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Morphometrics highlights subspecies differentiation of continental (*Rangifer t. tarandus*) and insular (*Rangifer t. platyrhynchus*) Norwegian reindeer

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Keywords: morphometrics; Norway; osteometrics; Svalbard; ungulate subspecies discrimination

Abstract: Reindeer (*Rangifer tarandus*) is an emblematic species with several recognized subspecies. Two reindeer subspecies are present in Norway: the wild and semi-domestic European tundra reindeer (*R. tarandus tarandus*) in continental Norway, and Svalbard reindeer (*R. tarandus platyrhynchus*) endemic to this archipelago. The main aim of this paper is to give a descriptive and quantified analysis of the modern wild reindeer morphological diversity. The morphometric variation was quantified, based on 262 adult specimens of both sexes, by both linear measurements, analysed through log shape ratio computed from post-cranial bones and teeth measurements, and landmarks and sliding semi-landmarks based geometric morphometrics (GMM) to quantify molars size and shape. All anatomical parts (teeth, metatarsals, metacarpals) highlighted differences between the continental and insular subspecies. Our main results pointed out morphometrics characteristics of nowadays reindeer subspecies, like differences in proportions between the size of metapodials or lower cheek teeth with the body size, that could be of great interest for archaeozoological research.

1 Introduction

Reindeer (*Rangifer tarandus* L., 1758) is an emblematic species with nine to fourteen recognized subspecies, depending of the criteria considered by biologists (Banfield 1961; Geist 1999; Kuntz 2011; Tryland and Kutz 2018). The species has a wide range of latitudinal distribution, from 46° N to 80° N, covering three continents: Europe (Scandinavia, Russia), Asia (Siberia, China, Mongolia) and North America (Canada, Alaska, Greenland) (Syroechkovskii 1995; Tryland and Kutz 2018). Such species then likely experiences a large range of environmental conditions, given their broad latitudinal range.

Reindeer skeletons have varied in size and shape and in time and space during the Pleistocene (Kuntz 2011; Weinstock 2000). DNA analyses have shown how Pleistocene climate fluctuation reshaped the geographic distribution of reindeer leading to the modern genetic diversity of the species (Yannic et al. 2014). However, the subspecies designation based on morphological differences does not reflect exactly the mitochondrial DNA phylogeography of the species, suggesting that morphological differences among subspecies may have evolved as adaptive responses to postglacial environmental changes (Flagstad and Røed 2003).

Two reindeer subspecies are present in Norway: the European tundra reindeer (*R. tarandus tarandus*) in continental Norway, and the insular Spitsbergen reindeer (*R. tarandus platyrhynchus*), endemic to the Svalbard archipelago north of the continental Norway. Norway is the only country that possesses both of these subspecies, while the distribution of the wild European tundra reindeer is also covering other parts of Eurasia.

We studied the morphometric differentiation in samples of these two reindeer subspecies from Norway and

Svalbard. Because they live under different environmental conditions, it might be possible to reveal differences in environmental factors attributed to differences in their morphology. As a highly sexually dimorphic species (Geist 1999), male and female reindeer are different in habitus, not only in body mass/size but also in feeding ecology as disclosed by e.g., dental textural microwear (Bignon-Lau et al. 2017). Therefore, we explored to what extent reindeer are sexually dimorphic in their skeletal morphometrics. Further, we examined the morphometric variation in cheek teeth of the lower jaw and anterior and posterior metapodials, which have the potential to reveal variations related to behavior and/or environmental interactions.

As an embranchment of morphometrics, osteometrics, which targets skeletal material, is frequently applied in biological and archaeological studies. Osteometrics can be used to discriminate taxonomy or groups, differences influenced by intrinsic (genetic, ontogeny) and extrinsic (diet, climate, geography, sickness, etc.) factors (Cucchi et al. 2015). Two main groups of morphometric methods are used in current archaeological studies, providing valuable taxonomical and environmental information. Firstly, linear morphometrics focus on measurements like length, width, anterior-posterior diameter or medio-lateral diameter of skeleton parts (Driesch 1976). Secondly, geometric morphometrics (GMM) quantify and visualize size and shape variation using (mainly) coordinates of homologous points or of points along curves (Adams et al. 2004, 2013; Rohlf and Marcus 1993). The latter group of methods is more and more used in archaeozoology (Cucchi et al. 2015).

The main aim of this paper was to give a descriptive and quantified dataset of Norwegian wild reindeer morphometric variation using both linear measurements and GMM. We chose to focus on morphometric data since (1) mainly bone remains are available from prehistoric periods, (2) numerous archaeological sites are rich in reindeer remains, (3) changes in reindeer anatomy reflected by skeleton measurements have been linked with past climatic and environmental changes (Kuntz 2011), (4) and most of the time the DNA information of past animal is not well preserved enough to allow molecular analyses for highlighting Palaeolithic reindeer evolution in Western Europe.

2 Materials and methods

2.1 Study populations

Today wild European tundra reindeer are found in 24 more or less separated populations or management units in continental Norway (<https://villrein.no/villreinomrader/>). These populations experience



Figure 1: Geographic location of the study populations. Dark red polygons represent the geographic range of the six populations in Norway. Hardangervidda, Knutshø and Forollhogna, localized in the south of continental Norway correspond to *R. tarandus tarandus*, while Grøndalen, Colesdalen and Sassendalen correspond to *R. tarandus platyrhynchus* from the island of Spitsbergen, Svalbard. Illustration by A. Lau-Bignon.

different habitats and ecological conditions depending on their geographic location (latitude, altitude, continental/island; Skogland 1989). Our study is based on the analysis of 6 reindeer populations, 3 from mainland Norway and 3 from the Svalbard archipelago (Figure 1).

Hardangervidda is the largest mountain plateau in Europe, located at an altitude of 1200 to 1600 m.a.s.l. This area holds the largest population of wild tundra reindeer in continental Norway (however fluctuating since many decades between 6.000 and 19.000 specimens; Skogland 1989; Strand et al. 2015a). Historically, this population has experienced several periods of high population density, overgrazing and consequently low vital rates. Today, the management aim is a population density of about 1.5 animal per km² in the winter population. Forollhogna (Jordhøy et al. 2010) and Knutshø (Strand et al. 2015b) are two similar sized (approx. 1800 km²), neighbouring reindeer areas located north of Hardangervidda. Both areas are situated within the low alpine to alpine zone, and are among the most productive wild reindeer areas in Norway. The present population management aims for Forollhogna and Knutshø equals respectively 2000 (1.1 animals/km²) and 1500 (0.8 animals/km²) animals in the winter population.

