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Randall J. Bayer, G. Ledyard Stebbins

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Chromosome Numbers, Patterns of Distribution, and Apomixis in *Antennaria* (Asteraceae: Inuleae)

RANDALL J. BAYER

Department of Biological Sciences, University of Windsor,
Windsor, Ontario N9B 3P4, Canada

G. LEDYARD STEBBINS

Department of Genetics, University of California,
Davis, California 95616

ABSTRACT. The current study presents 137 new chromosome determinations for *Antennaria* from throughout North America. Previously unreported species include *A. atriceps*, *A. marginata*, *A. rosulata*, and *A. stenophylla*. Although a few taxa remain uncounted, a reasonable summary of the chromosomal diversity for the entire genus can be made. Three groups of taxa are recognized based primarily on ploidy level and reproductive mode. One assemblage of taxa (group 1) is always sexual, primarily diploid, and is unrelated to the polyploid agamic complexes of group 3. Another category (group 2) consists of species that occur as diploids or tetraploids and are the probable diploid progenitors of the polyploids. The sexual diploid taxa are distinct morphologically and generally occur in southern latitudes and unglaciated regions. The polyploids (group 3) are frequently widely distributed in both southern latitudes and northern glaciated ones and are morphologically diverse.

Antennaria Gaertner is distributed primarily in temperate to arctic regions of the northern hemisphere and has centers of diversity in western North America that indicate it probably originated in the Rocky Mountains. Polyploidy, extensive hybridization, apomixis, and dioecy are all prevalent in *Antennaria* and have contributed to its well-known taxonomic complexity. Documentation of the occurrence, distribution, and association of these processes can provide an explanation for the taxonomic complexities within *Antennaria*. Conversely, a full knowledge of the biosystematics of *Antennaria* will undoubtedly add much to an understanding of the evolutionary significance of these processes. The current paper, which reviews the distribution of cytotypes in the genus, is a step in that direction.

Early investigations (Juel 1900; Stebbins 1932a, 1932b) established that the sexually reproducing diploid species of *Antennaria* have $2n = 28$ ($n = 14$). Lower numbers have not been encountered even among the morphologically most primitive species (Bayer 1984). Some European workers (Urbanska 1983a, 1983b; Gustafsson 1947-1948) have treated species with $2n = 28$ as tetraploids, an interpretation based primarily on the occurrence of diploid members with $2n = 14$ ($n = 7$) in *Gnaphalium* L., from which *Antennaria* was probably derived (Juel 1900;

Stebbins 1974; Bayer 1984). Species of *Antennaria* with $2n = 28$ are considered here to be diploids, although they are viewed as probable paleopolyploids that have become diploidized. Recent papers (Bayer and Stebbins 1981; Urbanska 1983a, 1983b; Bayer 1984; Chinnappa 1984) have revealed a polyploid series extending from diploid ($2n = 28$) to decaploid ($2n = 140$). Agamospermy is found only in polyploids, but polyploids can be either amphimictic or agamospermous (Bayer 1984). As far as is known, all diploid individuals are sexual and occur in approximate 1:1 sex ratios in populations (Bayer 1984).

The objectives of this paper are 1) to report new chromosome determinations for 137 collections and 2) to present a synopsis of cytological data for all of *Antennaria* synthesized from the data in the present and previous studies (principally, Bayer and Stebbins 1981; Urbanska 1983b; Bayer 1984; Chinnappa 1984).

MATERIALS AND METHODS

Chromosome number determinations were obtained by staining root tips using the Feulgen reaction as outlined in Bayer (1984). Root tips were used because these can be obtained throughout the year and because meiocytes from staminate individuals are lacking in agamosper-

TABLE 1. Chromosome numbers for North American species of *Antennaria*. Presented are state or province, county, and author's (R.J.B.) voucher numbers. Alphabetic prefixes in front of voucher numbers refer to state or province, county, or nearest city to a collection locality. The frequency of staminate clones, when determined, is presented in parentheses after the voucher number. Morphological resemblance of polyploids "toward" a particular diploid is indicated as [toward . . .]. * = first count for the species, ** = new number for the species.

A. anaphaloides, $2n = 28$. U.S.A. **Montana**: Granite Co., M-321, M-325; Lewis and Clark Co., M-314; Teton Co., M-304.

A. argentea, $2n = 28$. U.S.A. **California**: Nevada Co., C-367.

A. aromatica, $2n = 56$. U.S.A. **Colorado**: Summit Co., CO-458 [toward *A. media*]. **Montana**: Teton Co., M-302 (0.46).

A. atriceps (? = *A. alpina*), $2n = 56^*$. U.S.A. **Alaska**: Denali National Park, Therofare Pass, A-356.

A. corymbosa, $2n = 28$. U.S.A. **Colorado**: Gunnison Co., CO-437; Lake Co., CO-453. **Idaho**: Custer Co., I-305. **Montana**: Deerlodge Co., M-320.

A. dimorpha, $2n = 56^{**}$. U.S.A. **Idaho**: Blaine Co., Soreng 2420; Lemhi Co., I-302. **Montana**: Powell Co., M-319.

A. friesiana subsp. *alaskana*, $2n = 28^{**}$. U.S.A. **Alaska**: summit of Wickesham Dome, A-341; near summit of Wickesham Dome, A-342; 12 mile summit, 85 miles NE of Fairbanks, A-305; Eagle Summit, A-308; 34 miles NW of Nome on Nome-Teller hwy., A-386; Anvil Hill, N. of Nome, A-3100; Eagle Summit, A-309. $2n = 56$. **Alaska**: Port Clarence, A-395.

A. friesiana, subsp. *friesiana* $2n = 56^{**}$. U.S.A. **Alaska**: Mt. Fairplay, A-317; Donnelly Dome, S. of Delta, A-348; Reindeer Hills, 4 miles NE of Cantwell, A-353; Reindeer Hills, 4 miles NE of Cantwell (many monocephalous stems), A-354; Denali National Park, Eielson visitor center, A-355.

A. geyeri, $2n = 28$. U.S.A. **California**: Sierra Co., C-364. **Oregon**: Deschutes Co., O-343.

A. luzuloides, $2n = 28$. U.S.A. **California**: Sierra Co., C-365. **Idaho**: Custer Co., I-308. **Montana**: Ravalli Co., M-338.

A. marginata, $2n = 28^*$. MEXICO. **Chihuahua**: Soreng 8064. U.S.A. **Arizona**: Apach Co., AZ-500. **New Mexico**: Sandoval Co., NM-404; Sierra/Grant Co., Soreng 2168. $2n = 56^*$. U.S.A. **New Mexico**: Sante Fe Co., NM-411. $2n = 84^*$. U.S.A. **New Mexico**: Sandoval Co., NM-408 (0.00). $2n = 112^*$. U.S.A. **New Mexico**: Taos Co., NM-413. $2n = 140^*$. U.S.A. **New Mexico**: Sandoval Co., NM-405-A (0.00).

A. media, $2n = 28$. U.S.A. **Nevada**: Washoe Co., C-450. $2n = 56$. U.S.A. **Nevada**: Washoe Co., C-452. **Oregon**: Deschutes Co., Whitkus 2393. $2n = 98^{**}$. U.S.A. **Colorado**: Rio Grande Co., CO-409

TABLE 1. Continued.

(0.00). $2n = 112^{**}$. U.S.A. **Montana**: Glacier Co., GNP-264.

A. microphylla, $2n = 28$. U.S.A. **Colorado**: Gilpin Co., CO-462; Gunnison Co., CO-422, CO-438; Lake Co., CO-451; Saguache Co., CO-413, CO-418. **Idaho**: Blaine Co., CA-305. **Montana**: Granite Co., M-323 (0.02), M-528; Teton Co., M-307 (0.50). $2n = 42$. U.S.A. **Montana**: Powell Co., M-318; Teton Co., M-301 (0.09).

