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CONTRIBUTION TO THE TAXONOMY OF *OXYTROPIS CAMPESTRIS* (L.) DC. IN NORTHWESTERN NORTH AMERICA

by

© WAYNE J. ELISENS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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EDMONTON, ALBERTA

FALL, 1978

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 Contribution to the Taxonomy of *Oxytropis campestris* (L.) DC. in North-western North America

submitted by Wayne J. Elisens

in partial fulfilment of the requirements for the degree of Master of Science.

(Supervisor)

Date July 7th, 1981

ABSTRACT

The *Oxytropis campestris* complex in northwestern North America is a polyploid series comprised of at least seven morphologically and geographically distinct taxa. In light of the data of the present study, the author proposes that five taxa be reelevated to species status (*O. cusickii* Greenm., *O. gracilis* (A. Nels.) K. Schum., *O. columbiana* St. John, *O. jordalii* Porsild, *O. varians* (Rydb.) K. Schum.) and that two taxa be recombined as subspecies: *O. gracilis* (A. Nels.) K. Schum. subsp. *dispar* (A. Nels.) Elisens and *O. jordalii* Porsild subsp. *davisii* (Welsh) Elisens.

Three different chromosome numbers are present in the complex and represent the tetraploid (2n=32), hexaploid (2n=48), and dodecaploid (2n=96) condition. Although three species have uniform chromosome numbers (*O. cusickii*, 2n=48; *O. jordalii*, 2n=32; and *O. columbiana*, 2n=48), two taxa, *O. varians* and *O. gracilis* subsp. *gracilis*, each exhibit two different chromosome numbers. No attempt to subdivide *O. varians* was undertaken since, with the exception of guard cell size, no differences were observed between hexaploid and dodecaploid representatives. At least two distinct entities may be present in *O. gracilis* subsp. *gracilis*. Although morphologically, cytologically (2n=32), and ecologically uniform

east of the continental divide, subsp. *gracilis* is quite variable in appearance and has a different chromosome number (2n=48) west of the divide.

The chemical data indicate that of the thirty-three different flavonoid glycosides characterized, the majority were restricted in their occurrence. Only eleven glycosides were present in two or more taxa reinforcing the morphological, cytological, and geographical distinctiveness of the taxa examined in the present study.

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TABLE OF CONTENTS

CHAPTER		PAGE
1	INTRODUCTION	1
2	MATERIALS AND METHODS	25
	Collections and Field Studies ..	25
	Cultivation	25
	Herbarium Studies	26
	Guard Cell Measurements	26
	Cytological Studies	27
	Chemical Studies	27
3	RESULTS	35
	Morphological and Phytogeographical Studies	35
	Cytological Studies	35
	Guard Cell Measurements	43
	Chemical Studies	49
4	DISCUSSION AND CONCLUSIONS	138
LITERATURE CITED		187
APPENDIX		192

LIST OF TABLES

Table	Description	Page
1	Classification of the *Oxytropis campestris* (L.)DC. complex	19
2	Diagnostic characters of the taxa in the *Oxytropis campestris* (L.)DC. complex	20
3	Reported chromosome counts of *Oxytropis campestris* (L.)DC. in northwest North America	22
4	Comparative morphological characters in the *Oxytropis campestris* (L.)DC. complex	36
5	Chromosome counts for the *Oxytropis campestris* (L.)DC. complex	37
6	Collections of which chromosome counts are based	40
7	Statistical comparison of guard cell lengths between ploidy levels	44
8	Herbarium specimens from which chromosome numbers have been determined	45
9	Flavonoid glycosides of *Oxytropis campestris* var. *cusickii*	51
10	Flavonoid glycosides of *Oxytropis campestris* var. *gracilis*	53
11	Flavonoid glycosides of *Oxytropis campestris* var. *jordalii*	55
12	Flavonoid glycosides of *Oxytropis campestris* var. *varians* 2n=48	57
13	Flavonoid glycosides of *Oxytropis campestris* var. *varians* 2n=96	59
14	Flavone glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America	62

LIST OF TABLES (cont.).

Table	Description	Page
15	Flavonol glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America	65
16	Flavonoid glycosides present in only one taxon	133
17	Collections used in flavonoid analysis	136
18	Synopsis of the characters in the seven taxa of the *Oxytropis campestris* (L.)DC. complex in northwestern North America	139

LIST OF FIGURES

Figure	Description	Page
1	Somatic chromosomes of certain taxa in the *Oxytropis campestris* (L.)DC. complex	42
2	Guard cell length frequencies in the *Oxytropis campestris* (L.)DC. complex	48
3	Master chromatogram of the flavonoid glycosides of *Oxytropis campestris* var. *cusickii*	50
4	Master chromatogram of the flavonoid glycosides of *Oxytropis campestris* var. *gracilis*	52
5	Master chromatogram of the flavonoid glycosides of *Oxytropis campestris* var. *jordalii*	54
6	Master chromatogram of the flavonoid glycosides of *Oxytropis campestris* var. *varians* 2n=48	56
7	Master chromatogram of the flavonoid glycosides of *Oxytropis campestris* var. *varians* 2n=96	58
8	Master chromatogram of flavone glycosides of the *Oxytropis campestris* (L.)DC. complex	60
9	Master chromatogram of flavonol glycosides of the *Oxytropis campestris* (L.) DC. complex	63
10	Chromatographic and spectral data for Apigenin 7-O-glucoside isomer #1	67
11	Chromatographic and spectral data for Apigenin 7-O-glucoside isomer #2	69
12	Chromatographic and spectral data for Apigenin 7-O-diglucoside	71

LIST OF FIGURES (cont.)

Figure	Description	Page
13	Chromatographic and spectral data for Apigenin 7-O-triglucoside	73
14	Chromatographic and spectral data for Apigenin 7-O-sambubioside	75
15	Chromatographic and spectral data for Apigenin 7-O-rutinoside	77
16	Chromatographic and spectral data for Apigenin 7-O-glucosylvicianoside	79
17	Chromatographic and spectral data for Apigenin 7-O-vicianoside	81
18	Chromatographic and spectral data for Luteolin 7-O-glucoside	83
19	Chromatographic and spectral data for Luteolin 7-O-diglucoside	85
20	Chromatographic and spectral data for Luteolin 7-O-triglucoside	87
21	Chromatographic and spectral data for Luteolin 7-O-glucosylrutinoside	89
22	Chromatographic and spectral data for Luteolin 7-O-rutinoside	91
23	Chromatographic and spectral data for glycoside #14	93
24	Chromatographic and spectral data for glycoside #15	95
25	Chromatographic and spectral data for glycoside #16	97
26	Chromatographic and spectral data for glycoside #17	99
27	Chromatographic and spectral data for Kaempferol 3-O-glucoside	101

LIST OF FIGURES (cont.)

Figure	Description	Page
28	Chromatographic and spectral data for Kaempferol 3-O-sambubioside	103
29	Chromatographic and spectral data for Kaempferol 3-O-rutinoside	105
30	Chromatographic and spectral data for Quercetin 3-O-glucoside isomer #1	107
31	Chromatographic and spectral data for Quercetin 3-O-glucoside isomer #2	109
32	Chromatographic and spectral data for Quercetin 3-O-glucoside isomer #3	111
33	Chromatographic and spectral data for Quercetin 3-O-glucose-7-O-glucoside	113
34	Chromatographic and spectral data for Quercetin 3-O-sophoroside-7-O-glucoside	115
35	Chromatographic and spectral data for Quercetin 3-O-sambubioside	117
36	Chromatographic and spectral data for Quercetin 3-O-diglucosylxyloside	119
37	Chromatographic and spectral data for Quercetin 3-O-diglucosylxyloside	121
38	Chromatographic and spectral data for Quercetin 3-O-sambubioside-7-O-glucoside	123
39	Chromatographic and spectral data for Quercetin 3-O-glucosylrhamnoside	125
40	Chromatographic and spectral data for Quercetin 3-O-glucosylrhamnoside	127
41	Chromatographic and spectral data for Quercetin 3-O-rutinoside	129
42	Chromatographic and spectral data for glycoside #33	131

LIST OF FIGURES (cont.)

Figure	Description	Page
43	Flavonoid glycosides present in more than one taxon	134
44	Hypothetical view of the relationships in the *Oxytropis campestris* (L.) DC. complex in northwestern North America	183

LIST OF MAPS

Map	Description	Page
1	Distribution of *Oxytropis campestris* (L.)DC. in northwestern North America I.	14
2	Distribution of *Oxytropis campestris* (L.)DC. in northwestern North America II.	16
3	Distribution of the chromosome numbers in *Oxytropis varians* (Rydb.) K. Schum.	145
4	Distribution of *Oxytropis varians* (Rydb.) K. Schum.	148
5	Distribution of *Oxytropis gracilis* (A. Nels.) K. Schum.	155
6	Distribution of *Oxytropis cusickii* Greenm.	165
7	Distribution of *Oxytropis columbiana* St. John	171
8	Distribution of *Oxytropis jordalii* Porsild	177

LIST OF PHOTOGRAPHIC PLATES

Plate	Description	Page
1	Type specimen of *Oxytropis campestris* (L.) DC.	12
2	Type specimen of *Oxytropis varians* (Rydb.) K. Schum.	142
3	Type specimen of *Oxytropis gracilis* (A. Nels.) K. Schum. subsp. *gracilis*	152
4	Type specimen of *Oxytropis gracilis* (A. Nels.) K. Schum. subsp. *dispar* (A. Nels.) Elisens	159
5	Type specimen of *Oxytropis cusickii* Greenm.	163
6	Type specimen of *Oxytropis columbiana* St. John	169
7	Type specimen of *Oxytropis jordalii* Porsild subsp. *jordalii*	174
8	Type specimen of *Oxytropis jordalii* Porsild subsp. *davisii* (Welsh) Elisens	181

CHAPTER 1.

INTRODUCTION

The genus *Oxytropis* DC. is one of about 600 genera that comprise the Leguminosae, the third largest Angiosperm family. Second only to the grasses in economic importance, legumes provide many articles of food, fodder, dyes, gums, resins, oils, and ornament. The family is cosmopolitan in its distribution and is usually divided into three subfamilies: the Mimosoideae, the Caesalpinoideae, and the Lotoideae (Bentham, 1865; Taubert, 1894). These three taxa can be distinguished as follows:

Mimosoideae: flowers actinomorphic, calyx and corolla valvate in the bud.

Caesalpinoideae: flowers weakly or strongly zygomorphic, caesalpinaceous (upper petal innermost), aestivation imbricate-ascending.

Lotoideae: flowers strongly zygomorphic, papilionaceous (upper petal outermost), aestivation imbricate-descending, the two anterior petals often basally connate (the keel).

These taxa have, however, been accorded various taxonomic treatments; they have been classified by various authors as distinct families (Hutchinson, 1926; Taktahjan, 1959), reduced to two families (Wettstein, 1933), or

expanded to four subfamilies (DeCandolle, 1802). As Heywood (1971) notes, there is still no general agreement regarding the treatment of the major divisions.

The inclusion of *Oxytropis* in the tribe Galegeae (subfamily Lotoideae) has, to the contrary, rarely been disputed since Bentham's account of the Leguminosae in 1865. The second largest tribe in the legumes, the Galegeae is comprised of about fifty-four genera. Its members are primarily temperate in distribution and possess pinnately compound leaves with entire leaflets as well as ten stamens (usually diadelphous) with equal anthers. *Oxytropis*, with about 300 species worldwide, is one of the largest genera in the tribe. Best represented in Europe and Asia, there are only 20-30 species of *Oxytropis* currently recognized in North America (Barneby, 1952).

DeCandolle, working exclusively with Old World material, erected the genus *Oxytropis* in 1802 to contain a part of the Linnean *Astragalus*. As first described, *Oxytropis* was characterized by the beaked keel petals and the introflexion of the pod's ventral suture, as opposed to the muticous keel and bilocular pod (from the dorsal suture) of *Astragalus*. Since DeCandolle's treatise, certain authors have continued to combine the two genera (for example, Tidestrom, 1937; Shinners, 1958). Systematists in favor of reducing *Oxytropis* to subgeneric rank point to the lack of a distinctive habit and of any abso-

lute criteria by which the two genera can be set apart. Indeed, the description of two perfect astragali, *Astragalus nothoxys* Gray and *Astragalus acutrostis* Wats., with distinctly cuspidate keels resulted in several authors (for example, Rouy, 1897) removing the species of *Oxytropis* into a subgenus of *Astragalus*. However, Bunge (1869), the monographer of Old World *Astragalus* and of *Oxytropis*, Taubert (in Engler's Pflanzenfamilien, 1894), as well as Bentham and Hooker, and most contemporary botanists, have supported DeCandolle's treatment (see Wheeler, 1939). Barneby (1952), in his revision of the genus in North America, stated that until it could be shown that the gap between the two genera is no greater than that existing between sections within *Astragalus*, or that there are species of *Oxytropis* referable with equal justice to either genus, or that *Oxytropis* is polyphyletic, the submergence of *Oxytropis* in the older genus would do nothing to clarify relationships.

Chromosome data support the claim that *Oxytropis* presents a unified phyletic group related to, but distinct from, the *Astragalus* assemblage. The basic chromosome number in *Oxytropis* is consistently X=8, whereas *Astragalus* has basic numbers of 8 (Old World species) and 11, 12, or 13 in the New World (Ledingham and Fahselt, 1967).

OXYTROPIS DC.[1]

Oxytropis DC. Astragal. 24:77, 1802. *nom. cons.*

Aragallus Neck. Elem. 3:12, 1790.

Spiesia Neck. Elem. 3:13, 1790.

Astragalus L. Sp. Pl. 755, 1753. *pro parte.*

> Plants perennial, herbaceous, acaulescent to short caulescent; leaves alternate or basal, odd-pinnate, leaflets entire, without stipels; stipules mostly connate, adnate to the petiole or free; flowers violet, purple, white or yellow, in axillary racemes or spikes or arising from the caudex; bracts often small, membranous; bracteoles minute or absent; calyx-tube cylindric to campanulate, five subequal teeth; petals often with rather long claws; banner erect, ovate or oblong; keel equal to the wings or shorter, keel-tip produced into a beak, maculate or immaculate; wings oblong; stamens diadelphous, anthers uniform, ovary sessile or stipitate; style filiform straight or curved; pod sessile to stipitate, straight, erect or reflexed, two-loculed through intrusion of ventral suture to one-loculed; several seeded; seeds reniform, funicle filiform.

The first synopsis of the North American species of *Oxytropis* was by W.J. Hooker (1834) in his Flora Boreali-Americana. Although several species were first described in this important work (for example, *O. splendens*), the paucity of the material available limited Hooker's account of the genus as it did that of Torrey and Gray in their Flora of North America (1838). A similar problem faced Bunge (1869) in his monograph of *Oxytropis*. Asa Gray (based on his extensive collections and examination

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[1] synonymy based on Welsh (1967)

of the material at Kew) published the first North American revision (1884). He recognized sixteen species. The onset of the twentieth century witnessed further activity not only in the field, but in the proliferation of species proposed by various workers. Many of these species were hastily proposed, often based on one or two specimens, and, in Barneby's (1952) words, often contributed "... more to the literature and synonymy than to a true understanding of the genus."

In addition to the proliferation of newly described species, the resurrection of *Aragallus* Neck. and *Spiesia* Neck. by several authors, as well as the shifting back and forth between *Astragalus* and *Oxytropis*, resulted in chaos on the shelves of many herbaria. It was that disorder which prompted Barneby (1952) to attempt the first revision of the North American species of *Oxytropis* since Gray (1884). Barneby recognized twenty-two species; his account contributed greatly towards a definition of the major forms and a stabilization of the nomenclature. More recently, workers in the genus have generally supported Barneby's species concepts and have simply addended his original characterizations (for example, Boivin, 1967; Welsh, 1960, 1963, 1967).

Biosystematic studies within *Oxytropis* have been confined primarily to reports of chromosome numbers. As mentioned previously, the works of Ledingham and Fahselt

(1967) and Senn (1937) have consistently indicated that the basic number in the genus is X=8. These and other studies (for example, Ledingham, 1960; Holmen, 1962; Zhukova, 1966) indicate that *Oxytropis* is comprised of a number of polyploid species. In North America, chromosome counts range from 2n=16 in *O. deflexa* and *O. podocarpa* through 2n=32 (*O. viscida*) and 2n=48 *O.* (*sericea*) to a high of 2n=96 in *O. maydelliana* (Ledingham, 1960; Holmen, 1962). Aneuploidy does not appear to occur in the genus.

Although few chemosystematic studies have been carried out in *Oxytropis*, a wide variety of flavonoids have been identified in the Leguminosae from the numerous surveys conducted at the tribal and generic levels (Harborne, 1967; Peckett, 1959). Representative compounds from practically every one of the numerous flavonoid classes occur in the legumes as well as several compounds with unusual structures (Torck, 1976). The Leguminosae are particularly rich in methylated flavonols and flavones, additional hydroxylation in the flavonoid nucleus, and absence of hydroxylation at position 5 (Harborne, 1971). For example, 6- and 8- hydroxylated flavonols, methyl ethers related to the common flavonols (for example, isorhamnetin), and flavonols with a 2' hydroxylation are known in the family.

In addition to the several flavonoid structures

characteristic of the Leguminosae, each subfamily tends to have certain characteristic flavonoids or related phenolics (Harborne, 1967). While the Mimosoideae are rich in catechins, leucoanthocyanidins, and other tannins; the Caesalpinoideae have ellagitannins and the rare heartwood pigments haematoxylon and brazilin. Isoflavones and rotenoids characterize the Lotoideae; this subfamily is also particularly rich in anthocyanins and flavonol glycosides.

The few flavonoid surveys of *Oxytropis* reported in the literature have been carried out by Soviet workers (Pakanaev *et al*, 1969; Dungerdorzh and Petrenko, 1973; Blinova, 1974). Only Dungerdorzh and Petrenko's work has resulted in the identification of a flavonoid glycoside (rutin); most studies have been concerned with determination of the aglycone moieties in several Eurasiatic species. It is significant that the common flavonols quercetin and kaempferol are present in the majority of the species surveyed while rhamnetin and myricetin are more limited in their occurrence (Pakanaev *et al*, 1969; Blinova, 1974). No flavone aglycones are noted by any of these workers.

The present investigation is concerned with *Oxytropis campestris* (L.)DC. *sensu lato* in northwestern North America. Originally described in Linneus' (1753) Species Plantarum, *O. campestris* has been characterized by its

chartaceous pod texture, relatively small size of the flowers (<18mm.), and the more than six flowers per raceme. As with many Linnean species, further botanical exploration and study have revealed that *O. campestris sensu* Linneus is extremely variable with respect to its morphological features. Differences in stature, number of leaflets, length and density of the raceme, as well as the number and colour of the flowers have been noted by various authors (Porsild, 1951; Barneby, 1952; Welsh, 1963).

In addition to this morphological diversity, the circumboreal constellation of forms referred to as *O. campestris* (L.)DC. occur in a variety of geographic regions that exhibit much topographical and ecological diversity. In northwestern North America, where *O. campestris* is particularly widespread, its range extends from the Dakotas and northern Colorado to Alaska, the Yukon, and the western regions of the Northwest Territories (Barneby, 1952; Welsh, 1967). Within this region, several morphological taxa are common in, and, indeed, restricted to prairie, alpine, boreal, and arctic habitats. *O. campestris* is, therefore, comprised of a number of morphologically distinctive allopatric forms (Maps 1 & 2).

Oxytropis campestris (L.)DC.

Oxytropis campestris (L.)DC., Astrag., 59, 1802.
Astragalus campestris L., Sp. Pl.761. 1753, *sensu ampliatissimo*.

Oxytropis lambertii β Hook., Fl. Bor.-Amer., 1: 107. 1834.
Oxytropis monticola Gray, Proc. Amer. Acad., 20:6. 1884. *pro max. parte.*
Spiesia monticola (Gray) O. Kze., Rev. Gen., 206. 1891.
Aragallus monticola (Gray) Greene, Pittonia, 3:212. 1897.
Oxytropis cusickii Greenm., Erythea, 7:116. 1899.
Aragallus gracilis A.Nels., Erythea, 7:60. 1899.
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Aragallus alpicola Rydb., Mem. N.Y. Bot. Gard., 1:252. 1900.
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Oxytropis gracilis (A.Nels.) K. Schum., Just's Jahresb., 27:496. 1901.
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Oxytropis varians (Rydb.) K. Schum., Just's Jahresb., 29:543. 1903.
Aragallus luteolus Greene, Proc. Biol. Soc. Wash., 18:17. 1905.
Aragallus albertinus Greene, Proc. Biol. Soc. Wash., 18:15. 1905.
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Aragallus macounii Greene, l. c., *pro parte.*
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Oxytropis mazama St. John, op. cit., 101. 1928.
Oxytropis okanoganea St. John, op. cit., 102. 1928.
Oxytropis cascadensis St. John, op. cit., 105. 1928.
Oxytropis columbiana St. John, op. cit., 100. 1928.
Oxytropis albertina (Greene) Rydb., Fl. Prair. & Pl., 484. 1932.
Astragalus rydbergianus Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937. (*non. A. villosus*

Mchx).
Astragalus albertinus (Greene) Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937.
Astragalus alpicola (Rydb.) Tidestr., Proc. Biol. Soc. Wash., 50:19. 1937.
Astragalus mazama (St. John) G.N. Jones, Univ. Wash. Pub. Bot., 7:175. 1938.
Astragalus grayanus Tidestr., in Tidestr. & Kitt., Gl. Ariz. & New Mex., 216. 1941. *quoad nom. (non A. monticola* Phil.).
Oxytropis hyperborea Porsild, Sargentia, 4:53. 1943.
Oxytropis jordalii Porsild, Canad. Field-Nat., 65:77. 1951.

