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CONSUMPTION OF CANID MEAT AT THE GRAVETTIAN PŘEDMOSTÍ SITE, THE CZECH REPUBLIC

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Abstract: Předmostí is one of the most famous Gravettian sites in Central Europe. Its fame is based on a unique human assemblage, sadly largely destroyed during the Second World War, a huge mammoth assemblage and a very rich large canid assemblage. It has been shown previously that mammoth played an important role in the subsistence practices of the Gravettian inhabitants of Předmostí. Detailed analyses of the large canid postcranial material were carried out to investigate whether these canid remains can be assigned to different size groups and whether these remains show evidence of being butchered and consumed by humans. Based on defleshing marks and impact traces on the long bones, it is proposed here that large canids were consumed by the Gravettian inhabitants of Předmostí, thus further elucidating the specific human-large canid relationships that existed during the Upper Palaeolithic.

Key words: wolf, *Canis lupus*, dog, *Canis familiaris*, Upper Palaeolithic, Gravettian, domestication, canid meat consumption

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Introduction

Předmostí is part of a series of large Gravettian open-air sites located in Central Europe (Text-fig. 1) characterised by distinctive lithic tools (backed bladelets, micro-saws, geometric microliths), and by the presence of mammoth remains and ivory implements, ornaments, portable art and animal including human female representations. Mammoths played an important role in the Central European societies of Gravettian hunter-gatherers (Wojtal and Wilczyński 2015), both in life (e.g. ivory tools, ivory portable art, ornaments) and in death (several human burials were covered by mammoth scapulae) (Valoch 1981, Einwögerer et al. 2006, Trinkaus and Svoboda 2006, Svoboda 2008, Porr 2010, d'Errico et al. 2011, Lázničková-Galetová 2016). At Předmostí, the mammal assemblage is dominated by mammoth. Musil (1958, 1968) examined in detail the mammoth molars from this site. He concluded that the mammoth cows died at a relatively young age. Large canids are the second most abundant group at Předmostí based on the Minimum Number of Individuals (MNI) calculations (Pokorný 1951, Musil 2008).

Although the staple food of the Gravettian peoples from Předmostí has been shown to be mammoth (Absolon and Klíma 1977, Oliva 1997, Musil 2008, Bocherens et al. 2015), we investigated here whether the large canid assemblage present at this location shows evidence of butchery and consumption by humans, as is the case at other Gravettian

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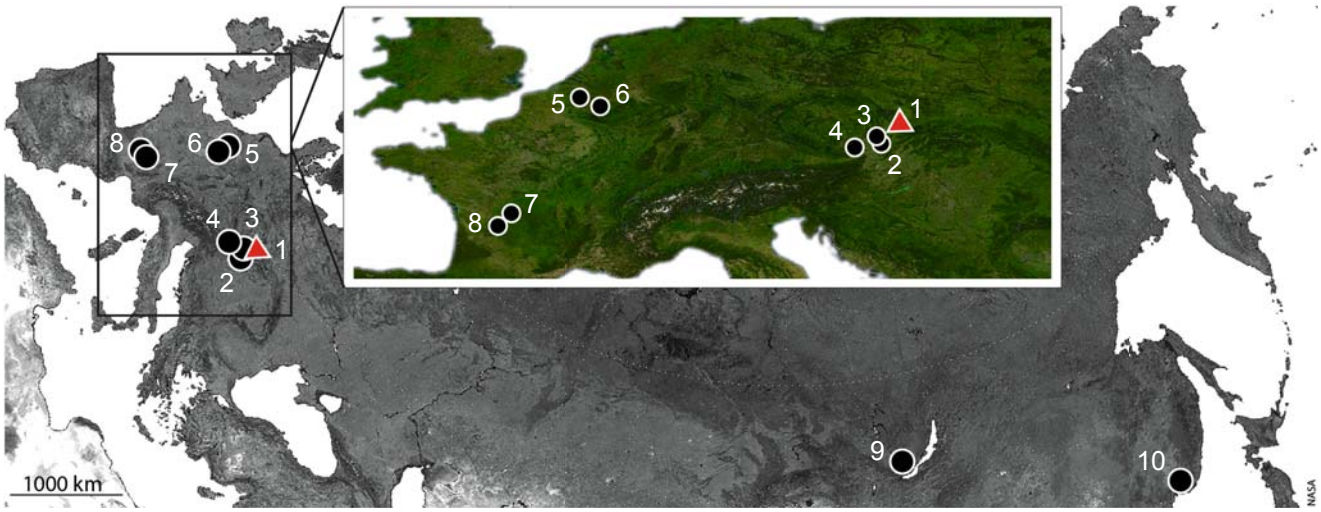


Text-fig. 1. Map of northern Eurasia with the most important sites discussed in the text: 1: Předmostí, 2: Pavlov, 3: Dolní Věstonice, 4: Krems Wachtberg, 5: Braives, 6: Trou des Nutons, 7: Jaurens, 8: Maldidier, 9: Lokomotiv, 10: Geographical Society cave.

sites from Central Europe (Fladerer 2001, Wojtal et al. 2012, Wilczyński et al. 2015). We aimed to verify if in the large canid assemblage from Předmostí human manipulation, as testified by cut marks and impact marks, can be discerned and furthermore looked for the possible presence of ochre traces. We also assessed plant root traces and carnivore gnawing. The osteometry of the long bones that had been modified by humans and carnivores was detailed and the size was characterised as "dog-like" or "wolf-like" (cf. Germonpré and Sablin 2017). We hope that this work will contribute to further clarification of the characteristics of human-canid relationships during the Gravettian.

Locality

Předmostí is situated on a south-facing slope in the Bečva valley in the so-called Moravian Corridor, the Czech Republic. The first organised excavations started here in the 1880s and continued well into the 2000s (Svoboda 2008, Wojtal and Wilczyński 2013). The lithic industry has traditionally been assigned to the Gravettian (Svoboda 2008). Two to three Upper Palaeolithic cultural layers have been noted at the site representing a long interval of prehistoric occupation. These can be considered to be composed of separate settlement units that are probably not contemporaneous but were in use during the Gravettian (Absolon and Klíma 1977, Svoboda et al. 1994, Svoboda 2008). Two AMS dates on bones from the upper and lower layer are available: 24,340 ± 120 BP (GrA-32641) for the upper layer and 26,780 ± 140 BP (GrA-32583) for the lower layer (Svoboda 2008); these dates result in a calibrated age range (95% probability) of 28,694 BP – 28,050 BP for the upper layer and a calibrated age range (95% probability) of 31,151 BP – 30,726 BP for the lower layer. A new AMS date, calculated from the cut marked femur (98-598-D) of a large canid, yielded an age of 24,492 ± 67 BP (ETH-76010), resulting in a calibrated age range (95%) of 28,754 BP – 28,328 BP. The calibrations were calculated using the Oxcal 3.4 program (https://c14.arch.ox.ac.uk/oxcal/OxCal.html).

Předmostí is well known for its rich human assemblage consisting of the remains of several individuals (Brůžek and Velemínská 2008). The funerary assemblage, for the most part excavated in 1894 by Maška, from the human burial area located near a rocky outcrop at the site, contained remains from mainly young people (Brůžek and Velemínská 2008). Sadly, most of these human remains were destroyed in a fire during the Second World War (Klíma 1991, Velemínská and Brůžek 2008).

The mammal assemblage at Předmostí is dominated by mammoth. Remains from more than 1,000 mammoths were discovered here (Musil 1968, Oliva 1997, Musil 2008). Maška (1884) excavated numerous remains and discovered that they were from young and subadult mammoths. Many mammoth long bones show clear traces of human modification, with evidence of intentional scraping of the bone or burning (Maška 1884). The mammoth age profile is dominated by young cows aged from 20 to 30 years (Musil 1958, 1968). This suggests a selective mortality, which is probably due to selective hunting of inexperienced females (Oliva 1997). The mammoth bones found at the site are probably remains from animals that most likely were hunted and eaten by the Gravettian inhabitants of Předmostí (Oliva 1997, Musil 2008, Bocherens et al. 2015). Furthermore, mammoth meat was probably the staple food of the Předmostí people (Absolon and Klíma 1977, Oliva 1997, Bocherens et al. 2015). Remains from other large herbivores such as bison, horse, and reindeer, are present but at low frequencies (Pokorný 1951, Musil 2008). Bones of the latter two species are highly fragmented having many carry cut marks (Maška 1884). Polar foxes are the third most numerous species in the mammal assemblage (Musil 2008).

