AN INTUITIVE PHYLOGENY
AND SUMMARY OF CHROMOSOME NUMBER VARIATION
IN THE GOLDENROD GENUS *SOLIDAGO* (ASTERACEAE: ASTEREAE)

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ABSTRACT

An intuitive phylogeny of the goldenrod genus *Solidago* is presented. The diagram was developed over three decades as data from field observations, morphological analyses, cytology, and limited molecular studies were considered. Chromosome numbers were mapped onto the phylogeny and highlighted in various ways to show the frequencies of diploids, tetraploids, hexaploids, octoploids, nonaploids, decaploids, and duodecaploid reports. Diploid-only taxa are most frequent. High polyploid (10x-14x) individuals occur in only three species. Taxa including polypoid series are more frequent than taxa with one polypoid cytotype.

No rigorous molecular phylogeny of the goldenrod genus *Solidago* L. (Asteaceae: Astereae) has been published. The only existing phylogeny featuring broad taxonomic sampling is that of Zhang (1996), in which cpDNA restriction fragment length polymorphism data were used to reconstruct relationships among 41 *Solidago* taxa. While support for certain relationships was strong, much of the topology received modest support. One of the Zhang (1996) trees was published in Semple, Ringius, and Zhang (1999). Schilling et al. (2008) published the most recent molecular phylogeny of *Solidago* using nuclear ribosomal ITS and ETS sequence data from 21 goldenrod species and one interspecific hybrid. They reported limited interspecific sequence variation, with pairwise comparisons revealing "ITS sequence divergence of generally less than 1%, with total differences between samples of 1–10 bp." While the phylogenetic limits of the genus *Solidago* have been established by these studies, these data have done little to clarify relationships within the genus. Semple and Cook (2006) estimated the number of *Solidago* species to be ca. 100 with 77 occurring in Canada and the USA, while Semple (2016b, frequently updated) includes 120 species and 42 subspecies/varieties. This species richness and the lack of resolution provided by previous analyses highlight the need for a dataset featuring both enhanced taxonomic sampling and phylogenetic signal. With this in mind, a detailed working intuitive phylogeny is presented in an effort to provide hypotheses on evolutionary relationships.

The intuitive phylogeny of all *Solidago* species and varieties is presented in Figure 1. This is the culmination of more than four decades of work on the genus by members of my Astereae Lab and is based on (1) observations on more 20,000 *Solidago* collections, (2) field observations of more than 100 of the approximately 122 species combined with single or multi-season greenhouse observations on most of the species with known ploidy level(s), (3) chromosome number determinations from nearly 4500 individuals, (4) published and unpublished multivariate morphometric studies including nearly 3000 specimens representing all sections and subsections of the genus, (5) several unpublished cladistics studies conducted by undergraduates in the Semple Astereae Lab, (6) existing molecular phylogenies (Zhang 1996; Beck et al. 2004; Schilling et al. 2008; Peirson et al. 2013), (7) relationships indicated in Nesom (1993), and (8) numerous discussions with colleagues and students over four decades. Sixty-two Semple Astereae Lab publications that include data on *Solidago* are listed online (Semple 2016a frequently updated, goldenrods) and are not cited here separately; the

first was Brouillet and Semple (1981) and the most recent was Semple and Lopez Laphitz (2016). The intuitive phylogeny includes three species not yet described.

The phylogeny diagram has been in development for about three decades. It began in the early to mid 1980s as a large poster board with taxon names and known chromosome counts placed in a rough phylogenetic pattern. The purpose was primarily to highlight which taxa remained to be studied cytologically and also to provide a quick overview of the genus for students. The diagram was converted into a computer graphic in the early 1990s using an early version of CorelDraw^{TM} and included in Zhang (1996). Layers were added to the diagram to highlight cytological information (Figs. 2-4) and the names of the about forty students who worked on the genus over four decades. Additional taxa were added as new names were published and changes were made to the branching topology, indicating revised hypotheses of evolutionary relationships based on new information. For example, the inclusion of *Solidago glomerata* Michx. in subsect. *Glomeruliflorae* was adopted based on the position of this taxon in Zhang (1996); Cronquist (1980) had grouped it with *S. squarrosa* and *S. puberula* Nutt. and other species placed here in subsect. *Squarrosae*. Changes in the ranks of some taxa were based on other cytological and molecular studies, e.g., Peirson et al. (2012, 2013) on subsect. *Humiles*.

