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Unveiling the Past: Exploring the Archaeology of Reindeer Domestication in Northern Fennoscandia through Geometric Morphometrics

For centuries, reindeer herding has been an integral part of the lifeway, socio-economy, and cosmology of the Indigenous Sámi of northern Fennoscandia. Despite its importance, the timing and details of reindeer domestication and early reindeer management remain unclear. Identifying domestic individuals in archaeological records remains challenging due to the presence of two interbreeding subspecies in Fennoscandia and a mixed socio-economic organisation of Sámi societies, which mainly combined wild reindeer hunting and small-scale reindeer herding. In recent decades, methodological advances in geometric morphometrics (GMM) have opened up new perspectives for studying domestication from archaeological records. This review summarises recent GMM research on reindeer domestication and examines its potential for the archaeological contexts of northern Fennoscandia. Considering analyses of reindeer bones and teeth, these studies offer valuable insights into changes in mobility and feeding behaviours induced by the domestication process, as well as the origins of domestication and early herd management strategies, contributing to the reconstruction of socio-economic changes within Sámi societies over time.

Menneisyyden paljastaminen: Porojen domestikaation tutkiminen pohjoisen Fennoskandian alueella geometrisen morfometrian avulla

Poronhoito on ollut satojen vuosien ajan keskeinen osa pohjoisen Fennoskandian alkuperäiskansan, saamelaisten, elämäntapaa, sosiaalitaloutta ja kosmologiaa. Merkittävyydestään huolimatta porojen domestikaation ja varhaisen hoidon ajoitus sekä yksityiskohdat ovat edelleen epäselviä. Kesytettyjen yksilöiden tunnistamista arkeologisesta aineistosta vaikeuttavat Fennoskandian alueella esiintyneet ja risteytyneet kaksi eri alalajia sekä saamelaisten yhteisöjen joustava sosiaali-

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taloudellinen järjestelmä, jossa yhdistyivät pääasiassa villipeurojen metsästys ja pienimuotoinen poronhoito. Viime vuosikymmeninä metodologiset edistysaskeleet geometrisessä morfometriassa (GMM) ovat mahdollistaneet uusia näkökulmia domestikaation tutkimukseen arkeologisen aineiston pohjalta. Tämä katsaus kokoaa yhteen uutta GMM-tutkimusta porojen domestikaatiosta ja arvioi sen soveltuvuutta pohjoisen Fennoskandian arkeologisiin konteksteihin. Porojen luiden ja hampaiden analyysien kannalta nämä tutkimukset tarjoavat valaisevaa tietoa domestikaatioprosessista johtuneista muutoksista liikkuvuudessa ja ravinnonkäytössä sekä jalostuksen alkuperästä ja varhaisista laumanhoitostrategioista. Nämä havainnot edesauttavat saamelaisyhteisöjen sosiaalitaloudellisten muutosten rekonstruointia aikojen saatossa.

Introduction

Evolution and Socio-Economic Dynamics of Reindeer Domestication in Fennoscandia

Since the Palaeolithic Age, the reindeer (*Rangifer tarandus Linnaeus*, 1758), one of the most emblematic species of Arctic ecosystems, has had a considerable impact on the lifestyles, economies, cultures, and cosmologies of numerous human societies across northern Eurasia. Initially, it was highly valued as prey for prehistoric societies, whose material cultures, hunting practices, and subsistence strategies varied widely depending on geographical location, local environment, and the behaviour of reindeer populations. In Fennoscandia, wild reindeer were hunted upon their arrival in these new territories during climatic warming and glacier melting, from the Mesolithic period until the early 19th century (e.g., Rankama & Ukkonen 2001; Halinen 2005; Helskog 2011). Meanwhile, an important event marked a turning point in the evolutionary and biogeographical history of the reindeer, as well as in the socio-economic and cultural dynamics of northern human societies: the advent of reindeer domestication. Genetic data suggest two main independent centres of reindeer domestication in Eurasia; one in northern Fennoscandia and the other in western Siberia (Røed et al. 2008, 2011). However, a notable genetic shift in the 16th and 17th centuries indicates the introduc-

tion of non-native reindeer to northern Fennoscandia during this period, implying that the maternal lineage of modern domestic reindeer herds in Fennoscandia originates from Siberia (Røed et al. 2018).

The earliest material evidence of reindeer management, such as sled runners (Murashkin et al. 2016) or harness parts (Losey et al. 2021), has been found in Siberia around 1500 BCE and 200 BCE, respectively. However, direct archaeological evidence of this nature is lacking in Fennoscandia during the initial stages of reindeer domestication. It is widely accepted that reindeer domestication gradually emerged in Fennoscandia from the Late Iron Age onwards, around 800–900 CE (Hansen & Olsen 2014), or perhaps even earlier around 600–700 CE (Salmi 2023) (Figure 1). Apart from the tentative mention of "domesticated" reindeer in historical documents, such as the account of the Norwegian navigator Ohthere of Hålogaland to King Alfred the Great of the Anglo-Saxon Kingdom of Wessex around 890 CE (Bately 2007), little is known of the reindeer-herding practices in this early stage. The utilisation of reindeer for transportation likely played a pivotal role in its domestication in these regions, particularly for transhumance and extensive trade. Some archaeological evidence, such as the analysis of habitation sites, also suggests early domestication around 800–1000 CE in the Scandinavian Mountains (i.e., on the high fells of Norway and Sweden), and approximately 800–1300 CE in northern Fennoscandia (Bergman et al. 2013; Seitsonen & Viljanmaa 2021). Nevertheless, direct evidence of domestication from fossilised reindeer remains is not evident until the late 13th century in northern Fennoscandian archaeological sites (Salmi et al. 2020a, 2021; Salmi 2023).

The gradual transition to reindeer herding and larger-scale nomadic pastoralism appears clear between 1400 and 1600 CE, where it became the basis of social organisation (Itkonen 1948; Kortesalmi 2008; Bergman et al. 2013; Hansen & Olsen 2014; Salmi et al. 2018; Salmi 2023). This transition, driven by various socio-economic factors such as colonial policies of emerging nation-states in southern Fennoscandia, intensified fur trade, or the expansion of Christianity, led to profound cultural changes in local societies (Hansen & Olsen 2014; Salmi et al. 2018; Salmi 2023). This was further exacerbated by the gradual disappearance of wild reindeer populations in northern Fennoscandia in the early 19th century (Figure 1). However, different stages in the development of herding at the expense of hunting may also have occurred during ecological instabilities and demographic declines of wild reindeer herds (Ingold 1986), following major climate fluctuations such as

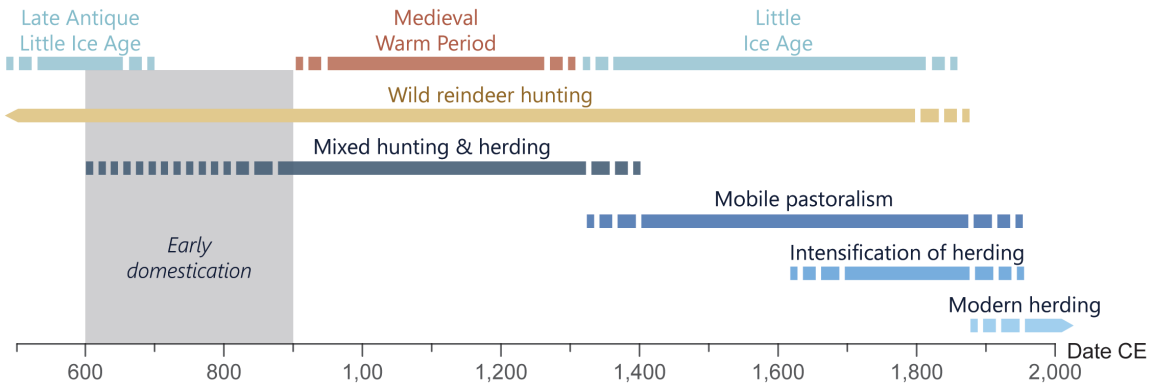

Figure 1. Chronology of the development of reindeer herding among the Sámi of northern Fennoscandia (Modified from Salmi 2023).

