SOLIDAGO VERACRUZENSIS, A NEW SPECIES OF GOLDENROD IN S. SUBSECT. TRIPLINERVIAE (ASTERACEAE: ASTEREAE) FROM MEXICO

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ABSTRACT

A new species in *Solidago* subsect. *Triplinerviae* is described from collections made primarily in Veracruz, Mexico. In multivariate analyses of *S. altissima*, *S. juliae*, *S. pringlei*, and the new species and in an analysis of the varieties of *S. altissima* and the new species, the new species had 100% a posteriori placement of specimens to the species. The new species generally resembles var. *pluricephala* in reduced upper stem leaf size, but with mean number of rays closer to var. *altissima* and mean ray floret lamina width closer to var. *gilvocanescens*. Upper stem leaves are usually serrate and the phyllaries of the new species are broader than those of *S. altissima* and sometimes multi-veined. The following new name is proposed: **Solidago veracruzensis** Semple, **sp. nov.**

Solidago subsect. Triplinerviae (Torr. & Gray) Nesom includes 20 species of goldenrods with 4 endemic to Mexico: S. durangensis Nesom, S. gypsophila Nesom, S. macvaughii Nesom, and S. pringlei Fern. (Semple 2018 frequently updated). Solidago altissima L. has been reported to be present in Coahuila, Nuevo León, Oaxaca, Tamaulipas, and Veracruz, Mexico (UNAM web site 2018; Nesom annotations 1989, 1990; more recent Villaseñor annotations; herbarium specimens from LL, MEXU, and TEX; Thiers continuously updated), but no collections that I have seen from these states are S. altissima. They are either S. pringlei (Hinton 20068 TEX; Hinton 25587 TEX; White & Chatters 42 LL), S. aff. pringlei (Encina & Portillo G. 822 MEXU-2 sheets, robust shoots), S. missouriensis Nutt (Villarreal & Carranza 8366 MEXU); Nesom annotated several other collections from the Sierra la Gavia region of Coahuila as S. missouriensis, but he did not annotate this sheet) or much less often S. velutina DC. of subsect. Nemorales (Mackenzie) Nesom (Semple et al. 2018) from Coahuila and Nuevo León, while collections from Veracruz, southern Tamaulipas, and northcentral Oaxaca are superficially similar to S. altissima var. pluricephala M.C. Johnston but have upper stem leaves that are more serrate, inflorescences that are often small and lack elongated lower branches, and have phyllaries that are generally wider than those of S. altissima and S. juliae, slightly wider than those of S. pringlei and S. macvaughii, and slightly narrower than those of S. gypsophila.

Multivariate analyses were performed in order to statistically assess differences between the Veracruz collections plus one each from southern Tamaulipas and north-central Oaxaca and specimens of *Solidago juliae, S. macvaughii, S. pringlei*, and *S. altissima* from throughout the range in Canada and the USA and representing all three races of *S. altissima* (var. *altissima*, var. *gilvocanescens* (Rydb.) Semple, and var. *pluricephala*). No specimens from Mexico were included in the multivariate study of *S. canadensis* and *S. altissima* reported by Semple et al. (2015). Also, no specimens from Veracruz were include the multivariate study of *S. altiplanities* C.&J. Taylor, *S. altissima* var. *gilvocanescens*, S. *chilensis* Meyen, *S. gypsophila*, *S. juliae* Nesom, *S. leavenworthii* Torr. & A. Gray, *S. microglossa* DC., *S. pringlei*, and *S. tortifolia* Ell. reported by Semple and Lopez Laphitz (2016). Semple et al. (2016) compared *S. durangensis* to specimens of several species of subsect. *Maritimae* (Torr. & Gray) Nesom and subsect. *Triplinerviae* but did not include specimens from Veracruz or any collections of *S. altissima*.

Multivariate Analyses

Multivariate analyses of 33 specimens of *Solidago altissima* var. *altissima*, 32 specimens of *S. altissima* var. *gilvocanescens*, 38 specimens of *S. altissima* var. *pluricephala*, 11 specimens of *S. juliae*, 1

specimen of *S. macvaughii* included a posteriori as unassigned, 12 specimens of *S. pringlei*, and 13 specimens of *S. veracruzensis* were undertaken following the methods described in Semple et al. (2015, 2016). Two analyses were run. <u>First</u>, specimens of *S. altissima*, *S. juliae*, *S. pringlei*, and *S. veracruzensis* were compared with 1 specimen of *S. macvaughii* included a posteriori. <u>Second</u>, specimens of the three varieties of *S. altissima* and *S. veracruzensis* were compared. All 30 traits scored are listed in Table 1.

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 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 dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
CAPLBRLN	Length of longest lower inflorescence branches (cm)
INVOLHT	Involucre height at anthesis (mm)
OPHYLL	Outer phyllary length (mm)
IPHYLL	Inner phyllary length (mm)
IPHYLLW	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 ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)
DACHPUB	Number of hairs on disc floret ovary/fruit body

Table 1. Traits scored for the multivariate analyses of 137 specimens of *Solidago* subsect. *Triplinerviae*.

Four species analysis

The Pearson correlation matrix yielded r > |0.7| for only mid stem leaf length and upper stem leaf length; the former was not included in the analysis. Midleaf traits and upper leaf width and serrations were included in the analysis. Ray floret ovary/fruit body traits were not included.

In the STEPWISE discriminant analysis of 137 specimens of four species level a priori groups (*Solidago altissima, S. juliae, S. pringlei*, and *S. veracruzenis*), the following seven traits were selected and are listed in order of decreasing F-to-remove values: mid stem leaf width (15.98), number of ray florets (14.79), inner phyllary length (13.36), disc corolla lobe length (13.28), involucre height (6.55), disc corolla length (6.45), and ray floret lamina length (5.51). 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 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. altissima* and *S. pringlei* (18.654); the smallest separations were between *S. juliae* and *S. veracruzensis* (4.043) and between *S. juliae* and *S. pringlei* (4.730).

Table 2. Between groups F-matrix for the four a priori groups in a STEPWISE analysis (df = 16 118).

