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# CHROMOSOME NUMBERS OF NORTH AMERICAN SPECIES OF ANTENNARIA GAERTNER (ASTERACEAE: INULEAE)[1]

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ABSTRACT

Chromosome numbers are presented for 99 populations of 13 species of *Antennaria*, including *A. plantaginifolia, A. neglecta, A. virginica, A. solitaria, A. racemosa, A. corymbosa, A. rosea, A. media, A. Parlinii, A. fallax, A. neodioica, A. canadensis*, and *A. petaloidea*. Four species from the eastern United States (*A. plantaginifolia, A. neglecta, A. solitaria*, and *A. virginica*) were determined as diploid ($n = 14$), and these are all sexual. Diploid counts were also obtained for two sexual species (*A. racemosa* and *A. corymbosa*) from the western United States. Chromosome counts are presented for two heteroploid agamic complexes occurring in the eastern United States; these include what have traditionally been referred to as *A. Parlinii, A. fallax, A. neodioica, A. canadensis*, and *A. petaloidea*. Determinations of $2n = 56$, 70, 84, and 112 were obtained for the *A. Parlinii* and *A. fallax* groups, where $2n = 84$ had been the only number previously reported. Numbers of $2n = 84$ were confirmed for *A. petaloidea* and *A. canadensis* and $2n = 56$ for *A. neodioica*. The western United States polyploid species (*A. rosea* and *A. media*) are reported as $2n = 56$. The presence of apomixis is correlated with polyploidy. The distribution of chromosome numbers in eastern United States *Antennaria* demonstrates that two diploids and many polyploids occur above the glacial margin, and thus there is an increase in the frequency of polyploidy with latitude. Colonization of the glaciated region by *Antennaria* following the recession of the Wisconsin ice sheet is also discussed. Many of the polyploids occur only in the glaciated region, thus suggesting a recent origin for these cytotypes. There is evidence indicating that the original base number in *Antennaria* may be $x = 7$.

*ANTENNARIA* GAERTNER is a dioecious member of the Inuleae (everlasting tribe) that has its greatest distribution in the cold temperate and Arctic regions of the Northern Hemisphere and three species in the southern Andes of South America. Apomixis in the genus was well documented by Juel (1900) in his work in European *Antennaria alpina* (L.) Gaertner, and was confirmed by Stebbins (1932b) in his work on northeastern United States *Antennaria*. The genus has about 20–30 species complexes (Gustafsson, 1947). Sexual diploid *Antennaria* has a base number of $n = 14$, but it has been suggested (Gustafsson, 1947) that the actual base number should be $x = 7$, and that what are considered to be diploids are actually tetraploids (amphidiploids). Polyploidy is extensive in *Antennaria* as is the associated agamospermy. The majority of the sexual diploid species of *Antennaria* occur in North America. In the eastern United States, four diploids and two polyploid complexes exist. In many of the agamic polyploid microspecies, male plants are rare or unknown, because the female plants that produce seed via agamospermy produce only female progeny, with the same genotype as themselves. In order that the phenomenon of agamospermy in *Antennaria* be better understood its causes must be recognized. It has long been known that polyploidy somehow facilitates the development of agamospermy since apomixis and polyploidy are usually associated with each other (Gustafsson, 1947). In all known cases the diploid species of *Antennaria* are always sexual. Other than the early work of Stebbins (1932a, b) on eastern *Antennaria* and a few miscellaneous chromosome counts on western *Antennaria* (Strother, 1972), little previous work has been done on the cytogenetics of North American *Antennaria*. The objectives of this study were: 1) to find the number and ranges of the sexual diploid species of eastern North American *Antennaria;* 2) to confirm the diploid chromosome number in these sexual diploids throughout their ranges; 3) to determine the range of the

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two heteroploid agamic complexes of eastern *Antennaria* and to detect different polyploid levels if they exist; and 4) to make first counts for some western United States *Antennaria*. These data will be used to discuss the relation of polyploidy and agamospermy in *Antennaria*, to expand upon the theory that the base number of *Antennaria* should be considered to be x = 7, to hypothesize on the parentage of the polyploid agamosperms, and to consider the cytogeography of eastern *Antennaria*.

