A MULTIVARIATE STUDY OF THE SOLIDAGO STRICTA COMPLEX (ASTERACEAE: ASTEREAE: SOLIDAGO SUBSECT. MARITIMAE)

JOHN C. SEMPLE, TROINA SHEA¹, MAMOOD EL-SWESI, HAMMAD RAHMAN, AND YUNFEI MA

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

¹Present address: CH2M, Calgary, Alberta, Canada

ABSTRACT

A multivariate morphometric study of the *Solidago stricta* complex of *S. subsect. Maritimae* was performed to assess statistical support for recognizing *S. austrina*, *S. chrysopsis*, *S. gracillima*, *S. pulchra*, *S. stricta*, and *S. virgata* as separate species. Ten analyses were run and discussed.

Solidago subsect. Maritimae (Torr. & Gray) G.L. Nesom includes all the bog and marsh goldenrod species with sheathing proximal basal rosette and lower stem leaves. The Solidago stricta Ait. complex includes six of the more inland or at least non-salt marsh inhabiting species native to the inner and outer coastal plains and southern piedmont regions of the eastern U.S.A. (Semple 2016 frequently updated; Semple et al. 2016): *S. austrina* J.K. Small (Fig. 1) native to wetter soils on the piedmont generally at 50 m elevation or higher; *S. chrysopsis* J.K. Small of South Florida and the keys (Fig. 2); *S. gracillima* Torrey & A. Gray (Fig. 3) native to the inner coastal plain and outer piedmont in habitats that may be rather wet in the spring but tend to be much drier in the summer and earlier fall; *S. pulchra* J.K. Small (Fig. 4) native to outer coastal plain boggy ground with *Sphagnum* in southeastern North Carolina; *S. stricta* Ait. (sensu stricto, not of authors; Figs. 5-6) native to moist argillaceous sand soils in eastern Virginia and the pine barons of southern New Jersey and disjunct in a few locations further south; and *S. virgata* Michx. (Fig. 7) native to the coastal plain at 5-40 m elevation from eastern North Carolina to Louisiana. The ranges of all six species are illustrated in Fig. 8.

Floristic treatments of the Solidago stricta complex have varied considerably during the past century and a half. Torrey and A. Gray (1841) misapplied the name S. stricta to the northern bog goldenrod S. uliginosa Nutt. and treated the southern species as S. virgata. In his large report on chromosome numbers in Solidago, Beaudry (1963) noted that S. stricta was "probably an aggregate of more than one species." Cronquist (1968) recognized the north species as S. uliginosa (stems usually hairy in the inflorescence), lumped several species into his S. stricta (stems usually glabrous in the inflorescence; rhizomatous) occurring from the Atlantic coastal plain of New Jersey to Texas, and separated out S. austrina as lacking rhizomes and occurring from Virginia to Georgia. Cronquist (1980) further divided his S. stricta into three species: S. stricta with long slender, stoloniferous rhizomes, S. *pulchra* without the rhizomes and with few heads (5-25) with many florets, and S. gracillima with many heads (more than 20) and fewer florets; he also stated that some S. uliginosa in North Carolina was transitional with S. gracillima (S. simulans Fernald treated as a synonym). Cronquist (1980) placed S. austrina, S. flavovirens Chapman, and S. perlonga Fern. in synonymy under his S. stricta. Semple and Cook (2006) followed Cronquist (1980) in recognizing S. pulchra but included S. gracillima in S. stricta as a subspecies (and S. austrina, and S. perlonga as synonyms of the subspecies); and they listed Solidago chrysopsis Small; S. flavovirens Chapman; S. stricta var. angustifolia (Elliott) A. Gray as synonyms of subsp. stricta. Based on multiple field trips after Flora North America was published, Semple (2012) selected a lectotype for S. gracillima, thereby restricting the species to plants of the complex with a few long to very long lower inflorescence branches, as is done here; he recognized S. austrina as a piedmont species with inflorescences with many branches that graded from short to distally short to proximately



Figure 1. Example of *Solidago austrina* used in the multivariate study: *Semple et al.* 11857 (WAT, unmounted when digital photograph was taken).



Figure 2. Example of *Solidago chrysopsis* used in the multivariate study: *Daggy 5943* (UNCC); note the very linear basal stem leaves.



Figure 3. Example of Solidago gracillima used in the multivariate study: Clewell s.n. (FSU).



Figure 4. Example of *Solidago pulchra* used in the multivariate study: *Taggart 101* (NCU), tip of inflorescence damaged resulting in lateral branch elongation lower on stem; color insert of heads in field, voucher is *Semple & Suripto 9755* (WAT).



Figure 5. Example of Solidago stricta used in the multivariate study, large shoot: Semple 11824 (WAT).



Figure 6. Examples of *Solidago stricta* used in the multivariate study: *Semple 11824* (WAT), small shoot; insert: lower stem leaves, *Semple 11575* (WAT), large shoot, scale bar = 1 cm.



Figure 7. Examples of *Solidago virgata* used in the multivariate study: *Semple 10917* (WAT), secund arrangement of heads due to stem leaning over rather than growing strictly erect; insert: lower stem leaves *Huck 1544* (NCU).



Figure 8. Distribution of the ranges and locations of multivariate samples of the species of the *Solidago stricta* complex (*Solidago subsect. Maritimae*): *S. austrina* (red dots), *S. chrysopsis* (white stars in insert), *S. gracillima* (light brown +s in insert), *S. pulchra* (yellow triangles), *S. stricta* (gray diamonds), *and S. virgata* (white dots).

mid length with the longest spreading and arching; he restricted *S. stricta* to outer coastal plain plants with short inflorescence branches regardless of the inflorescence size; and he recognized the Atlantic coastal plain plants of Virginia and New Jersey as *S. perlonga*, whose robust inflorescences had lower stem branches that were proximally ascending and diverging gradually away from the main axis of the inflorescence. After seeing an image of the holotype of *S. stricta*, Semple (2013) noted that the name had been misapplied to the southern race, which should be correctly labeled *S. virgata*, and that the name *S. stricta* was correctly applied to just the plants he treated as *S. perlonga* in 2012. In 2014, the first author examined the holotype of *S. stricta* at the British Museum of Natural History and confirmed his 2013 conclusion about the proper application of the name. In summary, the nomenclatural confusion about how to apply the name *S. stricta*, has been a problem for many decades and has required a combination of field observations of many populations over multiple decades, the accumulation of a large data base on chromosome number variation within the complex, and radical rethinking of how to treat the multiple ecologically distinct races occurring within the complex. Fernald's (1950) treatment of the complex would have been a better place to start than with Cronquist (1968, 1980), but Gray's Manual (8th edition) only covered the more northern members of the complex.

Semple et al. (2016) reported the results of a multivariate study of the *Solidago sempervirens* complex that includes five species. *Solidago azorica* Hochstetter ex Seubert is native in the Azores and introduced in the Bahamas and Bermuda. *Solidago mexicana* L. and *S. sempervirens* L. are native to salt marshes and coasts from Newfoundland, Canada to Tabasco, Mexico. *Solidago maya* Semple is native to wetter soils in the mountains of Chiapas, Mexico and the Maya Mountains of eastern Guatemala and western and central Belize. *Solidago paniculata* DC. is native to central Mexico in wetter areas of the Mexico City region (possibly extinct) and eastern Michoacán. Specimens of *S. maya* and eastern diploid *S. mexicana* can be similar to *S. virgata* and are included in one analysis in the study reported below.

Cytological sampling of the six species of the *Solidago stricta* complex ranges from just one known chromosome count to dozens of counts for a species. *Solidago chrysopsis* and *S. gracillima* are only known at the diploid level (2n = 18; Beaudry 1963; Semple et al. 1993; unpublished data). *Solidago pulchra* is only known at the tetraploid level (2n = 36; Semple et al. 1993; unpublished data). *Solidago stricta* is only known at the hexaploid level (2n = 54; Beaudry 1963; unpublished data). *Solidago austrina* is known at the diploid level in the eastern and southern parts of its range and at the tetraploid level in South Carolina, northern Alabama and southcentral Tennessee (2n = 18 and 2n = 36; unpublished data). *Solidago virgata* is known at the diploid, tetraploid and hexaploid levels (2n = 18, 2n = 36, and 2n = 54; usually reported as *S. stricta*; Beaudry 1963, 1969; Semple et al. 1981, 1984, 1993; Semple and Cook, 2004; unpublished data). A manuscript on the cytogeography of all species in *S. subsect. Maritimae* is in preparation by J.C. Semple and R.E. Cook and will include details on the unpublished counts noted here.

A multivariate morphometric analysis of the *Solidago stricta* complex has not been previously published. Specimens of *S. virgata* were included in Semple et al. (2016). The study presented here was designed to statistically explore the following questions: (1) Overall, into how many species can the *S. stricta* complex be usefully divided? (2) What traits best separate these species? (3) What are the consequences of including small shoots with small inflorescences in the analyses? (4) How well do habitat preferences and ranges fit with the morphologically defined species?

MATERIALS AND METHODS

In total, 211 specimens selected from a much larger number of specimens of *Solidago* subsect. *Maritimae* from BRIT, F, FLAS, FSU, GH, J.K.Morton in ROM, KY, LL, MO, MT, NCU, NY, TEX, UNCC, USCH, USF, and WAT in MT (Thiers, continuously updated) were scored and included in this study. Data were scored on *S. austrina* (41 specimens; Fig. 1), *S. chrysopsis* (19 specimens; Fig. 2), *S. gracillima* 18 specimens; Fig. 3), *S. pulchra* (15 specimens; Fig. 4), *S. stricta* (34 specimens; Figs. 5-6), and *S. virgata* (30 specimens; Fig. 7) of the *S. stricta* complex and *S. maya* (9 specimens; see Semple

2018 for illustrations) and eastern and western populations of *S. mexicana* (29 and 16 specimens respectively) of the *S. sempervirens* complex. Ranges of species in the *S. stricta* complex are shown in Fig. 8 along with the locations of samples included in a priori groups the multivariate analyses. Nineteen vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait.

