

**THE CYTOGEOGRAPHY OF *SOLIDAGO* SUBSECT. *RADULAE*
(ASTERACEAE: ASTEREAE)**

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ABSTRACT

The cytogeography of six of the seven species of *Solidago* subsect. *Radulae* is presented, based on 312 chromosome count reports. *Solidago altiplanities* is diploid $2n=18$ based on just one report. *Solidago californica* is mostly diploid $2n=18$ (36 reports) with just two tetraploid $2n=36$ reports. *Solidago gattingeri* is diploid $2n=18$ (2 reports). *Solidago mollis* includes tetraploids $2n=36$ (8 reports) and hexaploids $2n=54$ (8 reports). *Solidago radula* is mostly diploid $2n=18$ (11 reports) but includes some tetraploids $2n=36$ (4 reports) and one possible hexaploid $2n=54$ report. *Solidago velutina* includes diploids $2n=18$ (66 reports), tetraploids $2n=36$ (18 reports), and rarely hexaploids $2n=54$ (1 report). The chromosome number of *S. hintoniorum* is unknown.

As delimited by Semple and Beck (2021), based on the polygenomic phylogeny of Semple et al. (2023 in press), *Solidago* subsect. *Radulae* (Rydb.) Semple & J.B. Beck of sect. *Unilaterales* G. Don includes seven species: *S. altiplanities* C. & J. Taylor (Fig. 4 in Semple et al. 2015b), *S. californica* Nutt. (Figs. 1-2 in Semple et al. 2018), *S. gattingeri* Chapm. ex A. Gray (Figs. 1-2), *S. hintoniorum* Nesom (Figs 3-4 in Semple et al. 2018), *S. mollis* Bartl. (Figs. 5-6 in Semple et al. 2018), *S. radula* Nutt. (Figs. 12-13 in Semple et al. 2018), and *S. velutina* DC., the type species of the subsection (Figs. 14-17 in Semple et al. 2018).

Previously, *Solidago altiplanities* has been grouped with *S. canadensis* and *S. altissima* in subsect. *Triplinerviae* (Torr. & Gray) Nesom following Nesom (1993) and Semple & Cook (2006). Nesom (1989) reviewed the nomenclatural history of *S. velutina* and described *S. macvaughii* Nesom as similar. Nesom (1993) included *S. hintoniorum* Nesom in subsect. *Thyrsiflorae* A. Gray, but it was not included in subsect. *Thyrsiflorae* by Semple et al. (2017). Nesom (1993) included *Solidago macvaughii*, *S. mollis*, *S. radula*, and *S. velutina* (including *S. californica*) in subsect. *Nemorales* along with *S. nana* and *S. nemoralis* Ait. (including *S. decemflora*) as did Semple et al. (2018). Semple and Beck (2021) cited as the defining morphological traits of subsect. *Radulae* the more elongated rhizomes, more scabrous (stiffer) hairs on leaves, and large lower stem leaves with two, more pronounced lateral veins and the mid vein producing a trinervate appearance. *Solidago nana*, *S. nemoralis*, and *S. decemflora* are of subg. *Nemorales* (Mack.) Semple & Beck, which was defined by Semple and Beck (2021) as having leaves generally not triple-nerved, stem and leaf hairs soft, leaves gray-green to sometimes whitish, and basal rosettes often present at flowering. Semple and Beck (2021) placed *S. macvaughii* in subsect. *Triplinerviae* (Torr. & Gray) Nesom.

Raven et al. (1960) reported the first chromosome counts for *Solidago* subsect. *Radulae* with four diploid counts of $2n=9_{II}$ for *S. californica* and two diploid counts of $2n=9_{II}$ for *S. sparsiflora*, treated here as a synonym of *S. velutina*. Beaudry (1969) reported the first counts for *S. gattingeri* and *S. radula*, both diploid $2n=18$. Anderson et al. (1974) reported the first hexaploid count for *S. mollis*, and Semple et al. (1984) reported the first tetraploid count for *S. mollis*. Semple & Chmielewski (1987) reported the only count for *S. altiplanities* but under the name *S. speciosa* Nutt. var. *rigidiuscula* (Torr. & Gray) Porter, which Semple & Cook (2004) corrected to *S. altiplanities*. All previously reported counts are listed in Table 1 with identifications confirmed from herbarium vouchers for nearly all of the 310 reports.

MATERIALS AND METHODS

Chromosome counts were determined following the methods described in Semple (1985) and Semple & Cook (2004). Cytovouchers for nearly all reports were examined during visits to or in loans obtained from ASU, MT, NY, NMC, TEX, TRT, WAT in MT, and UC. Digital images of vouchers not seen in person were obtained via searches of SEINET (2023) and SERNEC (2022).



Figure 1. *Solidago gattingeri*, Rutherford Co., Tennessee, Kral 56466 (BRIT).

