

A Systematic Analysis of the Alpine Saxifrage Complex (Saxifragaceae) in the Canadian Arctic Islands Using Morphology and Chloroplast DNA Data

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The *Saxifraga nivalis* complex displays significant ecological, morphological and cytological variation. Most European studies suggest that the *S. nivalis* complex comprises two distinct species: *Saxifraga nivalis* sensu stricto and *Saxifraga tenuis*. However, the presence of intermediate morphotypes, inconsistencies in chromosomal counts and variability in morphological keys and descriptions have led to different taxonomic interpretations of the complex in North America. This study investigated the systematics of Canadian Arctic Island members of this complex from 157 specimens using 23 morphological characters. Principal component analysis of the morphological data revealed two adjacent clusters, corresponding to the two taxa and consistent with a close morphological similarity and the presence of hybrids. A preliminary restriction site analysis of five non-coding regions of the chloroplast genome, *trnH-trnK*, *trnT-trnF*, *trnF-trnV*, *trnV-rbcL* and *rbcL-ORF106*, was conducted using 21 restriction endonucleases. This analysis indicated a length difference between the *trnT-trnF* region of *S. nivalis* and that of *S. tenuis*, but no difference in restriction sites for any of the assayed regions. These results confirm that in the Canadian Arctic, the *S. nivalis* complex consists of two closely related, largely sympatric species, with notable morphological variability, and possible hybrids.

Key Words: Alpine Saxifrage, *Saxifraga nivalis*, *Saxifraga tenuis*, Canadian Arctic, systematics, morphology, chloroplast DNA restriction site analysis.

Saxifraga L., the largest genus in the Saxifragaceae, consists of nearly 400 herbaceous, mostly perennial species (Webb 1993; Soltis et al. 1993, 1996). *Saxifraga nivalis* L. sensu lato, commonly known as the Alpine Saxifrage, inhabits arctic and alpine environments throughout the northern hemisphere. The *S. nivalis* complex is dispersed throughout northern and alpine Europe, Siberia, arctic and subarctic North America and south in the alpine zone to Arizona and the Gaspé, Quebec (Britton and Brown 1913; Krause and Beamish 1973; Scoggan 1978; Webb 1993). Members of the *S. nivalis* complex display notable morphological, cytological and ecological variation, which has led to different taxonomic interpretations and classifications.

Linnaeus (1753) first described *S. nivalis*, a name that means snow saxifrage, as these plants are often found growing in snow patch plant communities (Britton and Brown 1913). Later, Wahlenberg (1812) recognized *S. nivalis* var. *tenuis* Wahlenb. for plants with a notably smaller stature, fewer flowers, smaller fruits and recurved stigmas. Smith (in Lindman 1918) elevated Wahlenberg's variety to *Saxifraga tenuis* (Wahlenb.) Harry Sm. However, the taxonomy of the *S. nivalis* complex remained problematic and the acceptance of *S. tenuis* as a species was controversial. For instance, Böcher (1938) recognized *S. nivalis* and *S. tenuis* as distinct species, but also suspected the presence of races and microspecies within the *S. nivalis* complex. Polunin (1940) found the two taxa difficult to separate morpho-

logically with intermediates and suggested the need for breeding and cytological studies before distinguishing them at the species level. Although accepted as a distinct species in Scandinavia and Greenland, based on samples from Alaska and the Yukon, Hultén (1945) concurred at the time with Polunin in treating the taxon as *S. nivalis* var. *tenuis* because of its minimal phenotypic distinction from *S. nivalis* and its low frequency of occurrence within the area of distribution of *S. nivalis*. However, in the Canadian Arctic, Porsild (1957, 1964) and Porsild and Cody (1980) recognized *S. nivalis* and *S. tenuis* as distinct species. Upon further examination of specimens from Alaska and neighboring regions, Hultén (1968) also recognized the two taxa at the species level. More recently Scoggan (1978) and Aiken et al. (1998) treat the two taxa as varieties of *S. nivalis*.

Taxonomic and nomenclatural ambiguity also stemmed from the description of additional varieties and microspecies, as well as the re-emergence of Haworth's (1812) suggestion to revise Linnaeus' concept of the genus *Saxifraga* (reviewed in Spongberg 1972). In 1905, Small divided the genus *Saxifraga* into 13 genera in North America (in Small and Rydberg 1905; reviewed in Soltis et al. 1996). Small treated *S. nivalis* as *Micranthes nivalis* (L.) Small, *S. nivalis* var. *tenuis* as *Micranthes tenuis* (Wahlenb.) Small, and distinguished an additional species in the Canadian eastern Arctic, *Micranthes kumlienii* Small. However, subsequent authors did not recognize the genus *Micranthes*,

and *M. kumlienii* was treated as belonging to *S. nivalis* (Polunin 1940; Aiken et al. 2000*). Fernald (1917) distinguished *Saxifraga nivalis* var. *labradorica* Fern., a variety localized in Labrador, and suggested that this plant corresponded to Small's concept of *Micranthes tenuis*. Subsequently, this variety was treated as a synonym of *S. nivalis* var. *tenuis* (Scoggan 1978) or as a luxuriant form of the latter (Polunin 1940). In the Gaspé Peninsula, Fernald (1917, 1950) identified another member of the *S. nivalis* complex, *Saxifraga gaspensis* Fern. Subsequently, this species was included under *S. nivalis* var. *tenuis* (Scoggan 1950, 1978), treated as *S. nivalis* var. *gaspensis* (Fern.) Boivin (Boivin 1966), and then considered as small *S. nivalis* s.s. (Blondeau 1989a). Most recently, Gervais et al. (1995) followed Fernald in treating the Gaspé population as a distinct species. In Alaska, Hultén (1968) considered *S. nivalis* as highly variable, recognizing *S. nivalis* var. *tenuis*, and describing *S. nivalis* var. *rufopilosa* Hultén for plants characterized by "densely pubescent, rufous-haired leaves and red petals" (page 579) found in Alaska and the Yukon. Porsild (1957, map page 188) appeared to treat *S. rufopilosa* under *S. tenuis* according to his map of that species (see also Porsild and Cody 1980, map page 403; Cody 1996). Later, Porsild (1975) recognized the latter as the distinct species, *S. rufopilosa* (Hult.) A. E. Porsild, and suggested that it was more closely related to *S. tenuis* than *S. nivalis*. Cody (1996) also recognized *S. rufopilosa* as a distinct species and considered *S. tenuis* as not present in the Yukon. In 1978, Scoggan's concept of *S. nivalis* var. *tenuis* encompassed *S. tenuis*, *S. gaspensis*, *S. nivalis* var. *labradorica* and *S. nivalis* var. *rufopilosa*.

Based on cytology and morphology, Löve (1983) and Webb (1964, 1993) discerned the species *S. nivalis* ($2n = 60$) and *S. tenuis* ($2n = 20$) in Europe. The taxonomic ambiguity regarding the *S. nivalis* complex in North America (Aiken et al. 2000*) appears to stem from the following factors: (1) several morphological characters used to distinguish the species in Europe do not hold up in North America; (2) taxa can be found growing together; and (3) intermediate morphotypes, as well as variation in chromosomal counts suggest hybridization. Various cytological studies of material from North America have demonstrated cytological diversity within the *S. nivalis* complex with chromosomal counts of $2n = 20, 40, c. 56, 58, 60$ or $c. 60$. While most support the above European counts for *S. nivalis* and *S. tenuis* (Mosquin and Hayley 1966; Hedberg 1967; Johnson and Packer 1968; Packer and McPherson 1974; Löve and Löve 1975), several studies found intermediate chromosome counts. Krause and Beamish (1973) provide counts for plants of the *S. nivalis-tenuis* complex from the Yukon ($2n = 20, 40$), British Columbia (60) and Idaho (20), which they were unable to identify to species. Intermediate chromosome counts have also been found in the Russian Arctic in a plant described as *S. nivalis* \times *S. tenuis* (Devaytov et

al. 1997). In the Gaspé Peninsula *S. gaspensis* is considered to be a putative endemic hybrid based on chromosome number ($2n = 40$) and apparent intermediate morphology (Gervais et al. 1995). Further confusion results from the variance and discrepancies among the morphological keys used in the identification of this complex and related species, such as *S. foliolosa* R. Br., which are occasionally misidentified as members of the *S. nivalis* complex. Consequently, accurate and consistent identification of North American plants belonging to this complex can be problematic.

The aim of this study was to investigate the distinctiveness of *S. nivalis* and *S. tenuis* in the Canadian Arctic Islands based on morphological and molecular differences, and to help reassess the taxonomic status of *S. tenuis*.

