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A comprehensive approach to wolf domestication

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## **Abstract**

In the past few decades studies on wolf domestication have been dominated by osteometric and DNA techniques, centred on establishing the time and place of dogs' appearance. This dissertation examines several methods used in the study of wolf domestication, including the above mentioned, and explores how ethnographic analogies contribute to our understanding of human-canid relationships in the past.

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## Abbreviations

aDNA	Ancient DNA
mtDNA	Mitochondrial DNA
13C	Ratio between 13C : 12C
15N	Ratio between 15N : 14N
Pm1-Pm2	Premolars

## Introduction

Humans have historically been very fond of their dogs (*Canis lupus familiaris*), to such an extent that they have been labeled man's best friend. Dogs have an extensive history with humans as they were the first animals to be domesticated (Clutton-Brock 2016:12), but they have not always been regarded in the same way. From hunter-gatherers' companions to becoming "family members" and producing a growing commodification of dogs (Power 2008:536), humans' relationship to dogs has sparked the interest of people, leading to significant investments and research into the topic.

Dogs' wild counterpart on the other hand, has suffered a different fate. Wolves (*Canis lupus lupus*) have been portrayed as voracious, deceitful, and greedy; they have been hunted and successfully eradicated from most of its territory (Marvin 2012:81). This tradition dates back as far as 812 AD when Charlemagne founded the Louveterie, an institution in charge of killing the wolves in the royal forests; this is the first known of systematic attempt to control wolves (Marvin 2012: 81).

These opposing views on such similar animals begs the question of how our relationship with wolves, and consequently dogs, started. There have been wolf bones in association with humans found that date to 400,000 years ago (Boxgrove, England), although there has been no physical evidence found for social interaction between the two species (Clutton-Brock 2016:8). So when did humans and wolves engage in meaningful interactions that lead to the process of domestication?

My interest in human/dog/wolf relationships evoked the following research questions:

1)How can we tell when the process of domestication was initiated?

2)Where did this happen?

3)How and why did it happen?

To this extent this dissertation looks at different methods used to identify dog remains, the problems involved in classifying dog remains, and how ethnohistoric data can offer an alternative model for early human-wolf/dog interactions. Particular attention is paid to late Pleistocene and Paleolithic remains of “early dogs”, as these are the most contentious findings.

## Chapter 1

### General information on wolf domestication

The definition of domestication, be it in reference to plants or animals, involves a two-way relationship between the target population and humans (Zeder 2012:227). It involves both cultural and biological components, constructing and crossing the boundaries between human and animal (Russell 2002:285). It is generally seen as a process, but people place emphasis on different sides of the partnership: some suggest humans as the dominant player, others see animals as the manipulators, and some see the process as a form of biological mutualism (Zeder 2012:228). It has been generally accepted that dogs evolved through the commensal pathway (**Figure 12**): a route which is generally initiated through an animal's own will (Zeder 2012:249). Part of this common belief is that wolves started scavenging around human settlements and refuse, and later have become assimilated into human societies (Clutton-Brock 2016:9). Provision of food resources has always played a central role in creating associations between humans and other species (Noske 1997:4), and whether wolves were feeding off humans scraps or humans were using wolves as a food source (as is explored in the later chapters), this seems to be the case with wolves' evolution into dog.

An animals' candidacy for domestication revolves around their behavioural characteristics, mostly their ability to reduce their "flight" response to external stimuli (Zeder 2012:232). Wolves are believed to be especially predisposed to living with humans due to their complex social groups and their high adaptability (Fogg et al. 2015:279).

It was not until later that the physiological changes seen, such as pedomorphism and general size reduction (Clutton-Brock 2016:11 ; Zeder 2012:236), appeared as a result of selective behavioural pressure (Zeder 2012:232).

## Chapter 2

### Literature review

Wolf domestication has been a much studied field but with no agreed conclusion as to where and when this process began (Pang et al. 2009). Within the field there are many contradictions and much of these arise due to researchers using different methods (Morey 2014:301) to interrogate data and evidence. In this chapter I look at several lines of evidence to advocate for a more holistic approach that includes different practices. As such this chapter reviews osteological and ancient DNA (aDNA) and DNA techniques, and variation in Pleistocene wolves.

A map of the most important specimen discussed in this section can be found in **(Figure 1)**

### *Osteometric studies*

A prototype and example of the morphological changes a canid undergoes during domestication can be seen in Belyaev's experiment on foxes. He created a program where silver foxes (*Vulpes vulpes*) were bred and selected for tameness and against aggression (Trut 1999:160). It was designed to observe how controlled breeding affected the foxes' phenotype; it tested the results of selective pressures and showed how animals' physiology changed. Belyaev believed that domestication selected for a behavioral instead of a quantitative trait; he considered genetic transformations of behavior to play a key role in triggering other genetic events (Trut 1999). This proved right; as the program progressed researchers noticed changes in the foxes'

neurochemical and neurohormonal mechanism, such as a steady drop in the hormone-producing activity of the animals' adrenal gland (Trut 1999: 166).

After forty years, 45,000 foxes and 30 to 35 generations, the study was left with a unique population of 100 foxes which have been described as "unmistakably domesticated" (Trut 1999:163). The changes started to become apparent from the 8th generation onwards. The first modifications were in alterations in the coat colour, mainly a loss of pigment, floppy ears and rolled tails. It was only after 15-20 generations that traits such as shorter tails and legs and overbites or underbites appeared (Trut 1999: 164). The changes also affected the skulls, in tendency they decreased in cranial height and width, and the snouts got wider and shorter. Overall the foxes' underwent considerable changes which were carried down to future generations. This experiment has the potential to act as a model of the changes that wolves experience during domestication.

The following three studies make use of von den Driesch's (1976) guide to canid skull measurements, a more traditional approach in identifying a canids' subspecies status.

Some of von den Driech's variables employed in the Germonpré et al.'s (2012) study are: total skull length, viscerocranium length, alveolar length of the tooth row, carnassial crown length, greatest braincase width, greatest palatal width, and minimal palatal width (**Figure 2**).

The researchers examined canids from Predmosti, spanning from 26,000 - 27,000BP, a site that held a minimum number of individuals of 22 canids, making them the second most abundant mammal.

Germonpré et al. (2012) results' indicated that three skulls had a greater affinity to Palaeolithic dogs, one to Pleistocene wolves, and three skulls had no clear affinity to anyone reference group indicating that they could have been hybrids or had closer affinity to a reference group not represented in this study (2012:194). All of the identified Gravettian Predmosti (Czech Republic) dogs conform to the typical skull morphology: shorter and broader snouts, wider palates, and wider braincases (2012:196). Although specifically shortened rostrums in Pleistocene wolves may have been the natural result of niche competition with Paleolithic human hunters (Crockford and Kuzmin 2012). Nonetheless, the Predmosti specimen had modified skeletal features that strongly suggested a close relationship with humans: large modified teeth, trauma on the skulls (**Figure 3**), and a "dog" with an artificially post-mortem placed bone in the mouth (**Figure 4**). The former is compared by Germonpre et al. to the practice of creating a hole in the skull in Alaskan wolves, bears, foxes and caribou to release the soul from the body in animism rituals (2012:199). Through nitrogen and carbon stable isotope analysis, it was shown that the humans on site did not consume reindeer as a significant part of their diet, whereas the canids did (Perri 2016:2). This suggests that human hunters were provisioning dogs with reindeer which they did not eat themselves. Perri argues that a more likely scenario would be the presence of multiple wolf ecomorphs in the region: one which functioned in a niche which included scavenging mammoth and taking larger prey like horses, and another which was migratory, targeting medium-sized migratory reindeer (2016:2).

Carbon and Nitrogen isotope studies can help elucidate the relationship between animals and humans found in the same site, as seen above in the Predmostí canids' case (Germonpré et al. 2012; Perri 2016). The case of the Lokomotive wolf and Shamanka (Siberia) dog is interesting because both canids were shown special treatment at death, attesting to their importance to humans, but analyses have shown

that they had different types of diets. The Shamanka dog was shown to have close  $^{13}\text{C}$  values to the humans in the same region ( $^{13}\text{C} = -16.1\%$ ) and  $^{15}\text{N}$  values also slightly lower than the humans inhabiting the Shamanka and Lokomotiv site ( $^{15}\text{N} = 13\%$ ) (Losey et al. 2011:185). The dog and humans' values differed from the terrestrial fauna indicating a large subsistence on aquatic resources (Losey et al. 2011:186). The Lokomotive wolf on the other hand had a completely different diet from both the Shamanka dog and the humans in both sites; the values ( $^{13}\text{C} = -20.2\%$  and  $^{15}\text{N} = 9.7\%$ ) suggest a diet based on terrestrial resources (Losey et al. 2011:186). This indicates that the dog was being fed by the humans whilst the wolf sourced its own food, conforming to behavioral characteristics and expectations of both subspecies. Dogs would have depended on their human companions to feed them or they would have scavenged their leftovers. Wolves on the other hand were (and are) better at hunting than dogs as they are better at cooperation which can lead to better hunting techniques such as the buffalo drives in North America (see Fogg et al. 2015).

Germonpre et al.'s (2016) later study analysed four canid skulls, dating from 50,000 years ago to 950 years ago, from the Sakha Republic in Siberia, the Razboinichya cave canid (34,200 BP) and the Shamanka dog (7400 BP). From the four Sakha canids, two were classified as dogs (**Figure 5**). In spite of Germonpré et al.'s decision, the skulls were found isolated and could not be related to any specific archaeological site (2016:2). The lack of archaeological context decreases the credibility of the researchers' identification of the Sakha canids as dogs.

