

A MULTIVARIATE MORPHOMETRIC ANALYSIS OF *SOLIDAGO* SECT. *SOLIDAGO* AND SECT. *MULTIRADIATAE* (ASTERACEAE: ASTEREAE)

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ABSTRACT

A multivariate morphometric study of the goldenrod groups *Solidago* sect. *Solidago* and *S.* subsect. *Multiradiatae* was conducted to assess the morphological differences among *S. virgaurea* and the closely related Eurasian species, *S. dahurica*, *S. decurrens* (including *S. insularis* and *S. praeflorens*), *S. horieana*, *S. kurilensis* (including *S. nipponica*), *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. yokusaiana* and the putatively related North American species *S. macrophylla* and *S. leiocarpa*, *S. multiradiata*, and *S. spithamea*. Analyses of a matrix of 217 specimens by 34 traits provided support for recognizing 12 species. Statistically, *S. macrophylla* was not as strongly separated from the Eurasian group of species as was the *S. multiradiata* group of three species. Some Eurasian taxa were not included in the a priori portions of the analyses. The following new combinations are proposed: **Solidago** ser. **Macrophyllae** Semple & J.B. Beck, **Solidago** sect. **Multiradiatae** (Semple) Semple & J.B. Beck; **Solidago decurrens** Loureiro var. **insularis** (Kitam.) Semple. A neotype is designated for *Solidago decurrens* and for *S. cantonensis*.

Solidago subsect./ser. *Solidago* includes 4 to 11 species depending upon the taxonomic treatment followed (Nesom 1993; Iwatsuki et al. 1995; Chen & Semple 2011; Sakaguchi et al. 2018; Semple 2020 frequently updated) — *S. virgaurea* L. (Figs. 1-2; including multiple European subspecies and varieties of uncertain status and numerous synonyms; this is the type species of the genus), *S. litoralis* Sav. (Figs. 3-4), *S. dahurica* (Kitag.) Kitag. ex Juz. (Figs. 5-6), *S. decurrens* Loureiro (Figs. 7-11; with numerous synonyms including *S. insularis* Kitam. and *Amphirhapis leiocarpa* Benth.), *S. horieana* Kadota (Fig. 12), *S. kurilensis* Juz. in Komarov (Figs. 13-15, including *S. nipponica* Semple), *S. minutissima* (Makino) Kitam. (Fig. 16), *S. pacifica* Juz. (Figs. 17-18), and *S. yokusaiana* Makino (Figs. 19-20). All members of ser. *Solidago* have large lower stem leaves, inflorescences that are narrow to broadly paniculiform (although most individuals in *S. kurilensis* have more corybiform inflorescences or inflorescence branches), and generally larger involucre for the genus. Inner pappus bristles are the longest and somewhat clavate. Cypselae bodies range from glabrous to densely and evenly strigulose. Details of the nomenclature of eastern Asia taxa names are presented in Table 1, which includes several new combinations and typifications.

Solidago ser. *Macrophyllae* Semple & J.B. Beck¹ includes one species, *Solidago macrophylla* Pursh (Figs. 21-22), which was included in subsect. *Glomeruliflorae* by Semple and Cook (2006), based on RFLP cpDNA results in Zhang (1996) and in the multivariate study of the subsection by Cook et al. (2009). Torrey and Gray (1842) included *S. macrophylla* Pursh as a synonym under *S.*

¹ *Solidago* ser. **Macrophyllae** Semple & J.B. Beck, **ser. nov.** **TYPE:** *Solidago macrophylla* Pursh. Involucre 8–10 mm tall; lower stem leaves largest, serrate; cypselae (± linear-obconic, glabrous, 1.4–4.4 mm, glabrous; pappi 4–7.3 mm. DNA sequence data (Beck et al. in prep.) indicate that *S. macrophylla* is the sister species to ser. *Solidago*.

squarrosa Muhl. with a question mark, noting the lack of type material at the time, and were uncertain whether it should be adopted as the older name for their *S. squarrosa*. Fernald (1950) placed *S. macrophylla* (No. 7) after *S. squarrosa* (No. 6) and before *S. calcicola* Fern. (No. 8) and *S. bicolor* L. (No. 9). Cronquist (1968) keyed out *S. macrophylla* first in having very large involucre and presented it as the first species in his floristic treatment of the genus in eastern North America. *Solidago squarrosa* and *S. multiradiata* were the second and third species treated by Cronquist. *Solidago macrophylla* has large lower stem leaves, inflorescence and phyllary traits like those of subsect. *Solidago*. The involucre are large for the genus. Inner pappus bristles are the longest and somewhat clavate.

Solidago sect. *Multiradiatae* Semple & J.B. Beck² includes three species: *S. multiradiata* Ait. (type species; Figs. 23-24), *S. leiocarpa* DC. (Figs. 25-26), and *S. spithamaea* M.A. Curtis ex A. Gray (Figs. 27-28). Torrey and Gray (1842) treated *S. multiradiata* as *Solidago virgaurea* var. *multiradiata* (Ait.) Torr. & Gray, noting it was most similar to *S. virgaurea* var. *cambrica* (Huds.) DC. All members of sect. *Multiradiatae* have large lower stem leaves, rounded corymbiform inflorescences or paniculiform inflorescences with rounded-corymbiform branches, and generally larger heads for the genus. Inner pappus bristles are the longest and somewhat clavate. Cypselae bodies are moderately strigulose.

The ranges of distributions of all taxa in *Solidago* ser. *Solidago* are shown in Fig. 29, including the locations of samples used in the multivariate analyses. All taxa in the series are native to Eurasia. Ranges of individual taxa vary from broad (*S. virgaurea*, *S. dahurica*, and *S. decurrens*) to very narrow (*S. horieana* and *S. minutissima*). The greatest diversity in taxa occurs in Japan. The range of distribution in eastern North America of *S. macrophylla* is shown in Fig. 30, including the locations of samples used in the multivariate analyses. The ranges of distribution of the three species of *S.* sect. *Multiradiatae* are shown in Fig. 31, including the locations of samples used in the multivariate analyses. *Solidago multiradiata* is widely distributed in western North America from northern Alaska to California and New Mexico in the mountain and across Canada to the maritime provinces of Canada; it also occurs in extreme eastern Russia. *Solidago leiocarpa* is confined to higher elevations in New England and adjacent northern New York. *Solidago spithamaea* is native to a few high elevation locations in western North Carolina.

Numerous chromosome number reports have been published for taxa in *Solidago* ser. *Solidago*, but all reports are for diploids ($2n=9\text{II}$ or $2n=18$): a review of the cytogeography is in preparation. All chromosome number reports for *S. macrophylla* are diploid (Cook & Semple 2008). Many chromosome number reports have been published for sect. *Multiradiatae*; a study of the cytogeography is in preparation by J.C. Semple and J.G. Chmielewski. Diploids and tetraploids ($2n=9\text{II}$ or $2n=18$; $2n=18\text{II}$ or $2n=36$) have been reported for *S. multiradiata* (e.g., Semple & Chmielewski 1987; Morton et al. 2018). Tetraploids ($2n=18\text{II}$ or $2n=36$) have been reported for *S. leiocarpa* mostly under the synonym *S. cutleri* Fern. (Beaudry 1963; Morton 1981 as *S. multiradiata*; Morton et al. 2018). A few hexaploid chromosome counts ($2n=27\text{II}$ or $2n=54$) have been reported for *S. spithamaea* (Semple et al. 1984, 2019; Semple & Cook 2004).

² *Solidago* sect. *Multiradiatae* (Semple) Semple & J.B. Beck, **comb. et stat. nov.** *Solidago* subsect. *Multiradiatae* Semple, Sida 21: 760. 2004. **TYPE:** *Solidago multiradiata* Ait. DNA sequence data (Beck et al. in prep.) indicate that the *S. multiradiata* species group is not closely related to sect. *Solidago*.



Figure 1. Large shoot of *Solidago virgaurea*, Moore 4617 (GH) from Germany.

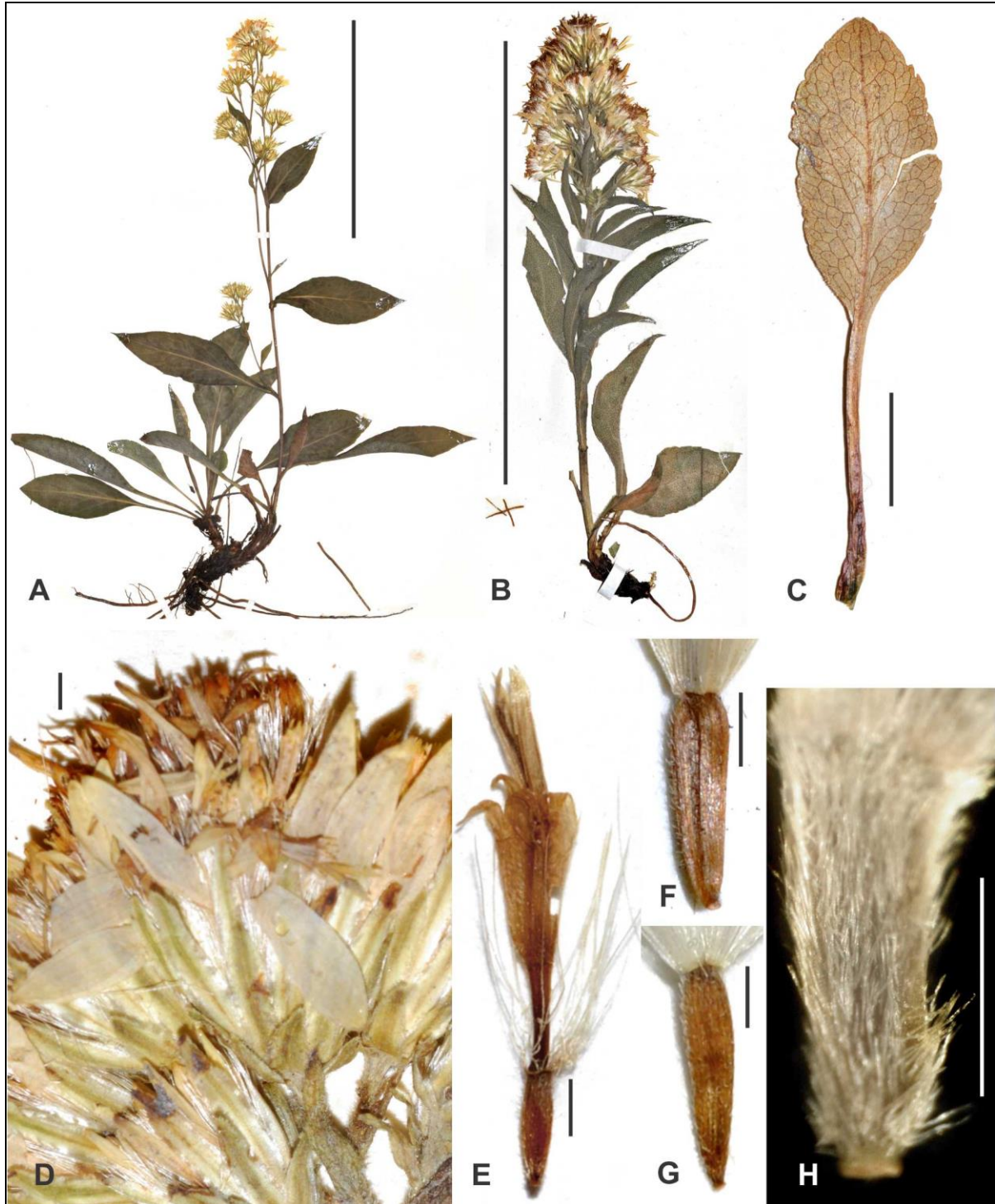


Figure 2. Details of the morphology of *Solidago virgaurea*. **A-B.** Small shoots, *Olgaard s.n.* (MO) and *Olgaard s.n.* (MO), Denmark. **C.** Lower stem leaf, *Montell s.n.* (MO), Finland. **D.** Heads, *Olgaard s.n.* (MO). **E.** Disc floret and sparsely hairy cypselas, *Moore 4617* (GH), Germany. **F-H.** Disc floret cypselas bodies, *Brandis 2846* (A) from Bosnia, *Lück s.n.* (WAT) from Hungary, and *Davis 50753* (BM) from Morocco (immature). Scale bar = 10 cm in A-B; = 1 cm in C; = 1 mm in D-H.



Figure 3. Shoots of *Solidago litoralis*, Fiori 976 (GH) from Viareggio, Lucca Prov., Italy (right two specimens).

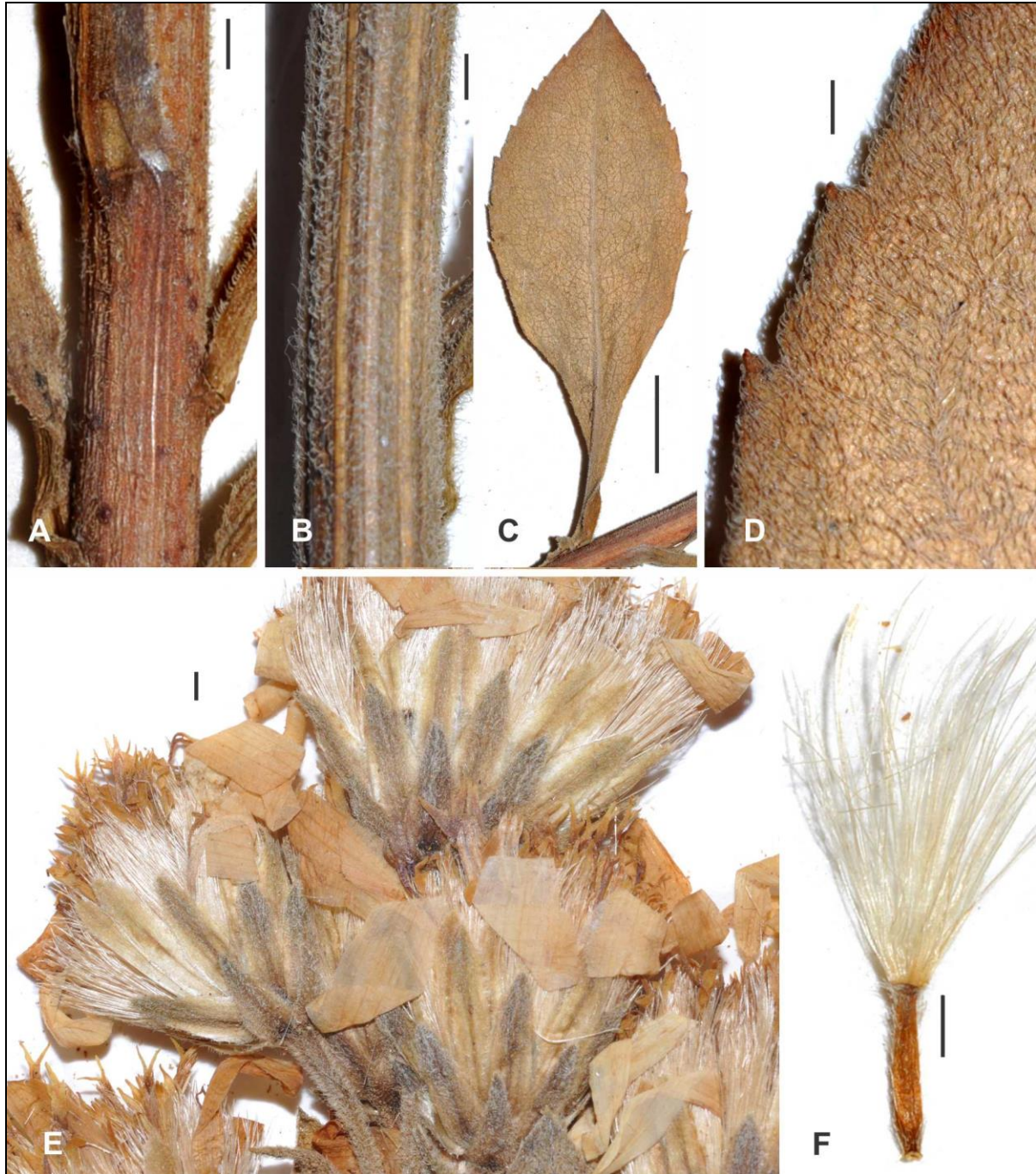


Figure 4. Details of morphology of *Solidago litoralis*. **A.** Lower stem, *Savi s.n.* (GH) . **B.** Mid stem, *Bussotti s.n.* (PI). **C-D.** Lower mid stem leaf and leaf margin, *Tomei s.n.* (PI). **D.** Heads, *Bussotti s.n.* (PI). **E.** Disc floret cysela, *Savi s.n.* (GH). Scale bars = 1 mm in A-B, D-E = 1 cm in C.



Figure 5. *Solidago dahurica*, Brummitt & Brummitt 232 (K) from Kamchatka, eastern Russia.



Figure 6. Details of the morphology of *Solidago dahurica*. **A-B.** Lower stems, *Kramer 10953* (K) and *Stainton et al 7839* (BM). **C.** Lower stem and upper stem leaves, *Sodombekov KPL-00126* (MO). **D-E.** Upper mid stem leaf margins, *Gomolitzky s.n.* (A) and *Sodombekov KPL-00126* (MO). **F.** Stem leaf in inflorescence, *Polunin 56-102* (BM). **G.** Heads, *Brummitt & Brummitt 232* (K). **H-I.** Distally hairy disc floret cypselae, *Stainton et al. 7839* (BM). **J.** Distally more hairy disc floret cypselae body, *Abel 110* (BM) from Pakistan. Scale bars = 1 mm in A-B and G-J; = 1 cm in C-F.



Figure 7. *Solidago decurrens* var. *decurrens*, Lin et al. 77 (A) from northeastern Taiwan.



Figure 8. Neotype of *Solidago decurrens* and holotype of *Amphirhapis leiocarpa* from Hong Kong (shoot on right Hinds s.n., K).



Figure 9. *Solidago decurrens* var. *insularis*, Koidzumi s.n. (KYO, image provided by Shota Sakaguchi) from Amami-Oshima, Ryukyo archipelago, Japan.



Figure 10. *Solidago decurrens* var. *praeflorens*, J. Nakai s.n. (TI, digital image provided by Tetsuo Ohi-Toma) from Hachijyo Is., Izu archipelago, Japan.



Figure 11. Details of the morphology of *Solidago decurrens*. **A-B.** Lower and upper stems, *Lin et al.* 77 (A). **C-D.** Lower stem leaf and margin detail, *Lai & Shan* 4428 (MO). **E.** Lower stem leaf, *Ding* 526 (MO). **F.** Heads, *An* 3963 (MO). **G.** Disc floret cypselid with corolla still attached, *Lin et al.* 77 (A). Scale bars = 1 mm in A-B, D, and F-G = 1 cm in C and E.



Figure 12. *Solidago horieana*, Horie s.n. (TNS) from Asahikawa, Hokkaido, Japan.

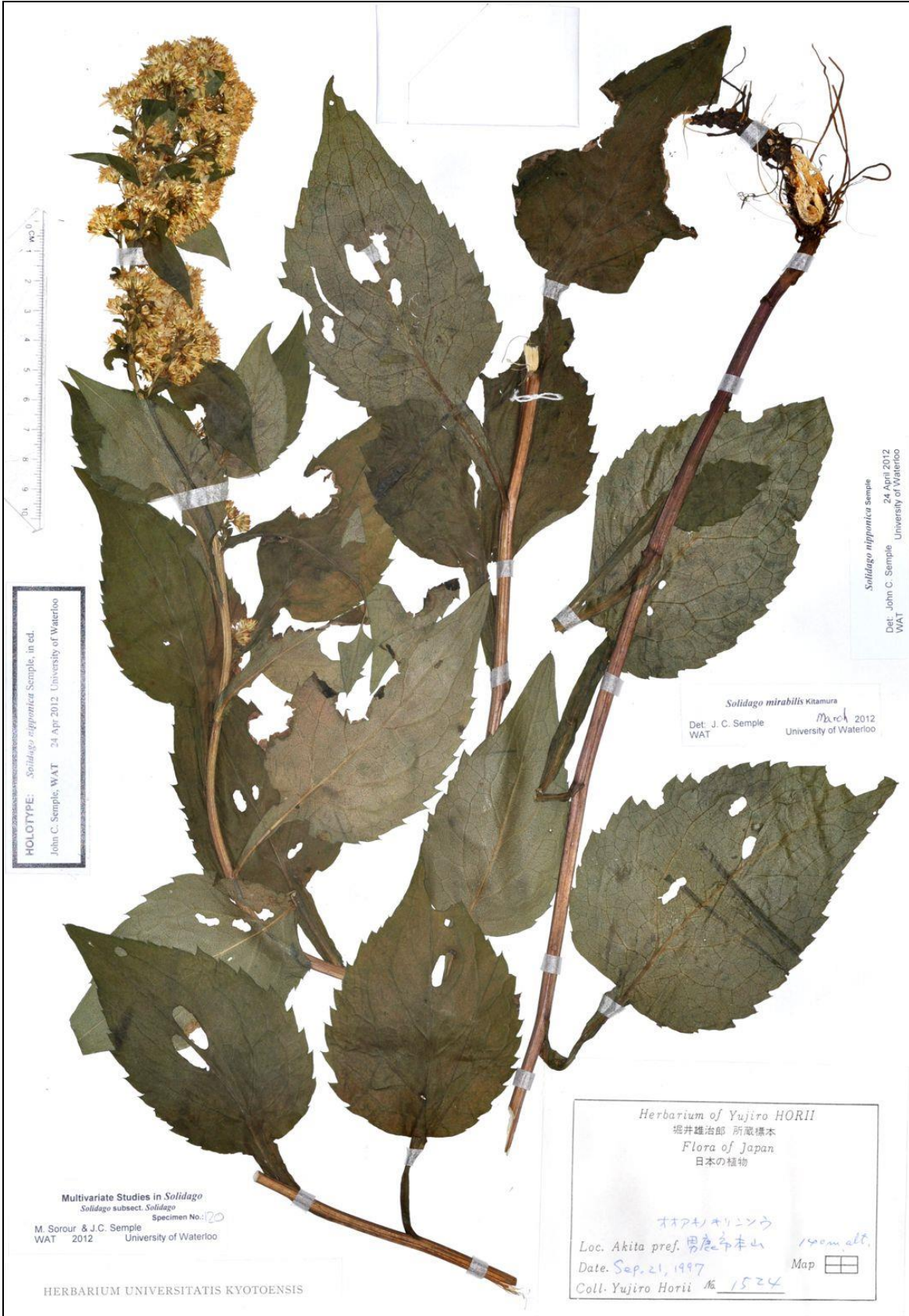


Figure 13. Large shoot of *Solidago kurilensis*, Hori 1524 (KYO; holotype of *S. nipponica*).