MATERIALS AND METHODS—Because most polyploid microspecies of *Antennaria* lack male plants, meiocytes could not be used for chromosome counting. Thus, root tips were used to obtain mitotic counts from all material. Plants were dug and transplanted to pots in the greenhouse. In most cases, several clones were secured from each population. After 2 to 8 wk, depending on the initial condition of the plants and time of year, root tips were harvested in the early morning and placed in 0.15% (w/v) solution of colchicine at 4 C for 8 hr. Root tips were then fixed in a 3:1 absolute alcohol : propionic acid (v/v) solution at 4 C for about 24 hr. After fixation, they were stored in a 70% solution of absolute alcohol at 4 C. Root tips were stained for 4 hr at 50 C in a modified solution of Snow's stain (Snow, 1963); the amount of HCl added to the standard Snow's stain being increased by a factor of 3. Increased acidity helped break down the relatively tough roots. Heavily stained portions of the root tips were thoroughly macerated in the drop of 45% acetic acid until a suspension of cells resulted. After adding the cover slip heavy pressure was applied to it with a new pencil eraser in order to squash the cells so that a good spread of the chromosomes would be achieved. Several counts were obtained from each population to assure accuracy in reporting chromosome numbers for each population.

RESULTS—Table 1 lists the chromosome number, collection number, and collection locality for the 102 populations of the 12 species of *Antennaria* examined in this study. Each entry represents an individual population. Voucher specimens are on deposit at OS. Figures 1 through 14 are photographs of chromosomes of 11 of the *Antennaria* species examined in this study. The distribution of diploid and polyploid populations in the *A. plantaginifolia* species complex is given in Fig. 15.

DISCUSSION—In order to understand the polyploid agamic complexes, the sexual diploid species must first be determined and studied (Babcock and Stebbins, 1938; Gustafsson, 1947). Thus, in the following discussion the sexual diploid species will be considered first followed by the polyploid agamic complexes.

*Sexual diploid species*.—Four sexual diploid species of *Antennaria* occur in the eastern United States. These are *A. plantaginifolia* (L.) Richardson in Hooker, *A. neglecta* Greene, *A. solitaria* Rydberg, and *A. virginica* Stebbins. As shown in Table 1, 14 populations of the first species, six of the second, six of the third, and three of the fourth species have been reported. The counts reported here for *A. plantaginifolia*, *A. solitaria*, and *A. neglecta* agree with those of Stebbins (1932a). The report of $2n = 28$ for *A. virginica* represents, as far as we are aware, the first determination for the species. *Antennaria solitaria* occurs in mesic wooded habitats south of the terminal margin of the Wisconsin glacial boundary. *Antennaria plantaginifolia* is confined to dry woods in the Appalachian Mountains region of the east. *Antennaria neglecta* occurs in prairies and grazed pastures throughout the east and is the most widespread of the four diploids. The spread of the range of *A. neglecta* was probably facilitated by deforestation and establishment of pastures by early settlers. *Antennaria neglecta* passes imperceptibly into *A. campestris* Rydberg, which is considered a synonym of *A. neglecta*, west of the Mississippi. It should be noted that OK-95 and OK-96, from Oklahoma, closely resemble *A. campestris* (Table 1). *Antennaria virginica* is restricted to shale barrens, mainly of West Virginia and Pennsylvania (Keener, 1970). It was long suspected that *A. virginica* is diploid (Stebbins, 1935) and this has been confirmed in plants from two locations, but it was found to be tetraploid in plants at a third location (Table 1). Stebbins (1935) postulated that *A. neodioica* Greene was the autotetraploid derivative of *A. virginica*, but this situation seems not to be the case since autotetraploid *A. virginica* closely resembles diploid *A. virginica*. *Antennaria neodioica* does not closely resemble diploid or tetraploid *A. virginica*, but it is possible that it is of allopolyploid origin, with *A. virginica* as one of its diploid parents.

