# TYPIFICATION OF WESTERN NORTH AMERICAN ANTENNARIA GAERTNER (ASTERACEAE: INULEAE); SEXUAL SPECIES OF SECTIONS ALPINAE, DIOICAE, AND PLANTAGINIFOLIAE

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Summary

It has been shown that eight well-defined species of Antennaria should be recognized (A. aromatica, A. corymbosa, A. marginata, A. media, A. microphylla, A. racemosa, A. rosulata, and A. umbrinella). A proposed synonymy for these eight diploid species, based on the similarity matrix and discriminant analysis, is presented here. These species appear to be the sexual progenitors for the polyploid agamic complexes comprising A. rosea and A. parvifolia. Relationships between the diploids and the polyploids are discussed.

## Introduction

Antennaria Gaertn. (Asteraceae: Inuleae: Gnaphalinae) is a taxonomically difficult genus because polyploidy, hybridization, and apomixis have led to the evolution of several polyploid agamic complexes. Each of these agamic complexes is composed of a large number of microspecies leading to a great deal of taxonomic confusion. From 1890 to 1940, several botanists, primarily E. L. Greene, M. L. Fernald, E. Nelson, P. A. Rydberg, and A. E. Porsild, discovered and named hundreds of Antennaria microspecies. Evolutionary studies in Antennaria (Bayer and Stebbins, 1981, 1982, 1983, 1987; Bayer, 1984, 1985a, b; Bayer and Crawford, 1986; Urbanska, 1983a, b) are just beginning to provide workable classifications, based on evolutionary relationships, for the different complexes within the genus.

Phenetic methodologies were used to study relationships among several species of western North American Antennaria from sects. Alpinae, Dioicae, and Plantaginifoliae (Bayer, 1987) and have shown that eight well-defined species should be recognized. It is likely that these eight taxa, 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., are the sexual progenitors of the A. rosea Greene and A. parvifolia Nutt. polyploid agamic complexes (Bayer, 1987). The purpose of this paper is to provide a list of taxonomic synonyms for the recognized taxa and to typify each name.

## Methods

Specimens were borrowed from CAN, DAO, GH, MONT, NDG, NY, RM, US, WIS, WOCB for morphological studies. A list of the 42 characters that were used to construct the basic data matrix (25 vegetative and 17 reproductive) from 138 OTUs (Operational Taxonomic Units) can be found in Bayer (1987). The basic data matrix can be obtained from the author. Type specimens have been compared to recognized taxa via a mean similarity matrix, which employs Pearson product-moment correlation coefficients (Sneath and Sokal, 1973) to relate average values for each taxon to the types as an aid in determining where each type belongs in synonymy. Discriminant analysis was used to compare the diploid taxa to the type specimens that were believed to be synonymous with them. Methodologies are similar to those employed in previous studies on North American species of *Antennaria* (Bayer, 1985a, b, 1987).

A stepwise discriminant analysis was computed by the BMDP program of Dixon (1981).

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An average similarity matrix, using average values (derived from the univariate statistics subroutine of BMDP) for each character from each taxon as well as values for each type, was computed by the NT-SYS program of Rohlf et al. (1974). The data were standardized using STAND subroutine of NT-SYS and the SIMINTVL subroutine and were employed to compute the similarity matrix. Computations were carried out on the IBM computer at the Computer Centre of the University of Windsor.

Two matrices were used in the analysis: 1) a 34 OTU matrix consisting of average values for the eight recognized taxa (A. aromatica, A. corymbosa, A. marginata, A. media, A. microphylla, A. racemosa, A. rosulata, and A. umbrinella), plus those for polyploid A. rosea (nine OTUs total) and 25 undetermined type specimens (listed in Tables 1 and 2) associated with these taxa, and 2) a 138 OTU matrix consisting of 15 specimens each of A. corymbosa, A. marginata, A. media, A. microphylla, A. racemosa, A. rosulata, and A. umbrinella, eight specimens of A. aromatica (only eight were available of this narrowly restricted endemic) and 25 undetermined type specimens. An average similarity matrix (correlation coefficients) was computed using matrix 1. The stepwise discriminant function was performed on matrix 2 and the posterior probabilities are disclosed in Table 2.

