

A MULTIVARIATE MORPHOMETRIC ANALYSIS OF *SOLIDAGO* SUBSECT. *HUMILES* (ASTERACEAE: ASTEREAE)

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ABSTRACT

A multivariate morphometric study of the goldenrod group *Solidago* subsect. *Humiles* was conducted to assess the morphological differences among *Solidago arenicola*, *S. austrocaroliniana*, *S. bellidifolia*, *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii*, *S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*. Eleven analyses were performed on different combinations of a priori species groups and traits using a matrix of 170 specimens by 39 traits and provided support for recognizing 13 species. An identification key to all 13 species in *S.* subsect. *Humiles* is included.

Solidago subsect. *Humiles* (Rydb.) Semple includes 5-13 species depending upon the taxonomic treatment (Nesom 1993; Semple and Cook, 2006; Semple and Peirson 2013; Semple 2019 frequently updated): *Solidago arenicola* B.R. Keener & Kral, *S. austrocaroliniana* Semple, *S. bellidifolia* E.L. Greene, *S. chlorolepis* Fern., *S. gillmanii* (A Gray) Steele, *S. glutinosa* Nutt., *S. kralii* Semple, *S. ontarioensis* (Ringius) Semple & J. Peirson, *S. plumosa* Small, *S. racemosa* E.L. Greene, *S. randii* (Porter) Britton, *S. simplex* Kunth, and *S. spathulata* DC. All members of the subsection have some resin on the phyllaries and peduncles and sometimes over much of the plant. The resin is produced by very small stipitate glands that are usually hidden under the resin. Basal rosette and lower stem leaves are generally the largest produced by plants of *S.* subsect. *Humiles*. Early formed rosette leaves are small, spatulate, and petiolate, while later formed rosette leaves can be similar but larger or oblanceolate and tapering to a shorter winged petiolate portion. Upper stem leaves are much reduced. Inflorescences are few to many headed and range from semi-corybiform in very small plants to narrowly to broadly paniculiform in most plants.

Peirson et al. (2013) looked at cpDNA haplotype variation using spatial analysis of molecular variance in 11 taxa in *S.* subsect. *Humiles* following the nomenclature of Semple and Cook (2006) but recognized here at the species level. Samples of *S. austrocaroliniana*, *S. bellidifolia*, and *S. chlorolepis* were not included. Peirson et al. (2013) concluded that “cpDNA variation was not strongly partitioned across species boundaries, geography or ploidy levels”, that the “highest haplotype diversity was located in western North America, followed by the southeastern USA and the formerly glaciated Great Lakes region”, and “six haplotypes were shared among species in *Solidago* subsect. *Humiles*”. Of note, the *S. simplex* sample from Mexico had a unique haplotype (arbitrarily assigned no. 46) which was placed in the parsimony network in a grouping with haplotypes radiating from haplotype 21, which also occurred in samples from the central Rocky Mts., and the southeastern US and was in turn connected to haplo group 4 common in eastern North America and one sample from British Columbia in western North America (Peirson et al. 2013, their Fig. 2). Peirson et al. (2018) also concluded that their “demographic analyses placed the main population expansion in *S.*

subsect. *Humiles* between the late Pleistocene and early Pliocene (well before the Wisconsinan glacial period hypothesis of Ringius & Semple, 1987)” but “also support the evolution of polyploid taxa within a Holocene timeframe”. Semple (2016) placed *S.* subsect. *Humiles* in a close relationship with subsect. *Multiradiatae* Semple native to North America and subsect. *Solidago* native to Eurasia.

Species in *S.* subsect. *Humiles* can be morphologically similar but have some critical differences. *Solidago arenicola* has large heads in a very open inflorescence (Figs. 1 and 2); cypselae are glabrous. *Solidago austrocaroliniana* is similar to *S. arenicola* in general appearance but has smaller involucre and blooms in the late spring (see Figs. 1 and 2 in Semple and Nelson 2018); cypselae are glabrous. *Solidago bellidifolia* includes short alpine plants with obviously spatulate rosette and lower stem leaves (Fig.3); cypselae are moderately to moderately-densely strigose. *Solidago chlorolepis* includes small plants with small heads (Fig. 4); cypselae are moderately densely strigose. *Solidago gillmanii* includes mid size to large plants with large serrate, acute, lanceolate basal and lower stem leaves, stems that are glabrate to moderately short hairy and larger heads (Figs. 5 and 6); the cypselae are moderately to densely short-strigose both proximally and distally. *Solidago glutinosa* includes small to mid size plants depending upon growing conditions and elevation (Figs. 7 and 8; see also Semple et al. 2016 Fig. 3); cypselae are moderately to moderately densely strigose over entire fruit body or slightly more so distally. In the Rocky Mountains, higher elevation plants of *S. glutinosa* can be confused with plants of *S. multiradiata* Ait. that mostly have broadly lanceolate to ovate leaves with long ciliate hairs on the margins and phyllaries that are lanceolate, attenuate and often subequal. *Solidago kralii* can be robust with many shoots from a single rootstock or much less robust with a single mid size stem (Figs. 9 and 10), and peduncles have 4-5 bracts; cypselae are glabrous. *Solidago ontarioensis* includes small to mid size plants with small compact to more open inflorescences (Figs. 11 and 12); cypselae tend to be rather strigose. *Solidago plumosa* can be similar to *S. kralii*, but the shoots are often smaller (Figs. 13 and 14), the leaves are narrower, and peduncles have 4-7 bracts; cypselae are glabrous. *Solidago racemosa* varies greatly in stem height depending upon whether rootstocks are growing in small cracks in rocks or in large ones with more soil or in rocky soil; stem leaves tend to be narrowly lanceolate and sharply acute and sometimes numerous (Figs. 15 and 16); cypselae are glabrate to sparsely strigose proximally and very sparsely to moderately strigose distally. *Solidago randii* includes small to robust plants with generally broadly lanceolate, serrate lower leaves with petioles that are broadly winged distally to less so proximally (Figs. 17-19); cypselae are very sparsely proximally to sparsely so distally to sparsely proximally to moderately so distally. *Solidago simplex* are generally small to midsize plants with heads with broad phyllaries for the subsection; phyllaries (Fig. 20; see Figs. 1 and 2 in Semple, Ma and Tong 2016); cypselae are glabrous to sparsely strigose. *Solidago spathulata* includes plants with often obviously resinous stems and leaves and heads (Figs. 21 and 22); upper stem leaves are generally obviously serrate with more teeth than other species; cypselae are moderately densely strigose.

The distributions of the thirteen species are allopatric to partially sympatric with one or more other species in the subsection (Figs 23 and 24). The most widely distributed species is *S. glutinosa* occurring from Alaska to Arizona and New Mexico in the Rocky Mount Cordillera and east across Canada to Ontario and northern Michigan (Fig. 23). *Solidago simplex* occurs in the central Sierra Madre Oriental of east-central Mexico (Fig. 23). *Solidago bellidifolia* occurs at higher elevations in the northern Cascade Mountains of northern Oregon, western Washington and Vancouver Island, British Columbia (Fig. 23). All other species occur in mostly allopatric disjunction populations in eastern North America. *Solidago ontarioensis* is confined to the islands and the mainland near Lake Huron and eastern Lake Superior (Fig. 24) in rocky soils and cracks in limestone and gneiss outcrops. *Solidago gillmanii* occurs in sandy soils along the eastern and northern shores of Lake Michigan and a few locations in northern Lake Huron (Fig 24). *Solidago randii* occurs in rocky soils in upland areas



Figure 1. Robust shoot of *Solidago arenicola*, Semple & B. Semple 11196 (WAT) from Alabama.

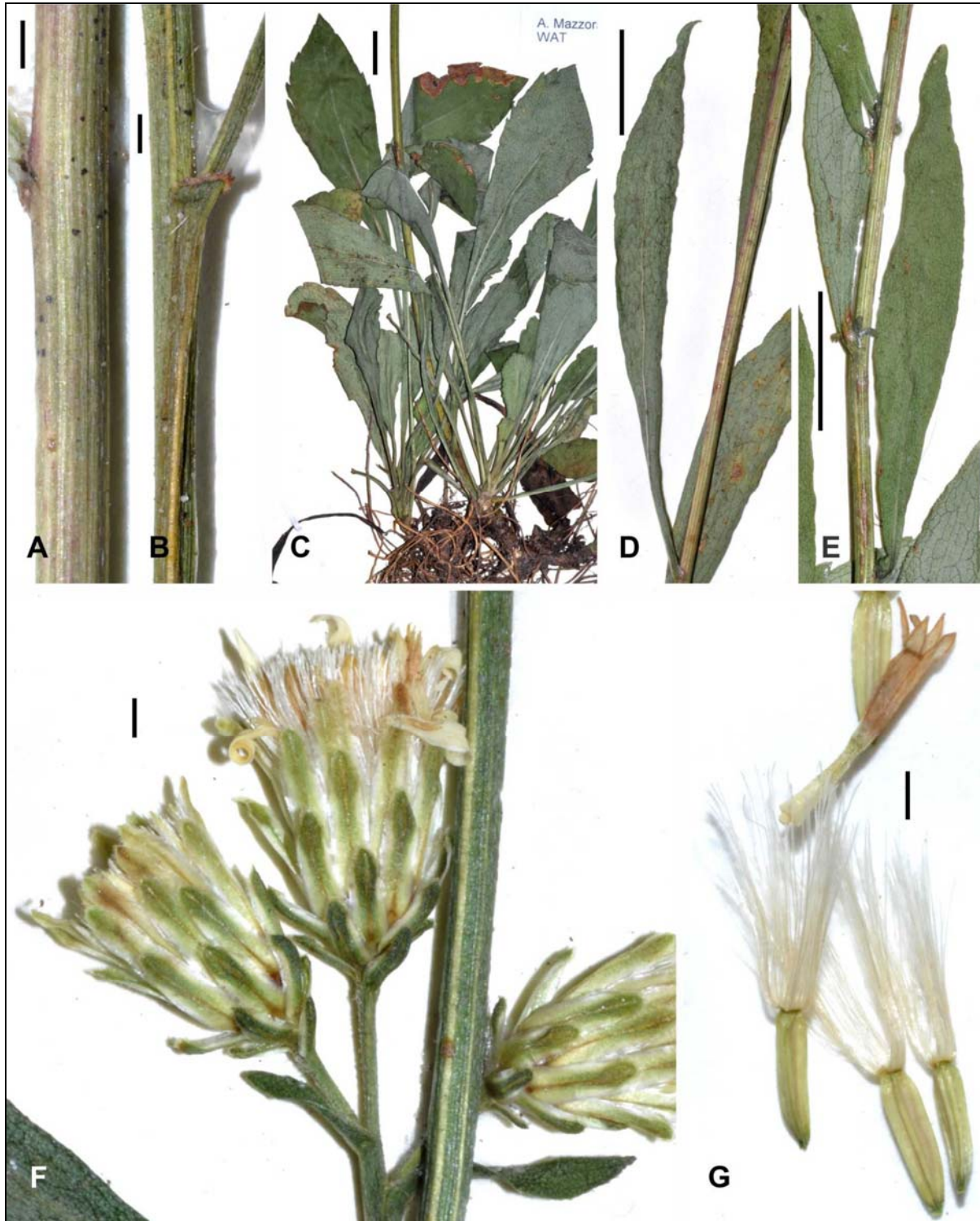


Figure 2. Details of the morphology of *Solidago arenicola*. **A.** Lower stem, *J. & B. Semple 11296* (WAT). **B.** Stem in inflorescence, *J. & B. Semple 11293* (WAT). **C.** Basal rosette and lower stem leaves, *J. & B. Semple 11291* (WAT). **D-E.** Mid and upper stem leaves, *J. & B. Semple 11296* (WAT). **F.** Heads, *J. & B. Semple 11291* (WAT). **G.** Disc floret cypselae, *J. & B. Semple 11293* (WAT). Scale bars = 1 mm in A-B, and F-G; = 1 cm in C-E.

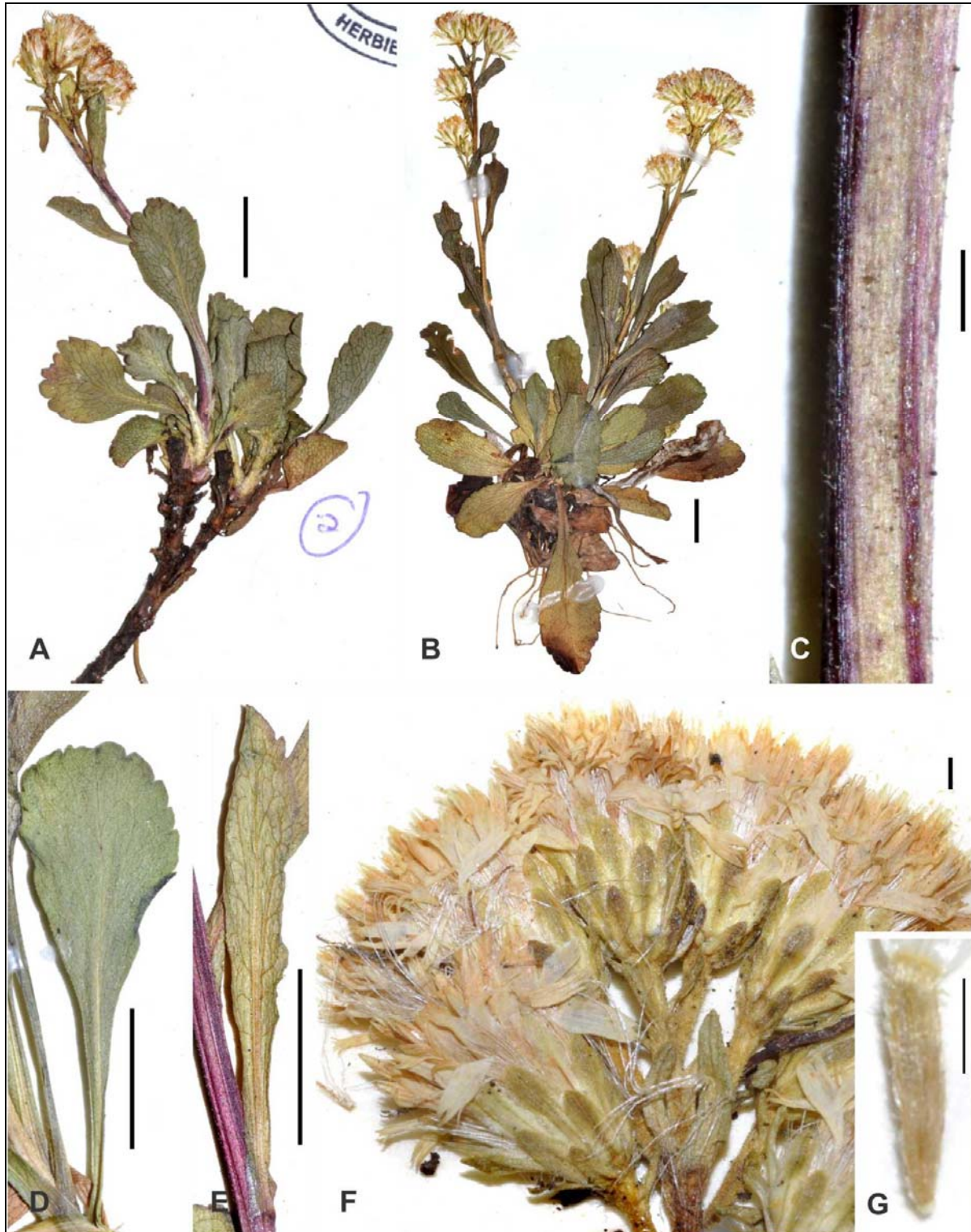


Figure 3. Morphology of *Solidago bellidifolia*. **A.** Mt. Hood, Oregon; *Semple & Xiang 10270* (WAT). **B.** Vancouver Is., British Columbia, *Ceska s.n.* (V). **C-D.** Lower stem and lower stem leaf, *Ceska s.n.* (V). **E.** Mid stem leaf, *Hardy s.n.* (V). **F.** Heads, *Ceska s.n.* (V). **G.** Cypselae body, *Semple & Xiang 10270* (WAT). Scale bars = 1 mm in C and F-G; = 1 cm in A-B, D-E.

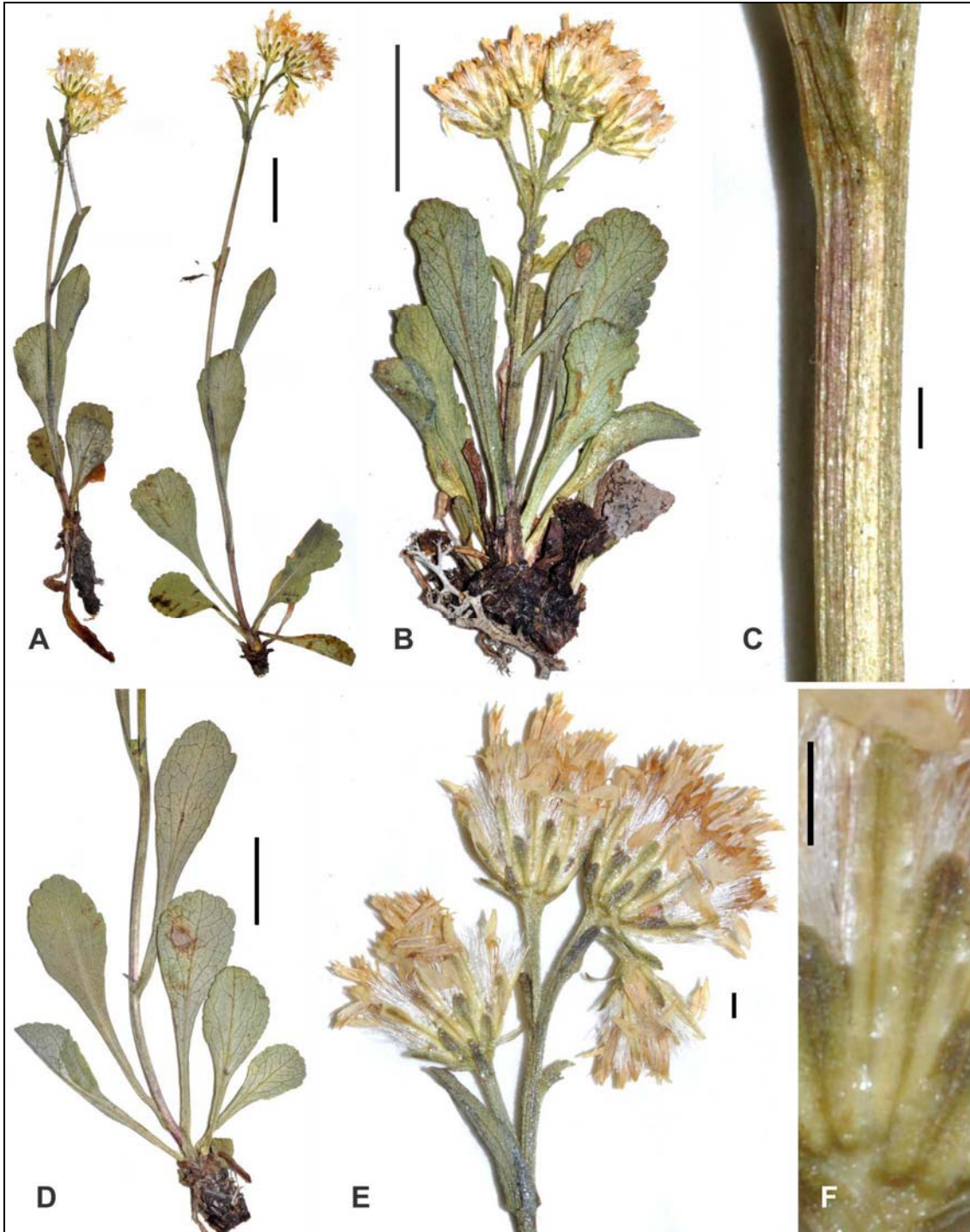


Figure 4. Morphology of *Solidago chlorolepis* from Mt. Albert, Québec. **A.** *Ringius 1694* (WAT). **B.** *Ringius 1700* (WAT). **C.** Mid stem, *Ringius 1691* (WAT). **D.** Lower stem leaves, *Ringius 1704* (WAT). **E-F.** Heads and phyllaries, *Ringius 1694* (WAT). Scale bars = 1 mm in C and E-F; = 1 cm in A-B, D.

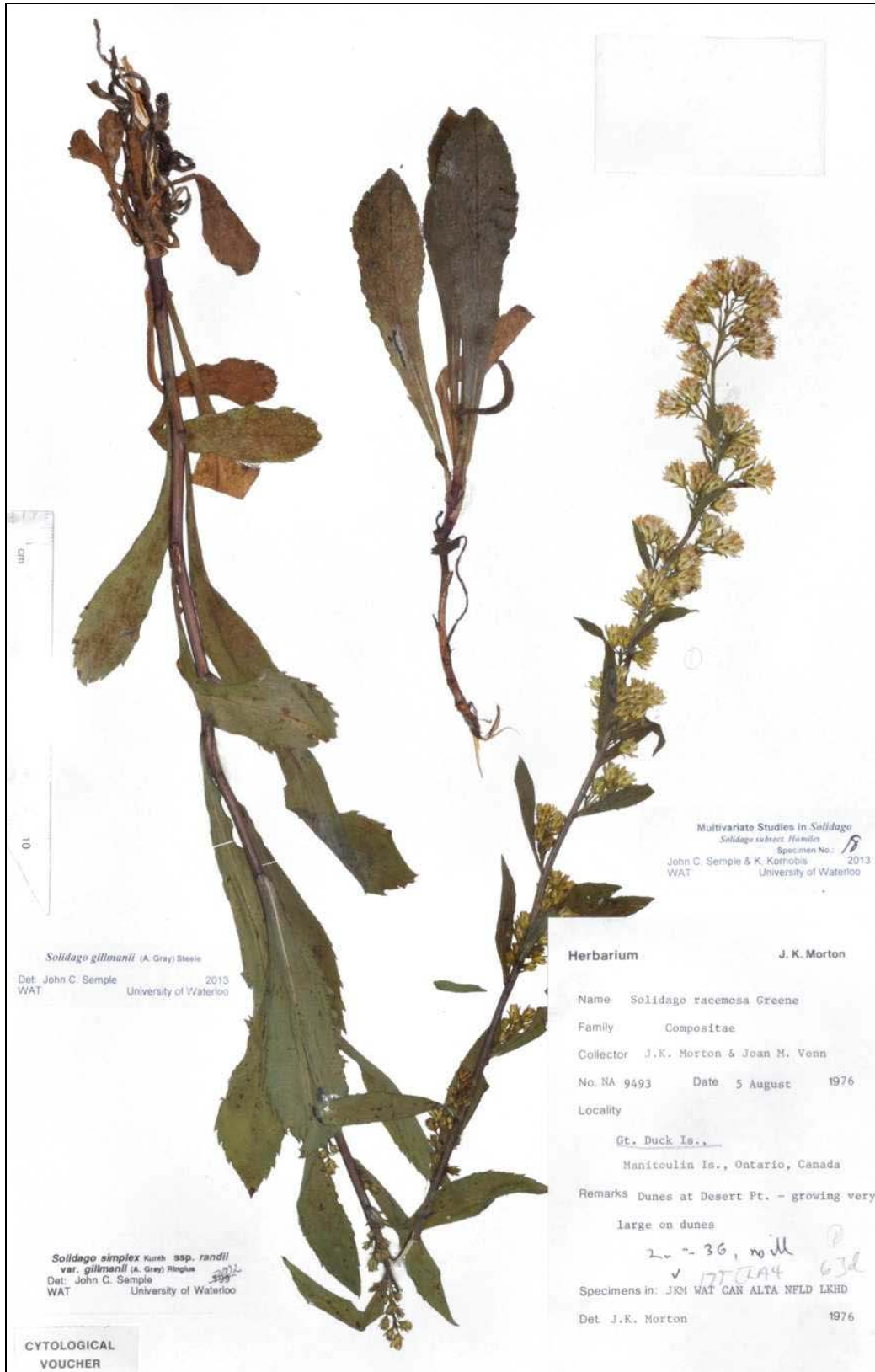


Figure 5. *Solidago gillmanii*, Morton & Venn NA9493 (TRT), Manitoulin Dist., Ontario.

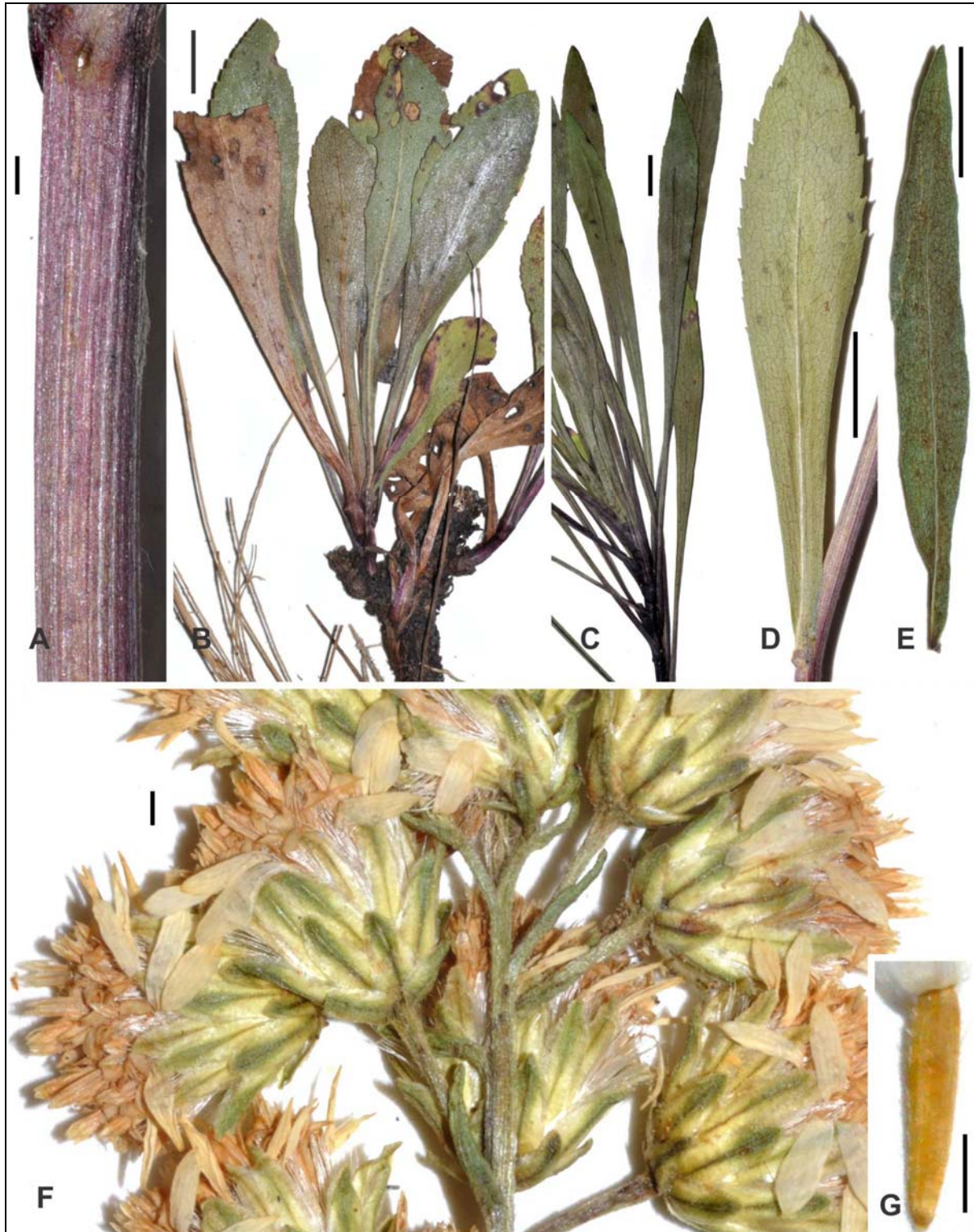


Figure 6. Details of the morphology of *Solidago gillmanii* from Michigan. **A.** Lower stem, *Ringius 1830* (WAT). **B.** Rosette leaves, *Ringius 1822* (WAT). **C.** Lower stem leaves, *Semple 11842* (WAT). **D.** Mid stem leaf, *Ringius 1830* (WAT). **E.** Upper stem leaf, *Semple 11843B* (WAT). **F.** Heads, *Ringius 1828* (WAT). **G.** Disc floret cypsela body, *Morton & Venn NA10911* (TRT). Scale bar = 1 mm in A and F-G; = 1 cm in B-E.