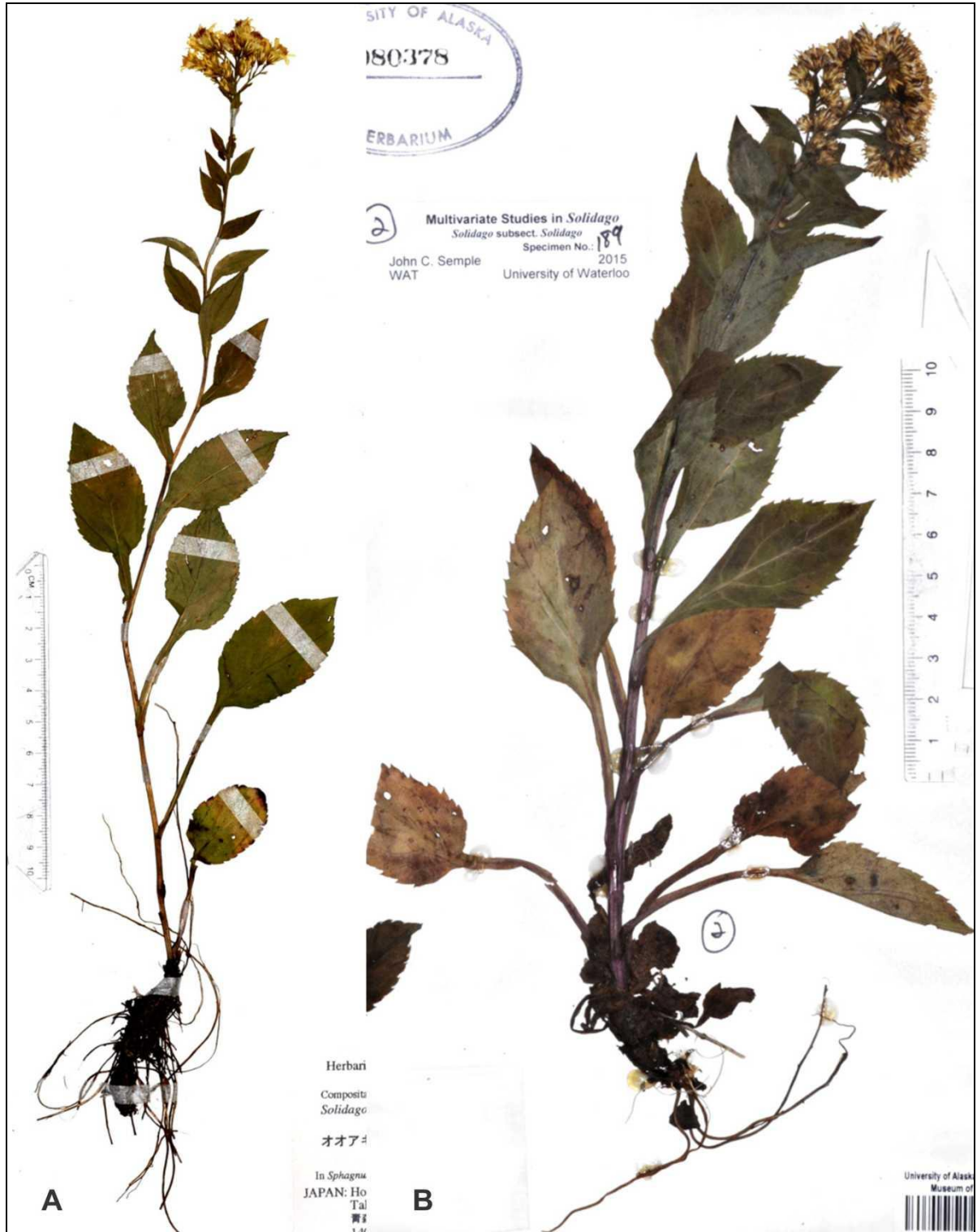


Figure 14. Small shoots of *Solidago kurilensis*. **A.** Yonekura 12919 (KYO), from Aomori Pref., Japan. **B.** *Barkalob* s.n. (ALA) from Iturup {Etorofu-to} Is., southern Kuril Islands, Kurilskiy Obl., Russia.

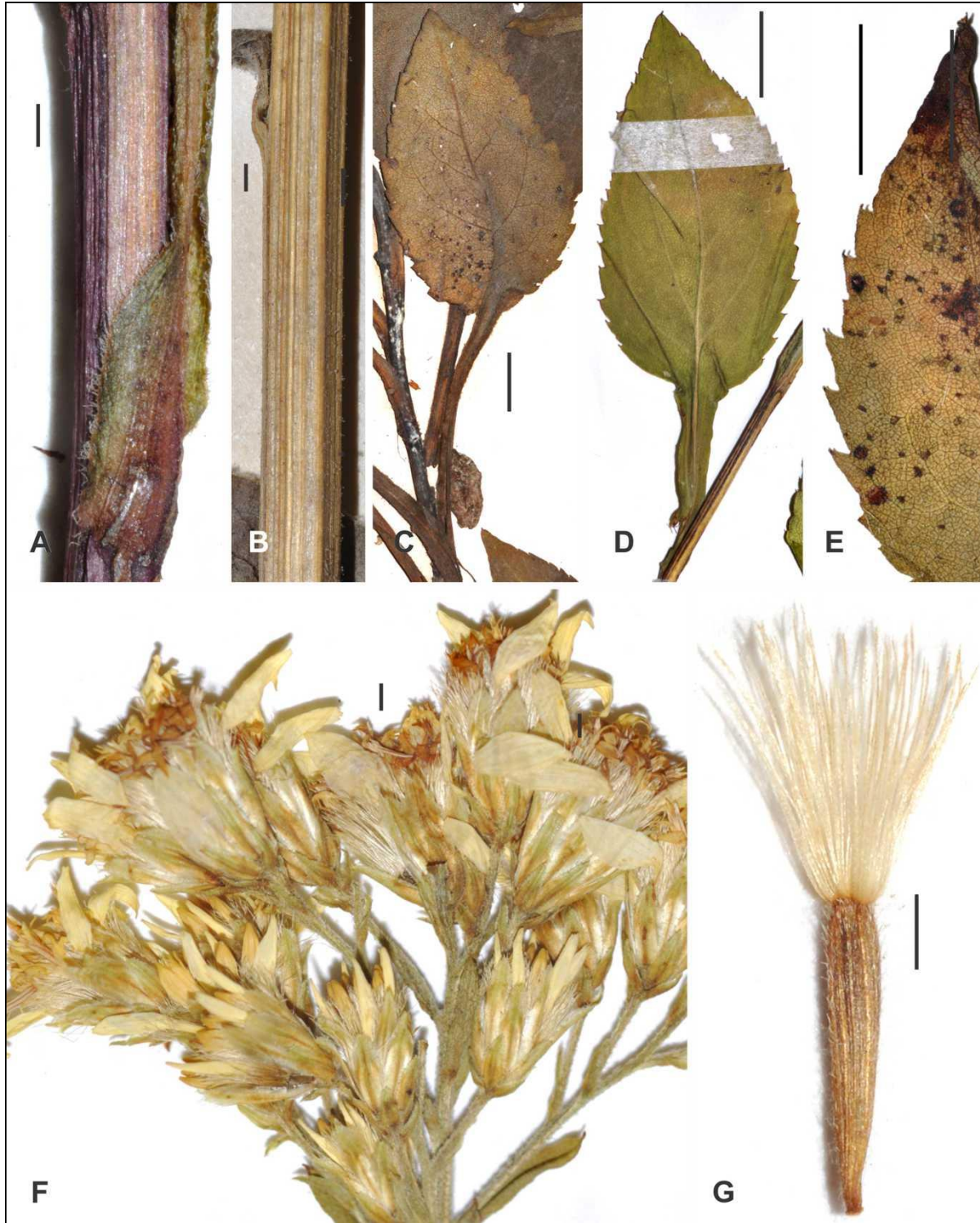


Figure 15. Details of the morphology of *Solidago kurilensis*. **A.** Lower stem and petiole base of lower stem leaf, *Barkalob s.n.* (ALA). **B.** Mid stem, *Hiroe 6808* (KYO). **C.** Small lower stem leaf, *Murata 6483* (KYO). **D.** Mid stem leaf, *Yonekura 12919* (KYO). **E.** Mid stem leaf margin, *Kurosaki 6416* (KYO). **F.** Heads, *Yonekura 12919* (KYO). **G.** Disc floret cypselid, *Kitamura s.n.* (KYO). Scale bars = 1 mm in A-B and F-G; = 1 cm in C-E.



Figure 16. Morphology of *Solidago minutissima* from Yakushima Is., Japan. **A.** Large shoot; *Furuse s.n.* (A). **B.** Small shoot; *Mitsuta 891* (KYO). **C.** Heads; *Murata 438* (KYO). **D.** Cypselae and old ray and disc corollas; *Mitsuta 891* (KYO). Scale bar = 1 cm in A and B; = 1 mm in C and D.

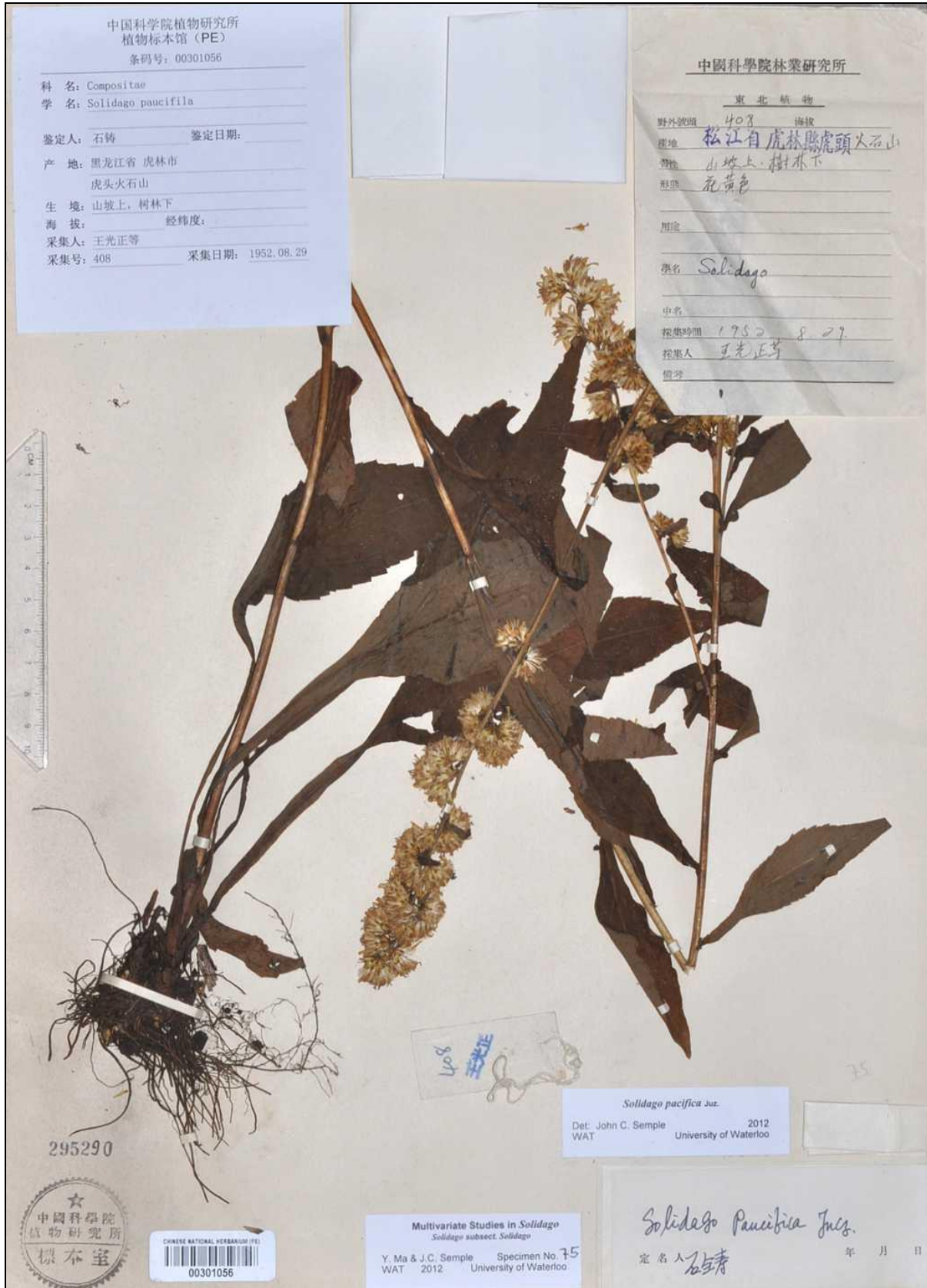


Figure 17. *Solidago pacifica*, Wang et al. 408 (PE) from Heilongjiang Prov., China.

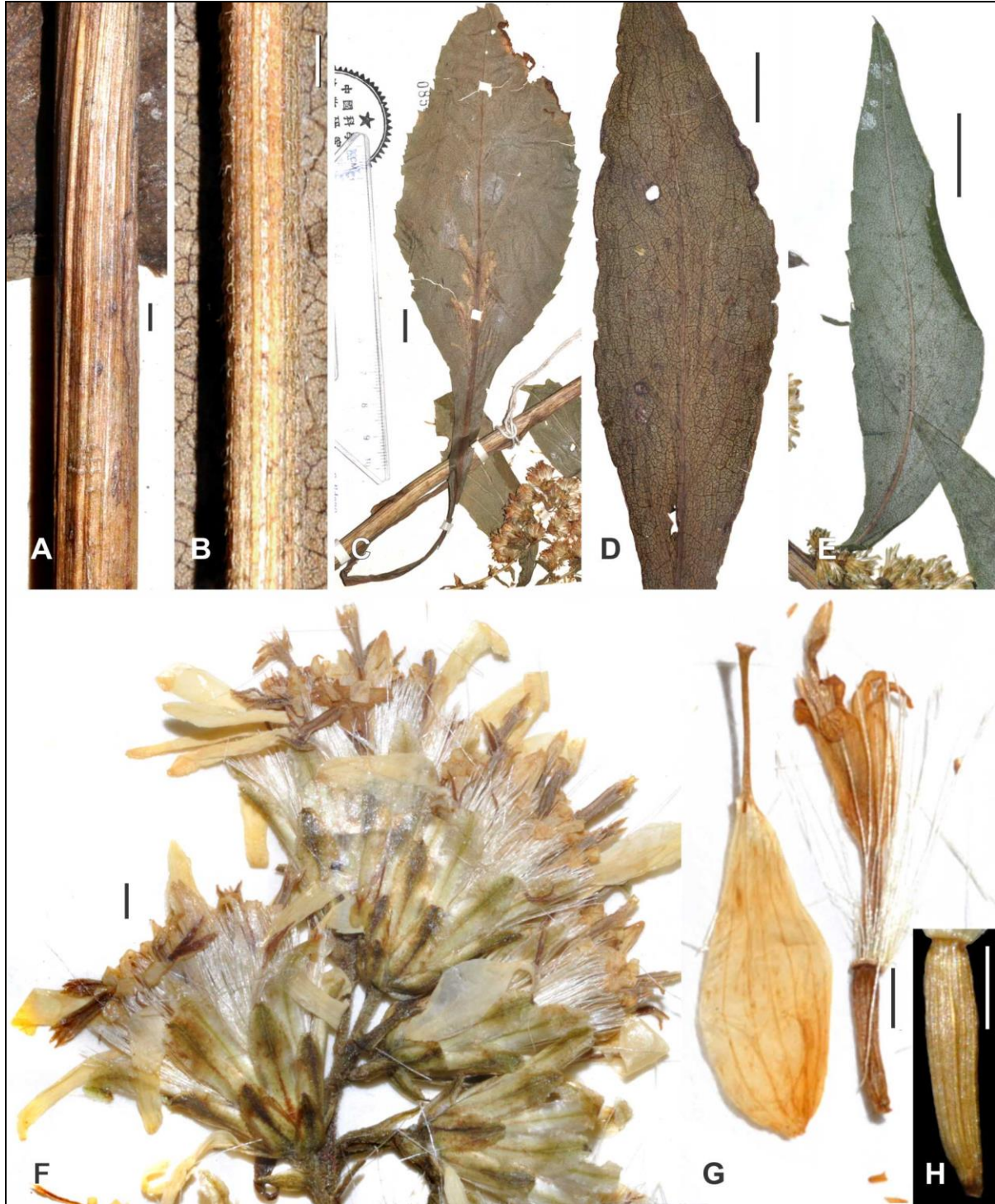


Figure 18. Details of morphology of *Solidago pacifica*. **A-B.** Lower and mid stems, *Wang et al. 408* (PE). **C.** Lower stem leaf, *Wang 563* (PE). **D.** Lower stem leaf venation, *Skvortsov s.n.* (MO). **E.** Stem leaf in inflorescence, *Wan & Chow 81116* (BM). **F.** Heads, *Wan & Chow 81116* (BM). **G.** Ray floret corolla and disc floret with immature cypsela, *Wang 592* (PE). **H.** Cypsela body, *Wan & Chow 81116* (BM). Scale bars = 1 mm in A-B and F-H-I = 1 cm in C-E.

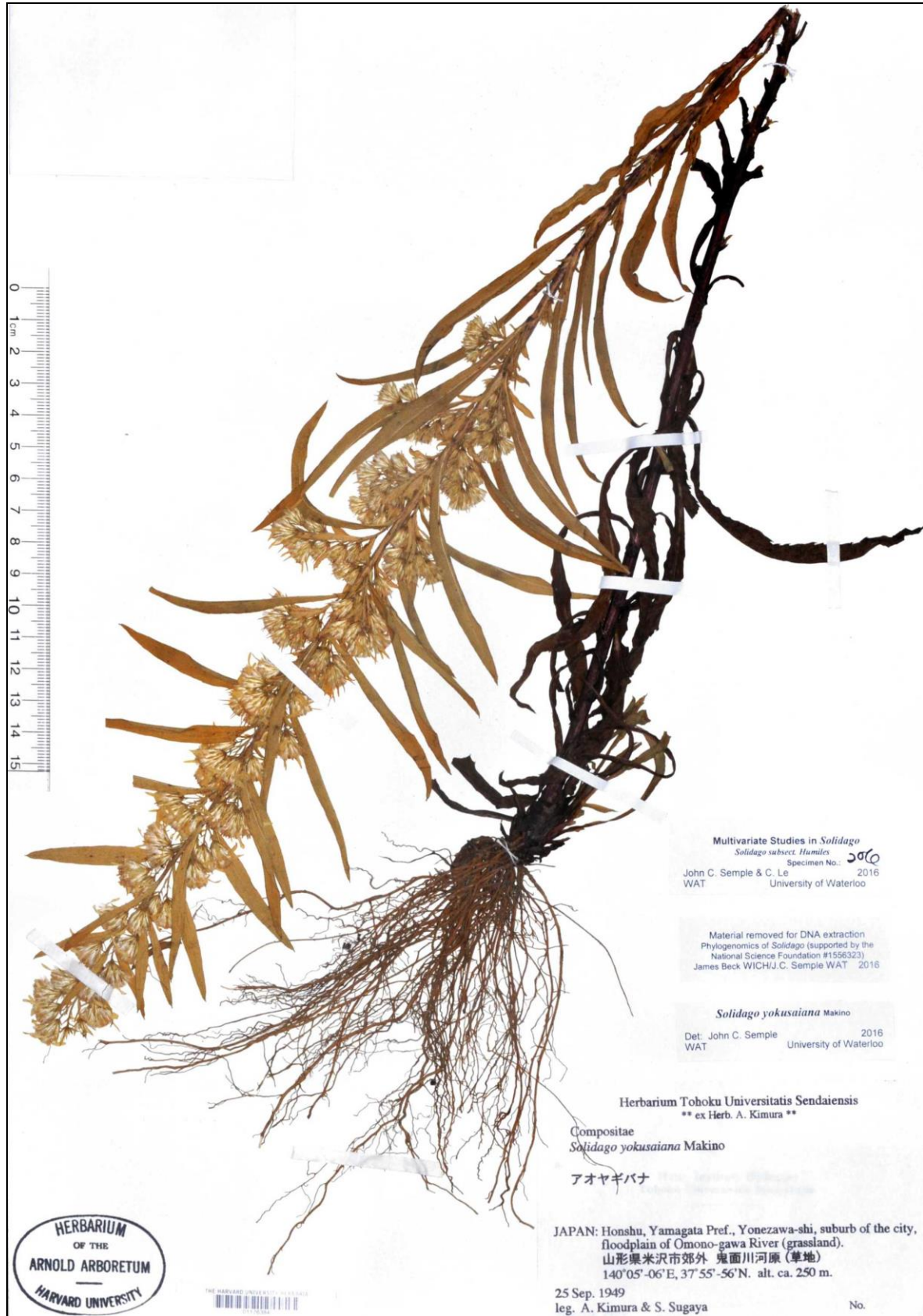


Figure 19. *Solidago yokusaiana*, Kimura & Sugaya s.n. (A) from Yamagata Pref., Japan.