Four species of *Antennaria* from western United States have been studied cytologically. Three of these chromosome counts represent first reports for the species. *Antennaria racemosa* Richardson in Hooker and *A. corymbosa* E. Nelson have both been determined to be diploids with $2n = 28$ (Table 1, Fig. 1 and 3). *Antennaria media* Greene is a tetraploid species with $2n = 56$ (Fig. 8). The count of

TABLE 1. *Chromosome numbers for 13 species of North American* Antennaria

| Species | 2n = | Location and voucher[a] |
|---|---|---|
| *A. solitaria* Rydberg | 28 | USA: KY: Bath Co., 4HS-44; McCreary Co., MBS-45. OH: Adams Co., BC-22; Hocking Co., HA-05. TN: Grundy Co. TE-38; Polk Co., QS-101. |
| *A. plantaginifolia* Richardson | 28 | USA: AL: Etowah Co., CO-102. KY: Edmonson Co., CSB-40; Hart Co., WSA-42, WSB-42, WSC-42, MT-50; Jackson Co., JC-52; Meade Co., MC-43; Whitley Co., WB-46. NC: McDowell Co., MD-105. PA: Centre Co., PA-15. SC: Abbeville Co., SB-104. TN: Campbell Co., CM-99; Polk Co., PO-100. |
| *A. neglecta* Greene | 28 | USA: OH: Delaware Co., BPN-56, KI-55; Fairfield Co., CT-06, CR-82. OK: Payne Co., OK-95, OK-96. |
| *A. virginica* Stebbins | 28[b] | USA: OH: Columbiana Co., AV-78. WV: Pendleton Co., BR-109. |
| | 56[b] | USA: WV: Grant Co., GR-110. |
| *A. racemosa* Richardson | 28[b] | USA: OR: Josephine Co., AR-89. |
| *A. corymbosa* E. Nelson | 28[b] | USA: CA: Eldorado Co., EL-115. |
| *A. neodioica* Greene | 56 | USA: OH: Delaware Co., ALC-53; Knox Co., KX-18. NY: Erie Co., EA-58. WV: Pendleton Co., ON-111. |
| | 84[c] | USA: OH: Fairfield Co., CR-82; Guernsey Co., CM-19. |
| *A. canadensis* Greene | 84 | USA: OH: Jefferson Co., AN-79. NY: Erie Co., EA-63. |
| *A. petaloidea* Fernald | 84 | USA: OH: Belmont Co., MO-80; Fairfield Co., CR-82; Jefferson Co., BZ-81. NY: Erie Co., AFG-61. CAN: ONT: Peterborough Co., BF-86, BF-87. |
| *A. media* Greene | 56[b] | USA: CA: Placer Co., AM-92. |
| *A. rosea* (D. C. Eaton) Greene | 56 | USA: CA: Eldorado Co., WL-114. |
| *A. Parlinii* Fernald sensu lato | 56[c] | USA: OK: Creek Co., OK-97-A. |
| (Bayer and Stebbins in prep.) | 70[c] | USA: KY: Lee Co., LC-48. |
| including *A. fallax* Greene) | 84 | USA: AR: Madison Co., AR-113. CT: New Haven Co., NH-20. IL: Vermillion Co., ILL-21, VC-32. IN: Monroe Co., MI-117; Perry Co., IN-116. KS: Greenwood Co., KA-119. KY: Bath Co., MB-41; Edmonson Co., CSA-40; Henry Co., HC-49; McCreary HB-47; Meade Co., OC-39; Rowan Co., TC-51. OH: Auglaize Co., FA-71; Belmont Co., MO-80; Coshocton Co., COS-17; Delaware Co., ALC-53, KI-54; Fairfield Co., BK-88, Franklin Co., DA-1-12; Highland Co., FH-30; Hocking Co. AC-27, AC-28, HS-65, HO-67, HG-83, HS-65-B; Knox Co., KX-18; Lawrence Co., SP-23; Noble Co., SL-64; Perry Co., PE-66; Ross Co., BB-25; Scioto Co., SF-26; Vinton Co., N-29, VC-24. OK: Creek Co., OK-97; Payne Co., OK-93; Rogers Co., OK-118; Tulsa Co., OK-94, OK-98. NY: Erie Co., EA-57. PA: Washington Co., WA-14. SC: Abbeville Co., AB-103; Lexington Co., SC-33 to -37. VA: Rockbridge Co., RB-106; Rockingham Co., RH-107. WV: Pendleton Co., PT-108. WI: Ashland Co., WI-112; Monroe Co., LA-186. CAN: ONT: Guelph, GU-185; Peterborough Co., KL-183. |
| | 112[b] | USA: OH: Knox Co., KX-18. |

[a] Collection numbers are those of the first author.
[b] First count for this species.
[c] New number for this species.