Traits used to define a priori groups were not included in the analyses to avoid circular logic. Differences in general inflorescence shape and branching characteristics were used to define a priori groups along with geographic location. Basal rosette and lower stem leaf traits were not included in the analyses because these were often not present on specimens. The numbers of longer branches in the inflorescence and their proximal angle of ascent and distal amount of outward curvature were used in defining a priori groups and were not included in the matrix in the discriminant analyses.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology are presented in Semple et al. (2016) and are not repeated here. Ten analyses were performed. In the first analysis, nine putative species level a priori were included: *Solidago austrina, S. chrysopsis, S. gracillima, S. maya*, eastern populations of *S. mexicana*, western populations of *S. mexicana, S. pulchra, S. stricta*, and *S. virgata*. In the second analysis, six species level a priori groups were included: *S. austrina, S. chrysopsis, S. gracillima* was excluded and only five species were included: *S. austrina, S. chrysopsis, S. pulchra, S. stricta*, and *S. virgata*. In the fouth analysis, four species were included: *S. austrina, S. chrysopsis, S. pulchra, S. stricta*, and *S. virgata*. In the fifth analysis, *S. austrina, S. chrysopsis*, and *S. virgata* were included. In the sixth analysis only *S. austrina* and *S. virgata* were included. In the seventh analysis only *S. stricta* and *S. virgata* were included. In the eighth analysis only *S. chrysopsis* and *S. virgata* were included. In the nineth analysis only *S. pulchra* and *S. virgata* were included. In the tenth analysis only *S. mexicana* and *S. virgata* were included. In the tenth analysis only *S. mexicana* and *S. virgata* were included.

RESULTS

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to either mid leaf or upper leaf length, upper leaf width, and usually either mid leaf or upper serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses. Ray floret lamina length sometimes correlated with involucre height and usually was not included in the STEPWISE analyses. Ray floret pappus length at anthesis usually correlated with disc floret pappus length and only the latter trait was included in STEPWISE analyses. Inflorescence length and width traits were generally used in defining a priori groups and were not included in the analyses.

Nine species groups analysis

In the STEPWISE discriminant analysis of nine putative species level a priori groups *Solidago austrina, S. chrysopsis, S. gracillima, S. pulchra, S. stricta,* and *S. virgata* of the *S. stricta* complex and *S. maya* and eastern and western populations of *S. mexicana* of the *S. sempervirens* complex, the following seven traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (15.06), number of disc florets (12.57), number of rays florets (12.42), upper leaf length (11.46), mid series phyllary width (7.91), number of nodes in distal 25% of the stem below the inflorescence (5.79), and involucre height (4.51). 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 3. F-values based on Mahalanobis distances between group centroids in N dimensional hyperspace indicated the largest separations were between eastern *S. mexicana* and *S. pulchra* (25.088), *S. gracillima* and *S. virgata* (23.649), and *S. gracillima* and western *S. mexicana* (1.487), *S. maya* and western *S. mexicana* (3.562), and *S. austrina* and *S. gracillima* (3.695).

Table 1. Traits scored for the multivariate analyses of specimens of *Solidago austrina*, *S. chrysopsis*, *S. gracillima*, *S. pulchra*, *S. stricta*, and *S. virgata*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip(cm)
UPSTMNOD25	Number of nodes in distal 25% of the stem below the inflorescence
UPSTMNOD 20	Number of nodes in distal 20% of the stem below the inflorescence
BLFLN	Basal rosette leaf length measured from the leaf base to tip (mm)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf dentation - number of serrations along (one side)
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf margin - number of serrations (one side)
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf margin - number of serrations (one side)
ULFLN	Upper leaf length measured form the leaf base to tip(mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf margin - number of serrations (one side)
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
CAPBRLN	Length of longest lower inflorescence branches (cm)
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
RPUB	Density of hairs on ray floret ovary at anthesis (1-5 scale)
DCORLN	Disc corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc corolla lobe length lobe (mm)
DACHLN	Disc achene length (mm)
DPAPLN	Disc pappus length (mm)
DPUB	Density of hairs on disc floret ovary at anthesis (1-5 scale)

In the Classificatory Discriminant Analysis of the nine putative species level a priori groups, a posteriori assignments of specimens ranged from 38-95% to their own group. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in decreasing order of percent correct placement. Eighteen of 19 specimens of the Solidago chrysopsis a priori group (95%) were placed a posteriori into the S. chrysopsis group: 7 specimens were placed a posterior with 90-95% probability; 3 specimens with 81-86% probability, 2 specimens with 71% and 78% probabilities, 4 specimens with 63-69% probability, 1 specimen with 42% probability (26% to S. maya and 20% to eastern S. mexicana), and 1 specimen with 28% probability (23% to S. maya; 20% to eastern S. mexicana, 13% to S. virgata, and 10% to S. stricta). One specimen of the S. chrysopsis a priori group was assigned to S. gracillima with 32% probability (29% to S. chrysopsis; 16% to S. austrina; and 15% to S. maya). Fourteen of 15 specimens of S. pulchra (93%) were assigned a posteriori to the S. pulchra group; 12 with 92-100% probabilities, and 2 with 64% and 51% probabilities. One specimen of the S. pulchra a priori group was assigned to S. maya with 42% probability (21% to S. chrysopsis; 15% to S. stricta, 4% to S. austrina, and 3% to S pulchra). Sixteen of the 18 specimens of the S. gracillima a priori group (89%) plus one additional specimen were assigned a posteriori to S. gracillima: 6 specimens with 80-93% probability; 5 specimens with 72-77% probability, 2 specimens with 64-65% probability, and 1 specimen with 59% probability (40% to S. austrina) and 1 specimen with 42% probability. Three specimens of the S. gracillima a priori were assigned to other species. All other taxa had much lower percents of correct assignment (38-63%) and are not discussed in detail; 69% of 16 specimens for western S. mexicana were assigned to that group a posteriori, but only 38% of 29 specimens of eastern S. mexicana were assigned to that group a posteriori; 62% of the 29 specimens of S. virgata were assigned to that group a posteriori. Among the specimens of S. virgata not assigned a posterior to S. virgata was Urbatsch 10776 (LSU) from Louisiana; the specimen was assigned to S. maya with 37% probability (15% each to S. chrysopsis and to S. stricta, 12% each to S. virgata and eastern S. mexicana and 8% to western S. mexicana).

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for 208 specimens of *Solidago austrina*, *S. chrysopsis*, *S. gracillima*, *S. maya*, eastern and western *S. mexicana* separately, *S. pulchra*, *S. stricta*, and *S. virgata* were not very informative due to considerable overlap in group distributions on the diagrams and are shown in Fig. 9. Only the symbols of *S. pulchra* are fairly well separated from other taxa on CAN1 versus CAN3. Eigenvalues on the first three axes were 1.882, 0.830 and 0.661.

Group	austrina	chrysopsis	gracillima	maya	<i>mexicana</i> E	<i>mexicana</i> W	pulchra	stricta
chrysopsis	18.522							
gracillima	3.695	16.406						
maya	9.6544	4.870	9.016					
<i>mexicana</i> E	19.311	12.273	17.474	1.487				
mexicana W	13.435	14.611	23.209	3.562	4.621			
pulchra	13.367	18.466	15.740	14.032	25.088	25.177		
stricta	16.290	12.995	16.754	4.215	12.453	9.089	23.184	
virgata	21.051	11.030	23.601	7.6871	16.343	10.965	25.329	4.549
-								

Table 2. Between groups F-matrix for the nine putative a priori groups analysis (df = 7 193).

Wilks' lambda = 0.05825 df = 7 8 199; Approx. F = 12.9701 df = 56 1044 prob = 0.0000

Group	austrina	chrysop-	gracil-	maya	mexicana	mexicana	pulchra	stricta	virgata	%
		sis	lima		E	\mathbf{W}				correct
austrina	18	2	10	0	1	0	5	1	2	46
chrysopsis	0	18	1	0	0	0	0	0	0	95
gracillima	1	0	16	0	1	0	0	4	1	89
maya	0	1	1	5	0	0	0	1	0	56
mexicanaE	3	0	0	5	11	5	0	4	1	38
mexicanaW	0	1	0	1	1	11	0	0	2	69
pulchra	0	0	0	1	0	0	14	0	0	93
stricta	1	3	0	4	2	2	1	19	2	56
virgata	1	2	0	3	0	0	0	5	18	62
Totals	24	27	28	19	17	18	20	30	25	63

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

Jackknifed classification matrix

Group	austrina	chrysop-	gracil-	maya	mexicana	mexicana	pulchra	stricta	virgata	%
		sis	lima		E	\mathbf{W}				correct
austrina	17	2	10	0	1	0	5	2	2	44
chrysopsis	0	17	1	1	0	0	0	0	0	89
gracillima	0	0	15	0	2	0	0	1	0	83
maya	0	1	1	5	1	0	0	1	0	56
mexicanaE	3	0	0	5	10	6	0	4	1	34
mexicanaW	0	1	0	3	3	8	0	0	2	50
pulchra	0	0	0	1	0	0	14	0	0	93
stricta	1	3	0	4	2	2	1	16	5	47
virgata	1	3	0	3	0	0	0	5	17	59
Totals	22	27	28	21	18	16	20	30	26	57

Figure 9. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 207 specimens of six a priori groups of the *Solidago stricta* complex and three a priori groups of the *S. sempervirens* complex: *S. austrina* (red dots), *S. chrysopsis* (gray stars), *S. gracillima* (orange +s), *S. maya* (green triangles), eastern *S. mexicana* (dark blue tringles), western *S. mexicana* (light blue triangles), *S. pulchra* (yellow triangles), *S. stricta* (gray diamonds), and *S. virgata* (white dots with black outline).

