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TAXONOMY OF *ARNICA* (ASTERACEAE)
SUBGENUS *ARCTICA*¹

STEPHEN R. DOWNIE AND KEITH E. DENFORD

ABSTRACT

Evaluation of systematic relationships in *Arnica* subgenus *Arnica* show that the complex consists of seven species. No new taxa have been proposed; however, names of several previously recognized taxa are treated as synonyms. *Arnica angustifolia*, *A. frigida*, and *A. lonchophylla*, each consisting of two subspecies, are extremely polymorphic and variable in chromosome number. *Arnica louiseana*, *A. rydbergii*, *A. fulgens* and *A. sororia* are morphologically distinct. A taxonomic revision of the subgenus includes descriptions, keys, synonymies, distribution maps, and a discussion of phylogenetic relationships.

Key Words: Asteraceae, *Arnica* subgenus *Arctica*, taxonomy, phylogeny, phytogeography, Northern Hemisphere

INTRODUCTION

Arnica subgenus *Arctica* is composed of a number of polyploid, predominantly agamospermous taxa distributed throughout temperate and arctic regions in the northern hemisphere. These rhizomatous perennial herbs are characterized by simple or occasionally branched stems bearing large hemispheric to campanulate-turbinate capitula, and a white, barbellate pappus. The subgenus is confined to latitudes between 45° and 80° N. in North America and 60° and 80° in the U.S.S.R., with disjunct members in northern Scandinavia. Taxonomic treatments of this complex have been influenced by the morphological variability encountered, particularly within *A. angustifolia* Vahl, *A. frigida* Meyer ex Iljin and *A. lonchophylla* Greene.

The basic chromosome number for *Arnica* is undoubtedly $x = 19$ (Böcher and Larsen, 1950; Ornduff et al., 1967; Downie, 1985), with cytotypes $2n = 38, 57, 76,$ and 95 reported for *Arnica angustifolia* and *A. frigida*, $2n = 38, 57,$ and 76 for *A. lonchophylla*, $2n = 76$ and 95 for *A. louiseana*, $2n = 38$ and 76 for *A. rydbergii*, and $2n = 38$ for both *A. fulgens* and *A. sororia* (Downie, 1987; Ph.D. dissertation,

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U. of Alberta, Edmonton). All previously reported chromosome counts for subgenus *Arctica* have been presented elsewhere (Downie, 1987; Ph.D. dissertation, U. of Alberta, Edmonton). Amphimictic ($2n = 38$) species of subgenus *Arctica* are closely correlated with non-glaciated regions; apomictic ($2n = 57, 76,$ and 95) phases are largely responsible for the recolonization of previously glaciated areas [Barker (1966; Ph.D. dissertation, U. of Wash., Seattle); Downie and Denford, 1986a; Downie, 1988].

Investigations of flavonoid constituents in *Arnica angustifolia* (Downie, 1988), *A. frigida* (Downie and Denford, 1986b), and *A. lonchophylla* (Downie and Denford, 1988) indicate extreme variability within taxa and a high similarity between taxa, and offer little of taxonomic value. In subgenus *Arctica*, flavonoid diversity appears to have accompanied high morphological variation. Flavonoid differences are apparent between *A. fulgens* and *A. sororia*, although populations of the two can be found with identical flavonoid chemistry (Downie and Denford, 1987). Only *A. louiseana* and *A. rydbergii* are clearly delimitable on the basis of their flavonoid chemistry (Downie and Denford, 1988).

Evaluation of systematic relationships in subgenus *Arctica* show that the complex, as circumscribed in this revision, consists of seven species, including six taxa ranked at the subspecific level. Names of seven taxa previously recognized by Maguire (1943) are treated as synonyms. This revision incorporates data from morphology, cytology, and flavonoid chemistry to elucidate the nomenclature and classification of the subgenus. This study is based on extensive field studies and collections from throughout the range of the complex and from an examination of approximately 2200 herbarium specimens (including types). A list of the herbarium specimens examined during the course of this investigation is on deposit at MO.

TAXONOMIC HISTORY

In the most recent monograph of *Arnica*, Maguire (1943) recognized 32 species in five subgenera, *Andropurpurea*, *Arctica*, *Austromontana*, *Chamissonis* and *Montana* and presented a comprehensive account of the taxonomic history of the subgenus. Subgenus *Austromontana* has recently been systematically investigated by Wolf and Denford (1984), who recognized nine species within the subgenus, reducing the number of taxa recognized by Maguire by four. Maguire's recognition of seven species and thirteen subspecies within subgenus *Arctica* was based primarily on an

examination of herbarium specimens. At that time, information on chromosome numbers and reproductive behavior within the genus was virtually unknown and resulted in a lack of knowledge of the morphological variation in these plants created by apomixis, polyploidy, and phenotypic plasticity.

In their revision of *Arnica* for North American Flora, Ediger and Barkley (1978) essentially adopted Maguire's (1943) treatment of subgenus *Arctica*, recognizing six species and seven varieties. *Arnica plantaginea* Pursh was combined with *A. alpina* subsp. *sornborgeri* (Fern.) Maguire, and the assemblage treated as *A. alpina* var. *plantaginea* (Pursh) Ediger & Barkl. The infraspecific taxa of *A. lonchophylla* were not recognized. At the same time, Douglas and Ruyle-Douglas (1978) treated *A. lonchophylla* as a subspecies of *A. angustifolia*, and *A. sororia* as a variety of *A. fulgens*.

MORPHOLOGY AND TAXONOMIC CRITERIA

Barker (1966, Ph.D. dissertation, U. of Wash., Seattle) demonstrated that the major populations of *Arnica angustifolia*, *A. lonchophylla* and *A. frigida* are autonomously apomictic; that is, agamospermy (seed production) can proceed without the stimulus of pollen tubes or fertilization of the polar nuclei. One of the effects agamospermy has on plant populations is the formation of microspecies, restricted in distribution to relatively small geographical areas (Grant, 1971). The morphological variability encountered in *Arnica* is attributable to apomixis and polyploidy [Afzelius, 1936; Gustafsson, 1947; Barker (1966; Ph.D. dissertation, U. of Wash., Seattle)]. Accordingly, the perplexing morphological and chemical variability in *Arnica* subgenus *Arctica* is likely the result of microspecies formation via apomixis. Other factors contributing to the complex variation patterns in the subgenus include: (1) phenotypic plasticity, (2) hybridization and introgression (perhaps between *A. angustifolia* and *A. lonchophylla*), (3) pollinator non-specificity, (4) geographical and (5) ecological isolation (Downie, 1987; Ph.D. dissertation, U. of Alberta, Edmonton).

In the past, attempts to give taxonomic credence to every morphological variant, or anomalous individual, resulted in complicated and confusing treatments. As a result of this study, the total number of taxa in subgenus *Arctica* is reduced from seventeen to ten, with one new combination proposed. Three species recognized in this treatment, *Arnica angustifolia*, *A. frigida* and *A. lonchophylla*, exhibit variability in morphology, ploidy level and foliar

flavonoid chemistry (Downie, 1987; Ph.D. dissertation, U. of Alberta, Edmonton). This variation has no doubt influenced previous taxonomic treatments. Characters useful in distinguishing taxa are: the presence or absence of short stipitate-glands on the leaves, achenes and involucre bracts, the shape of the capitulum, petiole length, the type of leaf margin, and achene pubescence.

PHYLOGENY

The genus *Arnica* is clearly defined, with the included species held together by similar phytochemistry, chromosome base number and structural characters. It is monophyletic, being derived from a hypothesized ancestor, *Protoarnica* (Maguire, 1943). Maguire considered *Arnica* to have originated in the arctic and subarctic regions of western North America from whence it spread eastward, westward, and southward. The paucity of *Arnica* species in Europe and Asia, and the presence of about 25 species confined primarily to the arctic, boreal and montane regions of northwestern North America, was used as supporting evidence. Based upon principal centers of dispersal and morphological similarity, Maguire (1943) recognized five subgenera, with subgenus *Arctica* representing the most ancestral group. The probable relationships of other subgenera in *Arnica* are not at all clear, and precise delineation is speculative. These subgenera may have arisen from subgenus *Arctica*, or independently from *Protoarnica* (Maguire, 1943). Maguire's delineation of taxa within the subgenus is also highly speculative, with numerous alternative origins proposed for many of the taxa.

The prevalence of apomixis, polyploidy and hybridization in *Arnica* makes phylogenetic analysis, and sister group designation, for subgenus *Arctica* difficult. The taxa comprising the remaining four subgenera, all plausible sister groups, have been used as the outgroup in this study. Subgenus *Arctica* is also monophyletic. All species possess (1) a large, broadly hemispheric to campanulate-turbinate capitulum, (2) a white, barbellate pappus, (3) a rhizome covered with dark, imbricate scales and leafbase remnants, (4) arctic/alpine ecology (with the exceptions of *A. fulgens*, *A. sororia* and *A. lonchophylla*), and (5) the prevalence of simple flavonols and flavones based on the glycosides of glucose and galactose. Based upon an examination of structural, phytochemical, ecological and phytogeographical data, we agree with Maguire that *Arctica* represents the archetypal group, being derived from the postulated precursor, *Protoarnica*.

Arnica angustifolia has been interpreted as the progenitor of all taxa within the subgenus (Maguire, 1943), and we concur with this view. It is the most widespread and only completely circumpolar species of *Arnica*. This taxon also protrudes in a southerly direction along three major radii: (1) along the coast of eastern Siberia, (2) in the alpine regions of northwestern North America, and (3) along the North Atlantic coast in eastern North America. In these regions it is sympatric, or close to, all other arnicas. With four ploidy races (including relictual diploid populations in unglaciated Alaska-Yukon), a seemingly ancient and diverse flavonoid chemistry, an arctic-alpine ecology, a wide geographic distribution, a non-specific habitat preference, an extremely polymorphic habit, and the possession of many plesiomorphous morphological features, *A. angustifolia* is almost certainly the ancestral species in subgenus *Arctica*, and perhaps the entire genus.

Arnica frigida and *A. louiseana* are early derivatives of *A. angustifolia*, for they maintain similar plesiomorphous morphological and phytochemical features, and occur in the same geographic areas as *A. angustifolia*. Maguire (1943) stated that *A. frigida* became segregated into two outlying geographical races, subsp. *griscomii* in eastern Canada, and *A. louiseana* (or more likely a precursor to present-day *A. louiseana*) to the south. There appears to be little doubt of the close genetic affinity between *A. frigida* subsp. *frigida* and *A. frigida* subsp. *griscomii*. Both taxa are similar chemically and morphologically, but are distinguished by geographical distribution, habitat specificity, and a few subtle morphological differences (Downie and Denford, 1986a). *Arnica louiseana*, with its glandular leaves, stems, involucre bracts, periclinium and achenes, is distinctive. The lack of luteolin 7-O-glucoside in *A. frigida* and *A. louiseana*, a flavone prevalent in all other species, and similar morphological characters, are unifying features suggesting that these two taxa originated from a common ancestor.

With a habitat specificity to more xeric conditions, *Arnica fulgens* and *A. sororia* evolved from the more common arctic-alpine regions to prairie and grasslands habitats. The marked degree of morphological, cytological, ecological, and flavonoid similarity between *A. fulgens* and *A. sororia* suggests that they are sister groups. This is in contrast to Maguire's (1943) proposed phylogenetic interpretation, in which these two taxa were treated as unrelated. All collections of *A. fulgens* had luteolin 6-O-methoxy 7-O-glucoside and apigenin, whereas only two collections of *A. sororia* had these compounds.

