

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

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ABSTRACT

A multivariate morphometric study of the goldenrod group *Solidago* subsect. *Nemorales* was conducted to assess the morphological differences among *Solidago californica*, *S. hintoniorum*, *S. mollis*, *S. nana*, *S. nemoralis* (subsp. *decemflora* and subsp. *nemoralis* combined), *S. radula*, and *S. velutina* (including *S. sparsiflora*). Analyses of a matrix of 335 specimens by 30 traits provided support for recognizing 7 species. The two subspecies within *S. nemorales* were previously investigated and were not reanalyzed. Based on the analyses and morphological studies, the *S. velutina* complex was split into a western *S. californica* and a Great Basin/Rocky Mountain cordilleran *S. velutina*; the results did not support dividing the latter species into a northern race (*S. sparsiflora* or *S. velutina* subsp. *sparsiflora*) and a more southern race (*S. velutina* subsp. *velutina*). The results indicated a close similarity between *S. mollis* and *S. radula*, although the two obviously differ in diagnostic leaf hair traits not included in the analyses and in growth pattern differences. One specimen (*Baker 722*, COLO) was strongly placed in *S. nana* and was not *S. rigida* as previously identified and reported in the literature.

Solidago subsect. *Nemorales* includes 5-9 species depending upon the taxonomic treatment (Nesom 1989a, b; Semple et al. 1990; Nesom 1993; Semple & Cook, 2006; Semple 2018 frequently updated): *S. californica* Nutt., *S. hintoniorum* Nesom, *S. macvaughii* Nesom, *S. mollis* Bartl., *S. nana* Nutt., *S. nemoralis* Ait., *S. radula* Nutt. *S. sparsiflora* A. Gray, and *S. velutina* DC. There are multiple synonyms under *S. nemoralis*, *S. sparsiflora*, and *S. velutina*. All members of the subsection have short to elongated rhizomes, densely short-hairy stems, leaves that are largest proximally and much reduced distally and sometimes trinervate, arrays of heads that are weakly to strongly secund conical, and phyllaries that are strongly graduated and either oblong or lanceolate. Species differ primarily in hair traits and leaf traits.

Solidago californica has densely short-wooly canescent stem hairs, densely hairy pedicels, and sparsely to moderately hairy ovate to broadly lanceolate outer phyllaries (Figs. 1-2); it has been treated as *S. velutina* subsp. *californica* (Nutt) Semple. *Solidago hintoniorum* (Figs. 3-4; Nesom 1989a) is the only Mexican endemic species in the subsection; it is distinguished by its often scabrous leaves with distally oriented hairs that create strong drag when a finger is run over the surface from leaf apex to base; hairs may be dense only near the leaf apex obscuring the scabrous condition. Nesom (1993) included *S. hintoniorum* Nesom (and *S. speciosa* Nutt.) in *S.* subsect. *Thyrsiflorae* A. Gray, but these were not included in subsect. *Thyrsiflorae* by Semple et al. (2017). *Solidago hintoniorum* has traits typical of subsect. *Nemorales* including large lower stem leaves. *Solidago macvaughii* is endemic to northern Aquascalientes, Mexico and is known from a few collections; it was considered to be closely related to or a synonym of *S. velutina* (Nesom 1989b), but Semple (2018) showed that its lower stem leaves were typical of species in the *Tortifoliae* group of *S.* subsect. *Triplinerviae* (Torr. & A. Gray) G.L. Nesom and it is excluded from further consideration here. *Solidago mollis* (Fig. 5-6) has usually broadly oblanceolate, trinervate lower and mid stem leaves that are moderately strigose and often somewhat grayish in color; individuals can form numerous-stemmed extensive rhizomatous clones. *Solidago nana* (Figs. 7-9) has short, densely hairy stems, grayish-green to whitish leaves, and arrays of heads that are very strongly secund to the point of

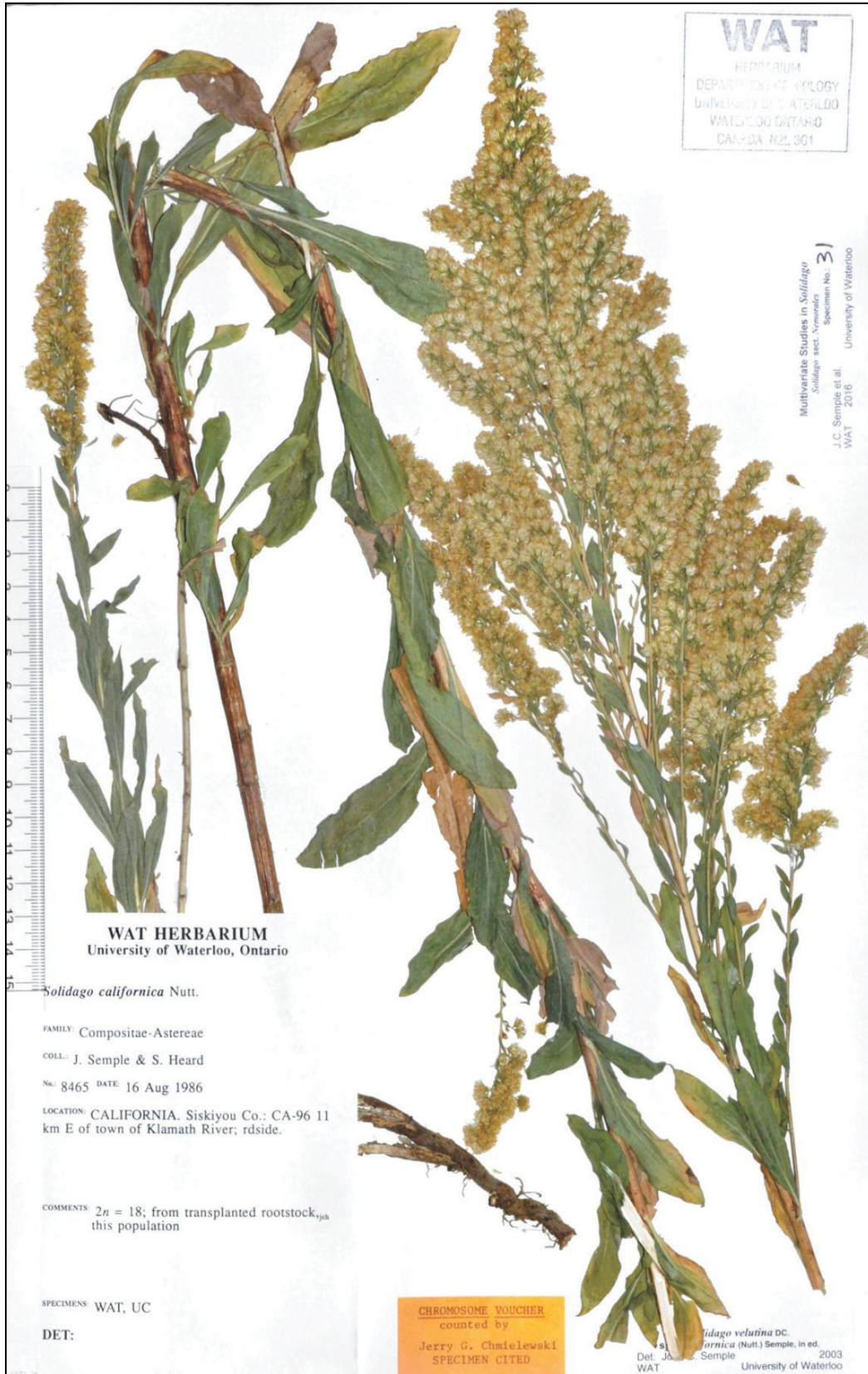


Figure 1. Very robust and small shoots of *Solidago californica*, Semple & Heard 8465 (WAT).

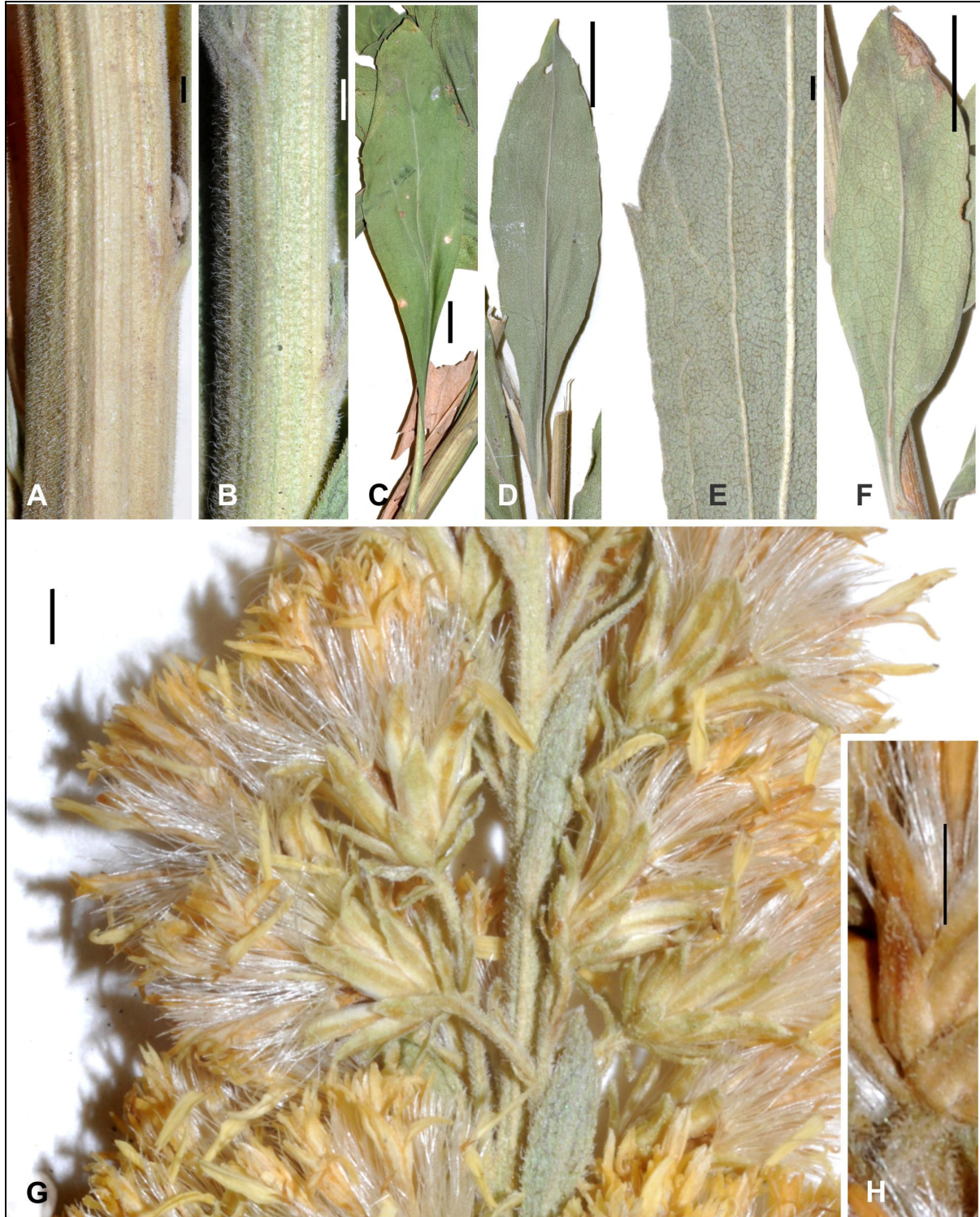


Figure 2. Details of the morphology of *Solidago californica*. **A-B.** Lower and upper stem, *Semple et al.* 9365 (WAT). **C.** Lower stem leaf, *Semple et al.* 9365 (WAT). **D.** Lower mid stem leaf, *Semple et al.* 9300 (WAT). **E.** Lower mid stem leaf mid vein and adaxial surface, *Semple & Brouillet* 7131 (WAT). **F.** Upper mid stem, *Semple & Heard* 8651 (WAT). **G.** Heads, *Semple & Heard* 8465 (WAT). **H.** Peduncle and outer phyllaries, *Dunkle* 3775 (RSA). Scale bars = 1 mm in A-B, E and G-H; = 1 cm in C, E-F.



Figure 3. *Solidago hintoniorum*, Patterswon 6331 (TEX) from Nuevo León, Mexico.

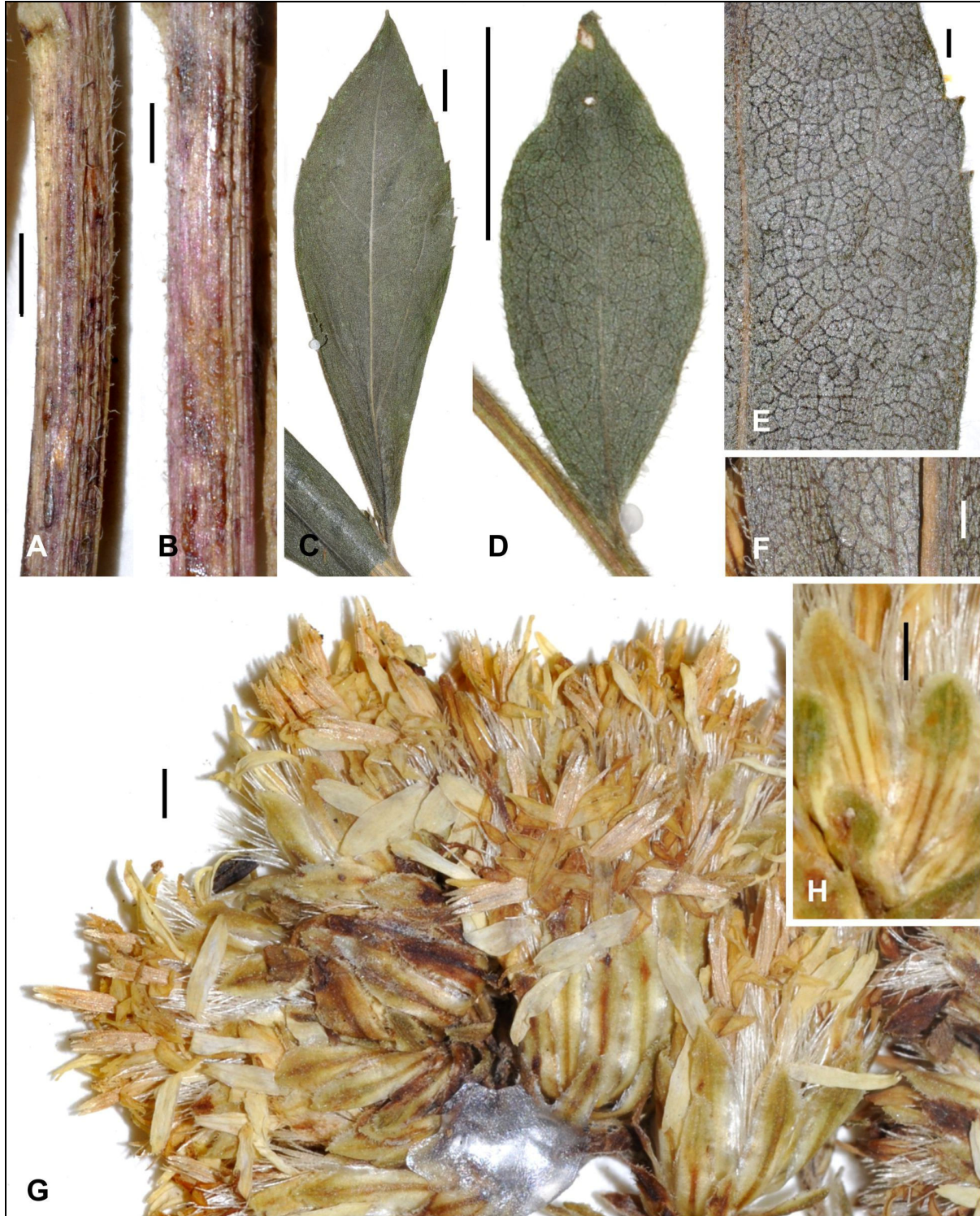


Figure 4. Details of the morphology of *Solidago hintoniorum*. **A-B.** Lower and mid stems, *Hinton 20867* (TEX). **C.** Lower mid stem leaf, *Hinton 22053* (TEX). **D.** Upper stem leaf, *Patterson 6331* (TEX). **E-F.** Upper stem leaf mid vein and adaxial surface detail. **E.** *Hinton 23323* (TEX). **F.** *Hinton et al 17884* (TEX). **G.** Heads, *McDonald 2561* (TEX). **H.** Multi-veined phyllaries, *Hinton et al. 17884* (TEX). Scale bars = 1 mm in A-B, F-H; = 1 cm in C-D.