Spitsbergen is the largest island in the Svalbard archipelago. The reindeer subspecies living here is a short-legged island form (Geist 1999). Unlike most of its relatives, Svalbard reindeer lives sedentary lives and

does not carry out seasonal migrations (Tyler and Øritsland 1989). The animals sampled for this investigation originated from three nearby valleys Figure, Grøndalen, Colesdalen and Sassendalen, located on Nordenskiöld Land (Pedersen et al. 2019). This area consists of multiple valley systems delimited and separated by glaciers, high mountains and fjords. Despite the physical barriers, animals may move between the different valley, and the overall population density in the area equals 5–6 animals per km² (Le Moullec et al. 2019). The arctic climate and the arctic tundra represent challenging conditions for a stationary ungulate, but the Svalbard reindeer is well adapted to the harsh conditions and limited food resources (Skogland 1984). This subspecies is known to store exceptional large deposits of fat and is smaller than the continental subspecies (Reimers and Ringberg 1983).

2.2 Sample collection

The material used in this study was collected from animals killed during the regular hunting season (from the middle of August to the beginning of October). Information on each specimen, like year and date of harvest, sex, and age, is stored in several databases (Norwegian Polar Institute, NINA, Natural History Museum; see Supplementary Appendix). For all samples, number of permanent erupted teeth and toothwear of the lower jaws were used for age estimation (Miller 1974; Reimers and Nordby 1968). Among the three continental reindeer populations, specimens hunted in 2014 at Hardangervidda and Knutshø are stored at MAE René-Ginouves (UMR 7041-ArScAn, Ethnologie préhistorique laboratory; Nanterre, France). Forollhogna teeth from 2017 have been stored at NINA, Trondheim and later destroyed by NINA (such annually culled specimens are not stored). Samples of reindeer from Spitsbergen are managed by the Norwegian Polar Institute (Tromsø) and formerly by the Natural History Museum, University of Oslo. Our measurements were taken in this latter institute, where specimens hunted before 2010

were stored. Teeth of the three Spitsbergen reindeer populations were from specimens hunted in 1998; while metacarpal and metatarsal measurements were taken from specimens hunted in 1984.

A total of 262 adult specimens of both sexes were studied (Table 1) of which 170 were from *R. t. tarandus* and 92 from *R. t. platyrhynchus* (Table 1). Teeth of all populations were analyzed through linear measurements ($N = 214$), while only two populations from Continental Norway were studied with a GMM approach ($N = 74$). Metapodes (metacarpal: $N = 126$, and metatarsal: $N = 124$) of four of the six groups of specimens, continental populations or subpopulations for Svalbard reindeer were studied (Table 1).

2.3 Data acquisition

2.3.1 Linear measurements and log shape-ratio: Our methodology based on skeleton measurements followed a published protocol ensuring comparability with other available data (Kuntz 2011), mainly inspired by previous well-defined measurements described by von den Driesch (1976).

Linear measurements were taken from lower cheek teeth at the tooth neck, metacarpals and metatarsals. Only two measurements (breadth and length, Figure 2A) were acquired from premolars (P_2 , P_3 and P_4), and from the third molar (M_3): L, length; and B, breadth. But three measurements were acquired from the first and second molars (M_1 and M_2 , Figure 2B): length (L); distal (Bd) and medial breadth (Bm). Lower cheek teeth measurements (exclusively made on permanent teeth) were taken at the tooth neck (at the very bottom of the crown), meaning that resulting data are less susceptible of age variations. All measurements on Forollhogna's teeth were measured by O. Bignon-Lau (O.B.-L.), while all other measurements were taken at least two times by F. Yu with the same vernier caliper as used by O.B.-L.

Table 1: Number of reindeer specimens studied per skeletal element, subspecies (*Rangifer t. tarandus*, *Rangifer t. platyrhynchus*) and the six populations or subpopulations in the case of Svalbard reindeer.

Subspecies	<i>Rangifer t. tarandus</i> ($n = 170$)						<i>Rangifer t. platyrhynchus</i> ($n = 92$)					
	Continental Norway						Island of Spitsbergen, Svalbard					
Localisation												
Population	Forollhogna ($n = 52$)		Hardangervidda ($n = 69$)		Knutshø ($n = 49$)		Colesdalen ($n = 32$)		Grøndalen ($n = 33$)		Sassendalen ($n = 27$)	
Gender of specimens	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Teeth – linear measurements	27	21	30	35	17	28	10	13	7	11	6	9
Teeth – GMM	0	0	28	20	15	11	0	0	0	0	0	0
Metacarpal	0	0	49 ^a	0	0	17	12	12	19	16	10	
Metatarsal	0	0	50 ^a	0	0	16	12	13	20	15	10	

^aNot specified in Kuntz (2011).

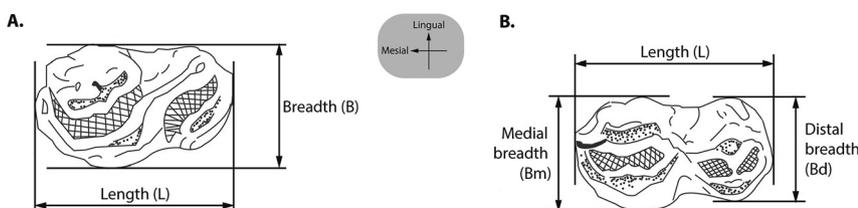


Figure 2: Occlusal view of measurements of reindeer mandibular cheek teeth. (A) Standards used for premolars P_2 , P_3 , P_4 and molar M_3 . (B) Standards used for M_1 and M_2 . Illustrated by A. Lau-Bignon and F. Yu.

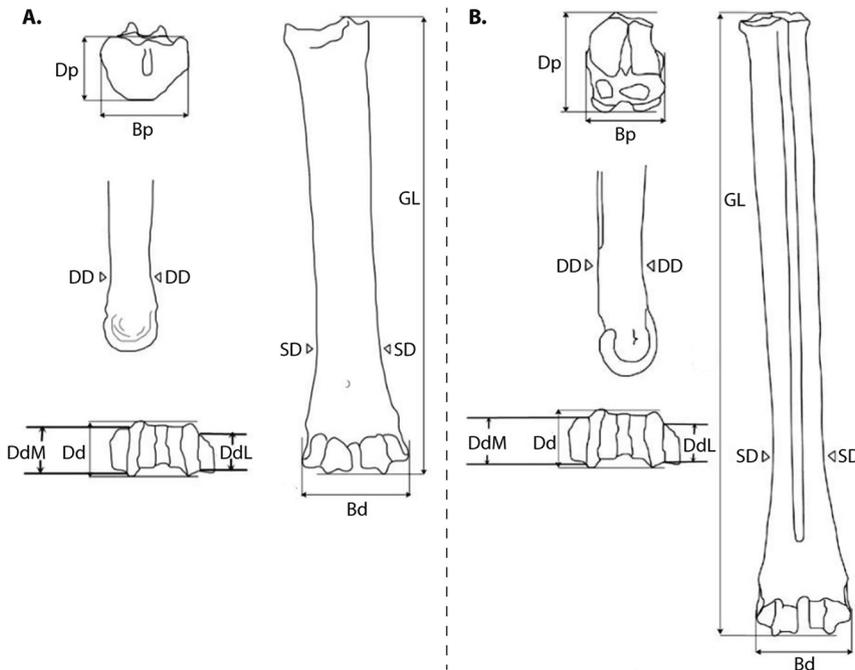


Figure 3: Measurements of reindeer's metacarpal (A) and metatarsal (B). Illustrations by Kuntz 2011, modified by F. Yu.

