

A SYSTEMATIC STUDY OF *ANTENNARIA MEDIA*,  
*A. PULCHELLA*, AND *A. SCABRA*  
(ASTERACEAE: INULEAE) OF THE SIERRA  
NEVADA AND WHITE MOUNTAINS

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ABSTRACT

*Antennaria pulchella* and *A. media* are a diploid progenitor–polyploid derivative pair of taxa that occur in the cordilleran system of western North America. *Antennaria scabra* is a glandular form of *A. pulchella* and is considered to be part of the variation within that taxon. The sexually reproducing diploid, *A. pulchella*, has a very restricted range, in the subalpine-alpine zones of the southern Sierra Nevada from the area around Lake Tahoe to the Mt. Whitney region. *Antennaria media* is a widespread polyploid that occurs throughout the cordilleran system of western North America from the Mexican border to the subarctic. They are both part of a large arctic/alpine species complex known as *A. alpina*. One of the diploid progenitors of *A. media*, and consequently the *A. alpina* complex, is *A. pulchella*.

*Antennaria media* E. Greene is a widespread polyploid species occurring throughout the alpine zones of most of the western North American mountain ranges from New Mexico and Arizona to southern Yukon. The type of *A. media* is from the high Sierra Nevada above Coldstream, Placer Co., California. Some authors follow the lead of Jepson (1925) and consider *A. media* to be an infraspecific taxon of *A. alpina* (L.) Gaertner, recognizing it as *A. alpina* var. *media* (E. Greene) Jepson. *Antennaria alpina*, in the strict sense, is a widespread circumboreal arctic-subarctic taxon, whereas *A. media* is a North American cordilleran segregate of the *A. alpina* complex (Bayer 1987, 1989B). *Antennaria media* is composed primarily of tetraploids ( $2n=56$ ), but higher ploidy levels up to octoploid ( $2n=112$ ) are frequently encountered (Bayer and Stebbins 1987; Bayer 1987) especially in the Rocky Mountains and other areas of its range away from the Sierra Nevada and Cascade Range. Staminate and pistillate plants occur in approximately equal frequencies in populations of *A. media* from the Sierra Nevada and Cascade Range, but in other parts of its range populations tend to be composed entirely of pistillate plants (Bayer and Stebbins pers. field and herbarium specimen obs.).

A series of diminutive herbarium specimens identified as *A. media*, including the type specimen of *A. pulchella* E. Greene from Mt. Goddard in the Sierra Nevada and *A. scabra* E. Greene (= *A. media*

subspecies *ciliata* E. Nelson) from the White Mountains, occur in the southern Sierra Nevada. Two sets of living plants, referable to *A. pulchella*, were collected in 1982 by G. L. Stebbins in the Sierra Nevada of California near Eagle Lake, Tulare Co. and Brainerd Lake, Inyo Co. These plants proved to have  $2n=28$  (Bayer 1984), indicating the fact that *A. pulchella* is a diploid. Studies of isozymes have established that diploid *A. pulchella* is fixed for one allele at the *Tpi-1* locus, but the polyploid plants of *A. media* are often fixed for an alternative allele not encountered in the diploids (Bayer 1989a). So although *A. pulchella* is probably one of the diploid progenitors of the *A. media* polyploids, they are probably not strict autopolyploid derivatives of *A. pulchella*, but instead of hybrid polyploid origin (Bayer 1989a). *Antennaria scabra* is often recognized as *A. alpina* var. *scabra* (E. Greene) Jepson, but its relationship to *A. media* and *A. pulchella* has been undecided and debatable.

These taxa had previously been treated as a single variable taxon, *A. media* (Bayer 1984; Bayer and Stebbins 1987; Bayer 1988). This circumscription should now be reviewed, especially in light of our recent field work (1987) in the Sierra Nevada with these taxa which yielded additional chromosomal and isozyme divergence data. Several questions need to be addressed. Is diploid *A. pulchella* morphologically distinct from polyploid *A. media* and, if so, what characters can be used most reliably to separate the taxa? What is the relationship of *A. scabra* to both *A. media* and *A. pulchella*? What is the range of the narrow endemics, *A. pulchella* and *A. scabra*, with respect to *A. media*? Morphometric and cytogeographic analyses are used to address these questions. The final outcome is a revised systematic treatment of these taxa.

#### METHODS

Herbarium specimens borrowed from ALTA, CAS, DAV, DS, GH, JEPS, NY, RM, UC, and US provided both morphological and distributional data. Chromosome counts were obtained from root-tip squashes using the Feulgen staining reaction outlined in Bayer (1984).