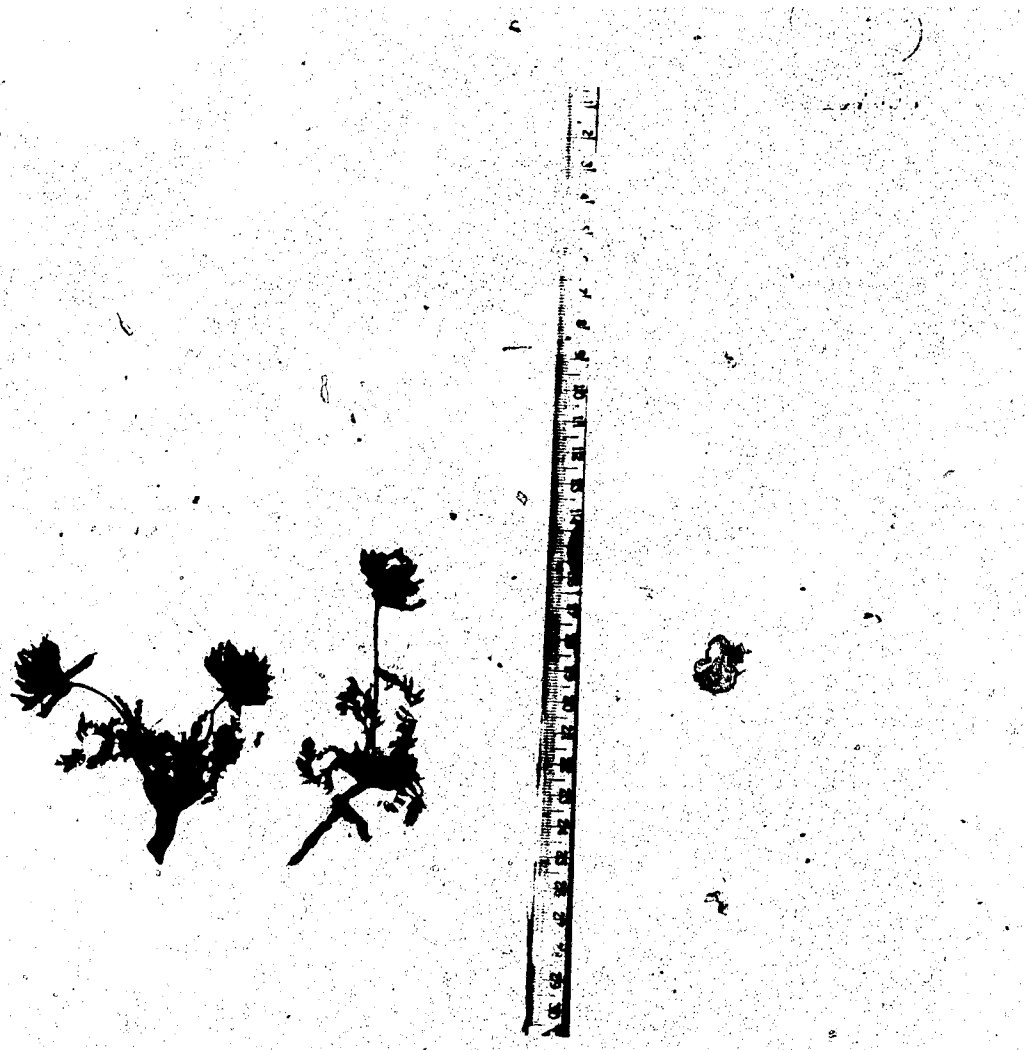
Description of *Oxytropis campestris* (L.) DC.

Variable in stature and pubescence, green and glabrate to densely silky-pilose, sometimes villous-hirsute especially the scape and petiole; caespitose and acaulescent from a branching caudex; stipules membranous, pale, glabrous to pilose dorsally, triangular to lanceolate acuminate, connate, adnate to the petioles, 1-3 nerved, the margins naked or ciliate with bristles or clavate processes; leaves 5-25 cm. long; leaflets 7-45, scattered, opposite or sometimes geminate and verticellate, 9-25 mm. long, 3-8 mm. wide; scapes 2.5-36 cm. long; bracts narrowly lanceolate, longer than the pedicels, pilose dorsally, rarely glabrate; racemes 5-30 flowered, 3-24 cm. long, capitate to oblong, becoming lax, 0.5-11 cm. long in fruit; calyx cylindrical with dark and light hairs, the tube 4.5-7 mm. long, teeth 1-4 mm. long, triangular; corolla white, ochroleucous, pale yellow, pinkish or purplish; banner 12-20 mm. long, 4-8 mm. wide; wings 10-17 mm. long, blades not much dilated upward, 3-4.5 mm. wide at apex; keel 10-15 mm. long, appendage small, maculate or immaculate; pod 8-16 mm. long, erect, sessile, pilose, with a beak about 5 mm. long, partially two-loculed by intrusion of the ventral suture. (Barneby, 1952; Welsh, 1967).

The taxonomic category assigned to these variants has varied considerably in the literature. For the most part,

PLATE 1.

Type specimen of *Oxytropis campestris* (L.) DC.



HERBARIUM LINNAEANUM

926.61

No.

Form of Savage Catalogue entries:

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

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

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

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

ASTRAGALUS

81 Astragalus 30 monospermis Orientalis. Astragalus tragacantha folio non ramoso, floribus luteis. Amm. ruth. 127. [→Pan.]/ Astragalus arcadius, foliis pennatis, calyce et fructu villosis. Hall. fasc. 367. t.13. [→Pan.]/ Habitat in Uralensibus montibus. [→Pan.]/

MAP 1.

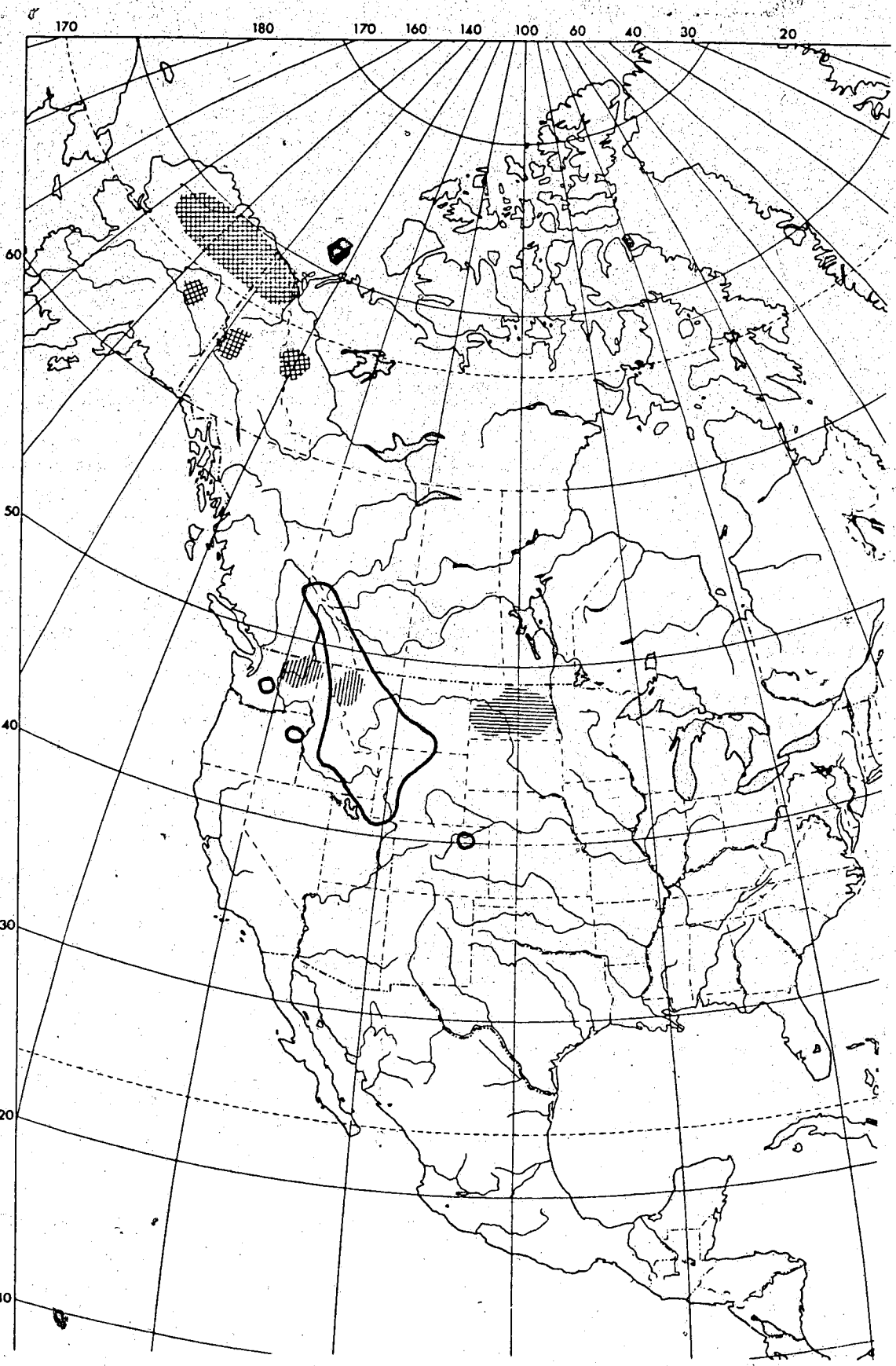
Distribution of *Oxytropis campestris* (L.)DC. in northwestern North America based on Barneby (1952), Welsh (1967), and Hultén (1968)


var. *columbiana* (St.John) Barneby


var. *cusickii* (Greenm.) Barneby


var. *dispar* (A.Nels.) Barneby


var. *jordalii* (Porsild) Welsh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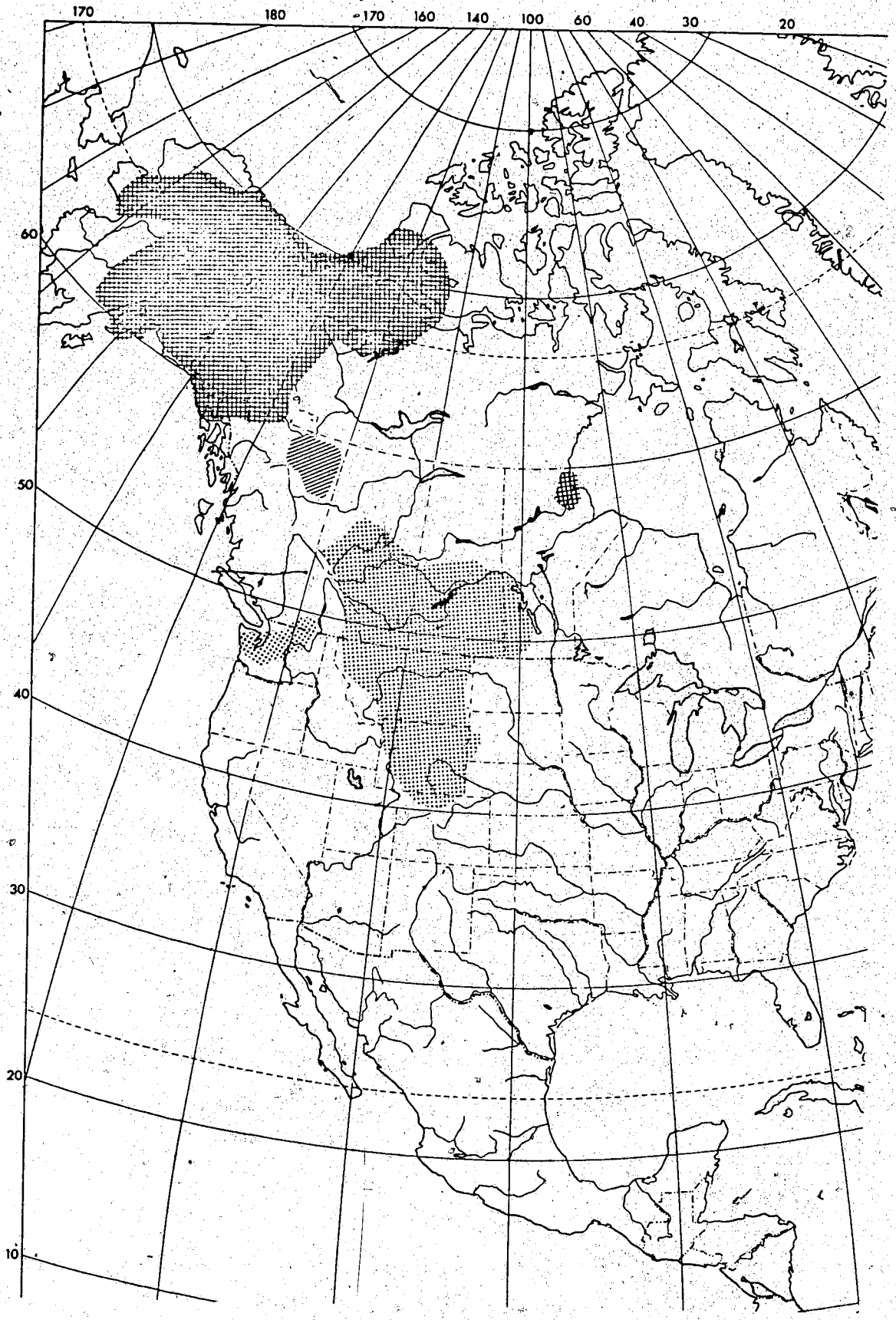
MAP 2.

Distribution of *Oxytropis campestris* (L.)DC. in northwestern North America based on Barneby (1952), Welsh (1967), and Hultén (1968)

var. *davisii* Welsh

var. *gracilis* (A.Nels.) Barneby

var. *varians* (Rydb.) Barneby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the plants of the New World have been held varietally distinct from *Oxytropis campestris* (L.)DC. In 1871, Watson recorded *O. campestris* as ranging from the arctic to Colorado while Bunge (1869) accepted the species as west European, east Asian, and western North American, noting, however, that the latter differed somewhat in stature and habit. Gray's revision (1884) excluded typical *O. campestris* from the American flora for the first time. The material which had been so named previously was divided into a western arctic *O. leucantha* and a new species, *O. monticola*, largely cordilleran and ochroleucous flowered. During the present century, the most western and Rocky Mountain forms have been variously segregated by different workers. Thus, in northwestern North America, where Watson could distinguish only *O. campestris sensu* Linneus, and Asa Gray only *O. monticola*; Nelson (1899), St. John (1928) and others collectively delineated fourteen species. This fact, coupled with the shifting back and forth between the genera *Astragalus* and *Oxytropis*, *Aragallus* and *Spiesia*, created an abundance of disordered synonyms and overall taxonomic confusion.

Barneby (1952) favored a return to the concept of an American *O. campestris*. He argued that while *O. campestris* in its original and narrowest sense is absent from the New World, the European and American plants can reasonably be ranked as geographic populations within a polymorphic,

circumboreal species, a view shared by Hultén (1967, 1968). Their "fundamental similarities" in structure and texture of the pod, in "flower", as well as orientation or amount of vestiture, indicated to Barneby the "inevitable acceptance" of an American *Oxytropis campestris* (L.)DC. In northwestern North America, he recognized five races (treated in the category of *varietas*) differentiated on the basis of petal colour, leaflet number, habitat, and stipule vestiture and ornamentation (see Tables 1 and 2).

Barneby's revision contributed greatly towards a stabilization of the nomenclature for the *O. campestris* complex and his species delimitations have been widely accepted. More recently, a number of authors have contributed to the taxonomy in this complex. Broadening Barneby's (1952) species concept, Welsh (1963) described two new varieties after examination and collection of specimens from British Columbia, the Yukon, and Alaska. One of these taxa, *jordalii*, had previously been described by Porsild (1951) as a new species confined to Alaska and the Yukon; it was accorded subspecific status by Hultén (1967). Thus, the examination of material using morphological criteria has resulted in the recognition of seven geographically and morphologically distinct subspecific taxa in *O. campestris* by Barneby (1952) and Welsh (1963).[2] Their

[2]Boivin (1967), in a rather cursory treatment of the *O. campestris* complex, recognized still another variety (var. *cervinus* (Greene) Boivin) characterized vaguely

TABLE 1.

Classification of the *Oxytropis campestris* (L.)DC. complex in Northwestern North America based on Barneby (1952) and Welsh (1963)

Oxytropis campestris (L.)DC var. *varians* (Rydb.) Barneby

Oxytropis campestris (L.)DC var. *gracilis* (A.Nels.) Barneby

Oxytropis campestris (L.)DC var. *cusickii* (Greenm.) Barneby

Oxytropis campestris (L.)DC var. *dispar* (A.Nels.) Barneby

Oxytropis campestris (L.)DC var. *columbiana* (St. John) Barneby

Oxytropis campestris (L.)DC var. *jordalii* (Porsild) Welsh

Oxytropis campestris (L.)DC var. *davisii* Welsh

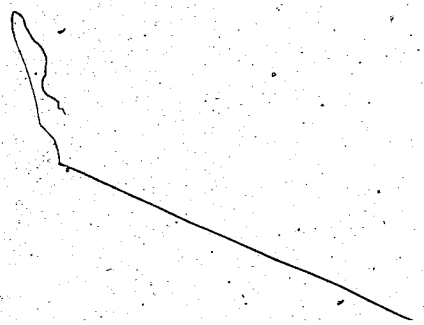

TABLE 2. Diagnostic Characters of the Taxa in the *Oxytropis campestris* (L.)DC. Complex in Northwestern North America (based on Barneby 1952, and Welsh 1963)

TAXA	DISTINCTIVE FEATURES
var. *varians* (Rydb.) Barneby	stipules with clavate processes; flowers white or ochroleucous; Alaska, Yukon, N.W.T.
var. *gracilis* (A.Nels.) Barneby	numerous leaflets (17-33); uniformly yellowish corolla; prairie habitats in the north-central states, prairie provinces, locally in B.C. and Washington
var. *dispar* (A.Nels.) Barneby	polychrome racemes and flowers; coriaceous pod texture; prairie habitats in North Dakota
var. *columbiana* (St.John) Barneby	whitish corolla; maculate keel; robust plants of riparian habitats in Washington and Montana
var. *cusickii* (Greenm.) Barneby	few leaflets/leaf (7-17); few flowers/raceme; low statured plants of alpine and sub-alpine meadows in central and northern Rocky Mts.
var. *jordalii* (Porsild) Welsh	pinkish or purplish corolla; small flowers (12 mm.); few flowers/raceme (6-14); alpine and arctic tundra habitats in Alaska, western N.W.T., Yukon, locally to Alberta
var. *davisii* Welsh	numerous verticellate leaflets (31-51); purple corolla; streamside habitats in northeast B.C.

classification of the complex is presented in Table 1. A major aim of this research project was to obtain new systematic information on several cryptic characters (for example, chromosome number, flavonoid glycosides) and use these data to test the conclusions of Barneby (1952) and Welsh (1963).

Prior to this study, biosystematic studies of *O. campestris* have been confined to cytological observations by a few workers; their published and unpublished chromosome counts are listed in Table 3. Published data indicate the presence of at least three chromosome numbers in *O. campestris*: 2n=32 (Ledingham, 1957; Knaben, 1968), 2n=48 (Ledingham, 1960), and 2n=>60 (Johnson and Packer, 1968). These data also suggest that there is no extant diploid race (2n=16); only a tetraploid (32), hexaploid (48), and an octoploid race or higher (>60) occur in northwestern North America. The 2n=48 reported for var. *gracilis* (A. Nels.) Barneby (Ledingham, 1960) from Kamloops indicates that Barneby's characterization of that taxon may be oversimplified. East of the continental divide, however, var. *gracilis* has a consistent mitotic count of 2n=32 (Ledingham, 1957).

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by few leaflets and lowland habitats in British Columbia and Washington. This study did not examine the validity of Boivin's new combination due to its poor characterization and description and the fact that it is included in Barneby's var. *gracilis*.

TABLE 3.

