Morphological, cytological, and flavonoid variability of the *Arnica angustifolia* aggregate (Asteraceae)

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The *Arnica angustifolia* aggregate is a circumpolar taxon previously consisting of a number of geographically distinct infraspecific taxa. Cluster and principal component analyses of 99 populations revealed the aggregate to be best represented by two subspecies: *A. angustifolia* subsp. *angustifolia* (a combination of the previously recognized subspecies *angustifolia, attenuata, sornborgeri, intermedia, iljinii*, and *alpina* and *A. plantaginea*) and *A. angustifolia* subsp. *tomentosa. Arnica angustifolia* subsp. *angustifolia* is polymorphic and varied in ploidy level and foliar flavonoid chemistry. No significant differences were found among the means of 14 characters in plants collected from six broadly delimited geographic areas. Four cytotypes ($2n$ = 38, 57, 76, and 95) and seven flavonoid glycosides (five flavonols and two flavones) were discerned. The aggregate is predominantly agamospermous with amphimictic phases in unglaciated Alaska and west central Yukon. Disjunct distributions are probably the result of survival in refugia during the late Wisconsinan.

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L'ensemble *Arnica angustifolia* est un taxon circumpolaire qui autrefois comprenait un certain nombre de taxons infraspécifiques géographiquement distincts. Des groupements et des analyses en composantes principales de 99 populations ont révélé que l'ensemble est mieux représenté par deux sous-espèces : *A. angustifolia* subsp. *angustifolia* (une combinaison des anciens sous-espèces *angustifolia, attenuata, sornborgeri, intermedia, iljinii* et *alpina* et *A. plantaginea*) et *A. angustifolia* subsp. *tomentosa*. L'*Arnica angustifolia* subsp. *angustifolia* est polymorphe et varié en ce qui concerne la ploïdie et la chimie des flavonoïdes foliaires. L'auteur n'a pas noté de différences significatives entre les moyennes de quatorze caractères chez des plants récoltés de six grandes régions géographique. Quatre cytotypes ($2n$ = 38, 57, 76 et 95) et sept glycosides flavonoïdes (cinq flavonols et deux flavones) ont été perçus. L'ensemble est surtout agamosperme avec des phases apomictiques en Alaska non glaciaire et vers l'ouest du Yukon central. Les distributions disjointes sont probablement le résultat de survie dans des refuges au cours du Wisconsinien supérieur.

[Traduit par la revue]

Introduction

Arnica angustifolia sensu lato (Asteraceae) is one of a number of complex aggregates in subgenus *Arctica*. Delimitation of taxa within this aggregate has been difficult owing to the polymorphic, apomictic, and polyploid nature of these plants. The apparent intergradation in morphology between the members of this aggregate has promoted considerable taxonomic confusion.

In his major treatment of the aggregate, Maguire (1943) recognized seven taxa: subspecies *angustifolia, attenuata, tomentosa, sornborgeri, intermedia, iljinii*, and *alpina* (subspecies *genuina* being illegitimate) of *Arnica alpina* (L.) Olin. Ferguson (1973), however, has rejected the commonly used name of *A. alpina* because it is a later homonym of *A. alpina* Salisb., a *Doronicum* species. The next available name, *A. angustifolia*, was proposed by Vahl in 1816 for plants collected in Greenland. Since then, the name *A. angustifolia* Vahl has been variously attributed to different plants of North America, Europe, and the USSR.

Circumpolar in distribution, these taxa occupy distinct geographical areas. Subspecies *angustifolia* is widespread throughout the North American arctic, found from Greenland west to Alaska and south to the Northwest Territories. Subspecies *attenuata* is more inland and southern, ranging from central Alaska eastward to northern Manitoba and Ontario. Subspecies *tomentosa* and *sornborgeri* form the southern radiants, the former found in western North America with disjunct populations in Newfoundland and the latter in eastern North America, distributed from Hudson Bay through northern Quebec to Newfoundland. Subspecies *intermedia* is a very localized population of the Okhotsk region in western USSR, whereas subspecies *iljinii*, according to Maguire (1943), is widespread throughout arctic Siberia. Subspecies *alpina* is found in northern Scandinavia and Spitsbergen.

Previous studies have recognized the morphological variation within *A. angustifolia* (Maguire 1943; Benum 1958; Polunin 1959; Engell 1970; Ediger and Barkley 1978; Douglas 1982). Plants have been described from the Northwest Territories (Raup 1947) and Greenland (Jorgensen *et al.* 1958) that fit into the circumscription of subspecies *alpina* from Scandinavia. Ediger and Barkley (1978) have stated that "the species consists of some seven thoroughly integradient varieties, each of which is variable and might sometimes be mistaken for another variety in the absence of geographic data." Characters previously used to distinguish these taxa include the presence of long stipitate-glandular hairs within the periclinium; plant height; number of pairs of cauline leaves; number of capitula; leaf and periclinium pubescence; and the lengths of the achenes, disc corollas, and teeth of the ray florets. However, I have observed that these characters are confluent and variable, suggesting that the subspecies may not be very well separated. In addition, a great deal of variability was evident within each taxon.

In North America, taxonomic treatments range from recognition of one species, composed of four confluent varieties (Ediger and Barkley 1978), to four separate species (Rydberg 1927). In Europe and the USSR, Iljin (1961) has recognized

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subspecies *alpina, intermedia*, and *iljinii* at the species level.

Arnica plantaginea Pursh, a taxon closely related to *A. angustifolia* subsp. *sornborgeri*, has been distinguished from the latter solely on possession of oblanceolate involucral bracts (Maguire 1943). Its range, similar to that of *A. angustifolia* subsp. *sornborgeri*, extends from Labrador westward to the northeastern shore of Hudson Bay. Ediger and Barkley (1978) have, without comment, combined this taxon with *A. angustifolia* subsp. *sornborgeri* as *A. alpina* var. *plantaginea*. During this study, I have noticed that the morphological differences between these taxa are minimal, and these oblanceolate bracts characteristic of *A. plantaginea* can be found in *A. angustifolia*. For this reason, specimens annotated as *A. plantaginea* have been included within the *A. angustifolia* aggregate.

The basic chromosome number for *Arnica* was shown by Böcher and Larsen (1950) and Ornduff *et al.* (1967) to be $x = 19$, with cytotypes of $2n = 38$, 57, 76, and 95 being reported. Previously reported chromosome counts are summarized in Table 1.

The primary purpose of this study was to investigate the presence and extent of morphological variability in geographically delimited samples of the aggregate from throughout its range and to correlate the morphological variability with chromosome number and flavonoid chemistry. A revised classification of the aggregate will be prepared based on the information obtained.

Materials and methods

Field studies and collections

Field collections of the western North American members of the *A. angustifolia* aggregate were made during the summers of 1982 to 1985. Materials for morphological, flavonoid, and experimental analyses were collected from 109 populations. A voucher specimen for each population collected from the field, as well as those cultivated in the greenhouse, was deposited at the University of Alberta Vascular Plant Herbarium (ALTA). Live plant material was transplanted from the field and transported to the University of Alberta Phytotron for cultivation. Achenes of taxa from Scandinavia, USSR, and eastern Canada were provided by the following botanic gardens: V. L. Komarov Botanical Institute, Leningrad; Main Botanic Garden, Moscow; Botanical Garden of Bochum, West Germany; Botanical Garden of the University of Uppsala, Sweden; and the Botanic Garden of the University of Copenhagen.

Phenetic analyses

A study of herbarium specimens from throughout the entire range of the aggregate, comprising type material and approximately 800 specimens, involved material from or visits to the following herbaria: ALA, ALTA, C, CAN, GH, ICEL, L, MT, NY, MONT, O, PH, RM, SASK, UBC, and US. A list of representative specimens, too numerous to be included in this paper, can be supplied by the author upon request. After tentative identification, a sample of 99 specimens was drawn which fell into the circumscription of the aggregate (refer to Downie, 1987, for a listing of these specimens). Since taxonomic boundaries among the previously recognized infraspecific taxa (*sensu* Maguire) were difficult to ascertain because of the polymorphism exhibited by these plants, the specimens used in the phenetic analyses were selected from six broadly delimited geographic areas throughout the aggregate's range. These specimens were also selected to reflect the apparent morphological variability encountered within each area. Delimitation of these areas was as follows: 1, eastern Canada; 2, central Canada and Montana; 3, arctic Canada and Alaska; 4, northern Scandinavia and Spitsbergen; 5, USSR, and 6, Greenland. The occurrence of regional morphological differentiation in *A. angustifolia* and *A. plantaginea* was investigated by determining the means, standard deviations, and ranges for 14 quantitative characters (see Table 2).

To assess phenetic relationships, 17 floral and 9 vegetative characters (comprising 16 strictly continuous characters and 10 ordered multistate characters) were chosen (Table 3). Criteria for character selection and quantification are described in Downie (1987).

To explore the taxonomic structure of the aggregate, cluster and principal component analyses (PCA) were performed using the SAS Statistical Package (SAS Institute Inc. 1985) and the computing facilities at the University of Ottawa. Data were standardized and used to calculate the dissimilarity matrix using squared Euclidean distance. Phenograms were generated using average linkage clustering (UPGMA) because it gave the least amount of distortion between the matrix and the phenogram, as indicated by the highest cophenetic correlation coefficient, than other similarity – dissimilarity coefficients. Standardized data were also used in the principal component analysis to observe variation in the data set. The data matrix utilized in these numerical analyses is presented in Downie (1987).

Cytological and pollen viability analyses

Methodologies used for acetocarmine root-tip squashes and pollen-grain viability testing have been previously published (Downie and Denford 1986*a*). Voucher slides for each examined collection are filed at ALTA.

Flavonoid analysis

Determination of foliar flavonoid constituents within the *A. angustifolia* aggregate was accomplished using the modified procedures of Mabry *et al.* (1970), Ribereáu-Gayon (1972), and Markham (1982). The precise methodology for the isolation and identification of *Arnica* flavonoids is reported in Downie and Denford (1986*b*). Owing to the limited availability of material from eastern Canada, Europe, and the USSR, extensive chemical analyses were only carried out for those taxa from western North America. Ninety-two collections of *A. angustifolia* were analyzed in this study. Collections from Greenland have also been included, but again, because of sparse material, flavonoid determination was not accomplished through exhaustive extraction and examination but rather by comparing the profiles obtained with those of *A. angustifolia* from Canada. Eight collections from Greenland were examined in this manner.

Results

Morphological variation

The wide range exhibited in plant height, leaf size and shape (Fig. 1), glandularity, number of capitula, capitulum size, and the length of the teeth on the ligulate florets is evident in *A. angustifolia*. By using Gabriel's modification of the GT2-method for multiple comparisons among pairs of means for unequal sample sizes (Sokal and Rohlf 1981), no significant differences ($P = 0.05$) were found among the means of 14 characters from specimens collected in six broadly delimited geographic areas (Table 2). Character variation among plants from each of these areas was found to be nearly continuous, suggesting that the taxa are not morphologically distinct. These characters have been previously used to delimit infraspecific taxa within *A. angustifolia* (Maguire 1943). A collection of OTUs (operational taxonomic units) possessing densely villous leaves and stems, small entire leaves, and a single (rarely three) capitulum from 2 of the 6 geographic areas was discerned.