Figure 20. Details of the morphology of *Solidago yokusaiana*. **A-B.** Lower and upper stems, *Furuse 1864* (K). **C.** Basal rosette leaves, *Furuse 1864* (K). **D.** Lower stem leaf venation, *Tanaka {Beaudry} 58-320-2* (MT). **E-F.** Mid and upper stem leaves, *Furuse 1864* (K). **G.** Heads, *Shiota 997* (GH). **H.** Disc floret with immature cypselum, *Lin et al. 77* (A). **I.** Cypselum body, *Kimura & Sugaya s.n.* (A). Scale bars = 1 mm in A-B and G-I = 1 cm in C-F.

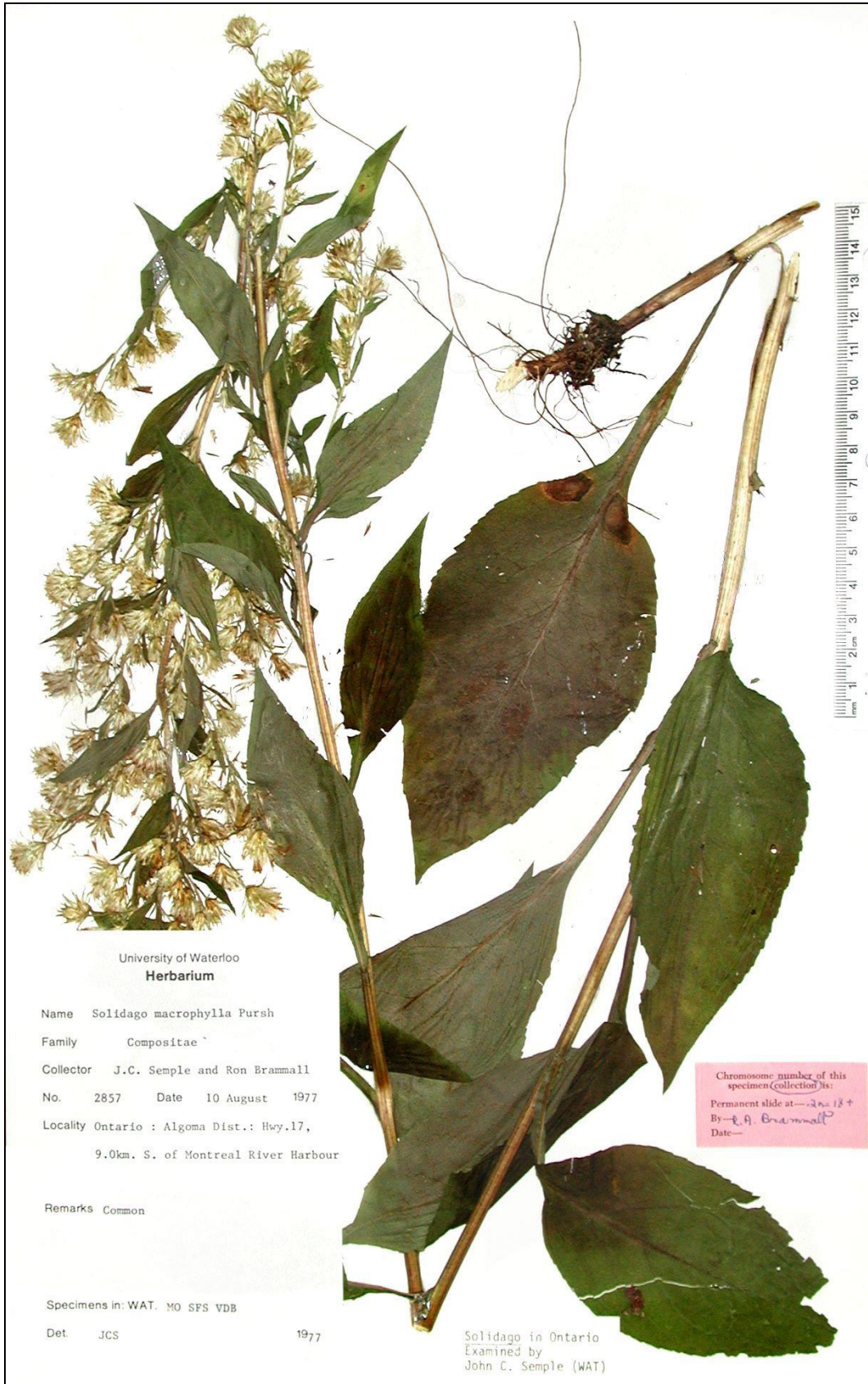


Figure 21. Large shoot of *Solidago macrophylla*, Semple & Brammall 2857 (WAT) from Algoma Dist., Ontario.



Figure 22. Details of the morphology of *Solidago macrophylla*. **A.** Small shoot, *Legault et al.* 8012 (MT). **B-C.** Lower and upper stems, *Morton & Venn* NA12155 (WAT). **D.** Small lower stem leaf, *Dodson* 25 (WAT). **E-F.** Lower mid stem leaf and undersurface midvein; *Rolland-Germain* 776 (MT). **G.** Heads, *Dodson* 25 (WAT). **H.** Disc floret cypsel with corolla still attached, *J. & B. Semple* 6768 (WAT). Scale bars = 1 mm in B-C, and F-H; D-E = 1 cm in C and E; and A = 10 cm.



Figure 23. *Solidago multiradiata*, Fraser 113 (WAT) from northern Québec.

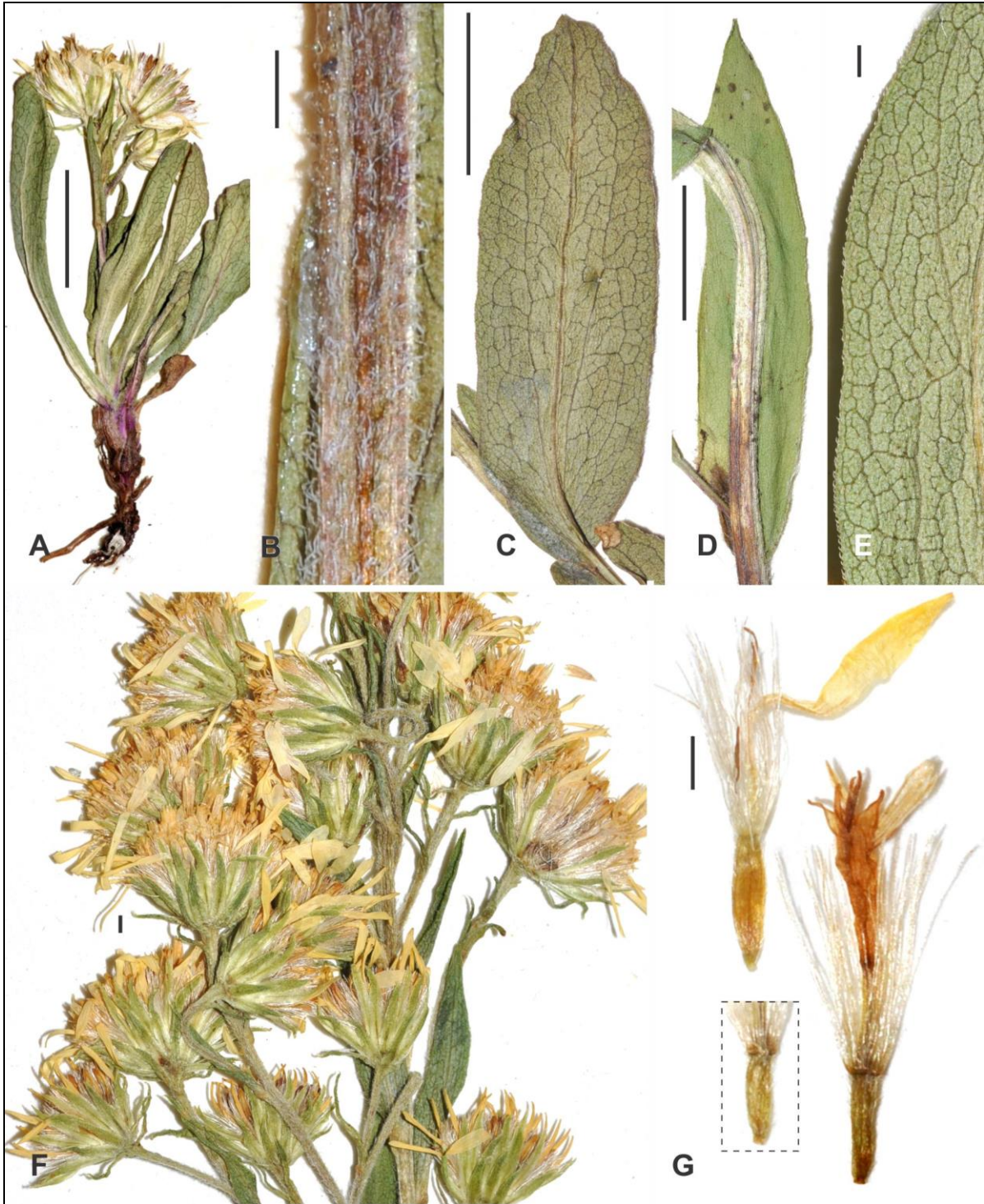


Figure 24. Details of the morphology of *Solidago multiradiata*. **A.** Dwarf shoot, *Semple et al* 9227 (WAT). **B.** Upper stem, *van Varneveld JvB73-454* (V). **C-E.** Upper stem leaves and margin detail, *Hawthorn s.n.* (WAT), *Semple & Heard 8693* (WAT), and *Semple et al. 11165* (WAT). **F.** Heads, *Clements s.n.* (WAT). **G.** Ray and disc floret cypselae with corollas still attached, *Semple et al. 11165* (WAT). Scale bars = 1 mm in B and F-G; = 1 cm in A and C-E.



Figure 25. *Solidago leiocarpa*, Ringius 1617 (WAT) from Mt. Washington, New Hampshire.

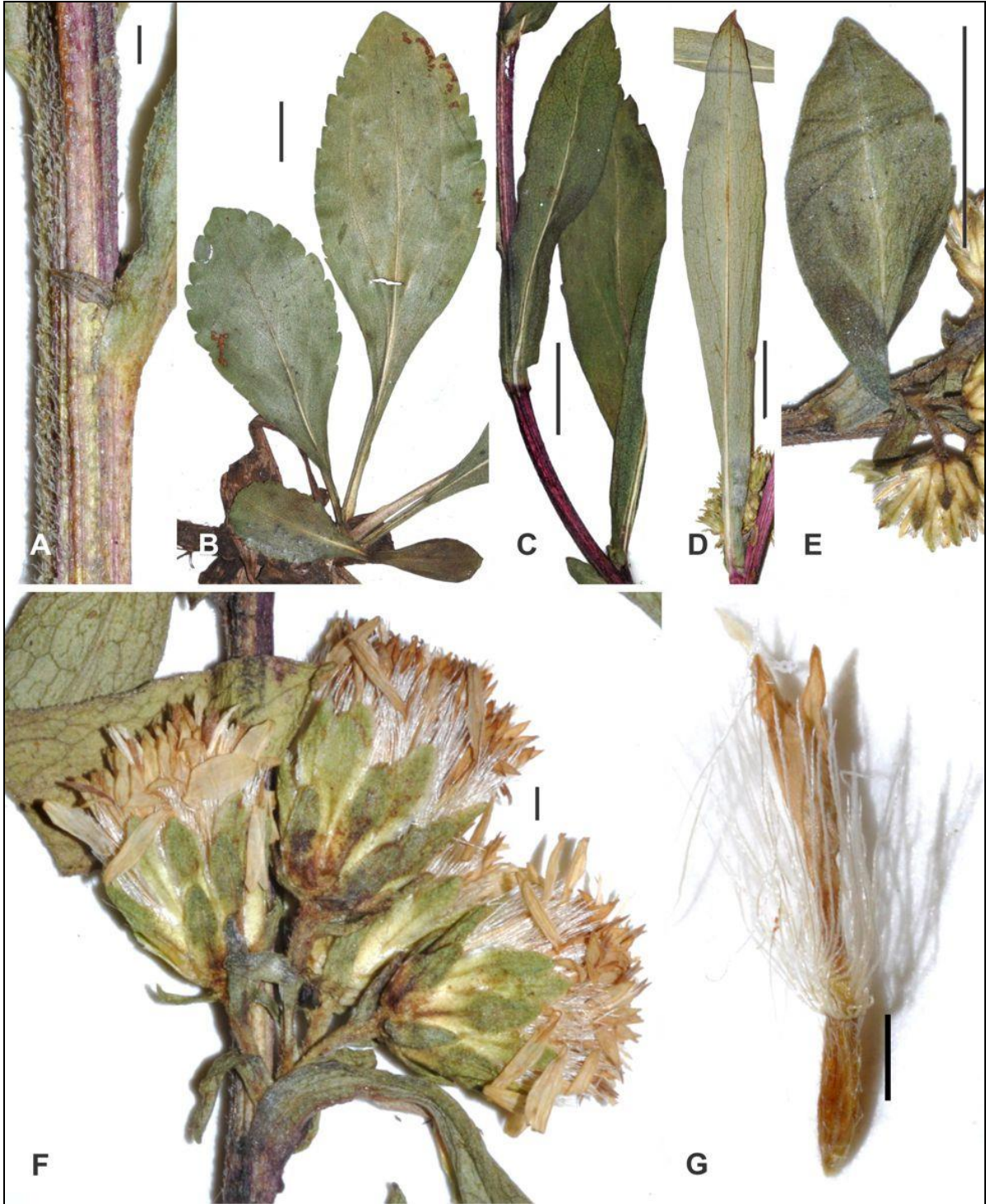


Figure 26. Details of the morphology of *Solidago leiocarpa*. **A.** Upper stem, *Ringius 1588* (WAT). **B.** Basal rosette leaves, *Ringius 1566* (WAT). **C.** Mid stem leaves, *Ringius 1613* (WAT). **D-E.** Upper stem leaves in inflorescence, *Ringius 1617* (WAT) and *Ringius 1561* (WAT). **F.** Heads, *Ringius 1557* (WAT). **G.** Disc floret cypsela with corolla still attached, *Ringius 1617* (WAT). Scale bars = 1 mm in A and F-G; = 1 cm in B-E.

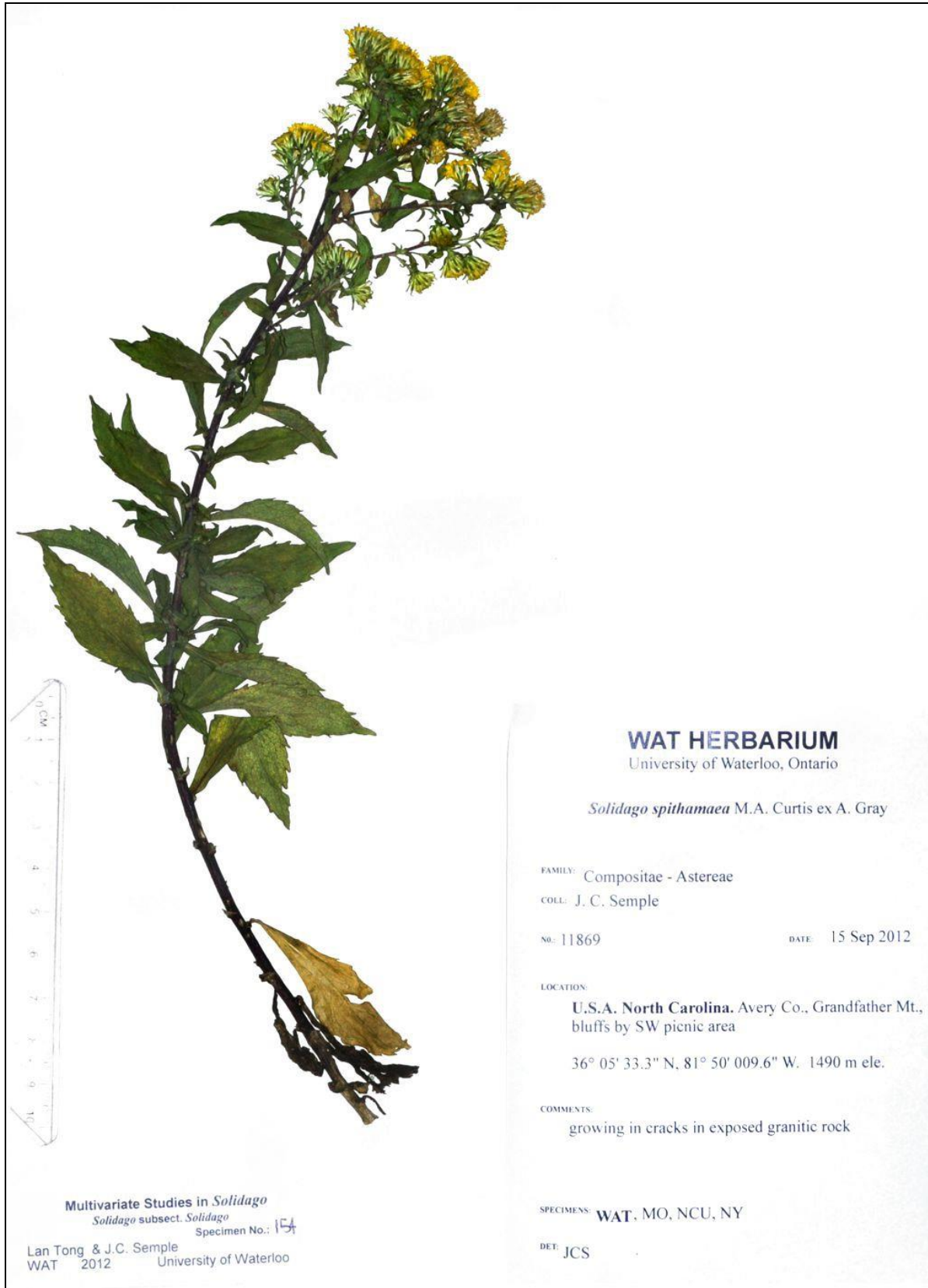


Figure 27. *Solidago spithamaea*, Semple 11869 (WAT unmounted) from Avery Co., North Carolina.

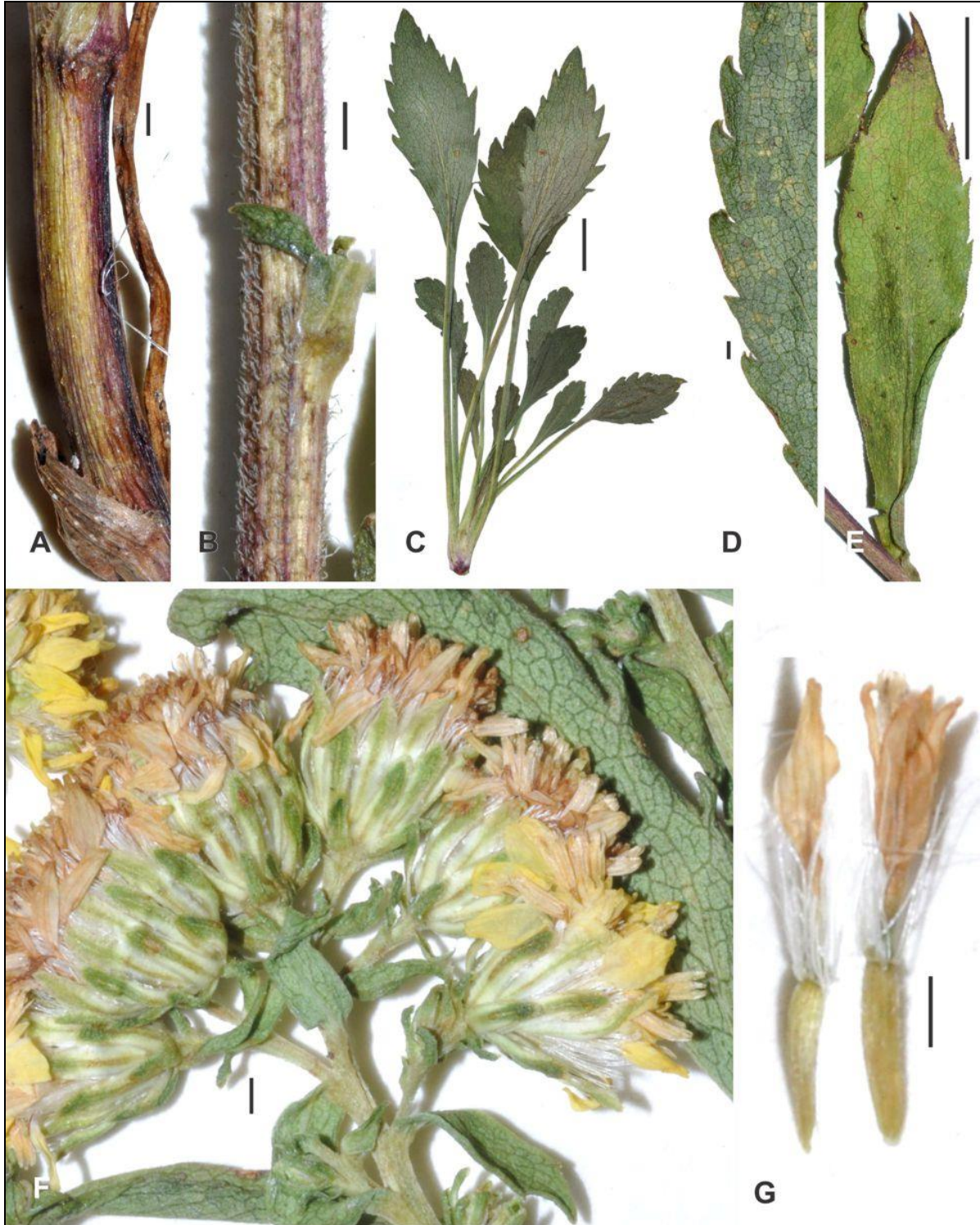


Figure 28. Details of the morphology of *Solidago spithamaea*. **A-B.** Lower and upper stems, *Semple & Suropto 9669* (WAT). **C.** Basal rosette leaves, *Semple 11869* (WAT). **D.** Lower stem leaf margin, *Semple & Suropto 9669* (WAT). **E.** Mid stem leaf, *Semple 11868* (WAT). **F.** Heads, *Semple 11869* (WAT). **G.** Ray and disc floret cypselae with corollas still attached, *Semple 11869* (WAT). Scale bars = 1 mm in A-B, D, and F-G; = 1 cm in C and E.

