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A biometric re-evaluation of recent claims for Early Upper Palaeolithic wolf domestication in Eurasia

Myriam Boudadi-Maligne [a,*], Gilles Escarguel [b]

[a] UMR 5199 PACEA, Université de Bordeaux, Avenue des Facultés B18, F-33405 Talence Cedex, France
[b] Laboratoire de Géologie de Lyon: Terre, Planètes, Environnement, UMR CNRS/Univ. Lyon 1/ENS-Lyon 5276, Boulevard du 11 Novembre 1918, F-69622 Villeurbanne Cedex, France

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ABSTRACT

The timing of wolf domestication remains a subject of intense debate, especially as recent genetic, morphological and radiometric analyses of relevant skeletal material apparently demonstrate the presence of canids on Eurasian Early Upper Palaeolithic sites to be more widespread than previously envisaged. However, numerous questions still surround wolf domestication, not least of which is satisfactorily explaining the process whereby this social carnivore progressively became a 'member' of human societies.

The analysis presented here emphasises the substantial variability of both modern and Pleistocene wolf populations, and in doing so, further highlights the need for caution when considering species attributions and, more particularly, accurately identifying dog rather than wolf remains in archaeological assemblages. A combination of biometric and morphological data provides a reliable basis for critiquing a series of recent publications purportedly demonstrating the presence of dogs alongside humans during the Early Upper Palaeolithic.

1. Introduction

The complexity, geography and still uncertain chronology of wolf domestication in Eurasia have rendered the subject a matter of continued and intense debate. While numerous questions persist concerning its precise origin, several hypotheses have nonetheless been proposed to explain the domestication process (e.g. Crabtree and Campana, 1987; Crockford, 2004; Vigne, 2004; Müller, 2005; Crockford, 2006; Morey, 2010). For example, did Palaeolithic groups intentionally domesticate wolves to assist in hunting and provide protection? Did they serve both as companions and eventual sources of meat (Morey, 2010; Boudadi-Maligne et al., 2012)? Did wolves 'naturally' become closer to humans over time, scavenging refuse left in and around campsites?

What little archaeological evidence that is available concerning wolf domestication can be divided into two broad categories, contextual and morphological. Identifying domesticated animals from contexts where they are not clearly linked to human occupation and associated archaeological material is difficult, if not impossible. On the other hand, instances where human and dog skeletons are found interred side by side within the same grave, such as at the Natufian site of Ain Mallaha, provide much more conclusive evidence for domestication (Davis and Valla, 1978).

The second source of evidence derives from skeletal morphology, particularly cranial measurements and changing patterns of dental growth and spacing (e.g. Gautier, 1990; Morey, 1992, 2010). All available information concerning domestication has in fact shown it to entail clear changes in the morphology, physiology and behaviour of the domesticated animal (e.g. Gautier, 1990; Morey, 1992; Clutton-Brock, 1995; Trut, 1999; Miklósi, 2007; Morey, 2010). In archaeological contexts, the most common criteria for discerning domesticated from wild specimens derive from morphometric data and, to a more debatable degree, the presence of skeletal or dental pathologies and modifications (Clutton-Brock, 1970; Gautier, 1990; Morey, 1992, 1994, 2010). Among these changes, the most significant are tied to an overall reduction in the size individuals, more specifically, facial aspects of the cranium (e.g. Davis, 1981; Tchernov and Horwitz, 1991; Morey, 2010; Zeder, 2012) and the retention of juvenile characters in domesticated adult canids (Morey, 2010), even if we now know that dogs are not simply paedomorphic wolves (Drake, 2011).

* Corresponding author.
E-mail addresses: m.boudadi-maligne@pacea.u-bordeaux1.fr, m.boudadimaligne@gmail.com (M. Boudadi-Maligne).

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Additionally, the rate in which these morphological changes appear has also been emphasised as evidence for domestication. For example, selective breeding experiments using foxes at the end of the 1950s by Belyaev, who privileged particular behaviours, namely tamability, have shown that only twenty generations, or about sixty years, suffice for morphological modifications to appear in canids (Belyaev, 1979; Trut, 1999, 2001; Arbuckle, 2005). In terms of archaeological material, determining dog remains from those of wolf essentially relies on comparing data collected from both fossil and modern specimens of both animals. However, the heavily fragmented nature of almost all known fossil specimens precludes the creation of a robust database of biometric data (Boudadi-Maligne, 2010). While data for modern canids is more numerous, reference collections employed in many studies illustrate only a portion of their variability, thus introducing important biases when fossil remains are considered. With this in mind, we focus on the fundamental importance of both the nature and structure of fossil and modern wolf reference collections, as well as how they are interpreted. In our view, this data constitutes the most convincing means for re-evaluating recent claims that several Early Upper Palaeolithic canids actually represent early domesticated dogs (Germonpré et al., 2009; Ovodov et al., 2011; Germonpré et al., 2012, 2013).

