

## Article

# Cytogeography of *Solidago* sect. *Erectae*, sect. *Villosicarpae*, sect. *Squarrosae*, and sect. *Brintonia* (Asteraceae: Astereae)

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**Abstract:** Chromosome numbers are reported for 67 individuals of 13 species of *Solidago* sect. *Erectae*, *S.* sect. *Squarrosae*, and *S.* sect. *Villosicarpae* from 65 locations in eastern Canada and the eastern United States: *S. bicolor*, *S. erecta*, *S. hispida*, *S. jejunifolia*, *S. pallida*, *S. puberula*, *S. pulverulenta*, *S. rigidiuscula*, *S. roanensis*, *S. sciaphila*, *S. speciosa*, *S. squarrosa*, and *S. villosicarpa*. Cytogeography maps based on new reports and all 258 previously published reports from 230 locations for the three sections plus *S.* sect. *Brintonia* (*S. discoidea*) are presented for 20 of the 30 species in the four closely related sections. The following are either first documented reports for the taxon or just first counts for a taxon from particular provinces and states: *Solidago bicolor*,  $2n = 18$  from Nova Scotia and Prince Edward Island; *S. hispida* var. *hispida*,  $2n = 18$  from New Hampshire, New Brunswick, and Wisconsin; *S. jejunifolia*,  $2n = 18$  from Michigan and Minnesota; *S. pallida*,  $2n = 18$  from Wyoming; *S. puberula*,  $2n = 18$  from Pennsylvania, Prince Edward Island, and Virginia; and first reports for *S. sciaphila*,  $2n = 36$  from Iowa, Illinois, and Wisconsin.

**Keywords:** biogeography; chromosome numbers; goldenrods**Citation:** Semple, J.C.; Cook, R.E.Cytogeography of *Solidago* sect. *Erectae*, sect. *Villosicarpae*, sect. *Squarrosae*, and sect. *Brintonia* (Asteraceae: Astereae). *Taxonomy* **2022**, *2*, 261–278. <https://doi.org/10.3390/taxonomy2030021>

Academic Editor: Emilio Cervantes

Received: 26 May 2022

Accepted: 29 June 2022

Published: 3 July 2022

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## 1. Introduction

*Solidago* sect. *Erectae* G. Don in Loudon is the second largest section in the genus with 26 species that are native to a range of habitats mostly in eastern North America varying from moist woods and wood margins to open sandy barrens and dunes, sandstone and limestone cliff tops and faces, and disturbed soil habitats such as roadsides and fields (Semple and Beck 2021 [1], Semple 2022 [2]). The section is defined by having lower stem and basal rosette leaves that are the largest on the plant and usually narrow elongated wand-shaped to club-shaped inflorescences and involucre and upper vegetative parts that are sometimes somewhat to obviously resinous. Most of the species were included in *S.* subsect. *Squarrosae* A. Gray and *S.* subsect. *Humiles* (Rydb.) Semple in Flora North America (Semple and Cook 2006 [3]). The number of species and varieties recognized in the section(s) or subsection(s) has differed among authors (Small 1903 [4], Fernald 1908 [5], Fernald 1915 [6], Fernald 1936 [7], Fernald 1950 [8], Radford et al., 1968 [9]) and over time by the same author or authors (e.g., Cronquist 1968 [10], Cronquist 1980 [11]; Semple et al., 2017a [12], Semple et al., 2017b [13], Semple et al., 2017c [14], Semple et al., 2020 [15], Semple and Nelson 2018 [16]) with 26 species recognized most recently [1]. Semple and Cook [3] adopted much of Cronquist's treatments [10,11] of taxa in their subsect. *Squarrosae* and recognized 9 species. Subsequent multivariate morphometric analyses [12–15] resulted in the breaking up of the *S. speciosa* complex into four separate species based on morphological and habitat preference differences of what had been treated as four varieties within the species and the breaking up of the *S. puberula* complex. Most recently Semple and Beck [1] presented a revised infrageneric classification based on an unpublished (currently in review) polygenomic DNA sequence data analysis that resulted

in the shifting of all but one species of subsect. *Squarrosae* to sect. *Erectae* and dividing the latter section into two subsections and three series; they also broke up subsect. *Humiles* sensu Peirson et al. (2012 [17]) into a smaller subsect. *Humiles* that retained the northern and western species: *S. bellidifolia* Greene, *S. chlorolepis* Fernald, *S. gillmanii* (A. Gray) E. S. Steele, *S. glutinosa* Nutt., *S. ontarioensis* (G. S. Ringius) Semple & J. A. Peirson, *S. randii* (Porter) Britt., *S. simplex* Kunth, and *S. spathulata* DC. Semple and Beck [1] placed the southeastern species of subsect. *Humiles* sensu J. A. Peirson into *S. ser. Erectae* (D. Don in Loudon) Hoffman of *S. subsect. Erectae* (D. Don in Loudon) Semple & J. B. Beck along with species or varieties previously grouped together in subsect. *Squarrosae* sensu Semple and Cook [3]: *S. arenicola* B. R. Keener & Kral, *S. austrocaroliniana* Semple & J. B. Nelson, *S. erecta* Pursh, *S. jejunifolia* Steele, *S. kralii* Semple, *S. pallida* (Porter) Rydb., *S. plumosa* Small, *S. rigidiuscula* (Torr. & Gray) Porter, and *S. speciosa* Nutt. *Solidago racemosa* Greene was also tentatively included in *ser. Erectae*, but it may belong in the revised subsect. *Humiles* of sect. *Erectae* pending further study. Species of the *S. bicolor/S. hispida* complex were included in *S. ser. Albigula* (Raf.) Semple & J. B. Beck [1]: *S. bicolor* L., *S. georgiana* Semple, *S. hispida* Muhl., *S. porteri* Small, and *S. sciaphila* E. S. Steele. Semple and Beck [1] placed three species with middle and upper stems densely very short canescent in *S. ser. Puberulae* Semple & J. B. Beck: *S. puberula* Nutt., *S. pulverulenta* Nutt., and *S. roanensis* Porter. Semple and Beck [1] retained just *S. squarrosa* Muhl. in *S. sect. Squarrosae* (A. Gray) Semple & J. B. Beck and placed *S. villosicarpa* LeBlond by itself in *S. sect. Villosicarpae* Semple & J. B. Beck. Semple and Beck [1] also placed *S. discoidea* (Ell.) Torr. & A. Gray by itself in *Solidago* sect. *Brintonia* (E. L. Greene) Semple & J. B. Beck between *S. sect. Squarrosae* and *S. sect. Thyrsiflorae* (A. Gray) Semple & J. B. Beck [18] that is not dealt with further in this paper but is the terminal clade in the greater *S. sect. Erectae* clade in *S. subg. Solidago*. *Solidago discoidea* was treated as *Brintonia discoidea* (Ell.) E. L. Greene in Flora North America [19] being the only goldenrod having pappus bristles that are tinted with anthocyanins, but otherwise the morphology is rather typical for *S. subg. Solidago*. *Solidago discoidea* was placed with *S. bicolor* and *S. hispida* in *S. subsect. Albigula* (Raf.) Nesom by Nesom 1993 [20].

The cytogeography (biogeography of chromosome count data) of the species now included in *S. sect. Erectae* (except those included in subsect. *Humiles* sensu Semple and Beck [1]), *S. sect. Squarrosae* and *S. sect. Villosicarpae* was investigated for this study building on a considerable amount of earlier research by multiple researchers between 1957 and 2019. The work of Jean Beaudry and his students and collaborators contributed much to the early cytotaxonomic knowledge of sect. *Erectae*, sect. *Squarrosae*, sect. *Brintonia* in a series of papers beginning in 1957 and ending more than a decade later with many first reports [21–24]. Numerous counts were reported in a series of cytotaxonomic papers over multiple decades by the Semple Astereae Lab [25–34]. Small numbers of counts were reported by various authors over the same period [35–40].

## 2. Materials and Methods

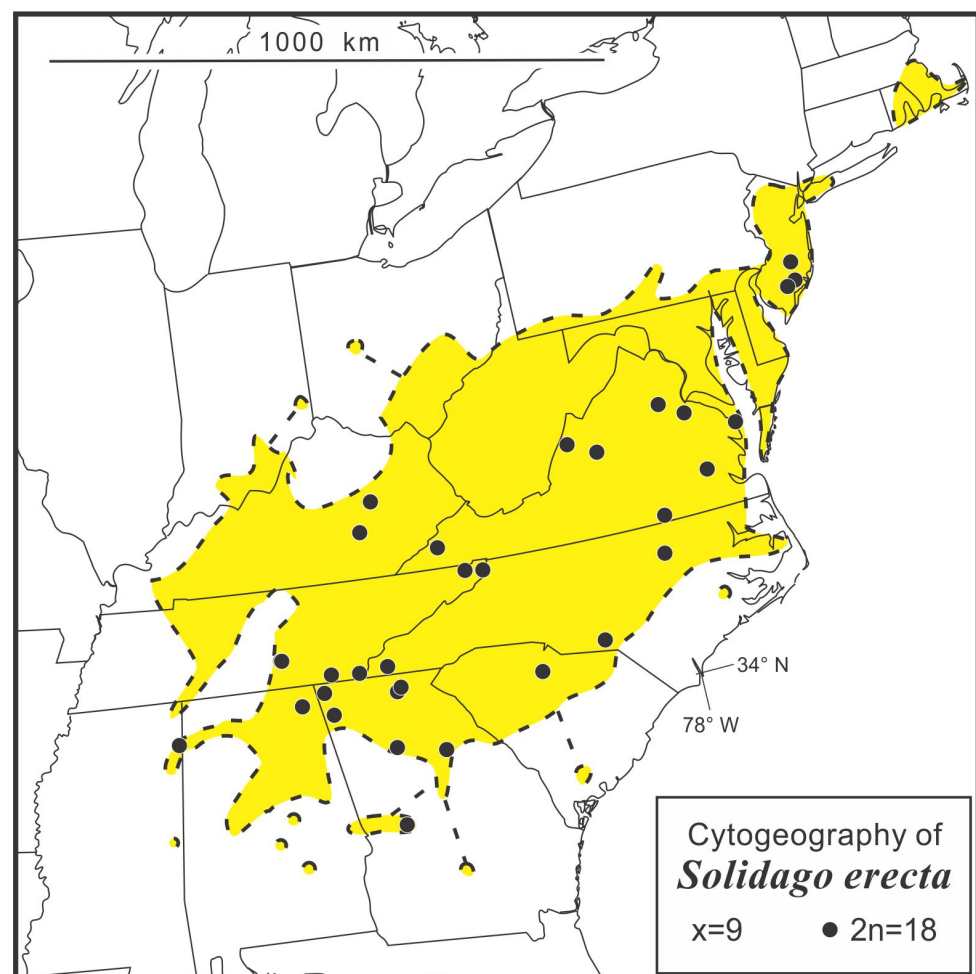
Meiotic counts ( $2n = 9_{II}$ ,  $2n = 18_{II}$ ,  $2n = 27_{II}$ ) were made from pollen mother cells dissected from buds fixed in the field in 3:1/EtOH: glacial acetic acid and subsequently stored under refrigeration in 70% EtOH. Mitotic counts ( $2n = 18$ ,  $2n = 36$ ,  $2n = 54$ ) were made from root tip cells taken from transplanted wild rootstocks or from seedlings grown from cypselae collected in the wild. Root tips were pretreated in 0.01% colchicine or saturated P.D.B. for 2–3 h, fixed in either Modified Carnoy's Fixative (4:3:1/chloroform: EtOH: glacial acetic acid) or Acetic Alcohol Fixative (3:1/EtOH: glacial acetic acid) and hydrolyzed in 1N HCl for 30 min at 60 °C before squashing. Anther sacs containing pollen mother cells and meristematic root tips were squashed in 1% acetic orcein, and counts of chromosomes were made from freshly prepared material. Herbarium vouchers for all new counts are deposited in WAT in MT unless otherwise indicated. Identifications were made by J.C.S. and follow the nomenclature in Semple and Beck [1].

