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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California Academy of Sciences (CAS)

Dudley Herbarium, Stanford University (DS)

Central Washington State University (ELRG)

Humboldt State University (HSC)

University of Idaho (ID)

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)

University of Victoria (UVIC)

British Columbia Provincial Museum (V)

Willamette University (WILLU)

Washington State University (WS)

University of Washington (WTU)

Crater Lake National Park

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 recieved 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 apomixis 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, α genuina and β 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 Barkley, 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 (see discussion under Arnica nevadensis).

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 Arnicas. 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

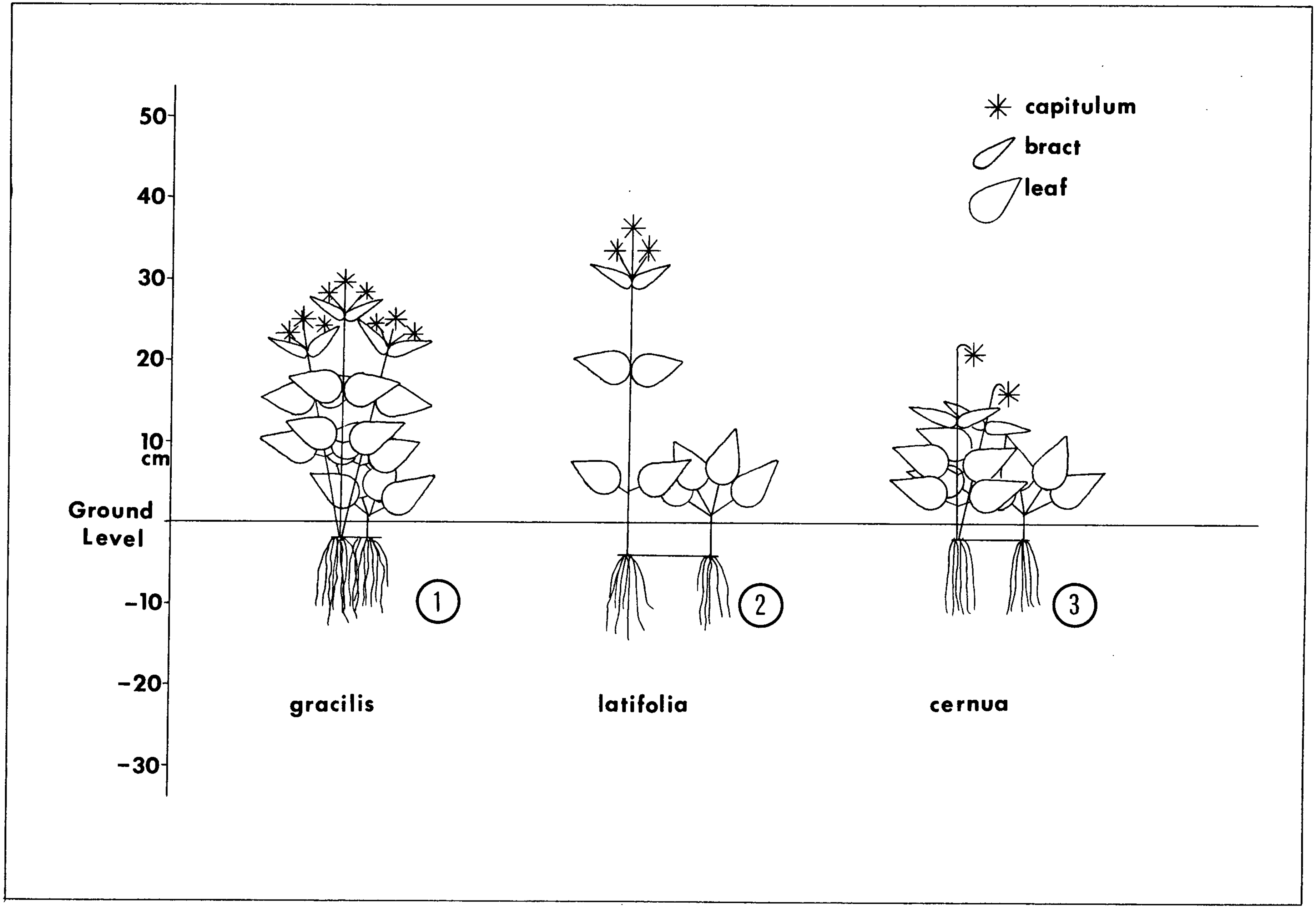
All species in Austromontana are rhizomatous. The rhizomes are usually slender (1-2 mm thick), dark brown, and unbranched or with a few predominantly terminal branches. They are naked or sparsely clothed with pairs of usually inpersistent brown scales. In some of the short-rhizomed species (especially 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 survace 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*


capitulum
bract
leaf
50
40
30
20
10
cm
Ground
Level
-10
-20
-30
1
2
3
gracilis
latifolia
cernua

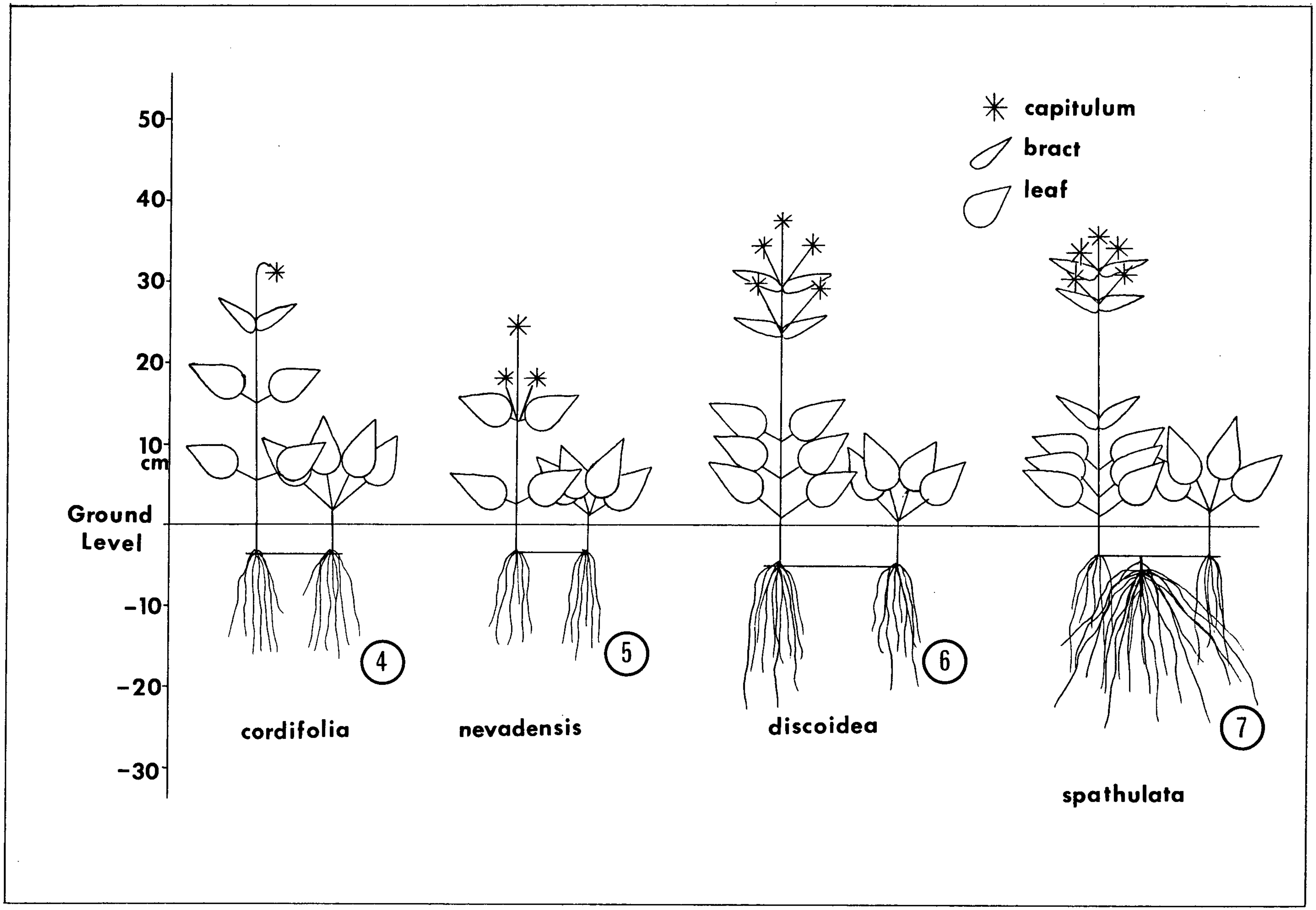
Figures 4-7. Schematic diagrams of habit and average branching pattern of *Arnica* species.

4. *Arnica cordifolia*

5. *Arnica nevadensis*

6. *Arnica discoidea*

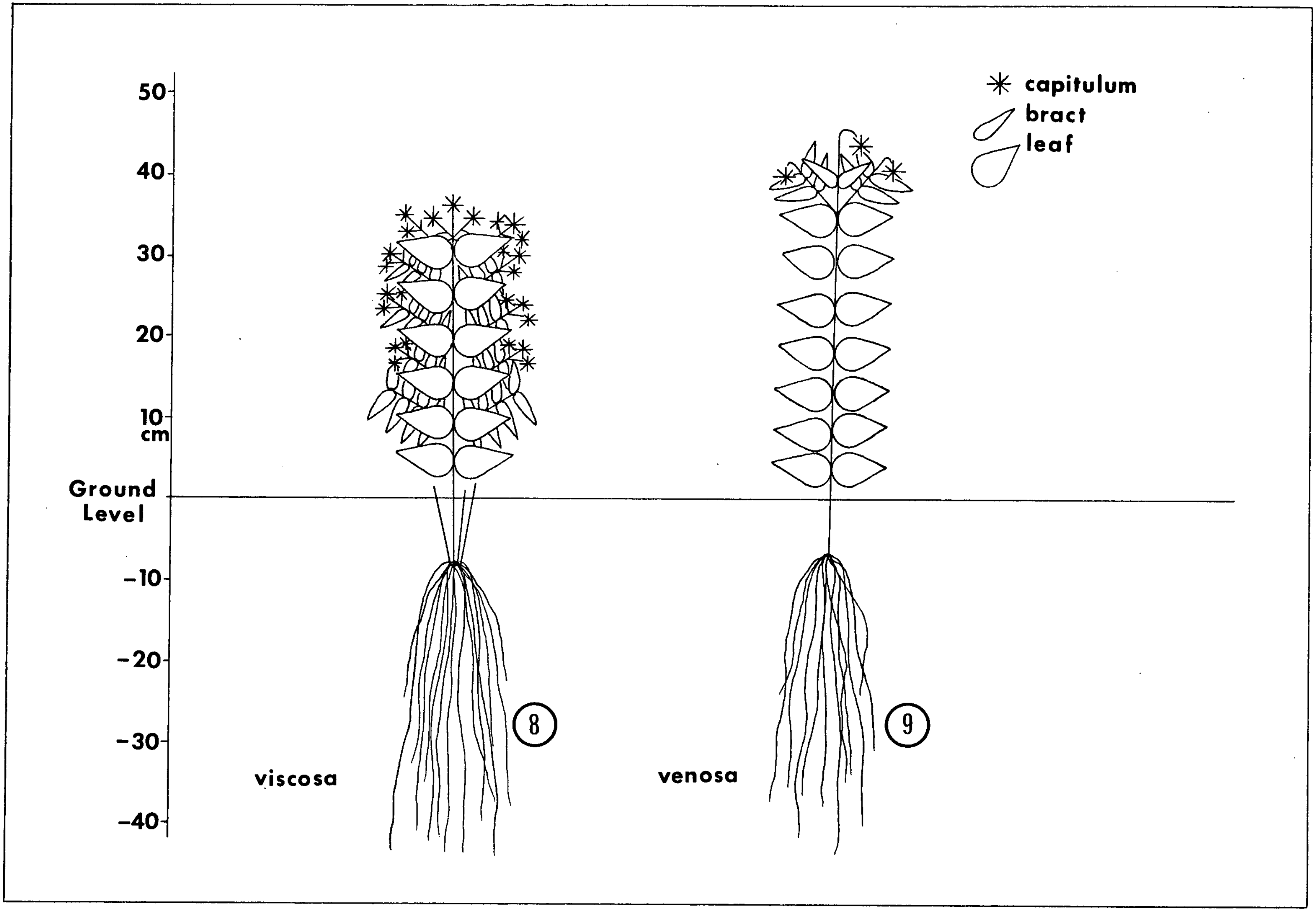
7. *Arnica spathulata*


capitulum
bract
leaf
50
40
30
20
10
cm
Ground
Level
-10
-20
-30
4
5
6
7
cordifolia
nevadensis
discoidea
spathulata

Figures 8, 9. Schematic diagrams of habit and average branching pattern of *Arnica* species.

8. *Arnica viscosa*

9. *Arnica venosa*


capitulum
bract
leaf
50
40
30
20
10
cm
Ground
Level
-10
-20
-30
-40
8
9
viscosa
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 membraneous 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.

10. Basal leaf of *Arnica latifolia S-1676*, WA, Clallam County.

11. Cauline leaf of *Arnica latifolia S-1654*, BC, Tod Mountain.

12. Basal leaf of *Arnica cordifolia S-1819*, OR, Wasco County.

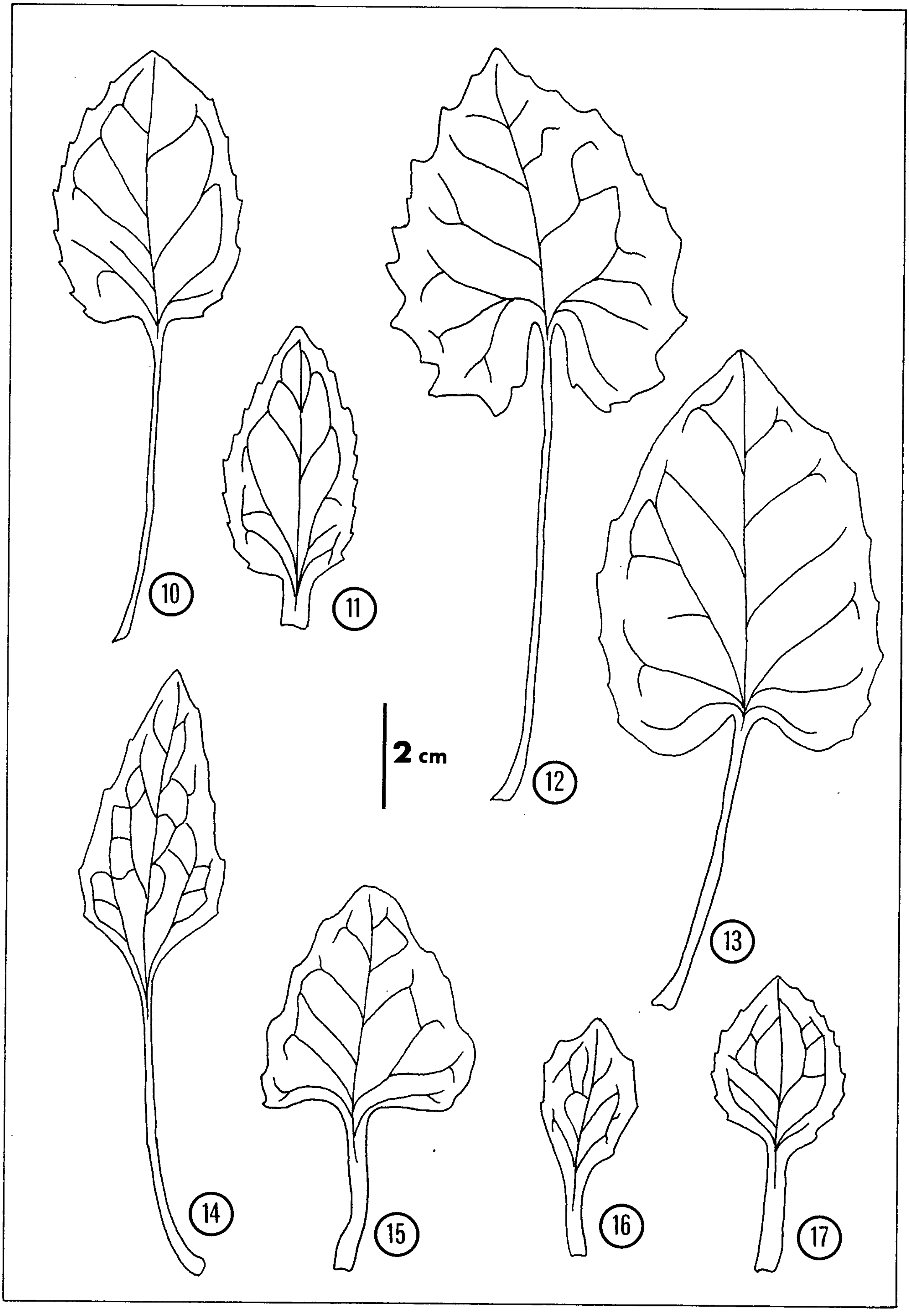
13. Cauline leaf of *Arnica cordifolia S-1354*, BC, Botanie Valley.

14. Basal leaf of *Arnica cernua S-1743*, OR, Josephine County.

15. Cauline leaf of *Arnica cernua Sweetser, s.n.* (ORE), OR, Josephine County.

16. Basal leaf of *Arnica gracilis S-1603*, AB, Lake Louise.

17. Cauline leaf of *Arnica gracilis Christ 19463* (ID), Elmore County.


10
11
12
13
14
15
16
17
2 cm

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.

20. Basal leaf of *Arnica discoidea* S-1789, CA, Marin County.

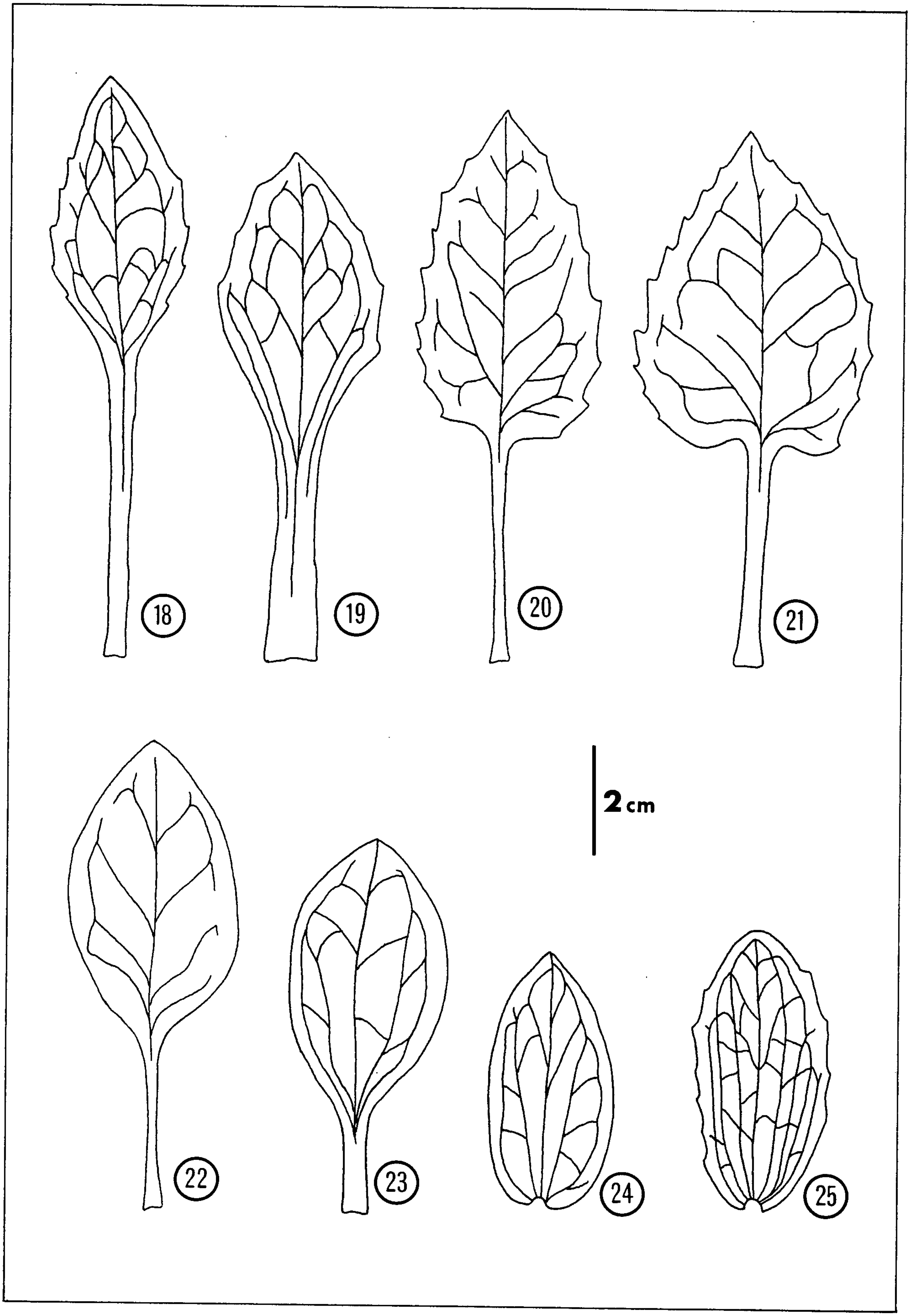
21. Cauline leaf of *Arnica discoidea* Copeland *s.n.* (ORE), CA, Butte County.

22. Basal leaf of *Arnica nevadensis* S-1910, NV, Washoe County.

23. Cauline leaf of *Arnica nevadensis* S-1910, NV, Washoe County.

24. Cauline leaf of *Arnica viscosa* Muth 733 (PUA), CA, Siskiyou County.

25. Cauline leaf of *Arnica venosa* S-1793, CA, Shasta County.


18
19
20
21
2 cm
22
23
24
25

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.

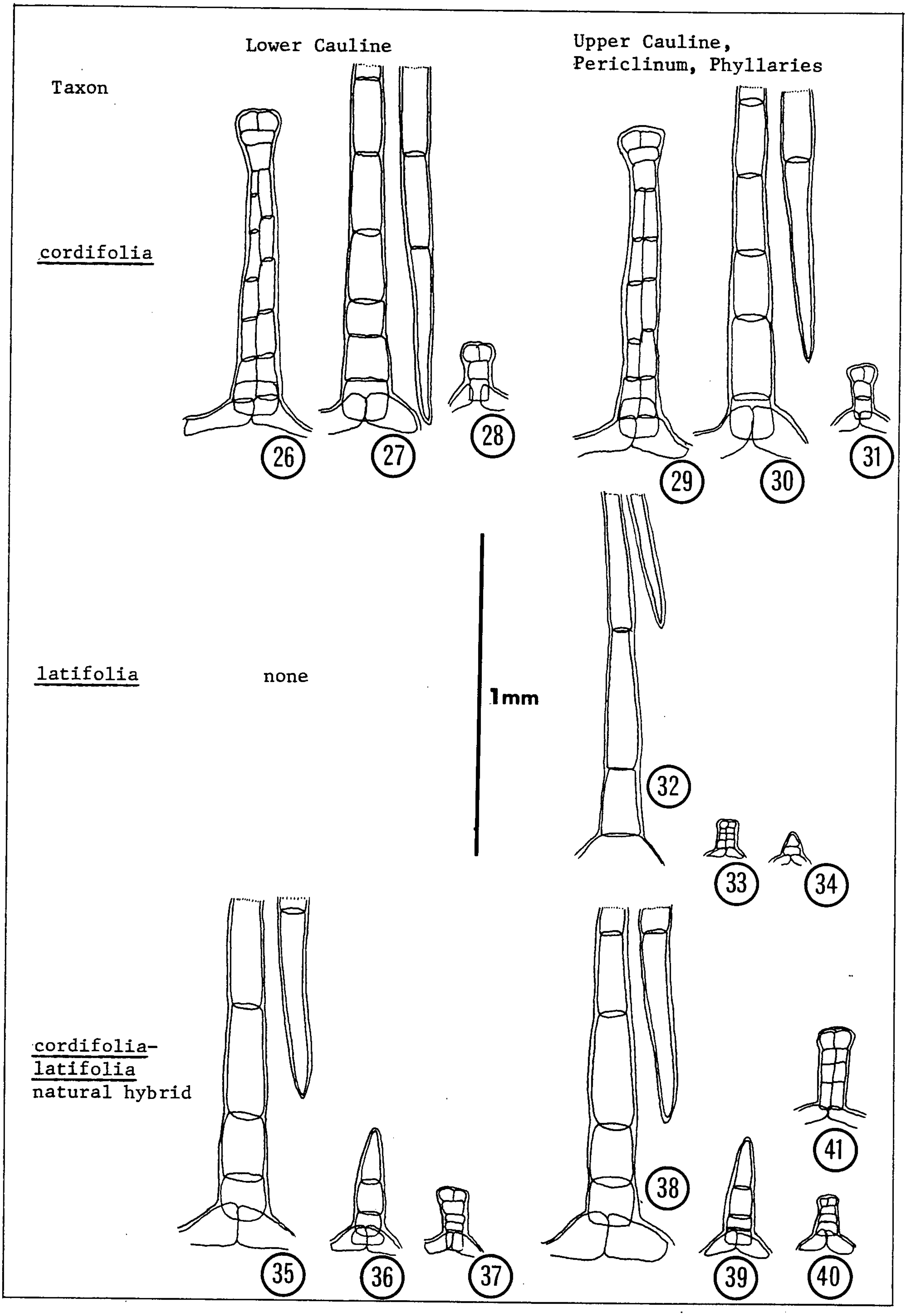
The degree of glandular pubescence imparts a more or less viscid or "clammy" and aromatic character to the leaves and stems of certain species, especially Arnica cordifolia, Arnica nevadensis, and Arnica viscosa. This character alone makes them readily separable in the field from those species largely 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.

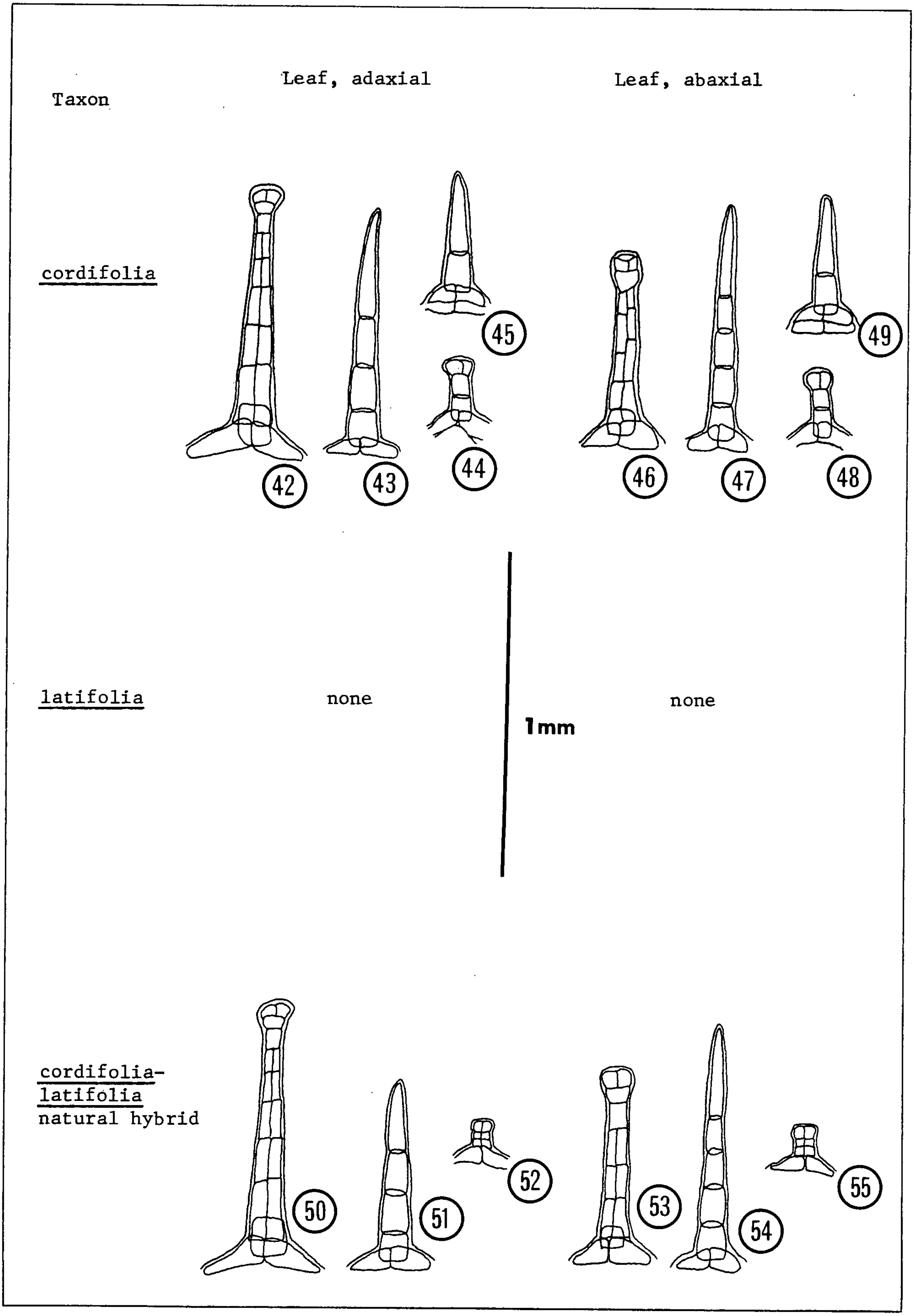
Non-glandular septate hairs are always one cell thick except at their bases and they are usually straight, the exceptions being on the lower part of the stems of some species, especially Arnica cernua. (Figure 62). Again two sizes of non-glandular hairs are seen, long ones 1-2 (-3) mm long and short 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.

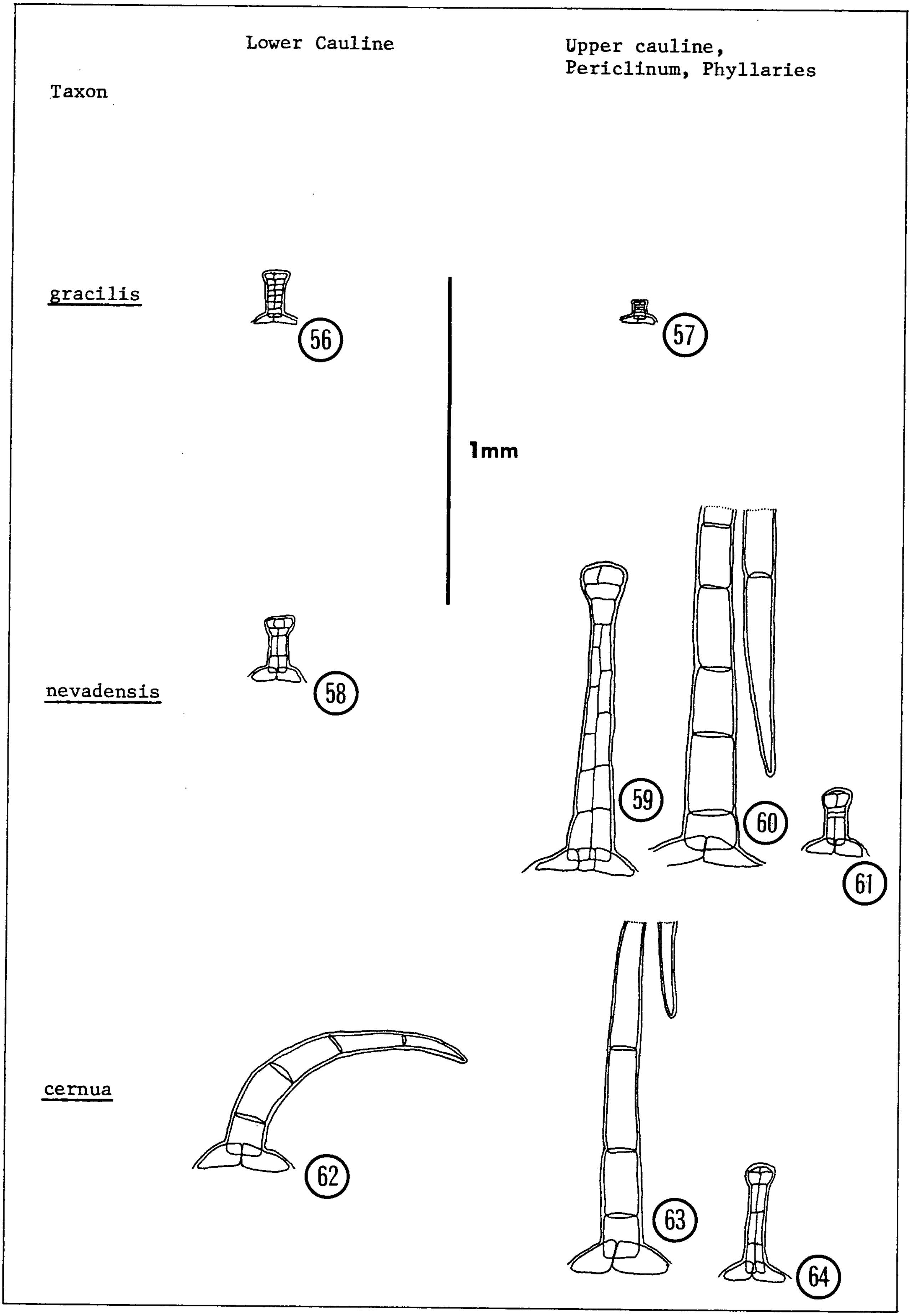
In certain species or populations the glandular hairs are colored, notably the yellow-tipped hairs of Arnica viscosa and the purple-tipped or based hairs of Arnica spathulata and to a lesser degree Arnica discoidea.

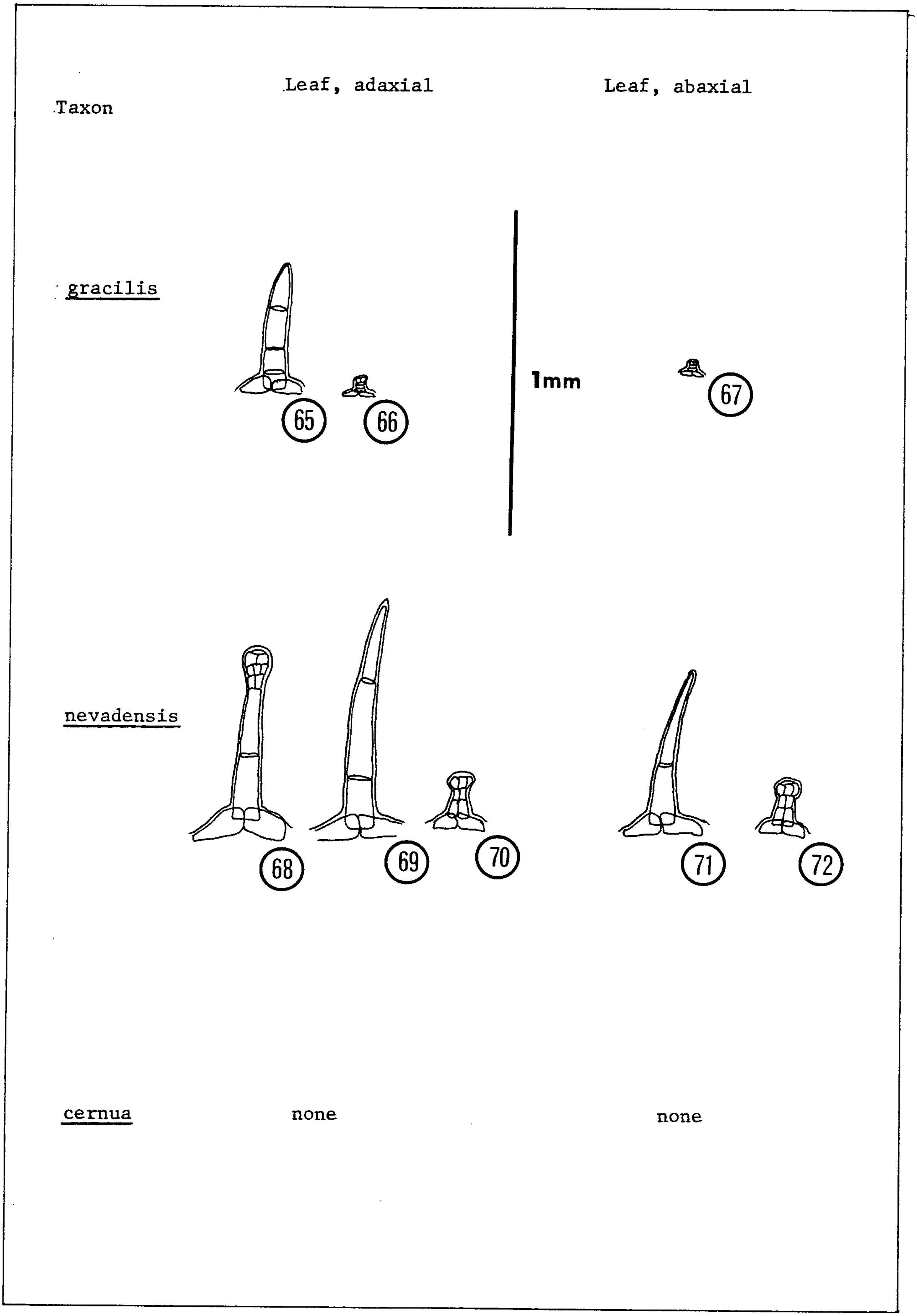
Figures 26 to 126 show the vestiture types of all vegetative parts of the species in these two subgenera, but with no indication of relative abundance of vestiture.

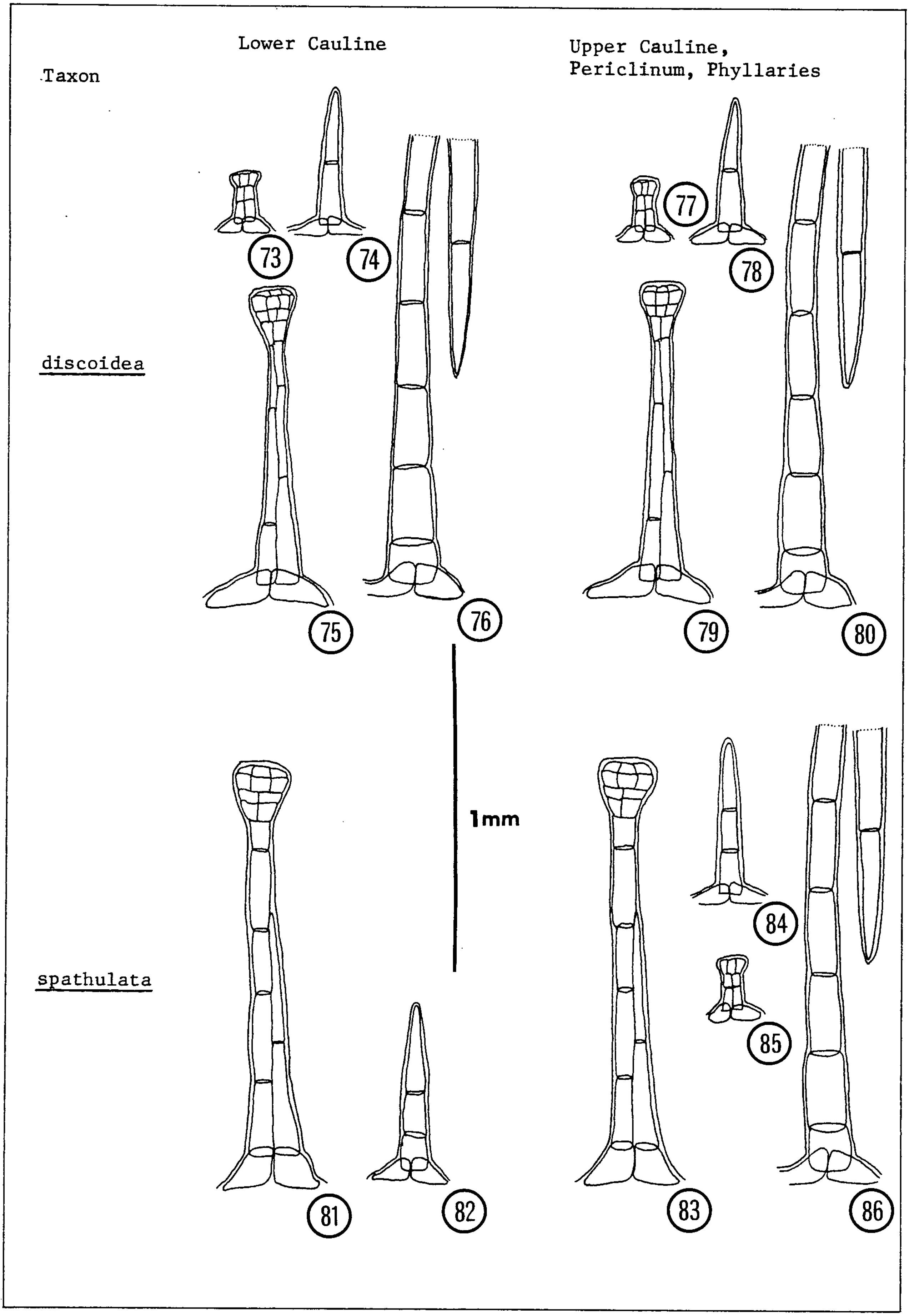
Figures 26-126. Comparison of Vestiture Types on Four Vegetative Parts of *Arnica* Species.