2. Material and methods

Geographic variability among modern European wolves was examined with recourse to osteological data collected from wild individuals in Portugal, Italy and Bulgaria (Boudadi-Maligne, 2010) combined with craniometrical characteristics of wild wolves from Poland, Russia, Finland and Sweden obtained with the help of Dr. H Okarma (Okarma and Buchalczyk, 1993; Boudadi-Maligne et al., unpublished data). All measurements involved adult individuals (*sensu* Nowak, 1973; Okarma and Buchalczyk, 1993) of known sex. In total, cranial measurements from 571 wild wolf specimens represented by 307 males and 264 females were analysed (Table 1).

In order to investigate inter-population variability, eight specific cranial measurements (Fig. 1) were selected based on published data (Von Den Driesh, 1976; Olsen, 1985; Crabtree and Campana, 1987; Morey, 1992; Nowak, 1995) and our own database. Statistical differences in size and shape across modern European wolf populations were compared using multiple statistical tests (ANOVA, CVA and an index of size variability (Boudadi-Maligne, 2010)). Here, we focus on size variability using Version 2 of the Multi-SIST (Size Index Scaling Technique) program developed by one of us (G.E). A modified index of size variability (VSI*index) was used that takes into account not only the standard deviation of the reference population but also that of each analysed group (Escarguel, 2008). Moreover, a Principal Coordinate Analysis of the allometric distance matrix combined with a Bootstrapped Spanning Network (Brayard et al., 2007; Escarguel, 2008) allowed us to both verify and quantify the distance between each group.

Table 1
Modern populations. The number of males (M) and females (F) is specified for each country.

Origin	Number of individuals	Sex
		M/F
Portugal (1)	20	13/7
Bulgaria (1)	40	20/20
Italy (2)	25	12/13
Sweden (3)	16	7/9
Finland (3)	25	13/12
Poland (3)	140	84/56
Russia (3)	303	156/147
Europe	**571**	**307/264**

Data collected by (1) Boudadi-Maligne; (2) Okarma and Boudadi-Maligne; (3) Okarma.

The reference collection of fossil populations includes only individuals reliably dated to the Upper Palaeolithic, the period commonly considered to witness the emergence of the domesticated dog, and includes new, unpublished data for Gravettian wolves from the site of Maldidier (Dordogne, France) and wolves from the Upper Pleniglacial natural-trap of Igue du Gral (Lot, France) (Boudadi-Maligne, 2010). Importantly, specific biometric analyses have conclusively demonstrated that these two populations can be safely attributed to *Canis lupus* (Boudadi-Maligne, 2010, 2012).

These two reference collections provide a robust sample significantly more representative of the actual morphological variability of wild wolves across Eurasia than those employed in previous studies, which relied solely upon either captive specimens or canids with uncertain species attributions. The variance of fossil and modern population was compared using univariate (Levene's and Brown-Forsythe's test) and bivariate (Box's M test) tests performed on both raw and log-transformed measurements. The resulting range of variability evident in the sample populations was then used as a basis for discussing a series of fossil canids recently reported as early dogs.

At present, putative fossil dog remains have been documented from more than twenty Eurasian sites (Fig. 3). Among these remains, only six examples, along with the specimen from Razboinichya Cave (Siberia), have been directly dated (Célérier et al., 1999; Chaix, 2000; Baales, 2006; Germonpré et al., 2009; Ovodov et al., 2011; Boudadi-Maligne et al., 2012; Napierala and Uerpmann, 2012). Difficulties surrounding the chronology of wolf domestication are further compounded by the lack of agreement as to whether particular remains can be reliably attributed to dog. This is especially the case not only for canids from Goyet, Předmostí and Razboinichya Cave (Detry and Cardoso, 2010; Morey, 2010; Napierala and Uerpmann, 2012; Crockford and Kuzmin, 2012; Larson et al., 2012) but also for the most recent northern European examples from Mezin, or Eliseevichi I (e.g. Benecke, 1987; Crabtree and Campana, 1987; Miklósi, 2007; Wang and Tedford, 2008; Morey, 2010; Larson et al., 2012), which have been excluded from the present analysis. Finally, as biometric data is inherently limited by the fragmentary nature and or conservation of certain fossil remains (for example, no measurable cranial elements are available for Pont d'Ambon) coupled with the lack of standardised measurements between researchers, we applied three different statistical tests to the fossil canid sample as a function of the available measurements.

The first statistical test compared cranial measurements of Upper Palaeolithic canids from Goyet, Předmostí and Maldidier to the modern reference collection of European wild wolves from Bulgaria and Portugal. As described above, bivariate Box's M tests for homogeneity of the variance-covariance matrices was first performed, followed by a MANOVA to compare the three populations. A Canonical Variate Analysis (CVA) was then carried out to find the shape features that best distinguish the groups. The second test involved a bivariate analysis using two cranial measurements (condylobasal length and palate width) employing two reference collections: securely identified archaeological dogs from postglacial contexts (Degerbøl, 1961; Morey, 2010) and modern European wild wolves from Poland, Portugal and Bulgaria.

Finally, a series of probabilistic distances (Maureille et al., 2001) were compared using the same two cranial measurements, alongside an additional index of skull robusticity calculated as the product of condylobasal length and palate width. Probabilistic distances (Maureille et al., 2001) were quantified between each canid skull assigned to either *C. lupus* (wild modern wolves and