

Morphometric analysis of western North American *Antennaria* (Asteraceae: Inuleae). I. Sexual species of sections *Alpinae*, *Dioicae*, and *Plantaginifoliae*

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Eight sexual species of *Antennaria* Gaertner from sections *Alpinae*, *Dioicae*, and *Plantaginifoliae* have been recognized based on morphometric analyses such as principal components and cluster analyses. These taxa include *A. aromatica* Evert (*Alpinae*), *A. corymbosa* Nelson (*Dioicae*), *A. marginata* Greene (*Dioicae*), *A. media* Greene (*Alpinae*), *A. microphylla* Rydb. (*Dioicae*), *A. racemosa* Hook. (*Plantaginifoliae*), *A. rosulata* Rydb. (*Dioicae*), and *A. umbrinella* Rydb. (*Dioicae*). Taxa having both diploid and polyploid cytotypes are *A. aromatica*, *A. marginata*, *A. media*, *A. microphylla*, and *A. umbrinella*, whereas *A. corymbosa*, *A. racemosa*, and *A. rosulata* are strictly sexually reproducing diploids.

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Huit espèces sexuées du *Antennaria* Gaertner des sections *Alpinae*, *Dioicae*, et *Plantaginifoliae* ont été reconnues à la suite d'analyses morphométriques tels que les analyses en composantes principales et les groupements. Ces taxons comprennent les *A. aromatica* Evert (*Alpinae*), *A. corymbosa* Nelson (*Dioicae*), *A. marginata* Greene (*Dioicae*), *A. media* Greene (*Alpinae*), *A. microphylla* Rydb. (*Dioicae*), *A. racemosa* Hook. (*Plantaginifoliae*), *A. rosulata* Rydb. (*Dioicae*), et *A. umbrinella* Rydb. (*Dioicae*). Les taxons ayant à la fois des cytotypes diploïdes et polyplloïdes sont les *A. aromatica*, *A. marginata*, *A. media*, *A. microphylla*, et *A. umbrinella*, tandis que les *A. corymbosa*, *A. racemosa*, et *A. rosulata* sont exclusivement des diploïdes se reproduisant sexuellement.

[Traduit par la revue]

The genus *Antennaria* (Asteraceae: Inuleae) is widely distributed in temperate to arctic regions of the northern hemisphere as well as in the Andes of South America. The greatest diversity in *Antennaria* with respect to morphology, chromosome number, and reproductive mode is in the cordillera of western North America. Polyploidy, agamospermy, and sexual dioecism have all contributed to the morphological diversity in the group, and as a result, there has been a great deal of taxonomic confusion surrounding the species of western North America. The current paper considers a group of species that share the features of sexual seed production (amphimixis), stoloniferous growth form, and diploid chromosome number (with some autotetraploidy). It is likely that these species are the sexual progenitors of the *A. rosea* and *A. parviflora* polyploid agamic complexes (Bayer 1987a). The species considered here include *A. aromatica* Evert, *A. corymbosa* Nelson, *A. marginata* Greene, *A. media* Greene, *A. microphylla* Rydb., *A. racemosa* Hook., *A. rosulata* Rydb., and *A. umbrinella* Rydb. These taxa all occur in the western cordillera and adjacent plains of North America, chiefly the Rocky Mountain Floristic Region and the Great Basin Province of the Madrean Floristic Region (in the sense of Cronquist 1982; see Bayer and Stebbins (1987) for distribution maps of each of the species), and excluding the Canadian Province of the Circumboreal Floristic Region.

The species have been variously treated and, to date, no entirely satisfactory classification has been proposed for the group. Authors of most floristic treatments (Scoggan 1979; Porsild 1950; among many others) present classifications that attempt to recognize, at the rank of species, many entities that are essentially agamosperous clones (agamospecies). These classifications are largely artificial and, as such, are inadequate because they indiscriminately lump sexual diploids and tetraploids together with polyploid gametophytic apomicts of diverse genetic composition. The final classification of the genus will be one which better reflects the evolutionary history of *Antennaria*.

When studying complex groups, such as those in *Antennaria*, it seems best to use a multifaceted approach, considering data from phyto geography, morphology, cytology, reproductive mode, and biochemistry (primarily enzyme electrophoresis) (Bayer and Stebbins 1981, 1982, 1983; Bayer 1984, 1985a, 1985b; Bayer and Crawford 1986; Beaman 1957; Dickinson 1986a, 1986b; Muniyamma and Phipps 1979, 1985; Phipps and Muniyamma 1980; Richards 1973).

This morphological study is the first of several studies that will provide a revised classification for this assemblage of *Antennaria* species. The purposes of the current study are to analyze the morphological variation among the taxa and to discuss morphological similarities and differences among the taxa.