Ovodov et al.'s study was different than the previous ones, as their analysis included only one canid which they sought to identify. On the one hand the Razboinichya cranium was nearly identical in size and shape to prehistoric Greenland dogs. On the other the carnassial teeth fell with the size range of modern wolves. Thus they

concluded that the Razboinichya canid represented an “incipient” dog in the early stages of domestication whose lineage did not survive the Last Glacial Maximum (2011:3). As to their material context, there was no direct evidence or artefacts to indicate human use or occupation of the cave where the canid was found, although some small charcoal pieces and burnt bones indicate the possibility of ancient humans visiting the cave occasionally (2011:2). However, there is no direct link to humans and identifying domesticated animals from contexts where they are not clearly linked to human occupation and associated archaeological material is difficult, if not impossible (Boudadi-Maligne & Escarguel 2014:80).

In order to achieve a more objective and unbiased comparison of morphometric canine remains, it is important to include an appropriate type and number of specimen reference groups tailored to each study. Germonpre et al.’s (2012) study compared canid cranium variables to the following reference groups: Pleistocene wolf, recent Eurasian wolf, Palaeolithic dog, prehistoric dog, recent archaic dog, and the recent other dog (2012:187). However, in their later study, Germonpré et al. (2016) used similar reference groups with the addition of two other groups which were more specific to the area where the canid remains they were investigating were found: recent northern dogs and recent northern wolves. Despite the more appropriate geographical samples, they excluded any recent archaic or prehistoric dog groups (Germonpre et al. 2016:6), taking their specimen out of their historical context and therefore making the comparisons inadequate. Ovodov et al.’s (2011) use of reference groups differed in that contrary to Germonpre et al.’s studies (2012; 2016) they had no modern dog groups. Their study used Pleistocene wolves from Predmosti (Czech Republic), modern wolves from Europe and North America, and prehistoric Greenland dogs from the Thule period (Ovodov et al. 2011:2-3). It is worth noting that even though the Predmosti canids are considered dogs by some (Benecke 1994; Germonpré et al.

2012), they are also highly contested by the conventional domestication dates 12,000 to 15,000 years ago (Morey 2014:300). Benecke (1994) (in Germonpre et al. 2012) identified the Predmosti dogs based on a high indice of polydonty on the lower jaws in comparison to that of wild wolf populations. Nonetheless, tooth crowding and polydonty have been criticised as a technique to classify specimen (Ameen et al. 2017) as it has been observed in similar amounts in domestic and wild populations, rendering the Predmosti an unsuitable reference group in Ovodov et al.'s (2011) study.

Even though there was no archaeological context in the two studies (Germonpre et al. 2012; Ovodov et al. 2011), the authors still deemed it tenable to classify the specimen as dogs. In the unlikely case that they were dogs, it implies that there was a detached or non-existent bond between early dogs and humans, which is highly unlikely and contradictory to the necessary condition (a relationship) to domestication. Humans would have invested significant time and resources on these animals and so some sort of relationship should theoretically be evident in the archaeological record. An absence of material association to humans indicates the lacking and essential relationship to humans that defined dogs.

Some studies have made use of other cranial measurements instead of von den Driech's; both Pitulko and Kasparov (2017) and Sablin and Khlopachev 2002 use alternative cranial measurements in their research. Scientists (Pitulko & Kasparov 2017) criticized the use of Von Den Driech's (1976) measurement scheme as in possible domestication scenarios it is easy to make a mistake, since a large dog could easily be classified as a wolf, based on its size (and vice versa, a small wolf can be identified as a dog). The width measurement variability, observed in any sample (especially an excavated one), is not useful in species identification, since no data regarding the sex/age of the animals exists. Because Ice Age dogs were the same size

as wolves (Sablin & Khlopachev 2002:795), smaller size cannot be used as evidence of domestication. Furthermore, at the end of the last glacial maximum (12,000 years ago) wild canids got smaller as a reduction in size was advantageous (Coppinger & Coppinger 2001:296).

This would mean that if canine remains from the Gravettian sites in Moravia were investigated as possibly belonging to dogs, (Germonpré et al., 2012), they would have to be compared with a reliable sample of wolves which inhabited Moravia 25,000–22,000 years ago, preferably taking into account sexual dimorphism, as it inevitably influences measurements (Pitulko & Kasparov 2017:494).

Pitulko and Kasparov determined through mtDNA analysis that the two Zhokhovo crania belonged to dog haplogroup A, which is widely spread throughout northern Eurasia (2017:493). They endeavored to clarify the nature of the Zhokhov dog crania, which they compared to the recent wolf crania from the coastal region of Siberian Arctic closest to the Zhokhov Island (2017:493). Proportional measurement used were the ratio of skull height in the cranial region to total skull length and the ratio of snout height at Pm1-Pm2 (**Figure 6**) to total skull length (2017:494). They used 24 wolf crania with mandibles and 32 crania (also with mandibles) of northern huskies from the native people of northern East Siberia. To avoid the contamination of cross-breeding that occurred in the post-word period they utilized skeletal material obtained by expeditions no later than the 19th century (2017:493).

The project analysed two canid crania from Bryansk Region, Russia, which were dated to 13,000–17,000 BP (Sablin & Khlopachev 2002:795) The ratio of greatest palatal breadth to condylobasal length of both these finds was compared with that for recent wolves from northern Europe, southern Europe, the Caucasus, Central Asia, the Middle

East and northern India , China, southern Siberia, northern Siberia, the Far East, and North America and that for Siberian huskies and Great Danes (Sablin & Khlopachev 2002:797). Although an extensive number of reference groups for extant wolves is given, there is a notable absence of ancient wolves and dogs. The results showed the Ice Age dogs from Eliseevichi differed from all recent wolves and had significantly shorter muzzles (shown in **Figure 7**) than Siberian huskies and Great Danes. Due to their morphology and the large number of mammoth bones found among the food debris at the site (2002:795), Sablin and Khlopachev determined the dogs to be a specific species, designed and bred in response to the needs of communal hunting. Dogs would have also served as a food source, a potential explanation for the hole on the side of the skull MAE 447/5298 (**Figure 7**) from Eliseevichi 1 site, as the brain could have been removed (2002:798). Nevertheless, the hole on the skull could also be interpreted as a ritualistic activity as seen has been suggested by Germonpré et al. (2012).

Another method which has been used to support the existence of “proto-domestic” dogs is tooth crowding. As there have been no previous definitions of tooth crowding, Ameen et al. proposed a standardised landmark-based protocol to measure and quantify tooth crowding, to be implemented in the context of dog domestication research (2017:41). They examined 750 modern dogs, 205 modern wolves, and 66 Late Pleistocene wolves from Alaska to test the hypothesis that mandibular tooth crowding is less frequent in ancient and modern wild wolf populations (2017:42). The Spacing Ratio between the 14 landmarks examined showed that 6.13% of dogs exhibit tooth crowding whilst Pleistocene and modern wolves exhibit 36.6% and 18.04% respectively (Ameen et al. 2017:46). Based on this and the fact that tooth crowding has been observed in dogs and wild and captive wolf populations, Ameen et al. advised that tooth crowding cannot be the only criteria used to determine whether a species is

wild or not (2017:47). To make sure that other factors did not influence the outcome, only adult specimen were used and sexual dimorphism was accounted for by use of a double ANOVA, which showed that it did not affect tooth crowding (2017:47). Nonetheless, the study recommends the use of cumulative tooththrow length for measuring tooth crowding in dogs and wolves and the Spacing Ratio value of 1.0 as a threshold for overall tooth crowding (2017:48). An additional limitation in the use of tooth crowding is the paucity of knowledge on the natural variation of crowding in Pleistocene wolves. This could be solved through a bigger compilation of data. A potential solution to this could be the use a new approach by Evin et al. which allows for a low-cost and portable reconstruction of 3D wolf crania (2016:89). They reconstructed models of five wolf crania using a high-resolution surface scanner and photogrammetry and compared them in terms of texture, colouration, topology, and geometry (2016:87). The photogrammetry approach consists of photographs, in this case 216 per cranium, taken from different angles to reconstruct the crania (2016:89). This method can help expand the number of reference specimen for future studies, especially for Pleistocene wolves which have been neglected despite their immense potential in resolving domestication disputes.

### *DNA and ancient DNA analyses*

The following studies use mitochondrial DNA (mtDNA) analysis though they differ in the type of specimen they sample, using only extant canids. Both Vila et al. (1997) and Savolainen et al. (2002) use mtDNA from dogs and wolves in Europe, Asia, and North America, although Savolainen also uses canids from Africa and has a larger number of samples (654 canids) compared to Vilà et al. (302 canids). The two studies created neighbour-joining phylogenetic trees. Vilà et al. found that dog haplotypes could not be separated into breeds and that wolves had haplotypes specific to their region

(1997:1687-1688). It is not surprising that wolves nowadays have haplotypes specific to their local region as they have a long history of persecution, with their habitat and population numbers having decreased dramatically over the years. In Vilà et al.'s tree clade 1's divergence implies an older origin of dogs than 14,000 years BP as suggested by the archaeological record (1997: 1689); they speculate from the sequence divergence between the most different genotypes in clade 1 that dogs could have appeared as early as 130,000 years ago (1689). On the other hand Savolainen et al.'s results indicate a single gene pool for all dog populations (2002:1610) and East Asia as the point of origin as this is where most of the genetic variation was. They calculate the time of origin for their dog clades by estimating the mean genetic distance in each clade to the original wolf haplotype, and the mutation rate (2002:1612). However they do not specify which the original wolf haplotype is and if by original they mean the ancestor of dogs, which is still unknown. Their sequence data suggest two possible timings for dogs: a) 40,000 years ago from clade A or b) 15,000 years ago involving clades A,B, and C (2002:1613). Savolainen et al. decide that 15,000 years ago is more likely to be the original date of domestication due to "circumstantial evidence" (2002:1613) and ascribe the absence of archaeological evidence for their proposed date and place to the lack of archaeological excavations in the area.