Material and Methods

Morphological Analysis

Specimens

Representative specimens from the Canadian Arctic were selected from the Canadian National Herbarium, Canadian Museum of Nature (CAN), and the Agriculture and Agri-foods Canada Herbarium, Central Experimental Farm, Ottawa (DAO). Morphological data were gathered from observations and measurements on 157 herbarium sheets (listed in Appendix I), including two chromosome count vouchers (*S. nivalis*, $2n = 60$, Calder et al. DAO 24148; *S. tenuis*, $2n = 20$, Calder et al. DAO 24149). One plant per sheet was sampled, except when sheets comprised mixed collections or included DNA vouchers, and then multiple plants per sheet were sampled. A total of 200 plants were sampled, 122 *S. nivalis* and 78 *S. tenuis*. More specimens of *S. nivalis* were available for study than of *S. tenuis*. Where identifications of examined specimens were judged questionable, specimens were re-identified based on a combination of published keys and preliminary results. Additionally, identifications of many *S. tenuis* specimens at CAN were subsequently confirmed for the Panarctic Flora Project (E. Reidar, 2001, 2002).

Morphological characters

Characters used in descriptions and keys of the *S. nivalis* complex (Simmons 1906; Polunin 1940; Porsild 1957; Löve 1983; Blondeau 1989a, 1989b; Webb 1993; Aiken et al. 1998, 2000*) were reduced to a set of 30 characters based on ease of observation or measurement on dried specimens as well as their taxonomic significance. Of these, 23 were selected for statistical analysis (Table 1). Petal length was excluded from all analyses due to difficulties in measuring petals that were often folded and partly included within the calyx. The qualitative characters, stem colour, petal shape, prominence of leafy bract on stem, leaf blade shape, leaf blade base shape and apex shape, were excluded due to variation within a plant or difficulties in determining discrete states.

TABLE 1. Morphological characters used in analyses of the *Saxifraga nivalis* complex in the Canadian Arctic.**Quantitative characters:**

1. Plant height (cm): HEIGHT; length from basal rosette to top of inflorescence
2. Stem width (mm): STWIDTH; measured midway along lower half of stem
3. Stem hair density (0, glabrous to 4, dense): STHRDENSITY
4. Stem hair length (mm): STHRLENGTH; measured midway along lower half of stem.
5. Leaf blade length (cm): LLENGTH; measurement made on the largest leaf
6. Leaf blade width (cm): LFWIDTH; measurement made on the largest leaf
7. Hair length on leaf lower surface (mm): UNDHRLGTH
8. Hair length along leaf margin (mm): MRGHRLGTH
9. Number of teeth on leaf: TEETH; count made on the largest leaf
10. Tooth width (mm): TTHWIDTH; measurement made on largest tooth on the largest leaf
11. Tooth length (mm): TTHLENGTH; measurement made on largest tooth on the largest leaf
12. Petal width (mm): PTWIDTH; measurement made on the largest petal

Qualitative characters:

1. Stem hair colour (rust-coloured; mixed rust and white; white)
2. Stem hair texture (short fine; long coarse)
3. Tooth apex shape (rounded; pointed)
4. Regularity of teeth (even in size; variable in size smaller towards leaf blade apex)
5. Hair presence on leaf lower surface (moderate to dense; sparse; absent)
6. Hair colour on leaf lower surface (rust; white)
7. Hair presence on leaf margin (moderate to dense; sparse; absent)
8. Hair colour on leaf margin (rust; white)
9. Inflorescence density (open; tight cluster)
10. Style shape (curved; straight or essentially so)
11. Petal colour (pink or essentially so; white or essentially so)

The software package DELTA (Dallwitz et al. 1993) and the character set for the "Flora of the Canadian Arctic Archipelago" (Aiken et al. 2002*) were used to generate preliminary taxon descriptions. These descriptions were then modified to read more easily, to exclude irrelevant characters, and to include important diagnostic characters not included in the Flora character set.

Statistical analysis

All statistical analyses were performed with SYSTAT version 8.0. For each quantitative trait, the means for *S. tenuis* and *S. nivalis* specimens were compared by performing t-tests. Separate variance values were calculated for each taxon. T-tests were conducted on both raw and log-transformed data. A principal component analysis (PCA) using the 12 quantitative characters indicated in Table 1 was conducted to visualize possible distinctiveness between *S. nivalis* and *S. tenuis*. The character MRGHRLGTH was excluded from some PCA analyses due to a large amount of missing data in *S. tenuis*, which sometimes lacked marginal hairs. The PCA analysis excluded all specimens with missing values. A discriminant function analysis was also performed on the quantitative data. For the 11 selected qualitative characters (Table 1) the percentages of specimens having each character state was determined for each taxon.

To determine if there was any geographical pattern to the morphological variation in *S. tenuis*, principal component analysis was performed only on the *S. tenuis* quantitative data (excluding MRGHRLGTH). This analysis also included five specimens from Alas-

ka (Calder 6107, 6511, 6249 DAO) and northern British Columbia (Calder & Kukkonen 28151 DAO, Taylor et al. 1204 DAO) not included in the larger analysis. Individuals were coded as occurring in one of three regions: high arctic (67), eastern arctic (11) or western montane (5).

Chloroplast DNA analysis*Plant material and DNA extraction*

A total of 15 plants, for which silica gel dried material was available, were selected for molecular analysis: seven individuals of *S. nivalis* (Gillespie 6165, 6675-1, 6826a-1, 6826a-2, 6977-2, 6984-5; Aiken 98-055-3), seven *S. tenuis* (Gillespie 6728-1, 6807-1, 6807-3, 6825-2, 6870-2, 6877-1, 6881-3), and one *S. foliolosa* (Gillespie 6841) (Appendix 1). The latter species was selected to provide perspective on the chloroplast DNA (cpDNA) data, based on its close phylogenetic relationship to the *S. nivalis* complex (Soltis et al. 1996). DNA was extracted following Doyle and Doyle's (1990) CTAB total DNA extraction procedure as modified by Gillespie et al. (1997).

Restriction site analysis

DNA extracts were PCR amplified using five pairs of universal primers for non-coding regions of chloroplast DNA. The five regions are: *trnH-trnK* (Demesure et al. 1995), *trnT-trnF* (Taberlet et al. 1991), *trnF-trnV* (Dumoulin-Lapegue et al. 1997), *trnV-rbcL* (Dumoulin-Lapegue et al. 1997), and *rbcL-ORF106* (Arnold et al. 1991). Amplification reaction mix and programs follow Gillespie and Boles (2001).

TABLE 2. Descriptive statistics and t-test comparing the means of *S. nivalis* and *S. tenuis* at the 95% confidence level for 12 quantitative morphological characters.

Character	Taxon	N	Mean (±SD)	Range		Difference in means	t value	df	p
				Min	Max				
Plant height (cm)	<i>S. nivalis</i>	122	9.12 (±3.37)	1.7	18.0	4.66	13.68	176.2	0.000
	<i>S. tenuis</i>	78	4.40 (±1.40)	1.8	8.5				
Stem width (mm)	<i>S. nivalis</i>	122	1.37 (±0.35)	0.7	2.5	0.82	23.06	178.6	0.000
	<i>S. tenuis</i>	78	0.56 (±0.15)	0.3	1.0				
Stem hair density	<i>S. nivalis</i>	122	3.2 (± 0.70)	1	4	2.0	24.94	205.0	0.000
	<i>S. tenuis</i>	78	1.2 (± 0.36)	1	3				
Stem hair length (mm)	<i>S. nivalis</i>	122	3.2 (± 0.70)	1	4	0.67	35.45	188.5	0.000
	<i>S. tenuis</i>	77	0.19 (±0.09)	0.1	0.5				
Leaf blade width (cm)	<i>S. nivalis</i>	119	0.96 (±0.34)	0.4	2.1	0.51	14.81	161.2	0.000
	<i>S. tenuis</i>	77	0.44 (±0.13)	0.2	0.8				
Leaf blade length (cm)	<i>S. nivalis</i>	119	1.38 (± 0.50)	0.6	3.6	0.69	13.51	166.5	0.000
	<i>S. tenuis</i>	77	0.67 (± 0.18)	0.4	1.5				
Hair length on lower leaf surface (mm)	<i>S. nivalis</i>	120	0.38 (±0.13)	0.2	1.2	0.10	7.25	197.0	0.000
	<i>S. tenuis</i>	78	0.27 (±0.06)	0.1	0.5				
Hair length on leaf margin (mm)	<i>S. nivalis</i>	121	0.19 (± 0.07)	0.1	0.4	0.07	8.47	167.4	0.000
	<i>S. tenuis</i>	55*	0.12 (± 0.04)	0.1	0.2				
Number of teeth on leaf blade	<i>S. nivalis</i>	118	10.3 (±1.74)	7	14	2.8	16.63	167.8	0.000
	<i>S. tenuis</i>	78	7.5 (±0.73)	6	9				
	<i>S. nivalis</i>	118	1.17 (± 0.42)	0.5	3.5				
Tooth width (mm)						0.37	7.86	195.6	0.000
	<i>S. tenuis</i>	78	0.80 (± 0.24)	0.5	1.6				
	<i>S. nivalis</i>	118	1.52 (±0.48)	0.8	3.2				
Tooth length (mm)						0.62	11.84	190.5	0.000
	<i>S. tenuis</i>	78	0.90 (±0.26)	0.4	1.8				
	<i>S. nivalis</i>	120	1.12 (±0.24)	0.7	1.8				
Petal width (mm)						0.40	14.16	202.0	0.000
	<i>S. tenuis</i>	77	0.72 (±0.16)	0.5	1.1				

