

A phylogenetic reconstruction of *Antennaria* (Asteraceae: Inuleae)

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A cladistic analysis of 32 sexually reproducing species of *Antennaria* Gaertn. revealed that the genus comprises five constitutive monophyletic groups: Geyeriae, Argenteae, Dimorphae, Pulcherrimae, and Catipes. Three of the groups, Argenteae, Dimorphae, and Geyeriae, have retained relatively large numbers of plesiomorphic characters. The members of these three groups are mostly nonstoloniferous and have not evolved characters often associated with sexual dimorphism that occur in the remainder of *Antennaria*. Consequently these three groups closely resemble the suprageneric outgroup, *Anaphalis* and *Gnaphalium*. The Pulcherrimae and Catipes represent the most specialized groups. These two groups have wider distributions and occur in a much greater diversity of habitats than the Argenteae, Dimorphae, and Geyeriae. Evolutionary advancement in the genus has been toward dioecism and coincident sexual dimorphism, probably as a method to promote outcrossing. In addition, polyploidy and two asexual means of reproduction, agamospermy and horizontal stolons, have evolved in the more specialized groups, the Pulcherrimae and Catipes. *Antennaria* probably arose from Mexican *Gnaphalium* sometime during the Oligocene or Miocene, migrated into the western United States where it has evolved and migrated into other areas of the northern hemisphere and South America.

Key words: *Antennaria*, Asteraceae, Inuleae, cladistics phylogeny, biogeography.

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Une analyse cladistique de 32 espèces du *Antennaria* Gaertn. se reproduisant sexuellement, a révélé que le genre comprend cinq groupes monophylétiques constitutifs : Geyeriae, Argenteae, Dimorphae, Pulcherrimae et Catipes. Trois de ces groupes (Argenteae, Dimorphae et Geyeriae) ont retenu des nombres assez importants de caractères plésiomorphes. Les membres de ces trois groupes sont surtout non stolonifères et n'ont pas évolué de caractères souvent associés au dimorphisme sexuel rencontré chez les autres *Antennaria*. Ainsi, ces trois groupes ressemblent étroitement au hors-groupe supragénérique, *Anaphalis* et *Gnaphalium*. Les Pulcherrimae et Catipes représentent les groupes les plus spécialisés. Ces deux groupes ont une plus grande distribution et se retrouvent dans une plus grande diversité d'habitats que les Argenteae, Dimorphae et Geyeriae. La tendance évolutive dans le genre a été vers la dioécie et le dimorphisme sexuel coïncidents, probablement comme une méthode de promouvoir la xénogamie. De surcroît, la polyploidie et deux types de reproduction asexuée, agamospermie et des stolons horizontaux, sont apparus dans les groupes les plus spécialisés, les Pulcherrimae et Catipes. L'*Antennaria* est probablement apparu au cours de l'Oligocène ou du Miocène, issu du *Gnaphalium* mexicain, et s'est déplacé vers l'ouest des États-Unis où il a évolué et s'est propagé à d'autres régions de l'hémisphère nord et de l'Amérique du Sud.

Mots clés : *Antennaria*, Asteraceae, Inuleae, cladistique, phylogénie, biogéographie.

[Traduit par la revue]

The genus *Antennaria* Gaertn. (Asteraceae: Inuleae: Gnaphaliinae) consists of 37 to 40 species in temperate to arctic regions of the Northern Hemisphere and South America, with its center of diversity in western North America. Thirty-two of these species are sexually reproducing diploids and (or) polyploids. The remaining species represent the several polyploid agamic complexes within the genus (Bayer 1987a). The majority of the taxonomic problems in the genus are associated with these polyploid complexes. The vast morphological variability in the polyploid complexes is the result of hybridization among the sexual species, these hybrid combinations being preserved by gametophytic apomixis (Bayer 1985a, 1985b, 1987a, 1990). Conversely, the sexual species are typically morphologically distinct from each other and consequently have fewer taxonomic problems (Bayer 1987a). Those isolated taxonomic problems that were present among the sexual species have been largely addressed (Bayer 1987b, 1988a, 1988b, 1989b, 1989d; Bayer and Stebbins 1982).

Antennaria is closely related to *Gnaphalium* L. (Bayer and Stebbins 1981; Bayer 1984; Bayer and Stebbins 1987). *Anaphalis* DC. could be the sister group to *Antennaria* because they are both dioecious and based on $x = 14$, while *Gnaphalium* is hermaphroditic or monoecious and based on $x = 7$. It is likely that both *Antennaria* and its close relative *Anaphalis* DC. were derived as dioecious (sometimes polygamodioe-

cius) offshoots of primarily hermaphroditic or polygamous *Gnaphalium* because dioecious breeding systems often evolve from hermaphroditic ones via monoecy (Bawa 1980). Additionally, most members of the subtribe Gnaphaliinae are either homogamous with hermaphroditic flowers or polygamous (Hilliard and Burt 1981). Some perfect florets are occasionally found in some *Antennaria* and quite frequently in *Anaphalis* species, indicating that some plants within these genera are polygamodioecious. However, it is uncertain whether dioecy in *Antennaria* and *Anaphalis* is a homologous or homoplastic feature.

Anaphalis is north temperate, primarily Asian, in distribution with 25–30 (65) species, whereas *Gnaphalium* is cosmopolitan with a disputable 150–200 species worldwide (Merxmüller 1974). Recently Hilliard and Burt (1981) proposed the split of *Gnaphalium* into two segregate genera, *Gnaphalium* sensu stricto and *Pseudognaphalium* Kirpiczn., based primarily on the characteristics of the stereome. The anatomy of the stereome, the thickened base of the phyllary, has been identified as an important taxonomic character at the generic level in the Gnaphaliinae (Drury 1970; Hilliard and Burt 1981). At this time it is uncertain whether these two groups will be accepted as taxonomically usable groups by other workers in the Inuleae, especially because the majority of the species of *Gnaphalium* sensu lato have not yet been reclassified. Until the new world species of *Gnaphalium* sensu lato

can be investigated systematically, I think it best to recognize all the species as belonging to *Gnaphalium*.

