


A CONTRIBUTION TO THE TAXONOMY AND PHYLOGENY OF *OXYTROPIS*

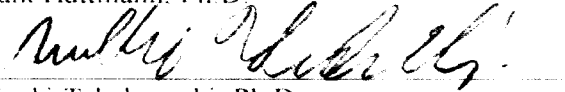
SECTION *ARCTOBIA* (FABACEAE) IN NORTH AMERICA


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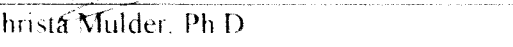
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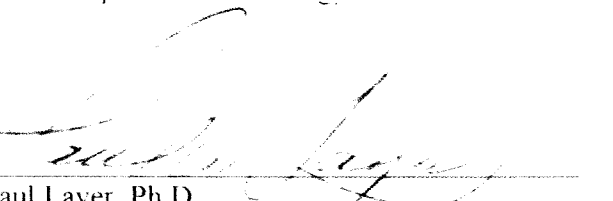

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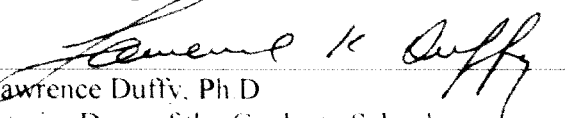

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A CONTRIBUTION TO THE TAXONOMY AND PHYLOGENY OF *OXYTROPIS*
SECTION *ARCTOBIA* (FABACEAE) IN NORTH AMERICA

A
THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Zachary J. Meyers, B.S.

Fairbanks, Alaska

August 2012

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Abstract

North American species of *Oxytropis* section *Arctobia* are reviewed through herbarium vouchers, scanning electron microscopy of seed coats, and phylogenetic analysis of sequence data to test the validity of the circumscription of section *Arctobia* as previously proposed. Morphologically, section *Arctobia* is characterized by few-flowered inflorescences, few leaflets per leaf, and a mainly cushion-like habit.

The micro-morphological data found considerable infraspecific variation in seed coat patterns. Sequence data from the nuclear *TRPT*, *CNGC5*, *GA3ox1* genes and the plastid *matK* gene were used to infer phylogenetic relationships among members of section *Arctobia*. Analyses using maximum parsimony, maximum likelihood and Bayesian inference of these sequences resulted in a phylogeny that unambiguously supports the monophyly of *Oxytropis*. None of the infrageneric subdivisions of *Oxytropis* were supported by our genetic analyses. Section *Arctobia* was found nested within species of section *Orobia*, *Glaeocephala*, and *Baicalia*. However, TRPT and *matK* sequence data support *Oxytropis arctobia* as a distinct species, which has previously been included under *Oxytropis nigrescens* under the North American treatment. Here eight species are recognized in section *Arctobia* for North America and a lectotype of *Oxytropis arctobia* is selected based on herbarium specimens.

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INTRODUCTION

The legume family (Fabaceae) includes many species that are economically important and harvested as oils, fibers, biofuel, timber, and medicines. Grain and forage legumes are grown on 15% of the Earth's arable surface (Graham & Vance 2003). They account for 27% of the world's primary crop production, including peas (*Pisum sativum*), chickpeas (*Cicer arietinum*), broad beans (*Vicia faba*) and forage crops such as *Medicago sativa* (Lewis et al. 2005). Legumes also are well known for their ability to fix nitrogen from the atmosphere via root-nodulating symbiotic bacteria and are often associated with mycorrhizae (Van den Bosch & Stacey 2003). This has resulted in the ability of many species to colonize barren lands, making them ecologically significant in most plant community assemblages. The Fabaceae is commonly divided into three subfamilies: Caesalpinioideae, Mimosoideae, and Papilionoideae (Doyle et al., 2000; Wojciechowski 2003; Wojciechowski et al. 2004). The largest and most widespread of the three subfamilies is Papilionoideae, with more than 13,000 species worldwide; is characterized by the absence of bipinnately compound leaves, unidirectional initiation of sepals and petals and a seed testa with a hilar valve (Polhill 1994). Based on these characters some authors have even treated this subfamily at the family level as Papilionaceae (Neill et al., 1999).

Reconstructing phylogenetic relationships within this ecologically and economically important family has received considerable attention (Crisp et al. 1999; Doyle et al., 2000; Pennington et al. 2000; Kajita et al. 2001; Herendeen et al., 2003 Luckow et al 2003; Wojciechowski 2003; Wojciechowski et al. 2000, 2004). In most

analyses, Papilionoideae as well as major subclades within the subfamily are strongly supported as monophyletic (Wojciechowski et al. 2004). Two large genera, *Oxytropis* DC. and *Astragalus* L., from the tribe Galegeae are strongly supported as monophyletic sister taxa, commonly referred to as locoweeds (Wojciechowski et al. 2000, Wojciechowski 2005). When the total number of species of these two genera is considered (*Oxytropis* with 350 species, Malyshev 2008; *Astragalus* with 1800-2500 species, Polhill and Raven 1981), they make up approximately 20% of the species diversity in subfamily Papilionoideae. *Oxytropis* is thought to have diverged from *Astragalus* approximately 12-16 Ma in Eurasia, both specializing in similar environments (Wojciechowski 2005). While these two taxa are closely related phylogenetically, they are taxonomically distinct. Morphologically, *Oxytropis* is distinguished from *Astragalus* by having beaked keel-petals, asymmetrical leaflets, and an acaulescent habit (Barneby 1952; Welsh, 2001; Zhu & Ohashi, 2000; Lewis et al., 2005).

Oxytropis (tribe Galegeae, Fabaceae) is a perennial plant genus with over 300 species recognized worldwide (Welsh, 2001; Zhu & Ohashi, 2000), primarily distributed in the mountainous regions of Europe, Asia, the Middle East, and western North America. The genus occupies a variety of ecotones including alpine scree slopes, wet meadows, arid sand dunes and riparian corridors (Yurtzev 1999). Within North America the genus is particularly speciose in the Arctic of Alaska, Canada and Western Russia on the Chukotka Peninsula. Malyshev (2008) recognizes 71 species and subspecies of *Oxytropis* in the Arctic, including two of the five subgenera as well as five of the 27 sections recognized by Bunge for the genus as a whole. Particularly, sect. *Arctobia*

Bunge dominates much of the alpine and tundra habitats in the Arctic with 18 known *Oxytropis* species (Yurtsev 1997). Species in section *Arctobia* are characterized by a reduced number of leaflets per leaf and fewer flowers per inflorescence as compared to other sections of *Oxytropis* in the Arctic (Bunge 1874). Since the circumscription of *Oxytropis* in 1802, taxonomists and botanists have struggled to systematically categorize the morphological diversity of the genus. In Alaska alone, the number of recognized species has fluctuated from 20 (Hultén 1958) to only a dozen (Welsh 2001). The species boundaries among closely related taxa in *Oxytropis* are not very clear resulting in different taxonomic interpretations of the species diversity (Barneby 1952; Hultén 1958; Yurtsev 1997,1999; Welsh 2001; Malyshev 2008).

Particularly in a group of plants where morphologically based taxonomy has been so difficult, the use of molecular sequence data provides an essential tool for resolving phylogenetic and taxonomic relationships. Molecular studies within *Oxytropis* are limited and even fewer have been conducted in the Arctic (But see Ledingham, 1960; Laguerre et al., 1997; Artyukova et al., 2003; Chung et al., 2004; Kulshreshtha et al., 2004; Schönswetter et al., 2004; Wojciechowski 2005; Gao et al. 2009; Schlee et al. 2010). Jorgensen et al. (2003) made the first attempt at evaluating species level relationships in Arctic *Oxytropis* using molecular data. Based on both ITS (internal transcribed spacer) sequences and RAPD (random amplified polymorphic DNA) markers, the study showed that northeastern arctic populations in both *Oxytropis arctica* R. Br. and *Oxytropis campestris* (L.) DC. are distinct from all other populations examined (Jorgensen et al. 2003). The observed geographic structuring was interpreted

as the result of a Pleistocene barrier formed by the Alaskan northern coastal ice shield. Evidence from molecular sequence data can further be used in an effort to date and resolve the evolutionary relationships of *Oxytropis* and section *Arctobia*. The present study seeks to increase our knowledge of the diversity and evolution within *Oxytropis* section *Arctobia* with an emphasis on the North American members of the section by applying a combination of morphological and molecular data approaches.

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Chapter 1. A survey of seed coat morphology in *Oxytropis* DC. sections *Arctobia*, *Baicalia*, *Glaeocephala*, *Mesogaea*, and *Orobia* (Fabaceae) from Alaska.¹

Abstract

Seed coat micromorphology of 22 out of 64 species of the genus *Oxytropis* from the Arctic in sections *Arctobia* (nine sp.), *Baicalia* (two sp.), *Glaeocephala* (three sp.), *Mesogaea* (one sp.) and *Orobia* (seven sp.) were studied using Scanning Electron Microscopy (SEM). Three main seed coat patterns (i.e., rugulate, lophate, and foveolate) and four distinct seed shapes (i.e., reniform, mitiform, globose, and ovoid) were found. Relationships among seed coat variation, taxonomic classification, seed dimensions and geographical distribution were tested using multinomial logistic regression analysis. In the analysis, sectional classification, length and L:W ratio of the seeds appear to be the main factors influencing the seed coat pattern. The relative frequency of seed coat patterns and seed shape compared to sectional classification revealed sections *Arctobia* and *Mesogaea* to be differentiated from sections *Baicalia*, *Glaeocephala*, and *Orobia*. *Oxytropis deflexa* is unique in having small, globose seeds as compared to the other Alaskan taxa with larger, reniform seeds. Overall, seed micromorphology among the Alaskan members of *Oxytropis* is highly variable, with species demonstrating all three seed coat patterns consistently with little to no taxonomic utility.

¹ Meyers, Z., Ickert-Bond S.M., and R. LaMesjerant. 2012 A survey of seed coat morphology in *Oxytropis* DC. sections *Arctobia*, *Baicalia*, *Glaeocephala*, *Mesogaea*, and *Orobia* (Fabaceae) from Alaska. In preparation for the International Journal of Plant Sciences.

Introduction

The genus *Oxytropis* DC. (Fabaceae, subfamily Papilionoideae, tribe Galegeae Dumort.) is taxonomically complex, comprising over 300 species worldwide (Yakovlev et al., 1996; Yurtsev 1999; Zhu and Ohashi 2000; Welsh 2001; Lewis et al., 2005). The genus is widely distributed throughout the Northern Hemisphere, with its greatest diversity found in the Tibetan plateau and circumpolar Arctic (Yurtsev 1999; Ranjbar et al., 2009). A total of 64 species are found in the Arctic, 22 of which occur in Alaska (Yurtsev 1999). *Oxytropis* is thought to have derived from *Astragalus* approximately 12-16 Ma and subsequently shares many morphological characteristics (Wojciechowski et al. 2005). A beaked keel, asymmetrical leaflets, and an acaulescent habit distinguish *Oxytropis* from *Astragalus* morphologically (Barneby 1952). Diversification in *Oxytropis* is thought to have been significantly influenced by interglacial and glacial periods in the Arctic (Yurtsev 1999).

During the Quaternary an ice-free, continuous land bridge called Beringia extended from the Russian Far East to Alaska and Canada and played a significant role in the history of many northern taxa (Hultén 1958; Elias et al. 1996; Ickert-Bond et al. 2009). *Oxytropis* taxa that are present in Beringia range in distribution from amphiberingian forms to groups endemic to Eastern (Alaskan) or Western (Russian) Beringia to circumpolar elements, some with extensions southward into the Rocky Mountains (Yurtsev 1997, 1999; Talbot et al. 1999). High levels of intraspecific morphological variation and phenotypic plasticity, coupled with a lack of definitive taxonomic

characters in some complexes, have led to difficulties and differences in species delimitation, resulting in a plethora of synonyms (reviewed in Welsh 2001).

Systematically, Alexander von Bunge's worldwide treatment of *Oxytropis* (1874) established four subgenera based on the presence of a septum in the legume and length of calyx teeth: I. *Oxytropis* (pod exerted above the calyx, with pod always ventrally and sometimes also dorsally septate), II. *Phacoxytropis* Bunge (pod exerted above torn calyx, without septum), III. *Physoxytropis* Bunge (small somewhat inflated legume enclosed by intact calyx), and IV. *Ptiloxytropis* Bunge (small pods enclosed by calyx with long villous calyx teeth). Bunge (1874) furthermore distinguished 17 sections within *Oxytropis* based on leaflet arrangement, raceme size and shape, legume shape and anatomy, presence of glandular hairs, and presence of spines on the petiole. Many of Bunge's infrageneric categories are still used in floristic works today (Barneby 1952; Yurtsev 1997, 1999; Zhu and Ohashi 2000; Polozhij and Malyshev 2006; Malyshev 2008a, b; Ranjbar et al. 2009).

Revisionary work on members of *Oxytropis* was completed by Vasil'chenko (1948), who added two subgenera exclusively of Old World taxa. In 1952 Barneby wrote a revision of *Oxytropis* for the North American taxa, clarifying much of the nomenclatural issues that had arisen. Yurtsev (1997; 1999) treated the genus from a Pan-arctic perspective and noted the importance of substrate affinity. Most recently, Welsh (2001) wrote a revision for *Oxytropis* in North America largely agreeing with the species concepts proposed by Barneby. These authors placed importance on characters such as stipule shape, pubescence type, legume shape and substrate affinity to delineate taxa.

Nevertheless, the observed high phenotypic plasticity that occurs in some taxa (i.e., sect. *Arctobia*, *O. nigrescens* complex) and intrinsic cultural differences in species concepts between Russian (Yurtsev 1999) and American taxonomists (Welsh 2001) have hampered a widely accepted unified panarctic taxonomy for the group.

Few reliable morphological characters are available for species delimitation and identification in *Oxytropis*. Section *Arctobia* of subgenus *Oxytropis* in particular has remained problematic to systematists due to the reduction in many morphological characters, which include few-flowered inflorescence (two to three flowers), few leaflets (eight to twelve), and species in this section frequently show a pulvinate or cushion-like habit. In contrast to the difficulty in delineating species belonging to sect. *Arctobia*, *Oxytropis deflexa* of subgenus *Phacoxytropis* is easily separated from other Alaskan oxytropes based on a number of distinct characters (e.g., mostly caulescent habit, pendulous, unilocular pods and stipules free from the petiole).

Within Fabaceae several studies have investigated the value of seed coat characters for identifying economically important taxa (Lersten 1981; Pandey and Jha 1988). Vural et al. (2008) examined seed morphology in forty-eight species of *Astragalus* and their study revealed two distinct seed coat patterns (i.e., rugulate and rugulate-reticulate consistent with terminology used in our study). This study also noted three distinct seed shapes within Turkish *Astragalus* using polar axis and equatorial diameter measurements: peroblate, suboblate, and oblate (comparable in our study to globose and ovoid or reniform and mitiform respectively). Seed shapes were concluded to be taxonomically useful only when combined with seed coat patterns in Turkish and

Iranian *Astragalus* (Vural et al. 2008; Ranjbar 2009). Seed coat patterns in *Oxytropis* have been documented to be rugulate, lophate and multi-reticulate, however, only a few species have been examined (i.e., *Oxytropis riparia*, *Oxytropis campestris*, *Oxytropis lambertii*), none of them from Alaska (Lersten 1981; Pandey and Jha 1988; Solum and Lockerman 1991). However, recently Erkul and Aytac (2010) examined 13 Turkish species of *Oxytropis* for a poster presentation and classified seed coats as striate-reticulate, psilate-reticulate, reticulate, and striate-rugulate.

Based on these recent studies, we examined whether seed micromorphology is of taxonomic utility in delimiting Alaskan oyxtropes of sections *Arctobia*, *Baicalia*, *Glaeocephala*, *Mesogaea* and *Orobia*. We examined seed shape, seed coat anatomy and micromorphology of two subgenera and five sections in *Oxytropis* using Scanning Election Microscopy (SEM).

Material and Methods

Our survey of seed coat micromorphology of *Oxytropis* includes 22 Alaskan taxa of the 64 arctic species that have been described (Yurtsev 1999; table 1.1). Most of the remaining arctic species are from the Old World (e.g., the Russian Far East, Siberia, and Scandinavia). Within the 22 Alaskan *Oxytropis* we included nine species from sect. *Arctobia* (of 13 classified in this section), two species from sect. *Baicalia* (of eight classified in this section), three species from sect. *Glaeocephala* (of 13 classified in this section), one species of sect. *Mesogaea* (of three classified in this section) and seven species from sect. *Orobia* (of 27 classified in this section; table 1.1). Taxa were sampled

primarily from Alaska but for four species in sect. *Arctobia* (*O. arctobia*, *O. bryophila* subsp. *lonchopoda*, *O. czukotica*, and *O. mertensiana*) we included additional samples that were collected from neighboring regions on the Chukotka or Kamchatka Peninsulas (Russia) and the Yukon Territory (Canada).

Mature, expanded seeds were removed from herbarium specimens; several immature, flattened or partially broken seeds were also examined, when insufficient material was available (table 1.1). Seeds were soaked in 90% ethanol for 24 hours and air-dried. For anatomical sections, seeds were soaked in a mixture of equal parts water, glycerol, and ethyl alcohol for 30 hours and samples were then sectioned with a razor blade. Seed anatomy was examined from representatives of each section. Whole and sectioned seeds were mounted on stubs with double-sided tape, sputter coated with a palladium target (60/40), in a Ladd model, and viewed with an ISI-SR-50 scanning electron microscope (SEM) at 15-20 kV at the Advanced Instrumentation Laboratory (AIL), University of Alaska Fairbanks. Seed coat patterns were examined adjacent to the hilum following Lersten (1981) at magnifications ranging from 500-2000X.

Measurements of seed length (L) and width (W) were made with an ocular micrometer on a stereoscopic microscope as well as from the SEM image file with a scale bar at 30-50X. Measurements given are the mean length (measured transversely to the hilum) and width (measured longitudinally to the hilum) in millimeters (table 1.1). A minimum of three specimens per taxon were examined; for every specimen three seeds were measured. Terminology used for seed shapes and seed coat patterns follow Lersten (1981) and Barthlott (1990).

Statistical analyses - We compared the relative frequency of seed coat patterns (i.e. rugulate, lophate, foveolate) with respect to taxonomic sections, species, latitude, and longitude to evaluate taxonomic and geographical correlations. Multinomial logistical regression was performed in R version 2.10.0 (R Development Core Team 2009) using the library (Venables and Ripley 2002) with the objective of testing potential predictive variables of seed coat patterns. Delimitation of taxonomic section, species, latitude, longitude, seed length, and seed length to width ratio (L:W) were used as independent variables (IVs) in the model, with seed coat pattern as the dependent variable (DV). We used an information theoretical approach to select the most parsimonious model of all candidates by minimizing Akaike's information criterion (AIC) to determine which IVs explain variation in seed coat pattern (table 1.2, Akaike 1974).

Results

Seed coat patterns and Shapes - The morphological characteristics of the seeds are summarized in table 1.1. All seeds examined appear smooth under the dissecting scope and show a uniform dark to light brown pigmentation (fig. 1.1). Seed shapes are classified according to the depth of the hilum and the height of both terminal lobes. Typically the seeds are reniform, but when the lobes are unequal in lengths they are classified as mitiform *sensu* Murley (1951) (fig. 1.1C-D). Fewer seeds are ovoid or globose as defined by the length to width ratio (table 1.1; fig. 1.1A-B). Seeds of

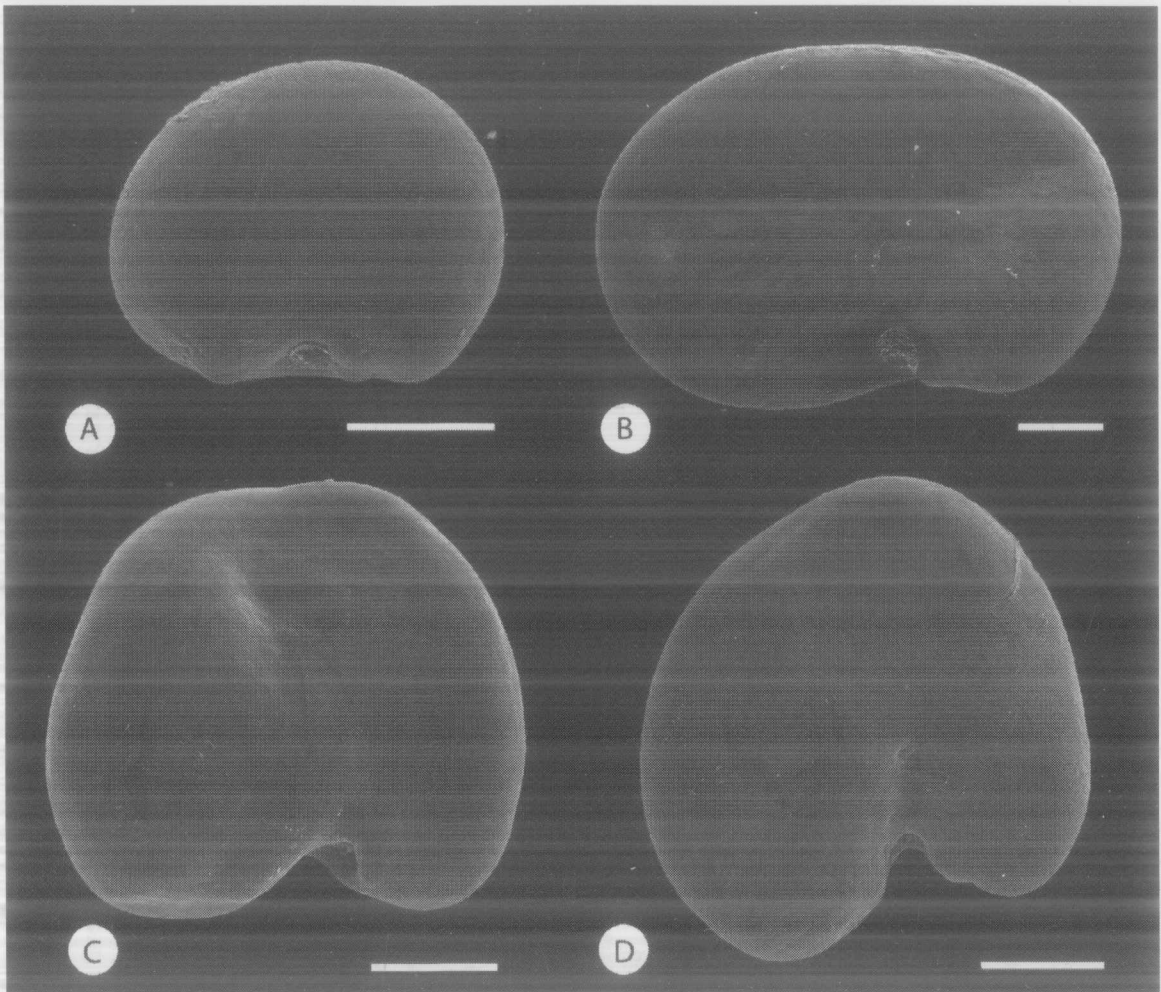


Figure 1.1 Seed shapes of *Oxytropis* in Alaska using scanning electron microscopy. *A*, *Oxytropis deflexa* (Ickert-Bond 1466); *B*, *Oxytropis tananensis* (Howenstein & Borron 40); *C*, *Oxytropis borealis* (Parker et al. 13030); *D*, *Oxytropis campestris* subsp. *gracilis* (Stensvold 5563). *A*, globose seed. *B*, ovoid seed. *C*, reniform seed. *D*, mitiform seed. Scale bars *A-D*, 500 μ m.

Table 1.1. Specimens examined along with voucher information and locality data. * All vouchers examined are deposited at the University of Alaska Museum of the North Herbarium (ALA) (unless otherwise noted). Herbarium acronyms follow Index Herbariorum (Thiers 2008). † denotes irregular or partially broken seeds. Surface ornamentation is categorized in five types: rugulate (R), rugulate reticulate (RR), multi-reticulate (MR), lophate (L) and lophate reticulate (LR). Latitude, longitude as well as the reported chromosome number for each taxon are recorded below (Index of Plant Chromosome Numbers, IPCN).

Species	Locality	Voucher information*	Mean Length (mm)	Mean Width (mm)	Seed Shape	Surface Ornament.	Lat	Long
<i>Oxytropis</i> subgen. <i>Oxytropis</i> sect. <i>Arctobia</i>								
(2n) = 16 <i>O. arctobia</i>	Canada: Southampton Island	Malte 119782	1.12	1.46	reniform	R, RR	64.10	-82.50
<i>O. arctobia</i>	Canada: Banks Island	Aiken 99-015 (CAN)	1.89	2.34	reniform	R, RR	73.22	-119.53
<i>O. arctobia</i>	Canada: Spence Bay.	McGrath s.n. (CAN)	1.46	1.64	reniform to mitiform	R, RR	69.53	-93.53
(2n) = 32 <i>O. bryophila</i>	Seward Peninsula	Murray, Yurtsev & Kelso 10658	2.05	1.77	reniform (†)	R, RR	65.69	-164.39
<i>O. bryophila</i>	Alaska Peninsula	Jansen & Carlson 02-127	2.05	2.2	reniform to mitiform	R, RR	58.61	-153.77
<i>O. bryophila</i>	Mt. Schwatka	Parker et al. 4949	1.44	1.99	reniform (†)	R, RR	65.88	-147.25
<i>O. bryophila</i>	Chugach Mts., Knik River	Barker 02-217	1.85	2.22	reniform to mitiform	R, RR	61.36	-148.91
<i>O. bryophila</i>	Nulato Hills, Debauch Mtn.	Parker et al. 7256	1.5	2.09	reniform	R, RR	64.51	-159.88
<i>O. bryophila</i>	Twelvemile Summit	Ickert-Bond 1526	1.63	1.95	mitiform	R, RR	65.39	-145.97
<i>O. bryophila</i> subsp. <i>lonchopoda</i>	Canada: Ogilvie Mts.	Cody & Ginns 34315	1.77	2.03	reniform	R, RR	65.29	-140.30

Table 1.1 Continued

(2n) = 32 <i>O. czukotica</i>	Russia: Kamchatka	Kharkevich 550a
<i>O. czukotica</i>	Russia: E Siberia	Koroleva & Petrovsky s.n.
(2n) = 16, 32 <i>O. gorodkovii</i>	Seward Peninsula, Minnie Creek	Murray, Yurtzev & Kelso 11565
<i>O. gorodkovii</i>	Ogotoruk Cr. drainage	Hultén <i>s.n.</i>
<i>O. gorodkovii</i>	Seward Peninsula, Lost R. Drainage	Lenarz 46
(2n) = 32 <i>O. huddelsonii</i>	Yukon-Tanana Upland, Yukon Fork	Parker et al. 6511
<i>O. huddelsonii</i>	Chugach Mts., Granite Range, E of Goat Cr.	Batten & Barker 96-321
<i>O. huddelsonii</i>	Yukon-Tanana Upland, Charley River	Roland 5713
<i>O. huddelsonii</i>	Alaska Range, Clearwater Mts.	Grundt <i>s.n.</i>
<i>O. huddelsonii</i>	Wrangel St. Elias N.P., Nicolai Ridge	Ickert-Bond 1640
<i>O. kokrinensis</i>	Vicinity of Akillik River	Duffy MD07-105
<i>O. kokrinensis</i>	Etivluk Test Well	Murray 6889
<i>O. kokrinensis</i>	Brooks Range, Bornite	Lewis <i>s.n.</i>

1.2	1.63	reniform	L, LR	62.35	168.90
2.28	1.82	mitiform	R, RR, MR	69.58	164.41
1.67	1.85	reniform	R, RR	65.33	-163.63
2.17	2.17	mitiform	R, RR	68.13	-165.66
1.86	2.25	reniform to mitiform	RR	65.45	-167.15
1.99	2.61	reniform to mitiform	R, RR	65.15	-143.70
1.89	1.94	reniform to mitiform	L, RR	60.99	-142.01
1.47	1.99	mitiform	R, RR	64.61	-143.68
2.21	2.36	reniform to mitiform	R, LR	63.03	-147.20
1.88	2.21	mitiform	R	61.45	-142.65
2.2	2.71	mitiform	R, RR	67.33	-159.96
1.5	1.43	reniform	RR	68.36	-156.75
1.6	1.5	mitiform	RR	67.08	-156.91

Table 1.1 Continued

(2n) = 16 <i>O. mertensiana</i>	Brooks Range, Mi 271 Dalton Hwy.	Murray 8541	1.93	1.77	mitiform	R, RR	68.45	-149.30
<i>O. mertensiana</i>	Brooks Range, Carnivore Cr.	Batten 856	1.18	1.25	reniform	R, RR	69.28	-145.03
<i>O. mertensiana</i>	Russia: Chukotka, Getlyanen River	Razzhivin et al. <i>s.n.</i>	1.95	1.92	mitiform	R, RR	65.25	172.16
(2n) = 16, 32 <i>O. scammaniana</i>	Wrangel St. Elias N.P., Nicolai Ridge	Ickert-Bond 1638	1.31	1.82	reniform	R, RR	61.46	-142.64
<i>O. scammaniana</i>	Etivluk Test Well	Murray 6890	1.5	1.7	reniform (†)	R, RR	68.36	-156.75
<i>O. scammaniana</i>	Ptarmigan Heart	Raup, Raup, & Drury Jr. 13739	1.3	1.33	reniform to globose (†)	R, RR	61.81	-138.58
sect. <i>Baicalia</i>								
(2n) = 16 <i>O. splendens</i>	Eagle Creek Campground	Ickert-Bond 1568	1.67	1.7	reniform	L	63.16	-143.20
<i>O. splendens</i>	Road to Chitina, W of Tosina River	Galen Smith 2342	1.78	1.69	reniform to mitiform	L, R	61.65	-144.65
<i>O. splendens</i>	Yukon River at mouth of Woodchopper Cr.	Parker & Batten 6218	2.63	2.51	mitiform	L, LR	65.36	-143.35
<i>O. tananensis</i>	Canada: Yukon Territory, Carmacks	Calder & Kukkonen 27976	1.5	1.63	ovoid †	RR	62.11	-136.26
<i>O. tananensis</i>	Porcupine River	Howenstein & Borron 40	2.24	3.01	mitiform to ovoid	L, LR	67.40	-141.08
<i>O. tananensis</i>	Yukon-Tanana Upland Gaffney Road	Duffy 95-710	1.46	1.49	mitiform to ovoid	L, LR, F	64.83	-147.64

Table 1.1. Continued

sect. <i>Glaeocephala</i>								
(2n) = 48, 98 <i>O. borealis</i>	Seward Peninsula, Salmon Lake	Murray, Yurtzev. & Kelso 10984	0.92	1.4	reniform	R, RR, LR	64.91	-164.95
<i>O. borealis</i>	Killik River valley, Ivisak Creek	Parker et al. 13030	1.58	2.01	reniform (†)	LR, MR	68.30	-154.05
<i>O. borealis</i>	Central Noatak R. valley, Sisiak Creek	Parker et al. 15056	1.22	1.71	reniform to mitiform	RR	68.00	-161.41
(2n) = 16 <i>O. glutinosa</i>	Mackenzie Delta's East Channel	Sim 6092	1.37	2.06	mitiform	RR, L	60.677	-134.129
<i>O. glutinosa</i>	Alaska Range, Tonzona River	Viereck 5368	2.1	2.45	reniform to mitiform	R, RR	62.83	-152.33
(2n) = 16 <i>O. viscida</i>	Canada: Yukon Territory, vic. Burwash Landing	Raup, Drury, & Raup 13962	1.74	1.76	mitiform	RR, MR, F, L, LR	61.36	-138.98
<i>O. viscida</i>	Akmalik Creek	Parker 7618	1.9	2.04	mitiform to ovoid	L, LR	68.40	-154.15
<i>O. viscida</i>	Canada: Yukon Territory, Kluane Lake	Raup & Raup 12908	1.57	1.70	reniform	RR	61.55	-138.66
sect. <i>Orobia</i>								
(2n) = 48, 80, 96 <i>O. arctica</i>	Seward Peninsula, Mystery Creek	Murray, Yurtzev. & Kelso 11640	1.79	2.17	reniform to mitiform	LR, RR	65.91	-163.5
<i>O. arctica</i>	Arctic Coastal Plain, Sagavanirktok River	Jorgensen & Batten JJ-9-9-9-7	1.18	1.67	reniform	LR, RR	69.56	-148.61

Table 1.1 Continued

(2n) = 48, 80, 96 <i>O. arctica</i> var. <i>barnebyana</i>	Baird Mts., Squirrel R., 'No Name Cr.'	Jorgensen et al. JJ-97-11-3	1.42
<i>O. arctica</i> var. <i>barnebyana</i>	Baird Mts., Squirrel R., 'No Name Cr.'	Jorgensen, et al. JJ-97-16-3	2.07
<i>O. arctica</i> var. <i>barnebyana</i>	Baird Mts., Squirrel R., 'No Name Cr.'	Jorgensen, et al. JJ-97-13-2	1.77
<i>O. arctica</i> var. <i>barnebyana</i>	Baird Mts., North Fork Squirrel R.	Jorgensen, et al. JJ-97-10-1	1.81
(2n) = 16, 32, 96 <i>O. campestris</i> subsp. <i>gracilis</i>	Dall Island, Grace Mtn. vic.	Stensvold 5563	1.67
<i>O. campestris</i> subsp. <i>gracilis</i>	Northway, Tetlin NWR bunkhouse	Moran 155	1.42
<i>O. campestris</i> subsp. <i>gracilis</i>	Brooks Range, Mile 180 Dalton Hwy	Jorgensen & Batten <i>s.n.</i>	1.92
(2n) = 32 <i>O. jordalii</i>	Alexander Archipelago	Calhoun & Kriekhaus 63	1.35
<i>O. jordalii</i>	Kenai Peninsula, Upper Nuka R. valley	Lipkin & Carlson 03- 310	1.38
<i>O. jordalii</i>	Mesa Archaeological Site	Jorgensen & Batten <i>s.n.</i>	1.18
<i>O. jordalii</i>	Brooks Range, Mi 271 Dalton Hwy.	Jorgensen & Batten JJ-99-10-11	1.01

1.98	reniform to mitiform	L, RR	67.44	-161.32
2.72	reniform to mitiform	L, LR	67.44	-161.32
2.66	reniform to mitiform	L, RR	67.44	-161.32
2.46	mitiform	L	67.49	-161.01
1.86	reniform to mitiform (†)	R, L, LR	54.91	-132.95
1.92	mitiform	L, LR	62.96	-141.93
2.28	reniform to mitiform	R, RR, L	67.31	-150.15
1.84	mitiform	MR, F	57.73	-136.06
1.65	reniform to mitiform to ovoid	LR, F	59.673	-150.69
1.55	reniform	L, R	68.41	-155.8
0.87	ovoid to globose	L	68.44	-149.35

Table 1.1 Continued

<i>O. jordalii</i>	Central Nigu R. valley	Parker 7562	1.78	2.09	mitiform to ovoid	L	68.33	-156.4
(2n) = 80 <i>O. kobukensis</i>	Kobuk Valley Nat. Park, Kobuk Dunes	Duffy MD07-123	1.82	2.55	mitiform to ovoid	L, LR	67.03	-158.76
<i>O. kobukensis</i>	Kobuk Valley Nat. Park, Kobuk Dunes	Duffy MD07-119	1.9	2.63	mitiform to ovoid	L, RR, R	67.03	-158.77
<i>O. kobukensis</i>	Kobuk R. valley, Paungaq Taugruk	Lipkin 84-47	1.74	1.94	reniform to mitiform	L, LR	67.18	-158.5
<i>O. koyukukensis</i>	Brooks Range, Mile 187.2 Dalton Hwy	Jorgensen & Batten JJ-99-11-12	1.67	1.87	mitiform	LR, L, RR	67.45	-150.13
<i>O. koyukukensis</i>	Brooks Range, Mile 187.2 Dalton Hwy	Jorgensen & Batten JJ-99-11-7	1.54	1.7	globose (†)	F, RR	67.45	-150.13
<i>O. koyukukensis</i>	Noatak River, N of Twelvemile Creek	Peter Ray N.06-10	1.51	1.43	mitiform	R, RR	65.40	-145.91
(2n) = 96 <i>O. maydelliana</i>	Seward Peninsula, VABM Bluff	Kildaw <i>s.n.</i>	2.45	2.4	reniform to mitiform	LR, RR	64.53	-163.75
<i>O. maydelliana</i>	Eagle Summit	Ickert-Bond 1549	1.53	1.77	reniform	R, RR	65.48	-145.40
<i>Oxytropis</i> subgen. <i>Phacoxytropis</i> sect. <i>Mesogaea</i>								
(2n) = 16 <i>O. deflexa</i>	Wrangel St. Elias N.P., Jack Creek	Ickert-Bond 1595	1.44	1.45	globose	L, LR	62.46	-143.10
<i>O. deflexa</i>	Central Noatak R. valley, Sisiak Creek	Parker et al. 15052	1.38	1.35	globose	R, L	68.00	-161.41
<i>O. deflexa</i>	Dalton Highway, station 5	Ickert-Bond 1466	1.08	1.25	globose	L, LR	67.05	-150.32

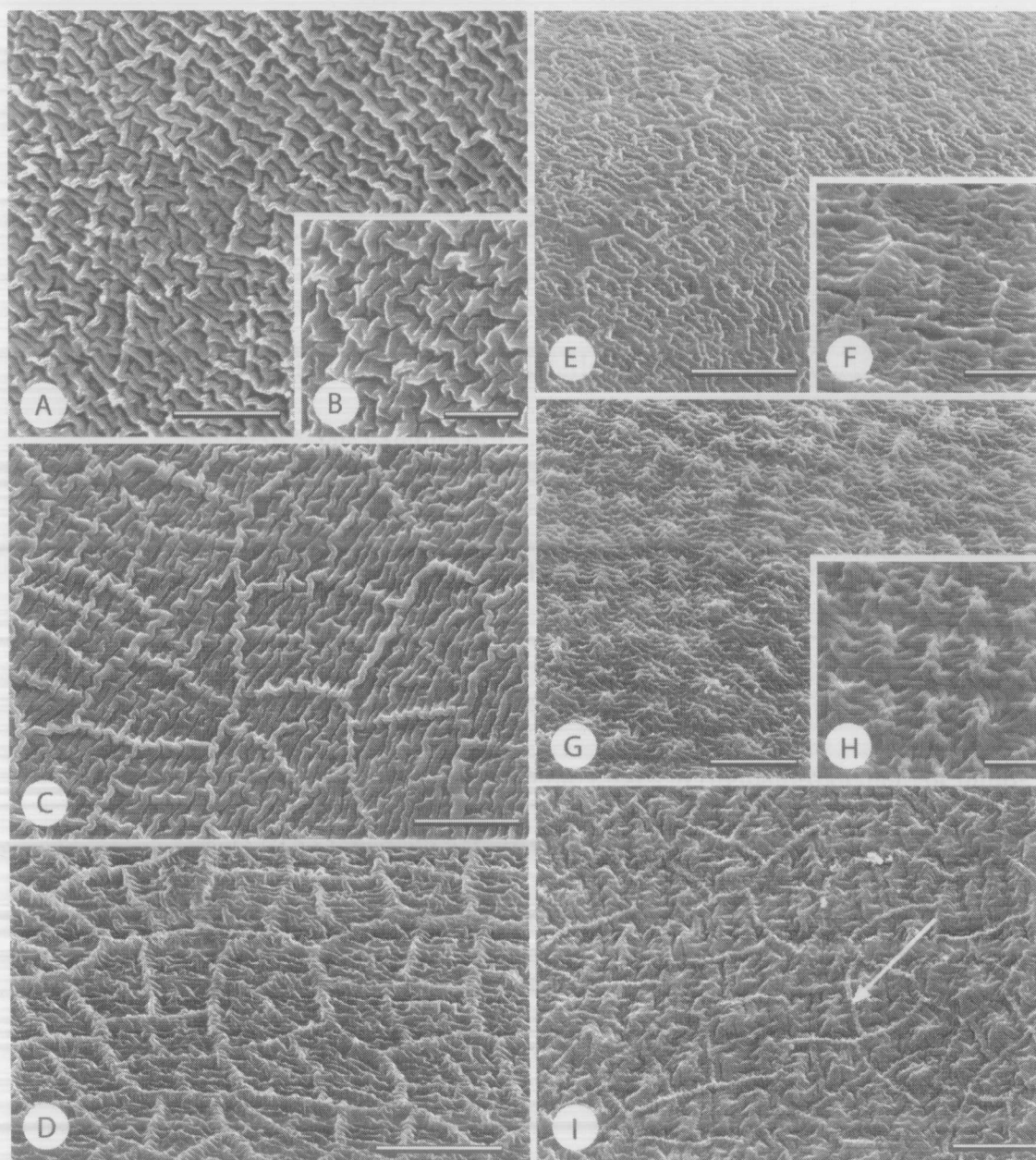


Figure 1.2 Seed coat patterns of *Oxytropis* in Alaska and the Russian Far East using scanning electron microscopy. A-C, *Oxytropis bryophila* (Murray, Yurtsev & Kelso 10658); D, *Oxytropis czukotica* (Koroleva & Petrovsky s.n.); E, *Oxytropis jordalii* (Lipkin & Carlson 03-310) rugulate; F, *Oxytropis viscida* (Raup, Drury, & Raup 13962); G, *Oxytropis arctica* var. *barnebyana* (Jorgensen et al. JJ-97-11-3); H, *Oxytropis koyukensis* (Jorgensen & Batten JJ-99-11-12); I, *Oxytropis kobukensis* (Duffy MD07-123). A, rugulate seed coat pattern. B, details of cuticular folding in rugulate seed coat. C, multi-reticulate seed coat. D, multi-reticulate seed coat pattern demonstrating details of cuticular folding. E, foveolate seed coat. F, foveolate seed coat pattern illustrating details of cuticular folding. G, lophate seed coat. H, details of the cuticular folding and regular spacing of the lophae. I, Lophate-reticulate seed coat showing additional ridges encircling the lophae. Scale bars A, C-E, G, I, 20 μ m; B, F, H, 10 μ m.

