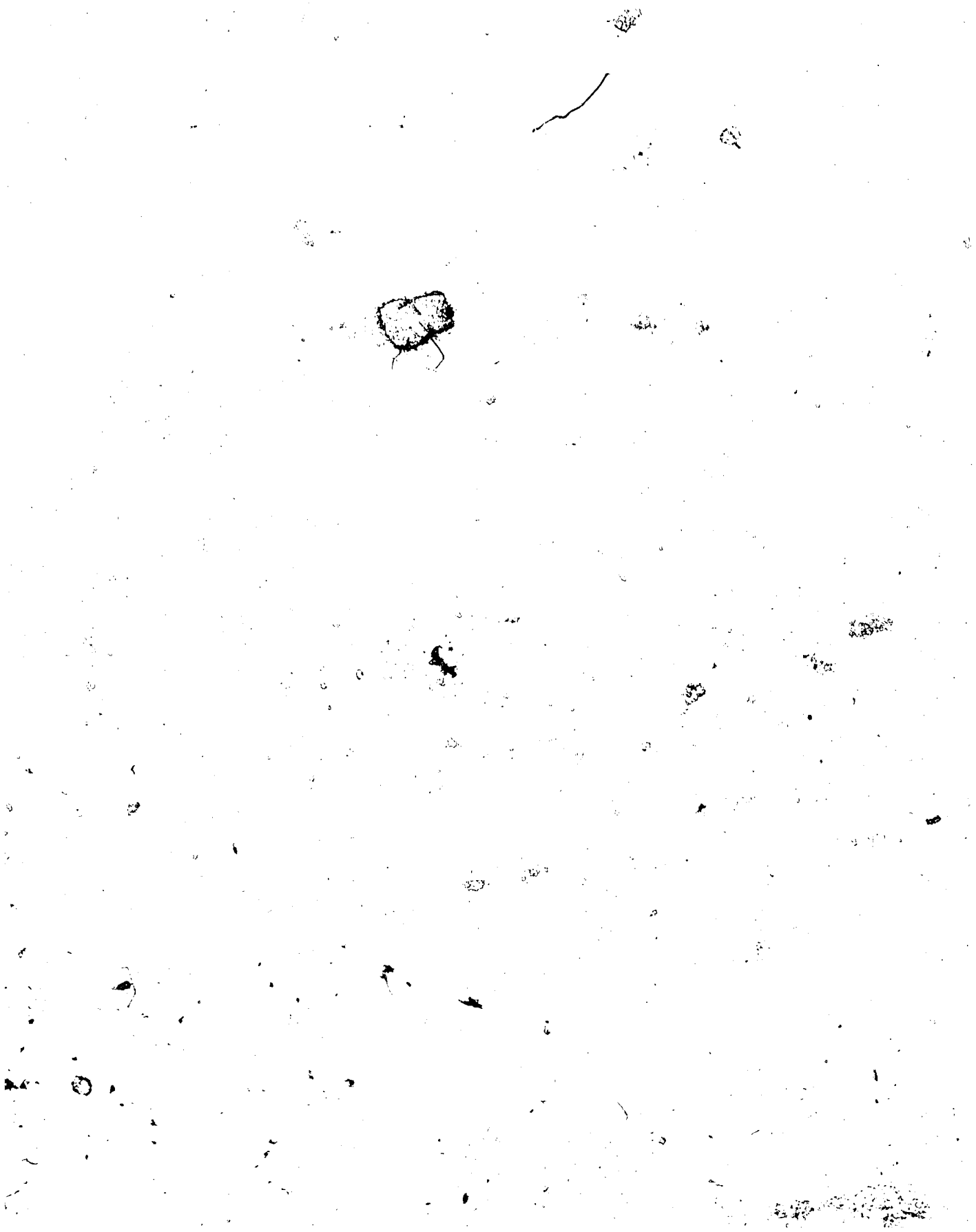
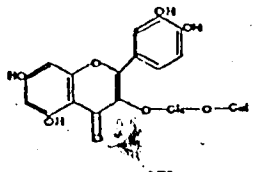


FIGURE 15. Chromatographic and spectral data for Quercetin 3-O-glucosylgalactoside.

Quercetin 3-O-glucosylgalactoside



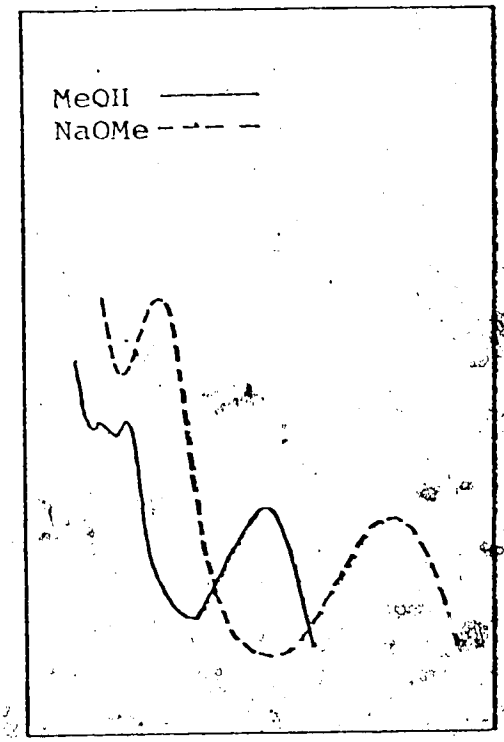
CHROMATOGRAPHIC DATA

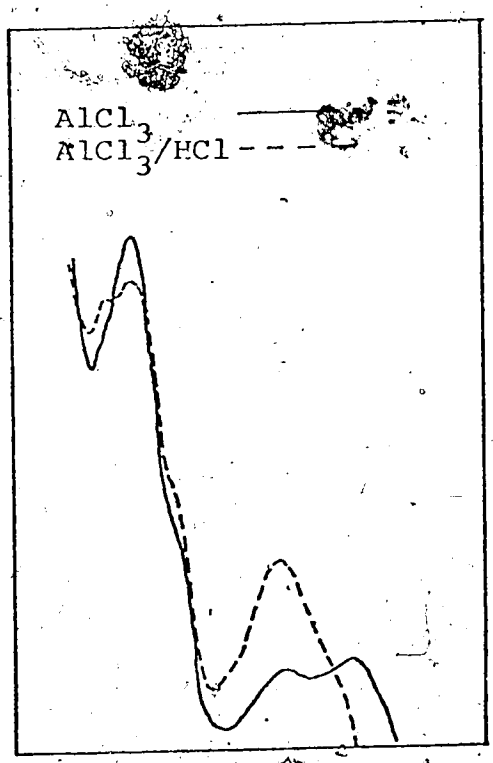
Spot Appearance: (UV) deep purple
(UV/NH_3) yellow-green

R_f Values: 0.22(BAW) 0.48(H_2O) 0.68(HOAc) 0.37(PNOH)

UV SPECTRAL DATA (nm)

MeOH	260, 273, 352
NaOMe	285, 418
$AlCl_3$	277, 302s, 360, 400
$AlCl_3$/HCl	262, 276, 300s, 358
NaOAc	272, 406
NaOAc/H_3BO_3	273, 378, 436s





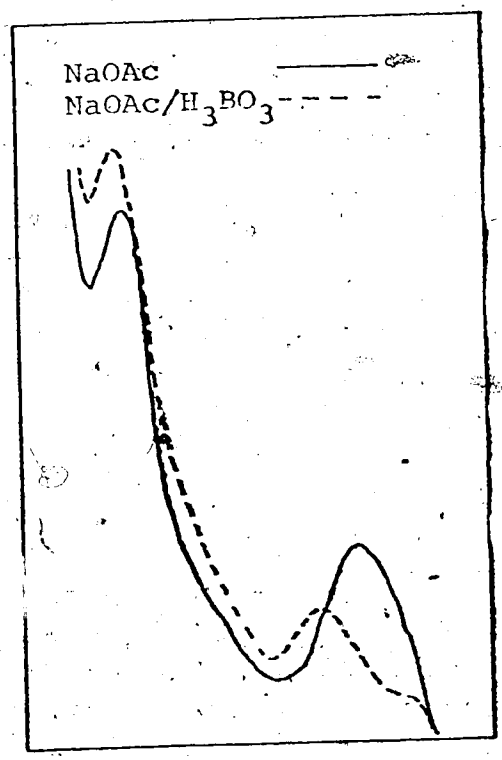
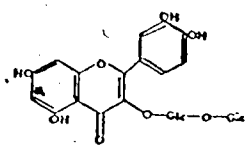


FIGURE 16. Chromatographic and spectral data for Quercetin 3-O-sophoroside.

