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ON *SOLIDAGO SIMPLEX* (ASTERACEAE: ASTEREAE): A MULTIVARIATE STUDY INCLUDING *S. GLUTINOSA*, *S. LEIOCARPA*, *S. MULTIRADIATA*, AND *S. SPATHULATA*

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ABSTRACT

Solidago simplex from the Sierra Madre Oriental of Mexico is included in a multivariate study with *S. glutinosa* and *S. spathulata* of subsect. *Humiles* and *S. leiocarpa* and *S. multiradiata* of subsect. *Multiradiatae* in order to assess statistical support for recognizing *S. simplex* as a separate species from *S. glutinosa* of the Rocky Mts and Great Plains and westerm boreal forest east to disjunct areas in Michigan and Ontario. *Solidago simplex* is statistically distinct and intermediate in a number of traits between *S. glutinosa* and *S. multiradiata*. The analyses indicate that *S. glutinosa*, *S. simplex,* and *S. spathulata* (subsect. *Humiles*) and *S. leiocarpa* and *S. multiradiata* (subsect. *Multiradiatae*) should be recognized as species.

Solidago simplex Kunth (Nov. Gen. 103. 1818; Figs. 1-2) was described from a collection from northeastern Mexico nearly two centuries ago:

TYPE: **MEXICO**. **Nuevo León**. Santa Rosa "Crescit prope pagum Sanctae Rosae mexicanorum," *Bonpland & von Humboldt 1300* (holotype: P, fiche!, digital image jSTOR!).

Application of the name *S. simplex* has varied considerably in floristic treatments. For much of the time, plants from Canada and the USA were treated under multiple species names that all belong in synonymy under *S. glutinosa* Nutt. (Fig. 3), *S. spathulata* DC. (Fig. 4), or *S. simplex*, depending upon whether or not Nesom (1989) was correct in lumping the Canadian, USA, and Mexican plants (Fig. 5) into a single species occurring from Hidalgo, Mexico, to Alaska in the mountains and east to Michigan and northwestern Ontario and whether or not *S. spathulata* native to the California and Oregon coast is included in the lumping. After *S. simplex*, *S. spathulata* DC. is the next oldest valid name: Prodr. 5: 339. 1836; *Solidago simplex* Kunth var. *spathulata* (DC.) Cronquist (Intermountain Fl. 5: 244. 1994):

TYPE: **USA**. **California**. Probably Monterey peninsula, *Haenke s.n.* (holotype: G-DC!; isotype?: P digital image jSTOR!).

Solidago glutinosa Nutt. follows is the next oldest valid name: Trans. Amer. Phil. Soc. n.s. 7: 328. 1841. *Solidago glutinosa* var. *glutinosa* (Nutt.) Cronq., Rhodora, 49: 76. 1947; *Solidago spathulata* subsp. *glutinosa* (Nutt.) Keck (Aliso 4: 104. 1958):

LECTOTYPE (Ringius, Taxon 35: 155. 1987): **USA**. [**Oregon**]. "On the Oregon and Wahlemet rivers," *Nuttall s.n.* (BM!); isolectotype: (PH!).

Solidago stricta Hook. (Fl. Boreali-Amer. 2: 4: 1834; non Ait. 1763, nec Moench 1802, nec Less. 1831) and *S. confertiflora* DC. (Prodr. 5: 339. 1836; non Nutt. 1836, non Fisch. & Mey. 1841. *Solidago virgaurea* L. var. *confertiflora* (DC.) Kurtz (Engl. Bot. Jahrb. 19: 386. 1894):

TYPE: **CANADA**. **British Columbia**. "Nootka" Sound on Vancouver Is., *Haenke s.n.* (holotype: G-DC!). — these two are not valid names.

The names *Solidago decumbens* Greene (Pittonia 3: 161. 1897), *S. aureola* Greene (Pittonia 4: 236. 1901), *Solidago aureola* Greene (Pittonia 4: 236. 1901), *S. yukonensis* Gandoger (Bull. Soc. Bot. France 50: 214. 1903), and *S. vespertina* Piper in Piper & Beattie (Fl. Northw. Coast. 365. 1915) have all been applied to specimens of *S. glutinosa* as treated here. Cronquist (1947) lumped *S. gillmanii* (Gray) Steele, *S. racemosa* Greene, and *S. randii* (Porter) Britt. as varieties in *S. glutinosa* subsp. *randii* (Porter)

Figure 1. Example of *Solidago simplex* used in the multivariate study: *Beaman 2736* (GH).