* Marginal hair was not present in all *S. tenuis*

PCR products were single digested with twenty one restriction endonucleases according to manufacturer's recommendations. These included nine 4-base pair (bp) cutting restriction enzymes: *AluI*, *HaeIII*, *HhaI*, *MspI*, *RsaI*, *DdeI*, *HinfI*, *Sau96I*, *TaqI*; two 5bp cutting restriction enzymes: *BstOI*, *SinI*; and ten 6bp enzymes:

ApaI, *BamHI*, *BglI*, *BglIII*, *DraI*, *EcoRI*, *EcoRV*, *HincII*, *PstI*, *XhoI*. To separate restriction fragments, 8 µL of the reaction mixture and 2 µL of buffer-dye mix were run on 1.1% agarose gels with ethidium bromide at 38 V for 2-3hrs. The restriction fragment patterns were visualized and photographed under ultraviolet light.

TABLE 3. Distribution of qualitative morphological character states in *Saxifraga nivalis* and *S. tenuis* in the Canadian Arctic. Numbers represent percentage of individuals having a particular character state.

Character	Character state	<i>S. nivalis</i>	<i>S. tenuis</i>
Stem hair colour	rust	1.3	74.4
	mixed	0	25.6
	white	98.7	0
Stem hair texture	short fine	1.6	100
	long coarse	98.4	0
Tooth apex shape	rounded	2.5	100
	pointed	97.5	0
Regularity of teeth	even-sized	18.3	87.2
	variable	81.7	12.8
Hairs presence on leaf lower surface	moderate-dense	91.7	84.6
	sparse	7.5	15.4
	absent	0.8	0
Hair colour on leaf lower surface	rust	40.0	79.5
	white	60.0	20.5
Hair presence on leaf margin	moderate-dense	91.7	10.3
	sparse	8.3	60.3
	absent	0	29.5
Hair colour on leaf margin	rust	20.7	60.0
	white	79.3	40.0
Inflorescence density	open	1.8	97.1
	tight cluster	98.2	2.9
Style shape	curved	25.9	84.7
	straight	74.1	15.3
Petal colour	pink	14.9	81.8
	white	85.1	18.2

Lengths of total amplified product and restriction fragments were estimated by comparison with known 100 bp ladder DNA markers.

Results

Morphological Analysis

To determine whether the means of the examined quantitative characters were different between *S. nivalis* and *S. tenuis*, t-tests were performed (Table 2). The analysis revealed a significant difference in means between the two taxa for all characters examined. Overall, plants belonging to *S. nivalis* are more robust than *S. tenuis* as implied by higher means in both plant height and stem width observed in *S. nivalis*. Similarly, leaves of *S. nivalis* are on average longer, wider and have longer, wider and more numerous marginal teeth than *S. tenuis*. Also, hairs on the stems are longer and denser and hairs on the lower surface and margin of leaves are on average longer in *S. nivalis*. Petal width was significantly greater in *S. nivalis* than in *S. tenuis*. However, the two taxa have notably different variances, with *S. nivalis* having a higher variance than *S. tenuis* for all quantitative characters examined. Considering the very low probability values and the robustness of t-tests for samples of this size, the differences in means can be considered as meaningful. Analyses were also performed on log-transformed data, with no significant differences.

The frequency of occurrence of states of qualitative characters differed considerably between the two taxa

for most characters (Table 3). The characters, stem hair colour and texture, tooth apex shape and inflorescence density, differed significantly between the two taxa, with less than a five percent overlap in states. Several characters, regularity of teeth, petal colour and style shape, exhibited an overlap in states of 10-26% between the two taxa. In contrast, one character, hair presence on lower leaf surface, displayed very similar frequencies of states between *S. nivalis* and *S. tenuis*, with hairs present in over 95% of the specimens examined in both taxa, although density was sometimes more sparse in *S. tenuis*. The remaining characters displayed considerable overlap in states between the taxa.

The principal component analysis of quantitative characters (excluding MRGHLGTH) revealed two clusters, positioned adjacent to each other with little overlap (Figure 1). Factor loading for the analysis was STWIDTH, LFWIDTH, LFLLENGTH, STHRLLENGTH, STHRDENSITY, HEIGHT, TEETH, PTWIDTH and TTHLENGTH for factor 1, and TTHWIDTH and UNDHRLGTH for factor 2, with 61% and 10% of total variance explained by factors 1 and 2, respectively. As noted above, there is considerable variation among *S. nivalis* plants for most examined characters. This can be observed on the graph through the large oblique spread of *S. nivalis* compared to *S. tenuis*. The PCA including the character MRGHLGTH produced very similar results (although displayed fewer individuals). The discriminant function analysis performed on the same data distinguished between the two taxa 100%

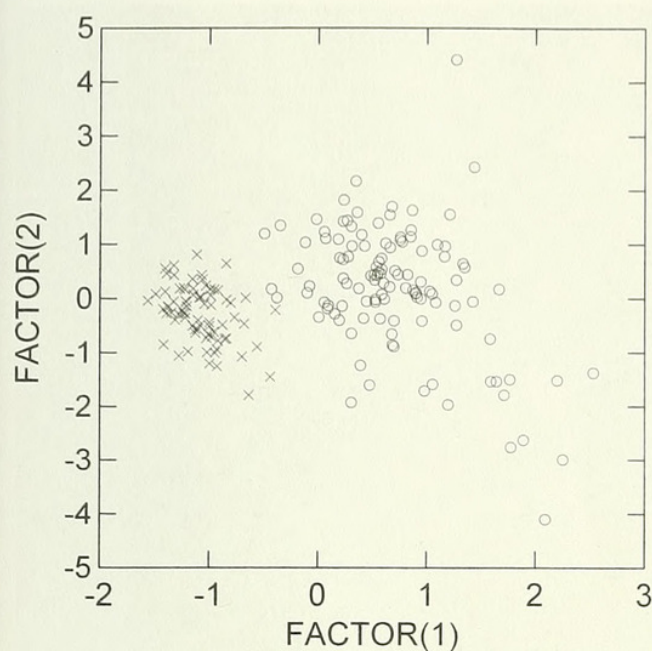


FIGURE 1. Principal component analysis on the quantitative morphological data set for the *Saxifraga nivalis* complex in the Canadian Arctic. Circles represent individuals of *S. nivalis*, crosses represent *S. tenuis*.

of the time, with one dimension accounting for the variation.

The PCA analysis examining geographical patterns to morphological variation in *S. tenuis* revealed very little geographical structure, with eastern arctic and high arctic plants almost completely overlapping.

Western montane plants separated from the majority of arctic plants on a combination of both factors (with LFWIDTH, LFLLENGTH, and TEETH, loading high on factor one, HEIGHT on factor two), but overlapped considerably with several eastern arctic plants. A discriminant function analysis performed on the three geographic groups produced similar results (correctly placing the western montane plants with 100% reliability, high arctic plants with 86% reliability, and eastern arctic plants with only 42% reliability).

Chloroplast DNA analysis

The *trnH-trnK* amplicons were estimated at 1600 base pairs (bp) for *S. nivalis* and *S. tenuis* and 1700 bp for *S. foliolosa*. The three largest regions, *trnF-trnV*, *trnV-rbcL* and *rbcL-ORF106*, were approximately 3000 bp in length in all three taxa. Interestingly, the *trnT-trnF* region was estimated to be 1800 bp, 1850 bp and 2000 bp in length for *S. nivalis*, *S. tenuis* and *S. foliolosa*, respectively.

Sixteen out of 105 enzyme restriction assays showed restriction site differences between *S. foliolosa* and the *S. nivalis* complex, including three site differences in the *trnH-trnK* region, three in the *rbcL-ORF106* region, three in the *trnV-rbcL* region, five in the *trnF-trnV* region and two in the *trnT-trnF* region (Table 4). No restriction site differences were detected between *S. nivalis* and *S. tenuis*. However, digestion of the *trnT-trnF* region with the restriction enzyme *AluI* showed clearly the length difference between *S. nivalis* and *S. tenuis* (Figure 2).

Table 4. Data matrix of restriction site characters for *S. nivalis* (N), *S. tenuis* (T) and *S. foliolosa* (F). "0" represents absence of restriction site; "1" represents presence of restriction site.

