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Archives of human-dog relationships: Genetic and stable isotope analysis of Arctic fur clothing

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ABSTRACT

Among Indigenous populations of the Arctic, domestic dogs (*Canis lupus familiaris*) were social actors aiding in traction and subsistence activities. Less commonly, dogs fulfilled a fur-bearing role in both the North American and Siberian Arctic. Examples of garments featuring dog skins were collected during the 19th-20th centuries and are now curated by the National Museum of Denmark. We sequenced the mitochondrial genomes of macroscopically identified dog skin garments. We conducted stable carbon and nitrogen isotope ratio analysis of the dog furs and of fur samples from contemporaneous pelts of Arctic (*C. lupus arctos*) and grey (*C. lupus*) wolves. Despite the presence of biocides used to protect the fur clothing during storage, we extracted well-preserved DNA using a minimally-invasive sampling protocol. Unexpectedly, the mtDNA genomes of one-third of the samples were consistent with wild taxa, rather than domestic dogs. The strong marine component in the diets of North American dogs distinguished them from Greenland and Canadian wolves, but Siberian dogs consumed diets that were isotopically similar to wild species. We found that dog provisioning practices were variable across the Siberian and North American Arctic, but in all cases, involved considerable human labor.

1. Introduction

Bioarchaeological approaches to the human–dog relationship are becoming increasingly commonplace. Previous studies have employed stable isotope analysis (carbon, nitrogen, sulfur) of dog bone collagen to investigate dietary relationships (Burleigh and Brothwell, 1978; Cannon et al., 1999; Guiry and Grimes, 2013; McManus-Fry et al., 2018; Monagle et al., 2018; Rick et al., 2011; Rogers et al., 2019; Tankersley and Koster, 2009), and genetic and radiogenic isotope analysis of preserved hard and soft tissues to track population movements (Ameen et al., 2019; Brown et al., 2013; Fillios and Taçon, 2016; Laffoon et al., 2015; Ní Leathlobhair et al., 2018; Ollivier et al., 2018). Dogs are frequently used as a proxy for human diet (Guiry, 2012) under the assumption that dogs could access similar foods as those consumed by humans either directly through provisioning, or indirectly through scavenging. Furthermore, by assuming that dogs travel in the company

of their owners, human migrations and/or cross-cultural interactions are revealed by tracking shifts in haplotypes or allele frequencies of dogs over geographic space (Ameen et al., 2019; Ollivier et al., 2018). While these approaches have received critique for oversimplifying human–dog dietary relationships (Eriksson and Zagorska, 2002; Perri et al., 2019a, 2019b), when biomolecular methods are combined with recent developments in social zooarchaeology, there is considerable potential to yield new insights into human–environment interactions (McGrath et al., 2019).

Applications of the Canine Surrogacy Approach (Cannon et al., 1999; Edwards et al., 2017; Guiry, 2012) to dog diets and later modifications that may characterize population genetic studies, need to be mindful of the often-fraught history of dogs in colonial North America and Siberia. During European exploration and settlement of these regions, the colonial agendas of Western geopolitical powers were furthered through the use of racially-charged language that positioned

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indigenous Arctic dog breeds as a metaphor for human Indigenous populations (Riche, 2015); control of domestic dog populations and forced resettlement policies further undermined traditional Indigenous lifeways (Laugrand and Oosten, 2002; Lévesque, 2010; Tester, 2010). Recent calls in anthropology and archaeology to reject anthropocentrism are creating more nuanced understandings of humans and their relationship to domestic dogs, wild canids, and at a broader scale, historical and modern landscapes and ecological webs (Conneller, 2004; Overton and Hamilakis, 2013; Viveiros de Castro, 1998: 478; Losey et al., 2018b). Social zooarchaeology repositions human beings relative to other species and focuses on the social, sensory, and environmental facets constituting the consumption of animals and their secondary products (Overton and Hamilakis, 2013).

In the world view of Inuit and Yup'ik cultures, humans share the landscape with non-human beings who are in possession of a spirit known as *inua* (Fitzhugh and Kaplan, 1983). Animals known to possess *inua* include dogs, seals, whales and wolverines, as well as a number of other beings (Bodenhorn, 1990; Fitzhugh and Kaplan, 1983). Reliant on animals for both food and raw materials, northern peoples were constantly engaged in social interactions with non-human beings. These relationships were maintained through the careful observance of food taboos and ritualized behaviours (Bodenhorn, 1990; Hill, 2011; Rasmussen, 1931, 1929). Dogs were unique in Inuit and Yup'ik cosmology; they were given names at birth, they received and wore amulets, they took part in ritual activities, and were considered to be members of society (Hill, 2018; Laugrand and Oosten, 2002; Whitridge, 2017). In contrast, wolverines did not behave according to the strict rules set out by arctic societies and represented dangerous and subversive figures (Laugrand, 2017).

Relational ontology and animism (Descola, 2013) have provided useful avenues to understand how the worldviews of arctic peoples are expressed in material culture. Connecting ontological perspectives with ecology is the concept of *habitus*. *Habitus* describes the corporeal bodies of humans and non-humans as 'an assemblage of affects or ways of being' (Viveiros de Castro, 1998). A *habitus* is constituted by the physical characteristics of a being that allow it to exist within an environment, and the interactions with other living and non-living things that shape its experiences and construct its perspective (Descola, 2013). The concept of *habitus* can provide similar insight into the use of fur clothing by arctic peoples. The functional properties of furs allow humans to inhabit the world in similar ways to wild species, literally providing humans with a 'second skin' (Bodenhorn, 1990: 62) and through biomolecular analyses of the furs, it is also possible to glimpse aspects of the *habitus* of the non-human arctic beings, namely those relating to diet. In the present study, we sought to access human-canid relationships through the combined methods of ancient mitochondrial DNA and stable carbon and nitrogen isotope analysis. We applied shallow DNA sequencing to genetically identify the source of the fur and verify macroscopic species identifications. These results were combined with stable isotopic analysis to yield new insights on regional variation in the diets of domestic dogs and wild species.

2. Background

2.1. Dogs in the Arctic

Human occupation of arctic environments was made possible through the use of domestic dogs for traction, hunting aids, companionship, and as a source of fur and food (Laugrand and Oosten, 2014; Morey, 2010; Strecker, 2018). North American Arctic and Subarctic dogs were historically relied on for sled traction, assistance with scenting seal-breathing holes and hunting polar bears (Rasmussen, 1931; Whitridge, 2017). The uses of dogs among Siberian Arctic cultures were more variable. Among the Nenets and Khanty reindeer herders of Western Siberia, dogs were used for traction, herding reindeer (caribou, *Rangifer tarandus*), and hunting wild game (Dwyer and

Istomin, 2008; Fitzhugh, 1997; Handford, 1998; Losey et al., 2018d). Dogs were tasked with pulling sleds in the coastal Kamchatka Peninsula until the introduction of domestic reindeer, 100 years ago (Strecker, 2018).

The presence of domestic dogs among Siberian and North American Indigenous communities is increasingly the focus of genetic and osteological research (Ameen et al., 2019; Brown et al., 2013; Losey et al., 2018c, 2018d; Perri et al., 2019a, 2019b). Dogs fall into seven identified mitochondrial clades, A-F and the recently identified X clade (Ameen et al., 2019; Ní Leathlobhair et al., 2018; Pang et al., 2009; Savolainen et al., 2002; Thalmann et al., 2013). Arctic dogs from Eastern Siberia and North America predominantly belong to the mitochondrial A-clade, based on samples ranging from the Early Holocene through to the current day (Ameen et al., 2019; Brown et al., 2015, 2013; Ní Leathlobhair et al., 2018). Specific A-clade haplotypes of North American dogs likely accompanied successive migrations of human groups from Siberia into the North American continent (Ameen et al., 2019; Ní Leathlobhair et al., 2018).