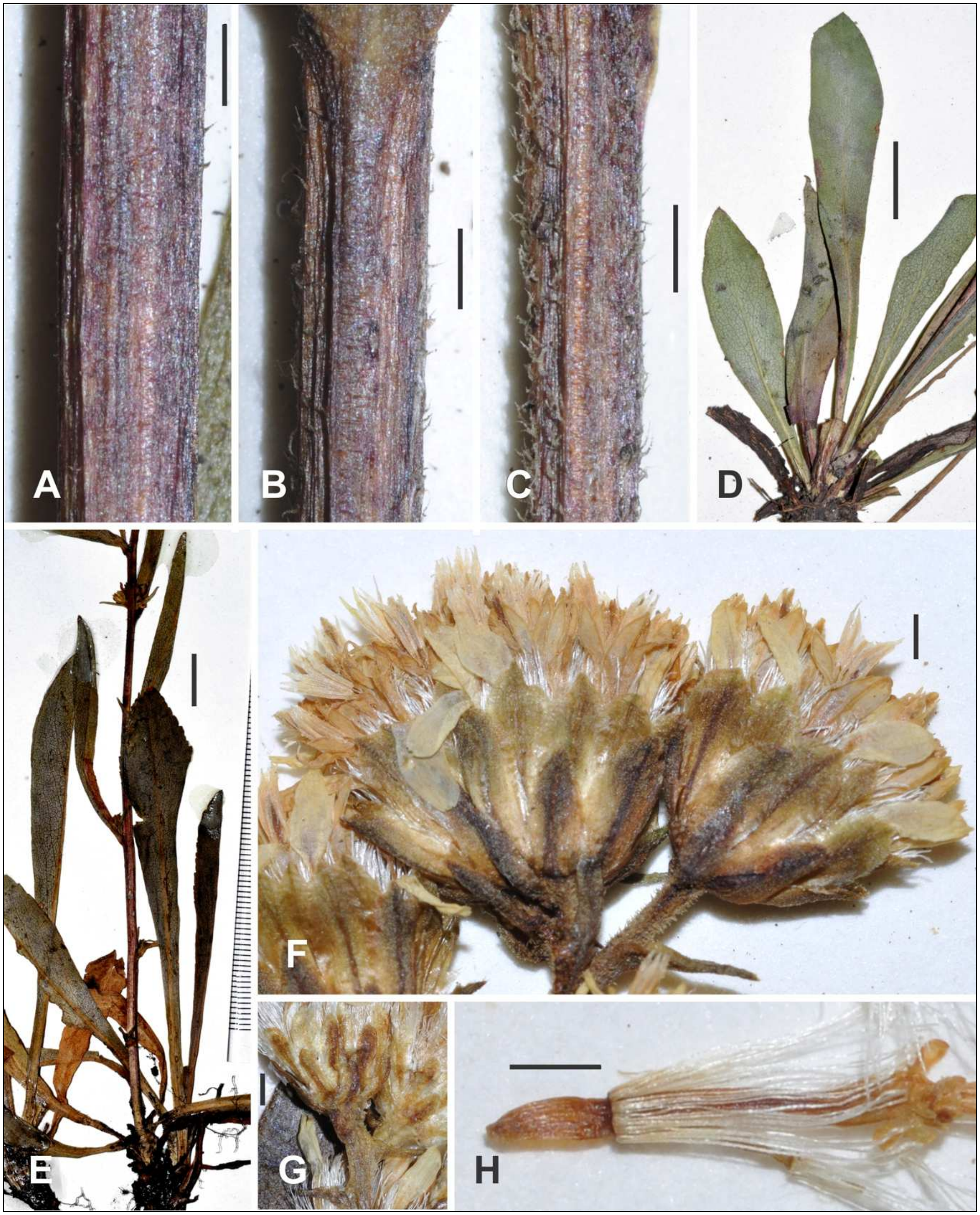

Figure 2. Details of morphology of *Solidago simplex*. **A-D.** *Beaman 2736* (GH). **A-C.** Lower, mid and upper stems. **D.** Basal rosette and lower stem leaves. **E**. Rosette and stem leaves, *Stanford et al. 2552* (TEX). F. Flowering heads, *Díaz-Barriga 6890* (TEX). G. Peduncle and phyllaries, *Hinton 22298* (TEX). H. Disc floret slightly past anthesis, *Roe et al. 247* (TEX). Scale bar = 1 cm in D and E; = 1 mm in A-C and F-H.

Figure 3. Examples of *Solidago glutinosa* used in the multivariate study: *Semple et al. 9370* (WAT unmounted): Insert A. Upper stem, *Semple & Brouillet 4218* (WAT). Insert B. Main stem, peduncle and head, *Semple & Brouillet 4218* (WAT). Scale bar = 1 mm in A-B.

Figure 4. Example of *Solidago spathulata* used in the multivariate study: *Ringius 1491* (WAT in MT); insert shows a peduncle and phyllaries with thick shiny resin.

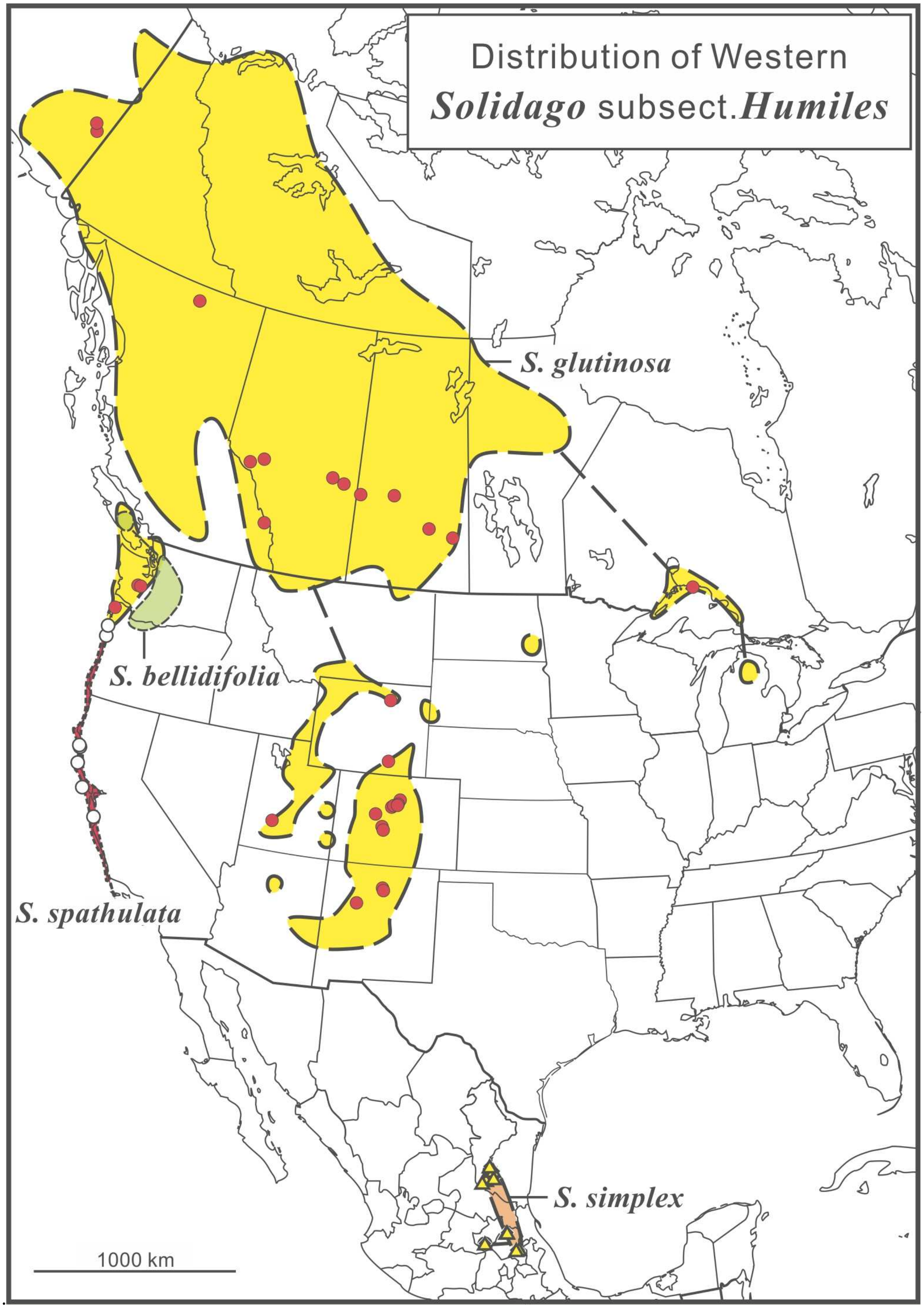

Figure 5. Distribution of the ranges and locations of multivariate samples of *Solidago simplex* (yellow triangles), *S. glutinosa* (red dots), and *S. spathulata* (white dots) of *Solidago* subsect. *Humiles*: *S. bellidifolia* was not included in the study.