Both of the studies acknowledge the possibility of multiple independent domestication events, Vilà et al. take it as a given due to the large and shared geographic areas that canids inhabited during the Palaeolithic and the possible and continuing genetic exchange between dogs and wolves (1997:1687). Contrary to them, Savolainen et al. only acknowledge this as possible if they establish the origin of dogs from clade A 40,000 years ago (2002:1613).

Pang et al. (2009) conducted their DNA study in order to find out which human culture achieved wolf "taming" (2009:2850) and where and by which mechanism domestication took place. They analyzed the control region for 1,543 dogs and the complete mitochondrial genomes for 169 dogs across the Old World to gain high phylogenetic resolution and geographical diversity (Pang et al. 2009:2862).

Pang et al. (2009) contradict each other in their study; they criticised earlier mtDNA studies (Vilà et al. 1997; Savolainen et al. 2002) which failed to establish the time and origin of dog domestication and attribute this to the number of base pairs studied in the control region (582 bp or less) which do not provide enough phylogenetic accuracy (2009:2850). However, they themselves use 582 base pairs in their study (2009) which alleged that their results provided evidence for a single event of dog domestication in the area of Asia south of the Yangtze River less than 16,300 years ago. Pang et al. (2009) also estimated that at least 51 female wolf founders were involved (2009:2859). They relate the time of domestication with the start of rice agriculture (Pang et al. 2009), implying that a more sedentary way of life would have made domestication easier and that "wolf taming was an important cultural trait" (2009:2849). Additionally they put forth the idea that dogs might have been domesticated for its use as a source of food as dogs have been eaten in this part of the world on a large scale from ancient time until today (2009: 2863). This idea does not support the hypothesis that dogs were domesticated in that area, not only does it imply that domestication was an intended and directed process by humans, but it would suggest that the use of dogs as a primary food source would follow the expansion of dogs themselves. Other societies have also been observed to use dog meat, particularly North America indigenous people (Fogg et al.)

Pang et al.'s study is based solely on extant populations of canids which proves problematic; some researchers such as Larson (2012) believe that early dogs' genetic signal might have been lost due to modern dog population's genetic admixture. The archaeological evidence for the presence of dogs or wolves around their suggested time (5,400–16,300 years ago) is vastly overlooked.

Germonpré et al. (2009) also use mtDNA in their studies, in which 57 base pairs in the mitochondrial control region are amplified from seven Belgian canids from the Goyet cave and Trou des Nutons (2009:477). In comparison to other DNA studies (Larson 2012) this seems like a low number, but Germonpré et al. justify the use of this region as it holds "the majority of informative nucleotide positions in the mitochondrial control region of wolves and dogs" (2009:477). The sequences from the ancient canids are then compared to those from extant dogs and wolves, available from GenBank (2009:480), leaving a lack of ancient wolf specimen. If Germonpré et al.'s (2009) aim in this study was to look at the relationship between the Belgian canids and modern day dogs then the genome sequences of ancient wolves would have been superfluous. However, if their aim was to determine the subspecies status of those canids, a reference to Palaeolithic wolves and dogs should have been included. I argue for an inclusion of older specimen as due to recent bottlenecks such as both world wars, genetic signatures have been obscured and any relation to pre-world war canids would not be detected by the comparison to the GenBank samples. Germonpré et al. come to the conclusion that because the sample's sequences are not found to be identical to the extensively genotype dog breeds, the Belgian canids are presumed wolves, although at the same time cautioning that mtDNA alone cannot determine a canids' status (2009:480). The use of dog breeds is not indicative of an ancient genetic composure as shown by Larson (2012), rendering the fact that the Belgian canids' sequence did not match the dogs' breeds irrelevant.

The use of the neighbor-joining tree (**Figure 8**) showed that five of the Belgian canids fell together with modern wolf sequences from Europe but also displayed haplotypes not described up to date, conducive to their conclusion that the large Belgian canids carried a large amount of genetic diversity and, as Thalmann et al. (2013) suggested, that these canids represented an extinct wolf lineage or a previously unknown extant wolf (2009:485).

This DNA study differs from the others already examined as it uses autosomal SNPs instead of mtDNA to analysis 137 dogs and 19 wolves. In total 49,024 autosomal SNPs (Larson et al. 2012: 8878) are analysed which is a considerable coverage in comparison to other genetic investigations. The aim of this study was to combine their data with that from previous studies to compare the genetic signature of 121 breeds with a worldwide archaeological assessment of the earliest dog remains (Larson et al. 2012:8878). Result showed that none of the “ancient” breeds derived from the areas where the earliest remains were found and that three of the “ancient” breeds (dingoes, basenjis, and New Guinea singing dogs) originate from regions outside the natural range of *Canis lupus* and where dogs were introduced 10,000 years after the conventional date (12,000-16,000 years ago) of domestication (Larson et al. 2012:8878). The analyses indicated that ancient breeds were only genetically distinct because the dog populations had been recently isolated from breeding with other dogs (2012:8878). Larson et al. deduce that bottlenecks throughout history where global dog populations have undergone episodes of diversification and homogenization, and with each successive event the power of genetic data from modern breeds to infer the history of dog population diminishes (Larson et al. 2012:8881). Even if studies were to sequence more than 10,000 SNPs they would only be recovering signatures that have resulted from a convoluted evolution in the 19<sup>th</sup> and 20<sup>th</sup> century (Larson et al. 2012:8882). Their starting hypothesis does not have a solid foundation, even if

“ancient” breeds could have been refined to a certain geographic location, early dogs would have migrated and potentially travelled long distances with human hunter gatherers. As this study has shown, autosomal SNPs methods are not preferable over mtDNA ones, especially when the study does not include any ancient canid remains. The results from Larson et al.’s study (2012) have made it clear that analysis of dog breeds and modern dogs post world wars are futile in elucidating dog origins as the genetic signaling is tampered and too intermixed.

Thalmann et al. (2013) studied the recovered genomes of 18 prehistoric canids and compared them to the sequences of 49 contemporaneous wolves and 77 dogs (2013:872). Due to the fragile nature of aDNA, mitochondrial genomes with less than 50% of length recovered were excluded (2013:872), as decayed DNA can be misleading and cause erroneous interpretation. With the use of their data the researchers created a well resolved phylogeny (**Figure 9**), forming four well defined dog clades, and even though the dogs and wolves were not reciprocally monophyletic all the modern dogs and most of the wolves fall into one of the clades (2013:872). To construct the phylogenetic tree Thalmann et al. used maximum likelihood, coalescence-based approaches, and Bayesian methods (2013:873). The most divergent specimen are three Belgian canids ranging from 36,000 to 26,000 years old, including the Goyet canid; these specimen’s haplotype have placed them as an ancient sister group to modern dogs and wolves instead of as a direct ancestor (Thalmann et al. 2013:872). The researchers have argued based on this phylogeny that the three Belgian canids could represent an aborted domestication episode or a phenotypically distinct but previously unrecognized Grey wolf population (Thalmann et al 2013:872). Furthermore, three of the dog clades (A,C, and D), which make up for 78% of dogs in the study, are sister to one or more ancient canids in Europe (2013:872). The three Belgian canids and the rest of the ancient canids in Europe are sister groups to modern

dogs, meaning that they shared a common ancestor but were not direct ancestors to today's dog population. This shows that even though the canids were identified as ancient dogs in the investigation, they did not contribute to modern dogs' genetic make up, implying there were several "aborted" domestic dog populations which did not survive until the present-day. Even though some researchers are cautious with older canid remains, there have not been any explicit explanations as to why the conditions in the earlier Palaeolithic would not have been conducive to some wolf populations' domestication as opposed to later conditions. Some have argued (Pang et al.2009; Ovodov et al. 2011) that the conditions in more sedentary hunter-gatherer societies would have been advantageous to the domestication of wolves but they have not provided further reasons as to why a sedentary life would afford a higher chance of taming or domesticating wolves. If using a domestication model based on the scavenging-for-food theory then it would not have mattered whether hunter-gatherers were highly mobile or not, as wolves are known to move long distances in search of mates, migratory prey, and territory (Perri 2016:2) and could have also tracked human movement.

Thalmann et al. also included pre-Columbian New World dogs in their study to test the hypothesis that dogs were domesticated before 13,000 years ago, which they did by through the calculation of the most recent common ancestor between dog clade A and ancient New World sequences (2013:872). This provided an estimate of 18,000 years ago, supporting the idea of shared ancestry and the theory that the first dogs arrived with the first humans to the New World (Leonard et al. 2002). Consequently Thalmann et al. conclude that dogs were first domesticated between 18,800 and 32,100 years ago in Europe (2013:873). Additionally, Thalmann et al. did not include any Middle Eastern or Chinese canids, which is interesting considering that the previous studies (Savolainen et al. 2002; Pang et al. 2009) examined in this paper have placed the

domestication of wolves in these regions. Indeed, the addition of specimen from the Middle East or China might have helped further disprove or prove the idea of dog origins in those areas (Pang et al. 2009; Savolainen et al. 2002), and therefore lend more credibility to Thalmann et al.'s (2013) discovery. Even though the study has an impressive and extensive number of canids, its phylogeny is based only on mitochondrial DNA, which means that even though the tree is well supported, it only represents part of the story of domestication as information from the Y-chromosome, and therefore the male lineage, is missing.

Genetic studies have led some researchers (Thalmann et al. 2013; Savolainen et al. 2002; Vila et al. 1997) to think that there were several domestication events as it has been shown that conditions conducive to this evolution were not specific to a place or time. This can be seen through sister groups in phylogenetic trees (Germonpré et al. 2009) that show aborted domestication events or dogs that did not survive or pass down their genetic inheritance. It would also explain why so many studies have come up with different domestication origins. Nonetheless the studies which have put forth the idea of multiple domestication events (Thalmann et al. 2013; Savolainen et al. 2002; Vila et al. 1997) have also had some flaws in their methodology, questioning the validity of their conclusions.