Large canids are the second most abundant group at Předmostí based on the MNI calculations (Pokorný 1951, Musil 2008). While excavating the northern zone in 1894, Maška discovered several complete wolf skeletons. Furthermore, he noted in his dairies that he had also excavated the remains of dogs (Absolon and Klíma 1977, Maška 2008: 185). Maška's idea that dogs could have been present at Předmostí was not taken up by later researchers

Table 1. List of the long bones of large canids used in this study. RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; MZM, Moravian Museum, Anthropos Institute, Brno, the Czech Republic; ZIN RAS, Zoological Institute of the Russian Academy of Science, Saint-Petersburg, Russia; SNM, Natural History Museum of Denmark, Copenhagen, Denmark; NRM, Swedish Museum of Natural History, Stockholm, Sweden; ISU, Irkutsk State University, Irkutsk, Russia.

Long bones large canids	Age/AMS	Collection	Reference	NISP
Site				
Předmostí (Czech Republic)	24,492 ± 67 BP (ETH-76010)	MZM	This study	1,167
Reference groups				
Pleistocene wolves (PlW)				
Trou des Nutons (Belgium)	21,810 ± 90 BP (KIA-25298)	RBINS	Germonpré et al. (2009)	2
Maldidier (France)	Pleniglacial		Boudadi-Maligne (2010)	7
Jaurens (France)	Pleniglacial		Boudadi-Maligne (2010)	5
Geographical Society cave (Russia)	Pleniglacial	ZIN RAS	Baryshnikov (2015)	11
Postglacial and Recent Eurasian wolves				
Recent Northern wolves (rNw)	19th & 20th century	ZIN RAS, NRM	Germonpré et al. (2009, 2012, 2014)	16
Postglacial Northern wolves (PNw)	Holocene	RBINS, ISU	This study, Losey et al. (2011)	8
Postglacial Danish wolves (PDw)	Holocene	SNM	Aaris-Sørensen (1977)	23
Recent Northern dogs (rNd)				
Sakhalin dog (Russia)	19th century	SNM	Germonpré et al. (2009, 2012, 2015a)	3
Siberian dogs (Russia)	19th & 20th century	ZIN RAS	Germonpré et al. (2009, 2012, 2015a)	4
Inuit dogs (Greenland)	19th & 20th century	SNM	Germonpré et al. (2015a)	37
Total				1,283

(Germonpré et al. 2015a). Pokorný (1951), while studying the canids, distinguished two size groups: *Canis lupus major* and *Canis lupus minor*. He assigned *Canis lupus medium*, a third type that according to Pokorný (1951) was described by Maška, to the *Canis lupus minor* group. Pokorný (1951), however, did not refer to this publication by Maška. In the publication of 1908, Maška (1908) mentioned that *Canis intermedius* could have been an ancestor of early dogs. Possibly, Pokorný (1951) was referring to that description. He considered some of the canid cranial material from Předmostí to have characteristics reminiscent of both the dhole and the dog (Pokorný 1951: 47–48). Musil (2000) followed Pokorný's (1951) subdivision of the large canid material and explained the size difference between the two groups in terms of the sexual dimorphism of wolves (but see also Musil 2014). Based on multivariate analysis of complete skulls and mandibles, we propose that at Předmostí two canid morphotypes are present, namely the Palaeolithic dog morphotype and the Pleistocene wolf morphotype (Germonpré et al. 2012, 2013, 2015a, b, 2017).

Material and methods

This study is based on the collections held in the depository of the Moravian Museum (Brno, the Czech Republic). The number of long bones in the large canid remains were assessed using Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) (Lyman 1994). The number of cut marked and impacted bones, bones with ochre traces and the number of carnivore damaged bones were expressed in NISP, MNI and the MNI based on each element (MNIe). Ornaments and bone tools are not included in this study (see Germonpré et al. 2012, 2015a). Human manipulation of the bone material was recognised by cut marks, impact marks and ochre traces left on the canid remains.The cut and impact marks are described based on the descriptions in Binford (1981), Lyman (1994) and Fernández-Jalvo and Andrews (2016). The butchering procedure is reconstructed based on the location of the marks in relation to the insertions of muscles and ligaments on the long bones and the position of joint capsules (Evans 1993). Use of the skeletal remains by carnivores was assessed by recording indications of gnawing. Carnivore damage is described based on Sutcliffe (1970), Binford (1981), Fernández-Jalvo and Andrews (2016) and Fosse et al. (2012).

Measurements of the long bones of the Předmostí large canids, given in mm, were made according to von den Driesch (1976). The Předmostí long bones are compared with several reference groups (Tab. 1). The first reference group consists of Pleistocene wolves from the Trou des Nutons cave in Belgium (Germonpré et al. 2009), the Jaurens and Maldidier caves in France (Boudadi-Maligne 2010) and the Geographical Society cave in the Primorskii territory in Russia (Baryshnikov 2015). All these sites presumably date from the Pleniglacial. A second reference group composed of Eurasian wolves contains recent northern wolves from Sweden and Russia. Two groups of postglacial wolves are added: a postglacial Danish wolf group (Aaris-Sørensen 1977) and a postglacial northern wolf group. The latter group contains two individuals: a Neolithic wolf

from Lokomotiv, Siberia (Losey et al. 2011) and a Roman wolf from Braives (Belgium). Recent northern dogs from Siberia, Sakhalin and Greenland form a further reference group because these dogs lived, as did the Weichselian canids, in a cold environment. Furthermore, they are presumed to represent a lack of recent admixture with modern breeds thanks to their geographic and cultural isolation (cf. Larson et al. 2012, Brown et al. 2013, van Asch et al. 2013).

As the mean total length of the skull and mandible of Palaeolithic dogs are significantly less than the corresponding mean lengths of Pleistocene and recent northern wolves (Germonpré et al. 2015a: tab. 4, Germonpré et al. 2017: tabs 5, 7), we presume here that the mean lengths and widths of the long bones are also likely to be less in the Palaeolithic dog morphotype than the mean values in the Pleistocene wolf morphotype. We propose that some long bones of the Předmostí canids can be termed "dog-like in size" when at least one of their measurements falls inside the observed range of the recent northern dogs and is smaller than the corresponding lower limit of the observed ranges in the wolf groups in our data set (cf. Germonpré and Sablin 2017). The canid specimens can be described as "wolf-like in size" when the measurements of the long bone fall outside the observed ranges of these measurements from the recent northern dog group, and if at least one dimension of the bone is larger than the largest mean of the observed ranges of this measurement in the wolf groups from our data set. The modified canid bones that match one of these assumptions are described in the following text as resp. "dog-like in size" or "wolf-like in size". The long bones in which measurements do not correspond to either of these assumptions are considered here as large canids. However, their sizes can be described as "overlapping in size" when their dimensions fall in the overlapping ranges of dogs and wolves, or "wolf-range in size" when their dimensions are larger than those of the recent northern dogs, but smaller than the mean of the ranges of the wolves.

One modified mandible (97-583-C Pr 5-90-92) was not assigned in Germonpré et al. (2015a) to the Palaeolithic dog morphotype nor to the Pleistocene wolf morphotype because it was too fragmented to be included in one of the discriminant function analyses (DFA). Two of its measurements are added to a biplot based on the height of the mandible behind the first molar (Hm1m2) versus the alveolar length of the premolar row (ALp1p4), measured according to von den Driesch (1976). For the biplot, JMP (version 13.1.0) was used and significance was set at <0.05. For four reference groups (Pleistocene wolves, recent northern wolves, recent northern dogs and Palaeolithic dogs: see Germonpré et al. (2015a) for more details on the reference groups of the lower jaws), density ellipses (0.95) were calculated. These ellipses are both density contours and confidence curves that show where a given percentage (here 95%) of the data is expected to lie; they are computed from the bivariate normal distribution fit to the X and Y variables. For clarity reasons, only the position of the modified mandible is shown.