Oxytropis in Alaska Range from 0.87 mm to 2.9 mm in width and from 1.0 mm to 2.1 mm in length, with an average length to width (L:W) ratio of 0.874 (table 1.1).

The majority of seeds in *Oxytropis* show a rugulate seed coat pattern with irregularly roughened cuticular folds (R, 63% of seeds examined; fig. 1.2A-D, 1.4). Within rugulate seed coats we recognized a multi-reticulate form. Multi-reticulate seed coats (MR) consist of a secondary mesh of interlacing ridges and irregularly roughened cuticular folds (50% of seeds examined; fig. 1.2C-D, 1.4). The second distinct seed coat pattern is lophate (L, 32% of seeds examined; fig. 1.2G-I, 1.4), which consists of distinct short ridges with irregular sides forming uplifted circular or rectangular patterns. We observed additional reticulation of the lophate pattern on a few specimens and recognize those as lophate-reticulate (LR; fig. 1.2G). The cuticular ridges on the lophate-reticulate pattern are relatively thin when compared to the ridges in rugulate-reticulate or multi-reticulate seed coats. The foveolate pattern is characterized by irregular circular folds with blunt edges and thick cell walls, which are raised above the seed surface (F, 5% of seeds examined; fig. 1.2E-F). The foveolate pattern (F; fig. 1.2E-F, 1.4) was found in only four species (i.e., *O. tananensis*, *O. jordalii*, *O. koyukensis*, and *O. viscida*).

Seed Anatomy - The cross-sections revealed the seed coat in all specimens to be well differentiated and exotestal with the outer integument providing the mechanical layer of the seed coat (fig. 1.3A). An uniseriate epidermis is covered by a cuticle on upper anticlinal walls (fig. 1.3A-C), and is composed of prominent macrosclereids (figs. 1.3B-C), followed by a single row of osteosclereids (hypodermis) and five to eight rows of

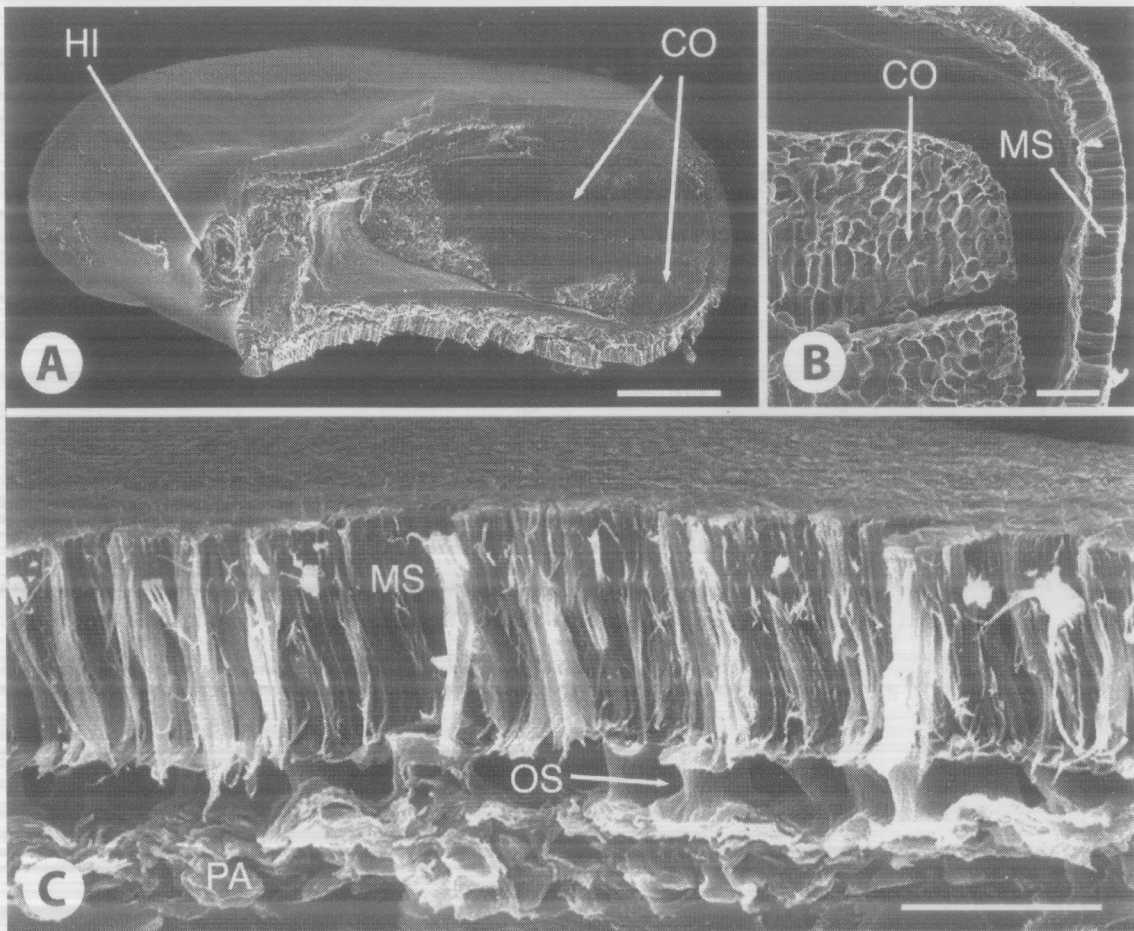


Figure 1.3. Seed anatomy of selected species of *Oxytropis* in Alaska using scanning electron microscopy. *A*, *Oxytropis huddelsonii* (Parker et al. 6511); *B*, *Oxytropis tananensis* (Ickert-Bond 1517); *C*, *Oxytropis bryophila* (Ickert-Bond 1526). *A*, Partially sectioned seed showing position of the hilum (HI), and two prominent cotyledons (CO) filling the embryo cavity. *B*, Cross section with detailed view of edge of the seed showing macroscleroids (MS) and outer cuticle layer. *C*, Cross section detailing uniform macroscleroids (MS) making up the outer epidermis, followed by a row of osteosclereids (OS) forming the hypodermis and tangentially elongated parenchyma cells (PA) of the nucellus. CO = cotyledon, HI = hilum MS = macroscleroids, OS = osteosclereids, PA = parenchyma. Scale bars *A* 500 μm , *B* 100 μm , *C* 50 μm .

compressed, tangentially elongate parenchyma cells of the nucellus (fig. 1.3C).

Statistical Analysis - Stepwise model selection of the multinomial logistic regression for the three major classes of seed coat patterns showed the strongest association with sectional classification, length of seed (size) and L:W ratio (shape). These factors produced the most parsimonious and descriptive model with an AIC score of 228.42

(table 1.2). Seed coat pattern was associated with taxonomic sectional classification, since the removal of this factor greatly increased the AIC score, indicating its significance to the overall variation observed. When seed coat ornamentation and seed shape were compared with sectional classification only sect. *Arctobia* and *Mesogaea* were found to differ from the other sections, with a unique seed shape found in sect. *Mesogaea*, and section *Arctobia* showing less variable seed coat patterns as compared to all other sections examined (table 1, fig 1.4). The other two independent variables (length and L:W ratio) contributed marginally to the overall variability of seed coat pattern when they were removed from the statistical model (table 1.2). Both distributional factors such as latitude and longitude as well as species classification were less informative of the independent variables (table 1.1, 1.2).

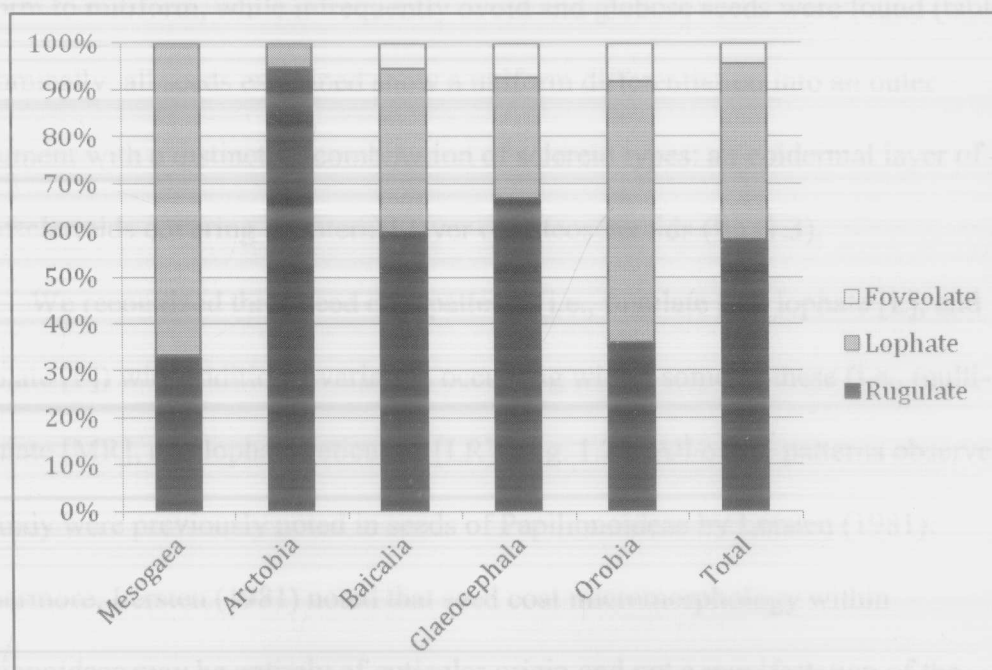


Figure 1.4 Frequency of the three main seed coat patterns found in each of the five sections of *Oxytropis* in Alaska. Primary pattern percentages are depicted on a gray scale (black = rugulate [R]; gray = lophate [L]; and white = foveolate [F]).

Table 1.2. Summary statistics of the multinomial logistic regression with AIC model selection of seed coat micromorphology. Delimitation of taxonomic section (referred to in table as “section”), species, latitude, longitude, length and length to width ratio. The data partition examines three primary seed coat patterns (i.e. rugulate, lophate, foveolate).

Independent Variables Selected	AIC Score
Section+Species+Latitude+Longitude+Length+L:W	241.1210
Section+ Latitude+Longitude+Length+L:W	231.4239
Section+Latitude+Length+L:W	228.8970
Section+Length+L:W	228.4271
Section+Length	232.7890
Section	234.1854

Discussion

The current study has revealed several distinct seed shapes, a uniform exotestal anatomy and several seed coat patterns among Alaskan oxytropes. Seeds are typically reniform to mitiform, while infrequently ovoid and globose seeds were found (table 1.1). Anatomically, all seeds examined show a uniform differentiation into an outer integument with a distinctive combination of sclereid types: an epidermal layer of macroscleroids covering an internal layer of osteoscleroids (fig. 1.3).

We recognized three seed coat patterns (i.e., rugulate [R], lophate [L], and foveolate [F]) with additional variation occurring within some of these (i.e., multi-reticulate [MR], and lophate-reticulate [LR]) (fig. 1.2). All of the patterns observed in our study were previously noted in seeds of Papilionoideae by Lersten (1981).

Furthermore, Lersten (1981) noted that seed coat micromorphology within Papilionoideae may be entirely of cuticular origin and not a manifestation of the underlying epidermal cells, which we show to be the case for *Oxytropis* as well (fig. 1.3A-C). Similarly, a study examining seed diversity in 48 species of Turkish *Astragalus*

found only two distinct seed coat patterns (rugulate and rugulate-reticulate) along with three seed shapes (Vural et al., 2008). They concluded that seed coat patterns at both the species and infrageneric levels were of limited taxonomic utility in *Astragalus* unless supported by macromorphological characters. The micrographs from Erkul and Aytaç (2010) exhibit similar seed coat microstructures as in our study; however their interpretation of the variation is not analogous to our classification criteria, the seed coat patterns (i.e., striate-reticulate, psilate-reticulate, reticulate and striate-rugulate) are not well defined, making it difficult to compare to our results.

We show that seed coat patterns are not useful to discriminate species of Alaskan *Oxytropis* and are of minor taxonomic utility. Some trends in seed coat frequency were observed at higher infrageneric ranks. The multinomial logistic regression analysis (table 1.2) demonstrates a relationship with seed coat patterns and seed shape to the sectional level for sections *Arctobia* and *Mesogaea*. Seed coat patterns were most conserved in section *Arctobia* with 97% of the taxa examined being strictly rugulate (table 1.1; fig. 1.2A-D; fig. 1.4). Greater variability was observed in the Alaskan members of sections *Orobia*, *Baicalia*, and *Glaeocephala* (fig. 1.4). Taxa examined from these sections all showed high intraspecific variability in seed coat pattern (table 1.1; fig. 1.4).

Despite the variability of seed shapes within sections in Alaskan *Oxytropis* (table 1.1), even within individual species, *Oxytropis deflexa* of subgenus *Phacoxytropis*, sect. *Mesogaea* is distinct by having exclusively small globose seeds, which range from 1 to 1.5 mm in length and 1.2 to 1.6 mm in width (table 1.1; fig. 1.1) as compared to seeds examined from other subgenera and sections, which are generally larger and reniform

(L= 0.92 to 2.45 mm, W =1.25 to 2.72 mm, table 1.1; fig 1.1). Subgenus *Phacoxytropis* including *O. deflexa* has been suggested by Bunge (1874) and was later adopted by Barneby (1952) as well as Yurtsev (1997) to be a distinct lineage within *Oxytropis* based on a number of vegetative and reproductive characters. In a recent phylogeny using *matK* sequence data for 637 legume taxa including seven species of *Oxytropis*, *O. deflexa* was shown to be the earliest diverging branch (personal communication, Marty Wojciechowski, Arizona State University, School of Life Sciences, Tempe, Arizona). Additional samples of Asiatic members in subgenus *Phacoxytropis* are needed to test whether small globose seeds represent the plesiomorphic seed shape and that reniform seeds represent the derived (apomorphic) condition in *Oxytropis*.

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Chapter 2. Taxonomy and phylogeny of *Oxytropis* section *Arctobia* (Fabaceae) in North America.²

Abstract

A taxonomic key, synonymy, species descriptions and molecular phylogeny of eight species of *Oxytropis* section *Arctobia* (Fabaceae) are presented. As circumscribed here section *Arctobia* in North America contains eight polymorphic species, restricted primarily to arctic and subarctic environments in Alaska and the Yukon Territory. This morphologically distinct group is defined by its few-flowered inflorescences (two to three flowers), limited number of leaflets (seven to fifteen), and frequent pulvinate or cushion-like habit. Phylogenetic analyses were conducted on 51 samples from a total of 21 species of *Oxytropis*, using nuclear *CNGC5*, *LE*, and *TRPT* as well as chloroplast *matK* sequences. Our analyses revealed *Oxytropis* section *Arctobia* to be nested within sections *Baicalia*, *Glaeocephala*, and *Orobia*. Two of the four molecular markers (i.e., *CNGC5* and *matK*) revealed weak biogeographical patterns, specifically in *Oxytropis arctobia* and *Oxytropis bryophila*, but overall little species resolution was recovered. A lectotype is selected for *Oxytropis arctobia*.

² Meyers, Z. and S.M. Ickert-Bond. 2012. Taxonomy and phylogeny of *Oxytropis* section *Arctobia* (Fabaceae) in North America. In preparation for *Systematic Botany*.

Introduction

Oxytropis DC. (tribe Galegeae, Fabaceae) contains 300 species worldwide (Lavin et al. 1990; Welsh, 1991; Yurtsev, 1999), distributed primarily in the mountainous regions of Europe, Asia, the Middle East, and western North America. The genus occupies a variety of ecotones including alpine scree slopes, wet meadows, arid sand dunes and riparian corridors (Yurtsev, 1999). The highest species diversity is found in the Russian Far East and the Tibetan plateau, as well as complex and intricate relationships within Beringia. In North America, *Oxytropis arctobia* Bunge extends as far north as Baffin Island in the Canadian Arctic, while several amphiberian species cross the Bering Sea into Chukotka and can be found as far east as the Lena River in Russia.

Since the circumscription of *Oxytropis* DC. in 1802, taxonomists and botanists have struggled to systematically categorize the morphological diversity of the genus. The similarity in morphology of *Oxytropis* to the closely related sister genus *Astragalus* caused confusion within the taxonomic community. Recent phylogenetic studies show that *Oxytropis* diverged from *Astragalus* approximately 12-16 million years ago (Ma) in Eurasia, with both genera diversifying in similar environments (Wojciechowski, 2005), with *Oxytropis* restricted to North America in the New World, while *Astragalus* is found throughout South America as well. While these two genera are closely related phylogenetically, they are taxonomically distinct and morphologically *Oxytropis* can be distinguished from *Astragalus* by having beaked keel-petals, asymmetrical leaflets, and

an acaulescent habit (Barneby 1952; Welsh, 2001; Zhu & Ohashi, 2000; Lewis et al. 2005).

Taxonomic History in North America

Oxytropis DC. was established by de Candolle based solely on the Old World species *Oxytropis montana* (L.) DC. Important collections of Old World *Oxytropis* from Russia and other arctic, subarctic and boreal floras had accumulated at the Royal Botanic Garden at Kew (K) and the British Museum of Natural History (BM) in London. There William Jackson Hooker used these early North American specimens for the first revision of *Oxytropis* in his *Flora boreali-americana* (Hooker 1831). His concept of species laid the foundation for all later works of the genus, which was accepted for the treatment of *Oxytropis* in the *Flora of North America* by Torrey and Gray (1838), except for the addition of six new species described by Thomas Nuttall (1786-1859).

Of the revisionary workers on North American *Oxytropis* Asa Gray stands out as the most thorough and systematic, even reviewing early North American material at K for his initial paper on the genus in 1864 and later for his revision of the genus in 1884. Meanwhile, the European botanist Alexander von Bunge published a monograph of the entire genus including four subgenera, 13 sections, and 181 species (Bunge 1874). Bunge's work is of limited value to the study of North American *Oxytropis*, since Bunge's knowledge of the genus in North America was largely derived from Gray's writings.

After the death of Asa Gray in 1888 the genus was placed in a state of disarray in North America by both Edward Lee Greene and Otto Kuntze, who combined many of the

older epithets in *Aragallus* Neck. (Greene 1897) and *Spiesia* Neck. (Kuntze 1891). In 1952 Rubert Barneby produced a detailed revision of the genus in North America. Barneby described the high intraspecific variation within the genus that he witnessed in the Rockies as well as artfully illustrated the complexities of the taxonomic history. His work has had long lasting affects. The last systematist to revise the genus in North America was Stanley Welsh (2001). His treatment primarily followed that of Barneby (1952) with the addition of two newly discovered taxa (i.e., *Oxytropis huddelsonii* A.E. Porsild and *Oxytropis kobukensis* S.L. Welsh).

Infrageneric Classification

The Old World systematist Alexander von Bunge established an infrageneric classification, in an attempt to address the morphological variability observed in the genus. Bunge (1874) distinguished 17 sections within *Oxytropis* based on leaflet arrangement, raceme size and shape, legume shape and anatomy, presence of glandular hairs, and presence of spines on the petiole. Many of Bunge's infrageneric categories are still used in floristic works today (Yurtsev 1999; Zhu and Ohashi 2000; Polozhij and Malyshev 2006; Malyshev 2008a, b; Ranjbar et al. 2009).

Since Bunge's monograph, few workers have reviewed the genus on a worldwide basis. Vasil'chenko (1948) added two subgenera, *Traganthoxytropis* Vass. and *Triticaria* Vass., exclusively of Old World taxa. Yurtsev (1997; 1999), who treated the genus from a Pan-arctic perspective, noted the importance of substrate affinity. Recently, Malyshev (2008b) investigated morphological diversification in relation to infrageneric

classifications of *Oxytropis*. The discovery of additional taxa in Asia by Russian botanists (Polozhij and Malyshev 2006; Malyshev 2008a, b) as well as Chinese colleagues (Zhu and Ohashi 2000; Wu et al. 2010) have offered new support for infrageneric relationships within *Oxytropis*.

Oxytropis section *Arctobia* — *Oxytropis* section *Arctobia* is prominently featured in Alaska with seven taxa currently recognized (Yurtsev 1997, 1999). This section is characterized by a reduced number of leaflets per leaf as well as a reduced number of flowers per inflorescence ranging from one to four per scape. Within section *Arctobia* Yurtsev (1997) includes five subsections (i.e., *Arctobiae*, *Kamtschaticae*, *Mertensianae*, *Podocarpae*, *Revolutae*), three series (i.e., *Arctobiae*, *Bryophilae*, *Nigrescentes*), and 18 species (see Table 2.1 for taxa included). Yurtsev (1997) also presents a ‘tentative scheme of phylogeny’ for section *Arctobia* based on overall morphological similarity, species distribution, and ecological affinities without any quantitative analysis provided (Fig. 2.1).

Phylogenetic Hypotheses to be tested

Currently, the phylogeny of *Oxytropis* section *Arctobia* proposed by Yurtsev (1997) serves as the most comprehensive treatment with taxa from Russia as well as the United States and Canada (Fig. 2.1). Our phylogenetic analyses are intended to test the taxonomic hypotheses proposed by Yurtsev (Fig. 2.1), in particular the monophyly of section *Arctobia*.

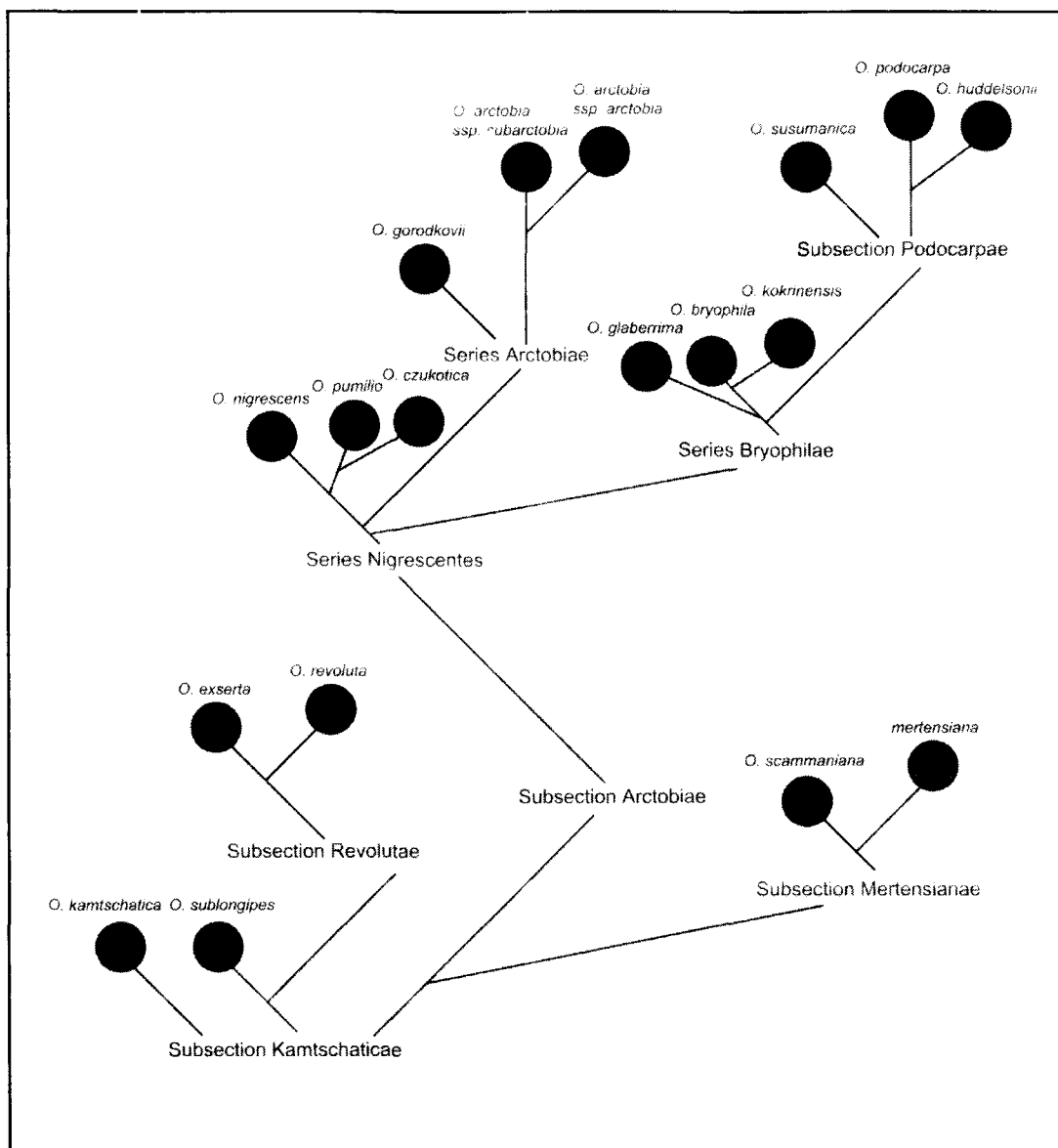


Figure 2.1. A tentative scheme of phylogeny of *Oxytropis* section *Arctobia* modified from Yurtzev (1997).

Table 2.1. Comparison of previous classifications with views presented in the current study for members of *Oxytropis* sect. *Arctobia*.

Barneby (1952) and **Welsh (2001)	Hulten (1968)	Yurtzev (1997) (Γ = strictly Russian taxa)	Present Study (2012) (\dagger = nigrescens complex) (\pounds = Incompletely known)
		Subgenus <i>Oxytropis</i> Sect. <i>Arctobia</i> Subsect. <i>Arctobia</i> Series <i>Nigrescentes</i>	Subgenus <i>Oxytropis</i> Sect. <i>Arctobia</i>
<i>O. nigrescens</i>	<i>O. nigrescens</i>	<i>O. nigrescens</i> Γ <i>O. czukotica</i> <i>O. pumilio</i> Γ	<i>O. nigrescens</i> \dagger <i>O. bryophila</i> \dagger \pounds
<i>O. nigrescens</i> var. <i>nigrescens</i>	<i>O. nigrescens</i> subsp. <i>bryophila</i>	Series <i>Bryophilae</i> <i>O. bryophila</i>	<i>O. bryophila</i> \dagger
<i>O. nigrescens</i> var. <i>lonchopoda</i>	<i>O. glaberrima</i>	<i>O. glaberrima</i>	<i>O. bryophila</i> \dagger
<i>O. kokrinensis</i>	<i>O. kokrinensis</i>	<i>O. kokrinensis</i>	<i>O. kokrinensis</i> \dagger
		Series <i>Arctobia</i> <i>O. gorodkovii</i> <i>O. arctobia</i> ssp. <i>arctobia</i> <i>O. arctobia</i> ssp. <i>subarctobia</i>	<i>O. gorodkovii</i> \dagger <i>O. arctobia</i> \dagger
<i>O. nigrescens</i> var. <i>uniflora</i>	<i>O. nigrescens</i> subsp. <i>pygmaea</i> <i>O. nigrescens</i> subsp. <i>arctobia</i>	Subsect. <i>Kamtschaticae</i> <i>O. sublongipes</i> Γ <i>O. kamtschatica</i> Γ	\pounds \pounds
	<i>O. revoluta</i> Γ	Subsect. <i>Revolutae</i> <i>O. revoluta</i> Γ <i>O. exerta</i> Γ	\pounds \pounds
<i>O. podocarpa</i> <i>O. huddelsonii</i> **	<i>O. huddelsonii</i>	Subsect. <i>Podocarpae</i> <i>O. podocarpa</i> <i>O. huddelsonii</i> <i>O. susumanica</i> Γ	<i>O. podocarpa</i> <i>O. huddelsonii</i> \pounds
<i>O. scammaniana</i> <i>O. mertensiana</i>	<i>O. scammaniana</i> <i>O. mertensiana</i>	Subsect. <i>Mertensianae</i> <i>O. scammaniana</i> <i>O. mertensiana</i>	<i>O. scammaniana</i> <i>O. mertensiana</i>

Materials and Methods

Herbarium Sampling — This study is based on herbarium material from the following herbaria (acronyms according to Thiers 2008): BM, BRY, CAN, DAO, GB, GH, LD, LE, MO, NDG, NY, O, PH, S, UPS, US. A total of 1200 specimens were used for morphological examination in evaluating species boundaries for this treatment. The locality data for all specimens were georeferenced using the description provided on the label. Distribution maps were generated through DIVA-GIS (Hijmans et al. 2004) using the WGS85 projection and datalayers provided by Scenarios Network for Alaska & Arctic Planning (SNAP). We followed the morphological species concept outlined in the Pan-arctic flora (Elven, 2011) to delimit species in this study. We recognize taxa as species on the basis of at least two different independent morphological characters. In addition, fertile intermediates should be rare. Intraspecific categories were omitted from this treatment.

Taxon Sampling — Species of section *Arctobia* Bunge (Yurtzev 1997) were included in the analysis, except for *O. pumilio*, *O. glaberrima*, *O. sublongipes*, *O. susumanica*, and *O. exerta* due to unavailability of material. Six outgroup taxa within *Oxytropis*, one representative each from section *Baicalia* Steller ex Bunge, *Glaeocephala* Bunge, *Xerobia* Bunge, two from section *Mesogaeae* Bunge, and seven species of section *Orobia* Bunge were chosen to determine infrageneric relationships (Not all outgroup taxa were amplified for each gene, see Appendix 1). For rooting purposes a total of twenty outgroup species were selected including three species of *Astragalus* L., one species of *Swainsona*

Salisb., two species of *Medicago* L., as well as *Vicia faba* L., based on previous phylogenetic studies (Martin et al. 1997; Wojciechowski et al. 2004; Steele et al. 2010).

Marker Selection — Four markers were selected to resolve species-level and infrageneric relationships. These include the plastid encoded *trnK-matK* gene region (*trnK /matK*), the nuclear encoded triosephosphate translocator gene (TRPT), the nuclear cyclic nucleotide gated channel 5 gene (CNGC5), and coding and non-coding regions of the single copy nuclear encoded GA3ox1 gene (LE). In most legume species the *matK* gene consists of 1500-1525 bp, while the flanking 5' and 3' *trnK* intron is approximately 1000 bp (Steele et al. 2010). Among the three nuclear markers used, the divergent exon of the nuclear encoded triosephosphate translocator gene (TRPT) is the shortest and approximately 345 bp in length (Flügge and Heldt 1984; Howard et al. 2007). It has shown variation within papilionoid legumes, providing suitable resolution of relationships at higher taxonomic levels (Howard et al. 2007). We also used the cyclic nucleotide gated channel 5 gene (CNGC5), which was recently used for resolving phylogenetic relationship in closely related species of *Medicago* by Maureira-Butler et al. (2008). They found CNGC5 to be approximately 843 base pairs in lengths in *Medicago*. The coding and non-coding regions of the single copy nuclear encoded *GA3ox1* gene were also amplified (approximately 1700 bp). The gene consists of a central intron flanked by two exons. In *Pisum sativum*, the combined length of both exons are 1125 bp long, and the intron sequence is 544 bp. This gene codes for gibberellin 3- β -hydroxylase (Martin et al. 1997; Lester et al. 1997) and has previously been used to discern

phylogenetic relationships among species of *Medicago* (Steele et al. 1999; Steele et al. 2010).

DNA Amplification and Sequencing – Sequences were produced from leaf material removed from herbarium specimens, preserved field collections and downloaded from GenBank (Appendix 1). Specimens were collected primarily in Alaska as well as from the Chukotka Peninsula of Russia, the Colorado Rockies, the Yukon Territory and the Canadian Archipelago. Total genomic DNA for all taxa (Appendix 1) was isolated following DNeasy Plant Mini Kit protocols (Qiagen Inc., California).

All four loci were amplified using primers as indicated in Table 2.2.

Amplifications were performed using 25 μ L reaction with 4.25 μ L of water, 2.5 μ L of 50% glycerol, 2.5 μ L of Taq buffer with KCl, 2 mM dNTPs, 1.25 μ L of the forward and reverse primers (varying from 3 μ M to 10 μ M), and 1.5 μ L of MgCl₂, 0.1 μ L of Taq DNA polymerase (Invitrogen) and 10 μ L of 10-30 ng/ μ L of DNA. While thermal cycling conditions for amplification of *trnK/matK* followed protocols outlined in Wojciechowski et al. 2004), those for LE and TRPT were optimized at 94°C for 2 min., 95°C for 30 seconds 57°C for 30 seconds, 72°C for 2.5 min and the cycle repeated 44 times with a final extension at 72°C for 7 min. For the amplification of CNGC5 we used 56°C as the annealing temperature, and an extension time of 1 min. at 72°C.

Sequence Alignment and Phylogenetic Analysis – Sequences were assembled into contigs in Sequencher 4.12 (GeneCodes, Ann Arbor, Michigan, USA). Sequence alignments

were initially made using MAFFT 6.859 (Kato et al. 2009) and then manually edited using MacClade (Maddison and Maddison, 1989). Ambiguous alignment sites were excluded. For phylogenetic analyses we prepared four matrices representing each of the four loci as well as a combined data matrix by concatenating *matK* and TRPT. All new sequences will be deposited in GenBank (see Appendix 1), and the final data matrices will be deposited in Tree-BASE (<http://www.treebase.org/treebase-web/home.html>) under study accession S#####.

Table 2.2. Sequences of oligonucleotide primers used. Sequences given are all 5' to 3'.

Marker	Primer Name	Sequence	Citation
TRPT	TRPT_F	CCATGATTCCTCGTTGAGACAAC	Howard et al., 2007
	TRPT_R	ATTAACACAACATTCAAAGCCCACCA	Howard et al., 2007
CNGC5	CNGC5_F	TCATCTCTGTYTGGCTTTAGTG	Maureira-Butler et al., 2008
	CNGC5_R	AAGCAGCCCARGTYCTCCAT	Maureira-Butler et al., 2008
matK	trnK685_F	GTATCGCACTATGTATCATTGA	Steele and Wojciechowski 2003
	trnKw1	GGGTTGCTAACTCAATGGTAGAG	Steele and Wojciechowski 2003
	matK1100L	TTCAGTGGTACGGAGTCAAATG	Steele and Wojciechowski 2003
	psbA_LR	GCAGTCATGGTAAAATCTTGGG	Ickert-Bond unpublished
	trnK4L_R	CATCTTTCACCCAGTATCGAAGG	Steele and Wojciechowski 2003
	matK4L	CTTCGCTACTGGGTGAAAGATG	Steele and Wojciechowski 2003
	LE	18F_ZJM	CCCTGACTTCAACTCC
	OD_3F	CTCCTCCTTCTTCCCAAACCTCA	Steele et al., 2010
	OD_5R	AATGTTGAGTCCGTGTGCGGGGC	Steele et al., 2010
	OD_7R	CTCTGACGGGTTCCGGTTCAC	Steele et al., 2010
	20R_SB	GGAATGAGTACCTTGGCACKA	This study

Phylogenetic analyses were conducted on all matrices and included maximum parsimony (MP) and maximum likelihood (ML) searches in PAUP* 4.0b10 (Swofford 2002), as well as Bayesian inference (BI) Markov Chain Monte Carlo (MCMC) in MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). All parsimony and bootstrap analyses were conducted using heuristic search methods and employed all addition sequence options (SIMPLE, CLOSEST, RANDOM addition sequences) in combination with tree-bisection reconnection (TBR) branch-swapping and the MulTrees option, which saves all minimal trees. Relative levels of clade support under MP and ML were assessed using nonparametric bootstrap analysis (BS; Felsenstein, 1985), with 1,000 bootstrap replicates, as implemented in PAUP* 4.0b10. The consistency index (CI; Kluge and Farris 1969), retention index (RI; Farris 1989) and rescaled consistency index (RC; Farris 1989) were also calculated to evaluate homoplasy (Table 2.3). All characters were equally weighted, and gaps were treated as missing characters as well as coded via complex indel coding (Simmons et al. 2007). For the ML analysis, the Akaike Information Criterion (AIC) was used in the program Modeltest 3.7 (Posada and Crandall 1998) to estimate the most appropriate model of DNA substitution for each data set.

