SYSTEMATICS OF ARNICA, SUBGENUS AUSTROMONTANA
AND A NEW SUBGENUS, CALARNICA (ASTERACEAE:SENECIONEAE)

by

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ABSTRACT

Seven species are recognized in *Arnica* subgenus *Austromontana* and two species in a new subgenus *Calarnica* based on a critical review and conservative revision of the species. Chromosome numbers are given for 91 populations representing all species, including the first reports for *Arnica nevadensis*. Results of apomixis, vegetative reproduction, breeding studies, and artificial hybridizations are given. Interrelationships of insect pollinators, leaf miners, achene feeders, and floret feeders are presented. *Arnica cordifolia*, the ancestral species consists largely of tetraploid populations, which are either autonomous or pseudogamous apomicts, and to a lesser degree diploid, triploid, pentaploid, and hexaploid populations. It has given rise to *Arnica nevadensis* which is tetraploid and autonomously apomictic, and to a complex of discoid populations treated here as a single polymorphic species, *Arnica discoidea*, with both diploid and tetraploid, sexual and pseudogamous apomictic races. *Arnica spathulata*, derived from *Arnica discoidea*, is largely restricted to serpentine soils and is a sexual diploid, with a few pseudogamous tetraploid apomictic populations. *Arnica latifolia*, the most polymorphic species, has arisen from *Arnica cordifolia*, although it has remained largely sexual and diploid. *Arnica latifolia* has given rise to *Arnica cernua*, the serpentine sexual, diploid endemic, and to *Arnica gracilis*, probably through hybridization with other species. *Arnica gracilis* now exists largely as a series of autonomously apomictic triploid races. The subgenus *Calarnica* was possibly derived from subgenus *Austromontana* by way of *Arnica spathulata* through *Arnica venosa*, the latter giving rise to *Arnica viscosa*. These latter two species are rare sexual diploids.
ARNICA CORDIFOLIA WITH BOMBUS MELANOPYGUS
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Jepson Herbarium, University of California (JEPS)
Kathryn Kalmbach Herbarium, Denver Botanic Gardens (KHD)
University of California, Los Angeles (LA)
Lakehead University (LKHD)
Museum of Northern Arizona (MNA)
Missouri Botanical Garden (MO)
University of Montana (MONTU)
Northern Arizona University (NAU)
California Polytechnic State University (OBI)
University of Oregon (ORE)
Pomona College (POM)
Pacific Union College (PUA)
Rancho Santa Ana Botanical Garden (RSA)
Santa Barbara County Museum (SBM)
Southern Oregon College (SOC)
University of British Columbia (UBC)
University of California, Berkeley (UC)
University of California, Santa Barbara (UCSB)
Utah State University (UTC)
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British Columbia Provincial Museum (V)
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INTRODUCTION

Arnica is a circumpolar genus of questionable tribal position in the Asteraceae, occurring from the northern limits of vascular plant growth at 85° north latitude, with four major southern radii of distribution; south in Asia to Japan; in Europe to Northern Jugoslavia and Northern Spain; in Eastern North America along the Atlantic Coast and Piedmont to Northern Florida; and in Western North America, where it reaches its greatest diversity, to Northern New Mexico and Southern California.

In the early years of Western North American exploration a vast number of species names were proposed, culminating in the Flora of North America in which Rydberg (1927) recognized 107 species in North America in 17 subgeneric groups. Rydberg presumably did not intend these groups to denote subgenera or sections, but rather convenient groups as an aid in identifying species. A much more conservative treatment, and the only comprehensive worldwide monograph, based largely on morphology, was proposed by Maguire (1943), in which he recognized 32 species (Appendix I) of which 27 are from Western North America. Maguire was the first to divide the genus into 5 subgenera, Arctica (7 species), Andropurpurea (3 species), Montana (2 species), Chamissonis (7 species), and Austromontana (13 species).

Since Maguire's works (1943, 1947), the genus has received little further study other than a few reports of chromosome numbers (Ornduff, et al., 1963, 1967; Strother, 1973; Straley, 1979), and an excellent survey of aposmixis in the genus by Barker (1966, unpublished). A recent monograph of the North American species (Ediger and Barkley, 1978) is based largely on Maguire (1943) with the reproductive information of Barker (1966). Ediger and Barkley (1978) recognize 23 species and 26 infraspecific taxa (Appendix II).
There remain few taxonomic problems in the subgenera *Andropurpurea*, *Montana*, and *Chamissonis*, although a re-evaluation of infraspecific taxa within the latter subgenus seems worthwhile. The greatest difficulties seem to be in the subgenus *Arctica*. However, owing to the circumpolar distribution of these species and their relative inaccessibility, particularly of the Asian taxa, a comprehensive systematic study of subgenus *Arctica* remains to be done. The subgenus *Austromontana* was selected for the present study because of unanswered taxonomic problems in this subgenus following Maguire's monograph and the number of taxonomic changes proposed since then (Maguire, 1947; Cronquist, 1955, 1960; Ediger and Barkley, 1978). Furthermore, partially due to cultural problems, Barker (1966) did less investigation of the reproductive behavior of *Austromontana* species than other subgenera. He states (Barker, 1966, p. 66), "The species belonging to the subgenus *Austromontana* have proved to be less amenable to investigation than those of other subgenera." Lastly, all the species in this subgenus are relatively easily accessible in Western North America.

**HISTORICAL BACKGROUND**

**Tribal Position of Arnica**

Although it has long been placed in the Senecioneae, *Arnica*, with its broad rays, opposite leaves, setose receptacle, base chromosome number of \(x=19\), and apomictic element, does not fit conveniently in this tribe. Nordenstam (1977) suggests either a close affinity to the Heliantheae or that possibly a new tribe, the "Arniceae", should be erected for *Arnica* and some eleven other genera. Baagøe (1977) presents evidence of ligule microcharacters for inclusion in the Heliantheae. Chemical data (Siegler et al.,
1974; Robins, 1977) supports the anomalous position in the Senecioneae. However, Turner and Powell (1977) believe that Arnica should be left in the Senecioneae. The pappus of capillary bristles is particularly out of place in the Heliantheae. The situation is well summarized by Cronquist (1977, p. 148), "It seems likely that these two genera Arnica and Doronicum will continue to be an embarrassment to future as well as present tribal organizations in the family." Further relationships of Arnica to Whitneya (Sierra Nevada), Arnicastrum (Northwest Mexico), Jamesianthus (Southeast United States), and Mallopatopus (Japan) and possibly other genera need more critical evaluation before they may be assigned with confidence to an existing tribe or placed in a new tribe.

Taxonomic History

Maguire (1943) gives an excellent historical account of the genus as a whole. While little more will be discussed concerning the remaining four subgenera (Arctica, Montana, Andropurpurea, and Chamissonis) a more detailed account of the taxa in Maguire's subgenus Austromontana, treated here as two subgenera, Austromontana and Calarnica, seems appropriate.

The first name proposed for a species in Austromontana was Arnica latifolia by Bongard (1832) which he described from material collected by Mertens at Sitka, Alaska. This proved to be the first in a long series of names applied to what are now interpreted as all variants or even typical specimens of the most polymorphic species in the subgenus, if not in the whole genus.

Hooker (1834) in the Flora Boreali-Americana named Arnica cordifolia from the Rocky Mountains, again the first name of many to be applied to a polymorphic, and the most widespread species in this subgenus. He also named
Arnica menziesii from the "Northwest Coast of America", the first of those species now considered as synonyms of Arnica latifolia.

Nuttall (1841) described a large-leaved plant from the Blue Mountains of eastern Oregon, Arnica macrophylla, now considered merely a large-leaved form of typical Arnica cordifolia. The first rayless taxon in the group was named Arnica discoidea by Bentham (1849) from material collected by Theodor Hartweg "in sylvis prope Monterey". Herder (1867) recognized two varieties of Arnica latifolia, A genuina and B angustifolia, and synonymized Hooker's Arnica menziesii under Arnica latifolia.

In the Synoptical Flora of North America, Asa Gray (1884) proposed three names which are now considered synonymous with other names, Arnica parviflora and Arnica cordifolia var. eradiata (now both = Arnica discoidea) and Arnica latifolia var. viscidula (= Arnica diversifolia in subgenus Chamissonis). However, he did name the very distinctive and rare Arnica viscosa from Mt. Shasta, California (Gray, 1878) and Arnica nevadensis from Lassen's Peak, California (Gray, 1884), both of which are considered good species today.

The three decades from 1897 to 1927 saw the greatest number of new names proposed, most of which are now relegated to synonymy under other species. Rydberg (1897, 1900, 1917, 1927), in a series of papers, proposed 18 new names, 17 of which are now considered synonymous with 5 older names. Only Arnica gracilis from the Rocky Mountains of Western Montana was retained as a good species by Maguire (1943) and in the present study, although others (Cronquist, 1955; Ediger and Barklý, 1978) considered it a variety of Arnica latifolia. Greene (1900, 1901, 1902, 1910) likewise proposed 16 new names, with only Arnica spathulata from Southwestern Oregon retained today, although Greene's Arnica tomentella still remains a questionably valid entity
Howell (1900) named the serpentine soil endemic which he collected in Josephine County, Oregon, Arnica cernua. It is one of the most distinctive of the radiate species, as well as one of the rarest. Nelson (1901, 1909) proposed the names Arnica platyphylla (= Arnica latifolia), Arnica columbiana, Arnica arcana (both = Arnica gracilis), and Arnica paniculata (? = Arnica cordifolia; see discussion under that species).

Jones (1910) proposed variety gracilis of Arnica betonicaefolia Greene (= Arnica latifolia). Hall (1915) named the rare but distinctive Arnica venosa which he collected in Shasta County, California. Gandoger (1918) named Arnica eripoda (= Arnica latifolia). Piper (1920) named Arnica andersonii from Skeena, British Columbia, another of the large-leaved shade forms of Arnica cordifolia, and Arnica aphanactis from Mt. Baker, Washington, which is a form of Arnica latifolia.

Fernald (1935) proposed the name Arnica whitneyi for plants from the Keewenaw Peninsula of Michigan, far disjunct from Western North American Austromontana species. It was considered a subspecies of Arnica cordifolia by Maguire (1943) and is not given taxonomic status by Ediger and Barkley (1978) or in the present treatment.

Williams (1935) placed Greene's Arnica teucriifolia as a variety of Arnica latifolia and St. John (1937) named Arnica hardinae (= Arnica cordifolia) from Benewah County, Idaho, the last new name proposed in the subgenus.

Maguire (1943), in his worldwide monograph of the genus, presented the most conservative treatment of the genus to that date, recognizing 13 species and 6 infraspecific taxa in Austromontana (see Appendix I). His treatment has been largely accepted by later workers and for the most part the findings of
the present study support his work. Although his work was based almost entirely on morphological characters, he seems to have had an excellent understanding of the genus. However, the greatest shortcoming of his work is that his keys are long and often very difficult to use.

Little taxonomic work has been done since Maguire's monograph other than some new combinations and arbitrary lumping of species. In a study of Great Basin plants Maguire (1947) recognized four varieties of Arnica cordifolia subsp. genuina: varieties cordifolia, macrophylla, pumila, and humilis.

Cronquist (1955), in the Flora of the Pacific Northwest, considered Arnica gracilis a variety of Arnica latifolia and he lumped Arnica parviflora and Arnica grayi under the new combined name Arnica discoidea var. eradiata (A. Gray) Cronquist. He later (Cronquist, 1958) changed the status of Arnica parviflora subsp. alata (Rydb.) Maguire to Arnica discoidea var. alata (Rydb.) Cronquist.

In the most recent classical monograph of the genus for North American Flora, Ediger and Barkley (1978) basically follow Maguire's work except that they use Cronquist's new combinations and that they treat Maguire's subspecies as varieties. They recognize 9 species with 8 infraspecific taxa in Austromontana (see Appendix II).

METHODS AND MATERIALS - GENERAL

Field collections were made from natural populations of Arnica species from British Columbia and Alberta to Ontario and Michigan and south to Colorado and Southern California during several extensive collecting trips from the fall of 1976 through the summer of 1979. Some plants or seeds were also obtained from other collectors and from botanical gardens.
Small, whole heads were fixed in the field in Carnoy solution (6 parts 95% ethanol : 3 parts chloroform : 1 part glacial acetic acid) and later transferred to 95% ethanol and refrigerated for cytological study.

Live plants or seeds of many populations were collected for further study in the experimental garden, greenhouse, and growth chamber. Observations and records were made in the field of pollinators and other insect visitors and feeders on the Arnica species. Insect specimens were collected for identification and further study. Rhizome growth was measured for a number of populations.

Specimens from more than 30 herbaria were studied to supplement field work. A morphological re-evaluation was made resulting in the conservative taxonomic treatment presented herein.

Voucher specimens of plants and insects are deposited at UBC.

DISCUSSION OF CHARACTERS

Among the morphological and other features used in elucidating taxa in the subgenera *Austromontana* and *Calarnica* and in determining phylogenetic relationships in these subgenera were the following:

Habit and Branching Patterns

All species in *Austromontana* are herbaceous perennials arising from rhizomes near the soil surface to several centimeters below the surface. The two species in *Calarnica* are also herbaceous perennials but they lack rhizomes. These have a thick woody caudex a few to several centimeters below the soil surface. Only the rhizomatous species produce sterile basal rosettes of leaves (innovations). Plants may be unbranched above ground to much-branched near ground level or higher on the plant. In the non-rhizomatous species,
and others with short rhizomes (as *Arnica gracilis*), the plant may be branched from below the ground level producing a clump. Heads may be erect or nodding and from one to many per stem. Figures 1–9 show a schematic representation of habit and average branching patterns.

**Underground Parts - Rhizomes, Caudices, and Roots**

All species in *Austromontana* are rhizomatous. The rhizomes are usually slender (1–2 mm thick), dark brown, and unbranched or with a few predominantly terminal branches. They are naked or sparsely clothed with pairs of usually inpersistent brown scales. In some of the short-rhizomed species (especially *Arnica gracilis*) and ecotypes of others (*Arnica cordifolia*, *Arnica latifolia*, and *Arnica cernua*) scales are more numerous or appear to be. These scales, in addition to persistent leaf bases and stem bases from previous years, give the rhizome a much more thickened appearance.

Rhizome length is relatively consistent within a majority of populations of most species, being markedly greater in some species (e.g., *Arnica cordifolia*) than in others (e.g., *Arnica gracilis* and *Arnica latifolia*). (See Table V). Within a species or population rhizomes are usually longer in shady than in sunny habitats. However, length seems to be largely genetically controlled. With few exceptions average yearly rhizome production under various artificial cultural regimes varied little from yearly average production in the same population in the field.

Rhizomes spread horizontally a few centimeters below the soil or duff surface in most species and in most forest and meadow habitats. However, in dry habitats, some populations, especially of *Arnica spathulata*, tend to have deeper rhizomes (6–10 cm) with vertical extensions which branch giving rise
Figures 1-3. Schematic diagrams of habit and average branching pattern of *Arnica* species.

1. *Arnica gracilis*
2. *Arnica latifolia*
3. *Arnica cernua*
gracilis

latifolia

cernua

* capitulum

◊ bract

◊ leaf
Figures 4-7. Schematic diagrams of habit and average branching pattern of Arnica species.

4. Arnica cordifolia
5. Arnica nevadensis
6. Arnica discoidea
7. Arnica spathulata
Graph showing plant growth stages:

- **4.** *cordifolia*
- **5.** *nevadensis*
- **6.** *discoidea*
- **7.** *spathulata*

Key:
- * capitulum
- ▲ bract
- ▽ leaf

Ground Level:
- -30 cm
- -20 cm
- -10 cm
- 10 cm
- 20 cm
- 30 cm
- 40 cm
- 50 cm
Figures 8, 9. Schematic diagrams of habit and average branching pattern of *Arnica* species.

8. *Arnica viscosa*

9. *Arnica venosa*
to horizontal rhizomes (Figure 7) closer to the ground surface.

Roots are sparsely produced along the rhizome, except toward the branching terminal origin of aerial portions. There are more roots produced on the shorter-rhizomed species and ecotypes. Primary roots are usually 0.5-1 mm thick and 20-30 cm long, rather vertical and simple or sparsely branched. In drier habitats and especially in serpentine soils the roots tend to be thicker (1-2 mm).

Rhizomes generally remain alive for about 3 years with the oldest growth dying as new rhizomes grow in the spring.

In Calarnica both species lack rhizomes but rather possess a thick woody perennial caudex, 4-5 cm in diameter from which usually many flowering stems are produced each year. The bases of old flowering stems remain on the caudices for several years giving them a rough character. The roots are quite thick (5-6 mm) and long (to 40 cm or more) and tend to be quite vertical and unbranched.

Leaves

All species of Austromontana produce basal rosettes of 4-6 pairs of usually long-petiolate leaves. Flowering stems have opposite pairs of brown membranous scales at the base, grading gradually, or more often abruptly, into small lower cauline leaves. There are typically 2-4 pairs of opposite cauline leaves, the largest produced toward the lower or middle portion of the stem, becoming smaller and bract-like and sometimes alternate below the inflorescence. Cauline leaves are sessile to long petiolate, with the petioles often winged, rarely wider than the blades. There is much variation in disposition of the leaves on the flowering stem as well as the angle at which the leaves are held.
Leaf outline ranges from lanceolate to broadly ovate, with acute to cordate bases and acute to rounded tips. Margins may be entire to crenate, serrate, dentate, or doubly serrate, dentate, or crenate, often undulate, and often combinations of these characters.

Leaves are one of the most reliable characters in separating taxa (Figures 10-25), although they are one of the most variable characters within some taxa. There is usually much interpopulational consistency, although there may be a great deal of phenotypic variation within a single population. Thick, relatively narrow sun-leaves or thin, relatively broad shade-leaves are often found within populations growing in open forest habitats, especially in *Arnica latifolia* and *Arnica cernua*. Leaves, especially in sunny locations and from plants growing in serpentine soils, are often flushed with red or purple.

There are no basal rosettes in subgenus *Calarnica*. Scales at the base of the flowering stems are very prominent and often several (6-12) pairs which grade gradually into cauline leaves. Stems of this subgenus are much leafier, with 7-15 or more pairs of sessile ovate leaves on the primary axis and smaller leaves and/or bracts on numerous lateral branches and in the leafy inflorescence. Upper bracts are usually sub-opposite or alternate.

### Odors of Herbage

Although difficult to describe qualitatively, pungent odors associated with those species bearing glandular hairs are excellent characters for separating some species. While odors are particularly useful in the field, herbarium specimens of certain species retain their odor for many years, notably *Arnica viscosa*.
Figures 10-17. Average Basal and Cauline Leaves of Arnica Species.

15. Cauline leaf of Arnica cernua Sweetser, s.n. (ORE), OR, Josephine County.
17. Cauline leaf of Arnica gracilis Christ 19463 (ID), Elmore County.
Figures 18-25. Average basal and cauline leaves of Arnica species.

18. Basal leaf of *Arnica spathulata* S-1381, OR, Josephine County.
19. Cauline leaf of *Arnica spathulata* Detling 4688 (ORE), OR, Josephine County.
21. Cauline leaf of *Arnica discoidea* Copeland s.n. (ORE), CA, Butte County.
24. Cauline leaf of *Arnica viscosa* Muth 733 (PUA), CA, Siskiyou County.
25. Cauline leaf of *Arnica venosa* S-1793, CA, Shasta County.
All species have odors when the leaves are bruised except Arnica latifolia and Arnica cernua. Rarely Arnica latifolia, or suspected hybrids of it and Arnica cordifolia are slightly fragrant, especially in younger, rapidly growing leaves. The odor is lost in older leaves. Among the fragrant-leaved species there are consistent differences in quality and degree of odors. Arnica viscosa has by far the strongest odor, while the closely related species, Arnica venosa, has only a slight fragrance, at least in the few populations studied in the field. There also seem to be consistent differences in the odors of closely related species, as in Arnica cordifolia and Arnica nevadensis, although there is some variation in odor in different populations of each of these species.

Vestiture

Maguire (1943, p. 403) comments on the use of pubescence as a critical character in work on Doronicum by Cavillier (1907) and the Russian Arnicas by Iljin (1926), but he cautions against relying too heavily on this character alone. Pubescence, or the lack thereof, is a good morphological character, especially in the field, when used in conjunction with other characters for determining Arnica taxa. With few exceptions all parts of all species are to some degree pubescent, most often densely so.