Based on present day distributions, it is probable that *Antennaria* and *Anaphalis* arose from different portions of the genus *Gnaphalium* sensu lato, *Antennaria* from the Mexican species of the genus and *Anaphalis* from the Asian species complex. It is not clear whether *Gnaphalium* or *Anaphalis* should be regarded as the sister group of *Antennaria*, which is partially the result of our very incomplete knowledge of both *Anaphalis* and *Gnaphalium*.

A monograph of *Antennaria* has never been presented and consequently the subgeneric relationships within the genus have never been discussed in any detail. Authors have often recognized subgeneric groups based on phenetic differences, but not on phylogeny. The purpose of this paper is to present a phylogeny of *Antennaria* that will help delimit monophyletic subgroups within the genus. This morphologically based phylogenetic hypothesis can then be compared to phylogenies based on other methods such as chloroplast DNA restriction analyses.

Materials and methods

Specimens of *Antennaria* were borrowed for morphological study from various herbaria, including ALA, CAN, DAO, F, MONTU, NDG, NY, RM, and US. Additionally, extensive collections at ALTA were utilized. *Gnaphalium* and *Anaphalis* were used as a suprageneric outgroup in this analysis. Specimens of about 30 species of Central American and a few North American *Gnaphalium* were borrowed from TEX. The species that were examined as members of the outgroup include *Anaphalis margaritacea* (L.) Benth. & Hook., *A. triplinervis* Benth., *Gnaphalium acediocephalum* (Grierson) L. O. Williams, *G. altamiranum* Greenm., *G. attenuatum* DC., *G. brachyphyllum* Greenm., *G. brachypterum* DC., *G. canescens* DC., *G. conoideum* HBK., *G. ehrenbergianum* Schultz-Bip., *G. eleagnoides* (Klatt) Blake, *G. greenmanii* Blake, *G. hintoniiorum* Turner, *G. inornatum* DC., *G. jaliscense* Greenm., *G. lavendulifolium* (HBK.) Blake, *G. liebmannii* Schultz-Bip., *G. macounii* Greene, *G. oxyphyllum* DC., *G. palustre* Nutt., *G. roseum* HBK., *G. schraderi* DC., *G. stolonatum* Blake, *G. stramineum* HBK., and *G. viscosum* HBK. In many cases several specimens of each species were examined to determine the degree of intraspecific variation of characters. The sizeable living collections of *Antennaria*, *Anaphalis*, and *Gnaphalium* maintained in the phytotron at the University of Alberta, as well as 10 years of field experience, were used as the basis for assessing the leaf-odor characteristics.

Four basic steps were followed in the phylogenetic analysis: selection of taxa, selection of characters and their states, polarization of the character states, and cladogram construction. These are discussed in detail below.

Selection of the taxa

Only those taxa that reproduce sexually and are of nonhybrid origin were included in this study. The term sexual is used throughout the paper to describe sporophytes that possess sexually reproducing gametophytes. Although it is possible to include hybrid polyploids (i.e., allopolyploids) within the analysis (Funk 1985), this leads to reticulations in the hierarchy. One method of dealing with hybrids in a cladistic analysis, assuming they can be identified, is to remove them prior to the analysis (Humphries and Funk 1984; Funk 1985). The five polyploid complexes in *Antennaria*, including *A. alpina* (L.) Gaertn. s.l., *A. howellii* Greene s.l., *A. parvifolia* Nutt. s.l., *A. parlinii* Fern. s.l., and *A. rosea* Greene s.l., are of multiple hybrid origin, sometimes involving up to as many as eight sexual species in the evolutionary history of the particular complex (Bayer 1985a, 1985b, 1987a, 1989c, 1990; Bayer and Crawford 1986). These hybrid poly-

ploids, having been identified based on both morphology and biochemical genetics, have been excluded from this analysis.

With respect to circumscription of taxa, I have followed recent revisions, treatments, and guidelines by Bayer and Stebbins (1982, 1987) and Bayer (1988a, 1989a, 1989d). I have included species from group 1 (diploids and polyploids from sections not containing apomicts) and group 2 (sexual diploids and polyploids from sections containing apomicts) as defined and outlined by Bayer and Stebbins (1987). Species circumscription within the Pulcherrima/Carpatia group, including *A. anaphaloides* Rydb., *A. carpatica* (Wahlb.) Bl. & Fingerh., *A. eucosma* Fern., *A. lanata* (Hook.) Greene, *A. pulcherrima* (Hook.) Greene, and *A. villifera* Boriss. follows the recommendations of Urbanska (1983a, 1983b). In most cases, my species delimitations agree with those recognized by Cronquist (1955) and Sharsmith (1960), which address most of the western North American species used in the analysis. Notable exceptions are my circumscription of *A. luzuloides* T.&G. to include *A. microcephala* A. Gray and the recognition of *A. microphylla* Rydb., which both Cronquist (1955) and Sharsmith (1960) subsume into *A. rosea*.

Selection of characters and their states

Characters chosen for inclusion within the cladistic analysis are those that had little or no infraspecific variation. Characters that have been traditionally used as diagnostic taxonomic characters have been included whenever possible. When a character was found to have some infraspecific variation, the predominant state was the one recorded. Small amounts of data are missing, the result of a lack of living material defeated the scoring of the leaf-odor character. Comparison of mature staminate and pistillate plant heights (Table 1; character 4) could not be scored in *A. rosulata* because the species essentially lacks the character due to extreme stem reduction. Twenty-seven, presumably homologous, characters were used in the final analysis (Table 1).