	<i>trnH-trnK</i>			<i>rbcL-ORF106</i>			<i>trnV-rbcL</i>			<i>trnF-trnV</i>			<i>trnT-trnF</i>		
	N	T	F	N	T	F	N	T	F	N	T	F	N	T	F
<i>Alu</i> I	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Apa</i> I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bam</i> H I	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0
<i>Bgl</i> I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bgl</i> II	0	0	0	1	1	1	0	0	0	1	1	0	0	0	0
<i>Bst</i> O I	0	0	1	1	1	1	0	0	1	0	0	0	1	1	1
<i>Dra</i> I	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1
<i>Eco</i> R I	0	0	0	1	1	1	0	0	0	0	0	1	0	0	1
<i>Eco</i> R V	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
<i>Hae</i> III	1	1	1	0	0	1	1	1	1	0	0	1	0	0	0
<i>Hha</i> I	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
<i>Hinf</i> I	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
<i>Msp</i> I	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
<i>Nci</i> I	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
<i>Pst</i> I	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
<i>Pvu</i> II	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0
<i>Rsa</i> I	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0
<i>Sau</i> 96 I	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Sin</i> I	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0
<i>Taq</i> I	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
<i>Xho</i> I	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0

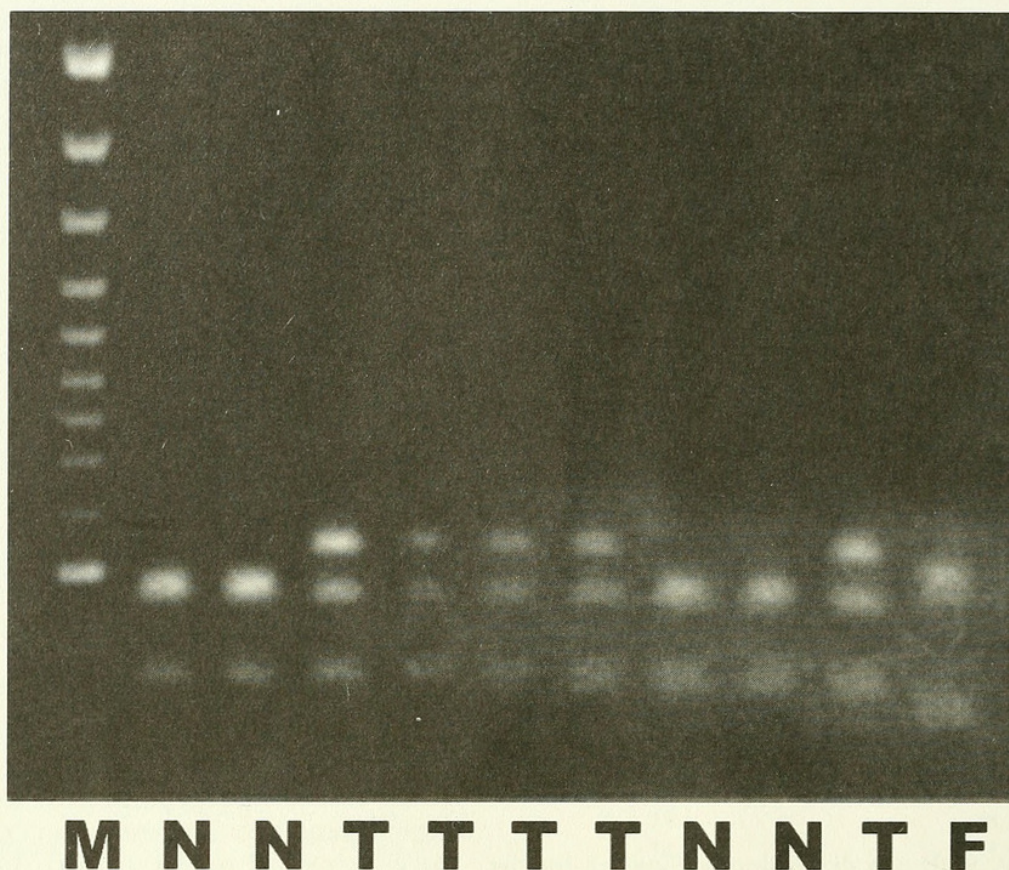


FIGURE 2. Digestion of the chloroplast DNA region *trnT-trnF* with restriction enzyme *AluI* for *Saxifraga nivalis* (N), *S. tenuis* (T) and *S. foliolosa* (F). The first lane contains a 100 bp DNA size marker (M). Note absence of the upper band on *S. nivalis*.

Discussion

The principal component analysis confirms that the *S. nivalis* complex in the Canadian Arctic is represented by two principal morphotypes, appearing as adjacent clusters on the PCA graph. The several plants occupying an intermediate position between the two clusters displayed a somewhat intermediate morphology, but nevertheless could readily be assigned to one of the two taxa. For example, several specimens of *S. nivalis* from Prince Patrick Island (e.g., Gillespie & Consaul 6869-4, 6926a-3) were very small with slender flowering stems, characters typical of *S. tenuis*, but otherwise had the morphological characteristics of *S. nivalis*. Although character states or ranges overlapped for the majority of characters examined, differences between the two taxa were statistically significant for all quantitative and for three qualitative characters.

Morphological variability

A significant amount of variance was observed for most characters measured. Since the *S. nivalis* complex is considered an environmental indicator (Aiken et al. 1998, 2000*), the variability observed may be due to phenotypic plasticity and variation in environment. For instance, *S. nivalis* plants growing in harsher habitats are usually shorter and less robust (e.g., the very short plant shown in Figure 3) than those grow-

ing in more nourishing environments. Also plants of *S. nivalis* may be taller with more slender stems in shady microhabitats as a result of etiolation. Another contributor to variance is the time of collection. Since stems elongate in the fruiting stage, particularly in *S. nivalis*, plants collected later in the season are more likely to be taller than their younger counterparts. However, most examined collections of *S. nivalis* and *S. tenuis* made at the same time and site displayed significant height differences on average between the two taxa. Leaf characters, such as leaf size and teeth number and size, showed much variation both within and between the two taxa. Although *S. tenuis* is usually found in wetter habitats than *S. nivalis*, the latter species in particular occupies a broad range of habitats and the two species sometimes co-occur in mixed populations. Some of the morphological variation in the complex, particularly within *S. nivalis*, may reflect this variation in habitat (Blondeau and Cayouette 2002; Aiken et al. 2000*). Such high intraspecific variation is apparently typical of Saxifrages, particularly in arctic and alpine environments, and several studies have demonstrated that such variation may not be of taxonomic significance (Soltis et al. 1996; Brysting et al. 1996).

The coloration of petals also varied within each taxon, but season and environment can be a large con-