There are two basic hair types in Arnica, septate glandular and non-glandular. Each of these types commonly occur in two types, long (1-2 mm) and short (0.1-0.2 mm), although there are numerous intermediate examples. The stipitate glandular hairs have septate stalks usually two cells thick except just beneath the gland where they are one-celled. The gland is composed of two to many cells. A majority of the stipitate glandular hairs are about 1 mm long on stalks composed of 6-8 cells, or they are quite short
(0.1-0.2 mm) with stalks 2-3 cells long.

The degree of glandular pubescence imparts a more or less viscid or "clammy" and aromatic character to the leaves and stems of certain species, especially Arnica cordifolia, Arnica nevadensis, and Arnica viscosa. This character alone makes them readily separable in the field from those species largely lacking glandular hairs, most notably Arnica cernua and Arnica latifolia. In Arnica gracilis the predominant hair type is the short, nearly sessile, glandular hair less than 0.1 mm long giving the leaves a rough appearance under 10X magnification. In the other species bearing glandular hairs there are mixtures of both the long and short hairs, except in Arnica viscosa which has only long glandular hairs.

Non-glandular septate hairs are always one cell thick except at their bases and they are usually straight, the exceptions being on the lower part of the stems of some species, especially Arnica cernua. (Figure 62). Again two sizes of non-glandular hairs are seen, long ones 1-2 (-3) mm long and short ones 0.3-0.5 mm long, with some intermediates. The number of non-glandular hairs imparts a softness to the leaves of Arnica cordifolia, Arnica discoidea, and Arnica venosa.

In certain species or populations the glandular hairs are colored, notably the yellow-tipped hairs of Arnica viscosa and the purple-tipped or based hairs of Arnica spathulata and to a lesser degree Arnica discoidea.

Figures 26 to 126 show the vestiture types of all vegetative parts of the species in these two subgenera, but with no indication of relative abundance of vestiture.
Figures 26-126. Comparison of Vestiture Types on Four Vegetative Parts of *Arnica* Species.
**Taxon**

**cordifolia**

**latifolia**

none

1 mm

**cordifolia-latifolia**

natural hybrid

**Lower Cauline**

**Upper Cauline, Periclinum, Phyllaries**
Taxon

leaf, adaxial

leaf, abaxial

cordifolia

latifolia

none

1 mm

none

cordifolia-
latifolia
natural hybrid
Lower Cauleine

Taxon

gracilis

nevadensis

cernua

Upper cauleine,
Periclinum, Phyllaries

1mm

56

57

58

59

60

61

62

63

64
Taxon

Leaf, adaxial

Leaf, abaxial

gracilis

1mm

nevadensis

none

cernua

none
Taxon

Leaf, adaxial

Leaf, abaxial

discoidea

spathulata

1mm
Lower Cauline
Taxon

Upper Cauline, Periclinum, Phyllaries

**viscosa**

**venosa**

1 mm
Capitula

Heads vary from turbinate to campanulate in the few-flowered species (i.e., *Arnica viscosa* and *Arnica gracilis*) to broadly hemispheric in most of the remaining species. They are less than 1 cm broad in the discoid *Arnica viscosa* to nearly 6 cm broad in terminal radiate heads of *Arnica cordifolia*. Heads in different species may be radiate with a single row of marginal ray florets or discoid, lacking ray florets. In the normally discoid species there may be elongated ray-like (ampliate) florets (Figures 154-156) and in the normally radiate species the ray florets may be absent. There are normally 1-3 heads per stem, with a larger terminal one and a pair or several pairs of lateral heads, with rarely as many as 30 or more heads per stem as in some populations of *Arnica latifolia*, *Arnica discoidea*, and *Arnica spathulata*. Heads are held erect at anthesis in most species. They are consistently nodding in bud in *Arnica cernua* and *Arnica venosa* and are often held at a 45-60° angle at anthesis in *Arnica cernua*, *Arnica cordifolia*, and *Arnica venosa*.

Phyllaries

Average number, size and shape of involucral bracts (phyllaries) are shown in Figures 127-136. These are variable characters within species and within populations, but offer some consistent differences in some taxa. All are lanceolate to ovate with acute tips, except *Arnica cernua*, *Arnica spathulata*, and *Arnica discoidea* which often have rounded tips. Phyllaries are consistently smaller and narrower in *Arnica viscosa* and *Arnica gracilis* than in other species. Putative natural hybrids between *Arnica cordifolia* and *Arnica latifolia* consistently have more phyllaries than either parent.
Figures 127-136. Average Involucral Bracts of Arnica Species.

127. Arnica nevadensis S-1870, CA, Sierra County.


129. Arnica cordifolia X Arnica latifolia (putative natural hybrid) 
S-1475, MT, Ravalli County.

130. Arnica latifolia S-1500, WA, Chelan County.

131. Arnica gracilis S-1605, AB, Moraine Lake.

132. Arnica cernua S-1386, OR, Josephine County.

133. Arnica discoidea S-1825, WA, Klickitat County.

134. Arnica spathulata S-1380, OR, Josephine County.

135. Arnica venosa S-1940, CA, Shasta County.

136. Arnica venosa S-1411, CA, Siskiyou County.
Margins of phyllaries are usually entire, although in rare cases they have a few irregular teeth. Bases of the phyllaries and the periclinum (area of attachment of phyllaries to the peduncle) are usually the most densely pubescent part of most plants and often have the longest hairs on the plant.

Ray Florets

All ray florets consist of a short tube and large flattened limb (Figures 137-142). The tube and lower surface of the limb are variably pubescent. The general outline of the limb is linear oblong to ovate with a rounded tip or more frequently one to several characteristic teeth. The sizes and shapes of these teeth are used in distinguishing between some species. These are especially good field characters, not always apparent in pressed herbarium specimens. The number of rays varies from typically five or rarely less in depauperate heads to occasionally twenty or more per head. Rays are always bright yellow and pistillate with an elongated style extending beyond the tube.

Disc Florets

Heads contain as few as 9-10 to more than 180 disc florets. These are mostly tubular or goblet-shaped (Figures 143-153). There is often a distinctive ring at the base where the tube attaches to the ovary and another ring about midway up the tube where the filaments are attached within. At this point the limb flares out, abruptly in some cases, very gradually in others. At the distal end of the limb are five recurved lobes. Disc florets are perfect with five anthers united around the pistil. Nectar is produced and the florets are fragrant. They are always bright yellow except in Arnica viscosa in which they are white or cream-colored. Walls of the tube and limb are often nearly translucent. Disc florets are sparsely to densely hairy on the
Figures 137-142. Typical ray florets of Arnica subgenus Austromontana.

137. Arnica cordifolia S-1353, BC, Botanie Valley.

138. Arnica cordifolia X Arnica latifolia hybrid S-1474, MT, Ravalli County.

139. Arnica latifolia S-1680, BC, Manning Park.

140. Arnica cernua S-1386, OR, Josephine County.

141. Arnica nevadensis S-1870, CA, Sierra County.

142. Arnica gracilis S-1605, AB, Moraine Lake.

143. Arnica cordifolia S-1353, BC, Botanie Valley.

144. Arnica cordifolia X Arnica latifolia S-1474 (putative natural hybrid), MT, Ravalli County.

145. Arnica latifolia S-1476, MT, Missoula County.

146. Arnica nevadensis S-1870, CA, Sierra County.

147. Arnica gracilis S-1605, AB, Moraine Lake.

148. Arnica cernua S-1386, OR, Josephine County.
Figures 149-152. Typical Disc Florets of *Arnica* Species in Subgenera *Austromontana* and *Calarnica*.

149. *Arnica discoidea* S-1789, CA, Marin County.

150. *Arnica spathulata* S-1742, OR, Josephine County.

151. *Arnica viscosa* S-1411, CA, Siskiyou County.

152. *Arnica venosa* S-1793, CA, Shasta County.
Figures 153-156. Florets of *Arnica discoidea*.

153. Typical disc floret, WA, Klickitat County, S-1825.

154. Marginal ampliate floret from same head.

155. Elongated marginal floret with abortive anthers, CA, Santa Barbara County, *Smith 8330* (SBM).

tube or throughout (especially in *Arnica venosa*). There are always a few hairs on the tips of the lobes as well as distinctive papillae on their inner surface. The florets are usually uniform in size and shape and symmetrical throughout the head. In many of the discoid heads of *Arnica discoidea* the marginal florets are asymmetrical, known as ampliate florets (Figure 155) or much elongated and ray-like with abortive anthers (Figures 154, 156).

**Pappus**

The pappus is composed of a ring or rings of about 27-65 multicellular bristles with lateral setae. The length of bristles varies according to the length of the floret, but the length of lateral setae is relatively consistent within some species or species groups. Maguire (1943, p. 402) treats these setae in three groups according to length: barbellate, with setae 0.1-0.2 mm; subplumose, 0.2-0.35 mm; and plumose, 0.35-0.6 mm. Most taxa in these two subgenera fall within the first two groups (Figures 157-165, 186). The pappus of the whole head forms a round ball 1-3 cm in diameter upon maturity of the achenes. Color of the mature pappus is usually pure white in most species or often tawny in *Arnica nevadensis*, *Arnica viscosa*, and *Arnica gracilis*.

**Achenes**

The best single reproductive character for separating some of the closely related species, is the vestiture of the achene surface (Figures 166-185). Table I gives a comparison of mature achenes. They are usually 5-8 mm long and 1 mm wide at their widest point, the distal end, linear oblong to clavate, weakly to strongly 5-10 angled. The surface is dark grey or brown to black
Figures 157-161. Photographs with light microscope of near mid-length of pappus.


158. Arnica latifolia S-1162, WA, Whatcom County.

159. Arnica cernua S-1772, CA, Humboldt County.

160. Arnica cordifolia S-1939, CA, Mono County.

161. Arnica nevadensis S-1870, CA, Sierra County.
Figures 162-165. Photographs with light microscope of near mid-length of pappus.

162. **Arnica discoidea** Detling 6050 (ORE), CA, Siskiyou County.

163. **Arnica spathulata** S-1381, OR, Josephine County.

164. **Arnica venosa** S-1940, CA, Shasta County.

165. **Arnica viscosa** S-1411, CA, Siskiyou County.

167. same, X130.

168. Arnica nevadensis S-1870, CA, Sierra County, X65.
169. same, X130.

170. Arnica discoidea S-1825, WA, Klickitat County, X65.
171. same, X130.
Figures 172-177. Scanning Electron Micrographs of Achene Surfaces (mid-length) of *Arnica* species.

172. *Arnica cernua* S-1772, CA, Humboldt County, X65.
173. same, X130.
174. *Arnica latifolia* S-1476, MT, Missoula County, X65.
175. same, X130.
177. same, X130.

178. Arnica spathulata S-1380, OR, Josephine County, X65.
179. same, X130.
180. Arnica venosa S-1940, CA, Shasta County, X65.
181. same, X130.
182. Arnica viscosa S-1411, CA, Siskiyou County, X65.
183. same, X130.
185. Photomicrograph with light microscope, achene surface of Arnica cordifolia S-1487, WA, Okanogan County, X500.
186. Scanning electron micrograph of pappus bristle (mid-length) of Arnica cordifolia S-1353, BC, Botanie Valley, X575.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Color</th>
<th>Length (mm)</th>
<th>Width Distally (mm)</th>
<th>Double Hairs</th>
<th>Glandular Hairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>cordifolia</td>
<td>dark grey</td>
<td>(6-)7-9(-10)</td>
<td>1+</td>
<td>uniform throughout or especially distally</td>
<td>uniform throughout</td>
</tr>
<tr>
<td>latifolia</td>
<td>grey-brown</td>
<td>(5-)6-8(-10)</td>
<td>1-</td>
<td>none or few distally</td>
<td>none or few distally</td>
</tr>
<tr>
<td>gracilis</td>
<td>black</td>
<td>(4-)5-6(-7)</td>
<td>1</td>
<td>none or very few distally</td>
<td>none or few throughout or many distally</td>
</tr>
<tr>
<td>cernua</td>
<td>dark grey</td>
<td>6-8</td>
<td>1+</td>
<td>many throughout or distally</td>
<td>none</td>
</tr>
<tr>
<td>nevadensis</td>
<td>dark grey to black</td>
<td>(4-)5-8</td>
<td>1+</td>
<td>few throughout or distally</td>
<td>uniform throughout</td>
</tr>
<tr>
<td>discoides</td>
<td>dark grey</td>
<td>6-8</td>
<td>1+</td>
<td>few to many throughout</td>
<td>few throughout</td>
</tr>
<tr>
<td>spathulata</td>
<td>black</td>
<td>7-9</td>
<td>1</td>
<td>none to few throughout</td>
<td>few throughout or distally</td>
</tr>
<tr>
<td>venosa</td>
<td>grey</td>
<td>6-8</td>
<td>1.5-2</td>
<td>many throughout</td>
<td>none</td>
</tr>
<tr>
<td>viscous</td>
<td>dark grey</td>
<td>5-6</td>
<td>1</td>
<td>none</td>
<td>uniform long-stipitate throughout</td>
</tr>
</tbody>
</table>
and minutely crested and undulate (Figure 184), although this is usually obscured by the surface hairs. There is a thick white ring, the annulus, at the base where the achene was attached to the receptacle and another ring located distally to which the pappus is attached. Achenes of ray florets are shorter and broader than those of the disc florets. Most achene coats have few to many double-pronged or "duplex" hairs (Figure 185), especially distally, in addition to long stipitate (Figure 183) to nearly sessile (Figure 184) glandular hairs. The position and relative abundance or sparsity of these hairs is used in this study as an important diagnostic character.

DISTRIBUTION AND ECOLOGY

Both of these subgenera are largely Western Cordilleran (in the broad sense) with eastern extensions or disjunct populations into the Cypress Hills of Saskatchewan, Black Hills of South Dakota, and around Lake Superior. None of these species is truly arctic as are some of the species in other subgenera. They occur in a variety of habitats from open alpine or mountain meadows, forest edges, open forests, disturbed roadside banks, stabilized rock slides, and stabilized burned-over areas, but mostly cool, mesic habitats. Only Arnica venosa is a plant of the hot, dry foothills of the upper Sacramento River Valley of Northern California. Two species, Arnica cernua and Arnica spathulata are restricted to or usually found on serpentine soils. Arnica viscosa is limited to high pumice slopes.

REPRODUCTIVE BIOLOGY

Phenology

Being montane or alpine plants, all species of Austromontana begin new
innovation growth and flowering stem elongation as soon as spring or summer
snows have melted. In coastal low mountains of California and Oregon this
may occur in April, while at higher altitudes and latitudes growth may begin
as late as September or October (or probably not at all some years where snow
cover is excessive). High alpine populations often have elongated flowering
stems under the melting snow or have stems emerging through the snow.

In areas where there is typically dry weather following the spring snow-
melt, as occurs east of the Cascade Mountains and in the Siskiyou and Klamath
Mountains, there is usually a brief flowering period of a few weeks with no
more lateral flower buds being produced after the monocephalous or few-headed
stems have flowered. This is the common condition in most species. In wetter
habitats populations of the same species or other species may continue to
branch and flower for months. Other species, especially Arnica latifolia,
produce only one "flush" of flowers regardless of the weather conditions
thereafter.

In a growth chamber under conditions of 16 hour days, 25°C, and adequate
moisture and fertilizer, populations of several species, Arnica cordifolia,
Arnica discoidea, Arnica venosa, and especially Arnica viscosa continued to
produce lateral branches and new growth from rhizomes and flowered continuous-
ly for more than a year. Other experimental populations of Arnica cordifolia,
Arnica discoidea, Arnica spathulata, Arnica gracilis, Arnica nevadensis, and
especially Arnica latifolia, produced only one "flush" of heads. Although
leaves remained green for months and new vegetative growth was produced, no
more flower buds were produced regardless of the growth regime. Only after
several weeks of vernalization and then increasingly warmer temperatures and
increased light were new flowering stems produced.
Actual flowering time from the opening of the first disc or ray floret to the opening of the last disc floret may be as brief as two days in the few-flowered species (e.g., Arnica gracilis) to more than a week in the larger flowered species.

During dry weather lateral buds often abort and at least during some years all the flower buds abort, as observed with numerous populations of Arnica cordifolia in central Wyoming during June 1978. Here, very large populations had flowering stems but no flowers.

Achenes ripen within a few weeks of flowering and are blown away. New rhizome growth begins about the time of flowering with the new innovations emerging during or just after flowering. All above-ground growth becomes dry and soon disappears except in wetter habitats where plants may remain green until fall frost.

In Calarnica the stems become much elongated and often branched before flowers are produced. Several weeks or months may elapse from emergence to flowering. Flowering may be rather brief with few heads per stem in Arnica venosa or longer for the much-branched Arnica viscosa.

Cytology

For chromosomal study, fixed anthers from small buds were excised on a glass slide, a drop of aceto-carmine was added, and the anthers were macerated with iron needles for about 1-3 minutes until the aceto-carmine became dark purple. A drop of Hoyer's medium (Beeks, 1955) was added to make the slide permanent, a cover slip was added, and the preparation was warmed briefly over a flame and squashed. Cover slips were later ringed with diaphane. Observations of chromosome number and meiotic behavior of microsporocytes were made
with a positive phase-contrast microscope. Tapetal cells were not used for chromosome number determinations since numerous observations of high polyploid numbers were made in tapetal cells surrounding diploid or tetraploid microsporocytes. Some chromosome number determinations were made from root-tips from potted plants grown in the greenhouse or growth chamber or from achenes germinated on moist filter paper. The root-tips were soaked in a supersaturated aqueous solution of paradichlorobenzene for 1-2 hours (Strother, 1969) before fixing and staining as for flower bud material.

Arnica chromosomes are small (ca. 5 µm), they do not fix well, and meiotic associations are often difficult to interpret, resulting in many of the previous reports being approximations or probable errors. Often many microsporocytes from a number of squashes had to be observed before accurate counts or pairing was determined. Although diploids usually form regular bivalents during metaphase I of meiosis (Figure 194), in the higher ploidy levels there is usually irregular behavior, with variable numbers of univalents, bivalents, multivalents, and chains present at metaphase I and lagging chromosomes and bridge formation during anaphase I (Figure 187), as has been noted previously by Ornduff, et al. (1963, 1967) and Barker (1966).

Table II lists all previously reported chromosome numbers for these two subgenera, a number of which are approximations. There is only one previous report for Arnica cernua and Arnica venosa and two each for Arnica gracilie, Arnica spathulata, and Arnica viscosa. Only for the two widespread species, Arnica cordifolia and Arnica latifolia, are there sufficient previous reports to show trends in ploidy levels. Table III shows new chromosome numbers observed during this study, more than twice the number of all previous reports. Counts for Arnica nevadensis are presented for the first time. Figures 187-
189 and 193, 194 show photographs of meiotic chromosomes of *Arnica gracilis*, *Arnica cordifolia*, and *Arnica discoidea*. Figures 195-207 show camera lucida drawings of all ploidy levels observed during this study, of all species recognized.

To summarize known chromosome numbers, five species in these subgenera are wholly diploid. These are *Arnica viscosa*, *Arnica venosa*, *Arnica cernua*, *Arnica latifolia* (one tetraploid reported), and *Arnica spathulata* (one tetraploid reported). Both diploid and tetraploid populations are known for *Arnica discoidea*. *Arnica gracilis* is predominately triploid, with one tetraploid and one hexaploid previously reported, although voucher specimens from these reports have not been seen. *Arnica nevadensis* is tetraploid, based on counts from three populations. *Arnica cordifolia* is the most variable, being predominately tetraploid, with a few diploid, triploid, pentaploid, and hexaploid populations known.

Apomixis

To determine if plants were apomictic, heads were bagged with cloth bags (Figure 211) before the rays opened on radiate species, or before the outer discs opened on discoid species. Barker (1966) showed that sexual diploids are self-incompatible, and there is additional data to support his findings. However, it was assumed that known polyploid populations producing viable achenes from bagged heads were indeed apomicts rather than self-compatible amphimicts (sexual plants). To insure that pollen was being transferred from anthers to stigmas, heads were gently rubbed on several successive days, as the florets matured and stigmas emerged from the surrounding anthers. When the achenes matured each was checked for contents. *Arnica* achenes are


188. Late anaphase I of same.

189. Late anaphase II of same.

190. "Quintad" and "Sextad" of same.


192. *Arnica nevadensis* S-1910, NV, Washoe County, SEM of pollen grains showing large and small grains, X1200.

193. *Arnica cordifolia* S-1416, CA, Sierra County, tetraploid (2n=76) with 37 chromosomes at each pole of the cell and one lagging pair.

