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Evidence for hybridization and introgression in two Canadian Arctic louseworts: *Pedicularis langsdorffii* subsp. *arctica* and *Pedicularis hirsuta*.

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Abstract

Hybridization and introgression between two closely related but taxonomically distinct Arctic lousewort species – the circumpolar *Pedicularis hirsuta* (predominantly eastern Arctic in Canada) and the amphiberingian, western Canadian *Pedicularis langsdorffii* subsp. *arctica* – is documented here for the first time, only the second confirmed case of introgression in this widespread genus. Multivariate and univariate analysis of morphological characters successfully delineate the two species as morphologically similar but distinct taxa. Analysis of nrDNA ITS sequences likewise differentiate the two taxa in all sampled instances. Analysis of cpDNA *atpI-atpH* sequences also separate these taxa, except in 12 individuals of *P. langsdorffii* subsp. *arctica*, which possess the same haplotype as *P. hirsuta*. Where these two species overlap in range in the Canadian High Arctic, chloroplast transfer from *P. hirsuta* to *P. langsdorffii* subsp. *arctica* is detected, and morphologically intermediate hybrids have been identified, indicating hybridization and subsequent backcrossing. Here we discuss the relationships between these two species, and provide a key useful in differentiating them.

Keywords: Arctic, *Pedicularis*, Orobanchaceae, Hybridization, Introgression

Introduction

Pedicularis L. is the largest genus of the ca. 89 genera in the Orobanchaceae (Bennett and Mathews 2006). This widespread family, which includes many notable parasitic members, now includes ca. 73 genera (like *Pedicularis*) that were formerly placed in the Scrophulariaceae (Wolfe et al. 2005). With over 600 species worldwide (Robart et al. 2015), *Pedicularis* is most diverse in temperate Eurasia, where over 70% of known species occur (Yang and Wang 2007). Many species can be found throughout the western hemisphere (Mill 2011), and approximately 40 are known from North America (Robart et al. 2011).

North American species of *Pedicularis* are thought to have radiated from Eurasian migrants (Li 1951; Robart et al. 2015). Previously, Savile (1977) suggested that up to 25 mid-latitude species on the continent evolved from a single species introduced in the Pliocene based on close morphological similarity; this is consistent with a recent phylogeny which estimates the number of North American ancestors to be only two (Robart et al. 2015).

Recent *rbcL* and *matK* DNA barcode data for the ten species of *Pedicularis* occurring in the Canadian Arctic indicate deep genetic divergence among several clades, suggesting six major lineages of this genus in the region (Saarela et al. 2013). One such lineage consists of three closely-related species: *Pedicularis lanata* Willd. ex Cham. and Schltdl., *Pedicularis hirsuta* L., and *Pedicularis langsdorffii* Fisch. ex Steven, all with extensive ranges in the Canadian Arctic (Aiken et al. 2007; Hultén 1964; Porsild and Cody 1980). Tkach et al. (2014), in their expanded *Pedicularis* phylogeny (including many Arctic species omitted from previous studies), also found this “*Pedicularis lanata/langsdorffii*” lineage, which included *P. hirsuta*. In this lineage *P. lanata* forms a well-supported clade with *P. alopecuroides* Steven ex Spreng., *P. dasyantha* (Trautv.) Hadac, and *P. pallasii* Vved., consistent with the *Pedicularis lanata* aggregate in Elven et al. (2011), and *Pedicularis hirsuta* and *P. langsdorffii* are resolved as sister species (Tkach et al.

2014). *Pedicularis hirsuta* is circumpolar; in North America it has a primarily eastern Arctic distribution, ranging from continental Nunavut and northernmost Quebec and Labrador, through to the eastern Canadian Arctic Archipelago and Greenland, with further occurrences on Banks Island, Melville Island, and coastal Alaska (Figure 1; Aiken et al. 2007; Elven et al. 2011). Considered a rare species in Alaska, it is found at only one location along the north coast (Cortés-Burns et al. 2009).

Pedicularis langsдорffii is an amphi-beringian species with two subspecies: subsp. *langsдорffii* in Chukotka in Far East Russia, the Bering Sea islands, and western Alaska; and subsp. *arctica* (R. Br.) Pennell ex Hultén, distributed from easternmost Siberia in Russia, through northwestern North America, and across to northeastern Greenland (Figure 1; Elven et al. 2011). These two taxa were initially treated as species, *P. langsдорffii* (sometimes misspelled as *P. langsдорffii*) and *P. arctica* R. Br. *Pedicularis arctica* was treated as an infraspecific taxon within *P. langsдорffii*, first as a variety by Polunin in 1940, and subsequently as a subspecies (Hultén 1968); however, the species level approach continued to be widely used in Canada (e.g., Porsild 1957, Porsild and Cody 1980). Here we follow recent treatments which ascribe them to the subspecies level (Cody 2000, Elven et al. 2011). *Pedicularis langsдорffii* subsp. *arctica*, the only subspecies of *P. langsдорffii* present in Canada, is predominantly western, with a range extending from British Columbia, Alberta, Yukon and the continental Northwest Territories (and western continental Nunavut) through to Ellesmere Island in the Canadian High Arctic (Figure 1) (Porsild 1957; Porsild and Cody 1980; Aiken et al. 2007). Although these authors indicated *P. langsдорffii* subsp. *arctica* as occurring on Baffin Island, these specimens (*Manning* 15 CAN 204697, *N. Polunin* 2471 CAN 97311, *Soper s.n.* CAN 97308, *Soper s.n.* CAN 97309) have since been redetermined to *P. hirsuta*, and the species is not considered present there. Both Porsild and Cody (1980) and Aiken et al. (2007) show *P. l.* subsp. *arctica* as occurring on nearby Bylot Island; however this specimen (Scotter 67143, DAO 334867) is likely a hybrid between *P. hirsuta* and *P. l.* subsp. *arctica* (see discussion for details)

Though largely allopatric, their ranges overlap in several places in Canada, including northwest mainland Nunavut, northeast Banks Island, Melville Island, Bathurst Island, and notably, throughout the High Arctic on Devon, Ellesmere, and Axel Heiberg Islands (Figure 1). Both *P. hirsuta* (Figure 2) and *P. langsdorffii* subsp. *arctica* (Figure 3) exhibit similar overall morphologies – often to a degree that the plants are easily confused with each other, particularly in the southern Arctic Archipelago where *P. hirsuta* grows larger. Conversely, the species are more easily differentiated in the northern portions of their ranges, where *P. langsdorffii* subsp. *arctica* in turn has much larger, more colourful flowers than *P. hirsuta* (Aiken et al. 2007).

These two species have been typically differentiated from each other on the basis of two small teeth located near the tip of the galea (the fused petals forming the “helmet” on top of each flower) – with *P. langsdorffii* subsp. *arctica* possessing these teeth, *P. hirsuta* lacking them (Porsild 1957). A later treatment by Porsild and Cody (1980) separated them on the basis of inflorescence pubescence; *P. hirsuta* possessing a white-woolly inflorescence, while *P. langsdorffii* subsp. *arctica* appearing nearly glabrous. However, where their ranges are sympatric, morphological intermediates between these two taxa have been suggested, specifically where the two species meet on Ellesmere Island and Greenland (Porsild 1957). This may indicate that hybridization is occurring between these two taxa. Additionally, DNA barcoding has detected the *matK* chloroplast haplotype of *P. hirsuta* in a specimen of *P. langsdorffii* which was thought to be due to sampling a hybrid, or detection of cpDNA Introgression (Saarela et al. 2013).

Most Arctic plant species are thought to be of hybrid origin, having undergone extensive reticulation through the Pleistocene (Abbott and Brochmann 2003), and have since been stabilized through polyploidy (Brochmann et al. 2004). While previous research asserted that polyploidy, apomixis (Bliss 1971) and autogamous reproduction strategies (Savile 1964) likely lowered the potential for recent

hybridization in Arctic plants, more current research indicates that rates of hybridization vary by taxon, and may be more prevalent than previously thought. Hybrids are noted in a diverse array of Arctic plant families, notable examples include *Potentilla* (Eriksen and Töpel 2006, Lèveillé-Bourret et al. 2014), *Papaver* (Solstad 2008), *Festuca* (Guldhal et al. 2001), *Salix* (Aiken et al. 2007), *Eriophorum* (Cayouette 2004), and *xPucciniphippsia* (Steen et al. 2004). As well, rates of hybridization in the Arctic may increase over time as climate change drives compatible species together (Brochmann and Brysting 2008).

Given reports of morphological intermediates between *P. hirsuta* and *P. langsдорffii* subsp. *arctica* where their ranges overlap, phylogenetic closeness (Saarela et al. 2013; Tkach et al. 2014), and overlapping flowering times (L.J. Gillespie, personal observation), which might enable interspecific cross-pollination via pollinator sharing (Macior 1983), we hypothesize that these two sister taxa may be hybridizing where they come into contact. Here, we conduct an in-depth molecular and morphological analysis of *P. hirsuta* and *P. langsдорffii* subsp. *arctica* in Canada to assess their taxonomic boundaries, and evidence for hybridization and/or Introgression.

Materials and Methods

Materials Examined

Specimens examined (Appendix A) for this study were selected to encompass the geographic range of both *Pedicularis* species across Canada, with a focus on regions where *P. langsдорffii* subsp. *arctica* and *P. hirsuta* are sympatric (Figure 1). In total, 58 specimens of *P. hirsuta* were examined; 54 were measured to collect morphological data (of which 50 specimens were used in the final analysis), and 47 specimens were DNA sequenced (only four of which did not have a corresponding voucher used in the morphology analyses). In *P. langsдорffii* subsp. *arctica*, 62 specimens were examined; 58 were measured for morphology (57 specimens in final analysis), and 49 specimens were DNA sequenced (only 7 of which did not have a corresponding morphology voucher).

PCR and Sequencing

Genomic DNA was extracted from both silica gel-preserved leaf tissue samples (50) and herbarium samples (52) according to protocols modified from Alexander et al. (2007). Not all extractions or amplifications were successful – see Appendix A for complete sample details. *Pedicularis lanata*, *P. albolabiata*, and *P. labradorica* were selected as outgroups so as to include congeners at varying phylogenetic distances (Robart et al. 2015) from the same geographic region (Porsild and Cody 1980). Samples were screened for sequence variation in 18 cpDNA regions. The *atpI-atpH* intergenic spacer region (Shaw et al. 2005) was selected for further sequencing, while the following regions were rejected due to low sequence variation: the core barcode loci for vascular plants *matK* (Fazekas et al. 2008) and *rbcL* (Levin et al. 2003; Kress and Erickson 2007), *trnH-psbA*, *trnC-rpoB*, *trnC-ycf6*, *trnD-trnT*, *trnS-trnG*, *trnS-trnfM* (Shaw et al. 2005), *atpB-rbcL* (Chiang et al. 1998), *trnT-trnL*, *trnL-trnF* (Taberlet et al. 1991), *rp32-trnL*, *trnV-ndhC*, *psbD-trnT*, *psbJ-petA*, *atpI-atpH*, and *petL-psbE* (Shaw et al. 2005).

