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A MULTIVARIATE MORPHOMETRIC ANALYSIS OF THE SOLIDAGO ULIGINOSA COMPLEX (ASTERACEAE: ASTEREAE; SOLIDAGO SUBSECT. MARITIMAE) IN EASTERN NORTH AMERICA

JOHN C. SEMPLE, TROINA SHEA, HAMMAD RAHMAN, YUNFEI MA¹, AND LAN TONG Department of Biology, University of Waterloo, Waterloo, Ontario Canada N2L 3G1 jcsemple@uwaterloo.ca

¹ Present address: Block Line Medical Clinic, Kitchener, Ontario N2C 0A5

ABSTRACT

A multivariate morphometric study of the *Solidago uliginosa* complex of *Solidago* subsect. *Maritimae* was conducted to assess the morphological differences among *Solidago austrina* as "outgroup," *S. simulans*, and *S. uliginosa* (including *S. humilis*, *S. klughii S. linoides*, *S. neglecta*, *S. purshii*, *S. terraenovae*, and *S. uniligulata*). An analysis of a matrix of 320 specimens by 37 traits of subsect. *Maritimae* was performed initially, then multiple analyses of the *S. uliginosa* complex with species limits defined in multiple ways to assess which taxa should be recognized and at what taxonomic rank within the *S. uliginosa* complex. Support was found for recognizing *S. simulans* and *S. uliginosa* and for recognizing 3 varieties within *S. uliginosa*: var. *uliginosa*, var. *peracuta, and* var. *terrae-novae*. A key to all species in *Solidago* subsect. *Maritimae* is included.

The Solidago uliginosa Nutt. complex consists of one to several species and multiple varieties, but with a tortuous history of names applied to them. Regardless of the names applied, the plants are all native to bogs and wet soils in eastern Canada and the northern midwest and northeastern regions of the U.S. and further south mostly at higher elevations in the Appalachian Mountains. All have lowest stem leaves with petioles sheathing the stem and blades that are lanceolate and finely to coarsely serrate on the margins. Sheathing lower stem leaves are found only in S. subsect. Maritimae (Torr. & Gray) Neson, which includes the following 13 species accepted by Semple (2019): S. austrina Small, S. azorica Hochstetter ex Seubert, S. chrysopsis Small, S. gracillima Torr. & Gray, S. maya Semple, S. mexicana L., S. paniculata DC., S. pulchra Small, S. sempervirens L., S. simulans Fern., S. stricta Ait., S. uliginosa, and S. virgata Michx. Multiple species include more than one ploidy level. Only S. uliginosa sensu lato and S. simulans are viewed here as being part of the S. uliginosa complex, with S. austrina being included for comparison. Previously published multivariate morphometric studies were presented on the S. sempervirens complex (Semple et al. 2016a) and the S. stricta complex (Semple et al. 2016b). Details of the cytogeography of all species will be described in a paper now in preparation and information on chromosome numbers will only be referenced in this paper when pertinent to presentation of morphological variation.

Multiple species have been described within the *Solidago uliginosa* complex over the past two centuries. Formal nomenclatural information is provided in Table 1. *Solidago humilis* Banks ex Pursh is the oldest name for what is treated here as *S. uliginosa* Nutt. but is a later homonym and was long rejected as the valid name for the species. Torrey and Gray (1842) proposed the names *S. neglecta* Torr. & Gray and *Solidago linoides* Torr. & Gray for the more southern members of the complex with secund inflorescences with spreading inflorescence branches. These more southern plants are known to be tetraploid (Beaudry & Chabot 1959; Beaudry 1963, 1969; Morton 1981; Semple et al. 1981, 1984, 1993, 2015, 2019; Chmielewski et al. 1987). Torrey and Gray (1842) treated the northern non-secund members of the complex under the misapplied name *S. stricta* Ait.

listing *S. uliginosa* as a synonym. Semple (2013) noted that the name *S. stricta* was correctly applied to the New Jersey to North Carolina hexaploid species that is part of the *S. stricta/S. virgata* complex in *S.* subsect. *Maritimae* (Semple et al. 2016b). *Solidago purshii* Porter was proposed as a new name to replace *S. humilis* with the same type specimen, and this was adopted by some botanists subsequently (e.g. Britton 1901, Fernald 1950; Beaudry et al. 1958). Cronquist (1947) discussed application of the names *S. uliginosa*, *S. neglecta*, *S. linoides*, and *S. uniligulata*, and he concluded that all applied to the same species with the oldest valid name being *S. uliginosa*.

Cronquist (1947) concluded that two varieties could be recognized within *Solidago uliginosa*: plants of var. *uliginosa* have a secund inflorescence, usually with long ascending-diverging lower branches (Figs. 1-2), while plants of *S. uliginosa* var. *peracuta* (Fern.) Friesner have non-secund inflorescences with lower branches that are either relatively short or if longer than ascending and not strongly diverging (Fig. 3-4). The epithet *peracuta* refers to the sharply acute leaf apices that Fernald emphasized in protologue. In 1946, Cronquist annotated the holotype of var. *peracuta* with the following: "I take this to be merely a young form of what has passed as *S. uliginosa* Nutt.. The type of the latter, however, is the plant which has secund inflorescence and has passed as *S. uniligulata* or *S. neglecta*." Plants with intermediate inflorescence traits occur.

Semple and Cook (2006) used the name *Solidago uliginosa* following Cronquist's application but did not recognize any varieties. Both var. *uliginosa* and var. *peracuta* include small to large shoots with smaller shoots being more common in the more northern portion of the range of distribution of the species. Stem height and the size of the inflorescence is strongly influenced by growing conditions and the length of the growing season. Rootstocks with very tall shoots in the field usually yielded only small shoots when transplanted to the greenhouse in confining pots, particularly after being in the greenhouse for more than one year.

Table 1. Species and variety names of taxa proposed in the Solidago uliginosa complex.

- Solidago humilis Banks ex Pursh, Fl. Sept. 1814. non Mill. (1768), nec Desf. (1829). Solidago virga-aurea L. var. humilis (Banks ex Pursh) A. Gray, Man. (ed.2) 202. 1856. TYPE: CANADA. Newfoundland. 1766, Banks s.n. (holotype: BM.!, annotated by A. Gray 1881 "The original of mss Solander (the No. 1 added subsequently)."
- Solidago uliginosa Nutt., J. Acad. Sci. Phila. 7: 101. 1834. TYPE: USA. New Jersey. C. Pickering s.n. (holotype: PH!).
- Bigelowia uniligulata DC., Prodr. 5: 329. 1836. Chrysoma uniligulata (DC.) Nutt., Trans. Amer. Phil. Soc. n.s.
 7: 325. 1841. Solidago neglecta Torr. & Gray var. uniligulata (DC.) B.S.P., Prelim. Cat. N. Y. Pl. 26.
 1888. Solidago uniligulata (DC.) Porter, Mem. Torr. Bot. Club 5: 320. 1894. TYPE: "in Nova-Caesarea [=New Jersey], in arenosis a Virginia ad Carolina", s.d., Greene s.n., (holotype: GDC jStor image g00455985!).
- Solidago neglecta Torr. & A. Gray, Fl. N. Amer. 2(2): 213. 1842. Solidago uniligulata Pursh var. neglecta (Torr. & Gray) Fern., Rhodora 23: 292. 1922. LECTOTYPE (designated here): Massachusetts. Essex Co.: Ipswich, Oakes s.n. (NY!: isolectotype: GH!). The protologue alluded to a group of collections: "In swamps, Massachusetts! and New York! to North Carolina! and Indiana! Aug.-Sept." Other syntypes are these: Massachusetts. Chapman s.n. (NY!). New York. Staten Is., Aug 1841, Torrey s.n. (NY!); Island of New York, Aug 1841, Torrey s.n. (NY!). North Carolina. Curtis s.n. (NY!). Ohio. Columbus, Lapham s.n. (NY!).
- Solidago linoides Torr. & A. Gray, Fl. N. Amer. 2: 216. 1842. Solidago neglecta Torr. & Gray var. linoides (Torr. & Gray) A. Gray, Syn. Fl. N. Amer. 1, pt. 2: 154. 1884. Solidago uliginosa Nutt. var. linoides (Torr. & Gray) Fern., Rhodora 49: 296. 1947. TYPE: USA. New Jersey. Wading River, pine barrens, sphagnous swamp, Sep 1833, A. Gray s.n. (holotype: GH!).
- Solidago humilis Banks ex Pursh var. microcephala Porter, Bull. Torrey Bot. Club 19: 129. 1892. **TYPE: USA. Maine**. Mt. Desert Island, Frenchman's Camp Road, Aug. 1891, *Redfield s.n.* (holotype: not seen); "very small heads for species, scarcely a line and a half long" in protologue is of uncertain application. The holotype was not found at GH or PH.

Solidago purshii Porter, Bull. Torrey Bot. Club 21: 311. 1894. TYPE: CANADA. Newfoundland. 1766, Banks s.n. (holotype: BM!).

Solidago klughii Fern. [Rhodora 17: 5 1915. TYPE: CANADA. Ontario. Bruce Co.: Oliphant, 14 Aug 1905, A.B. Klugh 3 (holotype: GH!).

- Solidago humilis Banks ex Pursh var. peracuta Fern., Rhodora 17: 6. 1915. Solidago uliginosa Nutt. var. peracuta (Fern.) Friesner, Butler Univ. Bot. Studies 3, no. 1: 55. 1933. Type: CANADA. Newfoundland. East Branch of Humber R., Middle Birchy Pond, open rocky woods, 13 Jul 1910, Fernald & Wiegand 4097 (holotype: GH!).
- Solidago uniligulata DC. var. levipes Fern., Rhodora 17: 7. 1915. Solidago uliginosa Nutt. var. levipes (Fern.) Fern., Rhodora 49: 296. 1947. **Type: USA. New York**. Penn Yan, Sartell s.n. (holotype: GH!).
- Solidago simulans Fern., Rhodora 38: 205. 1936. **TYPE**: **USA. North Carolina**. Macon Co.: near Highlands, moist rocks on the high mountains, 15 Sep 1897, *Biltmore Herb. 5730* (holotype: GH!; isotypes: NY!, US online image!).
- Solidago simulans Fern. [Rhodora 38: 205. 1936. **Type: USA. North Carolina**. Macon Co.: near Highlands, moist rocks on the high mountains, 15 Sep 1897, *Biltmore Herb. 5730* (holotype: GH!; isotypes: NY!, US online image!).
- Solidago humilis Banks ex Pursh var. *abbei* Boivin, Nat. Canad. 89: 73. 1962. **Type: CANADA**. **Québec**. Ungava, mainland south of Cairn Island, abundant in a wet, mossy and grassy spruce bog in the hills, 9 Aug 1939, *E.C. Abbe 3761* (holotype: DAO, not seen: isotype: MIN jStor image!).

Solidago humilis Banks ex Pursh var. microcephala Porter, [Bull. Torrey Bot. Club 19: 129. 1892. **TYPE: USA. Maine**. Mt. Desert Island, Frenchman's Camp Road, Aug. 1891, *Redfield s.n.* (holotype: not found); "very small heads for species, scarcely a line and a half long" in protologue] is of uncertain application. This is the oldest varietal name in the *S. uliginosa* complex and thus has priority and a new combination would be required under *S. uliginosa* if the holotype collection is located and found to be the same taxon as of *S. ulignosa* var. peracuta.