the Late Antique Little Ice Age (ca. 536–660 CE), the Medieval Warm Period (ca. 950–1250 CE) or the subsequent Little Ice Age cooling (ca. 1350–1850 CE) (Figure 1). Archaeologically, this transition has been evidenced through various data such as habitation structures (Bergman et al. 2013; Seitsonen & Viljanmaa 2021), the presence of harness or sled parts (Carpelan 1991, 1993), zooarchaeological studies (Harlin et al. 2019), stable isotope analysis (Salmi et al. 2015, 2020a; Fjellström et al. 2020), ancient DNA (Bjørnstad et al. 2012; Røed et al. 2018; Salmi & Heino 2019; Heino et al. 2021), and activity markers (Salmi et al. 2021).

Methodological Challenges and Innovations in Reindeer Domestication Studies

The discrepancy between historical sources (i.e., from the 9th century) and the earliest direct osteo-archaeological evidence on reindeer remains (i.e., from the 13th century) of the initial use of domesticated individuals by local human societies is explained by several obstacles encountered by archaeologists thus far:

- Fennoscandia is home to two subspecies of wild reindeer, the mountain reindeer (*R. t. tarandus*), inhabiting mainly the mountain regions (i.e., alpine

zone) of southern Norway, and the forest reindeer *(R. t. fennicus*), occupying the middle boreal zone (i.e., closed forest) in southern Finland. Semi-domestic reindeer, on the other hand, have been selected from wild mountain reindeer lineages (Røed et al. 2018), and are now distributed throughout Lapland in the high boreal (i.e., northern boreal/taiga zone) and alpine zones. While the two wild subspecies no longer naturally coexist in the landscape, and their overlapping ranges with semi-domestic lineages are very limited, the geographical distribution of these different populations was likely significantly different in the past compared to today. Wild mountain reindeer were found until the mountainous regions of northern Fennoscandia and wild forest reindeer were found throughout the taiga zone of central and northern Finland (Helle 1982). Until recently, osteological markers used to identify the two subspecies relied on specific characteristics of cranial elements or linear measurements on the postcranial skeleton of modern specimens (Nieminen & Helle 1980; Hakala et al. 1996; Puputti & Niskanen 2009). However, these methods are difficult to apply in the case of remains found in archaeological contexts where bones are often fractured to extract marrow.

- Prior to the transition to a reindeer-herding culture, Indigenous Sámi populations maintained their nomadic hunting, fishing, and gathering traditions, while engaging in small-scale reindeer herding. They possessed only small groups of semi-domesticated individuals used as decoys for wild reindeer hunting. Some male reindeer also performed various domestic tasks – such as pulling sledges during transhumance periods or carrying trade goods – while female reindeer could be used for milking (Tegengren 1952; Aronsson 1991; Korhonen 2008). These particular individuals had to be tamed and kept near the settlements under fairly close supervision by nomadic herders, rather than being kept in corrals. Thus, herders likely deliberately allowed wild reindeer to crossbreed with semi-domesticated individuals to prevent consanguinity (Sommerseth 2011). Furthermore, there was considerable geographic variation in the timing of the adoption and intensification of reindeer herding (Tegengren 1952; Sommerseth 2011; Bjørklund 2013; Salmi et al. 2018; Salmi 2023), such that no abrupt shift from hunting to pastoralism could be identified from the archaeological record, making it difficult to precisely identify the beginnings of reindeer domestication.

- Traditional methods used in zooarchaeology such as osteometry or activity markers have shown their limitations in identifying key moments at the onset of the reindeer domestication process. New protocols and methodological approaches have recently been developed to overcome these constraints and better exploit and interpret data from archaeological contexts in Fennoscandia. The emergence of cutting-edge techniques, such as stable isotope analysis and ancient DNA, has significantly advanced this field in recent years. However, these methods require specific study protocols and platforms, often expensive and not always straightforward to implement for the study of Sámi archaeological material (e.g., conservation of Sámi archaeological heritage and authorisation requests for sample destruction). Regardless of the method used, they have only benefited from extremely recent research dynamics and, for now, have only been applied to a few rare historical Sámi sites in northeastern Fennoscandia. Additionally, it is highly probable that reindeer herding is older and originated in the mountainous regions of Scandinavia rather than northeastern Fennoscandia (Wallerström 2000; Bergman et al. 2013; Heino et al. 2021).

The challenge of distinguishing semi-domesticated specimens in archaeological sites currently hinders the clear identification of the periods and main centres of the early reindeer domestication in Fennoscandia. To address these methodological challenges, recent advances in archaeological research have increasingly turned to geometric morphometrics as a powerful tool for analysing morphological variations in biological structures. This notably enables better detection of the early signs of phenotypic divergence related to the domestication process. This article aims to present the seminal works in geometric morphometrics on reindeer remains, highlighting new protocols, along with four examples of applications in the field of reindeer domestication, and their potential for studying archaeological contexts in northern Fennoscandia.

Geometric Morphometrics in Archaeology: Concepts and Methods

Morphometrics, a key tool in phenomics, explores variations in the geometry of biological forms and their correlation with other biological or ecological variables (Evin et al. 2022). The advancement of morphometrics in

recent decades, embodied by geometric morphometrics (GMM), allows for a comprehensive analysis of morphological changes in multidimensional spaces (Rohlf & Marcus 1993). By replacing the independent measurements of lengths or angles in 'traditional' morphometrics with point coordinates, GMM captures the geometric complexity of objects, facilitating precise visualisation of form differences (Bookstein 1991). The notion of form in morphometrics encompasses both size and shape, with the relationship expressed as 'form = size + shape' (Baylac 1996; Klingenberg 2016). Traditional morphometrics, however, suffers from varying definitions of size, described by different parameters (e.g., length, perimeter, etc.), and only a partial representation of shape, underestimating its geometric complexity. The evolution of GMM addresses these conceptual and methodological limitations, aiming to maximise biological information, better dissect size and shape components, and visualise shape variation more accurately.

Thus, GMM defines form of an object through a set of measured coordinates of points, referred to as landmarks. One of the main approaches in GMM used in zooarchaeology involves the use of the method of homologous landmarks and/or contour or surface sliding points (semilandmarks). Landmarks can be of several types: 1) Type I corresponds to strictly homologous anatomical structures (e.g., intersection of bone sutures); 2) Type II marks homology supported by geometry (e.g., maximum curvature); and 3) Type III geometric construction depends on other landmarks or specimen orientation (e.g., semilandmarks). Type I and II landmarks are generally preferred in studies because they offer better reproducibility (Bookstein 1991). The size of the object is specifically determined by the centroid size across all these landmarks. This centroid size is calculated as the square root of the sum of the squares of distances between the object's centre of gravity and each of these landmarks.