For amplification of the *atpI-atpH* intergenic spacer, two different reaction volumes were used: 15.5 µl for routine reactions, and 50 µl for older and/or degraded samples. The 15.5 µl reaction volumes contained 9.17 µl of ddH₂O, 1.5 µl of 10X reaction buffer (BioShop Canada), 1.94 mmol/L MgCl₂ (Sigma-Aldrich), 0.19 mmol/L dNTPs, 0.24 mmol/L of each primer at (Alpha DNA, Montreal), 0.02 µg/µL bovine serum albumin (Sigma-Aldrich), 0.08 µl of BioShop TAQ DNA Polymerase (BioShop Canada), and 1.5 µl genomic DNA. The 50 µl reaction volumes contained 26 µl of ddH₂O, 5 µl of 10X reaction buffer (BioShop Canada), 2.5 mmol/L MgCl₂ (Sigma-Aldrich), 0.2 mmol/L dNTPs, 0.3 mmol/L of each primer (Alpha DNA, Montreal), 0.02 µg/µL bovine serum albumin (Sigma-Aldrich), 1 µl of BioShop TAQ DNA Polymerase (BioShop Canada), and 5 µl genomic DNA. Amplification reactions for both cpDNA reaction volumes were run using the same thermocycler protocols: 95°C for 5 minutes, 30 cycles of: 95°C for 45 seconds, 48°C for 45 seconds, 72°C for 1 minute 30 seconds, and a final extension step of 72°C for 5 minutes.

We selected the internal transcribed spacer region (ITS) of the nrDNA for sequencing to assess variation using a nuclear marker (and to compare with the plastid data). We used the ITS1 and ITS4 primers described in White et al. (1990) to amplify and sequence the entire region. For the ITS PCRs, each 15.5 µl reaction volume contained 6.87 µl of ddH₂O, 1.5 µl of 10X reaction buffer (BioShop Canada), 2.41 mmol/L MgCl₂ (Sigma-Aldrich), 0.19 mmol/L dNTPs, 0.24 mmol/L of each primer (Alpha DNA, Montreal), 0.02 µg/µL bovine serum albumin (Sigma-Aldrich), 0.08 µl of BioShop TAQ DNA Polymerase (BioShop Canada), and 1.5 µl genomic DNA. The ITS PCRs were run using the following thermocycler protocols: 94°C for 3 minutes, 35 cycles of: 94°C for 1 minute, 42°C for 1 minute, 72°C for 1 minute 20 seconds, and a final extension step of 72°C for 5 minutes.

PCR products were purified by adding 6 µl of a 1:10 dilution of ExoSAP (1 µl of Exonuclease I [MJ Biolynx], 10 µl Shrimp Alkaline Phosphatase [MJ Biolynx], and 189 µl ddH₂O) to each successful reaction,

and incubating the mixtures at 37°C for 30 minutes, followed by 10 minutes at 90°C. Purified PCR products were sequenced on an ABI 3130xl Genetic Analyser using BigDye version 3.1 chemistry (Applied Biosystems). Sequence traces were assembled, visually verified, and aligned in Genious 6.0.3 using the ClustalW alignment method (Biomatters).

Phylogenetic Analysis

Models for nucleotide substitution were determined using the Akaike Information Criterion, calculated using MrModetest2 (Nylander 2004). For the *atpl-atpH* dataset the HKY+I model was selected, and for the ITS dataset the GTR+G model was chosen. There was no indel variation between or within *P. hirsuta* or *P. langsдорffii* subsp. *arctica*; accordingly indel characters were not included in our analysis.

Each marker (*atpl-atpH* and ITS) was analyzed separately. Bayesian analysis was run on each dataset in MrBayes 3.2.2 (Ronquist et al. 2012). In each analysis, two Markov chains were run for 20 000 000 generations, with trees sampled after every 100th generation, and 5000 trees discarded as the burn-in. Results were summarized as a majority rule consensus tree.

Maximum parsimony analyses were carried out in PAUP 4.0 (Swofford 2003) by running a heuristic search algorithm using the following parameters: 1000 replicates run to completion using random stepwise addition sequence and tree bisection reconnection (TBR) branch swapping. This resulted in 204 equally parsimonious trees for the ITS dataset and 24 equally parsimonious trees for *atpl-atpH* dataset, from which a strict consensus tree was generated for each dataset. Bootstrap support was obtained in PAUP 4.0 using the following parameters: 100 bootstrap replicates with a maximum of 10 000 trees generated per replicate through simple stepwise addition sequence and TBR branch swapping (Swofford 2003).

Morphology

A set of 32 characters were selected based on keys and descriptions of *P. hirsuta* and *P. langsdorffii* subsp. *arctica* from both Arctic floras and primary literature sources (Hultén 1968; Porsild 1955, 1957; Savile 1964, 1977; Welsh 1974; Aiken et al. 2007; Porsild and Cody 1980; Cody 2000; Robart 2005). These included 30 quantitative, and two qualitative characters (Table 1). Quantitative characters were directly measured using a ruler and digital calipers (Table 1; Figure 4). Qualitative characters (stem and inflorescence pubescence) were visually scored into six discrete character states: glabrous (no visible hairs on observed surface), glabrate (few hairs distributed sporadically over surface), sparse (approx. one to five hairs evenly distributed per cm², outer epidermis clearly visible under hairs), moderate (approx. 10-20 hairs evenly distributed per cm², outer epidermis partially hidden under hairs), dense (hairs covering surface, outer epidermis only partially visible under hairs), and very dense (surface completely covered in dense, wooly pubescence, outer epidermis completely hidden) (Table 1).

Four fruiting specimen characters (fruit width, fruit length, seed width, and seed length) were ultimately omitted due to missing data; fruiting specimens were rarely encountered in our herbarium search. As they seem to be infrequently collected, we did not find enough clearly identifiable specimens to analyze. Accordingly, specimens without flowers were omitted from the final multivariate analysis (Appendix A).

A total of 107 specimens (excluding fruiting specimens) from across the range of these taxa in the Canadian Arctic were measured. Based on measurements of key characters and our multivariate analysis (elaborated on in Results), 50 specimens were identified as *P. hirsuta*, 50 as *P. langsdorffii* subsp. *arctica*, and 7 specimens previously identified as *P. l.* subsp. *arctica* were identified as putative hybrids with intermediate or shared diagnostic characters from both species. These putative hybrids were omitted from both our univariate statistical analysis (though their measurements are included in Table 1) and our analysis of stem and inflorescence pubescence.

Three principal components analyses (PCA) were carried out on the data collected from the 26 remaining continuous variables in PAST 3.01 (Hammer et al., 2001); one PCA retaining just the 12 floral characters, one retaining the 14 vegetative characters, and one with all 26 characters.

Quantitative variables were tested for interspecific variation between the two taxa, excluding the putative hybrids, using a Mann-Whitney U test (as the data were not normally distributed) in PAST. We recorded the Mann-Whitney U statistic, the Z statistic, and the p value for these tests, and assessed their significance at the $p < 0.05$ and $p < 0.001$ levels. Median values and standard deviations for these variables were recorded and compared using boxplots.

Qualitative variable scores were transformed into percentages of specimens examined displaying each of six discrete character states for pubescence (Table 1), and charted using a stacked column chart.

Results

Phylogenetic Analysis

Analysis of both the nuclear (ITS) and plastid (*atpI-atpH*) datasets show that *Pedicularis hirsuta* and *Pedicularis langsdoerffii* subsp. *arctica* resolved together in a strongly supported clade, well separated from the outgroups, *P. lanata*, *P. albolabiata*, and *P. labradorica*, confirming that these two species are more closely related to each other (Figures 5, 6). This clade resolved as sister to *P. lanata* (Figure 5).

Both maximum parsimony and Bayesian analysis of the ITS dataset (both trees possessed identical topology) show that *P. hirsuta* and *P. langsdoerffii* subsp. *arctica* were each well resolved as a separate clade, with posterior probability scores of 0.73 and 0.68 and high levels of bootstrap support (92 and 98) respectively (Figure 5). There was no genotypic variation or geographic structuring in the two studied species: all specimens of *P. hirsuta* and *P. langsdoerffii* subsp. *arctica* displayed the same ITS genotype respectively.

Pedicularis hirsuta specimens display a genetically uniform haplotype and cluster together in analyses of the *atpI-atpH* dataset, differentiated from the majority of *P. langsdoerffii* subsp. *arctica* haplotypes with a posterior probability of 0.83 and a bootstrap value of 88 (Figure 6). *Pedicularis langsdoerffii* subsp. *arctica* possesses a variety of distinct haplotypes with all differentiated from *P. hirsuta* except for 12 specimens from Ellesmere, Banks, Devon, Melville, and Axel Heiberg Islands in the Canadian High Arctic and western Arctic islands (Figure 1, introgressed specimens), 11 of these 12 specimens possessed the same, and one a very similar haplotype as *P. hirsuta*. Most *P. langsdoerffii* subsp. *arctica* haplotypes were not resolved in the Bayesian analysis, thus we present the maximum parsimony tree here (Figure 6).

Morphology

Principal components analysis of the 12 floral morphological variables show both *P. hirsuta* and *P. langsдорffii* subsp. *arctica* as distinct clusters in multivariate space (Figure 7). The *P. langsдорffii* subsp. *arctica* specimens possessing a *P. hirsuta* haplotype (introgressed) exclusively cluster with *P. langsдорffii* subsp. *arctica*. PCA of the full 26 character dataset showed the same pattern as the floral dataset while explaining less of the variation in the data, and PCA of the 14 vegetative characters showed total overlap between the two taxa (Supplementary Figure S1). Specimens forming a third cluster (discussed in detail below), intermediate between the two species, were identified as putative hybrids.

Univariate analysis of the 12 continuous floral morphology variables measured indicate that, in general, the flowers of *Pedicularis langsдорffii* subsp. *arctica* are larger and more robust than flowers of *P. hirsuta*. There are significant differences between the two taxa for 11 of the 12 measured variables; for all of these variables *P. l. arctica* possessed the higher median value (Figure 8, Table 1). Only calyx short sepal length was not significantly different (Figure 8, Table 1). Notably, there was zero style protuberance in all *P. hirsuta* specimens measured, as opposed to a median length of 1.1 mm in *P. langsдорffii* subsp. *arctica*. Of the 14 vegetative characters measured, cauline leaf blade width, cauline leaf petiole length, cauline leaf lobe length, cauline leaf lobe width, bract blade width, and bract petiole length were all significantly different between the two taxa (Supplementary Figure S2, Table 1).

The vast majority of *P. hirsuta* specimens displayed dense inflorescence pubescence (85%), versus the nearly even split of sparse and moderate (and about 20% dense) character state proportions seen in *P. langsдорffii* subsp. *arctica* (Figure 9a). Both *P. hirsuta* and *P. langsдорffii* subsp. *arctica* have similar distributions for the stem pubescence qualitative character states, with mostly similar proportions of specimens displaying glabrate, sparse, and moderate stem pubescence; *P. hirsuta* possessed a higher

proportion of plants with moderately pubescent stems, and *P. l.* subsp. *arctica* has a higher proportion with glabrate stems. (Figure 9b).