Sixty-one specimens, including approximately equal proportions morphologically referable to *A. media* and *A. pulchella/A. scabra*, were used in the analysis. Type specimens for each of the three names were included among the 61 specimens, as well as several recent personal collections of known chromosome number. Specimens representing the range of morphological variation in all taxa were selected as a means of assuring that a representative sample of the morphological variability within each taxon was being analyzed. Thirty-eight vegetative and morphological characters were measured. The characters used in this study are identical with those listed in Bayer (1989c).

Morphological variation in the taxa was assessed using multivariate morphometric analyses, including principal components analysis (PCA) and cluster analyses. The analyses were implemented through the use of the NTSYS-pc programs (Rohlf 1987). The data were standardized so that each character had a mean of zero and a standard deviation of unity through the use of the STAND subroutine of NTSYS. A similarity matrix of product-moment correlations of the characters and a matrix of average taxonomic distances from the OTU's (Operational Taxonomic Units = specimens) were derived using the SIMINT subroutine. The EIGEN subroutine was used to calculate eigenvalue and eigenvector matrices from the matrix of product-moment correlations. The OTU's were subsequently projected onto axes, the eigenvectors, using the PROJ subroutine, thereby completing the PCA. A 3-dimensional graph of the OTU's on the first three principal components was plotted by the MOD3DG subroutine of NTSYS. A cluster analysis using the unweighted pair-group method (UPGMA) was generated by subjecting the distance matrix produced by SIMINT to analysis by the SAHN subroutine.

#### RESULTS

*Morphometrics.* The results of the PCA and cluster analysis (Figs. 1 and 2) indicate that two morphologically distinct groups can be recognized: *A. media* and *A. pulchella-A. scabra*. The cluster analysis, illustrated as a phenogram (Fig. 2), shows a distinct separation of *A. media* from the *A. pulchella* complex. A morphological gap is evident in the PCA between the two groups on the plot of factor 1 vs. factor 2 (Fig. 1), which accounts for 46.4% of the total variation. In both analyses, eight confirmed diploid specimens are grouped within the *A. pulchella* complex, whereas three verified tetraploids are within the *A. media* complex (Figs. 1 and 2). The type specimens of *A. media* and *A. pulchella* are clustered within the other specimens assigned to these taxa, but the type of *A. scabra* is grouped with the *A. pulchella* complex. In PCA, highest loadings for factor 1 were staminate and pistillate corolla length, pollen grain diameter, length of the longest (lowermost) cauline leaf, and height of the staminate involucre. Factor 2 has high loadings for pistillate pappus length, corolla length, achene length, and phyllary color, as well as length of the leaves in the basal rosettes. The two groups, *A. media* and *A. pulchella*, differentiate best along factor 1; consequently, characters having high loadings along this axis were examined as potential "key characters" that could be used confidently to separate the species. Investigation of these characters indicated that pistillate and staminate corolla length and length of the lowermost cauline leaves are the most reliable characters to separate the taxa. A trivariate plot of the OTU's using these three variables (Fig. 3) demonstrates the resolving power of these characters to distinguish the species.

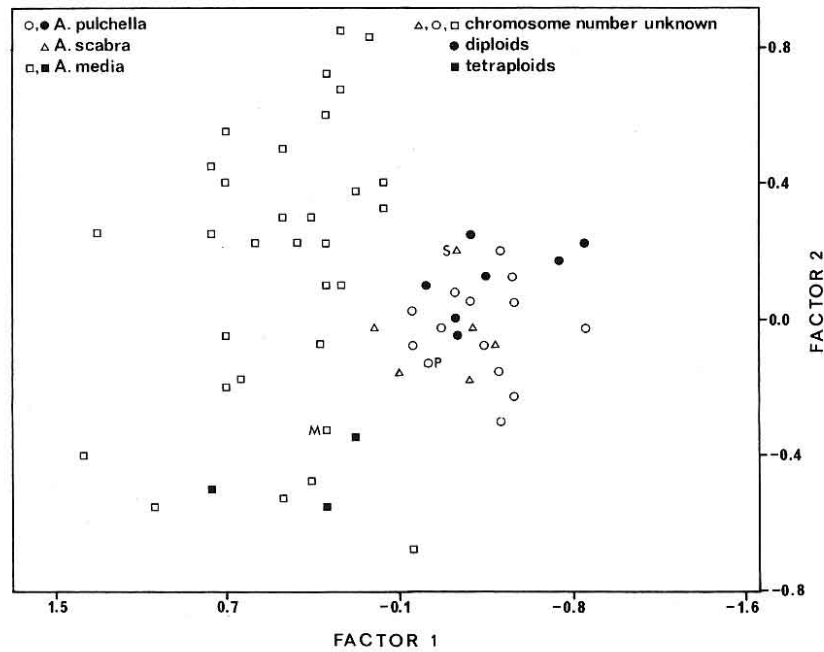


FIG. 1. PCA composed of a total of 61 OTU's (specimens) of *Antennaria media*, *A. pulchella*, and *A. scabra*. Holotypes of *A. media* (US), *A. pulchella* (US) and *A. scabra* (US) are marked with "M", "P", and "S", respectively.

