THE TAXONOMY OF ASTER SECTION MULTIFLORI (ASTERACEAE) — II. BIOSYSTEMATIC INVESTIGATIONS

ALMUT G. JONES

This paper is a continuation of the study presented in Rhodora Vol. 80, No. 823, pages 319–357, and it constitutes a summary of the biosystematic and phytogeographic data compiled in support of the taxonomic treatment of *Aster* sect. *Multiflori*. The core of the findings is based on my doctoral dissertation, deposited with the Graduate College of the University of Illinois at Urbana-Champaign in 1973, but research has been continued. Acknowledgments and bibliographic entries given in Part I will not be repeated. Two species are recognized: *Aster ericoides* Linnaeus [with the typical ssp. *ericoides* and ssp. *pansus* (Blake) A. G. Jones], and *A. falcatus* Lindley in Hooker [with the typical ssp. *falcatus* and ssp. *commutatus* (Torrey & Gray) A. G. Jones].

MATERIALS AND METHODS

For hybridization and uniform culture experiments, populations were transplanted to a research field in Urbana, Illinois, and to a greenhouse. Copious field notes were taken at the collection sites. The following states and provinces were visited: Alberta, Arizona, British Columbia, Colorado, Illinois, Indiana, Iowa, Kansas, Massachusetts, Minnesota, Montana, Nebraska, North and South Dakota, Oklahoma, Oregon, Washington, Wisconsin, and Wyoming. Vouchers (identified by numbers only) are deposited in the herbarium of the University of Illinois (ILL).

Morphological characteristics were examined in over 7,000 herbarium specimens covering the entire geographic range for *Aster* sect. *Multiflori*. In addition to specimens held at ILL, loans were

obtained from 40 other herbaria. The institutions for cited specimens are identified by their respective acronyms, as listed in *Index Herbariorum*, Ed. 6 (Holmgren & Keuken, 1974).

The technique for preparation and staining of chromosome squashes has been published (Jones, 1977). Countable figures were photographed at a camera magnification of 500 × using Kodak High Contrast copy film. Brovira No. 6 paper was used for printing.

MORPHOLOGICAL CONSIDERATIONS

In order to delimit the taxa in *Aster* sect. *Multiflori*, about 2,000 specimens were subjected to a quantitative and qualitative evaluation. The following diagnostic character groups presented themselves:

1. Number of florets per head (only number of disk flowers was scored).
2. Relative height of head, determined by adding height of the involucre to length of ligule (in mm).
3. Length and texture (firm vs. flexible) of the bract-like leaves of the peduncle.
4. Length of the peduncle.
5. Imbrication of the involucre, calculated as a ratio: length of outer to inner phyllaries.
6. Degree of herbaceousness of outer phyllaries, i.e., the fraction of the area that is green, in contrast to the chartaceous, indurate, basal portion.
7. Degree of squarrose spreading of outer phyllaries (this character is generally correlated with the previous: plants with stiff indurate outer phyllaries have a more strongly squarrose involucre than those with flexible green phyllaries).
8. Habit of rhizomes: stoloniferous vs. cormoid.
9. Habit of above-ground stems: cespitose vs. single-stemmed colonial.
10. Habit of the inflorescence: compound-racemiform, with heads secund, vs. diffuse-paniculate, with heads at apex of branchlets, not secund.
11. Type of stem pubescence, scored (on the major branches of the inflorescence) for three categories: divaricately hirsute, appressed strigose, and ascending (= intermediate).

Originally, seven of the contrasting character combinations were mapped for presence; data for some characters were subjected to an analysis of statistical significance, and those of others were employed for the construction of scatter diagrams (Jones, 1973, 1974).

Among the herbarium collections examined, many specimens exhibited intermediacy between the extremes of certain characteristics. In my own field work, I have also found many examples. The highest degree of intermediacy was observed among populations from Alberta, Saskatchewan, Montana, and western North Dakota, where three of the four subspecies are sympatric. Collections made by A. J. Breitung, A. H. Brinkman, B. Boivin, W. C. McCalla, E. H. Moss, H. M. Raup, and G. H. Turner in Alberta and Saskatchewan bear numerous annotations attesting to the problem of delimiting taxa within *Aster* sect. *Multiflori*. Only rarely can a collection from this area be identified with certainty on the basis of only one or two characters. However, specimens can usually be assigned to the subspecies by a combination of at least six or seven of the characteristics listed above, and most flowering or fruiting specimens can readily be distinguished at the specific level.

A comparison of mean, range, and standard deviation for quantifiable diagnostic characteristics in taxa of *Aster* sect. *Multiflori* is presented in Table 1. Four of the six categories in the table pertain to characters of the capitulum, one concerns the ultimate rameal leaves, and one constitutes the sum of four measurements.

Capitulum.   Head size is the most evident and constant morphological character by which the two species of *Aster* sect. *Multiflori* can be distinguished. *Aster ericoides* is a relatively small-headed species, while *A. falcatus* is relatively large-headed (Figure 1). Several traits contribute to head size: height of head, number of ligules, and number of disk florets. For statistical tests, relative height of head was computed by adding height of involucre in mm to the length of the ligule. In a 2 × 7 contingency table, a test of significance was performed on 956 samples, comparing relative height of head with number of disk florets (Table 2). Both the observed and the expected numbers are listed in each size class. The chi square value obtained corresponds to a probability of much less than 0.0005 for equal or more extreme deviations from a random distribution on the basis of chance alone. The correlation between these two characters is, therefore, statistically highly significant.

Table 1. **Comparison of morphological measurements for the taxa recognized in Aster sect. Multiflori.**

Characteristics		A. ericoides ssp. ericoides	A. ericoides ssp. pansus	A. falcatus ssp. falcatus	A. falcatus ssp. com mutatus
1. Number of disk	mean	9.0	14.7	20.5	18.6
flofrom florets per head	range	5–18	6–25	14–34	13–32
[Standard deviation] S (±)		2.85	4.33	4.70	4.16
2. Length of ligule	mean	5.14	5.33	7.18	7.52
(including corolla-tube),	range	3.0–8.0	3.0–8.0	6.0–10.0	6.0–11.0
in mm	S(±)	0.98	0.85	1.06	1.07
3. Height of involucre,	mean	4.06	4.36	5.41	5.81
in mm	range	2.5–5.5	3.0–5.0	5.0–8.5	4.5–9.0
	S (±)	0.66	0.57	0.74	0.89
4. Length of peduncular	mean	2.23	3.07	5.13	4.54
bract-like leaves,	range	1.5–4.5	1.5–5.5	3.5–9.0	2.0–10.0
in mm	S (±)	0.75	1.05	1.46	1.49
5. Sum of the above	mean	20.11	26.33	37.48	35.49
(1–4) measurements	range	14–31	15–34	29–52	27–55
	S (±)	3.85	4.77	5.03	6.87
6. Imbrication of involucre	mean	0.60	0.70	0.93	0.71
= ratio: length of outer	range	0.4–0.8	0.4–0.95	0.7–1.3	0.3–1.1
to inner phyllaries	S (±)	0.11	0.15	0.14	0.17

Number of disk florets was chosen for numerical evaluation, because ligules are often removed or broken off and cannot readily be scored with accuracy. Ligule number in *Aster ericoides* varies from (8–)10–18(–20), and in *A. falcatus* from (18–)22–32(–36). Consequently, the total number of florets separates the two species, with an approximate range of 18–33 in *A. ericoides* and 35–60 in *A. falcatus.* In reality, the correlation between height of head and number of florets is even stronger than is indicated in the statistical analysis. In typical *A. falcatus,* secondary heads on minor branchlets of the inflorescence are often considerably shorter than those terminating major branchlets. Number of florets, however, usually is not significantly affected by variability in height. There is hardly any overlap between the two species, as far as overall head size is concerned.

Table 2.   **Comparison of relative height and number of disk florets per head.**

Number of Florets per Head		Relative Height of Head 11.5 mm or less	12.0 mm or more	Totals
6 or less	observed	128	2	
	expected	94.10	35.90	130
7–10	observed	290	11	
	expected	217.88	83.12	301
11–14	observed	144	63	
	expected	149.84	57.16	207
15–18	observed	79	64	
	expected	103.51	39.49	143
19–22	observed	40	72	
	expected	81.07	30.93	112
23–26	observed	10	30	
	expected	28.95	11.05	40
27 or more	observed	1	22	
	expected	16.65	6.35	23
Totals		692	264	956

Chi Square: 330.24 (6 degrees of freedom)
Probability: $\ll 0.0005$

Degree of imbrication of the involucre, on the other hand, is subject to much variability. The character is significant, at best, at the subspecific level and must be evaluated in combination with other characteristics. When compared with height of head and rhizome habit in a scatter diagram, the results present a continuum (Jones, 1973, *f. 10*).

Inflorescence. Certain very diagnostic characters cannot readily be scored. Features of the inflorescence, for example, are very useful for separation of taxa in sect. *Multiflori.* In most populations of *Aster ericoides,* the inflorescence is a dense many-headed panicle with arching branches, the heads racemiform, on short peduncles, and typically secund. Within ssp. *pansus,* the secund exposure of heads is not as pronounced in plants of var. *stricticaulis* as in those of typical var. *pansus.* In var. *stricticaulis* the heads are nearly sessile, crowded, and inserted more or less uniformly around the flowering stalk.

Populations of both subspecies of *Aster falcatus* typically exhibit open panicles. The heads are long-pedunculate, not crowded, and not secund. Simple, short-stemmed, racemose inflorescences, observed in matted populations of *A. falcatus* ssp. *commutatus,* result from a phenotypic response to certain environmental conditions.

In a 2×2 contingency table, a sample of 956 specimens was tested statistically for correlation between height of head and type of inflorescence (Table 3). The extremely high chi square value indicates that the probability for a chance distribution of deviations from randomness is infinitesimal. The two species can, therefore, usually be distinguished on the basis of these two characteristics alone.

Many populations of the transition zone between the ranges of *Aster falcatus* ssp. *commutatus* and *A. ericoides* ssp. *ericoides* (i.e., from Manitoba, the Dakotas, western Minnesota, and Nebraska) tend toward intermediacy; the branches of the inflorescence are often arching and heads disposed more or less racemiform. Number of florets and height of head, however, are relatively high. If characters of pubescence are disregarded, many specimens of this kind identify with the description and the type of Rydberg's (1901) *A. crassulus* (=*A. falcatus* ssp. *commutatus* var. *crassulus*).