Figure 7. A robust individual of *Solidago glutinosa*, Pavlick 80-431 (V), British Columbia.

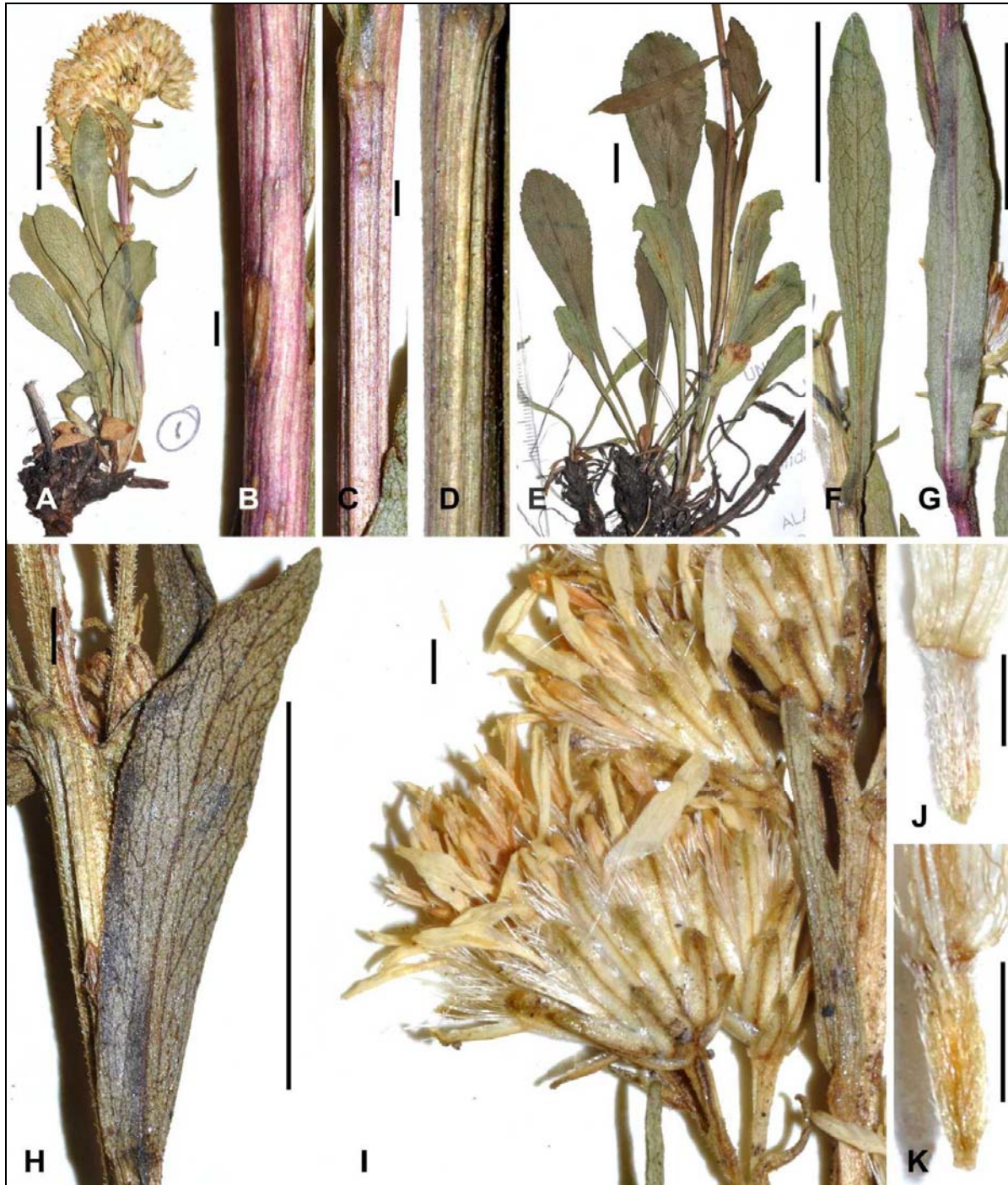


Figure 8. Details of the morphology of *Solidago glutinosa*. **A.** Alpine dwarf, Colorado, *Russell 66-129* (WAT). **B-C.** Lower and mid stem, *Semple & Brouillet 4218* (WAT). **D.** Mid stem, *Chmielewski et al. CCC4470* (WAT). **E-F.** Basal leaves and mid stem leaf, *Chmielewski et al. CCC4470* (WAT). **G.** Upper stem leaf, *Semple & Xiang 102011* (WAT). **H.** Upper stem and leaf, *J. & B. Semple 6556* (WAT). **I.** Heads, *Semple et al. 9370* (WAT). **J-K.** Densely and moderately strigose ovaries/immature cypselas bodies, *Montague & Montague 35* (WTU) and *Zika 22787* (WTU). Scale bars = 1 mm in B-D, and I-K; = 1 cm in C, A, E-H.

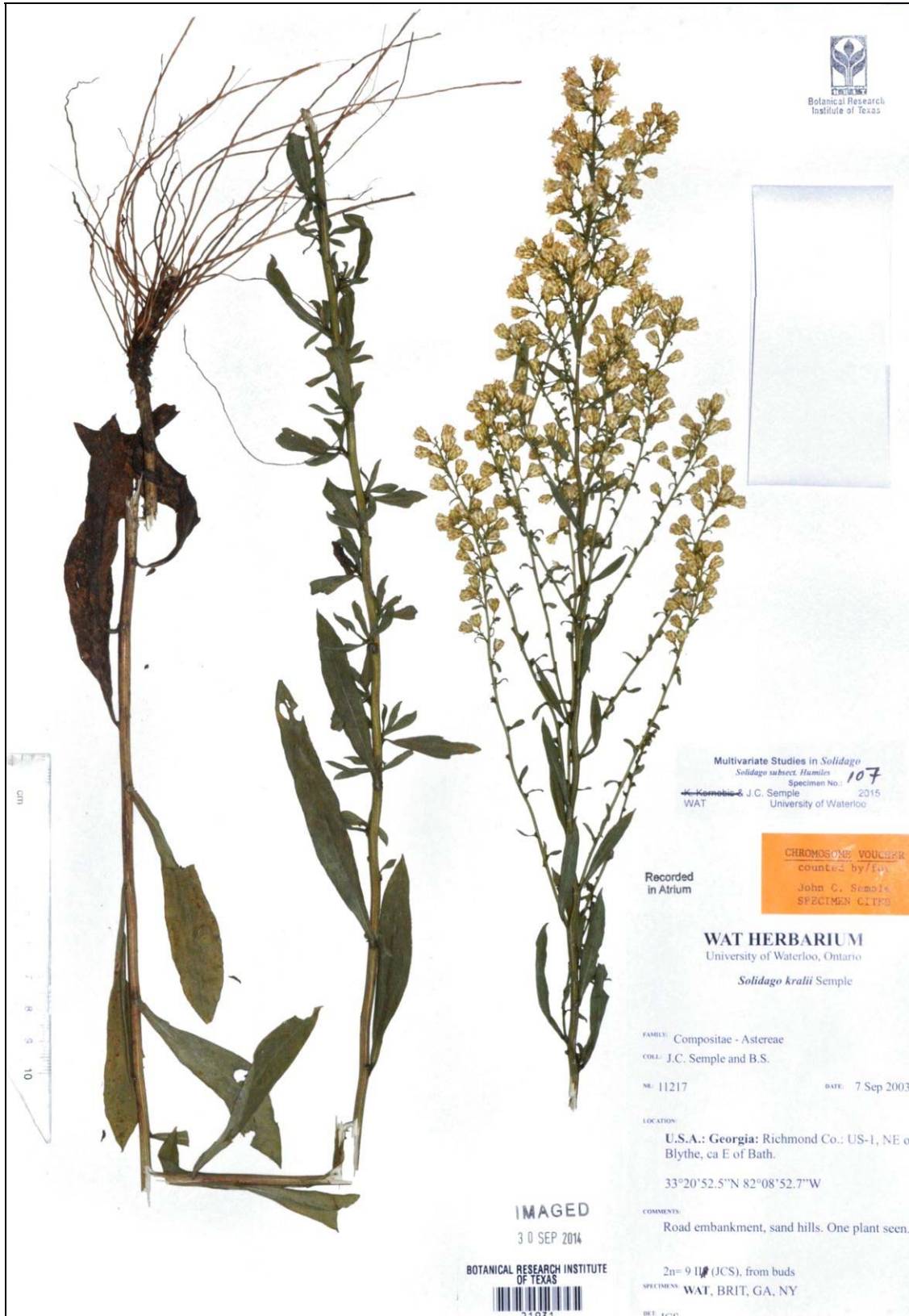


Figure 9. *Solidago kralii*. Semple & B. Semple 11217 (BRIT), Richmond Co., Georgia.

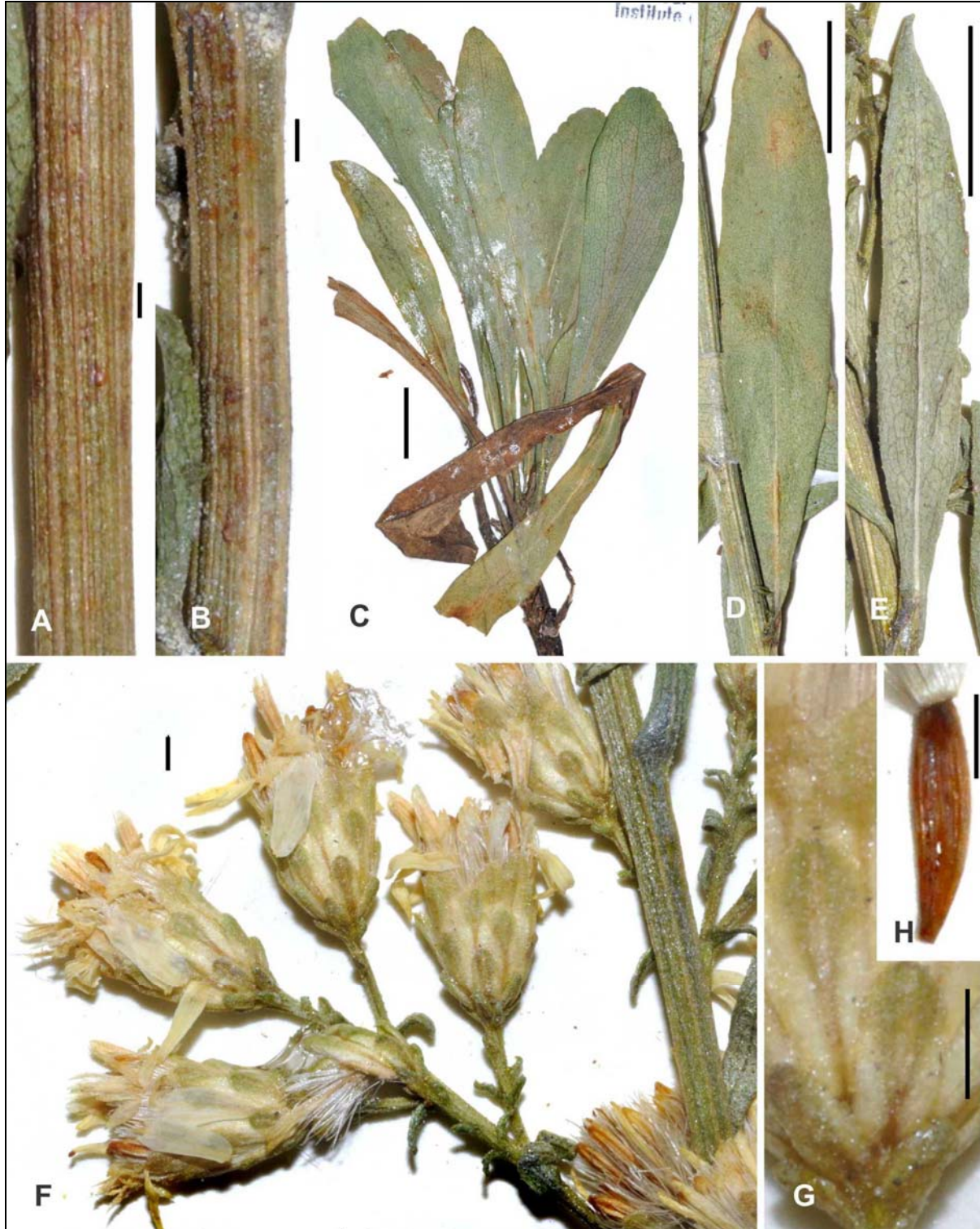


Figure 10. Details of the morphology of *Solidago kralii* from Georgia. **A.** Lower stem, *J. & B. Semple 11208* (WAT). **B.** Upper stem, *J. & B. Semple 11217* (WAT). **C-D.** Rosette leaves and mid stem leaf, *J. & B. Semple 11218* (BRIT). **E.** Upper stem leaf, *J. & B. Semple 11217* (BRIT). **F-G.** Heads and phyllaries, *J. & B. Semple 11217* (WAT and BRIT, respectively). **H.** Disc floret cypsela body, *Jones 15123* (USF). Scale bars = 1 mm in A-B and F-H; = 1 cm in C-E.

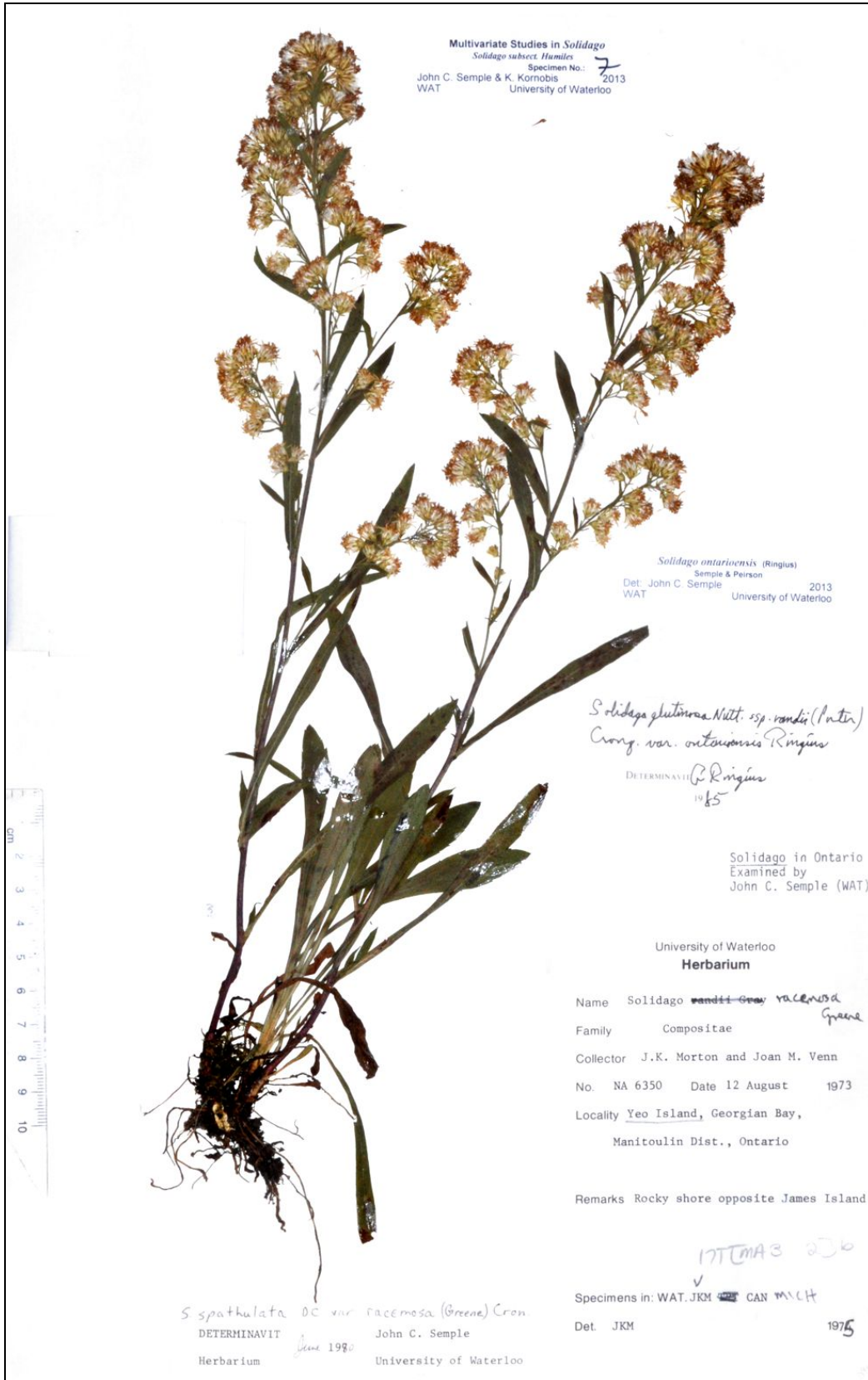


Figure 11. *Solidago ontarioensis*, Morton & Venn NA6350 (TRT), Ontario.

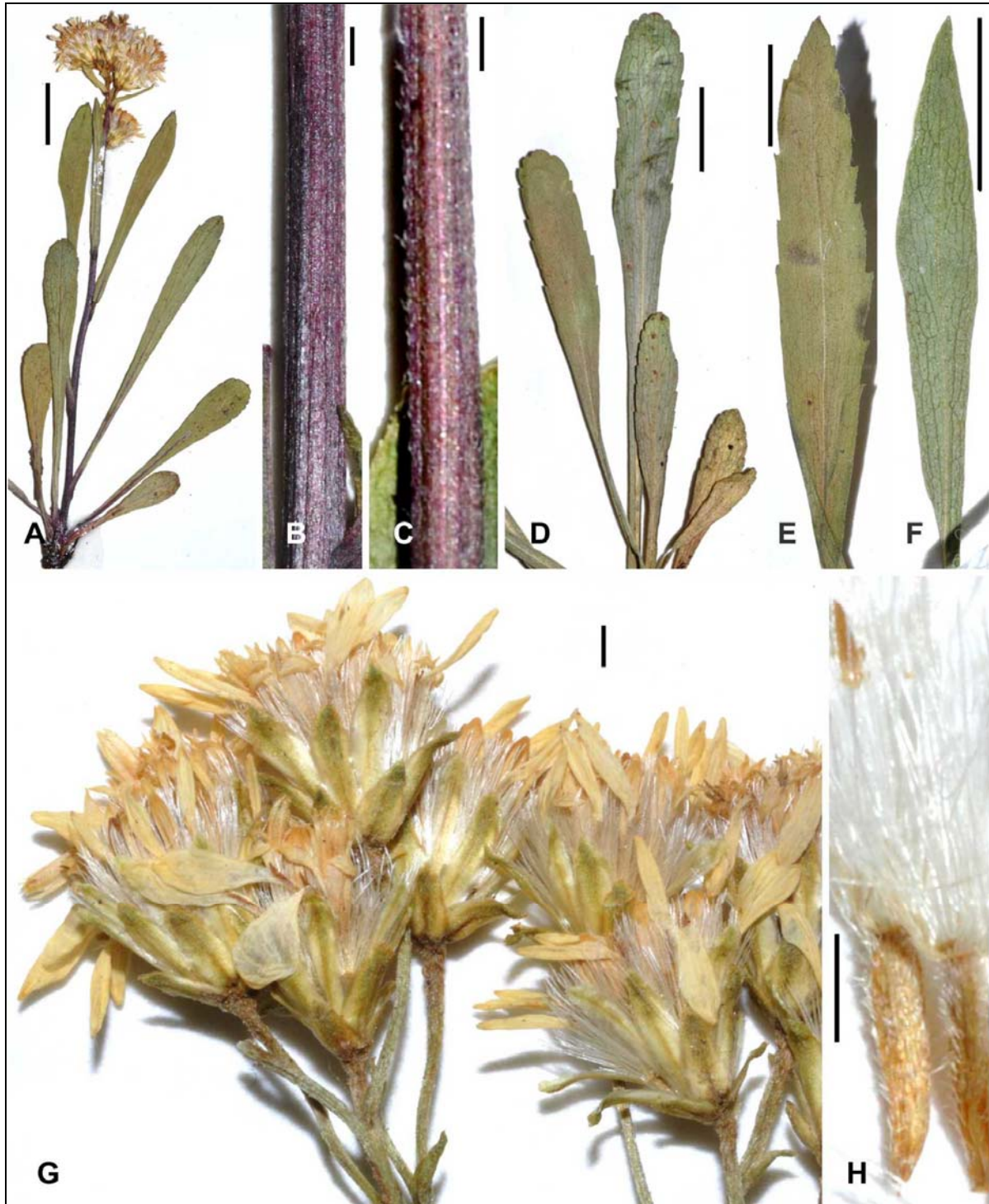


Figure 12. Details of the morphology of *Solidago ontarioensis*. **A.** Small plant, *Morton & Venn NA10586* (TRT). **B.** Lower mid stem, *Morton & Venn NA8061* (TRT). **C.** Mid stem, *Ringius 1448* (WAT). **D.** Basal rosette leaves, *Semple & Brammall 2780* (WAT). **E.** Lower stem leaf blade, *Semple & Brammall 2788* (WAT). **F.** Mid stem leaf, *Ringius 1448* (WAT). **G.** Heads, *Semple & Brammall 2780* (WAT). **H.** Disc floret cypselae, *Morton & Venn NA6350* (TRT). Scale bars = 1 mm in B-C and G-H; = 1 cm in A, and D-F.



Figure 13. *Solidago plumosa*, J.K. Small s.n. (MO), Stanley Co., North Carolina.

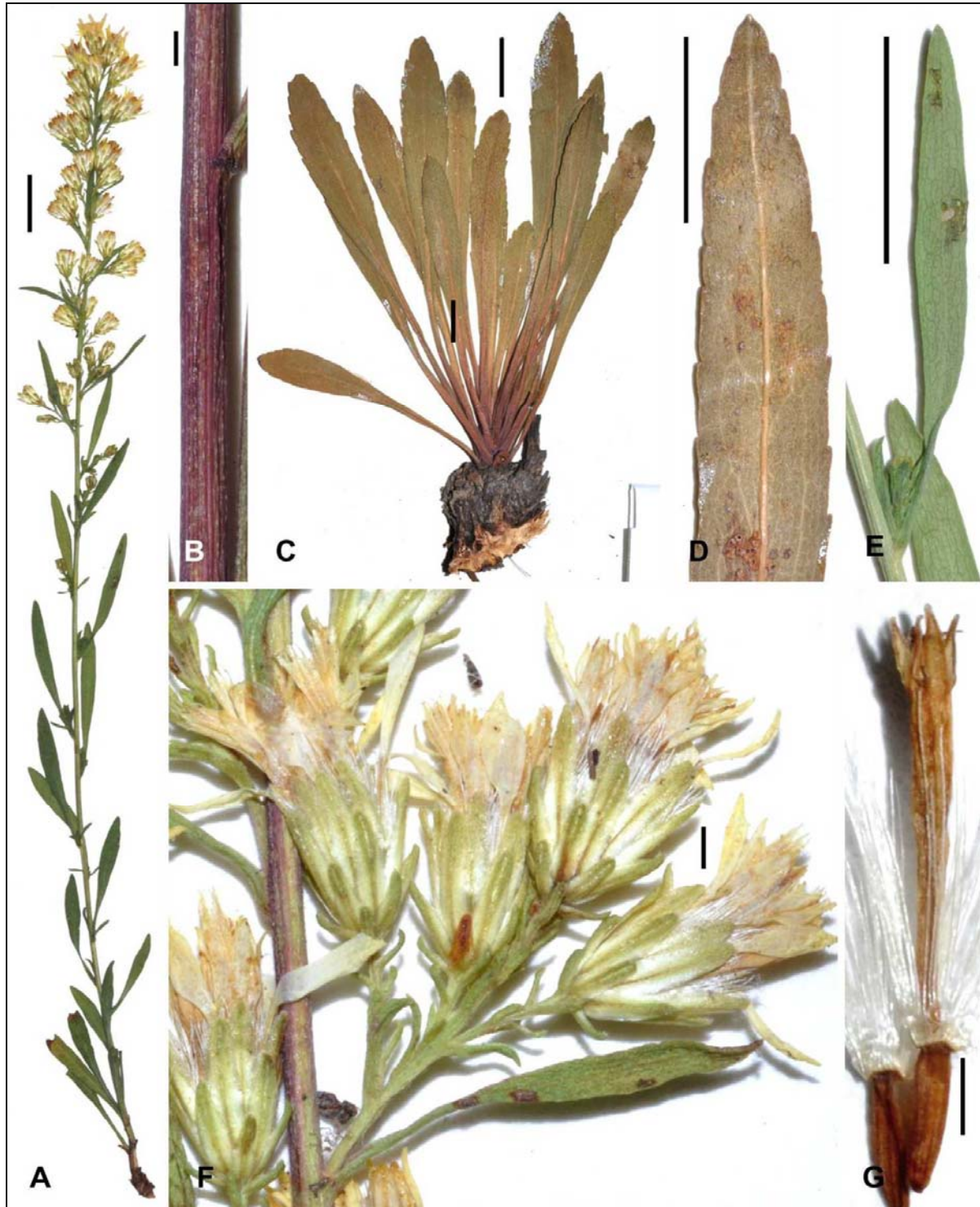


Figure 14. Details of the morphology of *Solidago plumosa*. **A.** Small shoot, *Peirson 604B* (MICH). **B.** Lower stem, *Peirson 604A* (MICH). **C-D.** Basal rosette leaves and detail of apex, *J.K. Small s.n.* (MO). **E.** Upper stem leaf, *Peirson 604B* (MICH). **F.** Heads, *Peirson 604A* (MICH). **G.** Disc floret cypselae, *J.K. Small s.n.* (MO). Scale bars = 1 mm in B and F-G; = 1 cm in A and C-E.