194. *Arnica discoidea* S-1787, CA, Napa County, diploid (2n=38) with 19 pairs of chromosomes at metaphase I. Bars = ca 50 μm.
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<tr>
<th>Taxon</th>
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<th>Locality</th>
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TABLE III. New Chromosome Numbers for *Arnica* Species in the Subgenera *Austromontana* and *Calarnica*.

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Putative Natural Hybrids

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Figure 195. *Arnica cernua* S-1772, CA, Humboldt Co. Microsporocyte, metaphase I plate, diploid with 19 pairs of chromosomes.

Figure 196. *Arnica latifolia* S-1529, BC, Vancouver Island, Forbidden Plateau. Microsporocyte, metaphase I plate, diploid with 19 pairs of chromosomes.
Figure 197. *Arnica cordifolia* S-1819, OR, Wasco County. Microsporocyte, late anaphase I, tetraploid with 38 chromosomes at each pole.

Figure 198. *Arnica cordifolia* S-1601, AB, Vermillion Pass. Microsporocyte, metaphase I plate, hexaploid with variable univalents, bivalents, and trivalents.
Figure 199. *Arnica cordifolia* X *Arnica latifolia* S-1475, putative natural hybrid, MT, Ravalli County. Microsporocyte, diakinesis, diploid with 19 pairs of chromosomes.

Figure 200. *Arnica cordifolia* S-1594, BC, E. of Windermere. Microsporocyte, late anaphase I, triploid with 30 chromosomes at one pole of cell and 27 at the other.
Figure 201. *Arnica gracilis* S-1613, AB, Peyto Lake. Microsporocyte, metaphase I plate, triploid, with variable univalents, bivalents, and trivalents.

Figure 202. *Arnica nevadensis* S-1870, CA, Sierra County. Microsporocyte, anaphase I, tetraploid, with 76 chromosomes.
Figure 203. *Arnica spathulata* S-1392, OR, Josephine County. Microsporocyte, metaphase I plate, diploid with 19 pairs of chromosomes.

Figure 204. *Arnica discoidea* S-1787, CA, Napa County. Microsporocyte, metaphase I plate, diploid with 19 pairs of chromosomes.

Figure 205. *Arnica discoidea* S-1821, OR, Wasco County. Microsporocyte, metaphase I plate, tetraploid with 38 pairs of chromosomes.
Figure 206. *Arnica viscosa* S-1411, CA, Siskiyou County. Microsporocyte, diakinesis, diploid with 19 pairs of chromosomes.

Figure 207. *Arnica venosa* S-1793, CA, Shasta County. Microsporocyte, metaphase I palte, diploid with 19 pairs of chromosomes.
produced regardless of the presence or absence of a viable seed within. These empty achenes are often as large as viable achenes and appear to be viable until examined closely or until the achene coat is removed.

According to Barker (1966) the two common types of apomixis found in Arnica are:

**Autonomous apomixis** - Seed production without pollination or fertilization.

**Pseudogamous apomixis** - Seed production does not occur unless the polar nuclei are fertilized to produce endosperm. Embryo development is parthenogenetic.

In addition to the bagging experiments, two emasculation methods were used to determine autonomous apomicts. In radiate populations disc florets were carefully removed from heads before the discs opened and before the rays had elongated (Figure 209). The head was then bagged, leaving the pistillate ray florets to mature in the absence of pollen. On other heads, either radiate or discoid, at the same stage of development, the whole top of the head from just above the ovary was removed with a razor blade, thus removing all anthers, stigmas, and the upper portion of the styles. The heads were then bagged and allowed to mature. Although severe, this treatment seems to have no detrimental effects on viable achene production in autonomous apomicts. The results of these bagging and emasculation procedures are shown in Table IV.

The breeding systems of the nine species are:

Sexual (self-incompatible)

*Arnica cernua* (Barker, 1966)

*Arnica discoidea* populations (Barker, 1966, as *Arnica parviflora*)
Figures 208-211. Experimental methods.

Figure 208. Arnica in cultivation in experimental field, UBC Botanical Garden Nursery.

Figure 209. Head of Arnica cordifolia S-1497, WA, Okanogan County, with disc florets removed.

Figure 210. Growth Chamber with plants in flower, seedlings in pots, and seeds germinating in petri dishes.

Figure 211. Arnica head bagged.
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<th>Diploid Chromosome #</th>
<th>Pollen Stainability</th>
<th># of Heads Selfed</th>
<th># of Heads Emasculated</th>
<th># of Achenes Produced</th>
<th># of Achenes With Seeds</th>
<th>% of Achenes With Seeds</th>
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<td>of Heads Emasculated</td>
<td>of Achenes Produced</td>
<td>of Achenes With Seeds</td>
<td>% of Achenes With Seeds</td>
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<p>| Taxon &amp;  | Diploid | Pollen | # of Heads | # of Heads | # of Achenes | # of Achenes | % of Achenes |</p>
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**Hybrids**

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<th># of Heads</th>
<th># of Achenes</th>
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</table>
**Arnica latifolia**  
**Arnica spathulata** populations  
**Arnica venosa**  
**Arnica viscosa**  

Autonomous Apomicts  
**Arnica cordifolia** populations  
**Arnica gracilis**  
**Arnica nevadensis**  

Pseudogamous Apomicts  
**Arnica cordifolia** populations  
**Arnica discoidea** populations  
**Arnica spathulata** populations (Barker, 1966)

**Pollen Stainability**

For pollen stainability tests, contents of freshly dehisced anthers of one or more florets of a plant from a wild-collected population or herbarium specimen was tapped out on a glass slide. Pollen grains were stained with a drop of cotton blue-lactophenol and a cover slip was added. The stainability of a 200-grain random sample for each population was scored after 24 hours. Large, well-formed grains stained dark blue were scored as "good". Those that did not stain or were small and misshapened were scored as "bad" (Figure 191).

The range of pollen stainability for each species is shown in Figures 212-221. Several of the species are so rare in nature and in herbaria that few specimens could be sampled.

Barker (1966) discussed the correlation between ploidy level, apomixis, and pollen stainability. The data presented here support his findings.
There are some distinct trends among certain species. The exclusively or predominately diploid, sexual species including *Arnica latifolia*, *Arnica cernua*, *Arnica spathulata*, *Arnica venosa*, and *Arnica viscosa* all show very high pollen stainability, mostly greater than 90%.

A second group of species includes *Arnica gracilis* and *Arnica nevadensis* which have mostly less than 10% stainable pollen. These two are known to be or presumed to be autonomous apomicts and mostly or entirely polyploids. A number of populations of *Arnica gracilis* sampled had no pollen produced in any florets. In known triploid populations of *Arnica gracilis* the production of small and unstainable normal sized pollen grains (Figures 191, 192) can be followed from irregular pairing of chromosomes to the production of more than four groups of chromosomes after anaphase II, the normal tetrad stage (Figure 189). Walls often form around these "quintads" or "sextads" resulting in micro pollen grains and normal sized grains (Figures 187-192). Even these large grains apparently lack a full complement of chromosomes and often fail to develop into a viable, or at least stainable, pollen grain.

A third group includes *Arnica cordifolia* and the closely related *Arnica discoidea* in which pollen stainability is erratic from 0-100% and does not seem to indicate anything specifically about the ploidy level or apomixis. In *Arnica discoidea* there are both diploid populations with high pollen stainability and tetraploid populations with lower pollen stainability. In *Arnica cordifolia* no definite sexual populations are known and for the known polyploid populations pollen stainability is variable. The best assumption for *Arnica cordifolia* is that lower pollen stainability probably represents autonomous apomictic populations and the higher pollen stainability represents pseudogamous apomictic populations. The few diploid populations which are
Figures 212-221. Range of pollen stainability for *Arnica* populations sampled.
Number of populations

% Pollen Stainability

cordifolia

latifolia

cordifolia-latifolia hybrids

10 20 30 40 50 60 70 80 90 100

Pollin Stainability
Number of populations

% Pollen Stainability
Number of populations

% Pollen Stainability

10 20 30 40 50 60 70 80 90 100

discoidea 218

spathulata 219

venosa 220

viscosa 221
known to exist may be sexual, although they have not been investigated experimentally.

Seed Production

Seed production both in nature and in cultivation is often quite low even in apomictic races. Although several dozen to a hundred or more achenes are produced in each head, many of these are empty. Also, in many populations of most or all species the heads are infested with one to several larvae of achene-feeding dipterans which often feed on most or all of the achenes in a head before the pappus expands and the seeds are dispersed. (See further discussion under Entomological Relationships).

Seed production in cultivation where there were no dipteran infestation was still low except in the autonomous apomictic populations of *Arnica gracilis* and *Arnica nevadensis*. Of achenes examined from 21 heads of *Arnica gracilis* 54-100% (mostly greater than 80%) of the achenes contained seed. Eight heads of *Arnica nevadensis* had 0-70% (mostly greater than 60%) full achenes. In the sexual populations of *Arnica latifolia* 0-72% (mostly less than 20%) of achenes from 25 heads examined contained seeds. Only wild collected achenes of *Arnica cernua* have been observed, with 6-14% full achenes from 5 heads from one population. Of the sexual, self-incompatible populations of *Arnica spatulata*, *Arnica viscosa*, and *Arnica venosa*, only one each has been grown successfully to the flowering and fruiting stage. Therefore, no data of seed production are available. One head of *Arnica venosa* collected in the wild had 47% full achenes.

There is poor seed set in cultivation of the predominately pseudogamous apomictic populations of *Arnica cordifolia* and *Arnica discoidea*. Of more than
50 heads of *Arnica cordifolia* examined, seed production was 0-64% (mostly less than 30%) of achene production. Wild collected achenes had 0-29% full achenes. In *Arnica discoidea* 0-20% of the achenes from 16 heads examined were full.

Seed Germination

Young seedlings in their alpine or montaine environment would be at a disadvantage if the achenes germinated immediately in late summer or fall after falling or being carried from the parent plant. It was suspected that the achenes needed a vernalization or scarification of the achene coat before the seeds would germinate. Germination probably occurs in nature after the spring snow-melt.

Achenes containing seeds were subjected to numerous schemes in an effort to induce germination, including the following:

1. Planted in pots of soil out-of-doors in the fall and allowed to overwinter under "natural" (i.e., Vancouver winter) conditions.

2. Stored dry or in moist sphagnum in the refrigerator (4°C) or freezer (0°C) or dry at room temperature (ca 20°C) for six weeks to several months before planting.

3. Achenes placed immediately after dispersal or after storage on moist filter paper in petri dishes in light (16 hours daylight) at 25°C. (Figure 210).

4. Same as #3 except total darkness.

5. Achene coats carefully removed after they had been soaked in distilled water for 24 hours, then placed on moist filter paper in 16 hours daylight at 25°C.
The results of these various tests have been mixed and there are still some unanswered questions concerning seed germination. The greatest success was had with soaked achenes, with achene coats removed, and then placing the seeds on moist filter paper under long days at 25°C. In no cases did any seed germinate on moist filter paper before the achene coat was removed. After removal, the hypocotyl often began to elongate within 12 hours.

Using the above method there was nearly 100% germination of seeds from some populations of some species, especially *Arnica cordifolia*, *Arnica graci­lis*, and *Arnica viscosa*. With other populations of the same species or other species, especially *Arnica cordifolia*, *Arnica nevadensis*, *Arnica discoidea*, and *Arnica spathulata*, none of the seeds germinated with this, or any other method. In some cases a few days after the achene coat was removed, the cotyledons reflexed, but there was no further sign of growth, even after months. In yet other populations of *Arnica cordifolia*, and especially *Arnica venosa*, a few seeds germinated immediately, while others remained plump and apparently capable of germination for up to six months, yet there were no signs of hypocotyl or epicotyl elongation. Often during the longer tests the dishes became infested with mold or algae, so that the seeds had to be discarded.

Vernalization is not needed for germination. Under artificial conditions germination was not enhanced by cooling or freezing the achenes. However, scarification of the achene coats seems to be essential for germination. Achenes planted directly in soil out-of-doors did not germinate the following spring. The achenes were very difficult to locate to determine if they still were viable or if they had decomposed during the winter.
Seedlings

Of more than 200 populations studied in the field, including all taxa recognized in this study, no seedlings were observed.

Seedlings grown from seeds germinated in the growth chamber were transplanted into a sterilized standard potting medium as soon as the first pair of true leaves started to develop. These were grown in the growth chamber under the same growing conditions as for germination. Mortality rate of the young seedlings was relatively high for the first few weeks. Most healthy seedlings were very slow growing, taking 1-3 months to develop three pairs of leaves. Seedlings of the serpentine endemic *Arnica cernua* grown both in potting medium and in serpentine soil grew equally slowly, the basal rosette reaching only 2-3 cm in diameter and with 3-4 pairs of leaves after 6-8 months. Others, especially *Arnica cordifolia*, *Arnica viscosa*, and *Arnica venosa* grew quickly after the third or fourth month and flowered by the sixth month (Figure 278). One seedling of *Arnica viscosa* had become much branched and produced more than 100 flowers by the eighth month. Seedlings of *Arnica latifolia* and *Arnica gracilis* produced robust basal rosettes and some rhizome growth within 6 months but no flowering stems were produced.

Two-month old seedlings grown in a growth chamber are shown in Figures 222-227. Even when quite young (by the first pair of true leaves) many of the seedlings assume the typical characters of the more mature plant, in leaf shape, roots, and especially in pubescence, although the seedlings are often more pubescent when young than they are later. After a few weeks the *Austromontana* species remain as a basal rosette with no stem elongation, while the *Calarnica* species form a definite stem by the time the second or third pair of true leaves have developed.
Figures 222-227. Arnica Seedlings ca 2 months after germination, 
grown in growth chamber.

Figure 222. Arnica cordifolia S-1497, WA, Okanogan County.

Figure 223. Arnica latifolia S-1855, AB, south of Grande Prairie.

Figure 224. Arnica gracilis S-1562, BC, Monroe Lake.

Figure 225. Arnica cernua S-1772, OR, Josephine County.

Figure 226. Arnica viscosa S-1411, CA, Siskiyou County.

Figure 227. Arnica venosa S-1940, CA, Shasta County.
Vegetative Reproduction

Considering the low seed production, infestations of achene feeding Diptera, and poor germination of seeds, vegetative reproduction by rhizomes in species of subgenus *Austromontana* is critical for their successful colonization.

Little or no information exists on vegetative reproduction potential in Arnicas. Herbarium specimens are of little value. Although Arnicas make nice herbarium specimens (i.e., they fit conveniently on a standard herbarium sheet) and they are frequently collected and are well-represented in herbaria, plants are usually pulled from the ground rather than dug, resulting in the rhizomes being left behind. Specimens with rhizomes usually show only one season's growth or a portion thereof. No known previously collected specimens of the two species in subgenus *Calarnica* had enough of the underground parts present to determine if they were or were not rhizomatous.

Records of annual rhizome growth have been kept on populations of all species seen in the field in addition to several years of records of growth of some populations in cultivation (Figures 228-231, Table V). These studies have been supplemented by measurements from herbarium specimens. In most instances the average growth is lower than the median. A few populations growing in relatively dense shade or in very loose soils tend to have the extremely long rhizomes. Examples are the low elevation populations of *Arnica gracilis* from forests at Monroe Lake, BC (Straley 1562) with rhizomes up to 6 cm long, whereas a majority of the populations as represented by those from high alpine rock scree slopes of Banff and Jasper National Parks, AB (Straley 1603, 1605, 1613) average only 1-2 cm of growth per year.
Figure 228. Rhizome growth measured over four years, *Arnica cordifolia* S-1512, UBC Botanical Garden, Native Garden. Plant originally from Kootenay District, BC.
Figure 229. Rhizome growth measured over 4 years, *Arnica latifolia* S-1162, WA, Whatcom County, Mt. Baker.
Figure 230. Rhizome growth measured over four years, *Arnica cernua* S-1772, CA, Humboldt County, Hoopa Mountain.
Figure 231. Rhizome growth measured over 3 years, *Arnica gracilis* S-1605, AB, Moraine Lake.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Annual Growth (cm)</th>
<th>Annual Average (cm)</th>
<th>Breeding System</th>
<th>Average Seed Viability</th>
</tr>
</thead>
<tbody>
<tr>
<td>cernua</td>
<td>(1-)4-15(-20)</td>
<td>6</td>
<td>Sexual</td>
<td>14%</td>
</tr>
<tr>
<td>cordifolia</td>
<td>2-20(-60)</td>
<td>10</td>
<td>Apomictic</td>
<td>30%</td>
</tr>
<tr>
<td>discoidea</td>
<td>5-15(-22)</td>
<td>7</td>
<td>Sexual and Apomictic</td>
<td>20%</td>
</tr>
<tr>
<td>gracilis</td>
<td>(0.5-)1-2(-6)</td>
<td>1.5</td>
<td>Apomictic</td>
<td>80%</td>
</tr>
<tr>
<td>latifolia</td>
<td>(0.5-)1-7(-10)</td>
<td>4</td>
<td>Sexual</td>
<td>20%</td>
</tr>
<tr>
<td>nevadensis</td>
<td>(1-)3-12</td>
<td>6</td>
<td>Apomictic</td>
<td>60%</td>
</tr>
<tr>
<td>spathulata</td>
<td>(1-)3-7(-14)</td>
<td>5</td>
<td>Sexual and Apomictic</td>
<td>?</td>
</tr>
</tbody>
</table>
There seems to be no distinct correlation between rhizome production and successful seed set or between the rhizome production of predominately sexual compared to apomictic species. However, there are some consistent differences between average rhizome growth of some of the closely related species. The average growth in *Arnica cordifolia*, for instance, is 2.5 times that of *Arnica latifolia* and the growth of *Arnica gracilis* is less than half as great as that of *Arnica latifolia*. The derived species (*Arnica cernua* and *Arnica gracilis* from *Arnica latifolia*, and *Arnica discoidea*, *Arnica spathulata* and *Arnica nevadensis* from *Arnica cordifolia*) all have lower rhizome production than do their presumed ancestral species.

Several of these species frequently invade landslides, burned-over areas, and other disturbed habitats. Particularly in *Arnica cordifolia* the yearly rhizome growth rates shown here could easily explain the vast coverage of an area by a single population after hundreds or thousands of years, from only one successful achene introduction.

**CULTIVATION OF ARNICA SPECIES**

*Arnica* populations have been transplanted from nature or grown from seed in the growth chamber, greenhouse, and experimental field at UBC with mixed results.

Some species, especially *Arnica cordifolia*, *Arnica nevadensis*, and *Arnica gracilis* have been most easily transplanted, with near 100% success, and with most populations flowering freely after transplanting. *Arnica spathulata*, *Arnica discoidea*, and *Arnica viscosa* have given mixed results. Some populations transplanted easily and flowered seasonally for several years. Others either did not survive or have lived for only a few months and flowered poorly
or not at all. The widespread *Arnica latifolia* usually survives moving, but flowers very poorly in future years, although it reproduces abundantly by rhizomes in cultivation. The serpentine endemic *Arnica cernua* has not been successfully transplanted. A few plants have survived for a year or two in the experimental garden but have become progressively smaller and have never flowered in cultivation. A few achenes have germinated and the resulting seedlings have grown very slowly both in serpentine soils and in a standard soil-less potting mixture. Two plants from different populations of the rare *Arnica venosa* have been unsuccessfully transplanted from the wild. However, unlike *Arnica cernua*, seedlings of *Arnica venosa* from achenes germinated on filter paper and transplanted to a soil-less potting mixture have grown quickly and flowered freely in cultivation.

In all cases, the tops died back to the rhizomes when plants were dug from the wild while in flower or just before or after. However, in most cases, there were new sprouts produced from the rhizomes within a few weeks of transplanting, often producing flowering stems several weeks later.

**HYBRIDIZATION**

**Sympatric Occurrence and Natural Hybridization**

There is very little evidence of recent hybridization occurring in nature between any of the species in *Austromontana* and *Calarnica*, or with species in other subgenera. There are a number of populations exhibiting intermediate characters between *Arnica cordifolia* and *Arnica latifolia*, usually not growing with one or either parent. These are considered old stabilized hybrids, usually apomicts, and will be discussed under *Arnica cordifolia*. 
Because of different ecological preferences, most of the nine species in these two subgenera do not occur sympatriically. Where two or more species do grow in close proximity or at least close enough for pollen exchange by insect pollinators (see Table VI), they often have little or no overlap in flowering times. This was observed in populations of *Arnica discoidea* and *Arnica cordifolia* growing sympatriically in Wasco County, OR (*Straley* 1820, 1821) and Klickitat County, WA (*Straley* 1825, 1826). In both of these populations the *Arnica cordifolia* was finishing flowering as the *Arnica discoidea* was just beginning to flower. A mixed population of *Arnica cernua* and *Arnica spathulata* (*Straley* 1385, 1386) in Josephine County, OR was observed in May of 1977 and 1978. The *Arnica cernua* was just finishing flowering as the *Arnica spathulata* was just beginning to flower. These two species have also been collected together in Del Norte County, CA (*Klipfel* 770, HSC), with no mention of any evidence of hybridization.