Löve and Löve (in Federov, 1969) for *A. rosea* (D. C. Eaton) Greene has been confirmed as 2n = 56 (Fig. 4, Table 1). Photographs of the chromosomes of all of the six diploids and tetraploid *A. media* and *A. rosea* can be seen in Fig. 1–8. One of the chromosomes in the genome is very long with a metacentric kinetochore. This phenomenon was observed in many preparations from all species when kinetochore regions were visible and is a distinctive feature of the *Antennaria* karyotype (Fig. 5 and 6, arrows).

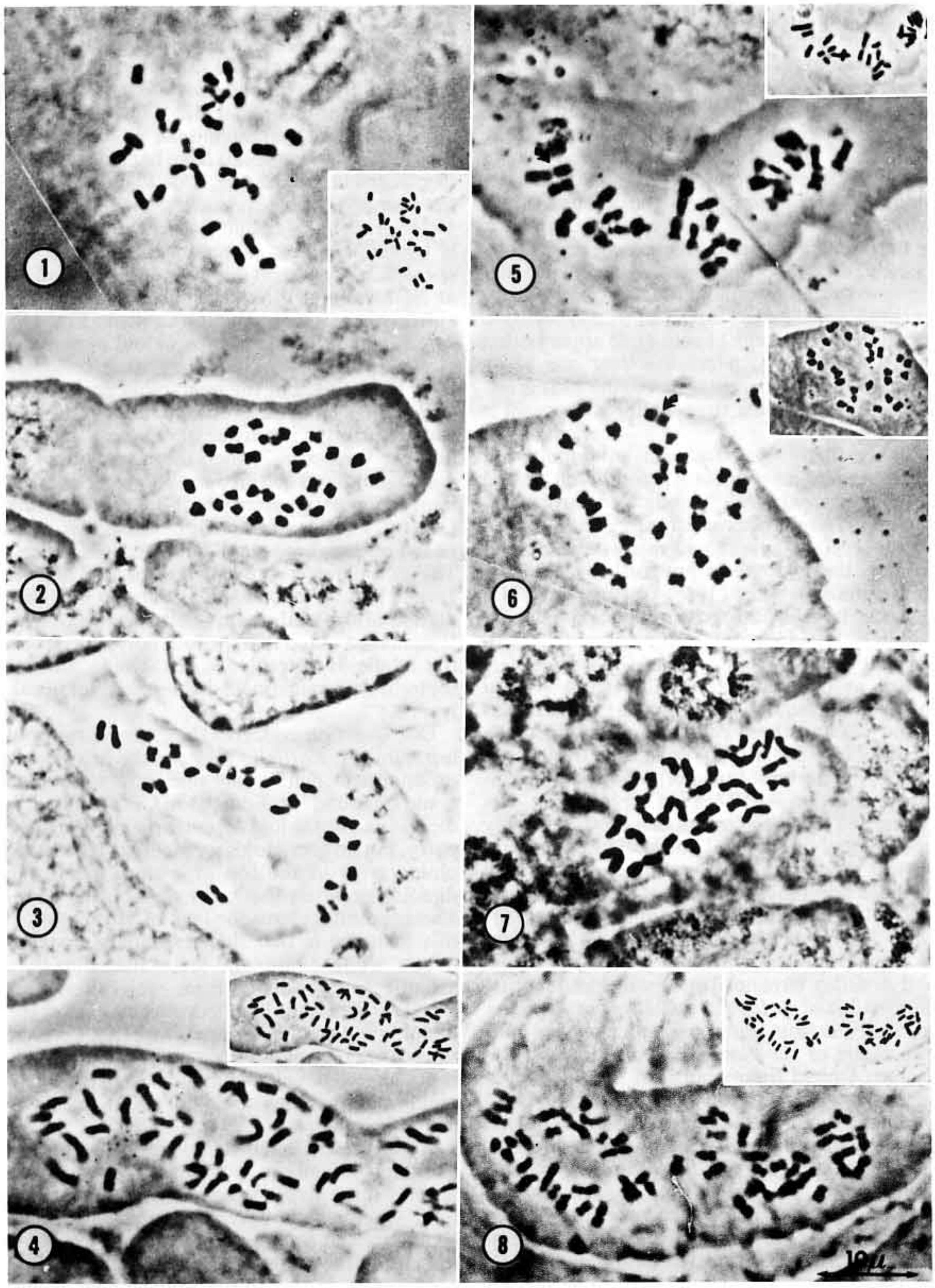


Fig. 1–8. Chromosomes of *Antennaria*. **1.** *A. corymbosa* $2n = 28$. **2.** *A. virginica* $2n = 28$. **3.** *A. racemosa* $2n = 28$. **4.** *A. rosea* $2n = 56$. **5.** *A. solitaria* $2n = 28$. **6.** *A. plantaginifolia* $2n = 28$. **7.** *A. neglecta* $2n = 28$. **8.** *A. media* $2n = 56$. Inked-in inserts are provided in some figures to aid in interpretation of the photographs. Arrows in Fig. 5 and 6 refer to the large metacentric chromosomes discussed in the text.