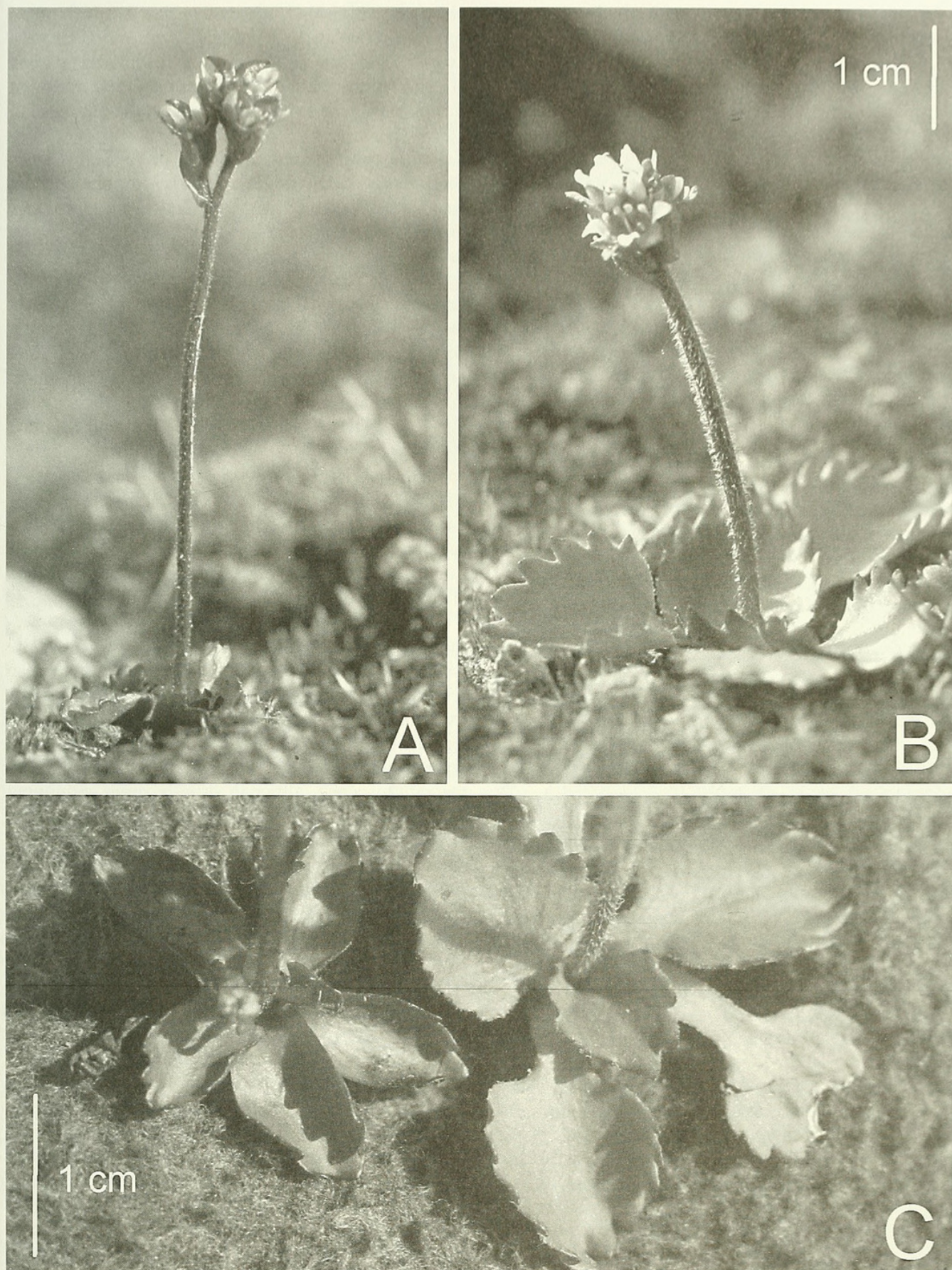


FIGURE 3. *Saxifraga nivalis* complex in the Canadian Arctic. A. *S. tenuis* (Gillespie & Consaul 6978-2), habit. B. *S. nivalis* (Gillespie and Consaul 6977-1), habit. C. Comparison of basal rosette of leaves of *S. tenuis* (on left, Gillespie & Consaul 6978-2) and *S. nivalis* (on right, Gillespie and Consaul 6977-1). A and B are the same scale.

tributor to petal coloration. Plants growing in more open, sunnier environments tend to have more pink or dark red anthocyanin pigment throughout the plant, including the petals. White petals may also sometimes turn pinkish with age. In contrast, little variation was observed within each taxon for the texture and coloration of stem hair, and these characters were significantly different between taxa.

Among traits traditionally used for identification of the *S. nivalis* complex, many displayed considerable intrataxon variance, with ranges often overlapping between taxa. Our results also indicate a greater degree of variability within *S. nivalis* than in *S. tenuis* in the Canadian Arctic. This pattern of variation results in a somewhat obscure morphological boundary between the two species and has led to difficulties in constructing good identification keys.

Characters and taxonomic identification

Despite the considerable intraspecific variation, most commonly used identification characters were significantly different between the two taxa. Indeed, plants of *S. nivalis* were overall larger and more robust than *S. tenuis*, and the latter often had a more reddish tinge on the petals and stem hair, as previously found by numerous authors (Simmons 1906; Polunin 1940; Porsild 1957; Böcher et al. 1968; Löve 1983; Blondeau 1989a; Webb 1993).

Flowering stem width was an excellent identification character apart from a few individuals, with *S. tenuis* characterized by a width of 1 mm or less, consistent with Webb's (1993) use of it as a key character. Consistently used by various botanists (e.g., Webb 1993), stem hair characters were among the most useful for identification. *Saxifraga nivalis* usually has a much more conspicuous, longer, denser, coarse crisped white vestiture, while *S. tenuis* has a less conspicuous, shorter, finer, usually glandular pubescence. Canadian Arctic *S. tenuis* was found to always have stem hairs, thus not conforming to descriptions of the taxon in Greenland and Svalbard as having mostly glabrous stems (Böcher et al. 1968, 1978; Rønning 1996). Generally, *S. nivalis* plants were taller than *S. tenuis*, but due to its variance, height was not useful for identification.

Saxifraga nivalis had more numerous teeth on the leaves than *S. tenuis*, and the latter had rounder obtuse teeth versus more pointed, as suggested in the literature (e.g., Böcher et al. 1968). The width and length of *S. tenuis* teeth were also found to be less than those observed on *S. nivalis*, but, this is not surprising considering that *S. nivalis* had on average longer and wider leaves. Interestingly, *S. nivalis* had a notably less regular dentition than *S. tenuis* in regards to the size of the teeth. The former generally had small teeth at the base with teeth becoming larger towards the apex, whereas *S. tenuis* had more evenly sized teeth. Although size of the largest leaf differed significantly between the two taxa, leaf size characters

make poor diagnostic characters due to overlap and age related variation. Also, leaf shape varied tremendously and thus should not be considered a good discriminating character. However, the leaf apices of *S. tenuis* did tend to be more rounded than those of *S. nivalis*.

Inflorescence compactness provides a useful identification character, with *S. nivalis* having one or more compact head-like clusters and *S. tenuis* a more open inflorescence (as described in Porsild 1957). Flower pedicels, especially of the lowermost flowers, are longer in *S. tenuis* than in *S. nivalis*. Since pedicels of the latter may elongate somewhat in fruit, this difference may be obscured later in the season. Although not constant, petals tend to be whiter, wider and ovate in *S. nivalis* and pink, narrower, more elongated and rounder at the apex in *S. tenuis*. Böcher (1938), Böcher et al. (1968), and more recently Löve (1983) and Rønning (1996) state that *S. nivalis* has straight or slightly spreading styles, while *S. tenuis* has styles that curve strongly downwards. This was not always the case in Canadian Arctic specimens we examined. The way specimens were pressed and the time of collection might be partly responsible for the variation in this character within the two species.

Other characters showed variation that was not useful in separating the two taxa. While *S. nivalis* usually had hairs on leaf margins, this character was also found to a lesser degree in *S. tenuis*. Most specimens examined had a purplish or reddish stem, thus not specific to *S. tenuis*. Also, the flowering stems of both taxa had on occasion a reduced leaf (bract) or two near the inflorescence, although usually more prominent in *S. tenuis*.

The presence of rust-coloured hairs on the lower surface of the leaves of *S. tenuis* has been commonly used to distinguish it from *S. nivalis* in the Canadian Arctic, and was used as a key character by several authors (Porsild 1957; Scoggan 1978; Porsild and Cody 1980). However, this study reveals that hairs are present on the leaf undersurface in over 99% of the plants examined of both species in the Canadian Arctic, and that hairs may be rust-coloured in both species, about 42% of *S. nivalis* plants examined and 74% of *S. tenuis* plants. This error may have resulted from Porsild's inclusion of *S. rufopilosa* within his concept of *S. tenuis* (distribution maps of *S. tenuis* in Porsild (1957) and Porsild and Cody (1980) appear to have included *S. rufopilosa*). *Saxifraga rufopilosa*, a species now considered to be endemic to unglaciated areas of the Yukon and Alaska, is characterized by a mat of long crinkly rusty hairs on the leaf undersurface (Cody 1996), much longer and denser than in either *S. tenuis* or *S. nivalis*. Whatever its origin, use of rust-coloured hair presence as a key diagnostic character in identifying Canadian Arctic material of the *S. nivalis* complex resulted in many misidentified specimens and much confusion as to the identity of *S. tenuis*.