Polarization of the character states

Several authors have discussed methods of determining character state polarization (Crisci and Stuessy 1980; Donoghue and Cantino 1984; Stuessy and Crisci 1984; Wiley 1980) and most agree that the outgroup method is most satisfactory. *Gnaphalium* and *Anaphalis* are used as the suprageneric outgroup in the phylogenetic reconstruction of *Antennaria*, because the determination of a sister group for *Antennaria* is problematical. Only those characters that have the same state in both *Anaphalis* and *Gnaphalium* have been included in the analysis as way of assuring that the characters are correctly polarized. The commonly occurring state in the suprageneric outgroup was taken as least derived (= plesiomorphous). One character, synflorescence branching (Table 1; characters 20a-c), is a multistate character and therefore the data were transformed into a series of three, two-state characters, following the procedure outlined in Felsenstein (PHYLIP manual, version 2.9).

Cladogram construction

The PHYLIP package of programs (Phylogeny Inference Package, version 2.9) developed by Joe Felsenstein was used to perform the cladistic analysis. The number of species in the analysis (32) is large and therefore a considerable number of trees are possible. The MIX program employing Wagner parsimony and the global branch swapping option (G) was used in an attempt to find the most parsimonious tree. An ancestor was specified using the ancestor option (A) of the MIX program, where all character states as they occur in the outgroup were designated as primitive. The MIX program was compiled, using TURBO PASCAL (Borland International, Inc.), and run on an IBM-PC compatible computer. The program was executed 15 times on the data set (Table 2) and the order of entry of taxa was varied for each run.

Results and discussion

Character selection and polarization

A list of 27 characters selected for inclusion in the phylogenetic reconstruction and their states is presented in Table 1.

The basic data matrix (Table 2) lists the 32 species and their states for each of the 27 characters. The majority of the *Gnaphalium* and both *Anaphalis* species that were investigated possess the plesiomorphous states for these characters. Eleven of the 23 *Gnaphalium* species possess the apomorphous state for some characters including the following: *Gnaphalium aecidiocephalum* (apomorphous state for characters 1, 14, 20, 23, 24, 26), *G. brachyphyllum* (25), *G. brachypterum* (21), *G. eleagnoides* (23, 24, 26), *G. hintoniorum* (15), *G. jaliscense* (21), *G. lavendulifolium* (11, 14, 20, 21, 24, 26), *G. macounii* (8, 15), *G. oxyphyllum* (8, 15), *G. stolonatum* (5, 9, 20, 24), and *G. viscosum* (8, 15, 21). The odor character (19) is sometimes difficult to evaluate in herbarium material, but my experience with fresh material of *Anaphalis* and *Gnaphalium* is that they are either odorless or have a strong cudweed (tobacco) odor. This cudweed odor is very strong even in some herbarium material (i.e., as in *A. margaritacea*). I don't know of any *Anaphalis* or *Gnaphalium* that has the citronella odor that is characteristic of some species of *Antennaria*.

Most members of *Gnaphalium* from Mexico and North America are herbaceous plants, much greater than 10 cm tall, that lack basal leaves, have cauline leaves of similar shape that remain the same size distally up the stem, lack flags and purple glandular hairs on the upper cauline leaves, bear short, erect, glabrous stolons or lack stolons, have adaxially and abaxially pubescent, sessile, more or less linear leaves that are thin in texture and lack the odor of citronella, possess a highly branched, polycephalous synflorescence of cylindrical to campanulate heads, have basally pubescent, light and uniformly colored, acute phyllaries of similar shape and size, produce unpigmented, actinomorphic corollas and have pappus that are only slightly dilated toward the tips. *Anaphalis* is similar to *Gnaphalium*, except it is rhizomatous and dioecious. The staminate *Anaphalis* plants at maturity are the same height as the pistillate plants, a feature considered plesiomorphous.

Reconstruction of the phylogeny

Fifteen cladograms were obtained from the analysis, ranging in length from 96 to 102 steps. The general topology remained the same in all the trees that were obtained; i.e., the basic groups or clades that are discussed in this paper (Geyeriae, Argenteae, Dimorphae, Pulcherrimae, and Catipes) were always present and always contained the same taxa. The greatest amount of variation in the cladograms appeared in the ultimate clades, especially in the relationships among the taxa in the Catipes group. The Alpinae clade usually contained the same taxa, although in some analyses *A. umbrinella* was included in the clade. The Dioicae and Umbrinellae clades obtained the least stable relationships among the trees. Consequently, a much greater amount of confidence can be placed on the structure of the major clades in the tree presented in this paper (Fig. 1), but less reliable are the relationships of members of the Dioicae/Umbrinellae clades.

One of the most parsimonious cladograms obtained contained 97 character state changes and is presented as Fig. 1. I present this cladogram because it most closely approached my intuitive phylogeny for *Antennaria* and was only one step longer than the most parsimonious tree. There are 26 reversals and 40 parallelisms, generating a total homoplasy of 68.0%. The high level of homoplasy is comparable to that obtained in other studies of Asteraceous groups (57% in *Coreopsis*, Jansen et al. 1987; 50% in *Acmella*, Jansen 1985; 80% in *Montanoa*,

Funk 1982). In the following discussion, numbers in parentheses refer to characters designated in Table 1 and portrayed in Fig. 1.