Group	altissima	juliae	pringlei
juliae	7.088		
pringlei	18.654	4.730	
veracruzensis	5.383	4.043	7.392

Wilks' lambda = 0.1191 df = 16 3 133; Approx. F= 7.6396 df = 48 351 prob = 0.0000

In the Classificatory Discriminant Analysis of 137 specimens of the four species level a priori groups (Solidago altissima, S. juliae, S. pringlei, and S. veracruzenis), percents of correct a posterori assignment to the same a priori group ranged from 84-100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. Twelve of 12 specimens of the S. pringlei a priori group (100%) were assigned a posteriori to the S. pringlei group; 11 specimens with 93-100% probability and 1 specimen with 52% probability (40% to S. juliae; Mueller 2062 GH from Nuevo León, this is the isotype of S. muelleri Standley a synonym of S. pringlei). Twelve of 12 specimens of the S. veracruzensis a priori group (100%) were assigned a posteriori to the S. veracruzensis group; 8 specimens with 92-100% probability (including the holotype and isotype of the species), 2 specimens with 84% and 82% probabilities, and 2 specimens with 75-76% probability. Ten of the 11 specimens of S. juliae (91%) were assigned a posteriori to the S. juliae group: 7 specimens with 93-100% probability, 2 specimens with 86% and 80% probability, and 1 specimen with 60% probability (32% to S. pringlei). One specimen of the S. juliae a priori group was assigned a posteriori to S. veracruzensis with 46% probability (29% to S. altissima and 25% to S. juliae; Nesom & Nesom 7219 BRIT from Blanco Co., Texas). 86 of 102 specimens of S. altissima a priori group (84%) were assigned a posteriori to the S. altissima group: 65 specimens with 90-100% probability, 10 specimens with 82-89% probability, 3 specimens with 73-79% probability, 2 specimens with 66% probability, and 3 specimens with 57% probability (43% to S. veracruzensis; Canning s.n. UBC from Penticton, British Columbia, var. gilvocanescens), 56% probability (44% to S. veracruzensis; Morton NA18776b TRT from Wilmington, North Carolina, var. pluricephala), and 53% probability (46% to S. juliae; Semple & B. Semple 6659 WAT from Walworth Co., South Dakota, var. gilvocanescens). Sixteen specimens of the S. altissima a priori group were assigned a posteriori to other species; 13 to S. veracruzensis with 52-94% probability (10 specimens were var. pluricephala, 2 were var. altissima, and 1 was var. gilvocanescens); 2 to S. juliae with 99% and 84% probability, and 1 to S. pringlei with 36% probability (35% to S. juliae and 28% to S. altissima). The single specimen of S. macvaughii only included a posteriori was assigned to S. veracruzensis with 93% probability.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 137 specimens of *Solidago altissima*, *S. juliae*, *S. mcvaughii* (included a posteriori), *S. pringlei*, and *S. veracruzensis* are presented in Fig. 1. Eigenvalues on the first three axes were 2.565, 0.445, and 0.215.

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

Group	altissima	juliae	pringlei	veracruzensis	% correct
altissima	86	2	1	13	84
juliae	0	10	0	1	91
pringlei	0	0	12	0	100
veracruzensis	0	0	0	12	100
Totals	86	12	13	26	88

Jackknifed classification matrix

Group	altissima	juliae	pringlei	veracruzensis	% correct
altissima	85	2	3	12	83
juliae	0	9	1	1	82
pringlei	0	1	11	0	92
veracruzensis Totals	0	0	0	12	100

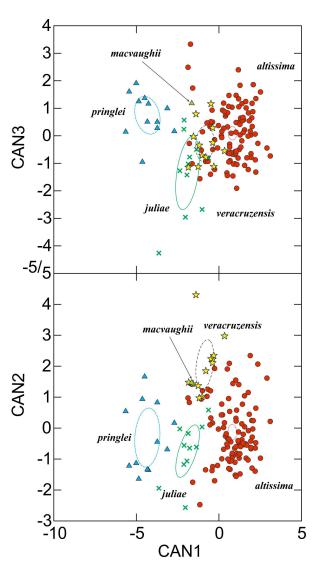


Figure 1. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 137 specimens of *Solidago* subsect. *Triplinerviae: S. altissima* (red dots), *S. juliae* (green \times s), *S. mcvaughii* (light green triangle), *S. pringlei* (blue triangles), *S. veracruzensis* (yellow stars).

Solidago altissima–S. veracruzensis analysis

The Pearson correlation matrix yielded r > |0.7| for most leaf traits and only upper leaf length, width and number of serrations were included. Involuce height and inner phyllary length were correlated and only the former was included. Also, ray floret ovary traits were not included.

In the STEPWISE discriminant analysis of 116 specimens of four a priori groups (*Solidago altissima var. altissima, S. altissima var. gilvocanescens, S. altissima var. pluricephla,* and *S. veracruzenis*), the following five traits were selected and are listed in order of decreasing F-to-remove values: involucre height (22.77), disc corolla length (9.49), ray floret lamina width (7.87), outer phyllary length (5.74), and disc corolla lobe length (4.46). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *S. altissima var. gilvocanescens* and *S. altissima var. pluricephala* (21.207) and *S. altissima var. gilvocanescens* and *S. altissima var. gilvoca*

Table 4. Between groups F-matrix for the four a priori groups in a STEPWISE analysis (df = 5 108).

Group	altissima	gilvocanescens	pluricephala
gilvocanescens	14.944		
pluricephala	3.408	21.207	
veracruzensis	12.537	18.648	12.490

Wilks' lambda = 0.2533 df = 5 3 112; Approx. F= 12.8019 df = 15 298 prob = 0.0000

