Let the winter sun shine on, let me feel the frost of dawn:
Rangifer tarandus osteology, anatomy, and identity.

by

Emily Hull

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Department of Anthropology
University of Alberta

Abstract

Rangifer tarandus, the species which encompasses both caribou in North America and reindeer in Eurasia, is a keystone species for both the cultures and the ecosystems of the circumpolar world. Because of this, human interactions with reindeer and caribou throughout history are of great interest to zooarchaeologists. Beyond the human-focused exploration of these relationships, these studies attempt to understand the experiences of the reindeer as well. This dissertation undertakes to explore, both quantitatively and qualitatively, the anatomy and life experiences of these animals. The studies include, first, a study of diagnostic differences between the phalanges of the fore and hindlimb, second, a study of the soft tissues of the hoof, third, an analysis of potential difference in entheseal changes between populations, fourth, a study of incidences of pathology between populations and sexes, and lastly, an osteobiography of a single remarkable animal. These studies highlight the use of osteology, anatomy, and paleopathology to explore animal life histories and create animal osteobiographies. As such, they present a collection of foundational studies designed for use by zooarchaeologists working with reindeer and caribou and for human-animal scholars examining the relationships between humans and *Rangifer tarandus.*

Preface

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Chapter 1:

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Chapter 2:

Emily Hull was the lead author for Chapter 2: Tendons and Ligaments of the *Rangifer tarandus* Metapodial and Hoof. She was assisted by co-authors Dr. Sirpa Niinimäki in research design and initial data acquisition, by Hanna-Leena Puolakka in data acquisition and Finnish translation, and by Mitchell Semeniuk in data analysis, comparative anatomy, and data organization.

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Emily Hull was the lead author for Chapter 3: Differences in Entheseal Changes in the Phalanges Between Ecotypes of Fennoscandian Reindeer. Study design was developed by Emily Hull, heavily assisted by co-authors Dr. Anna-Kaisa Salmi and Dr. Sirpa Niinimäki, based on their previous studies of entheseal changes in reindeer. Scoring assessment criteria was created by all three authors in concert. The data scoring, analysis, and statistical analyses were performed by Emily Hull. The majority of the article was written by Emily Hull, with contributions to the "Background" provided by Dr. Anna-Kaisa. The "Entheseal Changes" section was written by Dr. Sirpa Niinimäki with input, edits and section outline provided by Emily Hull.

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Introduction

If there is one thing that we truly know about reindeer, it is that they can fly. Whether through the dreams of hunters and herders, with ease across endless banks of snow, or across maudlin holiday cards, reindeer wander effortlessly along the edges of the Earth and the human imagination. Few animals straddle the public perception between mythological beast and working animal quite like the reindeer. From Rudolph's shiny nose to serious concerns over rapid depopulation of caribou herds, reindeer are, for many of us, a species too remote from our own experiences to be fully understood, and so take on a nearly fictional cast in our collective imagination. But the members of the species *Rangifer tarandus* themselves and their daily lives have been and remain of the utmost importance to the humans who know them intimately. Reindeer and caribou throughout the northern world have held many roles in our minds, imaginations, religions, households, and economies, as well as being a keystone species for Arctic and Subarctic ecological systems.

Humans have sought to describe the reindeer spirit in many ways. While Ingold (1980: 19) comments on the reindeer's "gaze of vacant melancholy", poet Marianne Moore (1935) only remarks, "Reindeer seem over-serious." For my part, each reindeer I have met has been different, observing me with looks that range from the wary, fearful, or challenging glances of unhabituated herd animals to the patient, long-suffering, or disdainful stares of working reindeer. As we seek to anthropomorphise and discern the emotions in reindeer eyes, we less often stop to wonder what they are trying to learn from us, although my suspicion is that their queries can often be boiled down to "what do they want *now*?"

My studies, with a few exceptions, focus on two groups of Fennoscandian reindeer from Finland, *Rangifer tarandus tarandus* and *Rangifer tarandus fennicus.* Finland is home to some of the most well-documented reindeer herding cultures in the world, as well as being home to groups of wild reindeer. The story of reindeer in Fennoscandia spans the human cultural shifts from nomadic hunting to sedentary pastoralism and ranching, with reindeer providing not only an avenue but also an impetus for these cultural adaptations (Butzer, 1982; Ingold, 1980; Riede, 2011). The two Finnish subspecies also represent two of the three globally recognized ecotypes of reindeer: barrenground and boreal. The difference in activity, behavior, and life experiences between ecotypes is a recurring theme in my research, as are the physical differences and similarities between the two. Over the course of my dissertation research, I have focused on skeletal and anatomical materials, using paleopathology and entheseal changes to examine life histories and experiences. Many of these skeletal and anatomical materials are those of the feet and hooves. There are multiple reasons for this focus. First, the minute study of the entirety of the reindeer body far is beyond the scope of one dissertation. Second, the hooves of *Rangifer tarandus* are unique but not well studied, making them ideal for more detailed study. Third, the interface between animal and earth taking place with the feet has symbolic as well as scientific importance, as the ground both holds us up in life and absorbs us as we die. The landscapes that reindeer traverse also add importance and interest to different ecotypes, as snow and forests play roles in their individual lives and their relationships with humans. The dichotomy between barrenground and boreal reindeer also divides domestic reindeer from wild forest reindeer, and this makes these ecotypes and their interactions with humans an area ripe for exploration. The questions surrounding the domestication of reindeer are extensive, and the reindeer of Fennoscandia lend themselves to the investigation of one of the potentially many loci of reindeer domestication. Common threads linking all of these questions are investigations of reindeer agency and identity, and whether that identity is defined by behavioral pattern, human interactions, or individual action.

Skeletal Material Culture

Osteobiographies, or skeletal life histories, are an attempt to retrace activity and trauma from patterns of entheseal change, disease, trauma, and attrition left on the skeleton. As Sofaer (2006) remarked, in this way the material body is examined in the same way we look at artifacts. We search for meaning in the physical bodies left behind after an individual's death, using the physical marks on bones to reconstruct a life history. Historically, osteobiographies have been exclusively used for the assessment and reconstruction of human lives, although exceptions have been made for the animals closest to us—primarily domestic animals who have been ritually sacrificed or slaughtered, or pets who have been given human or near-human funerary rituals (e.g., Losey et al., 2011; Tourigny et al., 2016). Rarely are wild or herded domestic animals given such treatment, which is unsurprising, as several factors complicate the study of such animal lives. First, in traditional archaeological approaches, less importance is bestowed by investigators on the lives of these animals, as they are understood as part of the natural realm rather than the human or cultural realm. This dichotomy, however, has been recently challenged by many scholars, particularly in anthropology (Boyd, 2017; Ingold, 2013; Russell, 2002; Stépanoff et. al., 2017; Stépanoff, 2012, 2017). Traditional perspectives also tend to place such animals under the purview of assemblage archaeology, wildlife biology, or paleontology, depending on their age and context. Second, lack of interment and use as food often leads to few intact skeletal materials. Analysts are left with intermixed and fragmented parts of multiple reindeer that are difficult to assign to specific individuals. Third, the remains of such animals are usually viewed in terms of patterns of species behavior rather than individual lives with complexities and personalities.

An examination of the individual lives of dead reindeer, whether being analysed as individuals within a group, or completely on their own, requires an osteobiographical approach. The understanding of an individual's lived trauma necessitates a full or partial reconstruction of their life history. With reindeer, however, this approach is limited by existing anatomical knowledge of reindeer, which is often quite limited and relies heavily on information drawn from other species, particularly other domestic ungulates. It was therefore important to establish better anatomical knowledge of Rangifer so that I could more accurately assess the implications of the pathologies found on their skeletons. In order to divide samples up into analytically useful groups, whether by ecotype, sex, or by individual, requires species-level understanding of bone function and musculoskeletal tissues that empower movement. Without this knowledge, analysis becomes limited to the functional anatomy that is shared between physically and evolutionarily divergent species.

In addition to better documenting the intricacies of animal bodies, an understanding of the unique form and function of a species may lead analysts to behave differently towards their remains in a theoretical context. When unique specializations are acknowledged, the group in which a individual is placed contracts, so that instead of "an ungulate," they become "a cervid," and then "a reindeer". At each level, these distinctions bring the human analyst closer to the acknowledgement of individual personhood and life history. As an archaeologist, I cannot directly access reindeer thought or behaviour. Only through their bodies and bones can I seek to learn more about their lives, both as ecotypes and as individuals. This requires a conceptual and methodological shift in how reindeer bodies are approached.

Ecotype and Ecotype Culture

Rangifer tarandus ecological niches are most often separated by groundcover (e.g., forest, tundra, heavy snow), leading to the division of reindeer and caribou into ecotypes based on adaptation to these ecological niches. Both domestic and wild cousins follow a three-pronged circumpolar morphological pattern, which based on DNA studies, appears to be the result of parallel evolution (Banfield, 1961; Røed, 2005, 2014). Divided into barrenground, boreal, and high arctic ecotypes, all occurring across Eurasia and North America, these ecotypes follow different cultural and behavioral patterns, and each have differing relationship with humans.

The small-bodied, densely coated, and often insular high arctic ecotype has the least habitual contact with humans. While sometimes hunted, they live in remote and inhospitable areas that prove difficult for long-term human habitation. Most high arctic populations remain small in number, vulnerable to predation, and unhabituated to human presence (Banfield, 1961; Hansen et al., 2010; Tyler, 1991). The most recognizable and numerous of the ecotypes, the barrenground or tundra reindeer, has the most contact with humans. Perhaps the only Fennoscandian ecotype to be domesticated, huge herds of barrenground reindeer provide subsistence and economic value to the humans who claim ownership of them. Even within the contexts of domestication, however, there is wide variation in human and reindeer relationships, and control over both movement and reproduction varies significantly (Banfield, 1961; Helle, 1982; Nieminen, 1995). The boreal or woodland ecotype of reindeer, which occupies the largest ecoregion, is the least social and most skittish. With a predilection for scattering rather than clustering in the face of threats, and a propensity to browse as well as graze, they are typified by large bodies, long legs, and high degrees of sexual dimorphism (Banfield, 1961; Drucker et al., 2010; Helle, 1982; Nieminen, 1995). They have never been domesticated in Fennoscandia, although they may have been elsewhere. They are understandably wary of humans, and their forest homes allow them to vanish into the trees like long-legged ghosts.

Ecotypes of *Rangifer tarandus*, despite their genetic similarities, have different shapes, adaptations, and behaviours. In fact, some of their behaviors vary between closely related herds and groups of the same ecotype. I believe that some of these behaviors may better be described as learned cultural behaviors rather than instinctive or adaptive behaviors, although some characteristic patterns certainly fall into the latter qualification. For this reason, I refer to reindeer cultural behaviors between groups as well as instinctive behavioral patterns throughout the dissertation.

Evolutionary History of *Rangifer Tarandus*

Before DNA studies of *Rangifer tarandus*, most phylogenetic theories on Rangifer evolution were based around osteometrics. As there are three distinct ecomorphs of *Rangifer tarandus* globally, it was hypothesized that during the Pleistocene, populations of *Rangifer tarandus (s.l.)* had been forced into isolated refugia, where genetic separation led to partial speciation. It was believed that this partial speciation was responsible for the polymorphy seen within this single species (Banfield, 1961). Banfield hypothesized that the ecomorphs had diverged first, that tundra and woodland subgroups had divided from one another in the early Pleistocene, and that both had migrated across Beringia. This implied that woodland ecotypes such as *R.t. caribou* and *R.t. fennicus* would have a closer phylogenetic relationship with each other than with tundra ecomorphs *R.t. tarandus* in Eurasia or *R.t. granti* in North America.

Banfield's structured his evolutionary model around ecomorphological differentiation rather than a continental divergence, and thus posited five different ancestral *Rangifer tarandus* subspecies. He saw all ecomorphs as synapomorphic, each defining a clade. In addition, he did not mention the subspecies recognized in Asia in his model, so *R.t. pearsoni* and *R.t. sibiricus* are conspicuously absent (Banfield, 1961). The primary assumption in this and all subsequent studies is that climatic changes at the beginning of the Wisconsin glacial period forced different populations of *Rangifer tarandus (s.l.)* into glacial refugia, where genetic isolation lead to partial but incomplete speciation. The major question regarding this theory is which populations and phenotypes diverged in what order.

One of the earliest continental studies of *Rangifer tarandus* DNA in North America was undertaken in 1991 using the subspecial populations defined by Banfield. This study attempted to assess genetic differences between populations based on the frequency of different alleles at the polymorphic locus that codes for serum transferrins (Røed et al., 1991). In the study, 469 modern Canadian caribou belonging to the subspecies of *R.t. granti, R.t. groenlandicus, R.t. pearyi, R.t. caribou,* and *R.t. tarandus* were analyzed. The investigators found that allele frequencies were highly correlated with geography, as caribou in Labrador showed the most divergence from those in the Northwest Territories. To the authors of this study, this strongly suggested a migration from Beringia progressing eastwards across northern North America (Røed et al., 1991).

In 2003, a study was performed on global mtDNA using *Rangifer tarandus* samples (Flagstad and Røed, 2003). One of the primary queries was whether ecotypes or geographic ranges were stronger indicators of genetic association. To this end, Flagstad and Røed utilized data from European and North American individuals to pinpoint a divergence point between these two geographic groups. The study identified three major haplogroups in *Rangifer tarandus* populations by assessing a 470 base-pair segment of mtDNA, and then applying the amplified samples to a Bayesian statistical approach to designate likely haplogroups. An analysis of

Rangifer mtDNA variability near the control region next to the tRNA^{pro} gene showed that *Rangifer tarandus* could be provisionally divided into three haplogroups, designated as haplogroups I, II, and III. Haplogroups I and II, strongly associated with North America and Eurasia, respectively, demonstrated enough genetic divergence to be assigned as clades, while haplogroup III "constitutes a wide subnetwork of crosslinked haplotypes […] located between haplogroups I and II (Flagstad and Røed, 2003:664)." Thus, the authors present haplogroup III as a "weakly supported clade (Flagstad and Røed, 2003:664)", but the crosslinked associations with haplogroups I and II would suggest that defining these phylogenetic groups as clades would be inaccurate, since clades, by definition, are monophyletic. Because of this, these haplogroups, especially haplogroup III, should perhaps be more accurately assessed as phylogenetic clusters rather than clades. Because members of haplogroup III include many high arctic populations, this strongly suggests additional migratory processes beyond a simple division between North American and Eurasian subspecies (Flagstad and Røed, 2003).

In 2005, Røed augmented the data from the 2003 study by adding transferrin allele frequencies, nuclear DNA microsatellite analysis, and additional samples of mtDNA. The goal was to clarify the relationships between reindeer and caribou populations further and hypothesize about evolutionary patterns and divergence. Røed assessed the genetic associations between subcategories of *R. tarandus* to determine whether ecotype, geography, or a combination of both was the strongest indicator of genetic similarity. Overall, a stronger association was found between geographically close populations than between the same ecotypes in different regions (Røed, 2005).

In both studies of reindeer dispersal and evolutionary history, geography proved to be a strong indicator of phylogenetic similarity, implying that observable *Rangifer* woodland and tundra ecotypes are due to postglacial parallel evolution rather than representative of pre-glacial refugial adaptations to ecological pressures. This is not completely clear-cut, as the circumpolar distribution of the high arctic ecomorphs results in more extensive genetic divergence and migratory history than would be expected from simple geographic divergence followed by parallel environmental adaptations. If the mtDNA divergence equations are correct, haplogroup III possibly represents the modern form of a parent haplogroup from which haplogroup II diverged after a Beringian migration (Flagstad and Røed, 2003; Røed, 2005). An alternate and more likely explanation is that the current data simply does not represent the entirety of divergence in ancient populations, or account for other non-Pleistocene migrations of animals across Eurasia. For example, recent research in Russia suggests that there is far more Asian genetic variation than has previously been considered (Anderson et al., 2017b; Kvie et al., 2016).

Bjørnstad et al.'s (2012) study involved the extraction and analysis of mtDNA of 68 archaeological reindeer remains from Norway, particularly in Finnmark. Both wild and domestic reindeer mtDNA was analysed, and the ancient haplotypes compared to those found in modern Fennoscandian populations. The results were quite startling. While no one had assumed that the genetic composition would have remained static with the rise of pastoralism in Fennoscandia, the haplotype clusters observed were completely different from those found in modern Fennoscandian domestic populations.

This divergence intersects with ethnographic records implying a vast change in reindeer husbandry in both Fennoscandia and Russia in the last 500 years, suggesting that the current DNA studies of *Rangifer tarandus* are missing an important component. This change may include a population crash or decline, or a second genetic migration replacing and intermingling with historic populations (Anderson, 2011; Bjørklund, 2013; Bjørnstad et al., 2012; Ingold, 1980; Krupnik, 1993; Røed et al., 2011, 2008, 2014).

The domestication of animals, although often presented as a linear process, can alternately be thought of as a form of evolution whereby an animal adapts, not only to ecological, environmental, or species pressures, but also to those of human intervention (Nyyssönen and Salmi, 2013; Russell, 2002; Stépanoff et al., 2017). Because of this, domestication may be seen as a continuation in the mosaic evolution of a species. A species such as *Rangifer tarandus*, which initially appears confusing based on existing domestication models, may in fact be an opportunity to observe domestication from a more nuanced perspective, where both human and animal are active participants in an evolutionary process.

Reindeer Bones and Hooves

As I studied reindeer ecotypes, by extension, I also examined their habitats and ecology. As a species that subsists mainly on lichens (with the occasional shrub, mushroom, lemming, and shed antler), and whose huge hooves both act as *de facto* snowshoes and shovels for digging lichens, their feet connect them to earth. This link, as well as a practical "from the ground up" approach, lead me to focus research on the limbs anchoring them to the ground.

Human butchery of *Rangifer tarandus* often involves practices that heavily fragment the head and major limb elements. As a result, metapodial and phalangeal bones (along with carpals and tarsal) often are the only whole elements remaining in archaeological assemblages (e.g., Binford, 1978). As such, these elements make ideal candidates for archaeological assessment. *Rangifer tarandus* are exceptionally well adapted to locomotion in snow and show marked overall morphological differences between ecotypes (Banfield, 1961; Takatsuki, 1992; Telfer and Kelsell, 1971, 1984). The differences in adaptation of the *Rangifer* foot, especially between ecotypes, was therefor seemed likely to prove informative if studied in detail.

Locomotory adaptions of animals in snow-heavy habitats have been investigated in previous studies. Most such studies measure hoof-load, which is defined as:

(whole animal body weight)/([forefoot area + hindfoot area]*2),

This formula provides a proportional measurement of body weight to foot area (Takatsuki, 1992; Telfer and Kelsell, 1971, 1984). Based on this equation, the smaller the hoof-load, the higher the proportion of foot area to overall body mass. In a survey of North American mammals, *R.t. caribou* had by far the smallest hoof-load of any cervid, falling in the same range as carnivores such as wolves (Telfer and Kelsell, 1971). While this technique of measurement was simple, it confirmed the advantageous morphological adaptation of *Rangifer tarandus* to snowy conditions (Blanco and Gambini, 2006; Formozov, 1946). This adaptation of oversized hooves makes the feet of reindeer and caribou even more interesting to study.

Domestication: Our House or Theirs?

Whether as prey for our ancestors or as modern domestic herd and draught animals, reindeer continue to be outliers among domestic animals. The timing and “level” of reindeer domestication in Eurasia has been a subject of great debate, as reindeer lack many of the characteristics that have been used to define other domestic herd animals such as goats, cattle, and sheep. In addition, reindeer display a range of tolerance to human companionship, with many herd animals remaining skittish and wary of humans, while others develop very close bonds with humans. There can be no argument that reindeer and caribou have been an integral prey animal for many human societies since the Pleistocene (Aaris-Sørenson et al., 2007; Gómez-Olivencia et al., 2014; Kuntz and Costamagno, 2011). In terms of Fennoscandian animal husbandry and management, rock art depicting reindeer corrals has been reported as early as 4700-4200 BC (Helskog, 2011).

A recurring issue in these discussions is the meaning of the term “domestication,” and, as Bahn (1979) argues, the notion of "domestication" as a discreet state rather than a variable cornucopia of potential relationships between humans and animals complicates, rather than clarifies, the relationships that reindeer have with the humans around them. Berthold Laufer’s (1917) early treatise on reindeer domestication mentions not only the 1555 documentation of Lapland reindeer by Olaus Magnus, Archbishop of Upsala, but also other early historical reindeer discourse: the Finnish epic poem, *Kalevala*, as well as the “Annals of the T’ang Dynasty,” which all mention reindeer domestication and utilization. In Mirov’s (1945:398) “Notes on Reindeer Domestication,” he refers to both reindeer who are tame enough to milk, and others who are “only slightly tamed and may be regarded as in a primitive state of domestication.” Eschewing the issue of domestication altogether, Mirov instead divides his descriptions into types of reindeer husbandry based around cultural resource use.

As the reindeer of Fennoscandia show few of the outward signs associated with purely physical definitions of domestication, such as coat color change, increased neotony, body size reduction, and overt morphological variation from their wild ancestors, other clues to domestication and human use must be sought (Zeder, 2012, 2015). Currently, the most powerful techniques in tracing reindeer husbandry are microsatellite DNA analysis osteological evidence, and the historical record.

DNA evidence for domestication in Fennoscandia is provided by variations in microsatellite DNA between herds of *R.t. tarandus*, which shows a genetic divergence at approximately 1300 AD (Bjørnstad et al., 2011). This date, however, should not be considered to mark the advent of reindeer domestication in Fennoscandia, as domestication is not an abrupt event. Genetic deviation requires the separation populations over multiple generations, and this process is complicated and masked by population crashes and bottlenecks due to climate change and introgression between wild and domestic groups (Hansen et al., 2011; Røed et al., 2014; Uboni et al., 2016). Historically, such dramatic genetic deviation occurred in Norway in the 1950s, and ostensibly occurred throughout the history and prehistory of reindeer management as a means to augment losses to both domestic and wild reindeer herds (Røed et al., 2014; Zeder, 2006). The fact that such a genetic divergence exists, however, provides a strong argument for reindeer domestication according to parts of its traditional definition.

Individual animal agency and the ease with which domestic reindeer feralise are often discussed in terms of animal management. Both topics, however, are overlooked in terms of historical domestication and species histories. Domestic reindeer, depending on their individual "jobs" and personal relationships with humans, occupy different rings of proximity to their human companions. It may be that these rings of proximity add to the confusion as to their "level" of domestication, because individual reindeer may occupy different domestic spaces at different stages of their lives (Stammler and Takakura, 2010). For example, an individual might spend portions of their life with little interaction with humans, while at other times be closely controlled or monitored by them. They seemingly range from states of wild or feral, to traditionally domestic. As Stammler and Takakura (2010:24 have aptly said, "reindeer seek out humans, but on the other hand can survive without humans. […] a domestic reindeer's behaviour can be characterized as ‘a broad continuum from great tameness to great ferality’ (Beach and Stammler, 2006:8-10)”.

Rangifer tarandus as a species has a complicated relationship with the term domestication. While some populations clearly have closer relationships to and work more closely with human populations, even they may not hold the traditional markers that have defied domestication in archaeology. Domestication is classically defined as a process where human breeding interventions transform a species or population so that domestic individuals are genetically, morphologically, and behaviorally different than their wild ancestors and counterparts (Clutton-Brock, 1999). Even closely managed reindeer show little such changes, and those contained by fences, corrals, and pens can maintain behaviors close to their wild brethren. Studies of wild and domestic reindeer DNA reveal conflicting results. While Røed et al. (2011) argue for a closer relationship between Asian and North American subspecies of *Rangifer tarandus*, they also reveal the complex relationships between wild and domestic *R.t. tarandus* in both Scandinavia and Asia, as well as the tenuous position of Finnish reindeer in between the two populations. Additionally, their paper brings to light the importance of hybridization with *R.t. fennicus* along ecological boundaries. Ultimately, every population border of *R.t. tarandus* and *R.t. fennicus* in Eurasia can be seen as a plastic hybrid zone where subspecial distinctions become fluid and blurred. This study also highlighted the fact that the genetics of *R.t. tarandus* in Fennoscandia, especially the more westerly portion of the population, are very distinct from those of *R.t. tarandus* in Asia, especially those to the far east (Røed et al., 2008). Archaeologically, this presents a serious challenge in the identification of faunal remains, as, while studies have been able to map some differences between *R.t. fennicus,* and *R.t.*

tarandus, there is still a morphological overlap between the two that makes the differentiation between them tricky at best (Nieminen and Helle, 1980; Puputti and Niskanen, 2009)

There is, however, less introgression than might be presupposed based on the close ranges and genetic similarities between ecotypes. One reason for this may be the timing of ruts, which may be offset by a few weeks between ecotypes; this seemingly slight difference in reproductive timing may make a significant difference in interbreeding (Helle, 1981:19). The root of the word domestication is the concept of bringing an animal out of the wild and into the household, and how this occurred with reindeer is a primary question in Northern zooarchaeology (Anderson et al., 2017; Hill, 2011, 2013; Ingold, 1980; Lien et al., 2018). If the traditional idea of the *domus,* a household living space, is explored in the context of an Arctic landscape, it becomes apparent that the definition of *domus* must be expanded to represent the nuances of northern life. In this way, all of a local environment, including homes—sea ice, inland ice, tundra, and taiga—can be seen as part of the domestic sphere. By their utilization, cultivation, and modification of these environments, *Rangifer tarandus* herds and individuals, whether wild or domestic, are key architects of these expanded households. In this way, it is the reindeer who hold the reins of domestication in the Arctic (Skarin and Åhman, 2014; Stépanoff et al., 2017).

The reasons reindeer were initially domesticated remain a subject of debate. While domestic reindeer pull sleds and now are ranched like other domestic ungulates, many scholars posit that reindeer were first tamed and domesticated in order to capture wild reindeer more efficiently. The concept of "hunting-embedded herding," *Fangstbasert reindrift* (Norwegian translation of the original Sami), refers to the practice whereby tamed animals were used to lure and hunt herds of wild animals (Bjørklund, 2013; Ingold, 1980; Sommerseth, 2010:115). These animals were either females in estrus or adult males, which were used to lure in wild males who were enticed by the possibility of either breeding or fighting. The "hunting-embedded herding" hypothesis suggests that this initial taming lead to the use of these more acclimated animals for other tasks, such as hauling sledges.

Perhaps the most comprehensive work on reindeer domestication and management is *Hunters, Pastoralists, and Ranchers*, published by Tim Ingold in 1980. This work is important in its organization and scope, and yet flawed in its focus on only one half of the human-animal relationship, with the origin of Eurasian reindeer management hinging upon human culture and environmental factors. Like most early reindeer scholarship, Ingold's focus radiates from a primarily Fennoscandian perspective and the Sámi. Ingold's thesis presents an evolution of reindeer management that began with a "primitive" hunting strategy, which subsequently developed into practices of hunting-embedded herding and corral-based ranching. It is the use of decoy deer and hunting-embedded herding, which Ingold credits with the first steps towards taming and then domesticating reindeer. Subsequent management practices evolved from increased docility of the deer themselves and the pressures of outside societies restricting ranges and offering monetary compensation for meat.

While not Ingold's intention, this depiction of a stepwise progression of cultural development cannot help but imply both advancement and progress. By extension, this advances the questionable idea that more "advanced" ranchers are more removed from their "natural" environments than the earlier hunters and therefore more civilized. When expanded beyond Fennoscandia, this hierarchy of reindeer strategy becomes more problematic, as people have relationships with *Rangifer tarandus* that fall all along and outside of the linear system of development laid out by Ingold. While his work remains invaluable for a basis from which to explore hunting, herding, and ranching systems, its use as a tool to track cultural development is limited. Ingold's primary purpose was to document the shift from wild to domestic reindeer, but, as has been discussed, reindeer domestication is a complicated set of practices that vary from region to region and between different cultural human-animal relationships (Ingold, 1980; Stepanoff et al., 2017; Vitebsky, 2006; Klokov, 2007; Baskin, 2000).

Humans studying domestication, especially those basing their studies on economy and product, may be biased in their determination of which species drive these ongoing relationships, thus developing theories that depend only on human economic needs, desires, and agency (Lien et al., 2018; Nyyssönen and Salmi, 2013; Poole, 2015; Puputti and Niskanen, 2008; Skarin and Åhman, 2014). Other players in this process need to be addressed. The cultural, biological, and sexual propensities of reindeer may have had a great deal to do with the mechanisms, instigation, and continuation of reindeer domestication. In the modern era, most "working" reindeer in Fennoscandia, who spent the most intimate time with humans, are castrated males. It is interesting that after a short rut where male reindeer aggression is high, males lose their antlers and congregate in more docile, social, non-hierarchical groups through the winter, while the antlered females remain aggressive and combative throughout their 203-240 day gestation period (Hirotani, 1990; Rowell and Shipka, 2005). Perhaps instead of a female being used to lure unsuspecting males in for the slaughter (which would seemingly work approximately one month a year), docile, antlerless males entered human settlements in search of bone scraps and patches of salty urine during the nutritionally lean winter months. While either following herds or employing other methods of hunting allows for the selection of both male and female animals for slaughter, having male animals around allows the most gregarious young males to be selected for castration and work, and a closer relationship with humans to develop. This system could also suggest why reindeer remain morphologically close to their ancestral forms. If genetic selection is often made to *remove* the reproductive capacity of the most desirable individuals rather than to retain it, reproduction is affected much differently than those animals who are breed for certain traits. This too may explain why the smaller but more social barrenground reindeer was domesticated in Fennoscandia and not the larger, stronger wild Finnish forest reindeer. While larger and stronger, the forest reindeer are much less social, even with one another. Forming smaller groups and heavily disposed to flight, these arguably more economically desirable reindeer may have lacked the cultural predisposition to lead them to contact humans or remain in contact with them, thus shunning domestication for their ecotype.

For many Arctic and subarctic cultures, it is integral to the hunt that an animal present itself for slaughter, offering itself up for sacrifice (Willerslev et al., 2015). In winter, hungry and desperate animals may have come to human settlements, willing to sacrifice some of their own in order to claim the benefits of human proximity, including protection from other predators. In this way, the indigenous theory of animals sacrificing themselves may have been the very way in which reindeer domestication began. While we may never know the exact events or processes that lead to the household coalescence of reindeer and humans, it is my intention here to acknowledge the agency of reindeer and caribou, both as cultural groups and as individuals, in shaping their own lives and destinies. Indeed, animal culture may have as much to do with domestication as human culture. In this sense, domestication questions become secondary to human-animal relationship questions.

Dissertation Structure

While the dichotomy between “hard” and “soft” sciences is indistinct, inaccurate, and steeped in the history of academic misogyny and outdated social hierarchies of science, it nonetheless remains in use (Cassell, 2004; Phillips, 2014; Storer, 1967). “Hard” sciences often refer to more quantitative, mathematical, and seemingly masculine scientific disciplines, while “soft” sciences more often describe the more qualitative, interpretive, and supposedly more feminine studies. Anthropology is unusual in that the discipline includes work at both ends of this spectrum, and the studies in this dissertation reflect this tendency, as I attempt to combine both inclinations. Animal agency and individuality are at the forefront of my inquiries, yet to make meaningful hypotheses about animal lives, we must know as many physical details about their anatomy as possible. These topics cannot be addressed solely from a theoretical perspective. The use of analogues is often necessary when little is known about a species, yet we must be aware that in ignoring or dismissing the physical details of animals, we are dismissing their unique biologies and identities. The fundamental goal underlying each chapter in this dissertation is the development of frameworks to study human and *Rangifer* relationships using the bodies of these animals. The chapters are organized from the most quantitative to the most qualitative.

In the first chapter, a new methodology to differentiate *Rangifer tarandus* first and second phalanges between forelimb and hindlimb is presented. This methodology is quantitative, using metrics and morphology to differentiate the phalanges of each limb. The proximal (PI) and medial (PII) phalanges are mathematically described via equations that can be used to determine whether a toe bone comes from a front or a rear leg. In the study of ungulate skeletal remains in zooarchaeology, the phalanges are almost always undifferentiated by limb. They are considered too similar in shape to make such distinctions and are thus lumped together. While I designed this methodology for use on faunal assemblages, my goals in developing this technique were not just the determination of more accurate MNI (minimum number of individuals) figures or better assessment of butchery patterns, but rather the identity of the limbs themselves. As phalanges root all terrestrial animals to the ground, the ways in which we use our limbs are unique to our own movement patterns. In order to learn more about how different reindeer used different feet, I first had to develop a method for telling their toes apart. Without this basic method, many of the subsequent studies would have far more limited application. This chapter was sole-authored, and has been published in *Rangifer* (Hull, 2019).

The second chapter described the *Rangifer tarandus* foot, particularly the soft tissue structures that join with and affect the bones that they shroud. These anatomical details were previous unavailable for *Rangifer*. The dissection of fore- and hindlimbs was undertaken and the soft tissue structures, particularly tendons and ligaments, were explored. With every incision, it became more apparent how unique and beautifully adapted reindeer hoves are, as well as how internally distinct the forelimb was from the hindlimb. From the delicate dewclaws of the hindlimb to the powerful flexor tendons and active and functional dewclaws of the forelimb, every part of each individual reinforced the need for species-level studies of these structures. This study was undertaken with the hope not only to guide future studies of entheseal change and activity reconstruction, but also to be of benefit to humans working with live animals. I believe these animals to be too important as individuals, both in antiquity and modernity, for us to relegate their beautiful and unique anatomical adaptations to interpretations from veterinary textbooks for cows and horses. The chapter was co-authored with Hanna-Leena Puolakka, Sirpa Niinimäki and Mitchell Semeniuk and is currently in review in *Polar Biology*.

The third chapter builds upon this anatomy to assess reindeer habitual activity. The methodologies from chapters one and two were necessary to undertake the study of differences in entheseal changes between wild and domestic reindeer hooves. In order to differentiate the lives and bodies of domestic animals, the entheseal sites of each phalanx of the fore- and hindlimb from adult *R.t. tarandus* and *R.t. fennicus* were scored. This study revealed very different patterns of activity between the groups, leading to the conclusion that the two ecotypes have different mobility and foraging patterns tied to the forms of landscapes they inhabit. The chapter was co-authored with Sirpa Niinimäki and Anna-Kaisa Salmi and is currently in review in the *International Journal of Osteoarchaeology*.

The fourth chapter expands the scope of investigation to the entire skeleton, as pathologies of adult *R.t. tarandus* and *R.t. fennicus* skeletons were explored. This study examined which groups, whether by sex or ecotype, were most likely to incur injury to which parts of the body. This study examined differences in patterns of pathology that could be used to assess the different lives of wild and domestic reindeer. While age-related pathologies remained constant across all groups examined, wild boreal reindeer were far more likely to be subject to long-term traumatic injuries, especially in the hooves. This provides information about the differing dangers reindeer face throughout their lives. Further, the patterns identified relate to their interactions with their environments, providing insight into their lives, and the cultural behaviors of each ecotype. The chapter was co-authored with Hanna-Leena Puolakka and Mitchell Semeniuk and is currently in review in *Animals on the Move: Archaeologies of Animal Movement*, edited by Anna-Kaisa Salmi and Sirpa Niinimäki.

The fifth and final chapter is the osteobiography of a severely injured male *R.t. caribou montanus* from 1930 whose body displays a traumatic and long-term pathology. The chapter chronicles both the investigation into his injury and healing, and my journey in recognition of non-human personhood, which I slowly experienced by proxy his life, injury, survival, and death. The emotional core of this story, developed through the osteobiography, revealed a major gap of understanding between humans and non-human persons, as well as a distinct lack of respect given to the lives and experiences of non-human persons. It challenged my views of the viability and quality of life of injured animals and raised questions related to reproductive ability and roles of non-reproductive individuals. This chapter is a love story between myself and a long dead caribou, as well as an examination of my 'speciest' biases. This chapter was sole-authored and is current *in press* in the journal *Society & Animals*.

The progression of these articles is not only from most quantitative to most qualitative, but also from minute to holistic, and species-based to individual-based. The metric and anatomical studies of chapters one and two describe the minutiae of bone and tendon on a species level. The investigation into entheseal changes in the phalanges shifted investigations into a more complete look at the body and activity, but also divided the samples by ecotype. The study of pathologies by body part, sex, and ecotype further divided the focus into individual animal lives, while also looking at the body, experiences, and life histories more holistically. The final chapter is completely individual, having arguably two subjects, myself and one caribou. His story and body are the focus of the study, as are the theoretical tangles of animal agency and life history that surround the construction of a wild animal osteobiography and studies surrounding non-human persons in general.

