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TAXONOMY OF *ARNICA* (COMPOSITAE) SUBGENUS *AUSTROMONTANA*[1]

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ABSTRACT

Nine species, with no infraspecific taxa, are recognized in *Arnica* subgenus *Austromontana,* a group primarily restricted to montane western North America. Previous treatments, which have variously recognized several infraspecific taxa, radiate and discoid sections, and two subgenera for these nine species, are viewed as artificial. Chromosome counts, all based on $x = 19$, are reported for 74 populations representing seven of the species. A discussion of comparative features, phylogenetic relationships, distribution maps, descriptions, synonymies and a key to the species are presented.

Key Words: *Arnica* subgenus *Austromontana,* taxonomy, chromosome counts, montane western North America

Arnica L. is a circumboreal, predominantly montane genus of about 32 species, most of which are confined to western North America. The genus, with its yellow florets, opposite leaves, capillary pappus and basic chromosome number of $x = 19$, is well defined. However, its tribal position within the Compositae has been the subject of considerable debate (Nordenstam, 1977; Robinson, 1981).

Members of the genus are extremely variable and numerous nomenclatural variants have been recognized. Apomixis has long been reported in *Arnica* (Afzelius, 1936) while Cronquist (1955) suggested that much of the perplexing morphological variability

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within the genus may be due to microspecies formation via apomixis. Cytologically, the genus is very diverse, with all ploidy levels from diploid to octoploid being reported (Wolf, 1980). Barker (1966) established that polyploidy within the genus always indicates apomixis and Straley (1980) confirmed this observation for the subgenus *Austromontana.*

Members of subgenus *Austromontana* are distinguished from the other four subgenera of *Arnica* by their turbinate to campanulate heads, white, barbellate pappus and broad leaves. The subgenus, as circumscribed in the present study, consists of nine species distributed in montane to alpine habitats from central Alaska through southern California and northern New Mexico, with a few disjunct populations of *A. cordifolia* occurring in Ontario and Michigan. Four of the nine species are relatively rare and restricted to the Klamath region of southwestern Oregon and northwestern California.

The only worldwide monograph of the genus *Arnica* (Maguire, 1943) was based largely on herbarium material; only two populations were available for study of some taxa, and the consequences of apomictic reproduction in the genus were largely unknown at the time. More recent taxonomic treatments of the genus in North America (Ediger and Barkley, 1978) and subgenus *Austromontana* (Straley, 1980) are based largely on Maguire (1943), with added observations on reproductive biology. The present revision of subgenus *Austromontana* incorporates observations from morphology, cytology, geography and flavonoid chemistry (Wolf, 1980; 1981; Wolf and Denford, 1983; 1984a; 1984b). More than 13,000 herbarium specimens were examined and over 250 populations were studied in the field.

TAXONOMIC HISTORY

The concept of subgenera in *Arnica* originated with Maguire (1943) when he described five subgenera: *Andropurpurea, Arctica, Austromontana, Chamissonis,* and *Montana.* Maguire (1943) recognized thirteen species and six subspecies in subgenus *Austromontana* and placed the seven radiate species and two subspecies in section *Eulatifoliae* and six discoid species and four subspecies in section *Eradiatae.* Maguire (1947) later recognized four varieties of *A. cordifolia* subsp. *genuina:* vars. *cordifolia, macrophylla, pumila*

and *humilis*. Cronquist (1955), in his treatment of *Arnica* for the Flora of the Pacific Northwest, included *A. grayi* and *A. parviflora* in the new combination *A. discoidea* var. *eradiata* (A. Gray) Cronquist and treated *A. gracilis* as a variety of *A. latifolia*. Shortly thereafter, Cronquist (1958) proposed the name *A. discoida* var. *alata* (Rydb.) Cronquist for *A. alata* Rydb.

In their revision of *Arnica* for the North American Flora, Ediger and Barkley (1978) essentially adopted Maguire's (1943) treatment of subgenus *Austromontana,* recognizing nine species and treating his (Maguire's) subspecies as varieties. Exceptions include their acceptance of Cronquist's (1955, 1958) treatment of *A. discoidea* with three varieties (var. *discoidea,* var. *alata,* and var. *eradiata*) and his recognition of *A. gracilis* as a variety of *A. latifolia*. In addition, Ediger and Barkley considered *A. paniculata* a possible hybrid between *A. cordifolia* and *A. parryi* A. Gray but did not give it formal taxonomic recognition.

In a recent systematic study, Straley (1980) retained Maguire's (1943) two sections and recognized seven species in a revised subgenus *Austromontana* and included *A. venosa* and *A. viscosa* in the newly erected subgenus *Calarnica*.

In the present revision of subgenus *Austromontana* nine of Maguire's (1943) species are recognized; however, in light of considerable evidence, particularly with respect to flavonoid chemistry and the morphological consequences of apomixis, we recognize no infraspecific taxa and reject Maguire's sections and Straley's (1980) new subgenus as artificial.

CHROMOSOME NUMBERS

Chromosome numbers from the species of subgenus *Austromontana* were determined for either mitotic or meiotic material using techniques previously outlined (Wolf, 1980).

Arnica chromosome numbers, including many species of *Austromontana,* published prior to 1980 have recently been reviewed (Wolf, 1980). Consequently, the following discussions will be largely limited to comments on more recent data which, in addition to the seventy-four new counts presented in Table 1, incorporates reports by Löve and Löve (1981) and Straley (1980, 1982). As previously noted, the basic chromosome number of the genus *Arnica* is $x = 19$ and all new counts within subgenus *Austromontana* conform to this

basic number. In the present study a new count of $2n = 57$ for *A. discoidea* is reported (Table 1).

Arnica cernua, A. venosa and *A. viscosa* are all uniformly diploid, while *A. nevadensis* is uniformly tetraploid. *A. spathulata* and *A. latifolia* are largely diploid; however, both have a few tetraploid populations. *A. gracilis* has both triploid and tetraploid chromosome races. *A. discoidea* has diploid, triploid and tetraploid races; however, the diploids are largely restricted to the Klamath region while the polyploids occur at the northern, eastern and southern limits of its distribution.

Arnica cordifolia, with five chromosome races, has previously been recognized as a mature polyploid complex (*sensu* Stebbins, 1971) (Wolf, 1980). Subsequent chromosome sampling, now totalling more than 150 populations from throughout its entire distribution, has confirmed this observation. Tetraploids are widespread, occurring throughout the entire species' range, triploids are found largely in the front ranges of the Rocky Mountains, and diploids, pentaploids and hexaploids are rare and of scattered occurrence. Diploids are largely restricted to northeastern Oregon and southern Yukon Territory, pentaploids are restricted to Colorado and hexaploids have been found in Alberta and central Washington.

MORPHOLOGY AND TAXONOMIC CRITERIA

In a discussion of the morphology of the genus *Arnica,* Maguire (1943) noted that there are some sharply defined species and a large number of other loosely-knit polymorphic ones. Within subgenus *Austromontana* most taxa fit into the latter category. Only *A. cernua, A. viscosa* and to some extent *A. venosa* are morphologically well defined. The remaining six species are highly polymorphic and show a wide range of morphological intergradation. In addition, superimposed upon this interspecific variability is a great deal of infraspecific variability. As Gustafsson (1947) and later Cronquist (1955) suggested, apomixis and polyploidy are probably largely responsible for this morphological variability within the genus. That *A. venosa, A. viscosa* and *A. cernua* are the only well defined species in subgenus *Austromontana* is not surprising since they are the only entirely sexual, diploid taxa in the subgenus. Although the several species of subgenus *Austromontana* are highly variable, a combination of several morphological features

in conjunction with ecological and distributional data are sufficient to distinguish among them. The following discussions detail morphological variation and characters of taxonomic significance within subgenus *Austromontana.*

HABIT. All species of subgenus *Austromontana* are herbaceous perennials. With respect to underground parts, both *Arnica venosa* and *A. viscosa* possess a thick woody caudex at or below the soil surface, which gives rise to several flowering shoots. The remaining species possess slender rhizomes which give rise to both flowering shoots and numerous sterile basal rosettes of leaves (innovations). Both rhizomes and caudices are frequently covered with dark scales and old leaf bases which give them a thickened appearance. In *A. gracilis* the tip of the rhizome may have several branches, thus producing a many-stemmed crown (approximate crown) with the flowering shoots appearing in dense clumps.

STEMS. Stems in the species of subgenus *Austromontana* range from simple, as in *Arnica cordifolia* and *A. cernua* to highly branched. *A. discoidea* and *A. venosa* are sometimes several branched above the middle while *A. viscosa* is several-branched throughout, sometimes so much that it resembles a small bush. In addition, virtually all species are much more branched when they occur on more exposed or disturbed sites. Stem height varies from 10–30 cm in the relatively small *A. cernua* and *A. gracilis,* up to 60–70 cm in robust specimens of *A. discoidea* and *A. cordifolia.* In general, stem pubescence resembles leaf pubescence, although it is usually denser above and reduced below.

VESTITURE. Virtually all parts of all species of subgenus *Austromontana* are to some degree pubescent. Both long (1–2 mm) and short (0.1–0.2 mm) septate glandular and non-glandular hairs occur in the subgenus. The long stipitate glandular hairs have stalks 6–8 cells long while the short stalks are 2–3 cells long. Both are two cells thick. *Arnica latifolia* generally lacks glandular pubescence, *A. viscosa* has only the long type, *A. gracilis* has only the short type and the remaining species have both long and short. In *A. viscosa* the entire plant is densely covered with long stipitate glandular hairs, so much so that it feels slimy to the touch.

Non-glandular hairs are one cell thick and either long (1–3 mm) or short (0.3–0.5 mm).

Table 1. New chromosome counts in *Arnica* subgenus *Austromontana*.

Taxon	*n* =	2*n* =	Location and voucher***
A. cernua	19		USA: CA: Humboldt Co.: Horse Mt., *W471*.
		38	USA: OR: Josephine Co.: Babyfoot Lake, *W464*.
A. cordifolia	19		CAN: YT: Canol Rd., km 16, *W507;* Squanga Lk, *W505*. *USA: OR: Wallowa Co.: Minam Park, W449;* Hwy 3, 8 km S Wa. state line, *W447*.
		57	CAN: YT: Skagway Rd., 19 km S. Carcross, *W499**. USA: MT: Flathead Co.: 8 km E Bigfork, *W496**; Lincoln Co.: 23 km W. Libby, *W444**; Missoula Co.: 34 km N Seeley Lk, *W495**.
	38		CAN: BC: Skagway Rd., 65 km S Carcross, *W500;* Hwy 93: 26 km N Jct Hwy 3, *W441;* 11 km S Jct Hwy 3, *W442;* Hwy 3, 15 km E Osoyoos, *B80055;* Hwy between Pavillion and Clinton, *B80060*. YT: Canol Rd., km 118, *W508;* Skagway Rd., 7 km S Carcross, *W498*. USA: CA: Nevada Co.: W side Donner Lk, *W476*. ID: Custer Co.: 15 km W Challis, *W486*. MT: Lincoln Co.: 25 km S Eureka, *W443*. Missoula Co.: 10 km E Bonner, *W493;* 22 km W Lolo City, *W491*. NV: White Pine Co.: Wheeler Peak, *W480*. OR: Grant Co.: 72 km S Ukiah, *W452;* Umatilla Co.: 14 km S Ukiah, *W451;* Union Co.: 40 km E Ukiah, *W450;* Wallowa Co.: 25 km N Enterprise, *W448;* Wheeler Co.: Ochoco Summit, *W453*. UT: Beaver Co.: 23 km E Beaver, *W482;* Cache Co.: Beaver Mt., *W484;* Iron Co.: 17 km E Cedar City, *W481;* Rich Co.: Bear Lake Summit, *W485;* Utah Co.: Mt. Timpanogos, *W483*. WA: Asotin Co.: Field Springs Park, *W446;* Spokane Co.: Mt. Spokane, *W445*.
		76	USA: CA: Plumas Co.: Gold Lake, *W478*. ID: Lemhi Co.: 5 km S Gibbonsville, *W487*. MT: Missoula Co.: Marshall Ski Area, *W492*. OR: Klamath Co.: Parker Mt. Summit, *W454*. UT: Duchense Co.: Hwy 33 at S border of Ashley Nat. Forest, *W396;* San Pete Co.: Jct Spring City-Skyline Drive Rd., *W393*. WA: Okanogan Co.: 23 km W Twisp, *W509*. WY: Teton Co.: Teton Nat. Park, Hidden Falls, *W429*.

A. discoidea	19		USA: CA: Humboldt Co.: 6 km W Briceland, *W472;* Mendocino Co.: 14 km W Boonesville, *W474;* San Mateo Co.: Kings Mt., *W475;* Siskiyou Co.: Baldy Mt., *W466;* Trinity Co.: 3 km E Burnt Ranch, *W470.*
		57**	USA: CA: Plumas Co.: Gold Lake, *W477**.
	38		USA: CA: Lake Co.: 13 km E Lower Lake, *W473;* Santa Barbara Co.: La Cumbre Peak, *W515.*
A. latifolia	19		CAN: ALT: Banff Nat. Park, Moraine Lake, *W513.* USA: OR: Curry Co.: Iron Mt., *W457.*
		38	USA: AK: Hatcher Pass, *W503.* WA: Chelan Co.: Swauk Pass, *W367;* Kittitas Co.: Snoqualmie Summit, *W510.*
	38		USA: CA: Siskiyou Co.: Bolan Lake, *W465;* 13 km W Etna, *W467.* ID: Idaho Co.: Lolo Pass, *W490;* Lemhi Co.: 9 km S Lost Trail Pass, *W488.* MT: Missoula Co.: Seeley Lake, *W494;* 27 km W Lolo City, *W489.*
		76	CAN: ALT: Waterton Nat. Park, Carthew Mt., *W440.*
A. spathulata	19		USA: CA: Del Norte Co.: French Hill, *W458;* 10 km N Gasquet, *W459.* OR: Josephine Co.: Hugo, *W455;* Merlin, *W456;* Selma, *W463;* Store Gulch Guard Station, *W462.*
	38		USA: OR: Josephine Co.: 17 km N Patrick, *W460;* 20 km N Patrick, *W461.*
A. venosa	19		USA: CA: Shasta Co.: Hwy 5, 3 km S Gibson turnoff, *W468;* Shasta Bally Rd., S Brandy Creek, *W469.*
A. viscosa	19		USA: OR: Klamath Co.: Crater Lake Nat. Park, Garfield Peak, *W511.*

* Count based on meiotic cells.

** New count for this taxon.

***Abbreviations of collectors: B = J. F. Bain; W = S. J. Wolf. Vouchers at ALTA.

LEAVES. Although highly variable, characters of the leaves are generally the most reliable in distinguishing the species of subgenus *Austromontana*. Characters considered important in the present study are leaf number, shape, margin, position and petiole width. Within the subgenus there is a general evolutionary trend from few, broad, coarsely dentate, narrowly petiolate leaves mostly below the mid-stem towards many, narrower, entire margined, sessile, evenly distributed leaves.

The number of cauline leaves varies from 2 to 4 pairs in such species as *Arnica cordifolia* and *A. latifolia* to more than 25 in *A. viscosa*. Species intermediate between these extremes include *A. spathulata* (3–5), *A. discoidea* (3–5) and *A. venosa* (6–10). Additionally, in the few-leaved species the leaves tend to be mostly below mid-stem while, in contrast, in the many-leaved species they are evenly distributed along both the stems and branches. This appears to be a trend within the genus *Arnica* in general (Maguire, 1943).

Leaf shape varies from broadly cordate in *Arnica cordifolia* to broadly lanceolate in *A. discoidea*. Intermediate conditions include: ovate to ovate-elliptic in *A. cernua, A. latifolia, A. venosa* and *A. nevandenis;* spathulate in *A. spathulata* and ovate-oblong in *A. viscosa*. Leaf margins vary from coarsely dentate in the primitive *A. cordifolia* to entire in its derivative *A. nevadensis* and the highly advanced *A. viscosa*. Intermediate forms include crenate in *A. cernua* and serrate to serrate-dentate in the remaining species.

Within the subgenus *Austromontana* there is a distinct evolutionary trend in petiole width from narrow to broad to completely sessile leaves, with the latter being considered most advanced. Five of the nine species have narrowly petiolate leaves (*Arnica cordifolia, A. cernua, A. discoidea, A. nevadensis* and *A. gracilis*), three species have sessile leaves (*A. latifolia, A. venosa,* and *A. viscosa*) while *A. spathulata,* with broadly winged petioles, represents the intermediate condition. Occasionally, the lower leaves of *A. latifolia* are short petiolate while the lower leaves of *A. cernua* and *A. gracilis* are infrequently narrowly winged. In addition, in all of the rhizomatous species, including the sessile-leaved species, the leaves of the innovations are narrowly petiolate. Leaves of innovations are otherwise similar to the cauline leaves. Additionally, in all species of the subgenus the upper leaves are often reduced, bract-like and not infrequently sub-opposite.

INFLORESCENCE. Within subgenus *Austromontana* several characters of the inflorescence are considered important in both delimitation of the species and determination of evolutionary relationships. Among these characters are head type (radiate vs. discoid), number and shape, phyllary shape and characters of the pappus. With the exception of *Arnica parryi* (subgenus *Chamissonis*), no discoid species of *Arnica* occur outside the subgenus *Austromontana.* Within the latter, *A. viscosa, A. venosa, A. spathulata* and *A. discoidea* are discoid while the remaining are radiate. In addition, in *A. discoidea* some marginal disc florets may be ampliate (elongated and ray-like), resulting in some pressed specimens of this species being confused with *A. cordifolia.* Results of the present study support Maguire's (1943) observation that the discoid condition represents the advanced state in subgenus *Austromontana.* Indeed, Cronquist (1977) considered the discoid condition to be derived within the Compositae in general.

The number of ray florets varies from 5 to 15 while the number of disc florets varies from 10 to 90. Within the subgenus there is a general trend of reduction in the number of disc florets, particularly in the discoid species. *Arnica cordifolia* and *A. latifolia,* with up to 90 disc florets, represent the primitive condition while *A. viscosa,* with as few as 10 florets, is viewed as highly advanced.

Cronquist (1977) considered yellow-colored corollas primitive within the Compositae in general. With the exception of *Arnica viscosa,* which has cream-colored florets, all other *Arnica* species possess yellow corollas. Clearly, the cream-colored florets of *A. viscosa* represent the derived condition in subgenus *Austromontana.*

Within subgenus *Austromontana* heads may occur singly as in *Arnica nevadensis, A. cordifolia,* and *A. cernua* or more commonly 3 to several heads are arranged in a corymbose inflorescence. Species with several heads include *A. viscosa* (10–20), *A. gracilis* (5–15) and *A. discoidea* (3–10, or up to 30). Maguire (1943) considered solitary heads primitive within *Arnica* in general and Cronquist (1977) noted a similar trend towards increasing head number in the Compositae in general. In the present study, the solitary condition is considered primitive in subgenus *Austromontana* while, in contrast, an increased number of heads is interpreted as an advanced state.

The pappus in the genus *Arnica* is composed of a ring of 25–70 capillary bristles of varying length. Based on seta length, Maguire

(1943) recognized three conditions within the genus: barbellate (0.1–0.2 mm), subplumose (0.2–0.35 mm) and plumose (0.35–0.6 mm). Also, within the genus pappus color varies from white to tawny. Maguire (1943) considered the white, barbellate pappus primitive, while the tawny, plumose pappus was considered advanced. Most species of subgenus *Austromontana* have retained the primitive white, barbellate pappus. However, in *A. cernua, A. discoidea, A. nevadensis* and *A. viscosa* the pappus is infrequently subplumose. Additionally, in both *A. nevadensis* and *A. viscosa* the pappus is sometimes slightly tawny.

Although somewhat variable, characters of the involucral bracts are often quite helpful in delimiting species. Phyllary shape varies from ovate-lanceolate (*Arnica cordifolia, A. cernua, A. discoidea, A. gracilis* and *A. venosa*) to lanceolate (*A. latifolia* and *A. viscosa*). *A. nevadensis* has distinctive oblanceolate phyllaries. Phyllary vestiture, like that of the leaves, consists of various combinations of short and long stipitate glandular and non-glandular hairs. The vestiture is always densest and longest at the bases of bracts, at the point of their attachment to the peduncle.

ACHENES. Achene color in subgenus *Austromontana* is mostly gray with the exception of *Arnica gracilis* (black), *A. spathulata* (black), and *A. latifolia* (brown). Length varies from 4.5–10 mm, with *A. gracilis* and *A. viscosa* being the shortest and *A. cordifolia* the longest. Achene width is almost uniformly 1 mm with the exception of *A. venosa* (1.5 mm). Achene vestiture, which is quite useful in delimiting species, consists of various combinations of both short and long glandular hairs and duplex (forked) hairs. For example, *A. viscosa* has only long stipitate glandular hairs, *A. gracilis* has a few short glandular hairs, *A. venosa* has an abundance of duplex hairs and *A. discoidea* has both duplex and glandular hairs.

PHYLOGENY AND PHYTOGEOGRAPHY

Maguire (1943) considered the genus *Arnica* to have arisen in Arctic or sub-Arctic western North America from where it spread eastward, westward and southward. Hultén (1937) listed 22 species of *Arnica* (some of which were not recognized by Maguire, 1943) that are of probable northwestern North American origin. As most species of the genus are adapted to cool montane habitats and 25 of the 32 species recognized by Maguire (1943) are largely confined to

northwestern North America this conclusion seems valid. Additional evidence to support this hypothesis is the presence of many relictual diploid races of otherwise widespread *Arnica* polyploid complexes in the unglaciated Alaska-Yukon region (Wolf, 1980). Phytogeographical evidence suggests that the genus *Arnica* is relatively old, and was part of the Arcto-Tertiary flora. The east-west disjunct distribution of *A. louiseana* Farr and *A. lonchophylla* D. C. Eaton, the circumpolar distribution of *A. angustifolia* Vahl and the close relationship between *A. montana* of Europe and *A. acaulis* of the eastern United States add support to this theory.

Raven and Axelrod (1978) included the genus *Arnica* within a group of genera that are well-developed in California, yet widespread elsewhere. They suggested that this recurrent pattern in the Californian flora is the result of spreading aridity from Upper Tertiary times in the western United States which culminated in the development of a full Mediterranean climate in the late Quaternary. A striking example of this distribution pattern occurs within subgenus *Austromontana* which contains both widespread species (e.g., *A. cordifolia* and *A. latifolia*) and several endemics (e.g., *A. cernua, A. venosa* and *A. viscosa*). In fact, the discoid species of *Austromontana* are confined almost entirely to the northern areas of the California Floristic Province, particularly within the Klamath region of southwestern Oregon and northwestern California. The occurrence of many endemics in the Klamath region and its significance in the evolution and development of the flora of the western states, particularly California, have been discussed by Whittaker (1960, 1961). Owing to its geological history, equable climate and diversity of parent soils, the Klamath region contains many endemics that probably represent both remnants of the Arcto-Tertiary flora and more recently derived taxa (Whittaker, 1961). In the case of subgenus *Austromontana,* the narrow endemics appear to be recently derived from the more widespread *A. cordifolia* and *A. latifolia* (Wolf & Denford, 1984b).

Speciation within the subgenus *Austromontana* has been accompanied by a number of ecological, morphological and chemical changes, some of which include: a shift from mesic to xeric habitats; temporal isolation of flowering periods; specialization to particular substrates; the replacement of solitary, radiate heads by more numerous, narrower, discoid heads with reduced numbers of disc florets; evolution from narrowly petiolate to sessile leaves; the

replacement of simple flavonol glycosides by more complex methylated flavone aglycones, and a secondary loss of flavonoids in several rare and geographically restricted species (Wolf, 1981; Wolf and Denford, 1983; 1984b). Additional factors contributing to speciation in the subgenus include hybridization, polyploidy and changes in reproductive systems (Wolf, 1980; Wolf and Denford, 1984a; Barker, 1967; Straley, 1980).