Solidago klughii Fern. was compared in the protologue to S. guiradonis A. Gray in phyllary and leaf traits. Solidago guiradonis is a member of S. subsect. Junceae and is a rare endemic in California and a close relative of S. confinis Nutt. and S. spectabilis (D.C. Eaton) A. Gray (Semple and Cook 2006; Semple 2019). In his annotation on the type specimen Cronquist in 1946 hypothesized that S. klughii was "only a phase of S. uliginosa var. peracuta (Fern.) Friesn." Klugh 3 (GH) has sheathing basal leaf bases and linear leaves. Similar plants are known to be tetraploid in the bogs on the west side of the Bruce Peninsula in Ontario; e.g., Semple & K. Shea Semple 2451 (WAT, CAN, MO, USF), reported in Semple et al. (1981) and included in the multivariate analyses below.

Two additional published names appear to be either minor variants or immature plants of *Solidago uliginosa*: (1) The holotype of *Solidago uniligulata* DC. var. *levipes* Fern. has large serrations on the narrowly oblanceolate to lanceolate lower leaves and a narrow, elongated inflorescence with immature heads. Fernald (1950) keyed the variety out as having "pedicels glabrous or glabrous and glutinous" and noted that plants came from "Bogs and wet sands centr. N.Y. to s. Ont." (2) *Solidago humilis* var. *abbei* Boivin was based on small shoots (30-33 cm) with few heads. Such diminutive shoots are frequent in northern collections of the *S. uliginosa* complex and not distinct from other northern collections seen. Both names belong in synonymy under var. *peracuta*.

The southernmost member at species rank of the *S. uliginosa* complex and most recently described is *S. simulans* Fern. As originally circumscribed, the species was limited to plants of the high mountains of Macon Co., North Carolina, in the southern Appalachian Mts. (Fig. 7), where it has been observed growing in shallow soil of seepage on exposed rock faces (Fig. 8). In the protologue, Fernald compared the species to *S. uliginosa* and *S. austrina* Small. The species can have some of the largest basal rosette leaves observed in the field of all species in the *S. uliginosa* complex (Fig. 9).

Shoots are similar to those of typical *S. uliginosa*. Cronquist (1980) included the species in a broadly defined *S. gracillima* Torr. & A. Gray and noted that *S. simulans* was "a broad-leaved extreme, approaching *S. uliginosa*." Semple and Cook (2006) treated *S. simulans* in synonymy under *S. uliginosa* but noted that it "might warrant recognition as a narrowly distributed endemic." Semple (2012) selected a lectotype for *S. gracillima* that effectively restricted that species to plants of the *S. stricta/S. virgata* complex with a few long to very long lower inflorescence branches, thereby excluding *S. simulans* from *S. gracillima*. *Solidago simulans* belongs in the *S. uliginosa* complex.

The ranges of distribution of *Solidago austrina*, *S. simulans* and *S. uliginosa* and locations of samples included in the multivariate analyses are shown in Fig. 10. *Solidago austrina* is the most southern of the three species occurring along the outer margins of the Piedmont from North Carolina to Alabama with populations extending north through eastern Tennessee to southern Kentucky and south into Panhandle Florida. As delimited here, *S. simulans* occurs in scattered locations on the Piedmont in North Carolina and at generally higher elevations in the Appalachian Mts. of northeastern Georgia, western North Carolina and eastern Tennessee and adjacent southwestern Virginia. *Solidago uliginosa* occurs over much of eastern North America from Newfoundland and Labrador to Hudson's Bay and southeastern Manitoba south to north central Illinois and New Jersey, Maryland and West Virginia, and scattered locations in Virginia in the mountains and further east in a range of boggy and marshy habitats (Fig. 10).

Numerous chromosome number reports have been published for taxa in *Solidago* subsect. *Maritimae*, including diploids 2n=9II or 2n=18, tetraploids 2n=18II or 2n=36, and hexaploids 2n=54. The cytogeography and a review of published chromosome counts will be presented in detail in a separate paper currently in preparation by the first author and Rachel Cook.

A multivariate analysis of 105 specimens of *S. austrina*, *S. simulans*, and *S. uliginosa* was undertaken to investigate the levels of similarities among taxa and to determine which traits most strongly differentiated these species and possible varieties within *S. uliginosa*. This has not been done previously. Specimens of *S. austrina* were included because the species can be similar to some morphs of *S. uliginosa*, although the latter have fewer leaves on the stems. Statistically supported answers to the following questions were the goals of the investigation: How many species should be recognized in the *S. uliginosa* complex? How many varieties, if any, should be recognized within *S. uliginosa* itself? Which traits are best at separating the taxa supported by the analyses?

MATERIAL AND METHODS

Herbarium specimens of *Solidago austrina*, *S. simulans*, and the *S. ulignosa* complex were borrowed and examined from the following herbaria (BRIT, FLAS, FSU, GA, GH, the J.K. Morton personal herbarium now in TRT, KYU, MT, NCU, NY, USCH, and WAT in MT; Thiers continuously updated). Digital images posted online by the following herbarium via the SouthEast Regional Network of Expertise and Collections (SERNEC Data Portal 2019) were examined to map distributions: ABLC, APSC, ASC, BHO, BRU, BUT, CALVIN, CLEMS, CMC, EMC, F, FSU, HUNT, ILL, IND, LSU, LYN, MCA, MICH, MIN, MOR, MSC, MUH, NO, NY, OSU, PH, UNC, UWL, VPI, WIS. Of the several thousand specimens examined, 105 were chosen and measured for the statistical analyses based on completeness of the specimen, state of maturity, and geographical distribution. In total, 20 vegetative and 17 floral traits were scored for the final analyses (Table 2). Additional stem, leaf, inflorescence, and phyllary indument traits were used in assigning specimens to a priori groups.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology were presented in Semple et al. (2016a) and are not repeated here. Eleven analyses were performed. In the <u>first</u> analysis, *S. austrina* (40 specimens), *S. azorica* (17 specimens), *S. chrysopsis* (19 specimens), *S.*



Figure 1. A robust shoot of tetraploid *Solidago uliginosa* var. *uliginosa*, *Semple & Suripto 5014* (WAT) from Mackinac Co., Michigan.



Figure 2. A robust shoot of tetraploid *Solidago uliginosa* var. *uliginosa*, *Semple & Suripto 9524* (WAT) from Ocean Co., New Jersey; very long inflorescence branches.



Figure 3. Robust shoots of diploid *Solidago uliginosa var. peracuta*, *Semple & Keir 4602* (WAT) from Wolfe Co., Québec.



Figure 4. Small shoots of *Solidago uliginosa* var. *peracuta*, *Gagnon* 74499 (MT) from Lac Nahalie in northwestern, Québec.



Figure 5. Solidago uliginosa var. terrae-novae, Rouleau 5165 (MT) from the Avalon Peninsula, Newfoundland.



Figure 6. Solidago uliginosa var. terrae-novae, Rouleau 5900 (MT) from Newfoundland.



Figure 7. Solidago simulans, Totten and party s.n. (NCU) from Satulah Mt., Macon Co., North Carolina.



Figure 8. Solidago simulans, Whiteside Mt., Jackson Co., North Carolina.



Figure 9. Solidago simulans, basal rosettes, Whiteside Mt., Jackson Co., North Carolina.



Figure 10. Ranges of distribution and source locations of multivariate samples in eastern North America of *Solidago austrina* (red dots), *S. simulans* (*brown* +*s*), and *S. uliginosa* (var. *uliginosa* s.l., orange triangles, mostly or exclusively tetraploid; var. *peracuta/"purshii"*, yellow triangles (mostly diploid); var. *terrae-novae*, light blue triangles); ranges of varieties based on conclusions drawn from the multivariate analyses and examination of online images of herbarium specimens.

S. gracillima (18 specimens), *S. maya* (9 specimens), *S. mexicana* (45 specimens), *S. paniculata* (13 specimens), *S. pulchra* (15 specimens), *S. sempervirens* (16), *S. simulans* (16 specimens), *S. stricta* (34 specimens), *S. uliginosa* (47 specimens), and *S. virgata* (29 specimens) were included in a STEPWISE discriminant analysis and then a COMPLETE discriminant analysis with seven traits because only eight specimens of *S. maya* could be included. In the <u>second</u> analysis, *S. austrina, S. simulans*, and *S. uliginosa* s.1. were included in a STEPWISE discriminant. In the <u>third</u> analysis, *S. austrina* and *S. uliginosa* s.1. were included in a STEPWISE discriminant. In the <u>fourth</u> analysis, *S. austrina* and *S. uliginosa* s.s. were included in a STEPWISE discriminant. In the <u>fifth</u> analysis, *S. austrina, S. purshii* (including *var. peracuta* and *var. terrae-novae*), *S. simulans*, and *S. uliginosa* s.s. were included in a STEPWISE discriminant. In the <u>fifth</u> analysis, *S. austrina, S. purshii* (including var. peracuta and var. terrae-novae), *S. simulans*, and *S. uliginosa* s.s. were included in a large back of the sixth analysis, *S. austrina, S. terrae-novae*, and *S. uliginosa* (including var. peracuta and var. uliginosa) were included in a STEPWISE discriminant analysis.

the <u>seventh</u> analysis, *S. austrina, S. purshii, S. simulans*, S. *terrae-novae*, and *S. uliginosa* s.s. were included in a STEPWISE discriminant analysis. In the <u>eighth</u> analysis, *S. purshii, S. terra-novae*, and *S. uliginosa* s.s. were included in a STEPWISE discriminant analysis. In the <u>ninth</u> analysis, *S. austrina, S. purshii*, S. *terrae-novae*, and *S. uliginosa* (including *S. simulans*) were included in a STEPWISE discriminant analysis. In the <u>ninth</u> analysis, *S. austrina, S. purshii*, S. *terrae-novae*, and *S. uliginosa* (including *S. simulans*) were included in a STEPWISE discriminant analysis. In the <u>tenth</u> analysis, *S. terrae-novae* and *S. uliginosa* (including *S. purshii*) were included in a STEPWISE discriminant analysis. In the <u>tenth</u> analysis. In the <u>eleventh</u> analysis, *S. purshii* and *S. terrae-novae* were included in a STEPWISE discriminant analysis. Numerous additional preliminary analyses were run over multiple years as the sample sizes of the taxa were increased but are not reported here. Specimens of *Solidago austrina* were included as an a priori group for comparative purposes in the multiple analyses of the *S. uliginosa* complex.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
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-number of serrations on 1 side of margin
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)
CAPBRNLN	Length of lower inflorescence branches (cm)
INVOLHT	Involucre height at anthesis (mm)
OPHYLLN	Outer phyllary length (mm)
MIDPHYLLN	Mid series phyllary length (mm)
MIDPHYLWD	Mid series phyllary width at widest point (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)

Table 2. Traits scored for the multivariate analyses of 320 specimens of *Solidago* subsect. *Maritimae*.

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
UPSTMNOD25	Number of nodes in the top 25% of the stem below the inflorescence
UPSTMNOD20	Number of nodes in the top 20% of the stem below the inflorescence

RESULTS

Analysis 1: Thirteen species level a priori groups analysis

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid stem leaf length, width, and number of margin serrations. Basal rosette leaves were often not present and were not included in the analyses. Lower stem leaves were present on many specimens but were not included in the analyses because their traits correlated highly among themselves and with mid and upper stem leaf traits. Among the floral traits scored, only ray floret pappus length and disc floret pappus length correlated highly; the former was included in the analyses. The numbers of nodes in the top 25% and 20% of the stem were highly correlated and only the number of nodes in the top 25% of the step were included in the analysis.