In the Classificatory Discriminant Analysis of 116 specimens of the four taxa a priori groups (Solidago altissima var. altissima, S. altissima var. gilvocanescens, S. altissima var. pluricephla, and S. veracruzensis), percents of correct a posterori assignment to the same a priori group ranged from 52-100%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. Thirteen of 13 specimens of the S. veracruzensis a priori group (100%) were assigned a posteriori to the S. veracruzensis group; 5 specimens with 98-100% probability, 3 specimens with 83-87% probability, 1 specimen with 74% probability, 2 specimens with 62-63% probability, 1 specimen with 53% probability (20% to var. gilvocanescens, 16% to var. altisssima, and 11% to var. pluricephala; Solano & Vara 378 TEX from Etla, Oaxaca), and 1 specimen with 33% probability (33% to var. pluricephala, 27% to var. altissima, and 6% to var. gilvocanescens; Ventura 10651 TEX from Mpio. Xalapa, Veracruz). Twenty-eight of the 32 specimens of the S. altissima var. gilvocanescens a priori group (88%) were placed a posteriori into the var. gilvocanescens group: 12 specimens with 90-100% probability, 4 specimens with 80-85% probability, 4 specimens with 73-79% probability, 3 specimens with 66-69% probability, 1 specimen with 57% probability (24% to var. altissima, 13% to var. pluricephala, and 6% to S. veracruzensis; Morton & Venn NA15967 TRT from Scott Co., Kansas). Four specimens of the S. altissima var. gilvocanescens a priori group were placed a posteriori in other taxa: 1 specimen to S. veracruzensis with 76% probability (13% to var. altissima and 10% to var. gilvocanescens; Canning s.n. UBC from Penticton, British Columbia), 1 specimen to var. pluricephala with 57% probability (43% to var. gilvocanescens; Morton & Venn NA15994 TRT from Lancaster Co., Nebraska), and two specimens to var. altissima with 51% probabability (37% to var. gilvocanescens and 13% to var. pluricephala; Morton & Venn NA16303 from Canadian Co., Oklahoma) and 50% probability (35% to var. gilvocanescens and 13% to var. pluricephala; Semple 6684 WAT from Eddy Co., North Dakota). Twenty-four or the 38 specimens of the S. altissima var. pluricephala a priori group (63%) were placed a posteriori into the var. pluricephala group: 2 specimens with 82% and 85% probabilities, 7 specimens with 70-79% probability, 7 specimens with 60-68% probability, 6 specimens with 53-59% probability, and 2 specimens with 44% probability (38% to S. veracruzensis and 17% to var. altissima; Anon. s.n. PERTH from Perth Station, Australia) and 38% probability (34% var. gilvocanescens and 25% var. altissima; Morton & Venn NA16455 TRT from Hancock Co., Mississippi). Fourteen specimens of S. altissima var. pluricephala a priori group were placed a posteriori in other taxa: 9 specimens to var. altissima with 66% probability (33% to var. pluricephala; Morton NA18778 TRT from Jones Co., North Carolina), 61% probability (33% to var. gilvocanescens; Semple & Chmiewlski 6297 WAT from Marshall Co., Alabama), 55% probability (38% to var. pluricephala; Morton & Venn NA16473 TRT from Butler Co., Alabama), 54% probability (46% to var. pluricephala; Morton & Venn NA1647154 TRT from Escambia Co., Alabama), 51% probability (46% to var. pluricephala; Morton & Venn NA16570 TRT from Sussex Co., Virginia), 50% probability (41% to var. pluricephala and 7% to S. veracruzensis; Forster PIF13192 K from Ipswich, Queensland, Australia), 43% probability (40% to var. pluricephala and 17% to var. gilvocanescens; Semple 3887 WAT from Okaloosa Co., Florida), 39% probability (29% to var. gilvocanescens and 26% to var. pluricephala; Johnston 12805 TEX from S of Brownsville, Texas), and 38% probability (35% to var. gilvocanescens and 26% to var. pluricephala; Cook et al. C-645 WAT); 3 specimens to S. veracruzensis with 85% probability (10% to var. pluricephala; Nesom et al. 7848 WAT from Natchitoches Par., Louisiana), 54% probability (21% to var. altissima, 17% to var. gilvocanescens, and 8% to var. pluricephala; Morton NA18776b TRT from Wilmington, North Carolina), and 37% probability (37% to var. pluricephala and 25% to var. altissima; Semple & Suripto 10069 WAT from Grimes Co., Texas); and 1 to var. gilvocanescens with 59% probability (33% to var. altissima and 8% to var. pluricephala; Morton & Venn NA16395 TRT from San Patricio Co., Texas). Seventeen or the 33 specimens of the S. altissima var. altissima a priori group (52%) were placed a posteriori into the var. altissima group: 1 specimen 81% probability, 4 specimens with 70-79% probability, 3 specimens with 61-68% probability, 3 specimens each with 50% probability (49% probability to var. pluricephala; Semple & Heard 8307 WAT from Boone Co., Arkansas; tetraploid 2n=36 / 39% to var. pluricephala and 11% to S. veracruzensis; Adelaide, South Australia, Uesugi SAUT no voucher, live collection / and 28% to var. pluricephala and 22% to var. gilvocanescens; Morton & Venn NA15993 TRT from York Co., Nebraska). Sixteen specimens of S. altissima var. altissima a priori group were placed a posteriori into other taxa: 2 specimens to S. veracruzensis with 76% probability (10% to var. altissima and 9% to var. pluricephala; Morton & Venn NA8550 WAT from N of Tobermory, Ontario) and 41% probability (38% to var. altissima and 18% to var. pluricephala; Morton & Venn NA16142 TRT from Randolph Co., West Virginia); 3 specimens to var. gilvocanescens with 87% probability (10% to var. altissima; Morton & Venn NA17660 TRT from S of Pinkham Notch, New Hampshire), 66% probability (17% to var. altissima and 11% to S. veracruzensis; Semple & Chmielewski 5251 WAT from Johnson Co., Kansas), and 46% probability (31% to var. altissima and 17% to S. veracruzensis; Semple 2908 WAT from Kent Co., Ontario); and 11 specimens to var. pluricephala with 72% probability (27% to var. altissima; Cook & Tereszchuk C-339 WAT from Monroe Co., West Virginia), 67% probability (28% to var. altissima; Morton NA18724 TRT from Effingham Co., Illinois), 59% probability (39% to var. altissima; Semple & Heard 8285A WAT from Yell Co., Arkansas), 57% probability (42% to var. altissima; Morton & Venn NA15996 TRT from transplant from Pottawattamie Co., Iowa), 53% probability (46% to var. altissima; Cook & Tereszchuk C-211 WAT from Garland Co., Arkansas), 53% probability (44% to var. altissima; Semple & Suripto 9737 WAT from Pitt Co., North Carolina), 53% probability (23% var. gilvocanescens and 22% var. altissima; Semple & Brammall 2791 WAT from Bruce Co., Ontario), 48% probability (48% to var. altissima; Morton & Venn NA17643 TRT from Portland, Maine), 46% probability (38% to var. altissima and 17% var. gilvocanescens; Semple 10872 WAT from Putnam Co., Georgia), 45% probability (36% to var. altissima and 16% to S. veracruzensis; Morton & Venn NA15993 TRT from York Co., Nebraska), and 42% probability (34% to var. altissima and 23% var. gilvocanescens; Semple & Heard 8284 WAT from Scott Co., Arkansas, tetraploid 2n = 36).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 116 specimens of *Solidago altissima* var. *altissima*, *S. altissima* var. *gilvocanescens*, *S. altissima* var. *pluricephala*, and *S. veracruzensis* are presented in Fig. 2. Eigenvalues on the first three axes were 1.121, 0.641, and 0.134. The placements of the holotype and isotype of *S. veracruzensis* are indicated in Fig. 2.