Seven specimens, four from the Truelove lowlands on Devon Island (*Mackenzie 14*, *Mackenzie 21*, *Mackenzie 45*, and *Pakarinen s.n.* [CAN 409449]), one from the Fosheim Peninsula on Ellesmere Island (*Gillespie 6138*), one from Tanquary Fjord on Ellesmere Island (*Gillespie 6478*), and one from Mokka Fjord on Axel Heiberg Island (*Parker 73061A*) were found to have intermediate morphology in both the floral and combined PCAs (Figure 7, Supplementary Figure S1a). The four Truelove Inlet individuals all possessed short, densely hirsute racemes, short calyces (both lengths), short distances from the tip of the galea to the teeth, and short corollas (all approaching *P. hirsuta*), wide corolla lips (approaching *P. l.* subsp. *arctica*), and intermediate anther length and intermediate galea width (Table 1). In this population both length of protruding style and tooth length were observed to be variable on the individual flowers of a single plant, and among different plants on the same herbarium sheet – ranging from non-exserted to extremely long-exserted styles, and calyx teeth ranging from absent to long, even on a single plant. Likewise exserted styles varied in orientation, from straight and perpendicular to the galea (as in *P. l.* subsp. *arctica*), to moderately-to-strongly recurved exserted styles (approaching the strongly recurved non-exserted styles of *P. hirsuta*). These plants all shared the same overall appearance, approaching an intermediate form between the two taxa, with the compact inflorescences and hirsute racemes characteristic of *P. hirsuta*, and the protruding styles (Table 1) characteristic of *P. l.* subsp. *arctica*.

The putative hybrid specimen from the Fosheim Peninsula (*Gillespie 6138*) also possessed variation in teeth presence and length, and style length, exsertion, and orientation, similar to the Truelove Inlet population. Morphologically, this specimen possessed narrow corolla lips, short corollas, and short galea teeth (all characters closer to the median values observed in *P. hirsuta*), and long anthers, longer

distances from the galea tip to the galea teeth, and wide galeas (closer to *P. l.* subsp. *arctica*) (Table 1). The other Ellesmere specimen from Tanquary Fiord (*Gillespie 6478*) possessed long corollas, wide galeas, well-exserted, erect styles, and long anthers characteristic of *P. l.* subsp. *arctica*, the short raceme, short calyces, and short (and sometimes absent) galea teeth characteristic of *P. hirsuta*, and intermediate measurements for lip width and galea teeth distance from tip (Table 1). The last specimen, *Parker 73061A* from Mokka Fiord, possessed short inflorescences, narrow corolla lips, and short (and sometimes absent) galea teeth (all character states approaching *P. hirsuta*), wide calyces, wide galeas, long anthers, exserted styles (all character states approaching *P. l.* subsp. *arctica*), and styles of variable orientation and intermediate corolla lengths (Table 1).

Of these seven putatively hybrid specimens, only one (*Mackenzie 21*) from the Truelove lowlands was included in our genetic analyses, where it was found to possess the nuclear genotype of *P. langsdorffii* subsp. *arctica*, and the plastid haplotype of *P. hirsuta* (Figures 5, 6 – recorded on these figures as *P. langsdorffii* subsp. *arctica* GIL2433 Devon). Another individual from the Truelove lowlands (*Kerik 40*, *P. langsdorffii* subsp. *arctica* GIL2418 Devon on Figures 5 and 6), identified as (non hybrid) *P. langsdorffii* subsp. *arctica*, and determined to be introgressed, was located well within the *P. langsdorffii* subsp. *arctica* polygon in our PCA (Figure 7).

Discussion

Our analysis of the *Pedicularis hirsuta*/*Pedicularis langsдорffii* subsp. *arctica* species complex indicates that these two species are taxonomically distinct entities, as supported by both molecular (Figure 5) and morphological (Figure 7) evidence. However, putative morphologically intermediate hybrids have been identified from their points of contact in the Canadian Arctic (Figure 7), and introgression between the two species has been detected at these points of contact through comparison of our chloroplast and nuclear DNA datasets (Figures 5, 6).

Taxonomic status and distinguishing characters of *Pedicularis hirsuta* and *Pedicularis langsдорffii* subsp. *arctica* in North America

Though there is clear evidence for hybridization and introgression in this group, our data indicates that these two largely allopatric species are distinct, though closely related entities. Analysis of the ITS sequences we generated clearly differentiates *P. hirsuta* from *P. langsдорffii* subsp. *arctica* (Figure 5). The same pattern is seen in the analysis of the chloroplast *atpI-atpH* sequences, save for the introgressed individuals (Figure 6).

Morphologically, when the putative hybrids are excluded, principal components analysis of the floral character matrix shows clear separation between the two taxa, with no overlap in multivariate space (Figure 7). This separation was driven by the eleven significantly different inflorescence characters measured between clearly identifiable, non-hybrid individuals for each taxon (Figure 8, Table 1).

These floral traits are consistent with Pennell's work on North American *Pedicularis* (1935), which is reliant on corolla and calyx characters in differentiating taxa. This was also noted in Aiken et al. (2007): "... the unusually large, dark purple, conspicuously spreading and clearly bidentate flowers of the far northern plants identify them with *P. langsдорffii*." when referring to confusion in differentiating *P.*

hirsuta from *P. langsдорffii* subsp. *arctica* (which they synonymized under *P. langsдорffii*). Böcher et al. (1968) also noted the large purple corollas of *P. langsдорffii* and the smaller pink corollas of *P. hirsuta* as useful distinguishing characters. Though we did not score flower color (very few dried specimens of either species retained their corolla colour), field observations (L.J. Gillespie) and floristic treatments (Porsild 1957; Böcher et al., 1968; Porsild and Cody 1980; Aiken et al. 2007) report a generally paler corolla in *P. hirsuta* when compared to *P. langsдорffii* subsp. *arctica*. Certainly our findings support the assertions of Böcher et al. (1968) and Aiken et al. (2007) of larger flowers, primarily statistically longer corollas, wider galeas, and wider corolla lips in *P. langsдорffii* subsp. *arctica* than in *P. hirsuta* (Figure 8). The length of the raceme (inflorescence length: Figure 8) was also found to be statistically longer in *P. langsдорffii* subsp. *arctica* than in *P. hirsuta*. Although inflorescence, corolla, and calyx size characters were found to be statistically significant between the two taxa, they cannot be used alone to distinguish the species due to the often large overlap (Figure 8).

Style protuberance and anther length were found to be the best diagnostic characters, since they had no or very little overlap, respectively, between the two taxa. Style protuberance, which was previously used to differentiate the taxa in Greenland (Böcher et al. 1968), was found to be exceptionally useful (Figure 8), as the style never protrudes from “good” *P. hirsuta* (Figure 2) – only *P. langsдорffii* subsp. *arctica* displays any style protrusion (Figures 3, 8). Anther length was found to be an excellent diagnostic character (Figure 8; 0.9-2.0 mm in *P. hirsuta*, 2.0-3.0 mm in *P. langsдорffii* subsp. *arctica*), and one that has not been used previously.

Our findings on floral morphology in each species – small, duller colored flowers with smaller anthers and retracted styles in *P. hirsuta*, and larger, brightly colored flowers with large anthers and protruding styles in *P. langsдорffii* subsp. *arctica* – is consistent with the pollination syndromes previously observed in these species. *Pedicularis hirsuta* is structurally adapted for self-pollination (Swales 1979), and was

found to have high reproductive success despite rare pollination events (Eriksen et al. 1993). Studies in West Greenland showing high seed set when pollinators were excluded (Philipp et al. 1996) and no variability in seven isozyme systems studied (Philipp 1998) also provide evidence for *P. hirsuta* as highly self-pollinating. Conversely, *P. langsdoeffii* subsp. *arctica* exhibits high reproductive success when insect pollinated – the large corolla lip, large anthers, and protruding style seem adapted for just this purpose (Williams and Batzli 1982). Macior (1975), in his studies of this species in the Yukon, determined that pollinators were almost exclusively bumblebees collecting both pollen and nectar, and that plants did not set seed in the absence of pollinators. Selfing versus outcrossing pollination syndromes may serve to reinforce species boundaries in this complex, but may also partially explain the hybridization and unidirectional chloroplast capture we observed, as we discuss below.

Fewer vegetative characters differed significantly (and most only at the $p > 0.05$ level) between the two taxa; these include cauline leaf blade width, cauline leaf lobe length and width, inflorescence bract blade width, bract petiole length ($p > 0.01$), and stem width (Suppl. figure S2, Table 1). Previous work has indicated that vegetative structures are conserved in *Pedicularis*, and are less variable and less useful when compared to floral structures (Li 1951). Savile (1977) hypothesized that the similar leaf morphologies seen in Canadian Arctic *Pedicularis* species were derived from a single mid-latitude alpine species through population isolation in the Pleistocene; the pinnatifid leaves were conserved in Arctic species and suggested to be not a disadvantage in open sites. Altogether, we found floral characters, and not vegetative characters, to be useful in distinguishing *P. hirsuta* and *P. langsdoeffii* subsp. *arctica*.

Prior to this study, there have been differences in opinion and some confusion on the taxonomic boundaries and morphological traits distinguishing *P. hirsuta* from *P. langsdoeffii* subsp. *arctica* (Simmons 1906; Hultén 1964; Polunin 1940; Porsild 1957; Porsild and Cody 1980). For example, Hultén (1964) used basal leaf breadth, filament hair density, and galea teeth to separate these species. While

galea teeth are easily observed and measured, filament hair density requires flowers collected when fully open, and basal leaves are rarely seen on herbarium sheets of these two species. This galea teeth character is one of two often cited characters used to distinguish these two species in the above mentioned treatments, the other being stem and inflorescence pubescence.

Porsild (1957) described *P. hirsuta* as lacking teeth on the galea, distinguishing it from teeth-bearing *P. langsdorffii* subsp. *arctica*. Böcher et al. (1968) also used the presence of galea teeth - though he qualified *P. hirsuta* as “usually without teeth” (pg. 163) - as a diagnostic character useful in differentiating the two species in Greenland. Our examination of the species complex found that typical *P. hirsuta* flowers do possess a pair of teeth on the galea; however, they are significantly shorter and closer to the distal tip of the corolla when compared with *P. langsdorffii* subsp. *arctica* (Figure 8, Table 1). This is consistent with Hultén (1964 – pg. 312), who asserted that *P. hirsuta* had “a less distinct tooth of the galea”. Even though both species bear teeth on the galea, our results indicate that the length of the teeth and their distance from the corolla tip are useful characters for differentiating these sister species, similar to their use in other members of *Pedicularis* (Li 1948).

Another previously unclear taxonomic character is the pubescence on the stem and surrounding the inflorescence in these two species. Previous work by Porsild and Cody (1980) suggested that the stem and inflorescence of *P. langsdorffii* subsp. *arctica* were glabrous or nearly so while in *P. hirsuta* they were “white-wooly”. Later, Cody (2000) also described the inflorescence of Yukon *P. langsdorffii* subsp. *arctica* as essentially glabrous. Our qualitative examination of the species complex showed that the stem and inflorescence of *P. hirsuta* were indeed frequently densely hairy, but very few of the *P. langsdorffii* subsp. *arctica* specimens were completely glabrous. Overall, stem pubescence showed similar levels of density for both species, but *P. hirsuta* possessed a greater number of specimens with very hairy inflorescences. While some variation in the amount of hair is likely due to phenotypic plasticity, the

higher density of hair on the inflorescence in *P. hirsuta* allows for it to be retained as a distinguishing character.