Vouchers for previously published counts were borrowed from or examined at MT and WAT [41] or examined online using SERNEC [42]. In some cases, the cited voucher

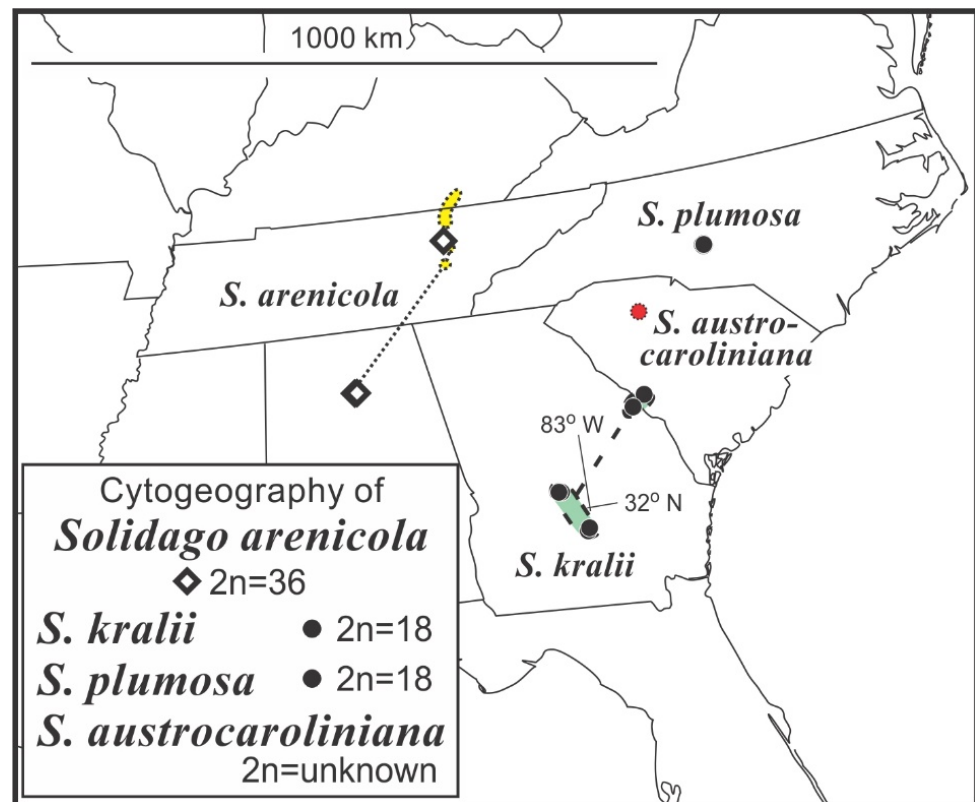
for a count could not be located and the likelihood that the identification was correct was assessed by examining other specimens of the same taxon collected by the author of the count from the same or approximately the same location.

### 3. Results

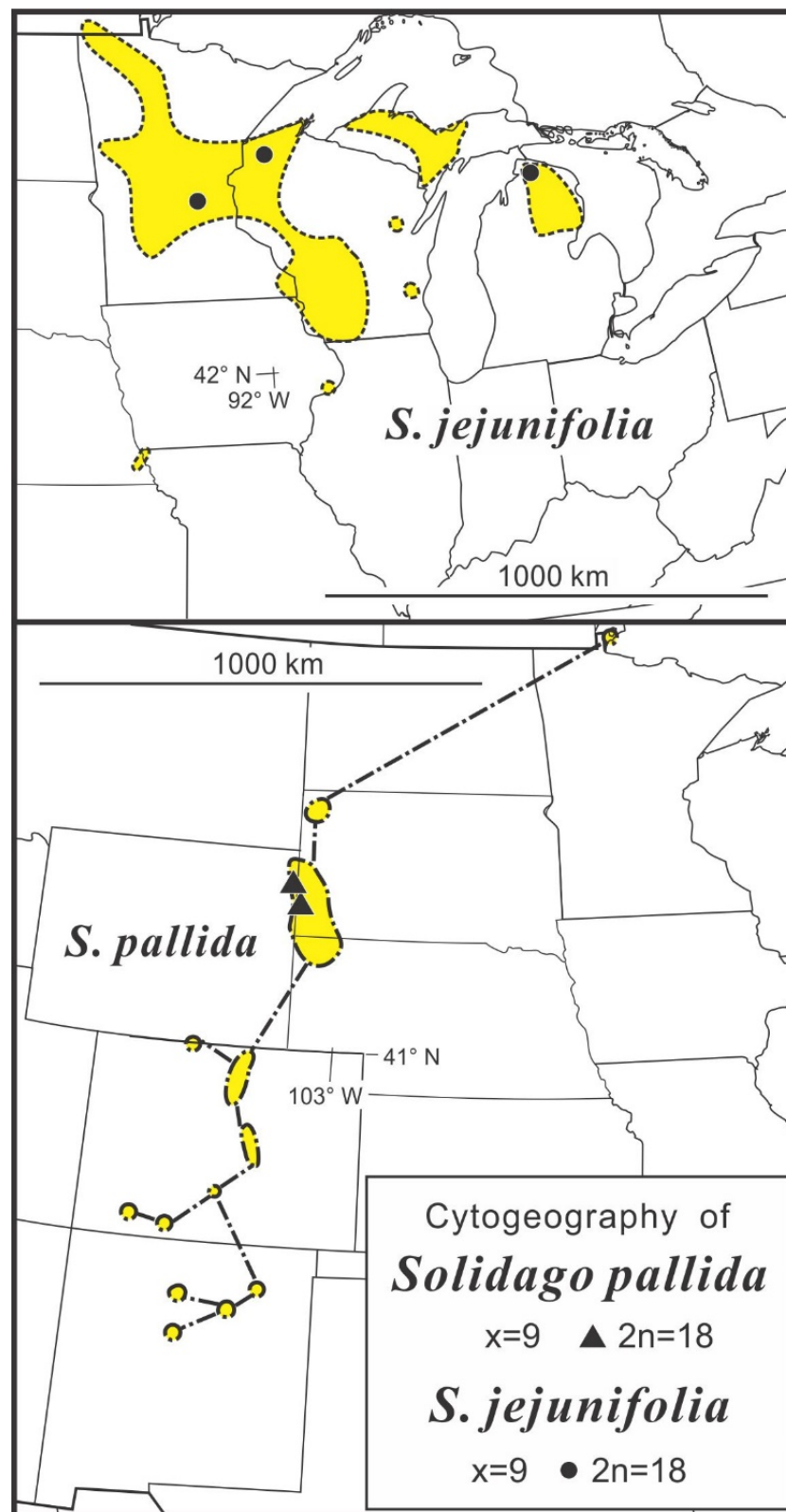
Identifications of vouchers were confirmed or revised for nearly all of the 258 previously published chromosome number reports from 230 locations for taxa in *Solidago* sect. *Erectae* (except subsect. *Humiles*), *S.* sect. *Squarrosae*, *S.* sect. *Villosicarpae* and *S.* sect. *Brintonia* and are listed in Appendix A. The previous report of  $2n = 18$  for *S. hispida* (Hooper 83091001 WAT [26]) was determined to be the first report for *S. hispida* Muhl. aff. var. *lanata* (Hook.) Fernald. Chromosome counts are reported for the first time in Appendix B for 67 individuals from 65 locations in eastern Canada and the eastern United States for 13 species of *Solidago* sect. *Erectae*, *S.* sect. *Squarrosae*, and *S.* sect. *Villosicarpae*. The following are either first documented reports for the taxon or for the taxon for particular provinces and states: *Solidago bicolor*,  $2n = 18$  from Nova Scotia and Prince Edward Island; *S. hispida* var. *hispida*,  $2n = 18$  from New Hampshire, New Brunswick, and Wisconsin; *S. jejunifolia*,  $2n = 18$  from Michigan and Minnesota; *S. pallida*,  $2n = 18$  from Wyoming; *S. puberula*,  $2n = 18$  from Pennsylvania, Prince Edward Island, and Virginia; and first reports for *S. sciaphila*,  $2n = 36$  from Iowa, Illinois, and Wisconsin. All 325 chromosome number counts from 295 locations for all taxa in *Solidago* sect. *Erectae* (except subsect. *Humiles*), *S.* sect. *Squarrosae*, *S.* sect. *Villosicarpae* and *S.* sect. *Brintonia* were used to create cytogeography maps for these taxa (Figures 1–9).