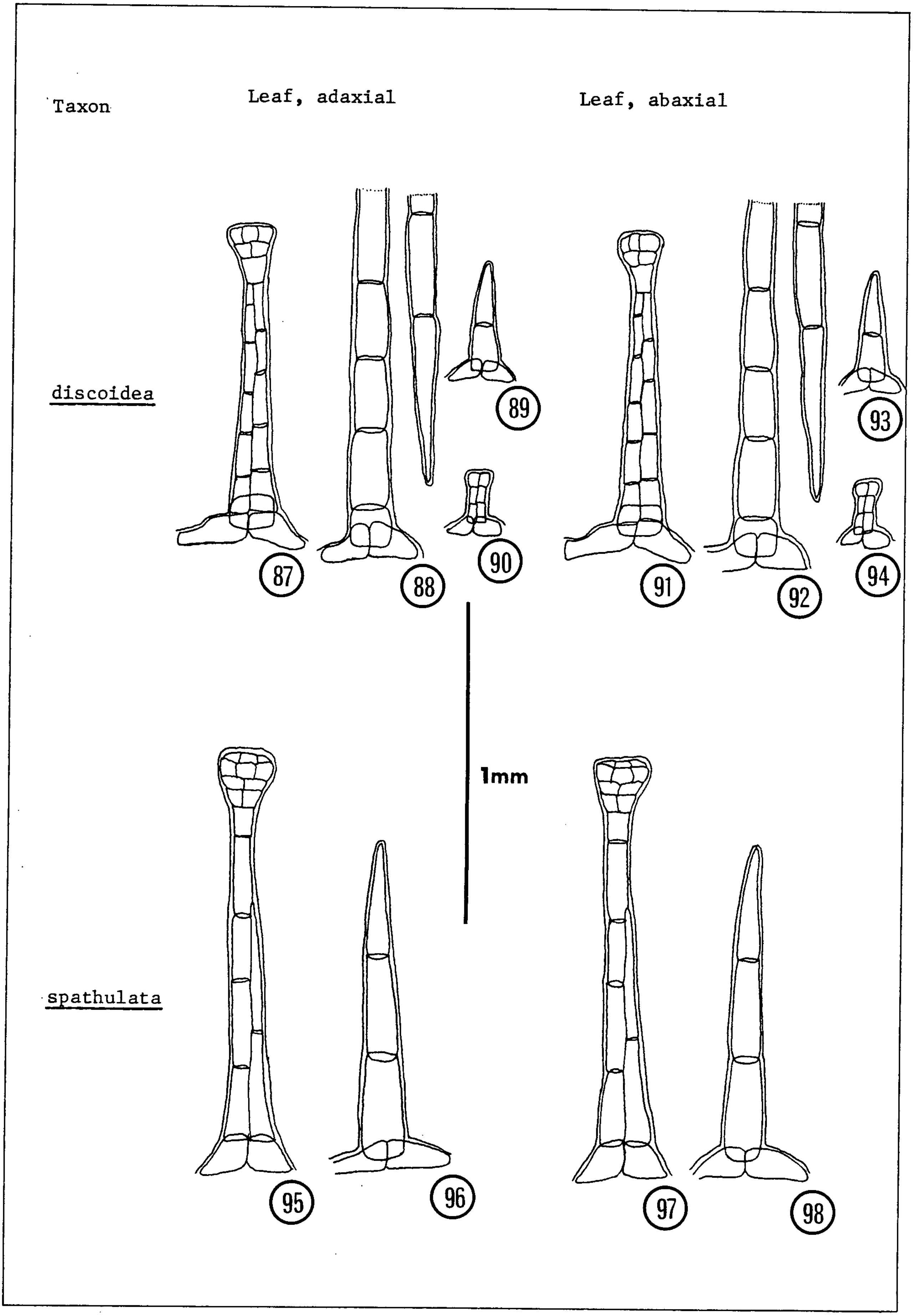

Lower Cauline
Upper Cauline,
Periclinum, Phyllaries
Taxon
cordifolia
latifolia
none
1mm
cordifolia-
latifolia
natural hybrid
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41

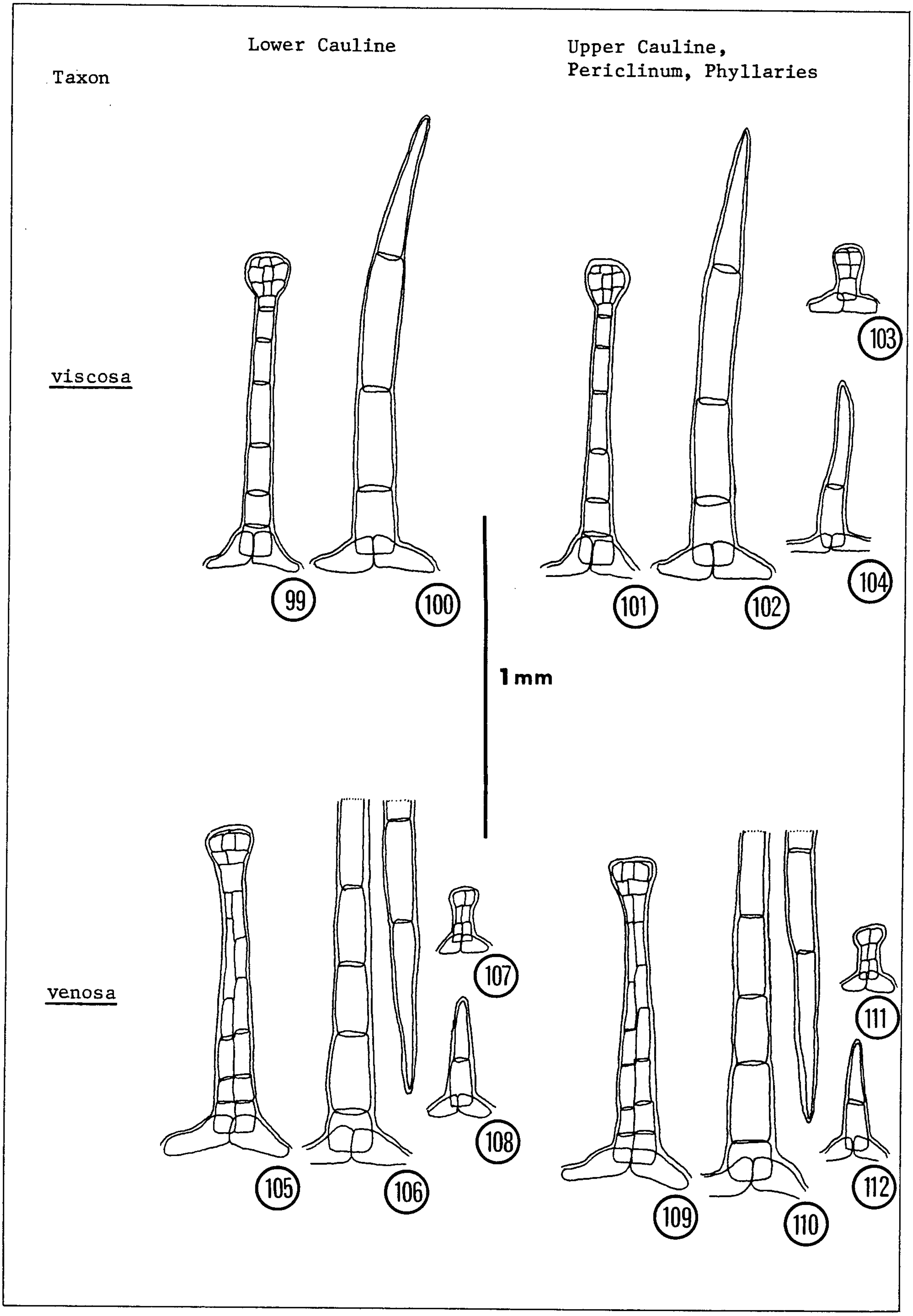

Taxon
Leaf, adaxial
Leaf, abaxial
cordifolia
42
43
44
45
46
47
48
49
latifolia
none
none
1mm
cordifolia-
latifolia
natural hybrid
50
51
52
53
54
55

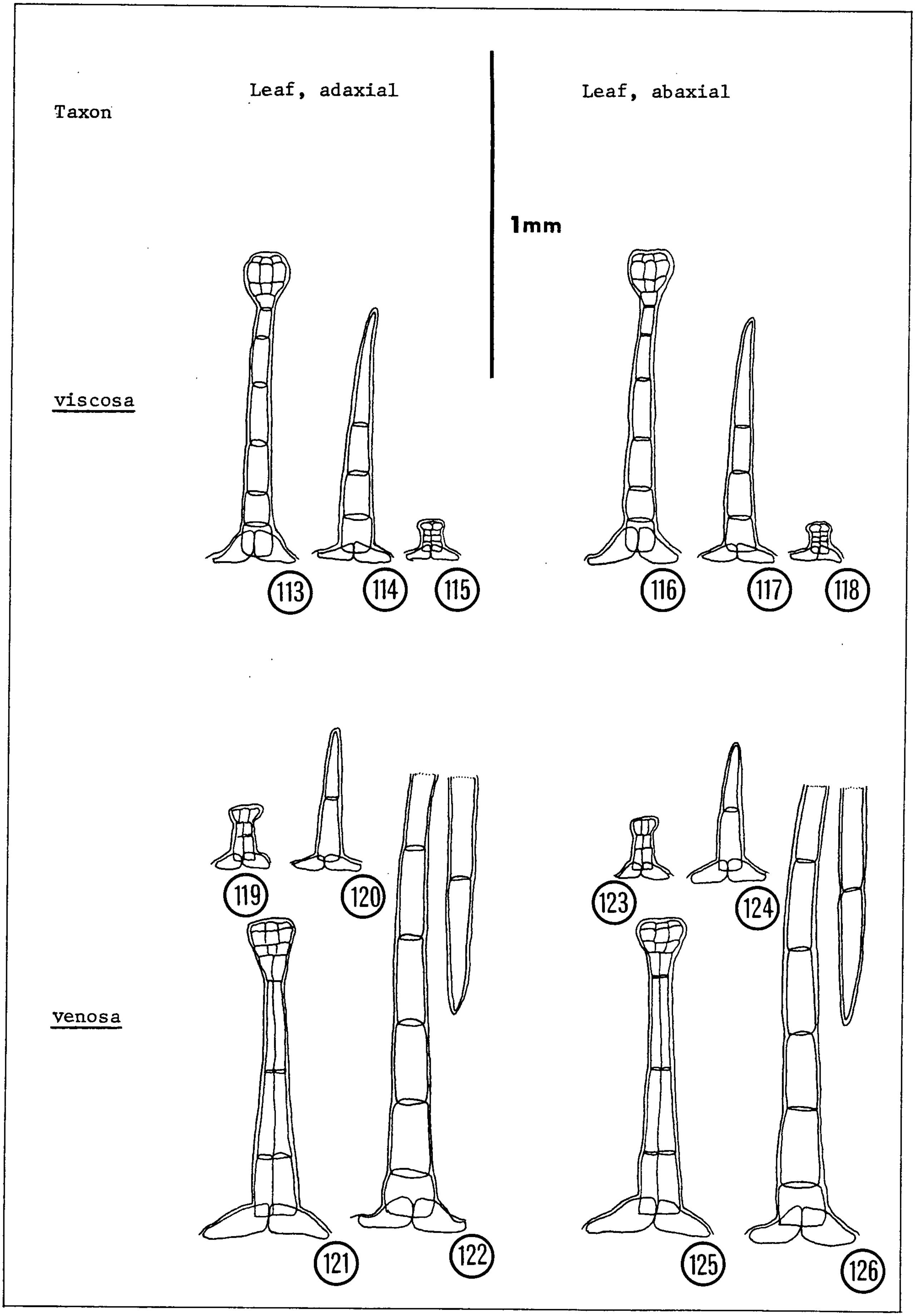

Lower Cauline
Upper cauline, Periclinum, Phyllaries
Taxon
gracilis
nevadensis
cernua
1mm
56
57
58
59
60
61
62
63
64


Taxon
Leaf, adaxial
Leaf, abaxial
gracilis
65
66
1mm
67
nevadensis
68
69
70
71
72
cernua
none
none


Taxon
Lower Cauline
Upper Cauline,
Periclinum, Phyllaries
discoidea
73
74
77
78
75
76
79
80
1mm
spathulata
84
85
81
82
83
86


Taxon
Leaf, adaxial
Leaf, abaxial
discoidea
spathulata
87
88
89
90
91
92
93
94
95
96
97
98
1mm


Taxon
Lower Cauline
Upper Cauline,
Periclinum, Phyllaries
viscosa
venosa
1mm
99
100
101
102
103
104
105
106
107
108
109
110
111
112


Taxon
Leaf, adaxial
Leaf, abaxial
1mm
viscosa
113
114
115
116
117
118
venosa
119
120
121
122
123
124
125
126

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.

128. *Arnica cordifolia* S-1343, BC, Botanie Valley.

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.

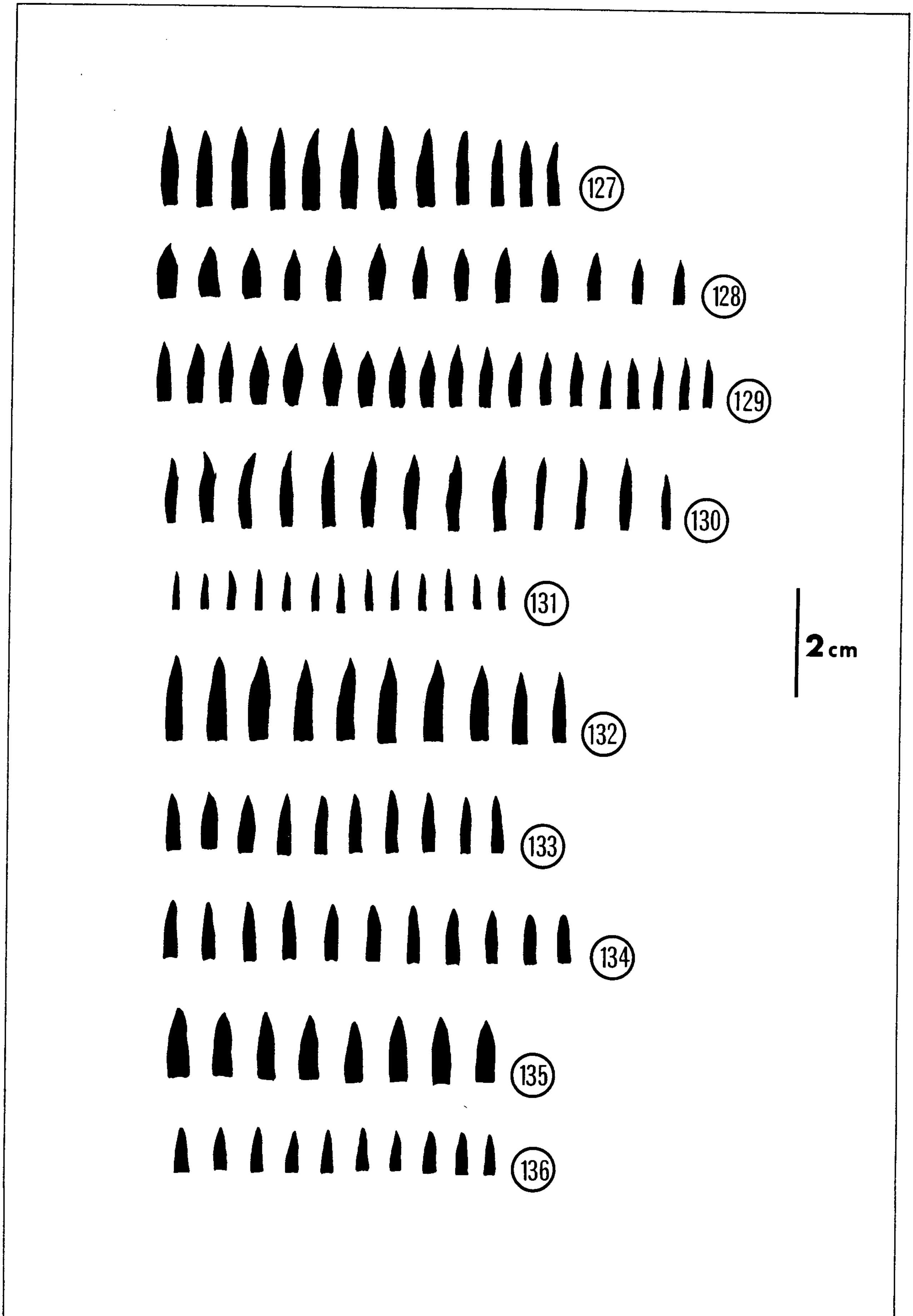
132. *Arnica cernua* S-1386, OR, Josephine County.

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.


127
128
129
130
131
2 cm
132
133
134
135
136

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.

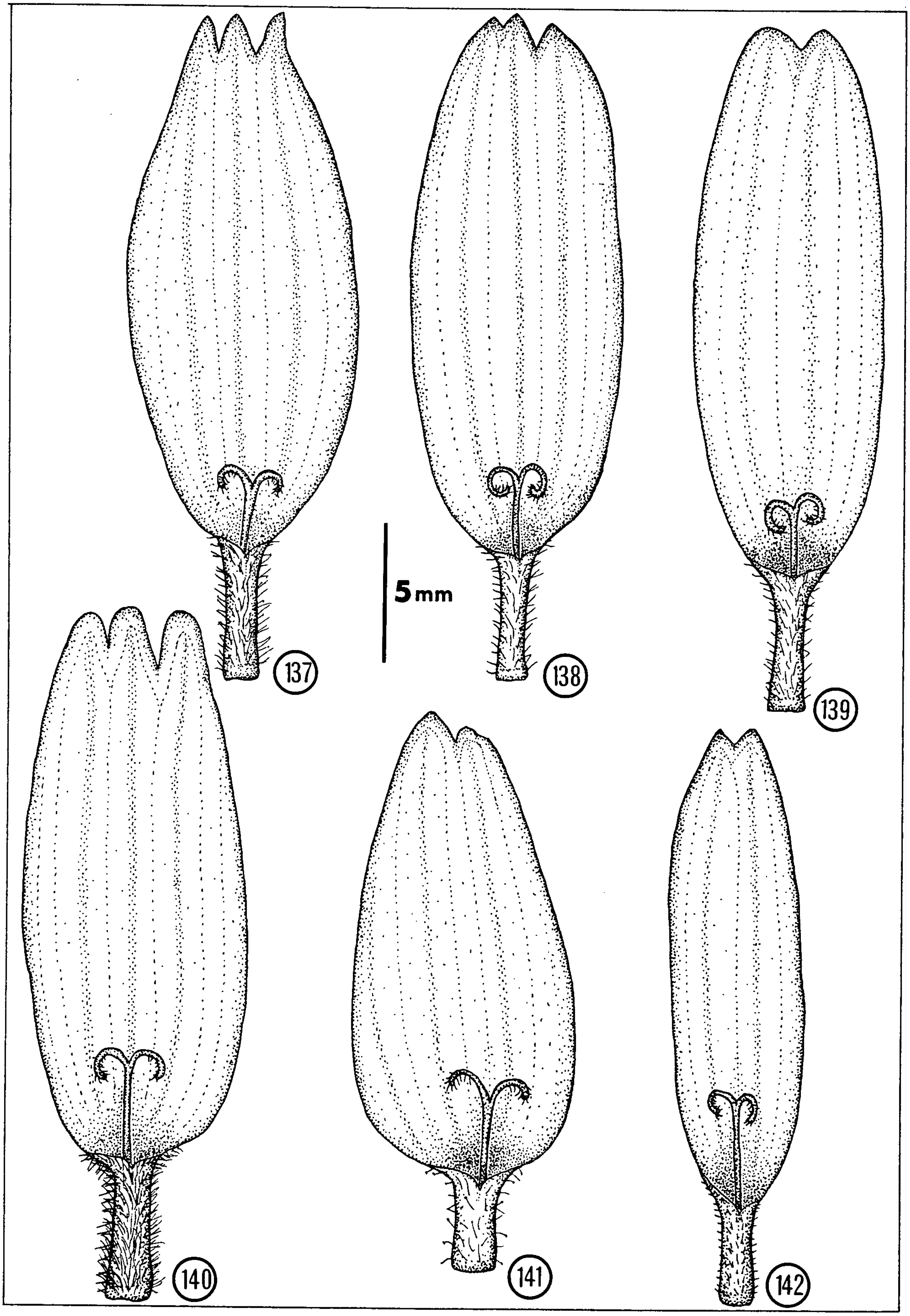
138. *Arnica cordifolia* X *Arnica latifolia* hybrid *S-1474*, MT, Ravalli County.

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.


5 mm
137
138
139
140
141
142

Figures 143-148. Typical Disc Florets of *Arnica* Species in Subgenus *Austromontana*.

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

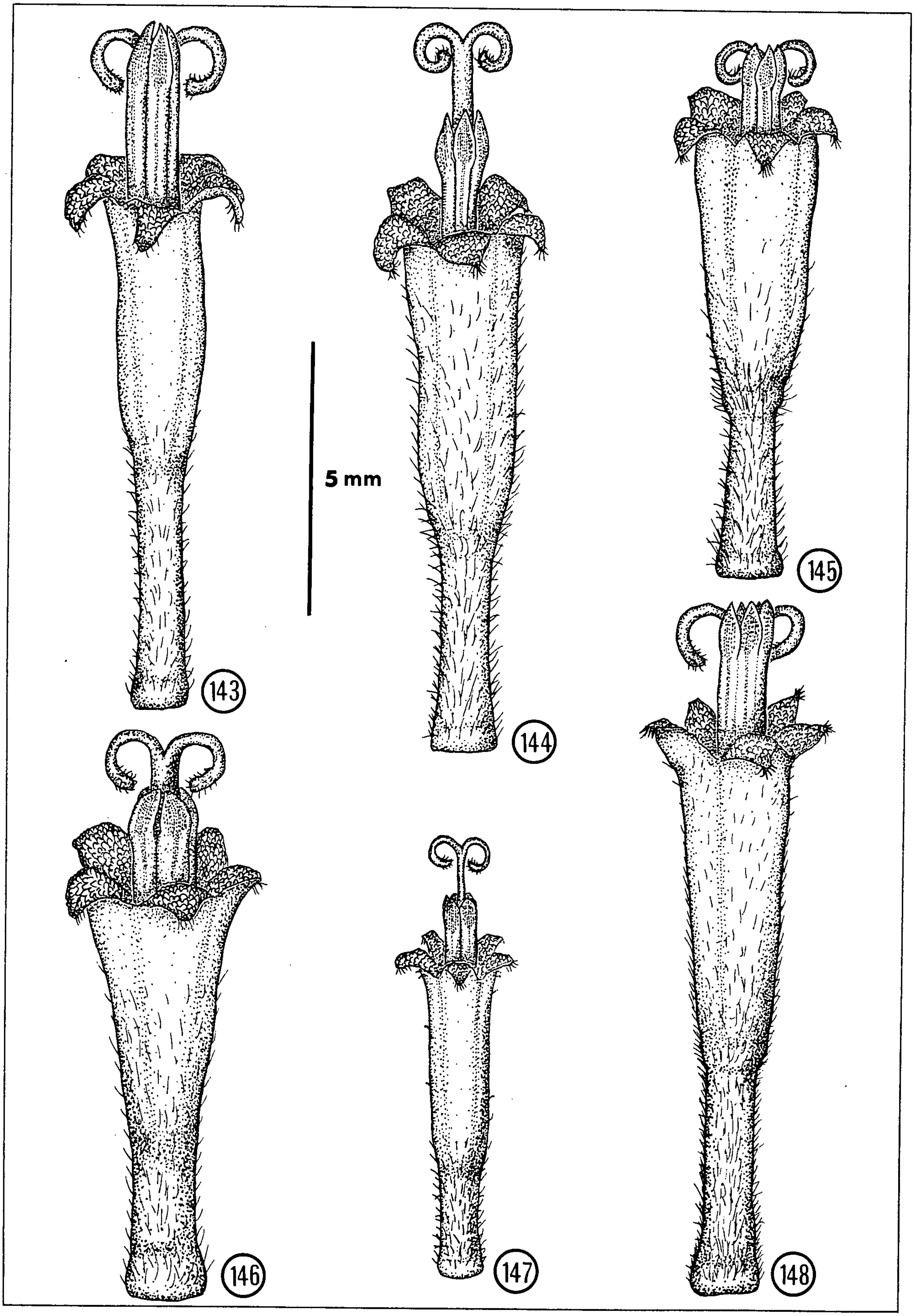
144. *Arnica cordifolia* X *Arnica latifolia S-1474* (putative natural hybrid), MT, Ravalli County.

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.


5 mm
143
144
145
146
147
148

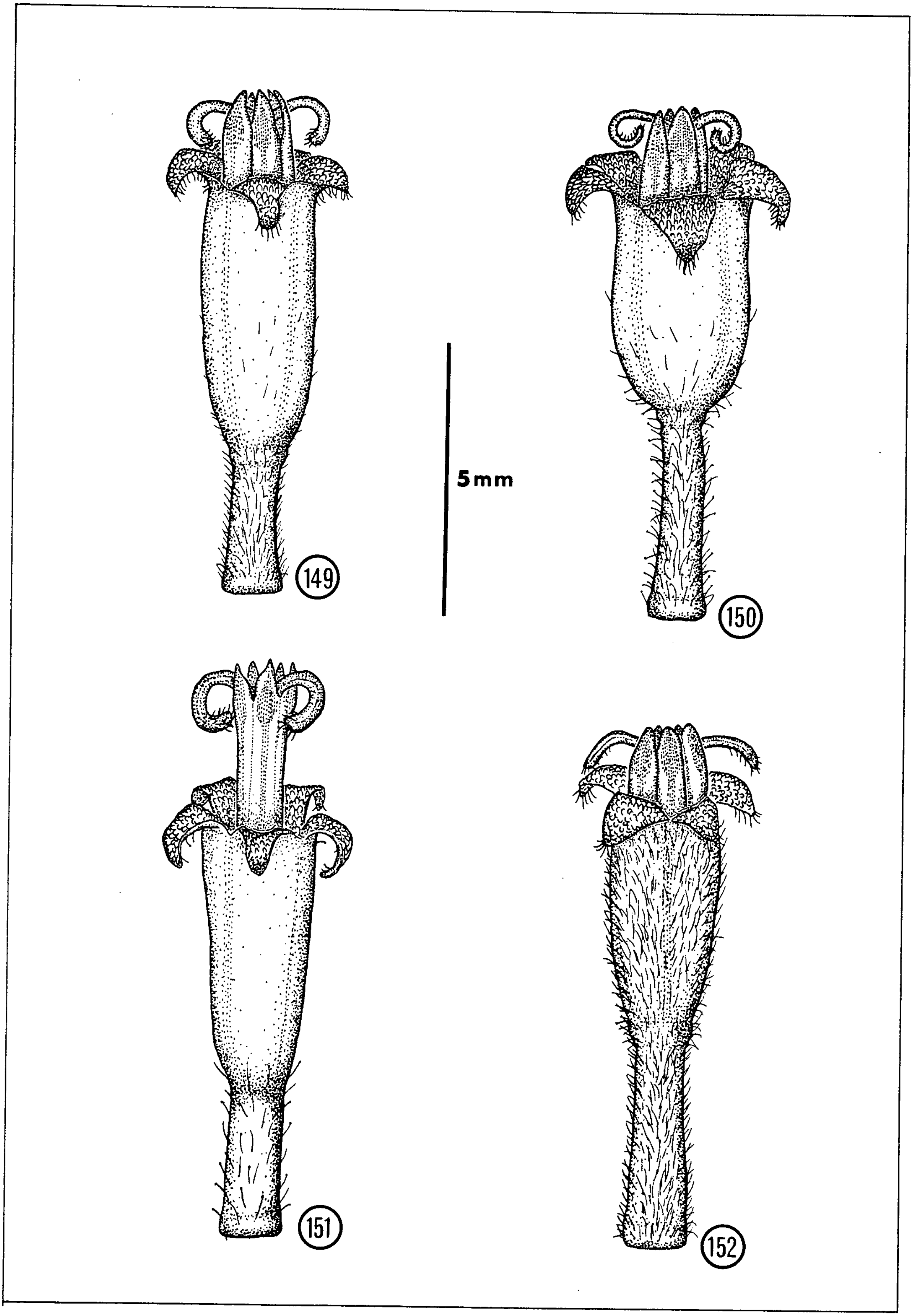
Figures 149-152. Typical Disc Florets of *Arnica* Species in Subgenera *Austromontana* and *Calarnica*.

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.


5mm
149
150
151
152

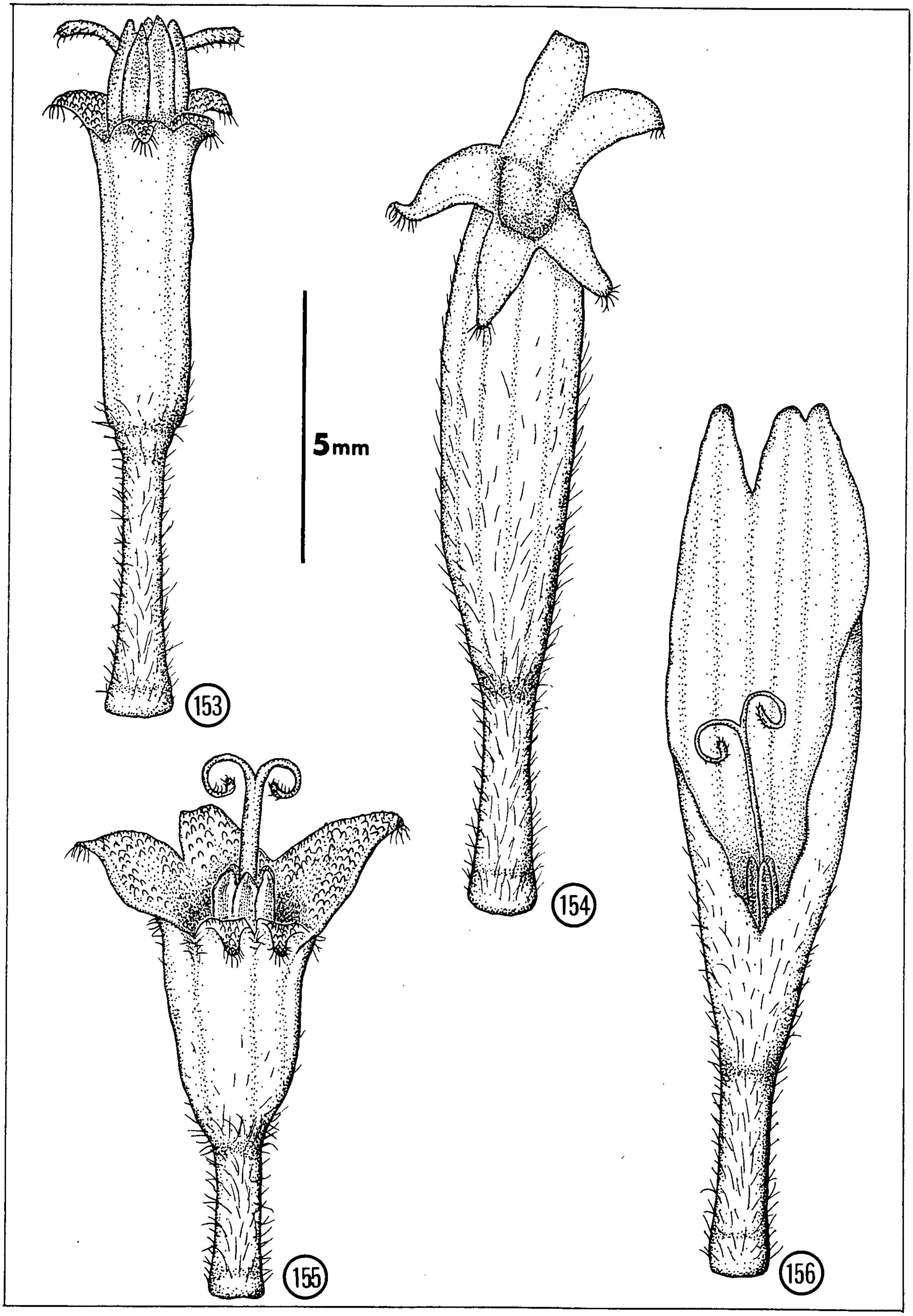
Figures 153-156. Florets of *Arnica discoidea*.

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).

156. Ray-like marginal floret with abortive anthers, CA, Mendocino County, *Nelson & Anderson* 843 (HSC).


5mm
153
154
155
156

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.

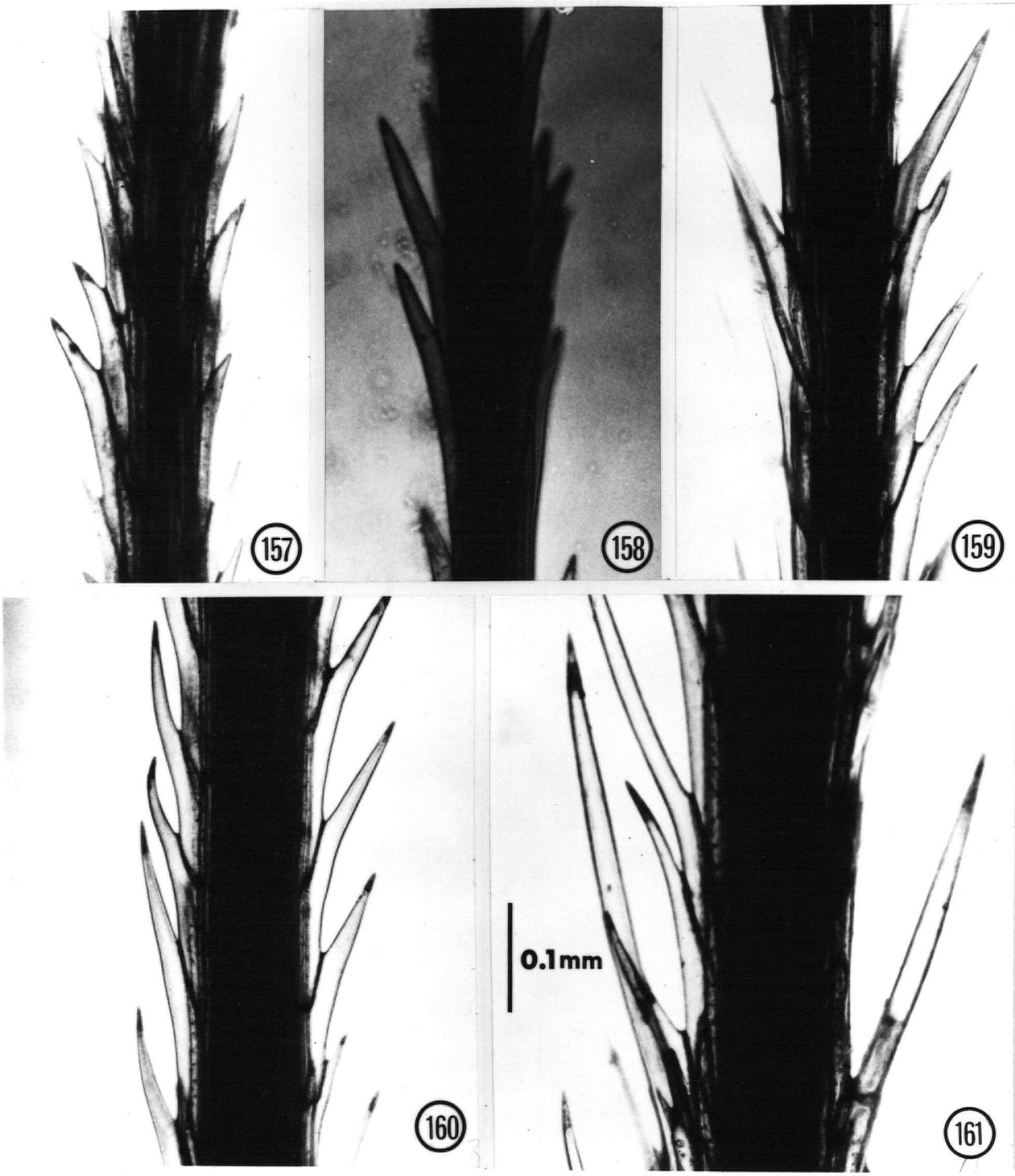
157. Arnica gracilis S-1603, AB, Lake Louise.

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.


157
158
159
160
161
0.1mm

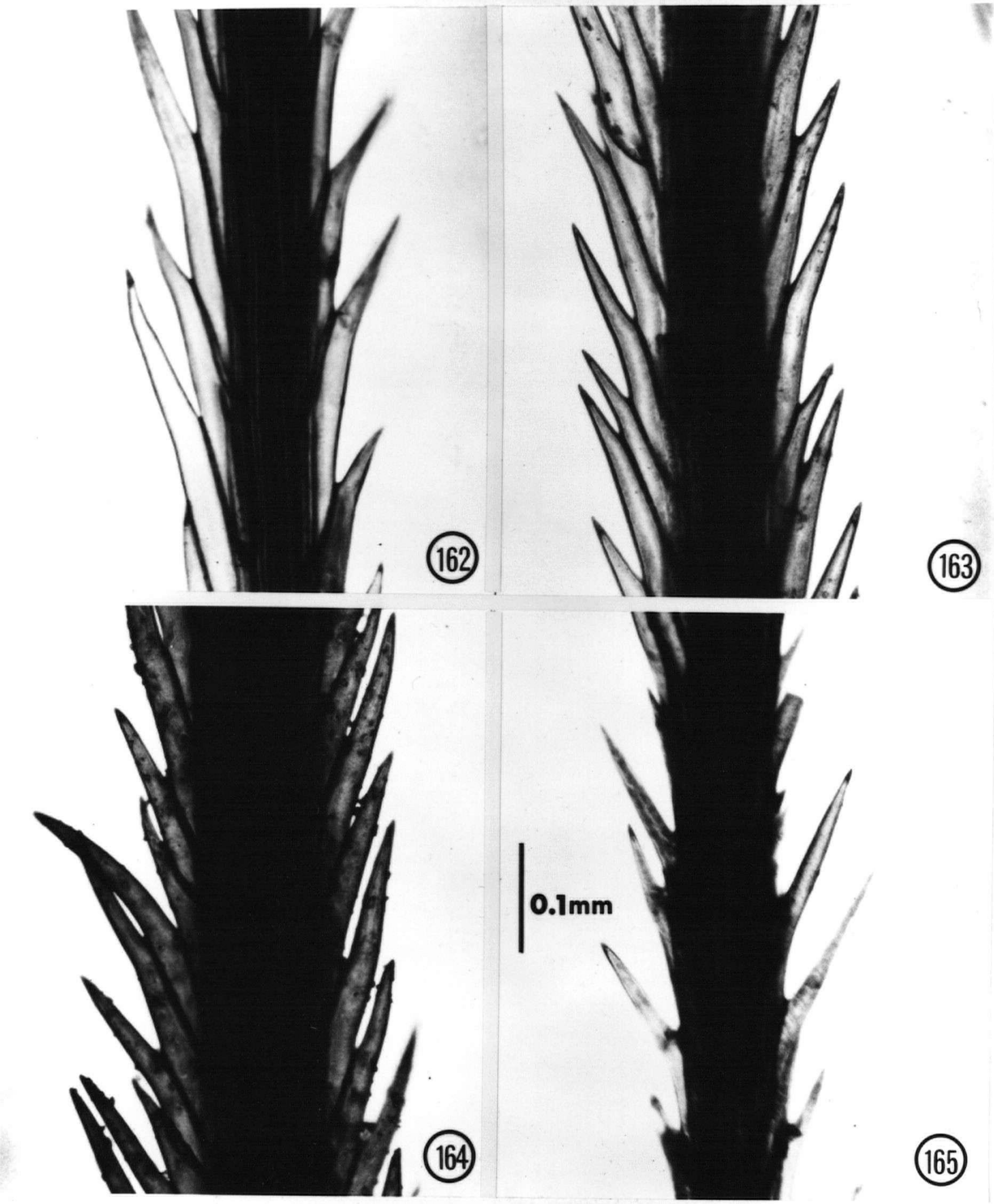
Figures 162-165. Photographs with light microscope of near mid-length of pappus.