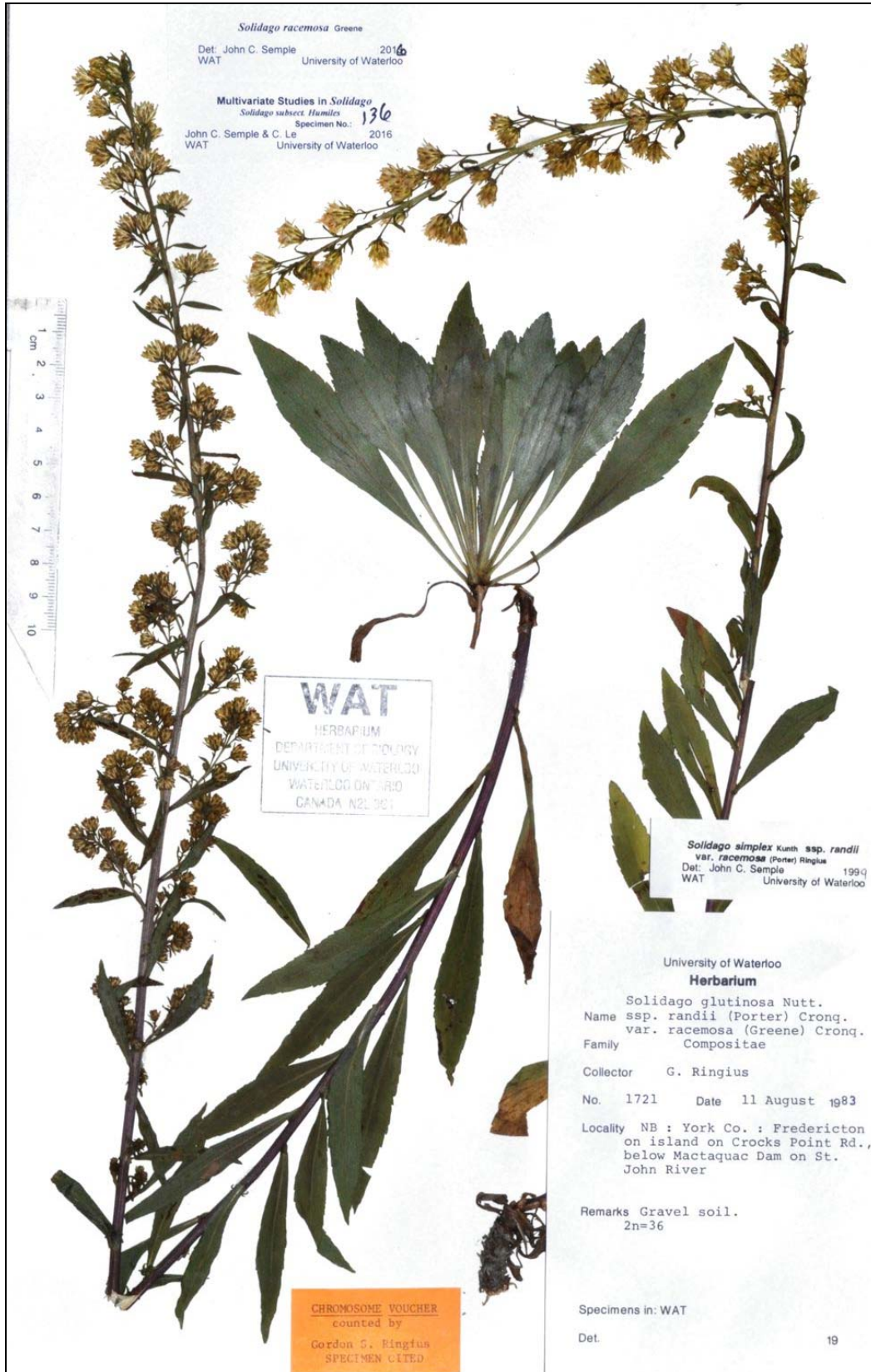


Figure 15. Robust *Solidago racemosa*, Ringius 1721 (WAT) from York Co., New Brunswick.

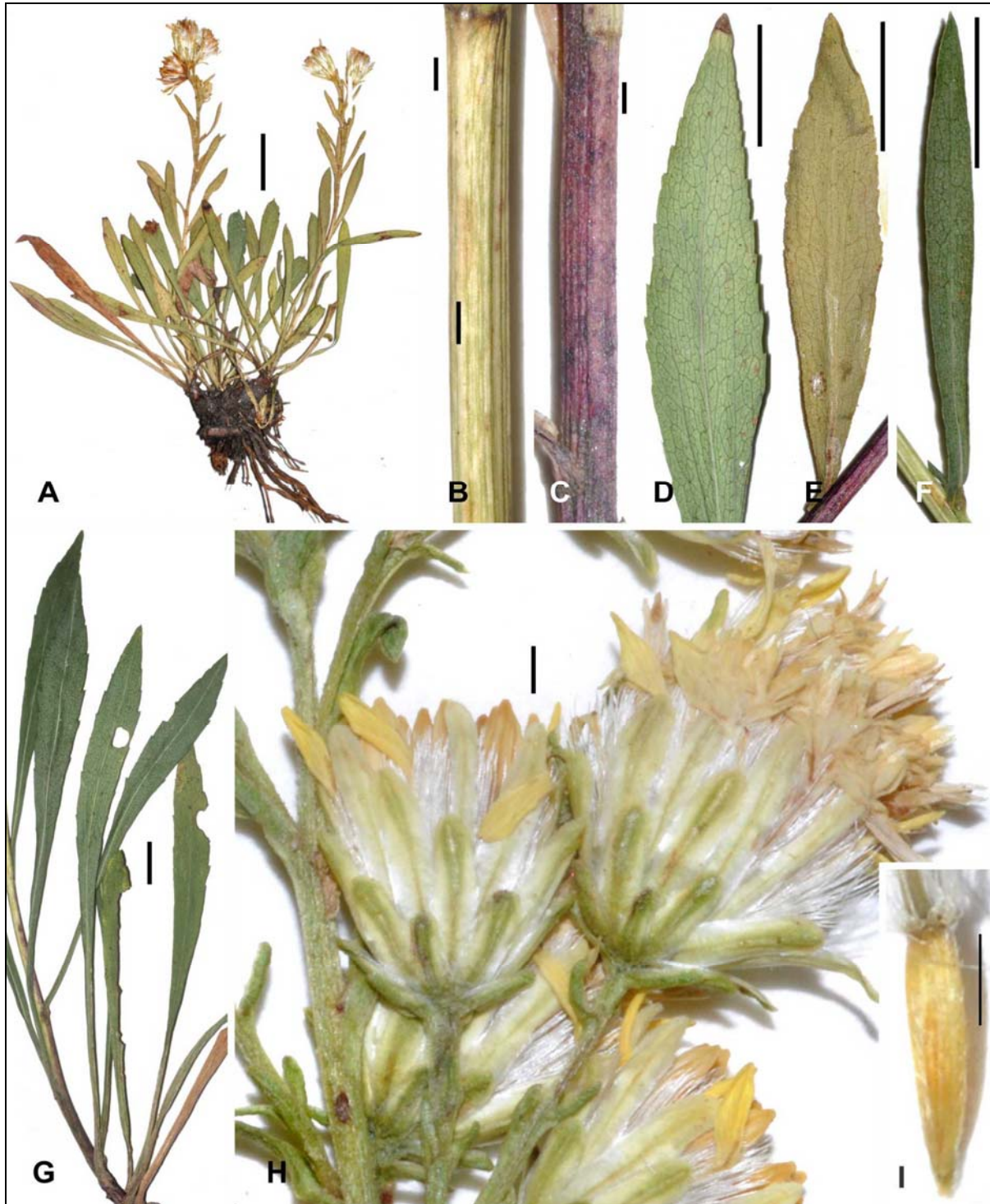


Figure 16. Details of the morphology of *Solidago racemosa*. **A.** Dwarf shoot, *Semple & Ringius 7612* (WAT). **B-C.** Lower stems, *Peirson 597* (MICH) and *Semple & Ringius 7612* (WAT). **D.** Lower stem leaf, *Semple & Ringius 7663* (WAT). **E.** Mid stem leaf, *Gagnon 5059* (QUE). **F-G.** Upper mid stem leaf and lower stem leaves, *Peirson 597* (MICH). **H.** Heads, *Peirson 601* (MICH). **I.** Disc floret cypsela body, *Semple & Ringius 7663* (WAT). Scale bars = 1 mm in B-C, and H-I; = 1 cm in A and D-G.



Figure 17. Robust *Solidago randii*. Pringle s.n. (NY), White Mountain Notch, New Hampshire.

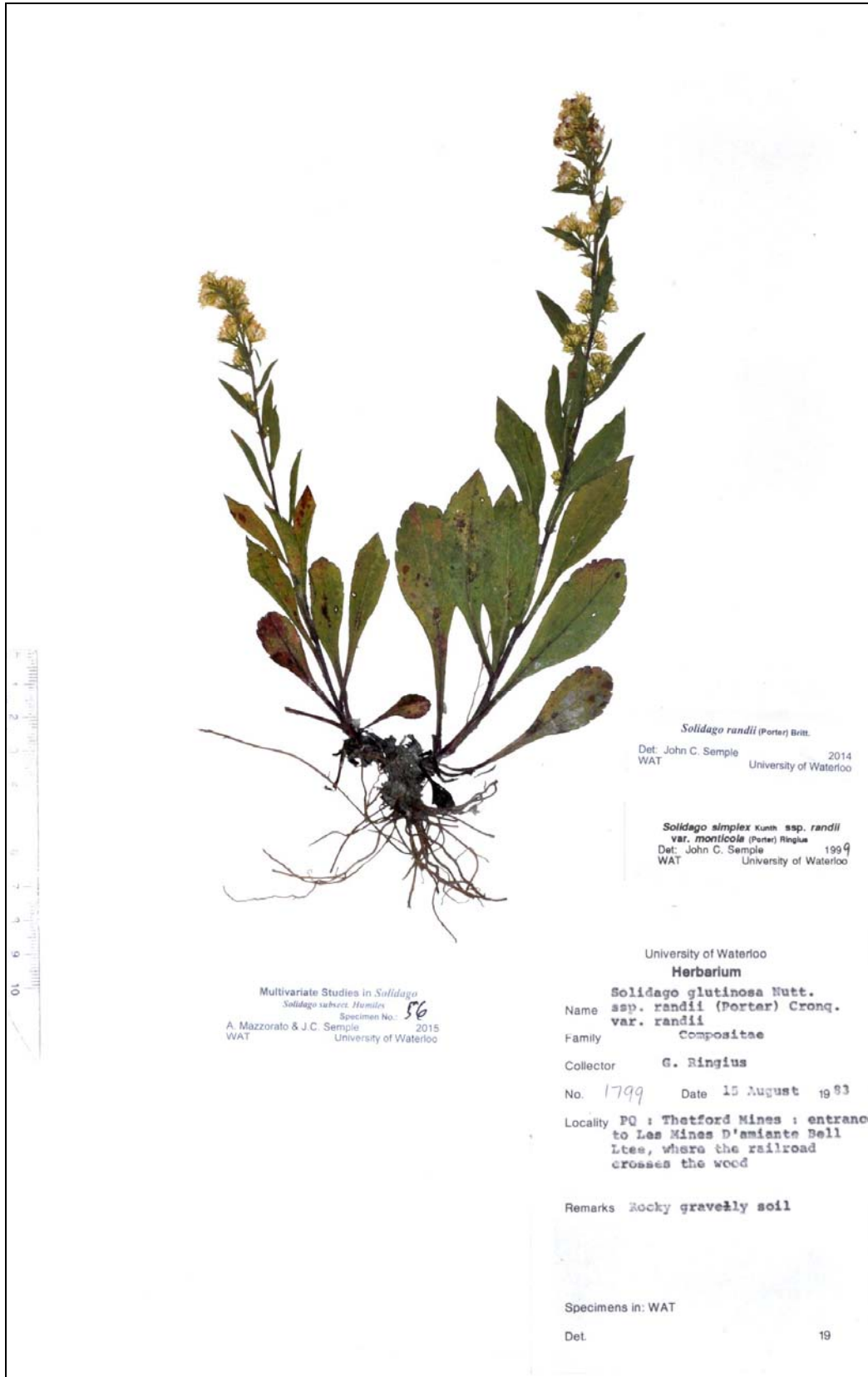


Figure 18. *Solidago randii*. Ringius 1799 (WAT), Thetford Mines, Québec.

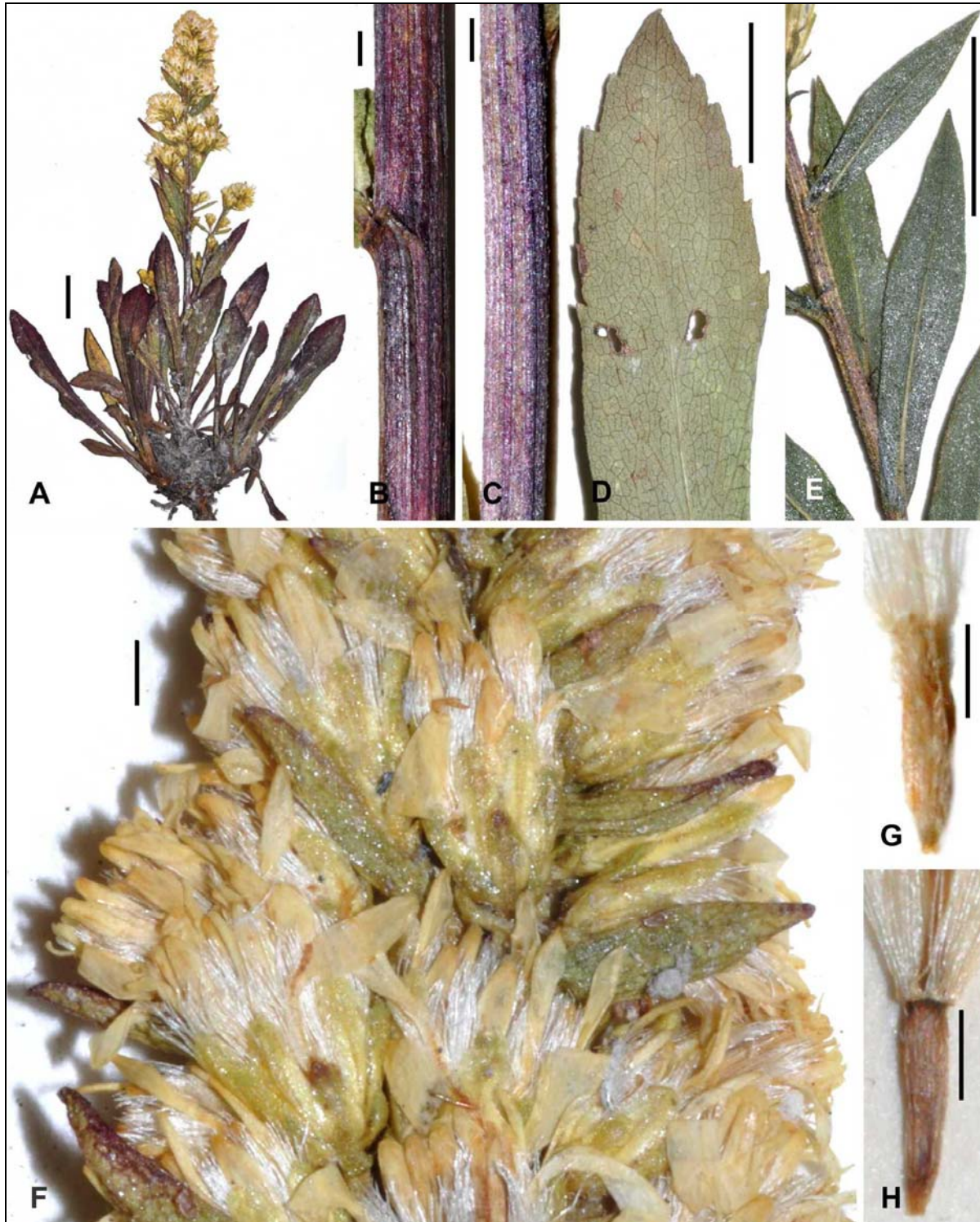


Figure 19. Details of the morphology of *Solidago randii*. **A.** Dwarf shoot, *Ringius 1800* (WAT). **B-C.** Lower and mid stems, *Marie-Victorin et al. 46678* (MT). **D.** Lower stem leaf distal blade, *Ringius 1807* (WAT). **E.** Resinous upper stem leaves, *Ringius 1763* (WAT). **F.** Heads, *Ringius 1800* (WAT). **G-H.** Disc floret cypselae, *Pringle s.n.* (NY) and *Grout s.n.* (NY). Scale bars = 1 mm in B-C and F-G; = 1 cm in A, D-E.



Figure 20. *Solidago simplex*, Hinton et al. 22120 (TEX), Mpio. Zaragoza, Nuevo Leon, Mexico.



Figure 21. *Solidago spathulata*, Ringius 1496 (WAT), Marin Co., California.

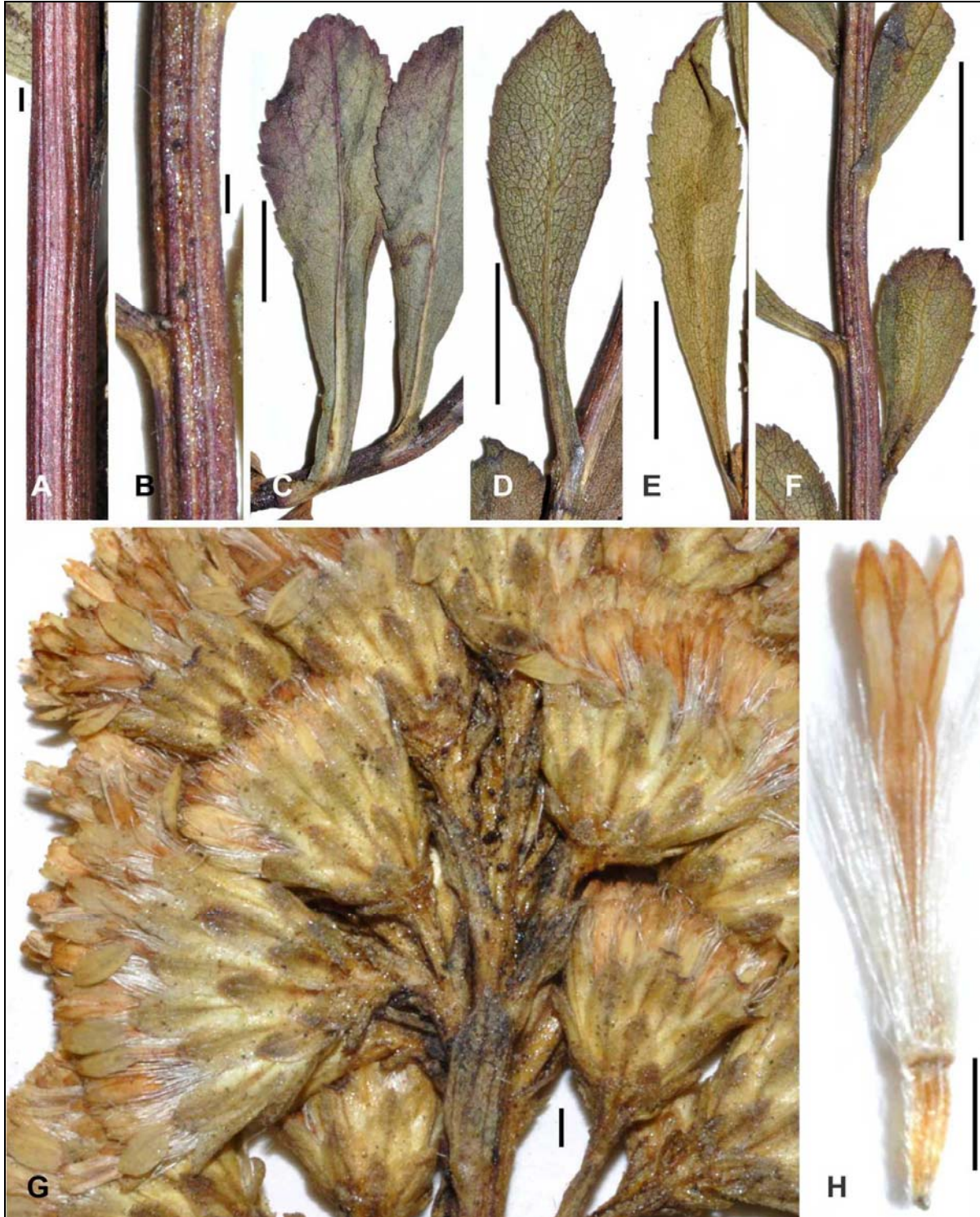


Figure 22. Details of the morphology of *Solidago spathulata*. **A.** Lower stem, *Morton & Venn NA15791* (TRT). **B.** Mid stem, *Ringius 1499* (WAT). **C.** Lower stem leaves, *Ringius 1501-2* (WAT). **D.** Upper mid stem leaf, *Semple & Heard 8465* (WAT). **E.** Upper stem leaf, *Ringius 1499* (WAT). **F.** Upper mid stem, *Semple & Heard 8651* (WAT). **G.** Heads, *Ringius 1499* (WAT). Scale bars = 1 mm in A-B, and G; = 1 cm in C-F.

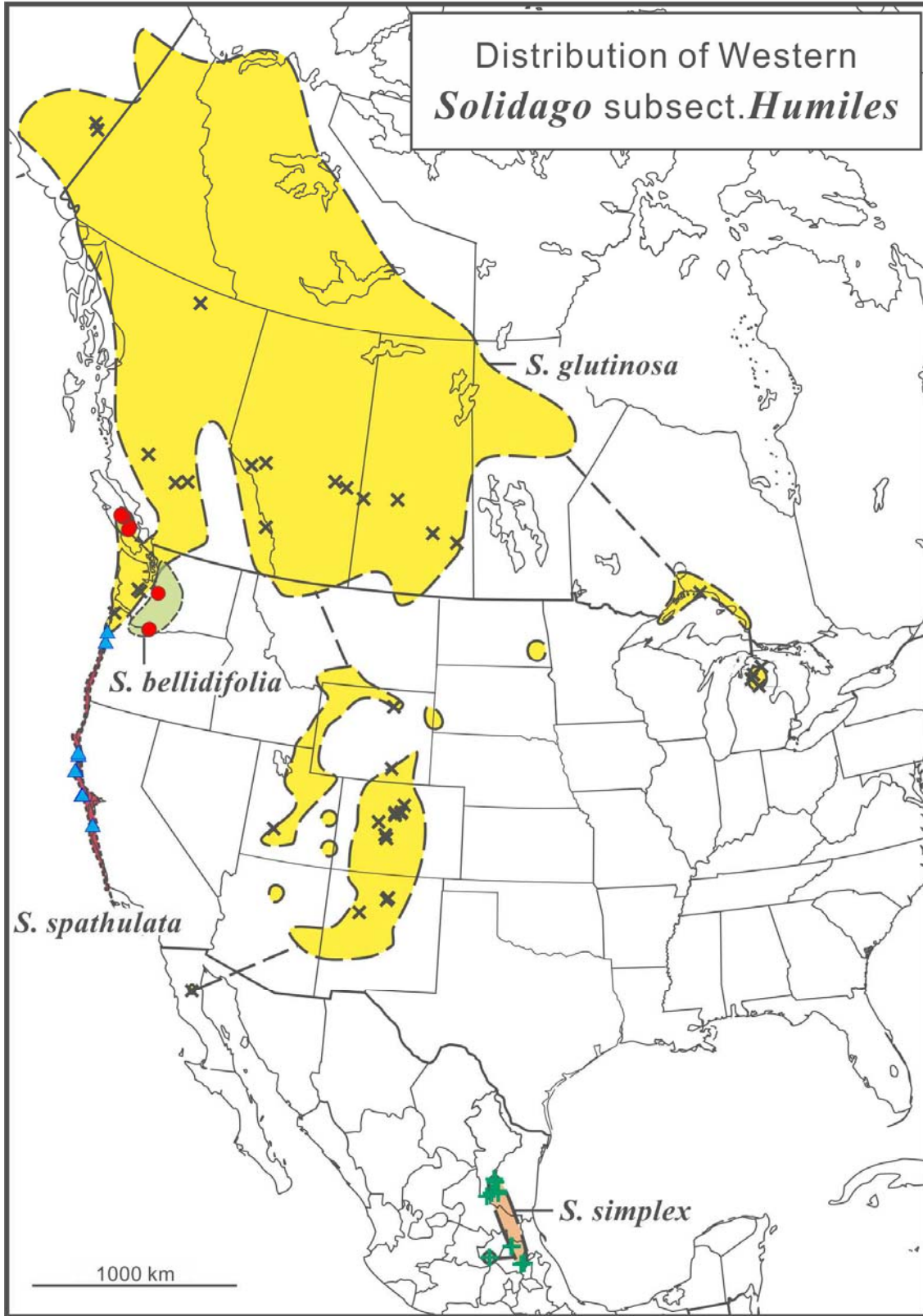


Figure 23. Ranges of distribution of western North American species and locations of samples included in analyses of *Solidago* subsect. *Humiles*; ranges based on all collections seen and literature.

