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Focus

A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation

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ABSTRACT

The process and timing of initial dog domestication is an important topic in human evolution and one which has inspired much recent debate. Findings of putative domesticated dogs have recently been reported from two Gravettian sites by Germonpré et al. (2015a), joining a handful of other reputed "Paleolithic dogs" dating to before the Last Glacial Maximum (LGM). Though these findings have been challenged previously, this paper draws attention to the most significant shortcoming in claims of early domesticated dogs – a lack of data on Pleistocene wolf variation. Without comprehensive data on the range of variation within Pleistocene wolf populations, the identification of domesticated dogs from prior to the Late Upper Paleolithic cannot be conclusively accepted or rejected.

1. Introduction

The timing of initial dog (*Canis familiaris*) domestication is critical to our understanding of human evolution. As our first domesticate, dogs are an important model for evaluating the pathways in which human populations may have initiated or responded to increasingly domestic interactions with animals (e.g. Zeder, 2012). Though domestication from a gray wolf (*Canis lupus*) ancestor is widely accepted (Vilà et al., 1997), recent research suggests this ancestor is from a now-extinct population of wolves (Freedman et al., 2014). Dog domestication poses additional complex questions about Pleistocene human–carnivore interactions, as unlike later domesticated livestock species, the wolf is a predator that would have been in competition with human hunters for local prey species. Moreover, wolves were the only animal known to have been domesticated by prehistoric hunter-gatherers (e.g. Thalmann et al., 2013), posing further questions about their initial uses, the process of domestication within a highly-mobile lifestyle, and the location of initial domestication events.

Based on substantial archaeological and genetic evidence, a Late Upper Paleolithic (ca. 16,000 BP) timing for dog domestication is generally accepted. A recent paper by Germonpré et al. (2015a) claims to identify earlier Paleolithic dogs from the Gravettian sites of Předmostí (ca. 31,000 BP, Czech Republic) and Kostenki 8 (c. 33,500–26,500 BP, Russia). These join three previously-contended "dogs" dating to before 16,000 years ago (Table 1). Though their identification as dogs is widely disputed, researchers have now begun to formulate hypotheses regarding the evolution of human groups in Eurasia based on earlier dates for dog domestication (Bocherens et al., 2015; Shipman, 2015a,b; but see Perri et al., 2015). The domestication of dogs predating the Last Glacial Maximum (LGM) also conflicts with most genetic evidence of a more recent divergence between wolves and dogs (e.g. Axelsson et al., 2013; Freedman et al., 2014; Larson and Bradley, 2014; but see Druzhkova et al., 2013; Thalmann et al., 2013). Importantly, comprehensive comparative data on Pleistocene wolf variation are severely lacking and poorly incorporated into discussions of dog domestication. This deficiency means morphological variations being used to identify putative Paleolithic dogs may actually be identifying natural variation in local wolves. Consequently, recently discovered "Paleolithic dogs" may simply represent previously unknown Pleistocene gray wolf subspecies.

2. Pre-LGM "Paleolithic dogs"

A date of roughly 16,000 years ago has long been the accepted time frame for initial dog domestication (Morey, 1992; Clutton-Brock, 1995; Freedman et al., 2014). Recently, there have been a handful of earlier Paleolithic *Canis* remains proposed as incipient

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Table 1
Putative incipient dogs dated to before 16,000 BP.

Site	Location	Age (cal. BP)	Reference
Goyet Cave	Belgium	ca. 36,500	Germonpré et al., 2009
Razboinichya Cave	Russia	ca. 33,500	Ovodov et al., 2011
Kostenki 8	Russia	ca. 33,500–26,500	Germonpré et al., 2015a
Předmostí	Czech Republic	ca. 31,000	Germonpré et al., 2012; Germonpré et al., 2015a
Eliseevichi 1	Russia	ca. 17,000	Sablin and Khlopachev, 2002