Maguire (1943) considered *Arnica cordifolia* to represent the ancestral species in subgenus *Austromontana* which gave rise to the rest of the subgenus. Results of the present investigation support this hypothesis. With respect to morphology, *A. cordifolia* exhibits most features considered primitive within the genus *Arnica* in general and the subgenus *Austromontana* in particular. Significant primitive features of *A. cordifolia* include: solitary, broad heads with white, barbellate pappus; unbranched stems with few, narrowly petiolate, broad, dentate leaves and dark gray achenes. In addition, the flavonoid profile of *A. cordifolia,* which lacks complex methylation, is relatively primitive (Wolf and Denford, 1983). Additionally, the mesic-montane habitat of *A. cordifolia* represents the ancestral condition within the genus *Arnica* in general (Maguire, 1943). Indeed, within subgenus *Austromontana* there is a distinct evolutionary trend from mesic-montane habitats towards drier habitats at both lower and higher elevations.

Phytogeographical, cytological and chemical evidence suggests that *Arnica cordifolia* was probably a relatively widespread diploid species prior to the Pleistocene. Hultén (1937) included *A. cordifolia* in a group of species widespread prior to the Pleistocene, but whose ranges were interrupted by glaciation. He hypothesized that these species survived the Pleistocene glaciations south of the ice and in unglaciated areas of the Yukon and Alaska. Upon retreat of the ice, these populations were rejoined to form a continuous distribution. This hypothesis is supported by the fact that the flavonoid profiles of populations north of the maximum limits of Pleistocene glaciation differ from those to the south (Wolf and Denford, 1983). Cytological evidence also supports the hypothesis that *A. cordifolia* was probably a relatively widespread diploid species prior to the Pleistocene. Barker (1966) noted that within the genus *Arnica* diploids were probably more widespread in the past and that polyploidy in the genus is a relatively recent, i.e., inter- or post-glacial phenomenon. Stebbins (1971) noted that most mature

polyploid complexes such as *A. cordifolia* are of Pliocene or Pleistocene origin. The occurrence of diploid populations of *A. cordifolia* in the unglaciated Yukon as well as south of the limits of glaciation (in Oregon) suggests a former, much wider distribution of diploid populations.

The geographical distribution, morphology, cytology and flavonoid chemistry of *Arnica latifolia* suggests that it is probably a pre-Pleistocene derivative of *A. cordifolia. A. latifolia* occurs throughout much of the range of *A. cordifolia* but in moister habitats at higher elevations. Morphologically the two species are very similar and are often difficult to distinguish on herbarium sheets. *A. latifolia* and *A. cordifolia* share several primitive features including: radiate heads with white, barbellate pappus; relatively few, broad leaves; innovations; and numerous, yellow disc florets. However, *A. latifolia* has several advanced features, including sessile leaves, narrow heads and phyllaries, and brown achenes. Its flavonoid profile, which consists largely of flavonol glycosides, is relatively primitive and similar to that of *A. cordifolia* (Wolf and Denford, 1984b). However, the two species, and their putative derivatives, differ largely with respect to the replacement of quercetin 6-methoxy-3-0-glucoside in *A. latifolia* for kaempferol 6-methoxy-3-0-glucoside in *A. cordifolia.* The largely diploid condition of *A. latifolia* suggests a pre-Pleistocene divergence from *A. cordifolia* prior to the elimination of the diploid level in the latter. *A. latifolia* may have been an ecological race of an archetypal "cordifolia" adapted to moister conditions, which became established after the advent of apomixis in the latter. The fact that *A. cordifolia* and *A. latifolia* probably hybridized to produce *A. gracilis* (Wolf and Denford, 1984a) also suggests a close relationship between the two species.

As previously noted (Wolf and Denford, 1984a), *Arnica gracilis* is probably a hybrid between *A. latifolia* and *A. cordifolia.* The flavonoid profile of *A. gracilis,* which consists of fourteen compounds, is essentially a summation of the two parental profiles. Although *A. gracilis* is somewhat intermediate between *A. latifolia* and *A. cordifolia,* it has several distinctive and advanced features of its own. These characters include a much more branched habit; narrower leaves; more numerous and smaller heads with a reduced number of disc florets; black, glandular achenes and the dry, alpine habitat. Since *A. cordifolia* is an apomictic, polyploid complex

(Wolf, 1980) with no known sexual populations and *A. latifolia* is largely sexual and diploid, *A. gracilis* was probably formed prior to or during the Pleistocene, before the elimination of the sexual condition in *A. cordifolia* (Wolf and Denford, 1984a).

As previously noted (Wolf and Denford, 1984b), there is little doubt that *Arnica discoidea* has been derived from *A. cordifolia.* Morphologically the two species are quite similar, almost to the extent that *A. discoidea* appears to be little more than a rayless *A. cordifolia.* However, *A. discoidea* is readily distinguished by several advanced features including: more numerous, narrower, discoid heads with a barbellate to subplumose pappus; more numerous, narrower leaves and glandular achenes. Additionally, *A. discoidea* and *A. cordifolia* are ecologically quite distinct. *A. cordifolia* is adapted to cool, mesic, montane habitats and is generally quite rare west of the Cascades. In contrast, *A. discoidea* occurs in hotter and drier habitats west of the Sierras and Cascades. In both instances where the two species have been observed in close association, in the Sierran foothills and in the central Cascades, *A. cordifolia* had flowered and set seed well over a month prior to the flowering of *A. discoidea.* Such early flowering of *A. cordifolia* is no doubt a means of escaping the relatively warm-dry summer conditions of these areas.

Cytological and chemical evidence suggests that *Arnica discoidea* was derived from *A. cordifolia* in the Klamath region. The flavonoid profiles of diploid Klamath populations of *A. discoidea* are strikingly similar to that of *A. cordifolia* while, in contrast, the polyploid populations outside the Klamath region have more advanced compounds and reduced flavonoid profiles (Wolf and Denford, 1984b). This suggests that *A. discoidea* has been derived from ancient diploid Klamath populations of *A. cordifolia* and that migration outward from this area has been accompanied by polyploidization and a change in flavonoid chemistry.

The Klamath region endemic *Arnica spathulata* has probably been derived from *A. discoidea* via saltational speciation into serpentine areas. Morphologically the two species are very similar, differing largely in leaf and petiole shape, and degree of pubescence. However, *A. spathulata* is readily distinguished by several advanced features including: narrow phyllaries; narrower, broadly petiolate leaves; and black achenes. Ecological distinctions between the two species are also readily apparent. *A. spathulata* occurs at lower

elevations and in drier habitats on serpentine soils. Additionally, the flavonoid profile of *A. spathulata,* which consists of eight compounds, is a subset of diploid Klamath populations of *A. discoidea* (Wolf and Denford, 1984b).

Whittaker (1961) noted that the diversity of soil types in the Klamath region has contributed greatly to the formation of many local endemics. Kruckeberg (1954, 1969) suggested that serpentine endemism results from an adaptation to serpentine followed by biotype depletion and the development of isolated populations into local endemics. Lewis (1962) noted that many serpentine endemics originate by saltation speciation in marginal populations. As Raven and Axel (1978) noted, marginal populations often occur in edaphic situations that are unique for the species as a whole. What these ideas suggest is that *Arnica spathulata* may have initially diverged from marginal populations of *A. discoidea* that gradually adapted to, and later became restricted to serpentine soils. The subsequent restriction of these populations to local isolated areas may have resulted in a gradual depletion of their flavonoid profiles. The fact that *A. discoidea* and *A. spathulata* are still morphologically somewhat similar suggests a fairly recent derivation of the latter. Indeed, Raven and Axelrod (1978) suggested that most herbaceous, localized serpentine endemics of the California Floristic Province (such as *A. spathulata*) originated in late Pleistocene or more recent time. *A. spathulata* is therefore probably a relatively recent derivative of *A. discoidea* that gradually became adapted to, and later restricted to serpentine areas.

The rare Klamath region endemic *Arnica venosa* is probably a very recent derivation of *A. discoidea.* Typical populations of *A. venosa* differ from *A. discoidea* by several advanced features including: numerous sessile leaves, a woody caudex and a lack of innovations. *A. venosa* is also distinguished by its strongly reticulate-veined leaves, more leafy and branched habit and preference for hotter, drier disturbed habitats. However, some specimens of *A. venosa* with thin, slightly woody rhizomes and few, broadly petiolate, weakly veined leaves tend to resemble *A. discoidea* and suggest the two species are related. *A. venosa* is diploid and its flavonoid profile, which consists of six compounds, is merely a subset of the profile of *A. discoidea.* Since *A. venosa* and *A. discoidea* occur sympatrically, have several flavonoids in common and are sometimes morphologically similar, it seems likely

that the former is derived from the latter. *A. venosa* is restricted to the foothills of Shasta County, California in the hottest and driest habitat of any *Arnica* species known. This represents considerable divergence from the ancestral cool-montane habitat characteristic of the genus *Arnica.* The very localized distribution of *A. venosa,* its preference for recently disturbed habitats and derived ecology suggest it is very recently derived, possibly during the post-glacial hypsithermal of 9,000 to 2,600 years ago (Flint, 1957).

Maguire (1943) and Straley (1980) considered the rare serpentine, Klamath endemic *A. cernua* to be derived from *A. latifolia.* However, both *A. cernua* and *A. cordifolia* share several primitive morphological features including: long, narrow petioles; broad solitary heads with pilose and glandular, ovate-lanceolate phyllaries; and dark gray achenes. In contrast, *A. latifolia* has sessile leaves; several narrow heads with lanceolate, sparsely pubescent phyllaries and brown achenes.

Raven and Axelrod (1978) suggested that *Arnica cernua* probably evolved from a more widespread species, in late Pleistocene or Recent times via saltation speciation in marginal populations that gradually became adapted to and later restricted to serpentine soils. It seems likely that *A. cernua* has been derived from the more widespread *A. cordifolia* prior to the elimination of the diploid condition in the latter.

Arnica nevadensis has been derived, at least in part, from *A. cordifolia. A. nevadensis* is an extremely variable species which sometimes resembles little more than a high altitude ecotype of *A. cordifolia.* In fact, in the past, many high altitude Rocky Mountain populations of *A. cordifolia* have been erroneously identified as *A. nevadensis. A. cordifolia* and *A. nevadensis* share several primitive features including: solitary, radiate heads and simple stems with few, relatively broad leaves. Additionally, the flavonoid profile of *A. nevadensis* is most similar to that of *A. cordifolia* (Wolf and Denford, 1984b). However, *A. nevadensis* is readily distinguished by its often tawny, subplumose pappus, entire leaves, oblanceolate phyllaries and relatively high altitude, exposed habitat. The extreme morphological variability of *A. nevandensis,* its tetraploid condition, apomictic reproductive system and resemblance to *A. cordifolia* suggests that either it is the result of introgression between the latter and another *Arnica* species or it is a high altitude microspecies

of *A. cordifolia* that has become established and more widespread via apomictic reproduction. The evolution of *A. nevadensis* may have been facilitated by the climatic cooling of the late Pliocene or Pleistocene and/or saltation speciation of high altitude populations of *A. cordifolia.*

Arnica viscosa is one of the rarest and most distinctive species of the genus *Arnica.* It is known from only seven populations on high alpine volcanic slopes, largely in the Klamath region of Oregon and California. Its opposite leaves and chromosome number of $n = 19$, among other features, clearly place it within the genus and its pappus characters, broad leaves and flavonoid profile warrant its inclusion in the subgenus *Austromontana. A. viscosa* exhibits virtually every advanced morphological, ecological and chemical feature of both the genus *Arnica* and subgenus *Austromontana.* Significant derived morphological features include: numerous, narrow discoid heads with a reduced number of cream-colored florets; highly branched habit; numerous, sessile, entire leaves; woody caudex; and a lack of innovations. Its restriction to very recent volcanic soils and dry, alpine habitat are also considered derived features. Additionally, the flavonoid profile of *A. viscosa,* which includes several highly methylated flavones and a 6-hydroxylated flavone, is considered highly advanced (Wolf and Denford, 1984b).

The very distinctive morphology, ecology and flavonoid chemistry of *Arnica viscosa* as well as its restriction to very recent habitats, i.e., less than 14,000 years old (McKee, 1972), makes an evaluation of its evolutionary history quite difficult and highly speculative at best. Maguire (1943) noted the similar leafy, branching habit and rootstock shared by *A. viscosa* and *A. venosa* and suggested they might be related. Straley (1980) considered *A. viscosa* to be a recent derivative of *A. venosa* and erected the new subgenus *Calarnica* to encompass the two species. However, even Maguire (1943) noted that the two species differ significantly in several features. In fact, except for the superficial similarity of habit shared by the two species, they bear little resemblance to each other. Although quite distinct, *A. viscosa* shares several features with *A. latifolia* including: very narrow heads with lanceolate phyllaries; sessile leaves; similarly glandular achenes which lack duplex hairs; the cool high altitude ecology; diploid chromosome number; and

several flavonoids (Wolf and Denford, 1984b). Additionally, in an extensive artificial hybridization program among the species of subgenus *Austromontana,* virtually the only successful crosses were between *A. viscosa* and *A. latifolia* (Straley, 1980).

The derivation of *Arnica viscosa* from *A. venosa,* as suggested by Straley (1980) also seems highly unlikely since the two species probably represent the two greatest ecological extremes within both the genus *Arnica* and subgenus *Austromontana. A. venosa* occurs at the lowest elevations and occupies the hottest and driest habitat of any *Arnica* while in contrast, *A. viscosa* is restricted to cold, high alpine habitats on volcanic soils. The derivation of *A. viscosa* from *A. latifolia,* a sub-alpine species, seems much more likely since it would require only a slight ecological shift. In addition, both *A. viscosa* and *A. latifolia* are diploid and occur sympatrically. Since *A. viscosa* shares several morphological, ecological and chemical features with *A. latifolia,* it seems more probable that *A. latifolia* has been involved, at least in part, in the derivation of *A. viscosa,* perhaps via saltational speciation onto very recent volcanic soils.

Assuming the above proposed phylogeny accurately represents evolutionary relationships, it is evident that the discoid condition has arisen independently at least twice within subgenus *Austromontana* and at least three times in the genus *Arnica* (cf. *A. parryi* A. Gray of subgenus *Chamissonis*). This is not surprising since the discoid condition has arisen independently numerous times in the Compositae (Cronquist, 1977). Maguire's (1943) recognition of radiate and discoid sections within subgenus *Austromontana* is therefore considered artificial and is rejected in the present study. Morphologically, both *A. venosa* and *A. viscosa* clearly belong in subgenus *Austromontana.* Additionally, both species contain two unusual quercetin glycosides common to all species of subgenus *Austromontana,* but lacking in the other subgenera of *Arnica* (Wolf and Denford, 1984b). Since *A. venosa* and *A. viscosa* do not appear to be related, as proposed by Straley (1980), his new subgenus *Calarnica* is also here rejected as artificial.

TAXONOMIC TREATMENT

Arnica L. subg. *Austromontana* Maguire, Brittonia. 432. 1943.
Type species: *A. latifolia* Bong.

Arnica L. sect. *Austromontana* Maguire, Brittonia. 432. 1943.

Arnica L. sect. *Eulatifoliae* Maguire, Brittonia. 432. 1943. Lectotype: *A. latifolia* Bong. (*nom. illegit.*).

Arnica L. sect. *Eradiatae* Maguire, Brittonia. 452. 1943. Lectotype: *A. discoidea* Benth.

Arnica L. subg. *Calarnica* Straley, Ph.D. diss., Univ. British Columbia. 1980. Type species: *A. viscosa* A. Gray. This name has been proposed, but at present it has not been validly published.

Perennial herbs; stems simple to much branched, arising from a scaly rhizome or woody caudex. Leaves simple, opposite, relatively broad, 1.0–2.5 times as long as wide, cordate to narrowly ovate or spathulate, entire to dentate or crenate, sessile to broadly or narrowly petiolate, uppermost leaves often reduced or bract-like. Heads solitary or numerous in a corymbiform inflorescence, radiate or discoid, broadly campanulate to narrowly turbinate; involucral bracts ovate to lanceolate, acute to acuminate. Ray florets yellow; disc florets yellow or cream-colored, anthers yellow; pappus white or rarely tawny, barbellate to subplumose. Achenes gray, brown or black, ± stipitate-glandular and/or ± hirsute with duplex hairs.

KEY TO THE SPECIES OF *ARNICA* SUBGENUS *AUSTROMONTANA*

1. Heads discoid (marginal corollas sometimes ampliate in No. 3).
   2. Leaves sessile.
      3. Leaves toothed, veins conspicuous; achenes hirsute with duplex hairs; florets yellow ..... 8. *A. venosa.*
      3. Leaves entire, veins inconspicuous; achenes stipitate-glandular; florets cream colored ..... 9. *A. viscosa.*
   2. Leaves petiolate, the petiole sometimes broad.
      4. Lowermost leaves ovate to subcordate or broadly lanceolate; petioles narrow or scarcely winged; achenes dark gray, stipitate-glandular with duplex hairs; species of southern Washington to southern California, including the Klamath region ..... 3. *A. discoidea.*
      4. Lowermost leaves spathulate; petioles broad, achenes black, stipitate-glandular, lacking duplex hairs; species mostly restricted to serpentine soils of Klamath region ..... 7. *A. spathulata.*
1. Heads radiate.
   5. Cauline leaves sessile; heads turbinate; achenes brown ..... 5. *A. latifolia.*
   5. Cauline leaves petiolate; heads campanulate to campanulate-turbinate; achenes dark gray or black.
      6. Leaves glabrous, thick, leathery; heads nodding in bud; plants restricted to serpentine soils of Klamath region ..... 1. *A. cernua.*
      6. Leaves variously pubescent, thin; heads erect in bud; plants not of serpentine soils, widespread.

7. Stems several-branched, mostly clumped; heads numerous (5–15); achenes black, mostly lacking duplex hairs ..... 4. *A. gracilis.*
7. Stems mostly simple, not clumped; heads solitary or few (1–3); achenes dark gray with duplex hairs.
   8. Leaves cordate, toothed; heads broadly campanulate; involucral bracts ovate-lanceolate; pappus white, barbellate; achenes ± hirsute and ± stipitate-glandular; widespread cordilleran species .... 2. *A. cordifolia.*
   8. Leaves ovate to elliptic, entire; heads campanulate-turbinate; involucral bracts oblanceolate; pappus white to tawny, barbellate to subplumose; achenes stipitate-glandular; species of Sierra Nevada, north less commonly to Washington ..... 6. *A. nevadensis.*

TREATMENT OF INDIVIDUAL TAXA

1. **Arnica cernua** Howell, Fl. NW. Am. 373. 1900. TYPE: Oregon, Josephine Co. On dry banks, base of the Coast mountains near Waldo, July 1884, *T. Howell 166* (HOLOTYPE, ORE!).

   Arnica chandleri Rydb., N. Am. Fl. 34: 339. 1927. TYPE: California, Humboldt Co., Hupi (Hoopa) Indian Reservation, June, 1901, *H. P. Chandler 1298* (HOLOTYPE, NY!; ISOTYPES, UC!, US!).

Stems simple, rarely branched, often reddish-purple, 10–30 cm high, 1.5–2.5 mm diameter, glabrous to sparsely villous; rhizomes 2–3 mm thick, 2–3 pairs reddish scales at the summit. Cauline leaves 3–4 pairs, often reddish-purple, elliptic to ovate, sometimes subcordate, 1.5–8 cm long, 1.5–4 cm broad, often thick and nearly succulent, glabrous to scabrous, acute to rounded, entire to serrate, commonly crenate or slightly lobed; petioles narrow or infrequently broadly winged on lowermost leaves, 2–6 cm long, 1–5 mm broad; uppermost leaves often reduced, lanceolate and sessile; leaves of the innovations 4–8, similar to cauline leaves. Inflorescence usually a single head or corymb of 3–5 heads, often nodding in bud; peduncle 3–15 cm long, sparsely to densely pilose and scabrous, heads radiate, campanulate-turbinate, 10–25 mm high; involucral bracts 8–14, ovate to broadly lanceolate, 8–16 mm long, 3–6 mm broad, sparsely to densely pilose and stipitate-glandular, acute to acuminate. Ray florets 5–10, yellow to slightly orange, broadly linear to elliptic, 10–20 mm long, 4–6 mm broad, 1–3 dentate; disc florets 20–60, yellow, tubular, 10–15 mm long, villous below; pappus of both ray and disc florets white, barbellate to subplumose. Achenes dark gray, 6–8 mm long, 1 mm broad, sparsely to densely hirsute with duplex hairs. Figure 1. Chromosome number $2n = 38$.

Figure 1. *Arnica cernua.*

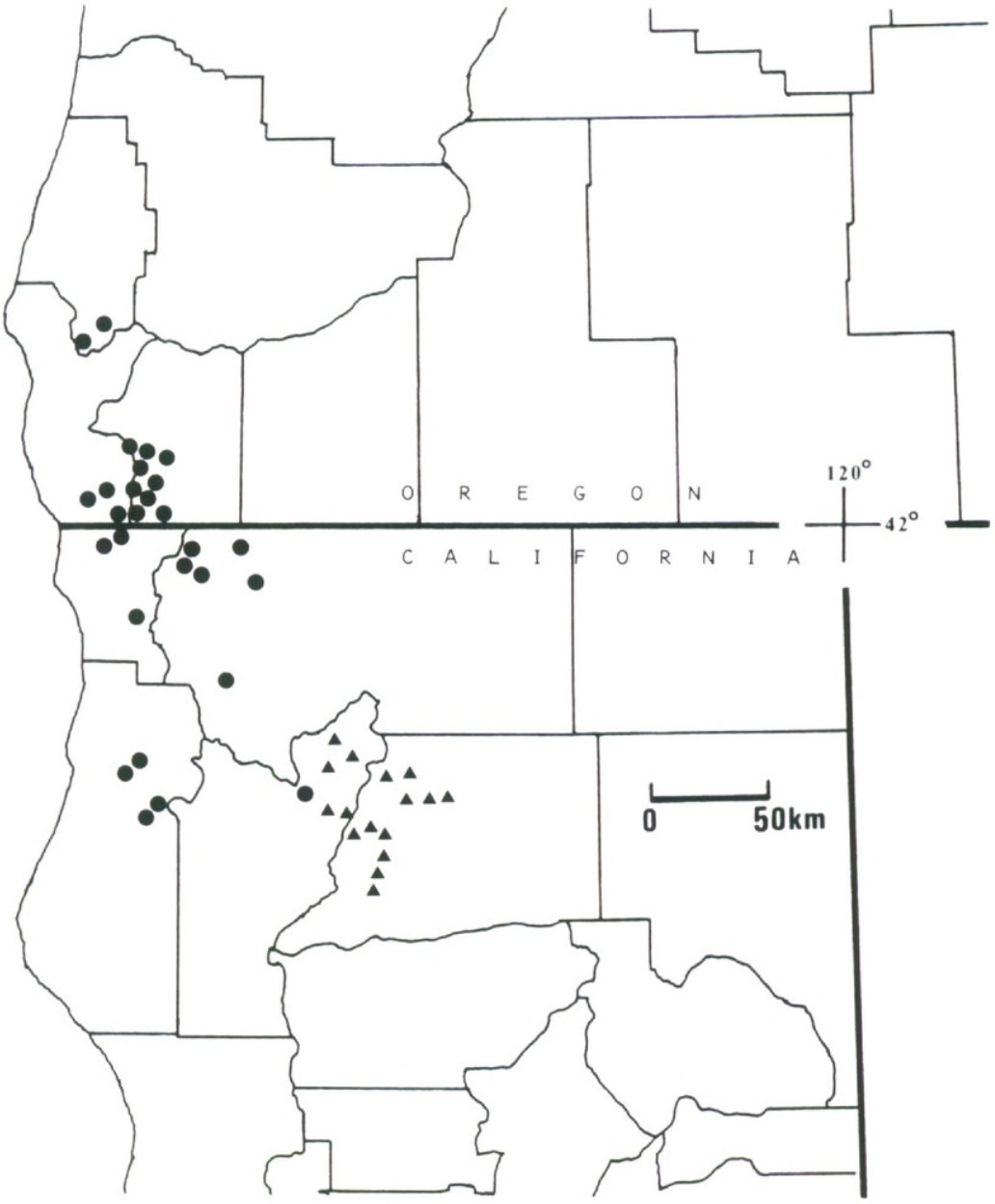

Figure 2. Distribution of *Arnica cernua* ● and *Arnica venosa* ▲.