Table 1. Basionyms and combinations of species and infraspecific names of taxa proposed in the *Solidago virgaurea* complex occurring in far eastern Asia in chronological order of basionyms.

- Solidago virgaurea* L., Sp. Pl. 880. 1753. **SYNTYPES:** Europe. Herb. 998.15 (LINN!; **LECTOTYPE** designated by Garbari & Cecchi in C.E. Jarvis AND N. Turland (eds). 1998. Herb. Linn. 998.16 (LINN!). *Clifford 409*, *Solidago 3* (BM). *Clifford 409*, *Solidago 3a*, (BM). *Clifford 409*, *Solidago 3b*, fol. A (BM). *Clifford 409*, *Solidago 3b*, fol. B (BM). *Clifford 409*, *Solidago 3[e]* (BM). Herb. Burser XV: 66 (UPS). Orthographic variant *S. virga-aurea*.
- Solidago decurrens* Loureiro, Fl. Cochinch. 501. 1790. **TYPE:** CHINA. Canton, date? Collector?. (HT: no collection seen at BM or P, F. Jabbour pers. com.). **NEOTYPE** (designated here: same as holotype of *Amphiraphis leiocarpa* Benth): CHINA. Hong Kong, 1841, *R.B. Hinds* (K!; Fig. 8).
- Solidago cantoniensis* Loureiro, Fl. Cochinch. 501. 1790. **TYPE:** CHINA. Canton, date? Collector? (HT: no collection seen at BM or P). **NEOTYPE** (designated here: same as holotype of *Amphiraphis leiocarpa* Benth): CHINA. Hong Kong, 1841, *R.B. Hinds* (K!; Fig. 8). = *S. decurrens* var. *decurrens*
- Amphiraphis leiocarpa* Benth. in Hook. f., Lond. J. Bot. 1: 488. 1842. *Solidago virgaurea* L. var. *leiocarpa* (Benth. in Hook.f.) A. Gray, Mem. Amer. Acad. n.s. 6(2): 395. 1859. non Miq. (1861). *Solidago virgaurea* L. var. *leiocarpa* (Benth. in Hook. f.) Nakai, Tokyo Bot. Mag. 31: 111. 1917. "in nota sub var. *coreana*", Nakai (1928). *Solidago virgaurea* L. subsp. *leiocarpa* (Benth. in Hook. f.) Hultén, Fl. Aleut. 315. 1937. **TYPE:** CHINA. Hong Kong, 1841, *R.B. Hinds* (T: K!; Fig. 8). = *S. decurrens* var. *decurrens*
- Solidago virga-aurea* L. var. *leiocarpa* Miquel, Neerl. J. Bot. 1: 101. 1861. non (Benth in Hook.f) Nakai (1917). **TYPE:** CHINA. Croit sur la montagne de Samkok, Su-heang, Oct, ?? (Type: not seen) No type specimens in L or U at Leiden, Netherlands (email from collections manager Thiejsse, 3 Apr 2013). = *S. decurrens* var. *decurrens*
- Solidago virgaurea* var. *taquetii* Lével. & Vaniot, Fedde Rep. 8: 141. 1910. **TYPE:** South Korea. Quelpaert, in herbis Hioton, 22 Aug 1908, *Taquet 940* (holotype: E digital image e00413380! jstor.org) = *S. decurrens* var. *decurrens*
- Solidago yokusaiana* Makino, Tokyo Bot. Mag. 28: 179. 1914. nom. nov. for *Solidago virgaurea* var. *angustifolia* Makino (1898). "Japan, southern. This grows always on rocks by rivers" **TYPE:** JAPAN. River side of Niyodo River, Ochi Village, Takaoka Country, Tosa, 30 Oct. 1891, *K. Watanabe s.n.* (lectotype designated by Semple & Ohi-Toma 2017: TI digital image from TI!).
- Solidago virgaurea* L. var. *minutissima* Makino, Tokyo Bot. Mag. 28: 179. 1914. *Solidago minutissima* (Makino) Kitamura, Acta Phytotax. Geobot. 3: 141. 1934. **TYPE:** JAPAN. {Kagoshima Pref., Kumage Co., Kamiyaku Town, Miyaura} Prov. Osumi, Mt. Miyaura-dake in Isl. Yakusima, Sep 1909, *T. Makino s.n.* (lectotype designated by T. Yahara, J. Fac. Sci. Univ. Tokyo 1987: MAK-175611 digital image on line!, digital image sent by MAK!).
- Solidago virgaurea* L. var. *coreana* Nakai, Bot. Mag. (Tokyo) 31(364): 110 (-111). 1917. Sylv. Koreana 14: 122. 1922. *Solidago decurrens* var. *coreana* (Nakai) Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 397. 1937. **TYPE:** Korea. in monte Bi-ru-bon, 16 Aug 1916, *Nakai 5921* (holotype: TI, digital image TI00011104 sent by Tetsuo Ohi-Toma from TI!).) = *S. decurrens* var. *decurrens*
- Solidago virgaurea* var. *asiatica* Nakai, Tokyo Bot. Mag. 42: 16. 1928. nom. invalid., nom. nud. "common in East Asia".) = *S. decurrens* var. *decurrens*
- Solidago virga-aurea* L. var. *yakusimensis* Nakai, Tokyo Bot. Mag. 62: 16. 1928. *Solidago yakusimensis* (Nakai) Masam., Mem. Fac. Sc. & Agric. Taihoku Imp. Univ. xi., Bot. No. 4, 439. 1934. **TYPE:** JAPAN. Kyushu Is. Prov. Osumi, in montibus insl. Yakusima, s.d., *Y. Yoshii s.n.* (holotype: TI, digital image TI00011108! sent by Tetsuo Ohi-Toma). = *S. minutissima*
- Solidago virgaurea* var. *praeiflorens* Nakai, Tokyo Bot. Mag. 42: 16. 1928. *Solidago decurrens* Loureiro var. *praeiflorens* (Nakai) Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 397. 1937. **TYPE:** JAPAN. Hachijyo Is., 15 Jun 1920, *J. Nakai s.n.* (holotype: TI, digital image TI0001110x sent by Tetsuo Ohi-Toma from TI! Fig. 10). = *Solidago decurrens* var. *praeiflorens*
- Solidago hachijoensis* Nakai, Tokyo Bot. Mag. 42: 16. 1928. nom. nud. validly published in Tokyo Bot. Mag. 42: 472. = *S. decurrens* var. *praeiflorens*
- Solidago virga-aurea* L. var. *gigantea* Nakai, Tokyo Bot. Mag. 62: 17. 1928. **TYPE:** JAPAN. {Hokkaido: Hokkaido Pref.,} Yeso, Nayoro Prov., {Teshio Dist.}, Teshio, 30 Aug 1919, *Nakai s.n.* (holotype: TI Herb. Imp. Univ., 3 sheets, one shoot in three parts) digital image provided by herbarium!) = *S. pacifica*
- Solidago japonica* Kitamura, Acta Phytotax. Geobot. 1932, 1(4): 286, in obs. **TYPE:** JAPAN. Hondo. Prov. Yamashiro, Mt. Hiei, Oct 1920, *G. Koidzumi* (Holotype: KYO, not seen). = *S. decurrens* var. *decurrens*

- Solidago mirabilis* Kitamura, Acta Phytotax. Geobot. 3: 140. 1934. non Small (1933). **TYPE:** JAPAN. Hondo. Prov. Ugo, Peninsula Oga, Shiodo, 4 Oct 1931, *H. Muramatsu s.n.* (holotype: not seen). = *S. kurilensis*
- Solidago insularis* Kitamura, Acta Phytotax. Geobot. 3: 141. 1934. *Solidago virgaurea* L. var. *insularis* (Kitam.) Hara, Enum. Spermatophytarum Japon. 2: 261 (1952). ***Solidago decurrens*** Loureiro var. *insularis* (Kitamura) Semple, comb. nov. **TYPE:** JAPAN. Liukiu, Is. Amani-oshima, Kaneku, 24 Apr 1923, *G. Kordsumi* (holotype: KYO, digital image!; Fig. 9) -Typus, Koniya, Dec. 1916 *leg?* (KYO, not seen), Insul. Utchina, Nawa, 3 Jan 1924, *Z. Tashiro* (KYO, not seen), Nakagamigun, Minjatamura, Osato, 9 Apr 1934, *N. Tawada* (KYO, not seen). = *S. decurrens* var. *insularis*
- Solidago virgaurea* L. var. *dahurica* Kitagawa, Rep. Inst. Sci. Res. Manchouchuo 1: 297(-298; t. 3, fig. 2). 1937. *Solidago dahurica* Kitagawa, Rep. Inst. Sci. Res. Manchoukuo 1: 297, in syn., as Kitag. mss. 1937. *Solidago virgaurea* L. subsp. *dahurica* (Kitag.) Kitag., Rep. Inst. Sci. Res. Manchoukuo 3(App. 1): 472. 1939 [Oct 1939]. *Solidago dahurica* (Kitag.) Kitag. ex Juz., Fl. URSS 25: 42. 1959. **TYPE:** CHINA. Heilongjiang Prov., "Prov. Hsing-an Orient, near Buheto", 22 Aug 1936, *Kitagawa s.n.* (Holotype: photograph in protologue!, digital image TI00011101 sent by Tetsuo Ohi-Toma from TI!).
- Solidago virgaurea* var. *paludosa* Honda, Bot. Mag. Tokyo 40: 95. 1937. *Solidago japonica* var. *paludosa* (Honda) Honda, Bot. Mag. Tokyo 40: 645. 1937. *Solidago decurrens* f. *paludosa* (Honda) Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 396. 1937. **TYPE:** JAPAN. Honshu. Prov. Sinano, n monte Kirigamine, 28 Jul 1936, *T. Osaka 34* (holotype: TI digital image TI00011103! sent by Tetsuo Ohi-Toma) = *S. decurrens* var. *decurrens*
- Solidago hachijoensis* var. *elata* Honda, Tokyo Bot. Mag. 51: 645. 1937. **TYPE:** JAPAN. Honshu. Osima, Prov. Izu, 1936, *J. Iwata* (H: Herb. Imp. U. Tokyo, not seen).
- Solidago virgaurea* subsp. *asiatica* Kitamura, Mem. Coll. Sci. Kyoto Univ. Ser. B. 13: 398. 1937. nom. nud. in syn.
- Solidago virgaurea* var. *asiatica* Nakai ex Hara, Bot. Mag. 52: 128. 1938 [nom. & stat.nov.], replaced syn. *Solidago japonica* Kitamura (1932). *Solidago virgaurea* subsp. *asiatica* (Nakai ex Hara) Kitam. ex Hara, Enum. Sperm. Jap. 2: 260. 1952. **TYPE:** same as *S. japonica* Kitamura. JAPAN. Hondo. Prov. Yamashiro, Mt. Hiei, Oct 1920, *G. Koidzumi* (holotype: KYO, not seen). = *S. decurrens* var. *decurrens*
- Solidago pacifica* Juz., Fl. URSS xxv. 576. 1959. **TYPE:** RUSSIA. Distr. Vladivostok, reg. Suifunensis, in vicin. Nikolsk-Ussuriensis, Krasnojarskayi sopka (ad fl. Suifun), 5 Sep 1927, *W. Transzchel sub n° 534* (holotype: LE digital image LE-01012705! provided by LE Aug 2015).
- Solidago kurilensis* Juzepczuk in Komarov, Fl. URSS, xxv. 577. 1959. *Solidago virgaurea* L. subsp. *kurilensis* (Juz.) V.N.Voroschilov in A.K. Skvortsov (ed.), Florist. issl. v razn. raionakh SSSR: 193 (1985): 1985. **TYPE:** RUSSIA. Insulae Kurilensis Merdionales, ins. Sikotan, in declivibus montium et in pratulis insularum Kurilensium, 27 Aug 1948, *A.I. Gizenko* (holotype: LE digital image LE-01012704 provided by LE Aug 2015).
- Solidago horieana* Kadota, J. Jap. Bot. 83(4): 235 (233-238; figs. 1-3, map). 2008 [Aug 2008]. **TYPE:** JAPAN. Hokkaido Island: Sorachi Subpref., Uryu-gun, Horokanai-cho, Osarunai, along the valley of Osarunai-gawa, 44° N, 142° 6' 34" E, 140 m, 7 Jul 1991, *K. Horie s.n.* (holotype: TNS 769414, digital image sent by Shinobu Akiyama Mar 2017; isotypes: KYO, SAPT, TI, TNS 769410, digital image sent by Shinobu Akiyama Mar 2017, TNS 769411 digital image! sent by Shinobu Akiyama Mar 2017, TNS 769412, digital image! sent by Shinobu Akiyama Mar 2017, TNS 769413, digital image! sent by Shinobu Akiyama Mar 2017).
- Solidago nipponica* Semple, Phytoneuron 2013-24: 1-9. 2013. **TYPE:** JAPAN. Honshu: Akita Pref., Oga city, Motoyama, 140 m ele., 21 Sep 1997, *Yojiro Horii 1524* (KYO!) = *S. kurilensis*

The purpose of this study was to determine statistical support for recognizing the species and varieties proposed within *Solidago* sect. *Solidago*, the levels of distinctiveness among the taxa, and what technical traits can be used to separate taxa besides those used to define the taxa as groups a priori. Also, taxa in ser. *Solidago* are compared with *S. macrophylla* and the three species of sect. *Multiradiatae*. The latter two North American taxa have been considered to be closely related to *S.* ser. *Solidago*. This is viewed as a preliminary study because not all taxa are included or available samples sizes were too small to include a taxon as an a priori group. No previous multivariate study has included all these species.

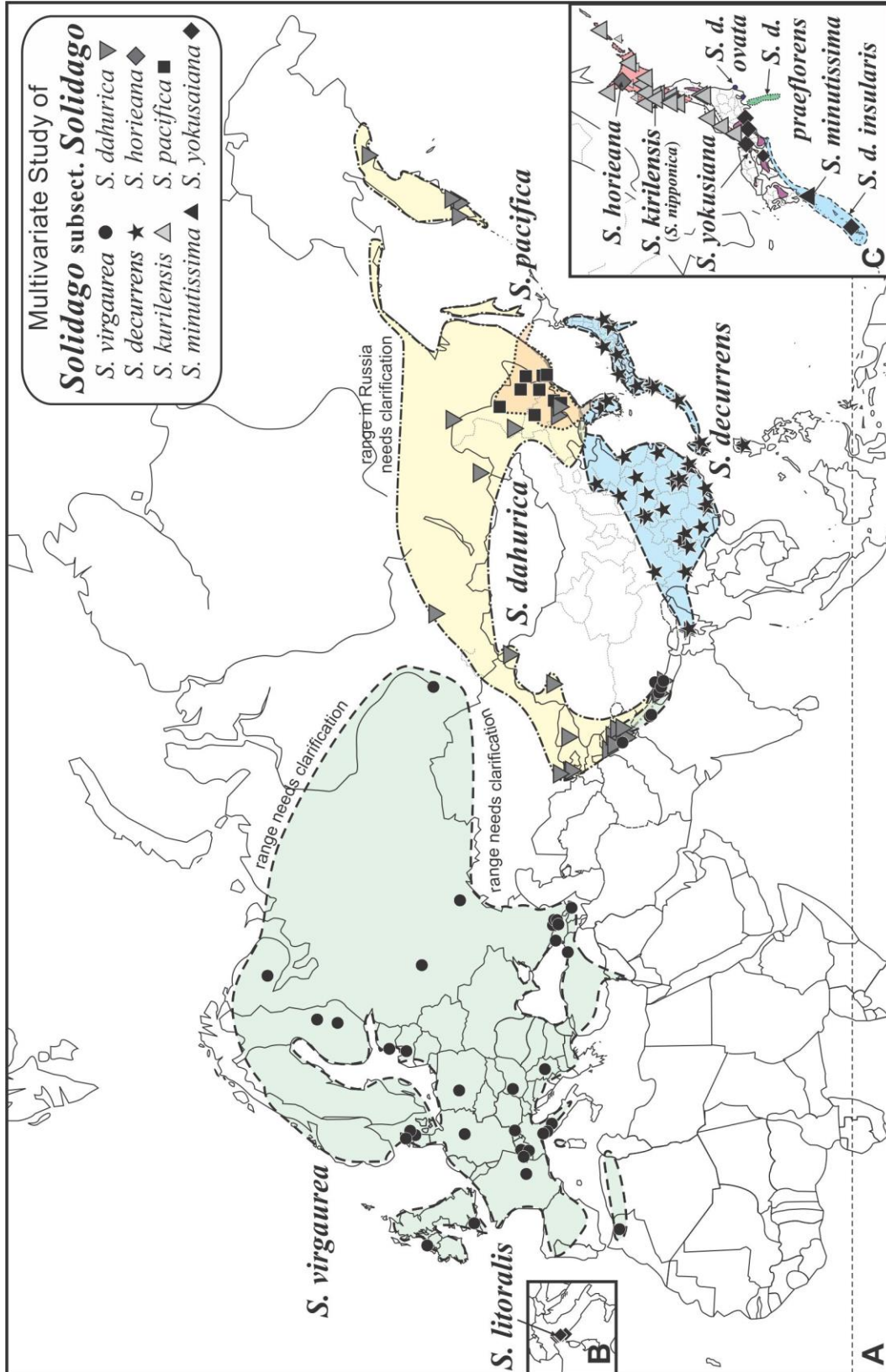


Figure 29. Ranges of distribution of taxa in *Solidago* ser. *Solidago* based on all collections seen and literature and locations of samples included in the multivariate analyses. **A.** Eurasia. **B.** Italy. **C.** Japan.

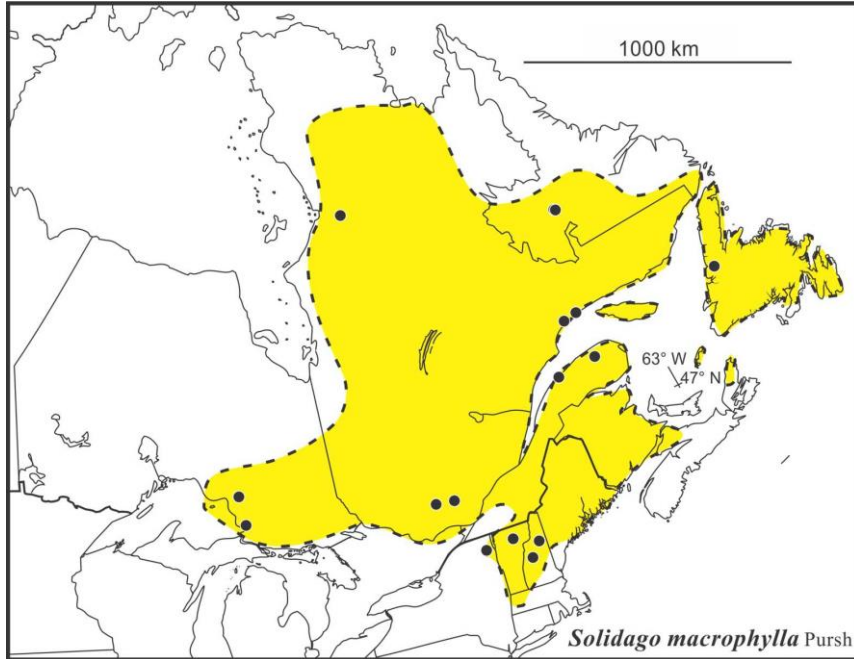


Figure 30. Range of distribution of *Solidago macrophylla* in eastern Canada and the adjacent US based on all collections seen and literature and locations of samples included in the multivariate analyses.

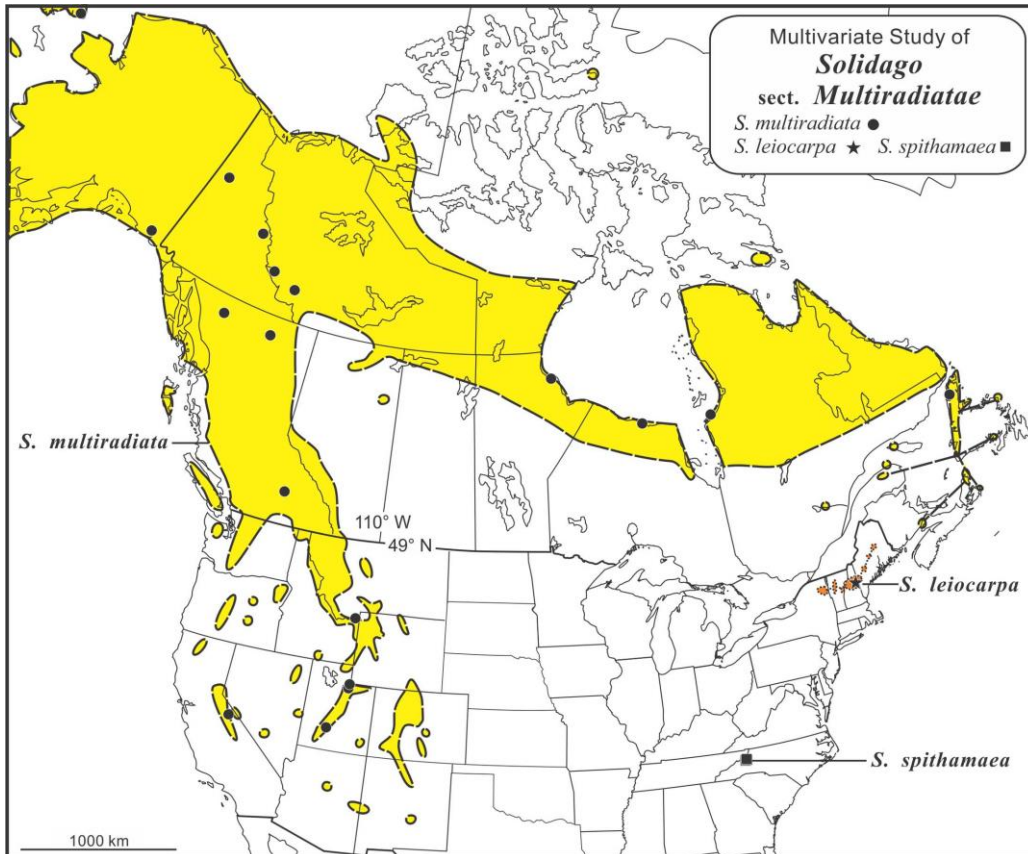


Figure 31. Ranges of distribution of *Solidago multiradiata*, *S. leiocarpa*, and *S. spithamea* in North America based on all collections seen and literature and locations of samples included in the multivariate analyses.