Collections from the southern portion of the range of *Aster* sect. *Multiflori* (Oklahoma, New Mexico, Texas, Mexico) often exhibit a particular inflorescence trait. The ultimate rameal leaves are very small and closely appressed to the peduncle or stem. They are stiff, often squarrose and phyllary-like and, in fact, usually intergrade with the phyllaries (Figure 2). This trait is predominantly correlated with appressed stem pubescence. Although mostly recorded for specimens of *Aster ericoides* ssp. *ericoides,* it has also been found in southern populations of *A. falcatus* ssp. *commutatus.* One trans-

Table 3.   **Comparison of relative height of head with type of inflorescence.**

| | | Inflorescence | | |
Relative Height of Head		racemiform, with heads short-peduncled or sub-sessile, secund, crowded on arching branches.	diffuse-paniculate, with heads long-peduncled, on divaricate or ascending branches, not secund.	Totals
11.5 mm or less	observed	567	125	692
	expected	457.47	234.53	
12.0 mm or more	observed	65	199	264
	expected	174.53	89.47	
Totals		632	324	956

Chi Square: 277.65 (1 degree of freedom)
Probability: $\ll 0.0005$

plant population of this form from southern Oklahoma (*893*) was successfully crossed with a population of typical *A. ericoides* from Indiana (*471*). Populations exhibiting the trait probably cannot be recognized above forma rank. In older floristic works, the plants may key out as *A. hebecladus* DC. Examples are: **Texas:** *W. F. Mahler 1396* (TEX); *H. Wurzlow 1891* (ILL); *E. Whitehouse 9491* (MICH, NY); *V. L. Cory 50291* (GH, ILL, MICH) and *50182* (MICH, NY); **New Mexico:** *F. R. Fosberg S3405* (COLO, GH) and *S3476* (UC); *O. E. Wooten, s.n.* (ILL, RM, KSC, UC); **Oklahoma:** *R. M. House 164* (OKL); *R. Bebb 5926* (OKL); *F. A. Waugh 229* (MO); *F. B. McMurry 1082* (OKL).

Habit.   This character is subject to extreme variability in response to environmental fluctuations. There is evidence of clinal variation along ecological gradients (Jones, 1978a), but there is also evidence of good morphological separation of genetically fixed features, at least at the subspecific level.

Ruth A. Nelson (1933) was the first to recognize the significance of underground parts as a diagnostic character in sect. *Multiflori.* She noted that plants with small heads (*Aster ericoides*) have a
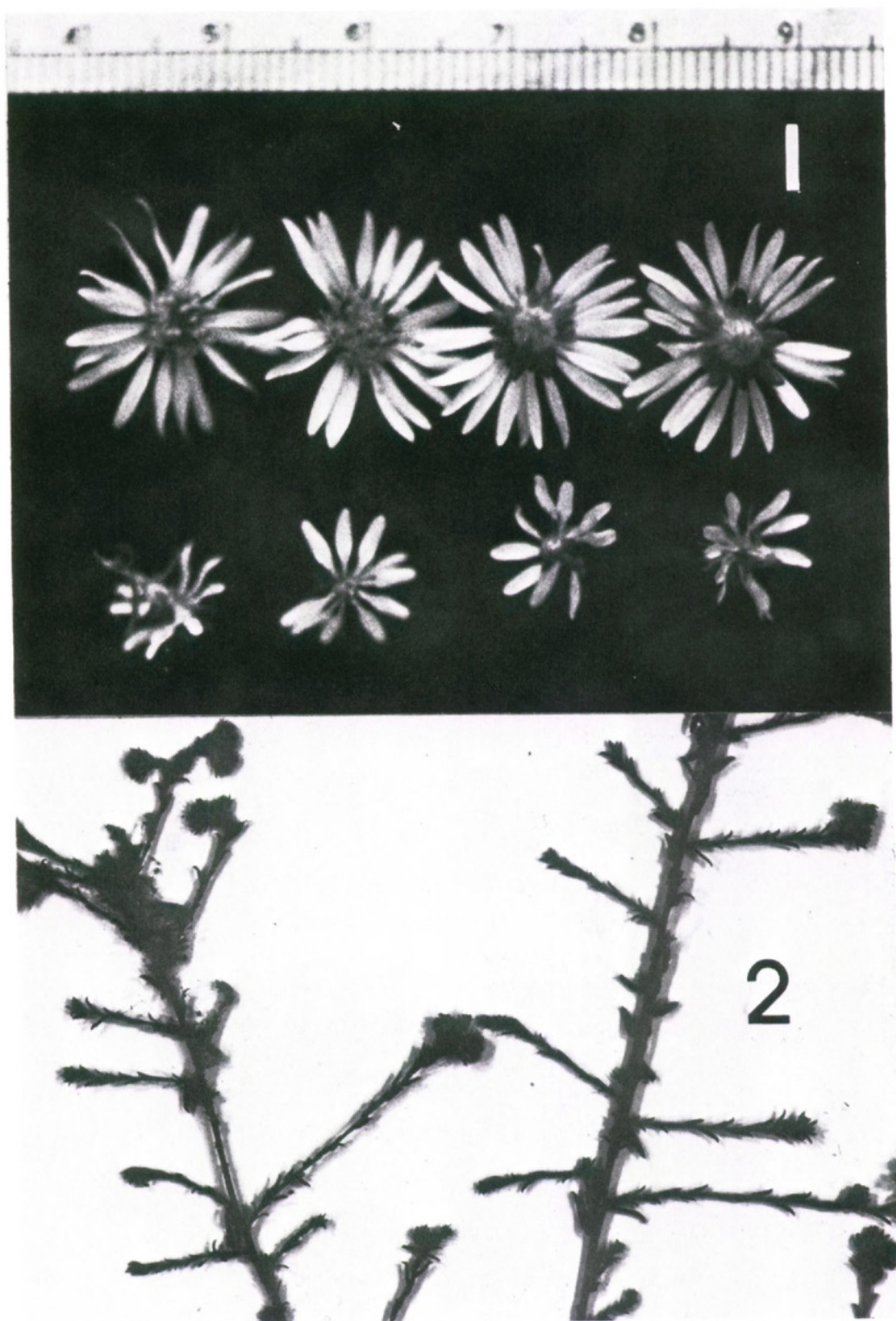
Figures 1 and 2.   **1.** Comparison of head size. Large heads: *Aster falcatus* ssp. *commutatus* var. *crassulus* (*424*, Nebraska); small heads: *A. ericoides* ssp. *ericoides* var. *prostratus* (*428*, South Dakota); **2.** *Aster ericoides* ssp. *ericoides:* form with appressed rameal leaves [portion of *W. F. Mahler 1396* (TEX)].

cespitose habit and short rhizomes, while plants with large heads ("*A. commutatus*") form extensive masses and have a creeping rhizome system. As she studied only Rocky Mountain collections from south of the Canadian border, her story was incomplete, and her interpretation led to confusion. Cronquist (1947) pointed out that all collections of *A. ericoides* from east of the Mississippi River have a creeping rhizome system, and that occasional large-headed specimens from the Cordilleran region have the cespitose habit. Later (1950) he gave specific status to the western small-headed taxon [*A. pansus* (Blake) Cronquist = *A. ericoides* ssp. *pansus* (Blake) A. G. Jones]. The holotype, Ellensburg, Washington, *K. Whited 853* (US! — Jones, 1978b, p. 337), lacks underground parts, but there is no doubt about the prevalence of this habit form in small-headed populations from the western states and provinces (Figure 3).

In populations with large heads, a similar dichotomy of underground habit can be observed. Plants of typical *Aster falcatus* have a short cormoid rhizome correlated with cespitose ascending stems (Figure 4). The type, "Arctic America," *Dr. Richardson* (K! — Jones, 1978b, p. 339), again lacks underground parts, but a nearly identical Richardson collection from Fort Franklin that is part of the type collection of *A. ramulosus* (K!) does exhibit a cormoid rhizome. In 68 specimens from Alberta, identified as typical *A. falcatus*, 60 had a short cormoid rhizome, and eight had a stoloniferous rhizome system. Over much of the range of *A. falcatus*, the typical subspecies is sympatric with ssp. *commutatus*. Plants of the latter taxon characteristically form extensive colonies or mats and exhibit a tangled, often woody and knobby, but clearly stoloniferous rhizome system (Figure 5). A certain degree of morphological intermediacy can be observed between the two subspecies, but they occupy somewhat different habitats and, in most places, plants of one taxon are much more abundant than those of the other.

Boivin (1962, 1972) considered the rhizome habit of mere ecological rather than taxonomic importance and, under *Aster ericoides* var. *commutatus*, he combined all elements of the large-headed *A. falcatus* plus the small-headed Great Plains variant of *A. ericoides* (= ssp. *pansus* var. *stricticaulis*). This judgment was based on the observation that, during the rainy spring season or in disturbed habitats, occasional horizontal rhizome strands may be produced by cormoid-cespitose plants. Herbarium specimens selected for me by

Figure 3.   *Aster ericoides* ssp. *pansus* var. *stricticaulis* — specimen with characteristic cormoid rhizome [*Ledingham, et al. 3973* (DAO)].

Boivin in support of his viewpoint included *McCalla 12101 & 12338; Boivin & Alex 10199; Boivin & Dore 8202* (DAO). For the far-western var. *pansus,* on the other hand, Boivin did accept the cormoid-tufted condition as a taxonomic character, and he also cited the stoloniferous condition as a diagnostic feature for the eastern var. *ericoides.* According to my observations, however, rhizome habit is a genetically fixed character in all the taxa because transplants of northwestern populations of *A. falcatus* (both sub-species) and *A. ericoides* ssp. *pansus* to the experimental field in Urbana always retained their original underground habit, season after season (Jones, 1978a).

Rhizome habit is correlated with above-ground habit. Popula-tions of *Aster ericoides* ssp. *ericoides* form colonies; the stems are erect, inserted singly, and typically branched above the middle in what is referred to as an excurrent growth habit (R. A. Nelson, 1933). Two variants have been observed in populations of *A. ericoides* ssp. *pansus.* The habit is cespitose in both, but in var. *pansus,* stems are erect and sturdy, with an excurrent branch system similar to ssp. *ericoides.* In var. *stricticaulis,* the stems are somewhat decumbent or ascending, typically more slender and not quite as tall as in var. *pansus.* In transplants to the experimental field in Illinois, populations of var. *pansus* from Oregon and British Columbia (*1130, 1152, 1153, & 1159*) retained the erect habit, while plants of var. *stricticaulis* from Alberta and western Minnesota (*450, 451, & 1203b*) exhibited a phenotypic response toward enhancement of the decumbent habit.

The habit of *Aster falcatus* ssp. *falcatus* resembles that of *A. ericoides* ssp. *pansus* var. *stricticaulis,* except that the stems are usually taller and sturdier, often nearly erect, and more diffusely branched. The colonial stands of *A. falcatus* ssp. *commutatus* are variable. In semi-arid regions of the Great Plains, they form matted growth with relatively short stems. In somewhat more mesic sites, the plants tend to be bushy, with stems decumbent or ascending, branched divaricately from near the base, often strongly sprawling. Transplants of both subspecies of *A. falcatus* from a more northern latitude (**Alberta:** *911, 1178, 1194, & 1195;* **Montana:** *1212;* **North Dakota:** *912, 914, & 1208;* **Wyoming:** *1082*) to the experimental field in Illinois experienced a phenotypic change toward more decumbent stems than were observed in their native habitats. A concurrent change in phenology was noted (Jones, 1978a). By contrast, trans-

Figure 4.　*Aster falcatus* ssp. *falcatus* — specimen with characteristic cormoid rhizome [*Cody & Gutteridge 7813* (NCU)].

plants from western states of the same latitude as Illinois (**Colorado:** *996, 1001, & 1053;* **Nebraska:** *424*) showed little or no change, either in habit or phenology.