Quercetin 3-O-sophoroside



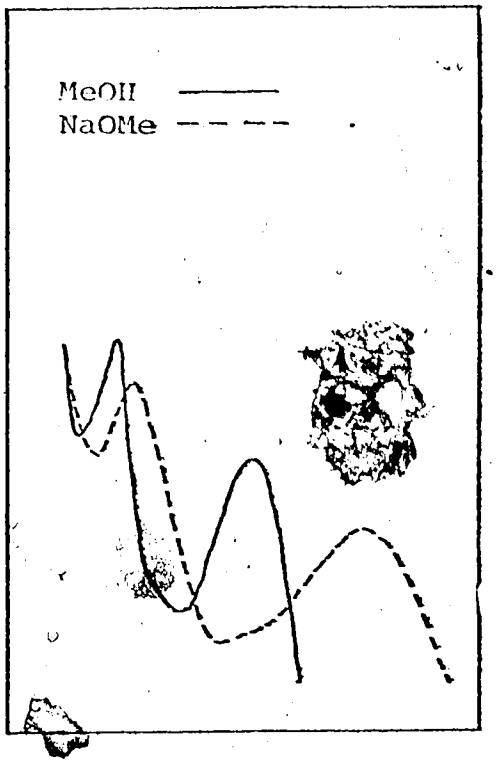
CHROMATOGRAPHIC DATA

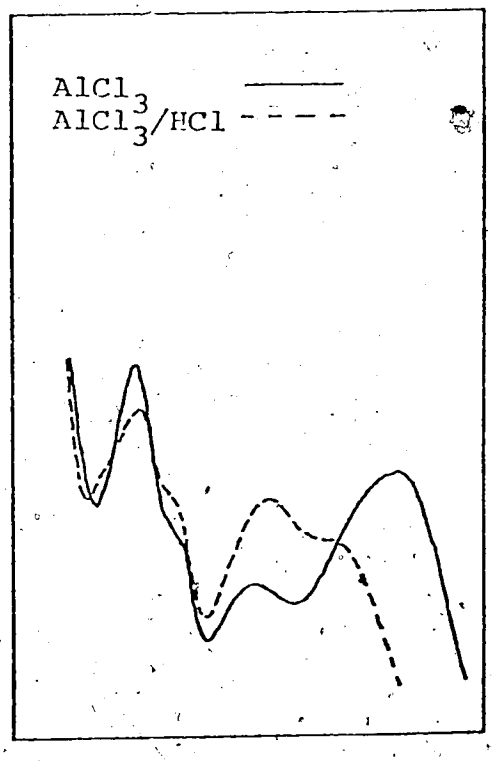
Spot Appearance: (UV) deep purple
(UV/NH_3) yellow-green

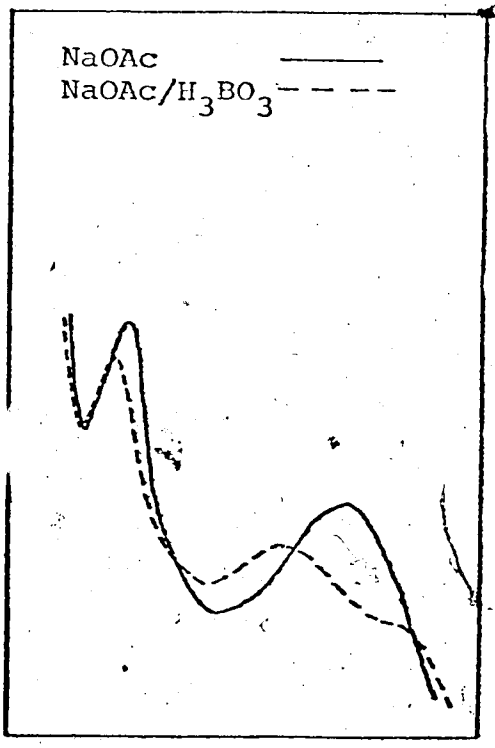
R_f Values: 0.42(BAW) 0.28(H_2O) 0.64(HOAc) 0.50@pH0H)

UV SPECTRAL DATA

MeOH	271, 347
NaOMe	282, 340s, 406
$AlCl_3$	278, 304s, 342, 422
$AlCl_3$/HCl	280, 300s, 352, 390s
NaOAc	276, 400
NaOAc/H_3BO_3	270, 310s, 364, 430s

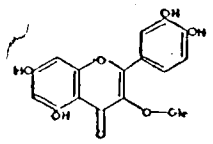






RE 17. Chromatographic and spectral data for Quercetin 3-O-glucoside.

Quercetin 3-O-glucoside



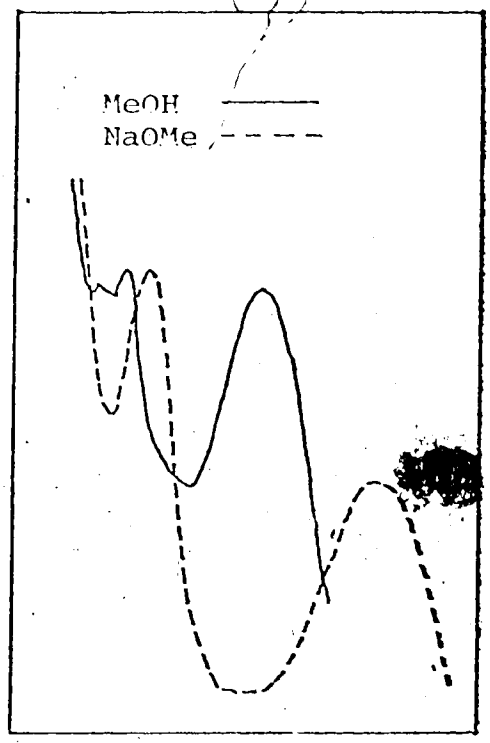
CHROMATOGRAPHIC DATA

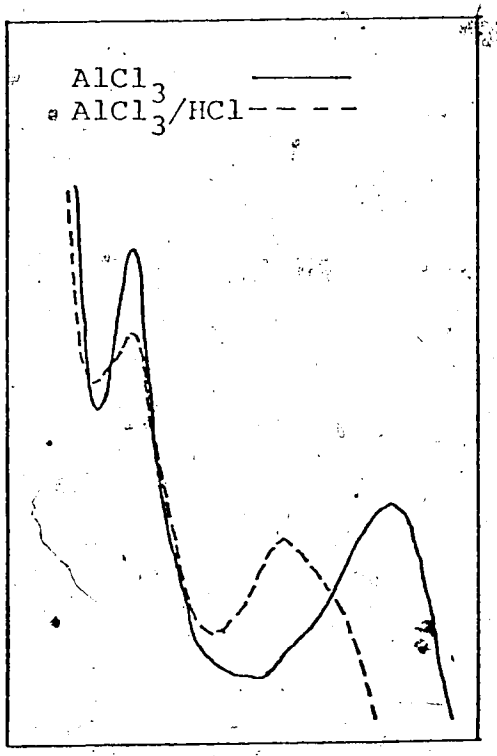
Spot Appearance: (UV) deep purple
(UV/NH_3) yellow-green

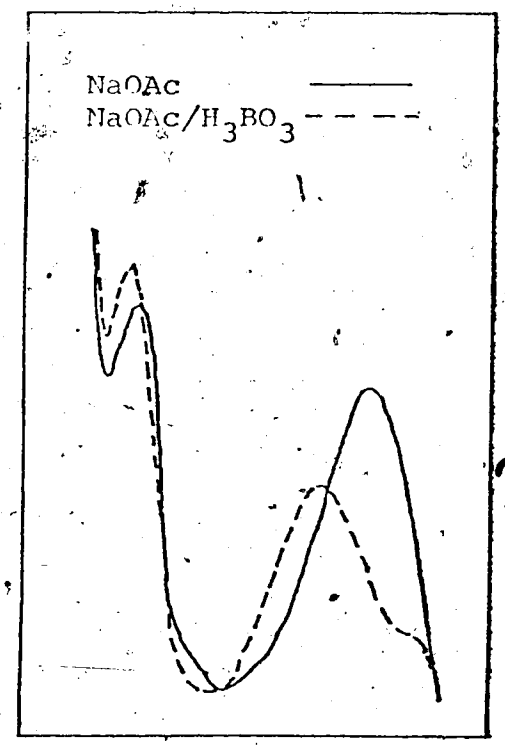
R_f Values: 0.60(BAW) 0.08(H_2O) 0.32(HoAc) 0.57(PhOH)

UV SPECTRAL DATA (nm)

MeOH	258, 274, 350
NaOMe	285, 336s, 414
$AlCl_3$	279, 335s, 425
$AlCl_3$/HCl	278, 364
NaOAc	274, 406
NaOAc/H_3BO_3	270, 378, 424s

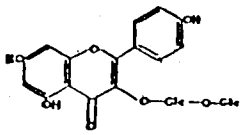






GURE 18. Chromatographic and spectral data for Kaempferol 3-O-sophoroside.