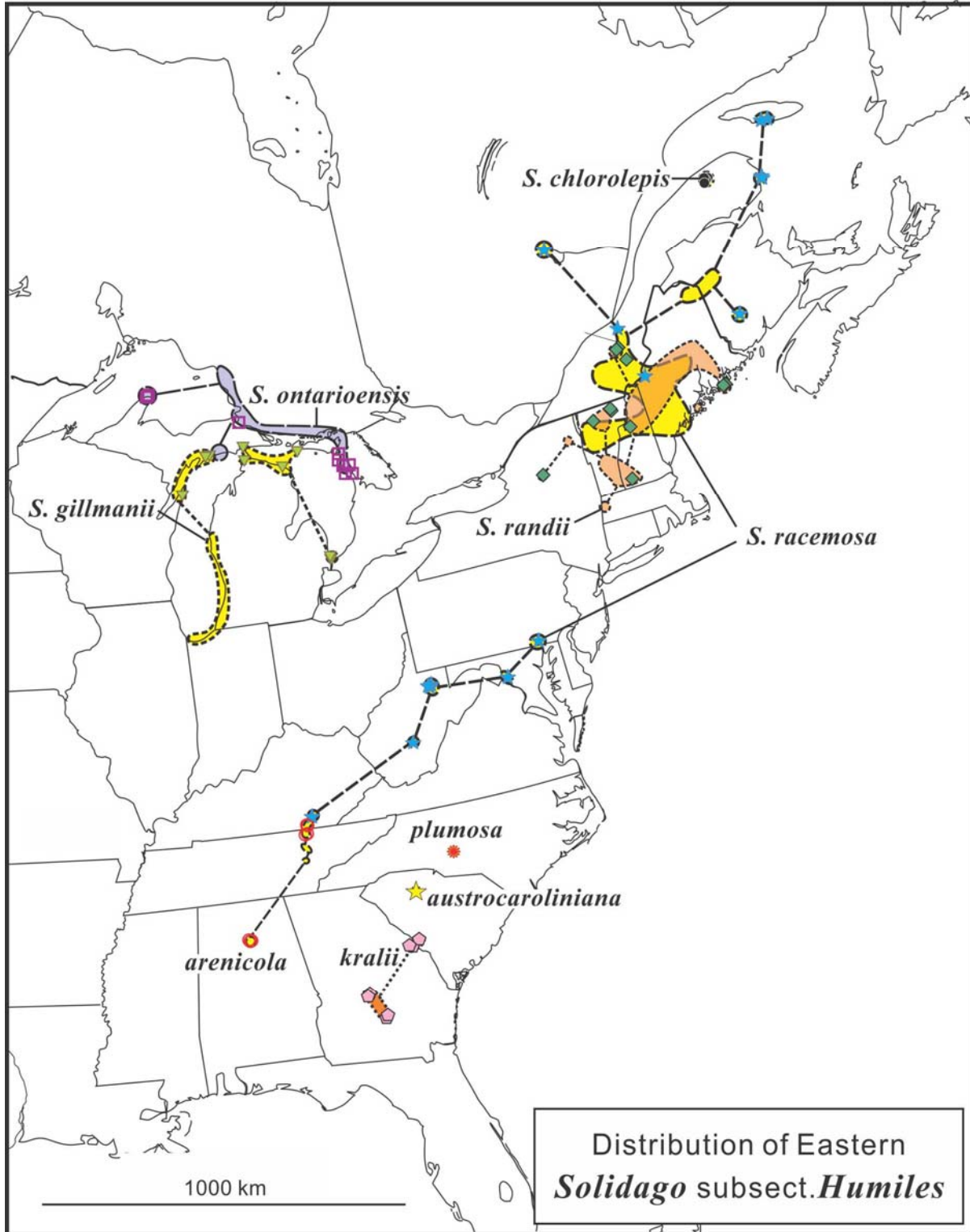


Figure 24. Ranges of distribution of eastern North American species and locations of samples included in analyses of *Solidago* subsect. *Humiles*; range based on all collections seen.

of northern New England, adjacent New York, eastern Québec, and northwestern New Brunswick (Fig. 24). *Solidago racemosa* occurs in cracks in rocks and rocky soils along streams and rivers in scattered locations from Anticosti Island in Québec south through New England to Pennsylvania, Maryland, West Virginia, and Kentucky (Fig. 24). The other five species are rare to extremely rare. *Solidago chlorolepis* occurs at higher elevations on Mt. Albert and adjacent peaks in the Gaspé region of Québec (Fig. 24). The other four occur in the southeastern U.S. *Solidago arenicola* occurs in sandy soils along rivers in southern Kentucky and adjacent Tennessee and in northern Alabama (Fig. 24). *Solidago kralii* occurs in sandy soils of the Fall Line counties in Georgia and just into South Carolina (Fig. 24). *Solidago plumosa* occurs in one location on rock outcrops along the Yadkin R., in North Carolina (Fig. 24). *Solidago austrocaroliniana* is known from a single collection from Union Co., South Carolina and is the only species that blooms in the late spring (Fig. 24).

Numerous chromosome number reports have been published for taxa in *Solidago* subsect. *Humiles*, including diploids $2n=9_{II}$ or $2n=18$, tetraploids $2n=18_{II}$ or $2n=36$, and hexaploids $2n=54$. *Solidago bellidifolia*, *S. spathulata*, *S. chlorolepis*, *S. kralii*, and *S. plumosa* have been reported to be diploid one to multiple times (Ringius and Semple 1987; Peirson et al. 2012 including references to previously published counts). *Solidago glutinosa* is diploid throughout its range with infrequent tetraploids having been reported from only northern Michigan (Peirson et al. 2012). *Solidago arenicola*, *S. gillmanii*, *S. ontarioensis*, *S. racemosa*, and *S. randii* are tetraploid with multiple counts for each species (Peirson et al. 2012). Hexaploids have been reported twice for *S. racemosa* (Beaudry 1963; Peirson et al. 2012). No counts have been reported for *S. austrocaroliniana* and *S. simplex*.

The purpose of this study was to determine statistical support for recognizing the species and subspecies/varieties proposed within *Solidago* subsect. *Humiles*, the levels of distinctiveness among the taxa, and what technical traits could be used to separate taxa besides those used to define the taxa as groups a priori. No previous study has included all species. Ringius (1986, Ph.D. thesis) compared *S. glutinosa* (with multiple infraspecific taxa) with *S. spathulata* and considered *S. plumosa* to be likely extinct. Rediscovery of *S. plumosa* and publication of *S. austrocaroliniana*, *S. arenicola*, and *S. kralii* subsequently expanded the taxa to be studied. Semple, Ma and Tong (2016) used multivariate statistical methods to demonstrate the distinctiveness of *S. simplex* from Mexico from *S. glutinosa* from Canada and the US. Nesom (1989) had placed *S. glutinosa* into synonymy under *S. simplex* following traditional taxonomic observation methods.

MATERIAL AND METHODS

Herbarium specimens were borrowed and examined from the following herbaria (BRIT, DES, GH, the J.K. Morton personal herbarium now in TRT, KY, LL, MICH, MT, NCU, QUE, TEX, USF, V, WAT in MT, and WTU; Thiers continuously updated). More than 3000 specimens were examined, from which 170 specimens were chosen and measured for the statistical analyses based on completeness of the specimen, maturity, and geographical distribution: 12 specimens of *S. arenicola*, 1 of *S. austrocaroliniana*, 13 of *S. bellidifolia*, 11 of *S. chlorolepis*, 10 of *S. gillmanii*, 34 of *S. glutinosa*, 12 of *S. kralii*, 12 of *S. ontarioensis*, 11 of *S. plumosa*, 18 of *S. racemosa*, 11 of *S. randii*, 11 of *S. simplex*, and 11 of *S. spathulata*. In total, 19 vegetative and 20 floral traits were scored for (Table 1). 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. (2016) and are not repeated here. Multiple analyses were performed over more than a decade as sample sizes were increased and samples of rarer species became available. In the first analysis, all samples of all species except *S. austrocaroliniana* were included in a STEPWISE discriminant. In the second analysis, all samples of all species except *S. austrocaroliniana* and *S. spathulata* were included in a STEPWISE discriminant. In the third

analysis, only specimens of the four western taxa *S. bellidifolia*, *S. glutinosa*, *S. simplex* and *S. spathulata*, were included in a STEPWISE discriminant. In the fourth, *S. bellidifolia* and *S. glutinosa* were investigated in a STEPWISE analysis. In the fifth, *S. glutinosa* and *S. simplex* were investigated in a STEPWISE analysis. In the sixth and seventh analyses, only specimens of the northeastern taxa *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa*, and *S. randii* were included in STEPWISE and COMPLETE analyses. In the eighth, only specimens of *S. glutinosa* and *S. ontarioensis* were included a STEPWISE analysis. In the ninth analysis, only specimens of *S. racemosa* and *S. randii* were included a STEPWISE analysis. In the tenth analysis, specimens of the four southeastern taxa *S. arenicola*, *S. kralii*, *S. plumosa*, and *S. racemosa*, were included in a STEPWISE analysis. In the eleventh analysis, only specimens of *S. arenicola* and *S. racemosa* were included a STEPWISE analysis. The single specimen of *S. austrocaroliniana* was included a posteriori in the first, second, and tenth analyses.

Table 1. Traits scored for the multivariate analyses of 170 specimens of *Solidago* subsect. *Humiles*.

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 from the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
UPSTMNOD25	Number of nodes on the top 25% of the stem below the inflorescence
CAPL	Length of inflorescence (cm)
CAPWD	Width of inflorescence (cm)
CBRNCHLN	Length of longest lower inflorescence branches (cm)
PEDBRCTS	Number of peduncle bracts and location
INVOLHT	Involucre height at anthesis (mm)
OPHYLLN	Outer phyllary length (mm)
MPHYLLN	Middle phyllary length (mm)
MPHYLWD	Middle phyllary width, widest point (mm)
MPHYLWD2	Middle phyllary width 1 mm below tip (mm)
RAYNUM	Number of ray florets per head

RSTRAPLN	Ray lamina length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray lamina 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)
RPUB	Density variation of hairs on ray floret ovary/fruit body (0-5 scale)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)
DPUB	Density variation of hairs on disc floret ovary/fruit body (0-5 scale)

RESULTS

Twelve 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, upper stem leaf width, and the number of upper stem leaf margin serrations. Basal rosette leaves were sometimes not present and were not included in the analyses. Stem height correlated strongly with basal rosette and lower stem leaf traits and was included as proxy for the lower stem and rosette leaf traits, although in most species stem height was highly variable. 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, involucre height and length of the disc corolla were strongly correlated as were ray floret lamina width and disc corolla lobe length, ray and disc floret ovary/fruit body lengths, ray and disc floret pappus lengths at anthesis, and ray and disc floret ovary/fruit body hair densities.

In the STEPWISE discriminant analysis of 168 specimens of twelve species level a priori groups (*Solidago arenicola*, *S. bellidifolia*, *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii*, *S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*), the following eight traits were selected and are listed in order of decreasing F-to-remove values: number of upper stem leaf margin serrations (23.33), stem height (11.53), number of peduncle bracts (10.95), involucre height (9.22), number of ray florets (8.34), upper stem leaf width (5.73), mid stem leaf length (5.66), and mid series phyllary width (5.60). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. plumosa* and *S. spathulata* (41.146); the smallest separations were between *S. bellidifolia* and *S. chlorolepis* (0.747) and between *S. glutinosa* and *S. randii* (1.884).

In the Classificatory Discriminant Analysis of 168 specimens of the twelve species level a priori groups (*Solidago arenicola*, *S. bellidifolia*, *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii*, *S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*) plus 1 specimen of *S. austrocaroliniana* include a posteriori, percents of correct a posteriori assignment to the same a priori group ranged from 53-100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. Ten of the 10 specimens of the *S. plumosa* a priori group (100%) were assigned a posteriori to *S. plumosa*: 9 specimens with 98-100% probability and 1 specimen with 79% probability. Eleven of the 12 specimens of the *S. arenicola* a priori group (92%) were assigned a posteriori into the *S. arenicola* group: 9 specimens with 96-100% probability and 2 specimens with 66% and 63% probability. One

Table 2. Between groups F-matrix for the twelve a priori groups in a STEPWISE analysis (df = 8 149)

Group	<i>areni- cola</i>	<i>bellidi- folia</i>	<i>chloro- lepis</i>	<i>gill- manii</i>	<i>glutin- osa</i>	<i>kralii</i>	<i>ontario- ensis</i>	<i>plum- osa</i>	<i>racem- osa</i>	<i>randii</i>	<i>simplex</i>
<i>bellidifolia</i>	26.518										
<i>chlorolepis</i>	25.668	0.747									
<i>gillmanii</i>	11.472	10.784	11.142								
<i>glutinosa</i>	32.939	6.791	4.722	13.220							
<i>kralii</i>	12.884	30.121	26.779	13.104	27.433						
<i>ontarioensis</i>	16.302	4.385	3.897	8.446	2.506	21.133					
<i>plumosa</i>	16.729	33.445	27.442	25.590	33.596	12.173	24.143				
<i>racemosa</i>	9.510	10.375	10.131	11.158	13.074	16.540	6.442	17.220			
<i>randii</i>	26.559	5.013	3.361	12.493	1.884	19.948	3.873	26.567	9.419		
<i>simplex</i>	15.462	6.849	6.243	7.236	4.810	11.872	3.415	23.059	7.727	2.834	
<i>spathulata</i>	38.441	26.764	25.670	27.743	31.300	34.733	23.277	41.146	31.156	28.510	24.081

Lambda = 0.0056 df= 8 11 156; Approx. F=13.4979 df= 88 986 prob = 0.0000

specimen of the *S. arenicola* a priori group was assigned a posteriori to *S. racemosa* with 36% probability (19% to *S. simplex*, 17% to *S. ontarioensis*, 8% to *S. arenicola*, and 6% to *S. plumosa* (Bailey B150 WAT from Scott Co., Tennessee; nearly all heads were immature). Ten of the 11 specimens of the Mexican *S. simplex* a priori group (91%) were assigned a posteriori to *S. simplex*; 2 specimens with 98% and 93% probabilities, 1 specimen with 87% probability, 2 specimens with 72% and 66% probabilities, 2 specimens with 55% (24% to *S. gillmanii*) and 51% probability (32% to *S. randii*), and 3 specimens with 44% probability (33% to *S. randii* and 11% to *S. glutinosa*), 33% probability (31% to *S. randii* and 14% to *S. glutinosa*) and 33% probability (28% to *S. gillmanii* and 22% to *S. racemosa*). One specimen of the *S. simplex* a priori group was assigned a posteriori to *S. randii* with 41% probability. Nine of the 10 specimens the *S. gillmanii* a priori group (90%) were assigned a posteriori to *S. gillmanii*; 5 specimens with 91-100% probability and 4 specimens with 81-89% probability. One specimen of the *S. gillmanii* a priori group was assigned a posteriori to *S. chlorolepis* with 23% probability (20% to *S. gillmanii*, 18% to *S. bellidifolia*, 14% to *S. ontarioensis*, 14% to *S. glutinosa* and 6% to *S. randii*; Ringius 1851 WAT from Door Co., Wisconsin). Ten of 12 specimens of the *S. spathulata* a priori group (83%) were assigned a posteriori to *S. spathulata*; 9 specimens with 100% probability and 1 specimen with 82% probability. Two specimens of the *S. spathulata* a priori group were assigned a posteriori to other species: 1 specimen to *S. glutinosa* with 54% probability (Morton NA3312 TRT from Newport, Oregon; upper stem leaves had multiple margin serrations and the involucre had a thick shiny resinous coating usual for of *S. spathulata*) and 1 specimen to *S. simplex* with 29% probability (26% to *S. gillmanii*, and 10% to *S. glutinosa*; Semple & Heard 8541 WAT from Medocino Co., California). Nine of 11 specimens of the *S. kralii* a priori group (82%) were assigned a posteriori to *S. kralii*; 6 specimens with 99-100% probability and 2 specimens with 74% and 70% probabilities. Two specimens of the *S. kralii* a priori group were assigned a posteriori to other species: 1 specimen to *S. arenicola* with 74% probability (Semple & B. Semple 11208 WAT from Pulaski Co., Georgia) and 1 specimen to *S. racemosa* with 46% probability (44% to *S. kralii*; Semple & B. Semple 11218 WAT from Aitken Co., South Carolina). Eight of 11 specimens of the *S. chlorolepis* a priori group (73%) were assigned a posteriori to *S. chlorolepis*; 6 specimens with 59-68% probability and 2 specimens with 49% probability (38% to *S. bellidifolia*; Ringius 1702 WAT) and 48% probability (34% to *S. bellidifolia*; Ringius 1800 WAT). Three specimens of the *S. chlorolepis* a priori group were assigned a posteriori to other species: 2 specimens to *S. bellidifolia* with 65% probability (27% to *S. chlorolepis*; Ringius 1702 WAT) and 26% probability (20% to *S. chlorolepis*, 18% to *S. ontarioensis*, 13% to *S. randii*, and 12% to *S. glutinosa*; Dignard & Gagnon 98-69 QUE), and 1 specimen to *S. glutinosa* with 44% probability (20% to *S. chlorolepis*, 14% to *S. ontarioensis*, 11% to *S. bellidifolia*, and 10 to *S. randii*; Ringius 1691c WAT). All specimens of *S. chlorolepis* were from Mt. Albert and nearby peaks on the Gaspé,

Québec. Thirteen of 18 specimens of the *S. racemosa* a priori group (72%) were assigned a posteriori to *S. racemosa*; 9 specimens with 90-99% probability, 1 specimen with 86% probability, 2 specimens with 57% probability (*Semple & Ringius 7612 WAT* from York Co., Pennsylvania; this was the most robust of the shoots collected from rocks above the Susquehanna R.) and 56% probability (44% to *S. arenicola*; *Peirson 603 MICH* from Nicholas Co., West Virginia), and 1 specimen with 36% probability (17% to *S. glutinosa*, 17% to *S. randii*, and 15% to *S. simplex*, *Dignard 99-114 QUE* from Île-d'Anticosti, Québec). Five specimens of the *S. racemosa* a priori group were assigned a posteriori to other species: 1 specimen to *S. arenicola* with 90% probability (*Peirson 601 MICH* from Barbour Co., West Virginia), 2 specimens to *S. randii* with 53% probability (*Labrecque s.n.* MT from Percé, Gaspésie, Québec) and 45% probability (*Semple & Keir 4621 WAT* from Franklin Co., Maine), 1 specimen to *S. ontarioensis* with 50% probability (*Dignard et al. 08-95 QUE* from Rivière Galiote, Île-d'Anticosti, Québec), and 1 specimen to *S. bellidifolia* with 24% probability (21% to *S. ontarioensis*, 17% to *S. randii*, 17% to *S. simplex*, and 13% to *S. glutinosa*; *Morton NA4142 TRT* from Percé Mt., Gaspésie, Québec). Results for the remaining four species are summarized but not presented in detail. Six of 11 specimens of the *S. ontarioensis* a priori group (55%) were assigned a posteriori to *S. ontarioensis*; 1 specimen with 96% probability, 1 specimen with 86% probability, and 5 specimens with 50-30%. Five specimens of the *S. ontarioensis* a priori group were assigned a posteriori to other species: 1 specimen to *S. spathulata* with 100% probability, 1 specimen to *S. simplex* with 46% probability, 1 specimen to *S. bellidifolia* with 39% probability, 1 specimen to *S. randii* with 35% probability, and 1 specimen to *S. glutinosa* with 28% probability. Seven of 11 specimens of the *S. bellidifolia* a priori group (54%) were assigned a posteriori to *S. bellidifolia*; 1 specimen with 90% probability, 1 specimen with 85% probability, 2 specimens with 79% and 71% probabilities, 2 specimens with 59 and 52% probabilities, and 1 specimen with 36% probability. Six specimens of the *S. bellidifolia* a priori group were assigned a posteriori to *S. chlorolepis* with 54%, 54%, 50%, 39% and 37% probability. Eight of 15 specimens of the *S. randii* a priori group (53%) were assigned a posteriori to *S. randii*; 1 specimen with 75% probability, 1 specimen with 69% probability, and 4 specimens with 58%, 58%, 53% and 44% probability. Seven specimens of the *S. randii* a priori group were assigned a posteriori to other species: 1 specimen to *S. simplex* with 92% probability, 3 specimens to *S. glutinosa* with 75%, 28% and 21% probabilities, 1 specimen to *S. ontarioensis* with 39% probability, and 2 specimen to *S. chlorolepis* with 30% and 28% probabilities. Thirteen of 34 specimens of the *S. glutinosa* a priori group (38%) were assigned a posteriori to *S. glutinosa*; 1 specimen with 88% probability, 3 specimens with 72-75% probability, 2 specimens with 69% and 65% probabilities, 2 specimens with 58% and 52% probabilities, and 6 specimens with 43%, 41%, 40%, 37%, 36% and 32% probabilities. Twenty-one specimens of 34 the *S. glutinosa* a priori group were assigned a posteriori to other species: 9 specimens to *S. randii*, 4 specimens to *S.*

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

Group	<i>areni-</i> <i>cola</i>	<i>bellidi-</i> <i>folia</i>	<i>chloro-</i> <i>lepis</i>	<i>gill-</i> <i>manii</i>	<i>glutin-</i> <i>osa</i>	<i>kralii</i>	<i>ontario-</i> <i>ensis</i>	<i>plum-</i> <i>osa</i>	<i>racem-</i> <i>osa</i>	<i>randii</i>	<i>simplex</i>	<i>spath-</i> <i>ulata</i>	% <i>correct</i>
<i>arenicola</i>	11	0	0	0	0	0	0	0	1	0	0	0	92
<i>bellidifolia</i>	0	7	6	0	0	0	0	0	0	0	0	0	54
<i>chlorolepis</i>	0	2	8	0	1	0	0	0	0	0	0	0	73
<i>gillmanii</i>	0	0	1	9	0	0	0	0	0	0	0	0	90
<i>glutinosa</i>	0	2	1	0	13	0	4	0	1	9	3	1	38
<i>kralii</i>	1	0	0	0	0	9	0	0	1	0	0	0	82
<i>ontarioensis</i>	0	1	0	0	1	0	6	0	0	1	1	1	55
<i>plumosa</i>	0	0	0	0	0	0	0	10	0	0	0	0	100
<i>racemosa</i>	1	1	0	0	0	0	1	0	13	2	0	0	72
<i>randii</i>	0	0	2	0	3	0	1	0	0	8	1	0	53
<i>simplex</i>	0	0	0	0	0	0	0	0	0	1	10	0	91
<i>spathulata</i>	0	0	0	0	1	0	0	0	0	0	1	0	83
TOTALS	13	13	18	9	19	9	12	10	16	21	16	10	68

Jackknifed classification matrix

Group	<i>arenicola</i>	<i>bellidifolia</i>	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>kralii</i>	<i>ontarioensis</i>	<i>plumosa</i>	<i>racemosa</i>	<i>randii</i>	<i>simplex</i>	<i>spathulata</i>	% correct
<i>arenicola</i>	10	0	0	0	0	0	0	0	2	0	0	0	83
<i>bellidifolia</i>	0	6	7	0	0	0	0	0	0	0	0	0	46
<i>chlorolepis</i>	0	2	8	0	1	0	0	0	0	0	0	0	73
<i>gillmanii</i>	1	0	1	8	0	0	0	0	0	0	0	0	80
<i>glutinosa</i>	0	2	1	0	13	0	4	0	1	9	3	1	38
<i>kralii</i>	1	0	0	1	0	6	0	1	2	0	0	0	55
<i>ontarioensis</i>	0	1	0	1	1	0	5	0	0	1	1	1	45
<i>plumosa</i>	0	0	0	0	0	0	0	10	0	0	0	0	100
<i>racemosa</i>	1	1	0	0	0	0	1	0	13	2	0	0	72
<i>randii</i>	0	0	3	0	3	0	1	0	0	6	2	0	40
<i>simplex</i>	0	0	0	1	0	0	0	0	0	3	7	0	64
<i>spathulata</i>	0	0	0	0	1	0	0	0	0	0	1	10	83
TOTALS	13	12	20	11	19	6	11	11	18	21	14	12	61

ontarioensis, 2 specimens to *S. bellidifolia*, 1 specimen to *S. simplex*, and 1 specimen to *S. spathulata*. The specimen of *S. austrocaroliniana* was assigned a posteriori to *S. simplex* with 42% probability (19% to *S. racemosa*, 14% to *S. gillmanii*, 8% to *S. ontarioensis*, and 6% to *S. arenicola*).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 170 specimens including all species *Solidago* subsect. *Humiles* are presented in Fig. 25. Eigenvalues on the first three axes were 4.267, 2.229, and 1.308.

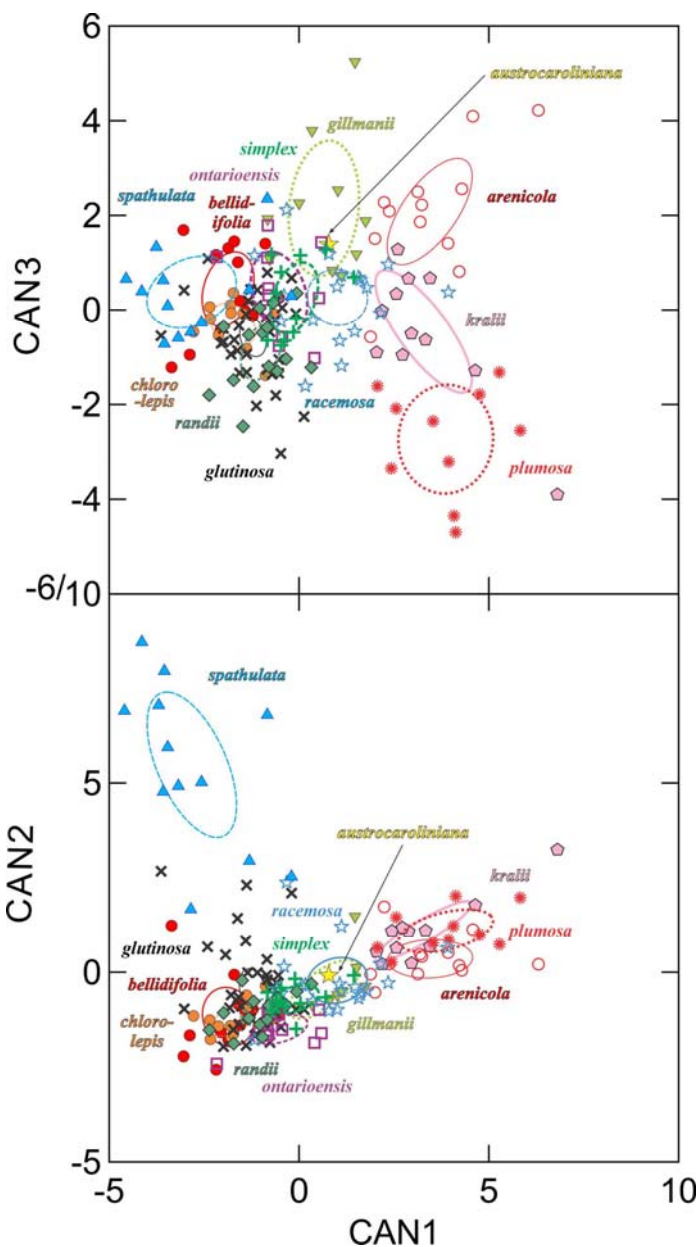


Figure 25. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 170 specimens of all species of *Solidago* subsect. *Humiles*: *S. austrocaroliniana* (yellow stars), *S. arenicola* (red circles), *S. bellidifolia* (red dots), *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black x's), *S. kralii* (pink pentagons), *S. ontarioensis* (magenta squares), *S. plumosa* (red star-bursts), *S. racemosa* (open blue stars), *S. randii* (green diamonds), *S. simplex* (green +s), and *S. spathulata* (blue triangles).

