

**ON *SOLIDAGO DURANGENSIS* (ASTERACEAE: ASTEREAE):
A MULTIVARIATE STUDY WITH SPECIMENS OF SUBSECT. *JUNCEAE*,
SUBSECT. *MARITIMAE*, AND SUBSECT. *TRIPLINERVIAE***

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ABSTRACT

Nesom (1991) described *Solidago durangensis* based on three collections from Durango, Mexico. The protologue was not illustrated; detailed illustrations of the species are presented here. The species has been included at different times in three different subsections of the genus. Multivariate morphometric analyses were performed on specimens of *S. argentinensis* and *S. missouriensis* of *Solidago* subsect. *Junceae*, *S. paniculata* of subsect. *Maritimae*, and *S. chilensis*, *S. juliae*, and *S. pringlei* of subsect. *Triplinerviae*. Two specimens of *S. durangensis* were scored and were not assigned to an a priori group but were included in the a posteriori classificatory discriminant analyses. Three multivariate analyses were performed. In the two 6-species analyses, the two specimens of *S. durangensis* were placed a posteriori into *S. chilensis* and *S. juliae*, respectively, and into *S. pringlei* and *S. juliae*, respectively. In the third analysis involving only the three species of subsect. *Triplinerviae*, the specimens of *S. durangensis* were placed a posteriori into *S. pringlei* and *S. juliae*. An additional specimen treated previously as either *S. pringlei* or *S. missouriensis* was also included in the analyses and was placed into *S. pringlei* in both 6-species group analyses and into *S. chilensis* in the third analysis. The results provide strong evidence that *S. durangensis* is most similar to species in subsect. *Triplinerviae* and on distinctive morphological features should be recognized as a very rare endemic species.

Nesom (1991) described *Solidago durangensis* Nesom (Figs. 1-4) but did not illustrate the new species. He stated that “the closest relative of the new species is hypothesized to be *S. paniculata* DC.”. *Solidago paniculata* (Figs 5-6) is the inland central Mexican member of *Solidago* subsect. *Maritimae* (Torr. & A. Gray) Nesom that includes the bog and marsh goldenrods: e.g., *S. mexicana* L., *S. sempervirens* L., *S. uliginosa* Nutt., and *S. virgata* Michx. (Semple 2016, frequently updated). Nesom (1993) included *S. durangensis* in subsect. *Triplinerviae* (Torr. & A. Gray) Nesom. When the first author examined limited herbarium material of *S. durangensis*, several traits were most striking. First the rather corymbiform inflorescence arrays were atypical in both subsect. *Maritimae* and subsect. *Triplinerviae*. Second, the dense, short hairy indument on the stems does not occur in subsect. *Maritimae* but is common in the *Tortifolia* group of subsect. *Triplinerviae*. The lack of lower stem material made it impossible to determine if the lower stem leaf petioles sheathed the stem as they do in all species of subsect. *Maritimae*. Semple (2016, frequently updated; versions in 2013-2016) placed *S. durangensis* into subsect. *Junceae* (Rydb.) Nesom in 2013 based on the fact that “Palmer 217 (F, MO) have fascicles of small leaves in the axes of some upper stem leaves” and that the “branching pattern of the inflorescence is more like *S. juncea* and *S. missouriensis* than members of *S.* subsect. *Triplinerviae*.” Densely hairy stems are not known in subsect. *Junceae*, but *S. argentinensis* Semple & Lopez Laphitz can be distally rather hairy, especially for the subsection. It was noted that additional research was needed on this rare species. Semple and Cook (2006) described the defining traits of each subsection. Regardless of its subsectional affinities, Nesom (1991) was correct in treating *S. durangensis* as a distinct species.



Figure 1. Isotype of *Solidago durangensis*; E. Palmer 363 (GH).