**Figure 1.** Cytogeography of *Solidago erecta* based on all counts; range based on all collections seen and the literature.



**Figure 2.** Cyto geography of *Solidago arenicola*, *S. kralii*, *S. plumosa*, and the range of *S. austrocaroliniana* (red dot indicates range); the subject. *Humiles*-like species of *S. ser. Erectae*; ranges based on all collections seen and the literature.



**Figure 3.** Cytogeography of *Solidago jejunifolia* and *S. pallida*; ranges based on all collections seen and the literature.

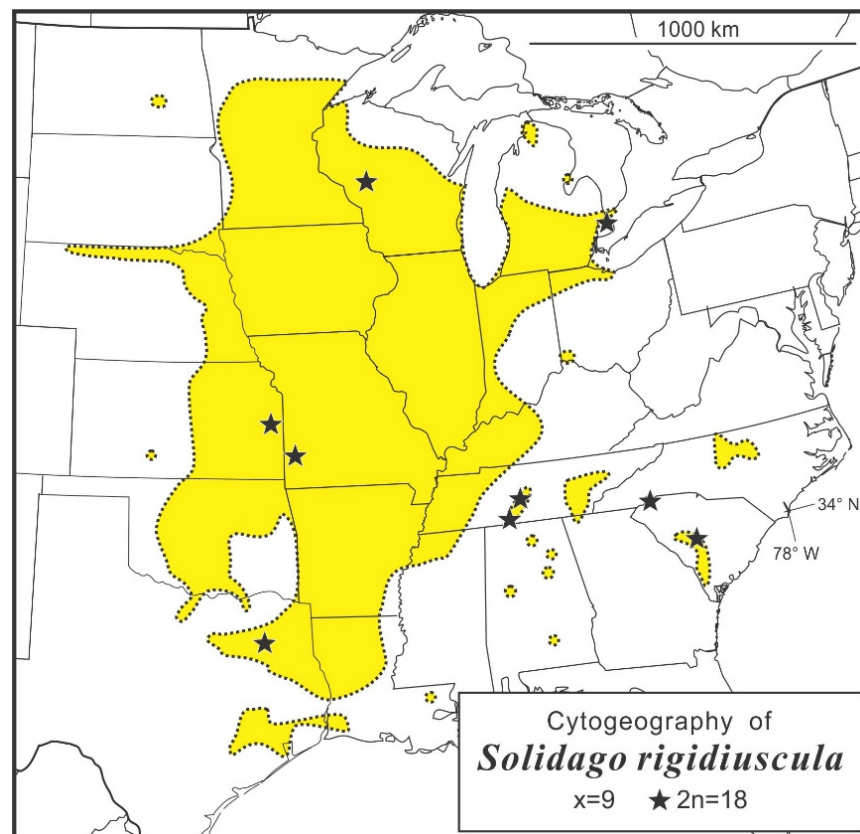


Figure 4. Cytogeography of *Solidago rigidiuscula*; range based on all collections seen and the literature.

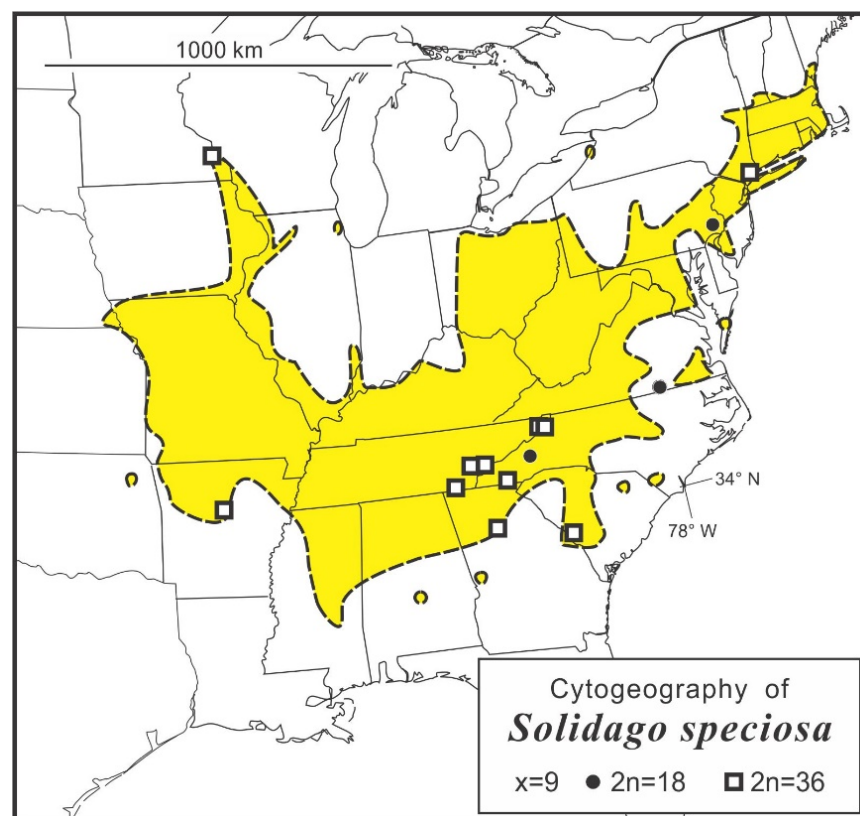
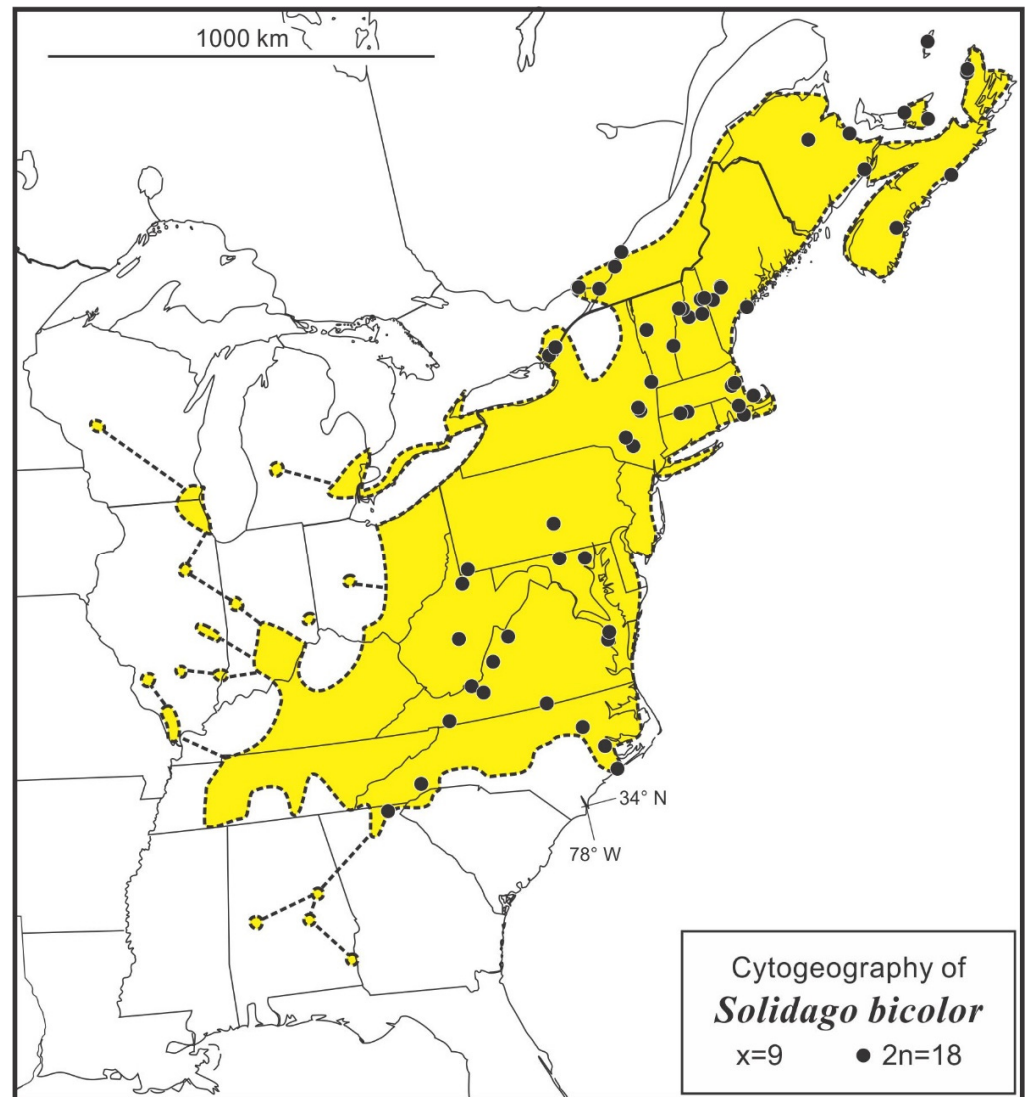
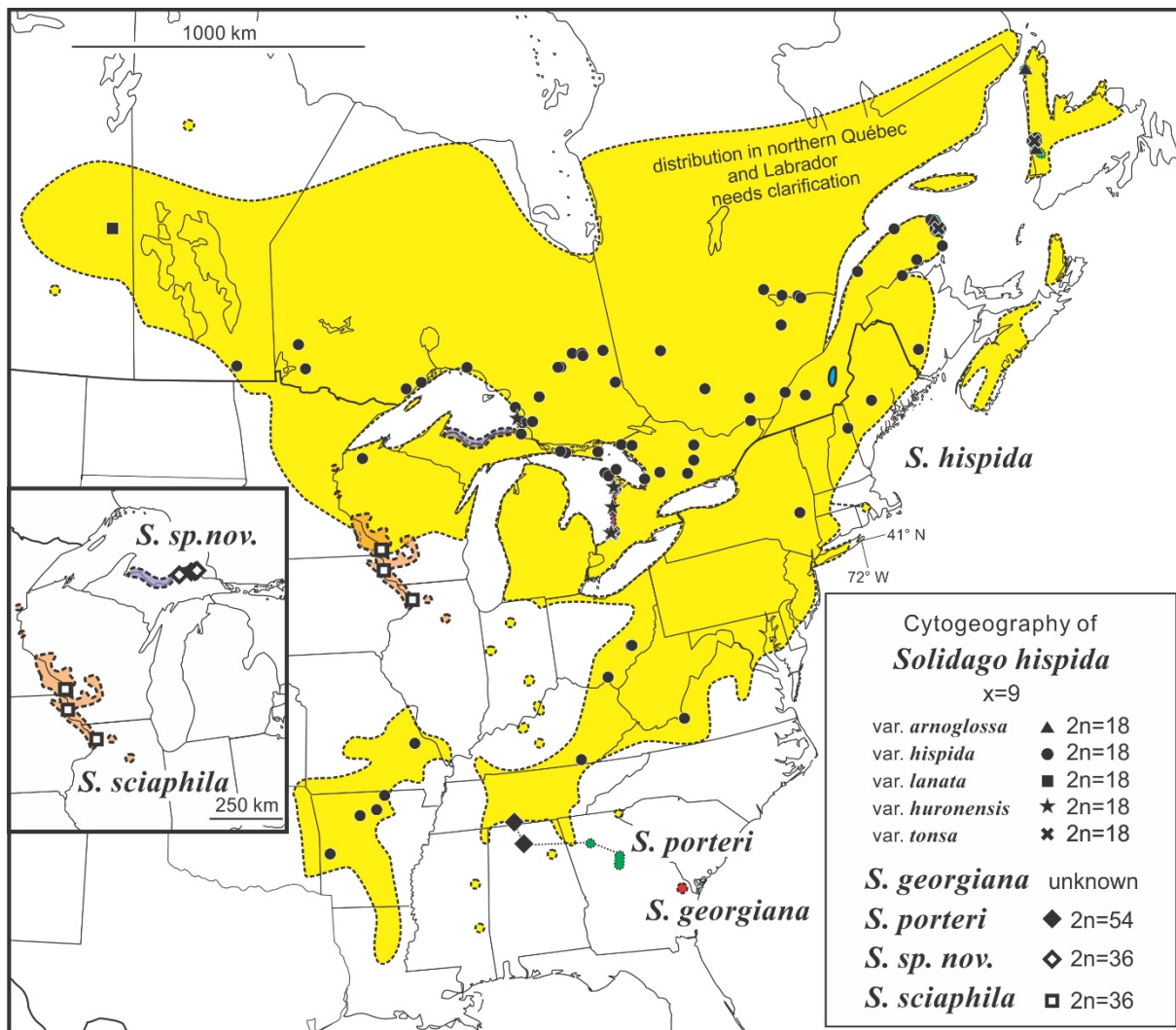