Cronquist and treated *S. bellidifolia* Greene as *S. glutinosa* (subsp. *glutinosa*) var. *nana* (Gray) Cronquist. Hitchcock and Cronquist (1955) treated the western plants as varieties in *S. spathulata* DC., as did others (e.g. Welsh & Moore 1973; Welsh 1974). Ringius (1985) and Ringius and Semple (1987) followed Cronquist's (1947) application of *S. glutinosa*. Nesom (1989) placed *S. glutinosa* in synonymy under *S. simplex*. Semple and Cook (2006) followed Nesom in treating the western plants as *S. simplex* (subsp. *simplex*). In their cytogeographic study of subsect. *Humiles* (Rydb.) Semple, Peirson et al. (2012) followed Semple and Cook (2006). Semple and Peirson (2013) split the subspecies and varieties out of *S. simplex* into six species with var. *nana* retained at that level in *S. simplex*. When the first author of this paper saw the digital image of the holotype of *S. simplex* posted on line by jStor, he was not certain that the name applied to Canadian and USA plants covered in Flora North America (Semple & Cook 2006) or in Semple and Peirson (2013).

Polyploidy is known to occur in three of the five species included in this study. *Solidago glutinosa* is diploid 2*n* = 18 throughout its range from Alaska to California and Arizona and east to Ontario (Beaudry & Chabot 1959; Mulligan et al. 1972; Hartman 1977; Keil & Pinkava 1979; Semple et al. 1981; Ward & Spellenberg 1986; Ringius & Semple 1987; Semple et al. 1992; Semple et al. 2001; Peirson et al. 2012) but includes some tetraploids in northern Michigan (Peirson et al. 2012). *Solidago leiocarpa* DC. (Fig. 6) is known only at the tetraploid level 2*n* = 36 (Beaudry 1963; Morton 1981; unpublished counts). *Solidago multiradiata* Ait. (Fig. 7) is known at the diploid level 2n = 18 throughout most of its range (Fig. 8) from Alaska south to California, Arizona and New Mexico and east to Newfoundland (Ward & Spellenberg 1968; Solbrig et al. 1969; Morton 1981; Löve & Löve 1982a; Semple et al. 1984; Semple & Chmielewski 1987; Semple et al. 2001; numerous unpublished counts) and as tetraploids from eastern Siberia south to Wyoming and east to Ontario (Zhukova & Tikhonova 1971; Witherspoon et al. 1974; Dawe & Murray 1979, 1980, 1981; Chinnappa & Chmielewski 1987; unpublished counts). Only diploids have been reported in *S. spathulata* (Raven et al. 1960; Beaudry 1969; Ringius & Semple 1987; Semple et al. 1989). No chromosome number has been reported the Mexican *S. simplex*.

A multivariate study has not been published previously on plants over the entire range of *Solidago glutinosa* and *S. simplex* as shown in Fig. 5. In his multivariate morphometric study of sect. *Humiles* as it was known at the time, Ringius (1985) did not include specimens from Mexico and treated the western plants as *S. glutinosa* subsp. *glutinosa* and *S. spathulata*. Observations on specimens of *S. simplex* from Mexico borrowed from GH, MO, LL, and TEX (Thiers, continuously updated) led to the decision that a multivariate study of Mexican *S. simplex* should be undertaken to compare the Mexican plants with samples of *S. glutinosa* and *S. spathulata* of subsect. *Humiles* and *S. multiradiata* Ait. and *S. leiocarpa* of subsect. *Multiradiatae* Semple (Fig. 8), due to some similarities of some of the samples of *S. simplex* from Mexico to both *S. multiradiata* and *S. glutinosa*. The results of the multivariate analysis are presented below.

MATERIALS AND METHODS

In total, 80 specimens selected from a much larger number of specimens from GH, J.K.Morton in ROM, K, LL, MO, TEX, and WAT in MT (Thiers, continuously updated) were scored and included in this study. Data was scored on *Solidago glutinosa* (27 specimens), *S. simplex* (11 specimens), and *S. spathulata* (12 specimens) of subsect. *Humiles* and *S. leiocarpa* (13 specimens) and *S. multiradiata* (17 specimens) of subsect. *Multiradiatae*. 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

Figure 6. Examples of *Solidago leiocarpa* used in the multivariate study: **A.** *Ringius 1557* (WAT). **B.** Upper stem and leaf, *Ringius 1586* (WAT). **C.** Lower portion of inflorescence, *Ringius 1557* (WAT). Scale bar = 1 cm in B; = 1 mm in C.

Figure 7. Examples of *Solidago multiradiata* used in the multivariate study: **A.** *Chmielewski et al. CC4753* (WAT). **B.** Head, *Clements s.n.* (WAT). **C.** Upper stem leaf, *Semple et al. 11165* (WAT). **D.** Peduncle, bracts, and phyllaries, *Fraser 113* (WAT). Scale bar = 1 cm in C; = mm in A, B, and D.