Research in support of the treatment of *Solidago* for Flora North America (Semple & Cook 2006) and the English language version of the Flora of China (Chen & Semple 2011) necessitated detailed examination of nearly all *Solidago* taxa and numerous multivariate studies incorporating 35-50 traits on large numbers of specimens. Early multivariate studies include Heard and Semple (1988) and Semple et al. (1990). More recent multivariate studies include Cook et al. (2009), Lopez Laphitz and Semple (2015), Semple et al. (2015), and Semple and Lopez Laphitz (2016). These detailed studies have led to insights into relationships among species within subsections. For example, the recent addition of multivariate data on *S. gypsophila* Nesom and *S. pringlei* Fern. (Semple & Lopez Laphitz 2016) resulted in multiple changes to the topology of subsect. *Triplinerviae*; the hypothesized relationships of much of the informal *Tortifoliae* group were changed to reflect the hypothesis that *S. pringlei* is likely basal or most similar to the ancestral species for the entire group. Also, the phylogenetic position of *S. altissima* L. was changed to reflect uncertainty about whether it belongs in the *Tortifoliae* group or the *Canadensae* group within the subsection. Traits of all the infrageneric groups were included in Semple and Cook (2006) and Lopez Laphitz and Semple (2015). Inflorescence shape and branching pattern, presence or absence of basal rosettes, size differences between lower and upper leaves, leaf shape and venation, numbers and sizes of leaf margin serrations and changes in these from lower to upper stem, and phyllary shape and venation are critical features of infrageneric taxa. Multivariate studies on all infrageneric groups in *Solidago* will be published as they are completed.

The Semple Astereae Lab *Solidago* chromosome number database currently includes reports for 4466 individuals; ploidy level determinations by flow cytometry are not included. More than 2000 of these were utilized in Semple (1992), a publication summarizing chromosome count data for *Solidago* taxa by provinces and states for Canada and the USA and including a long list of references not repeated here. Additionally, Watanabe (2016 frequently updated) includes a long list of published chromosome number reports for *Solidago* along with source publications. A significant number of counts included in the Semple Astereae Lab database have yet to be published, but efforts are underway to finalize and publish all cytogeographic studies. The following chromosome numbers are known in *Solidago*: $2n$=18, 27, 36, 45, 54, 72, 90, 108, and ca. 126. The Semple Lab database includes 2723 diploid counts ($2n$=9_{II}, $2n$=18; 60.9% of all counts), along with 1022 tetraploid counts ($2n$=18_{II}, $2n$=36; 22.8% of all counts), 637 hexaploid counts ($2n$=27_{II}, $2n$=54; 14.2% of all counts), one octoploid count ($2n$=72; and 23 flow cytometry ploidy level determinations), eight decaploid counts ($2n$=90), eight duodecaploid counts ($2n$=54_{II}, $2n$=108), and one 14x count ($2n$=ca.126). Also

included are three triploid counts (2*n*=27; 0.0672%) and two pentaploid counts (2*n*=45). The number of counts for a taxon ranges from 1-471 (*S. altissima* L.). No chromosome counts have been reported for the following ten species: *S. durangensis* Nesom, *S. gypsophila* Nesom, *S. hintoniorum* Nesom, *S. orientalis* (Nesom) Nesom, S. *paniculata* DC., and *S. pringlei* from Mexico; *S. pacifica* Juz. from eastern Asia; *S. argentinensis* Lopez Laph. & Semple from South America; and *S. buckleyi* Torr. & A. Gray and *S. capulinensi*s Cockerell & Andrews from the USA.

