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 infraspécific 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), indicat-
ing 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 autoploidy
derivatives of *A. pulchella*, but instead of hybrid polyploid origin
(Bayer 1989a). *Antennaria scabra* is often recognized as *A. alpina*
var. *scabra* (E. Greene) Jeppson, 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. Sev-
eral questions need to be addressed. Is diploid *A. pulchella* mor-
phologically distinct from polyploid *A. media* and, if so, what char-
acters 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

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 rep-
resenting the range of morphological variation in all taxa were se-
lected 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 mea-
sured. 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.
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 RMJ]). 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 sympathy 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.

Reflected in *A. pulchella* indicating that they are probably not simply autoploid 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 Sharpsmith 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**

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


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, scarious appendages at their tips (flags). Pistillate heads 4–6(3–7), in corymbose clusters; involucres 3.5–4.5(–6) mm high; phyllaries in 2 or 3 series, acute to blunt, scarious, 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 2.5(–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; involucres (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, Alberius 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); Pec-wec-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 Lebedyak CA-724 (ALTA, CAN, DAV, RM); trail to Matlock Lake, vicinity of Kearsarge Pass, 13 Jul 1987, Bayer, DeLuca, and Lebedyak 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 Lebedyak 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 Lebedyak CA-700 (ALTA, CAN, DAV, RM); exposed granite rocks, Pioche 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 Lebedyak CA-720 (ALTA, CAN, RM); H. M. Hall Natural Area, 30 Jun 1934, Blake 11822 (GH). Tulare Co.: Upper Franklin Lake,

**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-Ib*, 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-oblanceolate 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. monocarpa* DC., which occurs in mesic habitats on the margins of solifluxion 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. monocarpa*, so it cannot yet be compared to *A. corymbosa* or *A. pulchella*.


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

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 spathulate 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, scariosous appendages at their tips
(flags). Pistillate heads 4–7(2–9), in corymbose clusters and some-
times with elongate pedicels; involucre (4–)5–8 mm high; phyllaries
in 2 or 3 series, acute to blunt, scarios, 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–)4–6.5
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
17268 (ALTA); Jasper National Park, Sunwapt 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 Lilooet, 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

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