The presence of these two flavonoids in *A. sororia* is significant; however, a more thorough examination to determine the full range of flavonoid variability throughout the entire distribution of these plants is required before phylogenies based on flavonoid data can be positively assured. In *A. fulgens*, the unique occurrences of dense axillary tufts of hair at the base of the stem, disc corollas with septate-glandless hair, the possibility of polyploidy (Taylor and Brockman, 1966), and luteolin 6-O-methoxy 7-O-glucoside and apigenin suggests that this taxon is best considered derived from *A. sororia*.

Arnica fulgens and *A. sororia* are morphologically more similar to *A. angustifolia* than to *A. lonchophylla*. The large, hemispheric capitulum, entire to irregularly denticulate or dentate leaves, and the short, narrow or broad-winged petioles of *A. fulgens*, *A. sororia*, and *A. angustifolia* are in contrast to the numerous campanulate-turbinate capitula, and the long-petiolate, regularly dentate leaves of *A. lonchophylla*.

Of somewhat greater divergence from the ancestral condition are *Arnica lonchophylla* and *A. rydbergii*, the latter representing the most patristic taxon within the subgenus. Sessile leaves, narrowly campanulate-turbinate capitula, minutely denticulate or entire ligulate florets, linear-oblong to narrowly lanceolate involucral bracts, and the presence of both quercetin 3, 7-O-diglucoside and kaempferol 6-O-methoxy 3-O-glucoside in *A. rydbergii* clearly sets this taxon off from the remainder of the subgenus. It still, however, retains all the features characteristic of subgenus *Arctica*, and definitely belongs within this complex.

TAXONOMIC TREATMENT

Arnica Linnaeus, Sp. Pl. 884. 1753. TYPE species: *Arnica montana* L.

Stems herbaceous, simple or branched, arising from a perennial rhizome; leaves 1–12 pairs, simple, opposite (or apparently all basal), sessile or narrowly to broadly petiolate, the uppermost leaves sessile and reduced, rarely alternate; capitula solitary to many in a cymose inflorescence, radiate or discoid, broadly hemispheric to turbinate, the periclinium obvious; involucral bracts biseriate, or loosely uniseriate; receptacle convex, naked or with conspicuous tawny or stramineous hairs; ligulate florets pistillate, yellow to orange, the ligule entire or dentate; disc florets uniform, perfect, yellow to orange, tubular or goblet-shaped; anthers yellow or pur-

ple, the base minutely auriculate; styles exerted, bifurcate, revolutely coiled, the tip somewhat broadened and truncate, the outer surface papillose; achenes cylindrical or tapered, 5–10 nerved, with a conspicuous white annulus at base, variously pubescent with short-bifid or trifid double hairs, glandular or glabrous; pappus of numerous white to tawny, barbellate to plumose capillary bristles; chromosome number $x = 19$.

Subgenus *Arctica* Maguire, Brittonia 406. 1943.

Stems simple or occasionally 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 (excessively developed in *A. fulgens*); cauline leaves narrow, 1.5–20 times as long as wide, occurring below the middle of the stem, linear to ovate, or oblanceolate to spatulate, elliptic or oblong, margins entire, denticulate to dentate or occasionally undulate, sessile to broadly or narrowly-winged petiolate, the petioles mostly shorter than the blade (except in *A. lonchophylla*), 1–5 (–7) pairs of leaves, the uppermost sessile and reduced; periclinium very conspicuous, scantily to densely lanate-pilose; capitula large, 1–5 (–8), radiate, broadly hemispheric to campanulate-turbinate; involucre bracts biseriate, lanceolate to oblanceolate; ray and disc florets yellow to orange; anthers yellow; pappus white, barbellate.

KEY TO THE SPECIES OF SUBGENUS *ARCTICA*

1. Achenes glabrous below and sparsely hirsute above or glabrous throughout; lower cauline leaves broad, 1.5–7 times as long as wide; capitula 1 (–3) 2
2. Leaves conspicuously short stipitate-glandular; involucre bracts sparingly pilose otherwise glabrous, uniformly short stipitate-glandular; capitula nodding in anthesis; achenes glandular towards summit or occasionally densely glandular throughout 1. *A. louiseana*
2. Leaves sparsely or not at all short stipitate-glandular; involucre bracts pilose at base becoming glabrous or remaining pilose above, rarely short stipitate-glandular; capitula erect or nodding in anthesis; achenes rarely glandular 2. *A. frigida*
1. Achenes densely hirsute throughout; lower cauline leaves narrow, 3–20 times as long as wide; capitula 1–5 (–8) 3

3. Lower cauline leaves sessile or petiole very short and broad-winged; ligules entire or minutely 3-toothed, if toothed the teeth less than 0.5 mm long; stems caespitose 3. *A. rydbergii*
3. Lower cauline leaves distinctly petiolate; ligules obviously 3-toothed, the teeth 0.1–7 mm long; stems solitary or few 4
4. Lower cauline leaves regularly denticulate or dentate; petiole narrow and approximately equalling the blade in length; capitula campanulate-turbinate 4. *A. lonchophylla*
4. Lower cauline leaves entire or irregularly denticulate or dentate; petiole narrow or broad-winged and shorter than the blade; capitula broadly hemispheric or hemispheric 5
5. Leaves linear to broadly lanceolate, acute or acuminate, entire, denticulate or dentate; florets yellow; capitula hemispheric 5. *A. angustifolia*
5. Leaves narrowly oblong to oblanceolate, obtuse, entire or remotely denticulate; florets dark orange-yellow; capitula broadly hemispheric 6
6. Base of stem with dense tufts of long brown woolly hair in axils of basal leaves and persistent leaf bases; disc corollas densely pilose 6. *A. fulgens*
6. Base of stem lacking axillary tufts of brown hair, occasionally with few whitish hairs; disc corollas not at all pubescent 7. *A. sororia*

TREATMENT OF INDIVIDUAL TAXA

1. ***Arnica louiseana*** Farr, Ottawa Nat. 20: 109. 1906. *A. louiseana* Farr subsp. *genuina* Maguire, Brittonia 4: 419. 1943. TYPE: "Lake Louise, Canadian Rocky Mts. Rockslide on Fairview Mt. Alt. about 6000 ft. Aug. 18, 1905. *E. M. Farr 1067*." (HOLOTYPE: PH!; ISOTYPE: GH).

Plants 4–20 cm tall; rhizomes slender and covered with numerous dark imbricate scales and remnant leaf bases; stems solitary, simple, puberulent, stipitate-glandular, leaves to middle of stem or rarely all basal; leaves (0–) 1–3 pairs; upper cauline leaves sessile or narrowed to a short-winged petiole; lower cauline leaves 13–75 mm long, 4–20 mm wide; obtuse or occasionally acute or acuminate, elliptic to

oblong to ovate-lanceolate, petioles long and narrow, margins entire to saliently denticulate to slightly undulate, glabrous to hispidulous-puberulent, conspicuously short stipitate-glandular, 3–5 nerved; capitula nodding in anthesis, 1 (–3), campanulate-turbinate, 8–17 mm wide, 9–20 mm long; periclinium scantily to moderately pilose, yellow, short stipitate-glandular; involucrel bracts 8–15, 8–12 mm long, 1.5–3 mm wide, narrowly lanceolate, acuminate, sparingly pilose otherwise glabrous, uniformly short stipitate-glandular; ligulate florets 7–10, yellow, 12–20 mm long, 2.5–4.6 mm wide, the teeth 0.2–1.5 mm long; disc florets 6.2–8.4 mm long, narrowly goblet-shaped, stipitate-glandular, pilose, the tube 2–3.1 mm long; achenes 3.2–5 mm long, glabrous below and sparsely hirsute above or glabrous throughout, glandular towards summit or occasionally densely glandular throughout; chromosome number $2n = 76, 95$.

DISTRIBUTION AND HABITAT. Infrequent and localized on exposed tundra slopes and mature calcareous rock slides at 1800–2100 meters in the Canadian Rocky Mountains primarily in the vicinities of Waterton, Jasper and Banff National Parks (Figure 1). Flowers July to August.

Arnica louiseana can be separated from all other arnicas by its evident glandularity, its small size, and the nodding tendency of its peduncle.

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

Plants 0.5–4 dm tall; rhizomes short, slender, branched and covered with numerous dark imbricate scales and remnant leaf bases; stems solitary or several, rarely branching, glabrous to hispidulous-puberulent and sparsely stipitate-glandular below becoming sparsely to densely hispidulous-pilose and more glandular near the periclinium; leaves of small plants crowded at base, 1–4 pairs; upper cauline leaves sessile or narrowed to a short-winged petiole; lower cauline leaves 12–100 mm long, 5–35 mm wide, acute or obtuse, elliptic to lanceolate or ovate, or oblanceolate to spatulate, or occasionally lanceolate-oblong, acute to obtuse or abruptly pointed, petioles narrow and as long as the blade, margins inconspicuously denticulate or dentate to slightly undulate, rarely entire, glabrous to sparingly hispidulous-puberulent and sparsely or not at all short stipitate-glandular, 3–5 nerved; capitula erect or nodding in anthesis, 1 (–3), hemispheric to occasionally campanulate-turbinate, 8–20 mm wide, 11–30 mm long; periclinium sparsely to densely

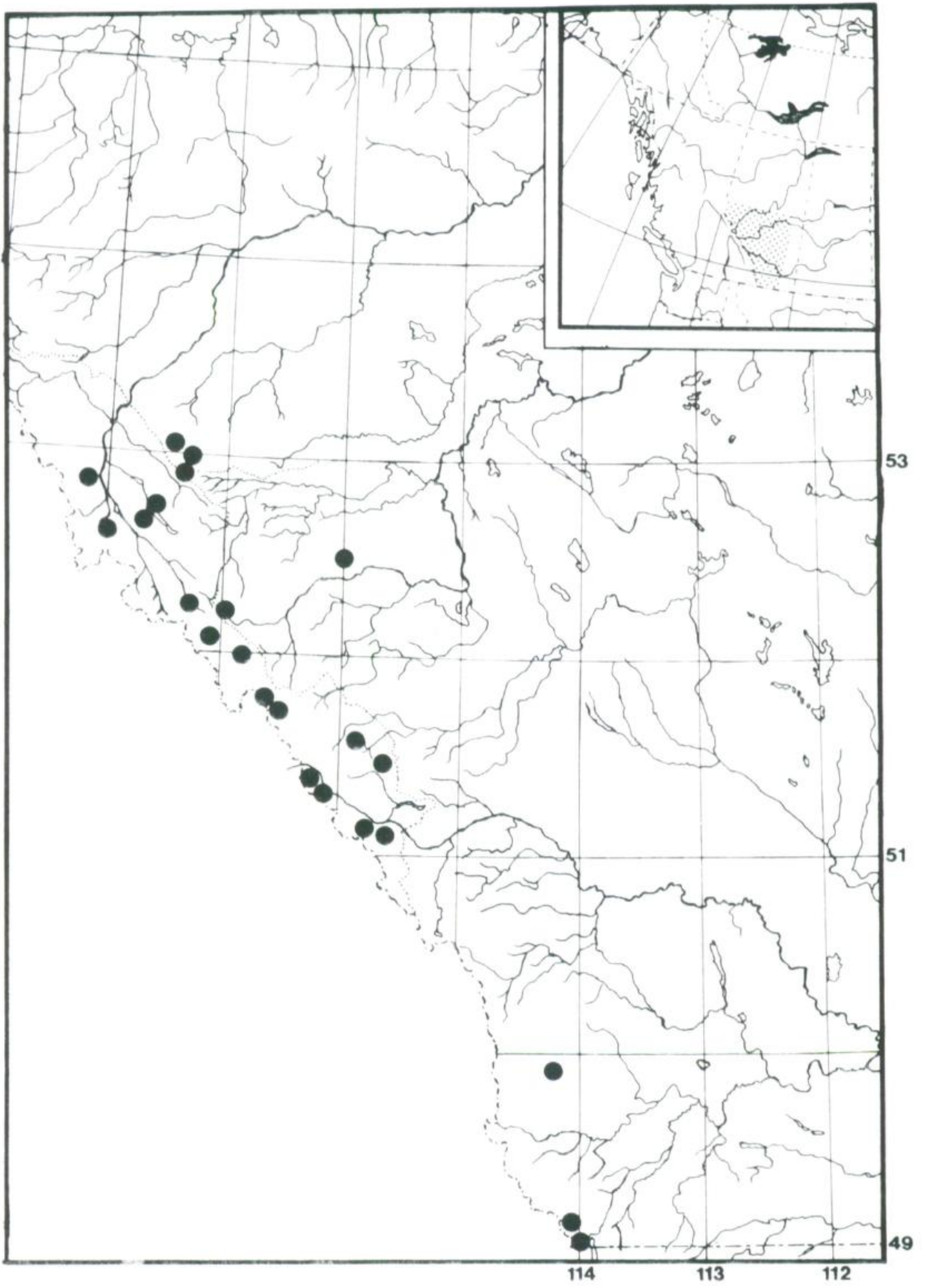


Figure 1. Distribution of *Arnica louiseana* in southwestern Alberta. Shaded area of inset corresponds to area covered by distribution map.