Figure 5. Cytogeography of *Solidago speciosa*; range based on all collections seen and the literature.

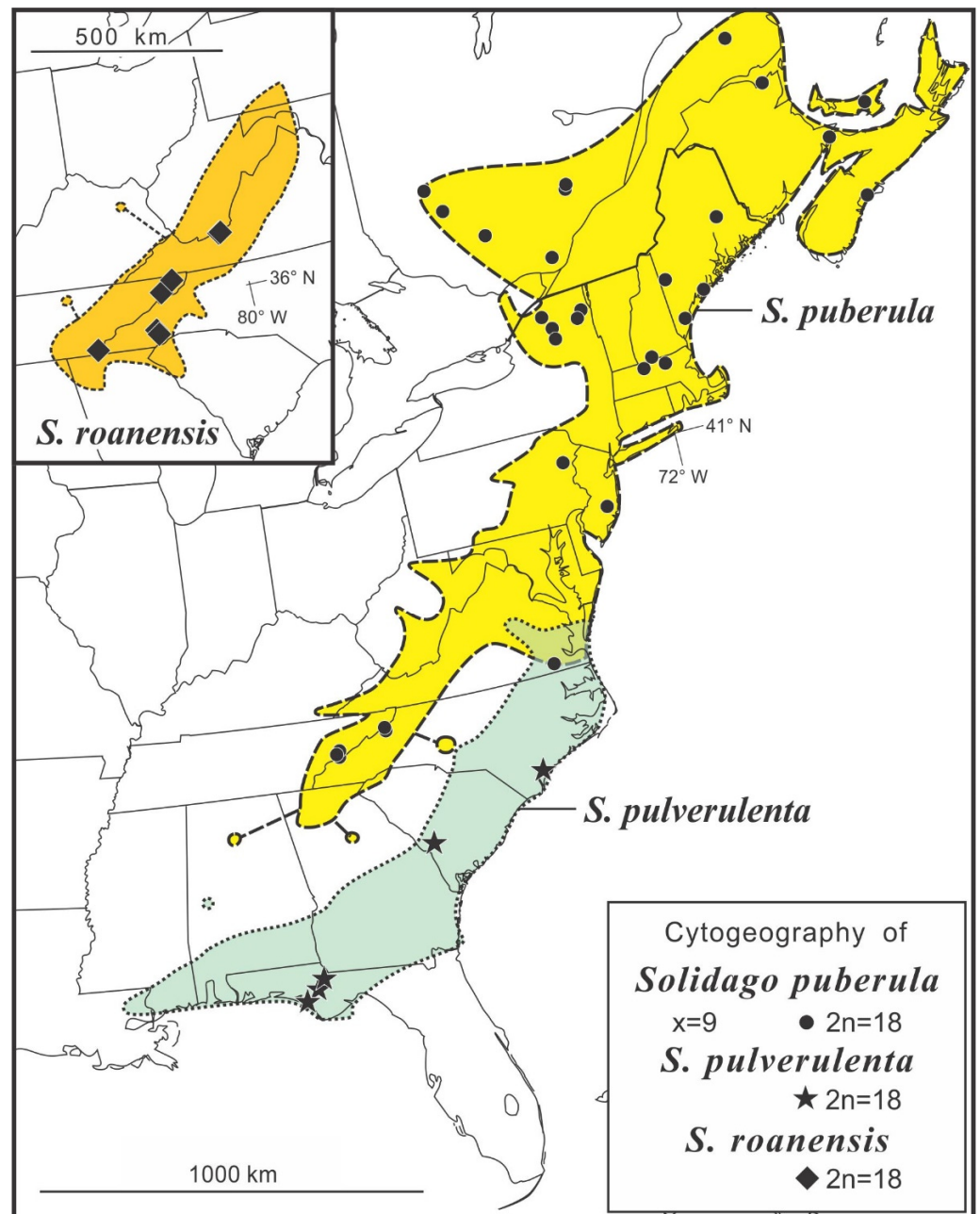


**Figure 6.** Cytogeography of *Solidago bicolor*; range based on all collections seen and the literature.

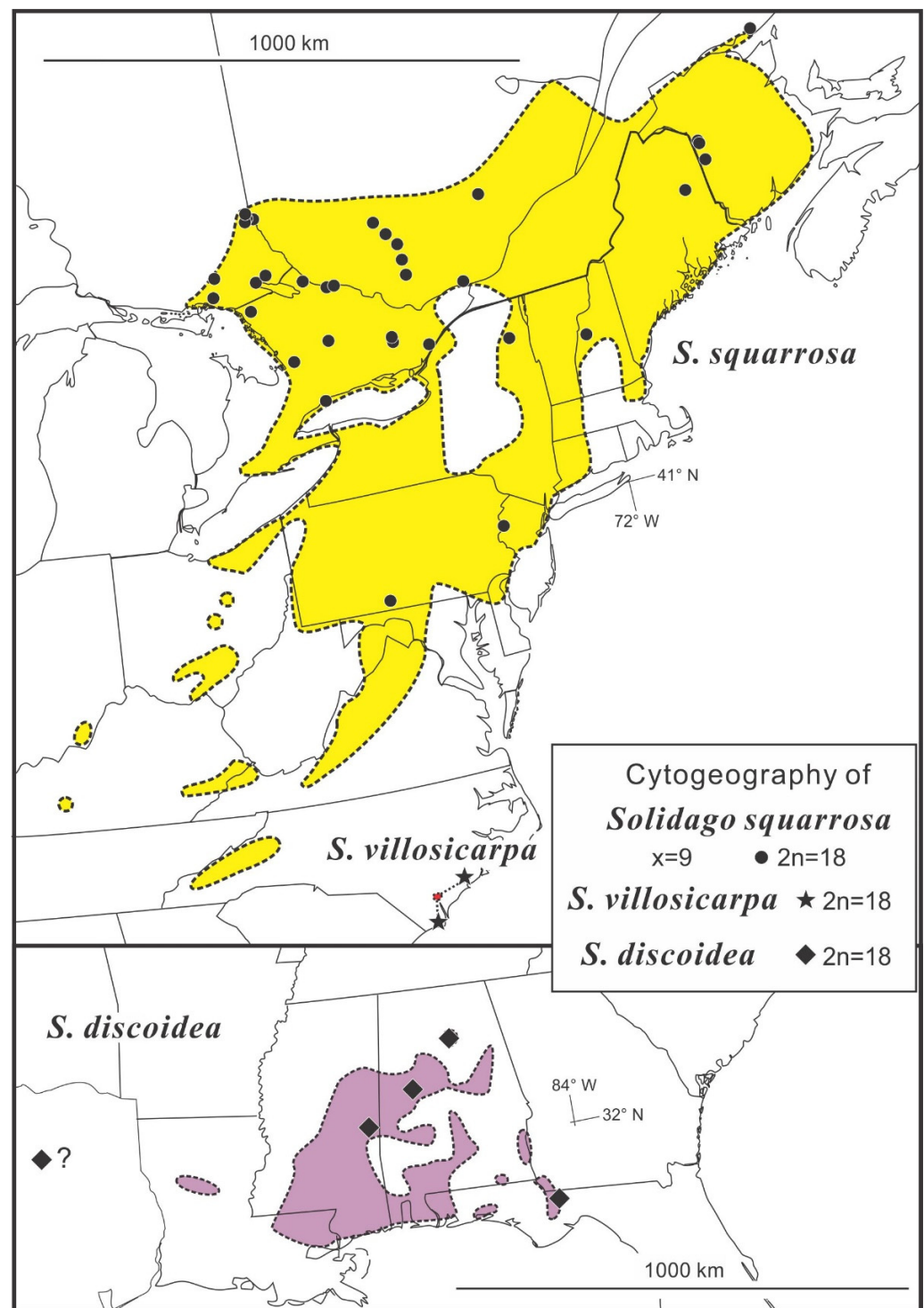


**Figure 7.** Cyto geography of *Solidago hispida*, *S. georgiana* (red dot indicates range), *S. porteri* (green dots indicate unsampled portions of range), *S. sp. nov.* (range in light purple), and *S. sciaphila* range indicated in orange); ranges based on all collections seen and the literature.