Nine variables were measured on metacarpals and metatarsals (Figure 3): Proximal antero-posterior diameter (Dp), proximal transversal diameter (Bp), smallest thickness of diaphysis (DD), distal antero-posterior diameter (Dd), distal mesial antero-posterior diameter (DdM), distal lateral antero-posterior diameter (DdL), distal transversal diameter (Bd), smallest breadth of diaphysis (SD), largest length (GL). Among these data of classical morphometrics, only metapodes from Hardangervidda were measured by Kuntz (2011), however this author did not measure the DdM and DdL.

Mosimann's log-shape ratios (LSR) (Mosimann 1970) were used to analyze separately the size and the shape of each tooth and bone. This analysis separates isometric size (i.e. the mean of the log-transformed measurements for each of the specimen) from shape ratio (i.e. the ratio of the logarithm of raw measurements and the corresponding isometric size), corresponding to univariate and multivariate data, respectively.

2.3.2 Geometric morphometrics (GMM): A landmark and sliding semi-landmark based GMM analysis were used to quantify the size and shape of M_1 . Analyses were performed in 2D on digital images using a Nikon 500 camera with Nikon lens AF-S ED micro Nikkor (60 mm). The occlusal surface of the teeth was set horizontally with a bubble level and in order to minimizing the amount of crown visible. A scale bar was included in all pictures. Left teeth were preferentially used, and alternatively, pictures of right teeth were mirrored to make them comparable.

The outline of the occlusal surface of each tooth was described using four landmarks (1–4 in Figure 4) and 60 sliding semi-landmarks (15 sliding semi-landmarks between each landmark). The shape of the mesial infundibulum was described using two landmarks (5 and 6; Figure 4) and 30 sliding semi-landmarks (15 for each side).

Coordinates were superimposed using a general Procrustes analysis (GPA; Rohlf and Slice 1990) using the Procrustes distance criterion for the sliding procedure. During this procedure, the centroid size (CS; Bookstein 1991) measures the dispersion of the landmarks around the centroid and is used as a size index, while the coordinate after the superimposition, called the Procrustes residuals, corresponds to shape data.

2.4 Statistical analysis

To give a descriptive and quantified analysis of the modern wild reindeer morphological diversity, we examined between-group differences in isometric and centroid sizes using Wilcoxon or Kruskal-Wallis, when two or more groups were compared respectively and visualized with boxplots. Shape data, corresponding to LSR or Procrustes residuals (coordinates after superimposition for GMM), were first explored by principal component analyses (PCAs) before applying Multivariate

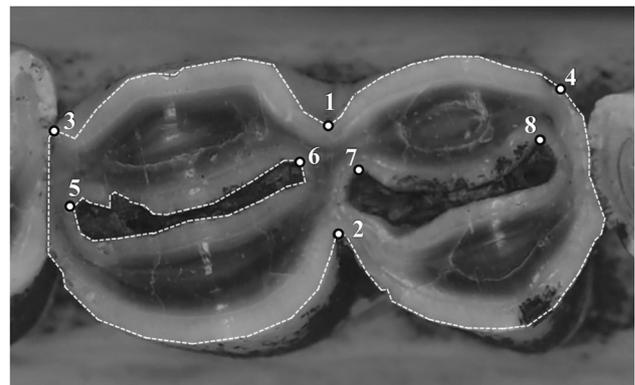


Figure 4: Geometric morphometrics protocol of the outline and the mesial enamel with the location of the eight landmarks (black dots) and the curve of sliding semi-landmarks (white dotted lines). Landmarks: 1-Lingual connection of paracone/metacone; 2-Buccal connection of protocone/hypocone; 3-Lingual/mesial crest of paracone; 4-Lingual/distal crest of metacone; 5-Lingual/mesial extremity of the first infundibulum (mesial half of molar); 6-Lingual/distal extremity of the first infundibulum (distal half of molar); 7-Lingual/mesial extremity of the second infundibulum (distal side); 8-Lingual/distal extremity of the second infundibulum (distal side). Photo/illustration by F. Yu.

analyses of Variance (MANOVAs) for comparing groups. When size or shape differences between groups were significant, discriminant analyses were performed. In addition, in order to visualize the dissimilarities in shape between the studied groups we performed neighbor joining networks built on the Mahalanobis distances obtained from the discriminant analyses. Because high number of variables can be misleading in LDA analyses (Kovarovich et al. 2011) the MANOVAs and discriminant analyses were performed on the first scores of the PCA maximizing the differences between the groups (Baylac and Friess 2005) following (Evin et al. 2013). The correct cross validation percentages (CVP) were provided as the mean CVP of 100 replicates of balanced samples and a 90 % confidence interval (CI) of the distribution (Evin et al. 2013). All analyses were performed in R 3.6.3 (R Core Team 2020) and mainly the package *geomorph* (Adams et al. 2019).

3 Results

3.1 Differences between subspecies

All anatomical parts (teeth, metatarsals and metacarpals) disclosed significant differences between the two subspecies based on log shape ratio data (Figure 5). The Svalbard reindeer had larger teeth regardless of the cheek tooth considered (Figure 5A, $W = 2880$, $p = 0.0001$), but smaller metacarpals (Figure 5B, $W = 2347$, $p = 0.001$) and metatarsals (Figure 5C, $W = 2238$, $p = 0.001$) than its continental counterpart. Log-shape-ratio sizes succeeded in correctly re-identified only 65.2 % (CI: 60.7–70.6 %) of the specimens based on their mandibles, 56.7 % (CI: 51.3–62.5 %) for the metacarpals, and 56 % (CI: 47.4–64.5 %) for the metatarsals. These low percentages reflect the large size overlaps between the two subspecies (Figure 5).

Moreover, while the principal component analysis of LSR teeth data (Figure 5A) revealed a complete overlap of the subspecies along the two first components (30.07 % and 19.3 % of the total variance, respectively), they however differed significantly ($F_{14,199} = 15.4$, $p \leq 2.2e-16$) with a correct CVP of 86.7 % (CI: 83–91.1 %).