ECOLOGY AND DISTRIBUTION: Relatively rare, but locally abundant in dry, open *Pinus–Pseudotsuga menziesii* forests at moderate elevations (500–1500 m). Known only from serpentine soils in Coos, Curry and Josephine Counties, Oregon and Del Norte, Trinity and Siskiyou Counties, California. Figure 2. Flowers late April to June.

REPRESENTATIVE SPECIMENS: **United States:** CALIFORNIA: Del Norte Co.: Gasquet-O'Brien Toll Rd., 7.7 mi. N. E. Patrick Creek Rd., *D. Breedlove 3178*

(CAS); Boundary Hill, near Telephone Point, *A. Eastwood s.n.* (CAS); Telephone Point, *A. Eastwood 148* (US). Humboldt Co.: Hoopa, *J. Davy and W. Blasdale 5645* (UC); Hoopa Indian Reservation, *H. Chandler 1298* (NY, UC, US); Ruby Creek, Willow Creek Canyon, *J. Tracy 7449* (UC); Horse Mt., *J. Tracy 15902* (CAS, UC), *S. J. Wolf 471* (ALTA); Willow Creek Canyon, *J. Tracy 7057* (CAS, UC); Hoopa Mt., *J. Tracy 7561* (UC). Siskiyou Co.: 15 mi. n. Happy Camp, *G. L. Stebbins 3269* (UC); Baldy Lookout, *F. Hoffman 3547* (UC); Klamath River Canyon, 1/2 mi. below mouth of Scott River, *R. Barneby 11513* (CAS). Trinity Co.: w. side Backbone Ridge on trail to Raymond Flat, *E. Carter 1116* (CAS); Mt. Bally, *S. Kleeberger s.n.* (CAS).

OREGON: Coos Co.: Iron Mt., *W. Baker 6822* (OSC, UC). Curry Co.: headwaters Chetco River, *R. J. Howell and G. True 48823* (CAS). Josephine Co.: base Coast Mts., near Waldo, *T. Howell 166* (ORE), *T. Howell 1446* (NDG, UC); Eight Dollar Mt., *L. Savage s.n.* (UC); Little Rock Creek, 2 mi. s.w. O'Brien, *L. Constance and R. Rollins 2993* (CAS, MICH, UC, WTU); Cedar Creek, Deer Creek Canyon, *L. Delting 4036* (UC); Siskiyou Mts., near O'Brien, *J. Thompson 1027* (CAS, NDG); Kerby, *A. Sweetser s.n.* (CAS); Babyfoot Lake Trail, *S. J. Wolf 464* (ALTA).

This species is easily distinguished by its glabrous, thick, ovate, crenate, petiolate leaves that are often reddish or purple; solitary, nodding heads, and serpentine habitat. Maguire (1943) considered *Arnica cernua* a derivative of *A. latifolia.* However, both *A. cernua* and *A. cordifolia* share several features including: long petiolate leaves, broad solitary heads with pilose and stipitate-glandular, ovate-lanceolate involucral bracts and dark gray achenes. In contrast, *A. latifolia* has sessile leaves, several narrow heads with narrow, sparsely pubescent bracts and brown achenes. In addition, the leaves of *A. cernua* are sometimes subcordate or even cordate (*T. Howell 1446, 1936* NDG) like *A. cordifolia.*

In the original description of *Arnica cernua* (Howell, 1900) no specimens were cited and no type was designated. Maguire (1943) designated a Howell collection (*T. Howell 1466* UC, NDG) as the lectotype for this species. However, as Rollins (1972) notes, "the existence of a holotype in the institution where the author worked is assumed until proven otherwise". Examination of Howell's collections at the University of Oregon has revealed that he did in fact designate a type by writing "Typ[sic] specimen" on one specimen (*T. Howell 166* ORE). According to the criteria of Rollins (1972) there would be no need to designate a lectotype since *Howell 166* would automatically be the holotype for *A. cernua.*

Rydberg (1927) described a smaller, more glandular form of *A. cernua* as *A. chandleri.* Examination of the type specimens (*Chandler 1298,* NY, UC, US) as well as two other collections of this taxon (*Davy and Blasdale 5645* UC and *Tracy 7449* UC) indicates that they are all referable to *A. cernua.*

2. **Arnica cordifolia** Hook, Fl. Bor. Am. 1: 331. 1834. TYPE: Alpine woods of the Rocky Mountains, on the east side, *Drummond s.n.* (HOLOTYPE, K photo!).

Arnica macrophylla Nutt., Trans. Am. Phil. Soc. II. 7: 408. 1841. *Arnica cordifolia* Hook. var. *macrophylla* (Nutt.) Maguire, Am. Midl. Nat. 37: 1947. TYPE: Blue Mountains of Oregon, *Nuttall s.n.* (HOLOTYPE, K photo!).

Arnica chionophila Greene, Pittonia 4: 171. 1900. TYPE: Ruby Mountains, Nevada, July 20, 1896, *E. L. Greene s.n.* (HOLOTYPE, NDG!).

Arnica subcordata Greene, Pittonia 4: 173. 1900. TYPE: on the Athabasca River, June 26, 1898, *W. Spreadborough* (*Geol. Surv. Can. No. 19644*) (HOLOTYPE, CAN!).

Arnica pumila Rydb., Mem. N. Y. Bot. Gard. 1: 433. 1900. *Arnica cordifolia* Hook. var. *pumila* (Rydb.) Maguire, Madroño 6: 154. 1942. TYPE: Gray's Peak, Colorado, Aug.-Sept., 1872, *Torrey s.n.* (HOLOTYPE, NY!).

Arnica parvifolia Greene, Pl. Baker. 3: 28. 1901. TYPE: Marshall Pass, Colorado, 10,000 ft., July 19, 1901, *C. F. Baker 515* (HOLOTYPE, NDG!; ISOTYPES, CAS!, POM!, UC!, US!, WS!).

Arnica paniculata A. Nelson, Man. Bot. Rocky Mts. 572. 1909. TYPE: moist timber, Bridger Peak, Carbon Co., Wyoming, Aug. 24, 1903, *L. N. Gooding 1974* (HOLOTYPE, RM!; ISOTYPES, CAS!, GH!, MO!, NY!, RM!, UC!, US!).

Arnica evermanii Green, Ottawa Nat. 23: 215. 1910. TYPE: shores of Petit Lake, Idaho, Aug. 13, 1895, *B. W. Evermann 318* (HOLOTYPE, US!).

Arnica abortiva Greene, Leaflets 2:47. 1910. TYPE: open spaces in timber, Wind River Mts., Wyoming, July 23, 1881 *W. H. Forwood s.n.* (HOLOTYPE, US!).

Arnica andersonii Piper, Proc. Biol. Soc. Wash. 33: 106. 1920. TYPE: Skeena, British Columbia, Sept. 11, 1910, *J. R. Anderson 677* (HOLOTYPE, US!; ISOTYPES, US!, WS photo!).

Arnica austinae Rydb., N. Am. Fl. 34: 340. 1927. TYPE: Lake City Canyon, California, July 1898, *Austin and Bruce 2165* (HOLOTYPE, NY!; ISOTYPES, NY!, UC!).

Arnica humilis Rydb., N. Am. Fl. 34: 341. 1927. *Arnica cordifolia* Hook. var. *humilis* (Rydb.) Maguire, Am. Midl. Nat. 37: 138. 1947. TYPE: on "the saddle", Lake Louise, Alberta, July 20, 1904, *J. Macoun* (*Geol. Surv. Can. No. 65504*) (HOLOTYPE, NY!; ISOTYPE, CAN!).

Arnica whitneyi Fernald, Rhodora 37: 334. 1935. *Arnica cordifolia* Hook. var. *whitneyi* (Fernald) Maguire, Brittonia 4: 452. 1943. TYPE: dry deciduous woods near Copper Harbor, Keweenaw Co., Michigan, July 4, 1934, *Fernald and Pease 3579* (HOLOTYPE, GH!).

Arnica hardinae St. John, Fl. SE. Wash. 419. 1937. TYPE: open woods, Lake Chatcolet, Benewah Co., Idaho, Oct. 2, 1927, *G. Weitman 226* (HOLOTYPE, WS!).

Stems mostly simple, sometimes branched, 10–40 (70) cm high, 2–3 mm diameter, glandular-puberulent to densely villous, especially above; rhizomes long, giving rise to several basal rosettes and flowering stems, 1.5–3.0 mm thick, 2–3 pairs of thin brown scales and often old leaf bases at the summit. Cauline leaves 2–4 (6) pairs,

cordate or subcordate to narrowly ovate, 3–10 cm long, 2–10 cm broad, puberulent to sparsely villous and sometimes stipitate-glandular, especially above, acute to rounded, dentate to coarsely dentate; petioles (2) 5–10 (20) cm long; uppermost leaves often reduced, ovate-lanceolate, short-petiolate or sessile, sometimes bract-like; leaves of the innovations 2–4, similar to cauline leaves or often more coarsely dentate. Inflorescence usually a single head or corymb of 3–5 (10) heads; peduncle 4–20 cm long, pilose and stipitate-glandular; heads radiate, broadly campanulate, 1.5–3.0 cm high; involucral bracts, 10–20, narrowly ovate to lanceolate, 10–20 mm long, 2–5 mm broad, pilose at base to puberulent above, sometimes glandular, acute to acuminate, margins scarious. Ray florets 6–13, yellow, elliptic-oblong, 15–30 mm long, 5–10 mm broad, subentire to 3-dentate; disc florets numerous, 20–90, yellow, tubular, 9–12 mm long, sparsely glandular above, sparsely to densely villous and stipitate-glandular below; pappus of both ray and disc florets white, barbellate. Achenes dark gray, 5–10 mm long, 1 mm broad, sparsely to densely hirsute with duplex hairs, also sometimes stipitate-glandular. Figure 3. Chromosome number $2n = 38, 57, 76, 95, 114$.

ECOLOGY AND DISTRIBUTION: Very common in mesic *Picea-Pinus-Pseudotsuga menziesii* forests or occasionally sub-alpine meadows from the central Yukon south through northern New Mexico, northern Arizona, Nevada and northern California. Also found in the Cypress Hills of Alberta and Saskatchewan and with outlying populations in the Black Hills of South Dakota, the Pasquia Hills of Saskatchewan and Riding Mt. Provincial Park, Manitoba. Also found in *Abies balsamea-Betula-Acer* forests in Keweenaw County, Michigan and Sibley Provincial Park, Ontario. Figure 4. Elevational distribution from 500 m in the Yukon to 3000 m in Colorado. Flowers May–July.

REPRESENTATIVE SPECIMENS: **Canada:** ALBERTA: Mt. Park, *M. Malte and W. Watson 1969* (UC); Jasper, near Icefields, *A. and R. Nelson 4889* (UC); Squaw Mt., *F. Lewis 92130* (CAN); Mt. Norquay, *B. LaSalle 45155* (CAN); Pyramid Mt., *A. E. Porsild and A. J. Breitung 16351* (CAN); Porcupine Hills, *Malte and Watson 603* (CAN); Lake Louise, *Malte and Watson 1014* (CAN); Mt. Park, *Malte and Watson 1995* (CAN); Mt. Edith Cavel, *J. Macoun 96072* (CAN); Cottonwood Creek, *E. H. Moss 4654* (ALTA, CAN); Mt. Eisenhower, *A. E. Porsild and A. J. Breitung 15808* (CAN); Sunshine Ski Lodge, *A. E. Porsild and A. J. Breitung 13604* (CAN); Medicine Lake, *M. Dumais 2816* (ALTA, CAN); Swan Dive Fire Tower, Swan Hills, *M. Dumais 4024* (ALTA, CAN); Palisades Mt., *A. E. Porsild 22526* (CAN). Mt.

Figure 3. *Arnica cordifolia.*

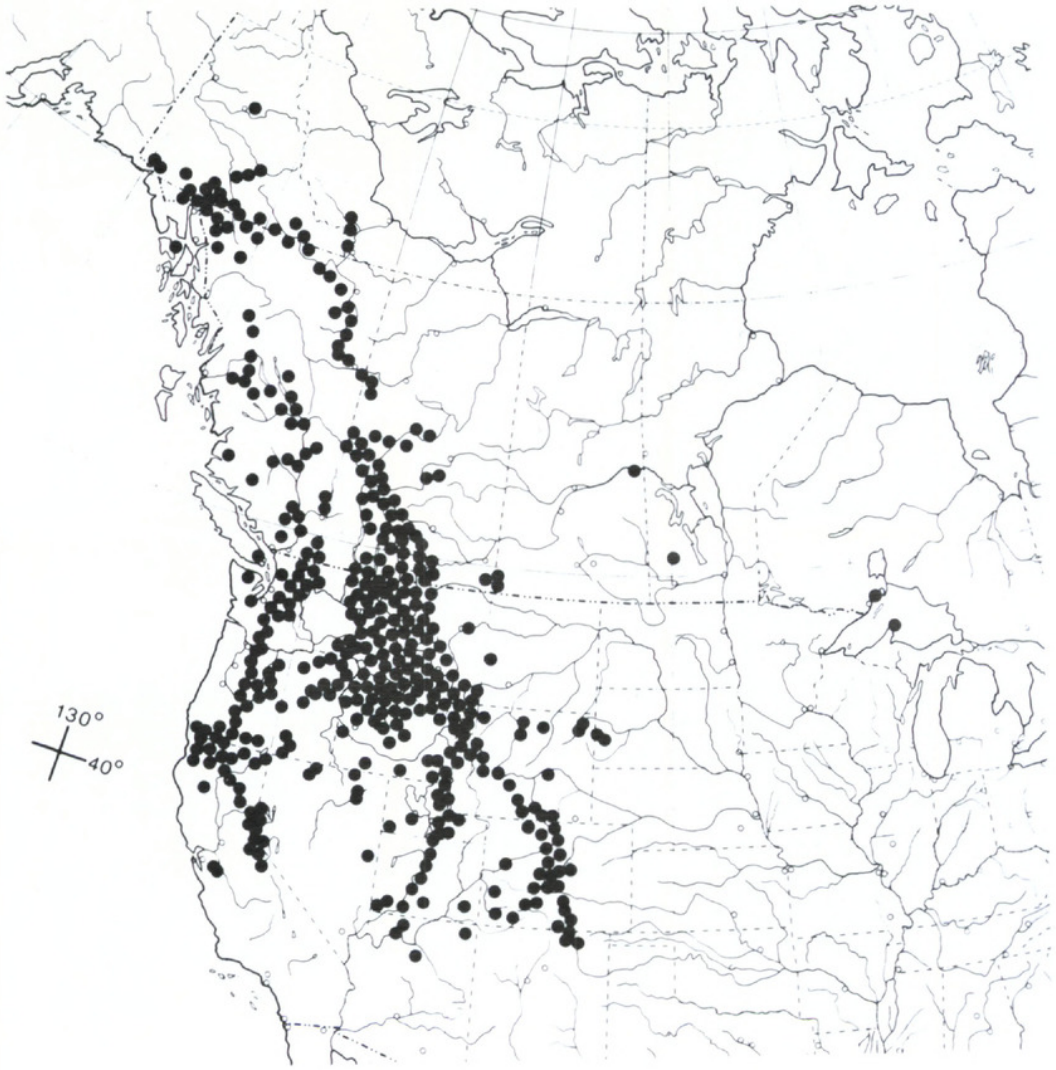

Figure 4. Distribution of *Arnica cordifolia.*

Norquay, *L. Jenkins 1586* (DAO); Waterton Lakes, *L. Carmichael 88* (DAO); Cypress Hills, Spring Creek, *R. S., A. J. Breitung 5661* (DAO); Saskatoon Mt., *L. Jenkins 738* (DAO); mi. 21, Jasper-Banff Hwy., *W. McCalla 4578* (ALTA); Lake Louise, *G. Turner 11517* (ALTA); Pyramid Lake, *T. Turner 6872* (ALTA); 20 mi. NW Edson, *I. Corns 12108* (ALTA); Ram Mt., *M. G. Dumais 7767* (ALTA); Lake George, *G. La Roi s.n.* (ALTA); Saskatoon Mt., *Prairie and Heywood 69* (ALTA); Swan Hills, *M. G. Dumais 4024* (ALTA); Surprise Lake, *M. G. Dumais 6212* (ALTA); Jarvis Lake, *M. G. Dumais 2420* (ALTA); Saddle Hills, N. of Sexsmith, *E. H. Moss 8464* (ALTA); Winfield, *F. Rusconi s.n.* (ALTA); Mercoal, *E. Woollven 23* (ALTA). Mt. Park, *E. Woollven 7* (ALTA).

BRITISH COLUMBIA: Alaska Hwy., 12 mi. NW Dawson Creek, *Calder and Kukkonen 26801* (UC); Revelstoke, *W. Spreadborough 64984* (NDG); Lake

Osoyoos, *J. Macoun 69323* (NDG); Skagit Valley, *J. Macoun 69325* (NDG); SW corner Dease Lake, *T. McCabe 8726* (UC); Crowsnest Pass, *T. McCabe 6463* (UC); Takla Landing, *T. McCabe 7835* (UC); Germansen Landing, *T. McCabe 7664* (UC); Clearwater, *T. McCabe 2078* (UC): 15 mi. SW Kleena Kleen, *T. McCabe 583* (UC); Atlin, *Setchell and Parks s.n.* (UC); Sinclair Pass, *T. McCabe 6219* (UC); Arnarchist Mt., *T. McCabe 5956* (UC); Atlin, *A. Eastwood 651* (CAS, UC); Bear Lake, *T. McCabe 7997* (UC); Pavilion Mt., *T. McCabe 213* (UC); Pinantan, *T. McCabe 2013* (UC); Skeena Crossing, *T. McCabe 7027* (UC); Princeton, *A. McCallum s.n.* (UC); Lake Bootahnie, *J. and E. Thompson 119* (MICH); 2 mi. E. Williams Lake, *J. Calder et al 16938* (DAO, OSC); Annaham Lake, *G. Bellinger 32395* (OSC); Cooper Mt., near Princeton, *Taylor and Szczawin s.n.* (OSC, UBC); Smithers, *J. Menzies 6016* (UBC); Cathedral Park, Twin Buttes, *R. Hainault 7879* (UBC); Mt. Edziza, *Annas and Klinka s.n.* (UBC); Hedley, *T. Taylor 2089* (UBC); 10 mi. E. Summit Pass, *H. Raup and D. Correll 10738* (UBC); 49 mi. E. Teslin, *H. Raup and D. Correll 11099* (CAN, UBC); Cassier, *T. Taylor et al 398* (CAN, UBC); mi. 81, Haines Rd., *T. Taylor et al 1342* (UBC). Mt. Defot, NW Dease Lake, *J. Teit 99* (UBC); mi. 206, Alaska Hwy., *A. E. Porsild 9111* (GH); Mt. Finlayson, Vancouver Island, *C. Newcomb 60* (GH); Laird Hot Springs, *A. E. Porsild and A. J. Breitung 22259* (CAN); Revelstoke, *J. Macoun 64984* (CAN). Mt. Brilliant, *H. Laing 687* (CAN); Osoyoos Lake, *J. Macoun 69323* (CAN); Telegraph Creek, *Dawson s.n. 14731* (CAN); Victoria, *J. Tolmie 1053* (DAO); Mt. Pope, *J. Whitehorn 382* (DAO); Blanchard River, 66 mi. S. Haines Jct., *Calder and Kukkonen 28185* (DAO); mi. 625 Alaska Hwy., *Calder and Gillet 25623* (DAO). Hurricane Creek, Atlin Dist., *J. Aitken 10* (DAO); Kootney Nat. Park, Sinclair Nature Trail, *K. Seel 27* (DAO); 12 mi. E. Field, *G. Turner 3899* (DAO); 8 mi. NE Ft. Steele, *R. Taylor and D. Ferguson 629* (DAO); 32 mi. W Prince George, *Mulligan and Woodbury 1688* (DAO); Kleena Kleen P.O., *Calder and Parmelee 19185* (DAO); 5 mi. N. Little Fort, *Calder and Saville 8638* (DAO); Nuttbide Lake, *Quiquet and Ritcey 57* (DAO); 9 mi. E. Williams Lake, *Calder and Parmelee 17040* (DAO).

MANITOBA: Rassburn Tower Cabin, Riding Mt. Provincial Park, *A. Lovaas 61-8* (DAO).

NORTHWEST TERRITORIES: Laird River between Nahanni Butte and Simpson, *C. Crickmay 114* (CAN); SW MacKenzie Mt., Laird Range, 15 mi. NW Ft. Laird, *W. Jeffrey 424* (CAN).

ONTARIO: Ravine Lake, Sibley Provincial Park, *C. Garton 15485* (CAN, MICH, UC): *15163* (UC), *15164* (CAN).

SASKATCHEWAN: Mt. Cabin, Pasquia Hills, *J. Rowe 983* (CAN); Cypress Hills; *C. Frankton 266* (DAO); *R. Newsome 394-64* and *470-64* (DAO); *Ledingham and Hudson 1788* (DAO); *G. Selleck 394* (DAO); *R. Russell s.n.* (DAO).

YUKON TERRITORY: Mi. 802, Alaska Hwy., *D. Bolinger s.n.* (OSC); Whitehorse, *J. Gillett and D. Mitchell 3862* (DAO, OSC); mi. 23, Campbell Hwy., *V. Harms 17193* (DAO, GH); mi. 116, Canol Rd., *A. E. Porsild and A. J. Breitung 10079* (CAN); St. Elias Mt., *A. Pearson 67-210A* (CAN); Keno, *G. Potack 119369* (CAN); Canol Rd., km 15.5, *S. J. Wolf 507* (ALTA); km 118, *S. J. Wolf 508* (ALTA); 3 mi. S Whitehorse, *J. Gillett 3259* (DAO, RM); lower Kathleen Lake, Kluane Nat. Park, *G. and G. Douglas 5884* (DAO); mi. 858, Alaska Hwy., *Calder and Gillett 25734* (DAO); mi. 777, Alaska Hwy., *Calder and Kukkonen 28318* (DAO); 16 mi. S. Haines Jct., *S. J. Wolf 300* (ALTA); km 196, Haines Rd., *S. J. Wolf 301* (ALTA); km

1479, Alaska Hwy., *S. J. Wolf 307* (ALTA); Alaska Hwy., 1.6 km E Squanga Lake, *S. J. Wolf 505* (ALTA).

United States: ALASKA: Sitka, *A. Paska s.n.* (UC); mi. 17.5 Haines Hwy., *M. Williams 1473* (OSC); Sitka, *A. Heller 14942* (WTU).

ARIZONA: Apache Co.: Lukachukai Mts., *Goodman and Payson 2865* (GH); rd. to Wide Lake, Lukachukai Mts., *C. Mason et al 2441* (UC). Coconino Co.: N. Rim, Grand Canyon, *U.S. Park Service 2007* (US); Indian Hollow, Kaibab Plateau, *L. Gooding 203* (UC); N. slope, San Francisco Peaks, *J. Leiberg 5897* (US).

CALIFORNIA: Alpine Co.: Hermit Valley, *F. Peirson 11593* (UC). El Dorado Co.: Magies Peak, *H. M. Hall 8810* (UC). Glenn Co.: Black Butte, *V. Rattan s.n.* (CAS). Humboldt Co.: Salmon Summit, *J. Tracy 14372* (UC). Lassen Co.: 1 mi. E Fredonyer Pass, *A. Heller* (UC). Madera Co.: Shadow Lake Trail, 1 mi. fm. Agnew Meadow, *J. and C. Reveal 427* (RM, UC, WTU). Mariposa Co.: Yosemite Valley, *G. Grant 4356* (UC); Signal Peak, *C. Quick 1997* (CAS). Modoc Co.: 15 mi. NE Alturas, *C. L. Hitchcock s.n.* (UC); Cedar Pass, *J. Weiler 61235* (UC); Emerson Creek, *Alexander and Kellogg 4668* (UC). Mono Co.: Slate Creek Basin, E. Mt. Conness, *J. Clausen 1124* (OSC); Mammoth Lakes, Lake Mary, *L. Rose 42194* (WTU). Nevada Co.: Donner Lake, *S. J. Wolf 476* (ALTA). Placer Co.: Deer Park, *H. Geis 38* (UC); W. side Donner Lake, *M. Denton 3901* (WTU). Plumas Co.: Gold Lake Rd., *S. J. Wolf 478* (ALTA); American Valley, *R. Austin s.n.* (NDG). Santa Clara Co: Mt. Hamilton, *R. Pendleton 873* (UC). Siskiyou Co.: Caribou Lake, *I. Wiggins 13562* (UC); English Lake, *F. Oettinger 1023* (UC); Marble Mt., *H. Chandler 1615* (UC); Salmon Mts., 10 mi. SW Etna, *A. Eastwood and J. Howell 5037* (CAS). Trinity Co.: Oregon Gulch Mt., *J. Tracy 7538* (UC); Musser Hill, *H. Yates 395* (UC). Tuolumne Co.: Gaylor Lakes, *H. Mason 11368* (UC).