**Figure 8.** Cytogeography of *Solidago puberula*, *S. pulverulenta*, and *S. roanensis*; ranges based on all collections seen and the literature.



**Figure 9.** Cytogeography of *Solidago squarrosa*, *S. villosicarpa*, and *S. discoidea*; ranges based on all collections seen and the literature.

#### 4. Discussion

The cytogeography for all taxa in *Solidago* sect. *Erectae* (except subsect. *Humiles*), sect. *Squarrosae*, sect. *Villosicarpae* and sect. *Brintonia* is based on 258 chromosome counts previously published (Appendix A) and 67 additional counts reported here (Appendix B). Only diploids are known in *S. bicolor* (Figure 6), *S. erecta* (Figure 1), *S. hispida* (Figure 7), *S. junifolia* (Figure 3), *S. kralii* (Figure 2), *S. pallida* (Figure 3), *S. plumosa* (Figure 2), *S. puberula* (Figure 8), *S. pulverulenta* (Figure 8), *S. rigidiuscula* (Figure 4), and *S. roanensis* (Figure 8)

of sect. *Erectae*, *S. squarrosa* (Figure 9) of sect. *Squarrosae*, *S. villosicarpa* (Figure 9) of sect. *Villosicarpae*, and *S. discoidea* (Figure 9) of sect. *Brintonia*.

The sizes of the ranges of species vary greatly in the genus *Solidago* as does the number of known populations within each range. Range size and frequency of occurrence within that range varies from very narrow and very rare, e.g., *S. porteri* (known only at the hexaploid level  $2n = 54$ ) and *S. villosicarpa* (known only at the diploid level  $2n = 18$ ), to relatively widely distributed and common, e.g., *S. hispida* (known only at the diploid level  $2n = 18$ ) and *S. speciosa* (known at both the diploid and tetraploids levels). The reasons for these differences are not known, although in some cases rare species appear to be found growing in rare habitats with distinct soil characteristics associated with particular communities of dominant plants, e.g., *S. villosicarpa* (LeBlond 2000 [43]). Semple and Cook [3] included comments on habitats of all species discussed below.

Polyploids occur in *S. arenicola* (Figure 2; tetraploids), *S. porteri* (Figure 7; hexaploids), *S. sciaphila* (Figure 7; tetraploids), *S. speciosa* (Figure 5; diploids and tetraploids occurring east of the Appalachian Mts. and only tetraploids occurring west of the Appalachian Mts.), and the tetraploid *S. sp. nov.* of J. Peirson [44] (Figure 7; insert in the *S. hispida* complex map) of subsect. *Erectae*. Polyploidy occurs in four of the eight species of subsect. *Humiles* (Peirson et al., 2012 [17]); *S. racemosa* includes only polyploids (tetraploids and hexaploids) and may belong in subsect. *Humiles* rather than subsect. *Erectae*. Out of the 27 species of *S. sect. Erectae*, no chromosome counts have been reported for two southeastern US species known only from type material, *S. austrocaroliniana* and *S. georgiana* of subsect. *Erectae*, and for the Mexican species *S. simplex* of subsect. *Humiles*. In comparison, only diploids are known in *S. sect. Solidago* native to Eurasia plus *S. macrophylla* native to eastern Northern America (Semple 2016 [45]). In *S. sect. Thyrsoiflorae* (A. Gray) A. Gray, the sixth section in *S. subg. Solidago*, 20 of 21 chromosome counts reported were diploid, with just one tetraploid count known [18,45]. Thus, the majority of taxa in *S. subg. Solidago* are diploid (27 out of 48 species; 73% of species have been counted), three species include diploids and tetraploids, five species include just tetraploids, 1 species includes tetraploids and hexaploids, and 1 species includes just hexaploids. Chromosome number data is unknown for 11 taxa (species and varieties) in *S. subg. Solidago*; *S. decurrens* Loureiro var. *praeflorens* (Nakai) Kitamura, *S. horieana* Kadota, *S. pacifica* Juz., and *S. yambaruensis* S. Sakaguchi & Mot. Ito of *Solidago* ser. *Solidago*; *S. austrocaroliniana*, *S. georgiana*, and *S. simplex* of *S. sect. Erectae*, and *S. buckleyi* Torr. & A. Gray, *S. capulinensis* Cockerell & Andrews, *S. orientalis* (Nesom) Nesom, and *S. spellenbergii* Semple of *S. sect. Thyrsoiflorae*.

**Author Contributions:** Conceptualization, J.C.S.; methodology, J.C.S.; investigation, J.C.S. and R.E.C.; resources J.C.S.; data curation, J.C.S.; writing—original draft preparation, J.C.S.; writing—review and editing, J.C.S. and R.E.C.; supervision, J.C.S.; project administration, J.C.S.; All authors have read and agreed to the published version of the manuscript.

**Funding:** This work was supported by Natural Sciences and Engineering Research Council of Canada Operating Grants to J.C.S. and an NSERC Postgraduate Scholarship and an Ontario Graduate Scholarship in Science and Technology (OGSST) to R.E.C.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** Data remains in position of J.C.S. and is available from him at jcsemple@uwaterloo.ca.

**Acknowledgments:** The following people are thanked for their assistance in the field: Jerry Chmielewski, Diana Cook, Richard Cook, Isolde Seiden, Brenda Semple, and Keith Tereszchuk. The help of the late Joan Venn is acknowledged for her assistance in the WAT herbarium.

**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A

Previously Published Chromosome Counts for *Solidago* sect. *Erectae* (Not Including Taxa of subsect. *Humiles*), sect. *Villosicarpae*, sect. *Squarrosae*, and sect. *Brintonia*; *B* = J.R. Beaudry; *Bt* = L. Brouillet; *C* = R.E. Cook; *C, C & C* = R. Cook, D. Cook and D. Cook; *Ch* = J. Chmielewski; *S* = J.C. Semple; and *S & S* = J.C. & B. Semple.

***Solidago* sect. *Erectae*** D. Don in Loudon

***Solidago* subsect. *Erectae*** (D. Don in Loudon) Semple & J.B. Beck

***Solidago* ser. *Erectae*** (D. Don in Loudon) Hoffmann

*Solidago arenicola* B.R. Keener & Kral (all as *S. arenicola*)— $2n = 36$  U.S.A. **Alabama:** Blount Co., Semple & B. Semple 11191 (WAT [30]), Semple & B. Semple 11196 (WAT [30]). — $4x$  by flow cytometry U.S.A. **Alabama:** Blount Co., Peirson 608 (MICH [17]), Peirson 608 (MICH [17]). **Tennessee:** Morgan Co., Peirson 610 (MICH [17]).

*Solidago austrocaroliniana* Semple & J.B. Nelson—No counts reported

*Solidago erecta* Pursh (all originally published as *S. erecta*)— $2n = 9_{II}$  U.S.A. **Alabama:** Jackson Co., G. Morton 4461 (NY [26]), G. Morton 4471 (NY [26]). **New Jersey:** Atlantic Co., S & Suropto 9501 (WAT [29]). **North Carolina:** Franklin Co., S & Suropto 9735 (WAT [29]). **Tennessee:** Hamilton Co., G. Morton 4446 (WAT [26]). **Virginia:** Culpepper Co., S & Suropto 9735 (WAT [29]); Rockbridge Co., G. Morton 6506 (NY [26]). — $2n = 18$  U.S.A. **Georgia:** Dade Co., S 10996 (WAT [30]); Dekalb Co., Morton & Venn NA16192 (TRT [33]); Greene Co., S 10868 (WAT [30]); Taylor Co., S 10974 (WAT [30]). **Kentucky:** Estill Co., S & Suropto 9454 (WAT [29]); Rockcastle Co., S & Suropto 9605 (WAT [29]). **Mississippi:** Itawamba Co., S & Suropto 10175 (WAT [29]). **New Jersey:** Burlington Co., B 57-197 (MT [23]). **North Carolina:** Richmond Co., S, Brammall & Hart 3046 (WAT [25]). **South Carolina:** Chester Co., S & Ch 6098 (WAT [26]). **Tennessee:** Sullivan Co., S10771 (WAT [30]). **Virginia:** Bath Co., S 10721 (WAT [30]); Essex Co., S & Ch 5969 (WAT [26]); Northumberland Co., S & Ch 5984 (WAT [26]); Wise Co., S & Ch 6281 (WAT [26]).

*Solidago jejunifolia* Steele— $2n = 9_{II}$  U.S.A. **Wisconsin:** Douglas Co., S 11848 (WAT [34]).

*Solidago kralii* Semple— $2n = 9_{II}$  U.S.A. **Georgia:** Pulaski Co., S & S 11208 (WAT [17]); Richmond Co., S & S 11217 (WAT [40]). — $2n = 18$  U.S.A. **Georgia:** Ben Hill Co., S & S 11216A (WAT [17]), S & S 11216-B (WAT [17]), S & S 11212 (WAT [17]); Pulaski Co., C, C & C 701 (WAT [40]). **South Carolina:** Aiken Co., S & S 11218 (WAT [17]). — $2x$  by flow cytometry U.S.A. **South Carolina:** Aiken Co., Peirson 605 (MICH [17]).