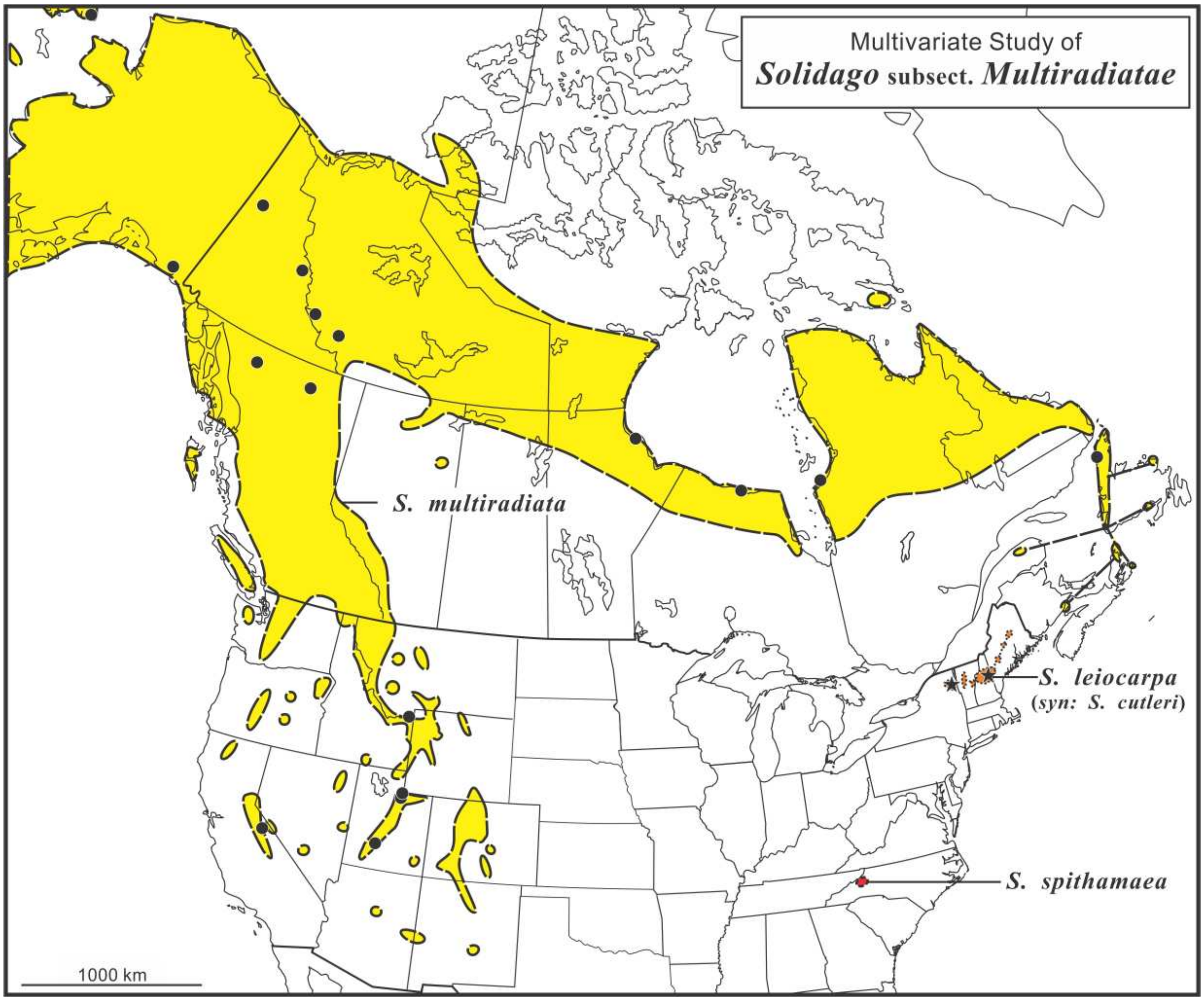

Figure 8. Distribution of the ranges and locations of multivariate samples of *Solidago leiocarpa* (stars) and *S. multiradiata* (black dots) of *Solidago* subsect. *Multiradiatae*: *S. spithamaea* was not included in the study.

groups along with phyllary shape and geographic location. Basal rosettes were not included in the analyses because these were often not present on specimens. Lower stem leaves were also not included because they were not always present.

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. Four analyses were performed. In the first analysis, five putative species level a priori groups were included: *S. glutinosa*, *S. leiocarpa*, *S. multiradiata*, *S. simplex*, and *S. spathulata*. In the second analysis, three species level a priori groups were included: *S. glutinosa*, *S. multiradiata*, and *S. simplex*. In the third analysis only *S. multiradiata* and *S. simplex* were included. In the fourth analysis only *S. glutinosa* and *S. simplex* were included.

RESULTS

Five species groups analysis

Two analyses including five species level a priori groups were run. The analysis including disc florets had slightly higher F-to separate values than the analysis including ray florets and the only the first of the two analyses is presented.

Table 1. Traits scored for the multivariate analyses of specimens of *Solidago glutinosa*, *S. leiocarpa*, *S. multiradiata*, *S. simplex*, and *S. spathulata*.

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 STEPWISE discriminant analysis including of 80 specimens of five species level a priori groups (*Solidago glutinosa*, *S. leiocarpa*, *S. multiradiata*, *S. simplex*, and *S. spathulata*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of mid margin serrations (42.16), involucre height (39.48), ray floret lamina length (21.11), number of disc florets (9.32), mid leaf length (8.32), and upper stem leaf width (8.18). 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 *Solidago multiradiata* and *S. spathulata* (47.915); the smallest separation was between *S. glutinosa* and *S. simplex* (3.851).

Table 2. Between groups F-matrix for the five a priori group analysis (df = 6 70).

Group	*glutinosa*	*leiocarpa*	*multiradiata*	*simplex*
leiocarpa	33.307			
multiradiata	29.628	32.678		
simplex	3.851	16.495	10.034	
spathulata	25.698	25.724	47.915	23.394

Wilks' lambda = 0.0195 df = 6 4 75; Approx. F = 21.3413 df = 24 245 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 100% down to 81%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. All 17 specimens of *Solidago multiradiata* (100%) were assigned a posteriori into the *S. multiradiata* group; 13 specimens with 90-100% probability; 2 specimens with 82-89%% probability; 1 specimen with 55% probability (43% to *S. simplex* and 2% to *S. glutinosa*, and 1 specimen with 52% probability (43% to *S. simplex* and 6% to *S. glutinosa*). All 12 of the specimens of the *S. spathulata* a priori group (100%) were assigned a posteriori to the *S. spathulata* group: 11 specimens with 99-100% probability and 1 specimen with 63% probability (34% to *S. glutinosa*). Twelve of the 13 specimens of the *S. leiocarpa* a priori group (92%) were assigned a posteriori to the *S. leiocarpa* group: 11 specimens with 100% probability and 1 specimen with 89% probability (9% to *S. simplex* and 2% to *S. glutinosa*). One specimen of the *S. leiocarpa* a priori group was assigned to *S. simplex* with 90% probability (10% to *S. glutinosa*). Nine of the 11 specimens of the *S. simplex* a priori group (82%) were assigned a posteriori to the *S. simplex* group: 1 specimen with 91% probability, 4 specimens with 80-87% probability, 1 specimen with 77% probability (22% to *S.*