Six species groups analysis

In the STEPWISE discriminant analysis of 157 specimens of the six species level a priori groups *Solidago austrina*, *S. chrysopsis*, *S. gracillima*, *S. pulchra*, *S. stricta*, and *S. virgata*, the following eight traits were selected as best separating the groups and are listed in order of decreasing F-to-remove values: length of the longest inflorescence branch (62.79), number of disc florets (18.96), disc floret pappus length at anthesis (18.80), mid leaf length (13.76), number of ray florets (8.63), involucre height (6.08), mid series phyllary width (5.52), and mid series phyllary length (4.22). 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 3. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *Solidago gracillima* and *S. virgata* (68.412), *S. gracillima* and *S. stricta* (54.317), *S. chrysopsis*, and *S. gracillima* (46.400), and *S. austrina* and *S. stricta* (8.205) and *S. stricta* and *S. virgata* (6.211).

Group	austrina	<i>chrysopsis</i>	gracillima	pulchra	stricta
chrysopsis	16.4892				
gracillima	46.089	46.400			
pulchra	14.268	14.684	48.452		
stricta	20.133	12.040	54.317	23.458	
virgata	21.856	8.205	68.412	19.742	6.211

Table 4. Between groups F-matrix for the six a priori group analysis (df = 8 144).

Wilks' lambda = 0.0228 df = 8 5 151; Approx. F = 21.7563 df = 40 633 prob = 0.0000

In the Classificatory Discriminant Analysis of the six species level a priori groups, a posteriori assignments of specimens ranged from 79-89% to their own group. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in decreasing order of percent correct placement. Seventeen of 19 specimens of Solidago chrysopsis (89%) were assigned a posteriori to the S. chyrsopsis group; 9 specimens with 90-99% probability, 5 specimens with 80-87% probability, and 3 specimens with 70-76% probability. Two specimens of the S. chrysopsis a priori group were assigned a posteriori to S. virgata with 62% probability (19% to S. chrysopsis and 16% to S. stricta; Correll et al. 44222 NCU from Dade Co., Florida) and 56% probability (37% to S. chrysopsis and 6% to S. stricta; McCart 11218 USF; Martin Co., Florida; narrow basal leaves, S. mexicana like inflorescence but 5% probability to eastern S. mexicana in the first analysis). Seventeen of 19 specimens of S. gracillima a priori group (89%) plus one additional specimen not included in the a priori group were placed a posteriori into the S. gracillima group: 16 specimens with 98-100% probability; 1 specimen with 73% probability (16% to S. austrina and 10% to S. stricta); and 1 specimen with 59% probability (41% to S. austrina; Smith s.n. NCU from Darlington Co., South Carolina). Two specimens of the S. gracillima a priori group were placed a posteriori into S. austrina: 1 specimen with 96% from Florida (Godfrey 60447 FSU with a possibly damaged inflorescence and atypical branching pattern), and 1 specimen with 62% from Florida (32% to S. gracillima; Godfrey 67758 FSU with a small inflorescence without long branches). Thirteen of the 15 specimens of the S. pulchra a priori group (87%): all 13 with 90-100%

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

07
83
89
89
87
79
83
84

Group	austrina	chrysopsis	gracillima	pulchra	stricta	virgata	% correct
austrina	30	1	0	5	5	0	73
chrysopsis	1	17	0	0	0	1	89
gracillima	3	0	16	0	0	0	84
pulchra	0	1	0	13	0	1	87
stricta	0	5	0	1	23	5	68
virgata	2	1	0	0	4	22	76
Totals	36	25	16	19	32	29	77

Jackknifed classification matrix

probability. Two specimens of the S. pulchra a priori group were assigned to other species: 1 specimen (Kologiski 512 UNCC from Brunswick Co., North Carolina) to S. chrysopsis with 60% probability (14% to S. virgata, 13% to S. stricta, and 11% to S. austrina); and 1 specimen (McCarthy s.n. NCU; from Willington, North Carolina), with 41% to S. virgata (25% to S. pulchra, 14% to S. chrysopsis, and 12% to S. austrina, and 8% to S. stricta). Thirty-four of the 41 specimens of S. austrina a priori group (83%) were assigned a posteriori to the S. austrina group: 19 specimens with 93-100% probability, 5 specimens with 81-87% probability, 3 specimens with 70-76% probability, 3 specimens with 63-66% probability, 3 specimens with 52-55% probability, and 1 specimen with 40% probability (40% to S. stricta, 12% to S. virgata and 8% to S. chrysospis; Heller 1284 NY from Rowan Co., North Carolina). Seven specimens of the S. austrina a priori group were assigned to other species: 4 specimens to S. pulchra with 45-99% probability (3 with very immature inflorescences without lower branches elongated including a tetraploid Semple & Suripto 9782 WAT from Kershaw Co., South Carolina), 1 hexaploid specimen (Semple & LeBlond 11788 WAT from Pender Co., North Carolina; with serrate narrow lower stem leaves) to S. chrysopsis with 78% probability (16% to S. austrina), and 1 specimen (Radford 18716 NCU from Chesterfield Co., South Carolina) to S. stricta with 58% probability (41% to S. virgata). Twenty-four of the 29 specimens of the S. virgata a priori group (83%) were assigned a posteriori to the S. virgata group: 9 specimens with 89-96%, 2 specimens with 81% and 79% probabilities, 2 specimens with 70% and 73% probability, 9 specimens with 59-68% probability, 1 specimen with 52% probability (Semple 11630 WAT from Pender Co., North Carolina; hexaploid; 28% to S. chrysopsis and 15% to S. stricta), and 1 specimens with 44% probability (Urbatsch 10776 from Tangipahoa Par., Louisiana; 37% to S. stricta and 18% to S. chrysospsis). Five specimens of the S. virgata a priori group were assigned a posteriori to the other species: 3 specimens to S. stricta with 51% probability (Ahles & Leisner 33442 NCU from Cumberland Co., North Carolina; 49% to S. virgata); 38% probability (Semple 11777 WAT from Orangeburg Co., South Carolina; hexaploid; 31% to S. virgata and 30% to S. chrysopsis), and 36% probability (Wright 3602 GH from Cuba; 30% S. chrysopsis, and 17% each to S. virgata and S. austrina); 1 specimen to S. chrysopsis with 42% probability (Semple & Suripto 10126 WAT from Mobile Co., Alabama; 39% to S. stricta and 19% to S. virgata); and 1 specimen to S. austrina with 46% probability (Smiley s.n. NCU from Collier Co., Florida; 25% to S. virgata and 15% to S. stricta). Twenty-seven of 34 specimens of the S. stricta a priori group (79%) were assigned a posteriori to the S. stricta group: 7 specimens with 90-100% probability, 8 specimens with 80-89% probability, 5 specimens with 71-75% probability, 3 specimens with 63-68% probability, 2 specimens with 53% and 55% probabilities, and 1 specimen with 46% probability. Seven specimens of the S. stricta a priori group were assigned a posteriori to two other groups, four had small inflorescences and three had larger inflorescences, two with long branches: 4 specimens to S. chrysopsis with 60%, 55%, 46%, and 35% probabilities; 3 specimens to S. virgata with 77%, 66%, and 49% probabilities.

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for 157 specimens of *Solidago austrina*, *S. chrysopsis*, *S. gracillima*, *S. pulchra*, *S. stricta*, and *S. virgata* are presented in Fig. 10. Eigenvalues on the first three axes were 4.376, 1.683 and 0.766.

Figure 10. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 157 specimens of six a priori groups of the *Solidago stricta* complex: *S. austrina* (red dots), *S. chrysopsis* (gray stars), *S. gracillima* (orange +s), *S. pulchra* (yellow triangles), *S. stricta* (gray diamonds), and *S. virgata* (white dots).

Five species groups analysis

In the STEPWISE discriminant analysis of 138 specimens of five species level a priori groups (Solidago austrina, S. chrysopsis, S. pulchra, S. stricta, and S. virgata), the following seven traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (23.74), number of disc florets (22.08), mid leaf length (17.98), involucre height (7.19), mid series phyllary width (6.45), number of ray florets (5.78), and mid series phyllary length (4.77). 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 6. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between Solidago pulchra and S. stricta (27.556); the smallest separation was between S. stricta and S. virgata (5.194).



Table 6. Between groups F-matrix for the five a priori group analysis (df = 7 127).