The estimated shoulder heights (SHe) of the canids were calculated based on the formulae given in Harcourt (1974) using the greatest length of complete long bones.The following formulae are used:

Humerus GL: $She = 3.43TL - 26.54$

Tibia GL: $She = 2.92TL + 9.41$

The mean and ranges of the body mass estimates (BMe) of the Předmostí canids and of the fossil and recent canid reference groups were calculated based on the regression equations given in Losey et al. (2015) and Losey et al. (2016). For the mandible fragment the following regression equation was used based on a combined wolf-dog set (Losey at al. 2015: tab. 5):

Mandible ALp1p4: $\log_{10}BMe = 2.487\log_{10} ALp1p4 - 2.707$ ($r^2 = 0.633$)

For the BMe based on the long bones of the Předmostí canids and of the wolf groups, regression equations were used on the basis of wolf limb dimensions (Losey et al. 2016: tab. 4). The following regression equations were used for the measurements in question:

humerus Dp: $lnBMe = 2.263lnDP - 5.459$ ($r^2 = 0.659$)
humerus Bd: $lnBMe = 1.781lnBd - 3.094$ ($r^2 = 0.670$)
ulna BPc: $lnBMe = 1.795lnBPc - 2.082$ ($r^2 = 0.620$)
femur Bp: $lnBMe = 1.744lnBp - 3.263$ ($r^2 = 0.659$)
femur Bd: $lnBMe = 2.113lnBd - 4.349$ ($r^2 = 0.561$)
tibia Bp: $lnBMe = 1.915lnBp - 3.765$ ($r^2 = 0.667$)

For the BMe based on the long bones of the recent northern dogs, regression equations were used on the basis of dog limb dimensions (Losey et al. 2016: tab. 2):

humerus Dp: $lnBMe = 2.268lnDP - 6.957$ ($r^2 = 0.852$)
humerus Bd: $lnBMe = 2.551lnBd - 6.025$ ($r^2 = 0.845$)
ulna BPc: $lnBMe = 2.122lnBPc - 3.145$ ($r^2 = 0.808$)
femur Bp: $lnBMe = 2.647lnBp - 6.677$ ($r^2 = 0.850$)
femur Bd: $lnBMe = 2.682lnBd - 6.372$ ($r^2 = 0.821$)
tibia Bp: $lnBMe = 2.766lnBp - 6.996$ ($r^2 = 0.858$)

Results

Skeletal representation

According to Musil (2008: tab. 2.1), the NISP of large canids from Předmostí totals 4,143 with a MNI of 103. Based on the mandibles present in the canid assemblage,

Table 2. NISP and MNIe of the long bones from the large canid assemblage from Předmostí. prox.: proximal, diaph.: diaphysis, dist.: distal.

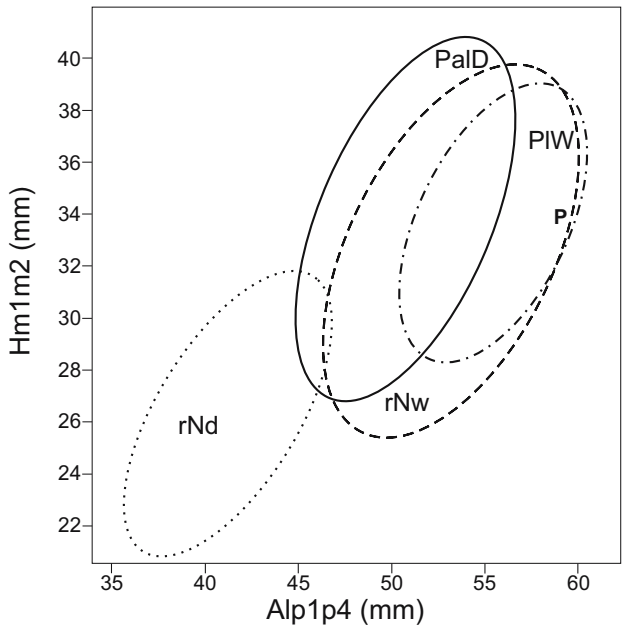
Předmostí: large canids	NISP					MNIe
	Complete	Prox.	Diaph.	Dist.	Total	Total
Humerus	53	94	6	129	282	95
Ulna	3	117			120	61
Radius	41	128	1	121	291	89
Femur	17	78	6	122	223	70
Tibia	36	123	3	89	251	80
Long bones total					1,167	102
All skeletal elements total					4,143[a]	120[b]

[a]Musil (2008)
[b]Germonpré et al. (2012)

a MNI of 120 was obtained (Germonpré et al. 2015a). All skeletal elements are represented (Pokorný 1951). We could reposition 1,167 long bones, and the MNI based on these long bones amounts to 102 (Tab. 2).

Measurements, estimated shoulder height and estimated body mass

The measurements of the long bones from the different groups in our data set are presented in Tables 3–6. Four modified bones from Předmostí can be described as "wolf--like in size", two modified bones as "dog-like in size" (Tabs 3–6). The observed range of the estimated shoulder heights for the Předmostí large canids is from 65 cm to 79 cm with a mean of 75 cm for the humerus and from 63 cm to 75 cm with a mean of 69 cm for the tibia (Tab. 7). The SHe of the wolf groups in our data set range from 66 cm to 82 cm based on the greatest length of the humerus and from 65 cm to 81 cm based on the greatest length of the tibia (Tab. 7), with means from resp. 73 cm to 78 cm and from 68 to 77 cm (Tab. 7). In recent northern dogs the SHe ranges from 53 cm to 70 cm with a mean of 62 cm, based on the humerus and from 53 cm to 66 cm with a mean of 59 cm, based on the tibia (Tab. 7). Body mass estimates are based on the widths and depths of the available bones (Tabs 8, 9). The Předmostí canids have BMe that ranges from 18 kg to 52 kg, with BMe means from 31 kg to 40 kg. The smallest BMe for a wolf in our data set is 29 kg and the largest BMe for a wolf is 47 kg, the means range from 33 kg to 43 kg (Tabs 8, 9). The observed range of the BMe for the recent northern dogs is from 21 kg to 38 kg, the mean BMe varies between 27 kg and 31 kg (Tabs 8, 9).



Text-fig. 2. Bivariate plot of the height of the mandible behind the first molar (Hm1m2: 19) by the alveolar length of the premolar tooth row p1 – p4 (Alp1p4: 11). P: Předmostí (97-583-C Pr 5-90-92); rNd: recent Northern dogs; PalD: Palaeolithic dogs; rNw: recent Northern wolves; PlW: Pleistocene wolves.

Table 3. The observed range (OR), mean and standard deviation of measurements, according to von den Driesch (1976), of the humerus from the large canid assemblage from Předmostí, from Pleistocene wolves, recent northern wolves. Postglacial Northern wolves (Aaris-Sørensen 1977), and recent northern dogs, and individual measurements of modified canid bones from Předmostí; dimensions are in mm; for details on the material see Table 1 and text. Value in bold: minimal value for "wolf-like in size", value in *italic*: measurement must be smaller for "dog-like in size". ≥: "wolf-like in size" measurement must be larger than or equal to the value that follows. ≤: "dog-like in size" measurement must be less than or equal to the value that follows.

		Humerus													
		GL					Dp				Bd				
Canis lupus/Canis familiaris		n	min	mean	max	sd	n	min	mean	max	sd	n	min	mean	max	sd
Předmostí: large canids	OR	53	195.85	215.92	238.89	12.35	75	47.05	55.20	62.04	3.38	170	34.22	45.15	51.36	3.23
Pleistocene wolves	OR	4	207.00	219.73	230.50	9.76	4	52.20	56.78	59.40	3.15	10	*39.20*	43.68	47.20	3.04
Recent Northern wolves	OR	5	219.60	231.44	247.20	11.25	5	54.40	**57.26**	59.10	1.86	5	45.50	**46.68**	47.50	0.85
Postglacial Northern wolves	OR	2	233.80	**235.40**	237.00							1			48.80	
Postglacial Danish wolves	OR	8	*201.00*	216.90	230.00		8	*52.00*	54.10	58.50		9	39.70	42.80	46.50	
Recent Northern dogs	OR	29	165.00	188.60	212.00	11.13	7	43.00	48.63	52.90	3.03	8	36.90	39.45	42.00	1.98
Canid "dog-like in size"	OR		≤ 201.00					≤ 52.00					≤ 39.00			
Canid "wolf-like in size"	OR		≥ 235.50					≥ 57.50					≥ 47.00			
Předmostí "wolf-like in size"																
98-594-B-P (2)			233.30					60.40					50.39			
98-594-C-P (2)			221.25					57.44					49.32			

Table 4. The observed range (OR), mean and standard deviation of measurements, according to von den Driesch (1976), of the ulna from the large canid assemblage from Předmostí, from Pleistocene wolves, recent northern wolves, Postglacial northern wolves, Postglacial Danish wolves (Aaris-Sørensen 1977), and recent northern dogs, and individual measurements of modified canid bones from Předmostí; dimensions are in mm; for details on the material see Table 1 and text. Value in bold: minimal value for "wolf-like in size", value in *italic*: measurement must be smaller for "dog-like in size", ≥: "wolf-like in size" measurement must be larger than or equal to the value that follows, ≤: "dog-like in size" measurement must be less than or equal to the value that follows.