*Cytology and cytogeography.* The results show that *A. pulchella* is diploid from eight localities in the Sierra Nevada of California and Nevada, based on three previously published reports (California, Inyo Co., C-235; Tulare Co., C-245 [Bayer 1984] and Nevada, Washoe Co., C-450 [Bayer and Stebbins 1987]) and five new determinations (California, Inyo Co., CA-700, CA-707, CA-724, CA-732; Mono Co., CA-720 [Voucher specimens are at ALTA and R.M.]). Previously published chromosome reports for *A. media* (Bayer and Stebbins 1981; Bayer 1984; Bayer and Stebbins 1987) indicate that the tetraploids are the most widespread and predominant cytotype in the species. Twenty-two chromosome counts of *A. media* from California and Oregon have yielded only tetraploid counts (Bayer and Stebbins 1987).

#### DISCUSSION

*Antennaria pulchella* should be recognized as a separate species from *A. media* because it is morphologically distinct from *A. media*. It is also presumably reproductively isolated because it is diploid, whereas *A. media* is tetraploid in the area of sympatry between the two taxa. Some tetraploids have allozymes that have not been de-

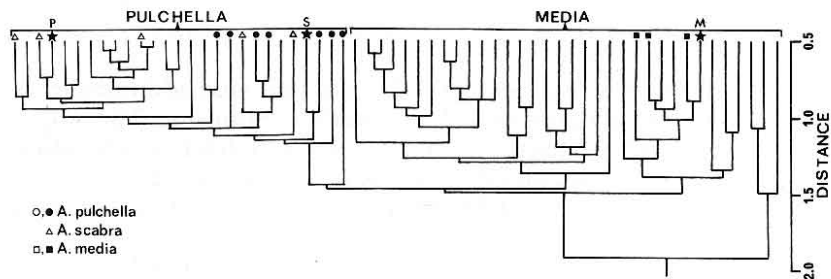


FIG. 2. Distance phenogram representing relationships among 61 OTU's of *Antennaria media*, *A. pulchella*, and *A. scabra*. Unlabeled OTU's belong to the taxon indicated at the top of the bracket that they cluster under. Holotypes of *A. media* (US), *A. pulchella* (US) and *A. scabra* (US) are marked with "M", "P", and "S", respectively.

tected in *A. pulchella* indicating that they are probably not simply autopolyploid derivatives of *A. pulchella* (Bayer 1989a). Also *A. pulchella* frequently possesses various quantities of glandular hairs, whereas *A. media* is usually non-glandular.

*Antennaria scabra* represents a very glandular form of *A. pulchella*. The type of *A. scabra* is included in the *A. pulchella* cluster. Other specimens of the taxon are very similar to typical *A. pulchella*, as indicated by morphometric analyses (Figs. 1 and 2), except they

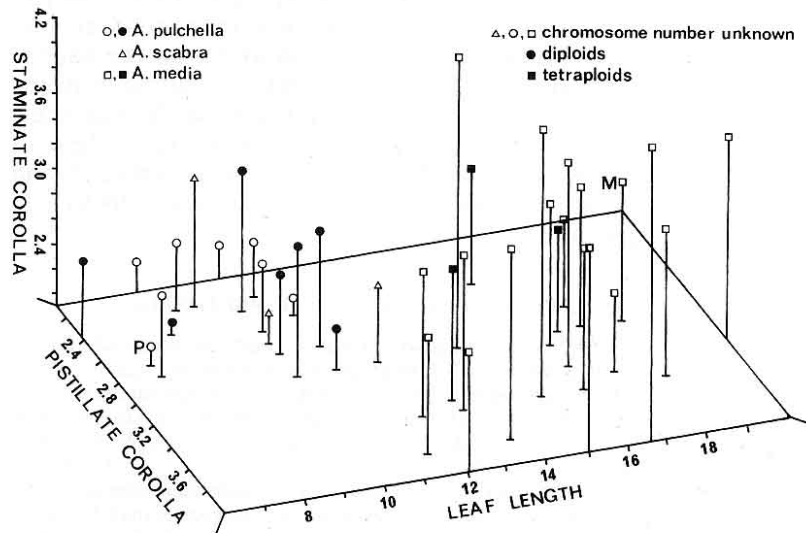


FIG. 3. Trivariate plot of *Antennaria media*, *A. pulchella*, and *A. scabra* specimens. The three axes consist of length of the staminate corolla, length of the pistillate corolla, and length of the lowermost cauline leaf. Holotypes of *A. media* (US) and *A. pulchella* (US) are marked with "M" and "P", respectively.

possess numerous stalked purple glandular hairs and are less pubescent than typical *A. pulchella*.