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

Group	altissima	gilvocanescens	pluricephala	veracruzensis	% correct
altissima	17	3	11	2	52
gilvocanescens	2	28	1	1	88
pluricephala	9	1	24	4	63
veracruzensis	0	0	0	13	100
Totals	28	32	36	20	71

Jackknifed classification matrix

Group	altissima	gilvocanescens	pluricephala	veracruzensis	% correct
altissima	14	3	14	2	42
gilvocanescens	3	26	2	1	81
pluricephala	10	1	23	4	61
veracruzensis	0	0	1	12	92
Totals	27	30	40	19	65

The results indicate that the specimens from Veracruz are statistically distinct from other species in Mexico and from Solidago altissima native to Canada and the USA and introduced into other locations around the globe. In both multivariate analyses, 100% of the S. veracruzensis specimens were placed a posteriori into that group with generally high probability. In the four species analysis, specimens of S. pringlei were most distantly separated from specimens of the other three species, particularly S. altissima. The least separation occurred between the group centroids of S. juliae and S. pringlei and between the group centroids of S. juliae and S. veracruzensis. Thirteen specimens of S. altissima were more similar to S. veracruzensis than to other species. In contrast, in the S. altissima varieties/S.veracruzensis analysis only 7 specimens of S. altissima was more similar to S. veracruzensis than to any of the three varieties of S. altissima. Thus, traits useful in separating S. pringlei and S. juliae from S. altissima and S. veracruzensis created a greater chance of specimens of S. altissima being assigned to S. veracruzensis. A sample size of only 1 meant S. macvaughii could not be included in the species level analysis as a separate a priori group. In the a posteriori classificatory analysis, the single specimen of S. macvaughii (McVaugh 23663 MICH; holotype of species) had a 93% probability of being in the S. veracruzensis group. Semple (2018) noted that S. macvaughii had traits typical of the informal Tortifoliae Group of subsect. Triplinerviae including persistent twisted wilted and pendent lower stem leaves, although Nesom (1989) had originally placed it near S. velutina in subsect. Nemorales (Mackenzie) Nesom. Specimens of S. altissima do not have such persistent senesced lower stem leaves. Very limited data on lower stem leaves was obtained from the collections of S. veracruzensis examined and they are discussed below.

Based on the results of the multivariate analyses, the broader phyllaries that are sometimes multveined, and the allopatric distribution of the *Solidago altissima*-like specimens from Veracruz, a new species of goldenrod endemic to eastern Mexico is proposed.

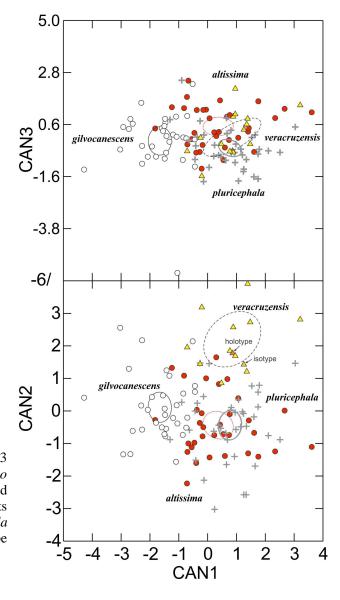


Figure 1. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 137 specimens of *Solidago* subsect. *Triplinerviae: S. altissima* var. *altissima* (red dots), *S. altissima* var. *gilvocanescens* (white dots with black outline), *S. altissima* var. *pluricephala* (gray +s), *S. veracruzensis* (yellow triangles; holotype orange triangles; isotype, pale orange triangles).

SOLIDAGO VERACRUZENSIS Semple, sp. nov. TYPE: MEXICO. Veracruz. Mpio. Jilotepec: El Esquilón, 7 Oct 1971, *F. Ventura A. 4382* (holotype: MEXU 835466; isotype: TEX). Figures 3-5.

Solidago veracruzensis is similar to S. altissima var. pluricephala from Texas but differs in having upper stem leaves with some serrations, phyllaries that are slightly broader and longer and sometimes multiveined, and in often having small thyrsiform inflorescences with very short lower branches.

Plants 80–106–150 cm, rhizomatous. **Stems** erect, proximally densely short villous-strigose canescent, sometimes becoming glabrate with age due to hair loss, distally densely short villous-strigose canescent. **Leaves**: basal rosette not observed; lower stem leaves were not observed with two exceptions discussed below; mid stem leaves sessile, blades oblanceolate, $55-72-115 \times 7-11-17$ mm, tapering to sessile base, apices acute, sparsely to moderately short strigose on adaxial surface, moderately short villous on abaxially surface, moderately to densely so on major veins, margins inrolled with 1-5-11 serrations, 0.5-1.5 mm long, ciliate; upper stem leaves sessile, blades narrowly lanceolate to linear lanceolate, $19-42-65 \times 3-6.2-12$ mm, much reduced distally, vestiture like mid stem leaves, margins with 0-3.4-9 small serrations. **Heads** 40-150+, in narrow thyrsiform or apically secund conical arrays