Cluster analysis

A phenogram for the 99 OTUs of the *A. angustifolia* aggregate was constructed using UPGMA (Fig. 2). The cophenetic correlation coefficient between the original dissimilarity matrix and the phenogram was 0.78. Seven major clusters of OTUs were established by arbitrarily drawing a phenon line at the 1.90 level. Cluster 1 is a rather large homogeneous group

TABLE 1. Previously reported chromosome numbers in the *Arnica angustifolia* aggregate. Presented are taxon, meiotic or somatic chromosome number, locality of specimen, and reference

Taxon	*n*	2*n*	Locality	Reference
A. angustifolia subsp. *alpina* (= subsp. *angustifolia*)		54	NRWY: Baatsfjord, Anneelv	Engelskjon and Knaben 1971
		56	NRWY: Alta, Altaelv	Engelskjon and Knaben 1971
		56	NRWY: Overbygd, Riidagierdo	Engelskjon and Knaben 1971
		56	NRWY: no locality information	Nygren 1954
		56	SPTSBRGN: Isfjorden	Flovic 1940
		57	NRWY: Vardo	Löve and Löve 1975
		57	SPTSBRGN: no locality information	Löve and Löve 1975
		60	SWDN: Abisko	Afzelius 1936
A. angustifolia subsp. *angustifolia*		38	YT: km 132 Dempster Hwy.	Wolf 1980
		38	YT: km 137 Dempster Hwy.	Wolf 1980
		50–60	GRLD: Clavering Island	Jorgensen *et al.* 1958
		ca. 57	NWT: Melville Island	Mosquin and Hayley 1966
		57	YT: km 138 Dempster Hwy.	Wolf 1980
		57	GRLD: Mesters Vig	Engell 1970
		76	GRLD: Sdr. Strømfjord	Böcher and Larsen 1950
		76	GRLD: Lyell's Land	Engell 1970
		76	GRLD: Holsteinborg	Engell 1970
		76	GRLD: Sdr. Strømfjord	Engell 1970
		95	GRLD: Marrait	Engell 1970
A. angustifolia subsp. *attenuata* (= subsp. *angustifolia*)	19		YT: Dawson	Wolf 1980
	19		YT: km 4 Dempster Hwy.	Wolf 1980
	19		YT: km 1.6 Mayo Road	Wolf 1980
	19		YT: 108 km N. Stewart Crossing	Wolf 1980
	19		YT: km 270 Klondike Hwy.	Wolf 1980
	19		AK: Boundary	Wolf 1980
	19		AK: km 2098 Alaska Hwy.	Wolf 1980
		38	YT: Dawson	Wolf 1980
		38	AK: km 79 Taylor Hwy.	Wolf 1980
		38	AK: no locality information	Barker 1967
		57	BC: km 132 Haines Hwy.	Wolf 1980
		57	YT: Dawson	Wolf 1980
		57	YT: 7.5 km S. Haines Junction	Wolf 1980
		57	YT: 26 km S. Haines Junction	Wolf 1980
		57	YT: 24 km W. Whitehorse	Wolf 1980
		57	YT: km 1788 Alaska Hwy.	Wolf 1980
		57	AK: 32 km S. Palmer	Wolf 1980
		57	YT: Whitehorse	Löve and Löve 1975
		ca. 57	YT: Ogilvie Mountains	Mulligan and Porsild 1970
A. angustifolia subsp. *sornborgeri* (= subsp. *angustifolia*)		76	PQ: Fort Chimo	Löve and Löve 1975
		76	PQ: no locality information	Hedberg 1967
A. angustifolia subsp. *iljinii* (=subsp. *angustifolia*)	19		USSR: no information given	Barker 1967
		56	USSR: Baranikha, W. Chukotka	Zhukova 1966
		56	USSR: Aljarmagtji R., Chukotka	Zhukova 1967
		56	USSR: Basseyna R., Komi	Sokolovskaya 1970
		56	USSR: Yagodniy R.	Zhukova and Petrovsky 1976
		56	USSR: Cherskiy	Zhukova *et al.* 1977
		56	USSR: Wrangell Island	Zhukova and Petrovsky 1972
		56	USSR: Siberia	Zhukova *et al.* 1973
		57	USSR: Archangelsk	Löve and Löve 1975
A. plantaginea (= subsp. *angustifolia*)		ca. 70	USSR: Arcto-Alpine Botanic Garden (original locality unknown)	Zhukova 1964
A. angustifolia subsp. *tomentosa*	38		ALTA: Banff Park	Wolf 1980
		57	ALTA: Banff Park	Wolf 1980
	38		ALTA: Mountain Park	Wolf 1980
		57	YT: Mackenzie delta	Löve and Löve 1975
		76	ALTA: Banff Park, Peyto Lake	Straley 1979

consisting of 58 OTUs of *A. angustifolia* from throughout its range. These OTUs represent collections obtained from Scandinavia, USSR, Spitsbergen, and across North America from Alaska to Greenland and south to Ontario and have been previously recognized as subspecies *angustifolia, alpina, attenuata, iljinii, intermedia*, and *sornborgeri*. Cluster 2 includes 13 OTUs possessing densely villous leaves, stems, and involucral bracts. These plants have been referred to as *A. angustifolia* subsp. *tomentosa*. Cluster 3 represents an isolated OTU from the USSR characterized by abundant involucral bract

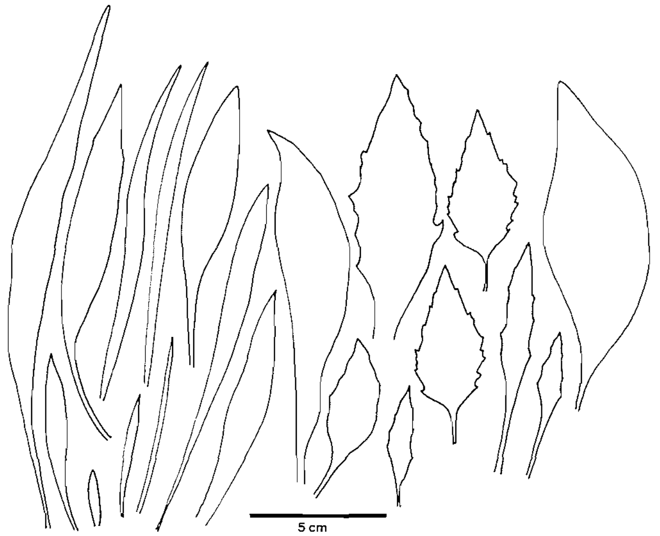

FIG. 1. Basal leaf shape variation among selected *Arnica angustifolia* subsp. *angustifolia* specimens.

glandularity and numerous narrow ligulate florets. With the exception of bearing these two anomalous traits, this plant is similar to those in cluster 1. Cluster 4 includes five OTUs from eastern Canada. These OTUs are represented by small plants with linear to narrowly lanceolate leaves, and short teeth on the ligulate florets. All 18 OTUs in cluster 5 possess three to five capitula per stem and are slightly larger in habit than those OTUs in cluster 1. Although most OTUs in this cluster represent plants from the southern and eastern North American ranges of *A. angustifolia*, some are representative of those from USSR and Greenland. These OTUs have been previously recognized as *A. plantaginea* and the subspecies *angustifolia, alpina, attenuata, iljinii,* and *sornborgeri* of *A. angustifolia*. The number of capitula and height of the plant have traditionally been used to distinguish between some of the subspecies of *A. angustifolia*. However, I have observed that when plants collected from throughout the range of the aggregate are grown alongside one another, all are morphologically indistinguishable and possess three or more capitula.

The hierarchical ordering prevalent during phenogram production cannot specify all inter-OTU relations. In addition, some linear ordering is necessary when the phenogram is produced on the printed page. Adjacent OTUs may be quite dissimilar, or OTUs in widely separated parts of the phenogram may be more similar to one another than to their neighbours. Cluster 6 comprises two OTUs from Alberta and Yukon that are characterized by smaller achenes and narrower involucral bracts than those plants in cluster 1. They represent no more than an end point in the normal range of morphological variation. Cluster 7 contains two anomalous specimens of *A. angustifolia* subsp. *tomentosa* collected in Newfoundland. These two specimens are characterized by large capitula, broadly lanceolate bracts that are not densely villous, and wide ligulate florets and should be most closely related to those OTUs in cluster 2. Results of UPGMA cluster analysis and greenhouse investigations suggest that the *Arnica angustifolia* aggregate may be composed of two major groups: a polymorphic *A. angustifolia* subsp. *angustifolia* and *A. angustifolia* subsp. *tomentosa*.

Principal component analysis

Of the 26 components that accounted for the total variance of the data, the first three principal component axes accounted for 49.8% (26.0, 14.8, and 9.0% respectively). The remaining 23 component axes each accounted for 8.1% or less of the remaining variance. Group separation was achieved by plotting the component scores for axes 1 and 2 (Fig. 3) and axes 2 and 3 (Fig. 4). In both plots, the 13 OTUs comprising *A. angustifolia* subsp. *tomentosa* formed isolated groups, with

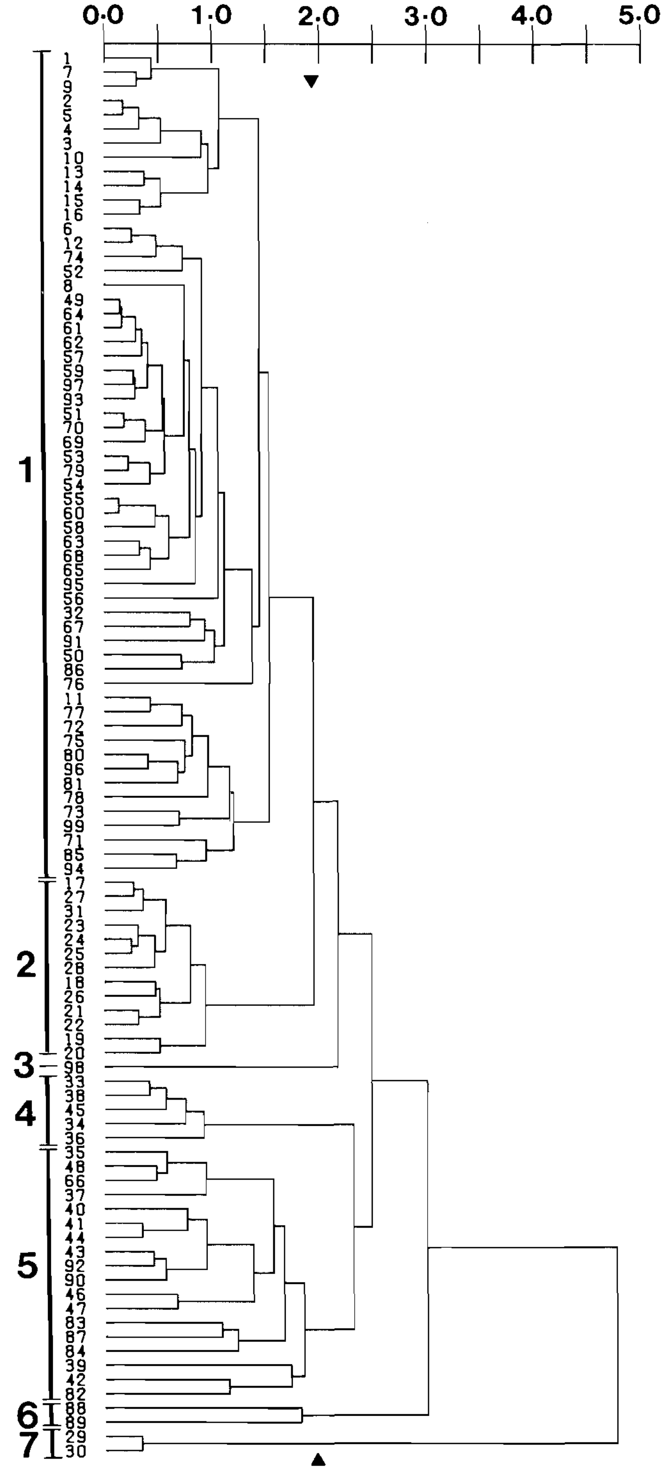

FIG. 2. UPGMA phenogram of 99 OTUs comprising the *Arnica angustifolia* aggregate based on Euclidean distance. Base nodes are labelled with OTU identity. The seven clusters are defined in text. Arrows indicate 1.90 phenon level.