A. monocephala, $2n = 28^{**}$. U.S.A. **Alaska**: Eagle Summit, 10 miles NE of Fairbanks, A-306; Denali National Park, Therofare Pass, A-357; Hatcher Pass, N of Palmer, A-360; Anvil Hill, just N of Nome, A-3102.

A. neodioica subsp. *howellii* (Greene) Bayer, $2n = 140^{**}$. U.S.A. **Montana**: Ravalli Co., M-348.

A. neodioica subsp. *neodioica*, $2n = 56$. U.S.A. **Kentucky**: Lawrence Co., COW-278. **Pennsylvania**: Greene Co., RO-301; Pike Co., BK-401 (probably the type locality), BK-402.

A. neodioica subsp. *petaloidea* (Fern.) Bayer & Stebb., $2n = 84$. U.S.A. **Montana**: Ravalli Co., M-349. CANADA. **Ontario**: Frontenac Co., MS-247.

A. parlinii subsp. *fallax* (Greene) Bayer & Stebb., $2n = 84$. U.S.A. **Illinois**: Jackson Co., ILL-270.

A. parlinii Fern. subsp. *parlinii*, $2n = 84$. U.S.A. **Kentucky**: Greenup Co., GR-275, GR-276, KE-277; Lawrence Co., CK-207; Menifee Co., MB-41.

A. parvifolia, $2n = 84$. U.S.A. **New Mexico**: Lincoln Co., NM-401 (0.00); Sandoval Co., NM-407 [typical] (0.01), NM-407 [toward *A. rosulata*]; Sierra/Grant Co., Soreng 2168 [toward *A. marginata*]. $2n = 112$. U.S.A. **Colorado**: Conejos Co., CO-405; Gunnison Co., CO-515, NM-417; Teller Co., L. Bayer 1. **New Mexico**: Bernalillo Co., NM-402; Rio Arriba Co., NM-417. $2n = 140$. U.S.A. **Colorado**: Grand Co., CO-470. **New Mexico**: Taos Co., NM-414.

A. plantaginifolia, $2n = 28$. U.S.A. **Kentucky**: Bath Co., BA-294; Greenbrier Co., GB-291; Lawrence Co., CK-207, COW-278; Magoffin Co., SV-279, PV-282; Morgan Co., GC-281.

A. pulcherrima, $2n = 28$. U.S.A. **Colorado**: Gilpin Co., CO-461; Gunnison Co., CO-420. $2n = 56$. U.S.A. **Montana**: Teton Co., M-312 (0.73).

A. racemosa, $2n = 28$. U.S.A. **Montana**: Carbon Co., BTP-214; Granite Co., M-330, M-350; Ravalli Co., M-336, M-337.

A. rosea, $2n = 42^{**}$. U.S.A. **Montana**: Lewis and Clark Co., M-317 [toward *A. umbrinella*] (0.00). $2n = 56$. U.S.A. **California**: Mono Co., C-216 [toward *A. media*]. **Colorado**: Clear Creek Co., CO-459 [toward *A. media*]; Conejos Co., CO-406 [typical]; Grand Co., CO-473 [toward *A. corymbosa*] (0.00), CO-469 [typical], CO-467 [toward *A. media*]; Gunnison Co., CO-440 [toward *A. umbrinella*]; Rio Grande Co., CO-410 [toward *A. media*]; Summit Co., CO-458 [toward *A. aromatica*]. **Montana**: Granite Co., M-326 [toward *A. cor-*

TABLE 1. Continued.

ymbosa], M-334 [toward *A. racemosa*] (0.00). **New Mexico:** Rio Arriba Co., NM-418 [toward *A. microphylla*] (0.00).

A. rosulata, $2n = 28^*$. U.S.A. **Arizona:** Apache Co., AZ-501. **Colorado:** Gunnison Co., CO-514. **New Mexico:** Rio Arriba Co., NM-505.

A. stenophylla, $2n = 56^*$. U.S.A. **Nevada:** Humboldt Co., N-502.

A. umbrinella, $2n = 28$. U.S.A. **Idaho:** Gooding Co., GO-304. **Montana:** Ravalli Co., M-339. $2n = 56$. U.S.A. **Colorado:** Jackson Co., CO-475. **Montana:** Granite Co., M-529; Lewis and Clark Co., M-315; Teton Co., M-303. **Wyoming:** Albany Co., W-401.

A. virginica, $2n = 28$. U.S.A. **Virginia:** Carroll Co., VA-303. **West Virginia:** Pendleton Co., AV-298. $2n = 56$. U.S.A. **West Virginia:** Hampshire Co., PV-300; Hardy Co., HY-299.

A. alaskana × *A. monocephala*, $2n = 28^*$. U.S.A. **Alaska:** Anvil Hill, N of Nome, A-3101.

A. argentea × *A. luzuloides?*, $2n = 28^*$. U.S.A. **California:** Sierra Co., C-366.

A. corymbosa × *A. media*, $2n = 42^*$. U.S.A. **Colorado:** Gunnison Co., CO-433. $2n = 56^*$. U.S.A. **Colorado:** Gunnison Co., CO-446.

A. corymbosa × *A. microphylla*, $2n = 28^*$. U.S.A. **Colorado:** Gilpin Co., CO-464.

A. corymbosa × *A. racemosa*, $2n = 28^*$. U.S.A. **Idaho:** Custer Co., I-306.

A. microphylla × *A. umbrinella*, $2n = 56^{**}$. U.S.A. **Colorado:** Grand Co., CO-478.

A. racemosa × *A. umbrinella*, $2n = 28^{**}$. U.S.A. **Wyoming:** Yellowstone National Park, WY-514.

mous populations of this dioecious genus (Bayer 1984). Root tips for cytological analysis were obtained from field-collected clones that were cultivated in the greenhouses of the Department of Biological Sciences at the University of Windsor. Voucher specimens are deposited in the following herbaria: numbers prefixed with A- (Alaska), C- (Colorado), or O- (Oregon) at DAV; prefixes CO- (Colorado), I- (Idaho), M- (Montana), and NM- (New Mexico) at RM; the rest at OS and WOCB. In recording chromosome counts from the literature, only those based upon field collections for which the locality is given have been included. Counts based upon botanical garden material have been omitted because identification and locality data are unreliable.

RESULTS

Chromosome number for 28 species of *Antennaria* and seven naturally occurring hybrids

collected in 15 U.S. states, one Canadian province, and one Mexican state are given in table 1. As far as can be ascertained, four of these species had not been determined previously. Seven of the determinations are new chromosome numbers for taxa that had been reported previously. Five of the seven hybrid combinations have not been reported before. A compilation of cytological data from the literature including the current study is given in table 2. Bayer and Stebbins (1981), Bayer (1984), and the present investigation were the main sources of information. Urbanska (1983b) presented a summary of data for the Carpaticeae (*A. carpaticea* s.l.) and this was incorporated into table 2. The counts for *A. microphylla*, *A. rosea*, and *A. umbrinella* were supplemented from Chinnappa (1984). Determinations for the primarily Eurasian species, *A. dioica* and *A. alpina*, were summarized from Fedorov (1969). A summary of relationships in *Antennaria*, based on chromosome numbers, morphology, and reproductive mode, is provided in table 3.

DISCUSSION

Most chromosome numbers of the major species of *Antennaria* are now known. Many need supplementary counts to establish the ploidy level(s). A few geographically restricted, endemic species, such as *A. gaspensis* and *A. soliceps*, still need to be collected and determined cytologically. The available data nevertheless allow a reasonable cytological analysis of the entire genus. Three groups of species within *Antennaria* can be recognized: 1) diploids and polyploids that are entirely sexual and are not progenitors of agamosperous taxa; 2A) diploids and 2B) polyploids that are sexual and are the progenitors of the polyploid agamic complexes; and 3) members of the polyploid agamic complexes (table 2).