MATERIAL AND METHODS

Herbarium specimens were borrowed and examined from the following herbaria: A, ALA, BM, GH, the J.K. Morton personal herbarium in TRT, K, KYO, MO, MT, PE, PI, TNS, WAT in MT (Thiers continuously updated). More than 1100 specimens were examined, from which 217 were chosen and measured for the statistical analyses based on completeness of the specimen, maturity, and geographical distribution: 161 specimens of ser. *Solidago* (36 specimens of *Solidago virgaurea* s.s., 25 specimens of *S. dahurica*, 44 specimens of *S. decurrens* including 5 specimens of var. *insularis*, 1 specimen of *S. horieana*, 20 specimens of *S. kurilensis* including the holotype of *S. nipponica*, 8 specimens of *S. litoralis*, 13 specimens of *S. minutissima*, 9 specimens of *S. pacifica*, and 5 specimens of *S. yokusaiana*) and 56 specimens of possibly related North American species (13 specimens of *S. leiocarpa*, 13 specimens of *S. macrophylla*, 17 specimens of *S. multiradiata* and 13 specimens of *S. spithamaea*). In total, 18 vegetative and 16 inflorescence and floral traits were scored for the final analyses (Table 2). Additional stem, leaf, inflorescence, and phyllary and cypsela 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. Seven analyses were performed. In the first analysis, *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. litoralis*, *S. macrophylla*, *S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea*, and *S. virgaurea* were included in a STEPWISE discriminant analysis and then a COMPLETE discriminant analysis with seven traits because only eight specimens of *S. litoralis* were included. In the second analysis, three a priori groups (ser. *Macrophyllae*, sect. *Multiradiatae*, and ser. *Solidago*) were included in a STEPWISE discriminant analysis. In the third analysis, *S. leiocarpa*, *S. multiradiata*, and *S. spithamaea* were included in a STEPWISE discriminant analysis. In the fourth analysis, *S. dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea*, were included in a STEPWISE discriminant analysis. In the fifth analysis, *S. litoralis* and *S. virgaurea* were compared in a STEPWISE discriminant analysis. In the sixth, *S. dahurica*, *S. decurrens*, and *S. virgaurea* were investigated via a STEPWISE analysis. In the seventh, *S. decurrens*, *S. kurilensis*, and *S. minutissima* were included in a STEPWISE discriminant analysis with specimens of *S. decurrens* var. *insularis*, *S. horieana*, and *S. yokusaiana* included a posteriori. Numerous preliminary analyses were run over multiple years as the sample sizes of the taxa were increased but are not reported here. One result of these preliminary analyses was the conclusion that *S. nipponica* was a synonym of *S. kurilensis*.

Table 2. Traits scored for the multivariate analyses of 217 specimens of *Solidago*.

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 the inflorescences at the widest point (cm).
CAPBLN	Length of the lower longest inflorescence branches (cm)
INVOLHT	Involucre height at anthesis (mm)
MIDPHYLWD	Width of mid series phyllary at widest point (mm)
MIDPHYLW1MM	Width of mid series phyllary 1 mm below apex (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	Total number of hairs on disc floret ovary/fruit body

RESULTS

Eleven 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 length of the mid stem leaf and 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 the following pairs of traits correlated highly: ray floret lamina length and disc floret pappus length, ray floret ovary/fruit body length and disc floret ovary/fruit body length, ray floret pappus length and disc floret pappus length, and disc corolla length and disc floret pappus length correlated highly; the underlined characters were included in the analyses.

In the COMPLETE discriminant analysis of 206 specimens of eleven species level a priori groups (*Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. macrophylla*, *S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea*, and *S. virgaurea*), the following seven of twelve traits selected in a STEPWISE analysis were used in the COMPLETE analysis and are listed in order of decreasing F-to-remove values: total number of disc floret ovary/fruit body hairs (33.63), mid series phyllary length (17.28), number of mid stem leaf margin serrations (16.96), number of ray florets (14.75), mid stem leaf length (11.96), mid series phyllary width 1 mm below apex (10.37), disc corolla lobe length (4.02). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 3. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. macrophylla* and *S. multiradiata* (58.318); the smallest separations were between *S. litoralis* and *S. spithamae* (4.559).

Table 3. Between groups F-matrix for the 11 a priori group analysis (df = 7 189).

Group	<i>dahurica</i>	<i>decurrens</i>	<i>kurilensis</i>	<i>leiocarpa</i>	<i>litoralis</i>	<i>macrophylla</i>	<i>minutissima</i>	<i>multiradiata</i>
<i>decurrens</i>	13.146							
<i>kurilensis</i>	15.060	19.816						
<i>leiocarpa</i>	25.682	36.000	29.797					
<i>litoralis</i>	14.301	19.603	18.891	1.226				
<i>macrophylla</i>	22.328	52.913	42.310	37.800	28.200			
<i>minutissima</i>	23.961	10.524	15.270	38.526	23.261	50.959		
<i>multiradiata</i>	34.185	41.676	31.314	23.448	16.850	58.318	31.927	
<i>pacifica</i>	4.922	4.532	11.358	17.403	12.157	24.464	14.928	26.154
<i>spithamaea</i>	15.408	19.203	13.310	7.438	4.559	27.839	20.826	25.142
<i>virgaurea</i>	15.334	22.882	9.414	15.994	6.470	52.969	23.681	23.729

Group	<i>pacifica</i>	<i>spithamaea</i>
<i>spithamaea</i>	12.714	
<i>virgaurea</i>	11.370	9.452

Wilks' lambda = 0.0086 df = 7 10 195; Approx. F= 19.9746 df = 70 1108 prob = 0.0000

In the Classificatory Discriminant Analysis of 206 specimens of the 11 species level a priori groups (*Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. litoralis*, *S. macrophylla*, *S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea*, and *S. virgaurea*), percents of correct a posteriori assignment to the same a priori group ranged from 56-100%. The Classification matrix and Jackknife classification matrix are presented in Table 4. Results are presented in order of decreasing percents of correct placement. Thirteen of 13 specimens of the *S. minutissima* a priori group (100%) were assigned a posteriori to the *S. minutissima* group with 93-100% probability. Twelve of 12 specimens of the *S. macrophylla* group (100%) were assigned a posteriori to the *S. macrophylla* group with 99-100% probability. Fifteen of the 17 specimens of the *S. multiradiata* a priori group (88%) were assigned a posteriori to *S. multiradiata* groups (88%): 13 specimens with 99-100% probability and 2 specimens with 87% and 82% probabilities. One specimen of the *S. multiradiata* a priori group (85%) was assigned a posteriori to *S. virgaurea* with 49% probability (23% to *S. dahurica*, 13% to *S. decurrens* and 9% to *S. multiradiata* (Semple et al. 11165 WAT from Nahanni N.P.R., Northwest Terr., Canada). Eleven of 13 specimens of the *S. spithamaea* a priori group were assigned a posteriori to the *S. spithamaea* group: 5 specimens with 94-99% probability, 1 specimen with 65% probability, 1 specimen with 56% probability, and 4 specimens with 45-49% probability (all 11 from Grandfather Mt., North Carolina). Two specimens of the *S. spithamaea* a priori group were assigned a posteriori to other species: 1 specimen to *S. dahurica* with 49% probability (26% to *S. spithamaea* and 22% to *S. macrophylla* (Semple & Suropto 9669 WAT) and 1 specimen to *S. kurilensis* with 41% probability (32% to *S. spithamaea* and 22% to *S. virgaurea*; Semple & Suropto 9669 WAT). Sixteen of 20 specimens of the *S. kurilensis* a priori group (85%) were assigned a posteriori to the *S. kurilensis* group: 7 specimens with 92-100% probability (including a shoot of *Barkalob s.n.* ALA from the southern Kuril Islands), 3 specimens with 83-89% probability, 2 specimens

with 77% and 73% probabilities, 1 specimen with 68% probability (the holotype of *S. nipponica*, Hori 1524 KYO; Fig. 13), 1 specimen with 57% probability (22% to *S. virgaurea*), and 2 specimens with 42% probability (42% to *S. spithamea* and 16% to *S. virgaurea*) and 42% probability (30% to *S. minutissima* and 22% to *S. decurrens*). Three specimens of the *S. kurilensis* a priori group were assigned to other species: 1 specimen to *S. virgaurea* with 92% probability (Konta 19657 A from Aomori Pref., Japan) and 2 specimens to *S. decurrens* with 60% probability (17% to *S. kurilensis* and 9% to *S. dahurica*; Staff of Bot. Gard. Tohoku U. 72905 MO from Ogachi-gun, Akita Pref., Japan) and 54% probability (28% to *S. minutissima* and 7% to *S. kurilensis*; Kurosaki 6416 KYO from Hokkaido, Japan). Thirty-seven of 44 specimens of the *S. decurrens* a priori group (84%) were assigned a posteriori to the *S. decurrens* group: 3 specimens with 90-93% probability, 12 specimens with 81-89% probability, 8 specimens with 73-79% probability, 6 specimens with 60-68% probability, 6 specimens with 50-58% probability, and 2 specimens with 46% probability (23% to *S. pacifica* and 22% to *S. dahurica*; Peng 12158 A from Taiwan; dwarf shoot) and 45% probability (34% to *S. dahurica* and 19% to *S. pacifica*; Wilson 1695 K from Hubei Prov., China; robust shoot). Seven specimens of *S. decurrens* were assigned a posteriori to other species: 3 specimens to *S. dahurica* with 73%, 62%, and 49% probabilities, 2 specimens to *S. pacifica* with 78% and 44% probabilities, 1 specimen to *S. spithamea* with 81% probability, and 1 specimen to *S. minutissima* with 68% probability (Tsang 2448 A from Guangxi Prov., China; 44 cm tall shoot). Six of 8 specimens of the *S. litoralis* a priori group (75%) were assigned a posteriori to the *S. litoralis* group: 1 specimen with 83% probability, 3 specimens with 64-68% probability, 1 specimen with 50% probability, and 1 specimen with 44% probability. Two specimens of the *S. litoralis* a priori group were assigned to other species: 1 specimen to *S. leiocarpa* with 59% probability (38% to *S. litoralis*; Bussotti s.n. PI) and 1 specimen to *S. pacifica* with 48% probability (16% to *S. litoralis*, 11% to *S. virgaurea*, 11% to *S. decurrens*, and 5% to *S. dahurica*; Nouoli s.n. PI). Seventeen of 25 specimens of the *S. dahurica* a priori group (68%) were assigned a posteriori to the *S. dahurica* group: 3 specimens with 95-100% probability, 5 specimens with 83-89% probability, 2 specimens with 70-71% probability, 2 specimens with 66% and 60% probabilities, 4 specimens with 50-58% probability, and 1 specimen with 46% probability (40% to *S. decurrens*; 40% to *S. decurrens* and 11% to *S. pacifica*; Konnikov-Galitsky 1218 MO from Zabaykasky Krai, eastern Russia). Eight specimens of the *S. dahurica* a priori group were assigned to other species: 4 specimens to *S. decurrens* with 77% probability (from Pakistan), 70% probability (from Nepal), 65% probability (from Pakistan) and 32% probability (32% to *S. dahurica*, 20% to *S. pacifica*, and 8% to *S. kurilensis*; from Kamchatka); 2 specimens to *S. pacifica* with 86% probability (from northeastern China) and 41% probability (26% to *S. kurilensis* and 23% to *S. decurrens*; Uzbekistan); 1 specimen to *S. macrophylla* with 52% probability, and 1 specimen to *spithamea* with 31% probability (28% to *S. dahurica*, 27% to *S. kurilensis* and 13% to *S. virgaurea*); and 1 specimen to *S. macrophylla* with 52% probability (36% to *S. dahurica* and 7% to *S. spithamea*; from India). Five of 9 specimens of the *S. pacifica* a priori group (56%) were assigned a posteriori to the *S. pacifica* group: 3 specimens with 91-100% probability, 1 specimen with 79% probability, and 1 specimen with 55% probability (33% to *S. decurrens* and 7% to *S. kurilensis*). Four specimens of the *S. pacifica* a priori group were assigned to other species: 2 specimens to *S. dahurica* with 82% probability and 53% probability; and 2 specimens to *S. decurrens* with 73% probability and 50% probability (49% to *S. pacifica*). Seven of 13 specimens of the *S. leiocarpa* a priori group (54%) were assigned a posteriori to the *S. leiocarpa* group: 3 specimens with 90-97% probability, 1 specimen with 84% probability, 2 specimens with 76% and 73% probabilities, and 1 specimen with 67% probability. Six specimens of the *S. leiocarpa* a priori group were assigned to other species: 3 specimens to *S. litoralis* with 91% probability, 73% probability, and 45% probability; and 2 specimens to *S. spithamea* with 93% probability and 59% probability. Sixteen of the 31 specimens of the *S. virgaurea* a priori group (52%) were assigned a posteriori to the *S. virgaurea* group: 4 specimens with 90-95% probability, 1 specimen with 82% probability, 4 specimens with 72-74% probability, 2 specimens with 47% probability and 45% probability. Fifteen specimens of the *S. virgaurea* a priori group were assigned a posteriori to other

species: 3 specimens to *S. litoralis* with 93% probability, 88% probability, and 53% probability; 3 specimens to *S. kurilensis* with 72% probability, 59% probability and 45% probability); 2 specimens to *S. dahurica* with 85% probability and 30% probability; 2 specimens to *S. spithamaea* with 61% probability and 55% probability; 2 specimens to *S. decurrens* with 55% probability and 36% probability; and 1 specimen to *S. multiradiata* with 88% probability.

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

Group	<i>dahurica</i>	<i>decurrens</i>	<i>kurilensis</i>	<i>leiocarpa</i>	<i>litoralis</i>	<i>macrophylla</i>	<i>minutissima</i>	<i>multiradiata</i>	<i>pacifica</i>	<i>spithamaea</i>	<i>virgaurea</i>	% correct
<i>dahurica</i>	17	4	0	0	0	1	0	0	2	1	0	68
<i>decurrens</i>	3	37	0	0	0	0	1	0	2	1	0	84
<i>kurilensis</i>	0	2	17	0	0	0	0	0	0	0	1	85
<i>leiocarpa</i>	1	0	0	7	3	0	0	0	0	2	0	54
<i>litoralis</i>	0	0	0	1	6	0	0	0	1	0	0	75
<i>macrophylla</i>	0	0	0	0	0	13	0	0	0	0	0	100
<i>minutissima</i>	0	0	0	0	0	0	13	0	0	0	0	100
<i>multiradiata</i>	0	0	0	0	0	0	1	15	0	0	1	88
<i>pacifica</i>	2	2	0	0	0	0	0	0	5	0	0	56
<i>spithamaea</i>	1	0	1	0	0	0	0	0	0	11	0	85
<i>virgaurea</i>	1	2	4	0	3	0	0	1	1	3	16	52
Totals	25	47	22	8	12	14	15	16	11	18	18	76

Jackknifed classification matrix

Group	<i>dahurica</i>	<i>decurrens</i>	<i>kurilensis</i>	<i>leiocarpa</i>	<i>litoralis</i>	<i>macrophylla</i>	<i>minutissima</i>	<i>multiradiata</i>	<i>pacifica</i>	<i>spithamaea</i>	<i>virgaurea</i>	% correct
<i>dahurica</i>	13	5	1	0	0	1	0	0	4	1	0	52
<i>decurrens</i>	3	36	0	0	0	0	2	0	2	1	0	82
<i>kurilensis</i>	0	2	16	0	0	0	0	0	0	1	1	80
<i>leiocarpa</i>	1	0	0	6	4	0	0	0	0	2	0	46
<i>litoralis</i>	0	0	0	3	3	0	0	0	1	0	1	38
<i>macrophylla</i>	0	0	0	0	0	12	0	0	1	0	0	92
<i>minutissima</i>	0	0	0	0	0	0	13	0	0	0	0	100
<i>multiradiata</i>	0	0	0	0	0	0	1	15	0	0	1	88
<i>pacifica</i>	2	3	0	0	0	0	0	0	4	0	0	44
<i>spithamaea</i>	1	1	1	1	0	0	0	0	0	9	0	69
<i>virgaurea</i>	1	2	4	0	5	0	0	1	1	3	14	45
Totals	21	49	22	10	12	12	16	16	13	17	17	68

Two dimensional plots of CAN1 versus CAN2 and CAN1 versus CAN3 canonical scores for 206 specimens of *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. leiocarpa*, *S. litoralis*, *S. macrophylla*, *S. minutissima*, *S. multiradiata*, *S. pacifica*, *S. spithamaea*, and *S. virgaurea* plus 1 additional specimen of *S. horieana*, 5 specimens of *S. virgaurea*, and 5 specimens of *S. yokusaiana* only included a posteriori and are presented in Fig. 32. Eigenvalues on the first three axes were 2.736, 2.698, and 1.144.

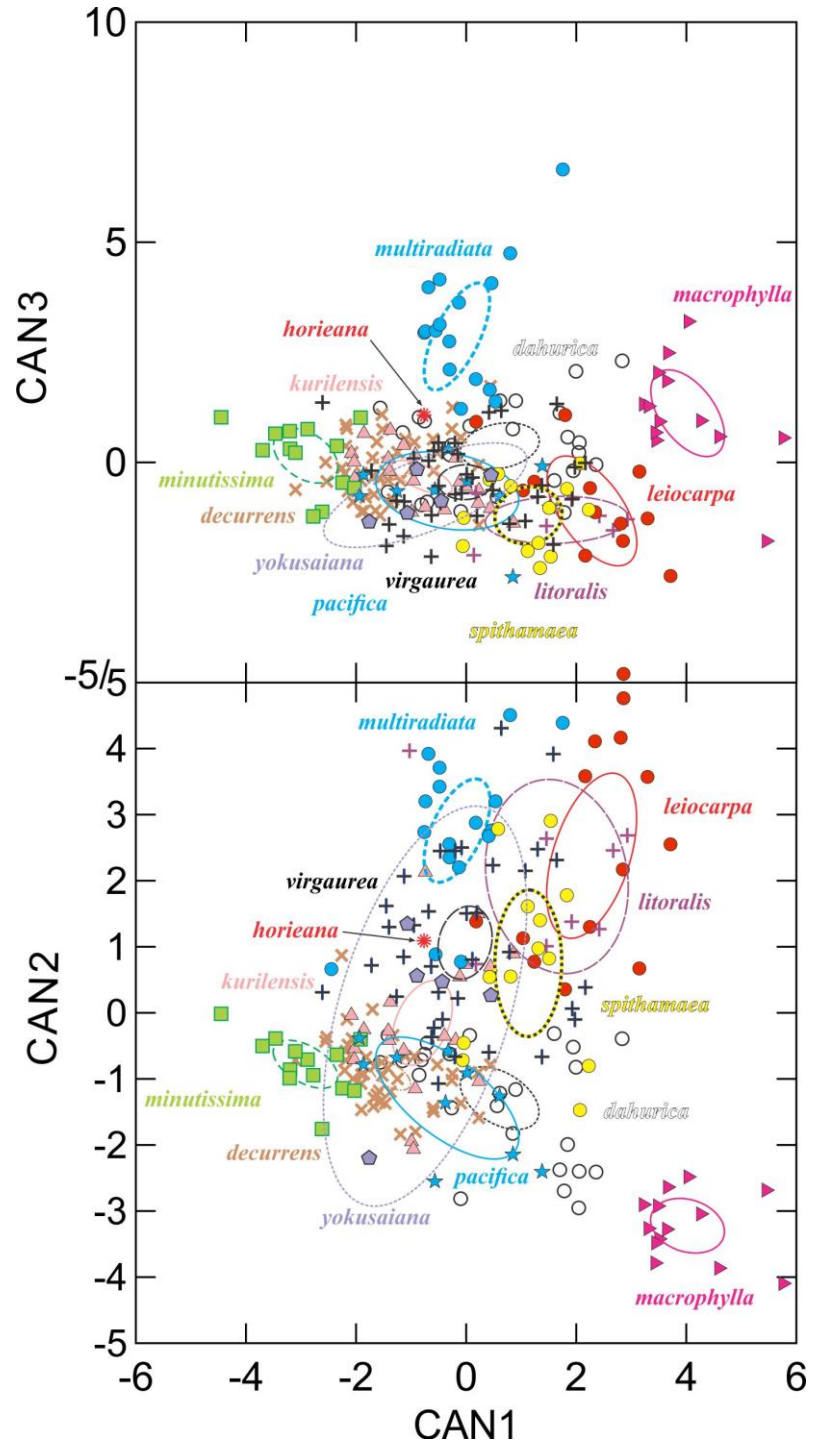


Figure 32. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 206 a priori specimens of species of *Solidago* ser. *Solidago*, *S. macrophylla*, and *S.* sect. *Multiradiata* and 11 a posteriori specimens based on a COMPLETE discriminant analysis using seven traits: *S. dahurica* (open black circles), *S. decurrens* (light brown x's), *S. horieana* (red star burst), *S. leiocarpa* (red dots), *S. litoralis* (purple +s), *S. macrophylla* (magenta right-oriented triangles), *S. minutissima* (light green squares), *S. multiradiata*, *S. pacifica* (light blue stars), *S. spithamaea* (yellow dots), and *S. virgaurea* (black +s); 95% confidence limits indicated by ellipses.

Three higher level a priori groups analysis

The Pearson correlation matrix for traits of specimens of ser. *Macrophyllae*, sect. *Multiradiatae*, and ser. *Solidago* was the same as in the eleven species analysis reported above.