On the other hand, PCA analyses of metatarsals and metacarpals showed that the two subspecies do not overlap on the two first PC axes (Figure 5B and 5C). The two subspecies clearly differ in their metapode shapes (metacarpals: $F_{7, 118} = 120.2$, $p \leq 2.2e-16$, metatarsals $F_{7,116} = 116.7$, $p \leq 2.2e-16$) with a CVP of 100 %.

3.2 Differences between populations

3.2.1 Teeth

Differences between populations were explored using both classical regression analyses and GMM. The Hardangervidda population was the only population that differed from the

others regarding its isometric teeth size (Table 2) and showed remarkably smaller teeth (Figure 6A and C). The six populations differed in shape (Table 2) with a cross validation of only 47.4 % (90 % CI: 38.8–54.4 %, i.e., well above the random cross validation since with six groups, the mean random CVP is 100/6). The dissimilarity network obtained from Mahalanobis distances (Figure 6B) revealed that the geographic origin of the populations structures the observed pattern, with the continental *R.t. tarandus* on one side of the network and the insular *R. t. platyrhynchus* subpopulations on the other side.

For the continental populations, the GMM approach provided congruent results with the specimens from Hardangervidda showing smaller M_1 than those from Knutshø (Figure 6C). The two first axes of the PCA (Figure 6D) showed a strong overlap between the two populations, with a greater variation among the specimens from Knutshø. The variation seems to reflect a proportionally less stretched mesial-distal shape of the distal side, as well as a more rounded buccal mesial side and a more developed lingual distal side (Figure 6E).

3.2.2 Metapodes

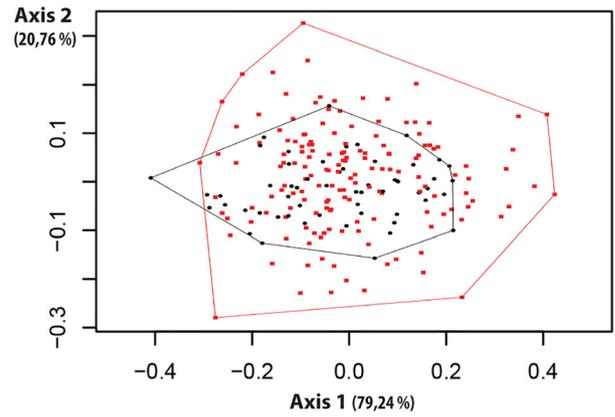
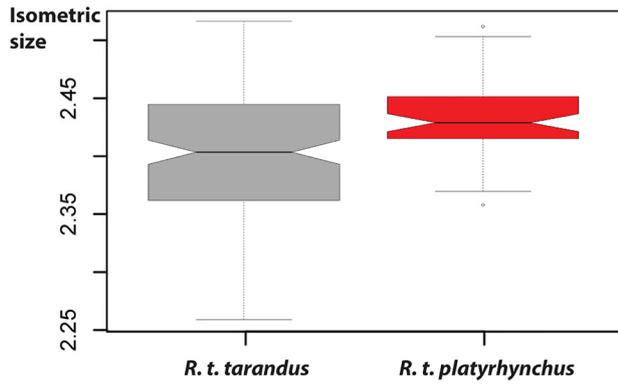
Four populations, three insular and one continental, were available for comparison of metatarsal and metacarpal metric data (Figures 7 and 8, Table 3). When raw measurements were compared to the single continental population from Hardangervidda, these data appeared slightly larger or of similar size than the insular populations, except for the smallest breadth of the diaphysis (SD) of both metapodials (Figures 7A and 8A, Table 3). The only measurement that fully discriminated between the insular and continental populations was the largest length (GL) of both metapodials. When measurements were combined using Log Shape Ratio, the proximal isometric size showed a greater overlap between populations than the distal isometric size (Figures 7B and 8B, Table 3), in agreement with observations on raw measurements. Analysis of shape variation (LSR) of both the metatarsal and metacarpal showed perfect discrimination between the continental and insular populations on the two first axes of the PCAs, that otherwise completely overlap (Figures 7C and 8C, Table 3).

3.3 Differentiation within populations: sexual dimorphism

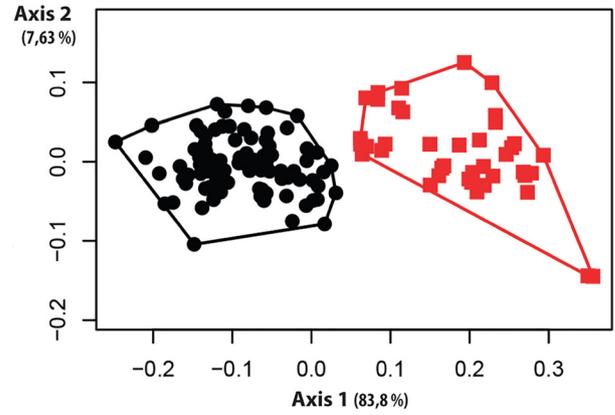
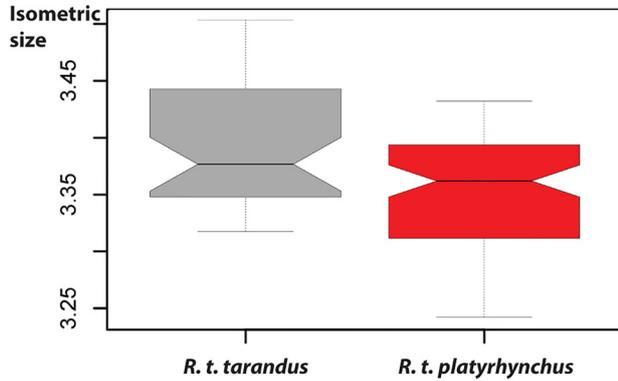
3.3.1 Teeth

Teeth measurements, captured by GMM, detected no sexual dimorphism neither in size nor in shape (all $p > 0.1$). Only the

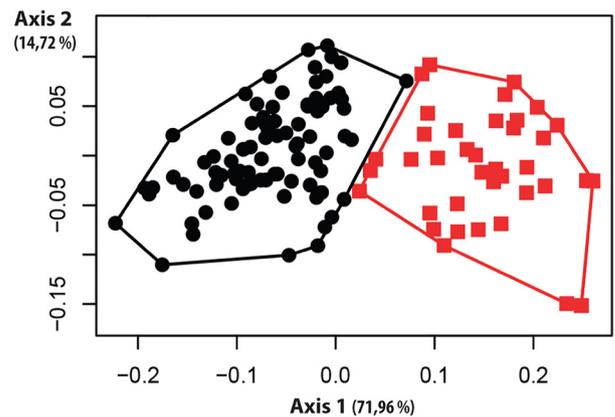
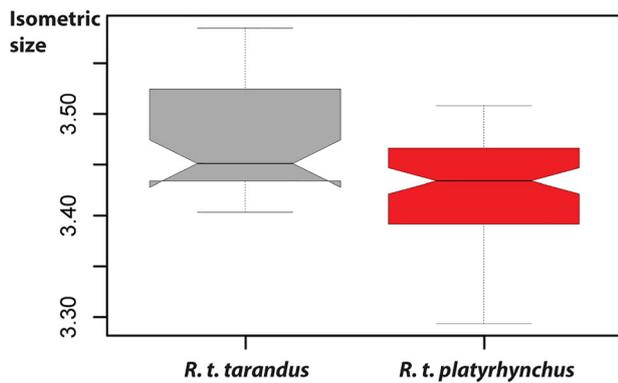
A.