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Chapter 1

Metric and Non-metric Guides for the Determination between Fore- and Hindlimb Phalanges of *Rangifer tarandus*

by Emily Hull

Abstract

Phalanges are a great untapped resource in the zooarchaeology of *Rangifer tarandus*. The utilization of this resource, however, is constrained by a current inability to consistently differentiate fore- from hindlimb phalanges in a mixed assemblage. The ability to separate and identify forelimb and hindlimb phalanx 1 (PI) and phalanx 2 (PII), as well as to recognize and identify other small bones of the hoof, leads to great opportunities for archaeologists. In large scale-analysis, this capacity allows a greater ability to determine minimum number of individuals and assess butchery and transport practices. In the examination of individual life histories of *Rangifer tarandus*, these designations allow a more precise study of pathology and entheseal change, which can shed light on adaptation, foraging strategy, and human-animal interactions. This study presents qualitative and quantitative methods for the differentiation of PI and PII of the fore- and hindlimbs and describes other bones of the hoof. Metric techniques were developed to differentiate fore- from hindlimb phalanges using non-invasive, non-destructive, and simple methods. The efficacy and accuracy of these methods were assessed using blind testing by students and staff. The average success rates of metric analysis yielded 87% accuracy for determinations of fore- versus hindlimb PI and 92% accuracy for determination of fore- versus hindlimb PII. These results show that this method could benefit researchers working with *Rangifer tarandus* remains.

Keywords: Rangifer tarandus, osteometrics, zooarchaeology, phalanges, metacarpal, metatarsal, osteology

Zooarchaeological Relevance of Phalanges

While often ignored due to their small size and difficulty in assessment, phalanges are nonetheless an untapped resource available to zooarchaeologists studying ungulates in general and *Rangifer tarandus* in particular. Because most cervid bones are broken or dispersed in archaeological deposits, either by human processing or by subsequent animal scavenging, intact skulls, long bones, or pieces of the axial skeleton are not commonly recovered. By contrast, the hooves, which have minimal meat, contain a network of tough tendinous and cartilaginous tissues, and are therefore less enticing for butchering or scavenging. Bones of the hoof are dense, small, and strong, and thus more often intact. In fact, whole phalanges are commonly found in human-kill and butchering deposits (Binford, 1981). Important osteometric studies of animal phalanges have been performed, especially in Bovids. These can be seen in the designation between fore- and hind-limb cattle phalanges (Dottrens, 1946), the use of phalanges in sex determination of bison (Duffield, 1973), and the subsequent study of metrics and paleopathology in the phalanges of cattle (Bartosiewicz, 1993; Bartosiewicz et. al., 1993). Cervids, however, have not been the subject of such studies, perhaps because *Rangifer tarandus* is the only domesticated cervid. This study describes both qualitative and quantitative methods for the study and distinction of *Rangifer tarandus* phalanges.

In zooarchaeological quantification, phalanges of *Rangifer* are often lumped together, with no attempts to divide fore- and hindlimb phalanges. The extreme difficulty in separating phalanges, due to similarities in morphology and size, may lead to the belief that phalanges of the fore- and hindlimb cannot be differentiated.

Separating both phalanx 1 (PI) and phalanx 2 (PII) of the fore- from hindlimb is significant to both assemblage-based analyses and individual life history studies in zooarchaeology. As phalanges are often among the most abundant complete bones in archaeological *Rangifer tarandus* assemblages, they offer a wealth of information. In assemblage-based analysis, more precise calculations of minimum number of individuals (MNI) are made possible by the specific identification of phalanges. For example, an assemblage with 400 first phalanges, assessed together without designations, must be initially considered to have an MNI of 50, as each individual *Rangifer tarandus* possesses 8 such elements. With more detailed assessment, MNI values can become much more precise. Further, the ratio of fore- to hindlimb phalanges may also give information as to human utilization, butchery practices, and preferential meat procurement (Binford, 1961; Binford, 1978; Steele, 2015). Identifying phalanges is also useful for analyses of *Rangife*r life histories. Different pathologies of fore- and hindlimb phalanges, as well as differences in entheseal changes at muscle attachment sites, may tell archaeologists much about the behavioral patterns of individual animals in life (Bartosiewicz & Gál**,** 2013; Villotte & Knüsel, 2013; Niinimäki & Salmi, 2016; Salmi & Niinimäki, 2016).

Background

Rangifer tarandus is a circumpolar and medium-sized cervid species with large hooves (Banfield, 1961). They are artiodactyls with cloven hooves and large dewclaws that often function as additional, rather than vestigial, toes. Their pattern of morphology follows that of the Telemetacarpalia, a subgroup of Cervidae. In this morphological adaptation, metacarpal (MC) I is not present, and metacarpals III and IV are fused into the central metapodial. Metacarpals II and V are foreshortened to become the dewclaws, which each include a vestigial metacarpal bone, and small PI, PII, and PIII, as well as a small sesamoid bone. In the metatarsal (MT), an analogous development is present, in which the vestigial metatarsals II and V are absent, leaving only the small PI, PII, and PIII, and small sesamoid bone. Metatarsals III and IV are fused into a single metatarsal (Nieminen, 1980, Nieminen, 1994; Cap *et. al.*, 2002).

The unique morphology of *Rangifer tarandus* is epitomized by the size of the feet, much of which is due to the dish-shaped cartilage which covers PIII and appears, in living animals, as the hoof. Telfer & Kelsall (1984) found that *Rangifer tarandus* hoof-to-body-size ratio is more similar to the paw-size of North American predators than to the hoof-size of other cervids. This may be due to their cold-weather adaptation, and again indicates that their morphology must be studied separately and not determined from proxy studies of other artiodactyls (Formozov, 1946; Nieminen, 1994; Geist, 1998).

Materials and Methods

Forty modern skeletal specimens from Finland housed at the University of Oulu were visually inspected. The collections contained both *Rangifer tarandus tarandus and Rangifer tarandus fennicus* of both sexes, all of which were skeletally mature. All had phalanges labelled by side and limb, and these were used in equation design and testing. In addition, six hooves belonging to domestic *Rangifer tarandus tarandus* were dissected for the study. The blind testing was done with a wider range of subspecies, including specimens of *Rangifer tarandus fennicus, Rangifer tarandus tarandus*, and *Rangifer tarandus caribou* from collections at both the University of Oulu and the University of Alberta, Canada. Each test was completed by 23-25 volunteers (dependent upon the test and the time volunteers had available). Volunteers for the blind test were all staff and students at the University of Oulu and the University of Alberta. The volunteers were comprised of 18 students with limited osteological experience, and 7 graduate students and staff with experience in osteology or zooarchaeology. Tests were discarded only for two reasons: first, in one case, improper use of the calipers led to measurements that were up to

220 mm larger than those found by their peers, or, second, the volunteer had written their name or other identification on the test. All tests were given in accordance to ethics approval by the University of Alberta.

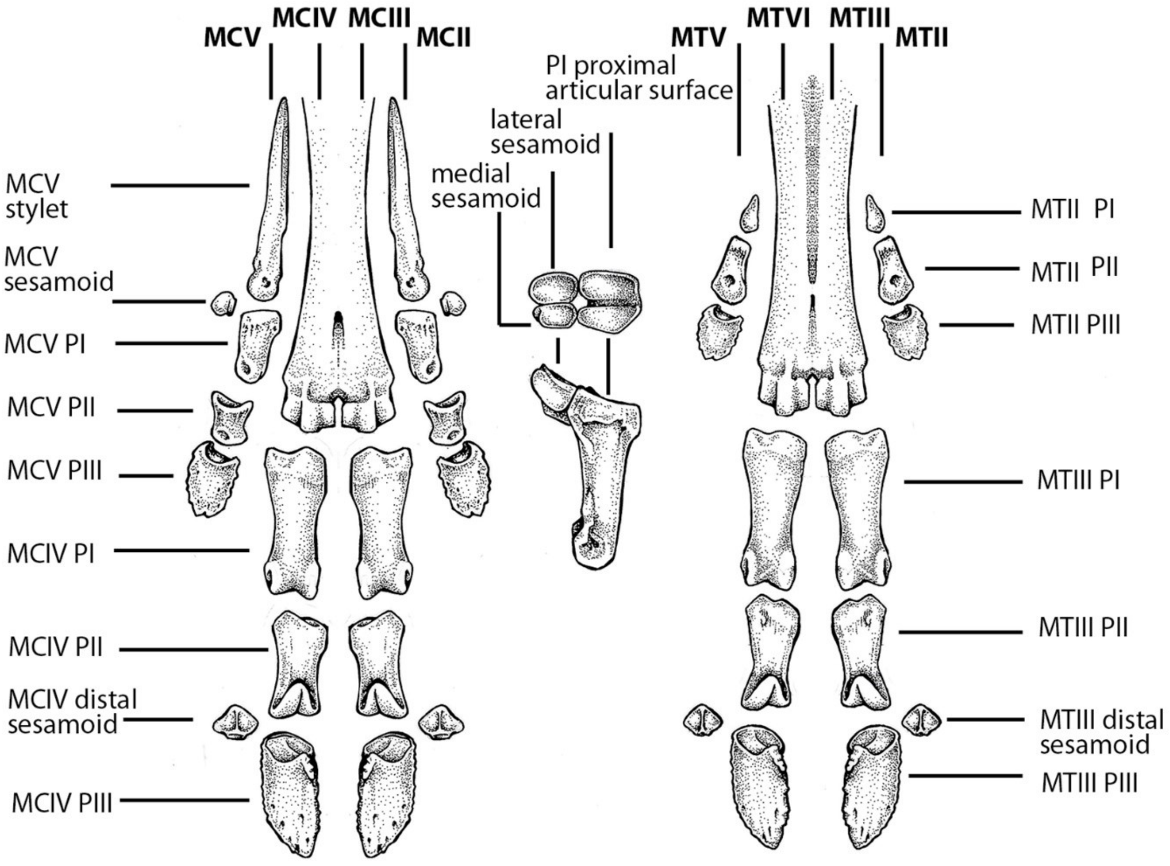


Figure 1. Metapodials, phalanges, and dewclaws, designated by metacarpal/metatarsal and phalanx number. Forelimb is pictured on the left and hindlimb on the right, with proximal sesamoids depicted in the center. (Both illustrations depict right limbs, although it should be noted that at this time there is no accurate test for determining right-limb from left-limb phalanges.) Illustration by author.

Initially, to develop specific written and illustrated descriptions of each bone that could be used to aid in siding and land-marking, each phalanx was examined in detail, and a representative description and diagram highlighting its anatomy and the differences between elements was produced (Fig.2).

Secondly, equations were devised systematically distinguish PI and PII from those of the hindlimb. The primary measurements were adapted from those described for the measurement of long bones by von den Driesch (1976) but were supplemented with other measurements to capture more variation of shape observed. Equations were derived and tested based on each phalanx's most distinct, definitive, and consistent morphological features. Six measurements were taken on each PI, and twelve on each PII, based on the most distinctive features of the bone. More measurements were taken on PII because of their extreme difficulty to separate visually. An additional goal was to ensure that the resulting equations were simple, straightforward, and require no mensuration that could not be expediently achieved with calipers and a calculator. To this end, no more than four measurements were eventually selected for each equation. The overall objective was simplicity and utility in an archaeological context. While both osteometric and morphological techniques are presented in this study, it is hoped that these techniques may be used in conjunction, as visual assessments by morphology are intrinsically subjective, while osteometric techniques are more reliable.

Measurements were collected in a spreadsheet, and trial and error equations, developed with consideration to shape dynamics, were used to find the greatest degree of separation in results. Initial results were also analyzed for differences between the sexes, however, all differences were found to be in size, not in shape. The size difference also included significant overlap, so was deemed unreliable for sexing without additional context.

General Anatomy of the Phalanges

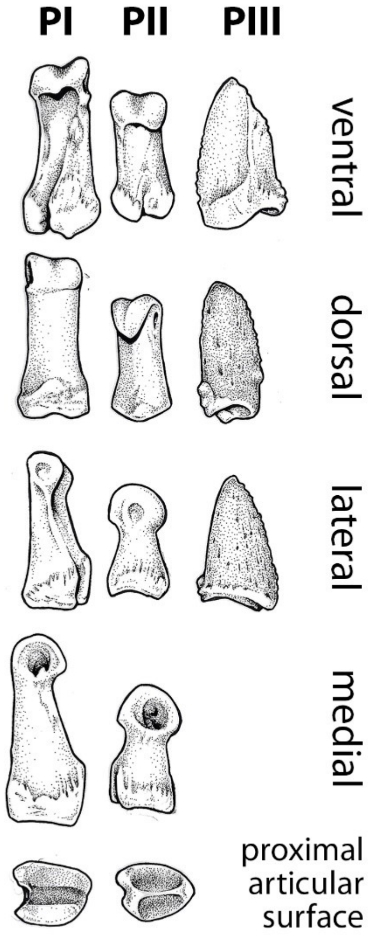


Figure 2. PI, PII, and PIII depicted from multiple angles, in reverse anatomical position. Illustration by author. As each hoof contains two digits, and as the differentiation between the analogous digit of the opposite hoof cannot yet be quantified, each hoof will be presented as the entire subject of study, rather than the entire body of the animal. For this reason, it is important to clarify directional terminology. Medial and lateral sides are designated as medial and lateral to the center of the hoof, not to the animal's body. Thus, the medial side of a phalanx would be the side that faces the center of the hoof, towards the other digit of the same hoof. (Both illustrations depict right limb bones, although it should be noted that at this time there is no accurate test for determining right-limb from left-limb phalanges.)

Phalangeal anatomy may be divided into four sections (Fig. 1): Phalanges I and II, PIII (or the terminal phalanx), sesamoids, and bones of the dewclaws.

Phalanges I and II. While very different in detail, PI and PII follow a general morphological form. These phalanges consist of a distally-oriented head, diaphyseal body, and a concave, proximal articular base.

While it may seem obvious to more experienced zooarchaeologists, it is important to differentiate PI from PII, as this may not be clear to novices (Fig.2). PII is a much shorter, smaller bone than PI, and can be identified by the heart shaped profile of its head when observed from the distal aspect. While the shape of the distal articular surface on PI resembles a spool or a bow with two rounded articular condyles separated by a central groove, the heart-shaped profile of PII is formed by two condyles, again separated by a central groove, which meet at a rounded point on the dorsal side of the phalanx. On the proximal articular surface, PI has a generally rectangular surface, with a central sulcus running dorsally to ventrally, while PII's proximal articular surface is again an inverted heart-shape, with a central ridge running from a small flat surface (often with vascular foramina) at the ventral aspect of the articular surface; this runs through the length of the articular surface before curling upwards to a pointed protuberance on the dorsal side of the phalanx. This surface articulates with the spool-shaped distal articular surface of PI.

Differentiating Medial from Lateral sides of PI. On the distal articular surface of PI are two articular condyles (Fig. 3). One condyle is higher and has a steeper angle than the other. This condyle also typically has much more development on the tendon attachment site just proximal to the articular condyle on the side of the phalanx. This condyle marks the medial side of the phalanx, facing the centerline of the hoof. Additionally, on the proximal articular surface, the medial articular facet is broader and deeper than the lateral articular facet, which often appears as a slightly raised platform.

Differentiating medial from lateral sides of PII. On the distal articular surface of PII are two circular, concave areas just proximal to the distal articular surface on the sides of the bone. The more distinct, concave area marks the medial side of the phalanx. The lateral side will often be quite smooth, with minor or indistinct concavity (Fig. 4). Additionally, on the ventral aspect of the proximal articular surface are two protuberances divided by the central ridge bisecting the articular surface. The side with the longer dorsal to ventral length is the lateral side. This projection will also be generally more robust and protuberant than the medial side.

Differentiating fore- and hindlimb PI. In the same individual, forelimb PI may be distinguished as consistently shorter in length with a more robust base than hindlimb PI, which have a noticeably longer diaphysis (Fig. 3). While the distal articular condyles are quite analogous between the fore- and hindlimb, the proximal articular surfaces at the base of the phalanges are a key distinguishing feature. When viewed from the proximal aspect, directly at the articular surface with the metapodial, the base of forelimb PI is roughly square or circular, with generally equal length and breadth. By contrast, the medial articular facet of hindlimb PI includes a styloid-like protuberance, which extends along the length of the medial articular surface significantly farther than the lateral surface. While the medial articular facet of forelimb PI is often slightly longer than the lateral facet, this difference is not so different to obscure the squared or circular shape of the proximal articular surface of the forelimb phalanx. In the hindlimb PI, the entire articular surface is rectangular, extending much more significantly ventrally-to-dorsally than medially-to-laterally.

In PI, the most diagnostic differences in measurement were found to be the ratio between overall length and breadth of the base. Visual inspection revealed that the shape of the PI base is most representative, with forelimb PI being square-shaped and hindlimb PI being more rectangular. This visual difference was backed up by measurement of the longest length and breadth of the proximal articular surface.

Overall, the difference between fore- and hindlimb PI can be assessed by examining the ratio of width to breadth of the proximal articular surface (Fig. 3). In forelimb PI, the ratio of breadth to width will be equal to or greater than one, and in hindlimb PI, this ratio will be less than one. The most reliable method of differentiation was found in the equation (Appendix, Fig. I): $A/B = X$, where A = the breadth of the proximal articular surface, and B = the longest length of the proximal articular surface. When $X \geq 1$, the phalanx is thoracic (forelimb), and when $X < 1$, the phalanx is pelvic (hindlimb). No results between 0.94 and 1.00 were recorded during the initial development of the equation (Fig.5).

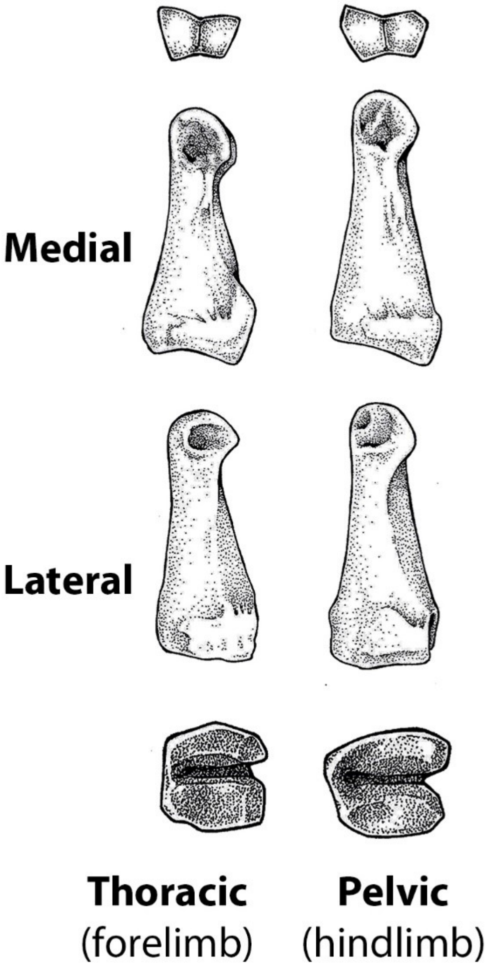


Figure 3. PI (Reverse anatomical position). Illustration by author.

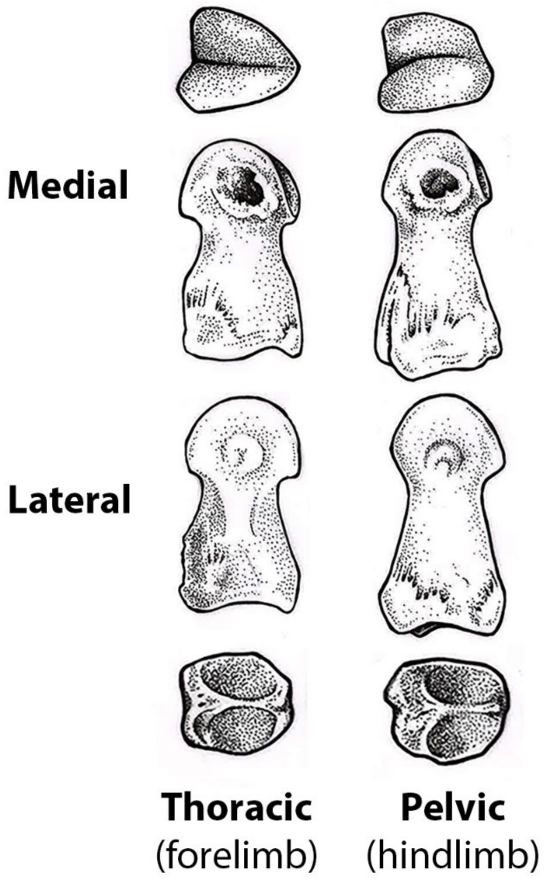


Figure 4. PII (Reverse anatomical position). Illustration by author.

Differentiating fore- and hindlimb PII. The difference between fore- and hindlimb PII in the same animal is subtle. If a single animal is present, the fore- and hindlimb PII can be sorted by general size and robusticity of several features (Fig.4). A forelimb PII is a shorter, more robust bone than a hindlimb PII. In both bones, the head of bone pinches in to create a neck at the distal end of the diaphysis before flaring out to a broad, heart-shaped base. The degree of constriction at this neck is much greater in a hindlimb PII than in a forelimb PII. An additional difference is the presence of more pronounced sharpness at the distal dorsal articular surface on a hindlimb PII, when the head of the phalanx is viewed from the side.

When analyzing disarticulated remains of incomplete or multiple animals, visual observation is not adequate to accurately separate the fore- and hindlimbs. There is significant overlap in the morphology in fore- PII and hindlimb PII from multiple individuals, especially those of different size, sex, and robusticity. For this reason, it is more reliable to use a metric system for analysis, especially for large numbers of individuals.

Several equations were tried using a multitude of variables (Appendix Fig. II), but the most consistent in separating fore- from hindlimb was (A+B)/C =X, where A= the longest total length, B= the length of the phalangeal base, and C= the smallest breadth of the neck. If X > 4.50, the phalanx is thoracic (forelimb); if X < 4.50, the phalanx is pelvic (hindlimb). No results between 4.45 and 4.55 were recorded during the initial development of the equation (Fig.6).

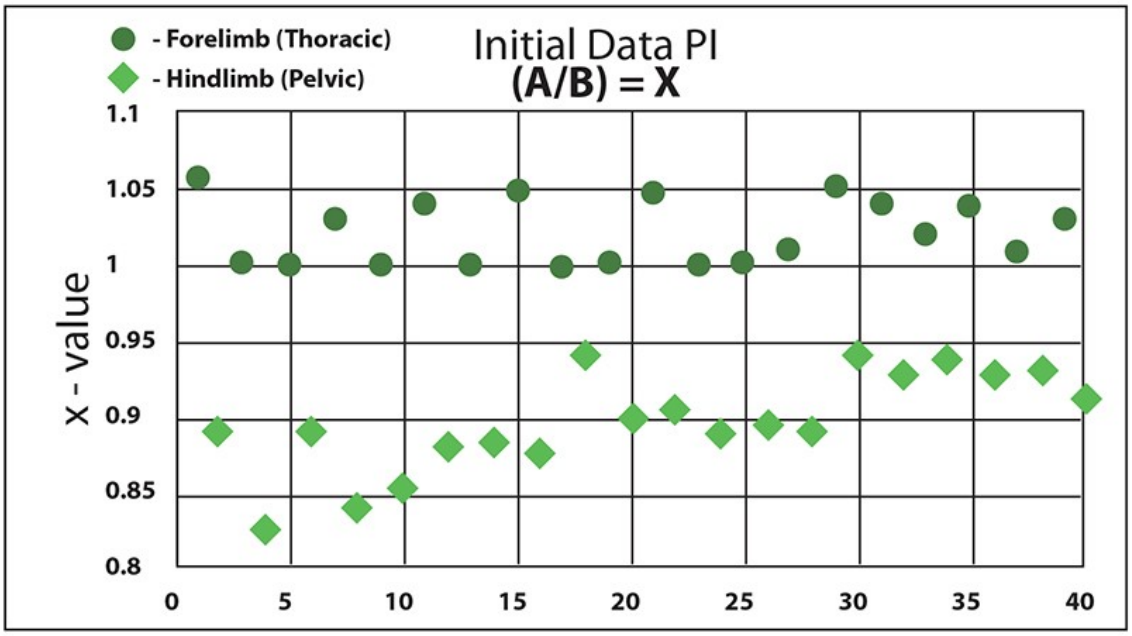


Figure 5. PI. Graph of values from the initial sample (n=40).

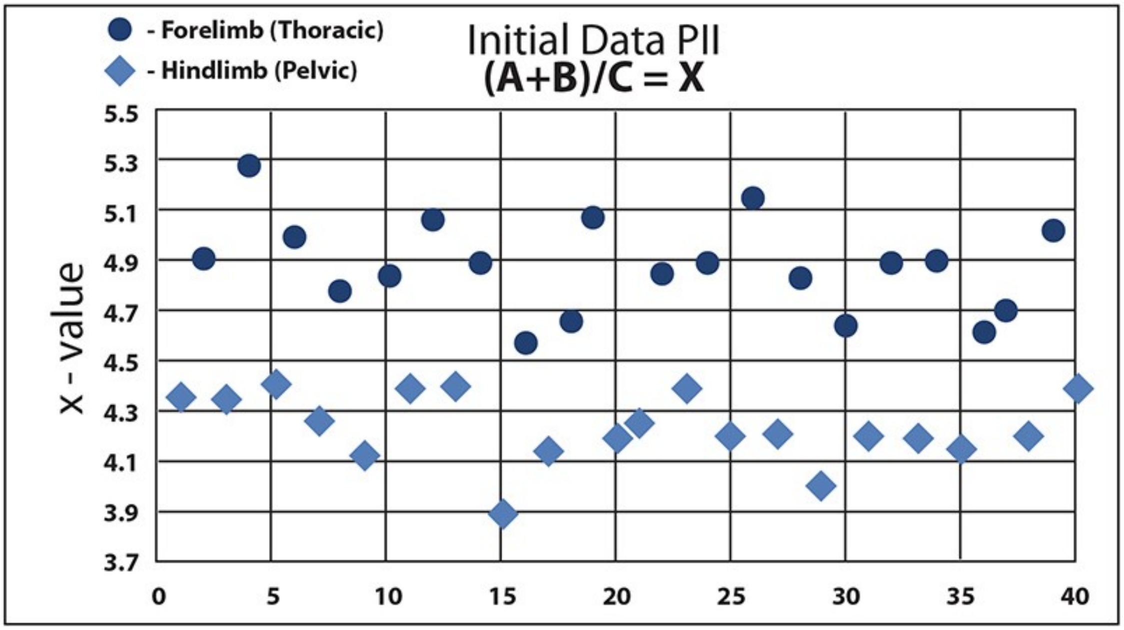


Figure 6. PII. Graph of values from the initial sample (n=40).

Anatomy and siding of PIII. In an individual animal, forelimb PIII may be differentiated from hindlimb PIII by its larger size (Fig.1). No reliable method has yet been found to differentiate fore- from hindlimb in a mixed-individual sample, and therefore must be the subject of further study. Siding, however, is quite clear. PIII is triangular in shape, with a proximal articular surface with three articular facets, and three generally flat surfaces converging to a pointed distal end. The largest, most curved of these surfaces forms the dorsal side of the hoof and can be additionally recognized by its high degree of ruggedness and plethora of vascular foramina. The ventral surface of PIII is quite smooth and often only shows ruggedness along muscle attachment sites at the proximal border and along the lateral edge of the surface. The medial surface of PIII is the smallest of the three sides, and houses two large vascular foramina just distal to the articular surface. The largest of these is present along the ventral edge of the surface. In order to side PIII, simply place it on the table in anatomical position, and the position of the medial surface will show whether it is on the medial or lateral side of the hoof. The two largest articular facets articulate with the head of PII. The smallest, on the most dorsal aspect of the articular surface, articulates with the distal sesamoid bone. This articular facet is also distinct between the fore- and hindlimb of the same individual, with the forelimb PIII's sesamoid articular facet being both smaller and more medially located than that of hindlimb PIII. Because of the range of inter-individual variation, however, neither this criteria nor size can be consistently used to separate fore- from hindlimb bones in a mixed assemblage.

Anatomy of the sesamoids.

Proximal sesamoids. Two proximal sesamoids (Fig.1) attach to the proximal dorsal aspect of PI and articulate with both the metapodials and PI in both the fore- and hind-limb. They can easily be differentiated into medial and lateral by their distinct shape. They are both lunate in shape, but the ventral, non-articular surface of the medial sesamoid is much more rounded. By contrast, the ventral, non-articular aspect of the lateral sesamoid extends to a rounded ridge. While the medial sesamoid is ovoid in shape with a flat base, the lateral appears more as a medially-to-laterally flattened trapezoid. The difference in morphology of these bones is consistent enough to be used to distinguish these bones in a mixed assemblage.

Distal/navicular sesamoid. The distal sesamoid bone makes up the heel of the hoof. It articulates with PIII on the proximal dorsal aspect and can be identified by its unique shape. This bone is shaped differently in the fore- and hindlimb hooves. The forelimb distal sesamoid is small and has the general shape of an equilateral triangle, with two dorsal articular facets of equal size articulating with PII. A round articulation at the distal end, at the opposite face from the apex of its triangular shape, articulates with PIII.

In the hindlimb, the distal sesamoid bone is larger, with uneven articular facets; the lateral facet has a larger surface area and creates the general shape of an obtuse triangle. Like the distal sesamoid of the forelimb, it has three articular facets in the same configuration: two articulating with PII, and one articulating with PIII. Despite these disparities, inter-individual variation makes these differences inappropriate for the determination of fore- from hindlimb phalanges in a multi-individual setting.

Dewclaws. Dewclaws of *Rangifer tarandus* (Fig. 2) contain their own unique skeletal anatomy, analogous to but distinct from the primary metapodials and digits of the hoof. They do not directly articulate at any point with the metapodial but are instead held in place by a network of connective tissue and ligaments. The forelimb dewclaws contain vestigial MCII and MCV which appear as sharp, linear stylet with a rounded distal articular surface (Barone, 1986). At this point, a rudimentary PI, PII, and PIII all articulate in succession beginning with the MCII/MCV and MCIIPI/MCVPI. In hindlimb dewclaws, the MCII/MCV stylet component is no longer present, and the complex contains only the phalangeal bones of MCIIPI/MCVPI, MCIIPII/MCVPII, and MCIIPIII/MCVPIII.

Differentiation between primary PIII and dewclaw PIII. The bones of the dewclaw are unlikely to be mistaken for any other bones of the hoof with one exception: PIII. While size is an important distinguishing factor between the PIII of the dewclaws and the primary PIII bones, it is important to note morphological differences, as the dewclaw PIII bones of a large adult animal may be close in size to the primary PIII bones of a small, young animal. Morphologically, PIII of the dewclaws have rough, vascularized edges around the entire border of the bone apart from the proximal articular surface, and is bifacial, having a front and a back surface running the length of the bone. By contrast, primary PIII bones have a triangular shape and have a rough, serrated edge only on the external margin. The internal border of the dewclaw PIII is smooth, straight, and flat, emerging nearly perpendicularly from the dorsal surface. Both PIII bones have large vascular foramina, which occurs on the dorsal surface of the dewclaw PIII and the interior surface of primary PIII bones.

Blind Tests

Students all used digital calipers to diminish errors that might be made while reading traditional dial calipers. Each bone was marked with a number or letter on tape, which also covered their collection specimen numbers, as these could have provided bias to the experienced osteologists.

Test A: Qualitative test. Volunteers (n= 25) were given ten randomly numbered PI and PII phalanges with red and blue dots randomly placed on the sides of each. They were asked to use the diagrams (Fig. 3 and 4) and the descriptions above to designate them as PI and PII as well as to identify the medial and lateral sides of each bone. The purpose of this test was two-fold: first, to assess the usefulness of the illustrated guide and descriptions, and second, to allow the novice volunteers to become more comfortable observing the phalanges.

Test B: Qualitative and quantitative differentiation between forelimb (TPI) and hindlimb (PPI). Volunteers (n= 23) were given a randomly numbered sample of ten PI phalanges and assigned (in separate sub-tests) to use illustrations and diagrams (provided in the Appendix) to divide them into fore- and hindlimb bones first, and then to use equations to do the same. This was done to compare the effectiveness of observation versus quantitative analysis.

Test C: Qualitative and quantitative differentiation between forelimb (TPII) and hindlimb (PPII). Volunteers (n= 23) were given a randomly numbered sample of ten PII phalanges and asked (in separate sub-tests) to use illustrations and diagrams (provided in the Appendix) to divide them into fore- and hindlimb bones first, and then to use equations to do the same. This was done to compare the effectiveness of observation versus quantitative analysis.

Projected test results. It was expected that the Test A would produce consistently good results, as the differences between PI and PII, and medial and lateral aspects were quite distinct once identified. It was projected that Test B, differentiating fore- and hindlimb PI, would result in a high rate of correct assessments as the equation is quite simple and the differences between the elements are often observable to the eye. It was thought that Test C would produce a lower rate of correct assessments, as the differences are very subtle to observe and the equation involves somewhat more complex measurements.

Blind test results.

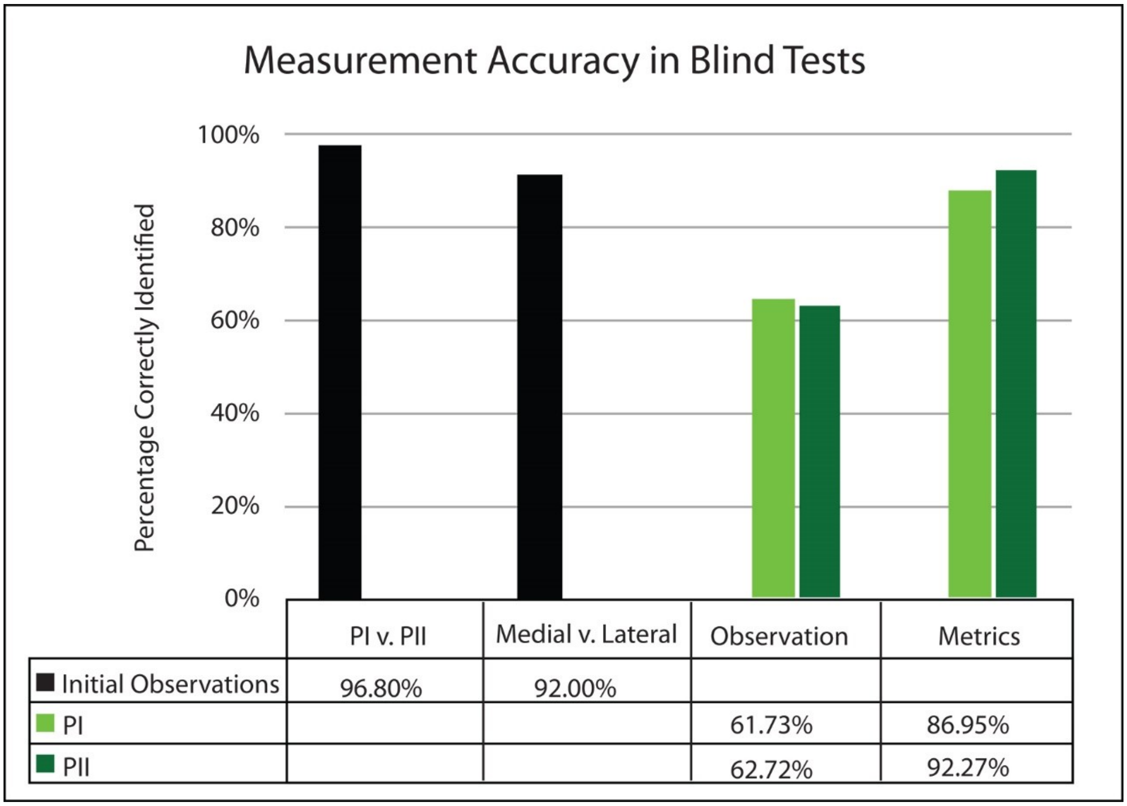
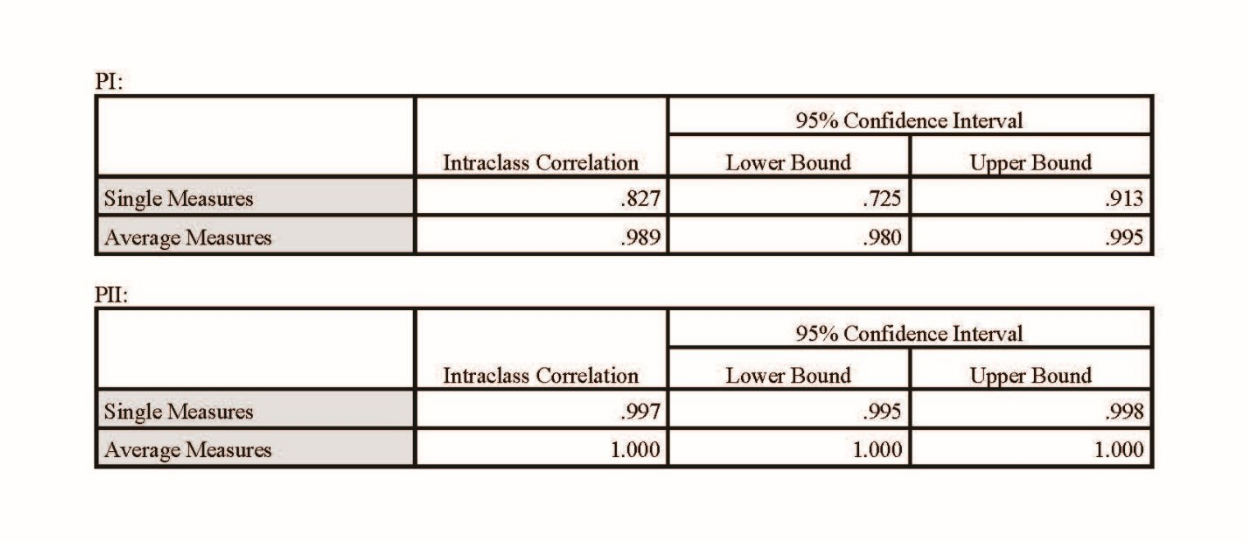


Figure 7. Graph of Blind Test Results. Black bars represent Test A; Light Green, PI Test B; Dark Green, PII Test C.