Eleven species level a priori groups analysis

The Pearson correlation matrix for traits of specimens of *Solidago arenicola*, *S. bellidifolia*, *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii*, *S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, and *S. simplex* included $r > |0.7|$ for multiple pairs of leaf and floral traits. The following traits were included: stem height, mid stem leaf length, upper stem leaf width, number of upper stem leaf margin serrations, number of peduncle bracts, involucre height, mid series phyllary length, mid series phyllary width, number of ray florets, ray lamina length, number of disc florets, disc corolla lobe length, disc floret ovary/fruit body length, and disc floret pappus length at anthesis.

In the STEPWISE discriminant analysis of 156 specimens of eleven species level a priori groups (*Solidago arenicola*, *S. bellidifolia*, *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii*, *S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, and *S. simplex*), the following eight traits were selected and are listed in order of decreasing F-to-remove values: stem height (14.76), number of peduncle bracts (11.08), number of ray florets (8.25), involucre height (7.70), upper stem leaf width (6.34), mid series phyllary width (6.07), mid stem leaf length (5.43), and disc floret pappus length at anthesis (4.44). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. bellidifolia* and *S. plumosa* (32.790); the smallest separations were between *S. glutinosa* and *S. randii* (2.006), between *S. glutinosa* and *S. ontarioensis* (2.450), between *S. randii* and *S. simplex* (2.808), and between *S. bellidifolia* and *S. chlorolepis* (2.904).

Table 4. Between groups F-matrix for the eleven a priori groups in a COMPLETE analysis (df = 8 138).

Group	<i>areni- cola</i>	<i>bellidi- folia</i>	<i>chloro- lepis</i>	<i>gill- manii</i>	<i>glutin- osa</i>	<i>kralii</i>	<i>ontario- ensis</i>	<i>plum- osa</i>	<i>racem- osa</i>	<i>randii</i>
<i>bellidifolia</i>	26.659									
<i>chlorolepis</i>	28.547	2.904								
<i>gillmanii</i>	12.786	13.220	11.935							
<i>glutinosa</i>	32.485	6.567	6.680	15.179						
<i>kralii</i>	12.437	30.760	30.676	15.161	27.935					
<i>ontarioensis</i>	17.337	4.593	4.488	9.555	2.450	22.555				
<i>plumosa</i>	16.160	32.790	28.292	25.247	33.174	12.256	24.159			
<i>racemosa</i>	10.679	10.620	10.715	11.653	12.414	18.167	6.178	16.825		
<i>randii</i>	28.510	5.907	3.611	13.471	2.006	22.947	3.704	26.540	9.285	
<i>simplex</i>	16.440	6.833	6.689	8.111	3.591	13.453	2.976	21.849	7.196	2.808

Wilks' lambda = 0.0120 df = 8 10 145; Approx. F = 11.1358 df = 80 883 prob = 0.0000

In the Classificatory Discriminant Analysis of 156 specimens of the twelve species level a priori groups (*Solidago arenicola*, *S. bellidifolia*, *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii*, *S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, and *S. simplex*) plus 1 specimen of *S. austrocaroliniana* included a posteriori, percents of correct a posteriori assignment to the same a priori group ranged from 100-45%. The Classification matrix and Jackknife classification matrix are presented in Table 5. All 10 of the specimens of the *S. plumosa* a priori group were assigned a posteriori to *S. plumosa* with 9 specimens with 98-100% probability and 1 specimen with 88% probability. All 11 specimens of the *S. chlorolepis* a priori group were assigned a posteriori to *S. chlorolepis*: 1 specimen with 95% probability, 1 specimen with 80% probability, 1 specimen with 77% probability, 4 specimens with 65-66% probability, and 3 specimens with 52-48%. Eleven of the 12 specimens of the *S. arenicola* a priori group (92%) were assigned a posteriori to the *S. arenicola*:

10 specimens with 94-100% probability and 1 specimen with 72% probability. One specimen of the *S. arenicola* a priori group was assigned a posteriori to *S. racemosa* with 38% probability (Bailey B150 WAT from Scott Co., Tennessee). Twelve of the 13 specimens of the *S. bellidifolia* a priori group were assigned a posteriori to *S. bellidifolia*: 2 specimens with 96-97% probability, 3 specimens with 80-84% probability, 2 specimens with 75% and 70% probabilities, 2 specimens with 69% and 60% probabilities, and 3 specimens with 46% probability (Ceska s.n. V from Mt. Arrowsmith, Vancouver Is., British Columbia), 41% probability (Semple & Xiang 10270 WAT from Mt. Hood, Oregon), and 32% probability (Semple & Xiang 10270 WAT from Mt. Hood, Oregon). Nine of the 10 specimens of the *S. gillmanii* a priori group specimens (90%) were assigned a posteriori to *S. gillmanii*: 7 specimens with 90-100% probability, 1 specimen with 88% probability, and 1 specimen with 57% probability. One specimen of the *S. gillmanii* a priori group was assigned a posteriori to *S. chlorolepis* with 41% probability (Ringius 1851 WAT from Door Co., Wisconsin). Nine of the 11 specimens of the *S. kralii* a priori group (82%) were assigned to the *S. kralii* a priori group: 7 specimens with 99-100% probability, 1 specimen with 87% probability, and 1 specimen with 69% probability. Two specimens of the the *S. kralii* a priori group were assigned to other species: 1 specimen to *S. arenicola* with 69% probability (Semple & B. Semple 11208 WAT from Pulaski Co., Georgia) and 1 specimen to *S. racemosa* with 52% (Semple & B. Semple 11218 WAT from Aiken Co., South Carolina). Nine of the 11 specimens of the *S. simplex* a priori group (82%) were assigned a posteriori to the *S. simplex* a priori group: 1 specimen with 93% probability, 2 specimens with 89% and 86% probabilities, 5 specimens with 51-59% probability, and 1 specimen with 33% probability. Two specimens of the *S. simplex* a priori group were assigned to *S. randii* with 38% and 28% probabilities. Thirteen of the 18 specimens of the *S. racemosa* a priori group (72%) were assigned a posteriori to *S. racemosa*: 8 specimens with 93-99% probability, 3 specimens with 83-85% probability, 1 specimen with 62% probability, and 1 specimen with 29% probability. Five specimens of the *S. racemosa* a priori group were assigned to other species: 1 specimen to *S. arenicola* with 86%, 2 specimens to *S. randii* with 51% and 38% probabilities, and 2 specimens to *S. ontarioensis* with 47% and 25% probabilities. For the other three species percents of correct assignment to the a priori species were much lower. Seventeen of the 34 specimens of the *S. glutinosa* a priori group (50%) were assigned a posteriori to *S. glutinosa*: 1 specimen with 82% probability, 2 specimens with 76% and 72% probabilities, 4 specimens with 61-69% probability, and 10 specimens with 54-33% probability. Seventeen specimens of the *S. glutinosa* a priori group were assigned a posteriori to 5 other species. Seven of the 15 specimens of the *S. randii* a priori group (47%) were assigned a posteriori to *S. randii*: 2 specimens with 83-84% probability, 1 specimen with 70% probability, 1 specimen with 61% probability, and 3 specimens with 57-45% probability. Eight specimens of the *S. randii* a priori group were assigned a posteriori to other species: 4 specimens to *S. chlorolepis* with 53-38% probability, 3 specimens to *S. glutinosa* with 68-39% probability, and 1 to *S. simplex* with 90% probability. Five of the 11 specimens of the *S. ontarioensis* a priori group (45%) were assigned a posteriori to *S. ontarioensis*: 2 specimens with 98-96% probability and 3 specimens with 53-40% probability. Six specimens of the *S. ontarioensis* a priori group were assigned a posteriori to other species: 3 specimens to *S. glutinosa* with 66-35% probability, 1 specimen to *S. bellidifolia* with 68% probability, 1 specimen to *S. simplex* with 41% probability, and 1 specimen to *S. gillmanii* with 34% probability. The 1 specimen of *S. austrocaroliniana* included a posteriori was assigned to *S. simplex* with 36% probability (27% to *S. gillmanii*, 20% to *S. racemosa*, and 7% to *S. ontarioensis*).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 158 specimens of all species of *S.* subsect. *Humiles* are presented in Fig. 26. Eigenvalues on the first three axes were 4.603, 1.384, and 1.110.

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

Group	<i>arenicola</i>	<i>bellidifolia</i>	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>kralii</i>	<i>ontarioensis</i>	<i>plumosa</i>	<i>racemosa</i>	<i>randii</i>	<i>simplex</i>	% correct
<i>arenicola</i>	11	0	0	0	0	0	0	0	1	0	0	92
<i>bellidifolia</i>	0	12	1	0	0	0	0	0	0	0	0	92
<i>chlorolepis</i>	0	0	11	0	0	0	0	0	0	0	0	100
<i>gillmanii</i>	0	0	1	9	0	0	0	0	0	0	0	90
<i>glutinosa</i>	0	3	0	0	17	0	5	0	1	7	1	50
<i>kralii</i>	1	0	0	0	0	9	0	0	1	0	0	82
<i>ontarioensis</i>	0	1	0	1	3	0	5	0	0	0	1	45
<i>plumosa</i>	0	0	0	0	0	0	0	10	0	0	0	100
<i>racemosa</i>	1	0	0	0	0	0	2	0	13	2	0	72
<i>randii</i>	0	0	4	0	3	0	0	0	0	7	1	47
<i>simplex</i>	0	0	0	0	0	0	0	0	0	2	9	82
TOTALS	13	16	17	10	23	9	12	10	16	18	12	72

Jackknifed classification matrix

Group	<i>arenicola</i>	<i>bellidifolia</i>	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>kralii</i>	<i>ontarioensis</i>	<i>plumosa</i>	<i>racemosa</i>	<i>randii</i>	<i>simplex</i>	% correct
<i>arenicola</i>	11	0	0	0	0	0	0	0	1	0	0	92
<i>bellidifolia</i>	0	11	1	0	0	0	0	0	0	1	0	85
<i>chlorolepis</i>	0	1	10	0	0	0	0	0	0	0	0	91
<i>gillmanii</i>	1	0	1	8	0	0	0	0	0	0	0	80
<i>glutinosa</i>	0	4	1	0	16	0	4	0	1	7	1	47
<i>kralii</i>	1	0	0	0	0	8	0	1	1	0	0	73
<i>ontarioensis</i>	0	1	0	1	4	0	3	0	0	0	2	27
<i>plumosa</i>	0	0	0	0	0	0	0	10	0	0	0	100
<i>racemosa</i>	1	0	0	0	0	0	2	0	12	2	1	67
<i>randii</i>	0	0	4	0	3	0	0	0	0	6	2	40
<i>simplex</i>	0	0	0	0	0	0	1	0	1	2	7	64
TOTALS	14	17	17	9	23	8	10	11	16	18	13	65

Four western species level a priori groups analysis

The Pearson correlation matrix for traits of specimens of *Solidago bellidifolia*, *S. glutinosa*, *S. simplex* and *S. spathulata* included $r > |0.7|$ for most pairs of leaf traits reducing those included to mid stem leaf width, upper stem leaf length and number of margin serrations, the number of upper stem nodes in the top 25% below the inflorescence, and the number of peduncle bracts. Basal rosette leaves were often not present and were not included in the discriminant analyses. Many floral traits were correlated, and only involucre height, the numbers of rays, ray floret lamina length and width, number of disc florets, the lengths of disc corolla and corolla lobes, fruit/ovary body, and pappus were included in the STEPWISE analysis.

In the STEPWISE discriminant analysis of 67 specimens of four species level a priori groups in (*Solidago bellidifolia*, *S. glutinosa*, *S. simplex*, and *S. spathulata*), the following four traits were selected and are listed in order of decreasing F-to-remove values: number of upper leaf margin serrations (50.21), upper stem leaf length (22.57), number of ray florets (10.78), and number of disc florets (7.65). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 6. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. glutinosa* and *S. spathulata* (46.606); the smallest separation was between *S. glutinosa* and *S. simplex* (8.389).

In the Classificatory Discriminant Analysis of 67 specimens of the four species level a priori groups (*S. bellidifolia*, *S. glutinosa*, *S. simplex*, and *S. spathulata*) plus 3 specimens included a posteriori, percents of correct a posteriori assignment to the same a priori group ranged from 82-100%.

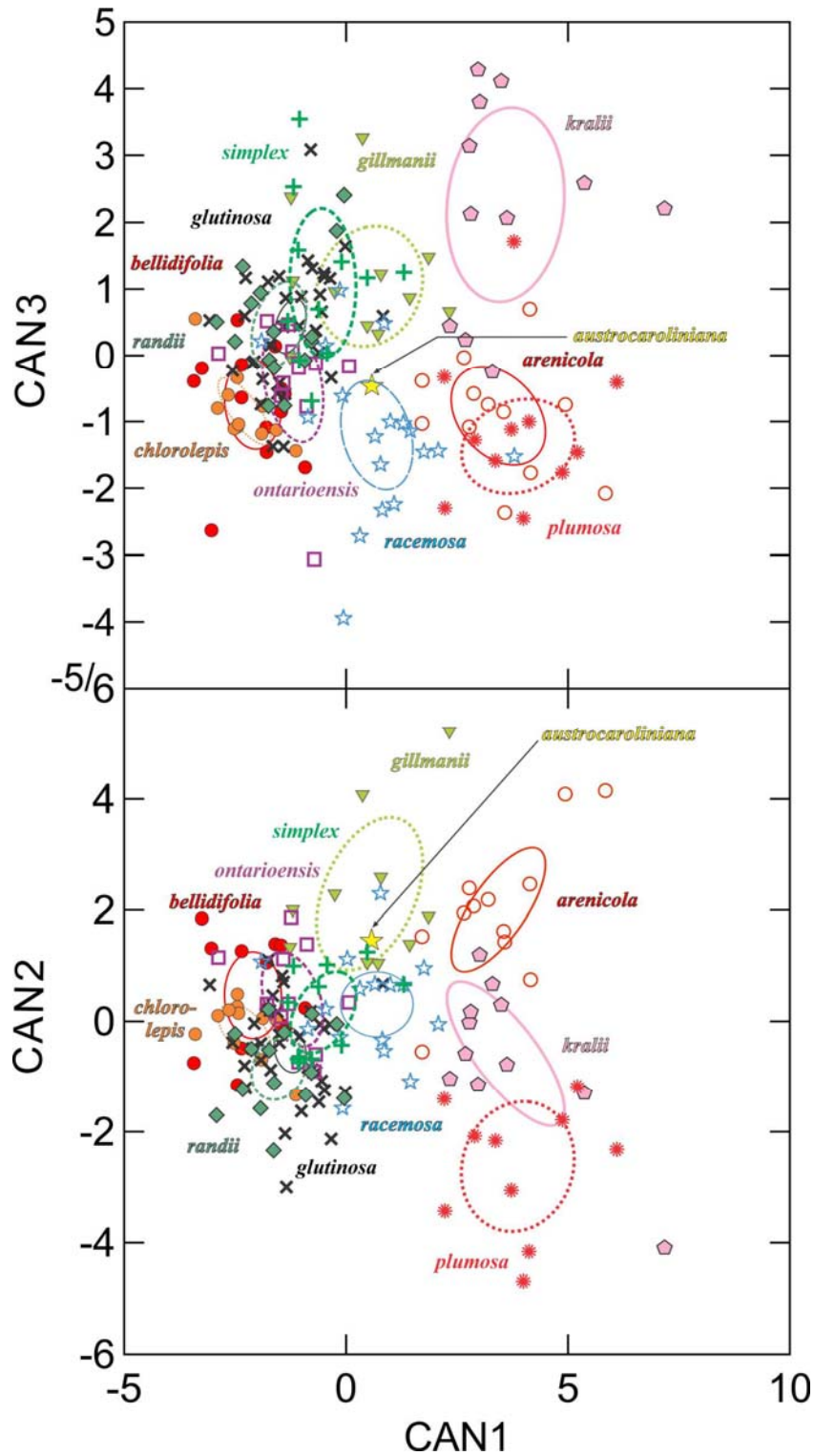


Figure 26. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 158 specimens of *Solidago* subsect. *Humiles*: *S. austrocaroliniana* (yellow stars), *S. arenicola* (red circles), *S. bellidifolia* (red dots), *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black x's), *S. kralii* (pink pentagons), *S. ontarioensis* (magenta squares), *S. plumosa* (red star-bursts), *S. racemosa* (open blue stars), *S. randii* (green diamonds), and *S. simplex* (green +s).

Table 6. Between groups F-matrix for the four species level a priori groups analysis (df = 4 60).

Group	<i>bellidifolia</i>	<i>glutinosa</i>	<i>simplex</i>
<i>glutinosa</i>	13.525		
<i>simplex</i>	13.907	8.389	
<i>spathulata</i>	30.057	46.606	36.388

Wilks' lambda = 0.0781 df = 4 3 63; Approx. F= 21.4788 df = 12 159 prob = 0.0000

The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 13 specimens of *S. bellidifolia* a priori group (100%) were assigned a posteriori into the *S. bellidifolia* group; 9 specimens with 90-100% probability 2 specimens with 83% and 81% probability, 1 specimen with 62% probability, and 1 specimen with 56% probability (43% to *S. glutinosa*; *Ceska s.n.* from Forbidden Plateau, Vancouver Is., British Columbia). Nine of 11 specimens of the *S. spathulata* a priori group (82%) plus 1 additional specimen included a posteriori were assigned a posteriori to *S. spathulata* with 95-100% probability. Two specimens of the *S. spathulata* a priori group were assigned to *S. bellidifolia* with 82% probability (13% to *S. spathulata*; *Semple & Heard 8541* WAT from Mendocino Co., California) and 66% probability (18% to *S. spathulata* and 15% to *S. glutinosa*; *J.K. Morton NA3312* TRT from Lincoln Co., Oregon, coastal dunes). Twenty-six of 32 specimens of the *S. glutinosa* a priori group (82%) were assigned a posteriori into the *S. glutinosa* group; 8 specimen with 91-99% probability, 2 specimens with 89% and 80% probabilities, 6 specimens with 70-75% probability, 6 species with 60-68% probability, and 2 specimens with 55% probability (37% to *S. simplex*; *Morton & Venn NA14135* TRT from Muncho Lake Prov. Park, British Columbia) and 53% probability (40% to *S. glutinosa*; *Semple & Heard 7747* WAT from Gunnison Co., Colorado; dwarf shoots 10-14 cm tall). Six specimens of the *S. glutinosa* a priori group plus 1 additional specimen included a posteriori were assigned to other species: 1 specimen to *S. spathulata* with 93% probability (*Zika 22787* WTU from Thurston Co., Washington; small shoots from rocky prairie, 70 m ele.); 3 specimens to *S. bellidifolia* with 67% probability (46% to *S. glutinosa*; *Russell 66-129* WAT from Pitkin Co., Colorado), 55% probability (40% to *S. glutinosa*; *Semple & B. Semple 11239* WAT from Summit Co., Colorado), and 54% probability (46% to *S. glutinosa*; *Morton NA2095* TRT from Mt. Fairplay, Alaska), and 3 specimens to *S. simplex* with 78% probability (21% to *S. glutinosa*; *Montague & Montague 35* WTU from Thurston Co., Washington; open prairie, 50 m ele.), 58% probability (42% to *S. glutinosa*; *Semple & B. Semple 6548* WAT from Boulder Co., Colorado), and 50% probability (53% to *S. glutinosa*; *Ringius 1978* WAT from Terrence Bay, Thunder Bay Dist., Ontario; 18 cm tall shoot). Eight of 10 specimens of the *S. simplex* a priori group (82%) plus 1 specimen included a posterior were assigned a posteriori to the *S. simplex* group: 5 specimens with 94-100% probability and 3 specimens with 83-89% probability. Two specimens of the *S. simplex* a priori group plus 1 specimen included a posteriori were assigned a posteriori to other species: 2 specimens to *S. glutinosa* with 68% probability (29% to *S. simplex*; *Pringle 10294* GH from Esdo. Hidalgo, Mexico) and 40% probability (31% to *S. simplex* and 29% to *S. bellidifolia*; *Hinton et al. 22298* TEX from Esdo. Nuevo Leon, Mexico); and 1 specimen to *S. bellidifolia* with 61% probability (29% to *S. glutinosa*; *Roe et al. 247* LL from Esdo. Hidalgo, Mexico).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 69 specimens of *Solidago bellidifolia*, *S. glutinosa*, *S. simplex*, and *S. spathulata* are presented in Fig. 27. Eigenvalues on the first two axes were 3.354 and 0.919.

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

Group	<i>bellidifolia</i>	<i>glutinosa</i>	<i>simplex</i>	<i>spathulata</i>	% correct
<i>bellidifolia</i>	13	0	0	0	100
<i>glutinosa</i>	3	26	2	1	81
<i>simplex</i>	1	2	8	0	73
<i>spathulata</i>	2	0	0	9	82
Totals	19	28	10	10	84

Jackknifed classification matrix

Group	<i>bellidifolia</i>	<i>glutinosa</i>	<i>simplex</i>	<i>spathulata</i>	% correct
<i>bellidifolia</i>	12	1	0	0	92
<i>glutinosa</i>	4	25	2	1	78
<i>simplex</i>	1	2	8	0	73
<i>spathulata</i>	2	0	0	9	82
Totals	19	28	10	10	81

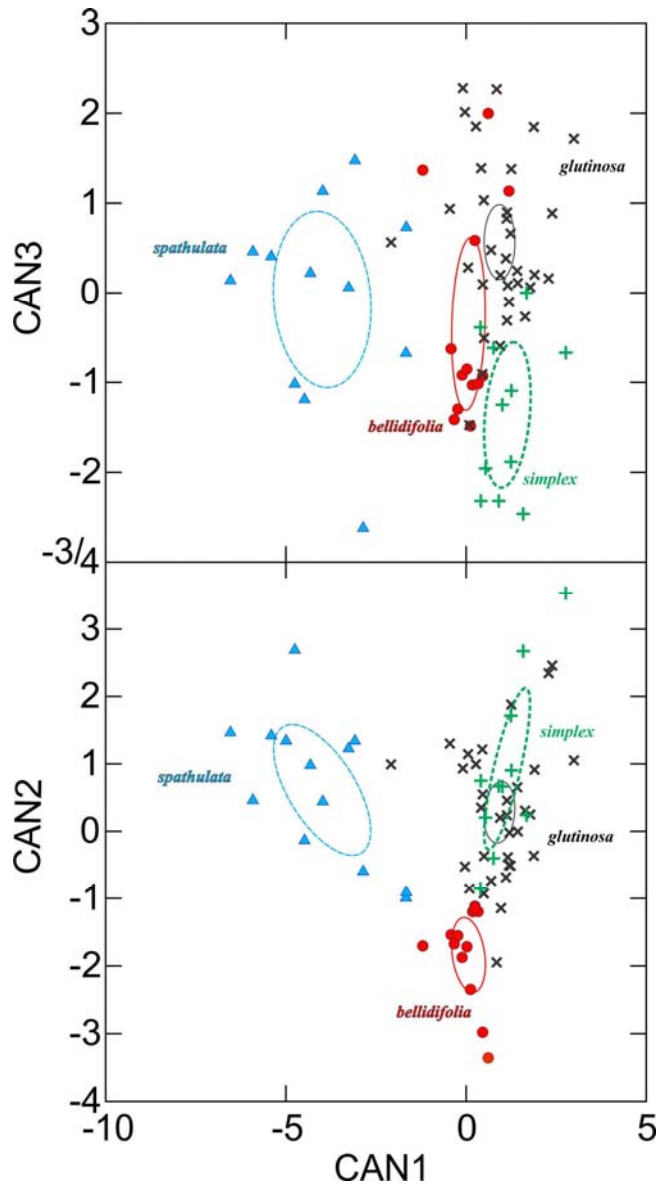


Figure 27. Plot of canonical scores (CAN1 vs CAN2) analysis for 69 specimens of *Solidago* subsect. *Humiles*: *S. bellidifolia* (red dots), *S. glutinosa* (black ×s), *S. simplex* (green +s), and *S. spathulata* (blue triangles).

Two species level a priori groups analysis: *Solidago bellidifolia* and *S. glutinosa*

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 serrations. Most floral traits were not highly correlated. Involucre height correlated with mid series phyllary length; the latter was excluded from the analysis. Ray floret fruit body and pappus lengths correlated with disc floret fruit body length and disc floret corolla length, respectively; the disc floret traits were included in the analysis.

In the STEPWISE discriminant analysis of 45 specimens of two species level a priori groups (*S. bellidifolia* and *S. glutinosa*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid leaf length (40.61), ray floret lamina width (9.82), and involucre height (6.22). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. *Solidago bellidifolia* and *S. glutinosa* had an F-to separate value of 19.607 (Wilks' lambda = 0.4107 df = 3 1 43; Approx. F= 19.6066 df = 3 41 prob = 0.0000).

In the Classificatory Discriminant Analysis of 45 specimens of the two species level a priori groups (*S. bellidifolia* and *S. glutinosa*), percents of correct a posteriori assignment to the same a priori group were 100% and 87%. The Classification matrix and Jackknife classification matrix are presented in Table 8. All 14 specimens of the *S. bellidifolia* a priori group (100%) were assigned a posteriori into the *S. bellidifolia* group; 10 specimens with 90-100% probability, 3 specimens with 83-89% probability, and 1 specimen with 76% probability. Twenty-seven of 31 specimens of the *S. glutinosa* a priori group (93%) were assigned a posteriori into the *S. glutinosa* group; 20 specimens with 90-100% probability, 2 specimens with 88-89% probability, 2 specimens with 77% and 75% probabilities, and 2 specimens with 60% probability each. Four specimens of the *S. glutinosa* a priori group were assigned to *S. bellidifolia* with 56% probability (*Ringius 1976* WAT from Terrence Bay, Thunder Bay Dist., Ontario; 19 cm tall shoot), 56% probability (*Semple & Xiang 102011* WAT from Johnston Co., Wyoming; small shoot 25 cm tall), 54% probability (*83 Semple & Heard 7747* WAT from Gunnison Co., Colorado; dwarf shoots 10-14 cm tall) and 51% probability (*Semple & Heard 7827* WAT from Beaver co., Utah; dwarf shoots 15-17 cm tall).

Frequencies of CAN1 canonical scores for 45 specimens of *S. bellidifolia* and *S. glutinosa* are presented in histograms in Fig. 28. The Eigenvalue on the first axis was 1.435.

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two a priori groups (*S. glutinosa* and *S. glutinosa*); a posteriori placement to groups in rows.