Ulna						
Canis lupus/ Canis familiaris		BPC				
		n	min	mean	max	sd
Předmostí: large canids	OR	42	15.75	21.35	25.93	2.34
Pleistocene wolves	OR	3	*22.90*	**24.20**	25.80	4.93
Recent Northern wolves	OR	1		23.80		
Recent Northern dogs	OR	7	19.74	21.26	23.26	1.17
Canid "dog-like in size"			≤ 22.50			
Canid "wolf-like in size"			≥ 24.50			

The position of the modified lower jaw (97-583-C-Př5-90-92) on the biplot of the height of the mandible behind the first molar (Hm1m2) versus the alveolar length of the tooth row of the premolars (Alp1p4) suggests that this specimen has more affinities with wild wolves since it falls completely outside the 95% density ellipse of Palaeolithic dogs and recent northern dogs, and inside the 95% density ellipses of the Pleistocene and recent northern wolves (Text-fig. 2). It has a BMe of 51 kg (Tabs 10, 11).

The measurements of nine modified Předmostí humeri are compared with corresponding measurements from the reference groups. Based on the criteria we proposed, one modified humerus (98-594-B-P (2)) is "wolf-like in size", not on the basis of its total length but on the basis of the maximum depth at its proximal end (Dp) and the maximum breadth at its distal end (Bd); both measurements exceed the means for these dimensions for the wolves in our data set (Tabs 3, 12). This wolf has a SHe of 77 cm and a BMe of 46 kg (Tabs 7–9, 12). The measurement of one modified ulna is compared to the ranges in our data sets. It falls outside the range of the recent northern dogs and inside the ranges of the wolves (Tabs 4, 12). Its BMe is 36 kg (Tab. 12). Three modified femora are compared to the data sets (Tabs 5, 12). One of these can be described as "wolf-like in size". This specimen has a BMe of 49 kg (Tabs 5, 8–9, 12). The comparison of the measurements of five modified tibiae with the data sets revealed that one tibia can be described as "wolf-like in size" with a BMe of 39 kg, two tibiae can be described as "dog-like in size". They have a BMe of resp. 28 kg and 29 kg (Tabs 6, 8–9, 12).

Human modifications

Several remains of large canids from Předmostí show evidence of human modification: cut marks (see also Valoch 2013), impact marks, ochre traces and inserted bone fragments could be discerned (Tabs 10–12, Text-fig. 3). Eight brain cases show evidence of perforation on the left and/or the right side. These manipulated skull fragments are described in Germonpré et al. (2012), two are from Palaeolithic dogs, one from a Pleistocene wolf (Germonpré et al. 2012). Human modified dentition, such as perforated and decorated teeth, is discussed in Germonpré et al. (2012). A skull from a Palaeolithic dog was found holding a bone fragment between its front teeth (Germonpré et al. 2012); a

Table 5. The observed range (OR), mean and standard deviation of measurements, according to von den Driesch (1976), of the femur from the large canid assemblage from Předmostí, from Pleistocene wolves, recent northern wolves, Postglacial northern wolves, Postglacial Danish wolves (Aaris-Sørensen 1977), and recent northern dogs, and individual measurements of modified canid bones from Předmostí; dimensions are in mm; for details on the material see Table 1 and text. Value in bold: minimal value for "wolf-like in size", value in *italic*: measurement must be smaller for "dog-like in size", ≥: "wolf-like in size" measurement must be larger than or equal to the value that follows, ≤: "dog-like in size" measurement must be less than or equal to the value that follows.

Femur											
Canis lupus/Canis familiaris		Bp					Bd				
		n	min	mean	max	sd	n	min	mean	max	sd
Předmostí: large canids	OR	56	47.33	53.91	62.51	3.19	66	37.79	43.57	50.70	2.41
Pleistocene wolves	OR	3	50.80	**55.13**	58.10	3.84	4	*39.10*	**43.78**	45.70	3.15
Recent Northern wolves	OR	5	49.40	54.34	57.00	2.96	5	41.40	43.88	45.20	1.46
Postglacial Northern wolves	OR	1			58.40		1			47.60	
Postglacial Danish wolves		7	*46.20*	51.10	53.80		6	39.50	41.20	46.00	
Recent Northern dogs	OR	8	39.50	44.00	48.80	3.17	8	35.00	38.43	41.30	2.28
Canid "dog-like in size"			≤ 46.00					≤ 39.00			
Canid "wolf-like in size"			≥ 55.50					≥ 44.00			
Předmostí "wolf-like in size"											
98-598-D			60.17								

Table 6. The observed range (OR), mean and standard deviation of measurements, according to von den Driesch (1976), of the tibia from the large canid assemblage from Předmostí, from Pleistocene wolves, recent northern wolves, Postglacial northern wolves, Postglacial Danish wolves (Aaris-Sørensen 1977), and recent northern dogs, and individual measurements of modified canid bones from Předmostí; dimensions are in mm; for details on the material see Table 1 and text. Value in bold: minimal value for "wolf-like in size", value in *italic*: measurement must be smaller for "dog-like in size", ≥: "wolf-like in size" measurement must be larger than or equal to the value that follows, ≤: "dog-like in size" measurement must be less than or equal to the value that follows.

Tibia														
Canis lupus/*Canis familiaris*		GL				Bp				Bd				
		n	min	mean	max	sd	n	min	mean	max	sd	n	min	mean	max	sd
Předmostí: large canids	OR	36	211.83	233.17	253.28	10.27	65	38.11	46.85	51.50	2.65	92	27.00	30.47	34.30	1.65
Pleistocene wolves	OR	4	*217.80*	230.60	245.30	11.67	3	*41.60*	47.13	51.20	4.97	7	28.70	**31.01**	34.30	1.91
Recent Northern wolves	OR	5	247.00	**258.82**	273.50	10.51	5	45.80	**48.32**	50.20	1.69	4	28.90	30.48	31.50	1.27
Postglacial Northern wolves	OR	2	255.00	256.50	258.00		1			51.11		1			32.00	
Postglacial Danish wolves		6	218.00	233.70	243.00		6	43.60	46.10	50.90		6	*28.00*	29.40	31.30	
Recent Northern dogs	OR	30	177.40	198.50	221.00	11.51	8	38.00	41.09	44.00	2.21	7	23.90	25.64	27.30	1.24
Canid "dog-like in size"			≤ 217.50					≤ 41.50					≤ 27.00			
Canid "wolf-like in size"			≥ 259.00					≥ 48.50					≥ 31.50			
Předmostí "wolf-like in size"																
98-598-B-Predm 1928								48.52								
Předmostí "dog-like in size"																
98-596-B (1) Pr15/5 83								41.40								
97-597-C-Pr85-1929								41.00								

Table 7. The observed range (OR), mean and standard deviation of the estimated shoulder heights (SHe) based on measurements according to von den Driesch (1976) calculated with the formule in Harcourt (1974) using the greatest length of the humerus and tibia from the large canid assemblage from Předmostí, from Pleistocene wolves, recent northern wolves, Postglacial northern wolves, Postglacial Danish wolves (Aaris-Sørensen 1977), and recent northern dogs, and of the individual SHe of modified canid bones from Předmostí; dimensions are in cm; for details see text. Value in bold: minimal value for "wolf-like in size", value in *italic*: measurement must be smaller for "dog-like in size", ≥: "wolf-like in size" measurement must be larger than or equal to the value that follows, ≤: "dog-like in size" measurement must be less than or equal to the value that follows.