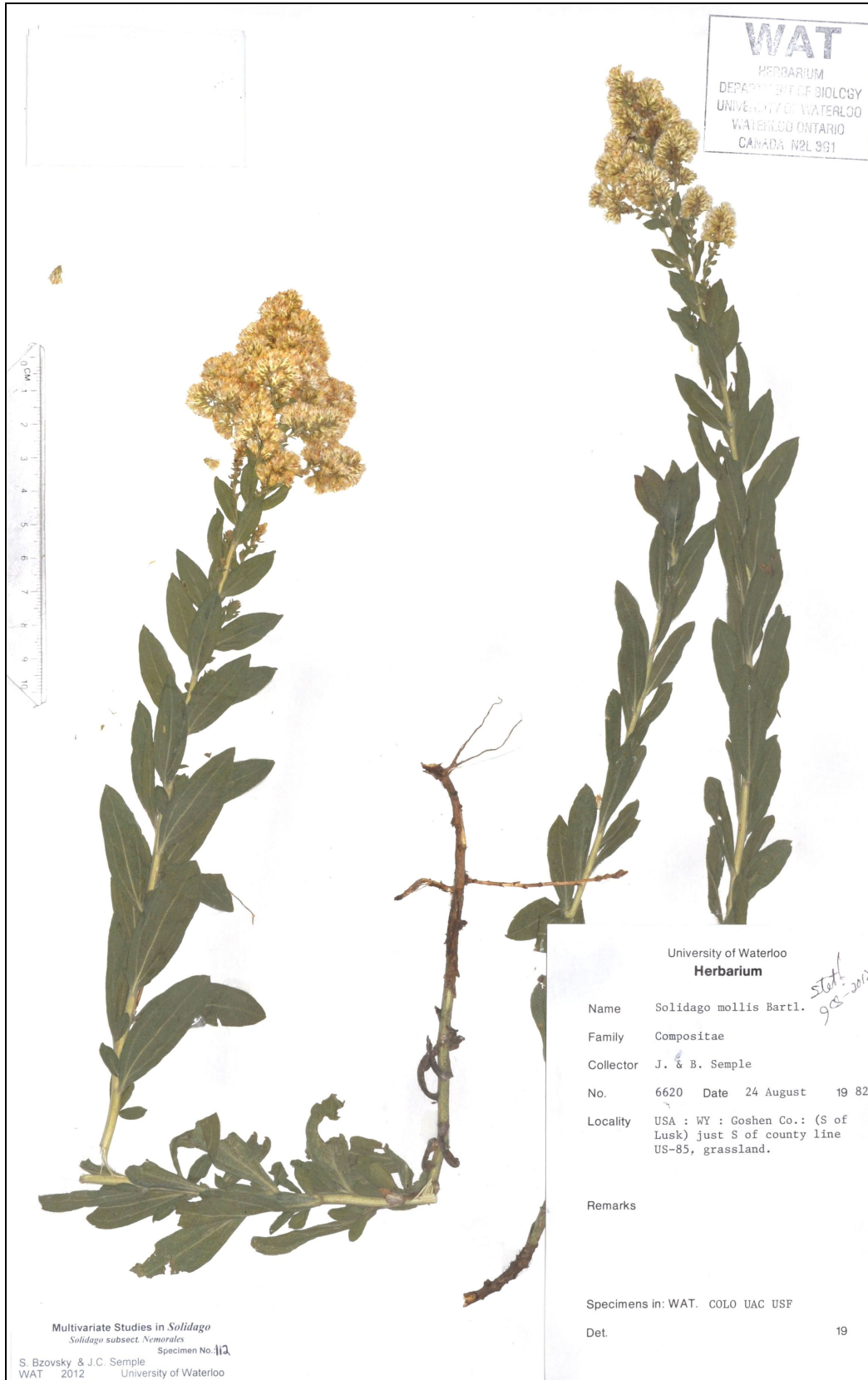


Figure 5. *Solidago mollis*, J. Semple & B. Semple 6620 (WAT) from Goshen Co., Wyoming.

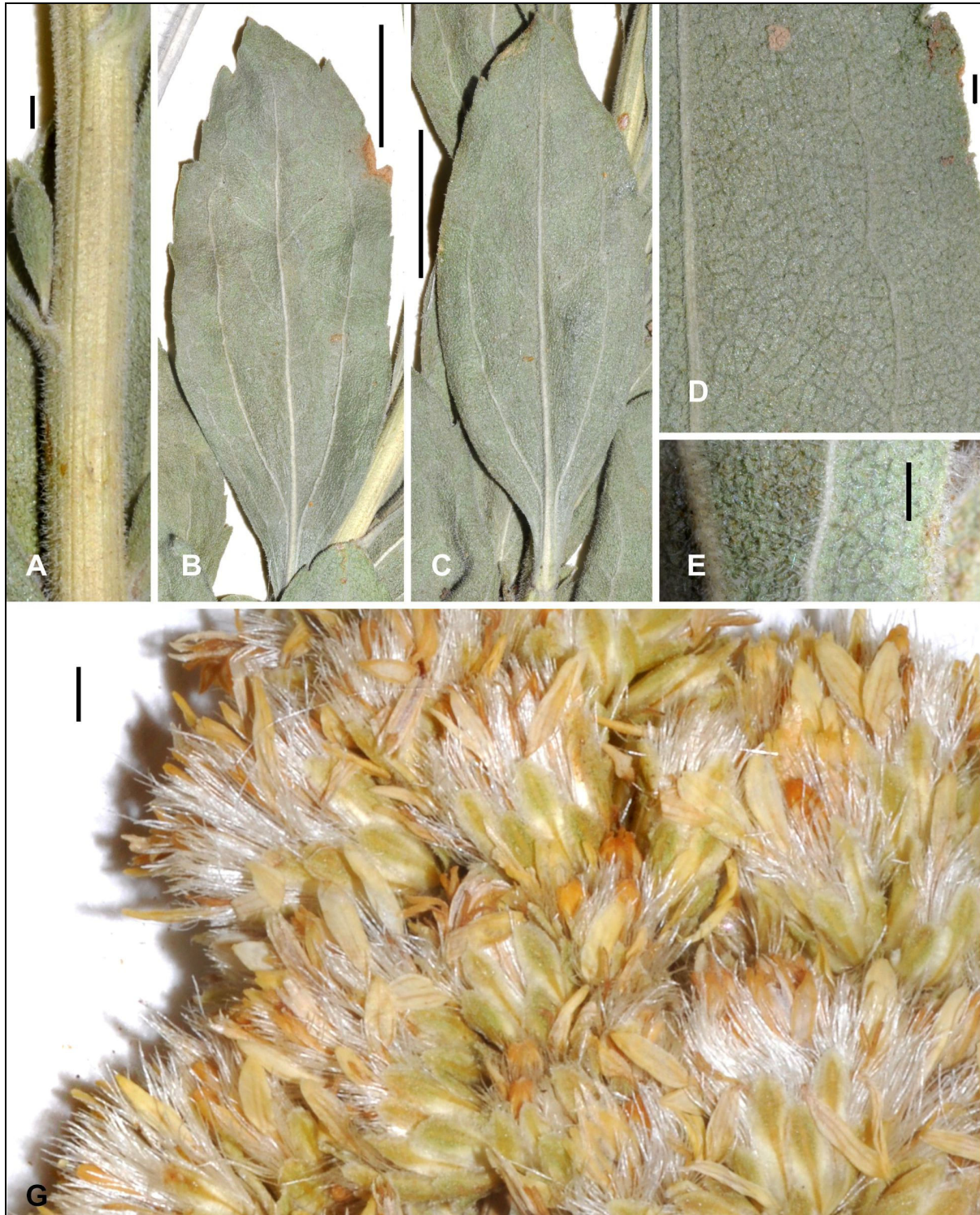


Figure 6. Details of the morphology of *Solidago mollis*. **A.** Upper stem, *J. & B. Semple 11391* (WAT). **B-C.** Lower mid stem and mid stem leaves, *Semple & Xiang 10201* (WAT). **D.** Mid stem leaf adaxial surface detail, *J. & B. Semple 10640* (WAT). **E.** Upper mid stem leaf adaxial surface detail, lateral vein, *J & B Semple 6655* (WAT). **F.** Heads, *J. & B. Semple 6655* (WAT). Scale bars = 1 mm in A, D-G; = 1 cm in B-C.



Figure 7. *Solidago nana*, Semple et al. 9235 (WAT) from Summit Co., Utah.

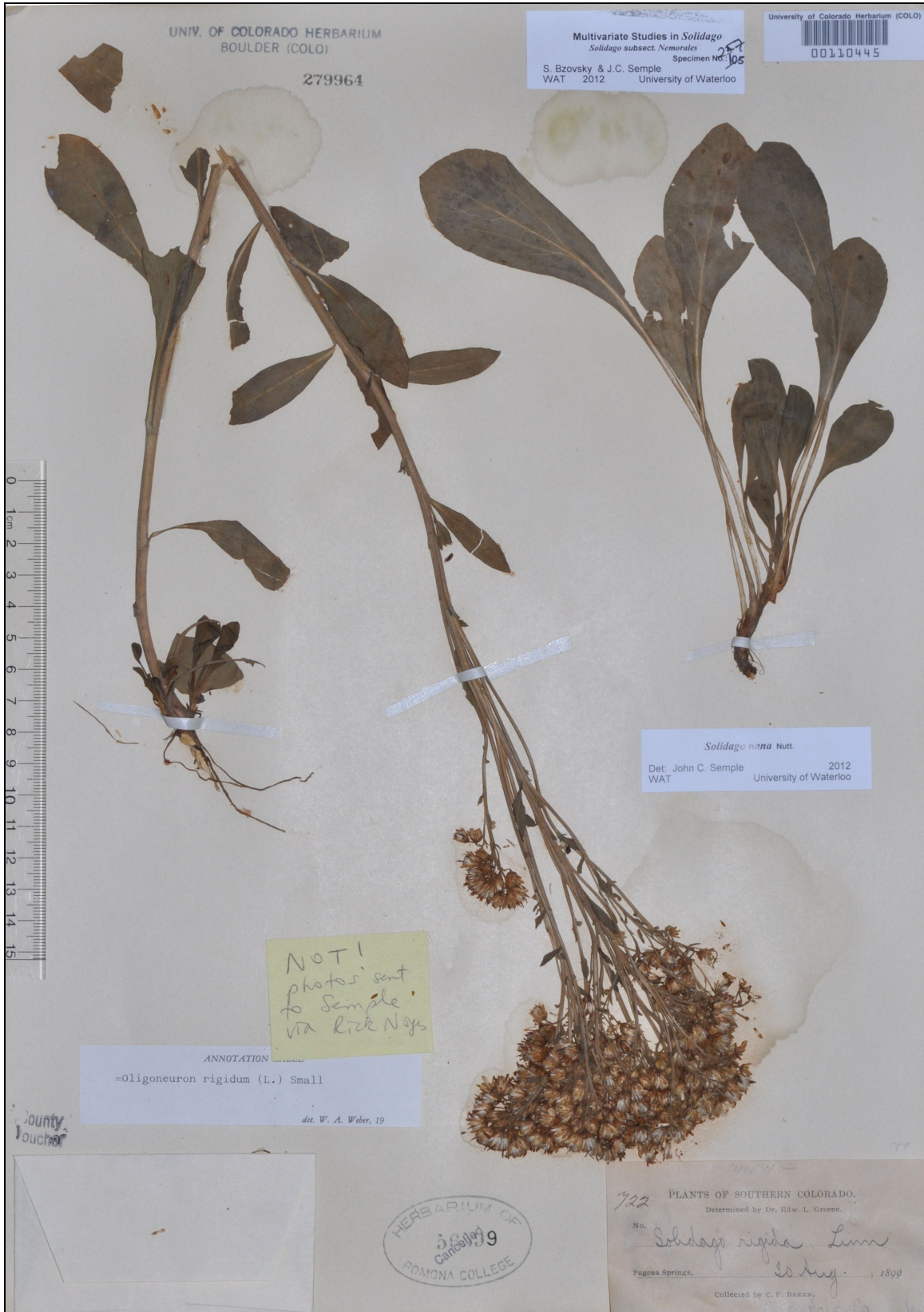


Figure 8. A robust plant of *Solidago nana*, Baker 722 (COLO) from Archuleta Co., Colorado.

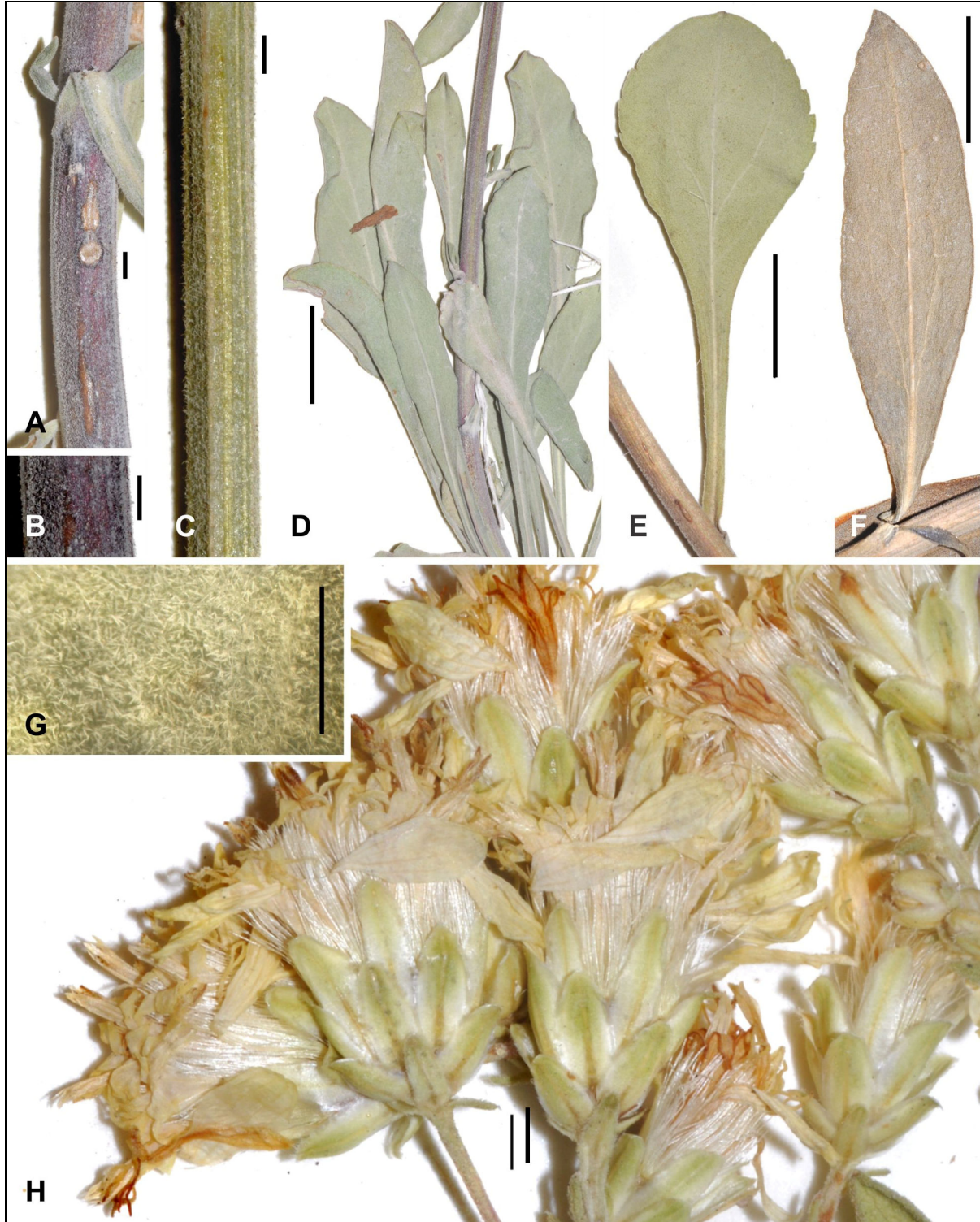


Figure 9. Details of the morphology of *Solidago nana*. **A-B.** Lower stem, *Semple et al.* 9267 (WAT). **C.** Mid stem, *Semple et al.* 9235 (WAT). **D.** Lower stem leaves, *Semple et al.* 9267 (WAT). **E.** Lower mid stem leaf, *Jones* 36536 (COLO). **F.** Mid stem leaf, *Baker* 722 (COLO). **G.** Mid stem adaxial surface, *Semple & Heard* 7803 (WAT). **H.** Heads, *Semple et al.* 9267 (WAT). Scale bars = 1 mm in A-B and G-H; = 1 cm in D-F.

appearing somewhat flat-topped. *Solidago nemoralis* (Figs. 10-11) includes mostly diploid eastern subsp. *nemoralis* and tetraploid subsp. *decemflora* on prairies; rhizomes are short to very short and basal rosette leaves are often present; stems and leaves are short canescent and often grayish-green; arrays of heads are secund conical and sometimes distally reflexed. *Solidago radula* (Figs. 12-13) is the other eastern North American species in the subsection and is distinguished by its scabrous leaves with hairs and texture like those of *S. hintoniorum*; it can be similar in appearance to *S. nemoralis* but the leaves are obviously scabrous.