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

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

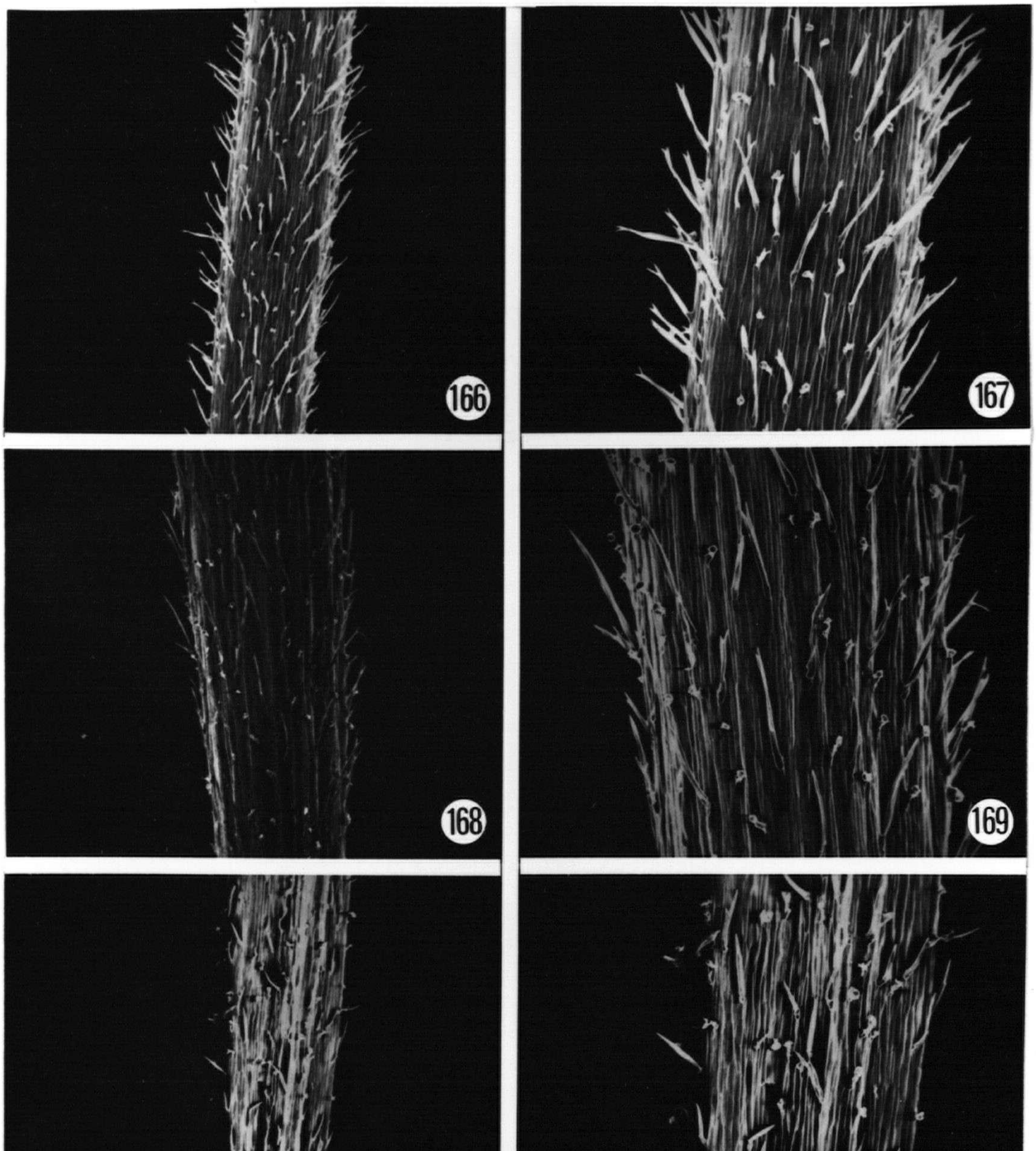
164. *Arnica venosa S-1940*, CA, Shasta County.

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


162
163
0.1mm
164
165

Figures 166-171. Scanning Electron Micrographs of Achene Surfaces (mid-length) of *Arnica* species.

166. *Arnica cordifolia S-1353*, BC, Botanie Valley, X65.
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.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Figures 172-177. Scanning Electron Micrographs of Achene Surfaces (mid-length) of *Arnica* species.

172. *Arnica cernua S-1772*, CA, Humboldt County, X65.

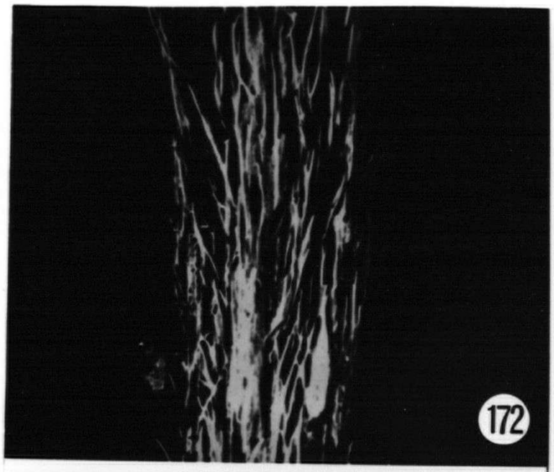
173. same, X130.

174. *Arnica latifolia S-1476*, MT, Missoula County, X65.

175. same, X130.

176. *Arnica gracilis S-1562*, BC, Monroe Lake, X65.

177. same, X130.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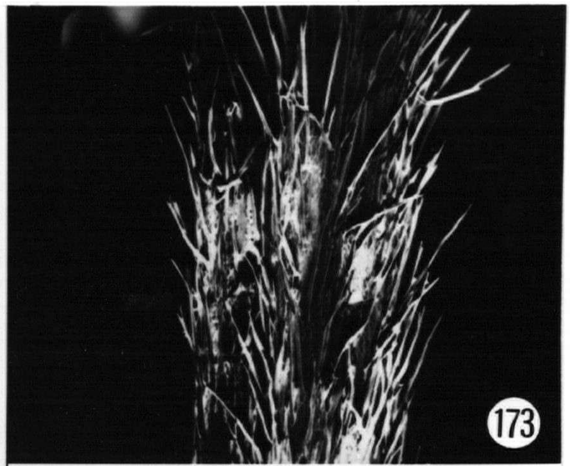
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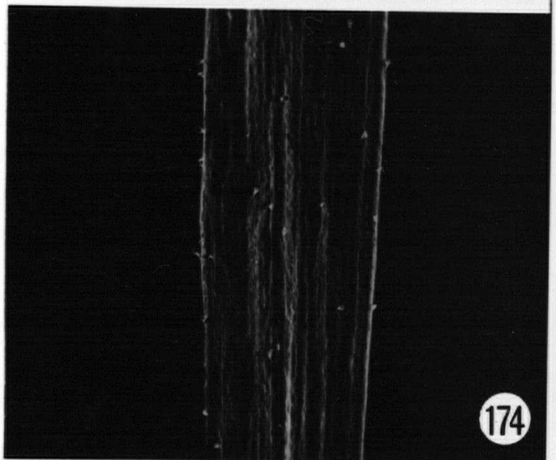
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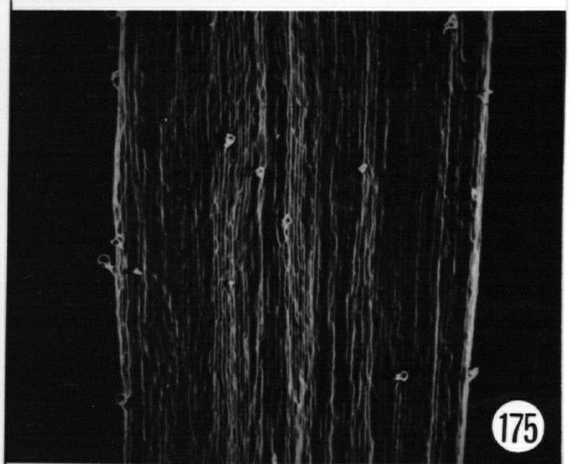
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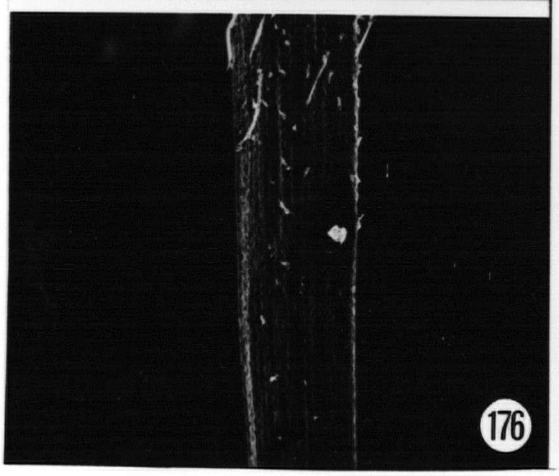
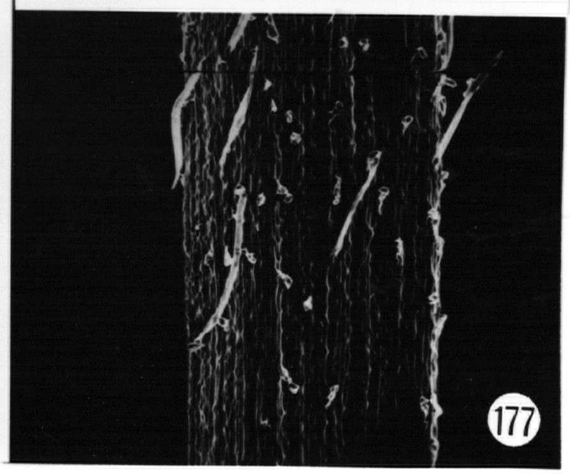

176


177

Figures 178-184. Scanning Electron Micrographs of Achene Surfaces (mid-length) of Arnica species.

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.

184. Arnica gracilis S-1562, BC, Monroe Lake, X250.

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.

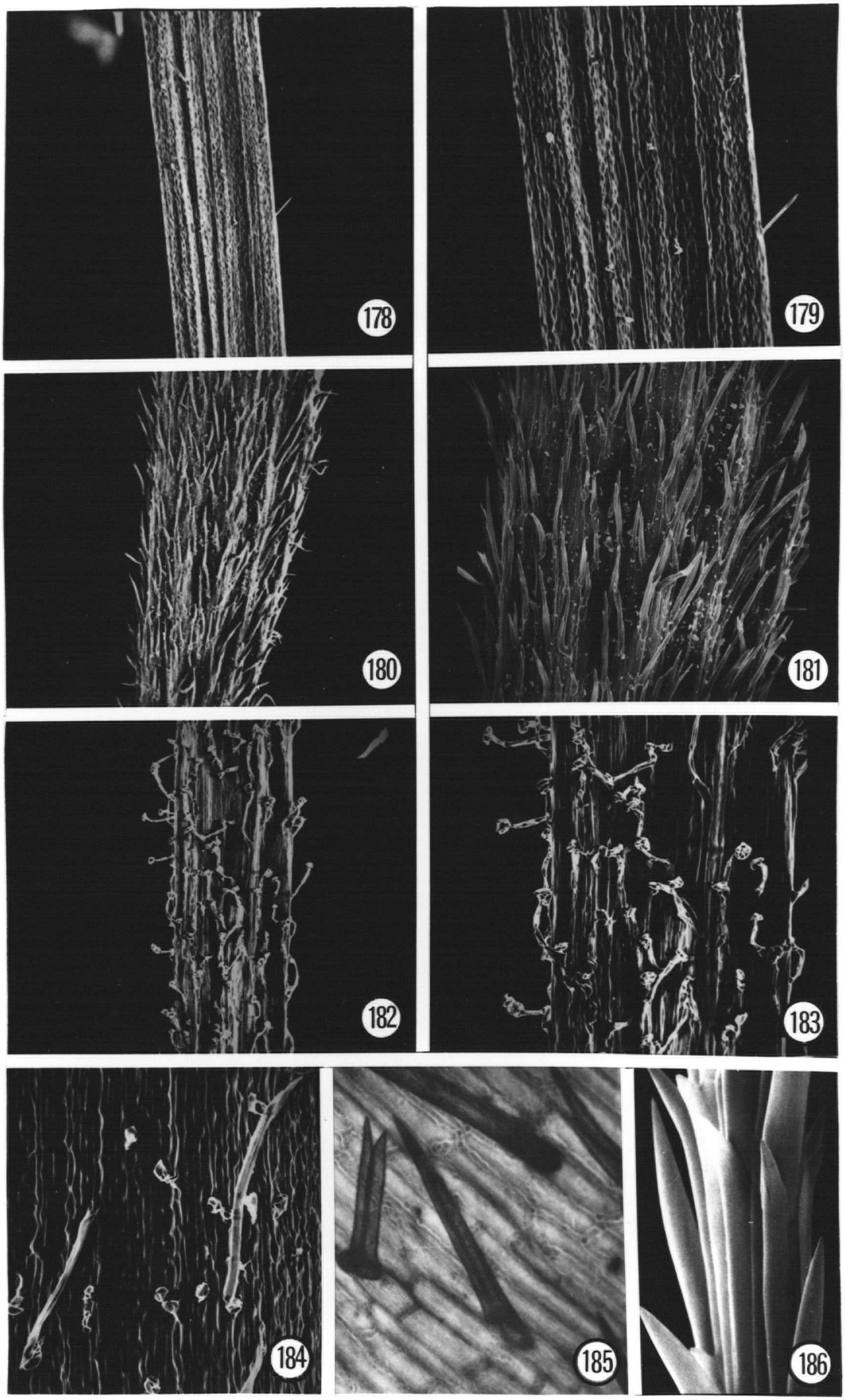

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TABLE I

COMPARISON OF MATURE ACHENES OF ARNICA SPECIES

Taxon	Color	Length (mm)	Width Distally (mm)	Double Hairs	Glandular Hairs
cordifolia	dark grey	(6-)7-9(-10)	1±	uniform throughout or especially distally	uniform throughout
latifolia	grey-brown	(5-)6-8(-10)	1-	none or few distally	none or few distally
gracilis	black	(4-)5-6(-7)	1	none or very few distally	none or few throughout or many distally
cernua	dark grey	6-8	1+	many throughout or distally	none
nevadensis	dark grey to black	(4-)5-8	1±	few throughout or distally	uniform throughout
discoidea	dark grey	6-8	1+	few to many throughout	few throughout
spathulata	black	7-9	1	none to few throughout	few throughout or distally
venosa	grey	6-8	1.5-2	many throughout	none
viscosa	dark grey	5-6	1	none	uniform long-stipitate throughout

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 snowmelt, 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 continuously 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 gracilis, 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

Figures 187-194. Meiotic Chromosomes, Microsporocytes, and Pollen Grains of *Arnica* Species.

187. *Arnica gracilis* S-1613, BC, Peyto Lake, anaphase I (upper cell), triploid with lagging chromosomes.

188. Late anaphase I of same.

189. Late anaphase II of same.

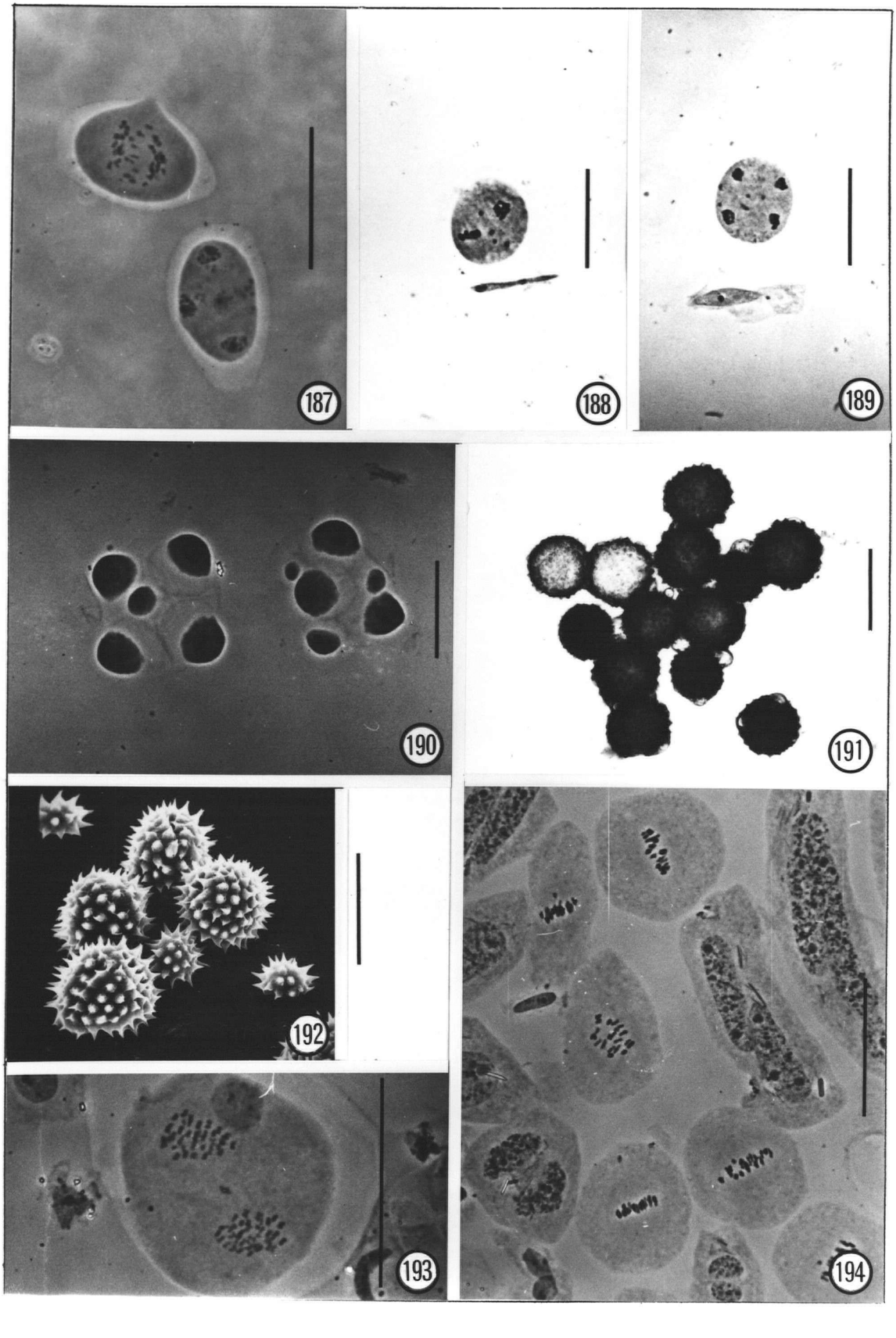
190. "Quintad" and "Sextad" of same.

191. *Arnica latifolia* S-1961, BC, Nancy Greene Provincial Park, pollen grains stained with cotton blue in lactophenol, showing two unstained grains.

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.


187
188
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191
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194

TABLE II. Previously Reported Chromosome Numbers for _Arnica_ Species in the Subgenera _Austromontana_ and _Calarnica_.

Taxon	Sporophytic Number	Locality	Reference
cernua	38	OR, Josephine Co.	Barker, 1966
cordifolia	76	BC, Lambly Creek	Taylor & Taylor, 1977
cordifolia	76	AB	Ornduff, et al., 1967
cordifolia	76	SK, Cypress Hills Provincial Park	Taylor & Brockman, 1966
cordifolia	ca76	WA, Stevens Co.	Barker, 1966
cordifolia	72-76	OR, Lake Co.	Strother, 1972
cordifolia	ca76	ID, Lewis Co.	Ornduff, et al., 1967
cordifolia	38	MT, Missoula Co.	Schaack, et al., 1974
cordifolia	ca90±6	CO, LaPlata Co.	Ornduff, et al., 1967
cordifolia	ca95±4	CO, Huerfana Co.	Ornduff, et al., 1967
cordifolia	ca95	CO, Larimer Co.	Love & Kapoor, 1968
cordifolia	60	Cult., USSR Arcto-Alpine Bot. Gdn.	Zhukova, 1967
discoidea (as _parviflora_)	ca72-76	OR, Josephine Co.	Ornduff, et al., 1963
discoidea (as _parviflora_)	38	CA, Trinity Co.	Barker, 1966
discoidea (as _parviflora_)	38	CA, Santa Cruz Co.	Ornduff, et al., 1967
discoidea	76	CA, Lake Co.	Ornduff, et al., 1963
discoidea	76	CA, Orange Co.	Ornduff, et al., 1963
gracilis	ca114	AB, Mt. Temple	Love & Love, 1964

Table II cont'd.

Taxon	Sporophytic Number	Locality	Reference
gracilis	ca76	ID, Valley Co.	Ornduff, et al., 1967
latifolia	38	BC, Queen Charlotte Is., Graham Is.	Taylor & Mulligan, 1968
latifolia	38	BC, Queen Charlotte Is., Moresby Is.	Taylor & Mulligan, 1968
latifolia	38	AB	Ornduff, et al., 1967
latifolia	38	WA, Kittitas Co.	Ornduff, et al., 1963
latifolia	38	WA, Whatcom Co.	Ornduff, et al., 1963
latifolia	38	WA, Lewis Co.	Barker, 1966
latifolia	38	MT, Ravalli Co.	Schaack, et al., 1974
latifolia	ca76	MT, Lake Co.	Powell, et al., 1974
spathulata	ca76	OR, Josephine Co.	Barker, 1966
spathulata	38	CA, Del Norte Co.	Ornduff, et al., 1967
venosa	38	CA, Shasta Co.	Barker, 1966
viscosa	38	CA, Siskiyou Co.	Barker, 1966
viscosa	38	CA, Trinity Co.	Strother, 1973

TABLE III. New Chromosome Numbers for *Arnica* Species in the Subgenera *Austromontana* and *Calarnica*.

Taxon	Sporophytic Number	Locality	Collection Number
cernua	38	CA, Humboldt Co. Horse Mtn.	S-1396
cernua	38	CA, Humboldt Co. west of Hoopa	S-1772
cordifolia	76	YT, Rancheria	S-1853
cordifolia	76	BC, Botanie Valley	S-1342
cordifolia	76	BC, Botanie Valley	S-1353
cordifolia	76	BC, Fountain Valley	S-1360
cordifolia	76	BC, Bonanza Pass	S-1549
cordifolia	57	BC, southeast of Windermere	S-1594
cordifolia	57	BC, Tod Mtn.	S-1652
cordifolia	76	BC, Hat Creek	S-2009
cordifolia	76	BC, Sunday Summit	S-2014
cordifolia	57	BC, Olalla	S-2022
cordifolia	76	BC, Apex Mountain	S-2025
cordifolia	76	BC, north of Kamloops	S-2028
cordifolia	76	WA, Okanogan Co., Slate Lake	S-1494
cordifolia	114	WA, Okanogan Co., Slate Lake	S-1497
cordifolia	76	WA, Okanogan Co., Slate Lake	S-1498

Table III cont'd.

Taxon	Sporophytic Number	Locality	Collection Number
cordifolia	76	WA, Klickitat Co., north of Lyle	S-1822
cordifolia	76	WA, Klickitat Co., Appleton	S-1823
cordifolia	76	OR, Wasco Co., Pine Grove	S-1819
cordifolia	76	OR, Wasco Co., Pine Grove	S-1820
cordifolia	76	CA, Sierra Co., Calpine	S-1416
cordifolia	76	CA, Placer Co., Lake Tahoe	S-1425
cordifolia	76	CA, Siskiyou Co., west of Meiss Lake	S-1797
cordifolia	76	CA, Mono Co., Saddlebag Lake	S-1937
cordifolia	57	CA, Mono Co., Saddlebag Lake	S-1939
cordifolia	114	AB, Vermillion Pass	S-1601
cordifolia	76	AB, Lake Louise	S-1604
cordifolia	76	AB, Moraine Lake	S-1610
cordifolia	76	AB, Peyto Lake	S-1616
cordifolia	76	ID, Bonneville Co., west of Aspen, WY	S-1836

Table III cont'd.

Taxon	Sporophytic Number	Locality	Collection Number
cordifolia	76	MT, Missoula Co., Pattee Canyon	S-1477
cordifolia	57	WY, Teton Co., Grand Teton Nat. Park	S-1464
cordifolia	57	WY, Teton Co., Flagg Ranch	S-1465
cordifolia	76	WY, Park Co., Yellowstone River, Upper Falls	S-1837
cordifolia	76	SD, Lawrence Co., Deadwood Gulch	S-1842
cordifolia	76	CO, Routt Co., Rabbit Ears Pass	S-1437
cordifolia	76	CO, Routt Co., Rabbit Ears Pass	S-1438
cordifolia	76	CO, Grand Co., Muddy Pass	S-1440
cordifolia	76	CO, Grand Co., Winter Park	S-1443
cordifolia	57	CO, Grand Co., Grand Lake	S-2035
cordifolia	76	CO, Clear Creek Co., Berthoud Pass	S-1458
cordifolia	76	CO, Boulder Co., Nederland	S-1460

Table III cont'd.

Taxon	Sporophytic Number	Locality	Collection Number
cordifolia	76	MI, Keweenaw Co., Copper Harbor	S-1846
cordifolia	76	MI, Keweenaw Co.	S-2005
cordifolia	57	Cult., BC, UBC Bot. Gdn., orig. from BC, Kootenay Dist.	S-1512
cordifolia	57	Cult., BC, UBC Bot. Gdn.	S-1513
discoidea	76	WA, Klickitat Co., Glenwood	S-1825
discoidea	76	OR, Wasco Co., Warm Springs Indian Reservation	S-1821
discoidea	38	CA, Mendocino Co., Little River	S-1775
discoidea	38	CA, Napa Co., south of Napa-Lake Co. line	S-1787
discoidea	38	CA, Marin Co., Mt. Tamalpias	S-1789
gracilis	57	BC, Monroe Lake	S-1562
gracilis	57	AB, Lake Louise	S-1603
gracilis	57	AB, Moraine Lake	S-1605
gracilis	57	AB, Peyto Lake	S-1613
gracilis	57	Cult., BC, UBC Bot. Gdn.	S-1762
latifolia	38	BC, Mt. Seymour	S-1503
latifolia	38	BC, Mt. Seymour	S-1504
latifolia	38	BC, Vancouver Island Forbidden Plateau	S-1529

Table III cont'd.

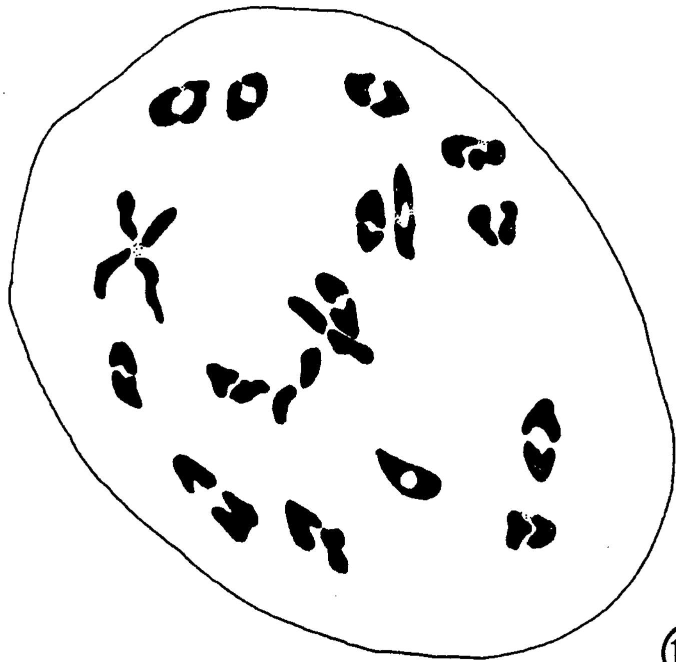
Taxon	Sporophytic Number	Locality	Collection Number
latifolia	38	BC, Vancouver Island Forbidden Plateau	S-1538
latifolia	38	BC, Bonanza Pass	S-1548
latifolia	38	BC, Kootenay Pass	S-1561
latifolia	38	BC, Manning Park	S-1680
latifolia	38	BC, Nancy Greene Prov. Pk.	S-1961
latifolia	38	BC, Black Tusk	S-2031
latifolia	38	BC, Cypress Bowl	S-2041
latifolia	38	WA, Whatcom Co., Mt. Baker	S-1161
latifolia	38	WA, Chelan Co., Washington Pass	S-1499
latifolia	38	WA, Chelan Co., Rainy Pass	S-1500
latifolia	38	AB, Peyto Lake	S-1612
latifolia	38	AB, south of Grand Prairie	S-1855
latifolia	38	MT, Missoula Co., Pattee Canyon	S-1476
nevadensis	76	CA, Sierra Co., Sierra Buttes	S-1870
nevadensis	76	CA, Mono Co., Saddlebag Lk.	S-1938
nevadensis	76	NV, Washoe Co., Mt. Rose	S-1910
spathulata	38	OR, Josephine Co., Kirby	S-1380
spathulata	38	OR, Josephine Co., east of Cave Junction	S-1381

Table III cont'd.

Taxon	Sporophytic Number	Locality	Collection Number
spathulata	38	OR, Josephine Co., O'Brien	S-1385
spathulata	38	OR, Josephine Co., Selma	S-1740
spathulata	38	OR, Josephine Co., north of O'Brien	S-1742
spathulata	38	CA, Del Norte Co., northwest of Gasquet	S-1390
spathulata	38	CA, Del Norte Co., east of Gasquet	S-1751
spathulata	38	CA, Del Norte Co., northwest of Gasquet	S-1392
venosa	38	CA, Shasta Co., Shasta Bally	S-1791
venosa	38	CA, Shasta Co., South Fork Lookout Mtn. Road	S-1792
venosa	38	CA, Shasta Co., Gibson	S-1793
viscosa	38	OR, Crater Lake Nat. Park, Garfield Peak	S-1946
viscosa	38	CA, Siskiyou Co., Mt. Shasta	S-1411
Putative Natural Hybrids			
cordifolia-latifolia	38	MT, Ravalli Co., Charles Waters Campground	S-1474
cordifolia-latifolia	38	MT, Ravalli Co., Charles Waters Campground	S-1475

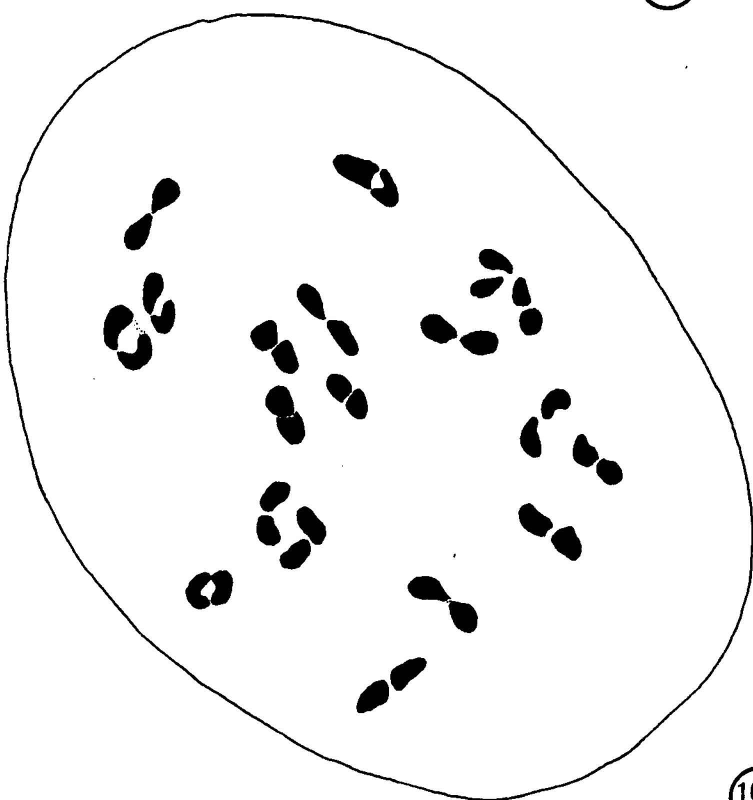
Figure 195. Arnica cernua S-1772, CA, Humboldt Co. Microsporocyte, Metaphase I plate, diploid with 19 pairs of chromosomes.

Figure 196. Arnica latifolia S-1529, BC, Vancouver Island, Forbidden Plateau. Microsporocyte, metaphase I plate, diploid with 19 pairs of chromosomes.



195

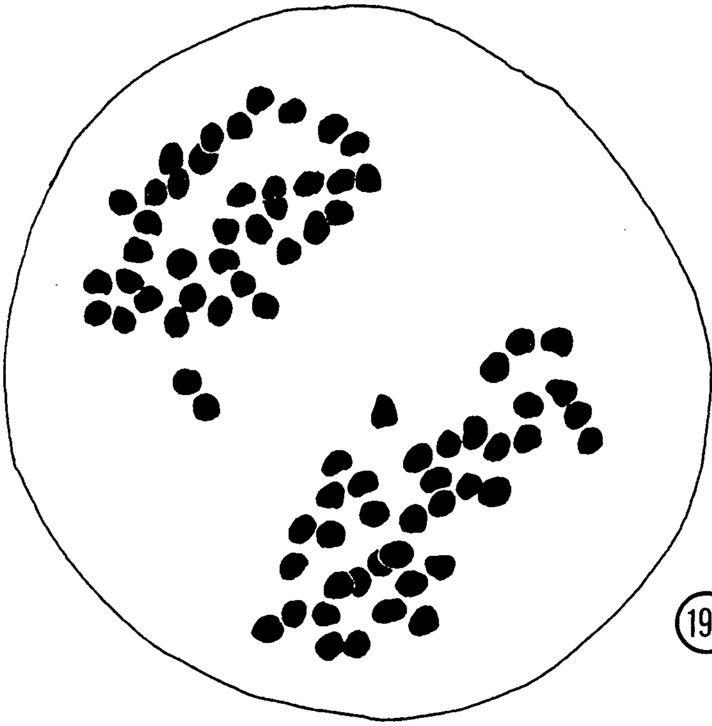
10 µm



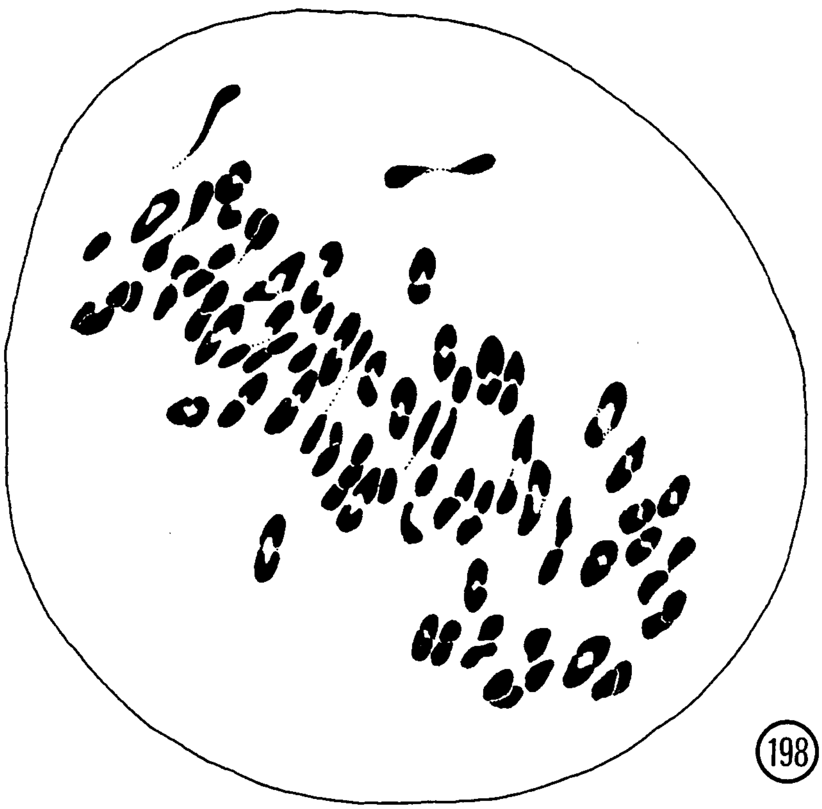
196

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.



197

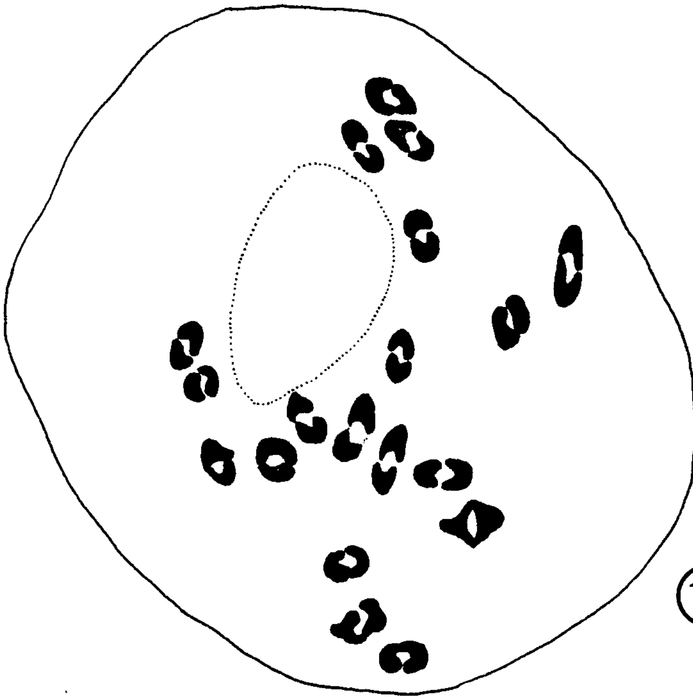


198

10 µm

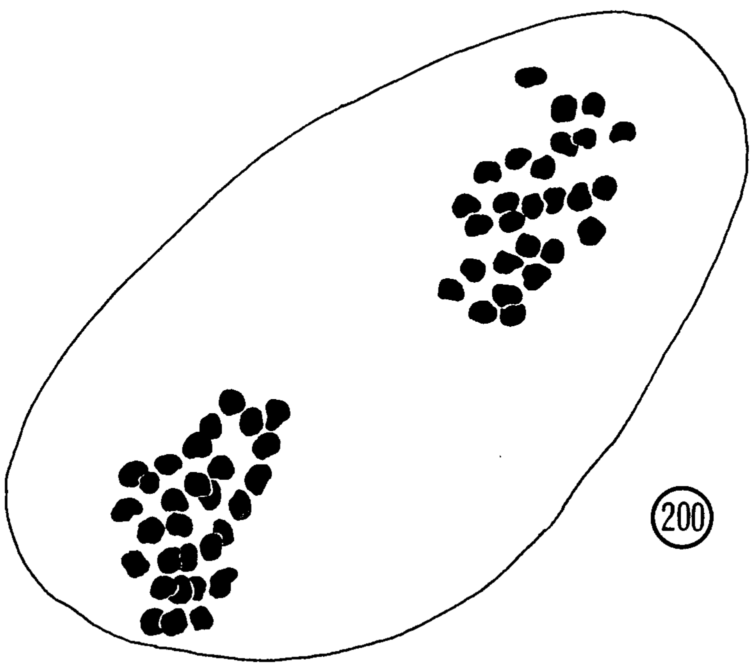
Figure 199. _Arnica cordifolia_ X _Arnica latifolia_ _S-1475_, putative natural hybrid, MT, Ravalli County. Microsporocyte, diakinesis, diploid with 19 pairs of chromosomes.

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.



