INVESTIGATIONS INTO THE EVOLUTIONARY HISTORY OF THE POLYPLOID COMPLEXES IN *ANTENNARIA* (ASTERACEAE: INULEAE).
II. THE *A. PARLINII* COMPLEX

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ABSTRACT

The *Antennaria Parlinii* polyploid complex is a widespread species occurring throughout deciduous forests of eastern United States and southern portions of adjacent Canada. This group consists of two variable subspecies, ssp. *Parlinii* and ssp. *fallax*. The complex is composed of both sexual and agamospermous populations with distinct geographic distributions. Crosses were made in all combinations among several sexual diploid species of *Antennaria* that morphologically resemble members of the *A. Parlinii* complex to aid in identifying its diploid ancestors. The hybrids were then compared by principal components, cluster, and discriminant analyses, to the naturally-occurring polyploids. Results indicated that *A. Parlinii* s.l. was of multiple hybrid origin involving three sexual diploid species, *Antennaria plantaginifolia, A. racemosa,* and *A. solitaria.*

Key Words: *Antennaria,* polyploidy, compilospecies, agamospermy, agamic complex, numerical taxonomy, interspecific hybrids

INTRODUCTION

The *Antennaria Parlinii* polyploid agamic complex occurs throughout deciduous forests from Georgia, west to Texas, north to the Thunder Bay District of Ontario, and east to Nova Scotia (Figure 7, Bayer and Stebbins, 1982). Populations of *A. Parlinii* are either sexually reproducing (with sex ratios near 1:1) or are asexual, and composed entirely of pistillate clones (Bayer and Stebbins, 1983). These sexual and asexual populations have distinct geographic distributions (Bayer and Stebbins, 1983), with the former occurring mainly in the southwestern portions of the range. Recently, Bayer and Stebbins (1982) defined *A. Parlinii* as consisting of two subspecies, *A. Parlinii* Fern. ssp. *Parlinii* and *A. Parlinii* Fern. ssp. *fallax* (Greene) Bayer and Stebbins. They differ in that the former has glabrous adaxial leaf surfaces and glands on the upper portion of the cauline stem while the latter has pubescent

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adaxial leaf surfaces and is glandless. Both subspecies are found over the entire range of the species, but ssp. *Parlinii* is rare in the southwestern portion of the range and more common in the northeast. Agamospermy in the *A. Parlinii* complex occurs via diplospory followed by diploid parthenogenesis, as was first demonstrated by Stebbins (1932b). Sexual members reproduce via the Polygonum-type embryo-sac (Stebbins, 1932a), as do sexual diploid members of the genus.

Antennaria Parlinii has basal leaves with 3–5 primary veins and capitulescences composed of 2–15 (median of 6) relatively large capitula. Chromosome numbers in the complex include tetraploids ($2n = 56$; $x = 14$), pentaploids ($2n = 70$), hexaploids ($2n = 84$), and octoploids ($2n = 112$) (Bayer and Stebbins, 1981; Bayer, 1984). Hexaploids are by far the predominant cytotype (Bayer, 1984), with pentaploids and octoploids so far only encountered rarely. Sexual tetraploids are occasional (Bayer, 1984), having been found at one site in Oklahoma, once in Missouri, and at five sites in the Driftless Area of Wisconsin. The frequent occurrence of tetraploid cytotypes in western portions of the range supports the hypothesis that the species originated in this area and spread eastward where it occurs both as sexual and agamospermous hexaploids (Bayer, 1984).

Workers on agamic complexes have often postulated that apomicts arise through hybridization between and among sexual diploid species (Gustafsson, 1947). Harlan and DeWet (1963) have termed polyploid complexes of multiple hybrid origin a *compilospecies*. The question can be asked: What were the most probable origins of the *Antennaria Parlinii* agamic complex? With this question in mind, crosses were made among five diploid species of *Antennaria: A. neglecta* Greene, *A. plantaginifolia* (L.) Richardson, *A. racemosa* Hook., *A. solitaria* Rydb., and *A. virginica* Stebb. to see whether any of the interspecific hybrids resembled members of the *A. Parlinii* complex (Bayer, 1985). These five diploid species were chosen for comparison with *A. Parlinii* because they are morphologically most similar to and largely sympatric with *A. Parlinii*. The five diploid species can be divided into two groups, the small-leaved section *Dioicae* with basal leaves having a single primary vein, and the large-leaved section *Plantaginifoliae* with basal leaves having 3–5 veins. Like the *A. Parlinii* complex, the diploids *A. plantaginifolia, A. racemosa,* and *A. solitaria* are of the large-leaved group and their

hybrids most closely resemble members of *A. Parlinii*. Hybrids from crosses between diploids of the small- and large-leaved groups usually produce single-nerved basal leaves (Bayer, 1985). Consequently, the three diploid species of *Antennaria* chosen for analysis along with *A. Parlinii* were *A. plantaginifolia, A. racemosa,* and *A. solitaria* (*Antennaria neglecta* and *A. virginica* were eliminated from further analysis). Several crosses were also attempted between sexual clones of *A. Parlinii* and two of the putative diploid parents to test whether introgression could still be occurring under natural conditions. The purposes of this paper are (1) to discuss the relationship of the *A. Parlinii* polyploid complex to several sexual diploids, (2) to test the hypothesis that the *A. Parlinii* complex is of multiple hybrid origin, (3) to discuss the relationship of *A. Parlinii* to the morphologically similar *A. neodioica* polyploid agamic complex, and (4) to comment on the mode of inheritance of some important morphological features.

