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MULTIVARIATE STUDIES OF *SOLIDAGO* SUBSECT. *SQUARROSAE*. III. *S. GEORGIANA, S. PORTERI, S. ROANENSIS, S. SQUARROSA*, AND *S. VILLOSICARPA* (ASTERACEAE: ASTEREAE)

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ABSTRACT

Solidago subsect. *Squarrosae* includes a number of larger-headed, often showy species that are native to eastern North America. *Solidago squarrosa* is widely distributed in eastern Canada south to the mountains in North Carolina, while *S. georgiana*, *S. porteri* and *S. villosicarpa* are narrowly distributed rare endemics in the southeastern USA. All five species have hairless lower stems and variously hairy mid and upper stems. A multivariate analysis of these four species and the smaller- headed *S. roanensis* was performed to compare and contrast the species.

Solidago subsect. *Squarrosae* A. Gray (Asteraceae: Astereae) includes more than a dozen species native primarily to eastern Canada and the midwestern and eastern portions of the USA (Semple et al. 2017). Semple and Cook (2006) recognized 9 species with multiple infraspecific taxa in several species, while Semple (2017, 2017 frequently updated) recognized 15 species: *S. bicolor* L., *S. erecta* Pursh, *S. georgiana* Semple, *S. hispida* Muhl., *S. jejunifolia* Steele, *S. pallida* (Porter) Rydb., *S. porteri* Small, *S. puberula* Nutt., *S. pulverulenta* Nutt., *S. rigidiuscula* (Torr. & A. Gray) Porter, *S. roanensis* Porter, *S. sciaphila* Steele, *S. speciosa* Nutt., *S. squarrosa* Muhl., and *S. villosicarpa* LeBlond.

All species of subsect. *Squarrosae* except *S. georgiana* were included in a multivariate study focusing on the *S. speciosa* complex (Semple et al. 2017). *Solidago porteri* (Figs. 1-2), *S. squarrosa* (Figs. 3-5) and *S. villosicarpa* (Figs. 6-8) were most strongly separated in that study and had larger heads than other species; *S. roanensis* was more centrally located in the plot of canonical scores and had smaller heads (see Figs. 5-6 and 13 in Semple et al. 2017). *Solidago georgiana* was described from a single collection by Semple (2017) in the companion paper to this study. *Solidago georgiana* has intermediate sized heads and stems that lack hairs proximally but become increasingly more hairy from mid stem to upper stem into the inflorescence (Figs 1-2 in Semple 2017), while stem hair distribution is similar in *S. porteri, S. roanensis, S. squarrosa* and *S. villosicarpa*; hair size varies within and between these five species.

Solidago roanensis, *S. squarrosa,* and *S. villosicarpa* have been reported to be diploid 2*n*=18 (Beaudry & Chabot 1959; Beaudry 1963; Beaudry 1969; Kapoor 1970; Kapoor 1977; Semple et al. 1981; Semple et al. 1984; Semple & Chmielewski 1987; Semple & Cook 2004; Semple et al. 2015; unpublished data). *Solidago porteri* was reported to be hexaploid 2*n*=54 (Semple & Estes 2015). The chromosome number of *S. georgiana* is unknown; Semple (2017) speculated that it might be a polyploid due to involucre size or a larger-headed diploid like *S. squarrosa* and *S. villosicarpa.*

Results of a multivariate analysis of *Solidago georgiana*, *S. porteri, S. squarrosa* and *S. villosicarpa* are reported here. *Solidago georgiana* (1 population in Georgia), *S. porteri* (5 populations in Tennessee, Alabama, and Georgia) and *S. villosicarpa* (3-4 populations in North Carolina) are narrowly distributed rare endemics in the southeastern USA (Fig. 9), while *S. squarrosa* is widely distributed in eastern Canada south to the mountains in North Carolina (Fig. 10).

Figure 1. Morphology of *Solidago porteri* (*Semple et al. 11861*, unmounted) from Giles Co., Tennessee.