B.



C.



● *R. t. tarandus* ■ *R. t. platyrhynchus*

Figure 5: Differences between the two subspecies based on size and shape extracted from the CLog Shape Ratio of linear measurements of lower cheek teeth, metacarpals and metatarsals. Boxplot of the isometric size (left) and visualization of the two first axes of the PCA of shape (right) based on teeth (A), metacarpals (B) and metatarsals (C).

Table 2: Differences in mandibular teeth between the 6 populations/subpopulations of reindeer located in the continental Norway mainland and the insular Svalbard archipelago.

	Colesdalen	Forollhogna	Grøndalen	Hardangervidda	Knushø	Sassendalen
Colesdalen	–	4.8e-19	8.8e-3	2.4e-8	1.1e-6	2.4e-2
Forollhogna	0.812	–	3.4e-13	4.8e-15	1.1e-17	9.3e-11
Grøndalen	0.948	0.972	–	1.3e-13	2.7e-7	4.1e-2
Hardangervidda	2.00E-10	4.4e-15	9.7e-8	–	3.7e-5	3.1e-6
Knushø	0.278	0.275	0.541	3.2e-11	–	6.4e-4
Sassendalen	0.073	0.089	0.166	1.4e-6	0.520	–

Isometric size (below the diagonal) and shape (Log Shape Ratios, above the diagonal) pairwise differences. p-Values of Wilcoxon-tests for size and of Manovas for shape. p-Values <0.05 in bold.

population from Forollhogna showed significant sexual size dimorphism, with the males being larger than the females (Table 4). All other size and shape comparisons between males and females were not significant (Table 4).

3.3.2 Metapodes

Unlike teeth, metapodials showed strong sexual size dimorphism (Table 5), with the males being larger than females (Figure 9). Only the subpopulation from Sassendalen showed non-significant sexual size dimorphism in metatarsal size, while males had larger metacarpal than females. Only the subpopulation from Grøndalen showed sexual dimorphism in metatarsal shape (Table 5), all the other shape comparisons were non-significant.

4 Discussion

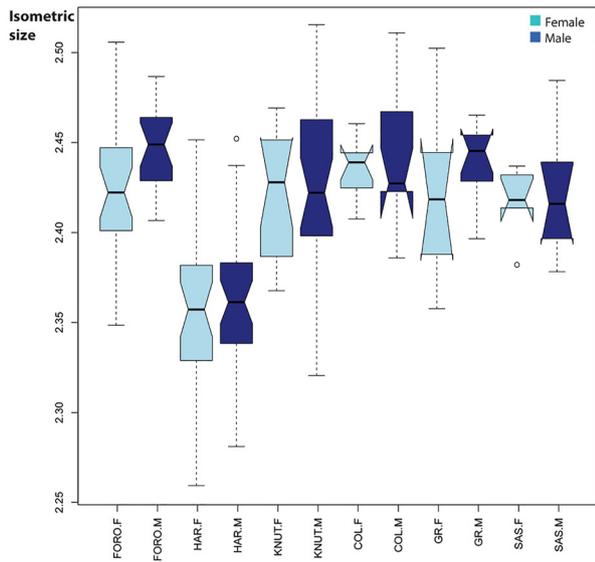
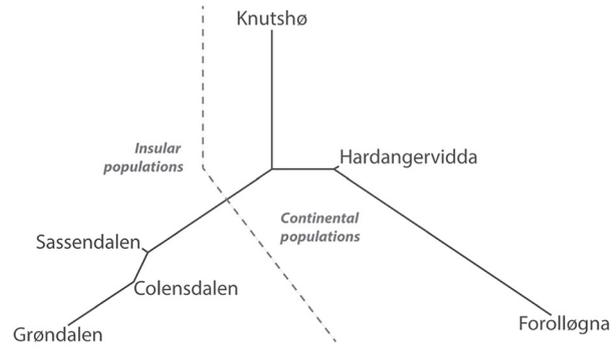
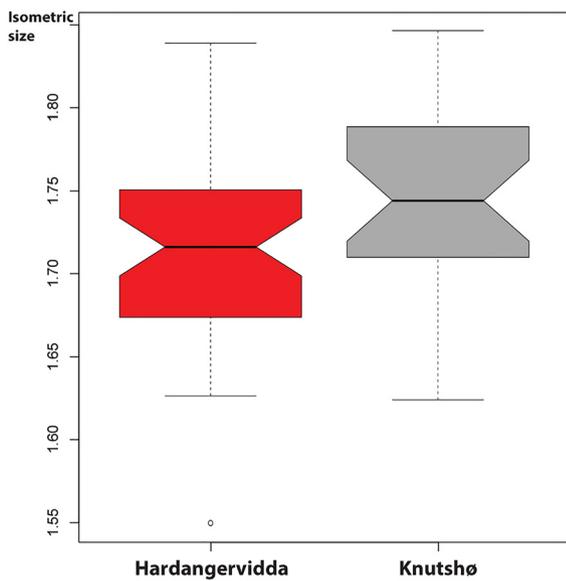
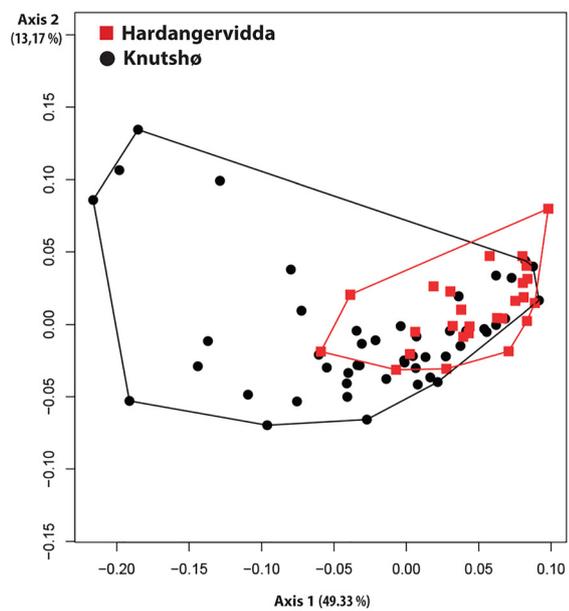
We examined osteological morphometric variation of two subspecies of reindeer from continental Norway and insular Svalbard using two complementary methods (linear morphometrics and GMM). These two datasets (mainland and island) are however separated by three decades. When both methods were applied to the same anatomical structure (e.g., teeth), the between groups differentiation in size and shape was highly consentaneous. Moreover, the application of GMM showed greater potential than ‘traditional’ approaches in morphometric studies to assess both within and between population differences. Especially, the possibility of visualizing shape differences provides a new way for discussing the morphology of animals in both future biological and archaeological studies. Our study complements recent studies, aiming at studying reindeer domestication, on the shape and shaft of the cortical thickness of long limb bones (Pelletier et al. 2021a) using 2D GMM, and the size and shape of forelimb (Pelletier et al. 2020) and hindlimb (Pelletier et al.