Shapes are then obtained by normalising the superimposed coordinates by this individual size, thus enabling the distinction of the intrinsic proportions of the object's geometry, regardless of its size, position, or orientation. This method is based on the concept of Procrustes superimposition, which aims to place all objects in the same morphological space (Figure 2). To achieve this, Procrustes superimposition consists of three distinct steps: 1) Translation of all configurations of homologous landmarks of the sample to their centroid, thus eliminating position effects; 2) Normalisation of all sample configurations to share the same centroid size, thereby preserving object proportions while neutralising size effects; and 3) Rotation of all

landmark configurations around their centroid to minimise distances between pairwise homologous landmarks, thereby eliminating rotation variations and minimising differences between all objects. The new Cartesian coordinates of the landmarks obtained after Procrustes superimposition are called Procrustes shape coordinates. The average of these coordinates represents the mean shape (consensus), while the distances between two sets of Procrustes coordinates in the shape space, called Procrustes distances, allow quantifying and visualising the similarity or dissimilarity between two or more shapes (Figure 2).

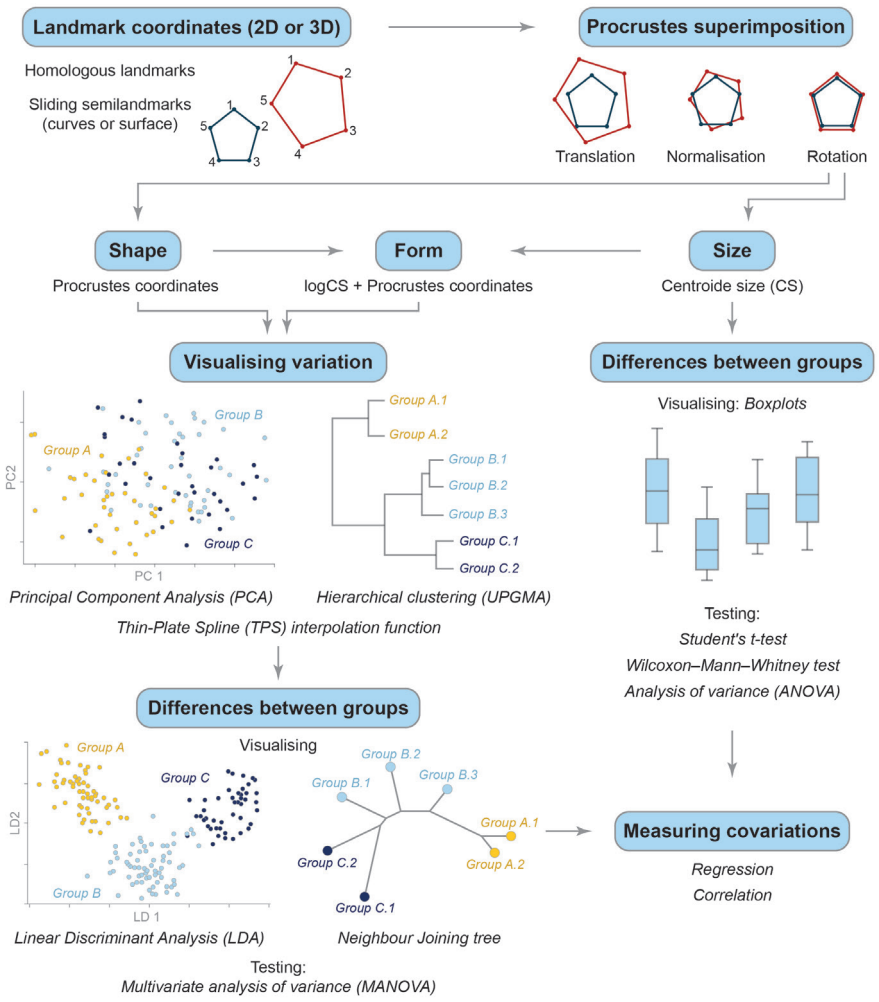

Figure 2. Statistical analysis of GMM data (Modified from Cucchi et al. 2015).

Then, two modes of graphical visualisation of shape differences can be used: one based on differences between superimposed point coordinates, and the other on thin plate splines, which quantify and remove the subjectivity of deformation grids. The first allows for observing differences between two point configurations, while the second visualises differences between the mean shape (consensus) and an object of interest by deforming a grid. These complementary approaches are used to compare objects or visualise the results of multivariate analyses such as principal component analysis or discriminant factorial analysis (Cucchi et al. 2015). By using multivariate regressions, these visualisations contrast differences between two extreme shapes but also allow visualising allometric differences, i.e., differences in proportions between objects associated with their size differences. Methodological advances in quantification and visualisation of shapes have been accompanied by the development of a rigorous statistical theory of shape (Dryden & Mardia 1998). While forms, measured from landmarks, reside in a simple Euclidean space, shapes, calculated from normalisations, lie in a curved space. This complexity of the shape space requires projection into a tangent space after superposition. This projection facilitates statistical analyses by making the data comparable and preserving observed correlations between objects. In GMM, statistical analyses are thus performed in this tangent space. Similarly, for centroid size, calculated on raw coordinates, it is necessary to transform it into logarithm to be compatible with the projections used in statistical analyses.

In zooarchaeology, animal remains are analysed in two or three dimensions, depending on their geometry and size (Figure 3). Teeth are typically examined in 2D using digital photographs. Besides being generally the best-preserved elements in archaeological assemblages, teeth have already demonstrated their potential for discriminating and characterising populations across a multitude of clades, both among large and small mammals (e.g., Evin et al. 2013; Cucchi et al. 2017, 2019; Pelletier 2019; Jeanjean et al. 2022). Cranial or postcranial bony elements, being more geometrically intricate, are now predominantly studied in 3D. This is often achieved through the reconstruction of 3D models obtained via computed tomography (e.g., Pelletier et al. 2020, 2022; Schoenebeck et al. 2021) or photogrammetry (e.g., Evin et al. 2016, 2019; Pelletier 2018; Ameen et al. 2019). GMM studies of dental and skeletal elements are complementary, as dental morphology is more influenced by the population signal (i.e., phyloge-

netic signal), while that of skeletal bones reflects more morpho-functional adaptations, following ecological or behavioural changes. In most cases, when a specimen is recovered, GMM analysis can be performed, provided that the necessary structures to capture the geometric characteristics are intact. Although it is preferable to study complete specimens, fragmented remains can still be analysed using an adapted version of the initial protocol, as fragmentation does not necessarily impede taxonomic identification (e.g., Owen et al. 2014; Cornette et al. 2015).

By harnessing the power of GMM, researchers have been able to delve into a wide range of archaeological questions, shedding light on aspects such as ancient animal domestication, human-animal interactions, and environmental changes over time. In the following section, I present recent case studies showcasing applications of GMM in reindeer domestication research, highlighting its effectiveness and potential for elucidating these questions in Sámi archaeological contexts of northern Fennoscandia.