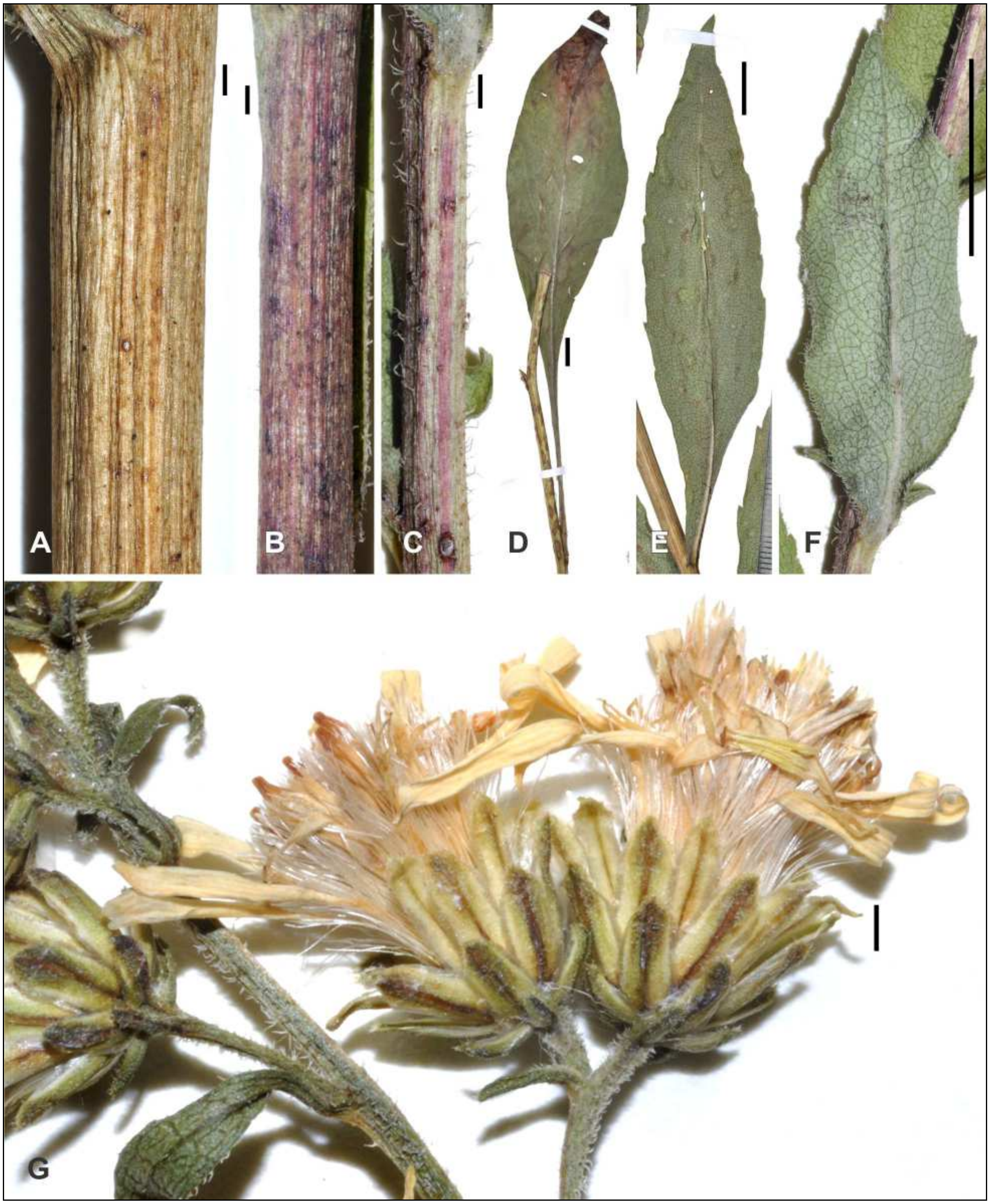

Figure 2. Details of the morphology of *Solidago porteri*. **A-C.** Lower, lower middle and upper stems. **A**. *Patrick et al 22001* (GA); robust shoot. **B-C.** *Semple & B. Semple 11190* (WAT). **D.** Lower stem leaf, adaxial surface, *Hill 1162b-1* (GA). **E.** Mid stem leaf, *Hill 1162a* (GA). **F.** Upper stem leaf, abaxial surface, *Semple & B. Semple 11190* (WAT). **G.** Heads, *Hill 1162c-6* (GA). Scale bars = 1 mm in A-C, and G; = 1 cm in D-F.

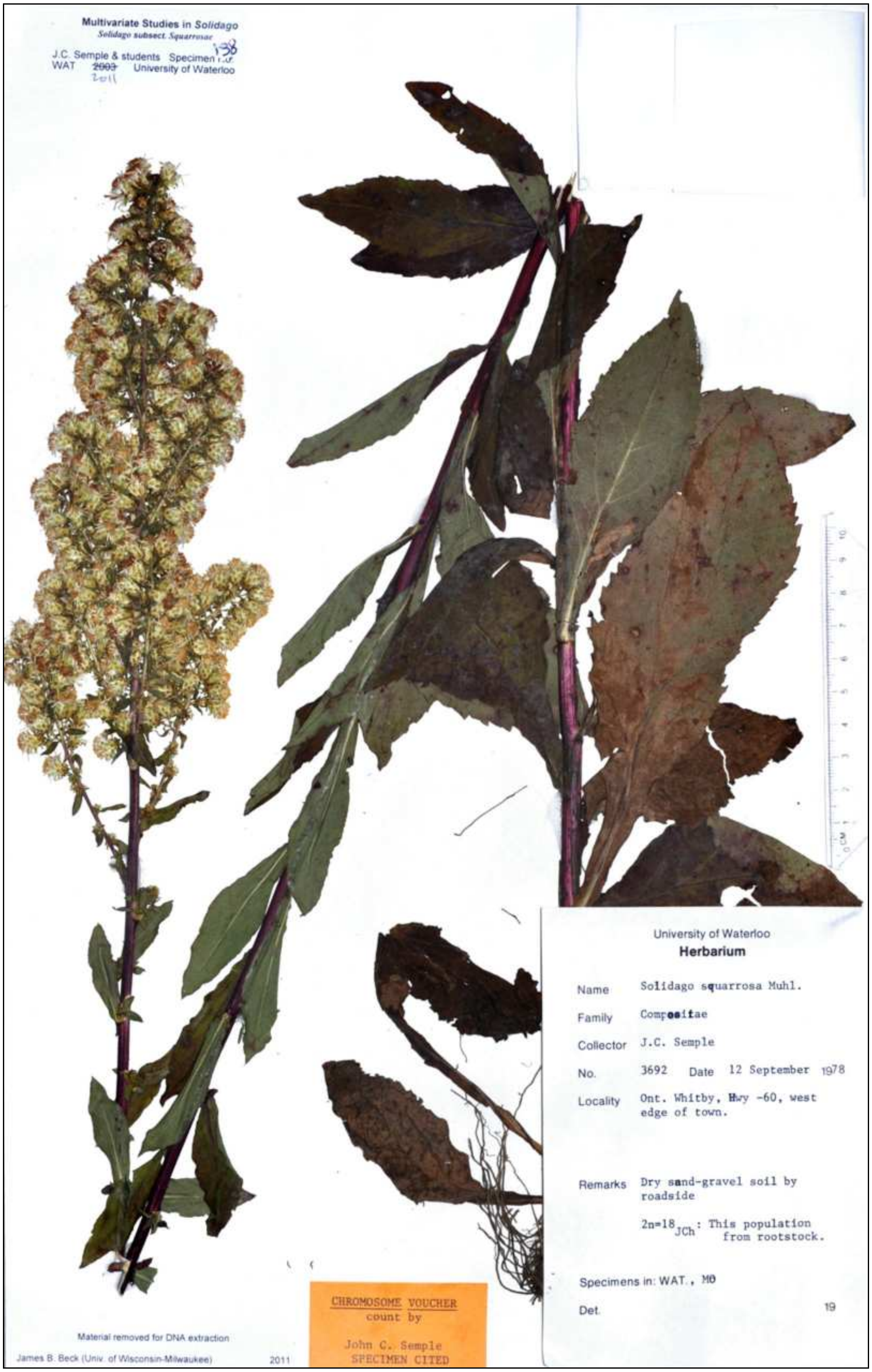

Figure 3. Morphology of *Solidago squarrosa*: *Semple 3692* (WAT) from Whitby, Ontario.