lanate-pilose, white or yellow, rarely stipitate-glandular; involucre bracts 9–20, 7.5–14.5 mm long, 1.8–4.9 mm wide, lanceolate to oblanceolate, acute, acuminate or rarely obtuse, pilose at base becoming glabrous or remaining pilose above, rarely short stipitate-glandular; ligulate florets 6–17, yellow, 10–39 mm long, 2.3–8 mm wide, the teeth 0.4–5 mm long; disc florets 6–10.2 mm long, goblet-shaped, sparingly stipitate-glandular, pilose, the tube 2–3.9 mm long; achenes 2.5–6 mm long, glabrous below and sparsely hirsute above or glabrous throughout, rarely glandular; chromosome number $2n = 38, 57, 76, 95$.

Arnica frigida is extremely variable in pubescence and leaf form. These plants are, however, characterized by their acute to obtuse or abruptly pointed apices; elliptic, lanceolate or spatulate leaves; achenes that are glabrous at the base and sparsely hirsute at the summit; and often with only a single capitulum. The two subspecies in *A. frigida* can be separated by the suite of characters in the key below. A discussion of the taxonomic history and synonymy of *A. frigida* is presented in Downie and Denford (1986a).

KEY TO THE SUBSPECIES OF *ARNICA FRIGIDA*

1. Periclinium yellow; involucre bracts pilose at base becoming glabrous or remaining pilose above, 1.8–4.9 mm wide; plants 0.6–4 dm tall **2a.** subsp. *frigida*
1. Periclinium white; involucre bracts pilose at base becoming glabrous above, 2.5–4.6 mm wide; plants 0.5–2.5 dm tall **2b.** subsp. *gricomii*

2a. *Arnica frigida* Meyer ex Iljin subsp. *frigida*, Trav. Musc. Bot. Acad. Sci. URSS. 19: 112. 1926. *A. louisiana* Farr subsp. *frigida* (Meyer ex Iljin) Maguire, Madroño 6: 153. 1942. *A. louisiana* Farr var. *genuina* Maguire, Madroño 6: 153. 1942. *A. louisiana* Farr var. *frigida* (Meyer ex Iljin) Welsh, Great Basin Nat. 28: 149. 1968. TYPE: "St. Laurence Bay (and Eschscholtz Bay), 1815–1818. *Eschscholtz s.n.*" (HOLOTYPE: LE, photo CAN!, UC!; ISOTYPE: LE, photo UC!)

A. nutans Rydb., N. Amer. Fl. 34: 328. 1927. TYPE: "Alaska, Vicinity of Port Clarence. Hillsides along Tuksuk Channel, near Port Clarence. July 30, 1901. *F. A. Walpole 1618.*" (HOLOTYPE: NY!, photo CAN!, UC!; ISOTYPE: US, photo UC!).

A. sancti-laurentii Rydb., N. Amer. fl. 34: 328. 1927. TYPE: "Sinu St. Laurentii. *Chamisso s.n.*" (HOLOTYPE: GH, photo CAN!, UC!).

A. brevifolia Rydb., N. Amer. Fl. 34: 329. 1927. *A. louisiana* Farr var. *brevifolia* (Rydb.) Maguire, Madroño 6: 153. 1942. TYPE: "Alaska, Copper River Region.

- Near Camp 6/15-19, in lateral moraine of Chitaslene Glacier. June 19, 1902. *W. L. Poto 46.*" (HOLOTYPE: US!, photo CAN!, UC!, drawing NY!).
- A. mendenhallii* Rydb., N. Amer. Fl. 34: 329. 1927. *A. louiseana* Farr var. *mendenhallii* (Rydb.) Maguire, Madroño 6: 153. 1942. TYPE: "Alaska. Fort Hamlin, Yukon River to Bergman, Koyukuk River. Found on Old Man Creek, a branch of the Koyukuk River. July 8, 1901. *W. C. Mendenhall s.n.*" (HOLOTYPE: US!, photo CAN!, UC!, drawing NY!).
- A. illiamnae* Rydb., N. Amer. Fl. 34: 331. 1927. *A. louiseana* Farr var. *illiamnae* (Rydb.) Maguire, Madroño 6: 15. 1942. TYPE: "Alaska. Lake Iliamna region. Open tundra along Nogheling Trail. July 20, 1902. *M. W. Gorman 163.*" (HOLOTYPE: US!, photo CAN!, UC!).
- A. louiseana* Farr var. *pilosa* Maguire, Madroño 6: 154. 1942. TYPE: "Alaska. Igloo Creek, McKinley National Park. July 13, 1932. *J. Dixon 29.*" (HOLOTYPE: UC!; ISOTYPE: US).
- A. snyderi* Raup, Sargentia 6: 250. 1947. TYPE: "Alpine crevices and slide rock. Vicinity of Brintnell Lake. App. Lat. 62° 5' N., Long. 127° 325' W, north slope of Colonel Mt., S. W. Mackenzie. July 5, 1939. *H. M. Raup & J. H. Soper 9383.*" (HOLOTYPE: RM!; ISOTYPE: CAN!).
- A. frigida* var. *glandulosa* Boivin, Rhodora 55: 56. 1953. TYPE: "Yukon Territory, Canada. Steep rocky slope by Klondike River. About 20 miles east of Dawson on road to McQuesten. July 17, 1949. *J. A. Calder & L. G. Billard 3767.*" (HOLOTYPE: DAO!).

Plants 0.6-4 dm tall; leaves 2-4 pairs; lower cauline leaves 12-100 mm long, 5-35 mm wide, acute or obtuse or abruptly pointed, lanceolate, elliptic to elliptic-lanceolate, spathulate or rarely oblanceolate; capitula 1 (-3), 8-20 mm wide, 11-30 mm long; periclinium sparsely to densely lanate-pilose, yellow; involucral bracts 7.5-14.5 mm long, 1.8-4.9 mm wide, lanceolate, acuminate or rarely obtuse, pilose at base becoming glabrous or remaining pilose above; ligulate florets 7-17, 10-39 mm long, 2.3-8 mm wide, the teeth 1-5 mm long; achenes 3.2-6 mm long; chromosome number $2n = 38, 57, 76, 95$.

DISTRIBUTION AND HABITAT. Abundant in alpine meadows, tundras and calcareous rocky outcrops from the Kolyma River, U.S.S.R., east to the islands of Bering Strait, Alaska, Yukon Territory to the Mackenzie River, Northwest Territories (Figure 2). Scattered populations found north of the Arctic Circle and east to the Coppermine River in Northwest Territories, and infrequent to rare in alpine areas of northern British Columbia. Flowers June to July.

- 2b. ***Arnica frigida*** Meyer ex Iljin subsp. ***griscomii*** (Fern.) S. R. Downie, Canad. J. Bot. 64: 1369. 1986. *A. griscomii* Fern., Rhodora 26: 105. 1924. *A. louiseana* Farr subsp. *griscomii* (Fern.) Maguire, Brittonia 4: 419. 1943. *A. louiseana* Farr var.

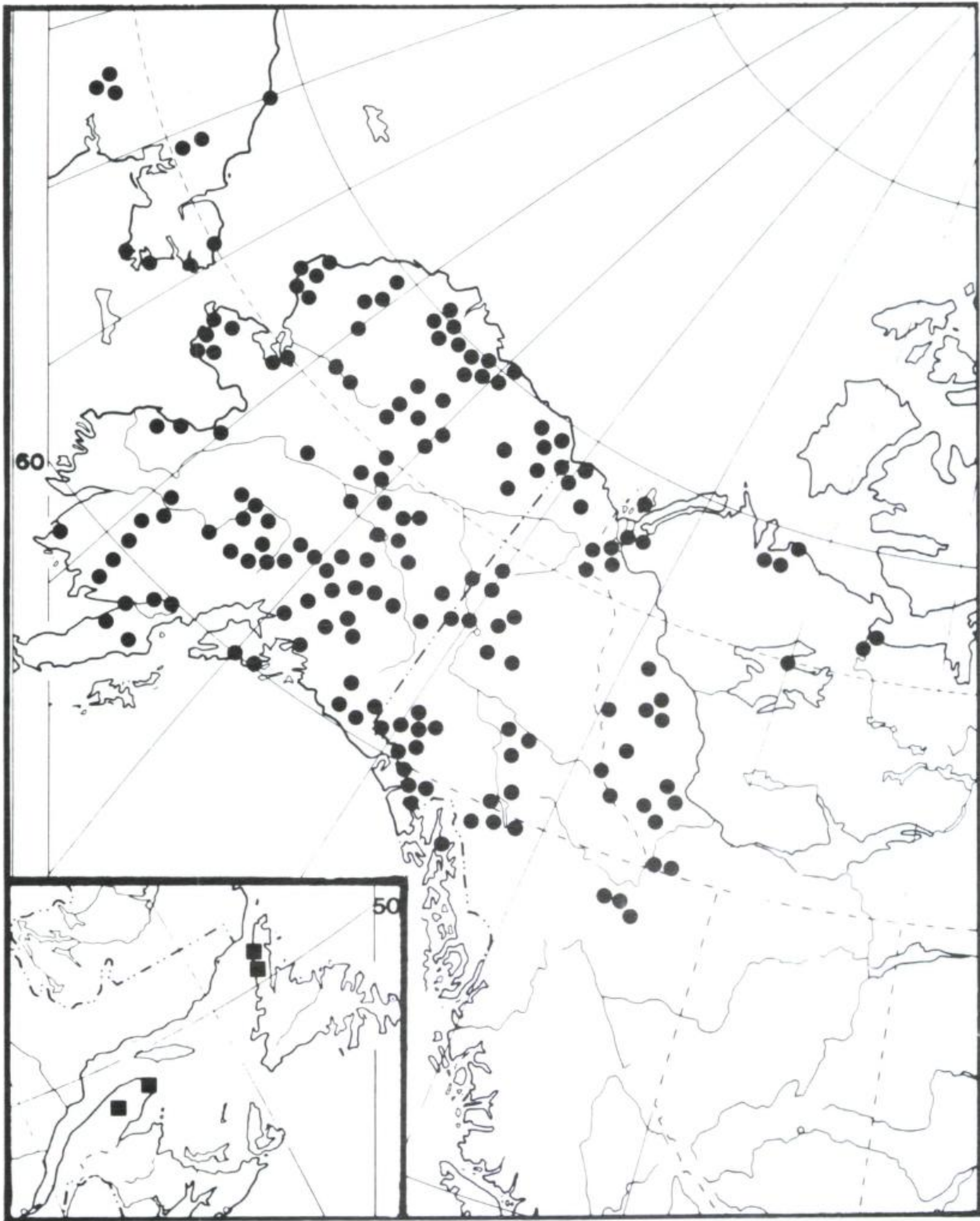


Figure 2. Distribution of *Arnica frigida* subsp. *frigida* (●) and *A. frigida* subsp. *griscomii* (■).

griscomii (Fern.) Boivin, *Phytologia* 23: 95. 1972. TYPE: "Québec. Matane County. Cold chimneys in the schist at about 900–1000 m altitude, south of Fernald Pass, Mt. Mattaouisse. Aug. 20, 1923. *M. L. Fernald & L. B. Smith* 26084." (HOLOTYPE: GH!, photo CAN!, ISOTYPES: CAN!; MT!, UC!, photo UC!).