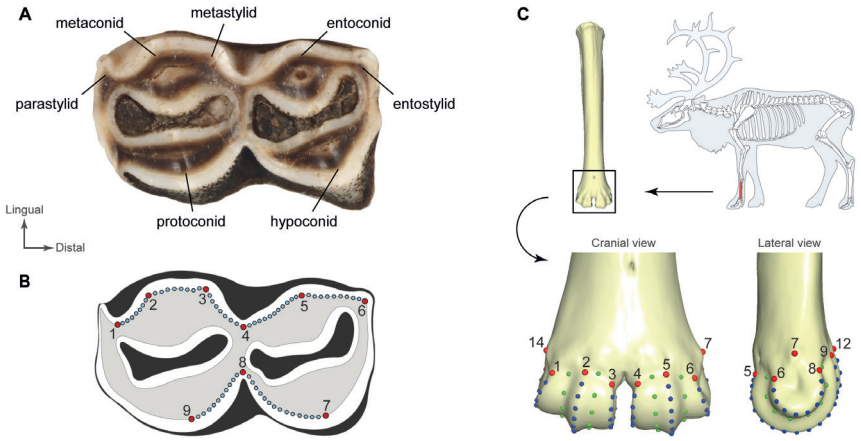

Figure 3. A. Occlusal view and nomenclature of a left lower first molar of reindeer (Photo: M. Pelletier). B. Positions of homologous landmarks (red circles) and curve semilandmarks (light blue circles). Landmarks are located at the maximum curvatures. Landmarks and semilandmarks are placed along the enamel-dentine junction (modified from Pelletier et al. 2023). C. Positions of homologous landmarks (red circles), curve semilandmarks (blue circles), and surface semilandmarks (green circles) on the distal end of a left metacarpal of reindeer (Modified from Pelletier et al. 2020)

Applications of Geometric Morphometrics in Reindeer Domestication Studies

Forelimb Long Bones: Indicators of Feeding Behaviour Changes and Reindeer Corralling

In the traditional reindeer herding of northern Fennoscandia, Sámi herders typically managed small groups of semi-domesticated individuals for various tasks (Tegengren 1952). These small herds were closely monitored by herders near their habitation sites yet allowed to roam freely in the landscape. This management approach contrasted with other traditional herding methods, such as those observed in Siberia, where some reindeer were kept captive in wooden enclosures, tethered by the neck to stakes or in pairs (e.g., Inamura 2005; Anderson et al. 2017; Haas et al. 2019). However, recent developments in reindeer herding in Fennoscandia since the 20th century have disrupted these traditional patterns due to the closure of state borders, resulting in a reduction of available lichen pastures (Heikkinen et al. 2012). These changes led to the adoption of a free-ranging system for herds with seasonal confinement in corrals (Helle & Jaakkola 2008), accompanied by supplementary feeding when environmental conditions made access to natural resources challenging (Itkonen 1948; Korhonen 2008). Nowadays, supplementary feeding is used not only to ensure the reindeers' sustenance but also to facilitate their domestication and training, as well as to maintain their overall health, particularly in a herding primarily focused on meat production (Holand 2007; Salmi et al. 2022).

Archaeologically, stable isotope analyses have suggested that this practice could date back to the 13th century (Fjellström et al. 2020; Salmi et al. 2020a). Other data, such as those related to skeletal changes associated with physical activity, support the hypothesis that some of the reindeer found in these archaeological contexts received additional feeding for the winter (Salmi & Niinimäki 2021). Winter feeding behaviour, particularly digging for lichen under the snow using repetitive movement of the forelimb, affects the muscle attachment sites on the bones of these joints to the extent that owner-fed reindeer can be distinguished from non-fed reindeer (Niinimäki & Salmi 2016). Indeed, free-ranging reindeer can spend over eight hours a day and seven months a year engaged in this activity

(Korhonen 2008). It is entirely possible that supplementary feeding may have been part of the early reindeer herding practices, but this practice would have been localised and not necessarily adopted by all Sámi reindeer herders from Fennoscandia (Salmi 2023). It is also conceivable that only certain reindeer, perhaps those intended for specific tasks and in closer contact with herders, benefited from this additional feeding. Thus, to better understand the morphological changes resulting from changes in mobility and feeding behaviours associated with herd management of semi-domesticated reindeer, a study of the long bones of reindeer forelimbs was conducted using morphological markers analysed through 3D geometric morphometrics.

This study was developed using the method of homologous landmarks and curve and surface semilandmarks on the long bones of the forelimbs (i.e., humerus, radius-ulna, and metacarpal) to help capture the three-dimensional structure of the epiphyses and compare their discriminatory potential between semi-domestic and wild reindeer (Pelletier et al. 2020). The 3D GMM approach was applied to 3D models obtained by computed tomography, including complete or partial skeletons of 123 modern reindeer individuals from central Finland, whose subspecies (i.e., mountain or forest reindeer), sex and activity pattern (i.e., free-ranging, corralled or draught reindeer) were known. Analyses were conducted on complete reindeer bones, but the methodology was adapted by focusing on proximal and distal parts not affected by entheseal changes and pathological lesions (Niinimäki & Salmi 2016; Salmi & Niinimäki 2016; Salmi et al. 2020b). Size differences were compared using boxplots based on log-transformed centroid sizes for the epiphyses analysed – distinguishing specimens based on subspecies, sex and activity pattern – and differences were tested using multiple Wilcoxon rank tests according to these different categories. Shape variations were visualised using a principal component analysis (PCA) based on Procrustes coordinates, and shape differences between these different groups were estimated using a multivariate analysis of variance (MANOVA). To better apprehend shape variations along the principal axes, 3D digital mesh was created for each of the elements at the ends of the principal component axes, based on the surface of the Procrustes mean configuration.

Comparisons of centroid sizes revealed that, for all analysed elements, forest reindeer are significantly larger than mountain reindeer, and males are noticeably larger than females within each subspecies. When considering subspecies and sex, the results further indicated that corralled individuals were significantly smaller than free-ranging individuals (Figure 4A). The skeletal size reduction among corralled individuals is a typical characteristic commonly used to document the effects of domestication. This rule appears to be particularly well observed in reindeer: the corralled individuals in this study did not have a long history of captivity, as most of these reindeer were born in the wild. The effects of reduced mobility on skeletal size are therefore evident without preferential selection. While there is no evidence to our knowledge that Fennoscandian reindeer have been kept in total captivity since the Late Iron Age, the control of mobility in these individuals likely led to lower levels of physical activity compared to free-ranging animals, which is crucial information for investigating the early stages of reindeer domestication. Additionally, draught reindeer are

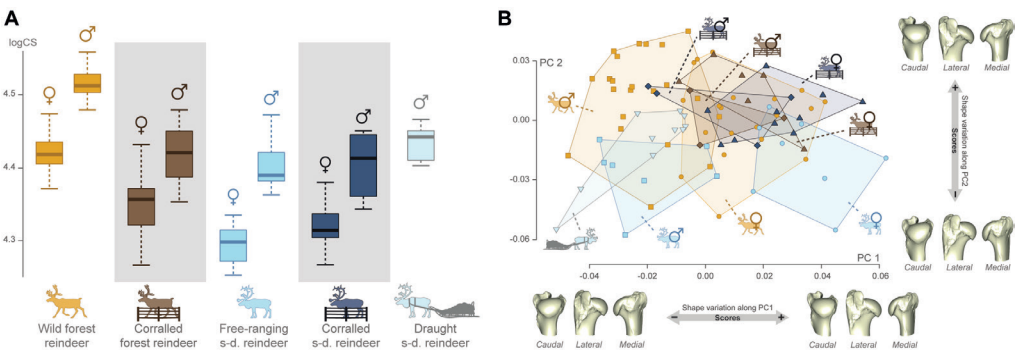

Figure 4. A. Boxplots of the variation in log-transformed centroid size (logCS) for the proximal metacarpal. B. Scatter plots of the two first axes (PC 1 and PC 2) of principal component analyses (PCA) performed on the shape data for the proximal humerus. Data are presented according to the subspecies (forest and mountain reindeer), sex (male = ♂ and female = ♀) and activity pattern (wild/free-ranging, corralled and draught reindeer) (Modified from Pelletier et al. 2020). s-d: semi-domestic.

larger than free-ranging ones, possibly due to the preferential selection of these individuals for their physical properties and abilities to perform domestic tasks.