Reported Chromosome Counts of the taxa in the *Oxytropis campestris* (L.)DC. Complex in Northwestern North America

Taxon	2n=	Locality	Reference
gracilis	32	Kananaskis Rd., Alberta	Mosquin, T., unpublished
gracilis	32	Olympic Park, Washington	Kruckeberg, A.R., unpubl.
gracilis	32	Burdick, Saskatchewan	Ledingham, G.F. 1957
gracilis	32	Crestwynd, Saskatchewan	"
gracilis	32	Regina, Saskatchewan	"
gracilis	32	Cypress Lake, Saskatchewan	"
gracilis	32	Moosomin, Saskatchewan	"
gracilis	48	Kamloops, B.C.	Ledingham, G.F. 1960
jordalii	32	White Mts., Alaska	Knaben, G. 1968
varians	>60	Ogotoruk Creek, Alaska	Johnson & Packer 1968

Other major objectives of the present study were to determine the distribution of the chromosome races in northwest North America and to identify and note the occurrence of the various flavonoid glycosides. No previous investigations of the flavonoids in *O. campestris* have been carried out although, as mentioned before, a few cursory examinations of Eurasiatic *Oxytropis* species were conducted. Flavonoid data have often proved invaluable in the resolution of taxonomic and evolutionary problems (for example, Adams and Turner, 1970). Their usefulness as "taxonomic markers" to aid the delimitation of generic and specific boundaries as well as their utility as "genetic markers" to indicate hybridization history is well documented in the literature (Peckett, 1959; Alston and Turner, 1963; Harborne, 1969). In addition, Denford (1973) and Packer (unpublished) have noted their potential as "historical markers" where refugial boundaries or migrational pulses could be indicated by flavonoid distribution.

In summary, seven morphologically distinctive and allopatric subspecific taxa are currently recognized in *Oxytropis campestris* (L.)DC. in northwestern North America by Barneby (1952) and Welsh (1963). There is evidence (Ledingham, 1957, 1960; Johnson and Packer, 1968) that this taxon represents a mature polyploid complex (Stebbins, 1971), possibly comprised of several species (Davis and

Heywood, 1963). For organizational and historical reasons, the data have been gathered and the results presented following the taxonomy of Barneby (1952) and Welsh (1963). In addition, a newly discovered chromosome race (2n=96) has served a similar organizing function.

CHAPTER 2

MATERIALS AND METHODS

Collections and Field Studies:

Field studies were undertaken to obtain plant material for laboratory and herbarium studies and to make ecological and breeding system observations, for example, substrate preference and possible hybridization. Collections of *Oxytropis campestris* (L.)DC were made throughout as much of its known range as possible (Barneby, 1952; Welsh, 1967) in northwestern North America. Material was obtained from twenty-six localities and included representative specimens of all seven taxa. Pressed herbarium specimens, air-dried and bagged material (for use in chemical studies), and live plants (for cytological, breeding system, and growth chamber studies) were collected for study.

Cultivation:

Live plants, transplanted into five-inch pots and grown in the University of Alberta greenhouses, were maintained under a diurnal temperature range of 10°-16°C with a relative humidity of 60% and a 16 hour photoperiod using natural lighting in the summer with supplemented light when required. Chlorotic plants were fertilized using a solution of 20-20-20 NPK fertilizer.

Further transplanting was often carried out due to root overcrowding and poor water retention of the native soils. Aphid and fungal infestations were treated using standard fungicides and insecticides.

Herbarium Studies:

Morphological and distributional studies were carried out on living and herbarium specimens from the following herbaria: University of Alberta, Edmonton (ALTA); Brigham Young University, Provo (BRY); the Gray Herbarium of Harvard University, Cambridge (GH); National Museum of Canada, Ottawa (CAN); University of Montana, Missoula (MONTU); University of Washington, Seattle (WTU); University of Calgary (UAC); Rocky Mountain Herbarium, Laramie (RM); United States National Museum, Washington, D.C. (US); and the University of Saskatchewan, Regina (USAS). The abbreviations used are those listed in Index Herbariorum (Holmgren and Keuken, 1974).

Guard Cell Measurements:

Various workers have found a correlation between cell size and ploidy level (Sax and Sax, 1937; Stebbins, 1971). In an effort to distinguish the chromosome races of *Oxytropis campestris* by cell size, measurements of epidermal guard cells were made. Leaves were soaked in boiling water for five minutes, the lower epidermis was then peeled off and placed on a microscope slide in a drop of water. Measurements were made using a micro-

meter eyepiece on an American Optical microscope (240X).

Cytological Studies:

Mitotic chromosome counts were made from actively growing root tips using the procedures of Tijo and Levan (1950) with slight modifications. Root tips were immersed in a 0.002 molar solution of 8-hydroxyquinoline (0.116 gm. in 400 mls. of water) for 2-3 hours at 13°-16°C; washed in distilled water for five minutes; then transferred to a watch glass and stained for thirty minutes in a solution of acetic orcein and 1N HCl (9:1). The solution was warmed over a bunsen burner 8-10 times during a thirty minute period. The tips were next placed on a slide in a drop of 45% acetic acid and a coverslip applied; then washed and made semi-permanent by ringing the coverslip with a mixture of gum mastic and paraffin wax (1:1). Chromosome counts were made under the oil immersion objective (1000X) of an American Optical microscope with a green filter. Several of the preparations were drawn using a camera lucida apparatus; these drawings were used in examination of chromosome morphology. Voucher specimens were deposited in the herbarium at the University of Alberta (ALTA).

Chemical Studies:

Identification of the flavonoid glycosides of five populations of *Oxytropis campestris* was carried out. In addition to the identification of the glycosides in these

five populations, chromatographic profiles of twenty-four populations were compared.

Above ground plant organs used in flavonoid extraction were collected in the field and dried in paper bags. Prior to chemical analysis, the collections were sorted to remove any contaminants. Stems, flowers, and leaves were uniformly used for extraction in every population sampled. Flavonoids were extracted using a blender; approximately 20 gm. (dry weight) of plant material were ground for 15 minutes in 500-700 mls. of 80% ethanol. The extract was then vacuum filtered through several layers of cheesecloth followed by Whatman #1 filter paper, then reduced in a rotoevaporator or flash evaporator under vacuum to 10-20 mls. Chlorophyll, other photosynthetic pigments, and lipids were removed by partitioning with multiple aliquots 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 mls. of the stock solution was combined with an equal amount of 2N HCl and refluxed at 110°C for three hours. The aglycones were then partitioned against ether, evaporated to dryness, and redissolved in a minimum volume of spectrograde methanol. Subsequently, they were spotted in varying concentrations on half sheets (23 X 57 cms.) of Whatman 1MM chromatography paper. Descending chromatogra-

phy was then carried out using three solvent systems: BAW (n-butanol-acetic acid-water, 4:1:5 upper phase), forestal (acetic acid-water-concentrated HCl, 30:10:3), and saturated phenol (phenol-water, 4:1). Identifications were made by comparison of R_f's with those reported by Harborne (1967, 1973) and Ribereau-Gayon (1972). UV spectral analysis was also carried out on certain purified aglycones; procedures as well as analysis of the data were based on Mabry *et al* (1969).

Seikel *et al* (1966) have reported that C-glycoflavonoids remain in the aqueous sugar layer after acid hydrolysis and ether extraction of the aglycones. To check for possible C-glycoflavonoids in the stock solution, the aqueous sugar layer was further extracted against amyl alcohol (Harborne, 1973). The amyl alcohol layer was then evaporated to dryness, redissolved in minimum methanol, and spotted on half sheets of Whatman 1MM paper. Descending chromatography of these sheets was then carried out in BAW, 15% acetic acid, and water.

Separation of the flavonoids of the stock solution was carried out on Whatman 3MM chromatography paper. To determine the optimum concentration for separation, varying volumes of the stock solution were spotted on 3MM paper and chromatographed descendingly in BAW for 16-19 hours. The sheets were then air-dried, rotated 90°, then run in 15% acetic acid for 6-8 hours. The chromato-

grams were 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 at least forty-eight sheets of Whatman 3MM paper and chromatographed in BAW and 15% acetic acid according to the procedures outlined above. The chromatograms were then viewed under UV light in the presence and absence of fuming NH_3. Spots resolved under either of these conditions were circled and their colors 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)[3]. Spots which yielded positive reactions to both treatments were cut out from the remaining sheets and eluted in 90% methanol. These solutions were evaporated to dryness and redissolved in minimum methanol.

To check flavonoid purity, the solutions were spotted on full sheets of Whatman 1MM paper and run, in the usual manner, in BAW and 15% acetic acid. Those solutions which were found to consist of more than one gly-

[3] 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.

coside (as indicated by the presence of two or more spots) were then streaked on Whatman 3MM paper in the solvent system which yielded the best separation.

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

UV spectral analysis using a Unicam SP 1800 spectrophotometer was carried out on each unknown using the procedures of Mabry *et al* (1969). These procedures included the comparison of methanol scans with those obtained after the addition of several diagnostic reagents to the methanolic solution. Scans were recorded for the effects of sodium methoxide, aluminum trichloride, aluminum trichloride plus hydrochloric acid, sodium acetate, and sodium acetate plus boric acid on the UV absorption of the compound in methanol.

The flavonoid glycosides were then hydrolyzed to their aglycone and sugar constituents by refluxing the methanolic solutions with an equal amount of 2N HCl at 100°C for twenty minutes to two hours depending on the suspected nature of the glycoside linkage (Ribéreau-Gayon, 1972). After hydrolysis, the solution was cooled and partitioned against 25 mls. of ethyl ether. The ether fraction, which contained the aglycone, was then evaporated to dryness, redissolved in minimum methanol, and chromatographed descendingly on Whatman 1MM paper in BAW, forestal, and saturated phenol. The aglycones were also chromatographed in 15% acetic acid to ensure that the sugar had been liberated during hydrolysis.

The lower aqueous layer contained the sugar component of the flavonoid glycosides. Identification of the flavonoid sugars was carried out using the procedures of Ribéreau-Gayon (1972). Neutralization of this acidic solution (although demonstrated experimentally to be unnecessary for purposes of identification) was carried out on approximately half of the isolated flavonoid sugars by using a 10% solution of di-n-octylmethylamine v/v in chloroform. Twenty-five mls. of this solution was partitioned against the acidic aqueous sugar fraction; the lower phase, containing the neutralized sugar solution, was then evaporated to dryness. The sugars were then redissolved in a minimum amount of 80% methanol and spot-

ted (two spots side by side) on half sheets of Whatman 1MM 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. In addition, a third solution, consisting of a mixture of five common sugars (glucose, rhamnose, xylose, galactose, arabinose) in 10% isopropanol, was applied next to the previously mentioned spots. Descending chromatography was then carried out in 80% isopropanol for 36 hours. Next, the sheets were air-dried, dipped in aniline hydrogenphthalate reagent, and heated in an oven at 55°C for twenty minutes in order to detect the sugars present. R_g's were calculated for each sugar and colour reactions compared with those reported by Zweig and Sherma (1972).

After the identification of the compounds of the five selected populations was completed, a chromatographic analysis of the spot patterns of twenty-four other populations was conducted. About 10 gms. dry weight of above ground flowering material was ground up with about 250 mls. of 80% ethanol. Concentration of the extract and determination of the optimum concentration for separation of the flavonoids were undertaken in the manner previously described. After the detection for phenolics and, more specifically, for flavonoids was carried out, the spot patterns and colour properties were noted. This information was then compared to the master

chromatogram in order to determine the distribution of the identified flavonoid glycosides.

CHAPTER 3.

RESULTS

Morphological and Phytogeographical Studies:

Examination of specimens revealed seven morphologically and geographically distinct taxa which, to a large extent, correspond to the seven varieties recognized by Barneby (1952) and Welsh (1963). The seven taxa were found to differ most significantly in habitat, leaflet number, stipule vestiture, number of flowers per raceme, pod texture, as well as corolla colour and length of the keel. The morphological differences are summarized in Table 4; they represent both vegetative and reproductive phases of the life cycle. Propagation in controlled environment facilities has indicated that these characters are not affected by varying environmental factors and therefore reflect genotypic differentiation.

Cytological Studies:

Cytological investigation confirmed the observation of Ledingham (1960) who noted that more than one chromosome number was present in *Oxytropis campestris* (L.)DC. *sensu lato*. Indeed, the data from the present study (Table 5) indicate that at least three chromosome numbers (32, 48, 96) are present in the species as defined by Barneby (1952), Welsh (1963), and Boivin (1967). These

TABLE 4.

Comparative morphological characters of the taxa in the *Oxytropis campestris* (L.)DC. complex in northwestern North America

Organ	Character	Taxa							
		varians 48 race	*varians* 96 race	*gracilis*	*dispar*	*cusickii*	*columbiana*	*jordalii*	*davisii*
Leaves	Number of leaflets	13-45	13-23	17-33	17-25	7-17	11-17	9-25	31-53
Stipules	Dorsal Vesture	pilose, glabrate	pilose, glabrate	pilose, glabrate	densely pilose	thinly pilose, glabrate	pilose, rarely glabrate	thinly pilose, glabrate	thinly pilose, glabrate
	Marginal Vesture	ciliate, clavate processes	ciliate, clavate processes	ciliate, glabrate, clavate processes rare	ciliate, clavate processes rare	ciliate, rarely glabrate	ciliate, clavate processes rare	ciliate, clavate processes	ciliate, clavate processes
Raceme	Number of flowers	10-25	8-15	6-30	8-15	6-15	6-28	6-14	10-16
Corolla	Colour	ochroleucous, whitish	ochroleucous, whitish	ochroleucous, whitish	ochroleucous whitish, pink, purplish	ochroleucous	whitish	ochroleucous, pink, purple	pink, purple
	Keel length (mm.)	10-12.5	13-15	10-14	12.5-14	11-14	11-14	10-11	11-12
Pod	Texture	Chartaceous	Chartaceous	Char.	Char. to Coriaceous	Char. to Coriaceous	Chartaceous	Chartaceous	Char.

TABLE 5.

Chromosome Counts for the *Oxytropis campestris* (L.)DC. Complex in northwestern North America determined in the present study

Taxon	2n=	Locality
var. *columbiana* (St. John) Barneby	48	Glacier Park, Montana
var. *cusickii* (Greenm.) Barneby	48	Anaconda Wilderness, Montana
	48	Jasper Park, Alberta
	48	Prospect Creek Rd., Alberta
	48	Waterton Park, Alberta
var. *davisii* Welsh	32	mile 403, ALCAN Hwy., B.C.
var. *dispar* (A. Nels.) Barneby	32	Morton Co., North Dakota
var. *gracilis* (A. Nels.) Barneby	32	W. of Calgary, Alberta
	32	Kananaskis Rd., Alberta
	32	Black Hills, South Dakota

TABLE 5.(cont.)

Taxon	2n=	Locality
var. *gracilis* (A. Nels.) Barneby	32	Albany Co., Wyoming
	32	Broadview, Saskatchewan
	32	Glacier Co., Montana
	48	Olympic Park, Washington
var. *varians* (Rydb.) Barneby	48	Dempster Hwy., Yukon
	48	Tok Jct., Alaska
	48	Kluane Lake, Yukon
	48	Moose Pass, Alaska
	48	Inuvik, N.W.T.
	96	mile 307 TAPS Hwy., Alaska
	96	S. of Mt. McKinley Park, Alaska
var. *jordalii* (Porsild) Welsh	32	Prospect Creek Rd., Alberta
	32	Richardson Mts., N.W.T.

numbers represent the tetraploid (32), hexaploid (48), and dodecaploid (96) condition and indicate that *Oxytropis campestris* (L.)DC. consists of a eupolyploid series in northwestern North America. The collections from which these chromosome counts were obtained are listed in Table 6.

The morphological taxa are generally correlated with chromosome number. Two taxa, however, are known to have more than one number; the taxon *gracilis* has both 2n=32 and 2n=48 while the taxon *varians* has 2n=48 and 2n=96. Map 3 shows the distribution of the chromosome numbers in the taxon *varians*. These data represent published chromosome counts (Table 3), the author's chromosome counts (Table 5), as well as chromosme numbers inferred by guard cell measurements (Table 8).

Analysis of the karyotype was conducted after treatment with 8-hydroxyquinoline for only the taxon *cusickii* (2n=48) and the taxon *gracilis* (2n=32). Observations of chromosome morphology (Figure 1) indicate that the medium-sized chromosomes are of fairly uniform length with median or sub-median centromeres. This condition, as noted by Stebbins (1971), is characteristic of a symmetrical karyotype commonly associated with unspecialized members of a family or genus. This contrasts with the asymmetrical karyotype where arm ratios and the relative lengths of the different chromosomes are heterogeneous. Asymmetrical

TABLE 6.

Collections of which Chromosome Counts are Based

Alaska: WJE #249, Tok Junction, June 24, 1976; WJE #268, Moose Pass, June 26, 1976; WJE #281, S. of McKinley Park, June 28, 1976; WJE #299, mile 307, TAPS Hwy., July 3, 1976; WJE #306, mile 322, TAPS Hwy., July 4, 1976.

Alberta: WJE #001a, 004a, Prospect Creek Rd., Cadomin, August 28, 1976; WJE #025, 217, Whitehorse Creek, Cadomin, June 24, 1976; WJE #043a, Hwy. #1, W. of Calgary, August 13, 1976; WJE #053, 060, Kananaskis Rd., July 15, 1975; WJE #110, Signal Mt., Jasper Park, August 23, 1975; WJE #222, Prospect Creek Rd., Cadomin, June 16, 1976; WJE #452, Carthew Mt., Waterton Park, July 12, 1977.

British Columbia: WJE #342, 343, mile 403, ALCAN Hwy., July 9, 1976.

Montana: WJE #099a, 100a, Goat Flats, Anaconda Wilderness, August 11, 1976; WJE #387,389, Mud Creek, Glacier Park, August 13, 1976; WJE #442, Glacier Co., July 9, 1977.

North Dakota: WJE #177, 181, Glen Ullin, Morton Co., May 26, 1976.

Northwest Territories: WJE #471, 472, Dolomite Lake,

TABLE 6. (cont.)

Inuvik, July 5, 1977.

Saskatchewan: WJE #190, Broadview, May 27, 1976.

South Dakota: WJE #162, 169, 170, Hwy. #16, Custer Co., Black Hills, May 25, 1976.

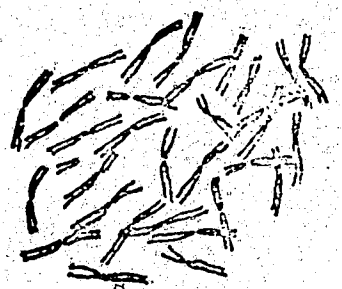
Washington: WJE #354, 356, Hurricane Ridge, Olympic Park, August 6, 1976.

Wyoming: WJE #154, Albany Co., May 24, 1976.

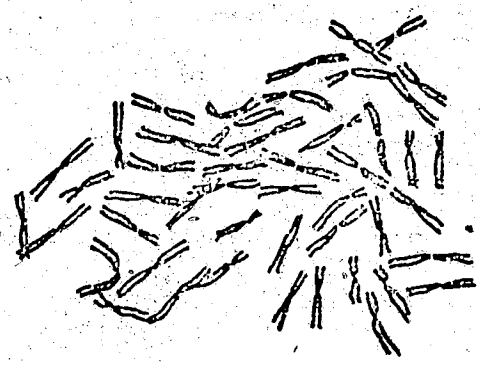
Yukon Territories: WJE #237, Kluane Lake, June 24, 1976; WJE #321, mile 82, Dempster Hwy., July 6, 1976.

FIGURE 1.

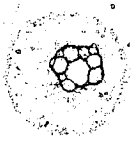
Somatic Chromosomes of certain taxa in the *Oxytropis campestris* (L.)DC. complex in northwestern North America



Oxytropis campestris (L.)DC var. *gracilis* (A.Nels.) Barneby
WJE #043 near Morley, Alberta
2n=32



Oxytropis campestris (L.)DC var. *cusickii* (Greenm.) Barneby
WJE #452 Carthew Mt., Waterton Park, Alberta
2n=48



karyotypes are characteristic of the more advanced or specialized members of a supraspecific taxon.

Attempts to observe meiotic pairing following fixation of flower buds in acetic alcohol proved unsuccessful.

Guard Cell Measurements:

Guard cell measurements indicated: 1) a positive correlation between guard cell size and ploidy level in the two taxa (*gracilis* and *varians*) with two chromosome numbers; 2) no significant difference between the mean guard cell length of the different taxa sharing the same chromosome number; and 3) that guard cell length in all taxa was positively correlated with ploidy level.

Within the taxon *gracilis*, the mean guard cell length for the tetraploid was 11.71 microns (N=485) while the mean for the hexaploid was 14.24 microns (N=75). A student's *t*-test showed a significant difference (Sdx=0.04, *t*=42.7) between the two means at the 0.1% level. Similar statistical procedures demonstrated that the mean (13.18 microns) of the hexaploid of the taxon *varians* differed significantly (Sdx=0.039, *t*=50) from the mean guard cell length (16.06 microns) of the dodecaploid.