COLORADO: Boulder Co.: Mts. between Sunshine and Ward, *F. Tweedy 4893* (RM); Boulder, *F. Ramaley 71* (RM). Chaffee Co.: Morass Creek, *I. Clokey 3474* (UC). Clear Creek Co.: Chicago Creek, *J. Ehlers 8402* (MICH). Custer Co.: Westcliffe, *C. Erlanson 1768* (MICH). Douglas Co.: 7.3 mi. SW Sedalia, *W. Weber 7440* (WTU). Eagle Co.: 2 mi. E. Tennessee Pass, *I. Tidstrom 4098* (US). El Paso Co.: 2 mi. W Palmer Lake, *G. Robbins 463* (DAO). Fremont Co.: Sierra Sangre de Cristo, *T. Brandegee 241* (UC). Gilpin Co.: Tolland, *E. Palmer 31255* (GH). Fontleroy Place, *H. Rodeck 58* (DAO). Grand Co.: Berthoud Pass, *J. Ehlers 8452* (MICH); Berthoud Pass, *F. Tweedy 5821* (RM). Gunnison Co.: Bonton Mine, *I. Clokey 3009* (UC). Hinsdale Co.: W. Slumgullion Pass, *J. Barrell 249-65* (US). Huerfano Co.: Mt. SW Blue Lake, *Mosquin and Gillett s.n.* (UC). Jefferson Co.: Lookout Mt., *H. Shacklette 5934* (MICH). Lake Co.: Lost Man Camp. 6 mi W Independence Pass, *U. Waterfall 11623* (UC); Leadville, *J. Ehlers 8218* (MICH). La Plata Co.: Eagle Pass, *Mosquin and Gillett 5430* (UC). Larimer Co.: Rocky Mt. Nat. Park, *D. McNeal 202* (RM). Mesa Co.: Grand Mesa, *U. Waterfall 11653* (UC). Mineral Co.: Wolf Creek Pass, *C. Wolf 3007* (CAS). Ouray Co.: Ouray, *Biltmore 1149* (US). Pitkin Co.: West Springs Creek, *J. Langenhein 1399* (UC). Sanguache Co.: Marshall Pass, *J. Barrell 29-66* (US). Summit Co.: Breckenridge, *K. Mackenzie 80* (RM).

IDAHO: Bannock Co.: 3 mi. above Pocatello, *A. Cronquist 2302* (GH). Bear Lake Co.: Aspen Range, Georgetown Canyon, *N. Holmgren and B. Bethers 4411* (UC). Benewah Co.: SE Plummer, *W. Baker 16085* (WTU). Bonneville Co.: Tie Canyon, 6 mi. SW Victor, *N. Holmgren and V. Marttala 5376* (UC). Butte Co.:

Craters of the Moon Nat. Monument, *Dole 49* (UC). Camas Co.: Soldier Mts., Ketchum-Featherville Rd., *C. L. Hitchcock and C. V. Muhlick 10417* (WTU). Custer Co.: 10 mi. W. Cape Horn, *C. L. Hitchcock and C. V. Muhlick 9654* (UC). Elmore Co.: 23 mi. NE Mountain Home, *Davidse and Collotzi 453* (UC). Franklin Co.: 2 mi. SW Franklin Basin R.S., *B. Maguire 21645* (WTU). Idaho Co.: Warren Summit, *R. Davis 2555* (UC). Kootenai Co.: Albany Falls, *C. Speilberg 452* (RM). Latah Co.: Moscow Mt., *L. Abrams 613* (UC). Lemhi Co.: Moccasin Creek, *C. L. Hitchcock and C. V. Muhlick 14287* (UC). Nez Perces Co.: Lake Waha, *A. and E. Heller 3170* (UC). Owyee Co.: Silver City, *J. Macbride 955* (RM). Rich Co.: Bear Lake Summit, *S. J. Wolf 485* (ALTA). Shoshone Co.: Bullion Pass, St. Line, *W. Baker* 13446 (OSC). Valley Co.: McCall, *W. Boone 29* (RM); 15 mi. N. Banks, *C. L. Hitchcock and C. V. Muhlick 8578* (WTU). Washington Co.: Mann Creek, *H. Tucker s.n.* (RM).

MICHIGAN: Keweenaw Co.: 3 mi. E. Agate Harbor, *F. Hermann 7995* (UC); Fort Wilkins State Park, *M. Feigley and L. Nagel s.n* (MICH); Copper Harbor Cemetery *C. Richards 3783* (MICH); *2221* (MICH); Grand Marias Harbor, *C. Richards 2144* (DAO, MICH); 1 mi. W. Copper Harbor, *F. Herman 7761* (MICH, RM); bluffs SE of Eagle Harbor, *M. Fernald and A. Pease 3580* (GH, MICH); Copper Harbor, *Pease and Ogden 25178* (GH).

MONTANA: Deerlodge Co.: Storm Mt. *S. J. Wolf 435* (ALTA). Flathead Co.: 8 km E. Bigfork, *S. J. Wolf 496* (ALTA). Gallatin Co.: Targhee Pass, *S. J. Wolf 433* (ALTA); Sage Creek, *D. Swingle s.n.* (MICH). Lake Co.: near Biological Station, Flathead Lake, *P. Smith 37* (NDG). Lewis and Clark Co.: 8 mi. W. Lincoln, *C. L. Hitchcock 17956* (UC). Lincoln Co.: Mt. Marston, *S. J. Wolf 343* (ALTA); 25 km S. Eureka, *S. J. Wolf 443* (ALTA). Madison Co.: E. of Brandon Lakes, *C. L. Hitchcock 16960* (UC). Meagher Co.: 35 mi. NW White Sulphur Springs, *C. L. Hitchcock 16225* (UC, WTU). Missoula Co.: Blackfoot Valley, *H. LaCasse 15* (MICH); Missoula, *Nawrodcki and Neff 2* (NDG); 34 km N. Seeley Lake, *S. J. Wolf 495* (ALTA); Marshall Ski Area, *S. J. Wolf 492* (ALTA). Ravalli Co.: 32 mi. E. Hamilton, *G. Hedgcock s.n.* (WTU). Saunders Co.: divide between Camas and Perry Basin, *F. Barkely 2568* (NDG). Sweetgrass Co.: 1 mi. below Rainbow Lakes, *C. L. Hitchcock 16506* (UC).

NEW MEXICO: Colfax Co.: Baldy Peak, *P. Standley 14307* (US); Hermatite Canyon, *D. St. John 52* (GH). Rio Arriba Co.: Chama, *P. Standley 6713* (US); Brazos Canyon, *P. Standley 10917* (US); Pecos River National Forest, Wuisor Creek, *P. Standley 4255* (US).

NEVADA: Elko Co.: Jarbridge Mts., Coon Creek, *P. Train 671* (NDG); Lamoille Lake, *A. Holmgren 14177* (UC); Steele Creek, Ruby Mts., *A. Borell s.n.* (UC); 8 mi. W. North Fork, *N. Nichols 321* (DAO). Humboldt Co.: Santa Rosa Range, *J. Gentry 1581* (DAO, NY, RM). Washoe Co.: Headwaters Galena Creek, *W. Archer 6677* (DAO, UC); Hunters Creek Rd., 9–11 mi. SW Reno *W. Archer 6295* (CAD). White Pine Co.: Wheeler Peak, *B. Maguire 21111* (GH, UC); *S. J. Wolf 480* (ALTA).

OREGON: Baker Co.: Eagle Creek, *T. Gustafson s.n.* (UC). Crook Co.: Ochoco N.F., *S. Warg s.n.* (OSC); 23 mi. NE Prineville, *F. Chisaki 780* (RM). Curry Co.: Summit of Pistol River Mt., *J. Thompson 4565* (CAS). Deschutes Co.: Pavilina Lake, *M. Peck 9658* (OSC). Grant Co.: Malheur N.F., Fields Park, *A. Kruckeberg 546* (UC). Harney Co.: Myrtle Creek Canyon, *M. Peck 2846* (OSC). Steens Mts., *C.*

Hansen 699 (OSC). Hood River Co.: Hood River, *T. Howell 477* (OSC). Jackson Co.: Mt. Ashland, *M. Peck 2934* (OSC). Jefferson Co.: Black Butte, *J. Johnson 470* (OSC). Josephine Co.: 4.6 mi. S. Hugo, *K. Chambers 2916* (OSC). Klamath Co.: Fossil Lake, near Crater Lake, *H. Furlong s.n.* (UC). Lake Co.: 2 mi. NW Crooked Creek, *M. Loveless 77* (UC). Morrow Co.: Tupper Guard Station, *E. Winn s.n.* (OSC). Umatilla Co.: 14 km S Ukaih, *S.J. Wolf 451* (ALTA). Union Co.: 40 km E Ukaih, *S. J. Wolf s.n.* (ALTA); Eagle Cap, *G. Mason 1395* (OSC). Jarboe Creek, *P. Standley s.n.* (OSC). Wallowa Co.: Lostine River, 18 mi. from Lostine, *J. Murphy 89* (UC); Hurricane Creek, *G. Mason 5365* (OSC); Lick Creek Rd. *H. Gilkey 8* (OSC). Wasco Co.: 2 mi. W. the Dalles, *M. Peck 2791* (OSC).Wheeler Co.: Fossil, *W. Lawrence 2988* (OSC).

SOUTH DAKOTA: Lawrence Co.: Spearfish Canyon, N Black Hills, *F. Bennett 941* (CAS); 10 mi. NW Deerfield, *P. Johnson 527* (MICH); top of Custer Peak, *E. Palmer 37547* (GH); Mt. Roosevelt, *W. Over 17639* (RM); Whitewood, *H. Hayward 1207* (RM).

UTAH: Beaver Co.: 23 km E. Beaver, *S. J. Wolf 482* (ALTA). Cache Co.: Logan Canyon, *B. Maguire 3881* (RM, UC). Carbon Co.: Willow Springs, 1 mi. E. Sunnyvale, *S. Blake 9587* (UC). Duchesne Co.: W. Mt. Agassiz, *B. Maguire et al 4317* (RM); Ashley Nat. Forest, *S. J. Wolf 396* (ALTA). Garfield Co.: Mt. Ellen, Henry Mts., *R. McVaugh 14652* (CAS, MICH). Iron Co.: 3 mi. N. Cedar Breaks Nat. Monument, *C. L. Hitchcock and C. V. Muhlick 4603* (UC, WTU); 17.2 km E. Cedar City, *S. J. Wolf 481* (ALTA). Juab Co.: Granite Canyon, *B. Maguire and R. Becraft 2853* (UC). Piute Co.: Marysvale, *M. Jones s.n.* (CAS). Rich Co.: Bear Lake Summit, *S. J. Wolf 485* (ALTA). Salt Lake Co.: Big Cottonwood Canyon, *P. Rydberg and E. Carlton 6652* (UC); City Creek Canyon, Salt Lake City, *K. Brizzee 7856* (WTU). San Pete Co.: Skyline Drive, B. Maguire 20033 (WTU); *S. J. Wolf 393* (ALTA). Summit Co.: Burntfork Creek, *E. Jensen s.n.* (UC). Tooele Co.: S. Willow Creek, Stansbury Range, *B. Maguire 21753* (GH, UC). Utah Co.: Mt. Timpanogos, *E. Applegate 8439* (CAS); 9.5 km E. Mt. Timpanogos, *S. J. Wolf 483* (ALTA). Washington Co.: Forsyth Creek, Pine Valley Mts., *P. Munz 16924* (WTU).

WASHINGTON: Asotin Co.: Field Springs Park, *S. J. Wolf 446* (ALTA). Chelan Co.: Tumwater Mt., *J. Thompson 6479* (WTU); Lookout Mt., *J. Thompson 6479* (WTU); Wenatchee Lake, *W. Dress 4228* (UC). Clallam Co.: Boulder Creek, Olympic Nat. Forest, *G. Jones 8475* (WTU). Columbia Co.: Wolf Fork, Touchet River, *H. St. John et al 6971* (UC). Garfield Co.: Blue Mts., *D. Peters 385* (UC); 15 mi. S. Pomeroy, *C. L. Hitchcock and C. V. Muhlick 8302* (UC, WTU). Kittitas Co.: Virden, *J. Thompson 11582* (UC, WTU); Lookout Mt., *J. Thompson 14512* (MICH; NDG). Klickitat Co.: NE Bingen, *W. Suksdorf 2760* (UC). Mason Co.: Mt. Elinor, *P. Freer 371* (WTU). Okanogan Co.: Salmon Creek, *C. Fiker 686* (WTU); 20 mi. W. Winthrop, *G. and G. Douglas 3514* (ALTA, DAO). Pend Oreille Co.: Calispell, *F. Kreager 351* (UC, WTU). Skamania Co.: Hamilton Mt., *L. Delting 7066* (UC). Snohomish Co.: Mt. Dickerson, *R. Owen s.n.* (WTU). Spokane Co.: Mt. Spokane, *S. J. Wolf 445* (ALTA). Stevens Co.: E. side Columbia River, 12 mi. above mouth of Spokane River, *H. Rogers 400* (UC). Yakima Co.: Mt. Aix, *J. Thompson 15016* (WTU); Chinook Pass, *J. Thompson 15136* (WTU); Bald Mt., *H. St. John 7854* (UC).

WYOMING: Albany Co.: 7.9 mi. W. Centennial, *S. J. Wolf 424* (ALTA); Woods Creek Canyon, *C. L. Porter and M. Porter 9810* (UC); Woods Creek, *L. Goodding*

1431 (UC); Centennial, *Kauffman and Erlanson 113* (MICH); University Camp, Medicine Bow Mts., *A. Nelson 7798* (RM). Big Horn Co.: 10–15 mi. E. Kane, *L. and R. Williams 3016* (RM). Carbon Co.: South Brush Creek Campground, *B. and L. Nelson 451* (RM). Crook Co.: 6 mi. NE Hulett, *M. Ownby 599* (RM, UC, WTU). Fremont Co.: Gannett Creek, *F. Jozwik 395* (UC); 1 mi. S. Pacific Spring, *C. L. Porter 4525* (RM). Lincoln Co.: Grover Park, Afton Area, *O. Harrison 55* (RM). Natrona Co.: Casper Mt., *R. Tresler 55* (RM). Park Co.: Crazy Woman Creek, Beartooth Mts., *L. and R. Williams 3518* (NDG). Saunders Co.: divide between Camas and Perry Basin, *F. Barkley 2568* (NDG). Sublette Co.: Green River Lakes, *A. Beetle 10534* (NDG); 16 km NE Pinedale, *S. J. Wolf 427* (ALTA). Teton Co.: Togowotee Pass, *S. J. Wolf 430; 432* (ALTA); Teton N. P., Hidden Falls, *S. J. Wolf 429* (ALTA); Jackson Hole, *J. and M. Reed 2250* (RM). Washakie Co.: 3 mi. E. Tensleep, *H. Fisser 784* (RM). Yellowstone N.P.: *W. Setchell s.n.* (UC); Mammoth Hot Springs, *F. Burglehaus 94* (MICH).

Arnica cordifolia is probably the most widespread *Arnica* in western North America, occupying fairly mesic habitats, in *Pinus-Pseudotsuga menziesii* or *Picea* forests throughout most montane areas of the region. In such areas as the foothills of Alberta, it forms extensive, nearly continuous populations for many kilometers. In the east *A. cordifolia* is restricted to only a few populations in *Betula-Acer* forests of Keweenaw Co., Michigan and Sibley Provincial Park, Ontario. *A. cordifolia* has also been recently collected in the Pasquia Hills, east of Saskatoon, Saskatchewan (*J. Rowe 983* CAN) and in Riding Mountain Provincial Park, Manitoba (*A. Lovaas 61-8* DAO).

In its typical woodland habitat, *Arnica cordifolia* displays little variability and is easily recognized by its large, solitary heads with broad rays and its cordate, dentate leaves. However, as Maguire (1943) noted, when it occurs in more exposed or disturbed habitats the leaves become smaller, narrower and lose their cordate bases; the pubescence becomes denser, harsher and more glandular; and the plants become smaller and more branched with several heads. This morphological form is characteristic of triploids and led to the suggestion that it may be the result of hybridization (Wolf, 1980). However, since recent flavonoid studies revealed no significant systematic differences among the chromsome races of *A. cordifolia,* including the triploids (Wolf, 1980), a hybrid origin can probably be ruled out.

Higher elevation forms of *Arnica cordifolia* tend to be much reduced, lack cordate leaf bases and have subentire leaves. This form has previously been recognized as *A. pumila* Rydb. or as *A. cordifolia* Hook. var. *pumila* (Rydb.) Maguire. However, when

such plants are transplanted to the greenhouse they revert to typical *A. cordifolia* (cf. *S. Wolf 306* ALTA). The high altitude form has often been confused with *A. nevadensis,* particularly in the mountains of Utah. However, the latter can be recognized by its narrower heads, oblanceolate phyllaries, less pubescent leaves and darker pappus with longer setae.

According to Maguire (1943), Drummond's explorations were largely in the vicinity of Jasper House, Alberta, along the Upper Athabasca River and at the headwaters of the North Saskatchewan River. Bird (1967) also concluded that most of Drummond's collections from the "Rocky Mountains" probably came from Jasper National Park. The type of *Arnica cordifolia* from "Alpine woods of the Rocky Mts.", was therefore probably collected in the front range of the Rocky Mountains, probably in Jasper National Park, Alberta. The type sheet consists of four specimens, the holotype collected by Drummond and three specimens collected by Douglas on the same expedition.

Maguire (1943) considered the rare *Arnica paniculata* A. Nelson a distinct species while noting it may be a hybrid between *A. cordifolia* and *A. parryi* A. Gray. Ediger and Barkley (1978) considered this taxon a hybrid and therefore did not give it taxonomic recognition. In fact, with the exception of its numerous heads and ovate leaves, *A. paniculata* differs very little from *A. cordifolia* as circumscribed in the present study. Additionally, a chromosome voucher of an *A. cordifolia* population with $2n$ = ca. 97 (*T. Mosquin and J. Gillett 5425* La Plata Co., Colorado; UBC) bears considerable resemblance to the type collection of *A. paniculata* (*L. N. Gooding 1974,* Carbon Co., Wyoming). It is very likely that *A. paniculata* represents an *A. cordifolia* with a high chromosome number and/or the product of introgression between the latter and some other taxon. It is therefore reduced to synonymy under *A. cordifolia.*

Arnica whitneyi of Keweenaw Co., Michigan was first described by Fernald (1935). It occurs as one large discontinuous population between Copper and Eagle Harbors (Straley, 1980). Recently it has also been located in Sibley Provincial Park, Ontario (*Garton 15164* CAN, *15486* MICH). Maguire (1943) noted that this taxon differed little from western populations of *A. cordifolia* but retained it as a subspecies of the latter because of its disjunct distribution. However, Ediger and Barkley (1978) did not give this taxon formal

taxonomic recognition. The facts that these eastern populations represent very typical *A. cordifolia,* share similar chromosome numbers (Wolf, 1980) and flavonoid chemistry (Wolf and Denford, 1983) with *A. cordifolia,* and that intervening populations of *A. cordifolia* in Saskatchewan and Manitoba also exist, support Ediger and Barkley's (1978) treatment. In the present study *A. whitneyi* is therefore reduced to synonymy under *A. cordifolia.*

3. **Arnica discoidea** Benth., Pl. Hartw. 319. 1849. TYPE: Monterey, California, *Hartweg 1805* (HOLOTYPE, K photo!; ISOTYPES, GH photo!, NY!).

Arnica parviflora A. Gray, Proc. Am. Acad. 7: 363. 1867. TYPE: Chaparral, Humboldt Co., California, Geol. Surv. Calif. 1867. *H. N. Bolander 6051* (HOLOTYPE, GH!; ISOTYPES, UC! K photo!, US!).

Arnica cordifolia Hook. var. *eradiata* A. Gray, Syn. Fl. N. Am. 1: 381. 1884. *Arnica discoidea* Benth. var. *eradiata* (A. Gray) Cronquist, Vasc. Pl. Pac. NW. 5: 49. 1955. TYPE: Hood River, Oregon, 1884, *Mrs. Barrett s.n.* (HOLOTYPE, GH!).

Arnica grayi A. Heller, Muhlenbergia 1: 5. 1900. TYPE: Hood River, Oregon, 1884, *Mrs. Barrett s.n.* (HOLOTYPE, GH!).

Arnica falconaria Greene, Ottawa Nat. 23: 215. 1910. TYPE: Falcon Valley, Washington, June 27, 1892, *W. N. Suksdorf 1617* (HOLOTYPE, US!; ISOTYPES, UC!, GH photo!, NY!).

Arnica alata Rydb., N. Am. Fl. 34: 342. 1927. *Arnica parviflora* A. Gray subsp. *alata* (Rydb.) Maguire, Brittonia 4: 455. 1943. *Arnica discoidea* Benth. var. *alata* (Rydb.) Cronquist, Contr. Dudley Herb. 5: 102. 1958. TYPE: Yosemite, California, 1865, *J. Torrey 258a* (HOLOTYPE, NY!).

Arnica sanhedrensis Rydb., N. Am. Fl. 34: 342. 1927. TYPE: Foothills of Mt. Sanhedren, Lake Co., California, *Heller 5985* (HOLOTYPE, NY!; ISOTYPES, POM!, UC!, US!).

Stems mostly simple to branched above, 15–60 cm tall, 2–5 mm diameter, villous and stipitate-glandular throughout; rhizomes giving rise to numerous basal rosettes and flowering stems, 2–5 mm thick, scales and old leaf bases crowded toward the summit. Cauline leaves 3–7 pairs, sometimes crowded toward stem base and often reduced above, ovate to broadly lanceolate, seldom subcordate, 2–12 cm long, 1–7 cm broad, glabrate to pilose and stipitate-glandular, serrate to coarsely dentate or crenate, rarely subentire; petioles narrow, 1.5–8.0 cm long, often broadly winged on upper reduced leaves; leaves of the innovations 4–10; similar to cauline leaves. Inflorescence a corymb of 3–10 (30) heads; peduncle 2–15 cm long, stipitate-glandular and densely pilose; heads discoid, the

marginal corollas sometimes ampliate, turbinate-campanulate, 12–22 mm high; involucral bracts 8–15, ovate-lanceolate to narrowly lanceolate, 8–13 mm long, 1–4 mm broad, densely pilose and stipitate-glandular, acute to acuminate. Florets 20–50, yellow, tubular, 8–11 mm long, stipitate-glandular and sparsely to densely villous; pappus white, barbellate (to subplumose). Achenes dark gray, 6–8 mm long, 1 mm broad, stipitate-glandular and hirsute with duplex hairs. Figure 5. Chromosome number $2n = 38, 57, 76$.

ECOLOGY AND DISTRIBUTION: Relatively uncommon in moderately dry *Quercus-Pinus* forests from Klickitat County in southern Washington, south sparingly in the Cascades through northern California, but more common in relatively exposed chaparral in the coast ranges of California south to Orange County. Figure 6. Elevational distribution ranges from near sea level to 1500 m. Flowers May–July.