199

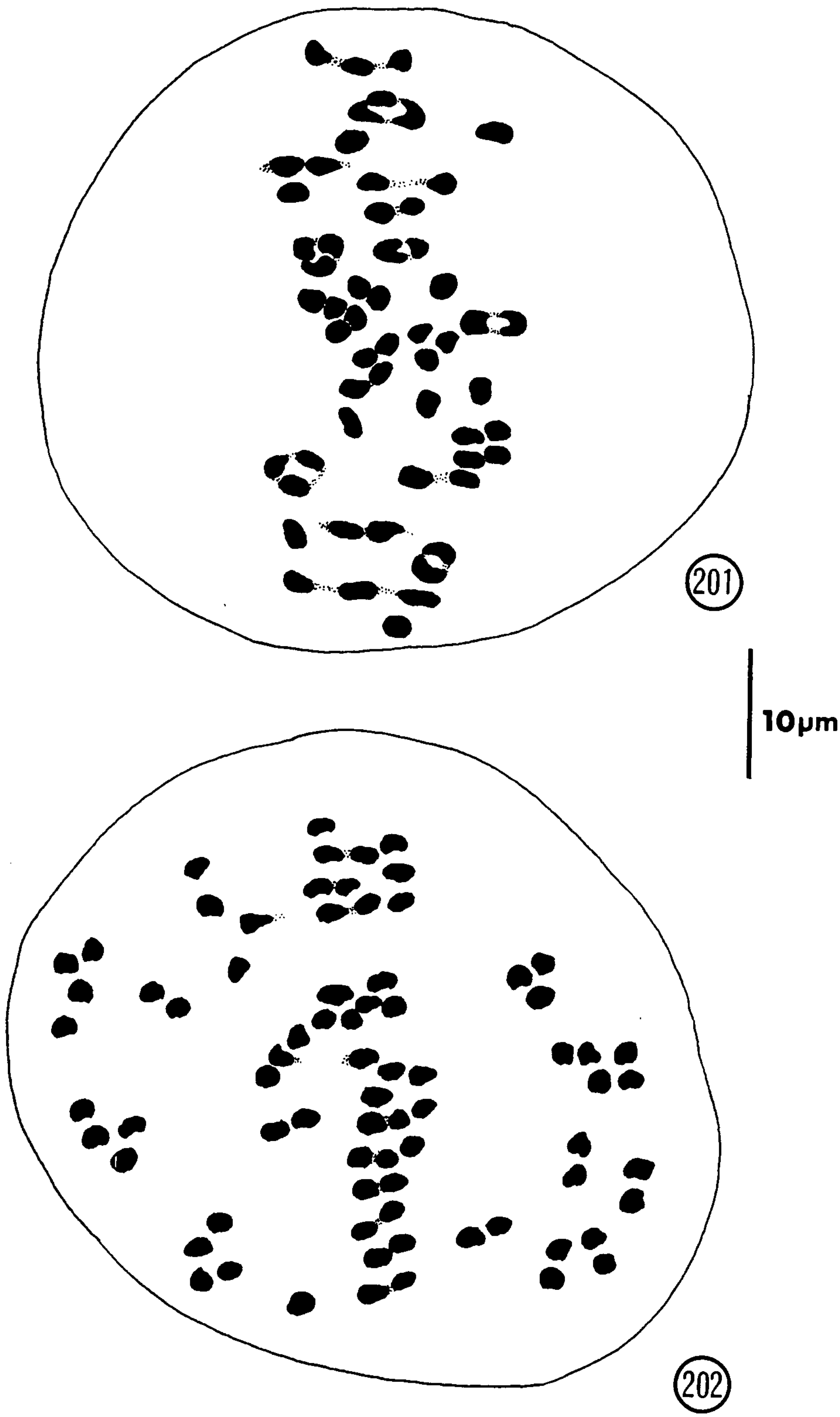
10 μm



200

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.



201

202

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.

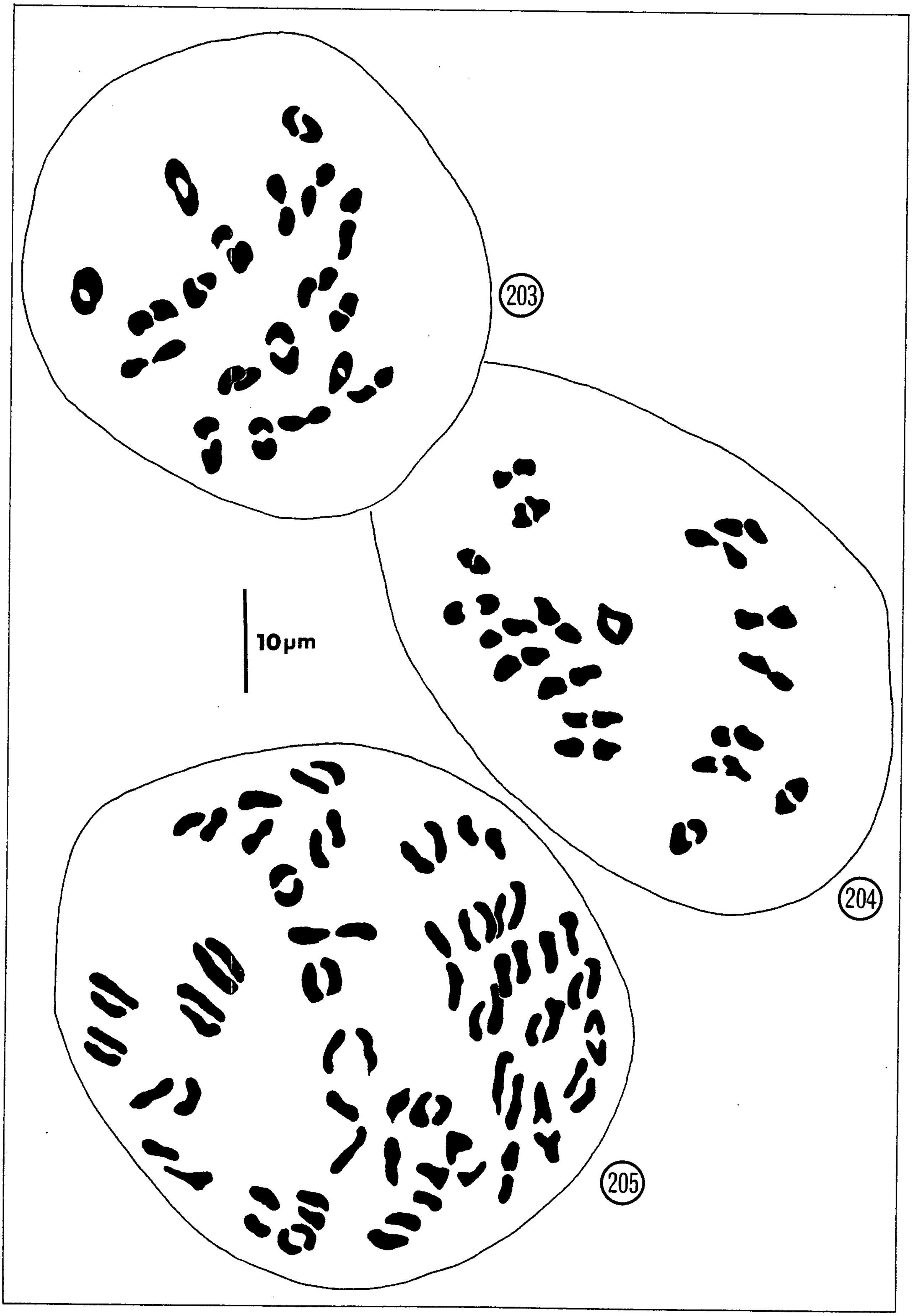
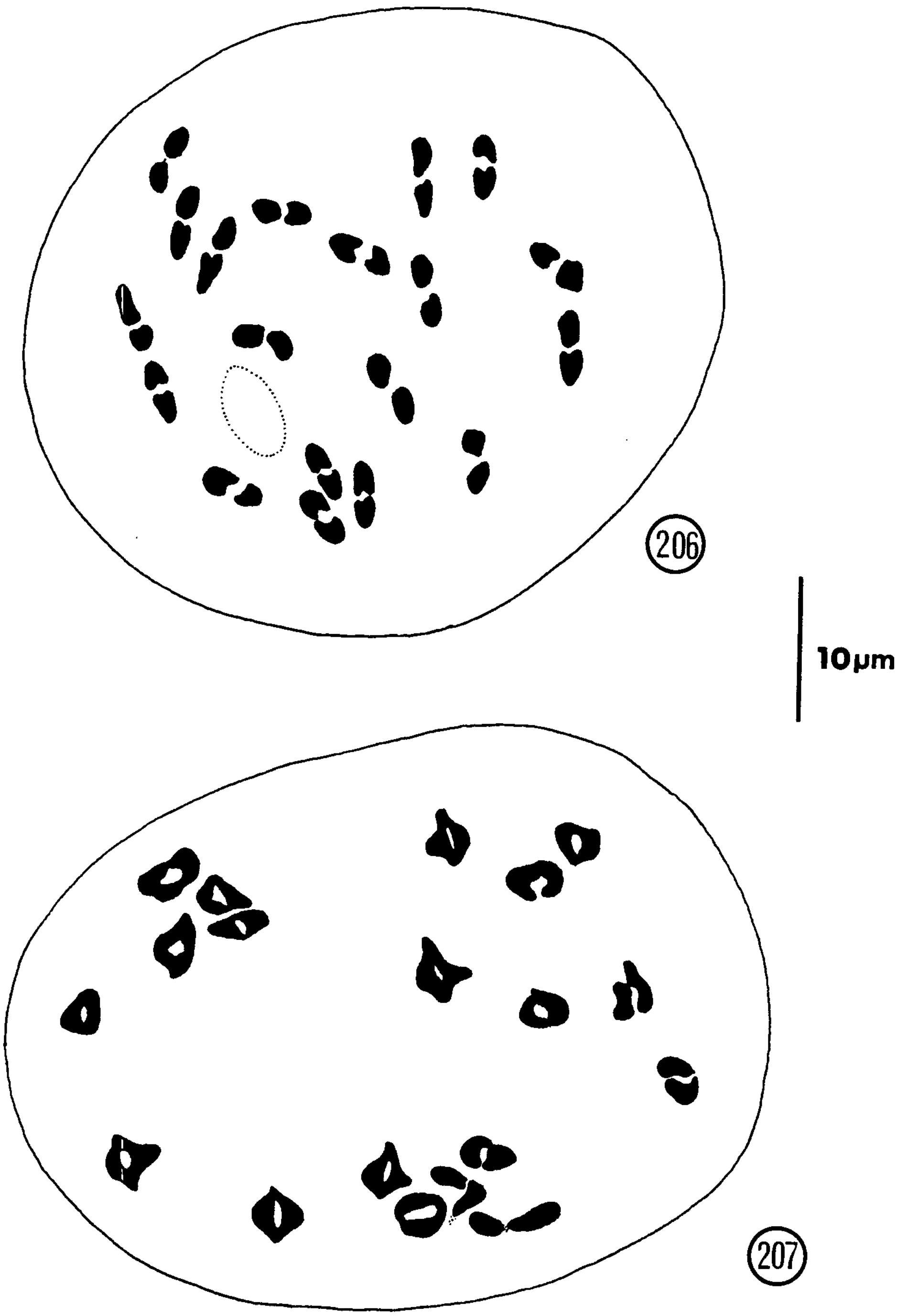

203
10µm
204
205

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.


206
10μm
207

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. Arnicas 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.

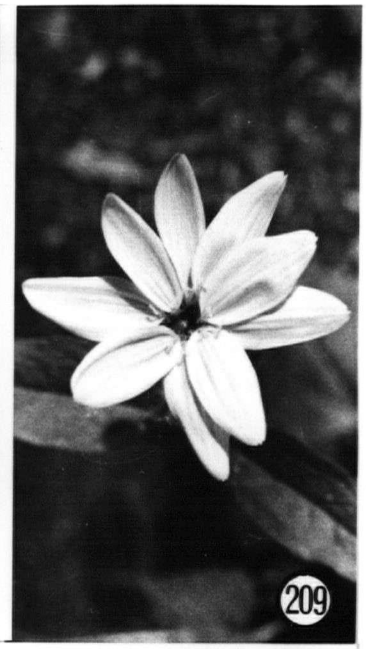


TABLE IV. Compatibility and Apomixis Experiments with *Arnica* species.

Taxon & Coll. #	Diploid Chromosome #	Pollen Stainability	# of Heads Selfed	# of Heads Emasculated	# of Achenes Produced	# of Achenes With Seeds	% of Achenes With Seeds
cordifolia 1342	76	69%	4	-	111	5	4.5
cordifolia 1343	?	89	4	-	221	38	17.2
cordifolia 1343	?	89	-	3	101	0	0
cordifolia 1353	76	83	2	-	112	7	6.2
cordifolia 1353	76	83	-	2	55	8	14.5
cordifolia 1359	?	38	2	-	96	13	13.5
cordifolia 1359	?	38	-	1	7	0	0
cordifolia 1360	76	42	4	-	157	2	1.3
cordifolia 1416	76	24	3	-	272	67	24.6
cordifolia 1458	76	82	1	-	189	0	0
cordifolia 1458	76	82	-	1	71	0	0
cordifolia 1477	76	32	6	-	371	24	6.5
cordifolia 1477	76	32	-	2	46	0	0
cordifolia 1487	?	49	1	-	52	9	17.3
cordifolia 1494	76	94	3	-	218	0	0
cordifolia 1494	76	94	-	2	52	0	0
cordifolia 1497	114	84	8	-	485	100	20.6

Table IV cont'd.

Taxon & Coll. #	Diploid Chromosome #	Pollen Stainability	# of Heads Selfed	# of Heads Emasculated	# of Achenes Produced	# of Achenes With Seeds	% of Achenes With Seeds
cordifolia 2005	76	81	3	-	314	4	1.3
cordifolia 2005	76	81	-	1	7	0	0
discoidea 1821	76	76	1	-	49	0	0
discoidea 1825	76	77	4	-	129	15	11.6
discoidea 1825	76	77	-	1	21	0	0
gracilis 1562	57	0	10	-	222	187	84.2
gracilis 1562	57	0	-	4	72	50	69.4
gracilis 1605	57	3	4	-	93	64	68.8
gracilis 1605	57	3	-	2	54	18	33.8
latifolia 1499	38	87	1	-	19	0	0
latifolia 1499	38	87	-	1	36	0	0
latifolia 1503	38	97	10	-	301	0	0
latifolia 1504	38	97	2	-	69	0	0
latifolia 1504	38	97	-	3	178	0	0
latifolia 1561	38	75	2	-	57	0	0
latifolia 1961	38	90	1	-	28	0	0

Table IV cont'd.

Taxon & Coll. #	Diploid Chromosome #	Pollen Stainability	# of Heads Selfed	# of Heads Emasculated	# of Achenes Produced	# of Achenes With Seeds	% of Achenes With Seeds
latifolia 1961	38	90	-	1	8	0	0
nevadensis 1870	76	43	2	-	122	59	48.4
nevadensis 1938	76	3	3	-	155	65	41.9
nevadensis 1938	76	3	-	3	74	23	31.1
spathulata 1380	38	99	3	-	113	0	0
venosa 1940	38	100	4	-	108	0	0
viscosa 1411	38	100	20	-	302	0	0
Hybrids							
cord.-lat. 1474	38	77	12	-	1570	0	0
cord.-lat. 1475	38	34	20	-	2051	0	0

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.

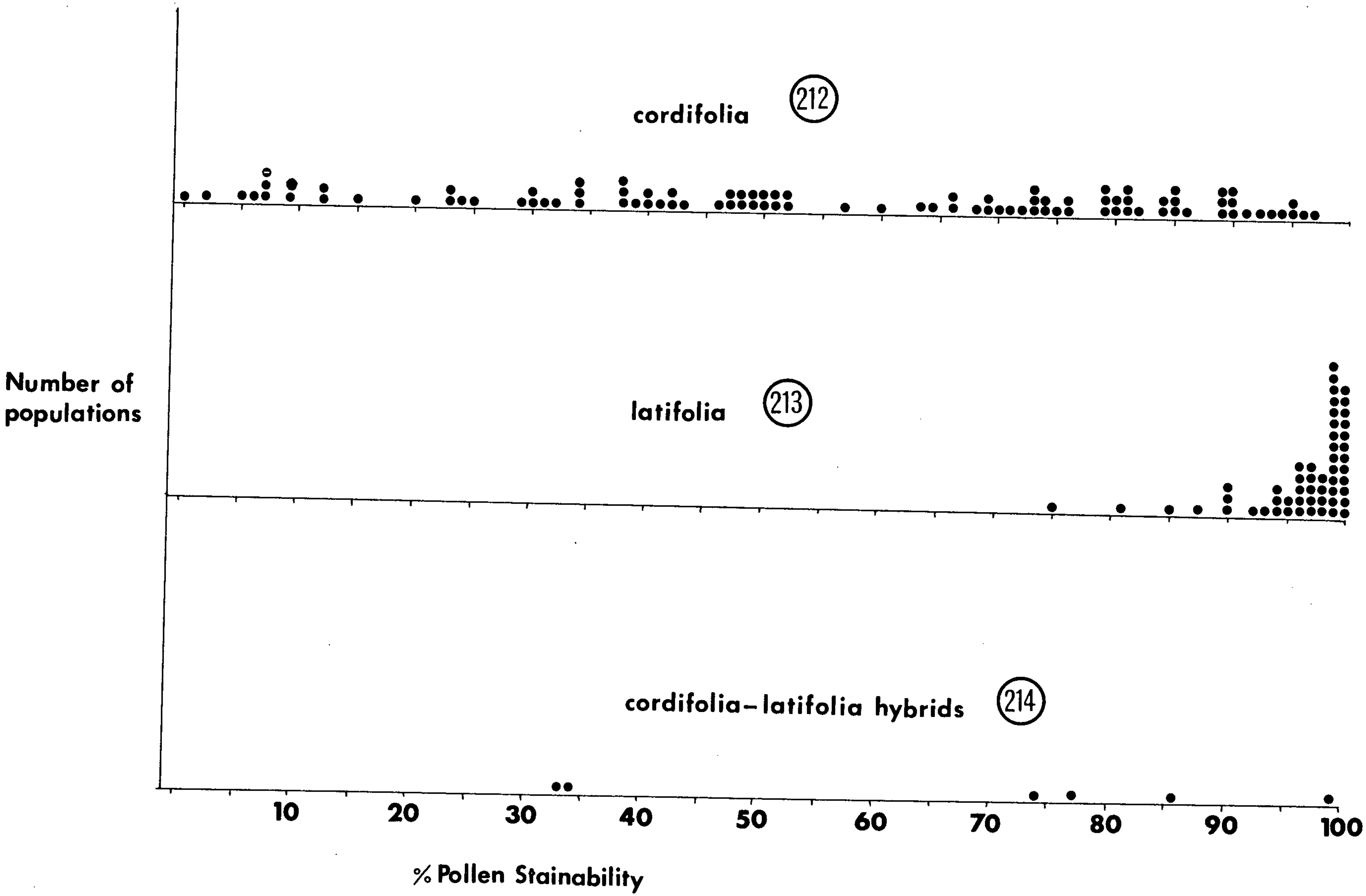
Barker (1966) discussed the correlation between ploidy level, apomixis, and pollen stainability. The data presented here support his findings.

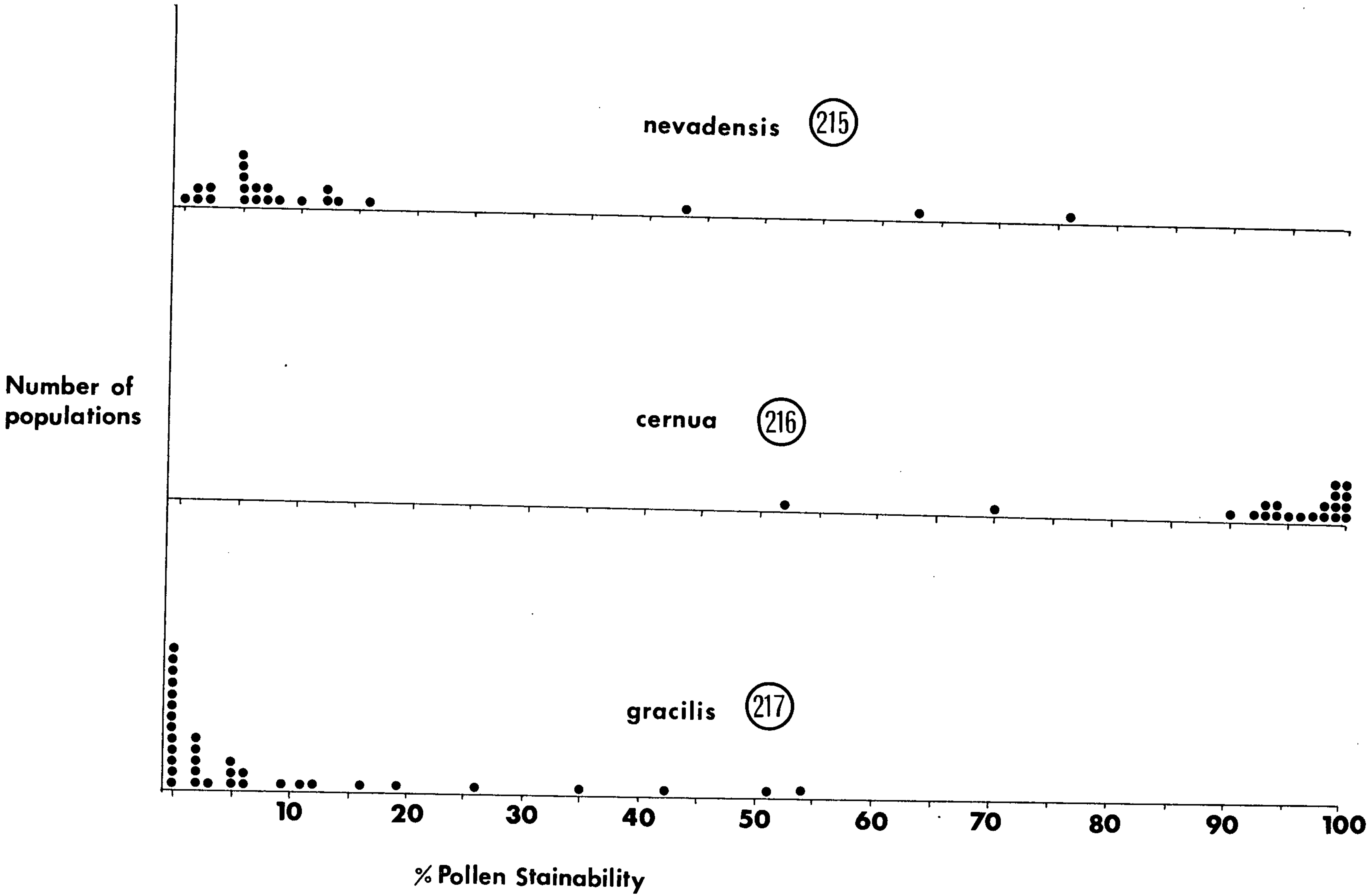
There are some distinct trends among certain species. The exclusively or predominately diploid, sexual species including Arnica latifolia, Arnica cernua, Arnica spathulata, Arnica venosa, and Arnica viscosa all show very high pollen stainability, mostly greater than 90%.

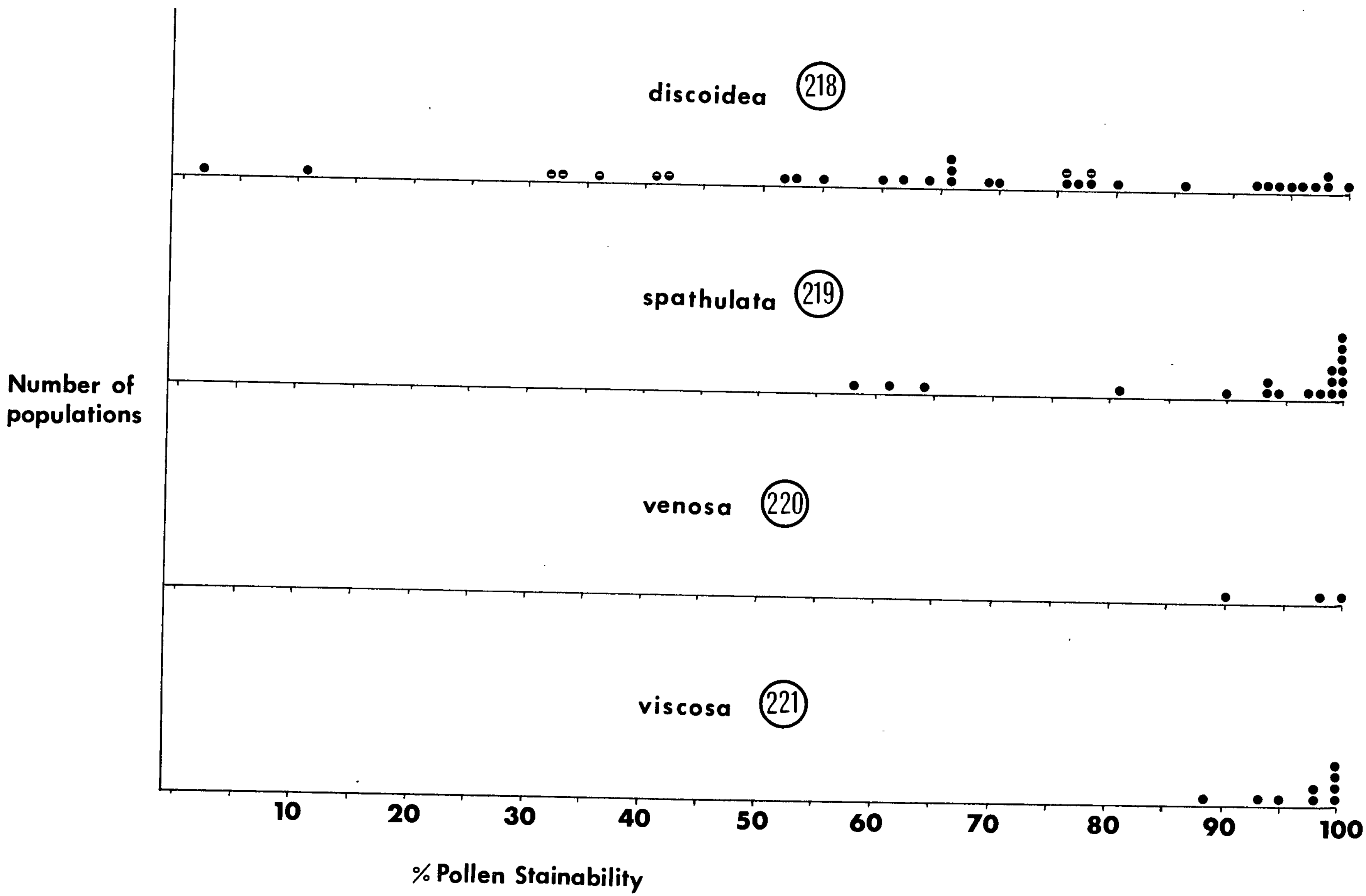
A second group of species includes Arnica gracilis and Arnica nevadensis which have mostly less than 10% stainable pollen. These two are known to be or presumed to be autonomous apomicts and mostly or entirely polyploids. A number of populations of Arnica gracilis sampled had no pollen produced in any 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.


cordifolia
212
latifolia
213
cordifolia–latifolia hybrids
214
Number of populations
10
20
30
40
50
60
70
80
90
100
% Pollen Stainability


nevadensis
215
cernua
216
gracilis
217
Number of populations
10
20
30
40
50
60
70
80
90
100
% Pollen Stainability



discoidea 218
spathulata 219
venosa 220
viscosa 221
Number of populations
10
20
30
40
50
60
70
80
90
100
% Pollen Stainability

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 spathulata*, *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 ($4^{\circ}C$) or freezer ($0^{\circ}C$) or dry at room temperature (ca $20^{\circ}C$) 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 $25^{\circ}C$. (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 $25^{\circ}C$.

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.

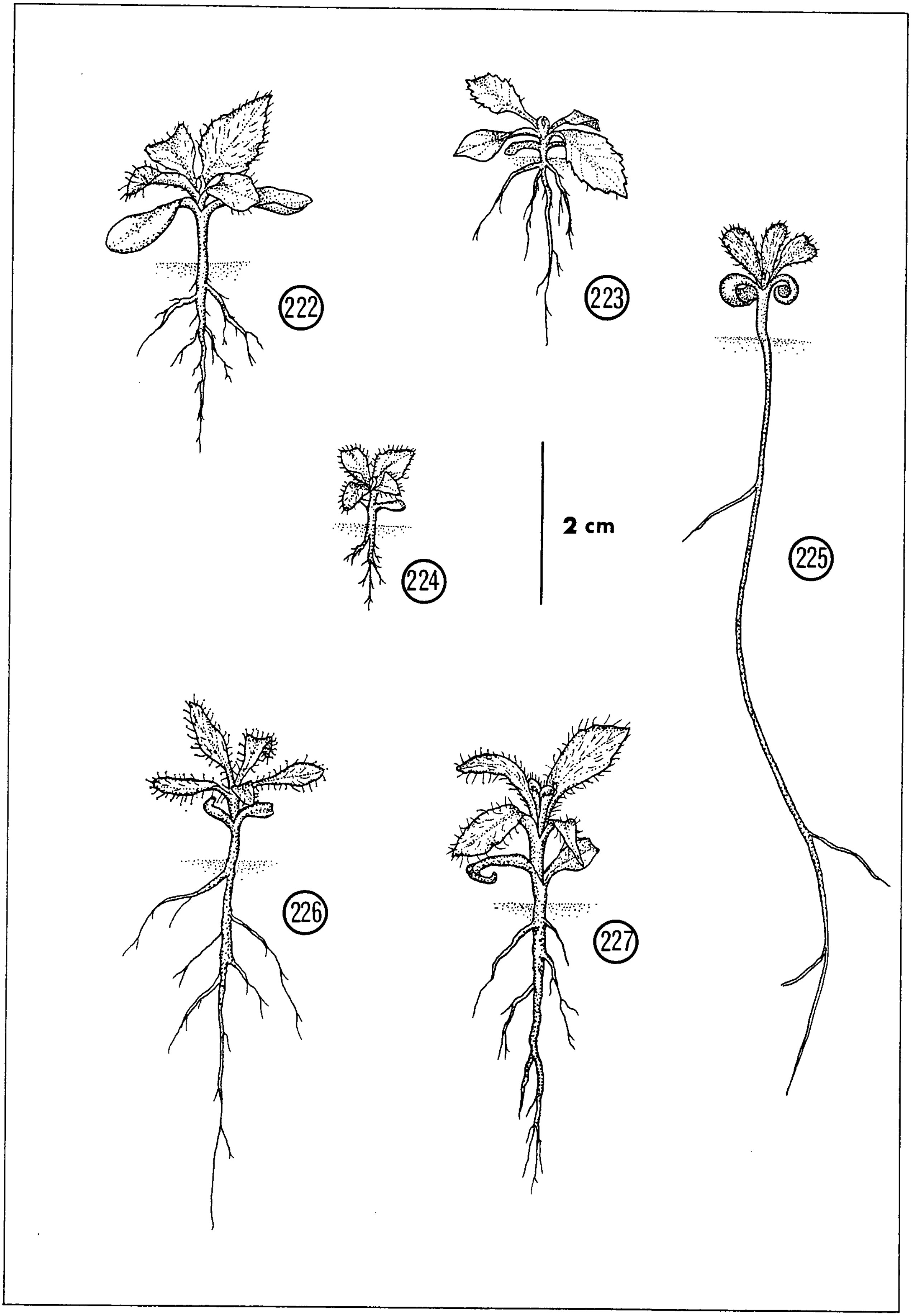
Figure 223. Arnica latifolia S-1855, AB, south of Grande Prairie.

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.


222
223
225
224
2 cm
226
227

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.

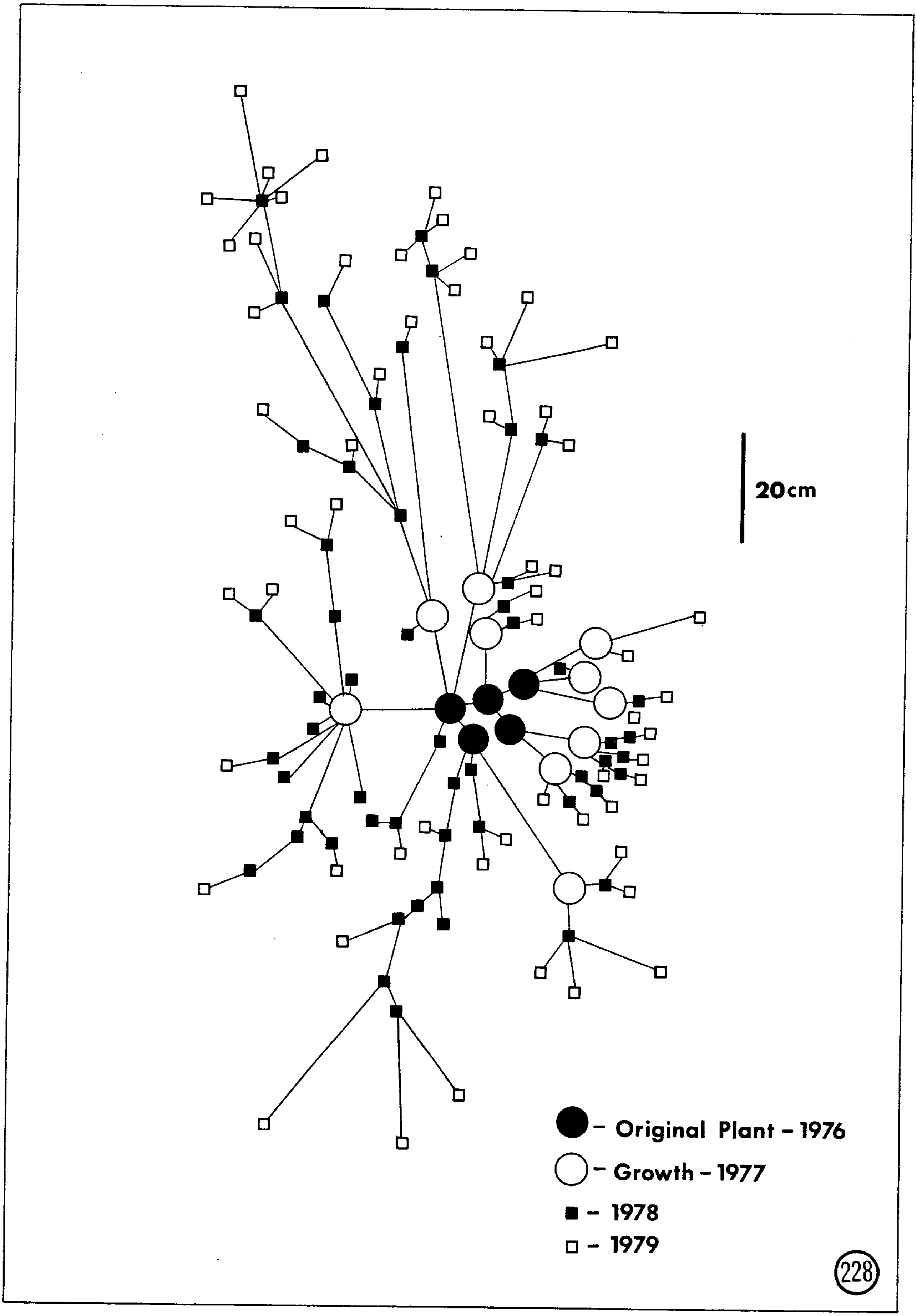

20cm
- Original Plant - 1976
- Growth - 1977
- 1978
- 1979
228

Figure 229. Rhizome growth measured over 4 years, Arnica latifolia S-1162, WA, Whatcom County, Mt. Baker.

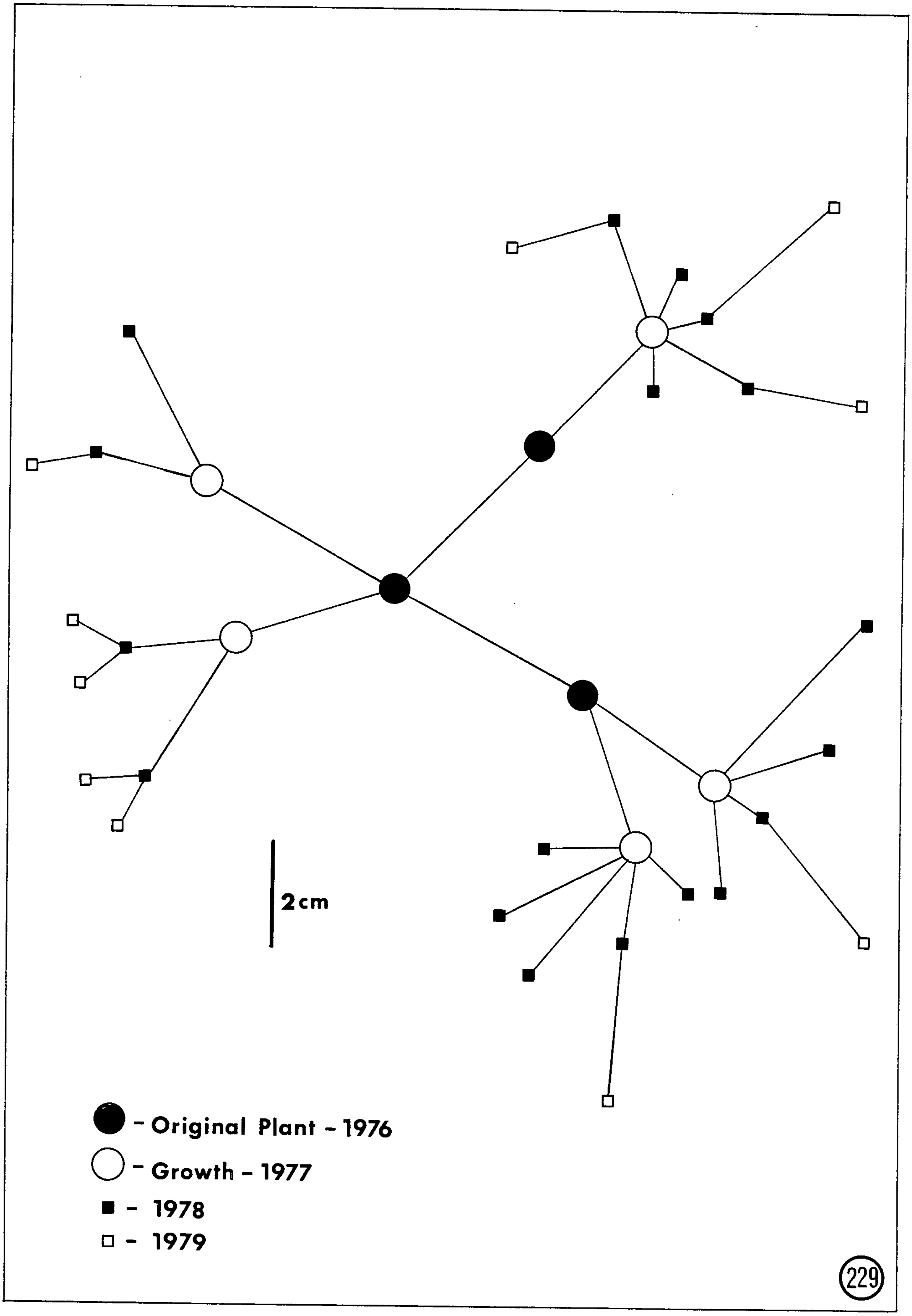
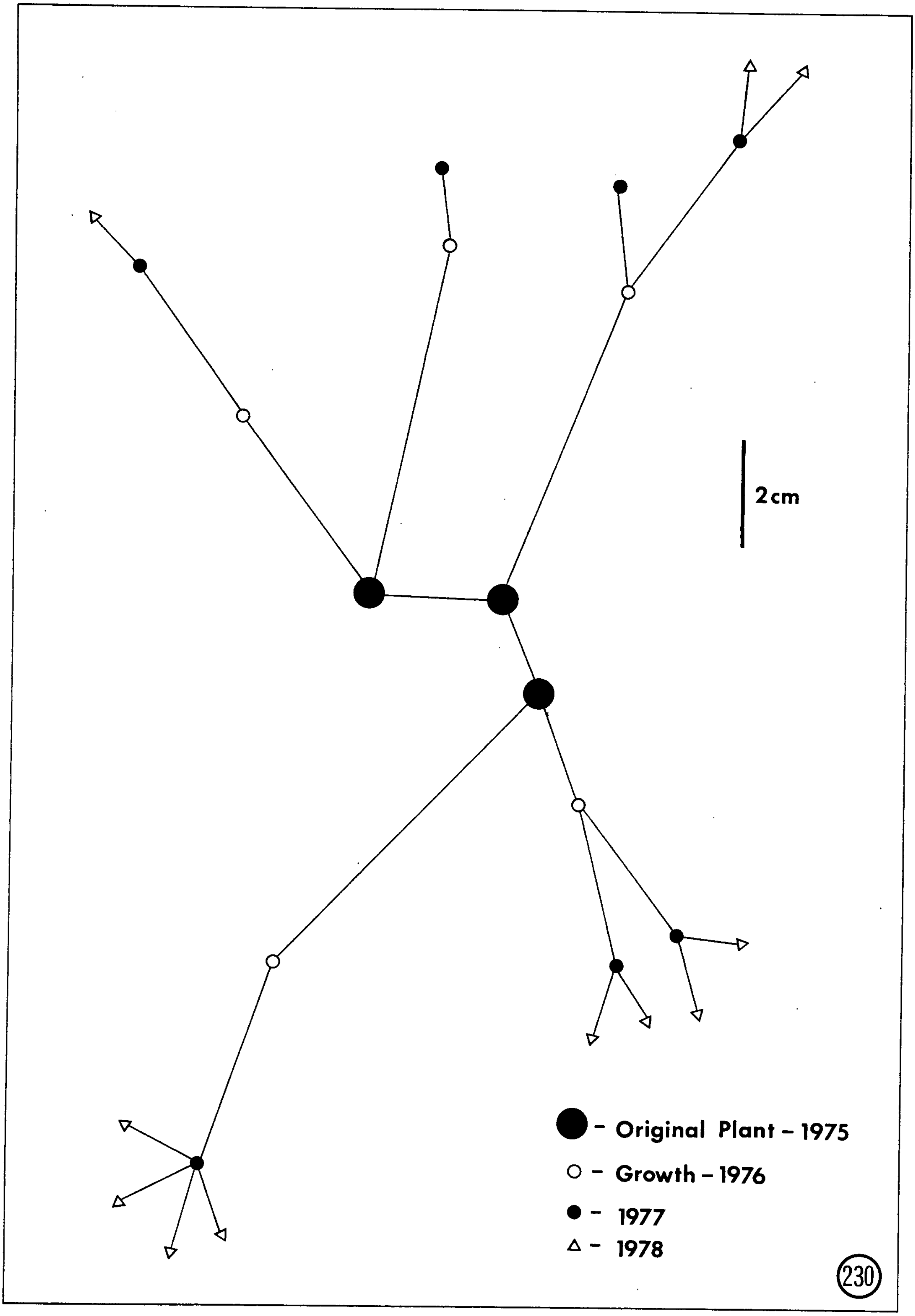
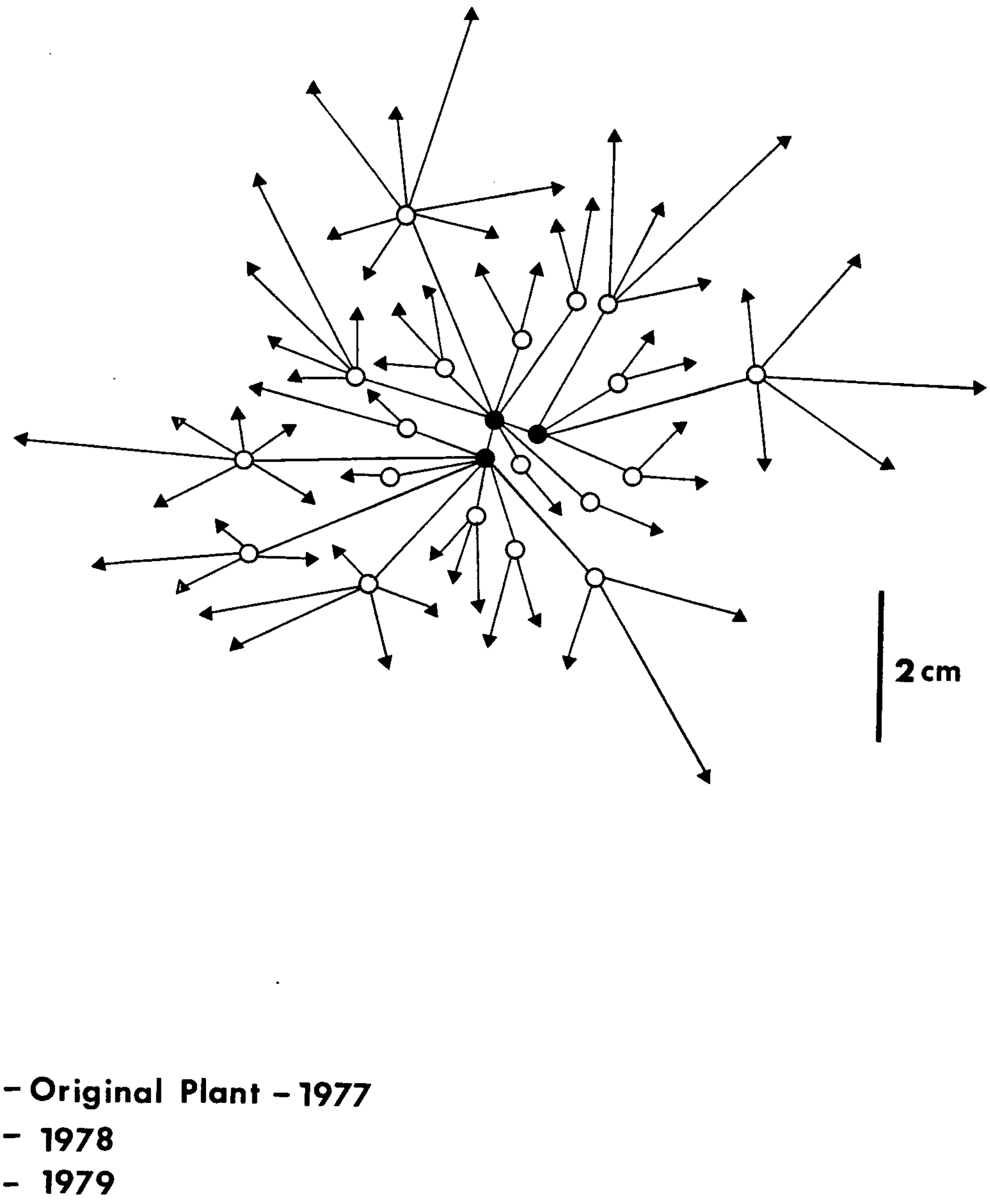

2cm
- Original Plant - 1976
- Growth - 1977
- 1978
- 1979
229

Figure 230. Rhizome growth measured over four years, *Arnica cernua S-1772*, CA, Humboldt County, Hoopa Mountain.