In most of the mixed populations there are also differences in ploidy levels, breeding systems, and viable pollen production, acting singly or usually in combination as barriers to natural hybridization.

A specimen from Custer County, ID (*Cronquist* 3375, UTC) represents an apparent hybrid population growing with both parents, *Arnica gracilis* and *Arnica longifolia*. The specimen is quite intermediate between the two parental types. This is the only herbarium specimen seen of what appears to be a hybrid population between two distinct species in two different subgenera (*Austromontana* and *Chamissonis*).
TABLE VI. Sympatric populations of *Arnica* subgenus *Austromontana* species with no evidence of natural hybrids.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Collection Number</th>
<th>Locality</th>
<th>Pollen Stainability</th>
<th>Diploid Chromosome Number</th>
<th>Breeding System</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>spathulata</em></td>
<td>S-1385</td>
<td>OR, Josephine Co.</td>
<td>100%</td>
<td>38</td>
<td>sexual</td>
</tr>
<tr>
<td><em>cernua</em></td>
<td>S-1386</td>
<td>OR, Josephine Co.</td>
<td>98%</td>
<td>-</td>
<td>sexual</td>
</tr>
<tr>
<td><em>cordifolia</em></td>
<td>S-1573</td>
<td>BC, Yahk Mountain</td>
<td>30%</td>
<td>-</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>latifolia</em></td>
<td>S-1576</td>
<td>BC, Yahk Mountain</td>
<td>100%</td>
<td>-</td>
<td>sexual</td>
</tr>
<tr>
<td><em>gracilis</em></td>
<td>S-1603</td>
<td>AB, Lake Louise</td>
<td>0%</td>
<td>57</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>cordifolia</em></td>
<td>S-1604</td>
<td>AB, Lake Louise</td>
<td>52%</td>
<td>76</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>latifolia</em></td>
<td>S-1612</td>
<td>AB, Peyto Lake</td>
<td>99%</td>
<td>38</td>
<td>sexual</td>
</tr>
<tr>
<td><em>gracilis</em></td>
<td>S-1613</td>
<td>AB, Peyto Lake</td>
<td>2%</td>
<td>57</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>cordifolia</em></td>
<td>S-1616</td>
<td>AB, Peyto Lake</td>
<td>32%</td>
<td>76</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>cordifolia</em></td>
<td>S-1653</td>
<td>BC, Tod Mountain</td>
<td>74%</td>
<td>-</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>latifolia</em></td>
<td>S-1654</td>
<td>BC, Tod Mountain</td>
<td>95%</td>
<td>-</td>
<td>sexual</td>
</tr>
<tr>
<td><em>cordifolia</em></td>
<td>S-1820</td>
<td>OR, Wasco County</td>
<td>85%</td>
<td>76</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>discoidea</em></td>
<td>S-1821</td>
<td>OR, Wasco County</td>
<td>76%</td>
<td>76</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>discoidea</em></td>
<td>S-1825</td>
<td>WA, Klickitat Co.</td>
<td>77%</td>
<td>76</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>cordifolia</em></td>
<td>S-1826</td>
<td>WA, Klickitat Co.</td>
<td>80%</td>
<td>-</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>nevadensis</em></td>
<td>S-1938</td>
<td>CA, Mono County</td>
<td>3%</td>
<td>76</td>
<td>apomictic</td>
</tr>
<tr>
<td><em>cordifolia</em></td>
<td>S-1938</td>
<td>CA, Mono County</td>
<td>8%</td>
<td>57</td>
<td>apomictic</td>
</tr>
</tbody>
</table>
Artificial Hybridization

Reciprocal crosses between all the species in these two subgenera are complicated by several factors. The difficulty in cultivation of some species or populations has been previously discussed. Getting plants to flower concurrently in cultivation is often a problem. In the experimental garden under natural spring conditions, most species produced only one set of flowering stems and the flowering duration was quite brief, especially in Arnica latifolia. While most of the montane and alpine species flower at the same time, Arnica viscosa takes several months for the flower stems to elongate, thus flowering much later than most other species. Under controlled conditions of the growth chamber Arnica viscosa, Arnica venosa, and some populations of other species could be kept flowering for many months, enabling experimental crosses with these and other more rapidly flowering species.

In radiate forms, the ray florets may be used as the female parent in crosses, but the reciprocal crosses cannot be made using the discoid forms with their complete florets as the female parent, without first proving the discoid form is self-incompatible. Emasculation of the small discoid florets before anthesis is tedious and often results in damage to the stigma or loss of the whole floret.

Polyploidy and apomixis are further complications, with sexual populations not known in several species, especially Arnica cordifolia, Arnica nevadensis, and Arnica gracilis. Not only can these species not be used as the female parent in reciprocal crosses, but with very low pollen fertility in many of them, they cannot be used as a pollen source for crosses.

The results of all reciprocal crosses are given in Table VII and summarized in Figure 232.
<table>
<thead>
<tr>
<th>Taxon &amp; Collection # (♀ Parent)</th>
<th>Diploid Chromosome #</th>
<th>Taxon &amp; Collection # (♂ Parent)</th>
<th>Diploid Chromosome #</th>
<th>Heads Crossed</th>
<th>Achenes Produced</th>
<th>Achenes With Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>latifolia 1499</td>
<td>38</td>
<td>cordifolia 1497</td>
<td>76</td>
<td>3</td>
<td>9</td>
<td>0</td>
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<tr>
<td>latifolia 1504</td>
<td>38</td>
<td>cordifolia 1512</td>
<td>57</td>
<td>2</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>latifolia 1961</td>
<td>38</td>
<td>cordifolia 2009</td>
<td>76</td>
<td>2</td>
<td>64</td>
<td>0</td>
</tr>
<tr>
<td>latifolia 1961</td>
<td>38</td>
<td>discoidea 1821</td>
<td>76</td>
<td>1</td>
<td>56</td>
<td>0</td>
</tr>
<tr>
<td>latifolia 1961</td>
<td>38</td>
<td>diversifolia 1419</td>
<td>76</td>
<td>3</td>
<td>118</td>
<td>3</td>
</tr>
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<td>latifolia 1961</td>
<td>38</td>
<td>gracilis 1605</td>
<td>57</td>
<td>1</td>
<td>28</td>
<td>0</td>
</tr>
<tr>
<td>latifolia 1961</td>
<td>38</td>
<td>viscosa 1411</td>
<td>38</td>
<td>1</td>
<td>53</td>
<td>0</td>
</tr>
<tr>
<td>latifolia 1503</td>
<td>38</td>
<td>mollis 1515</td>
<td>?</td>
<td>1</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>latifolia 1504</td>
<td>38</td>
<td>mollis 1515</td>
<td>?</td>
<td>1</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>spathulata 1380</td>
<td>38</td>
<td>cordifolia 1477</td>
<td>76</td>
<td>2</td>
<td>69</td>
<td>3</td>
</tr>
<tr>
<td>spathulata 1380</td>
<td>38</td>
<td>cordifolia 1497</td>
<td>76</td>
<td>2</td>
<td>37</td>
<td>0</td>
</tr>
<tr>
<td>venosa 1940</td>
<td>38</td>
<td>cordifolia 2005</td>
<td>76</td>
<td>1</td>
<td>53</td>
<td>0</td>
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<td>38</td>
<td>cord.-lat. hyb. 1475</td>
<td>38</td>
<td>1</td>
<td>25</td>
<td>0</td>
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<td>38</td>
<td>latifolia 2041</td>
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<td>26</td>
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<td>38</td>
<td>nevadensis 1938</td>
<td>76</td>
<td>1</td>
<td>26</td>
<td>0</td>
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<td>viscosa 1411</td>
<td>38</td>
<td>1</td>
<td>27</td>
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Table VII cont'd.

<table>
<thead>
<tr>
<th>Taxon &amp; Collection #</th>
<th>Diploid Chromosome #</th>
<th>Taxon &amp; Collection #</th>
<th>Diploid Chromosome #</th>
<th>Heads Crossed</th>
<th>Achenes Produced</th>
<th>Achenes With Seeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>viscosa 1411</td>
<td>38</td>
<td>cordifolia 1343</td>
<td>2</td>
<td>34</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>viscosa 1411</td>
<td>38</td>
<td>cordifolia 2005</td>
<td>1</td>
<td>22</td>
<td>0</td>
<td></td>
</tr>
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<td>55</td>
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<td>discoidea 1825</td>
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<tr>
<td>vicsosa 1411</td>
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<td>nevadensis 1870</td>
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<td>41</td>
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<tr>
<td>vicsosa 1411</td>
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<td>venosa 1940</td>
<td>2</td>
<td>36</td>
<td>2</td>
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<td>Hybrids</td>
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<td>spathulata 1380</td>
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<td>39</td>
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<tr>
<td>cord.-lat. 1475</td>
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<td>spathulata 1380</td>
<td>1</td>
<td>5</td>
<td>0</td>
<td></td>
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<tr>
<td>cord.-lat. 1475</td>
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<td>vicsosa 1411</td>
<td>3</td>
<td>40</td>
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</table>
Figure 232. Summary of all artificial crosses attempted between species in subgenus *Austromontana* and *Calarnica*. Solid lines indicate successful crosses. Dotted lines, unsuccessful crosses.
Many of the seedlings from crosses were very weak and did not survive beyond a few days or weeks, or did not survive the transplanting from petri dishes to soil.

As of this writing several seedlings are still too young to determine very much about their characters except some vegetative ones. Seedlings of Arnica viscosa X Arnica venosa do exhibit intermediate vegetative characters while quite young. The leaves are densely glandular as in Arnica viscosa, but with toothed margins as in Arnica venosa. One seedling from a cross between Arnica latifolia and Arnica viscosa has grown rapidly and has flowered. It is intermediate in most respects. The leaves are large, but nearly sessile and there are some glandular hairs and the odor of Arnica viscosa, yet greener than this parent. The few heads were narrow but bright yellow and with a few short, twisted ray florets. The pappus is tawny and the achenes have a few glandular hairs.

ENTOMOLOGICAL INTERRELATIONSHIPS

Although many of the Arnicas have showy heads and are a conspicuous part of the montane-alpine-arctic flora, very little has been recorded on pollination or any other plant-insect relationships, other than work done by Griffiths (1974) on host specific Phytomyza fly leaf miners.

Kunth (1908) has compiled records of a few insect visitors to Arnica montana (subgenus Montana), and some North American species cultivated in botanical gardens in Europe. Many of these pollinators were listed only as "bees" or "flies", etc. He records Arnica montana as being autogamous or geitonogamous (pollinated by adjacent florets in the same head), although the findings of Barker (1966) and in this current work suggest that all sexual
populations of Arnica species. With only one exception all these are confined to the genus Arnica. However, there seems to be no species-specific Phytomyza. Some of the Phytomyza species can be identified from the pattern of the mine, as they tunnel below the epidermis.

During this study mines were seen on all species in subgenus Austromon-tana, although none have been observed on either species of Calarnica. In most instances the mines occupy half or less of the leaf by the time the larvae pupate. There are some severe infestations observed in which most of the leaves on the plants have the whole surface mined by several miners per leaf. All collections identified are given in Table VIII, and representative mines are shown in Figures 233-240. No adult flies have been bred from either Arnica cernua or Arnica spathulata, so the species infesting those Arnica are not known.

Floret Feeders

There are occasional large host-specific or omnivorous herbivores including inch worms (Geometriidae) or cutworms, especially Autographa simplex Guéné (Noctuidae), which may devour leaves, heads and florets. There are also a number of smaller herbivores which feed on Arnica florets. At least half of the populations observed in the field of both radiate and discoid species had one or many small beetles (Buprestidae, mostly in the genus Anthaxia) feeding on the ray and/or disc florets (Table IX). In some extreme
TABLE VIII. *Arnica* specimens collected with leaf mines of *Phytomyza* species.

**Phytomyza oreas** Grif. or *Phytomyza arnicivora* Sehgal

*Arnica* cordifolia S-1472, MT, Lewis & Clark County

*Arnica* cordifolia S-1553, BC, Nancy Green Provincial Park

*Arnica* cordifolia S-1604, AB, Lake Louise

*Arnica* cordifolia S-1616, AB, Peyto Lake

*Arnica* cordifolia S-1819, OR, Wasco County

*Arnica* cordifolia S-1826, WA, Klickitat County

*Arnica* cordifolia Bohm 1109, BC, Osoyoos

*Arnica* cordifolia Guppy, s.n., BC, Botanie Valley

*Arnica* latifolia S-1676, WA, Clallam County

*Arnica* latifolia S-1680, BC, Manning Park

*Arnica* nevadensis S-1870, CA, Sierra County

**Phytomyza saximontana** Grif.

*Arnica* latifolia S-1538, BC, Vancouver Island, Forbidden Plateau

**Phytomyza species**

*Arnica* cernua S-1396, CA, Humboldt County

*Arnica* spathulata S-1385, OR, Josephine County
Figures 233-240. Leaf Mines of *Phytomyza* Species in leaves of *Arnica*.

Figures 233-237. Mines of *P. oreas* or *P. arnicivora*.

Figure 233. *Arnica latifolia* S-1680, BC, Manning Park.

Figure 234. *Arnica latifolia* S-1676, WA, Clallam County.

Figure 235. *Arnica cordifolia* S-1819, OR, Wasco County.

Figure 236. *Arnica cordifolia* S-1604, AB, Lake Louise.

Figure 237. *Arnica nevadensis* S-1870, CA, Sierra County.

Figure 238. Mine of *P. saximontana* on *Arnica latifolia* S-1538, BC, Vancouver Island, Forbidden Plateau.

Figure 239. Unidentified blotch mine on *Arnica cernua* S-1396, CA, Humboldt County.

Figure 240. Unidentified blotch mine on *Arnica spathulata* S-1385, OR, Josephine County.
TABLE IX. Buprestid Beetles Collected Feeding on Arnica Species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Collection Details</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arnica cordifolia S-1594, BC, Windermere</td>
<td>Anthaxia expansa Lec. - 2</td>
</tr>
<tr>
<td>Arnica cordifolia S-1819, OR, Wasco County, Pine Grove</td>
<td>Anthaxia expansa Lec. - 1</td>
</tr>
<tr>
<td></td>
<td>Anthaxia aenescens Casey - 1</td>
</tr>
<tr>
<td>Arnica cordifolia S-2022, BC, Apex Mountain</td>
<td>Anthaxia expansa Lec. - 2</td>
</tr>
<tr>
<td>Arnica cordifolia S-1842, SC, Lawrence County, Deadwood Gulch</td>
<td>Anthaxia expansa Lec. - 7</td>
</tr>
<tr>
<td>Arnica cordifolia S-1797, CA, Siskiyou County, Meiss Lake</td>
<td>Anthaxia sp. - 2</td>
</tr>
<tr>
<td>Arnica spathulata S-1381, OR, Josephine County, Cave Junction</td>
<td>Acmaeodera connexa Lec. - 1</td>
</tr>
<tr>
<td></td>
<td>Anthaxia california Obenb. - 1</td>
</tr>
<tr>
<td>Arnica venosa S-1793, CA, Shasta County, Gibson</td>
<td>Anthaxia california Obenb. - 8</td>
</tr>
<tr>
<td></td>
<td>Anthaxia sp. - 1</td>
</tr>
</tbody>
</table>
cases, as in *Arnica cordifolia* near Windermere, BC, S-1594, and in Grand County, CO, S-2035, the infestation was so severe that all the rays had been eaten, giving the plants a close superficial resemblance to *Arnica discoidea*. Severe infestations could affect pollinator visitation due to changed UV reflectance-absorbance patterns (see further discussion under UV section). The Buprestid beetles are mostly too small and glabrous to transfer pollen from one plant to another, thus are not likely aiding in pollination.

Achene Feeders

As discussed under "Seed Production" many populations of most or all species (observed in all species except *Arnica viscosa*) are infested with the larvae of one or more small flies of the genus *Xenochaeta* (Tephritidae).

The young larvae begin feeding on the ovaries before the first florets begin to expand. The larvae have usually pupated by the time the achenes are mature, occupying the remains of several achenes. In minor infestations the larvae usually feed upon only half a dozen or fewer achenes in the center of the head. The remaining achenes are undamaged. In more severe infestations, which occur commonly, most or all of the achenes are either eaten or the pappus on the viable achenes is damaged to the extent that it does not open properly. The uninfested achenes may drop to the ground as a solid unit rather than being carried away individually by the pappus blown in the wind.

Frequently the larvae of the tephritids are themselves infested with larvae of *Pteromalus* wasps (Pteromalidae), so that the adult wasps, rather than adult tephritids, emerge from the pupal cases. The achenes are still usually infested enough that they are not viable.
Ultraviolet Reflectance-Absorbance of Arnica Heads

Photographs of Arnica heads were taken out-of-doors on a sunny day with a tripod-mounted Minolta single-lense reflex camera using Kodak Tri-X Pan black and white film (ASA 400). At the same distance exposures were taken with a Wratten 18A filter attached and the camera stopped-down 3-4 f-stops to compensate for the lower light penetration through the opaque filter. The Wratten 18A filter allows only UV light in the 350-400 nm range to pass through. Arnica heads are large enough that the variation in focal length of the lens with and without the filter is not critical, although some distortion is seen at this distance (ca 30 cm). At distances closer than this the difference in focal length must be compensated for (Hill, 1977; Kennedy and Ganders, 1979).

The UV reflectance-absorbance pattern in Arnica heads, which appear completely yellow to the human eye (Figure 241), appear like those of Monoptilon belliioides (Kennedy and Ganders, 1979) in which the disc florets absorb UV light and appear dark, while the ray florets reflect UV and appear solid light (Figure 242). This is unlike the pattern in many other genera of the Asteraceae in which part of the ray florets reflect UV and an inner portion of the ray absorbs UV as in Rudbeckia spp. (Abrahamson and McCrea, 1977), Lasthenia chrysostoma (Kennedy and Ganders, 1979), or Coreopsis gigantea (Scogin et al., 1977).

In Arnica, after the heads have been in flower a few days and all the discs have opened and have probably been pollinated, the rays begin to absorb UV and the whole head appears dark (Figure 242). This post-pollination change in UV pattern has been noted by Scogin et al. (1977) for Coreopsis gigantea and a similar change was noted in older herbarium specimens of that species.
Figures 241-247. UV Reflectance-Absorbance in Arnica heads and Typical Heads of Three Species.

Figure 241. Arnica cordifolia X Arnica latifolia (putative hybrid) S-1474, MT, Rivalli County, photographed in natural sunlight.

Figure 242. Same photographed with Wratten 18A filter showing dark, absorptive UV discs and light, reflective UV rays in two recently opened heads on left and right, and dark, absorptive discs and rays of two post-pollination center heads.

Figure 243. Arnica discoidea S-1825, WA, Klickitat County, photographed in natural sunlight.

Figure 244. Same photographed with UV filter showing UV absorptive disc florets (dark).

Figure 245. Arnica cordifolia S-1497, WA, Okanogan County, very wide-rayed population.

Figure 246. Arnica latifolia S-1961, BC, Nancy Greene Provincial Park, typical head with "squared-off" rays.

Figure 247. Arnica gracilis S-1603, AB, Lake Louise, typical heads with few, narrow rays.
In the discoid species of *Arnica* the head absorbs UV and appears dark (Figures 243, 244).