REPRESENTATIVE SPECIMENS: **United States:** CALIFORNIA: Butte Co.: Jonesville, *E. Copeland* 400 (MICH, UC). Contra Costa Co.: Inner Black Hills, W. of "1970," *M. Bowerman 2173* (UC); Meridian Peak, *M. Bowerman 849* (UC). Del Norte Co.: Black Butte, *A. Eastwood 2137* (CAS); Smith River, above Rock Creek Lodge, *W. Cooke s.n.* (UC). Glenn Co.: Alder Springs, *M. Baker 10872* (UC). Humboldt Co.: Croghan Hole, *J. Tracy 19273* (UC); Bee Mt., *C. Quick 59-31* (CAS); Hoopa Mt., *Davy and Blasdale 5668* (UC); Trinity Summit, *J. Tracy 14154* (UC); *J. Tracy 18182* (UC); Horse Mt., *J. Tracy 17833* (UC); Briceland, *J. Tracy 6335* (CAS, UC); White Thorn Valley, *J. Tracy 5001* (UC). Lake Co.: Mt. Hull, *H. M. Hall 9564* (UC). Coff Mt., *H. M. Hall 9595* (UC); Ukiah, *H. Yates 3735* (UC); Elk Mt., *H. M. Hall 9587* (UC); Adam's Springs, *R. Hoover 5347* (NDG, UC); Eel River, *L. Benson 3726* (NDG). Marin Co.: Mt. Tamalpais, *A. Heller 8392* (UC); *K. Brandegee s.n.* (UC); *W. L. Jepson s.n.* (UC); *F. Boiletti s.n.* (NDG, UC); Blithdale Canyon, *J. Howell 26621* (CAS); Lagunitas, *H. M. Hall 8502* (UC). Mariposa Co.: Cathedral Rocks, *C. Sharsmith 2168* (UC); Sherlocks, *J. Congdon s.n.* (CAS); Yosemite Valley, *L. Abrams 4527* (UC); *H. M. Hall 8867* (UC); Vernal Falls, *H. M. Hall and E. B. Babcock 3443* (UC). Mendocino Co.: 5 mi. E. Point Arena, *L. Rose 39170* (UC); Point Arena, *A. Eastwood and J. Howell 6252* (CAS); Comptche, *H. Walker 342* (UC). Modoc Co.: John Henry Hill, *M. Manning 370* (UC). Monterey Co.: Pacific Grove, *A. Elmer 4402* (CAS, OSC, UC); Chews Ridge, S. Jonesburg, *L. Snyder 3774* (UC); Los Burros Creek, 15 mi. SW Jolon, *C. Hardham 7037* (OSC); Big Sur, *Y. Mexia s.n.* (CAS, UC); Point Lobos, *Helley s.n.* (CAS); Hanging Valley, Santa Lucia Mts., *D. Breedlove 36264* (CAS); Jolon, *C. Hardham 7037* (WTU). Napa Co.: Howell Mt., *J. Tracey 2224* (UC); White Sulphur Springs, St. Helena, *H. Chandler 7579* (UC); E. side of Mt. St. Helena, *R. Hoover 5014* (UC). Orange Co.: Santa Ana Mts., 4.8 mi. above gate on Silverado Canyon Truck Trail, *P. Raven 17751* (UC); Mojeska Springs, Santa Ana Mts., *W. Pequegnat s.n.* (WTU). Plumas Co.: S. E. Quincy, *C. Quick 41-60* (CAS); Taylorsville, *M. Glemens s.n.* (CAS). San Luis Obispo Co.: Ocean View Mine, N. of Cambria, *C. B. Hardman 6828* (CAS, UCSB);

Figure 5. *Arnica discoidea.*

Figure 6. Distribution of *Arnica discoidea*.

Pine Mt., Santa Lucia Mts., *R. Hoover 8018* (CAS). San Mateo Co.: Skyline Drive, *D. Demaree 9150* (NDG); Kings Mt. Rd., *D. Keck 1775* (CAS, OSC, WTU); Portola State Park, *J. Thomas 9558* (CAS). Santa Barbara Co.: Mudulee Lookout Trail from Big Pine Rd., *E. Blakley* 6056 (CAS); LaCumbre Peak, *D. Breedlove 3762* (CAS); *D. Breedlove 585* (CAS, UCSB); *S. J. Wolf 514* (ALTA). Santa Clara Co.: Loma Prieta, *W. Price s.n.* (UC); *P. Covel s.n.* (CAS); Mt. Hamilton, *R. Pendleton s.n.* (UC); summit Santa Cruz Mts., *R. Pendleton 394* (UC); Alma Soda Springs *A. A. Heller 7490* (UC); Mt. Hamilton, *H. Sharsmith 1051* (UC). Santa Cruz Co.: Loma Prieta Pk., *H. Mason s.n.* (UC); Eagle Rock, *R. Ferri 11114* (UC); Felton, *B. Schreiber 319* (UC); Boulder Creek, *T. Kearny s.n.* (CAS); Redwood Park, *S. Blake 11766* (WTU). Shasta Co.: Castle Rock, *H. Ripley and R. Barneby 9646* (CAS). Montgomery Creek, *E. Bethel s.n.* (CAS). Siskiyou Co.: Mt. Eddy, *Copeland s.n.* (CAS, MICH, NDG, UC, US); China Creek, S. Fork Salmon River, *I. Wiggins 13465* (UC); Mt. Shasta, *E. Palmer 2455* (UC); trail between Taylor and Cow Creeks, *G. Butler 322* (UC); McCloud, *A. Eastwood 1105* (CAS, UC); Castle Lake, *A. Eastwood 10719* (CAS). Sonoma Co.: Guernewood Park, *H. M. Hall s.n.* (UC); Dohrman Creek, N. E. Jensen's Ranch, *H. Mason 8063* (UC). Tehama Co.: 1.9 mi. above Whitlock Camp, *M. Baker and H. Wagon 12833* (UC); Fish Ridge, *F. Hoffman 3531* (UC). Trinity Co.: Morrison Gulch Trail, *E. Carter 1094* (CAS); Ripstein Campground *P. Munz s.n.* (CAS); 1.5 mi. above Peanut on Hwy. 36, *R. Ferris and L. Lorraine 11693* (UC); White Rock Ranger Station, N. of Yolla Bolly, *A. Alexander and L. Kellogg 5115* (UC); Coffee Creek Canyon, *J. T. Howell 1359* (GH, MICH); Dunsmuir Retreat, *H. M. Hall and E. B. Babcock 8537, 8539* (UC); Battle Creek, *J. T. Howell 13590* (CAS). Tuolumne Co.: Dodge Ridge, Pine Crest, *F. Hoffman 1764* (UC). Ventura Co.: Ocean View Trail, near Divide Peak, Santa Ynez Mts., *H. Pollar s.n.* (CAS).

NEVADA: Washoe Co.: Hunter Creek, *P. Kennedy 1869* (US).

OREGON: Curry Co.: Iron Mt., *W. Baker 5677* (UC); 3 mi. NE Brookings, *M. Peck 2803* (OSC); head of Lawson Creek, *J. Leach 2250* (ORE). Hood River Co.: base of Mt. Hood, *F. Lloyd s.n.* (NY); Bald Butte, *M. Armstrong 471* (NY); Hood River, *L. F. Henderson 452* (NY); Mt. Defiance Trail, Columbia Gorge, *L. Delting 7169* (CAS, ORE); Mt. Hood, near Tollgate, *Drake and Dickson s.n.* (WTU). Jackson Co.: Ashland, *M. Peck 2795* (OSC); *2395* (OSC). Josephine Co.: Noname Creek, SW of the Caves, *E. Applegate 11917* (CAS); Siskiyou National Forest, 5 mi E. Jct. 3941 and 3942, *M. Denton 2550* (WTU). Klamath Co.: Crater Lake, *A. Coonebe s.n.* (CAS); E. of Lake of the Woods, *E. Applegate 3799* (CAS); Crater Lake, *F. Colville and E. Applegate 332* (US); *F. Hummewell 7876* (GH). Wasco Co.: 4 mi. E. Bear Springs, *J. Thompson 4935* (CAS, WTU).

WASHINGTON: Klickitat Co.: Falcon Valley, *W. Suksdorf 7301* (CAS, NY, UC); *12047* (CAS, NY, UC, WTU); *1617* (GH, NY, UC, US).

Arnica discoidea is an extremely variable species and occurs in a variety of habitats from open chaparral to conifer forests from near sea level to 1500 m. As early as 1884 Gray recognized the similarity of this taxon to *A. cordifolia* and noted that "northwardly it seems to pass into *A. cordifolia.*" Indeed, in southerly portions of its range, *A. discoidea* is quite distinct and can easily be recognized by

its narrowly ovate leaves that are mostly crowded toward the base of the stem; broadly winged and reduced upper leaves; often numerous, narrower heads and frequently branched upper stem. However, northward it sometimes resembles little more than a rayless *A. cordifolia.* Further complicating its identification is the fact that ampliate marginal disc florets occur infrequently on some specimens of *A. discoidea* (e.g., *J. H. Thomas 4130* CAS and *H. M. Hall 9485* UC). When pressed, these florets resemble rays, causing some specimens to be erroneously identified as *A. cordifolia.* However, *A. discoidea* and *A. cordifolia* are distinct with respect to ecology, geographical distribution, flowering periods and a combination of several morphological features. *A. discoidea* occurs in hotter, drier, more exposed habitats at lower elevations west of the Sierras and Cascades and flowers 1–2 months later than *A. cordifolia.*

Based largely on leaf shape and geographical distribution, Maguire (1943) recognized four taxa within *Arnica discoidea sensu lato: A. grayi, A. discoidea sensu stricto, A. parviflora* ssp. *parviflora* and *A. parviflora* ssp. *alata.* Ediger and Barkely (1978) recognized the latter three taxa as varieties of *A. discoidea:* var. *discoidea,* var. *eradiata* (which included *A. grayi*) and var. *alata* respectively. However, since attempts to delimit these taxa produced no significant systematic correlations between morphology, chromosome number, geography or flavonoid chemistry (Wolf, 1981; Wolf and Denford, 1984b), *A. discoidea* is best treated as one highly polymorphic species with no infraspecific taxa.

4. **Arnica gracilis** Rydb., Bull. Torrey Bot. Club 24: 297. *Arnica latifolia* Bong. var. *gracilis* (Rydb.) Cronquist, Vasc. P. Pac. NW 5: 51. 1955. TYPE: Spanish Peaks (Madison Range, Montana). 6000 ft., July 14, 1896, *J. H. Flodman 901* (HOLOTYPE, NY!; ISOTYPES, NY!, US!).

Arnica columbiana A. Nelson, Bot. Gaz. 30: 200. TYPE: Columbia Falls, Montana, 1894, *J. J. Kennedy 24* (HOLOTYPE, MONT!).

Arnica multiflora Greene, Pittonia 4: 162. 1900. TYPE: Lake Pend d'Oreille, Idaho, June, 1891, *J. B. Leiberg 234* (HOLOTYPE, NDG!).

Arnica lactucina Greene, Ottawa Nat. 23: 214. 1919. TYPE: Hamilton Mt., Banff, Alberta, 5,800 ft., July 24, 1899, *W. C. McCalla 2014* (HOLOTYPE, US!, ISOTYPES, CU!, NY!).

Arnica betonicaefolia Greene var. *gracilis* (Rydb.) M. E. Jones, Bull. Univ. Mont. Biol. 15: 48. 1910.

Arnica puberula Rydb., Fl. Rocky Mts. 979. 1917. TYPE: Head of Lake Louise, Alberta, July 22, 1904, *J. Macoun (Geol. Surv. Can. No. 65523)* (HOLOTYPE, NY!; ISOTYPES, CAN!, US!).

Stems 3-several branched above, often in dense clumps of 5–10, 10–30 cm high, 1 mm diameter, mostly short stipitate-glandular above, becoming glabrate below; rhizomes 1–2 mm broad, covered with brown scales and old leaf bases; cauline leaves 2–3 pairs, ovate to ovate-lanceolate, 2–6 cm long, 1–3 cm broad, stipitate-glandular above, glandular below, acute, irregularly serrate to subentire; petioles narrow to broadly winged, 1–6 cm long; upper pair of leaves often reduced and connate-perfoliate; leaves of the innovations 5–14, similar to cauline leaves but narrowly petiolate. Inflorescence a corymb of (3)5–15 heads or rarely a single head; peduncle 1.5–7 cm long, stipitate-glandular, heads radiate, turbinate-campanulate, 10–15 mm high; involucral bracts 10–16, ovate-lanceolate, 6–12 mm long, 1–2 mm broad, short stipitate-glandular, acute to acuminate. Ray florets 5–12, yellow, linear-elliptic, 10–20 mm long, 3–5 mm broad, 3-dentate; disc florets 10–25, yellow, tubular, 4–6 mm long, short stipitate-glandular; pappus of both ray and disc florets white, barbellate. Achenes black, 4.5–7 mm long, 1 mm broad, short stipitate-glandular with few duplex hairs. Figure 7. Chromosome number $2n = 57, 76$.

ECOLOGY AND DISTRIBUTION: Dry, exposed, rocky, alpine slopes or occasionally sub-alpine meadows in the Rocky Mountains of Alberta, south irregularly to southern Wyoming, the Uintah Mountains, of Utah, Wallowa Mountains of Oregon and infrequently in the Cascade Mountains of southern British Columbia south to Mt. Rainier, Washington. Also known from Vancouver Island. Figure 8. Elevational distribution from 1200–2500 m. Flowers July–August.

REPRESENTATIVE SPECIMENS: **Canada:** ALBERTA: Peyto Lake, *W. Weber 2445* (GH, UBC, UC); Bertha Lake, *A. Breitung 16228* (UC); Lake Louise Trail, *Malte and Watson 164A* (UC); Lake Louise, *Butters and Holway 336* (GH, US); Tonquin Valley, *Beamish and Pindar-Moss 700151* (UC); Maligne Lake, *S. Brown 1287* (GH, WTU): Lake Louise, *S. Brown 703* (GH); Bertha Lake, *Gadd and Nagy 3573* (CAN); Bow Pass, *A. E. Porsild and A. J. Breitung 16208* (CAN); Mt. Bertha, *Blais and Nagy 1555* (CAN); Mt. Temple Ski Lodge *A. E. Porsild and A. J. Breitung 12722* (CAN); Whitehorse Creek, *M. Dumais 5248* (ALTA, CAN); Sunshine Ski Lodge, *A. E. Porsild and J. Lid 19570* (CAN); Mt. Eisenhower, *A. E. Porsild and A. J. Breitung 15807* (CAN); Goat Mt., *J. Macoun 96043* (CAN); Sofa Mt., *A. J. Breitung 17178* (DAO); Chief Mt., *A. Breitung 15867* (DAO); Sofa Mt., *P. Kuchar 2730* (ALTA);

Figure 7. *Arnica gracilis.*

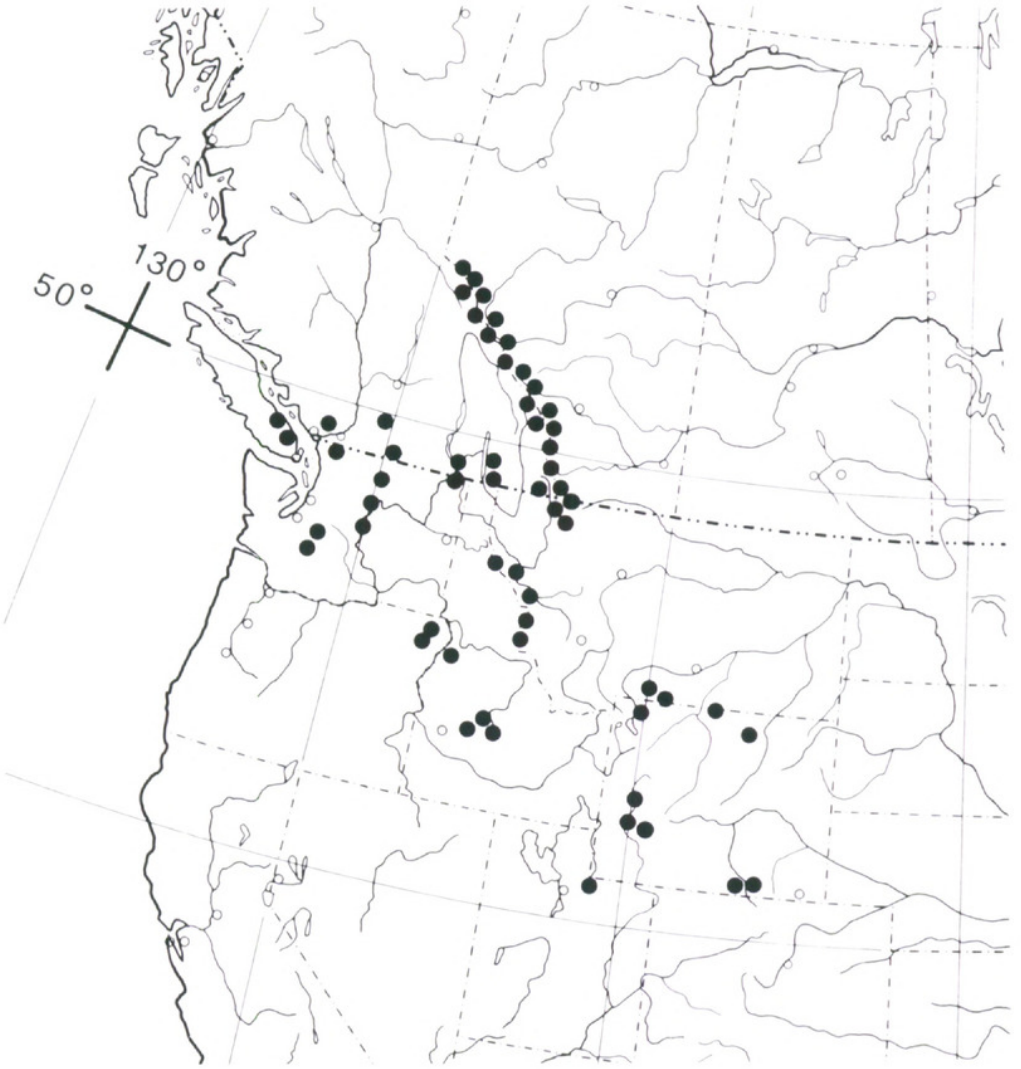

Figure 8. Distribution of *Arnica gracilis*.

Bertha Lake, *A. J. Breitung 16228* (ALTA); Maligne Lake, *H. Raup 2716* (ALTA); Red Rock Canyon, *E. H. Moss 374* (ALTA); Moraine Lake, *W. McCalla 4538* (ALTA); Lake Louise, *W. McCalla 7151* (ALTA); mi. 105, Banff-Jasper Hwy., *W. McCalla 7122* (ALTA).

BRITISH COLUMBIA: Ainsworth, *T. McCabe 5990* (UC); Kinbasket Lake, *T., McCabe 6275* (UC); between Burton and Fauquier, *T. McCabe 6629* (UC); trail, *J. Macoun 64977* (ND); Kicking Horse Valley, *S. Brown 298* (US); Mark Creek Falls, Kimberley, *F. Fedor 80* (UBC); Mt. Matier, *Pinder-Moss and Schofield 894* (UBC); Sage Creek Falls, *Bell and Davidson 359* (UBC); Commerce Mt., *Bell and Davidson 525* (UBC); Little Diamond Head, Garibaldi Park, *E. Peterson s.n.* (UBC); Boulder Creek, *F. Fedor 100* (UBC); Vancouver Island, Mt. Arrowsmith, *C. Rosendahl 1644* (GH); Mt. Assiniboine, *A. E. Porsild 18376* (CAN); Lake Agnes, *J. Macoun 14757* (CAN); Mt. Forget-Me-Not, *J. Macoun 22829* (CAN); Elk River, S. Elko, *J.*

Eastham 15629 (DAO); Flathead Summit, *Bell and Davidson 972* (DAO); Emerald Lake, Yoho Nat. Park, *W. McCalla 7032* (ALTA, DAO); Tuktakamin Mt., *J. Grant 65-5* (DAO); Vermillion Pass, *W. McCalla 2014* (ALTA).

United States: IDAHO: Clark Co.: West Camas Creek, 10 mi. above Kilgore, *A. Cronquist 1385* (ND, NY). Custer Co.: 3.5 mi. SW Stanley Lake, *Hitchcock and Muhlick 9630* (CAS, UC); 11 mi. NE Custer, *W. Baker 10790* (OSC); Seafoam, *Macbride and Payson 3653* (RM, US); McKay, *Nelson and Macbride 1497* (RM). Elmore Co.: 10 mi. W. Atlanta, *J. and C. Christ 19463* (OSC). Valley Co.: E. side Big Payette Lake, *P. Raven 18517* (CAS).

MONTANA: Carbon Co.: Rock Creek, 23 mi. SW Red Lodge, *A. Cronquist 8102* (CAN, CAS, MICH, NY, OSC, WTU). Gallatin Co.: Spanish Basin, *P. A. Rydberg and E. Bessey 5229* (US). Glacier Co.: Glacier Nat'l. Park. *B. R. and C. Maguire 15350* (UC). Lincoln Co.: Leigh Lake, Cabinet Mts., *D. Woodland 882* (CAS). Missoula Co.: Holland Creek, Holland Lake, *A. Cronquist* (CAS, UC); 5 mi. above Bonner, *Hitchcock and Muhlick 11432* (CAS, OSC, UC). Powell Co.: Shaw Creek R. S., Flathead N. F., *C. L. Hitchcock 18436* (WTU). Ravalli Co.: 4 mi. W. campground, Selway Bitterroot Wilderness, *D. Woodland 395* (CAS). Sweetgrass Co.: 6 mi. E. Box Canyon, Boulder River, *C. L. Hitchcock 16439* (UC, WTU).

OREGON: Wallowa Co.: Hurricane Creek, *M. Peck 22631* (UC); Boy Scout Ridge, *G. Mason 5981* (ORE, OSC).

UTAH: Summit Co.: 4 mi. N. Hayden Pass, *H. Bennett 8431* (CAS).

WASHINGTON: Chelan Co.: Mt. Stuart, *A. Kruckeburg 2638* (CAN, UC); Hwy. 2, 6 mi. NW Leavenworth, *W. Dress 4281* (UC). Kittitas Co.: Cle Elum River, *J. Thompson 10418* (CAS, CAN, WTU). Okanogan Co.: Angels Pass, *J. Thompson* (CAS, UC, US, WTU). Pend Oreille Co.: "Z" Canyon, 12 mi. N. Metaline Falls, *C. L. Hitchcock 2923* (UC, WTU). Pierce Co.: Mt. Rainier, *H. Leschke s.n.* (CAS). Whatcom Co.: Mt. Hermann, *J. Thompson 5352* (GH).

WYOMING: Albany Co.: Medicine Bow Mt., *A. and R. Nelson s.n.* (RM); Laramie Creek, *A. Nelson 7568* (RM). Carbon Co.: Chimneys of Pedro Mts., *L. Goodding 108* (RM, UC). Fremont Co.: Gannett Peak, *F. Jozwik 404* (RM, UC); Snow Lake, *R. Scott 9576* (RM). Johnson Co.: Headwaters of Clear Creek and Crazy Woman River, *F. Tweedy 3015* (RM). Park Co.: Olson's Meadow, *E. and D. Pearson 172* (RM). Sheridan Co.: Big Horn Mts., *J. Williams s.n.* (RM), *A. Nelson 8501* (RM). Sublette Co.: Fremont Lake, *E. and L. Payson 2834* (OSC, RM, UC, US); canyon above New Fork Lakes, *E. and L. Payson 4452* (GH); Horseshoe Lake, SE Pinedale, *C. L. Porter and B. Miller* 6069 (RM).

Arnica gracilis occurs on fairly exposed, rocky, alpine slopes or open sub-alpine meadows largely in the central Rocky Mountains. The close relationship of this taxon to *A. latifolia* has long been noted. Indeed, in his original description of *A. gracilis,* Rydberg (1897) noted it resembles a depauperate *A. latifolia.* Maguire (1943) considered *A. gracilis* a distinct species but called it "... a loose entity which is maintained as distinct from *A. latifolia* with some difficulty...". Cronquist (1955) and later Ediger and Barkely (1978) treated *A. gracilis* as a variety of *A. latifolia,* while Wolf and Denford (1984a) recently re-elevated it to specific status.