Humerus						
Canis lupus/*Canis familiaris*		Estimated shoulder height (cm)				
		n	min	mean	max	sd
Předmostí: large canids	OR	53	64.5	75.2	79.3	4.24
Pleistocene wolves	OR	4	68.4	72.7	76.4	3.35
Recent Northern wolves	OR	5	72.7	76.7	82.1	3.86
Postglacial Northern wolves	OR	2	77.5	**78.1**	78.8	
Postglacial Danish wolves	OR	8	*66.3*	71.7	76.2	
Recent Northern dogs	OR	29	53.9	62.0	70.1	3.82
Canid "dog-like in size"	OR		≤ 66.0			
Canid "wolf-like in size"	OR		≥ 78.5			
Předmostí "wolf-like in size"						
98-594-B-P (2)			77.4			
Tibia						
Canis lupus/*Canis familiaris*		Estimated shoulder height (cm)				
		n	min	mean	max	sd
Předmostí: large canids	OR	36	62.8	69.0	74.9	3.00
Pleistocene wolves	OR	4	*64.5*	68.3	72.6	3.41
Recent Northern wolves	OR	5	73.2	**76.5**	80.8	3.07
Postglacial Northern wolves	OR	2	75.4	75.8	76.3	
Postglacial Danish wolves	OR	6	64.6	69.2	71.9	
Recent Northern dogs	OR	30	52.7	58.9	65.5	3.36
Canid "dog-like in size"			≤ 64.5			
Canid "wolf-like in size"			≥ 77.0			

snout fragment from a large canid has a rib inserted in its nasal cavity (Text-fig. 4). Eight humeri (2.8 % $NISP_{humerus}$) from at least five individuals (5.3 % $MNI_{humerus}$) bear marks of human manipulation. An ulna (0.8 % $NISP_{ulna}$) and radius (0.3 % $NISP_{radius}$), from one individual (1.6% MNI_{ulna}, 1.1 % MNI_{radius}), were modified by humans.Three femora (1.4 % $NISP_{femur}$) from at least two individuals (2.9% MNI_{femur}) show traces of human modification. Six tibiae (2.4 % $NISP_{tibia}$) from at least four individuals (5% MNI_{tibia}) display signs of human involvement (Tabs 10, 11). In total, 19 long bones from large canids (0.5% $NISP_{all}$) from at least six individuals (5% MNI_{all}) show evidence that they had been modified by Gravettian people (Tabs 10, 11). Details of the modified bones are given below and in Tables 10–12.

Table 8. The observed range (OR), mean and standard deviation of the estimated body mass (BMe) based on the measurements according to von den Driesch (1976), calculated with the formules in Losey et al. (2016) using the depth of the proximal end (Dp) and the breadth of the distal end of the humerus and the breadth across the coronoid process of the ulna (BPC) from the large canid assemblage from Předmostí, from Pleistocene wolves, recent northern wolves, Postglacial northern wolves, Postglacial Danish wolves (Aaris-Sørensen1977), and recent northern dogs, and of the individual BMe of modified canid bones from Předmostí, dimensions are in kg; for details see text. Value in bold: minimal value for "wolf-like in size", value in italic: measurement must be smaller for "dog-like in size", ≥: "wolf-like in size" measurement must be larger than or equal to the value that follows, ≤: "dog-like in size" measurement must be less than or equal to the value that follows.

Humerus											
Canis lupus/Canis familiaris		Estimated body mass (Dp) (kg)					Estimated body mass (Bd) (kg)				
		n	min	mean	max	sd	n	min	mean	max	sd
Předmostí: large canids	OR	75	26.0	37.5	48.6	5.09	170	24.5	40.3	50.5	
Pleistocene wolves	OR	4	32.8	39.8	44.0	4.84	10	*31.2*	37.9	43.4	4.67
Recent Northern wolves	OR	5	36.1	**40.5**	43.5	2.93	5	40.7	**42.6**	43.9	1.38
Postglacial Northern wolves	OR						1			46.1	
Postglacial Danish wolves	OR	8	*32.6*	35.6	42.5		8	31.9	36.5	42.3	
Recent Northern dogs	OR	7	21.7	30.4	37.7	4.88	8	24.0	28.6	33.4	3.63
Canid "dog-like in size"	OR		≤ 32.5					≤ 31.0			
Canid "wolf-like in size"	OR		≥ 41.0					≥ 43.0			
Předmostí "wolf-like in size"											
98-594-B-P (2)			45.7					48.8			
98-594-C-P (2)			40.8					46.9			

Ulna						
Canis lupus/Canis familiaris		Estimated body mass (BPC) (kg)				
		n	min	mean	max	sd
Předmostí: large canids	OR	42	17.6	30.6	43.0	5.88
Pleistocene wolves	OR	3	*34.4*	**38.1**	42.6	15.42
Recent Northern wolves	OR	1	36.9			
Recent Northern dogs	OR	7	24.2	28.3	34.2	3.36
Canid "dog-like in size"			≤ 34.0			
Canid "wolf-like in size"			≥ 38.5			

Cut marks

Cut marks were observed on the humerus, ulna, radius, femur and tibia. Several types of cut marks could be discerned: marks related to disarticulation, defleshing, "repetitive" marks and a fourth type possibly in connection with bone tool manufacturing. Cut marks are absent on the skulls and mandibles, with the exception of a lower jaw from an Iron Age dog (Germonpré et al. 2015a), and were not observed on postcranial elements with the exception of the long bones here discussed.

Skinning marks

No specific cut marks related to skinning activities such as marks encircling the shaft of radius, tibia, metapodials or phalanges (cf. Binford 1981) were noticed.

Disarticulation marks

The vast majority of the large canids bones with disarticulation marks are from canids "wolf-like in size" or "wolf-range in size" (Tab. 12). Six humeri (1.77 % $NISP_{humerus}$) from at least five individuals (5.3 % $MNI_{humerus}$) carry cut marks related to the disarticulation of the humerus from the shoulder blade or the lower forelimb (Tabs 10–12, Text-fig. 3). Humerus 98-594-B-P (1) displays cut marks on the head. The purpose of this cut was likely to detach the m. infraspinatus just above its point of attachment on the humerus (near the facies m. infraspinati) near the more superficially located m. deltoideus (under its origin at the acromion) and to finally sever the articular capsule with its reinforcement strips (ligamentum glenohumeralia) (Text-fig. 5). The cutting on humerus 98-594-B-P (2) is comparable to the cut marks on 98-594-B-P (1), but here the m. supraspinatus and the joint capsule were cut dorsolaterally. This specimen is "wolf-like in size" (Tabs 3–6, 12). The cut marks on humerus 98-594-C-P (3) are comparable to the ones on humerus 98-594-B-P (1) which served the purpose of disarticulating the shoulder joint. Humerus 98-594-C-P (2) was deeply cut several times in succession (Text-fig. 6). These marks are most easily explained by disarticulation, taking into account their location, and do not seem related to decoration of the bone. The oblique deep cuts on the tuberositas teres minor suggest that the deep lying muscles teres minor and m. infraspinatus were cut to enable disarticulation from the scapula (Text-fig. 6). This specimen is also from a "wolf-like in size" individual

Table 9. The observed range (OR), mean and standard deviation of the estimated body mass (BMe) based on the measurements according to von den Driesch (1976), calculated with the formules in Losey et al. (2016) using the breadth of the proximal end (Bp) and the breadth of the distal end (Bd) of the femur and the tibia from the large canid assemblage from Předmostí, from Pleistocene wolves, recent northern wolves, Postglacial northern wolves, Postglacial Danish wolves (Aaris-Sørensen1977), and recent northern dogs, and of the individual BMe of modified canid bones from Předmostí, dimensions are in kg; for details see text. Value in bold: minimal value for "wolf-like in size", value in *italic*: measurement must be smaller for "dog-like in size", ≥: "wolf-like in size" measurement must be larger than or equal to the value that follows, ≤: "dog-like in size" measurement must be less than or equal to the value that follows.