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

Group	*glutinosa*	*leiocarpa*	*multiradiata*	*simplex*	*spathulata*	% correct
glutinosa	22	0	0	5	0	81
leiocarpa	0	12	0	1	0	92
multiradiata	0	0	17	0	0	100
simplex	2	0	0	9	0	82
spathulata	0	0	0	0	12	100
Totals	24	12	17	15	12	90

Jackknife Classification Matrix

Group	*glutinosa*	*leiocarpa*	*multiradiata*	*simplex*	*spathulata*	% correct
glutinosa	21	0	0	6	0	78
leiocarpa	0	12	0	1	0	92
multiradiata	0	0	15	2	0	88
simplex	2	0	1	8	0	73
spathulata	1	0	0	0	11	92
Totals	24	12	16	17	11	84

glutinosa), 1 specimen with 60% probability (26% to *S. glutinosa* and 14% to *S. multiradiata*), and 1 specimen with 58% probability (40% to *S. multiradiata* and 2% to *S. glutinosa*). Two specimens of the *S. leiocarpa* a priori group with assigned to *S. glutinosa*: 1 specimen 87% probability (13% to *S. simplex*) and 1 specimen with 58% probability (42% to *S. leiocarpa*). Twenty-two of the 27 specimens of the *S. glutinosa* a priori group (81%) were assigned a posteriori to the *S. glutinosa* group: 9 specimens with 90-99% probability, 6 specimens with 81-89% probability, 1 specimen with 74% probability (26% to *S. simplex*), 4 specimens with 61-67% probability (39-26% probability to *S. simplex*), and 2 specimens with 54% and 56% probabilities (46% and 41% to *S. simplex*, respectively). Five specimens of the *S. glutinosaa* a priori group with assigned to *S. simplex*: 1 specimen with 71% probability (27% to *S. glutinosa*), 3 specimens to 60-69% probability (40-30% to *S. glutinosa*), and 1 specimen with 49% probability (30% to *S. glutinosa* and 21% to *S. multiradiata*).

Two dimensional plots of CAN1 versus CAN 3 and CAN1 versus CAN2 canonical scores for 80 specimens of *S. glutinosa*, *S. leiocarpa*, *S. multiradiata*, *S. simplex*, and *S. spathulata* are presented in Fig. 9. Eigenvalues on the first three axes were 4.354, 2.855 and 0.082.

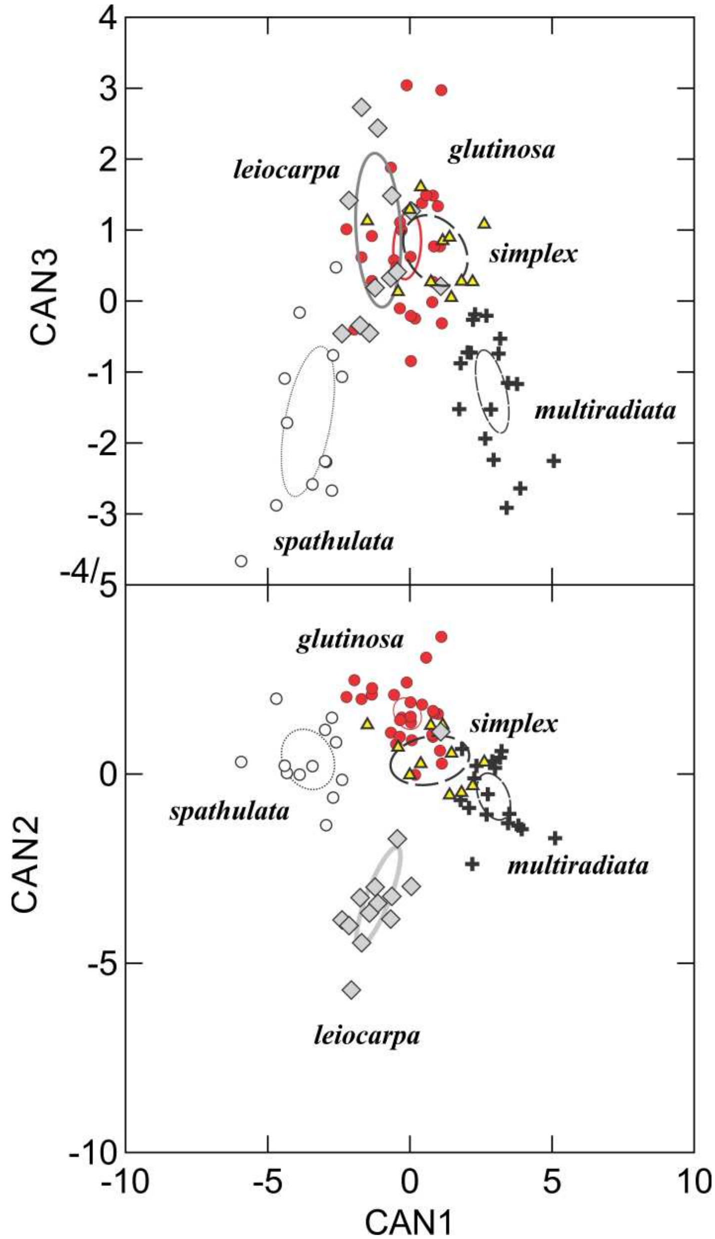

Figure 9. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 80 specimens of five a priori groups of *Solidago* subect. *Humiles* and *S.* subsect. *Multiradiatae*: *S. glutinosa* (red dots), *S. leiocarpa* (gray diamonds), *S. multiradiata* (black +s), *S. simplex* (yellow triangles), and *S. spathulata* (white dots).