Plants 0.5–2.5 dm tall; leaves 1–2 pairs; lower cauline leaves 15–80 mm long, 6–25 mm wide, acute or obtuse, spatulate to ovate or lanceolate-oblong; capitula 1 (–3), 11–20 mm wide, 12–23 mm long; periclinium moderately pilose, white; involucral bracts 9–13.5 mm long, 2.5–4.6 mm wide, broadly lanceolate to oblanceolate, acuminate or obtuse, pilose at base becoming glabrous above; ligulate florets 6–11, 15–22 mm long, 3–6 mm wide, the teeth 0.4–1.8 mm long; achenes 2.5–4.5 mm long; chromosome number $2n = 76$.

DISTRIBUTION AND HABITAT. Rare on exposed hornblende-schists and dry schistose talus in the alpine areas (850–1070 meters) of Mts. Logan and Saint-Alban of the Gaspé Peninsula in Québec; 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 (Figure 2). Flowers June to July.

3. ***Arnica rydbergii*** Greene, *Pittonia* 4: 37. 1899. TYPE: "Flora of Central Montana. Little Belt Mts., near the Pass. Aug. 10, 1896. *J. H. Flodman 891*." (HOLOTYPE: ND!, ISOTYPES: NY!, US!, photo CAN!).

A. caespitosa A. Nels., *Bot. Gaz.* 30: 203. 1900. TYPE: "Yellowstone National Park, on high stony ridges, Druid Peak, Wyoming. July 12, 1899. *A. & E. Nelson 5785*." (HOLOTYPE: RM!, ISOTYPES: RM!).

A. tenuis Rydb., *Bull. Torrey Bot. Club* 28: 20. 1901. TYPE: "Big Horn Mountains, Sheridan Co., Northwestern Wyoming. Aug. 1899. *F. Tweedy 2094*." (HOLOTYPE: NY, photo CAN!).

A. aurantiaca Greene, *Torreyia* 1: 42. 1901. TYPE: "Eastern Oregon Plants. Head of Keystone Creek, Wallowa Mtns. Aug. 2, 1900. *Wm. C. Cusick 2451*." (ISOTYPE: RM!, US).

A. lasiosperma Greene, *Leaflets* 2: 48. 1910. TYPE: Estes Park, base of Long's Peak, Colorado. 26 Aug. 1895. *Osterhout s.n. fide* Maguire (1943). Type not seen.

A. cascadiensis St. John, *Rep. Prov. Mus. Nat. Hist. B.C.* 1926: 10. 1927. TYPE: "Mt. McLean, British Columbia. July 11, 1926. *W. B. Anderson 8003*." (HOLOTYPE: WS, photo CAN!).

A. sulcata Rydb., *N. Amer. Fl.* 34: 344. 1927. TYPE: "Scott Mountain, Siskiyou County, California. Aug. 22, 1896. *E. L. Greene 1005*." (HOLOTYPE: GH, drawing NY!).

A. ovalis Rydb., *N. Amer. Fl.* 34: 338. 1927. TYPE: "Crow Nest Pass, Rocky Mtns. July 31, 1897. *J. M. Macoun 72719*." (HOLOTYPE: CAN!, photo CAN!).

Plants 0.8–3.5 dm tall; rhizomes moderately long and densely covered with scales and leaf base remnants; stems caespitose, several branches arising from the rhizome tip, simple, sparsely puberulent becoming moderately pubescent upwards, stipitate-glandular; leaves 2–4 pairs; upper cauline leaves sessile, lanceolate to broadly lanceo-

late; lower cauline leaves 2–7 cm long, 0.5–2.5 cm wide, acute to occasionally obtuse, oblanceolate to spatulate, sessile or petioles very short and broad-winged, margins entire to occasionally denticulate to sometimes predominantly dentate, glabrous to sparsely pilose, stipitate-glandular, 3–5 nerved; capitula erect, 1–3 (–5), campanulate-turbinate, 9–15 mm wide, 7–22 mm long; periclinium moderately pilose, white, short stipitate-glandular; involucre bracts 9–15, 7.3–14.5 mm long, 1.3–3.1 mm wide, linear-oblong to narrowly lanceolate, acute, glabrous to sparingly pilose, stipitate-glandular; ligulate florets 6–10, yellow, 13.5–29 mm long, 4–8.5 mm wide, entire or minutely 3-toothed, if toothed the teeth 0.1–0.5 mm long; disc florets 6.1–9.1 mm long, narrowly tubular, stipitate-glandular, densely pilose, the tube 2.3–3.7 mm long; achenes 3.8–7.1 mm long, densely hirsute throughout, not stipitate-glandular; chromosome number $2n = 38, 76$.

DISTRIBUTION AND HABITAT. Dry to mesic, exposed, rocky alpine slopes and ridges or alpine meadows in the Rocky Mountains of Alberta and British Columbia, south in the Cascade Mountains to Washington and Oregon, the Uinta Mountains of Utah and the Rocky Mountains of Wyoming and Colorado (Figure 3). Also known from Vancouver Island. Flowers July to August.

Confined to the cordillera of western North America, *Arnica rydbergii* is readily distinguished by its small, narrow heads; its minutely denticulate or entire ligule margins; few and narrowly tubular disc florets; clustered stems; and a strong tendency for the lower cauline leaves to be sessile.

During the period 1899 to 1901, four names were proposed for this species, including *Arnica rydbergii* Greene. As previously suggested by Maguire (1943), and observed in this study, the type specimens of *A. caespitosa*, *A. tenuis* and *A. aurantiaca* all fall within acceptable species limits and were undoubtedly named before the application of *A. rydbergii* was fully understood. The type of *A. cascadiensis*, although not seen in this study, was described as a glandless *A. rydbergii*, for it maintains all other diagnostic features (Maguire, 1943). The presence (or absence) of short stipitate-glandular hairs on the leaves and periclinium is not a critical character. *Arnica lasiosperma* is merely a depauperate specimen of *A. rydbergii* (Maguire, 1943).

The short-petiolate and large oval basal leaves led Rydberg to propose *Arnica ovalis* as a new species in 1927. However, its entire to indistinctly denticulate ligules, the narrow capitulum, and the sessile cauline leaves strongly suggest that this species conforms to

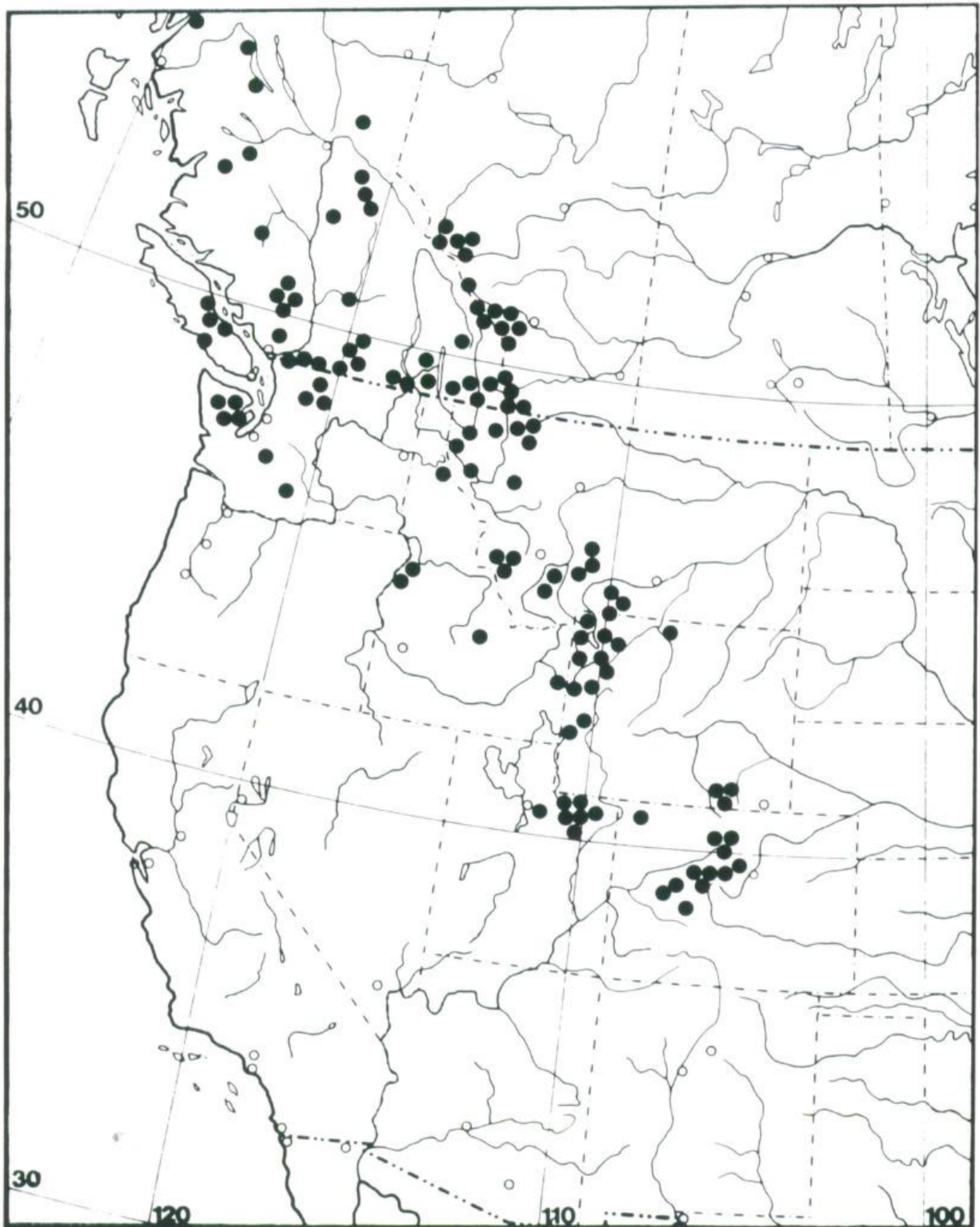


Figure 3. Distribution of *Arnica rydbergii*.

A. rydbergii. In the same year, Rydberg proposed *A. sulcata* for a single specimen possessing a short-plumose pappus, and a sulcate and copiously glandular stem. Maguire (1943) observed similarities between this and *A. rydbergii*, and placed *A. sulcata* in synonymy with the latter. With the presence of this plumose pappus it is doubtful if this species belongs in *A. rydbergii*. In addition, the range of *A.*

rydbergii does not extend south to California. However, without observing this specimen, it is difficult to assign it to a particular taxon. Until subsequent collections and observation reveal this taxon to be distinct, it should remain in synonymy with *A. rydbergii*.

4. ***Arnica lonchophylla***, Pittonia 4: 164. 1900.