*Polyploid agamic complexes*—Staminate plants are rare in the small-leaved agamic complex made up of *A. neodiocia, A. canadensis* Greene, and *A. petaloidea* Fernald. These species occur in the eastern United States mainly *above* the terminal boundary of the Wisconsin glacier, which suggests a recent origin for these apomicts. Originally the development of apomixis in the genus *Antennaria* was thought to be ancient, dating back to the old Quaternary or Tertiary periods (Gustafsson, 1947). *Antennaria neodioica* was determined to be tetraploid ($2n = 56$) at four locations and hexaploid ($2n = 84$) at two locations in its range (Table 1). It appears that in the range of *A. neodioica* near one of its probable diploid parents (*A. virginica*) it is tetraploid, but farthest from its diploid parent it is hexaploid.

Interestingly, *A. neodioica* is apomictic at the tetraploid level while *A. virginica* is sexual at the tetraploid level. As indicated earlier, tetraploid *A. virginica* is apparently of non-hybrid (autopolyploid) origin, and this would seem to support the hypothesis put forth by students of apomixis (Nygren, 1946; Gustafsson, 1947) that the hybrid nature of many apomicts facilitates, but does not cause apomixis. Both *A. canadensis* and *A. petaloidea* were determined as hexaploids ($2n = 84$) from several locations throughout their ranges (Table 1, Fig. 9 and 12) and these reports agree with those of Stebbins (1932b). Parentage of these apomicts is uncertain, but morphology would indicate the two small-leaved diploids, *A. virginica* and *A. neglecta* are involved. Probably both allopolyploidy and autopolyploidy are involved in varying degrees in the composition of these polyploids.

The large-leaved agamic complex of *Antennaria Parlinii* sensu lato (Bayer and Stebbins, in preparation) includes *A. Parlinii* Fernald and *A. fallax* Greene. The woolly indumentum on the adaxial surface of the leaves of *A. fallax* separates it from glabrous-leaved *A. Parlinii*. The range of *A. Parlinii* sensu lato is in the eastern United States north of the fall-line to southern Ontario, and west to Oklahoma and Minnesota (Fig. 15). The distributions of the diploid and polyploid populations in the *Antennaria plantaginifolia-Parlinii-fallax* species complex are shown in Fig. 15. *Antennaria plantaginifolia* is one of the probable diploid parents of the polyploid *A. Parlinii*; it resembles *A. Parlinii* except for being smaller especially with regard to floral parts. The species is sexual throughout its range. The polyploid *A. Parlinii* may occur as sexual or apomictic populations, the latter being discerned by a conspicuous lack of staminate clones. The distribution of these sexual and apomictic populations will be discussed in a later paper. Previously only hexaploid ($2n = 84$) *A. Parlinii* was known (Stebbins, 1932b), but now tetraploid ($2n = 56$), pentaploid ($2n = 70$), and octoploid ($2n = 112$) levels have been discovered (for distribution see Fig. 15). Photographs of the four polyploid levels are shown in Fig. 10, 11, 13, and 14. Hexaploid *Antennaria Parlinii* is by far the most common polyploid in the species, having been confirmed as a hexaploid at 52 locations throughout its range, and is either sexual or apomictic (Table 1, Fig. 15). The sexuality of the tetraploid and pentaploid clones is unknown since they were collected after blooming, but the pentaploid probably is apomictic because the odd ploidy level would cause sterility if it were sexual, unless the base number were $x = 7$, then the plant would be a decaploid and sterility would not be a problem. A population that was discovered in Knox County, Ohio is of interest because it is composed of both hexaploid and octoploid clones. The octoploids represent one of the highest counts known for *Antennaria* and in this population are sexual and exhibit a 1:1 sex ratio. It should be noted that the four polyploid levels (i.e., diploids, tetraploids, hexaploids, and octoploids) are indistinguishable morphologically.