This confusion with *Arnica latifolia* is not surprising since Wolf and Denford (1984a) have demonstrated that *A. gracilis* is a hybrid between *A. latifolia* and *A. cordifolia.* Although it is somewhat intermediate betwen these two species, *A. gracilis* has several distinctive features of its own. These include a much more branched habit; narrower leaves; more numerous and smaller heads with a reduced number of disc florets; black, glandular achenes; and the dry, alpine habitat. *A. gracilis* is relatively common, is morphologically distinguishable from its two parents and is an autonomous apomict that maintains itself quite vigorously in nature. It "behaves as a species" (Davis and Heywood, 1963) and is therefore recognized as such in the present study.

5. **Arnica latifolia** Bong., Mem. Acad. St. Petersb. VI 2: 147. 1832. *Arnica latifolia α genuina* Herder, Bull. Soc. Nat. Mosc. 40: 424. 1867. TYPE: Sitka, Alaska, *Mertens s.n.* (LECTOTYPE by Maguire, LE photo!).

Arnica menziesii Hook., Fl. Bor. Am. 1: 331. 1834. *Arnica latifolia β angustifolia* Herder, Bull. Soc. Nat. Mosc. 40: 424. 1867. TYPE: Northwest coast of America, *Menzies s.n.* (HOLOTYPE, K photo!).

Arnica betonicaefolia Greene, Pittonia 4: 163. 1900. TYPE: Mt. Steele, Olympic Mountains, Washington, 6000–7000 ft., Aug., 1895, *C. V. Piper 2002* (HOLOTYPE, NDG!; ISOTYPE, GH!).

Arnica teucriifolia Greene, Pittonia 4: 164. 1900. *Arnica latifolia* Bong. var. *teucriifolia* (Greene) L. Williams, Leafl. West. Bot. 1: 171. 1935. TYPE: Grassy mountain slopes, divide between St. Joe and Clear Water River, alt. 1820 m, region of the Coeur d'Alene Mountains, Idaho, July 10, 1895, *J. B. Leiberg 1229* (HOLOTYPE, US!; ISOTYPES, MO!, NY!, POM!, UC!).

Arnica ovalifolia Greene, Pittonia 4: 168. 1900. TYPE: Big Horn Mountains, Wyoming, 9000–10000 ft., July 17, 1890, *Blankinship s.n.* (HOLOTYPE, NDG!).

Arnica ventorum Greene, Pittonia 4: 173. 1900. TYPE: Union Pass, Wind River Mountains, Wyoming, Aug. 11, 1894, *A. Nelson 836* (HOLOTYPE, NDG!; ISOTYPES, MO!, NY!, RM!, WS!).

Arnica grandifolia Greene, Pittonia 4: 173. 1900. TYPE: Bridger Pass, Montana, July 28, 1896, *J. H. Flodman 896* (HOLOTYPE, NDG!; ISOTYPES, MO!, US!).

Arnica platyphylla A. Nelson, Bot. Gaz. 31: 407. 1901. TYPE: moist dark fir forests, Cascade Mts., Foothills, Hood River, Oregon, July 18, 1896. *L. F. Henderson s.n.* (LECTOTYPE by Maguire, RM!).

Arnica laevigata Greene, Ottawa Nat. 15: 279. 1902. TYPE: by springs in woods, Chilliwack Valley, B.C., alt. 3000 ft., Aug. 5, 1901, *J. M. Macoun (Geol. Surv. Can. No. 26926)* (HOLOTYPE, NDG!; ISOTYPES, CAN!, NY!).

Arnica aprica Greene, Ottawa Nat. 15: 280. 1902. TYPE: open ground along streamlets, Chilliwack Valley, B. C., alt. 3500 ft., July 10, 1901, *J. M. Macoun (Geol. Surv. Can. No. 26284)* (HOLOTYPE, NDG, photo UC!; ISOTYPES, CAN!, NO!, NY!). The holotype is listed at NDG but has not been located by the staff.

Arnica jonesii Rydb., Fl. Rocky Mts., 979. 1917. TYPE: Alta, Wasatch Mountains, Utah, July 31, 1879, *M. E. Jones 1119* (HOLOTYPE, NY!; ISOTYPES, NY!, POM!, UTC!).

Arnica eriopoda Gandoger, Bull. Soc. Bot. Fr. 65: 38. 1918. TYPE: Cascade Mountains, Oregon, July 27, 1902, *W. C. Cusick 2914* (HOLOTYPE, US photo!; ISOTYPES, MO!, NY!, POM!, UC!).

Arnica aphanactis Piper, Proc. Biol. Soc. Wash. 33: 105. 1920. TYPE: Mt. Baker, Washington, 1915, *G. W. Turesson s.n.* (HOLOTYPE, US!).

Arnica flodmanii Rydb., N. Am. Fl. 34: 334. TYPE: Spanish Peaks, Madison Range, Montana, July 14, 1896, *J. H. Flodman 898* (HOLOTYPE, NY!; ISOTYPES, MO!, NY!, US!).

Arnica glabrata Rydb., N. Am. Fl. 34: 335. TYPE: Crater Lake, Oregon, August 1898, *Austin and Bruce 1627* (HOLOTYPE, NY!).

Arnica paucibracteata Rydb., N. Am. Fl. 34: 336. 1927. TYPE: Medicine Bow Mountains, Wyoming, Aug. 3, 1900, *A. Nelson 7941* (HOLOTYPE, NY!; ISOTYPES, MO!, POM!, RM!, US!).

Arnica oligolepis Rydb., N. Am. Fl. 34: 336. 1927. TYPE: Hazelton, Skeena River, B. C., June 23, 1917, *J. M. Macoun (Geol. Surv. Can. No. 96048)* (HOLOTYPE, NY!; ISOTYPE, CAN!).

Arnica leptocaulis Rydb., N. Am. Fl. 34: 336. 1927. TYPE: Mt. Mark, Vancouver Island, B. C., July 25, 1887, *J. M. Macoun s.n.* (HOLOTYPE, NY!; ISOTYPES, CAN!, US!).

Arnica membranacea Rydb., N. Am. Fl. 34: 338. 1927. TYPE: Wimmer, Jackson Co., Oregon, June 13, 1892, *E. W. Hammond 231* (HOLOTYPE, NY!; ISOTYPES, US!, WS!).

Stems simple, sometimes sparsely branched above, 10–50 cm high, 2–3 mm diameter, glabrate to villous throughout; rhizomes 1–3 mm thick, giving rise to several basal rosettes and flowering stems, rhizomes with several thin brown scales, frequently covered with old leaf bases at the summit. Cauline leaves 2–4(6) pairs, mostly sessile to sub-sessile, the lower rarely petiolate, ovate to elliptic-lanceolate, 2–10 cm long, 1–6 cm broad, glabrous to very sparsely villous, obtuse to acute, serrate to dentate; lower leaves sometimes reduced and short-petiolate, the petioles 5–15 mm long, broadly winged; leaves of the innovations 2–10, similar to cauline leaves, petiolate, the petioles 2–10 cm long. Inflorescence usually a single head or corymb of 3–5(9) heads; peduncle 3–25 cm long, glabrate to sparsely villous above; heads radiate, narrowly turbinate, 8–20 mm high; involucral bracts 8–20, lanceolate to oblanceolate, 8–15 mm long, 1–3 mm broad, sparsely villous and glandular, acute to acuminate. Ray florets 8–15, yellow, oblong-linear, 10–25 mm long, 2–6 mm broad, 3-dentate; disc florets 20–90, yellow, tubular, 6–10 mm long, sparsely villous; pappus of both ray and disc florets white, barbellate. Achenes dark brown, 5–9 mm long, 1 mm broad,

sparsely short stipitate-glandular with few duplex hairs. Figure 9. Chromosome number $2n = 38, 76$.

ECOLOGY AND DISTRIBUTION: Common in relatively moist, montane *Picea-Abies* forests, or more commonly sub-alpine meadows from southern interior and coastal Alaska south along the coast and through the Cascades to northern California, and south in the Rocky Mountains from the Yukon through southern Colorado. Also common on Vancouver Island and the Queen Charlotte Islands. Figure 10. Elevational distribution from 500–3300 m. Flowers July–August.

REPRESENTATIVE SPECIMENS: **Canada:** ALBERTA: Lake Louise, *W. Setchell s.n.* (UC); Banff-Jasper Hwy., *W. A. Weber 2490* (UC); Banff, *H. Davis s.n.* (ND); Mt. Edith Cavell, *T. McCabe 8355* (UC); Sheep Mt., *J. Macoun s.n.* (MICH); Vermillion Pass, *R. Ogilvie s.n.* (UBC); Castlemont, *M. Malte and W. Watson 488* (CAN); Mt. Temple, *A. E. Porsild and A. J. Breitung 13753* (CAN); Bow River Pass, *A. E. Porsild and A. J. Breitung 14929* (CAN); tower, Waterton Nat. Park, *W. Blais and J. Nagey 1639* (CAN); Snowshoe Cabin, Waterton Nat. Park, *G. Armstrong and J. Nagey 4554* (CAN); Crandell Lake, *G. Armstrong and J. Nagey 3874* (CAN); Cameron Lake, *G. Armstrong and J. Nagey 4094* (CAN); Crows Nest Lake, *Dawson 14756* (CAN); Red Rock Canyon, *F. Sudol 43* (DAO), Mt. Rowe, *A. J. Breitung 16979* (DAO); Bow Pass, *W. McCalla 6771* (ALTA); Lake Agness, *W. McCalla 3730* (ALTA); Bald Hills, *P. Kuchar 521* (ALTA); Marmot Mt., *W. McCalla 3105* (ALTA).

BRITISH COLUMBIA: E. end Summit Lake, *Calder and Saville 10015* (UC); Mt. Fougner at Bella Coola, *Calder and Saville 20373B* (UC); Khutze Inlet, *T. McCabe 3480* (UC); Harrison Creek, 20 mi. N. Takla Landing, *T. McCabe* (UC); Nine Mile Mt., *T. McCabe 8181* (UC); Mt. Revelstoke, *T. McCabe 5392* (UC); Apex Mt., *R. Bowerman s.n.* (UC); Green Mt., near Haylmore, *J. and E. Thompson 691* (MICH); Mt. Selwyn, *H. Raup and E. Abbe 4164* (CAS); Emerald Lake, *C. Shaw 993* (US); Ft. St. James, *Calder and Saville 13720* (DAO, US); Dam Mt., *W. Taylor 5993* (UBC); Grouse Mt., *V. Krajina s.n.* (UBS); 44 mi. NNW Dease Lake, *S. MacDonald 511* (CAN, UBC); 12 mi. NE Smithers, *V. Krajina et al s.n.* (UBC); Goodchap Mt., *D. Martin s.n.* (UBC); Gold Fish Lake, *A. Szczawinski 174* (UBC); Duckling Creek, Germansen Landing, *G. Noel 158* (UBC); Mt. Semour, *V. Krajina 333* (UBC); Beatton River, *H. M. Raup and D. Correll 10066* (GH); Glacier Nat. Park, *E. Haber 1508* (CAN); mi. 85 Haines Rd., *C. Clarke 442* (CAN); White Pass, *M. Malte 364* (CAN); Tunjony Lake, *R. Pilfrey 21* (DAO); Yanks Peak, *Calder et al 18083* (DAO); Alpine Mt., 12 mi. NNE Nelson, *Calder and Saville 11129* (DAO); Red Rose Mine, *Calder and Saville 15190* (DAO); Mt. McLean at Lillooet, *Calder and Saville 15505* (DAO); 75 mi. S. Haines Jct., *Calder and Kukkonen 28154* (DAO); lake in Coast Range, 58°41′N, 133°04′W, *R. Pilfrey 79* (DAO). Queen Charlotte Islands: 20 mi. S. Morseby Logging Camp, *Calder et al 23046* (CAS, DAO, OSC, UBC, UC); Lake Takakia, *Calder and R. Taylor 36296* (DAO). Vancouver Island: Green Mt., *V. Krajina et al 5004* (UBC); Mt. Arrowsmith, *G. Allen s.n.* (UBC); Shaw Creek, *W. Spreadborough 96037* (CAN); Moat Lake, *J. Underhill 327* (DAO); Crest Lake, *A. Young and W. Hubbard 580* (DAO).

Figure 9. *Arnica latifolia.*

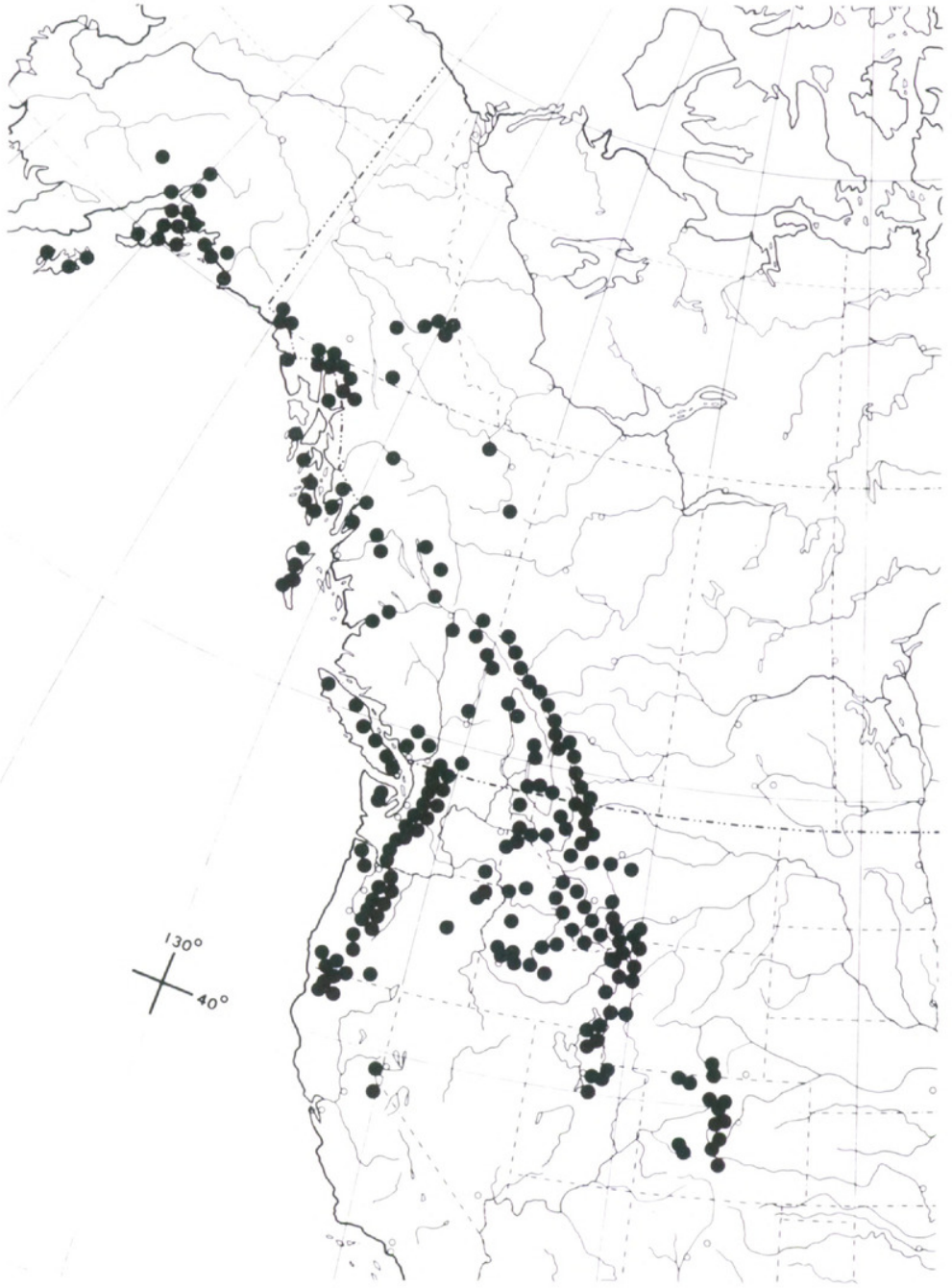

Figure 10. Distribution of *Arnica latifolia*.

NORTHWEST TERRITORIES: 62°46′N, 129°1′W, *L. Allison 29* (DAO).

YUKON TERRITORY: White Pass, *A. Eastwood 936* (UC); mi. 268, Canol Rd., *A. E. Porsild and A. J. Breitung 11374* (CAN, UC, US); mi 95, Canol Rd., *A. E. Porsild and A. J. Breitung 10228* (CAN, GH, UC, US, WTU); Upper Hyland Lake, *Calder and Kukkonen 27809* (CAS, DAO, GH); Kluane National Park, Alsek River, *G. and G. Douglas 8953* (DAO); Cassiar Mts., *W. Poole 49* (DAO); mt. 4 mi. W. Upper Hyland Lake, *Calder and Kukkonen 27909* (DAO); 62°11′N, 129°17′W, *L. Allison 40* (DAO).

United States: ALASKA: Hatcher Pass, *S. J. Wolf 503* (ALTA); Craig, *I. Norberg s.n.* (UC, US); Yakutat Bay, *F. Funston 79* (CAN, ND); Olga Bay, Kodiak Island, *S. Blake 553* (ND); Deer Mt., *F. Went 80* (UC); Yes Bay, *T. Howell 1634* (UC); Harris Peak, Prince of Wales Island, *D. Jaques 1569* (OSC); Indian River, Sitka, *L. Smith s.n.* (OSC); Duchess Mine, Latouche Island, *H. Shacklette 4704* (MICH); Cairn Ridge, near Juneau, *H. Shacklette* (MICH); Curry Lookout, *L. Jordal 2555* (MICH); Mt. Roberts, Juneau, *M. Williams 1392* (OSC); Kenai Lake, *J. Calder 6089* (CAS, DAO); Kuiu Island, *E. Walker 774* (CAS, US); 3 St's. Bay, Kodiak Island, *W. Eyerdam 602* (CAS, US); Eyak Lake, Cordova, *M. Hanna s.n.* (CAS); Skagway, *A. Eastwood 818* (CAS, US); Haines, *E. Scheuber s.n.* (US); Sitka, *C. Piper 4245* (US); Stikine Glacier, *W. Cooper 72* (US); Mt. Marathon, *J. Calder 5899* (UBC); Juneau, *E. Scamman 1123* (GH); Mt. Roberts, *A. and R. Nelson 4440* (GH); Mt. Crillion, *R. Bates 160* (GH); Barren Island, *I. Gabrielson s.n.* (GH); Alaska Range, 62°40′N, 152°30′W. *L. Viereck 5259* (CAN); Ketchican, *J. Anderson 2A691* (CAN); Orca, *I. Norbert s.n.* (CAN); Burma Rd., mi. 74, Richardson Hwy., *L. Spetzman 3319* (CAN); Palmer Creek Valley, SE Hope, *J. Calder 6233A* (DAO); Chugach Mts., Anchorage, *Dutilly et al 21143* (DAO).

CALIFORNIA: El Dorado Co.: S. side Echo Lake, *A. Heller 12544* (UC); Sugar Bowl Mt., *L. Kildale s.n.* (UC). Nevada Co.: Donner Pass, *A. Heller 7029* (MICH). Trinity Co.: Salmon Mts., Union Creek, *H. M. Hall 9648* (UC). Siskiyou Co.: Jackson Lake, *A. Alexander and L. Kellogg 183* (UC); Bolan Lake, *C. L. Hitchcock and J. Martin 5233* (UC), *S. J. Wolf 465* (ALTA); Hancock Lake Trail, Marble Mt. Wilderness, *F. Oettinger 460* (UC). Caribou Basin, Trinity Alps, *J. Howell* 13380 (CAS); 8.3 mi. from Etna on road to Sayer's Bar, *E. Balls 13942* (WTU), *S. J. Wolf 467* (ALTA).

COLORADO: Chaffee Co.: Monanos Creek, *I. Clokey 3500* (RM, UC). Clear Creek Co.: Loveland Pass, *S. J. Wolf 416* (ALTA). Gunnison Co.: Queen's Basin, *J. Langenheim 3908* (RM, UC). Lake Co.: Lake Creek, *I. Clokey 3515* (UC). Larimer Co.: Rocky Mt. National Park, Rainbow Curve Trail, *U. Waterfall 14958* (UC); Lock Vale, Estes Park, *I. Clokey 3962* (CAN, MICH, UC); Cameron Pass, *G. Osterhout 3795* (RM); Lake Helene Trail, Rocky Mt. National Park, *R. Ashton 70-g-7* (RM). Routt Co.: Hahn's Peak, *W. Weber 6929* (RM, WTU).

IDAHO: Bear Lake Co.: Bloomington Lake, *R. Davis 1613* (UC). Benewah Co.: Bald Mt., *W. Baker 13388* (OSC). Blaine Co.: 5 mi. from Alturas Lake, *C. L. Hitchcock and C. V. Muhlick 10534* (UC). Boise Co.: Jackson Peak, *C. L. Hitchcock and C. V. Muhlick 10026* (CAN, UC). Bonner Co.: Queen Mt., *W. Eggleston 9770* (US). Bonneville Co.: *E. Payson and G. Armstrong 3511* (RM). Custer Co.: 1 mi. E. Castle Peak, *C. L. Hitchcock and C. V. Muhlick 10913* (UC); Mt. Mogg, *C. L. Hitchcock and C. V. Muhlick 11236* (UC, WTU); 10 mi. S. Atlanta, *C. L. Hitchcock*

and C. V. Muhlick 10247 (RM, UC, WTU). Franklin Co.: 2 mi. SW Franklin Basin R. S., *B. Maguire 21643* (CAN, UC). Fremont Co.: Ponds Lodge, Targhee N. F., *W. Baker 9831* (OSC). Idaho Co.: Lolo Trail, 65 mi. E. Pierce, *C. L. Hitchcock and C. V. Muhlick 21921* (UC); Pilot Knob, *W. Elwood 36* (UC); Burnt Knob Lookout, *W. Baker 12638* (OSC). Lemhi Co.: 9 km S. Lost Trail Pass, *S. J. Wolf 488* (ALTA). Shoshone Co.: St. Maries River, *G. Wilson 103* (UC); 14 mi. E. Clarkia, *W. Baker 16208* (WTU). Valley Co.: Lick Creek Summit, *S. J. Wolf 357* (ALTA); Gold Fork Lookout, *J. Thompson 13745* (MICH, UC); Upper Payette Lake, *W. Baker 10357* (OSC).

MONTANA: Beaverhead Co.: Pintlar Falls, *C. L. Hitchcock and C. V. Muhlick 12784* (UC); Lake Waukena, *C. L. Hitchcock and C. V. Muhlick 13105* (OSC). Deerlodge Co.: Storm Lake, *C. L. Hitchcock and C. V. Muhlick 14830* (RM); Storm Lake Rd., *S. J. Wolf 435* (ALTA). Fergus Co.: Big Snowy Mts., 31 mi. SW Lewiston, *G. and F. Ownby 2417* (RM, UC). Flathead Co.: Bowman Lake, *R. Turley 212* (UC). Gallatin Co.: 8 mi. E. Eldridge, *C. L. Hitchcock and C. V. Muhlick 15149* (UC). Glacier Co.: Glacier National Park, *N. Carlson s.n.* (UC). Granite Co.: Burnt Fork Trail, *C. L. Hitchcock and C. V. Muhlick 14502* (WTU). Lake Co.: 10 mi. NE Polson, *J. Thomas 11051* (CAS). Lewis and Clark Co.: 25 mi. NW Agusta, *C. L. Hitchcock 17997* (RM, UC). Lincoln Co.: Mt. Marston Rd., *S. J. Wolf and P. and D. Wolf-Thompson 344* (ALTA) Madison Co.: Upper Brandon Lake, *C. L. Hitchcock 17045* (RM). Missoula Co.: 2 mi. E. Holland Lake, *C. L. Hitchcock 18357* (UC, WTU). Park Co.: 5 mi. E. Cooke City, *J. Witt 1755* (WTU). Powell Co.: 3 mi. W. Big Salmon Lake, *C. L. Hitchcock 17162* (WTU). Ravalli Co.: St. Mary's Creek, *C. L. Hitchcock and C. V. Muhlick* (CAN, UC). Stillwater Co.: Mt. Haystack, *C. L. Hitchcock and C. V. Muhlick 13429* (CAN, OSC, UC, WTU). Sweetgrass Co.: Crazy Mts., Big Timber Creek, *C. L. Hitchcock and C. V. Muhlick 13288* (OSC, UC).