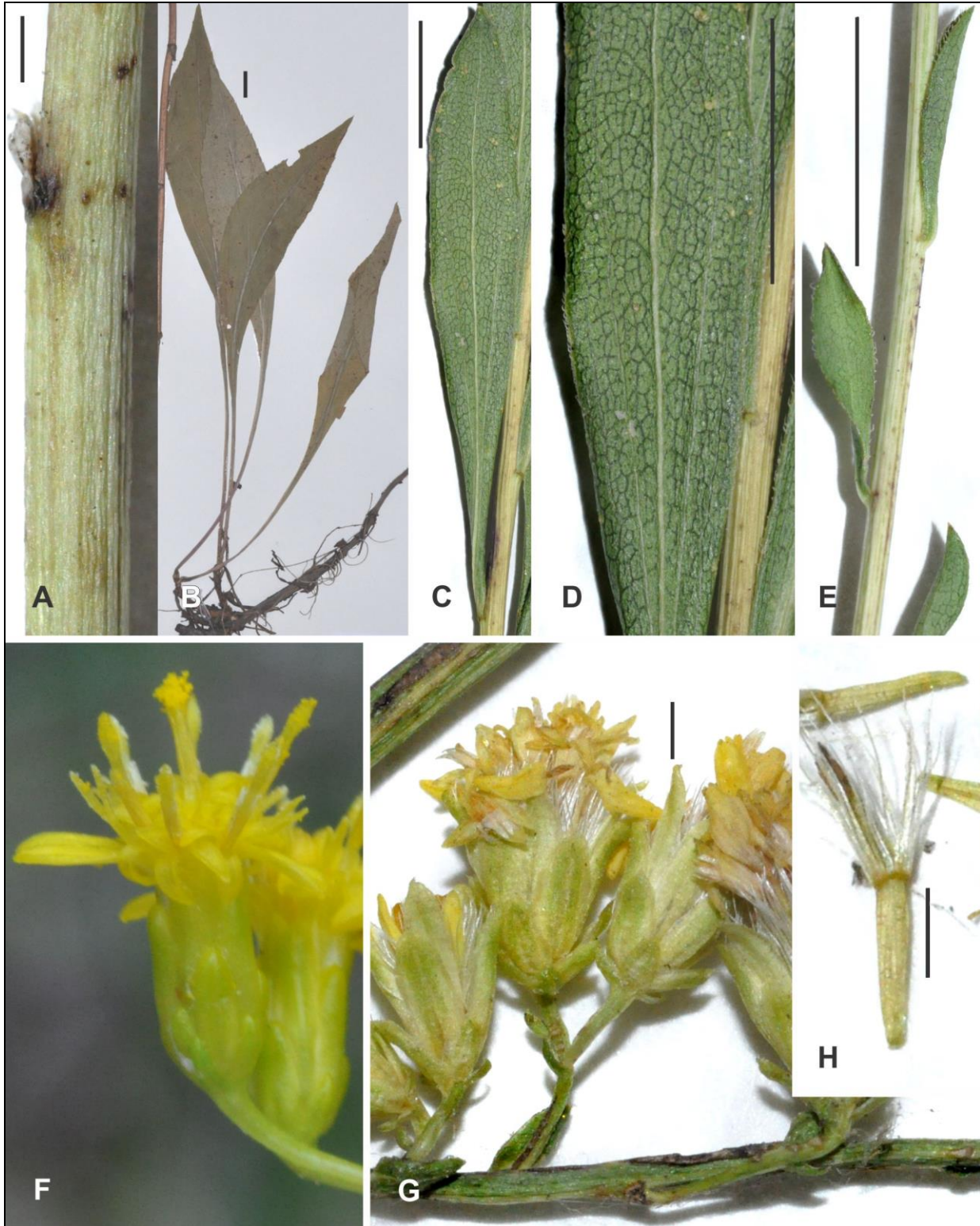


Figure 2. *Solidago gattingeri* — morphological details. **A.** Lower stem, *Semple et al. 11856* (WAT). **B.** Large basal rosette leaves, *Kral 40655* (MO). **C-D.** Mid stem leaf and blade detail, *Semple et al. 11856* (WAT). **E.** Upper stem stem leaves, *Semple et al. 11856* (WAT). **F-G.** In field and dried heads, *Semple et al. 11856* (WAT). **H.** Near mature fruit.

Table 1. Previously published chromosome number determinations in *Solidago* subsect. *Radulae*.