Materials and methods

Specimens were borrowed from CAN, DAO, GH, NDG, NY, RM, US, WIS, and WOCB for morphological studies. Table 1 lists the 42 characters that were used to construct the basic data matrix (25 vegetative and 17 reproductive) from 123 OTUs. The basic data matrix can be obtained from the author. Latitudes and longitudes of the collection sites were obtained from each specimen and were used to help determine whether any of the characters were correlated with geographic location.

Most of the species discussed in the paper are diploid and sexual, but with some notable exceptions. *Antennaria aromatica*, *A. marginata*, and *A. media* have presumed autopolyploid sexual and asexual derivatives that are almost indistinguishable morphologically from the sexual diploids (Bayer and Stebbins 1987). Asexual autotriploid and autotetraploid derivatives of *A. microphylla* are almost identical morphologically with the sexual diploid cytotypes (Bayer and Stebbins 1987). *Antennaria umbrinella* has sexual autotetraploid populations (Bayer and Stebbins 1987). To date, only *A. corymbosa*, *A. racemosa*, and *A. rosulata* are known to be strictly diploid and sexual (Bayer and Stebbins 1987). Further analysis may reveal ways to distinguish the different cytotypes of *A. aromatica*, *A. marginata*, *A. media*, *A. microphylla*, and *A. umbrinella*, but in this study they were considered as single entities. An effort was made to choose collections containing both staminate and pistillate individuals (i.e.,

TABLE 1. List of 42 characters and character states used in the numerical analysis of *Antennaria*. Numbers or letters following each character indicate the scale used or the qualitative state measurements. Latitude and longitude (characters 43 and 44) were determined for each OTU

Basal rosette characters

- (1) Length of entire basal leaf, mm. (2) Length of the petiole, mm. (3) Maximum width of the basal leaves, mm. (4) Length, along the mid-vein, from leaf tip to the maximum width, mm. (5) Shape of the anterior margin, i.e., length from tip to widest point in the leaf, mm. (6) Number of principal veins in the leaf. (7) Presence of a crinkled margin on the leaf, 0.0, absent; 1.0, present. (8) Adaxial leaf surface pubescence; 0.0, glabrous; 0.1, glabrous-villous; 0.2, villous; 0.3, pilose; 0.4, lanate; 0.5, tomentose; 1.0, canescent. (9) Number of leaves per basal rosette

Stolon characters

- (10) Number of leaves per stolon. (11) Length of the largest leaf, mm. (12) Width of the largest leaf, mm. (13) Length of the smallest leaf, mm. (14) Width of the smallest leaf, mm. (15) Stolon length, mm. (16) Number of stolons per basal rosette

Flowering stem (caulis) characters

- (17) Flowering stem height, mm. (18) Number of leaf nodes per caulis. (19) Width of the longest leaf, mm. (20) Length of the longest leaf, mm. (21) Width of the shortest leaf, mm. (22) Length of the shortest leaf, mm. (23) Presence of a scarious flaglike structure on the upper leaves; 0.0, absent; 1.0, present

Pistillate capitulescence characters

- (24) Height of the involucre, mm. (25) Number of heads per capitulescence. (26) Phyllary length, mm. (27) Phyllary width, mm. (28) Corolla length, mm. (29) Pappus length, mm. (30) Achene length, mm. (31) Phyllary colours; 1.0, green base, white tips; 2.0, green base, rose middle, white tips; 3.0, green base, black-brown middle, white tips; 4.0, green base, brown middle, rose tips; 5.0, green base, brownish tips; 6.0, brown base, white tips; 7.0, brown base, rose tips; 8.0, brown base, umber tips; 9.0, brown base, dark brown tips; 10.0, brown base, black or very dark green tips. (32) Number of florets per head.

Staminate capitulescence characters

- (33) Height of the involucre, mm. (34) Number of heads per capitulescence. (35) Phyllary length, mm. (37) Corolla length, mm. (38) Pappus length, mm

Miscellaneous characters

- (39) Presence of stalked glands on the surfaces of stems, leaves, etc.; 0.0, absent; 1.0, present. (40) Presence of staminate individuals in the population; 0.0, staminate absent (i.e., population all pistillate); 1.0, staminate present. (41) Pollen grain diameters (average of 25 grains), μm . (42) Chromosome number. (43) Latitude of collection site. (44) Longitude of collection site

amphimictic populations) for analysis. Taxa referred to as sexual and (or) diploid (e.g., *A. aromatica*, *A. marginata*, *A. media*, *A. microphylla*, and *A. umbrinella*) may in some cases include polyploids and (or) some asexuals.