**Pollinators**

An unexpectedly small number of insect pollinators has been observed visiting *Arnica* populations in these two subgenera, although many hours have been spent observing hundreds of populations at all hours of the day throughout most of the distribution of the species. In many of the largest populations with hundreds or thousands of heads in flower no pollinators were observed. There are several possibilities for the lack of pollinators in some populations. In forest habitats where the shade is relatively dense there may be fewer insects than in the more open habitats. In populations which are largely monocephalous, most of the heads may open within a few days of one another. Few or no pollinators may visit after the heads have been pollinated because of the changing UV reflectance-absorbance patterns. In alpine meadows, where there are many different plants flowering at the same time, there may be a preference for other genera or species of flowers by the pollinators. Many butterflies and bees have been observed visiting other flowers (i.e., *Valeriana* spp., *Lupinus* spp., and *Eriogonum* spp.) in preference to *Arnica* spp. In a few instances as on Yahk Mountain, BC, and Moraine Lake, AB, there seemed to be a pollinator preference for *Arnica* species in other subgenera. *Euphydryas* spp. (Nymphalidae) and *Hesperia* spp. (Hesperiidae) visited *Arnica rydbergii*, *Arnica mollis*, and *Arnica diversifolia*, but rarely visited *Arnica latifolia*, *Arnica cordifolia* or *Arnica gracilis*. At slightly lower elevations on Yahk Mountain and near the town of Yahk, BC, *Arnica latifolia* was commonly visited by several species of *Bombus*. These two
populations are the only Arnica species in these two subgenera where large numbers of insect pollinators were observed.

There seems to be no correlation between visitors to apomictic compared to sexual populations of Arnica species or between discoid and radiate species, although the UV patterns are different in the two groups.

Table X lists the Diptera, Hymenoptera, and Lepidoptera pollinators captured on Arnica heads. Nomenclature of butterfly pollinators follows Howe (1975), that of the other orders follows Borror et al. (1976) above the generic level.
TABLE X. Pollinators Collected on Arnica Heads.

Arnica cernua S-1772, CA, Humboldt County, Hoopa Mountain.
   Syrphidae sp.

Arnica cordifolia S-1464, WY, Teton County, Grand Teton National Park
   Lycaenidae
      Mitoura spinetorum (Hewitson) ♀

Arnica cordifolia S-1648, BC, Sheridan Lake
   Nymphalidae
      Speyeria electa beani (Barnes & Benjamin) ♀

Arnica cordifolia S-1797, CA, Siskiyou County, Meiss Lake
   Syrphidae
      Taxomerus occidentalis Curran ♀

Arnica cordifolia S-1819, OR, Wasco County, Pine Grove
   Syrphidae
      Syrphus opinator Osten Sachen ♂

Arnica cordifolia S-1823, WA, Klickitat County, Appleton
   Syrphidae
      Sphaerophoria sulphuripes (Thomson) ♀

Arnica cordifolia S-1826, WA, Klickitat County, Glenwood
   Andrenidae
      Andrena sp. ♂

Arnica cordifolia S-1836, ID, Bonneville County, Irwin
   Apidae
      Bombus bifarius Cresson ♀
   Andrenidae
      Andrena sp. ♂
Table X cont'd.

**Arnica cordifolia** S-2022, BC, Apex Mountain

Halictidae

*Halictus* sp.

**Arnica cordifolia** S-2028, BC, Kamloops

Megachilidae

*Megachile* sp.

**Arnica cordifolia** S-2029, BC, Sorrento

Syrphidae

*Eristalis tenax* (L.) ♀

**Arnica discoidea** S-1777, CA, Napa County, S. of Lake/Napa Co. line

Hesperiidae

*Erynnis propertius* (Scudder & Burgess) ♂

**Arnica latifolia** S-1567, BC, Yahk

Apidae

*Bombus mixtus* Cresson 4 ♂, 7 ♀ (=worker cast)

*Bombus bifarius* Cresson 2 ♀

*Psithyrus fernaldae* Franklin 1 ♂, 1 ♀

Anthophoridae

*Nomada* sp. ♀

Syrphidae

*Eristalis tenax* (L.) ♂

**Arnica latifolia** S-1574, BC, Yahk Mountain

Apidae

*Bombus bifarius* Cresson ♀
Table X cont'd.

**Arnica latifolia S-1576, BC, Yahk Mountain**

\begin{itemize}
  \item Apidae
    \begin{itemize}
    \item Bombus melanopygus Nylander \( \sigma \)
    \item Bombus mixtus Cresson \( 2 \sigma \)
    \end{itemize}
  \end{itemize}

\begin{itemize}
  \item Nymphalidae
    \begin{itemize}
    \item Euphydryas sp. \( 5 \sigma, 2 \varphi \)
    \end{itemize}
  \end{itemize}

**Arnica latifolia S-2031, BC, Black Tusk**

\begin{itemize}
  \item Sessidae
    \begin{itemize}
    \item Vespamina sp. ?
    \end{itemize}
  \end{itemize}

**Arnica spathulata S-1380, OR, Josephine County, Kirby**

\begin{itemize}
  \item Apidae
    \begin{itemize}
    \item Apis mellifera L.
    \end{itemize}
  \end{itemize}

\begin{itemize}
  \item Halictidae
    \begin{itemize}
    \item Halictus sp.
    \end{itemize}
  \end{itemize}

**Arnica spathulata S-1740, OR, Josephine County, Selma**

\begin{itemize}
  \item Apidae
    \begin{itemize}
    \item Bombus caliginosus (Frison) \( 2 \sigma \)
    \end{itemize}
  \end{itemize}

**Arnica venosa S-1793, CA, Shasta County, Gibson**

\begin{itemize}
  \item Halictidae sp.
  \end{itemize}
Genus **Arnica** L. Sp. Plant. 884. 1753.

**Artificial Key to the Subgenera of Arnica.**

A. Anthers purple; involucral bracts callous-tipped; plants of n. British Columbia and Yukon to Alaska and Japan... Subg. **Andropurpurea** Maguire

AA. Anthers yellow; involucral bracts not callous-tipped... B

B. Leaves all sessile; plants from woody caudex.... C

C. Cauline leaves strongly basally disposed on flowering stem; heads radiate; plants of se United States and central Europe........ Subg. **Montana** Maguire

CC. Cauline leaves not strongly basally disposed, stem leafy throughout; heads discoid; rare plants of sw Oregon and nw California........ Subg. **Calarnica** Straley

BB. Leaves mostly petiolate; plants rhizomatous, producing basal rosettes...... C

C. Pappus brown or tawny, subplumose................ Subg. **Chamissonis** Maguire

CC. Pappus white (rarely tawny), barbellate........ D

D. Leaf blades relatively narrow, mostly 3-10 times as long as wide; plants mostly densely tufted...... Subg. **Arctica** Maguire

DD. Leaf blades relatively broad, mostly 1-2.5 times as long as broad; plants mostly not densely tufted........ Subg. **Austromontana** Maguire
Species Recognized


Lectotype: Arnica latifolia Bongard


Lectotype: Arnica latifolia Bongard

1. Arnica cordifolia Hooker

2. Arnica nevadensis A. Gray

3. Arnica latifolia Bongard

4. Arnica gracilis Rydberg

5. Arnica cernua T. Howell


Lectotype: Arnica discoidea Bentham

6. Arnica discoidea Bentham

7. Arnica spathulata Greene

Subgenus Calarnica subgenus nov.

Type Species: Arnica viscosa A. Gray

8. Arnica viscosa A. Gray

9. Arnica venosa H.M. Hall

The following keys are designed to be useful for a majority of specimens of these two subgenera. An artificial key is provided for both live and pressed specimens, and a field key.

Artificial Key to the Species of Arnica, Subgenera Austromontana and Calarnica.

A. Leaves all sessile; non-rhizomatous perennials lacking sterile basal rosettes of leaves; heads discoid (Subgenus Calarnica) ........... B

B. Margins of leaves toothed; 2° veins prominent; leaves rugose; heads nodding in bud; florets bright yellow; achenes densely
strigose, non-glandular..........................9. Arnica venosa

BB. Margins of leaves entire; 2° veins inconspicuous; leaves smooth; heads erect in bud; florets creamy-yellow or white; achenes stipitate glandular..........................8. Arnica viscosa

AA. Leaves, at least lower ones, petiolate; rhizomatous perennials producing sterile basal rosettes; heads radiate or discoid (Subgenus Austromontana).........................................................B

B. Heads radiate (Section Eulatifoliae).................................C

C. Leaves mostly glabrous (if pubescent then sparsely scabrous and non-glandular).................................D

D. Heads erect in bud; achenes hirsute from middle to top; leaves thin; veins green; of widespread distribution in w. N.A.............3. Arnica latifolia

DD. Heads nodding in bud; achenes sparsely to densely pubescent throughout; leaves thick, leathery, veins reddish; restricted to serpentine soils of sw Oregon and nw California.....................5. Arnica cernua

CC. Leaves pubescent with glandular and non-glandular hairs..

.................................................................D

D. Pubescence of leaves glandular-puberulent only; plants mostly much-branched and clumped; mostly less than 20 cm tall; achenes black, glabrous to sparsely pubescent.

.................................................................4. Arnica gracilis

DD. Pubescence of leaves glandular stipitate and non-glandular; plants mostly unbranched and not clumped; greater than 20 cm tall; achenes grey, mostly densely hirsute at top or throughout.........................E
E. Leaves of innovations and lower cauline leaves with cordate bases; margins mostly toothed; pappus pure white.................1. Arnica cordifolia

EE. Leaves of innovations and lower cauline leaves with attenuated or rounded bases; margins mostly entire; pappus off-white or tawny..............

..................................................2. Arnica nevadensis

BB. Heads discoid (Section Eradiatae).................................................C

C. Leaves of innovations and lower cauline leaves spathulate; plants mostly restricted to serpentine soils of sw Oregon and nw California......................7. Arnica spathulata

CC. Leaves of innovations and lower cauline leaves with cordate or rounded bases; plants usually not of serpentine soils; s. Washington to s. California.........6. Arnica discoidea

Field Key to the Species of Arnica, subgenera Austromontana and Calarnica.

A. Leaves distinctly fragrant when bruised.........................B

B. Heads discoid.................................................................C

C. Leaves broadly sessile; cauline leaves and bracts greater than 6 pairs; basal rosettes lacking....................D

D. Margins of leaves toothed; plants predominately eglandular; leaves rugose; heads nodding in bud; florets bright yellow; rare at low elevations in Shasta Co., California...............9. Arnica venosa

DD. Margins of leaves entire; plants strongly glandular; leaves smooth; heads erect in bud; florets white to creamy-yellow; rare at high elevations in n. California
and sw Oregon......................8. Arnica viscosa

CC. Leaves of basal rosettes and lower cauline leaves distinctly petiolate; cauline leaves and bracts less than 6 pairs; basal rosettes present...........................................D

D. Lower cauline leaves spathulate; glandular hairs purplish or reddish; of serpentine soils in sw Oregon and nw California.................7. Arnica spathulata

DD. Lower cauline leaves not spathulate; leaves grey to green, lacking purplish or reddish hairs; usually not of serpentine soils, s Washington to s California...

.................................6. Arnica discoidea

BB. Heads radiate.................................................................C

C. Leaves appearing dark green, lacking non-glandular hairs; plants mostly densely clumped, from short rhizomes.......4. Arnica gracilis

CC. Leaves appearing greyish due to many non-glandular hairs; plants mostly not clumped, from long rhizomes...........D

D. Basal rosette leaves with cordate bases; plants with many long non-glandular hairs (1-2 mm); widespread in w. N.A. especially in open Pinus ponderosa and Pseudotsuga menziesii forests...1. Arnica cordifolia

DD. Basal rosette leaves with attenuated bases; plants lacking or with few long non-glandular hairs; rare species, mostly at high elevations in the Sierra Nevada..........................2. Arnica nevadensis

AA. Leaves not at all or very faintly fragrant when bruised.............B

B. Heads nodding in bud; plants dark reddish or purplish throughout,
especially along veins; rare species of serpentine soils in sw Oregon and nw California..................5. Arnica cernua

BB. Heads erect in bud; plants mostly greenish throughout except at base of stem; common widespread species not of serpentine soils..

.................................................3. Arnica latifolia

TAXONOMIC TREATMENT

Subgenus Austromontana Maguire

Perennial herbs from naked or scaly rhizomes or rarely a short woody caudex and rhizomes; roots slender or fleshy; sterile rosettes of leaves (innovations) produced; rosette leaves and lower cauline leaves usually the largest, mostly long petioled, decreasing in size upward, becoming bract-like and sessile below inflorescence; cauline leaves opposite, blades ovate to lanceolate, bases cordate to attenuate, tips acute to rounded, margins entire to crenate, serrate, dentate and undulate; stems simple to much-branched; vestiture of stems and leaves subglabrate to strigose, pilose, and stipitate glandular; inflorescence a solitary head or corymb; heads radiate or discoid; involucral bracts narrowly to broadly lanceolate, acute to acuminate; ray florets linear elliptic to oblong; disc florets tubular or goblet-shaped; achenes ribbed, subglabrate to hirsute and stipitate glandular; pappus white (rarely tawny), barbellate to subplumose.

Section Eulatifoliae Maguire

Heads radiate; otherwise, as with the subgenus.


Arnica macrophylla Nutt. Trans. Am. Phil. Soc. 7:407. 1841. TYPE:

Oregon, Blue Mountains, Nuttall (Herb. Hook., KEW).

(probable hybrid, also listed under synonymy of Arnica latifolia).


Arnica ovalis Rydb. N. Am. Fl. 34:338. 1927. TYPE: Alberta, Crow Nest Pass,
July 31, 1897, Macoun, Geol. Surv. Can. 72719 (CAN?) (not seen).


Arnica cordifolia Hook. subsp. whitneyi (Fern.) Maguire. Brittonia 4:452. 1943.


Strongly rhizomatous perennial herb; rhizomes 2-10(-60) cm growth/year, slender 1-2 mm thick, naked except for few scales and old leaf bases toward summit, unbranched or few branches near summit, forming large loose populations of sterile basal rosettes and flowering stems; stems single or rarely few, simple or branched near base or throughout, (10-)15-40(-55) cm high, sparsely to densely villous and stipitate glandular basally, more densely so higher, sometimes purplish or reddish at base; innovations with 2-6(-14) long-petiolate leaves, petioles (2-)6-10(-20) cm long, sometimes narrowly winged, blades ovate to broadly ovate or lanceolate, (1-)4-8(-12) cm long, (1-)3-6(-9) cm broad, bases cordate, subcordate, to sometimes rounded, tips acute to rounded, margins entire, subentire, to usually regularly dentate,
serrate, crenate, or rarely doubly dentate or serrate; cauline leaves 2-3(-5) pairs, often reduced basally and becoming bract-like toward summit, lower cauline leaves usually long-petiolate (1-)4-8(-10) cm long, blades (2-)5-10 (-13) cm long (2-)4-6(-9) cm broad, upper pairs of cauline leaves with progressively shorter petioles, uppermost pair usually bract-like and sessile; shape and margins of lower cauline leaves as in that of innovations, upper bracts usually ovate to lanceolate with subentire to entire margins; vestiture of herbage sparsely to densely strigose or villous on under surfaces, sparsely to usually densely strigose or villous and stipitate glandular, leaf margins ciliate; inflorescence usually a single head or open corymb of 3-7 (-35) heads; peduncles (4-)8-15(-20) cm long, peduncle and periclinum pilose and stipitate glandular; heads radiate, 15-25 cm high; involucral bracts (7-)10-15(-21) + uniseriate, 10-18 mm long, 2-4 mm broad, narrowly lanceolate, acute to acuminate; ray florets, (5-)8-11(-16) pale to dark golden yellow, tube 3-7 mm long, limb 10-25(-35) mm long, 4-7(-10) mm broad, linear elliptic, 1-3 teeth at tip, tube and base of limb sparsely villous and stipitate glandular; disc florets (15-)38-57(-94), tubular 8-12 mm long, sparsely to densely villous and stipitate glandular at base and sparsely glandular upward and on outer surface of lobes; pollen diameter 40-55 μm; achenes dark grey, 4-10 mm long, 1 mm broad, sparsely to densely hirsute with bifurcate hairs and few stipitate glandular hairs, especially distally; pappus white, barbellate, the lateral setae .07-.10 mm long, 38-52 bristles; apomictic; 2n=38,57,76,95,114.

Type: "Alpine woods of the Rocky Mountains", Drummond (Herb. Hook., KEW).

Distribution: Arnica cordifolia is common in many moderately dry habitats, especially in open Pinus ponderosa, Pinus contorta, and Pseudotsuga menziesii
forests or alpine meadows at many elevations from central Yukon and Eastern Alaska south to Northern New Mexico and Southern California, and east to the Black Hills of South Dakota and disjunct in *Abies balsamea*, *Acer* spp., and *Betula* spp. forests in Keweenaw Co., Michigan and Thunder Bay, Ontario. Figure 248.

Illustration: Figure 249.

This, the most widespread *Arnica* in Western North America, is usually abundant where it occurs, covering vast areas. It is often the dominant herbaceous plant in open forests in the Western Cordillera.

In its more typical form, where it grows in open pine or Douglas fir forests, it is distinctive with its deeply cordate, toothed leaves, large solitary heads, broad rays, and hirsute achenes. In other habitats there is great variability in form, which has led to the naming of a number of taxa. These are now generally accepted as falling within the range of variability of *Arnica cordifolia*.

In more shaded locations very large leaved forms often occur. These have been given taxonomic recognition in the past, as *Arnica macrophylla* Nutt. from the Blue Mtns. of Oregon, and *Arnica andersonii* Piper from Skeena, BC. However, this variation with large thin leaves can be seen from single collections or populations growing in sun, filtered shade, and dense shade, as in collections from Siskiyou Co., CA, S-1797 (Figures 250-259).

At the other extreme is a distinct series of ecotypes from high elevations and disturbed roadsides to which the names *Arnica pumila* Rydb. and *Arnica humilis* Rydb. have been applied. They are quite short, with small, usually entire leaves. They often resemble *Arnica nevadensis*, from which they can be
Figure 248. Distribution of *Arnica cordifolia* in Western North America. Populations in Michigan and Ontario are not shown.
Figure 249. *Arnica cordifolia* S-1494, WA, Okanogan County, habit.

X two-thirds.
Figures 250–259. Variation in basal leaves from single population of *Arnica cordifolia* S-1797, CA, Siskiyou Co.
distinguished, often only with difficulty, by the whiter, less plumose nature of the pappus, and usually a greater degree of pilosity of the leaves and stems than in *Arnica nevadensis* populations. Typical of these small ecotypes are collections from Slate Lake Trail, Okanogan Co., WA, S-1498 (Figures 260-267), and roadside in *Pinus contorta* forest, Pine Grove, Wasco Co., OR, S-1820 (Figures 268-276). Many herbarium specimens from Siskiyou Co., CA, Oettinger 1082, Sawyer 941, 1236 (HSC) combine many characters of both *Arnica nevadensis* and *Arnica cordifolia*. Only where there are several specimens or where they can be studied in the field can they be more easily assigned to one or the other of these species.

Larger, more typical *Arnica cordifolia* is separable from typical *Arnica nevadensis* in the generally narrower, paler rays, more densely pilose stems and leaves, more toothed margins, whiter, shorter lateral setae of the pappus, and more densely hirsute achenes of the former. There are some populations of *Arnica cordifolia* with broader rays (Figure 245) as in a population from Siskiyou Co., CA, S-1797. These rays are as broad as typical *Arnica nevadensis* rays. The two species are also usually ecologically separate. *Arnica cordifolia* usually grows at lower elevations and in more protected habitats of open forests. The two have been observed growing together at Saddlebag Lake, Mono Co., CA, S-1937, 1938, with *Arnica cordifolia* in the forest edge and *Arnica nevadensis* on more exposed rock outcrops.

Although *Arnica cordifolia* generally has only one or three heads per stem, some populations or individuals especially in wetter habitats, have much branched stems with many heads terminating each branch. The greatest extreme of this was seen in one plant with 35 heads from a collection from Tod Mtn., BC, S-1652.
Figures 260-267. Variation in basal leaves of high elevation population of *Arnica cordifolia* S-1498, WA, Okanogan Co.
Figures 268-276. Variation in basal leaves from population on disturbed roadside bank of *Arnica cordifolia* S-1820, OR, Wasco Co.
Other collections with several heads have been named *Arnica paniculata* by Nelson, a species retained by Maguire (1943), but considered a variant of *Arnica cordifolia* by Ediger & Barkley (1978). Maguire (1943) points out the possibility of this being a hybrid between *Arnica cordifolia* and *Arnica parryi* (subgenus Chamissonis), although both species are largely or wholly apomictic (Barker, 1966). A recent hybrid between the two is unlikely. It seems that the characters cited could fall within the range of variation of an apomictic race of *Arnica cordifolia*, and it is treated in this work as a variant thereof.