As in the inflorescence characteristics, many populations especially in the eastern portion of the range for *Aster falcatus* ssp. *commutatus* approach the habit of *A. ericoides* and match the type of *A. crassulus* Rydberg (1901). Stems are erect and sturdy, with somewhat excurrent branches (western **Iowa:** *553;* eastern **Nebraska:** *541;* eastern **South Dakota:** *553–556;* eastern **Colorado:** *1050*).

Another series of intermediates combines the sprawling divaricate branching habit of ssp. *commutatus* with floral characteristics of *Aster ericoides* (both subspecies). These plants were observed in the short-grass prairies and plains of Colorado, Kansas, Nebraska, Oklahoma, and Texas (*892, 893, 1045, 2199, 2204, & 3036*). Since the sprawling habit is found in both species, as well as in both plants with cormoid and stoloniferous rhizome systems, the populations are not taxonomically recognized. Examples are: *U. T. Waterfall 1821* (OKL) & *10394* (MICH); *A. & R. Nelson & G. J. Goodman 5292* (OKL, RM) & *5329* (OKL, RM, TEX); *G. Engelmann, s.n.* (MO); *J. W. Blankinship, s.n.* (MICH, RM, US); *W. C. Muenscher 11457* (GA); *F. D. Kelsey, s.n.* (ILL); *V. L. Cory 50291* (GH, ILL, MICH).

Pubescence.   In many older studies involving *Aster* sect. *Multiflori,* stem pubescence has been considered a character of primary taxonomic importance (Rydberg, 1906, 1917, & 1932). Most recent authors, however, recognize the significance of this character only at an inferior level. According to my observations, the dichotomy of spreading vs. appressed stem pubescence can be employed for each subspecies. In *A. ericoides,* colonies of either pubescence type often occur side by side in the same population, while the plants are nearly indistinguishable in other respects. Occasionally, stem pubescence may vary within one plant, especially in young vegetative growth (*413, 448, & 452*). Herbarium specimens of *A. ericoides* which exhibit this phenomenon are appressed strigose in the lower stem portion and divaricately hirsute in the upper branches, e.g., *E. Pammel, s.n.* (ISC) and *B. Shimek, s.n.* (ISC). Nearly all specimens of *A. falcatus* ssp. *commutatus* have spreading hairs in the lowermost few centimeters of the stem, regardless of whether the main stem portion has appressed or divaricate indument. If these plants were

keyed out with the aid of one of Rydberg's manuals, a collector might conceivably come up with a different name, depending on the portion of the stem he examined.

Many herbarium specimens of *Aster* sect. *Multiflori* have both appressed and spreading pubescence forms in different plant pieces on the same sheet, for example *G. H. Turner 2747* (ALTA); *A. H. Brinkman 788* (ALTA); *W. Krivda 2104* (COLO); *R. I. Cratty, s.n.* (ISC); *E. J. Hill, s.n.* (ILL), and *J. R. Churchill, s.n.* (MO). In other collections, one form may be represented on a sheet in one herbarium, while the other is represented on a duplicate sheet in another institution. Often the names originally applied to these specimens vary accordingly. For the most part, there is no doubt that the plants were collected in the same place and, with few exceptions, they are of the same species and subspecies.

Nevertheless, the results of experimental work indicate that the kind of indument is genetically determined. Both forms occur in all taxa, but ascending stem pubescence is a truly intermediate state between the appressed and the divaricate form. Within each subspecies, plants of the two forms can usually be successfully crossed. Stem pubescence cannot, therefore, be utilized as a key character in the separation of the species or subspecies.

Frequency of occurrence in any habitat or area usually favors one form over the other. At least to some extent, the differential distribution appears to be controlled by ecological forces. Tolerances and adaptations are not identical for the two pubescence forms (Jones, 1974). In my experimental work, I have found that plants of *Aster ericoides* with relatively sparse appressed pubescence were more adversely affected by excessive spraying with insecticides and fungicides than plants with copious hirsute pubescence. A 2:1 frequency ratio found in Illinois in favor of plants with spreading indument suggests that plants of the sparsely strigose form may be less well adapted to disturbance of habitat.

Stem pubescence was quantitatively compared with other characteristics for all four subspecies. The results for *Aster ericoides* ssp. *ericoides* have been published (Jones, 1974) and, on the basis of differential abundance and a combination of correlated morphological characteristics, varietal rank was assigned to the two pubescence types in that subspecies.

In *Aster ericoides* ssp. *pansus,* the two varieties can readily be distinguished on the basis of several characters other than pubes-
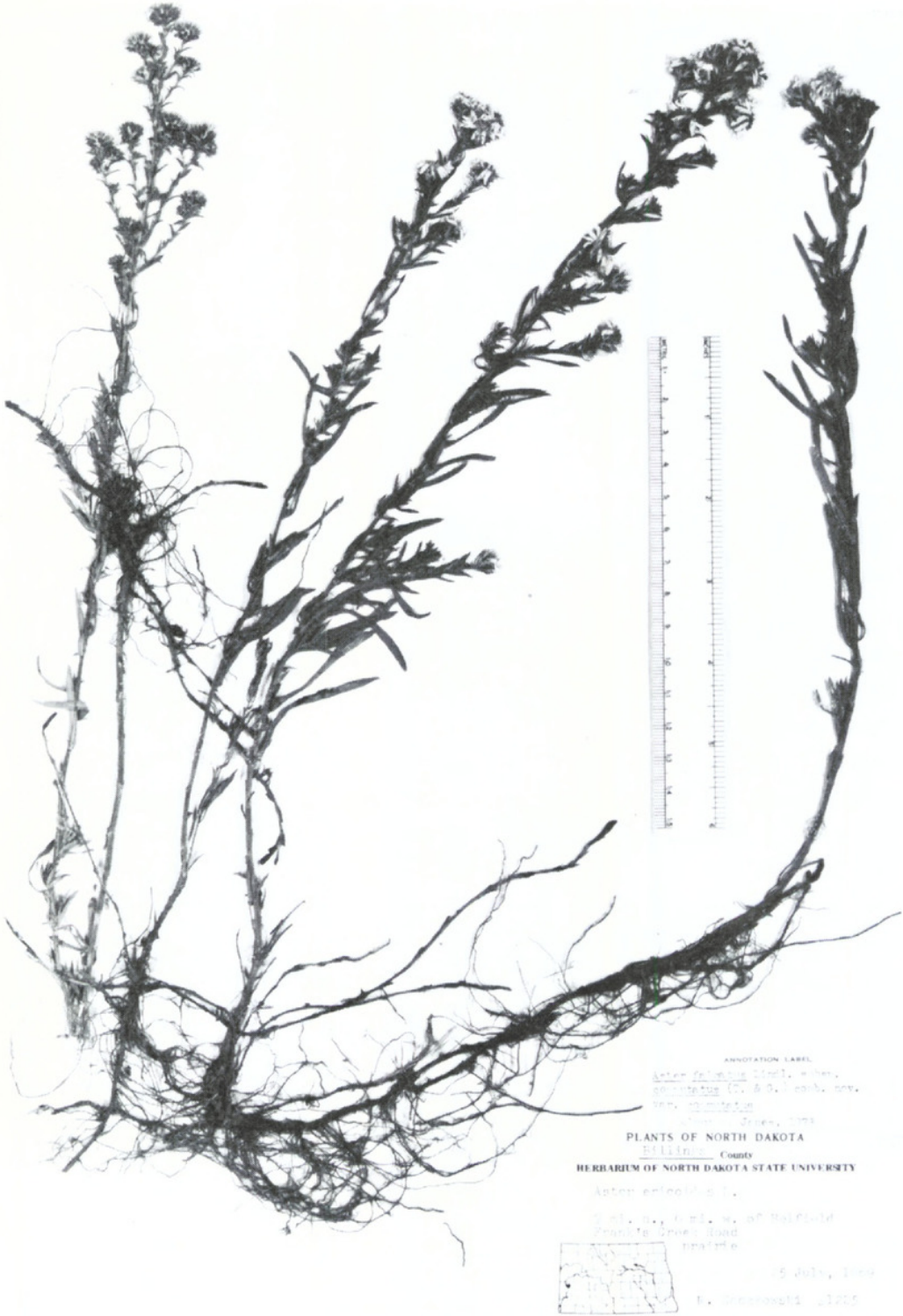
Figure 5. *Aster falcatus* ssp. *commutatus* — specimen with characteristic sto-
loniferous rhizome system [*Zaczkowski 1225* (NDA)].

cence. Plants of var. *pansus* have erect and sturdy stems, the inflorescences ample, with heads strongly secund. In plants of var. *stricticaulis* stems are slender, ascending or decumbent; inflorescences few-stemmed, with heads crowded, not strongly secund. A sample of 338 specimens was tested with a 2×2 contingency table for correlation of these character combinations with stem pubescence (Table 4). Intermediates, found to be only few in number, were omitted from the analysis. Expected frequencies were calculated under the null hypothesis that stem pubescence is of no significance. The high chi square value indicates, however, that the null hypothesis must be rejected. Probability for a chance association of the tested characters is less than 0.0005 and stem pubescence is a significant taxonomic character at the varietal level in ssp. *pansus*. Most plants in var. *pansus* have divaricate or reflexed trichomes, while plants of var. *stricticaulis* typically have appressed-strigose indument.

Specimens of *Aster falcatus* ssp. *falcatus* appear to be uniform. Quantity of indument is characteristically sparse in these plants. In a sample of 267 northwestern collections assigned to this subspecies, 24.7% were of the spreading pubescence form and 75.3% were of the strigose or closely ascending form. The strigose form clearly prevails in typical *A. falcatus;* the spreading form may have been introduced into the subspecies population by way of hybridization and introgression.

For *Aster falcatus* ssp. *commutatus,* the situation with regard to stem pubescence is complex. This subspecies is highly variable in several characteristics. It also has a wide geographic range, and is in contact and partly sympatric with all other subspecies of sect. *Multiflori.* The type, Upper Missouri, *Dr. James* (NY!), consists of a small branchlet with a few heads and appressed stem pubescence. Rydberg (1901) described *A. crassulus* to accommodate large-headed plants of the Great Plains and Rocky Mountains with spreading pubescence. The holotype, La Veta, Colorado, *Vreeland 690a* (NY! — Jones, 1978b, p. 341), as well as a possibly misnumbered duplicate (isotype), *Vreeland 190a* (RM!), are clearly of that pubescence form. Several paratypes, however, are strigose, except for the lowermost portion of the stem, e.g., Custer, South Dakota, *Rydberg 773* (NY); Rio Dolores, New Mexico, *Newberry* (NY); Madison County, Montana, *A. & E. Nelson 6839,* in part (GH, ILL, NY, US).

Table 4.   **Significance of stem pubescence in Aster ericoides ssp. pansus.**

Stem Pubescence		Habit Characteristics		
		var. *pansus*	var. *stricticaulis*	Totals
divaricate or reflexed	observed	82	38	120
	expected	37.633	82.367	
appressed	observed	24	194	218
	expected	68.367	149.633	
Totals		106	232	338

Chi Square: 115.504 (1 degree of freedom)
Probability: $\ll 0.0005$

Re-examination of the type material of *Aster multiflorus* γ *commutatus* and *A. crassulus,* evaluation of about 500 herbarium specimens, and observations made in the field revealed the presence in *A. falcatus* ssp. *commutatus* of two natural habit variants which are correlated with several other characteristics. The holotype of *A. crassulus* is a tall erect plant with spreading branches and a more or less racemiform inflorescence, the heads medium-large with about 16 disk florets and 20–22 ligules. Habit of the type for *A. multiflorus* γ *commutatus* can only be inferred by comparison with other collections from the same region, and with specimens annotated by A. Gray, as being that of a large-headed bushy plant with ascending stems and a diffuse-paniculate inflorescence.