Mr.Modeltest 2.3 (Nylander, 2004) and AIC were used to determine the model of evolution for the Bayesian analysis. We conducted BI/ MCMC analyses in MrBayes 3.2, which consisted of four linked chains, run for two million generations, sampled every 1000 generations. Each Bayesian analysis was repeated to confirm clade posterior probabilities and model estimates. Convergence was confirmed through the examination

of the summary statistic, potential scale reduction factor (PSRF), which approached 1 in all runs (Gelman and Rubin 1992). A 50% majority-rule consensus tree was obtained after the burn-in of 20,000. Bootstrap support (BS) from MP and ML analyses greater than or equal to 70% and Bayesian posterior probabilities (PP) greater than or equal to 0.8 are reported. Support was considered significant if ML and MP values were $> 70\%$ or if PP values were > 0.90 .

Conflict between the data sets was evaluated through visual comparison of the topologies and clade support by all three analyses (MP, ML, BI). In addition, the incongruence length difference test (ILD, Farris et al. 1994) was performed in PAUP* 4.0b10 using searches as described for maximum parsimony analyses (excluding uninformative characters) as well as by using 10 random addition sequence replicates per partition homogeneity replicate and by comparing a bootstrap consensus tree derived from the individual data partitions.

Hypothesis testing – Our phylogenetic analyses revealed section *Arctobia* to be nested within sections *Orobia*, *Glaeocephala*, and *Baicalia*, contradicting Yurtev's infrageneric classification. We tested whether our data are sufficient to statistically reject the hypothesis that section *Arctobia* is monophyletic. For the hypothesis testing, we used the Shimodaira–Hasegawa (SH) test (Shimodaira and Hasegawa 2001) as well as expected likelihood weight (ELW) test (Strimmer and Rambaut 2002) in TREE-PUZZLE 5.2 (Schmidt et al. 2002) as performed in Lumbsch et al. (2010).

Results

Size and Structure of Molecular Data Sets — The length of the TRPT gene ranges from 303 to 327 bases (Table 2.3). The aligned length of the TRPT data set is 327 bp, of which 97 sites are parsimony informative overall and 31 within section *Arctobia* (Table 2.3). An 18 bp indel was found, spanning positions 181 to 201. This deletion was only present in taxa within section *Arctobia*, however not all members within section *Arctobia* possessed this indel. The 18 bp indel discovered in the TRPT gene was coded using complex indel coding and analyzed using parsimony, but the resolution only marginally improved support (approximately 5%) and still lacked resolution of section *Arctobia* overall.

The CNGC5 gene varies in length from 741 to 876 bases. The aligned length of the CNGC5 data set is 918 bp, of which a total of 182 are parsimony informative overall and 61 parsimony informative sites are found among members of section *Arctobia* (Table 2.3). Two indels specific to samples of *O. mertensiana* were discovered at positions 227-309 bp as well as 448-490 bp, totaling 126 bp in the sequences. The indels were coded under simple indel coding as well as complex indel coding revealing species-level resolution of *O. mertensiana* with a bootstrap value of 86% (tree not shown).

The single copy nuclear LE gene varies in length from 1810-1850 bp (Table 2.3). Unsuccessful amplification coupled with low quality sequence reads greatly reduced the alignment. A sample of *Oxytropis podocarpa* was successfully amplified and sequenced with a total length of 1405 bp. The two flanking exons span a total of 919 bp (exon 1 from 1-438 bp and exon 2 from 943-1405 bp) with the intron spanning positions 439-942

Table 2.3 Summary of the molecular data sets and phylogenetic analyses

<i>Sequence characteristics</i>	TRPT	CNGC5	LE	matK	TRPT + matK
Number of species	35	21	16	40	40
Number of sequences	42	27	24	51	51
Length of complete sequence (range)	303 – 327	741 – 876	511 – 539	1512 – 1539	1805 – 1842
Aligned Length (maximum)	327	918	542	1563	1899
Number of Variable Sites	164	248	149	505	669
% informative characters in dataset					
Outgroup + Ingroup	97/327 = 29. 6%	182/918 = 19.9 %	117/542 = 3.86%	231/1563 =14.8 %	328/1899 = 17.9%
Ingroup	31/303 = 10. 2%	61/879 = 6.9%	33/514 = 6.4%	51/1539 = 3.3%	82/1842 = 4.5%
<i>Parsimony Analyses</i>					
# of trees	201,105	11,712	1,336	2	166,415
# of steps	329	300	200	766	1105
CI	0.657	0.917	0.870	0.792	0.745
RI	0.766	0.970	0.919	0.889	0.800
RC	0.503	0.889	0.799	0.657	0.596

Table 2.3 Continued

of groups with bootstraps > 70%

Outgroups + Ingroup	11	9
Ingroup	3	5

ML and BA Analyses

Model selection (ML)	TVM+G	K81uf+G
Model selection (BA)	GTR+G	HKY+G
AIC score	4325.0166	5653.4941

6	18	18
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5	8	5
---	---	---

HKY+G	TVM+G	GTR+G
-------	-------	-------

HKY+G	GTR+G	GTR+G
-------	-------	-------

3531.2271	12950.4424	17673.1914
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bp. The sequence and amplification primers designed in the current study for LE were based on the sequence from *Oxytropis podocarpa* (Table 2.2). The excised alignment of the LE data set is 542 bp long exclusively from exon 2 along the 3' end of the gene. A total of 117 characters are parsimony informative, while 33 characters are parsimony informative within section *Arctobia* (Table 2.3).

The length of the plastid *matK* gene ranges from 1512 to 1539 bases (Table 2.3). The aligned length of the *matK* data set is 1563 bp, of which 231 are parsimony informative. A total of 51 bp are parsimony informative within section *Arctobia* (Table 2.3). An insertion spanning 18 bp was discovered in three accessions of *O. bryophila* at positions 615-632.

These data sets differed in the sampling scheme, with 42 accessions sampled for TRPT, 27 for CNGC5, 24 for LE, and 51 for *matK*, respectively (Table 2.3; Appendix 1). The missing sequences are due to unsuccessful amplification and low quality sequence reads. A combined matrix of TRPT and *matK* was assembled with a total alignment length of 1899 bp. Visual examination of the tree topologies along with the incongruence length test between *matK* and TRPT revealed incongruence to not be significant ($p > 0.54$).

Analysis of the Nuclear TRPT Region — Parsimony analysis of the TRPT data set resulted in 201,105 equally parsimonious trees with 329 steps (CI=0.657, RI=0.766, RC=0.503; Table 2.3). Modeltest selected the TVM + gamma model for the ML analysis, while Mr.Modeltest selected the GTR + gamma substitution model for Bayesian inference. A 50% majority Bayesian consensus tree (Fig. 2.2) was constructed with an

AIC score of 4325.02 (Table 2.3). A well-supported clade (PP=1; ML=100%) of *Colutea arborescens*, *Swainsona pterostylis*, and *Sutherlandia frutescens* is resolved as sister to the locoweeds (PP=1; ML=100%). All analyses strongly support (PP=1; ML=100%) the monophyly of the genus *Oxytropis* as seen in the Bayesian consensus tree (Fig. 2.2), while none of the previously recognized infrageneric groupings are supported. A trifurcating branch of *Oxytropis* is illustrated (Fig. 2.2), with a highly-supported clade (PP=0.97; ML=96%) of *O. deflexa* and *O. pilosa*. An unsupported clade of *O. huddelsonii* and *O. podocarpa* diverges from the main clade of *Oxytropis* (Fig. 2.2). In addition, an unsupported clade of *O. kokrinensis* and *O. bryophila* appears in the main clade of *Oxytropis*. The Bayesian consensus tree also reveals strong to moderate support (PP=0.92; ML=0.77%) for the two accessions of *O. arctobia*, which grouped with *O. campestris* var. *roaldii*, *O. lambertii*, and *O. nigrescens*. All three analytical search algorithms performed (MP, ML, BI) resulted in highly reticulate trees with largely unresolved topologies for sect. *Arctobia*.

Analysis of the Nuclear CNGC5 Region — Parsimony analysis for the CNGC5 data set resulted in 11,712 equally parsimonious trees with a length of 300 steps (CI=0.917, RI=0.970, RC=0.889; Table 2.3). Modeltest selected the K81uf + gamma substitution model for the ML analysis and Mr.Modeltest selected the HKY + gamma for the BI. A Bayesian 50% majority consensus tree (Fig. 2.3) resulted with an AIC score of 5653.49 (Table 2.3). Strong support (PP=1; ML=100) of *Trigonella mesopotamica* and *Trigonella spruneriana* being sister taxa is illustrated within the basal *Trigonella* clade. In addition, a well-supported (PP=1; ML=100) monophyletic clade of *Medicago* is shown (Fig. 2.3).

All analytical approaches strongly support the monophyly of the genus *Oxytropis* (PP=1; ML=100%) as seen in the Bayesian consensus tree (Fig. 2.3). The BI phylogeny of CNGC5 revealed the polyphyly of sect. *Orobia* as well as sect. *Arctobia*. However, a strongly supported clade (PP=0.99; ML=100%) of *O. maydelliana*, *O. borealis*, and *O. arctica* var. *barnebyana* appears distinct from the rest of the species sequenced that form a large polytomy of all the remaining taxa (Fig. 2.3). Within this large unresolved clade (Fig. 2.3) a weakly supported clade of 14 accessions of section *Arctobia* (PP=0.90; ML=79) is shown. This weakly supported clade also contains a strongly supported clade of two accessions of *O. gorodkovii* (PP=0.99; ML=87%) and a moderately supported clade of two accessions of *O. arctobia* (PP=0.83; ML=70%), each distinct from the rest of the other taxa sampled.

Analysis of the Nuclear LE Region — The parsimony analysis of the LE data set resulted in 1,336 equally parsimonious trees with a length of 200 steps (CI=0.870, RI=0.919, RC=0.799; Table 2.3). Modeltest and Mr.Modeltest selected the HKY+gamma substitution model. All analyses strongly support *Oxytropis* as monophyletic (PP=1; ML=100%). A 50% majority Bayesian consensus tree was produced with an AIC score of 3531.23 (Table 2.3) showing sect. *Arctobia* (Fig. 2.4) to be nested within sect. *Glaeocephala* and *Orobia*. *Oxytropis mertensiana* and *O. kokrinensis* appear basal to the rest of the taxa sampled, which form a strongly supported clade (PP=0.95; ML=93%). Within this clade *O. scammaniana* is resolved as the first diverging node (PP=0.95; ML=93%), followed by the divergence of a moderately to well-supported clade

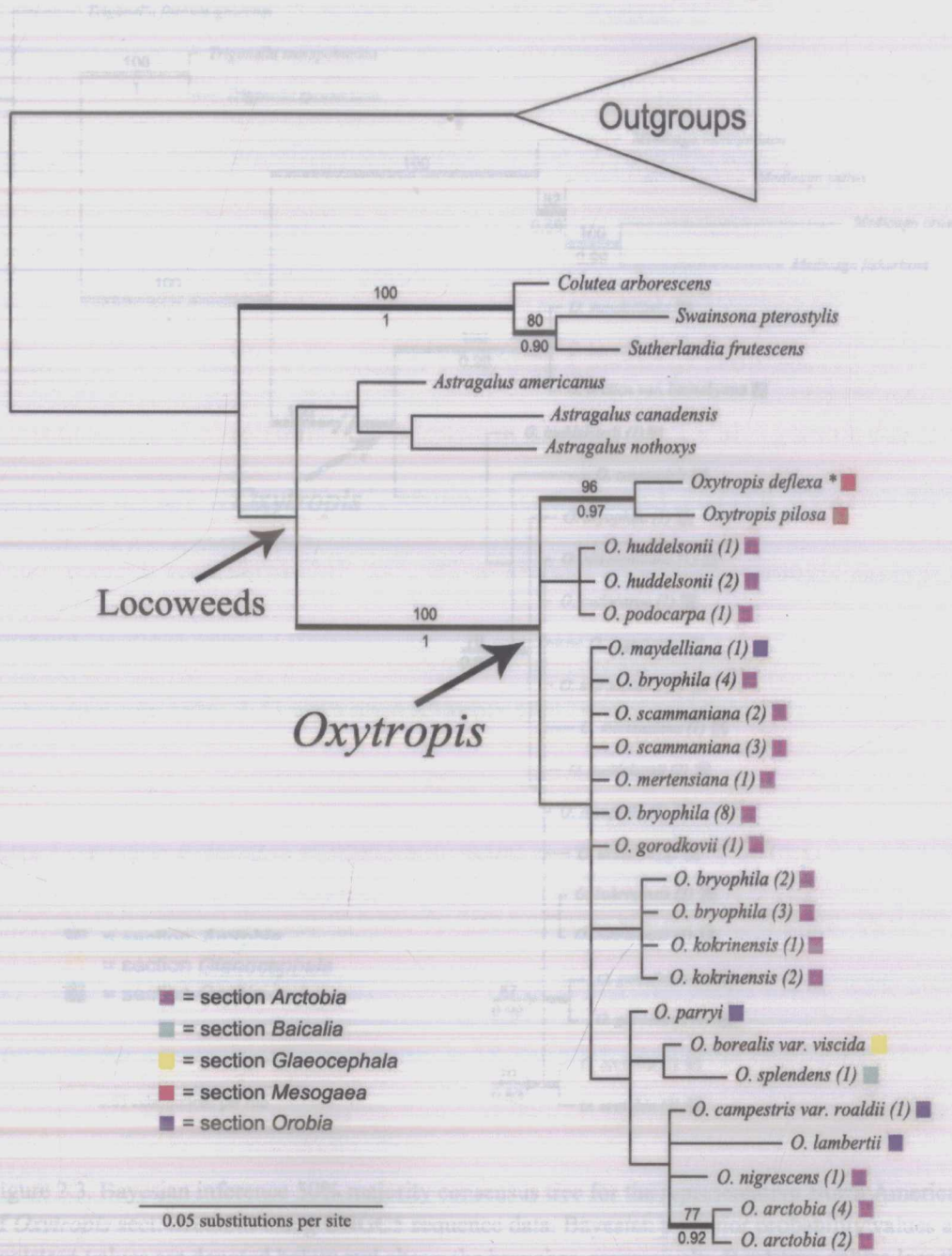


Figure 2.2. Bayesian inference 50% majority consensus tree for the representative North American species of *Oxytropis* sect. *Arctobia* using TRPT sequence data. Bayesian posterior probability values and ML bootstrap values are denoted below and above the branches, respectively. Bootstrap values less than 70% and posterior probabilities less than 90% are not depicted. Sections (left) and clade (arrows) names are provided. The numbers in parentheses denote the accessions from Appendix 1 and the * indicates a GenBank sample.

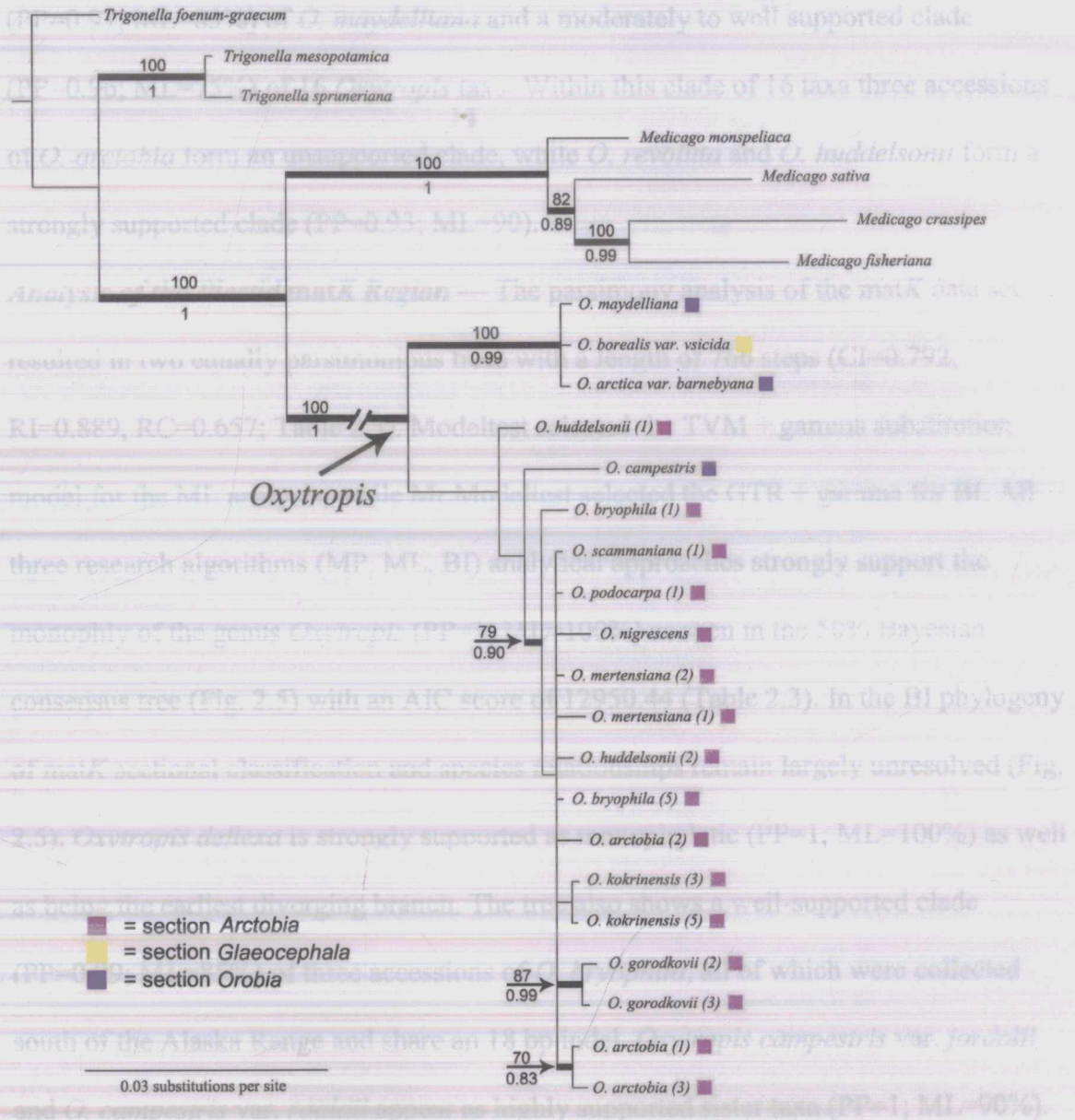


Figure 2.3. Bayesian inference 50% majority consensus tree for the representative North American species of *Oxytropis* sect. *Arctobia* using CNGC5 sequence data. Bayesian posterior probability values and ML bootstrap values are denoted below and above the branches, respectively. Bootstrap values less than 70% and posterior probabilities less than 90% are not depicted. Sections (left) and clade (arrow) names are provided. The // symbol indicates a break in the branch to allow the ingroup relationships to be illustrated in the figure. The numbers in parentheses denote the accessions from Appendix 1.

(PP=0.97; ML=83%) of *O. maydelliana* and a moderately to well supported clade (PP=0.96; ML=75%) of 16 *Oxytropis* taxa. Within this clade of 16 taxa three accessions of *O. arctobia* form an unsupported clade, while *O. revoluta* and *O. huddelsonii* form a strongly supported clade (PP=0.93; ML=90).

Analysis of the Plastid matK Region — The parsimony analysis of the matK data set resulted in two equally parsimonious trees with a length of 766 steps (CI=0.792, RI=0.889, RC=0.657; Table 2.3). Modeltest selected the TVM + gamma substitution model for the ML analysis, while Mr.Modeltest selected the GTR + gamma for BI. All three research algorithms (MP, ML, BI) analytical approaches strongly support the monophly of the genus *Oxytropis* (PP=1; ML=100%) as seen in the 50% Bayesian consensus tree (Fig. 2.5) with an AIC score of 12950.44 (Table 2.3). In the BI phylogeny of matK sectional classification and species relationships remain largely unresolved (Fig. 2.5). *Oxytropis deflexa* is strongly supported as monophyletic (PP=1; ML=100%) as well as being the earliest diverging branch. The tree also shows a well-supported clade (PP=0.99; ML=85%) of three accessions of *O. bryophila*, all of which were collected south of the Alaska Range and share an 18 bp indel. *Oxytropis campestris* var. *jordalii* and *O. campestris* var. *roaldii* appear as highly supported sister taxa (PP=1; ML=90%). In addition, a moderately supported clade (PP=0.99; ML=70%) of *O. borealis* var. *viscida*, *O. maydelliana*, *O. campestris*, *O. campestris* ssp. *sordida* and *O. splendens* is shown (Fig. 2.5), with a well-supported early diverging branch of *O. borealis* var. *viscida* (PP=0.97; ML=70%).

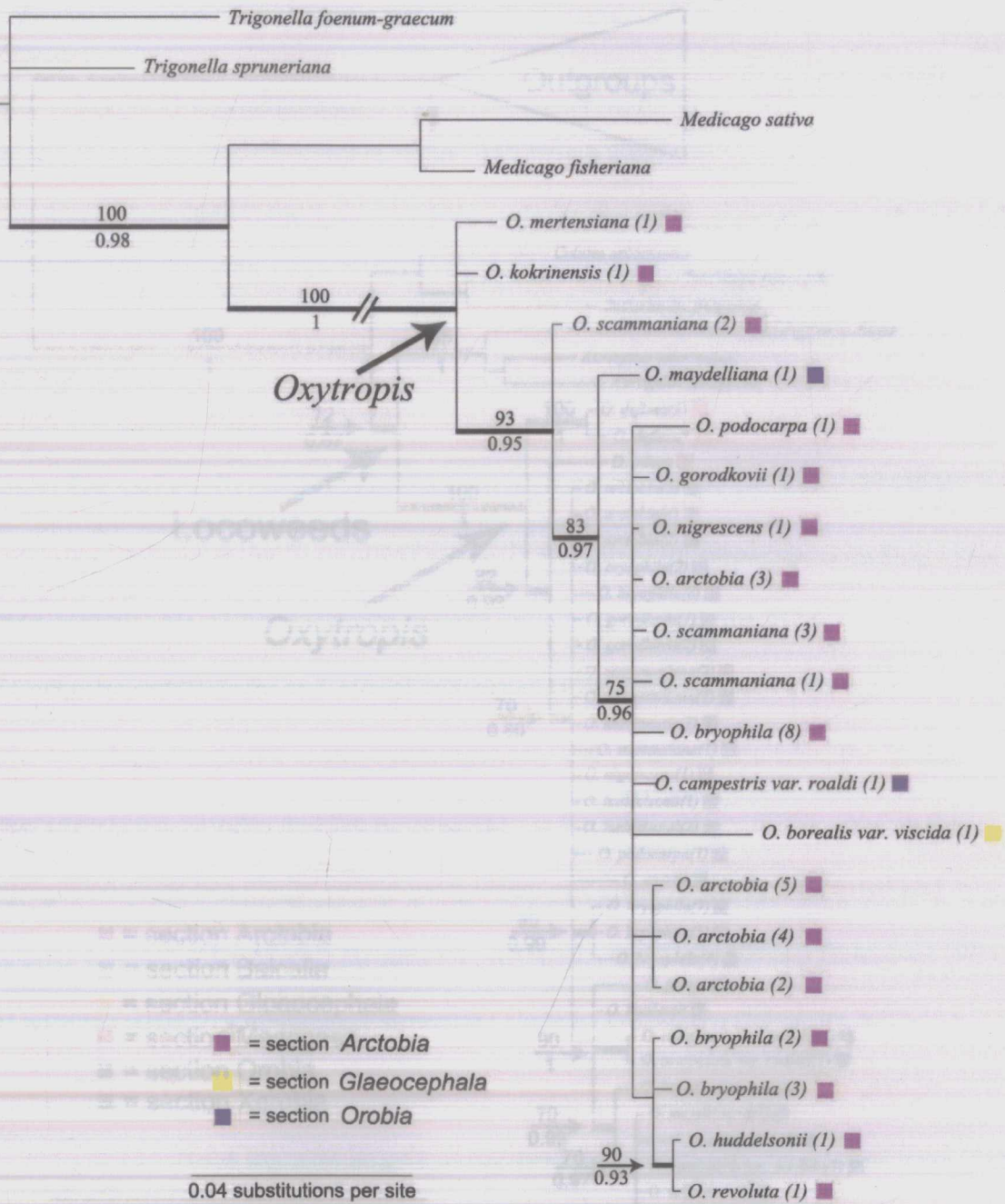


Figure 2.4. Bayesian inference 50% majority consensus tree for the representative North American species of *Oxytropis* sect. *Arctobia* using LE sequence data. Bayesian posterior probability values and ML bootstrap values are denoted below and above the branches, respectively. Bootstrap values less than 70% and posterior probabilities less than 90% are not depicted. Sections (left) and clade (arrow) names are provided. The // symbol indicates a break in the branch to allow the ingroup relationships to be illustrated in the figure. The numbers in parentheses denote the accessions from Appendix 1.

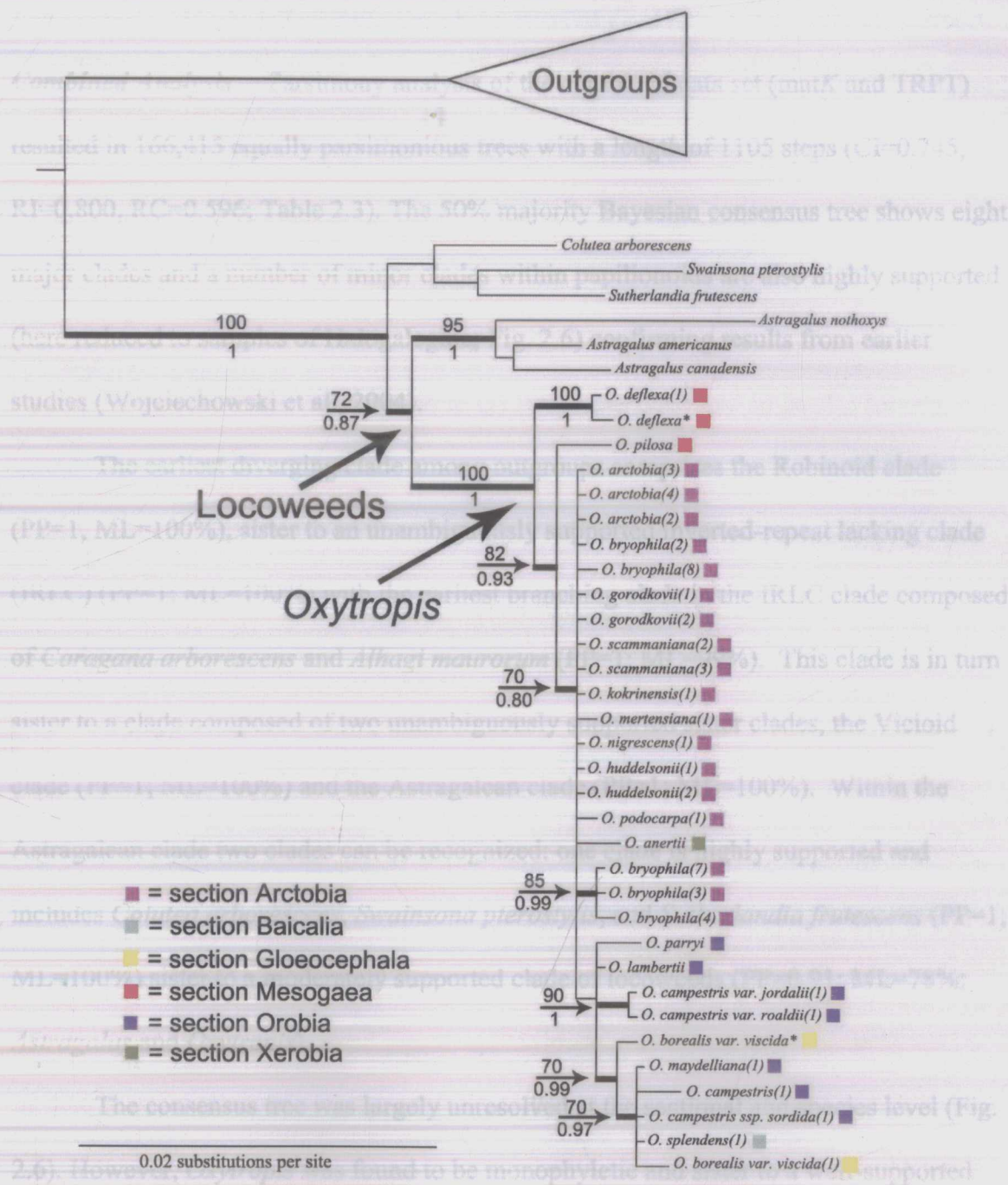


Figure 2.5. Bayesian inference 50% majority consensus tree for the representative North American species of *Oxytropis* sect. *Arctobia* using *matK* sequence data. Bayesian posterior probability values and ML bootstrap values are denoted below and above the branches, respectively. Bootstrap values less than 70% and posterior probabilities less than 90% are not depicted. Sections (left) and clade (arrows) names are provided. The numbers in parentheses denote the accessions from Appendix 1 and the * indicates a GenBank sample.

Combined Analysis — Parsimony analysis of the combined data set (matK and TRPT) resulted in 166,415 equally parsimonious trees with a length of 1105 steps (CI=0.745, RI=0.800, RC=0.596; Table 2.3). The 50% majority Bayesian consensus tree shows eight major clades and a number of minor clades within papilionoids are also highly supported (here reduced to samples of Halogalegina; Fig. 2.6) confirming results from earlier studies (Wojciechowski et al., 2004).

The earliest diverging clade among outgroups comprises the Robinoid clade (PP=1, ML=100%), sister to an unambiguously supported inverted-repeat lacking clade (IRLC) (PP=1; ML=100%) with the earliest branching clade in the IRLC clade composed of *Caragana arborescens* and *Alhagi maurorum* (PP=1; ML=99%). This clade is in turn sister to a clade composed of two unambiguously supported sister clades, the Vicioid clade (PP=1; ML=100%) and the Astragalean clade (PP=1; ML=100%). Within the Astragalean clade two clades can be recognized: one clade is highly supported and includes *Colutea arborescens*, *Swainsona pterostylis*, and *Sutherlandia frutescens* (PP=1; ML=100%) sister to a moderately supported clade of locoweeds (PP=0.91; ML=78%; *Astragalus* and *Oxytropis*).

The consensus tree was largely unresolved at the sectional and species level (Fig. 2.6). However, *Oxytropis* was found to be monophyletic and sister to a well-supported clade of *Astragalus* (PP=1; ML=98%). Within *Oxytropis*, the earliest diverging branch consisted of a moderately to weakly supported clade of *O. deflexa* and *O. pilosa* (PP=0.77; ML=77%), with the two accessions of *O. deflexa* being highly supported as

monophyletic (PP=1; ML=99%). Two accessions of *O. arctobia* were strongly supported within the main clade of *Oxytropis* (PP=0.94; ML=84%). The SH and ELW tests used in alternative hypothesis testing significantly ($p > 0.023$) rejected section *Arctobia* as being monophyletic at the 5% significance level.

Discussion

The classification of *Oxytropis* in the Arctic has remained enigmatic for over a century due to the lack of definitive taxonomic characters, convoluted nomenclatural history, and complex biogeography (Barneby 1952; Bunge 1874; Welsh 2001). Our study is the first contribution to understanding species relationships within *Oxytropis* sect. *Arctobia*.

Phylogenetic Relationships in Fabaceae – Higher-level phylogenetic relationships were observed in *matK*, TRPT, as well as in the combined analysis (Fig. 2.2; Fig. 2.5; Fig. 2.6). Support for the IRLC clade, which encompasses members of tribes Cicereae, Hedysareae, Trifolieae, and Vicieae is illustrated in the two Bayesian inference 50% majority consensus trees (Fig. 2.2; Fig. 2.5). All members of the IRLC clade share a loss of one copy of the large inverted repeat, approximately 25 kilobases (Wojciechowski et al. 2000). In addition, strong support for the Vicioid clade and Astragalean clade were observed (Fig. 2.5). The Vicioid clade includes tribes Cicereae, Trifolieae, and Vicieae, which appear a sister to the Astragalean clade. The Astragalean clade is one of the largest in the IRLC, with an estimated 3,000 species including the economically important genera such as *Medicago* (burclover), *Swainsona* (Sturt's Desert Pea), and *Cicer*

pinnatifidum (chickpeas). Recent molecular investigations of *matK* and other nuclear markers have shown that *Oxytropis* is in fact the monophyletic sister group to *Astragalus* and not nested within it (Wojciechowski et al. 2000, 2004), which was also shown by our analyses (Figs 2.2; 2.5; 2.6).

Infrageneric Level Phylogenetic Relationships – Yurtzev (1997) classified *Oxytropis* into numerous infrageneric categories (subgenera, sections, subsections, and series). None of the proposed infrageneric subdivisions of Yurtzev (1997) were supported with the genetic markers analyzed in this study with the exception of sect. *Mesogaea*. In both TRPT and *matK* sect. *Mesogaea* was found to be the earliest diverging clade, represented by *O. deflexa* and *O. podocarpa* (Figs. 2.2, 2.5). However, the results from the molecular data depict a largely unresolved phylogeny among members of sect. *Arctobia*.

Geographical Isolation – We found moderate to strong support of an *Oxytropis arctobia* clade using TRPT, CNGC5, and *matK* (Figs. 2.2, 2.3, 2.5), but the level of support varied depending on the marker used. Nevertheless, all markers indicated a slight divergence of the two accessions of *O. arctobia* from other members of section *Arctobia* under all three search algorithms used (Figs. 2.2, 2.3, 2.5). The samples of *O. arctobia* were collected in the Canadian Archipelago and the distinctiveness of the sequences may be indicative of geographic isolation since the last glacial maxima (Hulten 1937; 1958; Abbott and Brochmann 2003). *Oxytropis arctobia* is primarily distributed in the Canadian Archipelago, which has been suggested to harbor refugia (Eriksen and Töpel 2006), including those on Banks Island inhabited by *O. arctobia* used in our study.

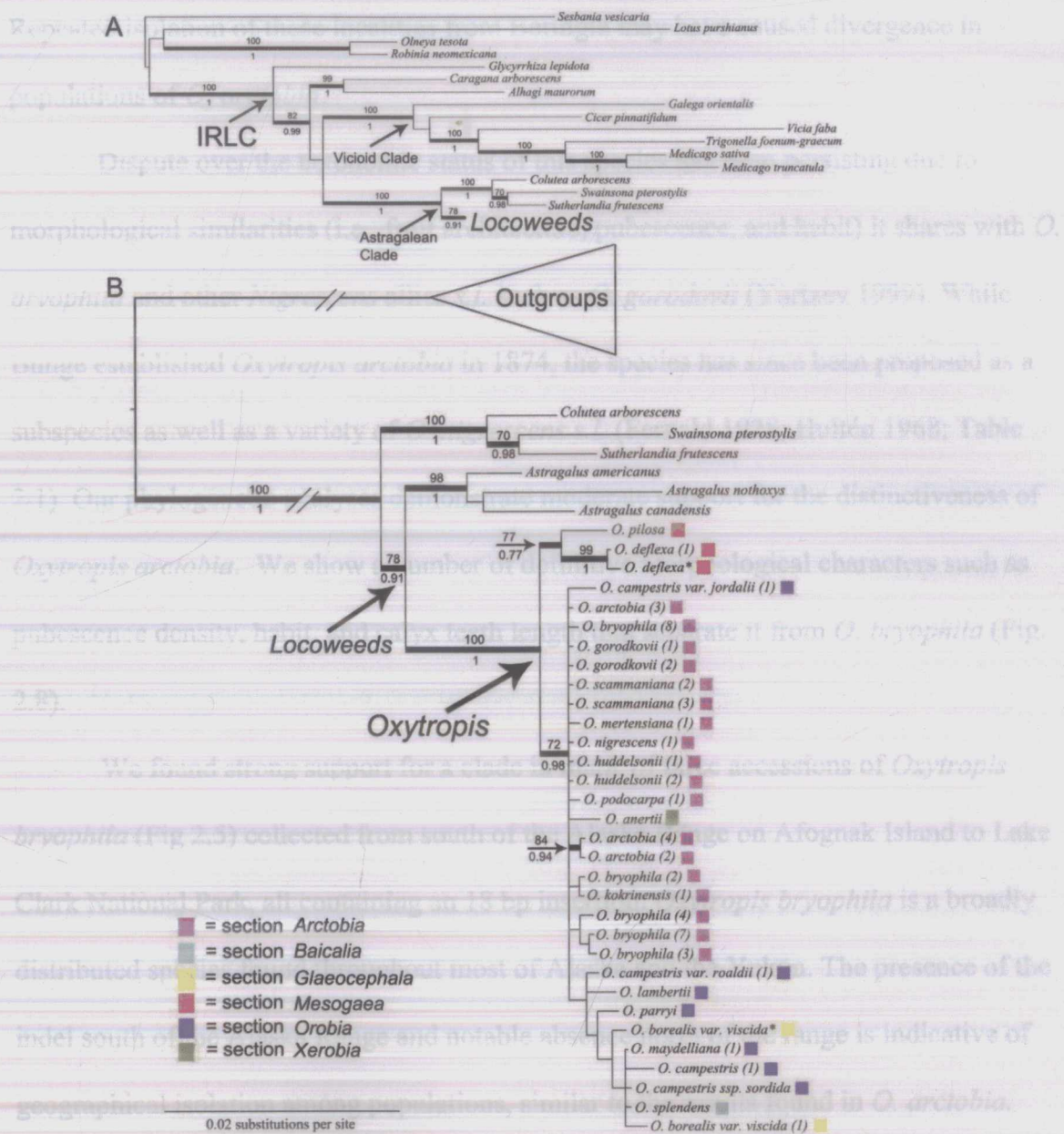


Figure 2.6. Bayesian inference 50% majority consensus trees for members of Fabaceae, with an emphasis on North American species of *Oxytropis* section *Arctobia* from the combined Bayesian analysis of *matK* and TRPT. A) Phylogenetic relationships within Hologalegina are shown at the top. Informal clade names follow Wojciechowski et al. (2004). B) Phylogenetic relationships of the locoweeds sampled are depicted below. Bayesian posterior probability values and ML bootstrap values are denoted below and above the branches, respectively. Bootstrap values less than 70% and posterior probabilities less than 90% are not depicted. Sections (left) and clade (arrows) names are provided. The // symbol indicates a break in the branch to allow the ingroup relationships to be illustrated in the figure. The numbers in parentheses denote the accessions from Appendix 1 and the * indicates a GenBank sample.