domesticated dogs (Table 1). These sites are all within Europe or Southern Siberia and include Goyet Cave (Germonpré et al., 2009), Razboinichya Cave (Ovodov et al., 2011), Kostenki 8 (Germonpré et al., 2015a), Předmostí (Germonpré et al., 2012, 2015a), and Eliseevichi 1 (Sablin and Khlopachev, 2002). Identifications of these putative dogs were made on the basis of cranial morphometrics, in particular analyses of skull variation, but also mandibles and teeth. These data were analyzed using univariate and multivariate approaches (e.g. ANOVA, Discriminate Function Analysis), utilizing comparative data from ancient and modern dogs and wolves from varying sample sizes. However, the comparative data used can be problematic. Current Pleistocene wolf data suffers from not only a lack of samples, but a bias towards incorporating large northern specimens in analyses, regardless of temporal or geographic parallels (Crockford and Kuzmin, 2012; Morey, 2014). Furthermore, modern wolves are not from the same lineage as domesticated dogs (Freeman et al., 2014), which may cause issues when using them as a comparative model. A continuous decline in wolf populations since ca. 20,000 years ago has also left these modern populations much less varied than during the pre-LGM (Pilot et al., 2014).

The classification of these canids as incipient domesticated dogs is highly contentious and issues related to their identification have been raised previously and will not be repeated here (see Crockford and Kuzmin, 2012; Napierala and Uerpmann, 2012; Boudadi-Maligne and Escarguel, 2014; Morey, 2014; Drake et al., 2015; Morey and Jeger, 2015; but see Germonpré et al., 2013; Germonpré et al., 2015b). Nevertheless, Germonpré et al. (2012) have speculated that these "Paleolithic dogs" were used to haul mammoth meat and recently Shipman (2015a) hypothesized that they helped humans actively hunt mammoth, leading to their outcompeting Neanderthals (but see Perri et al., 2015). Bocherens et al. (2015) also recently speculated that dietary variation among canids at Předmostí supported claims of both wolves and domesticated dogs from the site, suggesting humans were specifically provisioning these "dogs" with a special diet.

3. Variation in Pleistocene wolf populations

The range of natural variation among Pleistocene wolves is the most significantly overlooked factor affecting the identification of potential domesticated dogs. This problem holds similarities to debates regarding the identification of hominin species based on osteological data (e.g. White et al., 2009; Wood and Harrison, 2011) and larger questions about identifying speciation through morphology. Some discussions of dog domestication have recognized that proposed pre-LGM "Paleolithic dogs" may just represent variation within European gray wolf populations (Larson et al., 2012; Thalmann et al., 2013). Skoglund et al. (2015: 4) recently concluded that the more recent timing for dog domestication (ca. 16,000 BP) "would require that the majority of present-day dog ancestry originates from an extinct or presently unsampled wolf population" (see also Freedman et al., 2014; Morey and Jeger, 2015). This same paper (Skoglund et al., 2015) serves to highlight how little is known about multiple regional wolf populations. They sequenced a 35,000 year-old wolf from northern Siberia (Taimyr) and found that individual was from an unknown Pleistocene wolf lineage which diverged from both the modern wolves and the wolves that went on to become domesticated dogs. Similar findings of extinct late Pleistocene wolf types have been found previously (Leonard et al., 2007), suggesting significant variation in Pleistocene wolf populations.

Ecological factors such as prey specialization, predatory competition, habitat type and climate greatly affect the craniodental plasticity and genetic population structure of gray wolves (Carmichael et al., 2001, Carmichael, 2006; Geffen et al., 2004; Pilot et al., 2006; Musiani et al., 2007; Hofreiter and Barnes, 2010; Flowers and Schreve, 2014; Leonard, 2015). This means that within the Pleistocene gray wolf population, variation in local environments would have encouraged a range of wolf ecotypes that were genetically, morphologically, and ecologically distinctive. In locations where human groups were accessing a variety of environments (e.g. uplands, lowlands, arid regions) and in turn may have had contact with several different wolf ecomorphs, variation can be expected in wolf remains from Paleolithic sites. Pleistocene wolf variation may also be a relic of wolves moving into different niches as predator competition varies, as in Central Europe after 35,000 BP, when a significant change in the faunal community led to the disappearance of many species (Musil, 2010). This period also coincided with a warmer, more humid climate which may have encouraged smaller wolf morphs (e.g. Flower and Schreve, 2014). Additionally, wolves are highly mobile in search of mates, territory, or tracking migratory prey. Dispersal distances of several hundred kilometers are common and movements over 1000 km are recorded (Fritts, 1983; Mech, 1987; Mech et al., 1995). Some wolves are also migratory, instead of territorial, following herds of large migratory animals across distances of >1000 km (Mech and Boitani, 2003; Musiani et al., 2007). Given these wide-ranging movements, variation in *Canis* material from archaeological sites, especially in the case of a single individual, may also be the result of interactions between human hunters and transient non-local (dispersing or migratory) wolves.