A statistical analysis was made to determine the degree of correlation between stem pubescence and habit characteristics of specimens assigned to *Aster falcatus* ssp. *commutatus.* The sample consisted of 419 herbarium collections (duplicates not counted) from the entire range. The statistic used was a 2 × 2 contingency table solved for chi square (Table 5), and expected frequencies were calculated under the null hypothesis that stem pubescence is not correlated with habit characters. The small chi square value indicates that equal or more extreme deviations from random distribution would occur 70 times in 100 by chance alone, so that the null

hypothesis is highly acceptable. In a comparison of habit with inflorescence characteristics, stem pubescence is of no taxonomic significance within this subspecies. On a populational and geographic basis, one form is usually predominant, but in my own field work, intensive search revealed both pubescence forms in most collection sites.

GENETIC CONSIDERATIONS

Chromosome numbers. Literature reports of chromosome counts for *Aster* sect. *Multiflori* are as follows: $2n = 10$ for *A. amethystinus* [= *A. ericoides* × *novae-angliae*] (Van Faasen, 1963; Wetmore & Delisle, 1939). $2n = 10$ for *A. ericoides* (Delisle, 1937; Semple, 1976; Van Faasen, 1963; Wetmore & Delisle, 1939). $2n = 10$ for *A. pansus* [= *A. ericoides* ssp. *pansus*] (Löve & Löve, in Löve & Solbrig, 1964). $2n = 18$ (as $n = 9$) for *A. falcatus* (Anderson, et al., 1974). The voucher, *Raven 20610* (NY), from New Mexico, is *A. ericoides* with, perhaps, some intermediacy toward *A. falcatus* ssp. *commutatus.* The plant has relatively small heads, a divaricate branch system, spreading stem pubescence, and a stoloniferous rhizome.

My own cytological work consisted mostly of meiotic counts and revealed the presence of three ploidy levels in *Aster* sect. *Multiflori* (Figures 6–16). Plants of the small-headed *Aster ericoides* are usually diploid with a gametic chromosome number of $n = 5$, but tetraploid populations with $n = 10$ are not uncommon, especially in the southern part of the range. No hexaploid plants have been found in *A. ericoides*. The large-headed *A. falcatus,* by contrast, is typically a hexaploid with a gametic number of $n = 15$. Toward the eastern and southern part of the range, populations with $n = 10$ are common, but the meiotic number of $n = 5$ has not been encountered in large-headed plants. In most cases, chromosome number is correlated to head size, but not consistently.

Populations of *Aster ericoides* from east of the Mississippi River are morphologically very uniform, and most plants examined were diploid (*204, 239, 346, 347, 364, 365, 370, & 884* from Illinois, *474 & 905* from Indiana, and *586 & 1226* from Wisconsin). However, three populations from Indiana (*470, 471, & 904*) and one from Illinois (*457*), while morphologically indistinguishable from adjacent populations, were tetraploid with $n = 10$ chromosomes. Several populations from Kansas (*895*), eastern Colorado (*1045*), and Oklahoma

Table 5. **Significance of stem pubescence in Aster falcatus ssp. commutatus.**

Stem Pubescence		Habit Characteristics		Totals
		var. *commutatus*	var. *crassulus*	
divaricate or reflexed	observed	119	87	206
	expected	116.52	89.48	
appressed	observed	118	95	213
	expected	120.48	92.52	
Totals		237	182	419

Chi Square: 0.153 (1 degree of freedom)
Probability: 0.70 = 70%

(*892 & 894*) also were tetraploid. Although head size was small, some of these plants had the divaricate branching habit characteristic for *A. falcatus* ssp. *commutatus*. Again, there is no consistency, as one population from southern Oklahoma had the meiotic number of $n = 5$ (*891*). In populations from Nebraska, Iowa, South Dakota, and Minnesota, the correlation between ploidy level and head size was quite evident. Most diploid plants resembled populations from east of the Mississippi River, while tetraploid plants were characterized by slightly longer ligules and phyllaries, a somewhat higher number of florets, and a much stouter, often sprawling habit, approaching *A. falcatus* ssp. *commutatus* in appearance. Representative vouchers of diploid plants from these states are: *412, 413, 415, & 528* (Iowa), *428* (South Dakota), and *443, 445, & 1215* (Minnesota). Vouchers of tetraploid plants are: *424* (eastern Nebraska), *427* (western Iowa), *432* (South Dakota), and *450 & 451* (western Minnesota). Most populations from British Columbia and many from Alberta had a gametic chromosome number of $n = 5$ (*1151, 1159, 1202, & 1204*, occasionally $n = 10$ (*1152*). They all belong in *A. ericoides* ssp. *pansus*.

Hexaploid populations with $n = 15$ chromosomes were found in both subspecies of *Aster falcatus*. Collections of this kind were made in southern Alberta (*1178, 1194, & 1203a*), Wyoming (*1082*), Montana (*1206*), and North Dakota (*1208*). All tetraploid popula-
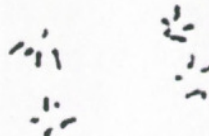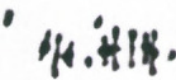
6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

tions found in this species belonged morphologically in *A. falcatus* ssp. *commutatus*. Collections were made in North Dakota (*912, 914, & 915*) and Colorado (*996, 1001, & 1050*).

Meiosis was regular in most preparations, although laggards and bridges during anaphase I were not uncommon (Figure 17). Occasionally pairing was incomplete, and univalents were observed during prophase and metaphase.

Hybridization. Of the many putative hybrids proposed in *Aster*, relatively few have been produced experimentally, for example, *A.* × *amethystinus* [= *A. ericoides* × *novae-angliae*] by Wetmore and Delisle (1939), *A.* × *herveyi* [= *A. macrophyllus* × *spectabilis*] by Uttall (1962), and *A.* × *blakei* [= *A. acuminatus* × *nemoralis*] by Pike (1970). A few experimentally produced interspecific hybrids that survived for several seasons can be added to the list from my work (Jones, 1973, and unpublished).

The procedure used for hybridization experiments and their evaluation has been published (Jones, 1974). Individual experimental results and tabulation of data obtained during the season of 1972, presented in my doctoral dissertation (Jones, 1973), are not repeated here. The results for sect. *Multiflori* can be summarized as follows.

Figures 6–20.   **6.** Diakinesis: *Aster ericoides* ssp. *ericoides* (*891s*, Oklahoma); $2n = 5_{II}$; **7.** Metaphase I: *Aster ericoides* ssp. *ericoides* var. *prostratus* (*239*, Illinois); $2n = 5_{II}$; **8.** Metaphase I: *Aster ericoides* ssp. *pansus* (*1159*, British Columbia); $2n = 4_{II} + 2_{I}$; **9.** Anaphase II: *Aster ericoides* ssp. *ericoides* (*346*, Illinois); $n = 5$; **10.** Diakinesis: *Aster falcatus* ssp. *commutatus* (*1050*, Colorado); $2n = 10_{II}$; **11.** Late Diakinesis: *Aster ericoides* ssp. *ericoides* (*471*, Indiana); $2n = 10_{II}$; **12.** Metaphase I: *Aster falcatus* ssp. *commutatus* var. *crassulus* (*424*, Nebraska); $2n = 9_{II} + 2_{I}$; **13.** Early Anaphase I: *Aster ericoides* ssp. *ericoides* (*457* × *470* = cross: Illinois × Indiana); $2n = 20$; **14.** Early Diakinesis: *Aster falcatus* ssp. *falcatus* (*1203b*, Alberta); $2n = 15_{II}$; **15.** Diakinesis: *Aster falcatus* ssp. *commutatus* (*1082*, Wyoming); $2n = 15_{II}$; **16.** Late Metaphase — Incipient Anaphase I: *Aster falcatus* ssp. *commutatus* (*1206*, Montana); $2n = 15_{II}$; **17.** Anaphase I: *Aster falcatus* ssp. *falcatus* (*1203b*, Alberta); note laggards and bridge resulting from translocation; **18.** Early Diakinesis: *Aster hesperius* × *falcatus* ssp. *commutatus* (*1111* × *1001*, Utah × Colorado); $2n = 2_{I} + 5_{II} + 1_{III} + 2_{IV}$ (= 23); **19.** Diakinesis: *Aster ericoides* × *falcatus* (*451* × *1178*, Minnesota × Alberta) $2n = 3_{I} + 8_{II} + 2_{III}$ (= 25); **20.** Early Anaphase I: *Aster ericoides* × *falcatus* (*451* × *1178*); $2n = 25$.

Many attempts were made to cross members of *Aster* sect. *Multiflori* with 15 species of other sections, but hybridization succeeded only if the species were cytologically related, with one exception. This exception was a cross between a population of *A.* cf. *hesperius* from Utah (*1110 & 1111*), with a gametic number of $n = 13$ chromosomes, and a population of *A. falcatus* ssp. *commutatus* from Colorado (*1001*), with $n = 10$ chromosomes. The hybrid exhibited $2n = 23$ chromosomes (Figure 18) in varying combinations of univalents, bivalents, and multivalents. The plants are vigorous and have survived for several seasons (*2595, 2780, 2965, 3072, 3155, 3206, 3278, 3684, 3687,* and others).

The work of Wetmore and Delisle (1939) was reproduced, with the difference that *Aster ericoides* (*314*) was the seed parent and *A. novae-angliae* (*348*) the pollen parent. The hybrids are vigorous and have survived for four seasons (*1565, 1644, 1826, 1845, 1990, 2519, 2782, 2847, 3115, 3223, 3657,* and others).

Hybrids between *Aster ericoides* (*365*) and *A. sericeus* (*608*) survived as weak plants in the greenhouse (*2715, 3178, & 3371*), but they did flower and set seed. The seedlings were the progeny from the only successful cross. Nine other crossing attempts failed to produce seed. Both parents and the hybrid had $n = 5$ chromosomes.

A cross between *Aster falcatus* ssp. *commutatus* (*996*) and *A. ascendens* (*1201c*) produced a few full achenes, but the seedlings died soon after emergence of the cotyledons and first rosette leaves.

In contrast to published reports (Ahles, in Jones & Fuller, 1955) and labeled herbarium specimens, I have not yet succeeded in crossing *Aster ericoides* and *A. pilosus.* Fourteen attempts were made involving about 5,000 potential achenes. One cross yielded a few achenes, but the seedlings died soon after emergence of the cotyledons.

Five attempts were made to cross *Aster ericoides* ssp. *pansus* from British Columbia with *A. campestris* from Alberta. These species are the putative parents of *A.* × *columbianus* Piper (pro sp., 1913). One cross (*1130* × *1184*) yielded a few full achenes, but the hybrid seedlings never grew beyond the rosette stage and died after one year.