2021b) long bones using 3D GMM, or lower mandibular teeth 2D GMM (Pelletier et al. 2023).

A remarkable phenomenon should be noticed, the insular Spitsbergen subspecies (*R. t. platyrhynchus*) has smaller metapodials, but a larger mandibular dentition compared to the continental Norwegian subspecies (*R. t. tarandus*). The only measurement showing smaller values for the continental subspecies is the smallest breadth of the diaphysis (SD), which is known to be greatly influenced by the way the measurement is acquired (i.e., positioning of the caliper; Kuntz 2011). In our study, the measurements of the Hardangervidda population came from published data (Kuntz *ibid.*), contrary to the other measurements that were acquired specifically for this study. It would therefore be of prime interest to confirm this trend by acquiring additional continental data.

Ecological studies have found that Svalbard reindeer possess a smaller, compressed body size due to extreme climate and the limited need for movement (Hansen et al. 2010; Meland 2014; Pedersen et al. 2018; Skogland 1989; Tyler and Øritsland 1989). Without the need to migrate or to hide and escape from polar bears predation (Derocher et al. 2000; Pedersen et al. 2019; Stempniewicz et al. 2021), they are short-legged, and this specialty of size is reflected by the morphology of the metapodes. Meanwhile, this observation reminds us that the body size of animals commonly affects limbs, while the cranial parts can be partly disjunct.

Furthermore, the three insular subpopulations showed similarities in their dentition and metapodials. On the contrary, the three continental populations present more differentiation, particularly in the dental shape. To discuss this distinction, the geographical distance between populations are important to considered. In the case of Spitzbergen, the three subpopulations of reindeer living in neighboring valleys, within only one hundred kilometers apart, are part of the same population (Côté et al. 2002; Peeters et al. 2020). However, the continental populations have a wider range, with seasonal migrations and dispersion (Geist 1999;

A.**B.****C.****D.****E.**

— Hardangervidda
— Knutshø

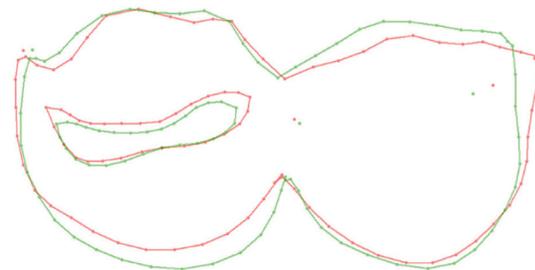
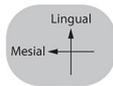


Figure 6: Differences of teeth between populations/subpopulations based on size and shape extracted from Log Shape Ratio (LSR) for the three populations (studied) in continental Norway (Knutshø, Forolløgna, Hardangervidda) and three populations in Svalbard (Grøndalen, Colesdalen, Sassendalen). (A) Boxplot of the isometric size, (B) network analysis of phenotype of shape based on LSR, (C) boxplot of centroid size, (D) two first axes of the PCA of geometric shape, and (E) visualization of mean shape differences.