In the COMPLETE discriminant analysis of 320 specimens of 13 species level a priori groups (Solidago austrina, S. azorica, S. chrysopsis, S. gracillima, S. maya, S. mexicana, S. paniculata, S. pulchra, S. sempervirens, S. simulans, S. stricta, S. uliginosa, and S. virgata), the following seven of ten traits selected in a STEPWISE analysis were used in the COMPLETE analysis and are listed in order of decreasing F-to-remove values: length of the longest inflorescence branches (43.26), mid stem leaf width (27.54), mid stem leaf length (18.99), ray floret pappus length (16.91), number of disc florets (16.34), number of mid stem leaf margin serrations (13.74), and mid series phyllary width (32.07). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 3. F-values based on Mahalanobis distances of the between group centroids indicated the that largest separations were between *S. gracillima* and *S. mexicana* (77.963), *S. gracillima* and *S. uliginosa* (77.914), and *S. gracillima* and *S. sempervirens* (75.558); the smallest separations were between *S. maya* and *S. virgata* (1.761), *S. chrysopsis* and *S. maya* (2.865), *S. simulans* and *S. uliginosa* (3.116), and *S. maya* and *S. stricta* (3.132).

In the Classificatory Discriminant Analysis of 320 specimens of the 13 species level a priori groups (*Solidago austrina, S. azorica, S. chrysopsis, S. gracillima, S. maya, S. mexicana, S. paniculata, S. pulchra, S. sempervirens, S. simulans, S. stricta, S. uliginosa, and S. virgata*), percents of correct a posterori assignment to the same a priori group ranged from 44-89%. The Classification matrix and Jackknife classification matrix are presented in Table 4. Results are presented in order of decreasing percents of correct placement. Percents of correct a posteriori assign to the same a priori group ranged from 84-89% for *S. chrysopsis, S. gracillima, S. pulchra,* and *S. paniculata*. Percents of correct a posteriori assign to the same a priori group ranged from 75-77% for *S. azorica, S. simulans,* and *S. virgata*. Percents of correct a posteriori assign to the same a priori group ranged from *S. sempervirens,* 56% for *S. stricta,* 53 percent for *S. uliginosa,* 50% for *S. austrina,* 44% for *S. maya,* and 38% for *S. mexicana.* The results are not discussed further.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 320 specimens of 13 species of *Solidago* subsect. *Maritimae* are presented in Fig. 11. Eigenvalues on the seven axes were 2.744, 1.861, 1.016, 0.880, 0.538, 0.327, and 0.028. Only symbols for *S*.

Group									s
	austrina	azorica	chrysopsis	gracillima	maya	mexicana	paniculata	pulchra	semperviren
azorica	43.155								
chrysopsis	13.922	50.723							
gracillima	63.067	96.655							
maya	4.130	25.362	56.681						
mexicana	14.455	46.667	2.865	32.694					
paniculata	24.131	44.949	8.747	77.963	0.661				
pulchra	10.708	47.036	17.871	45.193	5.520	8.895			
sempervirens	23.198	18.558	13.733	57.054	7.941	16.579	24.845		
simulans	8.572	20.277	29.280	75.558	9.224	13.245	11.047	24.635	
stricta	12.664	47.387	20.647	52.739	7.831	15.701	19.867	25.163	13.580
uliginosa	19.958	41.461	14.378	59.225	3.132	15.149	17.212	20.237	23.826
virgata	11.263	53.233	25.730	77.914	10.165	29.062	26.638	38.915	26.972
				-					
Group									
	simulans	stricta	uliginosa						
stricta	15.232			-					
uliginosa	3.116	35.894							
virgata	16.261	6.051	30.039						
				_					

Table 3. Between groups F-matrix for the 13 a priori group analysis of S. subsect. Maritimae (df = 10 288).

Wilks' lambda = 0.0117 df = 7 12 307; Approx. F= 23.4956 df = 84 1851 prob = 0.0000

Table 4. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of 13 a priori groups; a posteriori placements to groups in rows.

Group									S					
	austrina	azorica	chrysopsis	gracillima	maya	mexicana	paniculata	pulchra	semperviren	simulans	stricta	uliginosa	virgata	% correct
austrina	20	0	2	1	0	4	0	3	0	3	3	2	2	50
azorica	0	13	0	0	0	0	0	0	0	0	0	0	0	76
chrysopsis	0	0	17	0	1	0	0	0	0	0	0	0	1	89
gracillima	1	0	0	17	1	0	0	0	0	0	0	0	0	89
maya	0	0	0	0	4	3	0	0	0	0	0	0	2	44
mexicana	1	1	1	0	11	17	4	1	3	2	2	1	3	38
paniculata	0	0	0	0	1	1	11	0	0	0	0	0	0	85
pulchra	1	0	0	0	0	0	0	13	0	0	0	0	1	87
sempervirens	0	0	0	0	2	0	2	0	11	0	0	1	0	69
simulans	1	0	0	0	0	1	0	0	0	13	0	2	0	75
stricta	4	0	2	0	2	0	0	0	0	1	19	0	7	56
uliginosa	4	1	0	0	2	5	0	0	0	11	0	32	0	53
virgata	2	0	3	0	1	0	0	0	0	0	1	0	23	77
Totals	34	15	25	18	25	31	17	17	14	28	25	38	39	63

Group									SL					
	austrina	azorica	chrysopsis	gracillima	maya	mexicana	paniculata	pulchra	sempervireı	simulans	stricta	uliginosa	virgata	% correct
austrina	17	0	2	1	0	5	0	4	0	3	3	3	2	43
azorica	0	13	0	0	0	0	0	0	0	4	0	0	0	46
chrysopsis	1	0	16	0	0	0	0	0	0	0	0	0	2	84
gracillima	1	0	0	16	1	0	0	0	0	0	1	0	0	84
maya	0	0	1	0	2	4	0	0	0	0	0	0	2	22
mexicana	1	1	2	0	10	16	4	1	4	1	2	0	3	36
paniculata	0	0	0	0	1	2	10	0	0	0	0	0	0	77
pulchra	1	0	0	0	0	0	0	13	0	0	0	0	1	87
sempervirens	0	1	0	0	2	0	2	0	10	0	0	1	0	63
simulans	3	0	0	0	0	1	0	0	0	9	0	3	0	56
stricta	4	0	2	0	2	0	0	0	0	0	18	0	8	53
uliginosa	4	1	0	0	2	6	0	0	0	11	0	23	0	49
virgata	2	0	3	0	1	0	0	0	0	0	1	0	23	77
Totals	34	16	26	17	21	34	16	18	14	28	25	30	41	58

Jackknifed classification matrix

gracillima were separated from symbols for other taxa. There was partial to complete overlap of symbols for all other species.

Analyses 2-10: the S. uliginosa complex

The Pearson correlation matrix for traits of specimens of *Solidago austrina*, *S. simulans*, and *S. uliginosa* included r > |0.7| for most pairs of basal and lower leaf traits and mid and upper leaf traits reducing the number used to mid stem leaf length and the numbers of mid stem and upper stem leaf serrations. Basal rosette leaves were only sometimes present and were not included in the discriminant analyses. Only some floral traits were correlated. The following traits were included in all the subsequent STEPWISE analyses: length of the longest inflorescence branches, involucre height, mid series phyllary length and width, the numbers of ray and disc florets, the lengths of the ray floret lamina, ovary/fruit body, and pappus, the lengths of disc corolla, corolla lobes, fruit/ovary body, and pappus, and the number of nodes in the top 25% of the stem below the inflorescence.

Analysis 2: Three species level a priori groups analysis of the S. uliginosa complex

In the STEPWISE discriminant analysis of 105 specimens of three species level a priori groups *Solidago austrina*, *S. simulans* (including all specimens from northeastern Georgia, North Carolina, and Tennessee), and *S. uliginosa* (including all specimens from West Virginia north to northern Ontario, Québec and Newfoundland) the following six traits were selected and are listed in order of decreasing F-to-remove values: number of disc florets (42.78), number of ray florets (19.14), number of nodes in the top 25% of stem below the inflorescence (18.64), mid series phyllary length, (9.62), mid stem leaf length (6.35), and ray floret lamina length (6.06). 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 5. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. uliginosa* (52.645); the smallest separation was between *S. simulans* and *S. uliginosa* (10.216).

In the Classificatory Discriminant Analysis of 105 specimens of the four species level a priori groups (*S. austrina*, *S. simulans*, and *S. uliginosa*), percents of correct a posteriori assignment to the same a priori group ranged from 87-88%. The Classification matrix and Jackknife classification



Figure 11. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 320 specimens in 13 a priori groups of the Solidago subsect. Maritimae from a seven-trait COMPLETE Analysis: *S. austrina* (red dots), *S. azorica* (left oriented red triangles), *S. chrysopsis* (blue diamonds), *S. gracillima* (red star bursts), *S. maya* (gray diamonds), *S. mexicana* (black +s), *S. paniculata* (red circles), *S. pulchra* (magenta squares), *S. sempervirens* (green triangles), *S. simulans* (brown +s), *S. stricta* (yellow stars), *S. uliginosa* (orange triangles), and *S. virgata* (dark blue dots).

matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. Fourteen of the 16 specimens of the S. simulans a priori group (88%) were assigned a posteriori into the S. simulans group; 7 specimens with 92-100% probability, 1 specimen with 72% probability, 1 specimen with 62% probability (287), and 1 specimens with 59% probability (Godfrey 6949 GH from Scotland Co., North Carolina; originally identified by the collector as S. uniligulata var. neglecta and later annotated by M.L. Fernald in 1947 as S. uliginosa). Two specimens of the S. simulans a priori group were assigned to S. uliginosa with 80% probability (20% to S. simulans; *Chapman s.n.* NY from middle Florida; a problematic shoot that has a small inflorescence with short branches that is more like S. uliginosa but the provenance is much too far south for either species) and 79% probability (20% to S. simulans; Semple 11590 WAT from Whiteside Mt., North Carolina; Semple 11591 WAT from the same population was assigned to S. simulans with 89% probability; Fig. 6). Thirty-four of 39 specimens of the S. austrina a priori group (87%) plus 1 additional specimen only included a posteriori were assigned a posteriori into the S. austrina group; 32 specimens with 92-100% probability, 1 specimen with 72% probability, 1 specimen with 63% probability (Heller 1284 NY from Rowan Co., North Carolina), and 1 specimen with 58% probability (Semple & Suripto 9786 WAT a diploid from Clarendon Co., South Carolina). Five specimens of the S. austrina a priori group were assigned a posteriori to other species: 3 specimens to S. simulans with 90% probability (Lindholm s.n. GA from Liberty Co., Florida), 85% probability (Lazor 4587 MT from Liberty Co., Florida), and 79% probability (Radford 19485 NCU from Montgomery Co., North Carolina). Fortyone of 47 specimens of the S. uliginosa a priori group (87%) were assigned a posteriori into the S. uliginosa group; 28 specimens with 91-100% probability, 8 specimens with 81-89% probability, 3 specimens with 72-77%, 1 specimen with 66% probability (Umbach s.n. NCU from Indiana), and 1 specimen with 58% probability (Downs 6769 NCU from West Virginia). Six specimens of the S. uliginosa a priori group were assigned a posteriori to S. simulans with 83% probability (Semple & Suripto 9524 WAT from New Jersey; Fig. 2), 68% probability (Chase 3386 USCH from Tazewell Co., Illinois), 67% probability (Cusick 25744 NCU from West Virginia), 64% probability (Bouchard et al. 92408 MT from Newfoundland; small shoot with a var. peracuta-like inflorescence), 56% probability (Semple & Suripto 9590 WAT from York Co., Maine; a robust shoot with a large inflorescence with long ascending spreading branches), and 50% probability (Semple 11814 WAT from New Jersey).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 105 specimens of *Solidago austrina*, *S. simulans*, and *S. uliginosa* is presented in Fig. 12. Eigenvalues on the first two axes were 3.398 and 0.499.