Plants 1.2–5 dm tall; rhizomes slender, branched, covered with numerous dark imbricate scales and remnant leaf bases; stems solitary or few, simple or branched, glabrous to sparsely puberulent and moderately stipitate-glandular becoming densely pubescent and glandular upwards; leaves 3–7 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 3.5–14 cm long, 0.5–3.7 cm wide, acute, narrowly to broadly lanceolate to ovate, distinctly petiolate, petioles narrow and approximately equalling the blade in length, margins regularly dentate or denticulate, glabrous to moderately pilose, sparsely to densely stipitate-glandular, 3–7 nerved; capitula erect, (1–) 3–7 (–8), campanulate-turbinate, 7–20 mm wide, 8–16 mm long; periclinium glabrous to moderately pilose, white, stipitate-glandular; involucre bracts 10–15, 6.1–11.5 mm long, 1.2–3.5 mm wide, narrowly lanceolate, acute, glabrous to moderately pilose, stipitate-glandular; ligulate florets 6–14, yellow, 10–26 mm long, 3–7.1 mm wide, 3-toothed, the teeth 0.1–2.1 mm long; disc florets 5–9.5 mm long, narrowly goblet-shaped or goblet-shaped, moderately to densely pilose with long or short hairs, sparsely to densely stipitate-glandular, the tube 1.9–4 mm long; achenes 3–5.9 mm long, densely hirsute throughout, occasionally to regularly stipitate-glandular; chromosome number $2n = 38, 57, 76$.

In his monographic treatment of the genus, Maguire (1943) recognized three subspecies within *Arnica lonchophylla*: *genuina*, *chionopappa* and *arnoglossa*. The subspecific epithet *genuina* is illegitimate and should be treated as *lonchophylla*. Ediger and Barkley (1978), however, did not recognize infraspecific taxa within *A. lonchophylla* and maintained that the small differences among them do not warrant taxonomic recognition. Material from eastern Canada, previously recognized as subsp. *chionopappa*, is inseparable from widespread northwestern Canadian populations. Two subspecies are recognized within *A. lonchophylla*: *lonchophylla* and *arnoglossa*. The morphological characters delimiting these taxa are described below.

KEY TO SUBSPECIES OF *ARNICA LONCHOPHYLLA*

1. Periclinium and involucral bracts moderately pilose; disc corolla goblet-shaped, sparsely stipitate-glandular, densely long pilose; leaves sparsely stipitate-glandular, glabrous to moderately pilose, 3–11 times as long as wide **4a.** subsp. *lonchophylla*
1. Periclinium and involucral bracts glabrous to sparsely puberulent; disc corolla narrowly goblet-shaped, densely stipitate-glandular, moderately short pilose; leaves densely stipitate-glandular, glabrous to sparsely puberulent, 3–5 times as long as wide
 **4b.** subsp. *arnoglossa*

4a. *Arnica lonchophylla* Greene subsp. *lonchophylla*, Pittonia 4: 164. 1900. *A. lonchophylla* Greene subsp. *genuina* Maguire, Brittonia 4: 430. 1943. *A. alpina* (L.) Olin var. *lonchophylla* (Greene) Welsh, Great Basin Nat. 28: 149. 1968. *A. alpina* (L.) Olin subsp. *lonchophylla* (Greene) G. W. Douglas & G. Ruyle-Douglas in Taylor and MacBryde, Canad. J. Bot. 56: 185. 1978. *A. angustifolia* Vahl subsp. *lonchophylla* (Greene) G. W. Douglas & G. Ruyle-Douglas, Canad. J. Bot. 56: 1710. 1978. TYPE: "Athabasca River, Lat. 53° 30', Alberta. June 25, 1898. *W. Spreadborough 19647*." (HOLOTYPE: ND!; ISOTYPE: CAN!, photo CAN!).

A. wilsonii Rydb., N. Amer. Fl. 34: 332. 1927. TYPE: "W. of James Bay, 140 miles up Kapiscow River, Ont. July 15, 1902. *W. J. Wilson 54043*." (HOLOTYPE: CAN!).

Arnica chionopappa Fern., Rhodora 7: 148. 1905. *A. lonchophylla* Greene subsp. *chionopappa* (Fern.) Maguire, Brittonia 4: 430. 1943. TYPE: "Wet cliffs, Banks of the Grand River, Gaspé County, Québec. June 30–July 3, 1904. *M. L. Fernald s.n.*" (HOLOTYPE: GH!, photo CAN!).

A. gaspensis Fern., Rhodora 7: 148. 1905. TYPE: "Dry precipitous ledges of a hill at Cap Tourelle near St. Anne des Monts, Gaspé Co., Lower Canada. July 16, 1881. *J. A. Allen s.n.*" (HOLOTYPE: GH!, photo CAN!).

A. fernaldii Rydb., N. Amer. Fl. 34: 333. 1927. TYPE: "Newfoundland, Region of Port au Port Bay, Dry exposed ledges and shingle on the limestone tableland, Table Mountain, July 16 and 17, 1914. *M. L. Fernald & H. St. John 10875*." (HOLOTYPE: NY; ISOTYPES: CAN!, GH!, RM!).

Plants 1.2–5 dm tall; leaves 3–7 pairs; lower cauline leaves 3.5–14 cm long, 0.5–3.7 cm wide, narrowly lanceolate to ovate, margins regularly denticulate or dentate, glabrous to moderately pilose, sparsely stipitate-glandular, 3–5 nerved; capitula (1–) 3–5 (–8), 7–20 mm wide, 8–16 mm long; periclinium moderately pilose, white, stipitate-glandular; involucral bracts 7–11.5 mm long, 1.3–3.5 mm wide, moderately pilose throughout, stipitate-glandular; ligulate

florets 6–14, 13–26 mm long, 3–7.1 mm wide, the teeth 0.1–2.1 mm long; disc florets 5.1–9.5 mm long, goblet-shaped, densely long pilose, sparsely stipitate-glandular, the tube 1.9–4 mm long; achenes 3–5.9 mm long, occasionally short stipitate-glandular; chromosome number $2n = 57, 76$.

DISTRIBUTION AND HABITAT. Dry to mesic, open montane slopes of the Canadian Rockies extending northward in the interior lowlands to the Arctic Circle. Its range extends from the Yukon Territory, eastward through southwestern Northwest Territories, the northern regions of Saskatchewan and Manitoba to Hudson Bay with disjunct populations in northeastern Minnesota and adjacent Ontario, the Gaspé Peninsula, Anticosti Island, New Brunswick, Nova Scotia, and western Newfoundland (Figure 4). In eastern Canada, plants are found in open woodlands, river gravels, shorelines, and calcareous rocky outcrops, precipices and barrens. Flowers June to August.

In the past, *Arnica lonchophylla* subsp. *lonchophylla* from south central Ontario has either been regarded as a separate species (i.e., *A. wilsonii*; Rydberg, 1927), or a hybrid between *A. angustifolia* and *A. lonchophylla* (Maguire, 1943). Subsequent collections led Ediger and Barkley (1978) to place the name *A. wilsonii* in synonymy with *A. lonchophylla*. All material seen by the authors falls within the normal range of variation of typical *A. lonchophylla* subsp. *lonchophylla*.

In 1927, Rydberg reduced *Arnica chionopappa* to *A. arnoglossa*, and described the Newfoundland *A. chionopappa* as *A. fernaldii*. Fernald (1933) was unable to detect any differences between *A. chionopappa* from Gaspé, Anticosti Island, New Brunswick and Newfoundland, and inferentially reduced *A. fernaldii* to *A. chionopappa*. Maguire (1943) noticed that plants from Newfoundland are usually somewhat smaller and have narrower leaves than those from Québec. The greater number of herbarium specimens examined during this study showed no statistically significant differences between Newfoundland and Québec material.

Arnica gaspensis was proposed by Fernald in 1905 for plants similar to *A. chionopappa* but having larger, less hirsute achenes, oblanceolate bracts, more sharply toothed ligules, and a creamy-white pappus. These plants are similar to *A. lonchophylla* subsp. *lonchophylla*.

In northwestern Canada, where the ranges of *Arnica angustifolia* subsp. *angustifolia* and *A. lonchophylla* overlap, some specimens

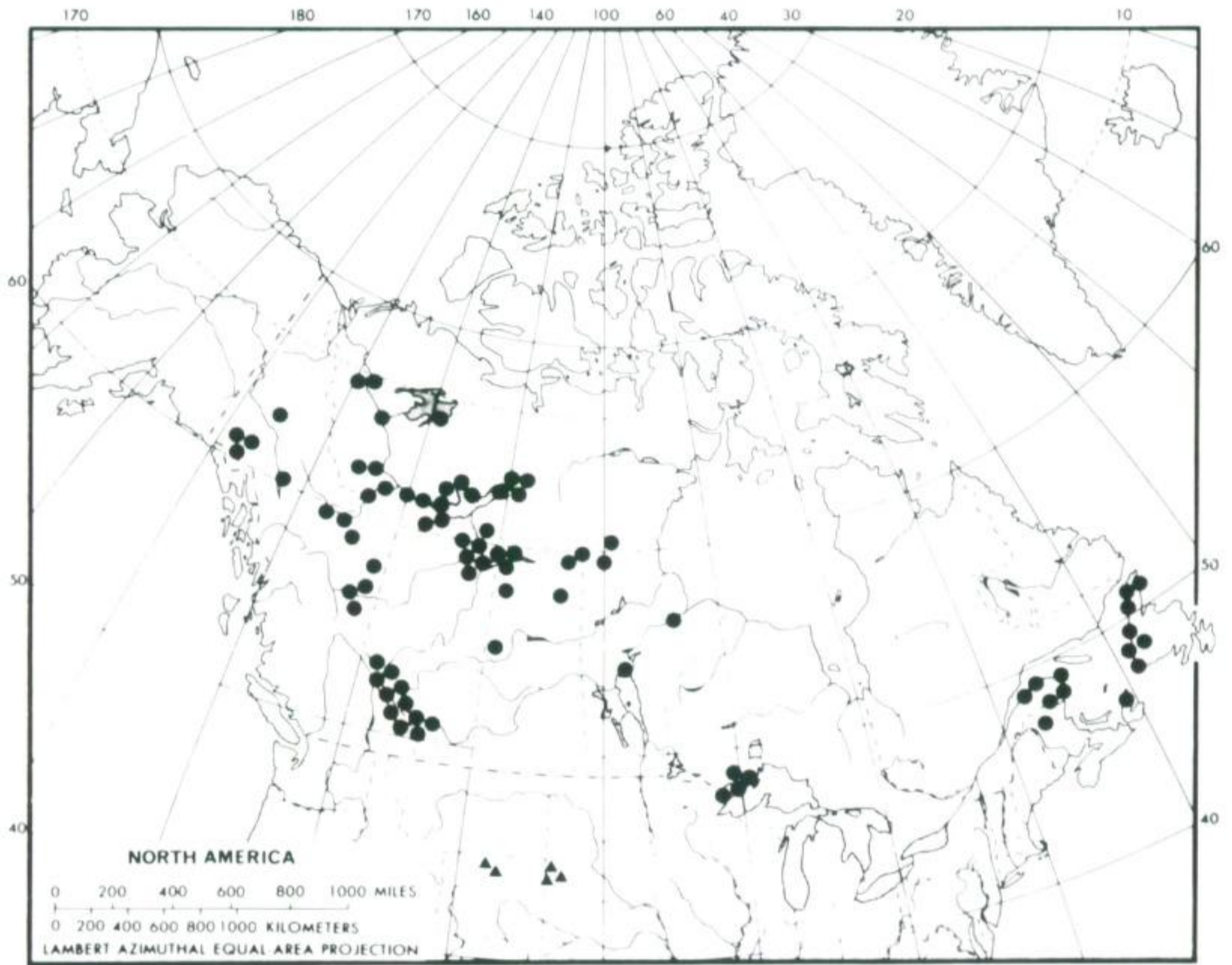


Figure 4. Distribution of *Arnica lonchophylla* subsp. *lonchophylla* (●) and *A. lonchophylla* subsp. *arnoglossa* (Δ).

cannot be assigned to either taxon without difficulty. This similarity in morphology led Douglas and Ruyle-Douglas (1978) to propose *A. angustifolia* subsp. *lonchophylla*. The status of these two taxa is further confounded by their flavonoid chemistry, for no differences are apparent. In addition, both share the same ploidy levels. Where the ranges do not overlap, *A. lonchophylla* and *A. angustifolia* are separated with ease. *Arnica lonchophylla* subsp. *arnoglossa* and the eastern Canadian disjunct of *A. lonchophylla* subsp. *lonchophylla* are evidently long-petiolate, have prominent regularly dentate teeth and obvious campanulate-turbinate capitula. Similarly, *A. angustifolia* from Scandinavia, the U.S.S.R., Greenland and eastern Canada show a great degree of morphological uniformity. *Arnica lonchophylla* is also typically a plant of montane or lowland habitats, whereas *A. angustifolia* is arctic and alpine. Nevertheless, in northwestern Canada, evidence suggests that these two taxa may be hybridizing; however, the actual extent of hybridization is unknown.