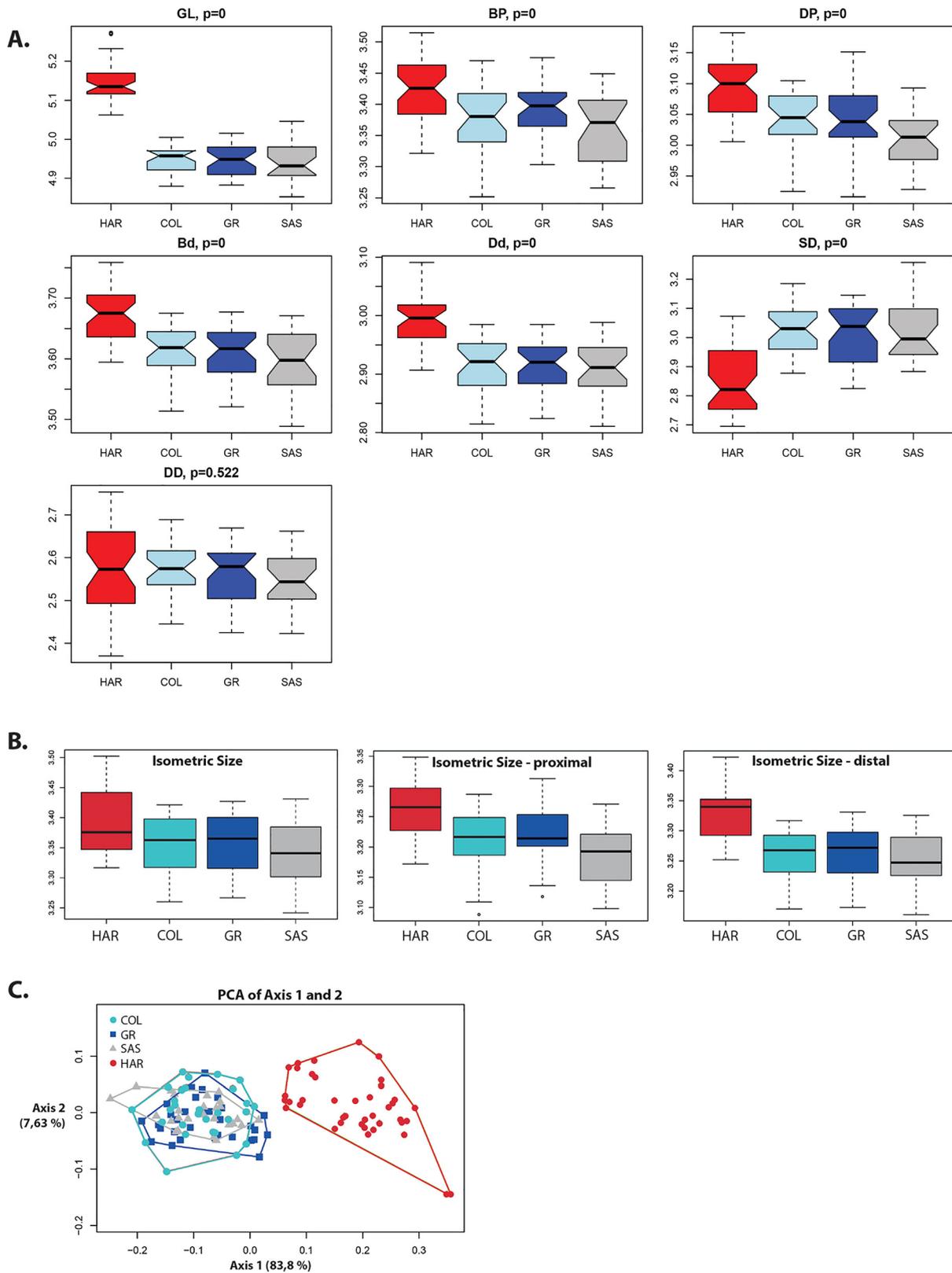


Figure 7: Between subpopulations/population differences in metacarpal size and shape. Boxplots of (A) the osteometric raw measurements (see Figure 3), (B) isometric size, and (C) two first axes of the PCA of Log Shape Ratio. HAR, Hardangervidda; COL, Colesdalen; GR, Grøndalen; SAS, Sassendalen; GL, largest length; SD, smallest breadth of diaphysis; BP, proximal transversal diameter; DP, proximal antero-posterior diameter; DD, smallest thickness of diaphysis; Bd, distal transversal diameter; Dd: distal antero-posterior diameter.

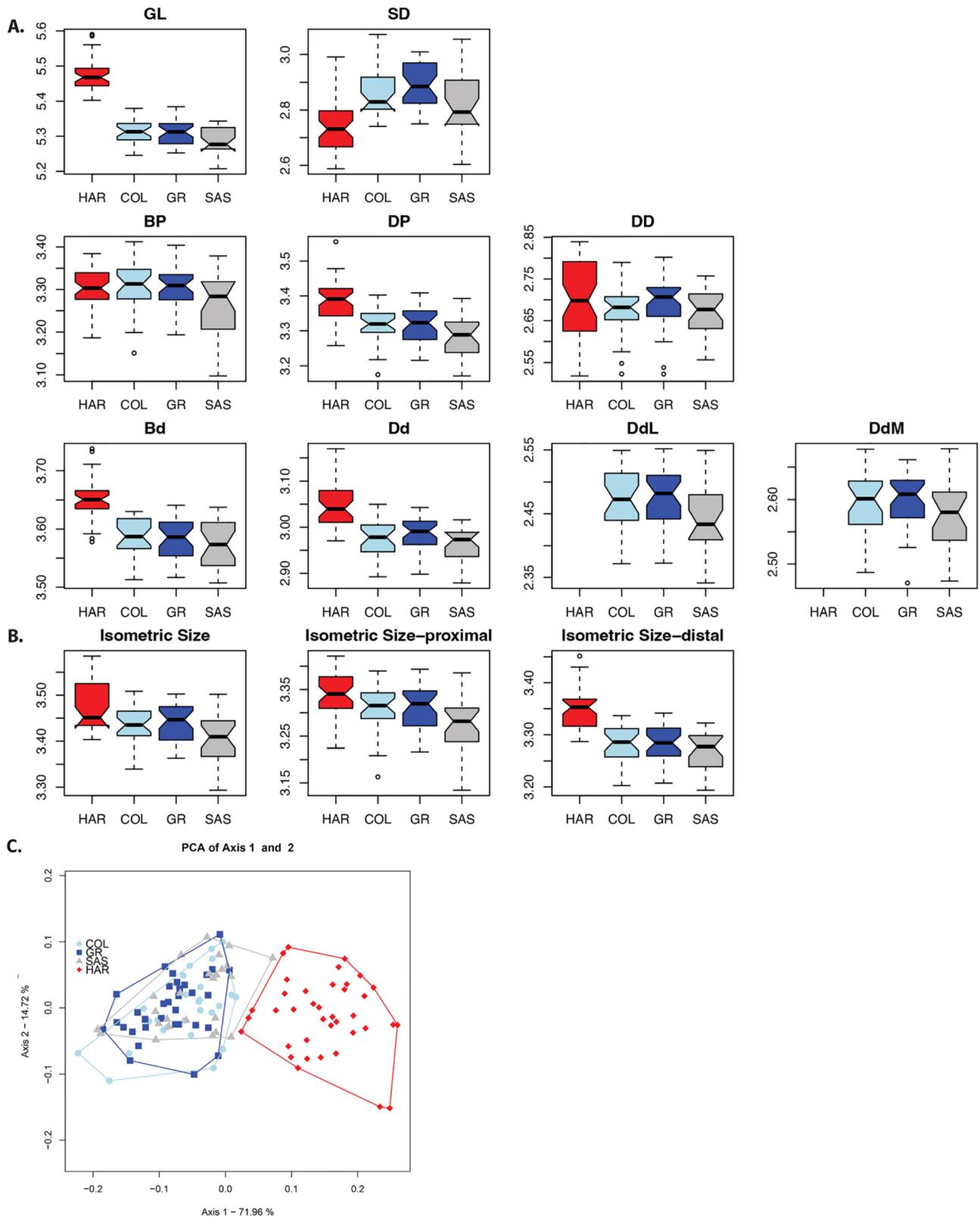


Figure 8: Between subpopulations/population differences in metatarsal size and shape. Boxplots of (A) the osteometric raw measurements (see Figure 3), (B) isometric size and (C) two first axes of the PCA of Log Shape Ratio. HAR, Hardangervidda; COL, Colesdalen; GR, Grøndalen; SAS, Sassendalen; GL, largest length; SD, smallest breadth of diaphysis; BP, proximal transversal diameter; DP, proximal antero-posterior diameter; DD, smallest thickness of diaphysis; Bd, distal transversal diameter; Dd, distal antero-posterior diameter; DdL, distal lateral antero-posterior diameter; DdM, distal mesial antero-posterior diameter.

Table 3: Pairwise comparison of continental populations and insular reindeer subpopulations in isometric size and Log Shape Ratio for the distal and proximal parts of the metatarsal and metacarpal.