Kaempferol 3-O-sophoroside



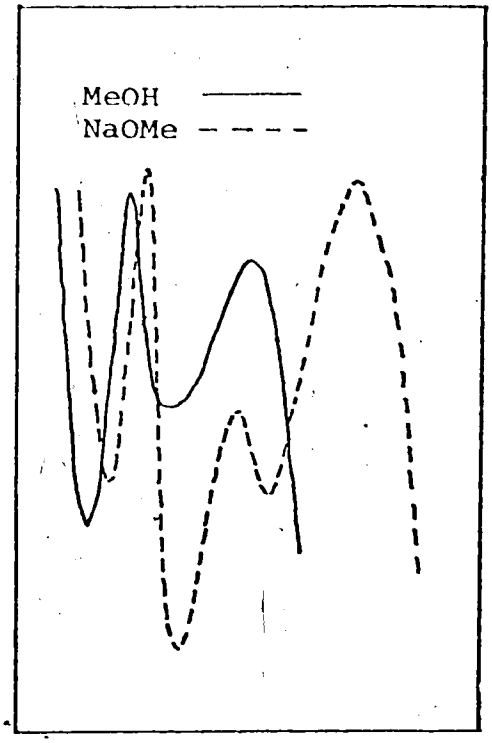
CHROMATOGRAPHIC DATA

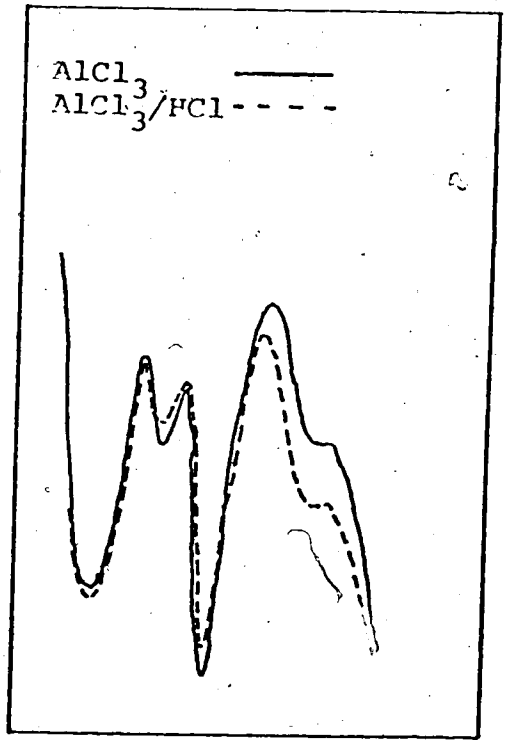
Spot Appearance: (UV) deep purple
(UV/NH$_3$) yellow-green

R_f Values: 0.51(BAW) 0.44(H_2O) 0.70(HOAc) 0.67(PhW)

UV SPECTRAL DATA

MeOH	273, 342
NaOMe	282, 335, 402
$AlCl_3$	282, 305, 353, 384
$AlCl_3$/HCl	282, 306, 348, 384
NaOAc	281, 309, 340s, 398
NaOAc/H_3BO_3	276, 312, 351





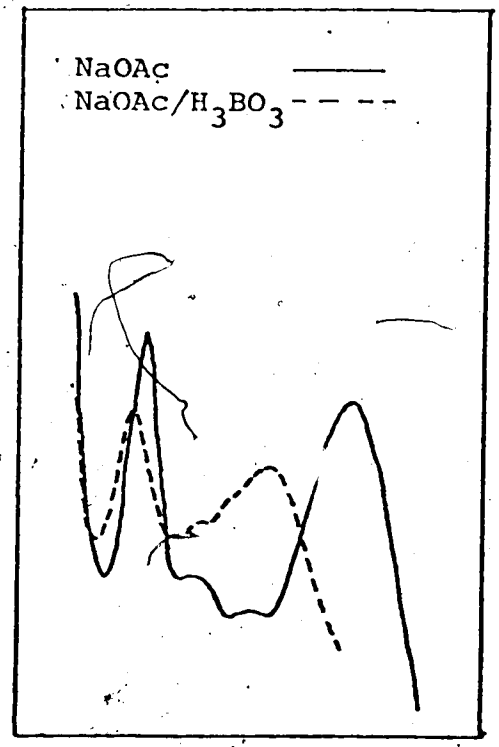


TABLE 6. Collections used in flavonoid analysis of the three subspecies of *Minuartia rossii*.

Subspecies *columbiana:*

Alberta: *W.J. Elis[illegible]* #79 Hailstone Butte, Kananaskis Forestry Rd., July 16/75; *SJW* #106 Prospect Mt., Mt. Park, June 20/75; *SJW* #124 Cardinal River Divide, Mt. Park, June 23/75; *SJW* #228 [illegible]thew Mt., Waterton Park, Aug. 16/75; *SJW* #229 Goat Lak[illegible]ark, Aug. 17/75; *SJW* #230 Nanton-Kananaskis Forestry Rd [illegible]. 18/75; #231 Highwood Pass, Kananaskis Forestry Rd., Aug. 18/75; *SJW* #235 Sunshine Village, Banff Park, Aug. 20/75; *SJW* #240 Signal Mt., Jasper Park, Aug. 28/75.

Montana: *SJW* #200 Beartooth Pass, Aug. 12/75; *SJW* #213 Goat Flats, Deerlodge Cty., Aug. 14/75; *SJW* #219 Choteau Mt., Teton Cty., Aug. 15/75

Subspecies *elegans:*

Alaska: *SJW* [illegible]50 McKinley Park, July 14/75; *SJW* #250 Mi. 12.5 Denali Highway, June 25/76; *SJW* #253 Mi. 108 Steese Highway, June 29/76; *SJW* #263 Mi. 307 TAPS Highway, July 3/76; *SJW* #282 Atigum Pass, Brooks Range, July 4/76.

Alberta: *J. Tande* Adam's Creek, Willmore Wilderness Park.

British Columbia: *SJW* #191 Summit Lake, July 27/75

Yukon: *SJW* #163 Southern Ogilvie Mts., 64 18'N, 137 20'W, July 20/75; *SJW* #183 Mi. 95.6, Dempster Highway, July 25/75; *SJW* #287 Mi. 57, Demster Highway.

Subspecies *rossii:*

Alaska: *SJW* #272 Prudhoe Bay, July 4/76; Northwest Territories: *P.A. Addison*, Resolute Bay, Cornwallis Island.

CHAPTER 4

DISCUSSION

Results of the present investigation of *Minuartia rossii* support the recognition of three closely related yet morphologically distinct taxa. Cytological, chemical, phytogeographical and breeding system data also corroborate the recognition of three taxa. The calciphilous habit and uniflorous inflorescence shared by the three taxa indicates that they are closely related.

Maguire (1958) described clinal modifications in *Minuartia rossii* which, he noted, take place in both westerly and southerly directions, and that proceeding from eastern to western populations, the sepals become acute; the petals narrower and shorter, and the leaves become less fleshy. Maguire (l.c.) also noted that southward the sepals become smaller and broader; the petals are inconspicuous or lacking, and the leaves remain more or less fleshy. Although the three taxa were found to differ in several characters of the leaves, sepals and petals, these differences were found to be taxon specific rather than clinal.

Subspecies *rossii* is a densely pulvinate plant occupying moist habitats throughout the North American arctic. It is distinguished by its small, purple, ovate, one nerved sepals; very small, fleshy, imbricate leaves; its rather long obovate petals and its largely sterile condition. Subspecies *elegans* is a loosely tufted plant of arctic and alpine Alaska, the Yukon and northeastern British Columbia. It is distinguished by its purple, ovate-lanceolate, weakly three nerved sepals; long, linear, ascending leaves and oblong petals which are as

long as the sepals. Subspecies *columbiana* is a caespitose plant of xeric alpine habitats of the front ranges of the northern and central Rocky Mountains. It has green, lanceolate, strongly three nerved sepals; somewhat fleshy, spreading leaves and is commonly apetalous.

Cytological evidence also supports the view that the *Minuartia rossii* complex is composed of three closely related taxa. All three taxa were found to possess a basic chromosome number of x=15. Subspecies *columbiana* has a chromosome number of 2n=30, subspecies *rossii* has 2n=60 and subspecies *elegans* has both 2n=30 and 2n=60. Although Briggs and Walters (1969) have noted that strict autopolyploids are relatively rare in nature, the tetraploid ssp. *elegans* is almost certainly derived from the diploid since no morphological differences between the two cytotypes were observed. Neither Favarger (1960, 1965) nor Baad (1969) observed any morphological differences between cytotypes of several species of *Arenaria*. Further evidence to support the autoploid derivation of the tetraploid from the diploid is that both cytotypes were found to possess identical flavonoid profiles. Flavonoids have been used extensively in detecting hybridization (Harborne, 1975) and if the tetraploid were an allopolyploid, one would expect some chemical differences to be evident.

The chromosome number of 2n=58 reported by Zukhova (1966) and confirmed in a later paper, Zukhova *et al.* (1973), for subspecies *rossii* from Wrangel Island is presumed to be derived via aneuploid reduction from the tetraploid 2n=60. Solbrig (1970) reports that reduction in chromosome number by fusion of chromosomes is the most common type of aneuploidy. Alternatively, the tetraploid could have lost two chromosomes, this phenomenon has been referred to as polyploidy drop by Grant

(1971). Since the tetraploid already possessed a double complement of chromosomes, the loss of two chromosomes could easily be tolerated.