Biosystematic studies of many of the problematic groups in *Antennaria* are in progress; therefore, the rank or status of some of these species will undoubtedly change. With the projected taxonomic changes in mind, most species are interpreted in the narrow sense to allow for future inclusion of some taxa within others. Distinguishing morphological characters for many previously discussed taxa may be found in Bayer and Stebbins (1982), Urbanska (1983a, 1983b), and Bayer (1984).

TABLE 2. Synopsis of chromosome numbers in *Antennaria*. Group designation—1 = sexual diploid and polyploid cytotypes not related to the polyploid agamic complexes, 2 = sexual diploids (2A) related to polyploid agamic complexes and (2B) the autopolyploid derivatives of these diploids, and 3 = members of the polyploid sexual and agamic complexes. Reference codes—a = current study; b = Bayer (1984); c = Bayer and Stebbins (1981); d = Chinnappa (1984); e = Fedorov (1969); f = Johnson and Packer (1968); g = Jorgensen et al. (1958); h = Löve and Löve (1982); i = Morton (1981); j = Mosquin and Haley (1966); k = Packer and McPherson (1974); l = Rune and Rönning (1956); m = Stebbins (1932a); n = Stebbins (1932b); o = Strother (1972); p = Urbanska (1983a, 1983b); q = Zhukova (1965); r = Zhukova (1968, 1969). * = most frequently encountered cytotype within a taxon.

Taxon	Group	Somatic number	Ploidy level	Reference
<i>A. alpina</i> (L.) Gaertner	3	84*	4x	e
<i>A. anaphaloides</i> Rydb.	1	28	2x	a, o
<i>A. arcuata</i> Cronq.	1	28	2x	b
<i>A. argentea</i> Benth.	1	28 + 2B	2x	o
	1	28	2x	a, b
<i>A. aromatica</i> Evert	2A	28	2x	b
	2B	56	4x	a, b
<i>A. atriceps</i> Fern.	3	56	4x	a
<i>A. carpatica</i> (Wahlb.) Bl. & Fingerh.	1	56	4x	p
<i>A. corymbosa</i> E. Nelson	2A	28	2x	a, b, c
<i>A. dimorpha</i> (Nutt.) Torrey & A. Gray	1	28	2x	b
	1	56	4x	a
<i>A. dioica</i> (L.) Gaertner	2A	28	2x	b, e
<i>A. eucosma</i> Fern.	1	56	4x	e, p
<i>A. flagellaris</i> (A. Gray) A. Gray	1	28	2x	b
<i>A. friesiana</i> (Trautv.) Ekman subsp. <i>alaskana</i> (Malte) Hul-tén	2A	28	2x	a
	2B	56	4x	a, f
<i>A. friesiana</i> (Trautv.) Ekman subsp. <i>friesiana</i>	3	56*	4x	a, g
	3	63	4x + 7	q
	3	100 +	7x +	j
	3	unknown	??	??
<i>A. gaspensis</i> Fern.	3	unknown	??	??
<i>A. geyeri</i> A. Gray	1	28	2x	a, b
<i>A. lanata</i> (Hook.) E. Greene	1	28	2x	b, p
<i>A. luzuloides</i> Torrey & A. Gray (including <i>A. microcephala</i> A. Gray)	1	28	2x	a, b
<i>A. marginata</i> E. Greene	2A	28	2x	a
	3	56	4x	a
	3	84	6x	a
	3	112	8x	a
	3	140	10x	a
<i>A. media</i> E. Greene	2A	28	2x	a, b
	3	56*	4x	a, b, c
	3	98	7x	a
	3	112	8x	a
<i>A. microphylla</i> Rydb.	2A	28	2x	a, b, d
	3	42	3x	a, d
	3	56	4x	b
<i>A. monocephala</i> DC.	2A	28	2x	a
	3	56	4x	r
	3	60	4x + 4	r
	3	70	5x	k
<i>A. neglecta</i> E. Greene	2A	28	2x	b, c, m
<i>A. neodioica</i> E. Greene s.l. (sensu Bayer & Stebbins, 1982)	3	56	4x	a, b, c, n
	3	84	6x	a, b, c
	3	140	10x	a
<i>A. nordhagiana</i> Rune & Rönning	2A	28	2x	l

TABLE 2. Continued.

Taxon	Group	Somatic number	Ploidy level	Reference
<i>A. parlinii</i> Fern. s.l. (sensu Bayer & Stebbins, 1982)	3	56	4x	b, c
	3	70	5x	b, c
	3	84*	6x	a, b, c, n
	3	112	8x	c
<i>A. parvifolia</i> Nutt. s.l.	3	56	4x	b
	3	84	6x	a, h
	3	112	8x	a, b
	3	140	10x	a, b
<i>A. plantaginifolia</i> (L.) Richardson	2A	28	2x	a, b, c, m
<i>A. pulcherrima</i> (Hook.) E. Greene	1	28	2x	a, p
	1	56	4x	p
<i>A. racemosa</i> Hook.	2A	28	2x	a, b, c
<i>A. rosea</i> E. Greene	3	42	3x	a
	3	56*	4x	a, b, c, d
	3	70	5x	b
<i>A. rosulata</i> Rydb.	2A	28	2x	a
<i>A. soliceps</i> S. F. Blake	3	unknown	??	??
<i>A. solitaria</i> Rydb.	2A	28	2x	b, c, m
<i>A. stenophylla</i> (A. Gray) A. Gray	1	56	4x	a
<i>A. suffrutescens</i> E. Greene	1	28 + 2B	2x	b
<i>A. umbrinella</i> Rydb.	2A	28	2x	a, b
	2B	56	4x	a, b, d
<i>A. villifera</i> A. Boriss.	1	28	2x	p
	1	42	3x	p
<i>A. virginica</i> Stebb.	2A	28	2x	a, b, c
	2B	56	4x	a, b, c

Group 1—Diploids and Polyploids from Sections not Containing Apomicts. Group 1 (table 2) consists of 14 species, many of which are not closely related taxonomically; however, all are united by the features of relatively low ploidy levels (diploid to tetraploid) and lack of agamosperous seed production. Species in this group are primarily diploid ($2n = 28$), but triploids and tetraploids are also known. As far as can be determined, agamospermy is absent from these species. This group contains *Antennaria* sect. *Carpaticeae*, which has been extensively studied by Urbanska (most recently, Urbanska 1983a, 1983b). Many other species in this group, especially *A. arcuata*, *A. luzuloides*, and *A. geyeri*, have characteristics that are considered to be primitive in *Antennaria* (Stebbins 1974; Bayer 1984).