Two aspects of *A. pulchella* and *A. scabra* provide additional evidence in support of the proposed conspecific relationship. The ranges of both narrowly restricted endemics are completely overlapping (Fig. 4) and congruent, and there are several mixed collections, e.g., Bayer *et al.* CA-700 (ALTA), Bayer *et al.* CA-724 (ALTA), and Sharsmith 3029A/3029B (UC) (representative specimens). Many *A. pulchella* have some glandular hairs on the upper cauline leaves and stem as well as on the involucre. Bayer *et al.* CA-700 and CA-724 contain a relatively small proportion of clones that could be referred to *A. scabra*; most are the *A. pulchella* phenotype with varying degrees of glandulosity. I suggest that glandulosity is a multistate character in *A. pulchella* and that *A. scabra* simply represents one extreme. The character segregates in some populations, therefore the mixed populations of the two morphotypes, *A. pulchella* and *A. scabra*, occur.

Staminate and pistillate corolla length, and length of the longest (lowermost) cauline leaf are the most reliable characters for separating the taxa. They can be used to construct a key to separate *A. media* from *A. pulchella* (*sensu lato*). Measurements should be made from mature specimens only, usually at anthesis or later. A good indication of maturity of corollas in *Antennaria* is their length when compared to the pappus bristles. At maturity the corolla of both genders almost equals the pappus in length (often about 1 mm shorter than the pappus). The pappus matures more quickly, consequently in immature heads the corollas are much shorter than the pappus bristles. In pistillate corollas, the measurement should be from the top of the ovary (achene) to the tip of the corolla, in staminate corollas from the summit of the rudimentary ovary to the base of the sinus between the perianth lobes. Glandulosity, gender ratio, and geographic distribution can also be used as minor characters to help differentiate the taxa.

#### KEY TO *ANTENNARIA MEDIA* AND *A. PULCHELLA*

- A. Pistillate corolla less than or equal to 3.0 mm at maturity; staminate corolla usually less than or equal to 2.75 mm at anthesis; lowermost cauline leaf less than or equal to 11 mm at maturity; glandular hairs often present on basal leaves, cauline leaves and stem; staminate plants always present in populations; plants of the Sierra Nevada from the Lake Tahoe region south to the Mt. Whitney area, California and adjacent Nevada. . . . . *A. pulchella*
- A'. Pistillate corolla greater than 3.0 mm at maturity; staminate corolla usually greater than 2.75 mm at anthesis; lowermost cauline leaf greater than 11 mm at maturity; glandular hairs absent from leaves, stems and involucres; staminate plants often absent from populations; plants widespread in western North America from California, Arizona, and New Mexico north to Yukon and Northwest Territories. . . . . *A. media*

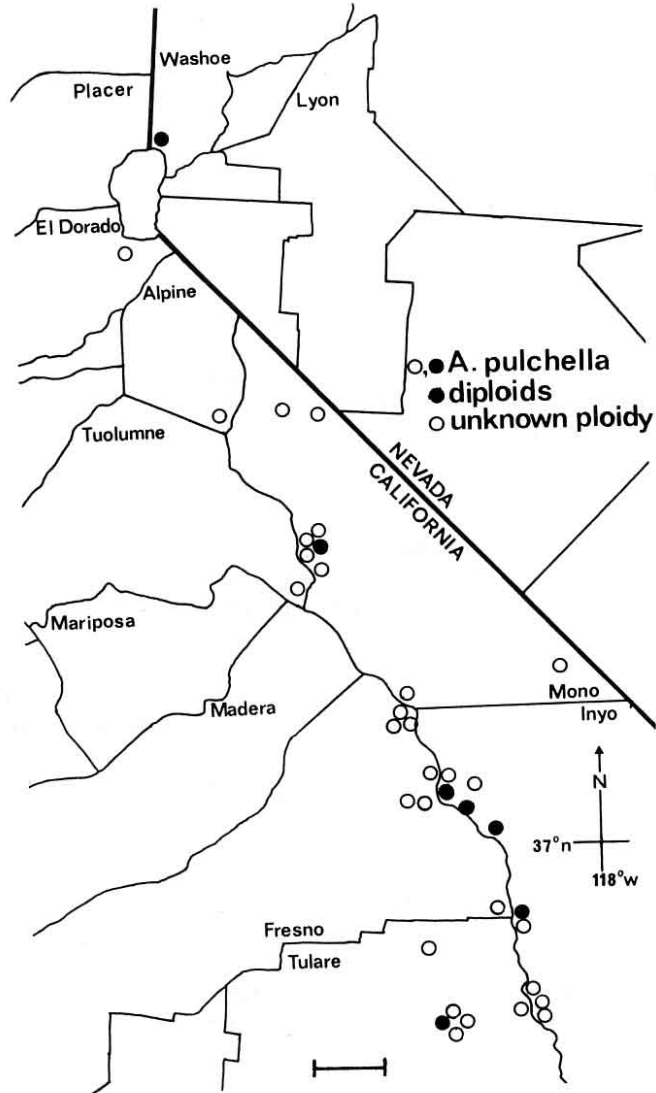


FIG. 4. Distribution of *Antennaria pulchella* (including *A. scabra*) in the Sierra Nevada and White Mountains of California and Nevada. Each symbol depicts one collection. Bar = 25 km.

