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A REVISED INTUITIVE PHYLOGENY OF *SOLIDAGO* (ASTERACEAE: ASTEREAE) BASED ON A PHYLOGENOMIC STUDY OF DIPLOIDS

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ABSTRACT

A revised intuitive phylogeny of *Solidago* was constructed using the results of a phylogeny of diploids published by Semple et al. (2023) overlaid with additional diploid taxa, taxa for which ploidy level is unknown, and polyploid taxa placed on the basis of morphology. This represents a substantial change to a previously published intuitive phylogeny (Semple 2016).

Semple (2016) presented an intuitive phylogeny of all species of *Solidago* based on morphological traits and the results of a cpDNA restriction fragment length polymorphisms study (Zhang 1996). The classification scheme of *Solidago* presented by Nesom (1993) was a critical guide in developing the 2016 intuitive phylogeny, along with modifications presented in the Flora of North America treatment of the genus (Semple and Cook 2006). Semple and Beck (2021) presented a radically revised classification of *Solidago* based on the at-the-time unpublished phylogenomic study of the genus, which included only diploid taxa and was inferred from 854 nuclear loci (Semple et al. 2023). The majority of the clades were strongly supported by Astral bootstrap analysis: 88/155 nodes (57%) received ≥95% bootstrap support.

Defining morphological traits for the subgenera, sections, and subsections were listed by Semple and Beck (2021). The 2021 classification scheme recognized many of the species groupings (section and subsection levels) found in Nesom (1993), but the subgenus level groups were radically different and all strongly supported. Semple et al. (2023) included only diploid samples in their phylogeny and these species are indicated in boldface in Figures 1 and 2. Although 47 polyploid and ploidy-level-unknown species were not included in Semple et al. (2023), the majority of these taxa have been placed with considerable confidence into sections, subsections, and series in the intuitive phylogeny presented here (Fig. 1). Semple and Beck (2021) listed nearly all of these taxa in their classification of *Solidago*. Placement of these 47 species plus multiple varieties is based on comparative morphology and is typically consistent with decisions reached in previous treatments (e.g. Fernald 1950; Cronquist 1980, 1994). More fine-scale relationships within a section or subsection are thus in part speculative and will require additional molecular phylogenetic study.

Semple and Beck (2021) recognized four subgenera in *Solidago* with *Chrysoma pauciflosculosa* (Mich.) Greene as the sister taxon (Semple et al. 2023). Within *Solidago*, subg. *Triactis* Raf. was the earliest-diverging lineage and included two sections. The semi-woody *S. ericamerioides* Nesom was the only species in sect. *Suffrutescentes* Semple & Beck and the herbaceous perennial sect. *Odorae* (Mack.) Semple & Beck included two diploid species, *S. odora* Ait. and *S. chapmanii* A. Gray. Subg. *Nemorales* (Mack.) Semple & Beck formed a clade sister to the remainder of *Solidago* and included *S. nemoralis* Ait., *S. nana* Nutt., and *S. decemflora* DC.

All other species in the genus were placed into two large subgeneric level clades; subg. *Solidago*, which included six very strongly supported sections and subg. *Pleiactila* Raf., which included eight weakly to strongly supported sections. Within subg. *Solidago*, sect. *Solidago* included one eastern North America species (*S. macrophylla* Banks ex Pursh) combined with all Eurasian *Solidago* taxa, including the type species *S. virgaurea* L. Subg. *Solidago* also included five North American clades: three monotypic sections — sect. *Villosicarpae* Semple & Beck, sect. *Squarrosae* (A. Gray) Semple & Beck, and sect. *Brintonia* (Greene) Semple & Beck — a large sect. *Erectae* G. Don (27 species), and a small sect. *Thyrsiflorae* (A. Gray) Semple & Beck (7 species). The monotypic sect. *Brintonia* included the rayless *S. discoidea* (Ell.) Torr. & Gray, which has previously been treated as separate genus *Brintonia* (e.g., Semple and Cook 2006).