2 cm
- Original Plant - 1975
- Growth - 1976
- 1977
- 1978
230

Figure 231. Rhizome growth measured over 3 years, Arnica gracilis S-1605, AB, Moraine Lake.



231

TABLE V. Yearly Rhizome Growth in Arnica, Subgenus Austromontana Species.

Taxon	Annual Growth (cm)	Annual Average (cm)	Breeding System	Average Seed Viability
cernua	(1-)4-15(-20)	6	Sexual	14%
cordifolia	2-20(-60)	10	Apomictic	30%
discoidea	5-15(-22)	7	Sexual and Apomictic	20%
gracilis	(0.5-)1-2(-6)	1.5	Apomictic	80%
latifolia	(0.5-)1-7(-10)	4	Sexual	20%
nevadensis	(1-)3-12	6	Apomictic	60%
spathulata	(1-)3-7(-14)	5	Sexual and Apomictic	?

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 sympatrically. 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 sympatrically 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.

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

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.

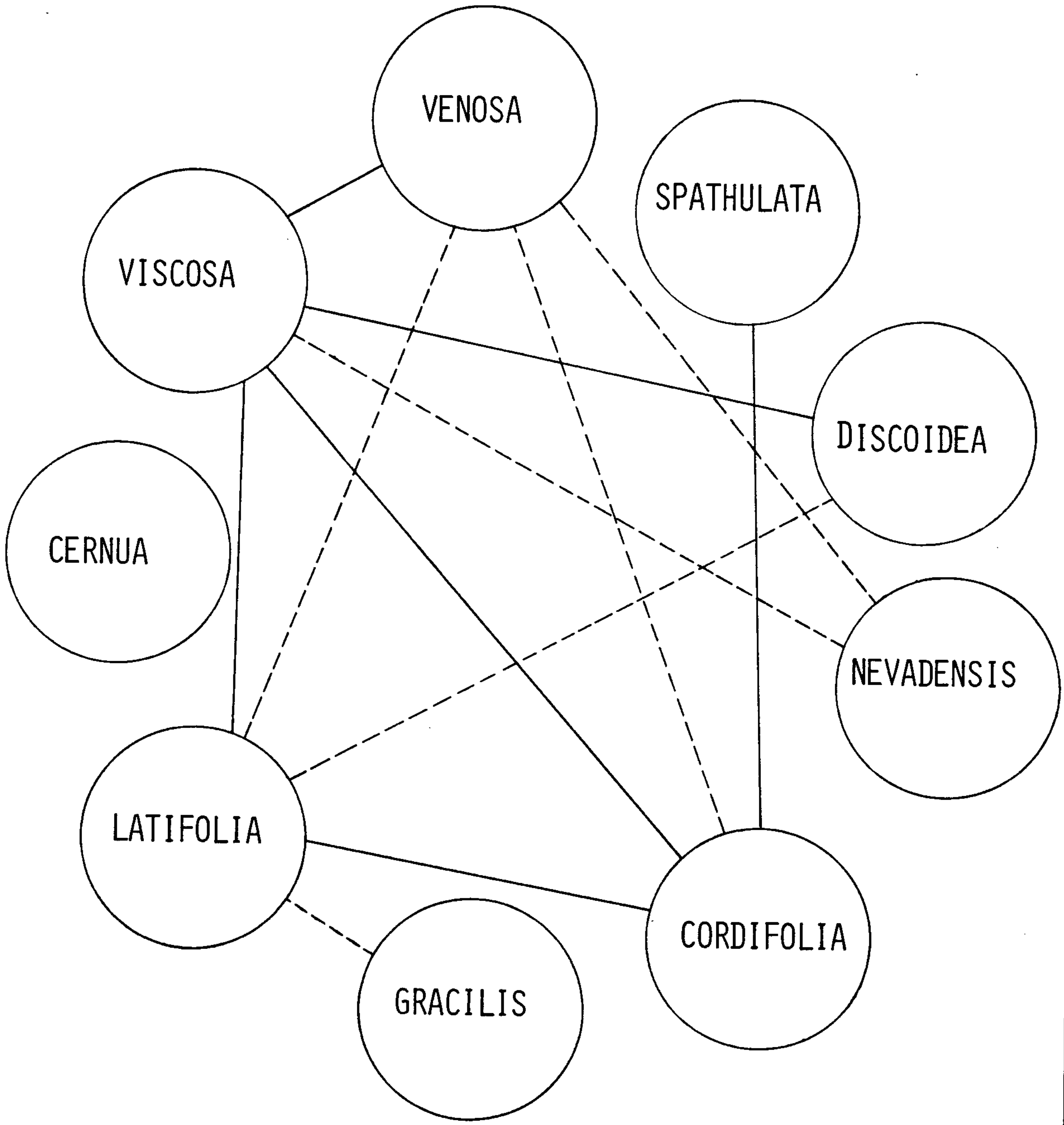
TABLE VII. Artificial Hybridizations Using Sexual Populations (known or supposed) of Arnica Species.

Taxon & Collection # (♂ Parent)	Diploid Chromosome #	Taxon & Collection # (♀ Parent)	Diploid Chromosome #	Heads Crossed	Achenes Produced	Achenes With Seeds
latifolia 1499	38	cordifolia 1497	76	3	9	0
latifolia 1504	38	cordifolia 1512	57	2	13	7
latifolia 1961	38	cordifolia 2009	76	2	64	0
latifolia 1961	38	discoidea 1821	76	1	56	0
latifolia 1961	38	diversifolia 1419	76	3	118	3
latifolia 1961	38	gracilis 1605	57	1	28	0
latifolia 1961	38	viscosa 1411	38	1	53	0
latifolia 1503	38	mollis 1515	?	1	8	0
latifolia 1504	38	mollis 1515	?	1	9	0
spathulata 1380	38	cordifolia 1477	76	2	69	3
spathulata 1380	38	cordifolia 1497	76	2	37	0
venosa 1940	38	cordifolia 2005	76	1	53	0
venosa 1940	38	cord.-lat. hyb. 1475	38	1	25	0
venosa 1940	38	latifolia 2041	38	1	26	0
venosa 1940	38	nevadensis 1938	76	1	26	0
venosa 1940	38	viscosa 1411	38	1	27	0

Table VII cont'd.

Taxon & Collection # (♂ Parent)	Diploid Chromosome #	Taxon & Collection # (♀ Parent)	Diploid Chromosome #	Heads Crossed	Achenes Produced	Achenes With Seeds
viscosa 1411	38	cordifolia 1343	?	2	34	5
viscosa 1411	38	cordifolia 2005	76	1	22	0
viscosa 1411	38	latifolia 1680	38	1	16	0
viscosa 1411	38	latifolia 1961	38	1	19	5
viscosa 1411	38	latifolia 2041	38	1	13	2
viscosa 1411	38	cord.-lat. hyb. 1474	38	2	45	0
viscosa 1411	38	cord.-lat. hyb. 1475	38	3	55	0
viscosa 1411	38	discoidea 1825	76	5	110	9
viscosa 1411	38	nevadensis 1870	76	2	41	0
viscosa 1411	38	venosa 1940	38	2	36	2
Hybrids						
cord.-lat. 1474	38	spathulata 1380	38	1	14	0
cord.-lat. 1474	38	viscosa 1411	38	1	17	0
cord.-lat. 1475	38	cordifolia 1353	76	1	61	0
cord.-lat. 1475	38	discoidea 1825	76	2	39	0
cord.-lat. 1475	38	spathulata 1380	38	1	5	0
cord.-lat. 1475	38	viscosa 1411	38	3	40	0

Figure 232. Summary of all artificial crosses attempted between species in subgenus Austromontana and Calarnica. Solid lines indicate successful crosses. Dotted lines, unsuccessful crosses.


VENOSA
SPATHULATA
VISCOSA
DISCOIDEA
CERNUA
NEVADENSIS
LATIFOLIA
CORDIFOLIA
GRACILIS

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 Arnicas are probably self-incompatible.

Leaf Miners

Griffiths (1974) records seven species of Phytomyza (Diptera:Agromyzidae) which form mines in the leaves 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 Austromontana, 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 Arnicas are not known.

Floret Feeders

There are occasional large host-specific or omnivorous herbivores including inch worms (Geometriidae) or cutworms, especially Autographa simplex Guenée (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.

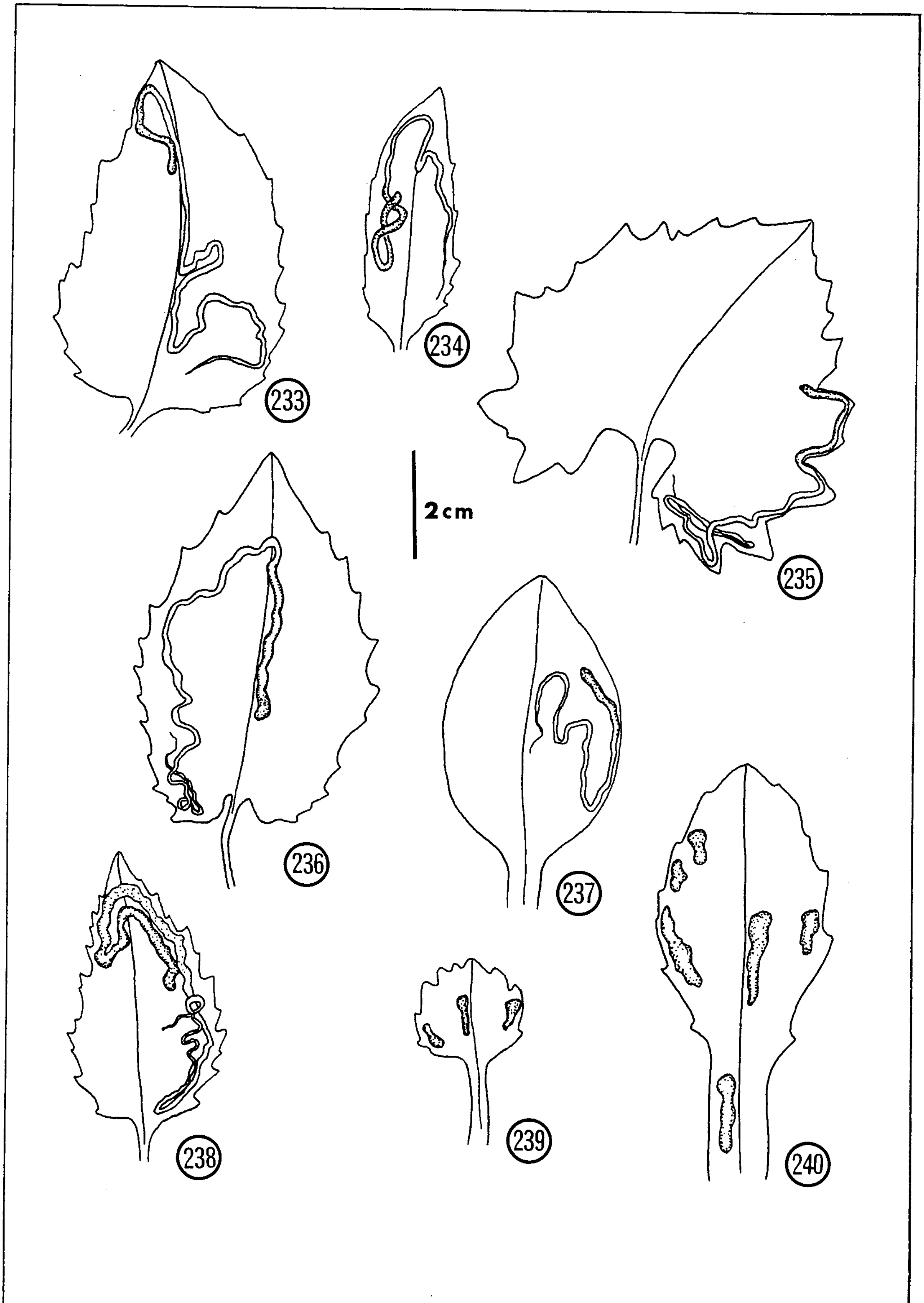

233
234
235
2cm
236
237
238
239
240

TABLE IX. Buprestid Beetles Collected Feeding on Arnica Species.

Arnica cordifolia S-1594, BC, Windermere

Anthaxia expansa Lec. - 2

Arnica cordifolia S-1819, OR, Wasco County, Pine Grove

Anthaxia expansa Lec. - 1

Anthaxia aenescens Casey - 1

Arnica cordifolia S-2022, BC, Apex Mountain

Anthaxia expansa Lec. - 2

Arnica cordifolia S-1842, SC, Lawrence County, Deadwood Gulch

Anthaxia expansa Lec. - 7

Arnica cordifolia S-1797, CA, Siskiyou County, Meiss Lake

Anthaxia sp. - 2

Arnica spathulata S-1381, OR, Josephine County, Cave Junction

Acmaeodera connexa Lec. - 1

Anthaxia california Obenb. -1

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

Anthaxia california Obenb. - 8

Anthaxia sp. - 1

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 damanged 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 bellioides* (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.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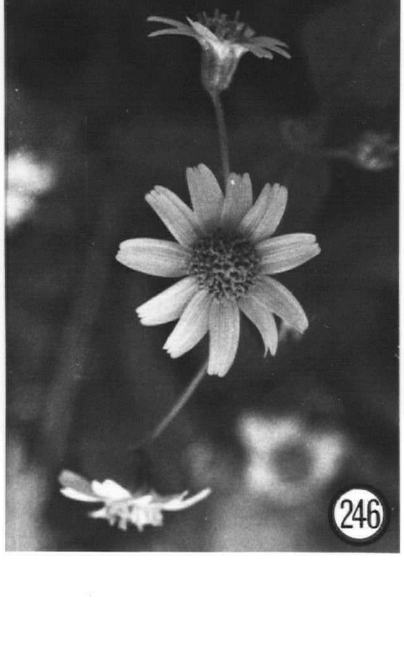
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247

In the discoid species of *Arnica* the head absorbs UV and appears dark (Figures 243, 244).

Pollinators

An unexpedtedly 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 Arnicas 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 Arnicas 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

Apidae

Bombus _melanopygus_ Nylander ♂

Bombus _mixtus_ Cresson 2 ♂

Nymphalidae

Euphydryas sp. 5 ♂, 2 ♀

Arnica _latifolia_ _S-2031_, BC, Black Tusk

Sessidae

Vespamina sp. ?

Arnica _spathulata_ _S-1380_, OR, Josephine County, Kirby

Apidae

Apis _mellifera_ L.

Halictidae

Halictus sp.

Arnica _spathulata_ _S-1740_, OR, Josephine County, Selma

Apidae

Bombus _caliginosus_ (Frison) 2 ♂

Arnica _venosa_ _S-1793_, CA, Shasta County, Gibson

Halictidae sp.

SYSTEMATIC TREATMENT

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

Subgenus *Austromontana* Maguire. Brittonia 4:432. 1943.

Lectotype: *Arnica latifolia* Bongard

Sect. *Eulatifoliae* Maguire. Brittonia 4:432. 1943.

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

Sect. *Eradiatae* Maguire. Brittonia 4:452. 1943.

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^{o} 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^{o} 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 cordiate 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 througout 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.

1. *Arnica cordifolia* Hooker. Fl. Bor. Am. 1:33. 1834.

Arnica macrophylla Nutt. Trans. Am. Phil. Soc. 7:407. 1841. TYPE: Oregon, Blue Mountains, *Nuttall* (Herb. Hook., KEW).

Arnica cordifolia Hook. var. macrophylla (Nutt.) Maguire. Am. Midl. Nat. 37:137. 1947.

Arnica grandifolia Greene. Pittonia 4:173. 1900. TYPE: Montana, Bridger Mountains, July 28, 1896, J.H. Flodman 896 (holotype, ND; isotype, MO) (probable hybrid, also listed under synonymy of Arnica latifolia).

Arnica subcordata Greene. Pittonia 4:173. 1900. TYPE: Alberta, Athabasca River, June 26, 1989, Spreadborough, Geol. Surv. Can. 19644 (UC).

Arnica pumila Rydb. Mem. N.Y. Bot. Gdn. 1:433. 1900. TYPE: Colorado, Gray's Peak, 1872, J. Torrey, s.n. (NY).

Arnica cordifolia Hook. var. pumila (Rydb.) Maguire. Madroño 6:154. 1942.

Arnica parvifolia Greene. Pl. Baker. 3:28. 1901. TYPE: Colorado, Marshall Pass, 3,000 m, July 19, 1901. C.F. Baker 515 (holotype, ND; isotypes, POM, WS).

Arnica paniculata A. Nels. Man. Bot. Rocky Mts. 572. 1909. TYPE: Wyoming, Carbon Co., Bridger Peak, moist timber, August 24, 1903, L.N. Gooding 1974 holotype, RM; isotype, MO).

Arnica evermannii Greene. Ottawa Nat. 23:215. 1910. TYPE: Idaho, Pittit Lake, 2160 m, August 13, 1895, B.W. Evermann 318 (US).

Arnica abortiva Greene. Leaflets 11:47. 1910. TYPE: Wyoming, Wind River Mountains, July 23, 1882, W.H. Forwood, s.n. (US).

Arnica granulifera Rydb. Fl. Rocky Mts. 978. 1917. TYPE: Montana, Little Belt Mountains, J.H. Flodman 896 (NY).

Arnica andersonii Piper. Proc. Biol. Soc. Wash. 33:106. 1902. TYPE: British Columbia, Skeene, Ellison, damp woods, September 11, 1910, J.R. Anderson 677 (US).

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 austinae Rydb. N. Am. Fl. 34:340. 1927. TYPE: California, Lake County, June 1898, R.M. Austin & Bruce 2165 (NY).

Arnica humilis Rydb. N. Am. Fl. 34:341. 1927. TYPE: Alberta, Lake Louise, "the saddle", 2100 m, Macoun, Geol. Surv. Can. 65504 (NY).

Arnica cordifolia Hook. var. humilis (Rydb.) Maguire. Am. Midl. Nat. 37:138. 1947.

Arnica whitneyi Fern. Rhodora 37:334. 1935. TYPE: Michigan, Keweenaw County, Copper Harbor, dry deciduous woods, July 4, 1934, Fernald & Pease 3579 (G).

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

Arnica hardinae St. John. Fl. SW. Wash. 419. 1937. TYPE: Idaho, Benewah County, Lake Chatcolet, open woods, G. Weitman 226 (holotype, WASH; isotype, WS).

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) $\pm$ 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; $2\underline{n}$=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.

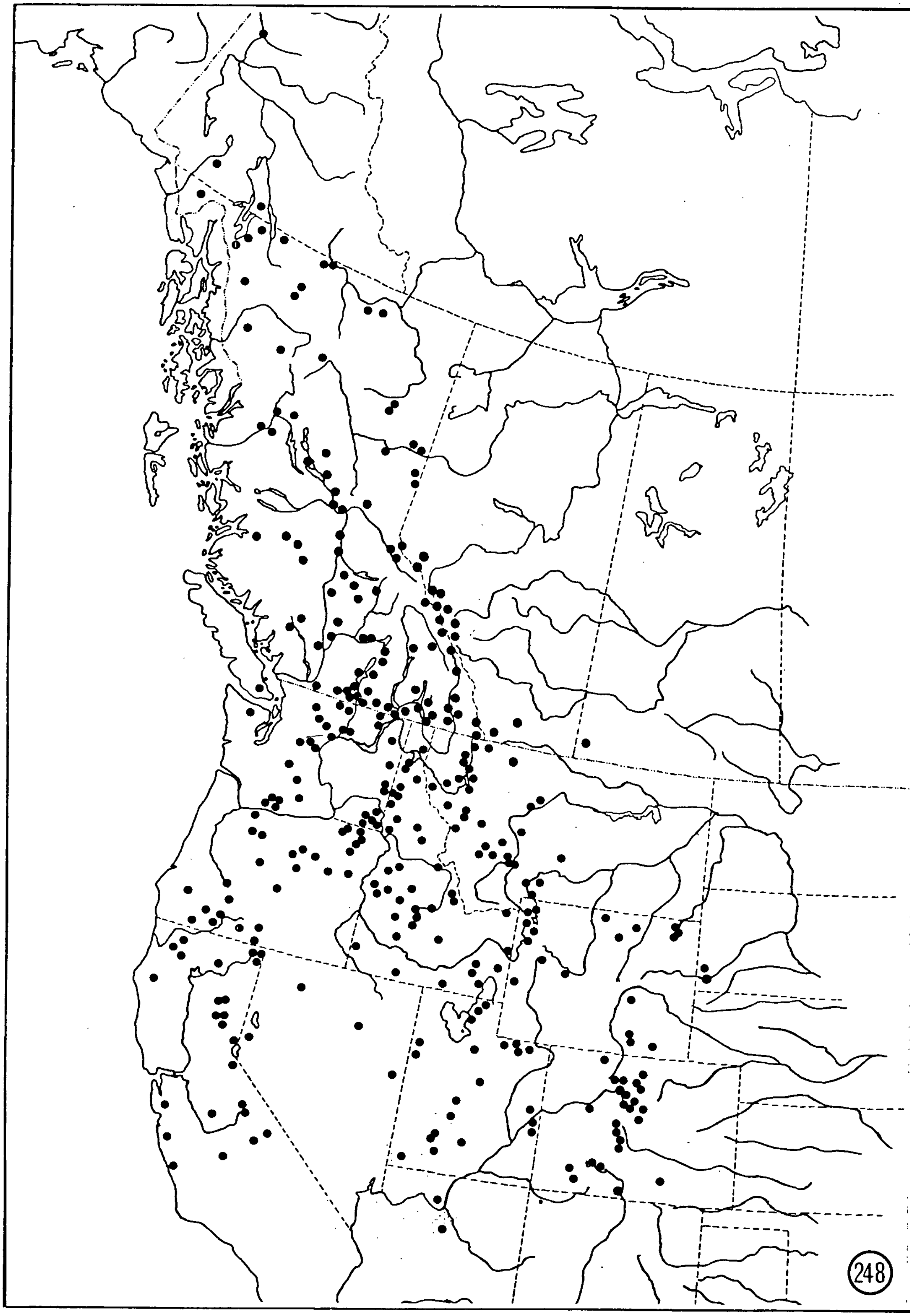
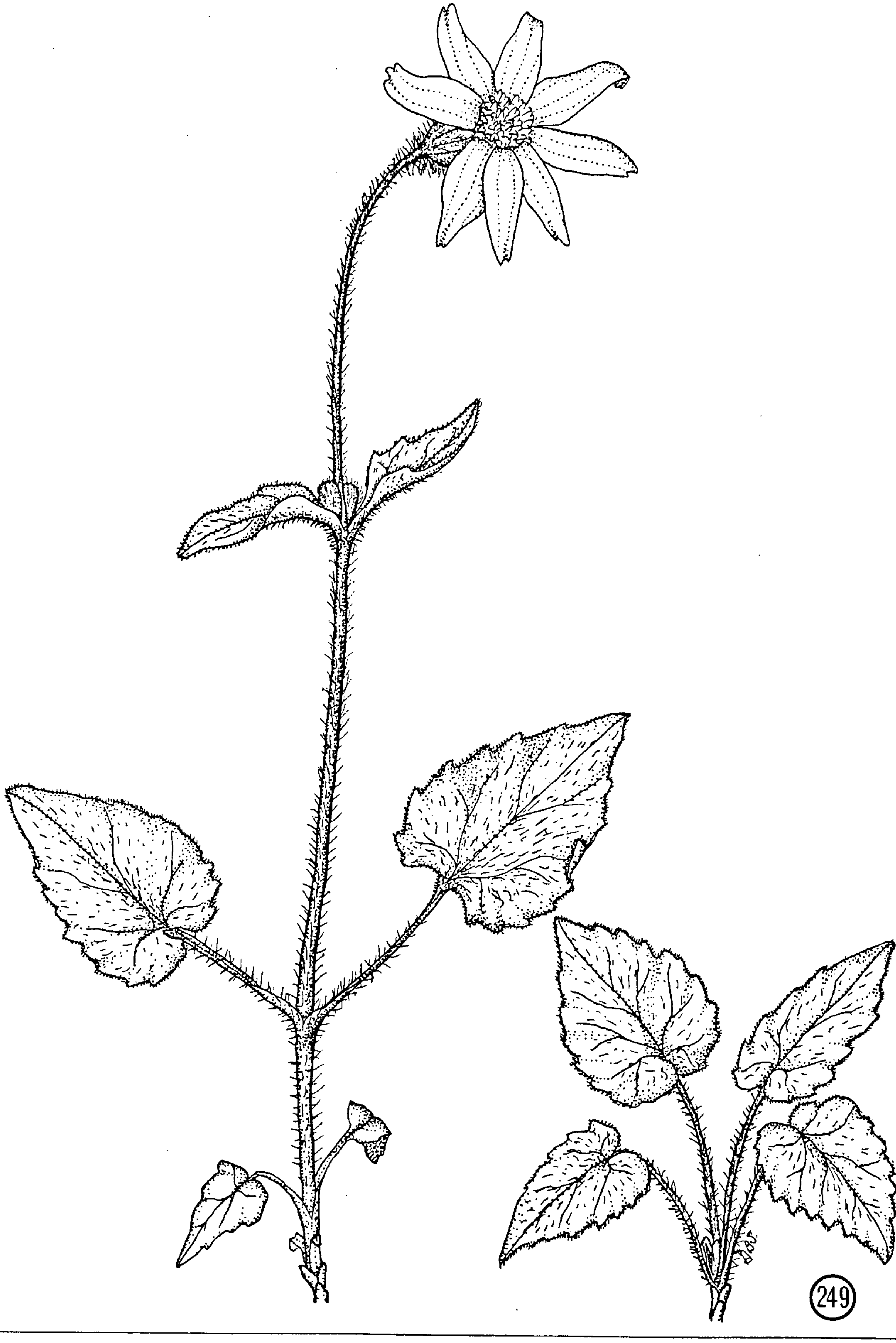

248

Figure 249. Arnica cordifolia S-1494, WA, Okanogan County, habit.
X two-thirds.



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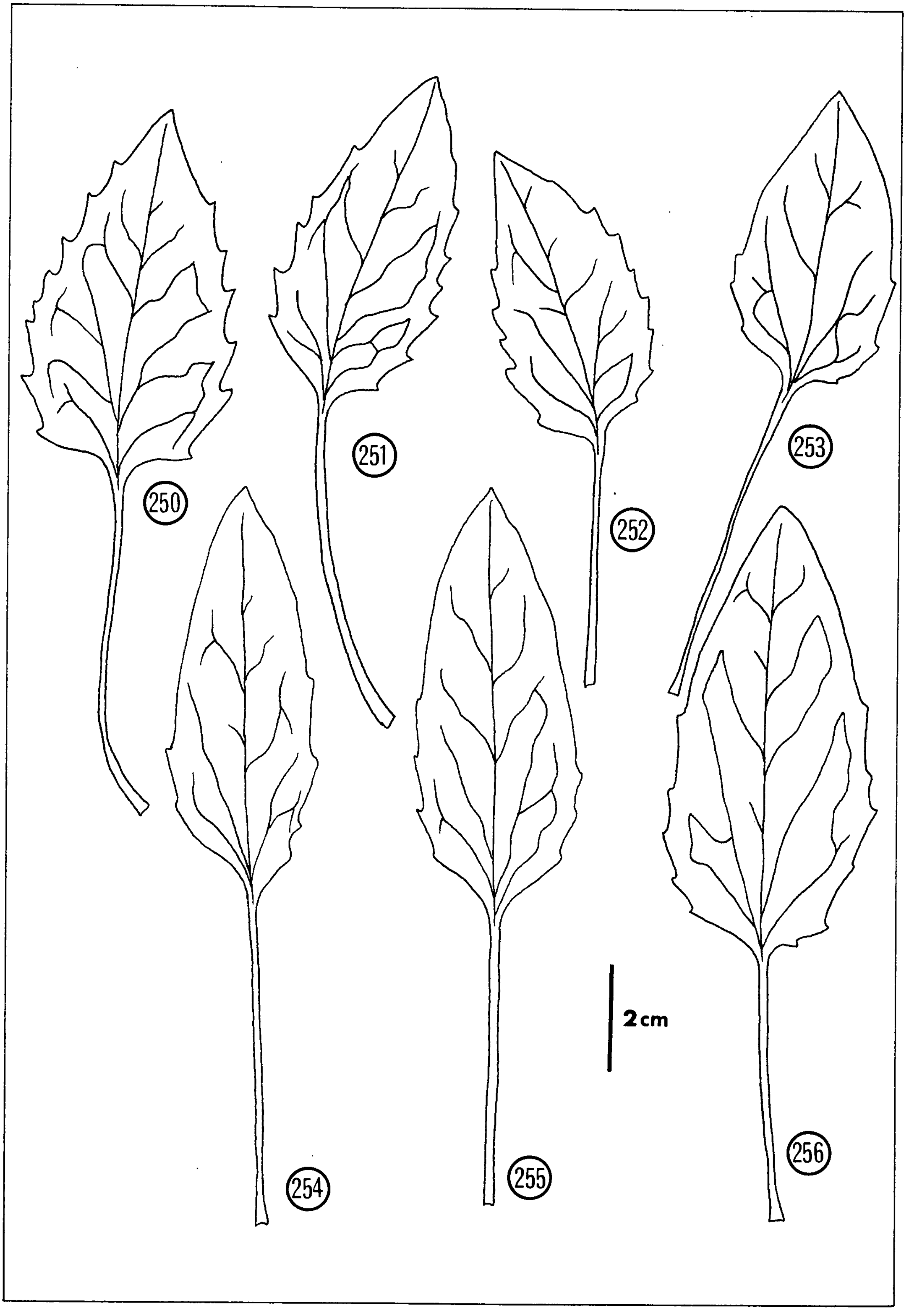
Figures 250-259. Variation in basal leaves from single population of *Arnica cordifolia* S-1797, CA, Siskiyou Co.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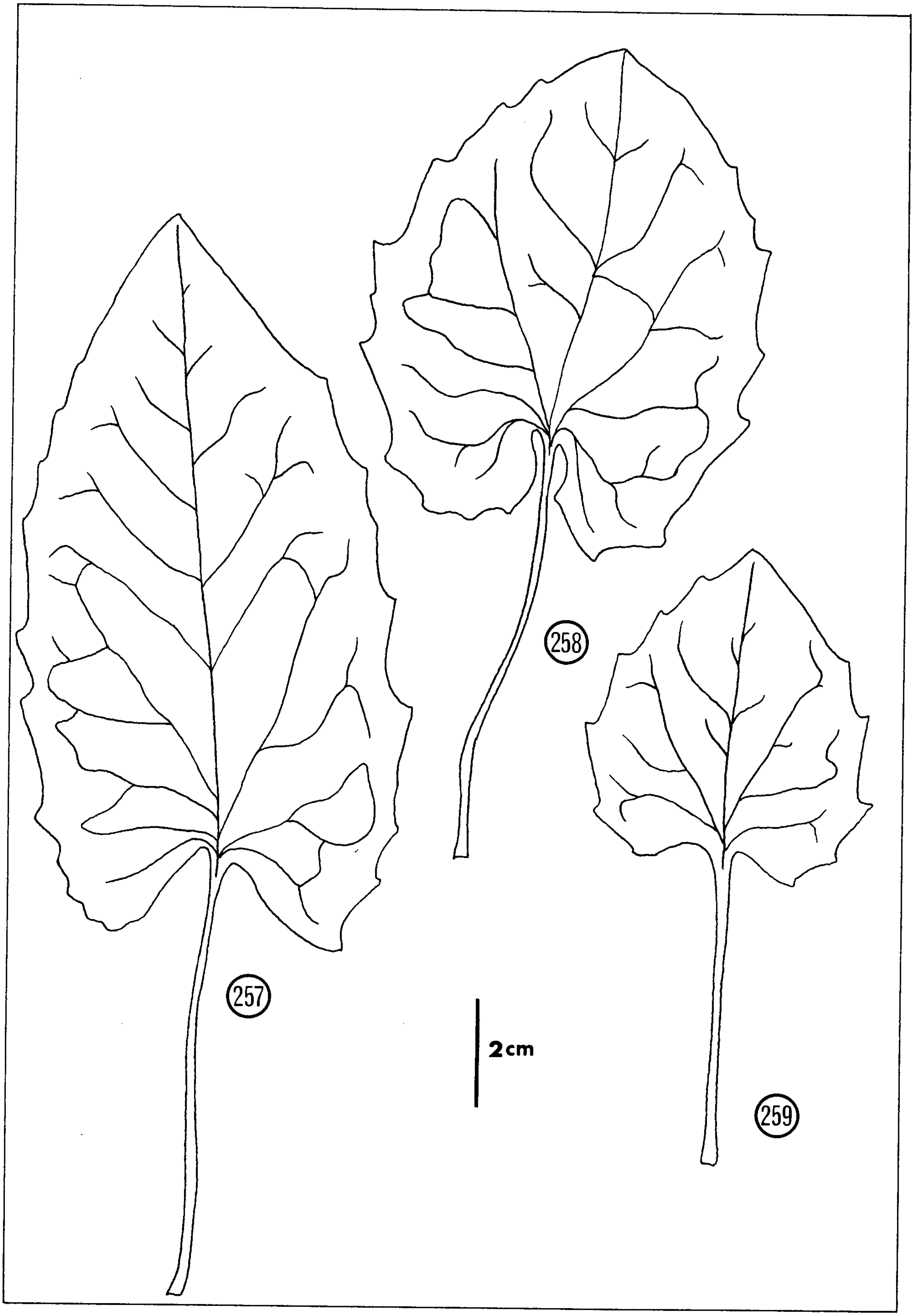
255
256
2 cm

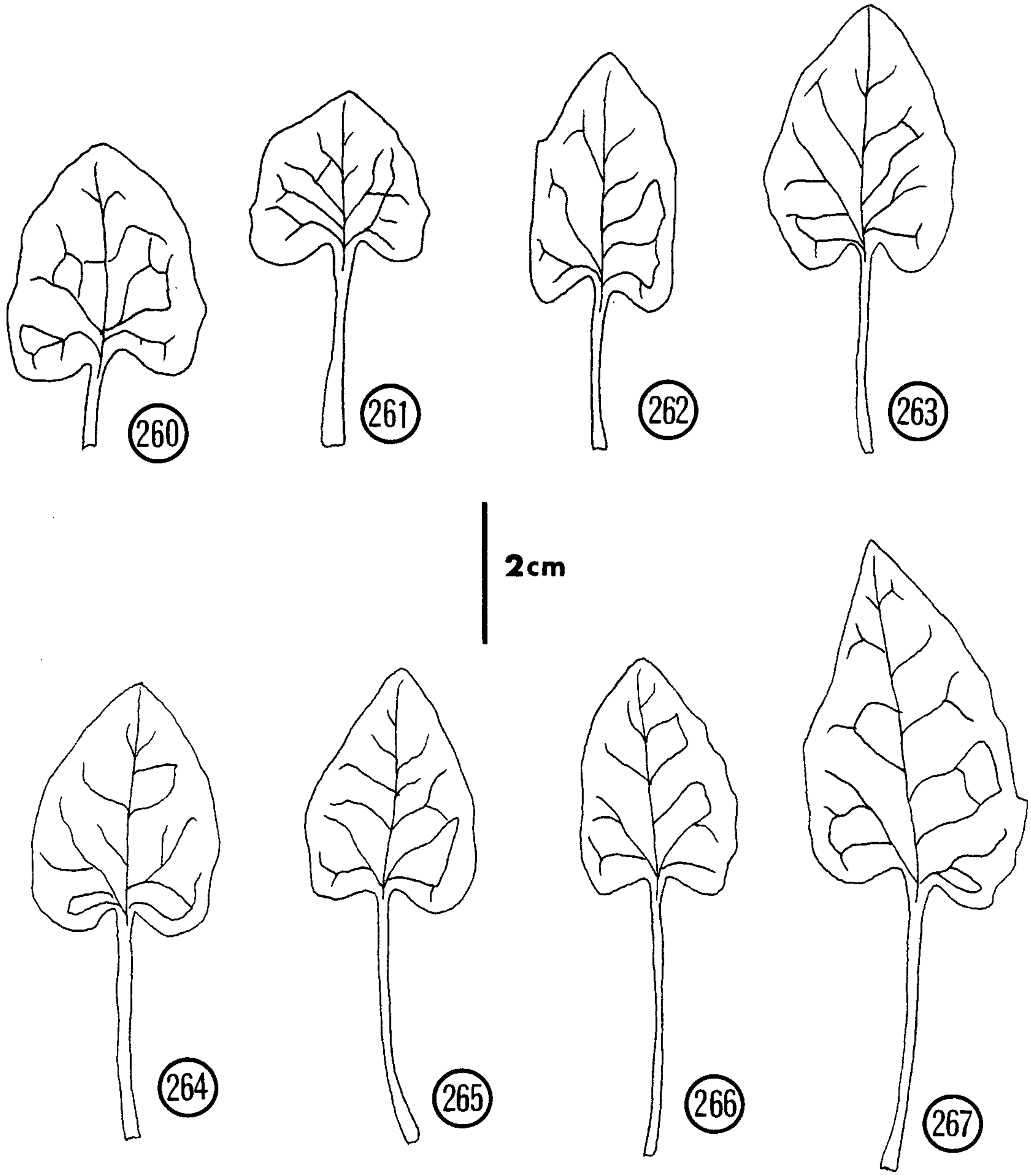

257
258
259
2cm

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.

