The taxonomy of *Arnica frigida* and *A. louiseana* (Asteraceae)

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The systematic relationships of the *Arnica frigida–louiseana* complex have been evaluated. This complex has been previously recognized as one species. *A. louiseana*, with three infraspecific taxa: subspecies *frigida*, *griscomii*, and *louiseana*. Morphological, phytogeographical, and cytological data support the recognition of *A. frigida* ssp. *frigida* and the newly proposed combination ***A. frigida*** spp. ***griscomii***. *Arnica louiseana* is also recognized at the specific level. All three taxa have distinct geographic distributions: *A. frigida* spp. *frigida* is found from eastern USSR, Alaska, Yukon, east to the Mackenzie River, N.W.T., with isolated populations east of the Mackenzie River and in northern British Columbia; *A. frigida* ssp. *griscomii* is extremely localized in Gaspé, Qué., and in northwest Newfoundland; and *A. louiseana* is restricted to high elevations in the Rocky Mountains of Alberta. The basic chromosome number for this complex is $x = 19$, with *A. frigida* ssp. *frigida* $2n = 38$, 57, 76, and 95, *A. frigida* ssp. *griscomii* $2n = 76$, and *A. louiseana* with chromosome complements of $2n = 76$ and 95. This complex is predominantly apomictic with amphimictic phases in unglaciated Alaska. Disjunct distributions are probably the result of Pleistocene survival in refugia with apomictic phases being responsible for the recolonization of glaciated areas.

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Les relations systématiques du complexe *Arnica frigida–louiseana* ont été évaluées. Ce complexe a été précédemment reconnu comme une seule espèce, le *Arnica louiseana*, avec trois taxons infraspécifiques: les sous-espèces *frigida*, *griscomii* et *louiseana*. Des données morphologiques, phytogéographiques et cytologiques soutiennent la reconnaissance du *A. frigida* ssp. *frigida* et la combinaison nouvellement proposée ***A. frigida*** ssp. ***griscomii***. *Arnica louiseana* est aussi reconnu au niveau spécifique. Chacun des trois taxons a une distribution géographique qui lui est propre: *A. frigida* ssp. *frigida* se retrouve en URSS orientale, en Alaska, au Yukon, et à l'est de la Rivière Mackenzie, T.N.-O., avec des populations isolées du côté est de la Rivière Mackenzie et au nord de la Columbie-Britannique; le *A. frigida* ssp. *griscomii* est extrêmement localisé en Gaspé (Qué.) et au nord-ouest de Terre Neuve, alors que le *A. louiseana* ne se retrouve que sur les hauteurs des Montagnes Rocheuses de l'Alberta. Le nombre chromosomique de base pour ce complexe est $x = 19$, le *A. frigida* ssp. *frigida* ayant $2n = 38$, 57, 76 et 95, le *A. frigida* ssp. *griscomii* $2n = 76$, et le *A. louiseana* ayant des compléments chromosomiques de $2n = 76$ et 95. Ce complexe est de prédominance apomictique avec des phases amphimictiques en Alaska non glaciaire. Des distributions disjointes sont les résultats probables de la survie, au cours du pléistocène, dans des réfuges accompagnée d'une recolonisation des régions ayant subi la glaciation, grâce à des phases apomictiques.

[Traduit par la revue]

Introduction

The interpretation of plant disjunctions has long been regarded as a central problem in plant geography. Familiar patterns of arctic species, disjunct in the cordillera of western North America, and extremely localized areas of northeastern North America, have received much attention (Fernald 1925; Wynne-Edwards 1937; Marie-Victorin 1938; Schofield 1969; Morisset 1971). A closely related assemblage of plants which typifies these disjunct distribution patterns is found within the *Arnica frigida–louiseana* complex (Asteraceae: Senecioneae).

In his major treatment of this complex, Maguire (1943) recognized three taxa: subspecies *frigida*, *griscomii*, and *genuina* of *Arnica louiseana* Farr. Subspecies *genuina* being illegitimate (see section 5, article 26, *International Code of Botanical Nomenclature*) is treated as ssp. *louiseana*. In the following discussion, evidence will be presented to justify the recognition of ssp. *frigida* and ssp. *louiseana* at the specific level and ssp. *griscomii* as a subspecies of *A. frigida* Meyer ex Iljin. Consequently, these taxa will be referred to as *A. frigida* ssp. *frigida*, *A. louiseana*, and the newly proposed combination, *A. frigida* ssp. *griscomii*.

Arnica frigida ssp. *frigida* was described (as *A. alpina* L.) in 1831 by C. F. Lessing in his report on the Synantherae from plant material gathered during the Romanzoffiana Expedition (1815–1818). The distribution of this taxon is quite extensive with plants found from east of the Kolyma River, USSR, through the islands of the Bering Strait, Alaska, Yukon Territory, to the Mackenzie River in the Northwest Territories (Maguire 1943; Hultén 1968). Isolated populations are also found in alpine areas of northern British Columbia (Buttrick 1977; Douglas 1982). *Arnica louiseana* is more restricted in its distribution, occurring at high elevations in the Canadian Rocky Mountains of Alberta and British Columbia (Douglas 1982; Moss 1983). It was described by Miss Edith Farr in 1906 from the vicinity of Lake Louise, Banff National Park, and can be separated from all others by its evident glandularity, its small size, and the nodding tendency of the peduncle (Farr 1906). *Arnica frigida* ssp. *griscomii* was originally described as *A. griscomii* by Fernald (1924). It exists in less than a half-dozen localities in the Gaspé Peninsula (Fernald 1933) and is a rare plant of Québec's flora (Bouchard *et al.* 1983). In Newfoundland, ssp. *griscomii* is restricted to limestone barrens and the alpine of the northwest (Fernald 1924, 1933). The distribution of these three taxa is illustrated in Fig. 1.

Taxonomic treatments of this complex have been influenced by the morphological variability encountered, particularly within *A. frigida* ssp. *frigida*. Rydberg (1927) recognized five taxa within the species, whereas Maguire (1943) placed these taxa in synonymy with *A. louiseana* ssp. *frigida*. Hultén (1930) maintained there are no discernible differences between those plants of arctic Asia and arctic North America and preserved the name *A. frigida*. Maguire (1943) suggested that in

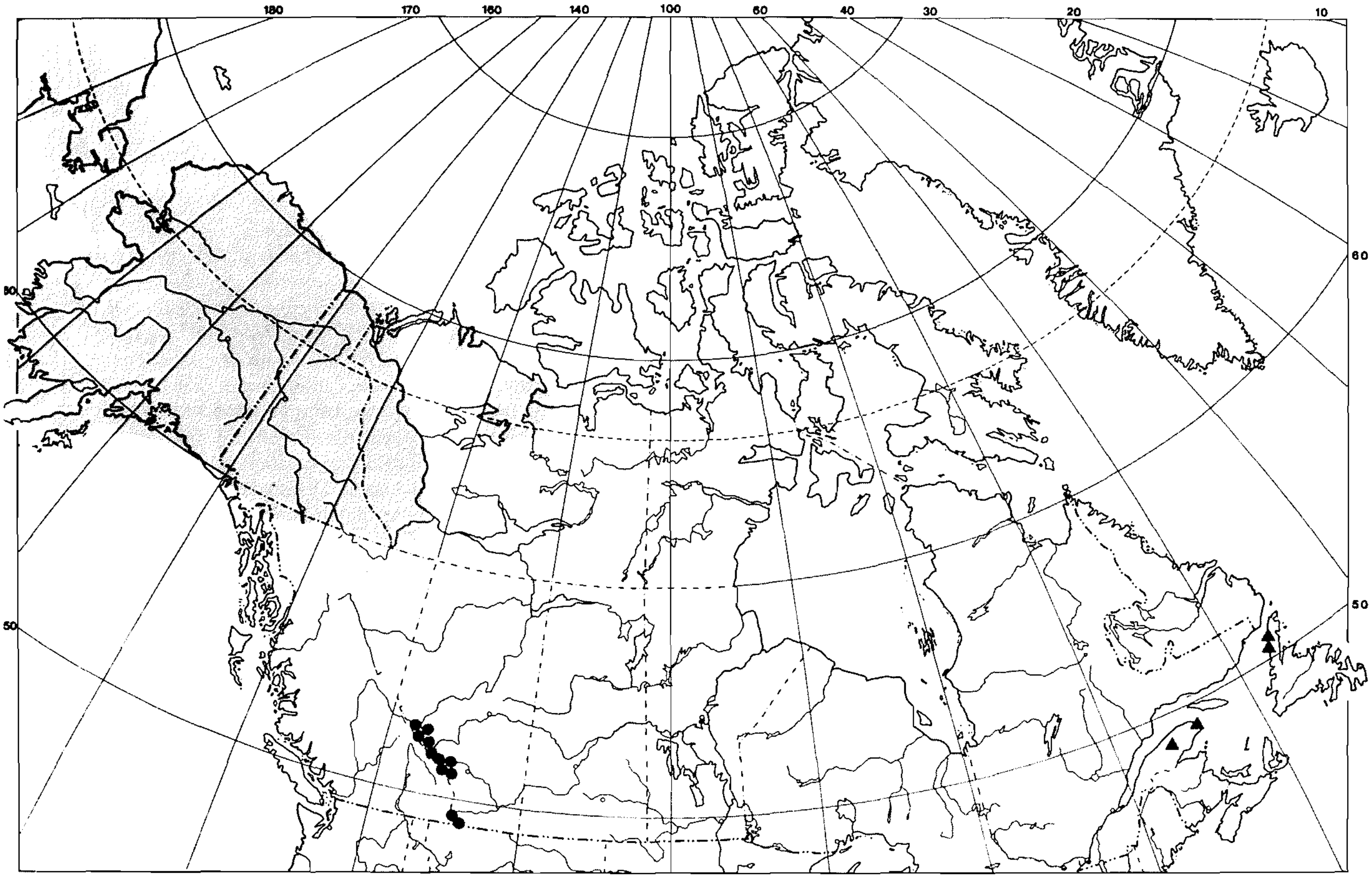

FIG. 1. Distribution of *A. frigida* ssp. *frigida*, shaded area; *A. frigida* ssp. *griscomii*, ▲; *A. louiseana*, ●.

TABLE 1. Previously reported chromosome numbers in the *Arnica frigida–louiseana* complex

Taxon	2*n*	Locality	Reference
A. frigida ssp. *frigida*	38	Alaska: Hatcher's Pass, W. Palmer	Wolf 1980
	38	Alaska: Caribou Creek, Glenallen Hwy.	Wolf 1980
	38	Alaska: Donnelly Dome	Wolf 1980
	38	Alaska: 11 km S. Delta Junction	Wolf 1980
	38	Alaska: Km 35 Denall Hwy.	Wolf 1980
	57	Alaska: Km 63 Taylor Hwy.	Wolf 1980
	58	USSR: Gusinaya River	Zhukova and Petrovski 1971
	60	USSR: Lorino	Zhukova 1965
	60	USSR: Arcto-Alpine Botanic Garden	Zhukova 1964
	70	USSR: Chukotsky Peninsula	Zhukova and Tikhonova 1971
	76	Yukon: Kluane Lake	Löve and Löve 1975
	76	USSR: Mt. Ulakhan-Tas	Zhukova *et al.* 1977
	ca. 76	Alaska: Ogotoruk Creek	Johnson and Packer 1968
A. louiseana	ca. 67	Alberta: Jasper National Park, Mt. Edith Cavell	Ornduff *et al.* 1967
	76	Alberta: Jasper National Park, Mt. Edith Cavell	Wolf 1980
	76	Alberta: Jasper National Park, Columbia Icefields	Wolf 1980
	76	Alberta: Jasper National Park, Maligne Lake	Wolf 1980
	76	Alberta: Banff National Park, Peyto Lake	Wolf 1980
	95	Alberta: Banff National Park, Moraine Lake	Straley 1982
A. frigida ssp. *griscomii*	76	Québec: Matane County, Mt. Logan	Gervais 1979

several respects *A. frigida* ssp. *griscomii* is more similar to *A. frigida* ssp. *frigida* than to *A. louiseana*. In describing a new species from the Northwest Territories, Raup (1947) acknowledged the similarity of this taxon to those plants of eastern North America. However, the consensus has been to maintain all three taxa in *A. louiseana* (Maguire 1943; Ediger and Barkley 1978; Scoggan 1979; Douglas 1982; Moss 1983).