TABLE 2. Data summary for 14 morphological characters in six geographically delimited samples

Character	Area 1 (n = 28)			Area 2 (n = 34)		
	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
Plant height (cm)	21.8	6.59	10.5–41.0	28.7	10.47	5.0–54.0
Basal leaf blade length (cm)	7.4	1.94	4.0–14.0	8.6	2.42	4.0–14.5
Basal leaf blade width (cm)	0.9	0.43	0.3–2.2	1.1	0.38	0.5–2.0
Capitulum width (mm)	20.5	3.29	13.0–27.0	19.7	3.43	13.0–25.0
Capitulum height (mm)	15.1	2.33	10.0–21.0	14.7	2.83	10.0–20.0
Achene length (mm)	4.9	0.59	3.9–7.0	4.9	0.50	4.0–5.8
Involucral bract length (mm)	12.2	1.78	7.5–17.6	10.7	1.73	7.0–15.0
Involucral bract width (mm)	2.5	0.38	2.0–3.6	2.5	0.51	1.5–3.5
Ligulate floret tooth length (mm)	1.4	0.73	0.3–5.0	1.4	0.66	0.5–3.0
Ligulate floret length (mm)	26.0	4.28	10.1–40.0	22.8	4.64	11.5–29.0
Ligulate floret width (mm)	5.9	0.95	4.0–8.5	5.7	1.21	3.8–9.1
Ligule number (per capitulum)	10.7	1.59	7.0–13.0	10.2	1.89	6.0–14.0
Disc corolla length (mm)	8.0	0.71	5.5–9.1	7.9	0.85	6.5–9.5
Disc corolla tube length (mm)	3.4	0.35	2.4–4.1	3.0	0.26	2.5–3.5

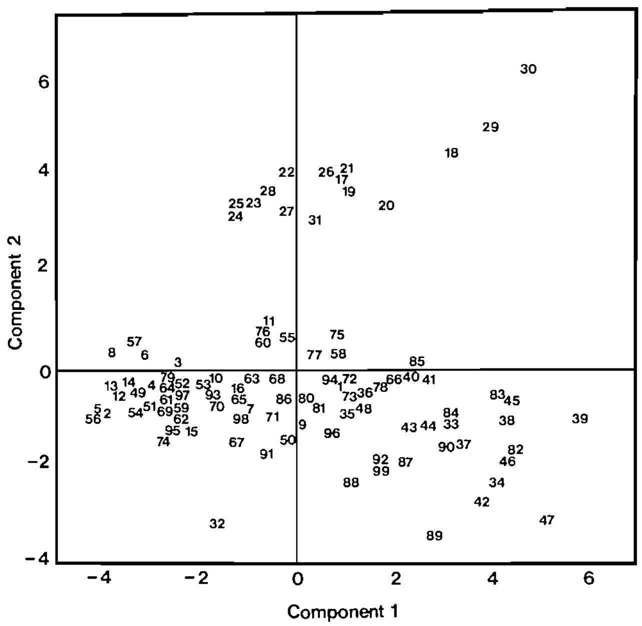

FIG. 3. Ordination of 99 OTUs of the *Arnica angustifolia* aggregate generated by plotting the first two principal components. Numbers refer to OTU identity.

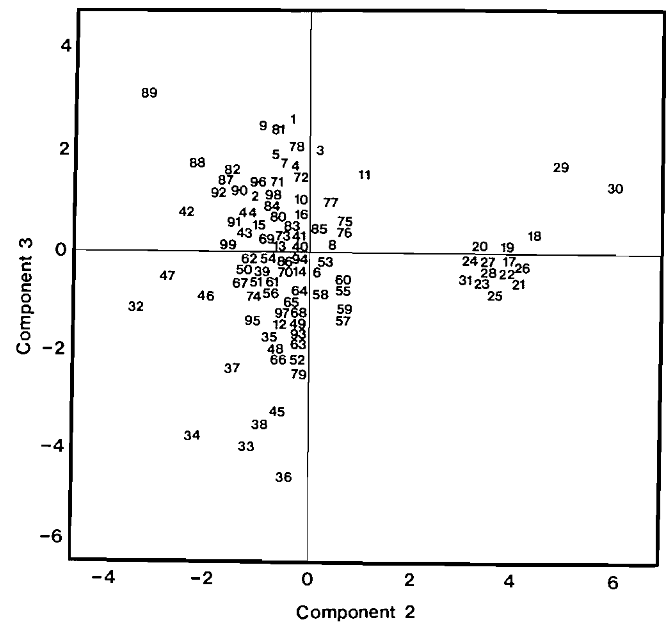

FIG. 4. Ordination of 99 OTUs of the *Arnica angustifolia* aggregate generated by plotting the second and third principal components. Numbers refer to OTU identity.

OTUs 29 and 30 marginal to the main groups. These two deviant OTUs also failed to cluster with subspecies *tomentosa* in the phenogram. All remaining OTUs could not be separated by the PCA but rather formed a large, loose group. Six characters contributed greatly to the total variance in principal component axis 1. In decreasing order of importance, these characters were disc corolla length, capitulum height, basal leaf length, disc corolla tube length, involucral bract length, and ligule length. OTUs with high positive loadings (e.g., OTUs 30, 39, 47) had large capitula, disc corollas, ligulate florets, involucral bracts, and basal leaves. Conversely, OTUs with high negative loadings (e.g., OTUs 5, 56) possessed low values with respect to these characters.

Characters having a pronounced effect on the ordination of OTUs in principal component axis 2 included, in descending order of importance, stem, leaf, involucral bract, periclinium, and peduncle pubescence and involucral bract width and achene length. OTUs with loadings greater than 3.0 (OTUs 17 to 31) possessed densely villous stems, leaves, and involucral bracts, long achenes, and wide involucral bracts. OTUs with loadings lower than −3.0 (e.g., OTUs 32, 47, 89) were characterized by sparse stem pubescence and glabrous leaves as well as shorter achenes and narrower involucral bracts.

Characters contributing significantly to the total variance in principal component axis 3 included, in decreasing order of importance, basal leaf shape, basal leaf width, ligule tooth length, periclinium and peduncle glandularity, and plant height. Five OTUs (OTUs 33, 34, 36, 38, 45) had loadings less than −3.0 and were represented by small plants possessing linear to narrowly lanceolate leaves, short teeth on the ligulate florets, and abundant glandularity on the periclinium and peduncle; they comprised cluster 4 in the UPGMA phenogram. Conversely, OTUs with high positive loadings on the same axis (e.g., OTUs 1, 9, 81, 89) were generally much taller of *Arnica angustifolia*. Geographic areas are defined in text. $\bar{x}$, mean; SD, standard deviation

Area 3 (n = 16)			Area 4 (n = 20)			Area 5 (n = 12)			Area 6 (n = 22)		
$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
18.2	7.46	7.0–39.0	16.4	6.52	7.0–30.0	23.2	9.83	10.0–51.0	16.0	5.84	5.0–30.0
5.9	1.99	2.0–13.0	5.3	1.45	2.0–10.5	6.8	2.72	3.0–14.0	5.4	1.65	2.3–12.0
0.9	0.32	0.3–1.9	0.9	0.33	0.4–2.1	1.0	0.50	0.3–2.6	0.8	0.20	0.4–1.2
18.9	2.93	15.0–30.0	18.0	2.49	13.0–23.0	18.5	2.29	15.0–23.0	16.7	2.59	12.0–23.0
13.7	2.08	10.0–20.0	12.6	1.86	10.0–17.0	13.0	1.80	10.0–17.0	13.1	2.35	9.0–19.0
4.7	0.80	3.5–7.6	4.3	0.41	3.5–5.2	4.5	0.51	3.8–5.6	4.2	0.56	3.1–6.0
11.3	1.20	8.5–14.5	10.1	0.95	7.3–11.6	9.9	1.48	6.5–12.2	10.1	1.24	7.9–14.0
2.6	0.53	1.8–4.1	2.5	0.40	2.0–3.9	2.6	0.55	1.7–4.0	2.5	0.40	1.6–3.5
1.8	1.10	0.4–5.6	2.7	1.40	0.6–7.0	1.8	0.80	0.5–4.0	1.1	0.42	0.2–3.0
22.1	4.12	13.0–30.0	18.8	3.60	10.0–25.0	20.6	4.03	13.0–27.0	18.8	4.32	12.7–32.0
6.0	1.29	4.0–9.5	4.8	0.71	3.5–6.5	5.8	1.09	4.0–8.0	5.3	1.17	3.0–8.5
9.6	1.80	6.0–16.0	10.9	1.83	7.0–15.0	10.1	1.98	7.0–14.0	9.9	1.56	7.0–14.0
7.3	0.69	6.0–10.0	6.8	0.72	5.0–8.0	7.1	0.66	6.0–8.5	6.9	0.80	5.2–9.0
2.8	0.38	2.0–4.0	2.8	0.42	1.9–3.5	2.7	0.29	2.3–3.2	2.8	0.40	2.0–3.5

and possessed broader basal leaves, longer teeth on the ligulate florets, and inconspicuous glandularity on the peduncle and periclinium. As previously stated, no significant differences were apparent among the means of these quantitative characters, measured from plants collected in six different geographic regions, which contributed significantly to the total variance in principal component axes 1 and 3. Furthermore, quantitative differences are reduced considerably when plants from these regions are grown together in a common greenhouse. The densely villous plants (OTUs 17 to 31) from Newfoundland and western Canada are effectively separated from all other OTUs and are sufficiently distinct to suggest taxonomic recognition. These OTUs have been previously recognized as *A. angustifolia* subsp. *tomentosa*. All remaining OTUs will be treated as *A. angustifolia* subsp. *angustifolia*.

Comparisons can be made between results of the cluster and principal component analyses. The OTUs comprising cluster 1 were all found to have loadings less than 2.5 on principal component axis 1, whereas the OTUs forming clusters 4 and 5 had loadings greater than 1.0 on the same axis. Sixteen OTUs were confluent between these values, suggesting that these clusters are not very well separated. It is virtually impossible to separate the OTUs forming clusters 1 and 5 on principal component axis 3; however, those OTUs represented by cluster 4 are easily defined as having loadings less than −3.0. In both plots, the outlying OTUs 88 and 89 clustered separately in the phenogram. With the exception of OTUs 29 and 30, cluster 2 includes all OTUs in the PCA with loadings greater than 3.0 on principal component axis 2. These OTUs have been defined as *A. angustifolia* subsp. *tomentosa*. OTUs 29 and 30, represented by cluster 6, were found to have the highest positive loadings on principal component axis 2 and, as observed in the PCA, are most similar to *A. angustifolia* subsp. *tomentosa*.

TABLE 3. Characters used in phenetic analyses of the *Arnica angustifolia* aggregate. Scale of measure presented in parentheses

No.	Description
1	Plant height (cm)
2	Basal leaf length (cm)
3	Basal leaf width (cm)
4	Capitulum width (mm)
5	Capitulum height (mm)
6	Achene length (mm)
7	Involucral bract length (mm)
8	Involucral bract width (mm)
9	Ligule tooth length (mm)
10	Ligule length (mm)
11	Ligule width (mm)
12	Ligule number (per capitulum)
13	Capitulum number (per stem)
14	Disc corolla length (mm)
15	Disc corolla tube length (mm)
16	Cauline leaves (number of pairs)
17	Stem pubescence: glabrous to sparse; moderate; dense
18	Leaf margin: entire to occasionally denticulate; denticulate to occasionally dentate
19	Leaf pubescence: glabrous to sparse; moderate; dense
20	Basal leaf petiole: sessile (or subsessile) or very short and broad winged; narrow or broad winged and shorter than blade; slender winged and approximately equaling the blade
21	Basal leaf shape: linear to narrowly lanceolate; narrowly to broadly lanceolate; broadly lanceolate
22	Periclinium and peduncle pubescence: glabrous to sparse; moderate; dense
23	Periclinium and peduncle glandularity: inconspicuous; abundant
24	Involucral bract pubescence: sparingly pilose, otherwise glabrous; pilose at base, glabrous above; pilose throughout; dense woolly-villous
25	Involucral bract shape: narrowly lanceolate; broadly lanceolate; oblanceolate
26	Involucral bract glandularity: inconspicuous; abundant

Chromosome numbers

Chromosome numbers are presented in Table 4 for 104 populations within the aggregate. Four ploidy levels are apparent in *A. angustifolia* subsp. *angustifolia*, in agreement with published counts by Engell (1970) and Wolf (1980). The counts of $2n = 57$ for Scandinavian material corroborate Engell's (1970) observation that these plants are most probably all triploid. Tetraploid counts for *A. angustifolia* subsp. *angustifolia* from western North America are, to my knowledge, the first published counts. Three counts of $2n = 57$ for plants collected in the USSR and three tetraploid counts counts for plants from eastern Canada suggest that these taxa may be entirely triploid and tetraploid, respectively. Chromosome counts of $2n = 57$ and $2n = 76$ for *A. angustifolia* subsp.