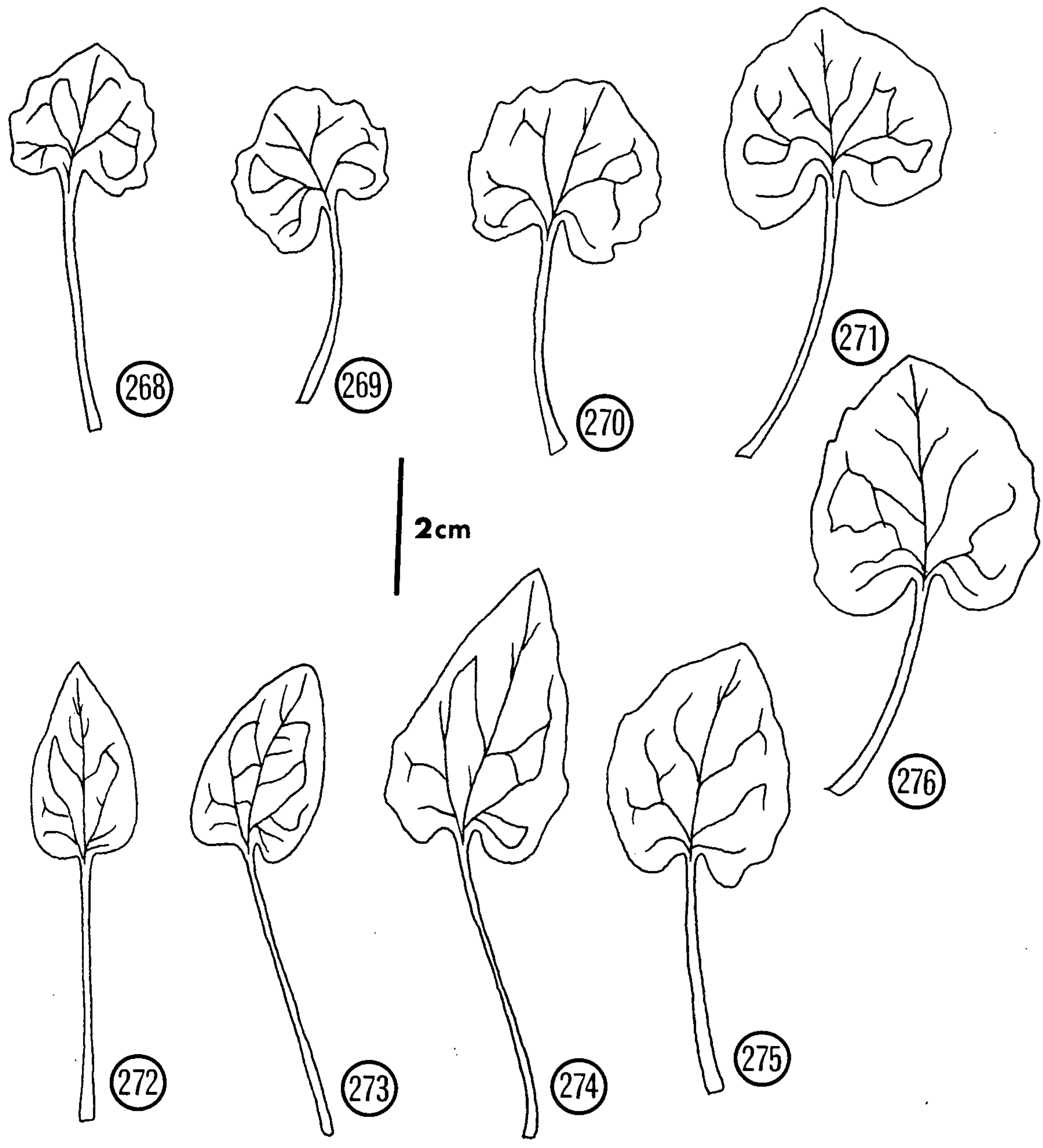
Larger, more typical Arnica cordifolia is separable from typical Arnica nevadensis in the generally narrower, paler rays, more densely pilose stems and leaves, more toothed margins, whiter, shorter lateral setae of the pappus, and more densely hirsute achenes of the former. There are some populations 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, Monó 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.


260
261
262
263
2cm
264
265
266
267

Figures 268-276. Variation in basal leaves from population on disturbed roadside bank of *Arnica cordifolia* S-1820, OR, Wasco Co.


268
269
270
271
2cm
272
273
274
275
276

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*.

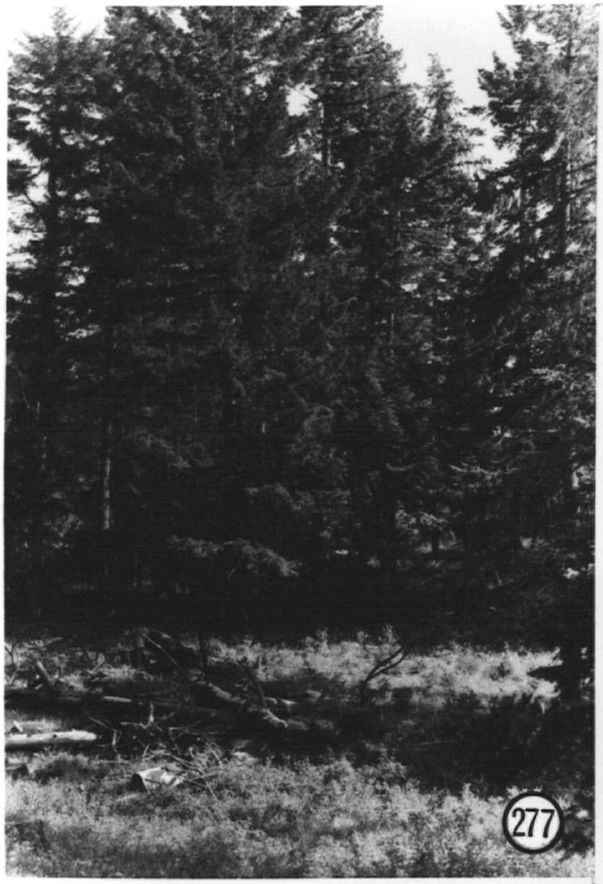
Figure 277. Habitat of *Arnica cordifolia*, WA, Klickitat Co., Appleton, (S-1823), open forest of *Pseudotsuga menziesii* and *Pinus ponderosa*.

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).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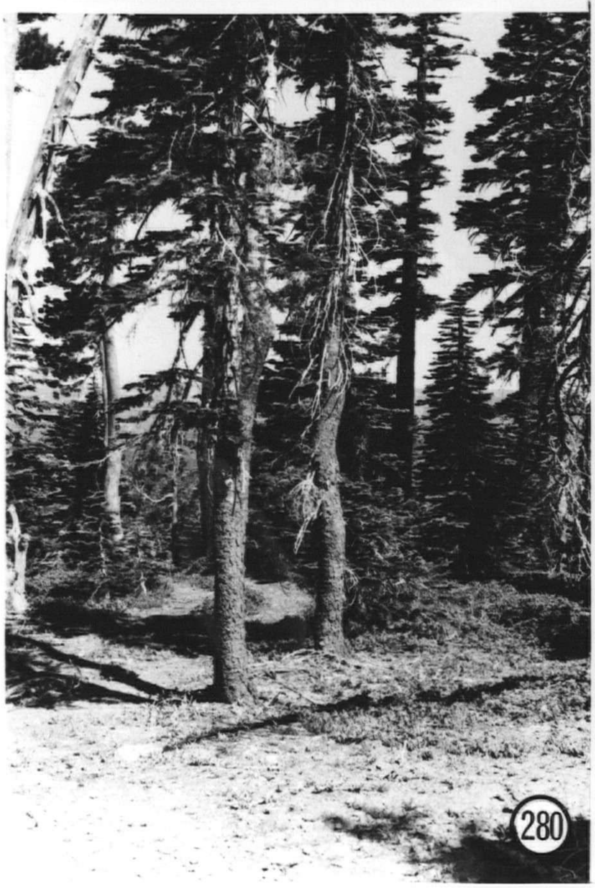

280

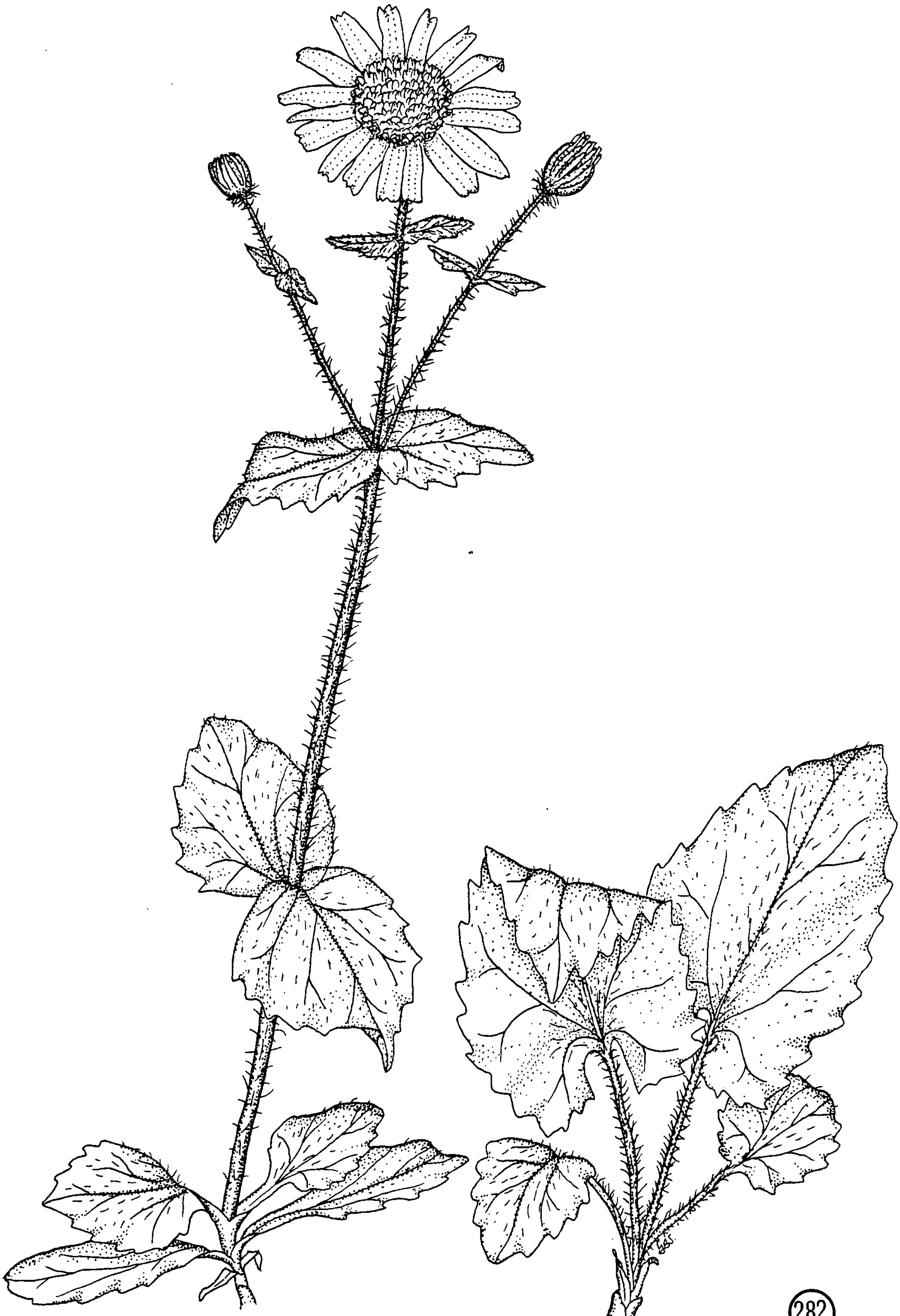

281

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.



282

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.

2. *Arnica nevadensis* A. Gray. Proc. Am. Acad. 19:55. 1883.
Arnica chionophila Greene. Pittonia 4:171. 1900. TYPE: Nevada, Ruby Mts., July 20, 1896, *E.L. Greene* (ND?) (not seen).

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 $\pm$ 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; involucral 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*.

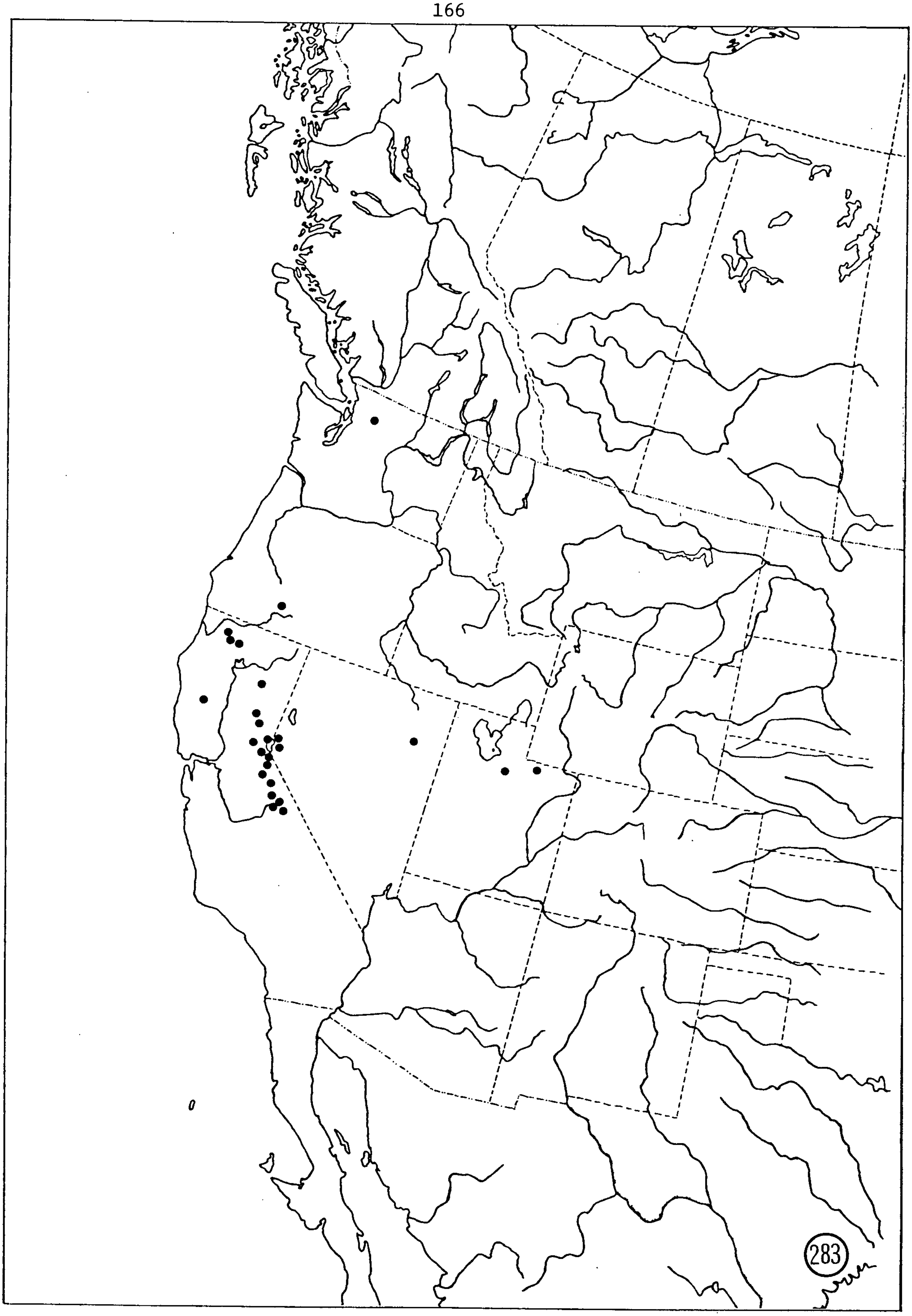
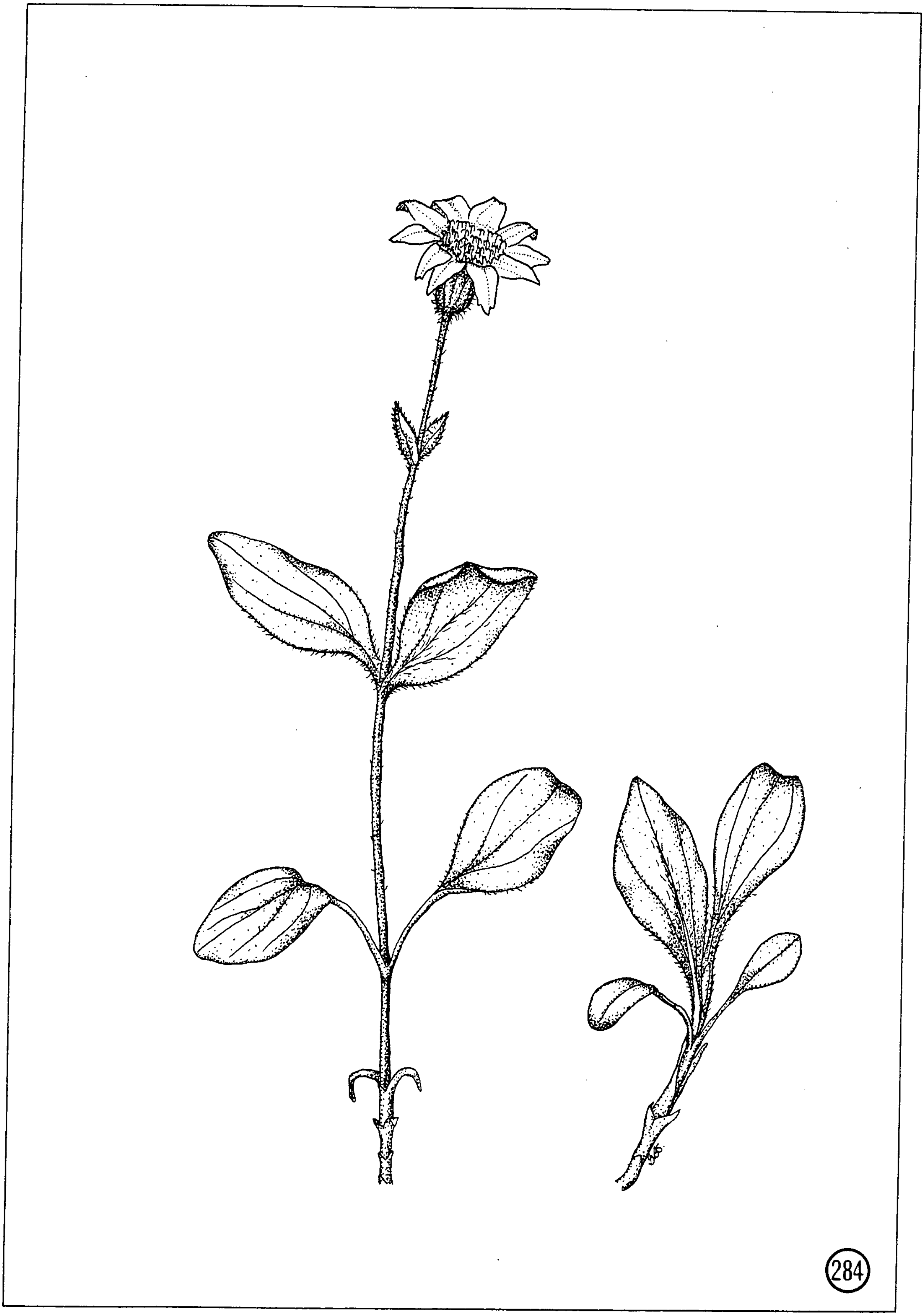

283

Figure 284. Arnica nevadensis S-1910, NV, Washoe Co. X two-thirds.


284

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 pubsecence 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.

3. _Arnica latifolia_ Bongard. Mem. Acad. St. Petersb. VI. 2:147. 1832.

Arnica latifolia α _genuina_ Herder. Bull. Soc. Nat. Mosc. 40:424. 1867.

Arnica latifolia β _angustifolia_ Herder. Bull. Soc. Nat. Mosc. 40:424. 1867.

Arnica latifolia A. Gray. Syn. Fl. N. Am. 1:381. 1884.

Arnica menziesii Hooker. Fl. Bor. Am. 1:331. 1834. TYPE: North West Coast of America, _A. Menzies_, _s.n._ (KEW).

Arnica betonicaefolia Greene. Pittonia 4:163. 1900. TYPE: Washington, Olympic Mountains, Mt. Steele, 1800 m, August 1895, _C.V. Piper 2002_ (ND).

Arnica teucriifolia Greene. Pittonia 4:164. 1900. TYPE: Idaho, Coeur d'Alene Mountains, divide between St. Joe and Clearwater Rivers, 1820 m, grassy mountain slopes, July 10, 1895, _J.B. Leiberg 1229_ (holotype, US; isotypes, MO, POM).

Arnica latifolia Bong. var. _teucriifolia_ (Greene) L. Williams. Leafl. West. Bot. 1:171. 1935.

Arnica ventorum Greene. Pittonia 4:173. 1900. TYPE: Wyoming, Wind River Mountains, Union Pass, August 11, 1894, _A. Nelson 836_ (holotype, ND; isotypes, MO, WS).

Arnica grandifolia Greene. Pittonia 4:173. 1900. TYPE: Montana, Bridger Mountains, July 28, 1896, _J.H. Floodman 896_ (holotype, ND; isotype, MO).

Arnica platyphylla A. Nelson. Bot. Gaz. 31:407. 1901. TYPE: Oregon, Cascade Mountains, Hood River, fir forests, July 18, 1896, _L.F. Henderson_, _s.n._ (RM).

Arnica laevigata Greene. Ottawa Nat. 15:279. 1902. TYPE: British Columbia, Chilliwack Valley, 900 m, by springs in woods, August 15, 1901, *J.M. Macoun, Geol. Surv. Can. 26926* (ND).

Arnica aprica Greene. Ottawa Nat. 15:279. 1902. TYPE: British Columbia, Chilliwack Valley, 1050 m, open ground along streamlets, July 10, 1901, *J.M. Macoun, Geol. Surv. Can. 26284* (holotype, ND; isotype, MO).

Arnica jonesii Rydb. Fl. Rocky Mts. 978. 1917. TYPE: Utah, Alta, Wasatch Mountains, 2700 m, July 31, 1879, *M.E. Jones 119* (holotype, NY; isotypes, POM, UTC).

Arnica puberula Rydb. Fl. Rocky Mts. 979. 1917. TYPE: Alberta, head of Lake Louise, July 22, 1904, *J.M. Macoun, Geol. Surv. Can. 65523* (NY).

Arnica eriopoda Gandoger. Bull. Soc. Bot. France 6538. 1918. TYPE: Oregon, Cascade Mountains, July 27, 1902, *W.C. Cusick 2914*, (holotype, US; isotypes, POM, MO).

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

Arnica flodmanii Rydb. N.Am. Fl. 34:334. 1927. TYPE: Montana, Madison Range, Spanish Peaks, 2100-2400 m, July 14, 1896, *J.H. Flodman 898*, (holotype, NY; isotype, MO).

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

Arnica oligolepis Rydb. N. Am. Fl. 34:336. 1927. TYPE: British Columbia, Skeena River, Hazelton, June 23, 1917, *J.M. Macoun, Geol. Surv. Can. 96048* (NY).

Arnica leptocaulis Rydb. N. Am. Fl. 34:336. 1927. TYPE: British Columbia, Vancouver Island, Mt. Mark, July 25, 1887, *J.M. Macoun, Geol. Surv. Can. 14570* (NY).

Arnica membranacea Rydb. N. Am. Fl. 34:338. 1927. TYPE: Oregon, Jackson Co., Wimmer, June 13, 1892, E.W. Hammond 231, (NY).

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), $\pm$ 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; 2*n*=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.

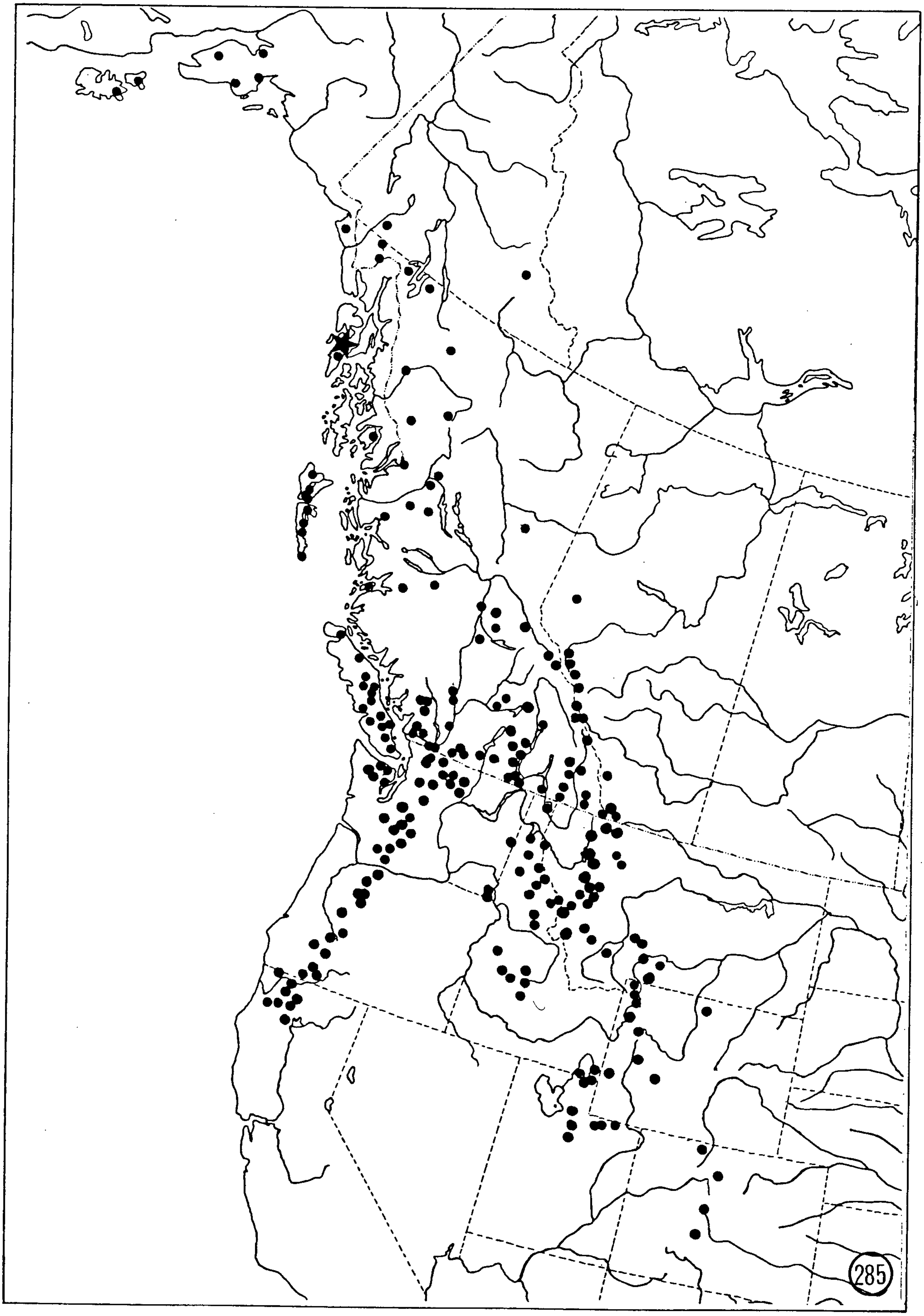
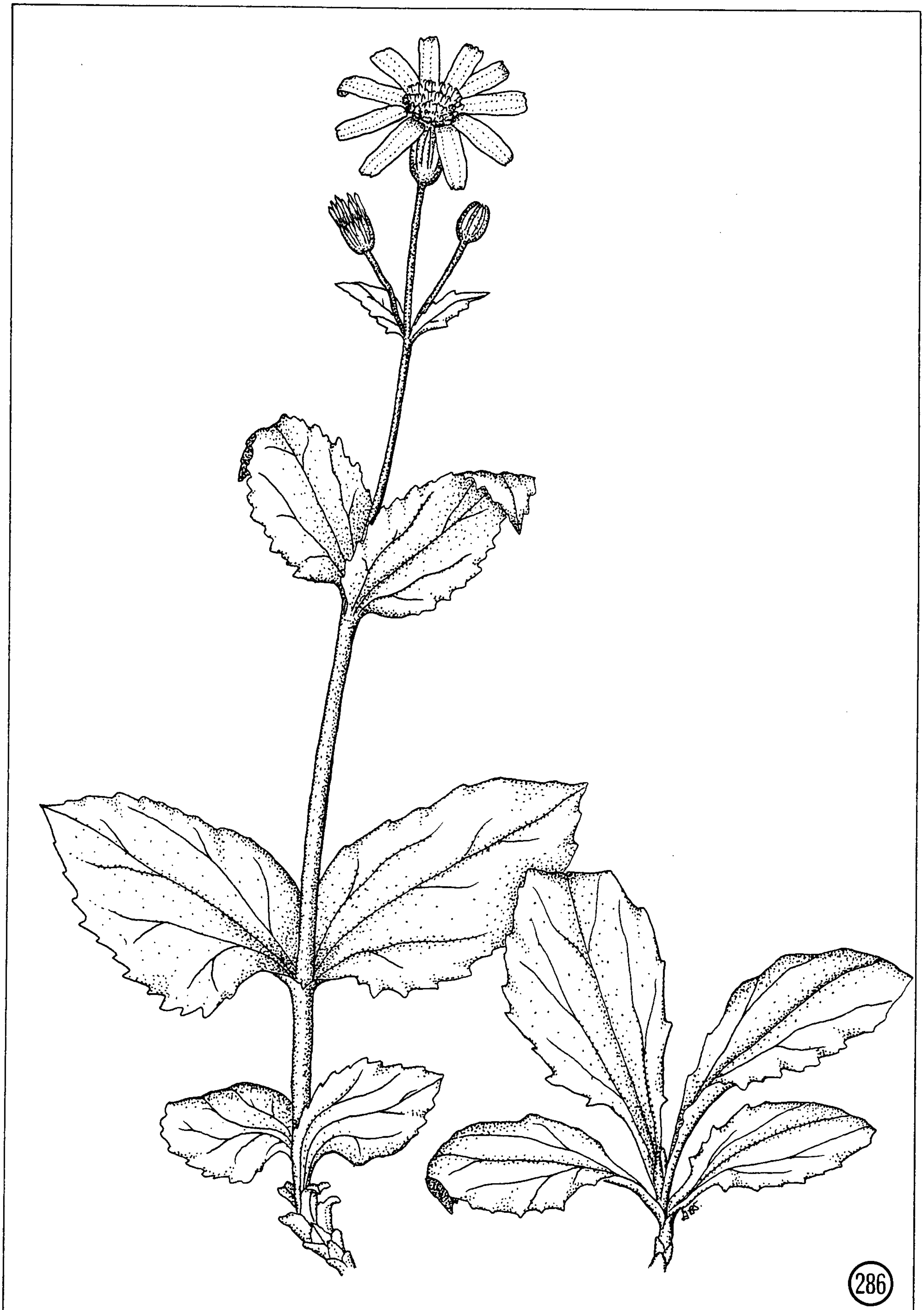

285

Figure 286. Arnica latifolia S-1500, WA, Chelan Co. X two-thirds.

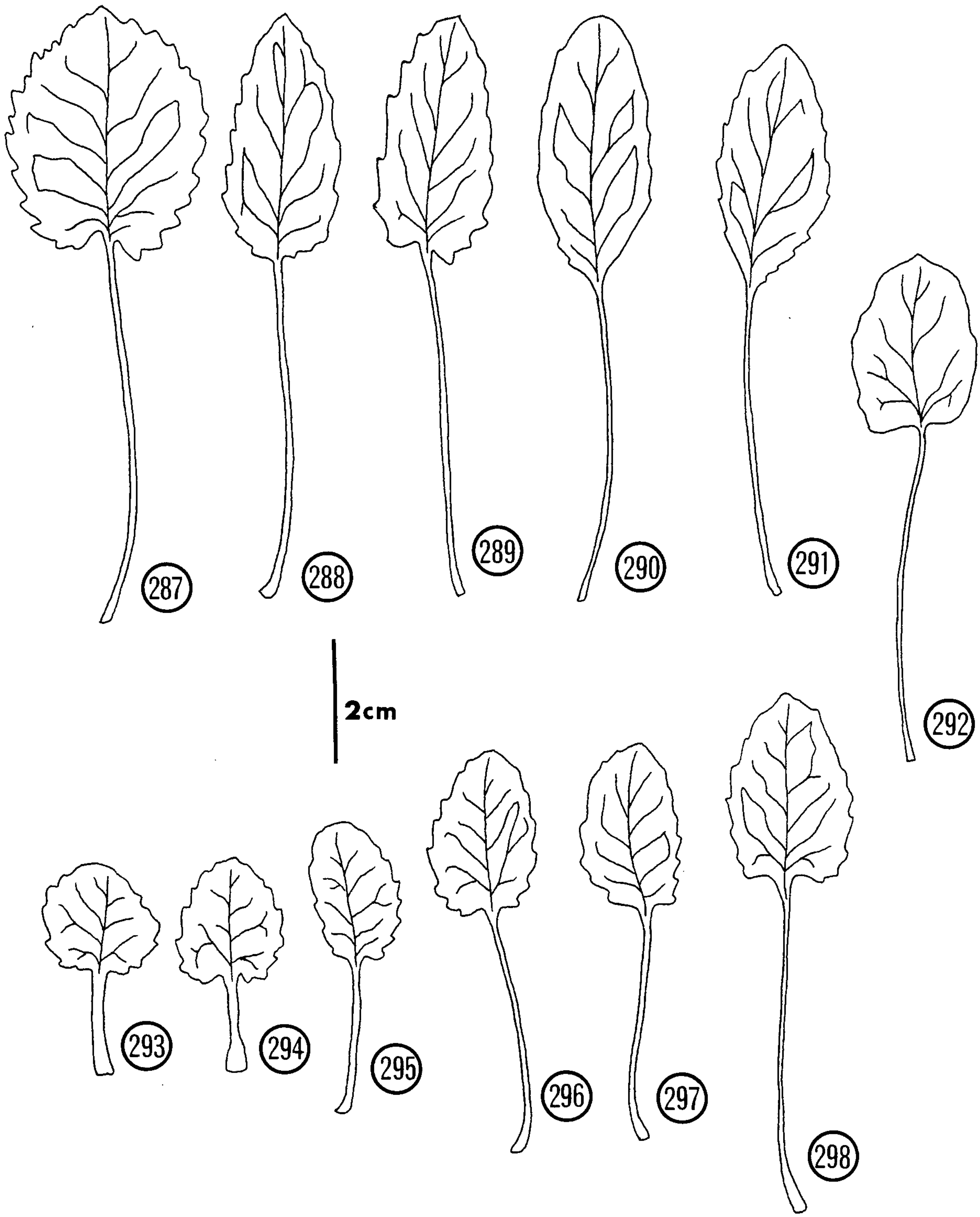

286

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 betonicaefolia 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.


287
288
289
290
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292
2cm
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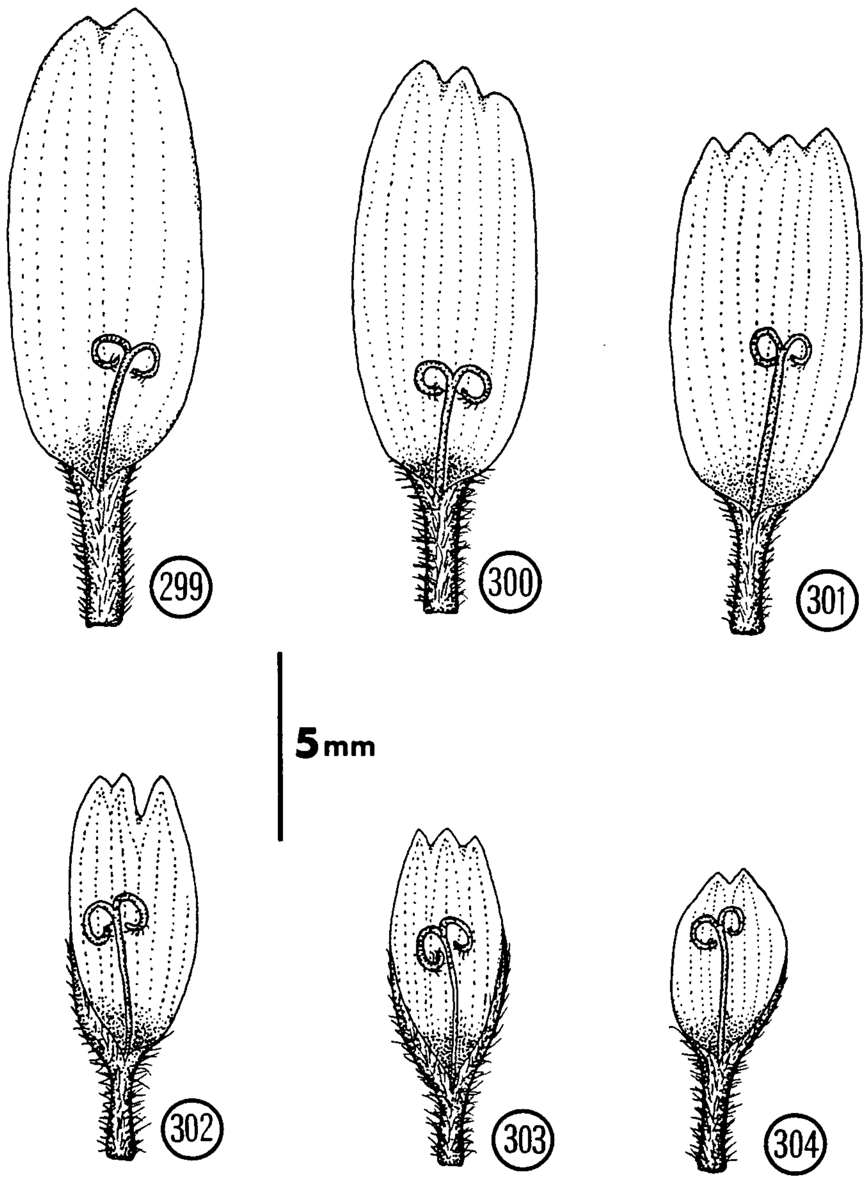
Figures 299-304. Variation in shortened ray florets from several heads on one plant of <u>Arnica latifolia S-1961</u>, BC, Nancy Greene Prov. Park.


299
300
301
5mm
302
303
304

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.

4. Arnica gracilis Rydberg, Bull. Torr. Bot. Club 24:297. 1897.

Arnica betonicaefolia var. gracilis (Rydb.) M.E. Jones, Bull. Univ. Mont. Biol. 15:45. 1910.

Arnica latifolia Bong. var. gracilis (Rydb.) Cronq. Vasc. Pl. Pac. NW. 5:51. 1955.

Arnica columbiana A. Nels., Bot. Gaz. 30:200. 1900. TYPE: Montana, Columbia Falls, R.S. Williams 1049 (RM).