## Results and Discussion

Over 350 names have been proposed for North American Antennaria, consequently the majority of them are synonymous with the recognized taxa. The majority of the types that pertain to A. aromatica, A. corymbosa, A. marginata, A. media, A. microphylla, A. racemosa, A. rosulata, and A. umbrinella have been examined and measured for morphological features. The types were compared to average values for each taxon via a mean similarity matrix (Table 1) as well as by discriminant analysis (Table 2).

A proposed synonymy based on the similarity matrix and discriminant analysis is presented (Table 2) along with the gender of the specimens given in the type description of each author (the correct genders were determined/verified as present on the type specimens). Gender(s) of the types is deemed important because the presence of staminate plants on the type indicates that the population that the specimens came from was probably sexually reproducing (Bayer and Stebbins, 1983) and that the specimen probably belongs to one of the sexual taxa. If only pistillate plants are present in a population it is possible that this specimen may have come from a population of polyploid apomicts (agamospermous), such as A. rosea Greene or A. parvifolia Nutt., because they have populations composed entirely of pistillate plants (staminate plants are rare). Sexually reproducing species have gender ratios of approximately 1:1 (Bayer and Stebbins, 1983; Michaels and Bazzaz, 1986). Table 2 demonstrates that most of the types that are synonymous with strictly sexual species have staminate plants. Only A. media is frequently asexual, thus staminate plants were probably absent from the type populations of names such as A. austromontana, A. candida, A. densa, A. modesta, and A. scabra. All types have been placed in synonymy with the diploid with which they have the highest affinity (Table 1); with the following exceptions, A. aizoides, A. austromontana, A. candida, A. modesta, and A. oblancifolia. The final list of synonymy in Table 2 is based not only on the phenetic analyses, geographic location of the type locality, genders of the type specimens, but intuitive gross morphological observations as well.

In areas where two or more sexual species co-occur, naturally occurring interspecific hybrids and backcross progeny may be found. Based on field experience and the morphology of hybrids collected from these native sites, three types have been classified as probable interspecific hybrids or their allopolyploid derivatives according to morphology (see Excluded Taxa). Antennaria erigeroides appears to be a hybrid between A. corymbosa and A. racemosa; A. oblancifolia a hybrid between A. racemosa and A. umbrinella; A. foliacea a hybrid between A. microphylla and A. racemosa. The accepted taxa and their taxonomic synonyms are presented at the end of the results and discussion section, as well as a list

Taxa	ARO	COR	MAR	MED	MIC	RAC	ROS	UMB	ROSEA
aizoides				0.395***			0.347**	0.200*	
aromatica	0.602***			0.253**			0.047*		
anstromontana	0.483***			0.428**			0.231*		
candida	0.503*			0.548**				0.587***	
corresposa		***199.0				*990.0			0.446**
erioeroides		0.489***				0.001*			0.473**
fondlori			0.354***			0.243**	0.203*		
Havescens				0.177**		0.160*		0.615***	
foliacea		0.222**				0.264***			0.087*
maronhila		0.819***				0.243*			0.401**
marginata			0.630***			0.100*	0.209**		
nedia	*0910			0.616***				0.517**	
microphylla					0.823***		0.182*		0.252**
modesta	0.526***			0.494**			0.285*		
nardina		0.632***						0.252*	0.260**
nitida	0.464**				0.685***		0.405*		
oblancifolia		0.402***	0.340*			0.382**			
eramoena			0.340***		0.128**				
nulchella	0.271*			0.652***				0.396**	
reflexa				0.445**				0.541***	0.272*
rosulata	0.401**		0.339*				0.770***		
scabra	0.824***			0.559*				0.624**	
sierrae-blancae							0.500***		
solstitialis	0.331*				0.493***			0.427**	
1 : 11				0.291**				0 341 ***	*092.0

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Table 2. Type specimens of Antennaria associated with A. aromatica, A. corymbosa, A. marginata, A. media, A. microphylla, A. racemosa, A. rosulata, and A. umbrinella. Given are type specific epithets, final synonymy, the gender(s) (S = staminate; P = pistillate) of the type materials, and the posterior probability (derived from stepwise discriminant analysis) that the specimen belongs to the group given as final synonymy. Dashed entries are those that could not be included in the discriminant analysis because of missing data for the specimen.