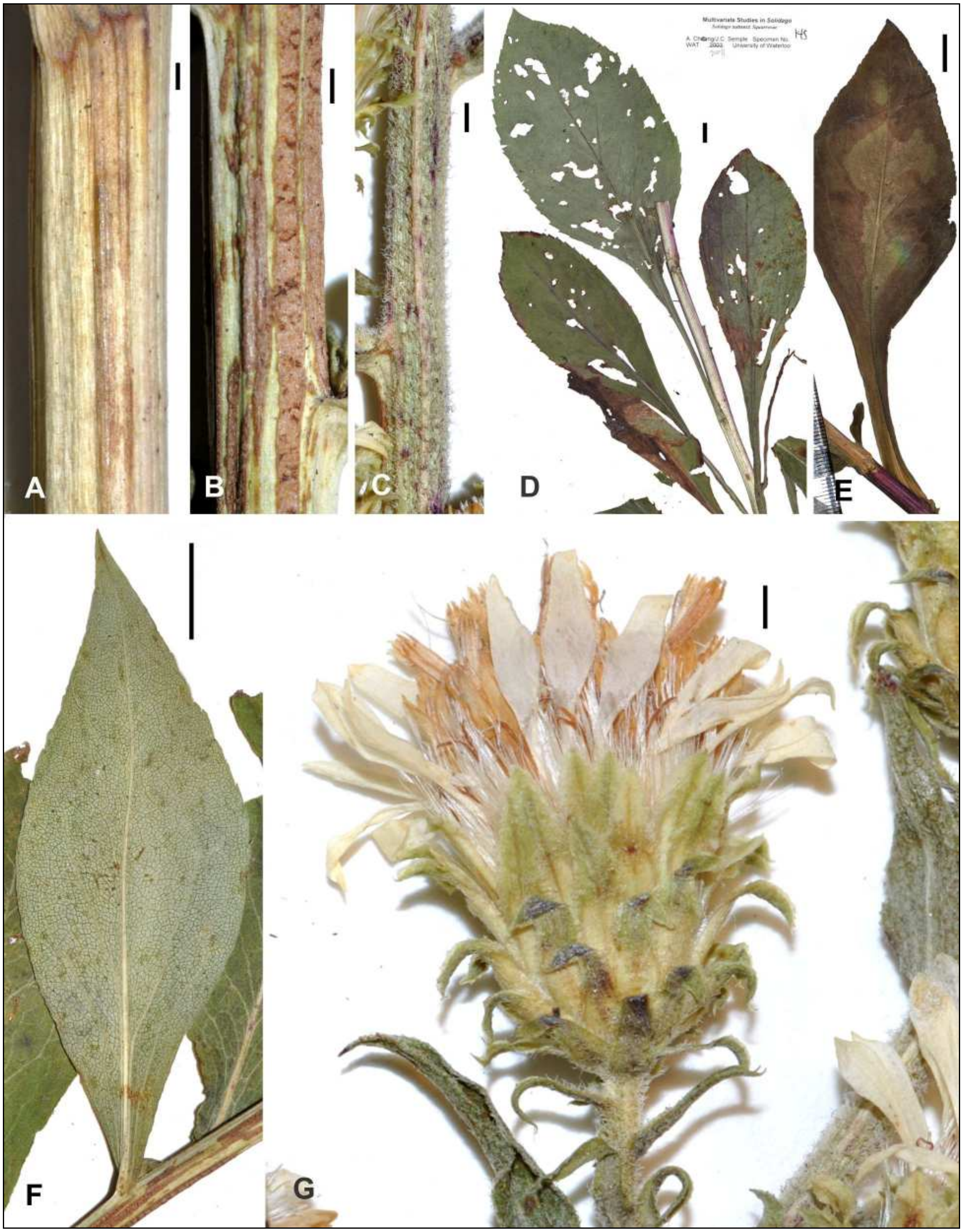

Figure 4. Details of the morphology of *Solidago squarrosa*. **A-C.** Lower, mid and upper stem in inflorescence, *Morton & Venn NA17632* (TRT), Maine. **D-E.** Lower stem leaves, *Semple & B. Semple 11529* (WAT) and *Morton & Venn NA11936* (TRT), New Brunswick and Maine, respectively. **F.** Mid stem leaf, *Morton & Venn NA17632* (TRT). **G.** Head, *Morton & Venn NA17632* (TRT). Scale bars = 1 mm in A-C, and G; = 1 cm in D-F.

Figure 5. *Solidago squarrosa* 1.3 m tall, *Semple & B. Semple 11529* (WAT) in Victoria Co., New Brunswick.