The basic chromosome number for *Arnica* was shown by Böcher and Larsen (1950) and Ornduff *et al.* (1967) to be $x = 19$, with chromosome races of $2n = 38$, 57, 76, and 95 being reported. Ornduff *et al.* (1967) have observed a high frequency of meiotic irregularities in triploids and tetraploids, which

Barker (1966) suggest may be due to aneuploidy. Previously reported chromosome counts are summarized in Table 1. A reported count for *A. louiseana* of $2n = 57$ (Wolf 1980) was based upon a misidentification of *A. rydbergii* Greene and is not included in this table.

There is a strong correlation between apomixis and poor pollen quality (Gustafsson 1947). Using pollen quality as an indicator of reproductive mode in *Arnica*, Barker (1966) was able to show that in collections where emasculation procedures and embryological observations indicated amphimixis, the pollen was well formed with better than 90% stainability in lactophenol – cotton blue. When apomixis was demonstrated experimentally, the pollen showed varying degrees of deformity and less than 80% stainability. The relationship between apomixis and polyploidy (Gustafsson 1946, 1947; Stebbins 1950) was exemplified in Barker's (1966) study in which all amphimicts were diploid and apomicts polyploid.

Considering the distribution of chromosome races in *Arnica*, Barker (1966) showed that no well-developed sexual species occurs in a glaciated area and no well-developed polyploid series occurs in an unglaciated area. The correlation between the existence of polyploids in previously glaciated areas and the presence of diploid cytotypes of the same species in unglaciated areas has been documented in *Iris versicolor* (Anderson 1936), *Calamagrostis* (Stebbins 1984), and *Minuartia elegans* (Wolf *et al.* 1979) and may have existed in the genus *Braya* in North America (Harris 1984).

Favarger (1961) and Johnson and Packer (1965) demonstrated that northern polyploids are more common in habitats most directly affected by climatic and edaphic deterioration during glaciation and that these habitats are of prime importance in determining the relative distribution patterns of diploids and polyploids. The greater genetic variability of polyploids, particularly when accompanied by ecotype or species hybridization, provides greater adaptability to new ecological conditions (Johnson and Packer 1965; Stebbins 1984). In contrast, diploids may succumb to these same selective pressures and be eliminated altogether (Stebbins 1971).

Arnica frigida was determined to be largely apomictic with a small amphimictic phase in the glaciated portion of south central Alaska (Barker 1966), with no location for the possible refugium of these sexual elements being found.

The present study was initiated to investigate the relationships between morphology, cytology, and geographic distribution of the *Arnica frigida* – *louiseana* complex. The influence of glaciation and the role of polyploidy on the evolution and phytogeographic history will also be investigated. The chemical relationships within this complex will be presented in a subsequent paper (S. R. Downie and K. E. Denford, in preparation).

Materials and methods

A study of specimens from throughout the entire range of the complex comprising approximately 700 specimens involved material from the following herbaria: University of Alaska (ALA); University of Alberta (ALTA); National Museum of Canada, Ottawa (CAN); Department of Agriculture, Ottawa (DAO); The Gray Herbarium of Harvard University (GH); Herbarium of the Komarov Botanical Institute, Leningrad (LE); Herbier Marie-Victorin, Montreal (MT); The New York Botanical Garden (NY); The Academy of Natural Sciences, Philadelphia (PH); University of British Columbia (UBC); Herbarium of the University of California at Berkeley (UC); and the United States National Herbarium (US).

Field collections were made in the Rocky Mountains of Alberta, northern British Columbia, Yukon Territory, southeastern Alaska, and in selected sites in the Gaspé Peninsula of Québec and western Newfoundland. A voucher specimen for each population collected was deposited at ALTA. Seeds, if available, were collected and stored in paper bags. Live plant material was transplanted from the field into 6-in. (1 in. = 25.4 mm) plastic pots and transported to the University of Alberta Phytotron for cultivation. The number of pots collected was dependent upon the size of the population and whether permission was received to collect in restricted areas.

Plants in the greenhouse were maintained under a 16-h photoperiod throughout the year. High-energy discharge lamps provided a minimum light intensity of 365 $\mu E \cdot m^{-2} \cdot s^{-1}$. Temperature was maintained at 22°C during the day and 18°C during the night. Relative humidity was maintained between 40 and 50%. At the end of their growing cycle, all leaf and stem tissue was removed and the pots containing the rhizomes were placed in a dark freezer at 3°C for 1–3 months. Afterwards, the pots were removed and returned directly into the greenhouse. Vegetative growth began immediately. To differentiate between genetic and environmentally induced traits, plants from all collections were grown in identical environmental conditions. Achenes were sown under a thin layer of sand in 3-in. clay pots and later transplanted to 5-in. plastic pots. Achene germination percentages for amphimictic collections were very low and pretreatment was necessary. In these cases, achenes were either scarified or placed in a freezer 5–9 days before sowing. Representative specimens of these cultivated plants have been preserved at ALTA.

Acetocarmine root-tip squashes were based upon a modification of the Chambers (1955) technique. Actively growing root tips were removed from greenhouse material, prefixed in a 0.002 *M* 8-hydroxyquinoline (0.116 g in 400 mL H_2O) solution for 2–2.5 h at 13–16°C and then fixed in absolute ethanol – glacial acetic acid (3:1, v/v). After fixation (24 h) root tips were rinsed thoroughly with distilled water, blotted dry, and immersed in a small amount of snail cytase ("glusulase") for 15 min at room temperature. The enzyme was used in prepared form. Further information regarding the use of this enzyme can be obtained in Roy and Manton (1965) and Soltis (1980). A longer period of time in the enzyme tended to digest the cells thoroughly and made staining more difficult. Subsequent to glusulase digestion, the root tips were placed in a small beaker of distilled water for a few minutes before being removed, blotted dry, and squashed using the conventional acetocarmine technique.

Slides were made semipermanent by ringing the cover slip with a melted mixture of gum mastic – paraffin wax (1:1, v/v). Chromosomes were examined and counted using an Olympus BHA, PM-10M photomicrographic system and photographed with an Olympus C-35 camera. A voucher slide for each examined collection was deposited at ALTA.

Pollen grain viability was determined by staining fresh pollen in a drop of lactophenol – cotton blue stain for 5 min. Pollen was collected in the field or greenhouse and placed directly into vials containing the stain. Vials were stored in the refrigerator before examination. Pollen grains were considered viable if they took up the stain and appeared a dark blue colour. Viability was estimated on the percentage of stained grains in the 500–600 grains examined per specimen. When fresh material was not available, pollen was judiciously removed from herbarium specimens upon the approval of the curators concerned.

The relationship between polyploidy and cell size is very well established (Sax and Sax 1937; Stebbins 1971) with guard cell size being a reliable means for the detection of polyploids (Sax 1938). Guard cell length measurements were taken from cultivated material with an ocular micrometer in an American Optical microscope. Preparations were made from living material by peeling off the abaxial leaf epidermis with tweezers, mounting the peel in water, and observing under the microscope. Measurements were taken from leaves of similar size and maturity and corresponding areas.

Herbarium specimens were examined initially for morphological differences and correlation of these differences with geographic distribution or habitat. In the phenetic analysis 122 specimens were used

TABLE 2. Collections used in TAXMAP analysis

OTU No.	OTU Code	OTU description
1	A-65519	Banff National Park, Mt. Paget, *Macoun s.n.* (US)
2	A-72	W. Hailstone Butte, *Norris 72* (DAO)
3	A-2938	Banff National Park, Mt. Wilson, *Breitung, Porsild & Boivin 2938* (DAO)
4	A-37189	Jasper National Park, Mt. Edith Cavell, *Calder 37189* (DAO)
5	A-56257	Whitegoat Wilderness, *Lee s.n.* (ALTA)
6	A-17454	Waterton Provincial Park, Mt. Richards, *Breitrung 17454* (NY)
7	A-16067	Banff National Park, Mt. Saskatchewan, *Porsild & Breitung 16067* (CAN)
8	A-5239	Whitehorse Creek, Nicanassin Range, *Dumais & Andrewchow 5239* (CAN)
9	A-1067	Banff National Park, Lake Louise, *Farr s.n.* (PH) Type specimen: *louiseana* Farr
10	A-7854	Cadomin, *Dudynsky 7854* (ALTA)
11	A-546	Jasper National Park, Bald Hills, *Downie 546* (ALTA)
12	A-547	Jasper National Park, Maligne Lake, *Downie 547* (ALTA)
13	A-544	Jasper National Park, Columbia Icefields, *Downie 544* (ALTA)
14	A-449	Banff National Park, Moraine Lake, *Downie 449* (ALTA)
15	A-450	Banff National Park, Peyto Lake, *Downie 450* (ALTA)
16	A-17457	Waterton Provincial Park, Mt. Richards, *Breitung 17457* (ALTA)
17	A-1607	Banff National Park, S.W. Moraine Lake, *Straley 1607* (DAO)
18	A-438	Prospect Mtn., 10 mi. S.W. Cadomin, *Mortimer 438* (ALTA)
19	N-2139	St. John Bay, Eastern Point, *Fernald, Long & Fogg 2139* (US)
20	N-2140	St. John Bay, Eastern Point, *Gernald, Long & Fogg 2140* (US)
21	N-2141	St. John Bay, Eastern Point, *Fernald, Long & Fogg 2141* (US)
22	N-2142	St. John Bay, S.W. Port Au Choix, *Fernald, Long & Fogg 2142* (US)
23	N-2143	Pointe Riche, St. John Bay, *Fernald, Long & Fogg 2143* (GH)
24	Q-26082	Matane Co., Mt. Mattaouisse, *Fernald et al. 26082* (US)
25	Q-26083	Matane Co., Mt. Logan, *Pease & Smith 26083* (NY)
26	Q-26084	Matane Co., Mt. Mattaouisse, *Fernald & Smith 26084* (GH) Type specimen: *griscomii* Fernald
27	N-29216	St. John Island, *Fernald et al. 29216* (GH)
28	N-74031	Port Au Choix, St. Barbe, *Hay & Bouchard s.n.* (CAN)
29	Q-49028	Forillion Park, Mt. Saint-Alban, *Marie-Victorin et al. 49028* (DAO)
30	BC-452	Stone Mtn Prov. Park, Summit Lake, *Downie 452* (ALTA)
31	BC-838	Teresa Island, Atlin Lake, *Buttrick 838* (UBC)
32	BC-916	Mile 83 Haines Road, *Taylor, Szczawinski & Bell 916* (CAN)
33	BC-1103	Mile 60 Haines Road, *Taylor, Szczawinski & Bell 1103* (CAN)
34	BC-7827	Mile 82 Haines Road, *Dudynsky 7827* (ALTA)
35	BC-10507	Summit Pass, *Raup & Correll 10507* (GH)
36	BC-60645	Spatsizi Plateau, *Krajina s.n.* (UBC)
37	BC-81811	Stonehouse Creek, Haines Road, *Beamish, Krause & Luitjens 681811* (UBC)
38	BC-78430	Stone Mtn. Prov. Park, Summit Lake, *Rose 78430* (UBC)
39	YT-33	Herschel Island, Beaufort Sea, *Cooper 33C* (NY)
40	YT-208	Firth River, near coast, *McEwen 208* (CAN)
41	YT-421	S. Mt. Klotz, 90 mi. W. Dawson City, *Greene 421* (ALTA)
42	YT-469	Km 32.5 Taylor Hwy., *Downie 469* (ALTA)
43	YT-470	Km 34.5 Taylor Hwy., *Downie 470* (ALTA)
44	YT-471	Km 38.5 Taylor Hwy., *Downie 471* (ALTA)
45	YT-474	Km 73.5 Dempster Hwy., *Downie 474* (ALTA)
46	YT-476	Km 75 Dempster Hwy., *Downie 476* (ALTA)
47	YT-477	Km 80 Dempster Hwy., *Downie 477* (ALTA)
48	YT-478	Km 76 Dempster Hwy., *Downie 478* (ALTA)
49	YT-3767	20 mi. E. Dawson City, *Calder & Billard 3767* (DAO) Type specimen: *glandulosa* Boivin
50	YT-6345	Profile Mtn., 16 mi. N.W. Dawson City, *G. W. & G. G. Douglas 6345* (DAO)
51	YT-8271	Mile 100 Haines Road, *Schofield & Crum 8271* (CAN)
52	YT-9755	Mile 132 Canol Road, *Porsild & Breitung 9755* (CAN)
53	YT-10080	Canol Road, Ross-Lapie R. pass, *Porsild & Breitung 10080* (CAN)
54	YT-11307	Little Atlin Lake, *Raup & Correll 11307* (GH)
55	YT-12158	Kluane Lake, *H. M. & L. C. Raup 12158* (GH)
56	YT-13760	N.E. Ptarmigan Heart, *H. M. Raup, Drury & K. A. Raup 13760* (GH)
57	NWT-83	Horn Lake, 37 mi. N.W. McPherson, *Youngman & Tessier 83* (CAN)
58	NWT-1530	Inuvik, Mackenzie River Delta, *Lambert s.n.* (DAO)
59	NWT-3964	5 mi. W. Horne Lake, Richardson Mtns., *Calder 33964* (DAO)
60	NWT-6647	Lone Mtn., lower N. Nahanni River, *Porsild 16647* (CAN)

