Comparative 2D-shape analyses of collared lemmings in the zone of possible sympatry between *Dicrostonyx groenlandicus* and *D. richardsoni* (Rodentia, Arvicolinae)

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Abstract

Morphological differentiation and relationships among collared lemmings (*Dicrostonyx*) remain unclear. This issue is particularly important in the Kivalliq Region, Nunavut, Canada, where *D. groenlandicus* and *D. richardsoni* ranges overlap. Possible sympatry of both species obscures the taxonomic status of collared lemmings from this area. We compared 2D outline shapes of the skull and three upper molars of collared lemmings collected from seven areas of the Canadian Arctic, including specimens from the Baker Lake-Aberdeen Lake area, in the Kivalliq Region, and *D. hudsonius* as an outgroup. Multivariate analyses revealed two distinct groups when considering the molars: *D. hudsonius*, and the remainder of lemmings. *D. richardsoni*, *D. groenlandicus*, and the lemmings from the Baker Lake-Aberdeen Lake area showed significant differences, especially when considering skull shapes, thus suggesting three distinct groups. However, skull shapes proved inefficient in discriminating between species. These differences suggest that collared lemmings from the Baker Lake-Aberdeen Lake area may not be correctly assigned to either of the two species without further genetic evaluation. They also suggest that these lemmings should have a peculiar taxonomic status. Our study calls for further taxonomical investigations for collared lemmings from the overlapping distribution ranges of *D. groenlandicus* and *D. richardsoni*.

Key words: *Dicrostonyx*, craniodental morphology, outline shape, elliptic Fourier analysis, Canadian Arctic

Introduction

Speciation in North American collared lemmings, of the genus *Dicrostonyx*, are thought to have taken place in the context of Pleistocene glaciations, with complete isolation of populations by glacial barriers resulting in allopatric speciation and intraspecific diversification. Fossil records indicated that an early form of *Dicrostonyx*, *Predicrostonyx hopkinsi*, occurred in Alaska, USA, more than 800,000-900,000 BP (Guthrie and Matthews 1971), possibly 1.5 M years ago (Harington 2011). Occurrence of the earliest *Dicrostonyx* dates as far back as the early Middle Pleistocene interglacial in North America, about 740,000 BP in the Yukon (Harington 2011) and 700,000 BP (reported as *D. torquatus*) on southern Banks Island, Northwest Territory, Canada (Harrington 1990). Separation between the Eurasian *D. torquatus* and North American *Dicrostonyx* was estimated to have occurred *ca.* 732,000 years ago based on genetic analyses (Fulton et al. 2013). Guthrie and Matthews (1971) reported a high rate of increase in molar complexity in *Dicrostonyx* during the Pleistocene, suggesting that speciation in this genus may have taken place during this era. Mitochondrial cytochrome *b* sequence data showed that the North American *Dicrostonyx* taxa started to diverge in the Middle Pleistocene, *ca.* 500,000 years ago (Fedorov and Goropashnaya 1999).

Kurtén and Anderson (1980) suspected an east–west continuum between the Nearctic collared lemming (*Dicrostonyx groenlandicus*) and the Ungava collared lemming (*D. hudsonius*) in the Wisconsin, in a possible periglacial continuous tundra belt. Similarity between *D. hudsonius* and fossils of *D. simplicitor* from the Yukon supports this early east-west continuum (Agadzhanyan 1984). Genetic evidence, however, indicated that *D. hudsonius* diverged as a monophyletic group in the Middle Pleistocene, *ca.* 425,000 BP, and occurred in isolated Wisconsin glacial refugia (Fulton et al. 2013), possibly in a mosaic-like environment (Guilday

1968; Youngman 1975; Mead and Mead 1989), which implies that this continuum should have existed well before the last glacial maximum. Regardless, the current geographical and reproductive isolation of *D. hudsonius* by the Hudson Bay and its morphological and genetic differences from the other *Dicrostonyx* have strengthened its taxonomic distinction (Jarrell and Fredga 1993; Engstrom et al. 1993; Eger 1995; Fedorov and Goropashnaya 1999; Wilson and Reeder 2005; Naughton 2012; Fulton et al. 2013).

The taxonomic distinction of the Richardson's collared lemming (*D. richardsoni*) from *D. groenlandicus* and their relationships have been more complex and highly debated due to their high morphological similarity and possible hybridization (Anderson and Rand 1945; Scott and Fisher 1983; Wilson and Reeder 2005). Yet, fossils identified as *D. richardsoni* were recently found in Iowa and South Dakota, which confirmed the isolation of this species in a southern refugium during the last glacial maximum (MacPherson 1965; Eger 1995; Fulton et al. 2013). Moreover, genetic data suggested a time of divergence between the two species occurring *ca*. 150,000 BP (Fulton et al. 2013), thus supporting possible pre-Wisconsinian isolation and divergence (Chaline 1987; Engstrom et al. 1993; Eger 1995). From the genetic perspective, the taxonomical status of the two species is mainly based on differences in the mitochondrial cytochrome *b* and karyotypes (Engstrom et al. 1993; Fedorov and Goropashnaya 1999). Morphological similarities between them, on the other hand, make species assignment very challenging (Eger 1995; Naughton 2012).

Speciation within this genus in North America can be regarded as relatively recent. As such, subsequent hybridization may potentially occur when natural reproductive barriers are disrupted, and may ultimately introduce adaptive variations or obscure the taxonomy and the relationships between closely related species (Arnold 1997; Barton 2001; Allendorf et al. 2001;

Sites and Marshall 2003; Mallet 2005; Abbott et al. 2016). Hybridization experiments between *D. richardsoni* from Churchill and *D. groenlandicus* from Baker Lake led by Scott and Fisher (1983) produced healthy but sterile lemmings. Presence of sterile hybrids in a certain area may create a biological barrier that may bring about reproductive isolation (Anderson and Rand 1945; Bigelow 1965; Scott and Fisher 1983; Abbott et al. 2016). Currently the distribution ranges of *D. richardsoni* and *D. groenlandicus* are thought to overlap around the Baker Lake and Aberdeen Lake area, in the Kivalliq Region, west of Hudson Bay, mainland Nunavut (Naughton 2012), but it is still uncertain if they are sympatric due to the difficulty in identifying them by external criteria and a lack of genetic-based studies (see Engstrom et al. 1993; Ehrich et al. 2000).