Three species groups analysis

In the STEPWISE discriminant analysis of 55 specimens of three species level a priori groups (*Solidago glutinosa*, *S. multiradiata*, and *S. simplex*), the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: upper stem leaf width (9.62), number of disc florets (8.76), disc floret pappus length at anthesis (4.88), number of mid stem leaf margin serrations (4.86), and mid stem leaf length (4.72). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. glutinosa* and *S. multiradiata* (19.039), and the smallest separation was between *S. multiradiata* and *S. simplex* (4.124) and only slightly larger between *S. glutinosa* and *S. simplex* (4.593).

Table 4. Between groups F-matrix for the three a priori group analysis (df = 5 48).

Group	*glutinosa*	*multiradiata*
multiradiata	19.039	
simplex	4.593	4.124

Wilks' lambda = 0.2940 df = 5 2 52; Approx. F= 8.1054 df = 10 96 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups, the percents of correct placement a posteriori ranged from 55-78%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Twenty of 27 specimens of *Solidago glutinosa* (78%) were assigned a posteriori to the *S. glutinosa* group; 7 specimens with 91-100% probability, 7 specimens with 80-89% probability, 2 specimens with 73% and 79% probabilities, 4 specimens with 60-68% probability (24-36% to *S. simplex* and 4-8% to *S. multiradiata*), and 1 specimen with 54% probability (46% to *S. simplex*). Six specimens of the *S. glutinosa* a priori group were assigned to *S. simplex* with 54-58% (31-49% to *s. glutinosa* and 1-5% to *s. multiradiata*). Thirteen of the 17 specimens of the *S. multiradiata* a priori group (76%) were assigned a posteriori into the *S. multiradiata* group; 7 specimens with 93-100% probability, 1 specimen with 86% probability, 1 with 79% probability, 2 with 63% and 66% probabilities (37% and 33% probabilities to *S. simplex*), and 2 specimens with 51% and 53% probabilities (37% and 35% probabilities to *S. simplex* and 14% and 10% to *S. glutinosa*). Four specimens of the *S. multiradiata* a priori group were assigned to the other two species: 3 specimens with 61%, 59% and 49% to *S. simplex* (27%, 37% and 43% to *S. multiradiata* and 12%, 3% and 8% to *S. glutinosa*, respectively). Six of 11 specimens of the *S. simplex* a priori group (55%) were assigned a posteriori to *S. simplex*: 2 specimens with 82-84% probability, 1 specimen with 71% probability (26% to *S. glutinosa*), 1 specimen with 64% probability (29% to *S. multiradiata* and 7% to *S. glutinosa*), and 2 specimens with 48% probability (1 with 48% to *S. multiradiata* and 1 with 46% to *S. glutinosa*). Five specimens of the *S. simplex* a priori group were assigned a posteriori into other species: 3 specimen was assigned to *S. multiradiata* with 65%, 52% and 50% probabilities (34%, 47% and 48% probabilities to *S. multiradiata*) and 2 specimens with 87% and 64% probabilities to *S. glutinosa* (13% and 33% to *S. simplex*).

Two dimensional plot of CAN1 versus CAN2 canonical scores for 55 specimens of *Solidago glutinosa*, *S. multiradiata*, and *S. simplex* are presented in Fig. 10. Eigenvalues on the first two axes were 2.003 and 0.133.

Two species groups analysis I

In the STEPWISE discriminant analysis of 28 specimens of *Solidago multiradiata* and *S. simplex*, the following four traits were selected in a STEPWISE analysis and are listed in order of decreasing F-to-

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

Group	*glutinosa*	*multiradiata*	*simplex*	% correct
glutinosa	21	0	6	78
multiradiata	1	13	3	76
simplex	2	3	6	55
Totals	24	16	15	73

Jackknifed classification matrix

Group	*glutinosa*	*multiradiata*	*simplex*	% correct
glutinosa	20	0	7	74
multiradiata	1	12	4	71
simplex	3	4	4	36
Totals	24	16	15	65

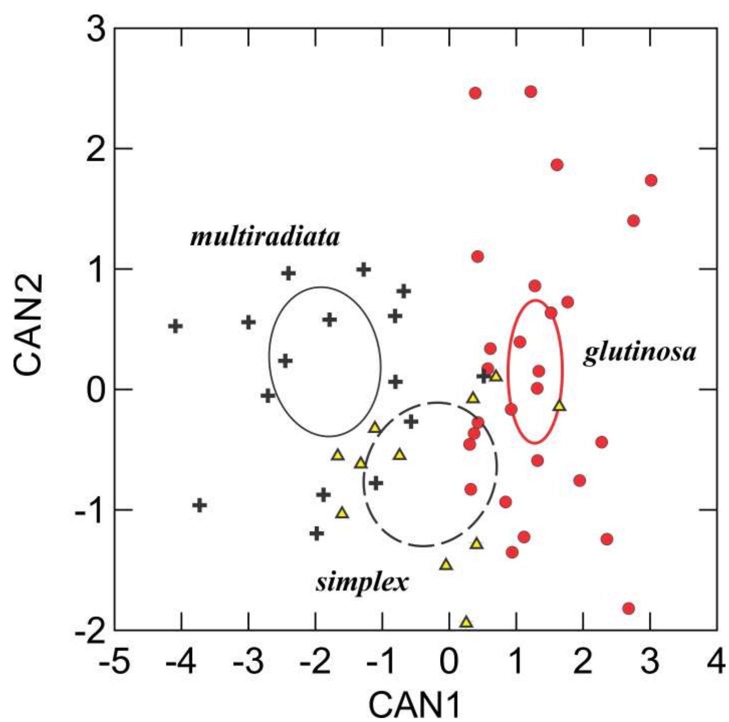

Figure 10. Two dimension plot of CAN1 versus CAN2 scores for 55 specimens in three a priori: *S. glutinosa* (red dots), *S. multiradiata* (black +s), and *S. simplex* (yellow diamonds).

remove values: disc floret corolla length (20.50), mid stem leaf length (11.30), number of ray florets (9.21), and mid stem leaf width (7.88). 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 multiradiata* and *S. simplex* had an F-to separate value of 11.553 (Wilks' lambda = 0.3323, df = 4 1 26; Approx. F= 11.5527, df = 4 23, 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 100% for *S. simplex* and 82% for *S. mutliradiata.* The Classification matrix and Jackknife classification matrix are presented in Table