Discussion

While the blind tests did support the higher accuracy of metric determinations versus observation, the projected comparative accuracies of each test were somewhat unexpected. Designation between PI and PII, as well as the determination of medial and lateral aspects were very consistent. Any errors may be explained by the inexperience of some of the volunteers. The unexpected results appear in the metric determination between PI and PII. Because of the simplicity and observability of fore- versus hindlimb PI, it was expected that both observation and metric tests of this digits would yield the highest accuracy. The actual results, however, belied this hypothesis (Fig.7). Results of observation were nearly indistinguishable between PI and PII (62% and 63%, respectively), and the PII metric blind tests yielded higher accuracy than the PI tests, with PII metric tests yielding a mean of 92% (mode= 100%) accuracy, and PI metric tests a mean of 87% (mode= 90%) accuracy. To check observer reliability, measurements from the volunteers were assessed by calculating Intraclass Correlation Coefficients. According to generally accepted standards, an Intraclass Correlation Coefficient (ICC) with a value over .750 is considered excellent, while an ICC value of between 0.60 and 0.74 is considered good (Cicchetti, 1993; Fleiss, 1986). In this study, the ICC values were calculated for absolute agreement between blind testers. The ICC for Test B showed an average measure value of .989. The ICC for Test C showed an average measure value of 1.000. All values are shown in Fig. 8.



PI:

	Intraclass Correlation	95% Confidence Interval	
		Lower Bound	Upper Bound
Single Measures	.827	.725	.913
Average Measures	.989	.980	.995

PII:

	Intraclass Correlation	95% Confidence Interval	
		Lower Bound	Upper Bound
Single Measures	.997	.995	.998
Average Measures	1.000	1.000	1.000

Figure 8. ICC values calculated for absolute agreement between blind testers.

There are multiple possible reasons for the discrepancy between measurement accuracy between PI and PII. First, perhaps a lack of familiarity with calipers led to minute measurement errors that became more apparent in the PI equation, which is a direct ratio, rather than in the PII equation, which is a more complex calculation. Second, as PI has a circumference-long area of rugosity and muscle attachment sites just distal to the edge of the articular surface (Fig. 1, Fig. 2), it is possible that the volunteers were measuring from this highly variable area, rather than from the edge of the articular surface. For this reason, the guidelines were amended to warn against this possibility. Another possible reason for the error margin is that participants may have paid more attention to the blind test with the more complex measurements, thereby giving this test more accuracy. The results, however, do support the usability and effectiveness of these measurement guidelines, especially with experience and practice.

Conclusions

While many current studies produce detailed results with advanced morphometrics, it was important in the design of this study to utilize simple measurements and to produce equations that could be done in the field or lab with only a set of calipers. The blind tests were done by students and staff who, with few exceptions, had never before studied or done metrics on *Rangifer tarandus* remains, and many had never practiced metrics analysis of any kind. The level of accuracy during their initial attempts suggests that with practice, accuracy would only increase. In the creation of these descriptions, diagrams, and equation-based determinations, the focus was on non-destructive usability, and this was demonstrated to be the case in the blind tests. With these guidelines and tools, more precise determination of fore- and hindlimb phalanges is clearly possible. Traditional zooarchaeology and assemblage-based analysis could utilize this technique for more precise determination of MNI, butchery practices, and preferential transport of meat. In studies of domestication, it has been shown that reindeer involved in different activities show different entheseal changes and pathologies; this technique could benefit this study by allowing the differential analysis of the habitual stressors on fore- versus hindlimb (Niinimäki & Salmi, 2016; Salmi & Niinimäki, 2016). Finally, in the emerging and expanding research areas of human-animal relationships, individual animal life histories, and animal ontologies, a more distinct understanding of the bones of the hooves may help elucidate topics from habitat, foraging techniques, and individual pathology. This technique has the potential to be an extra tool in the study of the osteology and archaeology of *Rangifer tarandus* in both modern and ancient America and Eurasia.

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Chapter 2

Tendons and Ligaments of the *Rangifer tarandus* metapodial and hoof

By Emily Hull, University of Alberta*, Mitchell Semeniuk, University of Alberta, Sirpa Niinimäki, University of Oulu, Hanna-Leena Puolakka, University of Oulu

Abstract

Rangifer tarandus, the northern species including both reindeer and caribou, is a pillar of northern ecosystems and the lives of northern peoples. As the only domestic cervid, reindeer are of great interest not only to the herders and hunters who presently interact with them, but also to zooarchaeologists and palaeontologists tracing their histories. Unfortunately, limited anatomical information on *Rangifer tarandus* muscles is available beyond descriptions of the large muscle groups. The hoof in particular is poorly documented. This is problematic, as this important body part has the potential to be informative in zooarchaeological analyses of habitual activity. Better understanding of the hoof can additionally be useful to herders and veterinarians seeking to provide veterinary care for living animals. This study undertakes dissections and comparisons of the reindeer hoof with other domestic ungulates to better document both the common and unique structures in *Rangifer tarandus* hooves.

Keywords: Rangifer tarandus, gross anatomy, hoof, phalanges, metapodials

Introduction

While reindeer and caribou are and have been a keystone species for human survival and ecological stability in the Arctic and sub-Arctic north, gaps in our knowledge of *Rangifer tarandus* anatomy persist. This is particularly true when discussing the hooves of reindeer. Veterinarians, hunters, and herders have first-hand knowledge of the anatomy and physiology of the reindeer hoof, but no guide for the novice has yet been produced. This study presents the origins, insertions, and primary actions of the tendons and ligaments of the hoof in order to further knowledge of *Rangife*r biology and anatomy.

In human osteology, osseous changes at the points of muscle, tendon, or ligament insertion, known as entheseal changes, are commonly examined to help reconstruct habitual activity (Villotte & Knüsel 2013). This technique is also beginning to be used in zooarchaeology in determining the habitual activities of domestic animals, particularly those of reindeer (Niinimäki & Salmi 2016, Salmi & Niinimäki 2016). In northern archaeology and human-animal studies, reindeer have been the subject of study as prey animals, herded animals, penned animals, ridden mounts, draught animals, and ritual offerings (Ingold 1980, International Centre for Reindeer Husbandry 2017, Mirov 1945, Nyyssönen & Salmi 2013, Salmi et. al. 2015, Sommereth 2011, Stammler & Takakura 2010, Stépanoff, et. al. 2017). Given this wide array of potential roles played by reindeer, determining the activities they undertook in life will help scholars better discern the specific ways in which these animals interacted with humans and their broader environments.

The study of entheseal changes as an analytical technique, however, is predicated on the knowledge of the exact muscles, tendons, and ligaments that act to cause habitual stress on the bone. Without this baseline information, accurate and effective assessments of habitual activity are impossible. In order to glean information from the entheseal changes of the phalanges, for example, it is first paramount to understand the soft tissues structures of the hoof and their functions.

This examination of the tendinous and ligamentary anatomy of the *Rangifer tarandus* hoof is designed to enable zooarchaeologists to study reindeer and caribou of the past, and to enable modern caretakers to more effectively promote the health of living reindeer. An additional concern in studies of *Rangifer tarandus* is the complications presented to these animals and the societies and cultures that depend on them. As climate change impacts the circumpolar north, habitat loss and social pressures threaten the lives of *Rangifer tarandus* and in turn, the people who herd and hunt them. As a keystone species of the north, understanding of the past and present of *Rangifer tarandus* is important in providing a viable future for these animals.

Background and Reference Species

Rangifer tarandus is a northern species with many subspecies and uniquely adapted ecotypes. Known as reindeer in Eurasia and caribou in North America, this species has been an important prey animal for humans since the Magdalenian (Kuntz & Costamagno 2011). Reindeer have become domestic herd animals who provide meat and fur, but also locomotion, traction, and milk (Aaris-Sørenson et al. 2007, Andersen 2011, Laufer 1917, Mirov 1945). The herding communities of Europe and Asia depend on the health and stability of this species, even as climate change and changing environments challenge the health and wellness of these animals. Reindeer are also of great interest to zooarchaeologists tracing cultural change and incipient domestication, as reindeer have held roles within human societies as unique as their biology.

While reindeer are far from the only domestic ungulate, they are the only domestic cervid. Even among cervids, reindeer hoof morphology is unique. Most studies of *Rangifer tarandus* musculoskeletal anatomy focus on the torso and upper limbs, as these are the most well-known and valuable areas of musculature to hunters and butchers. The most complete guide to the musculoskeletal anatomy of the *Rangifer tarandus* limbs is Wareing et al. (2011), which identifies and defines the gross anatomy of the limbs. However, the discreet attachment point of tendon insertion and ligamentory architecture of the lower limbs are not described in enough detail that points of insertion and connection on the phalanges can be determined. A precise and detailed guide to the soft tissue of the *Rangifer tarandus* lower limb and hoof is warranted.

Though a small portion of the overall body mass, *Rangifer tarandus* hooves are of primary importance to their health and viability. The foot is the interface between the environmental matrix and the body, but for the reindeer, the hoof functions in many other important ways. As a migratory species, *Rangifer tarandus* must depend upon their hooves to carry them long distances (Ferguson & Elkie 2003). Further, their chiniophilic adaptation requires strong forelimb digging, which involves using the front hooves to penetrate dense snowpack for lichens during snowy seasons (Formozov 1946, Nieminen 1993, Takatsuki 1992).

The far northern environments that constitute the habitat of most *Rangifer tarandus* have produced extreme cold weather adaptations. These include foraging adaptations to both tundra and the deep snow drifts of the taiga, both of which necessitate a broad hoof platform. Locomotory adaptions of animals in snow-heavy habitats have been investigated in previous studies. Most measure hoof-load (Telfer & Kelsell 1971, 1984; Takatsuki 1992), which provides a proportional measurement of body weight to foot area. The smaller the hoof-load, the higher the proportion of foot area to overall body mass. Caribou and reindeer have a much lower hoof-load than other ungulates, including *O. virginianus* and *O. hermonius*, a size ratio more akin to that of northern predator species than prey (Telfer & Kelsall 1971, 1984; Blanco and Gambini 2006). Their broad feet allow reindeer and caribou to walk over the snow, and their strong digging hooves can penetrate snowpack and deep, dense snow drifts. More southerly ecotypes such as boreal reindeer and caribou often wade through muddy waters and swamplands, and navigate rocky and rugged terrain, again depending on their broad hoof-spread to facilitate mobility and foraging in these environments (Nieminen 1990, 1993; Takatsuki 1992).

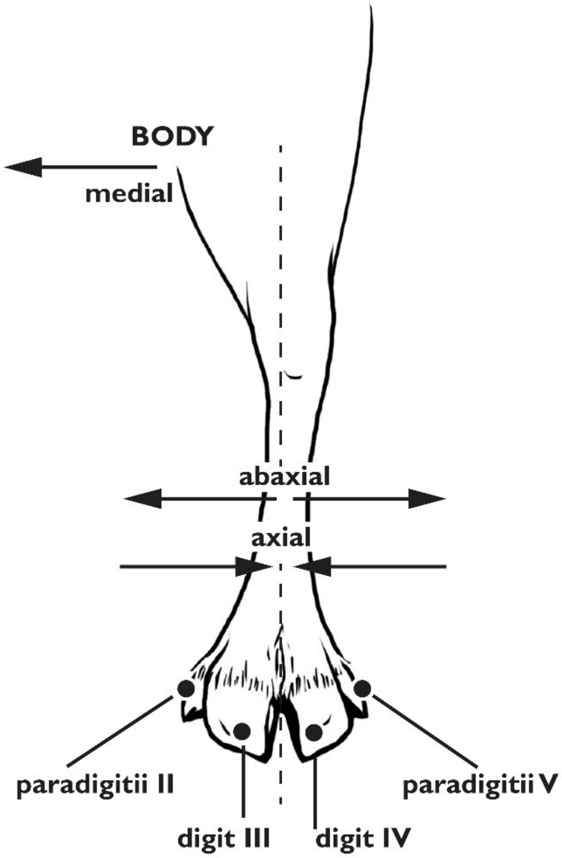

Figure 1. Directions and terminology. Left forelimb pictured. Illustration by E. Hull.

Despite the importance of these hoof adaptations to *Rangifer*, no comprehensive guide to the soft-tissue structures of the reindeer hoof is available. Other cervids suffer from the same gap in published information. This study, therefore, takes references from better documented species, particularly *Equus* and *Bos taurus*. Bovids are the most thoroughly documented domestic two-toed ungulates, and as such, bovid literature will provide the primary source for structure identification, nomenclature, and comparative physiology. This literature will be supplemented with information from equids. Specifically, soft tissue terminology was used or adapted from Budras et. al. (2011), Budras et. al. (2003), Smallwood (1992), and McLeod (1958), unless otherwise cited. Osteological nomenclature was adopted from Barone (1986), Budras et. al. (2011) and von den Dreisch (1976).

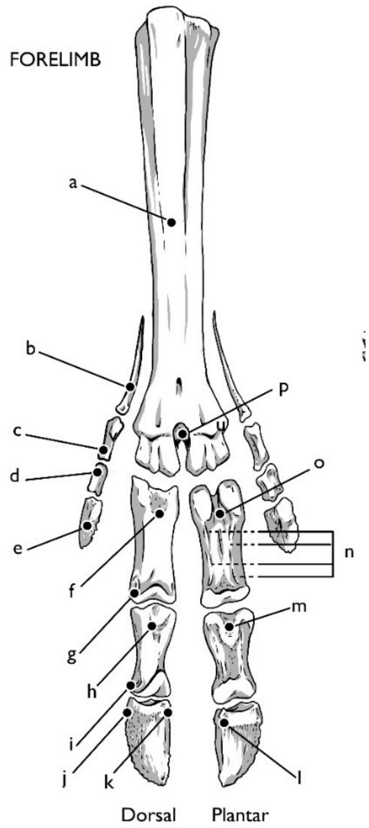

Figure 2. Bones of the forelimb. a) metacarpal (only dorsal aspect shown) b) MC V/II c) paradigitii PI d) paradigitii PII e) paradigitii PIII f) first phalanx (PI) g) head of PI h) second phalanx (PII) i) head of PII j) third phalanx (PIII) k) extensor process l) flexor tubercle m) flexor tuberosity n) axial and abaxial palmar eminences o) intercapital notch. Illustration by E. Hull.

Bones of the Lower Limb

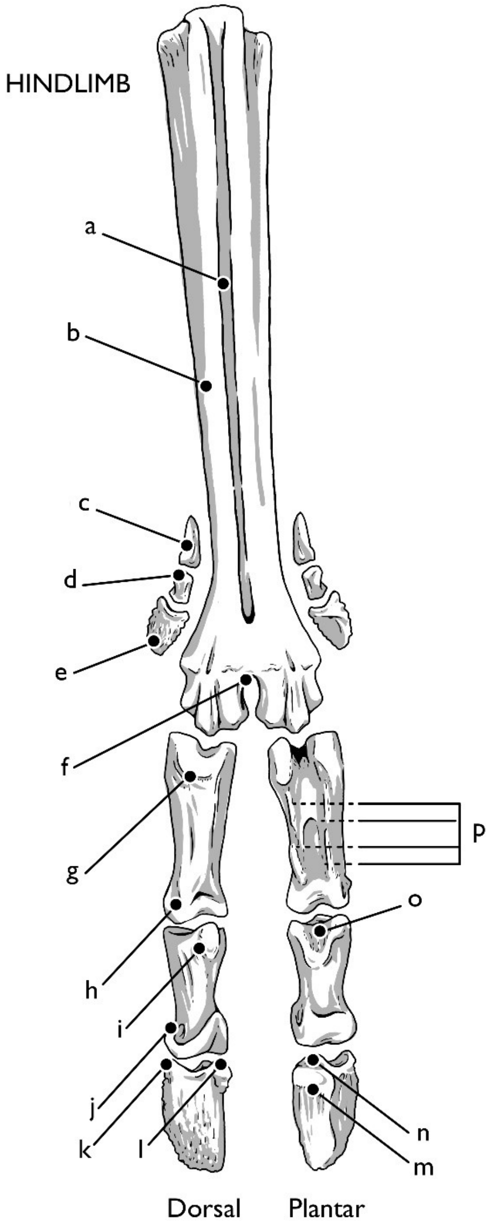

Figure 3. Bones of the hindlimb. a) longitudinal groove b) metatarsal (only dorsal aspect shown) c) paradigitti PI d) paradigitti PII e) paradigitti PIII f) intercapital notch g) first phalanx (PI) h) head of PI i) extensor tubercle of second phalanx (PII) j) head of PII k) third phalanx (PIII) l) extensor process m) plantar surface n) flexor tubercle o) concavity of flexor tuberosity p) axial and abaxial palmar eminences. Illustration by E. Hull.

Rangifer tarandus are artiodactyls, having two toes and two dewclaws per hoof, with a fused metacarpal/metatarsal III and IV to form the metapodial. Vestigial metacarpal II and V are present as stylets of the forelimb dewclaws, but absent in the hindlimb. Each limb contains (Fig. 1, Fig. 2, Fig. 3) a metapodial, three phalanges (three per each of two digits: PI, PII, PIII), dewclaws (each containing 4 bones in the forelimb and 3 in the hind), four proximal sesamoids, two distal sesamoids, and, in the forelimb, two dorsomedial sesamoids (Hull 2019). This osteology follows the pattern of other members of Telemetacarpalia (Nieminen 1994). Bovids, and artiodactyls in general, follow the same basic pattern, with the deviation of the dewclaws. In *Bos taurus*, the dewclaws rarely contact the ground, providing a different function than those of cervids. The dewclaws of *Rangifer tarandus* spread out against the ground, providing additional surface area for walking. When the forelimb is flexed, the dewclaws curl inward, providing a more efficient, shovel-shaped plantar surface for digging in the snow.

This increased functionality of the dewclaws leads to more substantial bones of the dewclaw, as well as more extensive ligamentary structures. Because of this, the suspensory ligaments connecting the dewclaw of *Rangifer tarandus* to the hoof proper should be considered as important as the other ligaments. While veterinary literature often glosses over the dewclaws of *Bos taurus*, they must be thoroughly discussed in *Rangifer tarandus* hoof anatomy.

Materials and methods. Dissections were conducted on the forelimbs and hindlimbs of three individuals, all juvenile male *Rangifer tarandus tarandus*. Despite being juvenile, all epiphyses of the lower limb were fused, making them appropriate for study. Dissection began at the proximal metapodial and continued throughout the hoof. Each specimen was first skinned, and dissection proceeded with each compartment, moving from superficial to deep. All dissections were photographed and video-recorded for reference. As the musculature of the fore- and hindlimb have been detailed by Waring et. al (2011), the dissections and study began distal to the carpals and tarsals, including the metapodials, phalanges, and dewclaws. Results are broken down by joint, with discussions focusing on the component structures of the fetlock, pastern, and coffin joints. As these structures are generally analogous between fore- and hindlimb, the use of domestic ungulate joint terminology is used, except in those places where the metacarpophalangeal joints differ from the metatarsophalangeal joints. Origins and insertions for each tendon and ligament are listed in Table 1 (listed at the end of the article).

All individuals dissected were culled and donated by a reindeer herder. The limbs were unwanted by-products after routine butchering, which would have been thrown out, as there was no useable meat on this portion of the animal. Remains were stored frozen at -22°C before the dissection process. All remains were treated with care, and guidelines for respect towards human cadavers were followed. No animals were killed to facilitate this study.

The metapodials. The metacarpal (MC) and metatarsal (MT) bones are similar in shape, with a few notable differences (Fig. 2, 3). Both are the fused third and fourth metapodials, and this double-sided form can be seen in the metacarpal from the proximal articular junction with the carpals. Here the tuberosity of MC III designates both the medial side of the metacarpal and division between MC III and MC IV. On the metacarpal, a long dorsal longitudinal groove follows the central line of the shaft, terminating at the intertrochanteric or intercapital notch between the two round articular surfaces of the head of the metacarpal. On the metatarsal, there is no tuberosity of MT III, but both dorsal and ventral longitudinal grooves vertically bisect the metatarsal shaft. The lateral aspect of the dorsal metatarsal shaft, divided by the dorsal longitudinal groove, is significantly more robust than the medial aspect. The interosseous ligaments and flexor tendons run through the dorsal groove the length of the metatarsal (and against the dorsal aspect of the length of the metacarpal), and the combined extensor capsule follows the length of the ventral longitudinal groove on both metapodials.

The round, spool-shaped trochanters on the head of the metapodials provide the platform for articulation of the first phalanx and the proximal sesamoid. The cup-shaped concavities on the sides of the metapodial heads provide the origin for the abaxial metacarpo- and metatarsophalangeal collateral ligaments. The deep indentation between the trochanters of the metapodial head are alternately referred to as the intercapital or intertrochanteric groove, which serves as the origin site of the axial metacarpo-/metatarsophalangeal collateral ligaments.

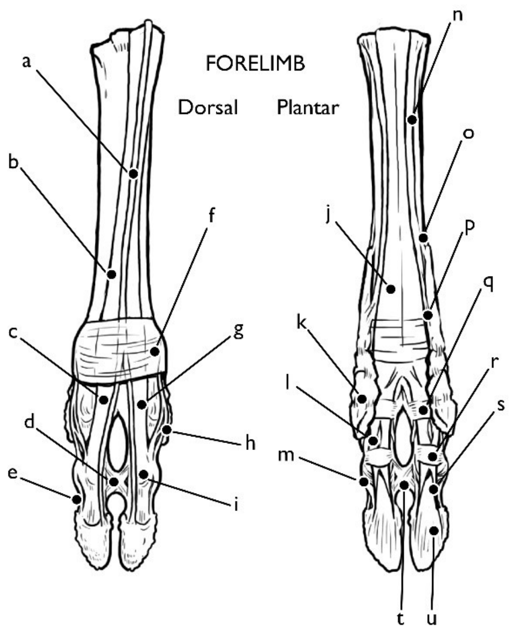

Figure 4. Forelimb tendons and ligaments

Dorsal: a) common digital extensor tendon b) medial/lateral extensor tendon c) lateral extensor tendon d) interdigital cruciate ligament e) lateral collateral distal interdigital ligament f) plantar annular ligament g) medial extensor tendon h) abaxial extensor branch i) extensor junction

Plantar: j) superficial and deep flexor capsule k) paradigitii/dewclaw l) separation of manicae flexoriae m) lateral collateral interdigital ligament n) interosseous ligament o) interosseous accessory branch to paradigitii II/V p) proximal accessory ligament to paradigitii II/V q) proximal annular ligament r) distal annular ligament s) superficial flexor tendon insertion t) interdigital cruciate ligament u) deep flexor tendon insertion. Illustration by E. Hull.

Metacarpophalangeal joint (forelimb fetlock joint). The fetlock joint is located where the metapodial articulates with the first phalanx, as well as with the proximal and dorsomedial sesamoids. The metacarpophalangeal joint is held together with collateral ligaments on the abaxial surfaces, axial collateral ligaments between the metacarpal and the first phalanx, and smaller cruciate ligaments supporting the plantar (proximal) sesamoids of each digit. The collateral ligaments of the fetlock joint run from the cup-shaped concavities on the abaxial aspects of the metacarpal capita and then divide, with one ligament going to the proximal plantar surfaces of the first phalanges. The other ligament combines with the cruciate ligaments holding the proximal sesamoids to the first phalanx. The large axial collateral ligaments, which attach the metacarpal to the first phalanges, run from each side of the interior intercapital notch of the metacarpal capita to combine with the axial portion of the small cruciate ligament of the same digit. These small cruciate ligaments, along with small sesamoidean ligaments, attach the metacarpal and proximal sesamoids to the axial eminences along the proximal axial and palmar surfaces of the first phalanx. The fibers of these cruciate ligaments run perpendicularly to the shaft of the first phalanx and may be distinguished by the direction of osseous build-up at the attachment point. This site is adjacent to the attachment point for the proximal annular ligaments, whose attachment site runs along the plantar surface, rather than extending along the axial surface.

Two layers of tendons run down the dorsal side of the metacarpal (Fig. 4). Superficially, the robust combined capsule of the superficial and deep flexor tendons run along the metacarpal, with the superficial flexor tendon creating a sheath (manicae flexoriae) around the deep flexor tendon until just proximal to the pastern joint. The combined tendons bifurcate at the fetlock joint to follow the individual digits III and IV. The interosseous ligaments run deep to the flexors. The interosseous ligaments begin as a thin, flat, fibrous structure that lays flat against the metacarpal. At the fetlock joint of the forelimb, the interosseous ligament divides into seven branches. The axial and abaxial extensor branches (divided into interosseous III and IV dependant on the digit which they serve) run on either side of each digit, while the medial branch inserts into the intercapital notch of the metapodial. The axial branches run on the internal surface of the hoof, crossing from the plantar to dorsal aspect of the hoof. The abaxial branches follow an analogous path on the outer surface of the hoof. The abaxial branch also subdivides, providing a small tendon to the proximal sesamoid bone. The axial and abaxial extensor branches of the interosseous ligaments recombine on the dorsal surface of the hoof, joining with the medial and lateral extensors at the extensor junction of the pastern joint. Two small accessory ligaments also subdivide, with the interosseous accessory ligament for paradigitii V subdividing from interosseous IV and the accessory ligament for paradigitii II subdividing from interosseous III. These ligaments attach to the axial aspect of the stylets of the dewclaws in the forelimb before continuing to a second attachment site on the proximal abaxial surface of PI proper and act to stabilize the dewclaw.

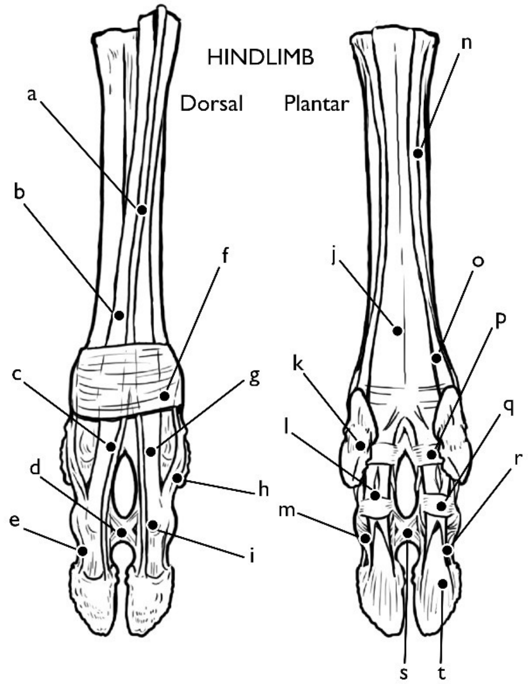

Figure 5. Hindlimb tendons and ligaments

Dorsal: a) long digital extensor tendon b) medial/lateral digital extensor tendon c) lateral digital extensor tendon d) interdigital cruciate ligament e) lateral collateral distal interdigital ligament f) plantar annular ligament g) medial digital extensor tendon h) abaxial extensor branch i) extensor junction

Plantar: j) superficial and deep digital flexor capsule k) paradigitii/dewclaw l) separation of *manicae flexoriae* m) distal interphalangeal collateral ligament n) interosseous ligament o) interosseous accessory branch to paradigitii II/V p) proximal annular ligament q) distal annular ligament r) superficial digital flexor tendon insertion s) interdigital cruciate ligament t) deep digital flexor tendon insertion. Illustration by E. Hull.

The proximal sesamoids of the hoof sit against the base of the first phalanx and provide a larger articular surface against which the rounded head of the metacarpal hinges. The entire fetlock joint is encased in a thick band of fascia covering the network of suspensory ligaments, as well as the tendons which pass along the dorsal and plantar sides of this joint. Superficially, the palmar annular ligament of digital flexors holds the tendon of the superficial and deep digital flexors in place, while the thin abaxial extensor branches run deep to this, further supporting the proximal sesamoids. They are held in place by the digital flexors until diverging just distally to the fetlock joint, where they curl around the axial and abaxial surfaces of the first phalanx before joining the other extensor tendons on the dorsal aspect of the digit.

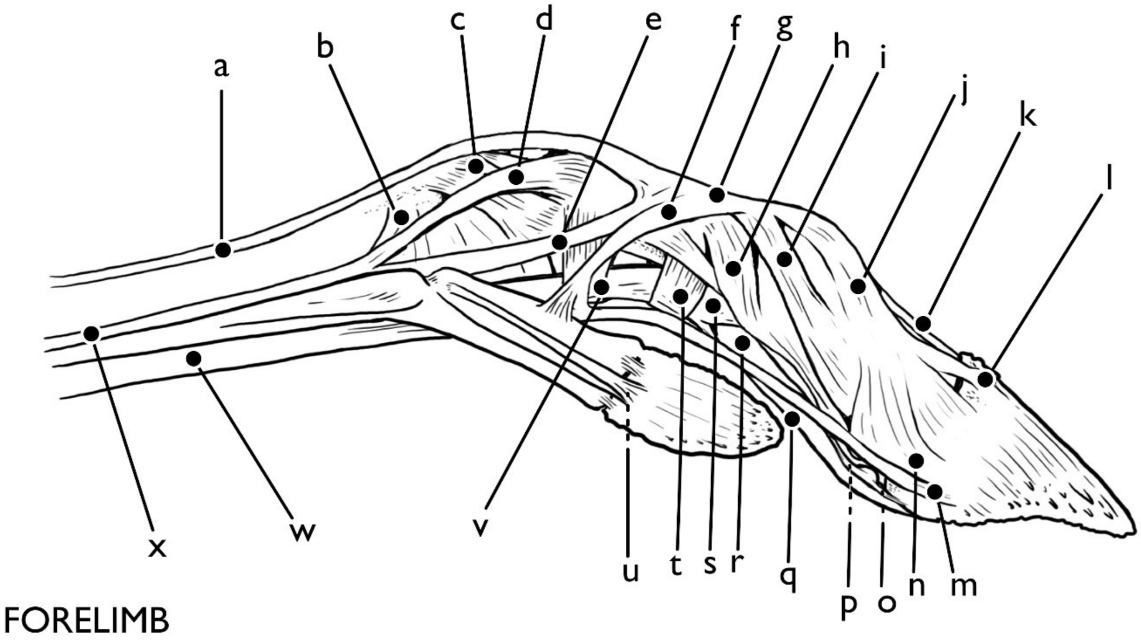

Figure 6. Forelimb, abaxial aspect: a) lateral digital extensor tendon b) sesamoidean ligaments c) metacarpophalangeal collateral ligament d) e) f) proximal accessory ligament of paradigitii II/V g) extensor junction h) abaxial proximal interphalangeal collateral ligament i) distal abaxial extensor branch j) distal lateral digital extensor tendon k) common digital extensor tendon l) distal lateral digital extensor tendon insertion m) distal accessory ligament of paradigitii II/V n) abaxial distal interphalangeal collateral ligament o) impar ligament p) collateral sesamoidean ligament q) deep digital flexor tendon r) deep digital flexor tendon s) superficial digital flexor tendon/separation of *manicae flexoriae* t) distal annular ligament u) paradigital distal interphalangeal collateral ligament v) proximal annular ligament w) combined superficial/deep digital flexor tendon x) interosseous ligament. Illustration by E. Hull.

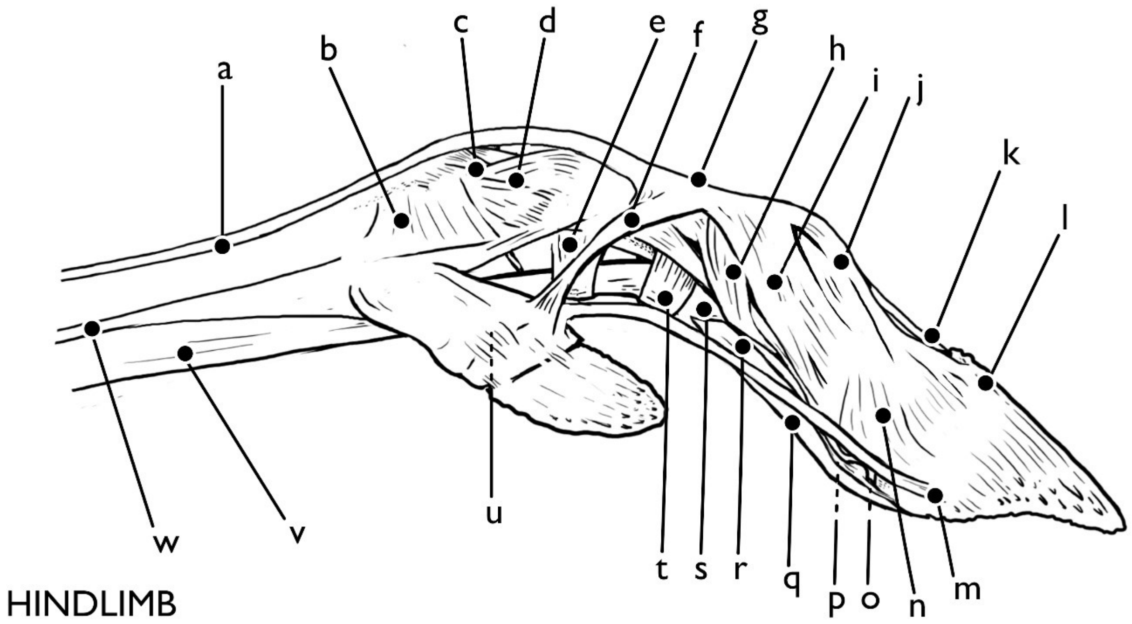

Figure 7. Hindlimb, abaxial aspect: a) lateral digital extensor tendon b) sesamoidean ligaments c) metacarpophalangeal collateral ligament d) metacarpophalangeal collateral ligament e) proximal annular ligament f) proximal accessory ligament of paradigitii II/V g) extensor junction h) abaxial proximal interphalangeal collateral ligament i) distal abaxial digital extensor tendon j) distal lateral digital extensor tendon k) long digital extensor tendon l) distal lateral digital extensor tendon insertion m) distal accessory ligament of paradigitii II/V n) abaxial distal interphalangeal collateral ligament o) impar ligament p) collateral sesamoidean ligament q) deep digital flexor tendon r) deep digital flexor tendon s) superficial digital flexor tendon/separation of manicae flexoriae t) distal annular ligament u) paradigital distal interphalangeal collateral ligament v) combined superficial/deep digital flexor tendon w) interosseous ligament. Illustration by E. Hull.

The dorsal compartment of this joint contains far less soft tissue than the plantar, as the belly of the combined superficial and digital flexor tendons are by far the most robust soft structure of the hoof. Along the dorsal portion of the joint there run two layers of extensor tendons, all contained within a single tendon sheath. The common digital extensor tendon is a thin, flat band which runs superficially along the dorsal surface of the metapodial, bifurcating at the fetlock joint into the digital extensor tendons for digits III and IV. Deep to this, the lateral and medial digital extensors run, crossing the joint and housing, in the forelimb, the dorsomedial sesamoid bones, one on each digit. These small bones act as miniature patellae, facilitating the extension of the first phalanx at the metacarpophalangeal joint (Hull 2019).