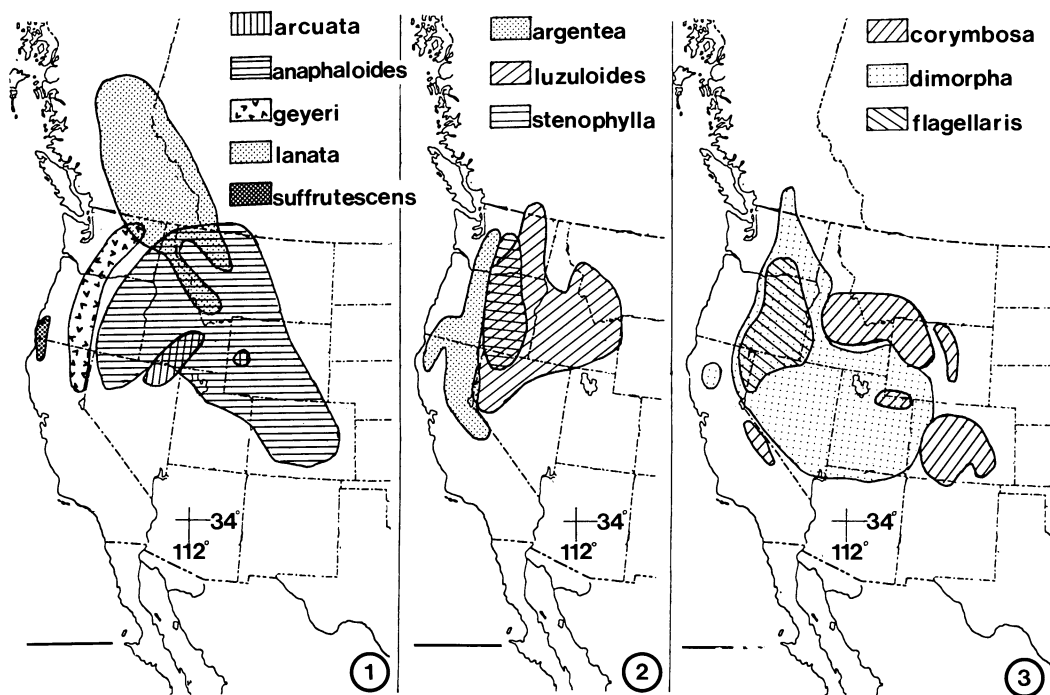
One of the rarest sexual species, *A. arcuata* (Bayer 1984), has been previously determined as a diploid (table 2; fig. 1). The present diploid reports and previous records (Bayer 1984; Strother 1972; Urbanska 1974) established *A.*

anaphaloides (fig. 1), *A. argentea* (fig. 2), *A. lanata* (fig. 1), and *A. luzuloides* (fig. 2) as $2n = 28$ from additional localities (tables 1 and 2; fig. 2).

Antennaria carpaticea, which occurs in the Carpathians, Alps, and Pyrenees (fig. 8), has been determined as tetraploid ($2n = 56$) from several localities (Urbanska 1983b; table 2). This is the only species in the group that is strictly European in distribution. Morton (1981) and Urbanska (1983b) have both found that *A. eucosma* like its close relative *A. carpaticea* is uniformly tetraploid (table 2). *Antennaria eucosma* typically occurs on limestone barrens in Newfoundland (Urbanska 1983a; fig. 4). Another member of the *Carpaticeae*, *A. pulcherrima*, occurs widely across Canada and south into the U.S. Rockies (fig. 8). It appears to be uniformly tetraploid throughout its range in Canada (Urbanska 1983b), but four diploid populations are now known from Montana (one population), Wyoming (one), and Colorado (two). Apparently this species arose in the Rockies as a diploid and presumed autopolyploid cytotypes spread north into Cana-

TABLE 3. Phylogenetic relationships in *Antennaria*. * = synonymized list of microspecies or agamospecies included within these taxa may be found in Bayer and Stebbins (1982). ** = diploid sexual members are those sexual species that have probably contributed to the genetic composition of the polyploid sexual and agamospecies of the group. Consequently some diploids may be listed under several groups if they have been implicated in their parentage. *** = only those agamospecies frequently encountered in floras have been included here.

Name of complex	Diploid sexual members**	Polyploid sexual members	Agamospecies
<i>parlinii</i>	<i>plantaginifolia</i> <i>racemosa</i> <i>solitaria</i>	<i>parlinii</i> s.l.*	<i>parlinii</i> s.l.*
<i>neodioica</i>	<i>neglecta</i> <i>plantaginifolia</i> <i>racemosa</i> <i>virginica</i>	absent from this group	<i>neodioica</i> s.l.*
<i>rosea</i>	<i>aromatica</i> <i>corymbosa</i> <i>media</i> <i>microphylla</i> <i>racemosa</i> <i>rosulata</i> <i>umbrinella</i>	absent from this group	<i>rosea</i> *** <i>alborosea</i> <i>arida</i> <i>bracteosa</i> <i>chilensis</i> <i>concinna</i> <i>gaspensis</i> <i>imbricata</i> <i>incarnata</i> <i>magellanica</i> <i>oxyphylla</i> <i>sedoides</i> <i>subviscosa</i>
<i>parvifolia</i>	<i>dioica</i> <i>marginata</i> <i>rosulata</i>	<i>marginata</i> <i>parvifolia</i>	<i>aprica</i> *** <i>fusca</i> <i>marginata</i> <i>parvifolia</i> <i>soliceps</i> ?
<i>alpina</i>	<i>aromatica</i> <i>friesiana</i> subsp. <i>alaskana</i> <i>media</i> <i>monocephala</i> <i>nordhagiana</i>	<i>friesiana</i> subsp. <i>friesiana</i> <i>media</i>	<i>alpina</i> *** <i>atriceps</i> <i>canescens</i> <i>friesiana</i> subsp. <i>friesiana</i> <i>media</i>
<i>carpatica</i>	<i>anaphaloides</i> <i>lanata</i> <i>pulcherrima</i> <i>villifera</i>	<i>carpatica</i> <i>eucosma</i> <i>pulcherrima</i>	absent from the remaining groups
<i>dimorpha</i>	<i>dimorpha</i>	<i>dimorpha</i>	
<i>luzuloides</i>	<i>argentea</i> <i>luzuloides</i> <i>stenophylla</i>	absent from the remaining groups	
<i>arcuata</i>	<i>arcuata</i>		
<i>flagellaris</i>	<i>flagellaris</i>		
<i>geyeri</i>	<i>geyeri</i>		
<i>suffrutescens</i>	<i>suffrutescens</i>		



FIGS. 1-3. Distribution of *Antennaria* species. 1. *A. arcuata*, *A. anaphaloides*, *A. geyeri*, *A. lanata*, and *A. suffrutescens*. 2. *A. argentea*, *A. luzuloides*, and *A. stenophylla*. 3. *A. corymbosa*, *A. dimorpha*, and *A. flagellaris*. Bar = 500 km.

da. Urbanska (1983b) reported that *A. villifera*, which occurs across Eurasia mainly above the arctic circle (Urbanska 1983b; fig. 8), is diploid and triploid (sensu Bayer and Stebbins 1981). Diploid and triploid races of *A. villifera* (syn. = *A. carpatica* var. *laestadiana* Trautv.) are apparently scattered over the entire range of this species. Irregular meiosis in the triploids (hexaploids sensu Urbanska 1983a, 1983b) may allude to its hybrid origin.

Antennaria dimorpha (fig. 3), originally reported as diploid from two localities (one each from Washington and Montana, Bayer 1984), is now known to be tetraploid from one Montana and two Idaho sites (table 1). Therefore, this species occurs as both diploid and tetraploid cytotypes (table 2), but additional counts are desirable to document the geographic distribution of the two. *Antennaria flagellaris* (fig. 3), which in some respects resembles *A. dimorpha*, was previously determined as diploid from a single locality (Bayer 1984). *Antennaria stenophylla*, which is morphologically and phyto-geographically similar to *A. luzuloides* (fig. 2), is

reported here as tetraploid ($2n = 56$). This is the first known count for this sexual species. Additional counts for *A. flagellaris* and *A. stenophylla* are needed before their ploidy level can be firmly established. The pattern appears to be uniform diploidy for *A. geyeri* (Bayer 1984; table 2; fig. 1) which resembles some members of the genus *Anaphalis* DC. (thought to be a sister-genus of *Antennaria*; Bayer 1984). The serpentine endemic, *A. suffrutescens*, is known as a diploid from only one locality (Bayer 1984; table 2; fig. 1).

