Chromosome Numbers and Taxonomic Notes for North American Species of Antennaria (Asteraceae: Inuleae)

Randall J. Bayer

Chromosome Numbers and Taxonomic Notes for North American Species of *Antennaria* (Asteraceae: Inuleae)

RANDALL J. BAYER

Department of Botany, Ohio State University,
Columbus, Ohio 43210

ABSTRACT. Chromosome numbers are presented for 132 populations of 27 taxa and three naturally occurring hybrids of *Antennaria*. Of the 27 taxa, 15 apparently have not been counted before and two counts are new numbers for species previously determined. Twenty taxa consist entirely or partially of sexual diploids ($2n = 28$): *A. arcuata, A. argentea, "aromatica," A. corymbosa, A. dimorpha, A. dioica, A. flagellaris, A. Geyeri, A. lanata, A. luzuloides, A. media, A. microcephala, A. microphylla, A. neglecta, A. plantaginifolia, A. racemosa, A. solitaria, A. suffrutescens, A. umbrinella,* and *A. virginica.* Six other species for which counts are not available are thought to exist as sexual diploids, bringing to 26 the total number of sexual diploids in the genus as a whole. Chromosome numbers are also presented for the five heteroploid complexes: *A. alpina* s.l. (including *A. media*), *A. neodioica* s.l., *A. parlinii* s.l., *A. parvifolia* s.l., and *A. rosea* s.l. While *A. alpina* s.l., *A. rosea* s.l., and *A. neodioica* s.l. each consist of one or two euploid chromosome levels, *A. parlinii* and *A. parvifolia* each have at least four different levels. *Antennaria parvifolia* has the highest chromosome number known in the genus, $2n = 140$ (decaploid). B-chromosomes were found in *A. suffrutescens.* Based on the counts presented and karyotypic information, it is hypothesized that the original base number in *Antennaria* was $x = 14$. A fourth subspecies of the *A. neodioica* complex, **Antennaria neodioica** subsp. **howellii**, is formally named.

Antennaria Gaertner comprises 25–30 sexual diploid species and several large polyploid agamic complexes distributed throughout the temperate to arctic regions of the northern hemisphere. It has long been thought that the base number of *Antennaria* is $x = 7$ even though $n = 14$ was the lowest number known (Gustafsson 1947). Bayer and Stebbins (1981) indicated that the base number could not be ascertained until more species had been counted. Chromosome reports now available for species viewed as primitive on morphological grounds, along with additional cytological information, suggest that $x = 14$ is the base number in *Antennaria*. The objectives of this paper are 1) to delimit the number and ranges of sexual diploid ($n = 14$) species of North American *Antennaria*, 2) to report the chromosome numbers of various members of the polyploid complexes, 3) to present evidence for a base number of $x = 14$ in *Antennaria*, and 4) to discuss several karyotypic features of the species.

MATERIALS AND METHODS

Root tips were used for chromosome counts for most collections owing to the lack of staminate plants in agamospermous species. Even in populations that have staminate members, the maturation of the meiocytes is completed over a very short period of time, which makes field collection of suitable meiotic material very difficult. For most counts, pieces of several individuals were uprooted from each population, potted, and grown in the greenhouse or growth chamber for several weeks until new roots had regenerated. Cuttings of some specimens were suspended in an aerated water bath to promote fast, active, root growth. Root tips were collected in the morning and placed in a solution of 0.015% colchicine (w/v) for 8–10 hours at 4°C. The root tips were then fixed overnight in Östergren and Heneen's fluid (Östergren and Heneen 1962), which provides excellent visualization of primary and secondary constrictions for karyotypic studies. Staining employed the Feulgen reaction (Feulgen and Rossenbeck 1924) according to the procedure of Östergren and Heneen (1962). The root tips were hydrolyzed in 1 N HCl at 60°C for 8 minutes and washed briefly in distilled water. They were then transferred to Schiff's reagent (leuco-basic fuchsin) for 2 hours and finally to a 5% pectinase solution for 1 hour. The root tips may be stored in 45% acetic acid at −20°C. In preparation for examination, root tips were macerated

in a drop of 45% acetic acid and pressure was applied to the coverslip with a new pencil eraser. Slides were then observed with phase contrast optics and photographed with Kodak technical pan film #2415. To make slides permanent, they were frozen according to the dry ice method (Conger and Fairchild 1953), air-dried on a warming plate overnight, and made permanent with the addition of one drop of Euparal and a new coverslip.

Meiotic material was fixed in 3:1 (v/v) 95% ethanol : glacial acetic acid and stored in 70% ethanol at −20°C. Individual florets were squashed and stained in acetocarmine stain (Löve and Löve 1975) and heated with an alcohol lamp before examination.

RESULTS

Table 1 lists the 132 populations of 27 taxa and three natural hybrids of *Antennaria* collected in 28 U.S. states, two Canadian provinces, and Switzerland. As far as can be determined, 15 taxa had not been counted previously and two new numbers have been obtained for taxa previously determined. Each entry represents an individual population. Voucher specimens are on deposit at DAV and OS, with duplicates of the WI- numbers at WIS. Figures 1–9 are photographs of some of the *Antennaria* chromosomes discussed. Photographs of chromosomes of other species of *Antennaria* may be seen in Bayer and Stebbins (1981).

DISCUSSION

In order to present the results in an evolutionary perspective the species will be discussed as three separate groups: 1) diploid species from sections not containing polyploid apomicts, 2) diploid species from sections containing polyploid apomicts, and 3) polyploid agamospermic and amphimictic species. It is probable that many of the polyploid agamospecies are of hybrid origin between two or more diploid members of the genus (Juel 1900; Bayer and Stebbins 1982).

