# A MULTIVARIATE MORPHOMETRIC ANALYSIS OF SOLIDAGO SUBSECT. THYRSIFLORAE (ASTERACEAE: ASTEREAE)

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#### **ABSTRACT**

A multivariate morphometric study of the goldenrod group *Solidago* subsect. *Thyrsiflorae* was conducted to assess the morphological differences among *Solidago buckleyi*, *S. capulinensis*, *S. correllii*, *S. orentialis*, *S. petiolaris*, *S. spellenbergii* and *S. wrightii*, and to compare the varieties within *S. petiolaris* and *S. wrightii*. Analyses of a matrix of 150 specimens by 39 traits provided significant support recognizing 7 species as well as for recognizing var. *angusta*, var. *petiolaris*, and var *wardii* in *S. petiolaris*. Varieties within *S. wrightii* were not recognized because the putative differences were based on continua of variation in phyllary gland and hair densities with no non-arbitrary way to split samples between densely glandular/non-hairy and non-glandular/densely hairy forms.

Solidago subsect. Thyrsiflorae includes 3-7 species depending upon the taxonomic treatment (Nesom 1989, 1990, 2008; Semple & Cook, 2006; Nesom & Lowrey 2011; Semple 2017 a, b; Semple 2017 frequently updated): S. buckleyi Torr. & A. Gray, S. capulinensis Cockerell & Andrews, S. correllii Semple, S. orientalis (Nesom) Nesom, S. petiolaris Ait., S. spellenbergii Semple, and S. wrightii A. Gray.

- \* **Solidago buckleyi** is generally distinguished by its large lower and mid stem leaves that are oblanceolate acuminate and obviously serrate (Figs. 1-2).
- \* Solidago capulinensis (Figs. 3-4) has generally not been recognized as a distinct species and was not included in Flora North America by Semple and Cook (2006). Nesom and Lowrey (2011) presented reasons for recognized the species.
- \* **Solidago correllii** is similar to both *S. petiolaris* and *S. wrightii* but differs in having often persistent lower stem leaves and rarely basal rosettes present at flowering (see Figs 1-4 in Semple 2017a). The lower stem leaves are narrowly oblanceolate tapering to a long petiole. Leaves can be rather silvery green when dried. Ovaries/fruit bodies are sparsely to moderately strigose. *Solidago correllii* was treated as *S. wrightii* var. *guadalupensis* Nesom by Nesom (2008) but was raised to species level and given a new name and type.
- \* **Solidago orientalis** is distinquished by it serrate stem leaves (Figs. 5-6). Nesom (1989) first described the taxon as *S. wrightii* var. *orientalis* Nesom but soon raised the taxon to species rank (Nesom 1990).
- \* Solidago petiolaris is distinguished by its stem leaves with very short (1-3 mm) petioles and the branching pattern of its infloresences. The species includes three sometime difficult to distinguish varieties that differ in leaf shape and indument traits and phyllary indument traits (Figs. 7-9). The var. petiolaris has broadly lanceolate-elliptic to ovate-elliptic usually entire leaves and has phyllaries that are non-glandular to very sparsely glandular and that are sparsely to densely strigose. The var. angusta (Torr. & A. Gray) A. Gray (Figs. 8-9) was first described as S. angusta Torr. & A. Gray (1842) defined as the name suggests by its narrow lanceolate leaves and later by its sparsely glandular resinous and not hairy phyllaries. The var. wardii (Britt.) Fern. was first described as S. wardii Britt.



Figure 1. Solidago buckleyi, Palmer 31571a (NY) Mine la Motte, Madison Co., Missouri.

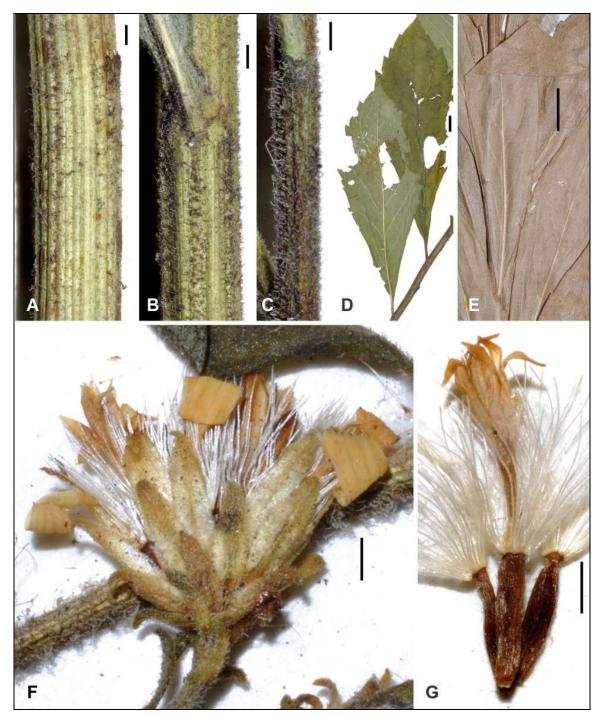


Figure 2. Details of morphology of *Solidago buckleyi*. **A-C.** Lower, mid and upper stem in inflorescence, *Keener 4013* (WAT). **D.** Lower stem leaves, *Semple & Suripto 9936* (WAT). **E.** Mid stem leaves, *Letterman* s.n. (NY). F. Pressed head, Brant et al. 753 (WAT). H. Disc floret cypselae, Eggleston 5397 (NY). Scale bars = 1 mm in A-C, and F-G; = 1 cm in D-E.



Figure 3. Solidago capulinensis, Lowrey 2190C (UNM unmounted) from Mt. Capulin Nat. Monument, Union Co., New Mexico.



Figure 4. Details of morphology of Solidago capulinensis: Lowrey 2190-B, -C, - E, -F and -4 (UNM unmounted). A. Basal of stem with new developing lateral shoots. B. Mid stem. C. Lower stem leaf. D. Mid stem leaves. E. Mid stem leaf, mid vein, abaxial surface. F. Heads. G. Disc floret cypselae. Scale bars = 1 mm in B, E, F-G; = 1 cm in A, C-D.

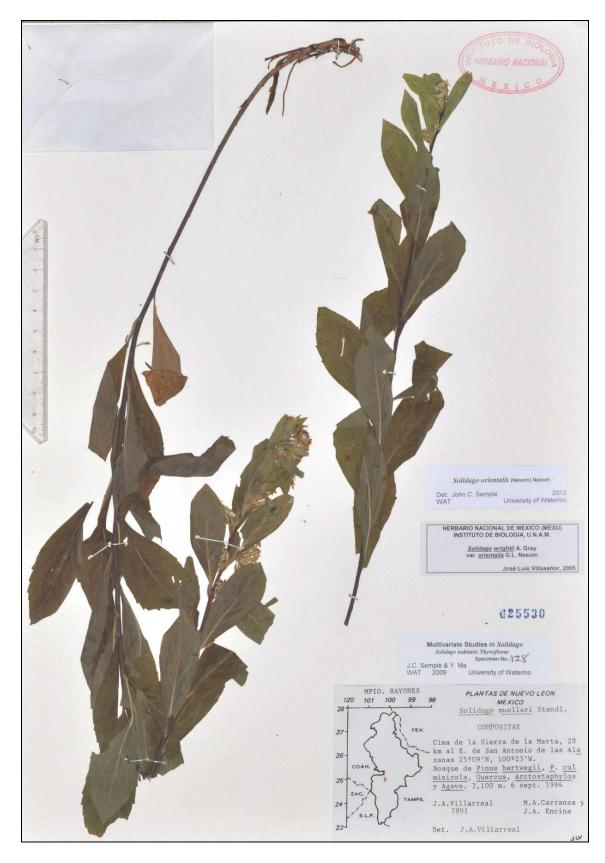


Figure 5. Solidago orientalis, Villarreal 7891 (MEXU), Cima de la Sierra de la Marta, Nuevo Leon, Mexico.

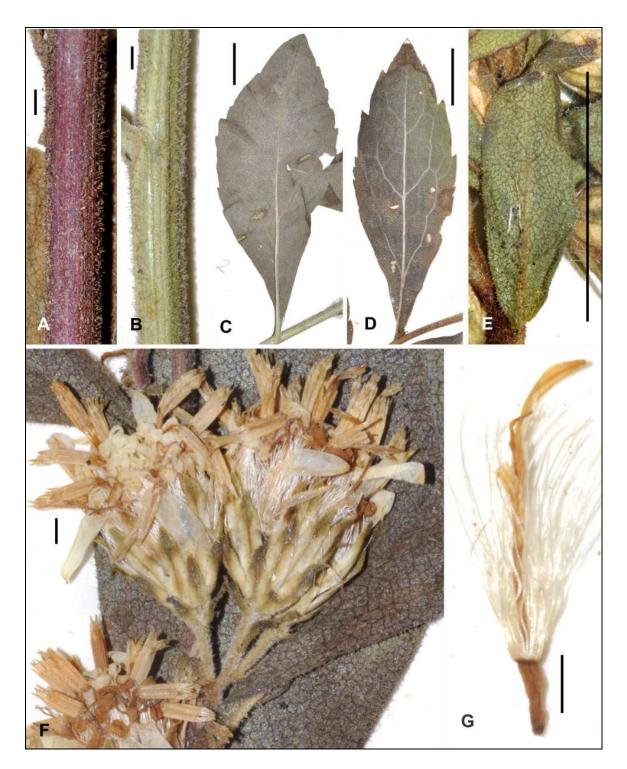


Figure 6. Details of morphology of Solidago orientalis: A-B. Mid stems; Villarreal 7891 (MEXU) and Hinton et al. 27489 (TEX). C-D. Mid stem leaves; Hinton et al. 27489 (TEX) and Hinton et al. 18613 (TEX). E. Peduncle bract; McDonald & Mayfield 2560 (MEXU). F. Heads; Hinton et al. 21617 (TEX). G. Ray floret cypsela and post flowering ray floret corolla, immature; Hinton et al. 18613 (TEX). Scale bars = 1 mm in A-B, F-G; = 1 cm in C-E.