The chromosomal base number of *Solidago* is *x*=9 (Semple and Cook 2006), and Figures 2-4 summarize chromosome number variation in the context of the intuitive phylogeny. Diploids-only species are most common (Fig. 2) with 79 taxa, although this includes several dozen taxa with only 1-4 individuals sampled. Taxa exhibiting a single polyploid cytotype are rare (Fig. 3); including 11 tetraploid taxa, four hexaploid taxa, and one octoploid taxon (*S. vossii* Pringle & Loreto). There are two decaploid-only taxa (Fig. 3): *S. faucibus* Weibolt and *S. lancifolia* (Torr. & Gray) Chapm. *Solidago glomerata* is the only known duodecaploid or higher (12x-14x) taxon (Fig. 3). There are 35 taxa with more than one ploidy level reported (Fig. 4); 19 with 2*x* and 4*x*; 11 with 2*x*, 4*x,* and 6*x*; and five with 4*x* and 6*x*. *Solidago* subsect. *Triplinerviae* exhibits both the largest number of taxa and the most number of multiple ploidy level taxa: *S. altissima* (471 counts), *S. gigantea* Ait. (426 counts), *S. canadensis* L. in the narrowest sense (261 counts), and *S. lepida* DC. (246 counts). Additional taxa with extensive numbers of counts include *S. nemoralis* Ait. (320 counts) in subsect. *Nemorales* and *S. rugosa* Mill. (252 counts) in subsect. *Venosae*. All of these species have been the subjects of long-term cytogeographic studies.

Several patterns emerge from mapping counts onto the intuitive phylogeny. No section or subsection of *Solidago* is only diploid or only polyploid. *Solidago* ser. *Odora* (Mackenzie in Small) Semple, *S.* ser. *Brachychaeta* (Torr. & Gray) Nesom, and *S.* ser. *Auriculatae* Semple are only known at the diploid level with multiple reports for each. Only subsect. *Thrysiflorae* comprises only diploids with one exception; two reports of tetraploids in *S. petiolaris* from Florida were in error (Semple and Cook 2004) and a third report from North Carolina has a correctly identified voucher (Semple et al. 1992). However, four of the nine taxa in subsect. *Thyrsiflorae* have no cytological data reported. All but three of the 18 taxon in subsect. *Squarrosae* are only diploid: *S. speciosa* Nutt. includes 2x and 4x individuals, *S. sciaphila* is 4x only, and the very rare *S. porteri* Small is the only 6x taxon in the subsection. All Eurasian taxa of subsect. *Solidago* are diploid, while the North American members *Multiradiatae* group include 2x and 4x or are exclusively polyploid. The taxa exhibiting the highest ploidy levels occur in only two subsections: one species in subsect. *Argutae* (Weiboldt & Semple 2003) and two species in subsect. *Glomeruliflorae* (Cook & Semple 2008). Taxa with multiple polyploid levels are more frequent (30) than taxa with a single known polyploid level (18). *Solidago* subsect. *Triplinerviae* includes the most taxa with multiple ploidy levels, which in part explains the taxonomic difficulties encountered in this group of species. It is also more intensively sampled than any other subsection, which may also account for its known cytological complexity. Finally, taxa of putative allopolyploid origin appear to be rare. The genus *Solidago* includes a large amount of morphological and cytological variation but surprisingly low levels of DNA sequence variation. This suggests relatively recent morphological and cytological divergence over a relatively short time.

