Journal of Archaeological Science 36 (2009) 473–490

Contents lists available at ScienceDirect

Journal of Archaeological Science

journal homepage: http://www.elsevier.com/locate/jas

Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes

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ARTICLE INFO

Article history:
Received 6 May 2008
Received in revised form
23 September 2008
Accepted 26 September 2008

Keywords:
Upper Palaeolithic
Canidae
Dog
Skull
Ancient DNA
Stable isotopes

ABSTRACT

Using multivariate techniques, several skulls of fossil large canids from sites in Belgium, Ukraine and Russia were examined to look for possible evidence of the presence of Palaeolithic dogs. Reference groups constituted of prehistoric dogs, and recent wolves and dogs. The fossil large canid from Goyet (Belgium), dated at c. 31,700 BP is clearly different from the recent wolves, resembling most closely the prehistoric dogs. Thus it is identified as a Palaeolithic dog, suggesting that dog domestication had already started during the Aurignacian. The Epigravettian Mezin 5490 (Ukraine) and Mezhirich (Ukraine) skulls are also identified as being Palaeolithic dogs. Selected Belgian specimens were analyzed for mtDNA and stable isotopes. All fossil samples yielded unique DNA sequences, indicating that the ancient Belgian large canids carried a substantial amount of genetic diversity. Furthermore, there is little evidence for phylogeographic structure in the Pleistocene large canids, as they do not form a homogenous genetic group. Although considerable variation occurs in the fossil canid isotope signatures between sites, the Belgian fossil large canids preyed in general on horse and large bovids.

1. Introduction

The evolutionary origin of the dog from wolves is well established via morphological (Benecke, 1987; Clutton-Brock, 1997; Morey, 1992; Nobis, 1986; Olsen, 1985) and genetic data (Savolainen et al., 2002; Vilà et al., 1997). Between 14,000 and 10,000 years ago dogs are known from Western Europe (Nobis, 1986; Chaix, 2000), Southern Europe (Altuna et al., 1985; Vigne, 2005), the Near East (Davis and Valla, 1978; Tchernov and Valla, 1997), the Russian Plain (Sablin and Khlopachev, 2002, 2003) and Kamchatka (Dikov, 1996). Dogs accompanied humans into the New World 12,000–14,000 years ago (Fiedel, 2005; Leonard et al., 2002). At that time the ancestral population of dogs in Eurasia was probably already large (Leonard et al., 2002). According to Savolainen et al. (2002) most recent dog populations have a common origin from a single gene pool in East Asia, descending from approximately five mtDNA lineages. Genetic results suggest a much older origin of dogs than indicated by prehistoric finds (Vilà et al., 1997). mtDNA data indicate that the domestication of the dog started either at around 40,000 years ago or at around 15,000 years ago (Savolainen et al., 2002). According to Lindblad-Toh et al. (2005), an ancient genetic bottleneck accompanying the domestication of dogs occurred around 27,000 years ago. With this in mind, the low frequency of recognised dog skulls in Upper Palaeolithic sites is somewhat surprising. In our opinion, it is likely that a number of Palaeolithic dog remains have so far not been recognized. We conducted an osteometric analysis of fossil large canids, which possibly could be either dog or wolf, found in Belgian, Ukrainian and Russian sites with the aims of identifying and distinguishing Palaeolithic dogs from fossil wolves. Our hypotheses are that changes in dog morphology compared to wolf morphology appeared rather abruptly, that they were linked to the effects of domestication and that these changes became fixed in the dog population. If evidence cannot be not found to support these hypotheses, the alternative hypothesis would then be that substantial morphological differences were present between Pleistocene wolf populations, before domestication, and between lineages of wolves that led later on to recent wolves and dogs. In this situation we would expect to see a gradual morphological change

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doi:10.1016/j.jas.2008.09.033

from wolves to dogs. The osteometrics of the fossil large canids were compared through univariate and multivariate analyses to those of prehistoric dogs, recent wolves and recent dogs in order to establish to which group the fossil specimens belong. We did not distinguish a priori a group of fossil wolves. A similar approach was developed by Morey (1986) on Amerindian dogs and Benecke (1987) on European Palaeolithic finds. We studied some of the same specimens as the latter investigation, but added material unknown at the time of Benecke's analysis.

Genetic analysis was undertaken on Belgian fossil large canids with the goal to compare the analyzed Belgian specimens with the recent dog and wolf mtDNA haplotypes described to date.

Isotopic analyses were conducted with the aims of reconstructing the diet of the Belgian fossil large canids and comparing them to those of other Pleistocene fossil canids. This dietary information may provide some insight into the relationship between humans and the Pleistocene canids. Whether identified as Palaeolithic dogs or fossil wolves by the morphometric and DNA analyses, we aimed to consider the diets of the fossil canids in context of the speculated broadening of human diets during the mid/late Upper Palaeolithic to include freshwater resources (Richards et al., 2001).

2. Material and methods

2.1. Osteometric analysis

Our sample comprised of 117 skulls of recent and fossil large canids (Table 1). The AMS age or the supposed age of the skulls is given in Table 1. The Belgian canids originate from six Palaeolithic caves and one postglacial cave, located in the Condroz, a region in the south of Belgium (Fig. 1).