Methodologies are similar to those employed in previous studies on eastern North American species of *Antennaria* (Bayer 1985a, 1985b). Principal components analyses (PCA) and cluster analyses were performed by the NT-SYS program of Rohlf *et al.* (1974). The data were standardized using STAND subroutine of NT-SYS, where the basic data matrix was transformed such that each character had a mean of zero and a standard deviation of unity (Sneath and Sokal 1973). The SIMINT subroutine was employed to compute the distance and similarity matrices. The distance coefficients were computed using the average taxonomic distance measure of Sokal (1961) as discussed by Sneath and Sokal (1973). Additionally, the similarity matrices of Pearson product moment correlation coefficients (Sneath and Sokal 1973) were computed by the SIMINT subroutine. Cluster analysis by the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal 1973) was computed by the TAXON subroutine, whereas the PCA (Sneath and Sokal 1973) was produced by the FACTOR subroutine of NT-SYS. Three factors were extracted by the PCA analysis. Three-dimensional coordinates produced by PCA were plotted by the MacSpin program (D², Software, Austin, Texas) and the axes were rotated using this program until suitable views were obtained. Univariate statistics (mean, median, mode, variance, and standard deviation) and bivariate analyses (bivariate scatter plots) were computed by the BMDP program of Dixon (1981). Principal components and cluster analyses were used to compare the diploid (and autotetraploid) taxa with each other. Computations were performed on the IBM computer at the Computer Centre of the University of Windsor.

Several data matrices were used in this study: (1) a 123 operational taxonomic unit (OTU) matrix consisting of 15 specimens each of *A. corymbosa*, *A. marginata*, *A. microphylla*, *A. media*, *A. racemosa*, *A. rosulata*, and *A. umbrinella*, 8 specimens of *A. aromatica* (only 8 were available of this narrowly restricted endemic), 1 type (holo- or lecto-type) specimen of each of these taxa (except *A. racemosa*; type not readily available), and the types of confused taxa such as *A. flavescens* Rydb., *A. macounii* Greene, and *A. pul-*

chella Greene; (2) a 105 OTU matrix, basically the same as matrix 1, except the 15 specimens of *A. racemosa* and the types of *A. flavescens*, *A. macounii*, and *A. pulchella* were removed; (3) a 41 OTU matrix with 15 specimens each of *A. media* and *A. umbrinella*, 8 specimens of *A. aromatica*, as well as the types (3 OTUs) of each of these taxa.

PCAs were performed on matrices 1 (displayed as Fig. 1), 2 (Figs. 2 and 3), and 3 (Figs. 4). Matrix number 1 (along with the 15 OTUs of *A. racemosa* removed) was used to construct a phenogram (Fig. 5) by the unweighted pair-group method (UPGMA) of cluster analysis. Bivariate analyses (bivariate scatter diagrams; Table 2) were performed on subsets of matrix 1 (each taxon analyzed separately), where each morphological character was plotted against latitude and longitude.

Results

The first PCA (Fig. 1) compares *A. racemosa* with the other diploid taxa. The first two factors account for 54.04% of the variation and the first seven factors have individual eigenvalues greater than 1.000 (indicating that the variables are not too highly correlated). High loadings for factor 1 are primarily vegetative features as well as the reproductive characters of phyllary colour and heads per capitulescence (aggregate of capitula). Factor 2 has high loadings for the characters such as pistillate involucre height and staminate and pistillate pappus length. Results for the first PCA (Fig. 1) show that *A. racemosa* is distinct from all other taxa. Because *A. racemosa* can be easily differentiated from the other taxa based on gross morphology, it was removed from the remaining analyses to allow a better scattering of the OTUs of the other taxa in three-dimensional space.

Figures 2 and 3 show two different views of the same PCA, in which the first three principal components account for 54.85% of the variation and the first nine factors have individual eigenvalues greater than 1.000. High loading for factor 1 include primarily vegetative characters as well as the features

TABLE 2. Correlation analysis of all characters contrasted with latitude and longitude

Character	ALL	ARO	COR	MAR	MED	ROS	UMB
1					+		-
2	-						
3	(-)				+		(-)
4	(-)						(-)
5	(-)						(-)
8	+,(+)						
9	-,(-)	-,(-)		(+)			
11					+		
12						-	(-)
14					+		
15				(-)			
16			-			(+)	(-)
17	-,(-)			(-)			
18	(-)						
20	+	+			+		
21	-						
24	-,(-)				(-)		
25	+						
26	-,(-)			(-)	(-)		
27	(-)				+,(-)	(+)	
28	-,(-)			(-)	(-)	(+)	
29	-,(-)			(-)	(-)		
31	+,(+)						
32	(-)						
33					+		
34	+	-,(-)					-
35	-				+		
36	-				+		
37	-				+		
38	-						