Studies on geographic variation of cranial characters can help in unraveling taxonomic and relationship issues in *Dicrostonyx* (Abramson and Tikhonova 2002). In our study we use 2D-shape analyses to assess patterns of variation in craniodental morphology in collared lemming populations from the Canadian Arctic, with a focus on collared lemmings from the Baker Lake-Aberdeen Lake area where the taxonomic status of many museum specimens remained unclear (see below). We included collared lemmings from the Canadian Arctic Archipelago, mainland Nunavut, Manitoba, and the Ungava Peninsula, Quebec. Using the elliptic Fourier analysis, we assessed the degree of differentiation of 2D outline shapes of four craniodental characters in seven groups of museum *Dicrostonyx* specimens, including *D. groenlandicus*, *D. richardsoni*, and *D. hudsonius*, used as an outgroup, and test for the validation of their distinction and morphological affinities in an attempt to shed new lights on the diversity puzzle of North American collared lemmings, degree of their reproductive isolation and relationships, and species boundaries.

Materials and methods

One hundred and fifty-six non-damaged skulls of museum specimens of collared lemmings were selected from eight geographic locations (Fig. 1, and supplementary material Table S1) to examine the outline shape of craniodental characters in *D. groenlandicus* collected from Adelaide Peninsula (n = 20), Cape Dorset (n = 19), and Ellesmere Island (n = 20), Nunavut, and Prince Patrick Island (n = 20), Northwest Territories, *D. richardsoni* (n = 27) collected from McConnell River area, Manitoba, and *D. hudsonius* (n = 30) collected from the Belcher Islands, Nunavut, and Nunavik, Quebec. We included a set of skulls of originally unidentified collared lemmings (pelts are currently non-existent) from the Baker Lake-Aberdeen Lake area, in the Kivalliq Region, Nunavut (n = 20). The specimens are now preserved in the Mammal Collection of the Canadian Museum of Nature (Natural Heritage Campus, Gatineau, Quebec). Species were formerly identified *in situ* according to pelage patterns solely (see Naughton 2012 for descriptions). The specimens were collected predominantly in the spring-summer season (May to September) between 1925 and 1978, including 22.2% being collected in 1960 (79% of which being collected from McConnell River) and 21.6% in 1949 (Fig. 2).

The external two-dimensions outlines of four craniodental characters, namely the skull (ventral view) and the occlusal patterns of the upper left molars (M1, M2, and M3), were analysed. Upper molars are less variable and were deemed much more reliable than lower molars in detecting morphological differences (Banfield 1974; Zazhigin 1984; Abramson and Tikhonova 2002; Abramson et al. 2004). To assess the outlines of these four craniodental characters, digital photographs (PNG format) were taken using a stationary Nikon Coolpix 4500 digital camera and Nikon SMZ 1500 stereomicroscope. The skulls and teeth were placed horizontally, bottom view up and at the same proximal-distal orientation. Photographs were directly uploaded into the open source image processing program *ImageJ*

(https://imagej.nih.gov/ij/), which was used to refine the image contours so that the outline shape of the craniodental characters could be extracted precisely. In some instances, technical glitches (i.e., sections of contours missing, non-true outline extracted, and pixel noise) due to poor contrast occurred while attempting to get the outlines of the molars using Image*J*. The teeth photographs were then scanned with a flatbed scanner and the outlines accurately redrawn by hand using a pigment liner pen (0.1 mm). The resulting images were uploaded into Image*J*.

DiaOutline was used to extract the actual shape for the four craniodental characters (Wishkerman and Hamilton 2018). The software R (version 3.3.1) was used to perform elliptic Fourier analysis (EFA) (Haines and Crampton 2000), as well as the following multivariate analyses. DiaOutline extracts x- and y-coordinate vector metrics and generates a series of harmonics (closed curves) using EFA to be further analyzed.

Linear Discriminant Analysis (LDA) was used as a classification method to quantify the separation of two or more *a priori* defined groups of specimens. It was performed on each craniodental character (i.e., M1, M2, M3, and skull) considered separately. The specimens were assigned to their respective groups according to their area of origin and not by species. The collared lemmings from Belcher Islands and Nunavik were lumped together to form one single group, i.e., Ungava Peninsula. Seven groups were thus considered for the analyses, Adelaide Peninsula, Baker Lake-Aberdeen Lake, Cape Dorset, Ellesmere Island, Prince Patrick Island, McConnell River, and Ungava Peninsula. Males and females were combined as there is no sexual dimorphism in the collared lemmings (Naughton 2012). Results were based on the combined information generated by the LDA dimensions. A non-parametric multiple analysis of variance using permutations (PERMANOVA) allowed to test for differences ($P \leq 0.05$) among the groups (Anderson 2001). F-values (F) were calculated to assess variability of distance

between points within the same group versus the variability in distance among points. R-squared values (R^2) were calculated as measurements of how well the proposed groups explain variation in the similarities or distances, interpreted as standard effect size (Cohen 1988). Percentage of nonoverlap between groups was inferred from R^2 (see Cohen 1988; Fritz et al. 2012) and used heuristically to estimate degree of similarity (the lower the percentage the higher the similarity). Finally, Mahalanobis' distances (D^2) were calculated to investigate affinities between the groups (Tabachnick and Fidell 1996).

We performed *a posteriori* LDAs to assess morphological affinities of the lemmings from the zone of possible sympatry with each recognized species. To this end we grouped lemmings according to their respective species (essentially by lumping together all *D. groenlandicus* groups) and kept those from the Baker Lake-Aberdeen Lake as a separate group. PERMANOVA F and P, R^2, and D^2 were calculated as above.