One question concerns the extreme rarity of tetraploid *A. Parlinii*. Why are the hexaploids predominant, while only one tetraploid clone could be found? In Edmonson Co., Kentucky, diploid and hexaploid *Antennaria* grow in sympatry, but no tetraploids were found. The hexaploids grow at the top of a slope while the diploids grow on the lower part of the slope. The apparent reason for lack of tetraploids in this instance is that the hexaploids are apomictic, while the diploids are sexual, thus they are effectively isolated from each other. This type of isolation probably occurs whenever the diploids and hexaploids are sympatric. Perhaps the reason tetraploids are rare is that apomixis is not as well developed in them as in the hexaploids and thus they could not colonize as well as the hexaploids.

As has been found in several other genera in which apomixis is prevalent, the diploid species have a restricted geographic distribution, whereas the polyploids are widespread (Babcock and Stebbins, 1938; Wolf, 1980). At the end of the last glaciation, *Antennaria* was probably restricted to the Appalachian Mountains and southeastern United States. After the glacial recession a large number of habitats were open to colonizing species (Adams 1905;

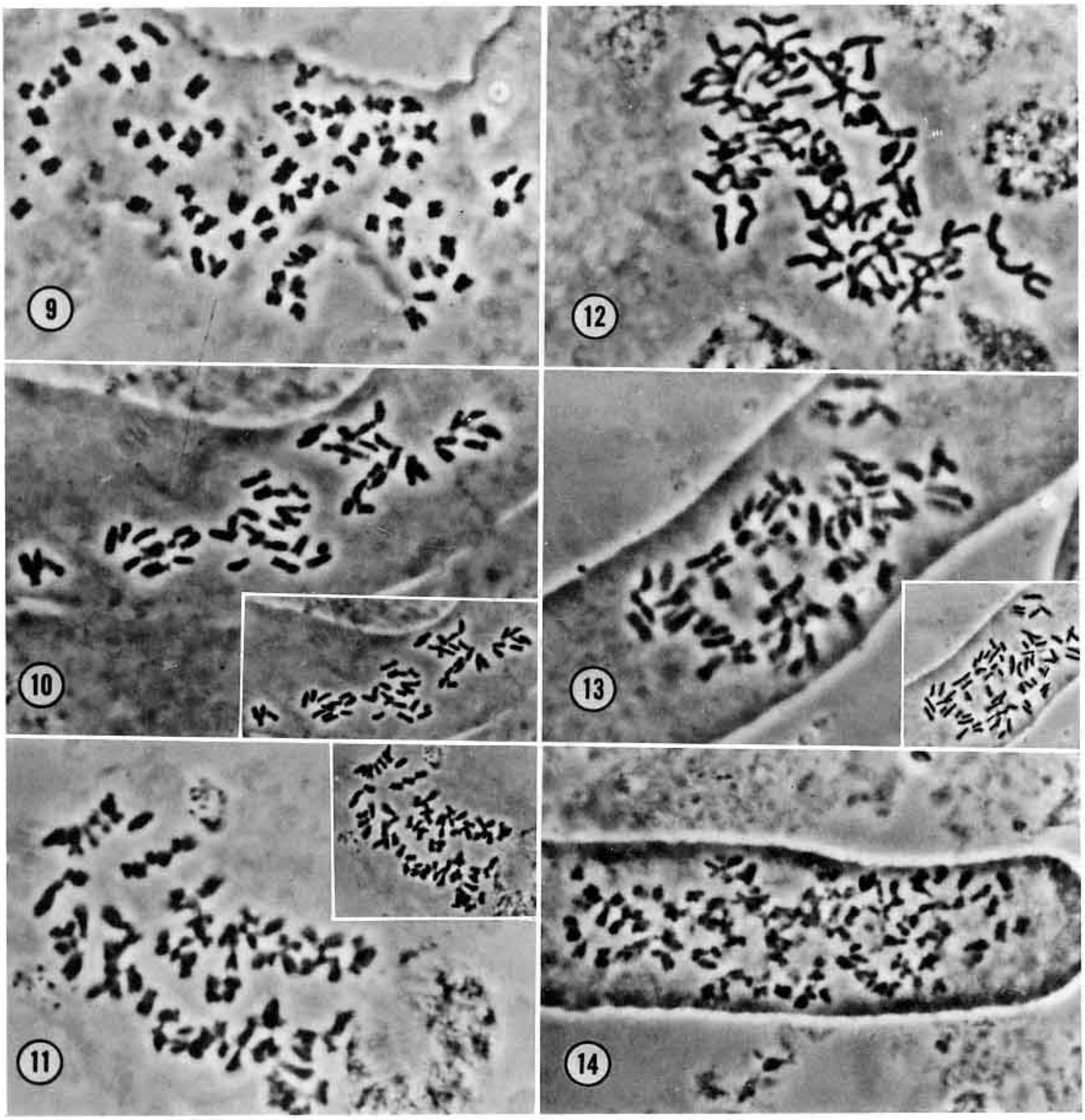

Fig. 9–14. Chromosomes of *Antennaria*. **9.** *A. canadensis* $2n = 84$. **10.** *A. Parlinii* $2n = 56$. **11.** *A. Parlinii* $2n = 84$. **12.** *A. petaloidea* $2n = 84$. **13.** *A. Parlinii* $2n = 70$. **14.** *A. Parlinii* $2n = 112$. Inked-in inserts are provided in some figures to aid in interpretation of the photographs.

Davis, 1976) such as *Antennaria*. Perhaps *Antennaria* migrated with oak and hickory (migration of the latter two is discussed by Davis, 1976) because it is usually associated with *Quercus* and *Carya* species. However, sexual *Antennaria* are not good colonizers due to their dioecious nature, thus apomictic polyploid females colonized the glaciated region and spread northward, whereas sexual diploids and sexual polyploids remained in the Appalachians and southeastern United States. As described by Adams (1905), these areas were the center of preservation for species during the Pleistocene glaciation.

Löve and Löve (1943, 1949 and 1974) and Johnson and Packer (1965) note that the frequency of polyploidy increases with latitude, and this is also true in *Antennaria* since, for the most part, all of the diploids are predominant below the glacial margin and the polyploids are predominant north of the glacial margin. Many polyploid microspecies of *Antennaria* exist in Arctic regions (Löve and Löve, 1975). Reasons why polyploids are able