Femur											
Canis lupus/*Canis familiaris*		Estimated body mass (Bp) (kg)					Estimated body mass (Bd) (kg)				
		n	min	mean	max	sd	n	min	mean	max	sd
Předmostí: large canids	OR	56	31.9	40.2	51.9	4.16	66	27.7	37.7	51.8	4.40
Pleistocene wolves	OR	3	36.1	**41.8**	45.7	5.00	4	*29.9*	38.1	41.6	5.55
Recent Northern wolves	OR	5	34.4	40.7	44.2	3.79	5	33.7	**38.2**	40.6	2.62
Postglacial Northern wolves	OR	1			46.1		1			45.3	
Postglacial Danish wolves	OR	7	*30.6*	36.5	39.9		6	30.5	33.4	42.1	
Recent Northern dogs	OR	8	21.2	28.5	37.1	5.40	8	23.7	30.6	36.9	4.79
Canid "dog-like in size"			≤ 30.5					≤ 29.5			
Canid "wolf-like in size"			≥ 42.0					≥ 38.5			
Předmostí "wolf-like in size"											
98-598-D			48.5								
Tibia											
Canis lupus/*Canis familiaris*		Estimated body mass (Bp) (kg)					Estimated body mass (Bd) (kg)				
		n	min	mean	max	sd	n	min	mean	max	sd
Předmostí: large canids	OR	65	24.7	36.8	44.0	3.94	92	30.1	37.7	46.9	3.77
Pleistocene wolves	OR	3	*29.2*	37.3	43.5	7.34	7	33.7	**39.0**	46.9	4.49
Recent Northern wolves	OR	5	35.1	**38.9**	41.9	2.59	4	*31.1*	37.7	40.0	2.88
Postglacial Northern wolves	OR	1			43.3		1			41.2	
Postglacial Danish wolves	OR	6	32.0	35.6	43.0		6	32.2	35.2	39.6	
Recent Northern dogs	OR	8	21.5	26.8	32.2	3.91	7	18.7	22.9	27.1	3.10
Canid "dog-like in size"			≤ 29.0					≤ 31.0			
Canid "wolf-like in size"			≥ 39					≥ 39			
Předmostí "wolf-like in size"											
98-598-B-Predm 1928			39.2								
Předmostí "dog-like in size"											
98-596-B (1) Pr15/5 83			28.9								
97-597-C-Pr85-1929			28.4								

(Tabs 3, 12). Humerus Předm 1928-P12404 bears cut marks below the cranial part of the tuberculum majus, just distal of the attachment site of m. infraspinatus. This mark could be related to cutting through the more superficially located muscles such as the m. deltoideus. One humerus (98-594-C-P (12)) bears cut marks on the distal epiphysis. Transversal cut marks occur on the medial trochlear ridge. The location of these marks suggests that the joint capsule, maybe together with the medial collateral ligament, was severed for disarticulation of the humerus from the lower forelimb.

Two femora (0.9% $NISP_{femur}$) from two individuals (2.9% MNI_{femur}) have cut marks that can be related to disarticulation (Tabs 10–12, Text-fig. 3). Femur 98-598-D carries marks in the neck related to cutting of the joint capsule to dismember the femur from the hip joint (Text-fig. 7). It is described as "wolf-like in size" (Tabs 5, 12). Femur 98-601a-D presents longitudinal cut marks on the posterior upper shaft which would cut through the m. quadratus femoris from which the end of the tendon inserts just below the fossa trochanterica. This muscle must be cut through in order to disarticulate the hip joint.

One tibia (98-589-B-Předmostí 1928) (0.4% $NISP_{tibia}$, 1.3% MNI_{tibia}) displays cut marks most likely related to dismembering the tibia from the femur and the patella (Tabs 10–12). Transversal marks on the tibial tuberosity and on the medial face below the medial condyle are connected with cutting loose the quadriceps femoris from the patella and the ligamentum patellae. The transversal marks on the tibial crest indicate cutting just above the end of the tendon to sever the m. sartorius, gracilis and semitendinosus (Text-figs 3, 8). This tibia is "wolf-like in size" (Tabs 6, 12).

Defleshing marks

Most large canid bones with defleshing marks are from canids which are "wolf-range in size" (Tab. 12). One

Table 10. The NISP and frequencies of cut marks, ochre traces, impact marks, gnawing traces and root traces observed on the cranial material and the long bones from the large canid assemblage from Předmostí. disartic.: disarticulation, deflesh.: defleshing, repetit.: repetitive, manu.: manufacturing, hum.: human; manip.: manipulation, gnaw.: gnawing.

Předmostí: large canids	Human modifications									Gnaw. traces	Root traces
	Cut marks					Ochre traces	Impact traces	Inserted bone	Total NISP hum. manip.		
	Disartic.	Deflesh.	Repetit.	Tool manu.	Total NISP cut marks						
Long bones											
Humerus (NISP)	6		1		6	1	1		8	1	86
$NISP_{humerus}$ %	2.13		0.35		2.13	0.35	0.35		2.84	0.35	30.50
Ulna (NISP)		1			1				1	1	17
$NISP_{ulna}$ %		0.83			0.83				0.83	0.83	14.17
Radius (NISP)				1	1				1		84
$NISP_{radius}$ %				0.34	0.34				0.34		28.87
Femur (NISP)	2	1	1	1	3				3		57
$NISP_{femur}$ %	0.90	0.45	0.45	0.45	1.35				1.35		25.56
Tibia (NISP)	1	3	1	2	5	2			6	1	106
$NISP_{tibia}$ %	0.40	1.20	0.40	0.80	1.99	0.80			2.39	0.40	42.23
$NISP_{long\ bones}$	9	5	3	4	16	3	1		19	3	350
$NISP_{long\ bones}$ %	0.77	0.43	0.26	0.34	1.37	0.26	0.09		1.63	0.26	29.99
$NISP_{all}$ %	0.22	0.12	0.07	0.10	0.39	0.07	0.02		0.46	0.07	8.45
Cranium + mandible											
Neurocranium[a] (NISP)							8		8		
$NISP_{cranium}$%							40.00		40.00		
Skull/snout[a] (NISP)								2	2		
$NISP_{skull/snout}$%								9.09	9.09		
mandible (NISP)							1		1		
$NISP_{mandible}$%							0.83		0.83		
$NISP_{all}$	9	5	3	4	16	3	10	2	30	3	350
$NISP_{all}$ %	0.22	0.12	0.07	0.10	0.39	0.07	0.24	0.05	0.72	0.07	

[a]Germonpré et al. (2012)

ulna (98-596-D) (0.8% $NISP_{ulna}$, 1.6% MNI_{ulna}) displays transverse cut marks on the lateral surface of the olecranon process related to cutting of the caput longum and the caput laterale of the m. triceps (Text-figs 3, 9, Tabs 10–12).

One femur (98-601a-D) (0.5% $NISP_{femur}$, 1.4% MNI_{femur}), which also carries disarticulation marks (see above), presents transversal cut marks on the anterior upper shaft below the neck probably to remove the meat of the quadriceps femoris muscle (Text-figs 3, 10, Tabs 10–12).

Three tibiae (1.2% $NISP_{tibia}$) from at least two individuals (2.5% MNI_{tibia}) bear cut marks suggesting filleting (Tabs 10–12). A tibia fragment from a subadult canid (98-601a 368F) carries longitudinal cut marks on the lateral face of the upper shaft probably where meat was extracted from the m. fibularis longus and maybe also the lateral part of the m. flexor digitorum profundus (Text-figs 3, 11). The longitudinal cut marks on the lateral face of the upper tibial shaft of complete tibia 97-597-A-Pr82 can also be related to the removal of

Table 11. The MNI and frequencies of cut marks, ochre traces, impact marks and gnawing traces observed on the cranial material and the long bones from the large canid assemblage from Předmostí. disartic.: disarticulation, deflesh.: defleshing, repetit.: repetitive, manu.: manufacturing, hum.: human; manip.: manipulation, gnaw.: gnawing.