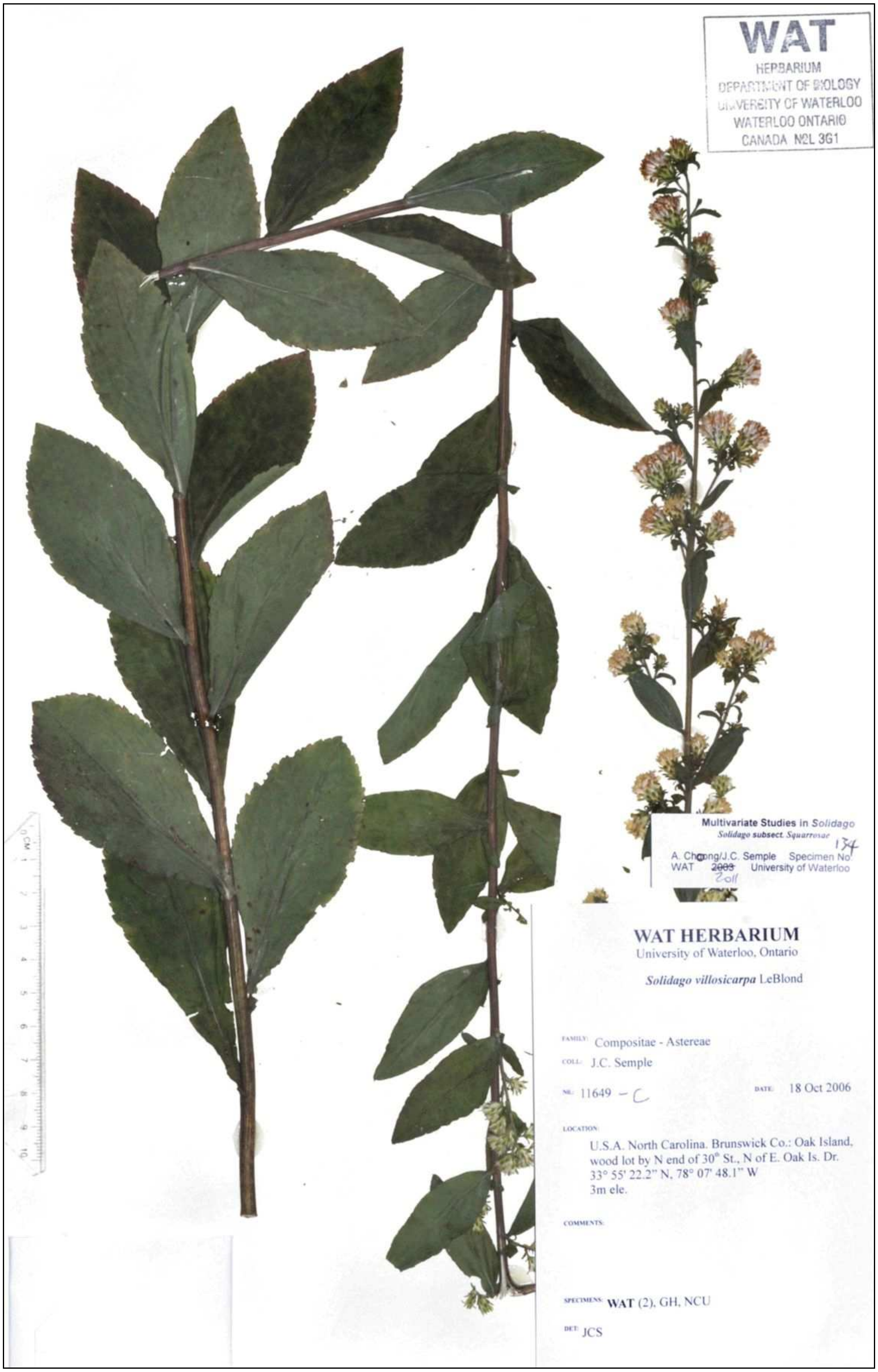

Figure 6. Morphology of *Solidago villosicarpa*: *Semple 11649 C* (WAT) from Brunswick Co., North Carolina.

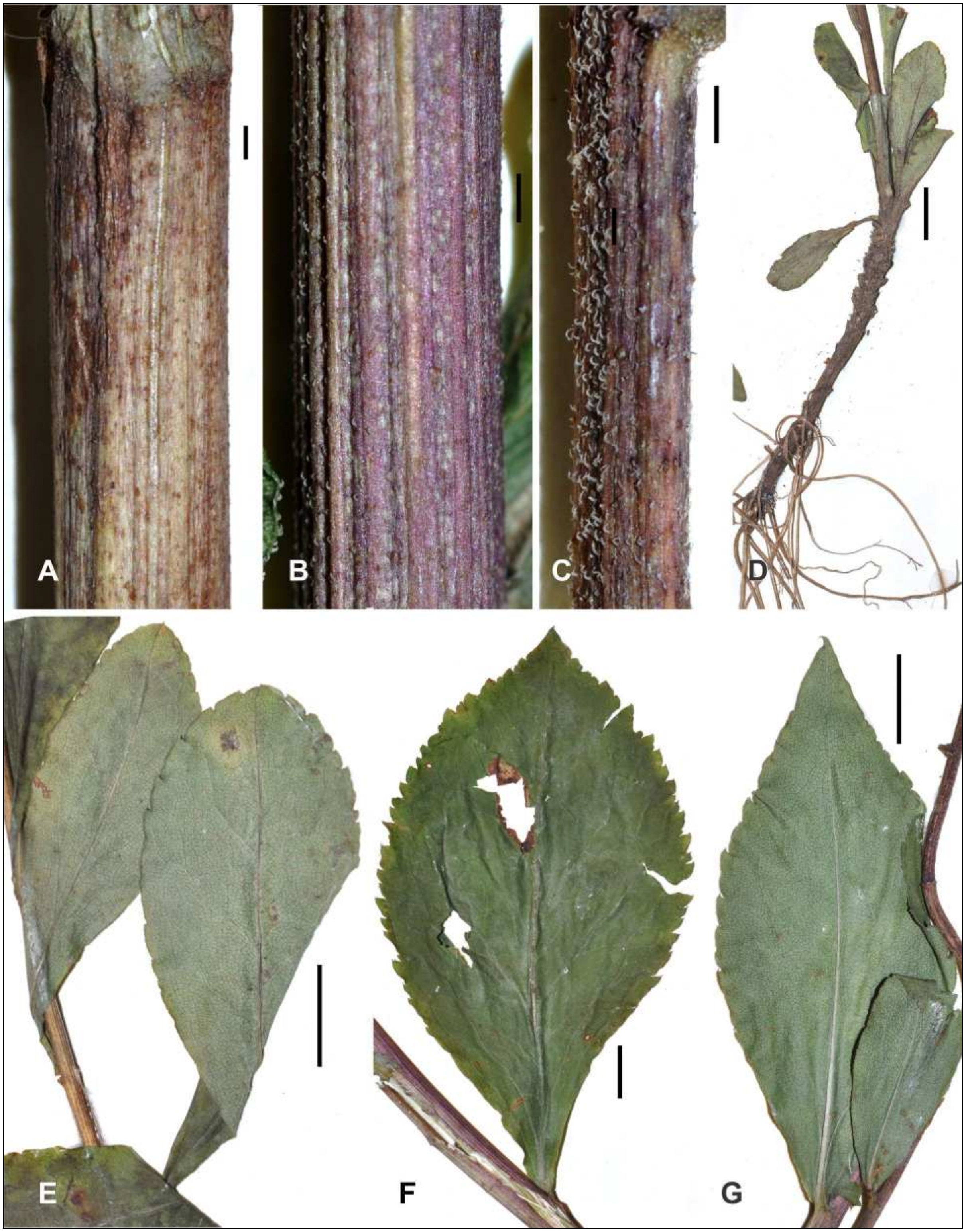

Figure 7. Details of the morphology of *Solidago villosicarpa*. **A-C.** Lower, middle and upper stem in inflorescence, *Semple 11645* (WAT). **D-E.** Portion of rootstock and lower stem leaves of small plant, *Semple 11649 B* (WAT). **F-G.** Mid and upper stem leaves of large plant, *Semple 11645* (WAT). Scale bars = 1 mm in A-C; = 1 cm in D-G.