Morphological variation analyses also revealed significant shape differences for most elements. Morphological differences between subspecies could reflect both behavioural and ecological distinctions. The forest reindeer is better suited to the closed conditions of the taiga, with deep and soft snow cover, while the mountain reindeer inhabits open environments and is better adapted to the hard-packed tundra snow. Additionally, males generally exhibit more robust bones, whereas females have a thinner and more slender morphology. These differences likely partly relate to the various support functions of the forelimbs, notably to bear the weight of larger and heavier antlers in males. Despite variations associated with phylogeny, ecology, and sex, the results primarily demonstrated that activity pattern, whether free-ranging, corralled, or working, also significantly impacts individual morphology (Figure 4B). Captivity directly influences bone shape. For instance, in corralled individuals, the proximal epiphysis of the humerus exhibits increased development of the lesser tubercle, enhancing shoulder stability and humerus adduction resistance. Conversely, the distal epiphysis of the humerus widens mediolaterally in free-ranging individuals, suggesting adaptation to activities such as foraging for lichens under snow during winter. Furthermore, the distal radius and metacarpal epiphyses appear to broaden in corralled individuals, likely in response to the need to reinforce joint areas during prolonged periods of static loading (Figure 5). These observations underscore the morphological changes induced by captivity, notably the tendency of long bones in the forelimbs toward a more slender morphology compared to their free-ranging counterparts.

Therefore, this 3D GMM approach enables understanding the direction of morphological variation under the influence of reduced mobility (i.e., corralled) or changes in feeding behaviour (fed or self-fed) induced by domestication (Figure 5). This study holds great potential for tracing the early stages of domestication from fossil reindeer remains and aiding in reconstructing the socio-economic changes of past Sámi populations in Fennoscandia over time.

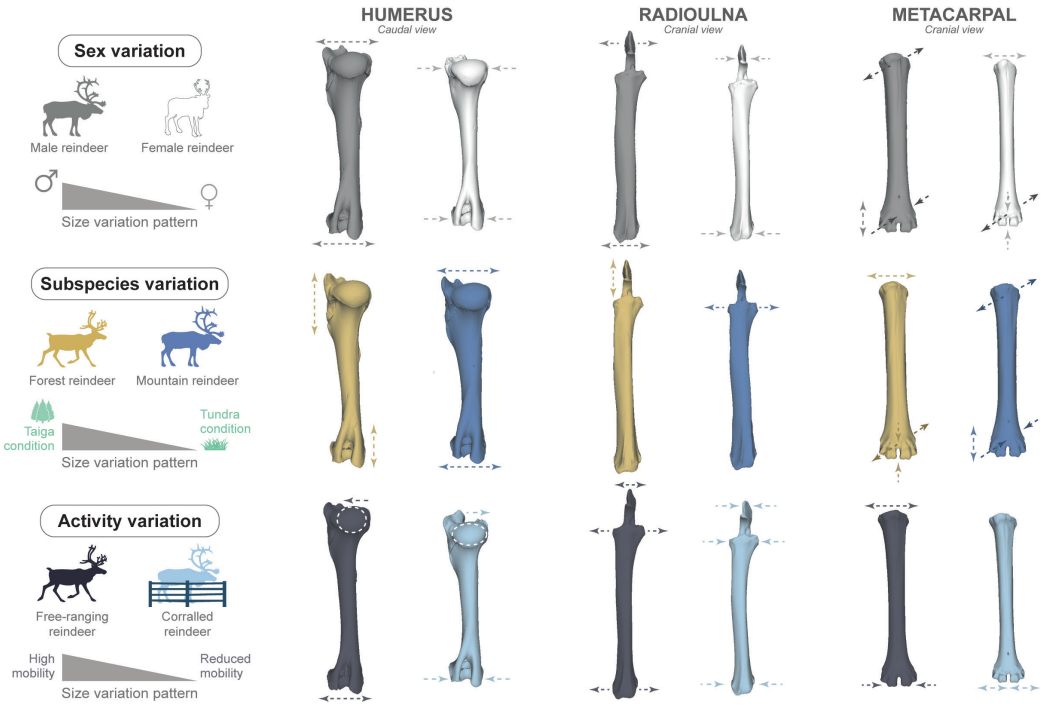

Figure 5. Visualisation of morphological changes in forelimb long bones of reindeer associated with sexual dimorphism (male in grey, female in white), phylogeny (forest reindeer in yellow, mountain reindeer in blue) and activity pattern (wild or free-ranging reindeer in dark purple, corralled reindeer in light blue). The arrows indicate the main variations in the different bones (mainly widening or narrowing).

Hindlimb Long Bones: Insights into Reindeer Domestication as Draught Animals

The use of reindeer for traction likely played a crucial role in their domestication among the Sámi people (Ingold 1986; Bately 2007; Bjørklund 2013). Draught and cargo reindeer were utilised for seasonal migrations and long-distance trade expeditions (Salmi & Heino 2019; Salmi 2023), as well as for transporting people and their possessions during movements and herding-related activities (Itkonen 1948; Korhonen 2008). However, the adoption of mobile pastoralism varied among Sámi groups, with some maintaining a hunter-gatherer-herder lifestyle until the 19th century (Itkonen 1948; Hansen & Olsen 2014; Harlin et al. 2019). Archaeological evidences of past reindeer use for traction or other domestic tasks can be explored

through the analysis of material artefacts, such as discoveries of harnessing and traction technology. This is evident, for example, in Siberia, with sled runners dating from ca. 1500 BCE (Murashkin et al. 2016) or harness parts from ca. 200 BCE (Losey et al. 2021). In northern Fennoscandia, discoveries of sleds similar to those later used by the Sámi for reindeer pulling date back to the 10th century (Svestad 2018). Reindeer harness pieces, although undated, from medieval Sámi habitation sites and the early modern period (Carpelan 1991, 1993), along with historical sources from the 16th century onwards, also attest to the use of reindeer for work and transportation (Salmi 2023).

Another possibility is to identify the early reindeer use for traction directly from the analysis of work-related skeletal changes, such as pathological lesions and entheseal changes (Salmi et al. 2020b). An analysis of these skeletal markers on reindeer remains from Sámi archaeological sites in northern Finland indicated that working reindeer were already integrated into the region's economy as early as the 13th century (Salmi et al. 2021). In practice, draught reindeer typically exhibit joint diseases or bone fusions, especially in the vertebrae, phalanges, and tarsal bones, which develop in response to the extra stress and loading caused by pulling. While the long bones of the forelimbs provide insights into feeding and mobility behaviour changes induced by domestication (cf. section "Forelimb Long Bones" in this article; Pelletier et al. 2020), the bones of the hindlimb are more subject to the constraints associated with body propulsion and are more impacted by external pressures (Schmidt & Fischer 2009; Hanot et al. 2017; Mallet et al. 2019). Consequently, the study of these skeletal elements using 3D GMM has promising and complementary potential for exploring reindeer domestication processes, particularly concerning human control over mobility or the use of reindeer as draught animals.

This study (Pelletier et al. 2022) focused on analysing the long bones of the hindlimbs (i.e., femur, tibia, and metatarsal) using the same methodology and sample of modern reindeer as in the previous study on the forelimbs (cf. section "Forelimb Long Bones" in this article; Pelletier et al. 2020). The results regarding centroid size data of the analysed epiphyses of the hindlimb long bones exhibited a similar size differentiation pattern as observed in the previous study (cf. Figure 4A), among subspecies (i.e., forest reindeer larger than mountain reindeer), sexes (i.e., males larger than females), and activity patterns (i.e., corralled individuals smaller

than free-ranging individuals, and draught reindeer larger than free-ranging ones), confirming that size variation in all skeleton elements reacts similarly to external stimuli. Shape analyses also revealed particularly strong congruence between subspecies morphological variation and phylogeny, indicating a relatively strong phylogenetic signal on the shape of the long bones (Figure 6). For example, the patellar surface of the distal femur and the lateral tibial plateau exhibited a more circular morphology in forest reindeer than in mountain reindeer, revealing adaptations to closed taiga-like environments. This allows for greater range of movement at the knee joint, enabling individuals to change direction more rapidly, such as zigzagging away from predators. In contrast, mountain reindeer morphology offers better stability in open environments and during higher loadings.