Combining the two diagnostic characters, style protuberance and anther length, with the statistically significant flower and inflorescence size characters allows us to create a key useful for separating these taxa. Of the many different keys in the literature, each focusing on a single or a set of different characters, the key of Böcher et al. (1968), which used style protruberance, corolla size, and corolla colour, best differentiated the two taxa.

Key to *Pedicularis hirsuta* and *Pedicularis langsdorffii* subsp. *arctica* in Canada

Style not protruding from tip of corolla galea; anthers 0.8-2.0 mm long; galea teeth absent or short (0-0.3 (-0.5) mm long), 0-0.8 (-1.1) mm from tip of galea; corolla pale pink, small (8.0-16.0 (-19.0) mm long, lip 3.0-10.0 mm wide); inflorescence usually shorter (14-47 (-160) mm long), moderately to densely hairy; primarily eastern Arctic species, common in Nunavut (Figure 2).

.....*Pedicularis hirsuta*

Style protruding 0.5-3.0 mm from tip of the corolla galea; anthers 2.0-3.2 mm long; galea teeth longer ((0.1-) 0.2-0.7 (-1.0) mm long), 0.5-1.8 mm from tip of galea; corolla deep pink to purple, larger (11.0-16.0-26.0 mm long, lip (5.0-) 7.0-19.0 mm wide), inflorescence usually longer ((24) 40-100 (-180) mm long), glabrate to moderately hairy (rarely densely hairy); primarily western Arctic species, common in the Northwest Territories, Yukon, northern and western Nunavut (Figure 3).

.....*Pedicularis langsdorffii* subsp. *arctica*

Phylogeography of *Pedicularis hirsuta* and *Pedicularis langsdorffii* subsp. *arctica*

The genetic variation observed within the cpDNA *atpI-atpH* sequences is similar to patterns seen in previous studies on Arctic plant evolution and phylogeography in North America (Tremblay and Schoen 1999; Abbott and Brochmann 2003; Eidesen et al. 2007): a genetically diverse taxon (*P. langsdorffii* subsp. *arctica*) centered on unglaciated Beringia, and a genetically-uniform taxon (*P. hirsuta*) with a Canadian centre of distribution in the glaciated Arctic Islands (Figures 1, 6). *Pedicularis langsdorffii* subsp. *arctica* likely spread from Beringia across the western Arctic islands and High Arctic after the last

glaciation. The observed cpDNA variation in this species did not have an obvious geographical component; high diversity in the western Arctic islands may suggest survival in refugia in situ (Tremblay and Schoen 1999; Fedorov and Stenseth 2002), however equally high diversity in the much less sampled western Arctic mainland suggests migration from Beringia. Based on geographic area analysis of multiple *Pedicularis* species, Robart et al. (2015) suggested an ancestral area in the Cascade Range and/or southern Rocky Mountains and subsequent continental glacial advance and retreat to explain the origin and biogeographic patterns of several Arctic species, including *P. langsдорffii*. Comprehensive sampling across its range with a focus on Beringian and alpine populations is needed to more adequately study the phylogeography of this species. The genetically uniform *P. hirsuta* obviously migrated to the Canadian Arctic from ice-free refugia after the last glaciation, however where these refugia were located is not evident from our data. One hypothesis is that *P. hirsuta* evolved from the *P. langsдорffii* subsp. *arctica* populations sheltered in the Beringian refugium (Abbott and Brochmann 2003) after the glaciers receded; however equally likely is an older origin and survival in refugia south of the ice sheet in North American and/or Eurasia. Comprehensive sampling across its circumarctic range would be necessary to address these hypotheses.

Hybridization of *Pedicularis hirsuta* and *Pedicularis langsдорffii* subsp. *arctica*

While the above key is based on clearly identifiable, non-hybrid individuals from each taxon, we did identify morphologically intermediate specimens from Axel Heiberg Island, Ellesmere Island, and Devon Island (see results). Based on their shared and intermediate character states (which are not necessarily the same between populations), and their intermediate, non-overlapping cluster in multivariate space, we have identified these specimens as putative hybrids.

The population of putative hybrids at Truelove Inlet on Devon Island all possessed character traits that marked them as a population of relatively uniform hybrids, including intermediate anther lengths and galea widths, and hybrid styles of variable exertion, length, and orientation. This style could be interpreted as a type of intermediate character: in *P. hirsuta*, the style is long and strongly recurved, but is never exerted from the galea, whereas the style in *P. langsdoeffii* subsp. *arctica* is always straight and exerted from the tip of the galea at a right angle. The Truelove Inlet styles exhibited a wide range of character states; some were not exerted at all, some were exerted as in *P. langsdoeffii* subsp. *arctica*, and some were recurved *and* exerted from the galea. This latter character state may represent a cross between the recurved, not exerted and straight, exerted styles. These recurved but exerted styles were also present in one of the other three identified putative hybrids (*Gillespie 6138*), but not in the other two (*Gillespie 6478*, and *Parker 73061A*). These three collections are all clearly identifiable as hybrids based on our multivariate analysis and on different suites of character states intermediate between and shared with the two parents.

Saarela et al. (2013) discussed two putative hybrids between *P. hirsuta* and *P. langsdoeffii* subsp. *arctica* based on observed discrepancies in *matK* and *rbcl* sequence data. Though we did not include these specimens in our morphology analyses, we did locate these specimens and identify one as an introgressed individual of *P. langsdoeffii* subsp. *arctica*, and the other as a putative hybrid⁶. The former, *Gillespie and Vogel 6105* from Axel Heiberg Island, possessed the *matK* haplotype of *P. hirsuta*, but was observed to possess the wide galeas, long galea teeth, long anthers, and wide corolla lips characteristic of *P. langsdoeffii* subsp. *arctica*.

The latter, *Gillespie and Vogel 6218* (but mistakenly referred to as *Gillespie 5218* in Saarela et al. 2013) from Lake Hazen, Ellesmere Island, was found to possess intermediate morphology, a plastid haplotype (*matK*) shared with *P. hirsuta* (Saarela et al. 2013), and the nuclear haplotype of *P. l.* subsp. *arctica*

(Figure 5, as GIL_2588), consistent with our previously identified putative hybrids. These characters included small anthers (1.6-2.0 mm long) and short galea teeth (0.3-0.5 mm), both character states closer to *P. hirsuta*, and long corollas (13.0-16.0 mm long), a *P. langsдорffii* subsp. *arctica* trait. Notably, this specimen possessed exerted styles of varying lengths, many of which were very long and recurved, a trait observed in the putative hybrid population at Truelove Inlet.

Additionally, we identified one potential hybrid specimen from Bylot Island, Nunavut, after we completed our data analysis. This specimen (*Scotter and Zoltai 67143*, DAO 334867), previously identified as *P. l.* subsp. *arctica*, possessed the larger stature and larger flowers of *P. langsдорffii* subsp. *arctica*, the hirsute inflorescences of *P. hirsuta*, and the sometimes-exserted, recurved styles identified as a hybrid character above. This specimen may in fact represent an eastern limit of the hybrid zone between these two taxa. Although Porsild (1957) mentioned intermediate forms on Baffin Island, we have identified neither “good” *P. l.* subsp. *arctica* nor hybrid specimens from there; however, this specimen from Bylot Island, adjacent to the north coast of Baffin Island, is geographically close.

Hybridization has previously been documented in temperate and boreal *Pedicularis* species, including ten species of European *Pedicularis* (Hegi 1909). Macior (1975) previously noted the possibility of hybridization in *Pedicularis* in the Yukon, specifically between *P. lanata* (as *P. kanei* Durand) and *P. langsдорffii* based on shared pollinators, and partial fertility in artificial crosses between the species. Both *P. langsдорffii* and *P. hirsuta* are diploids, $2n=16$ (Zhukova 1966, Hedberg 1967), so ploidy would not likely hinder hybridization. Compellingly, our putative hybrids were only found where both taxa came into contact (with the possible exception of the Bylot Island specimen discussed above) (Figure 1), and where introgressed individuals of *P. langsдорffii* subsp. *arctica* (as discussed below) have been detected; this supports our assertion that these eight specimens (including *Gillespie and Vogel 6218*) are hybrid individuals.

Evidence for Introgression between *Pedicularis hirsuta* and *Pedicularis langsдорffii* subsp. *arctica*

The presence of the *P. hirsuta* plastid haplotype in “good” *P. langsдорffii* subsp. *arctica* (i.e., their identity is supported by both morphology and ITS sequence data), and the detection of morphologically intermediate hybrids is strong evidence for hybridization, gene flow, and chloroplast introgression between the two taxa (Soltis et al. 1992). Introgression was recently described for the first time for this genus in Tibetan species of *Pedicularis* sect. *Cyathophora* by Eaton and Ree (2013), who detected recurrent introgression and reticulation between nearly all members of this clade – significantly affecting phylogenetic inference. Introgression has also been detected in *Rhinanthus* – another member of the Orobanchaceae (Ducarme and Wesselingh 2005).

Introgression happens when two taxa hybridize, and the hybrid backcrosses with the paternal parent, “capturing” the chloroplast of the maternal parent in subsequent offspring. Over evolutionary time these lineages remain taxonomically distinct from one other – subsequent hybridization between the taxa is rare – and the result is two stable species, with one possessing a chloroplast inherited from the other through these introgression events (Harrison and Larson 2014). Introgression has been previously documented in the Canadian Arctic Archipelago in *Poa hartzii* (Gillespie et al. 1997; Gillespie and Boles 2001), and suggested in some Canadian populations of the circumpolar legume *Astragalus eucosmus* (Sokoloff and Gillespie 2012).

Introgression may fit one of two patterns: localized or dispersed (Rieseberg and Brunsfeld 1992). In the former scenario, chloroplast capture occurs within a highly localized hybrid swarm, with extensive reticulation and morphological intermediates confined to a specific geographic area. This pattern is commonly seen in sympatric species (Rieseberg and Brunsfeld 1992). While both *P. hirsuta* and *P. langsдорffii* subsp. *arctica* are allopatric at the eastern and western parts of their ranges respectively (Figure 1), they may be considered sympatric where they come into contact in the north central

Canadian Arctic Archipelago, given their similar habitat preferences (moist tundra, riverbanks and pond edges) (Aiken et al. 2007), and previous collections of both species from the same site, notably on Ellesmere Island (Soper and Powell 1985).