In the following discussion a few taxa are interpreted narrowly (sensu stricto) to indicate the amount of variation present in the species. Inclusion or probable inclusion of these taxa within another species is indicated in parentheses after a name (table 1). For example, collections referable to the type of *A. brainerdii*

TABLE 1. Chromosome numbers determined for North American species of *Antennaria* Gaertner. Voucher specimens are on deposit at DAV and OS. Presented are state (province), county, and voucher designation for each collection (Bayer's voucher numbers consist of letters and numbers while Bayer and Stebbins' numbers are *80--* and *81--*). The frequency of staminate clones, when determined, is presented in parentheses after voucher designations. * = first count for the species, ** = new number for the species; *** = count from meiotic material.

A. arcuata Cronq. $2n = 28$*. Nevada, Elko Co., *NE-258, NE-259*.

A. argentea Benth. $2n = 28$. California, Sierra Co., *8001*.

"aromatica" Evert in press. $2n = 28$*. Montana, Carbon Co., *8092* (0.64). $2n = 56$*. Montana, Gallatin Co., *8105* (0.47).

A. brainerdii Fern. s.str. (=*A. parlinii* Bayer & Stebb. s.l.). $2n = 56$*. West Virginia, Pendleton Co., *SR-172*.

A. corymbosa E. Nelson. $2n = 28$. California, Mono Co., *C-218*; Eldorado Co., *ENF-269*. Wyoming, Johnson Co., *8051* (0.43).

A. dimorpha Torrey & A. Gray. $2n = 28$*. Montana, Carbon Co., *8066*. Washington, Spokane Co., *8141*.

A. dioica (L.) Gaertner. $2n = 28$. Switzerland, Davos, *K. Urbańska-Worytkiewicz s.n.*

A. farwellii E. Greene s.str. (=*A. parlinii* Bayer & Stebb. s.l.). $2n = 56$*. Michigan, Wexford Co., *MI-8001*.

A. flagellaris (A. Gray) A. Gray. $2n = 28$*. California, Lassen Co., *AF-227*.

A. geyeri A. Gray. $2n = 28$*. California, Siskiyou Co., *8030*. Washington, Spokane Co., *8139*.

A. lanata (Hook.) E. Greene. $2n = 28$*. Wyoming, Park Co., *8095****.

A. luzuloides Torrey & A. Gray. $2n = 28$*. Montana, Sanders Co., *8138*. Washington, Spokane Co., *8140*.

A. media E. Greene. $2n = 28$**. California, Inyo Co., *C-235*; Tulare Co., *C-245*. $2n = 56$. California, Inyo Co., *C-227, C-232, C-233, C-238, C-239, 8185*; Mono Co., *C-213, C-217, C-219, 8188*; Siskiyou Co., *MS-266* (0.00); Trinity Co., *JT-232*; Tulare Co., *C-246*. Oregon, Deschutes Co., *SW-222* (0.51), *DE-221* (0.47), *GL-229*; Douglas Co., *DO-224* (0.00); Klamath Co., *CL-225* (0.00); Lane Co., *DPW-223* (0.00).

A. microcephala A. Gray. $2n = 28$*. California, Sierra Co., *8003*.

A. microphylla Rydb. $2n = 28$*. Montana, Meagher Co., *8108* (0.24). North Dakota, Grand Forks Co., *JL-212*. Wyoming, Johnson Co., *8048*. $2n = 56$*. Montana, Carbon Co., *8088*. Wyoming, Johnson Co., *8056*.

A. neglecta E. Greene. $2n = 28$. Colorado, Boulder Co., *8020*. Ohio, Fairfield Co., *CE-201*. Iowa, Johnson Co., *UI-211*. Indiana, Bartholomew Co., *MZ-218, HV-216*; Dearborn Co., *DB-219*. Kansas, Cherokee Co., *KA-*

TABLE 1. Continued.

186. New Jersey, Sommerset Co., *NJ-240.* South Dakota, Custer Co., *8044.* West Virginia, Hampshire Co., *PV-166.*

A. neodioica Bayer & Stebb. s.l. $2n = 84$. Ontario, Peterborough Co., *KB-257.* Montana, Cascade Co., *8109* (0.00). South Dakota, Pennington Co., *8037* (0.00), *8045.* Wisconsin, Iowa Co., *WI-109.*

A. neodioica E. Greene subsp. *Howellii* (E. Greene) Bayer. $2n = 56^*$. South Dakota, Custer Co., *8046-B.* $2n = 84^*$. South Dakota, Custer Co., *8040, 8040-A.*

A. parlinii Bayer & Stebb. s.l. $2n = 56$. Missouri, Jasper Co., *8012-C.* Wisconsin, Dane Co., *DC-194, WI-204, WI-206;* Iowa Co., *WI-207, WI-212* (0.00). $2n = 70$. Missouri, Jasper Co., *8012-A, 8012-D.* $2n = 84$. Ontario, Guelph, *GU-185;* Peterborough Co., *KL-183.* Arkansas, Washington Co., *AR-189.* Indiana, Brown Co., *MZ-218.* Kentucky, Greenup Co., *GP-208.* Minnesota, Rice Co., *MN-191.* Ohio, Adams Co., *LX-253, BR-254;* Washington Co., *MG-215.* Oklahoma, Payne Co., *8010.* New York, Cattaraugus Co., *ASP-234, AL-235.* Wisconsin, Dane Co., *WI-203, WI-205;* Iowa Co., *WI-207, WI-208, WI-210;* Monroe Co., *LA-186;* Rock Co., *WI-211, WI-213* (0.50).