TABLE 2. (*concluded*)

OTU No.	OTU Code	OTU description
61	NWT-9197	Keele River, Mackenzie Mtns., *Cody & Scotter 19197* (DAO)
62	AK-19	White Mtns., central Alaska, *Gjaerevoll 19* (CAN)
63	AK-46	Chitaslene Glacier, Copper River region, *Poto 46* (US) Type specimen: *brevifolia* Rydberg
64	AK-71	Katmai Region, Alaska Peninsula, *Hagelbarger 71* (US)
65	AK-78	Tikchik Lakes, mtn. above Upnuk Lake, *Densmore 78* (ALTA)
66	AK-116	Onion Portage, Brooks Range, *Schweger 116* (ALA)
67	AK-163	Nogheling Trail, Lake Iliamna, *Gorman 163* (US) Type specimen: *illiamnae* Rydberg
68	AK-184A	Lake Iliamna, Alaska Peninsula, *Donaldson 184a* (ALA)
69	AK-196	Noluck Lake, Misheguk Mtn., *Parker 196* (ALA)
70	AK-273	Hwy. Pass, Mt. McKinley National Park, *Gornall 273* (UBC)
71	AK-283	E. Carnivore Creek, Brooks Range, *Batten 283* (ALA)
72	AK-367	138 mi. N.N.E. Arctic Village, *Hettinger 367* (CAN)
73	AK-379	70 mi. S. Point Barrow, near Atkasook, *Komarkova, Hansell & Seabert 379* (ALA)
74	AK-475	Mile 40 Taylor Hwy., *Downie 475* (ALTA)
75	AK-503	S. Delta Junction, *Downie 503* (ALTA)
76	AK-504	Mile 258 Richardson Hwy., *Downie 505* (ALTA)
77	AK-505	Mile 84.8 Steese Hwy., *Downie 505* (ALTA)
78	AK-506	Mile 105 Steese Hwy., *Downie 506* (ALTA)
79	AK-515	Mile 13 Denali Hwy., W. Paxson, *Downie 515* (ALTA)
80	AK-516	Mile 22 Denali Hwy., W. Paxson, *Downie 516* (ALTA)
81	AK-517	Mile 11 Denali Hwy., W. Paxson, *Downie 517* (ALTA)
82	AK-680	Mt. McKinley National Park, *Scamman 680* (GH)
83	AK-685	Arrigetch Creek Valley, Brooks Range, *Cooper CV-685* (DAO)
84	AK-1192	56 km. E. Chitina, McCarthy Road, *Harris 1192* (ALTA)
85	AK-1302	Anvil Mtn., 7 km. N.N.E. Nome, *Harris 1302* (ALTA)
86	AK-1366	Seward Peninsula, Mile 49 Nome-Taylor Hwy., *Harris 1366* (ALTA)
87	AK-1478	E. Oumalik, Arctic Alaska, *Ward 1478* (GH)
88	AK-1776	W. Burwash Landing, Rusty Glacier, *Murray 1776* (CAN)
89	AK-1833	Teller Reindeer Station, Port Clarence, *Walpole 1833* (US)
90	AK-1891	Anaktuvuk Pass, *Spetzman 1891* (CAN)
91	AK-1960	Umiat, *Hultén s.n.* (GH)
92	AK-2129	King Salmon, *Schofield 2129* (DAO)
93	AK-2610	10 mi. N. Isabel Pass, Richardson Hwy., *Smith 2610* (ALA)
94	AK-2654	Ogotoruk Creek, N. W. Alaska, *Packer 2654* (ALTA)
95	AK-2084	21 mi. S. Delta Junction, *Harms 2084* (GH)
96	AK-3492	Moose Pass, *A. & R. Nelson 3492* (ALA)
97	AK-4167	13 mi. W. Paxson on Denali Hwy., *Harms 4167* (GH)
98	AK-4248	Gold Bay, *Piper 4248* (US)
99	AK-5621	Mt. Marathon, Seward Peninsula, *Calder 5621* (US)
100	AK-6265	Mt. Fairplay, between Chicken and Tok, *Scamman 6265* (GH)
101	AK-6713	Mile 95 Yukon R. – Prudoe Bay Haul Rd., *Murray 6713* (ALA)
102	AK-6673	Mile 77-78 Dalton Hwy., *Khokhryakov, Yurtsev & Murray 6673* (ALA)
103	AK-7813	6.73 mi. S. Delta Junction, *Dudynsky 7813* (ALTA)
104	AK-7814	Donnelly Dome, *Dudynsky 7814* (ALTA)
105	AK-7817	Mile 79.5 Richardson Hwy., *Dudynsky 7817* (ALTA)
106	AK-7820	Hatcher's Pass, *Dudynsky 7820* (ALTA)
107	AK-7821	Caribou Creek, Mile 106 Glenn Hwy., *Dudynsky 7821* (ALTA)
108	AK-8371	12 mi. N.W. Kurupa Lake, Arctic Slope, *Hodgdon, Glazier & Piedeman 8371* (GH)
109	AK-19113	Thompson Pass, N. Valdez, *J. & C. Taylor 19113* (NY)
110	AK-20384	Iliamna Bay, *Gorman s.n.* (US)
111	AK-26069	Eielson Visitor's Center, Mt. McK. Park, *Richey s.n.* (ALA)
112	AK-52992	Naknek, *Norberg s.n.* (CAN)
113	AK-54238	Mt. McKinley National Park, *Frohne 54-238* (ALA)
114	AK-75132	32 km. N. Ambresvajun Lake, *A. R. & C. G. Batten 75-132* (ALA)
115	AK-77409	Old Man Creek, Koyukuk River, *Mendenhall s.n.* (US) Type specimen: *mendenhallii* Rydberg
116	UR-89929	Km 159 Route Egvekinot-lultin, *Petrovsky s.n.* (ALTA)
117	UR-89932	Chukotsky Peninsula, Lultin, *Zimarskaya, Korobkov & Yurtsev s.n.* (ALTA)
118	UR-89937	Chukotsky National Area, Anadyr Hills, *Karenin & Petrovsky s.n.* (ALTA)
119	UR-89938	Chukotsky National Area, Mt. Pevek, *Shamurin & Yurtsev s.n.* (ALTA)
120	UR-89939	Chukotsky Peninsula, Chegitun R., *Sekretareva, Sytin & Yurtsev s.n.* (ALTA)
121	UR-89940	Chukotsky Peninsula, Matuchan R., *Katenin et al. s.n.* (ALTA)
122	UR-89941	Chukotsky Peninsula, Lavrentiya, *Korobkov s.n.* (ALTA)

TABLE 3. Attributes used in TAXMAP analysis

No.	Attribute	Mode of assessment
1	Habit	0, stem unbranched; 1, stem branched
2	Stem glandularity	0, absent; 1, abundant
3	Leaf margin	0, entire; 1, inconspicuous dentate to slightly undulate
4	Leaf glandularity	0, inconspicuous; 1, abundant
5	Capitula position	0, erect; 1, nodding
6	Periclinium colour	0, white; 1, yellow to yellowish gold
7	Periclinium pubescence	0, sparse; 1, moderate; 2, dense
8	Periclinium glandularity	0, inconspicuous; 1, abundant
9	Achene pubescence	0, sparsely hirsute above middle, glabrous below; 1, sparse hirsute throughout; 2, dense hirsute throughout
10	Achene glandularity	0, inconspicuous; 1, abundant
11	Involucral bract pubescence	0, sparingly pilose, otherwise glabrous; 1, pilose at base, glabrous above; 2, pilose throughout; 3, dense woolly−villous
12	Involucral bract shape	0, narrowly lanceolate; 1, broadly lanceolate
13	Involucral bract glandularity	0, inconspicuous; 1, abundant
14	Capitula number (per stem)	
15	Plant height	Centimetres
16	Basal leaf length	Centimetres
17	Basal leaf width	Centimetres
18	Basal leaf length−width ratio	
19	Capitula length	Millimetres
20	Capitula width	Millimetres
21	Achene length	Millimetres
22	Involucral bract length	Millimetres
23	Involucral bract width	Millimetres
24	Involucral bract length−width ratio	
25	Ligule tooth length	Millimetres
26	Ligule length	Millimetres
27	Ligule width	Millimetres
28	Ligule length−width ratio	
29	Ligule number (per capitulum)	
30	Percent pollen stainability	0, 0−94%; 1, 95−100%
31	Geographic distribution	0, western North America; 1, eastern North America; 2, northern North America and USSR

(see Table 2). The specimens were chosen to reflect the apparent morphological variability exhibited by each taxon and to represent collections from throughout the range of the complex. To assess phenetic relationships, a list of 31 morphological and distributional characters was prepared (Table 3). The characters separating taxa within the *Arnica frigida−louiseana* complex were selected from previous authors' treatments (Rydberg 1927; Maguire 1943; Ediger and Barkley 1978) and our experience in the field and greenhouse. Each quantitative character represented a mean of 3 to 10 measurements, the total being dependent upon the number of plants per herbarium sheet. Characters were scored at the same relative position and developmental stage on each plant.

The TAXMAP classification program developed by Carmichael and Sneath (1969) and recently modified by Carmichael (1980) is a completely nonhierarchical method of cluster analysis. TAXMAP attempts to represent the OTUs (operational taxonomic unit) as points in n-dimensional space, where n is the number of characters. The information obtained is readily amenable to a two-dimensional diagrammatic representation (taxometric map) which preserves the maximum intracluster variation and the minimum intercluster discontinuity (Carmichael 1980). In this way, the main relations among all the OTUs are in a concise and interpretable form. The clustering procedure is outlined in detail in Carmichael *et al.* (1968).

The TAXMAP classification program was chosen over other classification programs because of its ability to cluster OTUs, using the information directly from the undistorted similarity matrix table. In this way all the OTU relations are specified, unlike that of models with reduced dimensionality. It can handle ordered and nonordered classes simultaneously and easily cope with missing data. It also allows for the weighting of characters according to their relative information content. Binary and continuous scale data are processed as the base 2 log of one more than the number of 95% confidence intervals included in the range between the largest and smallest values for that character (Carmichael 1980). Nonordered characters are processed as the base 2 log of the number of classes.

Using the TAXMAP program, data were standardized (Carmichael *et al.* 1965) and used to calculate the pairwise similarity matrix. Isolated subsets of similar items were then clustered. Carmichael *et al.* (1968) have defined these natural clusters to be continuous, relatively densely populated regions of space surrounded by continuous, relatively empty regions of space. Taxometric maps were drawn with the aid of the Calcomp plotter at the University of Alberta.

Results

Herbarium studies

An initial examination of herbarium specimens was done to gain an overall view of the structural variability encountered within this complex. The wide range in polymorphy exhibited in plant height, leaf size, pubescence, and floral characters is immediately obvious when examining specimens of *A. frigida* ssp. *frigida*. In contrast, those specimens identified as *A. louiseana* and *A. frigida* ssp. *griscomii* showed a high degree of uniformity in their morphological attributes. A number of characters were found to be useful in distinguishing the taxa; notably the presence or absence of short-stipitate glands and the colour of the periclinium. The periclinium in the Asteraceae, as defined by Maguire (1943), is the area between the transition of peduncle into capitulum and the base of the involucral bracts and is usually characterized by excessive pubescence.

Numerical analysis

Specimens representing 122 members of the *Arnica frigida–louiseana* complex were scored for 31 attributes and analyzed with the TAXMAP classification program. To aid in cluster interpretation, each OTU was assigned an OTU code indicating where the specimen was located (e.g., A, Alberta; AK, Alaska; U, USSR) and its collection number.