Subg. *Pleiactila* includes 82 species native to North and South America and is the most varied in terms of inflorescence branching patterns, leaf features, and ploidy levels. Sect. *Ptarmicoidei* (House) Semple & Gandhi was sister to the remainder of subg. *Pleiactila*. Nesom (1993) treated this group of species as the genus *Oligoneuron* Small, while Semple and Cook (2006) treated it as *Solidago* sect. *Ptarmicoidei*. Retaining *Oligoneuron* as a separate genus would require subdividing *Solidago* into a number of segregate genera, each of which would be difficult to define morphologically. Sect. *Glomeruliflorae* Torr. & Gray includes species with leafy terminal inflorescences with short branches and ploidy levels from 2*x* (2n=18) to 10*x* (2*n*=90) and 12x (2*n*=108, 126). Sect. *Multiradiatae* (Semple) Semple & Beck includes three species with somewhat flat-topped inflorescences. Sect. *Maritimae* (Torr. & Gray) Semple & Beck, sect. *Venosae* (G. Don) Semple & Beck, and sect. *Unilaterales* G. Don all have secund conical inflorescences that differ in branching pattern. One or more species in sections other than sect. *Ptarmicoidei* have phyllaries with multiple veins (the oligoneurate condition).

In some cases, large-scale differences between the intuitive diagram of Semple (2016) and our revised diagram (Fig. 1) are indicated by green lines (Fig. 2). For example in Semple (2016), subsect. *Nemorales* includes species placed here in both subg. *Nemorales* and subg. *Pleiactila* sect. *Unilaterales* G. Don subsect. *Radulae* (Rydb.) Semple & Beck. Semple (2016) recognized a large subsect. *Squarrosae* A. Gray, which is reduced here to the monotypic sect. *Squarrosae*, and nearly all remaining species are now included in sect. *Erectae*. Species with somewhat to obviously resinous stems, leaves, and phyllaries included in subsect. *Humiles* (Rydb.) Semple (in Semple 2016) are split between a smaller subsect. *Humiles* and subsect. *Erectae* (G. Don) Semple & Beck that tentatively includes *Solidago ayuhwasi* Brock & Estes and *S. racemosa* Greene. Thus, the resinous phyllaries trait is found in two subsections.

Lower stem leaves are trinervate with a prominent midvein and two prominent lateral veins in sect. *Unilaterales*. Three of the four subsections in sect. *Unilaterales* were strongly supported. Subsect. *Serotinae* (Rydb.) Semple & Beck included the North American *Solidago gigantea* Ait. and two South American species *S. chilensis* Meyen and *S. microglossa* DC. — no obvious morphological feature unites these three species. None of the five narrow endemic Mexican species of unknown ploidy level were included in the phylogenomic study and these were assumed by Semple and Beck (2021) to be closely related to *S. tortifolia* Ell. and *S. juliae* Nesom of subsect. *Triplinervae*. These had been assumed to be closely related to *S. chilensis* and *S. microglossa* previously (e.g., Lopez Laphitz and Semple 2015). Therefore, it is with significant uncertainty that the five Mexican species (*S. pringlei* Fern., *S. macvaughii* Nesom, *S. durangensis* Nesom, *S. gypsophila* Nesom, and *S. veracruzensis* Semple) and the North American polyploid *S. leavenworthii* Torr. & Gray are included in ser. *Tortifoliae* Semple & Beck of sect. *Triplinervae*. Lastly, all the species that have been previously treated at one time or another as part of *Solidago canadensis* are included in ser. *Canadenses* Semple & Beck as separate species. A much larger sample size of each of these taxa, along with an expanded sequence dataset, are needed to determine which of the species of ser. *Canadenses* listed here are monophyletic.