NOTE: Positive correlation ($p \leq 0.05$) of a character with latitude, +, negative, -; $p > 0.05$, blank. Correlation of characters with longitude is given in parentheses. The taxa are labeled with the first three letters of their specific epithets; ALL, all taxa analyzed as a single inclusive taxon. Character code designations are those given in Table 1 and only those characters that have significant correlation with latitude and longitude are included. *Antennaria microphylla* and *A. racemosa* lack significant correlation of characters with latitude or longitude.

of heads per capitulescence. Phyllary colour, adaxial leaf surface pubescence, and presence-absence of the scarious flag-like structure on the upper cauline leaves have the highest loadings in factor 2, whereas several vegetative features and phyllary colour have the highest loadings in factor 3. Phyllary colour is not highly correlated with any other morphological character but appears to be one of the best key characters for distinguishing among taxa. In Fig. 2, *A. corymbosa*, *A. microphylla*, and *A. rosulata* form well-defined groups of OTUs, while in Fig. 3, *A. marginata*, *A. corymbosa*, and *A. rosulata* are distinct. *Antennaria aromatica* is somewhat distinct (Figs. 2 and 3), although it overlaps with other clusters of OTUs. *Antennaria aromatica*, *A. media*, and *A. umbrinella* form a group of taxa that are similar morphologically.

In an effort to try to attain separation of these groups, morphologically distinct groups (*A. corymbosa*, *A. marginata*, *A. microphylla*, and *A. rosulata*) were removed from the next analysis. The result (Fig. 4) demonstrates that the three taxa *A. aromatica*, *A. media*, and *A. umbrinella* are morphologically distinct in that they do form rather well-defined morphological clusters. In this PCA (Fig. 4), the first three factors account for 56.17% of the variation and the first nine factors have individual eigenvalues greater than 1.000. High loading for factor 1 are several vegetative features, as well as char-

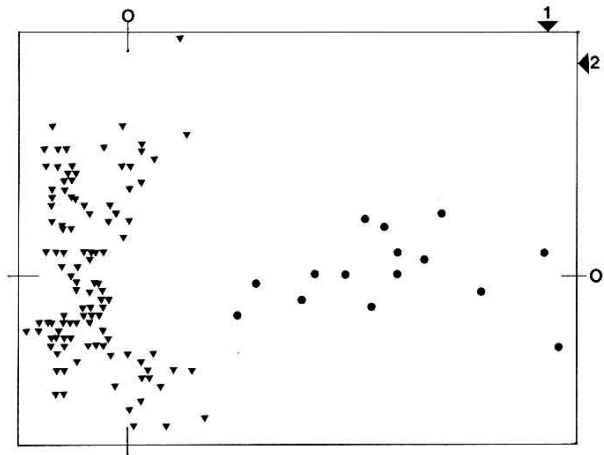


FIG. 1. PCA composed of 123 OTUs of *Antennaria racemosa* (●) and the small-leaved *Antennariae* (▲) composed of *A. aromatica*, *A. corymbosa*, *A. marginata*, *A. microphylla*, *A. media*, *A. rosulata*, and *A. umbrinella*. Factors 1 and 2 are labeled with arrowheads.

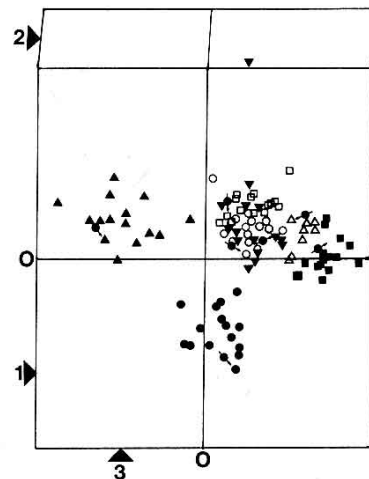


FIG. 2. PCA composed of 105 OTUs of *Antennaria aromatica* (△), *A. corymbosa* (▲), *A. marginata* (▼), *A. microphylla* (●), *A. media* (□), *A. rosulata* (■), and *A. umbrinella* (○). Types are indicated by circles with arrows pointing at an OTU with the same epithet as the type. Factors 1, 2, and 3 are labeled with arrowheads. This three-dimensional graph was obtained by rotation of PCA using the MacSpin program (D² Software, Austin, Texas).

acteristics of the staminate capitula. Factor 2 has highest loadings for pistillate reproductive characters and the "flag" character (Table 1, no. 23), whereas stolon features and phyllary colour have the highest loadings in factor 3. The type specimens of each of the taxa (except *A. racemosa*, which was unavailable for measurement) are included within each respective conspecific group in PCA.