and was defined by its lanceolate to broadly lanceolate leaves that are glabrous to sparsely strigose and phyllaries that are sparsely to densely strigose (Figs. 8-9). Application of the varietal names has varied in different floras or were not recognized. Britton (1901) keyed green leaved plants to S. petiolaris and silver leaved plants to S. wardii, but some of the silver leaved plants have more broadly lanceolate to ovate mid and upper stem leaves (Figs. 8F, 8I); such plants occur in the western Ozark Mts, and Ouachita Mts. in southwestern Missouri, western Arkansas, eastern Oklahoma and adjacent Texas. Fernald (1908) in making the combination var. wardii stated that these differed from typical S. petiolaris in having "firmer more glutinous and therefore more lustrous foliage." Nesom (1990) noted that the definition of var. angusta had shifted over time to define the taxon as having leaves that were "strongly glutinous, shiny, the lower surfaces glabrous or merely scabrous-hispidulous along the midrib and main veins" and involucres that were "granular glandular to glabrous" while var. petiolaris had leaves that were "scarely glutinous, not shiny, the lower surfaces densely spreading hairy to softly puberulent" and involuces "puberulent (often viscidulous) to occasionally glabrous. Nesom (1990) concluded that S. wardii should be treated as a synonym of S. petiolaris. Semple and Cook (2006) did not recognize varieties within S. petiolaris in the treatment of the species in Flora North America and listed the following as synonyms: Aster lindheimeranus (Scheele) Kuntze; A. petiolaris (Aiton) Kuntze; Solidago angusta Torrey & A. Gray; S. harperi Mackenzie ex Small; S. lindheimeriana Scheele; S. milleriana Mackenzie ex Small; S. petiolaris var. angusta (Torrey & A. Gray) A. Gray; S. petiolaris var. squarrulosa Torrey & A. Gray; S. petiolaris var. wardii (Britton) Fernald; S. squarrulosa (Torrey & A. Gray) Alph. Wood; S. wardii Britton. Yatskievych (2006) presented a useful summary of the problem of intergrading traits in his edition of the Flora of Missouri. Nesom (2008) discussed differences between the varieties and applications of the names and included maps showing differences in distribution of morphotypes. He applied the name var. angusta to plants with phyllaries that have slightly raised glands and no hairs (Figs. 9 C-E) regardless of whether the leaves are narrowly or broadly lanceolate to narrowly ovate (Figs. 8 F-I). Such plants occur from Missouri through Arkansas to Louisiana and west from southeastern Kansas to Texas and disjunct in northern Coahuila, Mexico. Phyllaries of var. wardii are obviously hairy (Fig. 9 H).

- \* Solidago spellenbergii is distinguished from S. wrightii by having longer lanceolate leaves than typically found in the latter and ovaries/fruit bodies that are nearly glabrous (see Figs 1-3 in Semple 2017b). The species is known from a single collection and might be a local ecotype of S. wrightii.
- \* Solidago wrightii is distinguished by its non-serrate stem leaves and inflorescences that are sometimes subcorymbiform and its moderately strigose ovaries/fruit bodies (Figs. 10-12). Several varieties have been recognized within the species but are not recognized here; S. wrightii var. adenophora Blake was distinguished by its upper leaves, stems and phyllaries being densely stipitate glandular and not hairy (Fig. 12I) while var. wrightii had sparsely to non-glandular upper leaves, stems, and phyllaries that were moderately to densely strigose (Fig. 12H). Kearney et al. (1960) recognized var. adenophora as a more southern form of the species in Arizona. Nesom (2008) concluded that there was considerable range of variation in the the numbers of hairs and glands on phyllaries and recognized the most glandular forms as f. adenophora (Blake) Nesom.

The distributions of the seven species are overall allopatric, with some sympatry at the margins. Solidago buckleyi is native to the open woods in eastern Missouri, southern Illinois and Indiana, and north central Alabama (Fig. 13; Semple & Keener 2016). The species is sympatric with S. petiolaris in Missouri and Arkansas. Solidago correllii is the only species present in the Guadalupe Mountains of Texas and New Mexico but possibly occurs in the White Mountains further north in New Mexico (Fig. 13) where S. wrightii is more common (Nesom 2008, as S. wrightii var. guadalupensis) and in possibly further south in the Davis Mountains of trans-Pecos Texas. Solidago orientalis is native to the Sierra Madre Oriental of northeastern Mexico (Fig. 13; Nesom 1990) and is allopatric with other species in the subsection.

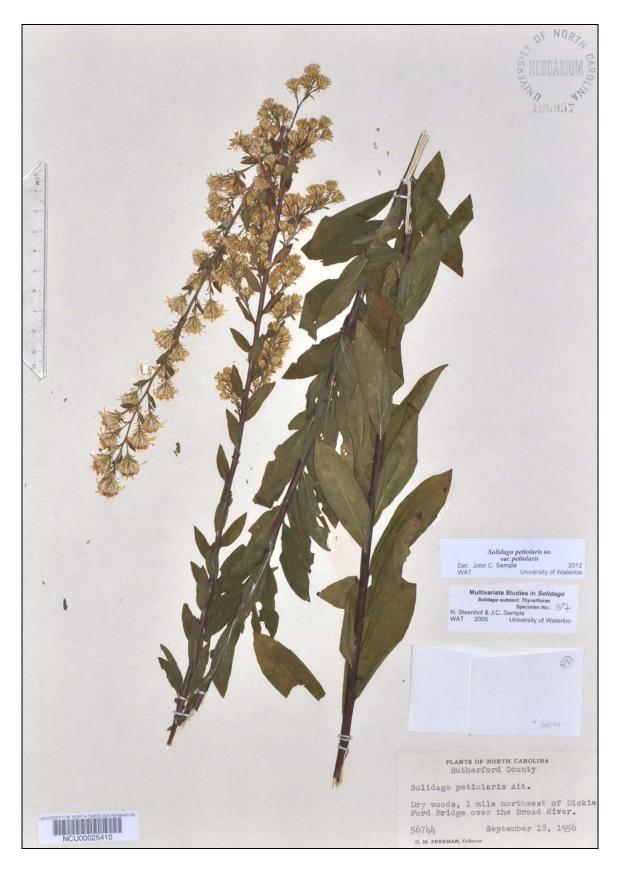


Figure 7. Solidago petiolaris, Freeman 56744 (NCU) from Rutherford Co., North Carolina.



Figure 8. Details of morphology of Solidago petiolaris: stems and leaves. A. Lower stem, Ward s.n. (GH isotype of S. wardii). B-C. Mid stems; var. petiolaris, Jones 22337 (NCU) and var. angusta, Thomas et al. 68478 (WAT). D. Stem in inflorescence, var. wardii, Drake 183 (TEX). E. Lower mid stem leaves, var. petiolaris, Ahles 36076 (NCU). F. Upper stem leaf, var. angusta, Semple & Heard 8274 (WAT). G-H. Mid stem leaves, var. angusta, Thomas 138410 (LSU) and Henrickson 11471 (LL). I-J. Upper mid stem leaves, var. angusta, Correll 26345 (LL) and var. petiolaris, Kral 41739 (WAT). K. Serrate secondary branch leaf, var. petiolaris, Radford 30544 (NCU). Scale bars = 1 cm.

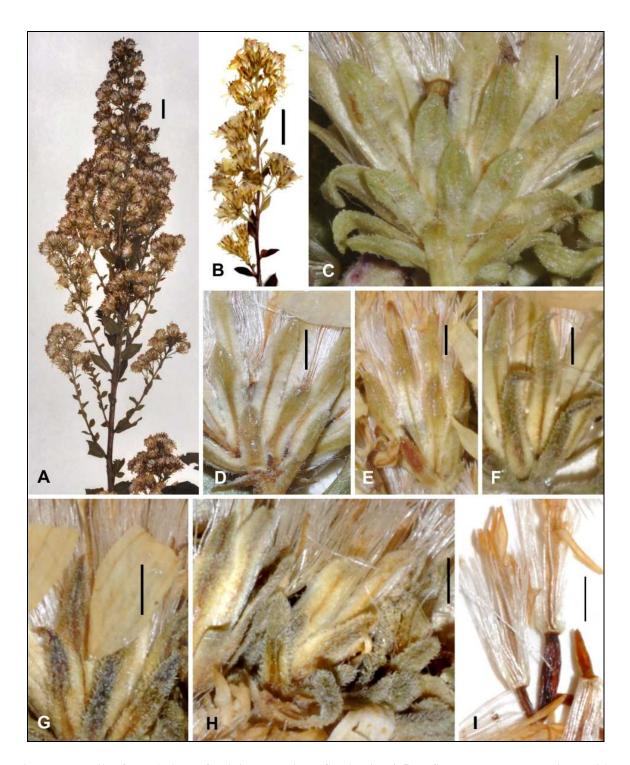


Figure 9. Details of morphology of Solidago petiolaris: floral traits. A-B. Inflorescences, var. petiolaris, wide, Radford 29536 (NCU) and small, Semple & Chmielewski 6186 (WAT). C-H. Phyllaries. C-E. Resinous, glandular. C. Broad leaved var. angusta, Semple & Heard 8268 (WAT). D. Ovate leaved var. angusta, Correll 26345 (LL). E. Var. angusta, Thomas 138410 (LSU). F-G. Var. petiolaris, Harbison s.n. (NCU) and Marsh 55-21 (TEX). H. Isotype of var. wardii, Ward s.n. (GH). I. Disc floret immature cypselae, var. wardii, Taylor 23743 (LSU). Scale bars = 1 mm in C-I = 1 cm in A-B.



Figure 10. Solidago wrightii, Wooton & Standley 3688 (NMC) from Lincoln Co., New Mexico.



Figure 11. Solidago wrightii, Semple & Heard 7988 (WAT) from Cochise Co., Arizona.