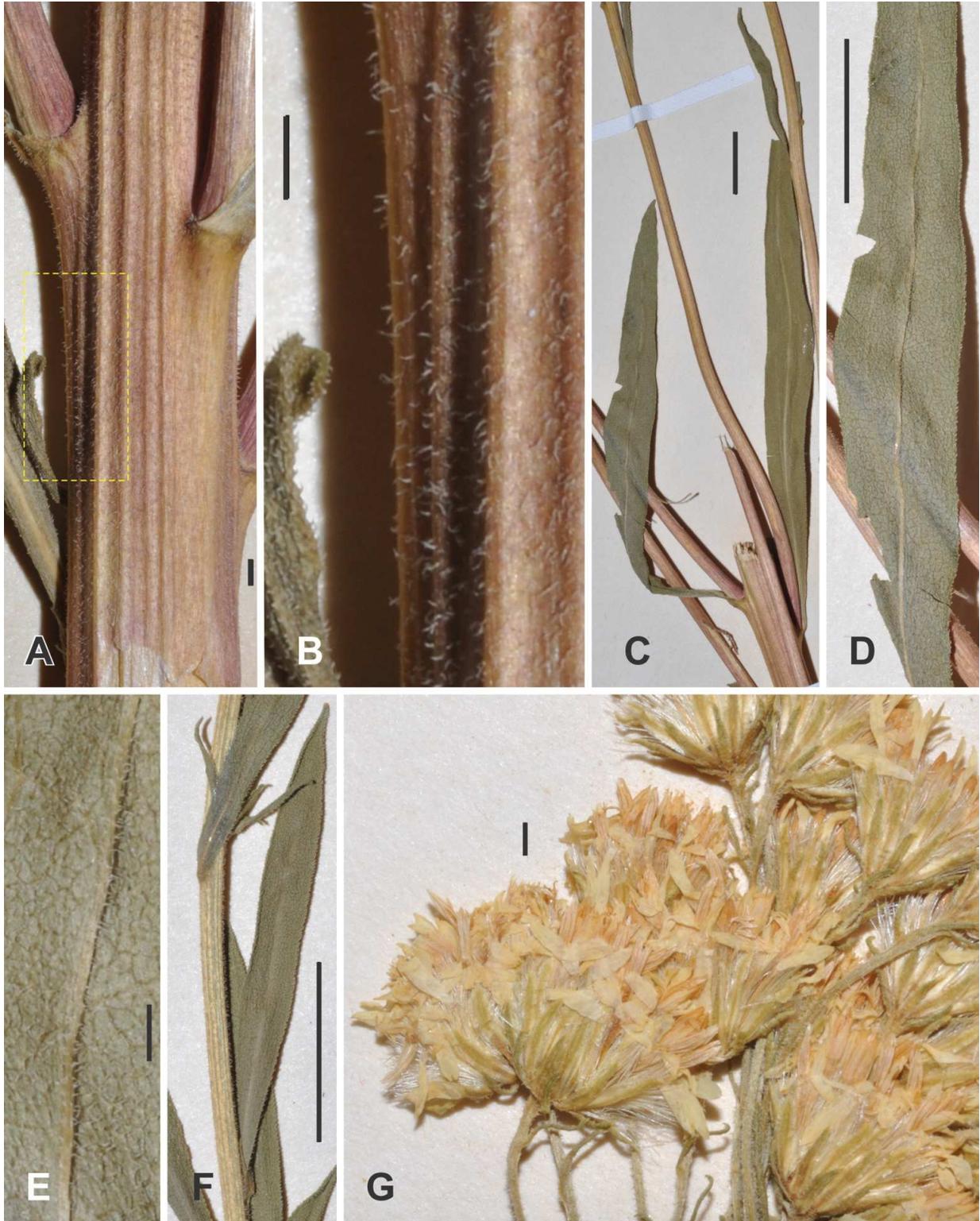


Figure 2. Details of isotype of *Solidago durangensis*, E. Palmer 363 (GH): stem, leaves and heads. **A-B.** Mid stem and enlargement of area in dashed outline. **C.** Mid stem leaves. **D.** Mid stem leaf, abaxial surface, weakly trinervate. **E.** Mid vein area of leaf in D. **F.** Upper branch and leaves. **G.** Heads. Scale bar = 1 mm in A, B, E, and G; = 1cm in C, D, and F.



Figure 3. *Solidago durangensis*; E. Palmer 217 (F) from Durango, Mexico.



Figure 4. *Solidago durangensis*; E. Palmer 217 (MO) from Durango, Mexico.



Figure 5. *Solidago paniculata*; Daniels 611 (F) from El Rosario, Dist. Federales, Mexico.



Figure 6. *Solidago paniculata*; Pérez Calix 845 (MEXU) from Agua Verde, Michoacán, Mexico.

In order to explore morphological similarities and differences among *Solidago durangensis* and possible related species, multivariate morphometric comparisons were performed on *S. argentinensis* and *S. missouriensis* Nutt. of subsect. *Junceae*, *S. paniculata* DC. of subsect. *Maritimae*, and *S. chilensis* Meyen, *S. juliae* Nesom, and *S. pringlei* Fern. of subsect. *Triplinerviae*. The results are presented below.

NOMENCLATURE

Solidago durangensis Nesom, Phytologia 70: 58. 1991. **TYPE: MEXICO. Durango.** City of Durango and vicinity, Apr-Nov 1896, *E. Palmer* 363 (holotype: US, digital image!; isotypes: GH! (Figs 1-2), US, digital image!).

Additional collections examined: **MEXICO. Durango.** Durango and vicinity, Apr-Nov 1896, *E. Palmer* 217 (F, Fig. 3; MO, Fig. 4).

MATERIALS AND METHODS

In total, 133 specimens from BRIT, F, GH, LL, LP, MEXU, MO, TEX, and WAT in MT (Thiers, continuously updated) were included in the analysis. Data on *Solidago chilensis* (80 specimens), *S. juliae* (11 specimens), and *S. missouriensis* (16 specimens) were measured by the second author for her M.Sc. thesis (Lopez Laphitz 2009) and for Lopez et al. (2011) and used in Lopez Laphitz and Semple (2015) and Semple and Lopez (2016). Specimens of *S. pringlei* (11 specimens) were scored by the first author and first used in Semple and Lopez (2016). New data on *S. durangensis* (two specimens), *S. paniculata* (10 specimens) were scored for this study by the third and fourth authors, and one *S. pringlei* specimen thought to be *S. "aff. missouriensis"* was scored for this study by the first author; this latter specimen was the smaller shoot on *Nesom & Morgan 5302* (TEX; Fig. 7) noted as being annotated as *S. missouriensis* (Semple & Lopez Laphitz 2016). For each specimen, 13 vegetative and 16 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, lower stem pubescence density, and leaf pubescence density were used to define a priori groups along with geographic location. Lower stem leaf traits were not included in the analyses because these were often not present on specimens.

All analyses were performed using SYSTAT v.10 (SPSS 2000). A pair-wise Pearson correlation matrix was created to determine which characters were highly correlated. One trait of each pair that had a $> |0.7|$ correlation value was excluded from the analysis to avoid possible pleiotropic effects of a single gene and to make the tests of null hypotheses more stringent. Stepwise discriminant analysis (STEPDISC) was used to select traits that best separated groups based on the Mahalanobis distances between a priori group centroids in N-dimensional hyperspace. Classificatory Discriminant Analysis was run on N-1 traits selected by the STEPDISC analysis, if more than N-1 traits were selected, where N = lowest sample size of the a priori groups; in this study N=10 and 7 (*Solidago paniculata*; not all traits could be scored on all specimens resulting in few collections being used in the second analysis). A COMPLETE analysis was then run using only five traits. Geisser probabilities of assignment to each a priori group were generated a posteriori for each specimen based on the Mahalanobis distances from the specimen location plotted in N-dimensional hyperspace to each a priori group centroid. Linear and Jackknifed analyses were run in each classificatory analysis to test the strength of group separation in terms of the numbers of discriminating traits. Results are presented in the form of F-value matrices based on Mahalanobis distances between group centroids and tables summarizing the results of the two methods of doing the classificatory discriminant analyses. Conclusions were reached based (1) on the percents of correct placements of specimens a posteriori, (2) on the probabilities of those placements being correct, and (3) on visual reexamination of each specimen via high resolution digital images or the actual