Group	austrina	chrysopsis	pulchra	stricta
chrysopsis	18.355			
pulchra	15.878	15.459		
stricta	24.461	14.532	17.556	
virgata	24.739	9.009	22.640	5.194

Wilks' lambda = 0.0829 df = 7 4 133; Approx. F = 16.3141 df = 282 459 prob = 0.0000

In the Classificatory Discriminant Analysis of the five species level a priori groups, percents of correct a posterori assignment to the same a priori group ranged from 74% to 89%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Results are presented in order of decreasing percents of correct placement. Seventeen of the 19 specimens of *Solidago chrysopsis* (89%)

were assigned a posteriori into the S. chrysopsis group; 7 specimens with 91-97% probability, 8 specimens with 81-89% probability, 3 specimens with 70-76% probability, and 1 specimen with 67% probability (29% to S. virgata; vanHoek & Wargo 985 USF from Highlands Co., Florida). Thirteen of 15 specimens of the S. pulchra a priori group (87%) were assigned a posteriori to the S. pulchra group: 12 specimens with 93-100% probability, and 1 specimen with 88% probability. Two specimens of the S. pulchra a priori group was assigned to other species: 1 specimen to S. chrysopsis with 60% probability (14% each to S. stricta, and S. virgata and 10% to S. austrina; Kologiski 512 UNCC from Brunswick Co., North Carolina; a tall plant for the species) and 1 specimen to S. virgata with 33% probability (25% to S. pulchra, 20% to S. chrysopsis, 13% to S. austrina, and 8% to S. stricta; McCarthy s.n. NCU from Willington, North Carolina). Twenty-four of the 29 specimens of the S. virgata a priori group (83%) were assigned a posteriori to the S. virgata group: 4 specimens with 92-95% probability, 5 specimens with 81-89% probability, 1 specimen with 74% probability, 8 specimens with 61-69% probability, and 4 specimens with 52-56% probability. Five specimens of the S. virgata a priori group were assigned to other species: 4 specimens to S. stricta with 40-70% probability and 1 specimen to S. austrina with 44% probability (26% to S. virgata, 14% to S. stricta and 2% to S. chrysopsis; Smiley s.n. NCU from Florida). Thirty-one of the 41 specimens of the S. austrina a priori group (76%) were assigned a posteriori to the S. austrina group: 20 specimens with 91-100% probability, 4 specimens with 85-89% probability, 4 specimens with 70-75% probability, 2 specimens with 63 % and 68% probabilities, and 1 specimens with 53% probability (37% to S. chrysopsis, and 7% to S. virgata). Ten specimens of the S. austrina a priori group were assigned to other species: 5 specimens to S. stricta with 45-57% probility; 3 specimens to S. pulchra with 99%, 85% and 74% probabilities; and 1 specimen to S. chrysopsis with 77% probability. Twenty-five of the 34 specimens of the S. stricta a priori group (74%) were assigned a posteriori to the S. stricta group: 8 specimens with 93-99% probability, 6 specimens with 81-89% probability, 2 specimens with 72% and 75% probabilities, 3 specimens with 66-69% probability, and 4 specimens with 53-57% probability, and 1 specimen with 43% probability (39% to S. virgata and 15% to S. chrysopsis). Nine specimens of the S. stricta a priori group were assigned to other species: 6 specimens to S. virgata with 49-69% probability, 2 specimens to S. chrysopsis with 54% and 45% probabilities, and 1 specimen to S. pulchra with 42% probability (23% to S stricta, 19% to S. chrysopsis, 9% to S. austrina and 7% to S. virgata).

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six a priori groups; a posteriori placements to groups in rows.

Group	austrina	chrvsopsis	pulchra	stricta	virgata	% correct
austrina	31	1	4	5	0	76
chrysopsis	10	17	0	0	1	89
pulchra	0	1	13	0	1	87
stricta	0	2	1	25	6	74
virgata	1	0	0	4	24	83
Totals	33	21	18	34	32	80

Jackknifed classification matrix

Group	austrina	chrysopsis	pulchra	stricta	virgata	% correct
austrina	31	1	4	5	0	76
chrysopsis	1	17	0	0	1	89
pulchra	0	1	13	0	1	87
stricta	0	3	1	24	6	71
virgata	2	1	0	5	21	72
Totals	34	23	180	34	29	77

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for 138 specimens of *Solidago austrina*, *S. chrysopsis*, *S. pulchra*, *S. stricta*, and *S. virgata* are presented in Fig. 11. Eigenvalues on the first three axes were 2.186, 1.049 and 0.549.

Figure 11. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 138 specimens of five a priori groups of the *Solidago stricta* complex: *S. austrina* (red dots), *S. chrysopsis* (gray stars), *S. pulchra* (yellow triangles), *S. stricta* (gray diamonds), and *S. virgata* (white dots).

Four species groups analysis

In the STEPWISE discriminant analysis of 101 specimens of four species level a priori groups (Solidago austrina, S. chrysopsis, S. pulchra, and S. virgata), the following nine traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (3.03), upper leaf length (19.09), disc floret pappus length at anthesis (17.83), mid series phyllary width (13.79), number of mid leaf serrations (9.03), number of upper leaf serrations (8.59), number of nodes in distal 25% of the stem below the inflorescence (6.46), number of ray florets (5.88), and involucre height (4.77). 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 8. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between S. pulchra and S. virgata (25.881); the smallest separation was between S. chrysopsis and S. virgata (8.6281).



Group	austrina	chrysopsis	pulchra
chrysopsis	19.972		
pulchra	20.989	15.540	
virgata	21.381	8.628	25.881

Table 8. Between groups F-matrix for the four a priori group analysis (df = 9 89).

Wilks' lambda = 0.0484 df = 9 3 976; Approx. F= 17.5300 df = 27 260 prob = 0.0000

In the Classificatory Discriminant Analysis of the five species level a priori groups, percents of correct a posterori assignment to the same a priori group ranged from 90-100%. The Classification matrix and Jackknife classification matrix are presented in Table 9. Results are presented in order of decreasing percents of correct placement. All 19 specimens of Solidago chrysopsis (100%) were assigned a posteriori into the S. chrysopsis group; 15 specimens with 91-100% probability, 2 specimens with 82-83% probability, 1 specimen with 76% probability, and 1 specimen with 68% probability (32% to S. virgata; Correll & Correll 50353 NCU from Big Pine Key, Monroe Co., Florida). All fourteen specimens of S. pulchra (100%) were assigned a posteriori to the S. pulchra group; 12 specimens with 100% probability, 1 specimen with 79%, and 1 specimen with 50% probability (45% to S. chrysopsis and 5% to S. virgata; McCarthy s.n. NCU from Willington, North Carolina). Thirty-four of the 39 specimens of S. austrina a priori group (90%) were assigned a posteriori to the S. austrina group; 29 specimens with 94-100% probability; 2 specimens with 80% and 86% probabilities; 2 specimens with 71% and 77% probabilities, and 1 specimens with 68% probability. Four specimens of the S. austrina a priori group plus 1 only included in the a posteriori classification were assigned to other species: 1 specimen, to S. virgata with 99% probability (Radford 18716 NCU from South Carolina; serrate lower stem leaves; this is likely a specimen of S. stricta); 1 specimen to S. pulchra with 93% probability (Godfrey & Fox 50299 NCU from Chatham Co., North Carolina with an atypical open few-branched inflorescence); 2 specimens to S. chrysopsis with 86% probability (Semple & Leblond 11788 WAT a hexaploid from Pender Co., North Carolina,; this is likely a specimen of S. stricta; and Semple 11826 WAT a diploid from Walton Co., Georgia with serrate lower stem leaves and a very immature lower inflorescence); and 1 specimen to S. virgata with 58% probability (39% to S. austrina; Godfrey & Fox 50514 SMU in BRIT from Harnett Co., North Carolina with serrate lower stem leaves and damaged inflorescence).

Group	austrina	chrysopsis	pulchra	virgata	% correct
austrina	35	1	1	2	90
chrysopsis	0	19	0	0	100
pulchra	0	0	14	0	100
virgata	1	2	0	26	90
Totals	36	22	15	27	93

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of five a priori groups; a posteriori placements to groups in rows.

Jackknifed classification matrix

Group	austrina	<i>chrysopsis</i>	pulchra	virgata	% correct
austrina	33	2	2	2	85
<i>chrysopsis</i>	0	19	0	0	100
pulchra	0	12	132	0	93
virgata	1	2	0	26	90
Totals	34	27	14	25	90

Two dimensional plot of CAN1 versus CAN2 canonical scores for 101 specimens of *Solidago austrina*, *S. stricta*, and *S. virgata* are presented in Fig. 12. Eigenvalues on the first two axes were 2.807 and 2.341.

Figure 12. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 101 specimens of four a priori groups of the *Solidago stricta* complex: *S. austrina* (red dots), *S. chrysopsis* (gray stars), *S. pulchra* (yellow triangles), and *S. virgata* (white dots).

Three species groups analysis

In the STEPWISE discriminant analysis of 102 specimens of three species level a priori groups (Solidago austrina, S. stricta, and S. virgata), the following six traits were selected in a STEPWISE analysis and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (37.33), number of disc florets (11.10), number of ray florets (10.83), mid leaf width (10.09), mid series phyllary length (9.15), and involucre height (5.71).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 10. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between S. austrina and S. virgata (28.729), and the smallest separation was between S. stricta and S. virgata (7.131).