Several characters, the secondary apomorphies, display a number of parallelisms and reversals within the group, including caulis height (2), cauline leaf shape (4), stolon pubescence (12), number of principal veins in basal leaves (18), synflorescence branching pattern (20), corolla pigmentation (26), and staminate pappus type (27). Conversely, some characters, the primary apomorphies, display few or no parallel character changes or reversals, including staminate plant height (unique change, 3), leaf pubescence on abaxial surface (an autapomorphy, 16), pistillate capitulum shape (unique change, 21), staminate phyllary shape (unique change, 22), basal rosette condition (unique change, 5), cauline leaf size (one reversal, 6), stolon type (one parallel change, 11), odor of young leaves (one parallel change, 19), and caudex characteristics (one parallel change, 1).

Inspection of the cladogram (Fig. 1) reveals that several monophyletic groups can be recognized within *Antennaria*. A careful search of the literature indicates that subgeneric categories in *Antennaria* have never been formally discussed at a generic level. Borissova (1959) devised some sections and series in *Antennaria* for the Eurasian taxa, but these account for only three of those discussed in this study. Rydberg (1922) divided *Antennaria* into 11 groups by means of a key, but these are invalid, since their rank was not indicated. Until formal taxonomic recognition can be affected, it seems best to implement the available names provided by Rydberg (1922) and Borissova (1959) for the different groups of *Antennaria*. These different monophyletic groups may eventually be recognized at the rank of either subgenera or sections within the genus.

Group Geyeriae consists of a single taxon, *A. geyeri*, which has a rather limited distribution in California, Oregon, and Washington. It is an isolated monophyletic group because the remainder of the genus shares two synapomorphies, presence of basal leaves (5) and dimorphic staminate phyllaries (22). *Antennaria geyeri* is similar to *Anaphalis* in that basal leaves are lacking, and even though it is dioecious, secondary reproductive characteristics are primarily monomorphic. Sexual dimorphism is poorly developed in *A. geyeri* and is apparent only in the slightly different shapes of the corollas. Sexual dimorphism, including secondary reproductive characters, is developed to differing degrees in all species of *Antennaria*. All sexually dimorphic characters are considered apomorphous, including differential height between staminate and pistillate plants and differences in the phyllary shapes and pappus type between the two types of sporophytes (Table 1). Interestingly, the pistillate head characteristics in *Antennaria* are similar to *Gnaphalium* and *Anaphalis*, whereas the staminate head characteristics of most species, such as broad phyllaries, dilated pappus bristles (Antennarioid type; Table 1), and vasiform corollas, are very different from the outgroup.

Antennaria argentea Benth., *A. luzuloides*, and *A. arcuata* Cronq. constitute the monophyletic group, Argenteae. The group is united by the possession of one synapomorphy, the presence of pubescent stolons (12). In addition, these species have retained the plesiomorphous characters of uniformly colored phyllaries (24), a character shared only with the *A. rosulata* and *A. microphylla* of the Dioicae group (Fig. 1), and a much-branched synflorescence (20a). The species in this group are all plants of the northwestern United States and adjacent

TABLE 1. Twenty-seven characters and character states used in a cladistic analysis of *Antennaria* where 0 designates the plesiomorphous state and 1, the apomorphic state

Habitat, habit, and flowering stem	
1. Base of plant	16. Leaf pubescence on abaxial surface
0, herbaceous or lignescent, virgate	0, pubescent
1, base a woody caudex	1, totally glabrous
2. Caulis height	17. Leaves
0, >10 cm	0, sessile
1, <10 cm	1, with distinct petiole
3. Staminate plant height at maturity	18. Number of principal veins in basal leaves
0, about the same height as pistillate	0, one
1, much shorter	1, many
4. Cauline leaf versus basal leaf shape	19. Odor of young leaves
0, same shape, monomorphic	0, odor of citronella absent
1, dimorphic	1, odor of citronella present
5. Basal rosette	Synflorescence
0, basal leaves absent or evanescent	20a-c. Synflorescence branching
1, basal leaves well developed and persistent	20a.
6. Cauline leaf size	0, branched, paniculate
0, same size as or larger than basal leaves	1, unbranched corymbose
1, gradually reduced to half the length/width or less	20b.
7. Flags; a flat, scarios tip resembling the tips of the phyllaries that occur at the apices of the upper cauline leaves	0, corymbose
0, absent	1, racemose
1, present	20c.
8. Purplish glandular hairs on upper stem and leaves	0, corymbose
0, absent	1, solitary
1, present	Capitula
Stolons	21. Pistillate capitulum shape
9. Stolon growth form	0, narrow, subcylindrical
0, short and erect	1, turbinate to campanulate
1, longer and horizontal, usually rooting at tips	22. Staminate phyllary shape; those then compared with the acute pistillate phyllaries
10. Leaf size along stolon	0, acute, the heads of both sexes monomorphic
0, not markedly reduced in size	1, blunt, the heads dimorphic
1, greatly reduced, rudimentary or lacking	23. Involucre pubescence
11. Stolon type	0, base of involucre wooly
0, herbaceous	1, glabrous
1, lignescent, the plant then suffruticose	24. Phyllary coloration
12. Stolon pubescence	0, median phyllaries uniformly colored
0, slightly pubescent, the surface of the stolon visible	1, colors distinctly zoned, multicolored
1, densely pubescent, the surface obscured	25. Phyllary tip coloration
13. Stolon length and leaf arrangement	0, tips of phyllaries light colored, white, stramineous, golden brown, or light pink
0, stolons relatively longer and the leaves not congested	1, dark colored, red, dark brown, dark olive-green, or black
1, stolons relatively shorter, leaves congested, cushion plants	Florets
Basal leaves	26. Corolla pigmentation
14. Basal leaf texture	0, corolla unpigmented, white
0, thin in texture	1, pigmented, usually red-colored
1, coriaceous and usually marcescent	27. Staminate pappus type
15. Leaf pubescence on adaxial surface	0, "gnaphalioid" type, similar to species of <i>Gnaphalium</i> , only slightly dilated at tips if at all, barbellate to denticulate
0, pubescent	1, "antennarioid" type, conspicuously dilated at tips, clavate
1, glabrous	

British Columbia (*A. luzuloides*) and occur at lower elevations in steppe to montane zones (Bayer and Stebbins 1987). *Antennaria arcuata* is one of the rarest *Antennaria* species and is known only from the type locality in Idaho and one Wyoming and two Nevada sites (Bayer and Stebbins 1987).