*Solidago pallida*— $2n = 18$  U.S.A. **South Dakota:** Custer Co., S & Bt 4476 (WAT [26]); corrected ident. in Semple and Cook 2004 [30], originally as *S. speciosa* var. *angustifolia*.

*Solidago plumosa* Small— $2n = 18$  U.S.A. **North Carolina:** Standley Co., Nesom s.n. (Guy Nesom, unpub., pers. comm. BRIT Feb 20 2003.)— $2x$  by flow cytometry U.S.A. **North Carolina:** Stanley Co., Peirson 610 (MICH [17]).

*Solidago rigidiuscula* (Torr. & Gray) Porter— $2n = 9_{II}$  U.S.A. **Missouri:** Jasper Co., Morton 3992 and 3993 (BRIT [26] as *S. speciosa* var. *rigidiuscula*). — $2n = 18$  CANADA. **Ontario:** Lambton Co., Lamb s.n (WAT [26] as *S. speciosa* var. *rigidiuscula*). U.S.A. **South Carolina:** Greenville Co., S & Ch 6180 (WAT [26] as *S. speciosa* var. *speciosa*). **Tennessee:** Marshall Co., S & Ch 9121 (WAT [28] as *S. speciosa*). **Wisconsin:** Jackson Co., S & Ch 5064 (WAT [26] as *S. speciosa* var. *rigidiuscula*).

*Solidago speciosa* Nutt. — $2n = 18$  U.S.A. **North Carolina:** Buncombe Co., S et al. 3028 (WAT [25] to sp.). **Pennsylvania:** Montgomery Co., B & Wherry 57-236 and 57-238 (MT [23] to sp.). — $2n = 18_{II}$  U.S.A. **New York:** Westchester Co., Morton 6794 (NY [26] as var. *speciosa*). — $2n = 18_{II}$  U.S.A. **South Carolina:** Edgefield Co., S & Suropto 9817 (WAT [29] as var. *speciosa*). — $2n = 36$  US. **Tennessee:** Blount Co., S & Ch 6228 (WAT [26] to sp.). Hamilton Co., Morton & Venn NA16201 (TRT [33] to sp.). — $2n = ca. 36$  U.S.A. **Arkansas:** Conway Co., Morton & Venn NA16265 (TRT [33] to sp.). **North Carolina:** Macon Co., Morton & Venn NA16180 (TRT [33] to sp.).

***Solidago* ser. *Albigulae*** (Raf.) Semple & J.B. Beck

*Solidago bicolor* L. (as *S. bicolor* unless otherwise noted)— $2n = 9_{II}$  U.S.A. **Maine:** Sagadahoc Co., S 10377 (WAT [29]). **Pennsylvania:** Perry Co., S & *Suripto* 9487 (WAT [29]). — $2n = 18$ . **BELGIUM.** seed from Bruxelles Garden, *Morton* s913 (TRT [33]). **CANADA.** **New Brunswick:** Northumberland Co., S & *Keir* 4690 (WAT [26]). **Ontario:** Leeds Co., S 2913 (WAT [25] as var. *bicolor*); Leeds Co., B et al. 62-210, 62-216, 62-230, 62-232 (all MT [24] as var. *bicolor*), S 10656 (WAT [30]). **Québec:** Argenteuil Co. S & *Keir* 4592 (WAT [26] as *S. hispida*); Deux-Montagnes Co., B & *Louis-Marie* 55G-228 (MT [22] as var. *bicolor*); Gaspé-Nord, Ruisseau-Sorel, B & *Louis-Marie* 58-249 (MT [23]). U.S.A. **Connecticut:** Hartford Co., S & *Bt* 3614 (WAT [25] as var. *bicolor*). **Maine:** Oxford Co., *Ringius* 1620a (WAT [26]). **Massachusetts:** Bristol Co., B & *Seymour* 57-160 (MT [24] as var. *bicolor*), S & *Bt* 3574 (WAT [25] as var. *bicolor*); Norfolk Co., B & *Seymour* 57-161 (MT [23] as var. *bicolor*), B & *Seymour* 57-165 (MT [23] as var. *bicolor*); Plymouth Co., S & *Bt* 3558 (WAT [25] as var. *bicolor*). **New Hampshire:** Carroll Co., S & *Bt* 3473 (WAT [25] as var. *bicolor*); Coos Co., *Cook & Tereszchuk* C-157 (WAT [34]), C & *Tereszchuk* C-161 (WAT [34]); Grafton Co., S & *Bt* 3483 (WAT [25] as var. *bicolor*), S & *Bt* 3460 (WAT [25] as var. *bicolor*). **New York:** Greene Co., S & *Bt* 3637 (WAT [25] as var. *bicolor*); Rennselear Co., B & *Beal* 57-134 (MT [23] as var. *bicolor*); Sullivan Co., S 6827 (WAT [26]). **North Carolina:** Carteret Co., *Morton & Venn* NA16560 (TRT [33]); Craven Co., S & *Ch* 6047 (WAT [26]); Edgecombe Co., S & *Ch* 6002 (WAT [26]). Henderson Co., S 10827 (WAT [30]). **Pennsylvania:** Greene Co., S 10676 (WAT [30]). **Vermont:** Addison Co., S 6904 (WAT [26]); Caledonia Co., S & *Bt* 3487 (WAT [25] as var. *bicolor*). **Virginia:** Allegheny Co., S 10732 (WAT [30]); Grayson Co., S 10744 (WAT [30]); Montgomery Co., B & *Massey* 57-312 (MT [23] as *bicolor* var. *ovalis*), B & *Massey* 57-313 (MT [23] as *bicolor* var. *ovalis*). **Wisconsin:** Marion Co., S 10681 (WAT [30]). — $2n = 18 + 0-1$  supernumerary. U.S.A. **Virginia:** Giles Co., B & *Massey* 57-328 (MT [23] as *bicolor* var. *ovalis*). — $2n = 18 + 0-3$  supernumeraries. **CANADA.** **New Brunswick:** Fundy N.P., *Kapoor* 69-xx-x ([36] not seen [36])— $2n = 18 + 0, 1, 3$  supernumeraries. **CANADA.** **Québec:** Co., Contrecoeur, B et al. 59-30 (MT [24] as var. *bicolor*).

*Solidago georgiana* Semple—No counts reported

*Solidago hispida* Muhl. var. uncertain— $2n = 18$  CANADA. **Québec:** *Boudreau* s.n. (QFA; Gervais et al., 1999; to sp.); *Ringius* 1653 (WAT [26] to sp.).

*Solidago hispida* Muhl. var. *arnoglossa* Fernald— $2n = 18$  CANADA. **Newfoundland:** Division No. 5, *Morton & Venn* NA12474 (TRT [37] to sp.); near Doctors Brook, *Morton & Venn* NA12336 (TRT [33] as var. *arnoglossa*). **Québec:** Bon Ami Pt., *Morton* s.n. (TRT [37] to sp.).

*Solidago hispida* Muhl. var. *hispida*— $2n = 9_{II}$  CANADA. **Ontario:** Algoma Dist.: S & *Brammall* 2861 (WAT [25] to sp.), S & *Brammall* 2868 (WAT [25] to sp.), S & *Brammall* 2870 (WAT [25] as to sp.); Bruce Co., S & *Brammall* 2789 (WAT [25] to sp.), S & *Brammall* 2300 (WAT [25] to sp.); Cochrane Dist.: S & *Brammall* 2830 (WAT [25] to sp.), S & *Brammall* 2831 (WAT [25] to sp.); Manitoulin Dist.: S & *Brammall* 2308 (WAT [25] to sp.); Parry Sound Dist.: S & *Brammall* 2891 (WAT [25] to sp.); Simcoe Co., S 2933 (WAT [25] to sp.); Thunder Bay Dist.: S & *Brammall* 2667 (WAT [25] to sp.); Timiskaming Dist., S & *Brammall* 2818 (WAT [25] to sp.); **Québec:** Laviolette Co., B 55-168 (MT [22] as var. *hispida*). U.S.A. **Arkansas:** Polk Co., S & *Heard* 8273 (WAT [27] to sp.). — $2n = 18$  CANADA. **Manitoba:** Roseau River Valley, *Löve & Löve* 6213 (not seen or located) [38] as *S. bicolor* var. *concolor*. **Newfoundland:** Gros Morne Natl. Park., *Morton & Venn* NA12163 (WAT [37] to sp.). **Ontario:** Bruce Co., S & *Brammall* 2979 (WAT [25] to sp.), S10671 (WAT [30] as var. *hispida*); Cochrane Dist.: Co., S & *Brammall* 2824 (WAT [25] to sp.); Kenora Dist.: S & *Bt* 4142 (WAT [26] to sp.), S & *B. Semple*. 6723 (WAT [26] to sp.); Lambton Co., C & *D. Cook* 74 (WAT [30] as var. *hispida*); Manitoulin Dist., *Morton & Venn* NA10743a (TRT [37] to sp.), *Morton & Venn* NA10749 (TRT [37] to sp.), S & *Brammall* 2328 (WAT [25] as to sp.); Sudbury Dist., S & *Brammall* 2836 (WAT [25] as to sp.), S & *Brammall* 2846 (WAT [25] to sp.); Thunder Bay Dist., *Morton* s.n. (WAT [37] to sp.), S et al. 6757 (WAT [27] to sp.). **Québec:** *Morton* s.n. (TRT [37] to sp.), *Dansereau* et al. 58-248 (MT [24] as *S. bicolor* var. *concolor*); Cap Jaseux, B 61-278, 61-279, 61-280 (MT [24] as *S. bicolor* var. *concolor*); Drummondville, *Ringius* 1653 (WAT [26] to sp.), *Ringius* 1663

(WAT [26] to sp.); Ile Maligne, Doucet 59-141 (MT [24] as *S. bicolor* var. *concolor*); Labelle Co., Marcellin-Sylvio 55-190 (MT [22] as var. *hispida*); Lac St-Jean Co., Rolland-Germain & Galiano 55-216 (MT [22] as var. *hispida*); Parc la Vérendrye, B & Doucet 59-66 (MT [24] as *S. bicolor* var. *concolor*). U.S.A. **Arkansas**: Fulton Co., S & Heard 8315 (WAT [27] to sp.); Searcy Co., S & Heard 8298 (WAT [27] to sp.); Stone Co., Morton & Venn NA16260 (TRT [33] as var. *hispida*). **Maine**: Somerset Co., S & Keir 4634 (WAT [26] to sp.). **Missouri**: Madison Co., S et al. 3774 (WAT [25] as *S. drummondii*, corrected det. by R.D. Noyes, MO duplicate). **New York**: Greene Co., S & Bt 3638 (WAT [25] to sp.); **Ohio**: Hocking Co., S et al. 2982 (WAT [25] to sp.); Scotia Co., S et al. 2987 (WAT [25] to sp.). **Virginia**: Allegheny Co., C & Tereszchuk 348 (WAT [34] as var. *hispida*). — $2n = 18 + 1$  supernumerary CANADA. **Ontario**: Cochrane Dist.: S & Brammall 2825 (WAT [25] to sp.); Sudbury Dist.: S & Brammall 2837 (WAT [25] to sp.)