It is also possible that the population of grey wolf that gave way to domestic dogs is extinct (Gopalakrishnan et al. 2017; Larson 2011). Larson theorized that early domestic dogs must have shared 100% of the same mitochondrial haplotypes with their ancestors but despite this, the number of shared between wolves and modern dogs is virtually 0% (2011:5488). As an explanation he proposed that the wild population that gave way to domestic dogs is extinct and the sampled wolves in genetic studies were not involved in the domestication process (2011:5488). Gopalakrishnan et al. also

believe that there was a full or partial extinction of the original wild lineages, which resulted in a loss of genetic diversity (2017:2).

Even though there have been some useful discoveries made through aDNA and DNA analyses, there seems to be several contradictions regarding the time and place of the first dogs, this means that researchers must be interrogating the data wrong by either using different techniques, such as the genetic loci used, or by sampling the wrong or insufficient specimen.

### ***Pleistocene wolf variation***

Wolf variation in the Pleistocene has been grossly overlooked in relation to dog origins and poorly incorporated into discussions of dog domestication (Perri 2016:1). Even so, it is of fundamental importance, especially during early stages of domestication when there appeared to be limited differences between wolves and dogs (Boudadi-Maligne & Escarguel 2014:87). However, due to the heavily fragmented nature of most known fossil canids, the creation of a robust database of biometric data is precluded (Boudadi-Maligne 2010).

This deficiency means morphological variations being used to identify putative Paleolithic dogs may actually be identifying natural variation in local wolves. (Perri 2016:1).

To prove the plasticity of wolves, Boudadi-Maligne and Escarguel (2014) sought to record the geographic variability among a total of 571 modern European wild wolves. They carried out their study by examining osteological data from wild wolves originating from Italy, Portugal and Bulgaria (Boudadi-Maligne, 2010), combined with

craniometrical characteristics of wild wolves from , Russia, Poland, Finland and Sweden (2014:81) Researchers focused on eight specific cranial measurements to investigate inter-population variability (**Figure 10**) (2014:81). As expected, the study highlighted the polymorphic character of *C. lupus* (2014:88). On top of this, there has been a continuous decline in wolf populations since ca. 20,000 years ago, leaving modern populations much less varied than before the last glacial maximum (Perri 2016:2); further emphasizing *Canis lupus*' diversity. In view of their results, Boudadi-Maligne and Escarguel no longer deemed tenable to consider the canids from Goyet, Predmostí and Razboinichya Cave as early examples of domestic dogs (2014:88). Perri also challenged the identification of domesticated dogs before 16,000 years ago as the material evidence cannot be resolutely accepted or rejected (2016:3). Perri (2016) put forward more problems in the current use of Pleistocene wolf data such as a bias towards incorporating large northern specimens in analyses, regardless of temporal or geographic parallels (2016:2). She also highlighted in her article that modern wolves are not from the same lineage as domesticated dogs (Perri 2016:2), causing potential issues when used as a reference and comparative model in studies. Some suggested ecological factors influencing cranio-dental plasticity are prey specialization, predatory competition, habitat type and climate (Perri 2016:2).

To see how ecological factors affect wolf variation, we turn to O'keefe et al., whom endeavored to quantify the variation in wolf skulls across North America and their correlation to climate, precipitation, taxonomy, and sex (2013:1224). The study used cranial morphometric data, such as the greatest length of cranium and zygomatic breadth, from 312 grey wolves from a historical study (2013:1225). O'keefe et al. also appended high-resolution climate data by referencing each location (2013:1224), so the study worked on the assumption that the wolves lived within the general area from where their remains were found (2013:1227). However, wolves are known to migrate and so even if a specimen is found in one place it is not guaranteed that it lived most of

its life in that environment. Wolves are highly mobile in search of mates, territory, or tracking migratory prey; it is not abnormal for dispersal distances to be of several hundred kilometers and movements over 1000 km have been recorded (Perri 2016:2). Despite this there have been some clear correlations in the study. Wolves in the wettest areas have shown larger frontal bones and longer and wider teeth which can be related to larger prey procurement (O'keefe et al. 2013:1234). Sexual dimorphism was also appreciable but males and females overlapped widely and so it cannot be the origin of skull variation (2013:1235). Lastly but most importantly, the choice of prey was found to have the most influence on morphology (O'keefe et al. 2013:1235).

## Chapter 3

### **Ethnographic analogies in the context of wolf domestication**

This chapter makes use of ethnography and ethnohistoric accounts in an effort to inform the possible type of relationship that humans had to early domesticated dogs. Through the particular lens of North American indigenous people I offer an alternative take on wolf/human interactions and a critical review of the problems with identifying potential “protodogs” and recently domesticated dogs.

Indigenous American peoples have had strong bonds with both wolves and dogs since before pre-Columbian times. This is evident in the large amount of dogs present in these peoples' daily life. Ethnographic accounts estimated that per Sheep Eater group (of approximately 20 humans) 30 dogs were kept as companions (Russell 1914 in Fogg et al. 2015:276), Cheyenne owned large groups of dogs (Fogg et al. 2015:267) and Pawnee people housed seven dogs per tent and roughly 4000 per encampment (Bozell 1988:96). Most of the relationships between American Indigenous hunter - gatherers and their dog and wolf companions seem to have been based on mutual cooperation (Fogg et al. 2015:263) and a peaceful symbiosis, where both species benefited from the partnership. From Western perspectives it is hard to grasp the concept of a positive association with wolves since there has been a long history of prosecution in Europe (Marvin 2012). However, due to their different way of life, ecology and other factors, indigenous people such as the Blackfeet consider wolves as friends to humans and do not believe in hunting them (Fogg et al. 2015:269), unlike Europeans who have targeted wolves since early history (as seen earlier with the Charlemagne example) (Marvin 2012). Like the Blackfeet, many indigenous peoples identified themselves with wolves and engaged with them as equals and in a reciprocal manner (Fogg et al. 2015). This type of relationship is likelier to allow for domestication

events to occur; even though Western mentalities are wary of wolves, a similar type of indigenous relationship and engagement with wolves must have been necessary for domestication to take place.

The Lakota or Sioux people and the Blackfeet people believed wolves to be instructors on hunting practices, social structure and behavior (Hernandez 2014), passed on through generations in the form of myths and stories, such as the Blackfeet ancient story "Wolf Man". Wolves and humans have very similar family or pack structures which is probably where the myth on social structure instructions come from, and why wolves were particularly prone to domestication. Wolves too live in socially complex groups with a specific pack hierarchy albeit a strong cooperation tendency, making it easier for them to be integrated into the human society. A wolf's pack usually consists of several generations of offspring and pair bonding is central and the base of the group (Fogg et al. 2015:273).

The Tsitsista (Cheyenne) tradition held that their people were taught to hunt by two wolves, a male and a female which were master hunters of the grasslands and, along with their fellow wolves, protector of all animals (Fogg et al. 2015:267). The male wolf, Maiyun, decided to teach the newcomers (humans) how to hunt. Blackfeet people believed this too as they duplicated wolves' buffalo drives down to the smallest detail (Hernandez 2013). Schleiser (1987) gave an account of how winter buffalo hunts took place on foot and how Indigenous peoples used their dogs to aid them. Both humans and dogs would surround a herd of buffalos and drive them into deep drifts, the dogs were in charge of redirecting any stray buffalos back into the drifts.

### *Canids as beasts of burden*

After hunting or in some other situation, such as moving camps, dogs would be used as beasts of burden. During hunting practice, once the Buffalo was killed it would be skinned and packed so that dogs could drag the bundles of meat over the ice and back to the camp (Fogg et al. 2015:268). Researchers have described Pawnee dogs wearing “dog sacks”, saddle-like bags, to carry the supplies of the likes of tent poles, meat, firewood, and other supplies in long distance hunts (Bozell 1988:97). Other indigenous tribes that used canids to carry burdens were the Cheyenne people and the Sheep Eaters (Fogg et al. 2015). The latter people owned and bred dogs that were stronger in the shoulders than normal dogs as these were expected to haul travois loads of 70 pounds and carr packs weighing up to 50 pounds (Loendorf & Stone 2006).

### *Dogs as a source of food*

An alternative use of indigenous dogs when there was a shortage and scarcity of food was the use of their canine companions as a food source (Bozell 1988: 95; Sablin & Khlopachev 2002:796); during such times dogs would also be a drain on resources as they would depend on humans to feed them. It has been suggested that this practice also took place in the gravettian site of Predmosti (Czech Republic), although it has not been specified whether the canids being consumed were wild or domesticated (Germonpre et al. 2017). Bozell (1988:105) suggests that indigenous American dogs' meat would have been relatively nutritious as it seems these dogs integrated maize and grasses into their diet, meaning their flesh contained more calories, potassium, calcium and other minerals. However, this is a generalisation as dogs would have had different feeding habits depending on their ecological resources; some may have had

more access to meat or aquatic resources depending on their location. Nevertheless it is true that dogs might have had a similar diet to their human keepers, and therefore more balanced, as is shown in the Shamanka dog case (Siberia) who largely subsisted on aquatic resources (Losey et al. 2010). The Pawnee people have been recorded to use dog meat in medicinal purposes and ceremonial events such as feasting (recorded during the 19th century by Irving and Carleton in Bozell 1988:97).

### *Dogs as hunting aids*

Early domestic dogs must have been trained and taught how to hunt with and by their human companions which would have required a considerable amount of time and energy. Nevertheless, it is not always beneficial to use dogs as hunting aids; the advantages conferred by domestic canids are dependent on circumstances (Lupo 2017:140), although there is limited data to show when and how humans benefit from them. Dogs do have the potential to reduce search costs and increase in prey encounter rates by flushing prey although they are not necessarily always deployed in hunts (Lupo 2017:145). The Xo hunters in Botswana pursue 29 different species but only use dogs when hunting six of them (Wilmsen & Durham 1988). When dogs are introduced into hunting communities, such as the Mayanga, there is a consequential effect of imbalance on the both of the species' diets, as dogs tend to focus more on smaller prey (Lupo 2017:145). Following this, dogs are most effective when used as a trained pack, especially in pursuit of large, mobile and high value prey (Lupo 2017:146) which correlates with the past ecological circumstances of North America indigenous people who used to pursue prey such as bison (Fogg et al. 2015).