Figure 8. *Solidago villosicarpa, Semple & C. Tinbrink 11*637 (WAT). **A.** Large plant after rain, USMC Camp Lejune, Onslow Co., North Carolina. **B.** Flowering heads, involucres 5-9-6.2 mm tall.

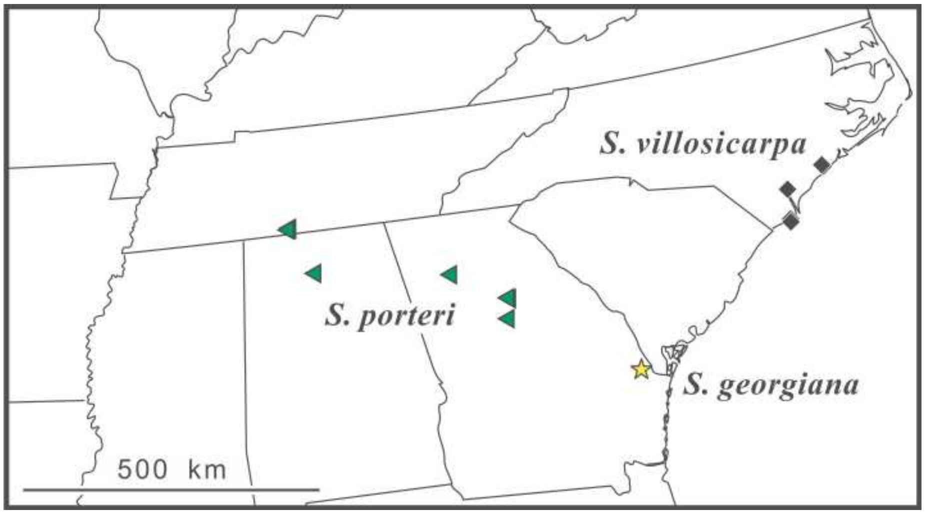

Figure 9. Ranges of distribution of *Solidago georgiana* (yellow star), *S. porteri* (green triangles), and *S. villosicarpa* (black diamonds) and locations of specimens included in the multivariate analyses.

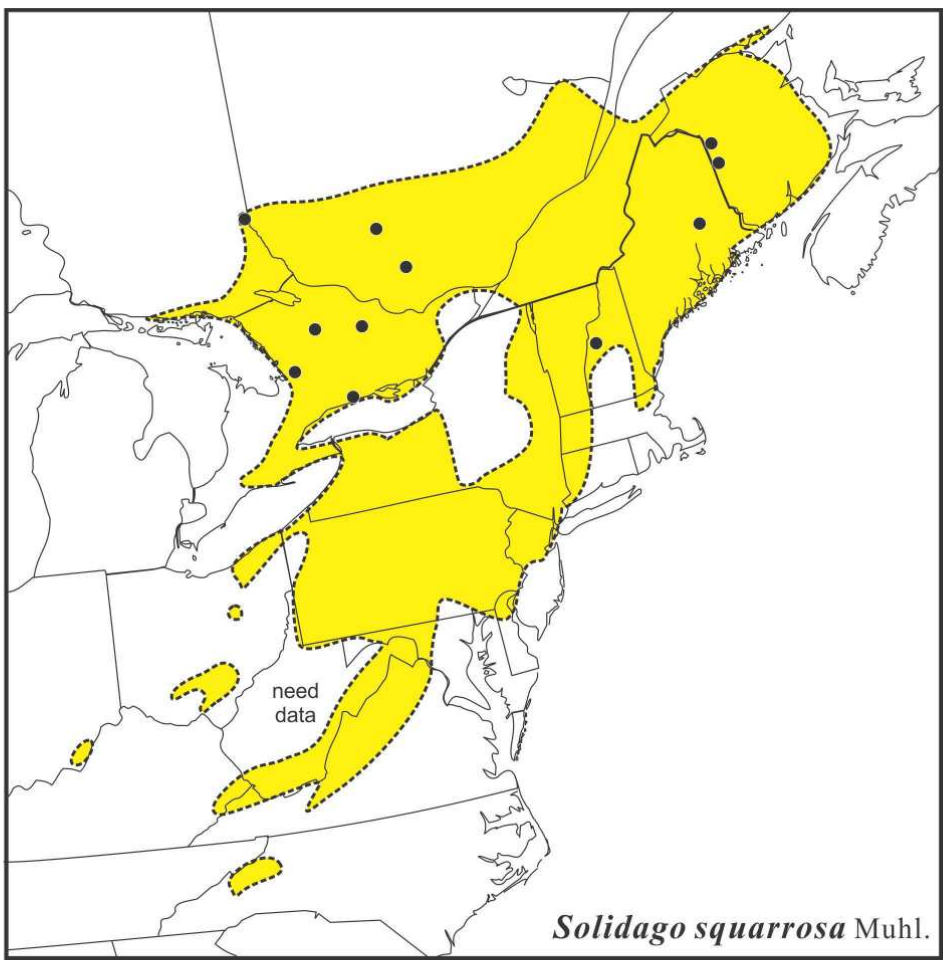

Figure 10. Range of distribution of *Solidago squarrosa* and locations of specimens included in the multivariate analyses.