#### TAXONOMIC TREATMENT

1. ANTENNARIA PULCHELLA E. Greene, Leaflet Bot. Observ. Crit. 2: 149. 1911.—TYPE: USA, California, "Plants of the Sierra Nevada Mtns., Mt. Goddard, alt. 11,000'" (fide label), 24–26 Jul

1900, *H. M. Hall and H. P. Chandler 686* (holotype, US! #390722).

*Antennaria media* E. Greene subsp. *ciliata* E. Nelson, Proc. U.S. Natl. Mus. 23:700. 1901.—TYPE: USA, California, "White Mts. Mono Co., Calif. 12,000 ft." (fide label), Jul 1886, *Wm. Shockley 444* (holotype, US! #47044).—*A. scabra* E. Greene, Leaf. Bot. Observ. Crit. 2:150. 1911.—*A. alpina* var. *scabra* (E. Greene) Jepson, Manual Fl. Pl. Calif. 1070. 1925.—TYPE: USA, California, "White Mts. Mono Co., Calif. 12,000 ft." (fide label), Jul 1886, *Wm. Shockley 444* (holotype, US! #47044). The taxon was first described as *A. media* subsp. *ciliata* by E. Nelson (1901), the type being *Shockley 444*. Nelson also mentioned a paratype, *Coville and Funston 2160*, in his protologue. Ten years afterward E. Greene (1911) described *A. scabra*, citing *Shockley 444* as the type and *Colville and Funston 2160* as a paratype, but not making any reference to the earlier description of *A. media* subsp. *ciliata* by Nelson. They are nomenclatural synonyms.

Mat-forming perennial herbs, odorless, with 3–6 leafy stolons per basal rosette; rosette-leaves spatulate to linear-cuneate, 5–14 in number, 6–12 mm long, 1.5–4.5 mm wide, usually with distinct petioles 1–3 mm long, glabrescent-scabrous to canescent, often also with purple glandular hairs. Stolons decumbent, 2–4(1–9) cm long, with 9–22 leaves, the proximal leaves 3–8 mm long, 0.5–2 mm wide, the distal leaves 6–12 mm long, 1.5–3.5 mm wide. Flowering stem (1–)3–12 cm high; cauline leaves 4–8(–9), linear, the lower 6–11(–13) mm long, 1–2.5 mm wide, the upper 3–8(–10) mm long, 0.5–1.5 mm wide, only those about the heads sometimes possessing linear-lanceolate, scarios appendages at their tips (flags). Pistillate heads 4–6(3–7), in corymbose clusters; involucre 3.5–4.5(–6) mm high; phyllaries in 2 or 3 series, acute to blunt, scarios, the longest 3.5–4.5(–5) mm long, 0.5–1.2 mm wide, colors various, the tips usually dark-green or black, but often brown, light brown, or white, with base of a darker brown or black. Florets 25–60 per head; corollas 2–3(–3.3) mm long, pappus 3.3–4(–4.5) mm long, achenes 0.7–1.3 mm long, with or without papillae. Staminate plant as frequent as pistillate, staminate heads 3–6, in corymbose clusters; involucre (3–)4–5 mm high; phyllaries 3.5–4.5 mm long; 0.7–2 mm wide, corolla 1.9–2.8(–3) mm long; pappus clavate, 2.5–3.5 mm long, pollen 16–22 micrometers in diameter;  $2n=28$ .

*Distribution and habitat* (Fig. 4). The known range of *A. pulchella* extends from Mt. Rose, Nevada, to Primrose Lake in the southern Sierra Nevada, where it is found primarily on the eastern slope with scattered sites on the western slope. Habitats are subalpine to alpine; 2800 m in the north to 3700 m in the south. One record indicates



2300 m, but may be in error (*McGregor 162*; representative specimens). Sites generally mesic, near the margins of tarns and streams or where there are intermittent streams or run-off from large snowmasses that provide moisture for most of the summer.