4b. *Arnica lonchophylla* subsp. **arnoglossa** (Greene) Maguire, *Brittonia* 4: 431. 1943. *A. arnoglossa* Greene, *Pittonia* 4: 166. 1900. *A. lonchophylla* Greene var. *arnoglossa* (Greene) Boivin, *Nat. Can.* 87: 27. 1960. TYPE: "Black Hills, near Fort Meade, S. Dakota. June 11, 1887. *W. H. Forwood* 323 1/2." (HOLOTYPE: US!, photo CAN!).

A. arcana A. Nels., *Bot. Gaz.* 37: 276. 1904. TYPE: Doyle Creek, Big Horn Mtns., Wyoming. July 26, 1902. *Goodding* 377 *fide* Ediger and Barkley (1978). Type not seen.

A. rydbergii var. *dubia* A. Nels. ex Hayward, *Bot. Gaz.* 85: 384. 1928, *Nomen nudum*.

Plants 1.7–4.5 dm tall; leaves 3–5 pairs; lower cauline leaves 4.5–11 cm long, 1.2–3 cm wide, broadly lanceolate to ovate, margins regularly denticulate to occasionally dentate, glabrous to sparsely puberulent, densely stipitate-glandular, 5–7 nerved; capitula (1–) 3–7 (–8), 7–13 mm wide, 9–13 mm long; periclinium glabrous to sparsely puberulent, white, densely stipitate-glandular; involucre bracts 6.1–10 mm long, 1.2–2.4 mm wide, glabrous to sparsely puberulent, densely stipitate-glandular; ligulate florets 7–10, 10–17.5 mm long, 3–5 mm wide, the teeth 0.2–1.1 mm long; disc florets 5–8.5 mm long, narrowly goblet-shaped, moderately short pilose, densely stipitate-glandular, the tube 2–3.2 mm long; achenes 3–5 mm long, regularly short stipitate-glandular; chromosome number $2n = 38$.

DISTRIBUTION AND HABITAT. Extremely localized in the Big Horn Mountains of north central Wyoming and the Black Hills region of South Dakota (Figure 4). Apparently quite rare. Plants of moist rocky soils and open woodlands. Flowers July to August.

Arnica lonchophylla subsp. *arnoglossa* is restricted to the Black Hills of South Dakota and the Big Horn mountains of Wyoming. It is readily distinguished from *A. lonchophylla* subsp. *lonchophylla* by its broader leaves, narrower disc corollas, and glandular but sparsely puberulent leaves, disc corollas, periclinium and involucre bracts.

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

Plants 0.5–5.4 dm tall; rhizomes slender, branched and covered in imbricate scales and leaf base remnants that may have tufts of long hairs in their axils; stems solitary or few, simple or rarely branched, sparsely to densely villous, short stipitate-glandular becoming increasingly villous and glandular upwards; leaves 1–5 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 2–20 cm

long, 0.3–4.1 cm wide, acute or acuminate, linear to broadly lanceolate, petioles short and broad-winged or narrow-winged and shorter than the blade, margins entire to irregularly denticulate or dentate, glabrous to densely spreading woolly-villous, stipitate-glandular, 3–5 nerved; capitula erect, 1–3 (–5), hemispheric, 12–30 mm wide, 9–21 mm long; periclinium very conspicuous, moderately to densely pilose, white, stipitate-glands occasionally lacking, obscured or dense; involucre bracts 9–22, 6.5–17.6 mm long, 1.5–4.1 mm wide, narrowly to broadly lanceolate to occasionally oblanceolate, acute or acuminate, densely to sparsely pilose throughout or evidently pilose at base becoming less so upwards, inconspicuously to obviously stipitate-glandular; ligulate florets 6–16, yellow, 10–40 mm long, 3–9.5 mm wide, 3-toothed, the teeth 0.2–7 mm long; disc florets 5–10 mm long, goblet-shaped, moderately to densely pilose, inconspicuously glandular or absent, the tube 1.9–4.1 mm long; achenes 3.1–7.6 mm long, densely hirsute throughout, inconspicuous or not at all glandular; chromosome number $2n = 38, 57, 76, 95$.

Arnica angustifolia, a circumpolar and circumboreal species, is the most widespread and most polymorphic in the genus. This taxon is identified by its long, linear to broadly lanceolate leaves, densely hirsute achenes, erect capitula, and yellow florets. Maguire (1943) segregated this species into seven geographical races; however, results of this investigation indicate that this aggregate is best treated as two distinct taxa: *A. angustifolia* subsp. *angustiifolia* (a combination of the previously recognized subspecies *angustifolia*, *attenuata*, *sornborgeri*, *intermedia*, *iljinii* and *alpina* of *A. angustifolia* and *A. plantaginea*) and *A. angustifolia* subsp. *tomentosa*. *Arnica angustifolia* subsp. *tomentosa* is a relatively small plant possessing one to three capitula and densely villous leaves, stems and involucre bracts. The periclinium is densely woolly-villous and conspicuously stipitate-glandular. *Arnica angustifolia* subsp. *angustifolia* is usually a much taller plant bearing one to five capitula per stem. Its leaves, stems and bracts are never densely villous. In many instances, the leaves are glabrous. The periclinium is usually pilose, but never woolly-villous, and stipitate-glands may be inconspicuous or lacking. A discussion of the taxonomic history and synonymy of *A. angustifolia* is presented in Downie (1988).

KEY TO SUBSPECIES OF *ARNICA ANGUSTIFOLIA*

1. Leaves glabrous to moderately villous, entire to denticulate or rarely dentate, linear to broadly lanceolate; periclinium mod-

erately to densely pilose, stipitate-glands occasionally lacking or obscured **5a.** subsp. *angustifolia*

1. Leaves densely spreading woolly-villous, entire or rarely denticulate, narrowly lanceolate; periclinium densely woolly-villous and densely stipitate-glandular **5b.** subsp. *tomentosa*

5a. *Arnica angustifolia* Vahl in Hornem. subsp. *angustifolia*, Fl. Dan. 9(26): 5. 1816. *A. alpina* (L.) Olin var. *angustifolia* (Vahl) Fern., Rhodora 36: 96. 1934. *A. alpina* (L.) Olin subsp. *angustifolia* (Vahl) Maguire, Madroño 6: 153. 1942. TYPE: "E. Groenlandia. Geiseke s.n." (HOLOTYPE: S!; ISOTYPE: C!).

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

A. alpina (L.) Olin 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 L. 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* Vahl 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* (L.) Olin subsp. *attenuata* (Greene) Maguire, Madroño 6: 153. 1942. *A. alpina* (L.) Olin var. *attenuata* (Greene) Ediger & Barkl., N. Amer. Fl. 10: 31. 1978. *A. angustifolia* Vahl subsp. *attenuata* (Greene) G. W. Douglas & G. Ruyle-Douglas, Canad. 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. Spec. Nov. Regni. Veg. 3: 388. 1907. TYPE: "Severn River (Keewatin) Ont. August 5, 1886. J. Macoun 14699." (HOLOTYPE: CAN!).

A. alpina (L.) Olin subsp. *attenuata* Greene var. *linearis* Hultén, Lunds Univ. Åarrskr. II. Sect. 2, 46: 1588. 1950. TYPE: Fort Yukon. *Murie 2204 fide* Ediger and Barkley (1978). Type not seen.

A. alpina (L.) Olin subsp. *attenuata* Greene var. *vestita* Hultén, Lunds Univ. Åarrskr. 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.

Arnica alpina (L.) Olin subsp. *iljinii* Maguire, Brittonia 4: 411. 1943. *A. iljinii* (Maguire) Iljin, Fl. URSS. 26: 658. 1961. *A. angustifolia* Vahl 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: LE, photo CAN!; ISOTYPES: GH!, O!).

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

Arnica sornborgeri Fern., Rhodora 7: 147. 1905. *A. alpina* (L.) Olin 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!).
- Arnica sornborgeri* Fern. var. *ungavensis* Boivin, *Nat. Can.* 75: 211. 1948. *A. alpina* (L.) Olin var. *ungavensis* Boivin, *Phytologia* 23: 94. 1972. TYPE: Québec. Fort Chimo, Baie d'Ungava. Aug. 17, 1945. Dutilly & Lepage 14768 fide Ediger and Barkley (1978). Type not seen.
- Arnica plantaginea* Pursh, *Fl. Amer. Sept.* 527. 1814. *A. alpina* (L.) Olin var. *plantaginea* (Pursh) Ediger and Barkl., *N. Amer. Fl. Ser. II, Pt. 10*: 32. 1978. TYPE: "Labrador. Herb. Dickson. Colmaster s.n. (HOLOTYPE: PH!, photo CAN!).

Plants 0.5–5.4 dm tall; stems sparsely to moderately villous; lower cauline leaves 2–20 cm long, 0.3–4.1 cm wide, acute or acuminate, linear to broadly lanceolate, petioles short and broad-winged or narrow-winged and shorter than the blade, margins entire to irregularly denticulate or rarely dentate, glabrous to moderately villous; capitula 1–3 (–5); ligulate florets 6–16, 10–40 mm long, the teeth 0.2–7 mm long; periclinium moderately to densely pilose, white, stipitate-glands occasionally lacking or obscured; involucre bracts sparsely to moderately pilose; achenes 3.1–7 mm long; chromosome number $2n = 38, 57, 76, 95$.

DISTRIBUTION AND HABITAT. A circumpolar taxon, occurring between 49° and 83° N. Latitude in North America, between 60° and 80° N. in the U.S.S.R., and in northern Scandinavia near the Arctic Circle. In North America, its range extends from Alaska eastward through northern Manitoba, Ontario and Québec, with isolated populations in northern Newfoundland (Figure 5); exposed tundras, gravelly and rocky slopes, roadsides, moist banks and open woodlands. In the southernmost portion of its range it is found on alpine slopes and ridges. Flowers May to September.

- 5b. *Arnica angustifolia* Vahl subsp. *tomentosa* (Macoun) G. W. Douglas & G. Ruyle-Douglas, *Canad. J. Bot.* 56: 1710. 1978. *A. tomentosa* Macoun, *Ottawa Nat.* 13: 166. 1899. *A. alpina* (L.) Olin subsp. *tomentosa* (Macoun) Maguire, *Madroño* 6: 153. 1942. *A. alpina* (L.) Olin var. *tomentosa* (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!).

