

DOCUMENTING A *SOLIDAGO BRENDAE* × *S. SEMPERVIRENS* HYBRID FROM THE GASPÉ, QUEBEC (ASTERACEAE: ASTEREAE)

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ABSTRACT

A collection from Mont-Louis, northern Gaspé, Québec, was originally identified as *Solidago canadensis* × *S. sempervirens*, but the location is outside the range of the first putative parent species. *Solidago brenndae* does occur along the north shore of the Gaspé. A multivariate analysis of 61 specimens of *S. brenndae*, *S. canadensis*, and *S. sempervirens* and the putative *S. brenndae* × *S. sempervirens* specimen was performed and confirmed that *S. brenndae* and *S. sempervirens* were the likely parents of the hybrid

During the process of examining and annotating all collections of *Solidago* in the Marie-Victorin Herbarium at the Jardin botanique in Montréal, (MT; Thiers continuously updated), a specimen identified as *Solidago canadensis* L. × *S. sempervirens* L. was encountered: *Labrecque & Lamoureux s.n.* (MT, Figs. 1-2; cited below). The collection site is on the northern shore of the Gaspé Peninsula, which is north of the range of *S. canadensis* but within the range of *S. brenndae* Semple (Semple 2013; Semple et al. 2013; Semple 2019 frequently updated). Therefore, the possibility that one of the putative parents was not *S. canadensis* but *S. brenndae*, which was only described in 2013, seemed more likely.

The second putative parent, *Solidago sempervirens*, is a member of subsect. *Maritimae* (Torr. & A. Gray) G.L. Nesom, which includes species with basal rosette and lower stem leaves that are generally much larger than upper stem leaves and have petioles that sheath the lower stem (Semple & Cook 2006). *Solidago brenndae* and *S. canadensis* are members of subsect. *Triplinerviae* (Torrey & A. Gray) G.L. Nesom, which generally have secund pyramidal shaped inflorescences and lower stem leaves that are 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 partway along the midvein; this is the “triple-nerved” condition of the subsection’s epithet.

Labrecque & Lamoureux s.n. was borrowed from MT and morphological traits scored for inclusion in a multivariate analysis of *Solidago brenndae*, *S. canadensis* var. *canadensis*, and *S. sempervirens* specimens. The results of the analysis are present below.

Materials and methods

In total, 62 specimens from MIN, the J.K. Morton personal herbarium now deposited in TRT, UNB, and WAT in MT (Thiers, continuously updated) were selected for inclusion in the analysis of *Solidago brenndae* (27 specimens), *S. canadensis* (21 specimens) and *S. sempervirens* (13 specimens), and one putative specimen of *S. brenndae* × *S. sempervirens*. All traits scored are listed in Table 1. Specimens of *S. brenndae* 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, New York, Nova Scotia, Ontario, Québec, and Vermont. Specimens of *S. sempervirens* came from Delaware, Louisiana, Michigan, New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Québec. Multivariate data on specimens of *S. brenndae* and *S. canadensis* were selected from specimens previously used in Semple et al. (2013).