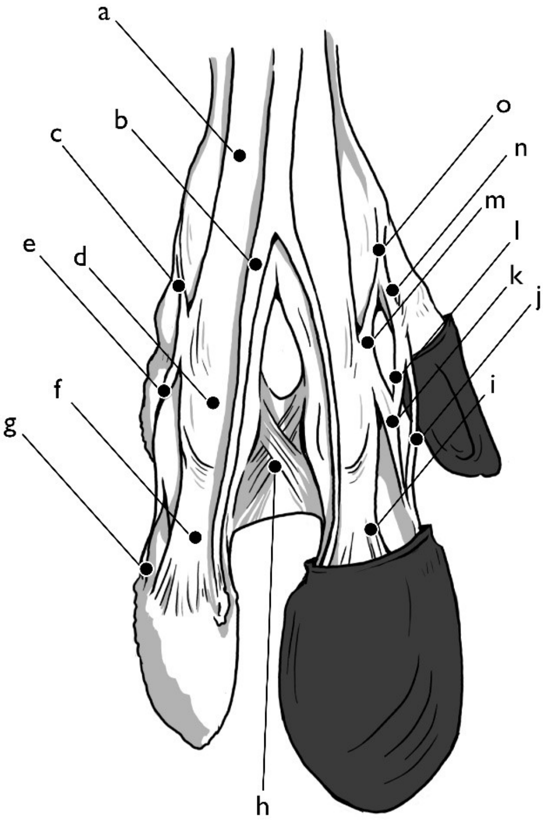

Figure 8. Hindlimb, dorsal view. Left side, hoof capsules removed, right side, hoof capsules present:

a) combined medial/lateral digital extensor ligament b) long digital extensor tendon c) axial extensor branch d) extensor junction e) proximal accessory ligament of paradigitii II/V f) deep lateral digital extensor tendon g) h) interphalangeal cruciate ligament i) deep lateral digital extensor tendon j) distal accessory ligament of paradigitii II/V k) distal interphalangeal collateral ligament l) proximal accessory ligament of paradigitii II/V m) n) interosseous accessory branch to paradigitii II/V o) axial extensor branch. Illustration by E. Hull.

It is also at the fetlock joint that the structure of *Rangifer tarandus* hooves wildly deviate from those of *Bos taurus*. While the tendons and ligaments mentioned above occur in different configurations and slightly different sites, they are nonetheless identifiable as analogous structures. Generally speaking, there are both more and more complex suspensory ligaments in the fetlock joint of *Rangifer tarandus* than in *Bos taurus*. These provide flexibility, especially in the abduction of the digits, at the cost of greater stability seen in the thick plantar annular ligament in *Bos Taurus*. This is expected considering differing habitats and behaviors. The *Rangifer tarandus* dewclaw, however, has structures without analog in *Bos taurus*, which are described below (Fig. 6, 7, 8).

Proximally, the dewclaws are held in place by both fascia as well as a paradigital accessory branch of interosseous III/IV in the forelimb. This tendon runs the length of the stylet and inserts on the first phalanx of the forelimb dewclaw. Two accessory abaxial ligament branches (the proximal and distal accessory ligaments of paradigitii II/V) also run from the proximal and distal ends of the dewclaw first phalanx. The proximal accessory extensor ligament combines with the abaxial extensor branches, and with the medial and lateral digital extensors, insert at the proximal dorsal aspect of the second phalanx of the digits proper. The action of these ligaments causes the abduction of the dewclaws to extend the digits of the hoof, causing the hoof to splay out, increasing surface area. The additional distal accessory ligament runs between the distal axial surface of the dewclaw to the proximal abaxial surface of the third phalanx proper, allowing the dewclaws to flex in concert with the other digits of the hoof. They are unable to flex independently. On the forelimb dewclaw, additional small interdigital collateral ligaments run between the small first and second phalanx, mirroring those of the proximal collateral interdigital ligaments on the hoof proper.

Several structures attach to the first phalanx between the fetlock and pastern joints. On the proximal dorsal aspect of the first phalanx, one insertion site of the deep medial and lateral extensor tendons occurs, keeping the dorsomedial sesamoid in place. On the plantar aspect, two important attachment sites produce two bilateral ridges along the shaft of the bone. These ridges are the attachment points for the proximal and dorsal digital annular ligaments, which encircle the strong flexor tendons of the digits. These ligaments are the primary stress points on the first phalanx when the digits are flexed.

Metatarsophalangeal joint (hindlimb fetlock joint). The metatarsophalangeal joint is similar to the metacarpophalangeal joint in structure. The collateral and sesamoidal ligaments of the metatarsal follow the same pattern as those of the metacarpal, as do the superficial and deep flexors. The interosseous accessory paradigital ligaments, however, are much more gracile and insert on PI of the dewclaw, as no stylets are present in the hind limb. In the dorsal compartment, the extensors follow a similar pattern, with the long digital extensor running superficially to the medial and lateral extensors, following a path analogous to the common digital extensor of the forelimb.

The tendons of the forelimb dewclaws are more developed than those of the hindlimb, and the forelimb dewclaws are both more robust and contain an additional bone: the vestigial MC II/V, or stylets. Despite this, they retain the same general tendinous and ligamentary structures, with a few important exceptions. Proximally, the dewclaws are held in place by fascia and the digital accessory branch of interosseous III/IV in the forelimb. This ligament runs the length of the stylet and inserts on the first phalanx of the forelimb dewclaw and continues to insert on PI of the digit proper. In the hindlimb, the stylet is absent, and this tendon attaches to and terminates at the first phalanx of the dewclaw. Because of the lack of stylet and reduced size of the first phalanx of the hindlimb dewclaw, the dewclaws are not able to abduct as broadly as in the forelimb. In the forelimb, the proximal accessory ligament of paradigitii II/V runs from the axial surface of the stylet of MC II/V, while in the hindlimb it originates from the proximal aspect of the first phalanx of MT II/V to attach to the extensor junction on PII of the digits proper. The distal accessory ligament of paradigitii II/V remains analogous. While small interdigital collateral ligaments are present on the hindlimb dewclaw, they are less developed than those of the forelimb, and the dewclaw itself has less flexibility between the joints of the dewclaw phalanges.

Proximal interphalangeal joint of the forelimb and hindlimb (Pastern joint). The proximal interphalangeal or pastern joint between the first and second phalanges is less complex than that of the fetlock joint (Fig 5, 6). Two proximal interphalangeal collateral ligaments run from the axial and abaxial depressions in the head of the first phalanx to insert along the palmar aspect of the second phalanx. Proximal to the pastern joint, the superficial and deep digital flexors run together, with the superficial digital flexor creating a tendinous sheath around the deep digital flexor. Just proximal to the pastern joint, the superficial digital flexor peels away from the deep digital flexor to insert into the flexor tuberosity on the proximal palmar surface of the second phalanx, as the deep digital flexor continues to run along the palmar/plantar aspects of the phalanges.

The medial and lateral digital extensors, axial and abaxial extensor branches of the interosseous ligament, and the proximal accessory paradigital ligament of the dewclaw insert on the dorsal surface of the body of the second phalanx at the extensor junction. This is a diffuse insertion site, much less discreet than that of the flexor tuberosity on the plantar side, where the superficial flexor tendon inserts, and the insertion site forms a noticeable trapezoidal platform. The medial and lateral digital extensor tendons bifurcate, with one branch inserting along the distal dorsal aspect of the second phalanx, and the other branch continuing to the third phalanx. The abaxial and axial extensor branches likewise partially insert at the extensor junction, then divide again, and continue to the third phalanx. Just below the pastern joint is a large interdigital ligament which is cruciate in form, which extends across the entire axial surface of the second phalanx and inserts at and just distal to the coffin joint on the second and third phalanges. This large, strong structure is without elasticity, providing protection against over-abduction of the hoof.

Figure 9. Exocrine gland. Photograph by H-L. Puolakka.

Exocrine Gland. Between the pastern joint and the distal cruciate interdigital ligament, a large exocrine gland is housed, which is present in both the fore- and hindlimb (Fig. 9). This gland is also present in other cervids, notably *Odocoileus virginianus*. This interdigital gland secretes kairomones to parasites and antimicrobial substances in *O. virginianus* (Hewitt 2011: 50). It may serve similar purposes in *R. tarandus*, although more research is necessary. The pelage of *R. tarandus* additionally increases in length adjacent to the capsule of the hoof, providing a ring of longer hairs around the junction between hide and cartilage at the hoof proper as well as the hoof capsules of the dewclaws.

Dorsal interphalangeal joint of both fore- and hindlimb (Coffin joint). The distal interphalangeal joint, or coffin joint, is covered by the transition from the dermis to the cartilaginous hoof capsule (Fig. 8). This joint also marks the terminus of most of the tendons and ligaments of the hoof. The third phalanx is pyramidal in shape, with dorsal, plantar, and axial sides, as well as coronary, soleal, and dorsal borders. It also contains an axial foramen, just proximal to the extensor process, and an abaxial foramen on the abaxial palmar surface proximal to the soleal border. The dorsal interphalangeal collateral ligaments run from the concave surfaces on the axial and abaxial sides of the head of the second phalanx. The axial dorsal interphalangeal collateral ligament partially divides into two branches, both inserting along the axial border of the dorsal aspect of the third phalanx. The abaxial dorsal interphalangeal collateral ligament inserts along the coronary border to the abaxial side of the dorsal border.

The abaxial digital extensor and the proximal accessory digital extensor of the dewclaw partially combine with the other digital extensors at the pastern joint, but both also have branches running to the third phalanx. Both curl around the second phalanx after partially inserting on the dorsal surface, to finally terminate on the plantar articular border of the third phalanx. Finally, the distal accessory paradigital ligament from the dewclaw extends to insert at the parietal groove on the abaxial surface of the third phalanx.

The long, thin, fibrous common digital extensor tendon of the forelimb and the long digital extensor tendon of the hindlimb insert on the extensor tubercle, an ovoid osseous structure at the proximal dorsal axial part of the third phalanx. Abaxial to this, along the border of the articular surface of the dorsal axial aspect of the third phalanx, the long branches of the medial and lateral digital extensor tendons insert on a small ridge of bone on the proximal edge of the abaxial surface. A small sesamoidal ligament runs from the proximal aspect distal sesamoid to the third phalanx, while the impar ligament runs from the distal aspect of the distal sesamoid to the third phalanx, further securing it in place. The deep digital flexor, after partially inserting at the flexor tubercle and passing over the distal sesamoid, fans out to make a diffuse insertion across nearly the entirety of the plantar surface of the third phalanx.

Additional aspects of the hoof. Compared to the rest of the metapodial and digits, the hoof capsule is much more densely packed with vascularized soft tissue structures. The surface of the hoof is divided into several parts. As per the definitions given in (Budras et. al. 2003, Habel 1949, McLeod 1958) for domestic cattle, the perioplic segment which defines the edge between the hide and the hoof is a slightly thicker band in *Rangifer tarandus*, which then gives way to the coronary segment, extending down the rest of the dorsal portion of the hoof. The sole segment covers the cranial point of the hoof, while the bulbar segment covers most of the plantar surface of the hoof and covers the hoof bulb, internally. The hoof bulb is a highly vascularized cushion of soft tissue covering the caudal portion of the internal hoof, running superficially to the deep digital flexor. This hoof bulb is innervated and vascularized by nerves, veins, and arteries running the length of the metapodials and digits to branch out into a network in the hoof capsule, with veins and arteries running through the abaxial and axial foramina of the third phalanx.

Discussion

The description of these structures in the hoof of *Rangifer tarandus* has implications for multiple fields, including wildlife biology, zooarchaeology, and veterinary science, but also providing resources for those who work closely with reindeer and caribou. In wildlife biology, any greater understanding of how the animal body functions can help inform studies of behavior, migration, foraging, and herd interactions by helping indicate where stress and injury may occur internally. Likewise, in veterinary science, a knowledge of the internal structures of reindeer feet may help veterinarians and herders give more precise and accurate medical care to ailing domestic animals, leading to a better quality of life.

For zooarchaeologists, understanding the points of attachment and stress, as well as the associated physiology, opens up many lines of inquiry. An understanding of tendinous and ligamentary insertions may help identify points of entheseal change, which may in turn help identify patterns of habitual activity. For skeletal specimens, entheseal changes can be informative in the identification of ecotype, foraging pattern, and even identification of domestic animals, particularly those that are working animals. Lastly, the understanding of these soft tissue structures may help scholars contextualize butchery marks and how they relate to conversion of reindeer bodies into specific products.

Rangifer tarandus hooves are similar to the feet of other ungulates in several ways. The large, basic forms of flexor, extensor, and collateral tendons and ligaments, while slightly different in placement, are very analogous to those other artiodactyls, especially *Bos taurus*. The greatest differences in foot anatomy between *Bos taurus* and *Rangifer* are seen in the form and function of the dewclaws. The vestigial MC/MT V (but not II) in *Bos taurus* is represented by the stifle, which descends from the proximal end of the metapodial, while the bones of the dewclaw are represented by one or two tiny bones (Budras 2011, Habel 1949, McLeod 1958). These dewclaws are non-functioning and rarely make contact with the ground. By contrast, the dewclaw of *Rangifer tarandus* is highly functional, especially in the forelimb, where the vestigial MC II/V form stylets which are connected by branches of tendons and activate in concert with the digits proper. The bones of the dewclaw in both fore- and hindlimb have identifiable first, second, and third phalanges. In addition, the strong accessory abaxial extensor tendon branches of the fore- and hindlimb dewclaw act to stabilize the hoof and prevent over-abduction. This creates a much larger hoof surface for locomotion and foraging. This unique adaptation shows the efficiency of the *Rangifer tarandus* body in snowy environments, but this may also open the hoof up to different injury and stress patterns compared to feet of other ungulates.

This study is limited, as it was done only on the limbs of a small number of domestic subadult male reindeer, and therefore may not represent the full range of variation present in the global populations of this species. Further research into the hoof anatomy that included female *Rangifer tarandus* specimens, as well as of *R.t. caribou* and *R.t. granti* in North America and high Arctic ecotypes of the far North would further expand our understanding of *Rangifer tarandus* anatomy. While this study provides only the basic anatomy of *Rangifer tarandus* hooves, it is hoped that this research will lead to more understanding of reindeer and caribou anatomy and assist in answering questions in both the past and present.

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Table 1. Origins and Insertions

Metacarpus	**Origin**	**Insertion**	**Action**
Superficial digital flexor tendon	Medial epicondyle of humerus (Waring et.al. 2011)	Flexor tuberosities of PII	Digital flexion; Forms **manicae flexoriae** around deep dig. flexor
Deep digital flexor tendon	Medial epicondyle of humerus (Waring et.al. 2011)	Flexor tubercle of PIII	Flexion of the hoof
Interosseous ligaments:	Proximal dorsal aspect of metacarpal		
Interosseii III (medial):			
Axial extensor branch	Interosseous III	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII	Extension and adduction of the digits
Abaxial extensor branch	Interosseous III	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII/ soleal border of PIII	Extension and abduction of the digits
Interosseous accessory branch to paradigitii II	Interosseous III	Axial aspect of MCII/proximal abaxial surface of PI of digit III	Stabilization and prevention of over-abduction of the dewclaw
Interosseii IV (lateral):			
Axial extensor branch	Interosseous IV	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII	Extension and adduction of the digits
Abaxial extensor branch	Interosseous IV	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII/ soleal border of PIII	Extension and abduction of the digits
Interosseous accessory branch to paradigitii V	Interosseous IV	Axial aspect of MCV /proximal abaxial surface of PI of digit IV	Stabilization and prevention of over-abduction of the dewclaw
Lateral digital extensor (runs jointly w/ med. dig. ext., bifurcates at fetlock joint.)	Lateral epicondyle of humerus (Waring et.al. 2011)	Extensor junction of the dorsal pastern joint/ dorsal border of	Extension of the digits

Extensor digitii quarti propruis		PIII	
Common digital extensor	Lateral epicondyle of humerus (Waring et.al. 2011)	Extensor process of PIII	Extension of the digits
Medial digital extensor (runs jointly w/ lat. dig. ext., bifurcates at fetlock joint.) *Extensor digitii tertii propruis*	Lateral epicondyle of humerus (Waring et.al. 2011)	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII/ axial border of PIII	Extension of the digits
Plantar annular ligament	Surrounds fetlock joint		Supports fetlock joint
Proximal sesamoidean collateral ligaments:			
Collateral ligaments of the proximal sesamoids	Intercapital notch of MC; concavities of metacarpal concavities	Abaxial aspects of proximal sesamoids	Connection and support of proximal sesamoids to the fetlock joint
Cruciate ligaments of the proximal sesamoids	Axial aspects of proximal sesamoids	Axial aspects of opposite proximal sesamoids	Connection and support of proximal sesamoids to the fetlock joint
Proximal annular ligament	Proximal palmar eminences of PI	Proximal palmar eminences of PI	Connection of flexor tendons to PI
Distal annular ligament	Distal palmar eminences of PI	Distal palmar eminences of PI	Connection of flexor tendons to PI
Proximal accessory ligament of paradigitii II and V	Axial portion of paradigital PI	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII	Extension of the dewclaw
Distal accessory ligament of paradigitii II and V	Axial portion of paradigital PI	Parietal groove of PIII	Flexion of the dewclaw
Metacarpophalangeal collateral ligaments (axial and abaxial)	Axial and abaxial aspects of trochanters of metacarpal capita	Lateral aspects of proximal PI	Support and connection of fetlock joint
Metacarpophalangeal collateral ligaments (medial)	Intercapital notch of metacarpal capita	Medial aspects of proximal PI	Support and connection of fetlock joint
Proximal interphalangeal collateral ligaments (axial and abaxial)	Axial and abaxial concavities on the head of PI	Concavity in the flexor tuberosity of PII	Support and connection of pastern joint
Distal interphalangeal collateral ligaments (axial and abaxial)	Axial and abaxial concavities on the head of PII	Dorsal surface of PIII	Support and connection of coffin joint
Distal interphalangeal cruciate ligaments	Proximal and distal medial surfaces of PII	Proximal and distal medial surfaces of PII	Support and connection of coffin joint
Distal collateral sesamoidean ligament	Deep digital flexor tendon	Plantar surface of proximal distal sesamoid	Connection of distal sesamoid/navicular bone and support of coffin joint
Impar ligament	Plantar surface of distal sesamoid below PIII articular surface	Plantar surface of PIII below sesamoidal articular surface	Connection of distal sesamoid/navicular bone and support of coffin joint

Metatarsus	Origin	Insertion	Action
Superficial digital flexor tendon	Supracondylar fossa of femur	Flexor tuberosity of PII	Digital flexion; Forms **manicae flexoriae** around deep dig. flexor
Deep digital flexor tendon	Lateral condyle of tibia	Flexor tubercle of PIII	Digital flexion
Interosseous ligaments:	Proximal dorsal aspect of		

	metatarsal		
Interosseii III:			
Axial extensor branch	Interosseii III	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII	Digital extension and adduction
Abaxial extensor branch	Interosseii III	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII/ soleal border of PIII	Digital extension and abduction
Interosseous accessory branch to paradigitii II	Interosseii III	Axial aspect of PI of paradigitii II	Stabilization and prevention of over-abduction of the dewclaw
Interosseii IV:			
Axial extensor branch	Interosseii VI	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII	Digital extension and abduction
Abaxial extensor branch	Interosseii VI	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII/soleal border of PIII	Digital extension and abduction
Interosseous accessory branch to paradigitii V	Interosseii VI	Axial aspect of PI of paradigitii V	Stabilization and prevention of over-abduction of the dewclaw
Lateral digital extensor (runs jointly w/ med. dig. ext., bifurcates at fetlock joint.)	Caudomedial aspect of proximal tibia (Waring et. al. 2011)	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII/ dorsal border of PIII	Digital extension of digit III
Long digital extensor	Lateral condyle of tibia *m. peroneus longus* (Waring et. al. 2011)	Extensor process of PIII	Digital extension
Medial digital extensor (runs jointly w/ med. dig. ext., bifurcates at fetlock joint.)	Lateral condyle of tibia *m. peroneus longus* (Waring et. al. 2011)	Extensor junction of the dorsal pastern joint/ extensor tuberosity of PII/axial border of PIII	Digital extension of digit IV
Plantar annular ligament	Surrounds fetlock joint	Surrounds fetlock joint	
Proximal sesamoidean collateral ligaments:			
Collateral ligaments of the proximal sesamoids	Intercapital notch of MC; concavities of metacarpal concavities	Abaxial aspects of proximal sesamoids	Connection and support of proximal sesamoids to the fetlock joint
Cruciate ligaments of the proximal sesamoids	Axial aspects of proximal sesamoids	Axial aspects of opposite proximal sesamoids	Connection and support of proximal sesamoids to the fetlock joint
Proximal annular ligament	Proximal palmar eminences of PI	Proximal palmar eminences of PI	Connection of flexor tendons to PI
Distal annular ligament	Distal palmar eminences of PI	Distal palmar eminences of PI	Connection of flexor tendons to PI

Proximal accessory ligament of paradigitii II and V	Axial portion of paradigital PI	Extensor junction of the dorsal pastern joint	Extension of the dewclaw
Distal accessory ligament of paradigitii II and V	Axial portion of paradigital PI	Parietal groove of PIII	Flexion of the dewclaw
Metatarsophalangeal collateral ligaments (axial and abaxial)	Axial and abaxial aspects of trochanters of metatarsal capita	Lateral aspects of proximal PI	Support and connection of fetlock joint
Metatarsophalangeal collateral ligaments (medial)	Intercapital notch of metatarsal capita	Medial aspects of proximal PI	Support and connection of fetlock joint
Proximal interphalangeal collateral ligaments (axial and abaxial)	Axial and abaxial concavities on the head of PI	Concavity in the flexor tuberosity of PII	Support and connection of pastern joint
Distal interphalangeal collateral ligaments (axial and abaxial)	Axial and abaxial concavities on the head of PII	Dorsal surface of PIII	Support and connection of coffin joint
Distal interphalangeal cruciate ligaments	Proximal and distal medial surfaces of PII	Proximal and distal medial surfaces of PII	Support and connection of coffin joint
Distal collateral sesamoidean ligament	Deep digital flexor tendon	Plantar surface of proximal distal sesamoid	Connection of distal sesamoid/navicular bone and support of coffin joint
Impar ligament	Plantar surface of distal sesamoid below PIII articular surface	Plantar surface of PIII below sesamoidal articular surface	Connection of distal sesamoid/navicular bone and support of coffin joint

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Chapter 3

Differences in Entheseal Changes in the Phalanges Between Ecotypes of Fennoscandian Reindeer

By Emily Hull, University of Alberta*, Sirpa Niinimäki, University of Oulu, and Anna-Kaisa Salmi, University of Oulu

Abstract

The identification and life histories of the different subspecies and ecotypes of *Rangifer tarandus* in Fennoscandia are of great interest to zooarchaeologists, as this species is a keystone animal of the North. The barrenground *Rangifer tarandus tarandus* has historically had closer bonds with humans, as a herded and domestic animal. By contrast, the boreal *Rangifer tarandus fennicus* has been a prey animal with a more fraught relationship with humans. Identifying which of these ecotypes were present and interacting with humans at different points in history provides information not only of human economies and subsistence strategies, but of the life histories and behavioral patterns of the reindeer themselves. This study uses entheseal changes on the phalanges of these animals to investigate different mobility, foraging, and limb-use patterns between ecotypes.

Introduction

Rangifer tarandus, the species which encompasses both reindeer and caribou, has been an integral animal for northern ecosystems and peoples. In Fennoscandia, the two native subspecies, or ecotypes of *Rangifer tarandus* have held different roles within human society. The more common barrenground *Rangifer tarandus tarandus* has shifted roles from prey to domestic animal, and in the modern era, all are domestic animals. By contrast, small populations of *Rangifer tarandus fennicus* represent the modern wild ecotype. While the possibility remains that *R.t. fennicus* may have contributed to current domestic herds through genetic introgression, the wild boreal *R.t. fennicus* has never been domesticated and has always been a prey animal. The reasons to investigate the differences between ecotypes come from the wealth of information that can come from the presence, absence, or proportions of different ecotypes present in an archaeological assemblage. These insights can then be used to more precisely explore animal life histories and the distinct forms of interactions reindeer had with humans in the past.

Separating these two subspecies in the archaeological record, however, comes with difficulties. Despite their different behaviors, habitats, and morphology, *R.t. fennicus* and *R.t. tarandus* overlap in size and in territory. Further, they are difficult to distinguish osteologically, especially in fragmentary and comingled assemblages where both subspecies may be present. In this study, entheseal changes in musculoskeletal attachments of the phalanges are compared between the two subspecies. We predict that the differing habitual activities of the two populations of reindeer generate distinct patterns of entheseal change in their feet Identifying such differences will potentially aid in identifying archaeological specimens to subspecies.

Background

Despite their similarities, the two ecotypes of *Rangifer tarandus* in Fennoscandia have very different lives. Today, all *R.t. tarandus* are domesticated, most managed in free-ranging herds divided by herding collectives. They naturally congregate in large herds, undergo long annual migrations, and are generally more docile and less skittish, perhaps due to their instinct to cluster together when faced with potential threats. They are part of the generally acknowledged "tundra ecotype" morphological pattern, being medium-sized reindeer with short legs. Despite being a "tundra ecotype," they are more accurately labelled as "barrenground," as they live not only on the alpine tundra of Fennoscandia, but on the Scandinavian montane located south of it.

R.t. fennicus, or wild forest reindeer, have diminished habitat areas in modern Finland, being restricted to small boreal and wetland areas in the mid-east of the country, near the Russian border. This subspecies is less social and less migratory and has a propensity to scatter and flee when threatened. Their habitual terrain is characterized by uneven topography and more dense foliage, leading this subspecies to graze as well as browse. Historically, *R.t. fennicus* were much more numerous and lived in the whole expanse of the boreal zone. Historically, wild reindeer of both types lived throughout the tundra, taiga, and boreal zones according to ecological niche (Luukko, 1954:111; Virrankoski, 1973:271–272; Lundmark, 1982:161).

Rangifer tarandus ecological niches are most often separated by groundcover (e.g., forest, tundra, heavy snow). While their ranges may overlap, the habitats and ecozones within those ranges are different; the two ecotypes primarily live in differing topographies. Reindeer interact habitually with these differing topographies in part through their feet, and it is expected that their feet should exhibit signs of change in relation to these differences in habitat and habitat-related activity. As a barrenground ecotype living in open, snowy tundra and taiga, we expect *R.t. tarandus* feet to show more pronounced adaptation for digging and foraging activities, especially in the forelimb. In contrast, *R.t. fennicus,* living in boreal zones with diverse topography, may show an adaptation to stability rather than specialized foraging.

As much human use of *Rangifer tarandus* bodies involves butchery practices that heavily fragment the head and major limb elements, phalangeal bones often are some of the only whole elements remaining in archaeological assemblages. Because of this, phalanges, especially the robust PI, make ideal candidates for archaeological assessment. Also, *Rangifer tarandus* are exceptionally well adapted to locomotion in snow and show extreme chionophilic adaptation, especially in the hoof (Telfer and Kelsall, 1971, 1984). The characteristics and composition of their snow-covered environments are integral to *Rangifer tarandus* foraging and locomotion, and therefore life history (Formozov, 1946). Because of this extreme environmental specialization, differences in ecological adaptations of the *Rangifer* foot, especially adaptation between ecotypes, is ripe for investigation.

Reindeer Use and Domestication

Reindeer herding in Fennoscandia most likely began at AD 800–1300 although some have posited that herding may have begun as early as 4700–4200 BC (Bergman et al., 2013; Hedman et al., 2015; Helskog, 2011). The exact mechanism by which reindeer hunting gave way to reindeer herding is a subject of great debate. (Sommerseth, 2011; Laufer, 1917; Mirov, 1945; Ingold, 1980; Willerslev et al., 2015). Larger-scale herding of tundra reindeer likely developed around AD 1500 from small scale reindeer keeping that formed part of diversified subsistence economies, and a broad aDNA change around this time period seems to reinforce this turning point (Bjørnstad et al., 2012). By around AD 1500, large scale reindeer pastoralism was practiced and formed the basis of economic systems (Bjørnstad et al., 2012; Bergman et al., 2013; Bjørklund, 2013; Hansen and Olsen, 2014: 195–206). This shift may have roots in the increasing trade, trade networks and emerging nation states of this period, which made closer control and individual ownership of individual reindeer economically advantageous (Hedman, 2003: 223-230; Odner, 2001; Vorren, 1974; 1977). Throughout this period of change for tundra reindeer, however, wild forest reindeer remained unmanaged and continued to be hunted by many groups (Tegengren, 1952; Kortesalmi, 2008: 23-24; Hansen and Olsen, 2014: 192-95).

Domestic reindeer in Fennoscandia, while all managed and owned in the modern era, do not show the same morphological changes by which many archaeologists may gage domestication in the archaeological record (Zeder et al., 2006; Zeder, 2012). Long-term reproductive selection by humans results in a series of morphological changes to an animal population. As reindeer have not been subject to the same degree and extent of reproductive restrictions in Fennoscandia, modern domestic reindeer remain morphologically analogous to their ancestral populations, which make wild and domesticated animals difficult to differentiate in the archaeological record (Puputti and Niskanen, 2009; Salmi et al., in press).

Both body size and composition differ somewhat between the two reindeer ecotypes. *R.t. fennicus* are larger animals with longer legs and more pronounced sexual size dimorphism, with male *R.t. fennicus* having an average body mass of 143 kg, while the average male *R.t. tarandus* is only 128 kg (Banfield, 1961; Puputti and Niskanen, 2008; 2009: 154; Nieminen and Helle, 1980). Females show less distinction between ecotypes, with *R.t. fennicus* females weighing an average of 88 kg, and *R.t. tarandus* females an average of 81 kg. Much overlap in size exists between smaller *R.t. fennicus* and larger *R.t. tarandus* individuals*,* especially among females and between female *R.t. fennicus* and male *R.t. tarandus*. In cases where no diagnostic skeletal elements are present and sex is unknown, only the very largest individuals can be extrapolated to be *R.t. fennicus*, as sexual dimorphism complicates the differentiation of other skeletal materials. While *R.t. fennicus* have much longer legs than *R.t. tarandus*, they seemingly do not have proportionally larger hooves, so the phalanges of each ecotype cannot be identified by size alone. Such overlapping body sizes make skeletal elements difficult to identify to the subspecies level, particularly when they are fragmentary or multiple individuals are represented.

Reindeer meat and other reindeer products were traded at least from the Medieval period onwards, so it is impossible to say based on archaeological site location whether bones are of *R.t. tarandus* or *R.t. fennicus.* Both aDNA evidence and historical accounts point to a mosaic structure of reindeer use where both domestic *R.t. tarandus* and *R.t. fennicus* were utilized for different purposes in the same areas (Salmi and Heino, 2019). Complicating matters even more, few reliable ways of sexing most individual reindeer skeletal elements are presently available. This being so, archaeologists must look for other clues to the relationships of reindeer and humans in the archaeological record.

Entheseal Changes

Entheseal changes, also known as musculoskeletal stress markers (Villotte et al., 2016), are sites where muscles attach to bone either directly in fibrous enthesis or via cartilage in fibrocartilaginous enthesis (Benjamin et al., 1986, 2002; Villotte, 2006). Variations in entheseal changes in human osteology are used to investigate subsistence strategies between groups, and division of labor between groups by social status and sex (e.g. Hawkey and Merbs, 1995; Churchill and Morris, 1998; Robb, 1998; Molnar, 2006, 2010). Utilization of entheseal changes to observe differences in activity patterns and/or intensity have recently been expanded to different animal species, where the methodology has been developed for reindeer (Niinimäki and Salmi, 2016) and horses (Binde et al., 2019). However, there are several methodological and etiological uncertainties involved (Jurmain et al., 2012). Several contributing factors have been identified, most notably age (Weiss, 2003; Niinimäki, 2011; Alves-Cardoso and Henderson, 2010; Michopoulou et al., 2015; Godde et al., 2018), regardless which entheseal observation method is used (Villotte et al., 2010; Milella et al., 2012; Acosta et al., 2017). In addition, body size has been identified as an issue where larger and heavier individuals have more developed entheses (Churchill and Morris, 1998; Niinimäki, 2011; Weiss et al., 2010; Michopoulou et al., 2015; Godde et al., 2018).

When considering how activity is reflected on entheses, there are two different viewpoints. On the other hand, activity effects are considered to result from overuse beyond the structural capacity of muscle-bone junction (Jurmain et al., 2012; Acosta et al., 2017). On the other, variation at an enthesis is considered subpathological where entheses modify to mechanical loading (Churchill and Morris, 1998; Lieverse et al., 2009; Niinimäki, 2012; Foster et al., 2014; Niinimäki and Salmi, 2016; Niinimäki et al., submitted). Depending on the above-mentioned viewpoints, research has focused on different features observed at an enthesis: bone resorption and bone formation. When overuse and thus pathological etiology is considered, studies focus on fibrocartilaginous entheses, specifically bone resorption as cortical defects in the form of erosion, porosity, and cavitation (cf. Drapeau, 2008, Mariotti et al., 2004, Milella et al., 2012; Henderson et al., 2013). When activity effects on entheseal changes are considered resulting from bone functional adaptation to mechanical loading, being thus subpathological, then focus is in the observation of bone formation or bone robusticity at an enthesis (Foster et al., 2014; Niinimäki and Salmi, 2014). It should be borne in mind that these two features at entheses, bone resorption and bone formation, may have different etiologies and should therefore be studied separately (Villotte and Knüsel, 2013; Foster et al., 2014).

Contribution of activity on entheseal changes remains heavily debated (Weiss, 2003; Molnar, 2006, 2010; Weiss et al., 2010; Alves-Cardso and Henderson, 2010; Niinimäki, 2011; Milella et al., 2012; Henderson et al., 2013; Michopoulou et al., 2015, 2017). In reindeer, bone formation at specific entheses has been observed to reflect activity. Free-ranging reindeer digging for lichen from under the snow have more developed morphology in bone formation at attachments of several elbow flexor muscles, and zoo reindeer have more developed attachments of *Subscapularis* muscle, likely resulting from standing long periods of time with their shoulder bracing apparatus activated (Niinimäki and Salmi, 2016). Working and zoo reindeer have similar degree of variability at elbow flexor attachment sites compared to free-ranging reindeer, the latter having the most robust entheses (Niinimäki and Salmi, 2016; Salmi and Niinimäki, 2016). This likely results from the fact that zoo and draught reindeer are fed and need not dig for lichen.

These prior studies on reindeer entheses as well as the supporting evidence from bone cross-sections and geometric morphometric studies encourage further development of methodology for observing changes at reindeer entheses on other bone elements. This study provides methodological reference categories for observing entheses at reindeer phalanges. This methodology is used to investigate differences in behavior and foraging strategy between the subspecies (*Rangifer tarandus tarandus* and *Rangifer tarandus Fennicus*) of Fennoscandian reindeer as apparent in their phalanges.

Materials and Methods

All analyzed individuals are adult specimens housed at the University of Oulu Biodiversity Unit. They included skeletal materials from both sexes of *R.t. tarandus* and *R.t. fennicus* whose remains include phalanges I (n=155), II (n=134), and III (n=133), with details provided in Table 1. The remains of *R.t. tarandus* far outnumber those of *R.t. fennicus*, especially in the cases of PII and PIII bones. The reason for the difference in sample size is two-fold. First, as *R.t. fennicus* is a protected species with diminishing numbers, its collection is highly restricted, and many of the available specimens were collected from deceased individuals partially dismembered by scavengers. Some of the small bones, especially PII and PIII, were not collected along with the rest of the body. Second, many of the deceased individuals collected had been in poor health, and many had pathologies of the feet, including extreme osteoarthritis, lipping and eburnation at articular surfaces, and occasional deformation of the bones as a whole, making them unsuitable for assessment. No animals of unknown provenance or subspecies designation were used. No hybrid, zoo-kept, or working animals were assessed in this study; all were free-ranging adults. Because the skeletal materials were collected with associated soft tissue, hides, and crania, often as well as antlers, all subspecies of specimens are known.

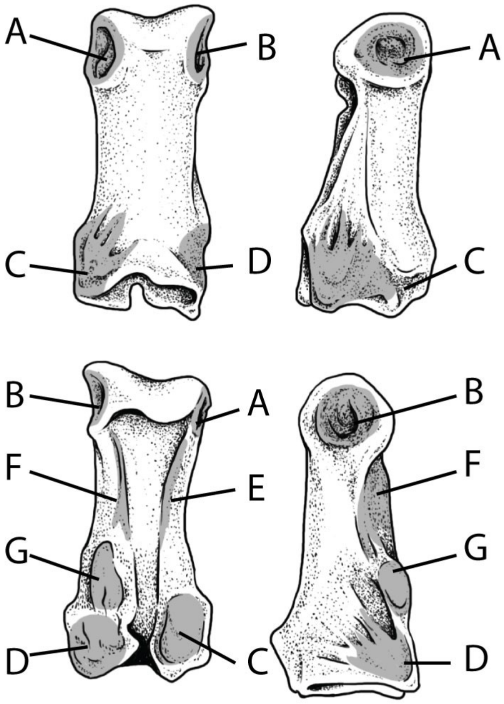

Figure 1: Entheseal sites scored on PI. Illustrations by E. Hull.