## *Selective breeding*

Breeding dogs would require a lot of effort for earlier prehistoric humans, it would entail culling the smallest and weakest puppies from the litters and only allowing the most desirable dogs to reproduce (as seen in Pawnee culture) (Bozell 1988:105). Isolated reproduction would have supposed a very big challenge in such mobile societies where there would not be enough physical barriers to stop wolves and dogs from mating. So even if hunter-gatherers in prehistory would have preferred large dogs capable of keeping up with their hunting activities, they probably would not have prioritised or maybe even thought about selectively breeding their canid companions based on morphological features. Nonetheless, Sablin and Khoplachev (2002) contradict this view as they propose that there was hybridization and deliberate selection for strong dogs in the Ice Age (2002:796) Nonetheless most “early dogs” would have retained wolf-like characteristics for several thousand years until more marked physical characteristics, such as skull neotenization, appeared. It is sensible to say that the first hunter-gatherers were probably not breeding their dogs and that it would have taken some time before humans and dogs could efficiently hunt together. This begs the question of whether dogs were domesticated for particular economic functions or whether hunting came secondarily as a side effect of domestication, challenging the conventional view that “protodogs” and early domesticated canids primarily served utilitarian functions such as means of transportation for gear or food and as hunting partners (Lupo 2017:139)

.

This brings us to the issue of introgression which is appreciable through modern examples in indigenous North American dogs and a recent breed developed in Europe. In North America Sheep Eaters used to make their dogs available to mate with wolves as they sought big and strong offspring (Fogg et al. 2015:274). In this example

interbreeding was desirable and even encouraged but it is not unlikely that this happened naturally without any human intervention. This type of mixing was not uncommon and probably continued after post-Columbus domestic dogs were introduced. Wolves in America with black fur coats have a melanistic K locus mutation which is first seen in domestic dogs (Anderson et al. 2009), proving that interbreeding and introgression occurred.

On the other hand, in Europe introgression occurred in a very directed and planned manner. In 1955 the Czechoslovakian army conducted an experiment in which they aimed to create a wolfdog lineage to use in the Cold War (Smetanová et al. 2015:2). To this purpose they mixed German Shepards (*Canis lupus familiaris*) with Carpathian wolves (*Canis lupus lupus*), looking for the offspring to retain the wolf's phenotype but dog-like behavior so that they could be used as working dogs to guard mountainous borders (Smetanová et al. 2015:2).

Through the similarity between the "recently domesticated" (Fogg et al. 2015) indigenous American dogs and their wild counterparts, we can observe the verisimilitude that was, as logic dictates, present in the early stages of domestication in the Palaeolithic.

In 1836 John Richardson (cited in Loendorf & Stone 2006) proclaimed that the dogs and wolves from the "fur countries" were so alike that even in short distances it was hard to distinguish them, he also described the offspring of the Indian dog and wolf as being stronger than an ordinary dog. Later on, in 1851 whilst travelling in Yellowstone, Frederick Kurz also noted dogs' astonishing resemblance to wolves in their overall physiognomy and lack of barking: "(dogs) howl like them, do not bark, and not infrequently mate with them" (cited in Loendorf & Stone 2006). Fogg et al. (2015:276)

suggested the possibility that as the dogs only differed in size to the wolves, they “may simply represent one aspect of naturally occurring variation”. Attached (**Figure 11**) is the image of a wolf and dog skull found in Yellowstone and a skull of a fully domesticated dog for reference. The image illustrates the resemblance between Indigenous American peoples’ dogs and wolves. Further examination of the skeletons found in Yellowstone Park have established that these dogs ranged in height between coyotes and wolves, had a robust frame and a large head comparable to that of wolves (Fogg et al. 2015:276). The closeness between these dogs and wolves highlights the problematic nature of identifying early dog remains and re-ignites the debate of what constitutes a dog.

In American Indigenous’ stories the wolf is always fed in return when it performs its service, for instance guiding and providing for people, yet some “Western” scholars contend that the first wolves associated with humans had to scavenge or hang around camps waiting for scraps (e.g., Coppinger and Coppinger 2001). In contrast, according to stories told by Indigenous Americans, humans voluntarily fed or shared food with the wolves with which they associated. Such traditions go back millennia to a time closer to the initiation of friendly relationships between humans and wolves. These stories represent and offer an alternative model of the first stages of domestication in comparison to those put forth by scholars like the Coppingers, who are limited by assumptions of fear and dominance-based relationships between humans and nonhumans (Fogg et al. 2015: 272).

## Chapter 4

### Discussion

I advocate for a holistic approach when researching dog domestication, as such all available lines of evidence and methods should be used when identify dog remains. One method on its own is not enough to securely identify remains, unless the remains are relatively recent and DNA analysis can identify dog haplotypes. Yet in the majority of cases the most important or relevant evidence is the archaeological context and the osteometry methods, especially in the context of early finds (i.e. older than 16,000 years). Each approach contributes in a different way towards a more wholesome understanding of human-canid relationships, and therefore domestication.

Belyaev's experiment (Trut 1999) has provided a list of morphological and physiological changes that occur in canids when they are selected for their tameness. Wolves are believed to have been selected for and successful in domestication because of their behavior (Zeder 2012) and their ability to be tamed or cohabit in close environment with humans; it is for this reason that the Belyaev's fox experiment offers such an effective insight, as it presents a number of changes that likely took place in wolf domestication. Not only does this study show the foxes' physical evolution, it also documented at what rate these changes appeared in terms of generation (Trut 1999). This can inform what material evidence archaeologists can look for when aiming to identify "protodogs" or early domesticates, such as changes in coat colour, ears, tails, and legs as these are the first features to diverge from their wild progenitors (as seen in Trut 1999).

However, the reality is that during the early Palaeolithic such selective pressures and isolations, as applied in Belyaev's experiment, would not have existed due to energy, resources, and knowledge. This solicits caution in trying to adapt the foxes' evolutionary model to a Palaeolithic wolf scenario. Even if hunter-gatherer were to

select canids for their tameness and these wolves mated, there was no isolation from other canids, making it easy for an interference and admixture between the desired “tamed” wolves and wild ones throughout the whole process. This mixing very likely staggered and slowed domestication during thousands of years. The development into dogs was likely to have looked more like an intricate pattern of tangled lines affected by introgression and aborted domestication events, instead of a single straightforward line as represented in most domestication hypothesis (**Figure 12**) (Zeder 2012). This is evident in North America where some wolves have the melanistic K locus mutation that produces black pelage and is favored in forested environments; this genetic trait appears to have originated in domestic dogs and introgressed into wild wolf populations through interbreeding at some point in the past (Anderson et al. 2009). Nevertheless, the experiment (Trut 1999) confirms the hypothesis that as wolves transitioned into dogs they developed neotenized skull features, which is observable and identifiable in some osteological remains.

Osteological methods have offered a more accessible and economical approach to canid remains. They have been used since the beginning of dog studies (e.g. von den Driesch’s measurements), but these methods can also be problematic as they are up to a certain extent open to interpretation. As the fox study (Trut 1999) shows there is a reduction in the snout length and overall cranium size, but there is no way to know at what exact moment a specimen can be labeled as domesticated, as there are no metric thresholds measurements to separate dogs and wolves. This can cause contentious interpretation of canid remains, as seen in the Razboinichya canid (Ovodov et al. 2011) and the Predmostí canids (in Germonpré et al. 2012), where metric values from the specimen being examined can resemble those of one reference group or another but do not fall into a specific category. Osteometric techniques are most unreliable when applied to older remains. In the case of Upper Palaeolithic remains,

osteological dilemmas are intrinsically linked to the high plasticity and diversity of Pleistocene Grey wolf populations (Perri 2016; Boudadi-Maligne & Escarguel 2014); meaning that different ancient Grey wolf populations might have been erroneously identified as dogs. Another obstacle to securely identify canid remains when they are older than 14,000 years is differentiating between small wolves and domestic dogs as size has proved problematic (Pang et al. 2009:2849). Nonetheless, cranial features and measurements remain one of the most reliable sources of diagnosis. Eventually skeletal physical differences became more apparent and easier to distinguish; with further isolated breeding and feeding habits dogs started conforming to the canon of shorter and wider snouts and broader braincases (Germonpré et al. 2012). Social learning would have also played a part in eventually speeding up the process of domestication, through knowledge of how to breed dogs being passed down through generations. In cases where remains are sufficiently distinct, and can be analysed using osteological methods, it is important to have adequate reference groups as seen in Pitulko and Kasparov (2017). Tooth crowding can be an auxiliary line of evidence in classifying remains but it is not reliable enough to be used on its own.

In regard to the identification of remains older than 16,000 years ago (Perri 2016:3), researchers (O'keefe et al. 2013; Boudadi-Maligne & Escarguel 2014) have voiced their apprehension over the lack of data on Pleistocene wolf variation. Wolf diversity has been emphasized in Boudadi-Maligne and Escarguel's study (2014) which sought to record the geographic variability of extant wild European wolves, whilst O'keefe et al. (2013) endeavored to quantify the variation in wolf skulls across North America. Due to the history of wolf persecution and their reduction in territory (Perri 2016), it can be safely assumed that *Canis lupus* had a higher plasticity than that already recorded in extant specimen. This shows that as long as there is an inadequate database on

Pleistocene wolves, the interpretation of Upper Palaeolithic canids' physical remains will be misguided and incomplete.