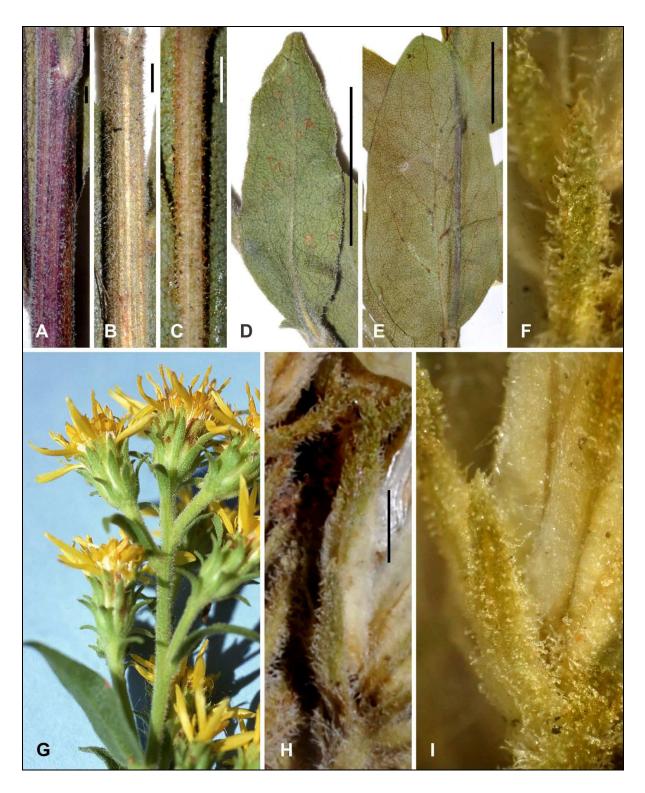
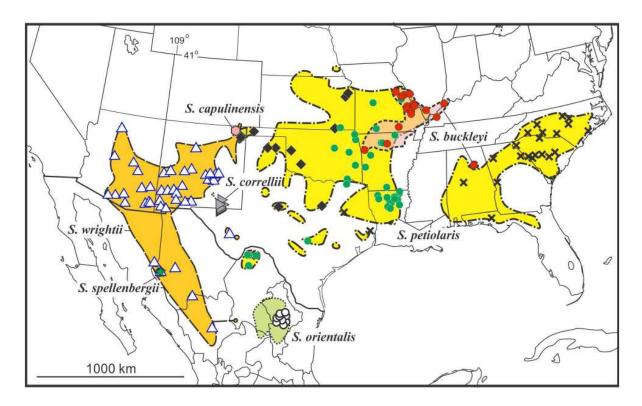


Figure 12. Details of morphology of Solidago wrightii. A-B. Mid and upper stems, hairy, Semple & Heard 8038 (WAT) and Sherman et al 202 (WAT). C. Upper stem, glandular, Van Devender 98-636 (NMC). D-E. Upper stem leaves, hairy, Semple & Chmielewski 9000 (WAT), and glandular, Bye 9883 (NMC). F. Peduncle bract, hairy, Semple & Heard 8038 (WAT). G. Fresh heads, glandular, Semple & Heard 7930 (WAT). H. Phyllaries, hairy, Semple & Heard 8038 (WAT). I. Phyllaries, glandular, Semple & Heard 7988 (WAT). Scale bars = 1 mm in A-C, and H; = 1 cm in D-E.

Solidago petiolaris is native to the southern USA from eastern New Mexico to North Carolina and south to Texas into northern Mexico in rocky soils in open woods and disturbed slopes (Fig. 13): var. petiolaris occurs mostly east of the Missisippi River with some collections coming from eastern Texas; var. angusta, occurs from Missouri and southeastern Kansas south to Louisiana and northeastern Texas with scattered populations in eastern and southern Oklahoma and across Texas in disjunct areas to the mountains of northern Coahuila, Mexico; var. wardii occurs from northeastern New Mexico to northeastern Kansas and south to Panhandle and central Texas (Nesom 2008). Solidago spellenbergii is known only from the type location in Parque Nacional de Cascada Basaseachic, western Chihuahua, Mexico. It was been collected along a trail on the slope to the base of the falls in moderately open woods with Ouercus and Pinus. Solidago wrightii is native to the mountains of Arizona, New Mexico, and trans-Pecos Texas in the USA and the eastern portions of the Sierra Madre Occidental in Sonora, western Chihuahua, and Durango and southwestern Coahuila in Mexico (Fig 13). It also occurs on the high plains in northeastern New Mexico and southeastern Colorado (Nesom 2008).

Nesom (1993) included Solidago hintoniorum Nesom and S. speciosa Nutt. (including S. harperi Mackenzie and S. jejunifolia Steele) in subsect. Thyrsiflorae, but these were not included in subsect. Thyrsiflorae by Semple (2017 frequently updated). Solidago hintoniorum has traits typical of subsect. Nemorales including large lower stem leaves. Solidago speciosa and S. jejunifolia are typical members of subsect. Squarrosae and have large lower stem leaves (Semple et al. 2017).



Distribution of 150 specimens included in the multivariate analyses of Solidago subsect. Thryrsiflorae: S. buckleyi (red dots), S. capulinensis (pink polygon), S. correllii (gray right-pointing triangles), S. orientalis (white-filled black circles), S. petiolaris (var. petiolaris, black crosses; var. angusta with more or less glandular resinous phyllaries and includes some silver leaved specimens, green dots; var. wardii with hairy phyllaries, black diamonds), S. spellenbergii (green star); S. wrightii (white-filled blue triangles).

All chromosome numbers reported for taxa in Solidago subsect. Thyrsiflorae are diploid, 2n=9II or 2n=18, with one exception. Diploid counts have been reported for S. correllii (Semple et al. 2001 as S. wrightii; corrected in Semple 2017a), S. petiolaris (Beaudry 1963, Semple et al. 1981; Semple et al. 1993; Semple & Cook 2004; Semple, Cook, & Owen 2015; Morton et al. in press; unpublished) and S. wrightii (Turner et al. 1962; Beaudry 1969; Anderson et al., 1974; Keil & Pinkava 1979, 1981; Windham & Schaak 1983; Ward & Spellenberg 1986; Semple & Chmielewski 1987; Keil et al. 1988; Semple et al. 1992, 2001; Morton et al. in press; unpublished). Semple et al. (1992) reported the single tetraploid count for S. petiolaris; the identity of the voucher Semple et al. 3044 (WAT) from Richmond Co., North Carolina, is confirmed below in the multivariate analyses, but the count itself cannot be confirmed to be from the field collected plant used as the voucher. Semple and Cook (2004) corrected the misidentification of two reports of tetraploids for S. petiolaris (Semple et al. 1984) to S. leavenworthii. Chromosome numbers have not been reported for S. buckleyi, S. capulinensis, S. orientalis, and S. spellenbergii.

The purpose of this study was to determine statistical support for recognizing the species and varieties proposed within Solidago subsect. Thyrsiflorae, the levels of distinctiveness among the taxa, and what technical traits could be used to separate taxa besides those used to define the taxa as a priori groups.

## MATERIAL AND METHODS

Herbarium specimens were borrowed and examined from the following herbaria (GH, LL, LSU, MEXU, NY, NCU, NMC, TEX, UNM, and WAT in MT; Thiers continuously updated). More than 700 specimens were examined, from which 150 were chosen and measured for the statistical analyses based on completeness, maturity, and geographical distribution (17 specimens of Solidago buckleyi, 10 of S. capulinesis, 13 of S. correllii, 7 of S. orientalis, 66 of S. petiolaris, 1 of S. spellenbergii included in a posteriori analyses, and 36 of S. wrightii). In total, 20 vegetative and 19 floral traits were scored for the final analyses (Table 1). Preliminary analyses not reported below included additional stem, leaf and phyllary indument traits scored on a smaller number of specimens.

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. Five analyses were performed. In the first analysis, Solidago buckleyi, S. capulinensis, S. correllii, S. orientalis, S. petiolaris, and S. wrightii were included in a STEPWISE discriminant analysis and a COMPLETE with six traits, plus one specimen of S. spellenbergii included a posteriori. In the second analysis, S. capulinensis, S. correllii, S. petiolaris, and S. wrightii were included in a STEPWISE discriminant analysis plus one specimen of S. spellenbergii included a posteriori. In the third analysis, S. petiolaris var. angusta, S. petiolaris var. petiolaris, and S. petiolaris var. wardii, were included in a STEPWISE discriminant analysis using Nesom's (2008) limits of the varieties with var. angusta including specimens with hairless phyllaries with either glands or resin. In the fourth analysis, S. petiolaris var. angusta, S. petiolaris var. petiolaris, and S. petiolaris var. wardii, were included in a STEPWISE discriminant analysis using alternative limits of the varieties with var. angusta defined by having narrow leaves and var. wardii by having broader leaves and phyllaries that were either hairy or not hairy. In the fifth analysis, the numbers of glands and hairs on upper stem leaves and phyllaries of specimens of S. wrightii were investigated and several ways including a STEPWISE analysis. A number of additional preliminary analyses were run but are not reported here.

Table 1. Traits scored for the multivariate analyses of 150 specimens of Solidago subsect. Thyrsiflorsae.

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
LEAGMM	Number of glands per mm <sup>2</sup> on upper stem leaf upper surface*
LEAHMM	Number of hairs per mm <sup>2</sup> on upper stem leaf upper surface*
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 inflorescence (cm)
INVOLHT	Involucre height at anthesis (mm)
OPHYLN	Outer phyllary length (mm)
PHYGD	Number of glands per mm <sup>2</sup> on mid series phyllary distal half
PHYHAIR	Number of hairs per mm <sup>2</sup> on mid series phyllary distal half
OPHYLW	Outer phyllary width (mm)
IPHYLN	Inner phyllary length (mm)
IPHYLW	Inner phyllary width (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	Number of hairs on disc floret ovary/fruit body

<sup>\*</sup>Preliminary analyses only

#### RESULTS

# Six species level a priori groups taxa analysis

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to the number of mid stem leaf margin serrations. Basal rosette leaves were present in only a few specimens of S. correllii and a single specimen of S. wrightii 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 stem leaf traits. Among the floral traits scored, only ray floret pappus length and disc floret pappus length correlated highly; the latter was included in the analyses.

In the COMPLETE discriminant analysis of 149 specimens of six species level a priori groups (Solidago buckleyi, S. capulinensis, S. correllii, S. orientalis, S. petiolaris and S. wrightii), the following six of seven traits selected in a STEPWISE analysis and used in the COMPLETE analysis are listed in order of decreasing F-to-remove values: number of mid stem leaf margin serrations (76.19), number of hairs on the disc floret ovary/fruit body (36.41), number of disc florets (15.85), involucre height (14.54), disc corolla lobe length (8.05), and disc floret pappus length at anthesis (7.21). 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 2. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between S. buckleyi and S. wrightii (73.695); the smallest separation was between S. buckleyi and S. orientalis (5.774).

Table 2. Between groups F-matrix for the five a priori groups analysis (df = 6 138).