Repeated isolation of these localities from Beringia may have caused divergence in populations of *O. arctobia*.

Dispute over the taxonomic status of this species has been persisting due to morphological similarities (i.e., fruit architecture, pubescence, and habit) it shares with *O. bryophila* and other *Nigrescens* allies *s.l.* such as *O. gorodovii* (Yurtzev 1999). While Bunge established *Oxytropis arctobia* in 1874, the species has since been proposed as a subspecies as well as a variety of *O. nigrescens s.l.* (Fernald 1928; Hultén 1968; Table 2.1). Our phylogenetic analyses demonstrate moderate support for the distinctiveness of *Oxytropis arctobia*. We show a number of definitive morphological characters such as pubescence density, habit, and calyx teeth length that separate it from *O. bryophila* (Fig. 2.8).

We found strong support for a clade in *matK* of three accessions of *Oxytropis bryophila* (Fig 2.5) collected from south of the Alaska Range on Afognak Island to Lake Clark National Park, all containing an 18 bp insertion. *Oxytropis bryophila* is a broadly distributed species found throughout most of Alaska and the Yukon. The presence of the indel south of the Alaska Range and notable absence north of the range is indicative of geographical isolation among populations, similar to the results found in *O. arctobia*.

Morphologically, *Oxytropis bryophila* is highly variable in habit, pubescence, and leaflet number. The observed morphological diversity continues to be interpreted at different levels of rank (Table 2.1). Barneby (1952) and Welsh (2001) do not recognize *O. bryophila* as being distinct from *O. nigrescens*, but rather as a singular polymorphic species with several varieties. Yurtzev (1997, 1999) treats the observed diversity at the

species level (Table 2.1), recognizing *O. bryophila*, *O. arctobia* and *O. gorodkovii* as being morphologically distinct from *O. nigrescens sensu strictu*.

Taxonomic Implications – Molecular work in closely related complexes of *Oxytropis* sect. *Arctobia* has yet to fully resolve phylogenetic relationships. Similarly, Jorgensen et al. (2003) examined ITS and RAPD sequences from members of the *O. campestris* and *O. arctica* complexes and found low genetic variation among these markers as well. However, a geographic split dividing the northeastern arctic populations from most other populations was discovered, similar to the findings in our study for *O. bryophila* when examining sequences of *matK*. The lack of genetic diversity among the species sampled here may be indicative of recent divergence (Abbott and Brochmann 2003; Holderegger and Abbott, 2003; Nordal et al. 1999). The ebb and flow of glacial maxima and minima caused populations to be isolated from each other during the Pleistocene (Abbott and Brochmann 2003). Three possible hypotheses may explain our observed lack of resolution in sect. *Arctobia* in North America: 1) The time interval between glacial maxima may have been sufficient to allow gene flow across the landscape, reducing overall genetic diversity and homogenizing the populations. 2) The populations did not have the required amount of time or conditions to diverge. 3) The species complex consists of a single broadly distributed polymorphic taxon influenced by geography and ecological variation. The results from this study do not support the monophyly of *Oxytropis* section *Arctobia* as suggested by Yurtzev (1997).

Use of next generation sequencing technologies such as restriction-site associated DNA sequencing (RADSeq) and whole genome datasets may provide additional

sequence resolution needed to better understand phylogenetic relationships in the recently evolved members of *Oxytropis* sect. *Arctobia*. In addition, increased sampling across the Russian Far East, Canada, and the contiguous United States may further elucidate infrageneric relationships.

TAXONOMIC TREATMENT

Oxytropis DC., *Astragalogia* ed quarto: 66, ed. Folio: 53. 1802, nom. cons. – TYPE: *O. montana* (Linnaeus) A.P. de Candolle (*Astragalus montanus* Linnaeus) (*typ. cons.*)

The genus is comprised of 300 species, occurring in meadows, riparian corridors, and the mountainous regions of Europe, Asia, and North America. Plants herbaceous, perennial, caulescent or acaulescent, with a robust taproot radiating into a simple to many-headed caudex. Stipules adnate to the petiole base, often forming a connate sheath. Leaves alternate, odd-pinnately compound, with 5 to many leaflets (rarely 1-3), the leaflets opposite, alternate or whorled. Racemes pedunculate or scapose, subcapitate to elongate, with 1 to many flowers. Calyx cylindrical to campanulate, five-toothed. Petals 5-merous, pink, purple, white, yellow, with an abruptly pointed keel. Legume sessile to stipitate, erect or reflexed, 1-loculed or partially 2-loculed. Seeds reniform to globose, seedcoats rugulate, lophate, and foveolate, with reticulate ridges. Ploidy levels range from diploid ($2n=16$) to dodecaploid ($2n=96$).

Section *Arctobia* Bunge

The section consists of approximately 18 species, occurring as far west as north-eastern Siberia in Russia and as far east as Labrador in northeastern Canada (Yurtzev 1997). Species richness is highest in Beringia, where species specialize in high alpine environments under xeric conditions. Overall the caudex branch length is reduced to 3-9 cm; leaves 2-7 cm long, opposite, odd-pinnately compound or simple to subpalmately 3-folioate with up to 13 (15) leaflets. Petioles sometimes persistent on the caudex. Flowers 1-3 (4) in North American taxa, up to 5 in *Oxytropis nigrescens* s. str. from Siberia, purple to pink; calyx tube campanulate, rarely cylindrical, lanceolate teeth shorter or subequal to tube. Bracts lanceolate or ovate. Cytological studies have reported chromosome counts of $2n=16$ or $2n=32$.

KEY TO THE NORTH AMERICAN SPECIES OF *OXYTROPIS* SECTION *ARCTOBIA*

1. Raceme with (2-) 3 (-4) flowers, scape strongly erect arising from a decumbent base; free blades of the stipules glabrous or nearly so.
 2. Leaves simple to subpalmately 3-folioate (rarely 5-folioate), leaflets glabrous below; free blades of the stipules often deltoid.

..... 6. *O. mertensiana*
 2. Leaves pinnately compound with more 9 – 13 (19) per leaf, leaflets pilose below; free blades of the stipules often ovate. 8. *O. scammaniana*
1. Raceme typically with 1 – 2 (3) flowers, scapes often spreading, sometimes suberect; free blades of the stipules distally ciliate.

3. Pods ovoid-ellipsoidal (two times longer than wide), inflated to semi-inflated.
 4. Pods ellipsoidal, semi-inflated, nearly glabrous or with short black pilose hairs; leaflets sparingly pilose. 3. *O. huddelsonii*
 4. Pods ovoid, inflated, black villous; leaflets often densely pilose. 7. *O. podocarpa*
3. Pods oblong-cylindrical-elliptical (three times longer than wide), not inflated.
 5. Stipules chestnut red, deltoid to linear with long acuminate apex. 5. *O. kokrinensis*
 5. Stipules pale yellow to green, linear-lanceolate to ovate with broadly acute apex.....6
 6. Pulvinate, caudex branches 2 to 5 cm in length; herbage densely lanate with white hairs (overall appearance white); leaves 1.5 – 2.5 (4) cm in length or less.....7
 7. Leaflets 2 – 3 (5) mm in length; hairs pilose, concentrated on the abaxial side of the leaflets with sparse pubescence on the adaxial side; restricted primarily in western Seward Peninsula of Alaska and Eastern Chukotka, with some populations along the coastal margin of northern Alaska. ..4. *O. gorodkovii*

7. Leaflets 2 – 3.5 (8) mm in length; hairs, villous, uniformly distributed on both sides of the leaflet, restricted in distribution to the Canadian Arctic and British Columbia.1. *O. arctobia*
6. Caespitose or loosely tufted, caudex branches 4 – 7 (8) cm in length; herbage sparingly pilose to lanate with an admixture of white and black hairs (overall appearance green); leaves 2.5 – 6 cm in length.2. *O. bryophila*

1. **Oxytropis arctobia** Bunge, Memoires de l'Academie Imperiale des Sciences de Saint

Petersbourg 22(1): 114. 1871. *Oxytropis nigrescens* var. *arctobia* (Bunge) A.

Gray, Proceedings of the Academy of Arts and Sciences 20: 3. 1884. *Spiesia*

arctobia (Bunge) Kuntze, Revisio Generum Plantarum 1: 206. 1891. *Astragalus*

nigrescens var. *arctobia* (Bunge) Tidestr., Proceedings of the Biological Society

of Washington 50(7): 19. 1937. *Oxytropis nigrescens* subsp. *arctobia* (Bunge)

Hultén, Arkiv for Botanik 7(1): 80. 1968. —TYPE: CANADA. “NE corner

Melville Peninsula, on Parry's Second Voyage”, *Edwards s.n.*” (lectotype, here designated, BM-45352!).

Oxytropis arctica β *uniflora* Hook., Parry's Second Voyage., Append 4: 396. 1825.

Oxytropis nigrescens var. *uniflora* (Hook.) Barneby, Proceedings of the California

Academy of Sciences 27(7): 209. 1952. —TYPE: CANADA. “Barrow River, E coast

Melville Peninsula, on Parry's Second Voyage”, *Edwards s.n.* (lectotype: BM-45452! isolectotype: GH-64419!).

Oxytropis arctobia var. *hyperarctica* Polunin, Bulletin of the National Museum of

Canada 92: 293-294. 1940. —TYPE: CANADA. “Franklin district, Baffin Island,

Arctic Bay, *Polunin 2583* (holotype: CAN-76863!).

Perennial; acaulescent from a branching subterranean caudex, caudex branches compact from 2.2 – 3.5 cm; stipule persistent, pale-green, partially adnate to petiole, connate at base, 3 – 5.5 mm long, blades deltoid, free, 1.5 – 3.5 mm long, ciliated margins with densely white or black pilose hairs; leaves, alternate, 1.5 – 2.5 (4) cm long,

the petioles 4 – 35 (40) mm long, covered in densely white pilose hairs; leaflets 5 – 11 (13), ovate to linear-lanceolate, 2 – 3.5 (8) mm long, 0.5 – 3 mm broad, pilose dorsally and ventrally, along the inrolled margin; scapes spreading, equaling the leaves, 0.6 – 2 (3) cm. villous-appressed; raceme loose, 1 – 2 flowered, bracts oblong to ovate, opaque, 1 – 1.5 mm long, black and white pilose dorsally as well as ventrally; calyx campanulate, 6.5 – 9 mm long, admixture of densely black and white villous hairs, the linear teeth 2 – 3 mm long; petals purple, banner obovate, emarginated, 12 – 15.5 mm long; wings 9 – 11 mm long, claw subequal; keel 9 – 11 mm long, claw subequal; legume sessile, rarely stipitate, the stipe 4 mm long, the body oblong to cylindrical, 22 – 30 mm long and 5 – 10 mm in diameter; seeds brown to reddish brown, reniform to mitiform, 1 – 2 mm long, 1.5 – 2 mm in diameter; seedcoat rugulate to rugulate reticulate. Fig. 2.7. Chromosome number: $2n=16$ (Gillett et al. 1999).

Phenology. *Oxytropis arctobia* flowers in mid-late June or early July.

Distribution (Fig. 2.8). Primarily distributed around the arctic and subarctic shores of Baffin Island and Hudson Bay to the gravel bars and rock outcrops of the Mackenzie Delta. This taxon has also been collected in the Rocky Mountains of Northern British Columbia, with a growth form similar to that of *Oxytropis bryophila*. *Oxytropis arctobia* is commonly found in tundra communities with *Dryas octopetala*, *Salix* sp., *Pedicularis lanata*, and *Saxifraga* sp. The elevation ranges from 25-240 m.

Notes. The taxonomy of *O. arctobia* has remained controversial due to the fact that the type specimen as designated by Bunge in 1871 has not been available for study by recent monographers. The most authoritative synoptic treatment of North American

Oxytropis (Welsh, 2001) quotes Bunge's citation as "v. s. sp. in herb. olim Fischeriano nunc h. bot. Petrop." = "I have seen a dried specimen in the herbarium, formerly Fischer's, now in the botanical garden of St. Petersburg." Bunge cites this specimen after the name *O. arctobia* as "*O. arctum* R. Br. beta ex herb. Fischer". Thus, the holotype for this name is a specimen that should be sought at LE. We have unsuccessfully tried to locate this specimen at LE with help from staff at the LE herbarium. Additional confusion regarding the identity of *Oxytropis arctobia* appears to come from the fact that *O. arctobia* Bunge has been cited as a synonym of *O. arctica* var. *uniflora* Hooker = *O. nigrescens* var. *uniflora* (Hook.) Barneby and the lack of locality or collector information for the *O. arctobia* type other than it was collected in arctic North America ("Habitat in arcticis Americanae borealis") and came from the Fischer herbarium ("ex herb. Fischer"). Hooker (1825) based his variety *uniflora* on specimens he saw at the British Museum (BM). Robert Brown's herbarium formed part of the nucleus of the BM holdings. Welsh designated one sheet as the lectotype for Hooker's variety in his 1995 paper and cites the locality for the lectotype as "Barrow River, E coast Melville Peninsula. Lat. 67°21', on Parry's second Voyage, *Edwards s.n.*, 1821-1823". In the introduction to "Chloris Melvilliana" Robert Brown (1820) thanks several people, including Parry and Fischer, for sending him specimens from Melville Island collected from the Parry voyage. Apparently Hooker studied the Parry collections at BM in Brown's care and was given a fragment for his herbarium (now part of Kew [K]). As Welsh (1995) mentions, "there are several sheets of this variety at BM taken on various Parry voyages (e.g., BM 45452, "*Oxytropis arctica*, Barrow River, 1822"). The isolectotype at K is similarly a mere fragment".

In order to resolve which exact specimen Bunge saw, it remains to be shown that the specimens Brown received from Parry and that the specimen Fischer had (which Bunge saw) were part of the same gathering; they may have been taken from different localities and/or on different days. It is also possible (likely!) that Brown sent Fischer a specimen from the gathering that Parry supplied to him, but even then the individuals may not have been taken from the same population. In order to decide on this we would need to make a careful comparison of all the original material. We cannot make such a careful comparison, since we cannot locate specimens at LE that might be what Bunge saw when describing *O. arctobia*. We consider the names *O. arctobia* Bunge and *O. arctica* var. *uniflora* Hooker are based on specimens from separate gatherings during the Parry voyage. Since we cannot locate the specimen cited by Bunge at LE, we are selecting a lectotype from among the other Parry material that Brown saw, since he sent the specimen to Fischer.

Oxytropis arctobia Bunge is easily distinguished from the *O. nigrescens* complex by its densely white pubescence and stout, broad calyx teeth. Two morphotypes of *O. arctobia* have been described, one as *O. arctobia* subsp. *subarctobia* Jurtz. occurs in the Canadian Arctic Archipelago demonstrating a strictly pulvinate habit, while the typical *O. arctobia* subsp. *arctobia* is more loosely matted and occupies a small disjunct population in British Columbia. Here we include these two subspecies as synonyms under *O. arctobia*.

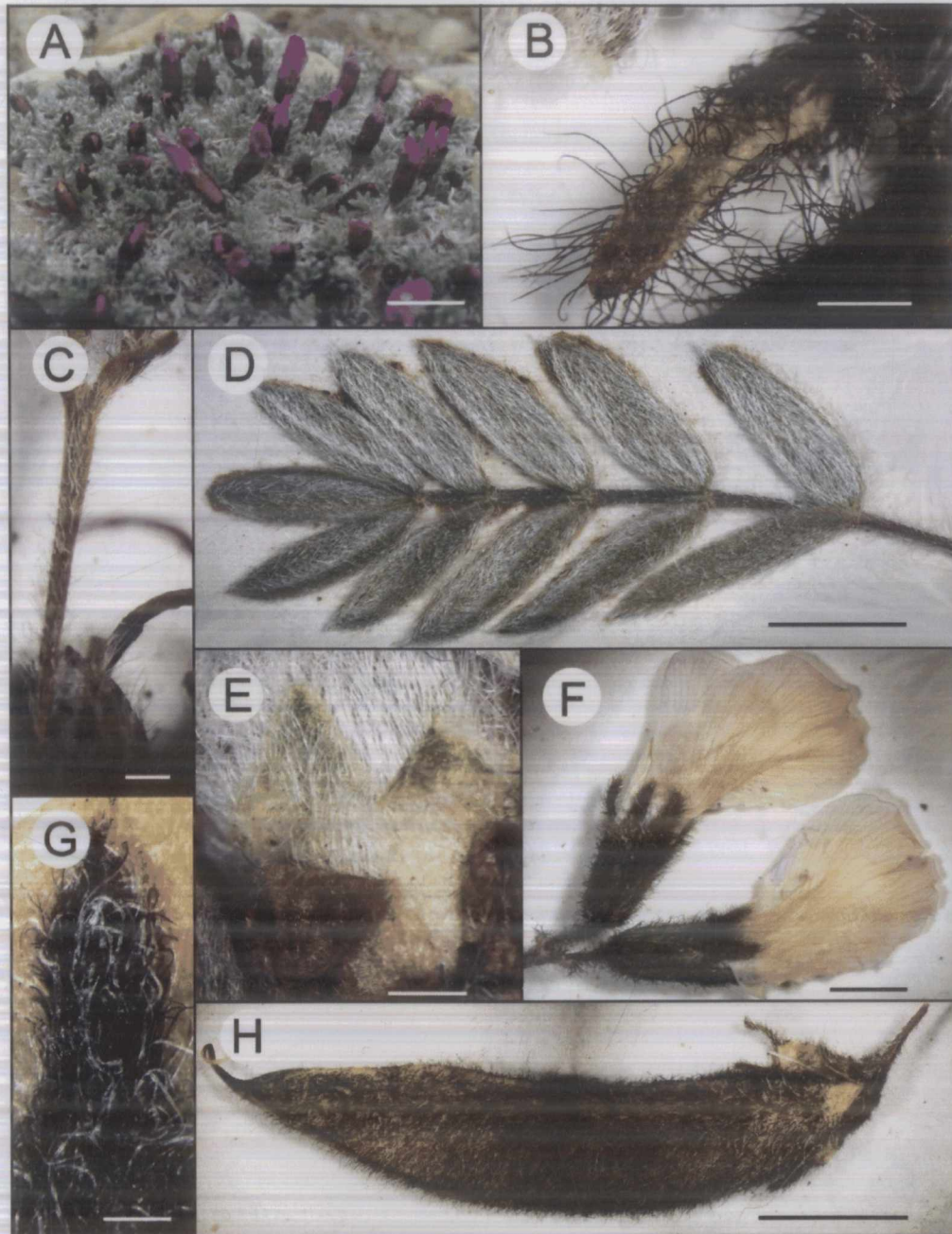


Figure 2.7. Morphological characteristics of *Oxytropis arctobia*. A. Extreme pulvinate habit (photo from Aiken et al. 2007). B. Lanceolate to linear-lanceolate flower bract (Aiken 99-011 CAN). C. Spreading scape with white pilose hairs (Gould CB-2 ALA). D. Odd-pinnately compound leaf with 5 leaflet pairs, leaflets lanceolate to oblong (Elven 2593/99 O). E. Membranous ovate to deltoid stipule covered with white pilose hairs (Cody 25685 CAN). F. Raceme 2 flowered covered with black villous hairs (Eriksen et al. 927 GB). G. Oblong to narrowly ovate calyx tooth covered in black villous hairs (Eriksen et al. 927 GB). H. Cylindrical legume covered with black villous hairs (Raup & Correll 10463 ALA). Scale bars A 1 cm; B, C, E, G 1 mm; D, F H 3 mm.

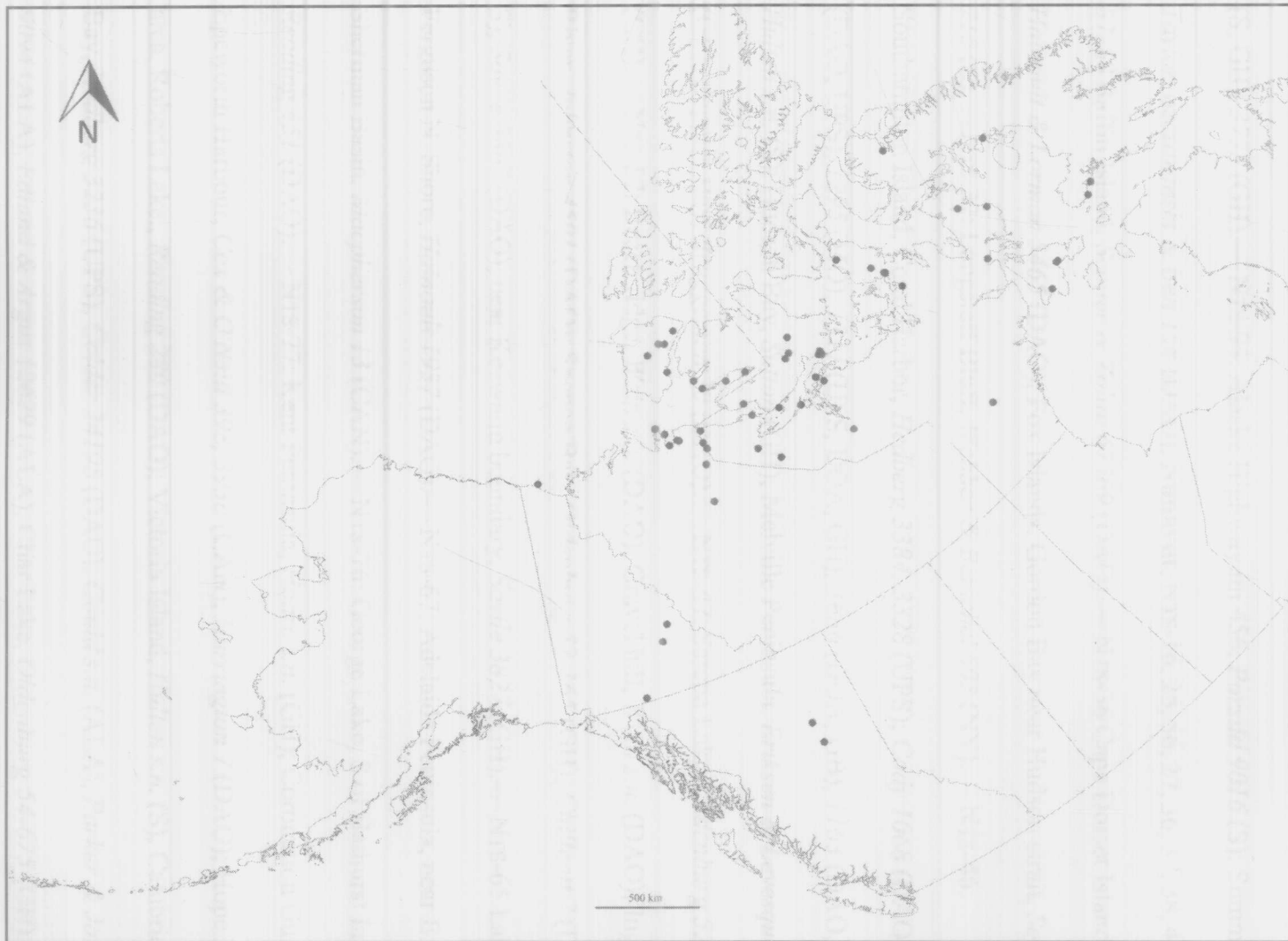


Figure. 2.8. Distribution map of *Oxytropis arctobia* in the Canadian Archipelago, the Yukon Territory and British Columbia.

ADDITIONAL SPECIMENS EXAMINED.

Canada, Alberta, NTS-84: Peace River Basin, Robb Lake, *Argus & Haber 10419* (ALA). **British Columbia**, NTS-82: Mt. Selwyn, *Raup & Abbe 3770 (S), 3907 (S), 3779 (S, GH), 3773 (GH)*.— NTS-94: Alaska Highway mi 456, *Porsild 9016 (S)*; Summit Pass, *Taylor, Szczawinski & Bell 158 (DAO)*. **Nunavut**, NTS-16, 25, 56, 27, 36, 37, 38, 47, 48, 57, 58 Baffin Island, *Scotter & Zoltai 67269 (DAO)*.— NTS-36 Cape Dorset Island, *Hainault & Lorman 5465 (DAO)*; Fox Islands, Gordon Bay near Hudson strait, *Soper 716 (S)*.— NTS-37: Longstaff Bluff, *Webber & Berschel 603 (NY)*.— NTS-46: Southampton Island, Coral Harbor, *Hedberg 3384, 3328 (UPS)*; *Cody 1068 (DAO), 1094 (DAO, UPS), 1295 (MO), 1311 (UPS, DOA, GH), 1886 (DOA, GB), 1163 (DAO, S), Hulten s.n. (S)*; Hudson Bay, *Sutton (GH)*; Melville Peninsula, *Eriksen & Levesque 772b (GB)*, Repulse Bay, *Bruggeman 70 (DAO)*.— NTS-47: Sarcpa Lake, *Oldenburg 52-287 (GH)*.— NTS-57: Beach ridge, *Wein s.n. (DAO)*; Gravel hill, *Wein s.n. (DAO)*; Inglis River, *Johnston 4501 (DAO)*; Spence Bay, *Oldenburg 52-165 (GH)*, *Chillcott 7 (DAO, S)*, *Savile 3867 (DAO)*; near Keewatin boundary, *Savile 3827 (GH)*.— NTS-65 Lake Ferguson N. Shore, *Hainault 1937 (DAO)*.— NTS-67: Adelaide Peninsula, near E. side of Sherman Basin, *Macpherson 13 (CAN)*.— NTS-76: George Lake, S of Bathurst Inlet, *Reading 451 (DAO)*.— NTS-77: Kent Peninsula, *Hoare s.n. (GH)*; Coronation Gulf, Epeworth Harbour, *Cox & O'Neill 398, 393a (CAN)*, *Harrington 7 (DAO)*; Hope Bay area, Roberts Lake., *Reading 280 (DAO)*; Victoria Island, *Hulten s.n. (S)*, Cambridge Bay, *Hedberg 3236 (UPS)*, *Calder 24198 (DAO)*, *Gould s.n. (ALA)*, *Parker & Jonsdottir 9094 (ALA)*, *Edlund & Argus 12629 (ALA)*, Char Lake, *Oldenburg 54-675 (GH)*.—

NTS-86: Coppermine River Area, *Reading 254, 533* (DAO).— NTS-87: Bluenose Lake Area, Site 16, *Scotter 90-454* (DAO); Site 3, *Scotter 90-198* (DAO); Site 6, *Scotter 90-248* (DAO); Site 41, *Scotter & Zoltai 90-772* (DAO); Victoria Island, Falaise Bay, *Parker 9108* (ALA), *Eriksen, Levesque, & Parker 927* (ALA); Bernard Harbour, *Johansen 294* (S). **North West Territory**, NTS-88,97,98: Banks Island, *Porsild & Breitung 17724* (S), *Scotter & Zoltai 31354* (DAO), *Stretton 127* (DAO); NE part Parker River Valley, *Elven RE2025/99* (O); “Porsito” Lake, *Oldenburg 54-321* (GH).— NTS-87: Victoria Island, Holman Island Hudson Bay Post, *Gray & Gibbard 20* (DAO), mouth of Minto River, *Oldenburg 54-224* (GH); Yellow Lake, *Oldenburg 54-246* (GH); Prince Albert Sound, *Weerstra 18* (DAO), *Shindman s.n.* (DAO).— NTS-88: Site B-13, *Scotter & Zoltai 31228* (DAO).— NTS-96: Great Bear Lake: Olmsted Bay, *Porsild & Porsild 5064* (S).— NTS-97: Just S of site, *Parmelee 2952* (DAO); Paulatuk, *Burn s.n.* (DAO); *Gillespie s.n.* (ALA); Site 1, Dewline Station, *Scotter & Zoltai 25485* (DAO); Tuklut Nogait National Park, *Gillespie s.n.* (ALA). **Yukon Territory**, NTS-105: Canol Rd., East side of Ross R. valley, *Porsild & Breitung 10181* (O); mi. 132, Lower Lapie R. Crossing, *Porsild & Breitung 9938, 9624* (S); Mt. Sheldon, *Porsild & Breitung 11086* (S); Tagish Lake, S of Nares Mtn., *Cody 25685* (ALA).— NTS-117: Herschel Island., *Oldenburg 44-420* (GH).

2. *Oxytropis bryophila* (Greene) Jurtz., Bot. J., URSS 53: 1539. 1968. *Aragallus*

- bryophilus* Greene, Proceedings of the Biological Society of Washington 18 (3): 17. 1905. *Oxytropis nigrescens* Pall. subsp. *bryophila* (Greene) Hultén, Flora of Alaska and Yukon 7: 1103. 1947. *Oxytropis nigrescens* Pall. var. *bryophila* (Greene) LePage, American Midland Naturalist 46(3): 758. 1951.— TYPE: U.S.A. ALASKA: St. Matthew's Island, Bering Sea, *Macoun 18,510* (holotype: NDG!).
- Astragalus nigrescens* Pall., Species Astragalorum 65. 1800.— TYPE: RUSSIA. "Hunc Astragalum inter Aldanum fl. et orientalem Oceanum", *D.D. Merk s.n.* (LE?). *Oxytropis nigrescens* Pall. f. *albida* Lepage, American Midland Naturalist 46(3): 758. 1952.— TYPE: U.S.A. ALASKA: Kodiak, Summit of Old Woman Mountain, *E. Lepage 25089* (CAN- 213260!).
- Oxytropis arctica* var. *subumbellata* Hook. in W.E. Parry, Sec. Voy. 4:396. 1825.— TYPE: CANADA. "Arctic shores and Islands of North America. "Dr. Richardson. 1/146. *Oxytropis arctica* Br. var. *subumbellata*. Coast", Dr. Richardson (lectotype: BM 45473!).
- Oxytropis nigrescens* Pall. var. *lonchopoda* Barneby, Leaflets of Western Botany 10(2): 23. 1963. *Oxytropis nigrescens* Pall. ssp. *lonchopoda* (Barneby) W.J. Cody, Canadian Field Naturalist 108: 94. 1994.— TYPE: CANADA. Yukon, Cathedral Rocks, Ogilvie Mountains, *J.A. Calder & J.M. Gillett 26013A* (holotype: DAO-9395!).
- Oxytropis czukotica* Jurtz., Byull. Moskovsk. Obshch. Isp. Prir., Otd. Biol. 85(6): 102. 1980.— TYPE: RUSSIA. West of Chukotka and the shore of the east bays of

Tschaunensi, near the village of Pevek, the mountain of Pekenei, *Jurtzev, Petrovsky, & Zhukova s.n.* (holotype: LE-3767, digital image!).

O. tschuktschorum auct., non Jurtz., Bot. Zhurn. (Moscow & Leningrad) 53: 1538. 1968.

Oxytropis glaberrima Hultén, Botanisk Tidsskrift 51: 124-125. 1954. — TYPE:

U.S.A. ALASKA. Kurupa Valley, 7 mi N of Kurupa Lake, *Hodgdon 8060* (holotype: S!).

Perennial; acaulescent from a subterranean caudex, caudex branches elongating from 4 – 7 (8) cm; stipules persistent, pale-green to yellow, partially adnate to petiole, connate at base, 5 – 12 (15) mm long, blades ovate to lanceolate, free, 1-nerved, 2 – 5 mm long, ciliated margins with pilose black and white hairs; leaves, alternate, 2.5 – 6 cm long, the petioles 7 – 30 mm long, slender sparsely to densely pilose; leaflets 5-15, linear-lanceolate to ovate, 2 – 9 mm long, 0.5 – 2 mm broad, ciliate along the inrolled margin; scape spreading, equaling or slightly surpassing the leaves, 0.5 – 4 cm, pilose; raceme loose, 1 – 2 (-3)-flowered; bracts linear to lanceolate, opaque, 1.5 – 3 mm long, black-pilose dorsally and ventrally; calyx campanulate, 6.5 – 10 mm long, densely black villous, teeth deltoid to lanceolate, 1 – 4 mm long; petals purple, banner obovate, emarginated, 12 – 18 (20) mm long; wings 10 – 16 mm long, claw subequal; keel 10 – 13 mm long, claw subequal; legume body cylindrical, 20 – 34 mm long, 5 – 9 mm in diameter; seeds brown, reniform to mitiform, 2 mm long, 2 mm in diameter; seedcoat rugulate to rugulate reticulate. Fig. 2.9. Chromosome number: $2n=16, 32$ (Murray and Kelso 1997).

Phenology. *Oxytropis bryophila* flowers in late June.

Distribution (Fig. 2.10). Amphiberingian, the most eastward distribution of *Oxytropis bryophila* occurs in the British Mountains of British Columbia, Canada. *Oxytropis bryophila* is broadly distributed throughout Alaska including the St. Elias Mountains, the Brooks Range, the Alaska Range, the Kodiak Archipelago, and the Seward Peninsula. The westernmost extent has been documented near the Lena River (Yakutsk Province). *Oxytropis bryophila* is found in arctic, acidic scree slopes. Common associates in alpine communities include *Dryas octopetala*, *Carex* ssp., *Douglasia arctica* and *Arnica alpina*; from sea level to 3500 m.

Notes. *Oxytropis bryophila* (Greene) Jurtz. constitutes the most phenotypically variable taxon within *Oxytropis* section *Arctobia* and thus the most problematic in terms of delineation. *Oxytropis bryophila* varies greatly in habit, density of pubescence, and size/shape of the stipules. Much of the morphological variation can be attributed to microclimate throughout the vast area this taxon occupies.

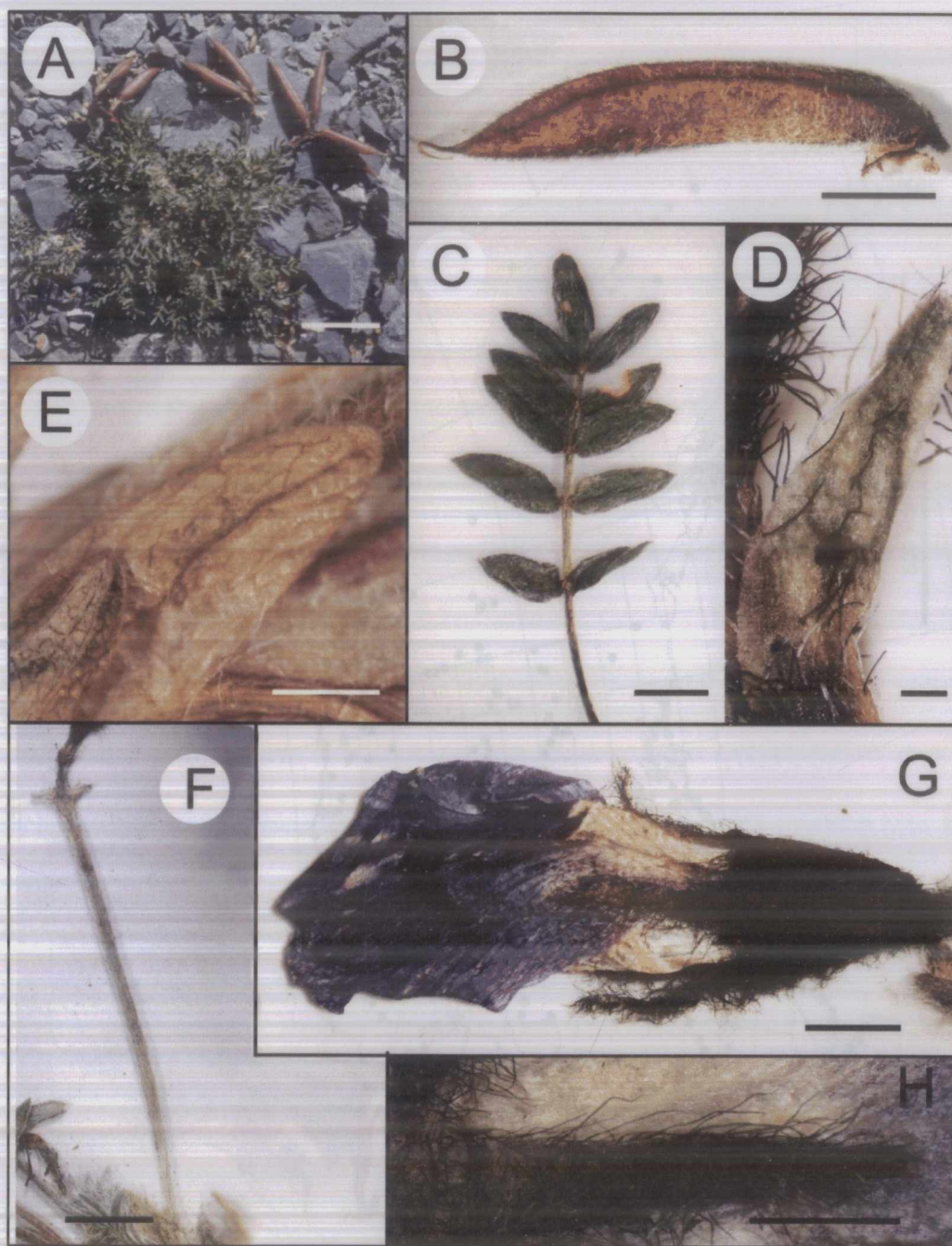


Figure 2.9. Morphological characteristics of *Oxytropis bryophila*. A. Spreading habit with cylindrical (photo provided by C. Parker). B. Cylindrical legume covered with an admixture of black and white villous hairs (Cody & Ginns 30426. NYBG). C. Odd-pinnately compound leaf with 5 leaflet pairs, leaflets lanceolate to oblong (Murray 6628 ALA). D. Lanceolate to linear-lanceolate flower bract (Batten 71 NYBG). E. Ovate to deltoid stipule covered with white pilose hairs (Hulten s.n. ALA). F. Spreading scape, with white pilose hairs (Rausch s.n. ALA). G. Flower covered with black villous hairs (Welsh 4252 NYBG). H. Linear to linear lanceolate calyx tooth covered in black villous hairs (Martensson P254 O). Scale bars A 5 cm; B, C, F, G 1 mm; D, E, H 0.5 mm.