A different line of evidence which has not been extensively explored in the context of canid-human relationship is carbon and nitrogen isotope analysis. As seen in the Shamanka dog and Lokomotive wolf, the carbon and nitrogen ratios can show what type of resources the canid was consuming, such marine or terrestrial food sources, and whether these were the same as human or not. If humans do have the same diet as the canid, this suggests a social relationship existed. If on the other hand specimen had different diets to the human populations they were associated with, as seen in the Predmostí canids' case (Germonpré et al. 2012; Perri 2016), then it is very likely that the canids were not domesticated.

Archaeological context remains arguably the most essential and decisive information relating to dog domestication. It can discredit or render reliable a canid classification; such is the case with the Zhokhov canids (eastern Siberian Arctic) (Pitulko & Kasparov 2017) and the Razboinichya canid (Ovodov et al. 2011). The Zhokhov canids were first identified as dogs through their cranial characteristics and the discovery of archaeological objects made of bone, mammoth ivory, and reindeer antler associated with harnessing (**Figure 13**) confirmed Pitulko and Kasparov's interpretation (2017). Whereas with the Razboinichya canid there was no circumstantial evidence found (except some small burnt bones) to directly associate it with humans. Therefore, negating any type of relationship with humans, which is essential in early dogs.

Relationships between canids and humans can be seen through the modification on skeletal remains and the context of burial. The most common dog remains which are modified are the skull and teeth as can be seen in the Predmostí and Eliseevichi

studies (Sablín and Khlopachev, 2002; Germonpré et al. 2012). In Shamanka grave 7, where a woman was buried in an extended supine position, several artefacts were located to the left of the body including ten teeth from an unknown canid, two of which were perforated (Losey et al. 2011:176-177). Losey et al. interpret the grave goods made out of or found in association with canids to represent an ontological model parallel to that of Northern indigenous people: animism (2011:175). The use of ethnohistoric and ethnographic data can aid in deducing the type of relationship which could have taken place between humans and canids in the past. Accounts of indigenous hunter-gatherers from North America (see Bozell 1988; Fogg et al. 2015) have been especially useful as they had a mobile lifestyle which might have had some parallels to that of Upper Pleistocene societies.

The importance of archaeological context in identifying liaisons between canids and humans is particularly well illustrated in the case of two canid burials in Shamanka and Lokomotiv (Siberia), both dating before 7000 years ago (Losey et al. 2011:174). At this time domestication of wolves had is thought to have already been successful (Larson et al. 2012; Pang et al. 2009). However, these burials show that even though some dogs were domesticated, humans still maintained some sort of social relationship with wolves. These are not the only specimen given preferential treatment in the area, but the other examples are more poorly documented.

The Lokomotiv canid was identified as a tundra wolf (*Canis lupus albus*) by a previous study, but no evidence was given for this classification (Losey et al. 2011:181). It appears that a severed human head was interred at the same time as the wolf (Losey et al. 2011:179); some other human remains were found around the tundra wolf but they were believed not to be contemporaneous to the wolf's burial (2010:180). The wolf was found fully articulated on its left side, the human head was located between its ribs

and legs and a patch of red ochre was drawn in the form of an oval, extending from the specimen's front limbs (Losey et al. 2011:180). Other finds in the grave consisted of bone needles, bone tool fragments, and simple lithic tools, none of which could be directly associated to the wolf (Losey et al. 2011:180).

The Shamanka canid was identified as a dog, although the specimen's cranium was missing; it seems it was dislodged during pit manipulation in further burials (Losey et al. 2011:178). The dog was laid on its right side and was directly associated to a large antler spoon, many other scattered human remains and artefacts were near the canid at around the same grave pit level (Losey et al. 2011:178). Upon pathological examination Losey et al. found that the spine and ribs showed evidence of trauma linked to conflict with prey or other dogs, blows from humans, or the use of the dog as a burden animal (Losey et al. 2011:182). It is instances like this when ethnohistoric data can help us identify what osteological trauma could mean; the Pawnee people used their dogs as beast of burden (Bozell 1988) and so the fact that the Shamanka dog had this type of pathology reflects the use of canids as a work force in Shamanka.

Ancient DNA analyses have been successful in identifying some individuals as dogs (e.g. Zhokhovo canids, see Pitulko & Kasparov 2017) but have failed in what most of them aimed to do, finding the founding wolf/dog population of modern dogs. Most early dogs have not been classified within a modern dog clade or do not share the same haplogroups with extant dogs, this can be due to several different reasons. Early dog specimen could represent aborted domestication events, there might not be enough appropriate references to compare them with, or they originate from different grey wolf populations. In studies involving ancient canids that construct neighbor-joining phylogenetic trees, it is essential to have appropriate reference groups which should

always include ancient canid samples and pre-world war samples to avoid bottlenecks and have greater diversity to compare the studied sample with. DNA studies are additionally limited when it comes to defining proto-domestic Palaeolithic dogs as the genomic signature of these early dogs has been mostly erased and will therefore not match modern day dog haplotypes. One example of the limitations of DNA analysis is when canids cannot be genetically classified either as wolves or dogs, such as the three Belgian specimens in Thalmann et al. (2013) which are placed as a sister-group to modern dogs but cannot be definitively classified. The investigation of early dogs' genetic composition is also reliant on the conservation and state of aDNA which deteriorates with age; this hinders the methods and samples that can be used.

The idea of a single founding wolf population is still present in many research articles and studies: this idea is either explicitly expressed (e.g. Pang et al. 2009; Clutton-Brock 2016:13) or implied when prominent academics suggest the hypothesis that the "original population" that gave birth to domestic dogs is extinct (Gopalakrishnan et al. 2017; Larson 2011). The search for the founding population of dogs has redirected the studies undertaken by scientists; instead of targeting the how and why of this event there has been a surge in the past couple of decades in DNA studies aiming to locate this mythological and elusive population.

In spite of the abundant research, dog domestication has not been associated to any one particular culture, with the exception of Pang et al. (2009) who argue that dog domestication might have been an important feature of rice agriculture although their study. Still, there has been no physical evidence to suggest that only a specific type of culture would be able to maintain a relationship with wolves favorable to domestication. It has been argued by some studies that conditions conducive to dog evolution were

not specific to a place or time (Savolainen et al. 2002;Thalmann et al. 2013; Vila et al. 1997). This is further shown in a relatively recent example of dog domestication in pre-Columbian America (Fogg et al. 2015). It is likely that many American indigenous peoples, especially those employing hunter-gatherer traditions, continued to maintain positive social relationships with wolves, or canids indistinguishable from wolves, conceiving more opportunities for domestication prior to, and continuing after, the arrival of Europeans in America (Fogg et al. 2015:263). The late naturalists, Audubon (1785-1851) and Bachman (1790-1874) emphasized that the Assiniboine used actual wolves as beasts of burden (in Fogg et al. 2015:264) instead of dogs.

Fogg et al. (2015:263) ventured to say that “suggested sites probably represent independent domestication events; thus, derivation of dogs from various types of wolves did not happen once, but probably continued into historic times” (Ovodov et al. 2011). However, some cases of putative early dogs are not well supported and there is no definitive evidence to show whether they were indeed dogs or wolves (e.g. Predmostí canids). Derr (2011:37) argued that the reason why we lack evidence is that the dog existed genetically before it did phenotypically; early animals called dogs were socialized wolves, dogs were essentially wolves still capable of looking like wolves. Additionally, the first dogs would have retained wolf-like genetics and only after isolated breeding would distinct genotypes divergent from the source wolf population appear in Palaeolithic dogs (Germonpré et al. 2009:485). Germonpré et al. suggested the separation of traits would only be perceivable after several thousand years due to bottlenecks during the early phases of domestication (2009:485). Although it is hard to tell the exact number, it is possible that humans had entered significant relationships with canids, to initiate the process of domestication, hundreds and maybe thousands of years before it was evident in the archaeological record.

The discovery of early dogs then involves the definition of the term “domesticate” and the flexibility with which it can be used.

From all the studies conducted until present it has not been possible to resolutely say where or exactly when dogs first became domesticated as there has been no general consensus (Pang et al. 2009; Germonpré et al. 2017). The archaeological record suggest domestication occurred at the beginning of the Holocene Epoch (Morey 2014); the earliest widely accepted dog remains in Europe (Bonn-Oberkassel) date back to 14,000 years ago. By 4000 to 5000 years ago, phenotypically distinct dogs started to appear in the archaeological record in northern Europe (Pitulko & Kasparov 2017:491). The place where domestication originated has been contentious: some studies have suggested East Asia (Savolainen et al. 2002; Pang et al. 2009) whilst other have proposed Eurasia (Sablin & Khlopachev 2002; Losey et al. 2011; Germonpré et al. 2012; Morey 2014) as the birthplace of dogs. Finds from Europe and Siberia (Germonpré et al. 2012; Boudadi-Maligne & Escarguel 2014; Germonpré et al. 2017) from the Upper Palaeolithic have made compelling cases for potential protodogs or early dogs but the evidence presented is too ambiguous and not sufficient to push back the date for wolf domestication. Perhaps with better methods and techniques in the future we will be able to determine whether dogs did in fact exist as early as before the Last Glacial Maximum.

## Limitations

The study of dog domestication is limited by the paucity of Upper Palaeolithic remains and the state they are found in. The field is also limited due to most of the efforts being put into finding the “original” wolf population and place, which are almost impossible to find with the current methods and techniques available to researchers, all studies aiming to do so until now have failed to gain full acceptance. Early dog remains have been especially difficult to find and characterize, as wolves and dogs are so similar that the biological and semantic differences would have taken thousands of years to set (Clutton-Brock 2016). So knowing this, maybe the focus of the field should be more centered on how we can track the progress and further evolution of dogs in human societies, instead of trying to define the exact time, place, and population that lead to the evolution of dogs.

This study is limited in the amount of literature and studies it reviews along with the methods examined. However, this study does not aim to present an exhaustive list of methods to use in the field of wolf domestication; its intent is to demonstrate the advantages in the use of several lines of evidence.

