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A MULTIVARIATE MORPHOMETRIC STUDY AND TAXONOMIC TREATMENT OF *SYMPHYOTRICHUM* SUBSECT. *PORTERIANI* (ASTERACEAE: ASTEREAE)

JOHN C. SEMPLE
Department of Biology
University of Waterloo
Waterloo, Ontario, Canada N2L 3G1
jcsemple@uwaterloo.ca

JERRY G. CHMIELEWSKI
Biology Department,
Slippery Rock University
Slippery Rock, Pennsylvania
jerry.chmielewski@sru.edu

ABSTRACT

Multivariate morphometric analyses were used to compare inflorescence and head traits of 313 individuals of *Symphyotrichum* subsect. *Porteriani*. The results of the numerical studies, notes on additional collections and distributional data, and field observations were incorporated into a taxonomic treatment of the subsection. Six taxa are recognized: *S. depauperatum*, *S. parviceps*, *S. kentuckiense*, *S. pilosum* var. *pilosum, S. pilosum* var. *pringlei*, and *S. porteri*. The taxa can be distinguished on the basis of differences in habit, pubescence, peduncular bract traits, involucre height, numbers of ray and disc florets, and the lengths of floret parts. White-rayed diploid *Symphyotrichum porteri* is native to the Front Range of the central Rocky Mountains; the other taxa are native to eastern North America. Three eastern species have restricted distributions: white-rayed *S. depauperatum* is a very rare diploid endemic to serpentine soils and outcrops in southeastern Pennsylvania and adjacent Maryland and disjunct in a small area in north-central North Carolina; white-rayed *S. parviceps* includes diploids and tetraploids native to a region generally northeast of the Ozark Plateau; usually blue-violet-rayed, octoploid *S. kentuckiense* occurs in central Tennessee, and northern Alabama and Georgia. Usually white-rayed *S. pilosum* occurs throughout most of the eastern USA and into parts of adjacent Canada; var. *pilosum* occurs throughout this area with tetraploids and hexaploids by and large allopatric; hexaploid var. *pringlei* occurs in a broad arch from Wisconsin to Nova Scotia and southward to northeastern North Carolina.

Symphyotrichum subsect. *Porteriani* (Rydb.) Semple is a well-delimited group of asters: all members have phyllaries with slightly to strongly inrolled margins near the tip, and all have a chromosomal base number of x = 8. These have historically were treated as members of *Aster* sect. *Dumosi* Torr. & Gray. With the exception of the type species *S. porteri* A. Gray, which is native to the foothills of the Front Range of the Rocky Mountains centering on Colorado, all taxa within the section are native to the eastern deciduous forest region of eastern North America. Members of the subsection, particularly the common and widely distributed *S. pilosum* (Willd.) Nesom, have been the subject of, or included in, a number of ecological and cytogeographic studies during the past five decades (Jones 1976, 1978; Peterson & Bazzaz 1978; Semple 1978; Baskin & Baskin 1979, 1985; Parish & Bazzaz 1982; Shackleford 1983; Semple & Chmielewski 1985; Chmielewski & Semple 1990; Levy & Wilbur 1990).

The cytology of the subsection is well known. Chromosome numbers for 650 individuals of the x = 8 subsection have been reported mostly under synonyms in the genus *Aster* (Avers 1954; Huziwara 1958; Van Faasen 1963; Van Faasen & Sterk 1979; Jones 1980b; Semple & Brouillet 1980b; Hill, 1983; Semple & Chmielewski 1985; Semple, Chmielewski, & Lane 1989; Chmielewski & Semple 1990; Levy & Wilbur 1990; Semple et al. 1992; Semple & Cook 2004; Semple et al. 2015, Semple et al. 2019). Karyotypes of *Symphyotrichum pilosum* were presented as camera lucida drawings by Huziwara (1958; 2*n* = 48; as *Aster pilosus*, variety not specified) and Van Faasen (1963; $2n = 24_{II}$; as *Aster pilosus*, voucher is var. *pilosum*). Photomicrographs of karyotypes of *S. pilosum* var. *pilosum* (as *Aster pilosus* var. *pilosus*) were presented in Shackleford (1983; 2*n* = 32 and 48) and Semple & Brouillet (1980b; just a single satellite chromosome).

There has been little disagreement on the within-genus affinities of subsect. *Porteriani*, but there has been disagreement on the rank and generic placement. Jones (1980a) treated Rydberg's (1906) species-group *Porteriani* as a section in *Aster* subg. *Symphyotrichum* (Nees) A.G. Jones, which is equivalent to subg. *Aster* sect. *Dumosi* Torr. & Gray sensu Semple and Brouillet (1980a). Cronquist (e.g., 1968, 1980) grouped species of subsect. *Porteriani* with species of subsect. *Dumosi*, although he did not use formal grouping labels. Semple and Brouillet (1980a) included the taxa of subsect. *Porteriani* in sect. *Dumosi*, the former not being mentioned. Semple (1985) separated the two groups of species and made the subsectional level combination in *Aster*. In the numerical analyses of Jones and Young (1983), a hypothetical OTU [based on *A. porteri* A. Gray, *A. pilosus*, and *A. pringlei* (A. Gray) Britt.] clustered with other *x* = 8 taxa, with which it was placed in their cladograms. Members of the complex recognized by Alexander in Small 1933 were included with *A. ramosissimus* sensu auct. (?non Mill.) in *Aster* sp-group XIII. *Ramosissimi*. Nesom (1994) transferred all *x*= 8 asters to *Symphyotrichum*, including those of subsect. *Porteriani*. Semple et al. (2002) accepted this placement within *Symphyotrichum*.

Within the subsection the number of taxa recognized and their ranks have varied among authors. Several dozen basionyms and another dozen combinations based on these have been put forward. In the last century, there was disagreement on what taxa should be recognized. Britton and Brown (1913; treatment with the assistance of Burgess) recognized the following taxa: *A. depauperatus* (Porter) Fern., *A. faxoni*, *A. ericoides* sensu auct. non L. (= *A. pilosus*), *A. priceae* (with a comment on the possible distinctiveness of *A. kentuckiensis* Britt.), and *A. pringlei*. Small (1933; treatment by Alexander) recognized *A. pilosus*, *A. faxoni*, *A. juniperinus* Burg., *A. priceae* Britt., and *A. ramosissimus*. Cronquist (1968, 1980) recognized the taxa *A. depauperatus* (Porter) Fern., *A. parviceps* (Burg.) Mack. & Bush, *A. pilosus* var. *pilosus*, *A. pilosus* var. *demotus* Blake, *A. pilosus* var. *priceae* (Britt.) Cronq., and *A. pilosus* var. *pringlei* (Gray) Blake. Fernald (1950) had recognized the same taxa, with two exceptions; a broad leafed *A. pilosus* var. *platyphyllus* (Torr. & Gray) Blake was accepted and *A. priceae* was considered anomalous and possibly a hybrid between var. *pringlei* and another undesignated species. Semple and Chmielewski (1985) accepted varietal status for *priceae* and *pringlei* within *A. pilosus* and presented reasons for placing var. *demotus* in synonymy under var. *pringlei*, which Jones (1980, 1983) treated as a separate species. Jones (1984) stated that if *A. pringlei* is to be treated as a var. of *A. pilosus*, then *A. depauperatus* and *A. parviceps* should be treated as varieties within *A. pilosus* subsp. *parviceps* (Mack. & Bush) A.G. Jones. Examples of habit and inflorescence variation are illustrated in Figures 1-2.

Because no comprehensive analysis of all taxa in subsect. *Porteriani* has ever been published and because there is uncertainty about what taxa to recognize and at what ranks, we undertook a study of the subsection based on field observations of all taxa and detailed examination of herbarium collections. The names used throughout the remainder of this paper are those adopted at the end of the study.

MATERIALS AND METHODS

Preliminary analyses were done using collections in WAT (now WAT in MT) in order to determine which variable characters would likely be useful in a full scale study. From specimens borrowed from GH, ILL, MO, NY, RM, TENN, and those in WAT, 313 individuals were selected for use in a final set of discriminant analyses with some specimens excluded ultimately. In several cases, shoots from the same plant grown in the wild and after transplanting to the garden at Waterloo were included for comparison. Specimens were chosen on the basis of stage of development (heads in anthesis), provenance, and tentative identity based on (a) Cronquist (1968) and (b) JCS's notes on type specimens and field and greenhouse observations.

Figure 1. *Symphyotrichum* subsect. *Porteriani*: habits. **A.** *S. porteri, Semple & B. Semple 11234*, Colorado. **B.** *S. pilosum* var. *pilosum*, Cambridge, Ontario. **C.** *S. parviceps*, *Semple & Brouillet 7378*, Adams Co., Illinois. **D.** *S. kentuckiense*, *Semple & Chmielewski 9126*, Davidson Co., Tennessee. **E.** *S. pilosum* var. *pilosum*, bluff habitat, *Semple & Chmielewski 5183*, Crawford Co, Wisconsin. **F.** Dwarf *S. pilosum* var. *pringlei*, *Semple & Brammall 2798*, Bruce Peninsula, Ontario.

Figure 2. *Symphyotrichum* subsect. *Porteriani*: heads. **A.** *S. parviceps*, *Semple & Brouillet 7378*, Adams Co., Illinois. **B.** *S. kentuckiense* (violet rays), *Semple & Chmielewski 9126* and *S. pilosum* var. *pilosum* (white rays), Davidson Co., Tennessee, North Carolina. **C.** *S. depauperatum*, *Semple 11627*, Hertford Co., North Carolina.

All taxa were observed growing in the wild and after transplantation to the greenhouse and/or garden. Efforts were made to include as many different morphotypes as possible and to include specimens similar to type collections in diagnostic features of the taxon (e.g., broad leaves, or ray floret color). The limits of the complex and distributions were determined from field observations made during 1975-2012 and type and general collections at B, CAN, DAO, GA, GH, ILL, MICH, MO, MT, NY, OAC, RM, TRT, TRTE, VDB, US, UWO, and WAT now in MT (Thiers updated continuously). The field locations of source populations for the 313 specimens utilized are indicated in figures in the taxonomic treatment at the end of this paper. In most cases, only one plant per site was included, but as many as 10 plants of *S. depauperatum* from one site and 27 plants of *S. kentuckiense* from one site were included, when either it was obvious from field notes that either a particular population contained several distinctive morphotypes or the number of populations available was very low. Over the course of 15 years, hundreds of populations throughout the range of the subsection were visited.

For the final set of analyses, 16 variable characters were selected to represent the morphological variation in reproductive structures (inflorescences, heads and florets). Character abbreviations and definitions are listed in Table 1. Each entry in the data matrix represented the mean of five measurements per character per individual. Reproductive features were chosen because they tend to be more stable than vegetative features such as leaf size and shape, and generally show less plasticity to changes in environmental factors. Measurements were made on parts at the same stage of development and position on the plant. Plants were also scored for the density of stem pubescent and the relative internode length between peduncular bracts.

Table 1. Characters scored for use in statistical analyses of *Symphyotrichum* subsect. *Porteriani.*

PRMBRANCH	Number of primary branches on upper stem
CAPITULA	Total number of heads on shoot
SUBBRACTLN	Length of bract subtending heads (cm)
INVOLHT	Height of the involucre (mm)
RAYS	Number of ray florets
RSTRPLN	Length of ray floret strap (mm)
RSTRPWD	Width of ray floret strap (mm)
RSTYLLN	Length of ray floret style (mm
RTUBLN	Length of ray floret tube (mm)
RACHLN	Length of ray floret ovary/cypsela at anthesis (mm)
RPAPLN	Length of ray floret pappus at anthesis (mm)
DISCS	Number of disc florets
PAPLN	Length of disc floret pappus at anthesis (mm)
DCORLN	Length of disc floret corolla (mm)
DLOBLN	Length of disc floret corolla lobes (mm)
DLIMBLN	Length of disc floret corolla limb (mm)

Analyses were performed in one of two ways. The first set of analyses presented below were performed using SYSTAT ver. 10 (SPSS Inc. 2000) and included 5 species level taxa (*S. depauperatum*, *S. kentuckiense*, *S. parviceps*, *S. pilosum* and *S. porteri*) and 3 taxa (*S. kentuckiense*, *S. pilosum* var. *pilosum* and *S. pilosum* var. *pringlei*). Analyses in SYSTAT followed the methods present in detail in Semple et al. (2015, 2016). All other analyses were performed on the mainframe computer facilities of the Department of Computing Services at the University of Waterloo using available packages of programs. Preliminary analyses were done with a system of clustering algorithms (CLUSTAN, Wishart 1978). Single linkage clustering was used to assess the relative similarity of the specimens and to establish preliminary groups that could serve as the bases for defining *a priori* groups to be compared by discriminant analysis. The characters ultimately used to determine membership in a group were not used as variables in the discriminant analyses. All other statistical analyses were done using subroutines UNIVARIATE, DISCRIM, STEPDISC, and CANDISC available in SAS (SAS User's Guide: Basics 1985; SAS User's Guide: Statistics 1985). Prior to analysis in SAS, length measurements were transformed with the logarithmic function to the base 10, and count data were transformed with the square root function in an attempt to satisfy the assumption of normality in univariate analyses and multi-normality in the multivariate analyses. Stepwise discriminant analysis (STEPDISC) was used to select a subset of characters that maximized differences among the *a priori* groups. The same subset also could be used as secondary characters in a key to the infraspecific taxa of the species. Classificatory discriminant analysis (DISCRIM) was used to classify, *a posteriori*, individuals into groups defined *a priori*. Correct classification rates and Geisser assignment probabilities indicate the strength of group separation. Canonical discriminant analysis (CANDISC) was utilized as a dimension-reduction technique to facilitate visualization of the results of the multidimensional analyses. This analysis was done because the first, or first few, canonical variables may reveal considerable differences among *a priori* groups, even when none of the quantitative variables do so independently. Tests for equality of group centroids (Wilks' Lambda, Pillai's Trace, Hotelling-Lawley Trace and Roy's Greatest Root) were performed as part of the canonical analysis.