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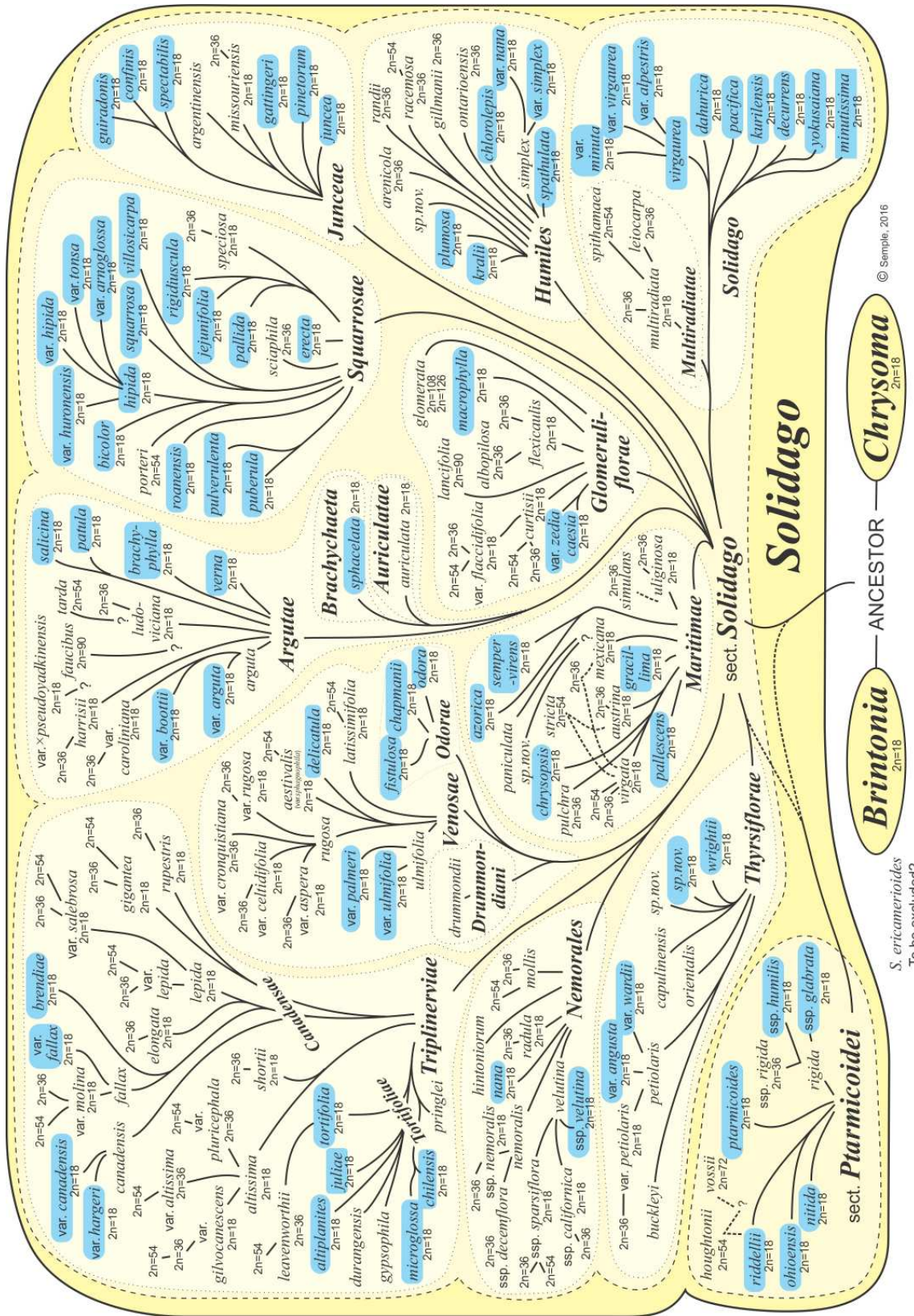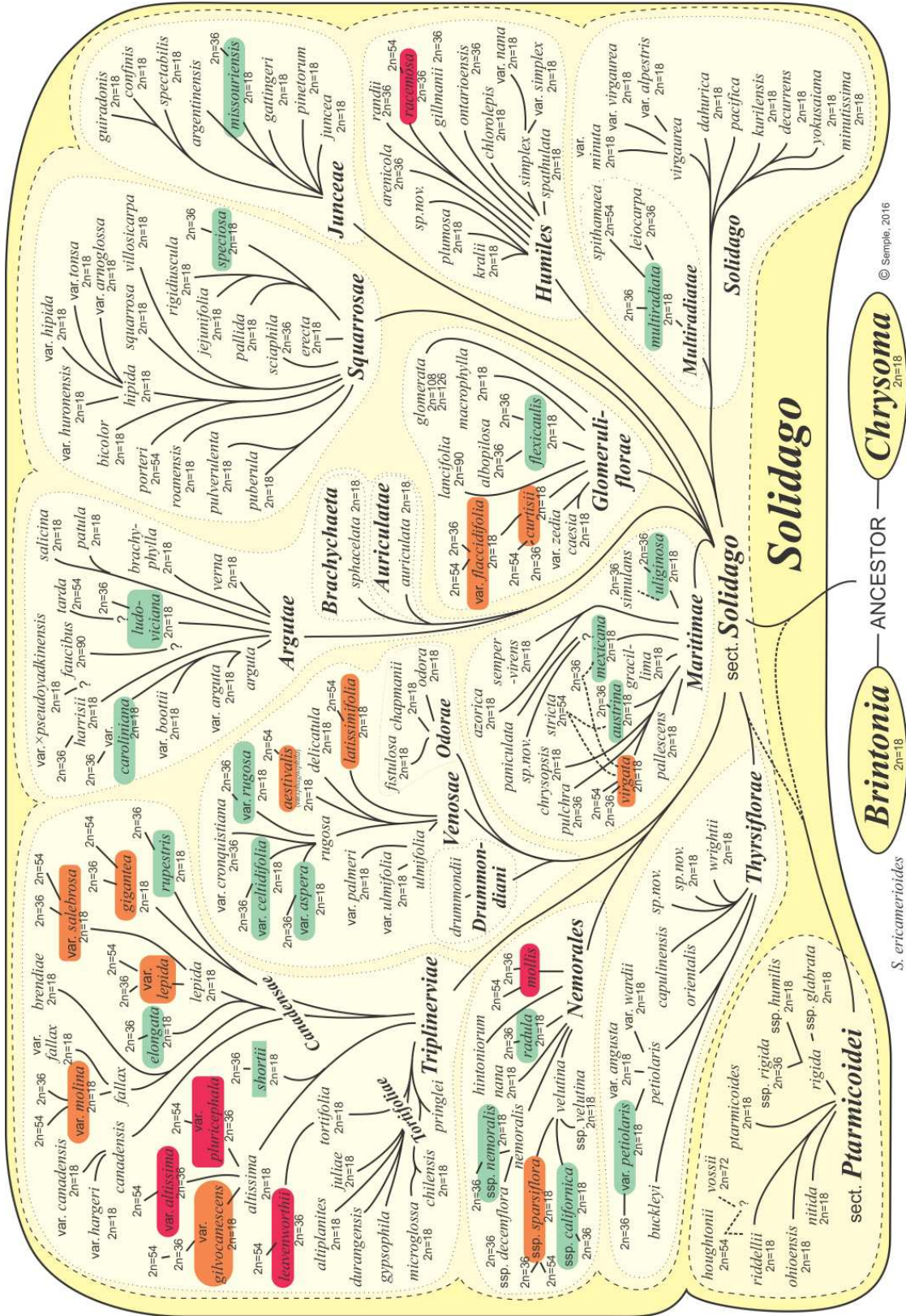
Figure 1. Intuitive phylogeny of the goldenrod genus *Solidago*.

Figure 2. *Solidago* taxa known only at the diploid 2*n*=18 ploidy level.

Figure 3. *Solidago* taxa known only at the tetraploid (green), hexaploid (orange), octoploid (red), decaploid (pink), or duodecaploid or higher (purple) ploidy levels.

Figure 4. *Solidago* taxa known at the two or more ploidy levels: 2*x* and 4*x* (green); 2*x*, 4*x* and 6*x* (orange); 4*x* and 6*x* (red).