Group	<i>bellidifolia</i>	<i>glutinosa</i>	% correct
<i>bellidifolia</i>	14	0	100
<i>glutinosa</i>	4	27	87
Totals	18	27	91

Jackknifed classification matrix

Group	<i>bellidifolia</i>	<i>glutinosa</i>	% correct
<i>bellidifolia</i>	14	0	100
<i>glutinosa</i>	4	27	87
Totals	18	27	91

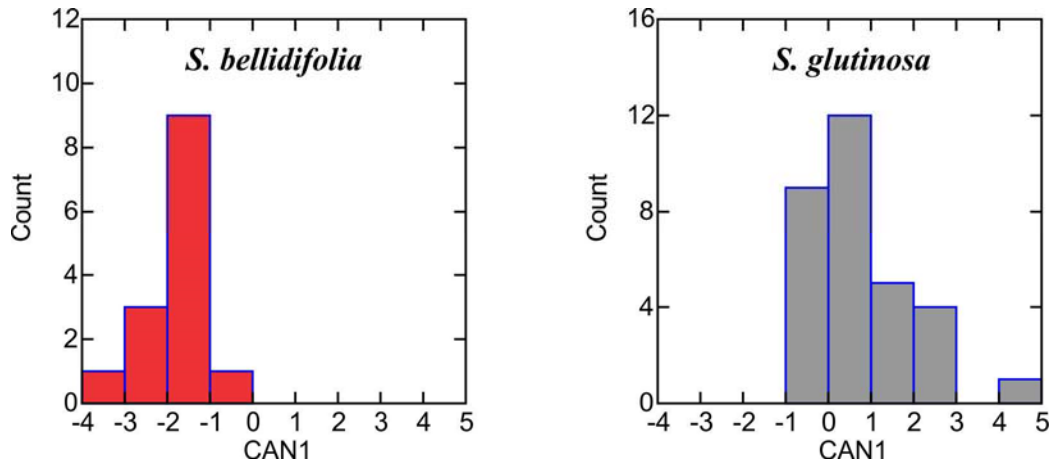


Figure 28. Histograms of CAN1 canonical scores for 45 specimens of *S. bellidifolia* (left) and *S. glutinosa* (right).

Two species level a priori groups analysis: Solidago glutinosa and S. simplex

The Pearson correlation matrix yielded $r > |0.7|$ for multiple pairs of leaf traits and floral traits. The following traits were included in the analysis: mid stem leaf length and numbers of margin serrations, upper stem leaf width and number of margin serrations, number of peduncle bracts, involucre height, mid series phyllary width, number of ray florets, ray floret lamina length and width, and number of disc florets, disc floret lobe, ovary/fruit body, and pappus lengths.

In the STEPWISE discriminant analysis of 44 specimens of two species level a priori groups (*S. glutinosa* and *S. simplex*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (29.71), number of ray florets (22.91), and upper stem leaf width (7.23), Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.0000$ that the null hypothesis was true. *Solidago glutinosa* and *S. simplex* had an F-to separate value of 16.245 (Wilks' lambda = 0.451 df = 14 1 42; Approx. F= 16.245 df = 4 40 prob = 0.0000).

In the Classificatory Discriminant Analysis of 44 specimens of the two species level a priori groups (*S. glutinosa* and *S. simplex*), percents of correct a posteriori assignment to the same a priori group were 97% and 91% respectively. The Classification matrix and Jackknife classification matrix are presented in Table 9. Thirty-two of the 33 specimens of the *S. glutinosa* a priori group (97%) were assigned a posteriori into the *S. glutinosa* group; 21 specimens with 90-100% probability, 3 specimens with 83-89% probability, 3 specimens with 73-77% probability, 1 specimen with 66% probability, and 4 specimens with 59% probability (*Semple & B. Semple 6548* WAT from Boulder Co., Colorado), 57% probability (*Semple & B Semple 5511* WAT from Mineral Co., Colorado), 53% probability (*Russell 66-129* WAT from Pitkin Co., Colorado), and 53% probability (*Hammond 10804* DES from San Pedro Martir Mts., Baha California, Mexico). One specimen of the *S. glutinosa* a priori group was assigned a posteriori to *S. simplex* with 77% probability (*Montague & Montague 35* WTU from Thurston Co., Washington). Ten of the 11 specimens of the *S. simplex* a priori group (91%) were assigned a posteriori into *S. simplex*: 7 specimens with 90-100% probability, 1 specimen with 87% probability, 1 specimen with 74% probability, and 1 specimen with 56% probability (*Hinton et al. 22298* TEX Esdo. Nuevo Leon, Mexico). One specimen of the *S. simplex* a priori group was assigned to *S. glutinosa* with 94% probability (*Roe et al. 247* LL from Esdo. Hidalgo, Mexico).

Table 9. 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	<i>glutinosa</i>	<i>simplex</i>	% correct
<i>glutinosa</i>	32	1	97
<i>simplex</i>	1	10	91
Totals	33	11	95

Jackknifed classification matrix			
Group	<i>glutinosa</i>	<i>simplex</i>	% correct
<i>glutinosa</i>	30	3	91
<i>simplex</i>	1	10	91
Totals	31	13	91

Frequencies of CAN1 canonical scores for 48 specimens of *S. glutinosa* and *S. simplex* are presented in histograms in Fig. 29. The Eigenvalue on the first axis was 1.564.

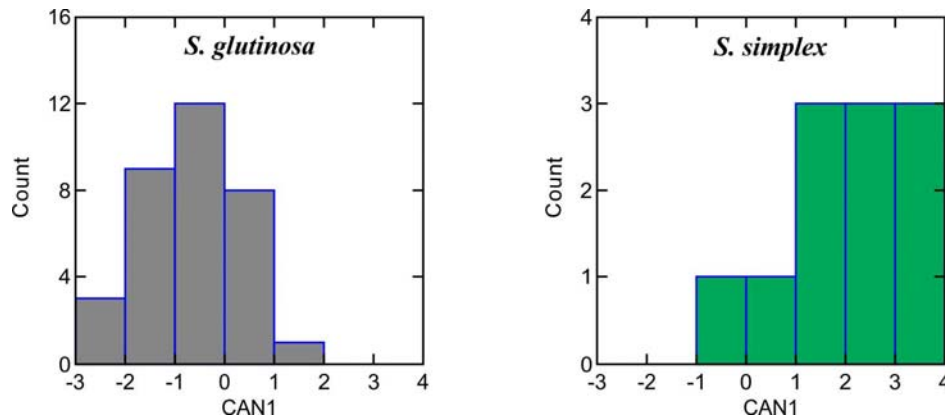


Figure 29. Histograms of CAN1 canonical scores for 44 specimens of *S. glutinosa* (left) and *S. simplex* (right).

Six northeastern species level a priori groups analysis 1

The Pearson correlation matrix yielded $r > |0.7|$ for multiple pairs of leaf traits reducing the number to be used to lower stem leaf length and number of margin serrations, mid stem leaf width, and upper stem leaf length. Involucre height correlated with mid series phyllary length and disc floret corolla length; the first trait was included in the analysis. Ray floret ovary/fruit traits correlated with disc floret ovary/fruit traits; ray floret pappus length and disc floret ovary/fruit body length were included in the analysis.

In the STEPWISE discriminant analysis of 94 specimens of six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*), the following eight traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: stem height (17.25), upper stem leaf length (12.93), mid series phyllary width (10.20), ray floret pappus length at anthesis (8.06), involucre height (7.76), mid stem leaf width (4.98), number of ray florets (4.66), and disc floret ovary/fruit body length (4.45). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had

probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 10. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. chlorolepis* and *S. glutinosa* (22.481); the smallest separation was between *S. chlorolepis* and *S. randii* (4.049).

Table 10. Between groups F-matrix for the six a priori groups of northeastern taxa (df = 8 81).

Group	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>ontarioensis</i>	<i>racemosa</i>
<i>gillmanii</i>	16.553				
<i>glutinosa</i>	11.538	22.481			
<i>ontarioensis</i>	7.556	10.516	5.696		
<i>racemosa</i>	11.319	12.082	14.537	5.058	
<i>randii</i>	4.049	19.478	6.340	8.406	11.382

Wilks' lambda = 0.0362 df = 8 5 88; Approx. F = 10.1288 df = 40 355 prob = 0.0000

In the Classificatory Discriminant Analysis of 94 specimens of the six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa*, and *S. randii*) plus 4 additional specimens included a posteriori, were assigned a posteriori to the same a priori group with percents correct of 75-100%. The Classification matrix and Jackknife classification matrix are presented in Table 11. All 11 of the specimens of the *S. chlorolepis* a priori group (100%) assigned a posteriori into the *S. chlorolepis* group; 6 specimens with 92-100% probability, 3 specimens with 87-89% probability, and 2 specimens with 56% probability (*Ringius 1691* WAT from Mt. Albert, Gaspé, Québec) and 50% probability (*Dignard & Gagnon 98-69* QUE from a peak WSE of Mt. Albert). Thirteen of the 14 specimens of the *S. randii* a priori group (93%) were assigned a posteriori to the *S. randii* group; 5 specimens with 95-100% probability, 2 specimens with 89% probability, 3 specimens with 60-66% probability, and 3 specimens with 51% probability and 42% probability (*Ringius 1759* WAT and *Ringius 1760b* WAT from Cadillac Mt. on Mount Desert Is., Maine), and 37% probability (*Ringius 1807a* WAT from Thetford Mines, Québec). One specimen of the *S. randii* a priori group plus 1 additional specimen included a posteriori were assigned a posteriori to *S. glutinosa* with 93% probability (*Beaudry 58-246* NY from Smuggler's Notch, Lamoille Co., Vermont) and 43% probability (*Ferguson & Attley s.n.* NY from Bald Mt., Fulton Chain, Herkimer Co., New York). Nine of the 10 specimens of *S. gillmanii* a priori group (90%) were assigned a posteriori to the *S. gillmanii* group with 98-100% probability. One specimen of the *S. gillmanii* a priori group was assigned to *S. chlorolepis* with 55% probability (35% to *S. gillmanii*; *Ringius 1851* WAT from Door Co., Wisconsin). Nine of the 11 specimens of the *S. ontarioensis* a priori group (82%) plus 1 additional specimen included a posteriori were assigned a posteriori to the *S. ontarioensis* group; 4 specimens with 92-100% probability, 2 specimens with 78% and 76% probabilities, 1 specimen with 61% probability, and 2 specimens with 57% probability (*Semple & Brammall 2787* WAT from Tobermory, Bruce Co., Ontario) and 53% probability (*Semple & Brammall 2788* WAT from E of Tobermory, Bruce Co., Ontario). Two specimens of the *S. ontarioensis* a priori group were assigned a posteriori to other species: 1 specimen to *S. glutinosa* with 69% probability (*Morton NA3691* TRT from Tobermory, Bruce Co., Ontario) and 1 specimen to *S. randii* with 65% probability (*Morton & Venn NA7620* TRT from Flower Pot Is., Bruce Co., Ontario). Twenty-six of the 32 specimens of the *S. glutinosa* a priori group (81%) were assigned a posteriori to the *S. glutinosa* group; 14 specimens with 91-99% probability, 2 specimens with 85% and 81% probability, 3 specimens with 72-78% probability, 4 specimens with 61-68% probability, and 2 specimens with 49% probability (48% to *S. simplex*; *Semple & B. Semple 6556* WAT from Summit Co., Colorado) and 46% probability (*Semple & Brouillet 4283* WAT from W of Mannville, Alberta). Six specimens of the *S. glutinosa* a priori

group plus 2 additional specimens included a posteriori were assigned a posteriori to other species: 3 specimens to *S. randii* with 91% probability (*Semple & Semple 11239* WAT from 10,400' ele., Summit Co., Colorado), 78% probability (*Morton NA1854* TRT from Bordon, Saskatchewan), 48% probability (47% to *S. glutinosa*; *Peirson 647* WAT from Otsego Co., Michigan; involucre were on average 3.5 mm high; Peirson et al. 2012 reported the population to be diploid), and 37% probability (33% to *S. glutinosa*; *Peirson 466* WAT from Presque Isle Co., Michigan; 63 cm tall shoot); 2 specimens to *S. ontarioensis* with 70% probability (22% to *S. glutinosa*; *Ringius 1976* WAT from Terrence Bay, Thunder Bay Dist., Ontario; 19 cm tall shoot) and 52% probability (29% to *S. glutinosa*; *Hammond 10804* DES from San Pedro Martir Mts., Baha California, Mexico); 1 specimen to *S. racemosa* with 94% probability (*Pavlick 80-431* V from 51° 55' N 122° 20' W, British Columbia; Fig. 7; robust plant); and 1 specimen to *S. chlorolepis* with 55% probability (31% to *S. simplex* and 12% to *S. glutinosa*; *Russell 66-129* WAT from 11000' ele, Independence Pass, Colorado; dwarf shoots 7-11 cm tall). Twelve of the 16 specimens of the *S. racemosa* a priori group (75%) plus 1 additional specimen included a posteriori were assigned a posteriori to the *S. racemosa* group; 10 specimens with 95-100% probability, 2 specimens with 63% probability and 62% probability, and 1 specimen with 52% probability (32% to *S. randii*; *Semple & Keir 4621* WAT from Franklin Co., Maine). Four specimens of the *S. racemosa* a priori group were assigned a posteriori to other species: 3 specimens to *S. ontarioensis* with 86% probability (*Labrecque s.n.* MT from Percé, Gaspésie, Québec), 77% probability (*Morton NA4142* TRT from Percé Mt., Gaspésie, Québec), and 70% probability (*Semple & Ringius 7612* WAT from York Co., Pennsylvania); and 1 specimen to *S. randii* with 31% probability (22% to *S. ontarioensis*, 19% to *S. racemosa*, 18% to *S. chlorolepis*, and 10% to *S. glutinosa*; *Dignard et al. 08-95* QUE from Île-d'Anticosti, Québec).

Table 11. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six species level a priori groups; a posteriori placements to groups in rows.

Group	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>ontarioensis</i>	<i>racemosa</i>	<i>randii</i>	% correct
<i>chlorolepis</i>	11	0	0	0	0	0	100
<i>gillmanii</i>	1	9	0	0	0	0	90
<i>glutinosa</i>	1	0	26	1	1	3	81
<i>ontarioensis</i>	0	0	1	9	0	1	82
<i>racemosa</i>	0	0	0	3	12	1	75
<i>randii</i>	0	0	1	0	0	13	93
Totals	13	9	28	13	13	18	85

Jackknifed classification matrix

Group	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>ontarioensis</i>	<i>racemosa</i>	<i>randii</i>	% correct
<i>chlorolepis</i>	10	0	0	0	0	1	91
<i>gillmanii</i>	1	9	0	0	0	0	90
<i>glutinosa</i>	1	0	23	2	1	4	72
<i>ontarioensis</i>	1	1	3	4	1	1	36
<i>racemosa</i>	0	1	0	3	10	2	63
<i>randii</i>	1	0	3	0	0	6	71
Totals	14	11	29	9	12	14	70

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 97 specimens of *Solidago chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa*, and *S. randii* are presented in Fig. 30. Eigenvalues on the first three axes were 2.699, 1.293, and 0.961.

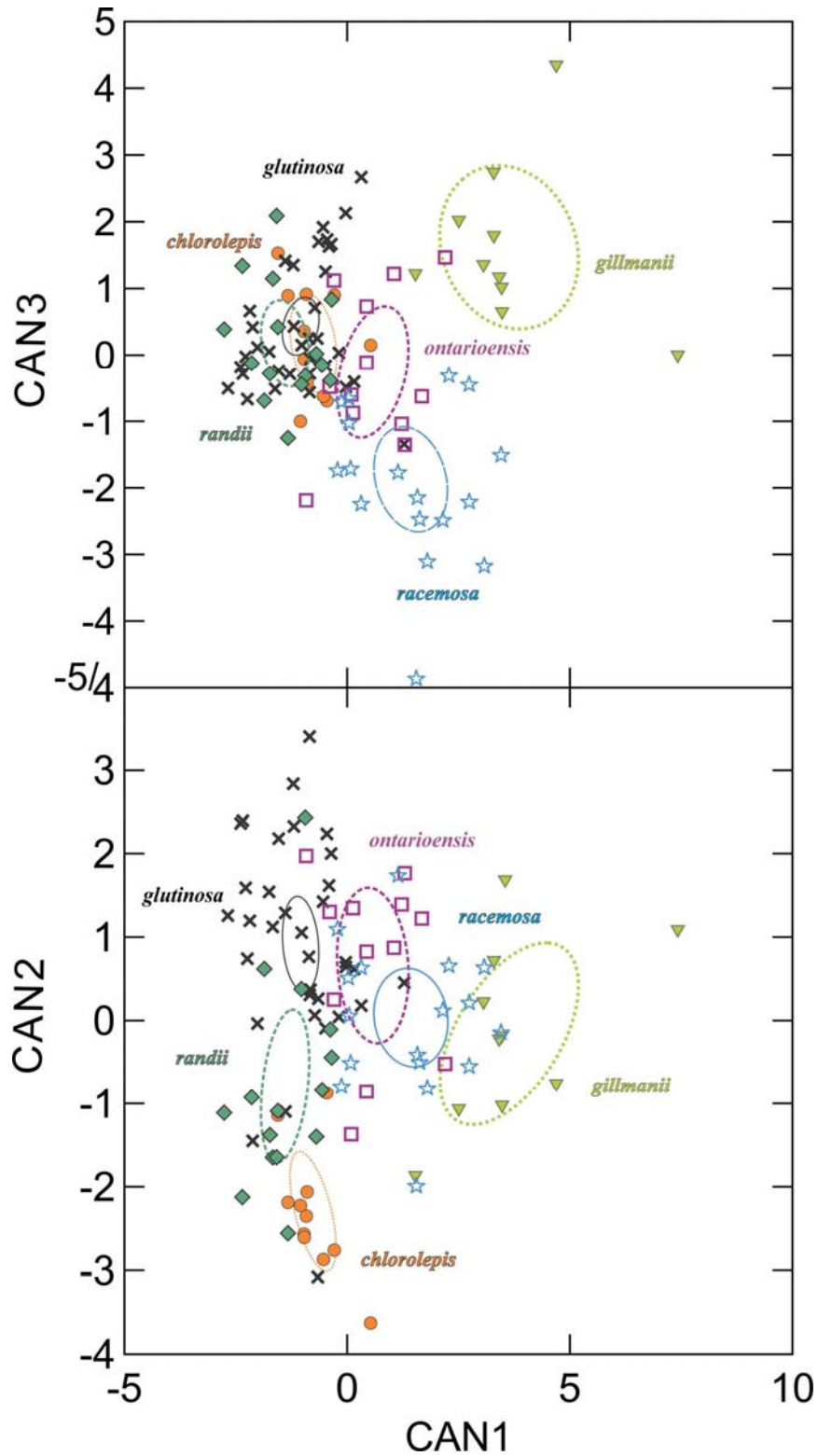


Figure 30. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) from the STEPWISE analysis of 94 specimens plus 3 additional ones a posteriori northeastern species of *Solidago* subsect. *Humiles*: *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black ×s), *S. ontarioensis* (magenta squares), *S. racemosa* (open blue stars), and *S. randii* (green diamonds).

Six northeastern species level a priori groups analysis 2

In order to determine how a large number of traits could be utilized to separate the six northeastern species into groups, a COMPLETE analysis was run using the following 21 traits ignoring the amount of correlation between traits: stem height, lower stem leaf length, width, and number of margin serrations, mid stem leaf length, width, and number of margin serrations, upper stem leaf length, width, and number of margin serrations, number of peduncle bracts, involucre height, mid series phyllary length, number of ray florets, ray floret lamina length and width, number of disc florets, disc corolla length and lobe length, disc floret ovary/immature fruit body length, and disc floret pappus length at anthesis.

In the COMPLETE discriminant analysis of 94 specimens of six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*), the following 8 traits had the highest F-to-removes values and are listed in order of decreasing F-to-remove values: stem height (9.65), disc floret pappus length at anthesis (4.82), involucre height (3.91), number of ray florets (3.91), number of peduncle bracts (3.43), number of upper stem leaf margin serrations (3.17), mid stem leaf width (2.92), and lower stem leaf width (2.80). 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 12. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. chlorolepis* and *S. ontarioensis* (6.919); the smallest separation was between *S. chlorolepis* and *S. randii* (2.278).

Table 12. Between groups F-matrix for the six a priori groups of northeastern taxa (df = 21 68).

Group	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>ontarioensis</i>	<i>racemosa</i>
<i>gillmanii</i>	5.897				
<i>glutinosa</i>	6.343	5.897			
<i>ontarioensis</i>	6.919	4.220	3.989		
<i>racemosa</i>	5.715	3.193	6.043	3.789	
<i>randii</i>	2.278	5.833	4.366	5.982	5.381

Wilks' lambda = 0.0124 df = 21 5 88; Approx. F = 4.6669 df = 105 337 prob = 0.0000

In the Classificatory Discriminant Analysis of 94 specimens of the six species level a priori groups (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*), percents of correct a posteriori assignment to the same a priori group were 75-100%. The Classification matrix and Jackknife classification matrix are presented in Table 13. All 11 specimens of the *S. chlorolepis* a priori group (100%) were assigned a posteriori into the *S. chlorolepis* group; 9 specimens with 97-100% probability and 1 specimen with 78% probability. All 10 of the *S. gillmanii* a priori group were assigned a posteriori to the *S. gillmanii* group: 8 specimens with 93-100% probability, 1 specimen with 89% probability, and 1 specimen with 71% probability. Ten of the 11 specimens of the *S. ontarioensis* a priori group (83%) were assigned a posteriori to *S. ontarioensis* with 91-100% probability. One specimen of the *S. ontarioensis* a priori group was assigned a posteriori to *S. glutinosa* with 69% probability (*Morton NA3691* TRT from Tobermory, Ontario; 21 cm tall shoot with small narrow inflorescence). Twenty-eight of the 32 specimens of the *S. glutinosa* a priori group (88%) were assigned a posteriori to *S. glutinosa*; 21 specimens with 90-100% probability, 3 specimens with 88-89% probability, 1 specimen with 77% probability, 1 specimen with 68% probability, 1 specimen with 52% (47% to *S. randii*; *Peirson 647* WAT from Otsego Co., Michigan), and 1 specimen with 40% probability (*Ringius 1976* WAT from Terrence Bay, Thunder Bay Dist., Ontario). Four specimens of the *S. glutinosa* a priori group were assigned a posteriori to other species:

3 specimens to *S. randii* with 93% probability (*Semple et al.* 9368 WAT from McKinley Co., NM), 76% probability (*Peirson* 466 WAT from Presque Isle Co., Michigan; 63 cm tall shoot), and 54% probability (40% to *S. chlorolepis*; *Semple & Semple* 11239 WAT from Summit Co., Colorado); and 1 specimen to *S. racemosa* with 58% probability (42% to *S. glutinosa*; *Pavlick* 80-431 V from 51° 55' N 122° 20' W, British Columbia; Fig. 7; robust plant). Twelve of the 13 specimens of the *S. randii* a priori group were assigned to the *S. randii* group: 9 specimens with 90-100% probability, 1 specimen with 76% probability, 1 specimen with 65% probability, and 1 specimen with 49% probability (49% to *S. chlorolepis*; *Ringius* 1760A WAT from Cadillac Mt., Mt. Desert Is., Maine). One specimen of the *S. randii* a priori group was assigned a posteriori to *S. glutinosa* with 83% probability (*Ringius* 1754 WAT from Cadillac Mt., Mt. Desert Is., Maine). Thirteen of the 16 specimens of the *S. racemosa* a priori group (81%) were assigned a posteriori to *S. racemosa*: 12 specimens with 90-100% probability and 1 specimen with 69% probability. Three specimens of the *S. racemosa* a priori group was assigned a posteriori to other species: 2 specimens to *S. ontarioensis* with 86% probability (*Morton* NA4142 TRT from Percé Mt., Gaspésie, Québec) and 50% probability (*Dignard et al.* 08-95 QUE from Île-d'Anticosti, Québec; this specimen has the lower stem leaves typical of *S. racemosa*), and 1 specimen to *S. chlorolepis* with 46% probability (39% to *S. racemosa*; *LaBreque* s.n. MT from Mt. Blanc, Percé, Gaspésie, Québec).

Table 13. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of six species level a priori groups using 20 traits; a posteriori placements to groups in rows.

Group	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>ontarioensis</i>	<i>racemosa</i>	<i>randii</i>	% correct
<i>chlorolepis</i>	11	0	0	0	0	0	100
<i>gillmanii</i>	0	10	0	0	0	0	100
<i>glutinosa</i>	0	0	28	3	1	3	88
<i>ontarioensis</i>	0	1	1	10	0	0	91
<i>racemosa</i>	1	0	0	2	13	0	81
<i>randii</i>	0	0	3	0	0	12	86
Totals	12	10	31	12	14	15	89

Jackknifed classification matrix

Group	<i>chlorolepis</i>	<i>gillmanii</i>	<i>glutinosa</i>	<i>ontarioensis</i>	<i>racemosa</i>	<i>randii</i>	% correct
<i>chlorolepis</i>	10	0	0	0	0	1	91
<i>gillmanii</i>	1	6	0	0	2	1	60
<i>glutinosa</i>	1	2	19	3	2	5	59
<i>ontarioensis</i>	0	0	3	6	1	1	55
<i>racemosa</i>	1	0	1	2	12	0	75
<i>randii</i>	2	0	3	0	0	9	64
Totals	15	8	26	11	17	17	66

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 94 specimens of *Solidago chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa*, and *S. randii* are presented in Fig. 31. Eigenvalues on the first three axes were 3.099, 2.200, and 1.040.

Two species level a priori groups analysis: *Solidago glutinosa* and *S. ontarioensis*

The Pearson correlation matrix yielded $r > |0.7|$ for multiple pairs of leaf traits and floral traits. The following traits were included in the analysis: mid stem leaf length, width and number of margin serrations, upper stem leaf number of margin serrations, involucre height, mid series phyllary width, number of ray florets, ray floret lamina width, number of disc florets, disc floret corolla, lobes, ovary/fruit body, and pappus lengths.