The five taxa with uniform chromosome numbers did not differ significantly when their mean guard cell lengths were compared to the means of other taxa sharing the same ploidy level. Thus the taxa *jordalii*, *davisii*, and *dispar* all share the same chromosome number (2n=32)

while their respective mean cell lengths are 11.48 microns (N=176), 11.91 microns (N=100), and 11.81 microns (N=75). Both 2n=48, the taxa *columbiana* and *cusickii* have means of 13.41 microns (N=77) and 13.62 microns (N=350) respectively.

Collective analysis of the guard cell length data indicated that cell length was significantly correlated with chromosome number. Table 7 lists the statistical results while Figure 2 illustrates the size frequency data graphically. Over two thousand measurements were taken.

TABLE 7.

Statistical comparison of guard cell length between ploidy levels in the *Oxytropis campestris* (L.) DC. complex in northwestern North America

Comparison	Standard Deviation between means (Sdx)	*t* value
2n=32 : 2n=48	0.024	41.6
2n=48 : 2n=96	0.033	55.75
2n=32 : 2n=96	0.034	83.0

The significant differences between mean cell lengths made possible the determination of ploidy levels from herbarium specimens (Table 8). Only those specimens

TABLE 8.

Herbarium Specimens from Which Chromosome Number has been Determined by Guard Cell Measurement

2n=	Locality	Collector(s)	Herbarium
32	Mt. Mansfield, B.C., Haines Rd.	J. Sias #19	CAN
32	Richardson Mts., N.W.T.	S.L. Welsh & J.K. Rigby #12062	BRY
32	mile 81, Dempster Hwy., Y.T.	R.T. Porsild #1486	CAN
32	Mackenzie Mts., N.W.T.	A.E. Porsild & A.J. Breitung #11817	CAN
32	Canol Rd., mile 111E, N.W.T.	V.C. Wynne-Edwards #8346	CAN
32	Wiseman, Alaska	H.M. Raup & A.J. Soper #9427	GH
32	Mackenzie Mts., N.W.T.	H. M. Raup & A.J. Soper #9449	GH
32	Juneau, Alaska	M. Williams #1397	GH
48	Brintnell Lake, N.W.T.	H.M. Raup & A.J. Soper #9427	ALTA
48	mile 81, Mackenzie Hwy., N.W.T.	S.S. Talbot #4630	ALTA
48	mile 22E, Canol Rd., N.W.T.	W.J. Cody & R.L. Gutteridge #7959	ALTA
48	Jago River, Alaska	J.E. Cantlon & W.T. Gillis #57-743	CAN
48	Chitina River, Alaska	H.M. Laing #125	CAN

TABLE 8. (cont.)

48	Jago River, Alaska	J.E. Cantlon & W.T. Gillis #57-1066	CAN
48	Lake Schrader, N. Slope, Alaska	L.A. Spetzman #518	CAN
48	Hayes River, N.W.T.	H.J. Scoggan #5893	CAN
48	Churchill, Manitoba	G.M. Keleher #31	CAN
48	Umiat, Alaska	I.L. Wiggins #13878	CAN
48	Umiat, Alaska	R.D. & M. Wood #421	CAN
48	Ewariege Lake, N.W.T.	V. Hawley #?	CAN
48	Richardson Mts., N.W.T.	J.G. Packer #1371	ALTA
48	Fairbanks, Alaska	E.Scaman #1654	GH
48	Churchill, Manitoba	A.E. Porsild #5480	GH
48	Firth R. & Mancha R., Alaska	E. Hulten #62767	BRY
48	Stevens Co., Wash.	H.T. Rogers #520	GH
48	Okanagan Co., Wash.	H. St. John #7703	GH
48	Savona, B.C.	C.L. Hitchcock & J. S. Martin #7396	GH
48	Mt. Wow, Wash.	J.W. Thompson #12578	GH
96	Ogotoruk Creek, Alaska	J.G. Packer #2582	ALTA
96	Cape Thompson, Alaska	R.D. & M. Wood #555	CAN

TABLE 8. (cont.)

96	Okpilak Lake, Alaska	J.E. Cantlon & W.M. Malcolm #58-0283	CAN
96	Richardson Hwy., Alaska	E. Scaman #4622	GH
96	Mt. McKinley Park, Alaska	E. Scaman #5103	GH
96	Gulkana, Alaska	E. Scaman #4547	GH
96	Curry, Alaska	E. Scaman #1617B	GH
96	Rapids Lodge, Alaska	E. Scaman #296	GH

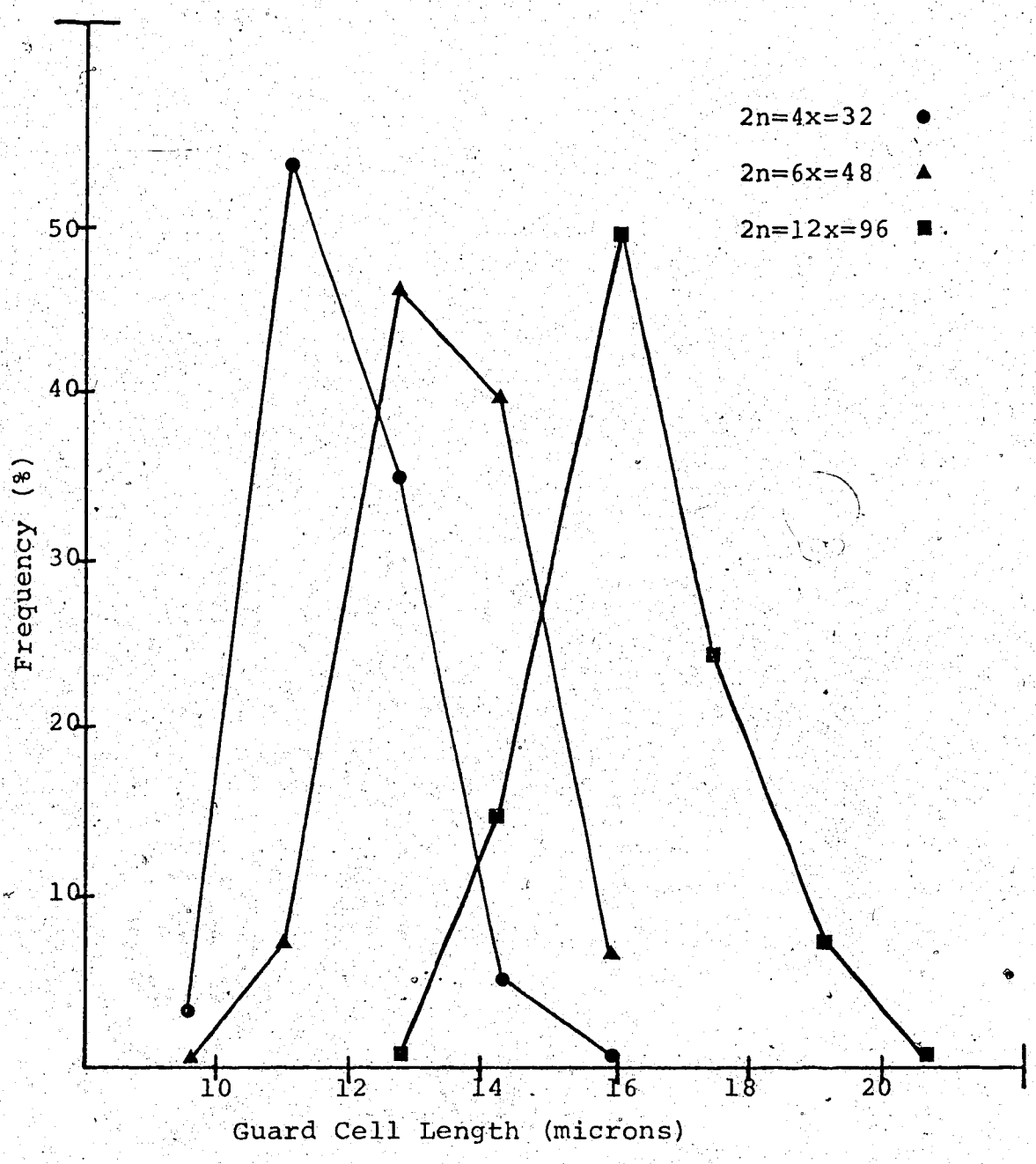


FIGURE 2. Guard Cell Length Frequencies in the *Oxytropis campestris* (L.)DC. Complex in Northwestern North America

in which the average cell length was within 0.75 microns of the predicted mean were used.

Chemical Studies:

The chemical aspects of this investigation involved detailed analysis of the flavonoid constituents in five populations. These five populations were deliberately chosen to represent four of the morphological taxa, the three ploidy levels, and material from glaciated and unglaciated regions of the continent. Figures 3-7 and Tables 9-13 show the fifty-eight compounds that were extracted, purified, and characterized using various chromatographic, hydrolytic, and optical procedures.

Comparison of these data revealed that at least thirty-three different flavonoid glycosides were present in the populations sampled (Figures 10-42). A total of seventeen flavone glycosides were found (Figure 8, Table 14) while the remaining sixteen compounds (Figure 9, Table 15) were flavonol glycosides. Apigenin and luteolin were the two flavone aglycones identified; similarly, there were only two flavonol aglycones: kaempferol and quercetin. Four glycosides had unidentified aglycone components.

Only three of the five populations examined contained glycosides of all four known aglycones. The sample population of the taxon *cusickii* lacked apigenin glycosides while that of the taxon *jordalii* lacked kaempferol glycosides.

FIGURE 3.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *cusickii* (Greenm.) Barneby WJE #021, Prospect Creek Road, Alberta

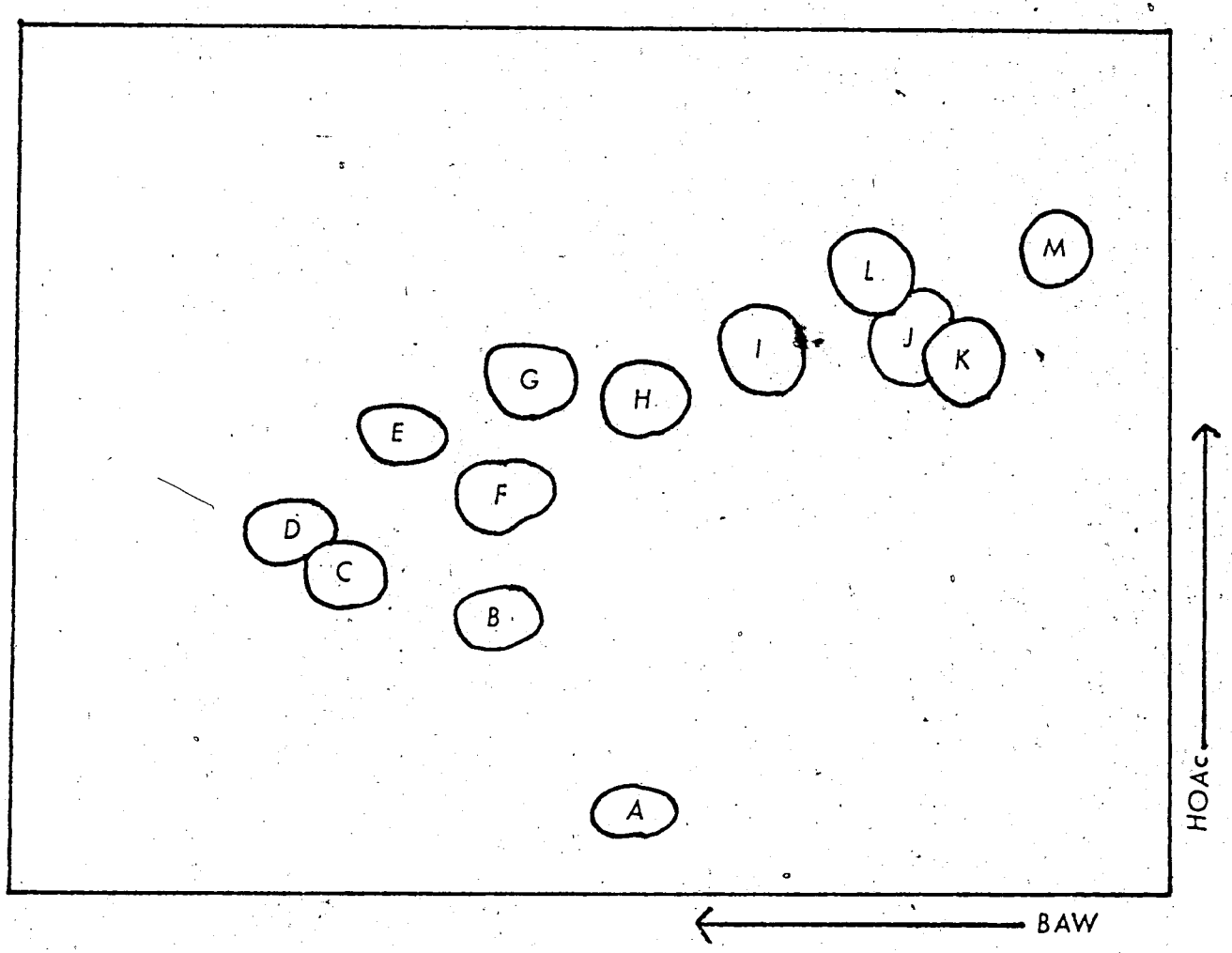


TABLE 9.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *cusickii* (Greenm.) Barneby

WJE #021, Prospect Creek Road, Alberta

Compound	Colour UV/NH_3	R_f's X 100 Solvents BAW	H_2O	HoAc	PhOH	MeOH *II	MeOH I	U.V. Spectral Data λ (in nm.) NaOMe I	$AlCl_3$ I	HCl I	H_3BO_3 I	NaOAc II	Aglycone	Sugar(s)	Attachment
A	p,y	47	02	11	56 38	256 270	346	56	79	-67	24	0	luteolin	glucose	7-O-glucoside
B	p,y	58	06	34	29	257 268sh	358	66	54	-48	16	17	quercetin	glucose	3-O-glucoside
C	p,y	70	09	38	70 41	256 268sh	358	60	[illegible]	-44	4	17	quercetin	glucose	3-O-glucoside
D	p,yg	76	13	43	68	268	306sh 351	55	48	---	5	6	kaempferol	glucose	3-O-glucoside
E	p,yg	66	23	53	62	267	350	60	50	---	4	8	kaempferol	glucose xylose	3-O-sambubioside
F	p,y	58	18	48	67 48	258 270sh	358	62	62	-58	12	18	quercetin	glucose xylose	3-O-sambubioside
G	p,yg	54	26	60	53	258 270sh	358	64	66	-62	18	14	quercetin	glucose xylose	3-O-diglucosyl- xyloside
H	p,yg	44	25	57	25	258 270sh	356	62	58	-54	12	10	quercetin	glucose xylose	3-O-diglucosyl- xyloside
I	p,y	36	38	61	47	276 286sh	344	70	54	---	18	0	?	?	?
J	p,y	24	43	65	44	256 270sh	358	64	72	-66	14	6	quercetin	?	?
K	p,y	19	30	62	28	258 268sh	358	72	62	-54	20	12	quercetin	glucose	3-O-glucose 7-O-glucoside
L	p,y	27	53	71	46	260 270sh	362	66	56	-52	18	8	quercetin	glucose xylose	3-O-sambubioside 7-O-glucoside
M	p,y	10	59	74	34	258 270sh	358	64	80	-72	20	8	quercetin	glucose	3-O-sophoroside 7-O-glucoside

p - purple, y - yellow, yg - yellow-green

FIGURE 4..

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *gracilis* (A.Nels.) Barneby WJE #048, Hwy. #1, West of Calgary, Alberta

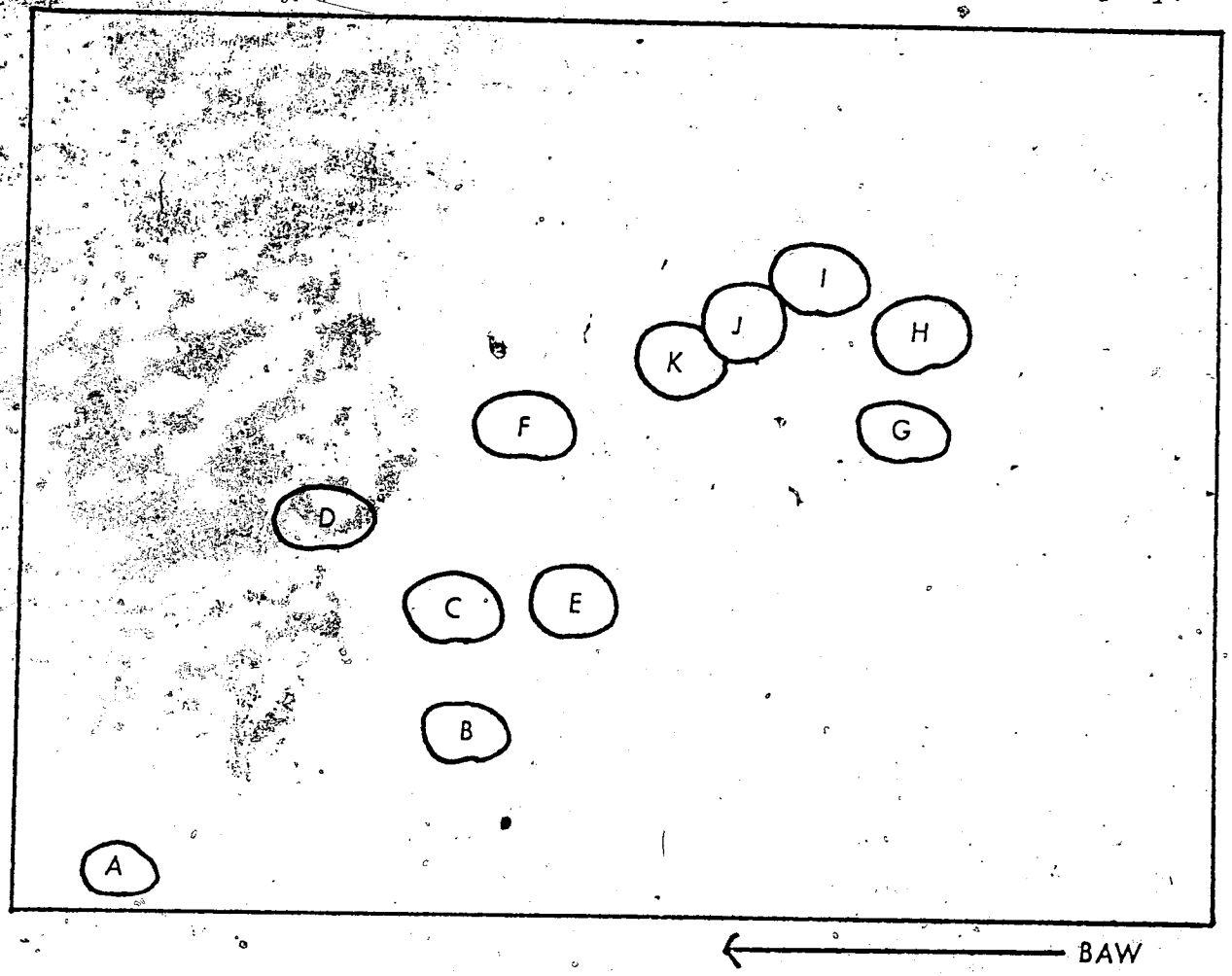


TABLE 10.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *gracilis* (A.Nels.) Barneby

WJE #048, Hwy. #1, west of Calgary, Alberta

Compound	Colour UV/NH_3	R_f's X 100 Solvents				U.V. Spectral Data λ (in nm.)							Aglycone	Sugar(s)	Attachment
		BAW	H_2O	HOAc	PhOH	MeOH II	MeOH I	NaOMe I	$AlCl_3$ I	HCl I	H_3BO_3 I	NaOAc II			
A	p,yg	90	01	04	87	264	324	80	86	---	0	6	?	glucose	?
B	p,y	62	03	23	81	272	326	70	60	-36	12	0	apigenin	glucose rhamnose	7-O-rutinoside
C	p,y	63	10	36	79 60 46	258 268sh	360	70	52	-50	10	18	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
D	p,yg	73	15	44	85 75	269	353	48		---	2	5	kaempferol	glucose	3-O-glucoside
E	p,y	54	52	33	29	258 268sh	356	65	56	-51	12	17	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
F	p,yg	58	54	54	61	268	350	88	68	---	0	8	kaempferol	glucose rhamnose	3-O-rutinoside
G	p,yg	26	69	53	58	274	338	64	50	-40	12	10	?	glucose	?
H	p,y	24	51	66	61	259 270	338	86	66	-42	18	9	luteolin	glucose	7-O-triglucoside
I	p,yg	33	33	71	54	270	340	62	61	---	10	4	?	glucose rhamnose	?
J	p,yg	40	40	66	77	268	344	42	56	---	2	2	apigenin	glucose	7-O-triglucoside
K	p,yg	45	28	63	74	272 284	324	70	75	---	0	0	apigenin	glucose arabinose	7-O-vicianoside

p - purple, y - yellow, yg - yellow-green

FIGURE 5.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *jordalii* (Porsild) Welsh WJE #223, Mt. Cheviot, Prospect Creek Road, Alberta