2.2. Dog fur clothing

The expert fabrication of fur clothing is regarded as a key adaptation to arctic environments (Issenman, 2011). Historically, the use of different furs was dependent upon a number of factors: the availability of species; trade with other northern groups (Arnold, 2016); the value of different furs as trade commodities; and opportunistic encounters with other species, such as polar and grizzly bear, while trapping foxes for European and Euro-American markets (Oakes, 1988). Generally, clothing across the North American and Siberian Arctic regions was made from the pelts of reindeer/caribou, harp seal (*Pagophilus groenlandicus*), or ringed seal (*Pusa hispida*) (Carlsen et al., 1995; Hatt and Taylor, 1969; Issenman, 2011). The furs of dogs, wolverines, and other species with dense fur, were used as a trim or ruff on the borders of clothing such as parkas, coats, and boots (Hatt and Taylor, 1969; Issenman, 2011; Krashennikov and Crownhart-Vaughan, 1955). The long guard hairs shared by these animals were useful for controlling temperature and humidity (Issenman, 2011). In subzero temperatures, the condensation from breath can collect on the fur trim around the hood and freeze, but this condensation can be shaken or brushed free from furs with long guard hairs (Issenman, 2011). When these furs line the edge of a hood, they can block the wind and aid in maintaining a warm environment around the face (Cotel et al., 2004; Issenman, 2011). Carnivore fur, such as dog, have a longer use-life as the fur is more resilient to fluctuations in humidity and moisture, whereas when the same processes occur to caribou fur, the fragile, hollow hairs will shed (Hatt and Taylor, 1969; Issenman, 2011; Steller, 1774). In some regions, certain dog furs were valued over others, for example in Kamchatka white fur from long-haired dogs was held in the highest regard (Krashennikov and Crownhart-Vaughan, 1955; Strecker, 2018). Dog fur has also been used in other regions outside of the Arctic such as the Salish coast where dog fur was woven into blankets up until European contact (Solazzo et al., 2011).

2.3. Canid diets and stable isotope analysis

The care and provisioning of domestic animals represent an investment, or storage of human labor, in return for assistance with subsistence activities, raw materials, and secondary products (Gudeman, 1977). As carnivores, dogs are one of the few domestic species that must be provisioned with meat and sources of dietary lipids (Losey et al., 2018b). In the Arctic, dogs were, and continue to be provisioned with readily available food sources, such as salmon or seal, which can be acquired in bulk and stored. In Greenland, the Canadian Arctic Archipelago, and coastal Labrador, between the 15th and 20th centuries, dogs were provisioned with seal, fish, shark, and caribou depending on the local availability of particular taxa (Coltrain et al.,

2004; Freuchen, 1921; Hantzsch, 1977; Jensen, 1961). Pre- and post-European contact populations of the Aleutian Islands and coastal Alaska harvested salmon and marine mammals to feed domestic dogs (Andersen, 1992; Dunlap et al., 2007; McManus-Fry et al., 2018; West and France, 2015). For at least 300 years, salmon has been a staple food for sled dogs of the Kamchatka Peninsula while hunting dogs were fed birds (Krashennikov and Crownhart-Vaughan, 1955; Steller, 1774; Strecker, 2018). Among the Nenets and Khanty of the Northern and Polar Urals, dogs were, and still are, fed reindeer meat and seasonal, locally available freshwater fish (Svoboda et al., 2011), which may demonstrate historical continuity with prehistoric practices (Losey et al., 2018a). Frequently, it is the scarcity of provisions for dogs that is responsible for the decline in their populations, in addition to epidemics of rabies and canine distemper virus (Degerbøl and Freuchen, 1935; Hjortlund, 1907; Strecker, 2018).

The day-to-day practices, such as feeding, that reinforced human–dog relationships in the Arctic have only recently begun to receive academic attention (Losey et al., 2018b). Stable carbon and nitrogen isotope ratio analysis provides an effective means to estimate the sources of dietary protein. Stable carbon isotope ratios ($\delta^{13}\text{C}$) can distinguish between the three main photosynthetic pathways used by different plant taxa (O’Leary, 1988), and between marine and terrestrial environments (Schoeninger and DeNiro, 1984). Cumulative enrichment occurs in ^{15}N between trophic levels linking stable nitrogen isotope ratios ($\delta^{15}\text{N}$) to a consumer’s trophic position and environment (Minagawa and Wada, 1984). Higher $\delta^{15}\text{N}$ values are measured in marine consumers (Britton et al., 2013; Byers et al., 2011; Coltrain et al., 2004; Guiry et al., 2012; McManus-Fry et al., 2018; Nelson et al., 2012b; Szpak et al., 2009) as aquatic food chains are longer than those of terrestrial environments.

Fur keratin is used as a dietary proxy in both modern and archaeological studies of diet (Darimont and Reimchen, 2002; McManus-Fry et al., 2018; Milakovic and Parker, 2011; Urton and Hobson, 2005) as it incorporates amino acids sourced from the diet during growth and, once formed, is metabolically inert (Petzke et al., 2005). Isotopic fractionation occurs in the metabolic processes that transform dietary amino acids, and those already found in the body, into new proteinaceous tissues, such as keratin (Macko et al., 1987). Diet–fur discrimination factors of +2 to +2.6‰ for $\delta^{13}\text{C}$ and +3.4‰ for $\delta^{15}\text{N}$ were originally determined for red foxes (Roth and Hobson, 2000) and appear to be appropriate for wolves (Darimont and Reimchen, 2002; Milakovic and Parker, 2011; Urton and Hobson, 2005). By comparison, bone collagen, the most common analyte in palaeodietary studies, tends to be elevated in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ relative to diet by +5‰ and +3 to +5‰, respectively (Ambrose and Norr, 1993; Bocherens and Drucker, 2003). Bone collagen and fur keratin record diet over different time periods of an animal’s life; bone collagen reflects the average protein sources consumed across a dog’s lifespan while fur keratin records dietary inputs only over the period of growth, approximately 14–15 weeks (Diaz et al., 2004). The growth rate of dog fur across different dog breeds is not thoroughly understood and can be expected to fluctuate seasonally (Al-Bagdadi et al., 1977; Diaz et al., 2004). Issenman (2011) reports that the husky’s winter fur, containing a mixture of long guard hairs and short wool-like underfur, would add a warm, moisture-resistant layer to clothing. We do not associate the sampled furs in the study with a particular season, but we assume that the fur samples would have grown over a period of three to four months.

3. Materials and methods

3.1. Fur clothing samples

The samples studied in this project were obtained from the ethnographic collections curated by the National Museum of Denmark (Supplementary Table 1). The fur clothing was collected from

Indigenous cultures across the North American and Siberian Arctic during the late 19th and early 20th centuries. The Fifth Thule Expedition, 1921–1924, purchased additional items in 1927 from Siberia (the so-called Eugen Alexander collections) that are currently curated by the National Museum. Further details can be found on the SkinBase database <http://skindragter.natmus.dk/Clothing> (Schmidt, 2016). The year of collection, the name of the Indigenous culture and location are recorded for some of the garments, but others are only associated with a general location, such as Alaska and the Aleutian Islands, or Kamchatka Krai. For this reason, we were unable to link the samples to particular locations or cultures and refer to the samples only by the general location of acquisition, which in some cases necessitated the use of colonial language.

Fur clothing or garments macroscopically identified as being dog/wolf fur were selected for inclusion in this study. We further collected paired samples from four additional garments with visually different ‘dog’ fur. A small sample of skin was removed from the garment roughly the size of a grain of rice with the fur intact upon the skin. The fur was removed from the skin using a sterile scalpel whereupon the fur and skin were processed for isotopic analysis and DNA sequencing, respectively. Mitochondrial genomes have been published from 11 dog furs in this collection from arctic communities spanning from St. Lawrence Island (Alaska) to Greenland (Ameen et al., 2019). The published mitochondrial genomes from these specimens were combined with samples included in this study to broaden the geographic range to western Siberia, test the macroscopic species identification, and to increase the coverage of published samples (Ameen et al., 2019).

3.2. Wolf pelt samples

The historical wolf samples from Greenland and Canada used in this study have been provided by the Natural History Museum of Denmark, the Natural History Museum, University of Oslo and the Danish Museum of Hunting and Forestry and were sampled from stuffed specimens or complete hides collected and listed as wolves.