In summary, 11 species occur in western North America (see figs. 1-3). *Antennaria carpatica* is strictly European (fig. 8); *A. eucosma* occurs in Newfoundland (fig. 4); and *A. villifera* is widely distributed across Eurasia (fig. 8). Both diploid and tetraploid cytotypes occur in *A. dimorpha* and *A. pulcherrima*, whereas diploids and triploids are known in *A. villifera* (table 2). One large group of species (the Carpaticeae) with close morphological affinities includes *A. anaphaloides*, *A. carpatica*, *A. eucosma*, *A. lanata*, *A. pulcherrima*, and *A. villifera* (see Urbanska 1983a,

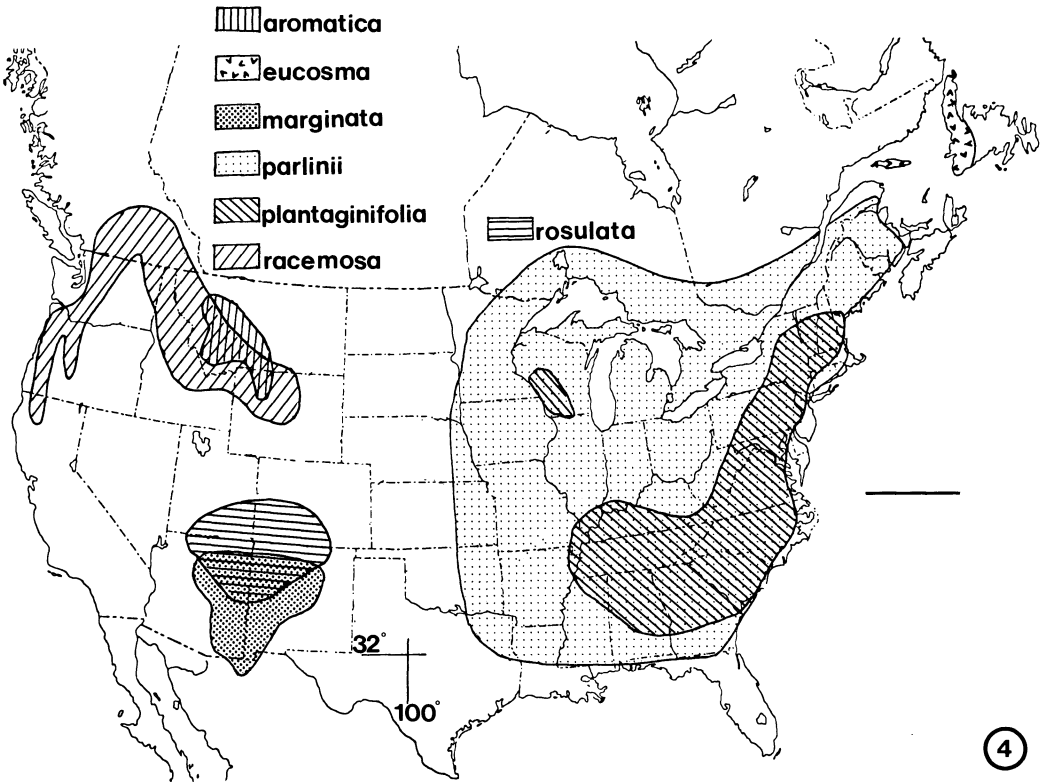


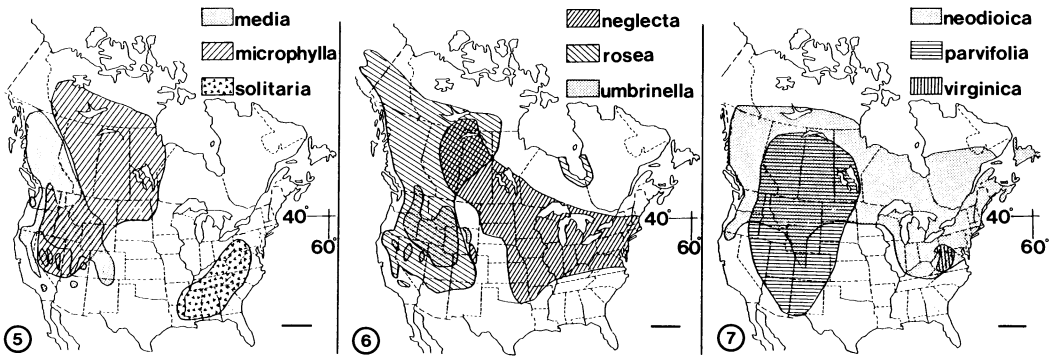
FIG. 4. Distribution of *Antennaria* species: *A. aromatica*, *A. eucosma*, *A. marginata*, *A. parlinii* s.l., *A. plantaginifolia*, *A. racemosa*, and *A. rosulata*. Bar = 500 km.

1983b for details; table 3). The similarity of the Eurasian *A. carpatica* and *A. villifera* to the North American *A. lanata* is so great that one author (Susnik 1969) recognized populations from the eastern Alps previously classified as *A. carpatica* as conspecific with *A. lanata*. *Antennaria argentea*, *A. luzuloides*, and *A. stenophylla* form an assemblage of morphologically similar, closely related species (table 3). Two xerophytic species that are strongly allied are *A. dimorpha* and *A. flagellaris*. *Antennaria arcuata*, *A. geyeri*, and *A. suffrutescens* remain as distinct species, the affinities of which are uncertain (table 3).

Group 2—Diploids and Sexuals from Sections Containing Apomicts. This group contains the sexual taxa from which the polyploid agamic complexes have been derived. Recent studies (Bayer 1985a, 1985b; Bayer and Crawford 1986) have elucidated the origins of the *A. parlinii* and *A. neodioica* complexes from among five of these diploid species (table 3). The species that are included in this list are based on past

taxonomic studies (Bayer and Stebbins 1982; Bayer 1985a, 1985b; Bayer and Crawford 1986) and recent field observations (Bayer and Stebbins unpubl. obs.).

Antennaria friesiana subsp. *alaskana* occurs in western and central Alaska and adjacent Yukon Territory (fig. 9). It has been reported as tetraploid ($2n = 56$) from near Point Hope (Johnson and Packer 1968) and is here recorded as diploid ($2n = 28$) from seven Alaskan localities and tetraploid from an additional locality (table 1). A closely related group of apomicts, *A. friesiana* subsp. *friesiana*, will be discussed in the next section. *Antennaria aromatica* (fig. 4) was first reported as occurring as diploid and tetraploid cytotypes and two additional determinations are also tetraploid (table 1), so it is one of several species in this group that have both diploid and tetraploid cytotypes (table 2). *Antennaria dioica* is unique in being the only member of this group that is not strictly North American, although it occurs in the western Aleutian Islands



FIGS. 5-7. Distribution of *Antennaria* species. 5. *A. media*, *A. microphylla*, and *A. solitaria*. 6. *A. neglecta*, *A. rosea* s.l., and *A. umbrinella*. 7. *A. neodioica* s.l., *A. parvifolia* s.l., and *A. virginica*. Bar = 500 km.

of Alaska (fig. 9). It has been reported as a diploid numerous times (table 2). We have not seen material of a proposed relative, *A. caucasica* Boriss., also reported as having $2n = 28$ (Fedorov 1969). *Antennaria nordhagiana* is another sexual diploid that is closely related to *A. dioica* (Rune and Rønning 1956). It occurs in a very restricted, remote area in northern Norway (fig. 9) and therefore little is known about it beyond its initial description (Rune and Rønning 1956).