Solidago velutina (Figs 14-16) includes considerable variation in stem height, leaf shape, leaf density, and inflorescence size and shape, some of which have been recognized nomenclaturally – *Solidago californica* Nutt. var. *nevadensis* A. Gray, Bot. Calif., 1: 319. 1876; *Solidago sparsiflora* A. Gray, Proc. Amer. Acad. 12: 58. 1877; *Solidago mollis* Rothrock in A. Gray, Wheeler Rep. Geogr. Surv. W100th Merid., Bot. 146. 1879. non Bartl. 1836; *Solidago trinervata* Greene, Pittonia 3: 100. 1896; *Solidago sparsiflora* A. Gray var. *subcinerea* A. Gray, Proc. Amer. Acad. Arts & Sci. 17: 197. 1882; *Solidago canadensis* L. var. *arizonica* A. Gray, Proc. Amer. Acad. Arts & Sci. 17: 197. 1882; *Solidago arizonica* (A. Gray) Woot. & Standl., Contrib. U.S. Nat. Herb. 16: 181. 1913.; *Solidago radulina* Rydb., Bull. Torrey Bot. Club 31: 650. 1904 [1905]; *Solidago howellii* Woot. & Standl., Contrib. U.S. Natl. Herb. 16: 181. 1913; *Solidago garrettii* Rydb. Bull. Torrey Bot. Club 37: 134. 1910; *Solidago velutina* DC. var. *nevadensis* (A. Gray) C. & J. Taylor, Sida 10: 246. 1984.; *Solidago velutina* DC. subsp. *sparsiflora* (A. Gray) Semple, Sida 20: 1616. 2003. Phyllaries tend to be lanceolate with somewhat attenuate acute tips and little surface indument (Fig. 17I), although rarely not attenuate and very rarely ovate in the southern end of the range in central Mexico, where the outer phyllaries are sometimes sparsely strigose. Phyllaries can be minutely stipitate glandular distally. Leaves of *S. velutina* are often triple-nerved (Fig. 17E) but variable in leaf density and shape (Figs. 17E-G). Some specimens lacking lower stem leaves could be mistaken for species in subsect. *Triplinervae* (Fig. 16). Morton et al. (2018) discussed such specimens in their presentation of chromosome numbers in the genus *Solidago*, noting that the holotype of *S. canadensis* var. *arizonica* A. Gray was one of these subsect. *Triplinerviae*-like specimens of *S. velutina*. *Solidago* × *scabrida* DC. appears to be a hybrid *S. velutina* × *S. paniculata* (Nesom 1989b), although the range of *S. velutina* shown below does not appear to overlap with that of *S. paniculata* (Semple 2018 frequently updated). Further research is needed on this taxon/hybrid.

The distributions of the seven species are allopatric to partially or completely sympatric with one or more other species in the subsection. *Solidago californica* is allopatric and native to disturbed soils and open habitats in much of California (except the eastern desert areas) and adjacent southern Oregon (Fig. 18). *Solidago hintoniorum* is native to disturbed soils in pine oak woods in south-central Nuevo León and adjacent Coahuila and Tamaulipas, Mexico (Fig. 19). *Solidago mollis* is native to the Great Plains from southern Alberta east to southern Manitoba south to Panhandle Texas and western Oklahoma and disjunct in central New Mexico (Fig. 20). *Solidago nana* is native to the eastern Great Basin mountains and western Rocky Mountains of Idaho south to New Mexico (Fig. 21); habitats include open pine woods, sagebrush and rabbit brush scrub, dry grasslands, roadsides and sandstone ledges. *Solidago nemoralis* is the most widely distributed species in the subsection and occurs in grasslands on the Great Plains from Alberta and Manitoba south to Texas and in disturbed habitats in much of eastern North America from eastern Manitoba to the Prince Edward Island south to Louisiana and northern Florida (Fig. 22). *Solidago radula* occurs in disturbed soils and open woods in the western portion of the eastern deciduous forest from Illinois southwest to Texas and on the prairies and in the Hill Country of Texas with scattered populations occurring eastward in the southeastern USA. (Fig. 23). *Solidago velutina* occurs in grasslands and open pine and oak forests and is frequently collected in disturbed roadsides of the Rocky Mountain cordillera and Great Basin from southern Montana and eastern California south to Zacatecas and San Luis Potosí, Mexico (Fig. 24).

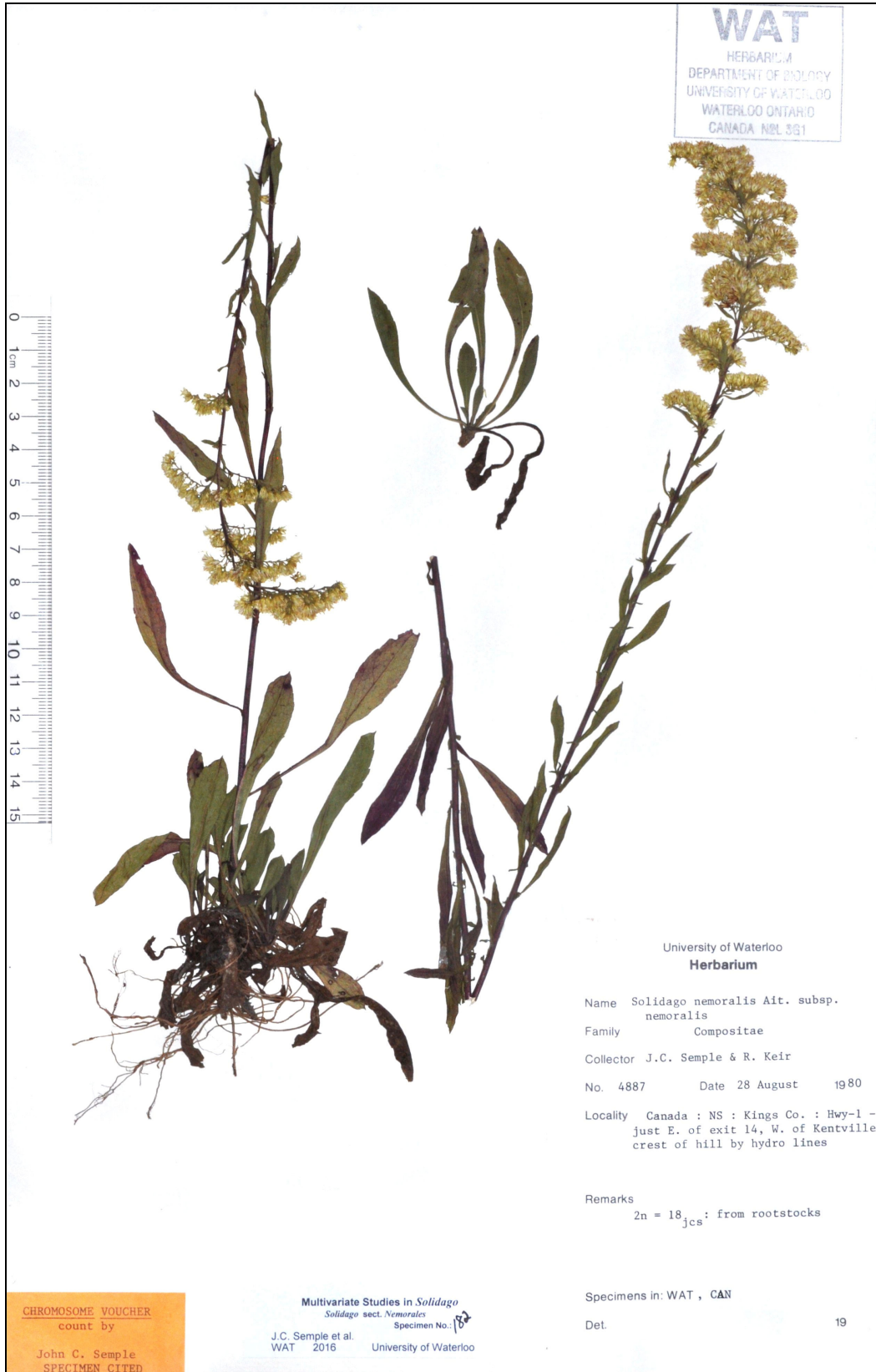


Figure 10. *Solidago nemoralis* subsp. *nemoralis*, Semple & Keir 4887 (WAT) from Kings Co., Nova Scotia.

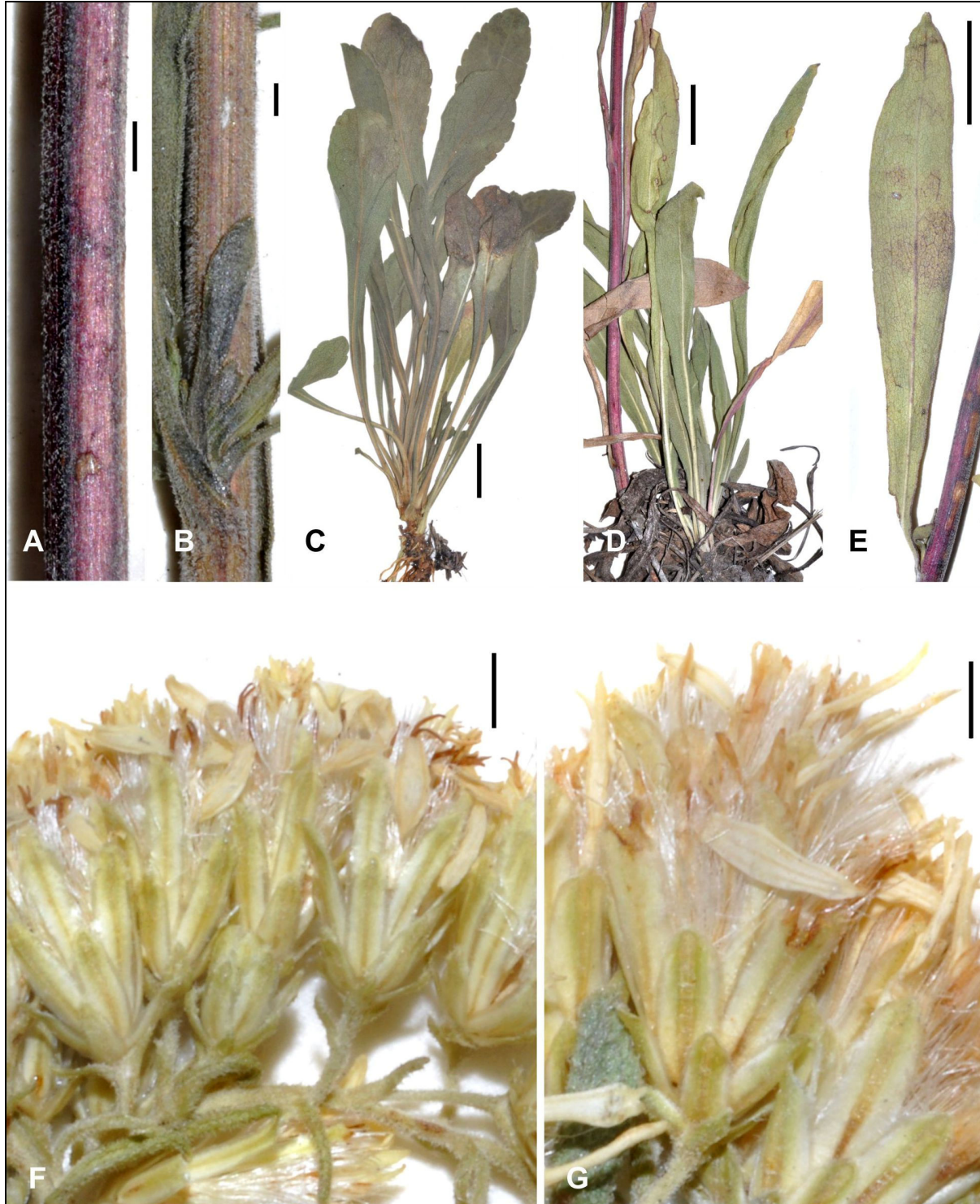


Figure 11. Details of the morphology of *Solidago nemoralis*. **A.** Lower stem, *Morton NA2285* (TRT). **B.** Mid stem, *Semple & Brammall 2305* (WAT). **C-D.** Basal rosettes, *Semple & Brammall 2305* (WAT) and *Semple & Brouillet 4216* (WAT). **E.** Mid stem leaf, *Semple & Brouillet 7131* (WAT). **F-G.** Heads, *Semple & Chmielewski 4990* (WAT) and *Semple & Brouillet 4489* (WAT); subsp. *nemoralis*, B, C and G; subsp. *decemflora*, A, D, E and G. Scale bars = 1 mm in A-B and F-G; = 1 cm in C-E.



Figure 12. *Solidago radula*, Thomas et al. 105653 (WAT) from Natchitoches Par., Louisiana.

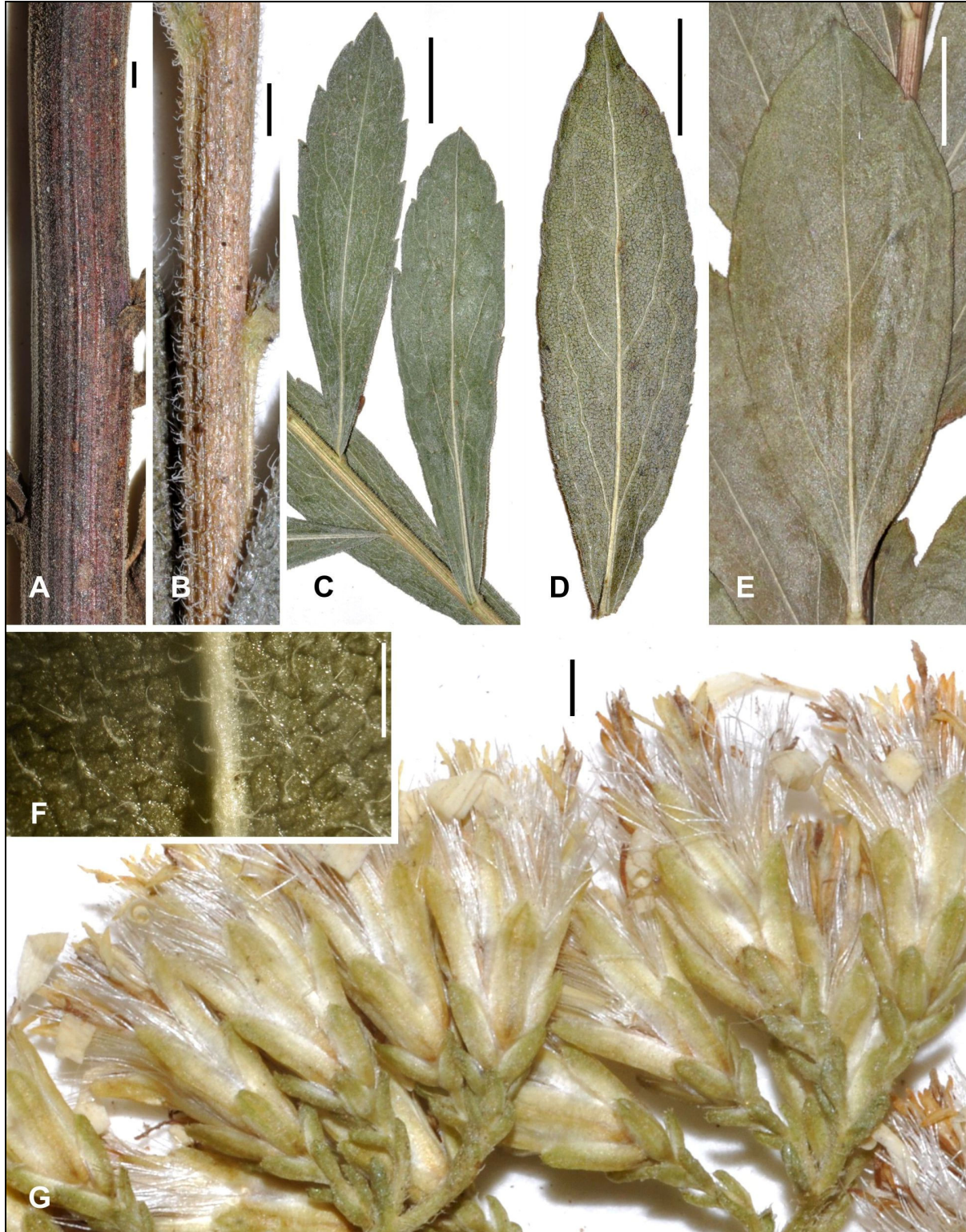


Figure 13. Details of the morphology of *Solidago radula*. **A.** Lower mid stem, *Thomas et al.* 91476 (WAT). **B.** Upper mid stem, *Thomas et al.* 105653 (WAT). **C.** Lower mid stem leaves, *Morton & Venn* NA16258 (TRT), greenhouse grown transplant. **D.** Mid stem leaf, *Redfearn & Shimizu* 33184 (WAT). **E.** Mid stem leaf, *Morton & Venn* NA16362 (TRT). **F.** Upper stem leaf mid vein and adaxial surface, *Redfearn & Shimizu* 33184 (WAT). **G.** Heads, *Taylor et al.* 5555 (WAT). Scale bars = 1 mm in A-B, F- G; = 1 cm in C-E.