## Conclusion

The fact that studies have not been able to determine the location and time of dog origins offers support to the idea that domestication was not restricted to one single event in the past. Instead, the different sites of putative dogs throughout the Old World suggest multiple and geographically extensive domestication processes. An example of how wolves have evolved into dogs during different times is the North American indigenous peoples and their dogs, as seen in chapter 3.

In order to identify canid remains in the archaeological record as accurately as possible, I propose a holistic and multimodal approach. The methods reviewed in the discussion are some of the most effective ones in providing a more complete narrative on human-canid relationships, but future research should not be limited to those. Unconventional methods such as ethnographic analogies can be pivotal tools in understanding the mechanisms and different types of inter-species alliances, as is the case with wolf domestication. Future research has much to reveal on how humans and canids associated in the past and how these interactions translated into domestication processes.

## Illustrations



**Figure 1** Important sites discussed in the literature review 1) Predmostí (Czech Republic) 2) Lokomotive and Shamanka canids (Baikal Lake/Russia) 3) Razboinichya (Altai mountains/Russia) 4) Zhokhovo canid (Russia) 5) Eliseevichi canid (Russia) 6) Goyet cave and Trou de nutons canids and (Belgium) (image from Maps of World 2017 and data compiled from Sablin & Khlopachev 2002; Losey et al 2011; Ovodov et al. 2011; Germonpré et al 2012; Pitulko & Kasparov 2017).

Measurements	TL (1)	VL (8)	ALP1-M2 (15)	P4CL (18)	GWBrC (29)	GWPal (34)	MWPal (35)	Ccl	Ccw	CBL (2)	BM (kg)
Predmostí OK 1060	238.08	116.30	85.40	26.39	68.91	82.62	44.43	12.40	8.46	225.00	36
Predmostí OK 1061	228.00	123.78	84.56	24.75	61.80	81.46	46.05	—	—	214.00	33
Predmostí OK 1062 (Pr 1)	264.16	143.17	89.45	24.50	64.99	82.19	46.52	13.63	8.56	249.00	46
Predmostí OK 1069 (Pr 3)	236.12	114.60	80.51	25.66	67.00	81.86	48.23	13.40	8.63	221.00	35
Predmostí (—)	232.00	111.57	77.00	24.50	66.11	83.50	46.00	12.27	—	217.00	34
Predmostí 1	276.54	135.04	91.61	25.89	63.00	90.62	49.77	14.43	9.77	254.00	48
Predmostí 1924	273.57	131.22	87.77	24.33	68.55	85.60	53.58	—	—	256.00	49
Goyet 2860	227.00	115.00	81.23	23.86	67.55	77.26	45.00	—	—	213.00	32
Eliseevichi dog 447	240.00	116.00	81.60	25.00	73.00	87.50	50.40	15.00	10.00	226.00	37
Eliseevichi dog 23781	256.00	117.00	92.00	27.30	68.00	91.00	51.50	—	—	236.00	41
Mezherichi 4493	225.70	112.00	79.00	24.60	63.50	77.20	43.10	13.00	7.80	212.00	32
Mezin 5490	225.80	110.30	81.10	24.50	61.60	77.20	44.90	—	—	215.50	33
Avdevo 911	246.00	123.00	82.00	24.20	66.30	83.00	46.70	—	—	228.00	38
Kostenki 17 36233	265.30	132.50	91.20	27.30	66.30	90.00	52.00	14.00	9.30	248.00	45
Trou des Nutons 2559	261.00	135.80	94.30	28.60	65.50	93.00	49.00	14.56	10.11	242.93	43
Anabar (Siberia) 29699	267.50	134.10	92.10	25.90	67.10	84.30	43.80	—	—	247.00	45
Mezin 5469	253.70	126.70	86.20	25.10	62.50	85.00	45.00	15.80	9.50	235.00	40
Mezin 5488	256.00	129.00	92.00	25.50	61.70	90.00	47.80	16.80	10.60	243.00	43

**Figure 2** Measurements, according to von den Driesch (1976), of the fossil large canids skulls used in Germonpré et al. 2012 (as seen in Germonpré et al. 2012:187)



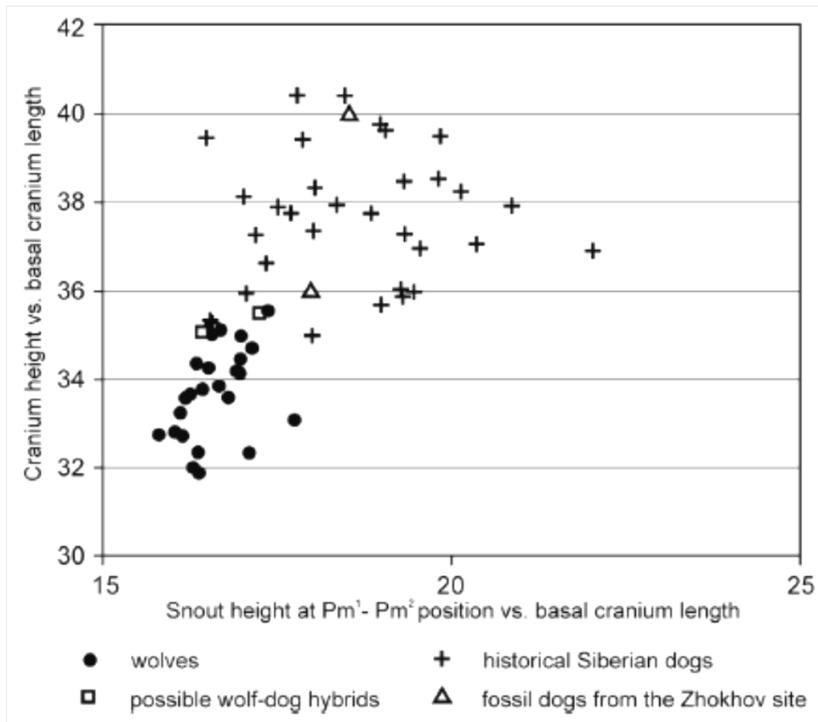
**Figure 3** Lateral view of Predmostí 1 skull with perforation on the lateral braincase (as seen in Germonpré et al. 2012:191)



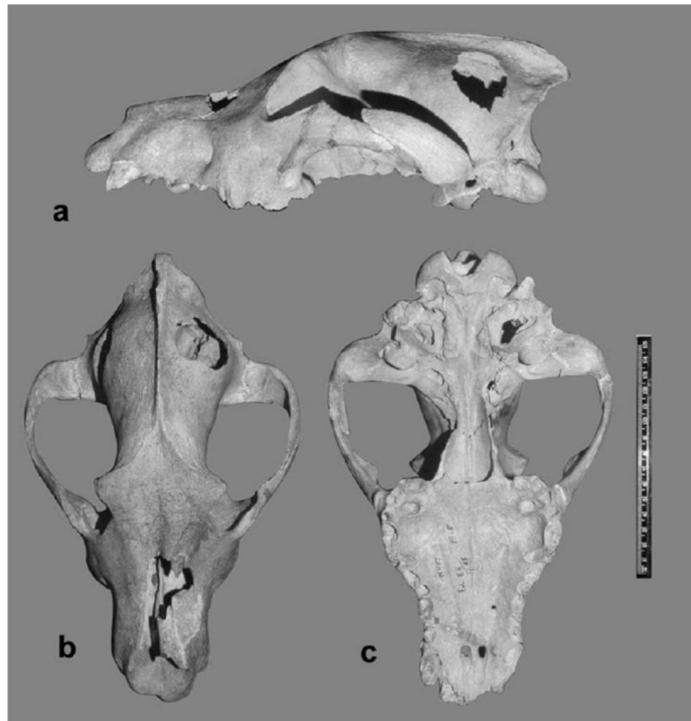
**Figure 4** Predmostí skull with bone inserted in jaws (as seen in Germonpré et al. 2012:191)

Specimen	Date	Closest affinity to reference group
Badyarikha canid	30,800 cal BP	Not identified at the moment but said to be between the wolf groups and the Palaeolithic dog group
Tirekhtyakha canid	>50,000 cal BP	Pleistocene wolves
Ulakhan Sala canid	17,200 cal BP	Palaeolithic dogs
Malyi Lyakhovsky canid	900 cal BP	Northern dogs
Razboinichya canid	33,000 cal BP	Palaeolithic dog
Shamanka canid	7,400 cal BP	Northern dogs