Group	buckleyi	capulinensis	correllii	orientalis	petiolaris
capulinensis	29.124				
correllii	44.705	18.173			
orientalis	5.774	14.340	18.179		
petiolaris	57.831	11.958	16.518	12.673	
wrightii	73.695	23.017	15.364	19.412	34.616

Wilks' lambda = 0.0346 df = 6 5 143; Approx. F= 24.3432 df = 30 554 prob = 0.0000

In the Classificatory Discriminant Analysis of 149 specimens of the six species level a priori groups (Solidago buckleyi, S. capulinensis, S. correllii, S. orientalis, S. petiolaris and S. wrightii) plus 1 specimen of S. spellenbergii, percents of correct a posterori assignment to the same a priori group ranged from 71-90%. The Classification matrix and Jackknife classification matrix are presented in Table 3. Results are presented in order of decreasing percents of correct placement. Nine of 10 specimens of the S. capulinensis a priori group (90%) were assigned a posteriori into the S. capulinensis group; 8 specimens with 96-100% probability, 1 specimen with 67% probability. One specimen of the S. capulinensis a priori group was assigned to S. petiolaris with 61% probability (37% to S. capulinenesis; Lowrey 2190-B UNM, unmounted when scored, from Mt. Capulin Nat. Mon., New Mexico). Ten of 13 specimens of the S. correllii a priori group (77%) were assigned a posteriori into the S. correllii group; 8 specimens with 98-100% probability, 1 specimen with 87% probability, and 1 specimen with 67% probability. Three specimens of the S. correllii a priori groups were assigned to other species: 2 specimens to S. capulinensis with 77% probability (10% to S. correllii and 9% to S. petiolaris; Ward 84-028 NMC from McKittrick Canyon, Guadalupe Mts., Texas; several shoots with linear-oblanceolate basal rosette and lower to upper stem and somewhat silvery-colored leaves and with few heads) and 50% probability (45% to S. petiolaris; Hershey s.n. NMC from Guadalupe Mts., Eddy Co., New Mexico; leaves are narrowly elliptic and green); and 1 specimen to S. wrightii with 95% probability (Correll 13948 LL from N. McKittrick Canyon, Guadalupe Mts, Texas; 29 cm tall shoot with persistent petiolate lower stem leaves and moderately

hairy ovaries/fruit bodies). Fifty of 66 specimens of the S. petiolaris a priori group (76%) were assigned a posteriori into the S. petiolaris group; 32 specimens with 91-95% probability (including 1 from panhandle Oklahoma and 1 from NE New Mexico), 10 specimens with 80-87% probability (including 1 from NE New Mexico), 4 specimens with 61-65% probability, and 1 specimen with 47% probability (35% to S. capulinensis and 17% to S. orientalis; Semple & Brouillet 3753 WAT from Franklin Co., Missouri). Sixteen specimens of the S. petiolaris a priori group were assigned to other species: 6 specimens to S. capulinensis with 99% probability (Riskind 2139 TEX from Coahuila, Mexico), 97% probability (Wendt 545 TEX from Coahuila, Mexico), 96% probability (Henrickson 11471 LL from Coahuila, Mexico), 84% probability (16% to S. petiolaris; Ahles 35335 NCU from Calhoun Co., South Carolina), 83% probability (17% to S petiolaris; Freeman 56744 NCU from Rutherford Co., North Carolina), and 73% probability (26% to S. petiolaris; Semple & Heard 8268 WAT from Leflore Co., Oklahoma); 6 specimens to S. correllii with 92% probability (Thomas 108653 LSU from Caldwell Co., Louisiana), 80% probability (Thomas et al. 61516 LSU from Morehouse Co., Louisiana), 77% probability (Thomas et al. 68478 WAT from Morehouse Co., Louisiana), 64% probability (Thomas 137913 TEX from Quachita Co., Louisiana), 64% probability (Morse & Roth 8800 WAT from Chautauqua Co., Kansas), and 63% probability (Thomas et al. 86196 WAT from Ouachita Co., Louisiana); 2 specimens to S. wrightii with 52% probability (40% to S. petiolaris and 8% to S. correllii; Ahles 34674 NCU from York Co., South Carolina) and 48% probability (40% to S. petiolaris and 6% each to S. capulinensis and S. correllii; Laing 575 NCU from Harnett Co., North Carolina); and 1 specimen to S. orientalis with 59% probability (41% to S. buckleyi; Croat 1186 TEX from Douglas Co., Kansas). Twenty-seven of 36 specimens of the S. wrightii a priori group (75%) were assigned a posteriori into the S. wrightii group; 18 specimens with 90-100% probability, 6 specimens with 84-88% probability, 1 specimen with 68% probability, and 1 specimen with 54% probability (39% to S. petiolaris; Wooton 325 NMC from Lincoln Co., New Mexico). Nine specimens of the S. wrightii a priori group were assigned to other species: 6 specimens to S. petiolaris with 88% probability (Ellis 288 NMC from Bernalillo/Sandoval Co., New Mexico), 72% probability (Wooton s.n. NMC from Dona Ana Co., New Mexico), 64% probability (Semple & B. Semple 10496 WAT from Gila Co., Arizona), 56% probability (32% to S. petiolaris and 11% to S. correllii; Ward 9 NMC from Coconino Co., Arizona), 47% probability (45% to S. wrightii and 5% to S. capulinensis; Spellenberg & Spellenberg 7926 NMC from Cascada de Basaeachic, Chihuahua, Mexico; upper stem leaves broadly lanceolate, ovary/fruit body moderately strigose), and 47% probability (40% to S. wrightii and 12% to S. correllii; Hess 2334 NMC from Catron Co., New Mexico); and 3 specimens to S. correllii with 63% probability (27% to S. wrightii; Noyes & Brant 202 WAT from Jeff Davis Co., Texas; broadly lanceolate to elliptic leaves, moderately strigose ovary/fruit body), 52% probability (48% to S. wrightii; Moir & Fitzhugh 476 NMC from Soccoro Co., New Mexico), and 45% probability (44% to S. petiolaris and 11% to S. wrightii; Todsen s.n. NMC from Hidalgo Co., New Mexico; narrowly oblanceolate lower stem leaves, sparsely strigose ovary/fruit body). Twelve of 17 specimens of the S. buckleyi a priori group (71%) were assigned a posteriori into the S. buckleyi group; 11 specimens with 90-100% probability and 1 specimen with 71% probability. Five specimens of the S. buckleyi a priori group were assigned to other species: 3 specimens were assigned to S. orientalis with 88% probability (Palmer 31511 NY from St. Francois Co., Missouri), 57% probability (37% to S. petiolaris; Semple & Suripto 9917 WAT from Oregon Co., Missouri; shoot with broadly lanceolate acuminate lower and mid stem leaves with serrate margins and a damaged leader with a few heads in axillary clusters), and 55% probability (43% to S. buckleyi; Letterman s.n., St. Louis Co., Missouri; shoot has broadly oblanceolate mid stem leaves with serrate margins); and 2 specimens to S. petiolaris with 96% probability (Deam 63848 NY garden grown transplant from Posey Co., Indiana; lanceolate acuminate mid stem leaves with serrate margins) and 77% probability (17% to S. orientalis; Semple & Suripto 9878 WAT from Union Co., Illinois; oblanceolate acuminate mid and upper stem leaves with serrate margins). Five of 7 specimens of the S. orientalis a priori group (71%) were assigned a posteriori into the S. orientalis group; 3 specimens with 96-100% probability and 2 specimens with 86% and 81% probabilities.

Two specimens of the S. orientalis a priori group were assigned a posteriori to S. buckleyi with 84% probability (Hinton et al. 21617 TEX from Galeana, Nuevo Leon, Mexico; broadly oblanceolate to ovate leaves with serrate margins) and 57% probability (43% to S. orientalis; Hinton et al. 27489 TEX from Purisima, Nuevo Leon, Mexico; broadly oblanceolate leaves with serrate margins). One specimen of S. spellenbergii (holotype: Spellenberg & Jewell 9266 NMC from Parque Nacional de Cascada Basasearchic, Chihuahua, Mexico) was included a posteriori and assigned to S. petiolaris with 51% probability and to S. orientalis with 42% and to S. wrightii with 0% probability. The specimen does not look like the first two species; the inflorescence is long-branched and lax, and it has very sparsely strigose ovaries/fruit bodies.

Table 3. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	buckleyi	capulinensis	correllii	orientalis	petiolaris	wrightii	% correct
buckleyi	12	0	0	3	2	0	71
capulinensis	0	9	0	0	1	0	90
correllii	0	2	10	0	0	1	77
orientalis	2	0	0	5	0	0	71
petiolaris	0	6	6	1	50	3	76
wrightii	0	0	3	0	6	27	75
Totals	14	17	19	9	59	31	76

Jackknifed classification matrix

Group	buckleyi	capulinensis	correllii	orientalis	petiolaris	wrightii	% correct
buckleyi	12	0	0	3	2	0	71
capulinensis	0	9	0	0	1	1	90
correllii	0	2	10	0	0	1	77
orientalis	2	0	0	5	0	0	71
petiolaris	0	7	6	1	49	3	74
wrightii	0	0	3	0	6	27	75
Totals	14	18	19	9	58	31	75

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 150 specimens of Solidago buckleyi, S. capulinensis, S. correllii, S. orientalis, S. petiolaris, S. spellenbergii, and S. wrightii are presented in Fig. 14. Eigenvalues on the first three axes were 3.630, 1.373 and 0.655.

# Four species level a priori groups taxa analysis

The Pearson correlation matrix yielded r > |0.7| for most pairs of lower leaf traits and mid leaf traits reducing the number to be used to mid stem leaf length, width, and serrations and upper stem leaf length. Basal rosette leaves were rarely present and were not included in the discriminant analyses: basal leaf length, basal leaf petiole length, and basal leaf length from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Most floral traits were not correlated, but ray floret pappus length and disc floret pappus length were highly correlated and only the latter was included in the STEPWISE analysis.