- Solidago altiplanities* C. & J. Taylor — $2n=9_{II}$ U.S.A. **Texas:** Cottle Co., *Semple & Heard* 8234 WAT (Semple and Chmiewski 1987, as *S. speciosa* var. *rigidiuscula*; corrected Semple and Cook 2004),
- Solidago californica* Nutt. — $2n=9_{II}$ U.S.A. **California:** Alameda Co., *Solbrig* 2814 not seen (Raven et al 1960); Los Angeles Co., *Semple et al.* 5610 WAT (Semple 1985); Riverside Co., *Solbrig* 2772 NY (Raven et al. 1960); San Benito Co., *Semple et al.* 9346 WAT (Semple et al. 1992); San Benito Co., *Chasaki et al* 2814 DS (Raven et al. 1960); Santa Cruz Co., *Semple & B. Semple* 5671 WAT (Semple 1985); San Diego Co., *Solbrig* 2761 NY (Raven et al. 1960); San Luis Obispo Co. *McLeod & Keil* K10975 not seen (Keil and Pinkava 1979). — $2n=9_{II+}$ supernumeraries U.S.A. **California:** Lassen Co., *G. Morton & Anderson* 5035 not seen (Semple et al. 1984). — $2n=18$ U.S.A. **California:** Kern Co., *Semple et al.* 9365 WAT (Semple et al. 2001), *Semple & Chmielewski* 8947 WAT (Semple et al. 2001), *Semple & Heard* 8651 WAT (Semple et al. 1989); Lassen Co. *G. Morton & Anderson* 5037 WAT (Semple et al. 1984); Los Angeles Co., *Semple & B. Semple* 5614 WAT (Semple et al. 1984); Mariposa Co., *Morton & Venn* NA15817 TRT, *Morton & Venn* NA15823 TRT (Morton, Venn and Semple 2018); Plumas Co., *Semple et al.* 9303 and 9307 WAT (Semple et al. 2001); Riverside Co., *Semple & Chmielewski* 8980 WAT (Semple et al. 1989); San Benito Co., *Semple et al.* 9346-1 WAT (Semple et al. 2001); San Bernadino Co., *Morton & Venn* NA15840 TRT ((Morton, Venn and Semple 2018)); San Diego Co., *Semple & B. Semple* 5580 WAT (Semple et al. 1984); San Mateo Co., *Beaudry* 59-199 and 59-200 MT (Beaudry 1969); Shasta Co., *Semple et al.* 9698 WAT (Semple 1985), *Semple et al.* 9300 WAT (Semple et al. 2001); Siskiyou Co., *Semple & Heard* 8465 WAT (Semple, Chmielewski & Lane 1989), *Morton & Venn* NA15780 TRT, *Morton & Venn* NA15782 TRT and *Morton & Venn* NA15784 TRT ((Morton, Venn and Semple 2018)), *Semple & Heard* 8498 WAT (Semple, Chmielewski & Lane 1989); Sonoma Co., *Semple & Heard* 8578 WAT (Semple, Chmielewski & Lane 1989); Tuolumne Co., *Morton & Venn* NA15813 TRT (Morton, Venn and Semple 2018), *Semple & Heard* 8730 WAT (Semple, Chmielewski & Lane 1989); Ventura Co., *Morton & Venn* NA15855 TRT (Morton, Venn and Semple 2018). **Oregon:** Douglas Co., *Semple & Brouillet* 7141 WAT (Semple et al. 1984). — $2n=36$ U.S.A. **California:** Sonoma Co. *Morton & Venn* NA15800 TRT and *Morton & Venn* NA15809 TRT (Morton, Venn and Semple 2018)
- Solidago gattingeri* Chapm. ex A. Gray — $2n=18$ U.S.A. **Tennessee.** Rutherford Co., *De Selm* 59-240-1 MT (Beaudry 1969).
- Solidago mollis* Bartl. — $2n=18_{II}$ U.S.A. **Kansas:** Ford Co., *Semple & Brouillet* 7296 WAT and *Semple & Brouillet* 7304 WAT (Semple 1985). **Oklahoma:** Greer Co. *Semple & Heard* 8235 WAT (Semple, Chmielewski & Lane 1989, as $2n=9_{II}$; corrected in Semple and Cook 2004). **South Dakota:** Minnehaha Co., *Semple & Xiang* 10181 WAT (Semple et al. 1993). **Wyoming:** Crook Co., *Semple & Xiang* 10188 WAT (Semple et al. 2001). — $2n=36$ U.S.A. **South Dakota:** Haakon Co., *Semple & B. Semple* 6644 WAT (Semple et al. 1984). **Wyoming:** Crook Co., *Morton & Venn* NA15697 TRT ((Morton, Venn and Semple 2018)). — $2n=27_{II}$ U.S.A. **Colorado:** Kit Carson Co., *G. Morton* 4991 NY(2) (Anderson et al. 1974); Pueblo Co., *Anderson* 3132 BYU, NY (Semple et al. 1984). **Montana:** Rosebud Co., *Semple & Brouillet* 6984 WAT (Semple 1985). — $2n=54$ CANADA. Manitoba, *Löve & Löve* S3797 not seen (Löve & Löve 1982a). U.S.A. **Montana:** Fergus Co. published as Judith Basin Co., *Semple & B. Semple* 11395 WAT (Semple et al. 2019). **North Dakota:** Emmons Co., *Semple et al.* 6668 WAT (Semple et al. 1984). **South Dakota:** Shannon Co., *Morton & Venn* NA15686 TRT (Morton, Venn and Semple 2018).
- Solidago radula* Nutt. — $2n=18$ U.S.A. **Arkansas:** Perry Co., *Demaree* 59-260-1, -3 MT (Beaudry 1969); Pope Co., *Semple & Heard* 8296 WAT (Semple & Chmielewski 1987 as *S. ulmifolia*; corrected Semple et al. 2019); Pulaski Co., *Demaree* 63-49-1, -2, -3, -4, -5 MT (Beaudry 1969). **Louisiana:** Natchitoches Par., *Semple & Surlito* 10038 WAT (Semple et al. 1993); Winn Par., *Thomas & Kessler* 79082 WAT (Semple and Chmielewski 1987). **Missouri:** Iron Co., *Cook & Parks* 468 WAT and *Cook & Parks* 469 WAT (Semple, Cook and Owen 2015); Washington Co., *Semple et al.* 9388 WAT (Semple et al. 1993). **Tennessee:** Dekalb Co., *Demaree* 63-40-1, -2, -3, -4, -5 MT (Beaudry 1969). — $2n=36$ U.S.A. **Arkansas:** Stone Co., *Morton & Venn* NA16258 TRT (Morton, Venn and Semple 2018). **Texas:** Erath Co., *Semple & Chmielewski* 6461 WAT (Semple et al. 1984 as *S. mollis* var. *angustifolia*; corrected here). Kerr Co., *Morton & Venn* NA16362 TRT and *Morton & Venn* NA16364 TRT (Morton, Venn and Semple 2018)
- Solidago* aff. *radula* Nutt. — $2n=18$ U.S.A. **Texas:** Gonzales Co., *Semple & Brouillet* 3351 WAT (Semple et al. 2019).