The cluster analysis of matrix 2 (Fig. 5) is concordant with the results obtained from the PCA (Figs. 2 and 3) of that matrix. *Antennaria aromatica*, *A. corymbosa*, *A. marginata*, *A. microphylla*, and *A. rosulata* each form very distinct morphological clusters, while *A. media* and *A. umbrinella* form small morphological units that are split and intermingled among one another. One unusual OTU, which was assigned to

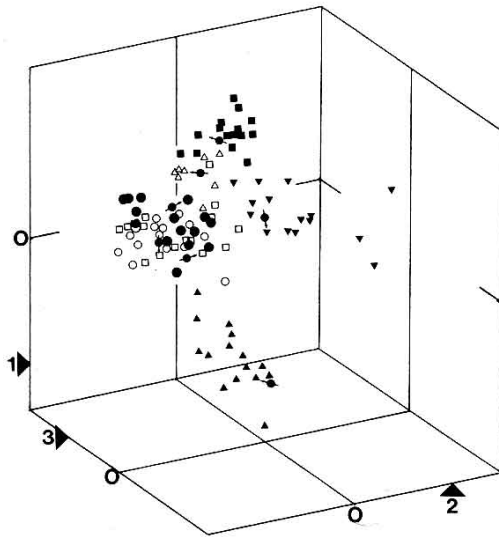


FIG. 3. PCA composed of 105 OTUs of *Antennaria aromatica* (Δ), *A. corymbosa* (\blacktriangle), *A. marginata* (\blacktriangledown), *A. microphylla* (\bullet), *A. media* (\square), *A. rosulata* (\blacksquare), and *A. umbrinella* (\circ). Types are indicated by circles with arrows pointing at an OTU with the same epithet as the type. Factors 1, 2, and 3 are labeled with arrowheads. This three-dimensional graph was obtained by rotation of PCA using the MacSpin program (D² Software, Austin, Texas).

A. media, clusters with *A. aromatica* and may actually be an allopolyploid that is intermediate between *A. aromatica* and *A. media*. The type specimen of each taxon is always associated within the proper conspecific group. The type of *A. pulchella* is associated closely within an *A. media* group with the type of *A. media*, whereas the types of *A. macounii* and *A. flavescens* are more closely allied to *A. umbrinella*.

Many characters appear to show some clinal variation with changes in latitude and longitude. This is true not only when all species are considered as a single taxon (Table 2, ALL) but when characters of individual taxa are compared with latitude and longitude. Many trends are evident, but some of the more general and (or) important ones are summarized below. As one considers a path from the south and eastern part of the ranges (New Mexico and Colorado, for example) to areas to the north and west, the leaves of *Antennaria* species become smaller in most respects and become increasingly pubescent. In general, there is a tendency toward shorter flowering stems with smaller and fewer leaves in the area toward the north and west. Plants in the north tend to have more staminate and pistillate heads per capitulescence. In the north and west, plants are generally smaller in all dimensions with respect to characters of the pistillate and, to a lesser extent, staminate heads. Phyllary colour is correlated with latitude and longitude and there is a trend toward the north and west for plants to have phyllaries that are darkest in colour. *Antennaria marginata*, *A. microphylla*, and *A. rosulata*, which have light-coloured phyllaries, are common in the southern parts of the range and *A. media* and *A. umbrinella*, with dark phyllaries, become more prevalent in the northern Rockies. The very dark-phyllaried *A. alpina* complex occurs in arctic Canada and Alaska. Most individual taxa show a few correlations of characters with latitude and longitude and these are concordant with the generalizations given above with a few notable exceptions. In *A. media*, many basal leaf characters, caulis characters, as well as characters of the

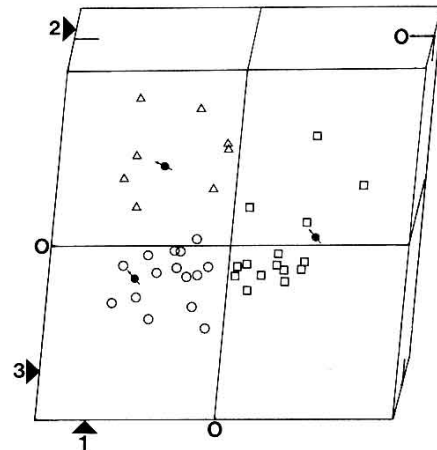


FIG. 4. PCA composed of 41 OTUs of *Antennaria aromatica* (Δ), *A. media* (\square), and *A. umbrinella* (\circ). Types are indicated by circles with arrows pointing at an OTU with the same epithet as the type. Factors 1, 2, and 3 are labeled with arrowheads. This three-dimensional graph was obtained by rotation of PCA using the MacSpin program (D² Software, Austin, Texas).

staminate involucre increase with latitude. Note that there is increased polyploidy in this species in the northern and eastern portions of the range of this taxon (see Bayer and Stebbins 1987). Clinal trends in *A. umbrinella* are all oriented in a latitudinal direction and the characters tend to decrease in size in the western part of the range.