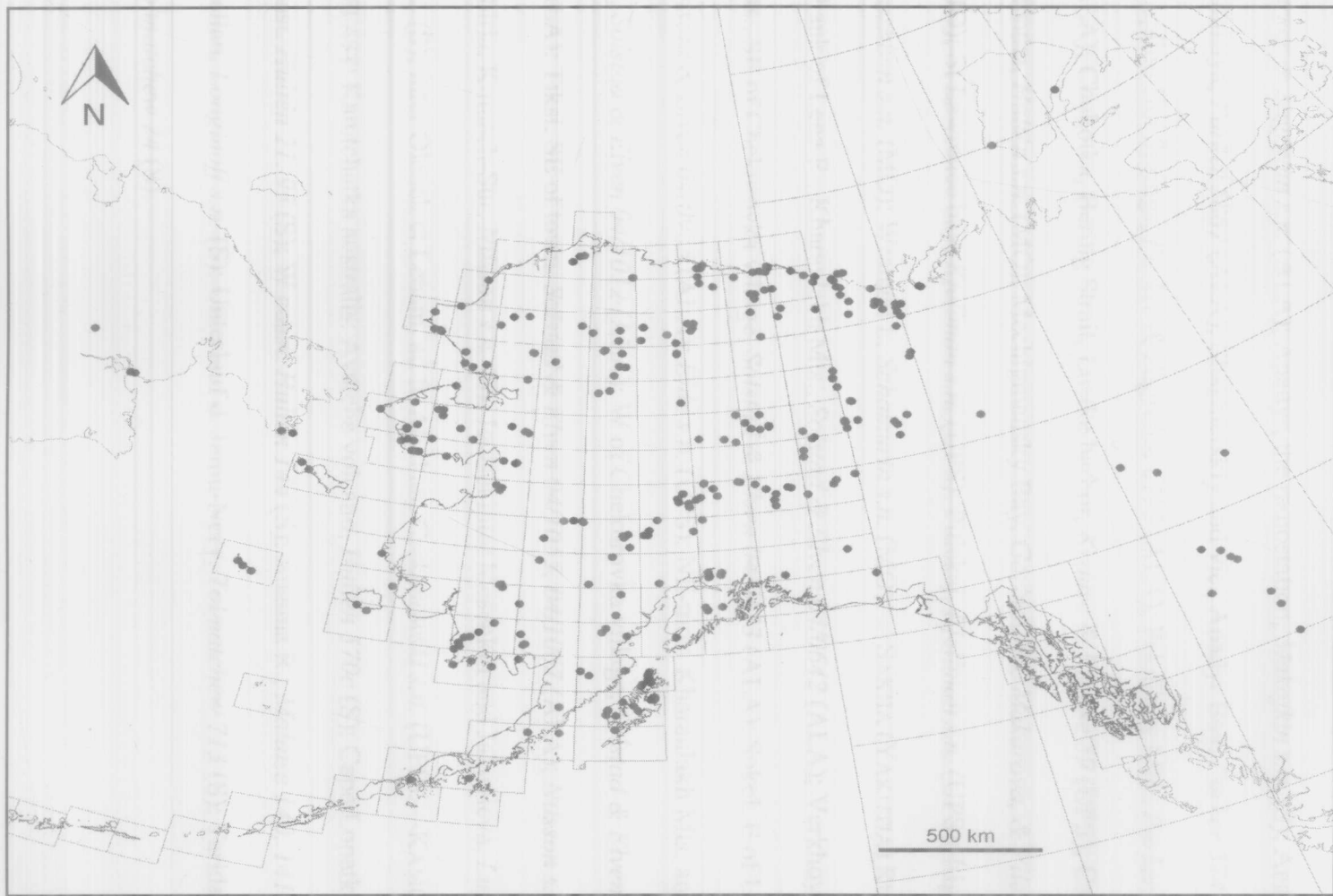


Figure. 2.10. Distribution map of *Oxytropis bryophila* in Alaska and neighboring Russian and Canadian territories

ADDITIONAL SPECIMENS EXAMINED.

Russia. CHUKOTKA AUTONOMOUS REGION: Chukotka Peninsula, Provideniya Bay, *Parker & Zagrebin s.n.* (ALA); Anadyr, the radiostation, *Makofkin s.n.* (S); Anadyr, Mt. Dionisiya, *Parker 5867* (ALA); Shakhterskiy and vic., Anadyr Bay, *Parker 5743* (ALA); Chaplino Hot Springs, *Parker & Zagrebin 6193* (ALA); Pekul'ney Mts., *Parker 5807* (ALA); Chukotka, Bering Strait, Luetke harbor, *Krause & Krause 59* (UPS); Cape Lopatka, *Hultén s.n.* (MO); Mechigmsky Bay, *Gorbunova, Makarova, & Plieva s.n.* (MO); St Lawrence bay, *Kjellman s.n.* (UPS); Pitlekaj, *Kjellman s.n.* (UPS); Itigran I., *Razhivin s.n.* (MO); Wrangel I., *Schamurin s.n.* (MO).— SAKHA (YAKUTIA) REPUBLIC: E bank of Lena R., Kharaulakh Mts., *Solstad & Elven 04/0642* (ALA); Verkhoyansk Mts., SE of Chekurovka village, *Solstad & Elven 04/0623* (ALA); Sokol, E of Lena R., *Solstad & Elven 04/0983* (ALA); *Ehle s.n.* (UPS); NE-most Kharaulakh Mts. and Lena R., *Solstad & Elven 04/1012* (ALA); W of Chekurovka village, *Solstad & Elven 04/0555* (ALA); Tiksi, SE of town, *Solstad & Elven 04/1055, 04/1067* (ALA); *Nilsson s.n.* (S); Sibiria, Kumach-Sur, *Nilsson s.n.* (S); Jenisei inter Mesenkin and Jakovieva, *Lundström s.n.* (S); inter Olenek et Lenam, ad fl. Atyrkan, *Czekanowski s.n.* (UPS).—KAMCHATKA OBLAST: Kamtchatka australis: Avatcha volcano, *Hultén 570c* (S); Cape Lopatka, E. coast, *Hultén 21, 93* (S); W coast, *Hultén 144* (S); Anauna R., *Malaise 140, 141* (S); Prallan, *Longinoff s.n.* (S); Unterlauf d. Jamu-Nery, *Tolmatchew 713* (S); Tarida, *Tolmatchew 24* (S).

U.S.A. Alaska. AFOGNAK QUAD.: Afognak I., Danger Cr. Valley, *Parker 2841* (ALA); Cloud Peak-Upper Malina Lake area, *Parker 3406* (ALA); S of Paramanof Bay, *Parker 3981* (ALA); Swikshak Lagoon, *Jansen & Carlson 02-127* (ALA); Blue Fox Bay, W entrance to bay, *Parker & Stuebaker 17473* (ALA); Devil Paw Mt., *Parker & Stuebaker 17406* (ALA); Hidden Lake, *Parker, Stuebaker & Pyle 17669* (ALA); Red Lake, SE end of ridge, *Parker & Stuebaker 17740* (ALA); Shuyak I., Big Bay vic., cape N of Eagle Cape, *Parker 3644* (ALA).— AMBLER RIVER QUAD.: Baird Mts., upper Akillik R. valley, *Parker, Batten & McIntyre 11466* (ALA).— ANCHORAGE QUAD.: Chugach Mts., W of Nike site, *Duffy & Tande 70, 197* (ALA); Ft. Richardson, site summit, *Lichvar & Marler 7994* (ALA); Knik R. drainage, upper Hunter Cr., *Barker 02-714* (ALA); Eklutna Gl., *Marvin 610, 1431* (ALA); Mt. Gordon, Lyon N of Arctic Valley, *Elven, Gabrielsen & Tove s.n.* (O).— ARCTIC QUAD.: Brooks Range, Old John Lake, *Smith 2539* (ALA); S Fork of the Canning R., *Wetzel 17* (ALA), *Hettinger 19. 32* (CAN).— BAIRD MTS. QUAD.: Baird Mts., Salmon R. headwaters, N of Mt. Angayukaqraq, *Parker, Batten & McIntyre 11379* (ALA), *Parker & Fowell 11296* (ALA).— BARTER ISLAND QUAD.: Arctic Coastal Plain, Arey I., *Mason 149* (ALA), *Polunin s.n.* (UPS); Okpilak R. delta, *Mouton 82912* (ALA).— BEECHEY POINT QUAD.: Arctic Coastal Plain, Prudhoe Bay, *Khokhryakov, Yurtsev & Murray 6757, Murray 4513, 4541* (ALA); Little Putuligayuk R., *Walker 84-42* (ALA); S of Prudhoe Bay, Percy Pingo, *Elven & Grundt s.n.* (ALA).— BELL RIVER QUAD.: Richardson Mts., Mt. Russell, *Cody & Ginns 29860* (ALA).— BENDELEBEN QUAD.: Seward Peninsula, Serpentine Hot

Springs, *Murray, Yurtsev & Kelso 10904 (ALA), Kelso 87-126 (ALA)*; Darby Mts., NE of Omilak Mt., *Murray & Lipkin 12274 (ALA)*; Eldorado Cr., *Murray, Yurtsev, & Kelso 10658 (ALA)*; Kuzitrin Lake, *Murray, Yurtsev & Kelso 11165 (ALA)*.— BERING GLACIER QUAD.: St. Elias Mts., Baldwin Glacier, *Cook & Eklund 4795 (ALA)*.— BETHEL QUAD.: Kilbuck Mts., Slate Cr., *Batten 06-95. (ALA)*.— BETTLES QUAD.: Finger Mt., Dalton Hwy., mi 100, *Khokhryakov, Yurtsev & Murray 6452 (ALA)*.— BLACK RIVER QUAD.: Keele Range, N of Salmon Fork of Black R., *Lipkin 91-113, 91-13 (ALA), Lipkin, & Herriges 16974 (ALA)*; 1 km W of Alaska-Yukon border Parker, *Lipkin, & Herriges 17116 (ALA)*.— CANDLE QUAD.: Seward Peninsula Highlands, Buckland R., *Lipkin 80-108, 80-193 (ALA)*; upper Tagagawik R. basin, *Lipkin 80-197 (ALA)*.— CAPE MENDENHALL QUAD.: Nunivak I., Chakwakamiut, *Utermohle 202 (ALA)*.— CHANDLER LAKE QUAD.: Arctic Foothills, Castle Mt., *Parker, Elven, Bennett & Guldager 12867, 12809 (ALA, O)*; Brooks Range, Shainin Lake, mouth of Alapah Cr., *Parker, Elven, Solstad & Bennett 13224 (ALA)*; Ulo Lake, head of N Fork Koyukuk R., *Chauvin 63 (ALA)*; Endicott Mts., Chandler Lake, *Parker, Elven & Solstad 12165 (ALA)*.— CHARLEY RIVER QUAD.: Ogilvie Mts., Mt. Casca, *Cook & Bennett 02-115, 02-106 (ALA)*; Monument 99, *Cook & Bennett 02-127 (ALA)*; NE flank of Jones Ridge, *Larsen & Batten 02-1299 (ALA)*; Yukon-Tanana Uplands, Mt. Sorenson, *Larsen & Person 02-1627 (ALA)*; Mt. Kathryn, *Larsen, Bennett & Flamme 02-1785 (ALA)*.— CHIGNIK QUAD.: Alaska Peninsula, Aleutian Range, Aniakchak Crater, *Lipkin, Duffy, Bosworth & Miller 04-222, 04-13 (ALA)*.— CIRCLE QUAD.: Yukon-Tanana Highland, Twelvemile

Summit, *Harms 2741-B, Gasser s.n., Scamman 3570* (ALA); West Crazy Mts., 1 km W of VABM Wolf, *Batten & Herriges 95-239* (ALA); Eagle Cr. vic. Berry Camp, *Bendock s.n.* (ALA); Mt. Prindle, SW of summit, *Murray 8524* (ALA); Lime Peak (Rocky Mt.) vic., *Parker & Batten 4766* (ALA).— COLD BAY QUAD.: Alaska Peninsula, Frosty Peak, *Talbot & Talbot s.n.* (ALA).— DE LONG MTS. QUAD.: Arctic Slope, Cape Sabine, Pitmegea R., *Cantlon & Gillis 57-143* (ALA).— DEMARCATION POINT QUAD.: Arctic Coastal Plain, Beaufort Lagoon, Nuvagapak Point, *Murray 3183, 3167* (ALA); Pingokraluk Lagoon, *Murray 3235* (ALA); Brooks Range, Jago Lake, *Cantlon & Gillis 57-1274, 57-748* (ALA).— DILLINGHAM QUAD.: Kilbuck-Kuskokwim Mts., Marsh Mt., *Roberson 199* (ALA); Jack-Knife Mt. *Caswell 350* (ALA); Lake Nerka, Mt. "2810" N of Amokuk Arm, *Caswell s.n.* (ALA).— EAGLE QUAD.: Yukon-Tanana Uplands, E and Middle Forks of Charley R., *Cook & Roland 02-327* (ALA); SW of Mt. Sorenson, *Larsen, Roland & Batten 02-1444* (ALA).— EAGLE RIVER QUAD.: Richardson Mts., W side of westernmost range, *Cody & Ginns 31022* (ALA); Rock River, *Russell s.n.* (ALA).— FLAXMAN ISLAND QUAD.: Arctic Coastal Plain, W of Sadlerochit R., *Sowl s.n.* (ALA).— GOODNEWS BAY QUAD.: Ahklun Mts., Limestone Ridge, Goodnews Bay village, *Parker 15802, 15529* (ALA); Kisogle Mtn., *Lipkin et al. 31, 82* (ALA); Nimgun Lake *Caswell 94-161* (ALA); Tatlignagpeke Mt., *Lipkin, Michaelson, & Blank 208* (ALA); Kilbuck-Kuskokwim Mts., Kagati Lake *Martin s.n.* (ALA); Platinum Spit, *Williams 3592* (ALA).— GOODPASTER RIVER.: headwaters of Goodpaster River, *Eck 8314* (ALA).— HAGEMEISTER ISLAND QUAD.: Bristol Bay Lowlands, Cape Peirce,

Schandelmeier 28 (ALA); Hagemeister I., *Talbot & Talbot s.n.* (ALA).— HARRISON BAY QUAD.: Arctic Coastal Plain, Inigok Well *Lipkin & Dawe s.n.* (ALA).— HEALY QUAD.: Alaska Range, Carlo Mtn., *Carwile 79-60* (ALA); Dry Cr., 50 miles E of Healy, *Viereck & Jones 5624* (ALA); Mile 39 Denali Park Rd., Sable Pass, *Smith 2261* (ALA); mi 46 Denali Park Rd., Polychrome Pass, *Nelson & Nelson 3811* (ALA, MO); Plateau between Teklanika R. canyon and Comb Peak, 8 km N of Stampede Trail, *Roland 3192* (ALA).— HEALY QUAD.: Alaska Range, Upper Sheep Cr., *Heimer s.n.* (ALA); vic. Bison Gulch, off Mile 243.6 Parks Hwy., *Kelso 84-79, Elven & Grundt s.n.* (ALA); W of VABM Comb, 1.7 km E of Teklanika R., *Larsen & Cook 01-6* (ALA).— HOOPER BAY QUAD.: Yukon-Kuskokwim Delta, Hooper Bay area, *Rausch s.n.* (ALA).— HOWARD PASS QUAD.: Lisburne Ridge, *Parker 7609* (ALA); Noatak National Preserve; W Feniak, *Duffy s.n.* (ALA), *Holmen & Mårtensson 61-1442* (UPS); Liberator Lake, *Holmen & Mårtensson 61-1607, 61-1689, 61-1743* (UPS).— HUGHES QUAD.: Norutak Hills, ridges S of Lower Kobuk Canyon, *Parker, Elven, & Solstad 13910* (ALA, O); Lockwood Hills, *Parker, Elven, & Guldager 13785* (ALA, O).— IDITAROD QUAD.: Kilbuck-Kuskokwim Mts., Beaver Mts., Tolstoi Lake, *DeLapp 732* (ALA); Chicken Mt., *Parker 1419* (ALA); Ganes Cr., *Drury, Jr. 3456* (ALA).— ILIAMNA QUAD.: Alaska Peninsula, Newhalen, *Avery N-9-52* (ALA); Roadhouse Mtn., 7 km N of Whistlewing Bay, *Parker 14100* (ALA); Aleutian Range, Chigmit Mts., S of Cottonwood Bay, *Batten & McWhorter 02-102* (ALA).— KARLUK QUAD.: Kodiak Archipelago, Kodiak I., Anvil Lake, *Parker & Studebaker 16462* (ALA); Olga Bay, *Loof & Loof 1351* (MO); Grant Lagoon, ridge 3 km

E of lagoon, *Parker & Stuebaker 16137, 16351* (ALA).— KILLIK RIVER QUAD.: Arctic Foothills, Mesa Archaeological Site, *Watson 49* (ALA); Brooks Range, Imiaknikpak Lake, Killik R., *Murray 4436, 4189* (ALA).— KODIAK QUAD.: Kodiak I., *Trelease & Saunders 4343, 4344, 4345* (MO), *Looff 16* (MO); Mt. Glottof, *Parker & Stuebaker 16887* (ALA); Pillar Mtn., *Rigby 10, Parker 3343* (ALA); Spiridon Pen., Chief Cove, *Talbot 71-13* (ALA); Uganik, Little Lake Cirque, *Gustafson 73-40* (ALA); Pyramid Mt. vic., *Parker 3952* (ALA); Three Sisters Mt., above Monashka Bay, *Stuebaker 40772* (ALA); Summit of Old Woman Mt., *Lepage 25089* (CAN), *25053* (MO).— KOTZEBUE QUAD.: Seward Peninsula, Cape Espenberg, *Parker, Elve, & Solstad 14392* (ALA).— LAKE CLARK QUAD.: Chigmit Mts., Tanalian Mt., *Miller, Meyers, Shulstad & Walton 2010-070* (ALA); Neacola Mts., tablelands N of Turquoise Lake Miller, *Meyers, Shulstad & Walton 2010-007* (ALA).— LIME HILLS QUAD.: Alaska Range, Head of Big R., *Drury, Jr. 4114* (ALA); Sparrevohn LRRS Air Force Station, *Parker, Batten, Meyers & Reynolds 8526* (ALA).— LIVENGOOD QUAD.: Mt. Schwatka, *Parker, Murray, Lipkin & Emers 4949, 4962* (ALA); Yukon-Tanana Uplands, Steese Hwy., mi 26, *Castle s.n.* (ALA); mi 30 Elliott Hwy., Wickersham Dome, *Harms 2938* (ALA); mi 110 Elliott Hwy., *Halliday A89-75* (ALA).— MCCARTHY QUAD.: Upper Skolai Valley, *Scott 1633* (ALA); Farewell Mt., *Drury, Jr. 2678, 2916* (ALA); Kuskokwim Valley, SE of Farewell, *Drury, Jr. 2829* (ALA); N of Post Lake, *Parker 678* (ALA); Tatalina Air Force Installation, *Smith 1730* (ALA).— MISHEGUK MT. QUAD.: Noatak National Preserve, Siniktanneyak Mt., *Miller s.n.* (ALA), Sisiak Cr., *Duffy s.n.* (ALA); De Long Mts.,

Noluck Lake, *Parker 150* (ALA, S); Inaccessible Ridge, Kagvik Cr. headwaters, *Parker & Beattie 11880* (ALA); Upper Utukok-Iligluruk R., *Boudreau & Reynolds s.n.* (ALA).— MT. HAYES QUAD.: Alaska Range, E of Miller Mine, *Parker 1355* (ALA); Molybdenum Ridge, *Duffy 98-323* (ALA); Rainbow Mt., Richardson Hwy., mi 212, *Harms 3568-B* (ALA); Sager's camp N of Mt. McGinnis, *Murray 3100* (ALA); Fielding Lake, *Smith 2613* (ALA); Horn Mt., *Spetzman 179* (ALA); Independent Ridge, *Spetzman 64* (ALA); Richardson Hwy., mi 213, *Chauvin 5* (ALA); Donnely Dome, Richardson Hwy., *Argus 1071* (UPS).— MT. KATMAI QUAD.: Aleutian Range, Dumpling Mt., *Hoffman 85-1, O'Donnell s.n.* (ALA); Kukak Bay, *Trelease & Saunders s.n.* (MO); Mt. Katolinat, *O'Donnell s.n.* (ALA).— MT. MCKINLEY QUAD.: Alaska Range, Muldrow Gl., *Viereck 1396* (ALA); Little Annie Mine, above Kantishna, *Foote 3678* (ALA); Kantishna Hills, N Fork Canyon Cr., *Larsen & Brodie 01-1017* (ALA); Mt. Eielson, NW slope to summit, *Viereck 1162* (ALA); Wonder Lake, *Nelson & Nelson 3932* (ALA).— MT. MICHELSON QUAD.: Arctic Coastal Plain, Hulahula R., *Lipkin 85-65* (ALA); Simpson Cove, *Meyers & Hayden 81-36* (ALA); Brooks Range, Kikiktat Mt., *Garner s.n.* (ALA); Carnivore Cr. drainage, *Batten 71* (ALA); Lake Peters drainage, *Batten 163* (ALA, MO); Sadlerochit R. drainage, W of Lake Schrader, *Batten 668* (ALA); Lake Shrader delta, *Mårtensson P 254* (UPS).— NOATAK QUAD.: Igichuk Hills, Hugo Cr. headwaters, *Parker, Elven, Solstad & Meyers 14936* (ALA); Mt. Noak, middle Situkoyok R. valley, *Parker, Elven, & Solstad 14785* (ALA); Kakagrak Hills, vic. 'radio tower' airstrip, *Parker, Batten, Denton & Heinlein 10235* (ALA); Mulgrave Hills, Tahinichok Mts.,

Parker, Elven & Solstad 14688 (ALA).— NOME QUAD.: Cape Woolley, Woolley Lagoon, *Strickland s.n.* (ALA); Glacier Cr. Rd., W side Anvil Mtn., *Kelso 83-204, 84-100* (ALA), *Parker 342* (ALA); Seward Peninsula Highlands, mi 4 Dexter Rd., *Heller 1013* (ALA); Crete Cr., *Murray, Yurtsev & Kelso 11339* (ALA); Glacial Lake, Sinuk R. valley, *Murray, Yurtsev & Kelso 11396* (ALA); Teller Rd., mi 11, *Williams 3362* (ALA); betw. Penny R. and Hungry Cr., *Elven, Gabrielsen, & Tove s.n.* (O).— NORTON BAY QUAD.: Nulato Hills, Christmas Mt., *Parker, Batten, Duffy & Cole 7389* (ALA); Debauch Mt., *Parker & Lipkin 7871, Parker, Batten, Duffy & Cole 7256* (ALA).— NUNIVAK ISLAND QUAD.: Yukon-Kuskokwim Delta, Nelson I., Tanunak, *Geist s.n.* (ALA).— NUSHAGAK BAY QUAD.: Bristol Bay Lowlands, Snake R., *Mesiar DCM-12* (ALA); Walrus Is., Round I., *Sherburne 20, Zabel & Taggart s.n.* (ALA).— PHILIP SMITH MTS. QUAD.: Arctic Foothills, Toolik Lake, *Walker 88-48-C* (ALA); Atigun Syncline GLORIA summit, *Batten 26877* (ALA); Galbraith Lake, W of lake, *Khokhryakov, Yurtsev & Murray 6628* (ALA); Imnavait Cr., 1 km NE of the INE trailer, *Managan, Prunier & Breen 4* (ALA); Uyamitqua Cr., near MS117, Dalton Hwy., *Walker 85-116* (ALA).— POINT HOPE QUAD.: Kipaloq and Angowlik Cr., Cape Dyer, *Viereck & Bucknell 4043* (ALA); Ogotoruk Cr. drainage, *Melchior & Melchior s.n., Johnson & Neiland 35, Piper 37* (ALA); Cape Sabine, Pitmeaga R., *Mårtensson C 63* (UPS).— PORT MOLLER QUAD.: Aleutian Range, Popof I., *Barker SP05-177* (ALA); *Trelease & Saunders 4347, 4348* (MO).— RUSSIAN MISSION QUAD.: Kilbuck-Kuskokwim Mts., Nyac vic., *Rutherford s.n.* (ALA); N of Tuluksak R., *Durst 140* (ALA).— SAGAVANIRKTOK QUAD.: Arctic

Foothills, Franklin Bluffs, *Klebesadel & Koranda s.n.* (ALA); Shaviovik R., *Spetzman 249* (ALA).— SELAWIK QUAD.: Waring Mts., *Parker, Meyers & Eagleson 9282, 9252* (ALA).— SELDOVIA QUAD.: Kachemak Bay, Poot Peak summit, *Berg 5* (ALA).— SEWARD QUAD.: Kenai Mts., Cooper Mt., *Klein 171* (ALA); Resurrection R. valley, S side of river, *Lipkin & Carlson 03-197* (ALA); Snow R., E of and above Paradise Lakes, *Hoef 143* (ALA).— SIMEONOF ISLAND QUAD.: Nagai I., *Harrington s.n.* (MO).— SLEETMUTE QUAD.: Canoe Mt., *Drury, Jr. 1849* (ALA).— SOLOMON QUAD.: Seward Peninsula Highlands, Kougarok Rd., mi 48, Kigluaik Mts., *Walker s.n.* (ALA); near Koyana Cr., *Kildaw s.n.* (ALA); Skookum Pass betw. Lower Solomon R. and Horton Cr., *Elven & Gabrielsen s.n.* (O).— ST. LAWRENCE QUAD.: Bering Sea Islands, SW Cape, St. Lawrence I., *Geist s.n.* (ALA); Kawuk Camp, *Rausch 6* (ALA); St Lawrence, *Kjellman s.n.* (S, UPS).— SEWARD QUAD.: Kenai Peninsula: Seward, *Hultén 7820* (S).— ST. MATTHEW QUAD.: St. Mathew Islands, *Trelease & Saunders 4352* (MO); Cape Upright, *Vacca 3* (ALA), *Ward & Ward 38* (ALA); Station 3, *Klein 116* (ALA); Hall I., *Trelease & Saunders 4351* (MO).— SURVEY PASS QUAD.: Brooks Range, Alatna R., *Murray 3926, 3777, s.n.* (ALA); *Hamilton 20* (ALA); Arrigetch Cr. valley, *Cooper CV-610, CV-650, 1030* (ALA); N end Walker Lake, *Smith 2461* (ALA); Unakserak R., S of Folly Lake, *Staender & Staender 30* (ALA).— SUTWIK ISLAND.: Ugaiushak I., *Lawhead 127* (ALA).— TABLE MT. QUAD.: Brooks Range, Ambresvajun Lake, Sheenjek R. valley, *Batten & Batten 75-477* (ALA); Firth R. drainage, VABM Silver, *Mouton s.n.* (ALA); Sheenjek valley 32 km N of Ambresvajun Lake, *Batten & Batten 75-2* (ALA).—

TALKEETNA QUAD.: Alaska Range, btw. Heart Mtn. and Swift Fork Kuskokwim R., *Roland 4405* (ALA); Shellabarger Pass, *Roland & Batten 4750* (ALA); Tonzona R., upper valley, *Viereck 5054* (ALA); Curry Ridge above Denali View, *Batten 2010-24* (ALA); Talkeetna Mts., Little Coal Cr. Drainage, Kesugi Ridge, *Williams s.n.* (ALA); W Fork Yentna R. Shadows Gl., *Larsen & Batten 01-824* (ALA).— TANACROSS QUAD.: Sheep Cr., E Alaska Range, *Winters Jr. 142* (ALA); Yukon-Tanana Upland, Divide Mt., *Dawe 79-7* (ALA); Mt. Fairplay, Taylor Hwy., *Smith 2430* (ALA), *Nava 64* (ALA).— TAYLOR MTS. QUAD.: Nishlik Lake, S shore, *Caswell 347* (ALA).— TELLER QUAD.: Seward Peninsula Highlands, Teller Hwy., mi. 63, *Elven & Grundt s.n.* (ALA); Teller Rd., mi. 68, *Williams 3392* (ALA); California River area, *Kaufman 2C* (ALA); Ear Mt., *Kelso 87-64* (ALA); Wales, *Mason 76-174-B* (ALA); Port Clarence, *Trelease & Saunders 4349* (MO).— TRINITY ISLAND.: Alitak, *Eyerdam 3028* (MO); Alitak Bay vicinity, Twin Peaks, *Studebaker 859, 23621* (ALA).— TYONEK QUAD.: Alaska Range, Neacola Mts. N of McArthur R., *Batten & Barker 09-147* (ALA); Frazer Lake, N end of lake, *Studebaker 02-532* (ALA).— UGASHIK QUAD.: Alaska Peninsula, Ugashik Narrows, *Talbot & Talbot s.n.* (ALA).— UNALAKLEET QUAD.: Nulato Hills, South R. and Rabbit Cr., SE of Unalakleet, *Parker & Batten 7897* (ALA), *Parker, Batten, Blank, Duffy & Cole 7031, 6988* (ALA); Unalakleet, *Stow 76* (NA).— VALDEZ QUAD.: Chugach Mts., Worthington Gl., *Hultén s.n.* (S); Blueberry Lake Campgr., Richardson Hwy., mi 24, *Harms 2893* (ALA).— WISEMAN QUAD.: Endicott Mts., Chimney Mt., *Parker, Elven*

& Solstad 12620 (ALA. O); Whiteface Mt., SW flanks, *Parker, Elven & Solstad* 12651, 12654 (ALA).

Canada, British Columbia. Alaska Hwy. Summit Pass, *Taylor, Szczawinski & Bell* 91, 158 (CAN), *Raup & Correll* 10463, 10685 (CAN); Mt. Selwyn, *Raup & Ernst* 3770, 3773, 3779, 3907 (CAN); Racing R., E of Summit Lake, *Porsild* 9016 (CAN); N of camp at bay, *Gillett & Boudreau* 17772 (CAN); Wokkpash Lake, Liard Riv., *George & Haber* 10817 (CAN); Spinel Lake, *Gillett & Boudreau* 17772 (UPS); Summit Lake below Mt. Saint George at mi 393, *Calder & Gillett* 24676 (UPS). **Northwest Territories.** Cache Cr., *Welsh s.n.* (ALA); E Cache Creek Dome, *Rigby* 30 (CAN); Mt. above Marengo Cr., *Meuleman* M5013 (CAN); E branch, *Porsild* 7037 (CAN); E slope of Richardson Mts., W of Mackenzie R. delta., *Porsild* 6841, 6699 (CAN); Jurassic Bug Cr. Sandstone., Cache Cr., *Welsh* 11968 (CAN); Liard R. btw. Nahanni Butte and Simpson, *Crickmay* 76 (CAN); Sachs Harbour 4 mi W, *Lambert s.n.* (CAN); Vic. of Brintnell Lake, N slope of Colonel Mt., *Raup & Soper* 9636, 9398 (CAN). **Yukon Territory.** Babbage R. NNW of Sam Lake, *Welsh & Rigby s.n.* (ALA); Ogilvie Mts., Windy Pass, *Parker s.n.* (ALA); 8 km N of Mt. King, *Cody & Ginns* 34315 (ALA); Blackfly, *Dickinson* 55, 60 (CAN); Old Crow R. valley, Snowdrift Camp, *Caswell, Henry & Martell s.n.* (ALA); Richardson Mts., *Cody & Ginns* 31661 (ALA); S end of Skull Range, *Cody & Ginns* 31614 (ALA); N slope of Skull Range, *Cody & Ginns* 31567-a (ALA); Bell R., White Mts., *Welsh & Rigby* 12190, 12178 (MO); Buckland Hills, *Elven* 2135/99 (ALA, CAN); Spear Mt., *Cody & Ginns* 31924 (ALA); Shingle Pt., *Aiken* 88-240 (CAN); Clarence Lagoon, Ivvavik National Park, *Cooper* 755 (CAN), *Consaul & Aiken* 958, 961 (CAN); Herschel

Island, *Cooper* 790, 1116, 1153, 1335 (CAN), E Pauline Cove, *Cooper* 831 (CAN); Buckland Hills, British Mts., *Cooper* 870, 927, 965, 1008 (CAN); Sheep Cr. NW of confluence of Sheep Cr., *Consaul & Aiken* 931 (CAN); Canol Rd., Lower Lapie R., *Porsild & Breitung* 9938 (S); NE shoulder of Mt. Sheldon, *Porsild & Breitung* 11086 (S); Mt. McIntyre, S of Whitehorse, *Gillett & Mitchell* 3439 (S); Bonnet Plume, Pinguicula Lake, *Bennett* 05-313 (ALA); Ogilvie and Wernecke Mts., 10 mi NW of Chapman Lake, *Cody & Ginns* 32992, 34143 (ALA); Blackstone Lake, 17 km W, *Cody & Ginns* 34403 (ALA).

3. **Oxytropis gorodkovii** Jurtzev Bot. J., URSS 53: 1538. 1968.—TYPE: RUSSIA.

Wrangel Island. The shore of Somnitelnaja, *Zhukova & Petrovsky s.n.* (holotype: LE-3767, digital image!).

Astragalus pygmaeus Pall., Species Astragalorum 66. 1800. *Oxytropis nigrescens*

var. *pygmaea* (Pall.) Cham., Linnaea 6 (4): 546. 1831. *Oxytropis pygmaea* (Pall.)

Fernald, Rhodora 30 (356): 153. 1928, non Tausch ex Beck, in Reichenb. Ic. Fl.

Germ. 22: 120. 1901. *Oxytropis nigrescens* subsp. *pygmaea* (Pall.) Hultén, Flora of

Alaska and Yukon 7: 1103. 1947.—TYPE: RUSSIA. Chukotka: “in terris arcticis

Siberiae ad orientem ultime, Tschucktschis habitatae”, *D.D. Merck s.n.* (LE?)

Oxytropis tschuktschorum Jurtzev pro min. p., quoad typam, nomen novum, Bot. J.,

USSR 53: 1538. 1968.

Perennial; acaulescent from a pulvinate subterranean caudex, caudex branches elongating from 2 – 3 (4) cm; stipules persistent, pale-green to yellow, partially adnate to petiole, connate at base, 5 – 8 mm long, blades ovate to lanceolate, free, 2 – 4.5 mm long, ciliated margins with lanate to densely pilose black hairs; leaves, alternate, 0.5 – 2.5 cm long, the petioles 2 – 5(15) mm long, slender densely pilose; leaflets 7 – 13, linear-lanceolate, 2 – 3 (5) mm long, 0.5 – 1.5 mm broad, pilose hairs restricted to abaxial side of the leaflet; scape spreading, equaling the leaves, 0.5 – 3 cm, pilose; raceme loose, 1 – 2-flowered; bracts linear to lanceolate, opaque, 1 – 4 mm long, black-pilose dorsally and ventrally; calyx campanulate, 6 – 10 mm long, densely black villous, teeth deltoid to lanceolate, 2.5 – 4 mm long; petals purple, banner obovate, emarginate, 12 – 15 mm long;

wings 9 – 12 mm long, claw subequal; keel 9.5 – 11 mm long, claw subequal; legume body cylindrical, 24 – 28 mm long, 4 – 8 mm in diameter; seeds brown, reniform to mitiform, 2 mm long, 2 mm in diameter; seedcoat rugulate reticulate, to lophate. Fig. 2.11. Chromosome number: $2n=16, 32$ (Petrovsky & Zhukova 1981; Zhukova 1983).

Phenology. *Oxytropis gorodkovii* flowers in late June.

Distribution (Fig. 2.12). Commonly found along the coastal margins of eastern Chukotka and the western Seward Peninsula and northern coast of Alaska. *Oxytropis gorodkovii* is uncommon in northern Alaska and the Yukon Territory with the populations being restricted to gravel bars. This taxon is commonly found with *Dryas octopetala*, *Hierochloe* ssp., *Carex* spp. Elevation ranges from 0 to 1000 m.

Notes. In 1968 Yurtzev considered *O. tschuktschorum* and *O. gorodkovii* to be separate species. In 1980 he lumped them [as to the types] and applied the name *O. czukotica* to most of the plants that had been called *O. tschuktschorum*. In 1980 he recognized two species, *O. czukotica*, the former including most of the plants to which the name *O. tschuktschorum* had been applied, and *O. gorodkovii*, the latter including the type of *Astragalus pygmaeus* Pall. [= *O. tschuktschorum*]. Here we recognize *O. czukotica* Jurtz. as a synonym of *O. bryophila* based on insufficient morphological boundaries between the two.

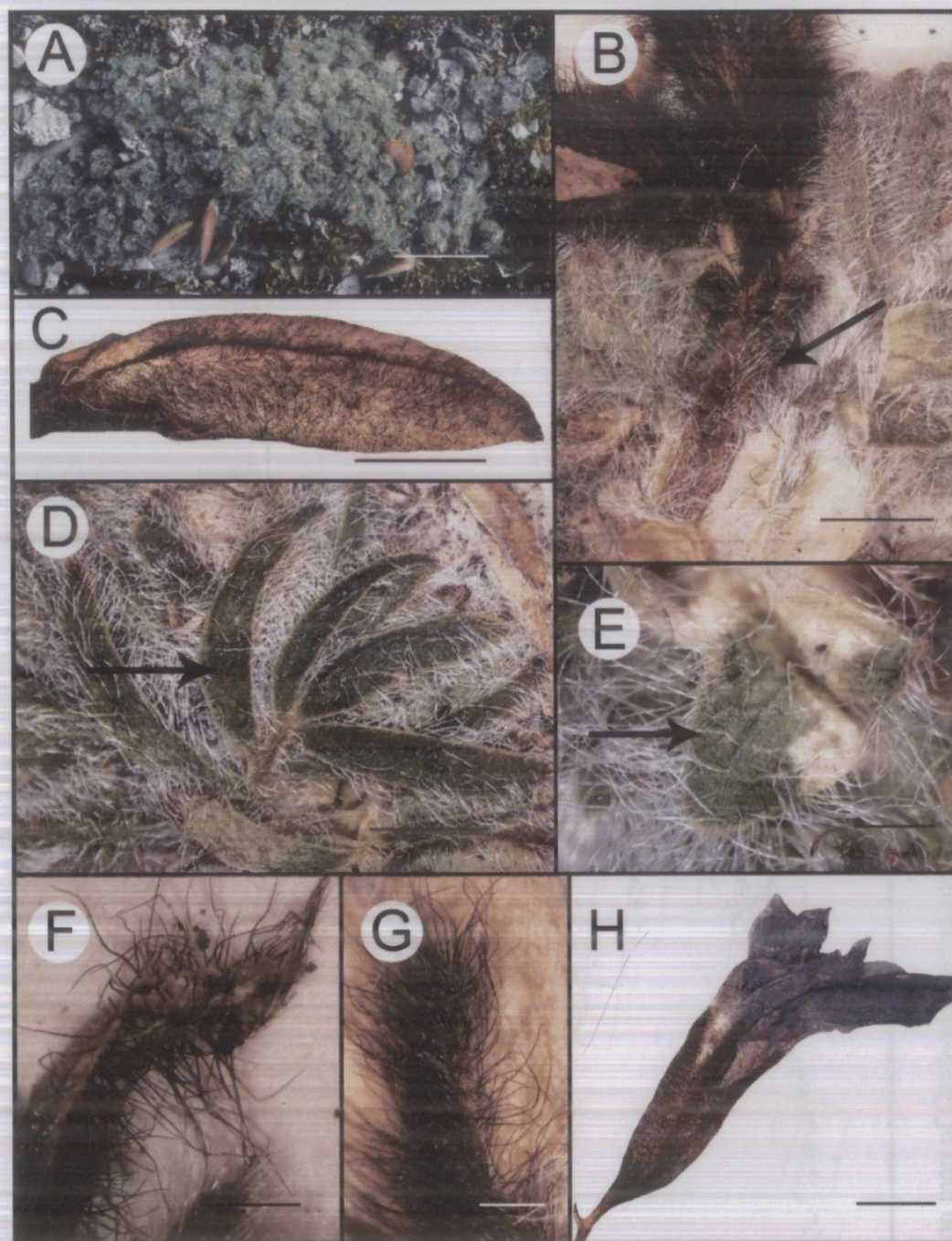


Figure 2.11. Morphological characteristics of *Oxytropis gorodkovii*. A. Extreme pulvinate habit (photo provided by C. Parker). B. Short scape, with white pilose hairs (Mason 7675 ALA). C. Cylindrical legume covered with black villous hairs, (Melchior & Melchior s.n. ALA). D. Odd-pinnately compound leaf with 5 leaflet pairs, leaflets lanceolate to oblong with white pilose hairs concentrated on the abaxial side (Mason 7675 ALA). E. Ovate to deltoid stipule covered with white pilose hairs, (Hulten s.n. ALA). F. Lanceolate to linear-lanceolate flower bract, (Aiken 99-011 MO). G. Oblong to narrowly ovate calyx tooth covered in black villous hairs, (Tikhmenev s.n. ALA). H. Flower covered with black villous hairs, (Kaufman 2C ALA). Scale bars A 1 cm; B, C, D, E, F, G 1 mm; H 3 mm.