Results

DiaOutline proved efficient in extracting the actual shape, including capturing minute inter-individual variations. Despite vetting the morphological attributes both on the specimens and the digital photographs, a few specimens notably departed from their respective groups, mainly in molars instances. However there was no obvious abnormality that would have warranted their removal from the dataset. In fact they rightly accounted for a proportion of the within group variation.

Results pertaining to the analyses considering the seven separate collared lemming groups are summarized in Table 1, Table 2, and Fig. 3. The LDAs revealed discrete outline shapes for each of the four craniodental characters representing each of the seven groups (Fig. 3). Analyses revealed highly significant differences ($P = 0.001$) among the groups and large standard effect

sizes (SES) (Cohen's d varied between 1.5 and 1.92, corresponding to $R^2 = 0.36$ and 0.48, respectively) (Table 1).

In LDAs relating to the 2D outline of the three upper molars, linear dimensions 1 and 2 (LD1 and LD2) combined 93.6% of the total variance when considering M1, 94.62% for M2, and 91.85% for M3. Summary of pairwise comparisons among LDA scores of the seven groups are given in Table 2. Results showed a neat separation between the Ungava Peninsula lemming group (*D. hudsonius*) and the rest on the LD1-LD2 plane (Fig. 3 a, b, and c). Lemmings of this group clustered tightly around the centroid, with low variability among individuals. The largest values for F, R^2 and Mahalanobis' D^2 were observed when comparing Ungava Peninsula lemmings with any of the other groups. The largest proportions of the variation in distances observed in the molar shapes, 47% to 75% ($R^2 = 0.47$ and 0.75, respectively), were accounted for when comparing this group with the other six, with the exception for the third upper molar (M3) of the Adelaide Peninsula and Ellesmere Island groups ($R^2 = 0.90$). By contrast, the six lemming groups pertaining to the *D. groenlandicus* and *D. richardsoni* species, including the Baker Lake-Aberdeen Lake group, showed larger variability along the LD1 and LD2 axes in the three LDAs for the molar shapes. This supports a higher heterogeneity in the molar shapes in *D. groenlandicus* and *D. richardsoni* than in *D. hudsonius*. These six groups overlapped more or less extensively on the LDA planes. As inferred from R^2, percentage of nonoverlap varies from ~27% for the smallest (small SES; corresponding to $R^2 = 0.04$, in M1) as observed between the McConnell River (*D. richardsoni*) and Cape Dorset (*D. groenlandicus*) groups, to ~62% for the largest (large SES; $R^2 = 0.26$, in M3) between the Baker Lake-Aberdeen Lake and Ellesmere Island groups. The largest values for F, R^2 and D^2, leaving out the Ungava Peninsula group, were

most often observed when comparing the Baker Lake-Aberdeen Lake group with any of the *D. groenlandicus* and *D. richardsoni* groups, particularly with the Ellesmere Island group.

With regard to the skull outlines, the first five dimensions (LD1-LD5) combined 96.8% of the total variance. Highly significant differences ($P = 0.001$) most often coupled with large SES were observed among groups, except for differences between the McConnell River and Ungava Peninsula groups. When considering only the six groups pertaining to *D. groenlandicus* and *D. richardsoni*, percentage of nonoverlap ranged from ~51% ($R^2 = 0.16$), as observed between Cape Dorset and Ellesmere Island groups, to ~69% ($R^2 = 0.34$), between the Baker Lake-Aberdeen Lake and Prince Patrick Island groups (Table 2). The lowest affinity (largest percentage of nonoverlap coupled with large D^2) was observed between the Adelaide Peninsula group and Baker Lake-Aberdeen Lake (nonoverlap = ~67%, $D^2 = 2.68$), Ellesmere Island (nonoverlap = ~65%, $D^2 = 2.74$), Prince Patrick Island (nonoverlap = ~66%, $D^2 = 2.58$), and Cape Dorset (nonoverlap = ~63%, $D^2 = 2.69$) groups. Similar results were obtained when restricting the analyses to the information available solely in the LD1-LD2 plane (58.9% of the observed variation; Fig. 3 b). In this case, however, differences were not significant when comparing Baker Lake-Aberdeen Lake with Prince Patrick Island ($P = 0.127$) and Cape Dorset ($P = 0.996$), and Cape Dorset with Prince Patrick Island ($P = 0.301$). In contrast to the observations made on the molars, the Ungava Peninsula group did not show the highest reported values, except for D^2 in the case of the pairwise comparisons with the Adelaide Peninsula and Ellesmere Island groups. Only 11% to 29% ($R^2 = 0.11$ and 0.29, respectively) of the variation in distances observed in the skull shape is accounted for when comparing this group with the others.

Results derived from the *a posteriori* analyses are summarized in Table 3 and Table 4. Highly significant differences ($P = 0.001$) were detected for each craniodental characters among

the four groups, i.e., *D. groenlandicus*, *D. richardsoni*, *D. hudsonius*, and Baker Lake-Aberdeen Lake (Table 3). *D. groenlandicus* and *D. richardsoni* showed significant differences in the shape of their three upper molars (Table 4) despite a close morphological affinity. Inferred percentages of nonoverlap between the two species were the lowest and varied between ~33% for the first upper molar (M1) and ~39% for M2 (Table 4). Mahalanobis' D^2 ranged between 1.11 for M1 and 1.35 for M2; only *D. richardsoni* and the Baker Lake-Aberdeen Lake group showed lower values in two instances (M1 and M3). The two species showed a more contrasted skull shape (nonoverlap = ~44%, and $D^2 = 1.56$; a large SES is also highlighted in Table 4); yet this contrast is weaker than between other groups, underlying in other words a greater similarity. The Baker Lake-Aberdeen Lake group displayed significant differences when compared with both species. When considering the three upper molars, percentage of nonoverlap was smaller when comparing this group with *D. richardsoni* (percentage ranged between ~41% and ~47% for M1 and M2, respectively, vs. ~43% and 54% with *D. groenlandicus* for M1 and M2, respectively). Mahalanobis D^2 supported this relatively closer proximity between the Baker Lake-Aberdeen Lake group and *D. richardsoni* (D^2 ranged between 0.73 and 1.49 for M1 and M2, respectively, vs. 1.60 and 2.18 with *D. groenlandicus* for M1 and M2, respectively). Conversely, the former showed a closer affinity in the skull shape with *D. groenlandicus* as supported by a relatively low percentage of nonoverlap (~59% vs. ~74% with *D. richardsoni*) and Mahalanobis D^2 (2.14 vs. 2.55). Finally, this analysis confirmed the sharp distinctiveness of *D. hudsonius* with regard to the shape of the three upper molars, with 71% ($R^2 = 0.71$) of the variation in distances observed in these craniodental characters being accounted for when comparing *D. hudsonius* with the other two species, and 83% ($R^2 = 0.83$) when comparing it with the Baker Lake-Aberdeen Lake group (Table 4). As observed in the first analyses considering the seven groups

