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DOCUMENTING A *SOLIDAGO BICOLOR* × *S. BRENDIAE* HYBRID (ASTERACEAE: ASTEREAE) FROM NOVA SCOTIA

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ABSTRACT

Hinds (1984) reported a wild hybrid between *Solidago bicolor* and *S. canadensis* and from Cape Breton Island, Nova Scotia, Canada. A single herbarium sheet *Hinds 3828* (UNB) was examined and initially determined to include voucher specimens of *S. bicolor*, *S. bicolor* × *S. brendiae* and *S. brendiae*. A multivariate analysis of 52 specimens of the three species *S. bicolor*, *S. brendiae*, and *S. canadensis* and the putative *S. bicolor* × *S. brendiae* specimen was performed and confirmed that *S. brendiae* was the likely second parent, not *S. canadensis*. The plot of first and second axes canonical scores for all specimens including the hybrid indicated that the putative hybrid was likely an interspecific *Solidago bicolor* × *S. brendiae* hybrid as did several other traits not included in the analysis.

Hinds (1984) reported a collection of putative *Solidago bicolor* L. × *S. canadensis* L. from Cape Breton Island National Park, Nova Scotia, Canada (roadside halfway to first salmon pool on Chéticamp R., gravelly roadside, one large plant with both parents, 11 Aug 1980, *Hinds 3828* UNB). The herbarium sheet includes voucher shoots of the two putative parent taxa and the putative hybrid (Figs. 1-4). Based on the distribution of *S. canadensis* and *S. brendiae* Semple (Semple 2013; Semple et al. 2013; Semple, frequently updated), the possibility existed that the second parent was not *S. canadensis* but *S. brendiae*, which was only described in 2013. *Solidago bicolor* is a member of *S.* subsect. *Squarrosae* A. Gray, which includes species with club- or wand-shaped inflorescences (elongated lower inflorescence branches are also wand- or club-shaped), with petiolate or subpetiolate and broadly oblanceolate to obovate basal rosette and lower stem leaves generally much larger than the upper stem leaves and with phyllaries tending to be oblong and obtuse to rounded tipped (Semple & Cook 2006). *Solidago brendiae* and *S. canadensis* are members of *S.* subsect. *Triplinerviae* (Torrey & A. Gray) G.L. Nesom, which generally have secund pyramidal-shaped inflorescences, lower stem leaves that not the largest and usually not present at flowering. Also, lower and often mid and upper stem leaves of species of subsect. *Triplinerviae* have two prominent lateral veins that arise part way along the midvein; this is the “triple-nerved” condition of the subsection epithet. *Hinds 3828* was borrowed from UNB and morphological traits scored up for inclusion in a multivariate analysis of *S. bicolor*, *S. brendiae*, and *S. canadensis* var. *canadensi*s specimens. The results of the analysis are presented below.

MATERIALS AND METHODS

In total, 52 specimens from the J.K. Morton personal herbarium (now deposited in ROM, MIN, UNB, and WAT in MT) were selected for inclusion in the analysis of 17 specimens each of *Solidago bicolor*, *S. brendiae*, and *S. canadensis* and one putative specimen of *S. bicolor* × *S. brendiae*. All traits scored are listed in Table 1. Specimens of *S. bicolor* came from Connecticut, Georgia, Maine, Maryland, New Hampshire, Nova Scotia, Ontario, Pennsylvania, Prince Edward Island, Québec, Virginia, and West Virginia. Specimens of *S. brendiae* came from New Brunswick, Newfoundland, Nova Scotia, Ontario, Prince Edward Island, and Québec. Specimens of *S. canadensis* (var. *canadensis* only) came from Maine, Massachusetts, New Brunswick, Nova Scotia, New York, Ontario, Québec, and Vermont. Multivariate data on specimens of *S. brendiae* and *S. canadensis* were selected from specimens previously used in Semple et al. (2013).