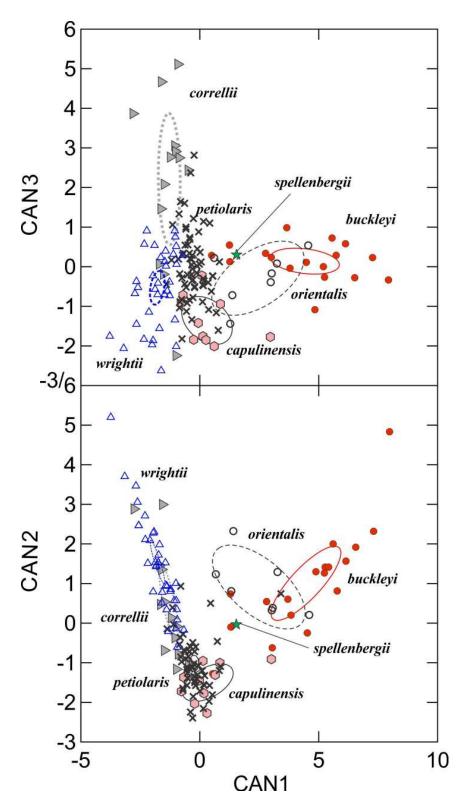


Figure 14. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 146 specimens of Solidago subsect. Thyrsiflorae: S. buckleyi (red dots), S. capulinensis (pink polygons), S. correllii (gray right-oriented triangles), S. orientalis (unfilled black circles), S. petiolaris (black ×s), S. spellenbergii (green stars; a posteriori) and S. wrightii (unfilled blue triangles).

In the COMPLETE discriminant analysis of 125 specimens of four species level a priori groups in (Solidago capulinensis, S. correllii, S. petiolaris, and S. wrightii), the following eight traits that had the highest F-to-remove values from the nine traits selected in a STEPWISE analysis were used in the COMPLETE analysis and are listed in order of decreasing F-to-remove values: number of disc floret ovary/fruit body hairs (51.86), number of disc florets (14.58), involucre height (11.69), upper stem leaf length (8.74), disc floret pappus length at anthesis (8.73), disc corolla lobe length (5.75), number of mid stem leaf margin serrations (4.90), and number of ray florets (4.68). 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 4. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between S. petiolaris and S. wrightii (24.738); the smallest separation was between S. correllii and S. wrightii (12.773).

Table 4. Between groups F-matrix for the four species level a priori groups analysis (df = 8 114).

Group	capulinensis	correllii	petiolaris
correllii	19.208		
petiolaris	14.136	14.674	
wrightii	22.089	12.773	24.738

Wilks' lambda = 0.0929 df = 8 3 121; Approx. F= 17.5043 df = 24 331 prob = 0.0000

In the Classificatory Discriminant Analysis of 125 specimens of the four species level a priori groups (Solidago capulinensis, S. correllii, S. petiolaris and S. wrightii) plus a posteriori 1 specimen each of S. spellenbergii and S. wrightii and 3 specimens of S. correllii, percents of correct a posterori assignment to the same a priori group ranged from 81-100%. The Classification matrix and Jackknife classification matrix are presented in Table 5. Results are presented in order of decreasing percents of correct placement. All 9 specimens of the S. capulinensis a priori group (100%) were assigned a posteriori into the S. capulinensis group; 8 specimens with 99-100% probability and 1 specimen with 81% probability. Eleven of 13 specimens of the S. correllii a priori group (85%) were assigned a posteriori into the S. correllii group; 9 specimens with 93-100% probability, 1 specimen with 87% probability, and 1 specimen with 78% probability (21% to S. petiolaris). Two specimens of the S. correllii a priori groups were assigned to other species: 1 specimen to S. petiolaris with 85% probability (13% to S. wrightii; Hershey s.n. NMC from Guadalupe Mts., Eddy Co., New Mexico; somewhat broader and larger mid stem leaves than most specimens of S. correllii); and 1 specimen to S. wrightii with 84% probability (Correll 13948 LL from N. McKittrick Canyon, Guadalupe Mts, Texas; 29 cm tall shoot with persistent petiolate lower stem leaves and moderately hairy ovaries/fruit bodies). Three addition specimens of S. correllii were included a posteriori: one shoot of Semple & Heard 8185 (WAT; Guadalupe Mts. N.P.) was assigned to S. correllii with 54% probability (37% to S. petiolaris and 9% to S. wrightii), a second shoot of Semple & Heard 8185 (WAT) was assigned to S. wrightii with 97% probability, and Carr et al. 16911 (TEX; NE tip of Bear Mt., Jeff Davis Co., Texas; leaves were narrowly lanceolate and had a slight silvery appearance to the green leaves) was assigned to S. correllii with 39% probability (35% to S. wrightii and 26% to S. petiolaris). Fiftyseven of 67 specimens of the S. petiolaris a priori group (85%) were assigned a posteriori into the S. petiolaris group; 48 specimens with 90-100% probability, 5 specimens with 81-89% probability, and 3 specimens with 72-77% probability. Nine specimens of the S. petiolaris a priori group were assigned to other species: 3 specimens to S. capulinensis with 100% probability (Croat 1186 TEX from Douglas Co., Kansas), 98% probability (56 Semple & Heard 8299 WAT from Searcy Co., Arkansas), and 53% probability (45% to S. petiolaris; Riskind 2139 TEX from Coahuila, Mexico); 3 specimens to S. correllii with 95% probability (Thomas et al. 86196 WAT from Ouachita Co.,

Louisiana), 87% probability (Morse with Roth 8800 WAT from Chautauqua Co., Kansas), and 65% probability (34% to S. petiolaris; Thomas 137913 TEX from Ouachita Co., Louisiana); and 3 specimens to S. wrightii with 66% probability (34% to S. petiolaris; Marsh 55-21 TEX from Anderson Co., Texas), 56% probability (39% to S. petiolaris; Semple 10948 WAT from Washington Co., Florida), and 55% probability (43% to S. petiolaris; Ahles 34674 NCU from York Co., South Carolina). Twenty-nine of 36 specimens of the S. wrightii a priori group (81%) were assigned a posteriori into the S. wrightii group; 21 specimens with 90-100% probability, 4 specimens with 81-87% probability, 1 specimen with 62% probability, 2 specimens with 58% probability (40% to S. petiolaris; Wooton 325 NMC from Lincoln Co., New Mexico) and 50% probability (47% to S. petiolaris; Ward 9 NMC from Coconino Co., Arizona), and 1 specimen with 46% probability (43% to S. petiolaris; Hess 2334 NMC from Catron Co., New Mexico). Seven specimens of the S. wrightii a priori group were assigned to other species: 4 specimens to S. petiolaris with 89% probability (Ellis 288 NMC from Sandia Mts., New Mexico), 68% probability (31% to S. wrightii; Wooton s.n. NMC from Dona Ana Co., New Mexico), 63% probability (35% to S. wrightii; Semple & B. Semple 10496 WAT from Gila Co., Arizona), and 51% probability (49% to S. wrightii; Spellenberg & Spellenberg 7926 NMC from Cascada de Basaeachic, Chihuahua, Mexico); and 3 specimens to S. correllii with 91% probability (Noyes & Brant 202 WAT from Jeff Davis Co., Texas), 66% probability (31% to S. wrightii; Ward 81-582 NMC from Lincoln Co., New Mexico; leaves are broadly lanceolate to narrowly ovate), and 47% probability (39% to S. petiolaris and 15% to S. wrightii; Todsen s.n. NMC from Hidalgo Co., New Mexico; narrowly oblanceolate lower stem leaves, sparsely strigose ovary/fruit body). The holotype collection of S. spellenbergii included a posteriori was placed in S. petiolaris with 64% (34% to S. capulinensis). One collection of S. wrightii (Nesom and Vorobik 5545 TEX; confluence of Rio Basaseachic and Rio Durazno Basaseachic, Chihuahua, Mexico; sparsely strigose ovaries/fruit bodies) included a posteriori was assigned to S. petiolaris with 78% probability (20% to S. wrightii).

Table 5. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of four a priori groups; a posteriori placements to groups in rows.

Group	capulinensis	correllii	petiolaris	wrightii	% correct
capulinensis	9	0	0	0	100
correllii	0	11	1	1	85
petiolaris	4	3	57	3	85
wrightii	0	3	4	29	81
Totals	13	17	62	33	85

Jackknifed classification matrix

Group	capulinensis	correllii	petiolaris	wrightii	% correct
capulinensis	9	0	0	0	10
correllii	0	11	1	1	85
petiolaris	4	4	56	3	84
wrightii	0	3	6	27	75
Totals	13	18	63	31	82

Two dimensional plots of CAN1 versus CAN3 and CAN1 versus CAN2 canonical scores for 127 specimens of Solidago capulinensis, S. correllii, S. petiolaris, S. spellenbergii, and S. wrightii are presented in Fig. 15. Eigenvalues on the first three axes were 2.106, 1.000 and 0.734.

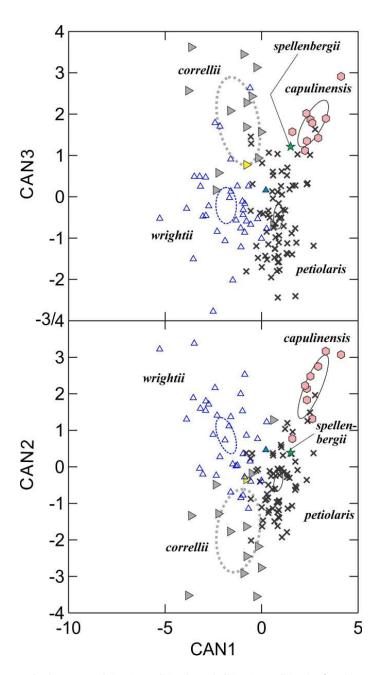


Figure 15. Plot of canonical scores (CAN1 vs CAN3 and CAN1 vs CAN2) for 127 specimens of *Solidago* subsect. *Thyrsiflorae*: *S. capulinensis* (pink polygons), *S. correllii* (gray right-oriented triangles; *Carr et al. 16911* TEX, yellow right-oriented triangles), *S. petiolaris* (black ×s), *S. spellenbergii* (green stars), and *S. wrightii* (unfilled blue triangles; *Nesom & Vorobik 5545* TEX, green-filled blue triangles).

## Three varietal level a priori group analysis of S. petiolaris I

The Pearson correlation matrix yielded r > |0.7| for some pairs of leaf traits reducing the number to be used to mid stem leaf length and width and upper stem leaf width. Basal rosette leaves were always absent and could not be included. Lower leaves were often absent and lower leaf traits were excluded from discriminant analyses. Most floral traits were not highly correlated. Only ray floret pappus lengths and disc floret pappus lengths were highly correlated and only the latter were included.