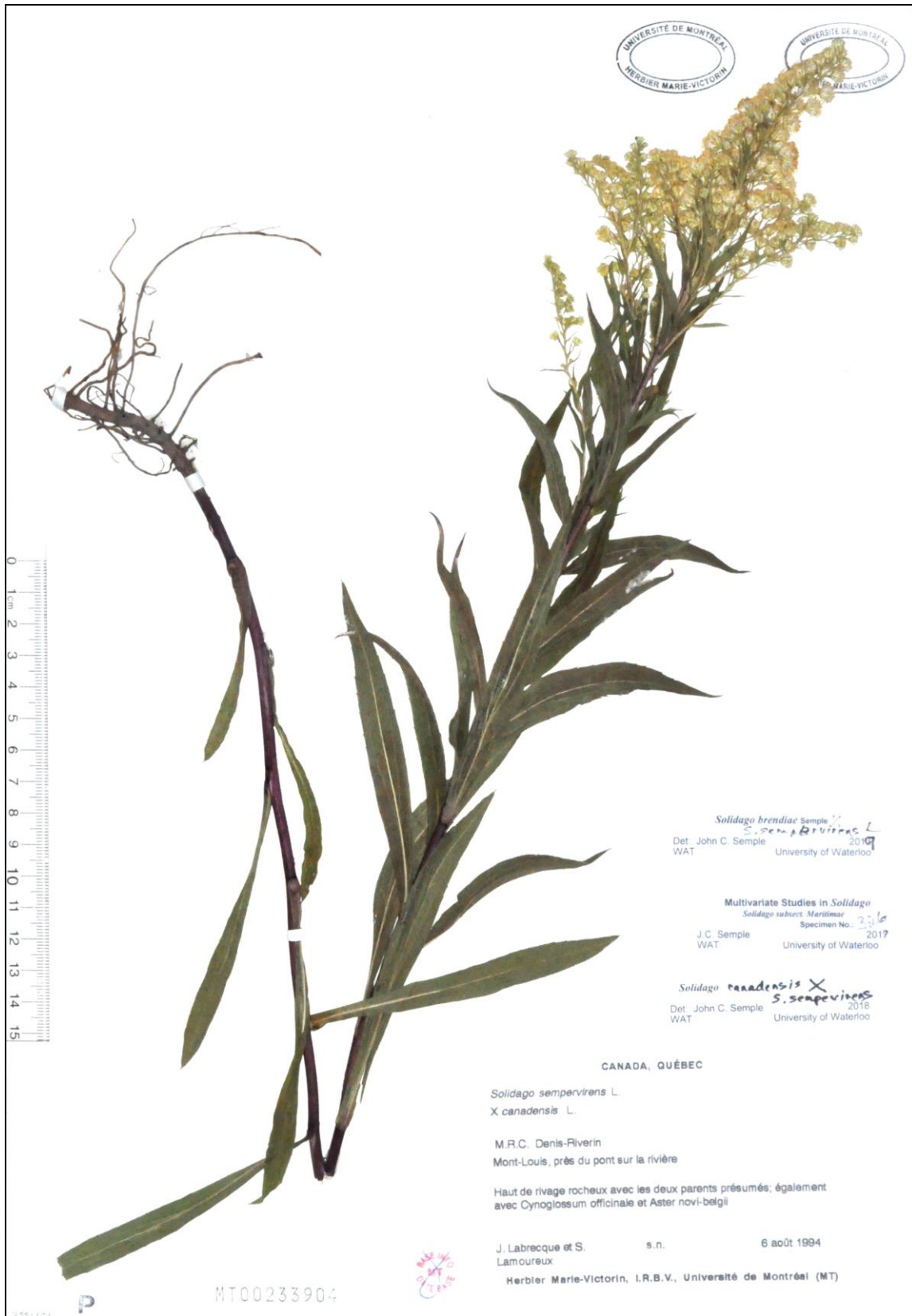


Figure 1. Labrecque & Lamoureux s.n. (MT); *Solidago brenidae* × *S. sempervirens* from Mont-Louis, northern Gaspé, Québec.



Figure 2. Details of *Labrecque & Lamoureux s.n.* (MT); *Solidago brendae* × *S. sempervirens*. **A-B.** Lower and mid stems. **C.** Lower stem leaf. **D-F.** Mid stem leaf, margin, and proximal abaxial surface. **G-H.** Upper stem leaf and raised veins on abaxial surface. **I.** Heads. Scale bar = 1 cm in A-B, E, and H-I; = 1 mm in C-D and F-G.

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

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 from 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)
CAPWD	Width of inflorescence (cm)
CBRNCHLN	Length of longest lower inflorescence branches (cm)
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)

Voucher, *Solidago brenidae* × *S. sempervirens*. Québec. M.R.C. Denis-Riverin, Mont-Louis, près du pont sur la rivière {near the bridge on the river}, haut de rivage rocheux avec les deux parents présumés, également avec *Cynoglossum officinale* et *Aster novi-belgii*, 6 Aug 1994, Labrecque & Lamoureux s.n. (MT). Figures 1 and 2.

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 in lower stem leaf traits were used to define a priori groups in part. Specimens of *S. sempervirens* usually had lower stem leaves that were the largest on the shoot. Specimens of *S. brenidae* 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 traits: mid leaf length, width, and number of margin serrations, upper leaf length, width, and number of margin serrations, involucre height, numbers of ray and disc florets, and disc floret corolla length.

Solidago brenidae and *S. canadensis* do not produce basal rosettes during the flowering season and usually lower stem leaves have senesced at flowering; all traits for basal and lower stem leaves were not included in the analysis because inclusion would have resulted in only individuals of *S. sempervirens* being included. All individuals of *S. sempervirens* have lower stem leaves that partially or fully sheath the stem, while the lower stem leaves of *S. brenidae* and *S. canadensis* do not sheath the stem.