In the Classificatory Discriminant Analysis of the three species level a priori

groups, the percents of correct placement a posteriori ranged from 76-88%. The Classification matrix and Jackknife classification matrix are presented in Table 11. Thirty-five of 40 specimens of *Solidago austrina* (88%) plus 1 additional specimen were assigned a posteriori to the *S. austrina* group; 31 specimens were assigned with 93-100% probability and 5 specimens with 83-87% probability. Five specimens of the *S. austrina* a priori group were assigned to *S. stricta* with 59% probability (36% to *S. austrina* and 5% to *S. virgata*; *Small s.n.* NY from with serrate lower leaves and a possibly damaged inflorescence, from Stanley Co. North Carolina), 54% probability (41% to *S. austrina* and 5% to *S. virgata*; *Small s.n.* NY from Stanley Co., North Carolina), 50% probability (46% to *S. austrina* and 3% to



S. virgata; Lindholm s.n. GA from Liberty Co. Florida, broadly lanceolate lower stem leaves with large serrations and small inflorescence), 50%+ probability (50%- to S. virgata; Radford 18176 NC from Chesterfield Co., South Carolina), and 43% probability (32% to S. virgata and 25% to S. austrina; Heller 1284 NY from Rowan Co., North Carolina). Twenty-four of the 29 specimens of the S. virgata a priori group (83%) plus one additional specimen were assigned a posteriori into the S. virgata group; 7 specimens with 91-97% probability, 8 specimens with 81-86% probability, 8 specimens with 69-76% probability, and 1 specimen with 51% probability (Semple & Suripto 9801 WAT from Colleton Co., South Carolina; a tetraploid with non-serrate lower stem leaves). Five specimens of the S. virgata a priori group were assigned to the other two species: 1 specimen to S. austrina with 71% probability (17% to S. virgata and 12% to S. stricta; Smiley s.n. NCU from Collier Co., Florida; with ovate crenate basal leaves) and 4 specimens to S. stricta with 66% probability (33% to S. virgata; Urbatsch 10776 LSU from Tangipahoa Par., Louisiana), 64% probability (36% to S. virgata; Semple & Suripto 10126 WAT from Mobile Co., Alabama with entire lower stem leaves), 64% probability (22% to S. austrina and 12% to S. virgata; Wright 3602 GH from Cuba with entire lower stem leaves), and 52% probability (47% to S. virgata; Semple 11777 WAT from Orangeburg Co., South Carolina, a hexaploid with entire lower stem leaves). Twenty-six of 34 specimens of the S. stricta a priori group (76%) were assigned a posteriori to S. stricta: 9 specimens with 91-100% probability, 5 specimens with 81-89% probability, 4 specimens with 71-75% probability (including 2 of the 6 specimens of Semple 11824 WAT from New Jersey; a 173 cm tall shoot with a 39 cm tall long-branched inflorescence and a 97 cm tall shoot with a 29 cm tall longbranched inflorescence), 3 specimens with 61-68% probability, 1 specimen with 55% probability (45% to S. virgata; Semple 11824 WAT, Fig. 5; a 94 cm tall shoot with a 33 cm tall long-branched inflorescence), 1 specimen with 53% (42% to S. virgata and 5% to S. austrina; McMillan & Kjellmark 1122 NCU from Liberty Co., Florida; 125 cm tall shoot with a 24 cm tall, long-branched inflorescence), 1 specimen with 52% probability (46% to S. virgata and 5% to S. austrina; Parker s.n. NY from New Jersey; 81 cm tall shoot with sparsely serrate lower stem leaves and a 10 cm tall narrow inflorescence), and 1 with 44% probability (40% to S. austrina and 16% to S. virgata; Brinton s.n. NCU from New Jersey; 75 cm stem with serrate lower stem leaves and a 12 cm tall inflorescence with a damaged tip and 5 elongated branches). Eight specimens of the S. stricta a priori group were assigned a posteriori to other species: 1 specimen was assigned to S. austrina with 85% probability (8% to S. stricta and 7% to S. virgata; Ahles 35961 NCU from Onslow Co., North Carolina; 125 cm tall shoot with serrate lower stem leaves and with 25 cm short-branched inflorescence); 7 specimens were assigned to S. virgata with 86% probability (12% to S. stricta; Ahles 36278 NCU from Pender Co., North Carolina; 109 cm tall shoot with serrate lower stem leaves and an 11 cm tall short-branched inflorescence), 83% probability (17% to S. stricta; Anderson 21472 FSU from Leon Co., Florida; 121 cm plus tall shoot with a 40 cm tall long-branched inflorescence; no lower stem leaves present), 76% probability (23% to S. virgata; Semple 11824 WAT, Fig. 6; 48.5 cm shoot with a 12 cm short-branched inflorescence; this was a second shoot taken from the base of the 173 cm shoot listed above and placed a posteriori into S. stricta), 61% probability (39% to S. stricta; Long 13368 GA from New Jersey; 51.5 cm tall shoot with a 5.5 cm tall short-branched inflorescence), 58% probability (42% to S. stricta; Semple 11824 WAT; 135 cm tall shoot with a 29 cm long-branched inflorescence), 52% probability (47% to S. stricta; Semple 11824 WAT; 84 cm tall shoot with a 16.5 cm short-branched inflorescence), and 48% probability (47% to S. stricta and 5% to S. austrina; MacKenzie 5588 NY from New Jersey; 76 cm tall shoot with a 20 cm tall shoot branched inflorescence with immature lower branches).

Table 10. Between groups F-matrix for the four a priori group analysis (df = 6 95).

Group	austrina	stricta
stricta	27.039	
virgata	28.729	7.131

Wilks' lambda = 0.2117 df = 6 2 100; Approx. F= 18.5786 df = 12 190 prob = 0.0000

Group	austrina	stricta	virgata	% correct
austrina	35	4	1	88
stricta	1	26	7	76
virgata	1	4	24	83
Totals	37	34	32	83

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

ackknifed classifica	kknifed classification matrix					
Group	austrina	stricta	virgata	% correct		
austrina	35	4	1	88		
stricta	2	23	9	68		
virgata	2	4	23	79		
Totals	39	31	33	79		

Two dimensional plot of CAN1 versus CAN2 canonical scores for specimens of *Solidago austrina*, *S. stricta*, and *S. virgata* are presented in Fig. 12. Eigenvalues on the first two axes were 2.276 and 0.442.



Figure 12. Two dimension plot of CAN1 versus CAN2 scores for 103 specimens in three a priori groups of the *Solidago stricta* complex: *S. austrina* (red dots), *S. stricta* (gray diamonds), and *S. virgata* (white dots).

Two species groups analysis I

In the STEPWISE discriminant analysis of 68 specimens of *Solidago austrina* and *S. virgata*, the following six traits were selected in a STEPWISE analysis and are listed in order of decreasing F-toremove values: disc floret pappus length at anthesis (34.03), number of disc florets (18.10), number of ray florets (14.84), number of upper leaf serrations on most serrate side (6.81), upper leaf length (4.77), and number of mid leaf serrations on most serrate side (7.02). 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. Group centroids of *Solidago austrina* and *S. virgata* had an F-to separate value of 30.0441 (Wilks' lambda = 0.2528, df = 6 1 66; Approx. F= 30.0441, df = 6 61 prob = 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori groups were 97% for *S. austrina* and 97% *S.*

virgata: one specimen of each species was assigned a posteriori to the other a priori group. The Classification matrix and Jackknife classification matrix are presented in Table 12. Thirty-eight of the 39 specimens included in the *S. austrina* a priori group (97%) were assigned a posteriori to that species: 36 specimens with 92-100% probability; 1 specimen with 88% probability (*Semple 11826* WAT from Walton Co., Georgia), and 1 specimen with 84% probability (*Godfrey & Fox 50514* SMU in BRIT from Harnett Co., North Carolina). One specimen of the *S. austrina* a priori group was assigned a posteriori to *S. virgata* with 100% probability (*Radford 18716* NCU from Chesterfield Co., South Carolina; serrate lower stem leaves). Twenty-eight of the 29 specimens of *S. virgata* a priori group (97%) were assigned a posteriori to the *S. virgata* group: 26 specimens with 93-100% probability; 1 specimen with 72% probability (*Wright 3602* GH from Cuba); and 1 specimen with 59% (*Semple et al. 3978* WAT from Sumter Co., Florida; non-serrate lower stem leaves). One specimen of the *S. virgata* a priori group was assigned a posteriori to *S. austrina* with 77% probability (*Smiley s.n.* NCU from Collier Co., Florida; this is the specimen with the ovate basal leaves with crenate margins).

Frequencies of CAN1 canonical scores for 68 specimens of *S. austrina* and *S. virgata* are presented in histograms in Fig. 13. The Eigenvalue on the first axis was 2.955.

Table 12. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	austrina	virgata	% correct
austrina	38	1	97
virgata	1	28	97
Totals	39	28	97

Jackknifed classification matrix

Group	austrina	virgata	% correct
austrina	37	2	95
virgata	2	27	93
Totals	39	28	94



Figure. 13. Histograms of CAN1 canonical scores for 68 specimens of S. austrina (left) and S. virgata (right).

Two species groups analysis II

In the STEPWISE discriminant analysis of 64 specimens of *Solidago stricta* and *S. virgata*, the following four traits were selected in a STEPWISE analysis and are listed in order of decreasing F-to-remove values: upper leaf width (15.94), mid series phyllary length (8.82), involuce height (7.26), and disc corolla length (3.87). 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. *Solidago stricta* and *S. virgata* had an F-to separate value of 12.769 (Wilks' lambda = 0.5360, df = 4 1 62; Approx. F= 12.7694 df = 4 59 prob = 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups Solidago stricta and S. virgata, the percents of correct placement a posteriori of specimens to the a priori group were 85% for S. stricta and 87% for S. virgata. The Classification matrix and Jackknife classification matrix are presented in Table 14. Twenty-nine of the 34 specimens of S. stricta (85%) were assigned a posteriori to that species: 14 specimens with 94-100% probability, 4 with 80-87% probability, 1 with 74% probability, 3 with 60-68% probability, and 7 with 52-59% probability. Five specimens of the S. stricta a priori group were assigned a posteriori to S. virgata: 1 specimen with 94% probability (Ahles 36278 NCU from Pender Co., North Carolina with serrate lower leaves), 1 specimen with 78% probability (Long 133368 GA from New Jersey), 1 specimen with 71% probability (Ahles 35961 NCU from Onslow Co., North Carolina with serrate lower leaves), 1 specimen with 59% probability (Semple 11824 WAT from New Jersey, the smallest shoot of the 6 specimen sample), and 1 specimen with 51% probability (Semple 11824 WAT from New Jersey, the second smallest shoot of the 6 specimen sample). Twenty-six of the 30 specimens of S. virgata (87%) were assigned a posteriori to the S. virgata group: 13 specimens with 90-99% probability, 51 specimens with 81-87% probability, 1 specimen with 75% probability, 4 specimens with 65-69% probability, and 3 specimens with 53-58% probability. Four specimens of the S. virgata a priori group were assigned a posteriori to S. stricta: 1 specimen with 82% probability (Semple & Suripto 10126 WAT from Mobile Co., Alabama, non-serrate lower leaves), 1 specimen with 81% probability (Urtbatsch 10776 LSU from Tangipahoa Par., Louisiana, non-serrate lower leaves), 1 specimen with 75% probability (Semple 11777 WAT from Orangeburg Co., South Carolina, hexaploid), and 1 specimen with 58% probability (Semple et al. 3913 WAT from Madison Co., Florida, haxaploid).