In the STEPWISE discriminant analysis of 216 specimens of three species level a priori eleven traits were selected and are listed in order of decreasing F-to-remove values: number of ray florets (62.08), mid leaf margin serrations (26.33), total number of disc floret ovary/fruit body hairs (24.05), mid series phyllary length (19.16), disc corolla lobe length (14.97), ray floret lamina length

(14.86), disc floret corolla length (8.71), ray floret pappus length (7.58), mid series phyllary width (7.01), involucre height (4.17), and mid stem leaf length (4.15). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 5. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between sect. *Multiradiatae* and ser. *Solidago* (40.103); the smallest separation was between ser. *Macrophyllae* and sect. *Multiradiatae* (29.317).

Table 5. Between groups F-matrix for the three higher level a priori groups analysis (df = 11 203).

Group	<i>Macrophyllae</i>	<i>Multiradiatae</i>
<i>Multiradiatae</i>	29.317	
<i>S. ser. Solidago</i>	32.560	40.103

Wilks' lambda = 0.1178 df = 11 2 213; Approx. F= 35.3061 df = 22 406 prob = 0.0000

In the Classificatory Discriminant Analysis of 216 specimens of the three higher level a priori groups (*Solidago ser. Macrophyllae*, *S. sect. Multiradiatae*, and *S. ser. Solidago*), percents of correct a posteriori assignment to the same a priori group ranged from 95-100%. The Classification matrix and Jackknife classification matrix are presented in Table 6. Results are presented in order of decreasing percents of correct placement. All 13 specimens of the *S. ser. Macrophyllae* a priori group (100%) were assigned a posteriori into the *S. ser. Macrophyllae* group; all specimens with 100% probability. One hundred and fifty-nine of 160 specimens of the *S. ser. Solidago* a priori group (99%) were assigned a posteriori into the *S. ser. Solidago* group; 144 specimens with 94-100% probability, 4 specimens with 81-89% probability, 4 specimens with 72-78% probability, 3 specimens with 62-66% probability, 2 species with 55% and 53% probabilities. One specimen of the *S. ser. Solidago* a priori group was assigned to the ser. *Macrophyllae* group with 51% probability (49% probability to the *S. ser. Solidago*; *Nouoli s.n.* PI, a densely hairy *S. litoralis* shoot from Calambrone, Italy). Forty-one of 43 specimens of the *S. sect. Multiradiatae* a priori group (95%) were assigned a posteriori to the *S. sect. Multiradiatae* group: 38 specimens with 97-100 probability, 2 specimens with 89% and 84% probabilities, and 1 specimen with 58% probability. Two specimens of the *S. sect. Multiradiatae* a priori group were assigned to *S. ser. Solidago*: 1 specimen with 100% probability (*Hawthorn s.n.* WAT; a *S. multiradiata* collection from Churchill, Manitoba) and 1 specimen with 97% probability (*Semple et al. 11165* WAT; a *S. multiradiata* collection from Nahanni NPR, Northwest Territories).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 216 specimens of *Solidago ser. Macrophyllae*, *S. sect. Multiradiatae*, and *S. ser. Solidago* is presented in Fig. 33. Eigenvalues on the first two axes were 2.280 and 1.588.

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

Group	<i>Macrophyllae</i>	<i>Multiradiatae</i>	<i>Solidago</i>	% correct
<i>Macrophyllae</i>	13	0	0	100
<i>Multiradiatae</i>	0	41	2	95
<i>Solidago</i>	1	0	159	99
Totals	14	41	161	99

Jackknifed classification matrix

Group	<i>Macrophyllae</i>	<i>Multiradiatae</i>	<i>Solidago</i>	% correct
<i>Macrophyllae</i>	13	0	0	100
<i>Multiradiatae</i>	0	40	3	93
<i>Solidago</i>	4	1	155	97
Totals	17	41	158	96

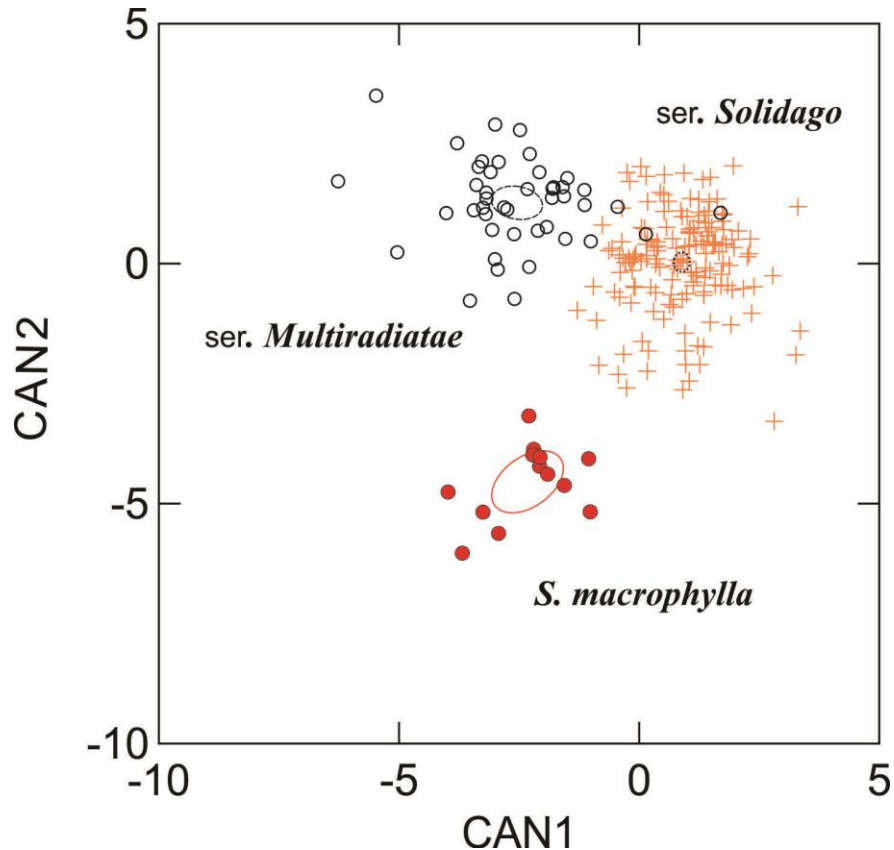


Figure 33. Plot of canonical scores (CAN1 vs CAN2) analysis for 216 specimens of *Solidago*: ser. *Macrophylla* (red dots), sect. *Multiradiatae* (black circles), and ser. *Solidago* (light brown +s).

Three species level a priori groups analysis: *Solidago* ser. *Multiradiatae*

The Pearson correlation matrix for traits of specimens of three species of sect. *Multiradiatae*, (*S. leiocarpa*, *S. multiradiatae*, and *S. spithamaea*) included $r > |0.7|$ for most pairs of basal and lower leaf traits and mid and upper leaf traits reducing the traits used to mid stem leaf length and number of serrations. Basal rosette leaves were often present but were not included in the discriminant analyses. Only two pairs of floral traits were highly correlated: 1) ray floret lamina length and ray floret pappus length and 2) ray floret pappus length and disc floret pappus length. Ray floret lamina length and disc floret pappus length were included in the STEPWISE analysis.

In the STEPWISE discriminant analysis of 43 specimens of three species level a priori groups in sect. *Multiradiatae*, (*S. leiocarpa*, *S. multiradiatae*, and *S. spithamaea*), the following seven traits were selected and are listed in order of decreasing F-to-remove values: mid series phyllary width 1 mm below apex (59.75), disc floret pappus length (23.73), mid series phyllary width (22.01), ray floret lamina width (15.55), number of mid stem leaf serrations (11.52), disc floret ovary/fruit body length (6.06), and mid series phyllary length (5.26). 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 separation was between *S. multiradiatae* and *S. spithamaea* (91.016); the smallest separation was between *S. leiocarpa* and *S. spithamaea* (25.406).

Table 7. Between groups F-matrix for the four species level a priori groups analysis (df = 7 34).

Group	<i>leiocarpa</i>	<i>multiradiata</i>
<i>multiradiata</i>	59.787	
<i>spithamaea</i>	25.406	91.016

Wilks' lambda = 0.0087 df = 7 2 40; Approx. F= 47.3623 df = 14 68 prob = 0.0000

In the Classificatory Discriminant Analysis of 43 specimens of the three species level a priori groups (*S. leiocarpa*, *S. multiradiatae*, and *S. spithamaea*), percents of correct a posteriori assignment to the same a priori group was 100% for all three groups with all specimens being placed in their appropriate groups with 100% probability. The Classification matrix and Jackknife classification matrix are presented in Table 8.

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

Group	<i>leiocarpa</i>	<i>multiradiata</i>	<i>spithamaea</i>	% correct
<i>leiocarpa</i>	13	0	0	100
<i>multiradiata</i>	0	17	0	100
<i>spithamaea</i>	0	0	13	100
Totals	13	17	13	100

Jackknifed classification matrix

Group	<i>leiocarpa</i>	<i>multiradiata</i>	<i>spithamaea</i>	% correct
<i>leiocarpa</i>	13	0	0	100
<i>multiradiata</i>	0	17	0	100
<i>spithamaea</i>	0	0	13	100
Totals	13	17	13	100

Two dimensional plot of CAN1 versus CAN2 canonical scores for 43 specimens of *Solidago leiocarpa*, *S. multiradiata*, and *S. spithamaea* is presented in Fig. 34. Eigenvalues on the first two axes were 20.430 and 4.394.

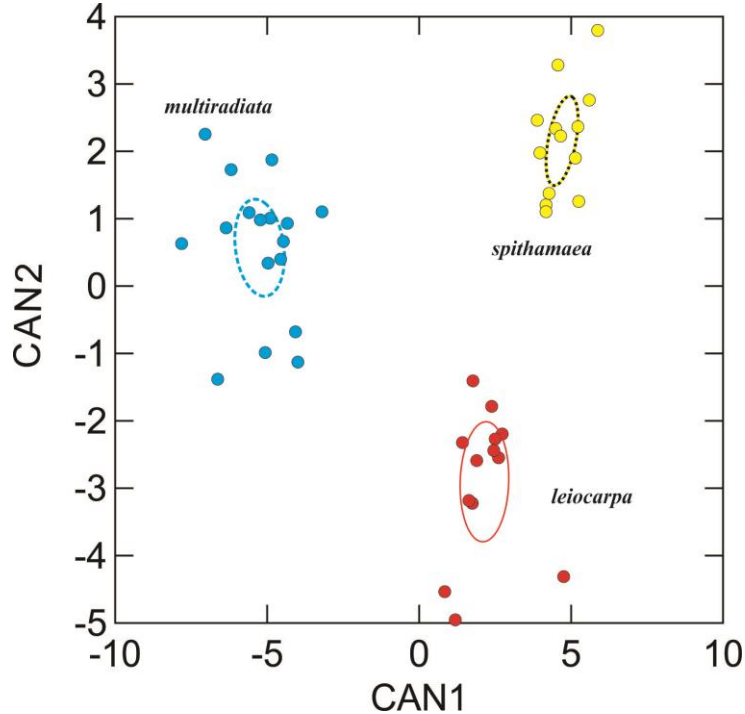


Figure 34. Plot of canonical scores (CAN1 vs CAN2) analysis for 43 specimens of *Solidago* sect. *Multiradiata*: *S. leiocarpa* (open blue stars), *S. multiradiata* (red circles), and *S. spithamaea* (yellow stars).

Seven species level a priori groups analysis: *Solidago* ser. *Solidago*

The Pearson correlation matrix yielded $r > |0.7|$ that was similar to that for all taxa in the first analysis. Only mid stem leaf length and number of serrations were used in the analysis of ser. *Solidago*. Floral traits used were the same as those in the first analysis.

In the STEPWISE discriminant analysis of 150 specimens of seven species level a priori groups (*S. dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea* plus 1 additional specimen of *S. horieana*, 5 specimens of *S. virgaurea*, and 5 specimens of *S. yokusaiana* only included a posteriori), the following seven traits were selected and are listed in order of decreasing F-to-remove values: total number of disc floret ovary/fruit body hairs (33.96), disc floret pappus length (16.48), number of mid stem leaf serrations (8.92), mid stem leaf length (7.07), ray floret lamina width (4.92), mid series phyllary width (4.29), and involucre height (3.94). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were the samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. F-values based on Mahalanobis distances of the between group centroids indicated the largest separations were between *S. litoralis* and *S. minutissima* (49.417) and *S. litoralis* and *S. decurrens* (40.840); the smallest separations were between *S. decurrens* and *S. pacifica* (2.447) and *S. dahurica* and *S. pacifica* (3.997).

Table 9. Between groups F-matrix for the 7 a priori species groups analysis (df = 7 137).

Group	<i>dahurica</i>	<i>decurrens</i>	<i>kurilensis</i>	<i>litoralis</i>	<i>minutissima</i>	<i>pacifica</i>
<i>decurrens</i>	21.638					
<i>kurilensis</i>	22.783	17.379				
<i>litoralis</i>	21.245	40.840	32.690			
<i>minutissima</i>	38.000	13.741	17.092	49.417		
<i>pacifica</i>	3.997	2.447	8.536	22.811	14.905	
<i>virgaurea</i>	19.657	29.447	12.178	16.365	34.455	10.290

Wilks' lambda = 0.03297 df = 7 6 143; Approx. F= 16.4651 df = 42 646 prob = 0.0000

In the Classificatory Discriminant Analysis of 150 specimens of seven species level a priori groups (*S. dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea*) plus 12 additional specimens only included a posteriori of (1 specimen of *S. dahurica*; 1 specimen of *S. horieana*; 6 specimens of *S. virgaurea* from Estonia, South Kazakhstan, Pakistan, India, Nepal; and 5 specimens of *S. yokusaiana*), percents of correct a posteriori assignment to the same a priori group ranged from 56-100%. The Classification matrix and Jackknife classification matrix are presented in Table 10. Results are presented in order of decreasing percents of correct placement. Thirteen of the 13 specimens of the *S. minutissima* a priori group (100%) were assigned a posteriori into the *S. minutissima* group with 93-100% probability. Eight of 8 specimens of the *S. litoralis* a priori group (100%) were assigned a posteriori into the *S. litoralis* group with 99-100% probability. Thirty-five of the 44 specimens of the *S. decurrens* a priori group (80%) were assigned a posteriori to the *S. decurrens* group: 2 specimens with 93% and 91% probabilities, 10 specimens with 80-89% probability, 11 specimens with 71-78% probability, 7 specimens with 61-69% probability, and 4 specimens with 59% probability (33% to *S. pacifica*; Miki et al. 81 MO from Honshu, Japan), 53% probability (42% to *S. pacifica*; Feng 12731 A from Yunnan Prov., China), 50% probability (25% to *S. pacifica*, 23% to *S. dahurica*; Peng 12158 A from Taiwan), and 50% probability (29% to *S. virgaurea*, 21% to *S. dahurica*; Clarke 18650 BM from India; holotype/lectotype of *S. virgaurea* var. *glabriuscula* Clark). Nine specimens of the *S. decurrens* a priori group were assigned to other species: 6 specimens to *S. pacifica* with 88% probability (*Sino-Amer. Exped. 2016* A from Hubei Prov., China), 72% probability (26% to *S. decurrens*; *Sino-Amer. Exped. 1257* A from Hubei Prov. China), 54% probability (22% to *S. decurrens*; *Togast 791* MO from Miyagi, Japan), 50% probability (41% to *S. decurrens*; *Hooker & Thomson s.n.* K from Khasia Hills, Meghalaya Prad., India), 49% probability (30% to *S. decurrens*, 17% to *S. dahurica*; *Niu 91401* MO from Jiangxi Prov., China), and 43% probability (42% to *S. decurrens*, 13% *S. dahurica*; *Furuse 1875* K from Okinawa Pref., Japan); 1 specimen to *S. dahurica* with 70% probability (20% to *S. minutissima*; *Wilson 1695* K from Hubei Prov., China); 1 specimen to *S. minutissima* with 54% probability (45% to *S. decurrens*; *Tsang 24487* A from Guangxi Prov., China); and 1 specimen to *S. kurilensis* with 44% probability (30% to *S. decurrens* and 25% to *S. pacifica*; *Boufford et al. 25836* A from South Korea). Sixteen of 20 specimens of the *S. kurilensis* a priori group (80%) were assigned a posteriori to the *S. kurilensis* group: 9 specimens with 90-100% probability, 6 specimens with 81-87% probability, and 1 specimen with 69% probability. Four specimens of the *S. kurilensis* a priori group were assigned to other species: 1 specimen to *S. virgaurea* with 97% probability (*Konta 19657* A from Aomori Pref., Japan); and 3 specimens to *S. decurrens* with 84% probability (10% to *S. virgaurea*; *Kitamura s.n.* KYO from Hokkaido Pref., Japan), 60% probability (18% to *S. virgaurea*, 17% to *S. kurilensis*; *Kurosaki 6416* KYO from Hokkaido Pref., Japan), and 38% probability (34% to *S. kurilensis*, 24% to *S. virgaurea*;

Staff of Bot. Gard. Tohoku U. 72905 MO from Ogachi-gun, Akita Pref., Japan). Nineteen of 25 specimens of the *S. dahurica* a priori group (76%) were assigned a posteriori to the *S. dahurica* group: 11 specimens with 90-99% probability, 4 specimens with 62-69% probability, 1 specimen with 50% probability (36% to *S. kurilensis*, 11% to *S. virgaurea*; *Russell 1729* BM from Jammu and Kashmir Prad., India), and 3 specimens with 44% probability (40% to *S. pacifica*, 11% to *S. decurrens*; *Stewart 13510* MO from Kashmir, Pakistan), 44% probability (35% to *S. virgaurea*, 20% to *S. kurilensis*; *Abel 110* BM from northeastern Pakistan; Fig. 6I), and 39% probability (32% to *S. decurrens*, 28% to *S. virgaurea*; *Eyerdam s.n.* MO from Kamchatka, Russia). Six specimens of the *S. dahurica* a priori group were assigned a posteriori to other species: 1 to *S. virgaurea* with 73% probability (24% to *S. dahurica*; *Yang 86-0886* WAT from Xinjiang Prov., China); and 5 specimens to *S. pacifica* with 55% probability (24% to *S. dahurica*, 17% to *S. decurrens*; *Kopronovich s.n.* MO from “Manchuria”, China), 48% probability (46% to *S. dahurica*; *Navnova 4493* MO from Ilansky, Krasnoyarsk Krai, Russia), 47% probability (35% to *S. dahurica*, 18% to *S. decurrens*; *Stewart s.n.* GH from Kamchatka, Russia), and 38% probability (32% to *S. dahurica*, 17% to *S. decurrens*, 13% to *S. virgaurea*; *Tabata et al. 13668* A from Nepal). Twenty of 31 specimens of the *S. virgaurea* a priori group (65%) were assigned a posteriori to the *S. virgaurea* group: 11 specimens with 91-100% probability, 3 specimens with 82-88% probability, 2 specimens with 78% and 70% probability, 2 specimens with 58% probability (41% to *S. kurilensis*; *King 11965* MO from Mont Ventoux, Dept. Vaucluse, France) and 56% probability (44% to *S. litoralis*; *Alm 2399* MO from Lake Tornetrask Dist., Switzerland), and 2 specimens with 49% probability (42% to *S. kurilensis*; *Parlatore s.n.* MO from Terni Prov., Italy) and 39% probability (30% to *S. pacifica*, 22% to *S. decurrens*, 8% to *S. kurilensis*; *Pankakoski s.n.* MO from Tyrväntö, Finland). Six of 9 specimens of the *S. pacifica* a priori group (56%) plus 1 specimen included a posteriori were assigned a posteriori to the *S. pacific* group: 3 specimens with 73-77% probability, 2 specimens with 56% probability (25% to *S. dahurica*, 16% to *S. kurilensis*; *Tonghua Team 152* PE from Jilin Prov., China) and 54% probability (27% to *S. decurrens*, 19% to *S. dahurica*; *Wang 563* PE from from Jilin Prov., China), and 3 specimens with 49% probability (43% to *S. dahurica*, 7% *S. decurrens*; *Wang 408* PE from Heilongjiang Prov., China; Fig. 17), and 43% probability (33% to *S. kurilensis*, 21% to *S. decurrens*; *Komarov 1499* K from “Manchuria”, China). Four specimens of the *S. pacifica* a priori group were assigned a posteriori to other species; 3 specimens to *S. decurrens* with 85% probability (14% *S. pacifica*; *Skvortsov s.n.* MO from vicinity of Vladivostok, Russia), 56% probability (44% to *S. pacifica*; *Wan & Chow 81116* MO from Changbaishan, Jilin Prov., China), and 43% probability (42% to *S. pacifica*; *Maack s.n.* GH near Amur River, “Manuchuria”, China); and 1 specimen to *S. dahurica* with 74% probability (23% to *S. pacifica*; *Wan & Chow 81116* BM from Changbaishan, Jilin Prov., China).

Ten additional specimens were not assigned to an a priori group in the analysis and were only included a posteriori in the Classificatory Discriminant Analysis. One specimen of *S. horieana* (*Horrie 1107* TNS) was assigned a posteriori to *S. kurilensis* with 75% probability (21% to *S. virgaurea*). Five specimens of putative *S. virgaurea* from central Asia were assigned a posteriori as follows: 3 specimens were assigned a posteriori to *S. virgaurea* with 73% probability (23% to *S. dahurica*; *Stainton et al. 8160* BM from Nepal), 55% probability (37% *S. dahurica*; *Thompson s.n.* GH from Hamachal Pradesh, India), and 47% probability (21% to *S. kurilensis*, 16% to *S. pacifica* and 10% to *S. dahurica*; *Tabata et al. 20280* A from Nepal); 1 specimen was assigned a posteriori to *S. litoralis* with 94% probability (*FeSissaw s.n.* K from South Kazakhstan); and 1 specimen was assigned a posteriori to *S. dahurica* with 67% probability (30% to *S. virgaurea*; *Polunin, Sykes & Williams 2610* BM from Nepal). Four specimens of the morphologically distinct *S. yokusaiana* were assigned a posteriori as follows: 1 specimen to *S. kurilensis* with 92% probability (*Tanaka s.n.* {*Beaudry 58-320-2* MT} cultivated from seed, Jardin botanique, Montréal, Québec; originally from Huzo Canyon, near Kyoto, Japan); 1 specimen to *S. virgaurea* with 85% probability (*Tanaka s.n.* {*Beaudry 58-320-1* MT} cult. F1, Montréal, Québec), 1 specimen to *S. dahurica* with 74%

probability (*Kimura & Sugaya s.n. A* from Yamagata Pref., Japan), and 1 specimen to *S. minutissima* with 48% probability (31% to *S. kurilensis*, 12% to *S. virgaurea*; Shiota 997 GH from Gifu Pref., Japan).