A. parvifolia Nutt. $2n = 56^*$. Montana, Carbon Co., *8067* (0.00). $2n = 112^*$. Colorado, Larimer Co., *8018.* North Dakota, Kidder Co., *La Duke 504.* South Dakota, Custer Co., *8019.* Washington, Spokane Co., *8142.* Wyoming, Johnson Co., *8047;* Park Co., *FC-213.* $2n = 140^*$. Colorado, Gunnison Co., *WR-271;* Larimer Co., *8019.*

A. plantaginifolia (L.) Richardson. $2n = 28$. Georgia, Chattooga Co., *GA-267.* Kentucky, Johnson Co., *SK-206;* Lawrence Co., *CK-207.* North Carolina, Halifax Co., *HX-230.* Virginia, Wythe Co., *RP-272.* Wisconsin, Columbia Co., *WI-201;* Dane Co., *WI-202.*

A. racemosa Hook. $2n = 28$. Montana, Gallatin Co., *8106;* Missoula Co., *8133* (0.43), *8134* (0.36). Wyoming, Park Co., *FC-214.*

A. rosea (D. C. Eaton) E. Greene. $2n = 56$. Alberta, Banff, *BNP-266.* California, Eldorado Co., *ENF-268.* Wyoming, Johnson Co., *8049.* $2n = 70^{**}$. Wyoming, Johnson Co., *8054.*

A. solitaria Rydb. $2n = 28$. Ohio, Fairfield Co., *MG-200;* Hocking Co., *SC-192, NE-197.* North Carolina, McDowell Co., *MD-195.*

A. suffrutescens E. Greene. $2n = 28 + 2B^*$. Oregon, Josephine Co., *O-201.*

A. umbrinella Rydb. $2n = 28^*$. Wyoming, Johnson Co., *8052.* $2n = 56^*$. Montana, Meagher Co. (type locality), *8111* (0.65). Wyoming, Johnson Co., *8058.*

A. virginica Stebb. $2n = 28$. West Virginia, Hampshire Co., *RA-250.* $2n = 56$. Maryland, Allegheny Co., *MY-236.* Pennsylvania, Bedford Co., *EV-180* (0.68), *WE-181* (0.56). West Virginia, Hampshire Co., *HR-162***.*

TABLE 1. Continued.

A. racemosa × *A. umbrinella.* $2n = 28^*$. Montana, Carbon Co., *8086.*

*A. media* × *A. umbrinella.* $2n = 56^*$. California, Mono Co., *C-222.*

A. media × *A. rosea* × *A. umbrinella.* $2n = 56^*$. California, Tulare Co., *C-243.*

Fern. were considered by us to belong to a more broadly circumscribed taxon *A. parlinii* s.l. (Bayer and Stebbins 1982).

Diploid species from sections not containing apomicts. Species in this group are all diploids, but tetraploids have been reported previously, e.g., *A. eucosma* $(2n = 56 + 4B)$ of the maritime provinces of Canada (Morton 1981). As far as is known, members of this group are strictly sexual. These species include *A. arcuata, A. microcephala, A. luzuloides, A. geyeri,* and *A. argentea,* all of which have retained a number of characteristics considered primitive for *Antennaria,* and they resemble members of *Gnaphalium* L. $(n = 7)$, the genus from which *Antennaria* is thought to be derived (Stebbins 1974).

Antennaria arcuata, which is known from only a few localities in northern Nevada, southern Idaho, and Wyoming, has been determined as diploid (table 1; fig. 1). It is unique in the genus in having long, arching stolons and ephemeral basal leaves and in occurring in seasonally moist meadows. Its basal leaves somewhat resemble those of *A. microcephala.* Another narrowly distributed species, *A. argentea,* occurs in dry open woods and hillsides in southern Oregon, extreme northern California, and western Nevada. The count of $2n = 28$ agrees with one made by Strother (1972) for *A. argentea,* although B-chromosomes were not observed in my mitotic material, as was seen by Strother in meiotic preparations.

Antennaria dimorpha and *A. flagellaris* occur on dry, open, stony slopes and are among the most xerophytic of all *Antennaria* species. *Antennaria dimorpha,* characterized by having a single large capitulum on a peduncle and closely cespitose habit, occurs from British Columbia and Alberta south to Washington, Oregon, and California, and east to Wyoming, Nebraska, and Montana. Long filiform stolons and solitary capitulae are characteristic of *A. flagellaris,* which is known from eastern Washington and Oregon
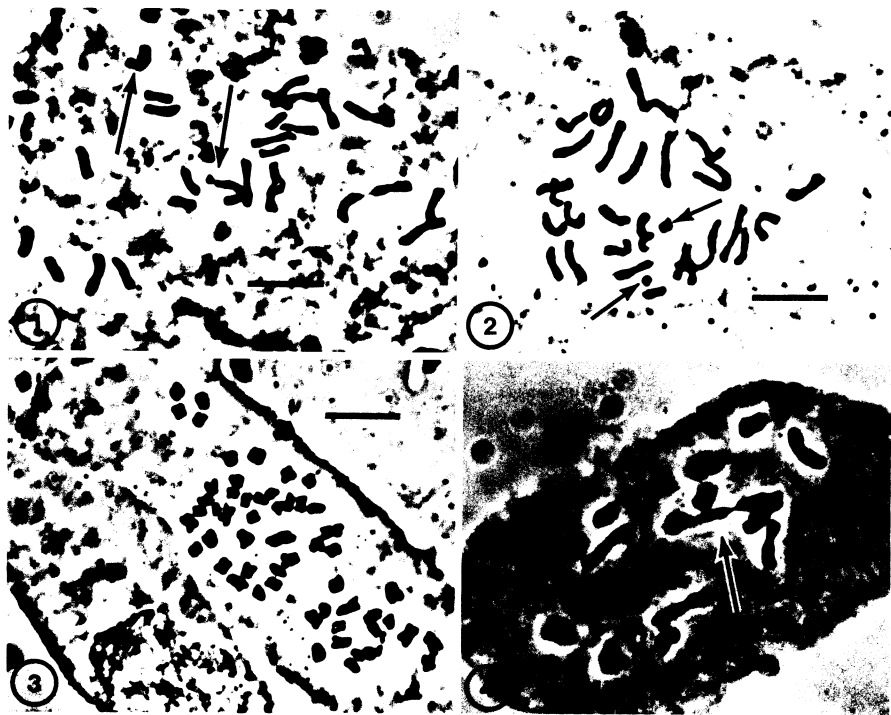
FIGS. 1–4. Chromosomes of *Antennaria* (cf. table 1). 1. Mitotic chromosomes ($2n = 28$) of *A. arcuata* (*NE-258*) with nucleolus organizing regions indicated by arrows. 2. Mitotic chromosomes ($2n = 28 + 2B$) of *A. suffrutescens* (*O-201*) with two B-chromosomes (arrows). 3. Mitotic chromosomes ($2n = 56$) of *A. media* (*C-227*). 4. Meiocyte at diakinesis of *A. plantaginifolia* × *A. solitaria* (*JC-52* × *TE-38-1*) showing multivalent (arrow). Scales = 10 μm.