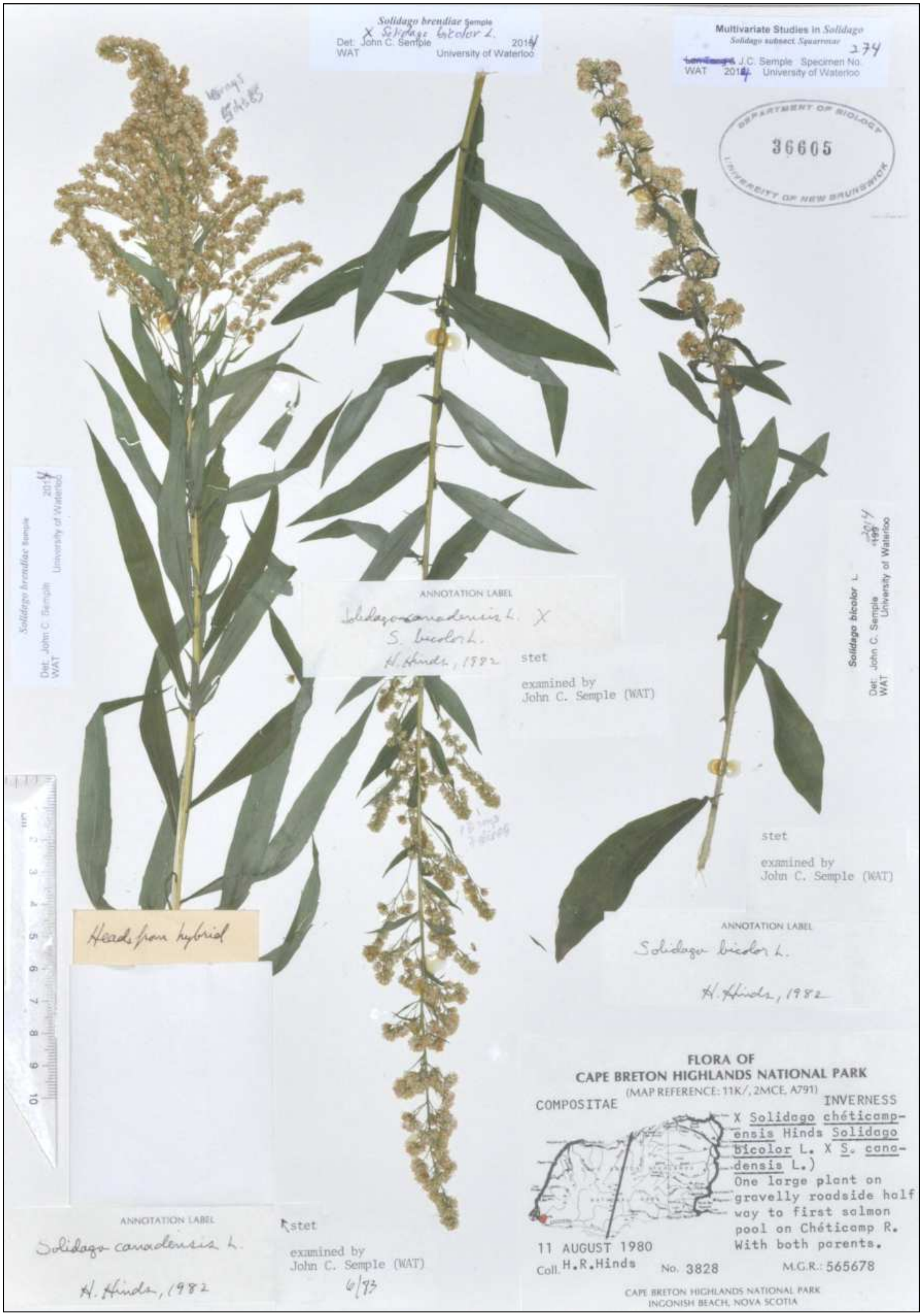

Figure 1. *Hinds 3828* (UNB); *Solidago brendiae, S. bicolor* × *S. brendiae*, and *S. bicolor* from Cape Breton Highlands National Park, Nova Scotia.