Table 5	Retween groun	F-matrix for	the four s	necies level	a priori groups	analysis (df - 6	94)
Table 5.	Detween group	s r-mainx 101	the four s	pecies level a	a priori groups	s analysis ($u_1 = 0$	94).

Group	austrina	simulans
simulans	19.218	
uliginosa	52.645	10.216

Wilks' lambda = 0.1517 df = 6 2 99; Approx. F= 24.5629 df = 12 188 prob = 0.0000

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

Group	austrina	simulans	uliginosa	% correct
austrina	34	3	2	87
simulans	0	14	2	88
uliginosa	0	6	71	87
Totals	34	23	45	87

Group	austrina	simulans	uliginosa	% correct
austrina	34	3	2	87
simulans	1	12	3	75
uliginosa	0	6	41	87
Totals	35	21	46	85

Jackknifed classification matrix



Figure 12. Plot of canonical scores (CAN1 vs CAN2) analysis for 105 specimens of *Solidago* subsect. *Maritimae*: *S. austrina* (red dots), *S. simulans* (brown +s), and *S. uliginosa* (orange triangles).

Analysis 3: Two species level a priori groups analysis: Solidago simulans and S. ulginosa s.l.

In the STEPWISE discriminant analysis of 63 specimens of two species level a priori groups (*S. simulans* and *S. uliginosa* including *S. purshii* and *S. terrae-novae*), the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid series phyllary length (43.34), number of ray florets (15.79), number of nodes in the top 25% of stem below inflorescence (6.53), and length or the longest lower inflorescence branches (5.87). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. *Solidago simulans* and *S. uliginosa* s.l. had an F-to separate value of 22.908 (Wilks' lambda = 0.3876 df = 4 1 61; Approx. F= 22.908 df = 4 58 prob = 0.0000).

In the Classificatory Discriminant Analysis of 63 specimens of the two species level a priori groups (*S. simulans* and *S. uliginosa* s.l.), percents of correct a posterori assignment to the same a priori group were 94% and 87%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Fifteen of the 16 specimens of the *S. simulans* a priori group (94%) were assigned a posteriori into the *S. simulans* group; 12 specimens with 90-100% probability, 1 specimen

with 88% probability, 1 specimen with 62% probability, and 1 specimen with 59% probability (*Semple 11590* WAT from Whiteside Mt., North Carolina; *Semple 11591* WAT from the same population was assigned to *S. simulans* with 100% probability; Fig. 6). One specimen of the *S. simulans* a priori groups were assigned to *S. uliginosa* with 79% (*Chapman s.n.* NY from middle Florida; a problematic specimen of uncertain identity and provenance). Forty of 47 specimens of the *S. uliginosa* s.l. a priori group (87%) were assigned a posteriori into the *S. uliginosa* s.l. group; 35 specimens with 94-100% probability, 4 specimens with 80-89% probability, and 1 specimen with 78% probability. Six specimens of the *S. uliginosa* s.l. a priori group (*Semple & Suripto 9524* WAT from New Jersey; a tetraploid, Fig. 2), 79% probability (*Cusick 25744* NCU from West Virginia), 72% probability (*Chase 3386* USCH from Tazewell Co., Illinois), 69% probability (*Semple 11814* WAT a tetraploid from Ocean Co., New Jersey), 54% probability (*Bouchard et al. 92408* MT from Newfoundland), and 54% probability (*Semple & Brouillet 3660* WAT from Oneida Co., New York; a 91 cm tall diploid).

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

Group	simulans	uliginosa	% correct	
simulans	15	1	94	
uliginosa	6	41	87	
Totals	21	42	89	
ckknifed class	sification matrix			
ckknifed class	sification matrix	uliginosa	% correct	
ckknifed class Group	sification matrix	uliginosa	% correct	
ackknifed class Group simulans uliginosa	sification matrix simulans 15 6	uliginosa 1 41	% correct 94 87	

Histograms of canonical scores (CAN1) for *S. simulans* and *S. uliginosa* s.l. are shown in Fig. 13. The eigenvalue on the first axis was 1.580.



Figure 13. Histograms of canonical scores (CAN1) for S. simulans (left) and S. uliginosa s.l. (right).

Analysis 4: Two species level a priori groups analysis: Solidago simulans and S. ulginosa s.s.

In the STEPWISE discriminant analysis of 28 specimens of two species level a priori groups (*S. simulans* and *S. uliginosa* var. *uliginosa* only), the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid series phyllary length (22.75),

number of ray florets (8.51), length of the longest lower inflorescence branches (5.14), and number of disc florets (4.54). 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 = 0.0000 that the null hypothesis was true. *Solidago simulans* and *S. uliginosa* had an F-to separate value of 12.477 (Wilks' lambda = 0.3155 df = 4 1 26; Approx. F= 12.4770 df = 4 23 prob = 0.0000).

In the Classificatory Discriminant Analysis of 28 specimens of the two species level a priori groups (*S. simulans* and *S. uliginosa* s.s.), percents of correct a posterori assignment to the same a priori group were 93% and 100%. The Classification matrix and Jackknife classification matrix are presented in Table 8. All of 13 specimens of the *S. uliginosa* s.s. a priori group (100%) were assigned a posteriori into the *S. uliginosa* s.s. group; 8 specimens with 97-100% probability, 4 specimens with 80-89% probability, and 1 specimen with 78% probability. Fourteen of the 15 specimens of the *S. simulans* a priori group (93%) were assigned a posteriori into the *S. simulans* group; 11 specimens with 92-100% probability, 2 specimens with 84-85% probability, and 1 specimen with 75% probability). One specimen of the *S. simulans* a priori groups were assigned to *S. uliginosa* s.s. with 53% probability (*Chapman s.n.* NY from middle Florida; a problematic specimen of uncertain identity and provenance).

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	simulans	uliginosa s.s.	%
			correct
simulans	14	1	93
uliginosa s.s.	0	13	100
Totals	14	14	96
ackknifed classifi	ication matrix		
ackknifed classifi Group	ication matrix simulans	uliginosa s.s.	%
ackknifed classifi Group	ication matrix simulans	uliginosa s.s.	% correct
ackknifed classifi Group simulans	ication matrix simulans 14	uliginosa s.s.	% correct 93
ackknifed classifi Group simulans uliginosa s.s.	ication matrix simulans 14 1	<i>uliginosa s.s.</i> 1 12	% correct 93 92

Histograms of canonical scores (CAN1) for *S. simulans* and *S. uliginosa* s.s. are shown in Fig. 14. The eigenvalue on the first axis was 2.170.



Figure 14. Histograms of canonical scores (CAN1) for S. simulans (left) and S. uliginosa (right).

Analysis 5: Four species level a priori groups analysis: Solidago uliginosa complex II

In the STEPWISE discriminant analysis of 105 specimens of four species level a priori groups *S. austrina*, *S. purshii* (combining predominantly diploid var. *peracuta* and *var. terrae-novae* of *S. uliginosa s.l.*), *S. simulans*, and *S. uliginosa* (including only tetraploid var. *uliginosa*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (29.35), number of nodes in the top 25% of stem below inflorescence (24.98), disc corolla lobe length (17.02), number of ray florets (16.91), mid series phyllary length, (7.44), and ray floret pappus length at anthesis (5.55). 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 = 0.0000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 9. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. purshii* (52.645); the smallest separation was between *S. simulans* and *S. uliginosa* (5.131).

Table 9. Between groups F-matrix for the four species level a priori groups analysis (df = 6 93).

	Group	austrina	purshii	simulans	
	purshii	59.038			
	simulans	14.420	20.069		
	uliginosa	17.399	10.455	5.131	
Wilks' lambda =	0.0960 df = 6	3 98; Approx	x. F= 18.8498	3 df = 18 2	63 prob = 0.000

In the Classificatory Discriminant Analysis of 105 specimens of the four species level a priori groups (S. austrina, S. purshii, S. simulans and S. uliginosa s.s.), percents of correct a posterori assignment to the same a priori group were 64% and 91%. The Classification matrix and Jackknife classification matrix are presented in Table 10. Thirty-one of the 34 specimens of the S. purshii a priori group (91%) were assigned a posteriori into the S. purshii group; 27 specimens with 92-100% probability, 2 specimens with 80-81% probability, 1 specimen with 73%, and 2 specimens with 68% (Rouleau 5142 MT from Newfoundland; has a var. terra-novae inflorescence) and 65% probability (Bouchard et al. 92408 MT from Newfoundland; has a var. peracuta inflorescence). Three specimens of the S. purshii a priori group were assigned to S. uliginosa with 82% (11% to S. purshii; Semple & B. Semple 8714 WAT from the Manitoba-Ontario border), 66% probability (Rouleau 5165 MT from Newfoundland), and 54% probability (Semple & Keir 4711 WAT from New Brunswick; 102 cm tall diploid shoot with an elongated inflorescence with short ascending lower branches). Thirteen of 16 specimens of the S. simulans a priori group (87%) were assigned a posteriori into the S. simulans group; 2 specimens with 92% and 96% probabilities, 7 specimens with 81-89% probability, 3 specimens with 72-76% probability, and 1 specimen with 68% probability (Totten s.n. NCU from Macon Co., North Carolina; Fig. 7). Two specimens of the S. simulans a priori group were assigned to S. uliginosa with 58% probability (32% to S. simulans: Semple 11590 WAT from Whiteside Mt., Jackson Co., North Carolina) and 49% probability (45% to S. simulans; Krouse s.n. NCU from Ashe Co., North Carolina). Thirty-three of 39 specimens of the S. austrina a priori group (85%) were assigned a posteriori into the S. austrina group; 28 specimens with 97-100% probability, 1 specimen with 86% probability, 2 specimens with 71-72% probability, 1 specimen with 62% probability (Orzell & Bridges 17342 GA from Colquitt Co., Georgia), and 1 specimen with 59% probability (Semple 11827 WAT from Walton Co., Georgia). Six specimens of the S. austrina a priori group were assigned to other species: 3 to S. simulans with 99% probability (Lindholm s.n. GA from Liberty Co., Florida), 98% probability (Lazor 4587 MT from Liberty Co., Florida), and 67% probability (Radford 19485 NCU from Montgomery Co., North Carolina); 2 specimens to S. uliginosa with 63% probability (Semple et al. 11857 WAT from Tennessee) and 60% probability

(*Beard 150* NCU from Lee Co., North Carolina; damaged inflorescence); and 1 specimen to *S. purshii* with 45% probability (*Heller 1284* NY from Rowan Co., North Carolina). Nine of the 14 specimens of the *S. uliginosa* s.s. a priori group (64%) were assigned a posteriori to *S. uliginosa*: 3 specimens with 92-100% probability, 3 specimens with 85-86% probability, 2 specimens with 76-77% probability, and 1 specimen with 60% probability (*Cusick 25744* NCU from West Virginia). Five specimens of the *S. uliginosa* s.s. a priori group were assigned a posteriori to other species: 2 specimens to *S. purshii* with 90% probability (*Gibson 1107* NCU from West Virginia) and 43% probability (*Downs 6769* NCU from West Virginia); and 3 specimens to *S. simulans* with 63% probability (*Chase 3386* USCH from Tazewell Co., Illinois), 59% probability (*Semple & Suripto 9590* WAT from York Co., Maine; a robust shoot with a large inflorescence with long ascending spreading branches), and 53% probability (*Semple & Suripto 9524* WAT from New Jersey; a tetraploid, Fig. 2).