Frequencies of CAN1 canonical scores for 64 specimens of *S. stricta* and *S. virgata* are presented in histograms in Fig. 15. The Eigenvalue on the first axis was 0.866.

Oroup	striciu	vii guiu	
stricta	29	5	85
virgata	4	26	87
Totals	33	31	86
Jackknifed class	ification matrix	K	
Group	chrysopsis	stricta	% correct
stricta	25	9	74
virgata	5	25	83
Totals	30	34	78

Table 14. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two a priori groups; a posteriori placements to groups in rows.

viroata

% correct

stricta

Crown



Figure. 15. Histograms of CAN1 canonical scores for 64 specimens of S. stricta (left) and S. virgata (right).

Two species groups analysis III

In the STEPWISE discriminant analysis of 44 specimens of *Solidago chrysopsis* and *S. virgata*, the following four traits were selected in a STEPWISE analysis and are listed in order of decreasing F-toremove values: mid series phyllary width (20.01), upper leaf width (5.59), disc floret pappus length at anthesis (4.77), and the number of ray florets (4.23). 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. *Solidago chrysopsis* and *S. virgata* had an F-to separate value of 23.861 (Wilks' lambda = 22.8612, df = 4 36; prob = 0.0000).

In the Classificatory Discriminant Analysis of the two species level a priori groups, the percents of correct placement a posteriori of specimens to their a priori group were 87% for Solidago chrysopsis and 96% for S. virgata. The Classification matrix and Jackknife classification matrix are presented in Table 15. Thirteen of the 15 specimens of S. chrysopsis plus four additional specimens included a posteriori were assigned a posteriori to that species with 94-100% probability (including vanHoek & Wargo 985 USF from Avon Park Air Force Range, Highlands Co., Florida; northern most symbol on the S. chrysopsis insert of Fig. 8; has a non-serrate basal leaf of 174×5.5 mm; possibly introduced from further south around Homestead A.F.B. in Dade Co., Florida): 1 specimens was assigned with 63% probability (Calvert s.n. WAT from Big Pine Key, Monroe Co., Florida). Two specimens of the S. chrysopsis a priori group were assigned a posteriori to S. virgata: 1 specimen with 64% probability (*McCarthy 11218* USF from Martin Co., Florida has a basal leaf 190×9 mm and an inflorescence that is S. mexicana like in shape) and 1 specimen with 60% probability (Correll & Correll 44222 NCU from just north of Everglades National Park, Dade Co. Florida; 2 small shoots on sheet, the right hand specimen has a mixture of basal leaves including a 120×10 mm leaf and a 150×5 mm leaf, the left hand specimen has only very narrow basal leaves; the specimen was annotated in 2011 by the first author as "Solidago aff. stricta / close to S. chrysopsis" but is now assigned to S. chrysospsis. Twenty-five of the 26 specimens of S. virgata (96%) plus three additional specimens included a posteriori were assigned a posteriori to the S. virgata group: 23 specimens with 94-100% probability, 1 specimen with 83% probability, 1 specimen with 65% probability (Semple 11777 WAT from Orangeburg Co., South Carolina, hexaploid). One specimen of the S. virgata a priori group plus one additional specimen excluded from the STEPWISE analysis were assigned a posteriori to S. chrysopsis with 97% probability (*Radford* 42645 NCU from Hyde Co., North Carolina; has non-serrate lanceolate basal leaves, 110×10.2 mm), and 61% probability (Semple et al. 3978 WAT from Sumter Co., Florida).

Frequencies of CAN1 canonical scores for specimens of *S. chrysopsis* and *S. virgata* are presented in histograms in Fig. 15. The Eigenvalue on the first axis was 2.651.

Table 15. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Group	chrysopsis	virgata	% correct
chrysopsis	13	2	87
virgata	1	25	96
Totals	14	26	93

Jackknifed classification matrix

Group	chrysopsis	virgata	% correct
chrysopsis	13	2	87
virgata	2	24	92
Totals	15	25	90



Figure. 15. Histograms of CAN1 canonical scores for 44 specimens of S. chrysopsis (left) and S. virgata (right).

Two species groups analysis IV

In the STEPWISE discriminant analysis of 44 specimens of *Solidago pulchra* and *S. virgata*, the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (45.28), disc floret pappus length at anthesis (21.55), upper leaf length (16.04), number of nodes in distal 25% of the stem below the inflorescence (8.95), and mid series phyllary length (4.62). The number of ray florets had the lowest F-to-remove value (0.07). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of p = 0.001 that the null hypothesis was true. *Solidago pulchra* and *S. virgata* had an F-to separate value of 65.883 (Wilks' lambda = 0.1034 df = 5 1 42; Approx. F= 65.8832 df = 5 38 prob. 0.0000.

In the Classificatory Discriminant Analysis of 44 specimens the two species level a priori groups (*Solidago pulchra* and *S. virgata*), all 44 specimens were assigned a posteriori to their a priori group species. Thirteen of the 14 specimens of *S. pulchra* were assigned a posteriori to *S. pulchra* with 100% probability, and 1 specimen with 94% probability. All 30 specimens of *S. virgata* included in the classification analysis were assigned a posteriori to the species with 100% probability.

Frequencies of CAN1 canonical scores for 44 specimens of *S. pulchra* and *S. virgata* are presented in histograms in Fig. 16. The Eigenvalue on the first axis was 8.669.



Figure. 16. Histograms of CAN1 canonical scores for 42 specimens of S. pulchra (left) and S. virgata (right).

Two species groups analysis V

In the STEPWISE discriminant analysis of 70 specimens of *Solidago mexicana* and *S. virgata*, the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: upper leaf width (13.35), number of nodes in distal 25% of the stem below the inflorescence (8.70), length of ray floret pappus at anthesis (5.93), number of disc florets (5.35), length of ray floret ovary at anthesis (5.20), and number of ray florets (4.19). 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. *Solidago mexicana* and *S. virgata* had an F-to separate value of 14.488 (Wilks' lambda = 0.4202 df = 6 1 68; Approx. F= 14.488 df = 6 63 prob = 0.0001).

In the Classificatory Discriminant Analysis of 70 specimens of the two species level a priori groups Solidago mexicana and S. virgata, the percents of correct placement a posteriori of specimens to the a priori group were 88% for S. mexicana and 89% for S. virgata. The Classification matrix and Jackknife classification matrix are presented in Table 15. Thirty-eight of the 43 specimens of S. mexicana (88%) were assigned a posteriori to the S. mexicana group: 30 specimens with 93-100% probability, 2 specimens with 85% and 89% probabilities, 2 specimens with 74% and 79% probabilities, 1 specimen with 67% probability, and 3 specimens with 51-59% probability. Four specimens of the S. mexicana a priori were assigned a posteriori to the S. virgata group with 96% probability (Correll 40681 NY from Grand Bahama Is.), 54% probability (Correll 40681 MO from Grand Bahama Is.), 51% probability (Moreno Casasola et al. BD-1099 from Tabasco, Mexico), and 50% probability (Lewis 7171 NY from Grand Bahama Is.). Twenty-four of the 27 specimens of S. virgata (89%) were assigned a posteriori to the S. virgata group: 18 with 91-100% probability, 2 specimens with 83-83% probability, 1 specimen with 71% probability (Ahles 35774 NCU from Duplin Co., North Carolina {ca 60 km inland from coast}, 1 specimen with 56% probability (*Smiley s.n.* NCU from Collier Co., Florida; basal leaves are broadly ovate and crenulate but not serrate). Three specimens of the S. virgata a priori group were assigned a posteriori to S. mexicana with 88% probability (Semple 11630 WAT from Pender Co., North Carolina; basal leaves entire, hexaploid 2n=54; ca. 25 km from coast roughly in line with Ahles 35774 NCU from further inland), 60% probability (Darst 113 NCU from Pinellas Co., Florida; wet open slash pine woods on barrier island), and 52% probability (Urbatsch 10776 LSU from Tangipahoa Par., Louisiana).

Group	mexicana	virgata	% correct
mexicana	38	5	88
virgata	3	24	89
Totals	41	29	88.5

Table 15. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three a priori groups; a posteriori placements to groups in rows.

Jackknifed class	ification matrix	x	
Group	mexicana	virgata	% correct
mexicana	34	9	79
virgata	5	22	81
Totals	39	31	80

Frequencies of CAN1 canonical scores for 70 specimens of *S. mexicana* and *S. virgata* are presented in histograms in Fig. 18. The Eigenvalue on the first axis was 1.380.



Figure. 18. Histograms of CAN1 canonical scores for 70 specimens of S. mexicana (left) and S. virgata (right).

DISCUSSION

The results of the multivariate analyses support the recognition of *Solidago austrina*, *S. chrysopsis*, *S. gracillima*, *S. pulchra*, *S. stricta*, and *S. virgata* as separate species. As noted in Semple et al. (2016), the ecological species concept is particularly useful in dealing with *Solidago* taxa (Peirson et al. 2012). As unpublished results became available over the past decade which supported splitting the *S. stricta* complex into multiple species occurring in different habitats and as unpublished and published results from other subsections of *Solidago* also began to indicate the same conclusion, the real problem in *Solidago* taxonomy was recognized: there had been too much lumping of distinct species in *Solidago* by Cronquist (e.g. 1980). Each species will be discussed below in alphabetical order.