Though these sympatric zones weren't directly observed for the purposes of this study, morphologically intermediate specimens (as mentioned in Porsild 1957) were encountered during examination of the herbarium specimens, namely on Axel Heiberg Island, Ellesmere Island, and Devon Island. Specimens from the Truelove lowlands, Devon Island – the only site where we identified multiple hybrid specimens (multiple plants on four herbarium sheets) – shared two putatively hybrid character states (intermediate anther length and galea width), while other character states (style protuberance, galea teeth presence/length) were variable within the population. This may indicate that this first pattern of introgression, hybrid swarming, is happening at this location. Notably, one morphologically “good”, introgressed *P. langsдорffii* subsp. *arctica* (Kerik 40) was identified at the same site – an indication that backcrossing and chloroplast capture (as discussed below) is occurring at this site as well.

In the second pattern of introgression described in Rieseberg and Brunsfeld (1992), dispersed introgression, gene flow occurs between two species from their point of contact – after the initial hybridization, backcrossing occurs preferentially with one of the two parents, giving rise to chloroplast capture in taxonomically “good” species – i.e., the chloroplast genome of one parent in a plant with the nuclear genome and morphotype of another (Rieseberg and Brunsfeld 1992).

This pattern was observed at multiple points of contact between *P. hirsuta* and *P. langsдорffii* subsp. *arctica*; these introgressed individuals (*P. langsдорffii* subsp. *arctica* specimens that exhibited the *P. hirsuta* cpDNA haplotype) were only found where the two species met in the Canadian High Arctic and western Arctic islands (i.e., Ellesmere Island, Devon Island, Axel Heiberg Island, Melville Island, Banks Island).

Under this model, backcrossing is generally unidirectional (Soltis et al. 1992). Ducarme and Wesselingh's work (2005) found unidirectional introgression into *Rhinanthus angustifolius* from *Rhinanthus minor*. They hypothesised that the direction of introgression could be influenced by several factors. The direction of most frequent crosses, the relative abundance of the different species, as well as other environmental conditions were suggested as playing a part in directing the evolution of mixed populations.

Based on our molecular and morphological evidence, pollination syndromes and floral morphology are likely the major drivers of unidirectional chloroplast introgression from *P. langsдорffii* subsp. *arctica* into *P. hirsuta*. As mentioned previously, *P. langsдорffii* subsp. *arctica* is structurally well adapted for outcrossing (Willams and Batzli 1982), and *P. hirsuta* is observed to be predominantly selfing (Eriksen et al 1993; Phillip 1998). Therefore, *P. hirsuta* would be less likely to be the pollen source and more likely to receive pollen from *P. langsдорffii* subsp. *arctica* (simply due to more pollinators visiting the latter species) and become the maternal parent of an F₁ hybrid. A pollinator visiting such a *P. langsдорffii* subsp. *arctica* × *P. hirsuta* hybrid (with *P. hirsuta* as the maternal parent) likely would be carrying *P. langsдорffii* subsp. *arctica* pollen having previously preferentially visited this species based on its pollinator-adapted flowers. This pattern, supported by our molecular evidence, suggests that all subsequent reproduction was likely entirely with members of *P. langsдорffii* subsp. *arctica* as the pollen parent, resulting in transfer of the *P. hirsuta* chloroplast into *P. langsдорffii* subsp. *arctica*. Conversely, the selfing-adapted flowers of *P. hirsuta* and fewer pollinator visits reduces the likelihood that this species would provide pollen, and additional nuclear genetic material, in backcrosses with the hybrids.

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Author Contributions

Conceived and designed the study: LJG CCC PCS. Gathered data: CCC PCS. Analyzed the data: PCS CCC..

Interpreted the data: LJG PCS CCC. Wrote the manuscript: PCS CC. Commented on and edited the manuscript: LJG.

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Table

Table 1. Morphological characters measured for *Pedicularis hirsuta* and *P. langsdoeffii* subsp. *arctica*, the number of specimens measured in each taxon per variable, the median and standard deviation, and the Mann-Whitney U and Z statistics, as well as the *p* value from the Mann-Whitney U pairwise comparisons. Measurements of putative hybrid specimens are given separately; for the Truelove site median values and standard deviations based on four specimens are given.

Continuous quantitative variables measured (mm)	n – <i>P. hirsuta</i>	Median – <i>P. hirsuta</i>	SD – <i>P. hirsuta</i>	n – <i>P. l. arctica</i>	Median – <i>P. l. arctica</i>	SD – <i>P. l. arctica</i>	Mann-Whitney U	Z	<i>p</i> value	Median – Truelove	SD – Truelove	Gillespie 6478	Gillespie 6138	Parker 73061a
A. Inflorescence length	50	37.1	22.90	53	66.0	30.31	609	-4.7214	2.34E-06	23.9	8.41006	25.1	42.1	19.2
B. Calyx long sepal length	50	7.2	1.14	53	8.3	1.33	670.5	-4.3166	1.58E-05	7.2	1.75404	6.2	7.3	6.2
C. Calyx short sepal length	50	5.9	1.28	53	6.5	1.43	1039.5	-1.8814	5.99E-02	5.25	1.23962	4.8	3.6	5.5
D. Calyx width	50	3.2	0.52	53	3.8	0.66	782	-3.5827	3.40E-04	3.55	0.55678	3.5	3.2	4.0
E. Corolla length	50	13.7	2.28	53	20.8	2.90	127	-7.9021	2.74E-15	14.8	2.69815	19.2	15.4	18.7
F. Corolla lip width	48	6.2	1.41	51	10.3	3.09	241	-6.8796	6.00E-12	9.6	2.49533	7.0	5.3	6.5
G. Galea width	50	2.1	0.44	53	3.3	0.46	81	-8.2082	2.25E-16	2.65	0.21602	2.9	3.2	3.8
H. Style protruberance	50	0	0	53	1.1	0.58	0	-9.2896	1.55E-20	1.15	0.57951	1.1	0.6	0.7
I. Anther length	50	1.5	0.23	51	2.4	0.28	1	-8.6651	4.51E-18	2.05	0.14142	2.3	2.6	2.2
J. Galea teeth distance to tip	49	0.4	0.25	53	1.0	0.29	224.5	-7.2025	5.91E-13	0.6	0.2708	0.7	1.0	0.4
K. Galea teeth length	50	0.1	0.11	53	0.4	0.17	216	-7.405	1.31E-13	0.3	0	0.1	0.2	0.1
L. Galea teeth width	49	0.15	0.08	53	0.2	0.07	905	-2.6976	6.98E-03	0.15	0.05774	0.2	0.1	0.1
M. Stem length	50	111.5	37.38	53	128.0	40.72	1071.5	-1.6696	9.50E-02	51.4	15.337	71.5	150.0	71.1
N. Stem width	50	2.6	0.68	53	3.1	0.93	926.5	-2.6969	8.62E-02	1.9	0.37749	2.0	3.2	2.7
O. Cauline leaf blade length	50	15.8	4.87	52	17.3	6.14	1220	-0.53	5.94E-01	7.35	1.14419	14.8	11.3	11.6
P. Cauline leaf blade width	50	4.4	1.13	52	3.6	1.25	944.5	-2.376	1.70E-02	2.4	0.54467	4.5	4.3	2.1
Q. Cauline leaf petiole length	50	11.5	3.07	52	12.2	4.25	1157.5	-0.95	3.40E-01	7.6	1.7519	12.0	10.0	12.5
R. Cauline leaf petiole width	50	2.5	0.73	52	1.2	0.90	1116	-1.2287	2.19E-01	1.9	0.6377	1.2	4.3	1.9
S. Cauline leaf lobe length	50	1.5	0.53	52	1.3	0.56	934	-2.449	1.43E-02	0.95	0.09574	1.4	1.2	0.8
T. Cauline leaf lobe width	50	1.1	0.36	52	0.9	0.34	932.5	-2.462	1.38E-02	0.5	0.17321	0.9	0.9	1.3
U. Bract blade length	50	9.3	3.52	51	10.7	5.35	1100	-1.1853	2.36E-01	6.1	1.97922	4.3	4.9	6.4
V. Bract blade width	50	3.3	0.92	51	2.8	0.94	919.5	-2.41	1.58E-02	2.35	0.9815	2.0	2.5	2.3
W. Bract petiole length	50	7.2	2.17	50	8.6	3.18	849.5	-2.75	5.80E-03	6.25	1.84572	5.8	4.6	8.0
X. Bract petiole width	50	2.9	0.94	51	2.5	1.24	993.5	-1.909	5.26E-02	2.25	0.86735	2.1	3.5	3.0
Y. Bract lobe length	49	1.2	0.36	50	1.1	0.48	947.5	-1.9431	5.20E-02	1.05	0.38622	0.6	1.1	0.8
Z. Bract lobe width	50	0.9	0.25	50	0.8	0.31	1206	-0.301	7.63E-01	0.55	0.3594	0.7	0.8	1.1
Qualitative characters measured														
AA. Stem hair density (0-glabrous, 1-glabrate, 2-sparse, 3- moderate, 4- dense, 5-very dense)														
BB. Inflorescence hair density (0-glabrous, 1-glabrate, 2-sparse, 3- moderate, 4- dense, 5-very dense)														

Figure Captions

Figure 1: Distribution of *Pedicularis hirsuta* and *Pedicularis langsдорffii* subsp. *arctica* in Canada based on National Herbarium of Canada (CAN) specimen data (top), and map of specimens sampled for DNA based on cpDNA genotype (bottom). Map created using SimpleMappr (Shorthouse 2010) using data in the Public Domain.

Figure 2: *Pedicularis hirsuta*, A. habit, B. inflorescence, C. flower showing galea with no teeth and non-protruding, strongly recurved style (Sokoloff 332a, CAN). Photos by P.C. Sokoloff.

Figure 3: *Pedicularis langsдорffii* subsp. *arctica*, A. habit, B. inflorescence, C. flower showing galea with teeth and protruding style (Saarela et al. 3618, CAN). Photos by P.C. Sokoloff.

Figure 4: Illustration of *Pedicularis langsдорffii* subsp. *arctica* flower showing ten morphological measurements performed on each specimen examined. Illustration by C.J. Chapman.

Figure 5: Bayesian phylogram of 82 ITS sequences of *Pedicularis hirsuta*, *P. langsдорffii* subsp. *arctica*, *P. lanata*, *P. albolabiata* and *P. labradorica*. Posterior probability scores are indicated above each branch, maximum parsimony bootstrap values are located below. Maximum parsimony tree consistency index (CI): 0.94.

Figure 6: Strict consensus of 24 most parsimonious trees generated from 78 *atpI-atpH* sequences of *Pedicularis hirsuta*, *P. langsдорffii* subsp. *arctica*, *P. lanata*, *P. albolabiata* and *P. labradorica*. Bayesian posterior probability scores are indicated above each branch, bootstrap values are located below. Maximum parsimony tree consistency index (CI): 0.93.

Figure 7: Principal components analysis of 50 *Pedicularis hirsuta*, 53 *P. langsдорffii* subsp. *arctica* (including nine introgressed), and seven putative hybrid specimens measured for 12 continuous floral morphology characters. Four putative hybrid specimens from Truelove Inlet, Devon Island (green polygon), three hybrid specimens from other localities (Gillespie 6138, Gillespie 6478, and Parker 73061A), and one introgressed *P. langsдорffii* subsp. *arctica* from Truelove Inlet (Kerik 40) are indicated.