	Proximal						Distal									
	Hardangervidda ^a		Colesdalen		Grøndalen		Sassendalen		Hardangervidda ^a		Colesdalen		Grøndalen		Sassendalen	
Metacarp	Hardangervidda ^a	-	0.40141	0.00089	0.00451	-	0.012	0.024	0.066							
	Colesdalen	0.00018	-	0.02263	0.08285	1.9e-7	-	0.573	0.478							
	Grøndalen	0.00045	0.65390	-	0.72177	1.9e-7	0.99	-	0.670							
Metatars	Sassendalen	5.7e-6	0.12495	0.04323	-	1.9e-7	0.60	0.60	-							
	Hardangervidda ^a	-	1.2e-14	1.2e-14	7.3e-10	-	0.35	0.83	0.34							
	Colesdalen	0.023	-	0.83	0.83	7.7e-8	-	0.34	0.64							
Sassendalen	Grøndalen	0.023	1	-	0.87	5.5e-8	0.75	-	0.34							
	Hardangervidda ^a	4.2e-5	0.023	0.023	-	3.2e-8	0.25	0.1	-							

p-Value of the size comparisons are in the lower hemi-matrices while the p-values for LSR comparisons are in the upper hemi-matrices. Significant p-value are presented in bold. p-Value were corrected for multi-test comparison for each pairwise analysis separately. ^aContinental population. Bold values mean significant tests.

Table 4: Test of sexual dimorphism in mandibular teeth size and shape for each of the six populations/subpopulations (significant statistical results (p < 0.05) are presented in bold).

Subspecies	Morphometric parameters			Shape		
	Tests	W	p	F	p	
Continental reindeer <i>Rangifer t. tarandus</i>	Forollhogna	155	0.007	0.77858	0.5708	
	Hardangervidda	499	0.7389	0.66636	0.6504	
	Knutshø	223	0.737	0.92948	0.4725	
Insular Svalbard reindeer <i>Rangifer t. platyrhynchus</i>	Colesdalen	68	0.8793	1.3164	0.3037	
	Grøndalen	25	0.2463	1.042	0.4372	
Sassendalen	27	1	2.0517	0.1646		

Results of Wilcoxon test (W statistic and p-value) for size and manova (F statistic and p-values) for shape. Bold values mean significant tests.

Table 5: Sexual dimorphism in metacarpal and metatarsal size and shape of the three insular Svalbard reindeer subpopulations.

Skeletal elements	Metacarpal				Metatarsal			
	Size		Shape		Size		Shape	
	W	p	F	p	W	p	F	p
Colesdalen	36	0.002	0.58	0.76	39	0.007	1.32	0.28
Grøndalen	65	0.048	2.23	0.069	51	0.002	3.48	0.009
Sassendalen	29	0.006	0.58	0.76	58	0.37	0.37	0.9

Results of Wilcoxon test (W statistic and p-value) for size and manova (F statistic and p-values) for shape. Bold values mean significant tests.

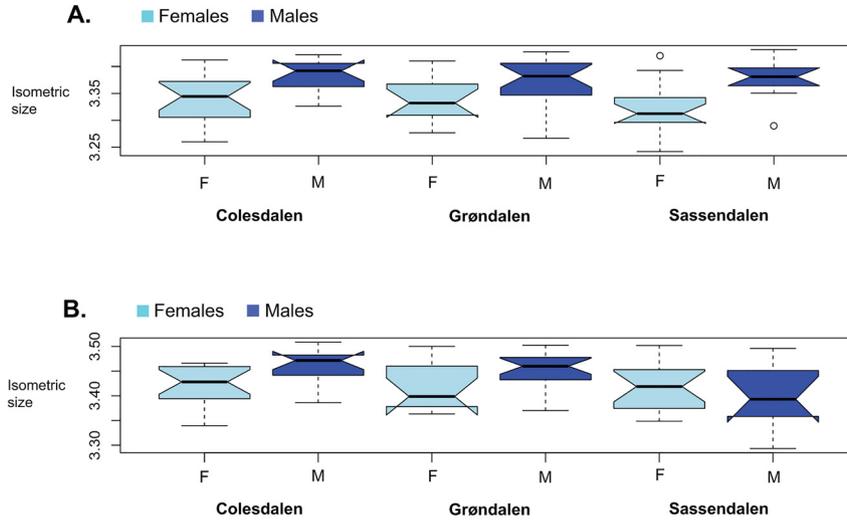


Figure 9: Differences of metapodes between genders based on size and shape extracted from Log Shape Ratio from Svalbard reindeer. Boxplot of the isometric size based on metacarpals (A) and metatarsal (B). p-Value of the tests comparing two genders are mentioned in posterior Table 5.

Skogland 1989). For this reason, it is possible that the distance between the habitats or distribution areas of the different populations influence the degree of their morphological differences, and potentially their degree of genetic exchanges. Populations living closer show more morphometric similarities, as in the case of the high-Arctic populations. Further, the only population that could be discriminated by its dental size was the Hardangervidda population. Though establishing the causality behind the comparatively smaller size of this population is only speculative, the Hardangervidda population experience different ecological condition, particularly related to relatively high population density and unstable resource of alimentation (Skogland 1984, *ibid.*; Tveraa et al. 2007).

At last, the morphometric discrimination between males and females is limited to size, with no noticeable shape dimorphism. In addition, microwear textural analyses confirmed that in the populations from Hardangervidda and Knutshø, males and females possessed different food habits during the summer-autumn period (Bignon-Lau et al. 2017), yet the morphometrics of dentition did not confirm this distinction, neither by classical morphometrics nor by GMM.

Nevertheless, the metapodial size only partially differs between genders. While some population exhibit a sexual dimorphism (e.g. Colesdalen, Grøndalen), the population of Sassendalen does not exhibit size differences between male and females. Considering that male reindeer usually has a larger body size than female, this sexual divergence deserves further investigations in both modern and archaeological populations to explore this differential sexual dimorphism in the skeletal elements and the differences between the populations.

5 Conclusions

The present research examined the morphometry of mandibular teeth and metapodials of modern insular Svalbard and continental Norway reindeer populations. We found that the variability of teeth morphology (namely isometric size) may have involvements for reindeer' feeding habits, as future dental microwear texture analyses will discuss it. We also found a positive relation between the metapodials and the teeth: we showed that insular reindeer

have smaller body size than continental reindeer, but conversely, have bigger lower cheek teeth.

This paper is demonstrating that GMM of reindeer teeth could be very useful for future studies (but see Pelletier et al. 2023; Rødven et al. 2006). As a main target in the hunter-gatherer societies, reindeer remains are widely discovered in paleolithic sites, particularly in Western Europe. Therefore, the differences between subspecies, populations, and genders quantified here, can certainly be used as an inspiration and standard in further archeozoological research.

Research ethics: No animals were handled or disturbed during this work. Observed specimens are listed in Annexes with their institutional reference numbers. We have worked with responsible of key Norwegian institutions (Natural History Museum, Oslo; Northern Norwegian Polar Institute, Tromsø; Norwegian Institute for Nature Research) in order to associate them in the research process.

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Data availability: Not applicable.

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Supplementary Material: This article contains supplementary material (<https://doi.org/10.1515/mammalia-2023-0004>).