Discussion

Generally, the sexual species of *Antennaria* are morphologically distinct without a morphological continuum between and among the taxa. This is true not only for *Antennaria* but also for sexual members of most agamic complexes such as those in *Crepis* (Asteraceae) (Babcock and Stebbins 1938) and *Hieracium* (Asteraceae), *Taraxacum* (Asteraceae) (Richards 1973), and *Rubus* (Rosaceae) (Grant 1981). In this study it has been shown that *A. corymbosa*, *A. marginata*, *A. microphylla*, *A. racemosa*, and *A. rosulata* are well defined morphologically. This is indicated by PCA (Figs. 1, 3), cluster analysis (Fig. 5).

Antennaria racemosa is the most recognizable of the taxa, with its large (three- to five-nerved) basal leaves; it is most similar morphologically (Bayer 1985b) and biochemically (Bayer and Crawford 1986) to large-leaved eastern species such as *A. plantaginifolia* (L.) Richards., *A. parlinii* Fern., and *A. solitaria* Rydb. *Antennaria marginata* and *A. rosulata* are the two species that commonly occur in steppe and montane habitats in the southern Rockies. The glabrous, bright green, white-margined basal leaves of *A. marginata* make it easily recognizable (Figs. 3, 5). *Antennaria rosulata* is characterized by having small, silvery, pubescent basal leaves with a capitulescence composed of solitary (rarely two) heads on a short (1–2 cm) flowering stem or caulis (Figs. 3, 5). The basal leaves of *A. rosulata* and *A. microphylla* are similar, but the two are very different with respect to their flowering stems and distribution. *Antennaria microphylla* has tall flowering stems (10.0–29.0 cm; 20.0 cm on average) that are pleiocephalous (6–13 heads; average of 10 heads/capitulescence) and occurs in the northern Rockies and adjacent plains. The phyllaries of *A. microphylla* are green based with white tips as