A: Lateral collateral metacarpo/metatarsophalangeal ligament; B: Medial collateral metacarpo/metatarsophalangeal ligament; C: Lateral collateral proximal interphalangeal ligament; D: Medial collateral proximal interphalangeal ligament; E: Distal annular ligament of PI; F: Distal annular ligament of PI; G: Proximal annular ligament of PI

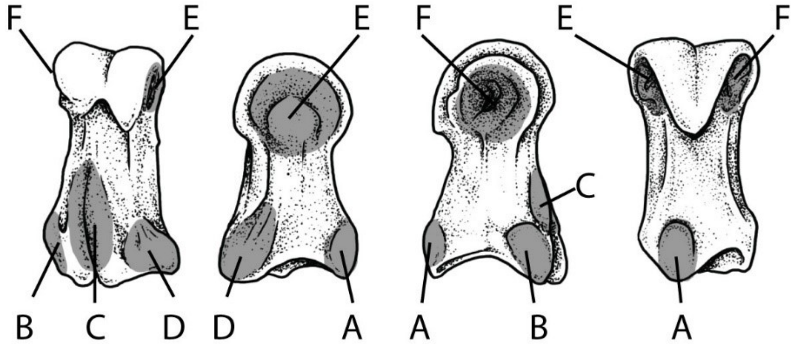

Figure 2: Entheseal sites scored on PII. Illustrations by E. Hull.

A: Extensor tuberosity; B: Lateral interphalangeal distal collateral ligament; C: Flexor tuberosity; D: Medial interphalangeal distal collateral ligament; E: Medial interphalangeal proximal collateral ligament; F: Lateral interphalangeal proximal collateral ligament

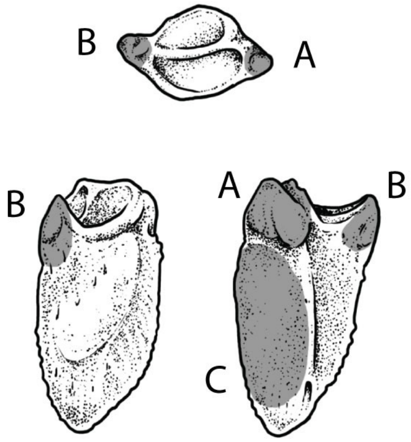

Figure 3: Entheseal sites scored on PIII. Illustrations by E. Hull.

A: Flexor tubercle (deep flexor tendon); B: Extensor tuberosity (common/long extensor tendon); C: Soleal surface (deep flexor tendon)

Mann Whitney U-tests were used during statistical analysis, as this test is robust when comparing samples of different sizes, and as the data was ordinal and not normally distributed. Each site of enthesis, while part of the foot as a whole, all are associated with individual tendons and ligaments that act on their own, so an independent sample test was appropriate in this case. Effect size was calculated by using Cohen's d, marking effect sizes to be small (<0.2), moderate (0.5) or large (>0.8). This numerical value refers to the magnitude of difference between groups (Cohen, 1994, 1988; Sullivan and Feinn, 2012). Statistics were calculated using IMB SPSS, JASP, and jamovi software systems. All pathological and juvenile specimens were removed from the sample.

Table 1. Numbers of Specimens and Individuals

	PI	**PII**	**PIII**
R.t. tarandus	n= 132, 23 individuals	n= 125, 23 individuals	n= 123, 23 individuals
R.t. fennicus	n= 23, 8 individuals	n= 9, 7 individuals	n= 10, 7 individuals

Before assessment could proceed, fore- and hindlimb phalanges were divided, as many of these were unlabelled in the sample. This division was based on metric assessment (Hull, 2019). Each phalanx was notated as fore- or hind, and each site was scored on each phalanx. The data was then analysed to investigate differences at each site between subspecies, as well as differences at each site between fore- and hindlimb ECs within subspecies. In the methodology created for observing human entheseal changes, a critique ensued when the method published by Hawkey and Merbs (1995), originally intended for specific muscle and ligament attachments, was applied on other entheses (e.g. Churchill and Morris, 1998; Weiss, 2003, 2007; Molnar, 2006). This is a major issue against the application of method beyond investigated entheses. Variation present at a specific enthesis in a specific bone (and in a specific species) should not be generalized as an expression of variability of all entheses. Thus, for the reindeer phalanges entheses, the observation method developed for entheses of reindeer long bones cannot be applied. In creating categories of entheseal appearance, total variation present in the material for a specific enthesis was observed, and then this observed variation was divided in to three-grade scores (0-2). This follows the protocol and rationale as published in the original study for reindeer entheses in Niinimäki and Salmi (2016).

Results

Inter-ecotype differences

Table 2. Pooled Phalanges compared by Ecotype

Site	Anatomical Point	Pooled difference between *R.t.tarandus (n= 133)* and *R.t. fennicus(n= 23)* PI	U	Effect Size (Cohen's d)	Subspecies	Mean	Median	SD
A	**Abaxial collateral metacarpo/metatarsophalangeal ligament**	***p* <.001**	**893**	**0.781**	***R.t.tarandus***	***1.000***	**1.000**	***0.798***
					R.t.fennicus	***1.609***	**2.000**	***0.656***
B	**Axial collateral metacarpo/metatarsophalangeal ligament**	***p* <.001**	**810**	**0.876**	***R.t.tarandus***	***1.030***	**2.000**	***0.720***
					R.t.fennicus	***1.652***	**2.000**	***0.647***
C	Abaxial collateral proximal interphalangeal ligament	*p* =.083	1206	0.390	*R.t.tarandus*	*1.015*	1.000	*0.738*
					R.t.fennicus	*1.304*	1.000	*0.765*
D	Axial collateral proximal interphalangeal ligament	*p* =.208	1293	-0.249	*R.t.tarandus*	*1.158*	1.000	*0.833*
					R.t.fennicus	*0.957*	1.000	*0.638*
E	**Distal annular ligament of PI**	***p* <.001**	**787**	**0.959**	***R.t.tarandus***	***0.842***	**1.000**	***0.716***
					R.t.fennicus	***1.522***	**2.000**	***0.665***
F	**Distal annular ligament of PI**	***p* <.001**	**551**	**1.266**	***R.t.tarandus***	***0.955***	**1.000**	***0.767***
					R.t.fennicus	***1.870***	**2.000**	***0.344***
G	Proximal annular ligament of PI	*p* =.346	1353	0.202	*R.t.tarandus*	*1.105*	1.000	*0.761*
					R.t.fennicus	*1.261*	1.000	*0.810*
Site	**Anatomical Point**	**Pooled difference between *R.t.tarandus (n= 125)* and *R.t. fennicus (n= 9)* PII**	**U**	**Effect Size (Cohen's d)**	**Subspecies**	**Mean**	**Median**	**SD**
A	Extensor tuberosity	*p* =.178	390	0.551	*R.t.tarandus*	*1.144*	1.000	*0.748*
					R.t.fennicus	*1.556*	2.000	*0.726*
B	Lateral interphalangeal distal collateral ligament	*p* =.929	525	0.163	*R.t.tarandus*	*1.312*	2.000	*0.817*
					R.t.fennicus	*1.444*	2.000	*0.726*
C	Flexor tuberosity	*p* =.343	449	-0.336	*R.t.tarandus*	*1.376*	2.000	*0.790*
					R.t.fennicus	*1.111*	1.000	*0.782*
D	Medial interphalangeal distal collateral ligament	*p* =.111	451	0.352	*R.t.tarandus*	*1.064*	1.000	*0.759*
					R.t.fennicus	*1.333*	2.000	*0.866*

E	Medial interphalangeal proximal collateral ligament	*p* =.791	551	-0.041	*R.t.tarandus*	*0.576*	1.000	*0.496*
					R.t.fennicus	*0.556*	1.000	*0.527*
F	Lateral interphalangeal proximal collateral ligament	*p* =.702	494	0.179	*R.t.tarandus*	*1.304*	1.000	*0.775*
					R.t.fennicus	*1.444*	2.000	*0.882*
Site	**Anatomical Point**	**Pooled difference between *R.t.tarandus (n= 123)* and *R.t. fennicus (n= 10)* PIII**	**U**	**Effect Size (Cohen's d)**	**Subspecies**	**Mean**	**Median**	**SD**
A	**Flexor tubercle (deep flexor tendon)**	***p* =.045**	**396**	**0.650**	***R.t.tarandus***	***1.016***	**1.000**	***0.735***
					R.t.fennicus	***1.500***	**2.000**	***0.850***
B	**Extensor tuberosity (common/long extensor tendon)**	***p* =.002**	**275**	**1.055**	***R.t.tarandus***	***0.862***	**1.000**	***0.813***
					R.t.fennicus	***1.700***	**2.000**	***0.483***
C	**Soleal surface (deep flexor tendon)**	***p* =.033**	**380**	**0.716**	***R.t.tarandus***	***1.033***	**1.000**	***0.809***
					R.t.fennicus	***1.600***	**2.000**	***0.516***

On PI, with both limbs pooled, the sites with statistically significant differences between *R.t.tarandus* and *R.t. fennicus* were A (U= 893; *p <.001*), B (U= 810; *p <.001*), E (U= 787; *p <.001*), and F (U= 551; *p <.001*) (Table 2). Specifically, the scores for *R.t. fennicus* were consistently higher for those four entheses (Table 2). An ecotype-based comparison between fore- and hindlimb was also conducted and is discussed below. The effect size values for all statistically significant sites were moderately high (A= 0.781) to very high (F= 1.266).

Pooled differences between ecotypes' PII bones are listed in Table 2. No sites were assessed as statistically different between the two ecotypes. Due to the small sample size of *R.t. fennicus* PII bones, an ecotype-based comparison between fore- and hindlimb was not feasible.

Table 3. Forelimb and Hindlimb compared by Ecotype

Site	**Anatomical Point**	***R.t.tarandus (n= 66)* v. *R.t. fennicus (n= 11)* PI forelimb**	**U**	**Effect Size (Cohen's d)**	**Subspecies**	**Mean**	**Median**	**SD**
A	**Abaxial collateral metacarpo/metatarsophalangeal ligament**	***p* =.013**	**202**	**0.826**	***R.t.tarandus***	***1.000***	**1.000**	***0.784***
					R.t.fennicus	***1.636***	**2.000**	***0.674***
B	**Axial collateral metacarpo/metatarsophalangeal ligament**	***p* =.006**	**187**	**0.918**	***R.t.tarandus***	***0.955***	**1.000**	***0.753***
					R.t.fennicus	***1.636***	**2.000**	***0.674***
C	Abaxial collateral proximal interphalangeal ligament	*p* =.290	294.5	0.33	*R.t.tarandus*	*1.106*	1.000	*0.767*
					R.t.fennicus	*1.364*	1.000	*0.809*
D	**Axial collateral proximal**	***p* =.003**	**187.5**	**-0.878**	***R.t.tarandus***	***1.591***	**2.000**	***0.679***

	interphalangeal ligament				***R.t.fennicus***	***1.000***	**1.000**	***0.632***
E	**Distal annular ligament of PI**	***p* =.040**	**234**	**0.725**	***R.t.tarandus***	***0.697***	**1.000**	***0.656***
					R.t.fennicus	***1.182***	**1.000**	***0.751***
F	**Distal annular ligament of PI**	***p* <.001**	**80.5**	**1.675**	***R.t.tarandus***	***0.773***	**1.000**	***0.791***
					R.t.fennicus	***1.909***	**2.000**	***0.302***
G	Proximal annular ligament of PI	*p* =.572	326.5	0.174	*R.t.tarandus*	*1.227*	2.000	*0.780*
					R.t.fennicus	*1.364*	1.000	*0.809*
Site	**Anatomical Point**	***R.t.tarandus (n= 67)* v. *R.t. fennicus (n=12)* PI hindlimb**	**U**	**Effect Size (Cohen's d)**	**Subspecies**	**Mean**	**Median**	**SD**
A	**Abaxial collateral metacarpo/metatarsophalangeal ligament**	***p* =.023**	**245**	**0.732**	***R.t.tarandus***	***1.000***	**1.000**	***0.816***
					R.t.fennicus	***1.583***	**2.000**	***0.669***
B	**Axial collateral metacarpo/metatarsophalangeal ligament**	***p* =.008**	**219**	**0.827**	***R.t.tarandus***	***1.106***	**1.000**	***0.682***
					R.t.fennicus	***1.667***	**2.000**	***0.651***
C	Abaxial collateral proximal interphalangeal ligament	*p* =.152	305	0.457	*R.t.tarandus*	*0.925*	1.000	*0.703*
					R.t.fennicus	*1.250*	1.000	*0.754*
D	Axial collateral proximal interphalangeal ligament	*p* =.360	340	0.251	*R.t.tarandus*	*0.731*	1.000	*0.750*
					R.t.fennicus	*0.917*	1.000	*0.699*
E	**Distal annular ligament of PI**	***p* <.001**	**156**	**1.197**	***R.t.tarandus***	***0.985***	**0.000**	***0.749***
					R.t.fennicus	***1.833***	**1.000**	***0.389***
F	**Distal annular ligament of PI**	***p* =.003**	**201**	**0.953**	***R.t.tarandus***	***1.134***	**0.000**	***0.776***
					R.t.fennicus	***1.833***	**1.000**	***0.389***
G	Proximal annular ligament of PI	*p* =.436	349	0.244	*R.t.tarandus*	*0.985*	0.000	*0.728*
					R.t.fennicus	*1.167*	0.000	*0.835*

All PIII bones were pooled, as there is currently no method for consistently determining fore- from hindlimb. In the pooled sample, all sites showed significant differences (Table 2). These sites are insertion points for the deep flexor tendon (A (U= 396; *p =0.045*) and C (U= 380; *p =0.033*)) and the long/common extensor tendon (B (U= 275; *p =0.002*)). In all cases, *R.t. fennicus* showed higher scores than *R.t. tarandus* (Table 2). The effect size values for all statistically significant sites were moderate (A= 0.650) to high (B= 1.055).

When fore- and hindlimb PI of *R.t. tarandus* and *R.t. fennicus* were analysed separately, the results remained generally consistent, with one deviation (Table 3). Site D (forelimb: U= 187.5; *p* = 0.003; hindlimb: U= 340; *p* = .360), exhibited significant difference in the forelimb, but not in the hind. This is the insertion site of the axial collateral proximal interphalangeal joint, or the insertion of the collateral pastern joint on the inner side of the hoof. In the forelimb, site D showed significantly lower EC scores among *R.t. fennicus* (mean = 1.000) than in *R.t. tarandus* (mean = 1.591) with a high effect size of -0.878. In the hindlimb, site D showed no significant difference, with *R.t. fennicus* having a mean score of 0.917 and *R.t. tarandus* a mean score of 0.731, with a small effect size of 0.251. Stress at this joint would occur during either flexion or extension of the medial and distal digits or during abduction of the toes.

Intra-Ecotype Differences *R.t. tarandus* shows significant differences between forelimb and hindlimb on sites D, E, and F on PI (Table 4). While site D (U= 959; $p < 0.001$), the medial interphalangeal collateral ligament, was more pronounced on the thoracic digits (thoracic mean = 1.591, pelvic mean = 0.731), sites E and F, the proximal annular ligament insertion sites, were more pronounced on the hindlimb (E: U= 1751; $p = 0.025$, thoracic mean = 0.697, pelvic mean = 0.985; F: U= 1649; $p = 0.007$, thoracic mean = 0.773, pelvic mean = 1.134). In *R.t. fennicus,* only site E (U= 33; $p = 0.021$) showed a significant difference, with thoracic mean = 1.182 and pelvic mean = 1.833, with a high effect size of -1.105. This shows that while *R.t. fennicus* may show more flexion in the hind digits than in the digits of the forelimb, this dichotomy between the use of the fore- and hindlimb is less distinct than in *R.t. tarandus*.

When analysing PII forelimb versus hindlimb, complete analysis of *R.t. fennicus* phalanges were hampered by a lack of samples. In *R.t. tarandus*, the pattern of differences in EC development between in the fore- and hindlimb continues to be present. On site A (U= 1557; $p = 0.036$), the pelvic limb showed higher EC scores (thoracic mean = 1.000, pelvic mean = 1.286; effect size = 0.388), while on site C (U= 1556; $p = 0.028$), the thoracic limb showed higher EC scores (thoracic mean = 1.532, pelvic mean = 1.222; effect size = -0.399).

Table 4. Forelimb and Hindlimb divided by Ecotype

Site	**Anatomical Point**	***R.t. tarandus* PI Forelimb (n= 66) v. hindlimb (n= 67)**	**U**	**Effect Size (Cohen's d)**	**Limb**	**Mean**	**Median**	**SD**
A	Lateral collateral metacarpo/metatarsophalangeal ligament	*p* =1.000	2211	0.000	Thoracic	*1.000*	1.000	*0.784*
					Pelvic	*1.000*	1.000	*0.816*
B	Medial collateral metacarpo/metatarsophalangeal ligament	*p* =.234	1936	-0.211	Thoracic	*0.955*	1.000	*0.753*
					Pelvic	*1.106*	1.000	*0.682*
C	Lateral collateral proximal interphalangeal ligament	*p* =.157	1918	0.246	Thoracic	*1.106*	1.000	*0.767*
					Pelvic	*0.925*	1.000	*0.703*
D	**Medial collateral proximal interphalangeal ligament**	***p* <.001**	**959**	**1.201**	**Thoracic**	***1.591***	**2.000**	***0.679***
					Pelvic	***0.731***	**1.000**	***0.750***
E	**Distal annular ligament of PI**	***p* =.025**	**1751**	**-0.409**	**Thoracic**	***0.697***	**1.000**	***0.656***
					Pelvic	***0.985***	**1.000**	***0.749***
F	**Distal annular ligament of PI**	***p* =.007**	**1649**	**-0.483**	**Thoracic**	***0.773***	**1.000**	***0.719***
					Pelvic	*1.134*	1.000	*0.776*
G	Proximal annular ligament of PI	*p* =.059	1818	0.321	Thoracic	*0.985*	1.000	*0.780*
					Pelvic	*1.227*	1.000	*0.728*
Site	**Anatomical Point**	***R.t. fennicus* PI Forelimb (n=11) v. hindlimb (n= 12)**	**U**	**Effect Size (Cohen's d)**	**Limb**	**Mean**	**Median**	**SD**
A	Lateral collateral metacarpo/metatarsophalangeal ligament	*p* =.819	62.5	0.079	Thoracic	*1.636*	2.000	*0.674*
					Pelvic	*1.583*	2.000	*0.669*
B	Medial collateral metacarpo/metatarsophalangeal ligament	*p* =.936	64.5	-0.046	Thoracic	*1.636*	2.000	*0.674*
					Pelvic	*1.667*	2.000	*0.651*
C	Lateral collateral proximal interphalangeal ligament	*p* =.688	59.5	0.146	Thoracic	*1.364*	2.000	*0.809*
					Pelvic	*1.250*	1.000	*0.754*
D	Medial collateral proximal interphalangeal ligament	*p* =.778	61.5	0.128	Thoracic	*1.000*	1.000	*0.632*
					Pelvic	*0.917*	1.000	*0.669*
E	**Distal annular ligament of PI**	***p* =.021**	**33.0**	**-1.105**	**Thoracic**	***1.182***	**1.000**	***0.751***
					Pelvic	***1.833***	**2.000**	***0.389***
F	Distal annular ligament of PI	*p* =.635	61.0	0.216	Thoracic	*1.909*	2.000	*0.302*
					Pelvic	*1.833*	2.000	*0.389*
G	Proximal annular ligament of PI	*p* =.571	57.0	0.239	Thoracic	*1.364*	2.000	*0.809*
					Pelvic	*1.167*	1.000	*0.835*
Site	**Anatomical Point**	***R.t. tarandus* PII Forelimb (n= 62) v. hindlimb (n=63)**	**U**	**Effect Size (Cohen's d)**	**Limb**	**Mean**	**Median**	**SD**
A	**Extensor tuberosity**	***p* =.036**	**1557**	**0.388**	**Thoracic**	***1.000***	**1.000**	***0.768***
					Pelvic	***1.286***	**1.000**	***0.705***
B	Lateral interphalangeal distal collateral ligament	*p* =.062	1609	0.330	Thoracic	*1.177*	2.000	*0.840*
					Pelvic	*1.444*	1.000	*0.778*
C	**Flexor tuberosity**	***p* =.028**	**1556**	**-0.399**	**Thoracic**	***1.532***	**1.000**	***0.718***
					Pelvic	***1.222***	**2.000**	***0.832***

D	Medial interphalangeal distal collateral ligament	*p* =.059	1595	-0.342	Thoracic	*1.194*	1.000	*0.743*
					Pelvic	*0.937*	1.000	*0.759*
E	Medial interphalangeal proximal collateral ligament	*p* =.411	1810	-0.147	Thoracic	*0.613*	1.000	*0.491*
					Pelvic	*0.540*	1.000	*0.502*
F	Lateral interphalangeal proximal collateral ligament	*p* =.100	1647	-0.297	Thoracic	*1.419*	1.000	*0.737*
					Pelvic	*1.190*	2.000	*0.800*

In summary, *R.t. fennicus* showed generally higher scores overall, while *R.t. tarandus* exhibited a higher diversity of scores between fore- and hindlimb. This pattern suggests that the two ecotypes use their limbs in different manners, and these differences manifest in visible ways within their feet

Discussion

Analysis has shown that some bones of the reindeer foot offer more information than others. Because of their positions as the beginning and end of the digit, PI and PIII show more marked entheseal changes between ecotypes. This makes anatomical sense, as the complex divisions and recombination of ligaments and tendons, as well as the stabilizing interdigital cruciate ligament of PII, protect this bone from the stressors placed on the proximal and distal phalanges (Hull et al., in review). While PIII shows consistently variable EC development, PI offers additional information, as forelimb bones can be decisively separated from hindlimb bones (Hull, 2019). This means that PI fore- and hindlimb ECs can be analysed separately, and the differences in development can be assessed between ecotype.

Using pooled samples to compare differences between ecotypes, significant differences in EC development are found on four attachment sites on PI associated with flexion and extension. No sites showed significant differences on PII. All three sites analysed on PIII show significant differences between ecotypes, and these three sites are also associated with tendinous insertion points responsible for flexion and extension. The inter-ecotype comparisons between pooled PII and PIII must be viewed conservatively however, as the small number of *R.t. fennicus* samples for these elements make these analyses less comprehensive than those of PI. While the size differences between *R.t. fennicus* and *R.t. tarandus* may have some effect on entheseal development, it is important to note that our study shows that some, but not all, entheseal sites show significant differences; *R.t. fennicus* do not show more entheseal development in all cases or on all sites.

When PI was separately assessed by both ecotype and limb, statistically significant sites remained the same, with the addition of the axial collateral metacarpophalangeal ligament on the thoracic limb (Tables 2, 3). When the thoracic and pelvic limbs were analysed between members of the same ecotype, an interesting pattern emerged. While only one site of significant difference in ECs was found between the fore- and hindlimb PIs of *R.t. fennicus* (Table 2), *R.t. tarandus* showed differences in three sites on PI (Table 3). While the small number of *R.t. fennicus* PII phalanges (n=9) make comprehensive statistics impossible, exploratory t-tests suggest that there are no significant differences between any sites, while *R.t. tarandus* show significant differences between fore- and hindlimb on two sites (Table 4). The most suggestive of these, sites A and C, or the extensor and flexor tuberosities, were calculated on the small number of *R.t. fennicus* specimens and showed no difference between limbs~~.~~

Inter-ecotype differences In the pooled analysis of PI, *R.t. fennicus* had higher EC scores than *R.t. tarandus* on sites A, B, E, and F. The sites A and B translate to the axial and abaxial collateral metacarpo-/metatarsophalangeal ligaments, which move with the flexion and extension of PI. These ligaments also function to stabilize the articulation between the metapodial and PI. Sites E and F are the insertion sites of each side of the distal annular ligament of PI. This ligament binds the flexor tendons to PI, creating a sheath that both allows mobility but stabilizes the tendons against PI. When the digits are flexed, this creates pressure against the distal annular ligaments, pulling them away from PI and causing stress at the insertion site.

Several interpretations may explain the difference in EC development between *R.t. tarandus* and *R.t. fennicus.* One important factor may be their differing habitats. *R.t. fennicus* are forest dwellers who will often traverse multiple ecozones in search of food and water. This includes wading in swamps and wetlands, climbing up rocky fells and cliffs, and dodging fallen trees and underbrush. This may produce more wear and tear on their feet as they adapt to changing ground conditions. By contrast, the barrenground *R.t. tarandus* are subject to far less diversity of habitat, with heavy snowdrifts often cushioning their movements in winter. These differences could account for the differences in ECs in the phalanges.

Behavioral adaptation and human habituation may account for additional difference. All *R.t. fennicus* are wild, and are by nature skittish and wary, fleeing at any signs of predators. The *R.t. tarandus* in the sample, while all free-range, are domestic animals who have some contact with humans and respond to predators by grouping, rather than dispersing. The heavy flight instinct of *R.t. fennicus* could lead to regular abrupt, powerful movements in the hooves that would in turn lead to entheseal development. The domestic *R.t. tarandus* likely experiences far fewer such abupt movements, resulting in lower EC scores.

Intra-ecotype differences While the differences in patterns between the ecotypes may allow zooarchaeologists to more easily identify the subspecies of reindeer in an assemblage, the differences in patterns between fore- and hindlimb within groups may shed light on different niche adaptations and behaviors. *R.t. tarandus* shows significantly different EC scores between fore- and hindlimb, while *R.t. fennicus* shows only slight differences between the two limbs. *R.t. tarandus* shows significant differences between sites D, E, and F on PI, two of which correspond to the insertions for the proximal annular ligaments, which are the primary sites holding the heavy flexor tendons to the digits. These sites combined suggest that there was more overall flexion in the hindlimb, whereas there appears to be more interdigital movement between PI and PII, as well as more abduction in the forelimb. In *R.t. fennicus,* only site E ($p = 0.021$) showed a significant difference. This indicates that while *R.t. fennicus* also shows more flexion in the hind digits, this dichotomy between the use of the fore- and hindlimb is less distinct. Our analysis suggests that while *R.t. fennicus* have more entheseal development in general, *R.t. tarandus* have more *differentiated* entheseal development. We propose that while *R.t. fennicus* may use the tendons and ligaments in their feet more, they do so holistically, with both limbs being subject to similar amounts and kinds of physical stressors. *R.t. tarandus* use different limbs for different purposes, leading to different entheseal changes between the limbs.

When analysing PII, complete analysis of *R.t. fennicus* phalanges were hampered by the small number of samples. In *R.t. tarandus*, however, we see evidence of a continued divergence between activity pattern in the fore and hindlimb, as sites A and C, the extensor and flexor tuberosities respectively showed significant differences. This difference is interesting because on site A, the extensor tuberosity, the pelvic limb showed higher EC scores, while on site C, the flexor tuberosity, the thoracic limb showed higher EC scores. The flexor tuberosity of PII is the insertion point of the superficial digital flexor and is congruent with the high thoracic EC scores of the medial interphalangeal collateral ligament of PI, as the development of both these sites are suggestive of repetitive flexion at the PI-PII interphalangeal joint (Hull et al. in review). This suggests that while both ecotypes flex their entire hindlimbs more habitually, *R.t. tarandus*, at least, flexes the smaller joints of the hooves in the forelimb, creating a scoop-shape out of their hoof. This may be consistent with more habitual pawing at the ground, digging, or using the forelimb hoof for foraging activities. If larger sample sizes confirm that this is untrue for *R.t. tarandus*, this may be an indication of less digging for forage, due to either more habitual browsing or less snow cover hampering foraging efforts.

Limitations. While the data shows a convincing pattern of differing hoof use between ecotypes of *Rangifer tarandus*, several limitations to this study must be discussed. First, the effect of sex on hoof use could not be analysed, primarily to the small sample of *R.t. fennicus*. Second, the size of the animals themselves may have affected levels of entheseal change. While *R.t. fennicus* are larger-bodied and had generally higher EC scores, they did not have universally higher EC scores, which suggests that size is not the only factor affecting the EC score differences between ecotype. Last, the age of each individual must be taken into account. While all specimens were adults, their exact age is unknown. A mitigating factor, however, is the removal of any specimens who showed age-related disease such as osteoarthritis. This is one way that senescent individuals may have been removed from the sample.

Conclusion

The data shows that there are significantly different EC patterns between the ecotypes of *R.t. tarandus* and *R.t. fennicus*, which may be caused by several factors. While the specific factors are not directly identifiable, the observed differences strongly suggest that there are significant behavioral, mobility, and/or foraging behaviors between these populations. The identification of these consistent differences has implications for studies of zooarchaeology, paleoecology, and domestication studies.

In zooarchaeological assemblages, *R.t. tarandus* and *R.t. fennicus* remains are nearly impossible to separate, especially in disarticulated and co-mingled remains. The differences in the ECs of the phalanges shown in this study present an additional tool for zooarchaeologists to determine whether *R.t. fennicus, R.t. tarandus*, or both, are present in an assemblage. Such identifications can, in turn, help establish which hunting, herding, or combined strategies were employed in the past. Fluctuation in the presence of the ecotypes in different areas of Finland is an additional clue to human interference in reindeer lives. For example, with the increase in herded reindeer, *R.t. tarandus* have shifted further south than their natural habitat, moving into the boreal zone, as they continue to do today (Kortesalmi, 2008: 29-63). A shift in faunal assemblage composition from *R.t. fennicus* to *R.t. tarandus* also may indicate a shift from hunting to herding, and a combined assemblage may indicate a mixed subsistence strategy.

Such subspecies identifications can likewise have implications for paleoecology. The presence of one or both of ecotypes may help show habitat and environmental change and elucidate shifting ranges of ecotypes. Habitat and range change is of increased importance in the current era, where climate change affects the ranges and viability of these animals. Understanding their historic habitats and environments helps us not only understand human history, but the species history of *Rangifer tarandus* in Fennoscandia.

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Chapter 4

Pathological Peculiarities between Modern Ecotypes of Fennoscandian Reindeer: Injury Patterns and Implications for Domestication and Paleoecology Studies

By Emily Hull*, Hanna-Leena Puolakka, and Mitchell Semeniuk

Abstract

The variety of relationships between humans and *Rangifer tarandus* in Fennoscandia are of interest to both zooarchaeologists and scholars of human-animal studies. Two subspecies of *Rangifer tarandus* are native to Fennoscandia. One of these, the tundra, or barrenground, reindeer ecotype *R.t. tarandus,* has been domesticated, while the boreal, or forest, ecotype *R.t. fennicus* has been hunted by humans but is not domesticated. Our study examines whether patterns of pathological lesions related to age, activity, and trauma in modern Finnish reindeer differ significantly between *R.t. tarandus* and *R.t. fennicus*. Because these ecotypes exhibit somewhat distinct behaviors and inhabit different environments, we explore whether these disparities affect the skeleton enough to create consistent patterns of pathological lesions. The patterns in lesions unique to each ecotype can be used to assess archaeological assemblages, potentially providing information about herding, hunting, and husbandry of reindeer in the past.

Introduction

Early in the history of Fennoscandia, there were at least two subspecies of wild *Rangifer tarandus*: the forest ecotype *R.t. fennicus* and the tundra ecotype *R.t. tarandus.* While both species were initially hunted, by the Medieval era, *R.t. tarandus* had begun the transition from prey animal to herd animal, with tamed decoy animals being used to facilitate hunting. Early ethnographic reports from Northern Finland also suggest that female animals were milked (Mirov, 1945).

The shift from predation to partnership with animals is an issue of great archaeological interest with few clear answers. Many domestic prey animals such as cattle, sheep, and goats underwent morphological and genetic changes once humans commenced multigenerational reproductive control. While the precise advent of domestication is difficult to pinpoint, established human reproductive control of animals can be seen archaeologically through changes in size, shape, pelage, disposition, and herd composition. These interspecies patterns of physical change form the core of traditional definitions of domestication, where morphological and genetic changes are seen as the key criteria for this evolutionary process (Zeder, 2006, 2012).

The history of reindeer domestication is challenging to determine, as reindeer have not undergone the extensive morphological change seen among many other domestic animals, in large part due to a lack of strict, continuous, or extended reproductive control. These ways of being with reindeer diverge from the traditional domestication narrative, and scholars have argued that reindeer domestication is in-progress, incomplete, or even non-existent (Kumpula & Colpaert, 2007; Nieminen & Helle, 1980). Reindeer play a variety of roles within societies, characterized by varying degrees of human control, ranging from very tame animals who live and work directly alongside humans, to loosely managed domestic animals who retain the behaviors and skittishness of their ancestors and wild cousins (Ingold, 1980; Klokov, 2007).

The belief that reindeer domestication is incomplete or incipient also ignores the plethora of secondary historical evidence, such as rock art, ancient name places, and reindeer husbandry tools, some of which have been present for thousands of years in Fennoscandia and the rest of

Eurasia (Andersen, 2011; Bahn, 1978; Bjørklund, 2013; Brännlund & Axelsson, 2011; Hedman et al., 2015; Helskog, 2011; Ingold, 1980; Sommerseth, 2011). Regardless, as the markers of morphological change used in traditional definitions of domestication are less overt in *Rangifer tarandus,* a persistent problem is ascertaining if the remains of reindeer are those of hunted wild or domestic individuals. Because of this, other types of investigations of reindeer bodies are needed to provide information on their ecological adaptations and relationships with humans. In Finland, the center of our analysis, only the tundra reindeer ecotype, *Rangifer tarandus tarandus*, has been domesticated. Their wild forest-dwelling cousins, *Rangifer tarandus fennicus*, are not domesticated, and live in different societies, follow different foraging techniques, and experience different environmental and human pressures (Banfield, 1961; Geist, 1998). The ranges of both subspecies in Finland can be seen in Figure 1.

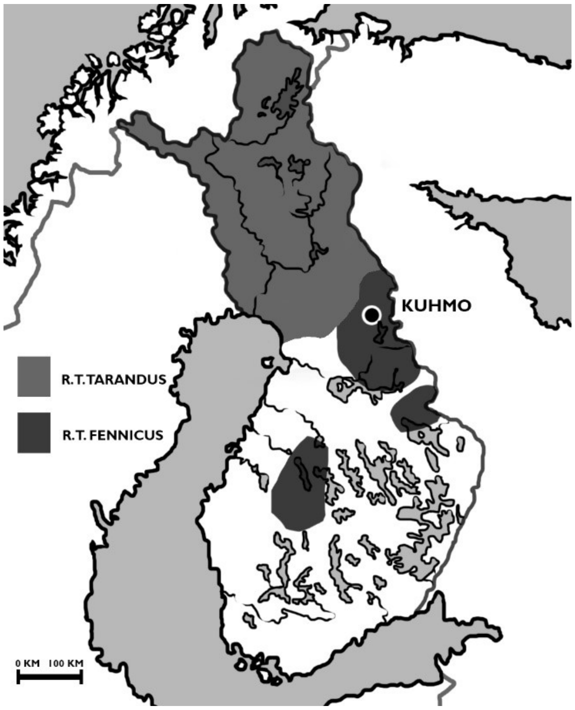

Figure 1. Ranges of *R.t. tarandus* and *R.t. fennicus* in Finland. (*illustration by E. Hull after CAFF. CARMA 8., 2019*).

Unfortunately, these ecotypes overlap in size and morphology, making conclusive subspecies determinations from skeletal remains difficult (Nieminen & Helle, 1980; Puputti & Niskanen, 2009). This study explores patterns of injury between the tundra ecotype from northern Finland and the forest-dwelling ecotyp*e*. Specifically, we examine how the differences in pathology and healing can give clues to both ancient environments and human interventions. The patterns of injury found in this analysis suggest differences in behavior, environment, and human use, which in turn may help to indicate whether archaeological *Rangifer tarandus* remains are those of hunted wild animals, butchered herd animals, or a combination of both.

Background

Ecotypes. Globally, while there are still many questions regarding *Rangifer* taxonomy, modern reindeer and caribou are customarily divided into three unique ecotypes: forest, tundra, and arctic. Each ecotype has representatives in both Eurasia and North America, and each has its own general phenotypic pattern. Behavior varies between ecotype, although some species-wide consistencies remain. *Rangifer tarandus* is the only species in which both males and females can grow antlers, and all subspecies undergo some seasonal migrations, although some are much more extensive than others. Ecotype groups vary in size, with tundra reindeer congregating in larger groups than arctic and forest ecotypes (Banfield, 1961; Geist, 1998).