(Fig. 4) 8–20–31 cm tall × 2–4.3–14.5 cm wide, branches 1-14 cm, usually diverging ascending-arching, heads secund on longest branches of large arrays, bracts, linear lanceolate. **Peduncles** 0.2–10 mm, moderately short villoso-hirtellous; bracteoles few, linear-lanceolate. **Involucres** likely cylindrical when fresh, but spreading distally when pressed, 3.1-4-5 mm. **Phyllaries** in 3–4 series, broadly to narrowly lanceolate, unequal (outer 1/4 – 1/3 length of inner), margins entire to slightly fimbriate distally, sparsely ciliate, apices acute, fimbriate, often with minute stipitate glands; central vein thicker proximally, rarely multi-veined. **Ray florets** 7–**10.5**–15; laminae yellow $1.3-1.6-2 \times 0.3-0.4-0.8$ mm; ovary 0.5–0.7–1.1 mm at anthesis, moderately strigillose, pappi 2–3–3.7 mm at anthesis, longest not clavate, others narrow, tapering. **Disc florets** yellow, 3–6–8; corollas 3–3.7–4.2 mm, lobes 0.76–0.9–1.13 mm; ovary (narrowly obconic) 0.7–0.8–0.9 mm at anthesis, moderately strigillose; pappi 2.6–3.3–4 mm, longest not clavate. Mature cypselae: fruit body 1–1.5 mm, pappi ca. 2–3.5 mm, very rare a 1-2 very short outer bristles. **Chromosome number**: unknown. (Means in **bold face**).

Dark sandy soil, red-clay soil, limestone hillside in scrub in canyon, disturbed oak vegetation, along road cuts in pine forest, grassy roadsides and pastures, in cut-over fields along ridge, and in relatively undisturbed grassland remnants. Elevations range from 650-2050 m (2130-6725 ft), averaging 1286 m. *Solidago veracruzensis* grows at generally higher elevations than *S. altissima* var. *pluricephala* in southern Texas and in mountainous areas versus flat outer coastal plain habitats.

Only a few specimens of *Solidago veracruzensis* had lower stem leaves. *Dressler 2309* (MEXU) from southern Tamaulipas had just one senesced proximal lower stem leaf that was pendent, slightly twisted proximally, serrate, and incomplete measuring ca. 33 mm \times ca. 6 mm wide (Fig 7A). The mid stem leaves of *Dressler 2309* (MEXU) were similar to those of the type specimens of *S. veracruzensis*. *Arriga C. 36* (MEXU) from Miahuatlan, Veracruz had several distal lower stem leaves with damaged apices that were 117 mm \times 11.5 mm and ca 104 mm \times 13 mm and were similar to the large lower mid stem leaves observed on the specimen. *Vibrans 7085* (MEXU:1128470) had some upper lower stem leaves; only one was senesced, not twisted, and it was ascending and damaged. All other collections of *S. veracruzensis* either lacked lower stems or had lower stems without any lower stem leaves attached. Lower stem leaves similar to the senescent, twisted and pendent brown to black lower stem leaves observed on some specimens of *S. juliae, S. macvaughii*, and *S. pringlei* and other species of the *Tortifoliae* group were not observed on any collections of *S. veracruzensis*. Specimens of *S. altissima* lack twisted lower leaves.

The mid and upper stem leaves of *S. veracruzensis* generally had moderately inrolled leaf margins with some specimens more pronouncedly so. In rolled leaf margins occur in all species of *S. subsect. Triplinerviae* varying from subtlety so (e.g., *S. canadensis, S. gigantea* Ait., *S. gypsophila*, and *S. juliae*) to obviously so other taxa (e.g., *S. altissima* var. *pluricephala* and *S. chilensis*). Inrolled margins vary from subtle to pronounced in some species (e.g., *S. pringlei, S. lepida* DC., and *S. tortifolia* Ell.). Slightly inrolled leaf margins also occur on many specimens of *S. subsect. Venosae* (G. Don in Loudon) Nesom, some specimens of *S. subsect. Nemorales* and *S. subsect. Solidago*, rarely in *S. subsect. <u>Humiles</u> (Rydb.) Semple, and very rarely in <i>S. subsect. Squarrosae* A. Gray and *S. sect. Ptarmicoidei* (House) Semple & Gandhi. Thus, inrolled leaf margins is not diagnostic for any one species or group or species, but is occurs in highest frequency in *S. subsect. Triplinerviae*.

Only two collections of *Solidago veracruzensis* had broad phyllaries with multiple veins (Fig. 6G), *Solano & Vara 378* (TEX) Mpio. San Juan Guelache Etla, Oaxaca, which is significantly disjunct from the main body of the species's distribution in central Veracruz and *Iltis et al. 860* (TEX) from Acajete, Mpio Xalapa, Veracruz in the center of the distribution of the species. Multi-veined phyllaries occur rarely in species of the *Tortifoliae* Group of subsect. *Triplinerviae: S. juliae, S. leavenworthii*, and *S. pringlei* in Mexico or the southern USA and *S. chilensis* and *S. microglossa*, native to South America. Multi-veined phyllaries have not been observed in the generally narrow phyllaries of *S. altissima*. Multi-



Figure 3. Holotype of Solidago veracruzensis Semple: Ventura 4382 (MEXU).

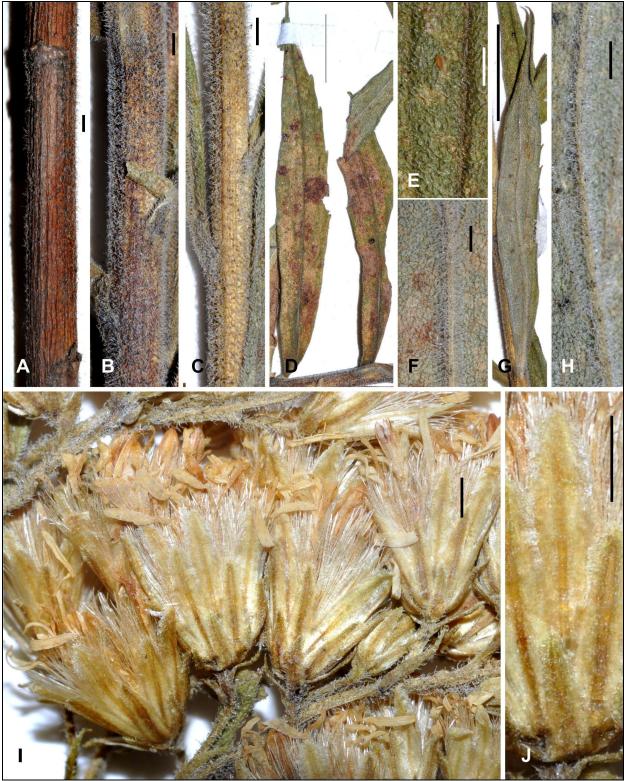


Figure 4. Details of the morphology of the holotype of *Solidago veracruzensis*, Ventura 4382 (MEXU). A-C. Lower, mid, and upper stems. D. Mid stem leaf. E-F. Mid stem leaf adaxial and abaxial surfaces. G-H. Upper stem leaf and abaxial midvein. I. Heads. J. Phyllaries. Scale bars = 1 mm in A-C, E-F, H-I; = 1 cm in D and G.