TABLE 4. Chromosome numbers determined for members of the *Arnica angustifolia* aggregate during this study

Taxon	2*n*	Locality and voucher
A. angustifolia subsp. *angustifolia*	38	CANADA: YUKON: km 471 Klondike Hwy., N. Pelly Crossing, *Downie 466*; km 610.5 Klondike Hwy., N.W. McQuesten, *Downie 467*; km 5 Dawson Boundary Rd. No. 9, *Downie 472*; km 12 Dempster Hwy., *Downie 473*; km 646 Klondike Hwy., *Downie 479*; km 547 Campbell Hwy., *Downie 487*; Carmacks, *Downie 682*; Kluane National Park, *Downie 499*. U.S.A.: ALASKA: 3 km N. Circle Hot Springs, *Downie 507*; Mile 314 Parks Hwy., N. Nenana, *Downie 649*; 1 km N.W. Circle Hot Springs, *Downie 654*; Circle Hot Springs Rd., *Downie 655*; mile 339 Hwy. 2, S.E. North Pole, *Downie 658*; Mile 267 Parks Hwy., *Downie 646*; mile 275 Parks Hwy., *Downie 647*
	57	CANADA: ALBERTA: Jasper National Park, Columbia Icefields, *Downie 544*; Jasper National Park, Mt. Edith Cavell, *Downie 721*; Jasper National Park, Bald Hills, *Downie 722*; Cardinal Divide, *Downie 725*; 2 km N. Pine Lake Campground, *Downie 582*; 5 km S. Pine Lake Campground, *Downie 583*; 20 km S. Pine Lake Campground, *Downie 585*; BRITISH COLUMBIA: Summit Lake, *Downie 616*; Muncho Lake Provincial Park, *Downie 619*; S. Muncho Lake Provincial Park, *Downie 618*; km 750 Alaska Hwy., *Downie 621*; km 895 Alaska Hwy., *Downie 623*; km 906 Alaska Hwy., *Downie 624*; km 625 Alaska Hwy., *Downie 625*; NORTHWEST TERRITORIES: km 174 Hwy., 3, *Downie 602*; km 160 Hwy. 3, *Downie 604*; km 327 Hwy. 3, *Downie 596*; km 308 Hwy. 3, *Downie 597*; km 282 Hwy. 3, *Downie 598*; km 180 Hwy. 3, *Downie 601*; 5 km E. Hay River, Hwy. 2, *Downie 575*; km 76 Hwy. 5, *Downie 578*; km 133 Hwy. 5, *Downie 579*; 46 km N. Enterprise, Hwy. 1, *Downie 588*; 1 km N. Blue Fish Creek, Hwy. 3, *Downie 591*; Fort Providence, *Downie 606*; km 233 Hwy. 1, *Downie 608*; km 299 Hwy. 1, *Downie 610*; 1 km E. junction Hwy. 7 and Hwy. 1, *Downie 612*; km 145 Hwy. 7, *Downie 614*; YUKON: km 1193 Alaska Hwy., *Downie 459*; km 1341 Alaska Hwy., *Downie 461*; 16 km S. Haines Junction, *Downie 480*; 88 km S. Haines Junction, *Downie 481*; km 134 Klondike Hwy., *Downie 484*; km 218 Canol Road, *Downie 489*; km 174 Canol Road, *Downie 491*; km 13 Canol Road, *Downie 522*; km 2 Canol Road, *Downie 521*; km 380 Campbell Hwy., *Downie 496*; km 1618 Alaska Hwy., *Downie 497*; Beaver Creek, *Downie 672*; km 1878 Alaska Hwy., Koidern, *Downie 676*; Carmacks, *Downie 682*; km 272 Klondike Hwy., *Downie 686*; km 36 Hwy. 8, S.W. Tagish, *Downie 687*. U.S.A.: ALASKA: mile 1239 Alaska Hwy., *Downie 631*; mile 1264 Alaska Hwy., Northway, *Downie 633*; 2 miles S. Tetlin Junction, *Downie 635*; 12 miles S. Tok, Hwy. 1, *Downie 637*; mile 66.5 Hwy. 1, *Downie 641*; mile 263 Richardson Hwy., S. Delta Junction, *Downie 659*; Mile 1372 Alaska Hwy., *Downie 669*; Mile 1324 Alaska Hwy., *Downie 671*. GREENLAND: Scoresby Sund. Nordvestfjord, *Böcher 10796*. SWEDEN: Torne lappmark, Jukkasjarvi, Loupakkte, *Nilsson s.n.* (Botanical Garden, U. of Uppsala). NORWAY: Troms, Tromso. Mt. Flojfjell, *Nilsson s.n.* (Botanical Garden, U. of Uppsala). USSR: Gydan Peninsula, Siberia (V. L. Komarov Botanical Institute, Leningrad); no locality information, Coll. no. 2965. (Main Botanic Garden, Moscow); no locality information, Coll. no. 632. (Main Botanic Garden, Moscow)
	76	CANADA: BRITISH COLUMBIA: Muncho Lake Provincial Park, *Downie 622*; NORTHWEST TERRITORIES: km 379 Hwy. 1, *Downie 611*; 56 km N. Fort Liard, Hwy. 7, *Downie 615*; km 222 Hwy. 3, *Downie 599*; km 1912 Alaska Hwy., *Downie 675*; QUEBEC: Fort Chimo, *Hedberg 1959* (Botanic Garden, U. of Copenhagen); no locality information *Böcher 10050* (Botanic Garden, U. of Copenhagen); no locality information. *Böcher 13666* (Botanic Garden, U. of Copenhagen); YUKON: km 1074 Alaska Hwy., *Downie 456*; km 1790 Alaska Hwy., *Downie 678*; km 354 Klondike Hwy., *Downie 684*. U.S.A.: ALASKA: 60 km E.S.E. Tok Junction, *Downie 501*; mile 1396 Alaska Hwy., *Downie 502*. GREENLAND: Holsteinborg, *Böcher 4749*; Sdr. Strømfjord, *Böcher 12080*; Sdr. Strømfjord, Sandflugtdalen, *Böcher 13354*; Lyell's Land, Polhemsdal, *Böcher 6059*; Disko, Godhavn, *Böcher 8158*; Disko, Brededal, *Böcher 8895*; Nugssuaq peninsula, Agatdalen, *K.J. 47*
	95	GREENLAND: Nugssuaq peninsula, Marrait, *Böcher 1*
A. angustifolia subsp. *tomentosa*	57	CANADA: ALBERTA: Ram Mountain, *Downie 535, 536*; Jasper National Park, Signal Mtn., *Downie 724*; Cardinal Divide, *Downie 728, 729*; Mile 92 Hwy. 4, N. Coleman, *Downie 734*; BRITISH COLUMBIA: Muncho Lake Provincial Park, *Downie 620*; NORTHWEST TERRITORIES: Hwy. 7 near Liard River, *Downie 746*
	76	CANADA: ALBERTA: Ram Mountain, *Downie 535A*; Cardinal Divide, *Downie 541A*

tomentosa are in agreement with those previously published by Löve and Löve (1975), Straley (1979), and Wolf (1980). No evidence of aneuploidy was found.

Plants having chromosome numbers of $2n = 38$ show a very close correlation with nonglaciated areas (Fig. 5). This sexual phase is prevalent throughout unglaciated Alaska and west central Yukon with some colonization of the glaciated areas (or perhaps a glacial relict) in Kluane National Park, Yukon. Triploid and tetraploid individuals are widely scattered throughout previously glaciated areas.

Pollen viability

Relationships among pollen quality, method of reproduction, and ploidy level in *Arnica* have been discussed previously (Barker 1966; Downie and Denford 1986*a*). Of 312 specimens, only 22 (7.1%) of *A. angustifolia* subsp. *angustifolia*

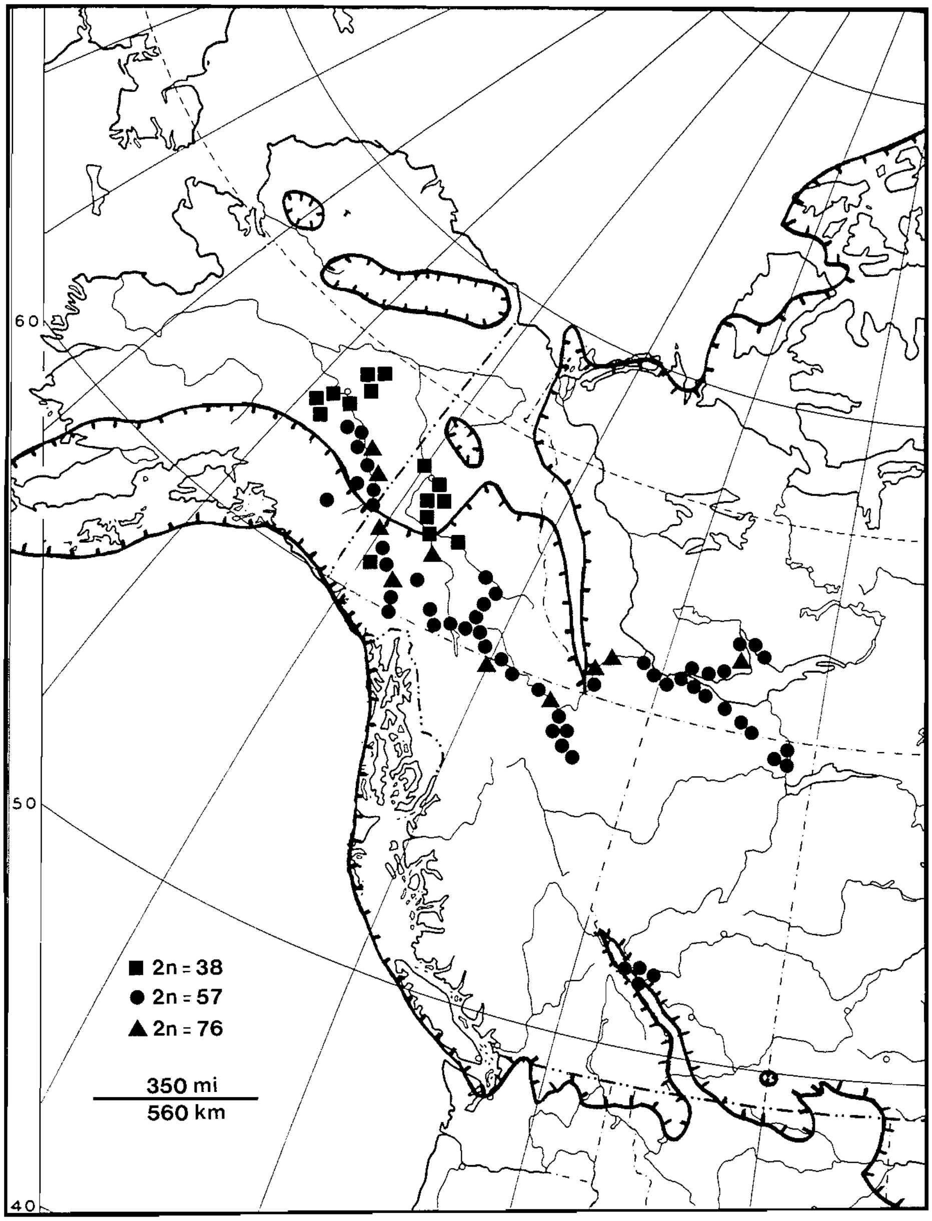

FIG. 5. Distribution of *Arnica angustifolia* subsp. *angustifolia* cytotypes in northwestern North America in relation to the maximum extent of the late Wisconsinan glacier complex (modified from Prest 1984).

possessed pollen more than 95% viable, indicative of amphimictic reproduction and $2n = 38$ (Barker 1966). These specimens were collected from areas in central Alaska and west central Yukon, which were largely free of ice during the time of the last glaciation (cf. Fig. 5). Specimens representing the disjunct populations of *A. angustifolia* subsp. *angustifolia*, comprising 34 collections from eastern Canada, 33 collections from Scandinavia and Spitsbergen, 10 collections from the USSR, and 33 collections from Greenland, all had less than 10% viable pollen. However, five plants from Greenland had between 25 and 51% viable pollen. Jorgensen *et al.* (1958) reported Scandinavian and Greenland tetraploids with fairly regular pollen mother cell meiosis that produce well-formed pollen, suggestive of a polyploid amphimict. Barker (1966), on the other hand, reports 0% pollen viability in all Greenland taxa investigated. In this study, all Greenland tetraploids possessed very little viable pollen and had irregularly shaped grains. Of the remaining 124 collections in *A. angustifolia* subsp. *angustifolia*, representing plants from northwestern North America, 59 collections (48%) had pollen which was 0% viable, 56 collections (45%) exhibited a pollen viability less than 50%, and 9 collections (7%) had between 50 and 85% stainable pollen. All 51 collections of *A. angustifolia* subsp. *tomentosa* possessed pollen which was less than 50% viable after staining. The pollen obtained from 32 of these collections (63%) was less than 10% viable. Throughout this study, in those collections where pollen viability was less than 80%, the pollen showed varying degrees of deformity.