Group	austrina	purshii	simulans	uliginosa s.s	% correct
austrina	33	1	3	2	85
purshii	0	31	0	3	91
simulans	0	0	13	2	87
uliginosa s.s.	0	2	3	9	64
Totals	33	34	19	16	84
ackknifed classi Group	fication matrix austrina	n purshii	simulans	uliginosa s.s	% correct
austrina	33	1	4	2	82
purshii	0	31	0	3	01
					91
simulans	0	0	13	2	91 87
simulans uliginosa s.s	0 0	0 2	13 3	2 9	87 64

Table 10. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four species level a priori groups; a posteriori placements to groups in rows.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 105 specimens of 4 species of *Solidago* subsect. *Maritimae* are presented in Fig. 15: groups (*S. austrina, S. purshii, S. simulans* and *S. uliginosa* s.s.). Eigenvalues on the three axes were 3.873, 0.718, and 0.0.224.

Analysis 6: Four species level a priori groups analysis: Solidago uliginosa complex III

In the STEPWISE discriminant analysis of 102 specimens of four species level a priori groups (*S. austrina*, *S. simulans*, *S. terrae-novae*, and *S. uliginosa* (including *S. purshii*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (28.27), number of ray florets (14.56), number of nodes in the top 25% of stem below inflorescence (14.20), mid series phyllary length (6.38), mid stem leaf length (6.06), and ray floret lamina length (5.95). 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 = 0.0000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 11. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. uliginosa* (47.624); the smallest separation was between *S. terrae-novae* and *S. uliginosa* (2.849).



Figure 15. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 105 specimens of 4 a priori groups of the *Solidago* subsect. *Maritimae*: *S. austrina* (red dots), *S. purshii* (yellow triangles), *S. simulans* (brown +s), *S. uliginosa* (orange triangles).

In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups (*S. austrina, S. simulans, S. terrae-novae*, and *S. uliginosa* including *S. purshii*), percents of correct a posteriori assignment to the same a priori group ranged from 68-87%. The Classification matrix and Jackknife classification matrix are presented in Table 12. Thirty-four of the 39 specimens In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups

Group	austrina	simulans	terrae-
			novae
simulans	19.115		
terrae-novae	19.985	7.003	
uliginosa	47.624	9.449	2.849

Table 11. Between groups F-matrix for the four species level a priori groups analysis (df = 6 93).

(S. austrina, S. simulans, S. terrae-novae, and S. uliginosa including S. purshii), percents of correct a posteriori assignment to the same a priori group ranged from 68-87%. The Classification matrix and Jackknife classification matrix are presented in Table 12. Thirty-four of the 39 specimens of the S. austrina a priori group (87%) plus 1 specimen only included a posteriori were assigned a posteriori into the S. austrina group; 31 specimens with 91-100% probability, 1 specimen with 88% probability, 1 specimen with 67% probability, and 2 specimens with 55% probability (Heller 1284 NY from Rowan Co., North Carolina) and 54% probability (Semple & Suripto 9786 WAT a diploid from Clarendon Co., South Carolina). Four specimens of the S. austrina a priori groups were assigned to other species: 3 specimens to S. simulans with 89% (Lindholm s.n. GA from Liberty Co., Florida), 81% probability (Lazor 4587 MT from Liberty Co., Florida), and 77% probability (Radford 19485 NCU from Montgomery Co., North Carolina); and 1 specimen to S terrae-novae with 90% probability (Beard 150 NCU from Lee Co., North Carolina; damaged inflorescence). Thirteen of 16 specimens of the S. simulans a priori group (81%) were assigned a posteriori into the S. simulans group; 7 specimens with 90-100% probability, 2 specimens with 85% and 81% probabilities, and 3 specimens with 75-79%. Three specimens of the S. simulans a priori group were assigned to other species: 2 specimens to S. terrae-novae with 62% probability (Chapman s.n. NY from middle Florida; a problematic specimen of uncertain identity and provenance) and 46% probability (Godfrey 6949 GH from Scotland Co., North Carolina); and 1 specimen to S. uliginosa with 49% probability (Semple 11590 WAT from Whiteside Mt., Jackson Co., North Carolina). Seven of the ten specimens of the S. terrae-novae a priori groups (70%) plus 1 specimen only included a posteriori were assigned to the S. terrae-novae group: 2 specimens with 96% probability, 2 specimens with 88% and 81% probability, 1 specimen with 78% probability, 1 specimen with 67% probability, and 2 specimens with 53% probability (Rouleau 5302 MT from SW Newfoundland) and 52% probability (Rouleau 7382 MT from SW Newfoundland; robust shoot with broad corymboid secund conical inflorescence). Three specimens of the S. terrae-novae a priori group were assigned a posteriori to S. uliginosa with 67% probability (Rouleau 5165 MT from Newfoundland; the second sheet of this number), 61% probability (Rouleau 5307 MT from SW Newfoundland; small and robust shoots with small corymboid inflorescences or a larger broad inflorescence with branches with small corymbiform arrangements of heads), and 40% probability (Rouleau 5165 MT from Newfoundland, Fig. 4). Twenty-five of the 37 specimens of the enlarged S. uliginosa a priori group (68%) were assigned a posteriori to the S. uliginosa group: 6 specimens with 91-98% probability, 3 specimens with 80-84% probability, 6 specimens with 70-79% proability, 4 specimens with 60-65% probability, 1 specimen with 47% probability (Rouleau 8411 MT from eastern Newfoundland), and 1 specimen with 39% probability (Downs 6769 NCU from West Virginia; the inflorescence has spreading arching lower branches typical for var. uliginosa). Twelve specimens of the enlarged S. uliginosa a priori group were assigned to other species: 6 specimens to S. simulans with 77% probability (Semple & Suripto 9524 WAT from New Jersey; a tetraploid, Fig. 2), 60% probability (Chase 3386 USCH from Tazewell Co., Illinois), 57% probability (Cusick 25744 NCU from West Virginia), 57% probability (Bouchard et al. 92408 MT from Newfoundland; small shoot with a var. peracuta-like inflorescence), 48% probability (Semple & Suripto 9590 WAT from York Co., Maine; a robust shoot with a large

Wilks' lambda = 0.1281 df = 6 3 98; Approx. F= 15.6023 df = 18 263 prob = 0.0000

inflorescence with long ascending spreading branches), and 42% (*Semple 11814* WAT from New Jersey); and 6 specimens to *S. terrae-novae* with 64% probability (*Rouleau 7022* MT from northcentral Newfoundland; a 74 cm tall shoot), 58% probability (*Gagnon 74499* MT from near James Bay in Québec; Fig. 4), 57% probability (*Semple & Keir 4897* WAT from New Brunswick; the inflorescence has long ascending diverging branches), 51% probability (*Semple & Suripto 9576* WAT, tetraploid from Massachusetts).

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

Group	austrina	simulans	terrae-	uliginosa	% correct
			novae		
austrina	34	3	2	0	87
simulans	0	13	2	1	81
terrae-novae	0	0	7	2	70
uliginosa	0	6	6	25	68
Totals	34	22	17	29	77
Jackknifed classi	fication matri	X			
Group	austrina	simulans	terrae-	uliginosa	% correct
			novae		
austrina	33	4	2	0	85
purshii	1	12	2	1	75
terrae-novae	0	0	7	3	70
uliginosa	0	6	6	25	68
Totals	34	22	17	29	75

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 105 specimens of 4 species of *Solidago* subsect. *Maritimae* are presented in Fig. 16: *S. austrina*, *S. simulans*, *S. terrae-novae*, and *S. uliginosa* (including *S. purshii*). Eigenvalues on the three axes were 3.408, 0.508, and 0.174.

Analysis 7: Five species level a priori groups analysis: Solidago uliginosa complex III

In the STEPWISE discriminant analysis of 102 specimens of five species level a priori groups (*S. austrina*, *S. purshii*, *S. simulans*, *S. terrae-novae*, and and expanded *S. uliginosa* (including *S. purshii*), the following seven traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (21.45), number of ray florets (12.82), number of nodes in the top 25% of stem below inflorescence (10.03), disc corolla lobe length (7.20), mid stem leaf length (6.01), mid series phyllary length (4.78), and ray floret lamina length (4.22). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of p = 0.0000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 13. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. austrina* and *S. purshii* (46.301); the smallest separations were between *S. purshii* and *S. terrae-novae* (2.722), *S. terrae-novae* and *S. uliginosa* (3.449), and *S. simulans* and *S. uliginosa* (4.686), and *S. purshii* and *S. uliginosa* (5.456).



Figure 16. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 104 specimens in 4 a priori groups of the *Solidago* subsect. *Maritimae: S. austrina* (red dots), *S. simulans* (brown +s), *S. terrae-novae* (including; light blue triangles), and an expanded *S. uliginosa* (including *S. purshii*; orange triangles).

Table 13. Between groups F-matrix for the four species level a priori groups analysis (df = 7 91).

Group	austrina	purshii	simulans	terrae- novae
purshii	46.301			
simulans	17.101	10.976		
terrae-novae	20.747	2.722	7.043	
uliginosa	17.303	5.456	4.686	3.449