TAXMAP recognizes six clusters and six isolated OTUs, or single-member clusters. The resulting taxometric map appears in Fig. 2. Evident from the taxometric map is the separation of *Arnica louiseana* and *A. frigida* ssp. *griscomii* into discrete clusters and the close similarity of the latter with *A. frigida* ssp. *frigida*. Within the *A. frigida* ssp. *frigida* group are 10 clusters. Many of these clusters simply represent extremities in morphological attributes or several unique characters which are not normally found within this group. The clusters can be described as follows. Cluster 1 represents the largest group and contains 63 OTUs of *A. frigida* ssp. *frigida*. Clusters 2 and 3 consist of all 11 OTUs of *A. frigida* ssp *griscomii* and all 11 OTUs of *A. louiseana*, respectively. Cluster 4 is most closely related to cluster 1 and contains 7 specimens which have a dense periclinium, achene, and involucral bract pubescence. Most members of this cluster have been previously described as *A. louiseana* var. *pilosa* (Maguire 1942). Cluster 5 includes 15 OTUs all represented by a high pollen viability ($2n$ = 38). This cluster is most closely related to cluster 4, which although characterized by a dense periclinium pubescence, is also represented by a high pollen viability. Cluster 6 includes 2 OTUs. With the exception of its prominent leaf glandularity and its high pollen stainability, it is identical with *A. frigida* ssp. *frigida* in cluster 1.

Isolated clusters 7, 10, and 11 are most closely related to *A. frigida* ssp. *frigida*. Cluster 7 is characterized by a specimen with a very large leaf width. Cluster 10 is represented by a plant with evident achene glandularity and cluster 11 is characterized by a plant with a very large capitulum and long ligulate florets. Since TAXMAP clusters OTUs on the basis of relative discontinuities in the proximities between OTUs, these three taxa are placed in isolated clusters. Cluster 8 represents the type specimen of *A. illiamnae* Rydb. This plant is characterized by a branching habit, three heads, and a prominent glandularity on the achenes and leaves. Maguire (1943) has recognized three specimens (*Mackis 4*, *Hagelbarger 258*, and *Palmer 55*) which have a branching habit and entirely oblanceolate leaves. On the annotation labels of these specimens, he suggests that these forms may represent a new species. During the course of this study, the oblanceolate leaf shape was found to be quite common in *A. frigida* ssp. *frigida*. Plants showing a tendency to branch were quite rare. These plants were found to be sporadic in distribution and represent no more than an abnormal growth form. These anomalous specimens were not included in the TAXMAP analysis. Cluster 9 contains a plant which is most closely related to the isolated OTU in cluster 10. This is due to its achene and involucral bract glandularity. Cluster 12 comprises an OTU which is characterized by its evident leaf glandularity and high pollen viability. Cluster 12 is most similar to cluster 5.

Cytology

Somatic chromosome numbers and information on the collection locality are presented in Table 4. The counts of $2n$ = 95 for *A. frigida* from Summit Lake, B.C., are the first reported pentaploids reported for this species. Tetraploid counts for *A. louiseana* and *A. frigida* ssp. *griscomii* confirm those reported by Wolf (1980) and Gervais (1979). No evidence of aneuploidy was found in any of the collections examined. The 31 new counts presented here strongly support the base chromosome number of 19 for the North American members of this complex.

When assessed for pollen viability, all diploid collections exhibited 90% or greater stainable pollen, whereas the triploids and tetraploids possessed 0 to 15% viable pollen. This corroborates Barker's (1966) hypothesis that poor pollen quality (less than 90%) is indicative of a polyploid nature in *Arnica*.

Pollen viability

The pollen quality of 300 specimens, representing 31 field collections and 269 herbarium specimens, was determined. Specimens were chosen to represent collections from throughout the entire range of the complex. Thirty collections of *A. louiseana* ($2n$ = 76) exhibited pollen viability of 0 to 3%. Eighteen collections of *A. frigida* ssp. *griscomii* ($2n$ = 76) also showed a very low percentage viability of 0 to 4%. Within the *A. frigida* ssp. *frigida* group, 10 collections from British

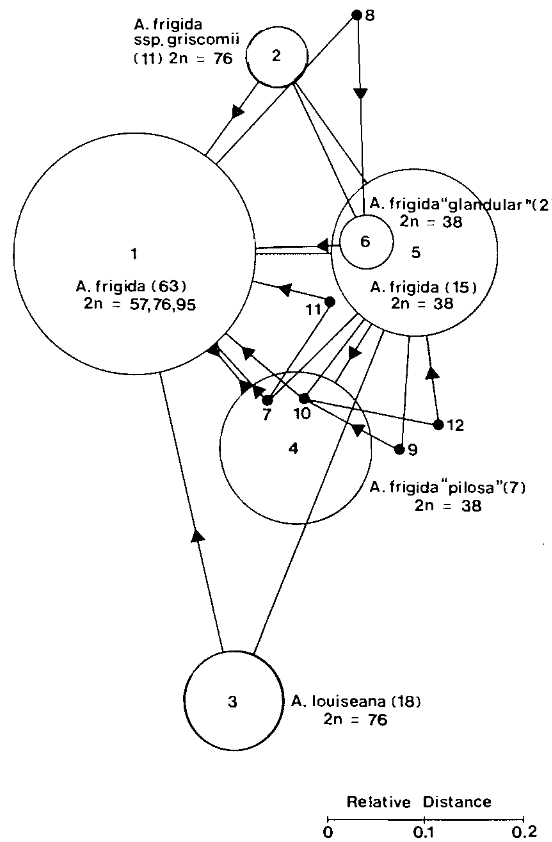

FIG. 2. Taxometric map showing the relations between members of the *Arnica frigida–louiseana* complex based on morphological, cytological, and distributional data. The numbers in parentheses represent the number of OTUs within the cluster. The diameters of the circles represent the maximum distance between any pair of OTUs included in the cluster. The lines connecting the margins of the circles represent the undistorted phenetic distance between the nearest neighbours in the two clusters. The arrows indicate the nearest neighbour to each cluster. Two arrows facing each other indicate the clusters are equidistant from each other.

TABLE 4. Diploid chromosome numbers determined for members of the *Arnica frigida–louiseana* complex

Taxon	2*n*	Locality and voucher
A. frigida ssp. *frigida*	38	U.S.A.: ALASKA: south of Delta Junction, *Downie 503*; Mile 250 Richardson Hwy., *Downie 504*; Mile 84.8 Steese Hwy., *Downie 505*; Mile 105 Steese Hwy., *Downie 506*; Mile 39 Elliott Hwy., *Downie 508*; Mile 39.3 Elliott Hwy., *Downie 508A*; Healy, *Downie 509*; Mile 106 Glenn Hwy., *Downie 514*; Mile 13 Denali Hwy., *Downie 515*; Mile 22 Denali Hwy., *Downie 516*; Mile 11 Denali Hwy., *Downie 517*; Donnelly Dome, *Downie 519*; South Mt. McKinley National Park, *Downie 524*
	57	*CANADA:* YUKON: Km 32.5 Taylor Hwy., *Downie 468*; Km 34.5 Taylor Hwy., *Downie 470*; Km 38.5 Taylor Hwy., *Downie 471*; Km 73.5 Dempster Hwy., *Downie 474*; Km 75 Dempster Hwy., *Downie 476*; Km 80 Dempster Hwy., *Downie 477*; Km 76 Dempster Hwy., *Downie 478*
		U.S.A.: ALASKA: Mile 40 Taylor Hwy., *Downie 475*
	95	*CANADA:* BRITISH COLUMBIA: Stone Mountain Provincial Park, Summit Lake, *Downie 452*; Stone Mountain Provincial Park, Summit Lake, *Downie 525*
A. louiseana	76	*CANADA:* ALBERTA: Banff National Park, Moraine Lake, *Downie 449*; Banff National Park, Peyto Lake, *Downie 450*; Jasper National Park, Columbia Icefields, *Downie 544*; Jasper National Park, Maligne Lake, *Downie 546*; Jasper National Park, Maligne Lake, *Downie 547*
A. frigida ssp. *griscomii*	76	*CANADA:* QUÉBEC: Forillion National Park, Mt. Saint-Alban, *Downie 531;* NEWFOUNDLAND: Southwest Port Au Choix, *Downie 533*; Pointe Riche, *Downie 534*

Columbia showed pollen viability of 0 to 1%, 28 collections from the Northwest Territories had pollen which was 0 to 6% viable, 53 collections from the Yukon Territory showed 0 to 15% viable pollen, and 15 collections from the USSR had 0 to 16% viable pollen. In Alaska, 61 collections exhibited pollen viability greater than 90% and 76 collections had 0 to 15% stainable pollen. Nine collections produced pollen which was 16 to 89% viable. In collections where pollen viability was less than 80%, the pollen grains showed varying degrees of pollen deformity.

No pollen was observed in the four collections from Summit Lake, B.C. (*Downie 452,525*, *Raup & Correll 10507*, *Rose 78430*). These collections represent the most southerly limit of the range of *A. frigida* ssp. *frigida* and are isolated by at least 200 km from the major northern populations. When we consider the isolation of this group and the pentaploid nature of its chromosomes, it is not surprising to find this absence of pollen. Barker (1966) has suggested that faulty chromosome pairing in pentaploids, meiotic disturbances in microsporocyte divisions, and the accumulation of random deleterious mutations may have caused this deterioration in microsporogenesis. Engell (1970) has reported on the degeneration of pollen mother cells in pentaploid populations of *A. angustifolia*, a closely related species to *A. frigida* (Maguire 1943). In these cells, all meiotic chromosomes appeared to be strongly contracted with chromosomal divisions stopping at prophase.

In Alaska and the USSR, 16 collections were also found not to produce pollen. Collections from Alaska (*Cantlon & Gillis 57-452*, *Geist s.n.*, *Hettinger 367*, *Murray & Johnson 6687*, *Packer 2654*, *Spetzman 835*, *Ward 1478*) were collected above 68° latitude, north of the Brooks Range. In the USSR, 9 collections from north and central Chukotsky are represented by *Afonina et al. s.n.*, *Korobkov s.n.* (3 collections), *Karenin & Petrovsky s.n.*, *Nechayev, Plieva & Yurtsev s.n.* (2 collections), *Yurtsev s.n.*, and *Zimarskaya, Korobkov & Yurtsev s.n.*

Herbarium collections having a pollen viability greater than 95% showed a very close correlation with nonglaciated areas (Fig. 3). The sexual phase is well developed throughout unglaciated central and southwestern Alaska with some colonization of the glaciated area in south central Alaska. The location for the refugium of these sexual elements has been confirmed and is more extensive than Barker (1966) realized. Plants which have been able to recolonize this glaciated area in the region of Lake Iliamna, are represented by five collections which have been utilized in the TAXMAP analysis. These collections (*Hagelbarger 71*, *Donaldson 184*a, *Gorman 163*, *Schofield 2129*, *Gorman s.n.*) were found to be morphologically distinct from the typical *A. frigida* ssp. *frigida* and characterized by obvious leaf, achene, and involucral bract glandularity. This glandularity was found to be restricted only to this area.

Guard cell measurements

Guard cell measurements for all field collections of the *Arnica frigida–louiseana* complex were determined (Fig. 4). Because of the magnitude of the unequal sample sizes, a GT2 method of multiple comparison after analysis of variance was chosen (Sokal and Rohlf 1981). A significant difference was observed ($p > 0.01$) between all pairs of ploidy levels, with the exception of the paired comparison between the triploids and the tetraploids (Table 5). Two triploid populations (*Downie 471,476*) represented anomalous guard cell measurements and showed a mean length of 49.7 (SD = 1.57) and 58.8 μm (SD = 1.44), respectively. These two collections were not included in the statistical analysis. No evidence of a difference in guard cell size was found between different taxa of the same chromosome number.