The Dimorphae clade, including *A. dimorpha* (Nutt.) T.&G., *A. flagellaris* (Gray) Gray, and *A. stenophylla* (Gray) Gray, are plants that occur in the most xerophytic habitats of any *Antennaria*. They are found in dry steppe habitats in the northwestern states, with *A. dimorpha* extending into areas of the southwestern states and southern Alberta and British Columbia. The group possesses one synapomorphy, dark colored phyllary tips (25). The group also displays symplesiomorphies for linear shaped capitula (21) and the "Gnaphalioid" type

pappus (27), which are synapomorphies shared by the remaining two groups, Pulcherrimae and Catipes.

It is interesting to compare the first three groups, Geyeriae, Argenteae, and Dimorphae, since they possess a large number of plesiomorphous features. They are all plants of the western United States and adjacent Alberta and British Columbia, occurring mostly in arid habitats at low elevations. All lack the apomorphic characters of campanulate or turbinate capitula (21), reduced and dimorphic basal vs. cauline leaves (4 and 6), petiolate leaves (excluding *A. argentea*) (17) and long, horizontal stolons that root at their tips (excluding *A. arcuata* and *A. flagellaris*) (9).

Group Pulcherrimae, which includes *A. anaphaloides*, *A. carpatica*, *A. eucosma*, *A. lanata*, *A. linearifolia* Wedd.,

TABLE 2. OTU by character data matrix for the phylogenetic analysis of the genus *Antennaria*

Taxa	Characters					
Outgroup	00000	00000	00000	00000	00000	0000
<i>A. alaskana</i>	01101	11100	00100	00000	01110	1111
<i>A. anaphaloides</i>	10001	00000	00000	00100	00110	1001
<i>A. arcuata</i>	00001	00011	01000	00000	00010	0000
<i>A. argentea</i>	10011	00000	01000	00100	00011	0001
<i>A. aromatica</i>	01111	10110	00110	01010	01110	1111
<i>A. carpatica</i>	10001	01000	00000	00100	01110	1111
<i>A. corymbosa</i>	00101	10010	00000	00000	00110	1011
<i>A. densifolia</i>	01111	11010	01110	01000	01110	1111
<i>A. dimorpha</i>	01001	00000	01100	00001	01010	1110
<i>A. dioica</i>	00111	10010	00001	01000	01110	1011
<i>A. eucosma</i>	10001	00000	00000	00100	00110	1101
<i>A. flagellaris</i>	01001	00011	00000	00001	01010	1100
<i>A. geyeri</i>	00000	00000	10000	00000	00000	0000
<i>A. lanata</i>	10001	01000	00000	00100	01110	1101
<i>A. linearifolia</i>	11001	00000	01110	001?0	01110	1011
<i>A. luzuloides</i>	10001	00000	01000	00100	00011	0001
<i>A. marginata</i>	00111	10110	01001	01010	01110	1011
<i>A. microphylla</i>	00111	10110	00100	01000	00110	0001
<i>A. monocephala</i>	01111	11110	00001	01001	01110	1110
<i>A. neglecta</i>	00111	11011	01000	00000	01110	1010
<i>A. nordhagiana</i>	01101	11110	00001	110?0	01111	1111
<i>A. plantaginifolia</i>	00111	10010	00000	01100	00110	1011
<i>A. pulchella</i>	01111	10110	00000	01000	01110	1111
<i>A. pulcherrima</i>	10001	01000	00000	00100	00110	1101
<i>A. racemosa</i>	00111	00110	01001	01110	11111	1010
<i>A. rosulata</i>	01-11	10110	00100	01001	01110	0001
<i>A. solitaria</i>	00111	11011	01000	01101	01110	1000
<i>A. stenophylla</i>	00001	00000	00000	00000	01011	1100
<i>A. suffrutescens</i>	01111	10110	11011	01001	01110	1000
<i>A. umbrinella</i>	00111	10010	00000	01000	01110	0101
<i>A. villifera</i>	10001	01000	00000	00100	01110	1111
<i>A. virginica</i>	00111	10010	00000	01000	00110	1011

NOTE: The sequence of characters follows that given in Table 1. A dash (-) indicates lack of that character in a particular taxon. A question mark indicates a lack of information about the taxon.

A. pulcherrima, and *A. villifera*, is monophyletic. The clade is delimited by two primary synapomorphies, the presence of a woody caudex at the base of the plant (1) and leaves with many parallel principal veins (18) and six symplesiomorphies, the lack of long horizontal stolons (9), staminate and pistillate plants of the same height (3), and cauline leaves of similar size and shape as the nonpetiolate basal leaves (4, 6, 17). The Pulcherrimae group is more widely distributed than any of the other groups, having Eurasian species, widely distributed North American species, and *A. linearifolia* of the South American Andes (Bayer and Stebbins 1987). The members of this group are primarily montane to arctic and alpine species with many occurring in rather mesic habitats. The fact that few character state changes occur in this clade (Fig. 1) may be an indication that some of the species should be subsumed into others. Additionally, they could be more stable species and consequently their patristic distances are less than species of *Antennaria* in other clades.