Each ecotype follows a general morphological pattern, influenced by their ecological niche. Arctic ecotypes have short legs, short rostrum, small body, thick pelage, and live in the high arctic. These include the subspecies *R.t. platyrhynchyus, R.t. pearyi,* and now disused subspecies such as *R.t. arcticus*, which is now usually lumped with *R.t. pearyi* (Banfield, 1961).

Tundra, or barrenground, reindeer are recognised by their broad antler spread, medium body, and long legs, and these include *R.t. tarandus* in Eurasia and *R.t. groenlandicus* in North America. Males and females of this ecotype use their large antlers in competition for reproductive opportunities and resources. They show sexual dimorphism in antler shape and size, and in body mass, but have less of a size difference between males and females than woodland reindeer. Individuals of this ecotype gather in large herds which undergo the longest migrations of any ecotype. While individual characteristics and personalities vary, as with any species, tundra reindeer tend to be less skittish and more communal than their boreal cousins, and therefore may have been more receptive to close human interactions (Helle, 1982). In addition, their large herds and varied societies also may have made them more accepting of a human element.

R.t. fennicus, the woodland subspecies, have a narrow antler spread, and up to 30% of females lack antlers (Banfield, 1961; Geist, 1998, Puputti and Niskanen, 2008; 2009: 15). All members have large bodies and long legs, and these reindeer exihibit most extreme sexual dimorphism in body size of any ecotype. Individuals of this ecotype, which also includes *R.t. caribou* in North America, live in much smaller communities, migrate much shorter distances, and are far more wary of humans than tundra reindeer. They have been hunted by humans, but not domesticated (at least in Fennoscandia). When confronted with potential threats, their propensity is to scatter rather than to cluster and circle as tundra reindeer do (Helle, 1982).

In Finland the forest- dwelling *R.t. fennicus* and the tundra *R.t. tarandus* have overlapping ranges (Figure 1). Although there is occasional introgression between these subspecies, this does not produce a significant number of hybrid individuals and thus does not confound community-wide studies of these two groups. It has been postulated that different timing of their ruts may decrease the possibility of hybridization (Helle, 1981:19).

Beyond having overlapping ranges, what complicates matters in archaeology is the overlap in size of *R.t. tarandus* and *R.t. fennicus* (Nieminen & Helle, 1980; Puputti & Niskanen, 2009). While *R.t. fennicus* are generally far larger than *R.t. tarandus,* a small female *R.t. fennicus* may be equal in size to a large male *R.t. tarandus.* As most reindeer body parts are found in comingled assemblages without distinct os coxae, crania, and attached antlers to determine sex, they are impossible to morphologically differentiate. Because of this, secondary clues to both ecotype and human intervention are key to further analysis of reindeer assemblages.

Paleopathologies in both humans and animals can be divided into many different areas of study. Pathological lesions of the bone can result from many factors, including disease or infection, cancerous growth, trauma, and age-or activity related pathologies such as osteoarthritis and entheseal changes. For this study, as we were looking at mechanical forces that shape pathological lesions, only lesions caused by trauma or age/activity will be examined.

Pathological lesions consistent with the unique stressors of animal work have been documented in a few species. For example, pathological studies of wild versus managed South American camelids have shown that modern domestic camelids are more vulnerable to congenital pathologies, while wild populations show a higher incidence of pathologies from environmental perils (Flensborg & Kaufmann, 2012.) In addition, Izeta and Cortes (2006) suggest the possibility of rough terrain acting as a compounding factor in working camelid paleopathologies.

Likewise, age/activity-related changes have been used to document activities associated with domestication, such as work activities like traction, bearing burdens, as well as with changes in foraging or feeding activities (Bartosiewicz & Gál, 2013; Niinimäki & Salmi, 2014; Salmi & Niinimäki, 2016). This study examines the possibility that the unique ecological niches and behaviors of domestic reindeer and wild forest reindeer create different environmental stressors and make the potential for differentiation by pathological lesion feasible.

Study Environment

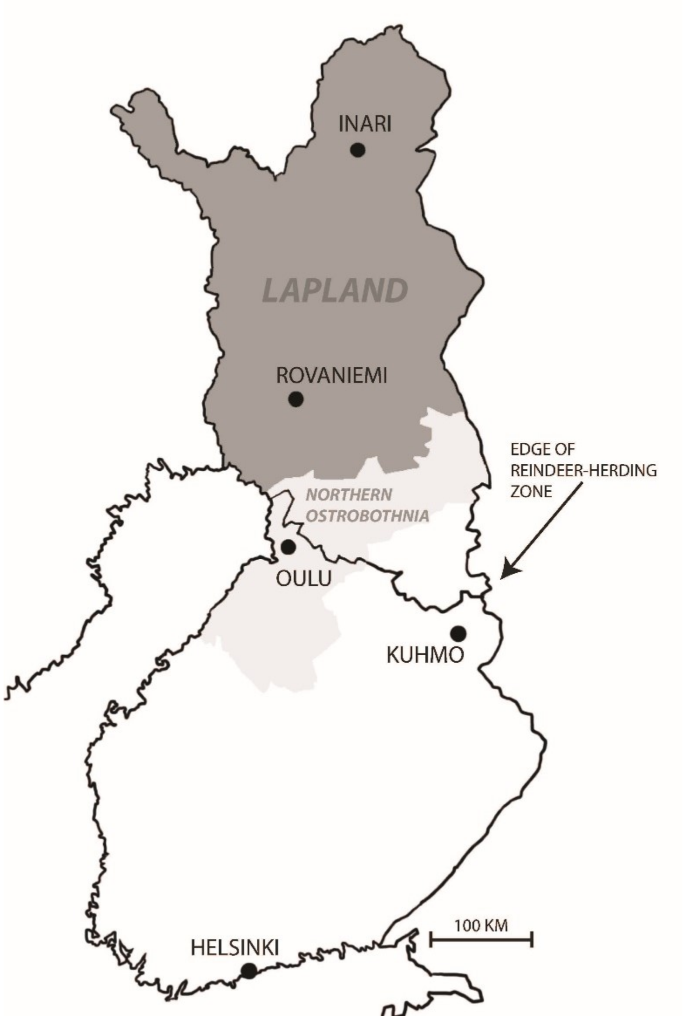

Figure 2. Areas of *R.t. tarandus* herding areas and *paliskutas* as well as notable regions and landmarks in Finland. (*illustration by E. Hull after National Geographic, Esri, Garmin, HERE, UNEP-WCMC, USGS, NASA, ESA, METI, NRCAN, GEBCO, NOAA, increment P Corp., 2019*).

Most of the rural areas of Finland consist of boreal forest or Scandinavian taiga with a subarctic climate. The northernmost parts of Finland are not considered arctic tundra as such, but rather a border zone of taiga and tundra, with open fells covered only by small trees and bushes and capped with alpine tundra. These latter areas are classified as the Scandinavian Montane Birch forests and grasslands ecoregion (WWF, 2019).

The vast majority of the *R.t. fennicus* in our sample come from the Kuhmo area (see Figure 2), and the following descriptions apply to the herds and individuals in that region. These wild reindeer prefer wetlands in the summer: bogs, marshes, coniferous swamps, and the watersides of small ponds, lakes, and streams. Such wetlands are plentiful in the Elimyssalo Nature Reserves, where the wild forest reindeer in the Kuhmo region mostly stay during the summer (Helle, 1982: 29). Wild forest reindeer remain in a small area in summer, and during the birthing season, their ranges may constrict to as small as a single square kilometer. They return to the same area every year, preferring habitually used spots to other similar areas nearby (Helle, 1982). In summer, wild forest reindeer subsist on dozens of plant species, so their foraging area is not based on the range of a single food source (Helle, 1982). In winter, wild forest reindeer congregate into larger herds and move to the Viiksimo and Lentua areas. These areas contain eskers: long, narrow, and steep ridges made of sand and gravel. Eskers are common in the Kainuu and Kuhmo region (Helle, 1982:30–31).

In the winter, both domestic and wild forest reindeer prefer to eat reindeer lichen (*Cladonia rangiferina*) and frequent the areas where it grows, mostly in dry pine forests, and other areas of dry and barren soil. Wild forest reindeer will wander between areas if the lichen starts to diminish or the snow cover becomes too deep or hard for them to forage efficiently. *R.t. tarandus* range over more restricted areas than their forest cousins. In fact, *R.t. fennicus* are more likely to move to areas where food is more plentiful, while *R.t. tarandus* may remain in an area without resources, even to the point of starving to death. Both subspecies will eat *Usnea*, a species of arboreal lichen, if reindeer lichen is unavailable or unreachable under snow cover (Helle, 1982).

The geology and ecology of their habitats also differ. The central habitat of wild forest reindeer consists of closed-canopy forests in the south, with floors covered in moss or shrubs. These give way to dry, lichenous woodlands further north, and then to sparse, tundra-like fells of northern Lapland, the home of tundra reindeer. In the *räkkä* season, the period between midsummer and early autumn, massive swarms of mosquitoes converge, and both wild and domesticated reindeer seek open areas such as fells, bogs, roads, and sands, looking for breezes to keep the mosquitoes away (Helle, 1981:20).

Herding practices

All *R.t.tarandus* in Finland are managed, meaning that they are owned by humans. There are 56 *paliskunta* or herding co-operatives (local organizations each comprised of several reindeer herders utilizing a defined area) in the reindeer herding zone, which together cover 36% of Finland, or ~123,000 square kilometers (Figure 2). This zone includes the northern and eastern parts of the North Ostrobothnia region, northern parts of the Kainuu region, and almost the whole of Lapland, excluding the municipalities around the Bothnian Bay (Ministry of Agriculture and Forestry of Finland, 2019).

The movement of domestic reindeer is partially restricted. In some places, fences between different *paliskunta* herding areas provide barriers to animal movement. In places without fences, the reindeer will often cross *paliskunta* borders. If a reindeer from a neighboring *paliskunta* is found during a separation event, they are returned to their owner. Separation events are annual herding roundups where reindeer are selected for slaughter or to receive veterinary care. *Paliskunta* have mostly formed around natural areas, on average 2,000 km^2 (600-15,000km^2), inside which specific reindeer herds stay all year. These *paliskunta* are usually bigger in the north, and smaller in the southern areas of the reindeer herding zone (Helle, 1982:23-24).

Humans interact with most domestic reindeer only twice a year: in the spring when earmarking the calves that represent the owner, and during the autumn annual separation roundups. As mentioned earlier, the reindeer are very loyal to their summer grazing areas and return to the same areas each year to give birth. This tendency facilitates the marking of the calves and allows humans to use reindeer behavior to their advantage (Helle, 1982: 25-27). A few domestic reindeer are taken in as a "home reindeer" in the autumn, who then live in pens over the winter or longer, for various reasons. Sick animals may be separated to be given veterinary care. Some males are castrated and taught to pull sleds or racers with skis, which now is almost entirely done for recreational and tourism purposes.

Materials and Methods

Materials. The specimens for this analysis are divided into two samples. The core sample consists of Finnish reindeer skeletons from 99 individuals. These individuals include domestic tundra (*R.t. tarandus*, n= 42) and wild forest (*R.t. fennicus*, n= 57) reindeer, all housed at the Biodiversity Unit, University of Oulu. While all of the *R.t. tarandus* samples are domestic reindeer, these individuals are managed animals from free-ranging herds. These herds are routinely gathered for culling, butchery selection, and to establish animal health. These roundups, however, do not occur so frequently as to prevent naturally occurring injuries. While the *duration* of an animal injury may be a sign of human intervention, these reindeer remain vulnerable to environmental injury that would have occurred in wild populations of *R.t. tarandus*. We thus consider this sample relevant for exploring injury occurrence rates. Furthermore, modern domestic reindeer have not been under the same levels of reproductive control as other domestic species. They retain a high level of similarity to their wild ancestors, meaning that modern populations remain osteologically relevant for zooarchaeological analogy. All known working or penned animals were excluded here, although some temporarily penned animals may be included, if this was not noted in their personal histories. While wild and domestic reindeer occasionally interbreed, no hybrids are included in the sample. Injuries in *R.t. fennicus* were also assessed by sex, where such information was available (n = 46). Too few individuals of known sex were available to perform sex-based assessment of *R.t. tarandus.*

Selection bias may be present in the *R.t. fennicus* specimens housed at the University of Oulu due to restrictions on hunting and collecting these animals. Because of these restrictions, the collected individuals are more likely to have been physically compromised due to injury, or to have been found dead. While the percentage of injury occurrence may be inflated due to collection bias, this should not affect the types and locations of the injuries present.

The second, smaller group of individuals (n= 11) includes the skeletons of tundra (*R.t. groenlandicus*) and arctic (*R.t. pearyi* and *R.t. arcticus*) individuals from North America, housed at the Canadian Museum of Nature. Although this subgroup is small, it was analyzed to assess the comparative pathologies of wild tundra and arctic animals to domestic tundra animals. While arctic subspecies are subject to different stressors than those from lower latitudes, such as high arctic predators, temperatures, and weather, the physical substrates on which they walk do not vary dramatically between arctic and tundra animals. These both include flat, mostly treeless stretches of land, exception for the gently rolling hills and taiga that tundra animals may encounter during their annual migration. Their environments are much more similar in topography than those frequented by forest reindeer, whose habitats include more variable and often unstable or dramatic changes in topography.

No zoo-kept, castrated, or working animals were included in this study, as these animals are subject to different mechanical stress than free-ranging individuals (Salmi & Niinimäki, 2016; Niinimäki & Salmi, 2014). Additionally, all analyzed individuals were adults of known subspecies and provenience. All study specimens were complete or nearly complete post-cranial skeletons, although several individuals were missing smaller, more fragile bones, especially ribs and phalanges.

Methods. All individuals were assessed for pathological lesions, and these lesions were divided into two types: those due to age and/or activity, and those due to trauma, e.g., fractures (Appendix 1).

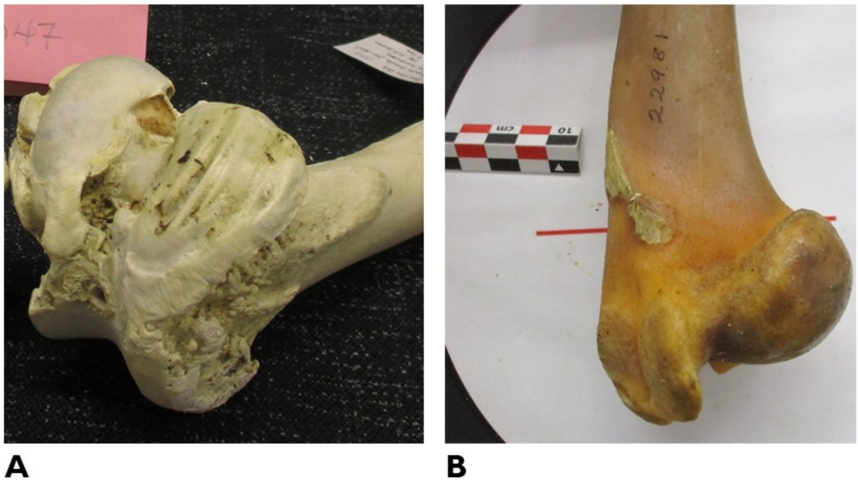

Figure 3. Age/activity-related pathologies. A) Long term, severe activity-related lesion associated with traumatic injury on the limb, counted with the associated traumatic pathology. B)

Activity-related lesion within the normal range unassociated with traumatic injury, noted separately from any traumatic pathology. *Photos by E. Hull.*

Age/activity. Frequency data was collected on mild age-related and activity-related pathological lesions, including entheseal change and osteoarthritis. These pathological lesions were documented only according to presence or absence on the entire skeleton. They were, however, divided by context. There were cases of severe osteoarthritis, eburnation, and osteophytic growth directly related to a site of trauma or obviously related to severe trauma on the opposite limb (Figure 1). These cases were not marked as age/activity-related, but rather noted as part of the trauma/healing complex of a long-term traumatic injury. Here mild age/activity-related pathologies include mild to moderate osteoarthritis, defined as limited osteophytic growth that did not deter full movement of the joint, with no eburnation (Figure 3), and isolated entheseal changes, namely those not associated with a traumatic lesion. The presence of these lesions were notated on specific limbs and analysed separately from traumatic injury.

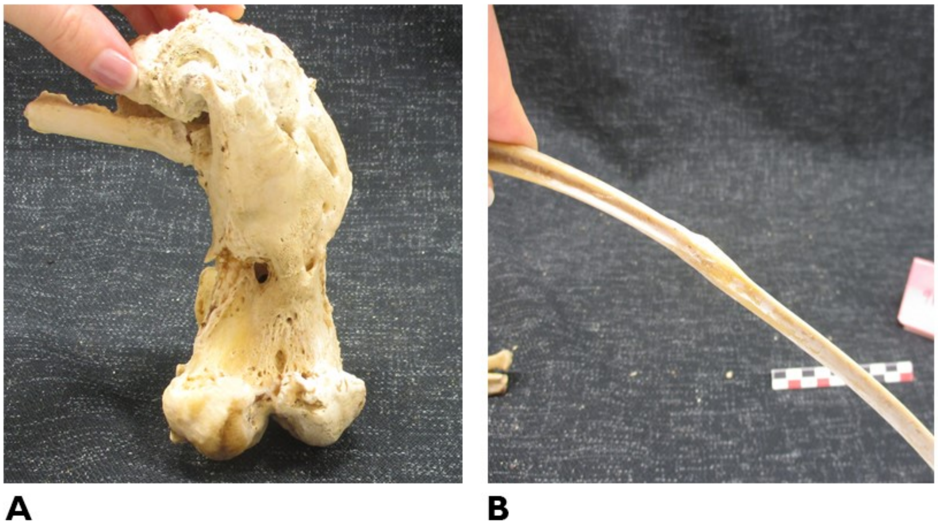

Figure 4. Traumatic pathological lesions. A) Long term, severe traumatic lesion, complex. B) Minor, healing lesion, non-complex. *Photos by E. Hull.*

Trauma. Initial analysis was qualitative, describing each pathology as specifically as possible. This primary analysis was then translated into a rubric which cross-referenced type of lesion to location of lesion. The lesion locations were divided into the following areas: post-cranial axial skeleton, forelimb (without hooves), forelimb hooves, hindlimb (without hooves), hindlimb hooves. Notation was made regarding extent/presence of healing in traumatic pathology as well as complexity and severity of the trauma (Figure 4).

Results

TABLE 1

Trauma frequencies between ecotypes

Ecotype	Presence	Number affected	Percent affected
Age/activity related (general)			
R.t. tarandus (n = 42)	No	42	100.0
	Yes	0	0.0
R.t. fennicus (n = 57)	No	34	59.6
	Yes	23	40.4
N. American (n = 11)	No	11	100.0
	Yes	0	0.0

Raw frequency data was analysed and crosstabulation of frequency data between groups was performed using chi-squared statistics employing Yates continuity correction. In an examination of raw frequency data, no *R.t. tarandus* showed signs of non-perimortem traumatic injury. At the same time, 40.4 percent of *R.t. fennicus* exhibited indications of longer-term trauma unrelated to cause of death (Table 1). The few examples of *R.t. fennicus* with potential perimortem injury also had longer-term traumatic pathologies present.

TABLE 2

Chi-Squared tests of trauma frequencies between *R.t. tarandus* and *R.t. fennicus*

	Value	df	p
X^2	22.076	1	< .001
X^2 continuity correction	19.872	1	< .001
N	99		

While the North American sample was too small for comprehensive statistical analysis, a chi-squared test of the *R.t. tarandus* and *R.t. fennicus* trauma frequencies showed a significant difference, with the continuity correction giving p<.001 (Table 2).

TABLE 3

Age/activity pathology frequencies between ecotypes

Ecotype	Presence	Number affected	Percent affected
Age/activity related (general)			
R.t. tarandus	No	30	71.4
	Yes	12	28.6
R.t. fennicus	No	39	68.4
	Yes	18	31.6
N. American	No	0	0.0
	Yes	11	100.0

In terms of age/activity-related pathologies, 28.6 percent of *R.t. tarandus* showed these pathologies, while they were present in 31.6 percent of *R.t. fennicus* individuals (Table 3). The small subsample of Canadian barrenground and arctic ecotypes (n=11) were compared to the base sample of Fennoscandian individuals. The Canadian caribou showed no incidence of trauma, but all of the individuals exhibited age/activity-related pathologies (Table 3). This suggests that while the Fennoscandian domestic reindeer sample may under-represent age/activity- related lesions in wild animals, it is consistent the incidence of traumatic injury. The chi-squared test results (Table 4) show that there is no statistically significant difference between the occurrence of age/activity related pathologies between *R.t. fennicus* and *R.t. tarandus.*

TABLE 4

Chi-Squared tests of age/activity pathology frequencies between *R.t. tarandus* and *R.t. fennicus*

	Value	df	p
X^2	0.104	1	0.748
X^2 continuity correction	0.010	1	0.920
N	99		

Delving more deeply into the specifics of the longer-term traumas and age/activity patterns present in the *R.t. fennicus* sample, differences between sexes were explored as to incidence or sites of trauma (Table 5).

TABLE 5

Frequency patterns of pathology between male and female *R.t. fennicus*

Sex	Presence	Number affected	Percent affected
Trauma (general)			
Female	No	14	58.3
	Yes	10	41.7
Male	No	10	45.5
	Yes	12	54.5
Trauma Forelimb (not hooves)			
Female	No	23	95.8
	Yes	1	4.2
Male	No	19	86.4
	Yes	3	13.6
Trauma Forelimb (hooves)			
Female	No	24	100.0
	Yes	0	0.0
Male	No	21	95.5
	Yes	1	4.5
Trauma Hindlimb (not hooves)			
Female	No	23	95.8
	Yes	1	4.2
Male	No	17	77.3
	Yes	5	22.7
Trauma Hindlimb (hooves)			
Female	No	23	95.8
	Yes	1	4.2
Male	No	20	90.9
	Yes	2	9.1
Trauma Axial skeleton			

Female	No	18	75.0
	Yes	6	25.0
Male	No	21	95.5
	Yes	1	4.5
Age/activity related (general)			
Female	No	19	79.2
	Yes	5	20.8
Male	No	9	40.9
	Yes	13	59.1
Age/activity Forelimb (not hooves)			
Female	No	21	87.5
	Yes	3	12.5
Male	No	16	72.7
	Yes	6	27.3
Age/activity Forelimb (hooves)			
Female	No	24	100.0
	Yes	0	0.0
Male	No	20	90.9
	Yes	2	9.1
Age/activity Hindlimb (not hooves)			
Female	No	22	91.7
	Yes	2	8.3
Male	No	15	68.2
	Yes	7	31.8
Age/activity Hindlimb (hooves)			
Female	No	22	91.7
	Yes	2	8.3
Male	No	19	86.4
	Yes	3	13.6
Age/activity Axial Skeleton			
Female	No	24	100.0
	Yes	0	0.0
Male	No	21	95.5
	Yes	1	4.5

While chi-squared tests showed no significant differences between overall trauma or trauma to specific regions, it did show statistically significant p-values for overall age/activity related trauma (p= .019), though this was not shown to be due to significance at any one site or region. All significance tests and frequency data, as discussed below, must be supplemented with the qualitative analysis of the lesions.

Discussion

Wild forest reindeer and tundra reindeer belong to the same species, but occupy distinct ecological niches, participate in different habitual behaviors, and for the individuals analyzed here, have different relationships with humans. These differences, in turn, can potentially provide information about human hunting and herding strategies, the development of reindeer herding, and human and reindeer mobility.

In this study, we examined the differences in typical pathologies between reindeer ecotypes, as they can potentially give information about the subspecies present in an assemblage. We then examined the rates of trauma and age/activity-based pathologies. This study is founded on the general supposition that animals in different ecological niches are subject to different stressors. Further, we postulate that reindeer in different ecological niches forage and move in different ways, but also that the nature of the ground surface can change an animal's posture and movement. More broadly, animals are subject to environmental hazards unique to their ecological niches.

The results of our analysis show several interesting trends. First, free-ranging tundra and wild forest reindeer have comparable incidences of age/activity related pathologies. Second, wild forest reindeer have a much higher incidence of traumatic pathologies. These data indicate that while both domestic and wild forest reindeer undergo similar amounts of everyday physical stressors, wild forest reindeer experience more traumatic injury, which is rare among barrenground or tundra ecotypes.

The fact that tundra and wild forest reindeer (and potentially also arctic ecotypes of *Rangifer tarandus*) have comparable incidences of age/activity-related pathologies suggests that some similar life-history patterns may be generally characteristic for the species regardless of ecological niche. This is important, especially as age/activity related pathologies can differ between working and nonworking animals of a given species (Bartosiewicz, 2008; Salmi & Niinimäki, 2016; Niinimäki & Salmi, 2014). Our study results confirm that overall patterns in the occurrence rates of such pathologies are not complicated by occupation of differing ecotypes, or even by the fact that the two ecotypes have differing average body masses. Our data also show a higher percentage of age/activity-related pathologies in fully wild reindeer than in husbanded free-range tundra reindeer, the latter admittedly being a very small sample. This pattern may be due to several factors, the first of which is collection bias. As herders donated the adult animals in the collection, they were more likely to be culled individuals, many of which were probably killed long before reaching senescence—maintaining animals to olde age is not cost-effective for herders. Because of this, these animals were less likely to have the time to develop age-related pathologies. The second factor is that domestic animals are more likely to be culled when they begin to show the first signs of age/activity-related disease, leading to fewer extreme examples in the sample. The third compacting factor is the winter foddering of domestic tundra reindeer. Such reindeer may have conducted less digging in the snow than their wild cousins, and therefore experienced less attritional pathologies on their bodies.

The most definitive result of this study was the difference in traumatic lesions between tundra and forest reindeer. Two causes appear to account for this pattern: differences in environment and differences in human management. A major reason for the significantly higher amount of traumatic injury in wild forest reindeer, especially in the limbs, may be due to environment. Kuhmo, where the majority of the boreal *R.t. fennicus* specimens originated, is an area of rocky forests and lakes near the Russia-Finland border. This terrain likely is a more unstable landscape for reindeer hooves to traverse, and the likelihood for injury in this landscape is perhaps compounded by the behavioral propensity of *R.t. fennicus* toward flight when threatened. Snow-covered tree-wells could present the threat of a broken hoof or leg, and unstable rocky slopes and streambeds offer additional hazards. Without human protection, wild forest reindeer are faced with potential threats from predators such as wolves, bears, and poachers. The panic inspired by predators could easily cause an animal to misstep, even in familiar territory, causing injury or death. Additionally, when faced with dwindling winter resources, wild forest reindeer will typically venture relatively long distances in search of food. While this allays the risk of starvation, the movement between different environments increases the risk of environmental injury.

By contrast, the *R.t. tarandus* from the collection were under some level of human protection and surveillance, although much less so than many other domestic species. Besides the two annual periods of intense interaction with humans, the domestic reindeer are mostly left to fend for themselves and act according to their own cultural and communal norms. Unlike the skittish and independent wild forest reindeer, these domestic reindeer prefer to remain in groups and congregate in known locations, even to the detriment of their health and wellness. As such, while environmental hazards probably remain consistent through time, the threat of starvation is now significantly reduced due to supplementary feeding, which has offset the recent loss of lichenous habitat. Additionally, these reindeer continually occupy landscapes well-known to them, and these places are characterized by flat or gently rolling topography, which further diminish the possibility of traumatic limb injuries.

An interesting dichotomy between male and female *R.t. fennicus* was also found. The occurrence of trauma to the axial skeleton shows where statistics without context do not represent the whole story. Because of the protected nature of *R.t. fennicus,* there are often more complete records of their provenance, deaths, soft-tissue trauma, lesions, or parasitic infestation. In the 33.33 percent of female *R.t. fennicus* who exhibited trauma to the axial skeleton, the trauma was always bilateral fractures to the lower ribs. There was only one occurrence of rib fracture in a male *R.t. fennicus,* individual 22070, whose injury was very different to those sustained by the females. This adult male *R.t. fennicus* suffered from multiple fractured cervical and upper thoracic vertebra and ribs, with an additional infection of his forelimb. The ranger reports state that he was 103 kg, making him extremely thin or malnourished, as *R.t. fennicus* males have an average body mass of 143 kg (Puputti and Niskanen 2008; 2009: 154). He was lying on his side, unable to rise, and was therefore euthanized. His extreme condition was distinct from the fractures observed on the females, which were universally on the lower ribs, present bilaterally, and either healed or in the process of healing. These lesions may be mating injuries, while individual 22070 was more likely the victim of a fall or being struck a glancing blow by a car. When looking into the trauma between sexes in terms of severity, male individuals were somewhat more likely to have severe injuries. Conversely, female injury patterns were generally, but not always, more minor. Overall, with the exception of axial skeletal trauma, male *R.t. fennicus* appear to suffer traumatic injury the same rate as females and overall greater age/activity-related pathologies of the limbs.

Humans often respond to domestic animal pathology by killing compromised animals, in which case there may be trauma without healing. In other cases, humans may employ veterinary intervention, resulting in the trauma being mitigated. We may also protect managed animals from some forms of gross trauma. An animal guarded by humans is less likely to fall victim to non-human predators and less likely to face starvation or death from a dangerous environment. When trauma does occur, however, these individuals are often “put out of their misery”, giving them reduced chances to heal. Beyond human responses to trauma, human foddering, herding, and penning shapes animal behaviour and experience, again leading to less starvation, non-human predation, and competition for resources.

The zooarchaeological implications of this study can be seen in the examination of the similarities and differences of wild and husbanded reindeer in Fennoscandia. As previously referenced, earlier studies have found differences in the entheseal changes and activity-related pathologies between penned and free-range reindeer (Salmi & Niinimäki, 2016; Niinimäki & Salmi, 2014). Our data show a lack of influence of ecological niche and mobility on the occurrence rates of activity-related pathological lesions. This suggests that previous studies on entheseal changes between penned versus free-ranging reindeer are not influenced by the ecotype of the reindeer—free-ranging domestic and wild reindeer have similar levels of age/activity-related pathologies.

The biggest difference between the populations, the incidence of trauma-based pathology, also has implications for zooarchaeology. Because husbanded and herded tundra reindeer generally lack traumatic pathologies, this study adds credence to hypotheses that an assemblage of animals with high rates of long-term pathologies is primarily composed of wild individuals of a forest ecotype. While human intervention may account for the lack of traumatic pathology among domestic tundra reindeer, the small North American subsample suggests that the environment may have as much to do with this discrepancy as human activity. Because barrenground and high arctic reindeer and caribou from the show little signs of these traumatic injuries, it can be presumed that the rugged environments frequented by forest ecotypes are a high-risk factor for the occurrence of these traumas. The fact that these traumas persist with more longevity on the hindlimb and axial skeleton is most likely due to reindeer foraging and feeding behaviors. As the forelimb is needed to dig for lichen, and as most of a reindeer's body weight is carried in the fronts of their bodies, a forelimb injury would be less survivable than a hindlimb or rib injury.

While these patterns should not be used in isolation to determine ecotype and domestication, they add an additional tool to the assessment of reindeer remains. Free-range reindeer of all ecotypes develop age and activity-related pathologies at the same rate, and thus unusual activity markers may be examined with more confidence in definitively assessing active domestic animal use. Conversely, tundra reindeer do not sustain traumatic injury at the same high rates as wild forest reindeer, and an assemblage with skeletal material of indeterminant ecotype may be assessed in this way. The presence of animals with long-term traumatic injury points strongly to the presence of hunted wild reindeer in an assemblage, while a complete lack of traumatic injury suggests herded and managed individuals.

This study shows how mobility and environment play important roles in the lives of reindeer in Fennoscandia, either highlighting their similarities or differences. The domesticated tundra ecotype shares the same high mobility as wild forest reindeer, but the differences in the terrains and surfaces that they traverse can be seen in their traumatic injuries. These similarities and differences add to our understanding of reindeer in both the modern and archaeological record.

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Chapter 5
Love and Death: A Theoretical and Practical Examination of Human-Animal Relations in the Creation of a Wild Animal Osteobiography.

By Emily Hull

Abstract

Osteobiographies are a common form of presenting the archaeological analysis of the life history of an individual. This form of analysis, however, is usually reserved for human subjects. Writing an osteobiography of a nonhuman person is complicated by the lack of human understanding of animal thought and experience. Such analysis is further complicated when the subject is a non-companion animal, and isolated from human funerary rituals which may shed light on the animal's life. The skeletal remains of an injured wild caribou from Alberta who was collected as a museum specimen present a unique opportunity to understand an individual animal's life, as well presenting an example of the complexities of human-animal relationships in an analytical setting. This study examines both the life of an extraordinary nonhuman person and the impact of reconstructing nonhuman life histories on the analyst.

Keywords: Rangifer tarandus, caribou, zooarchaeology, human-animal studies, animal paleopathology, osteobiography

Introduction

Historically, zooarchaeologists have focused on animals and animal remains as economic objects, reduced to their utility for meat and secondary by-products (Binford 1962, 1978, 2002). More recently, archaeological scholarship has expanded its focus to include the agency and personhood of animals (Nyyssönen & Salmi, 2013; Poole, 2015, Puputti, 2008). The remaining gap in this scholarship is due to its focus primarily on the collective experiences of wild animals, with the study of individuals mainly reserved for domestic species (Bear, 2011, p. 2). We also tend to divide our study of nonhuman persons into “known” animals, ones who had a relationship with humans, and “unknown” animals, or those seemingly only encountered around the time of their death (hunted animals), which are relegated to members of a group, rather than studied as individuals.

Osteobiographies have long been an analytical technique in physical anthropology (Saul, 1986, Sofaer, 2006). Occasionally, this technique is used in zooarchaeology for domestic animals, especially those given human or human-like burials (e.g. Tourigny et al., 2016). Osteobiographies of humans have also undergone a theoretical shift, with increasing thought given to both the individual and the context of burial, bring questions of interpersonal care, grief, and compassion to the forefront (Sofaer, 2006; Baadsgaard et al., 2012).

While nonhuman person osteobiographies are generally focused on individuals in burials, other scholars have used archaeological techniques to examine the lives of animals discovered in other archaeological contexts. Some have focused on the symbolic nature of the animal, either in death or life, while others have explored the relationships between nonhuman and human persons, animal agency, and the role of nonhumans in society (Bond, 1996; Boyd, 2017; Salmi et al., 2017; Serpell, 1996; Watts, 2013; Hill, 2013). Many such studies involve canids and their important connection to humans (Gräslund, 2002; MacKinnon, 2010; Losey et al., 2011; Losey et al., 2018). These studies have fundamentally reshaped the ways in which we consider animals in the archaeological record. In the majority of these papers, the animals in question were human companions, domesticates, or prey. While the subject of the current study was killed for his body, this killing was a scientific rather than an economic venture. He was a non-domestic, non-companion animal living outside of habitual human habitation zones. This presents new interpretive challenges.

Performing an osteobiography on such a wild animal is complicated by multiple factors. First, the lack of human burial of wild animals makes their remains difficult to find intact or as individual rather than comingled skeletons. Second, the usual lack or brevity of human records of wild animal deaths, even with animals from the historic period, limit the analysis of life history, as written records or verbal accounts are useful in guiding our interpretations. Third, the lack of direct human understanding of animal experiences, outside of speculation and anthropomorphism, makes the reconstruction of an individual nonhuman life challenging, although not impossible**.** Finally, the limited knowledge of the complexity of animal cultures and communities makes the context of an individual within their community difficult to discern.

Zooarchaeology has gained much from the theoretical developments in human-animal studies, especially a shifting focus on the individuality, agency, and personhood of the animals who are studied. While economically based analyses still serve important interpretative purposes, there is a growing understanding that animals are persons who make decisions, feel emotion, and experience both pain and pleasure **(**Aaltola, 2008; Balcombe, 2006; Bekoff, 2007; Hill, 2011). Most such research, however, has approached these subjects from a theoretical perspective rather than analytically engaging with animal remains themselves.

In this study, a disabled caribou collected for museum use in 1930 allows a rare opportunity to engage in a posthumous dialogue with a wild animal. His remains were collected and recorded in detail, and his activity just before death documented by the hunter who shot him. The caribou's well-preserved skeleton allowed precise osteological and paleopathological analysis, and his extreme and unusually healed injury presented a tangible locus from which to analyze his life.

This analytical journey was complicated by increasing theoretical and emotional questions that challenged and expanded my ability as a researcher to understand the possibilities of reconstructing the life of a nonhuman person. This journey led not only to insight into the life of this caribou, but also to a relationship between researcher and subject. While many scholars studying human remains develop an emotional bond with the subjects of their research, the emergence of this relationship with the remains of a wild animal may expand our understanding of how and where human-animal relationships may develop.