OREGON: Clackamas Co.: SW. slope Mt. Hood, *H. and J. Thomas 248* (UC). Clatsop Co.: Saddle Mt., *S. J. Wolf 379* (ALTA); Onion Peak, *L. Heckard 1606* (UC), *K. Chambers 3149* (CAS, OSC, WTU); Sugarloaf Mt., *K. Chambers 3764* (OSC, WTU). Curry Co.: Iron Mt., *S. J. Wolf 457* (ALTA); above Agness, *E. Applegate 7153* (CAS). Douglas Co.: Black Rock Lookout, *D. Overlander s.n. 1944* (OSC). Grant Co.: Strawberry Mt., *W. Cusick 3565* (WTU). Harney Co.: Stein's Mt., *P. Train s.n.* (OSC). Hood River Co.: Mt. Hood, *P. Munz 14461* (UC). Jackson Co: Mt. Ashland, *M. Peck 2934* (OSC). Jefferson Co.: *J. Johnson 462* (OSC). Josephine Co.: Big Meadow, SE Oregon Caves, *E. Applegate 11243* (UC); Bolan Lake, *J. Thompson 12510* (UC, WTU); Sexton Mt., *L. Savage s.n.* (UC). Lane Co.: Fairview Mt., *L. Constance s.n.* (UC); Horse Pasture Mt., *M. Peck 23841* (OSC); Fairview Mt., *W. Baker 5565* (OSC, WTU). Linn Co.: Breitenbush, *M. Peck 18718* (UC); Mt. Jefferson, *M. Peck 9109* (OSC); Monument Peak, *A. Aller 812* (OSC). Marion Co.: 1 mi. E. Breitenbush, *M. Peck 18718* (OSC); House Mt., *M. Peck* (OSC). Union Co.: Anthony Creek, Blue Mts., *W. Cusick 3820* (WTU). Wasco Co.: 5 mi. W. Mosier, *J. Thompson 4224* (WTU). Washington Co.: Tillamook Burn, N. of Wilson River Hwy., *K. Chambers 4052* (OSC).

UTAH: Cache Co.: Tony Lake, *A. Holmgren and C. Biddulph 8172* (UC); Mt. Naomi, *B. Maguire et al 14154* (GH, UC, US). Duchesne Co.: Blind Stream Rd., NW Hanna, *S. J. Wolf 397* (ALTA). Salt Lake Co.: Big Cottonwood Canyon, *W. Cooper 329* (RM); *A. Garrett 1509* (RM). Summit Co.: Stillwater Ford, Uintah Mts., *E. and L. Payson 4995* (RM). Utah Co.: Mt. Timpanogos, *B. Maguire 17507* (UC).

WASHINGTON: Chelan Co.: Mt. Stuart, *J. Thompson 7685* (CAS, UC). Clackamas Co.: Mt. Hood, *J. Thompson 3403* (WTU). Clallam Co.: Hurricane Ridge, *W. and M. Muenscher 10004* (UC); Mt. Angeles, *J. Thompson 7522* (CAS, UC, WTU). Columbia Co.: 1.5 mi. E. Table Rock, Umatilla N. F., *A. Kruckenberg 2514* (UC). Grays Harbor Co.: Colonel Bob L. O., *J. Thompson 7245* (WTU). Jefferson Co.: Olympic Mts., Mt. Constance, *R. Rollins and T. Chambers 2654* (UC). King Co.: Goldmeyer Hot Springs, *J. Broadbent s.n.* (WTU). Kittitas Co.: Mission Peak, *J. Thompson 14913* (CAS, MICH, UC, WTU). Klickitat Co.: Mts. NE Bingen, *W. Suksdorf 2760* (WTU). Mason Co.: Mt. Ellinor, *W. Eyerdam 1276* (UC). Pierce Co.: Yakima Park, Mt. Rainier N. P., *B. Maguire 17260* (UC); Mt. Rainier, *L. Benson 2337* (UC); Chinook Pass, *W. Eyerdam s.n.* (UC); Cowlitz Pass, *J. Thompson 11102* (CAS, WTU). Skamania Co.: Big Lava Beds, *J. Franklin 448* (OSC); Mt. St. Helens, *F. Coville 747* (US, WTU). Snohomish Co.: Mt. Pugh, *J. Thompson 14351* (CAS, MICH, UC). Whatcom Co.: Mt. Baker, *W. Muenscher 8030* (UC). Yakima Co.: Chinook Pass, *J. Thompson 15136* (CAS, MICH, UC, WTU); Mt. Aix, *J. Thompson 15016* (CAS, MICH, UC, WTU).

WYOMING: Albany Co.: 7.4 mi. W. Centennial, *S. J. Wolf 422* (ALTA). Lincoln Co.: Jackson's Hole, *E. and L. Payson 2276* (UC). Sublette Co.: 26 mi. W. Big Pinney, *F. and L. Meyer 2369* (UC). Teton Co.: Skyline Trail, Teton N.P., *L. Wehmeyer et al 5450* (MICH); 1 mi. E. Togwotee Pass, *S. J. Wolf 431* (ALTA). Yellowstone National Park: Obsidian Creek, *A. and E. Nelson 6108* (UC).

Arnica latifolia is one of the most polymorphic and widely distributed of western arnicas. This taxon is common in relatively cool, montane *Picea-Abies* forests or sub-alpine meadows from Alaska through Colorado and northern California. In its most typical form *A. latifolia* is easily recognized by its sessile, ovate, glabrous leaves; very narrow heads with narrow phyllaries and rays; and glabrous, brown achenes. However, both environmentally induced morphological variability and plants with petiolate lower cauline leaves are sometimes encountered. Consequently, this taxon is sometimes confused with both *A. cordifolia* and *A. gracilis.* Plants of shaded forests represent the typical form of the species while plants of more exposed areas are usually much reduced; have thicker, smaller, more glandular leaves; have broader heads with more glandular phyllaries and are often confused with *A. gracilis.* However, they are readily separable from the latter by their broader, sessile, petiolate leaves and fewer heads. Pressed specimens of *A. latifolia* with petiolate lower leaves are sometimes confused with *A. cordifolia;* however, they can be readily distinguished by leaf shape, margin and pubescence, head and phyllary shape and achene color.

The type sheet of *Arnica betonicaefolia* consists of two collections: *C. V. Piper 2202* and *2002.* Both were collected on Mt. Steele, Washington, in August, 1895; however, the former was collected at

7000 ft. while the latter was collected at 6000 ft. Maguire (1943) reduced *A. betonicaefolia* to synonymy under *A. latifolia* and cited *2002* as the holotype while Ediger and Barkley (1978), who reduced this taxon under *A. gracilis,* cited *2202*. Both collections represent the reduced high alpine form of *A. latifolia* and have ovate, serrate, sessile leaves and solitary narrow heads typical of this taxon. There is really no question as to which collection represents the holotype of *A. betonicaefolia* since Greene (1900) clearly designated *2002*.

6. **Arnica nevadensis** A. Gray, Proc. Am. Acad. 19: 55. 1883. TYPE: Lassen's Peak, California, *R. M. Austin s.n.* (LECTOTYPE by Rydberg, GH!; SYNTYPE, Summit Valley, California, Sept. 25, 1882, *C. G. Pringle s.n.* NY!).

Arnica tomentella Greene, Pittonia 4: 166. 1900. TYPE: open woods in Middle Tule River, California, alt. 5500 ft., April–Sept. 1897. *C. A. Purpus 5625* (HOLOTYPE, US!; ISOTYPES, GH!, MO!, UC!).

Stems simple, 10–50 cm high, 1.5–2.5 mm diameter, short stipitate-glandular throughout and puberulent above, rhizomes 1–2 mm thick, with several brown scales and old leaf bases at the summit. Cauline leaves 2–3 pairs, ovate to elliptic, 3–8 cm long, 2–4 cm broad, short stipitate-glandular throughout, acute to rounded, entire to denticulate; petioles narrow to broadly winged, 1.5–4.0 cm long; upper pair of leaves sometimes reduced, sessile and lanceolate; leaves of the innovations 4–6, similar to cauline leaves. Inflorescence a single head or corymb of 3 heads, peduncle 4–15 cm long, stipitate-glandular and somewhat villous, heads radiate, campanulate-turbinate, 15–20 mm high; involucral bracts 10–16, oblanceolate, 10–17 mm long, 2–4 mm broad, stipitate-glandular, acute to acuminate. Ray florets 6–14, yellow, linear to broadly elliptic, 15–25 mm long, 4–6 mm broad, 3-dentate; disc florets 20–60, yellow, tubular, 8–10 mm long, short stipitate-glandular; pappus of both ray and disc florets white to tawny, barbellate to subplumose. Achenes dark gray, 6–9 mm long, 1 mm broad, stipitate-glandular throughtout. Figure 11. Chromosome number $2n = 76$.

ECOLOGY AND DISTRIBUTION: Relatively uncommon in fairly dry *Tsuga-Pinus* forests or exposed rocky slopes of the Sierra Nevada Mountains from south of Yosemite National Park, California and adjacent Nevada, northward irregularly to the north Cascades and Olympic Mountains of Washington. Also known from the Ruby Mountains of Nevada. Figure 12. Elevational distribution 1500–3000 m. Flowers July–August.

Figure 11. Lectotype of *Arnica nevadensis*.

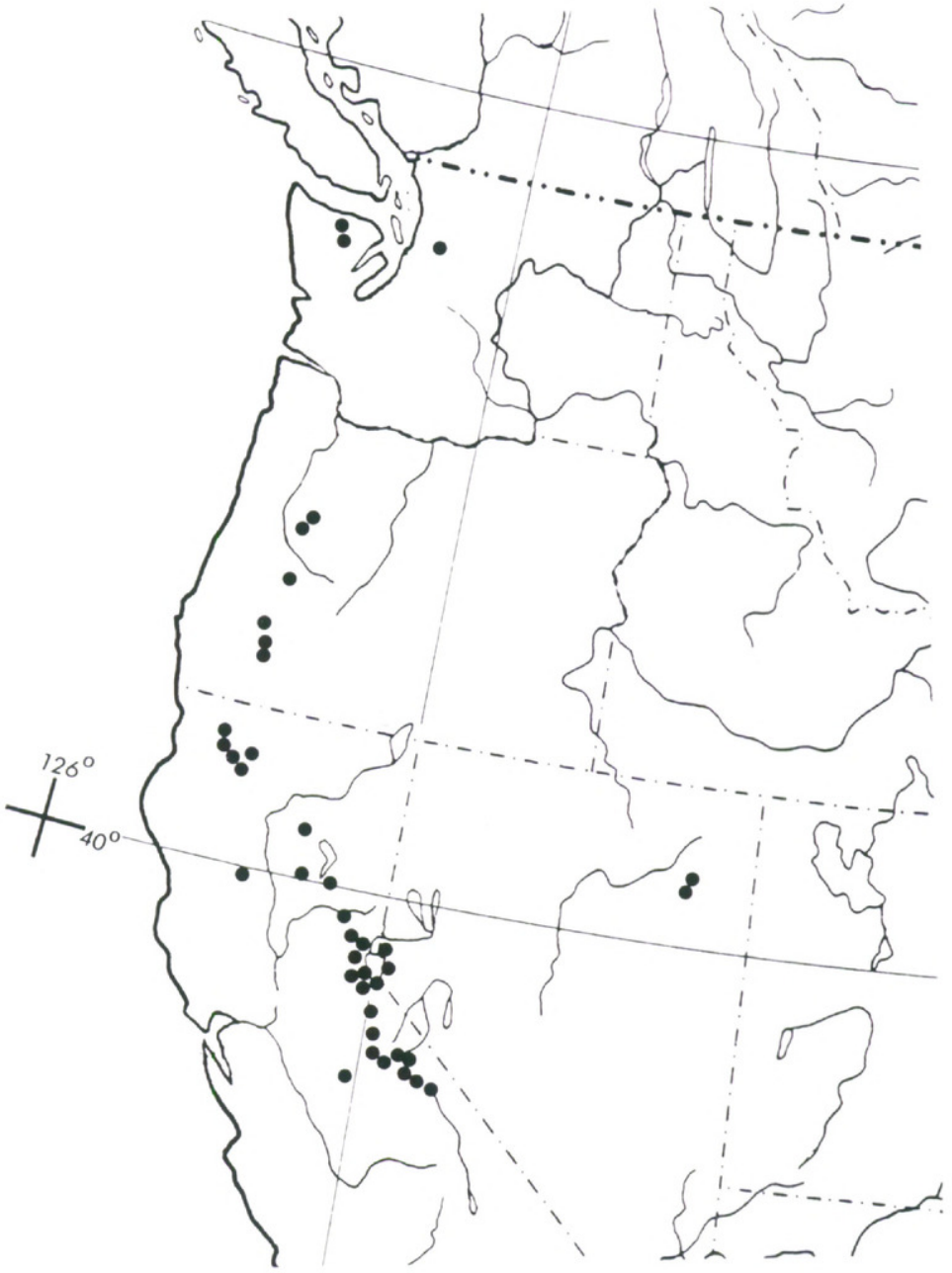

Figure 12. Distribution of *Arnica nevadensis*.

REPRESENTATIVE SPECIMENS: **United States:** CALIFORNIA: Truckee River, above Shingle Mill, *C. Sonne s.n.* (UC); open moist woods, middle Tule River, *C. Purpus 1540* (UC); Coburn Mill, *T. Brandegee s.n.* (UC); Middle Tule River, *C. A. Purpus 5625* (GH, UC, US). Amador Co.: *G. Hansen 416* (UC). Butte Co.: Jonesville, *A. Heller 12861* (OSC). El Dorado Co.: Fallen Leaf Lake, *G. L. Stebbins 2032* (UC); Angora Peaks, *H. M. Hall 8796* (UC); Velma Lakes Trail, above Eagle Lake, *G. Robbins 2054* (UC); Red Peak, *G. Robbins 1806* (CAS, UC); Fallen Leaf Lake, *M. Baker s.n.* (UC). Fresno Co.: Vidette Meadows, *J. Howell 24955* (CAS); Fish Camp, *P. Raven 5786* (CAS); Mills Creek, *P. Raven 5674* (CAS); Kip Camp, *P. Raven 7361* (CAS); Pocket Meadow, *P. Raven 6006* (CAS). Glenn Co.: Black Butte, *J. Howell 19250* (CAS). Inyo Co.: Flower Lake, *S. Austin 558* (UC); Big Pine Lakes, *J. Howell 23815* (CAS); Box Lake, *J. Howell 22445* (CAS); Rock Creek Lake, *J. Howell s.n.* (CAS). Madera Co.: Garnet Lake, *J. Howell 16479* (CAS); Shadow Lake, *P. Raven 3390* (CAS); Lake Ediya, *P. Raven 3527* (CAS). Mariposa Co.: Yosemite Park: Glacier Point, *H. M. Hall 9149* (UC); Fletcher Lake, *B. Schreiber 2013* (UC); Donohue Pass, *B. Schreiber 1787* (UC); Mt. Dana, *H. M. Hall and E. B. Babcock 3599* (UC); Lost Lake, *H. M. Hall 9068* (UC). Mono Co.: Mt. Lyell, *A. Hawbecker s.n.* (UC); Tiogo Crest, *H. Mason 11469* (UC); Harvey Monroe Hall Natural Area, *J. Clausen 1124* (UC), *P. Stockwell 1346* (CAS); Sonora Pass, *A. Eastwood* and *J. Howell 7565* (CAS). Nevada Co.: Stanford Peak, *A. Kellogg s.n.* (UC); Summit-Soda Springs, *Kennedy and Doten 274* (UC); Donner Pass, *J. Howell 18662* (CAS); S. side Donner Lake, *A. Heller s.n.* (CAS). Placer Co.: Mt. Anderson, *C. Sonne s.n.* (CAS, UC); Truckee River, *C. Sonne 7* (CH, UC); Truckee, *C. Sonne 27* (GH). Plumas Co.: Gold Lake Road, *J. Ewan 8206* (UC). Shasta Co.: Helen Mt., *G. Gillett 1078* (CAS); Lassen Peak, *R. M. Austin s.n.* (GH); Lassen National Park, *F. Hermann 11956* (UC). Sierra Co.: Gold Lake, *H. Baker 82* (CAS). Siskiyou Co.: Taylor Lake, *D. Barbe 129* (UC); Medicine Lake, *H. Baker 502* (UC); Upper English Lake, *F. Oettinger 1082* (UC); Wildcat Peak, *Alexander and Kellogg 204* (UC); Marble Mt., *H. Chandler 1615* (CAS). Tehma Co.: Brokeoff Mt., *G. Gillett 1066* (CAS). Tuolumne Co.: Elizabeth Lake, *H. Mason 692* (UC); Johnson Peak, *C. Sharsmith 217* (UC); peak between Matterhorn and Whorl Mts., *C. Sharsmith 3826* (UC). Trinity Co.: Grizzly Creek, Trinity Alps, *E. Carter 1011* (CAS).

NEVADA: Elko Co.: Three Lakes, Ruby Mts., *A. Borell s.n.* (UC). Clover Mts., near Deeth, *A. Heller 9242* (UC). Ormsby Co.: Fall Creek, *C. Baker 1432* (CAS, MICH, RM, UC, US). Washoe Co.: White Creek, E. slope Mt. Rose, *P. Train 4420* (UC).

OREGON: Douglas Co.: Mt. Bailey, *C. Geddes 18670* (OSC). Klamath Co.: Crater Lake National Park: Union Peak, *J. Simpson 9* (UC); Garfield Peak, *W. Baker 6184* (OSC, UC); *E. Applegate 9851* (CAS, OSC); W. Baker 7203 (WTU); Hillman Peak, *W. Baker 6401* (UC); *H. Sullen s.n.* (OSC). Lane Co.: N. Sister Mt., *M. Peck 14473* (CAS, OSC).

WASHINGTON: Chelan Co.: Nason Creek valley between Berne and Cascade, *I. Otil s.n.* (CAS). Clallam Co.: Mt. Angeles, *J. Flett 3325* (US). Jefferson Co.: Marmot Pass, Olympic National Forest, *J. Thompson 9907* (WTU).

Arnica nevadensis occurs mostly at high elevations in open *Tsuga–Pinus* forests or open rocky slopes of the Sierra Nevada and

sparingly northward in the Cascades and eastward into Nevada. In the southern part of its range this species is quite distinct and readily recognized by its entire, elliptic to ovate leaves; oblanceolate phyllaries; white-tawny, barbellate-subplumose pappus and relatively open, high altitude habitat. However, in the northern part of its range it is often confused with dwarf, high altitude forms of *A. cordifolia.* However, the entire leaves, darker pappus with longer seta and narrower heads of *A. nevadensis* distinguish it from the latter.

In his original description of *Arnica nevadensis,* Gray (1883) did not designate a type; however, he cited two specimens he had examined: *R. M. Austin s.n.,* Lassen's Peak, California (GH) and *C. G. Pringle s.n.* 1882, Summit Valley, California (NY). In his Flora of North America, Rydberg (1927) designated the first specimen cited (Austin) as the lectotype for this species. This choice was also later accepted by Maguire (1943). However, recently Ediger and Barkely (1978) rejected Rydberg's choice as arbitrary and designated the second specimen cited (Pringle) as the lectotype "... in order to preserve the traditional application of the name." According to the rules of the International Code of Botanical Nomenclature (Stafleu *et al*, 1978) this practice cannot be accepted without proper justifiction. Both Article 8 and the Guide to the Determination of Types specifically state that the first choice of a lectotype must be followed by subsequent workers unless it can be shown that the choice was based on a misinterpretation of the protologue or if the choice was made arbitrarily and without understanding the group concerned.

Ediger and Barkley (1978) based their decision on Recommendation 7B which states "Whenever the elements on which the name of a taxon is based are heterogeneous, the lectotype should be be selected as to preserve current usage ..." Although poorly pressed, the ovate, entire leaves, as well as the broad rays and tawny, subplumose pappus of the Austin specimen are typical of *A. nevadensis.* Further, it seems clear that Gray's (1883) description was based on the Austin specimen. He made specific reference to the cinereous color in both the type description and the discussion of the Austin specimen, while noting that the Pringle specimen was a "greener form". Although Rydberg (1927) gave no reason for his choice of the Austin specimen at the Gray Herbarium, he must have given it close examination since it would have been much easier for him to cite the Pringle specimen at the New York Botanical Garden.

Rollins (1972) has stressed the importance of selecting a lectotype from the institution where the author worked. Since both specimens cited by Gray (1883) are referable to *A. nevadensis,* but the first cited (Austin s.n.) was originally chosen as the lectotype by Rydberg (1927) and later accepted by Maguire (1943), it must be retained as the lectotype for this species.

Both Maguire (1943) and Ediger and Barkley (1978) recognized the rare *Arnica tomentella* of the Sierra Nevada. Maguire (1943) considered *A. tomentella* a close relative of *A. nevadensis.* This decision is not surprising since even a casual comparison of his (Maguire, 1943) description of the two taxa indicated they are nearly identical in most respects including: stem pubescence, leaf shape and margin, head shape, phyllary and ligule shape and all characters of the pappus. Only the taller stature and tuft of hairs on the phyllary tips distinguish *A. tomentella* from *A. nevadensis. A. nevadensis* is an apomictic, polyploid complex (Barker, 1967; Straley, 1980; Wolf, 1980) and the form previously recognized as *A. tomentella* probably represents an apomictic microspecies of the former.

Three specimens (*J. P. Tracy 19273* UC, *C. F. Sonne s.n.* UC #193450 and *G. D. Butler 643* UC) previously recognized as *Arnica tomentella* are *A. cordifolia.* Other specimens previously recognized as *A. tomentella* (*Lemmon s.n.* UC #337194; *C. F. Sonne s.n.,* June 6, 1886, GH, UC; *C. A. Purpus 1540* UC; *T. S. Brandegee s.n.* UC #91026; *C. A. Purpus 5625* GH, MO. UC, US) are all treated here as *A. nevadensis.* Another collection previously identified as *A. tomentella* (*Bolander 4937* UC) is *A. mollis* Hook.

7. **Arnica spathulata** Greene, Pittonia 3: 103. 1896. TYPE: Glendale, Oregon, June 30, 1887, *T. Howell s.n.* (HOLOTYPE, NDG!; ISOTYPES, CAN!, US!).

   Arnica eastwoodiae Rydb., N. Am. Fl. 34: 343. 1927. *Arnica spathulata* Greene subsp. *eastwoodiae* (Rydb.) Maguire, Brittonia 4: 458. 1943. *Arnica spathulata* Greene var. *eastwoodiae* (Rydb.) Ediger and Barkley. N. Am. Fl. II. 10: 43. 1978. TYPE: Gasquet, French Hill, Del Norte Co., California, Sept, 14, 1912, *A. Eastwood 221* (HOLOTYPE, NY!; ISOTYPES, NY!, US!).

   Arnica cusickii Rydb., N. Am. Fl. 34: 343. 1927. TYPE: dry western slopes, Cascade Mountains, southern Oregon, July 11, 1902, *W. C. Cusick 2873* (HOLOTYPE, NY!; ISOTYPES, MO!, ORE!, POM!, UC!, US!).

Stems simple to several branched, 15–50 cm high, 2–3 mm diameter, sparsely to densely villous and stipitate-glandular through-

out; rhizomes giving rise to several basal rosettes and flowering stems, 2–3 mm thick, covered with scales and old leaf bases at the summit. Cauline leaves 3–5 pairs, sometimes crowded towards stem base and reduced above, spathulate to elliptic-ovate, 2–8 cm long, 1–4 cm broad, sparsely to densely villous and stipitate-glandular, acute, sub-entire to mostly irregularly dentate; petioles mostly broadly winged, 1–9 cm long, 2–15 mm broad; leaves of the innovations 4–10, similar to cauline leaves. Inflorescence a solitary head or corymb of 3–9(25) heads; peduncles 2–20 cm long, sparsely to densely villous and long stipitate-glandular; heads discoid, turbinate-campanulate, 15–28 mm high; involucral bracts 8–15, broadly to narrowly lanceolate, 5–15 mm long, 1–4 mm broad, sparsely to densely villous and stipitate-glandular, acute to obtuse. Florets 15–50, yellow, tubular, 8–11 mm long, sparsely villous and glandular below; pappus white, barbellate. Achenes black, 5–10 mm long, 1 mm broad, sparsely short stipitate-glandular. Figure 13. Chromosome number $2n = 38, 76$.