Figure 8: Boxplots displaying median, interquartile ranges, and minimum/maximum values for interspecific differences for 12 continuous floral morphology characters measured in *Pedicularis hirsuta* (blue) and *P. langsдорffii* subsp. *arctica* (orange). Asterisks indicate statistical significance according to a Mann-Whitney U pairwise comparison: * $p < 0.001$.

Figure 9: Stacked column charts showing percent of specimens of *P. hirsuta* (50 specimens measured) and *P. langsдорffii* subsp. *arctica* (53 specimens measured) displaying each of six character states for two qualitative pubescence characters: A) inflorescence pubescence, B) stem pubescence.

Figure 1: Distribution of *Pedicularis hirsuta* and *Pedicularis langsdorffii* subsp. *arctica* in Canada based on National Herbarium of Canada (CAN) specimen data (top), and map of specimens sampled for DNA based on cpDNA genotype (bottom). Map created using SimpleMappr (Shorthouse 2010) using data in the Public Domain.

182x260mm (300 x 300 DPI)

Figure 2: *Pedicularis hirsuta*, A. habit, B. inflorescence, C. Flower showing galea with no teeth and non-protruding, strongly recurved style (Sokoloff 332a, CAN). Photos by P.C. Sokoloff.
169x148mm (300 x 300 DPI)

Figure 3: *Pedicularis langsдорffii* subsp. *arctica*, A. habit, B. inflorescence, C. Flower showing galea with teeth and protruding style (Saarela et al. 3618, CAN). Photos by P.C. Sokoloff.
169x148mm (300 x 300 DPI)

Figure 4: Illustration of *Pedicularis langsдорffii* subsp. *arctica* flower showing ten morphological measurements performed on each specimen examined. Illustration by C.C. Chapman.
39x41mm (300 x 300 DPI)

Figure 6: Strict consensus of 24 most parsimonious trees generated from 78 atpI-atpH sequences of *Pedicularis hirsuta*, *P. langsdorffii* subsp. *arctica*, *P. lanata*, *P. albolabiata* and *P. labradorica*. Bayesian posterior probability scores are indicated above each branch, bootstrap values are located below.

Consistency Index (CI): 0.93.

177x173mm (300 x 300 DPI)

Figure 7: Principal components analysis of 50 *Pedicularis hirsuta*, 53 *P. langsdorffii* subsp. *arctica* (including nine introgressed), and seven putative hybrid specimens measured for 12 continuous floral morphology characters. Four putative hybrid specimens from Truelove Inlet, Devon Island (green polygon), three hybrid specimens from other localities (Gillespie 6138, Gillespie 6478, and Parker 73061A), and one introgressed *P. langsdorffii* subsp. *arctica* from Truelove Inlet (Kerik 40) are indicated.

158x87mm (300 x 300 DPI)

Figure 8: Boxplots displaying median, interquartile ranges, and minimum/maximum values for interspecific differences for 12 continuous floral morphology characters measured in *Pedicularis hirsuta* (blue) and *P. langsдорffii* subsp. *arctica* (orange). Asterisks indicate statistical significance according to a Mann-Whitney U pairwise comparison: * $p < 0.05$, ** $p < 0.001$.
174x125mm (300 x 300 DPI)

Figure 9: Stacked column charts showing percent of specimens of *P. hirsuta* (50 specimens measured) and *P. langsdorffii* subsp. *arctica* (53 specimens measured) displaying each of six character states for two qualitative pubescence characters: A) inflorescence pubescence, B) stem pubescence.

Appendix A – Specimens verified for mapping, sampled for DNA sequencing, or measured for morphological analysis. Format of specimen citations is as follows: COUNTRY: PROVINCE: Locality, Collection date, *Collectors and number*, (Herbarium accession number), Extraction number, GenBank accession number for ITS, GenBank accession number for *atpI-atpH*, and a “M” if included in our morphology analyses, or a “F” if omitted from the analysis as the specimen was fruiting (only applicable to *P. hirsuta*, *P. langsdorffii* subsp. *arctica*, and hybrids). Missing or not applicable data is indicated with “-”.

Pedicularis albolabiata: CANADA: NORTHWEST TERRITORIES: Victoria Island, Minto Inlet, 71°33'N, 115°26'W, July 24, 2010, *L.J. Gillespie, J.M. Saarela, J. Doubt, R.D. Bull & P.C. Sokoloff 10199*, (CAN 599178), GIL_2603, KJ571370, KJ571288.

Pedicularis hirsuta: CANADA: NUNAVUT: Axel Heiberg Island, Diana Lake, Head of Mokka Fiord, 79°30'N, 88°30'W, August 1-8, 1953, *A.E. Porsild 18717*, (CAN 223362), -, -, -, M; Axel Heiberg Island, Expedition Fiord, 79°24'N, 90°48'W, July 18, 1996, *L.J. Gillespie & C. Vogel 6108-3*, (CAN 586297), GIL_2578, -, -, M; Axel Heiberg Island, Expedition Fiord, 79°24'N, 90°48'W, July 31, 1999, *L.J. Gillespie & L.L. Consaul 6540*, (CAN 586185), GIL_2423, KJ571312, KJ571232, M; Axel Heiberg Island, Expedition Fiord, 79°24'N, 90°48'W, July 19, 1996, *L.J. Gillespie & C. Vogel 6108*, (CAN 586297), GIL_2583, KJ571319, KJ571238, M; Axel Heiberg Island, Kanguk Peninsula, 79°16'N, 92°10'W, July 5-6, 1977, *G. Whalen 9*, (CAN 432818), GIL_2420, KJ571310, KJ571229, M; Axel Heiberg Island, Mokka Fiord, 79°29'N, 87°22'W, July 15, 1996, *L.J. Gillespie & C. Vogel 6084*, (CAN 607180), GIL_2575, -, -, M; Axel Heiberg Island, Mokka Fiord, 79°29'N, 87°22'W, July 15, 1996, *L.J. Gillespie & C. Vogel 6094*, (CAN 607184), GIL_2577, -, -, M; Axel Heiberg Island, Mokka Fiord, 79°29'N, 87°22'W, July 16, 1996, *L.J. Gillespie & C. Vogel 6098*, (-), GIL_2364, KJ571301, KJ571218, M; Axel Heiberg Island, Mokka Fiord, 79°29'N, 87°22'W, July 15, 1996, *L.J. Gillespie & C. Vogel 6077*, (CAN 607181), GIL_2573, KJ571314, KJ571234, M; Axel Heiberg Island, N. Colour Lake, -, July 22-23, 1967, *M. Kuc 525*, (CAN 331368), GIL_2429, KJ571317, KJ571247, M; Axel Heiberg Island, Thompson Valley, -, July 24, 1960, *R.E. Beschel 11065*, (CAN 267752), GIL_2634, -, KJ571249, M; Axel Heiberg Island, Vicinity of Upper House, -, July 22-23, 1967, *M. Kuc 542*, (CAN 331377), -, -, -, M; Baffin Island, 10km W of Nedlukseak Fiord, 67°50'N, 66°55'W, July 14, 1985, *R. Morrison 26-0*, (CAN 499381), GIL_2586, -, -, F; Baffin Island, Arctic Bay, Admiralty Inlet, 73°13'N, 84°0'W, August 12, 1927, *M.O. Malte 119164*, (CAN 97642), -, -, -, F; Baffin Island, Auyuittuq National Park, 67°25'N, 64°58'W, July 15, 1985, *R. Morrison s.n.*, (CAN 499382), -, -, -, M; Baffin Island, Beekman Peninsula, 63°24'N, 64°40'W, August 3, 1964, *I.A. McLaren s.n.*, (CAN 284048), GIL_2635, KJ571327, KJ571250, M; Baffin Island, Blacklead Island, 64°59'N, 66°11'W, August 21, 1924, *J. Dewey Soper 111519*, (CAN 97647), -, -, -, F; Baffin Island, Botany Bay, Kangerdluak Fiord, Nunavut Islands, 68°50'N, 68°30'W, July 20, 1967, *P.J. Webber 1235*, (CAN 312096), GIL_2627, KJ571323, KJ571244, M; Baffin Island, Bowman Bay Region, 65°38'N, 73°29'W, July 13, 1967, *D. Lamperd s.n.*, (CAN 312676), GIL_2629, KJ571324, KJ571245, M; Baffin Island, Cape Dorset, 64°10'N, 76°20'W, July 3, 1926, *J. Dewey Soper 125917*, (CAN 97646), -, -, -, M; Baffin Island, Cape Dorset, 64°10'N, 76°20'W, August 4, 1928, *M.O. Malte 120350*, (CAN 97635), -, -, -, F; Baffin Island, Clyde Inlet, 69°50'N, 70°40'W, July 3, 1950, *V.C. Wynne-Edwards 8891*, (CAN 204949), GIL_2628, -, -, M; Baffin Island, Clyde Inlet, 69°50'N, 70°40'W, June 29, 1950, *V.C. Wynne-Edwards 8861*, (CAN 204946), GIL_2630, KJ571325, KJ571246, M; Baffin Island,