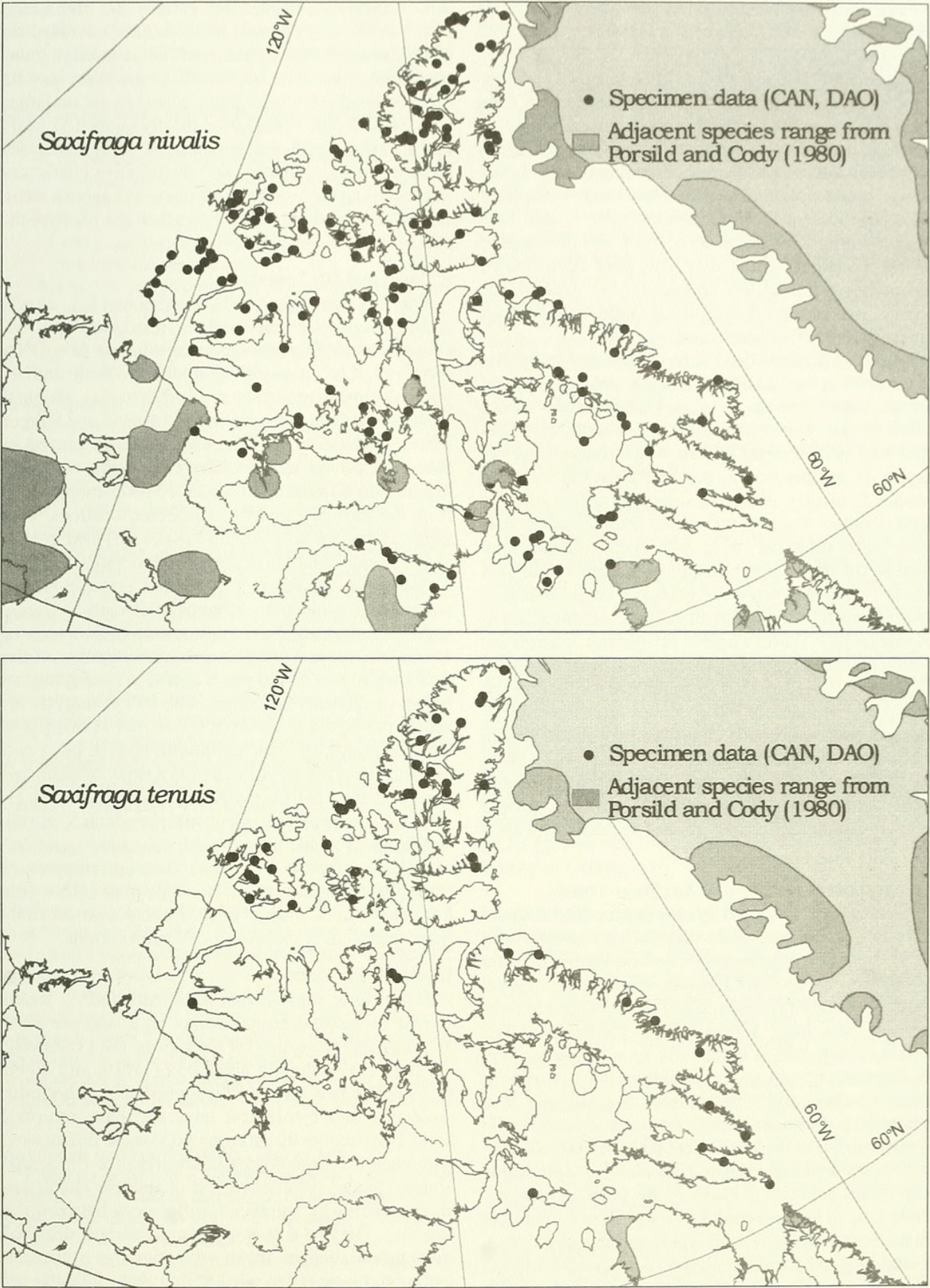


FIGURE 4. Distribution of the *Saxifraga nivalis* complex in the Canadian Arctic. (above) *S. nivalis*. (below) *S. tenuis*. Shading indicates approximate distribution outside of the Arctic Islands (from Porsild and Cody 1980, and CAN and DAO herbarium records).

The many herbarium collections having both *S. nivalis* and *S. tenuis* plants on the same sheet and under the same number (e.g., *Bruggeman* 358, *Savile* 4562, *Macdonald* 150, *Calder et al.* 24149) shows just how problematic identification of this complex in the Canadian Arctic has been. About 20% of herbarium specimens identified as *S. tenuis* at both CAN and DAO were in fact mixed collections including both *S. tenuis* and *S. nivalis* plants, or less often including small plants of *S. foliolosa* or *S. hieracifolia* Waldst. & Kit. Previous identification problems of the *S. nivalis* complex in the Canadian Arctic may also have been due to misinterpretation of key characters. For example, *S. nivalis* with several flower heads could be keyed out under lax (open) inflorescence.

Although *S. nivalis* and *S. tenuis* can be readily distinguished in the Canadian Arctic, a small percentage of specimens had one or a few characteristics of the other species. For example, some high arctic *S. nivalis* had very slender stems or fruit with strongly recurved styles. While this may be part of the natural variation within *S. nivalis*, it may also suggest a low level of hybridization. Some of the overlap in quantitative character states shown in our morphological analyses may also be the result of hybridization. Recent cytological studies have suggested the existence of *S. nivalis*-*S. tenuis* hybrids ($2n = 40$) in regions of the Russian Arctic and the Yukon where *S. nivalis* and *S. tenuis* are found growing together (Krause and Beamish 1973; Devyatov et al. 1997). The population in the Gaspé Peninsula has the same intermediate chromosome number and may represent a stabilized relictual hybrid in an area where neither parent now occurs (Gervais et al. 1995). In addition Polunin (1959) suggested that hybridization may also occur between the *S. nivalis* complex and other closely related species, such as *S. hieracifolia*.

Geographical variation in *Saxifraga tenuis*

Savile (1961) proposed that North American *S. tenuis* may be divided into three disjunct and morphologically distinct "populations." The first is a high arctic population composed of plants identical to material from the north of Greenland and hypothesized to have spread from there following the Pleistocene. The second population is apparently found mostly along Hudson Strait in southern Baffin Island, northernmost Quebec and Southampton Island, but also scattered northward to northeast Baffin Island. Savile treated plants in the Gaspé Peninsula of Quebec, considered by some as a separate species *S. gaspensis*, as part of this population. Plants of this population apparently tend to be larger and less purplish in colour than in the high arctic. The third highly variable population, found in Alaska and the Yukon, is usually characterized by a highly purplish pigmentation and whitish scape hairs, and was suggested to be intermediate between *S. nivalis* and high arctic *S. tenuis*.

Our analysis indicates that eastern and high arctic plants of *S. tenuis* cannot be distinguished based on examined quantitative characters, while western montane plants (based on our small sample size) may be differentiated from most arctic plants based on larger size. Since Savile (1961) used mostly qualitative characters to distinguish the three groups, further analyses based on both qualitative and quantitative characters and including more western montane and eastern arctic specimens should be made to further test his hypothesis.

Chloroplast DNA analysis

The five non-coding cpDNA regions of *S. nivalis* and *S. tenuis* were identical for restriction sites assayed. Considering the conservative nature of cpDNA evolution, it is not surprising to observe such similarity, with closely related species often having identical cpDNA restriction site profiles (Olmstead and Palmer 1994). However, *S. nivalis* and *S. tenuis* displayed an estimated 50 bp length difference in the *trnT-trnF* region. This difference was observed both among plants from the same site and from different locations. This suggests that the size variation in the *trnT-trnF* region is not background variation among populations or a phenomenon limited to a particular population, but represents a molecular difference between *S. nivalis* and *S. tenuis*, either a deletion event in *S. nivalis* or an insertion event in *S. tenuis*. Sequencing of the *trnT-trnF* region would prove useful in specifying the nature of this size difference. The RFLP analysis revealed molecular differences for 16 of 105 restriction enzyme assays between *S. foliolosa* and the other two species. These results are similar to a study of *Saxifraga* based on the cpDNA *matK* sequences (Soltis et al. 1996; plus sequences in Genbank), in which *S. nivalis* and *S. tenuis* would appear to be more closely related to each other than to *S. foliolosa*. Based on comparison of the Genbank sequences, the single plant of *S. tenuis* differed from *S. nivalis* in four nucleotide substitutions, and from *S. foliolosa* in 79 substitutions.

Implications

Our results suggest that *S. nivalis* and *S. tenuis* should be recognized as distinct taxa, and are most appropriately recognized at the species level following Porsild (1957), Porsild and Cody (1980), and Webb (1993). The two taxa are distinguishable at both the molecular and cytological level and have morphological differences that correspond to these differences. Although no morphological characters give 100% separation, many quantitative and qualitative characters show statistically significant differences between the two taxa. The two taxa overlap in geographic distribution in the Canadian Arctic, with the range of the less common *S. tenuis* included within that of *S. nivalis*. Although ranges of habitat preferences differ, there is considerable overlap, with the two taxa sometimes occurring in mixed populations. Lack of geographical

separation and considerable habitat overlap make recognition at the subspecific level inappropriate, while the morphological distinctiveness of the two taxa would make recognition at the varietal level inappropriate.

Saxifraga nivalis complex in the Canadian Arctic: key to species

- A. Inflorescence one to several dense head-like clusters of numerous flowers; petals white or essentially so (sometimes becoming pink with age); flowering stem (0.5-) 1-2.5 mm wide, moderately to densely hairy, with conspicuous long coarse white hairs; plant usually robust in appearance *S. nivalis*
- B. Inflorescence an open cyme of fewer flowers, flowers on distinct pedicels; petals pink or less often white; flowering stem 0.3-1 mm wide, usually sparsely hairy, with short fine hairs that are usually inconspicuous; plant delicate in appearance *S. tenuis*

Saxifraga nivalis L.