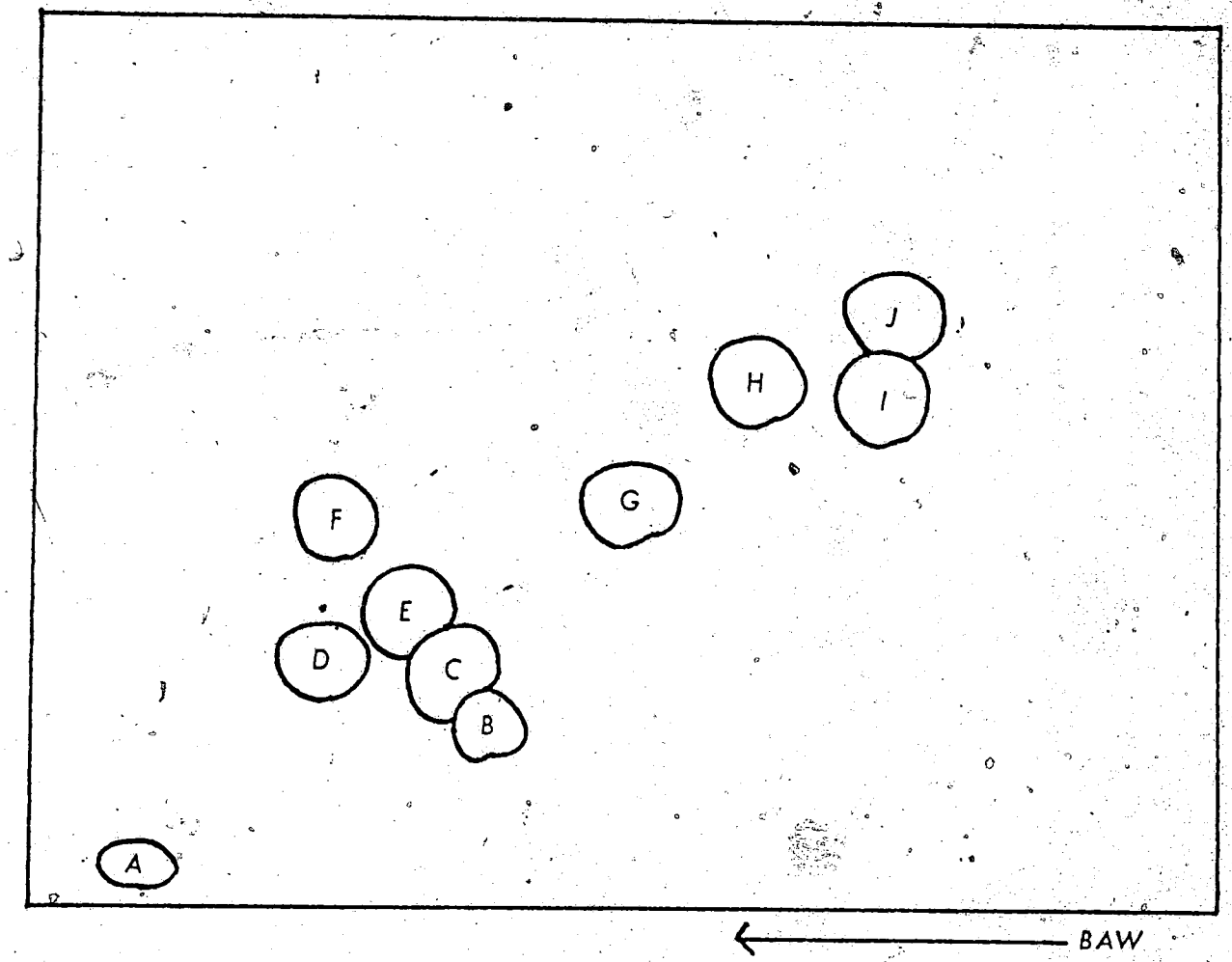


TABLE 11.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *jordalii* (Porsild) Welsh

WJE #223, Mt. Cheviot, Prospect Creek Road, Alberta

Compound	Colour UV/NH_3	R_f's X 100 Solvents				MeOH		U.V. Spectral Data λ (in nm.) NaOMe	$AlCl_3$	HCl	H_3BO_3	NaOAc	Aglycone	Sugar(s)	Attachment
		BAW	H_2O	HoAc	PhOH	II	I	I	I	I	I	II			
A	p,y	89	02	04	55	258 268sh	330	66	56	-44	0	16	?	glucose	?
B	p,y	60	03	22	80	270	330	66	56	---	0	0	apigenin	glucose	7-O-glucoside
C	p,y	62	12	27	78	270	324	64	60	---	4	8	apigenin	glucose	7-O-glucoside
D	p,y	74	08	28	78	256 268sh	352	66	52	-42	7	18	quercetin	glucose	3-O-glucoside
E	p,y	68	20	34	79	256 268sh	356	62	52	-46	7	18	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
F	p,y	72	15	45	56	268	330	82	70	---	26	4	apigenin	glucose	7-O-diglucoside
G	p,y	48	25	48	66	258 270sh	334	94	72	-46	26	12	luteolin	glucose	7-O-diglucoside
H	p,yg	41	29	61	79	272	326	70	72	---	22	0	apigenin	glucose xylose	7-O-sambubioside
I	p,y	29	35	59	71	272	330	70	70	---	6	0	apigenin	glucose	7-O-triglucoside
J	p,yg	28	31	68	47	258 268sh	338	84	60	-38	20	10	luteolin	glucose	7-O-triglucoside

p - purple, y - yellow, yg - yellow-green

FIGURE 6.

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *varians* (Rydb.) Barneby WJE #250, East of Tok Jct., Alaska 2n=48

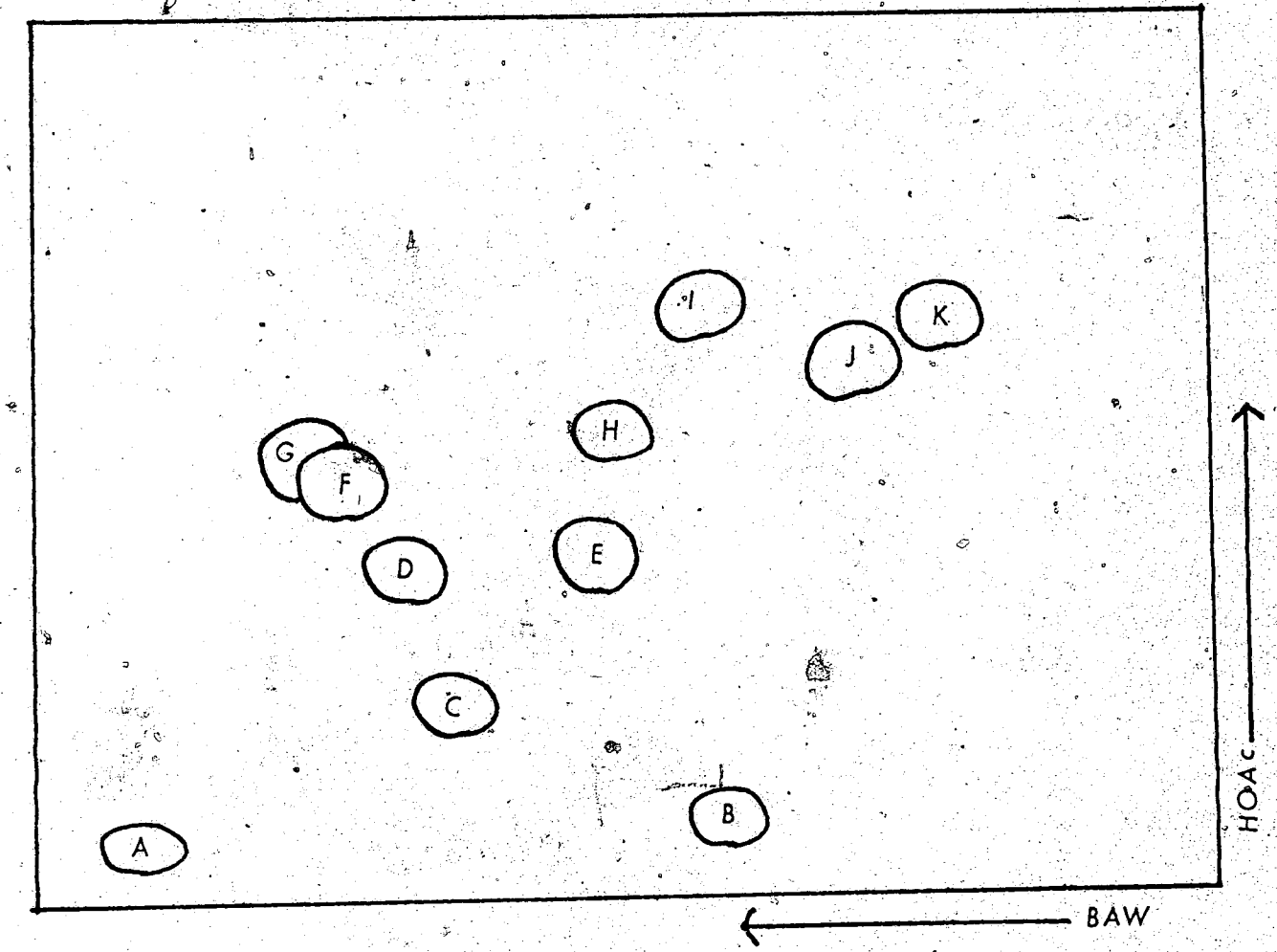


TABLE 12.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *varians* (Rydb.) Barneby

WJE #250, east of Tok Jct., Alaska 2n=48

Compound	Colour UV/NH_3	R_f's X 100 Solvents				U.V. Spectral Data λ (in nm.)							Aglycone	Sugar(s)	Attachment
		BAW	H_2O	HOAc	PhOH	MeOH II	MeOH I	NaOMe I	$AlCl_3$ I	HCl I	H_3BO_3 I	NaOAc II			
A	p,yg	89	00	08	90	270	328	68	62	50	4	6	?	glucose	?
B	p,y	41	02	11	85	258							luteolin	glucose	7-O-glucoside
C	p,yg	64	03	23	61	268	324	68	64	---	8	2	apigenin	glucose rhamnose	7-O-rutinoside
D	p,yg	67	13	39	76 48	256	356	64	54	-48	6	18	quercetin	glucose	3-O-glucoside
E	p,y	51	52	39	25	258 270sh	334	84	80	-52	26	14	luteolin	glucose rhamnose	7-O-rutinoside
F	p,yg	72	12	49	55	260 270sh	350	58	51	---	4	17	kaempferol	glucose	3-O-glucoside
G	p,yg	74	15	51	61 47	269	350	64	58	---	11	4	kaempferol	glucose	3-O-glucoside
H	p,yg	50	33	54	70 44	258 270sh	358	61	52	-46	18	18	quercetin	glucose rhamnose	3-O-rutinoside
I	p,yg	43	35	67	46	270	324	68	74	---	8	4	?	glucose rhamnose	?
J	p,yg	30	29	62	61	258 268sh	330	98	76	-42	30	0	luteolin	glucose rhamnose	7-O-glucosyl-rutinoside
K	-,y	23	44	66	41	256 268sh	330	103	68	-40	24		luteolin	glucose	7-O-triglucoside

p - purple, y - yellow, yg - yellow-green

FIGURE 7:

Master chromatogram of the flavonoid glycosides in *Oxytropis campestris* (L.)DC. var. *varians* (Rydb.) Barneby WJE #310, mile 322, TAPS Hwy., Alaska 2n=96

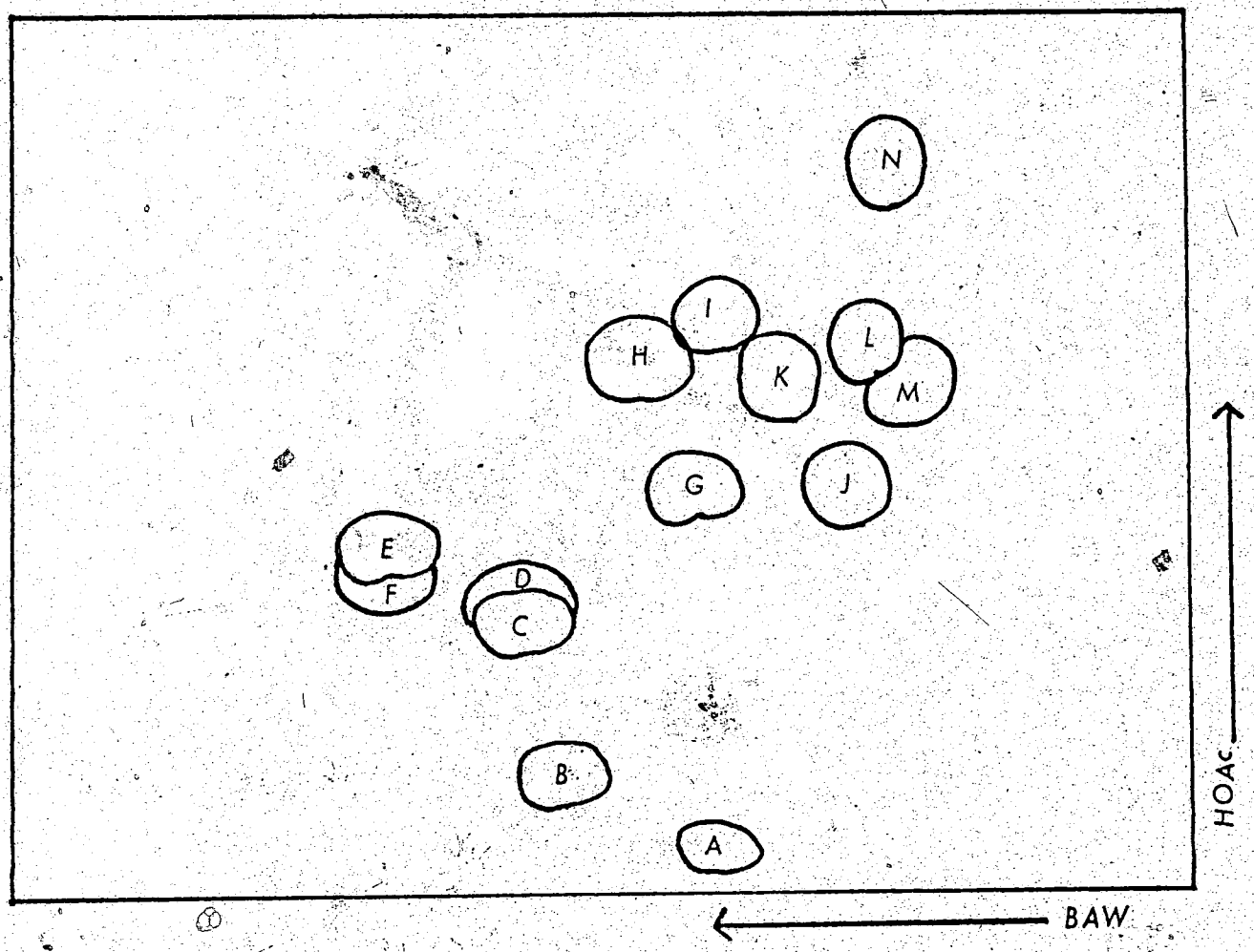


TABLE 13.

Flavonoid glycosides of *Oxytropis campestris* (L.) DC. var. *varians* (Rydb.) Barneby

WJE #310, mile 322, TAPS Hwy., Alaska 2n=96

Compound	Colour UV/NH_3	R_f's X 100 Solvents				U.V. Spectral Data λ (in nm.) MeOH		NaOMe	$AlCl_3$	HCl	H_3BO_3	NaOAc	Aglycone	Sugar(s)	Attachment
		BAW	H_2O	HoAc	PhOH	II	I	I	I	I	I	II			
A	p,y	41	01	07	54	272 286sh				---		0	luteolin		7-O-glucoside
B	p,yg	54	02	15	83	268 274sh	330		53	---			apigenin	glucose arabinose	7-O-vicianoside
C	p,y	57	14	32	75 51	258 268sh	356	58	64	-60	12	16	quercetin	glucose	3-O-glucoside
D	p,y	57	09	33	73 48	258 270sh	358	58	48	-44	4	18	quercetin	glucose	3-O-glucoside
E	p,yg	68	20	41	76	268	352	51	46	---	4	10	kaempferol	glucose	3-O-glucoside
F	p,yg	68	18	38	78	268	300 352	50	48	---	2	8	kaempferol	glucose	3-O-glucoside
G	p,y	42	35	47	74	256 268sh	358	60	50	-46	6	12	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
H	p,yg	47	40	62	79	270	326	84	72	---	26	0	apigenin	glucose-rhamnose	7-O-[illegible]
I	p,	40	26	57	78 67	270								glucose	?
J	p,	29	18	48	60	270	330							glucose	?
K	p,y	35	39	58	60	272	330	84	70	---	20	0	apigenin	glucose	7-O-triglucoside
L	p,	28	33	61	70	276						0		glucose	?
M	p,	25	48	59	60 39	258 282sh								glucose	?
N	-,	26	73	83	--	278 286sh						0		glucose	?

p - purple, y - yellow, yg - yellow-green

FIGURE 8.

Master chromatogram of the flavone glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

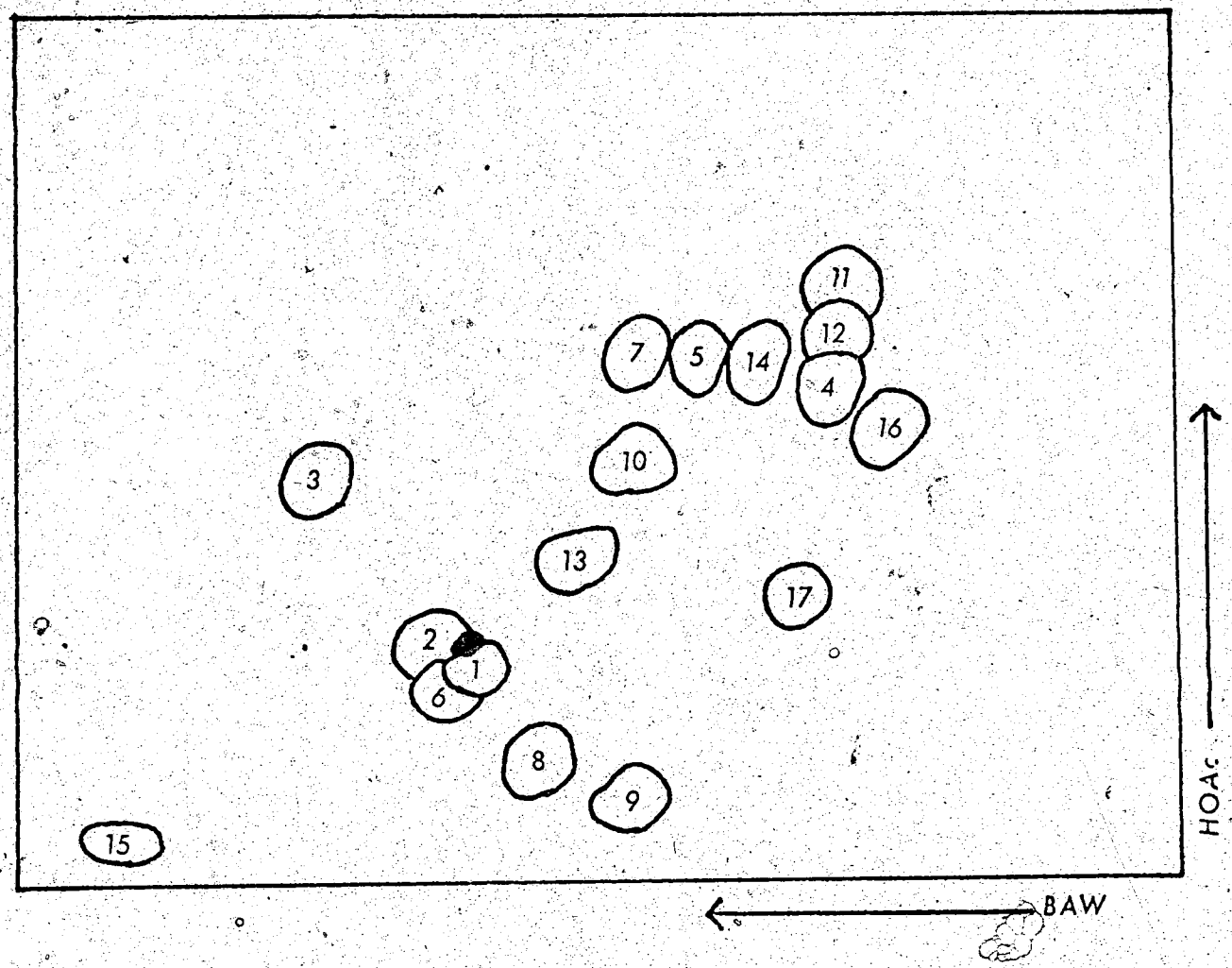


TABLE 14.