RESULTS

The results of a preliminary cluster analysis on a preliminary data set were not particularly informative and therefore were not used in establishing membership in *a priori* groups in subsequent analyses. A cluster analysis was not performed on the final data matrix of 304 specimens.

SYSTAT analysis on five species level a priori groups

In a SYSTAT discriminant analysis, 304 specimens of *Symphyotrichum* subsect. *Porteriani* were placed into one of five *a priori* species level groups usually recognized in the literature: *S. depauperatum* (N = 24), *S. kentuckiense* (N = 55), *S. parviceps* (N = 29), *S. pilosum* (N = 163), and *S. porteri* (N = 33). Eleven of the 27 characters scored were selected as significant in discriminating the 5 species and are listed in decreasing order of F-to-remove values: number of disc florets (37.92), length of subtending inflorescence bract (24.73), number of ray florets (12.79), ray floret strap width (5.87), disc floret limb length (5.51), disc floret pappus length at anthesis (4.98), ray floret tube length (4.55), number of primary branches on shoot (4.39), ray floret achene length (5.09), disc floret pappus length (4.82), disc floret corolla length (3.80), and ray floret style length (2.96). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *S. kentuckiense* and *S. depauperatum* (42.119), *S. kentuckiense* and *S. pariceps* (41.166), and *S. parviceps* and *S. porteri* (37.397); the smallest separations were between *S. depauperatum* and *S. parviceps* (5.915) and *S. parviceps* and *S. pilosum* (14.168).

In the SYSTAT Classificatory Discriminant Analysis of the five species level *a priori* groups (*Symphyotrichum depaupertum*, *S. kentuckiense*, *S. parviceps*, *S. pilosum*, and *S. porteri*), percents of correct *a posteriori* assignment to the same *a priori* group ranged from 79-92%. The Classification matrix and Jackknife classification matrix are presented in Table 2. Results are presented in order of decreasing percents of correct placement. Twenty-two of the 24 specimens of the *S. depaupertaum a priori* group (92%) were assigned *a posteriori* to the *S. depauperatum* group; 16 specimens with 91-99% probability, 4 specimens with 84-89%, 1 specimen each with 79%, 60%, and 59% probabilities. Two specimens of the *S. depauperatum a priori* group were assigned *a posteriori* to *S. parviceps* with

64% probability each. Forty-three of the 55 specimens of the *S. kentuckiense a priori* group (84%) were assigned *a posteriori* to the *S. kentuckiense* group: 11 specimens with 100% probability, 19 specimens with 90-99% probability, 4 specimens with 85-89% probability, 5 specimens with 71-77% probability, and 4 specimens with 61-68% probabilities. Nine specimens of the *S. kentuckiense a priori* group were assigned to other taxa: 6 specimens to *S. pilosum* with 78% 57% 55%, 53%, and 51% probabilities; and 3 specimens to *S. porteri* with 81%, 72%, and 62 probabilities. Twenty-five of the 33 specimens of the *S. porteri a priori* group (82%) were assigned *a posteriori* to the *S. porteri* group: 11 specimens with 100% probability, 7 specimens with 91-99% probability, 3 specimens with 81-88% probability, and 3 specimens with 76%, 65% and 56% probabilities. Six specimens assigned *a priori* to *S. porteri* were assigned *a posteriori* into 2 other species: 5 specimens to *S. pilosum* with 94%, 79%, 74%, 70% and 50% probabilities, and 1 specimen to *S. kentuckiense* with 69% probability. One hundred and twenty-four of the 166 specimens of the *S. pilosum a priori* group (82%) plus one included *a posteriori* were assigned *a posteriori* to the *S. pilosum* group: 42 specimens with 90-98% probability, 35 specimens with 80-86% probability, 21 specimens with 71-789% probability, 14 specimens with 61-67% probability, 12 specimens with 51-59% probability, and 1 specimen with 43% probability. Thirty-nine specimens of the *S. pilosum a priori* group were assigned *a posteriori* to other species: 10 specimens to *S. kentuckiense* with 100-45% probabilities; 8 specimens to *S. porteri* with 87-54% probabilities, 7 specimens to *S. parviceps* with 69-53% probabilities, and 4 specimens to *S depauperatum* with 77-38% probabilities. Twenty-three of the 29 specimens of the *S. parviceps a priori* group (79%) were assigned *a posteriori* to the *S. parviceps* group: 1 specimens with 100% probability, 9 specimens with 91-98% probability, 6 specimens with 80-86% probability, 3 specimens with 76-78% probability, 2 specimens with 76% and 78% probabilities, 2 specimens with 66-67%5 probability, and 2 specimens with 58-59% probability. Six specimens of the *S. parviceps a priori* group were assigned *a posteriori* to other species: 4 specimens to S. *depauperatum* with 89%, 61%, 58%, and 51% probabilities, and 2 specimens to *S. pilosum* with 86% and 78% probabilities.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 161 specimens of *Symphyotrichum depauperatum*, *S. kentuckiense*, *S. parviceps*, *S. pilosum*, and *S. porteri* are presented in Fig. 3. Eigenvalues on the first four axes were 2.760, 0.607, 0.386, and 0.081.

Table 2. F-matrix for the discriminant analysis of 5 species of *Symphyotrichum* subsect. *Porteriani*.

Group	***depauperatum***	***kentuckiense***	***parviceps***	***pilosum***
kentuckiense	42.119			
parviceps	5.915	41.166		
pilosum	20.872	28.944	14.168	
porteri	35.889	19.816	37.397	24.778

Wilks' lambda = 0.1038 df = 11 4 299; Approx. F= 20.3289 df = 44 1107 prob = 0.0000

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of seven *a priori* groups; a posteriori placements to groups in rows.

Group	***depauperatum***	***kentuckiense***	***parviceps***	***pilosum***	***porteri***	**% correct**
depauperatum	22	0	2	0	0	92
kentuckiense	0	46	0	6	3	84
parviceps	4	0	23	2	0	79
pilosum	4	12	7	130	10	80
porteri	0	1	0	5	27	82
Totals	30	59	32	143	40	82

Jackknifed classification matrix

Group	***depauperatum***	***kentuckiense***	***parviceps***	***pilosum***	***porteri***	**% correct**
depauperatum	21	0	3	0	0	88
kentuckiense	1	45	0	6	3	82
parviceps	4	0	20	4	0	69
pilosum	4	12	10	127	10	78
porteri	0	1	0	6	26	79
Totals	30	65	33	143	39	79

SYSTAT analysis on three polyploid taxa as priori groups

In a SYSTAT discriminant analysis, 217 specimens of *Symphyotrichum* subsect. *Porteriani* were placed into one of three polyploid *a priori* groups usually recognized in the literature: *S. kentuckiense* (N = 55), *S. pilosum* var. *pilosum* (N = 111), and *S. pilosum* var. *pringlei* (N = 51). Nine of the 27 characters scored were selected as significant in discriminating the 3 *a priori* groups and are listed in decreasing order of F-to-remove values: length of subtending inflorescence bract (26.29), number of ray florets (13.50), number of disc florets (9.41), ray floret tube length (4.91), disc floret limb length (4.81), ray floret strap width (3.72), disc floret achene length at anthesis (2.46), disc floret pappus length at anthesis (2.41), and ray floret style length (2.24). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. kentuckiense* and *S. pilosum* var. *pringlei* (26.766); the smallest separation was between *S. pilosum* var. *pilosum* and *S. pilosum* var. *pringlei* (6.844).

Table 4. Between groups F-matrix for the five species level *a priori* groups analysis (df = 10 205).

Group	***S. kentuckiense***	***S. pilosum* var. *pilosum***
S. pilosum* var. *pilosum	22.805	
S. pilosum var. pringlei	26.766	6.844

Wilks' lambda = 0.3205 df = 10 2 214; Approx. F= 15.7108 df = 20 410 prob = 0.0000

In the SYSTAT Classificatory Discriminant Analysis of the three polyploid *a priori* groups (*Symphyotrichum kentuckiense*, *S. pilosum* var. *pilosum*, and *S. pilosum* var. *pringlei*), percents of correct *a posteriori* assignment to the same *a priori* group ranged from 93%-68%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. Fifty-one of the 55 specimens of the *S. kentuckiense a priori* group (93%) were assigned *a posteriori* to the *S. kentuckiense* group: 10 specimens with 100% probability, 23 specimens with 90-99% probability, 3 specimens with 84-87% probability, 3 specimens with 73-77% probability, 2 specimens with 69% and 62% probabilities, 2 specimens with 54% and 50 probabilities, and 2 specimens with 42% and 40% probabilities. Four specimens of the *S. kentuckiense a priori* group were assigned to other taxa: 3 specimens to *S. pilosum* var. *pilosum* with 93%, 72%, and 42% probabilites; and 1 specimen to *S. pilosum* var. *pringlei* with 63% probability.

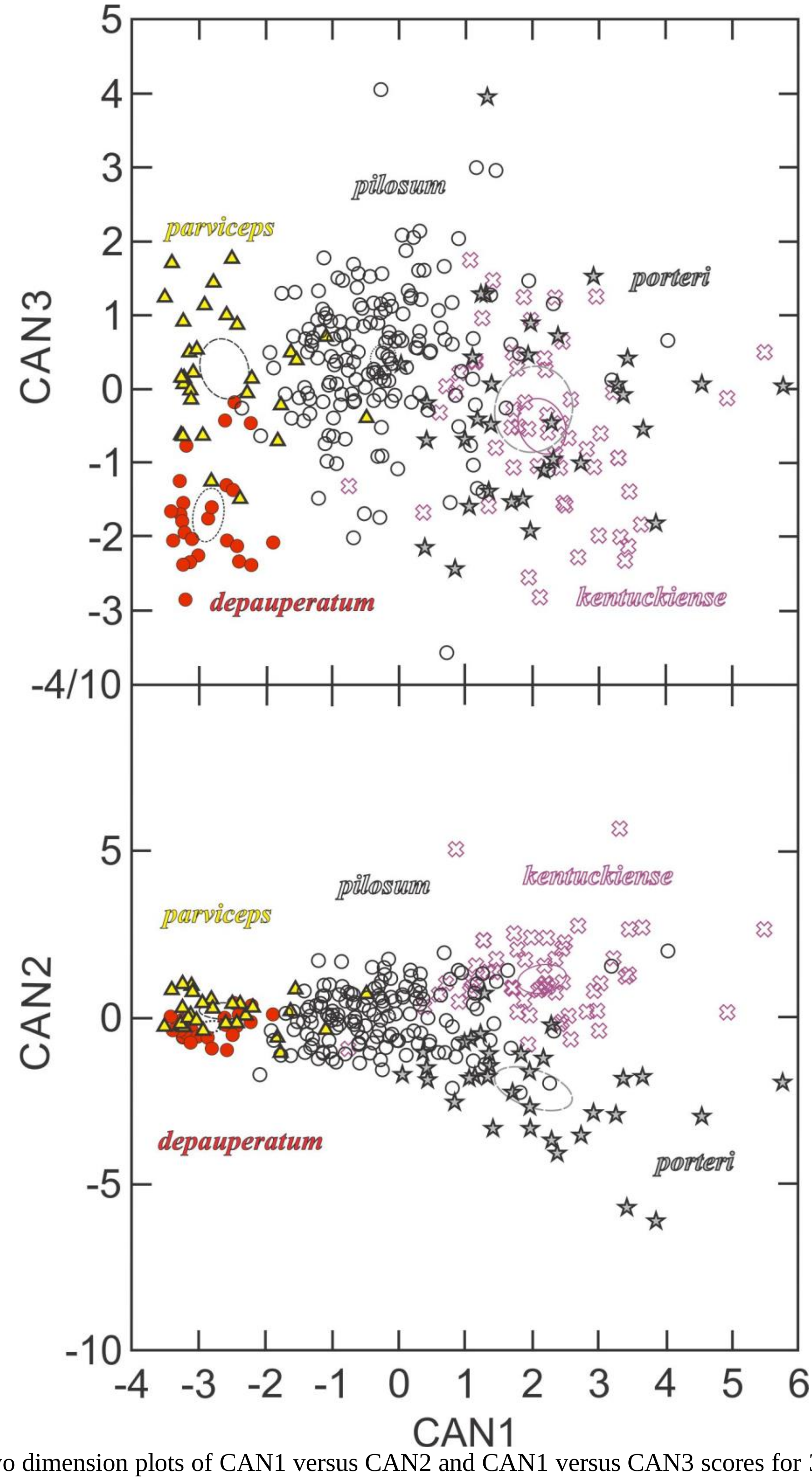


Figure 3. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 303 specimens of five *a priori* species groups of *Symphyotrichum* subsect. *Porteriani*: *S. depauperatum* (red dots), *S. kentuckiense* (open purple crosses), *S. parviceps* (black outline yellow triangles), *S. pilosum* (open black circles), and *S. porteri* (black outline gray stars).

Forty-two of the 51 specimens of the *S. pilosum var. pringlei a priori* group (82%) were assigned *a posteriori* to the *S. pilosum* var. *pringlei* group: 5 specimens with 91-97% probability, 11 specimens with 81-89% probability, 10 specimens with 70-79% probability, 8 specimens with 60-68% probability, 3 specimens with 58% and 54% (2 specimens), and 1 specimen with 44% probability. Ten specimens of the *S. pilosum* var. *pringlei a priori* group were assigned *a posteriori* to other species: 1 specimen to *S. kentuckiense* with 54% probability; and 8 specimens to the *S. pilosum* var. *pilosum* with 85%, 75%, 68%, 61%, 59%, 58%, 56%, and 54%. Seventy-six of the 111 specimens of the *S. pilosum* var. *pilosum a priori* group (68%) were assigned *a posteriori* to the *S. pilosum* var. *pilosum* group: 9 specimens with 90-97% probability, and 13 specimens with 80-89% probability, 17 specimens with 71-79% probability, 16 specimens with 60-69% probability, 13 specimens with 50-59% probability, and 2 specimens with 48% and 44% probabilities. Thirty-five specimens of the *S. pilosum* var. *pilosum a priori* group were assigned to the other two taxa: 25 specimens to *S. pilosum var. pringlei* with 95%, 86% (2 specimens), 81%, 80%, 7% (2 speciemns), 72% (2 speimens), 71%, 70%, 67%, 66%, 65%, 64%, 61%, 49% and 48%; and 10 specimens to *S. kentuckiense* with 100%, 97%, 91%, 90%, 84% (2 specimens), 62%, 55% (2 specimens), and 53%.