Solidago austrina

Confusion in separating *Solidago austrina*, *S. stricta*, and *S. virgata* is understandable and complicated by multiple ploidy levels known in *S. austrina* (2x, 4x) and *S. virgata* ((2x, 4x, 6x). *Solidago austrina* occurs in Piedmont and Fall Line moist soil habitats from central North Carolina to north central Georgia, where the range bifurcates in east central Georgia and heads southwest in a narrow zone to the

hills around Tallahassee, Florida, and northwest into northeastern Alabama then north into southern Tennessee and disjunct to southern Kentucky (Fig. 8). A few collections come from the Coastal Plain in North Carolina and Georgia. *Ahles 36276* (NCU) was placed a posteriori into *S. austrina* with 83% probability and is from Pender Co., North Carolina. *Bozeman 1962* (GA) was placed a posteriori into *S. austrina* with 97% probability and comes from Long Co., Georgia. The probabilities of a posteriori placement into *S. stricta* were only a few percent in each case. Thus, sometimes *S. austrina* gets onto the coastal plain, but only rarely and possibly does not establish itself in this atypical habitat. *Lazor 4587* (MT) from Liberty Co., Florida, was placed a posteriori into *S. austrina* with 46% probability (50% probability to *S. stricta*; the inflorescence is small and appears to be damaged). The ploidy level of these Florida collections is unknown. *Solidago austrina* is diploid in nearby and north central Georgia and northeast through South Carolina and North Carolina. One tetraploid from South Carolina has been found in the eastern portion of the range.

Plants of *Solidago austrina* in northern Alabama and adjacent Tennessee are tetraploids. *Semple & B. Semple 11203* (WAT and unmounted; from Cherokee Co., Alabama), *Semple & B. Semple 11198* (WAT; from Etowah Co., Alabama) were all placed a posteriori into *S. austrina* with 100% probability. *Semple et al.* 11857 (WAT) from Coffee Co., Tennessee, was assigned a posteriori to *S. austrina* with 96% probability in the three species analysis. *Campbell s.n.* (KY; Pulaski Co., Kentucky) was assigned a posteriori to *S. austrina* with 100% probability; this was originally identified as *S. uliginosa*; the ploidy level is unknown, but if the Kentucky population is disjunct from Tennessee or northeastern Alabama, then it is likely also tetraploid. Generally, even tall plants of *S. uliginosa* have fewer stem leaves that plants of *S. austrina*. Inflorescencences of southern *S. uliginosa* plants can be similar to those of *S. austrina* in having spreading and curved lower branches.

Solidago chrysopsis

Solidago chrysopsis has previously been ignored for the most part and treated as a synonym of *S. stricta* auth. non Ait. (i.e., *S. virgata*), e.g., Semple and Cook (2006). The species is a late-blooming goldenrod with very narrow lower stem leaves and a small inflorescence similar to that of *S. virgata*. It occurs in the Florida Keys and extreme southeastern Florida and in a few scattered locations further north in the Florida peninsula, which may be chance introductions (*S. chrysopsis* insert in Fig. 8). Statistical support for recognizing *S. chrysopsis* was strong in the five species analysis with 100% placement of all specimens of *S. chrysopsis* a priori group into *S. chrysopsis* a posteriori. In the two species analysis with *S. virgata*, two specimen of each species were assigned a posteriori to the other species. Based on the distribution of the specimens and the small number of technical characters selected in the STEPWISE analysis to separate the two species group centroids in N-dimensional hyperspace, all four specimens seem likely to belong to their respective a priori groups. *Solidago chrysopsis* can be confused with narrower-leaved small specimens of *S. virgata* where the ranges of the two species are sympatric in south Florida. Only one diploid chromosome count is known for *S. chrysopsis*. Only diploids are known in *S. virgata* from southern Peninsula Florida.

Solidago gracillima

Solidago gracillima can be one of the most distinctive species in the field due to its sparsely, but long branched inflorescence and very reduced mid and upper stem leaves. As delimited here, the range of *S. gracillima* extends from northern South Carolina to near Tallahassee in Panhandle Florida (Fig. 8). The greatest confusion with the species has been in the misapplication of the name, as was done in Semple & Cook (2006).

A possible collection from Carteret Co., North Carolina (*Angerman s.n.* USF; the one symbol for the species in North Carolina in Fig. 8) was included in the *Solidago gracillima* a priori group in the six species analysis and was placed a posteriori in that species with 98% probability, but it was annotated as

S. aff. *gracillima* in 2012 by the first author. This specimen represented a small number of collections from North Carolina that were identified by others as *S. gracillima* but that do not appear to be the same species as all other collections included in the analyses. The specimen was included in the analyses to see where it would be placed a posteriori; it was placed a posteriori in *S. gracillima* because of its long inflorescence branches. The leaves are less reduced upward than usual in the species and the arrangement of long branches in the inflorescence is not identical to specimens in South Carolina, Georgia, and Florida. Whether or not these plants are hybrids between *S. virgata* and other species of *Solidago* is unknown. Further research is needed to determine the correct identity of this small group of specimens that, in conclusion, are not *S. gracillima*, including *Angerman s.n.* (USF).

Solidago pulchra

Solidago pulchra was well separated in the analyses from S. virgata. Although the species has not historically always been recognized as distinct from S. virgata (i.e., S. stricta authors non Ait. in the literature, e.g., Radford et al. 1968, Cronquist 1968), Cronquist (1980) did recognize S. pulchra as distinct, based on its higher numbers of ray and disc florets, as did Semple and Cook (2006). Solidago pulchra is tetraploid and endemic to a narrow band of sphagnum depressions away from the coast in the southern coastal counties of North Carolina (S. pulchra insert in Fig. 8); our sample included one specimen cultivated at the North Carolina Botanical Garden on the Piedmont. No collections have been seen from South Carolina. Solidago pulchra is the only species to be well separated from the other eight species included in the first analysis of nine species. In the two species analysis including S. pulchra and S. virgata, all specimens were assigned a posterior to their a priori group species with 100% probability with the exception of one specimen of S. pulchra assigned with 94% probability. The involucres of S. pulchra are more broadly cylindrical than those of S. virgata and this was used in defining a priori groups. The mean number of disc florets was 15 for S. pulchra and 7.6 for S. virgata. This explains the difference in involucre shape because more receptacle area is needed to accommodate the much higher number of disc florets in S. pulchra. Shoots and lower stem leaves of S. pulchra tend to be much shorter than those of S. virgata but the most robust shoots of the former could cause possible confusion in identification.

Solidago stricta

Historically, true *Solidago stricta* Ait. non auth. has only recently been recognized as a species separate from *S. virgata* (as *S. stricta* auth. not Ait. in much of the literature). Semple (2013) reviewed the misapplication of the name to plants now treated either as *S. uliginosa* Nutt. or as *S. virgata*. The type of *S. stricta* Ait. is a European garden-grown specimen of North American origin. Eastern Virginia seems a likely source. Fernald (1938) described *S. perlonga* as a segregate of the *S. virgata* complex (referring to group as *Solidago* sp.-group *Uliginosae* Mackenzie in Small) native to southeastern Virginia and compared it to *S. austrina*, *S. flavovirens* Chapm. (a synonym of *S. austrina*), and *S. yadkinensis* (Porter) Small (= *S. austrina* × *S. arguta* Ait. *var. carolininana* A. Gray) and concluded it was most similar to *S. austrina*. Fernald also noted that his *S. perlonga* bloomed later than *S. austrina*, in contrast to the usual pattern of more northern plants blooming earlier than more southern plants. The explanation for the difference in phenology is likely that *S. austrina* is diploid and rarely tetraploid, while *S. stricta* is hexaploid. In *Solidago*, polyploid races tend to bloom later than diploids, e.g., *S. canadensis* L. versus *S. altissima* L. var. *altissima* at any particular location where the two are sympatric. The New Jersey plants of *S. stricta* sensu authors also belong with Fernald's species in *S. stricta* Ait. non auth. The range is more extensive than previously thought (Fig. 8), as noted below.

Six specimens representing 5 individuals of *Semple 11824* (WAT) from a single population in Burlington Co., New Jersey, were included in the analyses in the *Solidago stricta* a priori group; these all had serrate lower stem leaves but differed greatly in stem height, inflorescence height, and inflorescence lower branch length. Probabilities of placement into *S. stricta* ranged from 25-75% (75%-25% to *S. virgata*). One of the small shoots placed a posteriori into *S. stricta* was taken from the base of a large

shoot that was placed into *S. stricta*; both shoots were from the same individual. One chromosome count of 2n = 54 from a transplanted rootstock was obtained but cannot not be assigned to an individual voucher. These results clearly demonstrate the problem with identifying small shoots of *S. stricta* because such specimens lack an inflorescence large enough to allow lower inflorescence branches to bolt into the characteristic length and diverging pattern observed in larger specimens. If a specimen is hexaploid and has mid and lower stem leaves with serrations, then it is most likely *S. stricta*. Regrettably most herbarium collections do not include chromosome count data for the individual sampled.