Arnica multiflora Greene. Pittonia 4:162. 1900. TYPE: Idaho, Lake Pend Orielle, Leiberg 234 (holotype, ND; paratypes, MONTU, NY, WS).

Arnica ovalifolia Greene. Pittonia 4:168. 1900. TYPE: Wyoming, Big Horn Mountains, Blankinship, s.n. (ND).

Arnica arcana A. Nels., Bot. Gaz. 37:276. 1904. TYPE: Wyoming, Big Horn Mountains, Doyle Creek, N.L. Gooding 377 (holotype, RM; isotype, MO).

Arnica lactucina Greene, Ottawa Nat. 33:215. 1910. TYPE: Alberta, Banff, W.C. McCalla 2014 (ND).

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; periclinum densely short and longer stipitate glandular; heads (1-)3-11, radiate, 10-15 mm high; involucral bracts 6-14, $\pm$ 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.

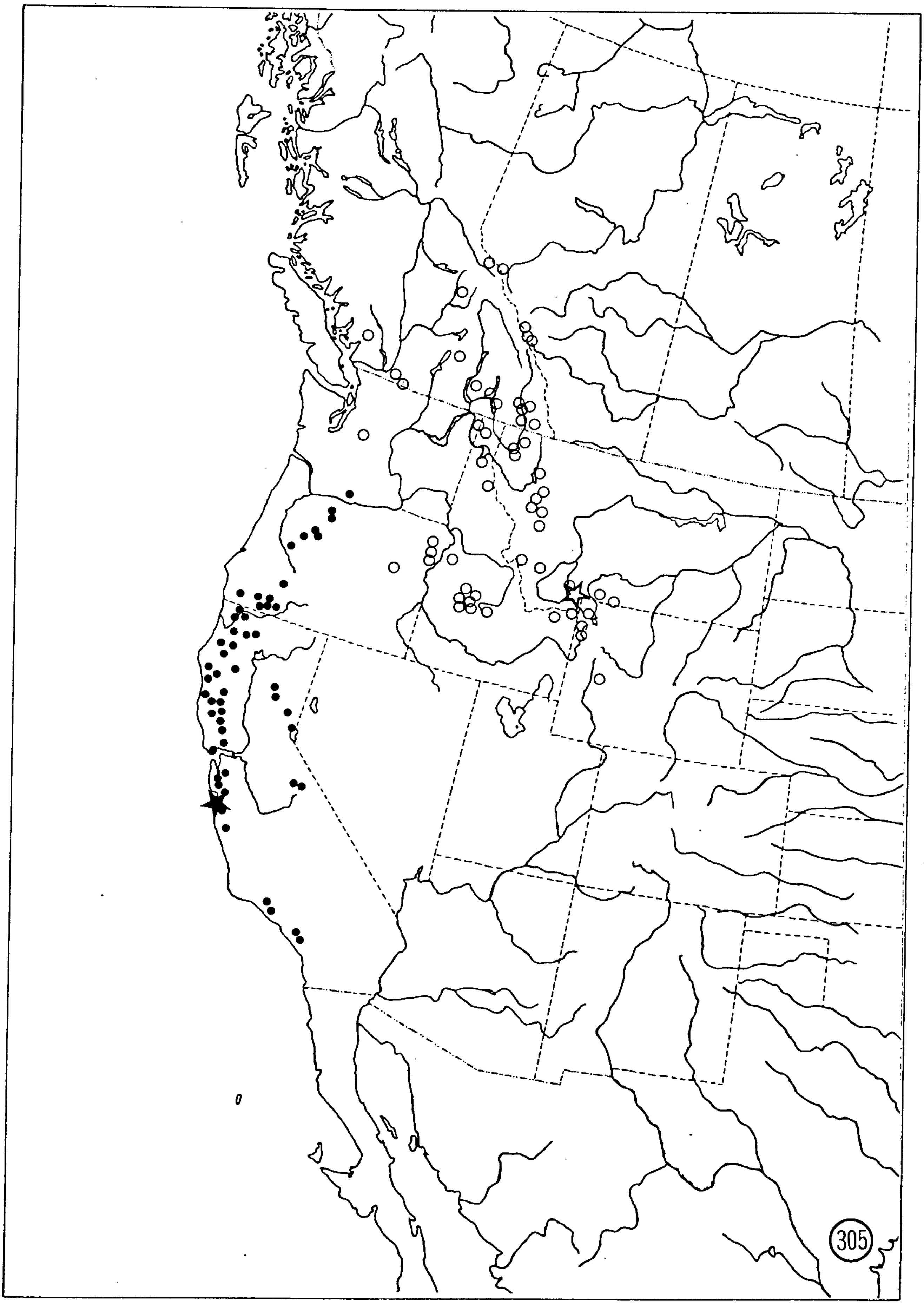

305

Figure 306. Arnica gracilis S-1605. AB, Moraine Lake. X two-thirds.

306

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.

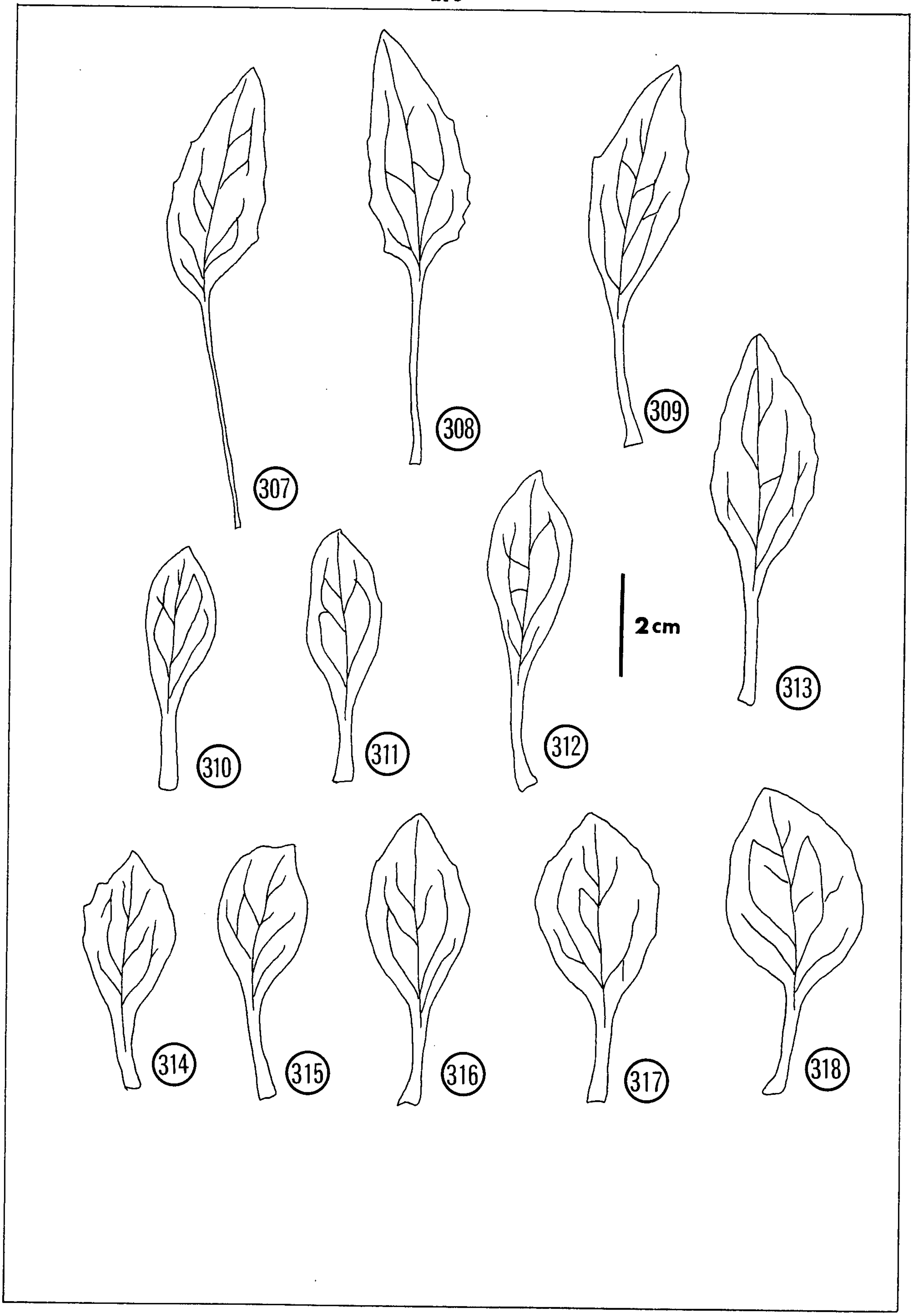
Artificial crosses between Arnica latifolia and Arnica mollis or Arnica diversifolia have been mostly unsuccessful. Arnica mollis has grown very poorly in cultivation and a few crosses between it as the male parent and Arnica latifolia as the female parent have produced no achenes. Arnica diversifolia 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.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2 cm
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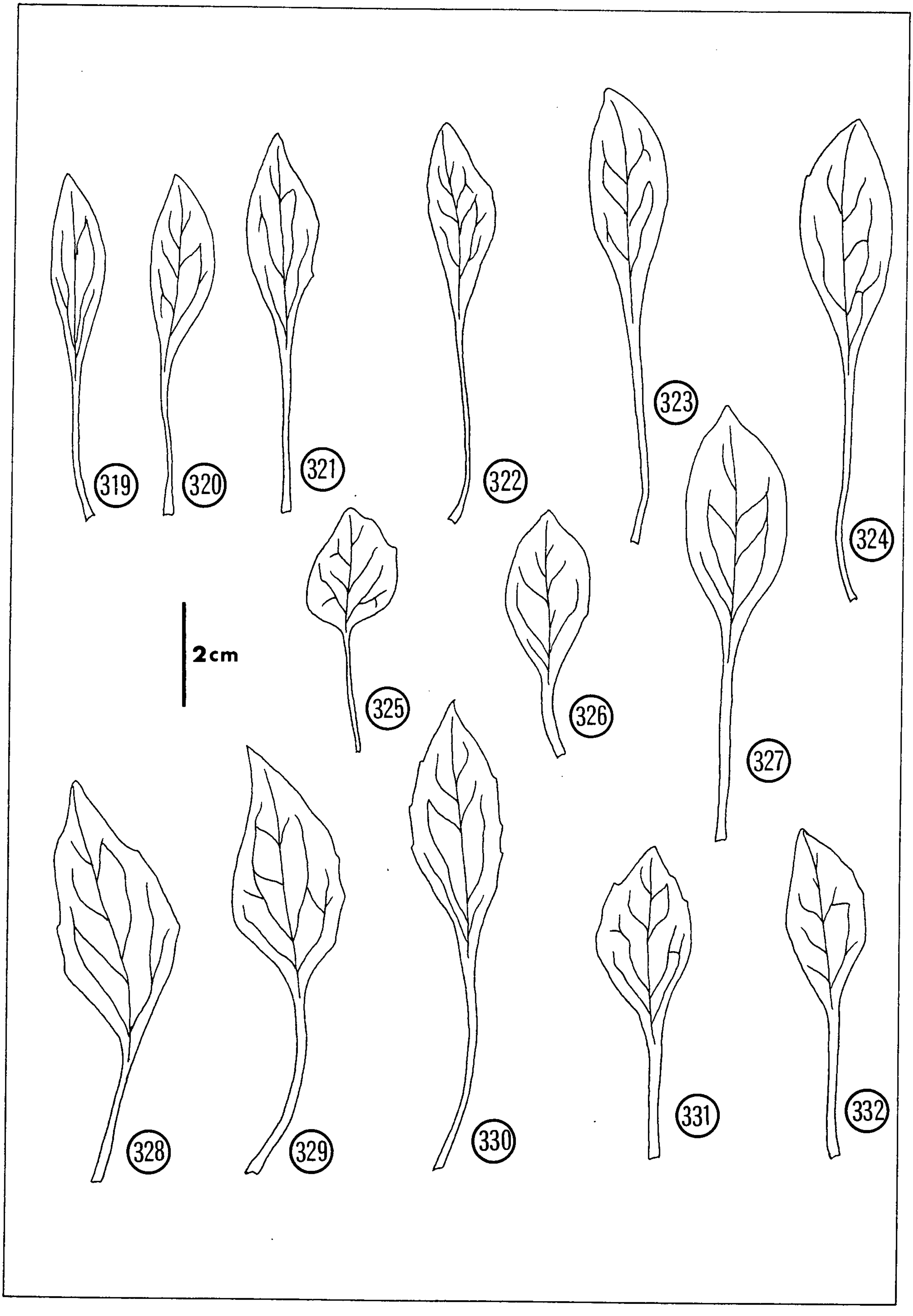
Figures 319-332. Variation in basal leaves of a single population of lower-elevation *Arnica gracilis* *S-1562*, BC, Monroe Lake.



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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), $\pm$ 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, 2*n*=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.

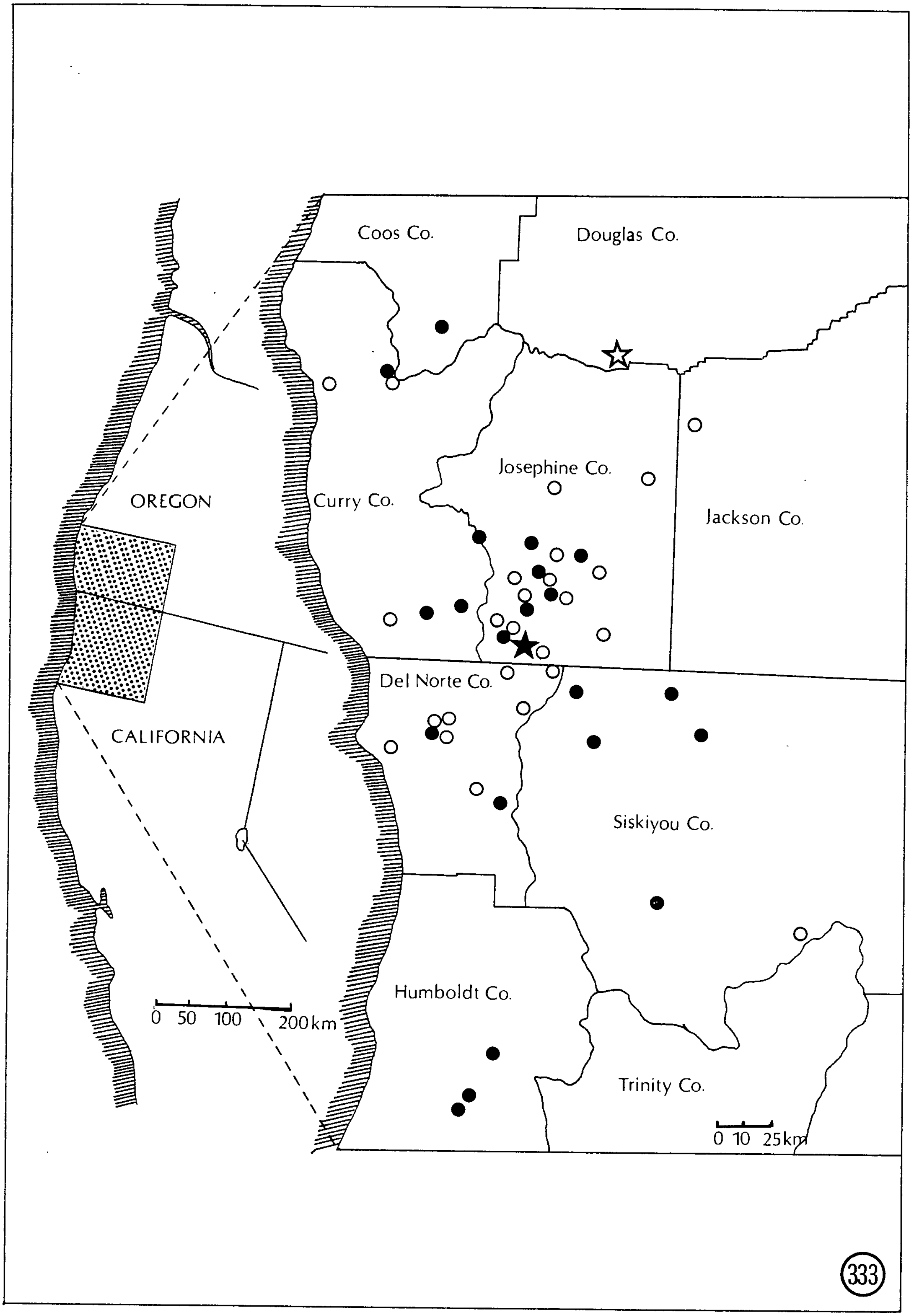

Coos Co.
Douglas Co.
Josephine Co.
OREGON
Curry Co.
Jackson Co.
Del Norte Co.
CALIFORNIA
Siskiyou Co.
0 50 100 200km
Humboldt Co.
Trinity Co.
0 10 25km
333

Figure 334. Habit of Arnica cernua S-1386. OR, Josephine Co.

X two-thirds.

334

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

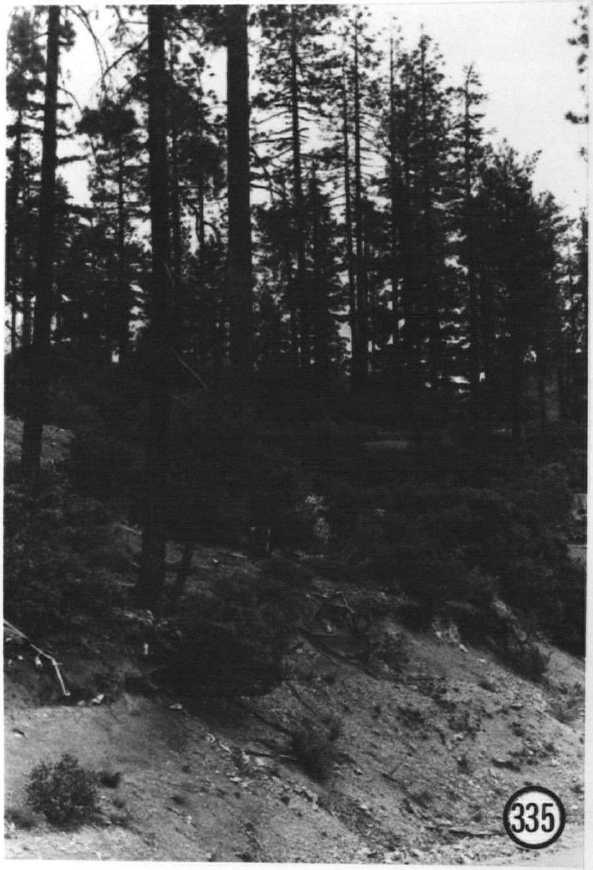
Figures 335-338. Habitat and habit of Arnica cernua.

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.



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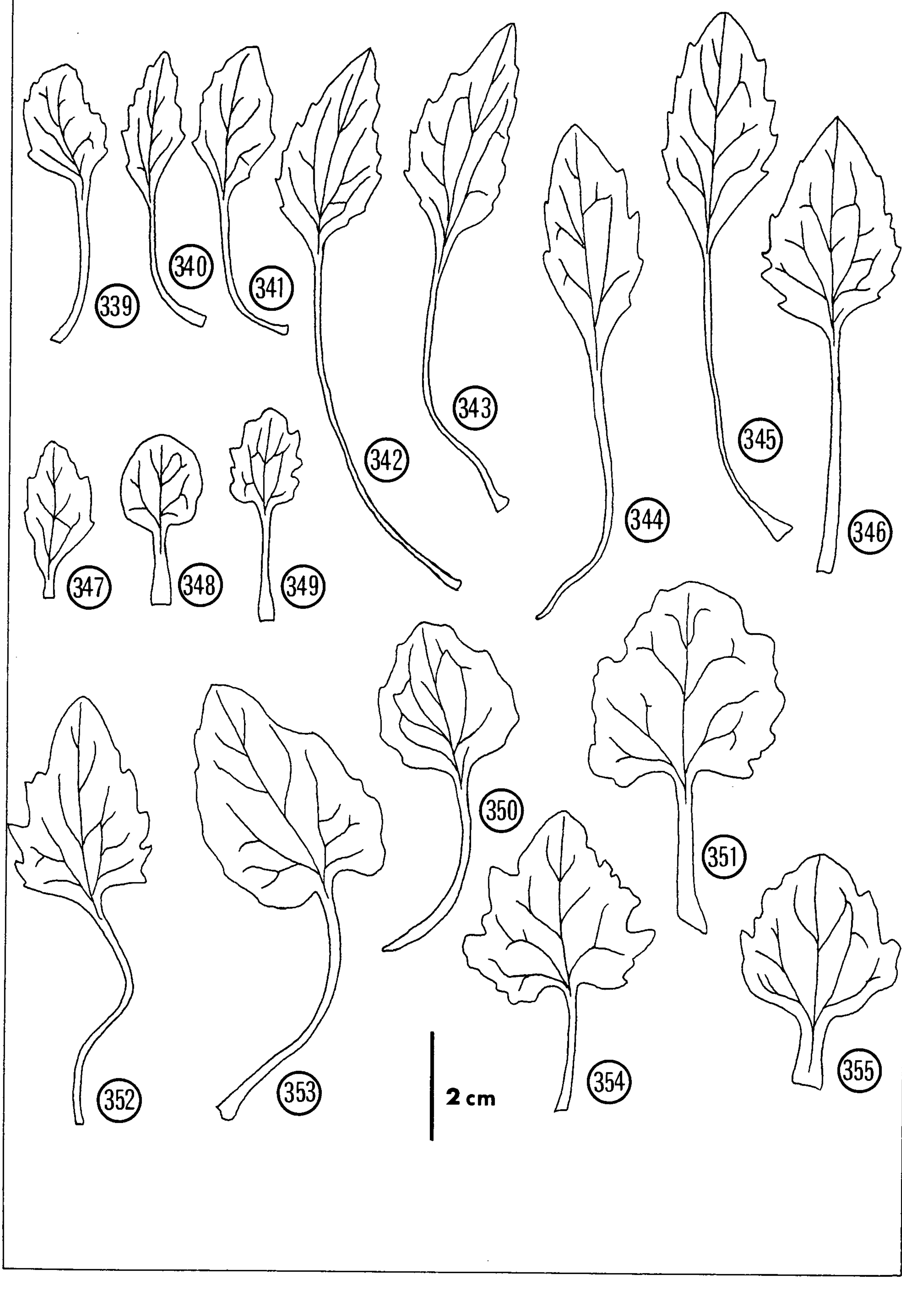
Figures 339-355. Variation in basal rosette leaves of _Arnica cernua_ _S-1772_, CA, Humboldt Co., small ecotype.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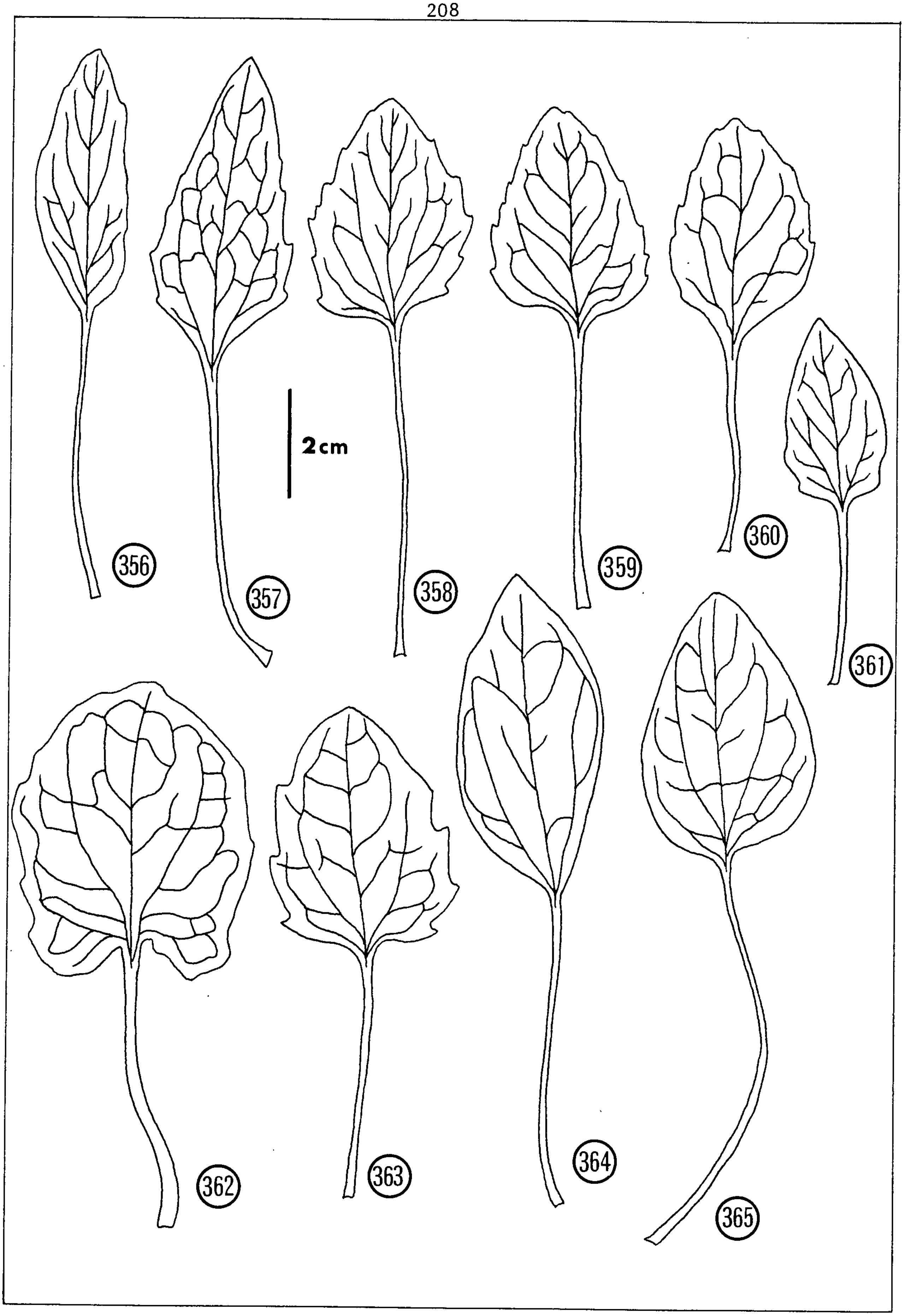
2 cm

Figures 356-365. Variation in basal rosette leaves of _Arnica cernua_ _S-1743_, OR, Josephine Co., large ecotype, from plants growing in full sun.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2cm
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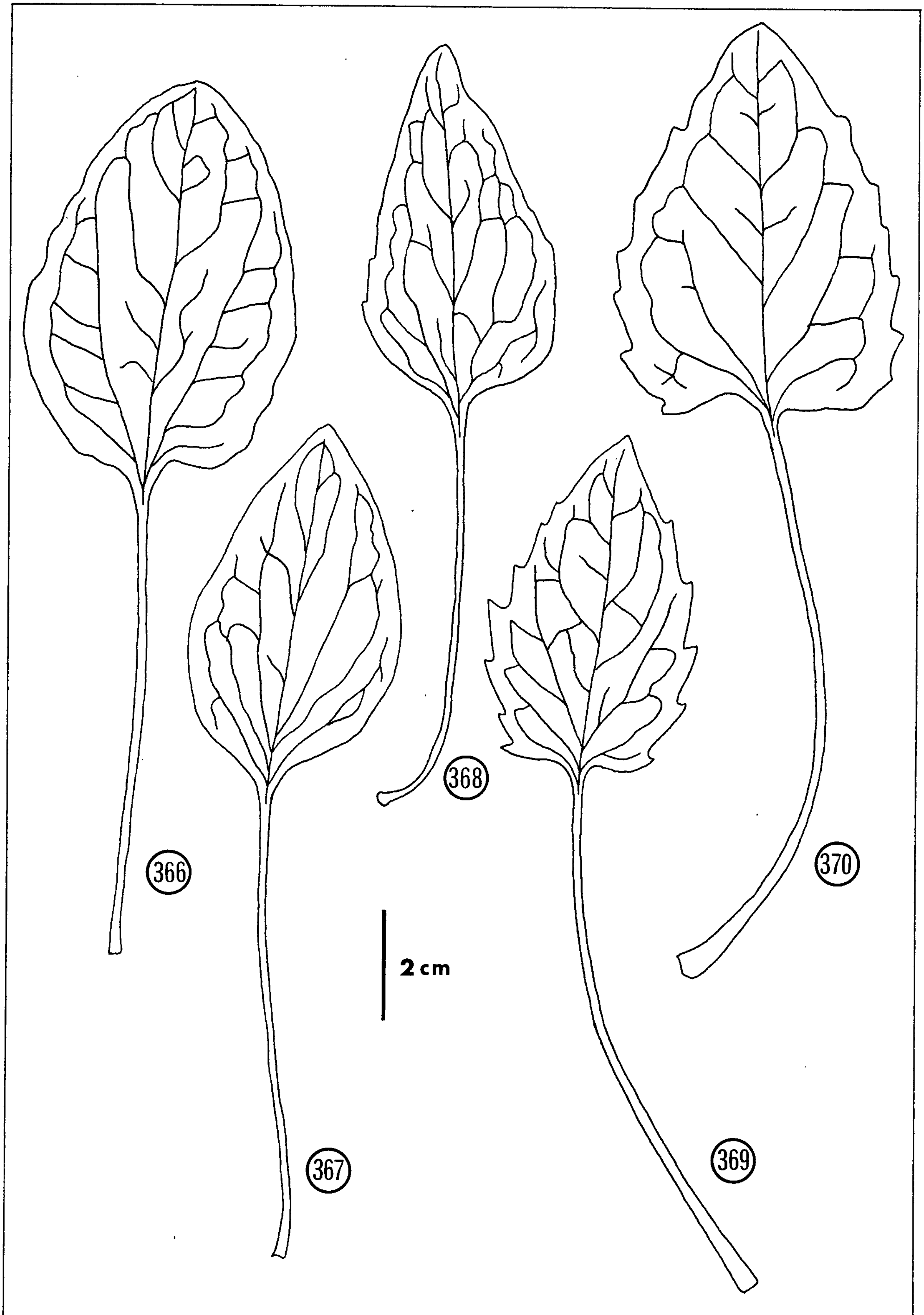
Figures 366-370. Variation in basal rosette leaves of Arnica cernua S-1743, OR, Josephine Co., large ecotype, from plants growing in shade.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2 cm

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.

6. *Arnica discoidea* Bentham. PL. Hartw. 319. 1849.

Arnica parviflora A. Gray. Proc. Am. Acad. 7:363. 1867. TYPE: California, Humboldt Co., chapparal, 1867, Geol. Surv. Calif., H.H. Bolander 6051. (holotype, G; isotype, KEW).

Arnica cordifolia Hook. var. *eradiata* A. Gray. Syn. Fl. N. Am. 1:381. 1884. TYPE: Oregon, Hood River, 1884, Barrett, s.n. (G).

Arnica discoidea Bentham var. *eradiata* (A. Gray) Cronquist. Vasc. Pl. Pac. NW. 5:49. 1955.

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

Arnica falconaria Greene. Ottawa Nat. 23:215. 1910. TYPE: Washington, Klickitat Co., Falcon Valley, June 27, 1892. *W. Suksdorf 1617* (ND).

Arnica alata Rydb. N. Am. Fl. 34:342. 1927. TYPE: California, Yosemite, 1865, *J. Torrey 258a* (NY).

Arnica parviflora A. Gray subsp. *alata* (Rydb.) Maguire. Brittonia 4:455. 1943.

Arnica discoidea Bentham var. *alata* (Rydb.) Cronquist. Contr. Dudley Herb. 5:102. 1958.

Arnica sanhedrensis Rydb. N. Am. Fl. 34:342. 1927. TYPE: California, Lake Co., south of Mt. Sanhedrin, July 25, 1902, *Heller 5985* (holotype, NY; isotype, POM).

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 (1-)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, sub-cordate, to rounded, or rarely attenuate, tips acute to rounded, margins subentire to usually regularly serrate, dentate, or crenate, 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 petiolate, 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.

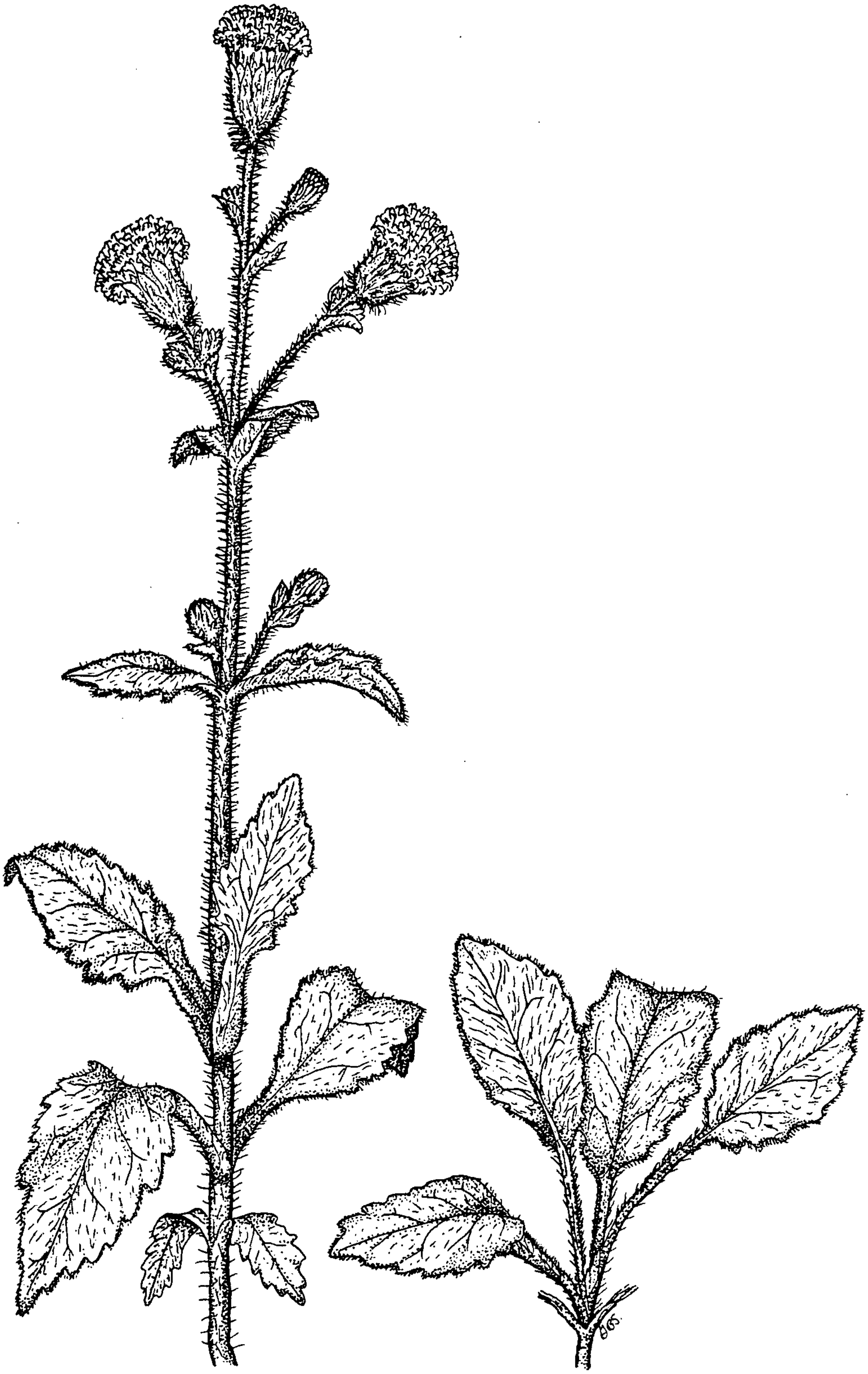
Type: California, Monterey Co., Monterey, in forest, Hartweg 1805 (KEW).

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.



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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 ampliate 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.


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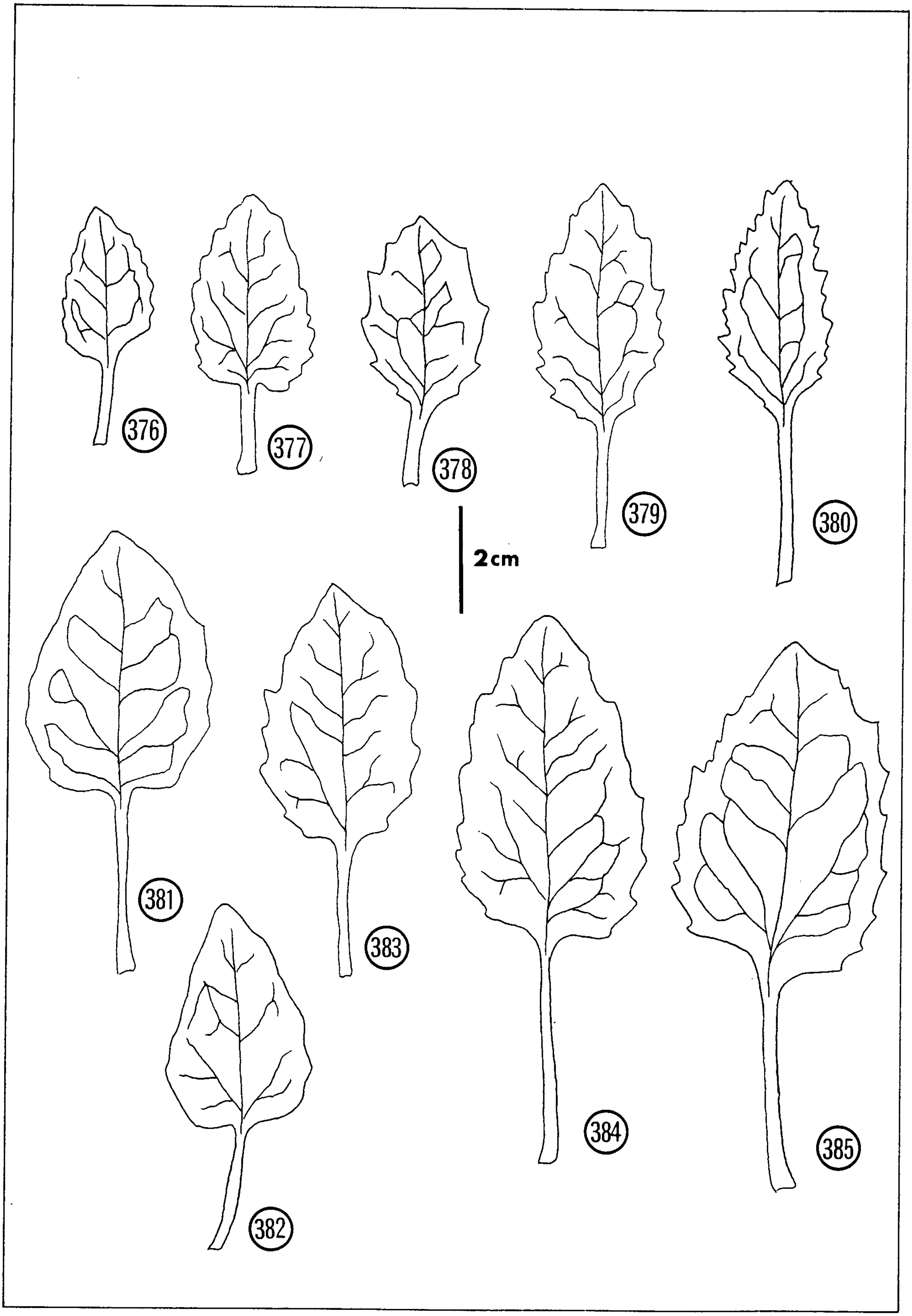
Figures 376-385. Variation in basal leaves of *Arnica discoidea* *S-1789*, CA, Marin County.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Arnica discoidea are discussed under *Arnica spathulata*.

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.

7. *Arnica spathulata* Greene. Pittonia 3:103. 1896.

Arnica eastwoodiae Rydb. N. Am. Fl. 34:343. 1927. TYPE: California, Del Norte Co., Gasquet, French Hill, September 14, 1912, *A. Eastwood 2211* (NY).

Arnica spathulata Greene subsp. *eastwoodiae* (Rydb.) Maguire. Brittonia 4:458. 1943.

Arnica spathulata Greene var. *eastwoodiae* (Rydb.) Ediger & Barkley. N. Am. Fl. II. 10:43. 1978.

Arnica cusickii Rydb. N. Am. Fl. 34:343. 1927. TYPE: Oregon, Cascade Mountains, dry western slope, July 11, 1902, *Cusick 2873* (holotype, NY; isotypes, MO, POM, US).

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, spathulate 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 ampliate 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.