A two dimensional plot of CAN1 versus CAN2 canonical scores for 217 specimens of *Symphyotrichum kentuckiense*, *S. pilosum* var. *pilosum*, and *S. pilosum* var. *pringlei* is presented in Fig. 4. Eigenvalues on the first two axes were 2.653 and 0.760. Thirty-four (74%) of the known tetraploids (2*n*=32) in var. *pilosum* were placed *a posteriori* into var. *pilosum* and 17 (54%) of the known hexaploids (2*n*=48) were placed *a posteriori* into var. *pilosum* while 14 hexaploids were placed *a posteriori* into *S. kentuckiense* (4 specimens) and *S. pilosum* var. *pringlei* (10 specimens). In contrast, 21 (81%) of the known hexaploids (2*n*=48) in var. *pringlei* were placed *a posteriori* into var. *pringlei* while 6 (22%) were placed *a posteriori* into *S. kentuckiense* (1 specimen) or *S. pilosum* var. *pilosum* (5 specimens). Thus, ploidy level was more significant in *a posteriori* placements to other taxa for hexaploids than for tetraploids.

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three *a priori* groups; *a posteriori* placements to groups in rows.

Group	***S. kentuckiense***	***S. pilosum*** var. ***pilosum***	***S. pilosum*** var. ***pringlei***	**% correct**
S. kentuckiense	51	3	1	93
S. pilosum var. ***pilosum***	10	76	25	68
S. pilosum var. ***pringlei***	1	8	42	82
Totals	61	87	68	78

Jackknifed classification matrix

Group	***S. kentuckiense***	***S. pilosum* var. *pilosum***	***S. pilosum* var. *pringlei***	**% correct**
S. kentuckiense	51	3	1	93
S. pilosum* var. *pilosum	10	76	25	68
S. pilosum* var. *pringlei	1	8	42	82
Totals	61	87	68	78

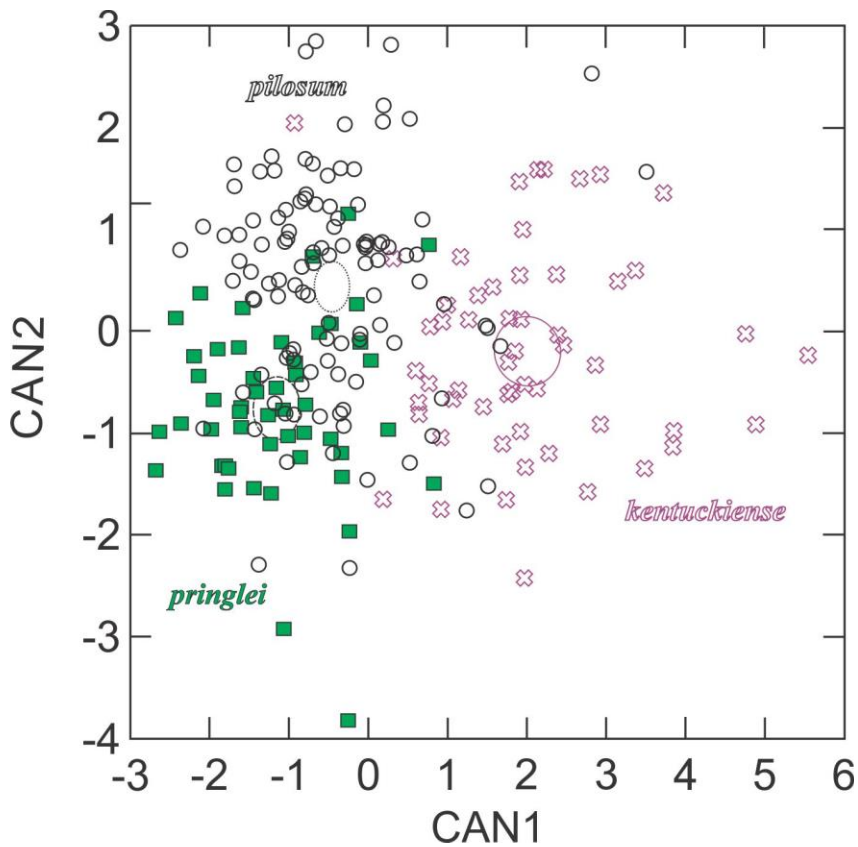


Figure 4. Two dimension plots of CAN1 versus CAN2 scores for 217 specimens of three polyploid *a priori* groups of *Symphyotrichum* subsect. *Porteriani*: *S. kentuckiense* (open purple crosses), *S. pilosum* var. *pilosum* (open black circles), and *S. pilosum* var. *pringlei* (black outline green squares).

SAS analysis on six a priori groups

In the SAS discriminant analysis, 314 specimens of *Symphyotrichum* subsect. *Porteriani* were placed into one of six *a priori* groups, which corresponded to six of the seven taxa usually recognized in the literature: *S. depauperatum* (N = 25), *S. kentuckiensis* (N = 60), *S. parviceps* (N = 29), *S. pilosum* var. *pilosum* (N = 115), and *S. pilosum* var. *pringlei* (N = 52; includes specimens assignable to var. *demotus* in some floras, but determined previously by Semple and Chmielewski (1985) to be a growth form only), and *S. porteri* (N = 33). All plants from the Rocky Mountain region were assigned to the *S. porteri a priori* group; all plants for which data were available were diploid (2*n*=16). Plants with glabrate stems, numerous peduncular bracts separated by short internodes, and small narrowly campanulate heads ascending phyllaries of unequal lengths were assigned to the *S. depauperatum a priori* group; three plants included in this group were known to be diploid, shoots from two of these were grown in the experimental garden or greenhouse. Plants with moderately pubescent stems, numerous peduncular bracts separated by short internodes, and small to mid-sized narrowly campanulate heads ascending phyllaries of unequal lengths were assigned to the *S. parviceps a priori* group; all plants for which data were available were either diploid (one plant) or tetraploid (2*n*=32; seven plants). Plants with sparsely to densely pubescent stems and mid-height turbinate involucres with the spreading to reflexed outer phyllaries much shorter than the inner ones were assigned to the *S. pilosum* var. *pilosum a priori* group; most plants were moderately to densely pubescent; plants for which data were available were either tetraploid (2*n*=32; 49 plants), pentaploid (2n=40; 1 plant), or hexaploid (2*n*=48; 30 plants). Plants with glabrate stems and mid-height turbinate involucres with the spreading to reflexed outer phyllaries much shorter than the inner ones were assigned to the *S. pilosum* var. *pringlei a priori* group; the 26 plants for which data were available were hexaploids (2*n*=48). Plants with glabrate stems and large generally taller involucres with non-reflexed outer phyllaries nearly equal in length to the inner ones were assigned to the *S. kentuckiense a priori* group; the six plants for which data were available were octoploid (2*n*=64).

SAS Analysis on six a priori groups

A SAS Stepwise discriminant analysis was performed to select a suite of variable traits useful in formulating discriminant functions to separate 6 *a priori* taxa (*S. depauperatum*, *S. kentuckiense*, *S. parviceps*, *S. pilosum* var. *pilosum*, *S. pilosum* var. *pringlei*, and *S. porteri*). Fourteen variable characters (in decreasing order of contribution to the discriminatory power of the model as measured by Wilks' Lambda, the likelihood ratio criterion) were determined (STEPDISC) to be important in discriminating among the six groups: NODISCS, BRACT, NORAYS, DISCPAPL, RAYACH, DISCLOBL, RAYSTRPL, DISCLIML, RAYSTRPW, NOHEADS, RAYPAPL, PRIBRANC, DISCL, and RAYTUBELN. In the classificatory discriminant analysis, discrimination among the six groups ranged between 72.2% and 93.9%, and Geisser assignment probabilities were generally greater than 0.80 for specimens correctly classified.

The eigenvalue for the first canonical variate (4.49) accounted for 68% of the variation. The Mahalanobis distances between pairs of groups and the associated F-values indicated that all groups differed significantly ($P < 0.0003$). Tests for equality of population centroids were significantly different ($P < 0.0001$).

SAS Analysis on four a priori eastern groups

A SAS Stepwise discriminant analysis was performed to select a suite of variable traits useful in formulating discriminant functions to separate 4 *a priori* taxa (*S. depauperatum*, *S. parviceps*, *S. pilosum*, and *S. porteri*). The results are illustrated in Fig. 6.

SAS Analysis on four a priori eastern groups

A SAS Stepwise discriminant analysis was performed to select a suite of variable traits useful in formulating discriminant functions to separate 5 *a priori* taxa (*S. depauperatum*, *S. parviceps*, *S. pilosum* var. *pilosum*, *S. pilosum* var. *pringlei*, and *S. porteri*). The results are illustrated in Fig. 7.

SYSTAT analysis of the two ploidy levels in S. pilosum var. pilosum

A STEPWISE discriminant analysis of 83 specimens of *Symphyotrichum pilosum* var. *pilosum* of known ploidy level using fewer traits compared 52 tetraploids, 1 pentaploid, and 30 hexaploids from much of the range of distribution. Only the number of disc florets was retained as a discriminating character in the final analysis. *A posteriori* placement of individuals into their respective groups was not high: 22 tetraploid specimens (42%) were correctly assigned *a posteriori* to the tetraploid group, the one pentaploid specimen was assigned to the pentaploid group (100%), and 13 of the hexaploid specimens (43%) were correctly assigned to the hexaploid group. Tetraploids and hexaploids in var. *pilosum* did not differ sufficiently to warrant recognition as separate taxa.

DISCUSSION

The results of the multivariate analyses indicated that all six *Symphyotrichum* groups investigated are well differentiated, but more so in the case of the three diploids (*S. porteri*, *S. parviceps*, and *S. depauperatum*) and the octoploid (*S. kentuckiense*) than the tetraploids and hexaploids. The tetraploids (*S. parviceps* and *S. pilosum* var. *pilosum*) and hexaploids (*S. pilosum* var. *pilosum* and var. *pringlei*) are more likely to be confused morphologically. Statistical analyses such as discriminant analysis, however, cannot dictate the ranks to be give each taxon, they can only be used to test hypotheses on the distinctiveness of the *a priori* groups included in the analysis. Thus, other information must be considered when determining the number of *a priori* groups and ultimately in assigning nomenclatural ranks to those groups determined to be significantly different.

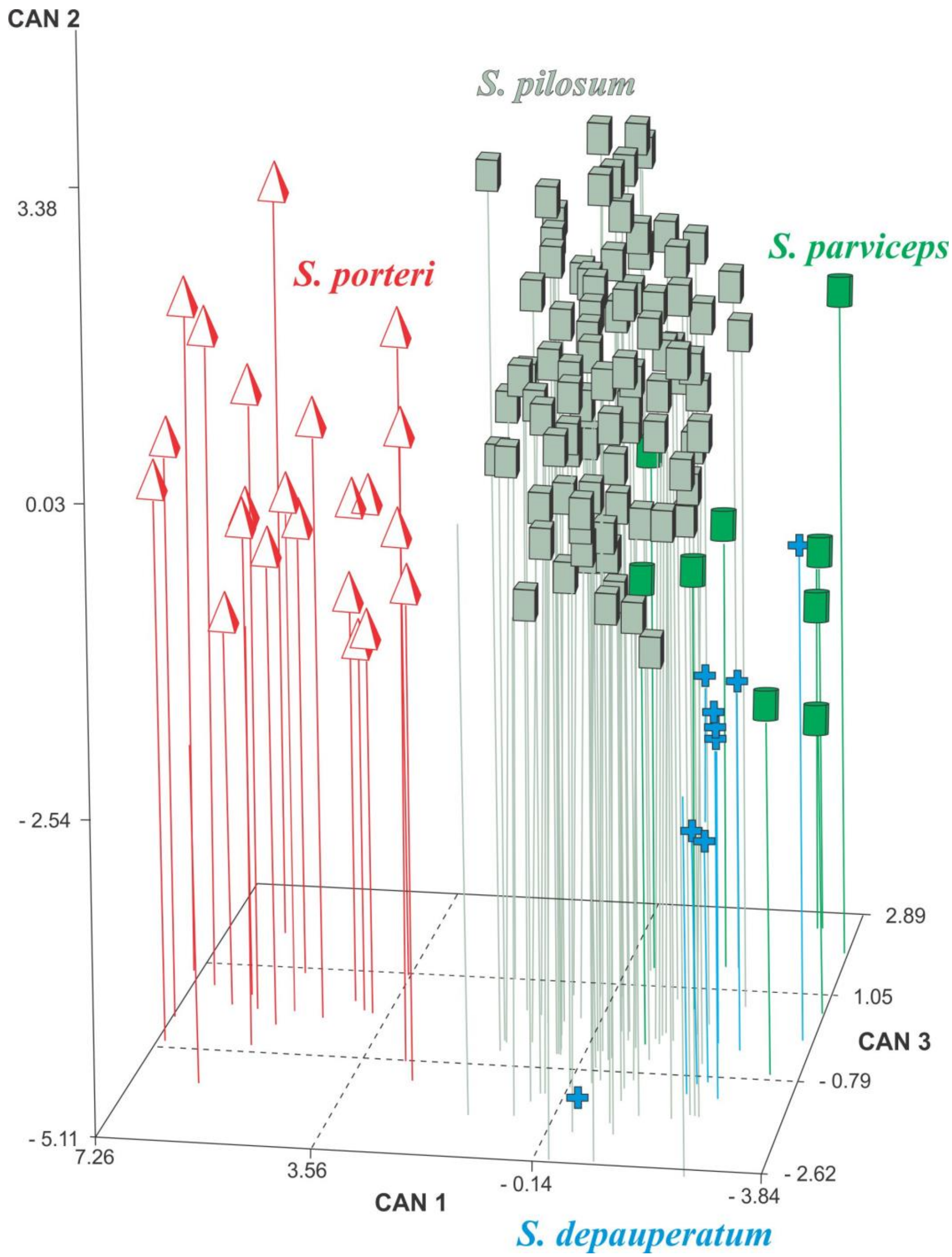


Figure 6. Plot of 138 specimens of *Symphyotrichum* subsect. *Porteriani* included in a SAS canonical analysis.