Maguire (1943) also gave taxonomic recognition to a population of *Arnica cordifolia* from Keweenaw Co., Michigan, treating it as subsp. *whitneyi*. Since 1943 additional populations have been discovered on the north shore of Lake Superior in Sibley Provincial Park, Thunder Bay District, Ontario *Garton 15164, 15486* (LKHD). Both of these populations have been studied in the field (S-1846, 1849). They are on the average taller, have more heads (3/stem), narrower rays, and less pubescence than average *Arnica cordifolia* populations in the Western mountains. However, there are numerous populations in the West which cannot be distinguished from the Michigan and Ontario populations. The population in Michigan is very rare and is on the endangered species list in that state. It is found as one large widely dispersed population (or several small populations) between Copper Harbor and Eagle Harbor, growing in open *Abies balsamea, Acer spicatum, Acer saccharum*, and *Betula* spp. forest. The dominant herbaceous cover in the area is *Aster macrophyllus*. When neither the *Aster* nor the *Arnica* are in flower, the basal rosettes of leaves are separable only with great difficulty. The *Arnica* leaves tend to be smaller, slightly greyer, and have a stronger odor. The *Arnica* may be
Figures 277-281. Habitats and Habits of Arnica cordifolia and Arnica nevadensis.

Figure 277. Habitat of Arnica cordifolia, WA, Klickitat Co., Appleton, (S-1823), open forest of Pseudotsuga menziesii and Pinus ponderosa.

Figure 278. Arnica cordifolia, 6-month old seedling, from seed collected at Hat Creek, BC, (Johns 648) (S-2009).

Figure 279. Arnica cordifolia X Arnica latifolia (putative hybrid), MT, Ravalli Co., Charles Waters Campground, (S-1475), normal radiate head and discoid head on same stem.

Figure 280. Habitat of Arnica nevadensis, CA, Sierra Co., Sierra Buttes, (S-1870), open forest of Pinus monticola, Tsuga mertensiana, and Abies sp.

Figure 281. Arnica nevadensis, NV, Washoe Co., Mt. Rose, (S-1910).
more common in the area than now presumed, but has been overlooked when not in flower because of the strong resemblance to the Aster. The plants from Sibley Provincial Park are ecologically and morphologically quite similar to the Michigan ones. This plant should be sought on Isle Royale in Lake Superior between the known populations in Michigan and Ontario. Arnica whitneyi Fern. is not given specific status or recognized as a subspecies of Arnica cordifolia in this treatment, despite the disjunct distribution.

Chromosomally they are like the dominant Western polyploid complex (2n=76) and morphologically they are less different than some of the other extremes, e.g., the dwarf forms discussed above, or the southern extremes in Arizona (Schreiber, s.n., Hemmingway, s.n. MNA).

There are numerous interesting populations which are in many morphological aspects intermediate between Arnica cordifolia and Arnica latifolia. Most notable are several collections from Josephine Co., OR, Lang 798 (SOC), Savage, s.n. (ORE), and Curry Co., OR, Leach 1544, 1545 (ORE), Ravalli Co., MT, S-1474, 1475 (Figure 282). These populations usually do not grow with one or either of the parents, and are considered to be old hybrids which have probably become apomictic after hybridization and have retained their intermediate characters. Pollen stainability ranges from 33%-99%. Diploid chromosome numbers have been obtained from two Montana collections. They appear to be sterile having never produced any viable achenes in cultivation, either when selfed or crossed with other species or similar populations.

These putative hybrids are usually much larger and more robust in all characters than either parent. They are strongly rhizomatous like Arnica cordifolia. The basal leaves and lower cauline leaves are usually + cordate, but the upper cauline leaves are sessile. The leaves are sparsely pubescent
Figure 282. *Arnica cordifolia* X *Arnica latifolia* S-1475, putative natural hybrid, MT, Ravalli County. X two-thirds.
and appear dark green as in *Arnica latifolia*. However, glandular hairs are present throughout giving the plants as strong an odor as in *Arnica cordifolia*. Heads are usually larger than in either parent, with more rays (up to 25), more disc florets (nearly 200) and more involucral bracts (up to 21). The shape of the rays (Figure 138) approaches that of *Arnica latifolia*, with more truncate tips. Disc florets (Figure 144) are more densely pubescent throughout than in either parent. There are numerous other populations or individuals closer to one or the other parent. All these are considered apomictic races and are not given taxonomic status.


Rhizomatous perennial herb; rhizomes (1-)3-12 cm growth/year, slender, 1-2 mm thick, naked except pairs of brown scales at nodes and crowded scales and old leaf bases toward the summit, unbranched or few branches apically, forming small to large populations of sterile basal rosettes and flowering stems; stems single or few, simple or branched from base or above, (10-)15-30 cm tall, very sparsely pilose and + densely short glandular throughout; innovations with (2-)4-6 long petiolate leaves, petioles 3-5 cm long, blades ovate, rotund, or elliptic to lanceolate, 4-7 cm long, 2-4 cm broad, bases rounded to attenuate, tips acute to rounded, margins entire, subentire, to rarely coarsely serrate or dentate; cauline leaves 2-3 pairs, lowest pair usually with longest petioles, (1-)2-3(-4) cm long, sometimes winged to 4 mm, next pair usually with largest blade 3-5.5 cm long, (1-)2-4 cm broad, upper pair usually reduced and bract-like, lanceolate, shape and margins of cauline
leaves like that of innovations; vestiture of herbage sparsely scabrous, pilose and short stipitate glandular throughout, margins ciliate; inflorescence usually of a single head or open corymb of 3(-7) heads; peduncles 4-12 cm long; peduncles and periclinum densely short and long stipitate glandular and sparsely pilose; heads radiate 15-20 mm high; involuclar bracts 10-15(-18) mm long, 2-4 mm wide, narrowly lanceolate, acute to acuminate; ray florets 5-13, dark golden yellow, tube 2-7 mm long, limb 15-20 mm long, 6-7 mm broad, villous and stipitate glandular on tube and lower back of limb, linear elliptic to broadly elliptic, 1-3 teeth at tip; disc florets 21-51, tubular 7-10 mm long, sparsely to densely villous and stipitate glandular at base and sparingly distally and on outer surface of lobes; pollen diameter 35-45 μm, achenes dark grey to black, 4-9 mm long, to 1 mm wide, sparsely hirsute with bifurcate hairs especially distally, short to long stipitate glandular throughout; pappus dull white to tawny, of 27-50 bristles, barbellate to subplumose, the lateral setae .15-.20 mm; apomictic; 2n=76.

TYPE: California, Sierra Nevada, 2700 m, Pringle s.n. (G).

Distribution: Mostly at high elevations (1500-3500 m) in open forests of Tsuga mertensiana, Pinus monticola, and Pinus contorta in the Sierra Nevada of California and Nevada and sparingly east to the San Juan Mountains of Utah and north in the Cascade Mountains to north-central Washington. (Figure 283).

Illustration: Figure 284.

Arnica nevadensis is a distinct species in the Sierra Nevada, where it can be readily separated from Arnica cordifolia most of the time. In much of its other distribution it is only separable from high elevation forms of Arnica cordifolia with difficulty, especially from herbarium specimens, as
Figure 283. Distribution of Arnica nevadensis.
Figure 284. Arnica nevadensis S-1910, NV, Washoe Co. X two-thirds.
further discussed under that species.

Occasional populations of *Arnica rydbergii* growing in shaded locations, as from Hurrican Ridge, Clallam County, WA (S-1677), are very atypical of that species and could easily be identified as *Arnica nevadensis*. Many individuals have broad rounded basal and lower cauline leaves. However, the narrower heads, pure white pappus, and densely hirsute achenes readily separate it from *Arnica nevadensis*.

In the Sierra Nevada, *Arnica nevadensis* is not infrequently found growing with *Whitneya dealbata*, with which it has often been confused. The persistent, more-papery rays on mature achenes and absence of pappus in *Whitneya* are distinctive.

*Arnica tomentella* Greene is a very dubious species retained as valid by both Maguire (1943) and Ediger & Barkley (1978). It is very rare in collections and has not been seen in nature by any of the recent workers on the genus. Most of the specimens have very insufficient data, including the Type, *Purpus 5625*, "open woods, middle Tule River, southeastern California" (holotype, US; isotype MO), so that relocating it in the field seems a matter of luck.

Maguire (1943) considered *Arnica tomentella* related to *Arnica cordifolia* or *Arnica nevadensis*. The plants are taller than average *Arnica nevadensis* and the involucral bracts are more pubescent, especially near the tips. The lateral setae are closer to those of *Arnica nevadensis*, although in old herbarium specimens the color of the pappus cannot be determined and the shape of the rays is difficult to determine.

Ediger & Barkley (1978) consider *Arnica tomentella* a possible hybrid between *Arnica cordifolia* and *Arnica chamissonis* var. *foliosa*, probably based
on the attenuate leaf bases and pubescent involucral bract tips. However, the general character of the pubescence is close to that of *Arnica nevadensis*, as are the leaves, and it is tentatively placed here as a probable apomictic race of *Arnica nevadensis*, until it can be found in the field again.


Arnica glabrata Rydb. N. Am. Fl. 34:335. 1927. TYPE: Oregon, Crater Lake, August 10, 1897, Austin & Bruce 1627, (holotype, NY; isotypes, POM).


Rhizomatous perennial herb; rhizomes 1-7(-10) cm/year, stout, 3-5(-7) mm thick, naked or densely clothed with old leaf bases and dark brown scales, unbranched or few-branched near summit, forming loose or dense clumps of sterile basal rosettes and flowering stems; stems single or few, simple or branched above upper pair of leaves/bracts, rarely branched lower, (10-)15-40 cm tall, glabrate to very sparsely villous throughout, distinctly purplish or reddish at base; innovations with 2-6(-12) long-petiolate leaves, petioles (2-)4-8(-12) cm, blades narrowly elliptic to ovate or rotund, (1-)3-5(-6) cm long, (0.5-)2-4(-5) cm broad, bases attenuate to rounded, subcordate, or rarely cordate, tips acute, margins entire to usually regularly dentate, serrate, or doubly dentate or serrate, or crenate; cauline leaves 2-4(-7) pairs, often reduced basally and toward summit, where bract-like, lower cauline leaves sessile or with short petioles 1-3(-5) cm long, often winged 2-5 mm, blades 2-6(-9) cm long, 1-4(-7) cm wide, upper cauline leaves progressively smaller, almost always sessile, shape and margins as in leaves of innovations; vestiture of herbage glabrate to sparsely (rarely densely) villous, strigose, and very rarely short stipitate glandular, margins often ciliate; inflorescence of a single head or open corymb; peduncles (1-)3-10(-20) cm long, becoming more villous upward; periclinum sparsely to densely villous; heads 1-3(-13), radiate, 10-20 mm high; involucral bracts (7-)11-16(-23), + uniseriate, 8-14 mm long, (1-)2-3 mm broad, narrowly lanceolate, acute to acuminate; ray florets (5-)8-15(-18), usually pale yellow, tube 3-5 mm, limb (5-)10-25 mm long, 2-5 mm wide, linear elliptic, truncate at tip, with 0-3 teeth, tube and base and back of limb sparsely villous; disc florets
(15-)50-90(-124), tubular, 5-10 mm long, sparsely to densely villous near base and on outer surface of lobes; pollen diameter 35-50 μm; achenes dark grey-brown, 5-10 mm long, 1 mm wide, few bifurcate hairs from mid-point distally, rarely throughout, few short stipitate glandular hairs distally or throughout, rarely glabrous; pappus white, barbellate, the lateral setae .05-.07 mm long, of 43-64 bristles; self-incompatible; 2n=38.

TYPE: Alaska, Sitka, Mertens, s.n. (Herb. Bongard, Leningrad).

Distribution: Arnica latifolia occurs in many habitats at varying elevations, mostly in cool mixed conifer forests in the mountains from Southern Alaska to Northern California and Central Colorado. (Figure 285).

Illustration: Figure 286.

Arnica latifolia is one of the commonest and most polymorphic of all species. It usually grows in wetter locations than Arnica cordifolia, especially in cool forests of Pseudotsuga menziesii, Picea spp., and Abies spp. and near stream margins.

There are so many ecotypes to which names have been applied that it is difficult to describe the "typical" Arnica latifolia. Most have sessile cauline leaves, the rays are usually truncate (Figure 139), the leaves and stems are usually glabrous, and the mature achenes are usually glabrous throughout or hirsute only on the distal half.

Among the variable ecotypes are a group of broad-leaved, robust populations with thin leaves from shady locations, and another group of smaller, narrower-leaved, often high elevation, sun forms with much thicker leaves. The extreme condition of the shade form is represented in collections from Mt. Baker, Whatcom Co., WA, S-1158, 1161. These are very robust plants to
Figure 285. Distribution of *Arnica latifolia*. Star indicates type locality.
Figure 286. *Arnica latifolia* S-1500, WA, Chelan Co. × two-thirds.
40 cm tall, with thin broad leaves and coarsely serrate margins. This large form has received taxonomic recognition in the past with several names having been applied (Arnica platyphylla Nels., Arnica aprica Greene, Arnica laevigata Greene). At the opposite extreme are plants which superficially resemble Arnica gracilis. These usually alpine plants are short (as little as 10 cm tall), clumped, and branched, with small heads, but lacking the glandular hairs (or lacking hairs of any type) of Arnica gracilis, and having paler, blunter rays than Arnica gracilis. Examples of these small ecotypes include collections from Mt. Arrowsmith, Vancouver Is., BC, Allen, s.n. (UBC), (Figures 287-298), and Green Mtn., Vancouver Is., BC, Krajina et al. 4987 (UBC). Records of Arnica gracilis from Vancouver Is. probably erroneously refer to these small ecotypes of Arnica latifolia. The name Arnica betonicae-folia Greene has been applied to these ecotypes in the past. One such form from Kootenay Pass, BC, S-1561 growing on a disturbed roadside, became much larger and more robust the following year when transplanted to the experimental garden in Vancouver. Every possible combination of intermediate individuals and populations exists between the large and small ecotypes from much of the distribution of the species.

There is a tendency in the northern part of the range for populations to have a greater pilosity to the leaves and stems (Buttrick 779, Atlin Lake, BC, and Taylor, et al. 5993, Ilgachuz Mtns., BC, and especially some collections from the Queen Charlotte Islands, BC, all UBC).

A truly discoid condition in Arnica latifolia has not been seen, although in one population from Nancy Greene Provincial Park, BC, S-1961, some plants had rays which were variously shortened (Figures 299-304), compared to typical rays for this species (Figure 139).
Figures 287-298. Variation in basal leaves of small alpine form of *Arnica latifolia* Allen s.n., BC, Mt. Arrowsmith.
The relationship of *Arnica latifolia* to *Arnica mollis* and *Arnica diversifolia* (both in Subgenus *Chamissonis*) deserves further investigation. *Arnica diversifolia* has been treated in previous works as a possible hybrid between the other two species. There are populations which strongly resemble *Arnica latifolia*, including several collections from Glacier National Park, MT, Harvey 5163, 5574 (MONTU), which have been determined as *Arnica diversifolia*.

Further discussions of the relationship of this species to *Arnica cernua*, *Arnica cordifolia* and *Arnica gracilis* may be found under the discussions of those species.


Rhizomatous, often clumped perennial herb; rhizome growth 0.5-3(-6) cm per year, slender, 1-2 mm thick, naked on older parts or with old leaf bases and brown scales especially toward the summit, unbranched or usually several branched forming clumps of sterile basal rosettes and flowering stems; stems single or usually several and often much branched throughout or above upper leaves/bracts, 10-30 cm high; glabrate below to sparsely short stipitate glandular, and sparsely scabrid or strigose, becoming densely short stipitate and sessile glandular above with yellowish hairs; innovations with 4-6(-12) long petiolate leaves, petioles 0.5-2(-6) cm long, rarely narrowly winged, blades elliptic to obovate, 2-3(-5) cm long, 1-2(-3) cm broad, bases cordate to attenuate, often oblique, tips acute, margins subentire to serrate; lower cauline leaves, 2-3 pairs and one or more pairs of opposite or alternate bracts, petioles 1.5-3(-4) cm long, often winged 2-3 mm, blades ovate to elliptic, 2-4(-5) cm long, 1-3.5 cm broad, bases usually attenuated, tips acute to rounded, subentire to irregularly serrate; upper cauline leaves reduced, ovate, usually sessile, often connate-perfoliate, 2-3(-6) cm long, 1-2(-3) cm broad, except uppermost bract-like, often alternate, 1-2 cm long, 1-2(-5) mm broad; vestiture of leaves sparsely strigulose and very short stipitate below, densely short stipitate or sessile stipitate above; inflorescence simple or open corymb; peduncles 2-8 cm; periclínium densely short and longer stipitate glandular; heads (1-)3-11, radiate, 10-15 mm high; involucral bracts 6-14, + uniseriate 5-10(-12) mm long, 1-2 mm broad, narrowly lanceolate, acute to acuminate; ray florets, 5-11, pale to bright yellow, tube 3-4 mm, limb 10-16(-20) mm long, 3-4(-6) mm broad, linear elliptic, tips acute with 1-3 blunt teeth at tip, glandular and sparsely villous on tube and lower back of limb; disc florets (9-)16-23(-44) tubular, 5-6 mm long, glandular and sparsely villous at base and on outer tips of lobes; pollen diameter
30-50 μm; achenes dark brown to black, 4-7 mm long, 1 mm wide, glabrous to short stipitate glandular throughout and few bifurcate hairs distally, pappus white, barbellate, the lateral setae .05-.07 mm long, 37-48 bristles. Apomictic. 2n=57.

**Type:** Montana, Madison Range, Spanish Peaks, 1800 m, July 14, 1896, J.H. Flodman 901 (NY).

**Distribution:** *Arnica gracilis* is found on alpine scree slopes and rocky slopes in open forests at mid to high elevations (1000-2400 m) in Cascade to Rocky Mountains from southern B.C. and Alberta to Wyoming and Oregon. Figure 305.

**Illustration:** Figure 306.

There has been much debate regarding the validity of *Arnica gracilis*. Maguire (1943) summarized his discussion of the species as "a loose entity which is maintained as distinct from *Arnica latifolia* with some difficulty."

In more recent floras (Cronquist, 1955; Taylor & McBryde, 1978; Ediger & Barkley, 1978) the authors have treated it as a variety of the widespread *Arnica latifolia*. In a subgenus (*Austromontana*) where there are no absolutely clear-cut species, and there are populations or individuals which are more or less intermediate or combine characters of two or more species, this assemblage of populations seems as good as most of the other species. In the present treatment it is without hesitation retained as a separate species.

Where *Arnica gracilis* grows in its typical form at high elevations on stabilized scree slopes, especially in the Rocky Mountains of British Columbia, Alberta, and Montana, it is densely clumped with little rhizome growth.
Figure 305. Distribution of *Arnica gracilis* (open circles) and *Arnica discoidea* (closed circles). Stars indicate type localities.
Figure 306. *Arnica gracilis* S-1605. AB, Moraine Lake. X two-thirds.
each year (S-1603, 1605, 1613). Plants branch from near ground level and often above each pair of leaves, producing many heads per stem and per plant (Figures 307-318). At the other extreme, in more shaded habitats often under Pinus ponderosa or Pinus contorta, as in stabilized rock slides at Monroe Lake, BC (S-1562), the rhizomes are much longer and plants form open clumps more in the nature of Arnica latifolia or Arnica cordifolia. These plants are rarely branched, producing only one head (rarely 3) per stem. Yet the shape of the leaves, ray florets, and the character of the short stipitate glandular hairs is typical of those plants from higher elevations. (Figures 319-332).

Arnica gracilis and Arnica latifolia are easily distinguished in the field. Arnica gracilis has a distinct fragrance and viscid nature to the leaves caused by the glandular hairs on the leaves. Arnica latifolia is usually glabrous and when it does have pubescence on the leaves (especially from more northern latitudes) the pubescence is non-glandular or predominately so, and it is usually not at all fragrant when bruised. Arnica gracilis leaves also look darker green, look and feel rough to the touch, and are noticeably rough under 10X magnification. Arnica gracilis also has fewer, narrower, more pointed rays (Figures 246, 247), long-petiolate ovate leaves, and broad ovate, usually sessile bracts. Very rarely, and only at high elevations, does Arnica latifolia have the very short rhizomes typical of Arnica gracilis.