A recent field excursion to New Mexico and Arizona yielded abundant material of the previously uncounted *A. marginata* (fig. 4). Mexican, Arizonan, and New Mexican collections of *A. marginata* are known as diploid from four localities, and as tetraploid, hexaploid, octoploid, and decaploid from one locality each (table 1). Diploid populations have sex ratios approaching 1:1 (Bayer and Stebbins unpubl. obs.), but the polyploid populations are entirely pistillate. Morphologically, the different cytotypes are indistinguishable from one another which suggests that the polyploid cytotypes are probably of non-hybrid origin (autopolyploids) from the diploids (table 3).

Antennaria media resembles *A. marginata* in that a number of polyploid cytotypes are known in addition to the diploid ones. Diploid cytotypes are reported from three California localities (Bayer 1984; table 1; fig. 5). Tetraploid cytotypes are apparently more common as they are known from 22 sites from California and Oregon (Bayer and Stebbins 1981; Bayer 1984; table 1). In addition, current studies have revealed the presence of septaploid ($2n = 98$) and octoploid ($2n = 112$) cytotypes from one locality each in the Rocky Mountains (table 1). As with *A. marginata*,

morphological studies need to be undertaken to determine if the sexual diploid cytotypes can be morphologically distinguished from the polyploid sexual and agamospermous ones.

Antennaria microphylla also comprises both sexual diploid populations and polyploid agamospermous ones (Bayer 1984; fig. 5). Totally agamospermous populations are easily detected by their lack of staminate clones, whereas sexual ones usually have a staminate frequency of 0.5 (Bayer and Stebbins 1983). Sexual diploid populations are quite common and are known from 42 localities (Bayer 1984; Chinnappa 1984; table 1). Asexual triploids are now known from seven localities (Chinnappa 1984; table 1); tetraploids are known from two sites. The polyploids are often found growing in sympatry with *A. rosea*. The two taxa are distinguishable by white phyllaries in *A. microphylla* as opposed to the red or rose-colored phyllaries in *A. rosea* (Bayer 1984). Presumably, the triploids could arise from fertilization of occasional sexual tetraploid embryo sacs of *A. rosea* or *A. microphylla* by pollen from a sexual diploid such as *A. microphylla*.

A distinctive species of the *A. alpina* complex, *A. monocephala*, has leaves that are green on the upper surface and monocephalous flowering stalks. It is common and widespread in Alaska and Yukon, but occurs sparingly in adjacent regions (fig. 8). Previous counts are $2n = \text{ca. } 70$ from Point Barrow (Packer and McPherson 1974) and $2n = 60$ and 56 from eastern Siberia (Zhukova 1968, 1969; table 2). Specimens from Siberia were not seen by us, but several collections from Barrow and the Rocky Mountains consist only of pistillate plants, so that these

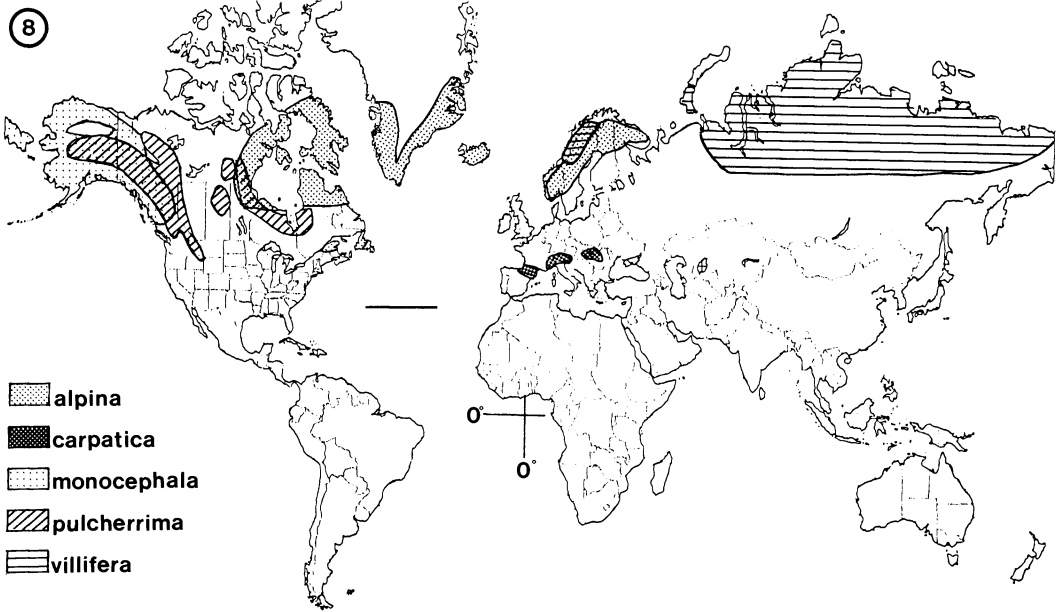


FIG. 8. Distribution of *Antennaria* species: *A. alpina* s. str., *A. carpatica*, *A. monocephala*, *A. pulcherrima*, and *A. villifera*. Bar = 2000 km.

polyploids appear to be apomictic. One of us (G.L.S.) collected *A. monocephala* from nine different localities in Alaska [Steese Highway northeast of Fairbanks, Talkeetna Mountains north of Palmer, two from Seward Peninsula, and five localities in the Alaska Range from the Richardson Highway west to Denali National Park (table 1). Staminate and pistillate plants were found in equal numbers at all localities; diploid counts were obtained from specimens collected at four localities (table 1)]. Examination of herbarium specimens from CAN, GH, and US showed that staminate plants are common throughout the Aleutian Islands, the southern half of the Alaska Peninsula, Yukon, and the MacKenzie Mountains, and that stomatal size of these plants is similar to specimens counted as diploid. Apparently, *A. monocephala* is diploid and sexual in the central part of its range (fig. 8), while peripheral localities to the north, northwest, and south contain polyploid apomicts. Borissova (1959), in her treatment of *Antennaria* for the flora of the USSR, recognized two monocephalous species from Kamchatka, *A. dioiciformis* Kom. and *A. komorovii* Juz. We have not seen specimens of these "species", and no chromosome counts are available, but judg-

ing from published descriptions, they may be apomicts that combine in different ways the characteristics of *A. dioica* and *A. monocephala*.

Antennaria neglecta, *A. solitaria*, and *A. plantaginifolia*, originally determined by Stebbins (1932a), have all been counted numerous times as uniformly diploid (Bayer and Stebbins 1981; Bayer 1984; table 1). These species all occur primarily in eastern North America (figs. 4, 5), but *A. neglecta* extends across the Great Plains (fig. 6). *Antennaria virginica*, also distributed in eastern North America, is found on Devonian shale barrens primarily in West Virginia and areas of adjacent states (fig. 7). This sexual species was determined as diploid from five localities and tetraploid from seven sites throughout its restricted range. From this limited sample, little can be concluded about distribution of the diploids and autotetraploids; however, the diploid cytotypes occur as widely as the polyploids. Diploids were found on the extreme margins of the range in Columbiana Co., Ohio (Bayer and Stebbins 1981), and recently in Carroll Co., Virginia (table 1).