Epithet	Final synonymy	Gender of types	Posterior probability
aizoides	=umbrinella	S	8 <del></del>
aromatica	=aromatica	S, P	1.00
austromontana	=media	P	0.91
candida	=media	P	0.79
corvmbosa	=corymbosa	S, P	0.99
densa	=media	P	9 <del></del>
erigeroides	=corymbosa × racemosa	P	0.60, 0.40
fendleri	=marginata	P	1.00
flavescens	=umbrinella	S, P	-
foliacea	=microphylla × racemosa	P	<del></del>
hygrophila	=corymbosa	S, P	1.00
marginata	=marginata	S	3 <del></del>
media	=media	S, P	0.90
microphylla	=microphylla	S, P	1.00
modesta	=media	P	0.59
nardina	=corymbosa	S, P	0.95
nitida	=microphylla	S	<del>-</del> .
oblancifolia	$=$ racemosa $\times$ umbrinella	S	0.82, 0.18
peramoena	=marginata	S	9 <del></del>
piperi	=racemosa	S, P	6 <del></del>
pulchella	=media	S, P	0.65
reflexa	=umbrinella	S, P	0.83
rosulata	=rosulata	S, P	1.00
scabra	=media	P	_
sierrae-blancae	=rosulata	S?	·
solstitialis	=microphylla	S, P	1 <u>1-1</u> -1
umbrinella	=umbrinella	S, P	0.75

of excluded taxa, which all appeared to be interspecific hybrids or their allopolyploid derivatives based on the above criteria as well as field observations of similar naturally occurring hybrids (Bayer, 1984; Bayer and Stebbins, 1987).

Babcock and Stebbins (1938), in their treatment of the American species of *Crepis* (Asteraceae), devised a system for classifying taxa within genera that were taxonomically complex as a result of polyploidy and apomixis. Bayer and Stebbins (1982) presented a system which is a modification of the original approach of Babcock and Stebbins (1938). In this revised system, sexual diploids and their autopolyploid derivatives are all given specific rank. The hybrid polyploids (allopolyploids) that are derived from two or more of these diploids, whether they are sexual or asexual, are given their own specific rank. The reasoning behind this is that because the polyploids are of diverse genetic composition they can not 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 and it seems best to continue to use this system when considering the taxa in this paper. Following is a typified list of synonymy for the eight recognized sexual taxa, as well as excluded taxa.

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Accepted Taxa

1) Antennaria aromatica Evert, Madroño 31: 109–112. 1984. TYPE: USA, Montana, Carbon Co., Beartooth range along Hwy. 212, ca. 0.8 km N of Quad Cr., 5 Aug 1981 Evert 3406 (Holotype, RM!; Isotypes, ALTA!, MO, MONT, MOR, NY, UC).