6. All 11 specimens included in the *S. simplex* a priori group (100%) were assigned a posteriori to that species: 9 specimens with 92-100% probability; 1 specimen with 85% probability (*Pringle 79*10 GH from 9800 ft. {= 2987 m}, Sierra de Pachuca, Hidalgo, Mexico; large basal rosette leaves, slightly resinous leaves and phyllaries), and 1 specimen with 84% probability (*Pringle 10294* GH from 9500 ft. {= 2895 m} Sierra de Pachuca, Hidalgo, Mexico; large basal rosette leaves, slightly resinous leaves, and thickly resinous phyllaries). Sixteen of the 17 specimens of *S. multiradiata* a priori group (94%) were assigned a posteriori to the *S. multiradiata* group: 12 specimens with 92-100% probability; 1 specimen with 84% probability, 1 specimen with 71% probability, 1 specimen with 53% probability (*Morton & Venn NA12401* WAT from the Northern Peninsula, Newfoundland), and 50% probability (Hawthorn s.n. WAT from Churchill, Manitoba). One specimen of the *S. multiradiata* a priori group was assigned a posteriori to *S. simplex* with 50% probability; *Kharkevich & Buck 836* K from Chukotka A.O. of extreme eastern Russia; the specimen includes three short shoots each with a small, few-headed inflorescence, upper stem leaves with long-haired ciliate margins, and subequal non-resinous very narrow triangular attenuate phyllaries that at typical for the *S. multiradiata*.

Frequencies of CAN1 canonical scores for 28 specimens of *Solidago multiradiata* and *S. simplex* are presented in histograms in Fig. 11. The Eigenvalue on the first axis was 2.009.

Table 6. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two a priori groups; a posteriori placements to groups in rows.

Group	*multiradiata*	*simplex*	% correct
multiradiata	16	1	94
simplex	0	11	100
Totals	16	12	96

Jackknifed classification matrix

Group	*multiradiata*	*simplex*	% correct
multiradiata	14	3	82
simplex	0	11	100
Totals	14	14	89

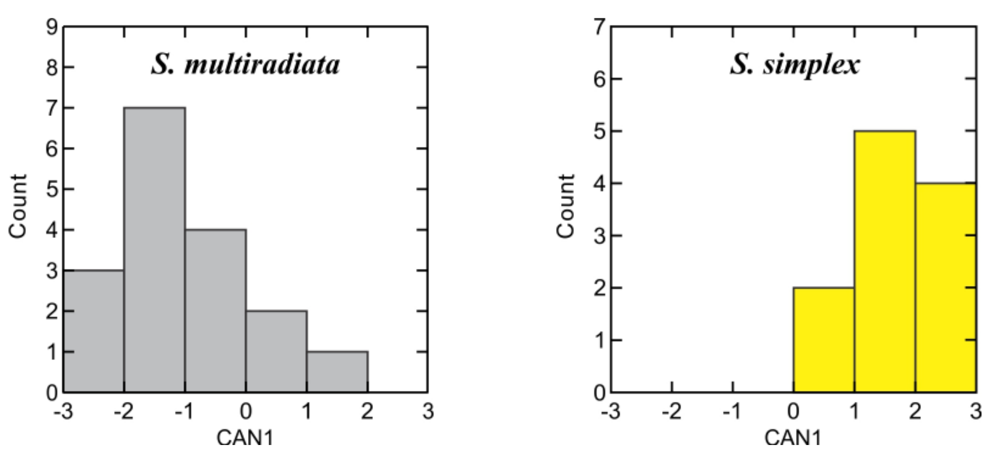

Figure. 11. Histograms of CAN1 canonical scores for 28 specimens of *S. multiradiata* (left) and *S. simplex* (right).

Two species groups analysis II

In the STEPWISE discriminant analysis of 38 specimens of *Solidago glutinosa* and *S. simplex*, the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (17.06), disc floret corolla length (12.07), width of the inflorescence (11.35), disc corolla lobe length (4.97). 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 glutinosa* and *S. simplex* had an F-to separate value of 10.624 (Wilks' lambda = 10.6240, df = 4 33; 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 group were 93% for *Solidago glutinosa* and 82% for *S. simplex*. The Classification matrix and Jackknife classification matrix are presented in Table 7. Twenty-five of the 27 specimens of *S. glutinosa* (93%) were assigned a posteriori to *S. glutinosa*: 18 specimens with 90-100% probability, 4 with 81-87% probability, 1 with 77% probability, and 1 with 63% probability. Two specimens of the *S. glutinosa* a priori group were assigned to *S simplex* with 60% probability (*Morton & Venn NA14134* JKM in ROM from Muncho L. Provincial Park, British Columbia; long narrow inflorescence with short hairs and heads with narrow phyllaries) and 55% probability (*Ringius 1976* WAT from Terrace Bay, Thunder Bay Dist., Ontario on coastal rocks of Lake Superior; short plants with small inflorescence with a few short hairs, heads with narrow resinous phyllaries). Nine of the 11 specimens of *S. simplex* (82%) were assigned a posteriori to the *S. simplex* group: 5 with 98-100% probability, 2 with 89% and 83% probabilities, 1 with 73% probability, and 1 with 62% probability. Two specimens of the *S. simplex* a priori group were assigned a posteriori to *S. glutinosa*: 1 with 95% (*Roe, Roe, & Mori 247* LL from NE of Jacala, Hidalgo, Mexico; inflorescence branches elongated, heads small, phyllaries narrow for *S. simplex*; cypselae glabrous with thickened brownish-red translucent ribs) and 1 specimen with 66% probability (*Stanford, Taylor & Lauber 2552* TEX from Cerro Pena Nevada, Tamaulipas, Mexico; short stems with small inflorescences with immature lower branches, hairs on main stem of inflorescence moderately dense to 0.3 mm long, somewhat villose, phyllaries broad).

Frequencies of CAN1 canonical scores for specimens of *S. glutinosa* and *S. simplex* are presented in histograms in Fig. 12. The eigen value on the first axis was 1.288.