MATERIALS AND METHODS

Field observations of *Antennaria* were made each spring from 1978–83 and over 400 collections were cultivated in the greenhouse. Interspecific hybrids and other crosses were made as outlined previously (Bayer and Stebbins, 1982; 1983). Pollen viability of certain hybrids was ascertained through the use of Alexander's differential staining method (Alexander, 1980). Three hundred grains/ individual were scored for viability.

Morphological studies were aided by the use of specimens borrowed from the following herbaria: CAN, CM, GH, MO, MONTU, NDG, NY, OS, PAC, RM, SDU, US, VPI, WIS, and WVA. Herbarium vouchers of field collections and artificial hybrids produced during this study are on deposit at OS. Numerical methods are explained in detail in Bayer (1985), and are discussed here briefly. Thirty-eight characters (16 vegetative and 22 reproductive; *see* Bayer, 1985, Table 1) were used to construct the initial basic data matrix. The basic data matrix may be found in Bayer (Appendix, unpub. Ph.D. dissertation, 1984. Ohio State Univ., Columbus). The NT-SYS program of Rohlf, Kishpaugh, and Kirk (1974) was used to compute the principal components analysis (PCA), cluster analysis (UPGMA), and a table of correlation coefficients. A stepwise dis-

criminant analysis and univariate statistics were generated by the
BMDP program of Dixon (1981). Computations were carried out at
The Instruction Research Computing Center at The Ohio State
University. Several data matrices were used for this study: (1) a 149
OTU (operational taxonomic unit) matrix consisting of members of
the *Antennaria Parlinii* (39 OTUs) complex, three related sexual
diploids (34 OTUs of *A. plantaginifolia*, 34 of *A. racemosa*, and 35
of *A. solitaria*), and their interspecific hybrids (7 OTUs), (2) a 117
OTU data matrix composed of members of the *A. neodioica* (72
OTUs) and *A. Parlinii* (45 OTUs) polyploid complexes, (3) a 153
OTU data matrix, basically the same as matrix number 1 (41 OTUs
of *A. Parlinii* s.l., 35 of *A. plantaginifolia*, 35 of *A. solitaria*, 35 of *A.
racemosa*, and 7 interspecific hybrids), and (4) an 11 OTU matrix
utilizing character averages for the three diploids and the *A. Parlinii*
polyploid complex, plus the individual interspecific hybrids (7
OTUs) among the three diploids. *Antennaria Parlinii* is used in the
sense of Bayer and Stebbins (1982) and includes all the agamo-
species included in synonymy under *A. Parlinii* ssp. *Parlinii* and ssp.
fallax. Specimens referable to several of the agamospecies (i.e. *A.
Brainerdii* (= ssp. *Parlinii*), *A. calophylla* (= ssp. *fallax*), and *A.
munda* (= ssp. *fallax*)) are occasionally discussed because some flo-
ras still recognize these taxa as distinct species. A three-dimensional
plot of PCA computed from matrix number 1 is presented as Figure
1. Matrix number 2 was used to compute a PCA; the results are
presented as two 2-dimensional plots (Figure 3) of the first three
factors. A cluster analysis was performed using matrix number 3;
the results are displayed as a phenogram (Figure 2). Matrix number
one was used to execute a discriminant analysis. Pearson product-
moment correlation coefficients (Sneath and Sokal, 1973) were used
to compare OTUs of matrix number 4.

<center>RESULTS</center>

Phenetics of the diploids, interspecific hybrids, and polyploids

The first three factors of the PCA composed of the three diploids,
their interspecific hybrids, and the *Antennaria Parlinii* complex
(Figure 1) accounted for 54.6% of the variation. The first 11 factors
have eigenvalues greater than 1.0, indicating that the characters are
not highly correlated. High loadings for factor 1 are reproductive
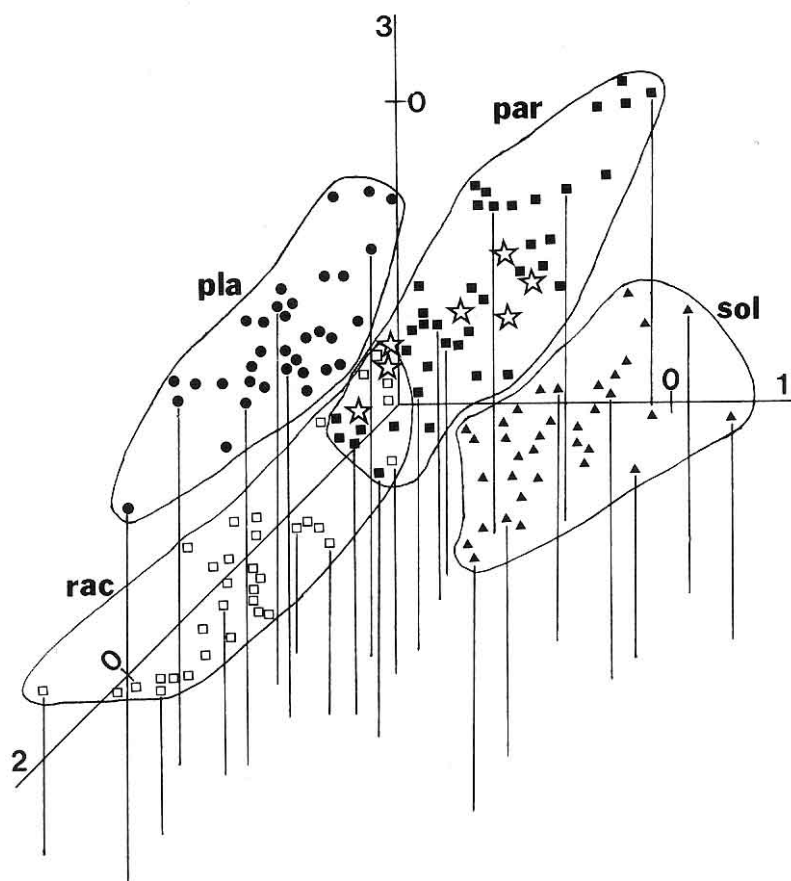characters such as number of heads per capitulescence, flowering