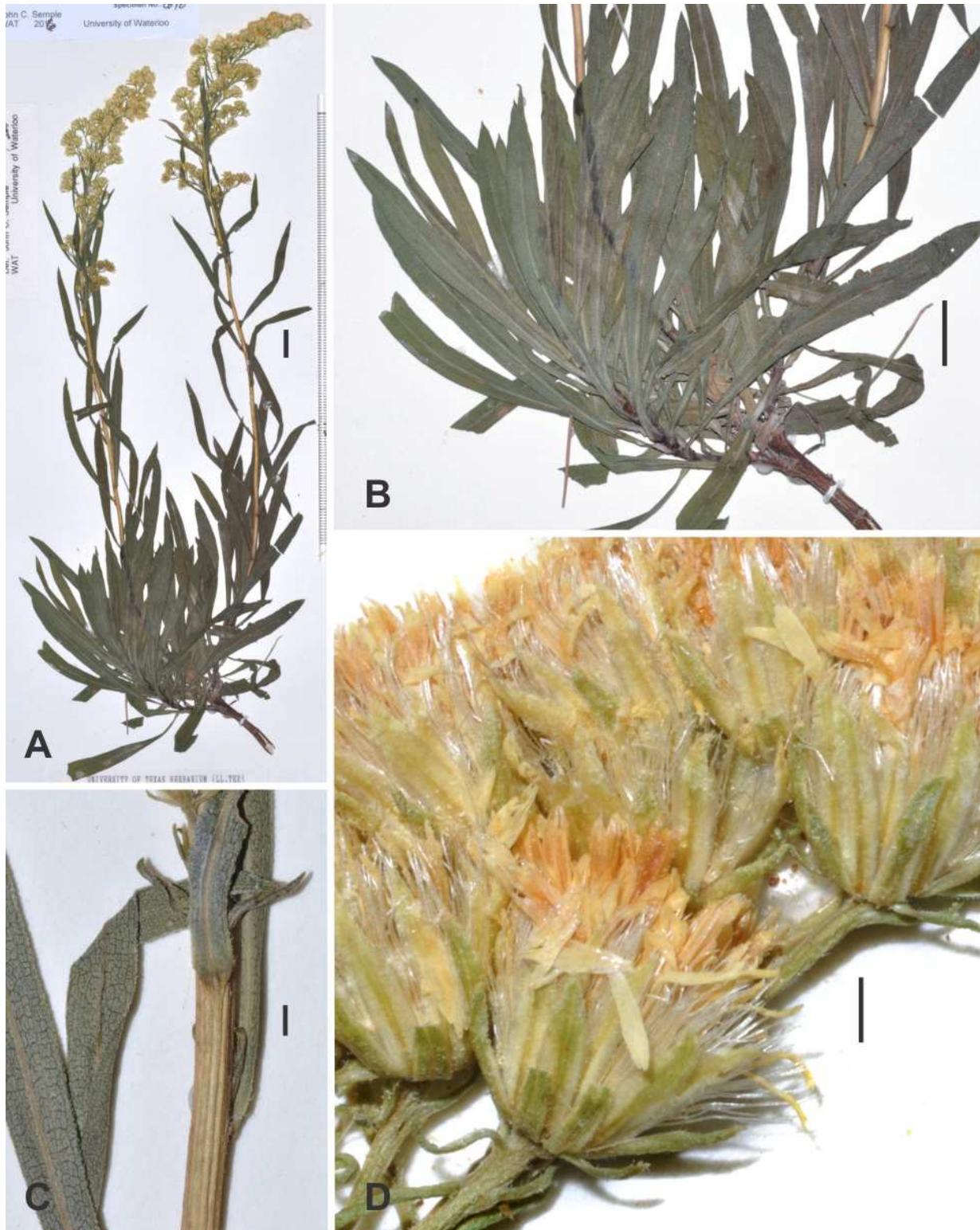


Figure 7. *Solidago* “*aff. missouriensis*” Nesom & Morgan 3502 (TEX) from Nuevo León, Mexico. **A.** Shoot. **B.** Lower or mid stem leaves depending upon how much of the whole shoot is present. **C.** Upper stem and leaves with several small lateral branch leaves in the axes. **D.** Heads. Scale bar = 1 cm in A, B; = 1 mm in C, D. The specimen is more likely an aberrant or damaged shoot of *S. pringlei*.

Table 1. Traits scored for the multivariate analyses of specimens of *Solidago argentinensis*, *S. chilensis*, *S. durangensis*, *S. juliae*, *S. missouriensis*, and *S. pringlei*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip(cm)
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 dentation-number of serrations of lower leaf
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 dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured from 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 dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (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)
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)

specimens. Lastly, a canonical analysis was performed as a dimension reduction technique to allow visualization of results in 1 to 3 dimensions with the number of dimensions being N-1, where in this case N equals the number of a priori groups in an analysis. While canonical analysis allows for a visual presentation of results, the plots are based on fewer axes than were used in the statistical analyses and thus do not fully show the multi-dimensional nature of the separation of a priori groups.

Three analyses were performed. Two six-species a priori groups analyses was performed including 136 specimens of *Solidago argentinensis* and *S. missouriensis* of subsect. *Junceae*, *S. paniculata* of subsect. *Maritimae*, *S. chilensis*, *S. juliae* and *S. pringlei* of subsect. *Tripinerviae*, plus a posteriori two collections of *S. durangensis* and one collection of *S. "aff. missouriensis."* In the first

analysis, mid stem leaf traits were included, but not upper stem leaf traits. In the second analysis, upper stem leaf traits were included but not mid stem leaf traits. The third analysis was performed including just the 102 specimens of *S. chilensis*, *S. juliae*, and *S. pringlei* plus a posteriori two collections of *S. durangensis* and one collection of *S. "aff. missouriensis."*

RESULTS

Six taxon analysis with mid stem leaf traits

In the COMPLETE discriminant analysis of six species level a priori groups *Solidago argentinensis*, *S. chilensis*, *S. juliae*, *S. missouriensis*, *S. paniculata*, and *S. pringlei*, the following five traits were included from a longer list selected in a preliminary STEPWISE analysis and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (27.52), disc corolla length (18.71), ray floret lamina length at anthesis (16.51), disc corolla lobe length (9.00), and mid leaf length (5.02). 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 $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances between group centroids indicated the largest separations were between *S. chilensis* and two species of subsect. *Junceae*, *S. missouriensis* and *S. argentinensis* (108.783 and 88.486, respectively), and the least separations (F-to separate) were between *S. juliae* and *S. pringlei* (5.967) and between *S. chilensis* and *S. pringlei* (9.146) of subsect. *Triplinerviae* and between *S. argentinensis* and *S. missouriensis* (9.824) of subsect. *Junceae*.

Table 2. Between groups F-matrix for the six a priori group analysis including mid stem leaf traits (df = 5, 130).