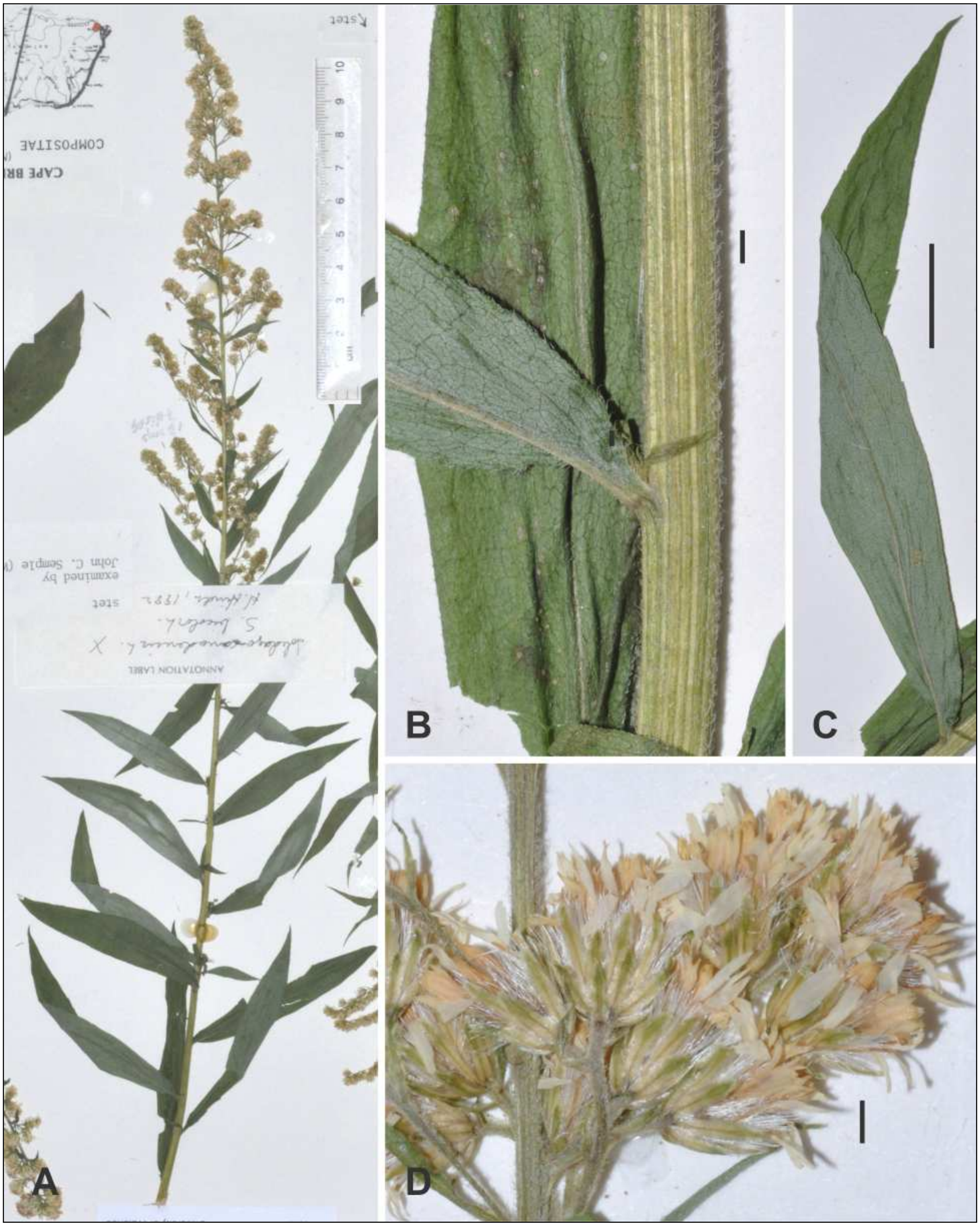

Figure 2. *Hinds 3828* (UNB): *Solidago bicolor* × *S. brendiae*. **A.** Upper portion of shoot. **B.** Lower stem leaves. **C.** Mid stem and leaf. **D.** Flowering heads. Scale bar = 1 cm in A and C; = 1 mm in B and D.