Solidago velutina DC. (many published as either *S. sparsiflora* or *S. velutina* subsp. *sparsiflora*) — $2n=9_{II}$ MEXICO. **Coahuila:** Roberts & Keil 10420 not seen (Keil and Stuessy 1977). **Durango:** King 3762 US, TEX (Turner et al 1962). **Nuevo Leon:** Nesom et al. 7740 TEX (Zhao Zai- Ming 1996). **Zacatecas:** Ward 80-061 NMC (Ward and Spellenberg 1986). U.S.A. **Arizona:** Cochise Co., Ward & Peterson 83-027 NMC and Ward & Petersen 83-067 NMC (Ward and Spellenberg 1986); Coconino Co., *Solbrig* 2795 not seen (Raven et al. 1960), *Pinkava et al.* P13715 ASU (Keil et al. 1988), *Keil* 11738 ASU (Keil and Pinkava 1979), *Semple et al.* 5547 WAT (Semple 1985); Gila Co., *Semple & Heard* 7926 WAT (Semple and Chmielewski 1987); Navajo Co., *Lehto, Pinkava & Keil* 18956A ASU (Keil and Pinkava 1981); Santa Cruz Co., *Keil & Pinkava* K11029 ASU (Keil et al. 1988); Yavapai Co., *Keil* K11457 ASU (Keil et al. 1988). **Colorado:** Garfield Co., *G. Morton & Anderson* 5013 WAT (Semple et al. 1984), *Spellenberg & Soreng* 5798 NMC (Ward and Spellenberg 1986); Pitkin Co., *Spellenberg & Soreng* 5802 NMC (Ward and Spellenberg 1986); Mesa Co., *G. Morton & Anderson* 5014 NY (Anderson et al 1974). **New Mexico:** Grant Co., *Ward et al.* 80-013 NMC, *Ward* 80-023 NY, *Ward & Spellenberg* 80-045 NMC, *Ward & Spellenberg* 81-586 NMC, and *Ward & Spellenberg* 80-047 NMC (Ward and Spellenberg 1986); Hidalgo Co., *Spellenberg* 6312b NMC (Ward and Spellenberg 1986); McKinley Co., *Ward* 81-492 NMC (Ward and Spellenberg 1986); Otero Co., *Ward* 81-461 NMC, *Ward* 81-576 NMC (Ward and Spellenberg 1986); Lincoln Co. (as Otero Co.), *Ward & Spellenberg* 80-033 NMC (Ward and Spellenberg 1986); San Juan Co., *Ward* 83-083 NMC (Ward and Spellenberg 1986). **Nevada:** Clark Co., *Raven* 13705 not seen (Raven et al. 1960). **Utah:** Washington Co., *Semple & Heard* 7863 WAT (Semple et al. 1989). — $2n=18$ MEXICO. San Luis Potosi; *Ward et al.* 80-059 NMC and *Ward et al.* 80-060 NMC (Ward and Spellenberg 1986). U.S.A. **Arizona:** Apache Co., *Morton & Venn* NA15901 TRT (Morton, Venn and Semple 2018); Cochise Co., *Morton & Venn* s.n. TRT (Morton, Venn and Semple 2018); Coconino Co., *Morton & Venn* NA15868 TRT, *Morton & Venn* NA15871 TRT, *Morton & Venn* NA15874 TRT, *Morton & Venn* NA15878 TRT, *Morton & Venn* NA15879 TRT, and *Morton & Venn* NA15880 TRT (Morton, Venn and Semple 2018); Navajo Co., *Morton & Venn* NA15892 TRT, and *Morton & Venn* NA15897 TRT (Morton, Venn and Semple 2018); Yavapai Co., *Morton & Venn* s.n. TRT (Morton, Venn and Semple 2018). **Colorado:** *Semple & B. Semple* 6536 WAT (Semple et al. 1984). **New Mexico:** Bernalillo Co., *Semple et al.* 9382 WAT (Semple et al. 2001); Catron Co., *Semple & Heard* 8028 WAT (Semple and Chmielewski 1987) *Morton & Venn* NA15914 TRT, *Morton & Venn* NA15915 TRT, *Morton & Venn* NA15916 TRT, *Morton & Venn* NA15918 TRT and *Morton & Venn* NA15921 TRT (Morton, Venn and Semple 2018); Colfax Co. *Morton & Venn* NA15960 TRT (Morton, Venn and Semple 2018); Lincoln Co., *Semple & Heard* 8120 WAT, *Semple & Heard* 8121 WAT, and *Semple & Heard* 8142 WAT (Semple and Chmielewski 1987); Taos Co., *Morton & Venn* NA15957 TRT and *Morton & Venn* NA15958 TRT (Morton, Venn and Semple 2018). **Texas:** Culberson Co., *Semple & Heard* 8175 WAT and *Semple & Heard* 8180 WAT (Semple et al. 1992). **Utah:** Beaver Co., *Semple & B. Semple* 11270 WAT (Semple et al. 2019); Garfield Co., *Semple & Heard* 7846 WAT (Semple and Chmielewski 1987); Kane Co., *Semple & Heard* 7852 WAT (Semple and Chmielewski 1987); Utah Co., *Semple & Chmielewski* 8882 WAT (Semple et al. 1989). **Wyoming:** Fremont Co., *Semple & Zhang* 10418 WAT (Semple et al. 2001), *Morton & Venn* NA15713 TRT (Morton, Venn, and Semple 2018). — $2n=18_{II}$ U.S.A. **New Mexico:** Grant Co., *Ward et al.* 80-028 NMC (Ward and Spellenberg 1986); Lincoln Co., *Ward* 81-581 NMC and *Ward* 81-585a NMC (Ward and Spellenberg 1986). **Wyoming:** Johnson Co., *Anderson* 2710 BRY (Anderson et al'74). — $2n=36$ U.S.A. **Arizona:** Coconino Co., *Semple & Chmielewski* 9003 WAT (Semple et al. 1992), *Morton & Venn* NA15881 TRT (Morton, Venn and Semple 2018). **Colorado:** Garfield Co., *Semple & Zhang* 10445 WAT (Semple et al. 2001). **New Mexico:** Colfax Co., *Morton & Venn* NA15963 TRT (Morton, Venn and Semple 2018); San Miguel Co., *Morton & Venn* NA15953 TRT (Morton, Venn and Semple 2018); Santa Fe Co., *Morton & Venn* NA15944 TRT (Morton, Venn and Semple 2018). **Nevada:** White Pine Co., *Semple et al.* 5749 WAT (Semple et al. 1984). **Utah:** Garfield Co., *Semple & B. Semple* 11247 WAT (Semple et al. 2019); Salt Lake Co., *Semple et al.* 9241 WAT (Semple et al. 2001); Summit Co., *Semple & Chmielewski* 8886 WAT (Semple et al. 1989); Wasatch Co., *Semple & Chmielewski* 8876 WAT (Semple et al. 1989). **Wyoming:** Teton Co., *Semple & Zhang* 10437 WAT (Semple et al. 2001). — $2n=c.36$ U.S.A. **Utah:** Cache Co., *Morton & Venn* NA15722 TRT (Morton, Venn and Semple 2018). Place of original unknown: from seed, Oslo Bot. Garden, 1951, *J.K. Morton* s952 TRT (Morton, Venn and Semple 2018). — $2n=54$ U.S.A. **Colorado:** Gilpin Co., *Semple & B. Semple* 5806 WAT (Semple et al. 1984).