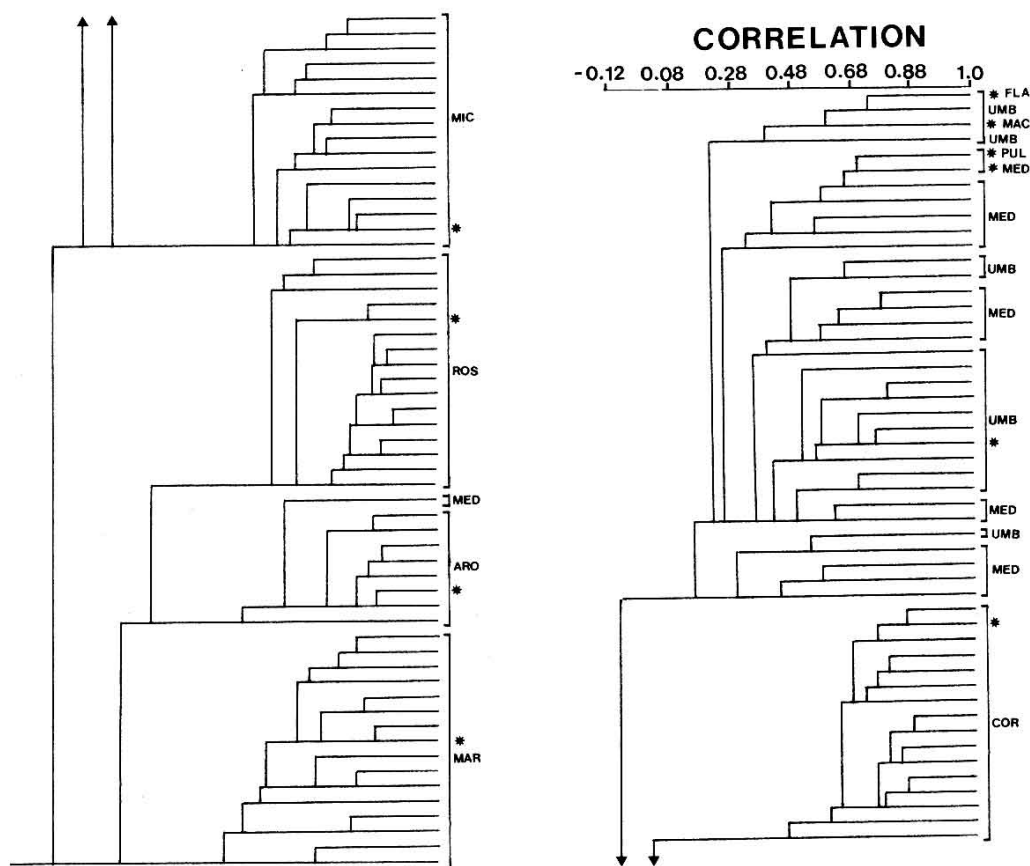


FIG. 5. Correlation phenogram (UPGMA) composed of 108 OTUs of seven species of *Antennaria* including *A. aromatica*, *A. corymbosa*, *A. marginata*, *A. microphylla*, *A. media*, *A. rosulata*, and *A. umbrinella*, their types (indicated by an asterisk), and the types of *A. flavescens*, *A. macounii*, and *A. pulchella*. Taxa are labeled with the first three letters of the specific epithets. Cophenetic correlation coefficient is 0.86.

opposed to those of *A. corymbosa*, which have a distinctive black dot at the base. *Antennaria corymbosa* is the most mesophytic of the taxa discussed, growing in *Salix* thickets, along streams and lakes, in the subalpine zone of the northern Rockies and Sierras and is differentiated based on its long, narrow basal leaves and characteristic phyllaries (Figs. 2 and 3).

Antennaria aromatica, *A. media*, and *A. umbrinella* remain as problematic taxa. They are similar morphologically and at times tend to intergrade into one another. *Antennaria aromatica* is perhaps the most distinct of the group (Figs. 3, 4). It occurs in a restricted area of southwestern Montana and adjacent areas of Idaho and Wyoming and is usually associated with strict edaphic conditions such as limestone talus in subalpine zones.

Antennaria media and *A. umbrinella* are usually well-defined morphological groups (Fig. 4). Douglas *et al.* (1977) found that phenolic substances (flavonoids) taken from *A. media* (= *A. alpina* var. *media*), *A. microphylla*, and *A. umbrinella* were very similar and as a result came to the conclusion that the three taxa should be merged into a single taxon. However, no mention is made of the reproductive mode of their sample populations. Additionally, phyllary colour was used to determine taxa, which can be an unreliable means of identifying taxa, especially when the reproductive mode of the population has not been determined or considered. Most of the

populations studied by Douglas *et al.* (1977) are probably segregates of *A. rosea* because (i) they were collected outside the known range of the species they have determined them as and (ii) because many *A. rosea* segregates resemble *A. umbrinella*, *A. media*, and *A. microphylla* because the latter have probably contributed genes to the *A. rosea* agamic complex (Bayer 1987a).

Antennaria umbrinella typically occurs in *Pinus ponderosa* woodlands or open *Artemisia tridentata* steppe, while *A. media* is strictly alpine or high subalpine. The species are best differentiated based on phyllary colour, those of *A. media* being very dark green or black, whereas those of *A. umbrinella* range from very light brown to dark brown. The stolons of *A. media* (especially the diploid cytotypes) are humifuse and herbaceous with reduced leaves at their proximal tips, but those of *A. umbrinella* are usually distinctly ascending and have a tendency toward woodiness. Additionally, the reproductive mode of plants in a given locality are useful. For example, *A. umbrinella* is always sexual and has equal frequency of staminate and pistillate individuals in its populations, but *A. media* is sexual primarily in California, eastern Oregon, and eastern Washington (G. L. Stebbins, unpublished observation), i.e., places where populations of *A. umbrinella* are absent or very infrequent. *Antennaria media* is asexual, having only pistillate clones in its populations, over most of its area of sympatry with *A. umbrinella*. Both species contain sexual

diploid and tetraploid cytotypes. Data on the distribution of cytotypes are scanty, but a general pattern is emerging (Bayer and Stebbins 1987). Diploid cytotypes of *A. media* (referable to the type of *A. pulchella*) occur in the Sierra Nevada and Inyo Mountains, while polyploids are widespread throughout its range (see Bayer and Stebbins (1987) for distribution maps). There is clinal variation (Table 2) in the size of the plants; those in the Californian part of the range tend to be smaller (i.e., are diploid or tetraploid), whereas those from the north-eastern part of the range are larger in most respects (i.e., tetraploids or higher). The diploid cytotype of *A. umbrinella* is known from only a few localities in Idaho, Montana, Oregon, and Wyoming and is tetraploid elsewhere including all of its range in Canada (Chinnappa 1983). If it is presumed that the polyploids were derived from diploids, then the two entities arose allopatrically in different areas of the western Cordillera. Ongoing crossing, ecological, and isozyme studies (R. J. Bayer, unpublished) seem to support *A. aromatica*, *A. media*, and *A. umbrinella* as distinct species based on the available cytological, phytogeographical, and morphological data. Whether diploid cytotypes of *A. media* (= *A. pulchella*) and *A. umbrinella* should be given taxonomic recognition will depend on whether morphological characters can be found that will reliably separate the two categories of cytotypes.