Wilks' lambda = 0.0840 df = 7 4 97; Approx. F= 11.6046 df = 28 329 prob = 0.0000

In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups (S. austrina, S. purshii, S. simulans S. terrae-novae, and S. uliginosa including S. purshii) plus 1 specimen each of S. austrina and S. terrae-novae only included a posteriori, percents of correct a posterori assignment to the same a priori group were 60-88%. The Classification matrix and Jackknife classification matrix are presented in Table 14. Fourteen of the 16 specimens of the S. simulans a priori group (88%) were assigned a posteriori into the S. simulans group; 5 specimens with 91-94% probability, 2 specimens with 89% and 84% probability, 4 specimens with 71-79% probability, 2 specimens with 64% probability (Krouse s.n. NCU from Ashe Co., North Carolina) and 63% probability (Godfrey 50724 GH from Moore Co., North Carolina), and 1 specimen with 55% probability (Godfrey 6949 GH from Scotland Co., North Carolina). Two specimens of the S. simulans a priori groups were assigned to S. uliginosa with 73% probability (Chapman s.n. NY from middle Florida; a problematic specimen of uncertain identity and provenance) and 40% probability (Semple 11590 WAT from Whiteside Mt., Jackson Co., North Carolina). Thirty-four of the 39 specimens of the S. austrina a priori group (87%) plus 1 additional specimen only included a posteriori were assigned a posteriori into the S. austrina group; 31 specimens with 96-100% probability, 1 specimen with 88% probability, 1 specimen with 63% probability (Sorrie 7711 NCU from Moore Co., North Carolina), and 1 specimen with 39% probability (Heller 1284 NY from Rowan Co., North Carolina). Five specimens of the S. austrina a priori group were assigned to other species; 3 specimens to S. simulans with 86% probability (Lindholm s.n. GA from Liberty Co., Florida), 83% probability (Lazor 4587 MT from Liberty Co., Florida), and 64% probability (Radford 19485 NCU from Montgomery Co., North Carolina); 1 specimen to S. terrae-novae with 61% probability (Beard 150 NCU from Lee Co., North Carolina; damaged inflorescence); and 1 specimen to S. uliginosa with 53% probability (Semple et al. 11857 WAT from Tennessee). Seventeen of 24 specimens of the S. purshii a priori group (71%) were assigned a posteriori to S. purshii; 6 specimens with 97-99% probability, 2 specimens with 88% and 84% probabilities, 1 specimen with 72% probability, 3 specimens with 58% probability (Shchepanek & White 2851 MT from Newfoundland), 54% probability (Semple & Brammall 2827 WAT from Cochrane Dist., Ontario; robust diploid), and 51% probability (Bouchard et al. 92408 MT from Newfoundland), and 2 specimens with 48% probability (Semple & Keir 4897 WAT from New Brunswick; robust diploid) and 44% probability (Ownbey & Hsi 4214 NCU from Minnesota). Six specimens of the S. purshii a priori group were assigned to other species: 4 to S. terrae-novae with 63% probability (Rouleau 7022 MT from northcentral Newfoundland), 60% probability (Torrey s.n. NY from New York), 55% probability (Semple & Keir 4897 WAT from New Brunswick, second shoot on sheet), and 50% probability (Gagnon 74499 MT from near James Bay in Québec; Fig. 4); 1 to S. simulans with 68% probability (Chase 3386 USCH from Illinois); and 1 to S. uliginosa with 61% probability (Semple & Keir 4711 WAT from New Brunswick; 102 cm tall diploid shoot with an elongated inflorescence with short ascending lower branches). Eight of 13 specimens of the S. uliginosa a priori group (62%) were assigned a posteriori to S. uliginosa; 3 specimens with 94-99% probability, 1 specimen with 88% probability, 1 specimen with 79% probability, 2 specimens with 67% probability and 60% probability (Semple 11814 WAT from New Jersey; tetraploid), and 1 specimen with 33% probability (32% to S. terrae-novae, 19% to S. austrina, and 16% to S. simulans; Downs 6769 NCU from West Virginia). Four specimens of the S. uliginosa a priori group were assigned to other species: 1 to S. purshii with 76% probability (Morton & Venn NA14272 TRT from Nipigon, Ontario; diploid with long diverging inflorescence branches); 3 specimens to S. simulans with 65% probability (Semple & Suripto 9524 WAT from New Jersey; a tetraploid, Fig. 2), 54% probability (Semple & Suripto 9590 WAT from York Co., Maine), and 51% probability (Cusick 25744 NCU from West Virginia); and 1 specimen to S. terrae-novae with 40% probability (38% to S. purshii and 21% to S. uliginosa; Gibson 1107 NCU from West Virginia). Six of 10 specimens of the S. terrae-novae a priori group (60%) plus 1 additional specimen only included a posteriori were assigned a posteriori to S. terrae-novae; 2 specimens with 94% and 91% probabilities, 1 specimen with 89% probability, 2 specimens with 78% probability and 76% probability, 1 specimen with 68%% probability, and 1 specimens with 55%

probability (*Rouleau 5302* MT from SW Newfoundland). Four specimens of the *S. terrae-novae* a priori group were assigned to other species: 3 specimens to *S. purshii* with 69% probability (*Rouleau 5307* MT from SW Newfoundland), 69% probability (*Rouleau 5165* MT from Newfoundland), and 48% probability (*Rouleau 7382* MT from SW Newfoundland); and 1 specimen to *S. simulans* 44% probability (*Rouleau 5165* MT from Newfoundland, Fig. 4).

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

Group	austrina	S. purshii	simulans	terrae-	uliginosa	% correct
				novae		
austrina	34	0	3	1	1	87
purshii	0	17	1	4	2	71
simulans	0	0	14	0	2	88
terrae-novae	0	3	1	6	0	60
uliginosa	0	1	3	1	8	62
Totals	34	21	22	12	13	77
Jackknifed classi	fication matri	x				
Group	austrina	S. purshii	simulans	terrae-	uliginosa	% correct
				novae		
austrina	32	0	3	1	3	82
purshii	0	16	1	5	2	67
simulans	1	0	13	0	2	81
terrae-novae	00	3	1	6	0	60
uliginosa	0	1	3	2	7	54
Totals	33	20	21	14	14	73

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 104 specimens of 5 species level groups (*S. austrina, S. purshii*, S. *simulans, S. terrae-novae*, and *S. uliginosa*) of *Solidago* subsect. *Maritimae* are presented in Fig. 17. Eigenvalues on the four axes were 4.234, 0.552, 0.243, and 0.179.

Analysis 8: Three varietal level a priori groups analysis of Solidago uliginosa

In the STEPWISE discriminant analysis of 47 specimens of three varietal level a priori groups in *S. uliginosa* (var. *peracuta*, var. *terrae-novae*, and var. *uliginosa*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret corolla lobe length (10.41), ray floret pappus length at anthesis (7.95), and number of nodes in the top 25% of the stem below the inflorescence (6.21). 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 = 0.0000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 15. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. *terrae-novae* and var. *uliginosa* (14.538); the smallest separation was between var. *terrae-novae* (5.425).

Table 15. Between groups F-matrix for the three varietal level a priori groups analysis (df = 3 42).

Group	peracuta	terrae-novae
terrae-novae	5.425	
uliginosa	14.538	12.875
Wilks' lambda = 0.3341 df = 3 2	44; Approx.	F = 14.538 df = 6



Figure 17. Two dimension plots of CAN1 versus CAN2 and CAN1 versus CAN3 scores for 104 specimens in 5 a priori groups of the *Solidago* subsect. *Maritimae*: *S. austrina* (red dots), *S. purshii* (yellow triangles), *S. simulans* (brown +s), *S. terrae-novae* (including; light blue triangles), and *S. uliginosa* s.s. (orange triangles).

In the Classificatory Discriminant Analysis of 47 specimens of the three varietal level a priori groups in S. uliginosa (var. peracuta, var. terrae-novae, and var. uliginosa) plus 1 additional specimen included a posteriori, percents of correct a posterori assignment to the same a priori group ranged from 67-90%. The Classification matrix and Jackknife classification matrix are presented in Table 16. Nine of the 10 specimens of the var. terrae-novae a priori group (90%) plus 1 specimen included a posteriori were assigned a posteriori into the var. terrae-novae group; 2 specimens with 90% and 93% probability, 2 specimens with 85-86% probability, 1 specimen with 74% probability, 3 specimens with 61-66% probability, and 2 specimens with 49% probability (Rouleau 5302 MT from SW Newfoundland; small shoots with broad compact inflorescences) and 48% probability (Rouleau 5165 MT from Newfoundland, Fig. 4). One specimen of the var. terrae-novae a priori group was assigned a posteriori to var. peracuta (37% to var. terrae-novae and 9% to var. uliginosa; Rouleau 5142 MT). Ten of 13 specimens of the var. *uliginosa* a priori group (77%) were assigned to that group: 6 specimens with 97-100% probability, 2 specimens with 73% and 75% probabilities, and 2 specimens with 64% and 62% probabilities. Three specimens of the var. *uliginosa* a priori group were assigned a posteriori to other varieties: 2 specimens to var. peracuta with 58% probability (Morton & Venn NA14272 TRT from Nipigon, Ontario; the inflorescence is rather broad for var. peracuta) and 41% probability (Downs 6769 NCU from West Virginia; the inflorescence has spreading arching lower branches typical for var. *uliginosa*) and 1 specimen to var. *terrae-novae* with 55% probability (Gibson 1107 NCU from West Virginia; the inflorescence is elongated and narrow). Sixteen of 24 specimens of the var. *peracuta* a priori group (67%) were assigned a posteriori to var. peracuta: 2 specimens with 97% and 95% probabilities, 5 specimens with 80-89% probability, 6 specimens with 72-79% probability, 2 specimens with 65-66% probability, and 1 specimen with 53% probability (45% to var. terrae-novae; Rousseau 51455 MT from L'Île-d'Anticosti, Québec; the shoot scored had a more compact inflorescence, while two other shoots not scored had larger more open inflorescences with spreading, arching lower branches more typical of var. terrae-novae). Seven specimens of the var. *peracuta* a priori group were assigned a posteriori to other varieties: 4 specimens to var. terrae-novae with 84% probability (Semple & Keir 4897 WAT from New Brunswick; the inflorescence has long ascending diverging branches; the other shoot on the sheet was also scored and assigned a posteriori to var. peracuta with 80% probability), 82% probability (Gagnon 74499 MT from near James Bay in Québec; Fig. 4), 61% probability (Semple 9072 WAT from Wisconsin; a robust diploid plant with an elongated inflorescence with short spreading arching branches), and 50% probability (48% to var. peracuta; Rouleau 7022 MT from northcentral Newfoundland; a 74 cm tall shoot with a large inflorescence with ascending branches typical of var. peracuta); 3 specimens were assigned a posteriori to var. uliginosa with 95% probability (Chase 3386 USCH from Illinois that should have been assigned var. *uliginosa* due to its long spreading inflorescence branches and geographic location), 61% probability (Semple & B. Semple 8714 WAT from near the Ontario-Manitoba border; a robust shoot with elongated inflorescence with ascending branches) and 53% probability (Ownbey & Hsi 4214 NCU from Minnesota; a mid size shoot with inflorescence with long diverging lower branches more typical of var. *uliginosa*).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 48 specimens of var. *peracuta*, var. *terrae-novae*, and var. *ulginosa* of *Solidago uliginosa* is presented in Fig. 18. Eigenvalues on the first two axes were 1.166 and 0.381.

Analysis 9: Alternative Analysis of four a priori groups: S. austrina, S. purshii, S. terrae-novae and S. uliginosa (including S. simulans)

In the STEPWISE discriminant analysis of 104 specimens of four species level a priori groups (*S. austrina, S. purshii, S. terrae-novae*, and *S. uliginosa* including *S. simulans*), the following six traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (24.82), number of nodes in the top 25% of stem below inflorescence (13.56), number of ray florets (12.67), disc corolla lobe length (11.55), mid stem leaf length (7.70), and ray



Table 16. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three variety level a priori groups in *Solidago uliginosa*; a posteriori placements to groups in rows.

floret lamina length (6.07). Lower inflorescence branch length was not selected as strongly discriminating (0.40). 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 = 0.0000 that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 17. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was

between *S. austrina* and *S. purshii* (53.771); the smallest separations were between *S. purshii* and *S. terrae-novae* (3.190) and *S. terrae-novae* and *S. uliginosa* s.s. (6.396)

Group	austrina	purshii	terrae- novae
purshii	53.771		
terrae-novae	24.771	3.190	
uliginosa	26.825	12.538	6.396

Table 17. Between groups F-matrix for the four species level a priori groups analysis (df = 6 93).