Greenhouse studies

Phenological differences were observed between parental populations and greenhouse-propagated material. Plants produced from achenes collected in the field and plants which had reestablished after a cold period showed a reduction in periclinium and involucral bract pubescence. In some instances the periclinium pubescence disappeared altogether. This was particularly evident in collections which can be described as var. *pilosa*. In these collections, the dense pubescence of the peduncle, periclinium, and involucral bracts that has been used to delimit this variant from *A. frigida* was lost. In addition, the characteristic yellow periclinium pubescence of *A. frigida* spp. *frigida*, so common in the field, was now white. Greenhouse-propagated material of *A. frigida* ssp. *frigida* was morphologi-

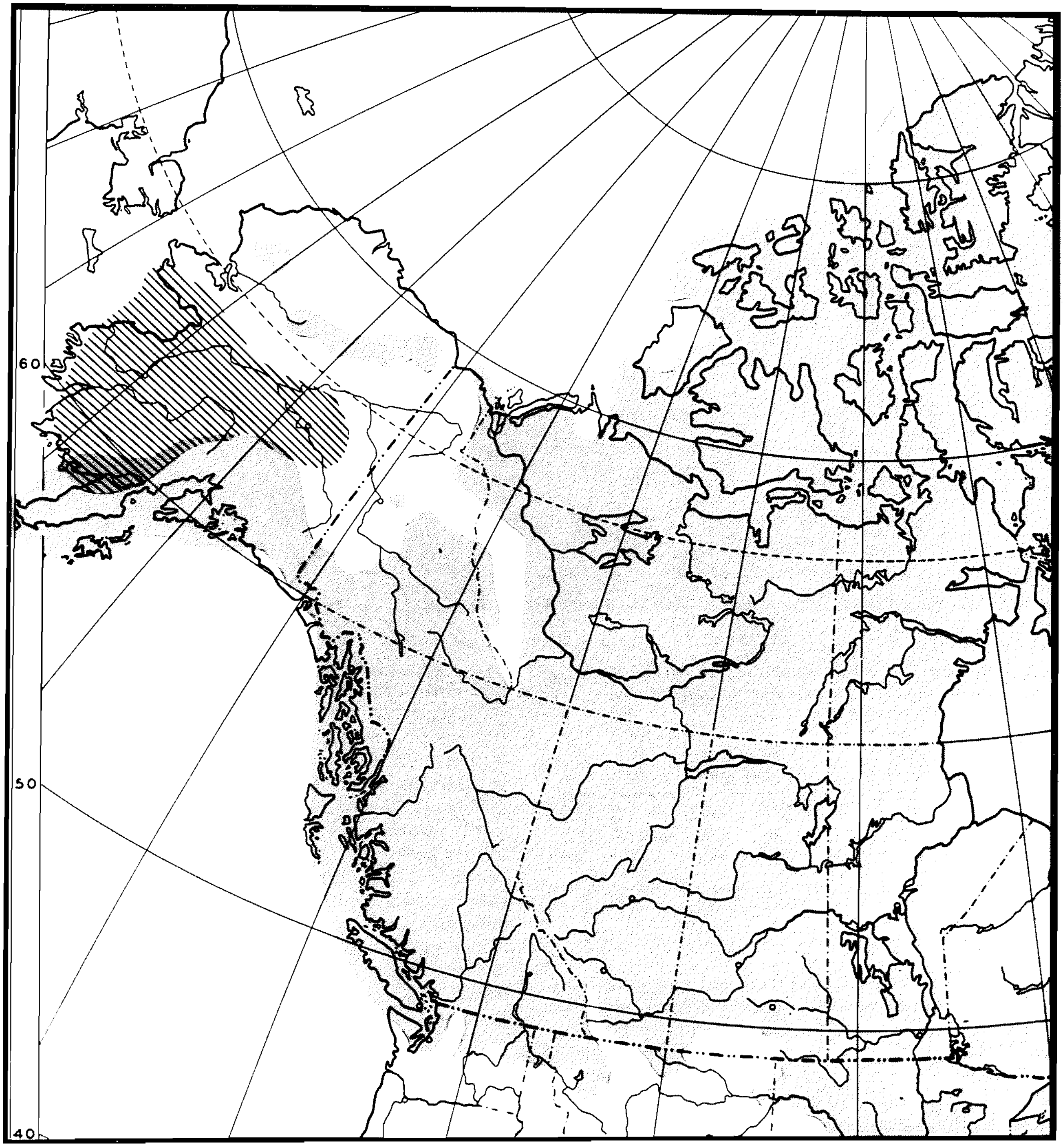

FIG. 3. Distribution of amphimictic *Arnica frigida* (hatched area) in relation to the approximate maximum extent of the Wisconsin glaciation (Prest 1969).

cally indistinguishable from *A. frigida* ssp. *griscomii*. No attempt was made to assess breeding compatability among the three taxa.

Field observations

There was no correlation between morphological differences and habitat; however, subtle differences were apparent between the cytotypes of *A. frigida* ssp. *frigida*. Plants representing the diploid condition were found growing in large rhizomaceous clumps along gravel roadsides, tundras, and meadows. The triploids were found either to be few in number and scattered randomly on rocky hummocks or to form dense mats along roadsides. The pentaploids of northern British Columbia were very infrequent and generally solitary in habit, although some very small clumps were apparent. The pappus on the achenes of *Arnica* greatly enhances their dispersability. However, very few seedlings were observed.

With regard to *A. frigida* ssp. *griscomii*, the only collection obtained from Québec was found to be precariously situated on the limestone precipices of Mt. Saint-Alban. This almost inaccessible population was quite abundant in this locality. Collecting trips to Mt. Logan and Mt. Mattaouisse (see Collins

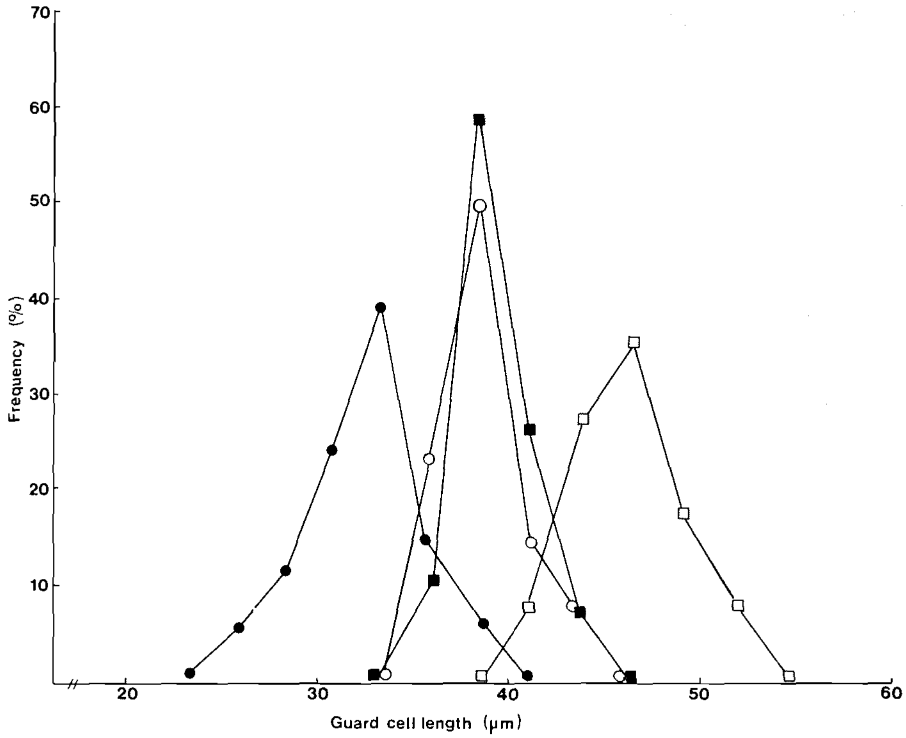

FIG. 4. Guard cell length in the *Arnica frigida–louiseana* complex. ●, diploids; ○, triploids; ■, tetraploids; □, pentaploids.

TABLE 5. Mean guard cell length, standard deviation, and number of cells examined in the *Arnica frigida–louiseana* complex

	Ploidy level			
	2*n*	3*n*	4*n*	5*n*
Mean guard cell length (µm)	12.66[a]	14.97[b]	15.26[b]	17.91[c]
SD	1.20	0.86	0.83	1.09
n	958	516	257	264

NOTE: Within a row, values followed by the same letter are not significantly different ($p > 0.01$). Based on a GT2 method of multiple comparison among pairs of means after analysis of variance.

and Fernald, 1925, for location of the latter) were to no avail. This taxon has been reported to make extensive vegetative carpets along the limestone barrens of northwestern Newfoundland (Fernald 1933). After extensive searching throughout the Port Au Choix area, only two small populations were found. It is feared that *A. frigida* ssp. *griscomii* is not as abundant as it once was and the definite probability of total extirpation exists.

The collecting of *A. louiseana* in Banff and Jasper National parks proved to be somewhat disappointing. This taxon was found to consist of solitary individuals intermittently scattered on alpine tundra slopes or nestled among calcareous rocks at lower elevations. The inaccessibility of many alpine areas precluded an accurate census of these plants in Alberta.

Discussion

The recognition of the three taxa as subspecies of *A. louiseana*, as proposed by Maguire (1943), is rejected on the basis of morphological and cytological evidence. This complex is best treated as *A. louiseana*, *A. frigida* ssp. *frigida*, and *A. frigida* ssp. *griscomii*. The similarity between *A. frigida* ssp. *frigida* and *A. frigida* ssp. *griscomii* strongly suggests that these two taxa are very closely related. *Arnica louiseana* exists as a separate entity, well differentiated from *A. frigida*. Although morphology does not permit the easy separation of *A. frigida* ssp. *frigida* from *A. frigida* ssp. *griscomii*, they can be distinguished on their geographical distribution, habitat specificity, chromosome number, and flavonoid chemistry (S. R. Downie and K. E. Denford, in preparation). The large solitary hemispheric or campanulate–turbinate head, the calciphilous habit, several similar leaf and floral morphological characters, and similar flavonoid profiles all indicate that these three taxa had common ancestry. The differences between these taxa are summarized in Table 6 and illustrated in Fig. 5.

Cytological evidence also supports the view that the *Arnica frigida–louiseana* complex is composed of three related taxa. *Arnica frigida* ssp. *griscomii* has a chromosome number of $2n = 76$ and *A. louiseana* has both $2n = 76$ and 95. Within *A. frigida* ssp. *frigida* is the full polyploid series, ranging from $2n = 38$ to $2n = 95$ (see Tables 1 and 4). The chromosome numbers of $2n = 58$ (Zhukova and Petrovski 1971) and $2n = 60$ (Zhukova 1964, 1965) for *A. frigida* in the USSR are presumed to have been derived from trisomic and pentasomic aneuploidy from the triploid $2n = 57$. Polyploids contain much duplication of genetic material and can tolerate the loss of one or more chromosome pairs (Grant 1971). This can lead to what Darlington (1963) has called a polyploid drop and may account for the $2n = 70$ in *A. frigida* (Zhukova and Tikhonova 1971) and the $2n =$ ca. 67 in *A. louiseana* (Ornduff *et al.* 1967), presumably having originated from the tetraploid $2n = 76$. Ornduff *et al.* (1967) have suggested that because of the small chromosome size in *Arnica*, counts which do not correspond to the base number of 19 are in error and are best treated as approximations. The difficulty in determining an accurate count for *A. frigida* from Ogotoruk Creek, AK (Johnson and Packer 1968) may be due to some unusual cytological be-

TABLE 6. Comparative characters of the *Arnica frigida–louiseana* complex

	A. frigida ssp. *griscomii*	*A. louiseana*	*A. frigida* ssp. *frigida*
Plant height, cm	5–25	4–20	6–40
Leaf glandularity	Absent or inconspicuous	Short stipitate	Absent or inconspicuous
Stem glandularity	Absent	Short stipitate	Absent
Periclinium			
Colour	White	Yellowish gold	Yellow
Glandularity	Absent or inconspicuous	Short stipitate	Absent or inconspicuous
Pubescence	Moderately pilose	Scantily or moderately pilose	Scantily to densely lanate-pilose
Involucre bract			
Shape	Broadly lanceolate	Narrowly lanceolate	Broadly to narrowly lanceolate
Glandularity	Absent or inconspicuous	Short stipitate	Absent or inconspicuous
Pubescence	Pilose at base, glabrous above	Sparingly pilose, otherwise glabrous	Pilose at base, glabrous above to dense wooly–villous
Achene glandularity	Absent or inconspicuous	Glandular towards summit	Absent or inconspicuous
Capitula position	Erect or nodding	Nodding	Erect or nodding
Ligule lobe length, mm	0.4–1.8	0.2–1.5	1.0–5.1
Pollen stainability, %	1–4	0–1	0–100
Chromosome number, 2*n*, and habit	76; rhizomaceous clumps	76; solitary 95	38; rhizomaceous 57; rhizomaceous–solitary 95; solitary
Habitat	Limestone cliffs and barrens in Newfoundland, shale scree in alpine areas of Gaspé	Mature rock slides, alpine slopes and ridges, 6000–7000 ft*	Rocky slopes, tundras, and meadows
Geographic distribution	Long Range Mtns. of western Newfoundland and Gaspé, Qué.	Canadian Rocky Mtns.	Eastern USSR east to Coppermine River, N.W.T., and south to northern British Columbia

*1 ft = 0.3048 m.

haviour which accounts for the lack of pollen produced by this specimen.