*Solidago hispida* Muhl. var. *huronensis* Semple— $2n = 18$  CANADA. **Ontario**: Bruce Co., S 2452 (WAT [25] as as var. *tonsa*), S & Brammall 2806 (WAT [25] as var. *tonsa*), S 10672 (WAT [30] as var. *huronensis*); Lambton Co., C & C C-73 (WAT [30] as var. *huronensis*).

*Solidago hispida* Muhl. aff. var. *huronensis* Semple— $2n = 18$  CANADA. **Ontario**: Algoma Dist., S & Brammall 2862 (WAT; Ringius & Semple 1987, as *S. glutinosa* var. *glutinosa*; corrected in [17] to *S. hispida*).

*Solidago hispida* Muhl. aff. var. *lanata* (Hook.) Fernald— $2n = 18$  CANADA. **Saskatchewan**: E of Shoal Lake, Hooper 83091001 (WAT to sp.).

*Solidago hispida* Muhl. var. *tonsa* Fernald— $2n = 18$  CANADA. **Newfoundland**: Table Mt., Morton & Venn NA12186 (WAT [37] to sp.).

*Solidago hispida* Muhl. aff. var. *tonsa* Fernald— $2n = 18$  CANADA. **Québec**: Gaspésie Co., St. Pierre des Monts, Morton NA4086 (TRT [37] to sp.).

*Solidago hispida* × sp.  $2n = 18$  CANADA. **Québec**: Comté de Gaspé-Ouest, Boudreau s.n. (QFA [39] as *S. simplex*).

*Solidago porteri* Small— $2n = 27_{II}$  U.S.A. **Alabama**: Morgan Co., S & S 11190 (WAT [31]). **Tennessee**: Giles Co., Estes 06795 (APSC [31]).

*Solidago* sp. nov. J.A. Peirson (in press)— $4x = 36$  (flow cytometry data) U.S.A. **Michigan**: 4 locations (MICH [43]).

*Solidago sciaphila* Steele—no previous counts reported

#### *Solidago* ser. *Puberulae* Semple & J.B. Beck

*Solidago puberula* Nutt. — $2n = 9_{II}$  CANADA. **Québec**: Laviolette Co., B 55-162 (MT [22] as var. *puberula*). U.S.A. **Maine**: Sagadahoc Co., S 10376 (WAT [29], as var. *puberula*); York Co., S & Suripto 9586 (WAT [29], as var. *puberula*). — $2n = 18$  CANADA. **Québec**: Mt. Albert, Morton s.n. (WAT [37] to sp.); Mont Ste-Anne, Dansereau 58-253 (MT; [23] as var. *puberula*); Rivière-aux-Rats, B & Doucet 59-119 (MT [24] as var. *puberula*). U.S.A. **Maine**: Oxford Co., Ringius 1621 (WAT [26] to sp.); Penobscot Co., Ringius 1629 (WAT [25] to sp.). **Massachusetts**: Franklin Co., S 6872 (WAT [26] to sp.); Worcester Co., S 6867 (WAT [26] to sp.). **New Hampshire**: Cheshire Co., Seymour 57-27-1, 57-27-1-2, 57-27-1-3 (MT [22], as var. *puberula*). **New Jersey**: Burlington Co., S & Ch 6259 (WAT [26] to sp.). **New York**: Essex Co., Ringius 1534 (WAT [26] to sp.), Ringius 1551 (WAT [26] to sp.); Hamilton Co., S & Bt 3670 (WAT [25] to sp.); St. Lawrence Co., S & Bt 3679 (WAT [25] to sp.), S & Bt 3686 (WAT [25] to sp.). **North Carolina**: Mitchell Co., S 10815 (WAT [30] as ssp. *puberula*). **Tennessee**: Blount Co., S & Ch 6227 (WAT [26], to sp.); Carter Co., S 10807 (WAT [30] as ssp. *puberula*); Sevier Co., Beaudry et al. 57-428 (MT; [23] as var. *puberula*), B et al. 57-441 (MT; [23] as var. *puberula*), Morton & J. Venn NA16169 (TRT [33] to sp.). — $2n = 18 + 0$  or 3 supernumeraries. CANADA. **New Brunswick**: Sackville, Kapoor 69-119-1 (SMUH not seen [36] to sp.). **Québec**: Rivière-aux-Rats, B & Doucet 59-120 (MT; [23] as as var. *puberula*), B & Doucet 59-220 (MT [24] as var. *puberula*).

*Solidago pulverulenta* Nutt. — $2n = 9_{II}$  U.S.A. **North Carolina**: Bladden Co., S & Suripto 9771 (WAT [29] as *S. puberula* var. *pulverulenta*). — $2n = 18$  U.S.A. **Florida**: Bay Co., Godfrey 63-35-2, 63-35-4, 63-35-5 (MT [24] as var. *puberula*); Calhoun Co., S & Godfrey 3112 (WAT [25] as *S. puberula*); Jackson Co., B & Godfrey 57-514 (MT; [23] as *S. puberula* var. *pulverulenta*).

*Solidago roanensis* Porter (all published as *S. roanensis*)— $2n = 9_{II}$  U.S.A. **Tennessee:** Carter Co., Morton 3853 (NY [26]), Morton 3854 (NY [26]); Polk Co., Morton 8546 (not seen; 8545 UTCH from same location is *S. roanensis* [26]).— $2n = 18$  U.S.A. **North Carolina:** Haywood Co., C, C, & C 557 (WAT [34]); Transylvania Co., B 57-473 (MT; [23]), 57-475 (MT; [23]). **Virginia:** Giles Co., B & Massey 57-321c, 57-322, 57-323, 57-324, 57-327 (all MT; [23]).— $2n = 18 + 0-1$  supernumerary. U.S.A. **Virginia:** Giles Co., B & Massey 57-316 (MT; [23]).

**Solidago** **subject.** *Humiles* (Rydb.) Semple See Peirson et al., 2012 [17] for review.  
Hybrids

*Solidago bicolor* × *S. puberula*— $2n = 18$  U.S.A. **Maine:** Oxford Co., S et al. 2989 (WAT [25] as *S. hispida*).

*Solidago hispida* × sp.— $2n = 18$  CANADA. **Québec:** mon Ste-Anne, Boudreau s.n. (QFA; [39] as *S. simplex* ssp. *simplex*).

**Solidago** **sect.** *Villosicarpae* Semple & J.B. Beck

*Solidago villosicarpa* LeBlond— $2n = 18$  U.S.A. **North Carolina:** Onslow Co., S & Tinbrink 11637 (WAT [32] to sp.), Semple 11639-A (WAT [34], Semple 11639-B (WAT [34], Semple 11639-C (WAT [34]).

**Solidago** **sect.** *Squarrosae* (A. Gray) Semple & J.B. Beck

*Solidago squarrosa* Muhl. (all published as *S. squarrosa*)— $2n = 9_{II}$  CANADA **Ontario:** Parry Sound Dist.: Co., S & Brammall 2890 (WAT [25]); Sudbury Dist.: Co., S & Brammall 2884 (WAT [25]). **Québec:** St-Maurice Co., B 55-61 (MT [22]). U.S.A. **New Jersey:** Warren Co., Morton 7891 (not seen [26]). **Pennsylvania:** Fulton Co., Morton 6564 (not seen [26])— $2n = 18$  CANADA. **New Brunswick:** Victoria Co., S & Keir 4673 (WAT [26]); Victoria Co., Ringius 1651 (WAT [26]). CANADA **Ontario:** Durham Co., S 3692 (WAT [25]); Frontenac Co., Ch 2319 (WAT [27]), S 10663 (WAT [30]); Haliburton Co., S 10667 (WAT [30]); Leeds Co., B et al. 62-212 (MT [24]); Muskoka Dist., Semple 2932 (WAT [25]); Nipissing Dist.: Ch 2301 (WAT [27]), Ch 2311 (WAT [27]); Renfrew Co., S 2426 (WAT [25]), Ch 2312 WAT [27]; Timiskaming Dist., S & Brammall 2819 (WAT [25]), Ch 2307 (WAT [27]). **Québec:** Argenteuil Co., Beaudry 55-205 (MT; Beaudry and Chabot 1959); Gaspé, Port Daniel, Kapoor 60-125-1 (SMUH not seen [36]), Kapoor 60-125-2 (SMUH not seen [36]); Ile du College, Chmielewski 2308 (WAT [27]); Parc La Vérendrye, B & Doucet 59-91 (MT [24]), B & Doucet 59-94 (MT [24]); Hwy-105 just S of Hwy-117, C & Seiden C-129 (WAT [34]); Rivière-aux-Rats, B & Doucet DO-59-122 (MT [24]). U.S.A. **Maine:** Aroostook Co., S & Keir 4660 (WAT [26]). **New Hampshire:** Grafton Co., S & Bt 3467 (WAT [25]). **New York:** Essex Co., Ringius 1543 (WAT [26]).