Figure 1. PCA composed of 149 OTUs including three diploid *Antennaria* species, interspecific hybrids, and the polyploid A. Parlinii s.l. Group outlines are indicated by a line. ● *A. plantaginifolia*, □ *A. racemosa*, ▲ *A. solitaria*, ■ *A. Parlinii*, and ☆ interspecific hybrids. Taxa are labeled with the first three letters of their specific epithets. Interspecific hybrid identifications are given as follows from uppermost to lowermost: HY41, HY01, HY42, HY02, HY03, HY04, HY40. Parentage of the hybrids is given in Table 1.

stem height, and width and length of the cauline leaves. A mixture of reproductive and vegetative characters such as degree of pubescence on the upper surface of the basal leaves, stolon length, and presence or absence of the scarious flag-like structure on the upper cauline leaves, have high loadings for factor 2. Factor 3 has high loadings for vegetative characters; the degree of pubescence of the upper leaf surfaces, width of the basal leaves, and number of stolons per basal rosette are examples. Inspection of Figure 1 shows that *A. Parlinii* is surrounded by the three diploids, *A. plantaginifolia, A. racemosa,* and *A. solitaria.* The diploid species are separated mainly by reproductive characters along component number 1. All of the interspecific hybrid combinations fall within the *A. Parlinii* group.

Although the two subspecies of *Antennaria Parlinii* are not shown as distinct in Figure 1, they do form somewhat distinct subgroups within *A. Parlinii* s.l. As expected, *A. Parlinii* ssp. *Parlinii* with its glabrous basal leaves and gland-bearing upper cauline stems, groups more closely to *A. racemosa,* with which it shares these characters. Subspecies *fallax* forms a subgroup in the upper portions of the *A. Parlinii* s.l. group and is most similar to *A. plantaginifolia* and *A. solitaria.* Several specimens referable to *A. calophylla* Greene (= *A. Parlinii* ssp. *fallax*) and *A. munda* Fern. (= *A. Parlinii* ssp. *fallax*) occupy positions at the upper end of the complex closest to *A. solitaria.*

The cluster analysis (Figure 2) has a cophenetic correlation coefficient of 0.857, and shows that the three diploids plus the *Antennaria Parlinii* polyploid complex each form a distinct group. The interspecific hybrids are either grouped within the *A. Parlinii* complex or with one of their parents. The two subspecies within *A. Parlinii,* although not represented separately in Figure 2, are scattered in small groups throughout the *A. Parlinii* complex. *Antennaria munda* Fern. (= *A. Parlinii* ssp. *fallax*) is a seldomly recognized agamospecies, which we have included within *A. Parlinii* s.l. (Bayer and Stebbins, 1982). In many respects it closely resembles *A. solitaria,* which is the reason it is grouped more closely to *A. solitaria* than to the remainder of *A. Parlinii.* Another seldomly recognized agamospecies, *A. Brainerdii* Fern., which has been included within *A. Parlinii* (Bayer and Stebbins, 1982), represents another extreme in the morphological variation of *A. Parlinii.* With its relatively small, glabrous, bright green leaves, *A. Brainerdii* closely resembles hybrids between *A. racemosa* and the other two diploids (Figure 2).
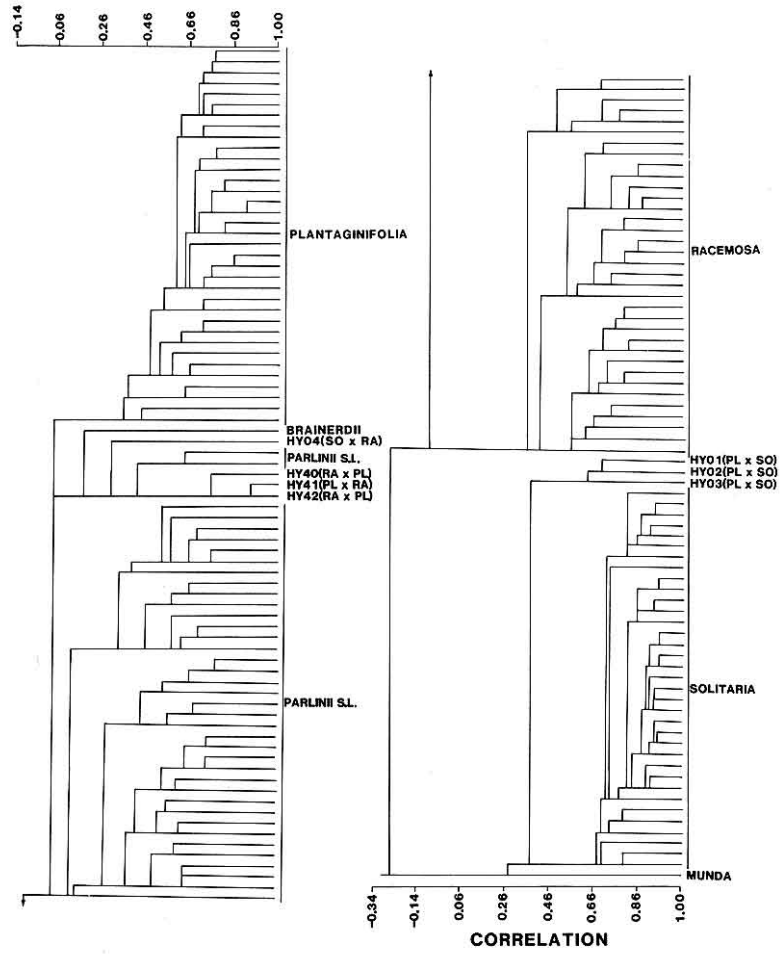
Figure 2. Correlation phenogram (UPGMA) composed of 153 OTUs including three diploid species of *Antennaria*, interspecific hybrids, and *A. Parlinii* s.l. Taxa are labelled with specific epithets. Two agamospecies, *A. munda* and *A. Brainerdii*, are represented separately from the remainder of *A. Parlinii* s.l. Parentage of hybrids is given in parentheses and are denoted by the first two letters of the parental specific epithets. Cophenetic correlation coefficient is 0.857.