Wilks' lambda = 0.1778 df = 6 3 98; Approx. F= 16.5093 df = 18 263 prob = 0.0000

In the Classificatory Discriminant Analysis of 102 specimens of the four species level a priori groups (S. austrina, S. simulans S. terrae-novae, and S. uliginosa including S. purshii) plus 1 each of specimens of S. austrina and S. terrae-novae only included a posteriori, percents of correct a posterori assignment to the same a priori group were 70% and 92%. The Classification matrix and Jackknife classification matrix are presented in Table 18. Thirty-six of the 39 specimens of the S. austrina a priori group (92%) plus 1 specimen only included a posteriori were assigned a posteriori into the S. austrina group; 31 specimens with 94-100% probability, 2 specimens with 85% and 88% probabilities, 1 specimens with 99% probability, and 3 specimens with 57% (Heller 1284 NY from Rowan Co., North Carolina), 56% probability (Semple & Suripto 9786 WAT a diploid from Clarendon Co., South Carolina), and 54% probability (Radford 19485 NCU from Montgomery Co., North Carolina). Three specimens of the S. austrina a priori groups were assigned to other species: 2 specimens to S. uliginosa with 87% (Semple et al. 11857 WAT from Tennessee) and 54% probability (Sorrie 7711 NCU from Moore Co., North Carolina); and 1 specimen to S. terrae-novae with 63% probability (Beard 150 NCU from Lee Co., North Carolina; damaged inflorescence). Eighteen of 23 specimens of the S. purshii a priori group (78%) were assigned a posteriori into the S. purshii group; 7 specimens with 91-99% probability, 1 specimen with 87% probability, 3 specimens with 72-75% probability, 3 specimens with 61-62% probability, 3 specimens with 58% probability (Shchepanek & White 2851 MT from Newfoundland), 56% probability (Gagnon 74499 MT from near James Bay in Québec; Fig. 4), and 54% probability (Semple & Keir 4897 WAT from New Brunswick; shoot on right side of sheet), and 1 specimen with 44% probability (Ownbey & Hsi 4214 NCU from Minnesota; a mid size shoot with inflorescence with long diverging lower branches more typical of var. *uliginosa*). Five specimens of the S. *purshii* a priori group were assigned to other species: 3 specimens to S. terrae-novae with 68% probability (Torrey s.n. NY from New York; the elongate inflorescence has long ascending lower branches), 66% probability (Semple & Keir 4897 WAT from New Brunswick; shoot on left side of sheet), and 66% probability (Rouleau 7022 MT from northcentral Newfoundland; a 74 cm tall shoot with a large inflorescence with ascending branches); and 2 specimens to S. uliginosa with 66% probability (Semple & B. Semple 8714 WAT from near the Ontario-Manitoba border; a robust shoot with elongated inflorescence with ascending branches) and 47% probability (Semple & Keir 4711 WAT from New Brunswick; 102 cm tall diploid shoot with an elongated inflorescence with short ascending lower branches). Seven of 10 specimens of the S. terrae-novae a priori group (70%) plus 1 specimen only included a posteriori were assigned a posteriori into the S. terrae-novae group; 3 specimens with 90-96% probability, 1 specimen with 81% probability, 1 specimen with 79% probability, 1 specimen with 68% probability, and 2 specimens with 57% probability (Rouleau 5302 MT from SW Newfoundland; small shoots with broad compact inflorescences) and 51% probability (Rouleau 7382 MT from SW Newfoundland; robust shoot with broad corymboid secund conical inflorescence). Five specimens of the S. terrae-novae a priori group were assigned to other species: 2 specimens to *S. purshii* with 73% probability (*Rouleau 5165* MT from SE Newfoundland, second sheet of this collection) and 72% probability (*Rouleau 5307* MT from SW Newfoundland; small and robust shoots with small corymboid inflorescences or a larger broad inflorescence with branches with small corymbiform arrangements of heads); and 1 specimen to *S. uliginosa* with 71% probability (*Rouleau 5165* MT from SE Newfoundland, Fig. 4).

Group	austrina	purshii	terrae-	uliginosa	% correct
			novae		
austrina	36	0	1	2	92
purshii	0	18	3	2	78
terrae-novae	0	2	7	2	70
uliginosa	2	1	1	26	87
Totals	38	21	12	31	85
Jackknifed classi	fication matrix	x			
Group	austrina	purshii	terrae-	uliginosa	% correct
			novae		
austrina	34	0	1	4	87
purshii	0	18	3	2	78
terrae-novae	0	3	6	1	60
uliginosa	2	1	1	26	87
Totals	34	21	11	33	82

Table 18. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four species level a priori groups; a posteriori placements to groups in rows.

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 104 specimens of 4 species groups are presented in Fig. 19: groups (*S. austrina*, *S. purshii*, *S. terrae-novae*, and *S. uliginosa* including *S. simulans*). Eigenvalues on the first three axes were 4.084, 0.415, and 0.180.

Analysis 10: Analysis of S. terrae-novae and S. uliginosa (including S. purshii)

In the STEPWISE discriminant analysis of 47 specimens of two species level a priori groups (*S. terrae-novae* and *S. uliginosa* including *S. purshii*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (35.24), number of ray florets (14.28), and ray floret pappus length (7.93). 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 = 0.0000 that the null hypothesis was true. *Solidago terrae-novae* and *S. uliginosa* had an F-to separate value of 18.363 (Wilks' lambda = 0.4384 df = 3 1 45; Approx. F= 18.3633 df = 3 43 prob = 0.0000).

In the Classificatory Discriminant Analysis of 47 specimens of the two species level a priori groups (S. *terrae-novae* and S. *uliginosa* including S. *purshii*) plus 1 specimen each of of S. *terrae-novae* and S. *uliginosa* only included a posteriori, percents of correct a posterori assignment to the same a priori group were 100% and 92%. The Classification matrix and Jackknife classification matrix are presented in Table 19. Ten of the 10 specimens of the S. *terrae-novae* a priori group (100%) plus 1 additional specimen only included a posteriori were assigned to the S. *terrae-novae* group: 8 with 92-100% probability, 2 with 89% and 85% probabilities, and 1 with 63% probability (*Rouleau 5165* MT from SE Newfoundland, second sheet of this collection). Thirty-three of the 36 specimens of the S. *uliginosa* a priori group (92%) plus 1 specimen only included a posteriori were



Figure 19. Plot of canonical scores (CAN1 vs. CAN2) for 104 specimens of *S. austrina* (red dots), *S. uliginosa*: var. *peracuta* (yellow triangles), var. *terrae-novae* (light blue triangles), and var. *uliginosa* including *S. simulans* (orange triangles).

into the *S. uliginosa* group; 27 specimens with 93-100% probability, 4 specimens with 86-88% probability, 1 specimen with 62% probability, and 2 specimens with 58% probability (*Gagnon 74499* MT from near James Bay in Québec; Fig. 4) and 52% probability (*Semple & Suripto 9576* WAT a tetraploid from Massachusetts; short divergent lower inflorescence branches). Three specimens of the *S. uliginosa* a priori group were assigned to *S. terrae-novae* with 94% (*Semple & Keir 4897* WAT from New Brunswick; the inflorescence has long ascending diverging branches), 54% probability (*Semple & Suripto 9590* WAT from York Co., Maine; a robust shoot with a large inflorescence with long ascending spreading branches), and 52% probability (*Semple 9072* WAT from Wisconsin; a robust diploid plant with an elongated inflorescence with short spreading arching branches).

Histograms of canonical scores (CAN1) for 49 individuals of *S. terrae-novae* and *S. uliginosa* (including *S. purshii*) are shown in Fig. 20. The eigenvalue on the first axis was 1.281.

Table 19. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Group	terrae-	uliginosa	% correct
	novae		
terrae-novae	11	0	100
uliginosa	3	34	92
Totals	14	34	96
ckknifed classif	ication matrix	x	
ackknifed classif	ication matriz terrae-	x uliginosa	% correct
ackknifed classifi Group	ication matriz terrae- novae	x uliginosa	% correct
ackknifed classifi Group terrae-novae	ication matrix <i>terrae-</i> <i>novae</i> 11	x uliginosa 0	% correct
ackknifed classifi Group terrae-novae uliginosa	ication matrix terrae- novae 11 4	uliginosa 0 33	% correct 100 89



Figure 20. Histograms of canonical scores (CAN1) for *S. terrae-novae* (left) and *S. uliginosa* (including *S. purshii*; right)

Analysis 11: Analysis of S. purshii and S. terrae-novae

In the STEPWISE discriminant analysis of 32 specimens of two species/varietal level a priori groups (*S. purshii* and *S. terrae-novae*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (33.98), mid series phyllary width (15.29), and number of ray florets (10.66). Lower inflorescence branch length was not selected as strongly discriminating (0.03). 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 = 0.0000 that the null hypothesis was true. *Solidago purshii* and *S. terrae-novae* had an F-to separate value of 22.924 (Wilks' lambda = 0.2893 df = 3 1 30; Approx. F= 22.9243 df = 3 28 prob = 0.0000).

In the Classificatory Discriminant Analysis of 32 specimens of the two species/variety level a priori groups (*S. purshii* and *S. terrae-novae*) plus 1 specimen of *S. terrae-novae* only included a posteriori percents of correct a posterori assignment to the same a priori group were 95% and 90%. The Classification matrix and Jackknife classification matrix are presented in Table 20. Twenty-one of the 22 specimens of the *S. purshii* a priori group (95%) were assigned a posteriori into the *S. purshii* group; 19 specimens with 97-100% probability, 1 specimen with 77% probability, and 1 specimen with 56% probability (2). One specimen of the *S. purshii* a priori group was assigned to *S. terrae-novae* with 91% (*Dutilly 11417* MT from the Mistassini Lake region of Québec; a 39 cm tall shoot with long strictly ascending lower inflorescence branches). Nine of the 10 specimens of the *S. terrae-novae* a priori group (95%) plus 1 specimen of *S. terrae-novae* only included a posteriori were assigned a posteriori into the *S. terrae-novae* group; 9 specimens with 92-100% probability and 1 specimen with 72% probability. One specimen of the *S. terrae-novae* a priori group (95%) plus 1 specimen of *S. terrae-novae* a priori group was assigned to *S. terrae-novae* a priori into the *S. terrae-novae* group; 9 specimens with 92-100% probability and 1 specimen with 72% probability. One specimen of the *S. terrae-novae* a priori group was assigned to *S. terrae-novae* a priori group was assigned

Group	purshii	terrae-	% correct
		novae	
purshii	21	1	95
terrae-novae	1	9	90
Totals	22	10	94
Group	purshii	terrae-	% correct
		novae	
purshii	21	1	95
terrae-novae	1	9	90
Totals	22	10	94

Table 20. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two species level a priori groups; a posteriori placements to groups in rows.

Histograms of canonical scores (CAN1) for 33 individuals of *S. purshii* and *S. terrae-novae* are shown in Fig. 21. The eigenvalue on the first axis was 2.456.

DISCUSSION

The results from the discriminant analyses support the recognition the following taxa in the *Solidago uliginosa* complex: *Solidago simulans, S. uliginosa* var. *peracuta, S. uliginosa* var. *terraenovae*, and *S. uliginosa* var. *uliginosa*. A key to all taxa in *Solidago* subsect. *Maritimae* is presented at the end of the discussion. Comments on each taxon accepted are present below.



Figure 21. Histograms of canonical scores (CAN1) for for S. purshii (left) and S. terrae-novae (right).

Excluding Analysis 1, in the five analyses that included *Solidago austrina* and *S. simulans* as separate taxa, the mean percent of correct a posteriori placement for both species was 87.6% with ranges of 85-92% for the former and 81-94% for the latter. *Solidago austrina* had means of 24.3 leaves on the upper 25% of the stem below the inflorescence, 3.2 rays, and 10.4 disc florets. *Solidago simulans* had means of 13.5 leaves on the upper 25% of the stem below the inflorescence, 3.2 rays, and 7.4 disc florets. *Solidago uliginosa* s.1. had means of 8.3 leaves on the upper 25% of the stem below the inflorescence, 5 rays, and 6.2 disc florets. The greater density of leaves (internode length versus leaf length) on stems of *S. austrina* and its allopatric distribution separate the species from members of the *S. uliginosa* complex. *Solidago austrina* was treated as a member of the *S. stricta/S.virgata* complex by Semple et al. (2016b).