MATERIALS AND METHODS

In total, 50 specimens from GA, the J.K. Morton personal herbarium now deposited in TRT, NY, TAWES, and WAT in MT (Thiers, continuously updated) were scored and included in the analysis: *Solidago georgiana* (1 unassigned a priori), S. *porteri* (11 specimens), *S. roanensis* (17 specimens), *S. squarrosa* (11 specimens from the northern half of the range), and *S. villosicarpa* (9 specimens). These were selected from more than 300 specimens examined. For each specimen, 18 vegetative and 19 floral traits were scored when possible: 1-5 replicates per character depending upon availability of material and whether or not the trait was meristic (Table 1). Basal rosette leaves were often not present. Lower stem leaves were sometimes not present. Mean values were used in the analyses, while raw values were used to generate ranges of variation for each trait. All traits scored are listed in Table 1.

All analyses were performed using SYSTAT v.10 (SPSS 2000). Details on the methodology are presented in Semple et al. (2016) and are not repeated here. One STEPWISE discriminant analysis was performed on four species level a priori groups (*Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*) with one specimen of *S. georgiana* not included in an a priori group but included in the a posteriori classificatory discriminant analysis.

Table 1. Traits scored for the multivariate analyses of 261 specimens of *Solidago* subsect. *Squarrosae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip (cm)
BLFLN	Basal rosette leaf length including petiole (mm)
BLFPETLN	Basal rosette leaf petiole length (not scored if winged margins broad)
BLFWD	Basal rosette leaf width measured at the widest point (mm)
BLFWTOE	Basal rosette leaf measured from the widest point to the end (mm)
BLFSER	Basal rosette leaf-number of serrations on 1 side of margin
LLFLN	Lower leaf length measured from the leaf base to tip (mm)
LLFWD	Lower leaf width measured at the widest point (mm)
LLFWTOE	Lower leaf measured from the widest point to the end (mm)
LLFSER	Lower leaf dentation-number of serrations of lower leaf
MLFLN	Mid leaf length measured from the leaf base to tip (mm)
MLFWD	Mid leaf width measured at the widest point (mm)
MLFWTOE	Mid leaf measured from the widest point to the end (mm)
MLFSER	Mid leaf dentation-number of serrations of mid leaf
ULFLN	Upper leaf length measured form the leaf base to tip (mm)
ULFWD	Upper leaf width measured at the widest point (mm)
ULFWTOE	Upper leaf measured from the widest point to the end (mm)
ULFSER	Upper leaf dentation-number of serrations of upper leaf
CAPL	Length of inflorescence (cm)
CAPW	Width of inflorescence (cm)
INVOLHT	Involucre height at anthesis (mm)
OPHYLN	Outer phyllary length (mm)
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)

IPHYLW	Inner phyllary width (mm)
RAYNUM	Number of ray florets per head
RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)

RESULTS

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid and upper stem leaf lengths, mid and upper stem leaf widths, and numbers of mid of upper stem leaf serrations. Basal rosette leaves were often absent and were not included in the discriminant analyses: basal leaf length, basal leaf petiole length, and basal leaf length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Many floral traits also were highly correlated. Involucre height correlated highly with inner phyllary length, ray floret pappus length, disc corolla length, and disc floret corolla length. Outer and inner phyllaries lengths were highly correlated. Inner phyllary length correlated highly with ray floret lamina length, ray floret pappus length, disc floret corolla length and disc floret pappus length. Ray floret lamina length correlated highly with ray floret lamina width, ray floret ovary length, ray floret pappus length, disc floret corolla length, and disc floret pappus length. Ray and disc floret ovary/fruit body lengths at anthesis were highly correlated. Ray floret pappus length correlated highly with disc floret corolla length and disc floret pappus length. Disc floret corolla length correlated highly with disc floret ovary/fruit body length and disc floret pappus length. Outer phyllary length, numbers of ray florets, ray floret lamina width, number of disc florets, disc floret corolla length, and disc floret corolla lobe length were included in the multivariate analysis.

In the STEPWISE discriminant analysis of 50 specimens of four species level a priori groups in (*Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*), the following eight traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of ray florets (12.57), disc corolla length (12.44), disc corolla lobe length (10.24), mid stem leaf width (8.46), outer phyllary length (6.40), mid stem leaf length (5.75), number of disc florets (5.71), and upper stem leaf length (4.14). 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. roanensis* and *S. squarrosa* (31.391; the smallest separations were between *S. squarrosa* and *S. villosicarpa* (10.130), *S. porteri* and *S. roanensis* (10.480), and *S. porteri* and *S. villosicarpa* (10.707).

In the Classificatory Discriminant Analysis of the four species level a priori groups (*Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*) plus 1 unassigned specimen of *S. georgiana*,

Table 2. Between groups F-matrix for the four a priori groups analysis (df = 8 38).

Group	***porteri***	***roanensis***	***squarrosa***
roanensis	10.480		
squarrosa	17.429	31.391	
villosicarpa	10.707	21.052	10.130

Wilks' lambda = 0.0156 df = 8 3 45; Approx. F= 14.6488 df = 24 110 prob = 0.0000

percents of correct a posterori assignment to the same a priori group ranged from 91-100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. All 9 specimens of the *S. villosicarpa* a priori group (100%) were assigned a posteriori into the *S. villosicarpa* with 100% probability. All 17 specimens of *S. roanensis* a priori group (100%) were assigned a posteriori to the *S. roanensis* group; 16 specimens with 98-100% probability and 1 specimen with 87% probability (13% to *S. porteri*). Eleven of the 12 specimens of the *S. porteri* a priori group (92%) were assigned a posteriori to the *S. porteri* group: 9 specimens with 99-100% probability, 1 specimen with 92% probability, and 1 specimen with 73% probability (12% to *S. squarrosa*, 10% to *S. villosicarpa*, and 6% *S. roanensis*). One specimens of the *S. porteri* a priori group was assigned a posteriori to the *S. villosicarpa* group with 69% probability (23% to *S. porteri*; *Porter s.n.* NY from Monticello, Georgia; a ca. 30 cm shoot with an inflorescence of only 5 heads; this is the smaller shoot on the lectotype of the species; the larger shoot on the lectotype was assigned a posteriori to *S. porteri* with 100% probability). Ten of the 11 specimens of the *S. squarrosa* a priori groups (91%) were assigned a posteriori to the *S. squarrosa* group with 99-100% probability. One specimens of the *S. squarrosa* a priori group was assigned a posteriori to the *S. villosicarpa* group with 48% probability (28% to *S. squarrosa* and 23% to *S. porteri*; *Semple & Brouillet 3467* WAT from Grafton Co., New Hampshire; the phyllaries are strongly squarrose and the leaves are typical for *S. squarrosa* but the heads had a mean value of only 7 ray florets). The single specimen of *S. georgiana* not assigned to an a priori group was assigned a posteriori to *S. porteri* with 67% probability (23% to *S. roanensis* and 10% to *S. villosicarpa*).