Antennaria corymbosa (fig. 3) and *A. racemosa* (fig. 4) are uniformly diploid ($2n = 28$) according to past determinations (table 2) and current

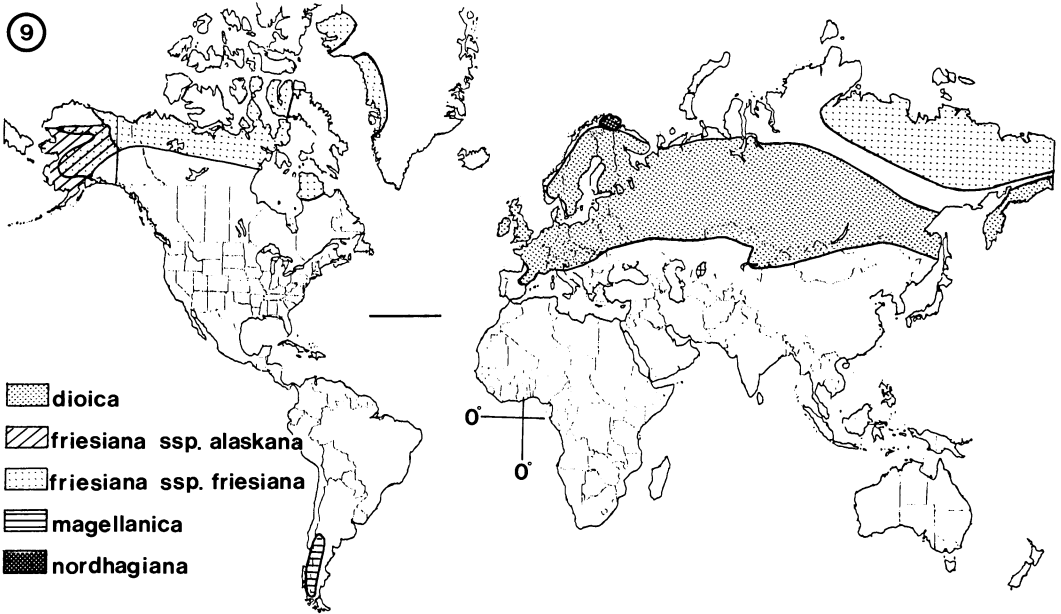


FIG. 9. Distribution of *Antennaria* species: *A. dioica*, *A. friesiana* subsp. *alaskana*, *A. friesiana* subsp. *friesiana*, *A. magellanica*, and *A. nordhagiana*. Bar = 2000 km.

ones (table 1). *Antennaria racemosa*, which occurs primarily in British Columbia, Alberta, Washington, Idaho, and Montana (fig. 4), is most closely related to the eastern *A. plantaginifolia*. This conclusion is based on recent morphological and artificial hybridization studies (Bayer 1985a) and enzyme electrophoretic studies (Bayer and Crawford 1986).

Xerophytic *A. rosulata* occurs in dry, sagebrush steppe and adjacent open *Pinus ponderosa* forests in an area centering on the four corners region of the southwestern United States (fig. 4). The first three determinations for this species are diploid (table 1). *Antennaria rosulata* may be one of the diploid progenitors of the *A. rosea* complex (table 3) and is also morphologically similar to *A. soliceps*, an apomictic microspecies known only from the Charleston Mountains near Las Vegas, Nevada, and also to the widespread *A. parvifolia*. *Antennaria umbrinella* also has both sexual diploid and autotetraploid cytotypes (table 2). The species is known as a diploid from only three localities (Bayer 1984; table 1) and as a tetraploid from 23 sites (Bayer 1984; Chinnappa 1984; table 1). Extensive sampling by Chinnappa (1984) has demonstrated that this species is consistently tetraploid in Canada. The diploids occur at widely spaced localities in Ida-

ho, Montana, and Wyoming. Additional sampling is needed in Colorado, Montana, Nevada, and Wyoming, the southern portions of the range (fig. 6), to establish the distribution of cytotypes. These data, however, do seem to fit an established pattern of diploids occurring in southern unglaciated areas with polyploids in glaciated northern regions (Bayer and Stebbins 1981; Ehrendorfer 1980; Wolf 1980).

All species in group 2 are sexual except *A. media* and *A. marginata* in which the polyploid cytotypes may be either sexual or asexual. This group includes 16 species, of which eight are strictly diploid (table 2). Five species, *A. aromatica*, *A. friesiana* subsp. *alaskana*, *A. media*, *A. umbrinella*, and *A. virginica*, have both sexual diploid and sexual tetraploid populations. *Antennaria microphylla* has sexual diploid cytotypes, as well as asexual (agamosperous) triploids and tetraploids. The species have two major centers of diversity and two minor ones. *Antennaria aromatica*, *A. corymbosa*, *A. marginata*, *A. media*, *A. microphylla*, *A. racemosa*, *A. rosulata*, and *A. umbrinella* all occur in the U.S. Rockies and some in parts of adjacent British Columbia and Alberta (figs. 3-6). This corresponds to the Rocky Mountain floristic region, the Great Basin province of the Madrean region, and the extreme

western edge of the North America prairies province of the Atlantic North American floristic region as described by Cronquist (1982). In this area (figs. 6, 7), two agamic complexes (*A. rosea* and *A. parvifolia*) reach their greatest morphological diversity because they are largely sympatric with their sexual diploid progenitors. The species occurring in eastern North America (Atlantic North American floristic region; see Cronquist 1982), *A. neglecta*, *A. plantaginifolia*, *A. solitaria*, and *A. virginica* (figs. 4, 7), are the diploid progenitors (along with *A. racemosa*) of *A. neodioica* s.l. (Bayer 1985a; Bayer and Crawford 1986) and the *A. parlinii* s.l. (Bayer 1985b; Bayer and Crawford 1986) agamic complexes. Two taxa, *A. friesiana* subsp. *alaskana* and *A. monocephala*, occur primarily in Alaska and Yukon Territory (circumboreal floristic region; figs. 8, 9); *A. dioica* and *A. nordhagiana* are primarily Eurasian in distribution (fig. 9).

Bayer and Stebbins (1982) suggested that reproductive isolating mechanisms among related sexual taxa of *Antennaria* are primarily ecological in that most species occur in different habitats. In addition, the sexual taxa can usually be hybridized easily in the greenhouse, although most F₁ hybrids are partially sterile and have irregular meiosis (Bayer and Stebbins 1982; Bayer 1984). In some habitats, sexual taxa do co-occur and in such places putative natural interspecific hybrids may often be found. The first of these, reported by Stebbins (1932a), is between *A. neglecta* and *A. plantaginifolia*. Other presumed hybrids were identified based on gross morphological features and are reported here (table 1) as primarily diploid. One hybrid (table 1; CO-433) was triploid, and probably a cross between diploid *A. corymbosa* and tetraploid *A. media*. Both species were found growing on the same slope as the hybrid. The discovery and identification of hybrids is deemed important because formation of the polyploids probably begins by interspecific hybridization among sexual individuals (Bayer 1985a, 1985b). The discovery of hybrids may indicate which diploid genomes could be present in the polyploids.

Group 3—Polyploid Sexual and Agamosperous Species Complexes. Five large agamic complexes may be recognized in *Antennaria*: *A. alpina* s.l., *A. neodioica* s.l., *A. parlinii* s.l., *A. parvifolia* s.l., and *A. rosea* s.l. *Antennaria neodioica* and *A. rosea* are entirely agamosperous

and therefore staminate clones are extremely rare in populations of these species. Conversely, *A. alpina* s.l., *A. parlinii* s.l., and *A. parvifolia* s.l. all have both sexually reproducing and agamosperous populations. Recent studies (Bayer 1985a, 1985b; Bayer and Crawford 1986) have maintained that agamic complexes arise through hybridizations among sexual diploid species of *Antennaria*. In general, the polyploids are sympatric with their sexual diploid relatives, but all have expanded their ranges beyond that of the diploids (figs. 3, 9).

The polyploid complex centering about *A. alpina* is among the most widespread in the genus. Major gene contributions to it have probably been made by five sexual taxa: *A. friesiana* subsp. *alaskana* and *A. monocephala* from Alaska, diploid *A. media* from the Sierra Nevada of California, diploid *A. nordhagiana* from northern Norway, and diploid *A. aromatica* from northwestern Wyoming and southwestern Montana. The apomicts belonging to the complex are most abundant and diverse in the arctic parts (fig. 8) of the Canadian province (Cronquist 1982). The *A. alpina* apomicts occur sparingly westward in Kamchatka and eastern Siberia, and extend eastward through Iceland to northern and alpine Scandinavia and the northwest corner of the USSR. Members of the complex are absent from western and central Siberia, where they are replaced by the northernmost populations of *A. dioica* (Borissova 1959).