Group	<i>argentinensis</i>	<i>chilensis</i>	<i>juliae</i>	<i>missouriensis</i>	<i>paniculata</i>
<i>chilensis</i>	88.486				
<i>juliae</i>	38.805	22.206			
<i>missouriensis</i>	9.824	108.783	31.507		
<i>paniculata</i>	79.157	28.961	30.267	91.114	
<i>pringlei</i>	35.641	9.146	5.967	28.861	27.034

Wilks' lambda = 0.0277 df = 5 5 134
 Approx. F = 34.4700 df = 25 484 prob = 0.0000

In the a posteriori Classificatory Discriminant Analysis of the six species level a priori groups plus the two specimens of *Solidago durangensis* and one specimen of *S. "aff. missouriensis"*, the percentage of correct placement to the a priori group ranged from 64-90% (Table 3). The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in decreasing order of percent correct placement. Nine of the 10 specimens of *S. paniculata* were placed a posteriori into the *paniculata* group with 90-100% probability; 1 specimen was placed into the *S. chilensis* group with 70% probability (28% into *S. paniculata*). Fourteen of 16 specimens of *S. missouriensis* (88%) were assigned a posteriori to the *S. missouriensis* group; 9 with 95-100% probability, 2 with 83% and 84% probability; 1 with 65%; and 2 with 52% and 57% probabilities; all other lower probabilities of placement were into the *S. argentinensis* group. Two *S. missouriensis* specimens were placed a posteriori into the *S. argentinensis* group with 69% and 68% probabilities (31% and 32% probabilities to *S. missouriensis*). Seventy of the 80 specimens of *S. chilensis* (88%) were assigned a posteriori to the *S. chilensis* group; 41 with 90-100% probability, 12 with 80-89% probability; 8 with 69-79% probability; and 9 with 45-62% probability. Ten specimens of the *S. chilensis* a priori group were assigned a posteriori to other species; 6 to *S. pringlei* with 59-87% probability; 2 to *S. juliae* with 87% and 98% probabilities; 1 to *S. argentinensis* with 100% probability; and 1 to *S. paniculata* with 55% probability (44% to *S. chilensis*).

Nine of the 11 specimens of *S. juliae* (82%) were assigned a posteriori to the *S. juliae* group; 6 with 95-100% probability; 1 with 74% probability (26% to *S. pringlei*); 1 with 59% probability (36% to *S. chilensis*); and 1 with 51% probability (40% to *S. juliae* and 1% to *S. chilensis*). Two specimens of the *S. juliae* a priori group were assigned a posteriori to *S. pringlei* with 69% and 59% probability (30% and 40% to *S. juliae*). Seven of the 11 *S. pringlei* specimens (64%) were assigned a posteriori to the *S. pringlei* group; 3 with 97-98% probability; 2 with 88% and 81% probabilities; and 2 with 74% and 72% probabilities. Four specimens of the *S. pringlei* a priori group were assigned a posteriori to other species: 2 to *S. chilensis* with 80% and 41% probabilities (20% and 41% *S. pringlei*, respectively); 1 to *S. juliae* with 57% probability (38% to *S. pringlei*); and 1 to *S. paniculata* with 46% probability (27% to *S. chilensis*, 24% to *S. pringlei*)

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six a priori groups using mid stem leaf traits; a posteriori placements to groups in rows.

Group	<i>argentinensis</i>	<i>chilensis</i>	<i>juliae</i>	<i>missouriensis</i>	<i>paniculata</i>	<i>pringlei</i>	% correct
<i>argentinensis</i>	10	0	0	2	0	0	83
<i>chilensis</i>	1	70	2	0	1	6	88
<i>juliae</i>	0	0	9	0	0	2	82
<i>missouriensis</i>	2	0	0	14	0	0	88
<i>paniculata</i>	0	1	0	0	9	0	90
<i>pringlei</i>	0	2	1	0	1	7	64
Totals	13	73	12	16	11	15	85

Jackknifed classification matrix

Group	<i>argentinensis</i>	<i>chilensis</i>	<i>juliae</i>	<i>missouriensis</i>	<i>paniculata</i>	<i>pringlei</i>	% correct
<i>argentinensis</i>	10	0	0	2	0	0	83
<i>chilensis</i>	1	69	2	0	2	6	86
<i>juliae</i>	0	1	7	0	0	3	64
<i>missouriensis</i>	4	0	0	12	0	0	75
<i>paniculata</i>	0	1	0	0	9	0	90
<i>pringlei</i>	0	2	1	0	1	7	64
Totals	15	73	10	14	12	16	81

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for specimens of *Solidago argentinensis*, *S. chilensis*, *S. juliae*, *S. missouriensis*, *S. paniculata*, and *S. pringlei*, and the two collections of *S. durangensis* and the one collection of *S. "aff. missouriensis"* are presented in Fig. 8. Eigen values on the first three axes were 7.050, 0.983, and 0.827.

Six taxon analysis with upper stem leaf traits

In the STEPWISE discriminant analysis of 120 specimens in six species level a priori groups *Solidago argentinensis*, *S. chilensis*, *S. juliae*, *S. missouriensis*, *S. paniculata*, and *S. pringlei*, the following six traits were selected and are listed in order of decreasing F-to-remove values: disc floret pappus length (28.16), disc corolla length (27.43), ray floret lamina length at anthesis (17.83), disc corolla lobe length (8.56), ray floret lamina width (6.17), and disc floret cypsela body length at anthesis (4.40). 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 between group centroids indicated the largest separations were between *S. chilensis* and *S. missouriensis* (102.792) and between *S. missouriensis* and *S. paniculata* (82.248) and the least separation was between *S. juliae* and *S. pringlei* (4.532) and between *S. argentinensis* and *S. missouriensis* (14.721).