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 50 specimens of *Solidago georgiana* (yellow stars), *S. porteri* (green triangles), *S. roanensis* (open blue stars), S. speciosa (yellow stars), *S. squarrosa* (red star bursts), and *S. villosicarpa* (black diamonds).are presented in Fig. 11. Eigenvalues on the first three axes were 7.458, 2.062 and 1.473.

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

Group	***porteri***	***roanensis***	***squarrosa***	***villosicarpa***	**% correct**
porteri	11	0	0	1	92
roanensis	0	17	0	0	100
squarrosa	0	0	10	1	91
villosicarpa	0	0	0	9	100
Totals	11	17	10	11	96

Jackknifed classification matrix

Group	*porteri*	*roanensis*	*squarrosa*	*villosicarpa*	% correct
porteri	9	10	0	2	75
roanensis	0	17	0	0	100
squarrosa	0	0	10	1	91
villosicarpa	0	0	0	9	100
Totals	9	18	10	12	92

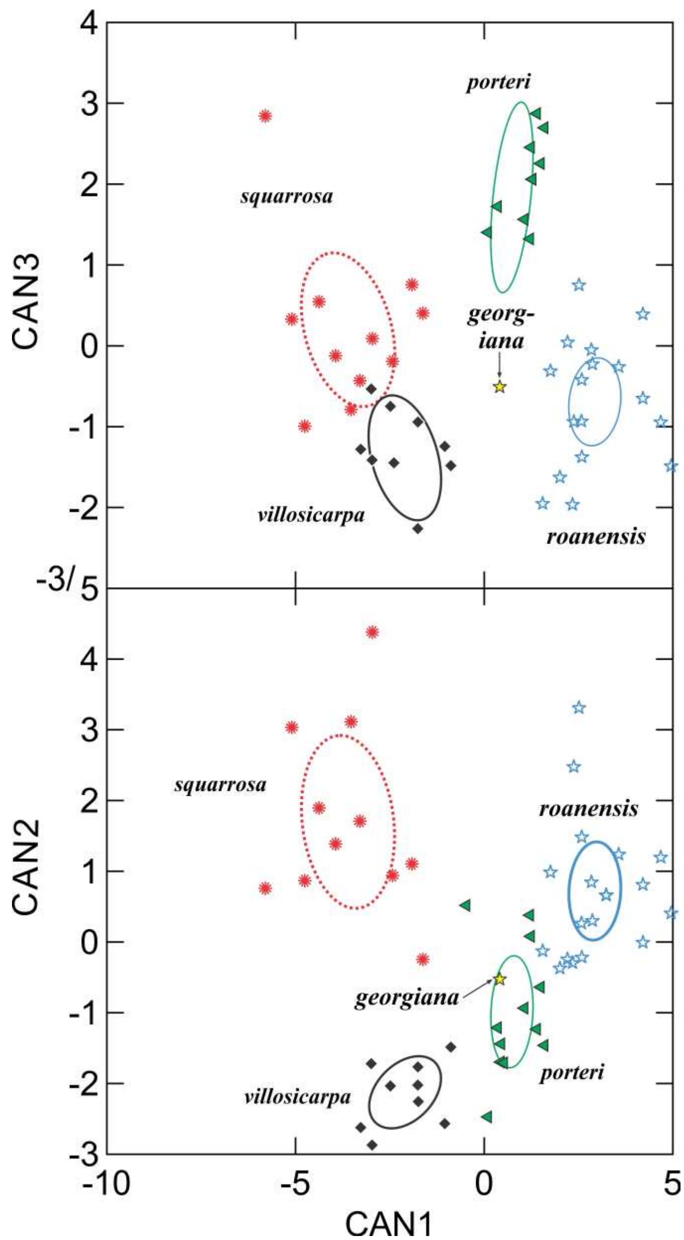

Figure 11. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 51 specimens of Solidago subsect. Squarrosae: *S. georgiana* (yellow stars), *S. porteri* (green triangles), *S. roanensis* (open blue stars), S. speciosa (yellow stars), *S. squarrosa* (red star bursts), and *S. villosicarpa* (black diamonds).

DISCUSSION

The results of the multivariate analysis strongly support recognition of *Solidago porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa as* distinct species. The results also indicate that *S. georgiana* does not fit strongly into the other four species although it is more similar to *S. porteri*. The yellow star symbol for the *S. georgiana* specimen was placed within the 95% confidence ellipse of *S. porteri* on the CAN1 versus CAN2 plot in Fig. 11, but the yellow star symbol for the *S. geogiana* specimen was placed by itself in between the other four species on the CAN1 versus CAN3 plot in Fig. 11. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis of the five species are presented in Table 4.

Solidago georgiana, *S. porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa* are not likely to be misidentified because each species has a set of distinct features and the ranges are allopatric. *Solidago squarrosa* is the only species in the subsection having long strongly reflexed outer phyllaries tips and cylindrical involucres when fresh. *Solidago porteri* is the only hexaploid in the subsection and has the largest involucres and the longest stem hairs of these five species. *Solidago roanensis* has the smallest heads and is the only species with multi-veined phyllaries. *Solidago villosicarpa* has the most showy heads with its long broad ray laminae and cylindrical involucres with broad appressed phyllaries. The little-known *S. georgiana* has mid-sized involucres with appressed phyllaries; it is the least distinctive of the five species although its ray floret laminae were the widest on average; it is the only one of the five species occurring on the outer coastal plain in southeastern Georgia.