Frobisher, 63°45'N, 68°31'W, July 25, 1982, *J.M. Gillett 19045*, (CAN 466226), GIL_2584, -, -, M; Baffin Island, Frobisher Bay, 63°44'N, 68°27'W, August 13, 1986, *S.G. Aiken, C. Campbell, E. Robinson 86-268*, (CAN 518125), GIL_2585, KJ571298, KJ571239, M; Baffin Island, Frobisher Bay, -, July 13, 1948, *C. Thacker s.n.*, (CAN 97628), GIL_2636, KJ571296, KJ571251, M; Baffin Island, Head of Clyde Inlet, 69°50'N, 70°40'W, June 25, 1950, *V.C. Wynne-Edwards 8831*, (CAN 204945), GIL_2631, KJ571326, KJ571248, M; Baffin Island, Inugsuin Fjord, 70°N, 68°30'W, July 28, 1965, *R. Hainault 3841*, (CAN 302021), GIL_2419, KJ571309, KJ571228, M; Baffin Island, Iqaluit, 63°45'N, 68°41'W, August 5, 1996, *L.J. Gillespie 6256*, (-), GIL_2366, KJ571300, KJ571219, F; Baffin Island, Nettilling Lake Burwash Bay, 65°57'N, 71°18'W, August 9, 1986, *S.G. Aiken 86-159*, (CAN 518022), GIL_2421, KJ571311, KJ571230, M; Baffin Island, Pangnirtung, Cumberland Gulf, 66°8'N, 65°41'W, August 21-22, 1927, *M.O. Malte 119180*, (CAN 97644), -, -, -, F; Baffin Island, Soper River, 63°5'42"N, 69°45'46"W, July 11, 2012, *J.M. Saarela, L.J. Gillespie, P.C. Sokoloff & R.D. Bull 2317*, (CAN 601957), GIL_2412, KJ571304, KJ571222, M; Baffin Island, Soper River, 63°14'N, 69°37'W, July 4, 2012, *J.M. Saarela, L.J. Gillespie, P.C. Sokoloff & R.D. Bull 2075*, (CAN 601958), GIL_2413, KJ571305, KJ571223, M; Baffin Island, Soper River, 63°15'N, 69°35'W, July 19, 2012, *J.M. Saarela, L.J. Gillespie, P.C. Sokoloff & R.D. Bull 2057*, (CAN 601955), GIL_2580, KJ571316, KJ571236, M; Bathurst Island, Bracebridge Inlet - south side, 5 miles east, -, July 12, 1973, *S.D. MacDonald s.n.*, (CAN 416035), GIL_2637, KJ571328, KJ571252, M; Bathurst Island, Polar Bear Pass, Research Station, 75°43'N, 98°25'W, August 7, 2000, *L.J. Gillespie & L.L. Consaul 6989*, (CAN 586199), GIL_2414, KJ571306, KJ571224, M; Coats Island, East Coast, Keewatin District, 62°49'N, 81°50'W, September 19, 1930, *A.E. Porsild 5935*, (CAN 97662), -, -, -, F; Ellesmere Island, Alexandra Fiord, 78°50'N, 76°25'W, July 25, 1996, *L.J. Gillespie & C. Vogel 6181*, (CAN 586184), GIL_2417, KJ571308, KJ571226, M; Ellesmere Island, Alexandra Fiord, 78°53'N, 75°45'W, July 26, 1996, *L.J. Gillespie & C. Vogel 6167*, (CAN 607182), GIL_2579, KJ571315, KJ571235, M; Ellesmere Island, Alexandra Fiord, 78°53'N, 75°50'W, July 18, 1979, *J.M. Gillett & M.J. Schepanek 18248*, (CAN 453948), GIL_2625, KJ571299, KJ571242, M; Ellesmere Island, Bache Peninsula, 79°4'N, 76°18'W, July 31, 1927, *M.O. Malte 119169*, (CAN 97639), -, -, -, F; Ellesmere Island, Bjerne Peninsula, 77°37'N, 87°15'W, July 30, 1961, *C.R. Harrington 286*, (CAN 270547), -, -, -, M; Ellesmere Island, Craig Harbour, 76°12'N, 81°20'W, August 2, 1927, *M.O. Malte 119175*, (CAN 97641), -, -, -, M; Ellesmere Island, Delta on E side of Lower Dumbell Lake, 82°26'N, 62°50'W, July 8, 1959, *C.R. Harrington 66*, (CAN 261598), -, -, -, F; Ellesmere Island, Forsheim Peninsula, Hot Weather Creek, 79°58'N, 84°26'W, July 20-21, 1996, *L.J. Gillespie & C. Vogel 6137-1*, (CAN 585252), GIL_2582, KJ571318, KJ571237, M; Ellesmere Island, Fort Conger, Discovery Harbour, Franklin Bay, 81°45'N, 64°47'W, July 30, 1984, *N.R. Morrison and C.D. Rubec 7648*, (CAN 490747), -, -, -, M; Ellesmere Island, Fosheim Peninsula, Hot Weather Creek, 79°58'N, 84°26'W, July 19, 1996, *L.J. Gillespie & C. Vogel 6126*, (-), GIL_2415, KJ571307, KJ571225, M; Ellesmere Island, Fosheim Peninsula, Slidre Fjord, 80°08'N, 86°20'W, August 9, 1955, *S.D. MacDonald 265*, (CAN 235332), GIL_2638, KJ571329, KJ571253, M; Ellesmere Island, Hazen Camp, N Shore of Hazen Lake, 81°49'N, 71°20'W, July 30, 1996, *L.J. Gillespie & C. Vogel 6240*, (CAN 607189), GIL_2569, KJ571313, KJ571233, M; Ellesmere Island, Johan Peninsula, 78°51'N, 75°50'W, July 14, 1979, *J.M. Gillett & M.J. Schepanek 18146*, (CAN 453879), GIL_2626, KJ571297, KJ571243, M; Ellesmere Island, Knud Peninsula, 79°02'N, 76°10'W, July 17, 1979, *J.M. Gillett 18233*, (CAN 453940), GIL_2608, KJ571321, KJ571240, M; Ellesmere Island, Lake Hazen, 81°45'N, 82°10'W, July 8, 1959, *J.M. Powell 519*, (CAN 483720), GIL_2624, KJ571322, KJ571241, M; Ellesmere Island, Lake Hazen vicinity, 81°45'N, 68°30'W, July 4, 1959, *J.M. Powell 508*, (CAN 483722), GIL_2439, KJ571295, KJ571217, M; Ellesmere Island,

Sverdrup Pass, 79°11'N, 79°25'W, July 13, 1979, *J.M. Gillett & M.J. Schepanek 18062*, (CAN 453815), GIL_2639, KJ571330, KJ571254, M; Ellesmere Island, Sverdrup Pass, 79°09'N, 79°25'W, July 17, 1979, *J.M. Gillett 18190*, (CAN 453906), GIL_2607, KJ571320, -, M; Ellesmere Island, Tanquary Fiord, 81°00'N, 79°45'W, July 21, 1964, *G.R. Brassard 1584*, (CAN 296315), -, -, -, M. GREENLAND: Melville Bugt, Tugtutligssuaq, 75°22'N, 58°32'W, July 31, 1979, *B. Fredskild & C. Bay 658*, (CAN 462393), GIL_2367, KJ571302, KJ571220, M; Qutdligssat, -, July 11, 1961, *R.E. Beschel 12036*, (CAN 274506), GIL_2368, KJ571303, KJ571221, M.

***Pedicularis labradorica*:** CANADA: NUNAVUT: Belcher Islands, Sanikiluaq, 56°32'N, 79°123'W, July 1, 2010, *L.L. Consaul, M. Ip & D. Charette 3867*, (CAN 599913), GIL_2373, KJ571371, KJ571289.

***Pedicularis lanata*:** CANADA: NORTHWEST TERRITORIES: Paulatuk, 69°20'N, 124°2'W, June 28, 2009, *L.J. Gillespie, J.M. Saarela, L.L. Consaul & R.D. Bull 8594*, (CAN 595018), GIL_2437, KJ571375, KJ571293; Tuktoyuktuk, near end of road to sewage pond ~ 5 km S of town, 69°26'N, 133°3'W, July 23 1995, *L.J. Gillespie 5936*, (CAN 586714), GIL_2365, KJ571372, KJ571290. NUNAVUT: Baffin Island, Soper River, 62°59'N, 69°43'W, July 15, 2012, *J.M. Saarela, L.J. Gillespie, P.C. Sokoloff & R.D. Bull 2479*, (CAN 601952), GIL_2435, KJ571373, KJ571291; Ellesmere Island, Fosheim Peninsula, Hot Weather Creek, 79°58'N, 84°26'W, July 20-21, 1996, *L.J. Gillespie & C. Vogel 6134*, (CAN 607188), GIL_2436, KJ571374, KJ571292; Ellesmere Island, Fosheim Peninsula, Hot Weather Creek, 79°58'N, 84°26'W, July 20-21, 1996, *L.J. Gillespie & C. Vogel 6140*, (CAN 586187), GIL_2438, KJ571376, KJ571294.

***Pedicularis langsдорffii* subsp. *arctica*:** CANADA: NORTHWEST TERRITORIES: Atkinson Point, 70°N, 131°20'W, August 1-3, 1927, *A.E. Porsild & R.T. Porsild 2657*, (CAN 97296), -, -, -, F; Banks Island, Aulavik National Park, 73°43'N, 119°55'W, July 11, 1999, *S.G. Aiken 99-054*, (CAN 582445), GIL_2431, KJ571344, KJ571260, M; Banks Island, De Salis Bay, 71°28'N, 121°53'W, July 21, 2003, *L.J. Gillespie, H. Bickerton & L. Consaul 7154-4*, (CAN 586094), GIL_2592, KJ571351, KJ571273, M; Banks Island, lake near north east corner of island, 73°24'N, 117°00'W, August 13-20, 1949, *A.E. Porsild 17726*, (CAN 128086), GIL_2633, KJ571369, KJ571287, M; Banks Island, Masik River Valley, 71°35'N, 125°8'W, July 18, 2003, *L.J. Gillespie, H. Bickerton & L. Consaul 7136-4*, (CAN 586096), GIL_2591, -, -, M; Banks Island, Masik River Valley, 71°35'N, 123°8'W, July 18, 2003, *L.J. Gillespie, H. Bickerton & L. Consaul 7136-2*, (CAN 586096), GIL_2370, KJ571334, KJ571265, M; Banks Island, Sachs Harbour south of Cape Kellett on S.W. coast, -, July 30th, 1949, *A.E. Porsild 17529*, (CAN 128085), GIL_2632, KJ571368, KJ571264, M; Banks Island, Shoran Lake, 73°31'N, 120°18'W, July 19, 1971, *K.L. MacInnes s.n.*, (CAN 535590), GIL_2613, KJ571357, KJ571263, M; Cape Dalhousie, 70°20'N, 129°55'W, August 7-14, 1927, *A.E. Porsild & R.T. Porsild 2793*, (CAN 97305), -, -, -, F; Cape Dalhousie, 70°20'N, 129°55'W, August 7-14, 1927, *A.E. Porsild & R.T. Porsild 2792*, (CAN 97295), -, -, -, M; Eskimo Lake Basin, -, July 23, 1947, *A.E. Porsild 16770*, (CAN 97290), -, -, -, M; Inuvik, Anderson R. Delta, 69°42'N, 129°W, June 29, 1963, *T.W. Barry 57*, (CAN 288024), GIL_2610, KJ571354, KJ571278, M; Liverpool Bay, Nicholson Island, 70°N, 129°W, August 15-16, 1927, *A.E. Porsild & R.T. Porsild 2933*, (CAN 97306), -, -, -, F; Liverpool Bay, Nicholson Island, 70°N, 129°W, August 15-16, 1927, *A.E. Porsild & R.T. Porsild 2932*, (CAN 97307), -, -, -, F; Liverpool Bay, Nicholson Island, 70°N, 129°W, August 15-16, 1927, *A.E. Porsild & R.T. Porsild 2931*, (CAN 97304), -, -, -, M; Mackenzie Delta, North end of Richards Island, -, July 29-August 5, 1947, *A.E. Porsild 16847*, (CAN 97292), -, -, -, F; Mackenzie Delta, Tuktoyaktok, -, July 22, 1953, *E.H. McEwen 100*, (CAN 226151), GIL_2609, -, KJ571277,