RESULTS AND DISCUSSION

Additional chromosome counts of $2n=18$ were determined from one individual of *Solidago gattingeri* and $2n=54$ from one individual of *S. radula* are reported here (Table 2). In total, 312 chromosome counts are known for individuals of *Solidago* subsect. *Radulae*. Only one diploid $2n=18$ has been sampled in *S. altiplanities* (Fig. 3, dot). Thirty-six diploid $2n=18$ and two tetraploid $2n=36$ individuals have been sampled in *S. californica* (Fig. 4, black dots for $2x$ and white squares with black outlines for $4x$). Only two diploids $2n=18$ from Tennessee have been sampled in *S. gattingeri* (Fig. 5, black dots for $2x$); no portion of the range west of the Mississippi has been sampled.

Table 2. Previously unpublished chromosome number determinations in *Solidago* sect. *Radulae* (vouchers in WAT).

Solidago gattingeri Chapm. ex A. Gray — $2n=18$ U.S.A. **Tennessee:** Rutherford Co., E of Murfreesboro, glade, Semple, Estes, Crabtree, Campbell, & Brock 11856 WAT.

Solidago radula Nutt. — $2n=18$ U.S.A. **Missouri:** Taney Co., Semple & Suario 9937 WAT. — $2n=54$ U.S.A. **Tennessee:** Cocke Co., S of Del Rio, TN-107 ca. 2 km S of US-25/70/TN-9, Cook & Family C-727 WAT (the identity of the transplanted rootstock was not confirmed to be the same as the voucher specimen because the transplant died before the count was made from stored and fixed root tips).

Eight tetraploid $2n=36$ and eight hexaploid $2n=54$ individuals of *Solidago mollis* have been sampled over much of the range of the species on the Great Plains (Fig. 6, white squares with black outlines for $4x$ and solid black squares for $6x$). Only hexaploids are known in the northern end of the range of *S. mollis* in Manitoba, North Dakota, and Montana, while only tetraploids are known from the southern end of the range in south-central Kansas and Oklahoma. Both ploidy levels occur in the central portion of the range. Much more sampling is needed to determine whether or not this pattern holds up.

Eleven diploid $2n=18$ individuals, four tetraploid $2n=36$ individuals, and one possible hexaploid $2n=54$ individual have been sampled over the range of *Solidago radula* (Fig. 7, dots for $2x$, white squares with black outlines for $4x$, solid black square for $6x$). The tetraploid samples from Texas could be treated as *S. radula* var. *laeta* (Greene) Fern., being similar to narrow leaved individuals of *S. mollis* but having leaves that are finely short scabrous (shark skin-like); these also have been treated as *Solidago mollis* Bartl. var. *angustata* Shinnars. The multivariate study of subsect. *Nemoralis* by Semple et al. (2018) included a comparison of specimens of *S. nana* (now in subg. *Nemorales*) and *S. mollis* and *S. radula* (now in subg. *Pleiactila* Raf. subsect. *Radulae*) with the two *S. radula* tetraploids from Kerr Co., Texas, the *S. radula* tetraploid from Arkansas, and one *S. radula* diploid from Iowa and cytologically unknown *S. radula* from Georgia being placed a posteriori into *S. mollis* with 54-68% probabilities based on similarities in leaf shape and floral part sizes; leaf indument traits were not included. Thus, some diploid and some tetraploid individuals of *S. radula* can be misidentified as *S. mollis* if indument traits are not emphasized. Further study on *S. radula* var. *laeta* in Texas is needed to justify recognizing the variety as more than just extremes at the end of a continuum in variation within *S. radula*.