Jensen and Eshbaugh (1976a, b) have demonstrated the utility of mean similarity matrices (correlation coefficients) for identifying hybrid taxa. A matrix of mean similarities (Table 1) shows that *Antennaria plantaginifolia* is most similar to *A. racemosa* and vice-versa. *Antennaria solitaria* is most similar to *A. Parlinii*, while *A. Parlinii* is about equally similar to *A. plantaginifolia* and *A. racemosa*. This analysis points to the overall similarity between the *A. Parlinii* polyploid complex and the three diploids. The interspecific hybrids are in all cases either most similar to one of their parents (e.g. HY02, HY03, and HY04) or to the *A. Parlinii* complex (e.g. HY01, HY40, HY41 and HY42). The method always associates the hybrid with one of its parents thereby showing the sensitivity of the technique. A discriminant analysis (Table 2), based on characters which best discriminate among the taxa, also demonstrates that these interspecific hybrids are always associated most closely with the polyploid complex or one of the diploid parents. A table of posterior probabilities derived from the discriminant analysis (Table 2) demonstrates that hybrids are identified as most probably belonging to either one of their parents (e.g. HY03 and HY42) or members of *A. Parlinii* (e.g. HY01, HY02, HY04, and HY41).

Relationship of the Antennaria neodioica complex to the A. Parlinii complex

The PCA (Figure 3) of members of *A. neodioica* (72 OTUs) and *A. Parlinii* (45 OTUs) was computed to demonstrate the morphological distinctness of the two closely related complexes. The first three principal components account for 51.5% of the variation. High loadings for factors 1 and 3 are vegetative characters, while those for factor 2 are reproductive characters. The *A. Parlinii* and *A. neodioica* complexes are separated chiefly on the basis of basal leaf characters along factor 1. The first eight factors have eigenvalues greater than 1.0, indicating that the characters are not highly correlated. The PCA (Figure 3) demonstrates that the two complexes do not overlap. Specimens of *A. neodioica* Greene ssp. *Howellii* (Greene) Bayer are morphologically closest to members of the *A. Parlinii* complex. *Antennaria Farwellii* Greene (= *A. Parlinii* ssp. *fallax*) is an agamospecies which has relatively small leaves when compared with the rest of *A. Parlinii* s.l. and is similar to members of the *A. neodioica* complex.

Table 1. Mean similarity matrix of *Antennaria* species with each other and with six artificial hybrid combinations. Taxa are labeled with the first three letters of the specific or subspecific epithet. Six artificial hybrids (HY —) and their parentage are presented along with their mean similarities to naturally occurring taxa. ** highest and * second highest similarity between each hybrid and the taxa are indicated.

	PAR	PLA	RAC	SOL
PAR	1.000	0.578	0.502	0.114
PLA	0.578	1.000	0.599	−0.100
RAC	0.502	0.599	1.000	−0.154
SOL	0.114	−0.100	−0.154	1.000
HY01 (PLA × SOL)	0.547**	0.352	−0.010	0.489*
HY02 (PLA × SOL)	0.485*	0.312	−0.122	0.678**
HY03 (PLA × SOL)	0.228	0.322*	0.005	0.482**
HY04 (SOL × RAC)	0.502*	0.416	0.581**	−0.116
HY40 (RAC × PLA)	0.691**	0.449	0.591*	−0.042
HY41 (PLA × RAC)	0.644**	0.563*	0.513	0.084
HY42 (RAC × PLA)	0.650**	0.514*	0.474	0.155

Table 2. Table of posterior probabilities derived from a discriminant analysis. Six artificial interspecific hybrids of *Antennaria* (HY——) and their parentage are presented along with the posterior probability to which of four naturally occurring groups of *Antennaria* they should belong. Taxa are labeled with the first three letters of the specific or subspecific epithet. Highest probabilities are **bold-faced**.