Figure 14. *Solidago velutina*, Jones 4453 (WAT) from Garfield Co., Colorado.



Figure 15. *Solidago velutina*, Correll & Johnston 20140 (LL) from W of Durango, Mexico.

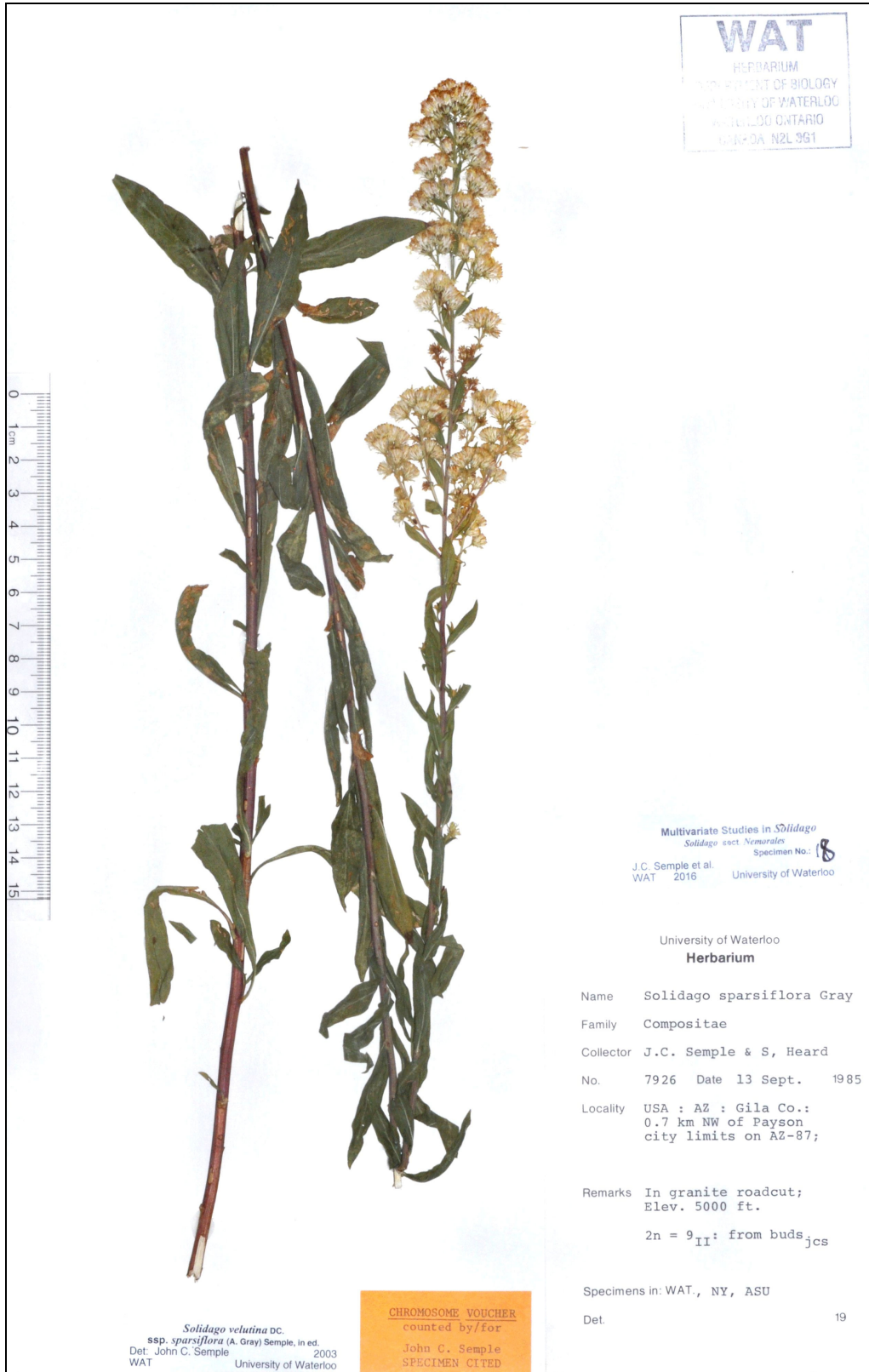


Figure 16. *Solidago velutina*, Semple & Heard 7926 (WAT) from Gila Co., Arizona; a tall shoot with narrow leaves and inflorescence.

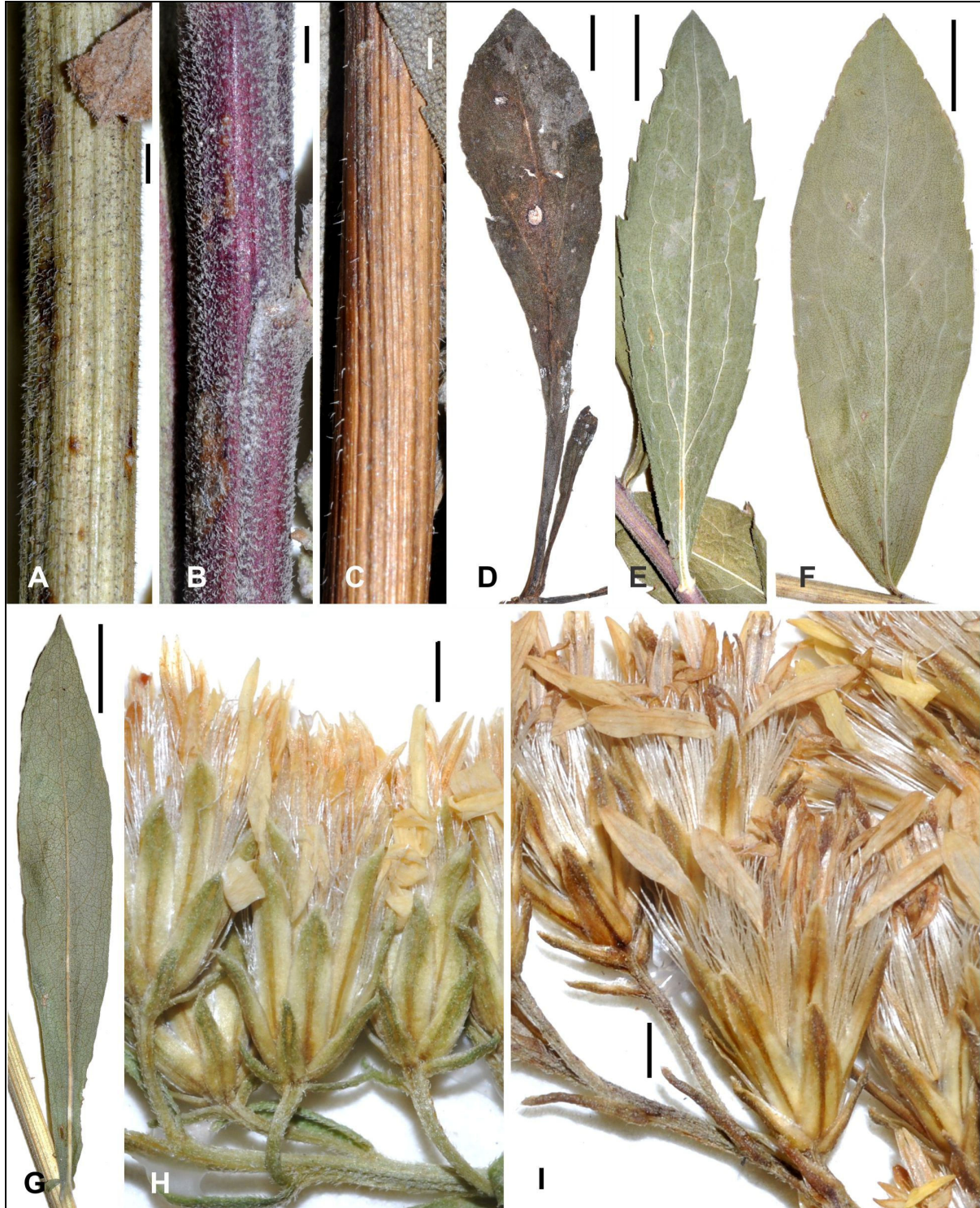


Figure 17. Details of the morphology of *Solidago velutina*. **A.** Lower stem, *Henrickson 22412* (TEX). **B.** Lower mid stem; *Davies & Turner A55* (TEX). **C.** Lower stem, *Hinton et al. 27924* (TEX). **D.** Lower stem leaf, *Hinton et al. 28069* (TEX). **E.** Lower stem leaf, *Jones 4453* (WAT). **F.** Mid stem leaf, *Bogler & Atkins 191* (TEX). **G.** Mid stem leaf, *Riskind 2215* (TEX). **H-I.** Heads, *Tenorio 1646* (TEX) and *Hinton 27918* (TEX). Scale bars = 1 mm in A-C and H-I; = 1 cm in D-G.

Numerous chromosome number reports have been published for taxa in *Solidago* subsect. *Nemorales* including diploids $2n=9II$ or $2n=18$, tetraploids $2n=18II$ or $2n=36$, and hexaploids $2n=54$. *Solidago californica* includes diploids and a few tetraploids (Raven et al. 1960; Beaudry 1969; Semple et al. 1984; Semple 1985; Semple et al. 1989; Semple et al. 1992; Semple et al. 2000; Morton et al. 2018). No chromosome number has been reported for *S. hintoniorum*. *Solidago mollis* is known to include tetraploids and hexaploids (Anderson et al. 1974; Löve & Löve 1982; Semple et al. 1984; Semple 1985; Semple & Chmielewski 1987; Semple et al. 1993; Morton et al. 2018). *Solidago nana* has been reported to be diploid a few times (Keil & Pinkava 1979; Semple & Chmielewski 1987 corrected identification in Semple et al. 1992; Semple et al. 1989; Semple et al. 2000). *Solidago nemoralis* includes mostly diploids and scattered tetraploids in subsp. *nemoralis* and only tetraploids in subsp. *decemflora* (Beaudry & Chabot 1959; Beaudry 1963; Kapoor 1977; Morton 1981; Semple et al. 1981; Löve & Löve 1982; Semple et al. 1984; Brammal & Semple 1990; Semple et al. 1993; Semple & Cook 2004; Semple et al. 2015; Morton et al. 2018; unpublished data); the cytogeography was presented by Brammal and Semple (1990). *Solidago radula* includes diploids and some tetraploids (Beaudry 1969; Semple et al. 1984 as *S. mollis* var. *angustifolia*; Semple & Chmielewski 1987; Semple et al. 1993; Semple et al. 2015; Morton et al. 2018); tetraploids occur in Arkansas and Texas, with the latter being similar to the type of *Solidago mollis* var. *angustifolia* from Texas treated here as a synonym of *S. radula*. *Solidago velutina* (often reported under the synonyms *S. sparsiflora* and *S. velutina* var. *nevadensis* (A. Gray) C. & J. Taylor) includes diploids, tetraploids, and a few hexaploids in the USA, while only diploids have been reported from Mexico (Raven et al. 1960; Turner et al. 1962; Anderson et al. 1974; Keil & Stuessy 1977; Keil & Pinkava 1979; Semple et al. 1984; Semple 1985; Ward & Spellenberg 1986; Semple & Chmielewski 1987; Keil et al. 1988; Semple et al. 1989; Semple et al. 1992; Zhao Zai-Ming 1996; Semple et al. 2001; Morton et al. 2018); based on involucre height variation it seems likely that some plants in Mexico are polyploid but this has not been documented.

The purpose of this study was to determine statistical support for recognizing the species and subspecies/varieties proposed within *Solidago* subsect. *Nemorales*, 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. Semple et al. (1990) compared *S. californica*, *S. sparsiflora*, and *S. nemoralis* (subsp. *decemflora* and subsp. *nemoralis*).

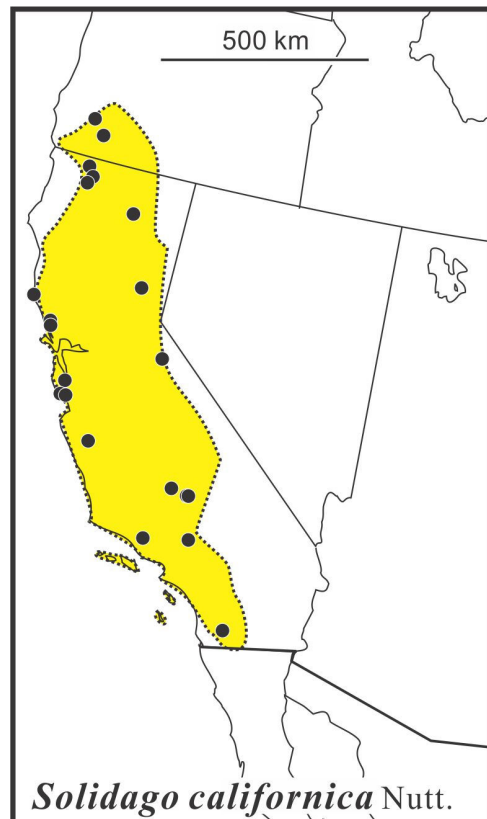


Figure 18. Range of distribution of *Solidago californica* in California and Oregon and the distribution of 21 specimens of included in the multivariate analyses of *Solidago* subsect. *Nemorales*; range based on all collections seen.

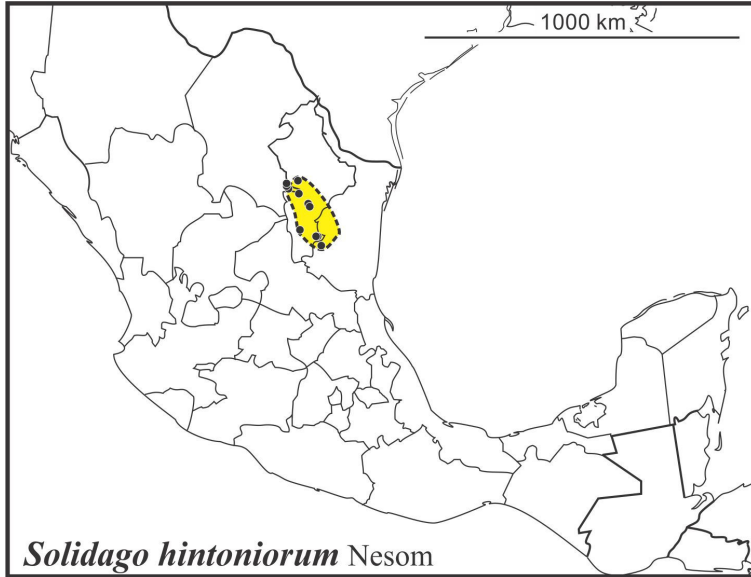


Figure 19. Range of distribution of *Solidago hintoniorum* in Nuevo León and Tamaulipas, Mexico, and the distribution of 5 specimens included in the multivariate analyses of *Solidago* subsect. *Nemorales* and other collections seen.

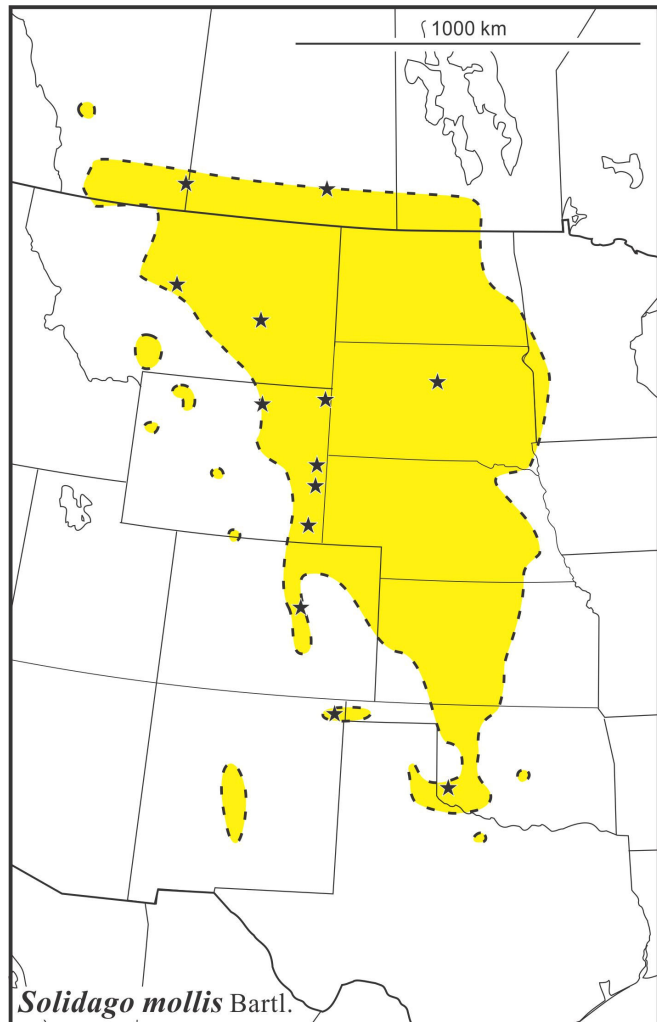


Figure 20. Range of distribution of *Solidago mollis* on the Great Plains in the USA and the distribution of 13 specimens included in the multivariate analyses of *Solidago* subsect. *Nemorales*; range based on all collections seen and literature.