The predominance of triploid apomictic populations has been demonstrated in this species. It probably represents a complex of apomictic races having originally arisen from hybridization between the diploid Arnica latifolia and the tetraploid races of Arnica mollis or Arnica diversifolia (the latter two both in Subgenus Chamissonis). The glandular pubescence of leaves and stems,
short scaly rhizomes, black, often glandular achenes, and often tawny pappus are all characteristics similar to the latter two species. Indeed, there are many populations which are separated only with difficulty from these species, especially when using herbarium specimens. Examples are Moraine Lake, Banff National Park, AB, where Arnica gracilis (S-1605) grows with a small form of Arnica diversifolia (S-1606) on a scree slope. The latter is distinguished in the field by the more viscid leaves, darker pappus, and less branched habit.

Artificial crosses between Arnica latifolia and Arnica mollis or Arnica diversifolia have been mostly unsuccessful. Arnica mollis has grown very poorly in cultivation and a few crosses between it as the male parent and Arnica latifolia as the female parent have produced no achenes. Arnica diversifolia has grown well in cultivation. However only one cross between this and Arnica latifolia has been successful, producing a few viable achenes. However, these did not survive beyond a few weeks. So, efforts to artificially produce an Arnica gracilis-like hybrid have not been successful.

There may also be confusion between Arnica gracilis and Arnica rydbergii (Subgenus Arctica), where they are growing in similar habitats. However, Arnica rydbergii usually has more sessile cauline leaves which have a very distinct pair of lateral veins nearly parallel to the mid-rib, giving the leaves a tri-nerved appearance. The pappus is pure white, the rays are darker orange-yellow, and the achenes are densely hirsute throughout in Arnica rydbergii.

5. Arnica cernua T. Howell, Fl. NW. Am. 373. 1903.

Arnica chandleri Rydb., N. Am. Fl. 34:339. 1927. TYPE: California, Humboldt Co., Hoopa Indian Reservation, June 1901, H.P. Chandler 1298 (holotype NY; isotypes MO, UC).
Figures 307-318. Variation in basal leaves of a single population of typical high-elevation *Arnica gracilis* S-1603, AB, Lake Louise.
Figures 319-332. Variation in basal leaves of a single population of lower-elevation *Arnica gracilis* S-1562, BC, Monroe Lake.
Rhizomatous perennial herb forming large open populations or tight clumps of sterile basal rosettes and flowering stems; rhizomes (1-)4-15(-20) cm growth/year, (1-)2-3(-5) mm thick, naked except pairs of brown scales at nodes, and crowded scales and old leaf bases toward summit, simple or sparsely to much branched especially toward summit; roots 2-3 mm thick, mostly unbranched, succulent; stems single or few, simple or rarely branched near base or higher, (5-)10-30(-45) cm high, glabrate to sparsely villous with incurved hairs, purplish or reddish at base or throughout; innovations with 4-8 long petiolate leaves, petioles (1-)4-6(-10) cm, blades 4-6(-7) cm long 2-4 (-5) cm broad, elliptic to ovate or rotund, bases rounded to subcordate, tips rounded to acute, margins entire or regularly or irregularly serrate, dentate, crenate, or laciniate and often undulate; cauline leaves 2-3(-5) pairs, the largest pair usually near base of stem, long petiolate, petioles (-1)2-4(-6) cm long, blade (0.5-)2-4(-6) cm long, (1-)2-4(-5) cm broad, petioles and blade size reduced upward, upper-most bract-like, often broadly sessile and often alternate; shape and margins of cauline leaves similar to that of innovation leaves, although often more deeply incised, leaves thick and succulent and often reddish or purplish especially along veins of lower surface; herbage glabrate to scabrid especially on margins and along main veins, rarely densely scabrid and pilose on upper surface; inflorescence usually a single head or an open corymb of 3-5 heads, nodding in bud, nodding or erect at anthesis, peduncles (2-)5-15(-22) cm long, upper peduncle and periclinum sparsely to densely pilose and scabrid; heads 15-25 mm tall, radiate; involucral bracts 7-12(-15), + uniseriate, 10-15 mm long, 3-5 mm broad, broadly lanceolate, acute to obtuse; ray florets (5-)7-9(-14), dark yellow, tube 4-6 mm long, limb 10-20 mm long, 4-8 mm broad, linear elliptic with 1-3 teeth at tip, tubes and base of limbs densely short villous; disc florets 24-57, tubular 10-15 mm
long, sparsely to densely villous at base and sparingly toward summit and on lobes; pollen diameter 35-50 μm; achenes grey, 6-8 mm long, 1+ mm broad, sparsely to usually densely hirsute with bifurcate hairs throughout or from mid-point distally; pappus pure white, 41-60 barbellate to subplumose bristles, the lateral setae .10-.15 mm long; sexual diploid, 2n=38.

Type: Oregon, Josephine County, near Waldo, on dry banks, base of Coast Mountains, June 1884, T. Howell 166 (ORE).

Distribution: *Arnica cernua* is restricted to serpentine soils at mid-elevations (400-1800 m) of the Coast Ranges and Siskiyou Mountains in three counties of Southwestern Oregon (Coos, Curry, and Josephine) and three counties of Northwestern California (Del Norte, Siskiyou, and Humboldt). Figure 333.

Illustration: Figure 334.

This distinct species is one of the rarest Arnicas, although it is often common where it does occur. Populations occupy rock crevices or rubble in open exposed habitats in open forests of *Pinus jeffreyi*, *Calocedrus decurrens*, *Garrya fremontii*, and *Arctostaphylos* spp., or at lower elevations are scattered in open forests of *Pinus ponderosa*, *Pseudotsuga menziesii*, and *Calocedrus decurrens*. It is not known to occur off serpentine soils.

*Arnica cernua* is obviously derived from *Arnica latifolia*, being most similar to that species, but differing from it in a number of characters other than their different ecological niches. The thick, leathery leaves, which are usually purple or red are distinctive in *Arnica cernua*. The leaves of *Arnica latifolia* are never as thick and fleshy nor are they often more
Figure 333. Distribution of *Arnica spathulata* (open circles) and *Arnica cernua* (closed circles). Stars indicate type localities.
Figure 334. Habit of *Arnica cernua* S-1386. OR, Josephine Co.

X two-thirds.
than slightly suffused with red or purple. The nodding or cernuous buds, from which *Arnica cernua* gets its name, may or may not become erect at anthesis. No specimens of *Arnica latifolia* have been seen with nodding buds. Both the phyllaries (Figures 130, 132) and the rays (Figures 139, 140) of *Arnica cernua* are larger and broader than those of *Arnica latifolia*. The distinct teeth at the tip of the ray florets of *Arnica cernua* differ from the more truncate tips of the *Arnica latifolia* ray florets. The achenes of *Arnica cernua* are much more densely hirsute distally or throughout than the smaller achenes of *Arnica latifolia*.

The species consists of two fairly distinct ecotypes, a small form (Figure 336) from exposed rocky slopes at higher elevations (750-1450 m) as in collections from Hoopa Indian Reservation and Horse Mountain, both from Humboldt Co., CA (Straley 1396, 1772) and a larger form (Figure 337) from lower elevations (400 m) in open forest habitats as from near O'Brien, Josephine Co., OR (Straley 1386). The smaller ecotype is barely rhizomatous, forming dense clumps with many stems, which often branch above producing 3-5 or more heads per stem. The leaves tend to be shorter-petioled and are relatively small (Figures 339-355). The larger ecotype is strongly rhizomatous forming large "loose" colonies. The stems are usually produced singly, are unbranched and consistently produce a single head per stem. Within populations of the larger ecotype there is a marked difference between plants growing in nearly full sun in that they have thicker, smaller, shorter petioled leaves (Figures 356-365) compared to the thinner, larger, longer petioled leaves of plants growing nearby in rather dense shade (Figures 366-370). Although Rydberg (1927) considered the small ecotype a separate species, recognizing it as *Arnica chandleri*, there are many collections with
Figures 335-338. Habitat and habit of *Arnica cernua*.

Figure 335. Habitat at summit of Hoopa-Redwood Valley Road, ele. 750 m, Hoopa Indian Reservation, Humboldt Co., CA, *Straley* 1772. Serpentine soils in open forest of *Pinus jeffreyi*, *Pinus lambertiana*, *Calocedrus decurrens*, *Arbutus menziesii*, and *Arctostaphylos* spp.

Figure 336. Dense clump with two open heads and many buds at above locality.

Figure 337. Larger form with one head per stem in dense forest of *Pinus ponderosa*, *Calocedrus decurrens*, and *Arctostaphylos* spp. at O'Brien, Josephine Co., OR, *Straley* 1386.

Figure 338. Seed head from above population.
Figures 356-365. Variation in basal rosette leaves of *Arnica cernua* S-1743, OR, Josephine Co., large ecotype, from plants growing in full sun.
Figures 366-370. Variation in basal rosette leaves of *Arnica cernua* S-1743, OR, Josephine Co., large ecotype, from plants growing in shade.
intermediate characters, so there seems to be no reason to give these populations separate taxonomic recognition.

There are a number of exceptional collections of this species, including extremely narrow-leaved specimens from Red Mountain, Curry Co., OR, Leach 3442 (ORE), with the largest cauline leaf blades only 1.5 cm long and 0.5 cm broad and a collection from Tennessee Pass, Josephine Co., OR, Savage s.n. (ORE) with the lower cauline leaf blades broader (5 cm) than long (3.5 cm) and deeply lobed. In an unusually pubescent specimen from Head Slide Creek, Curry Co., OR, Leach 2879 (ORE), all leaves and stems are scabrous throughout giving the plants a grey appearance. This population may represent a local ecotype or may reflect possible hybridization with one of the pubescent species, likely Arnica cordifolia.

The Type specimen, Howell 166 (ORE) consists of three flowering stems and one basal rosette. Two of the plants are similar to most of the later collections of the species. However, the third specimen on the sheet has two sets of distinct whorls of three leaves rather than opposite pairs, an unusual character for the genus.


(holotype, G; isotype, KEW).


TYPE: Oregon, Hood River, 1884, Barrett, s.n. (G).

Arnica grayi Heller. Muhlenbergia 1:5. 1900. TYPE: Oregon, Hood River, 1884, Barrett, s.n. (G).


Rhizomatous perennial herb; rhizomes 5-15(-22) cm growth/year, 2-5 mm thick, naked except for pairs of brown scales at nodes and crowded scales and old leaf bases toward summit, forming large populations of sterile basal rosettes and flowering stems; roots + succulent, 2-3 mm thick, relatively unbranched; stems single or few, simple or branched near base or throughout, (15-)20-45(-65) cm tall, sparsely to densely strigose, villous, and long stipitate glandular throughout; innovations with 4-8(-12) long petiolate leaves, petioles (l-)4-6(-10) cm long, blades, ovate or broadly ovate to broadly lanceolate, 3-5(-9) cm long, 2-4(-5) cm broad, bases cordate, subcordate, to rounded, or rarely attenuate, tips acute to rounded, margins subentire to usually regularly serrate, dentate, orcrenate, or rarely doubly serrate or dentate; cauline leaves (2-)3-5(-6) pairs, often reduced basally and becoming bract-like toward summit, lower cauline leaves usually the largest, long petiolar, petioles 2-6(-10) cm long, often winged 2-5(-14) mm,
blades (3-)4-7(-9) cm long, 2-6 cm wide, upper pairs progressively shorter petioled, and often subalternate, shape and margins of cauline leaves like that of innovations; vestiture of herbage usually moderately to densely scabrous and villous, especially along veins, and sparsely long stipitate glandular throughout; inflorescences an open corymb of 3-7(-20) heads, rarely subradiate, 12-15 mm high; involucral bracts, 7-12 + uniseriate, 10-15 mm long, 2-3(-5) mm wide, narrowly to broadly lanceolate, acute to acuminate; florets 19-45, tubular, 8-12 mm long, marginal florets often ampliate or rarely + ligulate, to 20 mm long, 5 mm wide, sparsely to densely villous and sparsely stipitate glandular at base and sparingly upward, and on outer surface of lobes; pollen diameter 45-60 μm; achenes dark grey, 6-8 mm long, 1 mm wide, sparsely to densely hirsute with bifurcate hairs, and stipitate glandular throughout, especially distally; pappus white, barbellate, of 42-64 bristles, lateral setae .05-.15 mm long; apomictic; 2n=38, 76.

Type: California, Monterey Co., Monterey, in forest, Hartweg 1805 (KEW).

Distribution: This species occupies a wide variety of habitats from open chapparal to conifer forests, near sea level to 1800 m, from Southern Washington (Klickitat County) to Southern California (Orange County). (Figure 305).

Illustration: Figure 371.

There has been much confusion and difference of opinion in the treatments of Arnica discoidea, the most widespread and most variable of the discoid species. Arnica discoidea, as presented here, contains elements recognized by Maguire (1943) as three species, Arnica discoidea, Arnica parviflora (with 2 subspecies), and Arnica grayi. Ediger & Barkley (1978) treat these as one species, Arnica discoidea, with three varieties.
Figure 371. Arnica discoidea S-1775. CA, Mendocino Co. X two-thirds.
At the northern limit of their distribution there are populations formerly known as *Arnica grayi* Heller, from Klickitat Co., WA (S-1825), Wasco Co., OR (S-1821), and Hood River Co., OR, Barrett, s.n. (G), growing with *Arnica cordifolia*. The leaves of these northern populations tend to be more densely strigose and with somewhat less cordate bases than in most of the southern populations. However, there are numerous intermediates throughout the range of the species, as in collections from San Mateo Co., CA, Keck 1775 (RSA).

Variability in leaf size, shape, and especially in margins can be seen in many populations (Figures 376-385) and is particularly notable in a collection from Mt. Eddy, Siskiyou Co., CA, Copeland 3909 (POM).

Many populations throughout the range of the species have marginal ampullate florets (Figure 155) or elongated ray-like florets (Figures 154, 156). This condition is especially pronounced in collections from Santa Barbara Co., CA, Smith 8330 (SBM), Trinity Co., CA, Baker 328 (HSC), and Eldorado Co., CA, Peirson 9517 (RSA). Superficially, these collections look very much like *Arnica cordifolia* and are often misidentified as such. However, none of the collections has true female ray florets, although they are likely often functioning as female. Even the elongated marginal florets are usually + tubular (Figures 154, 156) and have functional or abortive anthers.

*Arnica discoidea* differs from *Arnica cordifolia* in features other than an absence of ray florets. *Arnica discoidea* is usually more branched, has more heads (up to 20/stem), is less strongly rhizomatous, and usually prefers drier habitats than *Arnica cordifolia*. The discoid species also tends to be less pubescent, or at least the pubescence tends to be shorter than that of *Arnica cordifolia*. Trends toward, and differences between *Arnica spathulata* and
Figures 372-375. Habitat and habit of Arnica discoidea and Arnica spathulata.

Figure 372. Habitat of Arnica discoidea S-1825, WA, Klickitat Co., Klickitat River Gorge, open forest of Pinus ponderosa and Pseudotsuga menziesii.

Figure 373. same, flowering stems and basal rosettes.

Figure 374. same, three flowering heads and two seed heads.

Figure 375. Arnica spathulata S-1385, OR, Josephine Co., O'Brien.
Figures 376-385. Variation in basal leaves of *Arnica discoidea* S-1789, CA, Marin County.
Arnica discoidea are discussed under Arnica spathulata.

There does not seem to be any correlation between distribution, chromosome number, and size of heads, whether leaves are basally disposed or evenly distributed along the stem, or achene and pappus features in any of the discoid populations. These features have been used to separate the discoid species recognized in previous treatments. It seems best to treat these as one polymorphic species with both diploid, sexual and tetraploid, apomictic races.


Rhizomatous perennial herb often forming short woody caudex 0.5-1.5 cm broad, 1-2 cm high, 2-5(-7) cm below surface of ground, producing vertical and horizontal rhizomes (1-)3-7(-14) cm/year, generally naked except pairs of brown scales at nodes and crowded scales and some old leaf bases toward summit, forming large open populations of sterile basal rosettes and flowering stems; roots relatively few and succulent, 1-3 mm in diameter; stems single or few, simple to branched below and above, (15-)25-45(-55) cm tall, sparsely
to densely villous and long stipitate glandular throughout; innovations with 4–6(-10) long petiolate leaves, petioles 2–7 cm long, wingless or with wings 2–7(-12) mm broad, blades (2–)4–6(-8) cm long, 1–3.5 cm wide, spatulate to elliptic or obovate, bases attenuate or rarely rounded, tips rounded to acute, margins entire to coarsely and evenly serrate or crenate; cauline leaves 3–6 pairs, basally disposed to evenly distributed along stem, often subopposite, reduced and bract-like upward, where frequently alternate, with petioles as wide as or wider than blade, largest pair of cauline leaves with longest petioles, usually near base, petioles (1–)3–5(-8) cm, wings 2–10(-20) mm, blades (2–)3–6(-8) cm long, (1–)2–4(-5) cm wide, shape and margins as with leaves of innovations, veins usually prominent and reddish or purplish especially on lower surface; vestiture of herbage pilose and long stipitate glandular throughout, especially along veins, margins often ciliate; inflorescence a single head or an open corymb of 3–5(-25) heads, erect; peduncles (2–)4–8(-15) cm long, upper peduncles and periclinum long pilose and stipitate glandular; heads 15–25 mm high, discoid, rarely with amphiolate marginal florets; involucral bracts 7–13(-17), uniseriate, 10–15 mm long, 1–4 mm wide, lanceolate to broadly lanceolate, obtuse to acute; florets 18–52, goblet-shaped to tubular, 8–11 mm long, dark yellow, sparsely to densely villous and stipitate glandular toward base and sparsely upward and on lobes; pollen diameter 35–55 μm; achenes black, dark brown, or dark grey, short stipitate throughout or from mid-point distally, few or no bifurcate hairs distally, 6–9 mm long, 1 mm wide, pappus pure white, 37–56 bristles, barbellate, the lateral setae .07–.10 mm long; apomictic polyploid and self-incompatible sexual diploid; 2n=38, 76.

Type: Oregon, Douglas County, Glendale, June 3, 1887, T. Howell 1200 (US).
Distribution: *Arnica spathulata* occurs on open serpentine outcrops or open forests at low to mid-elevations (180-1400 m) of Coast and Cascade Ranges from Douglas and Curry Counties in SW Oregon to Siskiyou County in NW California. Figure 333.

Illustration: Figure 386.

This, the rarest of the species in section *Eradiatae* is known from about two dozen populations largely restricted to serpentine soils. Where it does occur the populations often consist of several dozen to hundreds of individuals. Populations or individuals are quite variable in size, branching habit, leaf shape, and pubescence. There is a small ecotype to which the name *Arnica eastwoodiae* Rydb. has been assigned. These populations, as in collections from French Hill Rd., Gasquet, Del Norte Co., CA, (S-1751, probably the type locality of *Arnica eastwoodiae*) are smaller, have narrower leaves with less-winged petioles (Figures 387-398), narrower heads, and shorter pubescence than most other populations of the species. They are found on open serpentine slopes in mixed forests of *Pinus attenuata*, *Calocedrus decurrens*, and *Pinus ponderosa* or *Pinus jeffreyi*. At the other extreme are a majority of populations, with taller stems, broader leaves, usually winged petioles (Figures 399-407), and long glandular hairs throughout. Typical populations of this larger ecotype are collections from Kirby, Cave Junction, and Selma, all in Josephine Co., OR, (S-1380, 1381, 1740). These populations are usually found on more densely forested hillsides of *Pinus ponderosa*, *Pseudotsuga menziesii*, *Arbutus menziesii*, and *Quercus kelloggii*. There are numerous populations which are intermediate in some or all of the above characters, including collections from Gasquet, Del Norte Co., CA, (S-1390) and O'Brien, Josephine Co., OR, (S-1385).
Figure 386. *Arnica spathulata* S-1740. OR, Josephine Co. X two-thirds.
Figures 399-407. Variation in basal rosette leaves of *Arnica spathulata* S-1740, OR, Josephine Co., large ecotype.
Occasionally in the large-leaved populations, as in a specimen from Pleasant Creek, Jackson Co., OR, Hammond 230 (MO), the petioles of cauline leaves are broad and are often wider than the blades. This character was not seen in any other Arnica. An unusual collection from Gold Basin, Curry Co., OR, Leach 2874 (ORE) has strongly basally disposed cauline leaves, and unusually dense, short-pilose vestiture.