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

Group	*glutinosa*	*simplex*	% correct
glutinosa	25	2	93
simplex	2	9	82
Totals	27	11	89

Jackknifed classification matrix

Group	*glutinosa*	*simplex*	% correct
glutinosa	25	2	93
simplex	3	8	73
Totals	28	10	87

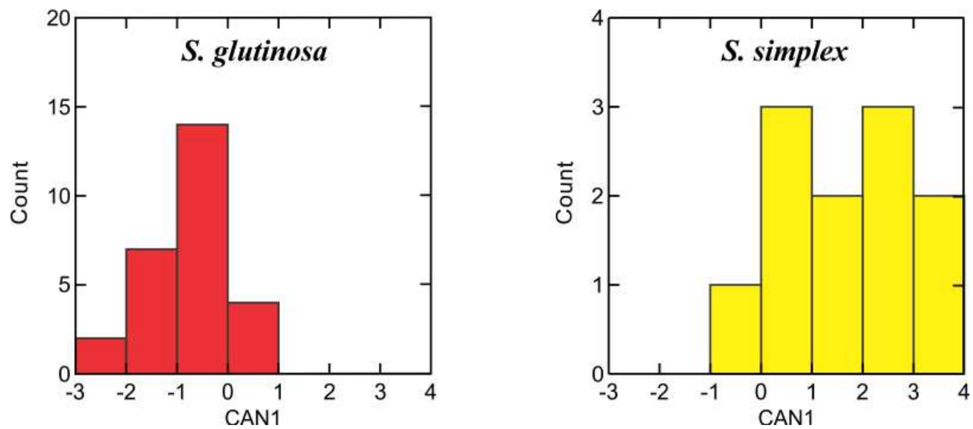

Figure. 12. Histograms of CAN1 canonical scores for 38 specimens of *S. glutinosa* (left) and *S. simplex* (right).

DISCUSSION

Based on the results of the multivariate analyses and additional observations on morphology the following taxa should be recognized as species: *Solidago glutinosa*, *S. simplex,* and *S. spathulata* in subsect. *Humiles* and *S. leiocarpa* and *S. multiradiata* in subsect. *Multiradiatae*. *Solidago glutinosa* should be treated as separate from *S. simplex* on the basis of the results of the multivariate analyses, its short branched elongated inflorescence versus the longer branched inflorescence of *S. simplex,* its short hairs (0.1-2 mm long) on the mid to upper stem and in the inflorescence, its usually narrower phyllaries, and its generally more densely short-haired cypselae. The ranges of *S. glutinosa* and *S. simplex* are separated by some 1000 km between the southernmost populations of *S. glutinosa* in New Mexico and the northern most populations of *S. simplex* in Nuevo León, Mexico. In the multivariate analyses, some specimens of *S. simplex* showed stronger similarities to *S. multiradiata* than to *S. glutinosa* confirming the first author's impression that some *S. simplex* specimens had features approaching those of *S multiradiata*.

In the intuitive phylogeny of *Solidago*, Semple (2016) did not separate *S. glutinosa* from *S. simplex* in the subsect. *Humiles* portion of the diagram; the branch labeled "*S. simplex*" is the *S. glutinosa* branch. *Solidago simplex* may be the most basal species in subsect. *Humiles* and a new branch for *S. simplex* can be added to the diagram lower down on the branch leading to other taxa in the subsection. *Solidago simplex* has phyllaries with rounded or obtuse ends like other species in subsect. *Humiles* and the leaves and phyllaries are somewhat to obviously resinous like other taxa in subsect. *Humiles*. In his cpDNA RFLP phylogenetic analyses, Zhang (1996) determined that *S. glutinosa* (as *S. simplex*), *S. multiradiata*, and *S. virgaurea* formed a clade, which is reflected in Semple (2016). Thus, it should not be surprising that there are morphological similarities between species of subsect. *Humiles*, subsect. *Multiradiatae*, and (across Eurasia) subsect. *Solidago*. *Solidago glutinosa* and *S. multiradiata* are both western cordilleran taxa that probably evolved from an ancestral taxon native to the mountains of eastern Mexico. *Solidago simplex* is the only species in either subsection still native to the mountains of eastern Mexico.

Solidago spathulata is the most densely resinous species in subsect. *Humiles* and has numerous serrations on lower and mid stem leaves and often on upper stem leaves. The numbers of leaf serrations accounts for the strong separation of *S. spathulata* from the other four species in the canonical analysis diagrams in Fig. 9. It is restricted to coastal sand dunes and headlands along the Pacific Ocean in Oregon and California (Fig. 5).

Solidago leiocarpa was strongly separated from the other four species on the CAN1 and CAN2 axes of the diagram in Fig. 9 with the exception of one specimen being more *S. simplex*-like. *Solidago leiocarpa* is native to higher elevations in the mountains of northeastern New York, north-central New Hampshire, and Maine in exposed alpine boulder plains, rock crevices, and alpine lawns, i.e. tundra like habitats. Tetraploid *S. leiocarpa* is likely a derivative of *S. multiradiata* that diverged in isolation as glaciers retreated northward in eastern North America.

All specimens of *Solidago multiradiata* were assigned a posteriori to that species in the five species analysis. Only two specimens were assigned with low percents of probability. However, in the plots of canonical scores diagram (Fig. 9), specimens of *S. multiradiata* did not separate out strongly from specimens of *S. simplex* in the first and second canonical axes, but they did separate out on the third axis. In the canonical scores diagram of *S. glutinosa*, *S. multiradiata*, and *S. simplex* (Fig. 10), symbols for *S. multiradata* and *S. simplex* are not fully separated. The ranges of distribution of *S. multiradiata* and *S. simplex* are separated by some 1000 km. The ranges of distribution of *S. multiradiata* and *S. glutinosa* are sympatric over much of the western range, with *S. multiradiata* occurring at higher elevations than *S. glutinosa*. In locations where the two ranges come into contact, the two species came be difficult to distinguish because both can be short and have small inflorescences. Differences in phyllary shape and size of the outer phyllaries usually is sufficient to allow relative ease in identification: *S. multiradiata* (Fig. 7B) and *S. glutinosa* (Fig. 3B). However, the two species appear to hybridize sometimes, when both occur together as diploids, as in the Colorado Front Range. Specimens of *S. multiradiata* have been misidentified as *S. simplex*, *S. glutinosa*, *S. randii*, and *S. racemosa* in different parts of the range of *S. multiradiata* across Canada. Species of subsect. *Humiles* never have phyllaries like those of *S. multiradiata*, whereas species of subsect. *Solidago* across Eurasia sometimes do have similar phyllaries to those of *S. multiradiata*.

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