	PAR	PLA	RAC	SOL
HY01 (PLA × SOL)	**1.000**	0.000	0.000	0.000
HY02 (PLA × SOL)	**0.998**	0.002	0.000	0.000
HY03 (PLA × SOL)	0.001	0.000	0.000	**0.999**
HY04 (SOL × RAC)	**0.962**	0.000	0.038	0.000
HY41 (PLA × RAC)	**0.997**	0.003	0.000	0.000
HY42 (RAC × PLA)	0.329	**0.671**	0.000	0.000

Inheritance of morphological characters

Most of the morphological characters that I have considered in *Antennaria* are inherited polygenically (Bayer, 1985) and are probably controlled by a few (4–5) genes. *Antennaria Parlinii* ssp. *Parlinii* has glabrous adaxial leaf surfaces while subspecies *fallax* has leaves that are pubescent adaxially. When representative clones of each subspecies are crossed, the F_1 hybrids (total of 37 observed) range from glabrous to slightly pubescent, indicating that leaf pubescence is controlled by several genes, with glabrity being dominant to pubescence.
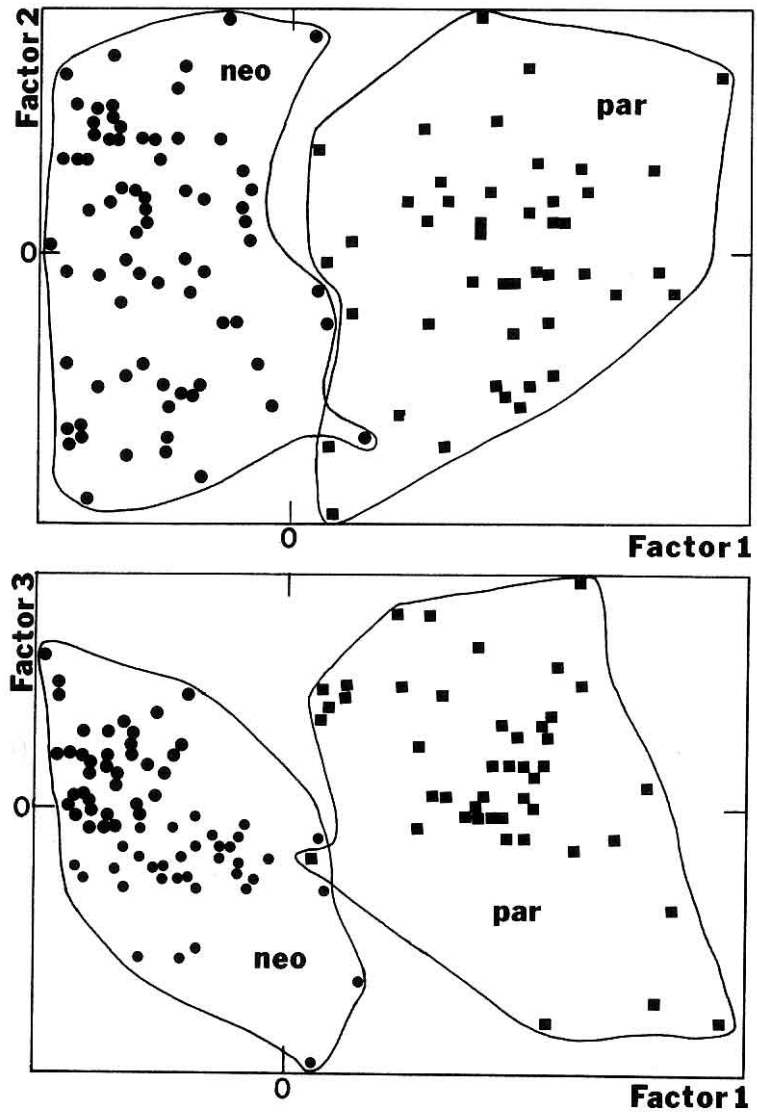
Figure 3. PCA composed of 117 OTUs of the *Antennaria Parlinii* (■) and *A. neodioica* (●) s.l. polyploid agamic complexes. Group outlines are indicated by a line. Taxa are labeled with the first three letters of their specific epithets.