The flavonoid profile of *Minuartia rossii* is unusual, being characterized by a combination of flavonols, acylated flavonols and C-glycoflavones. The kaempferol and quercetin glycosides of the species are relatively common, being found in numerous unrelated taxa (Harborne and Williams, 1975). In fact, quercetin and kaempferol glycosides are so widely distributed in flowering plants that Harborne (1975) considers their *absence* in a taxon to be of great significance. Since Bate-Smith (1962) found neither quercetin nor kaempferol in the species of *Arenaria* surveyed, the presence of these compounds in *Minuartia rossii* may be further justification for separating *Minuartia* from *Arenaria*. However, further chemical investigations of these two genera would be needed before making such a distinction solely on chemical grounds.

The acylated flavonol kaempferol 3-p-coumaroylglucoside is a relatively rare compound, being reported from *Tilia argentia* (Horhammer *et al.*, 1961) and *Pteridium aquilinum* (Wang *et al.*, 1973). This compound consists of a phenolic acid (p-courmaric acid) bound via an oxygen atom to the glucose molecule of kaempferol 3-O-glucoside. The presence of this compound in all three subspecies of *Minuartia rossii* indicates that they are very closely related because of shared enzyme systems and pathways involved in its synthesis.

Hegnauer (1964), Mabry *et al.* (1972) and Chopin and Bouillant (1975) have shown that many members of the Caryophyllaceae contain C-glycoflavones, particularly as glycosides of apigenin. Harborne (1972) has suggested that the distribution of C-glycoflavones supports the idea that they are primitive relicts, since they are present more in woody

families than herbaceous ones. Harborne (l.c.) suggested the possible evolutionary series: flanonol → C-glycoflanone → flavone. Swain (1975) however, considers flavonols and C-glycoflavones to be derived from the more simpler flavones. Chopin and Bouillant (1975) have shown that large numbers of C-glycoflavones are found in the more advanced angiosperm families, *e.g.* Leguminosae, Compositae and Umbelliferae. Swain (1975) has concluded that biochemically, the Caryophylidae is the most recently evolved sub-class of the angiosperms. The presence of many C-glycoflavones in the Caryophyllaceae may indeed be evidence that it is more advanced than previously thought.

The four C-glycoflavones found in *Minuartia rossii* have proved to be of great taxonomic interest. All four compounds were found to be isovitexin (apigenin 6-C-glucoside) derivatives. Several isovitexin derivatives have been reported in other members of the Caryophyllaceae (Hegnauer, 1964). Of particular interest are the studies of van Brederode and van Nigtevecht (1972, 1973, 1974) on the genetics of isovitexin glycosylation. These studies provide a possible mechanism for the production of the isovitexin glycosides found in *Minuartia rossii*. Glycosylation is controlled by several genes: gene G controls the transfer of glucose to the 7 position, gene A controls the transfer of arabinose to the 6-carbon bound glucose and gene Fg controls the transfer of glucose to the 6-carbon bound glucose. Several other genes were also shown to transfer other sugars to the 6 and 7 positions on the molecule.

The genes A and Fg however, would not be adequate to produce the triglucosides found in *Minuartia rossii*. If these two genes produced the triglycosides in a sequential manner, then one would expect

to find the intermediate diglycosides in the leaves also. A more plausible explanation would be that two other genes may be present which transfer glucose-glucose and arabinose-glucose complexes to the 6 position.

The flavone apigenin 6-C-arabinosylglucosyl-7-O-glucoside has been shown to be a taxonomic marker in *Minuartia rossii*, being present in ssp. *rossii* and *elegans* and absent in ssp. *columbiana*. Van Brederode and van Nigtevecht (1973) have shown that the formation of this compound from apigenin 6-C-glucoside is controlled by two genes. Gene A binds arabinose to the 6 position and gene Fg binds glucose to the 7 position. It can, therefore, be postulated that ssp. *columbiana* lacks gene G since it does not possess the 7-substituted flavone.

Van Brederode and van Nigtevecht (1972) reported that petal development in *Melandrium album* was correlated with 7 position glycosylation. They found that plants which possess an isovitexin 7-O-glucoside had well developed petals while those that lacked the 7 position sugar had very reduced petals. Results of the present investigation show no such correlation, since members of subspecies *elegans* with reduced or absent petals possess the 7-O glycoside. It can, therefore, be concluded that the 7-O-glucoside is taxon specific, being present in ssp. *rossii* and *elegans* and absent in ssp. *columbiana*. Thus the presence of the flavone apigenin 6-C-arabinosylglucosyl-7-O-glucoside correlates well with the cytological and morphological recognition of subspecies *columbiana* as a taxonomically distinct taxon.

The breeding systems of *Minuartia rossii* provide further evidence that this species is composed of more than one taxon. All three subspecies were found to be gynodioecious, however Radford *et al.*

(1974) have noted that this is a very common condition within the Caryophyllaceae. Likewise all three subspecies exhibit pronounced protandry, but as Baad (1969) noted this is also common in arenarias. Both the gynodioecious condition and protandry may be taxonomically without significance.

The production of bulbils is, however, taxonomically significant in *Minuartia rossii*. Simmons (1906) observed that arctic specimens of *Minuartia rossii* rarely flower and that he had not seen any fruits or seeds. He supposed that the plants must flower and ripen seed in some years, "....as it has no other means of propagation". Sorensen (1933) however, noted that the species propagates vegetatively by easily detached bulbils which, he noted, were probably carried along by streams of meltwater in the spring. Schischkin (1936) noted that subspecies *elegans* also possess small fascicles of leaves in the axils of the primary leaves.

Results of the present investigation have shown that all three subspecies of *Minuartia rossii* possess small fascicles of leaves in the axils of the primary leaves. It has been further shown that these fascicles of leaves function as vegetative propagules only in subspecies *rossii*. The 'propagules' of both ssp. *elegans* and *columbiana* were shown to be an ineffective means of vegetative reproduction, *i.e.* they do not detach readily in nature and they show very limited viability even under very advantageous artificial conditions. Subspecies *rossii*, on the other hand, exhibits almost total reliance on vegetative reproduction. It very rarely flowers and virtually never develops fruits or seeds. The presence of bulbils is, therefore, a good taxonomic character which can be used, along with morphological, cytological and

chemical characters, to distinguish ssp. *rossii* from ssp. *elegans* and ssp. *columbiana*.

Nannfeldt (1954) noted that the type specimen of *Minuartia rossii* did not possess bulbils, but instead had numerous well developed flowers. He therefore concluded that Richardson (1823) had based his description of *Minuartia rossii* on a dwarf specimen of *Minuartia stricta* (SW) Hiern. and therefore proposed the name *Minuartia rolfii* for this species. However, the type sheet of *Minuartia rossii* from Richardson's herbarium (*Arenaria rossii* R. Brown, Coast, BM) contains six specimens all of which are abundantly flowering, possess numerous vegetative propagules and are referable to this species. Examination of the type specimen of *Minuartia rolfii* (Simmons 2390, Ellesmereland, O) has revealed that it also is *Minuartia rossii* and the name *Minuartia rolfii* is therefore synonymous with *Minuartia rossii*.

The distribution of *Minuartia rossii* has been a subject of much misinterpretation. Its distribution has usually included Washington (Hitchcock *et al.*, 1964), California (Munz, 1968) and Colorado (Hitchcock *et al.*, 1964; Rydberg, 1906). Examination of herbarium material has revealed that *Minuartia rossii* does not occur in either California, Washington or Colorado. The specimens Munz (1968) reports from Mono Mesa and Tulare Counties, California (V. Duran 2829, UC, WTU and C. Sharsmith 3391B, UC) are *Minuartia stricta* and can be recognized by their long, bracteate, branching inflorescence. These specimens were also collected on granite rather than the limestone habitat *Minuartia rossii* normally occupies.

It is evident from herbarium specimens (*e.g.* J.W. Thompson 7433, Olympic Mountains, UC, WTU; W. Muenschen 10281, Whatcom County,

WTU) and from Hitchcock *et al.* (1964) illustration of *Minuartia rossii* that the reports of this species from Washington are erroneous. No reports of *Minuartia rossii* occurring in Washington have been substantiated by the present author. Likewise, no reports of *Minuartia rossii* from Colorado have been confirmed, such specimens as Hultén and Weber 11054A, Hoosier Ridge, COLO are also *Minuartia stricta*.