Recent research intended to verify claims of early domesticated dogs may actually support the concept of ecologically-driven variation in Pleistocene wolves. Dietary isotopic analysis of multiple canids from Předmostí found dietary variation between two groups, with one focusing primarily on mammoth and larger herbivores and the other on reindeer (Bocherens et al., 2015). Though analysis of humans from the same site did not find reindeer to be a significant component of the human diet, the authors suggest the canids with a reindeer-based diet were domesticated dogs. This would imply that human hunters were provisioning dogs with reindeer which they did not eat themselves. A more likely scenario is 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.

Additional support for multiple Pleistocene wolf subpopulations may also be found from the site of the oldest proposed "Paleolithic dog", Goyet Cave. Here, Germonpré et al. (2009) identified unique mtDNA haplotypes from each of the six canids sampled,

highlighting the level of wolf variation possible from one site. More recently, the Goyet "dog" has been identified as an ancient sister group to all modern dogs and wolves (Thalmann et al., 2013), like the Taimyr wolf above, not a direct ancestor, meaning it could easily represent "a phenotypically distinct, and not previously recognized, population of gray wolf" (Thalmann et al., 2013: 872). Germonpré et al. (2009) also demonstrated the range of dietary isotopic variation which can be present in wolves from the same site, with a difference of up to 3.4‰ in $\delta^{15}N$ values from Goyet wolves. This suggests that dietary isotopic differences recently used to support claims of domesticated dogs from Předmostí (up to 2.9‰ variation in $\delta^{15}N$ values between wolves and "dogs"; Bocherens et al., 2015) may not be evidence of human-mediated "dog" diets vs. wolf diets, but the result of natural subsistence variation in local wolf populations.

4. Discussion

The key to understanding initial dog domestication lies in a thorough analysis of Pleistocene wolf variation, while taking into account temporal and geographic variability. Reports of incipient dogs from prior to the generally accepted domestication period (ca. 16,000 BP) should be supported with data from local, contemporaneous wolf populations. Larson et al. (2012: 8878) previously argued that findings of early "domesticated dogs" (e.g. Germonpré et al., 2015a) could represent "a morphologically distinct local, now-extinct population of wolves". This remains the most plausible explanation. The difficulty of identifying subspecies in even modern wolf populations (e.g. O'Keefe et al., 2013; Fredrickson et al., 2015) underscores the complex nature of recognizing initial phases of dog domestication in the archaeological record.

Wolves are ecologically and morphologically plastic animals. Changes in size and shape, based on variation in prey, environment, climate and competition are well documented (e.g. Flower and Schreve, 2014). Claims of dog domestication around or before the LGM are based primarily on morphological characteristics thought to be associated with the process of domestication. These characteristics (e.g. shortened rostrum, tooth crowding, absence or rotation of premolars) are shown to be insufficient alone in determining dog domestication, as they have also been documented in ancient and modern wolves (e.g. Leonard et al., 2007; Boudadi-Maligne, 2010; Flower and Schreve, 2014; Dimitrijević and Vuković, 2015). Crockford and Kuzmin (2012) have also suggested morphological characteristics previously used to identify pre-LGM dog domestication, specifically shortened rostrums, may be the natural result of niche competition with Paleolithic human hunters, as seen in LGM Beringian wolves competing with short-faced bears (Leonard et al., 2007; Figueirido et al., 2010).

The goal of this paper is to draw attention to the lack of data on Pleistocene wolf variation, the insufficient integration of the existing data into current archaeological discussions, and the necessity of this data in pursuing future research into dog domestication. Findings of domesticated dogs in the pre-LGM Paleolithic have been largely based on one or a few individuals, discounting the importance of population-wide analyses. Moving towards a comprehensive understanding of dog domestication will require additional work on the genetic, morphological, isotopic and ecological history of Pleistocene wolf populations and their interactions with Paleolithic human groups, requiring collaboration between researchers from various fields. Until then, the identification of domesticated dogs from before 16,000 years ago cannot be resolutely accepted or rejected.

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