The results of this study and final conclusions on identifications indicate that Solidago stricta Ait. non auth. occurs in North Carolina and South Carolina on the coastal plain and possibly further south. Semple & LeBlond 11788 (WAT) is a hexaploid with serrate lower stem leaves from Pender Co., North Carolina, and is treated here in conclusion as S. stricta but was included in the S. austrina a priori group and placed in that group a posteriori in the three species multivariate analysis (S. austrina, S. stricta, and S. virgata). In the field at the time of collecting, Richard LeBlond suggested the possibility that a second collection from the same site (Semple & LeBlond 11787 WAT; a hexaploid without serrations and past bloom thus not included in the analysis but treated here as S. virgata) and the blooming collection Semple & LeBlond 11788 (WAT) were not the same species. He was correct because 11788 is most likely S. stricta. Another collection (Radford 41611 NCU from Pitt Co., North Carolina) was included in S. stricta in the three species multivariate analysis and had 71% probability a posteriori of being S. stricta (28% probability of being S. virgata). Ahles & Leisner 32434 NCU from Pender Co., North Carolina, was included in the S. stricta a priori group and was placed a posteriori into S. stricta with 81% probability in the three-species analysis. Radford 18716 (NCU) from Cash, Chesterfield Co., South Carolina was included in the S. austrina a priori group because it had serrate lower and mid stem leaves but was placed a posteriori in S. virgata with 55% probability and S. stricta with 45% probability. Cash appears to be a low area south of Cheraw, South Carolina at the upper edge of the coastal plain along the "Fall Line", although it is no longer labeled as a separate community in GoogleEarthTM. With very limited a posteriori probability of Radford 18716 (NCU) being S. austrina, the servate leaves indicate it to be S. stricta. No collections of S. stricta were seen from Georgia, but McMillan & Kjellmark 1122 NCU from Liberty Co., Florida, appears to be S. stricta as well and has the lower long inflorescence branches of the species, but with ambivalent a posteriori probability in the analyses. Thus, it appears that hexaploid S. stricta occurs rarely from southern New Jersey south to Panhandle Florida, following the inner coastal plain margin. Finding S. stricta in Georgia will be a challenge because confirmation will depend on determining that any individual from the inner coastal plain with serrate lower stem leaves is hexaploid. Finding a particularly robust individual with a large long-branched blooming inflorescence later in the season would be ideal. Confirming the presence of S. stricta in the Tallahassee area of Florida should also involve determining the ploidy level of possible individuals to be hexaploid.

Solidago virgata

All specimens of *Solidago virgata* included in the multivariate analysis had non-serrate lower stem leaves and inflorescences with short lower branches regardless of the length of the inflorescence array. All specimens of *S. virgata* came from the coastal plain from North Carolina south to Florida and likely west to eastern Louisiana (Fig. 8). Lower stem leaves are petiolate with lanceolate or oblanceolate blades, but can be narrowly so.

The identity of *Smiley s.n.* (NCU) from Collier Co., Florida, is uncertain because the basal stem leaves are ovate to very broadly lanceolate and crenate but not serrate. Such leaves are very atypical for *Solidago virgata*, but the inland Collier Co. location is well out of the range of other species in the *S. stricta* complex into which it might be placed. It was included in the *S. virgata* a priori group in the analyses but usually was placed into *S. austrina* or a mixture of taxa. The plant is not a specimen of *S. austrina*. It is treated here as *S. aff. virgata* for lack of a better solution. From the lower mid stem to the tip of the inflorescence, the specimens looks like *S. virgata*. This is not the only hard to place one-of-a-

kind specimen of *Solidago* encountered in herbaria by the first author. Additional data of some kind is needed in this case.

Only one possible specimen of Solidago virgata from Louisiana was included in the analyses (Urbatsch 10776 LSU from Tangipahoa Par.). Although S. virgata (under the name S. stricta auth. not Ait.) has been reported from Louisiana, there is very little evidence that it occurs in the state. All collections seen by the first author that were identified as S. virgata have turned out to be S. mexicana, with the exception of Urbatsch 10776 (LSU), which is similar to specimens of S. virgata from southern Alabama and Panhandle Florida. The overall appearance of the specimen fits well with specimens treated here as S. virgata, but the results of the nine a priori groups analysis that included S. mexicana are inconclusive as to the probable identify of the specimen. As well, Urbatsch 10776 (LSU) was placed a posteriori into S. stricta in the five-species and three-species analyses with low probabilities, and into S. stricta with 81% probability in the two-species analysis with S. virgata. Of note, a J.K. Morton & J. Venn collection of S. virgata from Mobile Co., Alabama, was hexaploid (unpublished data), as were collections of *S. virgata* from Walton Co., Bay Co., and Wakulla Co., in Panhandle Florida (Semple et al. 1993; unpublished data). Thus, it may be that the Urbatsch 10776 (LSU) is also hexaploid and the multivariate analyses indicates that hexaploids in S. virgata are often assigned a posteriori to the hexaploid species S. stricta, even though these plants do not have serrate lower stem leaves. Finding hexaploid plants without lower leaf serrations in Louisiana (and southern Mississippi) would confirm the presence of the species in these states. Urbatsch 10776 (LSU) is certainly not S. stricta morphologically.

In conclusion, the *Solidago stricta* complex is best treated as a group of six morphologically similar species occurring in different, but wetter soil habitats of the coastal plain and outer Piedmont from New Jersey to western Florida and adjacent states, with the range of Piedmont species *S. austrina* sweeping around the southern Appalachians into north Alabama and adjacent Tennessee and disjunct to southern Kentucky. The final statement in Semple et al. (2016) is repeated here: "Like members of other species complexes in *Solidago*, some difficulty in identifying some collections to species is to be expected. While the multivariate analyses reported here have led to a much better understanding of the complex, they do not provide a 100% fool proof solution to the challenges of identifying goldenrods in the complex."

ACKNOWLEDGEMENTS

This work was supported by a Natural Sciences and Engineering Research Council of Canada Operating and Discovery Grants to the JCS. Joan Venn is thanked for her curatorial assistance with loans. The following herbaria are thanked for loaning specimens and giving permission to dissect heads of selected specimens: AZU, BM, F, FSU, GH, J.K. Morton Herbarium in ROM, KY, LL, MEXU, MO, NCU, NY, TEX, USF, and WAT in MT. The following students assisted in recording location data and collecting morphological data on specimens of *Solidago*: Andrew Lam and Mariam Sorour.

LITERATURE CITED

- Beaudry, J.R. 1963. Studies on *Solidago* L. VI. Additional chromosome numbers of taxa of the genus. Canad. J. Genet. Cytol. 5: 150–174.
- Beaudry, J.R. 1969. Études sur les *Solidago* L. IX. Une troisième liste de nombres chromosomiques des taxons du genre *Solidago* et de certains genres voisins. Naturaliste Canad. 96: 103–122.
- Cronquist, A. 1968. *Solidago* L. Pp. 413-438, <u>in</u> H.A. Gleason (ed.). The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada. Hafner Pub. Co., New York.
- Cronquist, A. 1980. Vascular Flora of the Southeastern United States. I. Asteraceae. Univ. of North Carolina Press, Chapel Hill.
- Fernald, M.L. 1938. Noteworthy plants from southeastern Virginia. Rhodora 40: 364–424, 434–459, 467–485.

Fernald, M.L. 1950. Gray's Manual of Botany, 8th ed. Van Nostrand, New York.

- Radford, A.E., H.E. Ahles, and C.R. Bell. 1968. Manual of the Vascular Flora of the Carolinas. Univ. of North Carolina Press. Chapel Hill.
- Peirson, J.A., A.A. Reznicek, & J.C. Semple. 2012. Polyploidy, speciation, and infraspecific cytotype variation in goldenrods: The cytogeography of *Solidago* subsection *Humiles* (Asteraceae: Astereae) in North America. Taxon: 61: 197–210.
- Semple, J.C. 2012. Typification of *Solidago gracillima* (Asteraceae: Astereae) and application of the name. Phytoneuron 2012-107: 1–10.
- Semple, J.C. 2013. Application of the names *Solidago stricta* and *S. virgata* (Asteraceae: Astereae). Phytoneuron 2013-42. 1–3.
- Semple, J.C. 2016 (frequently updated). Classification and Illustrations of Goldenrods. https://uwaterloo.ca/astereae-lab/research/goldenrods/classification-and-illustrations
- Semple, J.C. and R.E. Cook. 2004. Chromosome number determinations in fam. Compositae, Tribe Astereae. VII. Mostly eastern North American and some Eurasian taxa. Rhodora 106: 253–272.
- Semple, J.C. and R.E. Cook. 2006. Solidago Linnaeus. Pp. 107–166, in Flora North America Editorial Committee (eds.). Flora of North America. Vol. 20. Asteraceae, Part 2. Astereae and Senecioneae. Oxford Univ. Press, New York.
- Semple, J.C., R.A. Brammall and J.G. Chmielewski. 1981. Chromosome numbers of goldenrods, *Euthamia* and *Solidago*, (Compositae-Astereae). Canad. J. Bot. 59: 1167–1173.
- Semple, J.C., Jie Zhang and ChunSheng Xiang. 1993. Chromosome numbers in Fam. Compositae, Tribe Astereae. V. Eastern North American taxa. Rhodora 95: 234–253.
- Semple, J.C., G.S. Ringius, C. Leeder, and G. Morton. 1984. Chromosome numbers of goldenrods, *Euthamia* and *Solidago* (Compositae: Astereae). II. Additional counts with comments on cytogeography. Brittonia 36: 280-292. Erratum. Brintonia 37: 121. 1985.
- Semple, J.C., T. Shea, H. Rahman, Y. Ma, and K. Kornobis. 2016. A multivariate study of the Solidago sempervirens complex of S. subsect. Maritimae (Asteraceae: Astereae). Phytoneuron 2016–73. 1-31.
- SPSS Inc. 2000. SYSTAT version 10 for Windows. SPSS Inc., Chicago. Ill.
- Thiers, B. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. Virtual Herbarium, New York Botanical Garden. http://sciweb.nybg.org/science2/IndexHerbariorum.asp