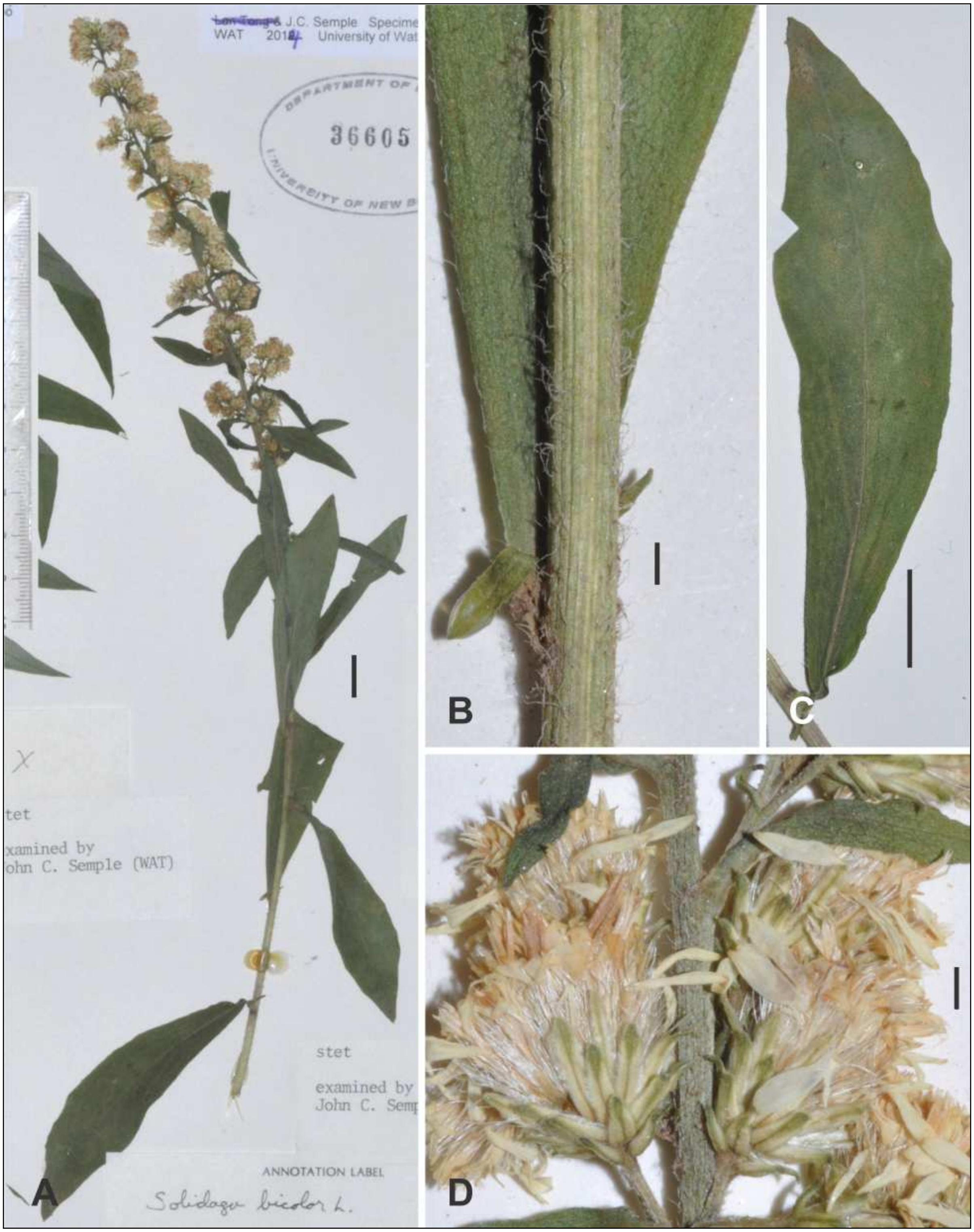

Figure 3. *Hinds 3828* (UNB): *Solidago bicolor*. **A.** Upper portion of shoot. **B.** Lower mid stem leaf. **C.** Mid stem and leaf. **D.** Flowering heads. Scale bar = 1 cm in A and C; = 1 mm in B and D.