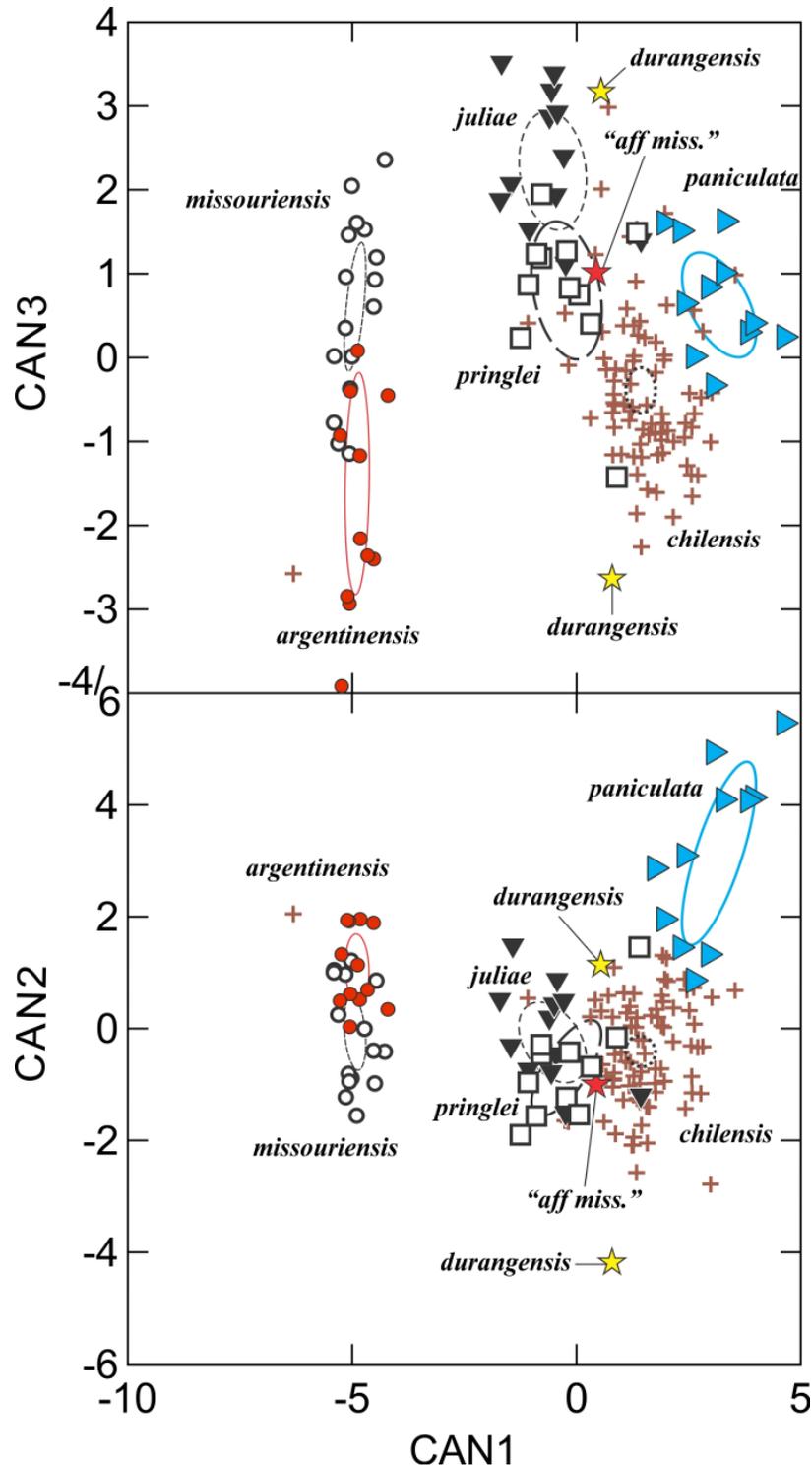


Figure 8. Plots of CAN1 versus CAN3 and CAN1 versus CAN2 of 136 specimens included in the first six a priori groups analysis: *Solidago argentinensis* (red dots) and *S. missouriensis* (circles) of *S.* subsect. *Junceae*, *S. paniculata* of *S.* subsect. *Maritimae*, *S. chilensis* (brown +), *S. juliae* (black triangles) and *S. pringlei* (white squares with black outlines) of *S.* subsect. *Tripinerviae*, and two collections of *S. durangensis* (yellow stars) and one collection of aff. "missouriensis" (red star) that is likely an aberrant *S. pringlei*; COMPLETE analysis with mid stem leaves; 95% confidence ellipses are shown for each group.

Table 4. Between groups F-matrix for the six a priori group analysis including upper leaf traits (df = 5, 130).

Group	<i>argentinensis</i>	<i>chilensis</i>	<i>juliae</i>	<i>missouriensis</i>	<i>paniculata</i>
<i>chilensis</i>	63.847				
<i>juliae</i>	31.199	21.801			
<i>missouriensis</i>	14.721	102.792	28.374		
<i>paniculata</i>	56.987	34.900	31.527	82.248	
<i>pringlei</i>	27.220	12.237	4.532	24.895	33.963

Wilks' lambda = 0.0277 df = 6 5 130
 Approx. F = 29.9599 df = 30 502 prob = 0.0000

In the a posteriori Classificatory Discriminant Analysis of the six species level a priori groups plus the two specimens of *Solidago durangensis* and the one specimen of *S. aff. missouriensis*, *S. paniculata* was the only a priori group with 100% placement of its specimens a posteriori to their a priori group; a posteriori assignments for other groups ranged from 73-94% to their own group (Table 5). The Classification matrix and Jackknife classification matrix are presented in Table 6. Results are presented in decreasing order of percent correct placement. All seven specimens of *S. paniculata* were assigned a posteriori with 100% probability to the species. Fifteen of 16 specimens of *S. missouriensis* (94%) were placed a posteriori into the *S. missouriensis* group: 12 specimens with 91-100% probability; and 3 with 81%, 73% and 58% probabilities (19%, 27% and 42% to *S. argentinensis*. Eleven of 12 specimens of *S. argentinensis* (91%) were assigned a posteriori to the *S. argentinensis* group *S. missouriensis* with 95% probability (5% to *S. argentinensis*). Ten of the 11 specimens of *S. pringlei* (91%) were assigned a posteriori to the *S. pringlei* group: 3 with 95-99% probability, 4 with 82-88% probability; 1 with 79% probability (21% to *S. chilensis*); and 2 with 64% probability (36% and 34% probability to *S. juliae*). One *S. pringlei* specimen was placed a posteriori into the *S. juliae* group with 51% probability (40% to *S. juliae* and 9% to *S. chilensis*). Seventy of the 80 specimens of *S. chilensis* (90%) were assigned a posteriori to the *S. chilensis* group; 55 with 90-99% probability, 9 with 80-89% probability; 5 with 76-79% probability (18-21% to *S. pringlei*), and 3 64%, 59% and 56% probabilities (35%, 39% and 38% to *S. pringlei*). Eight specimens of *S. chilensis* were assigned a posteriori to other species: 5 to *S. pringlei* with 75-88% probability; 7 to *S. juliae* with 97% and 60% probabilities; and 1 to *S. argentinensis* with 100% probability. Eight of the 11 specimens of *S. juliae* (73%) were assigned a posteriori to the *S. juliae* group: 6 with 91-99% probability; 2 with 68% (32% to *S. pringlei*) and 65% (28% to *S. chilensis* and 8% to *S. pringlei*). Three specimens of *S. juliae* were assigned a posteriori to *S. pringlei* with 61%, 61% and 54% probability (38%, 38% and 46% to *S. juliae*). The two specimens of *S. durangensis* were assigned to *S. juliae* with 93% probability (7% to *S. juliae*) and 84% to *S. pringlei* (16% to *S. juliae*). The one *S. "aff. missouriensis"* specimen was assigned a posteriori to *S. pringlei* with 60% probability (28% to *S. chilensis* and 11% to *S. juliae*).