Flavonoid analysis

Seven flavonoid glycosides, comprising five flavonols and two flavones, were isolated from 92 collections within the *A. angustifolia* aggregate from western North America and Greenland (Table 5). Only two sugar moieties, glucose and galactose, are associated with the flavonoids. All sugar attachments are in the 3 position in the flavonols and the 7 position in

TABLE 5. Flavonoid characters in *Arnica angustifolia* from western North America and Greenland

Taxon	No. of collections examined	Quercetin 3-*O*-galactoside	Kaempferol 3-*O*-glucoside	Quercetin 3-*O*-diglucoside	Kaempferol 3-*O*-galactoside	Quercetin gentiobioside	Apigenin 7-*O*-glucoside	Luteolin 7-*O*-glucoside
Subsp. *angustifolia* (Canada and Alaska)	19	+	+	+	+			
	16	+	+	+				
	12	+	+	+	+			+
	8		+	+				
	7	+	+	+				+
	5	+		+			+	+
	3	+		+				
	1		+		+			
	1	+		+		+		
	1	+		+	+			
	1	+		+				+
Subsp. *angustifolia* (Greenland)	5	+	+	+	+			
	3	+		+				
Subsp. *tomentosa*	6	+	+	+	+			
	4	+	+	+				

the flavones.

Arnica angustifolia subsp. *angustifolia* from Canada and Alaska exhibits the most divergent and numerous flavonoid profiles. However, this may be due primarily to the greater number of collections examined. No differences were apparent between *A. angustifolia* subsp. *angustifolia* from Greenland and western North America. Flavonoid profiles obtained from plants representing *A. angustifolia* subsp. *tomentosa* matched the two most common profile types in *A. angustifolia* subsp. *angustifolia*. Flavonoid variation in *A. angustifolia* did not correlate with ploidy. Such lack has been reported in other taxa (Glennie *et al.* 1971; Wolf 1981; Soltis and Bohm 1986). No intrapopulational variation in flavonoid constituents was observed.

Discussion

The results of this investigations indicate that this aggregate is best treated as two distinct taxa at the subspecific rank: *A. angustifolia* subsp. *angustifolia* (a combination of the previously recognized subspecies *angustifolia, attenuata, sornborgeri, intermedia, iljinii*, and *alpina* and *A. plantaginea*) and *A. angustifolia* subsp. *tomentosa*. These two phenetic groups are readily distinguished and identified on several continuous and descriptive characters. *Arnica angustifolia* subsp. *tomentosa* is a relatively small plant (0.6 to 2.0 dm) possessing one to three capitula and densely villous leaves, stems, and involucral bracts. The periclinium is densely pilose and conspicuously stipitate glandular. *Arnica angustifolia* subsp. *angustifolia* is usually a much taller plant (0.5 to 5.4 dm) bearing three to five capitula per stem. Its leaves, stems, and involucral bracts are never densely villous. In many instances, the leaves are often glabrous. The periclinium is usually pilose but never woolly villous; and stipitate glands may be inconspicuous or lacking.

This study also indicates the morphological, cytological, and flavonoid heterogeneity prevalent within *A. angustifolia* subsp. *angustifolia*. The transferal of field-collected plants, representing three ploidy levels, to a common garden resulted in diminution of morphological differences, indicating that much of the observed variation in this taxon is attributable to phenotypic plasticity. Davis and Heywood (1963) described good diagnostic characters as not being subject to wide variation nor being easily susceptible to environmental modification. Within *A. angustifolia* subsp. *angustifolia*, characters such as plant height; leaf, stem, and periclinium glandularity; capitula number, length, and width; and leaf size were found to be highly plastic and extremely variable. Taxonomic difficulty for this species in the past was primarily due to the frequent use of these characters. I have not seen enough USSR material to state unequivocally that plants representing subspecies *intermedia* and *iljinii* (*sensu* Maguire) are similar to those plants found in North America. Both these taxa are inadequately represented in herbaria and perhaps are not as widespread in the USSR as Maguire (1943) believed. However, the few available specimens annotated by Maguire are wholly confluent with the normal variation in *A. angustifolia*. When more information on chromosome number and flavonoid chemistry becomes available from the USSR, these plants can be assigned to *A. angustifolia* subsp. *angustifolia* with greater certainty.

Four ploidy levels were found within *A. angustifolia* subsp. *angustifolia* ($2n$ = 38, 57, 76, 95) and two within *A. angustifolia* subsp. *tomentosa* ($2n$ = 57, 76). Ornduff *et al.* (1967) have suggested that, owing to the small chromosome size in *Arnica*, counts that do not correspond to this base number are in error and are best treated as approximations. Chromosome counts of $2n = 56$ for plants from Norway, Spitsbergen, and the USSR (see Table 1) may represent monosomic aneuploidy, or more probably incorrect counts, since chromosome counts obtained from plants originating in these areas during this study were all $2n = 57$. Whether the polyploids represent autoploid or amphiploid derivatives of the $2n = 38$ diploids is difficult to ascertain. Further discussion is presented in Downie and Denford (1986*a*). A diversity of ploidy levels is found among plants in northwestern North America and Greenland, whereas plants from Scandinavia and the USSR are most probably all triploid, and plants from northern Quebec and Labrador are most probably all tetraploid.

Considering the distribution of chromosome races in *Arnica*, Barker (1966) has shown that no well-developed sexual species occurs in a glaciated area and no well-developed polyploid series occurs in an unglaciated area. The presence of relictual diploid elements of otherwise widespread *Arnica* species in unglaciated Alaska–Yukon has previously been reported by Wolf (1981) and Downie and Denford (1986*a*). Results of this study corroborate the existence of sexual elements in unglaciated areas and confirm the presence of $2n = 38$ *A. angustifolia*, evidently widespread, throughout this area.

Flavonoid profiles within the *A. angustifolia* aggregate are relatively simple, with two to five compounds per population. Within *A. angustifolia* subsp. *angustifolia*, 11 different flavonoid profiles are apparent; whereas *A. angustifolia* subsp. *tomentosa* has only two profile types. The two most common flavonoid profile types in *A. angustifolia* are prominent in *A. frigida* and *A. lonchophylla*, also of subgenus *Arctica* (Downie 1987). Flavonoid profile similarities between these taxa allude to their close affinity. Within *A. angustifolia* subsp. *angustifolia*, flavonoid diversity appears to have accompanied high morphological variability. With the prevalence of apomixis in this species (Barker 1966), and the large amount of morphological variability exhibited, much of the flavonoid variation probably reflects genetic heterogeneity from population to population. Considerable flavonoid variation has already been found in two other widespread and polymorphic species of *Arnica*: *A. cordifolia* (Wolf 1981) and *A. frigida* (Downie and Denford 1986*b*). In contrast, *A. angustifolia* subsp. *tomentosa*, consisting of only two chromosome races, exhibits little morphological and flavonoid variability. Gustafsson (1947) has suggested that apomixis and polyploidy are probably largely responsible for the morphological variability encountered within *Arnica*. In an investigation into the embryology of *A. angustifolia* subsp. *angustifolia* from Greenland, Engell (1970) observed "a number of apomictically propagating subunits." In this study, morphological differentiation (and flavonoid composition) was not found to correlate with ploidy. The interaction among plasticity, apomixis, and polyploidy has no doubt created the variable morphology and flavonoid chemistry evident in *A. angustifolia* subsp. *angustifolia*.

The similarities in morphology, cytology, and flavonoid chemistry between the two groups of taxa identify them as a species aggregate, separated by the suite of characters listed above. The gradation of these two groups has been previously suggested (Maguire 1943) but was not apparent during the course of this study. Putative hybrids between *A. frigida* subsp. *frigida* and *A. angustifolia* subsp. *tomentosa*, treated as *A. louiseana* var. *pilosa* (Maguire 1942), have already been shown not to occur (Downie and Denford 1986*a*). Intraspecific crosses between *A. angustifolia* subsp. *angustifolia* and *A. angustifolia* subsp. *tomentosa* were unsuccessful. Although Douglas (1982) has admitted *A. lonchophylla* Greene as a subspecies of *A. angustifolia*, recent evidence indicates that the former is a separate species, albeit closely related to *A. angustifolia* (Downie 1987).

Phytogeography

The allopatric distribution of *A. angustifolia* suggests that in pre-Wisconsinan times these taxa, or their precursors, had a more continuous distribution across North America, Europe, and the USSR. With the advance of the late Wisconsinan glaciation their intervening ranges were eradicated. To adequately explain the present-day distribution of *A. angustifolia*, it is necessary to postulate the survival of these plants during the late Wisconsinan in unglaciated areas north and south of the ice sheet or, perhaps, in smaller refugial areas surrounded by ice.

During the late Wisconsinan, extensive unglaciated refuges existed in eastern Siberia (Isayeva 1984; Velichko *et al.* 1984), northern Alaska (Hultén 1937; Prest 1984), northern and central Yukon (Rutter 1984), Banks Island, N.W.T. (Vincent 1984), and the Queen Elizabeth Islands, N.W.T. (Prest 1984); these acted as centres of biotic dispersal after glaciation. Portions of Kodiak Island, Alaska (Karlstrom and Ball 1969), coastal Greenland (Böcher 1963), and western Scandinavia (Gjaerevoll 1963) were also unglaciated during this time. Moreover, the lower sea level during maximum glaciation (Hopkins 1973) resulted in the emergence of the continental shelf between Alaska and the USSR, permitting plant migration between the two continents (Murray 1981).

Increasing evidence for an ice-free corridor, a strip of land positioned between the Laurentide and Cordilleran glaciers, which remained ice-free during the late Wisconsinan glaciation (Alley 1973; Stalker 1977; Fulton *et al.* 1984*a*; Rutter 1984), suggests that the area just east of the Rocky Mountains may have provided refuge for a number of plant species.

Late Wisconsinan glaciation in Atlantic Canada consisted largely of local ice caps (Fulton *et al.* 1984*b*). Geological and geographical evidence corroborates the existence of ice-free areas during this period in the Gaspé Peninsula of Quebec (Hétu and Gray 1981; Lafrenière and Gray 1981; Grant and King 1984; Prest 1984), western Newfoundland (Brookes 1977; Grant 1977), northern Labrador and southeastern Baffin Island (Ives 1963; Prest 1984), southwestern Nova Scotia (Grant 1977), and localized coastal and highland regions in New Brunswick (Grant and King 1984), which may have provided refugia for the late glacial vegetation. In addition, portions of the continental shelf remained unglaciated during the late Wisconsinan (Grant and King 1984; Prest 1984); from here vegetation later recolonized eastern Canada as the ice sheet melted (Morisset 1971; Terasmae 1973).

The prevalence of amphimictic ($2n = 38$) *A. angustifolia* in unglaciated parts of Yukon and Alaska intimates the survival of the species in this area during the late Wisconsinan, with subsequent migration of polyploid elements throughout the arctic and alpine after melting of the glacier ice. The greater genetic variability of polyploids in general, particularly when accompanied by ecotypic or species hybridization, provides greater adaptability to new ecological conditions (Johnson and Packer 1965; Stebbins 1984). The polyploid races of *A. angustifolia* have been particularly successful in recolonizing previously glaciated areas.