3.3. Ancient DNA analysis of skin samples

DNA was extracted from skin samples ($n = 68$) using a protocol, specific to ancient soft tissues, that removed inhibitors such as the biocides used to treat the garments in the museum collections (Ameen et al., 2019; Gilbert et al., 2007). The samples underwent a brief pre-digestion step to remove surface contaminants in an EDTA and proteinase K buffer for 30 min, followed by overnight digestion to extract the DNA. Purification of the extraction was performed according to Ameen et al. (2019) and Ersmark et al. (2015). Library building was conducted as per the BEST protocol for libraries (Ameen et al., 2019; Carøe et al., 2018). The amplified libraries were sequenced on the Illumina HiSeq2500 sequencing platform at Science for Life Laboratory in Stockholm, Sweden and further sequencing of previously published samples was conducted at the BGI sequencing facilities in Shenzhen, China on the BGISEQ-500 platform. Libraries prepared for sequencing on the BGISEQ-500 platform also follow the BEST protocol with the only alteration being the use of platform-specific sequencing adapters and indexes (Carøe et al., 2018).

The sequenced reads from each sample were initially mapped to the reference genome for the dog, CanFam3.1 under the assumption that the fur was of dog origin as indicated by the macroscopic assessment (Li and Durbin, 2009; Lindblad-Toh et al., 2005). The reads were also aligned to the NCBI NR protein database (14th Nov. 2019) using DIAMOND (Buchfink et al., 2015) to test whether the furs could have originated from other taxa. Briefly, DIAMOND aligns nucleotide data against a reference database composed of protein sequences from all three domains of life (bacteria, eukaryotes, and archaea). The taxonomic composition of a sample is computed based on these alignments using the LCA algorithm with MEGAN (Huson et al., 2016, 2007).

Subsequently, each sample was mapped to a concatenated panel of 28 mitochondrial reference genomes. These correspond to local mammalian taxa from the region which are reported to have been used for clothing (Hatt and Taylor, 1969; Issenman, 2011). Related species were used when mitochondrial references were not available, for example, the only relevant mitochondrial reference available for Arctic rodents were the Daurian ground squirrel and Siberian chipmunk mitochondrial genomes but ethnographic records also report the use of other ground squirrel species (Issenman, 2011). Each sample was mapped to the panel of mitochondrial reference genomes using BWA (Li and Durbin, 2009). A concatenated reference panel was used to mitigate the repeated mapping of the same reads to conserved or repetitive regions of the mitochondrial genomes. The alignments were then filtered to remove all reads with mapping quality below 30 and PCR duplicates were removed with Picard tools (<http://broadinstitute.github.io/picard/>), see Supplementary Table 2. The reads mapping to each mitochondrial reference in the concatenated reference panel were then extracted and quantified. Consensus sequences were called for samples that possessed complete mitochondrial genomes for the identified taxa with HTSbox (<https://github.com/lh3/htsbox>). Four of the previously published samples have increased coverage as a result of additional sequencing (Ameen et al., 2019). A maximum-likelihood tree of dogs and wolves was constructed with 1000 bootstrap replicates using RAxML (Stamatakis, 2006) from samples with at least 3x mean coverage of the mitochondrial genome, with publically available dog and wolf mitochondrial genomes using a coyote as the outgroup (Ameen et al., 2019; Frantz et al., 2016; Ní Leathlobhair et al., 2018; Pang et al., 2009; Thalmann et al., 2013). A maximum-likelihood tree was also constructed for fox samples following the same procedure, using one mitochondrial fox genome generated in this study and publically available arctic fox ($n = 3$) and red fox ($n = 6$) mitochondrial genomes using the dog mitochondrial reference genome (NC002008.4) as an outgroup, see Supplementary Fig. 1 for a list of NCBI accession numbers for fox mitochondrial genomes. For samples identified as dogs, and in cases with enough sequenced reads, biological sex was identified in cases through the comparison of reads mapping to the X chromosome in comparison to chromosome 1, which is similar in length (Skoglund et al., 2015, 2013).

Furthermore, we used FastQ Screen (Wingett and Andrews, 2018), a tool for searching against a reference panel to determine species source or metagenomic composition, with the same 28 mitochondrial genomes plus the human mitochondrial reference genome to evaluate the source of the furs. Due to the lack of complete whole genome references for all the candidate species, mitochondrial references were used to limit the disproportionate reference size for taxa with whole genome references available. FastQ Screen has been implemented on similar datasets to identify the animal source of clothing for Ötzi, the Tyrolean Iceman (O'Sullivan et al., 2016) and to assess the animal of origin for medieval vellum samples (Fiddyment et al., 2015). The FastQ Screen run was implemented also using BWA to align the sequenced reads to the reference panel. The results of FastQ Screen were visualised for the dataset used in the study with MultiQC (Ewels et al., 2016).

3.4. Isotope analysis of fur samples

The samples macroscopically identified as dog fur were pretreated at the Archaeological Research Laboratory, Stockholm University. The samples were cleaned by ultrasonication in a 2:1 chloroform-methanol solution (3×15 min). The solvent treated samples were then rinsed with deionized water and air-dried for 24 h. Between 0.7 mg and 1 mg of each fur sample was tightly folded into a tin capsule (5x9 mm, Säntis Analytical, Switzerland) for stable carbon and nitrogen isotope analysis. The fur samples were analyzed at the Jan Veizer Laboratory, University of Ottawa, Canada. Ten percent of the samples were analyzed in duplicate. The samples were combusted in a Vario EL Cube (Elementar, Germany) EA-IRMS interfaced via Conflo IV to Delta Advantage isotope

ratio mass spectrometer (Thermo, Germany). The raw isotope data were referenced to the VPDB (carbon) and AIR (nitrogen) scales using six calibration standards (IAEA-N1, IAEA-N2, USGS-40, USGS-41, NBS-22, and IAEA-CH-6). Three internal check standards were included in the analytical run: C-51 ($\delta^{13}\text{C}$: -23.0‰ ; $\delta^{15}\text{N}$: $+0.1\text{‰}$), C-52 ($\delta^{13}\text{C}$: -11.9‰ ; $\delta^{15}\text{N}$: $+16.6\text{‰}$), C-54 ($\delta^{13}\text{C}$: -16.6‰ ; $\delta^{15}\text{N}$: -34.5‰). Analytical error was monitored using a blind standard (C-55, Glutamic acid, $\delta^{13}\text{C}$: -4.0‰ ; $\delta^{15}\text{N}$: -28.5‰) run in triplicate and was better than $\pm 0.1\text{‰}$ for carbon and nitrogen.

The wolf fur samples were pretreated and analyzed at BioArCh, University of York. The samples were ultrasonicated in deionized water for 1 h to remove dirt and other debris. The samples were then soaked in a 7:1 dichloromethane/methanol solution (Tankersley and Koster, 2009) for 14 h after which time the solution was removed and the excess solvent allowed to evaporate. The samples were then ultrasonicated in deionized water ($330 \text{ min} \times$) (Britton et al., 2013) and oven-dried ($40 \text{ }^\circ\text{C}$, 24 h). Each dried sample was then homogenized using sterilized scissors. The samples (0.9 mg – 1.1 mg) were weighed in duplicate into tin capsules and combusted in a Sercon GSL Sample Preparation System module coupled to a Sercon 20–22 mass spectrometer. The raw isotope values were calibrated to the VPDB and AIR scales using international standards (Caffeine [IAEA 600] $\delta^{13}\text{C}$: $-27.8 \pm 0.1\text{‰}$, $\delta^{15}\text{N}$: $+1.0 \pm 0.1\text{‰}$; Cane sugar [IA-R006] $\delta^{13}\text{C}$: $-11.6 \pm 0.1\text{‰}$; and IAEA-N-2 $\delta^{15}\text{N}$: $+20.3 \pm 0.2\text{‰}$). Replicates of an internal fish gelatin standard ($\delta^{13}\text{C}$: $-15.2 \pm 0.1\text{‰}$, $\delta^{15}\text{N}$: $+15.3 \pm 0.2\text{‰}$) were run between every six samples to correct for instrumental drift. Three additional fish gelatin standards were used as check standards. Analytical error on replicate analyses of the samples was $\pm 0.2\text{‰}$ or better for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

We assessed sample preservation by comparing the atomic C/N ratios of the fur to published modern data sets from humans. In the papers we surveyed C/N ratios from the fur of modern canids included in stable isotope studies are rarely published. The C/N ratios of modern hair range from 3.0 to 3.8 (O'Connell et al., 2001; O'Connell and Hedges, 1999a), and are typically used to assess the preservation of human and non-human archaeological samples (McManus-Fry et al., 2018).