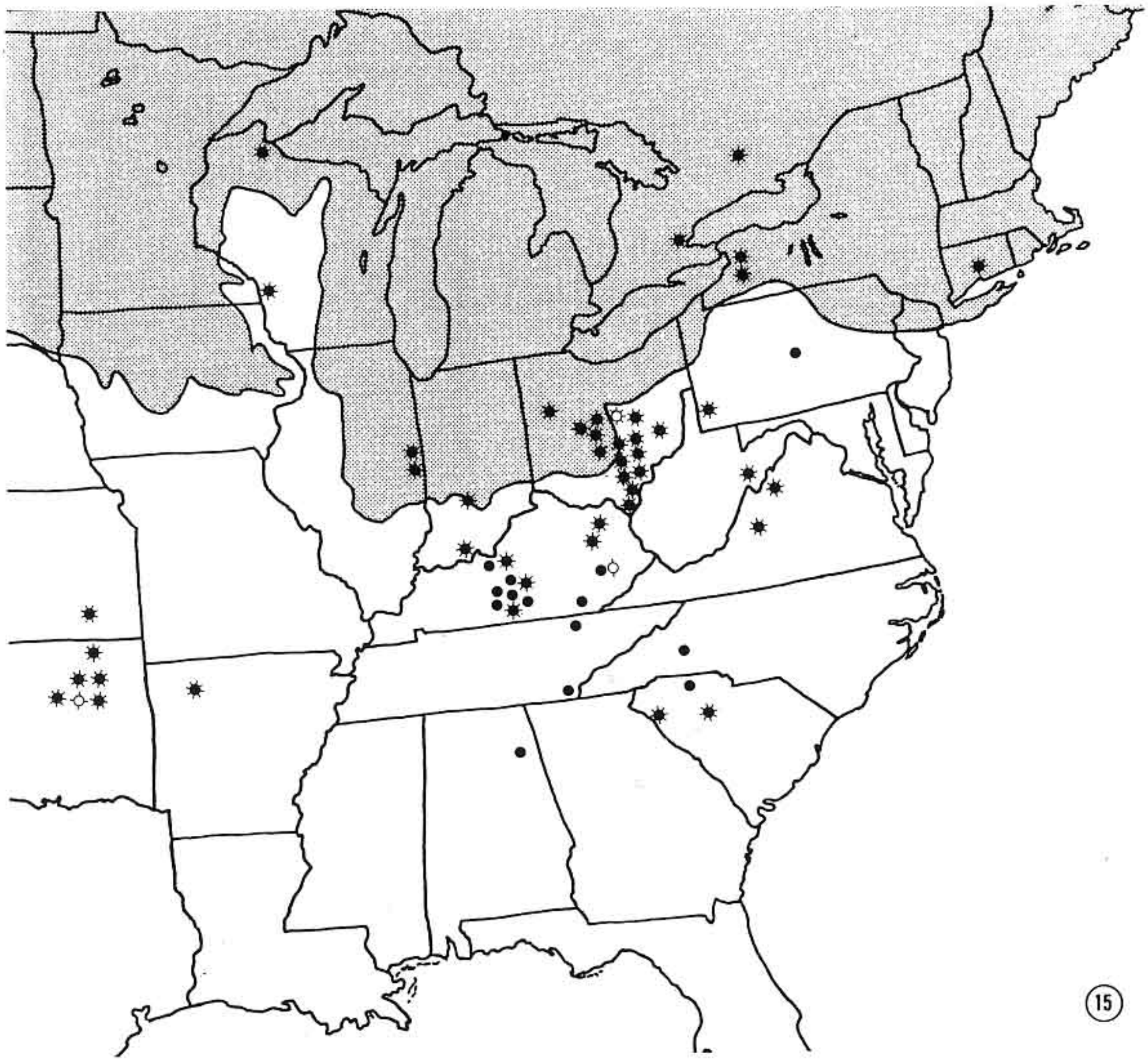


Fig. 15. Distribution of diplolid and polyploid populations in the *Antennaria plantaginifolia* species complex. Shaded areas show the maximum limits of the Wisconsin glaciation. ● $2n = 28$ (diploids), $2n = 56$, $2n = 70$, $2n = 84$, $2n = 112$.

to colonize pioneer or severely cold habitats have been discussed by Reese (1961), who says the polyploids are better adapted because of increased recombinational possibilities. This has been noted in *Antennaria,* where *A. Parlinii* is much more competitive than its putative diploid ancestor *A. plantaginifolia*. Specifically, the polyploid has the ability to grow in dense grassy areas, whereas the diploid *A. plantaginifolia* is usually confined to open habitats on relatively sterile soil, growing with *Danthonia spicata* (Poaceae), and does not compete well with other species. In the polyploid *A. Parlinii,* the increased chromosome number perhaps enhances the potential for new gene combinations that can be acted upon by natural selection (Löve and Löve, 1974). This increase in favorable gene combinations in polyploids permits them to colonize virgin soils far more steadily than the diploids.

Species of *Antennaria* having $2n = 28$ have generally been regarded as diploid, and in the complexes of *A. plantaginifolia* and *A. neodioica-neglecta* the species are multiples of 14, having somatic numbers 28, 56, 84, 112. Nevertheless, among species of western North America the somatic number 63 has been