east to Idaho and northern Wyoming, with a single locality in northeastern California. Both *A. dimorpha* and *A. flagellaris* were counted as diploid (table 1).

A very distinctive species, *A. geyeri* is found on dry hills and open woods from eastern Washington south to northern California and west to western Nevada. Typical of *A. geyeri* are its woody basal stolons, upright ascending stems with tomentose leaves, and often roseate phyllaries. In its lack of prostrate stolons and basal rosettes, this diploid resembles certain species of the closely related *Anaphalis* DC. *Antennaria lanata* occurs in alpine regions of British Columbia and Alberta, south to northeastern Oregon, and east to Montana and Wyoming. As the epithet implies, it is characterized by densely pubescent leaves and has been counted as diploid from one site in Wyoming (table 1).

Antennaria luzuloides and *A. microcephala* are two closely related diploid ($2n = 28$) species in-

habiting dry hillsides and meadows. The former is distributed from British Columbia south to eastern Oregon and Lassen County, California, east to Montana, Wyoming, and Colorado, while the latter is more narrowly distributed from southern Oregon to Lassen and Nevada counties, California, and adjacent western Nevada. Both species have a non-stoloniferous habit and numerous small capitulae but differ in the three-nerved leaves of *A. luzuloides* versus the one-nerved leaves of *A. microcephala*.

Lastly, *A. suffrutescens* occurs on dry serpentine ridges from Josephine and Curry counties, Oregon, and Del Norte and Humboldt counties, California. This very distinct species has small, coriaceous, bright green leaves and solitary heads and is diploid with two supernumerary or B-chromosomes ($2n = 28 + 2B$). The two B-chromosomes (fig. 2, arrows) were observed in most mitotic cells. B-chromosomes have been previously reported in *A. argentea*
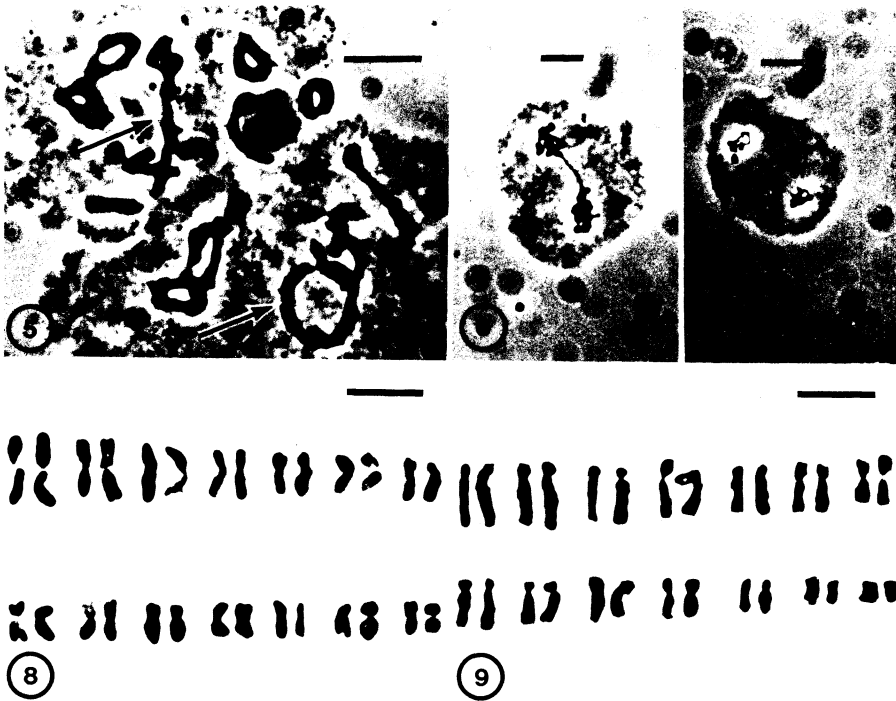
FIGS. 5–9. Chromosomes of *Antennaria* (cf. table 1). 5. Meiocyte at diakinesis of *A. plantaginifolia* × *A. solitaria* (*JC-52* × *TE-38-1*) showing probable multivalents (arrows) and a single bivalent with nucleolus organizing region associated with the nucleolus. 6. Meiocyte at anaphase I of *A. plantaginifolia* × *A. solitaria* (*JC-52* × *TE-38-1*) showing an anaphase bridge between the two groups of chromosomes. 7. Same as figure 6, but showing a fragment lagging at the metaphase plate. 8. Karyogram of *A. neglecta* (*UI-211*) showing 14 pairs of primarily metacentric chromosomes. 9. Karyogram of *A. plantaginifolia* (*CO-102*) showing 14 pairs of primarily submetacentric chromosomes. Scales = 10 µm.