Minuartia rossii is a pronounced calciphile and its present range appears to be the result of this very specific habitat preference. The species' occurrence in calcareous areas is well documented, *e.g.* Alaska (Johnson and Packer, 1968; Jordal, 1951), the Canadian Arctic Archipelago (Porsild, 1955), Greenland (Gelting, 1934) and Montana (Bamberg and Major, 1968). As expected, the species does not occur in the non-calcareous mountains of California or Washington. The only calcareous region of either Washington or Oregon is the Wallowa Mountains, Oregon where there are occasional outcrops of limestone (Franklin and Dyrness, 1973). This is consistent with the few records of subspecies *columbiana* from this region. Likewise, the only substantiated report of *Minuartia rossii* from Utah (B. and K. Harrison 10926, Unita Mountains, BRY) is attributable to the calcareous nature of this region. The calciphilous habit shared by the three subspecies of *Minuartia rossii* is therefore an indication of their close relationship and accounts for the restriction of subspecies *columbiana* to the calcareous front ranges of the Rocky Mountains.

The principally North American distribution of *Minuartia rossii* as well as the allopatric distribution of its three subspecies has generated considerable interest in the historical factors which may have caused such distributional patterns (Mattfeldt, 1922; Hultén, 1937;

Johnson and Packer, 1968). The present investigation has shown that the *Minuartia rossii* complex is composed of three morphologically and geographically distinct taxa which share certain cytological (x=15) and chemical characters. This suggests that while the three taxa are closely related they have had different histories. Mattfeldt (1922) suggested that *Minuartia rossii* was part of a group of plants from northeast Asia that migrated to North America during the Tertiary. He hypothesized that ssp. *elegans* and *rossii* became differentiated as they spread out to the arctic and Rocky Mountains. The present distribution of the *Minuartia rossii* complex, as well as its cytological condition suggests that the differentiation of the three taxa is correlated with the Pleistocene glaciations.

Stebbins (1971) has noted that polyploidy is a largely irreversible process, it can therefore be assumed that the tetraploid (2n=60) members of *Minuartia rossii* are derived from the diploids (2n=30). The present investigation has shown that ssp. *columbiana* lacks a specific gene for the glycosylation of isovitexin at the 7 position. Since the loss of a single gene is much more probable than a gain (Davis and Heywood, 1963), it can reasonably be concluded that the diploid ssp. *columbiana* has probably been derived from a diploid ssp. *elegans*. Since ssp. *rossii* and *elegans* share the same flavonoid profiles and the former is composed only of tetraploids, it can be concluded that ssp. *rossii* is probably derived from ssp. *elegans*. It appears then, that ssp. *columbiana* and ssp. *rossii* have been derived from the ancestral ssp. *elegans*.

Stebbins (1971) has concluded that the majority of polyploids have distribution patterns which suggest Pleistocene or more recent

origin. In North America Randawa and Beamish (1972) have shown that the diploids of *Saxifraga ferruginea* are restricted to areas south of the Pleistocene glaciers, while polyploids are confined to glaciated areas. This has been frequently observed in Europe for many other taxa. Stebbins (1950), in discussing the distribution of three taxa of a polyploid complex of *Iris*, has noted that the diploids are restricted to unglaciated areas of Alaska. The results of these studies indicate that the diploids tend to be restricted to unglaciated areas, either south of the maximum extent of glaciation or within unglaciated refugia while polyploids usually occupy glaciated areas. The same conclusion is maintained by Stebbins (1971) in a more recent publication.

A map depicting the maximum extent of the Wisconsin glaciation in North America is presented in Map 5. The present distribution of the two cytotypes of ssp. *elegans* (Map 4, Page 39) indicates that, in general, the diploids are restricted to the unglaciated Beringian region while the polyploids are found primarily in glaciated areas. The survival of large numbers of plants *in-situ* in the Alaska-Yukon region is well documented (Hultén, 1937; Johnson and Packer, 1967). The present southerly distribution of the diploid ssp. *columbiana* indicates that it probably existed south of the Pleistocene glaciers and possibly in known glacial refugia such as Mountain Park, Alberta (Packer and Vitt, 1974).

Stebbins (1971) has noted that, in general, polyploids are more aggressive than diploids and as a result, as polyploid complexes become older, the diploids become more restricted in geographical distribution. Likewise, Johnson and Packer (1965) have shown that polyploids are at a selective advantage in habitats which have been

MAP 5. Approximate maximum extent of Wisconsin glaciation in North America and Greenland (Gelting, 1934; Can. Geol. Surv.; 1968 Coulter *et al.*, 1962).

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GOODE BASE MAP SERIES

subjected to frequent and drastic fluctuations in climatic and edaphic factors. The distribution of the cytotypes of ssp. *elegans* appears to confirm this aggressiveness or selective advantage of polyploids over diploids, the polyploids have migrated out considerably from the central Alaska-region while the diploids seem to have extended their range only very slightly. Stebbins (1971) has noted that vegetative reproduction is very often correlated with polyploidy. The apparent lack of a diploid race of ssp. *rossii* may be the result of the diploid ancestor being out competed by the more aggressive tetraploids and/or the superiority of vegetative reproduction in the short arctic growing season.

The results of the present investigation have suggested the following historical sketch of the *Minuartia rossii* complex. Prior to the Pleistocene glaciations, a single ancestor of the complex probably occupied much the same range in North America as at present. This hypothetical ancestor was probably most similar to subspecies *elegans* and was diploid. As the ice sheets covered North America, populations of this ancestor became isolated in three major areas: both north and south of the ice and in Beringia. The center of the formation of the ice was in the Kewatin District, N.W.T. (A. Löve, 1959). As the ice moved northward it isolated the precursor of ssp. *rossii* in the high arctic. Known unglaciated areas of the arctic include a large part of Banks and Ellesmere Islands (Can. Geol. Surv., 1968), northern Greenland (Gelting, 1934) and Spitzbergen (Nannfeldt, 1954). Presumably the short growing season of these high arctic refugia would cause a shift in selection pressures to favor the vegetative reproduction characteristic of subspecies *rossii*. The present distribution and reproductive strategy of ssp. *rossii* indicate that it probably existed in refugia in the high

arctic during the Pleistocene from where it then migrated out upon retreat of the ice. Indeed, several workers have proposed such high arctic refugia (Porsild, 1955; A. Löve, 1959; D. Löve, 1959).

The *in situ* survival of ssp. *elegans* in the Beringian region is almost axiomatic. The presence of two chromosome races in this taxon and the restriction of the diploid race to unglaciated areas is strong evidence for its survival in Beringia during the Pleistocene.

The present southerly distribution of ssp. *columbiana* as well as its uniform diploid condition, indicates that it probably existed south of the ice margins and possibly in known glacial refugia such as Mountain Park, Alberta (Packer and Vitt, 1974) and Waterton Park, Alberta (Packer, 1971).