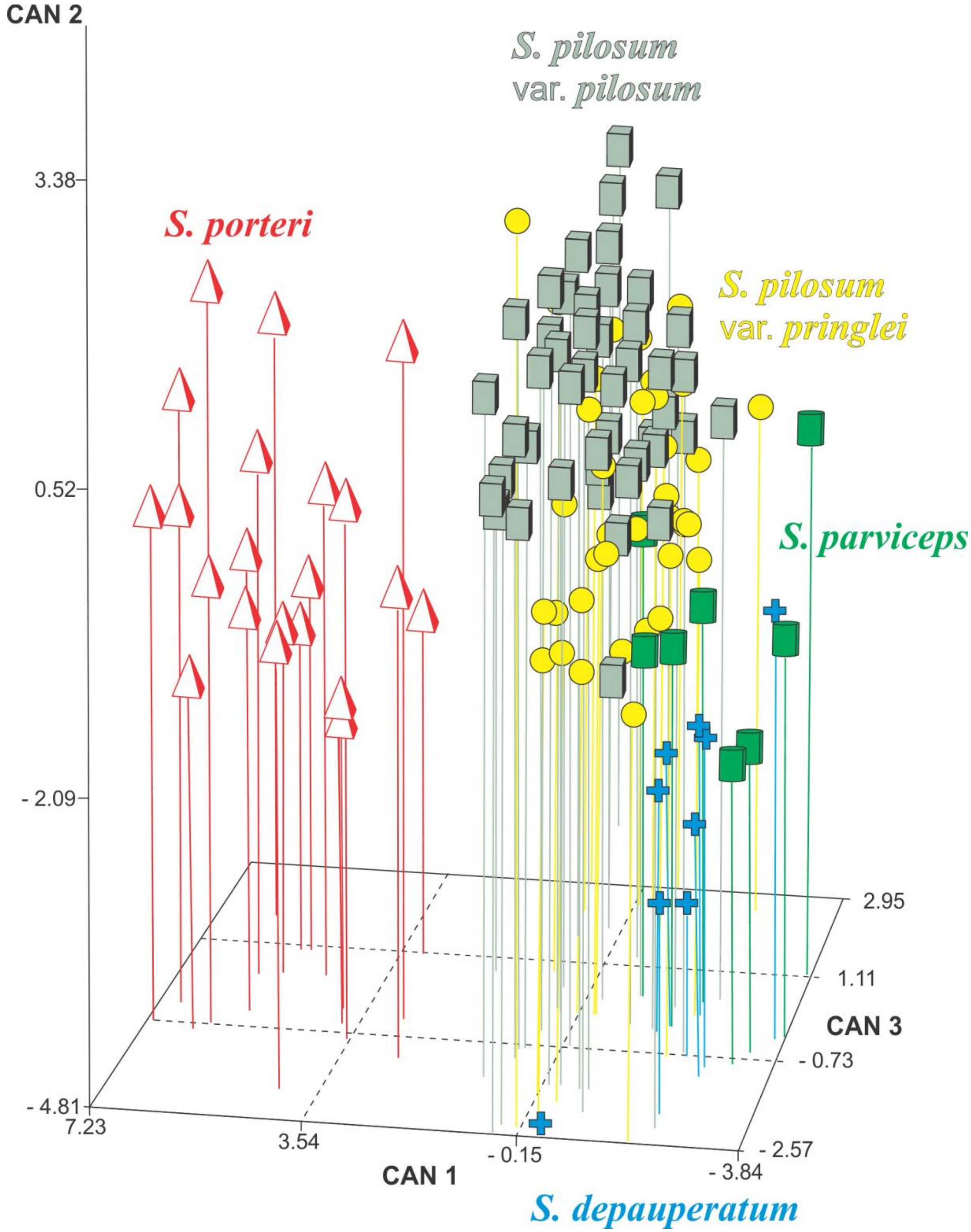


Figure 7. Plot of 121 specimens of *Symphyotrichum* subsect. *Porteriani* included in a SAS canonical analysis.

Our choice of six *a priori* groups, rather than more or less, is based on our greenhouse observations, preliminary numerical studies, the literature, and the sample size requirements imposed by the statistical procedures. We presented evidence earlier that *S. pilosum* var. *pringlei* and var. *demotus* were not distinct (Semple & Chmielewski 1985). We could find no non-arbitrary way of dividing the glabrate stemmed members of *S. pilosum* into two groups; stem height had been found to be dependent upon growing conditions. Our preliminary data analysis also indicated that the two "taxa" could not be maintained, and so only the one *a priori* group, var. *pringlei*, was included in the discriminant analyses.

Additional *a priori* groups might have been included based on the names we ultimately placed in synonymy. In some cases, type material was too fragmentary to provide data on the full character set. In other cases, the type specimen appeared to be nothing more than an aberrant growth form that we did not feel warranted recognition as an *a priori* group. Comments about disposition of names placed in synonym are included in the taxonomic treatment presented below.

In the case of subsect. *Porteriani* a number of nomenclatural ranks have been proposed for the taxa we recognize. Previous authors have almost never dealt with the western and eastern members of the subsection at the same time. *Symphyotrichum porteri* has been recognized at the species level (as *A. porteri* in much of the literature) with little disagree, and so our discussion will be restricted to the eastern taxa, about which there has been disagreement. Cronquist (1968, 1980) accepted the combinations *A. parviceps*, *A. depauperatus*, and *A. pilosus* var. *pilosus*, *A. pilosus* var. *pringlei*, *A. pilosus* var. *demotus*, and *A. pilosus* var. *priceae*, as did Semple and Chmielewski (1985). Jones (1980a) listed the following taxa: *A. depauperatus*, *A. pilosus* (including *A. parviceps*), *A. porteri*, and *A. pringlei*. Subsequently, Jones (1984) proposed the combinations *A. pilosus* ssp. *parviceps* (Burgess) A.G. Jones and *A. pilosus* ssp. *parviceps* var. *pusillus* (A. Gray) A.G. Jones (the varietal level name with priority for the *A. depauperatus* group).

Numerous chromosome number counts have been reported for members of subsect. *Porteriani* and were discussed by Semple and Chmielewski (1985). Semple, Chmielewski, and Lane (1989) reported several hexaploid counts of $2n$ = 64 for *A. priceae* (here treated as *Symphyotrichum kentuckiense*) and rejected the only other chromosome number published for the taxon. Semple and Chmielewski (1985) had reported a count of $2n$=32 under the name *A. pilosus* var. *priceae* based on a plant counted in northeastern Alabama. This plant was included in our numerical study and determined to be a member of *S. pilosum* var. *pilosum* in the classificatory discriminant analyses. All octoploid plants included in the analyses were found to be rather typical *S. kentuckiense*. Thus, we have rejected our own tetraploid report for *A. priceae* (treated here as *S. kentuckiense*) and acknowledge that unfamiliarity with the taxon at the time resulted in the misidentification of a glabrate, bluish-rayed individual of *S. pilosum* var. *pilosum* for *A. priceae*. The tetraploid plant collected in 1981 did not have the decumbent to ascending growth form nor the distinctive bluish-green leaf color typical of the many plants of *S. kentuckiense* we observed in the field at a number of sites in the fall of 1987. The generally larger size of floral parts of *S. kentuckiense* compared to other species of the section can be attributed in part, if not fully, to the higher ploidy level. Ploidy level can only in part account for the other distinctive features of the species.

By accepting *Symphyotrichum kentuckiense* as a distinct species, we have accepted the taxonomic rank commonly held during the first half of this century (in *Aster* by e.g., Burgess in Britton and Brown 1913; Alexander in Small 1933) and recently in *Symphyotrichum* by Medley (2021). Cronquist (1948) briefly presented reasons for treating *A. priceae* (here as *S. kentuckiense*) as a variety within *A. pilosus*. Important in his justification was the occurrence of apparent free hybridization between the two taxa at a population near Athens, Georgia (the eastern most known location for *A. priceae*; Fig. 5B). We did not find evidence of hybridization at the sympatric populations of the two species we visited in Tennessee, but this of course does not eliminate it as a possibility. The chromosome number difference between the two taxa at these sites may present some barrier to hybridization. Septaploids (2*n*=56) have been reported in other *x* = 8 taxa e.g., in *Symphyotrichum lanceolatum* (Semple et al. 1983, as *A. lanceolatus*), but not in subsect. *Porteriani*.

Cronquist (1948) also noted the instability of ray color as a character in separating *A. priceae* (here treated as *Symphyotrichum kentuckiense*) and *A. pilosus*, and in this we fully concur. White rayed forms of *S. kentuckiense* were present in both small and large populations we studied in the field in Tennessee, although most individuals had light to deep blue-lavendar rays. In *S. pilosum* var. *pilosum* and var. *pringlei* rays are usually white (occasionally light pink abaxially), and pale bluished rayed plants have been seen by us in the field. However, we have never seen any individuals of *S. pilosum* with rays as deeply blue-lavendar as those frequent in *S. kentuckiense*. Changes in ray color upon drying result in some intensification of pigment and this can further blur the distinction between taxa in herbarium specimens.

Specimens of *Symphyotrichum parviceps* from the western and southern portion of the species's range are more likely to be confused with other taxa than will be plants from the northern portion of the range. The two reports of tetraploid populations in *S. parviceps* are from the western and southern margins of the range (Semple, Chmielewski, & Chinnappa 1983; Semple & Chmielewski 1987; both as *A. parviceps*). The one diploid report is for a populations in west central Illinois (Semple & Chmielewski 1985). *Aster parviceps* was not listed as present in Arkansas by Smith (1988). Three collections of tetraploid *A. parviceps* from Fulton Co., Arkansas (Semple & Chmielewski 1987) were included in the multivariate study, but were classified *a posteriori* in var. *pringlei* or var. *pilosum* of *S. pilosum* with varying probabilities. Possibly significant is the fact that the only specimens of *S. parviceps* in the classificatory discriminant analysis with Geisser Assignment probabilities to the *S. parviceps* group of less than 0.92 were those from the southern and western portions of the range, the unglaciated region. One specimen from St. Genevieve Co., Missouri, was assigned *a posteriori* to the var. *pringlei* group, while other collections in eastern Missouri were assigned with high probabilities to the *S. parviceps* group. Further field work is needed to determine whether or not the distributions of diploids and tetraploids correlate with glaciated and unglaciated portions of the taxon's range or whether it is the case regardless of ploidy level that the more isolated, marginal populations in the species have diverged morphologically from the main body of populations in northeastern Missouri and western Illinois.

The convergence of tetraploids of *Symphyotrichum parviceps* with smaller-headed tetraploids and hexaploids of *S. pilosum* might be cited as support for merging the two species. However, the similarities are probably the direct result of the higher ploidy level, which in other species of *Symphyotrichum* correlates with the size of floral parts, e.g., *S. lanceolatum* Willd. (Semple & Chmielewski 1987 as *A. lanceolatus*). If *S. parviceps* is treated as a subspecies or variety of *S. pilosum*, then to be consistent all other taxa in the subsection also ought to be included in *S. pilosum* which would be an extreme "lumper's" approach to the systematics of subsect. *Porteriani*. We recommend against adopting such an approach. In our judgement, taken all together the morphological and distributional (and implied ecological) differences among the five species of subsect. *Porteriani* are greater than among the taxa of the *S lanceolatum* complex, which we treated as a single species (Semple & Chmielewski 1987 as *A. lanceolatus*) and equal to the differences among *S. lanceolatum*, *S. boreale* (Torr. & Gray) Löve & Löve, *S. dumosum* (L.) Nesom, *S. lateriflorum* (L.) Löve & Löve (sensu lato), *S. simmondsii* (Small) Nesom, and *S. tradescanti* (L.) Nesom. These latter species comprise a sister group in *S.* subsect. *Dumosi* (Torr. & Gray) Nesom to the species grouped in subsect. *Porteriani*. For example, the morphological differences between *S. kentuckiense* and *S. pilosum* are comparable to the differences between *S. dumosum* (most commonly diploid and tetraploid) and *S. simmondsii* (octoploid); also, both octoploid taxa have restricted distributions (and thus more specialized habitat requirements) compared to the related lower ploidy level species. The label of ‘sibling species complex’ is appropriately applied to members of both subsections.

Taxonomic Treatment

Symphyotrichum subsect. **Porteriani** (Rydb.) Nesom, Phytologia 77: 270. 1994. *Aster* sp.-group *Porteriani* Rydb., Fl. Colorado 352, 353. 1906. *Aster* sect. *Porteriani* (Rydb.) A.G. Jones, Brittonia 32. 235. 1980. *Aster* subsect. *Porteriani* (Rydb.) Semple, Phytologia 58: 429. 1985. **TYPE SPECIES**: *Aster porteri* A. Gray = *Symphyotrichum porteri* (A. Gray) Nesom

Aster sp.-group *Ramosissimi* Alexander in Small, Man. S.E. U.S. 1365. 1933. **TYPE SPECIES**: *Aster ramosissimus* Mill. ? = *A. pilosus* Willd.

Herbaceous perennials from fibrous-rooted, woody, shoot-rhizomed caudices. Basal rosettes developing at base of shoots by late in growing season and persisting through winter. Basal leaves oblanceolate to linear-oblanceolate, margins ciliate, sessile, cuneate-petiolate. Capulescences racemiform to paniculiform. Involucres narrowly campanulate to turbinate. Phyllaries with apical margins weakly to strongly inrolled, often spreading to reflexed; diamond-shaped chlorophyllous zone elongate. Cypselae compressed obconic, 1-2 ribs per side. Chromosome base number: $x = 8$.