separately, comparison between the skull shapes revealed highly significant differences coupled with large SES among groups. The greatest morphological affinity was observed between *D. hudsonius* and *D. richardsoni*, (nonoverlap = ~54%, with $D^2 = 0.99$), and the lowest ones between the Baker Lake-Aberdeen Lake group and these two species (*D. hudsonius*: nonoverlap = ~72%, $D^2 = 2.79$, and *D. richardsoni*: nonoverlap = ~74%, $D^2 = 2.55$).

Discussion

Our results from craniodental character 2D outlines reveal that collared lemmings in the Canadian Arctic show both intra- and interspecific morphological variability depending on their geographic location. Here we show that collared lemmings from the Baker Lake-Aberdeen Lake area in the Kivalliq Region, Nunavut, display significant differences in the shape of the upper molars and skull compared with the lemmings from elsewhere and identified as *D. groenlandicus* and *D. richardsoni*. This highlights a challenge in assigning lemmings from this area to either of the two species on the basis of craniodental criteria. The area of Baker Lake-Aberdeen Lake represents a junction point and a potential zone of overlap in the distribution ranges of *D. groenlandicus* and *D. richardsoni* (Fig. 1, adapted from Naughton 2012). However, no clear physical or biological barrier isolates the two species. When considering the shape of the three upper molars, we found that Baker Lake-Aberdeen Lake lemmings display a close morphological affinity (lesser overlap and smaller Mahalanobis' distances) with those from McConnell River; conversely, when considering the skull shape, the former display a closer morphological affinity with most of the other groups considered, except for those from Adelaide Peninsula and Ungava Peninsula. Such combination of morphological features of one species (i.e., *D. richardsoni*) with another's (*D. groenlandicus*) suggests the occurrence of putative F1 hybrid lemmings in the Baker Lake-Aberdeen Lake area. Although only sterile hybrids have

been observed in laboratory conditions (Scott and Fisher 1983), some observational evidences support hybridization events between the two species in the wild (Anderson and Rand 1945). The pattern of morphological overlap we observed between lemmings from this area and those from surrounding populations, however, was not suggestive of any intermediate form between *D. groenlandicus* and *D. richardsoni*, but pointed to the occurrence of three distinct groups whose biological and morphological features may reflect differential habitat characteristics. A note of interest in this respect is that Krebs (1963) reported a differential pattern of cycle in 1961 for lemmings in the Baker Lake area compared with adjacent populations.

Our *D. groenlandicus* samples include specimens from three insular populations, Baffin Island (Cape Dorset), Prince Patrick Island, and Ellesmere Island, which insularity should express a potential distinctiveness in craniodental shapes due to genetic isolation (see Ehrich et al. 2001). While lemmings from Cape Dorset can connect with populations on mainland Canada through Melville Peninsula owing to the very short distances (ca. 2-15 km) to be travelled, those from Prince Patrick Island and Ellesmere Island were and are isolated since the last glaciation and show genetic differentiation (Ehrich et al. 2001; Fedorov and Stenseth 2002). Isolation of *D. groenlandicus* populations was estimated to have been occurring since *ca.* 100,000 years ago (Fedorov and Goropashnaya 1999). In the current study, we reveal a strong effect of geographic locations on the skull shape, with a clear distinctiveness of lemmings from Adelaide Peninsula. In the same context, Eger (1995) noted that *D. richardsoni* populations from Churchill and McConnell River, Manitoba, were morphologically distinct, because of possible past isolation in different refugia. Our results show significant differential distributions of the four groups of specimens within the *D. groenlandicus* cluster, in congruence with partitions that recognized genetic (mtDNA) distinctions between Baffin Island, Prince Patrick Island, and Ellesmere Island

populations (Fedorov and Stenseth 2002). In addition, Ehrich et al. (2001) reported high genetic variability at four nuclear microsatellite loci in *D. groenlandicus* collected from various localities of the central and western Canadian Arctic. Such genetic variability could be paralleled with the variability in the skull shape we report for this species. Abramson and Tikhanova (2002) already reported good agreement between morphological and genetic (mtDNA) differentiations in Palaearctic collared lemmings. Conversely, we detected no such pattern of differentiation in *D. groenlandicus* groups when considering the upper molars, our results showing small effect size of geographic locations and a greater affinity between groups.

Our results confirm the molar complexity in present day collared lemmings. Smirnov and Fedorov (2003) found a discrepancy between genetic (mtDNA) differentiation and degree of development of triangles on the masticatory surface of the upper molars in *D. groenlandicus*. Their results suggest that variation in morphology of M1 and M2 while having limited utility to reveal phylogenetic relationships likely reflects convergence under environmental influence. Fedorov et al. (2020) reported a phylogenetic congruence between nuclear and mitochondrial genomes in *D. torquatus*, which would allow speculating to some extent about a possible discrepancy between molar morphology and nuclear genome as well. Regardless, this provides complimentary evidence to our findings suggesting a possible environmental influence, too, within the Baker Lake-Aberdeen Lake area. Thus, isolation of populations possibly in combination with genetic, environmental, and hybrids effects should account for a large part of the variation we report here on the shape of the craniodental characters.