3.5. Isotope data treatment

The challenge with interpreting stable isotope data from a wide geographic area lies in finding suitable comparative baseline data sets against which the target isotope data can be contextualized and interpreted (Casey and Post, 2011). As our samples date to the late 19th and early 20th century, the Suess effect on the $\delta^{13}\text{C}$ values of the samples was minimal and approximated analytical error. Therefore, we compared our samples to archaeological datasets and did not correct the fur data for the Suess effect. However, published modern salmon scale data (Satterfield and Finney, 2002) used in the paleodiet interpretation were corrected for the Suess effect after (Misarti et al., 2009) modified from (Hilton et al., 2006). This resulted in the addition of $+0.7\text{‰}$ to the salmon $\delta^{13}\text{C}$ values. This value is only an approximation of the change in $\delta^{13}\text{C}$ in the Pacific Ocean, as we did not account for changes due to phytoplankton productivity, sea surface temperature, and atmospheric CO_2 concentration. However, we deemed this acceptable because our intention was not to produce a comprehensive model of paleodiet.

Much of the comparative archaeological data available for arctic fauna is sourced from bone collagen, therefore, for ease of comparison, we adjusted the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of dog fur specimens by $+1.4\text{‰}$ and $+0.9\text{‰}$, respectively, after O'Connell et al. (2001). These discrimination factors were determined through experimental research on modern humans, but to the best of our knowledge, such data do not yet exist for domestic dogs, however, similar offsets have been used in dietary analyses of wolf fur and bone collagen (Kays and Feranec, 2011) and palaeodietary analyses of domestic dog fur and collagen (McManus-Fry et al., 2018).

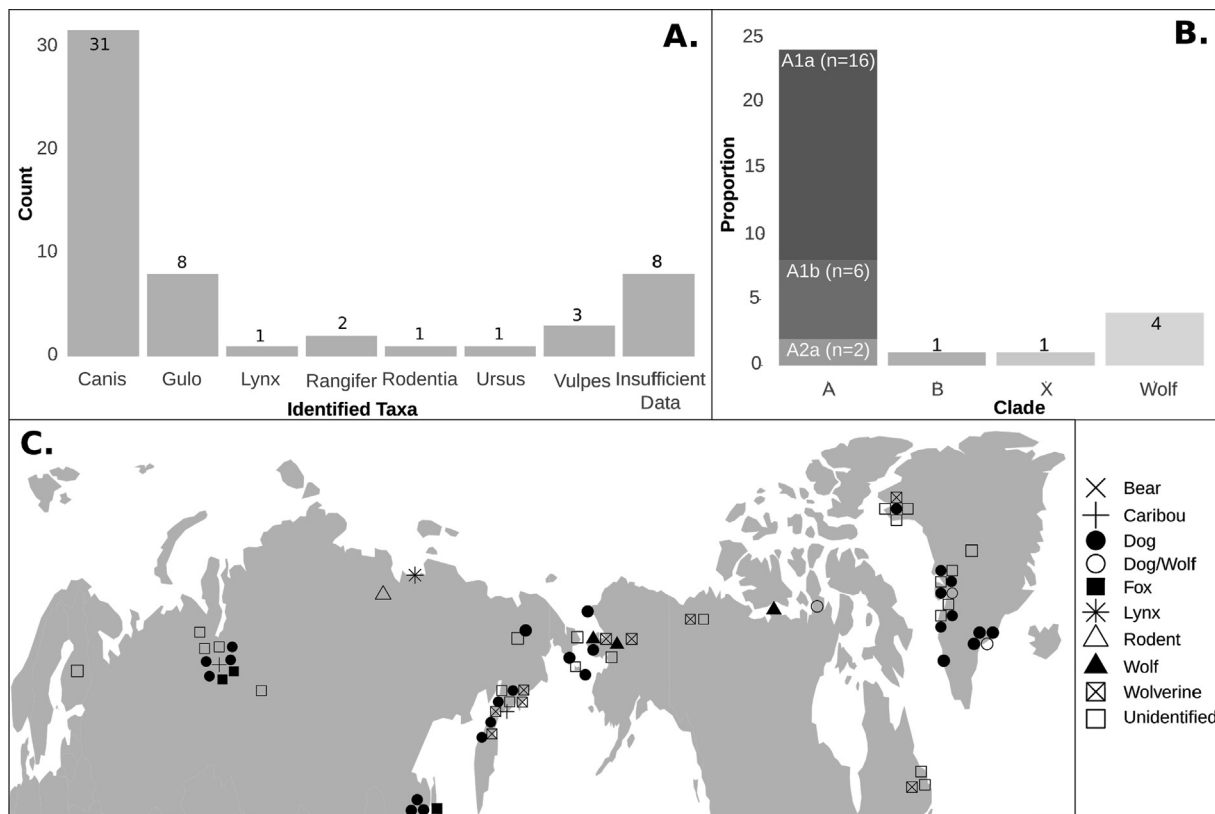


Fig. 1. Genetically identified taxa from fur samples. (A) Counts taxa identified genetically from this study and the published samples from the collection (Ameen et al., 2019). (B) Counts of dog/wolf haplotypes carried by dogs/wolves in the collection. (C) Genetically identified fur samples mapped to the region of collection.

4. Results

4.1. Genetic species identification of fur clothing

Samples were taken from 68 specimens to initially confirm the macroscopic species identification in order to ensure the appropriate interpretation of the isotopic results as well as to increase the number of complete mitochondrial genomes from historical arctic dogs in context with dietary data. Of the 68 specimens sampled DNA, DNA data on 11 of these specimens were previously (Ameen et al., 2019), in this study sufficiently concentrated for sequencing of 45 additional samples. In the previously published dataset two samples were identified as having been derived from animals with wolf mitochondrial haplotypes (Ameen et al., 2019); however, samples with low *Canis* sp. DNA content were excluded from analysis due to insufficient coverage of the mitochondrial genomes and as such were not tested for originating from non-*Canis* sources.

Based on mitochondrial and protein sequences, taxonomic assignment was possible for 36 of the samples from this study, and we confirmed the taxonomic assignment of the 11 published specimens (Fig. 1A, C). Four samples included in previously published studies underwent further sequencing improving the mitochondrial genome coverage (Ameen et al., 2019). The results of the alignment to the concatenated panel of mitochondrial genomes and the FastQ Screen results produced complimentary results after filtering out reads with low mapping quality and reads with no hits or hitting multiple genomes, respectively, see Supplementary Fig. 2 and Supplementary Tables 2 and 3. We were able to confidently identify 31 specimens as dogs or wolves on the basis of their DNA, including the 11 published individuals. A further 8 samples were identified genetically to be wolverine fur (*Gulo gulo*). Fox fur was identified on three of the garments; it was possible to identify one specimen (TRF.02.12) as a red fox (*Vulpes vulpes*) using phylogenetic tree construction, see Supplementary Fig. 1.

However, insufficient data was available for the other two specimens to provide confident species-level assignments. Two specimens showed the most reads mapping to the reindeer/caribou mitochondrial genome and both also had reads aligning to ruminant proteins in the DIAMOND analyses, see Supplementary Fig. 3 and Supplementary Table 4. Individual samples were also identified as a lynx (*Lynx lynx*) and a rodent related to the Dorian ground squirrel (*Spermophilus dauricus*). Concatenated reference panel alignment and the FastQ Screen analyses both showed the greatest proportion of reads aligned to the *Ursus* genus for one specimen, TRF.02.39. The light color of the fur, a high $\delta^{15}\text{N}$ value, and higher volume of reads mapping to the *Ursus maritimus* mitogenome over the *Ursus arctos* mitogenome, together suggest the fur originated from a polar bear. Due to an insufficient amount of data, with less than 50,000 reads, a confident taxonomic assignment was not possible for eight of the sequenced samples. For three additional samples with between 95,648 and 435,734 reads sequenced, no species in the mitochondrial panel or DIAMOND analysis could be identified as the taxa of origin for the fur. This likely occurred as the result of biases in the protein database which contained a disproportionate amount of data from dogs relative to other taxa of interest – even in the samples confidently identified as wolverine or fox, DIAMOND identified them as dog. Of the specimens confidently identified as dog, the endogenous DNA content ranged between 14 and 60% (mean 52.4%).