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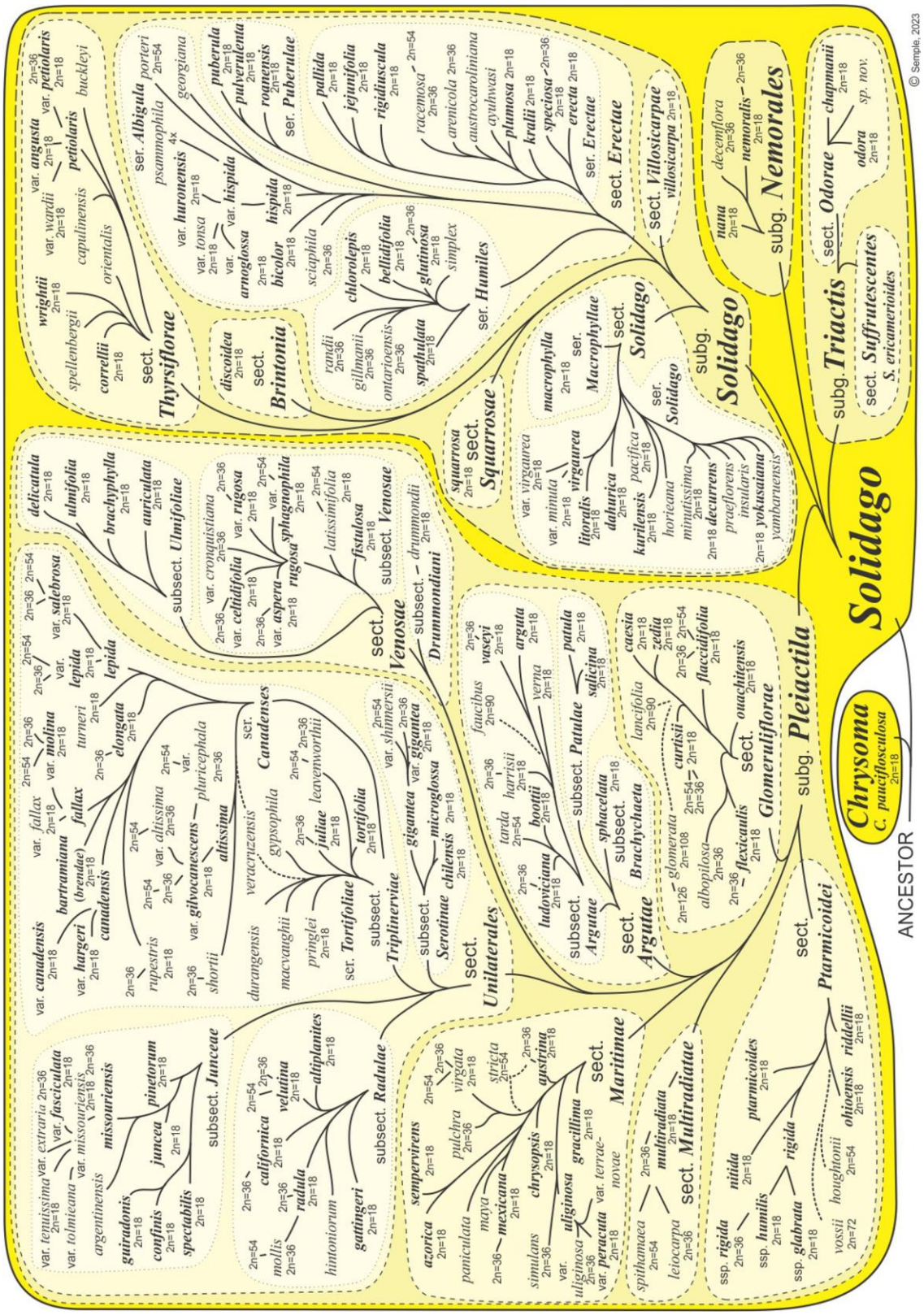

Figure 1. Revised intuitive phylogeny of *Solidago* based on a polygenomic phylogeny of diploids (Semple et al. 2023). Boldface names of taxa were included in the published phylogeny; the placements of remaining taxa are based on comparative morphology.