(Strother 1972) and *A. eucosma* Fern. & Wieg. (Morton 1981).

In summary, the aforementioned species have all been determined to be diploids and they probably reproduce via monosporic sexual embryo sacs of the *Polygonum*-type, as has been described for other sexual species of *Antennaria* by Juel (1900) and Stebbins (1932a). The presence of equal numbers of staminate and pistillate clones in populations of *Antennaria*, as is typical of these species (Bayer unpubl.), is a good indicator of the presence of an amphimictic reproductive mode (Bayer and Stebbins in press). These sexual diploid species, like others in *Antennaria* (Bayer and Stebbins 1981), are often quite narrowly distributed as compared to polyploid agamospermic species.

Sexual diploids and tetraploids from sections containing apomictic species. These species are im-

portant because they appear to be closely related to the polyploid, agamic complexes. They occur primarily as diploids, but tetraploids (presumably autopolyploids based on morphology) are known in four of them. It is likely that hybridization between and among these species has led to the formation of many of the polyploid apomictic complexes (Bayer and Stebbins 1982). Sexual embryo sacs occur in *A. neglecta* and *A. plantaginifolia* (Stebbins 1932a) and in *A. dioica* (Juel 1900). Sex ratios close to 1:1 suggest that the remaining species are also sexual (Bayer and Stebbins in press).

Antennaria corymbosa occurs in wet, alpine to subalpine meadows from Colorado and Utah, north to Montana and Idaho, west to Oregon, and sparingly in California and Nevada. It is probably the most mesophytic species of *Antennaria*, and it characteristically has a large dark

brown spot at the base of each white phyllary. It was first counted by us (Bayer and Stebbins 1981) and has been further verified as a diploid. *Antennaria corymbosa* appears to be related to the *A. rosea* agamic complex.

Antennaria dioica occurs from the British Isles eastward to the Aleutian Islands of Alaska, thus it occurs, albeit sparingly, in North America. It has been confirmed as a diploid by numerous European workers since the first count by Juel (1900) and is reported here also as a diploid from one locality in Switzerland (table 1). Morphologically, *A. dioica* closely resembles members of the *A. parvifolia* polyploid complex, which is common throughout the western United States.

Antennaria microphylla occurs as a sexual diploid (table 1) from eastern Washington east to western Minnesota and southward to Colorado. It has small, often spathulate, leaves and white phyllaries. A putatively (based on sex ratios) agamospermous form of *A. microphylla* is tetraploid ($2n = 56$) and is often found growing in sympatry with the tetraploid, agamospermous *A. rosea* (table 1). It differs from *A. rosea* mainly by its white phyllaries as opposed to the pink or red phyllaries of *A. rosea*, and this situation will be discussed further in the next section. Sexual *A. microphylla* is probably closely related to the *A. rosea* agamic complex and also the *A. gaspensis* Fern. [=*A. neglecta* var. *gaspensis* (Fern.) Cronq.] agamic complex of eastern Canada.

Another sexual species of *Antennaria* similar to *A. microphylla* is the brown-phyllaried *A. umbrinella*. *Antennaria umbrinella* occurs as a diploid and a tetraploid and is distributed on dry, subalpine slopes, meadows, and ridges from Alberta and British Columbia south through Washington, Oregon, California, and Montana to Wyoming, Colorado, and Arizona. A frequency of staminate clones of 0.68 (table 1) from the approximate topotype locality in Meagher Co., Montana, suggests that the tetraploid (presumed to be an autopolyploid) is sexual (Bayer unpubl.). Like *A. microphylla*, *A. umbrinella* appears most closely related to the *A. rosea* complex based on the often brownish phyllaries seen in many of the *A. rosea* segregates.

Two diploid counts (table 1; listed under *A. media*) have been obtained for plants that resemble *A. media* and occur in the Sierra Nevada. These plants closely resemble the type of

A. pulchella E. Greene, a species that further research may reveal is distinct from the tetraploid *A. media* (pers. comm. G. L. Stebbins, who is currently revising sect. *Alpinae*). A newly discovered species of the *Alpinae* group (Evert in press) is "*aromatica*" E. F. Evert, which is characterized by its dark brownish green phyllaries and pungently aromatic, cuneiform leaves. It occurs on limestone or talus in xeric subalpine areas of the mountains of Wyoming and Montana and has been counted as a diploid from the Beartooth Mountains of Montana and a tetraploid from the Bridger Mountains, east of Sacagawea Peak, Montana.

Diploid *A. racemosa*, with its glabrous, bright green leaves and raceme of capitula, is found in open woods and subalpine mountain slopes from Alberta and British Columbia, south and east to Washington, Oregon, northern California, Montana, Idaho, and Wyoming. The species appears to be closely related to the eastern diploids, *A. plantaginifolia* and *A. solitaria*, and the polyploid agamic complex of *A. parlinii* s.l. (Bayer and Stebbins 1982). A putative hybrid between two partially sympatric populations of *A. racemosa* and *A. umbrinella* is diploid (table 1). Hybridization between sympatric diploid species of *Antennaria* is not uncommon and is probably an important evolutionary factor leading to the production of the large, variable, taxonomically difficult, agamic complexes found in *Antennaria* (Juel 1900; Bayer and Stebbins 1982).