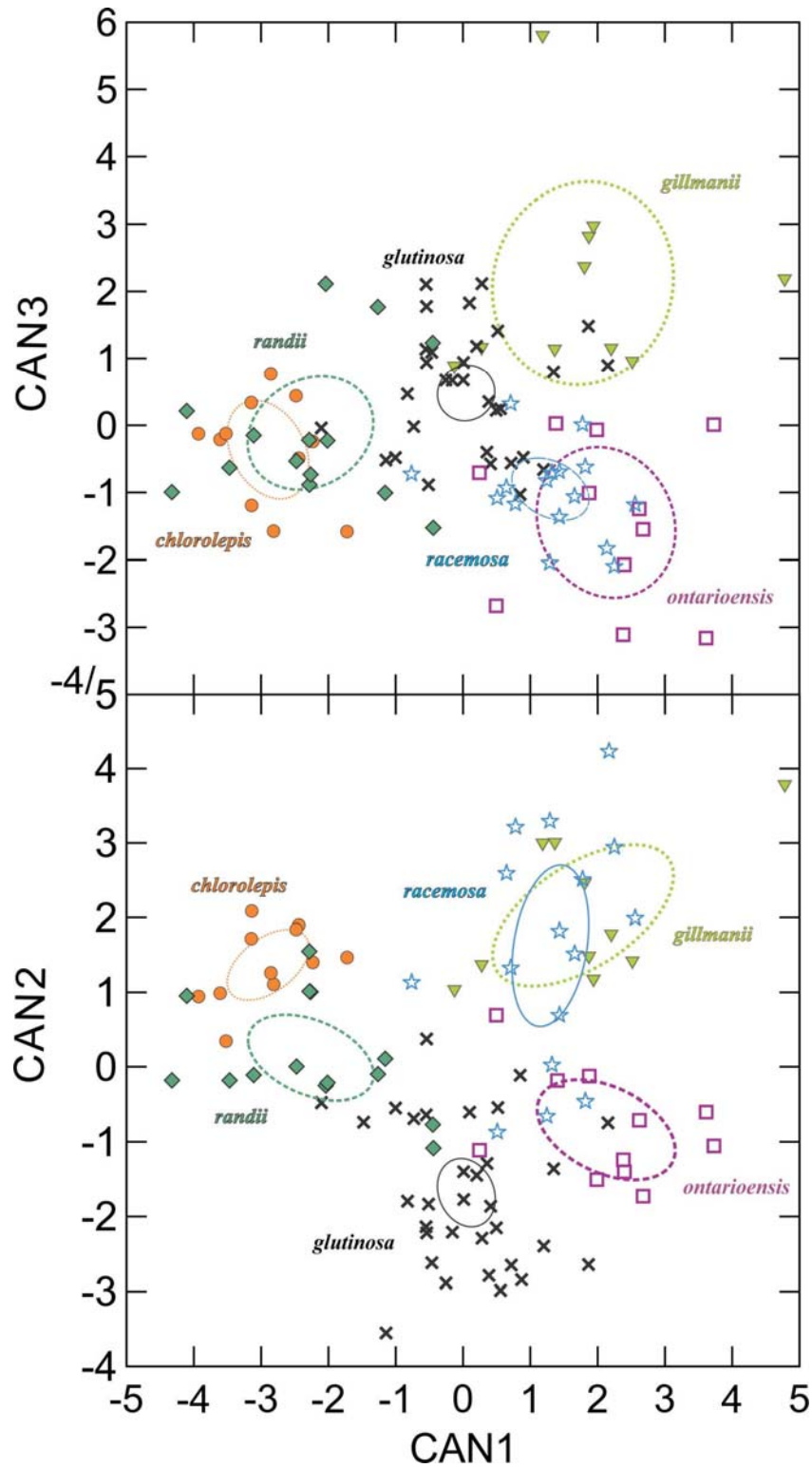


Figure 31. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 94 specimens of northeastern species of *Solidago* subsect. *Humiles* using 21 traits in a COMPLETE analysis: *S. chlorolepis* (orange dots), *S. gillmanii* (inverted green triangles), *S. glutinosa* (black ×s), *S. ontarioensis* (magenta squares), *S. racemosa* (open blue stars), and *S. randii* (green diamonds).

In the STEPWISE discriminant analysis of 47 specimens of two species level a priori groups (*S. glutinosa* and *S. ontarioensis*), the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: involucre height (27.53), disc floret ovary/fruit body (23.47), number of disc florets (12.90), and mid stem leaf width (4.11). 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 glutinosa* and *S. ontarioensis* had an F-to separate value of 16.419 (Wilks' lambda = 0.3901 df = 1 1 45; Approx. F= 16.4193 df = 4 42 prob = 0.0000).

In the Classificatory Discriminant Analysis of 47 specimens of the two species level a priori groups (*S. glutinosa* and *S. ontarioensis*) plus 1 additional specimen included a posteriori, percents of correct a posteriori assignment to the same a priori group were 92% and 91% respectively. The Classification matrix and Jackknife classification matrix are presented in Table 14. Thirty-three of the 36 specimens of the *S. glutinosa* a priori group (92%) were assigned a posteriori into the *S. glutinosa* group; 29 specimens with 91-100% probability, 3 specimens with 83-85% probably, and 1 specimen with 70% probability. Three specimens of the *S. glutinosa* a priori group were assigned a posteriori to *S. ontarioensis* with 98% probability (*Pavlick 80-431 V* from 51° 55' N 122° 20' W, British Columbia; Fig. 7; robust plant), 76% probability (*Ringius 1976 WAT* from Terrence Bay, Thunder Bay Dist., Ontario; 29 cm tall shoot) and 55% probability (*Morton & Venn NA14175 TRT* from Lavoy, Alberta). Ten of 11 specimens of the *S. ontarioensis* a priori group (91%) plus 1 additional specimen were assigned a posteriori into *S. ontarioensis*: 9 specimens with 95-100% probability, 1 specimen with 81% probability, and 1 specimen with 77%. One specimen of the *S. ontarioensis* a priori group was assigned to *S. glutinosa* with 61% probability (*Morton & Venn NA7620 TRT* from Flower Pot Is., Bruce Co., Ontario).

Frequencies of CAN1 canonical scores for 48 specimens of *S. glutinosa* and *S. ontarioensis* are presented in histograms in Fig. 32. The Eigenvalue on the first axis was 1.564.

Table 14. 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	<i>glutinosa</i>	<i>ontarioensis</i>	% correct
<i>glutinosa</i>	33	3	92
<i>ontarioensis</i>	1	10	100
Totals	34	12	91

Jackknifed classification matrix

Group	<i>glutinosa</i>	<i>ontarioensis</i>	% correct
<i>glutinosa</i>	32	4	89
<i>ontarioensis</i>	0	10	91
Totals	33	14	89

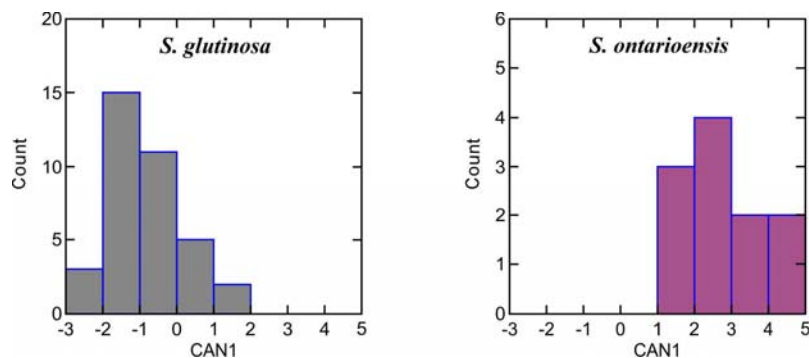


Figure 32. Histograms of CAN1 canonical scores for 48 specimens of *S. glutinosa* (left) and *S. ontarioensis* (right).

Two species level a priori groups analysis: *Solidago racemosa* and *S. randii*

The Pearson correlation matrix yielded $r > |0.7|$ for multiple pairs of leaf traits reducing the number to be used to mid stem leaf length and width and upper stem leaf length. Involucre height correlated with mid series phyllary length, ray floret pappus length and disc floret corolla and pappus lengths; involucre height was included in the analysis. Ray floret fruit body and pappus lengths correlated with disc floret fruit body length and disc floret corolla length, respectively; only disc floret ovary/fruit body length was included in the analysis.

In the STEPWISE discriminant analysis of 32 specimens of two species level a priori groups (*S. racemosa* and *S. randii*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc corolla lobe length (26.73), number of peduncle bracts (12.20), and upper stem leaf length (5.64). 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 racemosa* and *S. randii* had an F-to separate value of 20.710 (Wilks' lambda = 0.3107 df = 3 1 30; Approx. F= 20.7098 df = 3 28 prob = 0.0000).

In the Classificatory Discriminant Analysis of 32 specimens of the two species level a priori groups (*S. racemosa* and *S. randii*), percents of correct a posteriori assignment to the same a priori group were 94% and 87%, respectively. The Classification matrix and Jackknife classification matrix are presented in Table 15. Sixteen of the 17 specimens of the *S. racemosa* a priori group (94%) plus 1 additional specimen included a posteriori were assigned a posteriori into the *S. racemosa* group; 13 specimens with 90-100% probability and 3 specimens with 83-87% probability. One specimen of the *S. racemosa* a priori group plus 1 additional specimen included a posteriori were assigned a posteriori to *S. randii* with 66% probability (*Semple & Ringius* 7612g WAT from York Co., Pennsylvania; a 6.5 cm tall dwarf plant with small leaves; 3 other specimens from the same population was placed into *S. racemosa* with 97-100% probability) and 57% probability (*Peirson* 598 WAT from Barbour Co., West Virginia). Thirteen of 15 specimens of the *S. randii* a priori group (87%) were assigned a posteriori into the *S. randii* group; 11 specimens with 96-100% probability and 1 specimen with 74% probability. Two specimens of the *S. randii* a priori group were assigned to *S. racemosa* with 82% probability (*Beaudry* 58-2 NY from Smuggler's Notch, Lamoille Co., Vt.; lower stem leaves are broadly lanceolate/winged petiolate and like other specimens of *S. randii*), and 58% probability (*Ringius* 1760 WAT from summit of Cadillac Mt., Hancock Co., Maine; a similar shoot of the same collection was placed into *S. randii* with 98% probability).

Frequencies of CAN1 canonical scores for 34 specimens of *S. racemosa* and *S. randii* are presented in histograms in Fig. 33. The Eigenvalue on the first axis was 2.219.

Table 15. 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	<i>racemosa</i>	<i>randii</i>	% correct
<i>racemosa</i>	16	1	94
<i>ontarioensis</i>	2	13	87
Totals	18	14	91

Jackknifed classification matrix			
Group	<i>racemosa</i>	<i>randii</i>	% correct
<i>racemosa</i>	16	2	94
<i>randii</i>	2	13	87
Totals	18	14	91

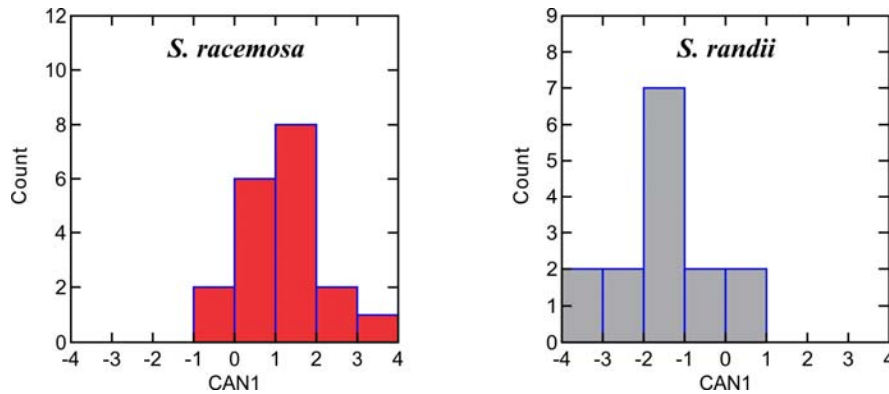


Figure 33. Histograms of CAN1 canonical scores for 34 specimens of *S. racemosa* (left) and *S. randii* (right).

Four southeastern species level a priori groups analysis

The Pearson correlation matrix yielded $r > |0.7|$ for multiple pairs of leaf traits and floral traits reducing the number that could be used. Mid stem leaf length, width, length from widest point to apex, and number of serrations were included in the analysis. Involucre height correlated highly with disc floret pappus length which correlated with mid series phyllary width; involucre height was included in the analysis. Ray floret ovary/fruit body length and ray floret pappus length correlated with disc floret ovary/fruit body length and disc floret pappus length respectively. Ray floret pappus length and disc floret ovary/fruit body length were included in the analysis.

Solidago racemosa was included for comparison because of reports that it is or might be present in Scott Co., Tennessee and northwestern Whitley Co., Kentucky in the range of *S. arenicola*. Specimens from these two counties can have glabrous cypselae like *S. arenicola* in some cases and sparsely strigose cypselae like *S. racemosa* in other cases.

In the STEPWISE discriminant analysis of 49 specimens of four species level a priori groups (*S. arenicola*, *S. kralii*, *S. plumosa*, and *S. racemosa*), the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid series phyllary width (10.57), involucre height (8.25), mid stem leaf width (7.28), number of peduncle bracts (6.00), and ray floret lamina length (5.59). Wilks’s lambda, Pillai’s trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. F-values based on Mahalanobis distances of the between group centroids are presented in Table 16. The largest separation (F value) was between *S. arenicola* and *S. plumosa* (19.315); the smallest separation was between *S. arenicola* and *S. kralii* (11.215).

Table 16. Between groups F-matrix for the twelve a priori groups in a COMPLETE analysis (df = 5 41).

Group	<i>arenicola</i>	<i>kralii</i>	<i>plumosa</i>
<i>kralii</i>	11.219		
<i>plumosa</i>	19.315	12.639	
<i>racemosa</i>	12.398	10.805	12.500

Wilks' lambda = 0.0616 df= 5 3 45; Approx. F= 13.1384 df= 15 113 prob= 0.0000

In the Classificatory Discriminant Analysis of 51 specimens of the four species level a priori groups (*S. arenicola*, *S. kralii*, *S. plumosa*, and *S. racemosa*) plus 1 additional specimen of *S. austrocaroliniana* and 2 additional specimens of other species included a posteriori, percents of correct a posteriori assignment to the same a priori groups were 70-100%. The Classification matrix and Jackknife classification matrix are presented in Table 17. All 17 specimens the *S. racemosa* a priori group (100%) plus 1 specimen included a posteriori were assigned a posteriori to the *S. racemosa* group; 11 specimens with 92-100% probability, 1 specimen with 89% probability, 3 specimens with 71-75% probability, and 2 specimens with 69% probability (18% to *S. kralii* and 8% to *S. arenicola*; Dignard et al. 08-95 MT from Île-d'Anticosti, Québec) and 63% probability (28% to *S. arenicola*; Pierson 603 MICH from Nicholas Co., West Virginia). All 10 specimens the *S. plumosa* a priori group (100%) were assigned a posteriori into the *S. plumosa* group; 9 specimens with 98-100% probability and 1 specimen with 69% probability. Eleven of 12 specimens of the *S. arenicola* a priori group (92%) were assigned a posteriori into the *S. arenicola* group; 8 specimens with 95-100% probability (including 1 specimen from Whitley Co., Kentucky and 2 from Scott Co., Tennessee), 2 specimens with 87% and 83% probabilities, and 1 specimen with 72% probability. One specimen of the *S. arenicola* a priori group was assigned a posteriori to *S. kralii* with 46% probability (27% to *S. racemosa* and 20% to *S. arenicola*; Bailey B150 WAT from Scott Co., Tennessee). Seven of 10 specimens of the *S. kralii* a priori group (70%) plus 1 additional specimen included a posteriori were assigned a posteriori into the *S. kralii* group; 7 specimens with 96-100% probability and 1 specimen with 67% probability. Three specimens of the *S. kralii* a priori group plus 1 additional specimen were assigned a posteriori to other species: 3 specimens to *S. racemosa* with 70% probability (20% to *S. arenicola* and 8% to *S. kralii*; Semple & B. Semple 11208 WAT from Pulaski Co., Georgia), 69% probability (39% to *S. kralii*; Semple & B. Semple 11218 WAT from Aiken Co., South Carolina), and 40% probability (21% to *S. plumosa*, 22% to *S. arenicola*, and 8% to *S. kralii*; S.B. Jones 15123 USF from Richmond Co., Georgia); 1 specimen was assigned to *S. plumosa* with 64% probability (20% to *S. racemosa* and 15% to *S. kralii*; Semple & B. Semple 11218 WAT from Aiken Co., South Carolina).

Table 17. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four southern species level a priori groups; a posteriori placements to groups in rows.

Group	<i>arenicola</i>	<i>kralii</i>	<i>plumosa</i>	<i>racemosa</i>	% correct
<i>arenicola</i>	11	1	0	0	92
<i>kralii</i>	0	7	1	2	70
<i>plumosa</i>	0	0	10	0	100
<i>racemosa</i>	0	0	0	17	100
Totals	11	8	11	19	92

Jackknifed classification matrix

Group	<i>arenicola</i>	<i>kralii</i>	<i>plumosa</i>	<i>racemosa</i>	% correct
<i>arenicola</i>	11	1	0	0	92
<i>kralii</i>	0	5	2	3	50
<i>plumosa</i>	0	0	10	0	100
<i>racemosa</i>	1	0	0	16	94
Totals	12	6	12	19	82

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 52 specimens of *Solidago austrocaroliniana*, *S. arenicola*, *S. kralii*, *S. plumosa*, and *S. racemosa* are presented in Fig. 34. Eigenvalues on the first three axes were 2.363, 1.312, and 1.087.

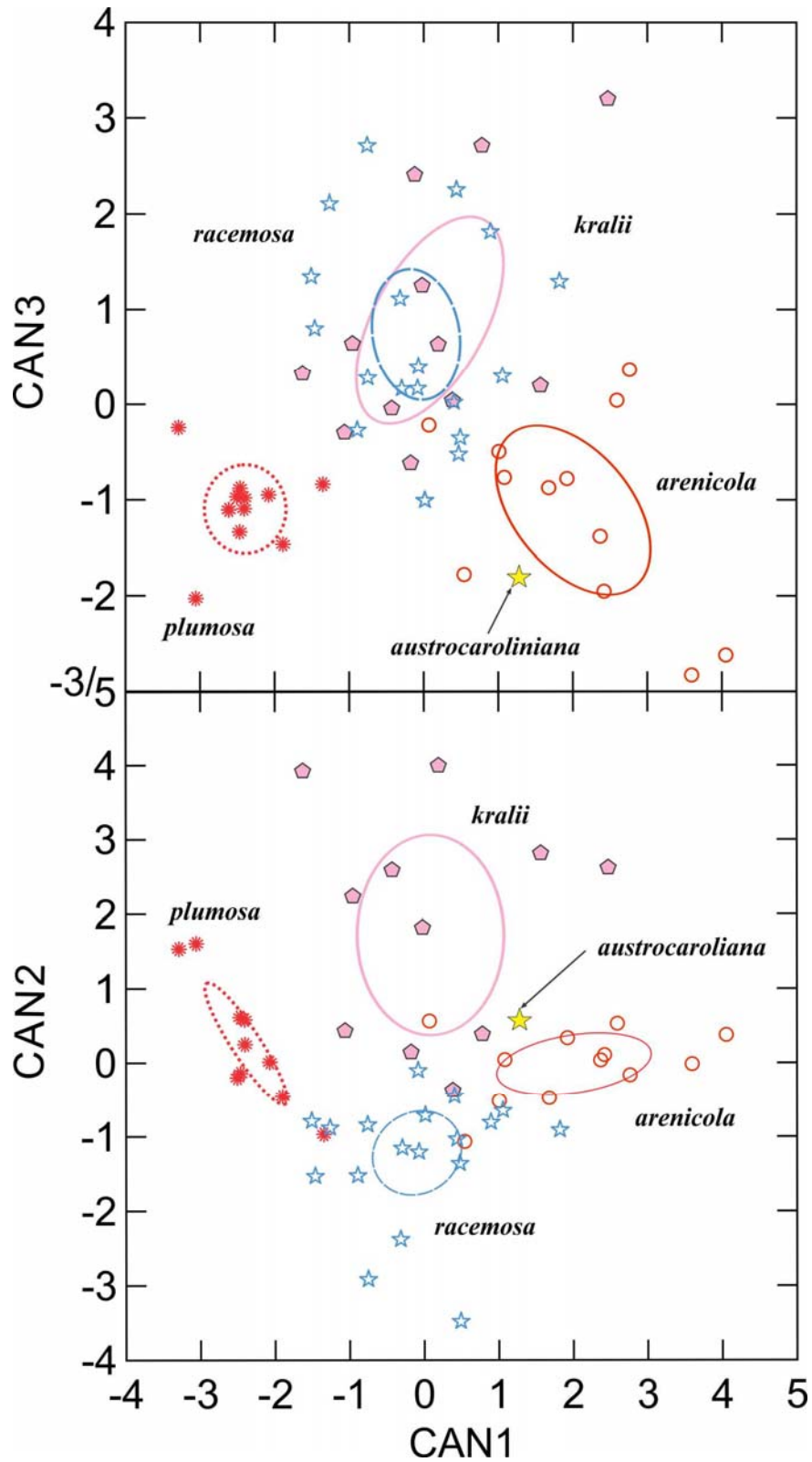


Figure 34. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) analysis for 52 specimens of *Solidago* subsect. *Humiles*: *S. austrocaroliniana* (yellow stars), *S. arenicola* (red circles), *S. kralii* (pink pentagons), *S. plumosa* (red star-bursts), and *S. racemosa* (open blue stars).

Two species level a priori groups analysis: *Solidago arenicola* and *S. racemosa*

The Pearson correlation matrix yielded $r > |0.7|$ for multiple pairs of leaf traits reducing the number to be used to mid stem leaf length, width and serrations. Number of peduncle bracts and the number of nodes in the upper 25% below the inflorescence were included in the analysis. Multiple floral traits were highly correlated and only involucre height, mid series phyllary width, number of ray florets, ray lamina length and width, ray floret pappus length at anthesis, number of disc florets, disc corolla length and lobe length, and disc floret ovary/fruit body length.

In the STEPWISE discriminant analysis of 29 specimens of two species level a priori groups (*S. arenicola* and *S. racemosa*), the following 7 traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: ray floret lamina length (16.35), mid stem leaf width (15.77), upper stem leaf length (10.28), disc corolla length (8.87), lower stem leaf width (7.43), disc floret pappus length (6.51), and involucre height (5.94). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. *Solidago arenicola* and *S. racemosa* had an F-to separate value of 19.045 (Wilks' lambda = 0.1361 df = 7 1 27; Approx. F= 19.0447 df = 7 21 prob = 0.0000).

In the Classificatory Discriminant Analysis of 29 specimens of the two species level a priori groups (*S. arenicola* and *S. racemosa*), percents of correct a posteriori assignment to the same a priori group were 100% and 94%. The Classification matrix and Jackknife classification matrix are presented in Table 18. All 12 specimens of the *S. arenicola* a priori group (100%) were assigned a posteriori into the *S. arenicola* group; 11 specimens with 100% probability (including *Medley 18343-87 KY* from Whitley Co., Kentucky) and 1 specimen with 99% probability (*Bailey B150 WAT* from Scott Co., Tennessee). Most specimens of *S. arenicola* had glabrous ovaries/disc floret cypsela. Sixteen of 17 specimens of the *S. racemosa* a priori group (94%) plus 1 additional specimen were assigned a posteriori to *S. racemosa*; 16 specimens with 100% probability (including *Peirson 612 MICH* from Whitley Co., Kentucky and specimens from several locations in West Virginia) and 1 specimen with 63% probability (*Semple & Ringius 7663c WAT* Montgomery Co., Maryland). One specimen of the *S. racemosa* a priori group was assigned a posteriori to *S. arenicola* with 95% probability (*Gagnon 5059 MT* from St-Isadore, Québec; ovaries/disc floret cypsela moderately dense strigose hairs distally and proximally).

Frequencies of CAN1 canonical scores for 29 specimens of *S. arenicola* and *S. racemosa* are presented in histograms in Fig. 35. The Eigenvalue on the first axis was 6.384.

Table 18. 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	<i>arenicola</i>	<i>racemosa</i>	% correct
<i>arenicola</i>	12	0	100
<i>racemosa</i>	1	16	94
Totals	13	16	97

Jackknifed classification matrix

Group	<i>arenicola</i>	<i>racemosa</i>	% correct
<i>arenicola</i>	12	0	100
<i>racemosa</i>	1	16	94
Totals	13	16	97

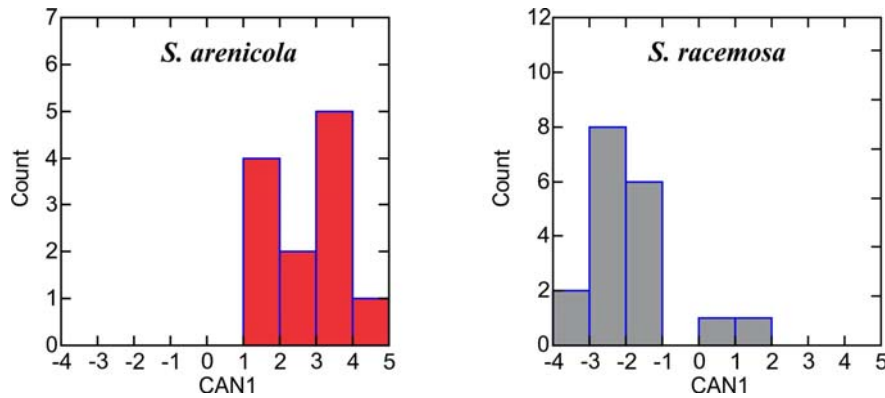


Figure 35. Histograms of CAN1 canonical scores for 29 specimens of *S. arenicola* (left) and *S. racemosa* (right).

DISCUSSION

The results from all the discriminant analyses support the recognition of the following 13 species in *Solidago* subsect. *Humiles*: *Solidago austrocaroliniana*, *S. arenicola*, *S. bellidifolia*, *S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. kralii*, *S. ontarioensis*, *S. plumosa*, *S. racemosa*, *S. randii*, *S. simplex*, and *S. spathulata*. However, not all *a priori* groups separated strongly in all analyses and the percentages of specimens assigned *a posteriori* to their corresponding *a priori* groups differed considerably and for some specimens the assignment probabilities were low. Overall, the thirteen species are likely closely related and have not diverged greatly in multiple characters in multiple cases. Historically, most of the species have been treated as varieties or subspecies within a single broadly defined transcontinental species, either as *S. spathulata* (Hitchcock and Cronquist 1973), *S. glutinosa* (Cronquist 1947; Ringius 1985), or *S. simplex* (Semple and Cook 2006). Semple and Peirson (2013) concluded that the eastern taxa all deserved species level rank based on the molecular work and species concepts discussions of Peirson et al. (2012) and Peirson et al. (2013). Each species occupies a different ecological niche with some graduation of niches into each other; e.g., lower to mid montane habitats grade into alpine habitats in the Pacific Northwest, and upland and river margin habitats can be very close to each other in the ranges of *S. randii* and *S. racemosa*. *Solidago glutinosa* as delimited here is the only widely distributed species and it shows considerable variation in stem height and leaf size over its range and is the only species that is predominantly diploid but includes some tetraploids in Michigan populations at the eastern limits of its range. While some species are consistently short, e.g., *S. bellidifolia* (4.5-14.5 cm) and *S. chlorolepis* (3.7-19 cm), others range from short to moderately tall, e.g., *S. glutinosa* (7-73 cm), to sometimes very tall for the subsection, e.g., *S. gillmanii* (31-88), *S. plumosa* (20-99 cm), *S. arenicola* (49-103 cm), and *S. kralii* (50-110 cm). Growing conditions greatly influence the final stem height attained in a single season by an individual plant. Even in the same local population stem height has been observed to vary considerably depending upon the amount of soil available in various size rock cracks and crevices, e.g. *S. ontarioensis* along the shore of Lakes Huron and Superior (Fig. 12A) and *S. racemosa* along rivers in Pennsylvania (Fig. 16A) and Maryland. Thus, while stem height was found to be useful in the first two analyses in separating *a priori* groups, generally stem height can only be used as a secondary character in keys to identification because it can be a misleading trait.