Sixty-six diploid $2n=18$ individuals, eleven tetraploid $2n=36$ individuals, and one hexaploid $2n=54$ individual have been sampled over the range of *Solidago velutina* (Fig. 8, dots for $2x$, white squares with black outlines for $4x$, solid black square for $6x$). Diploids occur through the range of the species from Wyoming to central Mexico. Tetraploids occur in Wyoming, Utah, Colorado, Arizona, and New Mexico, but have not been reported from Mexico. One hexaploid has been reported from Gilpin Co., Colorado, in the foothills of the Front Range of the Rocky Mountains.

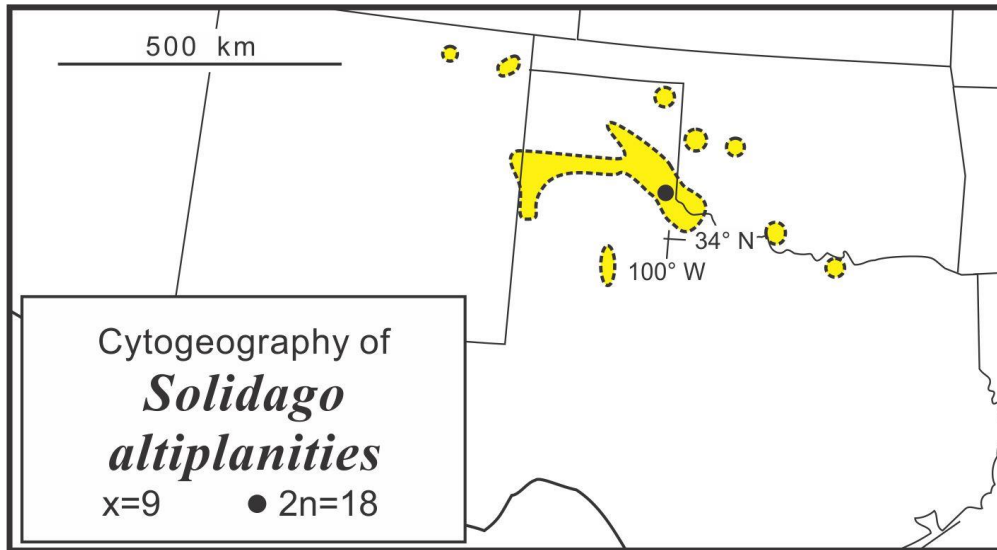


Figure 3. Cytogeography of *Solidago altiplanities*; range based on all collections seen and literature.

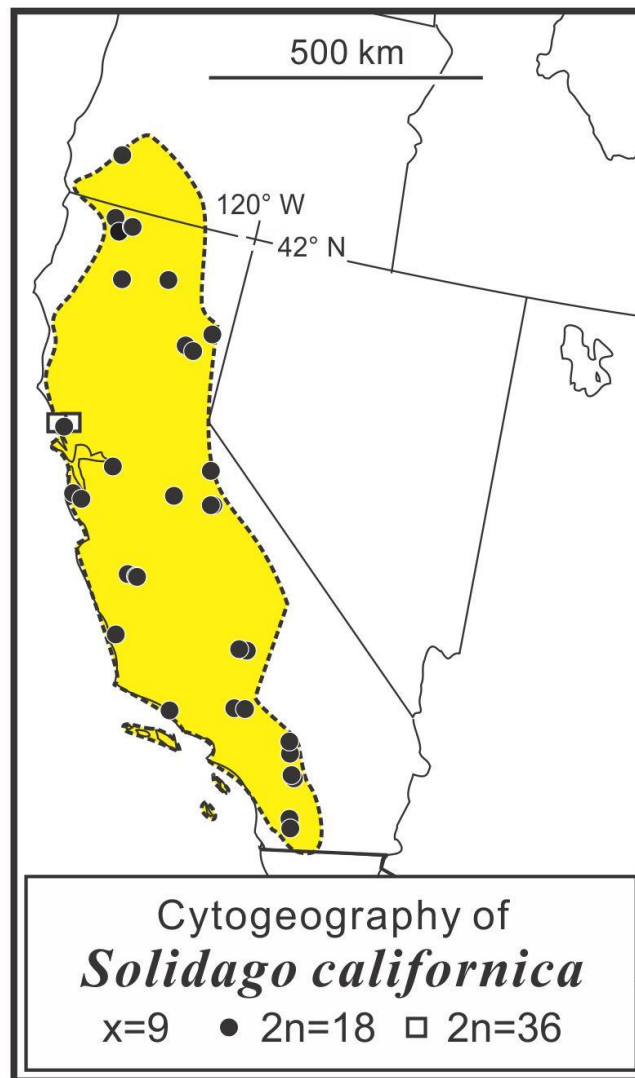


Figure 4. Cytogeography of *Solidago californica*. Range based on all collections seen and literature.

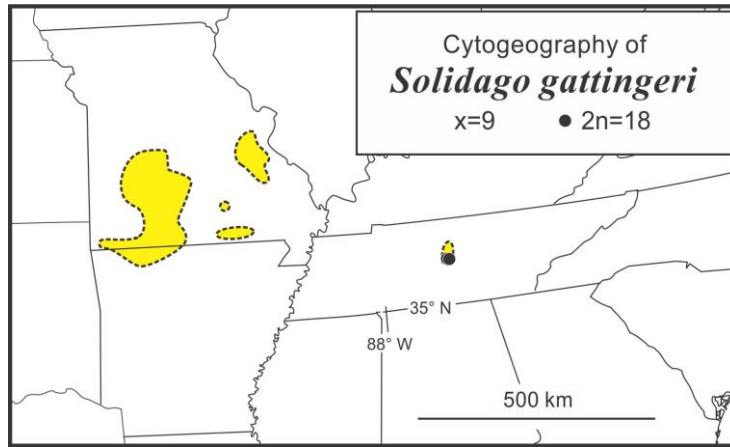


Figure 5. Cytogeography of *Solidago gattingeri*. Range based on all collections seen and literature.