Figure 5. Isotype of Solidago veracruzensis Semple: Ventura 4382 (TEX).

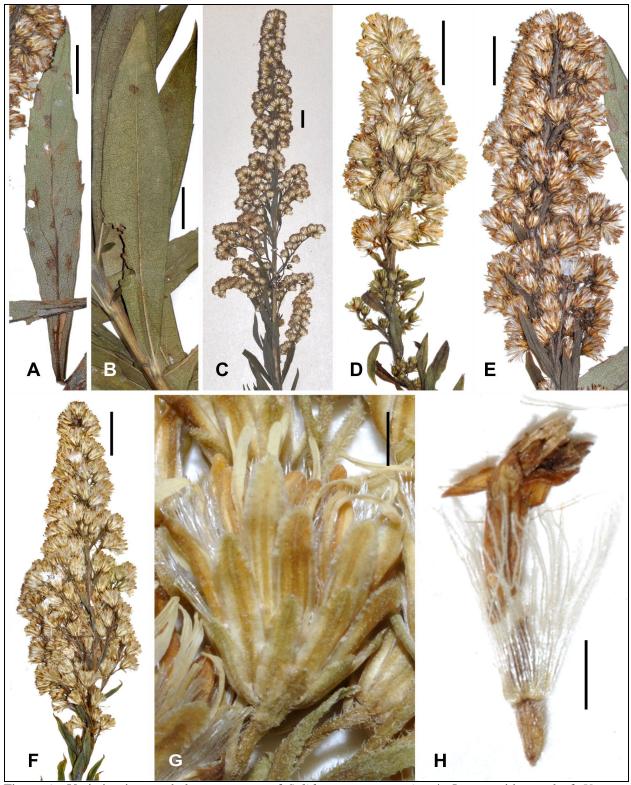


Figure 6. Variation in morphology non-type of *Solidago veracruzensis*. **A**. Lower mid stem leaf, *Ventura* 9132 (TEX). **B**. Mid stem leaf, abaxial surface, *Acosta & Dorantes* 537 (TEX). **C**. Elongated narrow inflorescence, *Boege* 2051 (MEXU). **D-F.** Small inflorescences, *Rzedowski* 12151 (TEX), *Ventura* 9132 (TEX), and *Garcia et al.* 1885 (TEX). **G**. Broad multi-veined phyllaries, *Solano & Vara* 378 (TEX). **H**. Disc floret, post anthesis, *Acosta & Dorantes* 537 (TEX). Scale bars = 1 mm in G-H; = 1 cm in A-F.



Figure 7. Lower stem leaves of *Solidago veracruzensis*. **A.** Wilted proximal lower stem leaf, *Dressler 2309* (MEXU). **B.** Distal lower stem leaves, *Arriga C. 36* (MEXU). Scale bars = 1 cm.

veined phyllaries also occur rarely to frequently in other species of other subsections in *Solidago* and thus the feature is not diagnostic for any one group of goldenrods.

Inflorescence size and shape varies from small club-shaped forms (Figs. 6D-F) to large secund conical forms with long lower branches (Fig. 5) and elongated narrow forms with short lower branches (Fig. 6C). About half of the specimens examined had small to midsize inflorescences with club or narrow second conical inflorescences. This might be a sampling bias favoring shoots that fit on herbarium sheets. The isotype from TEX has the largest inflorescence observed, while the holotype has one of smaller second conical ones observed with short lower inflorescence branches.

The distribution of Solidago veracruzensis in eastern Mexico is shown in Fig. 8 along with the distributions of S. durangensis, S. gypsophila, S. juliae, S. macvaughii and S. pringlei. With one northern disjunct exception in Tamaulipas and one disjunct collections from central Oaxaca, all collections included in the S. veracruzensis came from central Veracruz. The range of all species are allopatric, with those of S. durangensis, S. gypsophila and S. macvaughii being very restricted. This is in contrast to the distributions of S. wrightii A. Gray of subsect. Thyrsiflorae in the western cordillera (Semple et al. 2017, Fig. 13) and S. velutina DC. of subsect. Nemorales in the eastern cordillera (Semple et al. 2018, Fig. 24). The extensive ranges of distribution of the varieties of S. altissima are illustrated by Semple (2018 frequently updated). The range of S. juliae extends slightly further north in Texas. Only two of the collections of S. juliae illustrated at the UNAM website were thought to be that species. The single collection from Coahuila, Marsh 922 (MEXU:56696), includes just an upper portion of the stem with inflorescence and appears to be S. juliae. The single collection from Chihuahua, Pringle 1116 (MEXU:T33225), is treated here as S. aff. *juliae* because the leaves are more broadly lanceolate than seen in the Texas collections of the species. The collection was annotated as "S. juliae" by G.L. Nesom in 1990 and by J.L. Villaseñor in 2003 and originally identified as "S. canadensis var. canescens" by Pringle in the 1880s, which is a synonym of S. juliae. This may just be isolated marginal population divergence; further study is needed. A second collection from Chihuahua, Cronquist 10228 (MEXU 146256) annotated as "Solidago juliae" by G.L. Nesom in 1990 is here treated as S. velutina DC based on its

lowest stem leaves being the largest on the stem. Semple et al. (2018) noted that some collections of *S. velutina* could be misidentified to species of subsect. *Triplinerviae*, particularly if the lower stem leaves were absent.