The Catipes group is a large, monophyletic assemblage composed of three subgroups, Alpinae, Dioicae, and Umbrinellae (Fig. 1). The group contains the type species of the genus, *A. dioica* (L.) Gaertn., and so comprises *Antennaria* sensu stricto. The sexual progenitors of the polyploid agamic complexes all occur in the Catipes group and therefore subgroups containing the agamic complexes will presumably

also be circumscribed under this group. Polyploidy is prevalent among many species within this group of sexually reproducing species, whereas it is absent or uncommon in the other groups (especially groups Geyeriae, Argenteae, and Dimorphae). The group Dioicae consists primarily of North American species occurring in a diversity of habitats (excepting Scandinavian *A. nordhagiana* Rune and Rönning and Eurasian *A. dioica*). Several noteworthy synapomorphies delimit this group, including long, horizontal stolons (9), shorter staminate plants than pistillate ones at the time of seed dispersal (3), and the cauline leaves are much reduced in size when compared with the basal leaves (6) (except for a reversal in *A. racemosa* Hook.).

Antennaria umbrinella Rydb. comprises the monotypic, monophyletic subgroup Umbrinellae (a name based on the type species). It is delimited from other subgroups of the Catipes group by possession of the symplesiomorphic feature of unpigmented corollas (26), which is mostly absent from the taxa of other subgroups (Fig. 1). It differs from the Alpinae group in that it lacks the glandular hairs (8) and flags (7), and is taller than the dwarf arctic and alpine plants (2) of the Alpinae (Fig. 1). It is most similar to the Dioicae and is delimited from that group by possessing dark phyllaries (25), which are also characteristic of the Alpinae group. The Umbrinellae is a group that possesses characteristics of both of the other subgroups of the Catipes group, but is phenetically most similar to members of the Dioicae. *Antennaria umbrinella* occurs primarily in the montane and subalpine zone of the northern portion of the Rockies (Bayer and Stebbins 1987).

The monophyletic subgroup Alpinae consists of arctic-alpine species occurring primarily in western North America, including the western Arctic, and a narrow endemic, *A. nordhagiana*, in northern Norway (Bayer and Stebbins 1987). The subgroup possesses two principal synapomorphies in that they all have phyllaries with dark-colored tips (25) and cauline stems that are relatively short, 10 cm or less (2) (Fig. 1). The subgroup is also demarcated imperfectly by the presence of flags on their upper cauline leaves (7, exception is *A. pulchella* Greene) and purple or brown glandular hairs on the upper stem and upper cauline leaves (8, exception is *A. densifolia* Pers.). Within subgroup Alpinae, one monophyletic assemblage consists of *A. monocephala* DC. and *A. nordhagiana* recognized by the synapomorphy of glabrous adaxial leaf surfaces (15). Another monophyletic group within the subgroup Alpinae, comprising *A. alaskana* Malte, *A. aromatica* Evert, and *A. densifolia*, consists of plants with an alpine cushion plant growth form (13).

The Dioicae subgroup consists of three major clades, but the results of different analyses have demonstrated that the greatest number of changes between cladistic analyses occur within this group. Since a great deal of confidence cannot be placed on the clades within the Dioicae, they will not be discussed in any detail. *Antennaria marginata* Greene, *A. neglecta* Greene, *A. racemosa*, *A. solitaria* Rydb., *A. suffrutescens* Greene, and *A. virginica* Stebb. embody one monophyletic subgroup. All of the members of the subgroup possess pubescent stolons (12) and "Antennarioid"-type staminate pappus (27) (Fig. 1). One clade in the subgroup, consisting of the sister pair *A. neglecta* - *A. solitaria*, are species that are endemic to the deciduous forests and prairies of eastern and central North America. The second clade in the subgroup consists of *A. marginata*, *A. racemosa*, and *A. suffrutescens* united by two synapomorphies, glandular hairs on the upper