Our LDAs performed after grouping lemmings according to their respective species showed that both *D. groenlandicus* and *D. richardsoni* display somewhat yet significantly (with medium effect size) distinct occlusal patterns of the three upper molar, in agreement with genetic

data (Ehrich et al. 2000). These two species were deemed to be greatly similar in terms of their molar morphology (Jarrell and Fredga 1993). Besides, the skull shape may serve as a morphological criterion for discriminating between lemming groups, but not between species. Interestingly, these two species showed a closer skull shape affinity with one another than each did with the Baker Lake-Aberdeen Lake group (Table 4). In this sense, this finding underlines again the complexity in the morphological relationships between these two species. Eger (1995), using 13 skull linear measurements, showed no clear morphological differences between collared lemmings (*D. groenlandicus* and *D. richardsoni*) from the Kivalliq Region and adjacent mainland and island areas. Engstrom et al. (1993) reported that the morphology of the sex chromosome can reliably be used in discriminating between these two species, while autosomal chromosomes are not effective. Karyological and genetic variation, however, may not be expressed morphologically in Arvicolinae (Chaline 1987; Abramson and Tikhonova 2002). Hence, most determinations of collared lemming species are based on controversial pelage patterns (Youngman 1975; Hall 1981; Abramson and Tikhonova 2002; Naughton 2012).

With very distinctive upper molar shapes, *D. hudsonius* shows clear differentiation from the other collared lemmings, as anticipated from Agadzhanyan (1984), Jarrell and Fredga (1993), and Fedorov and Goropashnaya (1999). The clearest distinctions were observed when comparing the M2 outline shapes. M1 and M2 were reported to be species-specific (Banfield 1974; Kurtén and Anderson 1980), though the upper molars could prove to be unreliable in this respect in some circumstances (Youngman 1975; Jarrell and Fredga 1993). Kurtén and Anderson (1980) mentioned that *D. hudsonius* differs from *D. groenlandicus* due to the presence of accessory cusps on the three upper molars. Our results deriving from 2D-shape analyses confirm the great reliability of the upper molars in distinguishing *D. hudsonius* from both *D. groenlandicus* and *D.*

richardsoni. On the other hand, our results contrast with those of Eger (1995). The latter author showed that, while *D. hudsonius* and the Aleutian collared lemmings (*D. unalascensis*) are morphologically distinct, geographic variation among the other species were trivial (Ogilvie Mountains collared lemming, *D. nunatakensis*, was not included). However, the bulk of the craniometric variation that Eger (1995) observed was related to size; "shape" did not yield any clear distinction between species, save only *D. unalascensis*.

The collection dates of three out of the seven groups being biased for a single year (Adelaide Peninsula: 1957 [100%]; McConnell River: 1960 [100%]; Prince Patrick Island: 1949 [85%]) could affect in some ways the results of the comparisons in morphology. Body size of lemmings and voles has been shown to increase with population density (Chitty effect) (Chitty 1952; Boonstra and Krebs 1979; Fauteux et al. 2015) and changes in photoperiod (Mallory et al. 1981; Mallory et al. 1986), possibly as a consequence of phase-related allocation of energy for somatic and reproductive efforts (Oli 1999). Such effects were observed on *Dicrostonyx* and *Lemmus* skull size (Krebs 1964). Yet, no evidence for change in shape of skulls or molars was reported in this regard. In any case, our results mostly derive from samples whose collection dates randomly cover at least one population cycle period (i.e., four years), including the Ungava Peninsula group (Table S1), which can prove very insightful in this respect. In fact, the low variability in molar shapes as revealed by the LDAs indicates weak to no effect of collection year. Thus, the patterns of variation and differentiation we report here should reflect a strong genetic and geographic location effect.

The method by Wishkerman and Hamilton (2018) that we used here to extract the outline of craniodental characters proves efficient in detecting significant morphological variations in agreement with genetic data among collared lemming groups from Canada's Arctic. The pattern

of overlap we observed in the outline shape of the three upper molars and the skull among collared lemmings from the Kivalliq Region stresses out again the difficulty in assigning morphologically individuals from the Baker Lake-Aberdeen Lake area to either *D. groenlandicus* or *D. richardsoni*. With regard to the shape of the three upper molars, the McConnell River and Baker Lake-Aberdeen Lake groups generally show the closest morphological affinity (Table 2), suggesting a common *D. richardsoni* taxonomic status. The skull shape, however does not support such a common status. In addition, specimens from the Baker Lake-Aberdeen lake area kept in the Mammal Collection of the Canadian Museum of Nature were identified *in situ* as *D. groenlandicus* (Khidas and Shorthouse 2020). Our findings call for further studies on genetics, ecology and range distribution of collared lemmings in this possible zone of sympatry between *D. groenlandicus* and *D. richardsoni* for taxonomic purposes.

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Conflict of Interest statements

We, the three authors, declare that there is no real or perceived conflicts of interest that may arise from intellectual, personal, or financial circumstances of our research.

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Table 1. Value for PERMANOVA F and *P*, and R^2 for comparing 2D outline shape of the skull and three upper molars (M1, M2, and M3) among seven collared lemming groups from the Canadian Arctic (see text and Table 2 below for identification).

	F	*df*	R^2	*P*
M1	14.38	143	0.39	0.001
M2	21.0	142	0.48	0.001
M3	14.12	141	0.39	0.001
Skull	12.03	136	0.36	0.001

Table 2. Pairwise comparisons for craniodental affinity between seven collared lemming groups from the Canadian Arctic. MCR: McConnell River; AP: Adelaide Peninsula, CD: Cape Dorset; PPI: Prince Patrick Island; EI: Ellesemere Island; UP: Ungava Peninsula (Belcher Islands, Nunavut, and Nunavik, Quebec); BKL: Baker Lake (lemmings from the Baker Lake-Aberdeen Lake area). Bolded R^2 indicate large effect size (corresponding to Cohen's d > 0.8; Cohen 1988). Bolded D^2 indicate the largest distances between pairs of group centroids, hence the lowest affinity between groups.