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

Group	<i>argentinensis</i>	<i>chilensis</i>	<i>juliae</i>	<i>missouriensis</i>	<i>paniculata</i>	<i>pringlei</i>	% correct
<i>argentinensis</i>	10	0	0	1	0	0	91
<i>chilensis</i>	1	72	2	0	0	5	90
<i>juliae</i>	0	0	8	0	0	3	73
<i>missouriensis</i>	1	0	0	15	0	0	94
<i>paniculata</i>	0	0	0	0	7	0	100
<i>pringlei</i>	0	0	1	0	0	10	91
Totals	12	72	11	16	7	18	90

Jackknifed classification matrix

Group	<i>argentinensis</i>	<i>chilensis</i>	<i>juliae</i>	<i>missouriensis</i>	<i>paniculata</i>	<i>pringlei</i>	% correct
<i>argentinensis</i>	10	0	0	1	0	0	91
<i>chilensis</i>	1	72	2	0	0	5	90
<i>juliae</i>	0	1	6	0	0	4	55
<i>missouriensis</i>	2	0	0	14	0	0	88
<i>paniculata</i>	0	0	0	0	7	0	100
<i>pringlei</i>	0	0	1	0	0	10	91
Totals	13	73	9	15	7	19	88

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for 120 specimens of *Solidago argentinensis*, *S. chilensis*, *S. juliae*, *S. missouriensis*, *S. paniculata*, and *S. pringlei*, and the two collections of *S. durangensis* and the one collections of *S. aff. missouriensis* are presented in Fig. 9. Eigen values on the first three axes were 7.212, 1.629, and 1.150.

Three taxon analysis

In the STEPWISE discriminant analysis of 102 specimens in three species level a priori groups *Solidago chilensis*, *S. juliae*, and *S. pringlei*, the following eight traits were selected and are listed in order of decreasing F-to-remove values: disc floret pappus length at anthesis (19.47), ray floret lamina length (14.83), mid leaf width (9.68), disc floret cypselas body length at anthesis (8.81), outer phyllary length (6.97), number of mid leaf serrations (5.93), disc corolla lobe length (5.52), and mid leaf length (4.59). 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 between group centroids indicated the largest separations were between *S. chilensis* and the two North American species *S. juliae* and *S. pringlei* (18.965 and 14.423, respectively) and the least separation was between *S. juliae* and *S. pringlei* (5.931).

Table 6. Between groups F-matrix for the three a priori group analysis (df = 8, 92).

Group	<i>chilensis.</i>	<i>juliae</i>	<i>pringlei</i>
<i>chilensis</i>	0.000		
<i>juliae</i>	18.965	0.000	
<i>pringlei</i>	14.423	5.931	0.000

Wilks' lambda = 0.1589 df = 8 2 99

Approx. F = 13.6668 df = 16 184 prob = 0.0000

In the a posteriori Classificatory Discriminant Analysis of the three species level a priori groups plus the two specimens of *Solidago durangensis* and the one specimen of *S. "aff. missouriensis," S. pringlei* was the only a priori group with 100% placement to that group a posteriori; a posteriori assignments for other groups ranged from 91-96% to their own groups. The Classification and Jackknife Classification matrices are presented in Table 7. Results are presented in decreasing order of percent correct placement. Seven of 11 specimens of *S. pringlei* were placed a posteriori into the *S. pringlei* group with 90-100% probability; 3 with 77%, 76% and 74% (22% to *S. juliae*, 23% to *S. chilensis*, and 25% to *S. juliae*, respectively). Seventy-seven of the 80 specimens of *S. chilensis* (96%) were assigned a posteriori to the *S. chilensis* group; 70 with 90-100% probability, 4 with 81-88% probability; and 3 with 77%, 68% and 67% probabilities (23% to *S. pringlei*, 32% to *S. juliae*, and 21% to *S. pringlei* and 13% to *S. chilensis*). Three specimens of the *S. chilensis* group were assigned a posteriori to *S. pringlei* with 90%, 59% and 51% probabilities (10% to *S. chilensis*; 39% to *S. chilensis* and 10% to *S. juliae*; and 25% to *S. chilensis*

and 16% to *S. juliae*; respectively). One specimen of *S. durangensis* was assigned to *S. pringlei* with 98% probability and one was assigned to *S. juliae* with 56% probability (44% to *S. pringlei*). The one *S.* “*aff. missouriensis*” specimen was assigned a posteriori to *S. chilensis* with 95% probability (4% to *S. pringlei* and 1% to *S. juliae*).