The occurrence of arctic species, disjunct in the cordillera of western North America, and in extremely localized areas of northeastern North America, is very familiar (Fernald 1925; Schofield 1969). Hultén (1949) has described the Scandinavian members of *A. angustifolia* as "glacier survivers." The survival of *A. angustifolia in situ* in coastal or nunatak-type refugia or in close proximity to their present-day sites would have created the complex distribution patterns seen today.

Taxonomic treatment

Arnica angustifolia Vahl in Hornem., Fl. Dan. 9(26): 5. 1816

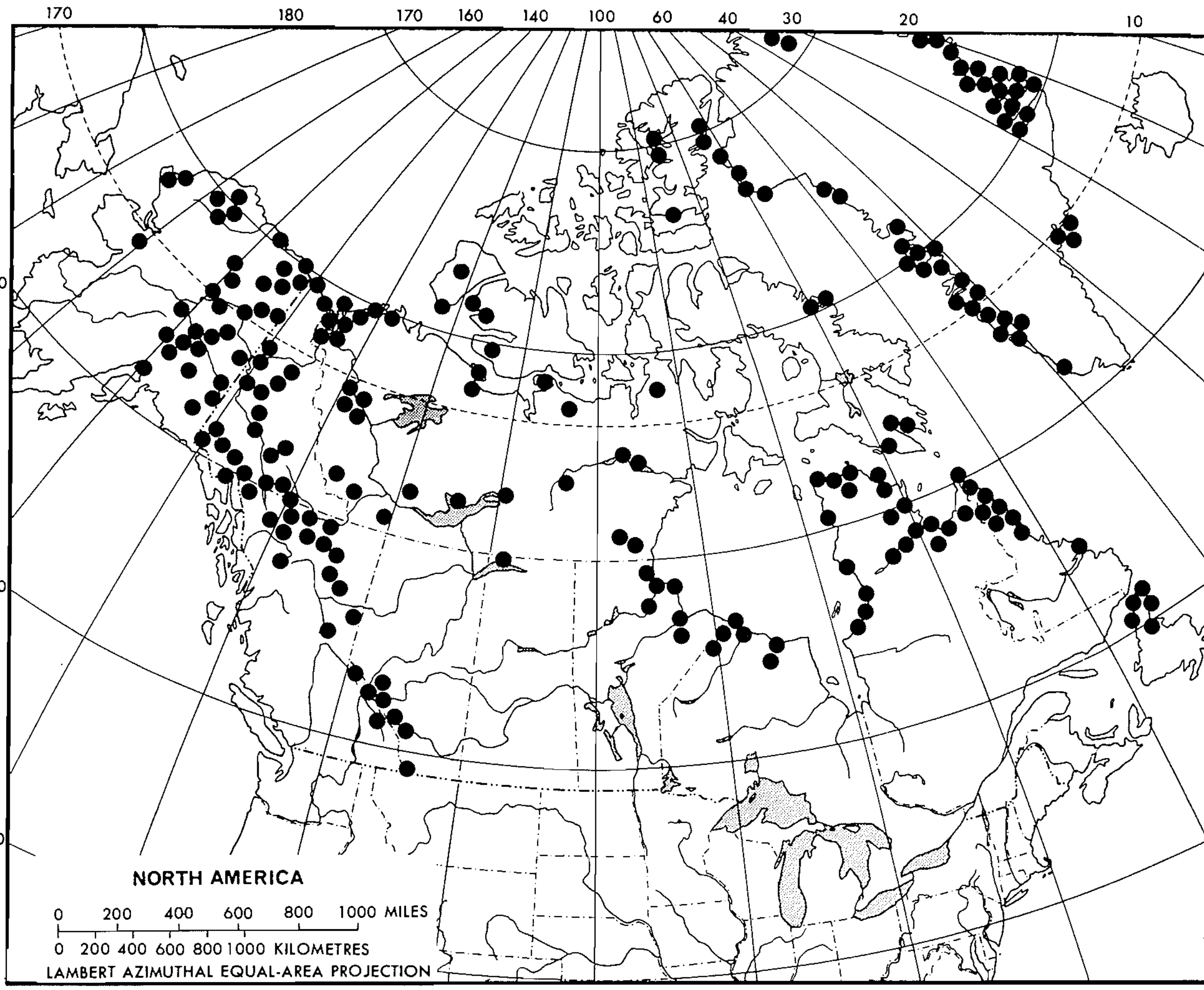

FIG. 6. Distribution of *Arnica angustifolia* subsp. *angustifolia* in North America.

Stems herbaceous, single or rarely branched, arising from a short branched rhizome covered in imbricate scales and leaf base remnants which may have tufts of long hairs in their axils, 0.5 to 5.4 dm high, sparsely to densely pilose, short stipitate-glandular, becoming increasingly villous and glandular upwards; cauline leaves 1 to 5 pairs, simple, opposite, mostly from below middle of stem; upper leaves sessile and reduced; lower cauline leaves 3 to 20 times as long as wide, 2.0 to 14.5 cm long, 0.3 to 2.6 cm broad, the blades linear, narrowly to broadly lanceolate to rarely oblanceolate, apex acute or acuminate, margins entire, denticulate or rarely dentate, petioles sessile, short and broad-winged or narrow-winged and shorter than the blade, glabrous to densely villous and stipitate-glandular, 3 to 5 nerved; capitula erect, 1 to 3 (rarely 5), large, hemispheric to broadly hemispheric, 12.0 to 30.0 mm broad, 9.0 to 21.0 mm high; periclinium very conspicuous, moderately to densely white pilose, stipitate glands inconspicuous or dense; involucral bracts 9 to 22, biseriate, narrowly to broadly lanceolate to occasionally oblanceolate, apex acute, 6.5 to 17.6 mm long, 1.5 to 4.1 mm broad, densely to sparsely pilose throughout or evidently pilose at base becoming less so upwards, inconspicuously to obviously stipitate-glandular; ligulate florets 6 to 16, yellow, 10.0 to 40.0 mm long, 3.0 to 9.5 mm broad, 3-toothed, the lobes 0.2 to 7.0 mm long; disc florets yellow, 5.0 to 10.0 mm long, goblet-shaped, moderately to densely pilose, inconspicuously glandular or absent, the tube 1.9 to 4.1 mm long; anthers yellow, the base minutely auriculate; styles exserted, bifurcate, revolutely coiled, the tip somewhat broadened and truncate, the outer surface papillose; achenes cylindrical or tapered, 5 to 10 nerved, with a conspicuous white annulus at base, 3.1 to 7.6 mm long, densely hirsute throughout, inconspicuous or not at all glandular; pappus white, barbellate; plants of arctic, subarctic, or alpine habitats; chromosome number $x = 19$.

Key to subspecies of *Arnica angustifolia*

Leaves glabrous to moderately villous, entire to dentate, linear to lanceolate or oblanceolate; periclinium moderately to densely white lanate-pilose, stipitate glands occasionally lacking or obscured; stems moderately villous . . . . subsp. *angustifolia*

Leaves densely villous, entire, lanceolate; periclinium densely pilose and conspicuously stipitate-glandular; stems densely villous . . . . subsp. *tomentosa*

Arnica angustifolia Vahl in Hornem. subsp. *angustifolia*, Fl. Dan. 9(26): 5. 1816

A. alpina var. *angustifolia* (Vahl) Fern., Rhodora, 36: 96. 1934. *A. alpina* subsp. *angustifolia* (Vahl) Maguire, Madroño, 6: 153. 1942. TYPE: "E. Groenlandia. *Gieseke s.n.*" (HOLOTYPE S!; ISOTYPE C!)

A. alpina forma *inundata* Porsild, Medd. Groenl. 58: 181. 1926. TYPE: Sargag, Greenland. *Porsild 200 fide* Maguire (1943). Type not seen.

A. alpina var. *vahliana* Boivin, Nat. Can. 75: 209. 1948. TYPE: "Baffin Island. 1937. *V. C. Wynne-Edwards 7364*" *fide* Ediger and Barkley (1978). Type not seen.

Arnica montana var. *alpina* L., Sp. Pl. 884. 1753. *A. alpina* (L.) Olin, Dissert. de Arnica, Upsaliae, 11. 1799. *A. alpina* (L.) Olin subsp. *genuina* Maguire, Brittonia, 4: 408. 1943. *A. angustifolia* subsp. *alpina* (L.) I. K. Ferguson in Heywood, Bot. J. Linn. Soc. 67: 282. 1973. TYPE: "Habitat in Alpibus and pratis Europae frigidioris," as described in Linnaeus' *Species Plantarum* (1753) *fide* Maguire (1943). Type not seen.

Arnica attenuata Greene, Pittonia, 4: 170. 1900. *A. alpina* subsp. *attenuata* (Greene) Maguire, Madroño, 6: 153. 1942. *A. alpina* var. *attenuata* (Greene) Ediger & Barkl., N. Am. Fl. 10: 31. 1978. *A. angustifolia* subsp. *attenuata* (Greene) G. W. Dougl. & G. Ruyle-Dougl., Can. J. Bot. 56: 1710. 1978. TYPE: "Open woods and river banks. Lewis River, Yukon Territory. June 13, 1899. *M. W. Gorman 1025*." (ISOTYPE CAN!, US!; PHOTO CAN!)

A. lowii Holm, Repert. Sp. Nov. 3: 388. 1907. TYPE: "Severn River (Keewatin) Ont. August 5, 1886. *J. Macoun 14699*." (HOLOTYPE CAN!) This specimen is typical of vigorous material of *A. angustifolia* subsp. *angustifolia*.

A. alpina subsp. *attenuata* var. *linearis* Hultén, Lunds Univ. Arrskr. II. Sect. 2, 46: 1588. 1950. TYPE: Fort Yukon. *Murie 2204 fide* Ediger and Barkley (1978). Type not seen. Scoggan (1979) has retained this name for plants belonging to subsp. *attenuata* having linear basal leaves, a character prevalent throughout the *A. angustifolia* aggregate. Ediger and Barkley (1978) had previously considered this name a synonym of subsp. *attenuata*. Material is typical of *A. angustifolia* subsp. *angustifolia*.

A. alpina subsp. *attenuata* var. *vestita* Hultén, Lunds Univ. Arrskr. II. Sect. 2, 46: 1588. 1950. TYPE: Tonsina Lodge, eastern Pacific Coast district of Alaska. *Anderson 1989 fide* Ediger and Barkley (1978). Type not seen. Since the range of *A. angustifolia* subsp. *tomentosa* does not extend into Alaska, Hultén had described plants which are covered in a grayish pubescence as var. *vestita*. Scoggan (1979) has questionably assigned these plants to *A. angustifolia* subsp. *tomentosa*, and Ediger and Barkley (1978) have placed this name in synonymy with subsp. *attenuata*. Until more specimens that have been annotated by Hultén as var. *vestita* can be seen, this taxon should remain in *A. angustifolia* subsp. *angustifolia*.

Arnica alpina subsp. *iljinii* Maguire, Brittonia, 4: 411. 1943. *A. iljinii* (Maguire) Iljin, Fl. URSS, 26: 658. 1961. *A. angustifolia* subsp. *iljinii* (Maguire) I. K. Ferguson in Heywood, Bot. J. Linn. Soc. 67: 282. 1973. TYPE: "Unterlauf des Jenissei, Ust-Jenisseiski Port (69°39′ n. Br.) Aug. 4, 1926. *A. Tolmachev 199*." (HOLOTYPE L; PHOTO CAN!; ISOTYPES GH!, O!)

Arnica intermedia Turcz., Bull. Soc. Nat. Mosc. 34: 203. 1851. *A. alpina* subsp. *intermedia* (Turcz.) Maguire, Brittonia, 4: 410. 1943. TYPE: Prope Alach-Jun 1835. *N. Turczaninow 836*. (HOLOTYPE L; PHOTO CAN!)

FIG. 7. Generalized illustrations of *Arnica angustifolia* subsp. *angustifolia*. (A) Based on *Downie 602A* (ALTA); (B) based on *Downie 624* (ALTA).