Complete mitochondrial genomes, where at least 90% of the sites had a mean coverage of 3x, were obtained from 17 dogs, 1 fox, 1 lynx, and 6 wolverines out of the 47 total samples sequenced. A phylogenetic tree was constructed with the dog/wolf mitochondrial genomes from this study and combined with 344 published mitochondrial genomes and the four previously discussed published mitogenomes with improved coverage (TRF.02.04, TRF.02.14, TRF.02.16, and TRF.02.29). Phylogenetic analysis revealed that only the two published samples were wolves (TRF.02.27 and TRF.02.28), the 17 previously unpublished mitochondrial genomes were all phylogenetically identified

Table 1Stable isotope results and preservation indicators from fur clothing samples genetically and macroscopically identified as *C. l. familiaris* (domestic dog).

Sample ID	MT. Cov.	Location	Year of collection	Sex	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	%C	%N	C/N
TRF-2-53	149.5	Kamchatka Krai, Russia	1961	M	-19.8	+6.5	45.3	14.7	3.5
TRF-2-54	14.7	Kamchatka Krai, Russia	1961	M	-20.4	+12.3	44.3	14.8	3.5
TRF-2-57	14.7	Kamchatka Krai, Russia	1961	F	-18.0	+7.3	44.1	14.7	3.5
TRF-2-23	29.7	Northern/Polar Urals, Russia	1927	M	-19.8	+7.1	44.3	14.6	3.5
TRF-2-25	44.5	Northern/Polar Urals, Russia	1927	M	-20.3	+8.5	43.7	14.2	3.6
TRF-2-14	73.2	Point Hope, Alaska	1926	M	-16.2	+14.6	40.6	13.3	3.6
TRF-2-29	101.2	Alaska/Aleutian Islands	1945	M	-16.5	+13.4	44.8	14.5	3.6
TRF-2-16	155.4	St. Lawrence Island, Alaska	1939	F	-14.2	+18.3	44.7	14.5	3.6
TRF-2-65	0.9	Nunavut, Canada	No date	F?	-16.1	+14.0	44.2	14.0	3.7
TRF-2-37	10.9	Tasiliak, Greenland	1911	M	-15.3	+16.4	44.3	14.4	3.6
TRF-2-70	12.0	Tasiliak, Greenland	1911	F	-14.7	+17.8	50.2	15.8	3.7
TRF-2-47	36.4	Uummannaq, Greenland	1926	F	-15.4	+19.8	39.6	13.1	3.5
TRF-2-41	4.0	West Greenland	1980	F	-16.5	+17.8	46.9	14.9	3.7
TRF-2-44	2.2	West Greenland	No date	M	-15.1	+18.3	40.0	12.8	3.6
TRF-2-45	2.2	West Greenland	No date	M	-14.6	+15.8	44.5	14.3	3.6

as dogs (Supplementary Fig. 4). One of the previously unpublished dog mitochondrial genomes, from a Nenets/Khanty coat, was found to have a mitochondrial genome from the B clade in the phylogenetic tree while the remaining 16 samples fell into the A clade. The A-clade dogs fell into three of the main A-subclades: A1a (n = 10), A1b (n = 4), and A2a (n = 2) (Fig. 1B).

4.2. Paleodiet of Arctic and Subarctic dogs, wolves, and wolverines

All but one of the samples met with published preservation criteria (O'Connell and Hedges, 1999b), with atomic C/N ratios ranging from 3.3 to 3.8. One sample (TRF-2-43), with exceedingly high weight % carbon and nitrogen, was removed from further analysis. The stable isotope data and preservation indicators from the samples genetically identified as *C. l. familiaris* and the wolf pelts are shown in Tables 1 and 2 and Fig. 2. Stable isotope results and preservation indicators from fur clothing samples genetically identified as wild species or with insufficient data for genetic identification are shown in Table 3.

We observed a broad range of $\delta^{13}\text{C}$ (-20.4‰ to -14.2‰) and $\delta^{15}\text{N}$ values (+6.5‰ to +19.8‰) in the dog fur samples, suggesting that dietary resources from marine, terrestrial, and potentially freshwater sources were used to provision dogs across the Arctic. The fur samples identified macroscopically as *C. l. familiaris* but for which no genetic identification could be obtained had a broader $\delta^{13}\text{C}$ range of -23.4‰ to -13.8‰, and $\delta^{15}\text{N}$ values ranging from +7.5‰ to +19.7‰.

The wolf pelts collected in Canada in the early 20th century had

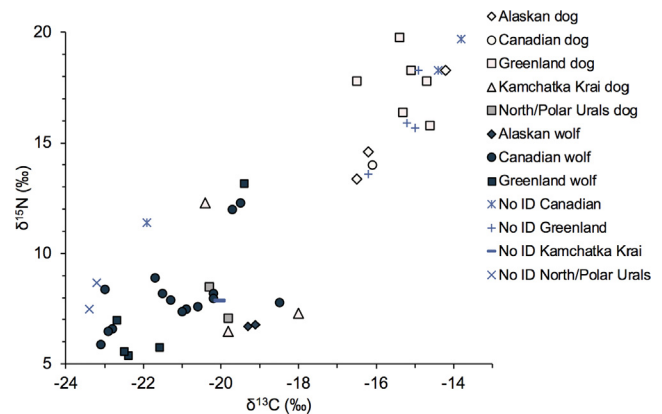


Fig. 2. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of genetically identified dog and wolf fur samples, and samples lacking a genetic species identification.

$\delta^{13}\text{C}$ values ranging from -23.1‰ to -18.5‰, and $\delta^{15}\text{N}$ values ranging from +5.9‰ to +12.3‰. The Greenland wolf pelts had $\delta^{13}\text{C}$ values ranging from -22.7‰ to -19.4‰, and $\delta^{15}\text{N}$ values ranging from +5.4‰ to +13.2‰. The genetically identified wolf fur samples from two Alaskan parka hoods had similar $\delta^{13}\text{C}$ values of -19.1‰ and -19.3‰, and $\delta^{15}\text{N}$ values of +6.8‰ and +6.7‰. The wolf samples are separated by latitude and plotted in Fig. 3. The Canadian wolf samples from high latitudes (> 75°N) generally had lower $\delta^{13}\text{C}$ values

Table 2

Stable isotope results and preservation indicators from wolf pelts.

Sample ID	Location	Region	Year of collection	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	%C	%N	C/N
1766	Itivleriaq, East Foxe Basin	Nunavut, Canada	1922	-20.9	+7.5	44.7	15.0	3.5
2046	Itibdjeriang, East Foxe Basin	Nunavut, Canada	ca. 1928	-20.6	+7.6	43.2	14.8	3.4
2047	Itibdjeriang, East Foxe Basin	Nunavut, Canada	ca. 1928	-21.0	+7.4	43.5	14.8	3.4
2043	Southampton Is.	Nunavut, Canada	1922	-20.2	+8.2	43.8	15.0	3.4
2044	Wilson Lake	Nunavut, Canada	1922/23	-20.2	+8.0	44.2	15.3	3.4
2048	Back River	Nunavut, Canada	1923	-21.3	+7.9	43.9	15.1	3.4
2049	Back River	Nunavut, Canada	1923	-19.5	+12.3	43.5	15.0	3.4
2050	Back River	Nunavut, Canada	1923	-19.7	+12.0	43.4	15.0	3.3
1458	Axel Heiberg Is.	Nunavut, Canada	1912	-23.1	+5.9	43.6	15.0	3.4
1460	Axel Heiberg Is.	Nunavut, Canada	ca. 1914	-22.9	+6.5	41.7	14.4	3.4
4093	Axel Heiberg Is.	Nunavut, Canada	1940	-21.7	+8.9	43.1	14.8	3.4
4094	Axel Heiberg Is.	Nunavut, Canada	1940	-21.5	+8.2	43.7	15.1	3.4
Eunr	Ellesmere Is.	Nunavut, Canada	1919	-23.0	+8.4	45.2	15.1	3.5
3456	Ellesmere Is.	Nunavut, Canada	1919	-22.8	+6.6	45.4	15.5	3.4
1921	Rosenvinge	Greenland	1925	-22.4	+5.4	44.9	15.4	3.4
1237	Hvalrosodden	Greenland	1922/23	-22.5	+5.6	43.4	14.9	3.4
4903	Kap Graah	Greenland	1926	-21.6	+5.8	42.9	14.7	3.4
8.1	East coast	Greenland	1901	-22.7	+7.0	43.7	14.9	3.4
1240	Skibshavnen	Greenland	1908	-19.4	+13.2	44.7	15.4	3.4

Table 3
Stable isotope results and mtDNA coverage from samples genetically identified as wild species or with insufficient data for identification.