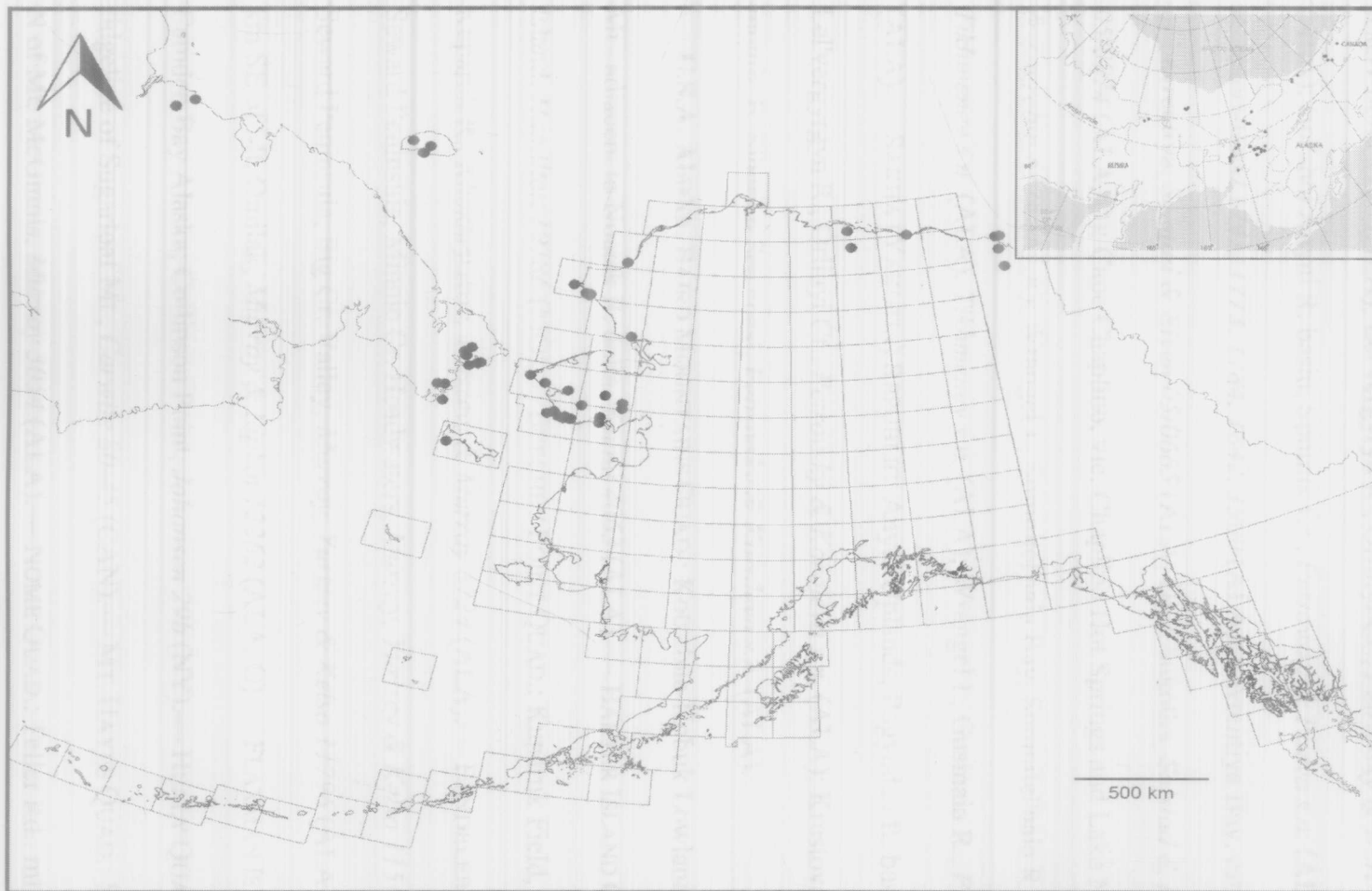


Figure. 2.12. Distribution map of *Oxytropis gorodkovii* in Alaska as well as neighboring Russian and Canadian territories (see insert map of far eastern occurrences).

ADDITIONAL SPECIMENS EXAMINED.

Russia. CHUKOTKA AUTONOMOUS REGION: 0.5 mi from road and 2 mi from Lorino *Ickert-Bond 1798* (ALA); *Lel'vergyryn R., Orlinyi Cr., Petrovsky & Koroleva s.n.* (ALA); *Bol'shoi Anyui R. basin, Sputnik Cr., Petrovsky & Plieva s.n.* (ALA); *Chegitun R. Ickert-Bond 1741, 1773, 1784, 1842, 1900* (ALA); *Lavrentiya Bay, estuary 15 km NW of Lavrentiya, Solstad & Elven 05/0665* (ALA, O); *Chukotka, Solstad & Elven 05/0272, 05/0974* (ALA, O); *Cape Chaplino, vic. Chaplino Hot Springs and Lake Naybak, Parker & Zagrebin 6174* (ALA); *Wrangel I., Somnitel'naia Bay, Somnitel'naia R., Levkovsky & Tikhmenev s.n.* (ALA), *Tikhmenev s.n.* (ALA); *Wrangel I., Gusinaia R., Petrovsky 80* (ALA).— SAKHA (YAKUTIA) REPUBLIC: *Anyui Uplands, Pogynden R. basin, Lel'vergyrgyn R., Orlinyi Cr., Petrovsky & Koroleva s.n.* (ALA); *Krestovaia River mouth, E. Siberian Sea coast, Petrovsky & Koroleva s.n.* (ALA).

U.S.A. Alaska. BAIRD MOUNTAINS QUAD.: *Kotzebue-Kobuk Lowlands, Napaktuktuk Mt., adjacent to Noatak R. delta, Young 4063* (ALA).— BARTER ISLAND QUAD.: *Barter Island, Hamilton 19786* (MO).— BEECHEY POINT QUAD.: *Kuparuk Field, E bank Kuparuk R., Khokhryakov, Yurtzev, & Murray 6724* (ALA).— BENDELEBEN QUAD.: *Seward Peninsula, Minnie Cr. Headwaters, Murray, Yurtzev & Kelso 11565* (ALA); *Seward Peninsula, Big Cr. Valley, Murray, Yurtzev & Kelso 11796* (ALA); *Darby Mts., 5 km SE of Mt. Omilak, Murray & Lipkin 12262* (ALA, O).— FLAXMAN ISLAND QUAD.: *Camden Bay Alaska; Collinson Point, Johansen 29b* (NY).— HEALY QUAD.: *Central N-S ridgeline of Sugarloaf Mt., Carwile 80-45* (CAN).— MT. HAYES QUAD.: *Sager's Camp, N of Mt. McGinnis, Murray 3054* (ALA).— NOME QUAD.: *Teller Rd., mi. 16-18, Walker*

s.n. (ALA), *Springer s.n.* (ALA); Arctic and Cleveland Cr., *Murray, Yurtzev & Kelso 11853*(ALA); Anvil Mt., N of Nome, *Parker 342, Welsh 5943* (ALA); 12 km NNE of Cape Rodney; *Parker & Beattie 15407* (MO); Moon Mts., *Parker, Lipkin, & Meyers 15941* (ALA); low uplands N of Sinuk, *Parker & Beattie 15407* (ALA); Dexter Rd., *Heller 919, 1228* (ALA); btw. Snake and Penny R., W of Nome, *Pegau 244* (ALA).— POINT HOPE QUAD.: vic. of Ogotoruk Cr., *Melchoir & Melchoir s.n.* (ALA), *Hultén s.n.* (ALA), *Johnson, Viereck, & Melchior 128, 334, 557* (ALA), *Wood & Wood 557-A* (ALA); Cape Thompson, *Belson s.n.* (ALA); Point Hope, *Mason 76-75* (ALA), *Welsh 5807* (MO).— SAINT LAWRENCE QUAD.: St. Lawrence Island, Boxer Bay, *Geist 192, 198* (ALA); Boxer Valley, dry hill-site NW of Boxer R., *Sauer s.n.* (ALA).— SOLOMON QUAD.: Seward Peninsula Highlands, Skookum Pass, on Council Road, *Kelso 83-34* (ALA); VABM Bluff at coast near Koyana Cr., *Kildaw s.n.* (ALA); Iviktook Lagoon, *Mason s.n.* (MO).— TELLER QUAD.: California River area, *Kaufman 2C* (ALA); Seward Peninsula Highlands, Lost R. Drainage, *Lenarz 46* (ALA); Cape Prince of Wales, *Kelso 82-140* (ALA); Port Clarence, *Trelease & Saunders 4350* (MO).

Canada, Northwest Territories, NTS-84: Caribou Hills, E Channel Mackenzie R., 3 miles NW of Reindeer Station, *Cody & Ferguson 10100* (ALA, NY). **Yukon Territory**, NTS-117: Babbage R., NNW of Sam Lake, *Welsh & Rigby 10084* (NY); Herschel Island, *Wood 194* (CAN), *Lindstrom s.n.* (NY); Ridge of Neroukpuk, N slope of Buckland Hills, 20 mi S of Herschel Island, *Welsh & Rigby 10153* (ALA).

4. **Oxytropis huddelsonii** A.E. Porsild., Bulletin of the National Museum of Canada 121:

252. 1951.—TYPE: CANADA. Yukon Territory, Goldenhorn Mts., south of Whitehorse, *C.W. Huddelson s.n.* (holotype: CAN-76836!).

Perennial; acaulescent from a branching subterranean caudex, caudex branches elongating from 2 – 5.5 cm; stipules persistent, pale-green to yellow, partially adnate to petiole, connate at base, 5 – 10 mm long, blades deltoid to lance-sublate, free, with red-purple discoloration along margins of apex, 2.5 – 6 mm long, ciliated margins with densely black pilose hairs; leaves, alternate, 1 – 5.5 cm long, the petioles slender, 7 – 46 mm long, subglabrous; leaflets 7-13, narrowly ovate to linear-lanceolate, 4 – 7 mm long, 0.5 – 3 mm broad, sparingly pilose dorsally and ventrally, along the inrolled margin; scape spreading, equaling the leaves, 2 – 4 cm, villous-appressed to pilose; raceme loose, 1 – 3-flowered; bracts oblong to ovate, opaque, 1 – 2 mm long, black-pilose dorsally and ventrally; calyx campanulate, 5.5 – 7.5 mm long, densely black villous, teeth linear to lanceolate, 1 – 3 mm long; petals purple, banner obovate, emarginated, 10 – 15 mm long; wings 10.5 – 13 mm long, claw subequal; keel 9.5 – 11.0 mm long, claw subequal; legume sessile, body ovoid nearly glabrous or with sparse short black pilose hairs, semi-inflated, 11 – 21.5 mm long, 4 – 10 mm in diameter, acuminate with linear to linear-lanceolate beak; seeds brown, reniform to mitiform, 1.5-2 mm long, 2-2.5 mm in diameter; seedcoat rugulate, rugulate reticulate, to lophate. Fig 2.13. Chromosome number: $2n=16$ (Dawe and Murray 1981).

Phenology. *Oxytropis huddelsonii* flowers in mid-summer.

Distribution (Fig 2.14). Restricted to the ridge tops and alpine tundra of southeast Alaska extending east to the Yukon Territory and southeast into British Columbia. This taxon is commonly found in alpine community assemblages, which include *Dryas octopetala*, *Arnica alpina*, *Vaccinium vitis-idaea*, and *Ledum palustre* var. *decumbens*. The elevation ranges up to 1500 m.

Notes. There have been some nomenclatural issues concerning the spelling of *Oxytropis huddelsonii*, but there is little dispute to the validity of the taxon as a distinct species due to its glabrous ellipsoidal legumes and ovate leaflets.

Additional specimens examined:

U.S.A. ALASKA. BERING GLACIER QUAD.: Chugach Mts., Granite Range, *Batten & Barker 96-321* (ALA).— EAGLE QUAD.: Mt. Veta tundra, *Spetzman 5076* (CAN); Taylor Hwy., near Jct. of Sixty-mile Rd., *Schmuck 286* (ALA); Open S-facing bluff, *Bennett & Larsen 02-197* (DAO).— HEALY QUAD.: Clearwater Mts.: Susitna drainage, *Grundt s.n.* (ALA).— MCCARTHY QUAD.: St. Elias Mts., Maccoll Ridge, *Parker 16701* (ALA); vic. Guerin Glacier, *Murray 2037* (ALA); vic. of Russell Glacier, *Murray 2168* (ALA); Nikolai Pass area, W of Nizina R., *Batten & Barker 96-49, 96-13* (ALA); Wrangle Saint Elias National Park, Nikolai Ridge, *Ickert-Bond 1641* (ALA).— MT. HAYES QUAD.: Denali Hwy., 6 mi., W of Paxson on Denali Rd., *Hultén s.n.* (S); 12.5 mi., *Williams 2301* (BRY); 12.6 mi., *Welsh 4771* (BRY, S, NY); 12.8 mi., *Klebesadel s.n.* (ALA, CAN); 13 mi., *Harms 4191* (ALA), *Davis 5060* (BRY); 14 mi, *Spetzman 4035* (CAN); 30 mi., *Welsh & Moore 8331* (BRY); Gulkana Glacier, *Viereck & Viereck 2155* (ALA).

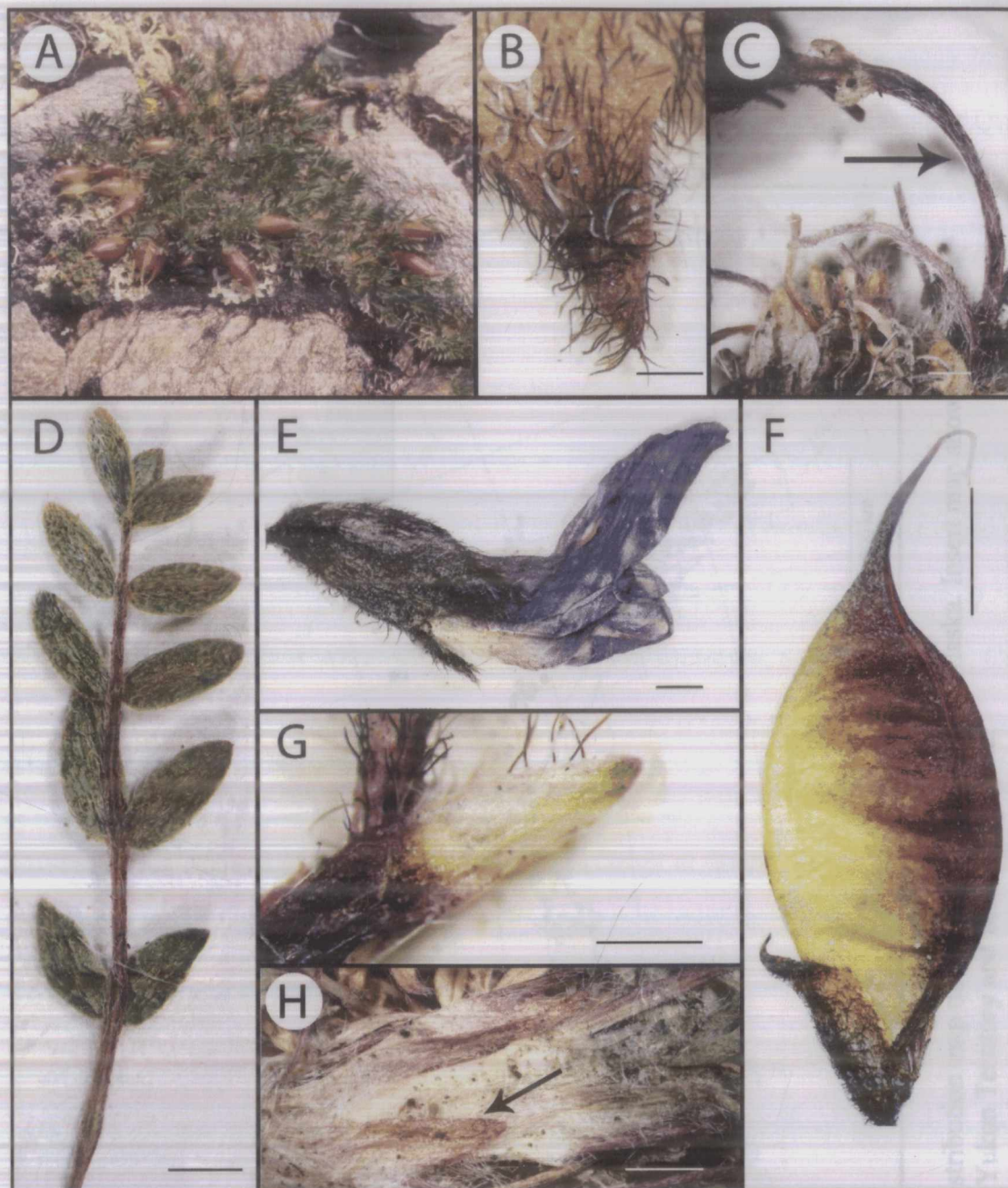


Figure 2.13. Morphological characteristics of *Oxytropis huddelsonii*. A. Spreading habit with semi-inflated legumes (photo provided by C. Parker). B. Deltoid to lanceolate calyx tooth (Murray & Murray 516, CAN). C. Spreading scape, with sparse white pilose hairs (Batten & Barker 96-49, ALA). D. Odd-pinnate leaf with 5 leaflet pairs, leaflets narrowly ovate to lanceolate (Murray & Murray 81, ALA). E. Flower covered with black and brown villous hairs (Murray 1561, CAN). F. Semi-inflated, elliptical legume with glabrous to sub-glabrous body (Murray 2037, ALA). G. Oblong to narrowly ovate flower bract (Murray 861, ALA). H. Membranous ovate to lanceolate stipule (Murray 1090, ALA). Scale bars B, H, G 0.5 mm; C- F 1 mm.

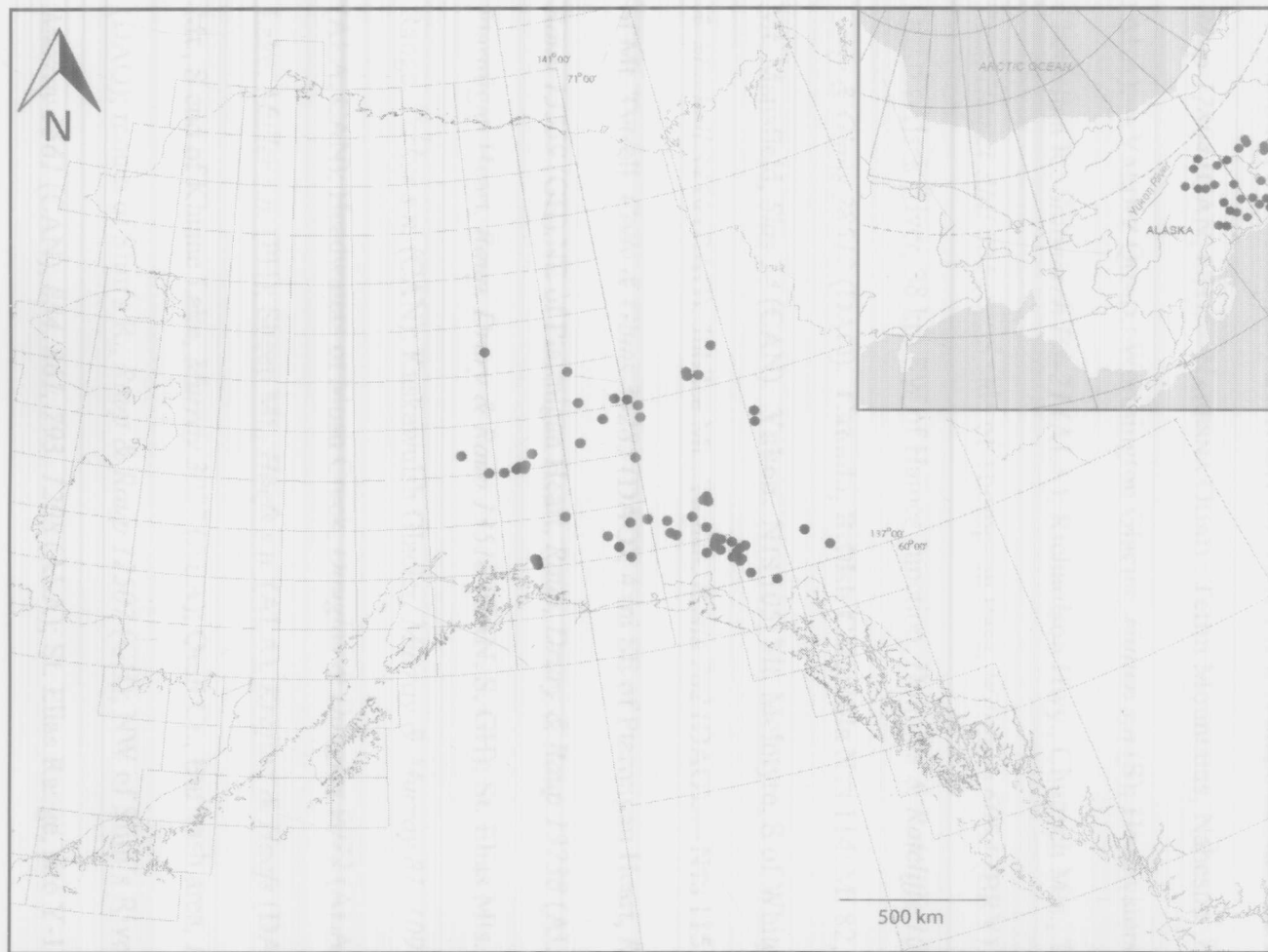


Figure. 2.14. Distribution map of *Oxytropis huddelsonii* in Alaska. Insert map shows additional localities in the Yukon Territory and British Columbia.

— MT. MCKINLEY QUAD.: Glenn Hwy., mi 120, Gunsight Mt., *Spetzman 4364* (CAN); Denali National Park, *Prevey JP-09-100* (ALA).— ST. ELIAS QUAD.: Chalcedony Mt., ca. 23 mi WSW of Haines Junction, *Douglas & Douglas 6788* (BRY).— TANACROSS QUAD.: Mt. Fairplay, Fortymile Hwy 29, *Anderson 10818* (S); N slope of Nutzotin Mts., *Raup & Raup 12804* (CAN, GH).— NABESNA QUAD.: Tetlin Mountains, Nabesna, *Teare 1620* (ALA).— VALDEZ QUAD.: Worthington Glacier, *Hulten s.n* (S); Headwaters of the Chetaslina R., *Saltmarch PA-21* (ALA); Richardson Hwy., Chugach Mts., Thompson Pass, *Hamet-Ahti 881* (S); S side of Thompson Pass, *Williams 605A* (BRY).— YAKUTAT QUAD.: Alsek River, 38 km SW of Haines Junction, *Douglas & Ratcliffe 10771* (BRY), *Cody & Ginns 28512* (DAO). **Canada, British Columbia** NTS 114: Mi 82, Haines Rd., Mt. Mansfield, *Sias 14* (CAN). **Yukon.** NTS 105: Mt. McIntyre, S of Whitehorse, *Gillett & Mitchell 3439* (DAO); Jubilee Mt., Tagish, *Rosie 782* (DAO).— NTS 115: 20 mi WSW of Mt. Tyrrell, *Cody & Ginns 35285* (DAO); 4 mi SE of Ptarmigan Heart, *Raup, Drury & Raup 13559* (GH), NE of Ptarmigan Heart, *Raup, Drury & Raup 13738* (ALA, S); SW of Ptarmigan Heart, *Raup, Drury & Raup 13518* (CAN, S, GH); St. Elias Mts., Centennial Range, *Tasker s.n.* (CAN); Kaskawulsh Glacier, *Murray & Murray 81, 1090* (ALA), *516* (ALA, CAN); Headwaters of Mush Creek, *Douglas & Douglas 9072* (ALA); Kluane Lake, *Muller s.n.* (PH); Sheep Mt., *Hoefs s.n.* (ALA), *Krajina & Hoefs* (DAO); Outpost Mt., S end of Kluane Lake, *Murray 3027* (ALA); Quill Cr., Burwash area, *Freedman s.n.* (DAO); mouth of Slim's R., *Raup & Raup 12507* (GH); NW of Slim's River, *Murray and Murray 1561* (CAN), *884, 861, 793, 1208* (ALA); St. Elias Range, site Y-17, *Scotter 20918* (DAO); site Y-20, *Scotter 21067* (DAO); site Y-21, *Scotter 21119* (DAO), *Scotter*

21147B (ALA); site Y-22, *Scotter 21292* (DAO); Mt. Desolei, *Cody & Ginns 28706* (DAO); Ethel Lake area, *Asquith 401* (DAO), *Kennedy 791b* (DAO); Mt. Hart, *Cody & Ginns 33826* (DAO, GH); S of Haines Rd. junction, *Harris s.n.* (GH); vic. Rusty Glacier terminus, W of Burwash Landing, *Murray 1330* (ALA); SW Haines Junction, Alsek River, *Pearson 181A* (CAN); Alaska Hwy. mi. 1022, Mt. Decoli, *Schofield & Crum 8061, 8148* (S).—NTS 116: 57 mi along Sixty-mile Rd., W of Dawson, *Calder 3595* (DAO), 50 mi, *Welsh & Moore 5604* (MO); Alaska border, *Friisch 122* (DAO); E of Hamilton Creek, *Cody & Ginns 34620b* (DAO); Tundra turf slope, *Cody & Ginns 32937a* (DAO); Mt. above Fish Creek, *Cody & Ginns 33134* (DAO); Hart R., *Cody & Ginns 34507b* (DAO); S of Klondike Loop Hwy., near Alaska border, *Cody & Ginns 33787* (DAO, NY); Fortymile Rd., mi 31.5, *Lutz 1141* (NY).

5. **Oxytropis kokrinensis** A.E. Porsild, *Rhodora* 41(486): 251-252, pl. 553. 1939.—

TYPE: U.S.A. Alaska, Kokrine Mts.: divide towards Melozitna R., elevation 2000' to 4000', A.E. & R.T. Porsild 762 (holotype: CAN-76828!).

Perennial; acaulescent from a branching subterranean caudex, caudex branches elongating from 2 – 4 (6) cm; stipules persistent, chestnut red, partially adnate to petiole, connate at base, 4 – 10.5 mm long, blades deltoid to linear, free, 1 – 6 mm long, with an abruptly acuminate apex, prominently 1- nerved, glabrous to subglabrous dorsally, densely black and white ciliate ventrally; leaves, alternate, 1 – 5 cm long, the persistent slender petioles 10 – 40 mm long, subglabrous; leaflets 7-9 (-13), narrowly ovate to linear-lanceolate, 2 – 8 mm long, 1 – 2.5 mm broad, pilose dorsally and ventrally, ciliate along the inrolled margin; scape spreading, equaling or slightly surpassing the leaves, 1 – 4 cm, villous-appressed to pilose; raceme loose, 1 – 2-flowered; bracts obelliptic to ovate, opaque to membranous, 1 – 1.5 mm long, sparsely black-pilose dorsally and ventrally; calyx campanulate, 5 – 9.5 mm long, densely black villous, teeth linear to lanceolate, 2.5 – 5 mm long; petals purple to pink; banner obovate, emarginated, 7 – 14.5 mm long; wings (9) 10 – 11.5 mm long, claw subequal; keel 8.5 – 10 mm long, claw subequal; legume sometimes sessile, frequently stipitate, stipe 1.5 – 4.0 mm long, the body oblong to cylindrical, 16.0 – 25.0 mm long and 5 – 8.0 mm in diameter, acuminate towards the base and apex; seeds brown, reniform, 1.0 – 1.5 mm long, 1.0 – 2.0 mm in diameter; seedcoat rugulate to rugulate reticulate. Fig 2.15. Chromosome number: unknown.

Phenology. *Oxytropis kokrinensis* flowers in late June to early July.

Distribution (Fig 2.16). Endemic to Alaska, found primarily in Northwest Alaska occurring near the Ray Mountains, the Buckland River, and the Selawik Hills, with disjunct populations in the central Brooks Range and the Kokrine Hills. *Oxytropis kokrinensis* is found in alpine scree slopes on disturbed soils ranging from acidic to calcareous, commonly in association with *Dryas octopetala*, *Oxytropis bryophila*, *Vaccinium vitis-idaea*, *Arnica alpina*, and *Ledum palustre* var. *decumbens*; elevation ranges from 450-1000 m.

Notes. In 1939 Porsild circumscribed *Oxytropis kokrinensis* on the basis of its strongly nerved rustic-red stipules. This distinct species is locally abundant in northwest and central Alaska. The chromosome number is unknown for *O. kokrinensis*, since the Holmen (1962) voucher that was cited for *O. kokrinensis* in the Pan-arctic Flora (Elven 2011) contains *O. bryophila* on the same herbarium sheet.

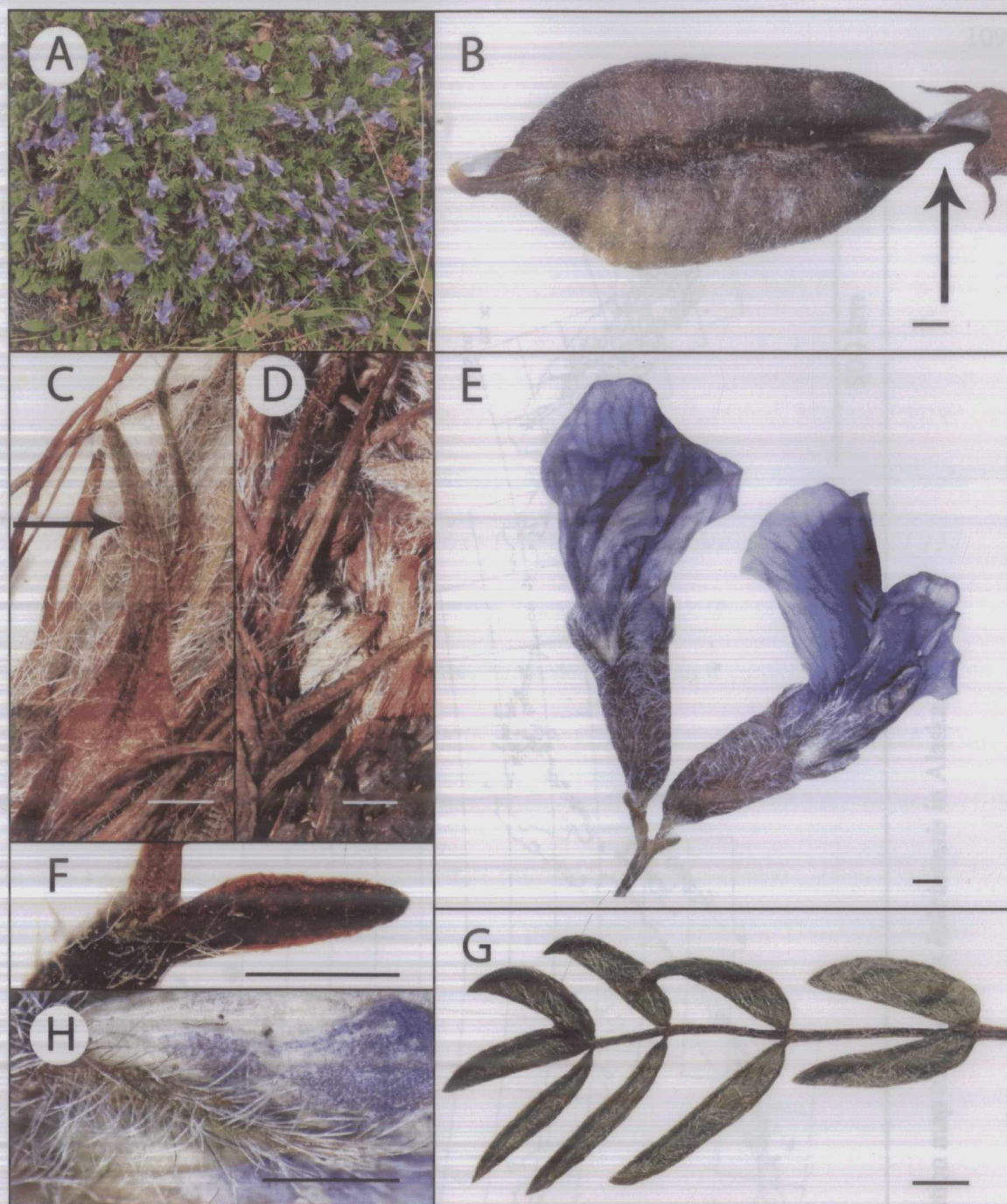


Figure 2.15. Morphological characteristics of *Oxytropis kokrinensis*. A. Subpulvinate habit. B. Elliptical legume with a prominent stipe (Parker, Elven & Guldager 13772, ALA). C. Red stipules with a strongly nerved linear free blade (Parker, Batten & McIntyre 11397, ALA). D. Scape with white pilose hairs (Lipkin 80-161, ALA). E. Two-flowered inflorescence (Parker & Meyers 10674, ALA). F. Oblong flower bract (Lipkin 80-196, ALA). G. Odd-pinnately compound leaf with 4 leaflet pairs, leaflets linear to linear-lanceolate (Lewis s.n., ALA). H. Linear calyx tooth covered with an admixture of white and black pilose hairs (Kassler 141, ALA); A, 2 cm; B, E 5 mm; C, D, F-G 1 mm.

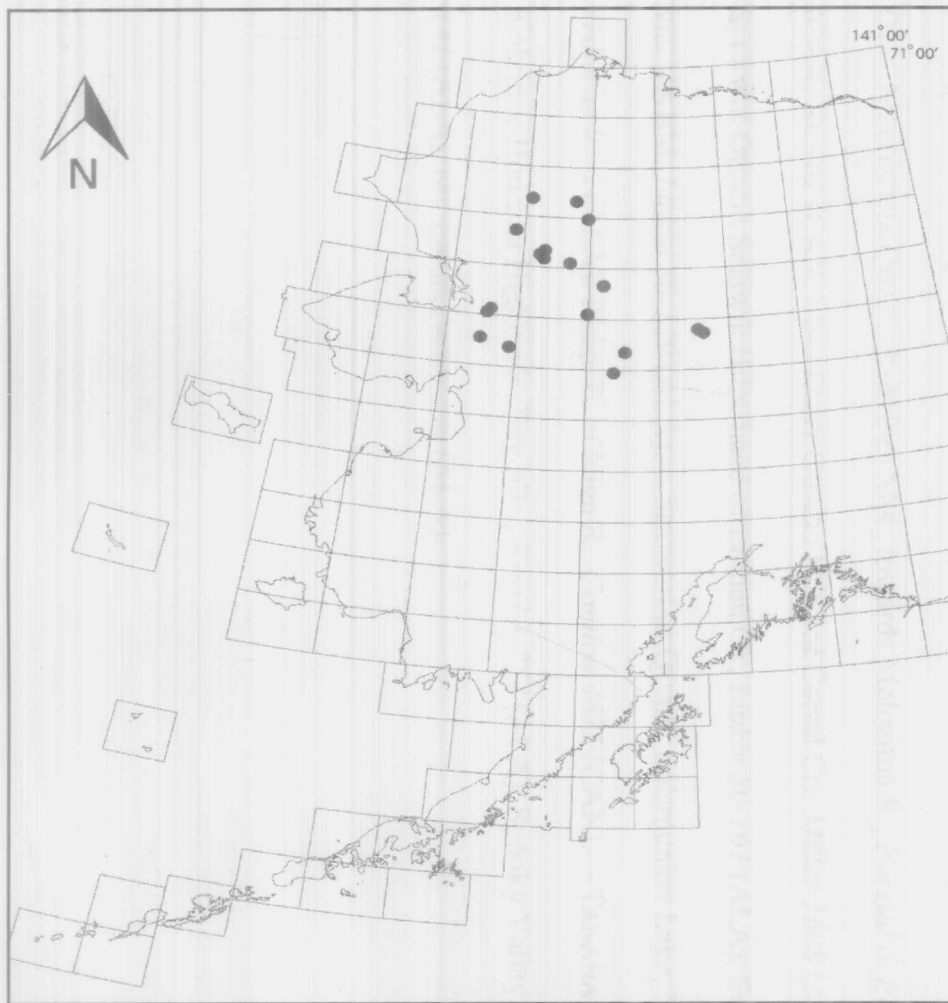
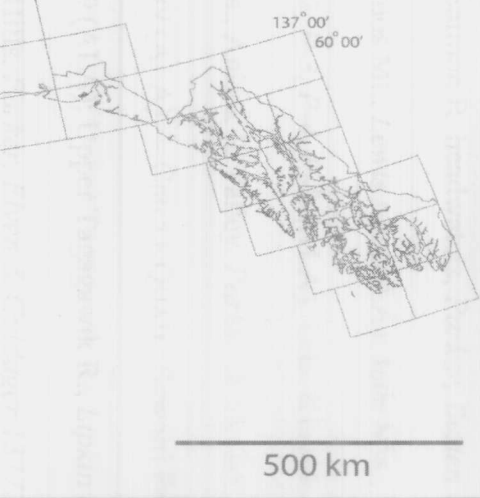
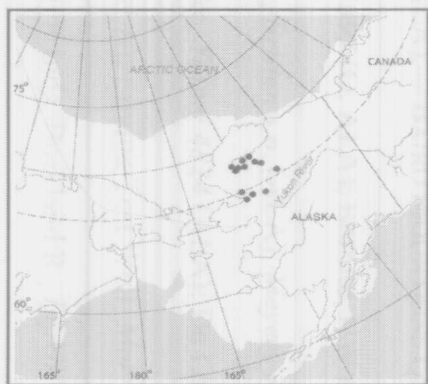


Figure. 2.16. Distribution map of *Oxytropis kokrinensis* in Alaska.