Spontaneous hybrids between *Aster ericoides* and *A. falcatus* possibly would be difficult to recognize with certainty. A considerable number of intermediates was found among herbarium speci-

mens. In the field, however, most populations could readily be placed into the respective species. Intermediacy and gene flow in areas of contact and overlap of taxa are evident but probably not found to the extent inferred from the prevalence of variants in collections of certain botanists who were cognizant of the existing taxonomic problems.

Average seed set of a total of over 130 crossing attempts between populations of *Aster ericoides* and *A. falcatus* was about 1%. This indicates the existence of a strong reproductive barrier between the two taxa. Even if only the 49 random crosses between typical *A. ericoides* and *A. falcatus* ssp. *commutatus* var. *crassulus* are evaluated, average seed set amounts to a mere 2%. A somewhat higher success is to be expected in these crosses, as the majority of populations of var. *crassulus* were found to be tetraploid with $n = 10$ chromosomes, and a considerable number of populations of *A. ericoides* also were tetraploid.

Crosses between *Aster* populations that were only varietally distinct generally yielded high, often nearly full (12% or more) seed set. In no case was a sterility barrier detected between the two different pubescence forms in populations of the same region that were morphologically similar in other respects. The reproductive barrier between var. *pansus* and var. *stricticaulis* appears to be somewhat stronger (7% average seed set in 4 attempts) than the barrier between var. *ericoides* and var. *prostratus* (17% average seed set in 12 attempts). Average seed set in 20 crosses between plants of typical *A. ericoides* and ssp. *pansus,* involving about 4,200 potential achenes, amounted to 9%.

Data for crosses within typical *Aster falcatus* are somewhat biased because a population from Edmonton, Alberta (*911*) could not be crossed with any other population in the whole section. Cytological examination suggests meiotic irregularity. Several other populations have been successfully crossed with an average seed set of about 10% in 4 attempts. Within *A. falcatus* ssp. *commutatus,* seed set in crosses between the two pubescence forms averaged about 13% in 5 attempts. When the two habit variants (var. *crassulus* and var. *commutatus* of this interpretation) were crossed, average seed amounted to 12% in 7 crossing attempts. Crosses between typical *A. falcatus* and ssp. *commutatus* yielded an average seed set of about 5% in 20 attempts, involving about 7,000 potential
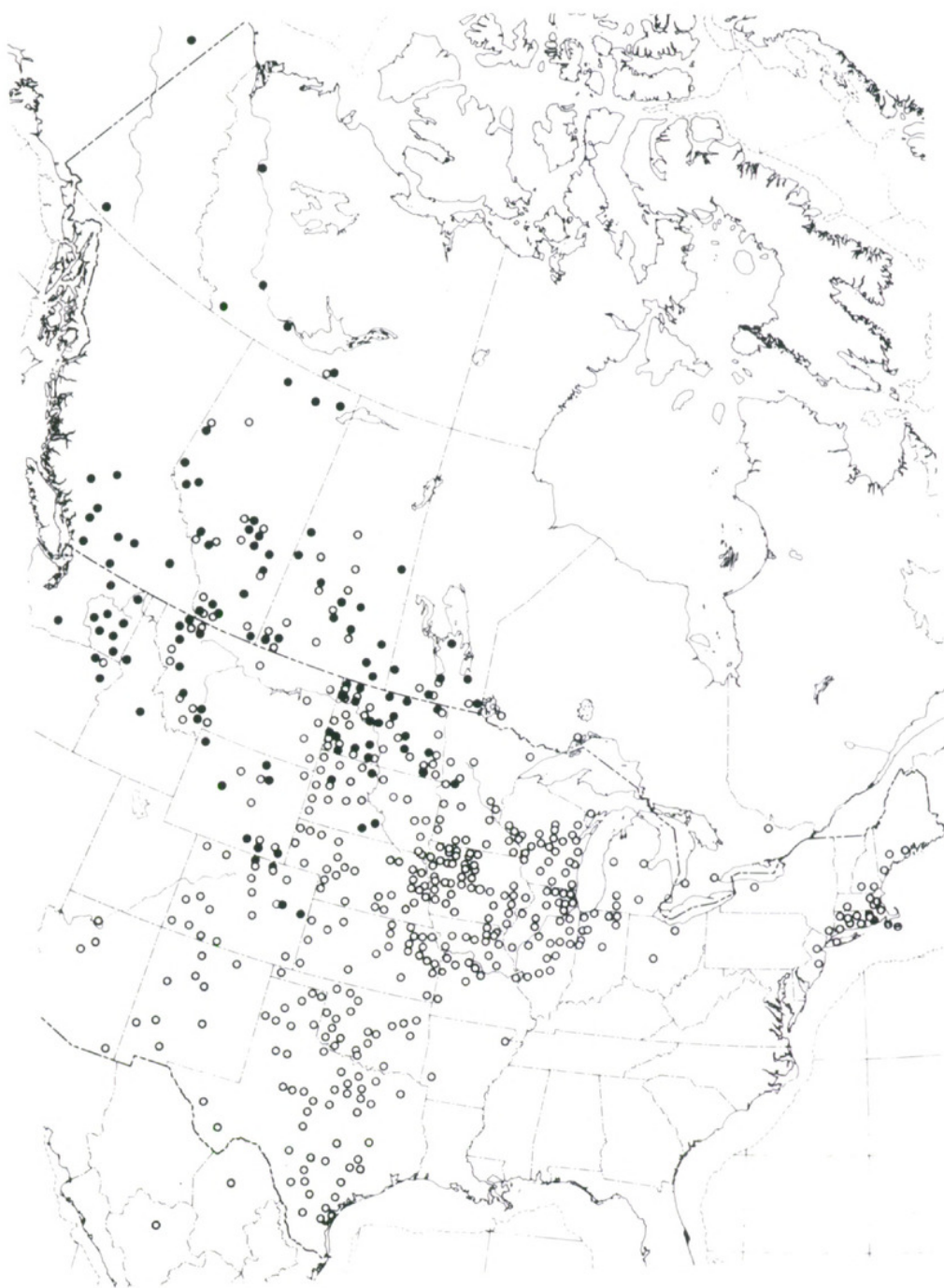
Figure 21.   Geographic distribution of rhizome habit. Circles: stoloniferous; full
dots: cormoid.

achenes. This relatively low yield indicates that genetic compatibility between the two subspecies of *A. falcatus* is somewhat impaired, but a considerable degree of intermediacy must be expected in regions of sympatry.

Cytological data offer an explanation for the fact that certain populations could not successfully be crossed with other morphologically indistinguishable populations from the same region. As far as tested, tetraploid plants could only rarely be hybridized with diploid plants. The few full achenes resulting from such crosses usually yielded plants that had the meiotic number of the seed parent, which may be the result of occasional selfing or contamination.

If artificial crosses between *Aster ericoides* and *A. falcatus* produced more than occasional full achenes, both parent plants were usually tetraploids, e.g., in a cross between *A. ericoides* from Oklahoma (*894*) and *A. falcatus* from Colorado (*996*), and another between *A. ericoides* from Minnesota (*451*) and *A. falcatus* from Colorado (*1001*). Exceptional hybrids between plants of different ploidy levels were obtained, however, e.g., *1194* ($n = 15$ from Alberta) $\times$ *457* ($n = 10$ from Illinois) and *451* ($n = 10$ from Minnesota) $\times$ *1178* ($n = 15$ from Alberta). Full seed set was obtained in these two crosses, and the progeny had $2n = 25$ chromosomes which exhibited irregular pairing during meiosis (Figures 19 & 20).

ECOLOGICAL CONSIDERATIONS

As a result of their extremely wide geographic range, species of *Aster* sect. *Multiflori* are found in a variety of ecological situations. However, the plants always grow in open places, never in woodlands; their natural habitat is grassland. In the forest-prairie ecotone, they have been recorded on glades and wind-exposed slopes that do not support tree growth, but these asters are absent from true forest areas. In the mountains, they are found on meadows, in the vicinity of streams and lakes, on well-drained ground in river valleys, occasionally on gravel bars, but not in wet seepage areas or low, moist, alluvial bottomlands. I have not found them in the extremely dry overgrazed plains which are dominated by *Artemisia tridentata,* but they are common in the bunch-grass prairies of the Great Plains. They are also found in dune habitats. In the tall-grass prairies, populations of sect. *Multiflori* generally grow in relatively

dry situations, while wet ground and ditch margins are favored by other *Aster* species, e.g., *A. simplex, A. praealtus,* and *A. puniceus.*

Tolerance of *Aster ericoides* toward disturbance of the natural vegetation appears to be very low. Occasional populations may be found at the margins of plowed fields but, at least in the region east of the Mississippi River, this species is mostly confined to remnants of prairie vegetation along railroads, to bluff prairies, and to dune areas (Jones, 1974).

By contrast, *Aster falcatus* may show a favorable response to disturbance or, at least, a considerable tolerance. This was noted by Boivin (1972), and it is evident from the exceptional vigor exhibited by several collections made in the vicinity of cities in Alberta [*McCalla 10218 & 12393; G. H. Turner 2812* (ALTA)]. Label data indicate that the plants grew in disturbed ground. The matted low-stemmed habit form with simple racemose inflorescences often found in plains populations of *A. falcatus* ssp. *commutatus* is commonly associated with pastured areas, and is probably a response to grazing. The plants form an integral part of the plant community in these man-made habitats. Observations made in my experimental fields, which during the spring season are much visited by rabbits and other wildlife, suggest that these asters may be of some importance as forage plants in the ranges of the Great Plains. A collection of this habit form (*G. H. Turner 7421*) was transferred by Dr. Turner to his garden and, in cultivation, grew into broadly branching sturdy plants about 60 cm tall, with paniculate inflorescences, the heads borne on long peduncles at the tips of branchlets [*G. H. Turner 7621, 7626, & 7627* (ALTA, DAO)].

My collecting experience with *Aster falcatus* ssp. *falcatus* is limited. This taxon appears to tolerate a wide climatic range, as it occurs from Alaska southward to Arizona and New Mexico. According to label data, northern populations were collected in dry prairie, on bluffs, and on river banks. In the southern portion of the range, the plants are found in grassland openings of the juniper-pine zone, at altitudes between 1,500 and 2,500 meters, i.e., in climatically moderate situations, rather than the hot deserts.

Asters of sect. *Multiflori* seem to display a notably high tolerance for salinity and alkalinity. Habitat information on herbarium sheets indicates that these plants were frequently collected in alkali flats and at edges of salt marshes. The presence of *A. ericoides* on the

islands of the Atlantic seaboard, in places exposed to salt spray, is also indicative of this tolerance. This adaptation appears to be correlated with a prevalence of the spreading pubescence form. Quantity of indument is usually exceptionally copious, often resulting in a cinereous appearance. Collections characteristic for this phenomenon are: **Montana:** *J. F. Brenkle & L. H. Shinners 41* (WIS); **New York:** *R. L. Crockett, s.n.* (GA); **Washington:** *W. J. Eyerdam 6382* (ILL); *H. St. John, W. D. Courtney & C. S. Parker 5499* (MO, UC, WS); **Manitoba:** *J. S. Rowe 197* (DAO); *H. J. Scoggan 4417 & 10404* (ALTA); **Mackenzie District:** *C. C. Loan 314* (DAO).