ECOLOGY AND DISTRIBUTION: Relatively rare and forming small populations in dry, open *Pinus-Quercus-Pseudotsuga menziesii* forests or such disturbed areas as roadcuts. Largely restricted to serpentine soils in Curry, Douglas, Jackson and Josephine Counties, Oregon and Del Norte and Siskiyou Counties, California. Figure 14. Elevational distribution 200–1500 m. Flowers April–July.

REPRESENTATIVE SPECIMENS: **United States:** CALIFORNIA: Del Norte Co.: Douglas Park, on Smith River, *J. Thompson s.n.* (CAS, NY); Smith River Canyon, 15 mi. E. Crescent City, *Ripley and Barneby 6798* (NY); Gasquet, *A. Eastwood 2211* (NY, US); French Hill, 2 mi. S. Gasquet, *J. Tracy 11461* (UC); Smith River at 18 mi. Creek, 3 mi. E. Gasquet, *J. Tracy 12284* (UC); Old Gasquet Toll Road, *J. Tracy 11208* (UC); State Line, N. Monumental, *J. Tracy 19423* (UC); Hayne's Flat Rd. on Coon Mt., *J. Tracy 18921* (UC); Grade from Patrick Creek to Shelly Creek, *A. Eastwood and J. Howell 3667* (CAS); Gasquet, *M. Peacock s.n.* (CAS); French Hill, *A. Eastwood 2211* (CAS); Patrick Creek, *A. Eastwood 12120* (CAS); Gasquet Mt., *A. Eastwood 12155* (CAS); along Hwy. 99, 3.2 mi. N. Gasquet, *D. Breedlove 3146* (CAS); Gasquet, *Parks and Tracy 11208* (UC); French Hill, *S. J. Wolf 458* (ALTA); 10 km N. Gasquet, *S. J. Wolf 459* (ALTA); 5.8 km NW Patrick, *S. J. Wolf 387* (ALTA). Siskiyou Co.: Humbug Mt. *G. Butler 985* (UC); Raspberry Lake, *D. Kildale 8706* (CAS).

OREGON: Curry Co.: 13 mi. SE Port Orford, *M. Peck 8933* (GH, OSC); Agness, *M. Peck 2794* (OSC); Iron Mt., *W. Baker 5677* (UC); Snow Camp, *J. Thompson 31* (CAS). Douglas Co.: Glendale, *T. Howell s.n.* (CAN, NDG, US). Jackson Co.: Wimer, *E. Hammond 230* (US). Josephine Co.: Caves City, *L. Rose 34218* (CAS,

Figure 13. *Arnica spathulata*.

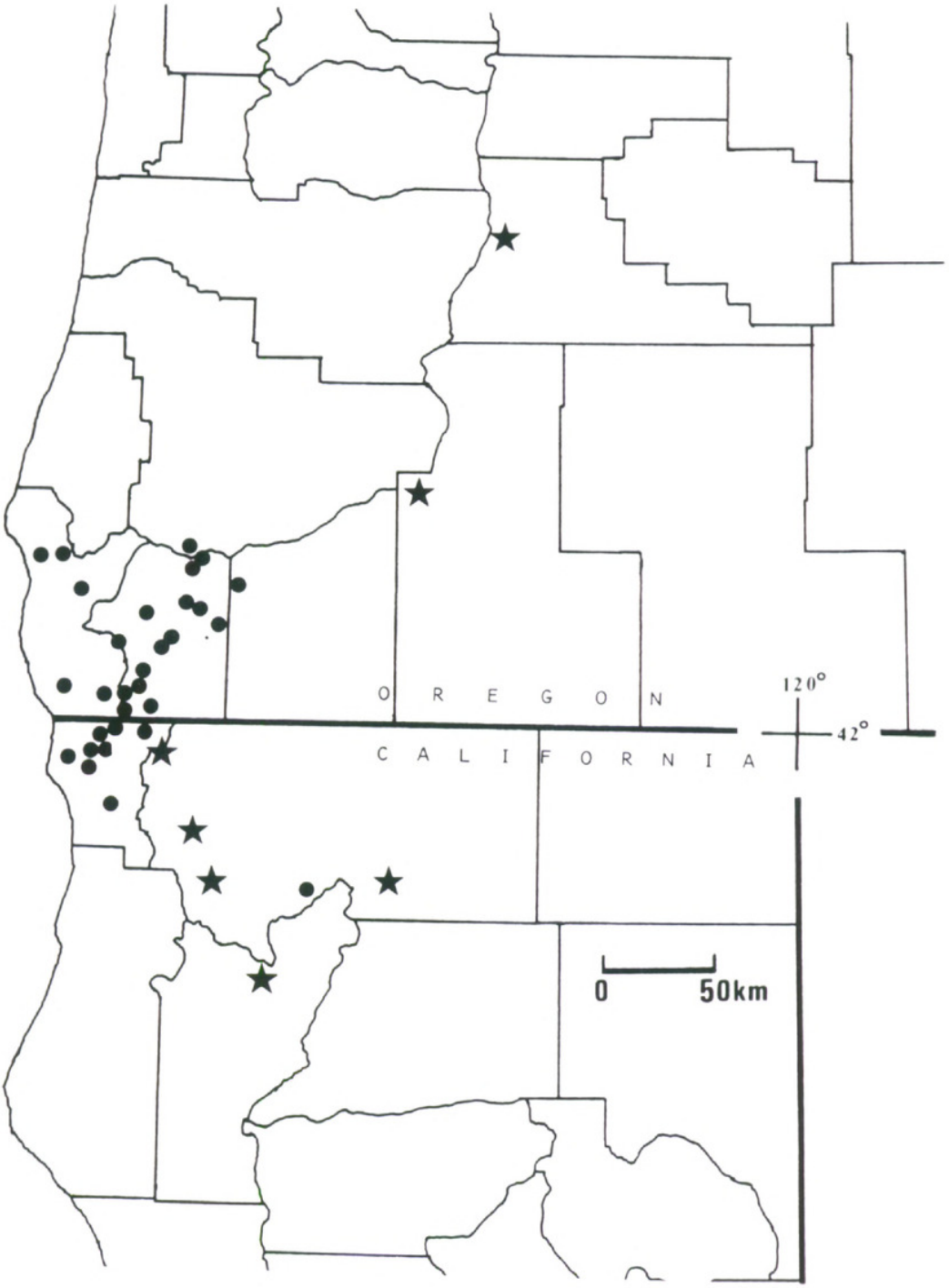

Figure 14. Distribution of *Arnica spathulata* ● and *Arnica viscosa* ★.

MICH, UC); 2 mi. S. Union Mt. Lookout, 12 mi. W. Waters Creek, *C. L. Hitchcock and J. Martin 5125* (CAS, UC, WTU); Oregon Mt., *A. Kruckeberg 1871* (UC), *A. Sweetser s.n.* (UC); Kerby, *L. F. Henderson s.n.* (OSC, UC); Grants Pass, *T. Howell s.n.* (MICH, OSC); Rough and Ready Creek, *E. Meola 99* (OSC); hwy. 99, 1 mi. N. Cave Jct., *K. Chambers 2912* (CAS, OSC); Hellgate, Rogue River, *M. Peck 8933* (OSC); Wonder Post Office, *M. Peck 23777* (OSC); 12 mi. W. Waldo, *M. Peck 2916* (OSC); Merlin, *L. Smith s.n.* (CAS); Finch Ranch, near Kirby, *L. F. Henderson 5900* (CAS); 2 mi. S. Wolfcreek, *Ripley and Barneby 9552* (CAS, NY); Waldo Jct., *D. Kildale 9623* (CAS); Selma, *N. Gale 14* (CAS), *H. and S. Parks 5947* (UC); Grants Pass, *T. Howell 131* (US), *C. Piper s.n.* (US), *Hammond 250* (NY); Caves Jct., near Kirby, *L. Rose 34218* (NY); 10 mi. S. Waldo, *J. Tracy 4617* (CAS); 17 km. N. Patrick, *S. J. Wolf 460* (ALTA); 20 km N. Patrick, *S. J. Wolf 461* (ALTA); Hugo, *S. J. Wolf 455* (ALTA); Merlin, *S. J. Wolf 456* (ALTA); Store Gulch Guard Station, *S. J. Wolf 462* (ALTA); Babyfoot Lake, *S. J. Wolf 384* (ALTA).

Arnica spathulata is a relatively rare, predominantly serpentine endemic, and occurs in dry, open forests at mid elevations in the Coast Ranges of the Klamath region. As previously noted (Wolf and Denford 1984b), this species is almost certainly derived from *A. discoidea.* However, it is readily distinguished by its spathulate, broadly winged, petiolate leaves, broader phyllaries and larger, black achenes which lack duplex hairs.

In more exposed habitats specimens of *Arnica spathulata* are often smaller, less hairy, with narrower, frequently reddish leaves crowded towards the base. Plants of this form have previously been recognized as *A. eastwoodiae* by Rydberg (1927). Maguire (1943) tentatively recognized this taxon as a subspecies of *A. spathulata* but noted it may, in fact, only represent an environmentally reduced form. These characters are probably environmentally induced and no correlations between morphology, chromosome number, geography or flavonoid chemistry could be discerned in this form (Wolf, 1981; Wolf and Denford, 1984b). Therefore it has not received formal taxonomic recognition in the present study.

In his original description of *Arnica spathulata* Greene (1896) did not designate a type or refer to any specimens examined. Maguire (1943) later designated a Howell specimen at the U.S. National Herbarium as the lectotype for this taxon (*T. Howell s.n.* Glendale, Oregon, June 30, 1887 (erroneously cited as June 3)). However, a specimen of *A. spathulata* on which Greene had written "Actual type of my *A. spathulata,* Pitt. iii, 103!" has been located in his personal herbarium at Notre Dame University. According to Article

8 of the International Code of Botanical Nomenclature (Stafleu *et al.*, 1978) this specimen supersedes Maguire's (1943) lectotype and is here treated as the holotype of *A. spathulata.* Both the U. S. National Herbarium specimen, previously chosen as lectotype, as well as a specimen at the National Museum of Canada are of the same collection as the holotype and are here recognized as isotypes.

8. **Arnica venosa** H. M. Hall, Univ. Calif. Publ. Bot. 6: 174. 1915. TYPE: Salt Creek, Shasta Co., California, alt. 430 m *H. M. Hall and E. B. Babcock 4013* (HOLOTYPE, UC!; ISOTYPES, GH!, NY!, RM!, UC!, US!).

Stems simple to 3-several branched, prominently ribbed, 20–60 cm high, 2–5 mm diameter, densely pilose and stipitate-glandular above to less so below; woody caudex 3–5 mm broad, covered with dark scales and old leaf bases. Basal rosettes lacking; cauline leaves 6–10 pairs, the middle largest, becoming reduced and bract-like above and scale-like below, broadly sessile or rarely short-broadly petiolate, ovate-elliptic to broadly lanceolate, 3–7 cm long, 1.5–4 cm broad, firm, 3–5 nerved above, strongly reticulate-veined below, glabrate to stipitate-glandular above, pilose and stipitate-glandular below, especially on veins below, acute to obtuse, irregularly and coarsely serrate. Inflorescence a solitary head on each branch, 1–7; peduncle 2–5 cm long, densely pilose and stipitate-glandular toward summit; heads discoid, turbinate-campanulate, 15–22 mm high; involucral bracts 8–19, 8–16 mm long, 3–5 mm broad, ovate to broadly lanceolate, pilose and stipitate-glandular, acute to obtuse. Florets 30–60, yellow, tubular, 8–10 mm long, densely pilose below; pappus white, barbellate. Achenes dark gray, angled and ribbed, 6–8 mm long, 1.5 mm broad, densely hirsute with duplex hairs. Figure 15. Chromosome number $2n = 38$.

ECOLOGY AND DISTRIBUTION: An extremely rare species of very dry, open *Pinus-Quercus* forests or, more commonly, of such disturbed sites as road cuts. Known from about thirty small populations, largely in western Shasta County and adjacent Trinity County, California. Figure 2. Elevational distribution 400–1400 m. Flowers May–June.

REPRESENTATIVE SPECIMENS: **United States:** CALIFORNIA: Shasta Co.: Salt Creek, *Hall and Babcock 4013* (GH, NY, RM, UC, US); Castella, *L. E. Smith 348* (CAS); Iron Mt., *L. E. Smith s.n.* (CAS, UC); road to Shasta Bally, 2.2 km S. Brandy

Figure 15. *Arnica venosa.*

Creek, S. Whiskeytown Lake, *G. Straley 1791* (UBC), *S. J. Wolf 469* (ALTA); bluff above mining road, E. of town of Iron Mt., *W. Barker 227* (WTU). Lamoine Quad: Baker Pine Plantation, W. of I-5, T36N, R5W, sec. 2, *S. Horner 112* (STNF), *G. Straley 1793* (UBC), *S. J. Wolf 468* (ALTA); Shell Mtn. Quad: 0.5 mi inside National Forest Boundary, Trinity Mt. Rd., T34N, R7W, sec. 10, *B. Williams 251* (STNF); W. of Dog Creek Rd. between Tollhouse and Grouse Springs, 7 mi. W. Delta, T35N, R6W, sec. 3, *B. Williams 369, 370, 371* (STNF), *M. Taylor 3195* (STNF); above forest service road, 1 mi. NW Damnation Peak, T36N, R6W, sec. 22, *M. Taylor 3196* (STNF). Trinity Co.: Swift Creek Rd., 0.7 mi. W. Hwy. 3, W of Trinity Center, T36N, R7W, sec. 18, *B. Williams 363* (STNF).

Arnica venosa is probably one of the rarest and most geographically restricted species of *Arnica.* It is known from about thirty populations, all within a 25 km radius, largely in western Shasta County, California. It is restricted largely to north-facing slopes, at elevations of 400–1400 m, in open *Pinus–Quercus* forests or more commonly on such disturbed sites as road cuts. Until very recently *A. venosa* was known from only six populations and, consequently, appeared on the California list of rare and endangered species (Smith *et al.,* 1980). However, based largely on the efforts of Ms. Barbara Williams of the Shasta-Trinity National Forest, many more populations have recently been discovered. The authors are greatly indebted to Ms. Williams for providing considerable information on *A. venosa* including both herbarium specimens and highly detailed and complete ecological observations.

In its typical form *Arnica venosa* is readily recognized by its rather stout, leafy stem; woody caudex; absence of innovations and broadly sessile, ovate-elliptic, reticulate-veined, coarsely dentate, very firm leaves. Since few specimens were available for examination, previous studies have concluded that this taxon exhibits little variability (Maguire, 1943; Straley, 1980). However, the availability and study of many newly collected specimens have revealed that *A. venosa,* like most other *Austromontana* species, exhibits considerable morphological variability and it appears to intergrade with *A. discoidea.* As previously noted (Wolf and Denford, 1984b), this taxon is probably derived from *A. discoidea.* At one extreme are typical forms of *A. venosa* with leafy stems and broadly sessile, veined leaves such as the type collection *Hall and Babcock 4013* (GH, NY, RM, UC, and US); *S. J. Wolf 468, 469* (ALTA) and *B. L. Williams 251* (STNF). At the other extreme are such specimens as *B. L. Williams 371* (STNF) with weakly veined,

long, narrowly petiolate leaves more characteristic of *A. discoidea.* This specimen is an otherwise typical form of *A. venosa* and is characteristically highly branched above with very reduced leaves. Additionally, it was collected near a population of *A. discoidea* and may represent some introgression from that species. However, without further evidence a hybrid hypothesis would be difficult to support. Another seemingly intermediate form is represented by *B. L. Williams 250* (STNF) which has very typical upper leaves, leafy stems and floral characters but has narrowly petiolate leaves below the mid-stem.

Whether these intermediate forms represent introgression between *Arnica discoidea* and *A. venosa* or natural variability in the latter is unclear. It is clear, however, that these two species are more similar than previously demonstrated. The flavonoid profile of *A. venosa* is a subset of that of *A. discoidea* and it is hypothesized that the former is a relatively recent derivative of the latter (Wolf and Denford, 1984b).

9. **Arnica viscosa** A. Gray, Proc. Am. Acad. 13: 374. 1878. TYPE: Mt. Shasta, California, 8000′, Sept. 1877, *J. D. Hooker and A. Gray s.n.* (HOLOTYPE, GH!).

Raillardella paniculata Greene, Erythea 3: 48. 1895. TYPE: near the limit of trees on Mt. Shasta, California, Aug. 4, 1894, *W. L. Jepson s.n.* (HOLOTYPE, NDG!).

Chrysopsis shastensis Jepson, Man. Fl. Pl. Cal. 1037. 1925. TYPE: Horse Camp, Mt. Shasta, California, 1000 ft., *W. L. Jepson 59i* (HOLOTYPE, JEPS!). In his original publication Jepson cited number *51i* as the holotype; however, according to his notes (Robbins, annotation on type sheet) as well as his designation of "Type" on number *59i*, this latter specimen is the holotype, and a typographical error occurred on publication.

Stems usually several branched, prominently ribbed, 20–50 cm high, 3–5 mm diameter, strongly stipitate-glandular, also becoming densely pilose above; woody caudex 3–5 mm broad, covered with dark scales, lacking basal rosettes; leaves numerous, 5–10 pairs on main stem, 2–6 pairs on branches, sessile, ovate-oblong to obovate-oblong, (1)2–4(5) cm long, 1–3 cm broad, sparsely to densely pilose and densely stipitate-glandular, more or less acute, entire. Inflorescence of 10–20 heads, peduncles 0.5–5 cm long, stipitate-glandular and pilose; heads discoid, narrowly turbinate, 1–2 cm high; involucral bracts 10–20, 6–10 mm long, 1–3 mm broad, broadly lanceolate, stipitate-glandular and pilose below, acute. Florets 10–30, cream colored, tubular, 6–10 mm long, stipitate-glandular;

pappus white, rarely tawny, barbellate to subplumose. Achenes dark gray, ribbed 4.5–6.5 mm long, 1 mm broad, stipitate-glandular. Figure 16. Chromosome number $2n = 38$.

ECOLOGY AND DISTRIBUTION: A very rare species of dry, exposed, pumice slopes at elevations of 1750–2500 m. Known localities in Oregon include three small populations in Crater Lake National Park, Klamath County and a single collection from the Three Sisters area of Deschutes County. Also known from four populations in Siskiyou County, California, a large population on Mt. Shasta, two populations in the Marble Mountains and a single collection from Preston Peak. An additional population is known from the Trinity Alps, Trinity County, California. Figure 14. Flowers August–September.

REPRESENTATIVE SPECIMENS: **United States:** CALIFORNIA: Siskiyou Co.: Mt. Shasta, *A. Eastwood 2055* (CAS, GH, UC), *W. B. Cooke 9228* (UC), *W. L. Jepson s.n.* (ND), *R. Bohmannson s.n.* (CAS); Horse Camp, Mt. Shasta, *J. D. Hooker and A. Gray s.n.* (GH), *W. B. Cooke s.n.* (UC), *11501* (CAS, DS, GH, OSC, UC), *13833* (CAS, DS, ND, NY, OSC, UC), *17828* (CAS, WTU), *P. Kamb 1488* (UC), *W. L. Jepson 59i* (JEPS), *W. Dress 3735* (UC), *A. A. Heller 13519* (CAS, DS, NY, US, WTU), *W. Barker 232* (WTU), *G. Straley 1411* (UBC), *S. J. Wolf 391* (ALTA); S. slope above ski lodge, Mt. Shasta, *R. Thorne and F. Oettinger 39010* (NY, RSA, UC); near Wagon Camp, Mt. Shasta, *M. De'Evelyn s.n.* (CAS); between Panther Meadow and ski lift, Mt. Shasta, *P. Hutchinson 938* (JEPS, K, US); South Gate, Mt. Shasta, *W. B. Cooke 25603* (GH, NY, WTU); Medicine Mt., 41°33′48″, 121°36′30″, *G. L. Clifton, s.n.* (PUS); Devils Punchbowl, 41°48′24″, 123°40′36″, *D. V. Hemphill s.n.* (PUA); Preston Peak, *C. A. Ground s.n.* (PUA); Upper English Lake, 41°24′36.2″, 123°12′53″, *F. W. Oettinger 668* (HSC, PUA, UC); Cliff Lake, *G. Muth s.n.* (PUA); Avalanch Gulch, 41°22′10″, 122°13′39″, *W. B. Cooke 2000* (UC). Trinity Co.: Trinity Alps: Boulder Creek, *W. J. Ferlatte 1286* (HSC, NY, UC); *W. J. Ferlatte 484* (HSC); Mirror Lake, *J. P. Smith 2361* (HSC).

OREGON: Deschutes Co.: Three Sisters area, Moraine Lake, E. Rock Mesa and S. of South Sister, *G. Van Vechten 219* (GH, OSC). Klamath Co.: Crater Lake National Park: Union Peak, *J. Mees s.n.* (CLNP), *F. Colville 1420* (RM, UC), *E. Applegate 10090* (CLNP); Hillman Peak, *E. Applegate 10126* (CLNP), *10134* (CAS); shore under Watchman Peak, *E. Applegate 9218* (CAS, CLNP); Wizard Island, *A. A. Heller s.n.* (CAS), *13820* (US); Garfield Peak, *W. Baker 7201* (NY, WTU), *G. Straley 1946* (UBC), *S. J. Wolf 511* (ALTA).

Arnica viscosa is one of the rarest and probably the most distinctive species of the genus *Arnica*. This species is restricted to volcanic soils and occurs on very open, rocky slopes at high elevations in the Cascades of northern California and southern

Figure 16. *Arnica viscosa.*

Oregon. It is known from a few populations in Crater Lake National Park, Oregon; Mt. Shasta, the Trinity Alps, Marble Mountains and Preston Peak, California. An additional collection was once made in the Three Sister Area of the central Oregon Cascades (*G. van Vechten 219* OSC, GH); however, repeated attempts by several workers, including the senior author, have failed to relocate this population.

Arnica viscosa is quite distinctive and easily recognized by its woody caudex; leafy branching habit; small, sessile, entire leaves; and narrow heads with cream-colored florets. In addition, virtually all parts of the plant are densely covered with long glandular hairs, so much so that it feels slimy to the touch. Additionally, it has a very distinctive odor which is retained almost indefinitely on herbarium sheets. All known collections of *A. viscosa* have been examined and this species appears to exhibit virtually no interpopulational variation. In fact the only atypical specimens examined were from Upper English Lake, Siskiyou Co., California (*F. Oettinger 668* HSC, UC). These plants were less viscid and the upper leaves and branches had a tendency to be sub-opposite to alternate.

The underground parts of *Arnica viscosa,* including the caudex and root sytem, are quite woody. This character is probably an adaptation to its rocky, relatively disturbed habitat on very steep slopes. Much of the root system is exposed, probably due to rock movement associated with heavy winter snows and runoff.

EXCLUDED TAXA

A. latifolia Bong. var. *viscidula* A. Gray, Syn. Fl. N. Am. 1: 381. 1884. TYPE: Sierra Nevada Mts., California, Sept. 25, 1882, *C. G. Pringle 2* (HOLOTYPE US!) ≡ *A. diversifolia* Greene, Pittonia 4: 171. 1900.

A. granulifera Rydb., Fl. Rocky Mts., 978. 1917. TYPE: Long Baldy, Little Belt Mt., Montana, Aug. 19, 1896, *J. H. Flodman s.n.* (HOLOTYPE, NY!) ≡ *A. mollis* Hook., Fl. Bor.-Am. 1: 331. 1834.

A. ovalis Rydb., N. Am. Fl. 34: 338. 1927. TYPE: Crowsnest Pass, Canadian Rocky Mts., *J. M. Macoun* (*Can. Geol. Surv. No. 72719*) (HOLOTYPE, CAN!) ≡ *A. mollis* Hook., Fl. Bor.-Am. 1: 331. 1834.

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