- 2) Antennaria corymbosa E. Nelson, Bot. Gaz. (Crawfordsville) 27: 212. 1899. TYPE: USA, Wyoming, Sierra Madre Mtns., "Battle Lake", 1 Aug 1897, A. Nelson 4160 (Holotype, RM!; Isotype, US! #344869). Date on holotype label reads "1" instead of "15" Aug, but collection number (4160) agrees with that cited in the original type description.
- =Antennaria nardina E. Greene, Pittonia 4: 82. 1899. TYPE: USA, Colorado, "on dry ground in Spruce belt, Mt. Massive near Leadville. 11,000 ft. alt.", 22 Aug 1899, T. Holm s.n. (Lectotype, here designated, NDG! #058336; Isolectotypes, here designated, WIS!(2), RM!). Pistillate plants are present on the herbarium sheet in NDG, but Greene stated that the specimens were only staminate.
- =Antennaria hygrophila E. Greene, Leafl. Bot. Observ. Crit. 2: 144. 1911. TYPE: USA, Nevada, "About Marlette Lake, Washoe County, 2460 M.", 10 Jul 1902, C. F. Baker 1296 (Lectotype, here designated, US! #419472; Isolectotypes, here designated, NDG! #058221 & 058222; US! #419471)
- 3) Antennaria marginata E. Greene, Pittonia 3: 290. 1898. TYPE: USA, New Mexico, "Plantae Novo-Mexicanae", 1847, A. Fendler 523 (Lectotype, here designated, US! #74056).
  - =Antennaria fendleri E. Greene, Leafl. Bot. Observ. Crit. 2: 143. 1911. TYPE: USA, New Mexico, "Plantae Novo-Mexicanae", 1847, A. Fendler 521a (Lectotype, here designated, US! #47045). This specimen is also a syntype of A. marginata Greene.
  - =Antennaria peramoena E. Greene, Leafl. Bot. Observ. Crit. 2: 144. 1911. TYPE: USA, New Mexico, "Wheeler's ranch", 11 Jul 1906, E. O. Wooton s.n. (Lectotype, here designated, US! #739921; Isolectotype, here designated, US! #563644).
- 4) Antennaria media E. Greene, Pittonia 3: 286. 1898. TYPE: USA, California, Placer Co., "Mts. above Coldstream", 31 July 1892, C. F. Sonne s.n. (Lectotype, designated by E. Nelson, Proc. U.S. Nat. Mus. 23: 700. 1901, U.S.! #310514; Isolectotype, here designated, RM!).
  - =Antennaria media E. Greene subsp. ciliata E. Nelson, Proc. U.S. Nat. Mus. 23: 700. 1901. TYPE: USA, California, "White Mts. Mono Co., Calif. 12,000 ft.", Jul 1886, Wm. Shockley 444 (Holotype, US! #47044).
  - =Antennaria austromontana E. Nelson, Proc. U.S. Nat. Mus. 23: 703. 1901. TYPE: USA, Utah, "Marysvale, Utah, Alt. 11,700 ft.", 28 Aug 1894, M. E. Jones 5522 (Holotype, US! #326693).
  - =Antennaria modesta E. Greene, Ottawa Nat. 30: 72. 1906. TYPE: CANADA, British Columbia, "Second summit w. of Skagit River, B.C. alt. 6,000 ft.", 29 Jul 1905, J. M. Macoun Canad. Geo. Survey #69.334 (Lectotype, here designated, NDG; Isolectotype, here designated, CAN! #106009; type description reads "25" July not "29" July).
  - =Antennaria pulchella E. Greene, Leafl. Bot. Observ. Crit. 2: 149. 1911. TYPE: USA, California, "Plants of the Sierra Nevada Mtns., Mt. Goddard, alt. 11,000", 24–26 Jul 1900, H. M. Hall & H. P. Chandler 686 (Holotype, US! #390722).
  - =Antennaria scabra E. Greene, Leafl. Bot. Observ. Crit. 2: 150. 1911. TYPE: USA, California, "White Mts. Mono Co., Calif. 12,000 ft.", Jul 1886, Wm. Shockley 444 (Holotype, US! #47044).
  - =Antennaria densa E. Greene, Leafl. Bot. Observ. Crit. 2: 151. 1911. TYPE: USA, California, "Mt. San Gorgonio, San Bernardino mountains, altitude 11,000 ft.", 12 Jul 1908, L. Abrams & E. A. McGregor 751 (Lectotype, here designated, US! #613419).
  - =Antennaria candida E. Greene, Leafl. Bot. Observ. Crit. 2: 151. 1911. TYPE: USA, California, "Mt. Ranier, alt. 9,000 ft.", 14 Aug 1895, O. D. Allen 141 (Holotype, US! #314044).
- 5) Antennaria microphylla Rydb., Bull. Torr. Bot. Club 24: 303. 1897. TYPE: USA, Montana, "Manhattan", 17 Jul 1895, P. A. Rydberg 2831 (Lectotype, here designated, NY!; Isolectotypes, here designated, NDG #58689; NY!).
  - =Antennaria nitida E. Greene, Pittonia 3: 283. TYPE: CANADA, Northwest Territories, "Dry ground, Charlton Island, James Bay.", 8 Jul 1887, Jas. M. Macoun Canad. Geo. Survey #11272 (Lectotype, here designated, CAN! #105305).