Plants perennial herbs, (2) 5-17 cm high, with a basal rosette of leaves. Leaves simple, alternate, all basal in a rosette, evergreen; petiole usually distinct, 0.2-2.5 mm long. Leaf blade ovate, obovate, orbicular or spatulate, 6-36 mm long (mean 14 mm), 4-21 mm wide (mean 10 mm), slightly leathery; green above, green or reddish-purple beneath, base obtuse and usually abruptly narrowed at petiole; apex obtuse, rounded or rarely acute; appearing single-veined or with inconspicuous lateral veins; upper surface glabrous; lower surface sparsely to densely hairy; hairs 0.2-1.2 mm long, rust-coloured, whitish or translucent; margins coarsely serrate or crenate, usually with rust-coloured or whitish hairs; teeth 7-14, usually increasing in size towards blade apex, tips usually pointed. Flowering stem erect, (0.5) 1-2.5 mm wide, green to purple, moderately to densely hairy, with hairs conspicuous, (0.5) 0.7-1.2 mm long, crisped (crinkly and irregularly wavy), white or translucent with tips and crosswalls white or sometimes rust-coloured or purplish, the tips sometimes glandular, usually leafless or occasionally with reduced leaves (bracts) close to the inflorescence. Inflorescence a dense head-like cluster of numerous flowers, sometimes with 1-2 smaller lateral clusters on short to long peduncles; flowers on very short pedicels, subtended by bracts. Flowers: sepals 5, free, green or purple, glabrous; petals 5, ovate or elliptic, 0.7-1.8 mm wide, equal to or longer than the sepals, white or cream-coloured, sometimes with reddish apex, mostly obtuse at apex; stamens 10; gynoecium partly inferior; carpels 2, partly fused; styles 2, free; placentation axile; ovules numerous. Fruit a capsule, spherical in lower half, with straight or slightly divergent free carpels above, 3-4 mm long, 4.5-5.5 mm wide, glabrous, dry, dehiscent; styles straight or slightly divergent, persistent; sepals persistent in fruit. Seeds numerous, 0.5-1 mm long, yellowish brown, with surface verrucose. Figure 3b, c; map 4a.

Saxifraga tenuis (Wahlenb.) Harry Sm.

Plants perennial herbs, 2-9 cm high, with a basal rosette of leaves. Leaves simple, alternate, all basal in a rosette, evergreen; petiole usually indistinct, ~0.5-2.5 mm long. Leaf blade narrowly ovate, obovate or spatulate, 4-15 mm long (mean 7 mm), 2-8 mm wide (mean 5 mm); slightly leathery, green to reddish-purple above, reddish-purple beneath; base obtuse or broadly attenuate and decurrent onto petiole; apex obtuse, rounded or rarely acute; appearing single-veined or with inconspicuous lateral veins; upper surface glabrous; lower

surface usually sparsely hairy, with hairs 0.1-0.4 mm long, rust-coloured, whitish or translucent; margins coarsely serrate or crenate, with sparse rust-coloured or whitish hairs or sometimes glabrous; teeth 6-9, usually evenly sized, tips usually rounded. Flowering stem erect, 0.3-1 mm wide, usually dark purple, sparsely hairy, with hairs mostly inconspicuous, 0.1-0.3 (0.5) mm long, fine, crinkled or straight, rust-coloured to translucent, often with purplish crosswalls and tips, the tips usually glandular; sometimes with a reduced leaf (bract) on the upper part of the stem. Inflorescence an open head of few flowers; flowers subtended by bracts; lower-most flowers often long-pedicellate and each subtended by a conspicuous bract. Flowers: sepals 5, free, green or purple, glabrous; petals 5, ovate or elliptic, 0.5-1.1 mm wide, equal to or longer than the sepals, usually pink, sometimes white, often with reddish apex, often rounded at apex; stamens 10; gynoecium partly inferior; carpels 2, partly fused; styles 2, free; placentation axile; ovules numerous. Fruit a capsule, spherical in lower half, with diverging free carpels above, 3-4 mm long, 4.5-5.5 mm wide, glabrous, dry, dehiscent; styles usually strongly re-curved at maturity, persistent; sepals persistent in fruit. Seeds numerous, 0.5-1 mm long, yellowish brown, with surface verrucose. Figure 3a, c; map 4b.

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Appendix 1: Collections examined of the *Saxifraga nivalis* complex from the Canadian Arctic.

Saxifraga nivalis

NUNAVUT. **Axel Heiberg Island:** 79°28'N 87°40'W, *Beschel 10979* (CAN); Bukken River, 80°31.57'N 92°21.83'W, *Gillespie et al. 6613* (CAN); Crusoe Glacier, 97°27'N 91°12'W, *Kuc 476-3* (CAN); Crusoe River, 79°24'N 90°50'W, *Kuc s.n.* (CAN 331187); Diana Lake, 79°30'N 88°30'W, *Porsild 16699-2* (CAN); Expedition Fjord, 79°20'N 92°W, *Kuc s.n.* (CAN 331189, CAN 331189); Mesa Brook, 79°37'N 95°W, *Beschel 13129* (CAN); Mokka Fiord, 79°45'N 87°W, *Parker 73061E* (CAN). **Baffin Island:** 63°24'N 64°35'W, *McLaren 91* (CAN); 66°40'N 70°W, *Soper s.n.* (CAN 65150); Admiralty Inlet, 73°13'N 84°W, *Malte 118993* (CAN); Apex, 63°43'N 68°27'W, *Gillespie & Soreng 6785* (CAN); Beekman Peninsula, 63°24'N 64°35'W, *McLaren 91* (CAN); Burwash Bay, 65°59'N 71°18'W, *Jacobs & Maus s.n.* (CAN 517697); Frobisher Bay, 63°45'N 68°31'W, *Gillett 19018* (CAN); Dorset Island, 64°12'N 76°32'W, *Hainaud & Norman 5698* (CAN); Foxe Peninsula, 66°23'N 83°13'W, *Manning 265* (CAN); Foxe Peninsula, 69°52'N 76°54'W, *Manning 231* (CAN); Frobisher Bay, 62°57'N 66°03'W, *Aiken et al. 86-260* (CAN); Frobisher Bay, 63°44'N 68°27'W, *Aiken et al. 86-493* (CAN); Frobisher Bay, 62°57'N 66°03'W, *Calder et al. s.n.* (DAO 24148); Frobisher Bay, 62°57'N 66°03'W, *Wynne-Edwards 7353* (CAN); Pond Inlet, 72°50'N 76°40'W, *Dutilly 1224a* (CAN); Stising Valley, *Weber 94* (CAN); Taverner Bay, 67°12'N 72°25'W, *Manning 44, 68, 77* (CAN). **Bathurst Island:** Polar Bear Pass, 75°43'N 98°23'W, *Aiken & Maus 92-022* (CAN); Goodsir Inlet, 75°45'N 97°45'W, *Lamothe 69-25* (CAN); Polar Bear Pass, 75°43.8'N 98°25.45'W, *Gillespie & Consaul 6984* (CAN) [DNA voucher, individuals 1-5 examined]. **Bylot Island:** 72°53'N 76°W, *Wilcox 125631* (CAN). **Cameron Island:** 76°19.5'N 104.5°W, *Aiken 92-039* (CAN). **Cornwallis Island:** Resolute, 74°40'N 94°50'W, *Aiken & MacCormac 98-055* (CAN 581909, plants 1-5; CAN 582554); Resolute, 74°40'N 95°04'W, *Aiken et al. 93-072* (CAN). **Devon Island:** Dundas Harbour, 74°31.3'N 82°33.5'W, *Gillespie et al. 6675-1* (CAN); Truelove Lowland, 75°40'N 84°40'W *Kerik s.n.* (CAN 409363). **Digges Island:** 62°32'N 77°45'W, *Gaston 25, 29* (CAN); 62°35'N 77°50'W, *Gaston 17* (CAN). **Ellef Ringnes Island:** Isachsen, 78°47'N 103°50'W, *Macdonald 242* (CAN). **Ellesmere Island:** 79°34'N 84°44'W, *Edlund & Roncato-Spencer 264* (CAN); Alexandra Fiord, 78°53'N 75°45'W, *Gillespie & Vogel 6165* (CAN); Alexandra Fiord, 78°53'N 75°50'W, *Gillett & Shchepanek 18108* (CAN); Craig Harbour, 76°20'N 81°30'W, *Dutilly 1267* (CAN); Hazen, 68°30'N 72°45'W, *Soper 8194* (CAN); Hazen, 81°49'N 71°20'W, *Gillespie & Vogel 6238* (CAN); Sawtooth Range, 79°43.54'N 83°09.44'W, *Gillespie et al. 6643* (CAN); Slidre Fjord, 80°N 86°15'W, *Tener 95* (CAN); Tanquary, 78°53'N 75°45'W, *Gillespie & Vogel 5982* (CAN). **King William Island:** Gjoa Haven, *Cooper 28* (CAN), 73 (CAN), 226 (CAN); Gjoa Haven, 68°38'N 95°53'W, *Larson 25* (CAN); Victory Point, *Cooper 164* (CAN), 122 (CAN). **Lougheed Island:** 77°30'N 105°38'W, *Edlund 2091* (CAN). **Meighen Island:** 79°55'N 99°30'W, *Kuc* (CAN 331171). **Pelly Bay:** 68°53'N 89°51'W, *Campbell s.n.* (CAN 282778). **Prince Charles Island:** 67°10'N 76°43'W, *Baldwin 1919* (CAN). **Victoria Island:** 68°53'N 105°W, *Edlund & Argus 12730-1* (CAN).