The single analysis was performed using SYSTAT v.10 (SPSS 2000) following the methods of Semple et al. (2013). STEPWISE discriminant analysis was used to select traits that most strongly separated the three a priori groups in N-dimensional hyperspace. 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-rank a priori groups *S. brenidae*, *S. canadensis* and *S. sempervirens*, the following four traits listed in order of decreasing F-to-remove values were selected (F-to-remove): involucre height (67.28), number of ray florets (55.84), number of disc florets (29.61), and upper leaf length (7.46). 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 *Solidago brenidae* and *S. sempervirens* (131.122) and between *S. canadensis* and *S. sempervirens* (130.623). The smallest separation was between *S. brenidae* and *S. canadensis* (34.737).

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

Group	<i>brenidae</i>	<i>canadensis</i>	<i>sempervirens</i>
<i>brenidae</i>	0.000		
<i>canadensis</i>	34.737	0.000	
<i>sempervirens</i>	131.122	130.623	0.000

Lambda = 0.0210 df = 4 2 54 Approx. F= 75.3145 df = 8 102 prob = 0.0000

In the Classificatory Discriminant Analysis of the three species level a priori groups *Solidago brenndae*, *S. canadensis*, and *S. sempervirens* the percents of correct classification were all 100% for all three species. The Classification matrix and Jackknife classification matrix are presented in Table 3. All 13 specimens of *S. sempervirens* a priori group were placed a posteriori into *S. sempervirens* with 100% probability. All 27 specimens of the *S. brenndae* a priori group were placed a posteriori into *S. brenndae* group: 18 specimens with 100% probability, 7 specimens with 92-99% probability, 1 specimen with 82% probability, and 1 specimen with 72% probability (28% to *S. canadensis*). All 17 specimens of the *S. canadensis* a priori group were placed a posteriori into *S. canadensis* plus 4 additional specimens included only a posteriori; 14 specimens with 100% probability and 7 specimens with 96-99% probability. Two specimens of *S. canadensis* not included a priori were placed a posteriori into *S. brenndae* with 75% probability each. The single putative *S. brenndae* × *sempervirens* specimen was placed a posteriori into *S. brenndae* with 100% probability.

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

	<i>brenndae</i>	<i>canadensis</i>	<i>sempervirens</i>	% correct
<i>brenndae</i>	27	0	0	100%
<i>canadensis</i>	0	17	0	100%
<i>sempervirens</i>	0	0	13	100%
Total	27	17	13	100%

Jackknifed classification matrix

	<i>brenndae</i>	<i>canadensis</i>	<i>sempervirens</i>	% correct
<i>brenndae</i>	27	0	0	100%
<i>canadensis</i>	0	17	0	100%
<i>sempervirens</i>	1	0	12	92%
Total	28	17	12	98%

A two dimensional plot of CAN1 versus CAN 2 canonical scores for 62 specimens of *Solidago brenndae*, *S. canadensis*, *S. sempervirens*, and the single collection of *S. brenndae* × *S. sempervirens* are presented in Fig. 3. Eigen values on the first two axes were 12.059 and 2.653.

Discussion

The results of the analysis plus the character states of several traits not included in the multivariate analysis support the revised identification of the *Labreque & Lamoureux s.n.* (MT) as *Solidago brenndae* × *S. sempervirens*, not the original identification as *S. canadensis* × *S. sempervirens*. 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. brenndae* with 100% probability (0% to *S. canadensis*). On this result, 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 place the hybrid specimen at the periphery the *S. brenndae* cluster of specimens, on the *S. sempervirens* side of the cluster and not on the side closer to *S. canadensis* (Fig. 3). 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 that could not be included in discriminant analyses. Like all specimens of *S. sempervirens*, *Labreque & Lamoureux s.n.* (MT) had lower stem leaves with petioles that sheathed or partially embraced the lower stem