In addition to the influence of phylogeny and sex on the bone morphology, activity pattern also has a significant impact. Large-sized males, especially wild forest reindeer and most draught reindeer, exhibit a more pronounced mediolateral development of the proximal femur epiphysis, thereby enhancing resistance to stresses associated with body propulsion and loading (Figure 6). This adaptation promotes more pronounced hip flexion and abduction, notably due to a deviated knee position. Moreover, the enlargement of the tibial tuberosity involved the presence of a stronger and larger patellar ligament, which reflects the strength of the quadriceps femoris muscles and therefore strengthens the knee joint. This general conformation, mainly of the femur and tibia, provides greater stability to the knee joint, in particular among cursorial cervids. This is attributed to repetitive flexion of the knee articulation, which are more involved during propulsion. In forest reindeer, this may be explained by their comparatively large body mass and adaptation to the taiga, while in draught reindeer, it could be due to increased range of motion in the hip and knee joint. However, this activity is reduced or even absent in corralled reindeer. Additionally, corralled reindeer show a mediolateral widening of the distal tibia and distal metatarsal epiphyses, likely in response to the need to strengthen articular areas during prolonged periods of static loading, a phenomenon similar to that observed in the forelimbs.

This 3D GMM approach also provides insight into the morphological variation of hindlimb bones influenced by both reduced mobility – such as that induced by captivity – and pulling in draught reindeer. Thus, this study holds promising potential for identifying the early use of draught reindeer from archaeological assemblages.

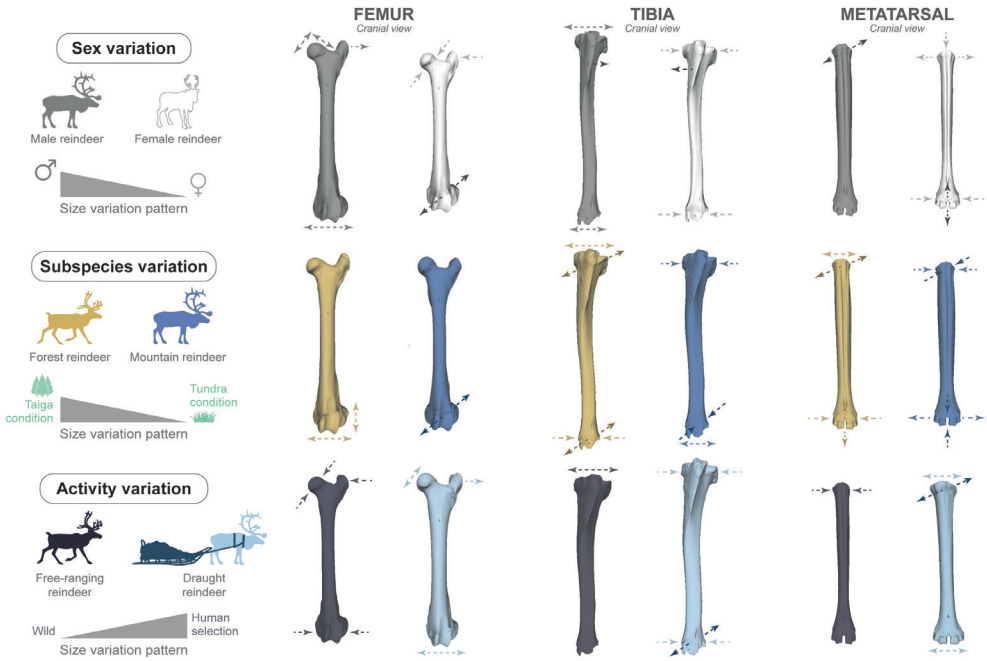

Figure 6. Visualisation of morphological changes in hindlimb long bones of reindeer associated with sexual dimorphism (male in grey, female in white), phylogeny (forest reindeer in yellow, mountain reindeer in blue) and activity pattern (wild or free-ranging reindeer in dark purple, corralled reindeer in light blue). The arrows indicate the main variations in the different bones (mainly widening or narrowing).

Limb Long Bone Cross-sectional Morphology: Markers of Selection and Mobility Reduction in Reindeer

In the preceding examples, I have emphasised significant changes in reindeer's activity patterns, including reduced mobility and their use as draught animals, as well as alterations in their feeding behaviour, notably the supplementary food provided by herders during seasonal confinement in corrals. These changes induce substantial phenotypic plasticity in the skeleton, particularly affecting the external morphology of the limb long bones – primarily at the proximal and distal bone ends – where muscle and ligament insertions determine crucial morphology for limb function (Pelletier et al. 2020, 2022). However, environmental and locomotor parameters can also influence the mechanical properties and internal structure of long bones (Pearson & Lieberman 2004; Shackelford et al. 2013; Kilbourne & Hutchin-

son 2019; Harbers et al. 2020; Niinimäki et al. 2021). Therefore, changes in habitual loading, such as increased loading in draught reindeer or decreased loading in corralled reindeer, along with alterations in foraging patterns, could alter the cortical bone along the shaft. The amount of cortical bone in long bone cross-sections correlates with shaft strength under weight constraints, while cross-sectional shape provides insight into the forces acting on the bone, revealing its function during locomotion. Additionally, reindeer bones found in archaeological contexts are rarely complete, often fractured due to marrow extraction (Harlin et al. 2019). Alongside frequently intact joint ends, bone shafts and diaphyseal fragments are commonly abundant in fossil assemblages. Thus, GMM analysis of the shape and thickness of cortical bone offers a promising and complementary approach to further characterise the direct impact of these activity changes on the overall morphology and structure of long limb bones.

Morphological variations in cross-sections were assessed using 2D GMM (Pelletier et al. 2021) on the same bone samples of modern reindeer as those utilised in the previous two studies (i.e., humerus, radioulna, metacarpal, femur, tibia, and metatarsal). Digital images of each cross-section were captured using a peripheral quantitative computed tomography (pQCT), with all bones scanned at 50 % of their inter-articular length. The cross-section form in proximal view was quantified through a method that combines landmarks positioned at the points of maximal curvature of the periosteum (i.e., the outer surface of the bone) and endosteum (i.e., the inner surface of the bone), along with semilandmarks on the contours of the periosteum and endosteum. This protocol offers the advantage of preserving the anatomical orientation of landmarks, enabling an examination of the directionality of shape changes. Comparisons and visualisations of size and 2D shape variations utilised the same methods employed for 3D analysis (see above). In this study, we also assessed whether skeletal size could serve as a good estimation of reindeer body mass by conducting a regression of body mass against centroid size for each bone.