In the STEPWISE discriminant analysis of 67 specimens of three varietal level a priori groups of Solidago petiolaris adopting Nesom's (2008) limits for groups (var. angusta, var. petiolaris, and var. wardii), the following seven traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: mid stem leaf width (31.93), mid stem leaf length (17.57), disc floret pappus length at anthesis (12.84), disc corolla lobe length (7.24), disc floret ovary/fruit body length at anthesis (6.74), ray floret lamina width (5.51), and disc floret corolla length (5.44). 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 6. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. angusta and var. petiolaris (24.186); the smallest separation was between var. petiolaris and var. wardii (4.876).

Table 6. Between groups F-matrix for the three varietal level a priori groups analysis (df = 7 58); Nesom (2008) varietal limits.

Group	angusta	petiolaris
petiolaris	24.186	
wardii	8.722	4.878

Wilks' lambda = 0.1722 df = 7 2 64; Approx. F= 11.6808 df = 14 116 prob = 0.0000

In the Classificatory Discriminant Analysis of 67 specimens of the three varietal level a priori groups in Solidago petiolaris (adopting Nesom's 2008 limits for var. angusta, var. petiolaris, and var. wardii), percents of correct a posteriori assignment to the same a priori group ranged from 80-92%. The Classification matrix and Jackknife classification matrix are presented in Table 7. Results are presented in order of decreasing percents of correct placement. Twenty-two of the 24 specimens of the var. petiolaris a priori group (92%) were assigned a posteriori into the var. petiolaris group; 14 specimens with 91-100% probability, 4 specimens with 82-86% probability, 1 specimen with 78% probability, and 3 specimens with 69% probability (30% to var. wardii; Radford 30382 NCU from Saluda Co., South Carolina), 67% probability (31% to var. wardii; Radford 30294 NCU from Edgefield Co., South Carolina), and 63% probability (37% to var. wardii; Ahles 34674 NCU from York Co., South Carolina). Two specimens of the var. petiolaris a priori groups were assigned to other varieties: 1 specimen to var. angusta with 84% probability (14% to var petiolaris; Ahles 35335 NCU from Calhoun Co., South Carolina); and 1 specimen to var. wardii with 57% probability (43% to var. petiolaris; McMillan 1993 NCU from Wake Co., North Carolina). Twenty-nine of 33 specimens of the var. angusta a priori group (88%) were assigned a posteriori into the var. angusta group; 24 specimens with 92-100% probability, 2 specimens with 88% and 84% probabilities, 2 specimens with 72% and 70% probabilities, and 1 specimen with 69% probability (19% to var. petiolaris and 13% to var. wardii; Semple & Suripto 9936 WAT from Taney Co., Mo; non hairy phyllaries with some glands). Four specimens of the var. angusta a priori group were assigned to other varieties; 3 specimens to var. wardii with 79% probability (Horr E573 LL from Montgomery Co., Kansas), 77% probability (Thomas et al 112964 TEX from Union Co., Louisiana) and 64% probability (22% to var. angusta and 14% to var. petiolaris; Steward 1409 LL from Coahuila); and 1 specimen to var. petiolaris with 69% probability (15% each to var. angusta and var. petiolaris; Semple & Heard 8299 WAT from Searcy Co., Arkansas; oblanceolate shiny green lower leaves to small broadly elliptic leaves above). Eight of 10 specimens of the var. wardii a priori group (80%) were assigned a posteriori into the var. wardii group; 6 specimens with 93-99% probability, 1 specimen with 79% probability, and 1 specimen with 56% probability (44% to var. petiolaris; Palmer 13049 TEX from Nolan Co., Texas). Two specimens of the var. wardii a priori group were assigned to var. petiolaris with 85% probability (15% to var. wardii; Taylor & Taylor 32588 NMC from Union, New Mexico; sparsely hairy phyllaries), and 52% probability (46% to var. wardii; Morse & Roth 8800 WAT from Chautauqua Co., Kansas; silvery lanceolate leaves and glandular phyllaries; this could have been assigned a priori to var. angusta).

Table 7. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three varietal level a priori groups; a posteriori placements to groups in rows; Nesom (2008) variety concept.

Group	angusta	petiolaris	wardii	% correct
angusta	29	1	3	88
petiolaris	1	22	1	92
wardii	0	2	8	80
Totals	30	25	12	88

Jackknifed classification matrix

Group	angusta	petiolaris	wardii	% correct
angusta	29	1	3	88
petiolaris	1	22	1	92
wardii	0	3	7	70
<b>Totals</b>	30	26	11	87

A two dimensional plot of CAN1 versus CAN3 canonical scores for 67 specimens of Solidago petiolaris (var. angusta, var. petiolaris and var. wardii) are presented in Fig. 16. Eigenvalues on the first two axes were 3.009 and 0.448.

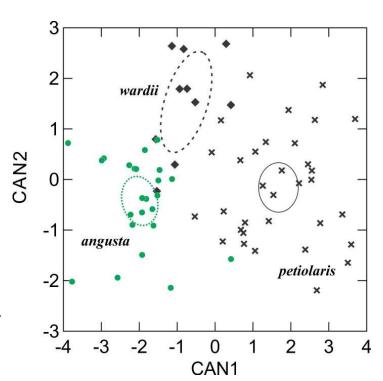


Figure 16. Plot of canonical scores (CAN1 vs CAN2) for 67 specimens of Solidago petiolaris: var. angusta (green dots), var. petiolaris (black ×s), and var. wardii (black diamonds); identifications based on Nesom (2008).

# Three varietal level a priori group analysis of S. petiolaris II

The same traits used in the first analysis of varieties of Solidago petiolaris were used except mid stem leaf width was excluded because it was used to define var. angusta (narrow leaves) and var. wardii (broader leaves). This meant that var. wardii extended into Missouri and Arkansas and var. angusta had a much more restricted distribution than shown in Fig. 13.

In the STEPWISE discriminant analysis of 67 specimens of three varietal level a priori groups of Solidago petiolaris (var. angusta, var. petiolaris, and var. wardii) adopting leaf width limits for var. angusta and ignoring phyllary indument features, the following three traits selected in a STEPWISE analysis are listed in order of decreasing F-to-remove values: disc floret pappus length (16.79), disc corolla length (14.60), and number of disc florets (8.37). 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 8. F-values based on Mahalanobis distances of the between group centroids indicated the largest separation was between var. angusta and var. petiolaris (20.919); the smallest separation was between var. angusta and var. wardii (5.545).

Table 8. Between groups F-matrix for the three varietal level a priori groups analysis (df = 3 62); alternative varietal limits.

Group	angusta	petiolaris
petiolaris	20.919	
wardii	5.545	11.756

Wilks' lambda = 0.4190 df = 3 2 64; Approx. F= 11.2619 df = 6 124 prob = 0.0000

In the Classificatory Discriminant Analysis of 67 specimens of the three varietal level a priori groups in Solidago petiolaris (adopting leaf width limits for var. angusta and ignoring phyllary indument features), percents of correct a posterori assignment to the same a priori group ranged from 56-88%. The Classification matrix and Jackknife classification matrix are presented in Table 9. Results are presented in order of decreasing percents of correct placement. Twenty-two of the 24 specimens of the var. petiolaris a priori group (92%) were assigned a posteriori into the var. petiolaris group; 14 specimens with 91-100% probability, 4 specimens with 82-86% probability, 1 specimen with 78% probability, and 3 specimens with 69% probability (30% to var. wardii; Radford 30382) NCU from Saluda Co., South Carolina), 67% probability (31% to var. wardii; Radford 30294 NCU from Edgefield Co., South Carolina), and 63% probability (37% to var. wardii; Ahles 34674 NCU from York Co., South Carolina). Two specimens of the var. petiolaris a priori groups were assigned to other varieties: 1 specimen to var. angusta with 84% probability (14% to var. petiolaris; Ahles 35335 NCU from Calhoun Co., South Carolina); and 1 specimen to var. wardii with 57% probability (43% to var. petiolaris; McMillan 1993 NCU from Wake Co., North Carolina). Thirteen of 18 specimens of the var. angusta a priori group (72%) were assigned a posteriori into the var. angusta group; 3 specimens with 92-99% probability, 1 specimen with 87% probability, 3 specimens with 70%-79% probability, 3 specimens with 60-69% probability, 2 specimens with 55% probability (Thomas et al. 112964 TEX from Union Par., Louisiana) and 51% probability (46% to var. wardii and 9% to var. angusta; Gilmore 3707 LSU from Winn Par., Louisiana), and 1 specimen with 48% probability (41% to var. wardii and 12% to var. petiolaris; Carr 14970 LSU from Lamar Co., Texas). Five specimens of the var. angusta a priori group were assigned to other varieties; 4 specimens to var. wardii with 67% probability (17% to var. angusta; Thomas & Kessler 79061 WAT from Winn Par., Louisiana), 56% probability (39% to var. angusta; Miller et al. 5847 TEX from Blanco Co., Texas), 52% probability (45% to var. angusta; Miller 19 TEX from Ottawa Co., Oklahoma), and 39% probability (37% to var. angusta and 24% to var. petiolaris; Thomas 138410 LSU from Webster Par., Louisiana); and 1 specimen to var. petiolaris with 65% probability (31% to var. wardii and var.

petiolaris; Thomas 138410 TEX from Webster Par., Louisiana). Thirteen of 25 specimens of the var. wardii a priori group (56%) were assigned a posteriori into the var. wardii group; 2 specimens with 85% probability, 1 specimen with 74% probability, 3 specimens with 60-62% probability, 4 specimens with 50-59% probability, and 1 specimen with 46% probability (32% to var. angusta; Freeman 118402 TEX from Roger Mills Co., Oklahoma). Eleven specimens of the var. wardii a priori group were assigned to the other two varieites: 6 specimens to var. petiolaris with 91% probability (9% to var. wardii; Taylor & Taylor 32588 NMC from Union, New Mexico; sparsely hairy phyllaries), 80% probability (18% to var. wardii; Semple & Suripto 9942 WAT from Hickory Co., Missouri), 59% probability (36% var. wardii; Semple & Suripto 9972 WAT from Logan Co., Arkansas; silvery leaves, non hairy resinous phyllaries), 57% probability (35% var. wardii; Semple & Heard 8299 WAT from Searcy Co., Arkansas; oblanceolate shiny green lower leaves to small broadly elliptic leaves above), 47% probability (43% to var. wardii; Semple & Suripto 9936 WAT from Taney Co., Mo; non hairy phyllaries with some glands), and 44% probability (34% to var. wardii and 22% to var. angusta; Taylor 32588 LSU from Union Co., New Mexico);); and 5 specimens to var. angusta with 95% probability (Taylor 16926 LSU from Choctaw Co., Oklahoma; silvery narrowly ovate leaves, non-hairy resinous phyllaries), 57% probability (36% to var. wardii; Semple & Heard 8268 WAT from Leflore Co., Oklahoma), 56% probability (40% var. wardii; Harding 407 TEX from Delaware Co., Oklahoma), 51% probability (49% to var. wardii; Riskind 2139 TEX from northern Coahuila), and 43% probability (Morse & Roth 8800 WAT from Chautauqua Co., Kansas; silvery lanceolate leaves and glandular phyllaries; this could have been assigned a priori to var. angusta).