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- =Antennaria solstitialis J. Lunell, Proc. Biol. Soc. Wash. 20: 39. 1907. TYPE: USA, North Dakota, "Leeds", 1 Jul 1902, J. Lunell s.n. (Lectotype, here designated, US! #413969).
- 6) Antennaria racemosa Hook., Fl. bor. amer. 1: 330. 1834. TYPE: NORTH AMERICA, "Rocky Mountains", *Drummond s.n.* (Lectotype, K; Phototype, CAN!).
  - =Antennaria Piperi Rydb., Bull. Torr. Bot. Club 28: 21. 1901. TYPE: USA, Oregon, "Herbarium of the U.S. exploring expedition under the command of Capt. Wilkes. Mountains of northern Oregon.", Wilkes expedition s.n. (Lectotype, here designated, NY!).
- 7) Antennaria rosulata Rydb., Bull. Torr. Bot. Club 24: 300. 1897. TYPE: USA, Arizona, "Allen's Park, Mogollon Mts. In grassy parks within the pine forests.", 25 May 1887, E. A. Mearns 40 (Lectotype, here designated, NY! (pistillate); Isolectotype, here designated, NY! (staminate)).
  - =Antennaria sierrae-blancae Rydb., Bull. Torr. Bot. Club 32: 127. 1905. TYPE: USA, Colorado, "Sierra Blanca, 12-13,500 ft.", 1877, J. D. Hooker & A. Gray s.n. (Holotype, GH!). The type specimen is very fragmentary and also immature, but should undoubtedly be referred to under A. rosulata.
- 8) Antennaria umbrinella Rydb., Bull. Torr. Bot. Club 24: 302. 1897. TYPE: USA, Montana, "Flora of Central Montana, Long Baldy, Little Belt Mts.", 19 Aug 1896, J. H. Flodman 859 (Lectotype, here designated, NY!; Isolectotypes, here designated, NDG! #58655, NY!, US! #291195).
  - =Antennaria aizoides E. Greene, Pittonia 3: 283. 1898. TYPE: CANADA, Alberta, "Dry rather barren soil, Cypress Hills, Sask.", 9 Jun 1884, J. M. Macoun Canad. Geo. Survey #11,245 (Lectotype, here designated, CAN!).
  - =Antennaria reflexa E. Nelson, Bot. Gaz. (Crawfordsville) 27: 208. 1899. TYPE: USA, Wyoming, "Centennial valley", 9 Jun 1895, A. Nelson 1265 (Holotype, RM!).
  - =Antennaria flavescens Rydb., Mem. New York Bot. Gard. 1: 411. 1900. TYPE: USA, Montana, "Bridger Mountains", 18 Jun 1897, P. A. Rydberg & E. A. Bessey 5145 (Lectotype, here designated, NY!; Isolectotypes, here designated, MONT! #7796, NDG #58169, US! #361269). Original description reads "11" July instead of "18" July, but collection numbers agree.

## Excluded Taxa

- Antennaria erigeroides E. Greene, Ottawa Nat. 20: 72. 1906. TYPE: CANADA, British Columbia, "Snow slides, alt. 4,500 ft. Lake House, Skagit River, B.C.", 24 Jun 1905, J. M. Macoun Canad. Geo. Survey #69,346 (Lectotype, here designated, CAN! #105648). This collection appears to be intermediate between A. corymbosa and A. racemosa and is probably a naturally occurring hybrid or allopolyploid derivative.
- Antennaria oblancifolia E. Nelson, Bot. Gaz. (Crawfordsville) 30: 121. 1900. TYPE: USA, Wyoming, Yellowstone Nat. Park, "In loose loamy soil among fallen timber. Open ground. Mammoth Hot Springs.", 3 Jul 1899, A. Nelson & E. Nelson 5640 (Lectotype, here designated, RM!; Isolectotype, here designated, US! #266130). This collection appears to be intermediate between A. racemosa and A. umbrinella and is probably a naturally occurring hybrid or allopolyploid derivative.
- Antennaria foliacea E. Greene, Pittonia 3: 279. 1898. TYPE: USA, Montana, "Flora of Central Montana, Little Belt Mts.", 18 Aug 1896, J. H. Flodman 867 (Lectotype, here designated, US! #291198). This collection appears to be intermediate between A. microphylla and A. racemosa and is probably a naturally occurring hybrid or allopolyploid derivative.

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