All five species share the glabrous lower stem condition with hairs occurring more densely distally on the mid to upper stem and into the inflorescence. Other species in the subsection are either hairy to the base of the stem or glabrous except in the inflorescence. The length of the stem hairs is shortest in *Solidago roanensis* and longest in *S. porteri*, which may be a gigas effect of the higher ploidy level in the latter species. Whether or not the stem hair distribution feature is a synapomorphy indicating these five species form a clade within subsect. *Squarrosae* needs to be tested using methods suitable for phylogenetic analysis.

Table 4. Descriptive statistics on raw data on morphological traits of specimens used in the multivariate analysis *S. georgiana*, *S. porteri*, *S. roanensis*, *S. squarrosa*, and *S. villosicarpa*: min-**mean-**max; * traits selected in STEPDISC analyses. Abbreviations of traits are described in Table 1.

Trait	***S. georgiana***	***S. porteri***	***S. roanensis***	***S. squarrosa***	***S. villosicarpa***
STEMHT cm	71	34–**71.5**–123	**26–61.2–101**	57.5–**96.1**–129	57–**95**–124
BLFLN mm	–	63	**9.5–93.3–185**	66–**214**–360	90–**131**–173
BLFPETLN mm	–	30	**4.5–48.8–110**	6–**89**–165	0–**38**–65
BLFWD mm	–	18	**2.3–20.4–36**	18–**51.2**–99	25–**40.71**–55
BLFWTOE mm	–	14	**2.3–25.9–80**	29–**51.7**–89	20–**38.3**–53
BLFSER	–	2	**4–10.2–21**	10–**18.4**–33	7–**16.5**–26
LLFLN mm	70–**100**–120	46–**125.4**–249	10.5–**85.6**–150	58–**141.2**–245	30–**87**–124
LLFPETLN mm	25–**30**–35	8–**25**–60	4.5–**48.8**–110	20–**47.8**–98	0–**13.5**–42
LLFWD mm	20–**27.7**–38	14–**28.6**–53	2.4–**20.9**–42	17–**42.3**–85	16–**38.5**–64
LLFWTOE mm	30–**45**–60	10–**44.5**–83	3.4–**31.5**–55	24–**44.4**–70	14–**38**–63
LLFSER	12–**16.7**–227	1–**7.1**–17	5–**11.1**–20	4–**14.5**–28	4–**14.7**–32
MLFLN* mm	30–**41.5**–50	38–**90.7**–169	7–**64.8**–125	48–**85.7**–123	30–**62.7**–96
MLFWD* mm	7–**9.5**–12	8–**20**–38	2–**16.3**–32	9–**24.9**–46	10–**26.7**–50

MLFWTOE mm	16–**20**–25	5–**42.5**–84	2.9–**31.2**–55	20–**34.1**–75	10–**27.3**–52
MLFSER	10–**11.5**–14	0–**4**–10	1–**7.7**–20	3–**9.7**–18	0–**8.6**–26
ULFLN* mm	18–**20.8**–23	20–**41.8**–92	4–**39.9**–81	19–**46.2**–75	17–**36.3**–75
ULFWD mm	4–**4.5**–5	6–**10.5**–23	1–**9.4**–19	4–**12.5**–27	9–**13.4**–34
ULFWTOE mm	9–**10.5**–12	6–**20.9**–50	2–**20.1**–41	9–**11.3**–22	7–**16.1**–37
ULFSER	0–**1.5**–5	0–**0.6**–9	0–**4.2**–14	0–**2.4**–12	0–**1.4**–10
CAPL cm	20	3.6–**15.5**–28	5.2–**16.4**–29.2	18–**33.4**–53.5	10–**30.4**–47
CAPW cm	2.5	2.2–**6.8**–12.8	1.8–**2.8**–7	3–**5**–11.5	1.6–**5.3**–12.4
INVOLHT mm	5–**5.0**–5.1	3.2–**6.1**–9.8	2.3–**3.9**–5.6	4–**6.4**–8.8	4.5–**6.2**–8
OPHYLN* mm	2–**2**–2.1	1.3–**1.95**–3.1	0.5–**1.6**–2.8	2–**2.8**–4.3	1.25–**2.1**–3.3
IPHYLN mm	4.5–**4.7**–4.8	3–**6.0**–8	2.1–**3.4**–4.8	3.9–**5.1**–7	4.3–**4.0**–6.3
RAYNUM*	4–**5**–6	1–**6.2**–9	2–**6**–13	4–**12.1**–20	4–**6.4**–11
RLAMLN mm	3.9–**4.1**–4.5	1.5–**3.0**–4.5	1–**1.9**–3	3–**4.0**–5.4	2–**4.5**–6.3
RLAMWD mm	1.5–**1.62**–1.7	0.3–**0.92**–1.9	0.4–**0.73**–1.6	0.5–**0.95**–1.6	0.7–**1.2**–2.0
RACHLN mm	1.2–**1.27**–1.4	0.8–**1.4**–2.13	0.5–**1.2**–2.1	1.0–**1.8**–2.7	1.2–**2.1**–2.7
RPAPLN mm	3.6–**3.7**–3.8	2.8–**4.21**–6	1.3–**2.3**–3.1	3–**4.1**–4.9	3.2–**4.1**–5.1
DISCNUM*	8–**9**–10	8–**12.2**–17	4–**8.6**–13	8–**15.4**–30	6–**13.2**–21
DCORLN* mm	4.3–**4.56**–4.8	2.3–**4.8**–6.6	2.5–**3.6**–4.9	4.7–**5.5**–6.7	4.1–**5.5**–6.5
DLOBLN* mm	0.7–**0.9**–1.1	0.8–**1.6**–2.8	0.2–**0.8**–1.7	0.7–0.**97**–1.5	0.75–**1.1**–1.25
DACHLN mm	1.1–**1.15**–1.2	0.9–**1.5**–3.3	0.6–**1.2**–2.3	1.3–**1.9**–2.8	1.2–**2.3**–3.6
DPAPLN mm	3.5–**3.65**–3.8	3.9–**4.6**–6	1.5–**2.8**–4.2	3.6–**4.6**–6	3–**4.7**–5.6

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