KEY TO THE SPECIES AND VARIETIES OF *SYMPHYOTRICHUM* SUBSECT. *PORTERIANI*

1. Stems glabrous; involucres 3.6-6 mm high; 12-42 rays (averaging 22-34) white to pink; (30)40-74(100) discs, disc corolla pappus averaging 0.5 mm shorter than corolla; foothills of Front Range of Rocky Mts. in WY, CO, northern NM .... *S. porteri* (1)
1. Not with the above combination of traits; fields and rocky outcrops throughout eastern deciduous forest
    2. Outer and inner phyllaries nearly equal in length; upper peduncular bracts generally exceeding head; involucres 4.7-8.5 mm tall, stems glabrous; (13)20-28(34) blue-violet rays (sometimes white); stems often decumbent to ascending; central TN and adjacent KT, northern AL and GA .... *S. kentuckiense* (5)
    2. Outer phyllaries much shorter than inner; involucres (2.7)3-5(6.5) mm tall; rays white (rarely pink to pale blue-violet); stems usually ascending, glabrous to densely pubescent; peduncular bracts not general exceeding involucres
        3. Peduncular bracts numerous; heads small (involucre generally 3-4 mm high, narrowly campanulate, averaging 9-17 rays and 6-16 disc florets); phyllary tips ascending, margins weakly inrolled
            4. Stem glabrous-glabrate; disc pappus not exceeding corolla tube; very rare on serpentine soils of southeastern PA, adjacent MD, possibly adjacent DL, and rare on diabasic soils in north central NC .... *S. depauperatum* (2)
            4. Stems pubescent; disc pappus slightly shorter to slightly longer than corolla; fields, sandy areas, and rocky outcrops of greater northern Ozark Plateau region to northern IL .... *S. parviceps* (3)
        3. Peduncular bracts few; heads larger (involucres usually 3.5-5.1 mm high, turbinate, averaging 16-28 rays and 17-39 disc florets); phyllary tips spreading to recurved, margins inrolled; throughout eastern deciduous forest .... *S. pilosum* (4)
            5. Stems sparsely to densely hispid; common in fields, disturbed soils, and on rock outcrops thoughout much of eastern U.S., southern Ontario, rare in southern Quebec .... *S. pilosum* var. *pilosum* (4a)
            5. Stems glabrous-glabrate, stem usually strictly ascending; common in the northeastern U.S. and across Canada to northern WI and NC .... *S. pilosum* var. *pringlei* (4b)

1. **Symphyotrichum porteri** (A. Gray) Nesom, Phytologia77: 289. 1994. *Aster porteri* A. Gray, Proc. Amer. Acad. 14: 99. 1881. Renaming of *Aster ericoides* var. *strictus* Porter and based on same type.

Aster ericoides L. var. *strictus* Porter, in Porter & Coulter, Synops. Fl. Colorado, U.S. Dept. Interior Misc. Publ. 4: 56. 1874. SYNTYPES: U.S.A. **Colorado Territory**. Rocky Mts., Lat. 39°-41°, 1862, *E. Hall & J. P. Harbour 254* (LECTOTYPE [A.Jones, on sheet 1986]: GH!). "Hayden's .S. Geological Survey, 1873, *Meechan s.n.* (GH!, on sheet with LT). Not *Parry 418* (GH!, G, K, P) as designated by A. Jones on sheet in 1982.

Herbaceous perennials from short branched rootstocks, or from elongated rhizomes. Stems ascending to erect, 1-5 dm tall, glabrate. Basal rosette leaves oblanceolate, spatulate to obovate, sessile, margins ciliate, apically sparsely serrate, glabrate, new rosettes of small leaves developing by flowering and persisting through winter. Lower stem leaves oblanceolate to linear oblanceolate, sessile, usually deciduous by flowering. Upper stem leaves linear, margins entire, sometimes ciliate, glabrous, somewhat falcate; branch leaves similar, reduced. Capitulescence paniculiform, few to many heads (5-120). Peduncles glabrous; bracts few, linear to narrowly lanceolate, glabrous, upper most (21)27-49(70) mm long. Involucres turbinate, 3.6-5.0(6.0) mm high. Phyllaries in 4-6 graduated series, glabrous, narrowly oblanceolate, tips spreading, margins of tip inrolled, diamond-shaped chlorophyllous zone much elongated. Rays (12)20-34(42), strap 6.8-12 mm long, 0.7-1.8 mm wide, white, very rarely pink. Disc corollas (30)40-75(103), (2.8)3.1-3.9(4.9) mm long, yellow becoming purple, somewhat ampliate, lobes (0.3)0.5-0.7(0.8) mm long. Achenes compressed obconic, 1 rib per side, glabrous to very sparsely strigose; single pappus whorl averaging 0.5 mm shorter than disc corolla. Chromosome number: 2*n* = 16.

Symphyotrichum porteri, Porter's Aster (Fig. 8), is the only western, lower montane member of subsect. *Porteriani* and is thus unlikely to be confused with other members of the subsection. It is also unlikely to be confused with any other species of *Symphyotrichum* in its range, except on a superficial level. In habit, capitulescence and indument traits, *S. porteri* is most similar to *S. pilosum* var. *pringlei*, but is distinguished by its more linear phyllaries and usually higher number of disc florets.

2. **Symphyotrichum depauperatum** (Porter) Nesom, 77: 289. 1994. *Aster ericoides* L. var. *depauperatus* Porter, Mem. Torr. Bot. Club 5: 323. 1894. Based on *Aster ericoides* L. var. *pusillus* A. Gray. *Aster depauperatus* (Porter) Fern., Rhodora 10: 94. 1908.

Aster ericoides L. var. *pusillus* A. Gray, Synop. Fl. N. Amer. 1,2: 184. 1884. *Aster parviceps* (Burgess) Mackenzie & Bush var. *pusillus* (A. Gray) Fern. in Robinson & Fern., Rhodora 11: 59. 1909. *Aster pilosus* Willd. ssp. *parviceps* (Burgess) A.G. Jones var. *pusillus* (A. Gray) A.G. Jones, Phytologia 55: 382. 1984. SYNTYPES: U.S.A. **Pennsylvania**. Lancaster Co.: barrens, 11 sept 1860, *Porter s.n.* (Holotype: GH!). "serpentine barrens," s.d., *Porter s.n.* (GH!).

Herbaceous perennials from short branched rootstocks, or from elongated rhizomes. Stems erect, 2-5 dm tall, glabrate. Basal rosette leaves oblanceolate, sessile, margins ciliate, apically sparsely serrate, sparsely pilose, new rosettes of small leaves developing by flowering and persisting through winter. Lower stem leaves narrowly to linearly oblanceolate, sessile, usually deciduous by flowering. Upper stem leaves linear, margins entire, sometimes ciliate, glabrate; branch leaves similar, reduced. Capitulescence paniculiform and sometime somewhat secund, few to many heads (11-344), often secund. Peduncles glabrous-glabrate; bracts numerous, linear, glabrous, upper most (10)13-19(2.2) mm long. Involucres narrowly campanulate, (3.2)3.4-4.0(4.3) mm high. Phyllaries in 3-5 graduated series, glabrate, oblanceolate, tips only slightly spreading, margins of tip somewhate inrolled, diamond-shaped chlorophyllous zone not much elongated. Rays 7-14, (3)3.8-5.4(6.2) mm long, 0.3-0.8(1.2) mm wide, white, very rarely pink. Disc corollas 7-17, (2.2)2.5-2.9(3.1) mm long, yellow becoming brown, somewhat ampliate, lobes 0.3-0.6(0.9) mm long. Achenes compressed obconic, 1 rib per side, sparsely to moderately strigose; single pappus whorl slightly shorter than disc corolla. Chromosome number: 2*n* = 16.

Symphyotrichum depauperatum, the Starved Aster, can be confused with short, smaller-headed plants of *S. pilosum* var. *pringlei*. The former has involucres that taper upward without a broader base (Fig. 7E) and ascending phyllaries with only slightly inrolled apical margins, while the latter has involucres broader near the base than mid portion (Fig. 9F) and more spreading phyllaries with more inrolled apical margins. In southeastern Pennsylvania and adjacent Maryland, var. *pringlei* is common, while *S. depauperatum* is very rare and apparently endemic to serpentine. In North Carolina, *S. depauperatum* is very rare and known only from three sites with diabasic rocky soil (Levy and Wilbur 1990).

Symphyotrichum depauperatum is one of only a few truly rare species of *Symphyotrichum*. It was listed as Category 2 Trend S in the U.S. Federal Register (1993 p. 51150).

Although *S. depauperatum* can occur in large populations with hundreds of plants, the total number of known extant populations is very low. Efforts to locate a number of populations sampled early in this century were unsuccessful, the sites now being covered by real estate developments of one sort or another. Even large populations are threatened because the range of the species is in such a highly populated area (Fig. 9I).

3. **Symphyotrichum parviceps** (Burgess) Nesom, Phytologia 77: 279. 1994. *Aster ericoides* L. var. *parviceps* Burgess in B. & B., 3: 379. 1898. *Aster parviceps* (Burgess) Mackenzie & Bush, Man. Fl. Jackson Co., Missouri. 196. 1902. *Aster depauperatus* (Porter) Fern. var. *parviceps* (Burgess) Fern., Rhodora 10: 94. 1908. *Aster pilosus* Willd. ssp. *parviceps* (Burgess) A.G. Jones, Phytologia 55: 381. 1984. TYPE: U.S.A. **Illinois**. Cook Co.: Englewood, 19 Sep 1879, *E.J. Hill 142/1879* (**NEOTYPE** [designated by A.G. Jones, Phytologia 55: 381. 1984]: ILL.

Aster ericoides L. var. *pusillus* A. Gray, Synop. Fl. N. Amer. 1,2: 184. 1884. *Aster parviceps* (Burgess) Mackenzie & Bush var. *pusillus* (A. Gray) Fern. in Robinson & Fern., Rhodora 11: 59. 1909. *Aster pilosus* Willd. ssp. *parviceps* (Burgess) A.G. Jones var. *pusillus* (A. Gray) A.G. Jones, Phytologia 55: 382. 1984. TYPE: U.S.A. **Pennsylvania**. Lancaster Co.: Barrens, 11 Sep 1860, *Porter s.n.* (possible **HOLOTYPE**: GH!)

Herbaceous perennials from short branched rootstocks, or from elongated rhizomes. Stems ascending to erect, 3-10 dm tall, sparsely to densely pubescent. Basal rosette leaves oblanceolate to narrowly oblanceolate, cunneate, sessile, margins ciliate, apically sparsely serrate, sparsely pilose, new rosettes of small leaves developing by flowering and persisting through winter. Lower stem leaves oblanceolate to linear oblanceolate, sessile, usually deciduous by flowering. Upper stem leaves linear oblanceolate, margins entire, ciliate, glabrate to sparsely pubescent; branch leaves similar, reduced. Capitulescence paniculiform, somewhat secund, few to many heads (6-330), usually secund. Peduncles sparsely to moderately pilose; bracts linear to narrowly lanceolate, glabrate, upper most 14-23(35) mm long. Involucres (narrowly) campanulate, (2.7)3.1-4.1(4.9) mm high. Phyllaries in 3-5 graduated series, very sparsely pubescent, oblanceolate, tips spreading, margins of tip inrolled, diamond-shaped chlorophyllous zone somewhat elongate. Rays (9)11-17(23), strap (3.7)5-5.5(7.3) mm long, 0.5-1.0(1.3) mm wide, white, very rarely pink. Disc corollas 5-16(28), (2.3)2.5-3.3(3.7) mm long, yellow becoming brown, somewhat ampliate, lobes 0.4-0.8 mm long. Achenes compressed obconic, 1 rib per side, sparsely to moderately strigose; single pappus whorl usually about as long as the disc corolla. Chromosome numbers: $2n = 16, 32$.

Symphyotrichum parviceps, the Small-headed Aster, is distinguished by its smaller narrow-involucred heads and pubescence (Fig. 10). It can be confused with smaller headed plants of *S. pilosum* var. *pilosum* with involucres with barely enlarged bases; the two taxa are sympatric (Fig. 10I and Fig. 15). Although occurring in unglaciated portions of the northern Ozark Plateau, *S. parviceps* is most common in central western Illinois and northeastern Missouri (Fig. 5A).

4. **Symphyotrichum pilosum** (Willd.) Nesom, Phytologia 77: 289. 1994. *Aster pilosus* Willd., Sp. Pl. 3: 2025. 1803. *Aster ericoides* L. var. *pilosus* (Willd.) Porter, Mem. Torr. Bot. Club 37: 323. 1894. **HOLOTYPE**: U.S.A. **Illinois**. *Richard s.n.* (B!, Schlect. No. 15857)

Herbaceous perennials from short branched rootstocks, or from elongated rhizomes. Stems ascending to erect, 2-12 dm tall, glabrate to densely pubescent. Basal rosette leaves oblanceolate, spatulate to obovate, sessile, margins ciliate, apically sparsely serrate, glabrous to sparsely pilose, new rosettes of small leaves developing by flowering and persisting through winter. Lower stem leaves oblanceolate to linear oblanceolate, cunneate, sessile, usually deciduous by flowering. Upper stem leaves linear to oblanceolate, margins entire, sometimes ciliate, glabrate to densely pubescent; branch leaves similar, reduced. Capitulescence paniculiform, sometime pyramidal and secund, rarely racemiform, few to many heads (8 to >300), sometimes secund. Peduncles glabrous to densely hispid; bracts linear to narrowly lanceolate, glabrous, (15)20-55(70) mm long. Involucres turbinate, (2.5)3.5-5.1(6.5) mm high. Phyllaries in 4-6 graduated series, glabrate to very sparsely pubescent, oblanceolate, tips spreading, margins of tip inrolled, diamond-shaped chlorophyllous zone elongate. Rays (10)16-28(38), strap (4.0)5.4-7.5(11) mm long, (0.4)0.8-1.3(1.7) mm wide, white, very rarely pink or pale blue. Disc corollas (13)17-39(67), (2.5)3.0-4.1(5.5) mm long, yellow becoming purple or brown, somewhat ampliate, lobes (0.4)0.6-0.8(1.0) mm long. Achenes compressed obconic, 1-2 ribs per side, sparsely to moderately strigose; single pappus whorl usually shorter than disc corolla. Chromosome numbers: $2\underline{n}$ = 32, 40, 48; many populations sampled throughout range.