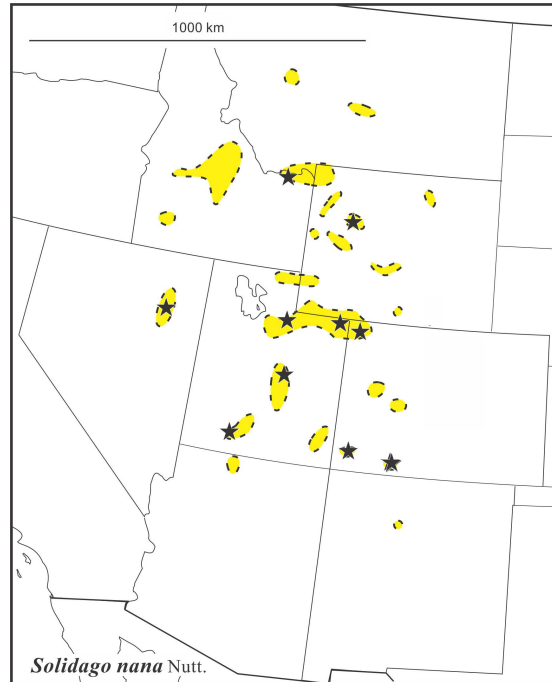


Figure 21. Range of distribution of *Solidago nana* in the Great Basin and central Rocky Mts. in the USA and the distribution of 12 specimens included in the multivariate analyses of *Solidago* subsect. *Nemorales*; range based on all collections seen and literature.

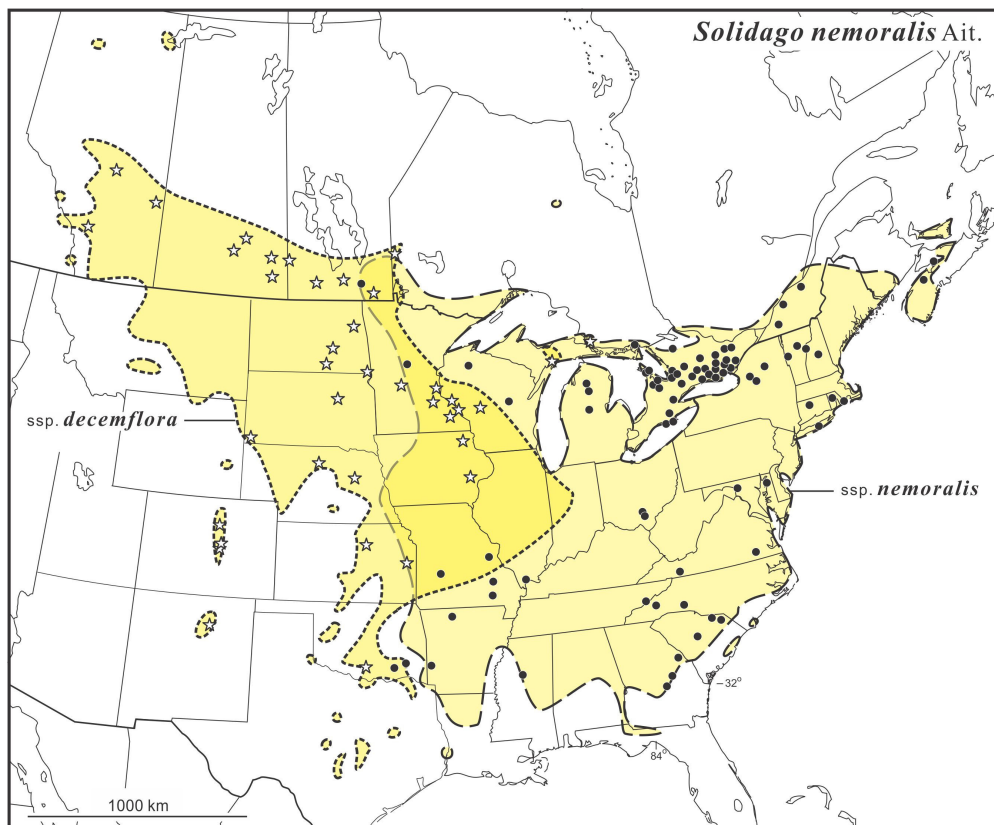


Figure 22. Range of distribution of *Solidago nemoralis* on the Great Plains and in eastern Canada and the USA and the distribution of 177 specimens included in the multivariate analyses of *Solidago* subsect. *Nemorales*; range based on all collections seen and literature; some symbols in densely sampled areas not shown for clarity.

Figure 23. Range of distribution of *Solidago radula* on the Great Plains and in western portion of the eastern deciduous forest area of the USA scattered in disjunction locations further east; the distribution of 13 specimens included in the multivariate analyses of *Solidago* subsect. *Nemorales* are indicated by stars; range based on all collections seen and literature.

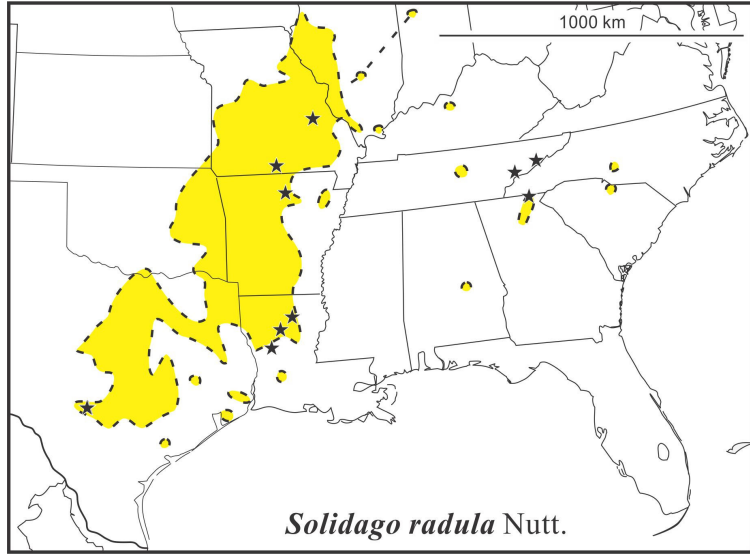
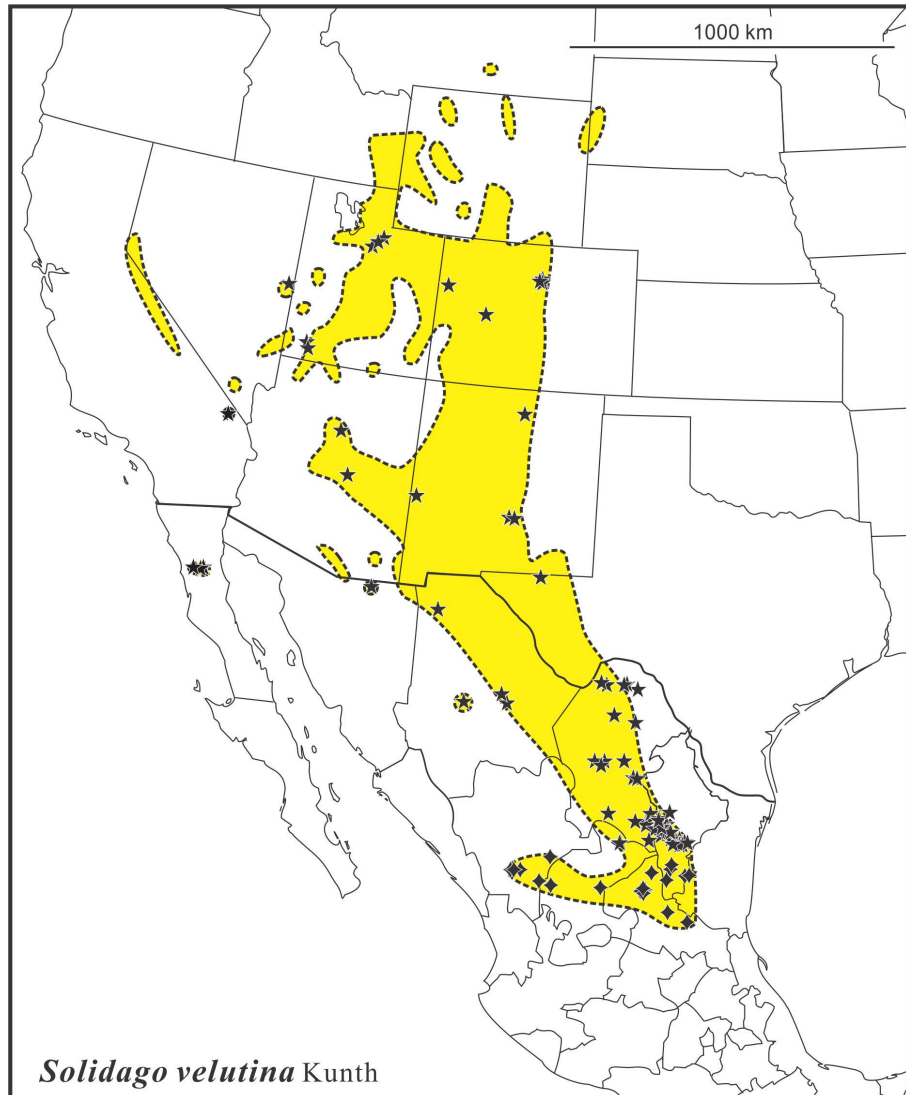


Figure 24. Range of distribution of *Solidago velutina* in the Great Basin and central Rocky Mts. in the USA south into central Mexico and the distribution of 96 specimens included in the multivariate analyses of *S. subsect. Nemorales* (putative subsp. *sparsiflora*, stars; putative subsp. *velutina*, diamonds; some symbols not shown due to density of sampling on southern Nuevo León); range based on all collections seen and literature.



MATERIAL AND METHODS

Herbarium specimens were borrowed and examined from the following herbaria: COLO, the J.K. Morton personal herbarium now in TRT, LL, MT, TEX, UNM, and WAT in MT (Thiers continuously updated). More than 1550 specimens were examined, from which 335 were chosen and measured for the statistical analyses based on completeness of the specimen, maturity, and geographical distribution: 21 specimens of *Solidago californica*, 5 of *S. hintonianum*, 12 of *S. mollis*, 12 of *S. nana*, 177 of *S. nemoralis*, 13 of *S. radula*, and 96 of *S. velutina*. In total, 18 vegetative and 12 floral traits were scored for the final analyses (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. Five analyses were performed. In the first analysis, *Solidago californica*, *S. hintonianum*, *S. mollis*, *S. nana*, *S. nemoralis*, *S. radula*, and *S. velutina* were included in a STEPWISE discriminant analysis and then a COMPLETE discriminant analysis with four traits because only five specimens of *S. hintonianum* could be included. In the second analysis, *S. mollis*, *S. nana*, and *S. radula* were included in a STEPWISE discriminant. In the third analysis, *S. mollis* and *S. radula*, were included in a STEPWISE discriminant. In the fourth, the *S. californica*/*S. sparsiflora*/*S. velutina* complex was investigated via a STEPWISE analysis. In the fifth, *S. californica* and *S. velutina* sensu lato (including *S. sparsiflora*) were included in a STEPWISE discriminant analysis. Numerous additional preliminary analyses were run over multiple years as the sample sizes of the taxa were increased but are not reported here.

Table 1. Traits scored for the multivariate analyses of 150 specimens of *Solidago* subsect. *Nemorales*.

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
CAPL	Length of inflorescence (cm)
INVOLHT	Involucre height at anthesis (mm)
RAYNUM	Number of ray florets per head

RSTRAPLN	Ray strap length top of the corolla tube to the tip of the strap (mm)
RSTRAPWD	Ray strap width measured at the widest point (mm)
RACHLN	Ray floret ovary/fruit body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
DCORLN	Disc floret corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc floret corolla lobe length lobe (mm)
DACHLN	Disc floret ovary/fruit body length at anthesis (mm)
DPAPLN	Disc floret pappus length at anthesis (mm)
DACHPUB	Number of hairs on disc floret ovary/fruit body

Placement of specimens of *Solidago velutina* into subsp. *velutina* was made based on geographic location. The lectotype (Nesom 1989b) of *S. velutina* is *Berlandier 930* (G-DC!), whose exact provenance is uncertain. *Berlandier 930* was in the range of *S. velutina* in late 1827 and January 1828 starting from Mexico City and passing through San Luis Potosí and Nuevo León to Saltillo and Monterey, and later again in April of 1830 in the Monterey area (Lawson 2012). Assuming *Berlandier 930* came from San Luis Potosí, then the southern portion of the range including Zacatecas would include plants of subsp. *velutina* and plants from further north could be assigned to subsp. *sparsiflora* as shown in Fig. 24. Nesom (1989b) did not divide the species in infraspecific taxa.

RESULTS

Seven 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 the number of mid stem leaf margin serrations. Basal rosette leaves were often not present and were not included in the analyses. Lower stem leaves were present on many specimens but were not included in the analyses because their traits correlated highly among themselves and with mid and upper stem leaf traits. Among the floral traits scored, only ray floret pappus length and disc floret pappus length correlated highly; the latter was included in the analyses.

In the COMPLETE discriminant analysis of 335 specimens of seven species level a priori groups (*Solidago californica*, *S. hintoniorum*, *S. mollis*, *S. nana*, *S. nemoralis*, *S. radula* and *S. velutina*), the following four of seven traits selected in a STEPWISE analysis were used in the COMPLETE analysis and are listed in order of decreasing F-to-remove values: disc corolla lobe length (98.31), ray floret lamina length (84.13), number of disc florets (77.89), and number of ray florets (32.07). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. nemoralis* and *S. velutina* (281.084); the smallest separations were between *S. mollis* and *S. radula* (1.548) and between *S. hintoniorum* and *S. radula* (9.861).

In the Classificatory Discriminant Analysis of 335 specimens of the seven species level a priori groups (*Solidago californica*, *S. hintoniorum*, *S. mollis*, *S. nana*, *S. nemoralis*, *S. radula* and *S. velutina*), percents of correct a posteriori assignment to the same a priori group ranged from 58-94%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. One-hundred and sixty-five of 176 specimens of the *S. nemoralis* a priori group (94%) were assigned a posteriori into the *S. nemoralis* group; 147 specimens with 90-100% probability, 7 specimens with 80-89% probability, 3 specimens

Table 2. Between groups F-matrix for the seven priori groups in a COMPLETE analysis (df = 4 325).