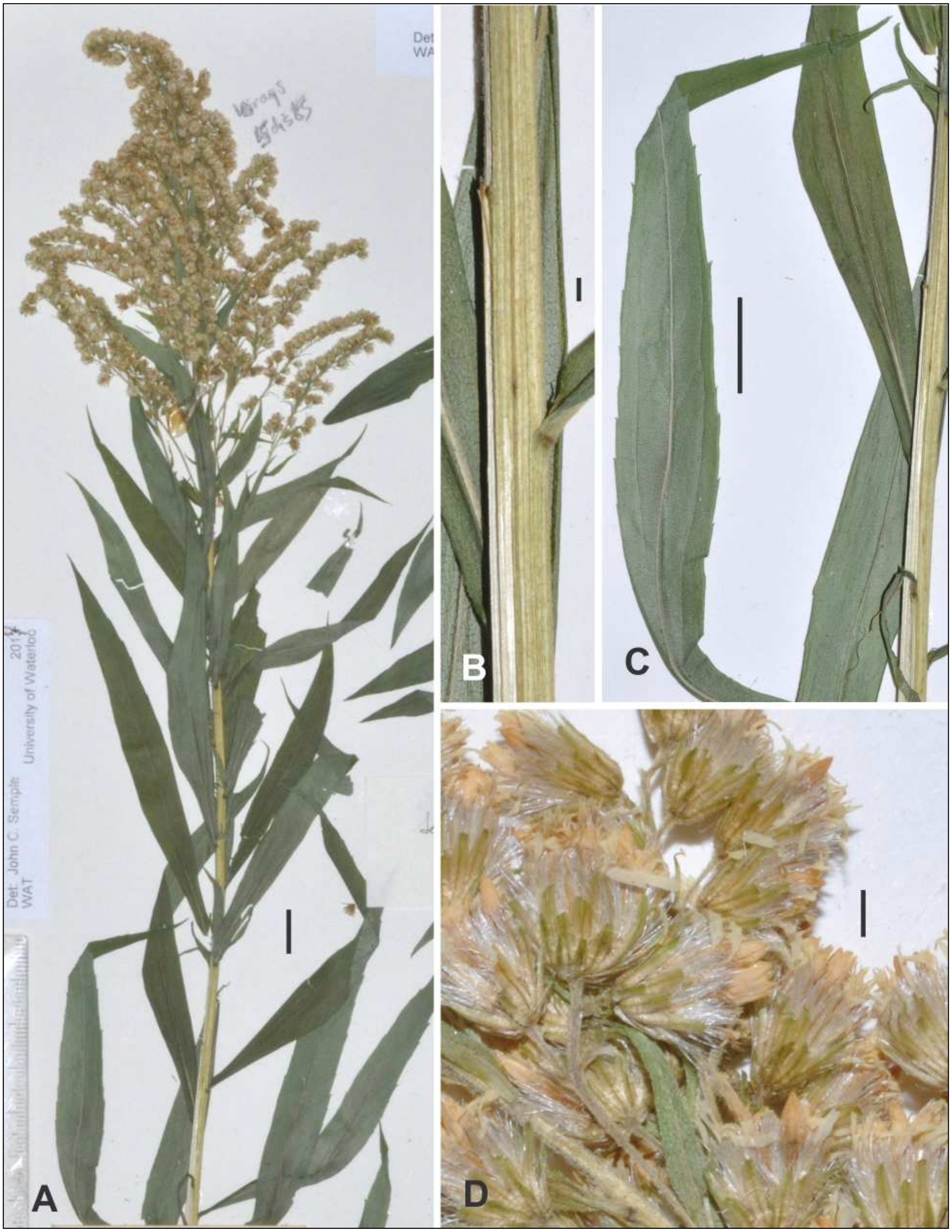

Figure 4. *Hinds 3828* (UNB): *Solidago brendiae*. A. Upper portion of shoot. B. Lower stem leaves. C. Mid stem and leaf. D. Flowering heads. Scale bar = 1 cm in A and C; = 1 mm in B and D.