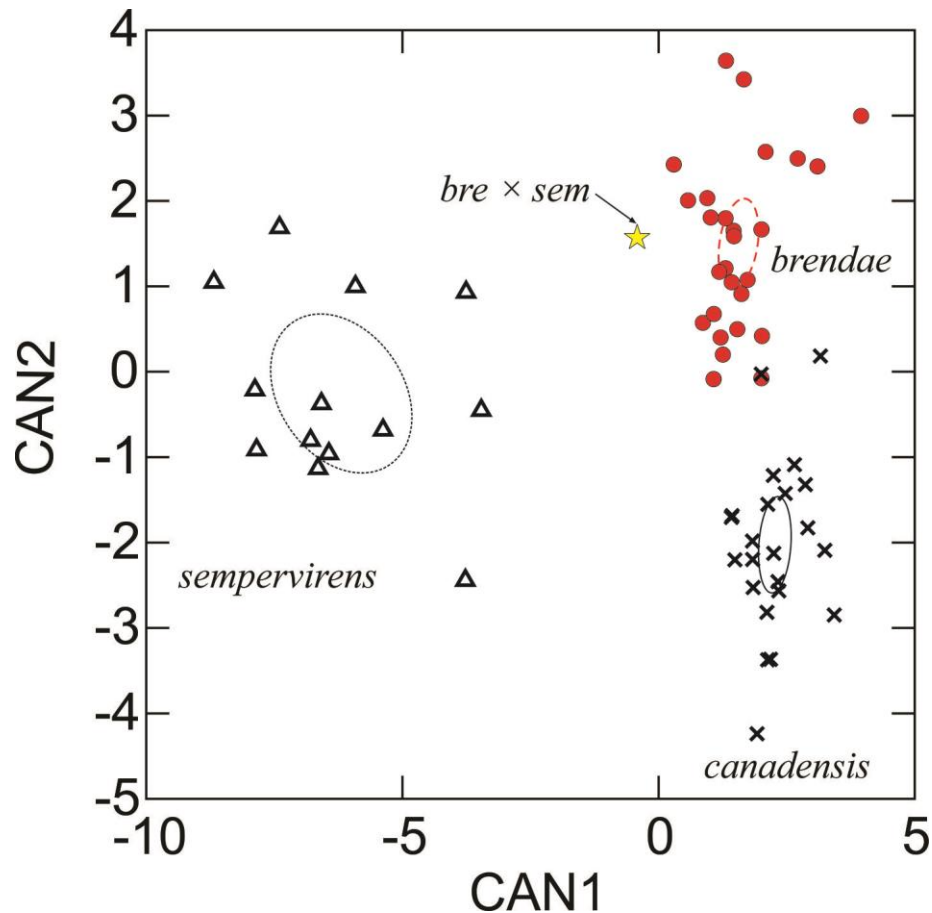


Figure 3. Plot of CAN1 versus CAN2 of specimens of *Solidago brenndae* (red dots), *S. canadensis* (red triangles; position of *Hinds* 3828 UNB indicated by P2), *S. canadensis* (black ×), *S. sempervirens* (black open triangles) and a *S. brenndae* × *S. sempervirens* specimen (yellow star).

(Figs. 2A and 2C). Also, the lowest leaves still present on the stem of *Labreque & Lamoureux s.n.* (MT) had only 2-3 serrations per side while those of *Solidago sempervirens* had none and those of *S. brenndae* and *S. canadensis* have multiple serrations on lower stem leaves (data are limited due to general absence of lower stem leaves on *S. brenndae* and *S. canadensis*). The triple-nerved condition of the hybrid mid and upper stem leaves is obvious (Figs. 2D-E), but venation was raised and not like that of *S. brenndae* and *S. canadensis*.

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 brenndae* parent. Such a specimen would have more traits in common with *S. brenndae* than the hybrid. No experimental hybrids were created as part of this analysis.

Chromosome numbers reported for *Solidago brenndae*, *S. canadensis*, and *S. sempervirens* are all diploid $2n=18$ (Semple 2019). 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 Labreque and Lamoureux did collect an interspecific hybrid in 1994 but they were understandably wrong in assuming it was a cross between *S. canadensis* and *S. sempervirens*. *Solidago brenndae* was not described until recently (Semple 2013) and would not have been an option as a parent at the time the collection was made and originally identified. Documenting

statistically or experimentally the occurrence of interspecific hybridization in *Solidago* needs to be done for multiple other putative cases.

Comment on the species epithet of Brenda's Goldenrod

The species epithet for Brenda's Goldenrod was first published as *S. brendiae* because the author and the honoree liked the sound of the name with an "i" included. This was considered by nomenclatural authorities as not appropriate for a feminine name in Latin based on the name "Brenda" and *S. brendae* was listed on IPNI.org. *Solidago juliae* Nesom includes the "i" because the name "Julia" (and the diminutive, "Julie") is Latinized by dropping the "a" and adding the generative ending "-ae". Some journals insist on using only tyrannically imposed formal Latinized names while others have accepted that the original author of the name deliberately included an extra syllable as a matter of auditory preference. In this publication, the author of the epithet begrudgingly bows to the strict rules of Latinizing feminine names as mandated by the International Code of Botanical Nomenclature (Turland et al. 2018).

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