Předmostí: large canids	Human modifications									Gnaw. traces
	Cut marks					Ochre traces	Impact traces	Inserted bone	Total MNI hum. manip.	
	Disartic.	Deflesh.	Repetit.	Tool manu.	Total MNI cut marks					
Long bones										
Humerus (MNI)	5		1	1	5	1	1		5	1
$MNI_{humerus}$ %	5.26		1.05	1.05	5.26	1.05	1.05		5.26	1.05
Ulna (MNI)		1			1				1	1
MNI_{ulna} %		1.64			1.64				1.64	1.64
Radius (MNI)				1	1				1	
MNI_{radius} %				1.12	1.12				1.12	
Femur (MNI)	2	1	1	1	2				2	
MNI_{femur} %	2.86	1.43	1.43	1.43	2.86				2.86	
Tibia (MNI)	1	2	1	1	3	2			4	1
MNI_{tibia} %	1.25	2.50	1.25	1.25	3.75	2.50			5.00	1.25
$MNI_{long\ bones}$	5	2	1	2	6	2	1		6	2
$MNI_{long\ bones}$ %	4.90	1.96	0.98	1.96	5.88	1.96	0.98		5.88	1.96
MNI_{all} %	4.17	1.67	0.83	1.67	5.00	1.67	0.83		5.00	1.67
Cranium + mandible										
Neurocranium[a] (MNI)							8		8	
$MNI_{cranium}$%							40.00		40.00	
Skull/snout[a] (MNI)								2	2	
$MNI_{skull/snout}$%								10.00	10.00	
mandible (MNI)							1		1	
$MNI_{mandible}$%							0.83		0.83	
MNI_{all}	5	2	1	2	6	2	8	2	9	2
MNI_{all} %	4.17	1.67	0.83	1.67	5.00	1.67	6.67	1.67	7.50	1.67

[a]Germonpré et al. (2012)

these same muscles. Tibia fragment 98-596-B (2) presents longitudinal cut marks on the lateral face of the mid tibial shaft that suggest the removal of the lateral located muscles: the dorsolateral m. tibialis cranialis and m. extensor digitorum longus, the lateral m. fibularis longus covering them, extensor digitorum lateralis, and caudolaterally the lateral part of the m. flexor digitorum lateralis.

"Repetitive" marks

Humerus Předm 1928-P12404 (0.4% $NISP_{humerus}$, 1.1% $MNI_{humerus}$), which shows evidence of disarticulation, also presents parallel transversal cut marks on the medial side of the upper shaft of the humerus (Text-figs 3, 12, Tabs 10–12). Femur Předm 1928-P12403 (0.5% $NISP_{femur}$, 1.4% MNI_{femur}) presents regularly spaced cut marks at its mid shaft (Text-figs 3, 13, Tabs 10–12). This specimen is described in Valoch (2013). Tibia 98-596- B(2) (0.4% $NISP_{tibia}$, 1.3% MNI_{tibia}) displays oblique parallel cut marks on its shaft (Tabs 10–12).

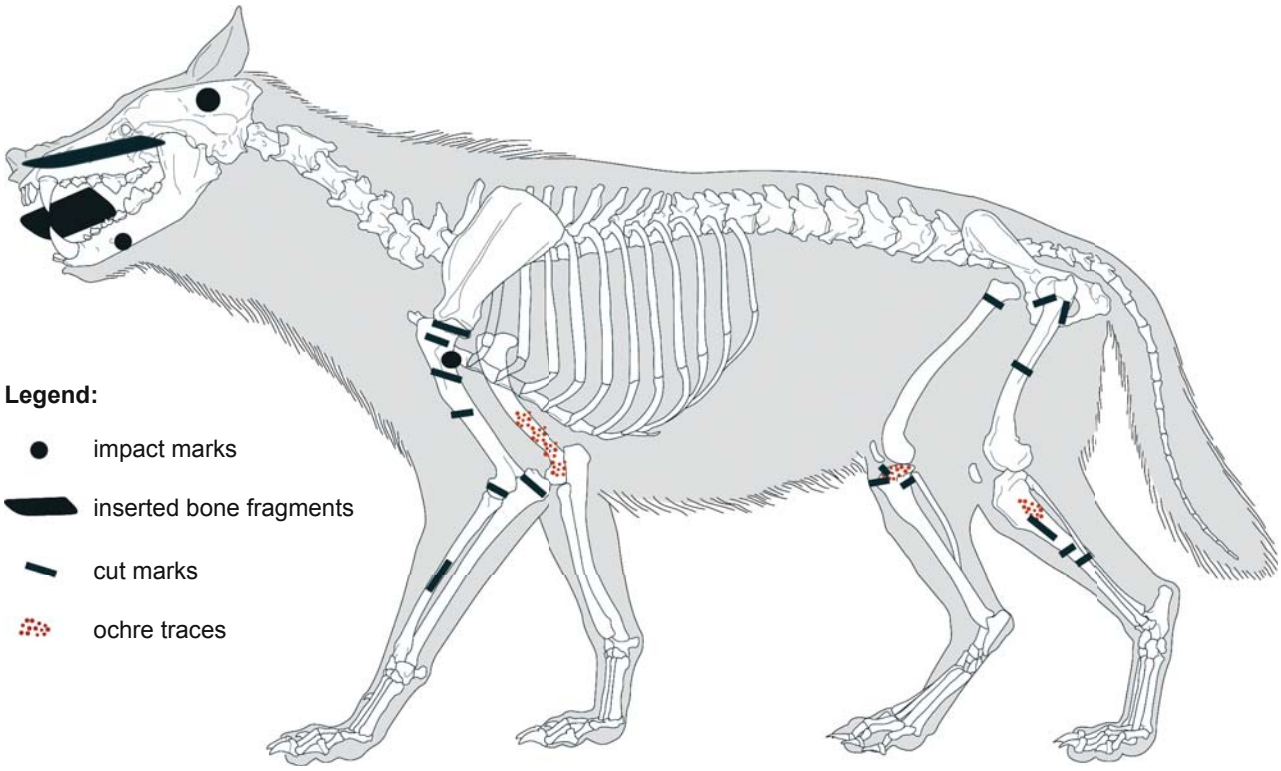
Marks related to manufacturing tools

A few bones present cut marks that could be related to bone tool manufacturing: a radius (0.3% $NISP_{radius}$, 1.1% MNI_{radius}), a femur (0.5% $NISP_{femur}$, 1.4% MNI_{femur}) and two tibiae (0.8% $NISP_{tibia}$, 1.3% MNI_{tibia}) (Tabs 10–12). Radius

Table 12. Overview of the modified canid bones from the Předmostí assemblage analysed for this study with individual measurements, estimated shoulder height (SHe), estimated body mass (BMe), general size and type of modification. w-l: "wolf-like in size", overl: "overlapping in size", w-r: "wolf-range in size", d-l: "dog-like in size", disartic.: disarticulation, deflesh.: defleshing, repetit.: repetitive, m.: manufacturing, gnaw.: gnawing, PD: Palaeolithic dog, PlW: Pleistocene wolf.

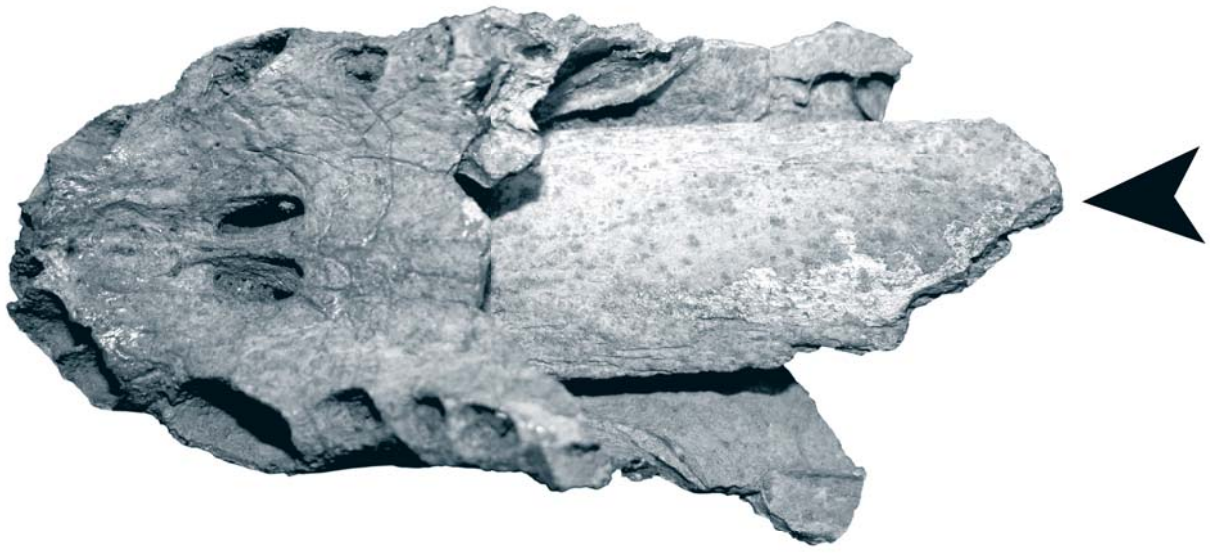
Předmostí: modified large canid bones	Metrics					Size	Human modifications							Gnaw. traces	Root traces
				SHe	BMe		Cut marks				Ochre traces	Impact marks	Inserted bone		
Element	mm	mm	mm	cm	kg		Disartic.	Deflesh.	Repetit.	Tool m.					
Skull															
neurocrania (NISP: 8)[a]						PD. PlW						X			
Předmostí (-)[a]						PD							X		
snout (NISP: 10)													X		
Mandible	ALp1p4	clm1	Hm1m2												
97-583-C Pr 5 90-92	59.54	30.64	33.63		50.9	w-l						X			
Humerus	TL	Dp	Bd												
98-594-B-P (1)	204.41	55.18	40.50	67.50	37.2	overl	X								
98-594-B-P (2)	233.34	60.40	50.39	77.40	45.7	w-l	X								X
98-594-C-P (3)	222.52	55.37		73.70	37.5	w-r	X								X
98-594-C-P (2)	221.25	57.44	49.32	73.20	40.8	w-l	X								X
Předmostí 1928-P12404		54.68			36.5	w-r	X		X						X
98-594-C-P (12)	210.00	54.15	42.28	69.40	35.7	overl	X								X
98-594-A-Př (1)			43.70		37.8	w-r					X				
98-594-A-Př Abs		55.64			37.9	w-r						X			
98-594-A-Př (2)			41.00		33.8	overl								X	
Ulna		BPc													
98-596-D		23.45			35.9	w-r		X							
98-599-B														X	
Radius															
98-595-B										X					X
Femur		Bp	Bd												
98-598-D		60.17			48.5	w-l	X								
98-601a-D		51.26			36.7	w-r	X	X							
Předm 1928-P12403			41.42		33.8	w-r			X	X					X
Tibia	TL	Bp	Bd												
98-598-B-Předm 1928		48.52			39.2	w-l	X								
98-601a-F								X			X				X
97-597-A-Př82	227.00	46.84	28.87	67.20	36.5	w-r		X							X
98-596-B(2)								X	X	X					X
98-596-B (1) Př15/5 83		41.40			28.9	d-l				X					X
98-596-E		45.65			34.9	w-r					X				X
97-597-C-Př82 1929		41.00			28.4	d-l								X	
NISP (total 33)							9	5	3	4	3	10	2	3	12