Group	<i>californica</i>	<i>hintoniorum</i>	<i>mollis</i>	<i>nana</i>	<i>nemoralis</i>	<i>radula</i>
<i>hintoniorum</i>	22.143					
<i>mollis</i>	28.057	15.848				
<i>nana</i>	44.090	20.792	20.175			
<i>nemoralis</i>	64.127	46.325	34.100	104.887		
<i>radula</i>	29.236	9.861	1.548	15.556	46.453	
<i>velutina</i>	34.437	11.294	39.829	90.162	281.084	34.065

Wilks' lambda = 0.0540 df = 4 6 328; Approx. F= 61.8377 df = 24 1134 prob = 0.0000

with 72-77% probability, 3 specimens with 62-65% probability, and 3 specimens with 59% (28% to *S. mollis*, 6% to *S. radula* and 6% *S. californica*; Semple & Brouillet 3472 WAT, subsp. *nemoralis*, from Carroll Co., New Hampshire; diploid), 54% probability (32% *S. velutina* and 13% *S. californica*; Semple & Heard 8079 WAT, subsp. *decemflora* from San Miguel Co., New Mexico; tetraploid), and 52% probability (33% *S. velutina* and 15% *S. californica*; Semple & Chmielewski 5094 WAT, subsp. *decemflora* from Pope Co., Minnesota; tetraploid). Eleven specimens of the *S. nemoralis* a priori group were assigned to other species: 6 specimens of subsp. *decemflora* to *S. californica* with 93% probability (Semple & Brouillet 4273 WAT from Banff N.P., Alberta), 89% probability (Semple & Brouillet 4212 WAT from E of Bredenbury, Saskatchewan; tetraploid), 59% probability (Semple & Brouillet 6960 WAT from Barnes Co., North Dakota; tetraploid), 49% probability (Semple & Heard 8079 WAT from San Miguel Co., New Mexico; tetraploid), 48% probability (Semple & B. Semple 6676 WAT from Stutsman Co., North Dakota; tetraploid), and 40% probability (Semple & Chmielewski 5258 WAT from Miami Co., Kansas; tetraploid); 3 specimens to *S. velutina* with 99% probability (Semple & Brouillet 4216 WAT from W of Springside, Saskatchewan; tetraploid), 90% probability (Semple & Chmielewski 5168 WAT from Winneskiek Co., Iowa; tetraploid), and 50% probability (29% *S. mollis*, 10% to *S. radula*; Brunton 18486 WAT from Burnt Lands Prov. Pk., Ontario); and 2 specimens of subsp. *nemoralis* to *S. mollis* with 46% probability (42% to *S. nemoralis*; Semple & Heard 8265 WAT from Pushmataha Co. Oklahoma) and 43% probability (27% to *S. nemoralis* and 26% to *S. radula*; Semple & Heard 8275 WAT from Polk Co., Arkansas). Eleven of 12 specimens of the *S. nana* a priori group (92%) were assigned a posteriori into the *S. nana* group; 10 specimens with 96-100% probability, and 1 specimen with 88% probability. One specimen of the *S. nana* a priori group was assigned to *S. radula* with 51% probability (36% to *S. mollis* and 14% to *S. nana*; Cronquist 8807 COLO from Clarke Co., Idaho). Ten of 13 specimens of the *S. mollis* a priori group (77%) were assigned a posteriori into the *S. mollis* group; 4 specimens with 71-79% probability, 1 specimen with 61% probability, and 5 specimens with 57% probability (42% to *S. radula*; 266 Semple & B. Semple 11391 WAT from Judith Basin Co., Montana), 56% probability (42% to *S. radula*; Semple & B. Semple 10644 WAT from E of Walsh AB in Saskatchewan), 54% probability (34% to *S. nemoralis* and 12% to *S. radula*; Semple & B. Semple 6624 WAT from Niobrara Co., Nebraska), 53% probability (43% to *S. radula*; Hubbard s.n. UNM from Union Co., New Mexico), and 51% probability (32% to *S. radula* and 12% to *S. velutina*; Semple & Brouillet 6984 WAT from Rosebud Co., Montana; hexaploid). Three specimens of the *S. mollis* a priori group were assigned to *S. radula* with 59% probability (38% to *S. mollis*; Calvert s.n. WAT from Lumsden, Saskatchewan), 56% probability (43% to *S. mollis*; Semple & Xiang 10188 WAT from Crook Co., Wyoming; tetraploid), and 50% probability (29% to *S. mollis* and 20% to *S. nana*; Semple & B. Semple 6655 WAT from Potter Co., South Dakota). Sixteen of the 21 specimens of the *S. californica* a priori group (76%) were assigned a posteriori to the *S. californica* group; 10 specimens with 90-100% probability, 3 specimens with 81-89% probability, 1 specimen with 78% probability, and 2 specimens with 57% probability (42% to *S. nemoralis*; Semple & Heard 8607

WAT from Monterey Co., California) and 53% probability (22% to *S. velutina* and 21% to *S. nemoralis*; Semple & Heard 8730 WAT from Tuolumne Co., California). Five specimens of the *S. californica* a priori group were assigned to other species: 4 specimens to *S. velutina* with 75% probability (25% to *S. californica*; Ringius 1473 WAT from Santa Cruz Co., California), 61% probability (35% to *S. californica*; Ringius 1495 WAT from Sonoma Co., California), 61% probability (14% to *S. radula*, 12% to *S. hintoniorum*, and 7% to *S. californica*; Semple & Heard 8465 WAT from Siskiyou Co., California; diploid), and 52% probability (28% to *S. mollis*, 8% to *S. radula*; Semple & Heard 8486 WAT from Siskiyou Co., California); and 1 specimen to *S. nemoralis* with 65% probability (17% to *S. velutina* and 14% to *S. californica*; Semple & Brouillet 7131 WAT from Jackson Co., Oregon). Sixty-nine of 96 specimens of the *S. velutina* a priori group (72%) were assigned a posteriori into the *S. velutina* group; 40 specimens with 91-100% probability, 13 specimens with 80-89% probability, 6 specimens with 72-78% probability, 3 specimens with 61-68% probability, and 3 specimens with 59% probability (25% to *S. nemoralis* and 16% to *S. californica*; Semple & B Semple 5547 WAT from Coconino Co., Arizona; diploid), 56% probability (25% to *S. californica* and 10% to *S. hintoniorum*; Chiang et al. 7883 LL from Zacatecas, Mexico) and 55% probability (45% to *S. californica*; Semple & B Semple 5748 WAT from Wheeler Peak, Nevada). Twenty-seven specimens of the *S. velutina* a priori group were assigned to other species: 9 specimens to *S. californica* with 50-100% probability; 8 specimens to *S. hintoniorum* with 36-79% probability, 3 specimens to *S. nemoralis* with 79-88% probability, and 3 specimens to *S. radula* with 46-56% probability; additional details on these specimens are not presented. Three of 5 specimens of the *S. hintoniorum* a priori group (60%) were assigned a posteriori to the *S. hintoniorum* group: 2 specimens with 100% probability and 1 specimen with 92% probability. Two specimens of the *S. hintoniorum* a priori group were assigned a posteriori to *S. velutina* with 99% probability (Hinton et al. 23323 TEX from Nuevo León, Mexico) and 66% probability (26% to *S. hintoniorum*; Hinton et al. 21492 TEX from Nuevo León, Mexico; this was an upper shoot on the same sheet with one of the specimens with 100% to *S. hintoniorum*). Seven of 12 specimens of the *S. radula* a priori group (58%) were assigned a posteriori into the *S. radula* group; 1 specimen with 79% probability, 4 specimens with 64-68% probability, and 1 specimen 51% probability (48% to *S. mollis*; Morton & Venn NA16362 TRT from Kerr Co., Texas; tetraploid). Five specimens of the *S. radula* a priori group were assigned a posteriori to other species; 1 specimen to *S. californica* with 68% and 4 specimens to *S. mollis* with 62% probability (38% to *S. radula*; Cook et al. C-628 WAT from Towns Co., Georgia), 62% probability (Morton & Venn NA16364 TRT from Kerr Co., Texas; tetraploid), 58% probability (42% to *S. radula*; Semple et al. 9388 WAT from Washington Co., Missouri; diploid), and 55% probability (45% to *S. radula*; Morton & Venn NA16258 TRT from Stone Co., Arkansas; tetraploid).

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>californica</i>	<i>hintoniorum</i>	<i>mollis</i>	<i>nana</i>	<i>nemoralis</i>	<i>radula</i>	<i>velutina</i>	% correct
<i>californica</i>	16	0	0	0	1	0	4	76
<i>hintoniorum</i>	0	3	0	0	0	0	2	60
<i>mollis</i>	0	0	10	0	0	3	0	77
<i>nana</i>	0	0	0	11	0	1	0	92
<i>nemoralis</i>	6	0	2	0	165	0	3	94
<i>radula</i>	1	0	4	0	0	7	0	58
<i>velutina</i>	9	8	2	0	4	4	69	72
Totals	32	11	18	11	170	15	78	84

Jackknifed classification matrix

Group	<i>californica</i>	<i>hintoniorum</i>	<i>mollis</i>	<i>nana</i>	<i>nemoralis</i>	<i>radula</i>	<i>velutina</i>	% correct
<i>californica</i>	15	0	0	1	1	0	4	71
<i>hintoniorum</i>	0	2	0	1	0	0	2	40
<i>mollis</i>	0	0	9	0	0	4	0	69
<i>nana</i>	0	0	0	11	0	1	0	92
<i>nemoralis</i>	6	0	2	0	165	0	3	94
<i>radula</i>	1	0	4	0	0	7	0	58
<i>velutina</i>	10	8	2	0	4	4	68	71
Totals	32	10	17	13	170	16	77	83

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 334 specimens of *Solidago californica*, *S. hintoniorum*, *S. mollis*, *S. nana*, *S. nemoralis*, *S. radula* and *S. velutina* are presented in Fig. 25. Eigenvalues on the first three axes were 3.829, 1.485, and 0.500.

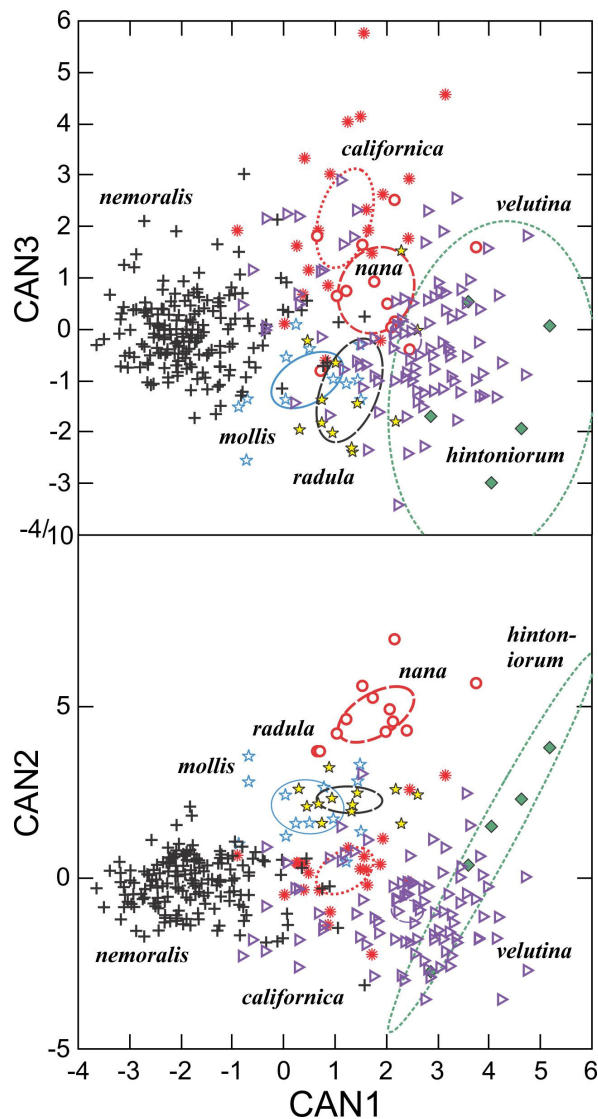


Figure 25. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 335 specimens of *Solidago* subsect. *Nemorales*: *S. californica* (red star bursts), *S. hintoniorum* (green diamonds), *S. mollis* (open blue stars), *S. nana* (red circles), *S. radula* (yellow stars), and *S. velutina* (right oriented violet triangles); COMPLETE discriminant analysis using four traits.

Three species level a priori groups analysis

The Pearson correlation matrix for traits of specimens of *Solidago mollis*, *S. nana*, and *S. radula* included $r > |0.7|$ for most pairs of basal and lower leaf traits and mid and upper leaf reducing the number used to mid stem leaf width and serrations. Basal rosette leaves were rarely present and were not included in the discriminant analyses. Many floral traits were correlated, and only the numbers of ray and disc florets and the lengths of disc corolla, corolla lobes, fruit/ovary body, and pappus were included in the STEPWISE analysis.

In the STEPWISE discriminant analysis of 37 specimens of three species level a priori groups in (*Solidago mollis*, *S. nana*, and *S. radula*), the following four traits were selected and are listed in order of decreasing F-to-remove values: number of disc florets (35.70), disc corolla lobe length (5.95), number of ray florets (4.19), and mid leaf width (4.01). 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. mollis* and *S. nana* (14.334); the smallest separation was between *S. mollis* and *S. radula* (1.574).

Table 4. Between groups F-matrix for the four species level a priori groups analysis (df = 7 26).

Group	<i>mollis</i>	<i>nana</i>
<i>nana</i>	14.334	
<i>radula</i>	1.574	11.642

Wilks' lambda = 0.1391 df = 8 2 34; Approx. F= 5.67263 df = 16 54 prob = 0.0000

In the Classificatory Discriminant Analysis of 37 specimens of the four species level a priori groups (*S. mollis*, *S. nana* and *S. radula*), percents of correct a posteriori assignment to the same a priori group ranged from 58-100%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 12 specimens of the *S. nana* a priori group (100%) were assigned a posteriori into the *S. nana* group; 11 specimens with 97-100% probability and 1 specimen with 55% probability (35% to *S. radula* and 10% to *S. mollis*). Eleven of 13 specimens of the *S. mollis* a priori group (85%) were assigned a posteriori into the *S. mollis* group; 1 specimen with 94% probability, 1 specimen with 82% probability, 4 specimens with 71-78% probability, 2 species with 67% and 62% probabilities, and 3 specimens with 55% probability (45% to *S. radula*), 52% probability (46% to *S. radula*), and 52% probability (47% to *S. radula*). Two specimens of the *S. mollis* a priori groups were assigned to *S. radula* with 69% probability (31% to *S. mollis*; *Sauleda & Sauleda* 6323 WAT from Elbert Co., Colorado; 39.5 cm tall shoots with congested smallish stem leaves and small involucre) and 61% probability (39% to *S. mollis*; *Calvert s.n.* WAT from Lumsden, Saskatchewan; 58.5 cm tall shoot with no lower stem leaves and 4.1 mm tall involucre). Seven of 12 specimens of the *S. radula* a priori group (58%) were assigned a posteriori into the *S. radula* group; 1 specimen with 96% probability, 1 specimen with 87% probability, 3 specimens with 79% probability, and 2 specimens with 69% probability (16% to *S. mollis* and 14% to *S. nana*; *Thomas et al.* 102874 WAT from Winn Par., Louisiana; a *S. nemoralis*-like general appearance) and 62% probability (38% to *S. mollis*; *Redfearn & Shimizu* 33184 WAT from Taney Co., Missouri). Five specimens of the *S. radula* a priori group were assigned to *S. mollis* with 68% probability (32% to *S. radula*; *Morton & Venn* NA16364 TRT from Kerr Co., Texas; tetraploid), 68% probability (32% to *S. radula*; *Morton & Venn* NA16258 TRT from Stone Co., Arkansas; tetraploid), 67% probability (33% to *S. radula*; *Morton &*

Venn NA16362 TRT from Kerr Co., Texas; tetraploid), 64% probability (36% to *S. radula*; Cook et al. C-628 WAT from Towns Co., Georgia), and 54% probability (46% to *S. radula*; Semple et al. 9388 WAT from Washington Co., Missouri; diploid).

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>mollis</i>	<i>nana</i>	<i>radula</i>	% correct
<i>mollis</i>	11	0	2	85
<i>nana</i>	0	12	0	100
<i>radula</i>	5	0	7	58
Totals	16	12	9	81

Jackknifed classification matrix

Group	<i>mollis</i>	<i>nana</i>	<i>radula</i>	% correct
<i>mollis</i>	7	0	6	54
<i>nana</i>	0	11	14	92
<i>radula</i>	5	0	7	58
Totals	12	11	14	68

Two dimensional plot of CAN1 versus CAN2 canonical scores for 37 specimens of *Solidago mollis*, *S. nana*, and *S. radula* is presented in Fig. 26. Eigenvalues on the first two axes were 3.999 and 0.213.

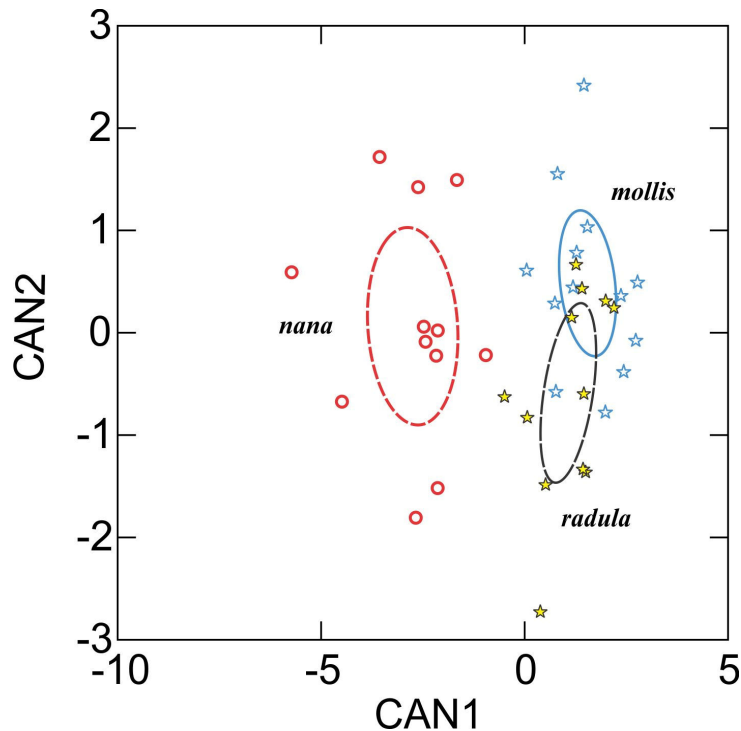


Figure 26. Plot of canonical scores (CAN1 vs CAN2) analysis for 37 specimens of *Solidago* subsect. *Nemorales*: *S. mollis* (open blue stars), *S. nana* (red circles), and *S. radula* (yellow stars).