In areas where two or more sexual species cooccur, naturally occurring interspecific hybrids and backcross progeny may be found. Naturally occurring hybrids in *Antennaria* have been documented many times (Juel 1900; Stebbins 1932a; Bayer and Stebbins 1982, 1987; Bayer 1984). Based on field experience and hybrids collected from these sites, three types have been classified as probable interspecific hybrids according to morphology. *Antennaria erigeroides* appear to be a hybrid between *A. corymbosa* and *A. racemosa* compared with another putative hybrid from Idaho (Bayer and Stebbins I-302 in DAV and OS). Several naturally occurring hybrids between *A. racemosa* and *A. umbrinella* (Bayer and Stebbins 8086 in DAV, OS, and ALTA; Bayer and Lebedyk WY-519 in RM and ALTA; Bayer, Lebedyk, and Joncas WY-619 in ALTA) are similar to the type of *A. oblancifolia*. Although hybrids between *A. microphylla* and *A. racemosa* have not been seen in the field, herbarium specimens, including the type of *A. foliacea*, are representative of what a hybrid between these two species might resemble.

Preliminary investigations into the ecology of these eight taxa (R. J. Bayer, unpublished) are beginning to demonstrate that each of them have distinct habitat requirements. The primary ecological parameters involved in determining which species of *Antennaria* may occur at a given site may include factors such as elevation, slope, and edaphic characteristics. Some species such as *A. aromatica* seem to have rather strict ecological requirements (i.e., usually occur on limestone talus in the subalpine zone), whereas others such as *A. umbrinella* have less strict requirements and occur on dry sagebrush steppe, through the Ponderosa pine zone, up to treeline.

The sexual diploid and autotetraploid species in *Antennaria*, as a rule, are morphologically distinct from one another. This was demonstrated when similar analyses were used when studying sexuals and polyploids of eastern North America (Bayer and Stebbins 1982; Bayer 1985a), where the diploids *A. neglecta* Greene, *A. plantaginifolia*, *A. solitaria*, and *A. virginica* Stebbins were found to be distinct morphologically from one another. Problems arise when the polyploid agamic complexes are considered because they are of multiple

hybrid origin from the diploids and may be confluent morphologically with them (Bayer 1987a). This was well noted by Babcock and Stebbins (1938) in their classic study of *Crepis* L. (Asteraceae) and in other genera in recent years (Grant 1981). It has been demonstrated that other agamic complexes in *Antennaria* are of hybrid origin and have absorbed genomes from few to many sexual diploid (or sexual tetraploid) species (Juel 1900; Stebbins 1932a, 1932b; Bayer and Stebbins 1983; Bayer 1985a, 1985b, Bayer and Crawford 1986).

The *A. rosea* polyploid agamic complex is certainly related to at least seven of the sexual taxa, especially, *A. corymbosa*, *A. media*, *A. microphylla*, and *A. umbrinella* and to a lesser extent *A. aromatica*, *A. racemosa*, and *A. rosulata* (Bayer 1987a). *Antennaria marginata* is probably more closely allied with the *A. parvifolia* agamic complex (R. J. Bayer, personal observation). Indeed most of the taxonomic difficulties among these species occur when the polyploid *A. rosea* is considered because some of the polyploid segregates tend to be morphologically confluent with their sexual progenitors. This leads to taxonomic problems because individuals that are asexual and polyploid and are derivatives of primarily one sexual species (agamic autopolyploids) must be treated taxonomically as belonging to the sexual species because they are morphologically inseparable from that species.

Babcock and Stebbins (1938) devised a system for classifying genera that were taxonomically complex as a result of polyploidy and apomixis, but which would reflect the evolutionary relationships among the species as well. In this system, sexual diploids and their autopolyploid derivatives were all given specific rank. The hybrid polyploids (allopolyploids) that were derived from two or more of these diploids, whether they were sexual or asexual, were given their own specific rank. The reasoning behind this is that because the polyploids are of diverse genetic composition, they cannot be referred morphologically or taxonomically to any of the diploids. Bayer and Stebbins (1982) followed this methodology when revising the species of *Antennaria* of the eastern United States. It is best to continue to employ this system when reclassifying the taxa considered in this paper and as a result eight sexually reproducing taxa are recognized: *A. aromatica*, *A. corymbosa*, *A. marginata*, *A. media*, *A. microphylla*, *A. racemosa*, *A. rosulata*, and *A. umbrinella*. A list of synonymy and typification for these taxa may be found in Bayer (1987b).

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