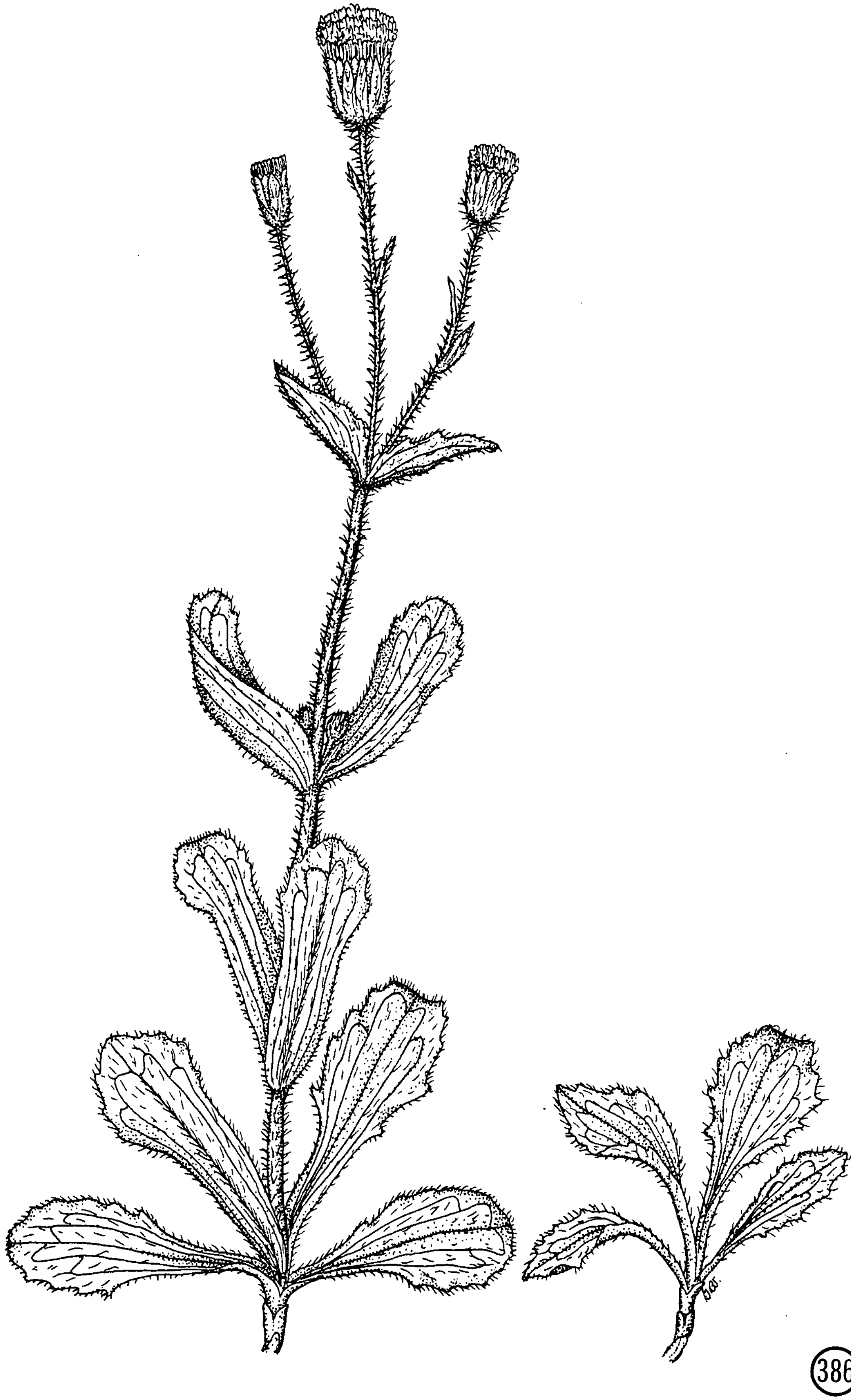
Type: Oregon, Douglas County, Glendale, June 3, 1887, T. Howell 1200 (US).

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.

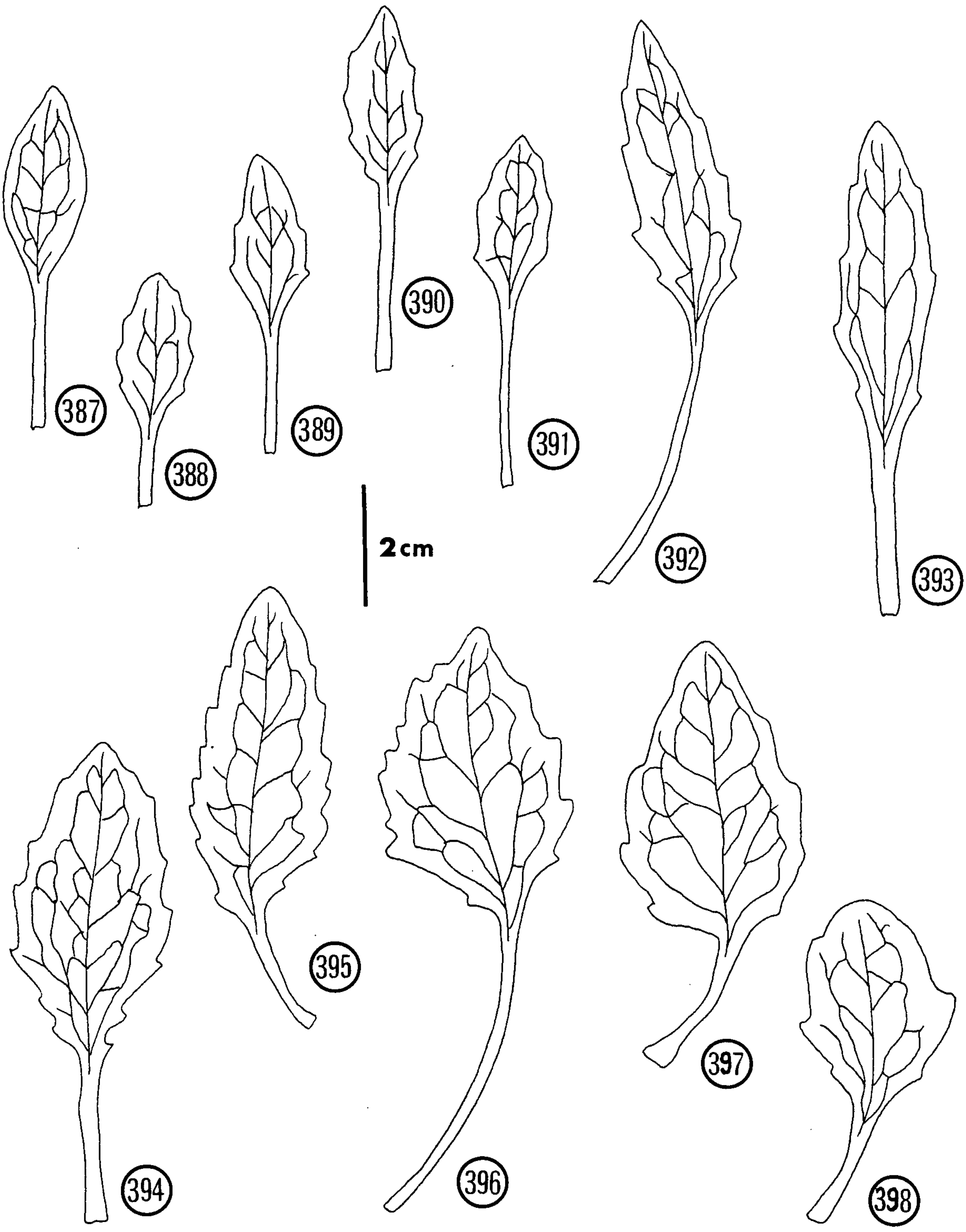
This, the rarest of the species in section Eradiatae is known from about two dozen populations largely restricted to serpentine soils. Where it does occur the populations often consist of several dozen to hundreds of individuals. Populations or individuals are quite variable in size, branching habit, 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.



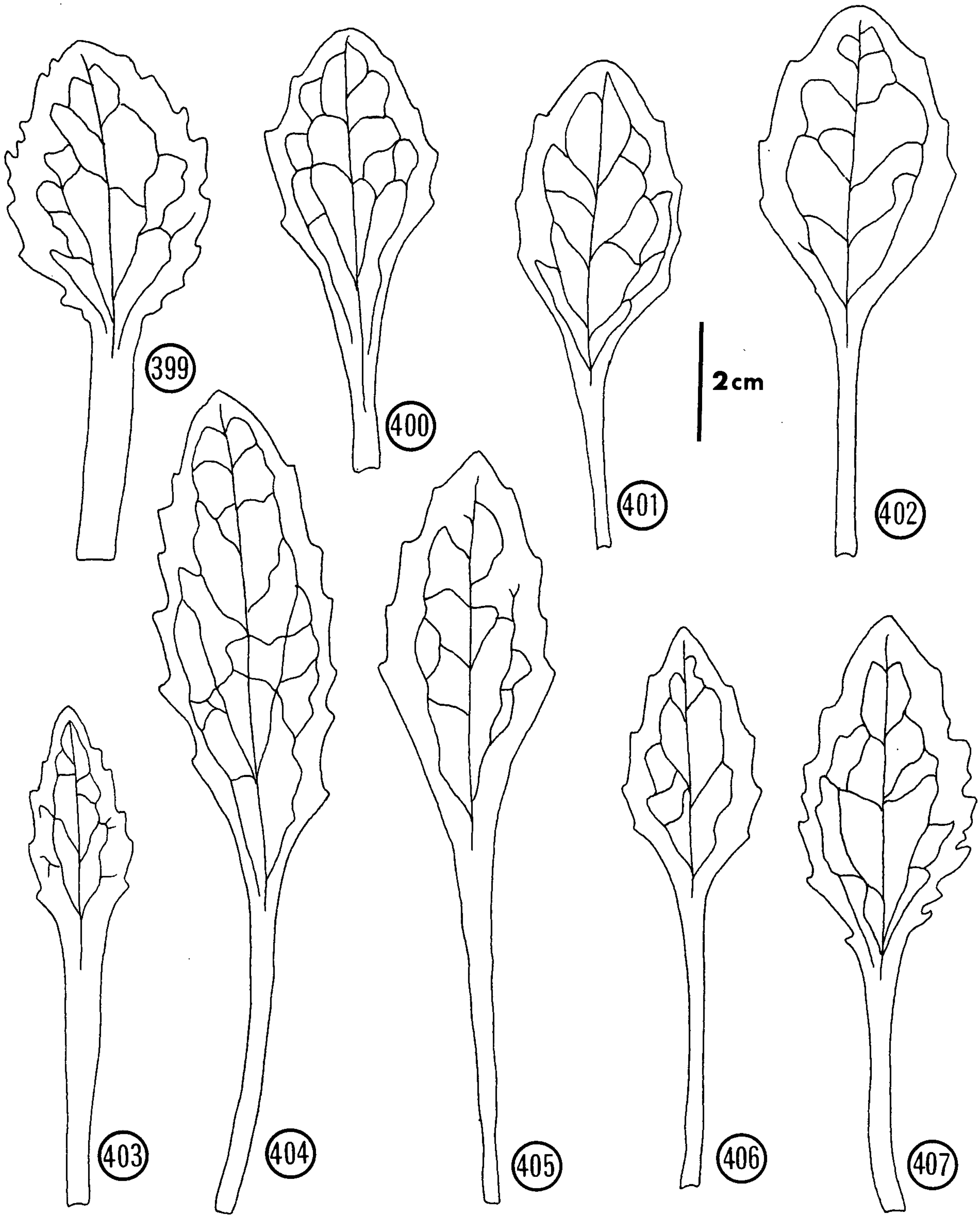
386

Figures 387-398. Variation in basal rosette leaves of *Arnica spathulata* *S-1751*, CA, Del Norte Co., small ecotype.



387
388
389
390
391
392
393
2cm
394
395
396
397
398

Figures 399-407. Variation in basal rosette leaves of *Arnica spathulata* *S-1740*, OR, Josephine Co., large ecotype.


399
400
401
402
2cm
403
404
405
406
407

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

8. *Arnica viscosa* A. Gray. Proc. Am. Acad. 13:374. 1878.

Raillardella paniculata Greene. Erythea 3:48. 1895. TYPE: California, Siskiyou Co., Mt. Shasta, near the limit of trees, August 4, 1894. *W.L. Jepson*, *s.n.* (not seen).

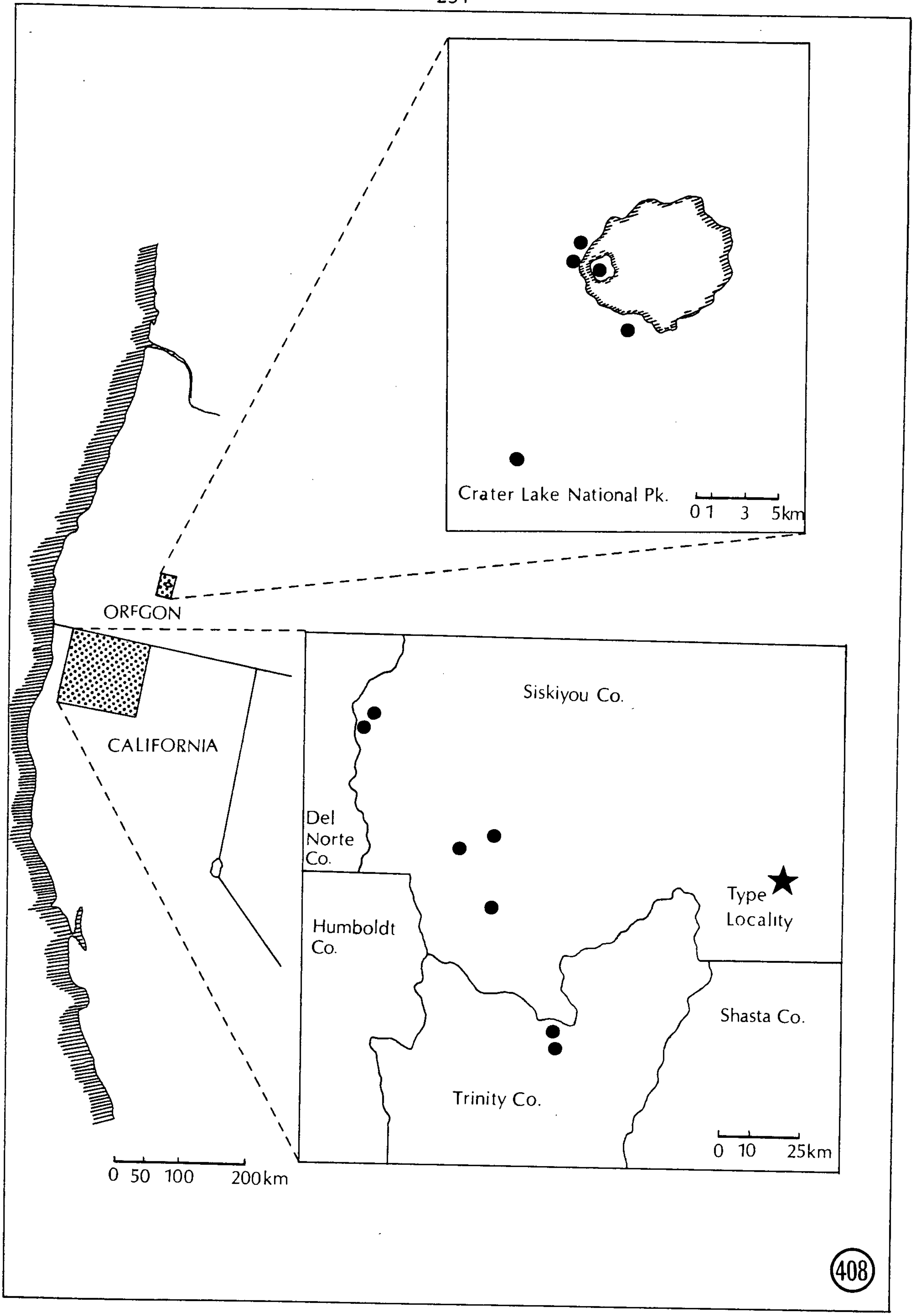
Chrysopsis shastensis Jeps. Man. Fl. Pl. Cal. 1037. 1927. TYPE: California, Siskiyou Co., Mt. Shasta, Horse Camp, 2400 m, *W.L. Jepson 51i* (JEPS).

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; 2*n*=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*.



Crater Lake National Pk.
0 1 3 5km
OREGON
CALIFORNIA
Siskiyou Co.
Del
Norte
Co.
Humboldt
Co.
Type
Locality
Shasta Co.
Trinity Co.
0 10 25km
0 50 100 200km

408

Illustration: Figure 409.

Arnica viscosa is the most distinctive and one of the rarest Arnicas. 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.

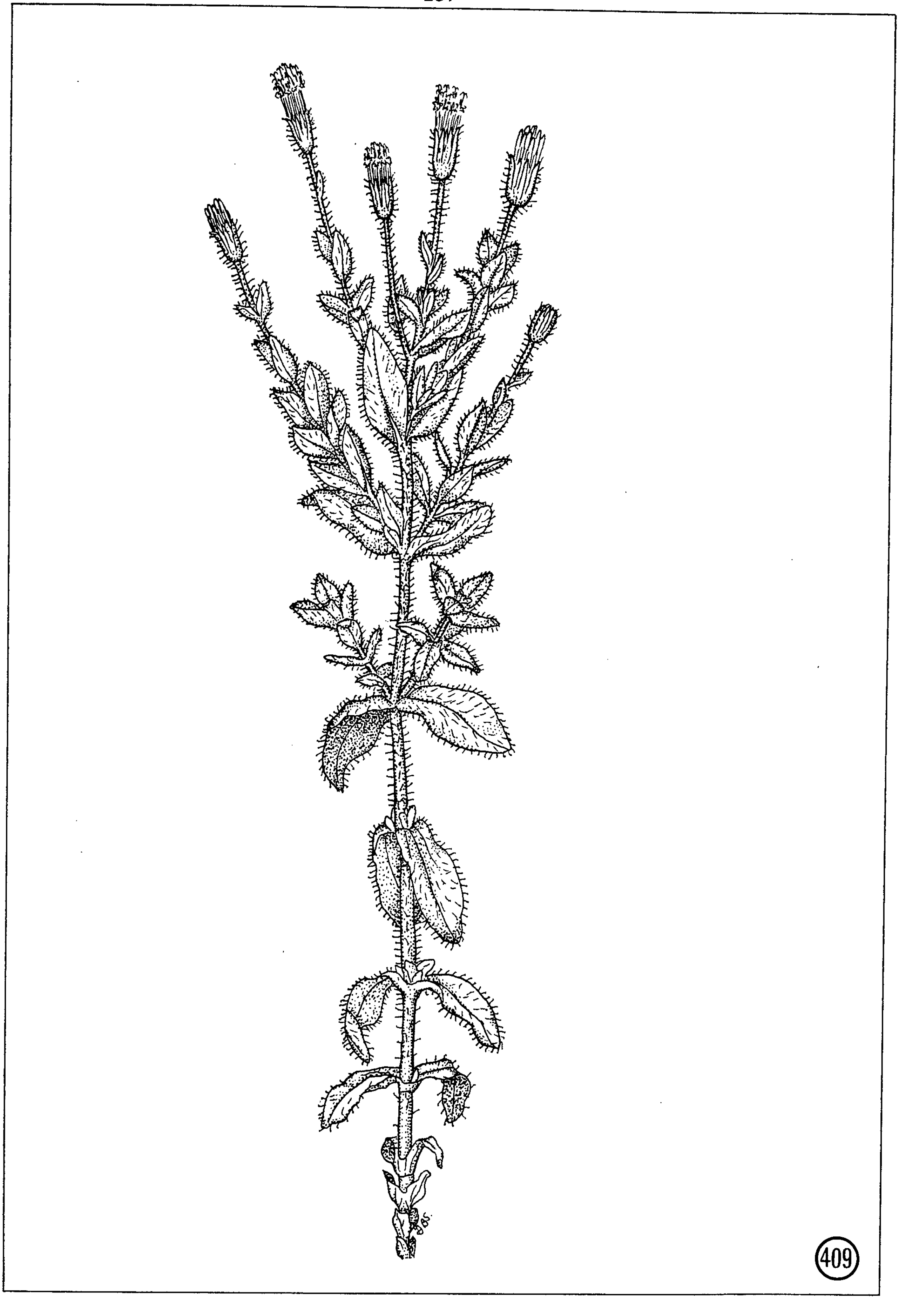
Arnica viscosa is strongly viscid throughout with long yellow-tipped glandular hairs on all vegetative parts and on florets and achenes. Its strong odor is unlike that of any other Arnica. The odor is retained in herbarium specimens for many years.

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.


409

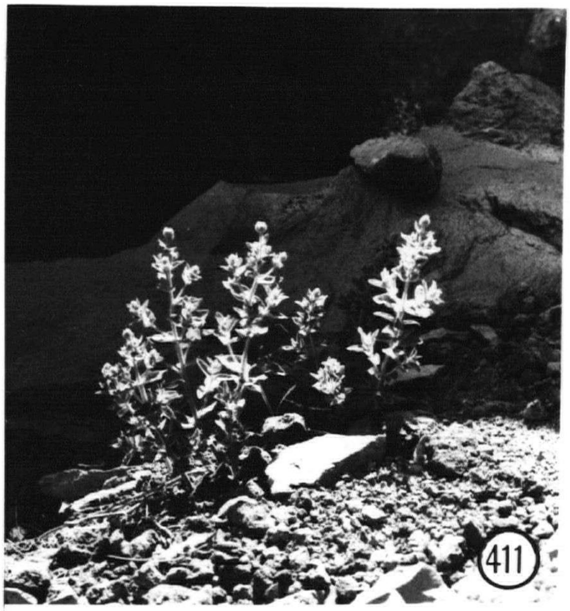
Figures 410-414. Habitats and habit of Arnica viscosa.

Figures 410-412. Habitat of Arnica viscosa S-1411. CA, Siskiyou Co., Mt. Shasta (Topotype).

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.

410



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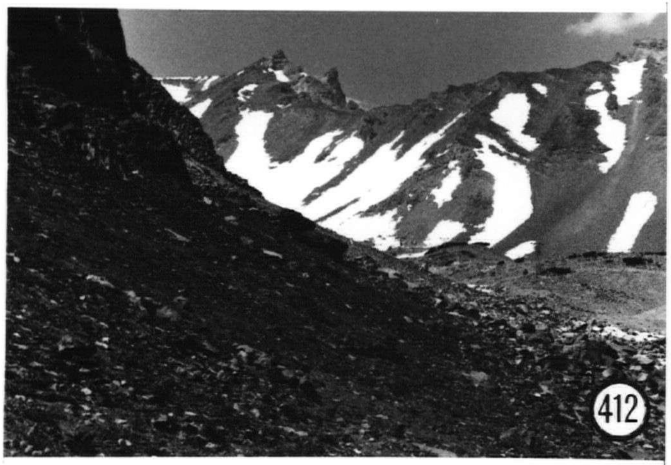

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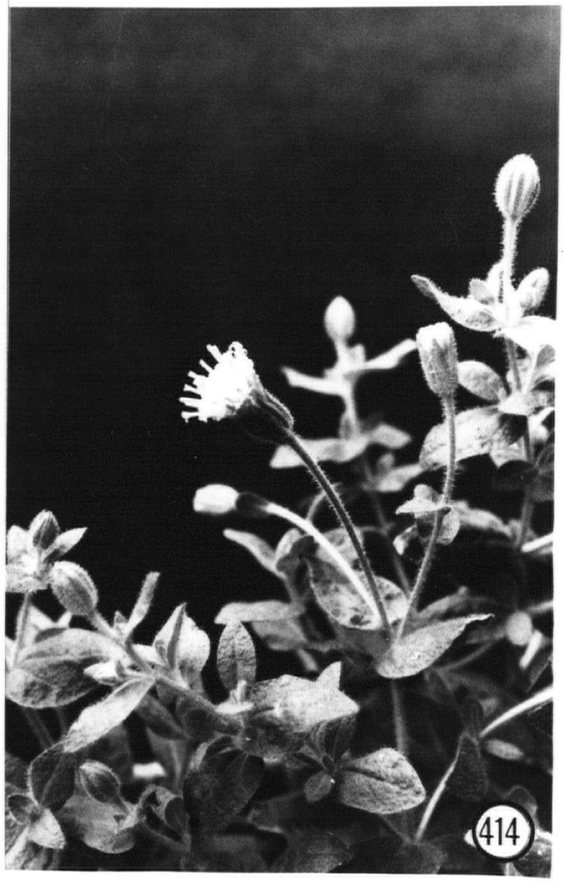


414

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.

9. *Arnica venosa* H.M. Hall. Univ. of Cal. Publs. Bot. 6:174. 1915.

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*.

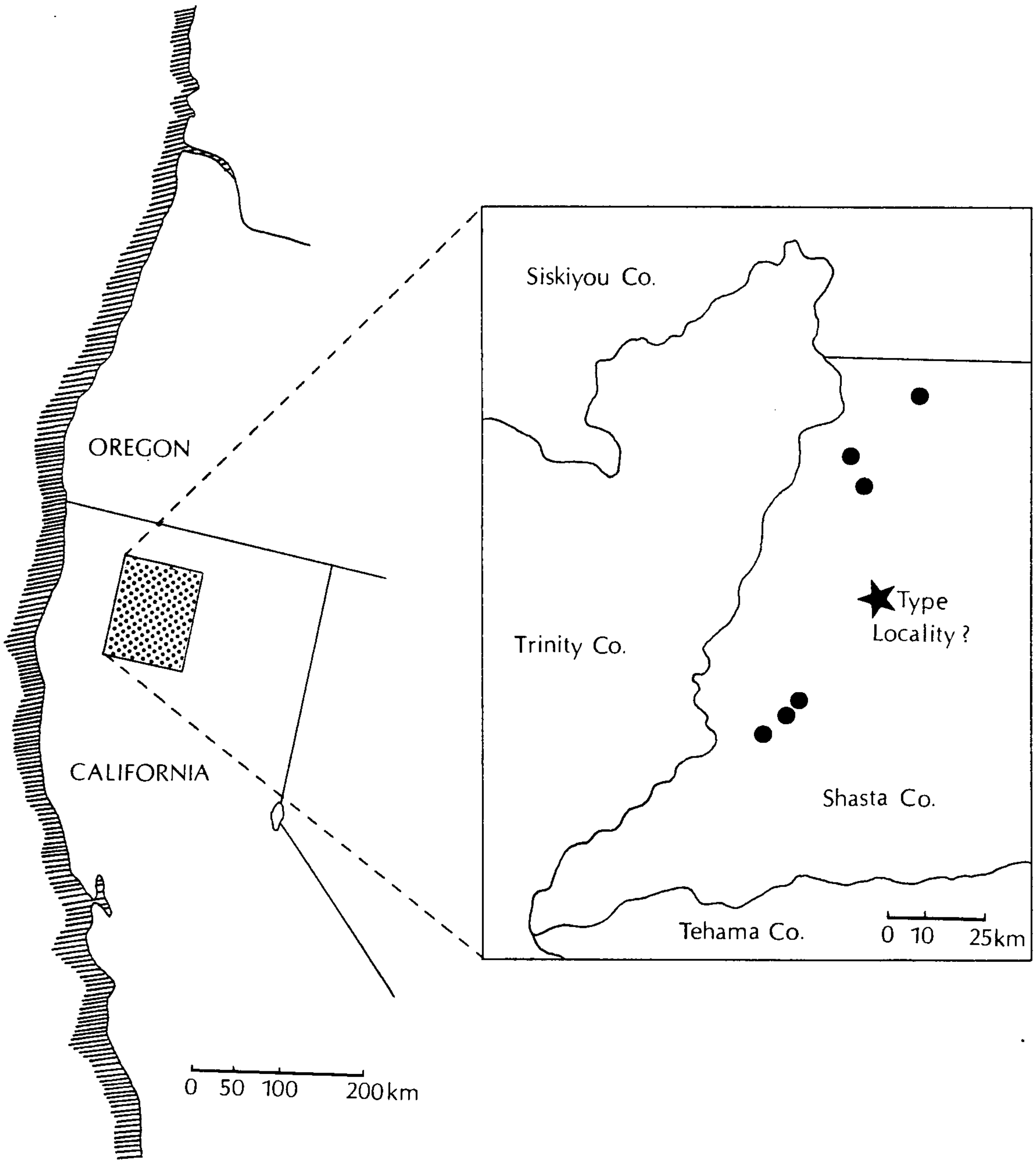
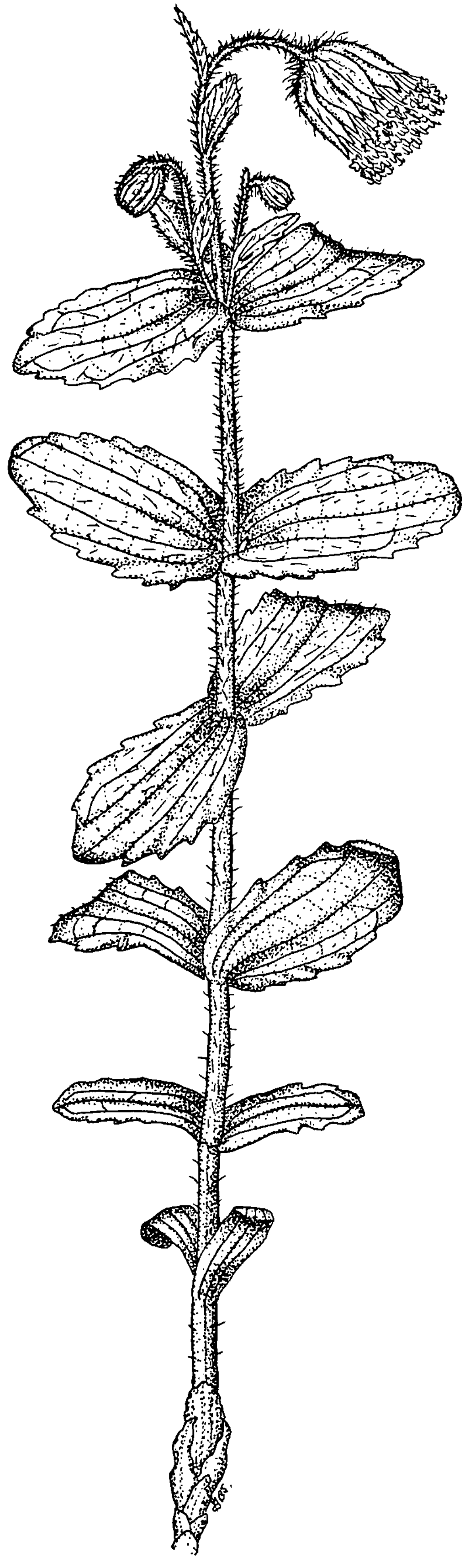

OREGON
CALIFORNIA
0 50 100 200km
Siskiyou Co.
Trinity Co.
Type
Locality ?
Shasta Co.
Tehama Co.
0 10 25km

Figure 416. Arnica venosa S-1793. CA, Shasta County. X two-thirds.



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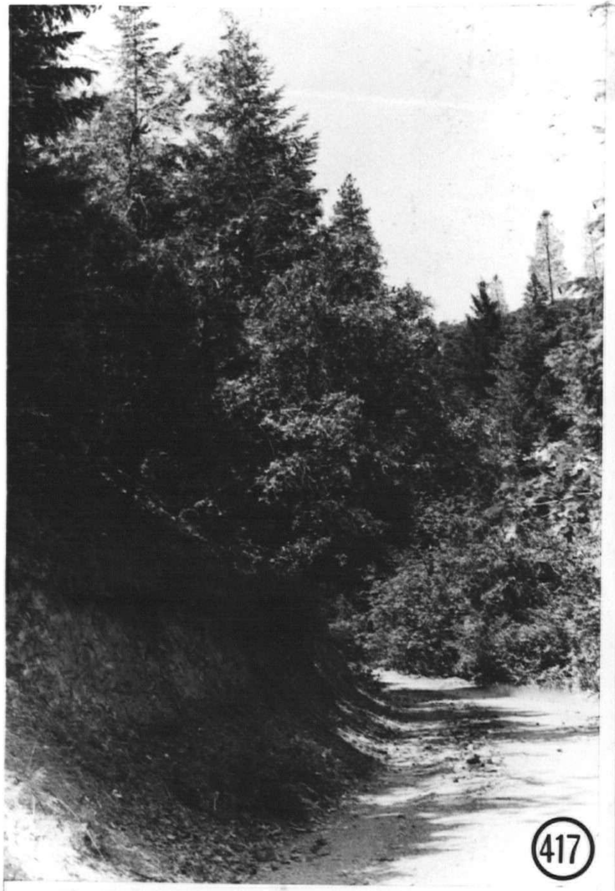
Figures 417-421. Habitat and habit of *Arnica venosa* S-1793, CA, Shasta Co., Gibson.

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.



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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.

PHYLOGENY

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.

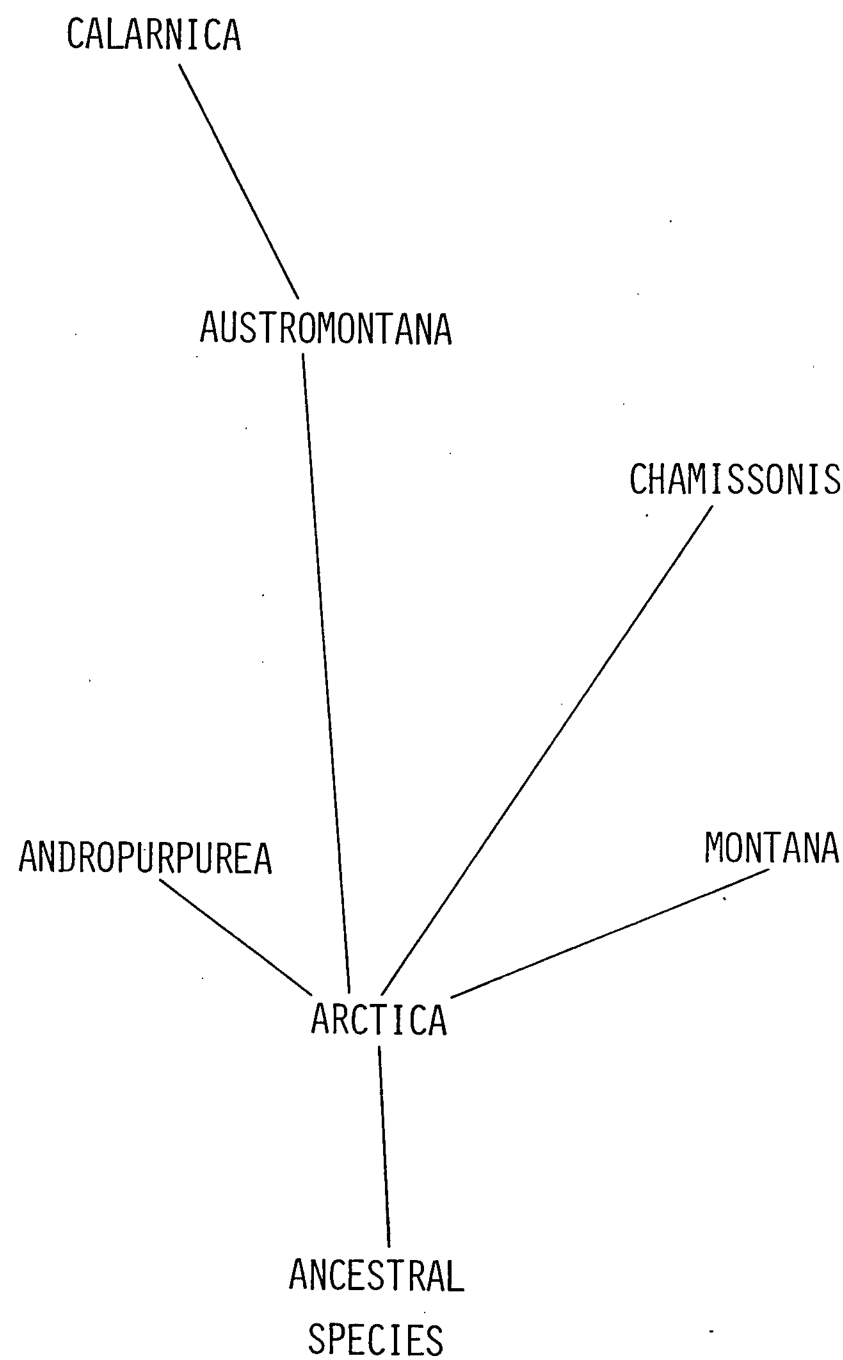
Arnica latifolia has in turn probably given rise to two other species. Arnica cernua, also a sexual diploid, is a rare serpentine soil endemic. It combines many morphological characters of Arnica latifolia but is ecologically distinct. A second species probably derived from Arnica latifolia, possibly 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

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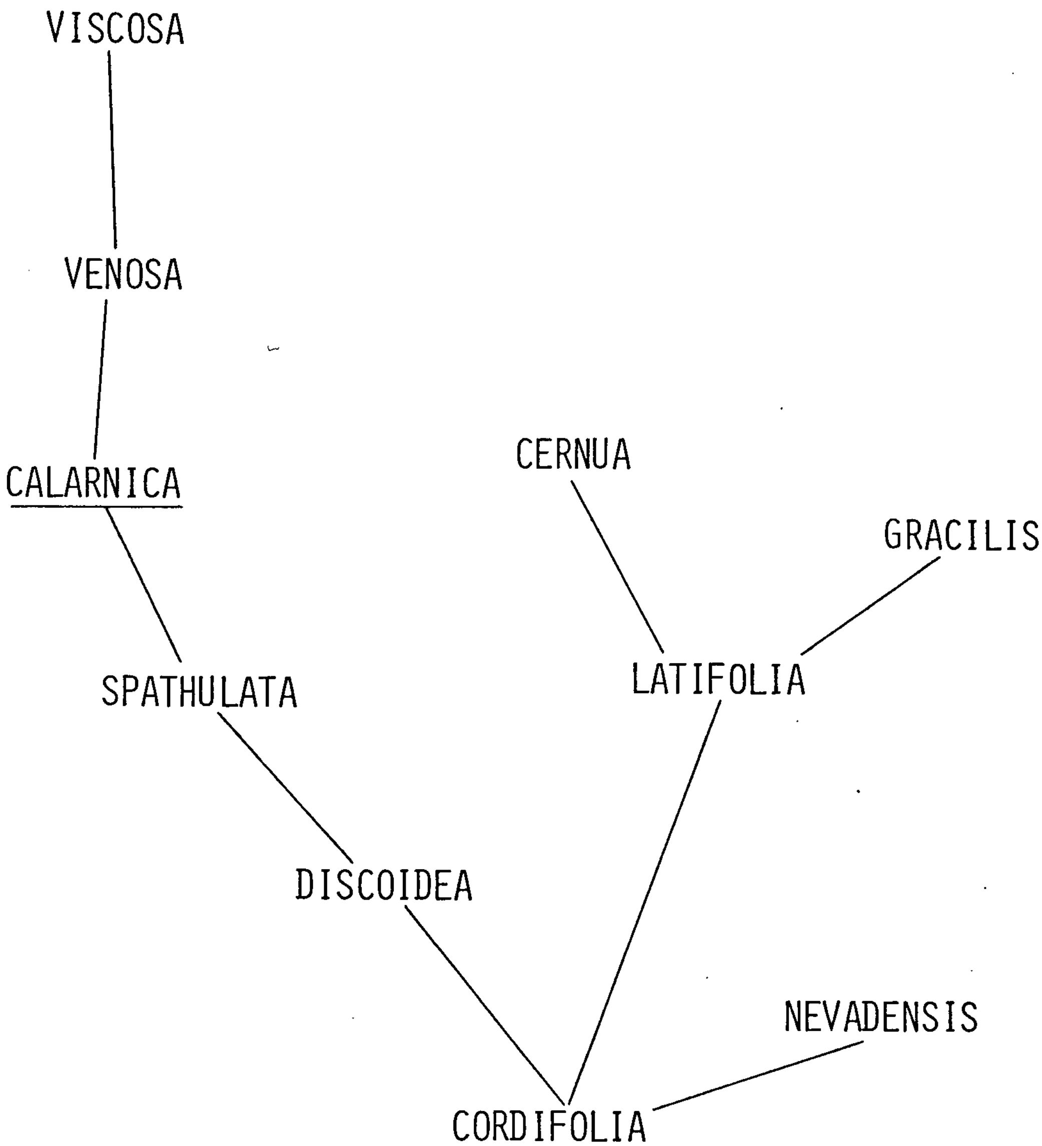
Figure 423. Possible Phylogenetic Relationships of *Arnica* Species in Subgenera *Austromontana* and *Calarnica*.



AUSTROMONTANA

423

SUMMARY

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 criteria 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 derivatives, 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.

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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
6. _Arnica_ _paniculata_ A. Nels.

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