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

Group	<i>dahurica</i>	<i>decurrens</i>	<i>kurilensis</i>	<i>litoralis</i>	<i>minutissima</i>	<i>pacifica</i>	<i>virgaurea</i>	% correct
<i>dahurica</i>	19	0	0	0	0	5	1	76
<i>decurrens</i>	1	35	1	0	1	6	0	80
<i>kurilensis</i>	0	3	16	0	0	0	1	80
<i>litoralis</i>	0	0	0	8	0	0	0	100
<i>minutissima</i>	0	0	0	0	13	0	0	100
<i>pacifica</i>	1	3	0	0	0	5	0	56
<i>virgaurea</i>	5	1	3	2	0	0	20	65
Totals	26	42	20	10	14	10	22	77

Jackknifed classification matrix

Group	<i>dahurica</i>	<i>decurrens</i>	<i>kurilensis</i>	<i>litoralis</i>	<i>minutissima</i>	<i>pacifica</i>	<i>virgaurea</i>	% correct
<i>dahurica</i>	15	1	1	0	0	6	2	76
<i>decurrens</i>	1	35	1	0	1	6	0	80
<i>kurilensis</i>	0	3	16	0	0	0	1	80
<i>litoralis</i>	0	1	0	7	0	0	0	100
<i>minutissima</i>	0	0	0	0	13	0	0	100
<i>pacifica</i>	2	3	1	0	0	3	0	56
<i>virgaurea</i>	5	1	4	3	0	1	17	65
Totals	23	44	23	10	14	16	20	77

Two dimensional plots of CAN1 versus CAN2 and CAN1 versus CAN3 canonical scores for 150 specimens of *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea* plus 1 additional specimen of *S. horieana*, 5 specimens of *S. virgaurea*, and 5 specimens of *S. yokusaitana* only included a posteriori and are presented in Fig. 35. Eigenvalues on the first three axes were 3.765, 1.532, and 0.692.

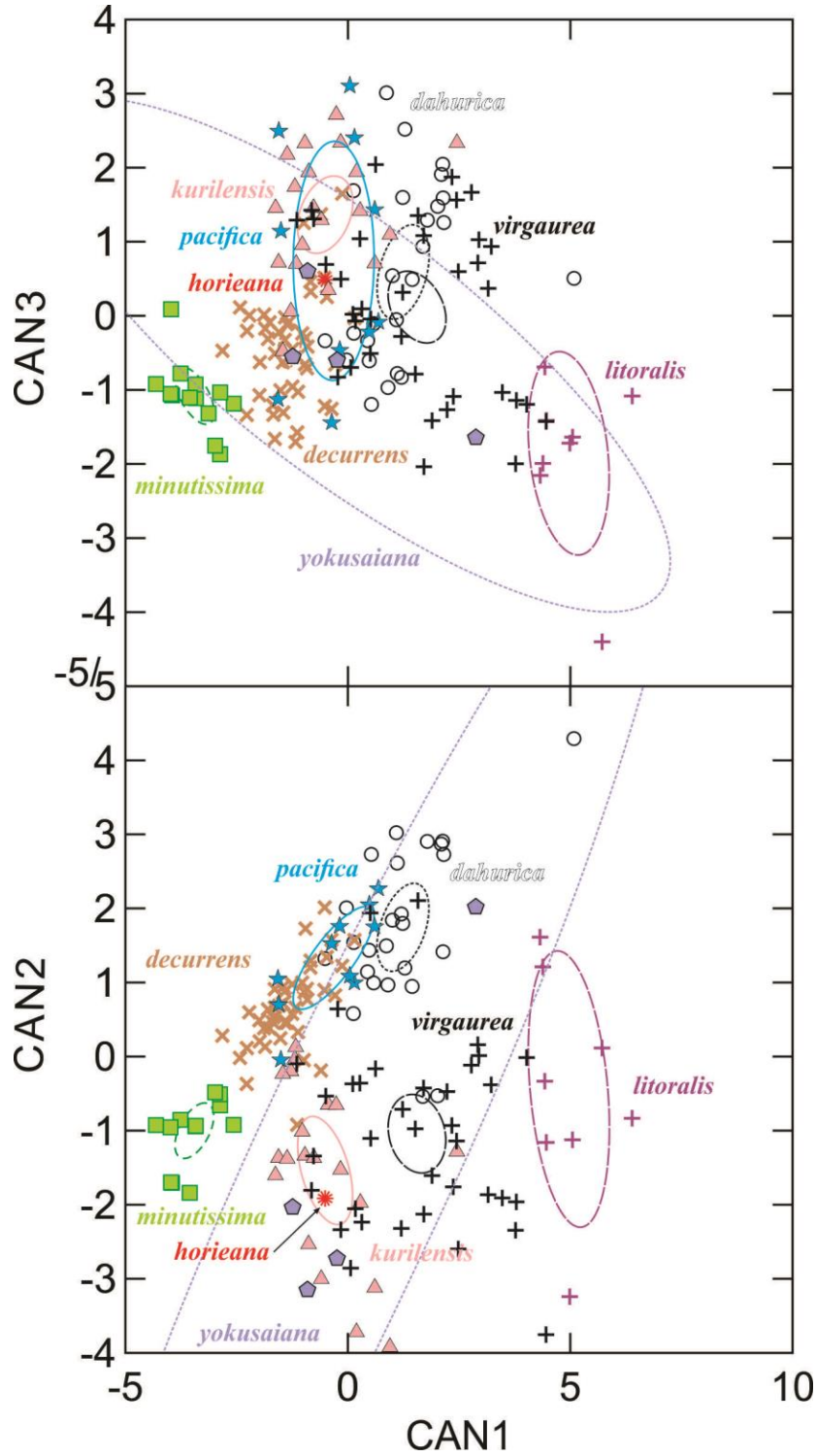


Figure 35. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 150 a priori specimens of species of *Solidago* ser. *Solidago*, and 11 a posteriori specimens *S. horieana*, *S. virgaurea* and *S. yokusaiana* based on a Stepwise discriminant analysis using seven traits: *S. dahurica* (open black circles), *S. decurrens* (light brown x's), *S. horieana* (red star burst), *S. litoralis* (purple +s), *S. minutissima* (light green squares), *S. pacifica* (light blue stars), *S. virgaurea* (black +s), and *S. yokusaiana* (lavender pentagons); 95% confidence limits indicated by ellipses.

Two species level a priori groups analysis of *S. litoralis* and *S. virgaurea*

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 and the numbers of serrations of mid and upper stem leaves. Multiple pairs of floret traits were correlated: involucre height correlated highly with mid series phyllary length and width, lengths of ray and disc floret pappi, and length of disc corolla, mid stem phyllary width correlated with length of ray and disc floret pappi, number of ray florets correlated with length, of ray and disc floret pappi, ray floret pappus length correlated with disc floret pappus length, and disc floret corolla length correlated with disc floret pappus length. Involucre height, numbers of ray and disc florets, ray floret lamina length and width, disc floret corolla and lobe lengths and total number of hairs on the disc floret ovary/cypsela body were included in the analysis.

In the STEPWISE discriminant analysis of 38 specimens of *Solidago litoralis* and *S. virgaurea*, one trait was selected in a STEPWISE analysis and is listed with F-to-remove value in parentheses: involucre height (17.26). 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 $p = 0.0002$ that the null hypothesis was true. *Solidago litoralis* and *S. virgaurea* had an F-to separate value of 17.259 (Wilks' lambda = 0.29888 df = 1 1 36; Approx. F= 17.259 df = 1 362 prob = 0.0002).

In the Classificatory Discriminant Analysis of the two species level a priori groups, the percents of correct placement a posteriori of specimens to the a priori group were 86% for *S. litoralis* and 84% for *S. virgaurea*. The Classification matrix and Jackknife classification matrix are presented in Table 11. Six of 7 specimens of *S. litoralis* (86%) were assigned a posteriori to the *S. litoralis* group: 2 specimens with 91-95% probability, 2 specimens with 87% probability, and 2 specimens with 77% and 71% probabilities. One specimen of the *S. litoralis* a priori group was assigned to *S. virgaurea* with 72% probability (*Savi s.n.* GH; stem and leaves densely hairy). Twenty-six of the 31 specimens of *S. virgaurea* (84%) plus 1 additional specimen included a posteriori were assigned a posteriori to the *S. virgaurea* group: 10 specimens with with 93-100% probability including 3 specimens from Italy, 5 specimens with 82-89% probability, 7 specimens with 70-79% probability, 1 specimen with 66% probability, and 3 specimens with 59% probability (*Kamavesh s.n.* MT from Georgia), 55% probability (Brandis 2846 A from Bosnia), and 52% probability (*Skvortsov s.n.* MO from near Moscow, Russia). Five specimens of the *S. virgaurea* a priori group were assigned a posteriori to *S. litoralis* with 86% probability (*Shlyakova 62-2* MT from Murmansk Oblast, Russia), 79% probability (*Davis 50753* BM from Morocco), 79% probability (*Ollgaard s.n.* MO from Denmark), 69% probability (*Alm 2399* GH from Switzerland), and 64% probability (*Davis 21097* MO from northeastern Turkey); none of these collections had densely hairy lower to mid stems and leaves.

Frequencies of CAN1 canonical scores for specimens of *S. litoralis* and *S. virgaurea* are presented in histograms in Fig. 36. The eigen value on the first axis was 0.479.

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

Group	<i>litoralis</i>	<i>virgaurea</i>	% correct
<i>litoralis</i>	6	1	86
<i>virgaurea</i>	5	26	84
Totals	11	27	84

Jackknifed classification matrix

Group	<i>litoralis</i>	<i>virgaurea</i>	% correct
<i>litoralis</i>	6	1	86
<i>virgaurea</i>	5	26	84
Totals	11	27	84

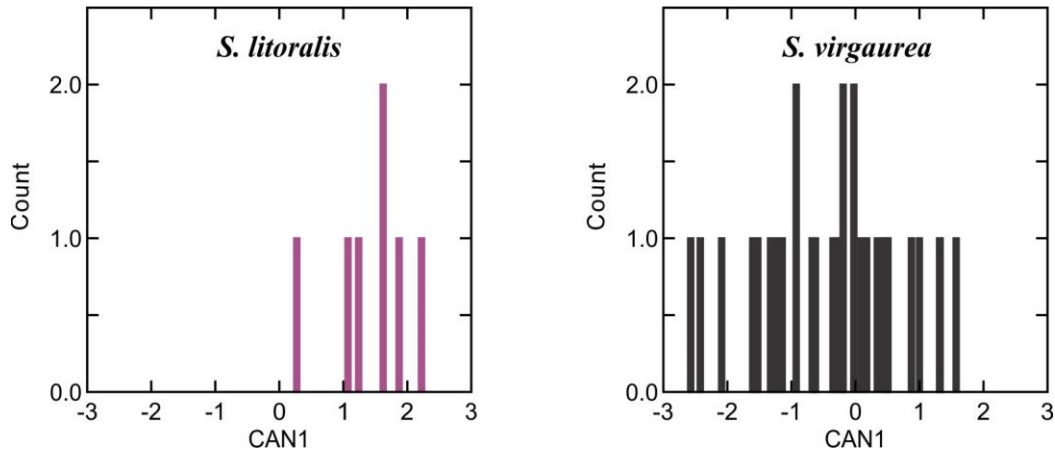


Figure. 36. Histograms of CAN1 canonical scores for 38 specimens of *S. litoralis* (left) and *S. virgaurea* (right).

Three species level a priori groups analysis of *S. dahurica*, *S. decurrens*, and *S. virgaurea*

The Pearson correlation matrix yielded $r > |0.7|$ for most pairs of leaf traits reducing the number used to mid stem leaf length and the numbers of serrations of mid and upper stem leaves. Three pairs of floret traits were correlated: involucre height and disc floret pappus length, ray floret lamina length and disc floret pappus length, and disc floret corolla length and disc floret pappus length. Disc floret pappus length was not included while the other three traits were along with all other floral traits.

In the STEPWISE discriminant analysis of 100 specimens of three species level a priori groups (*Solidago dahurica*, *S. decurrens*, and *S. virgaurea*) the following five traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret ovary/furit body total number of hairs (95.43), involucre height (14.06), , ray floret lamina length (12.29), ray floret lamina width (9.93), and number of mid stem leaf margin serrations (8.31). Wilks's lambda, Pillai's trace, and Lawley-Hotelling trace tests of the null hypothesis that all groups were samples of one group had probabilities of $p = 0.000$ that the null hypothesis was true. The F-matrix for the discriminant analysis is presented in Table 12. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation were between *S. decurrens* and *S. virgaurea* (47.459) and the smaller separations were between *S. dahurica* and *S. decurrens* (25.163) and *S. dahurica* and *S. virgaurea* (27.639).

Table 12. Between groups F-matrix for the four species level a priori groups analysis (df = 5 97).

Group	<i>dahurica</i>	<i>decurrens</i>
<i>decurrens</i>	25.163	
<i>virgaurea</i>	27.639	47.459

Wilks' lambda = 0.1323 df = 5 2 97; Approx. F= 32.5293 df = 10 186 prob = 0.0000

In the Classificatory Discriminant Analysis of 100 specimens of the three species level a priori groups (*Solidago dahurica*, *S. decurrens*, and *S. virgaurea*) plus 6 specimens only included a posteriori, percents of correct a posteriori assignment to the same a priori group ranged from 84-98%. The Classification matrix and Jackknife classification matrix are presented in Table 13. Forty-three of the 44 specimens of the *S. decurrens* a priori group (98%) were assigned a posteriori into the *S. decurrens* group; 33 specimens with 90-100% probability, 5 specimens with 80-85% probability, 1 specimen with 72% probability, 1 specimen with 62% probability, and 3 specimens with 59% probability (41% to *S. dahurica*; *Peng 12158 A* from Taiwan), 57% probability (43% to *S. dahurica*; *Niu 91401 MO* from Jiangxi Prov., China), and 49% probability (49% to *S. dahurica*; *Wilson 1695 K* from Hubei Prov., China). One specimen of the *S. decurrens* a priori group was assigned a posteriori to *S. dahurica* with 57% (38% to *S. decurrens*; *Tsang 20773 A* from Guangdong Prov., China). Twenty-seven of 31 specimens of the *S. virgaurea* a priori group (87%) plus 6 specimens only included a posteriori were assigned a posteriori to *S. virgaurea*: 23 specimens with 90-100% probability plus 1 specimen from Nepal with 98% probability and 1 specimen from southern Kyrgystan with 97% probability (assigned a priori to *S. dahurica* but having an atypically hairy cypselae body, 1 specimen with 87% probability plus 1 specimen from Nepal included a posteriori with 81% probability, 1 specimen with 79% probability plus 1 specimen from Nepal with 73%, 1 specimen with 62% probability, and 1 specimen with 53% probability (47% to *S. dahurica*; *Skvortsov s.n.* MO from near Golitsyno, Moscow Oblast, Russia; cypselae body sparsely but evenly hairy). Four specimens of the *S. virgaurea* a priori group plus one specimen include a posteriori were assigned a posteriori to other species: 3 specimens to *S. dahurica* with 97% probability (*anon. 3947 MO* of unknown provenance within the old USSR, if Asian than likely *S. dahurica*; only 5-8 few hairs on cypselae), 85% probability (*Alm & Smith 597 MO* from Switzerland; only 10-15 hairs on cypselae), and 64% probability (*Karjagin s.n.* A from Azerbaijan; 14-26 hairs mostly distal on cypselae); 1 specimen included a priori and 1 specimen only included a posteriori were assigned to *S. decurrens* with 95% probability (*Kerner 3768 MO* from Austria; 6-10 hairs on cypselae) and 86% probability (*Skvortsov et al s.n.* MO from Estonia; moderately evenly hairy cypselae). Twenty-one of 25 specimens of the *S. dahurica* a priori group (84%) were assigned a posteriori to the *S. dahurica* group: 14 specimens with 96-100% probability, 4 specimens with 80-83% probability, 2 specimens with 79% and 74% probabilities, and 1 specimen with 52% probability (*Konrokovits s.n.* MO from "Manchuria"; 5-12 hairs distal on cypselae). Four specimens of the *S. dahurica* a priori group were assigned to other species: 2 specimens to *S. virgaurea* with 93% probability (*Yang 86-0886 WAT* from western Xinjiang Prov., China; 44-50 hairs on distal half of cypselae) and 91% probability (*Abel 110 BM* from northeastern Pakistan; 45-50 hairs either mostly distal to on entire cypselae; Fig. 6I); 2 specimens to *S. decurrens* with 74% probability (*Ikonnikov-Galitsky 1218 A* from Zabaykasky Krai, Russia; 10-16 distal hairs on cypselae) and 64% probability (*Stewart s.n.* GH from Kamchatka; 0-4 distal hairs on cypselae).

A two dimensional plot of CAN1 versus CAN2 canonical scores for 106 specimens of *Solidago dahurica*, *S. decurrens*, and *S. virgaurea* are presented in Fig. 37. One additional specimen of *S. virgaurea* from Europe, 2 additional specimens of *S. dahurica* from Kyrgystan and Nepal, and 3 additional specimens of *S. virgaurea* from Nepal and Pakistan are included in the plot. Eigenvalues on the first two axes were 2.5222 and 1.128.

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

Group	<i>dahurica</i>	<i>decurrens</i>	<i>virgaurea</i>	% correct
<i>dahurica</i>	21	2	2	84
<i>decurrens</i>	1	43	0	98
<i>virgaurea</i>	3	1	27	87
Totals	25	46	29	91

Jackknifed classification matrix

Group	<i>dahurica</i>	<i>decurrens</i>	<i>virgaurea</i>	% correct
<i>dahurica</i>	20	2	2	80
<i>decurrens</i>	2	42	0	95
<i>virgaurea</i>	4	1	26	84
Totals	26	46	28	88

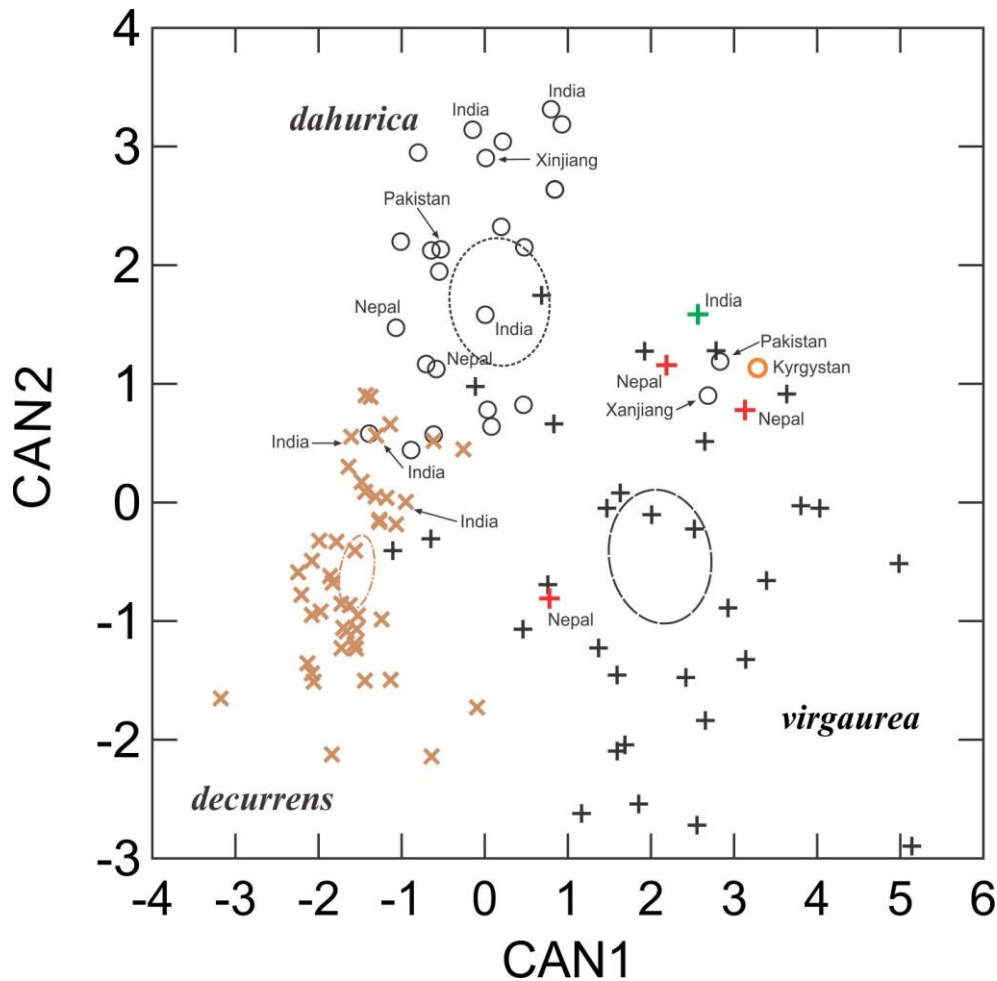


Figure 37. Plot of canonical scores (CAN1 vs CAN2) analysis for 106 specimens of *Solidago* ser. *Solidago*: *S. dahurica* (open black circles included a priori; orange circle include a posteriori), *S. decurrens* (light brown x's), and *S. virgaurea* (black +s included a priori, red and green +s included a posteriori); source locations of some collections are also indicated.