Arnica sornborgeri Fern., Rhodora, 7: 147. 1905. *A. alpina* subsp. *sornborgeri* (Fern.) Maguire, Brittonia, 4: 414. 1943. TYPE: "Rama, Labrador. Aug. 20–24, 1897. *J. D. Sornborger 157*." (HOLOTYPE GH! PHOTO CAN!; ISOTYPES NY!, RM!, US!; PHOTO CAN!)

Arnica terrae-novae Fern., Rhodora, 27: 90. 1925. TYPE: "Green Gardens, Cape St. George, Newfoundland. July 24, 1922. *K. K. Mackenzie & L. Griscom 11039*." (HOLOTYPE GH; PHOTO CAN!) Maguire (1943) has already observed that collections of *A. terrae-novae* are inseparable from *A. angustifolia* subsp. *angustifolia*.

Arnica sornborgeri var. *ungavensis* Boivin, Nat. Can. 75: 211. 1948. *A. alpina* var. *ungavensis* Boivin, Phytologia, 23: 94. 1972. TYPE: Québec. Fort Chimo, Baie d'Ungava, berge sablonneuse. Aug. 17, 1945. *Dutilly & Lepage 14768 fide* Ediger and Barkley (1978). Type not seen.

Arnica plantaginea Pursh, Fl. Am. Sept. 527. 1814. *A. alpina* var. *plantaginea* (Pursh) Ediger and Barkl., N. Am.

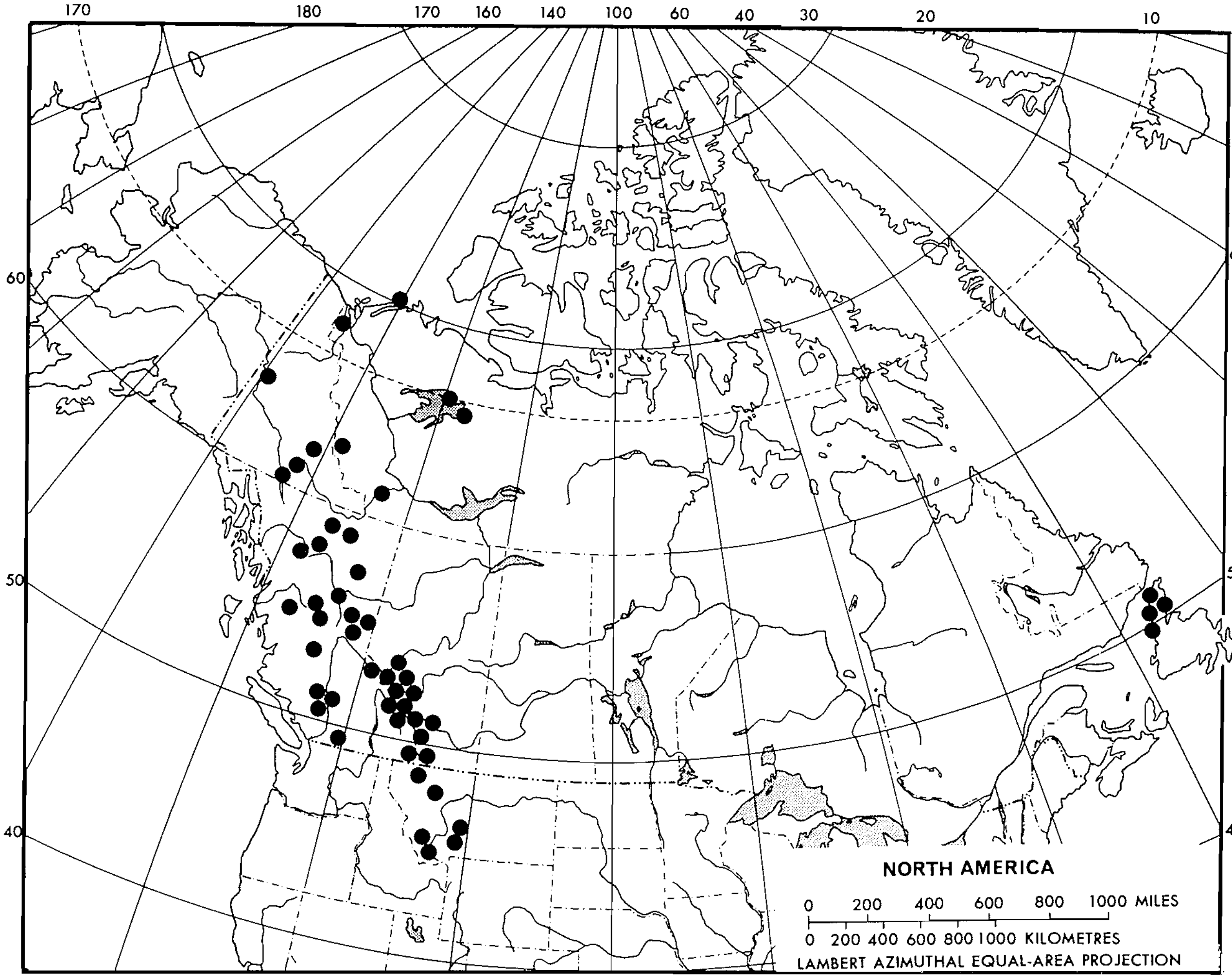

FIG. 8. Distribution of *Arnica angustifolia* subsp. *tomentosa* in North America.

Fl. Ser. II, Pt. 10: 32. 1978. TYPE: "Labrador. Herb. Dickson. *Colmaster s.n.*." (HOLOTYPE PH!; PHOTO CAN!) Plants described or annotated as *A. plantaginea* are few; to my knowledge less than 25 collections are available. There is no difference between these plants and those representing *A. angustifolia* subsp. *angustifolia*. *Arnica plantaginea* is treated as a synonym of the latter.

Plants 0.5 to 5.4 dm high; lower cauline leaves 2.0 to 20.0 cm long, 0.3 to 4.1 cm broad, linear, narrowly to broadly lanceolate to rarely oblanceolate, apex acute or acuminate, margins entire to denticulate or rarely dentate, petioles sessile, short and broad-winged or obviously narrow-winged and shorter than the blade, glabrous to moderately pubescent; capitula 1 to 3 (rarely 5); ligulate florets 6 to 16, 10.0 to 40.0 mm long, the lobes 0.2 to 7.0 mm long; periclinium moderately to densely pilose, stipitate glands evident or inconspicuous; achenes 3.1 to 7.0 mm long; chromosome numbers $2n$ = 38, 57, 76 and 95.

DISTRIBUTION AND HABITAT: A circumpolar taxon, confined primarily between 49 and 83° N latitude in North America and between 60 and 80° N in the USSR. Populations also found in northern Scandinavia near the Arctic Circle. In North America, its range extends from Alaska eastward through the northern regions of Manitoba, Ontario, and Quebec, with isolated populations in northern Newfoundland (Fig. 6). Also common from Greenland. Plants are found in a wide variety of habitats, notably exposed tundras, gravelly and rocky slopes, roadsides, moist banks, and open woodlands. In the southernmost portion of its range it is a plant of alpine slopes and ridges. See Maguire (1943), Selander (1950), and Benum (1958) for European and USSR distributions. Generalized illustrations Fig. 7.

Arnica angustifolia subsp. *tomentosa* (J. Macoun). G. W. Dougl. & G. Ruyle-Dougl., Can. J. Bot. 56: 1710. 1978. *A. tomentosa* J. Macoun, Ottawa Nat. 13: 166. 1899. *A. alpina* subsp. *tomentosa* (J. Macoun) Maguire, Madroño, 6: 153. 1942. *A. alpina* var. *tomentosa* (J. Macoun) Cronquist, Vas. Pl. Pac. N.W. 5: 46. 1955. TYPE: "Sheep Mountain, Waterton Lake, Rocky Mts., July 31, 1895. *J. Macoun 11606*." (HOLOTYPE CAN!; PHOTO CAN!)

A pulchella Fern., Rhodora, 27: 18. 1915. TYPE: "Table Mountain. Region of Port au Port Bay, Newfoundland. July 16 and 17, 1914. *M. L. Fernald & H. St. John 10874*." (HOLOTYPE GH; PHOTO CAN!; ISOTYPE GH!; PHOTO CAN!) After observing material of subsp. *tomentosa* from Newfoundland and noting very little difference between this taxon and *A. pulchella*, Fernald (1933) subsequently placed *A. pulchella* in synonymy with the former. *Arnica pulchella* is typical of *A. angustifolia* subsp. *tomentosa*.

A. tomentosa J. Macoun ex Greene, Pittonia, 4: 168. 1900. TYPE: "Mountains near Athabasca River near Lac Brûlé,

FIG. 9. Generalized illustration of *Arnica angustifolia* subsp. *tomentosa* (based on *Downie 620* (ALTA)).

Rocky Mts. June 20, 1898. *W. Spreadborough 19635.*" (ISOTYPE CAN!; PHOTO CAN!) Greene (1900) has also taken up the name *A. tomentosa* but has attributed it to Macoun in herb. This specimen is listed with Macoun's original description of the taxon and should be treated as a paratype.

Plants 0.6 to 2.0 (rarely 3.0) dm high; lower cauline leaves 3.5 to 10.5 cm long, 0.3 to 1.2 cm broad, narrowly lanceolate, apex acute, margins entire to rarely denticulate, petioles broad-winged and short, the leaves densely spreading woolly-villous; capitula solitary (rarely 3); ligulate florets 7 to 12, 14.5 to 30.0 mm long, the lobes 0.5 to 3.5 mm long; periclinium densely pilose and densely stipitate-glandular; achenes 4.5 to 7.6 mm long; chromosome number $2n = 57$ and 76.

DISTRIBUTION AND HABITAT: Infrequent in the Mackenzie delta region of the Northwest Territories, becoming more common southward in the Rocky Mountains of Alberta, British Columbia, and Montana (Fig. 8). Plants of bare rocky alpine slopes and subalpine meadows. Disjunct populations infrequent in exposed rocky areas and dry limestone barrens of northwestern Newfoundland. Generalized illustration Fig. 9.

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AFZELIUS, K. 1936. Apomixis in der gattung *Arnica*. Sven. Bot. Tidskr. **30**: 572–579.

ALLEY, N. F. 1973. Glacial stratigraphy and the limits of Rocky Mountains and Laurentide ice sheets in southwestern Alberta, Canada. Bull. Can. Pet. Geol. 21, pp. 153–177.

BARKER, W. W. 1966. Apomixis in the genus *Arnica* (Compositae). Ph.D. dissertation, University of Washington, Seattle.

——— 1967. I.O.P.B. chromosome number reports. Taxon, **16**: 156–157.

BENUM, P. 1958. The flora of Troms Fylke. Tromso Museum, Norway.

BÖCHER, T. W. 1963. Phytogeography of Greenland in the light of recent investigations. *In* North Atlantic biota and their history. *Edited by* A. Löve and D. Löve. Macmillan Publishing Company, New York.

BÖCHER, T. W., and LARSEN, K. 1950. Chromosome numbers of some arctic or boreal flowering plants. Medd. Groenl. **147**: 1–32.

BROOKES, I. A. 1977. Geomorphology and Quaternary geology of Codroy Lowland and adjacent plains, southwest Newfoundland. Can. J. Earth Sci. **14**: 2101–2120.

DAVIS, P., and HEYWOOD, V. H. 1963. Principles of angiosperm taxonomy. Oliver and Boyd, Edinburgh.

DOUGLAS, G. W. 1982. The sunflower family (Asteraceae) of British Columbia. Vol. I. Senecioneae. Occas. Pap. B.C. Prov. Mus. No. 23.

DOWNIE, S. R. 1987. The biosystematics of *Arnica* subgenus *Arctica* (Asteraceae). Ph.D. dissertation, University of Alberta, Edmonton.

DOWNIE, S. R., and DENFORD, K. E. 1986*a*. The taxonomy of *Arnica frigida* and *A. louiseana* (Asteraceae). Can. J. Bot. **64**: 1355–1372.

——— 1986*b*. The flavonoids of *Arnica frigida* and *A. louiseana* (Asteraceae). Can. J. Bot. **64**: 2748–2752.

EDIGER, R. I., and BARKLEY, T. M. 1978. *Arnica. In* North American flora. Ser. II. Part 10. *Edited by* C. T. Rogerson. New York Botanical Garden, New York.