CHAPTER 5

CONCLUSIONS

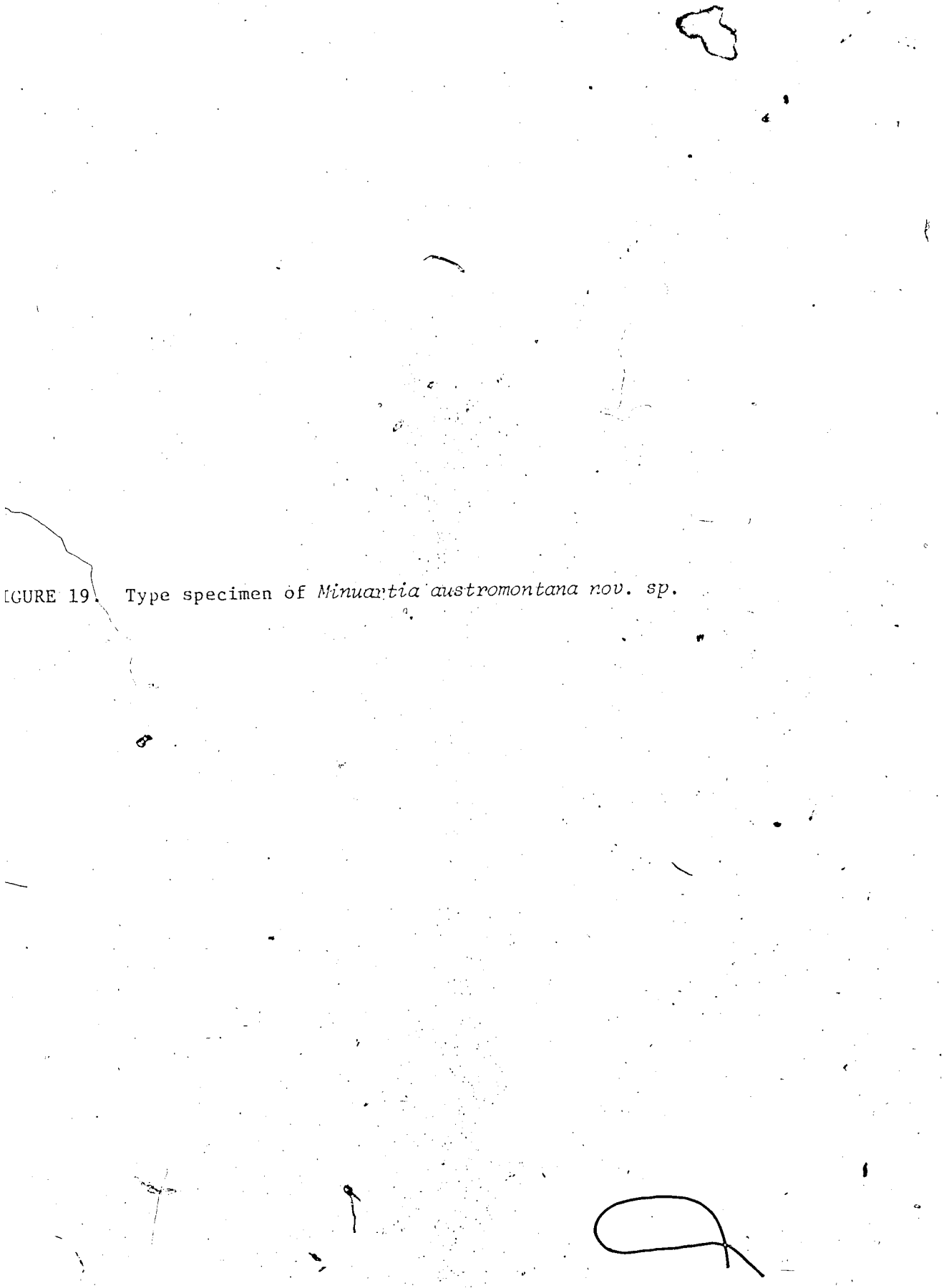
The present investigation has demonstrated that the *Minuartia rossii* complex is composed of three morphologically distinct taxa. Chemical, cytological, breeding system and phytogeographical data also support this conclusion. The differentiation of these taxa has been shown to be largely the result of isolation caused by the Pleistocene glaciations. Characters which distinguish the three taxa are summarized in Table 7. Maguire (1958) referred to the taxa as subspecies of *Minuartia rossii*; however, Davis and Heywood (1963) have noted that subspecies are distinguished by several small and usually quantitative differences, but these characters can break down individually. Davis and Heywood (l.c.) have noted that the morphological-geographical species concept is the most practical and takes into account all available evidence including morphology, chemistry, cytology, geography, etc.; but insists that the species so recognized must be delimitable by morphological characters. Reference to Table 7 shows that the three taxa of the *Minuartia rossii* complex are morphologically distinguishable on several characters and that the chemical, cytological and geographical characters corroborate the morphological data. Therefore, it seems appropriate to recognize the three taxa at the specific level. This practice has in the past been employed by several taxonomists who recognize both *Minuartia elegans* and *Minuartia rossii* for ssp. *elegans* and *rossii* (Schischkin, 1936; Nannfeldt, 1954; Hultén, 1958). It is recommended by the present author therefore that ssp. *rossii* and ssp.

TABLE 7. Comparison of characters of the three subspecies of *Minuartia rossii* (R. Br. *ex* Richards.) Graebn

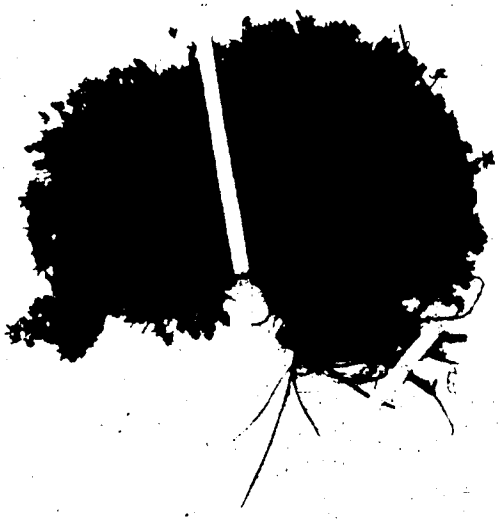
	rossii	*elegans*	*columbiana*
Habit	Pulvinate	loosely tufted	caespitose
	3-8(10)	5-20(30)	3-15
[illegible]	purple	purple	green
length (mm)	1.5-2.5	2-4	2-3
shape	oblong-ovate	ovate-lanceolate	linear to lanceolate
apex	obtuse to acuminate	acute	acute
venation	1-nerved	weakly 3-nerved	strongly 3-nerved
Petals - shape	obovate to spatulate	oblong to obovate	linear to oblong
size	1.5-2X calyx length	equal to calyx (sometimes lacking)	usually lacking (shorter than calyx)
Pedicel length (mm)	5-20	10-40	5-15
length (mm)	2-4	3-10	3-6
Leaves - shape	trigonous, subulate	linear, plane	subulate
position	imbricate	ascending	spreading to ascending
Bubils	present	absent	absent
Apigenin 6-C arabinosyl-glucosyl-7-0-glucoside	present	present	absent
Chromosome number (2n)	60	30, 60	30
Habitat	moist arctic	mesic arctic-alpine	xeric alpine
Distribution	high arctic North America	arctic-alpine Alaska-Yukon northeast British Columbia	northern and central Rocky Mountains

elegans be treated as *Minuartia rossii* (R. Br. ex Richards.) Graebn. and *Minuartia elegans* (Cham. and Schlecht.) Schischk. respectively. However, with respect to ssp. *columbiana*, this epithet cannot be used for the Rocky Mountain taxon of *Minuartia rossii* when recognized as a species. Examination of the type specimen of ssp. *columbiana* (J. Norman Henry 262, pass north of Robb Lake, B C., GH) has revealed that it is *Minuartia elegans*! The sepals are 3 mm long, purple, ovate-lanceolate, acute and weakly three nerved; the petals are oblong and equal to the sepals and the leaves are ascending. Subspecies *columbiana* is therefore a synonym of *Minuartia elegans*. In fact, ssp. *columbiana* has never been given formal taxonomic recognition. In view of this, the use of its epithet at the species level for the Rocky Mountain component of the *Minuartia rossii* complex would be extremely confusing. The present author proposes the name *Minuartia austromontana* for this taxon (type specimen A.J. Breitung 16415, summit of Mt. Lineham, Alberta, July 21, 1953, ALTA; Figure 19).

The distributions of the three recognized species of the *Minuartia rossii* complex are presented in Map 6.



IGURE 19. Type specimen of *Minuartia austromontana nov. sp.*

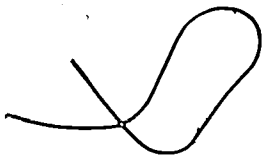


FLORA OF WATERTON LAKES NATIONAL PARK
ALBERTA, CANADA

Arenaria lanuginosa (Michaux.) Rohrb.

Summit of Mt. Lineham
Elev. 8800 feet.
July 21, 1923.
Shores.

Coll. August J. Rehring. No. 10215.



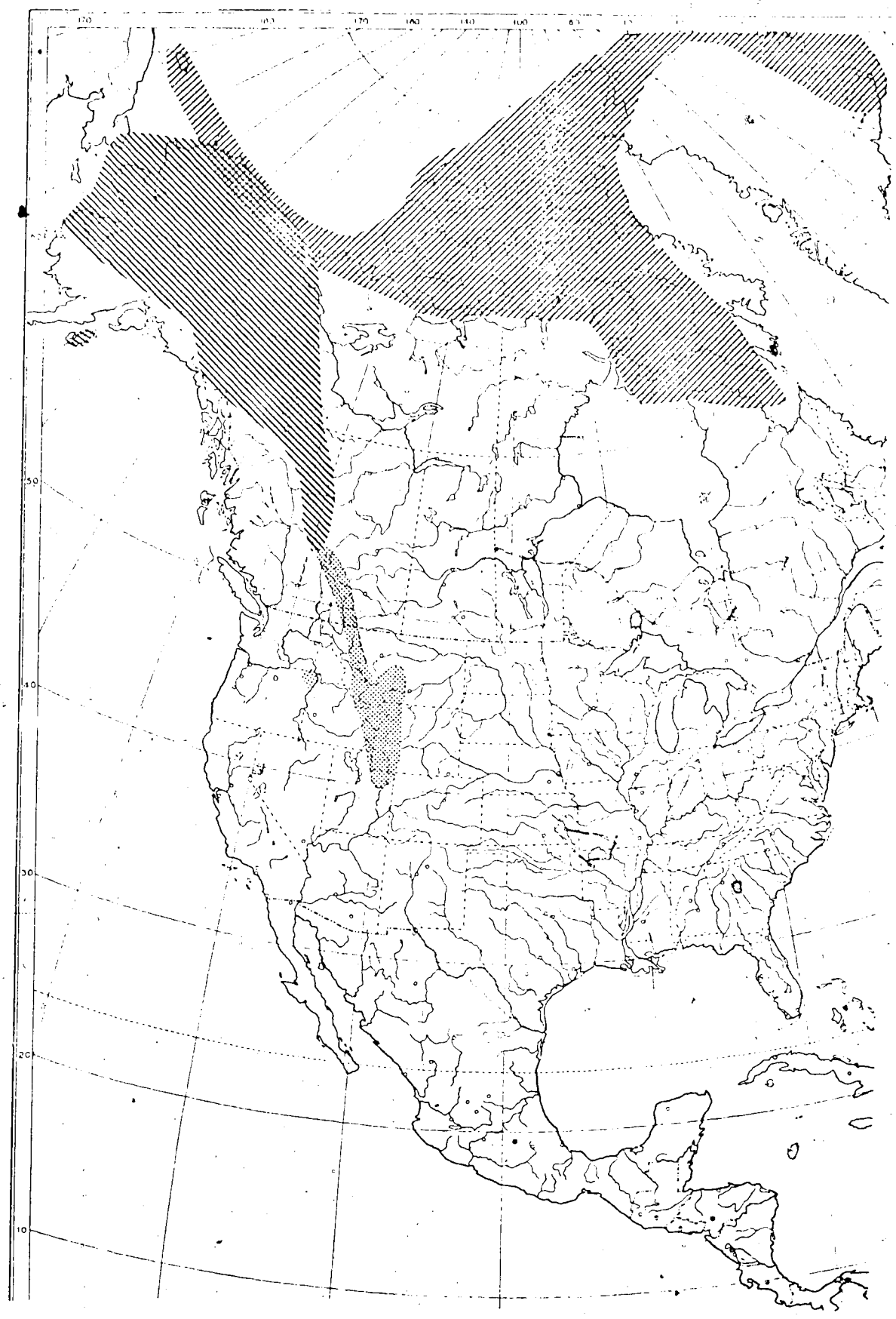
MAP 6. Distribution of the three species of the *Minuartia rossii* complex.