Symphyotrichum pilosum is the common Old Field Aster of much of the eastern USA. Two varieties are distinguished on the basis of indument: var. *pilosum* is pubescent, var. *pringlei* is glabrous to only very sparsely pubescent. Throughout the range where var. *pringlei* and var. *pilosum* are sympatric (Figs. 14-15), putative hybrids between var. *pringlei* and var. *pilosum* have been collected. These are either pentaploid ($2n$ = 40) or hexaploid ($2n$ = 48) depending upon the ploidy level of the var. *pilosum* parent, and they are sparsely to moderately pubescent. When the indument of the two parents is very different, then hybrids are readily recognizable. The common name White Heath Aster was first taken up when the taxon was incorrectly given the name *Aster ericoides* (sensu auct. non L.).

4a. **Symphotrichum pilosum** Willd. var. **pilosum**

?*Aster ramosissimus* Mill., Gard. Dict. ed. 8. no. 21. 1783. TYPE: not seen.

Aster villosus Michx., Fl. Bor. Amer. 2: 113. 1803. non Thunb. (1800). *Aster ericoides* L. var. *villosus* (Michx.) Torr. & Gray, Fl. N. Amer. 2: 124. 1841. **Holotype**/lectotype: "in pratis Illinoensibus." (P, seen on microfische).

Aster polyphyllus Willd., Enum. hort. Berol. 2: 888. 1809. **LECTOTYPE** (Jones and Hiepko, Willdenowia 11: 349. 1981): Sch. No. 15930 B!). The stems are sparsely pubescent. The LT may be a hybrid with var. *pringlei* or *Symphotrichum lanceolatum*.

?*Aster glabellus* Nees (attributed to Michx.), Syn. Aster. 31. 1818. non Lindl. in Hook. (1835) -- TYPE: not seen

?*Aster glabellus* Lindl. in Hook, Comp. Bot. Mag. 1: 97. 1835. non Nees (1818). **HOLOTYPE**: U.S.A. **Missouri**. St. Louis, *Boott s.n.* (not seen).

Aster ericoides L. γ *platyphyllus* Torr. & Gray, Fl. N. Amer. 2: 124. 1841. *Aster pilosus* Willd. var. *platyphyllus* (Torr. & Gray) Blake, Rhodora 32: 139. 1930. SYNTYPES: Indiana, *Dr. Clapp*, not seen), N. Carolina, *Schweinitz* (PH!). *Mr. Curtis* (**LECTOTYPO**, (designated here): NY!.

Aster juniperinus Burgess in Small, Fl. S.E.U.S. 1225, 1340. 1903. **HOLOTYPE**: Alabama. Choctaw Co.: Cocoa, 13 Oct 1896, *Schuchert s.n.* NY!) [Probably just a growth form of var. *pilosum*; stem horizontal allowing lateral branches of the capitulescence to elongate in a secund manner.]

Aster faxoni Porter, Mem. Torr. Bot. Club 37: 138-139. 1910. New name for *A. polyphyllus* Willd.

Aster pilosus Willd. f. *pulchellus* Benke, Rhodora 34: 11. 1932. **HOLOTYPE**: U.S.A. **Indiana**. Porter Co.: Valparaiso, 17 Sep 1929, *Benke 5083* F!; isotype: NY!)

The typical variety of *Symphyotrichum pilosum* (Fig. 11) is the most widely distributed taxon of the subsection (Fig. 14). Tetraploids and hexaploids (and hybrid pentaploids) are known and are allopatric over much of their respective ranges (Semple 1978; Semple & Chmielewski 1985; Chmielewski & Semple 1989). The range of habitats in which var. *pilosum* occurs and the plastic nature of its phenotype account for the much of the range in morphological variation included in the variety. The tallest plants in the wild will produce very short shoots under less favorable growing conditions. The leaf width to length ratio is influenced by growing conditions, but there appears to be a genetic component to this trait such that very broad leaved plants do not produce linear leaves. Rays are normally white, but can be pinkish under some conditions. The capitulescence can be somewhat to obviously conical in form with the apex leaning to one side (Fig. 11A) and rarely even wand or narrowly club shaped. Few-headed plants can be racemiform (Fig. 11B). This kind of variation does not warrant even the rank of *forma*.

4b. **Symphyotrichum pilosum** (Willd.) Nesom var. **pringlei** (A. Gray) Nesom, Phytologia 77: 289. 1994.

Aster pringlei A. Gray, Proc. Amer. Acad. 16: 99. 1880. nom. nud. *Aster ericoides* L. var. *pringlei* A. Gray, Synop. Fl. N. Amer. 1, 2: 184. 1884. *Aster pringlei* (A. Gray) Britt. in B. & B. Ill. Fl. 3: 379. 1898. *Aster pilosus* Willd. var. *pringlei* (Gray) Blake, Rhodora 32: 140. 1930. **LECTOTYPE**: Headlands of Lake Champlain, 3 Sep 1879, *Pringle s.n.* ([Almut Jones 1983 on sheet, not sheet marked as probable holotype by JCS'77]: GH. **ISOLECTOTYPE**: GH!(2), US!. Rocks of Gull Island, Lake Champlain, 10 Jul 1877, *Pringle 6a* (GH!, marked as probable holotype by JCS'77). **SYNTYPES**; Rocky headlands of Lake Champlain, Shelborne, Vt., 16 Oct. 1878, *Pringle 6b* (GH!).

Aster ericoides L. var. *randii* Britt. in B. & B. Ill. Fl. 3: 379. 1898. **LECTOTYPE** designated on sheet by J.C. Semple 1997 and here: **Maine**. Mt. Desert Island, 1 Sep 1892, *Rand s.n.* NY!, 2 Sep 1892, *Rand s.n*. (NY!)

Aster pilosus Willd. var. *demotus* Blake, Rhodora 32: 139. 1930. **HOLOTYPE**: U.S.A. **Virginia**. Princess Anne Co.: near Virginia Beach, 1 Oct 1898, *Kearney 2059* US-356711!

Pringle's Aster, *Symphyotrichum pilosum* var. *pringlei*, is readily distinguished from typical var. *pilosum* by its hairless to nearly hairless stems and leaves (Figs. 12). In the extreme, its heads are slightly smaller and have fewer florets; this may be due to the harsher environments it sometimes inhabits, e.g., seasonally very dry limestone pavements and shale outcrops and slopes. Smaller-headed plants can be mistaken for *S. depauperatum*.

Semple and Chmielewski (1985) presented data on the growth and development of individuals of var. *pringlei* that indicated that stem height was a highly plastic trait, and therefore should not be used to separate the taxon into two varieties. Thus, the often recognized taxon var. *demotus* was placed in synonymy. The name var. *demotus* has been applied to sparsely pubescent stemmed plants of var. *pilosum* as well occurring throughout the range of the latter.

5. **Symphyotrichum kentuckiense** (Britt.) Medley, Phytoneuron 2021-18: 2. 2021. *Aster kentuckiensis* Britt., Man. 960. 1901. **HOLOTYPE**: U.S.A. **Kentucky**. near Bowling Green, Oct 1898, *Price 4* NY!

Herbaceous perennials from short-branched rootstocks. Stems decumbent to ascending, sometimes erect, 3-10 dm tall, glabrous. Basal rosette leaves oblanceolate to obovate, sessile, margins ciliate, apically sparsely serrate, glabrate, new rosettes of small leaves developing by flowering and persisting through winter. Lower stem leaves oblanceolate to linear oblanceolate, sessile, usually deciduous by flowering. Upper stem leaves linear lanceolate, margins entire, glabrous, sometimes trinervate; branch leaves similar, reduced, often present as fascicles along much of the stem. Inflorescence racemiform or paniculiform, few to many heads (7-185), sometimes secund. Peduncles glabrous, elongate extensions of lateral branches; bracts linear to linear-lanceolate, glabrous, upper most (20)42-70 mm long. Involucres turbinate, (4.5)5.5-7.1(8.5) mm high. Phyllaries in 4-6 series, the outer nearly equal to the inner in length, glabrous, lanceolate to oblanceolate, tips spreading attenuate, margins of tip inrolled, diamond-shaped chlorophyllous zone elongate. Rays (13)20-28(34), strap 8.0-11.6(15.2) mm long, (0.7)0.9-1.5(1.9) mm wide, blue-violet to rarely white. Disc corollas (28)33-51(68), 3.4-4.6(5.5) mm long, yellow becoming purple, somewhat ampliate, lobes 0.5-1.0 mm long. Achenes compressed obconic, 1-2 ribs per side, sparsely strigose; single pappus whorl usually 0.3-0.4 mm shorter than disc corolla. Chromosome number: $2n = 64$; erroneously reported as $2n = 32$.

Symphyotrichum kentuckiense, Price's Aster or Kentucky Aster, is similar to *S. pilosum* var. *pringlei* in indument, but has a distinctive growth form (Fig. 13A) and has larger heads (Fig. 13E). In some plants the lower primary branches are long and bear raceme-like capitulescences. In many plants, most primary lateral branches do not elongate and consist of a number of linear, sometimes triple-nerved, leaves forming fascicules along the stem (Fig. 13A). Also distinctive for the subsection are the rather attenuate, long outer phyllaries (Fig. 13F); mid and inner series phyllaries are typical for the subsection (Figs. 13G-H). The color of the stems and leaves can be somewhat anthocyanotic giving the shoot a slightly bluish-green hue in more pigmented plants. *Symphyotrichum kentuckiense* is the only taxon in the subsection typically to have blue-violet rather than white rays. However, because otherwise similar white-rayed forms occur and because other taxa can have pinkish-blue rays, color cannot be used as the sole diagnostic trait.

Symphyotrichum kentuckiense occurs on broken limestone pavements of some cedar glades in Tennessee and northern Alabama (R. Kral, pers. comm.) but does not appear to be a strictly cedar glade endemic based on our field observations. It occurs in very disturbed sites in broken limestone by roadsides in Tennessee, as well as less disturbed sites. Populations can be large with hundreds of individuals.

Symphyotrichum kentuckiense blooms slightly earlier than *S. pilosum* var. *pilosum*, based on field and herbarium sheet data. This is similar to the situation in Ontario where *S. pilosum* var. *pringlei* blooms slightly earlier than var. *pilosum*. It is generally the case in asters, goldenasters and goldenrods that diploids bloom earlier than polyploids. For example, diploid *S. parviceps* blooms earlier than sympatric hexaploid *S. pilosum* var. *pilosum*. Thus, the earlier blooming time for the octoploid *S. priceae* is noteworthy.

6. Symphyotrichum × priceae (Britt.) Nesom (pro sp.), Phytologia 77: 290. 1994. *Aster priceae* Britt., Man. 960. 1901. *Aster pilosus* Willd. var. *priceae* (Britt.) Cronq., Rhodora 50:28. 1948. **HOLOTYPE**: U.S.A. **Kentucky**. Near Bowling Green, Oct 1898, *Price 8 (*NY!).

We accept Medley’s (2021) conclusion that the type material of *Aster priceae* Britt. consists of somewhat hairy stemmed hybrids between *S. kentuckiense* and *S. pilosum* var. *pilosum*.

Possible hybrid

Aster pilosus Willd. var. **× reevesii** (A. Gray) Blake (pro var.), Rhodora 32: 140. 1930. *Aster ericoides* L. var. *reevesii* A. Gray, Synop. Fl. N. Amer. 1, 2: 184. 1884. **HOLOTYPE**: U.S.A. **Tennessee**. near Nashville, dry river banks, *Curtiss 1279* (GH!)