Sets of traits are most useful in distinguishing species in *Solidago* subsect. *Humiles*. However, in the first analysis including all species, the numbers of serrations on upper leaf margins was found to separate *S. spathulata* from other species on the first canonical axis (Fig 24). Multiple species have obvious serrations on basal rosette and lower stem leaves, but only individuals of *S. spathulata* were consistently multi-serrate on the upper stem leaves. *Solidago glutinosa* and *S.*

bellidifolia had lower numbers of upper leaf margin serrations. All three species are western North American taxa. A few collections of eastern *S. gillmanii* and *S. racemosa* also have a few upper leaf serrations. The key to identification of all 13 species presented at the end of this paper uses sets of characters and geography and ecology to separate taxa.

Comments on Basal Rosette and Lowest Stem Leaves

Whether basal rosette and lower stem leaves are the largest or not is often used to split species into groups in the genus overall (e.g., Cronquist 1968; Semple and Cook 2006; Semple 2012). All taxa in *S.* subsect. *Humiles* have basal rosette and lower stem leaves that are the largest on the plant. Characteristics of basal and lower stem leaves have been used in keys to identification of taxa in *S.* subsect. *Humiles* (e.g., Ringius 1985; Semple and Cook 2006). In his doctoral thesis, Ringius (1985) separated the two subspecies of the broadly defined *S. glutinosa* on the basis of whether rosette and lower cauline leaves were spatulate and obtuse to orbicular with rounded apices (diploid subsp. *glutinosa*; here as *S. bellidifolia*, *S. chlorolepis*, *S. glutinosa* and *S. simplex*), or rosette and lower stem leaves were spatulate to obovate and usually sharp tipped (tetraploid subsp. *randii*; here as *S. gillmanii*, *S. ontarioensis*, *S. randii*, and *S. racemosa*). With the development of high resolution digital cameras, a digital library of all collections included in morphological studies such as this one can be created as a quick reference for checking morphological variation on larger structures such as leaves on all specimens included in a taxon. In *S.* subsect. *Humiles*, this became a critical way to compare printed numerical summaries of morphological traits used in the data matrix with the actual specimens even though some were not on hand for direct observation at the time of preparing the key to identification (i.e., some loans had already been returned). The first author's conclusion is that while Ringius (1985) was generally correct about differences between basal rosette and lower stem leaves of different groups of species, the range of variation within some species and even within a single individual was problematic for splitting taxa into groups. All the rosette and lower stem leaves of *S. bellidifolia* and *S. chlorolepis* were generally small for the subsection, narrowly to broadly obovate with more or less rounded apices and with more abruptly to only gradually tapering bases into a petiolate lower portion. This was true for some specimens of *S. glutinosa* although most had more broadly lanceolate leaves with mostly broadly obtuse but pointed apices and tapering leaf bases. Some collections shifted from having the oldest smaller outer leaves in a rosette that matched the first option of the key to having larger inner leaves of the rosette that matched the second option of the key. Even some individuals of *S. gillmanii*, *S. ontarioensis*, *S. randii*, and *S. racemosa* produced a few small outer rosette and lower stem leaves that were apically rounded and not pointed, although most of the larger younger leaves were acute and sharply pointed. Thus, differences in basal rosette and lower stem leaf traits are useful traits to include in keys to *S.* subsect. *Humiles*, but secondary traits, such as cypselae hair characteristics and especially geography and habitat may be critical in moving through the key to the correct identification for a particular specimen. In short, if the collection comes from along a river in the eastern U.S., ignoring those really small spatulate and rounded rosette leaves will get you to *S. racemosa*. If the collection comes from the mountains of northeastern central Mexico, then it is *S. simplex* even if basal leaf traits are confusing. Developing a key to all 13 species was more challenging than expected.

Comments on Western North American Taxa

There are some distinct differences between the four western North American species *S. bellidifolia*, *S. glutinosa*, *S. simplex* and *S. spathulata* and the ranges are fully to mostly allopatric (Fig. 22). *Solidago spathulata*, the California and Oregon coastal dune and headland species is the most distinct of the four western species with its obviously serrate middle ($x = 12.7$ serrations per side, 6-27 range) and upper stem leaves ($x = 7$ serrations per side, 2-14 range). *Solidago glutinosa* has few-many to no serrations on its middle ($x = 3.6$ serrations per side, 0-11 range) and upper stem leaves ($x = 0.96$ serrations per side, 0-6 range). Vegetative parts and the involucre of *S. spathulata* are usually very obviously resinous compared to the other three western species.

Solidago bellidifolia was treated as *S. glutinosa* var. *nana* by Ringius (1985) and as *S. simplex* var. *nana* in Flora North America (Semple and Cook 2006), but the results from this study indicate that it is both morphologically distinct from *S. glutinosa* and ecologically isolated by occurring at higher elevations in the Pacific Northwest where the ranges of the two species appear to be sympatric (Fig. 22), but are locally allopatric. The basal rosette and lowest stem leaves of *S. bellidifolia* are on average about 3.5 times as long as wide, while those of *S. glutinosa* are on average about 8.2 times as long as wide, although some individuals of *S. glutinosa* can have leaves approach the length to width ratio of those of *S. bellidifolia*. While shoots of *S. bellidifolia* scored for this study were consistently small ($x = 9.8$ cm, range 4.5-15.5 cm tall), shoots of *S. glutinosa* were generally much taller ($x = 35$ cm, range 7-63 cm tall). In more stressful habitats, *S. glutinosa* can approach *S. bellidifolia* in stature either at higher elevations in the Rocky Mts. or growing in cracks in rocks along the north shore of Lake Superior in Ontario or near the coast at low elevations on Vancouver Is., British Columbia.

Solidago simplex is treated here as a species limited in distribution to just northeastern central Mexico following Semple, Ma, and Tong (2016) with *S. glutinosa* treated as a separate much more widely distributed species in Canada, the US, and northern Baja California, Mexico (Fig. 22). Earlier, Semple and Cook (2006) had followed Nesom (1989) in treating *S. glutinosa* as a synonym of *S. simplex*. The multivariate analyses of 12 species, the four western species, and just *S. glutinosa* and *S. simplex* presented above provided additional support for treating *S. simplex* and *S. glutinosa* as a species and included more individuals of *S. glutinosa* than had been scored in Semple, Ma, and Tong (2016). Using just three traits (number of disc florets, number of ray florets, and upper stem leaf width), 97% of the 33 *S. glutinosa* specimens included in the two species analysis were assigned a posteriori to *S. glutinosa* and 91% of the 11 *S. simplex* specimens were assigned a posteriori to *S. simplex*. The ranges of the two species are separated by more than 1000 kms. In the first two analyses including 12 and 11 species, a few individuals of other species were assigned a posteriori to *S. simplex* indicating that there are some similarities between *S. simplex* and other species as well as to *S. glutinosa*, at least using the traits selected by the analyses. In reality, it is not likely that there were chance introductions of *S. simplex* individuals into the ranges of *S. ontarioensis* or *S. racemosa*, even if a specimen of each of the latter species happened to have some traits more similar to *S. simplex* than to either eastern species in the first two analyses, in which multiple species were not well differentiated by the traits selected as most suitable to separate the majority of species. In the *S. glutinosa*/*S. simplex* analysis in Semple, Ma, and Tong (2016), number of disc florets, disc floret corolla length, width of the inflorescence, and disc corolla lobe length were selected in a STEPWISE analysis to be useful in separating the two species. While some individuals of *S. simplex* possessed a narrow inflorescence with short peduncles, some had a more open inflorescence with longer inflorescence branches and peduncles (Fig. 20). Only some individuals of *S. ontarioensis* produced more open long-branched inflorescences (Fig. 11), but these were more leafy than those of *S. simplex*.

Comments on northeastern North American Taxa

The collective results of all the multivariate analyses indicate that the six species native to the northeastern US and eastern Canada (*S. chlorolepis*, *S. gillmanii*, *S. glutinosa*, *S. ontarioensis*, *S. racemosa* and *S. randii*) are distinct taxa but are more challenging to identify than species from other parts of the range of subsect. *Humiles*. This may be because all five taxa include dwarf individuals and more robust individuals due to differences in growing conditions even within their respective habitats. For example, both plants of *S. glutinosa* from western higher elevation habitats in the Rocky Mts. and from near the shore of Lake Superior in Ontario and plants of *S. ontarioensis* from rocky shores near the eastern Lake Superior and limestone pavements near Lake Huron can be only 10-15 cm tall; small plants have few leaves and very small compact inflorescences. Involucre size is generally smaller in diploid *S. glutinosa* than tetraploid *S. ontarioensis*, but there are rare tetraploids in *S. glutinosa* in Jack Pine barrens of northcentral Michigan where *S. ontarioensis* does not occur.

Ringius (1985) and Semple and Cook (2006) emphasized basal rosette and lower stem leaf traits in their keys to separating the northeastern North American taxa (*S. chlorolepis*, *S. gillmanii*, *S. ontarioensis*, *S. racemosa* and *S. randii*; all treated as varieties within *S. glutinosa* s.l. or *S. simplex* s.l.) from the western North American taxa (*S. bellidifolia*, *S. glutinosa* and *S. simplex*; again all treated as part of *S. glutinosa* s.l. or *S. simplex* s.l.). Rosette and lower stem leaf traits were ultimately retained as useful in the key even though some confusion can arise due to variation in leaf traits even on the same individual. Involucre height differences resulting from being diploid versus tetraploid were not as clear as expected because involucres of tetraploid *S. randii* were smaller than for other tetraploids in some of the plants scored.

The four Gaspésie and Île-d'Anticosti, Québec collections of *S. racemosa* warrant discussion. A collection included in the analyses as a member of *S. racemosa* (Morton NA4142 TRT from Percé Mt., Gaspésie, Québec) was reported to be diploid (Morton 1981) and was discussed by Ringius (1985) but not assigned to any variety within *S. glutinosa* sensu lato. The specimen was weakly assigned to *S. bellidifolia* (24% probability in the first analysis of 12 species), to *S. ontarioensis* (25% in the second 11 species analysis; 77% probability in the six northeastern species STEPWISE analysis, 48% probability in 21 trait COMPLETE analysis of the northeastern taxa), and to *S. racemosa* (92% probability in the four species southeastern taxa analysis; 77% probability in the *S. racemosa/S. randii* analysis). If the diploid count (Morton 1981) was made from the rootstock of the specimen on the voucher herbarium sheet, then it is the only diploid count for *S. racemosa* and the only diploid count for the *S. gillmanii*, *S. ontarioensis*, *S. racemosa*, *S. randii* group of eastern species. A second collection included in the analyses as a member of *S. racemosa* (LaBreque s.n. MT from Mont Ste.-Anne, Gaspésie, Québec) was assigned a posteriori to *S. randii* (53% probability in the first 12 species analysis; 51% probability in the 11 species analysis), to *S. ontarioensis* (86% probability in the six northern species STEPWISE analysis), to *S. chlorolepis* (46% probability in the 21 trait COMPLETE analysis of the northeastern taxa), and to *S. racemosa* (100% in the *S. racemosa/S. randii*) analysis. The ploidy level of LaBreque s.n. (MT) is unknown. The two northern most collections of *S. racemosa* were from Île-d'Anticosti, Québec. Dignard et al 08-95 (QUE) was assigned a posteriori to *S. ontarioensis* (50% probability in the first 12 species analysis; 47% probability in the 11 species analysis; 50% probability in the six northern species 21 trait COMPLETE analysis), to *S. racemosa* (83% in the *S. racemosa/S. randii* analysis) and to *S. randii* (31% probability in the six northern species STEPWISE analysis). Dignard 99-114 (QUE) was assigned a posteriori to *S. racemosa* (36% in the 12 species analysis; 29% probability in the 11 species analysis; 62% probability in the six northern species STEPWISE analysis; 69% in the six northern species 21 trait COMPLETE analysis; and 90% in the *S. racemosa/S. randii* analysis). Our conclusion is that all four plants are *S. racemosa* but atypical in some traits for the species, which is not unexpected considering their isolated northern locations. *Solidago chrysolepis* Fern., *S. anticostensis* Fern., *Solidago victorinii* Fern., and *Solidago* × *raymondi* Rousseau (putatively *S. racemosa* × *S. victorinii*) have been proposed for distinctive plants from eastern Québec, but all are treated here as synonyms of *S. racemosa*.

Comments on southeastern North American Taxa

The only species in *S.* subsect. *Humiles* that consistently had more than three peduncle bracts were *S. kralii* and *S. plumosa*. Both species have glabrous ovaries/cypsela bodies. The mid stem leaves of *S. kralii* are 5-7 times as long as wide and those of *S. plumosa* are more linear and 7-21 times as long as wide. Upper stem leaves of *S. kralii* are slight less linear than the mid stem leaves, while those of *S. plumosa* are slightly more linear than the mid stem leaves. Both species usually have very few or no serrations on upper stem leaves. The ranges of the two species are allopatric (Fig. 23) and may be the result of vicariant biogeography of a shared ancestral species.

Solidago racemosa was included in the analysis of the southeastern taxa because Floden (2012) indicated the range of the species (reported as *S. simplex* var. *racemosa*) extends into northern Tennessee and adjacent Kentucky in disjunct populations along separate river systems of the Cumberland Plateau. Floden (2012) cited Peirson et al. (2012) who reported tetraploids of *S. arenicola* in Tennessee. Floden (2012) included comments on *S. erecta* Pursh, which is a member of *S.* subsect. *Squarrosae* A. Gray (Semple et al. 2017) and easily distinguished from members of subsect. *Humiles* by the latter having resinous phyllaries. The resinous quality is produced by minute glands that Floden (2012) noted were not always visible on specimens at 40x. Such glands are often not easily seen even at 70x, but the resin is present and makes the phyllaries shiny at least near the tip. The first author has observed in the process of taking high resolution digital images of all collections included in multivariate analyses of *Solidago* that the light of the camera flash adds white highlights to surfaces that otherwise do not appear to be resinous, but in fact have a thin resinous coating. Adjusting the angle of dissecting scope light can result in the same phenomenon. The phyllaries of *S. arenicola* and *S. racemosa* have a thin resinous coating that reflects light in a few bright spots (Figs. 2F and 16H), while the phyllaries and peduncle surfaces of *S. kralii* are much more obviously resinous (Figs. 10F-G).

Some collections of subsect. *Humiles* from Tennessee and adjacent Kentucky seen during this investigation had glabrous ovaries/fruit bodies and were identified as *S. arenicola*. Some collections had some hairs on the ovary/fruit bodies and were identified as *S. arenicola* on general appearance or as *S. racemosa*. No specimens of *S. arenicola* included in this study were assigned a posteriori to the *S. racemosa* group, and one specimen of *S. racemosa* a priori group was assigned a posteriori to *S. arenicola* with 95% (*Gagnon 5059 QUE* from from St-Isadore, Québec; ovaries/disc floret cypselae moderately densely strigose hairs distally and proximally). Both species include tetraploids with larger involucres which may account for the confusion about the identity of the Tennessee/adjacent Kentucky collections. Peirson et al. (2013) included specimens of *S. arenicola* from Kentucky in their cpDNA study including material vouchered as *Peirson 612* (MICH) which was labeled as S104 on their map in their Figure 1. In our multivariate study, *Peirson 612* (MICH) was included as a sample of *S. racemosa* based on the identification on the herbarium sheet label, although the cypselae bodies were completely glabrous. In the two species analysis (*S. arenicola* and *S. racemosa*), *Peirson 612* (MICH) was placed a posteriori into *S. racemosa* with 100% probability and is shown on our map Fig. 23 as being the only Kentucky sample of *S. racemosa*. Four Peirson collections of *S. racemosa* from West Virginia were also included in the our multivariate study and all were assigned a posteriori in the two species analysis to *S. racemosa* with 100% probability. The only collection of *S. arenicola* from Kentucky included in our multivariate study as *S. arenicola* was *Medley 18343-87* (KY; glabrous cypselae bodies) which was placed a posteriori into *S. arenicola* with 100% probability. The three *S. arenicola* collections from Scott Co., Tennessee included in our study all had some short hairs on the distal portion of the ovary/cypselae fruit bodies; these were placed a posteriori into *S. arenicola* with 99-100% probability. Our conclusion is that *S. arenicola* is present in Kentucky and Tennessee and some individuals are either very *S. racemosa*-like in multiple traits (*Peirson 612* MICH) or *S. racemosa* is also present in Kentucky and maybe Tennessee at the same or different locations. These northern populations of *S. arenicola* may just be divergent from the Alabama populations in ovary/cypselae indumenta features and do not include *S. racemosa*. The results of the molecular and morphological studies are contradictory. Further morphological or DNA basal analyses of the populations in Alabama, Tennessee and Kentucky may clarify the matter. If both species are present at the same location then hybridization is possible.

Solidago austrocaroliniana is known only from a single collection. This necessitated that it only be included in the analyses a posteriori and could not be included as a separate a priori group. In the first two analyses, the single specimen of *S. austrocaroliniana* was assigned a posteriori into *S. simplex* (42% and 26% probability respectively; 6% and 0% to *S. arenicola* respectively). In the

analysis of the five southeastern US species, the single specimen of *S. austrocaroliniana* was assigned a posteriori to *S. arenicola* (98% probability); the yellow star symbols for the collection of *S. austrocaroliniana* were placed outside the 95% confidence limits ellipses for *S. arenicola*, *S. kralii*, and *S. plumosa*, but closer to *S. arenicola* group centroid. In the protologue of the species Semple (2018) noted that the holotype of *S. austrocaroliniana* looked more like *S. arenicola* than other southeastern species but had smaller involucres. Additional specimens of *S. austrocaroliniana* need to be found in order to resolve questions about its relationships to southeastern taxa of *S.* subsect. *Humiles*.

Key to taxa in *Solidago* subsect. *Humiles*

- 1 Mid and upper stem leaves with (2-)6-27 serrations; coastal dunes of OR and CA *S. spathulata*
- 1 Mid and upper stem leaves with very few or no serrations
 - 2 Peduncles with 4-7 bracts
 - 3 Mid stem leaves 7-21 times as long as wide; North Carolina *S. plumosa*
 - 3 Mid stem leaves 5-7 times as long as wide; Georgia, Aiken Co. South Carolina *S. kralii*
 - 2 Peduncles with 1-3 bracts
 - 4 Involucres 7–11 mm tall; cypselae glabrous (sometimes sparsely strigose in TN and KY); southeastern KY to northern AL *S. arenicola*
 - 4 Involucres 3–7(–8) mm; cypselae sparsely to moderately densely strigose
 - 5 Spring to early summer blooming; upland South Carolina *S. austrocaroliniana*
 - 5 Summer to fall blooming; western and northeastern North America
 - 6 Basal rosette and lower stem leaves spatulate to obovate, apices rounded to very obtuse and slightly pointed; stem 2-15(20) cm tall
 - 7 Basal rosette and lowest stem leaves averaging 3.5-4 times as long as wide; cypselae moderately to moderately densely strigose distally and proximally; high alpine habitats in OR, WA and Vancouver Is., BC *S. bellidifolia*
 - 7 Basal rosette and lower stem leaves averaging 4-7 times as long as wide; cypselae sparsely to moderate strigose distally and proximally; Mt. Albert region, PQ *S. chlorolepis*
 - 6 Basal rosette and lower stem leaves spatulate to obovate, apices obtuse with a point to acute and sharply pointed (sometimes rounded in *S. glutinosa*); stem (10-)20-110 cm; high alpine and rock shoreline plants sometimes <20 cm (see *S. glutinosa*, *S. ontarioensis*, *S. racemosa*)
 - 8 Involucres 4–5.5 mm tall at flowering (larger as fruit develops); western North America, east in Canada to Ontario and Michigan
 - 9 Basal and lower stem leaves averaging 7-8 times as long as wide; prairie and montane habitats, AK to AZ and NM, east to MI and northern ON *S. glutinosa*
 - 9 Basal and lower stem leaves averaging 5-6.5 times as long as wide; montane habitats, central Mexico *S. simplex*
 - 8 Involucres (4.1-)5-8 mm tall; Great Lakes area, uplands, and along rivers from PQ to WV and southeastern KY
 - 10 Involucres 4.1-5(-5.5) mm tall; cypselae very sparsely to sparsely strigose proximally, more so distally; barren, rocky, non-alpine uplands; se PQ, n. New England, ne. NY *S. randii*
 - 10 Involucres 5-7 mm tall; cypselae sparsely to moderately strigose or sparsely strigose proximally, to more so distally

- 11 Cypselae moderately to densely strigose proximally and distally; larger infls open branched; stems 1-4 dm; cauline leaves (2-)4-13(-24); rocky shores, L. Superior, northern L. Huron *S. ontarioensis*
- 11 Cypselae glabrate to moderately strigose proximally, sparsely to densely so distally; stem to 8 dm tall; cauline leaves often numerous (except for small plants); sand dunes or on rocks near river banks
- 12 Cypselae glabrate to sparsely strigose proximally, very sparsely to moderately distally; lower cauline leaves usually less than 10 mm wide; calcareous rocky riverbanks, e PQ south to MD and WV and rarely KY *S. racemosa*
- 12 Cypselae sparsely strigose proximally, sparsely to moderately dense distally; lower cauline leaves usually more than 10 mm wide; sand dunes, L. Michigan, northern L. Huron *S. gillmanii*

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LITERATURE CITED

- Anderson, L.C., D.W. Kyhos, T. Mosquin, A.M. Powell, and P.H. Raven. 1974. Chromosome numbers in Compositae. IX. *Haplopappus* and other Astereae. Amer. J. Bot. 61: 665-671.
- Beaudry, J.R. 1963. Studies on *Solidago* L. VI. Additional chromosome numbers of taxa of the genus Canad. J. Genet. Cytol. 5: 150-174.
- Cronquist, A. 1947. Notes on the Compositae of the northeastern United States IV. *Solidago*. Rhodora 49: 69-79.
- Cronquist, A. 1968. *Solidago* L. pp. 413-438, in H. A. Gleason, ed. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. Hafner Pub. Co., New York.
- Fernald, M.L. 1950. Gray's manual of Botany, 8th ed. Van Nostrand, New York.
- Floden, A. 2012. Notes on two rare *Solidago* (Asteraceae) in Tennessee: *S. arenicola* and *S. simplex*. Phytoneuron 2012-63: 1-4.
- Hitchcock, C.L. and A. Cronquist. 1973. Flora of the Pacific Northwest: an illustrated manual. University of Washington Press. Seattle.
- Nesom, G.L. 1989. *Solidago simplex* (Compositae: Astereae), the correct name for *S. glutinosa*. Phytologia 67: 155-157.
- Nesom, G.L. 1993. Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and observations on the phylogenetic position. Phytologia 75: 1-44.

- Peirson, J.A., A.A. Reznicek, & J.C. Semple. 2012. Polyploidy, speciation, and infraspecific cytotype variation in goldenrods: The cytogeography of *Solidago* subsection *Humiles* (Asteraceae: Astereae) in North America. *Taxon*: 61: 197–210.
- Peirson, J.A., C.W. Dick and A.A. Reznicek. 2013. Phylogeography and polyploid evolution of North American goldenrods (*Solidago* subsect. *Humiles*, Asteraceae). *J. Biogeography*. 40: 1887–1898.
- Ringius, G.S. 1985. A biosystematic study of the *Solidago spathulata* DC. - *S. glutinosa* Nutt. complex Compositae: Astereae). Ph.D. dissertation. Univ. of Waterloo: Waterloo, Ontario.
- Ringius, G.S. and J.C. Semple. 1987. Cytogeography of the *Solidago spathulata* - *S. glutinosa* complex (Compositae: Astereae). *Canad. J. Bot.* 65: 2458–2462.
- Semple, J.C. 2012. *Solidago* pp. 421-422, in B. G. Baldwin et al. (eds.), *The Jepson Manual, Vascular Plants of California*. 2nd Ed. University of California Press, Berkeley.
- Semple, J.C. 2016. An intuitive phylogeny and summary of chromosome number variation in the goldenrod genus *Solidago* (Asteraceae: Astereae). *Phytoneuron* 2016-32. 1-9.
- Semple, J.C. 2019, frequently updated. Classification and Illustrations of Goldenrods. <<https://uwaterloo.ca/astereae-lab/research/goldenrods/classification-and-illustrations>>
- Semple, J.C. and R.E. Cook. 2006. *Solidago* Linnaeus. Pp. 107–166, in *Flora North America* Editorial Committee (eds.). *Flora of North America*. Vol. 20. Asteraceae, Part 2. Astereae and Senecioneae. Oxford Univ. Press, New York.
- Semple, J.C. and J.B. Nelson. 2018. *Solidago austrocaroliniana* (Asteraceae: Astereae), a new species of subsect. *Humiles* from South Carolina. *Phytoneuron* 2018-75: 1-6.
- Semple, J.C., and J.A. Peirson. 2013. A revised nomenclature for the *Solidago simplex* complex (Asteraceae: Astereae). *Phytoneuron* 2013-41. 1-5.
- Semple, J.C., Y. Ma and L. Tong. 2016. On *Solidago simplex* (Asteraceae: Astereae): a multivariate study including *S. glutinosa*, *S. leiocarpa*, *S. multiradiata* and *S. spathulata*. *Phytoneuron* 2016-87. 1-21.
- Semple, J.C., L. Tong, and Y.A. Chong. 2017. Multivariate studies of *Solidago* subsect. *Squarrosae*. I. The *Solidago speciosa* complex (Asteraceae: Astereae). *Phytoneuron* 2017-18: 1–23.
- Semple, J.C., L. Tong, Y. A. Chong and M. Kaddoura. 2017. Multivariate studies of *Solidago* subsect. *Squarrosae*. II. The *Solidago bicolor*–*S. hispida* complex (Asteraceae: Astereae). *Phytoneuron* 2017-33: 1–44.
- Semple, J.C., T. Shea, H. Rahman, Y. Ma, and K. Kornobis. 2016. A multivariate study of the *Solidago sempervirens* complex (Asteraceae: Astereae: *S.* subsect. *Maritimae*). *Phytoneuron* 2016-73. 1-31.