M; Mackenzie River delta, East branch, -, July 5, 1935, *A.E. Porsild* 7393, (CAN 97298), -, -, -, M; Mackenzie River Delta, N end of Richards Island, 69°40'N, 134°40'W, July 22-24, 1947, *A.E. Porsild* 2274A, (CAN 97299), -, -, -, M; Melville Island, Bailey's Point, 74°4'N, 114°40'W, July 19, 2004, *A.A. Archambault* 123, (CAN -), GIL_2601, -, -, -; Melville Island, Canrobert Hills, 75°57'N, 115°00'W, July 25th, 1984, *S. Edlund* 407, (CAN 489907), GIL_2618, GIL_2606, KJ571362, -, F; Melville Island, Ibbett Bay, -, July 20, 1961, *J.S. Tener & C.R. Harington* 345, (CAN 270544), GIL_2619, KJ571363, -, M; Melville Island, Marie Bay, 76°15'N, 115°27'W, July 23, 1985, *S. Edlund* 232, (CAN 495886), GIL_2616, KJ571360, KJ571282; , M Melville Island, Marie Bay, 76°12'N, 114°55'W, July 17th, 1984, *S. Edlund* 287, (CAN 489142), GIL_2617, GIL_2605, KJ571361, KJ571283, M; Melville Island, Murray Inlet, on Hecla Bay, 75°26'N, 113°30'W, July 26, 1984, *S. Edlund* 421, (CAN 502397), GIL_2614, KJ571358, -, M; Melville Island, Shellabear Point, N side of Dundas Peninsula, 76°51'N, 113°23'W, July 6, 1980, *S. Edlund* 022, (CAN 486676), GIL_2615, KJ571359, KJ571281, M; Paulatuk, 69°18'46"N, 123°54'15"W, June 30, 2009, *L.J. Gillespie, J.M. Saarela, L.L. Consaul & R.D. Bull* 8639, (CAN 595153), GIL_2596, -, -, F; Paulatuk, 69°18'46"N, 123°54'15"W, June 29, 2005, *L.J. Gillespie, J.M. Saarela, L.L. Consaul & R.D. Bull* 8634, (CAN 595144), GIL_2371, KJ571335, KJ571266, M; Six miles E of Kittigazuit, 69°20'N, 133'W, July 24-28, 1927, *A.E. Porsild & R.T. Porsild* 2518, (CAN 97294), -, -, -, F; Six miles E of Kittigazuit, 69°20'N, 133'W, July 24-28, 1927, *A.E. Porsild & R.T. Porsild* 2519, (CAN 97293), -, -, -, M; Tuktuyaktok, 69°40'N, 133'W, July 25, 1935, *A.E. Porsild* 7433, (CAN 97297), -, -, -, F; Victoria Island, Boot Inlet, 71°30'35"N, 117°20'3"W, July 8, 2010, *L.J. Gillespie, J.M. Saarela, J. Doubt, R.D. Bull & P.C. Sokoloff* 9519-5, (CAN 599170), GIL_2372, KJ571336, KJ571267, M; Victoria Island, Minto Inlet, 71°12'N, 116°23'W, July 14, 2010, *L.J. Gillespie, J.M. Saarela, J. Doubt, R.D. Bull & P.C. Sokoloff* 9798, (CAN 599172), GIL_2599, -, -, M; Victoria Island, Minto Inlet, 71°31'N, 115°6'W, July 25, 2010, *L.J. Gillespie, J.M. Saarela, J. Doubt, R.D. Bull & P.C. Sokoloff* 10247, (CAN 599168), GIL_2602, -, -, -; Victoria Island, Minto Inlet, 71°37'N, 115°26'W, July 7, 2010, *L.J. Gillespie, J.M. Saarela, J. Doubt, R.D. Bull & P.C. Sokoloff* 9479, (CAN 599169), GIL_2597, KJ571353, KJ571275, M; Victoria Island, S.W. coast, vicinity of Holman Island trading post., -, August 8th, 1949, *A.E. Porsild* 17330, (CAN 128087), GIL_2612, KJ571356, KJ571280, M; Victoria Island, Ulukhatok, 70°N, 117°W, July 6, 2010, *J.M. Saarela & R.D. Bull* 1496, (CAN 599179), GIL_2600, -, KJ571276, M. NUNAVUT: Axel Heiberg Island, Gypsum Hill, 79°56'N, 87°14'W, August 4, 1999, *L.J. Gillespie, L.L. Consaul & R.J. Soreng* 6581, (-), GIL_2424, KJ571338, KJ571257, -; Devon Island, TrueLove Lowland, 75°40'N, 84°40'W, August 4, 1972, *J. Kerik* 40, (CAN 409447), GIL_2418, KJ571331, KJ571227, M; Ellesmere Island, Tanquary Camp, National Park Reserve, 81°24'N, 76°52'W, July 21, 1999, *L.J. Gillespie & L.L. Consaul* 6477, (-), GIL_2416, KJ571337, KJ571255, M; Ellesmere Island, Fosheim Peninsula, 79°58'N, 84°26'W, July 20-21, 1996, *L.J. Gillespie & C. Vogel* 6133, (CAN 585211), GIL_2589, -, -, -; Ellesmere Island, Fosheim Peninsula, Hot Weather Creek, 79°58'N, 84°26'W, July 20-21, 1996, *L.J. Gillespie & C. Vogel* 6139, (-), GIL_2369, KJ571333, KJ571256, M; Ellesmere Island, Fosheim Peninsula, Hot Weather Creek, 79°58'N, 84°26'W, July 19, 1996, *L.J. Gillespie & C. Vogel* 6125-2, (CAN 586292), GIL_2427, KJ571341, KJ571270, M; Ellesmere Island, Hazen Camp, 81°49'N, 71°20'W, July 30, 1996, *L.J. Gillespie & C. Vogel* 6239-1, (-), GIL_2428, KJ571342, KJ571258, M; Ellesmere Island, Hazen Camp, N Shore of Hazen Lake, 81°49'N, 71°20'W, July 30, 1996, *L.J. Gillespie & C. Vogel* 6218-2, (CAN 586715), GIL_2588, KJ571349, -, -; Ellesmere Island, Mokka Fiord, river flowing into Bernard Lake, 79°29'N, 87°22'W, July 15, 1996, *L.J. Gillespie & C. Vogel* 6093, (-), GIL_2576, KJ571348, KJ571262, M; Ellesmere Island, Vendom Fiord, 78°02'N, 82°22'W, July 11, 1973, *P. Blachut & S. Wilkins* 32/31, (CAN 472947), GIL_2430, KJ571343,

KJ571259, M; Melville Island, 5km from south central coastline, 74°54'17"N, 109°35'34"W, July 11, 2009, *L. Bosquet* 27, (CAN 593622), GIL_2422, KJ571332, KJ571231, -; Melville Island, McCormick Inlet, 75°47'N, 112°26'W, August 2, 2000, *L.J. Gillespie & L.L. Consaul* 6960-3, (CAN 586205), GIL_2426, KJ571340, KJ571269, M; Prince Of Wales Island, South Inner Browne Bay, 73°8'N, 97°30'W, July 5, 1958, *E. Macpherson* 220, (CAN 255633), GIL_2432, KJ571345, KJ571271, M; Queen Elizabeth Islands, Eglington Island, -, July 10, 1968, *M. Kuc s.n.*, (CAN 331356), GIL_2611, KJ571355, KJ571279, M; Victoria Island, Johansen Bay, 68°39'N, 110°42'W, July 13, 2008, *L.J. Gillespie, J.M. Saarela, L.L. Consaul & R.D. Bull* 7896, (CAN 592802), GIL_2594, -, -, -; Victoria Island, Long Point Beach, 69°5'37"N, 105°16'12"W, July 27, 2008, *L.J. Gillespie, J.M. Saarela, L.L. Consaul & R.D. Bull* 8472, (CAN 592814), GIL_2425, KJ571339, KJ571268, M; Victoria Island, Oterkvik Point, 68°36'23"N, 112°34'7"W, July 4, 2008, *L.J. Gillespie, J.M. Saarela, L.L. Consaul & R.D. Bull* 7507, (CAN 592392), GIL_2434, KJ571347, KJ571272, M; Victoria Island, Sinclair Creek, 68°43'N, 109°6'W, July 22, 2008, *L.J. Gillespie, J.M. Saarela, L.L. Consaul & R.D. Bull* 8287, (CAN 592806), GIL_2595, KJ571352, KJ571274, -. Axel Heiberg Island, Mokka Fiord, 79°29'N 87°22'W, July 15, 1996, *L.J. Gillespie* 6078, (CAN 607183), GIL_2574, -, -, -; Ellesmere Island, Tanquary Camp, 81°24'N 76°52'W, July 29, 1996, *L.J. Gillespie & C. Vogel* 6211, (CAN 607150), -, -, -, M; Ellesmere Island, Tanquary Camp, 81°24'N 76°52'W, July 28, 1995, *L.J. Gillespie & F. Chatenoud* 5954 (CAN 582567), -, -, -, M. YUKON: 3 miles S of Shingle Point, -, June 29, 1971, *G. Ironside s.n.*, (CAN 375973), -, -, -, M; Between Bell River and Driftwood River, Western Richardson Mountains, 67°55'N, 137°23'W, June 30, 1973, *S.L. Welsh & J.K. Rigby* 12309, (CAN 383370), GIL_2623, KJ571367, KJ571286, M; Clarence Lagoon, 69°36'N, 140°47'W, July 9, 1990, *L.L. Consaul & S.G. Aiken* 960, (CAN 550825), GIL_2622, KJ571366, -, M; Clarence Lagoon, 69°35'N, 140°44'W, July 9, 1990, *L.L. Consaul & S.G. Aiken* 989B, (CAN 550862), GIL_2621, KJ571365, KJ571285, M; Gladstone Creek Drainage, Ruby Range, 61°20'N, 138°37'W, July 10, 1966, *J.A. Neilson* 752, (CAN 312169), -, -, -, M -; Ivavik National Park, Buckland Hills, 69°25'N, 139°38'W, August 3-5, 1999, *R. Elven* 2243/99, (CAN 583858), -, -, -, M; Mountain Slopes east of mouth of Slim's R., Kluane Lake, 60°57'N, 138°25'W, July 18, 1944, *H. M. & L. G. Raup* 12546, (CAN 277773), -, -, -, M; Vicinity of Alaska Highway Mile 837, 60°33'N, 133°6'W, June 30, 1959, *S.G. Shetler & K.J. Stone* 3100, (CAN 297421), GIL_2620, KJ571364, KJ571284, M.

***Pedicularis langsдорffii* subsp. *arctica* × *Pedicularis hirsuta*:** CANADA: NUNAVUT: Axel Heiberg Island, Mokka Fiord, 79°40'N, 87°00'W, July 27, 1973, *G. Parker* 73061A (CAN 368203), -, -, -, M; Devon Island, Truelove Inlet, 75°41'N, 84°40'W, July 15, 1974, *K. Mackenzie* 14, (CAN 397501), -, -, -, M; Devon Island, Truelove Inlet, 75°41'N, 84°40'W, July 16, 1974, *K. Mackenzie* 21, (CAN 397509), GIL_2433, KJ571346, KJ571261, M; Devon Island, Truelove Inlet, 75°41'N, 84°40'W, July 21, 1974, *K. Mackenzie* 45, (CAN 397547), -, -, -, M; Devon Island, Truelove Lowland, 75°40'N, 84°40'W, August 9, 1972, *P. Pakarinen s.n.* (CAN 409449), -, -, -, M; Ellesmere Island, Hot Weather Creek, 79°58'N, 84°26'W, July 20-21, 1996, *L.J. Gillespie & C. Vogel* 6138, (CAN 607185), GIL_2590, KJ571350, -, M; Ellesmere Island, Tanquary Camp, 81°24'N, 75°7'W, July 21, 1999, *L.J. Gillespie & L.L. Consaul* 6478 (CAN 607186), GIL_2571, -, -, M.