Sample ID	Macroscopic species ID	Genetic species ID	Location	MT. Cov.	Year of collection	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	%C	%N	C/N
TRF-2-27	<i>C. l. familiaris</i>	<i>C. lupus</i>	Alaska/Aleutian Is., USA	4.9	1945	-19.1	+6.8	45.3	15.0	3.5
TRF-2-28	<i>C. l. familiaris</i>	<i>C. lupus</i>	Alaska/Aleutian Is., USA	10.7	1945	-19.3	+6.7	44.7	14.1	3.7
TRF-2-69	<i>C. l. familiaris</i>	<i>C. lupus</i>	Kent Peninsula, Canada	38.0	1927	-18.5	+7.8	43.7	14.5	3.5
TRF-2-03	<i>C. l. familiaris</i>	<i>Gulo gulo</i>	Kamchatka Krai, Russia	0.4	1966	-20.2	+6.7	52.7	17.6	3.5
TRF-2-50	<i>C. l. familiaris</i>	<i>Gulo gulo</i>	Kamchatka Krai, Russia	0.1	1961	-21.0	+6.6	45.3	15.1	3.5
TRF-2-55	<i>C. l. familiaris</i>	<i>Gulo gulo</i>	Kamchatka Krai, Russia	5.4	1961	-17.1	+11.9	44.2	14.6	3.5
TRF-2-56	<i>C. l. familiaris</i>	<i>Gulo gulo</i>	Kamchatka Krai, Russia	4.3	1961	-18.9	+8.2	38.0	12.6	3.5
TRF-2-32	<i>C. l. familiaris</i>	<i>Gulo gulo</i>	Labrador, Canada	4.5	1924	-16.6	+13.6	44.4	14.9	3.5
TRF-2-35	<i>C. l. familiaris</i>	<i>Gulo gulo</i>	MacKenzie Delta, Canada	1.7	1936	-20.4	+6.9	42.1	13.9	3.5
TRF-2-30	<i>C. l. familiaris</i>	<i>Gulo gulo</i>	Alaska/Aleutian Is. USA	10.0	1945	-22.0	+6.3	44.3	14.4	3.6
TRF-2-39	<i>C. l. familiaris</i>	<i>U. maritimus</i>	Kap York, Greenland	0.0	1905	-15.0	+18.5	49.1	16.1	3.6
TRF-2-62	<i>C. l. familiaris</i>	<i>V. lagopus</i>	Northern/Polar Urals, Russia		1927	-22.2	+9.1	45.6	14.7	3.6
TRF-2-61	<i>C. l. familiaris</i>	<i>V. lagopus?</i>	Northern/Polar Urals, Russia		1927	-19.4	+11.9	44.4	14.2	3.6
TRF-2-66	<i>C. l. familiaris</i>	-	Kap York, Greenland		1905	-15.2	+15.9	36.9	12.1	3.6
TRF-2-33	<i>C. l. familiaris</i>	-	Labrador, Canada		1922	-13.8	+19.7	43.8	14.6	3.5
TRF-2-34	<i>C. l. familiaris</i>	-	Labrador, Canada		1922	-14.4	+18.3	45.2	14.5	3.6
TRF-2-72	<i>C. l. familiaris</i>	-	MacKenzie Delta, Canada		1926	-21.9	+11.4	44.5	14.4	3.6
TRF-2-52	<i>C. l. familiaris</i>	-	Kamchatka Krai, Russia		1961	-20.0	+7.9	45.0	15.0	3.5
TRF-2-63	<i>C. l. familiaris</i>	-	Northern/Polar Urals, Russia		1881	-23.2	+8.7	45.5	14.6	3.6
TRF-2-67	<i>C. l. familiaris</i>	-	Northern/Polar Urals, Russia		1927	-23.4	+7.5	45.4	14.1	3.8
TRF-2-17	<i>C. l. familiaris</i>	-	West Greenland		No date	-14.9	+18.3	45.2	14.5	3.6
TRF-2-43	<i>C. l. familiaris</i>	-	West Greenland		No date	-15.0	+15.7	77.3	29.4	3.1
TRF-2-46	<i>C. l. familiaris</i>	-	West Greenland		1870	-16.2	+13.6	44.3	14.1	3.7

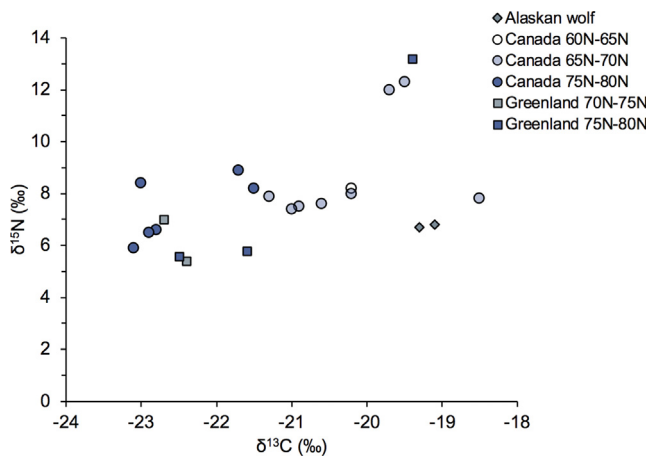


Fig. 3. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of early 20th century wolves plotted according to latitude.

than those from lower latitudes, but the sample size was too small for statistical testing. One Greenland wolf pelt collected from a latitude above 75°N had a very high $\delta^{15}\text{N}$ value and higher $\delta^{13}\text{C}$ value relative to the other Greenland wolves. This suggests some dietary contributions from marine or anadromous species.

The ~5‰ range in $\delta^{13}\text{C}$ values and ~7‰ range in genetically identified wolverine $\delta^{15}\text{N}$ values was a surprising result of our study (Fig. 4). Wolverines have not been the subject of frequent isotopic study but the existing published bone collagen data from Alaska is tightly clustered around -20‰ reflecting a diet of terrestrial herbivore protein (Dalerum et al., 2009a). Wolverine diets are typically comprised of hunted and scavenged terrestrial ungulates (Dalerum et al., 2009b; Koskela et al., 2013), but the isotopic values of two wolverines from Kamchatka and Labrador are suggestive of inputs of protein from marine or anadromous species.

5. Discussion

Fur clothing acts as a material archive and mnemonic of the social interactions between humans, dogs, and other species (Overton and Hamilakis, 2013). Living dogs were simultaneously working with each

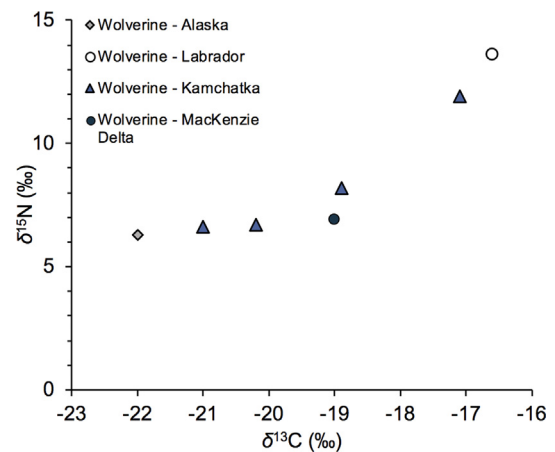


Fig. 4. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fur from genetically identified wolverines from Canada (Labrador and MacKenzie Delta), Alaska, and Kamchatka Krai.

other alongside humans to sustain life in the Arctic and, among some communities in Kamchatka, being tended to as a future source of fur. As the fur was expertly fashioned into warm clothes it may have acted as a reminder of the owner-dog relationship during life and continued to testify to both the interactions of the dog with other species via their consumption, and to the long-term genetic history of domestic dogs among Arctic cultures. The following section will review the methodological implications of this study, followed by a discussion of the results with respect to the reciprocal interactions of humans and dogs, and, as a contrast, the adversarial relationship between people and wolverines.