**Figure 5** Canids' affinity to reference groups (data collected from Germonpré et al. 2016)

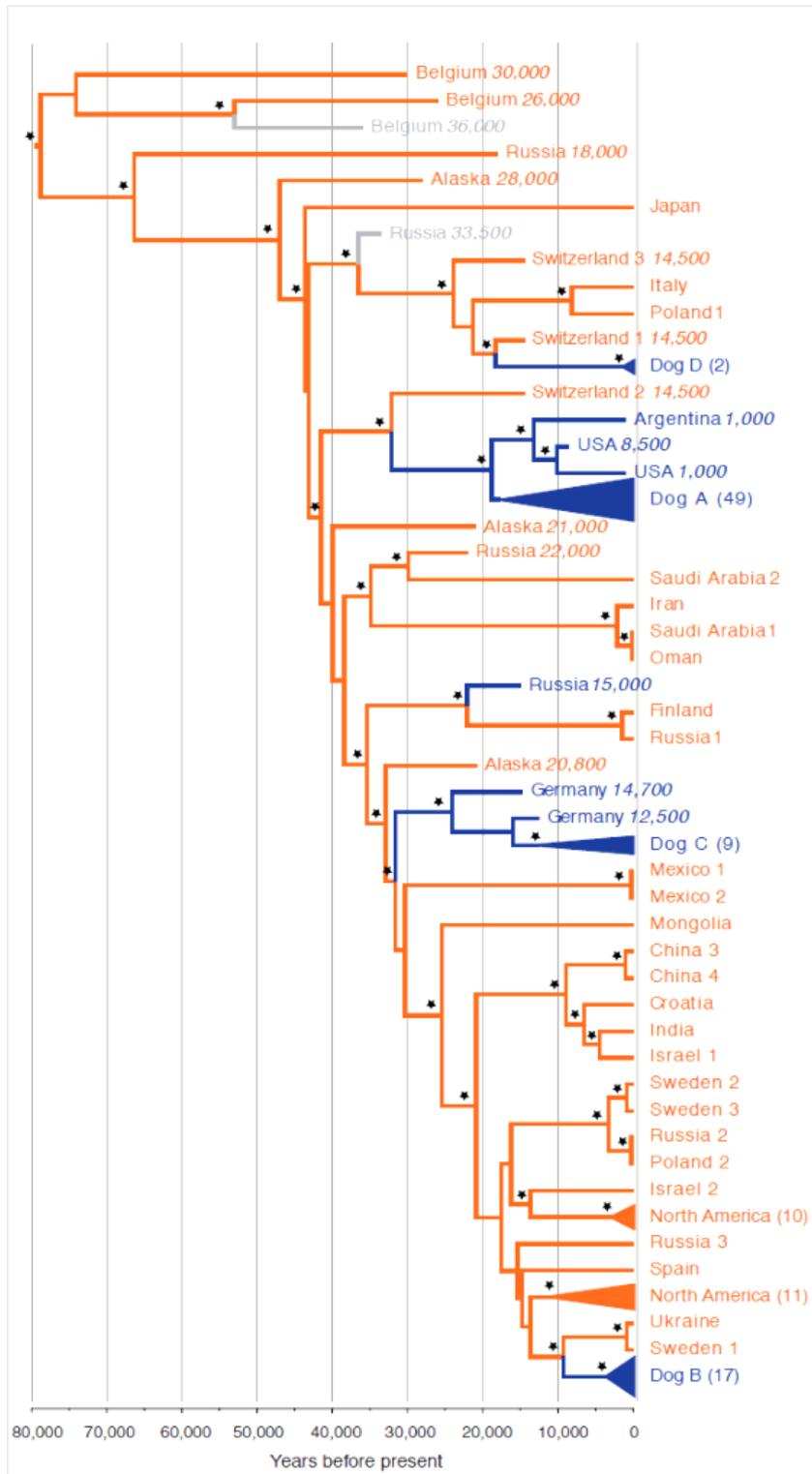


**Figure 6** Proportional characteristics of the crania of dogs and wolves from Arctic Siberia (as seen in Pitulko & Kasparov 2017:507)

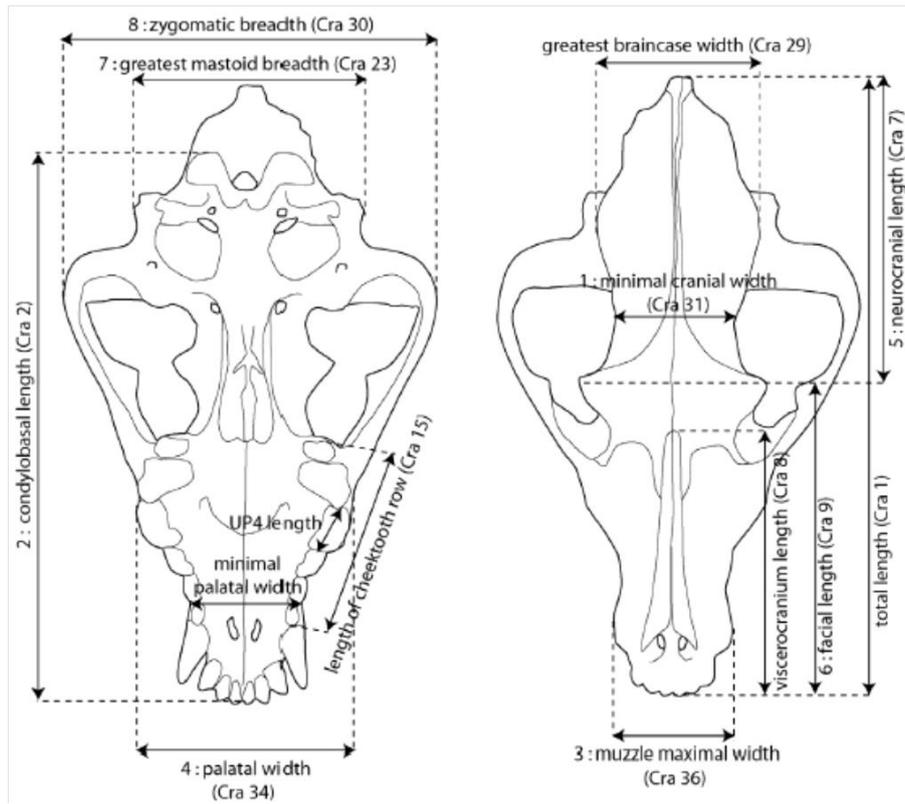


**Figure 7** Dog cranium from Eliseevichi 1 skull MAE 447/5298 (as seen in Sablin & Khlopachev 2002:796).





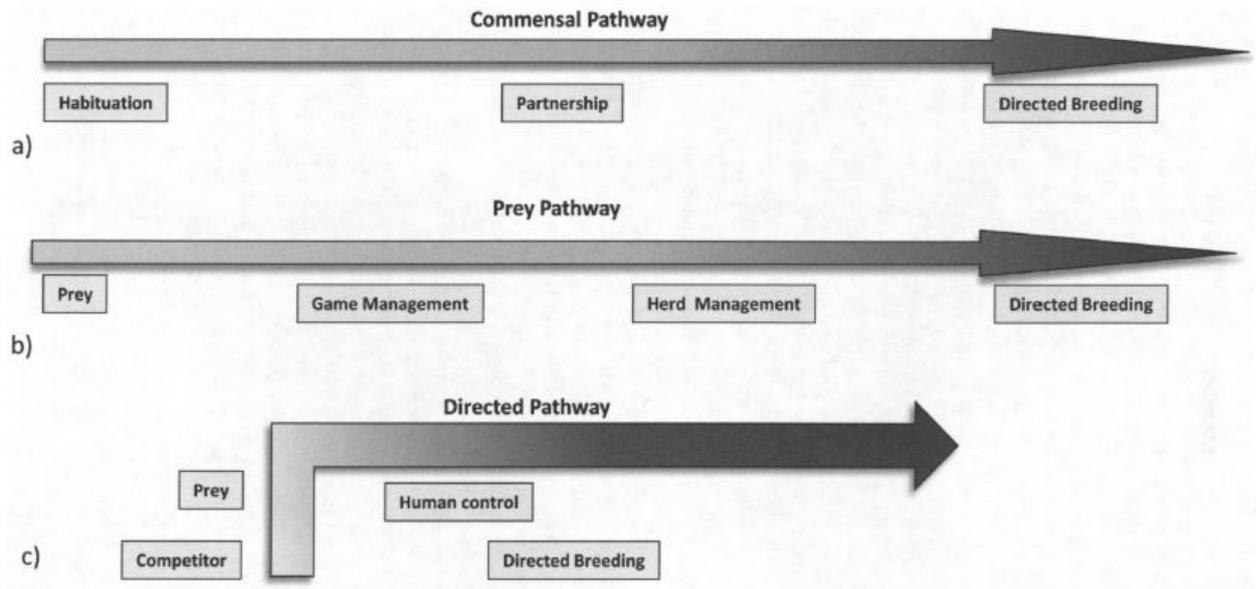
**Figure 9** Phylogenetic arrangement of modern and ancient dog (blue) and wolf sequences (as seen in Thalmann et al. 2013:873)



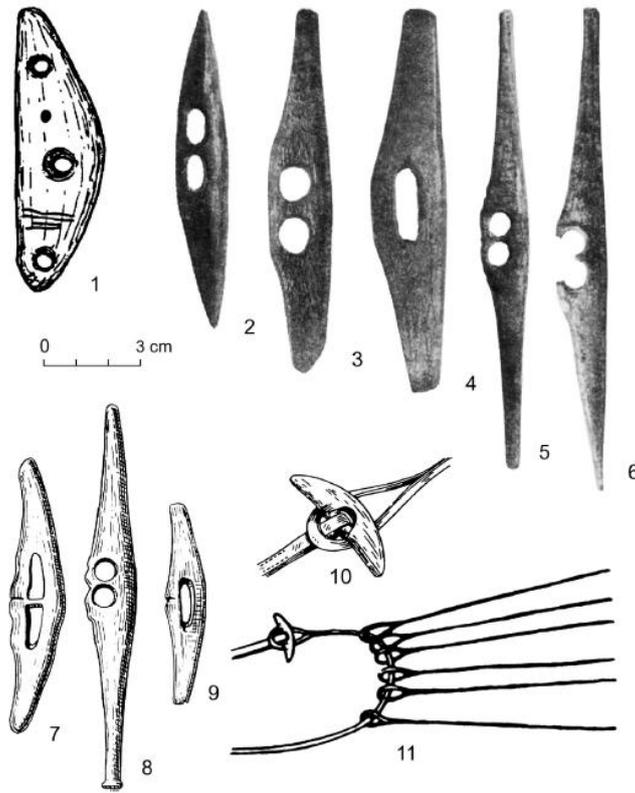
**Figure 10** measurement used in Boudadi-Maligne and Escarguel's study (2014) (as seen in Boudadi-Maligne and Escarguel 2014:82)



**Figure 11** comparison of wolf skull (top), Shoshone “dog” (middle), domesticated dog (bottom)  
(as seen in Fogg et al. 2015:275)



**Figure 12** Pathways to animal domestication (as seen in Zeder 2012:249)



**Figure 13** archaeological objects made of bone, mammoth ivory, and reindeer antler associated with harnessing (as seen in Pitulko & Kasparov 2017)

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