		MCR-BKL	MCR-AP	MCR-CD	MCR-PPI	MCR-EI	MCR-UP	BKL-AP	BKL-CD	BKL-PPI	BKL-EI	BKL-UP
M1	F	1.88	3.70	1.53	2.08	7.78	40.57	5.57	3.68	4.85	12.00	36.00
	P	0.072	0.001	0.17	0.060	0.001	0.001	0.001	0.002	0.001	0.001	0.001
	R^2	0.05	0.08	0.04	0.05	**0.16**	**0.47**	0.13	0.10	0.12	**0.25**	**0.47**
	D^2	0.75	1.39	0.79	0.84	**2.14**	**3.67**	1.85	1.43	1.52	**2.53**	**3.00**
M2	F	3.44	4.66	2.48	2.27	4.80	55.49	7.14	10.06	9.89	10.44	91.34
	P	0.001	0.001	0.014	0.041	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	R^2	0.08	0.10	0.06	0.05	0.11	**0.56**	**0.17**	**0.22**	**0.22**	**0.22**	**0.70**
	D^2	1.45	1.89	1.17	1.20	1.70	**4.76**	2.08	2.26	2.31	2.08	**4.09**
M3	F	2.57	1.94	2.21	3.08	6.91	40.04	5.95	7.22	8.76	12.75	56.36
	P	0.030	0.087	0.040	0.003	0.001	0.001	0.001	0.001	0.001	0.001	0.001

	R^2	0.06	0.05	0.05	0.07	**0.15**	**0.48**	**0.15**	**0.17**	**0.20**	**0.26**	**0.58**
	D^2	0.83	0.96	0.88	1.31	**2.19**	**3.68**	1.68	1.66	**2.13**	**2.57**	**2.85**
Skull	F	14.81	10.35	8.40	9.95	19.99	6.35	14.37	9.11	13.22	16.38	14.06
	P	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	R^2	**0.27**	**0.21**	**0.17**	**0.22**	**0.31**	0.11	**0.32**	**0.22**	**0.34**	**0.32**	**0.24**
	D^2	1.84	**2.25**	1.88	1.23	**2.56**	1.10	**2.68**	0.04	0.66	0.85	**2.22**

		AP-CD	AP-PPI	AP-EI	AP-UP	CD-PPI	CD-EI	CD-UP	PPI-EI	PPI-UP	EI-UP
M1	F	4.91	1.72	2.59	61.94	1.93	9.13	44.96	3.86	55.69	93.17
	P	0.001	0.10	0.020	0.001	0.068	0.001	0.001	0.004	0.001	0.001
	R^2	0.12	0.04	0.06	**0.59**	0.05	**0.20**	**0.52**	0.09	**0.56**	**0.68**
	D^2	1.81	0.77	0.75	**4.81**	1.04	**2.53**	**4.04**	1.48	**4.50**	**5.42**
M2	F	2.62	3.03	2.40	106.21	1.45	3.91	122.57	3.14	113.68	115.24
	P	0.011	0.006	0.045	0.001	0.20	0.001	0.001	0.004	0.001	0.001
	R^2	0.07	0.07	0.06	**0.72**	0.04	0.10	**0.75**	0.08	**0.73**	**0.73**
	D^2	1.29	1.35	0.27	**6.15**	0.07	1.02	**5.93**	1.08	**5.96**	**6.11**

M3	F	2.26	2.13	3.59	61.96	1.43	4.28	64.60	4.40	56.64	72.58
	P	0.029	0.05	0.006	0.001	0.20	0.001	0.001	0.001	0.001	0.001
	R^2	0.06	0.05	**0.90**	**0.60**	0.04	0.10	**0.61**	0.10	**0.57**	**0.63**
	D^2	0.20	0.63	1.45	**4.50**	0.52	1.65	**4.50**	1.86	**4.98**	**5.00**
Skull	F	11.24	10.58	14.12	14.73	9.87	7.00	11.40	11.46	8.75	19.40
	P	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	R^2	**0.27**	**0.31**	**0.30**	**0.26**	**0.27**	**0.16**	**0.20**	**0.28**	**0.18**	**0.29**
	D^2	**2.69**	**2.58**	**2.74**	**3.35**	**2.26**	0.81	**2.26**	1.49	1.58	**3.07**

Table 3. Value for PERMANOVA F and *P*, and R^2 for comparing 2D outline shape of the skull and three upper molars (M1, M2, and M3) among four collared lemming groups (*D. groenlandicus*, *D. richardsoni*, *D. hudsonius*, and Baker Lake-Aberdeen Lake) from the Canadian Arctic.

	F	*df*	R^2	*P*
M1	43.71	143	0.48	0.001
M2	78.47	142	0.63	0.001
M3	48.41	141	0.51	0.001
Skull	26.61	136	0.38	0.001

Table 4. Pairwise comparisons for craniodental affinity between four collared lemming groups from the Canadian Arctic. Dr: *D. richardsoni* (lemmings from McConnell River, Manitoba); Dg: *D. groenlandicus* (lemmings from Adelaide Peninsula, Cape Dorset, and Ellesmere Island, Nunavut, and Prince Patrick Island, Northwest Territories, are lumped altogether in this group); Dh: *D. hudsonius* (lemmings from the Belcher Islands, Nunavut, and Nunavik, Quebec); BKL: Baker Lake (lemmings from the Baker Lake-Aberdeen Lake area). Bolded R^2 indicate large effect size (corresponding to Cohen's d > 0.8; Cohen 1988). Bolded D^2 indicate the largest distances between pairs of group centroids, hence the lowest affinity between groups.