Flavone glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

Compound Number	Colour UV/NH_3	Rf's X 100						U.V. Spectral Data λ (in nm.)					Aglycone	Sugar(s)	Attachment
		Solvents				MeOH		NaOMe	$AlCl_3$	HCl	H_3BO_3	NaOAc			
		BAW	H_2O	HoAc	PhOH	II	I	I	I	I	I	II			
1	p,y	60	03	22	80	270	330	66	56	---	0	0	apigenin	glucose	7-O-glucoside
2	p,y	62	12	27	78	270	324	64	60	---	4	8	apigenin	glucose	7-O-glucoside
3	p,y	72	15	45	56	268	330	82	70	---	26	4	apigenin	glucose	7-O-diglucoside
4	p,y	29	35	59	71	272	330	70	70	---	6	-4	apigenin	glucose	7-O-triglucoside
5	p,y	41	29	61	79	272	326	70	72	---	22	0	apigenin	glucose xylose	7-O-sambubioside
6	p,yg	62	03	23	81	272	326	70	60	---	8	0	apigenin	glucose rhamnose	7-O-rutinoside
7	p,yg	45	28	63	74	272 284	324	70	75	---	0	0	apigenin	glucose arabinose	7-O-glucosyl-vicianoside
8	p,yg	54	02	15	83	268	330		53	---			apigenin	glucose arabinose	7-O-vicianoside
9	p,y	47	02	11	56 38	256 270	346	56	79	-67	24	0	luteolin	glucose	7-O-glucoside
10	p,y	48	25	48	66	258 270sh	334	94	72	-46	26	12	luteolin	glucose	7-O-diglucoside
11	p,yg	28	31	68	47	258 268sh	338	84	60	-38	20	10	luteolin	glucose	7-O-triglucoside
12	p,yg	30	29	62	61	258 268sh	330	98			30	0	luteolin	glucose rhamnose	7-O-glucosyl-rutinoside
13	p,yg	51	52	39	25	258 268sh	334	84	80	-52	36	14	luteolin	glucose rhamnose	7-O-rutinoside
14	p,y	36	38	61	47	276 286sh	344	70	54	---	18	-4	?	?	
15	p,y	89	02	04	55	258 268sh	330	66	56	-44	0	8	?	glucose	
16	p,yg	26	69	53	58	274	338	64	50	-40	12	10	?	glucose	
17	p,yg	33	33	71	54	270	340	62	61	---	10	4	?	glucose rhamnose	

p - deep purple, y - yellow, yg - yellow-green

FIGURE 9.

Master chromatogram of the flavonol glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

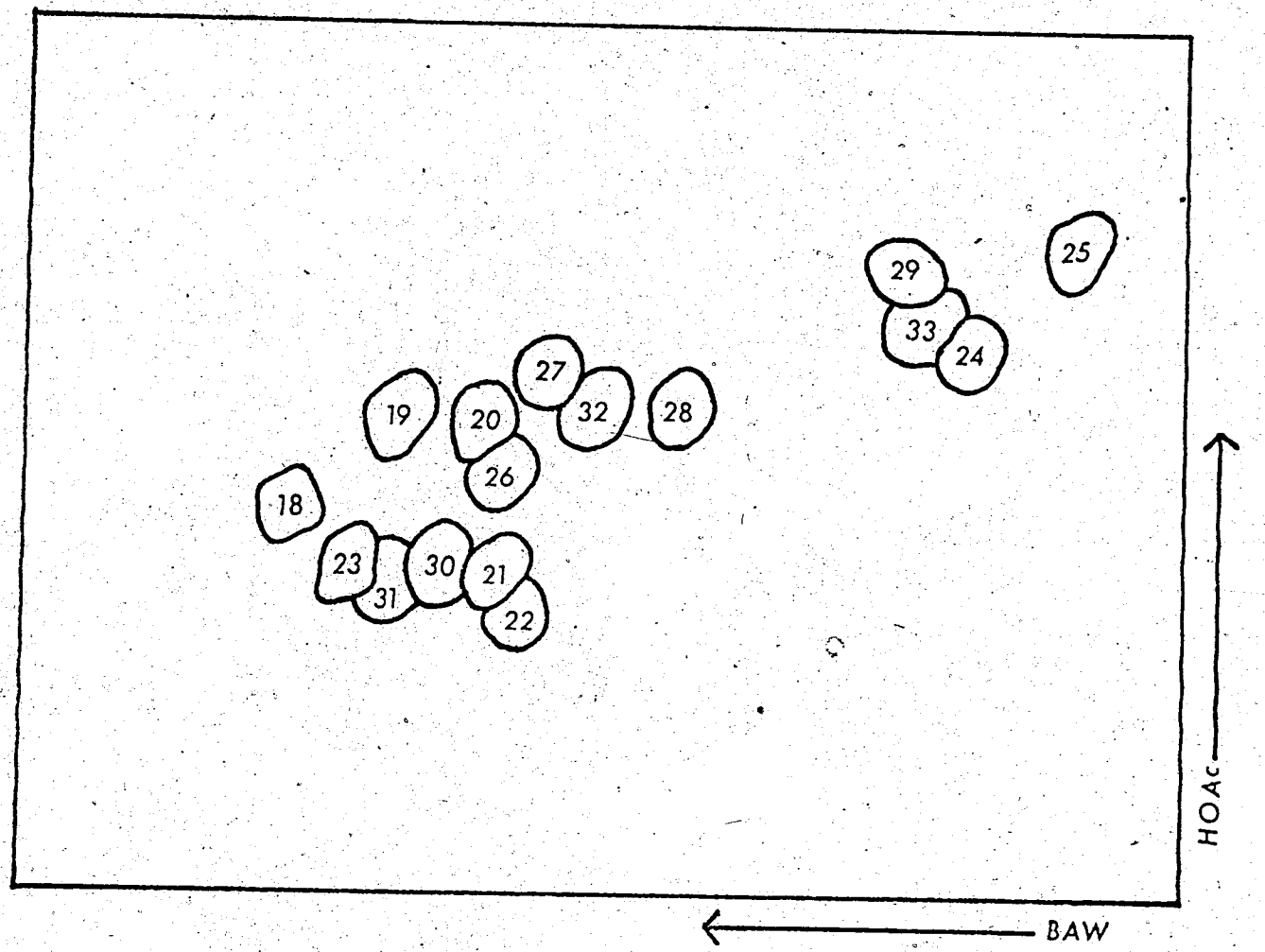


TABLE 15.

Flavonol glycosides of the *Oxytropis campestris* (L.)DC. complex in northwestern North America

Compound Number	Colour UV/NH_3	R_f's X 100						U.V. Spectral Data λ (in nm.)					Aglycone	Sugar(s)	Attachment
		Solvents				MeOH		NaOMe	$AlCl_3$	HCl	H_3BO_3	NaOAc			
		BAW	H_2O	HOAc	PhOH	II	I	I	I	I	I	II			
18	p,yg	76	13	43	68	268	351	55	48	---	5	6	kaempferol	glucose	3-O-glucoside
19	p,yg	66	23	53	62	267	350	60	50	---	4	8	kaempferol	glucose xylose	3-O-sambubioside
20	p,yg	58	54	54	61	268	350	88	68	---	0	8	kaempferol	glucose rhamnose	3-O-rutinoside
21	p,y	58	06	34	29	257 268sh	358	66	54	-48	16	17	quercetin	glucose	3-O-glucoside
22	p,y	57	14	32	75 51	258 268sh	354	60	66	-60	14	14	quercetin	glucose	3-O-glucoside
23	p,y	70	09	38	70 41	256 268sh	358	60	48	-44	4	17	quercetin	glucose	3-O-glucoside
24	p,y	19	30	62	28	258 268sh	358	72	62	-54	20	12	quercetin	glucose	3-O-glucose 7-O-glucoside
25	p,y	10	59	74	34	258 270sh	358	64	80	-72	20	8	quercetin	glucose	3-O-sophoroside 7-O- glucoside
26	p,y	58	18	48	67 48	258 270sh	358	62	62	-58	12	18	quercetin	glucose xylose	3-O-sambubioside
27	p,yg	54	26	60	53	258 270sh	358	64	66	-62	18	14	quercetin	glucose xylose	3-O-diglucosyl-xyloside
28	p,yg	44	25	57	25	258 270sh	356	62	58	-54	12	10	quercetin	glucose xylose	3-O-diglucosyl-xyloside
29	p,y	27	53	71	46	260 270sh	362	66	56	-52	18	8	quercetin	glucose xylose	3-O-sambubioside 7-O-glucoside
30	p,y	63	10	36	79 60 46	258 268sh	360	70	52	-50	10	18	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
31	p,y	68	20	34	79	256 268sh	356	62	52	-46	12	18	quercetin	glucose rhamnose	3-O-glucosyl-rhamnoside
32	p,yg	50	33	54	70 44	258 268sh	358	61	52	-46	18	18	quercetin	glucose rhamnose	3-O-rutinoside
33	p,y	24	43	65	44	256 270sh	358	64	72	-66	14	6	quercetin	?	

p - deep purple, y - yellow, yg - yellow-green

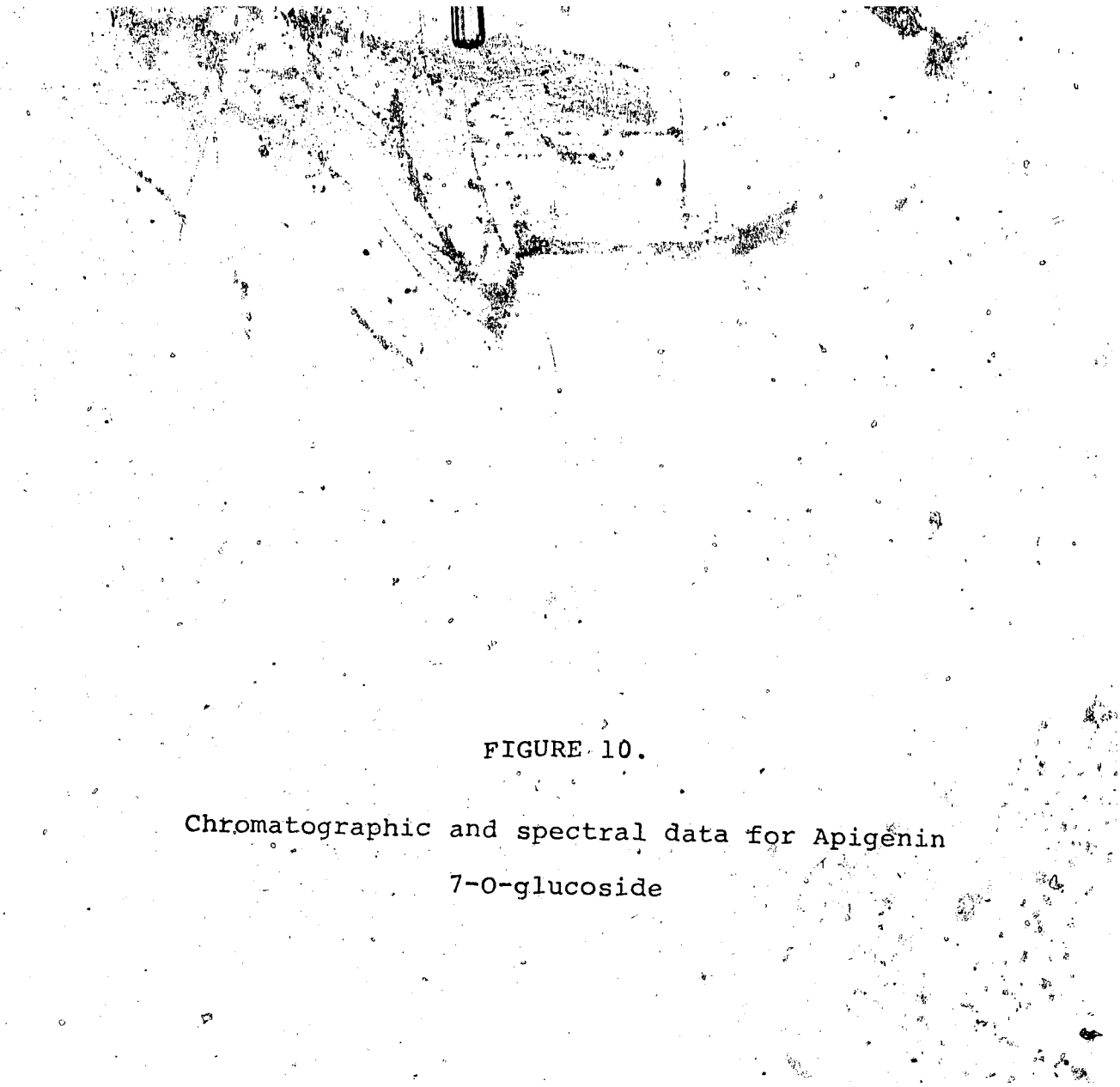
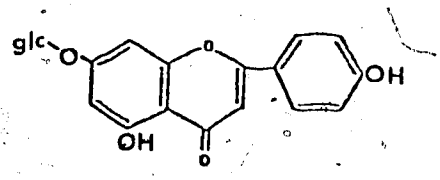


FIGURE 10.

Chromatographic and spectral data for Apigenin 7-O-glucoside

#1 Apigenin 7-O-glucoside

isomer #1

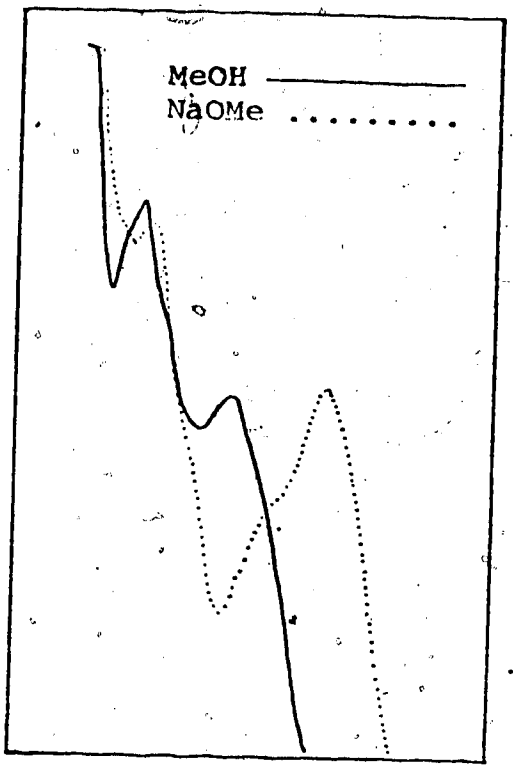


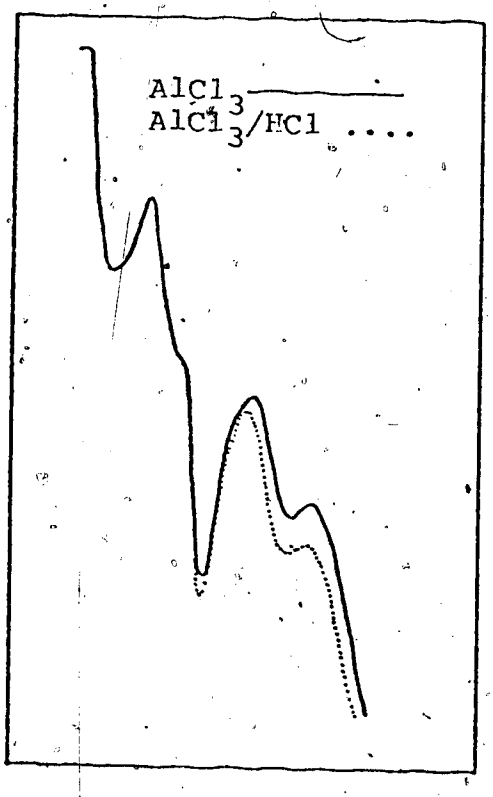
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HOAc	PhOH	UV	UV/NH_3
60	03	22	80	ppl	ylw

UV Spectral Data

MeOH	270, 330
NaOMe	275, 358sh, 392
$AlCl_3$	278, 346, 386
$AlCl_3$/HCl	278, 342, 384
NaOAc	270, 388
H_3BO_3	272, 330





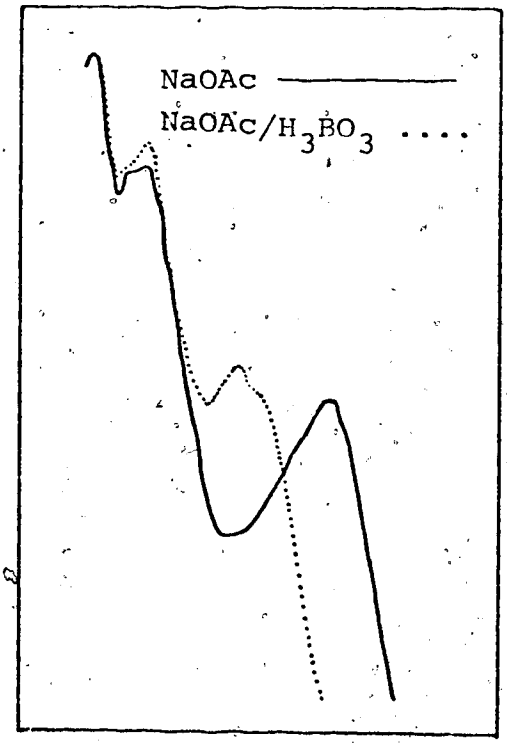
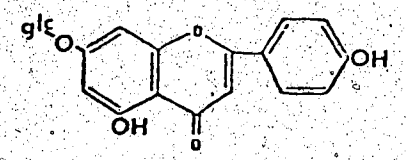


FIGURE 11.

Chromatographic and spectral data for Apigenin 7-O-glucoside

#2 Apigenin 7-O-glucoside

isomer #2

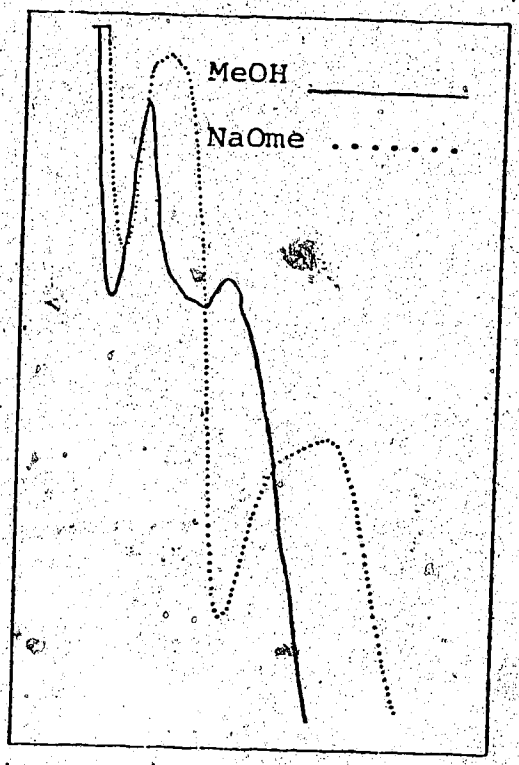


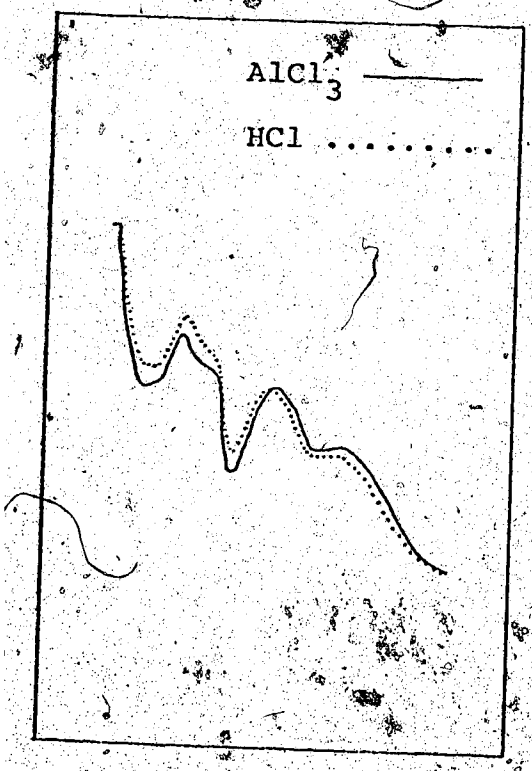
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
62	12	27	78	ppl	ylw

UV Spectral Data

MeOh	270, 324
NaOMe	280, 358sh, 384
$AlCl_3$	278, 302sh, 341, 384
$AlCl_3$/HCl	280, 302sh, 336, 384
NaOAc	278, 366
H_3BO_3	272, 328





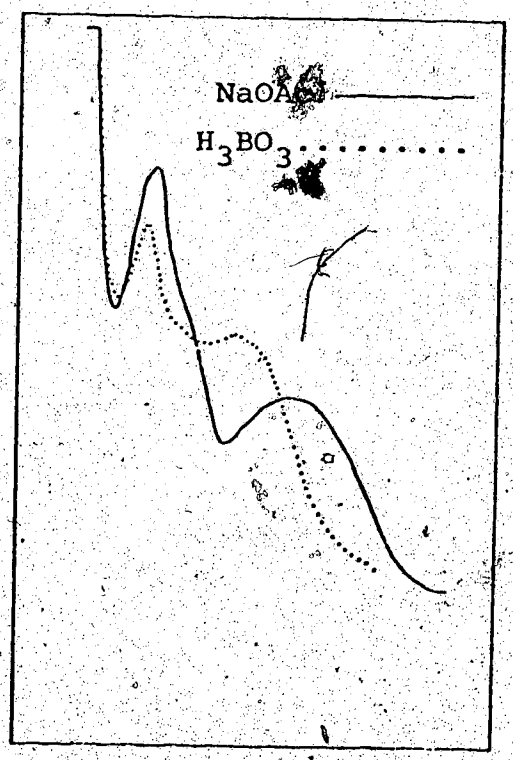
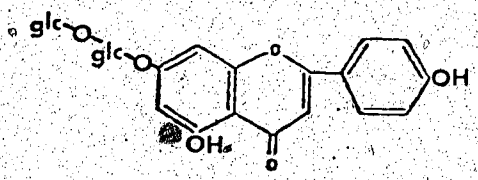


FIGURE 12.