The variations in centroid size of bone cross-sections align with those observed at the proximal and distal epiphyses of the same bones (cf. Figure 4A). Additionally, the results showed a strong significant correlation between centroid size and body mass, suggesting that bone size could serve as a reasonable estimate of body mass for this species (Figure 7A). However, significant variations in body mass were noted among male forest reindeer (i.e.,

wild) – often with body mass even lower than that of male mountain reindeer (i.e., semi-domesticated) – contrasting with observations of centroid size where forest reindeer were generally larger than mountain reindeer. Similarly, corralled individuals displayed body masses similar to those in the wild, contradicting previous differences observed in centroid size where corralled reindeer were smaller. These observations are consistent with the captivity-induced increase in body weight (e.g., O'Regan & Kitchener 2005; Harbers et al. 2020), as well as with significant changes in feeding and reproductive behaviours. In the wild, reindeer experience significant seasonal variations in body mass (Reimers 1983; Weladji et al. 2002). Before winter, reindeer achieve their maximum weight to cope with the harsh winter climate and generally become relatively lean by the end of winter. At the end of the rutting period (i.e., autumn), adult males are also lean as a result of fights related to reproduction and lack of feeding. In comparison, competition among males is reduced in semi-domestic herds due to herd management practices by herders, which may explain greater variation in body mass among wild male reindeer. Furthermore, reindeer kept in corrals according to the free-ranging system are primarily fed during winter, avoiding winter food shortages or difficulty in finding food. This practice may also explain

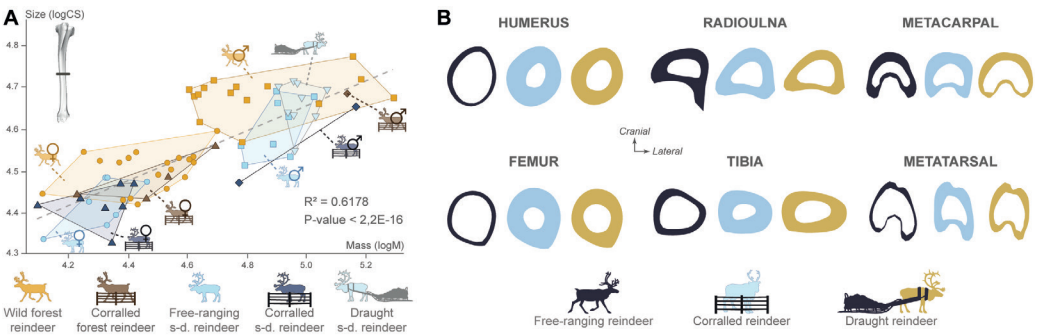

Figure 7. A. Regression between log-transformed centroid size (CS) of the tibia and log-transformed body mass (M), amongst subspecies (forest and mountain reindeer), sex (male = ♂ and female = ♀) and activity pattern (wild/free-ranging, corralled and draught reindeer). A significant contribution was considered for p-value < 0.05. (Modified from Pelletier et al. 2021). B. Visualisation of morphological changes in cortical bone thickness associated with selection in Fennoscandian reindeer (Modified from Heino & Pelletier 2022).

why mountain reindeer in this sample (i.e., semi-domestic) are proportionally heavier than forest reindeer and exhibit less variation in body mass despite their smaller body size.

Regarding the overall morphology of bone cross-sections, females exhibited an elongated section in the craniocaudal direction, whereas in males, the sections were more circular and extended mediolaterally. This trend suggests a morpho-functional adaptation in heavier individuals (i.e., males) to resist mediolateral bending, linked to the strong sexual dimorphism in reindeer. Corralled and draught individuals displayed more circular cross-sectional morphology, associated with an increase in cortical bone thickness compared to wild reindeer (Figure 7B). This confirms the impact of changes in locomotor and feeding behaviours in semi-domesticated reindeer, as well as the effect of increased body mass on bone shape and volume of the shaft, indicating greater bone strength. For corralled reindeer, better adapted to prolonged periods of static loading, this could result from the cumulative and interdependent consequences of increased body mass, a richer diet, and stereotypical behaviours increasing the frequency of muscle use. As for draught reindeer, specially selected for their physical abilities and trained for several months to run and pull, this could partially explain the increase in muscle volume compared to wild individuals, as well as significantly higher selective pressures, resulting in increased cortical bone thickness.

Through environmental, (i.e., populations mainly from central Finland), genotype (i.e., forest and mountain reindeer) and phenotype (i.e., free-ranging, corralled and draught reindeer) control, this study allowed us to highlight the interdependent variations of body weight and the morphology of the internal structure of the bone shafts, mainly due to human selection. These variation patterns associated with behavioural changes in semi-domestic versus wild reindeer provide valuable information on the early effects of the selection on bone morphology and could be benefit the archaeological record.

Cheek Teeth: Insights into the Biogeographical History of Reindeer and Reconstruction of Human Subsistence Strategies

Identifying subspecies on archaeological sites in northern Fennoscandia is crucial for understanding the history of Sámi communities, particularly regarding the domestication and early management of reindeer. This identification can reflect various subsistence strategies and cultural in-

terpretations. For instance, the exclusive presence of forest reindeer at a settlement, offering, or hunting site would likely indicate a hunting-based subsistence strategy, as this subspecies has apparently never been domesticated in Fennoscandia. Conversely, the coexistence of both subspecies at an archaeological site would suggest a mixed socio-economic organisation of Sámi societies, combining wild reindeer hunting and semi-domesticated reindeer herding. Interpreting the exclusive presence of mountain reindeer could be more complex without additional contextual data, as it could imply either a mixed economy or exclusive herding, depending on the region. Additionally, since both subspecies have different behaviours and ecological requirements, this could have influenced the hunting strategies of past human societies, such as mass hunting in the case of mountain reindeer, more gregarious, or individual hunting in the case of forest reindeer (Rankama & Ukkonen 2001).

The analysis of skeletal morphology in different reindeer populations has highlighted the impact of taxonomy, etho-ecology, and sex on morphological variation. However, significant overlaps in the size and shape of skeletal elements, stemming from behavioural variability, sexual dimorphism, and environmental factors, can complicate the distinction between subspecies at an archaeological site, thus rendering socio-cultural interpretation more complex. To better differentiate subspecies without being influenced by the significant impact of human selection, it is necessary to identify other relevant and less plastic phenotypic markers. Hence, the study of teeth, often employed in GMM studies, could complement analyses of postcranial skeletal elements, as they carry a taxonomic signal, are generally well-preserved, and abundantly present in archaeological assemblages. This approach can contribute to identifying the subspecies of isolated reindeer teeth, as well as distinguishing between wild and domestic individuals in archaeological records. To achieve this, biosystemic signals were tested by examining the morphology of the enamel-dentine junction using a 2D landmark and semilandmark protocol applied to the occlusal surface of first and second lower molars (m1 and m2) (Pelletier et al. 2023). These teeth were selected due to their similar conformation, clear distinction from premolars and m3, different degree of wear compared to the latter, and their abundance in archaeological assemblages. This approach can also address other underlying questions, such as improving the identification of the minimum number of individuals at an archaeological site. A total of 389 modern specimens were

analysed, including both wild reindeer subspecies (i.e., mountain reindeer from southern Norway and forest reindeer from southern Finland), as well as semi-domestic populations (from northern Finland). Tooth morphotypes were compared using a multivariate analysis of variance (MANOVA), and visualisation of phenotypic similarities was performed using Procrustes distances and the Neighbour Joining method.