5.1. DNA analysis of fur clothing

Until the 1970s, the National Museum of Denmark routinely treated fur garments with chlorinated biocides to preserve the furs from insects, but despite this treatment, we were still able to extract sufficient endogenous DNA for analysis. The preservation of DNA in the skin samples proved to be very good in most cases. In cases where the endogenous content of dog DNA appeared to be low (< 10% dog DNA) closer investigation showed this to be the result of incorrect

macroscopic identification rather than poor preservation. However, low endogenous content alone cannot distinguish between dog/wolf and non-dog/wolf samples. Samples with between 10 and 56% endogenous 'dog DNA' were, in turn, either dog samples with reduced preservation or from other carnivore species with similar DNA sequences, such as foxes and bears.

The phylogenetic analysis showed that, with only two exceptions, the dog mitogenomes from the collection all fall into the A clade. This is consistent with previous studies that show that Arctic dogs, prior to European colonization over the last century, possess mitochondrial haplotypes within this clade (Ameen et al., 2019; Brown et al., 2015, 2013). One of the exceptions is a Nenets/Khanty dog with a B clade haplotype, suggesting that this dog likely has at least some ancestry from outside of the Arctic where this haplotype is prevalent. Unfortunately, a sufficient amount of hair was unavailable for isotopic analysis, therefore we cannot compare the isotopic composition of the individual to other dogs from the region. The second exception is a dog carrying an X-clade haplotype as identified previously (Ameen et al., 2019). The specimens with A clade haplotypes generally cluster geographically, with dogs from Greenland grouping with other dogs from Greenland, and the different regions of Siberia clustering together.

The paired samples from garments with visually different dog fur provided some insight into the use of dogs in arctic communities. The coat featuring fur from the B clade haplotype had dog fur of two different colors, both of which were sampled and sequenced. The white fur possessed the B clade haplotype, while the sample with black fur carried an A clade haplotype demonstrating that dogs with both haplotypes were contemporaneously present in the region. Two individuals, male and female, were identified in a second set of paired samples taken from a coat made predominantly of dog skin. In the third set of paired samples the mitochondrial and sex data were insufficient to determine if the fur originated from different individuals. In the final set of paired samples both were identified as *C. lupus* with no phylogenetic distinction between the two and neither sample could be confidently assigned a sex. It appears that as dogs worked together to pull sleds, they were physically united after death, frequently with wild animals, in the task of protecting human bodies from the Arctic environment. Although domestic dogs were in possession of a unique perspective, and occupied a distinct position in the cosmology of arctic peoples (Laugrand and Oosten, 2014), from the perspective of humans, the similarities between wild and domestic species may have been more important when choosing furs for clothing.

5.2. Isotopic analysis of fur clothing

Isotopic analysis of the sampled furs provided further characterization of the species composing the clothing of Arctic hunter-fish-gatherers and herders. For samples with insufficient genome coverage, we hypothesized that diet may provide an indication of canid species, but this proved to be highly context-dependent. Domestication is associated with behavioral, morphological, and genetic changes and, in the case of dogs, increasing dependence on humans for food, shelter, and protection (Zeder, 2006). In the archaeological past, and among modern societies with limited access to commercial dog food, dogs could have accessed locally available foods, either through scavenging or direct provisioning by their owners (Guiry, 2012). Dietary dependence would be particularly apparent among the dogs of mobile or semi-sedentary coastal arctic hunter gatherers. In such communities, marine resources were collected in bulk and dried or frozen to serve as dog food (Ames, 1977; Strecker, 2018), and these practices are revealed in the stable isotope values of archaeological dogs (Coltrain et al., 2004; McManus-Fry et al., 2018; West and France, 2015).

To enable comparison with published bone collagen data, the domestic dog, wolf, and unidentified fur samples were adjusted to estimated bone collagen values. The Greenland dog samples (Fig. 5A) plotted with local marine mammals suggesting these formed a

dominant dietary component, similar to archaeological humans in the same region (Nelson et al., 2012a). Four of the wolf samples had diets consistent with terrestrial sources of protein, while the fifth may have consumed a mixed marine-terrestrial diet. Greenland-based studies of Arctic wolf scat show that musk ox, hare, lemmings, and Arctic foxes feature in wolf diets (Dalerum et al., 2018; Maquard-Peterson, 1998). The unidentified samples from Greenland and Labrador (Fig. 5B) plot among the genetically identified dogs and published dog bone collagen samples. Dogs from the central and south coasts of Labrador were historically provisioned with small species of seal (ringed, harp and harbor) which would result in high $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to local marine species (Harris et al., 2020). Two of the dog fur samples from Alaska (Fig. 5C) are consistent with published dog bone collagen data from coastal Alaska and the Aleutian Islands and suggest a mixed salmon-marine protein diet, while the third dog consumed food more consistent with a diet of marine mammals (Ameen et al., 2019; McManus-Fry et al., 2018; West and France, 2015). The two wolf fur samples had much lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relative to marine taxa and genetically identified dogs. The wolf fur samples (Fig. 5D) from Nunavut had isotopic compositions consistent with a diet of terrestrial protein, while the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the domestic dog were consistent with a marine protein-based diet (Coltrain et al., 2004). The unidentified fur sample from the MacKenzie Delta plotted among the wolf samples. These results suggest that the unidentified samples with isotopic values consistent with marine environments may be from domestic dogs, but similar isotopic values from polar bear fur (Table 3) ultimately undermine this assumption. However, future isotopic studies of canid bones from the Eastern Arctic may reasonably assume that diet can be used as a general indicator of behavioral domesticity.

The diets of the Kamchatka Krai (Fig. 5E) and Northern and Polar Ural (Fig. 5F) dogs were less indicative of dietary dependence. The dogs from Kamchatka Krai had isotopic compositions inconsistent with a diet dominated by salmon, which was unexpected given the abundant literature describing the salmon-rich diets of Kamchatkan sled dogs (Krasheninnikov and Crownhart-Vaughan, 1955; Strecker, 2018). Instead the results suggested a mixed diet of terrestrial with limited contributions from salmon (Satterfield and Finney, 2002). This could be attributed to seasonal variation in the types of foods fed to sled dogs, or the fur samples may have been taken from hunting dogs, who were reportedly fed with birds, rather than fish (Krasheninnikov and Crownhart-Vaughan, 1955; Strecker, 2018). The dogs from Nenets and Khanty communities in the Urals occupied a region of isotopic space between anadromous fish and reindeer which also suggests a mixed diet. The two unidentified samples (TRF-2-63 & TRF-2-67) potentially consumed freshwater fish which could be caught in the Ob River that passes through the traditional territories of the Nenets and Khanty, or other terrestrial game.

Some of the interactions that reinforce domestication and underpin human-dog relationships are revealed here through biomolecular analyses of ethnographic collections. In the North American Arctic, humans engaged in reciprocal relationships with dogs and other species (Hill, 2011); dog-human interactions were characterized by labor on behalf of both parties to procure marine mammals, fish, and caribou (Coltrain et al., 2004; McManus-Fry et al., 2018; West and France, 2015). The effort was well-spent as properly nourished sled dogs helped to maintain connections between communities in winter, and increased access to geographically dispersed resources (Taylor, 1974). In Siberia, herders provisioned dogs with reindeer and fish remains, and devoted significant energy to the actions involved in preparing dog food (Svoboda et al., 2011; Tuisku, 2001). The fish and reindeer soups prepared for dogs required not only the ingredients of the dish but also the collection of firewood and water (Tuisku, 2001). Dog provisioning was not an afterthought, but a critical component of daily life. While it is not possible to determine what proportion of food was acquired through direct feeding versus scavenging, the available isotopic data reveal a correspondence between human and dog diets (Coltrain et al.,