 - *Minuartia rossii*[10]

 - *Minuartia elegans*

 - *Minuartia austromontana*

[10]range also includes Spitzbergen


50
40
30
20
10

Synopsis of the *Minuartia rossii* complex

Plants mostly sterile; leaves imbricate, 2-4 mm long; sepals oblong-ovate, obtuse to acuminate, 1.5-2.5 mm long, one nerved; petals obovate to spatulate, conspicously surpassing the sepals; densely pulvinate plants of Arctic North America, Greenland, Spitzbergen and eastern Siberia..... *Minuartia rossii*

Plants rarely, if ever, sterile; leaves spreading to ascending, 3-10 mm long; sepals ovate-lanceolate to linear, acute, 2-4 mm long, three nerved; petals oblong to linear, equaling or shorter than the sepals or absent; caespitose to loosely tufted plants of arctic-alpine eastern Siberia, Alaska-Yukon and southward in the Rocky Mountains to Wyoming.

Sepals purple, ovate-lanceolate; petals oblong to obovate, equaling the sepals; leaves linear, plane; loosely tufted plants of arctic-alpine eastern Siberia, Alaska-Yukon and southward in the Rocky Mountains to central Alberta.., Alberta..... *Minuartia elegans*

Sepals green, linear to lanceolate; petals mostly lacking, linear to oblong, shorter than the sepals; leaves subulate, fleshy; caespitose alpine plants of the front ranges of the Rocky Mountains, central Alberta through Wyoming; eastern Oregon; northern Utah..... *Minuartia austromontana*

Minuartia rossii (R. Br. *ex* Richards.) Graebn., *Arenaria rossii* R. Br. *ex* Richards., *Alsine rossii* Richards. Fenzl, *Alsinopsis rossii* (Richards.) Rydb., *Arenaria rossii* Richards. var. *daethiana* Polunin, *Minuartia rolfii* Nann., *Alsinanthe rossii* (Richards.) Löve and Löve.

Plants densely pulvinate to loosely tufted, 3-8(10) cm broad, often purplish; sepals purple, 1.5-2.5 mm long, oblong-ovate, obtuse to acuminate, keeled, one nerved; petals obovate to spatulate, obtuse, from one and a half to twice as long as the sepals; pedicels 5-20 mm long (almost lacking in densely pulvinate forms); leaves 2-4 mm long, fleshy, trigonous, keeled, subulate, obtuse, imbricate; rarely flowering; reproducing vegetatively by small globular fascicles of leaves in the axils of the primary leaves; capsules as long as the sepals, very rare;

chromosome number 2n=60; inhabits moist depressions high Arctic North America, eastern Siberia, Greenland and Spitzbergen.

Holotype: *Arenaria rossii* R. Brown, Coast, *Richardson* (BM).

Minuartia elegans (Cham. and Schlecht.) Schischk., *Arenaria elegans* Cham. and Schlecht., *Alsine elegans* (Cham. and Schlecht.) Fenzl, *Arenaria rossii* Richards. var. *columbiana* Raup, *Arenaria rossii* Richards. ssp. *elegans* (Cham. and Schlecht.) Maguire, *Arenaria rossii* Richards. ssp. *columbiana* (Raup) Maguire, *Alsinanthe elegans* (Cham. and Schlecht.) Löve and Löve.

Plants loosely tufted, 5-20(30) cm broad, often purplish; sepals purple, 2-4 mm long, ovate-lanceolate, acute, somewhat keeled, weakly three nerved; petals oblong to obovate, obtuse to emarginate, equal to or shorter than calyx, sometimes rudimentary or lacking; pedice 1-4 cm long; leaves 3-10 mm long, linear, obtuse, ascending, small leafy fascicles present in the axils of primary leaves; capsule as long as calyx; chromosome number 2n=30 and 2n=60; inhabits mesic arctic and alpine areas of eastern Siberia, Alaska, the Yukon and central Alberta.

Holotype: St. Lawrence Bay, Chuckchi Pensinsula *Chamisso* and *Schlechtendal* (LE).

Minuartia austromontana nov. sp.[9]

Plants caespitose, 3-15 cm broad; sepals green, 2-3 mm long, linear to lanceolate, acute, strongly 3-nerved, sometimes scarious margined; petals usually lacking or rudimentary, linear to oblong, shorter t sepals; pedicels 5-15 mm long; leaves 3-6 mm long, somewhat fleshy and keeled,

[9]to be validly published at a later date.

subulate, obtuse, spreading to ascending; small leafy fascicles sometimes present in axils of primary leaves, capsule as long as calyx, chromosome number 2n=30; inhabits xeric alpine areas principally in the front ranges of the Rocky Mountains, central Alberta through Wyoming; northern Utah and northeastern Oregon.

Holotype: Mt. Lineham, Alberta, July 21, 1953, *A.J. Breitung* 16415 (ALTA).

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APPENDIX

REPRESENTATIVE SPECIMENS

Minuartia rossii (R. Br. *ex* Richards.) Graebn.

Alaska: Prudhoe Bay, *E. Schofield and M. Williams* P-G16 (ALA); Kurupa River, *A.R. Hodgdon* 8510 (GH).

Greenland: Dragon Point, *T. Wulff* (CAN, GH); Kong Oscars Fjord, *H.M. and L.G. Raup and T. Washburn* 693 (GH); Ymer Island, *T. Sorensen* 3312 (CAN).

Northwest Territories: Resolute Bay, Cornwallis Island, *Beschel* 10695 (GH, NY); Hazard Inlet, Somerset Island, *D.B.O. Savile* 3616 (GH, NY); Arctic Bay, Baffin Island, *N. Polunin* 2587 (GH); South Bay, Southampton Island, *N. Polunin* 2282 (GH); Bernard River, Banks Island, *W.J. Maker and S. MacLean* 82 (RM); Albert Sound, *A.E. Porsild* 17384 (CAN); Isortog River, Baffin Island, *P.J. Webber* 635 (CAN); Hall Beach, Melville Peninsula, *P.J. Webber* 666 (CAN); Foxe Basin, Prince Charles Island, *W. K.W. Baldwin* 1939 (CAN); Ward Hunt Island, *R.L. Christie* 50 (CAN); Axel Heiberg Island, *Beschel* 11194 (CAN); Dundas Harbour, Devon Island, *N. Polunin* 2554 (CAN); Craig Harbour, Ellesmere Island, *N. Polunin* 872 (CAN); Coral Harbour, Southampton Island, *D.B.O. Savile and I. Kukkouen* 24234 (COLO); Devon Island, *P. Barrett* 710 (UBC); Ellesmere Island, *H.G. Simmons* 2390 (O).

Spitzbergen: Northern Svalbard, det. *P.F. Schelander* (S); *E. Anderson* (S); Wahlenbergsbay, *A.J. Malmgren* (S); Lommibay, *A.J. Malmgren* (S).

Wrangel Island: *Zhukova* (LE); *Zhukova and Petrovsky* (LE).

Yukon: Shingle Point, 68°56'N, 137°12'W, *J.A. Parmelee* 2775A (UBC).

Minuartia elegans (Cham. and Schlecht.) Schischk.