Table 9. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of three varietal level a priori groups; a posteriori placements to groups in rows; alternative variety concept.

Group	angusta	petiolaris	wardii	% correct
angusta	13	1	4	72
petiolaris	1	21	2	88
wardii	5	6	14	56
Totals	19	28	20	72

Jackknifed classification matrix

Group	angusta	petiolaris	wardii	% correct
angusta	13	1	5	67
petiolaris	1	20	3	83
wardii	5	7	13	52
Totals	18	28	21	67

A two dimensional plot of CAN1 versus CAN3 canonical scores for 67 specimens of Solidago petiolaris (var. angusta, var. petiolaris and var. wardii) are presented in Fig. 17. Eigenvalues on the first two axes were 3.009 and 0.448.

## Varietal level analyses within S. wrightii

A preliminary analysis including specimens for which densities of the numbers of hairs and glands on upper stem leaves were scored was run. A plot of the number of hairs versus the number of glands on upper stem leaves is shown in Fig. 18. While specimens with no glands or no hairs could easily be assigned to var./f. wrightii and var./f. adenophora a priori groups, specimens with few to many hairs and glands could not be assigned unambiguously. More specimens had both many hairs and glands than did specimens with no hairs or no glands.

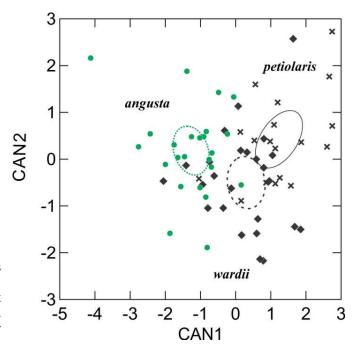


Figure 17. Plot of canonical scores (CAN1 vs CAN2) for 67 specimens of Solidago petiolaris: var. angusta (green dots), var. petiolaris (black ×s), and var. wardii (black diamnds); identification based on leaf width, phyllary hairs, and distribution.

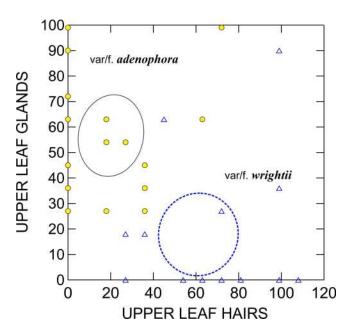


Figure 18. Plot of gland and hair numbers for 36 specimens of Solidago *wrightii*: var. *adenophora* morph (yellow dots) and var. *wrightii* morph (unfilled blue triangles); 95% confidence limits indicated by ovals; identification based on numbers of phyllary glands and hairs.

The Pearson correlation matrix yielded r > |0.7| for most pairs of leaf traits reducing the number to be used to mid and upper stem leaf lengths, mid and upper stem leaf widths, and numbers of mid of upper stem leaf serrations. Basal rosette leaves were nearly always absent and were not included in the discriminant analyses: basal leaf length, basal leaf petiole length, and basal leaf length

from widest point to tip were all highly correlated. Lower leaves were sometimes absent and lower leaf traits were excluded from discriminant analyses. Many floral traits also were highly correlated.

In the STEPWISE discriminant analysis of 36 specimens of two varietal/form level a priori groups in (Solidago wrightii var. adenophora and var. wrightii), the following trait was selected in a STEPWISE analysis: number of disc florets (9.48). 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 = 0.0041 that the null hypothesis was true. The var. adenophora and var. wrightii had an F-to separate value of 9.483 (Wilks' lambda = 0.78192 df = 1.134; Approx. F= 9.483 df = 34 prob = 0.0041).

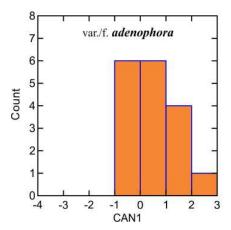
In the Classificatory Discriminant Analysis of 36 specimens of the two varietal level a priori groups of Solidago wrightii (var. adenophora and var. wrightii), the percents of correct placement a posteriori of specimens to the a priori group were 65% var. adenophora and 63% for var. wrightii. The Classification matrix and Jackknife classification matrix are presented in Table 10. Eleven of the 17 specimens of var. adenophora (65%) were assigned a posteriori to the var. adenophora group: 1 specimen with 91% probability, 1 specimen with 82% probability, 4 specimens with 72-79% probability, 4 specimens with 60-69% probability, and 1 specimen with 52% probability (Semple & B. Semple 10496, WAT, from Gila Co., Arizona). Six specimens of the var. adenophora a priori were assigned a posteriori to the var. wrightii group with 69% probability (Earle 393, NMC, from Lincoln Co., New Mexico), 59% probability (Carter & Carter 1218, NMC, from Catron Co., New Mexico), 59% probability (Bye 9883, NMC, from Mpio. Bocoyna, Chihuahua, Mexico), 56% probability (Carter s.n., NMC, from Swift Trail, Graham Co., Arizona), 56% probability (Todson s.n., NMC, from Hidalgo Co., New Mexico), and 52% probability (Metcalfe 1324, NMC, from Sierra Co., New Mexico). Twelve of the 19 specimens of var. wrightii (63%) were assigned a posteriori to the var. wrightii group: 2 specimens with 93% and 97%% probabilities, 1 specimen with 82% probability, 2 specimens with 78% and 73% probabilities, 5 specimens with 63-69% probability, and 2 specimens with 56% probability (Columbus 1686, NMC, from Luna Co., New Mexico) and 52% probability (Wooton 325, NMC, from Lincoln Co., New Mexico). Seven specimens of the var. wrightii a priori group were assigned a posteriori to var. adenophora with 82% probability (Van Devender 98-636, NMC, from Mpio. Sonora, Mexico), 71% probability (Semple & Heard 8038, WAT, from Grant Co., New Mexico), 62% probability (Anderson et al. 921, NMC, from Graham Co., Arizona), 62% probability (Ward 81-582, NMC, Lincoln Co., New Mexico), 52% probability (Semple & Heard 8147, WAT, from Lincoln Co., New Mexico), 52% probability (Hess 2334, NMC, from Catron Co., New Mexico), and 52% probability (Ward & Peterson 83-070, NMC, from Hidalgo Co., New Mexico).

Table 10. Linear and jackknife classification matrices from the Classificatory Discriminant Analysis of two varietal/form level a priori groups; a posteriori placements to groups in rows; alternative variety concept.

Group	adenophora	wrightii	% correct
adenophora	11	6	65
wrightii	7	12	63
Totals	18	18	64

Jackknife classification matrix

Group	adenophora	wrightii	% correct
adenophora	11	6	65
wrightii	7	12	63
Totals	18	18	64



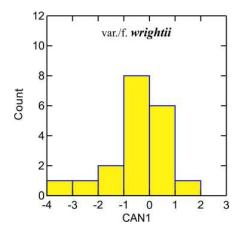


Figure 19. Histograms of CAN1 scores for 36 specimens of *Solidago wrightii*: var./f. *adenophora* morphs and var./f. *wrightii* morphs (black diamonds); identifications based on numbers of phyllary glands and hairs.

Frequencies of CAN1 canonical scores for 36 specimens of var. *adenophora* and var. *wrightii* are presented in histograms in Fig. 19. The Eigenvalue on the first axis was 0.279.

#### **DISCUSSION**

The results from all the discriminant analyses support the recognition the following taxa in the *Solidago* subsect. *Thyrsiflorae: S. buckleyi, S. capulinensis, S. correllii, S. petiolaris* (var. *angusta*, var. *petiolaris*, and var. *wardii*), *S. orientalis, S. spellenbergii*, and *S. wrightii* (no varieties or forms recognized). However, not all *a priori* groups separated strongly and the percentages of specimens assigned *a posteriori* to their corresponding *a priori* groups varied and the assignment probabilities were not consistently high. Overall, the seven species are likely closely related and have not evolutionarily diverged greatly in multiple characters.

Of the two new species *Solidago correllii* and *S. spellenbergii*, (Semple 2017a and b) support was strong for recognizing *S. correllii* as a species and not just as var. *guadalupensis* in *S. wrightii*. There were similarities more frequently between *S. correllii* and *S. petiolaris* than to *S. wrightii*. Of note, one collection (*Carr et al. 16911*, TEX) annotated as *S.* aff. *correllii* (assigned a posteriori to *S. correllii* with 39% probability, 35% probability to *S. wrightii* and 26% to *S. petiolaris*) came from Jeff Davis Co., Texas and was the only specimen from that county not identified as *S. wrightii*. All other collections of *S. correllii* seen as part of this study came from the Guadalupe Mts. of Eddy Co., New Mexico, and Culberson Co., Texas, ca 80-100 mi NNW of the Jeff Davis Co. location. Although the one specimen of *S. wrightii* from Jeff Davis Co. (*Sherman et al. 202* WAT) included in the study was assigned a posteriori in the first and second analyses to *S. correllii*, it had broadly lanceolate to narrowly ovate green leaves and did not look like specimens of *S. correllii*, but the specimen had 18-24 disc florets, which is more typical of *S. correllii*, with a mean of 25 disc florets than typical of *S. wrightii* with a mean of 15 disc florets. With its elliptic-narrowly ovate leaves, *Sherman et al. 202* (WAT) was clearly not *S. correllii*, even if some floral traits were atypical.

The leaves of some specimens of *S. correllii* and some plants of *S. petiolaris* var. *angusta* were silvery from some viewing angles, but could look greener when viewed from directly above. In the field, silvery leaves of plants of var. angusta tended to be silvery and much lighter in color than other individuals of var. angusta. Thus, the silvery color is the result of light being reflected off the shiny leave surfaces (both abaxial and adaxial faces). The term "silvery" has to be used with caution because it is dependent upon the angle at which light is observed coming off leaves and because it has

been sometimes used to describe densely hairy leaves that are reflecting light of the surfaces of the hairs rather the leaf epidermis.