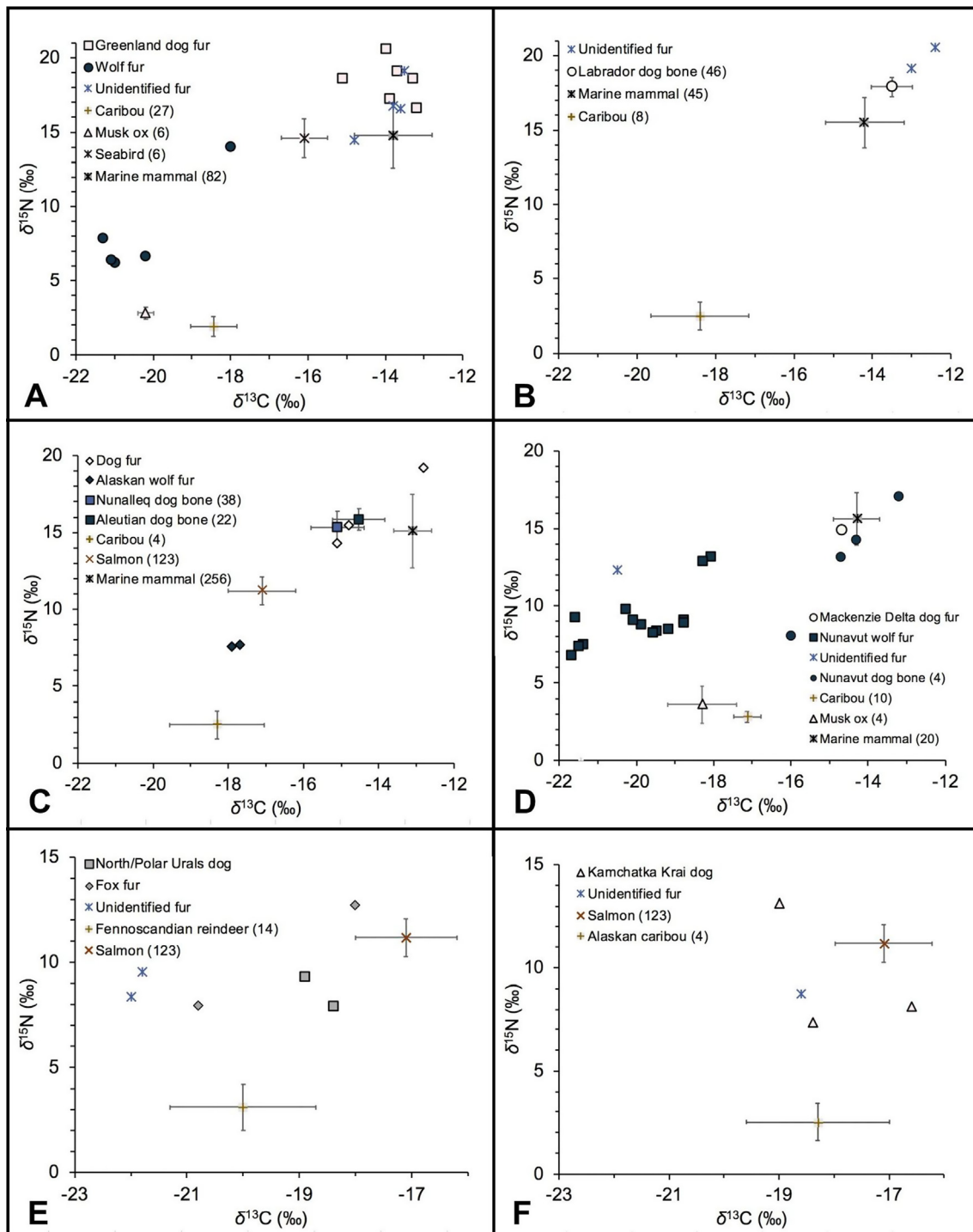


Fig. 5. Fur samples adjusted to bone collagen isotope values per geographical region: A) Greenland B) Labrador C) Alaska D) Nunavut E) Urals F) Kamchatka. Published comparative bone collagen data were taken from the following sources: Greenland - (Nelson et al., 2012b); Labrador - (Harris et al., 2020), modern Arctic char - (Guiry et al., 2016); Hudson Bay - (Coltrain et al., 2004); Alaska - (Britton et al., 2013; Clark et al., 2019; McManus-Fry et al., 2018; Szpak et al., 2017; West and France, 2015), Pacific salmon data - (Satterfield and Finney, 2002); Fennoscandian data - (Dury et al., 2018).

2004; McManus-Fry et al., 2018). As sled dogs consumed food, they were engaging in social relationships with their owners, with other dog team members, and with other animals (Whitridge, 2017).

A complex relationship with a dietary element also existed between humans and wolverines, but it was not characterized by reciprocity or cooperation as between dogs and people. Like humans, wolverines relied on the flesh of other animals for survival but unlike humans and other wild animals possessing inua, the wolverine violated the social contract by stealing food from meat caches and scavenging (Laugrand,

2017). The range of isotopic composition among the wolverine furs sampled in this study suggest that wolverines could have been encountered in a variety of locales, and through careful observation of these animals within their environment hunters could discern where best to place traplines. Despite the contempt fostered by the wolverine's assaults on carefully constructed meat caches, amulets made of wolverine teeth and claws were believed to imbue the wearer with strength (Laugrand, 2017), and wolverine pelts were prized among the Canadian Inuit for their warming and protective properties (Cotel et al., 2004;

Oakes, 1988). The mixed marine-terrestrial isotope signatures of two wolverines may have resulted from consumption of cached marine mammal meat or fish signifying the tenacity of this species, and its presence in arctic communities.

The aim of this research was to consider the social relationships of humans and dogs using biomolecular methods and there are two important limitations to the data that require consideration. The curated assemblage of clothing reflects the collection practices and interests of 19th and early 20th century ethnographers and anthropologists. Therefore, the frequency of garment components made from dog pelts may not be a reflection of the frequency with which dog pelts were actually used among arctic communities. Dogs were crucial for life in the Arctic, but their major contribution was labour, not furs. At the National Museum of Denmark, the items that include dog fur only constitute about 100 pieces of approximately 1650 garments in the collections (ranking fourth after seal, caribou, and polar bear). Secondly, while we found that species of some of the furs were misidentified by macroscopic examination, the study was not designed as an explicit test of macroscopic methods. Further research designed to examine the rate of error in macroscopic methods and the conditions under which error is more likely to occur may be warranted, but we cannot, at this point, quantify the failure rate associated with macroscopic identification of animal fur.

6. Conclusion

Many of the properties of animal skins allowed, in a very literal sense, the limitations of the human body to be transcended by co-opting some of the physical characteristics of dogs and wild species. Of the samples with sufficient data for genetic identification which had also been macroscopically identified as dogs, 34% were revealed to be sourced from other taxa, highlighting the limitations in identifying small pieces of fur in clothing macroscopically. The generally excellent preservation of DNA in these skin samples, some of which were collected in the late 19th century, attests to the potential of this DNA reservoir for the investigation of population genetics before globalisation. Stable isotope analysis of the furs allowed the exploration of short-term provisioning practices and revealed the diversity of dog diets across the Arctic region. Museum-curated ethnographic collections are a largely untapped resource as that can, using minimally invasive methods, form the basis for a range of ecological and cultural studies.

CRedit authorship contribution statement

Alison J.T. Harris: Investigation, Formal analysis, Visualization, Writing - original draft, Writing -review & editing. **Tatiana R. Feuerborn:** Investigation, Formal analysis, Visualization, Writing - original draft, Writing -review & editing. **Mikkel-Holger S. Sinding:** Investigation, Formal analysis, Supervision, Writing - original draft. **James Nottingham:** Investigation. **Robert Knudsen:** Formal analysis. **Alba Rey-Iglesia:** Supervision. **Anne Lisbeth Schmidt:** Resources, Writing - review & editing. **Martin Appelt:** Resources, Writing - review & editing. **Bjarne Grønnow:** Resources, Writing - review & editing. **Michelle Alexander:** Supervision, Funding acquisition, Resources, Writing - review & editing. **Gunilla Eriksson:** Supervision, Funding acquisition, Resources, Writing - review & editing. **Love Dalén:** Supervision, Resources, Funding acquisition, Writing - review & editing. **Anders J. Hansen:** Supervision, Resources, Funding acquisition, Methodology, Writing - review & editing. **Kerstin Lidén:** Supervision, Funding acquisition, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial

interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaa.2020.101200>.

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