Solidago veracruzensis is likely closely related to S. pringlei Fern., S. durangensis, S. gypsophila, and S. macvaughii of Mexico based on similar involucre and floral traits. All five species may be derived from a common ancestor via vicariant biogeographic events splitting the ancestral taxon into disjunct populations and habitats. Solidago veracruzensis is also likely closely related to S. altissima of the USA and Canada based on general similarities in leaf features such as the general lack of persistent, dark, twisted lower stem leaves. A polygenomic multi-loci molecular study of all taxa is needed to really determine relationships among species in S. subsect. Triplinerviae.

Additional collections of S. veracruzensis seen. MEXICO. Tamaulipas. Mpio. Aldama: Sierra de Tamaulipas: region of Rancho Las Yucas, ca. 40 km NNW of Aldama, 9 Oct 1957, Robert L. Dressler 2309 (MEXU 48751, digital image). Veracruz. Mpio. Banderilla: Banderilla, 12 Oct 1973, Acosta & Dorantes 537 (TEX). Mpio. Calcahualco: 11 km al N de Coscomatepec, por la terracería a Escola, 30 Sep 1984, García, Koch, González, & Hernández 1885 (MEXU 484202). Mpio. Coacoatzintla: Entrada al Rancho La Palma, carretera Jilotepec-Coacoatzintla, 2 Nov 1998, Lizama M.J. 1227 (MEXU 260258, digital image). Mpio. Juchique de Ferrer: alrededores de Juchique camino Juchique ple de las Hayas, 28 Apr 1976, Aponte et al. C-240 (TEX). Mpio. Miahuatlán: Miahuatlán, 15 Nov 1979, Arriga C. 36 (MEXU 564021, digital image); Naolinco, camino a Miahuatlán, 7 Nov 1981, Ventura A. 19079 (MEXU 338837); above the Cascades at Noalinco, 10 Nov 1983, Turner & Tapia 15473 (TEX). Mpio. Orizaba: NW of Orizaba, Cerro del Borrego, 14 Dec 1959, Rzedowski 12151 (TEX). Mpio. Tequila: S of Rizaba along road to Zongolica, 5.0 mi N of Tequila, 9 Oct 1984, Sundberg & Lavin 3074 (TEX). Mpio. Xalapa: vicinity of Acajete, ca 15 km NW of and above Xalapa on road to Perote, 8 Oct 1978, Iltis, Castillo C., & Lasseigne 860 (TEX, MEXU 835466); Casa Blanca, 28 Oct 1976, Ventura 13474 (MEXU, TEX); Jardin Botanico Clavijero, 25 Apr 1978, Ortega & Calzada 0-789 (TEX); Cerro Macuiltepetl Ladera W, 15 Nov 1979, Garcia & Palma 80 (MEXU 352141); Colonia Azteca, 9 Apr 1974, Ventura A. 9864 (TEX); 9 km al E del Castillo, 20 Oct 1971, Dorantes 400 (TEX, MEXU 219617); near Jalapa, 6 Jul 1908, Pringle 15605 (LL); Jalapa, 4 Feb 1894, Smith 1603 (TEX); Marties de Chicago, 16 Oct 1974, Ventura 10651 (TEX, MEXU); camino al Sumidero, 22 Sep 1976, Zola B. 761 (MEXU) 259921); Cd. Xalapa, 8 Sep 1970, Ventura A. 2310 (MEXU 350141, TEX); Rancho Guadalupe, 3 km W de Jalapa carretera vieja Jalapa-Coatepec, 8 Sep 1970, Monroy et al. 33 (MEXU 260258); en las afueras de la ciudad (entre rancherías), hacia el sur, 14 Dec 2000, Vibrans 7085 (MEXU 1128470); Rancho Guadalupe 3 km W de Jalapa carretera vieja Jalapa Coatepec, 20 Aug 1975, Calzada & colaboradores 1888 (MEXU 213054, digital image); W of turn off to Lago Farfan, along road to Juchique, 6 Sep 2001, Bye 28262 (MEXU 1012466, digital image); Jalapa-Consolapan, 1 Sep 1971, Boege 2051 (MEXU 194191).

A summary of descriptive statistics on morphological traits based on all raw values in the data matrix used in the multivariate analysis of *Solidago altissima*, *S. juliae*, *S. pringlei*, and *S. veracruzensis* is presented in Table 6. Disc floret ovary/fruit body measurements were for florets at flowering; mature cypselae have larger values.

Key to Solidago veracruzensis and related species

- 1. Inner phyllaries averaging (0.5-)0.6–0.8-(10) mm wide.

 - 2. Smaller veins of leaves under surfaces raised, densely hairy; Coahuila S. gypsophila
- 1. Inner phyllaries averaging 0.4–0.6 mm wide.
 - 3. Inflorescences broadly secund conical and somewhat corymbiform; Durango S. durangensis
 - 3. Inflorescences secund conical to narrowly second conical, not corymbiform.

- 4. Stems and leaves sparsely to moderately villous-canescent or more densely so on Great Plains in the US.

 - 5. 10-**20**-33 florets per head; leaves narrowly lanceolate; lower stem leaves if present, twisted, pendent, senescent, achlorophyllous; Mexico.

6. Mid stem leaves linear-lanceolate, serrations usually few; Coahuila, Nuevo León S. pringlei

6. Mid stem leaves oblanceolate, serrations numerous; Aguascalientes S. macvaughii

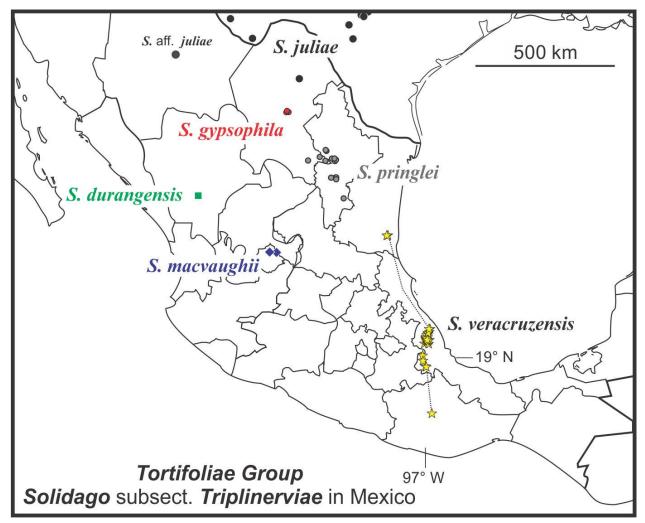


Figure 8. Distribution of species of the *Tortifoliae* Group of *Solidago* subsect. *Triplinerviae* in Mexico. See text for comments on the *S*. aff. *juliae* collection from Chihuahua.