*Representative specimens.* USA, California, Alpine Co.: White Mts., 8 Sep 1936, *Albertus 370* (USFS). El Dorado Co.: Desolation Valley, 18 Aug 1909, *McGregor 162* (NY). Fresno Co.: basin just N of Mono Pass, head of Mono Creek, 8 Aug 1937, *Sharsmith 3029A* and *3029B* (NY, UC); Mt. Goddard, 24–26 Jul 1900, *Hall and Chandler 686* (UC); Rae Lakes Basin, Kings Canyon National Park, isthmus between first and second Rae Lakes, 3 Aug 1978, *Burke 669* (DAV); Muir Pass, 11,955 ft, 28 Jul 1952, *Raven 4707* (CAS); slope W of Second Recess, 11,000 ft, 30 Jul 1953, *Raven 5947* (CAS); McGee Lakes to Wanda Lake, 25 Jul 1952, *Raven 4687* (CAS). Inyo Co.: Slim Lake, SE of Kearsarge Pass, W of Independence, 8 Aug 1942, *Alexander and Kellogg 3285* (GH); Cottonwood Lakes, SW of Lone Pine, about rocks, E side from fifth lake, 29 Aug 1942, *Alexander and Kellogg 3407* (NY, UC); Mt. Whitney, Consultation Lake, E slope, 23 Jul 1935, *Rose 35498* (CAS); Big Pine Creek, near Brainerd Lake, 10 Sep 1982, *Vasey C-235* (DAV); Pee-wee-pot-hole, NE of Dingleberry Lake, above Lake Sabrina, 11 Aug 1950, *Raven and Stebbins 295* (UC); Coyote Ridge, Sierra Nevada, 11,700 ft, 7 Aug 1950, *Raven and Stebbins 211* (UC); Inyo National Forest, Trail from Blue Lake to Dingleberry Lake, 16 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-724* (ALTA, CAN, DAV, RM); trail to Matlock Lake, vicinity of Kearsarge Pass, 13 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-707* (ALTA, CAN, DAV, RM); lake basin below Chocolate Mt. and Hurd Pk., steep rocky slope between Mary Louise Lakes and Bull Lake, 16 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-732* (ALTA, CAN, DAV, RM); Sierra Nevada, near first Cottonwood Lake, common among grasses and sedges adjacent to Cottonwood Creek, 12 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-700* (ALTA, CAN, DAV, RM); exposed granite rocks, Piute Pass, 22 Jul 1934, *Ferris 8940* (DS). Mono Co.: Sweetwater Mts., Deep Creek, common among rocks up the stream, 5 Aug 1944, *Alexander and Kellogg 4011* (GH); Yosemite National Park, Mono Pass, 21 Aug 1907, *Eastwood 570* (CAS); H. M. Hall Natural Area, 25 Jul 1954, *Kruckeberg 3576* (NY, RM); Dana Plateau, in gravels of unglaciated granitics, vicinity of Mt. Dana, 13 Jul 1937, *Sharsmith 2433* (UC); mountains above Saddlebag Lake, 14 Aug 1927, *Hastings s.n.* (NY); alpine fell-field at head of Sweetwater Creek, Sweetwater Mts., 24 Jul 1955, *Munz 21220* (NY); vicinity of Tioga Pass, moist drainage area at S end of Saddlebag Lake, 14 Jul 1987, *Bayer, DeLuca, and Lebedyk CA-720* (ALTA, CAN, RM); H. M. Hall Natural Area, 30 Jun 1934, *Blake 11822* (GH). Tulare Co.: Upper Franklin Lake,

Mineral King Game Refuge, Sequoia National Park, 28 Jun 1966, *Rice, Pemble, and Fleschner 187* (DAV); W side of Eagle Lake, above Mineral King, 16 Sep 1982, *Stebbins, Vasey, and Stephens C-245* (DAV); Sequoia National Park, S end of Eagle Lake, 3 mi above Mineral King, (in part) 13 Sep 1932, *Bracelin 726* (GH, NY); S shore of Twin Lakes, Sequoia National Park, 7 Sep 1932, *Bracelin 703* (GH); Primrose Lake, 11,500 ft, 24 Jul 1949, *Howell 25702* (CAS); SE of Farewell Gap, 20 July 1951, *Howell 28008* (CAS). Tuolumne Co., Kuna Crest above Helen Lake, Parker Pass region, 20 Jul 1937, *Sharsmith 2620* (NY). Nevada, Washoe Co., S of the summit of Mt. Rose, along Third Creek, 15 Jul 1984, *Stebbins, Kunz, and Vasey C-450* (DAV).