ADDITIONAL SPECIMENS EXAMINED.

USA. Alaska. AMBLER RIVER QUAD.: Baird Mts., SE of Akillik R. valley, *Parker & Fowell 11764* (O, ALA); N of lower Nuna Cr., *Parker, Batten & McIntyre 11712* (ALA).—BAIRD MOUNTAINS QUAD.: Salmon R. headwaters, *Parker, Batten & McIntyre 11397* (O, ALA); Bornite, NW of Cosmos Mt., *Lewis s.n.* (ALA); Jade Mts., N of Kobuk R., *Britten s.n.* (ALA), *Meyers P-1, P-2, P-3, P-4, P-5* (ALA); Lake Kipmik, S side of lake, *Young 4824* (ALA); De Long Mts., Anisak R. valley, *Parker & Meyers 10674* (ALA); Etivluk Test Well, *Murray 6889* (ALA).—CIRCLE QUAD.: Seward Peninsula Highlands, Buckland R., *Lipkin 80-100* (ALA); Upper Tagagawik R., *Lipkin 80-196* (ALA).—HUGHES QUAD.: Lockwood Hills, *Parker, Elven & Guldager 13772* (ALA, O).—MELOZITNA QUAD.: Kokrines Mts., towards Melozitna R., *Porsild & Porsild 761* (CAN, S), *762* (CAN, S).—RUBY QUAD.: Head of Corral Cr., *Miller 1608* (ALA, S).—SELAWIK QUAD.: Selawik Hills, head of Lomen Cr., *Lipkin 80-161* (ALA); Selawik Hills, vic. VABM, *Lipkin 80-129* (ALA).—SHUNGNAC QUAD.: Solsmunket Lake, NE of lake, *Osborne 91-5* (ALA); Ridge E. of Nigu R., *Cantlon 4675* (CAN).—TANANA QUAD.: Kokrines-Hodzana Highlands, Ray Mts., *Kassler 252* (ALA), Spooky Valley, *Kassler 141* (ALA), Mt. Eakin, *Juday s.n.* (ALA).

6. **Oxytropis mertensiana** Turcz., Bulletin de la Société Impériale des Naturalistes de Moscou 13 (1): 68. 1840. *Spiesia mertensiana* (Turcz.) Kuntze, Revisio Generum Plantarum 1: 207. 1891. *Aragallus mertensianus* (Turcz.) Greene, Pittonia 3 (17A): 211. 1897.—TYPE: RUSSIA. East Chukotka, “ad sinum Sancti Laurentii,” *Mertens s.n.* (holotype: KW-001001230, digital image!).

Perennial; acaulescent from a branching subterranean caudex, caudex branches elongating from 3 – 11 cm; stipules persistent, pale-green to yellow, partially adnate to petiole, connate at base, 7.5 – 15 mm long, blades deltoid to linear-lanceolate, free, 1.5 – 9 mm long, glabrous to subglabrous dorsally, sparsely black and white ciliate ventrally; leaves unifoliate or trifoliate, rarely quinquefoliate, 2.5 – 7 cm long, unifoliate leaf ovate to elliptic, 6 – 25 (29) mm long, 1 – 6 mm broad, trifoliate leaf palmate to subpalmate, leaflets 3-nerved, glabrous dorsally, sparsely pilose ventrally, ciliate along the inrolled margins; scape erect, equaling or surpassing the leaves, 2 – 8 cm long, villous-pilose; raceme erect, (2–) 3 (–4) -flowered; bracts linear, membranous, 1 – 6 mm long, densely black-pilose dorsally, glabrous to subglabrous ventrally; calyx campanulate, 4 – 10 mm long, densely black villous, teeth linear-subulate, 1 – 4 mm long; petals purple; banner obovate, emarginate, 12 – 15 mm long; wings 9.5 – 11 mm long, claw subequal; keel 8 – 10 mm long, claw subequal; legume sessile to stipitate, stipe 0.5 – 2 mm long, body ellipsoid-oblong, 10 – 17 mm long, 4 – 5 mm in diameter, short acuminate recurved beak; seeds brown, reniform to mitiform, 1 – 2 mm long, 1 – 2 mm wide; seed coat rugulate to

rugulate reticulate. Fig. 2.17 Chromosome number: $2n=16$ (Krogulevich 1976; Zhukova 1983).

Phenology. *O. mertensiana* flowers in mid-late June or early July.

Distribution (Fig. 2.18). Amphiberingian, the most eastward (disjunct) distribution of *Oxytropis mertensiana* is limited to the Richardson Mountains in the Yukon Territory, Canada. Otherwise, *O. mertensiana* is found primarily in the Interior of Alaska west to the Seward Peninsula, Cape Lisburne, islands of the Bering Sea and the Chukotka Peninsula, extending westward to the Lena River (Yakutsk Province). *Oxytropis mertensiana* is found in moist arctic tundra near upland river terraces, margins of frost boils, and in calcareous substrates, commonly associated with tundra and alpine communities including *Dryas octopetala*, *Carex* ssp., *Luzula nivalis*, *Douglasia arctica* and *Arnica alpina*; from sea level to 1900 m.

ADDITIONAL SPECIMENS EXAMINED.

Russia. CHUKOTKA AUTONOMOUS REGION: Anadyr basin, Sokh River, Lake Drumlinnoye, *Petrovsky & Plieva s.n.* (ALA); Drumlinoje, *Petrovsky & Plieva 6329* (S); vicinity of Lake Drumlinnoye, *Petrovsky & Plieva s.n.* (ALA, CAN, NY); Anyui Uplands, Pogyn den R. basin, Lel'vergyrgyn R., *Petrovsky & Koroleva s.n.* (ALA). Eastern Chukotka, *Sukhorukova, Efros & Kozhevnikov 26122, 26152* (CAN); Konyam Bay, *Kjellman s.n.* (S, UPS); Lavrentiya Bay and vic. Lavrentiya village, *Sekretaryeva & Yurtsev s.n.* (ALA), *Solstad & Elven 05/0670* (O); southeastern end, Getlyanen Lagoon, *Razhivin, Sekretaryeva & Yurtsev s.n.* (ALA); Lorenz-Bay, *Krause & Krause 60* (UPS);

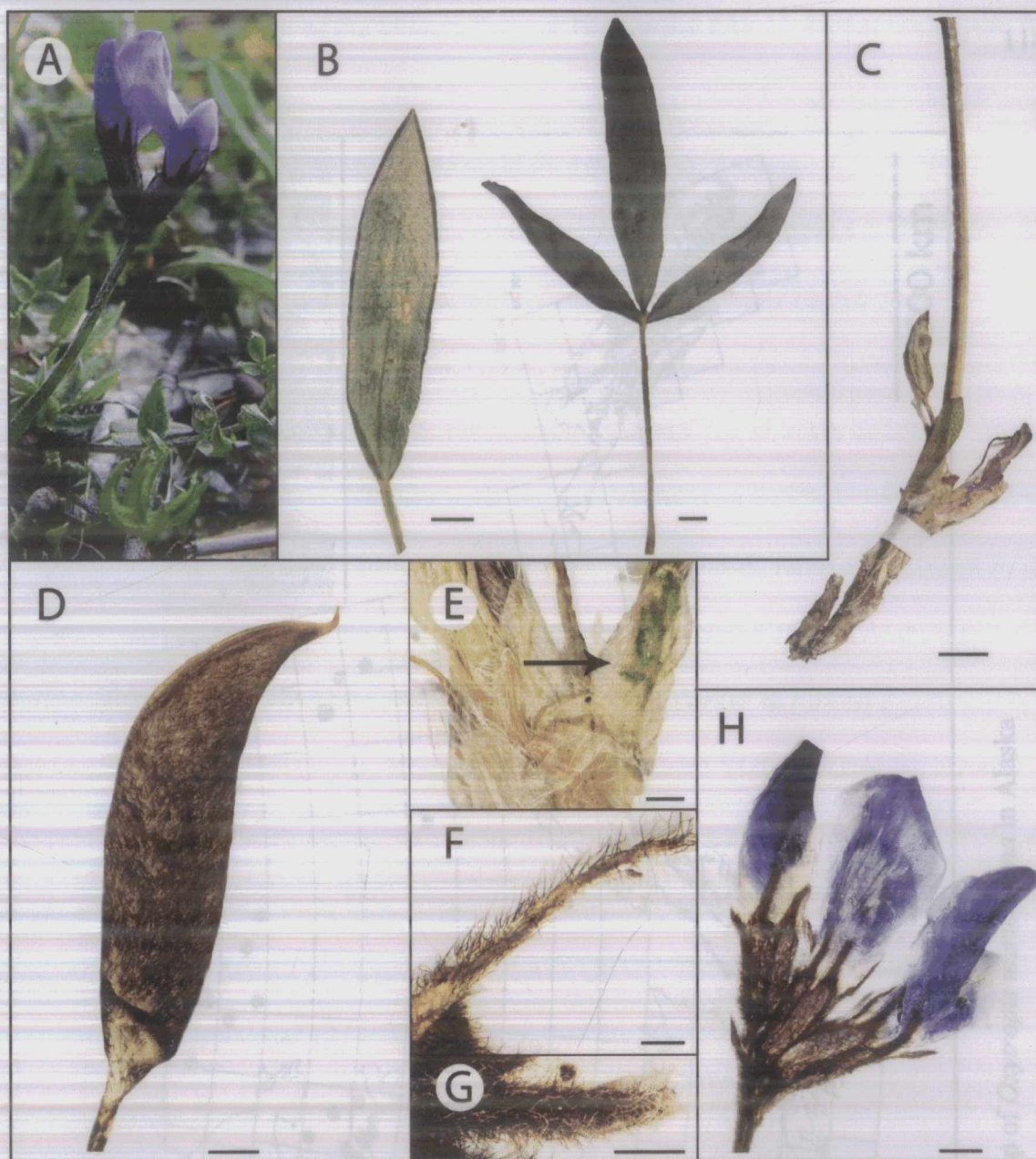
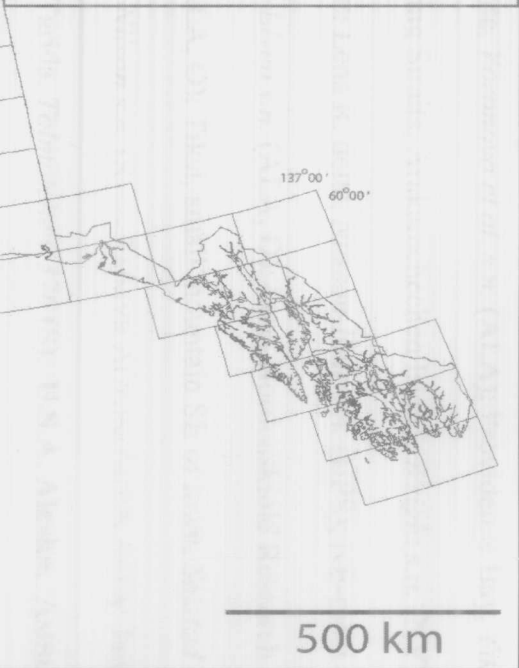
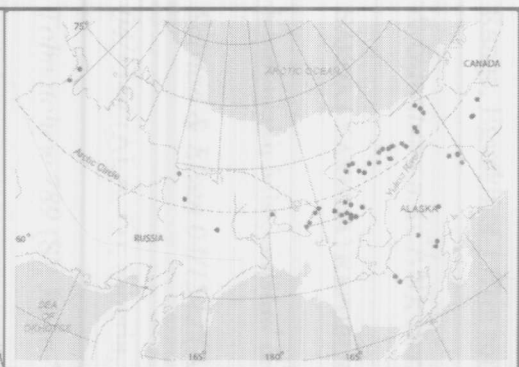


Figure. 2.17. Morphological characteristics of *Oxytropis mertensiana*. A. Erect habit. B. Unifoliate (left) and trifoliate leaf (right) (Parker & Beattie 11792 - left, Murray 6938 - right, ALA). C. Erect scape with decumbent base (Murray 6734, ALA). D. Elliptical legume with recurved beak (Lipkin & Moran 353, ALA). E. Membranous ovate stipule (Parker 289, ALA). F. Linear flower bract (Kildaw s.n., ALA). G. Linear calyx tooth (Kelso & Milheisler s.n., ALA). H. Three-flowered raceme covered with densely villous hairs (Parker & Beattie 11792, ALA). Scale bars B-D, H 2 mm; E-G 1 mm.



Figure. 2.18. Distribution map of *Oxytropis mertensiana* in Alaska



Uelen vic., 2.5 km south of the village, *Sytin & Yurtsev s.n.* (ALA); Upper Ioniveyem R., *Nechaev, Plieva & Yurtsev s.n.* (ALA); Rauchua River, *Yurtzev s.n.* (CAN); Iskaten' Range, Egvekinot-Iul'tin route, *Voronova et al. s.n.* (ALA); Providence Bay, *Tikhomirov & Garriluk s.n.* (CAN); Bering Straits, Arakamchechen Island, *Wright s.n.* (NY).—

SAKHA (YAKUTIA) REPUBLIC: Lena R. delta, *Nilsson-Ehle s.n.* (UPS); NE-most Kharaulakh Mts., *Solstad & Elven s.n.* (ALA, O); Lena-Nordenskiold Research Station, *Solstad & Elven 04/1522* (ALA, O); Tiksi, small mountain SE of town, *Solstad & Elven 04/1544* (ALA, O); Siberia, *Nilson s.n.* (S).—TAIMYR AUTONOMOUS AREA: Jamu-Nery, *Tolmatchew 789* (S); Jamu-Tarida, *Tolmatchew 376* (S). **U.S.A. Alaska.** AMBLER RIVER QUAD.: Schwatka Mts., Igning R. headwaters, *Parker & Solstad 13747* (ALA, O).—

BAIRD MTS. QUAD.: Baird Mts., Salmon R. headwaters, *Parker & Fowell 11320* (ALA).—BENDELEBEN QUAD.: Kougark Rd., mi. 50, *Kelso 83-196* (ALA, S); Seward Peninsula Highlands, Humboldt Cr., *Kelso 87-429* (ALA); Kuzitrin Lake, 5 km S of Lake Charles, *Racine 326* (ALA, US); Nome River valley, *Welsh 5869* (ALA); Etchepuk River valley, *Pegau 247* (BRY).—CHANDALAR LAKE QUAD.: Endicott Mts., Chandler Lake, *Parker, Elven & Solstad 12135* (ALA, O); upper Encampment Cr., 3 km NNE of Inualurak Mt., *Parker & Solstad 13381* (ALA, O); Brooks Range, Mikado Mine Camp, *Klebesadels s.n.* (ALA).—CIRCLE QUAD.: Yukon-Tanana Uplands, S. Fork of Birch Cr. drainage, *Parker, Batten & Herriges 6383* (ALA, O); Eagle Cr. vic. Berry Camp, *Trent 150-65* (ALA); Steese Hwy., 85.5 mi NE of Fairbanks, *Wetherell & Finzel 738* (NY, US); Eagle Summit, *Anderson 2471* (ALA, DOA, S), *Anderson 7569* (PH), *Ickert-Bond 1547* (ALA), *Klebesadel s.n.* (ALA), *Parker 2308* (O), *Scamman 5218, 3568, 4743* (GH);

Carter, 1678 (MO), Eagle Summit area, Porcupine Dome, *Scamman 809* (S), 3586 (CAN), *Viereck 7394* (ALA); Mountain W of Mastodon Dome, *Hultén s.n.* (BRY, S).— CHARLEY RIVER QUAD.: Upper Woodchopper Cr., *Bennett & Larsen 02-034* (DAO).— DEMARCATION POINT QUAD.: Beaufort Lagoon, Nuvagapak Point, *Meyers 80-33* (ALA), *Murray 3508* (ALA), 3172 (ALA, CAN, O); Jago R., *LaFlamme 91* (ALA). *Cantlon & Gillis 57-948* (ALA); Jago R. valley, lake on W side of river, *Murray 6938* (ALA); 3 mi downstream of Okpilak R., *Cantlon & Malcolm 58-0031* (CAN).— EAGLE QUAD.: Yukon-Tanana Uplands, mountains dividing Goodpaster and Charley River drainage, *Larsen, Bennett & Flamme 28157, 02-1977, 02-1993a* (ALA); Glacier Mt., *Welder s.n.* (S).— FORT YUKON QUAD.: Birch Creek District, *Anderson s.n.* (UPS).— GOODNEWS BAY QUAD.: Ahklun Mts., valley between Cone and Twin Mtn., *Parker 15670* (ALA, O); Eagle Bluff, *Lipkin & Moran 353* (ALA).— HAGEMEISTER ISLAND QUAD.: Bristol Bay, Slug Mtn., *Caswell 92-245* (ALA).— HEALY QUAD.: 0.5 mi N of mi 68, Denali Hwy., *Davis 5044A* (BRY).— HOWARD PASS QUAD.: De Long Mts., Feniak Lake, *Holmen & Martensson 61-1241* (UPS), *Young 4581* (ALA); Anisak R. valley vic., *Parker 10798* (ALA); Desperation Lake, *Parker & Meyers 10546* (ALA).— IDITAROD QUAD.: 6 km NE of Camelback Mtn., *Parker 1535* (ALA).— IKPIKPUK RIVER QUAD.: Vicinity of the upper Kurupa River valley, *Hodgdon, Piedaman & Glazier 8275* (GH, S).— LAKE CLARK QUAD.: Neacola Mts., Turquoise Lake, *Caswell 96-384* (ALA); valley between Turquoise Lake, *Caswell & Lipkin 01-118* (ALA).— MT. MCKINLEY QUAD.: Clearwater Cr. drainage near Myrtle Cr., *Duffy MD02-272* (ALA).— MESHEGUK MTN. QUAD.: De Long Mountains, Kagvik Cr. headwaters, *Parker & Beattie 11792* (ALA).— MT. MICHELSON

QUAD.: Lake Peters, *Hultén s.n.* (S), *Martensson 281* (UPS), *Scholander & Flagg S-384* (US); Lake Schrader delta, *Martensson 271* (UPS), *Spetzman 790* (ALA, CAN, US, S), *823* (CAN, S), *Spetzman, Scholander & Flagg S-377* (US); Carnivore Cr. Drainage, *Batten 229, 403, 856* (ALA).—NOME QUAD.: Nome, *Anderson 3756* (ALA, CAN, GB, S), *Hill 57* (US); Glacier Cr., *Zachel s.n.* (ALA); E of Cooper's Gulch, *Sigafoos 3003* (US); Crete Cr., W side Kigluaik Mts., *Kelso & Milheisler s.n.* (ALA); Kigluaik Mts., Grand Singatook, *Elven, Gabrielsen & Jorgesen s.n.* (O); Anvil Mt., *Harris 1316* (BRY), *Solstad & Elven s.n.* (O), *Williams 2679* (ALA); between Snake and Penny R., *Pegau 246* (ALA, BRY); between Hungry Cr. and Penny R., *Elven, Gabrielsen & Jorgesen s.n.* (O); 2 mi. W of Snake R. and 6 mi. W of Nome, *Welsh 5960* (BRY); Mt. Brynteson, *Sigafoos 3550* (S); Teller Rd., mi. 13.8, *Dawe 79-101* (ALA); Teller Rd., headwaters of Arctic and Cleveland Creeks, *Elven, Gabrielsen & Jorgensen 219445* (ALA); mountainridge N of Cripple Cr., *Solstad & Elven s.n.* (O); vicinity of Nome, Anvil Mt., *Kelso 81-412* (CAN), *Thornton 321* (US); Kougarak Rd., mi. 25, *Walker s.n.* (ALA); mi. 255, *Walker 94918* (ALA); Upper Kougarak, *Atwater s.n.* (GH); Dexter Rd., mi. 4, *Heller 874, 921* (ALA), *Thomton 2265* (S); between Nome and Girl Scout Camp, *Welch 19414, 19392, 22104* (NY); Anvil Rd., 25 km from Nome, *Heller 1039* (ALA); Dexter Creek, ca. 10 km NE of Nome, *Heller 1240* (ALA), *Porsild 1372* (CAN).—PHILIP SMITH MTS. QUAD.: Dalton Hwy., Mt. Hultén, *Elven & Grundt s.n.* (ALA, O), *Murray 8541* (ALA); Toolik Lake, *Walker 88-35-B* (ALA), *Khokhryakov, Yurtsev & Murray 6656* (ALA); Dalton Hwy., mi. 242 at Chandalar Camp, *Murray 6734* (ALA, DAO).—POINT HOPE QUAD.: Cape Beaufort, *Hultén s.n.* (S), *Argus & Chunys 5648* (BRY, CAN, DAO,

GH); Cape Lisburne, *Anderson 4541* (ALA).— POINT HOPE QUAD.: Crowbill ridge, *Packer 2175* (DAO).— SOLOMON QUAD.: Cape Nome, *Blaisdell s.n.* (GH, NY, US); hill on S side of Council Rd., *Walker s.n.* (ALA); Council Rd., mi. 40, Solomon R., *Parker 289* (ALA); Kougarak Rd., mi. 44, *Kelso 84215* (ALA); Darby Mts., upper Dry Canyon Cr., *Murray & Lipkin 12357* (ALA, O); VABM Bluff at coast near Koyana Cr., *Kildaw s.n.* (ALA, DAO).— SURVEY PASS QUAD.: NW of Walker Lake, *Jordal 3994* (CAN, US); ridge to E of lake, *Smith 2458* (ALA, NY, S).— TELLER QUAD.: Gold Run Cr., Teller Rd., mi. 55, *Williams 3407* (ALA, BRY); Wales, *Mason 76-142* (ALA); Cape Prince of Wales, *Kelso, Flock & Colson 149* (ALA, NY).— WISEMAN QUAD.: Wiseman, *Jordal 1990* (ALA, S, US); Endicott Mts., *Hardam 21055* (NY); Chimney Mt., *Parker, Elven & Solstad 12596* (ALA, O). **Canada, Yukon.** NTS-117: Richardson Mts., *Cody & Ginns 30415* (ALA, GH), *30542* (DOA).— NTS-116: Tombstone Territorial Park, Angelcomb Mt., *Pojar, Hamilton & Pojar s.n.* (DOA).

7. **Oxytropis podocarpa** A. Gray, Proceedings of the American Academy of Arts 6: 234. 1864. *Spiesia podocarpa* (A. Gray) Kuntze, Revisio Generum Plantarum 1: 207. 1891. *Aragallus podocarpus* (A. Gray) A. Nels., New Manual of Botany 294. 1909.—TYPE: CANADA. Labrador, *Schweinitz s.n.* (lectotype: GH-00064377!).

Oxytropis arctica δ *inflata* Hook, Flora Boreali-Americana 1(3): 146. 1834. *Spiesia inflata* (Hook.) Britton, Memoirs of the Torrey Botanical Club 5: 201. 1894.

Aragallus inflatus (Hook.) A. Nelson, Erythea 7(6): 59. 1899. *Oxytropis inflata*

(Hook.) Steffen, Beihefte zum Botanischen Centralblatt 58: 162. 1938. *Oxytropis*

podocarpa var. *inflata* (Hook.) B. Boivin, Le Naturaliste Canadien 94(1): 78. 1967.

—TYPE: U.S.A. Highest summit of Rocky Mts., *Drummond s.n.* (Isotype: GH-

00064419!). *Oxytropis hallii* Bunge, Mémoires de l'Académie Impériale des

Sciences de Saint Pétersbourg 22(1): 162. 1874. *Spiesia hallii* (Bunge) Kuntze,

Memoirs of the Torrey Botanical Club 5: 201. 1894. *Aragallus hallii* (Bunge) Rydb.,

Bulletin of the Torrey Botanical Club 33(3): 144. 1906.—TYPE: No locality

recorded, *E. Hall & J.P. Harbour 143* (Isotype: GH 00064436!).

Perennial; acaulescent from a branching subterranean caudex, caudex branches elongating from 2 – 6 cm; stipules persistent, pale-green to yellow, partially adnate to petiole, connate at base, 5 – 10 mm long, blades deltoid to lanceolate, free, 1.5 – 6 mm long, ciliated margins with densely black pilose hairs; leaves, alternate, (0.5)1 – 4(6) cm long, the petioles slender densely to sparsely pilose; leaflets (5)7-13, linear to linear-lanceolate, 1 – 10 mm long, 0.5 – 2.5(4) mm broad, pilose dorsally and ventrally; scape

spreading to semi-erect, equaling the leaves, 0.5 – 5 cm, sparingly pilose; raceme loose, 1 – 2(3)-flowered; bracts ovate to lanceolate, opaque, 1 – 4 mm long, black-pilose dorsally and ventrally; calyx campanulate, 6 – 11 mm long, densely black villous, teeth deltoid to lanceolate, 1 – 3 mm long; petals purple, banner obovate, emarginated, 12 – 16(17) mm long; wings 10 – 13 mm long, claw subequal; keel 9 – 11 mm long, claw subequal; legume stipitate, stipe 1 – 3 mm long, body ovoid, black and white hairs sparse, inflated, 10 – 34 mm long, 5 – 17 mm in diameter, acuminate with linear to linear-lanceolate beak; seeds brown, reniform to mitiform, 2 mm long, 2 mm in diameter; seedcoat rugulate reticulate, to lophate. Fig 2.19. Chromosome number: unknown.

Phenology. *Oxytropis podocarpa* flowers in late June.

Distribution (Fig. 2.20). Commonly found along the alpine ridges of the Rocky Mountains in Colorado, Montana, Wyoming and Alberta. *Oxytropis podocarpa* is also disjunctly distributed in the Canadian Arctic along the coasts of Northern Labrador, Southern Baffin Island, and the Hudson Strait. This taxon is commonly associated with *Dryas octopetala*, *Hierochloa* sp., *Carex* sp., and *Saxifraga oppositifolia*. Elevation ranges from 5 to 3850 m.

Additional specimens examined:

U.S.A. COLORADO — CLEAR CREEK COUNTY: E of Loveland Pass, *Beaman & Erbisch 1326* (GH).— COSTILLA COUNTY: Sangre de Cristo, *Brandeger 885* (MO).— GUNNISON COUNTY: 4.5 mi. NE of Gothic on Virginia Peak, *Osborn 2447* (US); head of Cement Cr., *Breedlove 17600* (NY). 1.5 mi NNE of Gothic, *Spongberg 64-69* (GH, US); head of Cement Cr., *Breedlove 19711* (DAO); 5 mi N of Gothic, *Spongberg 65-92* (GH).

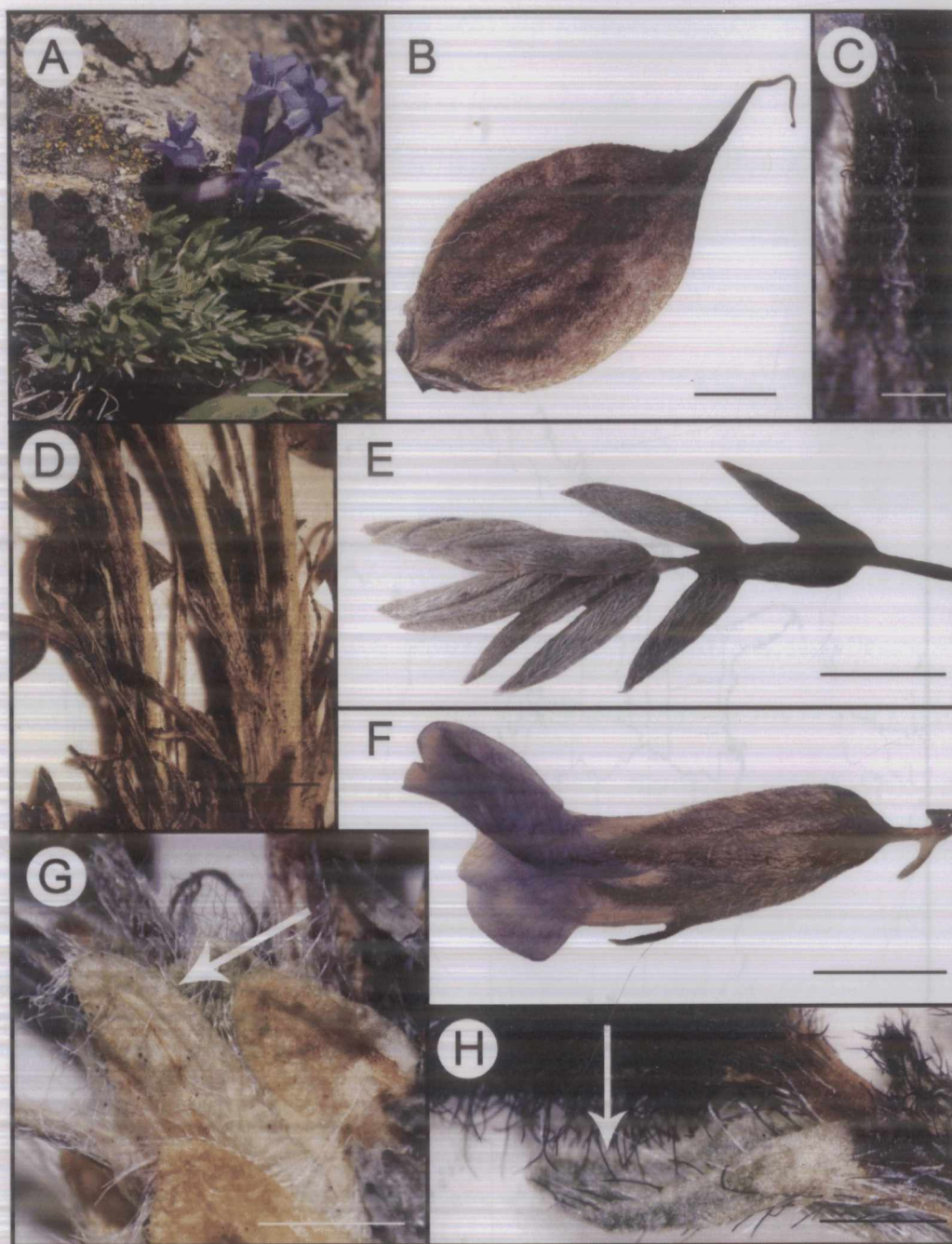


Figure 2.19. Morphological characteristics of *Oxytropis podocarpa*. A. Erect (photo provided by D. Waylett). B. Inflated ovoid legume with acuminated beak (Kirkpatrick 1848, ALA). C. Linear calyx tooth (Hartman 19055, CAN). D. Spreading scape with decumbent base (Spongber 65-92, GH). E. Odd-pinnately compound leaf with four leaflet pairs, leaflets linear to linear-lanceolate (Porsild 23005, CAN). F. One-flowered raceme covered with densely villous hairs (Porsild 18318, CAN). G. Membranous ovate stipule (Spellenberg & Soreng s.n., DAO). H. Linear flower bract (Porsild 21425, CAN). Scale bars B, D, F 2 mm; C, E, G, H 1 mm.

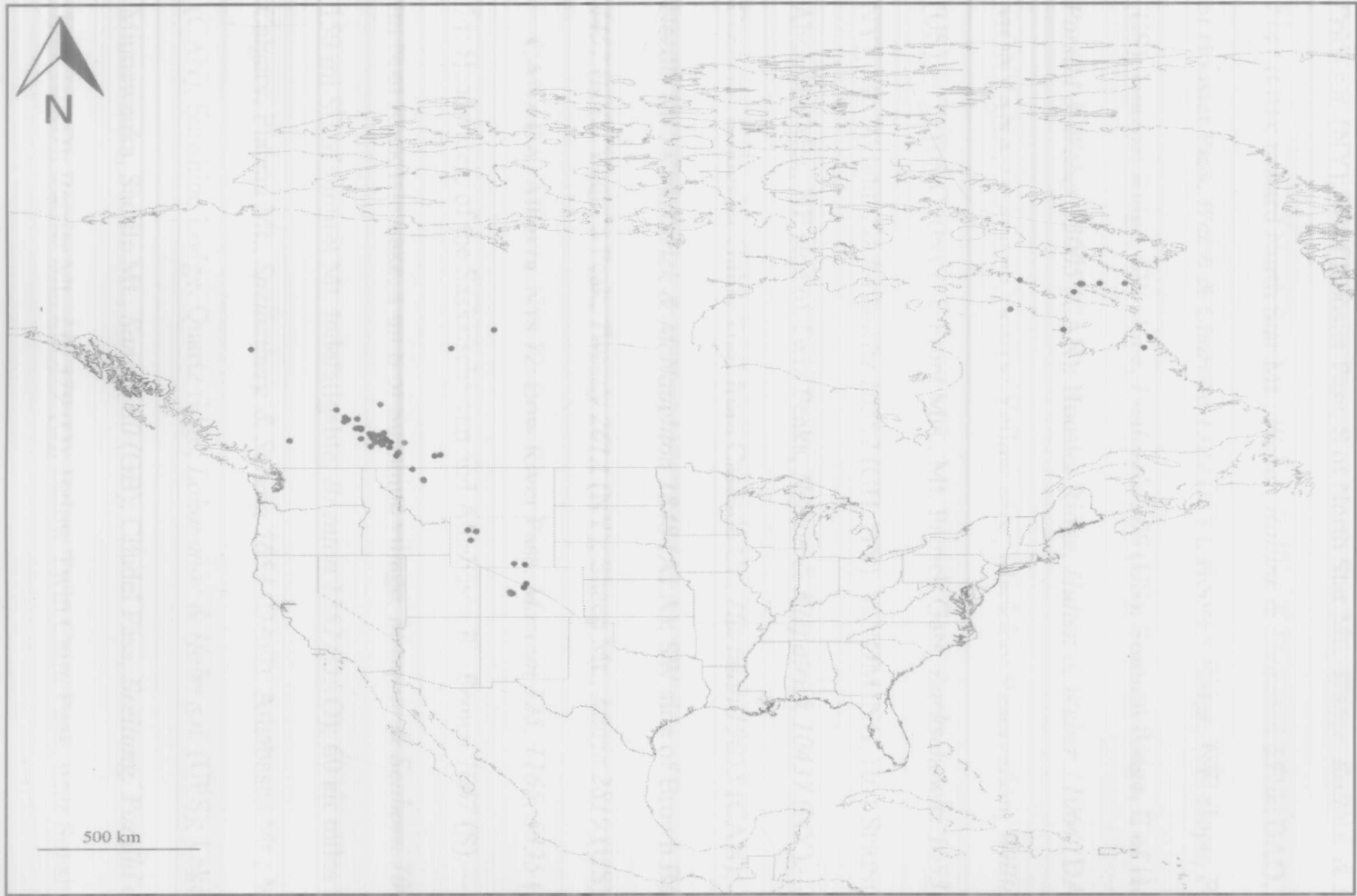


Figure. 2.20. Distribution map of *Oxytropis podocarpa* in North America.

— GUNNISON COUNTY: 0.5 mi NW of Frigid Air Pass, *Seagrist & Bohn 233* (MO); 0.75 mi NW of Frigid Air Pass, *Seagrist & Bohn 354* (MO).— PARK COUNTY: Hoosier Pass, *Price s.n.* (NY); W of Hoosier Pass, S of North Star Mt., *Weber, Rollins, & Livingston 7147* (GH); toward North Star Mt., *Weber, Rollins & Livingston 6510* (DAO, GH); 1.5 E of Hoosier Pass, *Welsh & Charette 1322* (NY); Hoosier Ridge, NW slope, *Penland s.n.* (US); Hoosier Ridge, SW slope, *Penland 1300* (US); Summit Ridge, E of Hoosier Pass, *Porsild & Weber 23005* (CAN); Hoosier Ridge, *Hultén & Weber 11064* (DAO, S).

MONTANA, GLACIER COUNTY: Yellow Mts., Blackfoot Reservation, *Williams 1086* (US).— TETON COUNTY: E Front Mts., Mt. Patrick Gass, *Lackschewitz 10535* (CAN, NY); Mt. Wright, *Lackschewitz 10502* (GH, NY). **WYOMING**, HOT SPRINGS COUNTY: Absaroka Mts., NE side of Twin Peaks, *Nelson & Kikpatrick 10437* (NY).— PARK COUNTY: Smuggler Gulch Trail from Cascade Cr., *Hartman 19055* (CAN); 1 mi SW of Needle Mt., *Kirkpatrick & McNaughton 1848* (ALA); SW side of Brown Basin, *Dorn 4457* (NY); Yount's Peak, *Tweedy 261A* (NY); Sheep Mt., *Murie 2819* (US).