Trait	S. altissima	S. juliae	S. pringlei	S. veracruzensis
STEMHT cm	33- 87 -200	60– 95 –180	32 49 70	73– 99 –150
LLFLN mm	30- 82.8 -158	74– 108 –127	38- 67.4 -110	103– 110 –117
LLFWD mm	5– 13.5 –35	5.5– 11 –15	4.7– 5.8 –8.5	11.5– 12.3 –13
LLFWTOE mm	16– 40.7 –80	17– 41.4 –60	15– 27 –55	40– 42.5 –45
LLFSER	0-7-22	9- 12 -18	0-4.5-15	5- 6.5 -8
MLFLN mm	33– 69.3 –133	27– 49.7 –88	14– 34.1 –102	55– 73.3 –115
MLFWD mm *	5– 11.5 –30	4– 7.2 –17	3- 9.5 -30	7.2– 10.6 –17
MLFWTOE mm	14– 36.2 –70	9– 23 –35	12– 27 –45	20– 32.2 –50
MLFSER	0-6-17	0– 3.1 –14	0- 4.7 -14	1- 5.6 -11
ULFLN mm	17– 45.7 –102	12– 29.6 –80	16– 41.4 –86	19– 43 –65
ULFWD mm	2- 8.0 -10	2.5– 4.6 –9	1.5– 4.1 –10	3- 6.1 -12
ULFWTOE mm	6– 24.8 –60	6– 14.1 –28	10– 19.8 –40	10– 19.7 –33
ULFSER	0– 3 –11	0 –0.8 –6	0– 2.1 –11	0– 3.6 –10
CAPL cm	5– 18.2 –38	11– 21.7 –37	3.5– 8.9 –14.5	5.5– 12.8 –24
CAPW cm	1.5– 11.8 –35	5.5– 8.3 –11	2– 4.5 –10	2- 7.8 -19
INVOLHT mm *:	2– 3.3 –4.8	2.6– 3.4 –4.1	3– 3.5 –4.5	3.1– 4.05 –5.1
OPHYLN mm	0.5-1.15-2.3	0.8– 1.3 –2	0.9– 1.4 –2	1– 1.3 –2
IPHYLN mm *	2– 2.6 –4.5	2.3.– 2.8 –3.5	2.6– 3.4 –4.3	3– 3.9 –5
IPHYLW mm	0.4– 0.5 –0.6	0.4– 0.55 –0.7	0.4– 0.6 –0.8	0.6– 0.8 –1
RAYNUM	1– 9.1 –21	6– 10.4 –18	7– 12.6 –20	7– 10.7 –15
RLAMLN mm *	0.9– 1.3 –2.8	0.7– 1.26 –1.8	1.4– 1.8 –2.9	1.3– 1.7 –2.3
RLAMWD mm	0.1– 0.3 –0.7	0.1– 0.34 –0.6	0.2– 0.5 –1	0.3– 0.45 –0.8
DISCNUM *	1– 4.5 –13	2- 5.8 -9	3– 8.5 –13	3- 5.7 -8
DCORLN mm *	2.5– 3.6 –6	2.5– 3.2 –4	2.9– 3.3 –4.1	3– 3.7 –4.2
DLOBLN mm *	0.3– 0.8 –1.1	0.5– 1.1 –2	0.7– 1.0 –1.4	0.5– 0.86 –1.1
DACHLN mm at anthesis	0.3– 0.7 –1	0.5– 0.8 –1.3	0.6– 0.8 –1.2	0.7– 0.8 –1
DPAPLN mm at anthesis	1.5– 3.0 –3.5	2– 2.7 –4	2.1– 2.7 –3.6	2.6– 3.2 –4

Table 6. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analyses *S. durangensis*, *S. gypsophila*, *S. juliae*, *S. macvaughii*, *S. pringlei*, and *S. veracruzensis*: min-mean-max. The lowest stem leaves are also generally absent by flowering.

* Traits selected by the STEPWISE analysis as useful in separating a priori groups

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LITERATURE CITED

Nesom, G.L. 1989. Taxonomy of *Solidago velutina* (Asteraceae: Astereae) with a new related species from Mexico. Phytologia 67: 297–303.

- Semple, J.C. 2018. On *Solidago macvaughii* (Asteraceae: Astereae) a rare Mexican endemic in the *Tortifoliae* Group of *S.* subsect. *Triplinerviae*. Phytoneuron 2018–35: 1-6.
- Semple, J.C. and R. Lopez Laphitz. 2016. On Solidago gypsophila and S. pringlei (Asteraceae: Asteraee), rare and not so rare Mexican endemics: A multivariate study of the Tortifolia group of S. subsect. Triplinerviae. Phytoneuron 2016-29: 1–20.
- Semple, J.C., K. Kornobis, and S. Bzovsky. 2018. A multivariate morphometric analysis of *Solidago* subsect. *Nemorales* (Asteraceae: Astereae). Phytoneuron 2018-42: 1–40.
- Semple, J.C., R. Lopez Laphitz, H. Rahman, and Yunfei Ma. 2016. On Solidago durangensis (Asteraceae: Astereae): A multivariate study with specimens of S. subsect. Junceae, S. subsect. Maritimae, and S. subsect. Triplinerviae. Phytoneuron 2016-49: 1–19.
- Semple, J.C., Y. Ma, U. Naik, N. Steenhof, and L. Tong. 2017. A multivariate morphometric analysis of Solidago subsect. Thyrsiflorae (Asteraceae: Astereae). Phytoneuron 2017-77: 1–37.
- 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. New York Botanical Garden's Virtual Herbarium.
- UNAM. 2018. Portal de Datos Abiertos UNAM. https://datosabiertos.unam.mx/