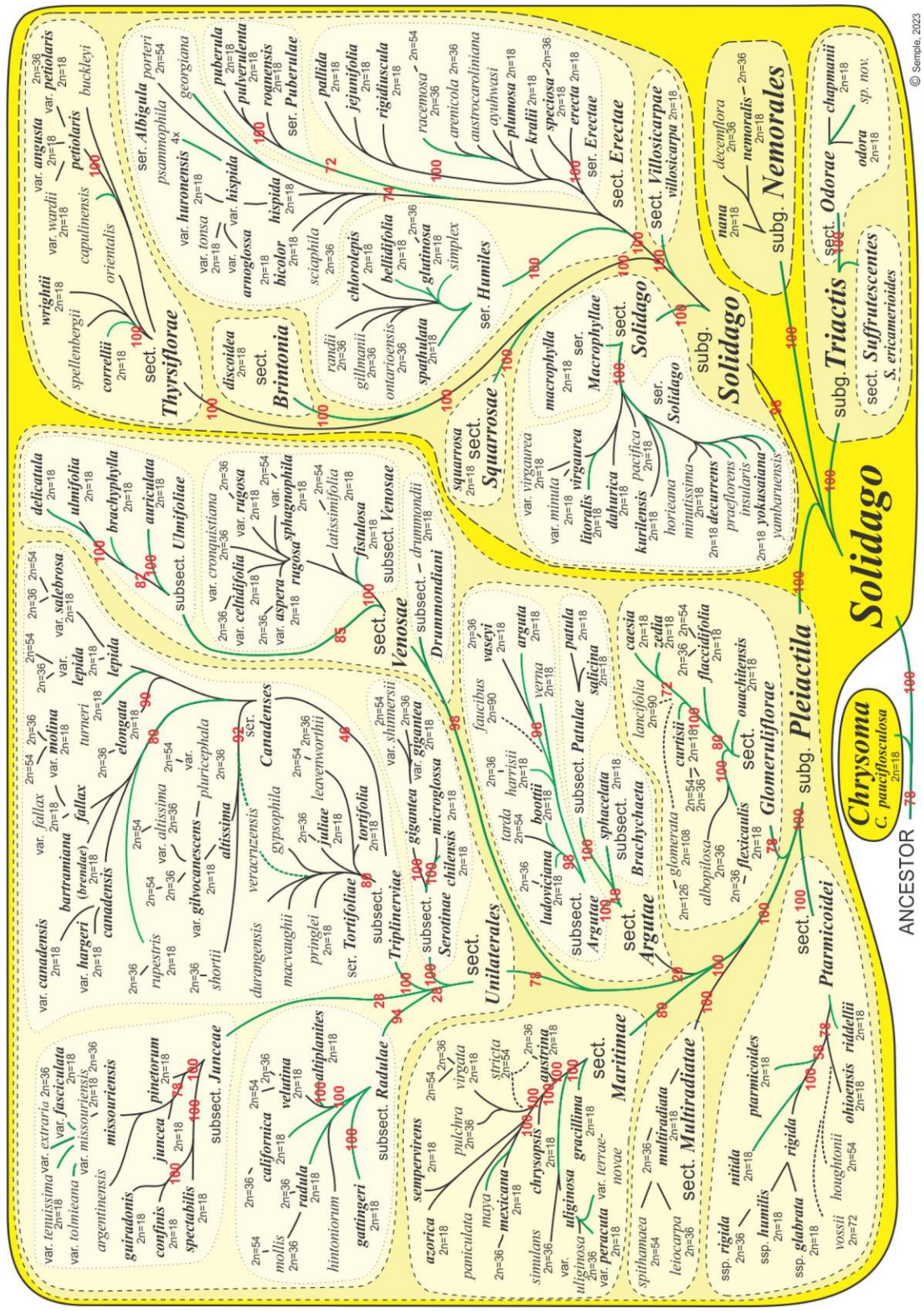

Figure 2. Revised intuitive phylogeny of *Solidago* based on a polygenomic phylogeny of diploids (Semple et al. 2023; boldface text here). Green lines indicate changes resulting from the phylogenomic study and other work. Red numbers indicate Astral bootstrap values (Semple et al. 2023).