Background

Finding CNM10759. CNM10759 is the archival code for the remains of a large male caribou who lived in Jasper National Park, Alberta in the 1920s until his death on July 4, 1930. CNM10759 was killed by Ian McTaggart Cowan, a noted naturalist who worked throughout Canada. During his collection trips, he provided notes in his journals on the behavior of the animals he collected. Because of this, we have a unique look into the premortem behavior of a wild animal with a peculiar injury, one that most would assume would foreshorten his life and impair wellness and viability.

When I first met CNM10759 (Fig. 1), I was analyzing differences in phalangeal changes between broad populations of caribou and reindeer. His remains lie in a large wooden box, with the most delicate being wrapped in bubble-wrap and tissue paper. His container feels more like a casket than a specimen box, and the care given to the caribou's remains by the museum curators is related in large part to the fact that he exhibits remarkable pathological lesions--he was an injured animal. Such severely injured animals typically would be excluded in population level studies, as they would be considered aberrant cases that would distort or bias a sample. My initial reaction was much the same, but my sentiments eventually shifted from dismissal and pity to complete fascination and admiration. Due to his unique injury, and the availability of the historical documentation about this individual, I came to feel that CNM10759's life history should be the focus of my study. My initial assumptions about his life and death were challenged as I delved into the written records of his death and the intricacies of his body.

Figure 1. CNM10759's skull.

The osteobiography as personal history. Traditional osteobiographies are life histories written from the evidence left on bone, forming a cornerstone of archaeological osteology (Saul, 1986; Sofaer, 2006). Almost all osteobiographies are written based on human skeletal remains, with the occasional exception of companion animals. The nature of an osteobiography is intrinsically personal. They are the life story of an individual, their health, wellness, habitual activities, and injuries. Because wild animals are generally perceived as members of a group, they are usually studied using assemblage-based analysis. This is often the only plausible way to study fragmented and mixed nonhuman remains processed by humans (Reitz & Wing, 1999; Steele, 2015). The remains of collected or culled wild animals in museum collections represent a unique opportunity to look at the skeletal morphology of wild individuals, but there is often little context to their lives. CNM10759 is notable not only in that we have written records of his last moments of life, but also because he was the survivor of an extreme injury. His injury, a severely broken and misaligned femoral contusion, allows us to explore how wild animals are hurt and heal. Further, this individual's life challenges notions of how injury progresses in the wild without human interference, and how we perceive health and viability in wildlife.

It is natural for an analyst to feel sympathy, compassion, and develop affection for their subject, even if that subject is present only as skeletal remains. While it is important to be as unbiased as possible, the study of remains could not exist if we did not sympathize or empathize with the skeletons laid out on our study benches. Although we must be careful not to place our own values onto the dead, we should also openly acknowledge that without our recognition of piles of bones as the remains of a once living individual, we would not be attempting to reconstruct their lives. It is within this balance that ethical, compassionate, and edifying osteobiographies are written. When the subject is a nonhuman person, this balance is further shifted, as a different way of being must be considered. Further, we must consider how we assess health and viability. In this study I consider health and wellness holistically, including factors beyond simply biological health. A healthy individual is therefore one who is free from disease, infection, malnutrition, and starvation, and who is an active part of a social group.

Materials and Methods

All analyses on CNM10759 were done using comparative animal and human pathologies for reference. 3D images were taken of his injured femur, courtesy of the Canadian Museum of Nature, and CT scans were taken of his entire skeleton with the facilitation and expertise of Ottawa Hospital. Additional information was obtained from specimen tags and the notes made by Cowan in his journals, curated at the University of Victoria, Canada.

Section One: First Impressions

Initial observations of the skeleton. When I opened the box containing CNM10759, I was initially confused. His femur was fragmented and contained bizarre growths and chunks of bone that I could not immediately identify. Once his skeleton was unpacked, it was obvious he had been the survivor of a traumatic injury, as his femur was in two pieces, each covered in twisted networks of unusual bone growth. By modern standards, he was a physically imposing adult male. His remains consist of an intact skull with antlers removed, a right humerus, a left femur, both ulnae, both tibiae, and all carpals, tarsals, metapodials, and phalanges from all limbs. CNM10759 measured 2160 mm from shoulder to tail, with a hind hoof width of 640 mm, making him large for a modern caribou. Written records from 1900 of caribou collected in the same area identify three males as being of relatively similar size, with shoulder to tail lengths of 2083 mm, 2057 mm, and 2210 mm, and hind foot sizes of 610 mm, 635 mm, and 597 mm. While we do not have a measurement of CNM10759’s height in life, these similarly sized males measured from 1321 to 1397 mm at the shoulder, suggesting CNM10759 fell within a similar range (Allen, 1900).

Besides his large size, his most notable feature was his broken and twisted femur. Because of this skeletal deformation, I was immediately morbidly fascinated and overcome with pity, as my first assumption was that the life of this caribou would have been painful and lonely, and that this injury had ultimately led to his demise. Once I began to dig deeper into his documented history and skeletal life story, I realized that only this last assumption was correct, but not in the way I had presupposed.

Pity and assumptions of animal pain. When presented with a body with a dramatic injury, it is perhaps natural to feel both pity and interest. A common narrative of wild animal injury is that an injured animal will be shunned as a liability by their community, left in loneliness and isolation (Hanger & Tribe, 2005; Kirkwood & Best, 1998; Bradshaw & Bateson, 2000; Paquet & Darimont, 2010). Facing extreme vulnerability to predators, they will die a slow and painful death, eventually succumbing to infection or starvation. While this sequence of events does occur, it also presents a speciesist perspective on physical disability and the ability to overcome or heal from traumatic injury. Survival of injuries, especially debilitating injuries, is often seen as a technologically facilitated process where humans with "superior" intellect employ medical care to prolong life. The notion of nature as brutal and uncaring, "red in tooth and claw," has formed a touchstone in the philosophical dichotomy between "nature" and "civilization." Because of these human ideas, the notion of a wild animal having successfully survived a severe injury seems not only unlikely, but almost unimaginable. Due to this initial bias, I was utterly confused as to how an injury so severe could have yielded such dramatic osteological changes, as bone growth takes time. When I first examined his remains, I had no doubt that this injury had been the primary cause of his death, and that the tangled knot of bone that I saw was the result of painful secondary pathology. It did not enter my mind that this injury could have healed and that he could have had social standing and even quality of life within his community.

Section Two: Fascination and Exploration

Osteological assessment of the skeleton and results of CT scans. The most evocative trait of CNM10759 was the injury and healing of his left hindlimb, as seen in Fig. 2. His femoral diaphysis was split in two via a fracture, with the displaced distal portion becoming dislodged and shifted upwards. It eventually joined with an osseous growth emerging from the diaphysis of the femur, having been rotated in the injury. The head of the femur was snapped off at the point of epiphyseal fusion. The proximal end of the femur shows osseous resorbsion, or the thinning of the bone as it is broken down and the base components absorbed into the blood stream. As the head of the femur was not found with the rest of the collection, it is unknown if the bone was completely resorbed or if a portion of the femoral head was still present in the acetabulum (hip joint), which was not saved by the collector. The rotation of the distal femur and the shearing off of the femoral head, as well as the lack of damage to the rest of the leg, all suggest an injury where the femur was twisted, perhaps due to a fall or a misstep into a hole or unexpected slope.

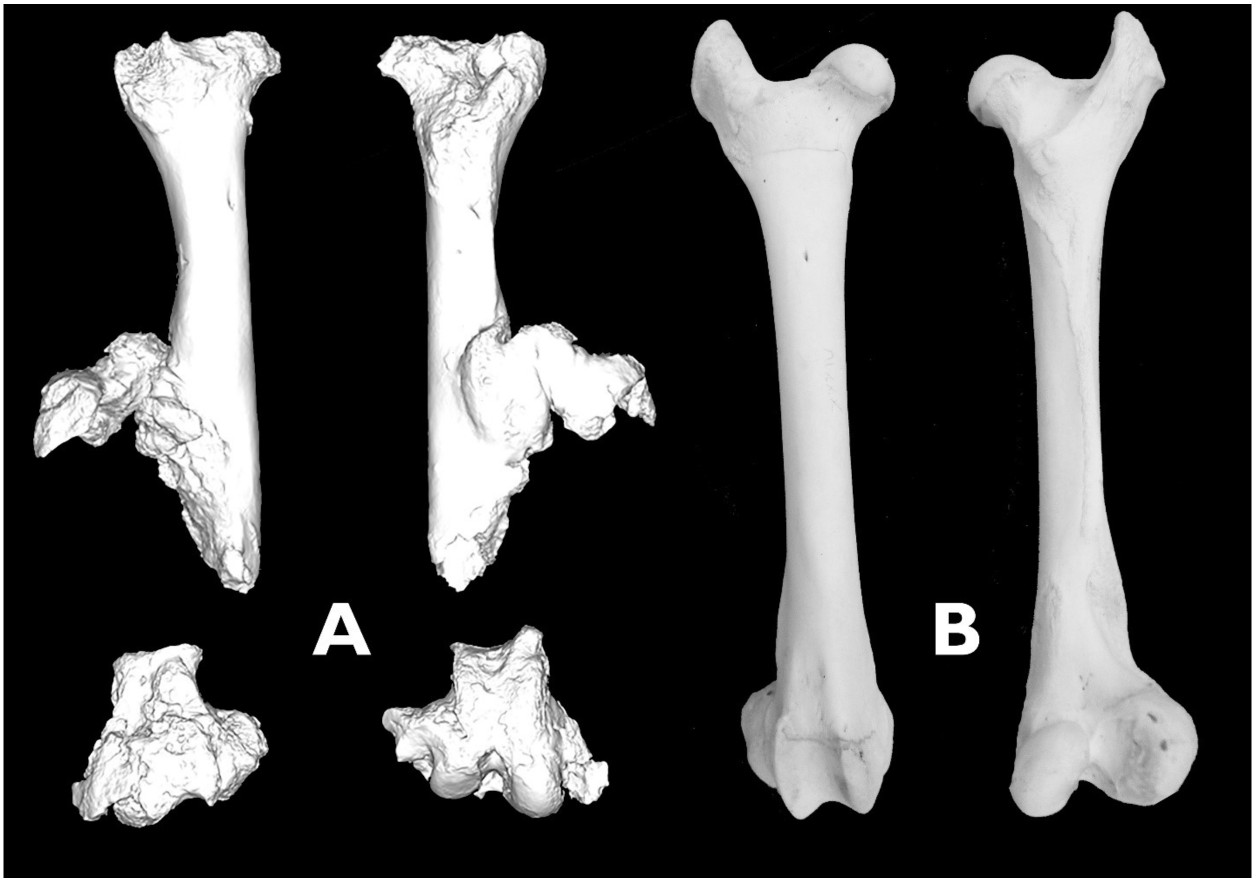

Figure 2. A) 3D scans of CNM10759's injured femur, showing the abnormal growth on the side of the shaft, as well as the broken off distal portion at the bottom. B) A healthy caribou femur.

The growth in the middle of the femoral diaphysis is ~six by eight cm. This growth is smooth and dense on the cranial surface, with continuous bumps, grooves, and growths on the caudal aspect. The growth is c-shaped in cross-section, and when placed with the displaced distal femur, covers it like a cupped hand. There is no fusion between the two, but although there may have been some slight movement of the distal femur and the bony growth, there are no sites of eburnation (polishing due to bone rubbing against bone) or articulation, so the placement would have been relatively stable. This growth and situation of the distal femur left the articular surface of the distal femur still able to articulate with the tibia at the "knee" joint, albeit at an unusual angle (Fig.3). The articular surface (area of the knee joint) of the proximal tibia shows signs of continued articulation, although on a foreshortened axis, as surfaces of normal articular wear show lack of continuous use. The ongoing use of the injured limb can also be seen in the tarsal (ankle) bones, which show osteoarthritis on the left side but not on the right, indicating unusual but habitual use of the left hind limb.

Figure 3. The left image shows the motion of the bent knee joint between femur and tibia with the detached end of the femur secured in the “cup” formed by the heterotopic ossification. The right image shows the component parts in linear view, illustrating how they fit together.

The bony growth protruding from the diaphysis may at first be attributed to remodeling after the initial fracture. When a bone is broken, it usually heals in a series of stages: a temporary healing callous of spongey bone binds the fracture site together, eventually remodeling itself into cortical bone as the fracture heals. If the fracture is reset correctly, with no displacement of the bone, the bone can reattach itself with little evidence of the initial break. In a displaced fracture, this healing callous may develop in strange patterns, attempting to connect with a broken off portion of bone that is no longer where it is supposed to be. In these cases, the interior surfaces of the bone (the endosteum and medullary cavity) often show the line of fracture internally, even after the bone is healed.

In the case of CNM10759, however, CT scans showed that the medullary cavity and endosteum of that area of the diaphysis remain undamaged (Fig. 4), and that the boney growth protrudes from the original periosteal (external) surface rather than from a fracture site. In short, the growth is located on the outer surface of an undamaged area of the bone. Because of this, this growth, rather than being a continually growing healing callous at the site of fracture, is rather interpreted as a *heterotopic ossification traumatica* (bone growth within the soft tissue around an injury) caused by the irritation of the diaphyseal periosteum by the displaced distal femur (Shehab et al., 2002; McCarthy & Sundaram, 2005; Doblare et al. 2004; Aufderheide et al., 1998). This growth then anchored the distal articulation so that walking would again be possible. CT scans also showed differences in cortical thickness between the left and right radioulnae, with the opposite limb showing greater cortical thickness, indicating greater weight was placed on this side (Shackelford et al., 2015). This implies that while he was bearing weight on his injured leg, he was either still favoring his left side, or that his asymmetrical gait placed greater mechanical stress on his right forelimb.

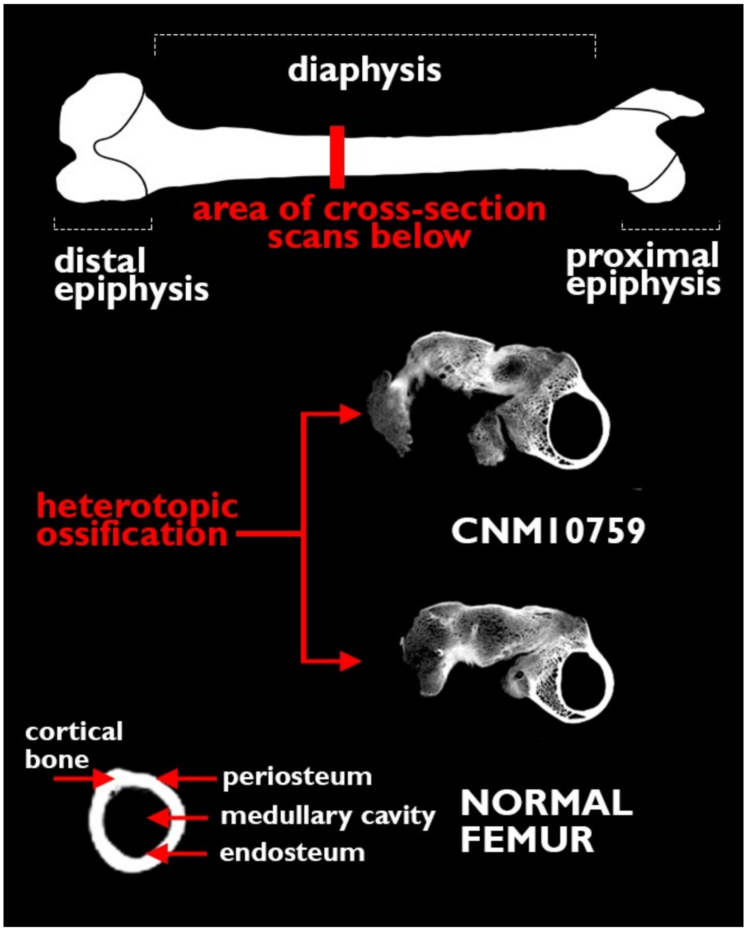

Figure 4. Diagrams and CT Scans showing the mid-femoral cross-section of a healthy caribou versus that of CNM10759. The maturity of the heterotopic ossification can be seen in the thickness of the white border surrounding the growth.

CNM10759's patella (kneecap) is fully fused to the displaced distal femur, which then articulates with a heterotopic ossification on diaphysis of the femur, as shown in Fig. 3. The distal femur, while displaced, continues to articulate with the tibia. Evidence of osteoarthritis on the articular surfaces of both distal femur and proximal tibia show that CNM10759 was still walking on his injured leg, rather than walking only on his three uninjured legs. CT scans show that the heterotopic ossification was mature at the time of his death, with pseudo-cortical bone present around the periphery of the growth.

The site closest to the articulation of the distal femur with the tibia, where the most mechanical stress was occurring, shows a cortical density similar to that on sites of the original cortical bone. The distal portion of the fractured femoral diaphysis shows advanced resorbsion, and the proximal femur shows both enlarged nutrient foramina and development of auxiliary vascular channels leading to the osseous growth on the diaphysis. This suggests that bone was being absorbed from the now useless distal end of the fractured bone, while the proximal end was developing new blood and nutrient channels to fuel the new bone growth and useable area created by the heterotopic ossification.

Outside of the trauma and remodeling of the hindlimb long bones, long-term use can be seen in the development of osteoarthritis of the tarsal bones only on the left side. This bilateral asymmetry shows not only long-term use, but that the limb had reconfigured to act viably but not as efficiently as the uninjured limb.

Additional proof of long-term use can be seen in osteoarthritis of the first phalanges of the left hind foot, the heavy development and increased ruggedness of the surface of the astragalus and calcaneus, and heavy development of muscle attachment sites in the lower left hind limb and the upper right forelimb (Claudepierre & Voisin, 2005; Wareing et al., 2011). All of these adaptations take time to develop, so there is no doubt that CNM10759 lived with his initial injury and then with his displaced but healed limb for a significant amount of time.

Breaking with assumptions of misery. Besides his injured femur, CNM10759's skeleton shows no other signs of ill health or malnutrition. In fact, his collection was not a "mercy killing," but rather one of curiosity; his injury and resulting gait made him attractive as an unusual specimen. His skeleton shows that despite my initial assumptions, this was a caribou who was walking on all four legs, and that the network of bone on his femur was the result of his body healing, providing a new way for his limb to function and to locomote (Fig. 5). The length of time that this had taken to form shows that he was not simply “limping along,” literally and figuratively. He had survived at least one (and possibly several) winters with his injury and was providing himself with the food necessary to grow a nutritionally expensive new network of bone.

Heterotopic ossifications do not occur without irritation (Shehab et al., 2002). The formation of the heterotopic ossification in CNM10759's leg shows us that not only did his body create a new platform on which to walk, but that he was actively trying to walk on his leg soon after his injury, or else the boney network would not have formed. It was his walking on the injured limb that caused the secondary effect of this healing pattern. Had he not been using this limb, the bone would have continued to resorb, and the density of his tibia and femur would have greatly reduced. The new articular platform on his tibia and the bilateral asymmetry of the bones of his injured left leg show more activity patterns than the right, meaning there is no doubt that he was walking and bearing weight on this leg.

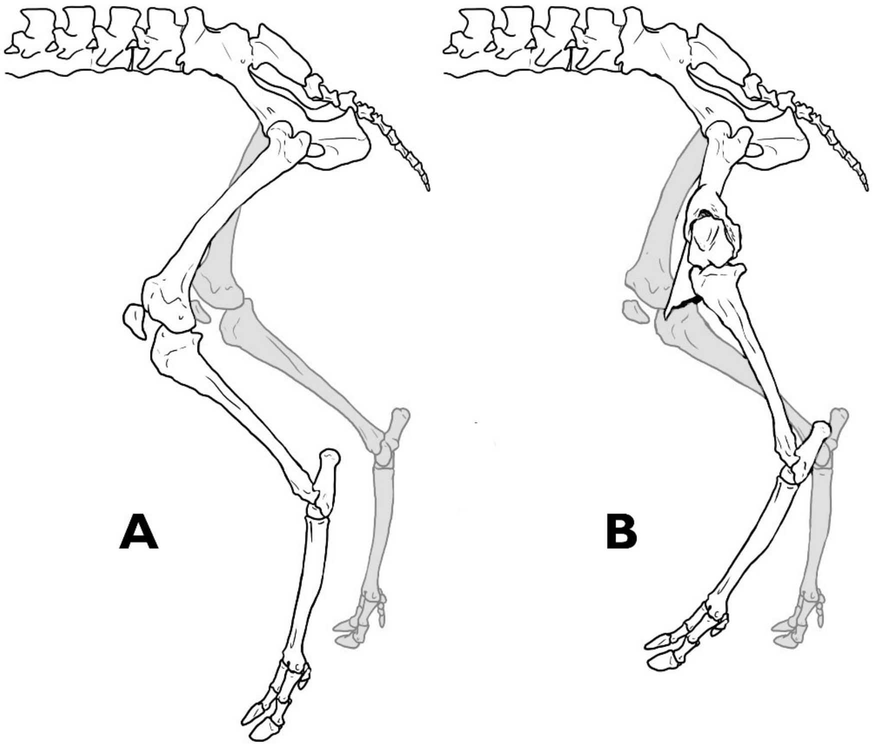

Figure 5. A) Normal articulation of the caribou hindlimb, B) CNM10759's hindlimb. Illustration by author.

While we know that animals experience pain, we cannot know exactly how they process the pain that they feel, which limits what can be said about the suffering he may have endured (Dawkins, 2008). We can be sure that the initial injury caused CNM10759 extreme pain, but it is impossible to know what he felt as he walked on his injured leg. As I continued to study CNM10759's remains and learned about his incredible recovery, he ceased to be a pathological outlier in my studies. He became an individual at whom I could no longer pity. Pity felt condescending towards a nonhuman person who had overcome hurdles I could only imagine.

Section Three: Sympathy and Recognition of Personhood

Life history reconstruction. One of the most important sets of questions about CNM10759 is when during his life he sustained the severe injury and what was his age at death. Further, how did the timing of the injury affect his overall development? Age estimation of caribou is usually done through epiphyseal fusion or tooth wear. Tooth wear can be quite reliable but is contingent on the rate of wear of a known community eating the same foods. As most age estimation models have been established using barrenground or tundra *Rangifer tarandus*, it is important to be conservative and reflexive when using these guides. Barrenground caribou graze more than forest caribou, who will also habitually browse when tender growth on trees and shrubs is available (Pasda, 2009; Drucker et al. 2010). This difference in diet can lead to a difference in the rate of tooth wear. Tooth eruption can be used to age younger individuals, but CNM10759 had all his adult teeth. Based on tooth wear estimations by Pasda (2009), CNM10759 was conservatively 36-84 months old. The examination of the fusion of his epiphysis based on estimations by Hufthammer (1995) of European reindeer likewise suggest an age within this range, based on the full fusion of the epiphyses of all of his long bones, with the proximal ulna (one of the last epiphyses to fuse in *Rangifer tarandus*) showing the last stages of fusion. This suggests that CNM10759 was fully adult but still young, placing his age at death at five-and-a-half to ten years, with his tooth wear suggesting an age of up to seven-and-a-half years.

While age at death can only be established within a broad range, the age at which CNM10759 sustained his injury falls between a baseline of what can be proved, and speculation regarding what is deemed most likely. What is certain is that CNM10759's distal femur was fused when he sustained his injury, as the displaced bone shows complete epiphyseal fusion that could not have occurred once the bone was broken off. This fusion occurs at 36-48 months (Hufthammer, 1995).

The breakage of the femoral head is suggestive. The proximal femoral epiphysis fuses within the same temporal range as the distal epiphysis, but most often completes fusion following the distal end (Hufthammer, 1995). If CNM10759 was one of the individuals whose distal femur fused earlier than his femoral head, this would explain why the head of his femur was so cleanly sheared off. This would place his injury before 48 months of age, the latest age at which this end of the element fuses. An alternate explanation is that his injury led to his femoral head being snapped off at the neck due simply to the torsion of the entire limb. This, however, does not explain why the break did not occur further down the neck of the femur, or along the proximal diaphyseal shaft. The fact that only the head of the femur was broken off suggests that this epiphysis was not fully fused, and that the break occurred along the lines of fusion. This suggests the injury was sustained around three to five years of age, coinciding with him coming into adulthood.

Several factors show that this was an old injury, and that his recovery after the injury was complete. First, the extent and maturity of the heterotopic ossification takes both time and nutrition. The development of a vascular system within the medullary cavity of the femur illustrates both duration and operation. The osteoarthritis on his carpal bones also shows that his healed but misaligned limb was being used for long enough and with enough pressure for the carpals on the left side to develop different wear patterns than the right. Finally, the bone resorbsion from the lateral side and cortical expansion on the medial side of the femur distal to the attachment of the remodeled distal femur shows not only the passage of time. This also indicates mechanical stress moving to the medial side of the femur as the bone itself was rearranged. As auxiliary evidence of his health, his remaining epiphyses on other limb bones continued to fuse, suggesting that his development was not deterred by the injury.

This evidence strongly suggests that CNM10759 was injured around three to five years of age, and that he died at five-and-a-half to ten years of age. It is technically possible that his injury occurred anywhere from one year to seven years prior to death, but I find both extremes unlikely. Because of the stage of maturation of the heterotopic ossification, the development of complex vascular systems in his femur, the activity-related osteoarthritis in his lower limbs, and differences in cortical thickness in his radioulnae, such changes likely did not occur in a single year. Conversely, I believe that with a duration as long as seven years, a thicker pseudo-cortical bone border would have developed around the heterotopic ossification, and that more severe osteoarthritis would be present in his limbs. Regardless of the exact timing, CNM10759 would have had this injury for a significant portion or all of his adult life.

Recovery and quality of life. While many scholars have debated and presented varying philosophies of measuring animal pleasure, happiness, and emotion, I take a rather parsimonious stance (Balcombe, 2006; Bekoff, 2007; Griffin, 2001). CNM10759 and I are divided not only by species and community, but also by time. Caribou culture and behavior may have changed in the intervening 90 years, and, as the human descriptions of his behavior are limited to a few lines written on a single day (see below), explicit explorations of his emotional state are not possible.

McMillan (2008) posits a rubric for nonhuman quality of life based on the following factors: social relationships, mental stimulation, health, "stress," and control. Based on Cowan's accounts of CNM10759's circumstances at death, as discussed in the following section, CNM10759 still had a place within his community and was able to continue social relationships. We cannot directly know what kinds of mental stimulation caribou need or desire, but as CNM10759 was not rendered immobile by his injury, he was able to experience changes in landscape, eat a variety of food, and interact with other individuals. As discussed above, CNM10759's injury did not greatly affect his overall health, and while a misaligned femur is a serious limitation, it was not affecting his growth, nutrition, and was not the cause of secondary infection or illness. "Stress" is another factor that is impossible to gauge in this situation. Although CNM10759 may have been subject to greater stress than his peers, the complexities of "stress" as described by McMillan cannot be speculated upon in this instance. Control, the last factor in determining quality of life, refers to the real or perceived control an individual has over their situation or themselves. We cannot know what or how CNM10759 thought about his situation, but his continued participation in the herd would imply that he had as much individual agency as other wild caribou. According to this rubric, CNM10759 was a nonhuman person experiencing quality of life at the time of his death.

As I came to this conclusion, my initial response of pity gave way to feelings of injustice. While the collection of animals has a long history throughout the world, it seemed increasingly unfair and tragic that this magnificent being had overcome such a horrible injury only to be killed and taken as a curiosity. Understanding that this was the custom of the time, and not blaming the collectors for their participation in this system, I still felt that CNM10759 had died before his time.

Section Four: Admiration

The written record. On the day CNM10759 died, Cowan wrote in his journal:

> "July 4, 1930. In morning went up Maccarib Creek to Pass. Tracks of coyote, fox, marten, bear, wolverine, porcupine, caribou, goat and deer. Saw signs of Richardson's vole and *Synaptomys.* Saw male caribou with broken left hind leg. Mr. Curran and I went out after crippled caribou. Jumped 5-4 fine bulls and a cow and another 5, 2 young bulls and a cow. After stalk shot cripple which was with a cow. Cows much lighter in color. Skinned it out and arrived camp 6 o'clock. Went out again and brought in hide and head and some meat (Cowan, 1930)."

In the case of most wild animals, we not only lack documentation of their deaths, but also accounts of their specific behavior, appearance, or socialization. For CNM10759, we have the short journal entry of his collector, which gives us a rare but brief glimpse into his last day alive, which provides some clues to his life history and wellness.

We can see from the account that CNM10759 was mobile, although his gait designates him as a "cripple" to Cowan. He was spotted and then moved rapidly enough that a stalk was required to kill him. The animals who were jumped during the stalk constitute what likely were part of a mixed sex community, which is typical for woodland caribou in the spring and summer (Ferguson & Elkie, 2004; Hirotani, 1990; Wittmer, 2005). The fact that he was shot while in the company of a cow further solidifies that he was still a part of his community, and not, as the traditional narrative of animal injury tells us, shunned because of his injury. Lastly, the fact that meat was taken from CNM10759 after death tells us that he was not holistically unhealthy. Meat would not be taken from an individual with infection or obvious ill health.

While the consideration of CNM10759's role within his society or his own agency and right to life were seemingly not topics common among collectors in 1930, the notes on his killing reveal an individual who was viable and thriving. We can see from CNM10759's brief life history that traumatic injury does not immediately signify death or expulsion from an animal community, and that long-term healing and quality of life can be achieved without human intervention. As we study nonhuman persons and societies, it would be advantageous to consider overall health as well as adaptability and resiliency when determining the fitness of members of a group. In terms of overall fitness, there is no way to conclusively determine whether CNM10759 was reproductively viable. His antler pedicles are robust in size, and, while his antlers were removed and are no longer part of the collection, there was no mention of them being malformed or unusual. In cervids, damage to testes changes hormone levels, which in turn dramatically change antler development. Naturally occurring cryptorchidism in cervids also results in similar patterns of unusual antler growth. A collector with an interest in the unusual would have most likely commented on such antler growth, had it existed. CNM10759's femoral fracture was mid-diaphyseal, and therefore not close to his genitalia. Even if his reproductive organs were still functioning, this does not mean that he would have been able to participate in dominance battles with other males or had the ability to mount a cow. His ability to reproduce is an unknown. This said, reproductive fitness is not the only way to measure the viability of an individual in a community. Male animals are not simply sperm banks who exist only to perpetuate their own genetic lineages. As a member of his community, CNM10759 may have held other important roles, including that of a behavioral model and protector to younger community members and a companion to other individuals in his herd. During the winter months, when sexes separate and same-sex groups are the norm, males often feed together and live in docile cohabitation (Wittmer, 2005; Brown, 1986). During the spring and summer, when mixed-sex groups travel together, large males such as CNM10759 provide additional buffers between predators and vulnerable members of the community. CNM10759's role in his community was not contingent solely on his procreative status.

Animal societies and multispecies studies. Throughout this study, CNM10759 moved through many spaces in my mind. He was first an object, the remains of an animal who had been born nearly a century ago. This object inspired curiosity and pity, and I exclaimed "Oh, poor thing!" out loud when I unboxed his remains. As I studied him, he became an individual who had once lived, breathed, suffered, and survived. I began to see him as a person, and my emotional journey became one of interest and adoration. He became all that I wanted to talk about, and I felt a kind of emotional ownership over him. He was my "special case," and although I could see him as a person, I still did not fully acknowledge his agency. It was only with some glimpses of his function in his society, his agency, and his autonomy that I truly began to appreciate him as the unique individual that he was. He was a member of a community, the survivor of a bizarre and extreme injury, and an adult nonhuman person. CNM10759's case exposes that the condescension or infantilization that animals, especially those that are injured, often provoke is a speciesist reaction to individuals with complex and complete lives.

Conclusions

This study leads me to two conclusions. First, injured animals have individual and cultural importance that may be over-looked by zooarchaeologists because of our assumptions of animal fitness, pain, and healing. CNM10759 was not killed because he was weak, but because he was unique; this may also be the case in archaeological assemblages, where recovered animals have the potential to be seen as symbols of strength rather than easy targets. CNM10759 was also still an active member of his community who had the potential to be reproductively viable, challenging our ideas of what constitutes potential breeding partner. Reproductive fitness aside, he still may have had cultural knowledge and value to his community by both protecting and teaching younger members of his community. We may be missing the importance of disabled animals to both human and animal communities due to our assumptions of injured animal viability. Our narratives about the challenges faced by and quality of life of these animals may need to be rewritten, and we must not assume that past human cultures viewed injured animals with the same biases that we do today.

Second, this study leads to a reflection on the relationship that develops between researcher and subject, even when the subject is both nonhuman and long dead. From a reflexive, agency-based perspective of human-animal relationships, it is important to discuss the emotional and theoretical impact that such studies have on the researcher. Intense study may lead to us developing unexpected relationships with our subjects, relationships not limited by species, time, space, or death. The process of working through the understanding of an animal’s life often changes our own perceptions of animals as individuals, as persons, and as members of a social group. This change in our own understanding can lead to a more nuanced interpretation of animal lives in both a social and archaeological context.

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Conclusion

Research Summary

My research was entirely focused on *Rangifer tarandus*, and although each project looked at a different aspect of reindeer and caribou, all projects used physical remains to examine, explore, or reconstruct animal lives and life histories. All of the projects were developed with the hope of being useful to future zooarchaeological studies but were constructed using the bodies of modern animals from Fennoscandia and Canada. The majority of these studies focused specifically on the two ecotypes of reindeer in Fennoscandia: domestic *Rangifer tarandus tarandus*, and wild *Rangifer tarandus fennicus*. Through an investigation of their bodies, I aimed to find clues as to ecological, behavioral, and cultural differences between the two, particularly those that might have led *Rangifer tarandus tarandus* to become domesticated and *Rangifer tarandus fennicus* to remain wild. My projects ranged from quantitative to theoretical, but all involved the body as a means by which to study animal life.

In the first two projects, I focused on expanding anatomical knowledge of *Rangifer tarandus* by examining the intricacies of the bones of the hoof, the soft tissues of the hoof, and the differences in structure between the fore- and hindlimb. These studies were foundational to further studies. They also examined aspects of animal anatomy that are fundamentally important to the health and wellness of modern animals, and the minute examination of these small bones in zooarchaeology. These studies found that the anatomy of *Rangifer tarandus* is unique and that a specific species-level knowledge is necessary for further analysis. In other words, species such as cattle or horses do not have the same structural anatomy as *R. tarandus* and therefore are misleading proxies for them. Additionally, the first study showed that metric analysis could consistently differentiate the bones of the fore- from hindlimb, allowing for more precise examinations of zooarchaeological remains.

My third project was built off of findings from the first two. Specifically, the knowledge acquired from these foundational studies made possible the study of the differences in entheseal changes (ECs) in the hooves between *R.t. tarandus* and *R.t. fennicus*. This study looked at how entheseal variation in the hoof might signal different behaviors between the two ecotypes, especially in terms of mobility and foraging. The results of this project showed significant differences in ECs between the two ecotypes.

My fourth project expanded upon the idea of differences between Fennoscandian ecotypes. Instead of examining the microtraumas of one area of the body, I concentrated on the pathologies throughout the post-cranial skeleton. This project examined the pathologies, both traumatic and age/activity-based, between ecotypes and also between male and female *R.t. fennicus*. This exploration between ecotypes was supplemented with a small subsample of wild Canadian caribou from the barrenground and arctic ecotypes to compare wild and domestic traumatic injuries. This study found both no substantial differences in age/activity-based traumas such as osteoarthritis, but clear difference between ecotypes in traumatic injury. *R.t. fennicus,* who showed substantially more traumatic injuries, also exhibited significant differences in the location of injury between males and females. The differences in male and female pathological certainly deserve additional study, with appropriate sex-separated samples of other subspecies present. From the injury patterns, it appears that there is reproductive trauma in the ribs of female animals that may be affected by the size and sexual dimorphism of each ecotype.

My fifth project was a combination osteobiography and theoretical examination of anthropocentrism in the study of animal remains. In this project, I chronicled the evolution of my assumptions as I examined the body of a male Canadian caribou with a long-term traumatic injury. By examining the longevity of his injury, my assumptions about the survival and viability of injured wild animals were contested. This challenged a very fundamental human narrative: the idea that non-human persons are made vulnerable or unviable by injury and that only humans have the ability, through cooperation and modern medicine, to survive and thrive through traumatic injuries. This narrative is one that informs our current views on wildlife culling and euthanasia but leaves out the agency and ability of non-human persons to heal and maintain overall health and well-being regardless of physical constraint or disability.