Alaska: upper Koujarok River, *C.B. Atwater* 1909 (GH); Anvil Hill, Nome, *A.E. and R.T. Porsild* 1335 (GH); Norton Sound, *A.E. and R.T. Porsild* 984 (GH, CAN); Teller, Port Clarence, *E. Scamman* 5481 (GH); Mi. 105 Steese Highway, *J. Trent* 96 (GH); Mastadon Dome, Miller House, *E. Scamman* 4824 (GH); Wiseman, *E. Scamman* 2247 (GH); Meade River, 45 Mi. S. of Pt. Barrow, *I.L. Wiggins* 12658 (GH, CAN); Mi. 12.5 Denali Highway, *M. Williams* 1644 (BRY); Sable Pass, McKinley Park, *A. and R. Nelson* 4080 (RM); Polychrome Pass, McKinley Park, *A. and R. Nelson* 3777 (RM); Marsh-fork River, 46 Mi. N.N.W. Arctic Village, *L. Hettinger* 824 (CAN); Eagle Summit, *E. LaPage* 23277 (CAN); Sheep Creek, White Mts., *O. Gjaerevoll* 456 (CAN); 5 Mi. S. of Eagle, *G. Smith* 2413 (CAN); Muldrow Glacier, Anderson Pass, *L.A. Viereck* 1400 (ALA, COLO); Ogotoruk Creek, *J.G. Packer* 2053 (COLO); Ukinyik Creek, Bering Strait, *L. Viereck and A. Bucknell* 4357 (COLO); Amara Lake, Kodiak Island, *E. Hultén* (S); Ogotoruk Creek, *J.G. Packer* 2329, 2178, 1284, 1963 (ALTA).

Alberta: Persimmon Range, Wilderness Provincial Park, *J.G. Packer* 3380, 3231B (ALTA).

British Columbia: Summit Pass, *H.M. and D.S. Correll* 10683 (GH); Mt. Selwyn, *H.M. Raup and E.C. Abbe* 3951 (GH, NY); Good Hope Lake, 2 Mi. N. of Cassiar, *K.I. Beamish, K. Wade and J. Pojar* 730376 (UBC).

Northwest Territories: Mi. 44E, Canol Rd., *W.J. Cody and R.L. Gutteridge* 7719 (ALTA, NY, GH, UBC); West Cache Creek, 68°15'N, 136°24'W, *S.L. Welsh and J.K. Rigby* 12073 (BRY); Brintell Lake, Mackenzie Mts., *H.M. Raup and J.H. Soper* 9655 (ALTA, GH, RM, NY, UBC); Richardson Mts., 68°N, 136°W, *A.E. Porsild* 6792 (CAN), Mi. 82E Canol Rd., *A.E. Porsild and A.J. Breitung*

11804 (CAN); Richardson Mts., 68°08'N, 136°28'W, *V.J. Krajina* 63071282 (UBC).

Siberia: St. Lawrence Bay, Chukchi Peninsula, *Chamisso and Schlectendal* (LE); Chukchi Peninsula, *Petrovsky* (LE).

Yukon: Kluane Lake, *H.M. and L.G. Raup* 12592 (GH); Mi. 57, Demster Highway, *R.T. Porsild* 224' (GH); Sam Lake, 68 34'N, 139 23'W, *S.L. Welsh and J.K. Rigby* 10397 (BRY); Mi. 105 Canol Rd., *A.E. Porsild and A.J. Breitung* 10891 (CAN); Mi. 83 Dempster Highway, *R.T. Porsild* 1523 (CAN); Herschel Island, *R. Wood* 146 (CAN); Mi. 1022 Alaska Highway, *W.B. Schofield and H.A. Crum* 7941 (UBC); Summit Lake, 67°42'N, 136°28'W, *J.G. Packer* (NY).

Minuartia austromontana nov. sp.

Alberta: Medicine Lake, Jasper Park, *E. Scamman* 2528 (GH); Crow's Nest Pass, *J. Macoun* 18270 (GH); Waterton Lakes, *A.S. Pease* 22570 (GH); Sulphur Mt., Banff Park, *S. Brown* 146 (GH, NY); Avion Ridge, Waterton Park, *S.B. Waite* 178 (BRY); Highwood Pass, *A.E. Porsild and J. Lid* 19351 (CAN); Sunshine Lodge, Banff, *A.E. Porsild and J. Lid* 19464 (CAN); Mt. Saskatchewan, Banff, *A.E. Porsild and A.J. Breitung* 16056 (CAN); Mt. Brett, Banff, *A.E. Porsild and A.J. Breitung* 13802 (CAN); Carthew Mt., Waterton Park, *T.M.C. Taylor* 8634 (UBC); Carthew Pass, Waterton Park, *A.J. Breitung* 16689 (NY); Whitehorse Creek, *J.G. Packer* 2802 (ALTA); Mountain Park, *J.G. Packer* 3049b (ALTA); Highwood Pass, *J.G. Packer* 1969-436 (ALTA); Mi. 89 Kananaskis Forestry Rd., *J.G. Packer* 1969-475 (ALTA); Avion Ridge, Waterton Park, *J.G. Packer* 3735 (ALTA); 10 Mi. S.W. of Cadomin, *M.G. Dumais* 4235a (ALTA); North Kootenay Mt., *J.G. Packer and G. Silberhorn* 1971-35 (ALTA).

Idaho: Mt. Borah, Custer Co., *C.L. Hitchcock and C.V. Muhlick* 10951 (WTU).

Montana: Piegan Pass, Glacier Park, *A.S. Pease and W.S. Drew* 132 (GH); upper Marias Pass, *J. Wauby* 43 (GH); Beartooth Pass, Carbon Co., *A. Cronquist* 8003 (NY, UC, GH, COLO); Siyeh Pass, Glacier Park, *L.H. Harvey and R.H. Pemble* 7146 (WTU); Black Lion Mt., Pioneer Range, *C.L. Hitchcock and C.V. Muhlick* 12908 (WTU); Pintlar Peak, *C.L. Hitchcock and C.V. Muhlick* 12860 (WTU); Shale Mt., Flathead National Forest, *C.L. Hitchcock* 18624 (WTU); Queener Peak, Granite Co., *K.H. Lackschewitz* 618 (MONTU); Mt. Baldy, Powell Co., *K.H. Lackschewitz* 6181 (MONTU); Choteau Mt., Teton Co., *K.H. Lackschewitz* 4428 (MONTU, NY); Goat Flats, Deerlodge Co., *K.H. Lackschewitz* 3043 (MONTU); Scapegoat Mt., Lewis and Clark Co., *J. Craighead* 50 (MONTU); E. Flattop Mt., Glacier Park, *S. Bamberg* 71 (COLO); Mt. Henry, Glacier Park, *R.H. Pemble and Harvey* 178 (MONTU); Black Lion Mt., Beaverhead Co., *C.L. Hitchcock and C.V. Muhlick* 12908 (NY).

Oregon: Wallowa Mts., *W.C. Cusick* 2299 (UC, GH); Hurricane Creek, Wallowa Mts., *M.E. Peck* 22576 (UC, OSC).

Utah: Black Fork, Uinta Mts., Summit Co., *B.F. and K. Harrison* 10926 (BRY).

Wyoming: Beartooth Range, Park Co., *P. Johnson* 131E (RM); Green River Lakes, Sublette Co., *E.B. and L.B. Payson* 4494 (RM).

TABLE 8. Chemical and spectral characteristics of flavonoid glycosides in the *Minuratia rossii* (R. Br. ex Richards.) Graebn. complex.

Compound	Colour UV/NH_3*	Rf's x 100 Solvents BAW	H_2O	15%HOAc	PhOH	U.V. Spectral Data MeOH BI	BII	NaOMe BI	NaOAc BII	$AlCl_3$ I	HCl I	H_3BO_3 I	Aglycone	Sugar and attachment
Kaempferol 3-p-Coumaroylglucoside	p,y	80	10	39	75	338	277	70	-1	15	-4	14	Kaempferol	3-O-glucose
Apigenin 6-C-glucoside	p,y	61	15	42	77	334	274	65	7	51	-1	14	Isovitexin	none
Apigenin 6-C-arabinosyldiglucoside	p,y	26	46	66	62	334	274	68	8	16	-4	12	Isovitexin	6-C-arabinose
Apigenin 6-C-triglucoside[1]	p,y	24	51	68	53	330	259	72	1	16	-2	28	Isovitexin	6-C-glucose
Apigenin 6-C-arabinosylglucosyl-7-O-glucoside	p,y	29	42	66	68	326	276	52	6	17	-3	16	Isovitexin	6-C-arabinose 7-O-glucoside
Quercetin 3-O-glucosylgalactoside	p,y	22	48	68	37	352	260	66	8	48	-42	26	Quercetin	3-O-glucose + galactose
Quercetin 3-O-sophoroside[2]	p,y	42	28	64	50	347	271	59	5	75	-70	17	Quercetin	3-O-glucose
Quercetin 3-O-glucoside	p,y	60	08	32	57	350	258	64	16	75	-61	28	Quercetin	3-O-glucose
Kaempferol 3-O-sophoroside[2]	p,y	51	44	70	67	342	273	60	8	11	-5	9	Kaempferol	3-O-glucose

*p, deep purple; y, yellow-green; (1) glycoside linkages undeter- ; (2) 2-β-glucosylglucoside (β1→2).