Chromatographic and spectral data for Apigenin 7-O-diglucoside

#3 Apigenin 7-O-diglucoside

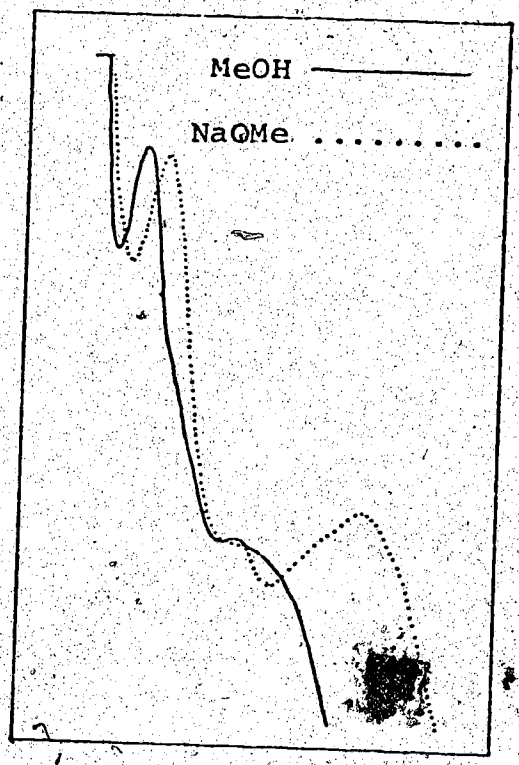


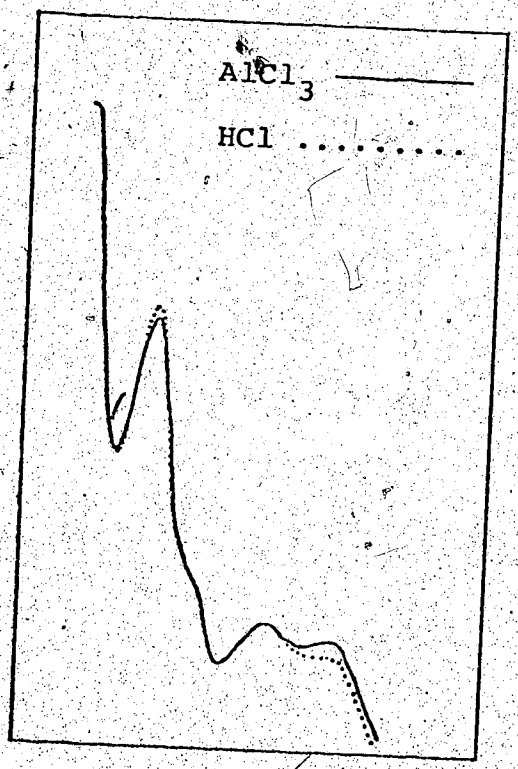
Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
72	15	45	56	ppl	ylw

UV Spectral Data

MeOH	268, 330
NaOMe	280, 334, 412
$AlCl_3$	276, 306sh, 354, 400
$AlCl_3$/HCl	276, 306sh, 354, 400
NaOAc	272, 378
H_3BO_3	268, 356





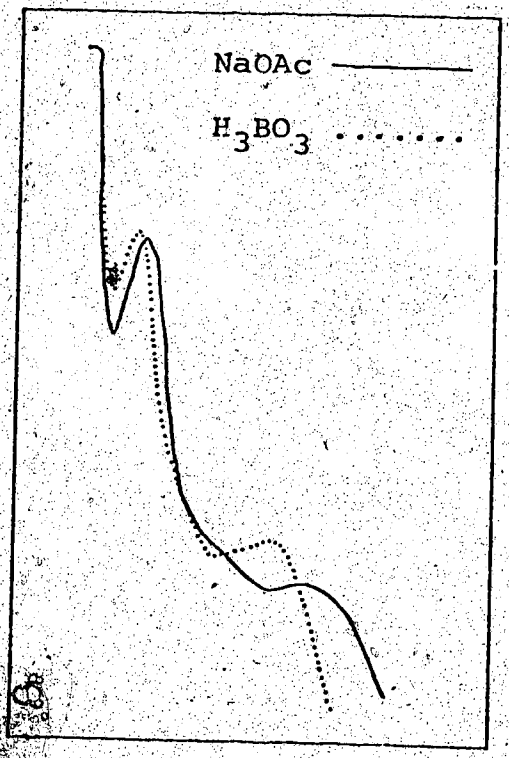
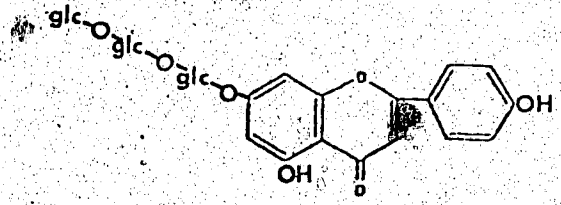


FIGURE 13.

Chromatographic and spectral data for Apigenin 7-O-triglucoside

#4 Apigenin 7-O-triglucoside

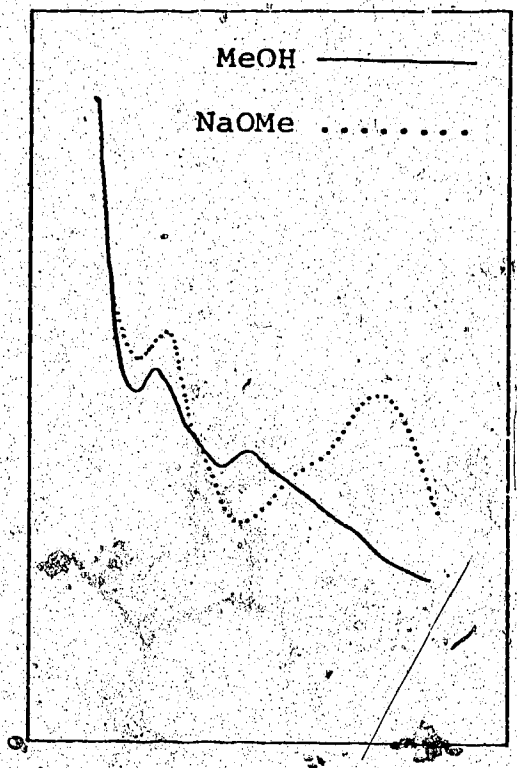


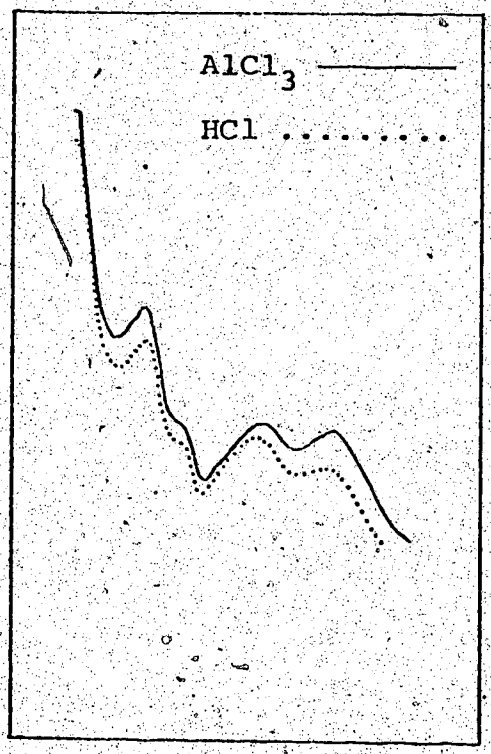
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
29	35	59	71	ppl	ylw

UV Spectral Data

MeOH	272, 330
NaOMe	278, 400
$AlCl_3$	276, 304sh, 354, 400
$AlCl_3$/HCl	276, 304sh, 350, 400
NaOAc	268, 358
H_3BO_3	268, 336





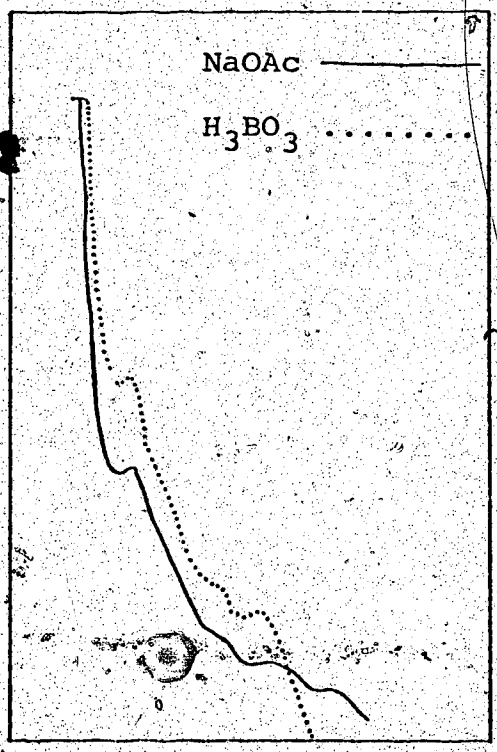
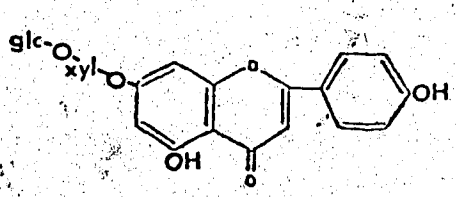


FIGURE 14.

Chromatographic and spectral data for Apigenin 7-O-sambubioside

#5 Apigenin 7-O-sambubioside

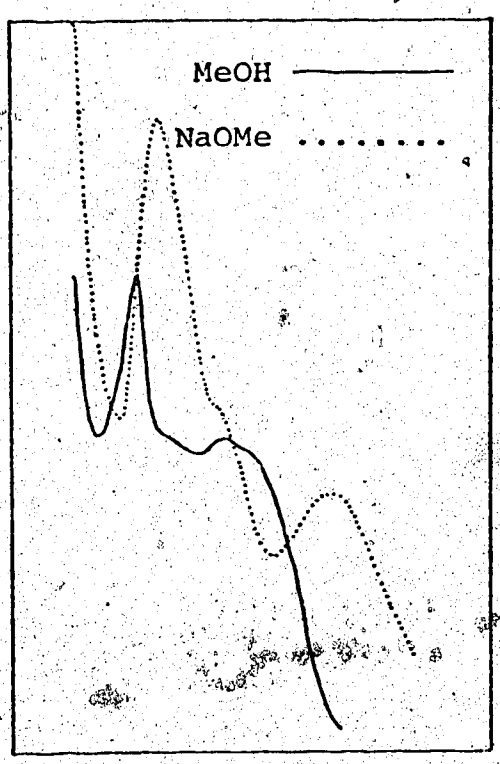


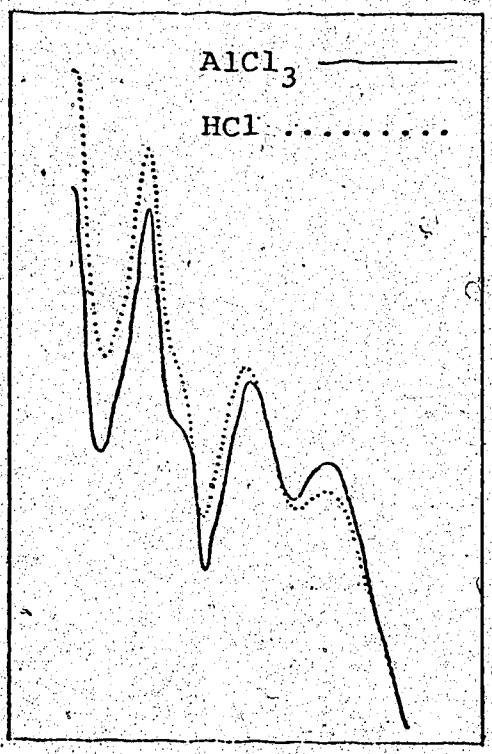
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HOAc	PhOH	UV	UV/NH_3
41	29	61	79	ppl	ylw

UV Spectral Data

MeOH	272, 326
NaOMe	284, 326sh, 398
$AlCl_3$	274, 294sh, 344, 398
$AlCl_3$/HCl	280, 294sh, 346, 398
NaOAc	272, 326
H_3BO_3	270, 348





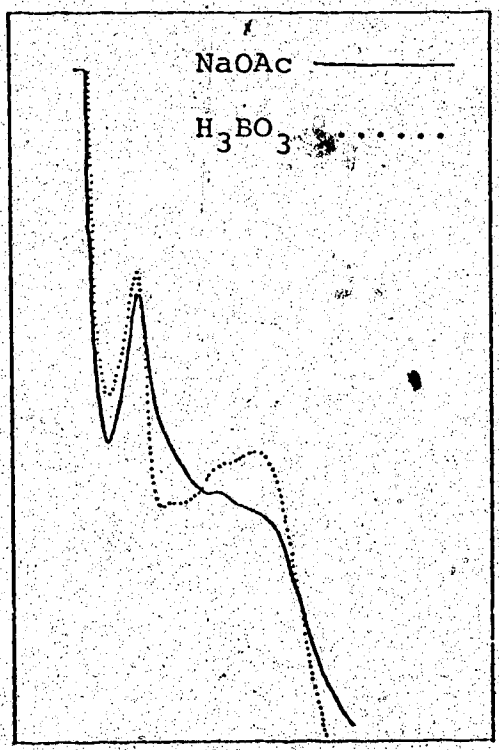
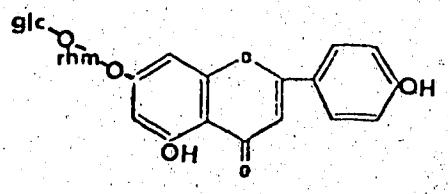


FIGURE 15.

Chromatographic and spectral data for Apigenin 7-O-rutinoside

#6 Apigenin 7-O-rutinoside

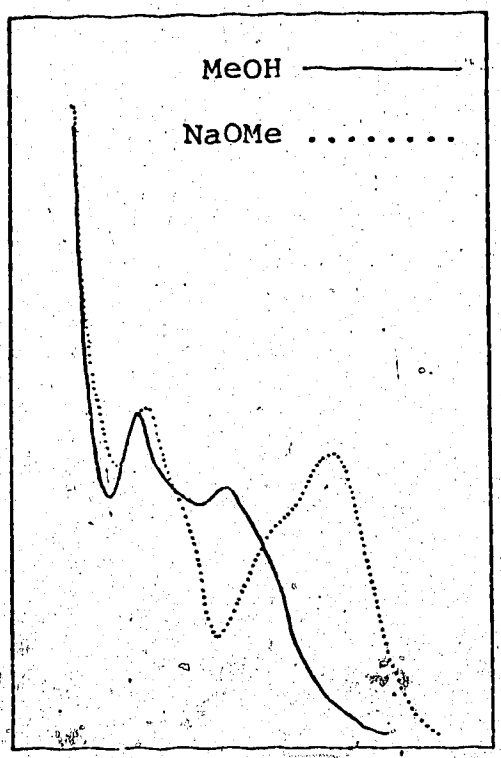


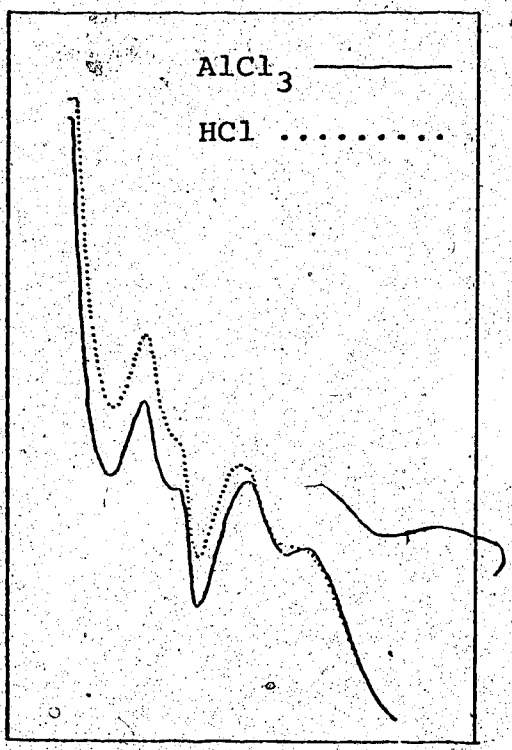
Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
62	03	23	81	ppl	yg

UV Spectral Data

MeOh	272, 326
NaOMe	278, 354sh, 396
$AlCl_3$	278, 302sh, 346, 386
$AlCl_3$/HCl	278, 302sh, 340, 386
NaOAc	272, 370
H_3BO_3	270, 334





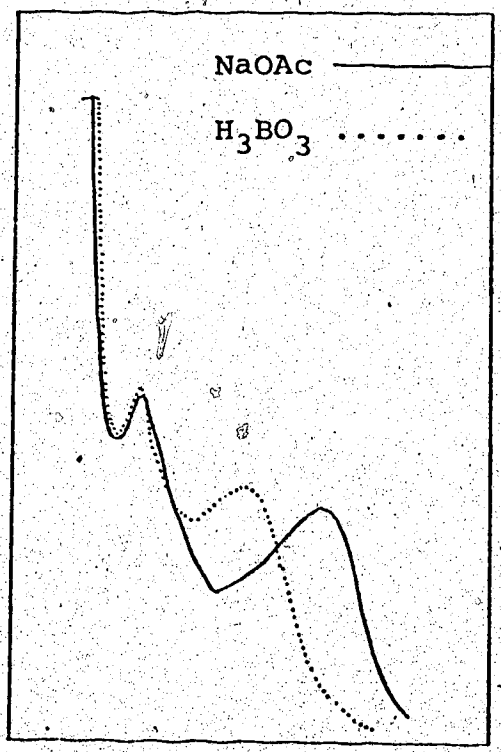
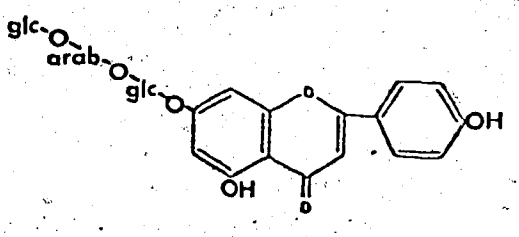
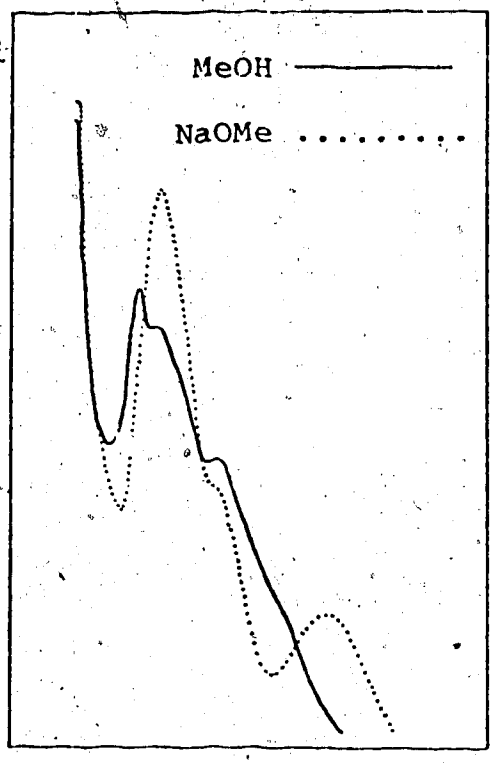


FIGURE 16.