*Relationships.* *Antennaria pulchella* is perhaps most closely related to *A. corymbosa* E. Nelson, a sexual diploid species of the northern Rockies that has disjunct populations in the Sierra Nevada (Bayer and Stebbins 1987). *Antennaria pulchella* possesses *Tpi-1<sup>b</sup>*, an allele that is shared only with *A. corymbosa* and some tetraploid segregates of *A. media* (Bayer 1989a). Both species occur in mesic habitats at subalpine elevations. Many individuals of *A. pulchella* have linear-oblongeolate basal leaves and phyllaries that are white tipped with a black base, characteristics that distinguish *A. corymbosa*. *Antennaria pulchella* is also perhaps closely related to arctic *A. monocephala* DC., which occurs in mesic habitats on the margins of solifluction lobes. It differs from *A. pulchella* in its monocephalous flower stalks and glabrous adaxial leaf surfaces. Unfortunately, isozyme variation has not yet been investigated in *A. monocephala*, so it cannot yet be compared to *A. corymbosa* or *A. pulchella*.

2. *Antennaria media* E. Greene, Pittonia 3:286. 1898.—*Antennaria alpina* (L.) Gaertn. var. *media* (E. Greene) Jepson, Manual Fl. Pl. Calif. 1070. 1925.—LECTOTYPE (Nelson 1901, Proc. U.S. Natl. Mus. 23:700.): USA, California, Placer Co., “Mts. above Coldstream” (fide label), 31 Jul 1892, *C. F. Sonne s.n.* (US! #310514).
- Antennaria austromontana* E. Nelson, Proc. U.S. Natl. Mus. 23:703. 1901.—TYPE: USA, Utah, “Marysvale, Utah, Alt. 11,700 ft.” (fide label), 28 Aug 1894, *M. E. Jones 5522* (holotype, US! #326693).
- Antennaria modesta* E. Greene, Ottawa Naturalist 30:72. 1906.—LECTOTYPE (Bayer 1988, Taxon 37:292–298.): CANADA, British Columbia, “Second summit W of Skagit River, B.C. alt. 6,000 ft.” (fide label), 29 Jul 1905, *J. M. Macoun Canad. Geo. Survey #69,334* (NDG; Type description reads “25” July not “29” July).
- Antennaria densa* E. Greene, Leaf. Bot. Observ. Crit. 2:151. 1911.—TYPE (Bayer 1988, Taxon 37:292–298.): USA, California, “Mt.

San Gorgonio, San Bernardino mountains, altitude 11,000 ft.” (fide label), 12 Jul 1908, *L. Abrams and E. A. McGregor 751* (lectotype, US! #613419).

*Antennaria candida* E. Greene, *Leaf. Bot. Observ. Crit.* 2:151. 1911.—TYPE: USA, California, “Mt. Rainier, alt. 9,000 ft.” (fide label), 14 Aug 1895, *O. D. Allen 141* (holotype, US! #314044).

Mat-forming perennial herbs, odorless, with 3–6 leafy stolons per basal rosette; rosette-leaves spatulate to linear-cuneate, 5–11 in number, (6–)9–19 mm long, 2.5–6 mm wide, usually with distinct petioles 1–5 mm long, canescent and usually non-glandular. Stolons decumbent, 1–4 cm long, with 7–20 leaves, the proximal leaves 3–10(–14) mm long, 0.5–3 mm wide, the distal leaves 6–19 mm long, 1.5–5.5 mm wide. Flowering stem (2–)5–13 cm high; cauline leaves 4–10, linear, the lower (9–)11–20 mm long, 1.5–4 mm wide, the upper 5–11 mm long, 0.5–2 mm wide, only those about the heads infrequently possessing subulate, scarious appendages at their tips (flags). Pistillate heads 4–7(2–9), in corymbose clusters and sometimes with elongate pedicels; involucre (4–)5–8 mm high; phyllaries in 2 or 3 series, acute to blunt, scarious, the longest (3.5–)4–6.5 mm long, 0.7–1.6 mm wide, colors various, the tips usually dark-green or black, but much less often brown, light brown, or white, with base of a darker brown or black. Florets 35–80 per head; corollas (2.5–)3–4.5 mm long, pappus (3.5–)4–5.5 mm long, achenes 0.6–1.6 mm long, with or without papillae. Staminate plant as often as frequent as pistillate, but often completely lacking from populations, staminate heads 3–7, in corymbose clusters; involucre (3.5–)4.5–6.5 mm high; phyllaries (3.5–)4–6 mm long; 0.7–2 mm wide, corolla (2.5–)2.8–4.5 mm long; pappus clavate, 2.5–4.5 mm long, pollen 19–25 micrometers in diameter;  $2n=56, 98, 112$ .

*Distribution and habitat.* *Antennaria media* occurs in subalpine to alpine/arctic tundra zones from New Mexico and Arizona into the North American subarctic. In California, it occurs at elevations and in habitats that are similar to those of *A. pulchella*. A detailed distribution map of *A. media* must wait until its status in the northern portions of its range can be investigated more closely.