Limitations

My research projects were subject to many limitations but can be summarised as those restraints due to sample size, constraints due to collection information, restrictions of my own geographical mobility, and limitations due to language and interspecies communication. My sample size was restricted by the nature of the collections I was able to access. My main collection sites were the University of Oulu Biodiversity Unit and the Zoological Collections of the Canadian Museum of Nature. In both these collections, I was able to access complete or nearly complete skeletons with age and location documented. Unfortunately, in many cases, especially with ecotypes that show less sexual dimorphism, sex was not recorded. Additionally, in the Canadian samples, the rarer arctic and barrenground ecotypes were well represented, but, ironically, the more common Canadian *Rangifer tarandus caribou* was less well represented. This pattern holds true throughout many of the collections in North America in Europe, limiting the cross-continental ecotype comparisons that could be made.

Although both of my primary collection sites contained many specimens, many consisted only of long bones, and the bones of the toes and the axial skeleton were incomplete or non-existent. This limited the sample sizes that I was able to examine. Many specimens had incomplete sex information that made pooling by sex necessary, and may have led to nuances between the sexes being overlooked. Simply put, large and comprehensive skeletal collections of reindeer really do not exist, but they are clearly needed for many future studies of these animals in zooarchaeology and related disciplines.

Because the projects required the largest samples I could find from the smallest areas (so as to represent a single subspecies or group), this further limited my work to the two collections. There are, however, far more ecotypes and subspecies than are represented in my work. Even within my research I came to believe that the universality of the three commonly recognised ecotypes is suspect, especially in regards to animal cultures. The only European samples with which I worked came from Finland, and, while these may be representative of the reindeer of Fennoscandia, they cannot be representative of all Eurasian reindeer. The domestication paradigms within which I compared wild and domestic animals are different from the reindeer cultures in other parts of Europe and Asia. In fact, the dichotomy between the domestic barrenground reindeer and the wild boreal reindeer may not hold true in other cultures, where boreal or mixed communities of reindeer may have been domesticated. Because of this, my research is of most use in Fennoscandia, and its application to other regions will require care.

Limitations in communication created issues in two directions. First, a lack of Finnish language skills inhibited my ability to access all of the data for the Finnish specimens. This was largely resolved, however, due to my Finnish friends and colleagues who kindly helped with translations. Second, I also had no way to communicate with reindeer themselves and had an extremely limited time in which to observe live animals. This disconnect with live animals may lead to misinterpretations, as much of what I learned about this animals was through their skeletal remains and the literature. Although reindeer and I can never speak a common language, the opportunity to observe their natural behaviors and modes of communication with one another clearly would have led to a deeper understanding of their lives.

Future Directions

As often happens, working with reindeer and caribou, especially with CNM 10759, has left me with far more questions than answers. There remains a desire to delve into more wild animal osteobiographies, as I find their lives so poorly unchronicled. In this vein, I am also interested in the lives and life histories of non-reproductive group members as well as their importance in animal communities. I believe that viewing herds as distinct cultural groups within a species or subspecies might shed light on animal cultural transmission and unique behaviors between herds of animals. For example, I intend to study sexual dynamics and trauma caused by reproductive and gestational activities of wild and domestic reindeer, especially in light of interesting rib fracture patterns found in females. Regarding human-animal relationships, I am interested in pursuing studies and theoretical models of how animal and human cultures create an environment where human and animal relationships can flourish and where mutualism and domestication is more likely to occur. Lastly, I am interested in studying natural versus human-created pathologies and injury patterns in animals over time. The unfortunate truth is that many working animals, both historic and modern, have brutal, punishing lives that leave painful signs on their bodies as they are worked, sometimes literally, to the bone. Trauma and lesions from the human punishment of working animals can lead to additional clues about an animal's occupation and the conditions of its life. The physical abuse of animals by humans is an emotionally difficult but culturally valuable subject to explore. The extent and types of physical abuse within a culture can help us determine the social role of that animal within the human culture, and lead to the better understanding of animal lives through time. As well as pathologies caused by humans, I am interested in pathologies in humans caused by living and working with animals, and I am curious to explore these pathologies as a form of mutual harm. I intend to continue studying cervids and other ungulates and their relationships with humans, which seem both more distant and more complex than those of purely "companion animals." While studies of reindeer have advanced in dashes and bounds in the last few years, there is still much work to be done to understand the lives and histories of these symbols of the North, who have left their hoofprints and shed antlers littered inexorably across the snows of history.

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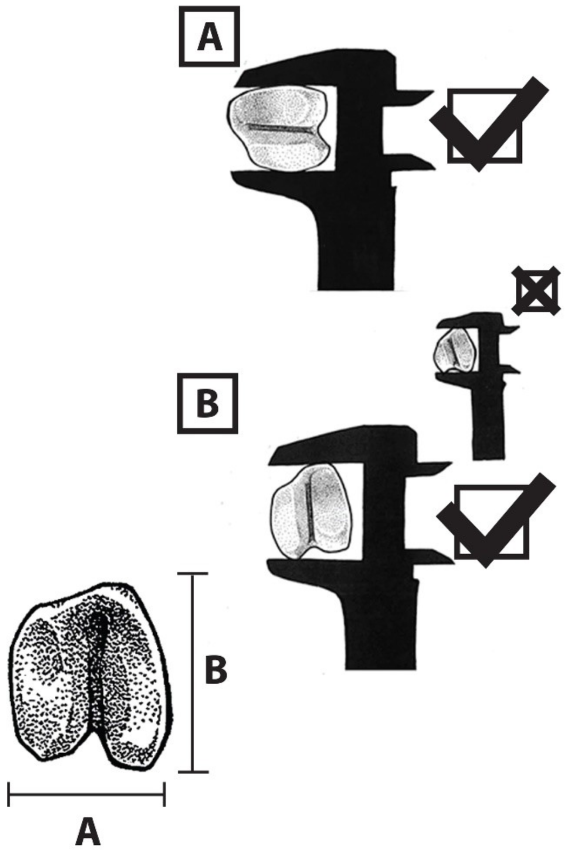
Appendices

Appendix 1: Guidelines for Differentiation between Fore and Hindlimb PI and PII for Chapter 1

For consistency and expedience, forelimbs were marked as “thoracic” limbs (TPI and TPII), and hindlimbs were marked as “pelvic” limbs (PPI and PPII).

PI: Metric analysis.



[Figure I: Measuring guidelines for PI]

Measuring Instructions.

A: Measure the widest breadth of the phalanx.

B: Measure the longest length of the base of the phalanx, making sure that the central groove is parallel to the calipers. Do not lean the bone so that both dorsal protuberances rest against the calipers.

Note: Be sure that the measurement is taken from the edge of the articular surface not from the rugged area distal to it.

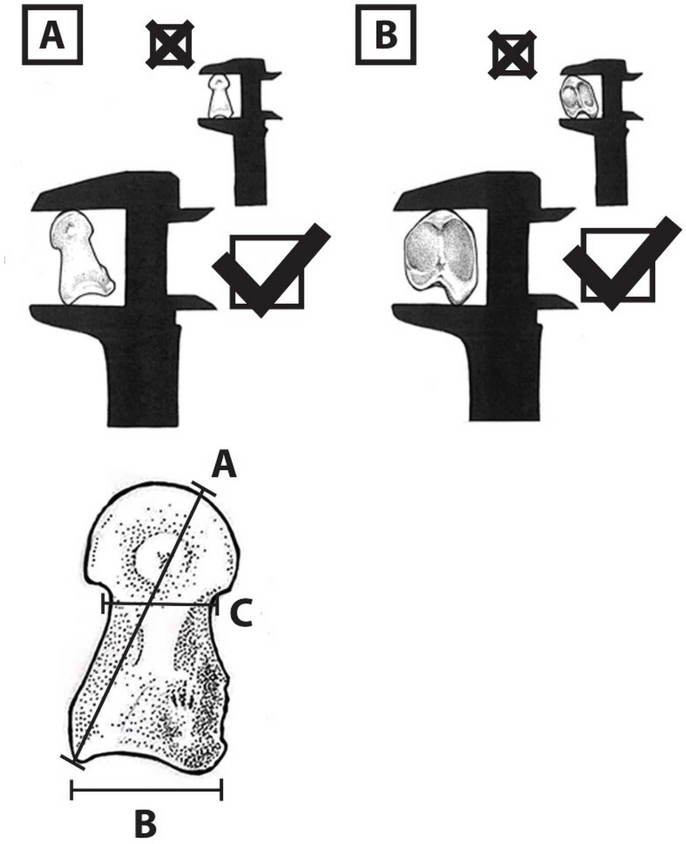
EQUATION: A/B = X.

$X \geq 1$= Thoracic (Fore)

$X < 1$= Pelvic (Hind)

PII: Metric analysis

[Figure II: Measuring guidelines for PII]



Measuring Instructions.

A: Measure the longest length from the head of the phalanx on the lateral side to the apex of the proximal ventral protuberance. Measure from the highest point on the head. Once correctly positioned, the phalanx may rotate freely between measurement points in the calipers. This is a sign that the phalanx is in the correct measurement position.

B: Measure the longest length of the base of the phalanx, making sure that the central ridge is parallel to the calipers. <u>Do not lean the bone so that both dorsal protuberances rest against the calipers.</u> To ensure this, identify the small, flat ovoid surface on the proximal dorsal aspect of the phalanx and rest this flat area flush against the calipers during measurement.

C: Measure the narrowest area of constriction on the neck of the phalanx, from the side of the phalanx, measuring from the dorsal to ventral surfaces, not side to side.

EQUATION: $(A+B)/C = X$

Round your results to the nearest hundredth, e.g. 4.01.

If $X < 4.50$: Thoracic (Fore)

If $X > 4.50$: Pelvic (Hind)

If $X = 4.50$: Please re-check your measurements. If you still get 4.50, this bone must be marked as “undetermined”

Appendix 2: EC Scoring Criteria for Chapter 3

*Criteria for all sites investigated are listed, illustrations are provided for significant sites. All illustrations by E. Hull

<u>PI</u>

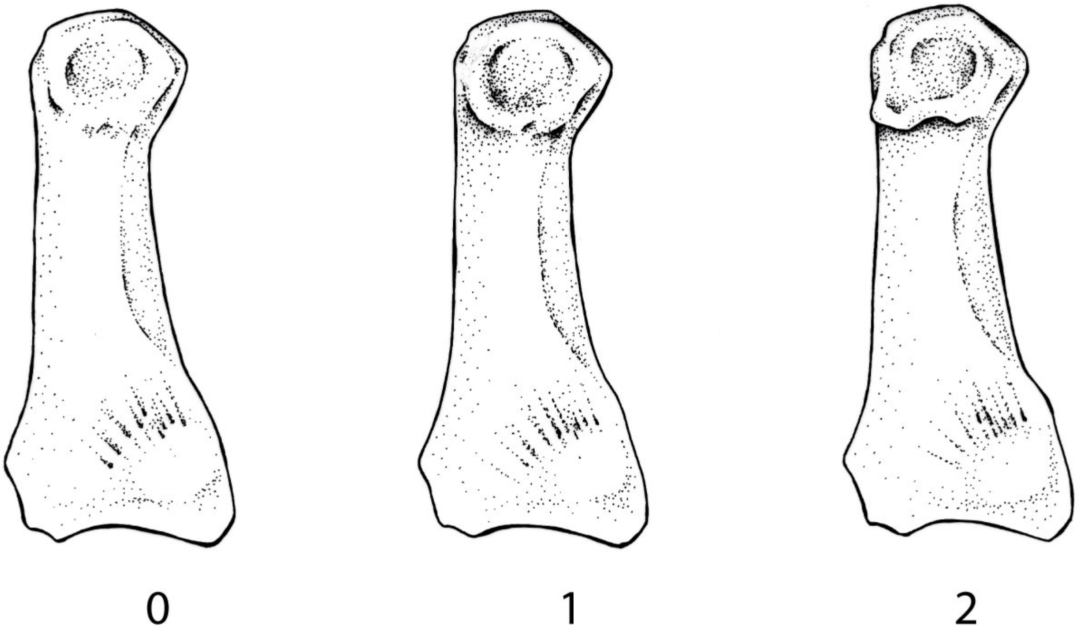
PI: Site A:

Site: The side of the distal surface adjacent to the articulation with PII. Site A is located on the side of the bone with the lower (less elevated) articular condyle (the lateral side). The site is circular, and the areas of EC are the rim of the circular attachment site, specifically the proximal and dorsal edges, with the proximal edges showing the most development.

Scoring Criteria:

0- Minimal to no elevation of either border area
1- Elevation of one or both borders, but with diffuse, not discrete edges
2- Discrete edges at both borders, with sharp elevation sometimes leading to lipping, especially at the proximal border.

Figure S1. Site PI:A



PI: Site B

Site: The side of the distal surface adjacent to the articulation with PII. Site B is located on the side of the bone with the higher (more elevated) articular condyle (the medial side). The site is circular, and the areas of EC are the rim of the circular attachment site, specifically the proximal and dorsal edges, with the proximal edges showing the most development. While this site is analogous to Site A, Site B is more developed, so be sure not to confuse the sites.

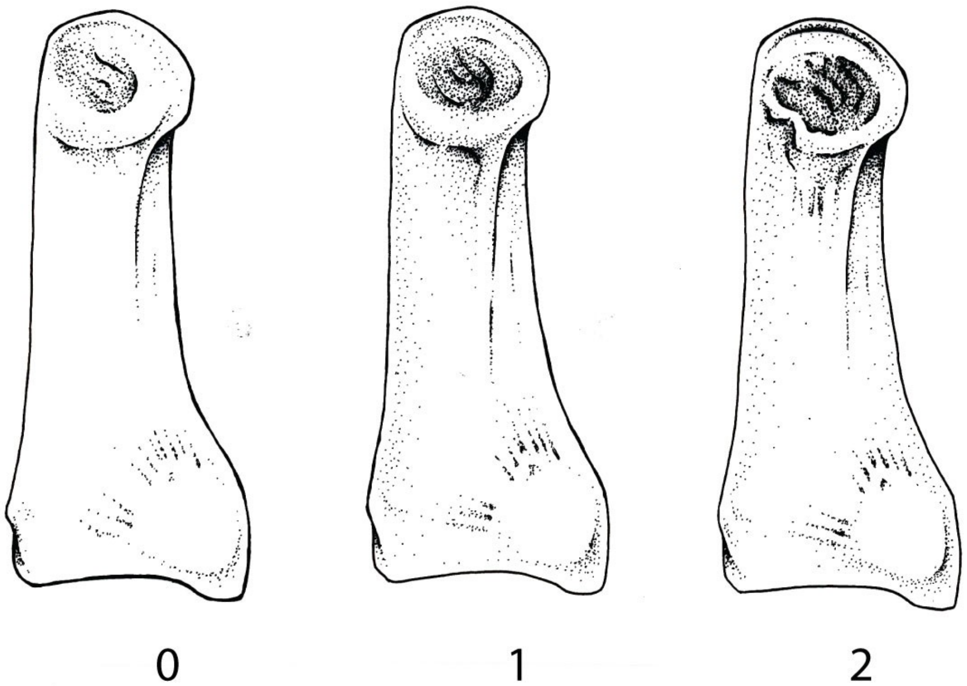
Scoring Criteria:

0- Edges are present with minimal to moderate elevation
1- Moderate elevation with discrete edges, especially on the proximal border
2- Distinct discrete elevation of both borders, high development of proximal border with edges elevated up to lipping.

NOTES:

Porosity present in some cases around the area between the attachment site and the adjacent articular surface.

Figure S2. Site PI:B



PI Site C:

Site: Proximal to sites E and A, on the side of the phalanx, extending to dorsal and ventral sides. This site is a combination of two attachment sites, but as the fibers of the tendons combine and are subject to the same tensions, they are scored together, as differentiation of the sites is difficult or impossible.

Traits: Angle of elevation, ruggedness

Scoring Criteria:

0- 0°-30° between diaphysis and attachment site, minimal to no elevation
1- 30°-60° between diaphysis and attachment site, discernable elevation
2- 60°-90° marked ruggedness on Thoracic; marked, discrete elevation in Pelvic

NOTE: Observe from ventral aspect.

Notes: Site attachment follows morphological platform, scoring may be assessed by the angle between the diaphysis of the phalanx to the distal edge of attachment site, as EC to this area will create bone disposition angle between the two.

NOTE: Porosity observed, but not scored, as it was most like caused by uneven bone formation, not bone erosion, and thus is not scorable.

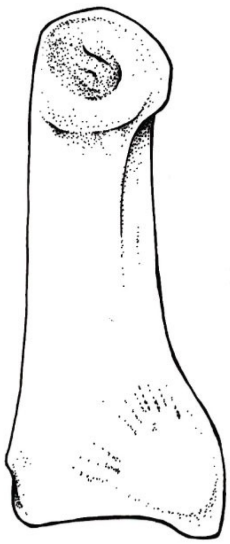
PI: Site D

Site: Proximal to B and F. The directionality of bone formation at attachment site is parallel with diaphysis.

Scoring Criteria

0- Area of projection with no or minimal border
1- Area of projection with elevation and diffuse border
2- Area of projection with high elevation with a distinct and discrete edge or border.

Figure S3. Site PI:D



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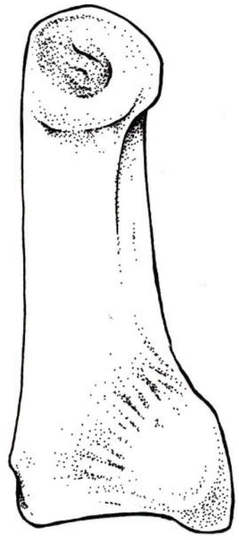
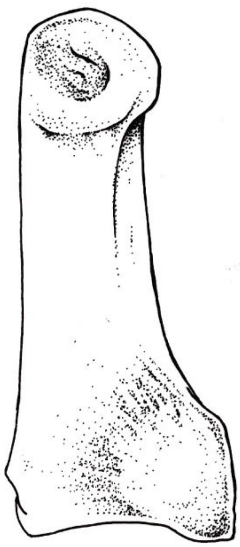


1



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PI: Site E:

Site: Ovular or two-pronged site on side or ventral surface of PI, proximal to lower articular condyle (same side as site A); do not confuse with site C.

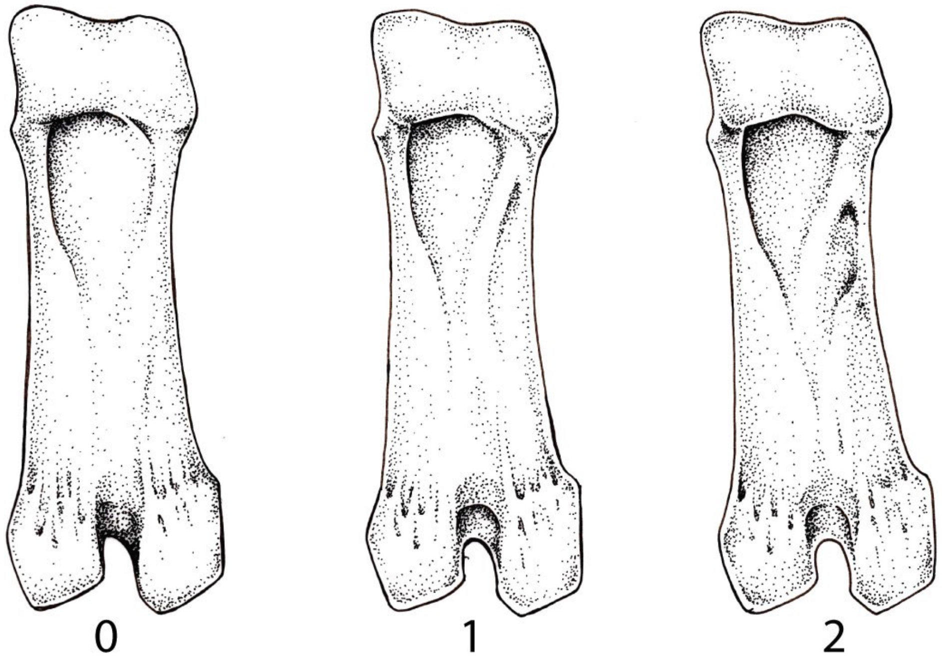
Formation:

- 0- Minimal to no elevation, minimal ruggedness
- 1- Moderate elevation, moderate ruggedness
- 2- Distinct elevation, distinct ruggedness

Note:

Do not confuse the morphological crest with bone deposition, although EC develops along morphological ridge.

Figure S4. Site PI:E



PI Site F:

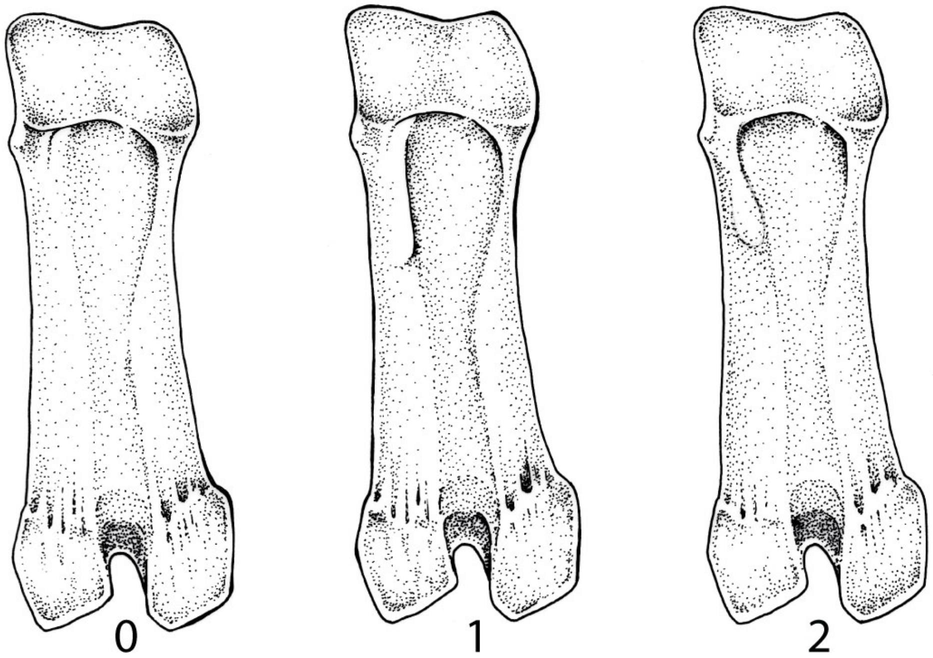
Site: Site F is on the medial dorsal side of PI, between Site B and Site G. Site F is opposite and analogous to Site E, although the presence of erosion, and the two-pronged shape of the attachment site are not present.

Traits: Ruggedness and elevation

Scoring Criteria:

0- Minimal to no elevation; minimal to no ruggedness
1- Slight elevation, slight to moderate ruggedness
2- Moderate elevation, moderate ruggedness up to the development of a distinct (often) ovular protuberance, which is surrounded by additional ruggedness.

Figure S5. Site PI:F



PI: Site G:

Site: Proximal to site D, with deposition and development oriented perpendicular or at an obtuse angle to length of phalangeal diaphysis.

Criteria:

0- Presence of site visible with minimal to moderate elevation. Attachment edges are diffuse.
1- Moderate elevation with banding following the morphological edge of the bone perpendicular to diaphysis. Diffuse terminus of site. Striations may be present.
2- Distinct elevation, distinct banding, distinct and elevated terminal border of site on or near dorsal aspect of bone.

PII

PII Attachment Site A:

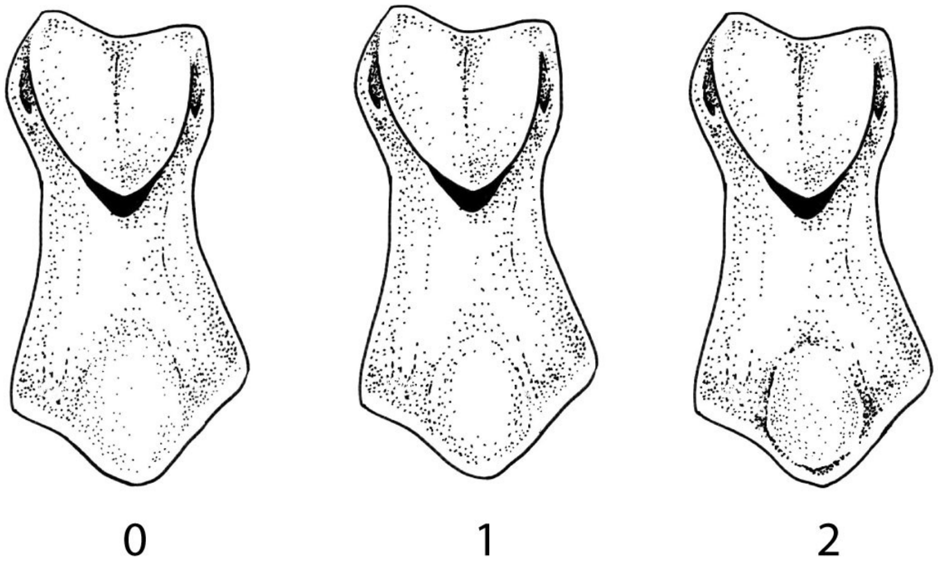
Site A:

Circular or ovular attachment site on the central proximal dorsal surface of PII just distal to articular surface with PI

Scoring Criteria:

0. No raised element, no raised border (may be slight ruggedness of surface).
1. Development of raised circular platform, no perpendicular linear border, increased ruggedness.
2. Clearly defined raised circular platform, clearly defined linear borders, well defined parallel edge and bone build-up following the morphology of the bones, clear border at distal edge of attachment site at perpendicular border.

Figure S6. Site PII:A



PII Site B

Site: Site on the medial proximal end of the done on the ventral side. This end of the bone is divided into protuberances with site C in the middle. Site B is located on the medial protuberance beginning on the ventral aspect and extending to the medial side. Care must be taken to separate this site from Site C.

Scoring Criteria:

- 0- Site present, with no elevation that is not morphological.
- 1- Raised area or part of area with a discernable edge. Entire area not elevated.
- 2- Distinct elevation of attachment area with clear edge of attachment site with a wider than 1mm raised band.

NOTES:

1. Striations may be present, but should not be used as criteria for scoring
2. Attachment should be assessed first from superior view and then from a profile view from the dorsal side to avoid unconscious influence from other sites.

PII – Attachment Site C

Site C:

Attachment site on the proximal ventral surface of PII occurring between sites B and D, occurring at the proximal 1/3 of the center of PII just distal to the articulation with PI.

Scoring Criteria:

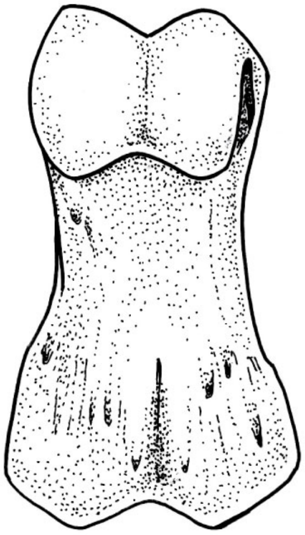
0. No elevation, minimal or no delineation.

1. Clear delineation of attachment site, minimal to no elevation.

2. Clear, discrete delineation and elevation of site with clearly and sharply defined U-shaped border.

NOTES: Sharp edge running parallel with bone along same side as site D is morphological and not indicative of development of the site.

Figure S7. Site PII:C



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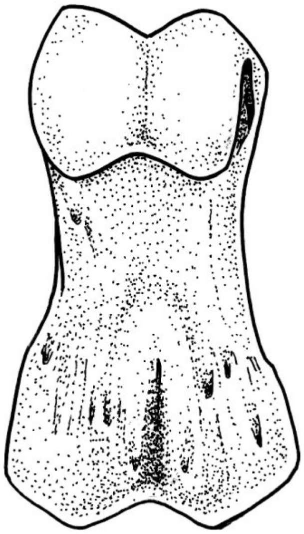

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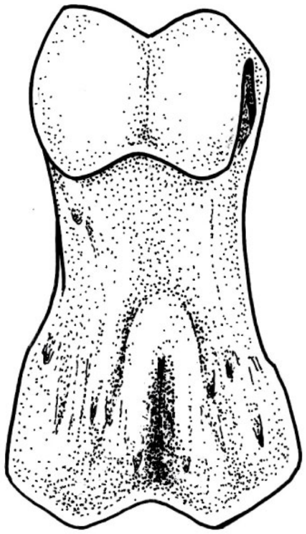

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PII Site D:

Site:

Edge of the attachment site at proximal ventral aspect of PII, on and around the lateral morphological protuberance. The attachment site abuts the protuberance, and the sharp development of the edge closest to site C is an area of bone development and stress.

Scoring Criteria:

0- Attachment site present with no or minimal elevation, minimal developed distal edge although it be present.
1- Small, elevated, often ovular process present, but does not extend throughout the entirety of the attachment site. The development of the distal edge is present, but minimal to moderate.
2- Whole attachment site developed and elevated. The development of the edge of the distal area of the site is moderate to sharply defined.

NOTES:

Flaring at the proximal end of bone is morphological, not developmental.

PII Site F:

Site: Circular, concave attachment site on the medial, distal aspect of bone, on the side of the bone just proximal to the articular surface with PIII.

Scoring Criteria:

0- No or minimal edge of attachment site, no elevation.
1- Distinct and lightly elevated edge of attachment site, which may be continuous with the rest of the articular surface.
2- Distinct, discrete and elevated proximal edge of attachment site.

Note:

Porosity observed distal to surrounding entheseal site in some specimens but not scored.

PII Site E

Site: Circular attachment site on the lateral side of the distal aspect of PII, just proximal to the articular surface with PIII. Often quite smooth.

Trait: Presence/Absence of ruggedness at proximal edge of circular attachment site

0- Presence
1- Absence

<u>PIII</u>

PIII: Site A:

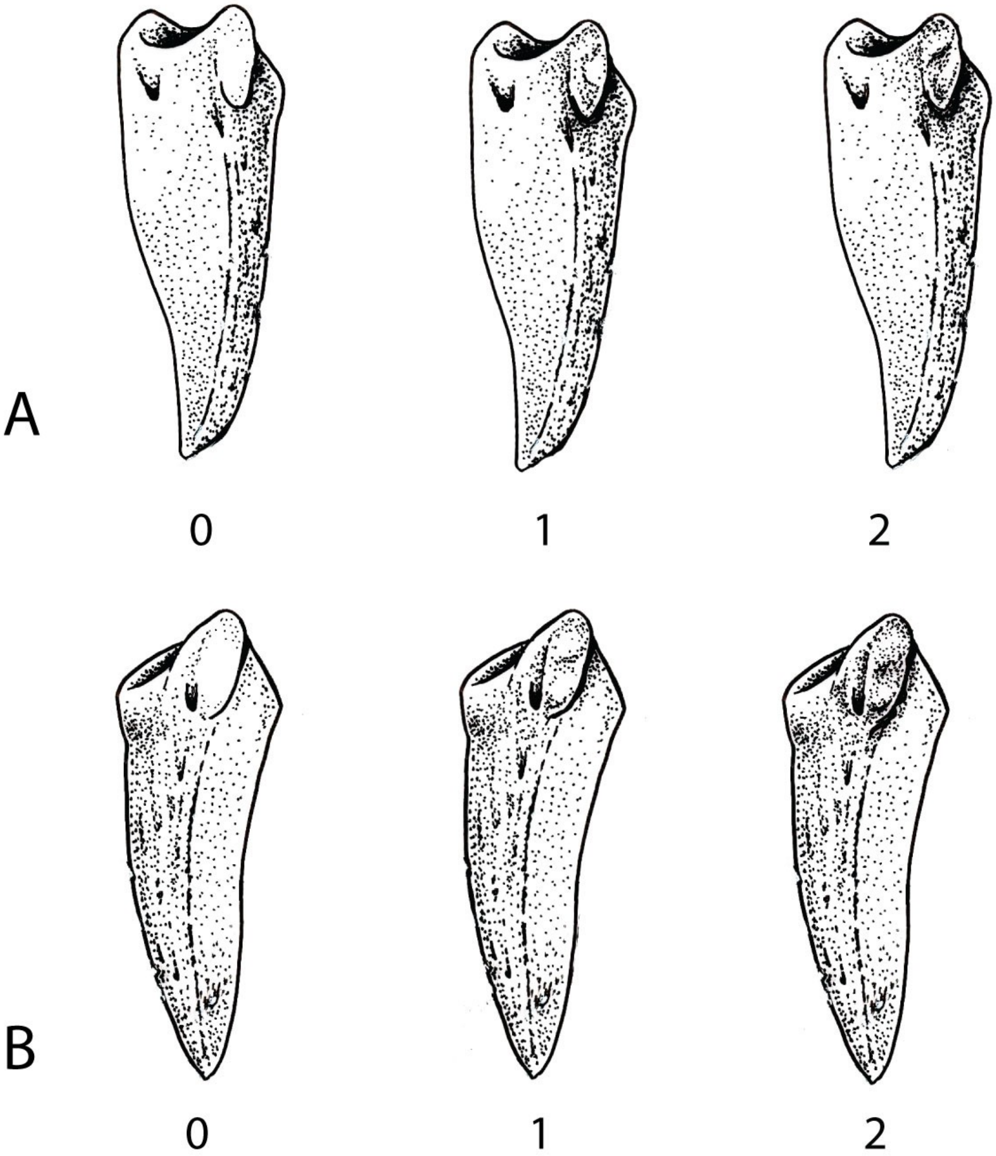
Site: An elevated, ovular process on the proximal ventral apex of the bone, just distal to the articulation with PII.

Scoring Criteria:

0- Site elevated but smooth, free from ruggedness, ridges or depressions. An ovoid, elevated process may be present, but will be smooth and follow the morphology of the site.
1- Mild ruggedness with no more than two small grooves, ridges and/or bumps present. Porosity may be present but is due to bone deposition rather than absorbsion.

2- Rugged, distinctly elevated attachment area with a rough, wrinkled appearance caused by a complex of multiple groves, bumps and ridges. Porosity may be present but is due to bone deposition rather than absorbsion.

Figure S8. Site PIII: A&B



PIII: Site B

Site: The triangular process at the proximal end of the soleal border just distal to the lateral articular process on the outside edge of the bone. The soleal border just distal to this site may appear slightly concave, but should not be considered when assessing this site

Scoring Criteria:

0- Site is smooth and free from irregularity of the border of the site. The site may be slightly elevated but will be free from any ruggedness.
1- Site is elevated, with mild to moderate ruggedness, including the development of bumps and grooves. The site border will remain free from irregularity.
2- Moderate to extreme ruggedness of the site with uneven borders of the site, which may make the triangular border of the site irregular and rugged.

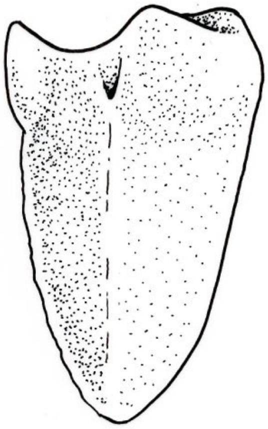
PIII: Site C:

Site: The attachment site extends across the breadth of the proximal palmar surface of PIII, a few millimeters below the groove which separates the articulation site of the distal sesamoid bone with the plane of the palmar surface of the bone. The attachment site is on the plane of the palmar surface, not on the groove above it, running perpendicular to the length of the bone. A color difference may be visible but should not be used for scoring assessment.

Scoring Criteria:

0- Site may be visible, with no to minor striations present which run parallel with the length of the bone. The site is smooth and barely or not distinguishable from the rest of the palmar surface.
1- Site is distinctly visible and mildly to moderately elevated, with notable parallel striations. Site edges are diffuse, with no distinct edge or elevation at the proximal border of the site.
2- The site is distinctly visible and elevated with a distinct and discrete elevation of the proximal border of the attachment site creating an elevated band running perpendicular to the length of the bone. Parallel striations are highly visible, and the distal border remains diffuse.

Fig S9. Site PIII:C



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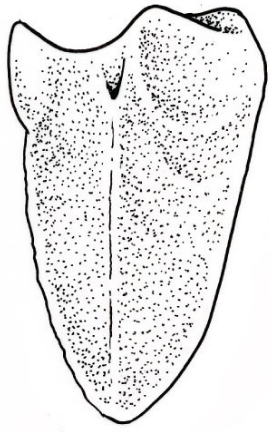

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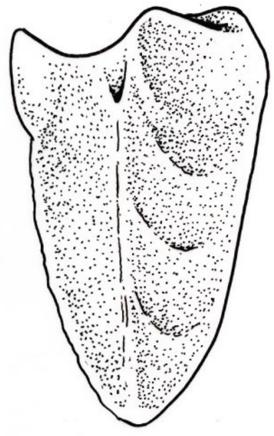

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