When the distribution of populations of sect. *Multiflori* is mapped, not with regard to taxa but to contrasting pairs of characteristics, one branch of the dichotomy always transcends the entire range, while the other finds expression only in the western half (Jones, 1973, and Figure 21). The eastern limit for the western element roughly coincides with the 100th meridian. Several writers in the fields of ecology and plant geography have recognized this meridian as a climatic and vegetational boundary (Jenny, 1930; Livingston & Shreve, 1921; McDougall, 1925; Merriam, 1892; Oosting, 1956; and Transeau, 1935); it separates the true prairies from the more sparsely vegetated Great Plains. The controlling climatic parameter is precipitation.

Ranges of the four subspecies recognized in sect. *Multiflori* are determined largely by their response to climatic factors. *Aster ericoides* ssp. *ericoides* grows predominantly in the true prairie under moderate moisture stress. In the northern portion of its range, this taxon does not extend west of the 100th meridian. In the southern portion, for example Texas, the plants occur in the blackland prairies, in open areas associated with the *Dalea-Prosopis-Populus* community, and in the post-oak belt, again under fairly mesic conditions.

Aster ericoides ssp. *pansus* is limited to the area west of the 95th meridian. Variety *pansus* grows mostly west of the continental divide, in the narrow grassland strips of river valleys and in the Palouse Prairie. The tall erect habit exhibited by these plants may be indicative of their association with the relatively dense, tall vegetation prevailing in this region of moderate climatic conditions. The somewhat decumbent or sprawling var. *stricticaulis,* on the other hand, is more common in the dry plains east of the continental

divide. These plants are found in thinly vegetated habitats domi-
nated by bunch-grasses. Other forbs in association with these asters
are *Lesquerella ludoviciana, Tephrosia virginiana, Astragalus* spp.,
Sphaeralcea coccinea, Artemisia frigida, Heterotheca villosa, Pen-
stemon spp., *Geum triflorum,* and *Solidago* spp. All these plants are
characterized by a similar cespitose habit. In the early-season stage,
several stems arise from a caudex-like rhizome in all directions at an
angle of less than 90° with the horizontal, thereby providing
maximum ground cover (Jones, 1973, *pl. 11 a, c, & f*). The general
prevalence of this habit form in many unrelated plains species
strongly suggests an adaptive response toward protection against
wind and excessive soil moisture loss.

Aster falcatus ssp. *commutatus* is found in habitats of variable
climatic conditions, which is to be expected from the morphological
heterogeneity found in this taxon. Variety *commutatus* tolerates the
xeric conditions that prevail in the high plains and is often
sympatric with plants of *A. ericoides* ssp. *pansus* var. *stricticaulis.*
Populations of the var. *crassulus* prevail in the transition zone
between the true prairies and the dry plains, i.e., in more mesic
situations. Populations of typical *A. falcatus* also seem to favor
somewhat more moderate situations than those of var. *commutatus.*
My own collections of ssp. *falcatus* (e.g. *1160, 1178, 1194, & 1208*)
were made mostly in the vicinity of rivers or on gravelly slopes.

GEOGRAPHIC DISTRIBUTION

An understanding of the geographic distribution of sect. *Multi-
flori* proved to be critical for a solution of the taxonomic problems.
After extensive field and experimental work, all herbarium collec-
tions available were again scrutinized. Using the morphological
criteria established and summarized in Table 1, it was possible to
estimate relative frequency of occurrence of the four subspecies in
any given area. Representation in the herbarium is, of course, often
biased and, at best, a crude approximation of the conditions that
actually prevail. Bias can be minimized, however, by having a large
sample from a variety of sources. Not counting duplicates, the total
sample for this particular presentation consisted of 3,209 collec-
tions. After sorting them geographically, the specimens under each
subspecies were counted, and the frequencies calculated in percent
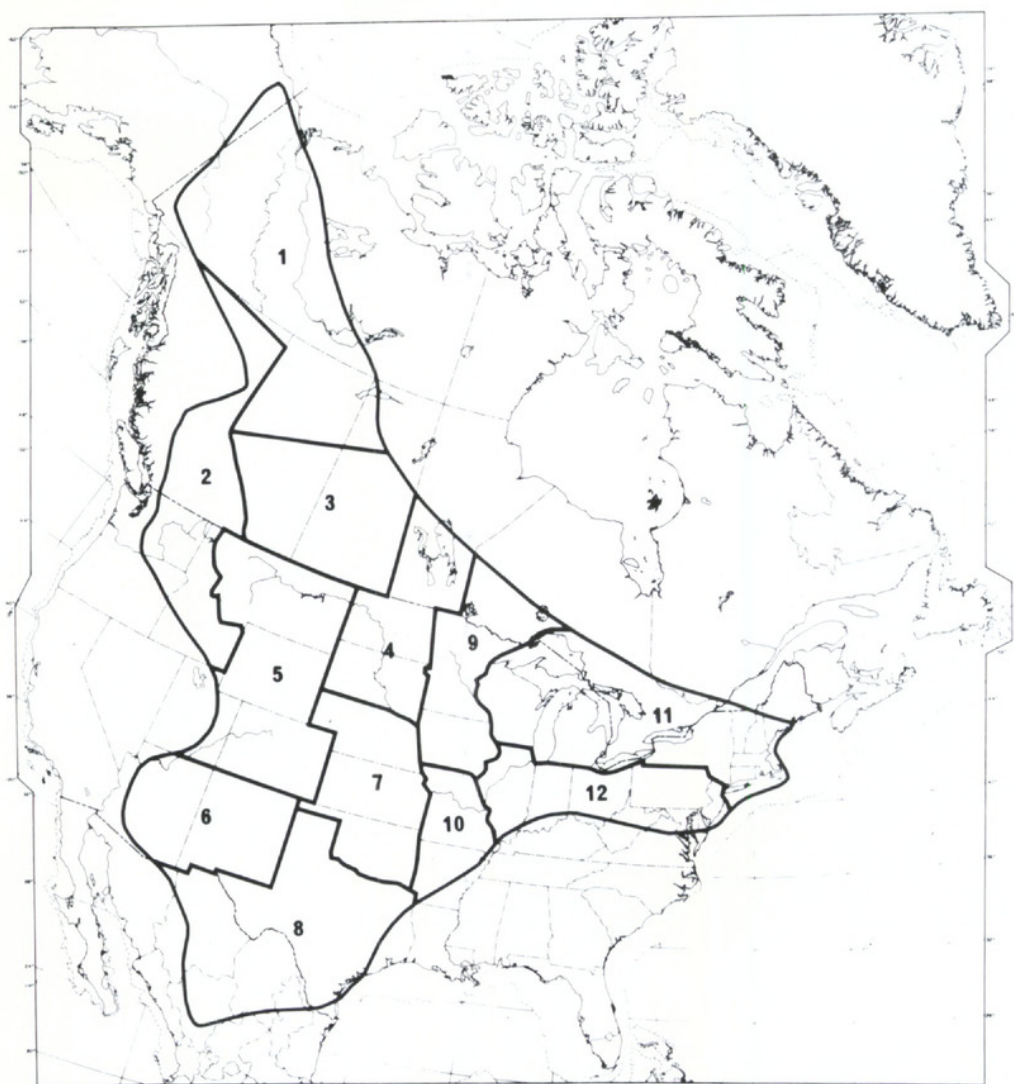of total sample from each state or province. On the basis of the

Figure 22.   Range of *Aster* sect. *Multiflori*, subdivided into 12 more or less natural zones.

percentages obtained, the total range for sect. *Multiflori* was subdivided into 12 zones (Figure 22). Although they follow political boundaries (except in Canada), these zones represent more or less natural assemblages. The tabulated results (Jones, 1973, p. 217) are not repeated here, but the summaries are presented diagrammatically (Figures 23–25). Shaded sections in the large pies for each zone represent the subspecies occurring in that zone, and the blank sections represent morphological intermediates. Smaller pies below each of the zones give a breakdown of the varietal frequencies.

Discussion of Results.   Zone 1 represents the northern extreme of range, northern Alberta, the Northwest Territories, and Alaska, a large area, in which relatively few collections were made. While both species occur in the area, typical *Aster falcatus* is predominant. In *A. ericoides* ssp. *pansus,* variety *stricticaulis* prevails. A high percentage of intermediates is, at least in part, a reflection of small sample size.

Zone 2, the northwestern limit of range, hosts the same two subspecies as Zone 1, but the frequencies differ significantly. This zone is separated from all the others by the continental divide. Populations of the small-headed *Aster ericoides* ssp. *pansus* var. *pansus* predominate in British Columbia and in the Palouse Prairie.

Zone 3 reveals the presence, in nearly equal proportions, of three subspecies, the two subspecies of *Aster falcatus* plus *A. ericoides* ssp. *pansus.* This zone constitutes the "trouble" area of southern Alberta and Saskatchewan referred to before. The number of morphological intermediates is relatively small, however, in comparison to the number of collections that can readily be placed. Similar to Zone 1, in *A. ericoides* ssp. *pansus,* variety *stricticaulis* is more common than typical var. *pansus.* In *A. falcatus* ssp. *commutatus,* variety *commutatus* is predominant. If pubescence forms are considered in this subspecies, the proportions of the two variants are approximately equal.

Zone 4 is characterized by the occurrence of all four subspecies. Manitoba and the Dakotas form the northern half of a corridor bounded by the 95th and 105th meridians, i.e., the transition zone between the true prairies and the plains. *Aster falcatus* ssp. *commutatus* and *A. ericoides* ssp. *pansus* are more common than typical *A. falcatus* and *A. ericoides.* In *A. ericoides* ssp. *pansus,* only var. *stricticaulis* is represented, while frequency ratios are about equal between the varieties of ssp. *ericoides* and *A. falcatus* ssp. *commutatus.* This equal division also applies to the pubescence forms.