DISCUSSION

Juel (1900) first concluded that the polyploid agamic species of *Antennaria* were probably the result of hybridization between sexual diploid species. It has been documented that most agamospermous groups arise in this way (Grant, 1981). With regard to the origins of *A. Parlinii*, Stebbins (1932b) suggested that while *A. fallax* Greene (= *A. Parlinii* ssp. *fallax*) was most closely related to *A. plantaginifolia*, other cytological features indicated *A. solitaria* or *A. neglecta* were also involved. *Antennaria Parlinii* Fern. (= *A. Parlinii* ssp. *Parlinii*), although similar to *A. plantaginifolia*, had several morphological features not present in *A. plantaginifolia* such as bright green adaxially glabrous leaves; it was undoubtedly of allopolyploid origin (Stebbins, 1932b). With respect to this character in ssp. *Parlinii*, Beals and Peters (1966) stated that "the very characteristic glabrous upper leaf surface and occasional purple glands on the stem suggest that introgression may have occurred in the past with some unknown, now extinct species." They were undoubtedly unaware of *A. racemosa*, the only sexual diploid *Antennaria* with adaxially glabrous leaves that are as large (3–5 veined) as those of *A. Parlinii* ssp. *Parlinii*. *Antennaria racemosa* also has the purple glands found in ssp. *Parlinii*.

Previously, it was demonstrated by the use of PCA that the three diploids examined as progenitors of *Antennaria Parlinii* are morphologically distinct from one another (Bayer, 1985). It has also been shown (Bayer and Stebbins, 1982; Bayer, 1985) that the diploids are isolated by both spatial and reproductive factors. Further, it has been noted that these isolating mechanisms (Bayer, 1985) occasionally break down and allow hybridization among the diploid species. I have recently observed populations of *A. plantaginifolia*, *A. solitaria*, and polyploid *A. Parlinii* growing side by side in Kentucky; the same observation is reported from West Virginia (G. L. Stebbins, pers. comm.). Recently, field observations and crossing studies (Bayer and Stebbins, 1982) indicate ample opportunity for hybridization and introgression between the two eastern diploids, *A. plantaginifolia* and *A. solitaria*, and the polyploid *A. Parlinii* s.l. The existence of tetraploid, pentaploid, and octoploid cytotypes of *A. Parlinii*, in addition to the predominant hexaploid cytotype, could be cited as evidence of hybridization and introgression between polyploids and diploids. In the *A. neodioica* complex

($2n = 56, 84$), which is totally apomictic, there are only two cyto-
types; this reduced number of cytotypes could be attributed to a
reduction in crossing between the apomictic polyploids and
diploids.

Both *Antennaria plantaginifolia* and *A. solitaria* are sympatric
with the *A. Parlinii* complex throughout their entire ranges in the
eastern United States (*see* Figures 2, 3, and 7, Bayer and Stebbins,
1982). *Antennaria solitaria* occurs in moist woodlands in the eastern
United States mainly south of the Wisconsin glacial margin, while
A. plantaginifolia is found throughout the Appalachian region,
Atlantic Coastal Plain, and north into New York. *Antennaria plan-
taginifolia* also is known from disjunct populations in the Driftless
Area of Wisconsin, as has been confirmed recently (Bayer, 1984; G.
L. Stebbins, unpubl. obs.). A single specimen of *A. solitaria* from
the Driftless Area of Jackson Co., Wisconsin, has been seen in the
collection of WIS and thus it apparently occurs there. *Antennaria
racemosa* is found in the coniferous forests of British Columbia and
Alberta, south to Washington, Oregon, northern California, Mon-
tana, Idaho, and Wyoming. It has been reported as far east as the
Black Hills of South Dakota (McIntosh, 1931; Dorn, 1977). Thus,
although *A. racemosa* is not sympatric with *A. plantaginifolia* or *A.
solitaria* at the present, they may have been sympatric during the
last glacial period, 10,000 years ago, when forests probably
extended across what is now prairie (Wells, 1970). It is likely that
many Cordilleran species migrated eastward during the last glacial
period (Wells, 1970; Whitehead, 1972; Marquis and Voss, 1981). For
example, *A. rosea* Greene, a chiefly Cordilleran species which
occurs sympatrically with *A. racemosa,* has disjunct populations on
the north shore of Lake Superior (Hyypio, 1952). If *A. rosea* once
migrated or dispersed eastwards, it is possible that *A. racemosa*
could have similarly migrated.

The overlap of *Antennaria Parlinii* and *A. racemosa* in the PCA
(Figure 1) indicates that *A. racemosa* was probably involved in the
ancestry of the complex despite its present-day geographic isolation.
The position of the diploid species also indicates that no single one
of them is predominantly responsible for the genetic composition of
the polyploids. In his original description, E. L. Greene (1898) made
the perceptive observation that *A. calophylla* (= *A. Parlinii* ssp.
fallax) was "related to the exclusively southern *A. solitaria*"; based

on the PCA he was apparently correct. Likewise *Antennaria munda* (= *A. Parlinii* ssp. *fallax*) has basal leaves which are shaped like those of *A. solitaria.* Thus, these agamospecies (*A. calophylla* and *A. munda*) appear to have a predominance of genes from *A. solitaria;* this relationship is indicated by PCA in that the agamospecies occupy positions closest to *A. solitaria.* The positioning of certain OTUs of *A. Parlinii* s.l. beyond the morphological types found in *A. plantaginifolia* or *A. solitaria* (Figure 1) could be attributed either to the effects of polyploidy or to transgressive segregation. Transgressive segregation was earlier noted (Bayer, in press) in hybrids between *A. solitaria* and *A. neglecta.* Hiesey and Nobs (1982) have also reported this phenomenon in diploid and polyploid agamic complexes in *Poa.* The cluster analysis indicates that the two subspecies within *A. Parlinii* s.l. are scattered in small groups throughout the *A. Parlinii* complex. This lack of grouping of the two subspecies of *A. Parlinii* is probably the result of segregation of genes from the genomes of several diploids and also because ssp. *Parlinii* and ssp. *fallax* are separated mainly on the basis of only one character, namely pubescence of the adaxial surface of the basal leaves.