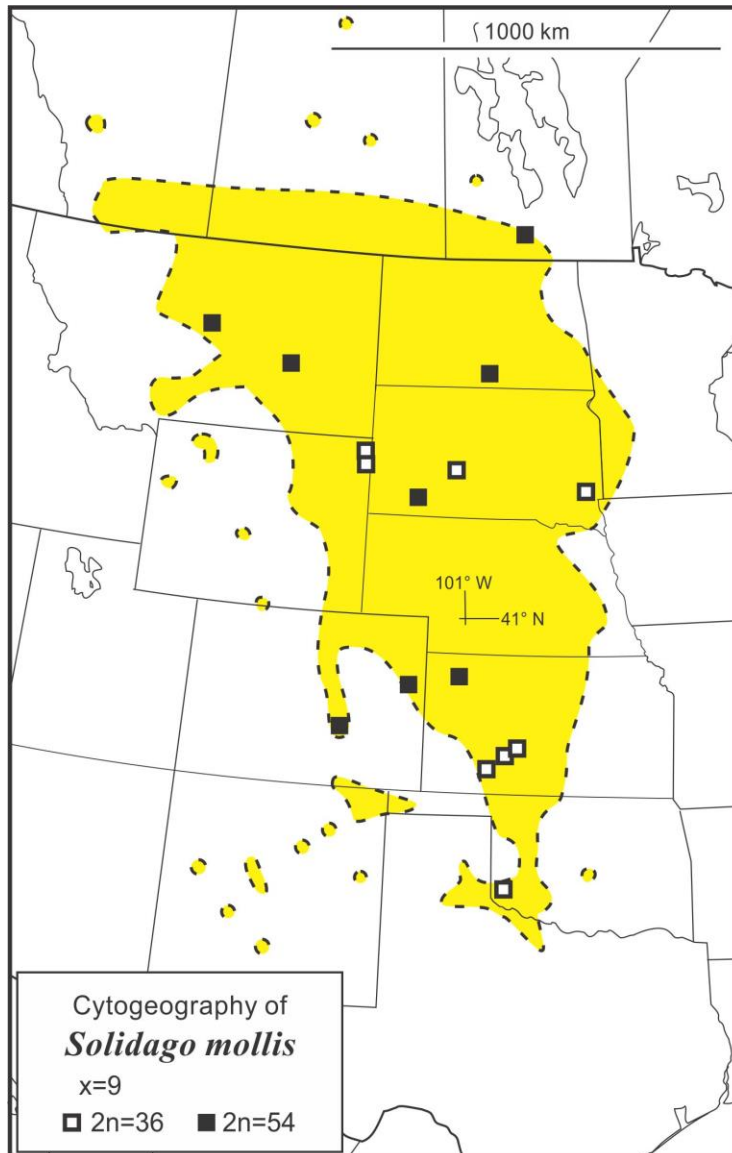


Figure 6. Cytogeography of *Solidago mollis*. Range based on all collections seen and literature.