Several authors (Fernald, Greene, Malte, Nelson, and Porsild) have described as species various apomicts or clusters of apomicts belonging to this complex (table 3), but its taxonomic limits are as yet poorly defined. Apomicts occur in western Canada that are transitional between the *A. alpina* and *A. rosea* complexes. In the western U.S., there are apomicts that are intermediate between *A. alpina*, *A. corymbosa*, *A. media*, and *A. umbrinella*, whereas some of the entities recognized by Borissova (1959) may represent intermediates between *A. alpina* and *A. dioica*. These intermediates are possible because many of the predominantly apomictic populations give rise, presumably via chromosomal segregation, to staminate plants. These may pollinate pistillate plants of sexual species wherever the two come into contact. The relationships within this vast complex are still poorly understood. Establishing these relationships by both traditional and modern methods is one of the most

important fields for future research in the genus.

Chromosome numbers recorded for apomicts in the *A. alpina* complex range from $2n = 56$ to ca. 100. Tetraploids, previously known from Greenland (Jorgensen et al. 1958), have been determined by us in *A. friesiana* subsp. *friesiana* from three localities in the Alaska Range, from Mt. Fairplay, near the eastern boundary of Alaska, and from a population from Denali National Park that is similar to *A. atriceps* (table 1). The number 63 is recorded for *A. friesiana* subsp. *friesiana* from eastern Siberia (Zhukova 1965) and for two different "species" from Greenland (table 2). Hexaploids ($2n = 84$) occur in Greenland and are predominantly or exclusively present in apomicts from Iceland and Scandinavia, including the topotype locality of *A. alpina*. The highest count, $2n = \text{ca. } 100 (\pm 20)$, was recorded by Mosquin and Hayley (1966) from Melville Island in the Canadian arctic. Apparently, the greatest diversity of chromosome numbers of apomicts in this complex exists in the Canadian arctic and adjacent Greenland, as well as in the Canadian and U.S. Rockies, based upon high numbers found in Alberta (Chinnappa 1984), Montana (Bayer 1984), and Colorado (Bayer 1984).

Antennaria neodioica is recognized as containing four subspecies, viz. *A. neodioica* subsp. *canadensis* (E. Greene) Bayer & Stebbins, subsp. *howellii* (E. Greene) Bayer, subsp. *neodioica*, and subsp. *petaloidea* (Fern.) Bayer & Stebbins. The species as a whole has tetraploid, hexaploid, and decaploid cytotypes and the first two cytotypes are most frequently found in this species. The tetraploids occur primarily near the proposed origin of the species (Bayer 1984), which is the mid-Appalachian region. Higher ploidy levels occur in areas where the species has expanded its range (fig. 7) beyond the Appalachians (Bayer 1984). For example, the highest number (decaploid) for the species is from a Montana collection of *A. neodioica* subsp. *howellii*. Biosystematic studies have demonstrated that *A. neglecta*, *A. plantaginifolia*, *A. racemosa*, and *A. virginica* are the most likely diploid progenitors of the compilospecies *A. neodioica* (Bayer 1985a; Bayer and Crawford 1986).

The *A. parlinii* complex occurs as tetraploid from seven localities, pentaploid from two localities, hexaploid from 50+ localities, and octoploid from a single locality (Bayer and Stebbins

1981; Bayer 1984; table 1). Two subspecies, *A. parlinii* subsp. *parlinii* and subsp. *fallax* (E. Greene) Bayer & Stebbins constitute *A. parlinii* s.l. This complex has both sexual and agamosperous populations (Bayer and Stebbins 1983; Bayer 1984) with sexual populations occurring primarily in the southwestern portions of the range (fig. 4). Undoubtedly, *A. parlinii* arose in this area (the midwest) where it is both sexual and occasionally tetraploid, but predominantly hexaploid (Bayer and Stebbins 1982; Bayer 1984, 1985a). Presumably, *A. parlinii* spread northward and eastward where it survives as agamosperous hexaploids. *Antennaria plantaginifolia*, *A. racemosa*, and *A. solitaria* are the diploid ancestors of the *A. parlinii* agamic complex (Bayer 1985b; Bayer and Crawford 1986). The *A. parlinii* and *A. neodioica* polyploid agamic complexes have been examined in several studies (Stebbins 1932a, 1932b; Bayer and Stebbins 1981, 1982, 1983; Bayer 1984, 1985a, 1985b; Bayer and Crawford 1986) making them the best understood of the polyploid complexes in *Antennaria*.

Antennaria parvifolia occurs as sexual, asexual, and intermediate (mixed sexual, facultatively sexual, and asexual) populations. Preliminary field investigations (Bayer and Stebbins unpubl. obs.) indicate that sexual and intermediate populations occur in the southern parts of the range (fig. 7) of the species in New Mexico, Arizona, and Colorado, while apomictic ones occur north into Manitoba, Alberta, and British Columbia. Chromosome numbers ranging from tetraploid to hexaploid, octoploid, and decaploid have all been encountered (table 2). Sexuality and agamospermy in *A. parvifolia* are apparently not correlated to ploidy level; both are known to occur in both high and low (tetraploid) cytotypes (Bayer 1984; Bayer and Stebbins, unpubl. obs.). Decaploids, which are the highest cytotype known in *Antennaria*, are quite commonly encountered in *A. parvifolia* (Bayer 1984; tables 1 and 2). *Antennaria dioica*, *A. marginata*, and *A. rosulata* appear to be likely diploid relatives (table 3) of *A. parvifolia* (considering gross morphological observations made on field and herbarium specimens; Bayer and Stebbins pers. obs.). Some specimens morphologically resemble one of the probable diploid parents and this relationship is indicated in table 1.

Antennaria rosea has been determined as tetraploid ($2n = 56$) from 48 localities throughout its range (fig. 6) in the Rockies and Sierra Ne-

vada (tables 1 and 2). Triploidy and pentaploidy are known from one locality each (tables 1 and 2). Recent field observations (Bayer and Stebbins unpubl. obs.), suggest that *A. rosea* is apparently of hybrid origin involving perhaps seven sexual diploid species including *A. aromatica*, *A. corymbosa*, *A. media*, *A. microphylla*, *A. racemosa*, *A. rosulata*, and *A. umbrinella* (table 3). Combinations of these different diploid genomes along with polyploidy and agamospermy have led to a great diversity of apomictic clones and consequently an extreme degree of taxonomic confusion in *A. rosea* s.l. An *Antennaria* known from the southern hemisphere (fig. 9), the apomictic *A. magellanica* Schultz-Bip (= *A. chilensis* Remy), has $2n = 56$ and probably belongs to this complex (Bergman 1937).

In conclusion, the polyploid agamic complexes are very diverse both morphologically and chromosomally. Many of the polyploids have a single predominant cytotype as well as several other less frequent ploidy levels, for example *A. rosea* is usually tetraploid, although triploid and pentaploid cytotypes are known (table 2). *Antennaria media* and *A. friesiana* subsp. *friesiana* are usually tetraploid, while *A. alpina* s. str. and *A. parlinii* are most frequently hexaploid (table 2). Several cytotypes are known in *A. neodioica* and *A. parvifolia*, but based on available counts (table 2) no single cytotype is predominant. Many more determinations will be required before geographical distribution of cytotypes within the polyploids are completely known because morphological features alone for use as indicators of ploidy level are as yet unavailable. In general, the polyploids are much more widely distributed than are any of the diploids and they occur more often in northern glaciated areas while the diploids are found in southern unglaciated regions. Polyploidy and agamospermy are associated because apomicts are always polyploid, but not vice versa.

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