**Solidago** **sect.** *Brintonia* (Greene) Semple & J.B. Beck

*Solidago discoidea* (Ell.) Torr. & Gray— $2n = 9_{II}$  U.S.A. **Mississippi:** Lauderdale Co., Jones 15336 (GA not seen [46]; other collections of species from MS by S.B. Jones are correctly identified).— $2n = 18$  U.S.A. **Alabama:** Blount Co., S & S 11194 (WAT; [32]); Tuscaloosa Co., B & Harper 57-560, 57-562, 57-563, 57-564 (MT; [23] as *S. delicatula* in error). **Florida:** Gadsden Co., B & Godfrey 57-732, 57-333, 57-335, 57-336 (MT; [23] as *S. delicatula* in error [-332, -333, -334] and *S. discoidea* [-335, -336]). **Texas:** Dallas Co., B & Shinnars 57-631 (MT; there are two sheets in MT with this number, one is *S. delicatula* [23] and one is *S. discoidea* indicating a clerical error and making this report questionable).

## Appendix B

Previously Unreported Chromosome Number Determinations of Taxa in *Solidago* sect. *Erectae*, sect. *Squarrosae*, and sect. *Villosicarpae* from Canada and the United States Are Arranged Alphabetically by Section, Subsection, Series, and Species. Bt = L. Brouillet; C = R. Cook; C, C & C = R. Cook, D. Cook and R. Cook; S = J.C. Semple; S & S = J.C. & B. Semple; and T = K. Terezhuk; All Vouchers in WAT in MT.

***Solidago* sect. *Erectae******Solidago* subsect. *Erectae******Solidago* ser. *Erectae***

*Solidago erecta* Pursh— $2n = 18$  U.S.A. **Georgia:** Chattooga Co., US-27 S of Sommerville, C & T 248; Union Co., GA-60 W of Suches, C, C & C 616; GA-180 1 km N of Vogel St. Park, C, C & C 622. **New Jersey:** Atlantic Co., NE of Egg Harbor City, Bremen Ave. (Co.Rd.-674), S 11817. **North Carolina:** Cherokee Co., US-64 ca 3 km E of Murphy, S 11586. **Tennessee:** Coffee Co., S of Manchester, Arnold Center R., S & S 11189; US-41 SE of Manchester, S & S 11187. Johnson Co., US-421 N of Mountain City, C & T C-322; Polk Co., US-64/74 W of Greasy Branch Creek, C & T 270. **Virginia:** Mecklenburg Co., E side of La Crosse, US-58 3.8 km E of I-85, S 11611. Prince George Co., VA 10 4 km W of Burrowsville, S 11761.

*Solidago jejunifolia* Steele— $2n = 18$  U.S.A. **Michigan:** Cheboygan Co., Indian River, S of Burt Lake, Indian River Snowmobile Trail, S 11838. **Minnesota:** Sherburne Co., SE of Orrock, Sand Dunes State Forest, Ann Lake Campground, S 11850.

*Solidago pallida* (Porter) Rydb. — $2n = 18$  U.S.A. **Wyoming:** Crook Co., NW of Sundance, F.S.Rd-838 6.2 km N of US-24, S & S 11401.

*Solidago rigidiuscula* (Torr. & Gray) Porter— $2n = 9_{II}$  U.S.A. **Tennessee:** Giles Co., ca. 4 mi NW of Minor Hill (SW of Pulaski), W side of Little Texas Rd. S of intersection with Kennedy Rd., S 11866.— $2n = 18$  U.S.A. **Kansas:** Miami Co., US-169 3 mi N and 3.8 mi E of Beagle, S & Chmielewski 5259. **South Carolina:** Lexington Co., N end of Gaston, US-321, road right of way, S 11775.

*Solidago speciosa* Nutt. — $2n = 18$  U.S.A. **Virginia:** Mecklenburg Co., E side of LaCrosse, US-58 3.8 km E of I-85, S 11613. — $2n = 36$  U.S.A. **Georgia:** Gwinnett Co., W of Loganville, Old Loganville Rd just E of Fox Chase Rd., S 11677. **Minnesota:** Winona Co., SW of Winona, MN-43 5.4 km NE of I-90, bluffs of Mississippi R., S & S 11321. **Tennessee:** Carter Co., TN-131 S of TN-67, C & T 313; Johnson Co., US-321 near NC state line, C & T 310. Monroe Co., S of Sweetwater, TN-68 2.7 km SE of US-11/TN-2, S 11568. **Wisconsin:** Vernon Co., S of Stoddard, WI-35 Scenic Bluff Overlook Area, *Semple* 11951.— $2n = 54$ . U.S.A. **North Carolina:** Avery Co., NC-194 ca. 3.2 km E of US-19E, C & T 291 (Identity of voucher correct, but identity of plant transplanted to greenhouse from which count was made could not be confirmed subsequently; count not included in Figure 6).

***Solidago* ser. *Albigulae***

*Solidago bicolor* L.— $2n = 18$  CANADA. **New Brunswick:** Westmoreland Co., W of Bouctouche, junction of NB-11 and NB-475/505, S & S 11466. **Nova Scotia:** Queens Co., Ten Mile Lake Prov. Park, S & S 11510. **Prince Edward Island:** Queens Co., PEI-222, S of Pleasant Grove, S 11472. U.S.A. **Maine:** Oxford Co., US-2 W of Rumford, C & T C-168. **New Hampshire:** Coos Co., US-2 5 km E of Gorham, C & T C-157, between Gorham and Shelburne, off US-2 on Old Man Park rd., C & T C-161. **Vermont:** Windsor Co., VT-12 ca 2 km W of Hartland, C & T C-189. **Virginia:** Augusta Co., US-250 at Highland Co. line, Shenandoah Mt., C & T C-388.

*Solidago hispida* Muhl. var. *hispida*— $2n = 9_{II}$  U.S.A. **Wisconsin:** Douglas Co., W of Solon Springs, US-53, S 11847. — $2n = 18$  CANADA. **New Brunswick:** Restigouche Co., Campbellton, 11 Val D'Amour Rd., vicinity of Quality Inn, S 11450; York Co., W of Pokiak, NB-2 ca 2 km W of NB-105, S & S 11527. **Ontario:** Algoma Co., Dist.-Rd.-556 between Searchmont and Ranger Lake, 47 km E of Hwy-1, S & S 11093; Haliburton Co., S of Bancroft, Bay Lake Rd, by Bay Lake, S 11059; Parry Sound Dist., Hwy-522 at Stumpy Bay Rd. 27.4 km W of Loring, S & S 11071; Peterborough Co., 7 km N of Woodview, Hwy-28 roadside picnic area by river, S & S 11056; Renfrew Co., Hwy-62 N of Combermere, S & S 11065. **Québec:** Hwy-132 W of Bic, S & S 11426; Gaspésie, N of Grande-Cascapédia, Hwy-299, fishing access site #27, by Rivière Cascapédia, S & S 11444; Hwy-117 between Val D'Or and Louvicourt, C & IS 112. U.S.A. **New Hampshire:** Coos Co., US-2 ca 1 km E of Gorham, C & T 156. **Virginia:** Augusta Co., US-250 ca 0.2 km E of Calf Pasture Creek, C & T C-382.



*Solidago sciaphila* Steele— $2n = 18$  U.S.A. **Wisconsin:** Vernon Co., S of Stoddard, WI-35, bluff scenic overlook, S 11853.— $2n = 36$  U.S.A. **Iowa:** Clayton Co., McGregor, S & Chmielewski 5179. **Illinois:** Carroll Co., Mississippi Pallasades St. Pk., Ossei Pt., S 11854. **Wisconsin:** Vernon Co., S of Stoddard, WI-35, bluff scenic overlook, S 11851, S 11853.

#### **Solidago ser. Puberulae** Semple & J.B. Beck

*Solidago puberula* Nutt. — $2n = 18$  CANADA. **New Brunswick:** Gloucester Co., Hwy-11 ca 4 km S of Janeville, S & S 11456. **Nova Scotia:** Lunenburg Co., Bayswater, provincial park beach, dunes, S & S 11496. **Prince Edward Island:** Queens Co., PEI-2 between Tenmile House and Tracadie, S & S 11479. **Québec:** Hwy-117 S of Louvicourt, C & IS C-114; Reserve la Verendrye, Hwy-117 just S of Rd-30, rest stop, C & IS C-126, Hwy-117 S of Rd-30; C & IS C-118. U.S.A. **Pennsylvania:** Monroe Co., NW of Mt. Pocono, PA-6111 N of Sussex Dr., S 11805. **Virginia:** Southampton Co., S of Sebrell, Co.Rd.-647, S 11615.

*Solidago pulverulenta* Nutt. — $2n = 18$  U.S.A. **North Carolina:** Pender Co., NE of Clark's Landing, Clark's Landing Loup Rd., S 11635.

*Solidago roanensis* T. C. Porter— $2n = 18$  U.S.A. **Tennessee:** Sullivan Co., US-421 W of Shady Hollow, top of mountain, C & T 332.

#### **Solidago sect. Villosicarpae** Semple & J.B. Beck

*Solidago villosicarpa* LeBlonde— $2n = 18$  U.S.A. **North Carolina:** Brunswick Co., Oak Island, 32 St. S of East Oak Island Dr., S 11645.

#### **Solidago sect. Squarrosae** A. Gray

*Solidago squarrosa* Muhl. — $2n = 18$  CANADA. **New Brunswick:** Victoria Co., E of Perth-Andover, NB-109, road embankment, S & S 11529. **Ontario:** Temiskaming Dist.: Harris Twp., Hwy-65 E of New Liskeard, 1.7 km W of Twp. Conc. Rd. 3 & 4, C & Seiden C-83. **Québec:** Hwy-105 just S of Gracefield, C & Seiden C-134; S of Mikamic, Hwy-105, C & Seiden C-132; La Vallée-de-la-Gatineau Co., Hwy-117, S boundary of Reserve la Verendrye, rest stop, C & Seiden C-125.

## References

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