Chromatographic and spectral data for Apigenin 7-O-glucosylvicianoside

#7 Apigenin 7-O-glucosylvicianoside



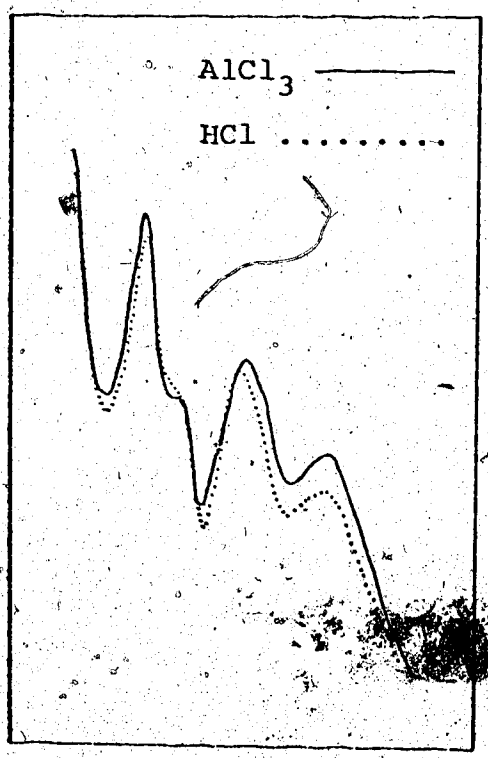


Chromatographic Data

Rf Values				Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
45	28	63	74	ppl	yg

UV Spectral Data

MeOH	272, 284, 324
NaOMe	286, 316sh, 394
$AlCl_3$	278, 302sh, 346, 399
$AlCl_3$/HCl	278, 302sh, 346, 398
NaOAc	272, 326
H_3BO_3	270, 324



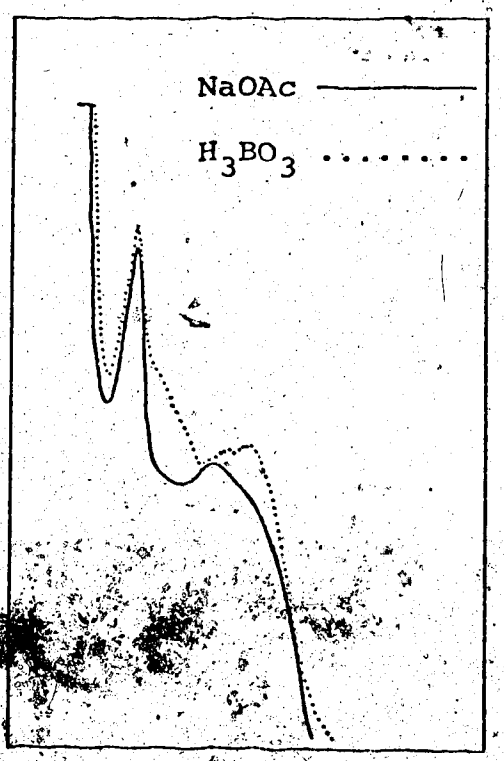
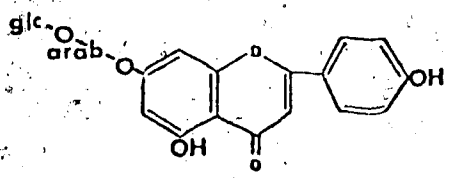


FIGURE 17.

Chromatographic and spectral data for Apigenin 7-O-vicianoside

#8 Apigenin 7-O-vicianoside

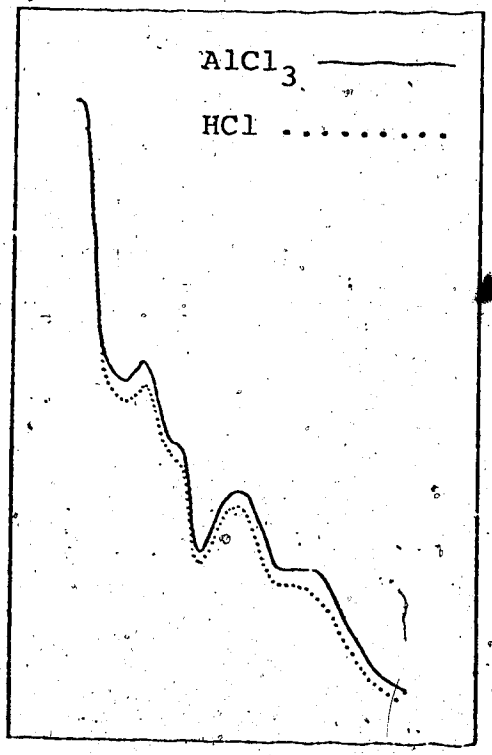


Chromatographic Data

	Rf Values			Spot Colour	
BAW	H_2O	HoAc	PhOH	UV	UV/NH_3
54	02	15	83	ppl	yg

UV Spectral Data

MeOh	268, 330
NaOMe	
$AlCl_3$	274, 302sh, 340, 383
$AlCl_3$/HCl	274, 302sh, 340, 380
NaOAc	
H_3BO_3	



Oxytropis jordalii Porsild subsp. *davisii* (Welsh) Elisens *comb.* and *stat. nov.*

based on
Oxytropis campestris (L.)DC. var. *davisii* Welsh, Leafl. West. Bot., 10:25. 1963.

Acaulescent herbs from a branching caudex; leaves pinnate, 4-10 cm. long; leaflets 25-51, ovate to lanceolate, some fasiculate 5-9 mm. long, 2-3 mm. broad, acute, pilose above and below with simple hairs; leaf-rachis and petiole grooved ventrally, strigulose to pilose; stipules 12-14 mm. long, the free ends 5-6 mm. long, sparsely pilose, ciliate, clavate processes often present; scape 5-15 cm. long, strigulose; raceme 2-4 cm. long, 10-16 flowered; petals pink-purple; calyx cylindric, with dark and light hairs, tube 4.2-4.7 mm. long, teeth 1.5-2 mm. long; chromosome number, 2n=32; gravelly disturbed habitats in northeastern British Columbia.

Holotype: mile 403.4, ALCAN Hwy., British Columbia; 1962, R.J. Davis 6076 (BRY)!

O. jordalii subsp. *davisii* was first described as a variety of *O. campestris* by Welsh (1963). Distinguished by commonly verticellate leaflets and pink-purple flowers, it demonstrates affinity with subsp. *jordalii* by its chromosome number (2n=32), pink-purple flowers, and small papery legumes. Subspecies *davisii* is restricted to the area around northeastern British Columbia (Map 8) where its occurrence suggests Pleistocene survival. No detailed flavonoid data was obtained.

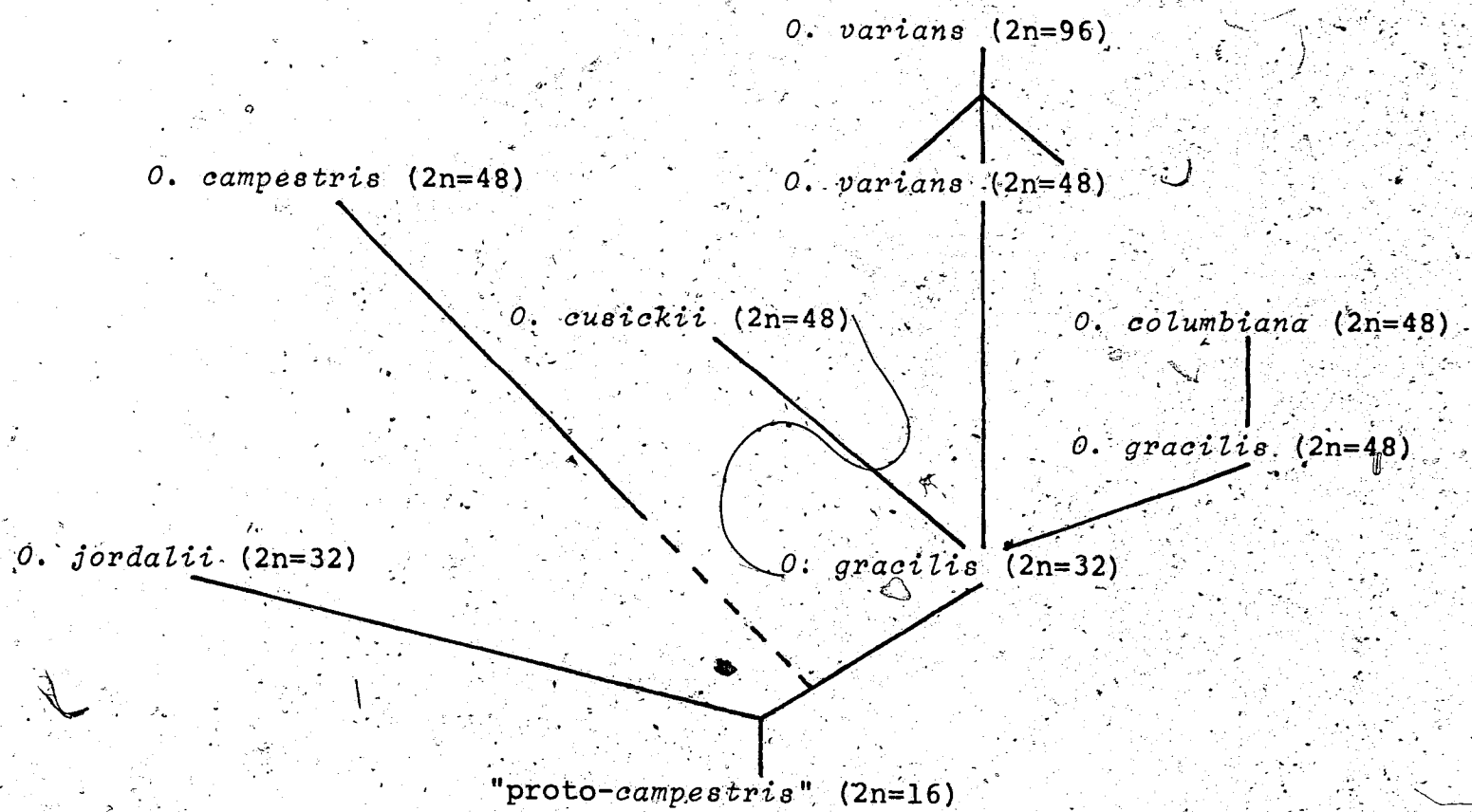
PLATE 8.

Type specimen of *Oxytropis jordalii* Porsild subsp. *davisii* (Welsh) Elisens

The cytological data of the present study and the distribution of the taxa (Maps 4-8) suggest that *Oxytropis campestris sensu* Barneby (1952) and Welsh (1963) represents a mature polyploid complex (Stebbins, 1971) which has undergone several cycles of polyploidization followed by periods of diversification and differentiation. Since trends of polyploidy are generally from lower to higher levels, polyploid complexes are particularly useful in analysis of problems of plant geography and phylogeny. Stebbins (1971) states that most mature complexes originated during the Pliocene or Pleistocene. Indeed, the relative antiquity of this complex is indicated by the fact that there is no extant diploid (2n=16) *Oxytropis* similar to any of the taxa. The species with the lowest ploidy level (2n=32) in the complex, *O. jordalii* and *O. gracilis*, represent the morphological, geographical, and ecological extremes. The variable *O. gracilis* with its many leaflets, numerous ochroleucous, whitish, or pinkish flowers, and small chartaceous pods is probably most similar to a hypothetical "proto-*campestris*" (Figure 44). Survival south of the glacial margin is suggested by its present distribution. On the other hand, the low-statured, alpine taxon *O. jordalii*, with 6-12 small flowers per raceme, is ecologically and morphologically specialized. Its narrowly restricted, widely disjunct distribution, confined principally to unglaciated areas, suggests that

FIGURE 44.

Hypothetical view of the relationships in the *Oxytropis campestris* (L.) DC. complex in northwestern North America



it could be considered a patroendemic (Favarger and Contandriopoulos, 1961).

Morphological similarity (for example, the large number of leaflets, numerous flowers, small chartaceous pods) indicates that *O. varians* (2n=48, 96) and the Eurasiatic *O. campestris* (2n=48) are closely related to *O. gracilis* (2n=32, 48). The data of the present study, however, suggest that these three taxa diverged ecologically, geographically, and cytologically and have had very different evolutionary histories. The changing environments and subsequent contraction and intermixing of floras characteristic of the Quarternary might explain the relatively rapid evolutionary diversification within this polyploid complex. For example, the dodecaploid race of *O. varians* is possibly of recent hybrid origin and is still expanding its range.

In marked contrast, the differentiation of *O. cusickii* (2n=48) and *O. columbiana* (2n=48) from *O. gracilis* was, perhaps, pre-Pleistocene and a result of the late Tertiary orogenies in western North America. This long period of isolation and evolution might explain the morphological and ecological distinctiveness of these taxa.

The present investigation does not presume to have resolved all the problems in this widespread and polymorphic complex. It does, however, provide some guidance for an appropriate reclassification. Neither the

modern general practice of recognizing only a single highly variable species nor that of older workers, who recognized many species, was adopted. As is so often the outcome of systematic research, a middle course has been followed.

Key to the *Oxytropis campestris* complex in northwestern North America

a_1 Stipules generally bearing clavate processes on the margins of the free blades; plants found north of 56° N. (except locally in the Alberta Rockies); Alaska, northern British Columbia to western MacKenzie district, N.W.T. .....b

b_1 leaflets commonly whorled; corolla pink, purple; plants of gravelly disturbed habitats in northeastern British Columbia .....*Oxytropis jordalii* subsp. *davisii*

b_2 leaflets not whorled; corolla yellow, white, or, if pink-purple, the distribution not as above c

c_1 racemes 10-25 flowered; flowers mostly 12-17 mm. long; leaflets 19-45 .....*Oxytropis varians*

c_2 racemes 6-12 flowered; flowers mostly 14 mm. long or less; leaflets 9-21 ...*Oxytropis jordalii* subsp. *jordalii*

a_2 Stipules generally lacking clavate processes on the margins of the free blades; plants found south of 56° N.; British Columbia, Oregon to Manitoba, northern Colorado .....d

d_1 leaflets 7-17; plants of low alpine habitats in the Rocky Mountains or riparian habitats in northeastern Washington and northwestern Montana

.....e

e_1 petals white, blue-veined, with prominently maculate keel; scapes 13-30 cm.; tall plants of riparian habitats in northeastern Washington and northwestern Montana

.....*Oxytropis columbiana*

e_2 petals yellowish, rarely, if ever, maculate; scapes 5-19 cm.; low alpine plants of the Rocky Mountains

Oxytropis cusickii

d_2 leaflets 17-33, or, if less, than plants of middle elevations in northwestern Washington and British Columbia; plants of prairies, open woodland, or mountain meadows

.....f

f_1 corolla pink, purple, or polychrome; pod coriaceous; prairies of North Dakota

.....*Oxytropis gracilis* subsp. *dispar*

f_2 corolla whitish or ochroleucous; pod chartaceous; prairies, open woodland, and mountain meadows from British Columbia to Manitoba, south to Colorado

...*Oxytropis gracilis* subsp. *gracilis*

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APPENDIX

REPRESENTATIVE SPECIMENS

Oxytropis varians (Rydb.) K. Schum.

Alaska: Jago River, *J.E. Cantlon & W.T. Gillis #57-743*, (CAN); Chitina River, *H.M. Laing #125*, (CAN); Lake Schrader, north slope, *L.A. Spetzman #518*, (CAN); Umiat, *I.L. Wiggins #13878*, (CAN); Fairbanks, *E. Scamman #1654*, (GH); Firth and Mancha Rivers, *E. Hulten #62767*, (BRY); Ogotoruk Creek, *J.G. Packer #2582*, (ALTA); Richardson Hwy., *E. Scamman #4622*, (GH); Gulkana, *E. Scamman #4547*, (GH).

British Columbia: Cassiar, *J.W. Eastham #389*, (CAN).

Manitoba: Churchill, *G. M. Keleher #31*, (CAN).

Northwest Territories: Hayes River, *H.J. Scoggan #5893*, (CAN); Ewariege Lake, *V. Hawley s.n.*, (CAN); Richardson Mts., *J.G. Packer #1371*, (ALTA); Dolomite Lake, Inuvik, *W.J. Elisens #460*, (ALTA); Great Bear Lake, *A.E. and R.T. Porsild #5328*, (CAN).

Yukon Territories: South shore Kluane Lake, *W.J. Elisens #234*, (ALTA); Bear Creek, mile 1021 ALCAN Hwy., *H.M. Raup, W.H. Drury and K.A. Raup #13136*, (CAN); Miles canyon, Whitehorse, *M.O. Malte #336*, (CAN); Haines Rd., Dezadeash, *A.E. and R.T. Porsild #22308*, (CAN).

Oxytropis gracilis (A. Nels.) K. Schum. subsp. *gracilis*

Alberta: Pincher Creek, *E.H. Moss #114*, (GH); Blairmore, *A.S. Pease #22545*, (GH); west of Calgary, *W.C. McCalla #8749*, (GH); Entrance, *M.G. Dumais & K. Anderson #2450*, (CAN).

British Columbia: Keremeos, *H.J. Scoggan #16030*, (CAN); Savona, *C.L. Hitchcock & J.S. Martin #7396*, (GH); Kamloops, *J.W. & E.M. Thompson #45*, (CAN).

Colorado: Fraser, Grand Co., *S.L. Welsh & L.A. Charette #1261*, (BRY).

Manitoba: Riding Mountain Park, *G.B. Ownbey #2881*, (CAN); Miniota, *H.J. Scoggan #11199*, (GH); Cowan, *H.J. Scoggan & W.K. Baldwin s.n.*, (GH).

Montana: St. Mary's Lake, Glacier Park, *B. & R. Maguire #15539*, (GH); Westby, *E.L. Larsen #10*, (GH).

Saskatchewan: Saskatoon, *G.W. Argus #9069*, (CAN); McKague, *A.J. Breitung #1218*, (GH).

South Dakota: Nemo, Lawrence Co., *S.L. Welsh #994*, (BRY).

Washington: Okanogan Co., *H. St. John #7703*, (GH).

Wyoming: Laramie Range, Albany Co., *C.L. & M.W. Porter #9824*, (GH); Four Corners, Weston Co., *C.L. Porter #5340*, (GH).

Oxytropis gracilis (A. Nels.) K. Schum. subsp. *dispar* (A. Nels.) Elisens

North Dakota: Glen Ullin, *W.J. Elisens #186*, (ALTA); Belfield, *O.A. Stevens #501*, (GH); Leeds, Benson Co., *S.L. Welsh #878*, (BRY).

Oxytropis cusickii Greenm.

Alberta: Snow Creek Pass, Banff Park, *A.E. Porsild #21424*, (CAN); Mt. Cheviot, Cadomin, *W.J. Elisens #011*, (ALTA); Mt. Carthew, Waterton Park, *W.J. Elisens #130*, (ALTA).

British Columbia: Quiniscoe Lake, Ashnola Range, *J.A. Calder #19599*, (GH).

Montana: Beartooth Mountains, Carbon Co., *A. Cronquist #7988*, (GH); Anaconda-Pintlar Wilderness, Beaverhead Co., *C.L. Hitchcock & C.V. Muhlick #12861*, (RM).

Oregon: Ameroid Lake, Wallowa Mts., Wallowa Co., *A.R. Kruckeberg s.n.*, (RM).

Washington: Mt. Wow, *J.W. Thompson #12578*, (ALTA); Heliotrope Ridge, Mt. Baker, *H. Weitman #10591*, (GH).

Wyoming: Warren Peak, Crook Co., *C.L. & M.W. Porter #10150*, (GH); Medicine Bow Mts., *A. Nelson #9228*, (GH); Boyd, Weston Co., *A. Nelson #9433*, (GH); Gannett Peak, Fremont Co., *F. Jozwik #417*, (GH).

Oxytropis columbiana St. John

Montana: Mud Creek, Glacier Park, *W.J. Elisens #387*, (ALTA); Big Prairie, Glacier Park, *L.H. Harvey #5686*, (MONTU).

Washington: Kettle Falls, Ferry Co., *H.T. Rogers #426*, (GH); Gifford, Stevens Co., *L. Boner & V. Weldert #180*, (GH).

Oxytropis jordalii Porsild subsp. *jordalii*

Alaska: Wiseman, *H.M. Raup & A.J. Soper #9427*, (GH); Juneau, *M.Williams #1397*, (GH); Arctic Village, *L.H. Jordal #3644*, (CAN).

Alberta: Mt. Cheviot, near Cadomin, *W.J. Elisens #224*, (ALTA).

British Columbia: Mt. Mansfield, Haines Rd., *J.Sias #19*, (CAN).

Northwest Territories: Richardson Mts., *S.L. Welsh & J.K. Rigby #12062*, (BRY); MacKenzie Mts., *A.E. Porsild & A.J. Breitung #11817*, (CAN); mile 111E, Canol Rd., *V.C. Wynne-Edwards #8346*, (CAN).

Yukon Territories: mile 81, Dempster Hwy., *R.T. Porsild #1486*, (CAN).

Oxytropis jordalii Porsild subsp.

davisii (Welsh) Elisens

British Columbia: mile 403.5, ALCAN Hwy., *W.J. Elisens #350*, (ALTA); mile 588.5, ALCAN Hwy., *S.L. Welsh & G. Moore #7440*, (BRY); mile 160, ALCAN Hwy., *S.L. Welsh & G. Moore #5431*, (BRY).