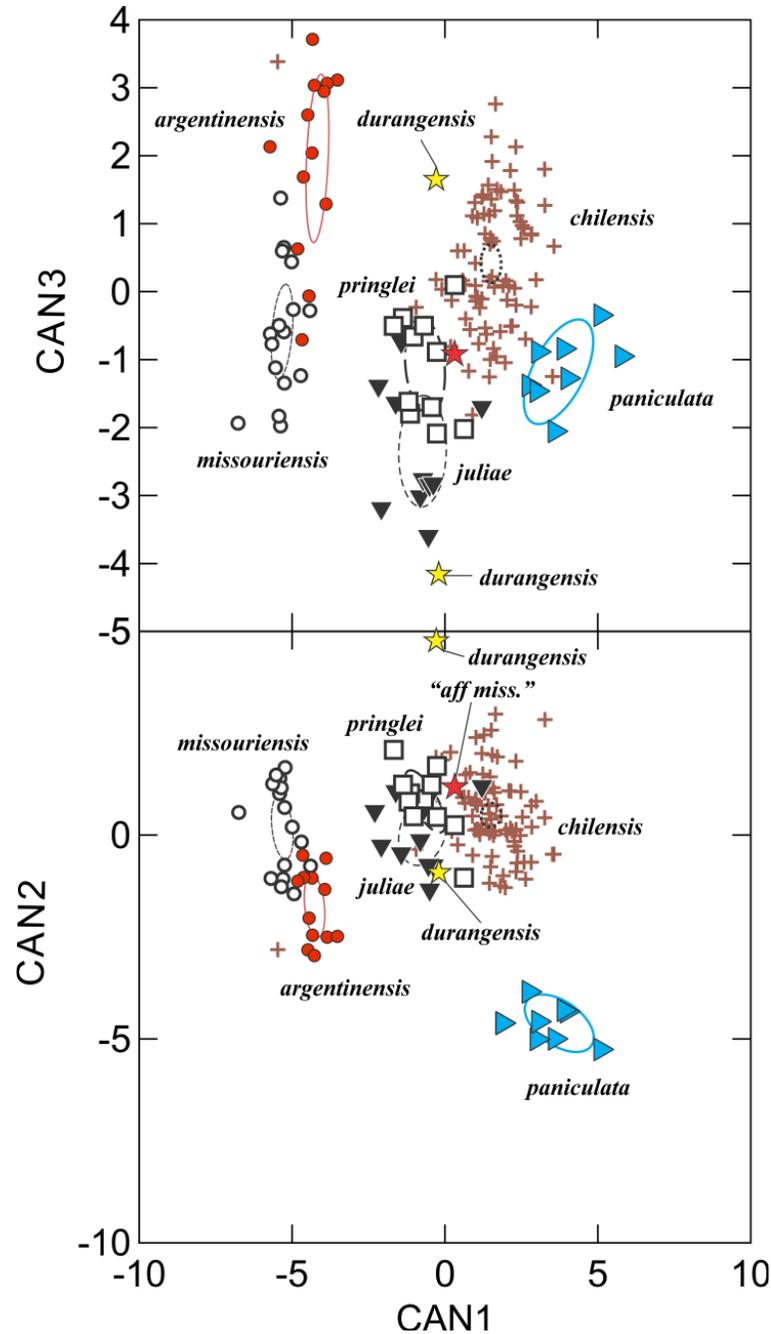


Figure 9. Plots of CAN1 versus CAN3 and CAN1 versus CAN2 of 136 specimens included in the second six a priori groups analysis: *Solidago argentinensis* (red dots) and *S. missouriensis* (circles) of subsect. *Junceae*, *S. paniculata* of subsect. *Maritimae*, *S. chilensis* (brown +), *S. juliae* (black triangles) and *S. pringlei* (white squares with black outlines) of subsect. *Tripinerviae*, and two collections of *S. durangensis* (yellow stars) and one collection of “*aff. missouriensis*” (red star) that is likely an aberrant *S. pringlei*; STEPWISE analysis with upper stem leaves; 95% confidence ellipses are shown for each group.

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

Group	<i>chilensis</i>	<i>juliae</i>	<i>pringlei</i>	% correct
<i>chilensis</i>	77	0	3	96
<i>juliae</i>	0	10	1	91
<i>pringlei</i>	0	0	11	100
Totals	77	10	15	96

Jackknifed classification matrix

Group	<i>chilensis</i>	<i>juliae</i>	<i>pringlei</i>	% correct
<i>chilensis</i>	74	3	3	93
<i>juliae</i>	0	9	2	82
<i>pringlei</i>	1	1	9	82
Totals	75	13	14	90

A two dimensional plot of CAN1 versus CAN2 canonical scores for 102 specimens of *Solidago chilensis*, *S. juliae*, *S. pringlei*, and the two collections of *S. durangensis* and the one collection of *S. "aff. missouriensis"* are presented in Fig. 10. The positions of the two *S. durangensis* specimens and one *S. "aff. missouriensis"* specimen are indicated by two yellow stars and one red star, respectively. Eigen values on the first two axes were 2.209 and 0.492.

DISCUSSION

The results support Nesom's (1993) inclusion of *Solidago durangensis* in subsect. *Triplinerviae* but do not support his (Nesom 1991) protologue comparison with *S. paniculata* of subsect. *Maritimae*. Also, Semple's 2013-2016 (Astereae Lab web site of that time period) placement of *S. durangensis* in subsect. *Junceae* is not supported. The two specimens of *S. durangensis* were assigned a posteriori in the classificatory discriminant analyses to *S. chilensis*, *S. pringlei*, or *S. juliae* with high probabilities in the three analyses. These species are all members of subsect. *Triplinerviae*. The *S. durangensis* specimens were never assigned to species of subsect. *Junceae* or subsect. *Maritimae*. Additional specimens of *S. durangensis* are needed in order to be able to include them in an analysis as their own a priori group. The limited number of collections that Nesom (1991) and we saw for this study were all collected in 1896. A search of the Durango, Mexico, area is needed to determine if the species is still extant. The two specimens of *S. durangensis* did not cluster tightly together in the three analyses. Both specimens were incomplete shoots, which may have resulted in the leaves scored being at upper and lower ends of the ranges of variation for these traits and subsequent differences in canonical scores involving these traits.

This is the first multivariate analysis that has included *Solidago durangensis*, *S. paniculata*, and species of the informal *Tortifolia* group of subsect. *Triplinerviae*. Lopez Laphitz and Semple (2015) did not include *S. pringlei* in their analysis, but Semple and Lopez Laphitz (2016) did. Specimens of *S. chilensis* were placed a posteriori more often into *S. pringlei* than *S. juliae* in all three of the analyses, although in each study the number was low. This indicates that *S. pringlei* shares more similarities with *S. chilensis* than *S. juliae*. All specimens of *S. pringlei* including the isotype of *S. muelleri* Standl. were placed a posteriori into *S. pringlei* only in the three species analysis of this paper, further supporting treating *S. muelleri* as a synonym of *S. pringlei*.