Whether the polyploids represent autoploids or amphiploids is difficult to ascertain. Although amphiploidy is far more common in vascular plants (Stebbins 1950), the origin of the polyploid races in the *Arnica frigida–louiseana* complex is debatable. Since a close morphological resemblance between a polyploid and a diploid is not a valid criterion for autoploidy (Grant 1971), other criteria must be used. These include observations of chromosome pairing, fertility, and segregation ratios (Grant 1971) and chemical comparisons (Harborne 1975). Ornduff *et al.* (1967) and Engell (1970) have observed some unusual cytological characteristics in meiotic chromosome pairing in *Arnica*, suggestive of an autoploid origin. Stebbins (1959) stated that autoploids may have been created by hybridization between differently adapted diploids of the same species. The large degree of polymorphism exhibited by *A. frigida* ssp. *frigida* is a function of the variety of adaptative niches that the populations are able to occupy and exploit (Dobzhansky 1950). Grant (1971) has described three primary factors which are necessary to promote polyploidy. These are (*i*) the existence of diploid species to carry different genomes. (*ii*) natural hybridization between species or adapted forms of the same species, and (*iii*) a long-lived growth habit to increase the chances of somatic doubling. Along with the severe arctic climate and the exposed disturbed habitats of Quaternary origin, these three factors may have created the complex polyploid series prevalent within this complex.

Phytogeography

The allopatric distribution of the *Arnica frigida–louiseana* complex suggests that in pre-Pleistocene times these taxa, or their precursors, had a more continuous distribution across North America and the USSR. The ancestor of the present-day *A. frigida* was diploid and may have originated in Alaska where present-day diploids are to be found. Hybridization between diploid ecotypes, or closely related taxa, would promote genetic variability and polyploidy, permitting migration and colonization of areas previously covered by the pre-Wisconsin ice sheets. These ancestors migrated southward and eastward, with the outlying populations represented by higher ploidy levels. This would account for the presence of the present-day tetraploids in western and Atlantic Canada and the pentaploids isolated in northern British Columbia and Alberta. The establishment of ancestral *A. louiseana* in the Canadian Rockies would have had to be very early, probably during the Tertiary, to create the divergence in morphology observed between this taxon and *A. frigida*. The close similarity between *A. frigida* ssp. *frigida* and *A. frigida* ssp. *griscomii* suggests that this group remained confluent for a much longer period of time. With the advance of the Wisconsin glaciation, the intervening portions of their range were eradicated, leaving the plants to survive in northeastern North America and in alpine areas of western North America.

Extensive unglaciated refugia existed in both eastern Siberia and the northern half of Alaska (Hultén 1937; Prest 1969); these acted as a centre for biotic dispersal after glaciation. The Wisconsin glaciation removed *A. frigida* from much of its former range and left the diploids to survive in this arctic refugium (Fig. 3). Subsequent to glacial retreat, the newly created polyploids, and those polyploids persisting from pre-Wisconsin times, were successful in recolonizing these glaciated areas.

There has always been considerable interest in the historical factors which may have produced a disjunction similar to that

FIG. 5. Habit of *Arnica frigida* and *A. louiseana*. (A) *Arnica frigida* ssp. *frigida* (based on *Downie 476* (ALTA)); (B) *Arnica frigida* ssp. *griscomii* (based on *Fernald, Long & Fogg 2140* (MT)); (C) *Arnica louiseana* (based on *Straley 1607* (DAO)).

found in the *Arnica frigida – louiseana* complex (Marie-Victorin 1938; Stebbins 1935; Wynne-Edwards 1937, 1939; Hultén 1937; Rousseau 1953; Drury 1969). To adequately explain the present-day distribution of this complex, it is necessary to postulate the survival of these species in unglaciated areas north and south of the ice sheet, or perhaps in smaller refugial areas surrounded by ice.

To explain the survival of cordilleran and arctic disjuncts in eastern Canada, Fernald (1925) proposed the nunatak hypothesis. This hypothesis has been subject to much controversy in the light of geologic and ecological evidence (Alcock 1935, 1944; Wynne-Edwards 1937; Marie-Victorin 1938; Flint *et al.* 1942; Morisset 1971). In northwestern Newfoundland, recent geological evidence (Brookes 1977; Grant 1977*a*, 1977*b*); corroborates the existence of ice-free areas which may have provided refugia for the glacial and late-glacial vegetation. However, the extreme environment likely to be found during this time may have been detrimental to the survival of many plant species (Morisset 1971). Without further substantiated geological evidence indicating that these refugial areas remained unglaciated throughout the Wisconsin, and information on the glacial and postglacial ecology of the area, the idea of *Arnica* surviving on nunataks during the last glaciation is at best speculative.

Some parts of the continental shelf may have provided refugia for plants during the last glaciation (Ives 1963; Morisset 1971; Terasmae 1973). Terasmae (1973) has reported that at maximum glaciation the sea level would have lowered as much as 130 m and that during the period of deglaciation this level would have increased only 50–60 m. Conditions would no doubt be milder in refugia bordering upon a sea that was not frozen all year round (Morisset 1971). The presence of late-glacial vegetation on the continental shelf (Emery *et al.* 1965; Sirkin 1967; Livingstone 1968; Terasmae 1973) indicates that at least some parts of this area provided refugia from which vegetation later recolonized eastern Canada as the ice sheet retreated.

The definitive signs of total glaciation in all parts of the Gulf of St. Lawrence region (Alcock 1944; Ives 1963; Morisset 1971) precludes the survival of *A. frigida* ssp. *griscomii* on nunataks in the Gaspé Peninsula. It is suggested that these plants would have had to migrate northward from a coastal continental shelf refugium or from a much larger refugium south of the ice sheet. They became established in habitats which provided a cool environment and where they were removed from competition with the better adapted mesophytic flora.

Another explanation to account for the eastern disjuncts of *A. frigida* is long-distance dispersal. The ingestion of the achenes by birds and the presence of the pappus to facilitate wind dispersal are means allowing these arctic plants to reach eastern Canada. However, no intermediate stations of

A. frigida are found, even though equable edaphic conditions exist in central Canada (Given and Soper 1981). The isolated presence of *A. frigida* ssp. *griscomii* on Mt. Logan, Mt. Mattaouisse, and Mt. Saint-Alban in Québec and the localized distribution of this taxon in northwestern Newfoundland would have involved successful colonization by at least four propagules.

In Alberta, it is now generally accepted that portions of the Rocky Mountains remained largely ice-free during maximum Pleistocene glaciations. The concept of an ice-free corridor has received much attention, for there is increasing geologic (Rutter 1980, 1984), stratigraphic (Reeves 1973; Stalker 1977; Stalker and Harrison 1977), palynological (Schweger *et al.* 1981; Ritchie 1984), and chronostratigraphic (Westgate *et al.* 1972; Jackson 1979) evidence for its existence. Present-day plant distributions have also been used as evidence for the existence of unglaciated refugia in Alberta (Packer 1971; Packer and Vitt 1974). *Arnica louiseana* may have survived *in situ* in the Rocky Mountains during the last glaciation or perhaps survived glaciation in close proximity to their present-day sites.

Davis and Heywood (1963) have described subspecies to be regional representatives of a species. A subspecies may be found to differ in chromosone number or be isolated geographically or ecologically (Heywood 1958). These entities lack, however, a sufficient degree of morphological differentiation to be treated as a separate species. We accept this usage and therefore feel that the eastern disjunct of *A. frigida* is best treated as *A. frigida* ssp. *griscomii*.

The most pragmatic approach to species recognition is in utilizing the morphological–geographical species concept (Davis and Heywood 1963). To fulfill this concept, a complete undertaking of biosystematics is inevitable, bringing together information obtained from cytogenetics, phytochemistry, morphology, phytogeography, etc. However, Davis and Heywood (1963) insist that the species recognized must be delimitable by morphological attributes. Reference to Table 6 and Fig. 2 indicates that *A. louiseana* and *A. frigida* conform to this model.

Key to the *Arnica frigida – louiseana* complex

Leaves conspicuously short-stipitate glandular; plants 4–20 cm high; stem glandular; periclinium scantily or moderately yellow–gold pilose; involucral bracts 1.5–3.0 mm broad, sparingly pilose, otherwise glabrous, uniformly short-stipitate glandular; capitula nodding in anthesis; achenes glandular towards summit . . . . *A. louiseana*

Leaves sparsely or not at all glandular; involucral bracts scarcely glandular; capitula erect or nodding in anthesis; achenes rarely glandular

- Plants 6–40 cm high; periclinium sparsely to densely yellow lanate–pilose; involucral bracts 1.8–4.9 mm broad, pilose at base becoming glabrate or remaining densely pilose above . . . . *A. frigida* ssp. *frigida*
- Plants 5–25 cm high; periclinium moderately white pilose; involucral bracts 2.5–4.6 mm broad, pilose at base becoming glabrate above . . . . *A. frigida* ssp. *griscomii*

Arnica frigida Meyer ex Iljin ssp. *frigida*, Trav. Musc. Bot. Acad. Sci. URSS, 19: 112. 1926

A. alpina L., Linnaea, 6: 233. 1831

A. angustifolia Vahl. North Am. Flora, 2: 449. 1843

A. nutans Rydb., North Am. Flora, 34: 328. 1927 (NY!)

A. sancti-laurentii Rydb., North Am. Flora, 34: 329. 1927 (GH!)

A. brevifolia Rydb., North Am. Flora, 34: 329. 1927 (US!)

A. louiseana var. *brevifolia* (Rydb.) Maguire, Madroño, 6: 153. 1942

A. mendenhallii Rydb., North Am. Flora, 34: 329. 1927 (US!)

A. louiseana var. *mendenhallii* (Rydb.) Maguire, Madroño, 6: 153. 1942

A. illiamnae Rydb., North Am. Flora, 34: 331. 1927 (US!)

A. louiseana var. *illiamnae* (Rydb.) Maguire, Madroño, 6: 153. 1942

A. louiseana var. *pilosa* Maguire, Madroño, 6: 154. 1942 (UC!)

A. louiseana ssp. *frigida* (Meyer ex Iljin) Maguire, Madroño, 6: 153. 1942

A. snyderi Raup, Sargentia, 6: 250. 1947 (RM!)

A. frigida var. *glandulosa* Boivin, Rhodora, 55: 56. 1953 (DAO!)

A. louiseana var. *frigida* (Meyer ex Iljin) Welsh, Great Basin Nat. 28: 147. 1968

TYPE: "St. Laurence Bay (and Eschscholtz Bay), 1815–1818. *Eschscholtz s.n.*" (HOLOTYPE LE, PHOTO UC!; ISOTYPE LE, PHOTO UC!).

Plants 6–40 cm high; stems solitary or several from a short branched caudex, rarely branching, glabrate to hispidulous–puberulent below becoming sparsely to densely hispidulous–pilose near the periclinium, leaves to middle of stem, rarely above, leaves of small plants crowded at base; cauline leaves 2–4 pairs, sessile or narrowed to a short-winged petiole; basal leaves tufted with slender petiole as long as the blade, 5–35 mm broad, 12–100 mm long; leaves lanceolate, elliptic to elliptic–lanceolate, spathulate or rarely oblanceolate, apex acute or rarely obtuse, upper leaves frequently reduced and alternate, margins inconspicuously dentate to slightly undulate, rarely entire, glabrate to sparingly hispidulous–puberulent and sparsely or not at all glandular, rarely abundant glandular; periclinium sparsely to densely yellow lanate–pilose, rarely short-stipitate glandular; involucral bracts 7.5–14.5 mm long, 1.8–4.9 mm broad, 2-serial, lanceolate, acuminate, rarely obtuse, pilose at base becoming glabrate or remaining densely pilose above, rarely also somewhat glandular; ligulate florets 7 to 17, 10–39 mm long, 2.3–8 mm wide, the lobes 1.0–5.0 mm long; achenes 3.2–6.0 mm long, usually glabrous below and sparsely hispid at the summit, or seldom uniformly sparsely hispid, rarely glandular; capitula nodding or erect in anthesis, solitary, rarely 3 or more, campanulate–turbinate, 11–30 mm high, 8–20 mm broad; chromosome number $2n$ = 38,57,76,95.

DISTRIBUTION AND HABITAT: Abundant in alpine meadows, tundras, and calcareous rocky outcrops from the Kolyma River, USSR, east to the islands of the Bering Strait, Alaska, Yukon Territory to the Mackenzie River, N.W.T. Scattered populations found north of the Arctic Circle and east to the

Coppermine River, N.W.T., and infrequent to rare in alpine areas of northern British Columbia.

In the earliest revision of North America *Arnica*, Torrey and Gray (1843) placed the first described *A. alpina* L. into the much confounded *A. angustifolia* Vahl complex. Within this complex were also placed *A. fulgens* Pursh, *A. plantaginea* Pursh, and members of the *A. angustifolia* aggregate. Herder (1867) was able to give a much better interpretation of *Arnica* after viewing many collections brought to him from throughout the USSR and Alaska (which at that time was owned by the USSR) and retained *A. alpina L. sensu* Lessing.

Although the actual type specimen was not seen, a photograph was provided by UC. The specimen was collected by Eschscholtz as *A. alpina* L. and appears identical with *A. frigida*. In 1926 Iljin proposed *A. frigida* Meyer ex Iljin.