The final four sexual species to be considered, *A. neglecta*, *A. plantaginifolia*, *A. solitaria*, and *A. virginica*, all occur in the eastern United States and have been discussed by us both taxonomically (Bayer and Stebbins 1982) and cytologically (Bayer and Stebbins 1981). *Antennaria neglecta* has been verified as diploid from ten localities across its range, confirming the previous counts of Stebbins (1932a) and Bayer and Stebbins (1981). The seven diploid counts of *A. plantaginifolia* presented here confirm the previous reports by Stebbins (1932a), Bayer and Stebbins (1981), and Löve and Löve (1982). Monocephalous *A. solitaria* has been verified as diploid, thus confirming previously published counts (Stebbins 1932a; Bayer and Stebbins 1981).

The shale barren endemic *A. virginica* occurs in West Virginia and Virginia and in limited areas in Maryland, Pennsylvania, and Ohio (one

locality). Originally suspected to be a diploid (Stebbins 1935), it was confirmed to occur both as a diploid and a tetraploid (Bayer and Stebbins 1981). One additional diploid and four tetraploids are reported here (table 1). The frequencies of staminate clones (table 1) from two of these tetraploid populations indicate a sexual mode of reproduction. The situation of diploids and autotetraploids occurring in *A. virginica* parallels the condition previously mentioned for *A. umbrinella, A. media,* and "*aromatica.*" Many more determinations will be needed before meaningful statements can be made about geographic distributions of diploids and tetraploids of these species.

As far as relationships are concerned, *A. plantaginifolia* and *A. solitaria* are most closely allied to the *A. parlinii* s.l. polyploid complex (Bayer and Stebbins 1982; Bayer unpubl.). Morphologically, *A. neglecta, A. plantaginifolia,* and *A. virginica* are most similar to the *A. neodioica* s.l. polyploid agamic complex (Bayer and Stebbins 1982; Bayer unpubl.). Interspecific hybrids among the four eastern diploids (Bayer and Stebbins 1982) indicate that the diploid species differ primarily by a few structural rearrangements of the chromosomes. Meiosis in hybrids between *A. plantaginifolia* and *A. solitaria* typically exhibits irregularities such as multivalents (figs. 4–5), but generally 12 to 14 II are observed. Meiotic irregularities such as bridge chromosomes (fig. 6) at anaphase I and lagging fragments (fig. 7) at telophase I suggest that *A. plantaginifolia* and *A. solitaria* differ by one or more inversions.

In summary, it is probable that all the abovementioned species have a sexual mode of reproduction and are for the most part diploid ($2n = 28$) with some sexual tetraploids known in four of the species. Morphologically, all the species are characterized by having prostrate stolons, considered to be an advanced characteristic in *Antennaria* (Stebbins 1974). As is true of almost all of the sexual diploids (and tetraploids) these species are morphologically well-defined and represent the sexual relatives of the widespread polyploid, agamospermous species complexes to be discussed in the next section. While some of them (e.g., *A. neglecta* and *A. dioica*) are broadly distributed, most are not as widespread geographically as are their derived polyploid agamic complexes.

Nearly all the sexual species of *Antennaria* are now known cytologically. Other probable sexual diploids or tetraploids in need of investigation are: *A. marginata* E. Greene (SW U.S.A.), *A. rosulata* E. Greene (SW U.S.A.), *A. stenophylla* A. Gray (NW U.S.A.), *A. alaskana* Malte (Alaska), *A. monocephala* DC. (Alaska), and *A. anaphaloides* Rydb. (NW U.S.A.).

Polyploid sexual and agamospermous species complexes. *Antennaria* appears to contain five large polyploid species complexes namely, *A. alpina* s.l., *A. parvifolia* s.l., *A. neodioica* s.l., *A. parlinii* s.l., and *A. rosea* s.l. *Antennaria rosea* and *A. neodioica* are composed entirely of polyploid agamospermous populations that are completely pistillate. By contrast, *A. alpina, A. parvifolia,* and *A. parlinii* (Bayer and Stebbins in press) contain some sexual populations with both staminate and pistillate clones and some that are agamospermous. The sexual populations in each species generally occur in the southern parts of the respective ranges of the species complexes. Agamospermous seed production occurs via diplospory followed by diploid parthenogenesis, as was first demonstrated for *A. alpina* (Juel 1900) and later for members of the *A. parlinii* and *A. neodioica* complexes by Stebbins (1932b).

Included within sect. *Alpinae* is *A. media* (including *A. scabra* E. Greene and *A. pulchella* E. Greene), which occurs on alpine tundra from Alberta and British Columbia south to the Sierra Nevada of California and east to Montana, Wyoming, and Colorado. *Antennaria media* is known as both sexual and asexual populations; it has been confirmed as tetraploid (fig. 3). At two localities (table 1; *8185* and *8188*) the specimens match the type of *A. scabra,* which is considered a synonym for *A. media.* Greenish brown phyllaries are a distinctive characteristic of tetraploid *A. media.* This species is viewed as the southern relative of the circumboreal, fully agamospermous, primarily hexaploid ($2n = 84$; Fedorov 1969) *A. alpina* (L.) Gaertner s.str. Two unusual collections of *A. media* from California may represent introgressant segregates (G. L. Stebbins pers. comm.). The first of these, *C-222* (table 1), while being very similar to *A. media,* also bears characteristics of *A. umbrinella.* Another collection, *C-243* (table 1), is also morphologically most like *A. media,* but probably also has genes from *A. corymbosa* and *A. rosea.*

Antennaria rosea is a widespread polymorphic group of fully agamospermous populations, which was first reported as a tetraploid by Löve

and Löve (in Fedorov 1969) and confirmed by us (Bayer and Stebbins 1981). Morton (1981) reported *A. rosea* from the Yukon as $2n = $ ca. 68 (approximately pentaploid). It occurs in montane subalpine zones from Alaska, Yukon, and Northwest Territories, east to Hudson Bay, south to Alberta, British Columbia, and California, and east to Colorado, Wyoming, and Montana. I have verified *A. rosea* s.str. (with pink or red phyllaries) as being tetraploid (table 1). A white-bracted form of *A. rosea* s.l., which can be referred to as *A. microphylla* s.str., has also been counted as tetraploid. Frequently the white-bracted form (*A. microphylla* s.str.) and the rose-bracted form (*A. rosea* s.str.) are found growing in sympatry. An extremely rare staminate clone, discovered in Wyoming, was determined as pentaploid ($2n = 70$; table 1). Such clones could have arisen from the fertilization of an occasional sexual embryo sac produced by tetraploid *A. rosea* by pollen from an unknown hexaploid to produce a pentaploid hybrid.