Aster reevesii hort., A. Gray, Synop. Fl. N. Amer. 1, 2: 184. 1884. in syn. = *Symphyotrichm pilosum* var. *pilosum* × *S. priceae*

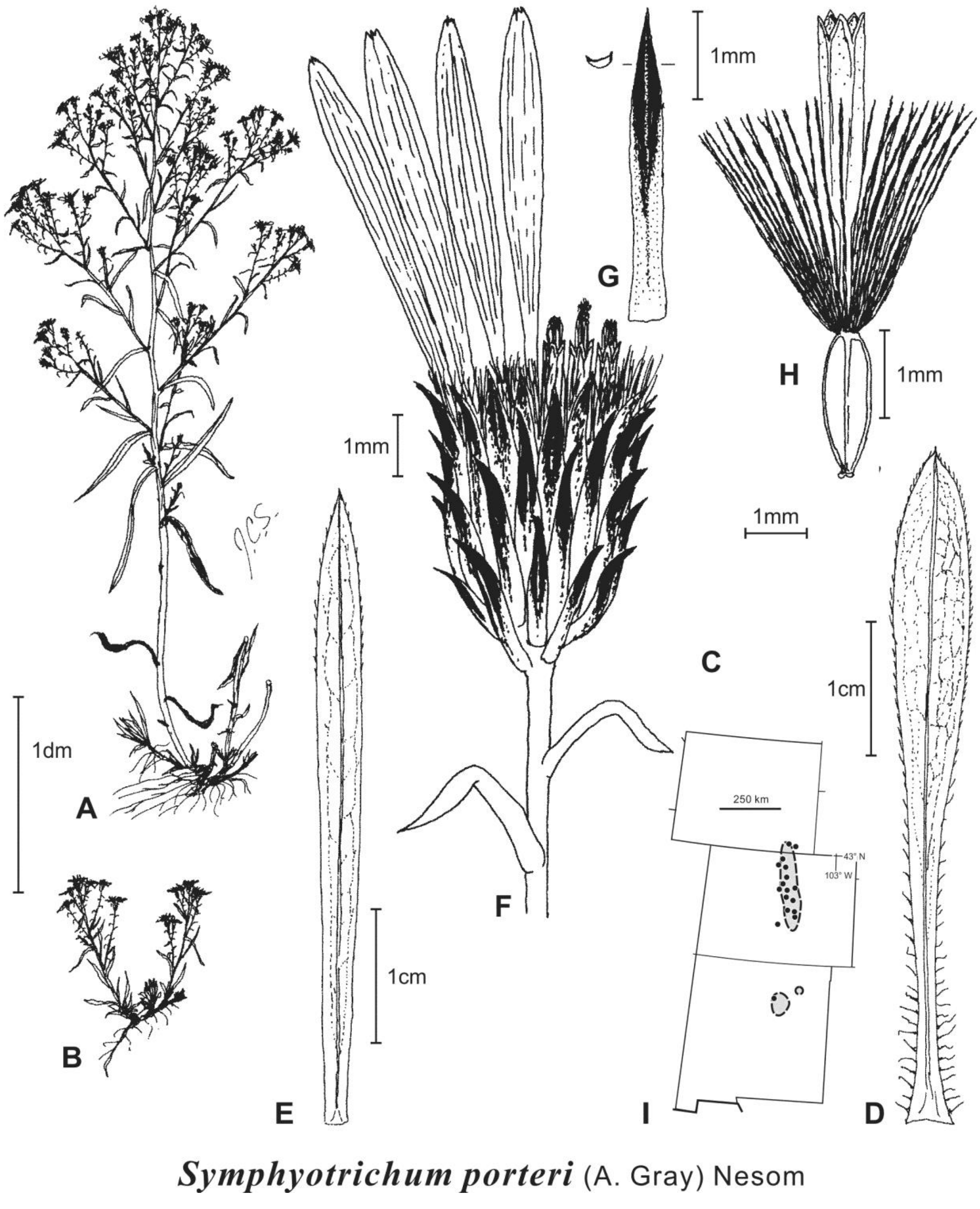


Figure 8. Morphology of *Symphyotrichum porteri*. **A-B.** Habits of mid-size and small shoots. **C.** Mid stem. **D.** Small outer basal rosette leaf. **E.** Mid stem leaf; surface hairs not illustrated. **F.** Head with only some florets drawn, diploid. **G.** Mid series phyllary; chlorophyllous zone dark. **H.** Mature cypsela with disc floret attached, diploid. **I.** Range map in WY, CO, and NM and locations of samples used in analyses.

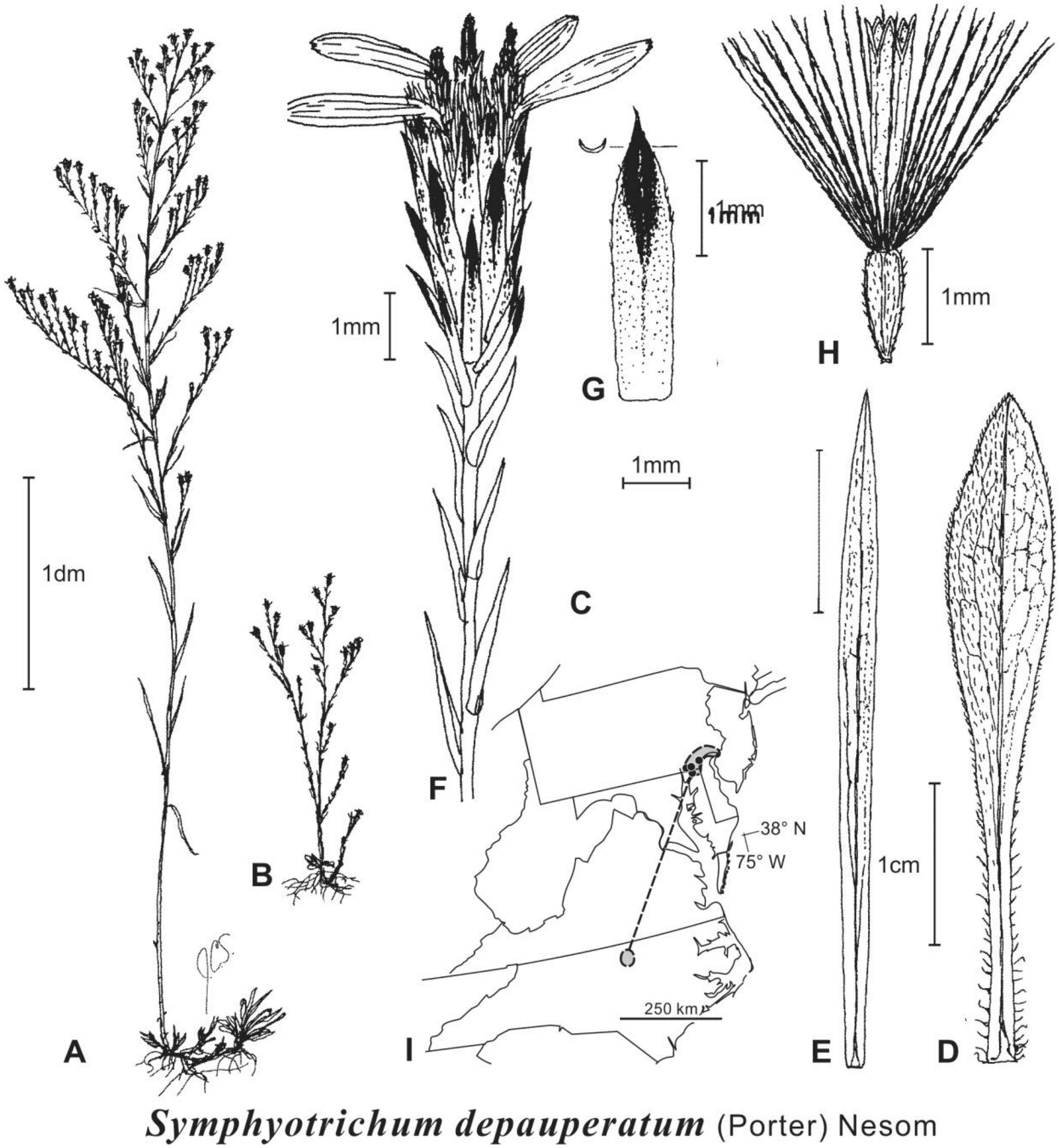


Figure 9. Morphology of *Symphyotrichum depauperatum*. **A-B.** Habits of mid-size and small shoots. **C.** Mid stem. **D.** Small outer basal rosette leaf. **E.** Mid stem leaf; surface hairs not illustrated. **F.** Head with only some florets drawn, tetraploid. **G.** Mid series phyllary; chlorophyllous zone dark. **H.** Mature cypselae with disc floret attached, diploid. **I.** Range map in PA, MD, and NC and locations of samples used in multivariate analyses.

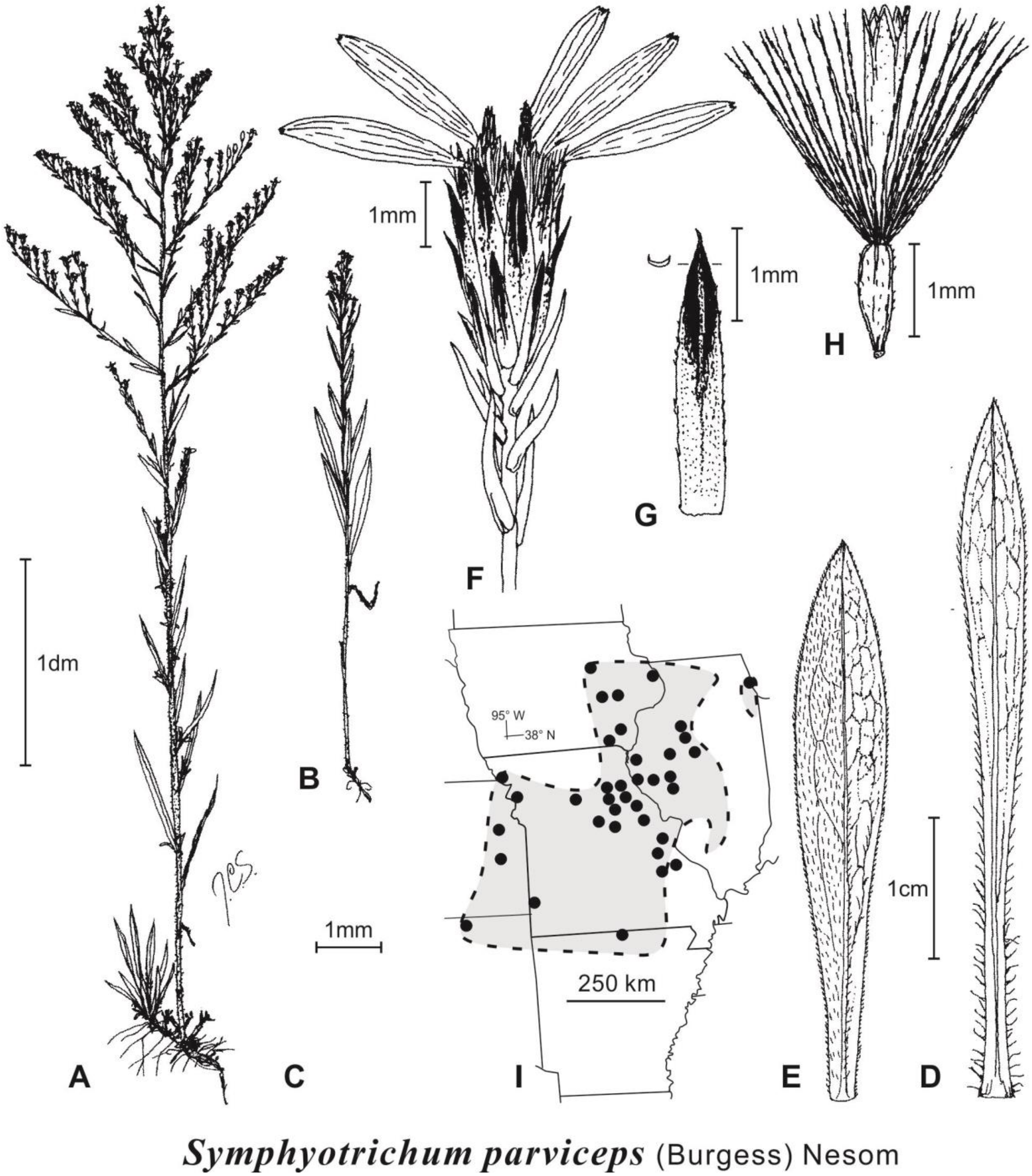


Figure 10. Morphology of *Symphyotrichum parviceps*. **A-B.** Habits of mid-size and small shoots. **C.** Mid stem. **D.** Small outer basal rosette leaf. **E.** Mid stem leaf; surface hairs not illustrated**. F.** Head with only some florets drawn, diploid. **G.** Mid series phyllary; chlorophyllous zone dark. **H.** Mature cypsela with disc floret attached, diploid. **I.** Range map in IA, IL, MO, OK, and AR and locations of samples used in multivariate analyses.