ENGELL, K. 1970. Embryological investigations in *Arnica alpina* from Greenland. Bot. Tidsskr. **65**: 225–244.

ENGELSKJON, T., and KNABEN, G. 1971. Chromosome numbers of Scandinavian arctic–alpine plant species. II. Opera Bot. **52**: 1–38.

FERGUSON, I. K. 1973. *Arnica. In* Flora Europaea, Notulae systematicae ad florum Europaeam spectantes, No. 14. *Edited by* V. H. Heywood. Bot. J. Linn. Soc. **67**: 275–283.

FERNALD, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Am. Acad. Arts. Sci. **15**: 237–342.

——— 1933. Recent discoveries in the Newfoundland flora. Rhodora, **35**: 364–369.

FLOVIC, K. 1940. Chromosome numbers and polyploidy within the flora of Spitsbergen. Hereditas, **26**: 430–440.

FULTON, R. J., FENTON, M. M., and RUTTER, N. W. 1984*a*. Summary of Quaternary stratigraphy and history, western Canada. *In* Quaternary stratigraphy of Canada—a Canadian contribution of IGCP Project 24. *Edited by* R. J. Fulton. Geol. Surv. Can. Pap.

84-10. pp. 69–83.

FULTON, R. J., KARROW, P. F., LASALLE, P., and GRANT, D. R. 1984*b*. Summary of Quaternary stratigraphy and history, eastern Canada. *In* Quaternary stratigraphy of Canada—a Canadian contribution of IGCP Project 24. *Edited by* R. J. Fulton. Geol. Surv. Can. Pap. 84-10. pp. 193–210.

GJAEREVOLL, O. 1963. Survival of plants on nunataks in Norway during the Pleistocene glaciation. *In* North Atlantic biota and their history. *Edited by* A. Löve and D. Löve. Macmillan Publishing Company, New York.

GLENNIE, C. W., HARBORNE, J. B., ROWLEY, G. D., and MARCHANT, C. J. 1971. Correlations between flavonoid chemistry and plant geography in the *Senecio radicans* complex. Phytochemistry, **10**: 2413–2417.

GRANT, D. R. 1977. Glacial style and ice limits, the Quaternary stratigraphic record, and changes of land and ocean level in the Atlantic Provinces, Canada. Geogr. Phys. Quat. **31**: 247–260.

GRANT, D. R., and KING, L. H. 1984. A stratigraphic framework for the Quaternary history of the Atlantic Provinces. *In* Quaternary stratigraphy of Canada—a Canadian contribution of IGCP project 24. *Edited by* R. J. Fulton. Geol. Surv. Can. Pap. 84-10. pp. 173–191.

GUSTAFSSON, A. 1947. Apomixis in the higher plants. III. Biotype and species formation. Lunds Univ. Arsskr. **44**: 183–370.

HEDBERG, O. 1967. Chromosome numbers of vascular plants from arctic and subarctic North America. Ark. Bot. Ser. 2, **6**: 309–326.

HÉTU, B., and GRAY, J. T. 1981. The late Wisconsin deglaciation from the Gulf of St. Lawrence to the Chic-Choc mountains, Gaspésie. *In* Excursion et colloques en Gaspésie, Québec. *Edited by* J. T. Gray. University of Montreal, AQQUA/CANQUA, August 23–29, 1981. pp. 88–105.

HOPKINS, D. M. 1973. Sea level history in Beringia during the past 250,000 years. Quat. Res. **3**: 520–540.

HULTÉN, E. 1937. Outline of the history of arctic and boreal biota during the Quaternary period. Bokforlags Akticbolaget Thule, Stockholm, Sweden.

——— 1949. On the races in the Scandinavian flora. Sven. Bot. Tidskr. **43**: 383–406.

ILJIN, M. 1961. *Arnica*. *In* Flora URSS. Vol. XXIX. Akademiia Nauk SSSR, Botanicheskii Institute, Moscow.

ISAYEVA, L. L. 1984. Late Pleistocene glaciation of north-central Siberia. *In* Late Quaternary environments of the Soviet Union. *Edited by* H. E. Wright, Jr., and C. W. Barnosky. University of Minnesota Press, Minneapolis.

IVES, J. D. 1963. Field problems in determining the maximum extent of Pleistocene glaciation along the eastern Canadian seaboard—a geographer's point of view. *In* North Atlantic biota and their history. *Edited by* A. Löve and D. Löve. Pergamon Press, New York.

JOHNSON, A. W., and PACKER, J. G. 1965. Polyploidy and environment in arctic Alaska. Science (Washington, D.C.), **148**: 237–239.

JORGENSEN, C. A., SORENSEN, T., and WESTERGAARD, M. 1958. The flowering plants of Greenland. Biol. Skr. K. Dan. Vidensk. Selsk. **9**: 1–172.

KARLSTROM, T. N., and BALL, G. E. (*Editors*). 1969. The Kodiak Island refugium: its geology, flora, fauna and history. Ryerson Press, Toronto, Ont.

LAFRENIÈRE, L. B., and GRAY, J. T. 1981. The problem of glacial limits of alteration in the Gaspésie Highlands. *In* Excursion et colloques en Gaspésie, Québec. *Edited by* J. T. Gray. University of Montreal, AQQUA/CANQUA, August 23–29, 1981. pp. 48–68.

LÖVE, A., and LÖVE, D. 1975. I.O.P.B. chromosome number reports. Taxon, **24**: 671–678.

MABRY, T. J., MARKHAM, K. R., and THOMAS, M. B. 1970. The systematic identification of flavonoids. Springer-Verlag, New York.

MAGUIRE, B. 1942. *Arnica* in Alaska and Yukon. Madrono, **6**: 153–155.

——— 1943. A monograph of the genus *Arnica*. Brittonia, **4**: 386–510.

MARKHAM, K. R. 1982. Techniques of flavonoid identification. Academic Press, Toronto.

MORISSET, P. 1971. Endemism in the vascular plants of the Gulf of St. Lawrence. Nat. Can. (Que.), **98**: 167–177.

MOSQUIN, T., and HAYLEY, D. E. 1966. Chromosome numbers and taxonomy of some Canadian arctic plants. Can. J. Bot. **44**: 1209–1218.

MULLIGAN, G. A., and PORSILD, A. E. 1970. I.O.P.B. chromosome number reports. Taxon, **19**: 102–113.

MURRAY, D. F. 1981. The role of arctic refugia in the evolution of the arctic vascular flora—a Beringian perspective. *In* Evolution Today, Proceedings of the second international congress of systematic and evolutionary biology. *Edited by* G. G. E. Scudder and J. L. Reveal. Hunt Institute for Botanical Documentation, Carnegie-Mellon University, Pittsburgh.

NYGREN, A. 1954. Apomixis in angiosperms. II. Bot. Rev. (Lancaster), **20**: 577–649.

ORNDUFF, R., MOSQUIN, T., KYHOS, D. W., and RAVEN, P. 1967. Chromosome numbers in Compositae. VI. Senecioneae. II. Am. J. Bot. **54**: 205–213.

POLUNIN, N. 1959. Circumpolar arctic flora. Oxford University Press, London.

PREST, V. K. 1984. The late Wisconsinan glacier complex. *In* Quaternary stratigraphy of Canada—a Canadian contribution to IGCP Project 24. *Edited by* R. J. Fulton. Geol. Surv. Can. Pap. 84-10. pp. 21–36 and map 1584-A.

RAUP, H. M. 1947. The botany of southwestern Mackenzie. Sargentia, **6**: 249–252.

RIBERÉAU-GAYON, P. 1972. Plant phenolics. Oliver and Boyd, Edinburgh.

RUTTER, N. W. 1984. Pleistocene history of the western Canadian ice-free corridor. *In* Quaternary stratigraphy of Canada—a Canadian contribution to IGCP Project 24. *Edited by* R. J. Fulton. Geol. Surv. Can. Pap. 84-10. pp. 49–56.

RYDBERG, P. A. 1927. *Arnica*, Carduaceae: Senecioneae. North Am. Flora, **34**(4): 321–357.

SAS INSTITUTE INC. 1985. SAS user's guide: statistics. Version 5 ed. SAS Institute Inc., Cary, NC.

SCHOFIELD, W. B. 1969. Phytogeography of northwestern North America: bryophytes and vascular plants. Madrono, **20**: 155–207.

SCOGGAN, H. J. 1979. The flora of Canada. Vol. 4. Natl. Mus. Nat. Sci. (Ottawa) Publ. Bot. No. 7(4).

SELANDER, S. 1950. Floristic phytogeography of south-western Lule Lappmark (Swedish Lapland). Vol. II. Almquist and Wiksell, Stockholm.

SOKAL, R. R., and ROHLF, F. J. 1981. Biometry. 2nd ed. W. H. Freeman and Company, San Francisco.

SOKOLOVSKAYA, A. P. 1970. Kariologicheskoe issledovanie flory Basseyna R. Usy (Komi, ASSR). *In* Cytotaxonomical atlas of the arctic flora. *Edited by* A. Löve and D. Löve. 1975. J. Cramer, Germany.

SOLTIS, D. E., and BOHM, B. A. 1986. Flavonoid chemistry of diploid and tetraploid cytotypes of *Tolmiea menziesii* (Saxifragaceae). Syst. Bot. **11**: 20–25.

STALKER, A. MACS. 1977. The probable extent of Classical Wisconsin ice in southern and central Alberta. Can. J. Earth Sci. **14**: 2614–2619.

STEBBINS, G. L. 1984. Polyploidy and the distribution of the arctic–alpine flora: new evidence and a new approach. Bot. Helv. **94**: 1–13.

STRALEY, G. B. 1979. I.O.P.B. chromosome number reports. Taxon, **28**: 278.

TERASMAE, J. 1973. Notes on late Wisconsin and early Holocene history of vegetation in Canada. Arct. Alp. Res. **5**: 201–222.

VELICHKO, A. A., ISAYEVA, L. L., MAKEYEV, V. M., MATISHOV, G. G., and FAUSTOVA, M. A. 1984. Late Pleistocene glaciation of the Arctic shelf, and the reconstruction of Eurasian ice sheets. *In* Late Quaternary environments of the Soviet Union. *Edited by* H. E. Wright, Jr., and C. W. Barnosky. University of Minnesota Press, Minneapolis.

VINCENT, J.-S. 1984. Quaternary stratigraphy of the western Canadian Arctic Archipelago. *In* Quarternary stratigraphy of Canada—a Canadian contribution to IGCP Project 24. *Edited by* R. J. Fulton. Geol. Surv. Can. Pap. 84-10, pp. 87–100.

WOLF, S. J. 1980. Cytogeographical studies in the genus *Arnica* (Compositae: Senecioneae). I. Am. J. Bot. **67**: 300–308.

——— 1981. A biosystematic revision of *Arnica* L. (Compositae) subgenus *Austromontana* Maguire. Ph.D. dissertation, University of Alberta, Edmonton.

ZHUKOVA, P. 1964. The karyology of some species of Compositae growing in the Arcto-Alpine Botanic Garden (Kola Peninsula). Bot. Zh. (Leningrad), **49**: 1656–1659.

——— 1966. Chromosome numbers in some species of plants of the northeastern part of the USSR. Bot. Zh. (Leningrad), **51**: 1511–1516.

——— 1967. Chromosome numbers in some species of plants of the northeastern part of the USSR. II. Bot. Zh. (Leningrad), **52**: 983–987.

ZHUKOVA, P., and PETROVSKY, V. V. 1972. Chromosome numbers of some flowering plants of the Wrangel Island. II. Bot. Zh. (Leningrad), **57**: 554–567.

——— 1976. Chromosome numbers of some western Chukota plant species. II. Bot. Zh. (Leningrad), **61**: 963–969.

ZHUKOVA, P., PETROVSKY, V. V., and PLIEVA, T. V. 1973. The chromosome numbers and taxonomy of some plant species from Siberia and far east. Bot. Zh. (Leningrad), **58**: 1331–1342.

ZHUKOVA, P., KOROBKOV, A. A., and TIKHONOVA, A. D. 1977. Chromosome numbers of some plant species in the eastern arctic Yakuta. Bot. Zh. (Leningrad), **62**: 229–234.

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