Table 1. Traits scored for the multivariate analyses of *Solidago bicolor*, *S. brendiae*, and *S. canadensis* and one specimen of *S. bicolor* × *S. brendiae*.

Abbreviation	Description of trait scored
STEMHT	Stem height measured from the stem base to tip(cm)
BLFLN	Basal leaf length measured from the leaf base to tip(mm)
BLFPETLN	Petiole length of basal leaf- measured from the petiole base to tip of basal leaf (mm)
BLFWD	Basal leaf width measured at the widest point (mm)
BLWTOE	Basal leaf measured from the widest point to the tip(mm)
BLFSER	Basal leaf dentation-number of serrations of basal leaf
LLFLN	Lower leaf length measured from the leaf base to tip(mm)
LLPLETLN	Petiole length of lower leaf- measured from the petiole base to tip of the lower leaf (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
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
INVOLHT	Involucre height (mm)
OPHYLN	Outer phyllary length (mm)
IPHYLN	Inner phyllary length (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 cypsela body length at anthesis (mm)
RPAPLN	Ray floret pappus length at anthesis (mm)
RPUB	Number of pubescence per ray achene (mm)
DCORLN	Disc corolla length from the base to tip of the corolla lobes (mm)
DLOBLN	Disc corolla lobe length lobe (mm)
DACHLN	Disc achene length (mm)
DPAPLN	Disc pappus length (mm)

Not all traits scored were included in the analyses. Traits used to define a priori groups were not included in the analyses to avoid circular logic. Differences between upper leaf traits and ray floret color were used to define a priori groups. Specimens of *Solidago bicolor* usually had lower stem leaves that were the largest on the shoot. Specimens of *S. brendiae* and *S. canadensis* lacked lower stem leaves and therefore traits on lower stem leaves were excluded. A Pearson pairwise correlation matrix was generated and only one trait of a pair of traits with a correlation value $|r| > 0.7$ was included in the analyses. The analyses included the following less correlated traits: MLFLN, MLFWD, MLFSER, CAPL, CAPW, INVOLHT, OPHYLL, RAYNUM, RSTRAPL, RSTRAPWD, and DISCNUM.

All analyses were performed using SYSTAT v.10 (SPSS 2000) following the methods of Semple et al. (2013). Initially STEPWISE discriminant analysis was used to select traits that most strongly separated the three a priori groups in N-dimensional hyperspace. Because the number of traits selected was less than N-1 where N equals the smallest sample size for any of the a priori groups there was no need to select traits and run a complete analysis subsequently. In this study, N-1=16 and so the results of the STEPDISC analysis are presented. A complete analysis using all 11 traits was also run for comparison. Classificatory discriminant analyses were run to place a posteriori the single hybrid specimen into one of the three a priori species level groups.

RESULTS

In the STEPWISE discriminant analysis of three species level a priori groups *Solidago bicolor*, *S. brendiae* and *S. canadensis*, the following eight traits listed in order of decreasing F-to-remove values were selected (F-to-remove): number of ray florets (28.00), involucre height (13.12), number of disc florets (11.89), inflorescence length (11.28), ray floret strap length (7.09), inflorescence width (6.72), mid lead length (5.70), and outer phyllary length (4.53). 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 between group centroids indicate the largest separations were between *S. bicolor* and *S. canadensis* (53.426) and between *S. bicolor* and *S. brendiae* (47.482). The smallest separation was between *S. brendiae* and *S. canadensis* (13.078).

In the Classificatory Discriminant Analysis of the three species level a priori groups *S. bicolor, S. brendiae* and *S. canadensis* the percents of correct classification were all 100%. The Classification matrix and Jackknife classification matrix are presented in Table 3. All 17 specimens of *S. bicolor* were placed a posteriori into the *S. bicolor* group with 100% probability. Fifteen of the 17 specimens of *S. brendiae* were placed a posteriori into the *S. brendiae* group with 97-100% probability; one was placed into the *S. brendiae* group with 91% probability; and one was into the *S. brendiae* group with 73% probability (27% to the *S. canadensis* group).

Table 2. Between groups F-matrix for the three a priori group analysis (df = 11, 38).