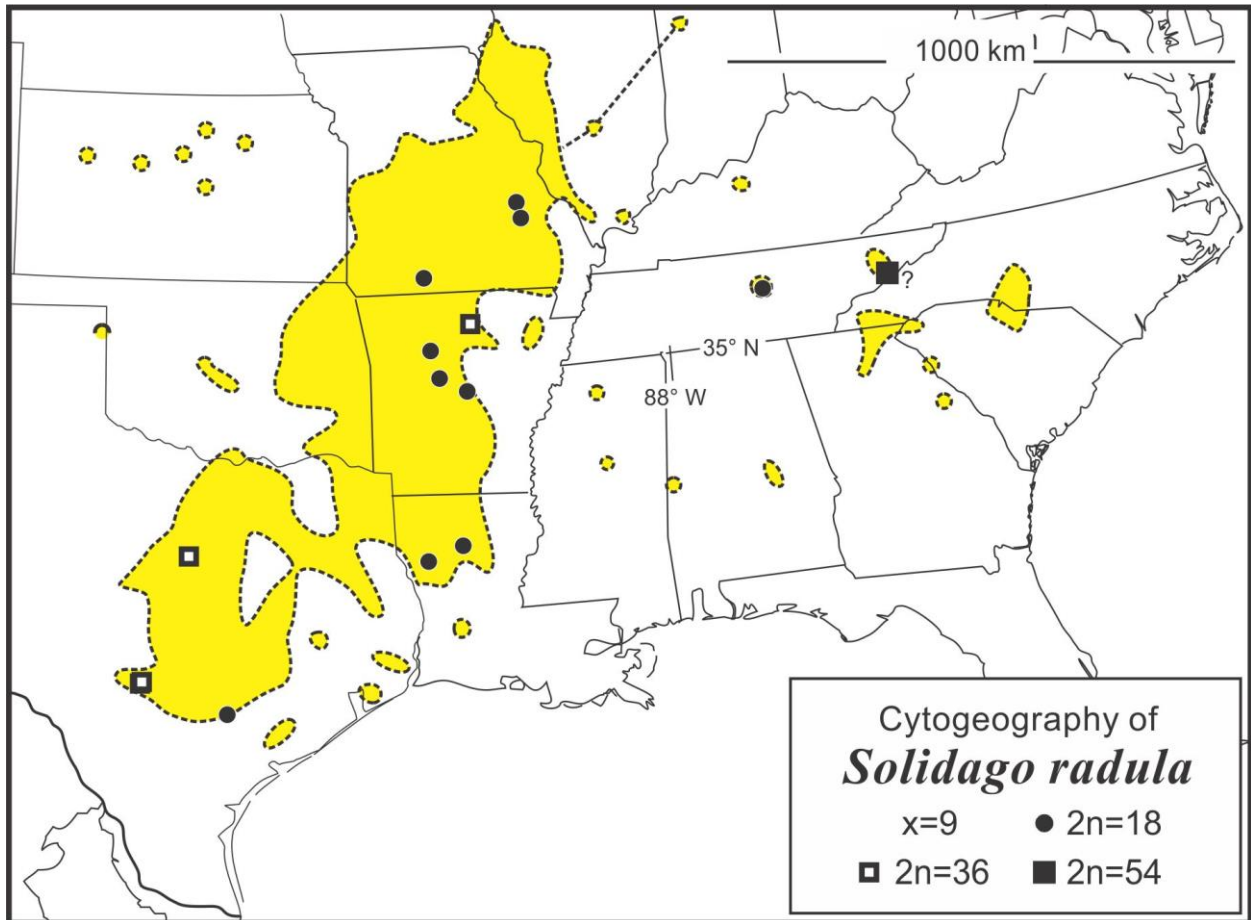


Figure 7. Cytogeography of *Solidago radula*. Range based on all collections seen and literature.

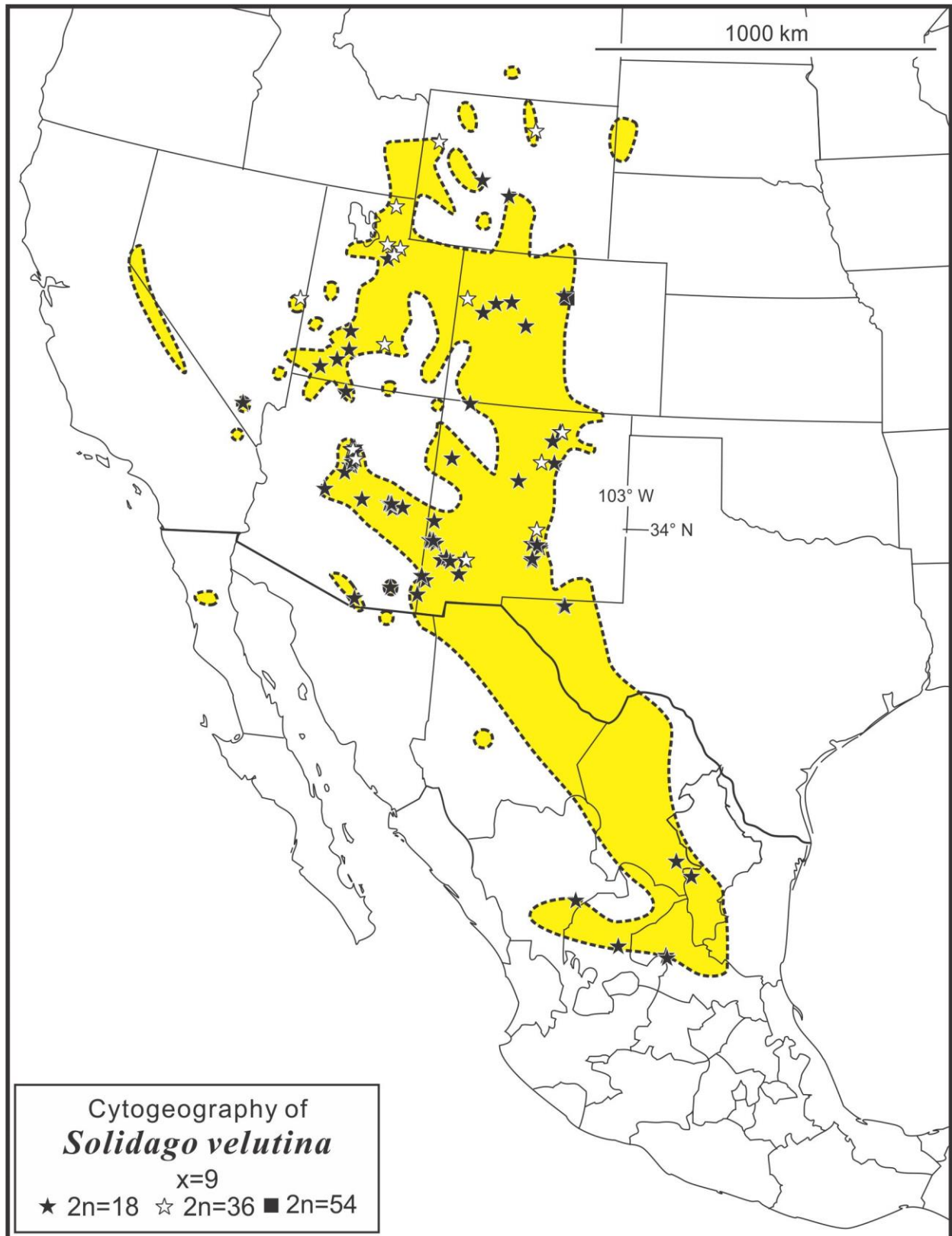


Figure 8. Cytogeography of *Solidago velutina*. The single hexaploid count is from north-central Colorado. Range based on all collections seen and literature.

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