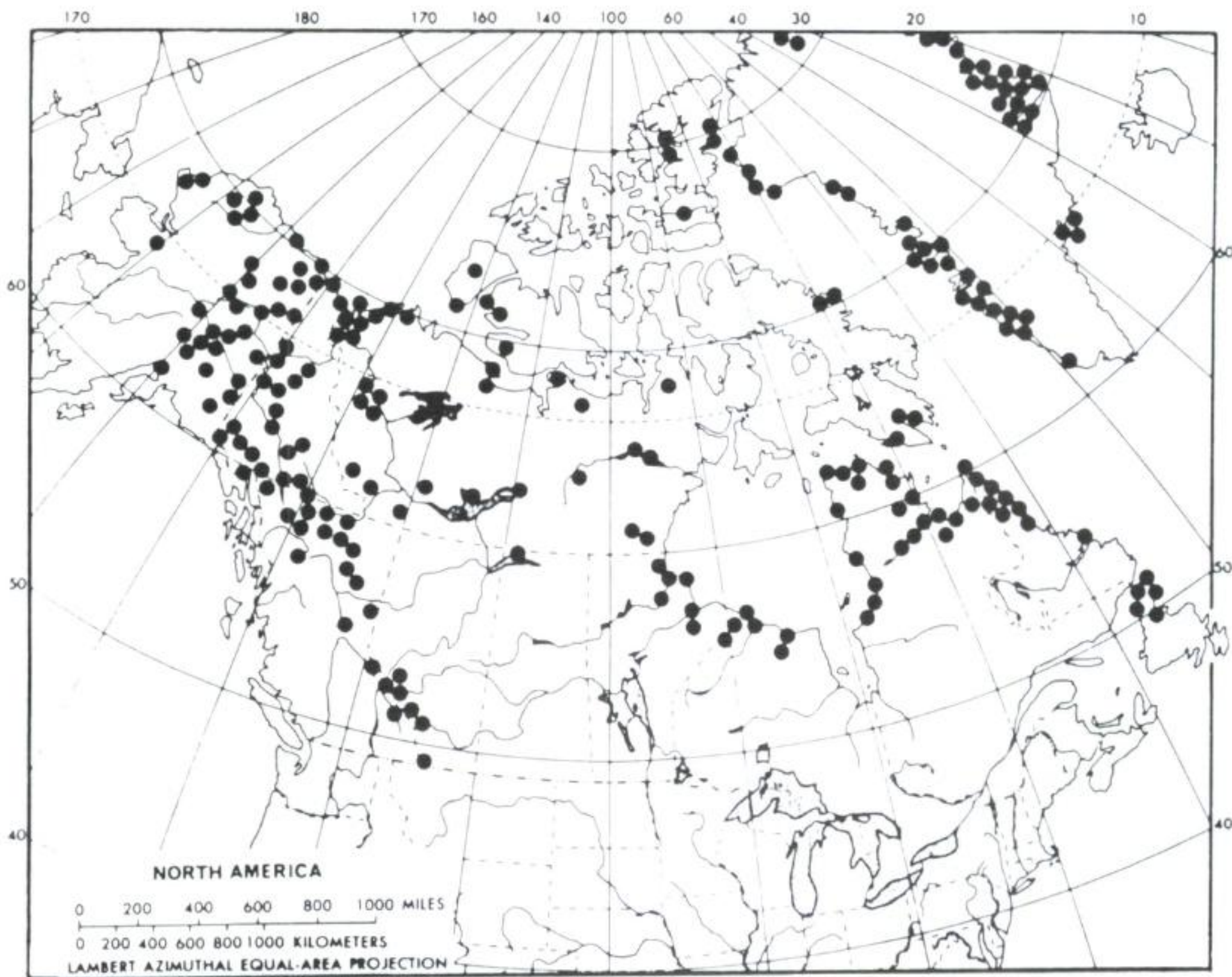


Figure 5. North American distribution of *Arnica angustifolia* subsp. *angustifolia*.

A. tomentosa Macoun ex Greene, *Pittonia* 4: 168. 1900. *non A. tomentosa* Macoun, *Ottawa Nat.* 13: 166. 1899. TYPE: "Mountains near Athabasca River near Lac Brule, Rocky Mts. June 20, 1898. *W. Spreadborough* 19635." (ISOTYPE: CAN!, photo CAN!)

Plants 0.6–2 (–3) dm tall; stems densely villous, lower cauline leaves 3.5–10.5 cm long, 0.3–1.2 cm wide, acute, narrowly lanceolate, petioles short and broad-winged, margins entire or rarely irregularly denticulate, densely spreading woolly-villous; capitula 1 (–3); ligulate florets 7–12, 14.5–30 mm long, the teeth 0.5–3.5 mm long; periclinium densely woolly-villous and densely stipitate-glandular, white; involucre bracts densely woolly-villous; achenes 4.5–7.6 mm long; chromosome number $2n = 57, 76$.

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 (Figure 6); bare rocky alpine slopes and subalpine meadows. Disjunct and infrequent in exposed rocky areas and dry limestone barrens of northwestern Newfoundland. Flowers July to August.

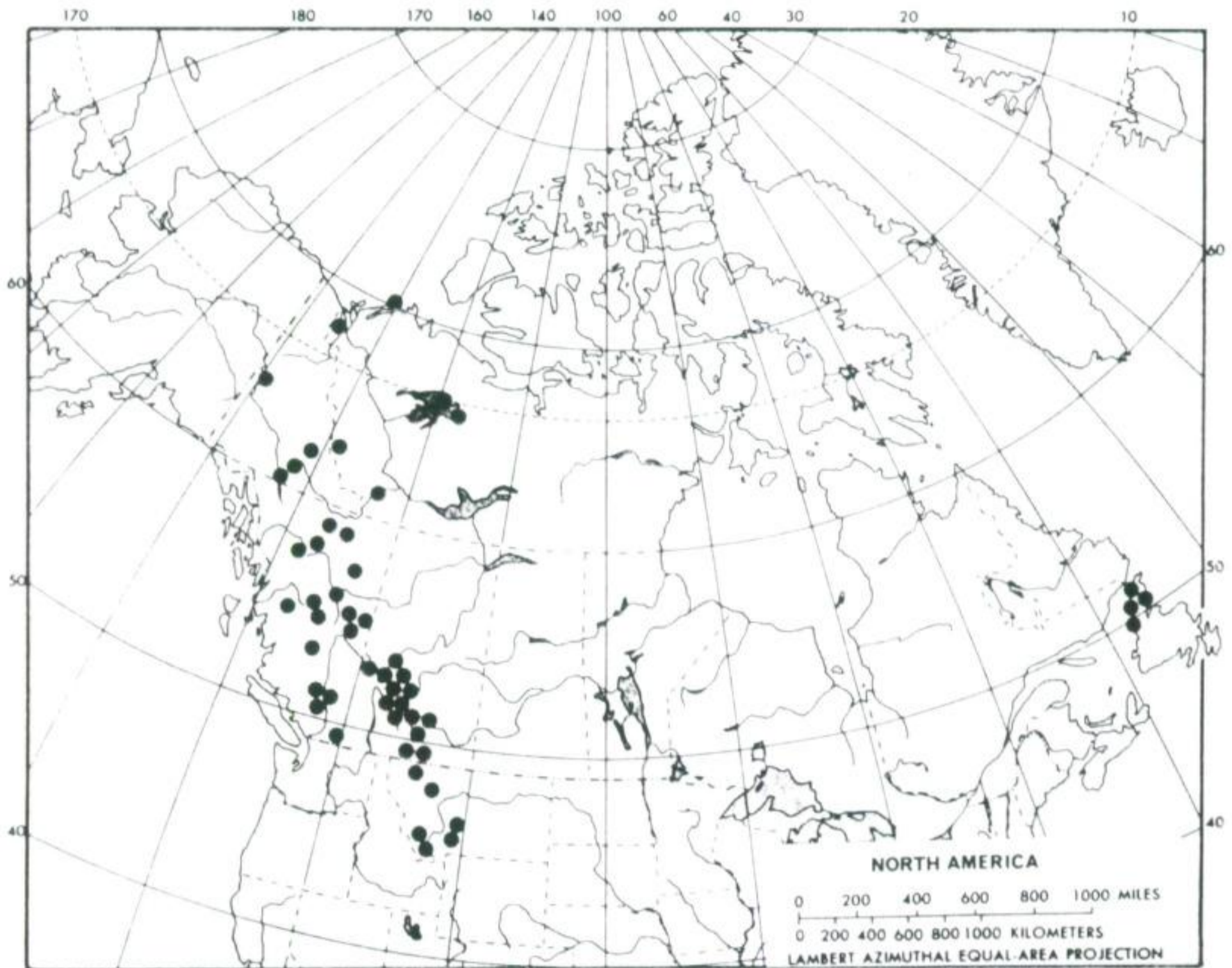


Figure 6. Distribution of *Arnica angustifolia* subsp. *tomentosa*.

6. ***Arnica fulgens*** Pursh, Fl. Amer. Sept. 527. 1814. *A. montana* var. *fulgens* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 164. 1818. TYPE: "On the banks of the Missouri" (Pursh 1814). (HOLOTYPE indicated by Maguire (1943) to be in BM was not found by staff; ISOTYPE, without locality, PH!, photo CAN!).
- A. pedunculata* Rydb., Bull. Torrey Bot. Club 24: 297. 1897. TYPE: "Flora of Central Montana, Spanish Basin, Madison Range. July 11, 1896. J. H. Flodman 899." (HOLOTYPE: NY!).
- A. monocephala* Rydb., Mem. N. Y. Bot. Gard. 1: 435. 1900. *A. pedunculata* Rydb. var. *monocephala* (Rydb.) Lunell, Amer. Midl. Nat. 5: 241. 1918. *A. pedunculata* Rydb. forma *monocephala* (Rydb.) Cockerell, Torreyana 18: 183. 1918. TYPE: "Exploration of Montana and Yellowstone Park. Bridger Mountains, Mont. 14 June 1897. P. A. Rydberg and E. A. Bessey 5221." (HOLOTYPE: NY!; ISOTYPE: CAN!).
- A. pedunculata* Rydb. var. *tubularis* Cockerell, J. Hered. 7: 428. 1916. TYPE: "Boulder, Colorado. June 1915. W. P. Cockerell s.n." (HOLOTYPE: GH!).

Plants 1–7.2 dm tall; rhizomes short, densely scaly, thick; stems solitary or few, simple, moderately puberulent becoming increasingly pubescent upwards, stipitate-glandular, base with conspicuous dense tufts of long brown woolly hair in axils of basal leaves and

persistent leaf bases; leaves 3–5 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 4.5–20 cm long, 0.6–2.5 cm wide, obtuse, narrowly oblong to oblanceolate, petioles narrow or broad-winged and shorter than the blade, margins entire or sometimes irregularly remotely denticulate, moderately uniformly pubescent, stipitate-glandular, 3–5 nerved; capitula erect, 1 (–3), broadly hemispheric, 14–30 mm wide, 11–17 mm long; periclinium moderately to densely pilose, white, stipitate-glandular; involucre bracts 13–21, 10–15.5 mm long, 1.5–4.5 mm wide, narrowly to broadly lanceolate to elliptic-oblong, obtuse to occasionally acute, uniformly pilose throughout, the tips pilose within, stipitate-glandular; ligulate florets 8–16, dark orange-yellow, 16–32 mm long, 2.9–8 mm wide, 3-toothed, the teeth 0.3–2.1 mm long; disc florets 6–9.1 mm long, goblet-shaped, stipitate-glandular, densely pilose, the tube 2.5–5 mm long; achenes 3.5–7 mm long, densely hirsute throughout, occasionally sparingly glandular; pappus white or nearly so; chromosome number $2n = 38$.