Group	*bicolor*	*brendiae*	*canadensis*
bicolor	0.000		
brendiae	47.482	0.000	
canadensis	53.426	13.078	0.000

Wilks' lambda
Lambda = 0.0214 df = 8 2 48
Approx. F= 29.8996 df = 16 82 prob = 0.0000

A two dimensional plot of CAN1 versus CAN 2 canonical scores for specimens of *Solidago bicolor, S. brendiae, S. canadensis*, and the single collection of *S. bicolor* × *S. brendiae* are presented in Fig. 5. The positions of the *S. bicolor* and *S. brendiae* specimens mounted with the hybrid on *Hinds 3828* (UNB) are indicated by P1 and P2, respectively. Eigen values on the first two axes were 12.321 and 2.506.

The results of the complete analysis using all 11 characters was overall similar but with a slight decrease the average probabilities of correct assignments a posteriori of specimens to *Solidago brendiae* and *S. canadensis*, including the *S. bicolor* × *S. brendiae* specimen to *S. brendiae* (93%). These additional traits were useful in the case of a few specimens but weakened the overall results in terms of group centroid separation. The full details are not presented here.

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

Linear classification matrix

	bicolor	***brendiae***	***canadensis***	% correct
bicolor	17	0	0	100%
brendiae	0	17	0	100%
canadensis	3	0	17	100%
Total	17	17	17	100%

Jackknifed classification matrix

	bicolor	***brendiae***	***canadensis***	**% correct**
bicolor	17	0	0	100%
brendiae	0	15	2	88%
canadensis	0	1	16	94%
Total	17	16	18	94%

DISCUSSION

The results support the identification of the hybrid as *Solidago bicolor* × *S. brendiae*. Because a single specimen cannot be treated as an a priori group in discriminant analyses, the hybrid specimen was not assigned to an a priori group but was included in the a posteriori classificatory discriminant analysis, which assigned the specimen a posteriori to *S. brendiae* with 90% probability (10% to *S. canadensis*). On these results, the putative hybrid could be rejected as a hybrid. However, in the canonical discriminant analysis (a dimension reduction technique), the first and second canonical scores for the hybrid placed the specimen between the *S. bicolor* group of specimens and the *S. brendiae* group of specimens, but closer to the latter (Fig.5). The position of the hybrid is close to the two specimens of *S. brendiae* placed a posteriori in *S. brendiae* with the 73% and 91% probabilities. The specimens of the two parent taxa on *Hinds 3828* (UNB) are indicated in Fig.5 (P1 and P2); the hybrid is positioned on the diagram about half between these two specimens, which is where one would expect a hybrid to be placed on such a diagram.

A more traditional scatter plot diagram (e.g., see Fig. 13 in Semple and Semple 1977) could have been constructed and would have allowed the inclusion of traits difficult to score for inclusion in discriminant analyses. The rays of *Solidago bicolor* are white (Fig. 3D). The rays of the hybrid are lighter yellow in color (Fig. 2D) than those of the *S. brendiae* (Fig. 4D) and *S. canadensis* species, although this trait is less reliable on dried collections than the color difference would be on fresh plants in the field. The fresh rays of *S. brendiae* are the typical bright yellow of most goldenrods (see Fig 3E in Semple 2013). Hinds (1984) stated that "The hybrid occurred with both parents growing nearby and combined the characteristics of both." I suspect that what caught the late Harold Hinds' attention was the lighter creamy yellow color of the rays of the hybrid. Ray color was not included as a trait in the discriminant analysis. The triple-nerved condition of the hybrid leaves was less obvious (Figs. 2B-C) than on specimens of the two species of subsect. *Triplinerviae* (Fig. 4C). Another obvious indicator of the hybrid condition would be the size and shape of lower stem leaves, which differ greatly between members of subsect. *Squarrosae* and those of subsect. *Triplinerviae* (Semple & Cook 2006). *Hinds 3828* does not include the lower portions of the stems of the hybrid shoot or its parents. Therefore, lower stem leaf traits were not available for comparison.