The sample size of N=1 for Solidago spellenbergii meant it could not be treated in the analyses as a separate a priori group. The a posteriori assignments of the holotype of S. spellenbergii to S. petiolaris with 51% in the first analysis and 64% in the second analysis and to S. wrightii with 0% and 1% certainly indicate that the holotype is not just an atypical form of S. wrightii, which is the only other species of subsect. Thyrsiflorae present in the Sierra Madre Occidental of Mexico. Four collections that were treated as S. wrightii and were from the Basaseachic area of Chihuahua and adjacent Sonora were included in the analyses and these were placed a posteriori into either S. wrightii or S. petiolaris (and less so to S. wrightii); none of these were as tall as the holotype of S. spellenbergii and none had mid and upper stem leaves like those of the holotype of S. spellenbergii. Semple (2017b) recommended additional sampling of the Cascada Basaseachic local area to find additional collections of S. spellenbergii. Additional sampling of the few mountainous areas between the Sierra Madre Oriental where S. orientalis occurs and the Sierra Madre Occidental might reveal additional undescribed narrowly endemic taxa in S. subsect. Thyrsiflorae.

In our first analysis, Solidago buckley and S. orientalis were found to be rather similar. In reality, this is not the case because there are a big differences in lower stem leaf size and shape; S. buckleyi has much bigger lower stem leaves than those seen of S. orientalis. In fact, the largest leaves in the subsection are the lower stem leaves of some S. buckleyi individuals. As well, S. buckleyi grows in the northeastern Ozarks and eastward, while S. orientalis is native to the Sierra Madre Oriental of mostly Nuevo Leon, Mexico (Fig. 13). In the analyses, the similarities between S. buckleyi and S. orientalis are the result of mid stem leaf serrations being selected in the STEPWISE analysis portion of the first analysis. These are the two species that consistently had obviously serrate lower and mid stem leaves. Rarely, lower and mid stem leaves of S. petiolaris var. petiolaris can be serrate but the teeth are generally smaller than those of *S. buckleyi*.

The results indicate that Solidago petiolaris and S. wrightii differ in a number of technical traits with numbers of hairs on the disc floret ovary/fruit body being significant. All specimens of S. wrightii had some hairs on disc floret ovaries/fruit bodies. Two-thirds of the S. petiolaris specimens had no hairs on the disc floret ovaries/fruit bodies, but a third did but mostly in very low numbers on the distal portions of some fruits and no hairs on others. Six collections of S. petiolaris included in the analyses did have sparsely to moderately hairy fruits and five of these were var. petiolaris plants from South Carolina, Georgia, Alabama and eastern Texas; some of these were placed a posteriori into S. petiolaris in the first two analyses, and some into S. correllii and S. wrightii. One plant of var. wardii from Kansas had sparsely strigose disc floret ovaries/fruit bodies. The ranges of the two species are essentially allopatric but are potentially sympatric in northeastern New Mexico and adjacent Colorado. It is highly unlikely that a plant with moderately hairy fruits found growing in the Carolinas, Georgia, Alabama, or eastern Texas in the Eastern deciduous woods would be a disjunct S. wrightii. The S. petiolaris plant with the hairiest fruit include the analyses came from eastern Texas and had the characteristic elongated narrow inflorescence and hairy phyllaries of var. petiolaris.

The two analyses of the three varieties within Solidago petiolaris clearly show that delineation and distribution of var. angusta and var. wardii presented by Nesom (2008) is a reasonable solution to dealing with the problem of defining the two western varieties of the species. Our results are in full agree with Nesom's observation that leaf features and phyllary features are not correlated. Presumably var. angusta was originally designated as a separate species on the basis of its narrow leaves and nearly glabrous phyllaries, while var. wardii was designated as a separate species on the basis of its silver leaf color (light reflecting off hairs?) and its canescent phyllaries. The confusion regarding the applications of the names to silver leaved specimens (either broad or narrow

leaves) and glandular or resinous non-hairy phyllaries is understandable in places like eastern Oklahoma, western Arkansas and much of Missouri where the majority of specimens do not match either the type of S. angusta or the type of S. angusta. However, by defining var. angusta on the basis of phyllary vestiture and accepting both green or silver, narrow lanceolate leaved morphs and green or silver ovate-leaved morphs because all these morphs have phyllaries that are not hairy and are sparsely to densely resinous (due to varying numbers of small glands), the confusion is for the most part eliminated. In this case, the silvery color is due to light reflecting of the shiny non-hairy leaf surfaces. Either a more broadly defined var. angusta (see the first varietal level analysis of S. petiolaris) or a more broadly defined var. wardii (see the second varietal level analysis of S. petiolaris) was needed. Our results indicate that the first alternative of a broadly defined var. angusta is much more strongly supported statistically than the latter alternative.

Support for dividing Solidago wrightii into a hairy var. wrightii and a glandular var. adenophora is low for both the percents of correct placement a posteriori and in the low probabilities for the correct placements. While the null hypothesis was not rejected statistically, there was no obvious way of separating plants with glandular upper leaves and phyllaries and those with hairy upper leaves and phyllaries, except by group centroid thinking, that is, forcing all specimens into one or the other group. Both the numbers of glands and the numbers of hairs were continua of variation that could not be split in a non-arbitrary way into distinct groups. In our sample, more specimens had both hairs and glands that did those with just glands or just hairs. While admittedly, the most glandular non-hairy plants are very distinct from the most hairy non-gland/minimally glandular plants, the details reveal that such plants are just the ends of continua. Nesom (2008) opted to reduce the rank of the two varieties to just forms. Our conclusion is that even this is not justified and var. adenophora belongs in synonymy under the species name S. wrightii.

In conclusion, the seven species of Solidago subsect. Thyrsiflorae are clearly closely related but differ sufficiently in obvious and some technical traits that identification of most specimens to species should not be a great challenge when geography is also considered. Most significant is the general lack of data on basal rosette leaves. Unlike some groups of goldenrods, basal rosettes are not obvious and generally not present in the field at the time of flowering. If they were, then many more collections would include rosettes. The vast majority of specimens have no basal rosette leaves and often lacked most lower stem leaves at the time of flowering. One collection (Wooton s.n., NMC) included in the study did have a well developed basal rosette and lower stem leaves and these are illustrated in Figs. 20 A-B. A second collection of S. wrightii (Powell & Flyr 1493, TEX) seen but not included in the analyses had several young rosettes present on the rootstooks; the rosette leaves were similar to those of S. correllii (Semple 2017a, Fig 5), but the mid and upper stem leaves were like those of S. wrightii and not narrowly lanceolate. The presence or absence of rosette leaves has been used in keys to identification (Semple & Cook 2006). The basal leaves in Fig. 20 are rather typical of those occurring in the genus Solidago, larger than some and smaller than others but possessing the winged petiolate proximal portion.

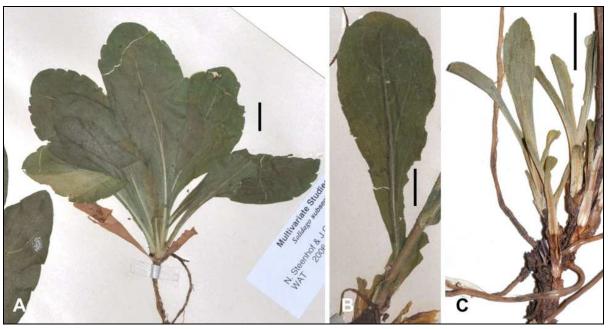


Fig. 20. Basal rosette and lower stem leaf (B) of *Solidago wrightii*. **A-B.** *Wooton s.n.* (NMC) from Dona Ana Co., New Mexico. **C.** *Powell & Flyr 1493* (TEX) from Jeff Davis Co., Texas. Scale bars = 1 cm.

# Key to taxa in Solidago subsect. Thrysiflorae

- - - 3. Cauline leaves serrate, proximal oblanceolate, distal oblanceolate to elliptic; cypselae moderately to moderately densely strigose; Sierra Madre Oriental, mostly Nuevo León, Mexico

      Solidago orientalis
    - 3. Proximal cauline leaves entire to sparsely serrate (rarely serrate in *S. petiolaris*), oblanceolate to obovate; distal lanceolate to narrowly to broadly elliptic; much of the southern USA and Sierra Madre Oriental in Mexico.
      - 4. Cypselae very sparsely to moderately densely strigose (rarely glabrate).

        - 5. Cypselae very sparsely strigose.
          - 6. Phyllaries long attenuate, outer ½ or more the length of the inner, glandular, resinous; cauline leaves green, resinous glandular, glabrate to very sparsely strigose;

stems very sparsely villose-strigose; arrays with elongated lower branches, open; Parque Nacional de Cascada Basaseachic, Chihuahua Solidago spellenbergii 6. Phyllaries lanceolate, graduated, sparsely glandular and moderately strigose distally, cauline leaves grayish-green, moderately short strigose; stems densely short villose-canescent; arrays congested narrowly paniculiform; Mt. Capulin, Union Co., 

4. Cypselae glabrous (rarely glabrate to very sparsely strigose; very rarely strigose); arrays of heads often narrow, elongated; cauline leaves entire except rarely in SE USA; SE USA to northeastern New Mexico, southeastern Colorado, Texas, northern Coahuila, Mexico

- 7. Middle and inner series phyllaries glabrous, usually minutely glandular or resinous and shiny; mid and upper stem leaves usually narrowly lanceolate, rarely broadly lanceolate to ovate, green to shiny silvery; Missouri to Louisiana west to eastern Kansas to eastern 7. Middle and inner series phyllaries sparsely to moderately strigose, sometimes minutely glandular; mid and upper stem leaves lanceolate-elliptic to ovate-elliptic.
  - 8. Involucres at anthesis 6-8 mm (mean = 7.5 mm), mid leaves 12-21(-32) mm wide; North Carolina to northern Florida west to Alabama, disjunct in east Texas

......var. **petiolaris** 8. Involucres at anthesis 4.3-6.3(-7; mean = 5.3 mm); southern Nebraska, Kansas, western Oklahoma, western Texas, northeastern New Mexico, southeastern Colorado

var. **wardii** 

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