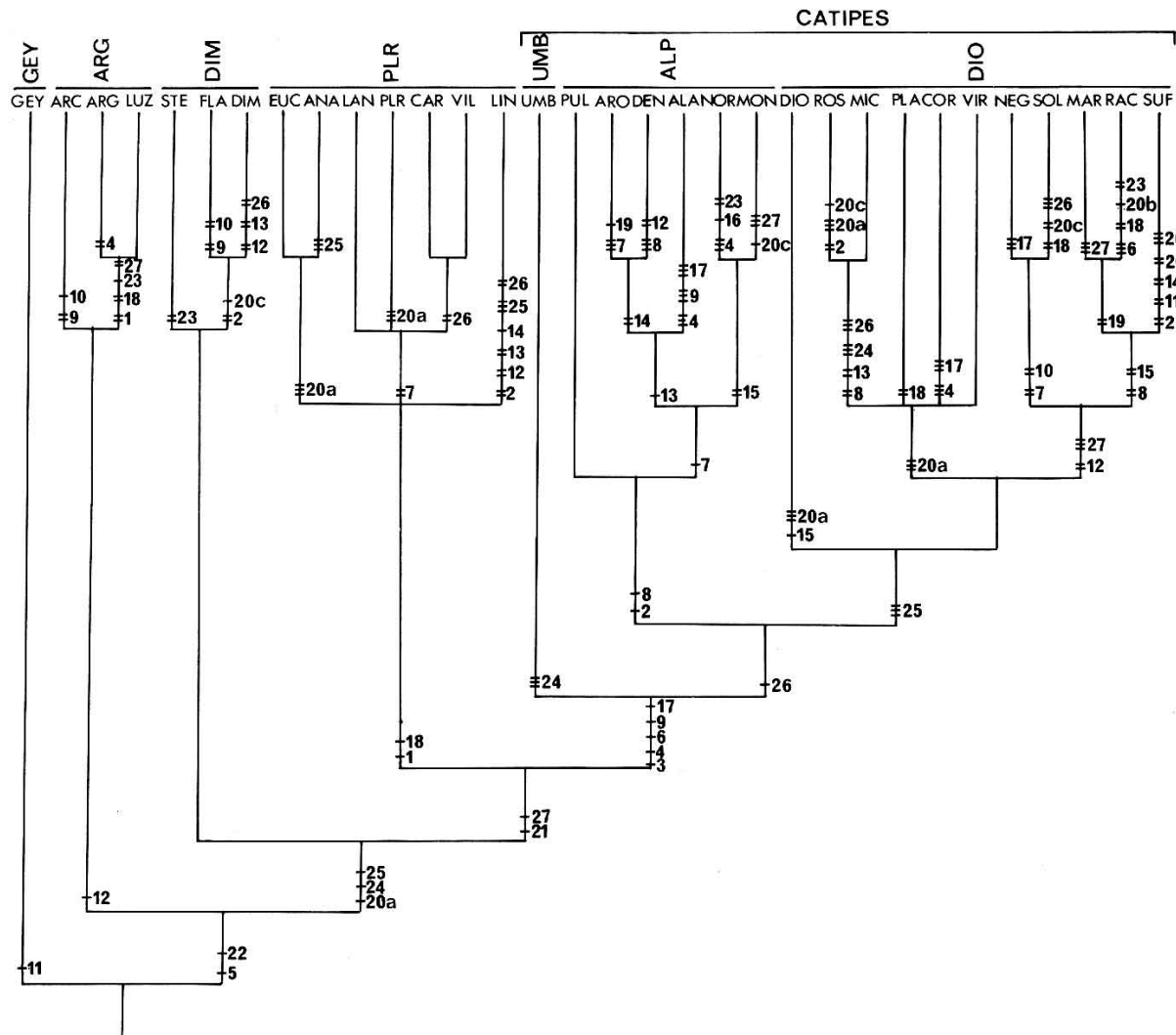


FIG. 1. Cladogram depicting cladistic relationships of sexual species of *Antennaria*. Numbers refer to characters given in Table 1. The species are labeled with the first three letters of their specific epithets (see Table 2), except for *A. pulcherrima* (PLR) to distinguish it from *A. pulchella* (PUL). Monophyletic groups and subgroups are indicated above the species and are abbreviated as follows: GEY, Geyeriae; ARG, Argenteae; DIM, Dimorphae; PUL, Pulcherrimae; UMB, Umbrinellae; ALP, Alpinae; DIO, Dioicae. Single bars denote unique character changes, double bars indicate parallelisms, and triple bars signify reversals.

cauline leaves and stem (8) and glabrous adaxial leaf surfaces (15). *Antennaria marginata*, *A. racemosa*, and *A. suffrutescens* are montane species that occur in western North America, but have nonoverlapping ranges (Bayer and Stebbins 1987).

The second subgroup of the Dioicae (Fig. 1), comprising *A. corymbosa* E. Nels., *A. microphylla* Rydb., *A. plantaginifolia* (L.) Richardson, *A. rosulata* Rydb., and *A. virginica* Stebb., is a monophyletic group that is allied on the basis of two symplesiomorphies, possess nonpubescent stolons (12), and "Gnaphalioid"-type staminate pappus (27) (Fig. 1). The third clade containing a single species, *A. dioica*, differs from the previous clade only by the possession of glabrous adaxial leaf surfaces (15).

Conclusions and summary

The genus *Antennaria* comprises five major monophyletic groups: Geyeriae, Argenteae, Dimorphae, Pulcherrimae, and

Catipes (Fig. 2). Three of the groups, Argenteae, Dimorphae, Geyeriae, have retained a relatively large number of plesiomorphic features and occur in arid habitats with rather restricted ranges, principally in the western United States (Fig. 2). The members of these three groups are mostly non-stoloniferous and have not evolved characters often associated with sexual dimorphism that occur in the remainder of *Antennaria*, and thus they most closely resemble species of *Anaphalis* and *Gnaphalium* (Fig. 2). *Antennaria* probably arose in western North America or Central America, from Mexican *Gnaphalium*. This is supported by the fact that western North America is not only the center of diversity for *Antennaria*, but is also where the species having the largest number of plesiomorphic features are centered (Fig. 2).

The Pulcherrimae and Catipes (Fig. 1) represent the most specialized groups and have attained more extensive distri-

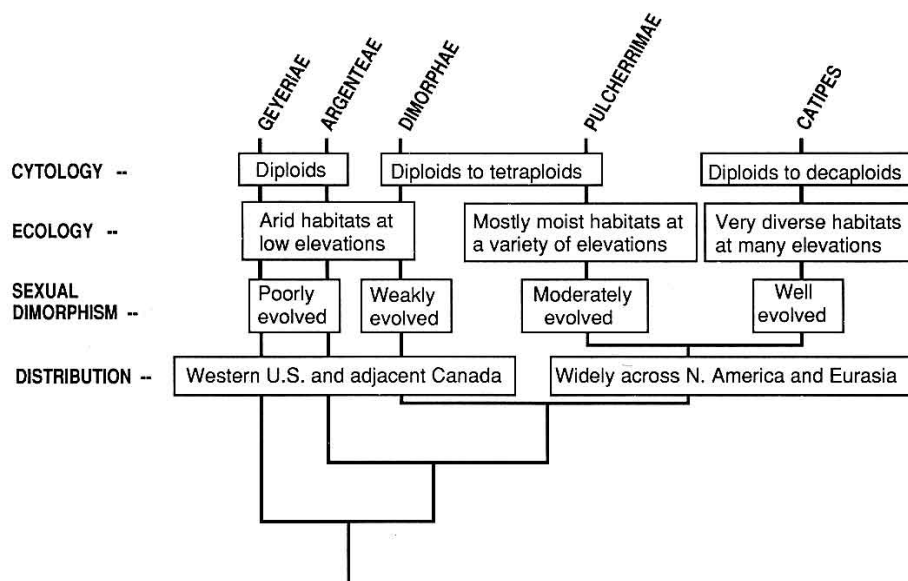


FIG. 2. Reduced cladogram portraying relationships among the five groups of sexual species of *Antennaria*. Cytological and ecological aspects, breeding system evolution, and distribution patterns of the various groups are superimposed on the cladogram.