*Arnica spathulata* most closely resembles *Arnica discoidea* from which it certainly has been derived. The former differs in its spathulate leaves which are more often purple or red, in its taller heads, larger, darker achenes, and in the character of its rhizomes. A somewhat intermediate population has been called *Arnica cusickii* Rydb., Cusick 2873 (NY, POM, MO, US). The exact locality is not known, only "dry western slope of the Cascade Mountains, Southern Oregon." The several specimens are variable, but the character of the basally disposed cauline leaves with cordate bases closely resembles some *Arnica discoidea* specimens, so much so that in the most recent monograph of the genus (Ediger and Barkley, 1978), it is listed in the synonymy under *Arnica discoidea*. However, in the characters other than the leaves, especially in the vestiture, rhizomes, and achenes, it seems to fit best in *Arnica spathulata* and is herein retained as a synonym of that species.

Ampliate or elongated ray-like marginal florets seem to be much rarer in this species than in *Arnica discoidea*. Only one specimen, Tracy 19424 (UC) from Del Norte Co., CA, north of Monumental, has been seen with long ray-like ampliate florets. It was reported as growing with typical discoid plants.
Subgenus Calarnica subgen. nov.

Herbae perennes erectae a caudice ligno subterraneo; rhizomata carentes; radices succulentae, verticales; caules ramosi; folia caulina ovata, sessile; plantae dense vel sparsim stipitato-glandulosae et pilosae; capitula eradiata; pappus albusve subinfuscatus suffusus, barbellatusve subplumosus; chromosomatum numerus gamatae n=19.

Erect perennial herbs from woody caudex, non-rhizomatous; roots fleshy, vertical and unbranched; lacking sterile basal rosettes (innovations); flowering stems branching from base, or sparingly to much-branched above; stems equably leafy, cauline leaves sessile, ovate, margins entire to serrate, bases rounded, apex acute to rounded; stems and leaves pilose and long stipitate glandular; inflorescence a single head or much-branched leafy corymb; heads discoid; involucral bracts narrowly to broadly lanceolate, acute; florets tubular; achenes ribbed, hirsute and stipitate glandular; pappus white to tawny, barbellate; gametic chromosome number n=19.

Type: Arnica viscosa A. Gray

W.L. Jepson, s.n. (not seen).


Perennial herb from woody caudex 1-4 cm broad, covered with old stem bases and brown scales; rhizomes lacking; roots succulent, mostly vertical
and unbranched to 40 cm long, 3-6 mm thick; stems solitary or several, much branched throughout, 25-50 cm tall at anthesis, sparsely short stipitate glandular and pilose below, densely long stipitate glandular and pilose above; innovations not produced; cauline leaves with 6-10(-12) pairs, largest near middle of stem, reduced and scale-like toward base, reduced and bract-like above, upper or all leaves/bracts often alternate or subopposite, largest cauline leaves 3-5 cm long, 1.5-3.5 cm broad, narrowly to broadly elliptic, broadly sessile, margins entire, bases rounded to acute, tips acute to obtuse, both surfaces sparsely to densely pilose, especially along veins and margins, densely long stipitate glandular, with yellow-tipped hairs; heads solitary terminating all upper branches; peduncles 0.5-5 cm long, peduncles and periclinum long stipitate glandular; heads erect, discoid, 1.5-2 cm high; involucral bracts, 8-14(-21), + uniseriate, 6-12 mm long, 1-3 mm wide, narrowly lanceolate, acute; florets 9-32(-54) tubular, 8-12 mm long, white to creamy-white, densely long stipitate glandular below; pollen diameter 40-45 μm; achenes grey to brown, sparsely to densely long stipitate glandular throughout, shallowly ribbed, 4-6 mm long, to 1 mm wide, pappus off-white to tawny, 36-48 bristles, barbellate, 5-9 mm long, lateral setae .05-.15 mm long; self-incompatible diploid; 2n=38.

TYPE: California, Siskiyou County, Mt. Shasta, 2400 m, 1877, J.D. Hooker & A. Gray, s.n. (G).

Distribution: This species occurs on loose pumice slopes at high elevations (1750-2500 m) in Crater Lake National Park, Klamath County, Oregon and in Western Siskiyou and Northern Trinity Counties, California. Figure 408.
Figure 408. All known populations of *Arnica viscosa*.
Arnica viscosa is the most distinctive and one of the rarest Arnica species. Its much-branched habit, small, entire, sessile leaves, narrow, white, discoid heads, and tawny pappus set it apart from all other species. It is the only species with white florets, a character strangely never mentioned in previous descriptions or monographs. The prominent yellow anthers give the heads a definite yellowish cast which may be the reason why the white florets have not been observed previously.

Arnica viscosa is strongly viscid throughout with long yellow-tipped glandular hairs on all vegetative parts and on florets and achenes. Its strong odor is unlike that of any other Arnica. The odor is retained in herbarium specimens for many years.

Described from Mt. Shasta, California in 1887 by Asa Gray, Arnica viscosa was long known only from the type locality (Figures 410-412) and from Garfield Peak in Crater Lake National Park, Oregon. Only in the past 20 years has it been noted from at least four other places in Crater Lake, five localities in Western Siskiyou County, California, and two localities in Northern Trinity County, California, in the Salmon Mountains and Trinity Alps.

Where Arnica viscosa has been observed on Mt. Shasta and Garfield Peak there is virtually no other vascular plant life. The very deep roots are able to grow almost vertically among the loose pumice into the soil below. Both of these populations are quite large, composed of several hundred plants.

A study of 25 herbarium specimens and two populations in the field showed less variability in this species than in many of the others. There is a great tendency for upper branches, leaves, and bracts to be subopposite to completely alternate. An extreme example of this is a specimen from Upper English
Figure 409. *Arnica viscosa* S-1411. CA, Siskiyou County, Mt. Shasta (Type Locality). X two-thirds.
Figures 410-414. Habitats and habit of *Arnica viscosa*.


Figure 413. Habitat of *Arnica viscosa* S-1946, OR, Klamath Co., Crater Lake.

Figure 414. Flowering head of *Arnica viscosa* S-1411, CA, Siskiyou Co., Mt. Shasta.
Lake, Siskiyou County, CA, Oettinger 668 (HSC). One unusually pilose specimen in which the stem and veins are predominately long pilose rather than predominately long stipitate glandular as usual was collected on Preston Peak, Siskiyou County, CA, Ground 820 (PUA).

There is a questionable collection by W.L. Jepson from Mt. Shasta, named Raillardella paniculata by Greene. It fits the description and exact locality of Arnica viscosa. As mentioned earlier there is virtually no other plant life growing near the Arnica at that elevation on Mt. Shasta, so this collection must be this species and is listed under the synonymy although a voucher specimen was not cited in the original description and has not been located.


Perennial herb from woody caudex 3-5 cm broad covered with old stem bases and dark brown scales; rhizomes lacking; roots succulent, mostly unbranched, to 30 or more cm long, 2-5 mm thick; stems solitary or few, simple to rarely branched above upper pairs of leaves/bracts, 30-50 cm high at anthesis, sparsely scabrous and pilose below, becoming more densely pilose and stipitate glandular above; cauline leaves 7-10 pairs, largest near middle of stem, reduced and becoming scale-like toward base, and reduced and bract-like above, upper leaves and bracts often subopposite or alternate, largest cauline leaves (3-)4-6(-7) cm long, (1.5-)2-3(-4) cm broad, narrowly elliptic to broadly so, broadly sessile, margins evenly coarsely serrate or rarely doubly serrate, bases rounded, tips acute to obtuse, rugose, veins prominent, especially on lower surface, lower surface sparsely to densely pilose and sparsely stipitate glandular; inflorescence a single head terminating main
stem and lateral branches, if any; peduncles 1.5-5 cm long, peduncles and periclinum densely pilose; heads nodding, especially in bud, discoid, 2-2.5 cm high; involucral bracts 8-14, + uniseriate, 10-15 mm long, 4-6 mm broad, broadly lanceolate, acute to obtuse; florets 32-56(-70), tubular, 8-10 mm long, dark yellow, densely villous, especially below; pollen diameter 35-40 μm; achenes grey, strongly angled and ribbed, 6-8 mm long, 1.5 mm broad, densely hirsute with bifurcate hairs; pappus white, of 45-55 bristles, 6-10 mm long, barbellate, the lateral setae 0.1-0.2 mm long; self-incompatible; 2n=38.

TYPE: California, Shasta County, Salt Creek, 430 m, June 1903, H.M. Hall & E.F. Babcock 4013 (UC).

Distribution: Arnica venosa is found in foothills (430-530 m) of the Sacramento River Valley in mixed conifer and Quercus spp. forest of Shasta County, California. Figure 415.

Illustration: Figure 416.

This distinctive species, closely related to Arnica viscosa, has toothed leaves, nodding buds, yellow florets, and a paucity of glandular hairs, setting it apart from that species. This too, is one of the rarer Arnica species. For many years it was known from only two localities in Shasta County, California, Iron Mountain and Salt Creek, the latter the type locality. The exact location of "Salt Creek" is not known. There are several Salt Creeks in Shasta County, including one which is now partially under Lake Shasta. Iron Mountain is now the site of an active copper mining operation and the Arnica may have been exterminated from that locality. The mine owners will not allow botanists to search the area. Having not been collected
Figure 415. All known populations of *Arnica venosa*.
Figure 416. *Arnica venosa* S-1793. CA, Shasta County. X two-thirds.

Figures 417-418. Habitat, roadside bank in open mixed forest of *Quercus* spp. and conifers.

Figure 419. Habit of numerous branches from base.

Figure 420. Strongly nodding bud.

Figure 421. Head with first florets open and nodding buds, and rugose leaves.
for more than 50 years, it was thought to be possibly extinct. Only in recent years has there been renewed interest by the National Forest Service personnel in the area to find it, and at least 5 other localities have been found, all in Shasta County.

It is found in discrete populations of a few individuals to a few dozen plants, in open forests of *Pinus ponderosa*, *Pinus lambertiana*, *Pinus attenuata*, *Pinus sabiniana*, *Pseudotsuga menziesii*, *Quercus kelloggii*, *Quercus chrysolepis*, *Calocedrus decurrens*, *Arctostaphylos* spp. and *Ceanothus* spp., and along open roadsides in these forests. Plants sparingly colonize the disturbed roadside banks. Plants begin to flower in mid- to late May and bloom for a few weeks before the hills become very hot and dry, although a few stragglers may continue to flower throughout the early summer months. In cultivation seedlings continued to flower for many months when grown under wetter conditions.

Specimens are very rare in herbaria. Of about 6 specimens seen from 3 localities plus 3 other populations studied in the field during the spring and summer of 1978, there seems to be very little variability in the plants.
Maguire (1943) suggests that the genus *Arnica* probably arose in arctic or subarctic Western North America and spread from there to the east and south. He recognized five subgenera with *Arctica* as the ancestral subgenus. He considered the large, hemispheric or turbinate heads and densely pubescent periclinum as being primitive characters. If these morphological characters are considered primitive, then the possible phylogenetic scheme shown in Figure 422 can be deduced for the other subgenera. This is a modification of Maguire's phylogenetic scheme for his five subgenera, plus my newly proposed subgenus *Calarnica*.

Within subgenus *Austromontana*, *Arnica cordifolia* is the probable link between the two subgenera, *Arctica* and *Austromontana*. This species has large, usually solitary heads, and densely pilose periclinum. From *Arnica cordifolia*, the other species in *Austromontana* and *Calarnica* could logically have evolved as shown in Figure 423.

*Arnica cordifolia* occurs today largely as a series of apomictic polyploid populations, from triploid to hexaploid, with tetraploid predominating. However, diploid populations do occur rarely. Whether or not any of these diploids are sexual has not been demonstrated. Based on pollen quality and the usually strong correlation of diploidy with sexuality in the genus, there is a strong possibility that some of these diploid populations are sexual. Barker (1966) hypothesized that apomixis in the genus is a relatively recent development (inter- or post-glacial). Sexual diploids are assumed to have been more common and widespread in the past.

Diploid *Arnica cordifolia* probably gave rise to *Arnica latifolia* in generally wetter habitats. *Arnica latifolia* usually has narrower heads, with
fewer florets, and a less-pilose periclinum than Arnica cordifolia. These characters are considered as being derived. Arnica latifolia is the most polymorphic species in the subgenus, although it exists almost entirely as sexual diploid populations, with many ecotypes. The close relationship of these two species can be seen in numerous populations which combine many of the morphological characters of both species.

Arnica latifolia has in turn probably given rise to two other species. Arnica cernua, also a sexual diploid, is a rare serpentine soil endemic. It combines many morphological characters of Arnica latifolia but is ecologically distinct. A second species probably derived from Arnica latifolia, possibly through hybridization, is Arnica gracilis. It is considered a variety of Arnica latifolia by many authors. However, in my opinion, most populations can be easily distinguished from Arnica latifolia. Arnica gracilis is largely a triploid, autonomous apomict, found mostly at higher elevations or in rockier habitats than Arnica latifolia. Arnica gracilis is more branched and has much smaller heads, with fewer florets than Arnica latifolia. I interpret these characters as being advanced. Arnica gracilis has the glandular pubescence found in Arnica diversifolia and Arnica mollis in subgenus Chamissonis. Both of these latter species have been shown to have tetraploid elements.

The chromosome number and morphology of Arnica gracilis suggests it may be of hybrid origin between diploid Arnica latifolia and tetraploid Arnica diversifolia or Arnica mollis, although attempts to make this cross artificially have been unsuccessful. Arnica latifolia often grows with either or both Arnica diversifolia and Arnica mollis, but there are presently barriers to hybridization between the sexual diploid and the apomictic tetraploids. Both of the latter two species usually have very low pollen fertility.
Arnica nevadensis closely resembles Arnica cordifolia in morphology and in being a series of tetraploid autonomous apomictic races. The former is usually ecologically distinct, being found at higher elevations and in more exposed habitats. There are populations of these two species which are difficult to assign to one species or the other. Arnica nevadensis may have arisen as selections of apomictic races of Arnica cordifolia, without hybridization with other species. However, the longer pappus setae, tawny pappus, shorter pubescence, and attenuated or rounded leaf bases of Arnica nevadensis suggest that some other species may have been involved in its early evolution. Based on morphology, Arnica nevadensis could have originated as the result of hybridization between Arnica cordifolia and Arnica chamissonis in the subgenus Chamissonis.

Arnica discoidea differs little from Arnica cordifolia except in its lack of ray florets. The usually, more-branched habit, more heads, and discoid condition of Arnica discoidea are interpreted as derived characters. Arnica discoidea is a plant of chaparral and other drier habitats than that of Arnica cordifolia. Another discoid species, Arnica spathulata, seems to be a serpentine endemic derivative of Arnica discoidea. Both of these discoid species occur as both diploid and tetraploid populations.

The subgenus Calarnica with two species, Arnica viscosa and Arnica venosa is considered as distinct from subgenus Austromontana as the latter is from any of the other subgenera. I consider subgenus Calarnica to be advanced with its numerous small heads, sessile leaves, lack of rhizomes, and adaptation to drier habitats. The relationship of this subgenus to other subgenera is unclear. It is possibly derived from Arnica spathulata. The pappus, pubescence, and woody caudex of Arnica venosa are closer to that of Arnica
spathulata than any other species. *Arnica viscosa* is probably a high-elevation derivative of *Arnica venosa*. They are both sexual diploids. I consider *Arnica viscosa*, with its very narrow heads and white florets, the most advanced member of the genus.
Figure 422. Possible Phylogenetic Relationships of Arnica Subgenera (modified after Maguire, 1943).
PHYLOGENETIC RELATIONSHIPS IN ARNICA SUBGENERA
Figure 423. Possible Phylogenetic Relationships of *Arnica* Species in Subgenera *Austromontana* and *Calarnica*.
A conservative taxonomic treatment of *Arnica* subgenus *Austromontana* with seven species and a new subgenus, *Calarnica*, with two species has been presented. This treatment is based on field studies, cytology, breeding systems, artificial hybridizations, insect interrelationships, and a morphological re-evaluation. In a monograph of the genus *Arnica* by Maguire (1943) these two subgenera were recognized as one, *Austromontana*, with 13 species and three infraspecific taxa. I recognize the following species in subgenus *Austromontana*:

**Sexual, incompatible diploids**

*Arnica latifolia* (one tetraploid population reported)

*Arnica cernua*

*Arnica spathulata* (one tetraploid population reported)

**Pseudogamous apomictic polyploids**

*Arnica cordifolia* (some autonomous apomicts and rarely, diploids)

**Pseudogamous apomictic polyploids and sexual, incompatible diploids**

*Arnica discoidea*

**Autonomous apomictic polyploids**

*Arnica gracilis*

*Arnica nevadensis*

I recognize the following sexual, incompatible diploids in subgenus *Calarnica*:

*Arnica venosa*

*Arnica viscosa*
No infraspecific taxa are recognized. Although several species contain two or more relatively distinct elements, there is, in my opinion, too much overlap in characters to warrant giving them taxonomic recognition. There also does not seem to be any consistent geographical or ecological isolation of these populations.

There is a strong correlation between high pollen stainability, diploidy, and sexuality. Autonomous apomictic polyploids have very low pollen stainability, or pollen is not produced at all. Pseudogamous apomictic polyploids have higher pollen stainability than the autonomous apomictics, but usually lower than the sexual diploids.

Seed set and viability is quite low in most of the species, and those achenes which are produced are often fed upon by insect predators. On the other hand, vegetative reproduction by rhizomes has been shown to be an important factor in short distance dispersal of several of the species in subgenus *Austromontana*.

There are no completely clear-cut species in subgenus *Austromontana*. Every species, as I recognize them, intergrades into one or more other species. In the sexual diploids there are a number of local ecotypes which are very plastic, responding to the local environmental conditions. Individuals have been shown to exhibit morphological differences from year to year under varying environmental conditions in cultivation. Species in these sexual diploids are recognized as a series of outbreeding populations, with high pollen stainability, similar morphology, and similar ecological niches.

The two sexual, diploid species in subgenus *Calarnica* are very clear-cut species. These two rare species show very little interpopulational variation.

In the apomictic species, a number of apomictic races have received taxonomic recognition in the past. In reality every population may be
considered a species. These are self-breeding entities with barriers to
interbreeding with other morphologically similar populations, even though
they may have recently evolved from a common ancestor. To treat each of
these populations as a species would be completely impractical. Other cri-
teria such as pollen stainability or chromosome numbers are of little help in
elucidating species. It seems best to recognize groups of morphologically
and ecologically similar apomictic races as species.

In one species, Arnica discoidea, there are both sexual, diploid and
apomictic, tetraploid populations. The tetraploids are probably recent de-
rivatives, which have not become morphologically distinct. I can see no
characters which can be used to separate the tetraploids from their diploid
counterparts, other than their different breeding systems. They are treated
as a single species with both sexual and apomictic elements.
LITERATURE CITED


APPENDIX I

Taxa recognized by Maguire (1943)

Subgenus Austromontana

1. *Arnica latifolia* Bongard
2. *Arnica gracilis* Rydb.
3. *Arnica cernua* Howell
4. *Arnica tomentella* Greene
5. *Arnica nevadensis* A. Gray
7a. *Arnica cordifolia* Hook. subsp. *genuina* Maguire
7b. *Arnica cordifolia* Hook. subsp. *whitneyi* (Fernald) Maguire
8. *Arnica grayi* Heller
9a. *Arnica parviflora* A. Gray subsp. *genuina* Maguire
9b. *Arnica parviflora* A. Gray subsp. *alata* (Rydb.) Maguire
10. *Arnica discoidea* Bentham
11a. *Arnica spathulata* Greene subsp. *genuina* Maguire
11b. *Arnica spathulata* Greene subsp. *eastwoodiae* (Rydb.) Maguire
12. *Arnica venosa* H.M. Hall
13. *Arnica viscosa* A. Gray
APPENDIX II

Taxa recognized by Ediger & Barkley (1978)

Subgenus Austromontana

1a. Arnica latifolia Bongard var. latifolia
1b. Arnica latifolia Bongard var. gracilis (Rydb.) Cronquist
2. Arnica cernua Howell
3. Arnica tomentella Greene
4. Arnica nevadensis A. Gray
5a. Arnica cordifolia Hooker var. cordifolia
5b. Arnica cordifolia Hooker var. pumila (Rydb.) Maguire
6a. Arnica discoidea Bentham var. alata (Rydb.) Cronquist
6b. Arnica discoidea Bentham var. eradiata (A. Gray) Cronquist
6c. Arnica discoidea Bentham var. discoidea
7a. Arnica spathulata Greene var. spathulata
7b. Arnica spathulata Greene var. eastwoodiae (Rydb.) Ediger & Barkley
8. Arnica venosa H.M. Hall
9. Arnica viscosa A. Gray