DISTRIBUTION AND HABITAT. Throughout interior British Columbia and southern Alberta extending north into the Peace River drainage area, southern Saskatchewan, southwestern Manitoba, south to northern California, northern Nevada, northern Utah, northern Colorado, and east to western North and South Dakota (Figure 7); prairies and grasslands at low elevations in the northern part of the range, montane up to 3,000 meters in Wyoming and Colorado. Plants commonly found in moist depressed areas, often growing in dense clumps. Flowers May to July.

Arnica fulgens is a densely rhizomatous species occupying montane to grassland habitats throughout the northern United States and adjacent southwestern Canada. It is distinguished by having a large broadly hemispheric capitulum, entire leaves, dense axillary tufts of brown woolly hairs at the base of the stem, and dense glandless hairs on the disc corollas. A discussion of the taxonomic history and synonymy of *A. fulgens* and *A. sororia*, is presented in Downie and Denford (1987).

7. ***Arnica sororia*** Greene, Ottawa Nat. 23: 213. 1910. *A. fulgens* Pursh var. *sororia* (Greene) G. W. Douglas and G. Ruyle-Douglas in Taylor and MacBryde, Canad. J. Bot. 56: 185. 1978. TYPE: "Near International boundary between Kettle and Columbia rivers. Cascade, B.C. June 30, 1902. *J. M. Macoun* (*Geol. Surv. Can. No. 64987*)." (HOLOTYPE: ND!; ISOTYPES: CAN!, GH!, photos CAN!, UC!).

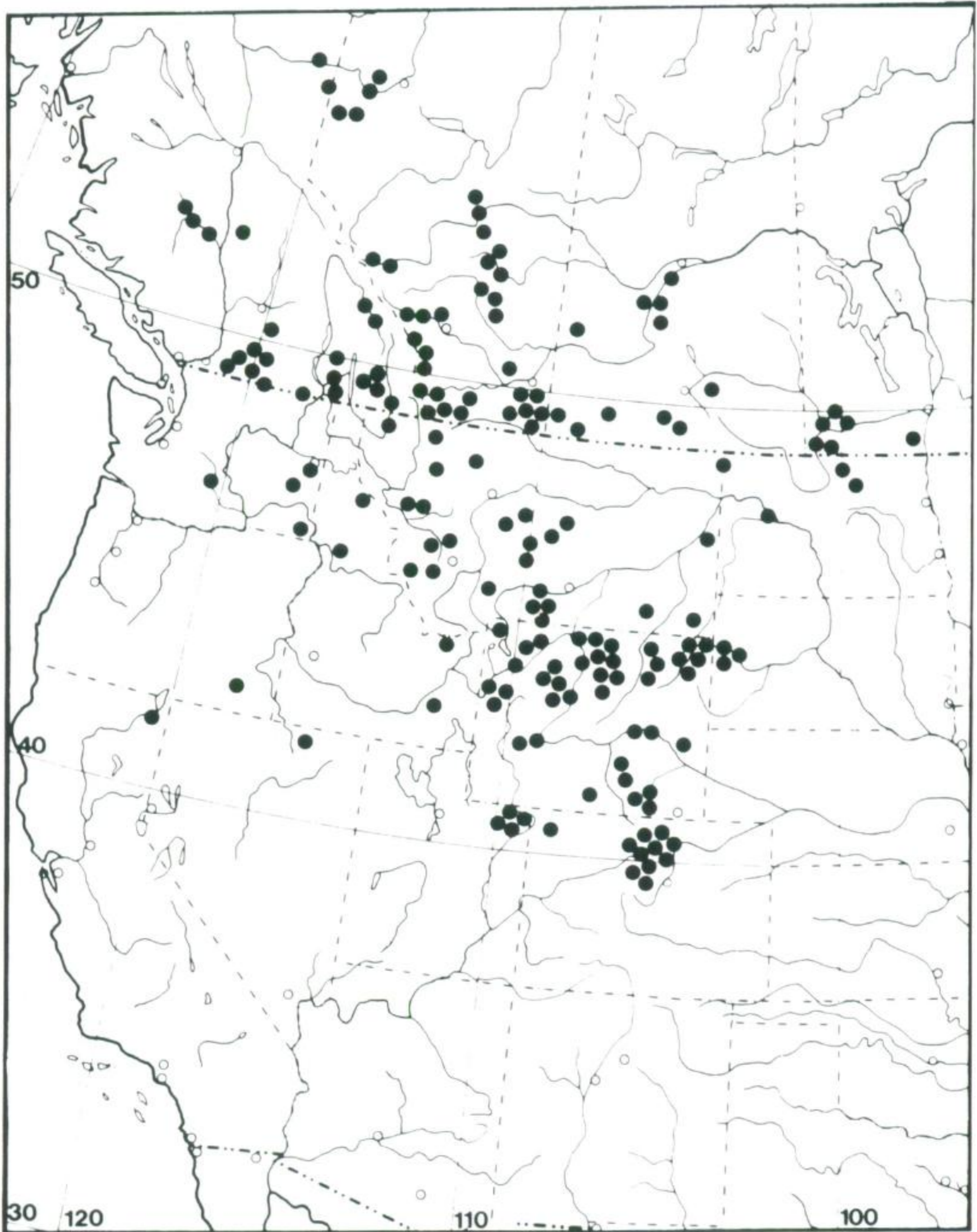


Figure 7. Distribution of *Arnica fulgens*.

A. stricta Greene, Ottawa Nat. 23: 214. 1910, non *A. stricta* A. Nels., Ottawa Nat. 23: 214. 1910. *A. trinervata* Rydb., N. Amer. Fl. 34: 344. 1927. TYPE: "Near International Boundary between Kettle and Columbia Rivers. June 30, 1902. J. M. Macoun (Geol. Surv. Can. No. 64979)." On isotypes: "W. of Cascade, B.C." (HOLOTYPE: ND!, ISOTYPES: CAN!, NY, photos CAN!, UC!).

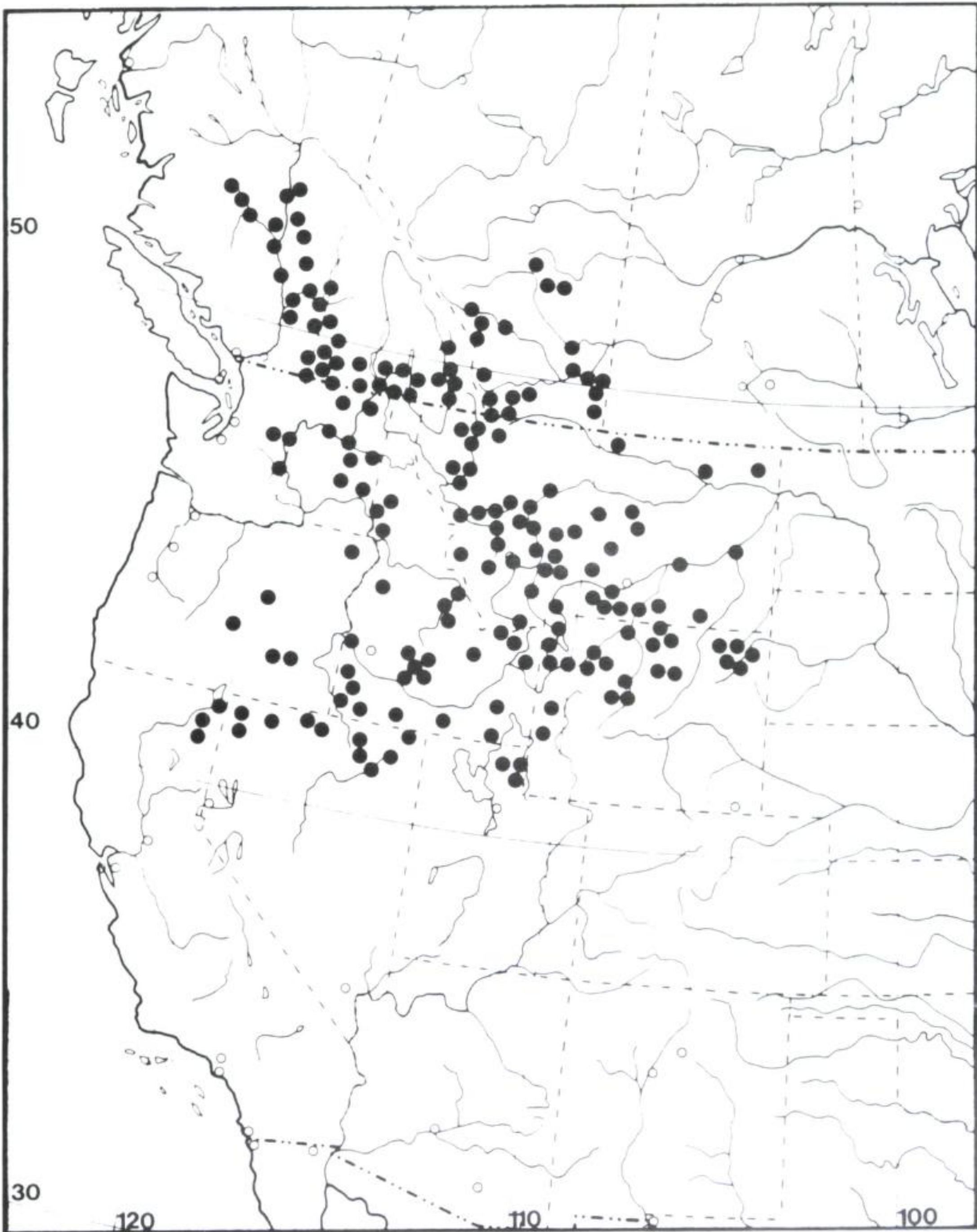


Figure 8. Distribution of *Arnica sororia*.

Plants 1.5–5 dm tall; rhizomes short, less scaly than in *A. fulgens*, slender; stems solitary or few, simple to branched, base lacking axillary tufts of brown hair, occasionally with few whitish hairs or none at all, moderately puberulent below becoming increasingly pubescent upwards, stipitate-glandular; leaves 3–6 pairs; upper cauline leaves sessile and reduced; lower cauline leaves 3.5–14.5 cm

long; 0.6–2.4 cm wide (usually narrower than in *A. fulgens*), obtuse, narrowly oblong to oblanceolate, the petioles narrow-winged and shorter than the blade, margins entire to sometimes irregularly remotely denticulate, moderately uniformly pubescent, short stipitate-glandular, 3–5 nerved; capitula erect, 1–5, broadly hemispheric, 11–27 mm wide, 9–17 mm long; periclinium moderately to densely pilose, white, stipitate-glandular; involucral bracts 13–20, 9.5–14.2 mm long, 1.2–3.1 mm wide, narrowly to occasionally broadly lanceolate, acute, uniformly pilose throughout, tips not at all pilose within, glandular; ligulate florets 9–17, dark orange-yellow, 15–31 mm long, 2.5–7.5 mm wide, 3-toothed, the teeth 0.2–1.8 mm long; disc florets 6.9–10 mm long, goblet-shaped, stipitate-glandular, not at all pubescent, the tube 3–5.5 mm long; achenes 3–5.5 mm long, densely hirsute throughout, occasionally sparingly glandular; pappus white or nearly so; chromosome number $2n = 38$.

DISTRIBUTION AND HABITAT. Throughout the interior of southern British Columbia, southern Alberta, south to northern California, northern Nevada, northern Utah and east to northwestern Wyoming and eastern Montana (Figure 8); prairies and grasslands at low elevations particularly in very dry areas; in less dense populations, in drier habitats and at lower elevations than *Arnica fulgens*. Flowers May to July.

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