		Dr-Dg	Dr-Dh	Dr-BKL	Dg-Dh	Dg-BKL	Dh-BKL
M1	F	5.82	86.76	4.10	122	11.84	86.35
	P	0.002	0.001	0.008	0.001	0.001	0.001
	R^2	0.06	**0.66**	0.10	**0.54**	0.11	**0.69**
	D^2	1.11	**3.61**	0.73	**4.43**	1.60	**2.90**
M2	F	9.29	106.21	6.23	243.42	22.27	191.61
	P	0.001	0.001	0.001	0.001	0.001	0.001
	R^2	0.086	**0.71**	**0.14**	**0.71**	**0.19**	**0.83**
	D^2	1.35	**4.81**	1.49	**6.06**	2.18	**4.15**
M3	F	7.30	69.05	4.36	138.93	18.22	101.06

	P	0.001	0.001	0.01	0.001	0.001	0.001
	R^2	0.07	**0.61**	0.10	**0.58**	**0.16**	**0.72**
	D^2	1.16	**3.69**	0.85	**4.70**	2.01	**3.00**
Skull	F	23.63	12.52	27.56	39.90	23.14	27.46
	P	0.001	0.001	0.001	0.001	0.001	0.001
	R^2	**0.21**	**0.19**	**0.40**	**0.30**	**0.23**	**0.38**
	D^2	1.56	0.99	**2.55**	**2.47**	**2.14**	**2.79**

Figure 1: Sample localities (solid squares) of specimens used in comparative 2D-shape analysis in collared lemmings from the Canadian Arctic. Distribution range is delineated for each recognized species (adapted from Naughton 2012). The base map image used to create this map is freely available at https://www.simplemappr.net/. Gold: *Dicrostonyx groenlandicus*; Yellow: *D. richardsoni*; Brown: *D. hudsonius*; Gold-Yellow stripes: area of possible sympatry between *D. groenlandicus* and *D. richardsoni*.

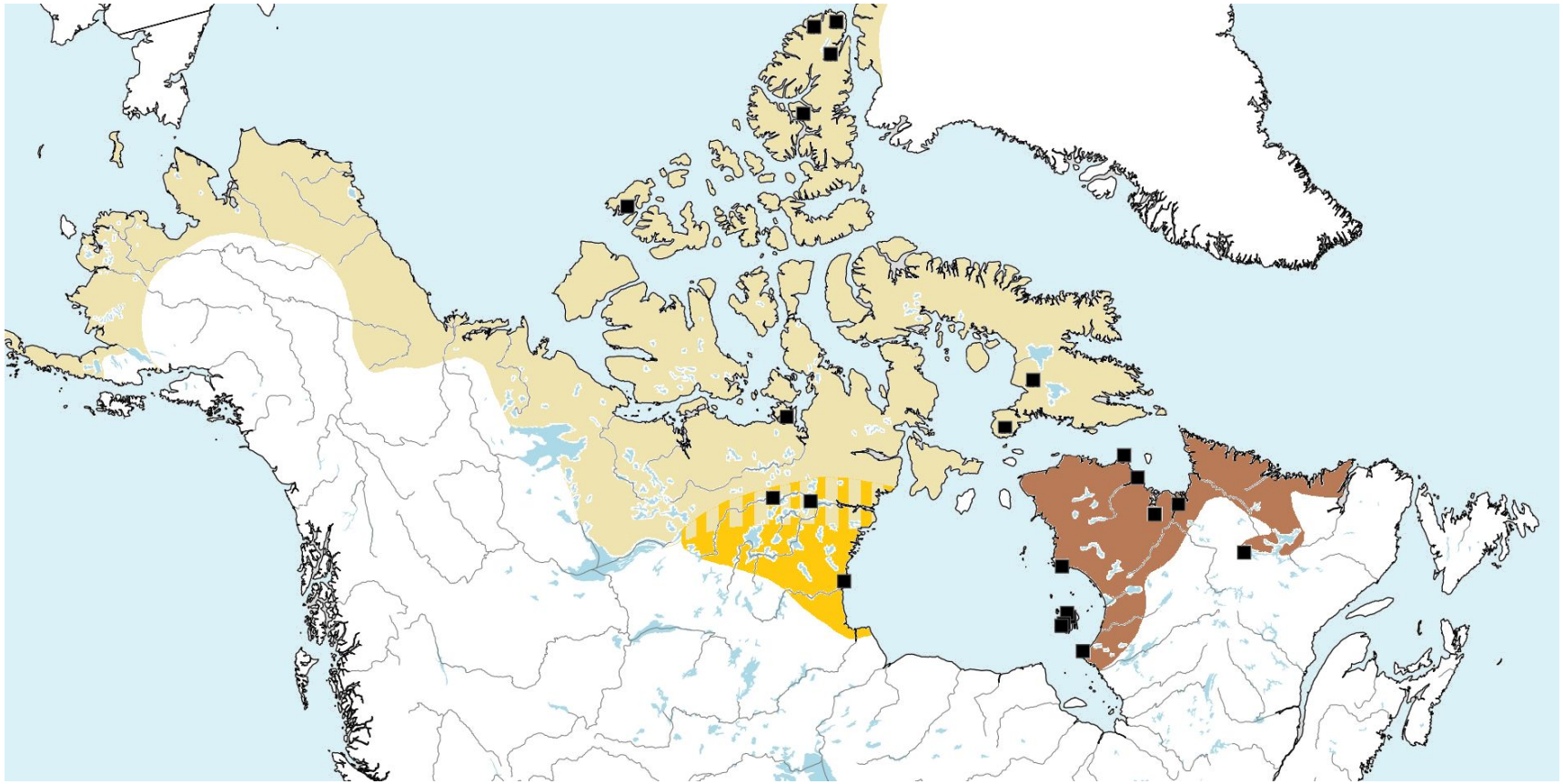


Figure 2. Sample years of specimens used in comparative 2D-shape analysis in collared lemmings from the Canadian Arctic.