The following year, Rydberg (1927) proposed five names for the polymorphic *A. frigida* ssp. *frigida*, with the typical species being described as *A. nutans*. Rydberg had probably not been aware of the work of Iljin. The much variable size of *A. frigida* ssp. *frigida* had led Rydberg to give the name *A. mendenhallii* to such large specimens and *A. brevifolia* to the smallest specimens. With the exception of size, these plants are identical with *A. frigida* ssp. *frigida*. The type specimen of *A. sancti-laurentii* was collected at St. Laurence Bay by A. C. Chamisso at the same time as Eschscholtz selected the type of *A. frigida*. Maguire (1943) has observed that these two plants are identical. Chamisso accompanied Eschscholtz on the collecting expedition.

Arnica illiamnae is represented by a specimen which has a distinct glandularity on the herbage and a branching habit. This branching habit is very rarely seen within this species and represents no more than an abnormality in growth form. The glandularity is more prominent than normally found, but otherwise these plants are identical with *A. frigida* ssp. *frigida* and do not warrant taxonomic consideration.

In the vicinity of Mt. McKinley National Park, AK, plants have been found that Maguire (1942, 1943) suggests may represent hybrids between *A. frigida* and *A. angustifolia* ssp. *tomentosa* (Macoun) G. W. Dougl. & G. Ruyle-Dougl. These plants are characterized by erect heads and a dense periclinium and involucral bract pubescence. These plants were described by Maguire (1942) as *A. louiseana* var. *pilosa* and subsequently placed in synonymy with *A. frigida* (Ediger and Barkley 1978). With the exception of the dense pubescence no differences were found between these plants and the typical *A. frigida* ssp. *frigida*. In contrast, Boivin (1953) proposed *A. frigida* var. *glandulosa* for plants lacking a pilose involucre and periclinium. Maguire (1943) has stated that the periclinium frequently furnished an excellent character for the delimitation of specific and subspecific categories. However, the periclinium pubescence is lost or may just be composed of a few white hairs when the plants are transplanted into the greenhouse subsequent to tissue turnover. The degree of periclinium pubescence is undoubtedly a poor character and taxonomic delimitations based upon this character would have to be reevaluated in the light of this environmentally induced trait.

REPRESENTATIVE SPECIMENS: CANADA: YUKON: 20 mi. E. Dawson, *Boivin 3767* (DAO); Quill Creek area, *Freedman s.n.* (DAO); Mt. Peters, *Scotter 20775* (DAO); Mt. Maxwell, *Scotter 21169A* (DAO); Profile Mtn., *Douglas 6345* (DAO); Ogilvie Mts., *Porsild 198* (GH,CAN); 7 mi. E. Little Atlin Lake, *Raup & Correll 11214* (GH,CAN,UBC); N.E. Red Tail Lake, *Raup, Drury & Raup 13465* (GH,CAN); N.E. shoulder Mt. Sheldon, *Porsild & Breitung 11102* (GH,CAN,UC,US); N.E. Ptarmigan Heart, *Raup, Drury & Raup 13760* (GH,CAN); Mtn. S. Haines Rd. Jnctn., *Harris 12068* (GH); S. Kluane Lake, *H. M. & L. C. Raup 12158* (GH); Mile 132 Canol Rd., *Porsild & Breitung 9755* (GH,CAN,NY,UC,US); Mile 95 Canol Rd., *Porsild & Breitung 10467* (GH,CAN, US); Burwash Landing, *Clarke 292* (GH,CAN); Keno Hill, *Porsild 729* (CAN); E. Dempster Hwy. Pass, *Beamish, Krause & Luitjens 681725* (CAN,NY,UBC); McQuesten area, *Campbell 469* (CAN); Ross-Lapie R. Pass, Canol Rd., *Porsild & Breitung 10080* (CAN); Mile 100 Haines Hwy., *Schofield & Crum 8271* (CAN); Firth R., *McEwen 208* (CAN); 13 mi. N.E. Lapierre House, *Youngman & Tessier 600* (CAN); 12 mi. S.W. Haines Jnctn., *Pearson 142* (CAN); E. Herschel Island, *Cooper 33C* (NY); N.W. Dawson City, *Greene 225* (ALTA); Mile 58 Dempster Hwy., *Greene 529* (ALTA); Sunblood Mtn., Virginia Falls, *Carbyn 30* (DAO); Kluane Game Sanctuary, *Freedman 291* (CAN); Mt. Decoeli, *Brink s.n.* (UBC); Whitehorse, *Beamish, Krause & Luitjens 681463* (UBC). BRITISH COLUMBIA: Mile 83 Haines Rd., *Taylor, Szczawinski & Bell 916* (CAN,DAO,UBC); Mile 60 Haines Rd., *Taylor, Szczawinski & Bell 1103* (CAN,DAO); Summit Pass, *Raup & Correll 10507* (GH,CAN,DAO,UBC); Storehouse Creek, *Beamish, Krause & Luitjens 681811* (CAN,UBC); Teresa Island, Atlin Lake, *Buttrick 838* (UBC); Summit Lake, *Rose 78430* (UBC); Spatsizi Plateau, *Krajina s.n.* (UBC). NORTHWEST TERRITORIES: Mount Cody, *Cody & Spicer 11798* (DAO,NY,UBC); Coppermine, *Findlay 129* (DAO); Dodo Canyon, *Cody & Gutteridge 7694* (DAO); Richardson Mts., *Krajina 63071211* (DAO,UBC); Inuvik, *Lambert s.n.* (DAO); Caribou Hills, *Cody & Ferguson 10057* (DAO); Canoe Lake, *Cody & Johansson 12878* (DAO); 5 mi. S. Horne Lake, *Calder 33964* (DAO); Clinton Point, *Parmelee 3185* (DAO,UBC); Mackenzie Mts., *Cody & Scotter 19197* (DAO); Nahanni National Park, *Talbot T6148-3* (DAO); Hornaday River region, *Scotter & Zoltai 25732* (DAO); Mackenzie River Delta, *Porsild 6968* (GH); Britnell Lake, *Raup & Soper 9492* (CAN); 37 mi. N.W. McPherson, *Youngman & Tessier 83* (CAN); S. Richards Island, *Porsild 7080* (CAN); Lone Mt., *Wynne-Edwards 8526* (CAN); W. Cache Creek, *Welsh & Rigby 12060A* (CAN,NY); Cape McDonnel, Great Bear Lake, *A.E. & R.T. Porsild 5162* (CAN). UNITED STATES: ALASKA: Donnelly Dome, *Harms 2804* (ALA,CAN,DAO,GH); Eagle Summit, *Harms 6262* (ALA,DAO,GH); Upper Kurupa River Valley, *Hodgdon & Riedenans 8607* (DAO); Kanayut Lake, *Spetzman 2086* (CAN,DAO); Endicott Mtn., *Cooper CV-685* (DAO); Mile 12 Paxton-Cantwell Hwy., *Webster 188* (DAO); Curry, *Schofield 1850* (DAO); King Salmon, *Schofield 2129* (DAO,GH,NY); Mt. Marathon, *Calder 5621* (DAO,NY,US); Umiat, *Hultén s.n.* (ALA,GH,NY,US); Chandler Lake, *Wiggins 13692* (GH,US); 3–4 mi. downstream from Georgetown, *Drury 1903* (ALA,GH); along Ganes and Yankee Rd., *Drury 3449* (ALA,GH); Moose Pass, *A. & R. Nelson 3492* (ALA,GH, NY,UC,US); Mt. Fairplay, *Scamman 6265* (GH); Wiseman, *Scamman 2302* (GH); Manley Hot Springs, *Scamman 3770* (GH); Takotna, *Anderson & Gasser 7390* (ALA,GH); Norton Sound, *A. E. & R. T. Porsild 930* (GH); Livengood, *Scamman 1766* (GH,US); 12 mi. N.W. Kurupa Lake, *Hodgdon, Glazier & Piedeman 8371* (GH); 13 mi. W. Paxson, *Harms 4167* (ALA,GH); 2 mi. N. Igiugig, *Harms 4317* (ALA,GH); E. Oumalik, *Ward 1478* (CAN,GH,UC,US); Sadlerochit River, *Spetzman 835* (CAN,US); Grayling Lake, *Hettinger 51*

(CAN); Kongakut River Hill, *Hetting 367* (CAN); Anaktuvuk Pass, *Spetzman 1891* (CAN,US); 3 km S.S.E. Cape Sabine, *Shetler & Stone 3162* (CAN); Naknek, *Norberg s.n.* (CAN, GH,UC,US); White Mts., *Gjaerevoll 19* (CAN); S. Tanana River valley, *H. M. & L. G. Raup 12659* (CAN); 2 mi. N. Aniak, *Drury 1501* (ALA,CAN); Guerin Glacier terminus, *Murray 2015* (ALA,CAN); Head Chitina River, *Liang 203* (CAN); Mile 49 Richardson Hwy., *McBeth 360* (NY); Healy, *Anderson 5724* (CAN,NY); Thompson Pass, *J. & C. Taylor 19113* (NY); 7 mi. N. Palmer, *Welsh 4217* (NY); Mile 39 Elliott Hwy., *Welsh 4434* (ALA,NY); Polychrome Pass, *McBeth 223* (NY); Mendenhall, near Juneau, *Anderson 2A375* (PH); Port Clarcua, *Sharp s.n.* (PH); Kigluaik Mts., *Harris 1366* (ALTA); Anvil Mtn., Seward Peninsula, *Harris 1302* (ALTA); 56 km E. Chitina, *Harris 1192* (ALTA); Summit Lake, 10 km N. Paxson, *Harris 1208* (ALTA); Ogotoruk Creek, *Packer 2654* (ALTA); 138 mi. N.N.E. Arctic Village, *Hettinger 367* (ALTA); Utakok R. below Driftwood Creek, *Ward 1269A* (US); Middle fork of Koyokuk River, *Marshall s.n.* (US); Dumpling Mtn., *Hagelbarger 258* (US); Sheenjek Valley, *Mertie s n.* (US); Headwaters of Mulchatna River, *Sargent & Smith 51* (US); Road from Martel to Post, *Muller 697* (US); Johnston Hill, *Muller 1104* (US); N.E. Wonder Lake, *A. & R. A. Nelson 3937* (ALA,US); Bessey Rd., Nome, *Miller 108C* (ALA,US); 12 mi. S. Napamuta, *Miller 289C* (ALA, US); Mt. McKinley National Park, *Mackis 4* (US); Katmai Region, *Hagelbarger 71* (US); Ansktoobak River, *Schrader s.n.* (US); Yukon R. between Rampart and Tanana, *Palmer 55* (ALA, US); Gold Bay, *Piper 4248* (US); Talstoi, *Harrington 35* (US); Lake Schrader, *Scholander & Flagg S-529* (US); Chandler Lake, *Wiggins 13694* (US); S.W. Takotna Mtn., *Layden 165* (US); above Wiseman, *Jordal 2116* (US); downstream from Okpilak River, *Cantlon & Malcolm 58-0023* (US); Pitmegea River, *Cantlon & Gillis 57-452* (ALA,US); between Yukon R., Nation R., and Boundary, *Mertie 113* (US); Richardson Glacier, *Rausch s.n.* (US); Teller Reindeer Station, Walpole 1833 (US); W. side Jago River, *Cantlon & Gillis 57-732* (US); Iliamna Bay, *Gorman s.n.* (US); White Mtn., *Collier s.n.* (US); Wild Lake, N. Bettles, *Jordal 2463* (US); Wahoo Lake, *Chapman 51* (ALA); Tikchuk Lakes, *Densmore 78* (ALA); Marsh Mtn., near Aleknagik, *Roberson 184* (ALA); Killeak Lake, *Racine 99* (ALA); Rainbow Mtn., *Parker RM-75* (ALA); Lava Lake, *Racine 167* (ALA); Finger Mtn., *Murray & Johnson 5067* (ALA); Mile 40 Council Rd., *Parker 235* (ALA); Mile 103 Steese Hwy., *T. P. & J. T. O'Farrell 49* (ALA); Onion Portage, *Scheweger 116* (ALA); Ray Mts., *Kassler 61* (ALA); Noluck Lake, *Parker 196* (ALA); Philip Smith Mts., *Murray & Johnson 6101* (ALA); Wrangell Mts., *Alf et al. 432* (ALA); Lake Peters, *Batten 496* (ALA); Carnivore Creek, *Batten 283* (ALA); Ambresvajun Lake, *A. R. & C. G. Batten 75-401* (ALA); Mile 77-78 Dalton Hwy., *Khokhryakov, Yurtsev & Murray 6673* (ALA); South Hill, *Trent JNT-87-1965* (ALA); Meade River, *Geist s.n.* (ALA); Selawik Hills, *Lipkin 80-135* (ALA); Mile 33 Taylor Hwy., *Nava 38* (ALA); Mt. Hayes, *Anderson 549* (ALA); near Atkasook, *Komarkova et al. 379* (ALA); Cantwell, *Palmer 1915* (ALA); Mile 141.5 Taylor Hwy., *Harms 4920* (ALA); Miller Creek, *Hatler 22* (ALA); Ballaine Lake, *Hatler 5* (ALA); University of Alaska, *Alt 5* (ALA); Oumalik, *Ebersole & Bowman 244* (ALA); Seward, *Helmstetter 80-208* (ALA); Lost River, *Lenarz 80* (ALA); Cape Dyer, *Viereck & Bucknell 4156* (ALA); Fish Creek, *Murray & Johnson 6687* (ALA); Sadlerochit River, *Hendrick 78-100* (ALA); Kipmik Lake, *Young 4874* (ALA); Ikpikpuk River, *Geist s.n.* (ALA); Kokrines, *Miller 1563* (ALA); Serpentine Hot Springs, *Springer s.n.* (ALA); Cape Beaufort, *Stone 915* (ALA); Unalakleet, *Becker 23* (ALA); Takahula Lake, *Jorgensen T191* (ALA); Cape Thompson, *Johnson, Viereck & Melchior 527* (ALA); Dexter Rd., *Heller 986* (ALA); Mile 15.5 Teller Rd., *Walker s.n.* (ALA); Lake Iliamna, *Donaldson 184A* (ALA); 85 mi. N.E. Fairbanks, *Seim s.n.* (ALA); Kilo Hot Springs, *Kassler 270* (ALA); between Castner and Fels glaciers, *Shaughnessy 72-114* (ALA); N. Grayling Lake, *Murray 6713* (ALA); Canning River, *Spetzman 375* (ALA); Independent Ridge, *Spetzman 100* (ALA); Kalubik River, *Mason 76-423* (ALA); Newhalen, *Thomas N-11-52* (ALA); Fielding Lake, *Spooner RSS-P-98* (ALA); Arrigetch Creek, *Cooper CV-685* (ALA); Feather River, *Pegau 273* (ALA); Mt. McKinley National Park, *Gornall 273* (UBC); Marshall, *Harrington 148* (US); Carlo Creek Forest above Carlo Creek, *Carwile 79-161* (ALA); Mount McKinley National Park, *Dixon 56* (UC); on summit between American Creek and King Salmon Creek along Taylor Hwy. to Eagle from Liberty, *Langenheim 4144* (UC); Mile 29 Elliott Hwy., *Harms 3841* (ALA); Feniak Lake, Nakpik Creek, *Young 4355* (ALA); Thompson Pass, Richardson Hwy., *Frohne 53-161* (ALA); Angel Creek and Chena River, *Keller 155* (ALA); Mt. Osborn, Central Kigluaik Mtns., *Kelso 84352* (ALA); Post Lake and Post River, *Parker 475* (ALA); Tin Creek, *Parker 606,649* (ALA); tributary of Big Salmon Fork, *Parker 725* (ALA). USR: Arakamtchetchene Island, *Wright s.n.* (NY); Arakamtchetchene Island, *Anonymous* (NY); Plover Bay, *Dall s.n.* (US); Chukotsky Peninsula, Lake Yoni, *Nechayer, Plieva & Yurtsev s.n.* (ALTA); Chukotsky Peninsula, Chegitun River, *Sekretareva, Sytin & Yurtsev s.n.* (ALTA); Chukotsky National Area, Mt. Pevek, *Shamurin & Yurtsev s.n.* (ALA); Chukotsky Peninsula, Matuchan River, *Karenin et al. sn.* (ALTA); Chukotsky National Area, Anadyr Hills, *Karenin & Petrovsky s.n.* (ALTA); Chukotsky Peninsula, Lavrentiya, *Korobkov s.n.* (ALTA); Chukotsky Peninsula, Leningrad, *yurtsev s.n.* (ALTA); Chukotsky Peninsula, Lultin, *Zimarskaya, Korobkov & Yurtsev s.n.* (ALTA); Chukotsky Peninsula, Yoniveem River, *Nechayev, Plieva & Yurtsev s.n.* (ALTA).