Two species level a priori groups analysis: *Solidago mollis* and *S. radula*

The Pearson correlation matrix yielded $r > |0.7|$ for most pairs of leaf traits reducing the number to be used to mid stem leaf width and number of serrations and upper stem leaf length. Most floral traits were not highly correlated. Involucre height correlated with ray floret pappus length and disc floret corolla length. Ray floret fruit body and pappus lengths correlated with disc floret fruit body length and disc floret corolla length, respectively; the latter two traits were included in the analyses.

In the STEPWISE discriminant analysis of 23 specimens of two species level a priori groups (*S. mollis* and *S. radula*), the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: involucre height (5.91), number of ray florets (4.73), and disc floret lobe length at anthesis (4.09). 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 $p = 0.0143$ that the null hypothesis was true. *Solidago mollis* and *S. radula* had an F-to separate value of 4.505 (Wilks' lambda = 0.5967 df = 3 1 22; Approx. F= 4.5054 df = 3 20 prob = 0.0143).

In the Classificatory Discriminant Analysis of 23 specimens of the two species level a priori groups (*S. mollis* and *S. radula*), percents of correct a posteriori assignment to the same a priori group were 77% and 73%. The Classification matrix and Jackknife classification matrix are presented in Table 6. Ten of the 13 specimens of the *S. mollis* a priori group (77%) were assigned a posteriori into the *S. mollis* group; 3 specimens with 91-98% probability, 3 specimens with 82-88% probability, 2 specimens with 79% and 77% probabilities, and 2 specimens with 67% and 64% probabilities. Three specimens of the *S. mollis* a priori groups were assigned to *S. radula* with 79% (*Calvert s.n.* WAT from Lumsden, Saskatchewan), 58% probability (*Sauleda & Sauleda 6323* WAT from Elbert Co., Colorado), and 53% probability (*Semple & Brouillet 6984* WAT from Rosebud Co., Montana; hexaploid). Eight of 11 specimens of the *S. radula* a priori group (75%) were assigned a posteriori into the *S. radula* group; 4 specimens with 91-99% probability, 2 specimens with 72% and 71% probabilities, 1 specimen with 68% probability, and 1 specimen with 51% probability (*Thomas et al. 102874* WAT from Winn Par., Louisiana). Three specimens of the *S. radula* a priori group were assigned to *S. mollis* with 67% probability (*Taylor et al. 5555* WAT from Ouachita Par., Louisiana), 66% probability (*Morton & Venn NA16364* TRT from Kerr Co., Texas; tetraploid), and 64% probability (*Morton & Venn NA16362* TRT from Kerr Co., Texas; tetraploid).

Frequencies of CAN1 canonical scores for 23 specimens of *S. mollis* and *S. radula* are presented in histograms in Fig. 27. The Eigenvalue on the first axis was 0.676.

Table 6. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three varietal level a priori groups; a posteriori placements to groups in rows; Nesom (2008) variety concept.

Group	<i>mollis</i>	<i>radula</i>	% correct
<i>mollis</i>	10	3	77
<i>radula</i>	3	8	73
Totals	13	10	75

Jackknifed classification matrix

Group	<i>mollis</i>	<i>radula</i>	% correct
<i>mollis</i>	10	3	77
<i>radula</i>	4	7	64
Totals	14	10	71

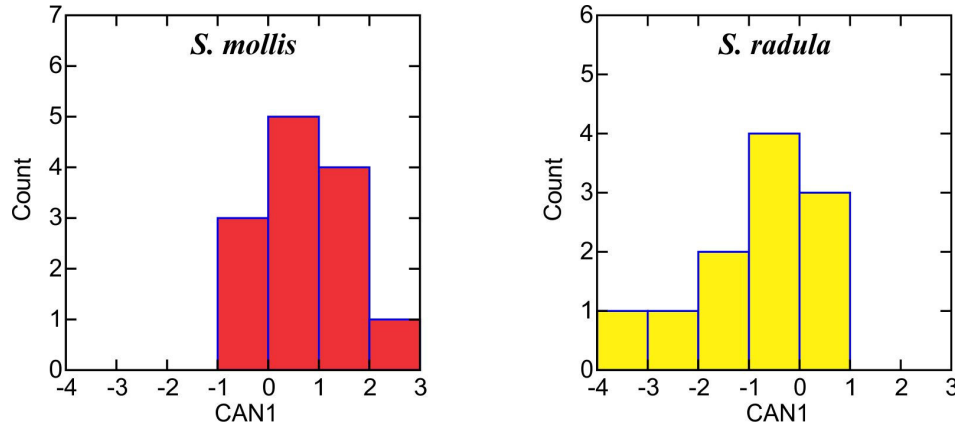


Figure. 27. Histograms of CAN1 canonical scores for 23 specimens of *S. mollis* (left) and *S. radula* (right).

Three species/subspecies level a priori groups analysis of *S. velutina* s.l.

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 and upper stem leaf length. Multiple floret traits were correlated and involucre height, ray floret number, ray floret lamina length and width, disc floret number, and disc floret corolla, lobe and fruit body lengths were included in the analyses.

In the STEPWISE discriminant analysis of 99 specimens of three subspecies level a priori groups of *Solidago velutina* s.l. (subsp. *californica*, subsp. *sparsiflora*, and subsp. *velutina*) plus 14 specimens only included a posteriori, the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret number (9.90), disc corolla length (9.40), and ray floret lamina length (4.57). 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 7. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between subsp. *californica* and subsp. *sparsiflora* (22.426) and subsp. *californica* subsp. *velutina* (20.332); the smallest separation was between putative subsp. *sparsiflora* and putative subsp. *velutina* (1.146).

Table 7. Between groups F-matrix for the three varietal level a priori groups analysis (df = 3 91); alternative varietal limits.

Group	<i>californica</i>	<i>sparsiflora</i>
<i>sparsiflora</i>	22.426	
<i>velutina</i>	20.332	1.146

Wilks' lambda = 0.5387 df = 3 2 93; Approx. F= 10.9958 df = 6 182 prob = 0.0000

In the Classificatory Discriminant Analysis of 99 specimens of the three species/subspecies level a priori groups in *S. velutina* s.l. (subsp. *californica*, subsp. *sparsiflora*, and subsp. *velutina*) plus 14 specimens only included a posteriori, percents of correct a posteriori assignment to the same a priori group ranged from 32-92%. The Classification matrix and Jackknife classification matrix are presented in Table 8. Results are presented in order of decreasing percents of correct placement. Ten

of the 11 specimens of the *S. californica*/subsp. *californica* a priori group (92%) plus 6 specimens included a posteriori were assigned a posteriori into the subsp. *californica* group; 12 specimens with 91-100% probability, 2 specimens with 83% and 85% probabilities, 2 specimens with 72-73% probability, and 1 specimens with 69% probability, and 1 specimen with 52% probability (28% to subsp. *sparsiflora* and 20% to subsp. *velutina*; Semple et al. 9365 WAT from Kern Co., California). One specimen of the *S. californica*/subsp. *californica* a priori group plus one specimen included a posteriori were assigned to subsp. *sparsiflora* with 53% probability (29% to subsp. *californica* and 18% to subsp. *velutina*; Ringius 1495 WAT from Sonoma Co., California) and 52% probability (27% to subsp. *californica* and 21% to subsp. *velutina*; Semple & Brouillet 7131 WAT from Jackson Co., Oregon). Nine of the 16 specimens of the subsp. *velutina* a priori group (56%) plus 3 specimens only included a posteriori were assigned a posteriori into the subsp. *velutina* group; 1 specimen with 75% probability, 9 specimens with 50-59% probability, and 1 specimen with 49% probability (47% to subsp. *velutina*; Nesom & Wells 6698 TEX from southern Nuevo León). Seven specimens of the subsp. *velutina* a priori group plus 1 specimens included a posteriori were assigned a posteriori to subsp. *sparsiflora* with 56% probability (44% to subsp. *velutina*; Chiang et al. 8001 LL from southern Nuevo León, Mexico), 55% probability (44% subsp. *velutina*; Reyes A. 820 TEX from San Luis Potosi, Mexico), 52% probability (48% subsp. *velutina*; Gonzalez 435 TEX from southern Durango, Mexico), 50% probability (50% subsp. *velutina*; Lundell 5104 TEX from San Luis Potosi, Mexico), 49% probability (47% subsp. *velutina*; Nesom & Wells 6726 TEX from southern Nuevo León, Mexico), 49% probability (45% subsp. *velutina*; Wilson 10979 TEX from Zacatecas, Mexico), and 48% probability (48% to subsp. *velutina*; Rzedowski 6815 TEX from San Luis Potosi, Mexico). Twenty-two of 68 specimens of the subsp. *sparsiflora* a priori group (32%) plus 6 specimens included a posteriori were assigned a posteriori to the subsp. *sparsiflora* group; 2 specimens with 60-61% probability, 21 specimens with 50-49% probability, 3 specimens with 40-49% probability, and 1 specimen with 34% probability. Thirty-eight specimens of the subsp. *sparsiflora* a priori group plus 7 specimens included a posteriori were assigned to other subspecies; 11 specimens to subsp. *californica* with 38-99% probability and 41 specimens to subsp. *velutina* with 49-61% probability); the details are not presented here.

A two dimensional plot of CAN1 versus CAN3 canonical scores for 118 specimens of *Solidago velutina* (subsp. *californica*, subsp. *sparsiflora*, and subsp. *velutina*) are presented in Fig. 28. Eigenvalues on the first two axes were 0.636 and 0.021.

Table 8. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three varietal level a priori groups; a posteriori placements to groups in rows; alternative variety concept.

Group	<i>californica</i>	<i>sparsiflora</i>	<i>velutina</i>	% correct
<i>californica</i>	11	1	0	92
<i>sparsiflora</i>	8	22	38	32
<i>velutina</i>	0	7	9	56
Totals	19	30	47	44

Jackknifed classification matrix

Group	<i>californica</i>	<i>sparsiflora</i>	<i>velutina</i>	% correct
<i>californica</i>	11	1	0	92
<i>sparsiflora</i>	10	17	41	25
<i>velutina</i>	0	9	7	44
Totals	19	27	48	36

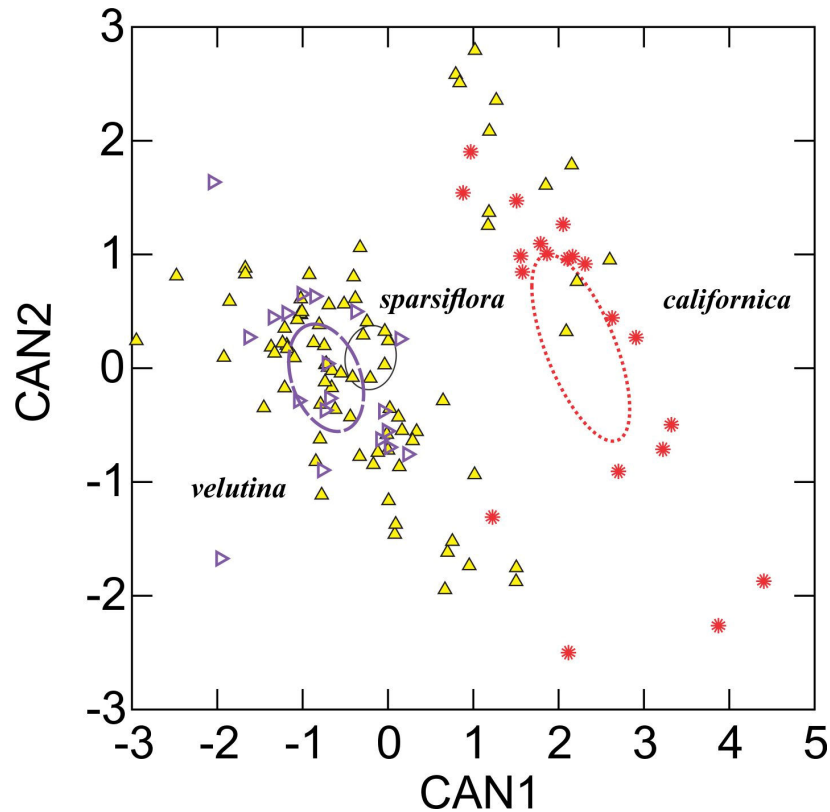


Figure 25. Plot of canonical scores (CAN1 vs CAN2) analysis for 119 specimens of *Solidago* subsect. *Nemorales*: *S. californica* (red starbursts), putative *S. sparsiflora* (yellow triangles), and putative *S. velutina* (right oriented violet triangles).

Two species level a priori groups analysis: Solidago californica and S. velutina

The Pearson correlation matrix yielded $r > |0.7|$ for some pairs of leaf traits reducing the number to be used to mid stem leaf length, width and upper stem leaf width. The traits used in the analyses were the same as used for the subspecies analyses within *S. velutina*.

In the STEPWISE discriminant analysis of 109 specimens of two species level a priori groups (*S. californica* and *S. velutina*), the following four traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: number of disc florets (17.77), ray floret lamina length (5.27), disc floret corolla length at anthesis (4.62), and disc floret ovary/fruit body length at anthesis (4.38). 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 californica* and *S. velutina* had an F-to separate value of 15.3231 (Wilks' lambda = 0.6292 $df = 4$ 1 107; Approx. F= 15.3231 $df = 4$ 104 $prob = 0.0000$).

In the Classificatory Discriminant Analysis of 109 specimens of the two species level a priori groups (*S. californica* and *S. velutina*) plus 16 additional specimens included a posteriori, percents of correct a posteriori assignment to the same a priori group were 92% and 89%. The Classification matrix and Jackknife classification matrix are presented in Table 9. Eleven of the 12 specimens of the *S. californica* a priori group (92%) plus 7 specimens include a posteriori were assigned a posteriori into the *S. californica* group; 11 specimens with 92-100% probability, 2 specimens with 86% and 88% probabilities, 3 specimens with 70-78% probability, 1 specimen with 64% probability, and 1 specimen with 58% probability (Semple & Heard 8607 WAT from Monterey Co., California).

One specimen of the *S. californica* a priori group and 1 additional specimen included a posteriori were assigned a posteriori to *S. velutina* with 58% probability (*Semple & Brouillet* 7131 WAT from Jackson Co., Oregon) and 56% probability (*Ringius* 1495 WAT from from Sonoma Co., California). Eighty-six of the 97 specimens of the *S. velutina* a priori group (89%) plus 10 additional specimens included a posteriori were assigned to the *S. velutina* a priori group: 72 specimens with 90-100% probability, 7 specimens with 83-88% probability, 7 specimens with 70-78% probability, 3 specimens with 65-66% probability, and 3 specimens with 57% probability (*Semple & Heard* 8142 WAT from Lincoln Co., New Mexico; diploid), 55% probability (*Semple & Heard* 7863 WAT from Washington Co., Utah; diploid), and 53% probability (*Powell et al.* 1474 TEX from Coahuila, Mexico). Eleven specimens of the *S. velutina* priori group plus 1 specimen included a posteriori were assigned a posteriori to *S. californica* with 99% probability (*Semple & B Semple* 5749 WAT from Wheeler Peak, Nevada; peduncles sparsely strigose, outer phyllaries not strigose, tetraploid), 97% probability (*Semple & B Semple* 6536 WAT from Boulder Co., Colorado; diploid), 95% probability (*Semple & B Semple* 5812 WAT from Boulder Co., Colorado), 87% probability (*Semple & B Semple* 5806 WAT from Gilpin Co., Colorado; tetraploid), 87% probability (*Semple & B Semple* 5748 WAT from Wheeler Peak, Nevada), 83% probability (*Semple & Heard* 7926 WAT from Gila Co., Arizona; diploid; Fig. 16), 83% probability (*Henrickson* 11780 LL from Coahuila, Mexico), 82% probability (*Johnston* 2603 TEX from Coahuila, Mexico), 74% probability (*Jones* 4453 WAT from Garfield Co., Colorado; Fig. 16), 72% probability (*Semple & Chmielewski* 8876 WAT from Wasatch Co., Utah; tetraploid), 59% probability (*Semple & Chmielewski* 8882 WAT from Utah Co., Utah; diploid), and 55% probability (*Cowan et al* 5373 TEX from Coahuila, 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>californica</i>	<i>velutina</i>	% correct
<i>californica</i>	11	1	92
<i>velutina</i>	11	86	89
Totals	22	87	89

Jackknifed classification matrix

Group	<i>californica</i>	<i>velutina</i>	% correct
<i>californica</i>	11	1	92
<i>velutina</i>	12	85	88
Totals	23	86	88

Frequencies of CAN1 canonical scores for 125 specimens of *S. californica* and *S. velutina* are presented in histograms in Fig. 30. The Eigenvalue on the first axis was 0.589.