Zone 5 comprises the states of the high plains. *Aster falcatus* ssp. *commutatus* predominates, providing nearly half of the sample of 334 collections. Typical *A. falcatus* also has fairly high representation, and the degree of morphological intermediacy is considerable. Plants with hirsute pubescence are about twice as abundant as plants with strigose indument. *Aster ericoides* is mostly represented by ssp. *pansus* var. *stricticaulis,* while ssp. *ericoides* barely enters the eastern portion of this zone.
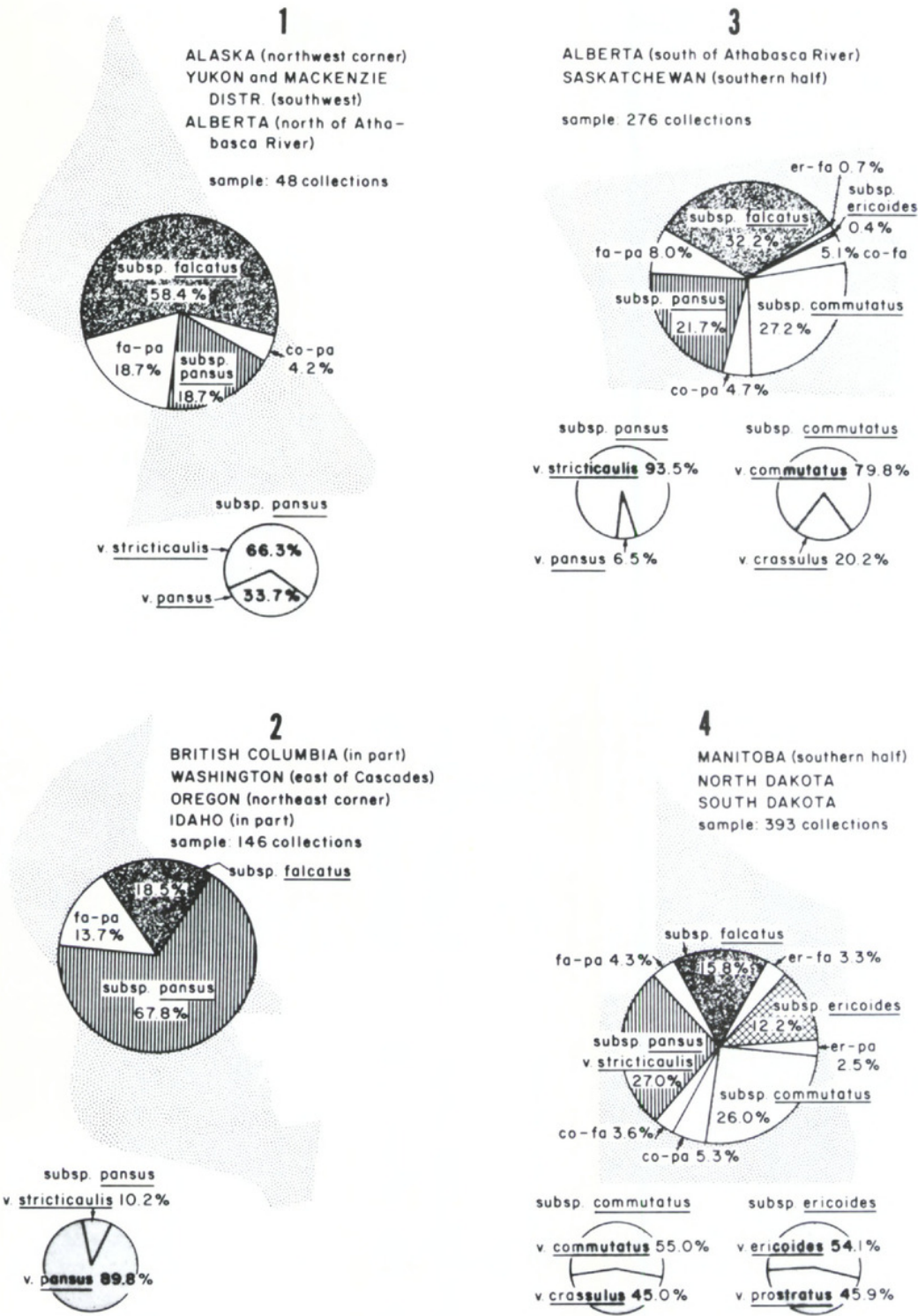
1

ALASKA (northwest corner)
YUKON and MACKENZIE
    DISTR. (southwest)
ALBERTA (north of Atha-
    basca River)

sample: 48 collections

3

ALBERTA (south of Athabasca River)
SASKATCHEWAN (southern half)

sample: 276 collections

2

BRITISH COLUMBIA (in part)
WASHINGTON (east of Cascades)
OREGON (northeast corner)
IDAHO (in part)
sample: 146 collections

4

MANITOBA (southern half)
NORTH DAKOTA
SOUTH DAKOTA
sample: 393 collections

Figure 23.   Frequency of occurrence for taxa represented in zones 1–4.

Zone 6 reveals that the southern limit of *Aster ericoides* ssp. *pansus* has been reached; this taxon is essentially absent in Arizona and New Mexico. Instead, ssp. *ericoides* occurs with increased frequency. *Aster falcatus* is mostly represented by ssp. *commutatus*, but ssp. *falcatus* has been collected at higher altitudes. Within ssp. *commutatus*, variety *crassulus* prevails with 63%. Approximately 56% of the collections have hirsute stems.

Zone 7, comparable to Zone 4 in the north, forms the southern half of a corridor bounded by the 95th and 105th meridians. Distribution of taxa is different, however; *Aster ericoides* ssp. *ericoides* is the predominant taxon in Nebraska, Kansas, and Oklahoma, and the strigose var. *ericoides* is more abundant than the hirsute var. *prostratus*. *Aster falcatus* ssp. *commutatus* is represented mostly by var. *crassulus* and, again, the form with strigose pubescence prevails, with ratios similar to those found for *A. ericoides*.

Zone 8 forms the southern limit of range for sect. *Multiflori*. The plants are mostly *Aster ericoides* ssp. *ericoides*, although southern populations often differ morphologically somewhat from populations east of the Mississippi River. *Aster falcatus* ssp. *commutatus* occurs mostly in the form of var. *crassulus*, with plants of the strigose pubescence form prevalent. Representation of typical *A. falcatus* is minor in Texas and Mexico.

Zones 9–12 can be considered as a unit. This is the area east of the 95th meridian, where populations of sect. *Multiflori* are characterized by considerable uniformity. Only along the northwestern boundary do plants of *Aster falcatus* enter the area to any extent, mostly in the form of ssp. *commutatus* var. *crassulus*. *Aster ericoides* ssp. *pansus* usually exhibits some intermediate traits. Without underground parts, herbarium specimens are indistinguishable from the typical subspecies. All populations in Zones 11 and 12 are typical *A. ericoides*. This area (east of the Mississippi River) was the subject of an earlier publication (Jones, 1974).

Brief mention must be made of regions adjoining the range of sect. *Multiflori*. I have seen no specimens from either California or Nevada which can be placed in this section. Most specimens from these states labeled as such were misidentified plants with affinities to *Aster ascendens* (e.g., *E. Palmer 143*, from San Diego Co., California — NY). There are two sheets from Fremont's expedition
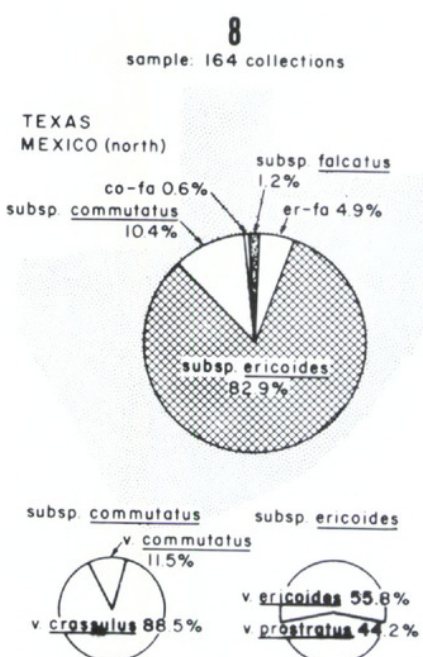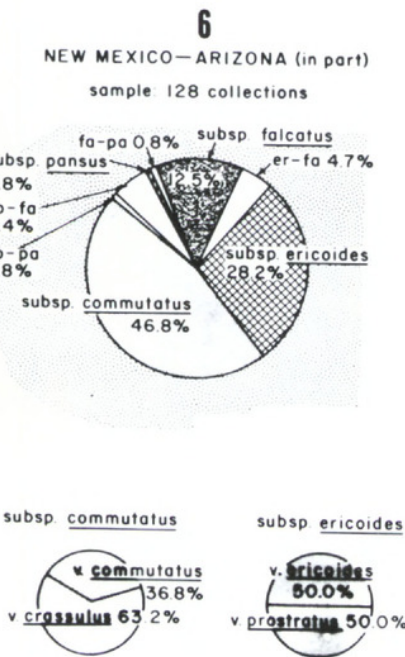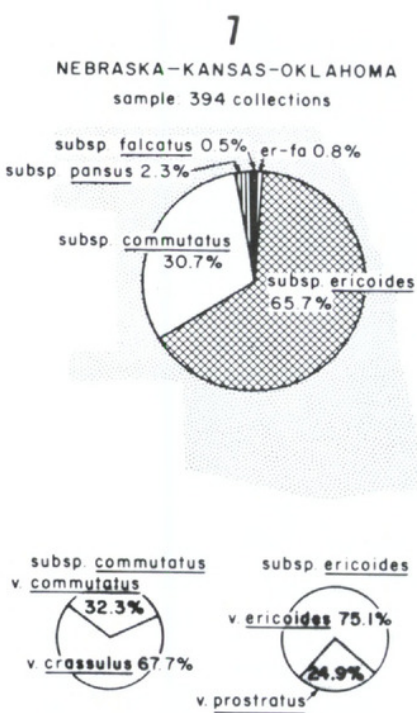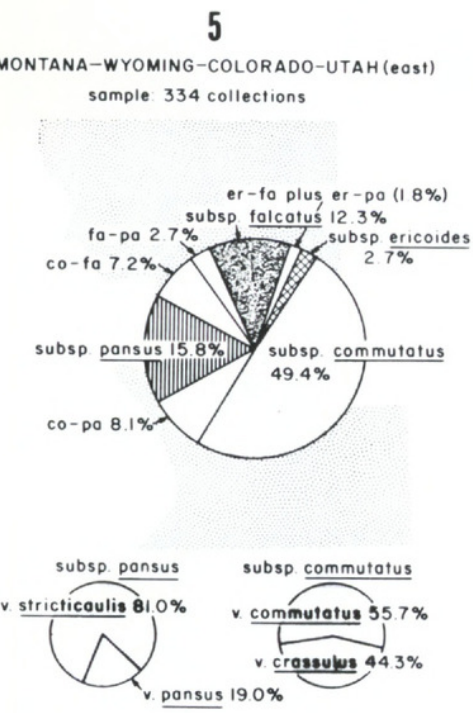
Figure 24. Frequency of occurrence for taxa represented in zones 5–8.

to California, 1845–47, one of which is *A. ericoides* (labeled *A. multiflorus*) from "Turkey Creek"; the other consists of two dissimilar pieces, one of which is *A. falcatus* ssp. *commutatus*. That sheet bears Nuttall's number *64* (NY); it was labeled *A. Nuttallii* by Asa Gray and annotated by him: "or new — Nuttall's specimen is poor." One does not know where these plants were collected. In *Botany of California,* Asa Gray (1876) does not list sect. *Multiflori* among the asters from that state.

In the northeastern part of the range, the sect. *Multiflori* does not extend beyond southeastern Ontario and the extreme southwest corner of Quebec. Although I have seen no specimens from Quebec, I have seen a photograph of a stand of *Aster ericoides* labeled Hull County, Templeton, *W. Scott 13342* (DAO). The locality is in the vicinity of Ottawa.

In the southeastern United States, there is only one authentic record from Virginia [Fauquier County, 8 miles from Aldie, etc., *H. A. Allard 12196* (TEX, US, WIS)], but I have found many misidentified sheets from that state, which probably account for some of the counties listed for the occurrence of *Aster ericoides* in Virginia (Massey, 1961). Peattie (1930) cited his own collection *2521* from Polk County, North Carolina. I have not located that collection, but all other collections from the Carolinas were misidentified, except one piece on a sheet marked Anderson, South Carolina, John Davis. The other piece on that sheet is *A. parviceps,* and a collection exists with the same date, also by John Davis, from Hannibal, Missouri (MICH). Another questionable North Carolina record is a collection by P. O. Schallert, marked Winston-Salem (GH). Schallert was a prolific collector in the Southwest, and Winston-Salem was his place of residence.