This study has shown that tooth wear had a major impact on the size and shape of m1 and m2, potentially overshadowing the perceptible differences between subspecies or populations. As the tooth became worn, the centroid size of the tooth increased. Shape was also directly impacted by the wear with an attenuation of the enamel folds on the lingual side and a deepening of the interlobal grooves. The analyses were therefore subdivided into wear classes, more or less correlated with age (i.e., Class 0: <1 year; Class 1: 1–3 years; Class 2: 3–6 years; Class 3: 6–10 years; and Classe 4: >10 years) in order to better capture the taxonomic signal. Unworn (Class 0) and highly worn (Class 4) teeth were excluded from the study, as they were difficult to integrate into the landmarking protocol, and avoided incorporating the noise inherent in these wear classes into the analyses. In addition, these categories are generally not the most abundant individuals in the Fennoscandian fossil record (Puputti & Niskanen 2009; Hedman et al. 2015; Harlin et al. 2019), which could be an advantage for application to the Sámi archaeological contexts of northern Fennoscandia. This method demonstrated that analysing tooth shapes through 2D GMM allowed for quantifying divergences between the two subspecies of wild reindeer on one hand, but also subtler divergences between wild and semi-domestic mountain reindeer, and linking them to selection pressures related to domestication (Figure 8A). Another strong aspect of this study is that sexual dimorphism was not significant in all the populations studied, both in terms of tooth size and shape, contrasting with previously observed results on postcranial skeletal remains. This could also be explained by the fact that sexual selection in polygynous male ungulates favours skeletal size over tooth size (Carranza & Pérez-Barbería 2007).

This study has identified specific tooth characteristics for modern wild and semi-domestic populations, alongside a dichotomy in tooth shape space that separates wild phenotypes, while also highlighting the morphological similarity between wild and semi-domestic mountain reindeer (Figure 8A). Of particular note, forest reindeer exhibit a squarer dental morphology with a deep lingual interlobal groove and a narrower vestibular one, along with

mesial and distal lobes of similar proportions. They also feature a narrower mesiolingual fold between the metaconid and parastyle. In contrast, mountain reindeer display more tapered teeth with a flatter lingual edge, a deeper vestibular interlobal groove, and a larger mesial vestibulo-lingual diameter compared to the distal diameter. The congruence of these morphotypes with phylogeny has confirmed the relatively strong phylogenetic signal on the shape of the lower molar, which can significantly aid in distinguishing different ecotypes in the archaeological record. Applied to four Finnish archaeological sites between the 13th and 19th centuries, this methodology enabled the identification of subspecies and the earliest evidence of a domesticated reindeer economy among the Sámi people in the region. The sites of Juikenttä, Nukkumajoki, and Markkina yielded teeth belonging to both subspecies, confirming the presence of forest reindeer in northern Finland between the 13th and 17th centuries, which is no longer the case nowadays (Figure 8B). Indeed, during this period, local climatic conditions were more conducive to the development of the boreal forest, as evidenced by pollen analyses (Finsinger et al. 2013), and thus to the presence of this subspecies. However, the proportion of forest reindeer compared to mountain reindeer was significantly higher at archaeological sites in northeastern Finland than in the northwest (Figure 8C). These regional variations could be attributed to both specific environmental conditions and/or different hunting strategies adopted by Sámi communities. Archaeological and historical evidence of the use of draught reindeer has also been found at these three sites, indicating a mixed socio-economic organisation among the Sámi populations (Harlin et al. 2019; Salmi et al. 2021). Finally, all individuals identified at the Pappila site, located in the fell region with a high and arid landscape, were mountain reindeer (Figure 8C). The environment of the region likely never favoured the presence of forest reindeer. Sámi communities practiced reindeer herding in this region during the 17th century, but subsistence was primarily based on hunting and fishing (Itkonen 1948), meaning that some of these reindeer could also be wild and/or semi-domestic mountain reindeer.

This new protocol has facilitated a highly reliable taxonomic distinction at the subspecific level, as well as an analysis of morphological variations among wild and domestic individuals within modern populations. It has primarily allowed for the identification of subspecies present in various archaeological sites in Northern Finland, thereby demonstrating that the reindeer's biogeography has significantly evolved since the 13th century.

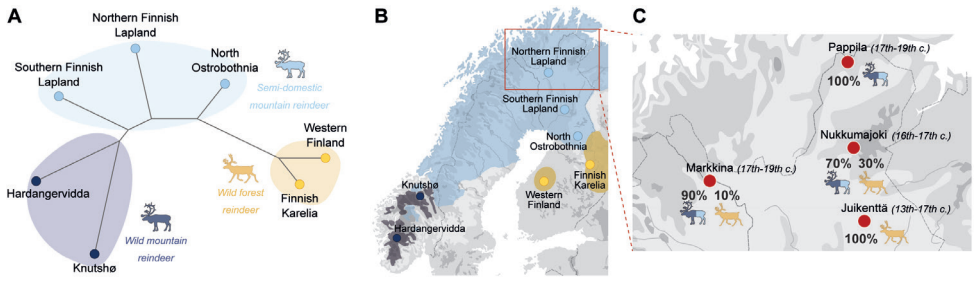

Figure 8. A. Neighbour-joining tree using Mahalanobis distances based on m1 shape data (Class 1) from modern Fennoscandian populations (modified from Pelletier et al. 2023). B. Current geographical distribution of the two reindeer subspecies including wild and domestic populations in Fennoscandia (Modified from Heino & Pelletier 2022), with location of the modern populations used in this study. C. Location of the four Finnish archaeological sites cited in the text and proportion of subspecies identified at each site based on lower molars (m1 and m2). In this case, the GMM was unable to distinguish between wild and semi-domestic individuals within the mountain reindeer subspecies. The presence of semi-domesticated individuals was confirmed by other proxies such as activity markers and body proportions based on postcranial bone measurements.

Conclusion and Archaeological Perspectives for the Identification of Early Domesticated Reindeer

Historically, the reindeer is likely one of the most recently domesticated species by humans, but identifying the time and place of its domestication through archaeological records remains a complex task. Zooarchaeologists require powerful biomarkers on fossil reindeer remains to document the origins of the earliest domesticated reindeer. The various studies presented in this article have demonstrated the potential of GMM studies on bones and teeth to identify subspecies, sexes, and also to better understand the impact of selection and domestication on reindeer morphology. Understanding the morphometric variability of modern reindeer is a crucial prerequisite to better comprehend what governs individual, intra- and inter-population variation before applying it to the fossil record.

As I have demonstrated through the presentation of these princeps studies in GMM on reindeer remains, the study of teeth and skeletal bones is highly complementary. Teeth primarily provide information on taxonomy, and while limb bones can also contribute to this subject, they

are more informative regarding sexual dimorphism or changes in feeding behaviour (e.g., additional food provided by herders) or mobility (e.g., corralled or pulling). The identification of subspecies on archaeological sites appears to be a crucial prerequisite for understanding the history of past Sámi communities, as it may reflect different subsistence strategies or cultural interpretations. Indeed, the presence of forest reindeer in a deposit could directly imply a subsistence strategy based on hunting, while the presence of mountain reindeer could imply herding. Sex identification also holds significant implications for research on semi-domestic individuals in archaeological contexts, as semi-domestic males were preferentially used for transport and traction, although females may also have been present in Sámi reindeer herds, particularly for milking purposes. Finally, the identification of corralled or draught reindeer, through their specific morphological markers, directly enables discussion of the behavioural changes in mobility and feeding induced by domestication.

These protocols will enable archaeologists to better estimate the presence of wild or semi-domestic reindeer in archaeological assemblages, thus understanding the evolution of socio-economic patterns among Sámi reindeer herding communities in northern Fennoscandia. However, caution is warranted in the accurate identification of semi-domestic reindeer due to the significant variability in the chronology and spread of the domestication process in Fennoscandia, as well as genetic introgression between wild and semi-domestic herds. Each parameter such as size, shape, and allometry must be meticulously analysed to identify individuals and gain a better understanding of reindeer morphometric variability in Fennoscandia. This should also be systematically linked to archaeological contexts, material cultures, dating, and ideally with other methodologies such as analysis of entheseal changes and pathological lesions, ancient DNA, or stable isotopes. Such holistic studies would refine research on archaeological sites to better identify the early practices of reindeer domestication and herding in Fennoscandia over time and space.

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