DISCUSSION

The results from all the discriminant analyses support the recognition the following taxa in the *Solidago* subsect. *Nemorales*: *Solidago californica*, *S. hintoniorum*, *S. mollis*, *S. nana*, *S. nemoralis* (subsp. *decemflora* and subsp. *nemoralis*), *S. radula* and *S. velutina* (including *S. sparsiflora* in synonymy). However, not all a priori groups separated strongly 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 seven species are likely closely related and have not diverged greatly in multiple characters in multiple cases. Historically, *S.*

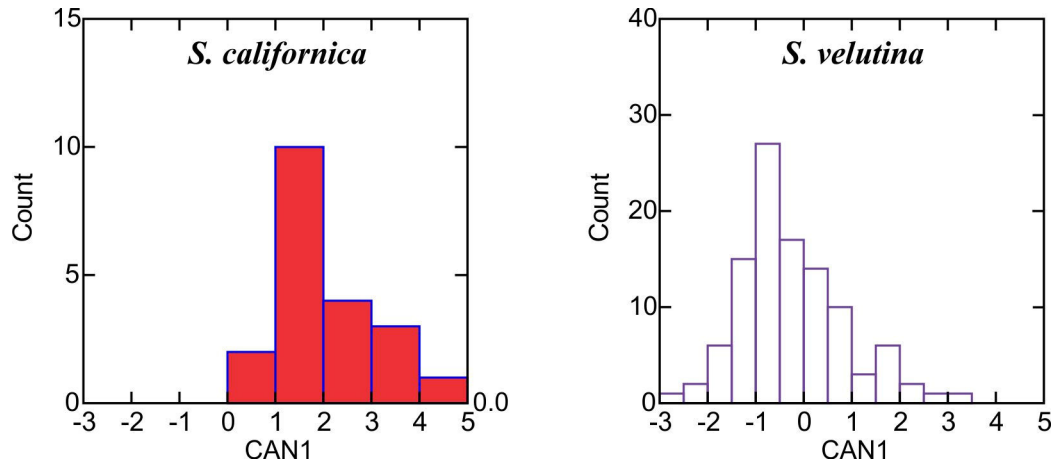


Figure. 30. Histograms of CAN1 canonical scores for 125 specimens of *S. californica* (left) and *S. velutina* (right).

californica has been included in *S. velutina* either as a subspecies (Semple & Cook 2006) or as a synonym of *S. velutina* (Nesom 1989b). *Solidago nemoralis* was found to be the most morphologically distinct species in the subsection with 94% of the 176 specimens being placed into the species group a posteriori even though only four floral traits were used in the discriminant analysis. Semple et al. (1990) concluded that *S. nemoralis* should be divided into two subspecies. This conclusion was not tested again because only one additional specimen of *S. nemoralis* was added to the matrix in the current study.

Solidago nana was also found to separate strongly from the other species using only four floral characters. This is not surprising because the species is easily recognized by its generally dense indument of soft canescent hairs and its often superficially corymbiform inflorescence. Its range is in part sympatric with that of *S. velutina*, but the two are not likely to be confused. Included in the analysis was Baker 722 (COLO; Fig. 8) from Pagosa Springs, Archuleta Co., Colorado which was placed a posteriori into *S. nana* with 100% probability. Baker 722 (COLO) was the unseen voucher that Semple and Nesom (2013) cited as the only specimen of *S. rigida* being present in the Flora of the Four Corners Region and noted it to possibly be introduced. The specimen had been first identified by E.L. Green as *S. rigida* and annotated later as *Oligoneuron rigidum* (L.) Small by W.A. Weber. The specimen is just a robust individual of *S. nana* and is now annotated as such. The phyllaries of *S. rigida* are multi-veined, while those of *S. nana* are always single veined. There is no known collection of *S. rigida* from the area covered by the Flora of the Four Corners Region.

The results presented here support the conclusion of Semple et al. (1990) that *S. californica* should be treated as a separate species but that *S. sparsiflora* should be reduced to a synonym under *S. velutina* as Nesom (1989b) suggested. In the analysis of the three possible subspecies within *S. velutina*, the *californica* group was supported as distinct, but only 34% of the *sparsiflora* group specimens were placed into that group in the a posteriori classification analysis. When *S. californica* and *S. velutina* including all the putative *S. sparsiflora* specimens were compared, 19 of the 21 specimens of *S. californica* were placed into that species, and 92 of 105 specimens of *S. velutina* were placed a posteriori into the that species. In all cases, the misplaced specimens had the diagnostic traits of the species they were assigned to a priori. Our conclusion is that sometimes floral traits of the two species overlap in ranges of variation, but when all traits are considered, identification to the correct species is likely. This includes the few collections of *S. velutina* from the Mohave Desert in eastern and southeastern California and the few collections of *S. velutina* from the San Pedro Martir region of northern Baja California, Mexico.

The most unexpected result of the multivariate analyses was the lack of strong separation of *Solidago mollis* and *S. radula*. *Solidago mollis* was found to be very similar to *S. radula* based on the traits used in the analyses, but differences in stem density in clones, inflorescence shape, leaf hair density, and leaf shape make placement of specimens into one of the two species reliable. Tetraploids of *S. radula* had technical traits similar to those of the tetraploid/hexaploidy *S. mollis*. The ranges are allopatric but approach each other closely in western Oklahoma and southern Panhandle Texas in the Red River region. We conclude that the two species are closely related. *Solidago mollis* may be derived from *S. radula*.

Lastly, *Solidago hintoniorum* was not well differentiated from *S. velutina*. The sample size of only five specimens for *S. hintoniorum* accounts for some of the statistical results. Additional specimens of *S. hintoniorum* were examined in this study, but these had immature heads and thus could not be scored for floral traits. In the protologue of *S. hintoniorum*, Nesom (1989a) compared the species to *S. petiolaris* and *S. wrightii*. Later, Nesom (1993) included *S. hintoniorum* in *S.* subsect. *Thyrsiflorae* in his overview of the entire genus. In this study in Table 2, the F-value based on the Mahalanobis distance is slightly lower for the group centroids of *S. hintoniorum* and *S. radula* than for *S. hintoniorum* and *S. velutina*, although two of the five specimens of *S. hintoniorum* were assigned a posteriori to *S. velutina* and none to *S. radula*. Some specimens of *S. hintoniorum*, e.g. *Patterson 6331* (TEX; Fig. 3), not included in the multivariate analysis due to missing data points look very similar to some specimens of *S. radula*. As noted by Nesom (1989a) and confirmed in this study, the phyllaries of some specimens annotated by Nesom in 1989 as *S. hintoniorum* have broad oblong multi-veined phyllaries (Fig. 4H) that would be very atypical in *S. velutina* but fit better with the single-veined phyllaries of *S. radula*. At this point, conclusions about the status of *S. hintoniorum* are tentative. Further field work is needed to collect more flowering samples of *S. hintoniorum* and to ascertain how different its habitat is from *S. velutina* in the southern half of Nuevo León, Mexico.

In conclusion, the seven species of *Solidago* subsect. *Nemorales* are clearly closely related but differ sufficiently in some obvious and some technical traits, so that identification of most specimens to species should not be a great challenge when geography is also considered.

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

1. Heads secund, in rounded, secund, pseudo-corymbiform paniculiform arrays; often alkaline meadows and flats, Montana and Idaho south to New Mexico and Arizona ***Solidago nana***
1. Heads usually in narrowly to broadly pyramidal, paniculiform arrays, branches secund.
 2. Plants with short-branched caudices; leaves softly canescent; arrays secund to apically recurved; prairies and open ground in eastern deciduous forests ***Solidago nemoralis***
 3. Pappus bristles usually not or barely exceeding ray floret corolla tubes and bases of disc floret lobes; disc corolla lobes 0.5–0.9(–1) mm; involucre usually 2.6–4.2 mm (tetraploids have larger heads); cypselae usually only sparsely strigose; basal leaves usually crenate, oblanceolate to obovate; open areas and open woods in eastern deciduous forest ***Solidago nemoralis* subsp. *nemoralis***
 3. Pappus bristles usually exceeding ray floret corolla tubes and bases of disc corolla lobes; disc corolla lobes (0.6–)0.8–1.5 mm; involucre usually 4.6–5.8 mm; cypselae moderately strigose; basal leaves usually not crenate, often linear-oblanceolate; prairies (rarely in forested areas) from Indiana westward to the Rocky Mountains, British Columbia to New Mexico ***Solidago nemoralis* subsp. *decemflora***
2. Plants with short to long creeping-rhizomatous; heads in thyriform to secund-pyramidal, paniculiform arrays.
 4. Leaves finely scabrous, not or weakly 3-nerved; central and eastern USA ... ***Solidago radula***

4. Leaves coarsely scabrous, hispid or soft-canescens, sometimes strongly 3-nerved; prairies and w USA to central Mexico.
5. Heads in paniculiform arrays, usually compact, branches broadly thyriform to somewhat secund pyramidal, proximal branches reflexed-recurved distally, basal leaves withering by flowering; prairies of Great Plains ***Solidago mollis***
5. Heads in cone-shaped arrays with branches narrowly secund, or open, lax, pyramidal; basal leaves often present at flowering; from near sea to mid montane elevations, Wyoming to s Oregon, south to central Mexico.
6. Peduncles moderately to densely strigose; outer phyllaries lanceolate to ovate, sparsely strigose; stems densely villose-strigose; California and s Oregon ***Solidago californica***
6. Peduncles very sparsely to moderately strigose; outer phyllaries lanceolate with attenuate acute tips, usually glabrous (rarely sparsely strigose in Zacatecas); stems moderately to densely short-canescens; Great Basin and Rocky Mountain USA to central Mexico.
7. 7.3 mean number of ray florets; inner phyllaries single-veined ***Solidago velutina***
7. 4.3 mean number of ray florets; inner phyllaries sometimes multi-veined ***Solidago hintoniorum***

ACKNOWLEDGEMENTS

This work was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grants to the first author. Joan Venn is thanked for her curatorial assistance with loans. The following herbaria are thanked for loaning specimens of *Solidago* subsect. *Nemorales* and giving permission to dissect heads: COLO, the J.K. Morton personal herbarium now in TRT, LL, MT, TEX, UNM, and WAT in MT. Andrew Lam assisted in recording location data on specimens of *Solidago* subsect. *Nemorales*. Specimens used in the multivariate study of *S. nemoralis*, *S. californica*, and *S. sparsiflora* (Semple et al. 1990) were included in this study. The staff of the de Candolle Herbarium at Conservatoire et Jardin botaniques de la Ville de Genève is thanked for providing a high resolution digital image of the type material of *Solidago velutina* DC. Kanchi Gandhi is thanked for guidance on determining the provenance of the lectotype of *S. velutina*.

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.
- Beaudry, J.-R. 1969. Études sur les *Solidago* L. IX. Une troisième liste de nombres chromosomiques des taxons du genre *Solidago* et de certains genres voisins. *Naturaliste Canad.* 96: 103–122.
- Beaudry, J.-R. and D.L. Chabot. 1959. Studies on *Solidago* IV. The chromosome numbers of certain taxa of the genus. *Canad. J. Bot.* 37: 209–288.
- Brammall, R.A. and J.C. Semple. 1990. The cytotaxonomy of *Solidago nemoralis* (Compositae: Astereae). *Canad. J. Bot.* 68: 2065–2069.
- Kapoor, B.M. 1977. Further observations on the chromosome morphology of some *Solidago* species. *Cytologia* 42: 241–253.
- Keil, D.J. and D. Pinkava. 1979. In A. Löve (ed.). In IOPB chromosome number reports LXIII. *Taxon* 28: 271–273.
- Keil, D. and T. Stuessy. 1977. Chromosome counts of Compositae from Mexico and the United States. *Amer. J. Bot.* 64: 791–798.

- Keil, D.J., M.A. Luckow, and D.J. Pinkava. 1988. Chromosome studies in Asteraceae from the United States, Mexico, the West Indies, and South America. *Amer. J. Bot.* 75: 662–668.
- Lawson, R.M. 2012. *Frontier Naturalist: Jean Louis Berlandier and the Exploration of Northern Mexico and Texas*. Univ. of New Mexico Press.
- Löve, A and D. Löve. 1982. IOPB Chromosome number reports LXXV. *Taxon* 31: 344–360.
- Morton, J.K. 1981. Chromosome numbers in Compositae from Canada and the U.S.A. *Bot. J. Linn. Soc.* 82: 357–368.
- Morton, J.K, Joan Venn and John C. Semple. In press. Chromosome number determinations in *Solidago* (Asteraceae: Astereae). *Rhodora* 119: in press.
- Nesom, G.L. 1989a. New species of Mexican *Solidago* (Compositae: Astereae). *Phytologia* 67: 142–147.
- Nesom, G.L. 1989b. Taxonomy of *Solidago velutina* (Asteraceae: Astereae) with a new related species from Mexico. *Phytologia* 67: 297–303.
- Nesom, G.L. 1993. Taxonomic infrastructure of *Solidago* and *Oligoneuron* (Asteraceae: Astereae) and observations on the phylogenetic position. *Phytologia* 75: 1–44.
- Raven, P., O. Solbrig, D. Kyhos and R. Snow. 1960. Chromosome numbers in Compositae. I. Astereae. *Amer. J. Bot.* 47: 124–132.
- Semple, J.C. 1985. Chromosome number determinations in Fam. Compositae tribe Astereae. *Rhodora* 87: 517–527.
- Semple, J.C. 2018 frequently updated. Classification and Illustrations of Goldenrods. <<https://uwaterloo.ca/astereae-lab/research/goldenrods/classification-and-illustrations>>
- Semple, J.C. and J.G. Chmielewski. 1987. Chromosome numbers in Fam. Compositae, Tribe Astereae. II. Additional Counts. *Rhodora* 89: 319–325.
- Semple, J.C. and R.E. Cook. 2004 Chromosome number determinations in fam. Compositae, Tribe Astereae. VII. Mostly eastern North American and some Eurasian taxa. *Rhodora* 106: 253–272.
- 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 G. L. Nesom. 2013. *Solidago* L. Pp. 288–291, in K.D. Heil, S.L. O’Kane, L.M. Reeves, and A. Clifford. 2013. *Flora of the Four Corners Region, Vascular Plants of the San Juan River Drainage: Arizona, Colorado, New Mexico, and Utah*. Monographs in Systematic Botany from the Missouri Botanical Garden, Vol. 124. Missouri Botanical Garden Press, St. Louis.
- Semple, J.C., R.A. Brammall and J. Chmielewski. 1981. Chromosome numbers of goldenrods, *Euthamia* and *Solidago* (Compositae-Astereae). *Canad. J. Bot.* 59: 1167–1173.
- Semple, J.C., J.G. Chmielewski, and R.A. Brammall. 1990. A multivariate morphometric study of *Solidago nemoralis* (Compositae: Astereae) and comparison with *S. californica* and *S. sparsiflora*. *Canad. J. Bot.* 68: 2070–2082.
- Semple, J.C., J.G. Chmielewski & M. Lane. 1989. Chromosome numbers in Fam. Compositae, Tribe Astereae. III. Additional counts and comments on some generic limits and ancestral base numbers. *Rhodora* 91: 296–314.
- Semple, J.C., J.G. Chmielewski, and ChunSheng Xiang. 1992. Chromosome numbers in Fam. Compositae, Tribe Astereae. IV. Additional reports and comments on the cytogeography and status of some species of *Aster* and *Solidago*. *Rhodora* 94: 48–62.
- Semple, J.C., R.E. Cook & E. Owen. 2015. Chromosome numbers in Fam. Compositae, Tribe Astereae. VIII. Eastern North American taxa. II. *Rhodora* 117: 80–91.
- Semple, J.C., Jie Zhang and ChunSheng Xiang. 1993. Chromosome numbers in Fam. Compositae, Tribe Astereae. V. Eastern North American taxa. *Rhodora* 95: 234–253.
- Semple, J.C., G. S. Ringius, C. Leeder, and G. Morton. 1984. Chromosome numbers of goldenrods, *Euthamia* and *Solidago* (Compositae: Astereae). II. Additional counts with comments on cytogeography. *Brittonia* 36: 280–292. Erratum. *Brittonia* 37: 121. 1985.

- Semple, J.C., T. Shea, H. Rahman, Y. Ma, and K. Kornobis. 2016. A multivariate study of the *Solidago sempervirens* complex of *S.* subsect. *Maritimae* (Asteraceae: Astereae). *Phytoneuron* 2016-73: 1–31.
- Semple, J.C., ChunSheng Xiang, Jie Zhang, M. Horsburgh and R.E. Cook. 2001. Chromosome number determinations in Fam. Compositae, Tribe Astereae. VI. Western North American taxa and comments on generic treatments of North American asters. *Rhodora* 103: 202–218.
- Turner, B.L., A.M. Powell, and R.M. King. 1962. Chromosome numbers in Compositae. VI. Additional Mexican and Guatemalan species. *Rhodora* 64: 251–271.
- Ward, D.E. and R.W. Spellenberg. 1986. Chromosome counts of angiosperms of western North America. *Phytologia* 61: 119–125.
- Zhao, Zai-Ming. 1996. Documented chromosome numbers 1996.2. Miscellaneous U.S.A. and Mexican species, mostly Asteraceae. *Sida* 17: 259–263.