The PCA and the cluster analysis demonstrate that while many segregates of *Antennaria Parlinii* ssp. *fallax* morphologically resemble the diploid *A. plantaginifolia,* other segregates of the complex referable to ssp. *fallax* (including *A. calophylla* and *A. munda*) and ssp. *Parlinii* (including *A. Brainerdii*) have characteristics suggesting the presence of genes from both *A. solitaria* and *A. racemosa.* Both *A. Parlinii* s.l. and the *A. solitaria* × *A. plantaginifolia* hybrids are intermediate between *A. solitaria* and *A. plantaginifolia* with respect to number of heads and number of florets per head (Figure 4). Inspection of the basal leaves and capitulescences of the three diploid species, hybrids, and naturally-occurring polyploids demonstrates the close resemblance of all the artificial interspecific hybrids with *A. Parlinii* segregates. The resemblance is evident not only with respect to shape of the basal leaves, but also in the number and arrangement of heads, and on closer inspection the number of florets per head. The mean similarity matrix (Table 1) and the discriminant analysis (Table 2) also point to the similarity of most of the interspecific hybrids to members of the *A. Parlinii* complex. Many hybrids having *A. solitaria* as one of the their parents fre-

5cm
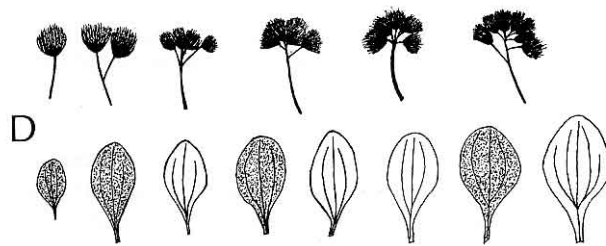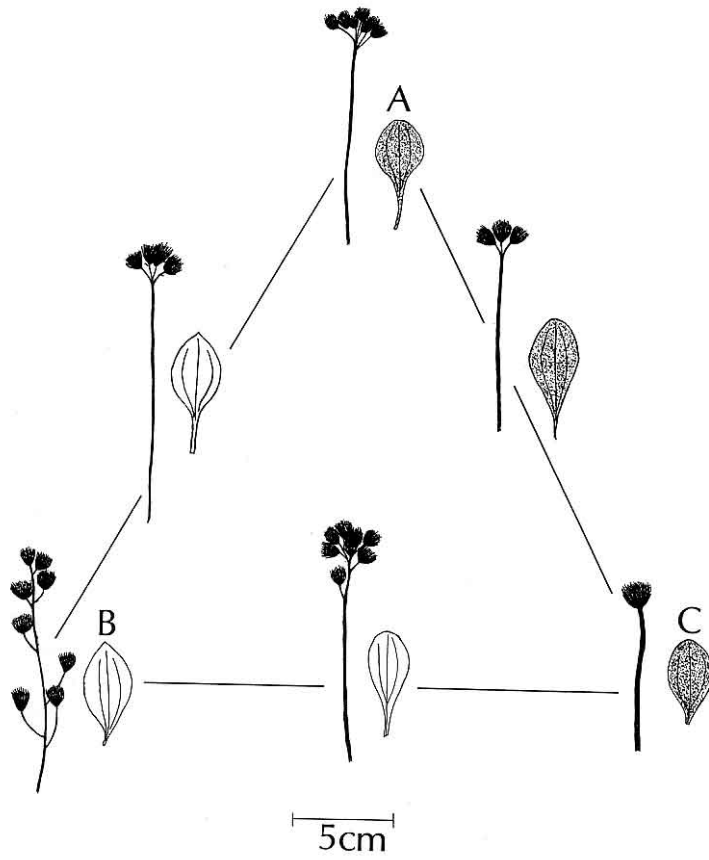
quently have high affinities with *A. solitaria* and this resemblance could be from the expression in these hybrids of several dominant traits present in *A. solitaria* (Bayer, 1985).

Antennaria Parlinii s.l. and *A. neodioica* s.l. both occur sympatrically in the deciduous forests of the eastern United States and adjacent Canada, but *A. neodioica* s.l. also occurs as far west as British Columbia and as far north as Hudson Bay and the Canadian Northwest Territories (Bayer and Stebbins, 1982; Bayer, 1985). The two polyploids are most easily separated taxonomically by the number of primary veins in the basal leaves, *A. Parlinii* having 3–5 and *A. neodioica* having only a single nerve. Beals and Peters (1966) and Beals (1968), in studying *Antennaria* in Wisconsin, came to the conclusion that members of these two complexes form a continuum and that species names are convenient labels when applied to them. They postulated that the complex was the product of hybridization and polyploidy. Although some segregates of the *A. Parlinii* complex do resemble members of the *A. neodioica* complex and vice-versa, they can always be positively identified on the basis of number of veins in the basal leaves. In addition, *A. neodioica* consists entirely of asexual populations (Bayer, 1985), while *A. Parlinii* s.l. is composed of both sexual and asexual populations (Bayer and Stebbins, 1983). The PCA (Figure 3) demonstrates that the two complexes are morphologically separable; their evolutionary history, reproductive mode differences, and chromosome number distinctions (Bayer, 1984) support this argument. The two complexes are morphologically similar at the extreme limits of their variation because they probably share the two sexual diploid progenitors *A. plantaginifolia* and *A. racemosa* (Figure 5). The *A. Parlinii* complex has one unique diploid progenitor, *A. solitaria*, while *A. neodioica* has two, *A. neglecta* and *A. virginica*. Figure 5 further portrays the proposed relationships of *A. Parlinii*, *A. neodioica*, and their extant