The placement of a specimen of *Solidago chilensis* into *S. argentinensis* was surprising because Lopez Laphitz et al. (2011) noted this did not happen in an analysis that they had run on just *S. argentinensis*, *S. chilensis*, and *S. microglossa*. Lopez Laphitz et al. (2011) and Lopez Laphitz and Semple (2015) included some very short specimens of *S. chilensis* that on stem height alone might be

misidentified as *S. missouriensis*. Also, some specimens of *S. chilensis*, e.g. the shorter shoot on *Nesom & Morgan 5302* (TEX) have pairs of lateral branch leaves, a feature typical of, but thus not exclusive to, subsect. *Junceae*.

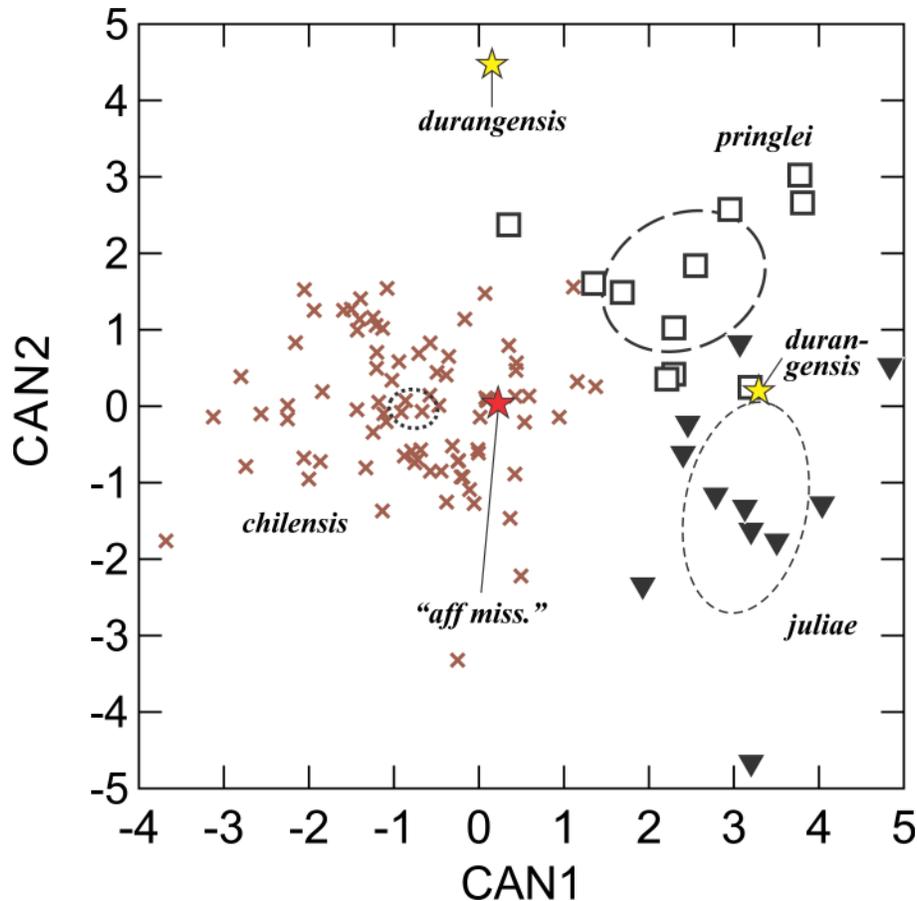


Figure 10. Plots of CAN1 versus CAN2 of canonical scores for 136 specimens of *Solidago chilensis* (brown +), *S. juliae* (black triangles) and *S. pringlei* (white squares with black outlines), and two collections of *S. durangensis* (yellow stars) and one collection of aff. “*missouriensis*” (red star) that is likely an aberrant *S. pringlei*; 95% confidence ellipses are shown for each group.

Multivariate analyses based on the sizes and numbers of parts can sometime yield unexpected results because the traits show some variation due to environmental factors or due to stem damage. This is likely the explanation for a specimen of *Solidago chilensis* being weakly assigned a posteriori in the first analysis to *S. paniculata*, which is the central Mexican endemic species of subsect. *Maritimae*. The *S. chilensis* plant (*Thüngen 127*, LP) came from General Alvarado, Buenos Aires Prov., Argentina, and had lower stem leaves and leaf bases typical of subsect. *Triplinerviae*, i.e., not the largest and without sheathing leaf bases typical of subsect. *Martimae*. In the second analysis, the same specimen was placed a posteriori into *S. chilensis* with 99% probability. Multiple analyses emphasizing different traits can be a useful way to clarify surprising results in one analysis.

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LITERATURE CITED

- Lopez Laphitz, R.M. 2009. The genus *Solidago* L. (Astereae, Asteraceae) in South America and related taxa in North America. M.Sc. dissertation. Univ. of Waterloo. Waterloo, Ontario.
- Lopez Laphitz, R. and J.C. Semple. 2015. A multivariate morphometric analysis of the *Solidago chilensis* complex in South America and related taxa in North America (Asteraceae: Astereae). *Ann. Missouri Bot. Gard.* 100: 423-441.
- Nesom, G.L. 1991. *Solidago durangensis* (Asteraceae: Astereae), a new species from Mexico. *Phytologia* 70: 58-59.
- Nesom, G.L. 1993. Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and observations on the phylogenetic position. *Phytologia* 75: 1-44.
- 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. 2006. *Solidago* Linnaeus. Pp. 107-166, in *Flora North America* Editorial Committee (eds.). *Flora of North America North of Mexico*. Vol. 20. Asteraceae, Part 2. Astereae and Senecioneae. Oxford Univ. Press, New York.
- Semple, J.C. and R. Lopez Laphitz. 2016. On *Solidago gypsophila* and *S. pringlei* (Asteraceae: Astereae), rare and not so rare Mexican endemics: A multivariate study of the *Tortifolia* group of *S.* subsect. *Triplinerviae*. *Phytoneuron* 2016-30. 1–20.
- Semple, J.C., H. Rahman, S. Bzovsky, M.K. Sorour, K. Kornobis, R. Lopez Laphitz, and L. Tong. 2015. A multivariate morphometric study of the *Solidago altissima* complex and *S. canadensis* (Asteraceae: Astereae). *Phytoneuron* 2015-10. 1–31.
- Thiers, B. [continuously updated]. *Index Herbariorum*: A global directory of public herbaria and associated staff. Virtual Herbarium, New York Botanical Garden, Bronx. <<http://sciweb.nybg.org/science2/IndexHerbariorum.asp>>