reported, which is not a multiple of 14, but could be interpreted as 9-ploid on $x = 7$. Since the plants counted were probably apomicts, and in some genera such as *Poa* (Gustafsson, 1947) apomicts have aneuploid chromosome numbers, their number does not necessarily imply that species of *Antennaria* (with $2n = 14$) directly ancestral to those discussed in the present paper either exist at present or existed in the past. The presence of x = 7 in several species of the neighboring genus *Gnaphalium* (Federov, 1969) suggests strongly that x = 14 was derived originally from x = 7, but whether this doubling took place before or after the differentiation of *Antennaria* as a distinct genus cannot be determined until many more of its species have been counted.

CONCLUSIONS—Polyploidy has played a dominant role in the evolution of species of *Antennaria*. Polyploid seems to be correlated with the appearance of apomixis in *Antennaria*, since all diploid *Antennaria* are strictly sexual. Many polyploid *Antennaria* species are apomictic and occur as pistillate plants only. The occurrence of diploids is mainly below the glacial margin whereas the frequency of agamospermous polyploids increases above the glacial margin. Thus, the theory of Hagerup (1932) that polyploidy increases with increasing latitude is supported by studies in eastern North American *Antennaria*. Evidence indicates that the actual base number in *Antennaria* may be x = 7.

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