Another widespread complex, *A. parvifolia* s.l., occurs in dry plains and slopes in arid areas from Manitoba south to Oklahoma and west to New Mexico, Arizona, Utah, Washington, and British Columbia. As previously mentioned, it appears to be primarily sexual in the southern part of its distribution and predominantly agamospermous in the northern part of its range, from which most of my determinations have been made. It has rather large capitula that usually have pink or white phyllaries except for the brownish phyllaries found in *A. aprica* E. Greene s.str., which is here included in the *A. parvifolia* complex. It is quite polymorphic chromosomally with tetraploids, octoploids ($2n = 112$), and decaploids ($2n = $ ca. 140) known for the complex. The count of $2n = $ ca. 140 (approximate decaploid) represents the highest recorded in the genus. One of the decaploid counts, *WR-271* (table 1) is the only count made from a sexual population of *A. parvifolia*. This sexual decaploid is noteworthy for *Antennaria* because the polyploids are usually agamospermous, or if they are amphimictic they are generally at the lower tetraploid or hexaploid levels. Sexuality was known previously as high as the hexaploid level in *A. parlinii*. Recently Löve and Löve (1982) counted *A. parvifolia* Nutt. (listed by them both as *A. aprica* and incorrectly named as *A. parviflora* Nutt.) as a hexaploid ($2n = $

84). Thus, *A. parvifolia* s.l. occurs as a polyploid at four euploid levels ranging from tetraploid to decaploid and contains populations with the highest chromosome numbers known in *Antennaria*.

Antennaria neodioica s.l. (Bayer and Stebbins 1982) is composed of obligately agamospermous populations (Stebbins 1932b; Bayer and Stebbins 1982) that are widely distributed (see Bayer and Stebbins 1982, fig. 6). It is distinguished by its single-nerved often spathulate basal leaves and has been determined previously as a tetraploid (Stebbins 1932b; Bayer and Stebbins 1981) and a hexaploid (Bayer and Stebbins 1981). *Antennaria neodioica* appears to be tetraploid primarily in regions where it is not too distant from its closest diploid progenitor, *A. virginica* (Bayer and Stebbins 1981). In regions more distant from *A. virginica*, which occurs mainly in Virginia and West Virginia, *A. neodioica* is primarily hexaploid and this is confirmed by additional hexaploid counts obtained from localities in Ontario, Wisconsin, South Dakota, and Montana (table 1).

Antennaria howellii, a western relative of *A. neodioica* s.l., is characterized by one- to three-nerved glabrous basal leaves with heads in corymbiform cymes. It occurs in montane woods from Alberta and British Columbia, south to Oregon, Washington, northern California, Idaho, Wyoming, Montana, and South Dakota and is here reported as a tetraploid and a hexaploid. It seems to consist entirely of obligate apomicts with staminate plants being rare. The results of a numerical analysis using 38 vegetative and reproductive characters (Bayer unpubl.) suggest *A. howellii* be recognized as a subspecies of the polymorphic *A. neodioica* s.l. complex (see Bayer and Stebbins 1982 for details). Subspecies *howellii* can be distinguished from *A. neodioica* E. Greene subsp. *neodioica* and subsp. *petaloidea* (Fern.) Bayer & Stebb. by its glabrous adaxial basal leaf surfaces. It is separable from subsp. *canadensis* (E. Greene) Bayer & Stebbins by its lack of a flag-like appendage on the upper cauline leaves and basal leaves usually greater than 9 mm wide.

Antennaria neodioica E. Greene subsp. **howellii** (E. Greene) Bayer, comb. et stat. nov.— *Antennaria howellii* E. Greene, Pittonia 3: 174. 1897.—*Antennaria neglecta* E. Greene var. *howellii* (E. Greene) Cronq., Leafl. W.

Bot. 6:43. 1950.—LECTOTYPE (here designated): U.S.A., Oregon, St. Helens, 20 May 1887, *Thomas Howell s.n.* (NDG!; isolectotype: MO!). E. L. Greene erred in this original description by stating that the locality from Howell's specimen was "Oregon, Mt. St. Helens" because obviously Mt. St. Helens is in Washington. The specimen (actually from near the town of St. Helens, Oregon) is actually from a locality that is nearer to the typical habitat of the species.

Antennaria Parlinii s.l. (Bayer and Stebbins 1982) is distributed throughout the deciduous forests of the eastern United States and adjacent areas in southern Ontario (see Bayer and Stebbins 1982, fig. 7). It has been discussed in detail with respect to cytology (Bayer and Stebbins 1981), taxonomy (Bayer and Stebbins 1982), and populational reproductive modes (Bayer and Stebbins in press). Both sexual and agamospermous populations are known (Bayer and Stebbins in press) and it has been previously reported (Bayer and Stebbins 1981) as a tetraploid, pentaploid, hexaploid, and octoploid. Tetraploids, previously known from only one site (in Oklahoma), have now been found to occur at one locality in Missouri and five localities in the Wisconsin driftless area. The presence of sexual tetraploids at the western limits of the range of the species strongly supports the hypothesis that they arose in this area (the Midwest) and spread eastward and northward, where they occur primarily as sexual and agamospermic hexaploids. Pentaploids ($2n = 70$) have been verified at one locality in Missouri and the common hexaploids have been verified at 18 localities throughout its range. *Antennaria farwellii* s.str. and *A. brainerdii* s.str. are two small-leaved agamospecies that Bayer and Stebbins (1982) included in synonymy under *A. parlinii* s.l. Specimens collected in the field are referable to the types of *A. brainerdii* and *A. farwellii* and are so referred here (table 1). Each agamospecies has been determined as tetraploid (table 1).