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Figure 4.   Line drawings of capitulescences and basal leaves of representative specimens among three diploid species of *Antennaria*, their interspecific hybrids, and *A. Parlinii* (both subspecies). Adaxial leaf pubescence is indicated by stippling. Variation among taxa is apparent with respect to leaf shape and pubescence, number of veins in basal leaves, and number, size, and arrangement of heads in the capitulescence. A. *A. plantaginifolia,* B. *A. racemosa,* C. *A. solitaria,* and D. *A. Parlinii* (both subspecies). Bar = 5.0 cm.
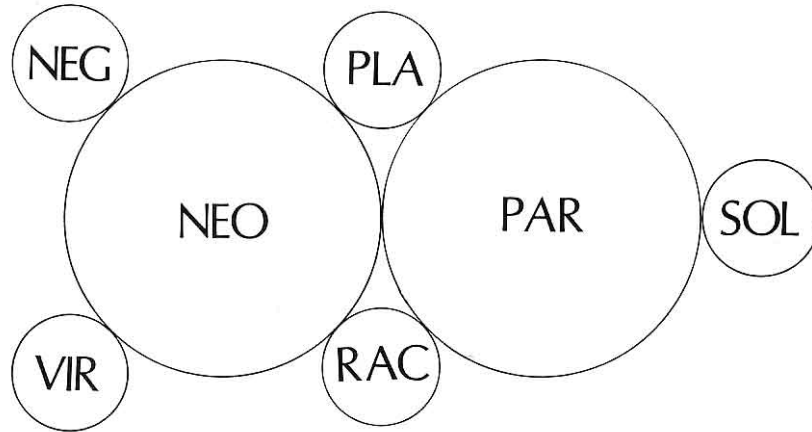
Figure 5.   Proposed relationship of the *Antennaria neodioica* s.l. (NEO) and *A. Parlinii* s.l. (PAR) agamic complexes to the sexual diploids *A. neglecta* (NEG), *A. plantaginifolia* (PLA), *A. racemosa* (RAC), *A. solitaria* (SOL), and *A. virginica* (VIR). Degree or relatedness is indicated by proximity of the circles to each other. Relative morphological variability within each taxon is indicated by the size of the circles. See text for detailed explanation.

sexual diploid progenitors. *Antennaria plantaginifolia* and *A. racemosa* can be viewed as pivotal genomes because they are shared by both polyploids. The diploids unique to the ancestry of each complex are responsible for their morphological distinctness.

Antennaria Parlinii s.l. is often found growing with two of its probable diploid progenitors, *A. plantaginifolia* and *A. solitaria.* The question arises whether introgression is still possible between the polyploid and its diploid progenitors. Many populations exist in which asexual clones of *A. Parlinii* s.l. are found growing with sexual clones of *A. plantaginifolia* (Bayer and Stebbins, 1981); in such cases the species are obviously reproductively isolated. In populationš where sexually reproducing clones of the polyploids and diploids are sympatric, introgression may still be occurring. In crosses conducted in the greenhouse between *A. Parlinii* s.l. and the diploids *A. plantaginifolia* and *A. solitaria,* the *A. Parlinii* s.l. × *A. plantaginifolia* crosses set 1.0% of their seeds (Bayer and Stebbins,

1982) while the *A. Parlinii* s.l. × *A. solitaria* hybrids set 0.5%. As a result of the crosses, a single hybrid from each was obtained; both were expected to be and were confirmed as tetraploids ($2n = 56$). The *A. Parlinii* × *A. plantaginifolia* hybrid was pistillate and was not analyzed further with respect to fertility, but the *A. Parlinii* × *A. solitaria* hybrid had a pollen stainability of 77.3%. The stainability is high, especially when compared with results obtained for interspecific crosses among diploid species (Bayer, 1985). Diploid species of *Antennaria* have pollen stainabilities greater than 85.0% (Bayer, 1985). The *A. Parlinii* × *A. solitaria* hybrid should be quite fertile; it is likely that introgression is still occurring among the polyploids and diploids.

The contention that polyploid agamic complexes should be retained as distinct from their diploid relatives at the specific level (Bayer and Stebbins, 1982) is viewed as the most desirable solution to the species problem in *Antennaria*. Because the polyploids are of multiple hybrid origin, it is inappropriate to include them simply as varieties of one of the diploid relatives as did Cronquist (1945) when he included members of *A. Parlinii* as varieties of *A. plantaginifolia*. *Antennaria Parlinii* is certainly of hybrid origin because it has characteristics not found in diploid *A. plantaginifolia*. Although one can not rule out the possibility that diploid progenitors have become extinct, the most simple and plausible explanation is that which has been presented.

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