The Goyet cave is situated in a limestone cliff in the Samson valley, a tributary of the Meuse River. The cave consists of several chambers in which a large number of Middle and Upper Paleolithic artefacts were discovered along with numerous remains of ice age mammals (Dupont, 1873). Many of the fossil bones are broken, have cut marks, or display traces of ochre (Germonpré, 1996; Germonpré and Hämäläinen, 2007). The Palaeolithic artefacts date from the Mousterian, Aurignacian, Gravettian, and Magdalenian, which indicates recurrent occupations of the cave from the Pleniglacial until the Late Glacial. Unfortunately, it is not always clear from which horizon the artefacts and bones originated (Dewez, 1987; Otte and Groenen, 2001; Ulrix-Closset, 1975). Aurignacian ivory beads were discovered in Horizon 3 (Otte, 1979). This horizon is a palimpsest of multiple occupations (Miller, 2001). Other spectacular finds include "batons de commandement", needles, perforated teeth, a bone harpoon and shell necklaces from the Magdalenian (Horizons 1 and 2) (Dewez, 1987). Deeper inside the cave Dupont (1873) distinguished a fourth and fifth horizon containing mainly bones from cave bear and cave lion. The fossil canid skull found during Edouard Dupont's excavations in the 1860s has an AMS age of c. 31,700 BP. According to Dupont's unpublished notes, the skull was found in a side gallery of the cave, in Horizon 4, together with remains from mammoth, lynx, red deer and large canids.

The Trou des Nutons (Furfooz), Trou Bailleux and Trou de la Naulette caves are situated in limestone cliffs on the banks of the river Lesse, a tributary of the Meuse. In the 1860s, Dupont excavated in Trou des Nutons cave a partly associated skeleton of a large canid that he identified as wolf (Dupont, unpublished notes). The right humerus displays cut marks; the skull has an AMS age of 21,800 BP. However, the main bone horizon produced Magdalenian artefacts and a cut-marked phalanx of horse has been dated by AMS to 12,630 y BP (Charles, 1998). Trou de la Naulette is a famous Neanderthal site excavated by Dupont in the 1860s (Dupont, 1873). According to the notes of Dupont, the fossil canid skull was found in the Second Horizon, the same containing the Neanderthal remains. Trou Baileux (Balleux) was excavated in 1866 and in the 1980s (Dupont, unpublished notes; Depaepe, 1988). Dupont (unpublished notes) discovered remains from beaver, red deer, roe deer, horse, bison, sheep/goat and pig. The species present point to a postglacial age for this assemblage. The canid skull most probably forms part of the postglacial assemblage discovered by Dupont; its appearance is similar to that of the bones from this assemblage.

The cave of Grands Malades was situated on the left bank of the river Meuse. Several bones of large canids were discovered at the site, as were Mousterian artefacts (Ulrix-Closset, 1975).

The Ukrainian and Russian fossil large canids are from the Russian Plain and Siberia (Fig. 1). One skull from Siberia was found in the permafrost in fluvial deposits on the bank of a tributary of the Anabar River (Yakutia). This isolated find is not related to any prehistoric site and therefore it is assumed that this specimen is from a fossil wolf. The other skulls were discovered at Upper Palaeolithic sites from the Russian Plain. The fauna at the Gravettian site of Avdeevo includes mammoth, rhinoceros, horse and reindeer. The large quantity of arctic fox and wolf bones suggests the existence of fur hunting. Most of the artefacts and art pieces are made from mammoth tusks (Gvozdover, 1995). The Epigravettian Mezin is well known for its round mammoth bone dwelling. At Mezherich, also dating from the Epigravettian, four mammoth bone dwellings are present (Pidoplichko, 1998; Soffer, 1985).

Dogs and wolves were used as reference groups (Table 1). The first reference group consisted of European prehistoric dogs, containing the two Palaeolithic dogs from the Epigravettian Eliseevich I site (Russian Plain), with an age of around 13,900 BP (Fig. 1). Here, remains of at least eight mammoth bone complexes and large quantities of worked ivory were discovered (Sablin and Khlopachev, 2002, 2003). The most complete dog skull (447) was found in a hearth deposit, near a concentration of mammoth skulls (Polikarpovich, 1968). Its braincase has been perforated on the left and right side (Sablin and Khlopachev, 2002, 2003). Cut marks are present on the zygomatic and frontal bones. With exception of the canines and some premolars, all its teeth are missing. In addition the left and right carnassials were apparently removed by damaging the alveoli.

In order to have a larger reference group, that contained more than two specimens, we added to the prehistoric dog group three younger and smaller dogs: the Epipalaeolithic dog of Saint-Thibaud, France (Chaix, 2000) and the Mesolithic dogs from the German sites Bedburg (Street, 1989) and Senckenberg (Degerbøl, 1961).

The second reference group was made up of recent dogs. Breeds of dogs whose genetic relationships are known from molecular marker studies were specifically selected (Parker et al., 2004). Phylogenetic analysis separated several dog breeds with ancient origins (Chow Chow, Siberian Husky) from a larger group of breeds with modern origins (Parker et al., 2004). Thus the recent dogs in our study were divided into two sub-groups: the recent archaic dogs (including Chow chow and Siberian Husky) and recent other dogs. The other modern breeds appear to represent a more recent radiation from shared European stock (Parker et al., 2004). We selected large animals with a wolf-size skull (Irish Wolfhound, Mastiff, Tibetan Mastiff, Great Dane, Doberman Pinscher, German Shepherd Dog) along with Malinois and Rottweiler, comparable in size to the Husky. We also added one skull of a Central Asian Shepherd Dog as an unclassified specimen.

Recent or historical wolves from Belgium, northwestern Russia, Caucasus, Jamal, Yakutia, Kamchatka and the Far East formed the last reference group. Two skulls from wolves kept in captivity in Belgian zoos were considered as unclassified specimen.

Only animals with the permanent dentition in place and complete fusion of the dorsal cranial sutures were considered in