*Representative specimens.* CANADA, Alberta, Waterton Lakes National Park, alpine summit of Mt. Crandell, 9 Aug 1953, *Breitung 17368* (ALTA); Jasper National Park, Sunwapta Pass, shoulder of Wilcox Mtn., 13 Jul 1939, *Moss 4974* (ALTA); Jasper National Park, along Tonquin Valley trail, switchback area, 19 Jul 1971, *Scotter 16858* (ALTA). British Columbia, hillside, road from Anahim Lake to Bella Colla, 8 Jul 1956, *Calder, Parmelee, and Taylor 18518* (DAO); Mt. McLean at Lillooet, shale flat, 6 Sep 1954, *Calder, Savile, and Ferguson 15510* (DAO); on coarse talus at treeline on E slope of Starvation Peak, 29 Jul 1958, *Taylor, Calder, and Ferguson 3206*

(DAO). Vancouver Island, trail to summit of Mt. Albert Edward, Forbidden Plateau, 6 Aug 1961, *Calder and MacKay 32168* (DAO); Vancouver Island, Mt. Arrowsmith near Alberni, 26–27 Jul 1956, *Calder, Parmelee, and Taylor 19451* (DAO). USA, California, Inyo Co.: on trail from North Lake to Piute Pass, 9 Sep 1982, *Stebbins and Vasey C-232* (DAV). Mono Co.: White Mts., above McAfee Meadows, 6 Aug 1945, *Maguire and Holmgren 28086* (NY). Tulare Co.: S Margin of southwest lake, Maggie Lakes, 14 Sep 1982, *Stebbins, Vasey, and Stephens C-243* (DAV); N end of Eagle Lake, above Mineral King, 16 Sep 1982, *Stebbins, Vasey, and Stephens C-246* (DAV). Colorado, Grand Co.: ski slopes E of Berthoud Pass, summit of peak near microwave tower, 4 Aug 1984, *Bayer, Dunford, Soreng, and Stebbins CO-468* (RM). Gunnison Co.: alpine peaks and slopes just S of Cottonwood Pass, 20 Jul 1985, *Bayer and Lebedyk CO-520* (RM); alpine summit E side of Cumberland Pass, 1 Aug 1984, *Bayer, Dunford, Soreng, and Stebbins CO-442* (RM). Idaho, Custer Co.: alpine summit of Twin Peaks near fire lookout tower, 31 Jul 1986, *Bayer, Lebedyk, and Joncas ID-604* (CAN, DAO, DAV, RM). Montana, Deerlodge Co.: alpine tundra at Storm Lake Creek Pass (Goat Pass), 26 Jul 1987, *Bayer, DeLuca, and Lebedyk MT-722* (ALTA, CAN, RM). Gallatin Co., E slopes and summit of Mt. Sacajawea, 6 Aug 1986, *Bayer, Lebedyk, and Joncas MT-629* (ALTA, CAN, DAO, RM). Nevada, Nye Co.: Toiyabe Range, in open aspen, head of North Twin River, 27 Jul 1945, *Maguire and Holmgren 25993* (GH). Oregon, Deschutes Co.: N side of Bachelor Butte, 26 Aug 1984, *Stebbins OR-450* (DAV); base of Middle Sister below Renfrew Glacier, 25 Aug 1984, *Stebbins OR-436* (DAV); Three Sisters Wilderness, along trail at Obsidian Falls, 25 Aug 1984, *Stebbins OR-416* (DAV). Utah, Salt Lake Co.: Alta, slopes below Mt. Tuscarora, 24 Jul 1986, *Bayer, Lebedyk, and Joncas UT-604* (RM). Summit Co.: Uinta Mts., S slope of Bald Mtn., 26 Jul 1986, *Bayer, Lebedyk, and Joncas UT-616* (CAN, DAO, RM). Wyoming, Big Horn Co.: Cloud Peak Wilderness, along middle Tensleep Creek near Mirror Lake, 11 Aug 1986, *Bayer, Lebedyk, and Joncas WY-636* (DAV, RM). Fremont Co.: Wind River Range, alpine slopes of Cony Mt., 22 Jul 1985, *Bayer and Lebedyk WY-503* (RM). Park Co.: Hoodoo Basin trail, about 5–6 air mi NW of Stinkingwater Peak, 22 Jul 1985, *Hartman and Nelson 21306* (RM).

#### ACKNOWLEDGMENTS

Support for this research was granted by the Natural Sciences and Engineering Research Council of Canada (NSERC grant #A3797) and by a University of Alberta Central Research Fund Grant (#55-47930). I thank Rob DeLuca, Dan Lebedyk, and Ledyard Stebbins for accompanying me in the field on various occasions and the curators of CAS, DAV, DS, GH, JEPS, NY, RM, UC, and US for the loan of specimens. I am grateful to Jim Morefield, Brett Purdy, Ledyard Stebbins, and John Strother for their helpful comments on earlier versions of this paper.

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(Received 18 Sep 1989; revision accepted 4 Jan 1990.)