Arnica frigida ssp. ***griscomii*** (Fern.) S. R. Downie, comb. nov.

A. griscomii Ferald, Rhodora, 26: 105. 1924

A. louiseana ssp. *griscomii* (Fern.) Maguire, Brittonia, 4: 419. 1943

A. louiseana var. *griscomii* (Fern.) Boivin, Phytologia, 23: 95. 1972.

TYPE: "Quebec, Matane County. Cold chimneys in the schist at about 900−100 m altitude, south of Fernald Pass, Mt. Mattaouisse, August 20, 1923. *M. L. Fernald and L. B. Smith 26084*" (HOLOTYPE GH!; ISOTYPES MT!, UC!; PHOTO UC!).

Plants 5−25 cm high; stems several from a short branched caudex, simple, glabrate below to sparingly villous above, leaves to middle of stem; cauline leaves 1 or 2 pairs, sessile or narrowed to a short-winged petiole; basal leaves tufted with slender petiole as long as the blade, 6−25 mm broad, 15−80 mm long; leaves spathulate to ovate or lanceolate−oblong, apex acute or obtuse, margins dentate to slightly undulate, glabrous to sparingly hispidulous−puberulent and sparsely or not at all glandular; periclinium moderately white pilose, rarely short-stipitate glandular; involucral bracts 9−13.5 mm long, 2.5−4.6 mm broad, 2-serial, broadly lanceolate to oblanceolate, apex acuminate to obtuse, pilose at base becoming glabrate above, rarely sparsely glandular; ligulate florets 6 to 11, 15−22 mm long, 3−6 mm broad, the lobes 0.4−1.8 mm long; achenes 2.5−4.5 mm long, mostly glabrous below middle, short-hirsute above, rarely glandular; capitula nodding or erect in anthesis, solitary, hemispheric to occasionally turbinate, 12−23 mm high, 11−20 mm broad; chromosome number $2n = 76$.

DISTRIBUTION AND HABITAT: Rare on exposed hornblende schists and dry schistose talus in the alpine areas (850−1070 m) of Mt. Logan, Mt. Mattaouisse, and Mt. Saint-Alban of Gaspé, Qué., and infrequent in the turfy talus of limestone sea cliffs and gravelly limestone barrens in the areas of Ingornachoix Bay, St. John Bay, St. Barbe Bay, and the Doctor Hill Range of northwestern Newfoundland.

While studying specimens of *A. louiseana* and observing no morphological differences between this taxon and *A. frigida* ssp. *griscomii*, Fernald (1933) combined his previously proposed *A. griscomii* (Fernald 1924) to the earlier proposed name of *A. louiseana*. However, the apparent differences led Maguire (1943) to propose *A. louiseana* ssp. *griscomii*.

REPRESENTATIVE SPECIMENS: CANADA: NEWFOUNDLAND: St. John Bay, *Fernald, Long & Fogg 2141* (DAO,GH,MT, NY,PH,US); St. John Bay, *Fernald, Long & Fogg 2139* (DAO,GH,MT,NY,PH,US); S.W. Port Au Choix, *Fernald, Long & Fogg 2142* (GH,MT,NY,PH,US); region between St. John Bay and Ingornachoix Bay, *Fernald, Long & Fogg 2143* (GH,MT,PH); St. John Bay, *Fernald, Long & Fogg 2140* (GH,MT,NY,PH,US); St. John Island, *Fernald et al. 29216* (GH,PH); St. Barbe S. District, Port Au Choix, *Hay & Bouchard 74031* (CAN); Doctor's Hill, St. Barbe, *Tuomikoski 343* (CAN,MT); Old Port Au Choix, *Penson s.n.* (MT,US); QUÉBEC: Mt. St-Alban, *Marie-Victorin, Rolland-Germain & Dominique 49028* (DAO,MT); Matane Co., Mt. Mattaouisse, *Fernald, Griscom, Mackenzie, Pease & Smith 26082* (MT,NY,US); Matane Co., Mt. Logan, *Pease & Smith 26083* (MT,NY); Matane Co., Mt. Mattaouisse, *Fernald & Smith 26085* (NY,US).

Arnica louiseana Farr, Ottawa Nat. 20: 109.1906
A. louiseana ssp. *genuina* Maguire, Brittonia, 4: 419. 1943

TYPE: "Lake Louise, Canadian Rocky Mts. Rockslide on Fairview Mt. Alt. about 6000 ft., August 18, 1905. *E. M. Farr 1067*" (HOLOTYPE PH!, ISOTYPE GH).

Plants 4−20 cm high; stems solitary from a short branched caudex, simple, glandular−puberulent, leaves to middle of stem or rarely all basal; cauline leaves 1−3 pairs or none, sessile or narrowed to a short-winged petiole; basal leaves 4−20 mm broad, 13−75 mm long; leaves elliptic to oblong to ovate−lanceolate, apex obtuse or occasionally acute or acuminate, margins entire to saliently denticulate to slightly undulate, uniformly short-stipitate glandular; periclinium scantily to moderately yellowish gold pilose, short-stipitate glandular; involucral bracts 8−12 mm long, 1.5−3.0 mm broad, 2-serial, narrowly lanceolate, acuminate, sparingly pilose otherwise glabrous, uniformly short-stipitate glandular; ligulate florets 7 to 10, 12−20 mm long, 2.5−4.6 mm broad, the lobes 0.2−1.5 mm long; achenes 3.2−5.0 mm long, glabrate below, short-hirsute and glandular towards the summit or occasionally uniformly pubescent; capitula nodding in anthesis, solitary, campanulate−turbinate, 9−20 mm hign, 8−17 mm broad; chromosome number $2n = 76, 95$.

DISTRIBUTION AND HABITAT: Infrequent and localized on exposed alpine tundra slopes and mature calcareous rock slides at 1800−2100 m in the Canadian Rocky Mountains of Alberta in the vicinities of Waterton, Jasper, and Banff national parks. Although it can be reasonably expected to find *A. louiseana* in the Rocky Mountains of British Columbia, to date Kootenay National Park is the only location *A. louiseana* has been found (Douglas 1982).

REPRESENTATIVE SPECIMENS: CANADA: ALBERTA: top of Mt. Bourgeau, *Scotter 10062* (DAO); Flanc N. du N. Saskatchewan, *Boivin 5093* (DAO); Mt. Wilson, *Breitung, Porsild & Boivin 2938* (DAO); W. Hailstone Butte, Livingstone R., *Norris 72* (DAO); Mt. Edith Cavell, *Calder 37189* (DAO); Mt. Anderson, *Breitung, Porsild & Boivin s.n.* (DAO); Maligne Lake, *Scotter 9797* (DAO); Moraine Lake, *Straley 1607* (DAO); Mt. Paget, *Macoun* (CAN,GH,NY,US); S. Peyto Lake, *Weber 2446* (GH,NY,UC); Mt. Patterson, *Porsild & Breitung 16164* (CAN); Snow Creek Pass, *Porsild 22666* (CAN); Clearwater Forest Reserve, N. Nordegg, *Porsild 20718* (CAN); Panther Mtn., *Porsild & Breitung 16280* (CAN); Bow River Pass, *Porsild & Breitung 14927* (CAN); Mt. Saskatchewan, *Porsild & Breitung 16067* (CAN); Columbia Icefields, *Scoggan 16440* (CAN); Sulphur Mtn., *Sanson 309* (CAN); Whistler Mtn., *Laing s.n.* (CAN); Lake Louise, *Macoun 65520* (CAN,NY); Mt. Richards, *Breitung 17454* (NY); Mt. Richards, *Breitung 17457* (ALTA); Lake Louise, *Farr s.n.* (PH); Whitehorse Creek, *Dumais & Andrewchow 5239* (ALTA); 3 mi. S. Cadomin, *Dumais 6274C* (ALTA); Bald Hills, *Kuchar s.n.* (ALTA); Prospect Mtn., *Mortimer 438* (ALTA); Anderson Peak, *Kuchar 2901* (ALTA); Whitegoat Wilderness, *Lee s.n.* (ALTA); Lake Louise, *Brown 665* (GH,NY,PH); Peyto Lake, *Dudynsky 7841* (ALTA); Columbia Icefields, *Dudynsky 7842* (ALTA); Bald Hills, Maligne Lake, *Dudynsky 7849* (ALTA); Cadomin, *Dudynsky 7854* (ALTA).

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