In summary, the polyploid sexual and agamic complexes have much wider distributions than their diploid relatives. In *Antennaria* agamospermy is always associated with polyploidy, but polyploidy is not necessarily always associated with agamospermy. Two of the polyploid complexes, i.e., *A. media* and *A. rosea*, are predominantly one ploidy level while other complexes such as *A. parlinii* s.l. and *A. parvifolia* s.l. each contain four euploid levels.

KARYOTYPE MORPHOLOGY

As discussed by Bayer and Stebbins (1982), a number of European workers (e.g., Gustafsson 1947) have suggested that the base number in *Antennaria* is $x = 7$ even though the lowest number found is $x = 14$. The reasons for suggesting a base number of $x = 7$ in *Antennaria* include the following: 1) Some counts of $2n = 63$ have been reported (Fedorov 1969), and these could be interpreted as nine-ploid based on $x = 7$; and 2) the presence of $x = 7$ in the related *Gnaphalium* suggests $n = 14$ was originally derived from $x = 7$. Although the $2n = 63$ determinations can be neither discounted nor easily explained, all the counts reported here are multiples of 14 with several of them being pentaploid (odd-ploid) based on $n = 14$ ($2n = 70$). Species such as *A. arcuata, A. geyeri,* and *A. microcephala* are regarded as having retained primitive characters found in *Gnaphalium*, and these are all $2n = 28$. If an $n = 7$ *Antennaria* were to be found it would most likely have been among these species of *Antennaria*, yet it was not.

Additional evidence supporting an $x = 14$ base number in *Antennaria* comes from karyotypic studies. Chromosomes can be most parsimoniously paired into 14 groups of two (figs. 8–9), not into seven groups of four. The presence of one pair with nucleolus organizing regions (NOR; cf. fig. 1) indicates the presence of two genomes in these cells. The presence of a single paired chromosome attached to the nucleolus in early prophase of meiosis I, similar to those seen in figure 5, indicates that in this $n = 14$ individual there are two genomes present. Thus karyotypic data also support an $x = 14$ base number in *Antennaria*. These preliminary karyologic data demonstrate karyotypic differences between certain species in the genus. For example, chromosomes of *A. neglecta* are primarily metacentric (fig. 8) while those of *A. plantaginifolia* are mostly submetacentric (fig. 9).

LITERATURE CITED

BAYER, R. J. and G. L. STEBBINS. 1981. Chromosome numbers of North American species of *Antennaria* Gaertner (Asteraceae: Inuleae). Amer. J. Bot. 68:1342–1349.

———— and ————. 1982. A revised classification of *Antennaria* (Asteraceae: Inuleae) of the eastern United States. Syst. Bot. 7:300–313.

———— and ————. In press. Distribution of sexual and apomictic populations of *Antennaria parlinii.* Evolution 37.

CONGER, A. D. and L. M. FAIRCHILD. 1953. A quick-freeze method for making smear slides permanent. Stain Technol. 28:281–283.

EVERT, E. F. In press. A new species of *Antennaria* (Compositae) from Montana and Wyoming. Madroño.

FEDOROV, A. A. 1969. *Chromosome numbers of flowering plants.* Acad. Sci. USSR. V. L. Komarov Botanical Institute.

FEULGEN, R. and H. ROSSENBECK. 1924. Mikrosko-
pish-chemisher Nachweis einer Nucleinsäure vom Typus der Thymonucleinsäure und die darauf beruhende elektive Farbung von Zellkernen in mikroskopischen Praparatin. Hoppe-Seyler's Z. Physiol. Chem. 135:203–252.

JUEL, H. O. 1900. Vergleichende Untersuchungen uber typische und parthenogenetische Fortpflanzung bei der Gattung *Antennaria.* Kongl. Svenska Vetenskapsakad. Handl. 33(5):1–59.

GUSTAFSSON, Å. 1947. Apomixis in higher plants. Acta Univ. Lund. 42–44:1–370.

LÖVE, A. and D. LÖVE. 1975. *Plant chromosomes.* Leutershausen, Germany: J. Cramer.

———— and ————. 1982. IOPB chromosome number reports LXXV. Taxon 31:356.

MORTON, J. K. 1981. Chromosome numbers in Compositae from Canada and the U.S.A. J. Linn. Soc., Bot. 82:357–368.

ÖSTERGREN, G. and W. HENEEN. 1962. A squash technique for chromosome morphological studies. Hereditas 48:332–341.

STEBBINS, G. L. 1932a. Cytology of *Antennaria.* I. Normal species. Bot. Gaz. (Crawfordsville) 94:134–151.

————. 1932b. Cytology of *Antennaria.* II. Parthenogenetic species. Bot. Gaz. (Crawfordsville) 94:322–345.

————. 1935. A new species of *Antennaria* from the Appalachian region. Rhodora 37:229–237.

————. 1974. *Flowering plants: Evolution above the species level.* Cambridge, Mass.: Belknap Press, Harvard Univ. Press.

STROTHER, J. L. 1972. Chromosome studies in western North American Compositae. Amer. J. Bot. 59:242–247.