NORTHWEST TERRITORIES. **Banks Island:** 73°N 117°W, *Aiken 99-203* (CAN); 73°24'N 117°0'W, *Porsild 17711* (CAN); 74°31'N 121°07'W, *Manning & Macpherson 164* (CAN); Bernard River, 73°22'N 121°47'W, *Maher & Maclean 75* (CAN); Egg River, 72°27'N 124°36'W, *Lambert s.n.* (CAN 535943); Lambton, 71°05'N 123°09'W, *Porsild 17579* (CAN); Shoran Lake, 71°51'N 113°23'W, *MacInnes s.n.* (CAN 535570, 535598, 535733). **Fitzwilliam Owen Island:** 77°07'N 113°47'W, *Kuc s.n.* (CAN 331114). **Melville Island:** 75°56'N 114°48'W, *Edlund & Aiken 148* (CAN); Canrobert Hills 75°47.30'N 115°56'W, *Edlund 179* (CAN); Ibbett Bay, 75°54'N 114°30'W, *Edlund 43* (CAN); Kitson River, 76°02'N 113°05'W, *Edlund 18* (CAN); Marie Bay 76°12'N 114°55'W, *Edlund 305* (CAN); McCormick Inlet, 75°46.2'N 112°31.64'W, *Gillespie & Consaul 6977* (CAN, plants 1, 2), 6964a (CAN); Shellabear Point, 71°51'N 113°23'W, *Edlund 115* (CAN); Sherard Bay, 76°08'N 108°07'W, *Dugal s.n.* (CAN 535598); Winter Harbour, 74°17'N 110°42'W, *Kuc s.n.* (CAN 400104); Winter Harbour, 74°17'N 110°42'W, *Tener & Harington 149* (CAN). **Prince Patrick Island:** Green Bay, 76°33.67'N 118°53.09'W, *Gillespie & Consaul 6869* (CAN, plants 1-6); Intrepid Inlet, 76°22.01'N 118°35.45'W, *Gillespie*

& *Consaul* 6876 (CAN); Mould Bay 76°12'N 119°25'W, *MacDonald* 146 (CAN); Mould Bay, 76°14.50'N 119°21'W, *Gillespie & Consaul* 6806 (CAN, plants 1-5); Mould Bay, 76°14'N 118°57'W, *Gillespie & Consaul* 6827 (CAN, plants 1, 2), 6826 (CAN, plants a1-a5); Mould Bay, 76°21.50'N 119°30.50'W, *Gillespie & Consaul* 6884 (CAN, plants 1, 2), 6984 (CAN, plants 1-5), 6806 (CAN, plants 1-5). **Victoria Island:** Minto, 71°34'N 115°21'W, *Edlund* 594 (CAN).

Saxifraga tenuis

NUNAVUT. **Axel Heiberg Island:** Bastion Ridge, 79°21'N 90°48'W, *Beschel* 12920 (CAN); Mesa Brook, 79°35'N 95°30'W, *Beschel* 13129 (CAN 295548); 80°17'N 88°27'W, *Scotter & Zoltai* 45133 (DAO), 45181 (DAO). **Baffin Island:** Resolution Island, 61°20'N 64°55'W, *Wynne-Edwards* 7225 (CAN); Erik Harbour, 72°40'N 76°30'W, *Calder s.n.* (DAO 30869, 30871); Ogac Lake, 62°51.7'N 67°21'W, *McLaren s.n.* (CAN 274125); Frobisher Bay, 63°45'N, 68°32'W, *Senn* 3658 (DAO); Blackhead Island, 64°59'N 66°19'W, *Soper s.n.* (CAN 125598); Savage Islands, 61°49.15'N 65°42.62'W, *Gillespie et al.* 6728 (CAN), 6732 (CAN); Inugsuin Fjord, 69°50'N 69°08'W, *Beschel* 3649A (CAN). **Bathurst Island:** 76°36'N 100°04'W, *Blake* 24a (DAO). **Bylot Island:** 73.03'N 80.07'W, *Scotter & Zoltai* 6751A (DAO). **Ellef Ringnes Island:** Isachsen, 78°49'N 103°37'W, *Savile* 4275 (DAO), 4219 (DAO), 4224 (DAO), 4285 (DAO), 4355 (DAO), 4293 (DAO); Isachsen, 78°47'N 103°30'W, *MacDonald* 251 (CAN), 252 (CAN); Christopher Peninsula, 78°59'N 101°35'W, *Savile* 4194 (DAO); 78°45'N 102°50'W, *Savile* 4148 (DAO). **Ellesmere Island:** Eureka, 79°59'N 85°50'W, *Scotter & Zoltai* 45294-B (DAO); Eureka, 80°10'N, 85°39'W, *Bruggemann* 805 (DAO); Fosheim Peninsula, 79°34'N 84°44'W, *Edlund & Roncato-Spencer* 262 (CAN 535348, 533280); Fosheim Peninsula, 79°58'N 84°26'W, *Edlund & Roncato-Spencer* 275 (CAN); Hazen, 81°49'N 71°21'W, *Savile* 4485 (DAO), 4752 (DAO), 4655 (DAO); Hazen, 81°45'N 68°30'W, *Powell* 338 (CAN); Hazen, 82°N 70°W, *Soper* 8273 (CAN); Makinsen Inlet, 76°41'N 81°37'W, *Blake* 7 (DAO); Mount Pullen, 82°25'N 62°17'W, *MacDonald* 46 (CAN); 81°45'N 62°11'W, *Powell* 520 (CAN); Mt. Pullen, 82°26'N 62°11'W, *Bruggemann* 215 (DAO); Tanquary Fjord, 79°12'N 83°29'W, *Brassard* 3306 (CAN); Van Hauen Pass, 81°07'N 86°55'W, *Brassard* 3047 (CAN); Vesle Fjord, 79°12'N 83°29'W, *Edlund & Roncato-Spencer* 282 (CAN). **Somerset Island:** 72°56'N 94°57'W, *Zoltai* 741044 (DAO).

NORTHWEST TERRITORIES. **Melville Island:** 74°58'N 115°02'W, *Parker* 44f (DAO); Bailey Point, 74°58'N, 115°02'W, *Parker* 48b (DAO); McCormick Inlet, 75°46.2'N 112°31.64'W, *Gillespie & Consaul* 6978 (CAN, plants 1, 2), 6964b (CAN). **Prince Patrick Island:** Green Bay, 76°33.67'N 118°53.09'W, *Gillespie & Consaul* 6870 (CAN, plant 1); Intrepid Inlet, 75°46.9'N 112°22.09'W, *Gillespie & Consaul* 6877 (CAN, plant 1); Mould Bay, 76°21.5'N 119°30.5'W, *Gillespie & Consaul* 6881 (CAN, plants 1-6); Mould Bay, 76°14'N 118°57'W, *Gillespie & Consaul* 6825 (CAN, plants 1-3); Mould Bay, 76°14.5'N 119°21'W, *Gillespie & Consaul* 6807 (CAN, plants 1-5). **Victoria Island:** Ulusartok Peninsula, 70°44'N 117°44'W, *Edlund* 875 (CAN).

ALASKA. Kenai Peninsula. 60°49'N 149°33'W, *Calder* 6511, 6249, 6107 (DAO).

BRITISH COLUMBIA. Haines Junction, *Calder & Kukkonen* 28151 (DAO); Haines, *Taylor et al.* 1204 (DAO).

Mixed collections - *Saxifraga tenuis* and *Saxifraga nivalis* on same sheet

NUNAVUT. **Baffin Island:** Apex, 63°43'N 68°27'W, *Calder et al. s.n.* (DAO 24149); Home Bay, 68°45'N 67°10'W, *Smith VP-53-61* (CAN). **Ellesmere Island:** Tanquary Fjord, 79°12'N 83°29'W, *Brassard* 3317 (CAN); Hazen, 81°49'N 71°21'W, *Savile* 4562 (DAO).

NORTHWEST TERRITORIES. **Victoria Island:** near Holman, 70°43'N 117°43'W, *Edlund* 719 (CAN). **Prince Patrick Island:** Mould Bay, 76°12'N 119°25'W, *MacDonald* 150 (CAN, *S. tenuis*: 1, 3, 4, 7, 8, 9; *S. nivalis*: 2, 5, 6, 10).



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