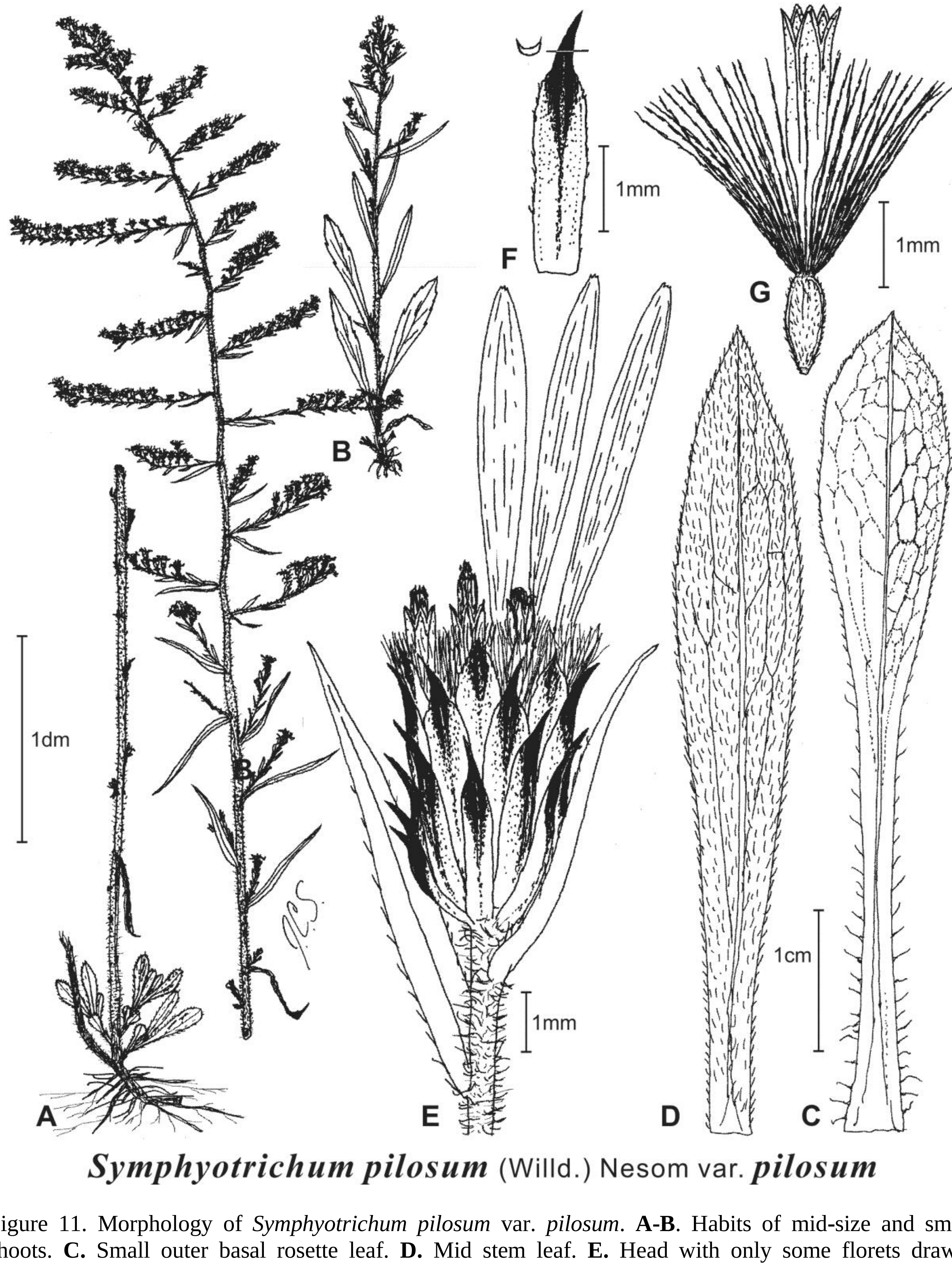
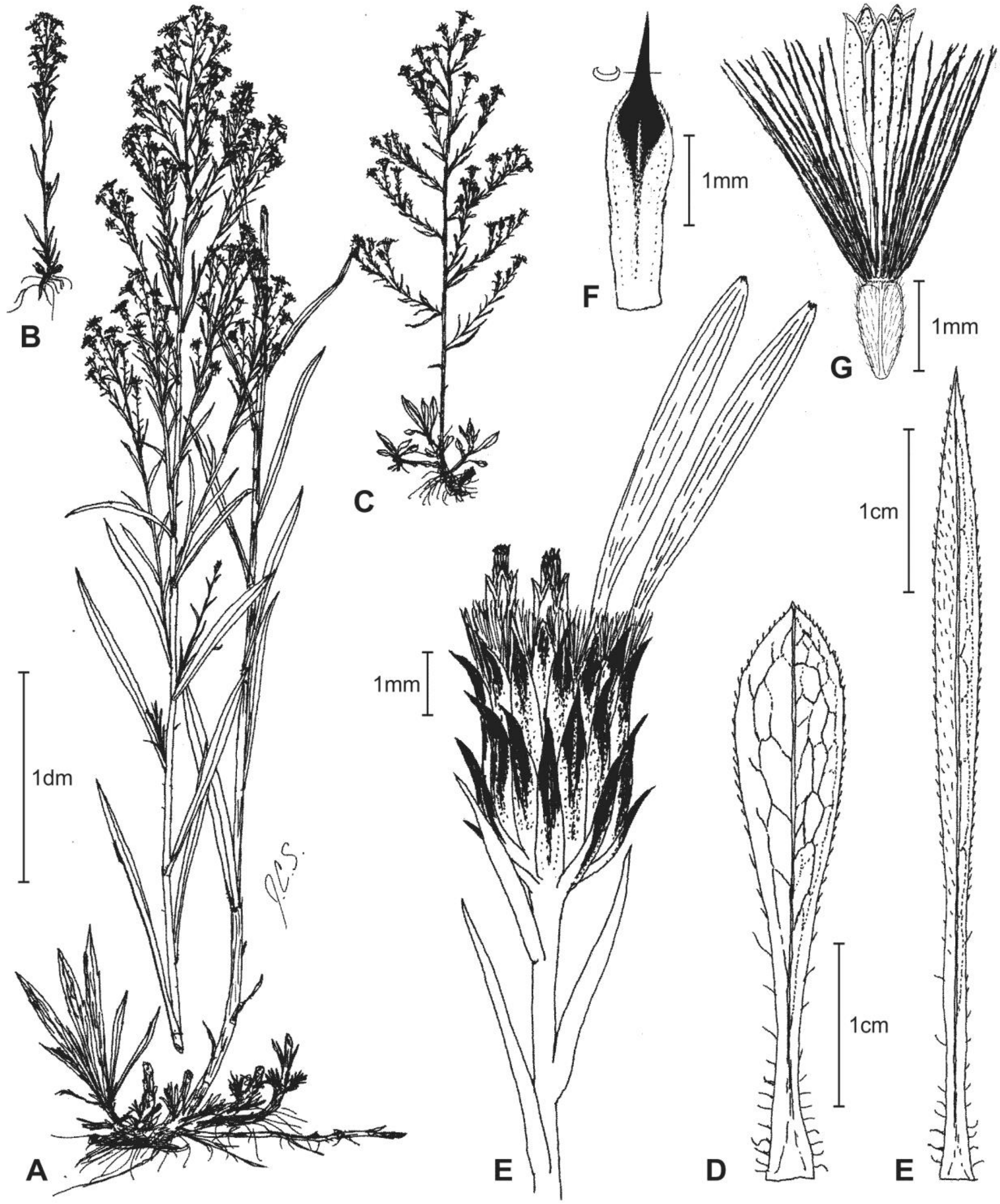


Figure 11. Morphology of *Symphyotrichum pilosum* var. *pilosum*. **A-B**. Habits of mid-size and small shoots. **C.** Small outer basal rosette leaf. **D.** Mid stem leaf. **E.** Head with only some florets drawn, hexaploid. **F.** Mid series phyllary; chlorophyllous zone dark. **G.** Mature cypsela with disc floret attached, tetraploid.



Symphyotrichum pilosum var. ***pringlei*** (A. Gray) Nesom

Figure 12. Morphology of Symphyotrichum *pilosum* var. *pringlei*. A-B. Habits of mid-size and small shoots. **C.** Small outer basal rosette leaf. **D.** Mid stem leaf. **E.** Head with only some florets drawn, hexaploid. **F.** Mid series phyllary; chlorophyllous zone dark. **G.** Mature cypsela with disc floret attached, tetraploid.

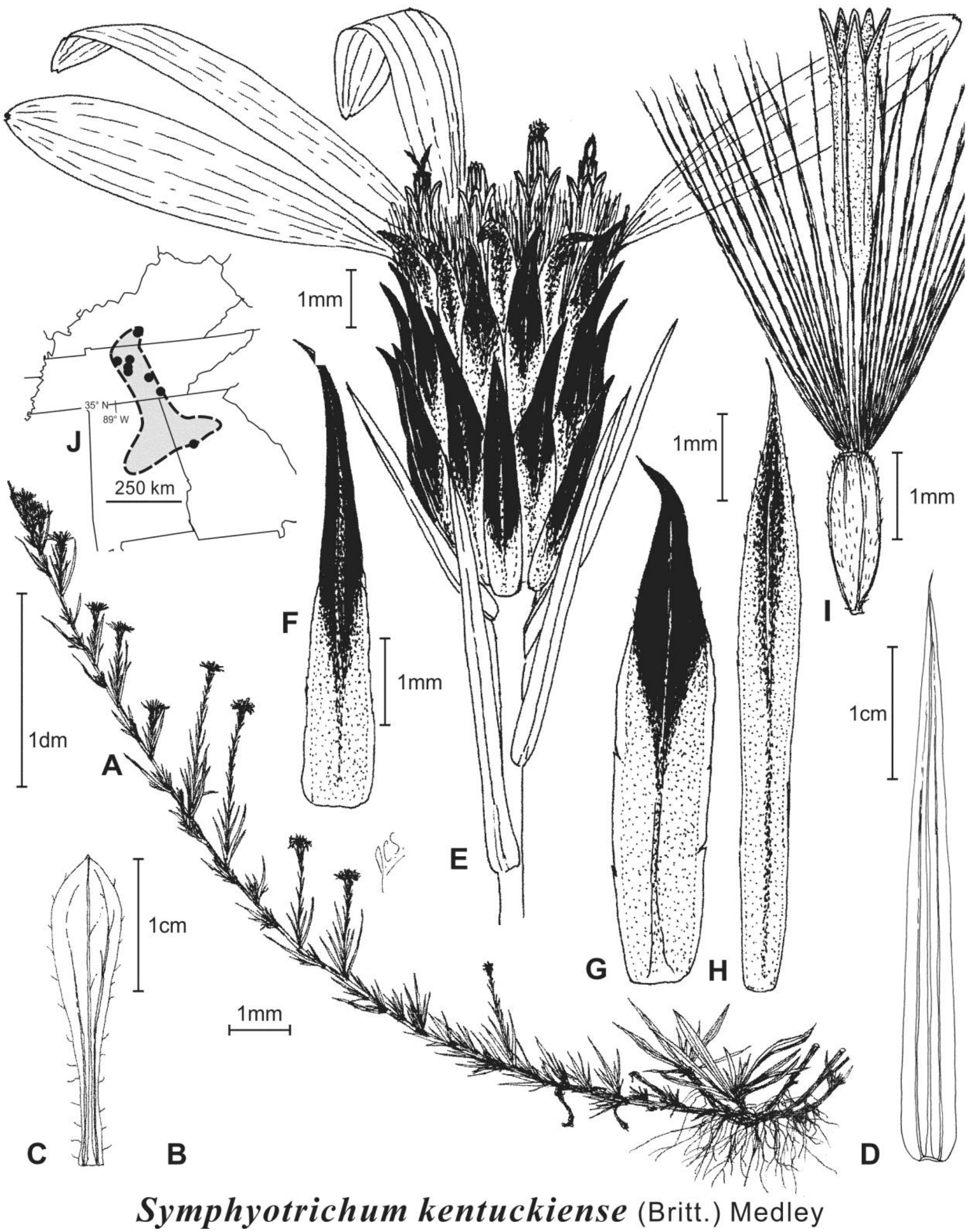


Figure 13. Morphology of *Symphyotrichum kentuckiense*. **A.** Habit of mid-size shoot. **B.** Mid stem. **C.** Small outer basal rosette leaf. **D.** Mid stem leaf; surface hairs not illustrated. **E.** Head with only some florets drawn, diploid. **F-H.** Outer, mid, and inner series phyllares; chlorophyllous zone dark. **I.** Mature cypsela with disc floret attached, hexaploid. **J.** Range map and locations of samples used in multivariate analyses.

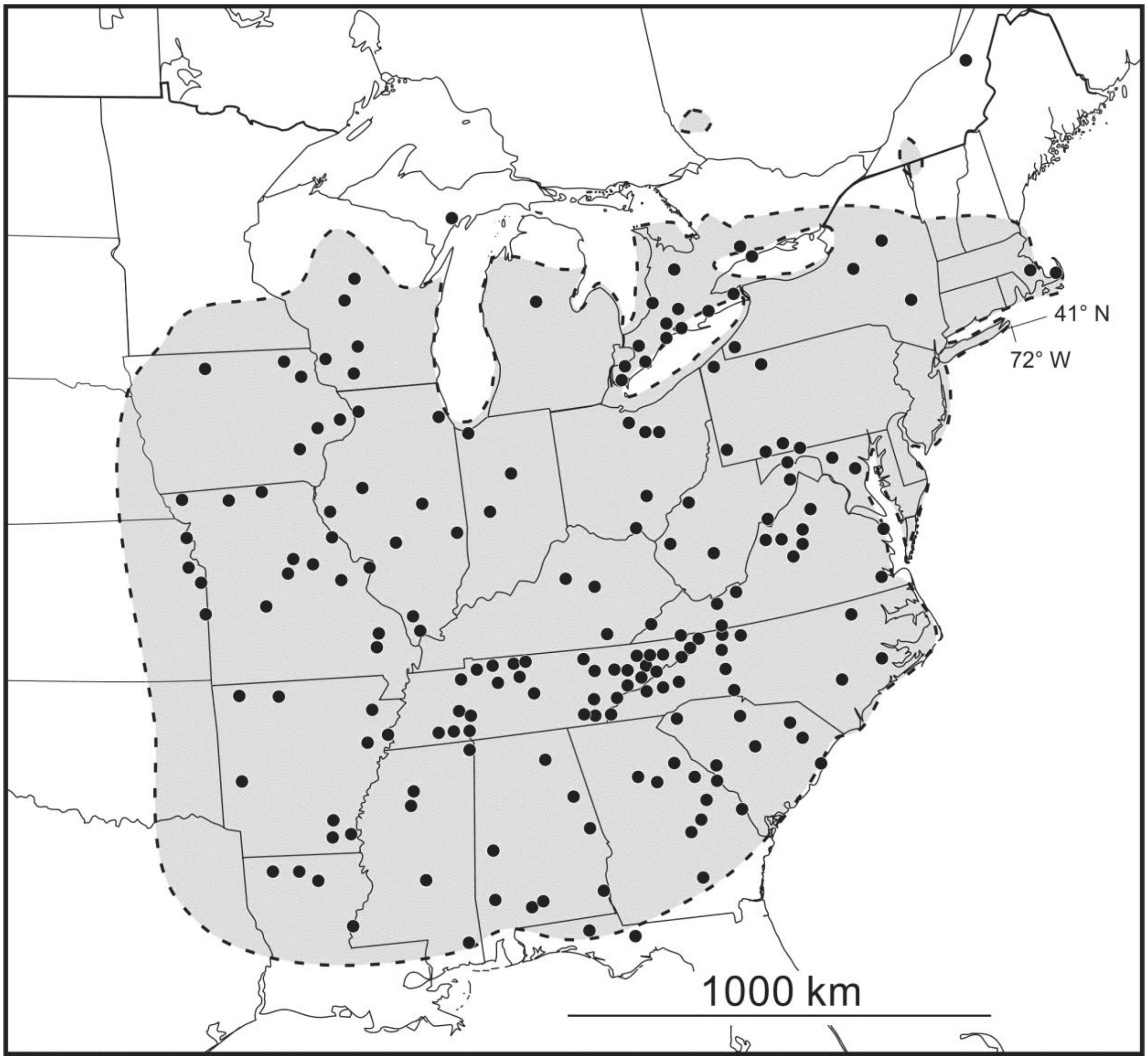


Figure 14. Distribution of scored samples of *Symphyotrichum pilosum* var. *pilosum* and range of variety in the eastern United States and adjacent Canada.

Figure 15. Distribution of scored samples of *Symphyotrichum pilosum* var. *pringlei* and range of variety in the eastern United States and adjacent Canada. See text for comments on the Alabama and Kentucky specimens.

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