Results of the Analyses 3 and 4 indicate that Solidago simulans and S. uliginosa both sensu stricto and sensu lato can be distinguished with high probability by sometimes subtle technical differences. The length of mid series phyllaries, number of ray florets, and the length of the lower longer inflorescence branches were selected in both analyses as most important in separating the two taxa, but the latter trait was more important in Analysis 4 including just var. *uliginosa* individuals; number of disc florets was the fourth trait selected. In Analysis 3, S. uliginosa included individuals of var. peracuta (S. purshii), var. terrae-novae, and var. uliginosa with the result that the number of nodes in the upper 25% of the stem was selected as the third most significant trait and inflorescence branch length was fourth in separating S. simulans and S. uliginosa s.l. Differences in numbers of upper stem leaves is a reflection of the fact that individuals of S. uliginosa tend to be shorter in northern portions of the range and thus have fewer nodes per stem overall than individuals from more southern populations. This is also true if S. austrina is added to the comparison because it is both taller and more southern in distribution than S. simulans and S. uliginosa. In Analysis 2, number of nodes in the upper 25% of the stem was selected as the third most significant trait in separating S. austrina, S. simulans and S. uliginosa s.l., but S. austrina has more congested leaves over the whole stem than the other two species. The number of nodes on the upper 25% of the stem below the inflorescence was the same for both S. simulans and S. uliginosa var. uliginosa: on average 13 nodes (leaves) for both taxa were present on the upper 25% of the stem. The mean length of mid stem phyllaries was 3.4 mm for samples of S. simulans and 2.8 mm for S. uliginosa var. uliginosa, but total involucre length at flowering was essentially the same, 5.06 mm and 4.93 mm, respectively. The difference in numbers of florets was also critical but small: averaging 3.2 rays and 7.5 disc florets for samples of S. simulans and 4.5 rays and 5.8 disc florets for samples of S. uliginosa var. uliginosa. On average, S. simulans has fewer rays and more discs than S. uliginosa var. uliginosa. Solidago simulans also had slightly longer, wider and more serrate basal leaves and less hairy but longer ray and disc floret ovaries at flowering than S. uliginosa var. uliginosa on average, but the traits were not selected as significant in discriminating the two taxa. Such differences do indicate that the two taxa differ on average in multiple traits even if the ranges of variation overlap considerably. Overall, we conclude that it is useful to recognize *S. simulans* as a distinct southern species in the *S. uliginosa* complex.

Included in the *Solidago simulans* a priori group was a problematic specimen, *Chapman s.n.* NY from middle Florida. It was provisionally assigned to S. simulans for the analyses; it was not assigned to species on the original collection label or the FNA label; Max Medley annotated it as Solidago cf. uliginosa in 1992; JCS annotated the species to genus only in 2012. Middle Florida is way outside the range of S. uliginosa and outside the range of S. simulans, but not far outside the range of S. austrina (Fig. 10). Two shoots are present on the herbarium sheet. The lower leaves have petiole bases that are slightly expanded and are obviously serrate. The inflorescences are short and the lower branches are not elongated; one is somewhat secund. The specimen was assigned a posteriori into S. uliginosa in Analysis 1 (92%; 6% to S. simulans, and 1% to S. austrina), Analysis 2 (80%), Analysis 3 (52%), Analysis 4 (53%), and Analysis 7 (73%) and to S. terrae-novae in Analysis 6 (62%). If the specimen is correctly identified as S. uliginosa, then the question is how did that species get to central Florida in the mid 1800s. It makes more sense that it is an outlier in S. austrina disjunct from the Tallahassee area of the Florida Panhandle; superficially it might fit into that species morphologically, but the results of the analyses indicated otherwise. Alternatively, the collection was labeled in New York with the wrong label and is in fact from much further north. *Chapman s.n.* (NY) from middle Florida remains problematic. DNA analysis might clarify the identification.

Two collections observed online from the same area in southwestern Virginia indicate the problem with easily separating Solidago simulans and S. uliginosa. Bentley 337 (VPI) from Big Spring Bog, 2615 ft. (797 m), Grayson Co., Virginia has a small inflorescence with short ascending lower branches. Ogle s.n. (VPI) from The Glades, Grayson Co., Virginia has a large inflorescence with ascending-diverging lower branches. Both collections were identified as S. uliginosa and posted on line under that name on SERNEC. Krouse s.n. (NCU) from a bog near the top of Bluff Mt. (ca. 1550 m), Ashe Co., North Carolina has an inflorescence similar to Ogle s.n., but with more mature heads on the lower branches; it was placed a posteriori in Analysis 3 of this study into S. simulans with 62% probability. Thus, it is likely that the two southwest Virginia collections are also S. simulans, although Bentley 337 has an inflorescence more typical of S. uliginosa var. peracuta, which does not occur in Virginia. The next geographically nearest collection observed from Virginia was Bills s.n. (VPI) from Allegheny Mt., Highland Co., Virginia; this has an inflorescence similar to that of Downs 6769 (NCU) from Grant Co., West Virginia which was placed a posteriori in Analysis 3 into S. uliginosa with 89% probability. There is a gap of multiple counties separating the southern most collections of S. uliginosa var. uliginosa in the Appalachian Mts. of Virginia and West Virginia from the northern most collections of S. simulans in the Appalachian Mts. of northern North Carolina and adjacent southwestern Virginia. Both species extend eastward at lower elevations onto the Piedmont and all of these lower elevation collections are treated here as S. uliginosa in Virginia and as S. simulans in North Carolina.

The results of Analyses 5-11 support recognition of three varieties within *Solidago uliginosa*, although an argument could be made for separating the generally more southern tetraploid var. *uliginosa* as a separate species from a more northern mostly diploid *S. purshii* including var. *peracuta* and var. *terrae-novae*. We choose not to do so because many of the differences are the result of ploidy level gigas effect and the shorter growing season for more northernly distributed plants resulting in shorter stems with generally shorter inflorescences. Ploidy level differences alone are not considered to be a basis for separating species in *Solidago* because it is likely that in most cases polyploids evolved as autopolyploids within single taxa, and potentially more than once, e.g. tetraploids in *S. nemoralis* Ait. ssp. *nemoralis* (Brammall and Semple 1990). If ploidy differences are

the base for separating diploids from tetraploids and from hexaploids into separate species, then in many cases only traits known to be influenced by ploidy level (e.g., involucre height, disc corolla length, ovary/cypsela body and pappus length) would have to be used to separate many two ploidy level and three ploidy level taxa into two or three unreliably distinguishable species: e.g., *S. altissima* L. var. *gilvocanescences* (Rydb.) Semple into three species, *S. altissima* L. var. *pluricephala* M.C. Johnston into two species, *S. gigantea* Ait. into three species, *S. missouriensis* Nutt. into two or more species, *S. velutina* DC. into three species, and *S. virgata* into three species, to name just a few examples of many in *Solidago* (Semple 2016).

The three varieties of Solidago uliginosa (var. peracuta, var. terrae-novae, and var. uliginosa) are best separated on inflorescence branching pattern traits. In all three varieties, taller stems tend to have the largest inflorescences. The typical race var. *uliginosa* usually has longer diverging inflorescence branches, although small inflorescences often have lower branches too short to show much divergence away from the main axis with stems short to very tall (52-136 cm tall). The var. *uliginosa* is allopatric in the southern part of its range but is sympatric in the parts of its range that extends north along the Maine coast in the east and in the Great Lakes area near the shores of Lake Huron and Lake Michigan near populations of var. peracuta in the western portion of the range. Only tetraploids are known in var. *uliginosa*, which means involucres and cypselae will be somewhat larger than found in the other two varieties. Field and garden grown vouchers for the tetraploids reported from Oka, Québec (Beaudry and Chabot 1959), have inflorescences typical for var. uliginosa, even though this location is well within the range of var. peracuta. Several dozen diploid counts for var. *peracuta* have been made in eastern Ontario, southern Quebec and adjacent New York and Vermont. Perhaps the Oka area tetraploids were introduced from the Great Lakes area. Diploids occur throughout the range of var. peracuta (Fig. 10), which includes very short to very tall stems (9-102 cm tall) with small to larger inflorescences with lower branches strongly ascending and diverging only slightly from the main axis; a few tetraploids have been reported from near James Bay in Ouébec (Beaudry and Chabot 1959; Beaudry 1969) and the field and garden grown vouchers have either typical inflorescences for var. peracuta or ones with rather long ascending lower branches. The inflorescences of individuals of var. terrae-novae (ploidy level unknown) have long lower branches that ascend and are somewhat divergent making the inflorescence often nearly as wide as tall and somewhat corymbiform in overall shape with stems generally very short to short (8-43 cm tall). This can be obvious even in small shoots with small inflorescences (Fig. 6). Intermediates with var. peracuta occur and inflorescence branching pattern can grade from one form to the other. The var. terrae-novae is aptly named as it is known only from Newfoundland and mostly from the southern portion of the province. Cronquist (1968) noted that plants of var. *peracuta* had "leaves seldom much toothed", but numbers of serrations of middle and upper leaves were not selected as significant traits in separating the varieties in our Analysis 8. In fact, for mid stem leaves of var. peracuta the mean number of margin serrations on one side of the leaf was higher (8.74) than for var. *uliginosa* (4.77), but slightly lower than for var. terrae-novae (9.73).

Key to taxa in Solidago subsect. Maritimae

[Short plants with short inflorescences can be a problem to identify when traits or large inflorescences are critical in separating similar species.]

- 1. Disc florets 3-12; Gulf coastal and southern Mexico, eastern Canada and USA.
 - 2. Upper leaves somewhat reduced from mid and lower leaves.
 - 3. Middle stem leaves broadly lanceolate to ovate; Azores, Bermuda Solidago azorica
 - 3. Middle stem leaves narrowly lanceolate; coastal from Newfoundland to northern North Carolina, introduced inland along heavily salted roads in the eastern USA

...... Solidago sempervirens

- 2. Upper leaves much reduced from lower leaves.
 - 4. Upper stem leaves not congested, relatively few.

 - 5. Inflorescence either elongate and narrow or lower branches variously ascending to spreading, many and grading in length into short upper branches.
 - 6. Lower and mid stem leaves entire; mountains in Chiapas, Mexico, Guatemala, Belize
 - 6. Lower and mid stem leaves serrate; eastern Canada and USA.

 - 7. Rays averaging 5, discs averaging 6; Newfoundland to northern Virginia west to Hudson's Bay and southeastern Manitoba south to central Illinois
 - Solidago uliginosa

 - 8. Inflorescence not somewhat corymbiform and usually much longer than wide.
 - 4. Upper stem leaves congested, relatively many.
 - 10. Basal and lower stem leaves serrate; inflorescence sometimes secund.
 - 10. Basal and lower leaves not serrate; inflorescence always narrow, sometimes secund.

 - 12. Inflorescence never with secund apex; outer coastal plain.
 - 13. Disc florets averaging 14 (10-21); basal and lower stem leaves averaging 31 (22-37) mm × 5.4 (3-8) mm; outer coastal plains North Carolina and adjacent South Carolina
 Solidago pulchra
 - 13. Disc florets averaging 7-8 (4-12); basal and lower leaves averaging 56-60 (17-155) mm \times 5.5-9.2 (1-27) mm.

 - 14. Basal and lower stem leaves linear; south Florida and Keys

...... Solidago chrysopsis

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