butions and occur in a much greater diversity of habitats than the Argenteae, Dimorphae, and Geyeriae (Fig. 2). The Catipes is the most highly specialized group because sexual dimorphism is highly developed in many primary and secondary sexual characteristics. Also, the plants possess horizontal stolons, an efficient means of asexual reproduction, and are the sexual progenitors of the polyploid agamic complexes (Fig. 2). Polyploidy is most common and its euploid levels are most numerous (up to decaploid) among members of group Catipes. The Geyeriae and Argenteae are strictly diploid, whereas members of the Dimorphae and Pulcherrimae have some autotetraploid cytotypes. (See Bayer and Stebbins (1987) for a complete discussion of chromosome diversity in the genus.)

Evolutionary advancement in the genus has obviously been toward dioecism and coincident sexual dimorphism, probably as a method to promote outcrossing (Fig. 2). Also, polyploidy and two asexual means of reproduction, agamospermy and horizontal stolons, have evolved in the more specialized groups (Fig. 2). The evolutionary movement in the genus has been toward species occurring in increasingly specialized habitats (Fig. 2), and indeed several edaphic endemics, including *A. suffrutescens* (serpentine endemic) and *A. aromatica* (limestone talus endemic), are among the most advanced species of *Antennaria*.

I offer the following scenario to explain the phylogeography and evolution of *Antennaria*. I suggest that *Antennaria* arose from Madrean *Gnaphalium* sometime during the Oligocene or Miocene. A species such as *G. stolonatum*, which bears a striking resemblance to some species of *Antennaria*, would be illustrative of the archetype that could have given rise to *Antennaria*. As aridity increased in western North America during the late Tertiary, the newly evolved group migrated into the Great Basin and Columbia Plateau region, where the least specialized *Antennaria*, groups Argenteae and Geyeriae, still occur today in open forest habitats at relatively low elevations. Furthermore, other asteraceous groups with Madrean affinities

that were adapted to xeric conditions had spread rapidly into this area during the Miocene as well (Taggart and Cross 1980; Taggart et al. 1982; Leopold and Denton 1987; Wolfe 1987). Suitable habitats for the early *Antennaria* groups, the montane zone with *Pinus ponderosa*, were present in the Columbia Basin and Great Basin in the Middle Miocene (Taggart and Cross 1980; Leopold and Denton 1987). Axelrod and Raven (1985) have suggested that several herbaceous perennial genera, such as *Aster*, *Astragalus*, *Eriogonum*, *Haplopappus*, *Penstemon*, and *Senecio*, developed initially in montane woodland environments and as the climate and topography changed and diversified during the Tertiary, these groups evolved numerous species that radiated into sites from desert to alpine. *Antennaria* likewise appears to fit into this pattern. Aridity increased as the Miocene progressed into the Pliocene, especially as the result of the continual rising of the Cascade (Leopold and Denton 1987) and Sierra Nevada ranges (Chabot and Billings 1972). In response to this increasing aridity, the most xerophytic group, the Dimorphae, evolved. The Dimorphae, like the Argenteae and Geyeriae, are presently distributed in western North America, south of the Wisconsinan glacial terminus (Fig. 2). The Pulcherrimae and Catipes were apparently the most recent groups to arise. Both groups have extended their ranges beyond the western United States into Eurasia and to a much lesser extent South America. Land bridges have existed intermittently across Beringia from the Mesozoic up until as recently as 13 000 years BP (Matthews 1979) and so *Antennaria* could have migrated to Eurasia at any time from the Middle Miocene through to the end of Pleistocene. I think it more likely that the genus migrated to Eurasia via Beringia instead of across a European - North American land bridge. Weak evidence in support of this includes the fact that the present day diversity of *Antennaria* in northeastern North America is low, especially when compared with Alaska and the Yukon. *Antennaria nordhagiana* of Norway is certainly most closely related to and most derived than Alaskan

A. monocephala. There is also an apparent decrease in the number of species from west to east across Eurasia. The paucity of species in Eurasia and South America may indicate that the groups simply haven't had enough time to speciate there because of their relatively recent migration to those areas.

The Pulcherrimae have colonized both glaciated and unglaciated areas of North America and Eurasia, but the fact that a large number of diploid members of the group, *A. anaphaloides*, *A. lanata*, and *A. pulcherrima*, occur primarily in the western United States and adjacent southern Canada points to this region as the center of origin for this group (Urbanska 1983b). The sexual tetraploid members of the Pulcherrimae have been very successful in migrating across Canada and Eurasia. The sexual species of the Catipes evidently evolved prior to the Quaternary because they occur primarily in unglaciated regions and indeed some are found in areas that have been proposed as glacial refugia (Dahl 1955; Rutter 1984), such as *A. nordhagiana* in northern Norway and *A. densifolia* in unglaciated portions of the Northwest Territories and Yukon (Bayer 1989b). Three centers of diversity for sexual members of the Catipes exist, the western United States is a primary center, while the Alaska-Yukon area and the eastern United States are secondary (Bayer and Stebbins 1987). The polyploid sexual and agamic complexes, such as *A. alpina*, *A. howellii*, and *A. rosea*, were the most recent to evolve as they were derived from the sexual progenitors of section Catipes (Bayer 1987) and have colonized the previously glaciated regions of North America and Eurasia. The overwhelming success of the Catipes seems to be correlated with the high incidence of polyploidy and agamospermy in certain species of this group.

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