Three species level a priori groups analysis of *S. decurrens*, *S. kurilensis* and *S. minutissima*

The Pearson correlation matrix yielded $r > |0.7|$ for most pairs of leaf traits reducing the number used to mid stem leaf length and the number of serrations of upper stem leaves. Three pairs of floret traits were correlated: involucre height and disc floret pappus length, ray floret pappus length and disc floret corolla lobe length, and disc floret corolla lob length and disc floret pappus length. Disc floret pappus length and disc floret lobe length were not included. Involucre height and ray floret pappus length were included along with all other floral traits.

In the STEPWISE discriminant analysis of 100 specimens of three species level a priori groups (*Solidago decurrens*, *S. kurilensis*, and *S. minutissima*), the following six traits were selected and are listed in order of decreasing F-to-remove values: disc floret ovary/fruit body total number of hairs (20.21), number of upper stem leaf serrations (15.23), mid stem leaf length (10.74), disc corolla length (9.58), involucre height (9.46), and mid series phyllary width 1 mm below apex (7.95). 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 14. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between *S. decurrens* and *S. kurilensis* (38.629); the smaller separation was between *S. decurrens* and *S. minutissima* (27.689).

Table 14. Between groups F-matrix for the four species level a priori groups analysis (df = 65 69).

Group	<i>decurrens</i>	<i>kurilensis</i>
<i>kurilensis</i>	38.629	
<i>minutissima</i>	27.689	31.432

Wilks' lambda = 0.0678 df = 6 2 74; Approx. F= 32.6722 df = 12 138 prob = 0.0000

In the Classificatory Discriminant Analysis of 77 specimens of the three species level a priori groups (*Solidago decurrens*, *S. kurilensis*, and *S. minutissima*) plus 1 specimen of *S. horieana* and 5 specimens of *S. yokusaiana* only included a posteriori, percents of correct a posteriori assignment to the same a priori group ranged from 85-100%. The Classification matrix and Jackknife classification matrix are presented in Table 15. All 44 specimens of the *S. decurrens* a priori group (100%) were assigned a posteriori into the *S. decurrens* group; 42 specimens with 94-100% probability, 1 specimen with 83% probability, and 1 specimen with 78% probability. All 13 specimens of the *S. minutissima* a priori group (100%) were assigned a posteriori to the *S. minutissima* group: 12 specimens with 96-100% probability and 1 specimen with 82% probability. Seventeen of 20 specimens of the *S. kurilensis* a priori group (85%) were assigned a posteriori to the *S. kurilensis* group: 16 specimens with 96-100% probability and 1 specimen with 86% probability. The holotype specimen of *S. nipponica* (Horie 1524 KYO) and the two shoots on the collection from Iturup Is., Kuril Arch., Russia were included among the specimens assigned a posteriori to *S. kurilensis* with 100% probability. Three specimens of the *S. kurilensis* a priori group were assigned a posteriori to *S. decurrens* with 91% probability (*Murata 6483* KYO from Sado Is., Niigata Pref., Japan), 83% probability (*Kitamura s.n.* KYO from Hakodate, Hokkaido Pref., Japan), and 55% probability (44% to *S. kurilensis*; *Staff of Bot. Gard. Tohoku U. 72905* MO from Ogachi-gun, Akita Pref., Japan); all three plants had rounded corymbiform inflorescences or truncate lower stem leaves typical of *S. kurilensis*). Six additional specimens were included a posteriori in the analysis. One specimen of *S. horieana* (*Horie s.n.* TNS from Kamikawa, Hokkaido Pref., Japan) was assigned to *S. kurilensis* with 100% probability, although leaf and inflorescence traits did not fit into *S. kuriensis*. Five specimens of *S. yokusaiana* were assigned a posteriori to three different species: 2 specimens to *S. kurilensis* with

100% probability and 99% probability (*Tanaka cult* by *Beaudry* 58-320-2 MT originally from Hozu Canyon near Kyoto, Japan), 1 specimen to *S. decurrens* with 100% (*Kimura & Sugaya s.n.* A from Yamagata Pref., Japan; Fig. 19), and 2 specimens to *S. minutissima* with 100% probability (*Furuse 1864* K from Kunigami Dist., Okinawa Pref., Japan) and 58% probability (38% to *S. kurilensis*; *Shiota 997* GH from Mino Dist., Gifu Pref., Japan).

Table 15. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	<i>decurrens</i>	<i>kurilensis</i>	<i>minutissima</i>	% correct
<i>decurrens</i>	44	0	0	100
<i>kurilensis</i>	3	17	0	85
<i>minutissima</i>	0	0	13	100
Totals	47	17	13	96

Jackknifed classification matrix

Group	<i>decurrens</i>	<i>kurilensis</i>	<i>minutissima</i>	% correct
<i>decurrens</i>	44	0	0	100
<i>kurilensis</i>	3	17	0	85
<i>minutissima</i>	0	0 </td <td>13</td> <td>100</td>	13	100
Totals	47	17	13	96

A two dimensional plot of CAN1 versus CAN2 canonical scores for 77 specimens of *Solidago decurrens* (var. *decurrens* and var. *insularis* treated a priori as a single groups, but shown by different colored symbols in diagram), *S. kurilensis*, and *S. minutissima* are presented in Fig. 38. One additional specimen of *S. horieana* and 5 additional specimens of *S. yokusaiana* included a posteriori are shown in the plot. Eigenvalues on the first two axes were 3.368 and 2.378.

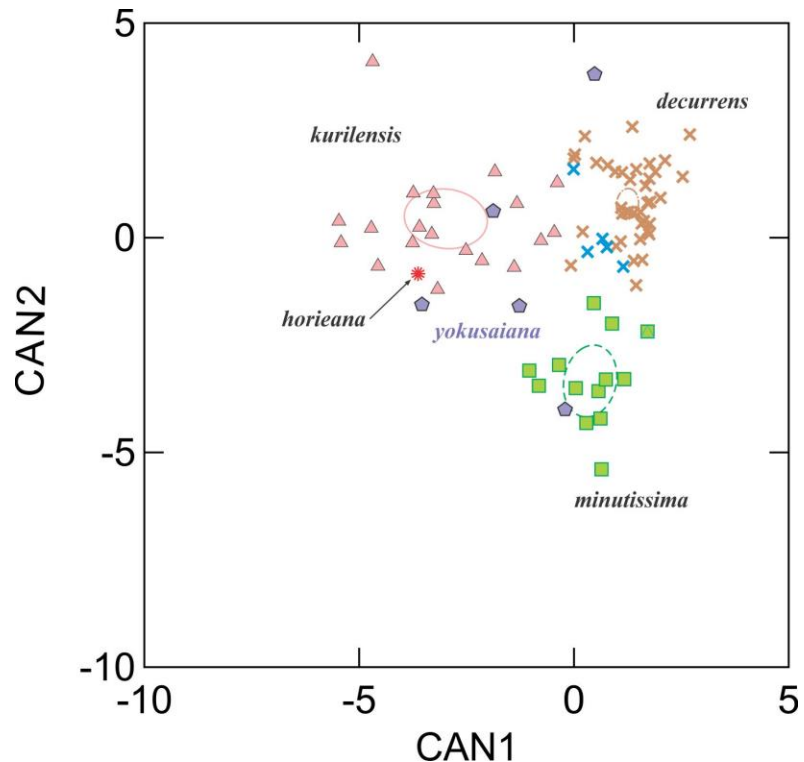


Figure 38. Plot of canonical scores (CAN1 vs CAN2) analysis for 77 specimens of *Solidago* ser. *Solidago* from eastern Asia: *S. decurrens* (var. *decurrens* are light brown x's; var. *insularis* are blue x's; 95% confidence ellipse includes a specimens of species), *S. kurilensis* (pink triangles), and *S. minutissima* (green squares) posteriori); specimens of *S. horieana* (red star burst) and *S. yokusaiana* (lavender pentagons) included a posteriori.

DISCUSSION

The results of the multivariate analyses provide support for recognizing the following species: *Solidago dahurica*, *S. decurrens*, *S. kurilensis*, *S. litoralis*, *S. minutissima*, *S. pacifica*, and *S. virgaurea* in ser. *Solidago*, *S. macrophylla* in ser. *Macrophyllae*, and *S. leiocarpa*, *S. multiradiata*, and *S. spithamaea* in sect. *Multiradiatae*. *Solidago nipponica* was found to be the same taxon as *S. kurilensis* and thus belongs in synonymy under the older name. Although data were limited for some taxa in ser. *Solidago* the following taxa are also recognized: *S. decurrens* var. *insularis*, *S. horieana*, and *S. yokusaiana*. Just the digital image of the holotype collection of *Solidago virgaurea* var. *praeiflorens* was available during this study, but this also appears to be an island arch race and is treated here as *Solidago decurrens* var. *praeiflorens*.

The results of the ser. *Macrophyllae*, ser. *Solidago* and sect. *Multiradiatae* analysis indicate that the latter group is more morphologically distant from ser. *Solidago* than is ser. *Macrophyllae*. *Solidago macrophylla* is more similar to taxa in ser. *Solidago* than is *S. multiradiata*. This contradicts the results of the RFLP cp DNA-based study by Zhang (1996; Fig. 1 in Semple et al. 1999), which we conclude was the result of homoplasies between cpDNA fragments of *S. multiradiata* and *S. virgaurea*. Different mutations yielded approximately similar molecule weight fragments with the target DNA location at different positions within the fragments. Polygenomic sampling of the entire genome yields more historically accurate results (Beck et al. in prep.).

Further work is needed to determine if *Solidago virgaurea* sensu stricto should be split into species and varieties. At least 62 different names and combinations have been proposed for European variants of *S. virgaurea*. Most of these are undoubtedly just early published names that belong in synonymy under *S. virgaurea* var. *virgaurea*, if other varieties are recognized. Proposals to treat dwarf plants as distinct varieties, subspecies, or separate species are based on either geographically narrowly limited samples (e.g., Kiełtyk & Mirek 2014) or are really just alpha level taxonomic proposals that require much more work to document the distinctiveness of the proposed taxon. Based on how taxa of the genus *Solidago* in North America have apparently rapidly diverged, it seems reasonable to assume that some of the proposed names for European taxa occurring in isolated mountain ranges or distinct habitats might warrant some level of taxonomic recognition within *S. virgaurea*. In the analyses, *S. virgaurea* was not strongly supported and generally fell among the taxa with the lower levels of correct a posteriori placement. This is likely in part the result of significant emphasis being placed on the total number of ovary/cypsela body hairs, which varies more in *S. virgaurea* than any other taxon. In all cases, regardless of the number of hairs, individuals of *S. virgaurea* had some hairs covering the entire cypselae body, evenly in most cases and sometimes with more hairs distally than proximally. The results of the analyses indicate that *S. virgaurea* occurs in Europe and adjacent mountains in Morocco in North Africa and eastern Turkey in northwestern Asia. A gap in the distribution appears to occur between these western plants and those found in the mountains of northeastern Pakistan, northern India, and Nepal. The two allopatric portions of the range of *S. virgaurea* are separated by very dry areas of mountains and lowlands in Afghanistan, Turkmenistan, Uzbekistan, and western and central Kazakhstan. A polygenomic study comparing large numbers of samples of *S. virgaurea* and *S. dahurica* is needed to clarify the geographic limits of the two species. Such a study could also show whether or not high alpine forms of the *S. virgaurea* are derived multiple times from closely related lower elevation populations or if all of the high alpine forms across Europe are of a single origin. In short, is *S. minuta* L. a real taxon or a polyphyletic assemblage of regional dwarf alpine ecotypes? Such a molecular study is also likely to reveal whether *S. virgaurea* is native to the Himalaya Mountains or if the plants with hairs over much or all of the fruit body surface are in fact extremely hairy forms of *S. dahurica*. Individuals treated a priori as *S. dahurica*, *S. decurrens*, and *S. virgaurea* in the analysis of just those species were placed a posteriori into those species with significant probability for a high majority of the specimens, but the analysis heavily weighted the total numbers of ovary/fruit body hairs. Two specimens from Pakistan

and two from Xinjiang Prov., China were included in the *S. dahurica* a priori group. One specimen each from Pakistan and Xinjiang were placed with very high probability into *S. dahurica*, while the other specimens were placed with high probability into *S. virgaurea* among the cluster of specimens that included the specimen from Kyrgyzstan (Fig. 37). Of the 5 specimens of *S. virgaurea* assigned to other species, all were from Europe and had sparsely hairy ovary/cypsela bodies and were assigned a posteriori to either *S. dahurica* or *S. decurrens*, although it is highly unlikely that specimens from Austria, Estonia, and Switzerland belong to those two Asian species.

The names *Solidago virgaurea* subsp. *leiocarpa* and *S. virgaurea* var. *leiocarpa* have been misapplied in the literature for many decades (e.g. Iwatsuki 1985; Sakaguchi et al. 2018). The basionym *Amphirhapis leiocarpa* was proposed in 1842 based on *Hinds s.n.* (K!) collected in Hong Kong (see Table 1). There is only one species of *Solidago* native to southern China, *S. decurrens*, which was based on an unknown collection from Canton. No type collections appear to exist, but a neotype *Hinds s.n.* (K!) is designated in Table 1. The choice of neotype was logical because it is a historically significant collection and comes from the same provenance as the original material on which the name *S. decurrens* was based. The choice of neotype for *S. decurrens* also results in *Amphirhapis leiocarpa* and names based on the basionym being relegated to complete synonymy under the older name *S. decurrens*. Iwatsuki (1995) stated that var. *leiocarpa* was native to the southern Kuril Islands, Hokkaido, Sakhalin, Kamchatka and E. Siberia, but no taxon in *Solidago* as treated here has a range that includes all those locations (see Fig. 29). *Solidago dahurica* is native to E. Siberia, Kamchatka, and Sakhalin, but not northern Japan or the Kuril Islands. *Solidago pacifica* is native to the provinces and oblasts along the lower Amur River in China and Russia and “Manchuria” China, North Korea, and a few locations on northern Hokkaido Island, Japan. The names *S. virgaurea* subsp. *leiocarpa* and *S. virgaurea* var. *leiocarpa* cannot be legitimately applied to plants native to E. Siberia, Kamchatka, and Sakhalin. Such plants are either *S. dahurica*, *S. kurilensis*, or *S. pacifica*. *Solidago decurrens* does not occur in the southern Kuril Islands, Hokkaido, Sakhalin, Kamchatka, and E. Siberia. Sakaguchi et al. (2018) applied the name *leiocarpa* to a set of plants native to higher elevations on Hokkaido and Honshu. Sakaguchi (pers. comm.) indicated that these are somewhat genetically differentiated from *S. decurrens* and *S. kurilensis* (synonym *S. nipponica*) and may be the result of possible hybridization and introgression of *S. decurrens* and *S. kurilensis* at higher elevations where the ranges of the two parent species are locally sympatric. Regardless of exactly what these plants are (a mixture of hybrids or ecotypes?), the name *leiocarpa* is not correctly applied to them.

The status of *Solidago pacifica* is problematic in terms of species limits. In the two multispecies analyses that included *S. pacifica* specimens, a posteriori placement into *S. pacifica* was only 56% in both analyses; nearly half the specimens assigned a priori to *S. pacifica* were placed into either *S. dahurica* or *S. decurrens*. The range of distribution of *S. pacifica* connects the allopatric ranges of *S. dahurica* and *S. decurrens* in northeastern China and North Korea where the ranges of all three are potentially sympatric. A large sample of plants from throughout North Korea is needed to increase the sample size of *S. pacifica*, but obtaining such collections seems unlikely at this time. Molecular data might reveal that *S. pacifica* is in fact an assemblage of robust *S. decurrens* and *S. dahurica* specimens that are atypical forms in marginal populations. Further work on *S. pacifica* is needed. In Table 1, the type of *S. virgaurea* var. *gigantea* Nakai from Hokkaido is listed as a synonym of *S. pacifica*. Sakaguchi et al. (2018) did not include specimens under the name *S. pacifica*, although some of the Korean peninsula collections they sampled may belong in that species. It is also possible that some of the northern Hokkaido collections labeled under the misapplied Bentham epithet *leiocarpa* or all of their Hokkaido samples belong in *S. kurilensis* (including *S. nipponica*).

It seems highly likely that all the native Eurasia taxa in *Solidago* are derived from a single North American branch of the genus and *S. macrophylla* is the only species native to North America

that is part of that branch today (J.B. Beck, pers. comm.). It also seems highly likely that *Solidago* migrated into Eurasia via Beringia at some time in the past during glacial times. Interestingly, only diploids are known in ser. *Solidago* and ser. *Macrophyllae*. *Solidago multiradiata* is the only native North American species that also is native to extreme eastern Eurasia (Chukotka Autonomous Okrug, Russia; a tetraploid count has been reported from Chukotka by Zhukova and Tikhonova 1971), but *S. multiradiata* is not closely related to the Eurasian ser. *Solidago*. Assuming the ancestor of ser. *Solidago* migrated via the same route and ultimately diverged into the species recognized here in the same way and for the same reasons that the genus has diverged into more than 100 species relatively quickly in North America, the more distant a Eurasia population of *Solidago* is from extreme northeastern Russia the more divergent it is from the original ancestor of ser. *Solidago*. Traditionally, *S. virgaurea* has been defined very broadly to include nearly all taxa in the genus native to Eurasian in multiple subspecies and varieties. The only exceptions recognized as separate species in Iwatsuki et al. (1995) were *S. minutissima* and *S. yokusaiana*, but these are native to southern Japan and are adapted to well defined habitats and are morphologically distinct from *S. decurrens* (synonym: *S. virgaurea* var. *asiatica*). It is not logically consistent to include most of the Eurasian *Solidago* taxa in *S. virgaurea* but to separate these two taxa as species. *Solidago horieana* was not described in 1995, but might also have been treated as a distinct species by Iwatsuki et al. (1995) because it too is confined to a specific habitat on Hokkaido Island. The highly informative results of Sakaguchi et al. (2018) indicate that there is a north to south divergence of genomes within Japan with divergence into special habitats in Hokkaido (*S. horieana*), central and southern Honshu (*S. yokusaiana*), the Izu archipelago (*S. decurrens* var. *praeflorens*) and the Ryukyu Arc (*S. minutissima* on Yaku-shima and *S. decurrens* var. *insularis* further south). Sample sizes in this multivariate study for var. *praeflorens* and var. *insularis* were too small to reach final conclusions about whether or not they differ sufficiently from *S. decurrens* to warrant species rank, although the differences among the three varieties of *S. decurrens* are not large in our opinion. It might be logically more consistent to also treat *S. minutissima* as a variety within *S. decurrens*, but the results of the multivariate study indicate that species status is not unwarranted. The results of Sakaguchi et al. (2018) are basically in agreement with the results of this multivariate study, although their nomenclatural choices obscure this similarity in findings. Our conclusion is that the same kind of divergence in molecular traits will be found following ser. *Solidago* from east to west across Eurasia as Sakaguchi et al. (2018) found following the series from north to South in Japan. Expanding the molecular sample to include plants from southern China, Vietnam, and the northern Phillipines and eastern India could reveal whether or not *S. decurrens* diverged in a similar fashion and whether all three of these possible migration routes are examples of repeated founder effect reduction in overall genome diversity, with *S. dahurica* being the most diverse genetically in ser. *Solidago* and the most phylogenetically basal taxon in the series. Do the Kamchatka populations represent persistent early members of ser. *Solidago* or are they also the result of divergence via founder effect from a possible glacial peak refugium for the entire series somewhere further south on mainland eastern Asia? Multivariate methods are not suited to resolving these questions.

Key to taxa in *Solidago* ser. *Solidago*

1. Cypselae very sparsely to densely strigulose over the entire ovary/fruit body; Europe, Morocco, Turkey, and the Himalaya mountains of India and Nepal
 2. Lower stems and leaves glabrous to only very sparsely strigose; Europe, Morocco, Turkey, and Himalaya mountains of India and Nepal ***Solidago virgaurea***
 2. Vegetative portions of plants densely strigose to villose-strigose; sand dune habitats along coast between the mouths of Magra (Liguria) and Cecina (Tuscany) rivers, Italy ***Solidago litoralis***
1. Cypselae glabrous or sparsely to moderately strigulose only distally (some *S. dahurica* individuals can be more hairy on the upper lower half of the fruit body).

2. Inflorescences usually somewhat corymbiform; blade of lower leaves truncate; Kuril Islands, Hokkaido, northern Honsho, Japan ***Solidago kurilensis***
2. Inflorescences narrowly to broadly paniculiform; blade of lower leaves tapering; most of temperature zone Asia
3. Stem 2-15 cm tall; higher elevations, Yaku-shima, Japan ***Solidago minutissima***
3. Stems 20-100 cm tall; most of temperature zone Asia
4. Stem leaves narrow, gradually reduced upward, sometimes somewhat triple-nerved; rheophyte on rocks along rivers in southern Japan ***Solidago yokusaiana***
4. Stem leaves much reduced upward, leaves never triple-nerved; various habitats in Asia
5. Involucres (5-)7-8-10 mm tall
 6. Cypselae usually only sparsely hairy distally; central Asia to northern China and Kamchatka ***Solidago dahurica***
 6. Cypselae densely strigose; rheophyte on rocks in streams of serpentine areas of northern Hokkaido, Japan ***Solidago horieana***
5. Involucres 3.5-5.6-7 mm tall; various habitats in eastern Asia and eastern India
 7. Phyllaries somewhat obtuse; plants robust; greater lower Amur R. drainage China and southeastern Russia, North Korea, "Manchuria" China ***Solidago pacifica***
 7. Phyllaries lanceolate, acute; stems short to rarely 1+ m tall but leaves much reduced upward; eastern India, central, eastern and southern China, northern Viet Nam, higher elevations on Luzon Is., Philippines, Taiwan, Japan ***Solidago decurrens***
 8. Flowering January to May; mid stem leaves crowded on mid stems, lower above ground stems persisting for years; Ryukyu Is., Japan ***S. d. var. insularis***
 8. Stems blooming in summer and fall; mid stem leaves not crowded; stems dormant in winter
 9. Cypselae strigose distally; Izu archipelago, Japan ***S. d. var. praeflorens***
 9. Cypselae glabrous; South Korea, eastern China south into northern Vietnam and Luzon Is., Philippines, eastern India, Taiwan and Japan ***S. d. var. decurrens***

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