Two authentic disjunct collections are: **Alabama:** Hale County, Rosemary, *R. M. Harper, s.n.* (NY); **Mississippi:** Oktibbeha County, Starkville, *J. D. Ray 7669* (NCU).

In this age of long-distance motor travel, it would be surprising if one would not occasionally find plants growing outside their natural range. The fact that so few specimens do exist outside the range of sect. *Multiflori* indicates that these plants have no weedy tendencies. In my own recent travels, I have been unable to find *Aster ericoides* in southern Indiana, Kentucky, Tennessee, the Carolinas, and Georgia.
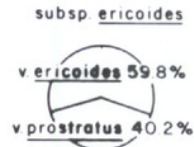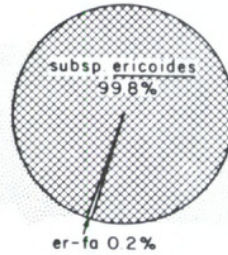
9

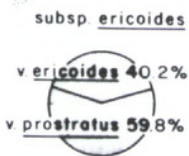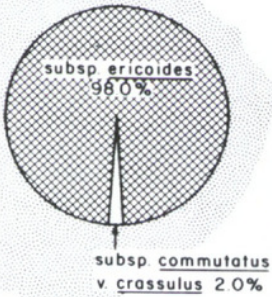ONTARIO (west) — MINNESOTA — IOWA
sample: 335 collections

subsp. pansus 0.3%
er-pa 3.0%   er-fa 1.8%
subsp.
commutatus
5.7%

subsp. ericoides
89.2%

subsp. commutatus   subsp. ericoides

v. crassulus 94.7%   v. ericoides 54.3%

                                v. prostratus 45.7%
         v. commutatus
         5.3%
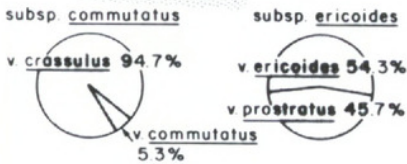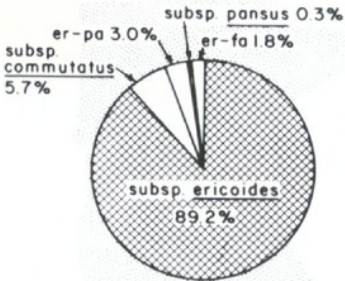
11

WISCONSIN — MICHIGAN — ONTARIO (southeast)
NEW YORK — NEW ENGLAND STATES

sample: 416 collections

subsp. ericoides
99.8%

er-fa 0.2%

subsp. ericoides

v. ericoides 59.8%

v. prostratus 40.2%

10

MISSOURI — ARKANSAS (in part)
sample: 99 collections

subsp. ericoides
98.0%

subsp. commutatus
v. crassulus 2.0%

subsp. ericoides

v. ericoides 40.2%

v. prostratus 59.8%

12

ILLINOIS — INDIANA — OHIO — PENNSYLVANIA
NEW JERSEY — DELAWARE — VIRGINIA (north)

sample: 476 collections

subsp. ericoides
99.8%

subsp. commutatus
v. commutatus 0.2%

subsp. ericoides

v. ericoides 30.2%
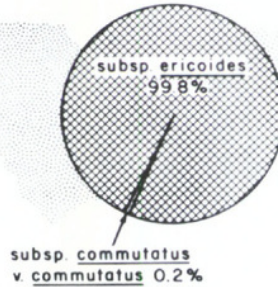
v. prostratus 69.8%
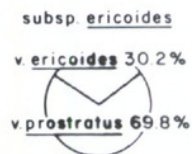
Figure 25.   Frequency of occurrence for taxa represented in zones 9–12.

PHYLOGENETIC CONSIDERATIONS

The ease with which many *Aster* species can be hybridized suggests that the genus is actively evolving. Three series of chromosome numbers occur in *Aster,* with the basic numbers $x = 5, 8,$ and 9. Considerations of chromosome evolution in the genus revolve around the question of which base number is the ancestral one, the high $x = 9$ or the low $x = 5$. Literature on the subject has been discussed in a previous paper (Jones, 1977). The available evidence suggests that the progenitor of *Aster* had a basic chromosome number of $x = 4$, and that all taxa of the three extant chromosome number series are derived by way of aneuploidy and polyploidy.

Species of *Aster* sect. *Multiflori* belong in the $x = 5$ series. According to accepted criteria, *A. ericoides* is phylogenetically older than *A. falcatus*. Populations of *A. ericoides* are predominantly diploid and, with the exception of the far northern reaches, this taxon has been recorded throughout the range for the whole group. The typical ssp. *ericoides* is characterized by a high degree of morphological uniformity and by relatively limited ecological requirements and tolerances. The taxon is predominant in the southwestern portion of range and the sole representative of the section in the eastern one-third of the area. There is hardly any sympatry with ssp. *pansus,* which is confined to the northwestern part of range. The two subspecies are morphologically and ecologically well differentiated, but a genetical barrier is lacking or very weak. Data on abundance of populations, and information on postglacial migration of floras (Benninghoff, 1964; Hanson, 1947; Hultén, 1937) suggest that the probable center of distribution for *A. ericoides* is the prairie area between the Missouri and Mississippi Rivers. Several factors suggest that ssp. *pansus* is a derivative of the typical subspecies, for example, a higher degree of heterogeneity and a relatively narrow range, as compared to typical *A. ericoides.* Gene flow from sympatric populations of *A. falcatus* may be partly responsible for the lack of uniformity in *A. ericoides* ssp. *pansus.*

Aster falcatus is typically hexaploid, but a considerable number of populations were found to be tetraploid. On the basis of the polyploidy, one can assume that this species is a derivative of *A. ericoides,* and the wide northern extent of range, into Alaska, suggests that differentiation of the two species took place before the Wisconsinan glaciation. Typical *A. falcatus* is, perhaps, a species of

the flora element that survived maximum glaciation in nunataks or unglaciated pockets in the mountains (Fernald, 1925; Hultén, 1937). Highest frequency of occurrence for this subspecies is recorded from the northwestern portion of range. In the extreme north, it is the only representative of sect. *Multiflori.*

The hexaploid chromosome number has been found in both subspecies of *Aster falcatus,* although no populations from north of Edmonton, Alberta, have been examined. The two subspecies are well differentiated morphologically but rather weakly in their ecological requirements. *Aster falcatus* ssp. *commutatus* is sympatric with all other recognized taxa of sect. *Multiflori* over at least part of their ranges, but it is absent from the extreme northern region. These plants appear to be more tolerant toward disturbance of habitat, and reproductively more aggressive than plants of typical *A. falcatus,* a fact which suggests that the ssp. *commutatus* may be phylogenetically younger than the typical subspecies. However, hexaploidy can have arisen more than once. A certain degree of genetic isolation between the two subspecies is indicated by a relatively low average seed set (5% of the potential) in the successful crosses. Perhaps the two subspecies originated separately, and the species boundaries were obliterated relatively recently, after the Pleistocene.

Tetraploid populations are found mostly in the central range of sect. *Multiflori,* and they are characterized by a high degree of heterogeneity. At least theoretically, this ploidy level may have originated in two ways: by duplication of the chromosomes in diploid parents, or by hybridization between hexaploid and diploid plants. Subsequent crossing and recombinations between populations, followed by fixation of genotypes, may account for the heterogeneity observed.

LITERATURE CITED
(except entries listed in Part I)

ANDERSON, L. C., D. W. KYHOS, T. MOSQUIN, A. M. POWELL, & P. H. RAVEN. 1974. Chromosome numbers in Compositae — IX. Haplopappus and other Astereae. Am. Jour. Bot. **61:** 665–671.

BENNINGHOFF, W. S. 1964. The prairie peninsula as a filter barrier to post-glacial plant migration. Proc. Indiana Acad. Sci. **73:** 116–124.

DELISLE, A. L. 1937. The influence of auxin on secondary branching in two species of *Aster.* Am. Jour. Bot. **24:** 159–167.

FERNALD, M. L. 1925. Persistence of plants in unglaciated areas of boreal America. Mem. Am. Acad. Arts and Science 15: 241–342.

GRAY, A. 1876. Gamopetalae. *In:* Botany of California. Geol. Survey of California. Welch, Bigelow & Co., Cambridge, Massachusetts. Vol. 1.

HANSON, H. P. 1947. Postglacial vegetation of the northern Great Basin. Am. Jour. Bot. 34: 164–171.

HOLMGREN, P. K., & W. KEUKEN. 1974. Index Herbariorum, part I: The herbaria of the world. Ed. 6. Regnum Vegetabile, Vol. 92.

HULTÉN, E. 1937. Outline of the history of arctic and boreal biota during the Quaternary Period. Bokförlags Aktiebolaget Thule. Stockholm.

JENNY, H. 1930. The nitrogen content of the soil as related to the precipitation-evaporation ratio. Soil Science 29: 123–206.

JONES, A. G. 1977. New data on chromosome numbers in *Aster* section *Heterophylli* (Asteraceae), and their phylogenetic implications. Systematic Botany 2: 334–347.

———. 1978a. Observations on reproduction and phenology in some perennial asters. Am. Midl. Nat. 99: 184–197.

———. 1978b. The taxonomy of *Aster* section *Multiflori* (Asteraceae). I. Nomenclatural review and formal presentation of taxa. Rhodora 80: 319–357.

LIVINGSTON, B. E., & F. SHREVE. 1921. The distribution of vegetation in the United States as related to climatic conditions. Carnegie Inst. Washington Publ. 284.

LÖVE, A., & O. SOLBRIG. 1964. *In:* IOPB Chromosome number reports. Taxon 13: 100–110, 201–209.

McDOUGALL, E. 1925. The moisture belts of North America. Ecology 6: 325–332.

MERRIAM, C. H. 1892. The geographic distribution of life in North America with special reference to the Mammalia. Proc. Biol. Soc. Washington 7: 1–64.

OOSTING, H. J. 1956. The study of plant communities. Ed. 2. W. H. Freeman & Co. San Francisco and London.

PIKE, R. B. 1970. Evidence for the hybrid status of *Aster* × *Blakei* (Porter) House. Rhodora 72: 401–426.

SEMPLE, J. C. 1976. The karyotype of *Aster ericoides* (Asteraceae): some Canadian populations. Can. Jour. Genet. Cytol. 18: 661–664.

TRANSEAU, E. N. 1935. The prairie peninsula. Ecology 16: 423–437.

UTTALL, L. J. 1962. Synthesis of *Aster herveyi*. Rhodora 64: 113–117.

VAN FAASEN, P. 1963. Cytotaxonomic studies in Michigan asters. Michigan Botanist 2: 17–27.

WETMORE, R. H., & A. L. DELISLE. 1939. Studies in the genetics and cytology of two species in the genus *Aster* and their polymorphy in nature. Am. Jour. Bot. 26: 1–12.

DEPARTMENT OF BOTANY
UNIVERSITY OF ILLINOIS
URBANA
ILLINOIS 61801