CANADA, Alberta, NTS 72: Bow River Pass, *Macoun 525, 1165, 5335* (CAN).— NTS 74: Headwaters of the Saskatchewan and Athabasca R., *Brown 1067* (S).— NTS 82: 12 mi N of Rock Isle Lake, 1 mi S of Sunshine village, *Masquin & Seaborn 7093* (DAO); 150 mi SE of summit Mt. Indefatigable, *Brunton 1352* (DAO); 60 air miles SSW of Calgary, Plateau Mt., *Spellenberg & Soreng 5654* (DAO); Athabasca Mt., *Moss 4927* (CAN); Sunshine Lodge, Quartz ridge, *Lohammar & Holm s.n.* (UPS); Lake Minnewauka, Saddle Mt., *Sanson 80* (GB); Citadel Pass, *Breitung, Porsild & Bolvin 3369* (DAO); Barrier Mt., *Lid 379* (O); Below Twin Cairn Peak, near Sunshine Ski lodge,

Calder & Holm 24076 (DAO); Elbow R., *Macoun s.n.* (S, US); Fatigue Mt., *Boisin 4917* (DAO); Fatigue Pass, *Scotter 10749* (DAO); Lake Louise station, *Walcott s.n.* (S, US); Mt. Aylmer, *Fletcher 456* (DAO); Mt. Inglismaldie, *Pelluet 205* (CAN); mountain S of Peyto Lake, Bow Summit, on the Banff-Jasper Hwy., *Weber, Rollins & Livingston 2437* (GH, NY); N Fork Old Man's R., *Dawson s.n.* (NY); Pasque Mt., 40 mi N of Coleman, *Mountjoy 33* (DAO); Pipestone Pass, *Macoun s.n.* (NY, US); Plateau Mt., E of Wilkinson Summit on Kananaskis Rd., *Calder 37296* (DAO); ridge above Sunshine Lodge, *Ogilvie s.n.* (DAO); Saddle Mt., *Macoun 742* (O); shoulder of Athabaska Mt., *Moss 4927* (DAO); Slope of Mt. Temple, *Bankam s.n.* (PH); near Laggan, Banff National Park, *Macoun s.n.* (NY); Slope of Mt. Temple Snow Cr., Pass 30 mi N of Banff, *Calder 23956* (DAO); Summit and upper slopes of Baldy Mt., N of Nordegg, *Porsild & Breitung 20574* (CAN); Sunshine Area, *Scotter 10375* (DAO); Twin Cairn Mt., *Scotter 11231* (DAO); Upper Red Deer R., E of Scalp Cr., *Porsild 18318* (CAN); vic. of Sunshine Ski Lodge, S of Healy Cr., *Porsild & Breitung 13200* (ALA), *15932* (CAN); vic. of Banff, *McCalla 2126* (NY, US); Wonder Pass, near Mt. Assiniboine, *Walcott s.n.* (US).—NTS 83: Athabasca Valley, *Lohammar & Holm s.n.* (UPS); Snow Cr. Pass, *Porsild 21425* (CAN); N flank of Mt. Saskatchewan, *Boivin 5111* (DAO); Cardinal Pass, *Kojima s.n.* (DAO); ENE of Saskatchewan Glacier near Sunwapta Pass, *Calder & MacKay 32687* (DAO); Jasper National Park, *Laing 330* (CAN), *Cavell 37187* (DAO); Headwaters of Saskatchewan and Athabasca Rivers, *Brown 1069* (PH); Mt. Clithroe, *Scotter 17099* (DAO); slope near Jasper, *Moss 2719* (GH). **British Columbia**, NTS 82: Citadel Peak, *Lid & Porsild 652* (O); Goat Mt., *Taylor & Ferguson 3023* (DAO); Kicking Horse lake, *Macoun s.n.* (CAN,

GH, NY, UPS, US); Kootenay National Park, Floe Lake-Numa Pass, *Seel 159* (DAO); Mt. Paget, *Macoun s.n.* (NY, US); Nub Mt., *Taylor & Ferguson 3797* (DAO); Simpson Pass area, slopes of Twin Cairn, *Holm 632a, b* (UPS); Sunburst Lake Camp, Mt. Assiniboine, *Scamman 6668* (GH); Sunshine Ski Lodge, 12 mi SW of Banff, *Breitung, Porsild, & Bolvin* (DAO); W slope of Tornado Mt., *Taylor & Ferguson 3151* (DAO).— NTS 92: Mt. Bowman, 15 mi NW of Clinton, *Calder, Parmelee, & Taylor 17702* (NY).

Newfoundland and Labrador, NTS 14: Kangalaksiorvik Bay, *Bryant s.n.* (GH).

Northwest Territories, NTS 75: S of Brazean Lake, *Brown 1067* (NY, MO). **Nunavut**, NTS 25: Baffin Island, Frobisher Bay, *Sewall 260* (GH, S), *Hedberg 3115* (UPS), *Senn 3542* (DAO, S), *Senn 3657* (DAO), *Senn & Calder 3689, 3815, 3864* (DAO), *Senn & Calder 3737* (DAO, US), *Senn & Calder 3946* (ALA, DAO, GH, S), *Senn & Calder 3955* (DAO, UPS), *Hultén s.n.* (S), *Aiken, Campbell, & Robinson 86-466* (CAN), *Cody 3955* (MO), *Hainault & Norman 5409* (CAN, DAO, O), vic. of airport, *Wynee-Edwards 9205* (CAN), Sylvia Grinnell R., *Collins 46* (US), Summit of Apex Hill, 5 km E of Iqaluit, *Brunton & McIntosh 9889* (CAN).— NTS 35: Baffin Island, Amadjuak Bay, *Soper 912* (CAN, GH, NY, S). **Quebec**, NTS 25: Baie Kayak, *Rousseau 1466* (GH, S, US). — NTS 35: Raglan Lake, *Brown 1067* (S). **Saskatchewan**, NTS 74: vic. of Summit Pass, *Raup & Correll 10463, 10685* (GH).

8. **Oxytropis scammaniana** Hultén, Ark. Bot., 33B: 4, fig. 2, 3 (map). 1947.—TYPE:
U. S. A. Alaska: Eagle Summit, near Steese Highway, 109 miles north of

Fairbanks, *Scamman 806* (holotype: S-8878! isotype: GH-00064381!).

Perennial; acaulescent from a branching subterranean caudex, caudex branches elongating from 3 – 8.5 cm; stipules persistent, pale-green with purple margins near the apex, partially adnate to petiole, connate at base, 6 – 13 mm long, blade ovate to lanceolate, free, 1 – 6 mm long, prominently 1-nerved, glabrous to subglabrous dorsally, sparsely black and white bristly-ciliate ventrally; leaves, alternate, 1.5 – 8 cm long, the persistent slender petioles subglabrous; leaflets 9 – 13 (19), narrowly ovate to lanceolate, 2.5 – 10 mm long, 1 – 3 mm broad, pilose dorsally and ventrally, ciliate along the inrolled margin; scape erect, surpassing the leaves, 1.5 – 7 cm, villous-appressed to pilose; raceme loose, 2 – 3-flowered; bracts linear, opaque, 2 – 6 mm long, black-pilose dorsally and ventrally; calyx campanulate, 5 – 10 mm long, densely black villous, teeth linear, 1.5 – 4 mm long; petals purple; banner obovate, emarginated, 10 – 14 mm long; wings 9 – 11.5 mm long, claw subequal; keel 6 – 10 mm long, claw subequal; legume sessile, body ovoid-oblong to elliptical, 11 – 17.5 mm long, 4-6.5 mm in diameter, short acuminate recurved beak; seeds brown, reniform to mitiform, 1 – 2 mm long, 1 – 2 mm wide; seedcoat rugulate to rugulate reticulate. Fig 2.21. Chromosome number: $2n = 16, 32$ (Dawe & Murray 1981).

Phenology. *Oxytropis scammaniana* flowers in mid-late June.

Distribution (Fig. 2.22). Found primarily in the major mountain ranges of Alaska and adjacent Yukon Territory, which includes the Brooks Range, the Alaska Range, the

Wrangell Mts., the Ray Mts., and the White Mts. *Oxytropis scammaniana* is found on alpine scree slopes and tundra benches, commonly in alpine and heath community assemblages including *Dryas octopetala*, *Vaccinium vitis-idaea*, and *Ledum palustre* var. *decumbens*; 550 m to 1500 m.

ADDITIONAL SPECIMENS EXAMINED.

U.S.A. Alaska. CIRCLE QUAD.: Eagle Summit, *Anderson* 7569 (ALA, GH, S), *Anderson & Brown* 10220 (ALA), *Batten & Batten* 74-52 (ALA), *Chauvin* 36 (ALA), *Gjaerevoll* 921, 1141 (S), *Leon* 52 (ALA), *LePage* 23308 (DAO), *Klebesadel s.n.* (ALA), *Scamman s.n.* (ALA), *Scamman* 806 (S), *Viereck* 7359 (ALA, S); Steese Hwy., mi. 104, *Young s.n.* (ALA); Steese Hwy., mi. 105, *Spetzman* 805 (NA); Steese Hwy., mi. 107, *Cross s.n.* (ALA, DAO); Steese Hwy., mi. 112, *Welsh & Moore* 8510, 8539 (ALA); near Steese Hwy., 109 mi N of Fairbanks, *Scamman* 299, 5217, 4744 (GH), *Scamman* 3571-B, 3767, 2115, 5256 (S), *Scamman* 2112 (ALA), *Cody & Webster* 5311 (DAO); White Mts., Lion Peak, *Gjaerevoll* 232 (S); Hope Cr. headwaters, 10 km N of Steese Hwy., *Halliday A-372-75* (ALA); Twelvemile Summit, *Anderson* 2406 (S), *Elliott s.n.* (ALA), *Harms* 2741 (ALA, GH), 2750 (ALA), *Kessel s.n.* (ALA), *Klebesadel s.n.* (ALA), *Parker & Murray* 2143 (DAO), *Sparrow* 85-19, 85-18 (ALA); Eagle Cr. area, Steese Hwy., mi. 105, *Trent* 16 (ALA, GH), *Densmore* 2188 (ALA); Sourdough Cr., 70 miles NE of Fairbanks, *Smith* 2003 (ALA, NY); NE of Fairbanks, Steese Hwy. mi 88, *Hultén s.n.* (S); Sourdough Cr., 6 mi N of the Steese Hwy., *Smith* 1953 (ALA, NY); Harrison Cr., 10 km S of Miller House, *Smith* 1773 (ALA, NY, S), *Scamman* 413 (GH), 2 km SW of Lime Peak, *Parker & Batten* 4790 (ALA); 3 km S of Lime Peak, *Parker, Batten & Moran* 5502 (ALA); 6

km S of Lime Peak, *Parker & Batten 4859* (ALA); Mastodon Dome, 12 miles SW of Miller House, *Scamman 4848* (GH); Mt. W of Mastodon Dome, *Hultén s.n.* (S); Porcupine Dome, *Ickert-Bond 1548* (ALA); 12 mi from Miller House, *Scamman 807* (GH); Ridge above Miller Cr., *Scamman 6235* (GH); S Fork of Birch Cr. drainage, *Parker, Batten & Herriges 6382* (ALA).—CHANDLER LAKE QUAD.: Endicott Mts., Chandler Lake, *Parker, Elven & Solstad 12174* (ALA, O), *Parker, Bennett & Guldager 12351* (ALA); Shainin Lake, *Bennett & Elven 02-342* (DAO); upper Encampment Cr., 3 km NNE of Inualurak Mt., *Parker & Solstad 13348, 13283* (ALA).—CHANDALAR QUAD.: St. Mary's Pass, 10 mi E of Chandalar Lake, *Klebesadel s.n.* (ALA); Bettles River, 20 miles NE of Wiseman, *Jordal 2276-B* (S).—CHARLEY RIVER QUAD.: Ogilvie Mts., Mt. Casca vic., *Parker & Hasselbach 6273* (ALA); Alder Cr., Yukon Fork of S Fork Birch Cr., *Larsen & Bennett 02-20380* (ALA).—EAGLE QUAD.: Mt. Fairplay, Fortymile Hwy., *Anderson 10819* (ALA, S); Copper Hills, 1.5 km S of VABM Copper, *Larsen 02-2094* (ALA); 6.6 km SW of Mt. Sorenson, *Larsen, Roland & Batten 02-1435* (ALA); Upper Charley R., 20 km E of VABM, *Cook & Roland 02-427* (ALA); Mts. dividing Goodpaster and Charley R., *Larsen, Bennett & Flamme 02-1891* (ALA).

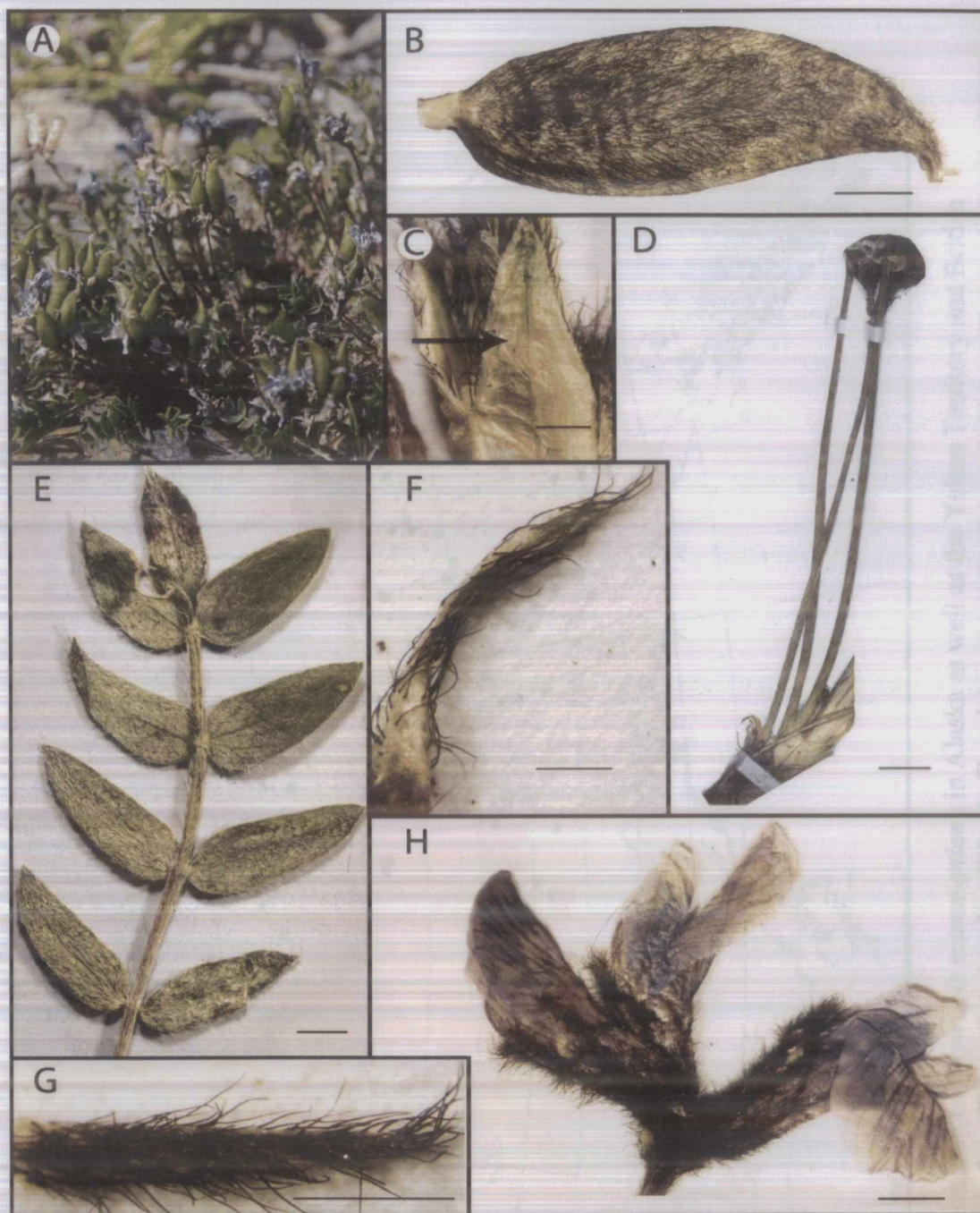


Figure 2.21. Morphological characteristics of *Oxytropis scammaniana*. A. Erect habit (photo provided by S. Ickert-Bond). B. Elliptical legume with recurved beak (Smith, Purdy & Chengalath 563129, CAN). C. Opaque deltoid to ovate stipule (Parker, Elven & Solstad 2416, O). D. Erect scape arising from a decumbent base (Cody & Webster 5960, DAO). E. Odd-pinnately compound leaf with four leaflet pairs, leaflets narrowly ovate to lanceolate (Hultén s.n., ALA). F. Linear flower bract with black villous hairs (Viereck 5043, ALA). G. Linear calyx tooth (Wethesell & Finzel 747, NY). H. Three-flowered raceme covered with black villous hairs (Hultén s.n., ALA). Scale bars C, F, G 1 mm; A, D, E, H, 3 mm.

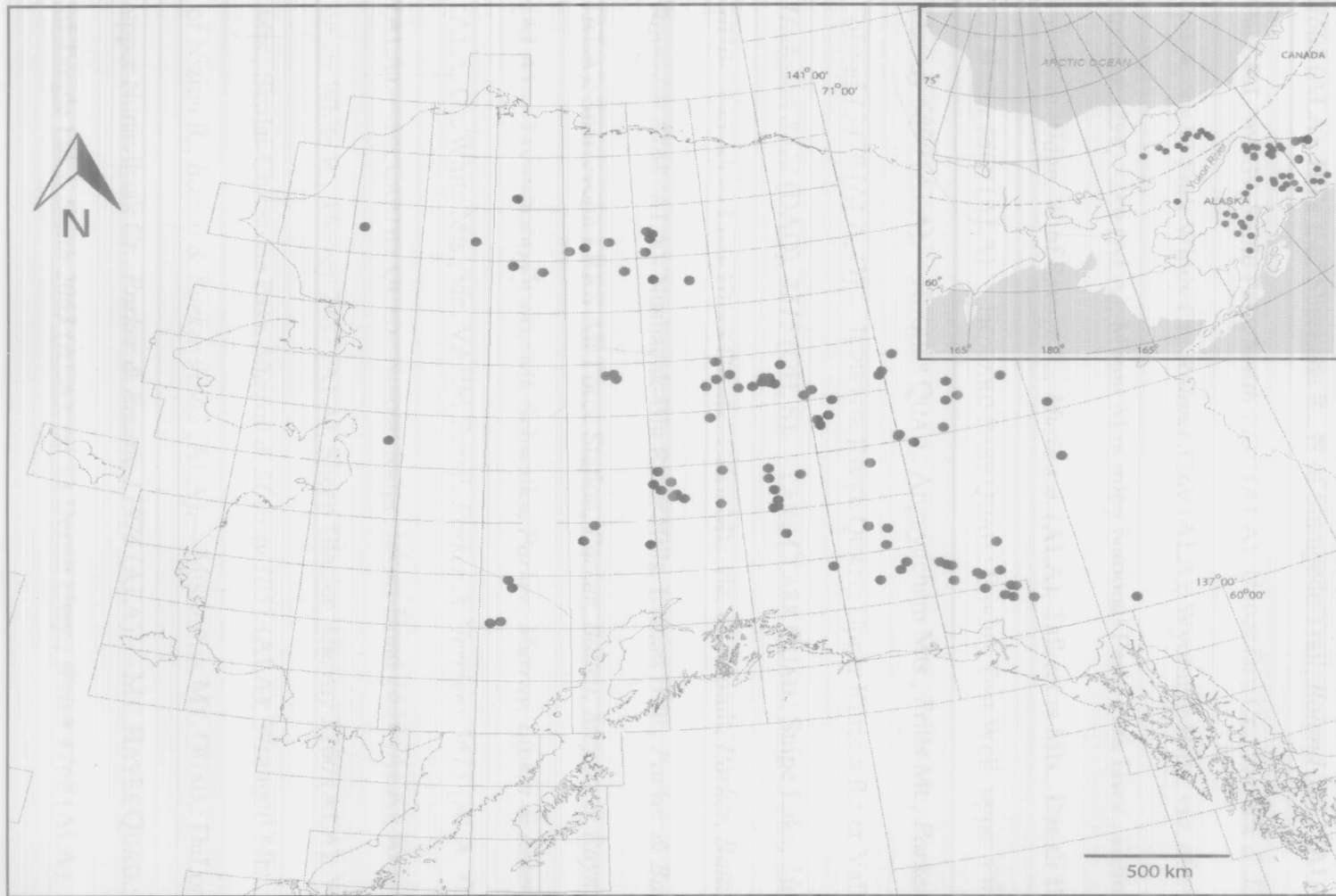


Figure. 2.22. Distribution map of *Oxytropis scammaniana* in Alaska as well as the Yukon Territory and British Columbia (see insert map for additional eastern localities in Canada).

— FAIRBANKS QUAD.: UAF Campus, *Gasser s.n.* (ALA).— HEALY QUAD.: Cantwell, *Palmer 1951* (ALA); N of Foggy Pass above E fork Cantwell Cr., *Roland & Carwile 4605* (ALA); Hills E of Shushana R., N of Stampede Trail, *Roland 3052* (ALA); Denali Park Rd., mi. 39, Sable Pass, *Smith 2259* (ALA); Upper Dry Cr., *Viereck & Jones 6071* (ALA, S); W Fork Windy Cr., *Roland 3269* (ALA); Wyoming Hills, vic. of peak 5840, *Roland 3294, 3286* (ALA); Mount McKinley National Park, Park Hwy., *Hultén s.n.* (S); Primrose Ridge, W of Savage R., *Murie s.n.* (ALA); Talkeetna Mts., Denali Hwy., mi. 87, *Welsh 4800* (ALA).— HOWARD PASS QUAD.: Etivluk Test Well, upper Etivluk R., *Murray 6890* (ALA).— HUGHES QUAD.: Angayucham Mts., Fritts Mt., *Parker, Elven & Solstad 13470* (ALA, O).— IKPIKPUK RIVER QUAD.: Upper Kurupa River Valley, *Hodgdon 8412* (DAO), *8515* (GH, S).— LAKE CLARK QUAD.: Snipe Lake, *Meyers ZJM 2010-2* (ALA).— LIME HILLS QUAD.: Cairn Mt., vic. of summit, *Parker, Batten & Raynolds 8768* (ALA); Nushagak-Big River Hills, Lyman Hills, *Parker & Batten 8948* (ALA); Sparrevohn LRRS Air Force Station, *Parker, Batten, Meyers & Raynolds 8525* (ALA).— LIVENGOOD QUAD.: Mt. Schwatka, *Parker, Murray, Lipkin & Emers 5021* (ALA, O); White Mts., vic. VABM Fossil, *Parker & Herriges 5615* (ALA, DAO), *4908* (ALA).— MCCARTHY QUAD.: Nikolai Ridge, Ickert-Bond *1639* (ALA); Russell Glacier, upper White R., *Murray 2187* (ALA); Sheep Glacier, *Murray 2260* (ALA); Wrangell Mts., Skolai-Chitistone Pass, *Murray & Murray 1051* (ALA); Wrangell Mts., plateau W of Nizina R., *Batten & Barker 96-62* (ALA).— MISHEGUK MT. QUAD.: DeLong Mts., upper Nunaviksak Cr., *Parker & Beattie 11976* (ALA).— MT. HAYES QUAD.: 8 km ENE of Tangle Lake, *Smith 2063* (ALA); mi 13 Denali Hwy., *Welsh 4768* (ALA), *Harms 4190*

(ALA); between Castner and Fel Glaciers, *Shaughnessy 72-117* (ALA); Bear Cr., mi 233 Richardson Hwy., *Batten, Dawe & Murray 78-55* (ALA); Denali Hwy., 12.6 miles W of Paxon, *Welsh 4768* (NY); Horn Mt., *Spetzman 179-A* (ALA, S); Castner Glacier, *Cody & Webster 4960* (DAO); Richardson Hwy. mi 207, *Anderson & Brown 10202* (ALA); Rapids Lodge, Richardson Hwy. mi 233. *Anderson 2244* (ALA).—NABESNA QUAD.: Mentasta Mts., vic. Nabesna R., *Moran 61-A* (ALA); Stuver Cr., *Bennett & Loomis 03-325* (DAO); Wrangell Mts., Euchre Mt. near Chisana, *Bennett & Loomis 03-848* (ALA).—NORTON BAY QUAD.: Nulato Hills, N Fork Unalakleet R., *Parker, Batten & Lipkin 8065* (ALA).—PHILIP SMITH MTS. QUAD.: Toolik Lake, *Meyers PopNI* (ALA); Atigun Syncline GLORIA summit, *Batten 08-79* (ALA); 5 m N of Chandalar Camp & ca 2 mi S of Atigun Pass, *Welsh & Ostler 1146* (NY, ALA); Endicott Mts., mi 275 Dalton Hwy., *Murray & Johnson 6054* (ALA); mi 271 Dalton Hwy., Mt. Hultén, *Lipkin 80-81* (ALA).—SURVEY PASS QUAD.: Alatna R., Headwaters Lake, *Murray 4082, 3879* (ALA); 5 km S of Folly Lake, *Staender & Staender 31* (ALA).—TALKEETNA QUAD.: upper valley of the Swift Fork of the Kuskokwim River, *Viereck 5043* (S), 8 km N of Heart Mt., *Roland 4404* (ALA); Tonzona R., *Viereck 5043* (ALA); Park Hwy., mi 61, *Hultéen s.n.* (S).—TANACROSS QUAD.: Mt. Fairplay, 30 miles N of the Alaska Hwy., *Smith 2430-A* (ALA, NY); mi 34 Taylor Hwy., *Calder & Gillett 26431* (DOA, NY), *Smith & Viereck 2381* (ALA).—TANANA QUAD.: Ray Mts., Kilo Hot Springs, *Dawe 79-177* (ALA); NW of Kanuti Kilolitna R., *Kassler 90* (ALA); Spooky Valley and Mt. Eakin, *Juday s.n.* (ALA).—VALDEZ QUAD.: Wrangell Mts., Cheshnina Plateau, *Cook & Baker 4735* (ALA).—WISEMAN QUAD.: Endicott Mts., Chimney Mt., *Parker, Elven & Solstad 12616*

(ALA). **Canada, British Columbia.** NTS-82: McArthur/Ethel Lake area, site 312, *Kennedy 422* (DAO).—NTS-93: 16 mi SW of Chapman Lake, *Cody & Ginns 33432* (DAO); W of Dempster Hwy km 93, *Friisch 128* (DAO). **Yukon.** NTS-105: Mt. Caribou, 5 mi N of Carcross, *Gillett & Mitchell 4574* (DAO).—NTS-106: S Wernecke Mts., above Sorrel Pass, *Friisch 126* (DAO); N of Mayo, *Thomlinson 6* (DAO); Snake drainage, *Schroeder, Loewen & Mickle SPE-LDS-203* (DAO).—NTS-115: Asi Keyi SMA, Brooke Cr., *Bennett, Caswell & Mueller 04-0944* (DAO); Asi Keyi, Wolverine Plateau, *Rosie 2258* (DAO); Kluane National Park, Duke R., *Asquith, Majinski & Morgan 12* (DAO); Hogue Pass, *Saniforth 97-48* (DAO); Mt. Hart, *Cody & Ginns 33837* (DAO); Mt. Maxwell, *Scotter 21150* (DAO); 60-mile Hwy., AK Border, *Friisch 125* (DAO); Sheep Mt., SW plateau, near Kluane Lake, *Krajina. & Hoefs* (DAO); St. Elias Range, *Scotter 20792, 20870* (DAO), near Klutlan Glacier, *Scotter 20959* (DAO); Amphitheatre Mt., 16 mi. SW Burwash Landing, *Pearson 203* (DAO); Kluane Lake, E of the mouth of Slim's R., *Raup & Raup 12527* (ALA, GH); Observation Mt., Kaskawulsh Glacier, *Murray & Murray 646* (ALA); vic. of Rusty Glacier, *Murray 1331* (ALA).—NTS-116: Oglivie Mts., Mt. Abraham, Dempster Hwy. 130 km, *Solstad & Elven 03/0310* (O), VABM station, *Cook & Bennett 02-250* (ALA); Cloudy Range, W of headwaters of Canadian R., *Cody & Ginns 33514* (ALA, DAO); S of Klondike Loop Hwy., near Alaska border, *Cody & Ginns 33788* (DOA, GH, NY); Head of Kandik R., *Hughes* (DAO); N and E of Hart R., *Cody & Ginns 34507-A* (DAO); Near junction of Kaskawulsh, Dezadeash and Aisek rivers, *Pearson 67-120* (DAO).

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APPENDIX 2.1. Voucher information including collection locality, collector and collection number, herbarium, and GenBank accession numbers (*TRPT*, *CNGC5*, *matK*, *LE*) for specimens used in this study. Letters in parentheses refer to multiple accessions (i.e., different specimens) used in the molecular analysis. “—” indicates no sequence for the DNA region and * represents the GenBank accession for a duplicate taxon that was sampled in the phylogenetic analysis.

OUTGROUP *Alhagi maurorum* Medik.; EU258906, —, AY386880, —; *Astragalus canadensis* L.; EU258910, —, AY386875, —; *Astragalus nothoxys* Gray; HQ730403, —, AY386877, —; *Astragalus americanus* (Hook.) M.E. Jones; HQ730405, —, AY386876, —; *Caragana arborescens* Lam.; EU258905, —, AF142737, —; *Cicer pinnatifidum* Jarb. & Spach; EU258922, —, AF522081, —; *Colutea arborescens* L.; EU258912, —, AY386874, —; *Galega orientalis* Lam.; EU258923, —, AF522083, —; *Glycyrrhiza lepidota* Nutt.; EU258904, —, AY386883, —; *Lotus purshianus* (Benth.) Clem. & E.G. Clem.; EU258901, —, AF142729, —; *Medicago crassipes* (Boiss.) E. Small; —, DQ662657, —, —; *Medicago fisheriana* (Ser.) Trautv.; —, DQ662656, —, HM159562—; *Medicago monspeliaca* (L.) Trautv.; —, DQ662658, —, —; *Medicago sativa* L.; EU258921, DQ662602, AY386881, HM211141; *Olneya tesota* Gray; EU258903, —, AF543857, —; *Robinia neomexicana* A. Gray; EU258902, —, AF543856, —; *Sesbania vesicaria* (Jacq.) Elliott; EU258899, —, HQ730417, —; *Sutherlandia frutescens* (L.) R. Br.; EU258914, —, AY386913, —; *Swainsona pterostylis* Bakh. f.; EU258915, —, AF142735, —; *Trigonella foenum-graecum* L.; HQ730413, DQ662659, HM211164, —; *Trigonella mesopotomica* Hub.-Mor.; —, DQ662660, —, —; *Trigonella spruneriana* Boiss.; —, DQ662666, —, HM211170—; *Vicia faba* L.; EU258919, —, AY386899, —;

INGROUP Sect. *Arctobia*, ***Oxytropis arctobia*** Bunge (1) — CANADA: Thompson River, *Aiken s.n.* (CAN); (2) Cambridge Bay, *Edlund & Argus s.n.* (CAN); (3) Paulatuk, NWT, *Gillespie et al. 8662* (CAN); (4) Tuktot Nogait National Park, *Gillespie et al. 8662* (CAN); (5) Lower Brock River *Gillespie et al. 9389* (CAN); ***Oxytropis bryophila*** (Greene) Jurtzev. (1) — CANADA: Whitehorse, *Bennett 07-300* (ALA); (2) U.S.A. Alaska: Twelvemile Summit, *Ickert-Bond 1526* (ALA); (3) Afognak Island, *Parker 17406* (ALA); (4) Pickeral Lake, *Meyers 2010-01* (ALA); (5) Seward Peninsula, *Ickert-Bond 1719* (ALA); (6) Toolik Lake, *Meyers 2009-01* (ALA); (7) Lake Clark National Park, Snipe Lake, *Meyers 2010_02* (ALA); (8) — RUSSIA: Chukotka: Anadyr Bay, *Parker 5743* (ALA); ***Oxytropis gorodkovii*** Jurtzev (1) — U.S.A. Alaska: Seward Peninsula; Darby Mts., *Murray & Lipkin 12262* (ALA); (2) Noatak; Kakagrak Hills, *Parker et al. 10235* (ALA); (3) Seward Peninsula, *Ickert-Bond 1704* (ALA); ***Oxytropis huddelsonii*** A.E. Porsild (1) — U.S.A. Alaska: Wrangell St. Elias N.P., Nicolai Ridge, *Ickert-Bond 1641* (ALA); (2) Denali National Park, *Joseph P JP-09-100* (ALA); ***Oxytropis kokrinensis*** A.E. Porsild (1) — U.S.A. Alaska: Kobuk Valley National Park, *ABR T42-01* (ALA); (2) Kobuk Valley National Park, *ABR T84-01* (ALA); (3) Kobuk Valley National Park, Jade Mts., *Meyers 6-7* (ALA); (4) *Meyers 2-5* (ALA); (5) *Meyers 1-9* (ALA); ***Oxytropis nigrescens*** (Pall.) Fisch. ex DC. — RUSSIA: Lena River estuary, *Solstad & Elven 04/0983* (ALA); ***Oxytropis nigrescens*** (Pall.) Fisch. Ex DC. *var.* ***lonchopoda*** Barneby (1) — CANADA: Ogilvie Mts., *Cody & Ginns 32992* (ALA); (2) Ogilvie Mts., *Cody & Ginns 34143* (ALA); ***Oxytropis mertensiana*** Turcz. U.S.A., Alaska, Eagle Summit, *Ickert-Bond 1547* (ALA); ***Oxytropis podocarpa*** A. Gray (1) —

U.S.A. Colorado: Silver Hills, *Hilpman s.n.* (ALA); (2) Absaroka Mts., *Kirkpatrick & McNaughton 1848* (ALA); *Oxytropis revoluta* Ledeb. (1) — RUSSIA: Kurile Islands, *s.n.* (ALA); (2) Kamchatka; Munovsky Volcano, *Eriksen & Tupel 1722* (ALA);

Oxytropis scammaniana Hultén (1) — U.S.A., Alaska: Wrangell St. Elias National Park, Nicolai Ridge, *Ickert-Bond 1639* (ALA); (2) Porcupine Dome, Eagle Summit, *Ickert-Bond 1548* (ALA); (3) Toolik Lake, *Meyers 2009_P1/1*, (ALA); **Sect. *Baicalia*** Bunge.

Oxytropis splendens Douglas — CANADA: Yukon, *Bennett 07-308* (ALA); **Sect. *Glaeocephala*** Bunge, *Oxytropis borealis* DC. **var. *viscida*** (Nutt.) S.L. Welsh

*HQ730407, —, EU025909, —; (2) USA: Alaska: Atigun Pass, *Ickert-Bond 1508* (ALA); **Sect. *Mesogaeae*** Bunge, *Oxytropis deflexa* (Pall.) DC. **var. *sericea***; *EU258911, —, AY38878, —; (1) CANADA: Hotsprings Rd., *Bennett 07-255* (ALA) *Oxytropis pilosa* (L.) DC.; HQ730408.1, —, AY920452.1, —; **Sect. *Orobia*** Bunge, *Oxytropis arctica* R. Br. **var. *barnebyana*** S.L. Welsh — USA: Alaska: Seward Peninsula, *Ickert-Bond 1710* (ALA); *Oxytropis campestris* (L.) DC. — CANADA: Yukon, *Bennett 07-253* (ALA); *Oxytropis campestris* (L.) DC.; **var. *jordalli*** (A.E. Porsild) S.L. Welsh — CANADA: Yukon, *Bennett 07-81* (ALA); *Oxytropis campestris* (L.) DC. **var. *roaldii*** (Ostenf.) S.L. Welsh — CANADA: Yukon, *Bennett 07-81* (ALA); *Oxytropis campestris* (L.) DC. **ssp. *sordida*** C. Hartm. — NORWAY: Finnmark, vic Vadso, *Parker et al. s.n.* (ALA); *Oxytropis lambertii* Pursh; EU258913.1, —, AY386915, —; *Oxytropis maydelliana* Trautv. — USA: Alaska: Eagle Summit, *Ickert-Bond 1549* (ALA);

Oxytropis parryi A. Gray; HQ730406.1, —, HQ293020.1, —; **Sect. *Xerobia*** Bunge, *Oxytropis anertii* Nakai; —, —, HM142266.1, —;

CONCLUSION

The present-day Arctic flora is of recent origin (i.e., 2-3 million years), with an estimated 2218 species of which 5% are endemic to the region (Murray 1995; Brochmann & Brysting 2008; Elven 2011). The ebb and flow of massive ice sheets, along with fluctuating ice-free regions (i.e., refugia) facilitated the dynamic distribution of the Arctic flora. As a result of the glacial ice sheets, sea levels plummeted forming the Bering Land Bridge, which acted as a barrier, filter, and vector for much of the Arctic flora. (Hultén 1958; Abbott et al. 2000; Abbott and Brochmann 2003; Eidesen et al. 2007; Ickert-Bond et al. 2009). This in turn has created complex post-glacial dynamics across much of the arctic landscape creating numerous cryptic, enigmatic Arctic taxa.

The use of molecular phylogenetics and divergence time estimations, along with findings of fossil pollen as well as macrofossils has enhanced our knowledge of community assemblages and species distributions in the Arctic during the Pleistocene (Short and Nichols 1977; Anderson et al. 1994; Koch et al. 2006; Abbott and Comes 2004; Sheen et al. 2004). A molecular clock approach by Tkach et al. (2008) revealed several Arctic lineages of *Artemisia* to be considerably older in origin than previously assumed, however evidence of younger dispersal events were also documented. Many Arctic genera demonstrate this pattern of evolution due to high levels of extinction caused by glacial and interglacial cycles (Hoffmann and Roser 2009). Low levels of genetic differentiation which have been documented in *Cassiope tetragona* (Eidesen et al. 2007) and *Rubus chamaemorus* (Ehrich et al. 2008), as well as high morphological variability are often indicative of a more recent origin. Many Arctic taxa demonstrate

these characteristics, most notably the genus *Oxytropis*.

In Chapter 1 we investigated seed coat micromorphology of *Oxytropis* section *Arctobia* in order to assess its taxonomic utility. Other studies have previously shown that seed coat micromorphology is of taxonomic utility in delineating species within the Brassicaceae (Murley 1951), Scrophulariaceae (Chuang and Heckard 1972) and Orchidaceae (Molvray and Kores 1995) as well as within Fabaceae, although sampling in Fabaceae was largely restricted to few samples per genus (Lersten 1981; Pandey and Jha 1988). We show that of the 22 species of *Oxytropis* examined, only *O. deflexa* significantly differed in the size and shape of the seed, having small globose seeds as compared to the other Alaskan taxa with larger, reniform seeds. Three main seeds coat patterns were observed (i.e., rugulate, lophate, and foveolate), although high levels of infraspecific variation between the patterns provided no taxonomic resolution between species.

In Chapter 2 we used four genetic markers (i.e., TRPT, CNGC5, LE, and matK) that have been previously used to infer phylogenetic relationships at various taxonomic levels within Fabaceae (Wojciechowski et al. 2004; Howard et al. 2007; Maureira-Butler et al. 2008; Steele et al. 2010). The molecular data supports the monophyly of the genus *Oxytropis* from its closely related sister genus *Astragalus*. We found moderate support for a distinct *O. arctobia* lineage from the Canadian Archipelago as well as three accessions of *O. bryophila* collected south of the Alaska Range, which share an 18bp indel in matK. Both the Canadian Archipelago as well as the regions south of the Alaska Range have been suspected of containing small refugial areas that are remnants from the

last glacial maxima (Hultén 1958; Abbot and Brochmann 2003). The findings of this research demonstrated similar biogeographic patterns in *O. bryophila* as those found by Jorgensen et al. (2003), who showed that northeastern Arctic populations in both *O. arctica* and *O. campestris* are distinct from all other populations examined in Alaska.

Further work is required to fully elucidate the complex relationships among species of *Oxytropis* section *Arctobia*. While earlier studies have utilized microsatellites and AFLP (amplified fragment length polymorphisms) to resolve relationships among populations of *Oxytropis* or closely related species (Herendeen et al 2003; et al. 2004; Schönswetter et al. 2004; Schlee et al. 2010), most recently next-generation sequencing technologies such as restriction-site associated DNA sequencing (RADSeq) show strong promise for its ability to resolve recent divergences (Davey and Blaxter 2010). Furthermore, whole genome datasets, coupled with ecological work investigating substrate affinities and ecological niche modeling may provide additional insight into understanding diversification and species boundaries among members of *Oxytropis* section *Arctobia* (Bennett and Leitch 2005; Taberlet et al. 2012).

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