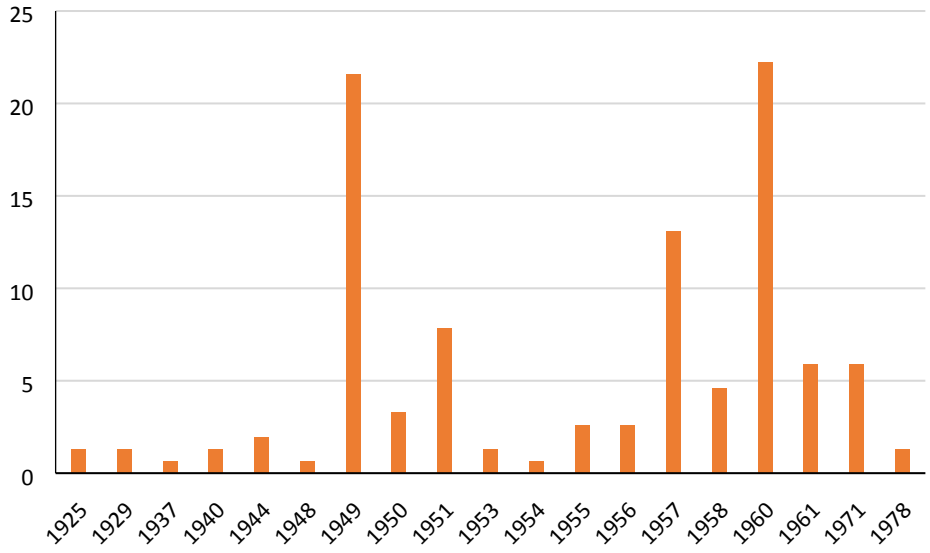
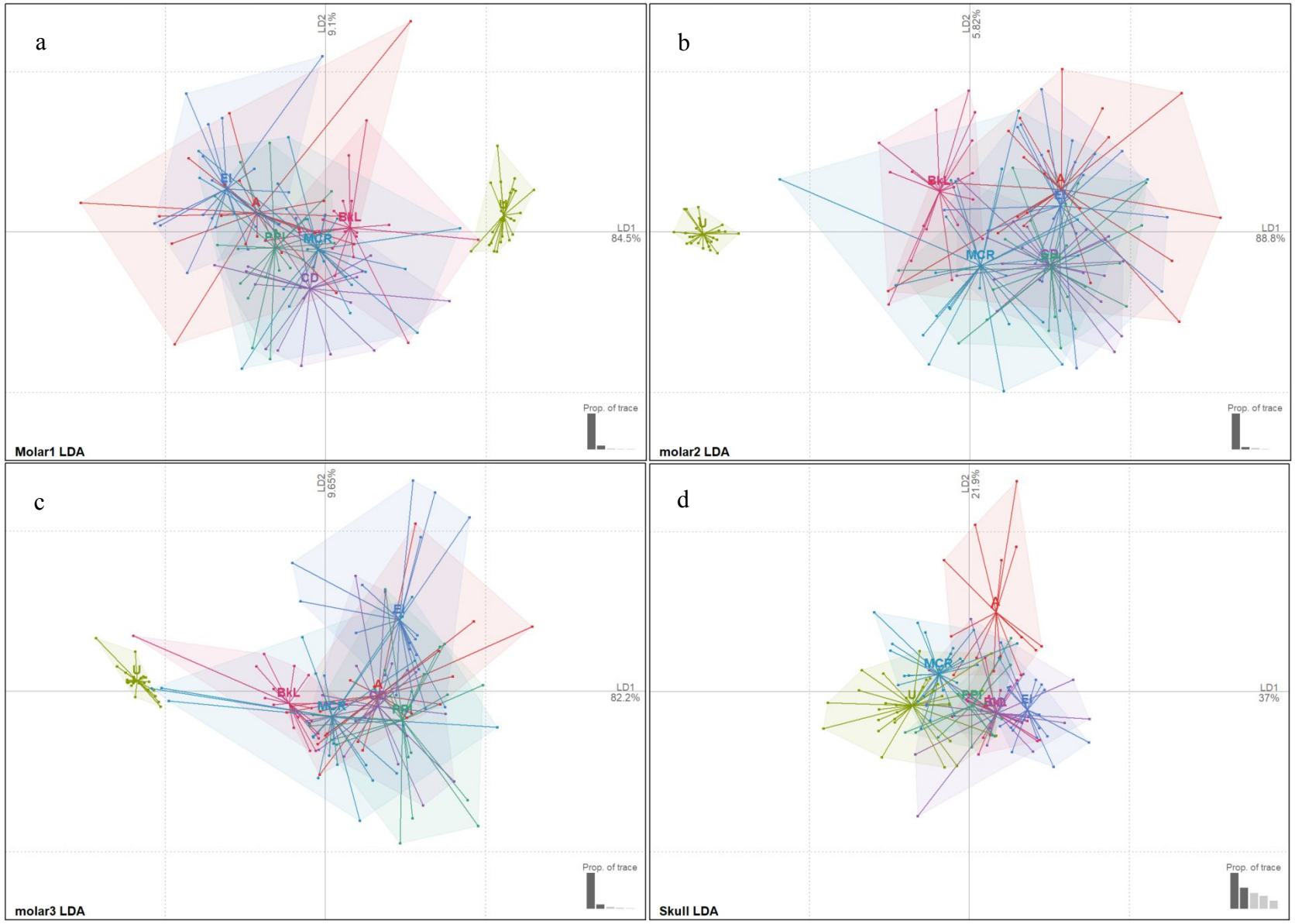


Figure 3: Linear discriminant analysis plots representing the collared lemming groups from the Canadian Arctic examined in the current study. Results are shown for the three upper molars (i.e., M1, M2, and M3) and skull outlines. a: M1, b: M2, c: M3, d: skull. A: Adelaide Peninsula; BKL: Baker Lake; CD: Cape Dorset; EI: Ellesmere Island; MCR: McConnell River; PPI: Prince Patrick Island; U: Ungava Peninsula.



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