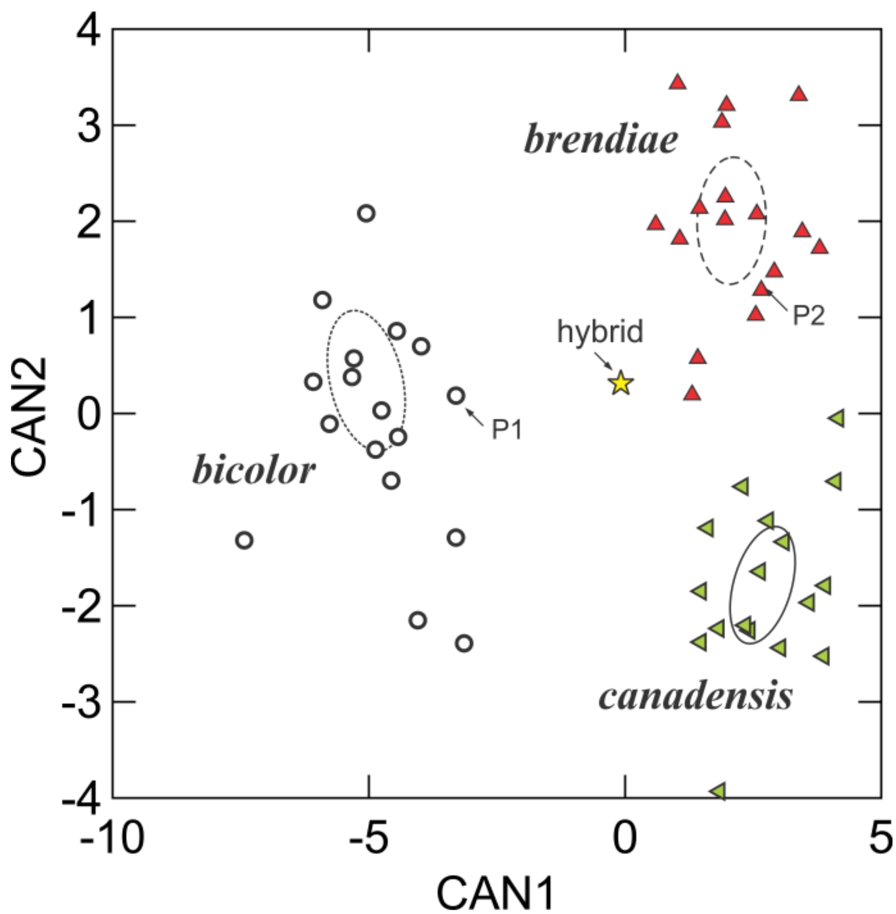

Figure 5. Plot of CAN1 versus CAN2 of specimens of *Solidao bicolor* (open circles; position of *Hinds 3828* UNB indicated by P1), *S. brendiae* (red triangles; position of *Hinds 3828* UNB indicated by P2), *S. canadensis* (green triangles), and a *S. bicolor* × *S. brendiae* specimen (yellow star).

There is also the possibility that the hybrid specimen is not an F1, but is an F2 backcross of an F1 individual with the *Solidago brendiae* parent. Such a specimen would have more traits in common with *S. brendiae* than the hybrid. No experimental hybrids were created as part of this study. Additional sympatric populations of *S. bicolor* and *S. brendiae* need to be explored in the field to assess whether or not F2 plants occur or hybridization is restricted to just F1 interspecific hybrids.

The known chromosome numbers for *Solidago bicolor*, *S. brendiae* and *S. canadensis* are all diploid, $2n = 18$. Hybridization would be facilitated by the parents having the same ploidy level.

Also, the lack of known polyploids in the three species means that ploidy level was not a factor in differences between morphological traits of the three species and the hybrid.

My conclusion is that Hinds did collect an interspecific hybrid in 1980 but he was understandably wrong in assuming it was a cross between *Solidago bicolor* and *S. canadensis*. *Solidago brendiae* was not described until recently (Semple 2013) and would not have been an option for him to choose as a parent at the time he made the collections and published his interpretation in 1984. Documenting statistically or experimentally the occurrence of interspecific hybridization in *Solidago* needs to be done for multiple other putative cases.

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