[a]Germonpré et al. (2012)

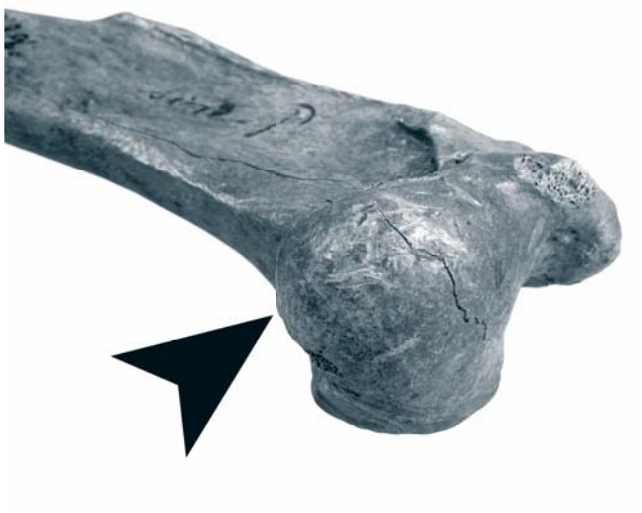


Text-fig. 3. Schematic position of the human modifications (cut marks, impact marks, ochre traces, inserted bones) recognised on the canid remains from Předmostí, indicated on a wolf skeleton; the frequencies of the modifications are not shown. Modified after © 2003 ArcheoZoo.org / Michel Coutureau (Inrap).

98-595-B (Text-figs 3, 14), femur Předmostí 1928-P12403, which also displays "repetitive" marks (Text-fig. 13) and tibia 98-596-B(2), which also has defleshing and "repetitive" marks, plus scraping marks that run oblique or parallel to the long axis of the bone. These scrapings could be related to removal of the periosteum in preparation for work with the bone itself. Oblique cut marks on the mid shaft of tibia 98-596-B (1) could have faciliated subdivision of the shaft into two halves (Text-figs 3, 15). This specimen is described as "dog-like in size" (Tabs 3–6, 12).



Text-fig. 4. Rib fragment inserted in the nasal cavity of canid skull fragment (10).



Text-fig. 5. Disarticulation marks on the head of humerus 98-594-B-P (1) to disarticulate the shoulder joint, for the metrics of this bone see Table 12.

Text-fig. 6. Disarticulation marks on humerus 98-594-C-P (2) for disarticulation from the scapula, for the metrics of this bone see Table 12.

Impact marks

The two specimens with impact marks are from large individuals (Tab. 12). One lower jaw, a right mandible (98-583-C-Př5-90-92), presents a fracture morphology that can be related to human action (Text-figs 3, 16). The break on the ventral edge of this lower jaw presents an oblique angle to the bone cortical surface. On the fracture surface, conchoidal scars indicate that flakes of bones have been detached, probably they were chipped off during impact. This jaw can be described as from a Pleistocene wolf (Text-figs 2, Tab. 12).

One large canid long bone presents clear evidence of impact marks. The proximal part of humerus 98-594-A-Předm (0.4% $NISP_{humerus}$, 1.1% $MNI_{humerus}$) was broken by percussion that produced a curved edge with a flake still attached to the shaft (Text-figs 3, 17, Tabs 10–12).

Text-fig. 7. Disarticulation marks on the neck of femur 98-598-D to dismember it from the hip joint, for the metrics of this bone see Table 12.

Ochre traces

Three large canid bones from Předmostí carry ochre traces: humerus 98-594-A-Předm (0.4% $NISP_{humerus}$, 1.1% $MNI_{humerus}$), tibia 98-596-E and tibia 98-601a-F (0.8% $NISP_{tibia}$, 2.5% MNI_{tibia}) (Tabs 10–12). The latter bone also presents defleshing marks (Text-figs 3, 11).

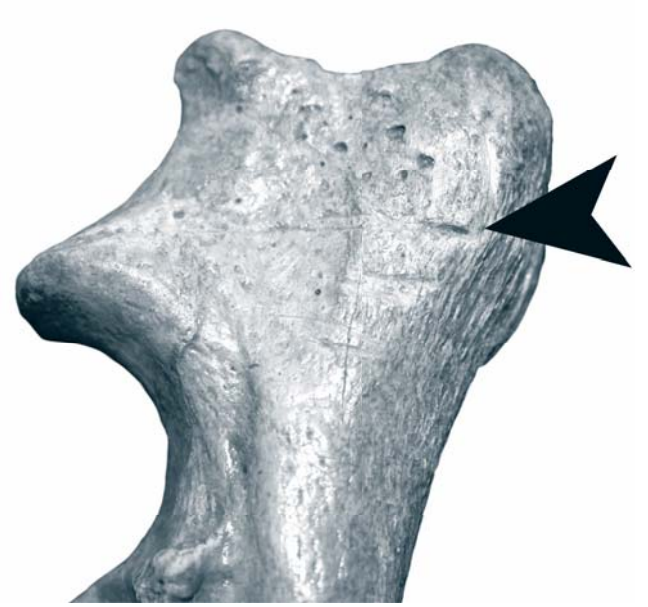
Specific human manipulation

The nasal cavity of a skull fragment (10) contains a rib fragment. This rib fragment was probably inserted after the snout was broken off from the neurocranium (Text-figs 3, 4). Another canid skull (Předmostí (-)) had a bone fragment inserted into its mouth (Germonpré et al. 2012: figs 7, 8).

Carnivore modifications

Three long bones (0.07% $NISP_{all}$) from at least two individuals (1.7% MNI_{all}) display modifications made by carnivores (Tabs 10–12). Humerus 98-594-A-Př (2) bears carnivore chewing traces on the medial trochlear ridge. This part of the trochlea displays typical scooping out of the cancellous bone characterised by a reduced thickness of the walls of the trochlea surrounding the pit (Text-fig. 18). The olecranon process of ulna 98-599-B was chewed by a carnivore; along the edges puncture marks occur (Text-fig. 19). The proximal part of tibia 97-597-C- Př82 1929 displays a puncture mark that presents an inverted cone shape, with depressed cortical bone covering the walls of the puncture (Text-fig. 20). This specimen is "dog-like in size" (Tabs 3–6, 12).

Text-fig. 8. Disarticulation marks on tibia 98-589-B-Předmostí 1928, transversal cut marks on the tibial tuberosity and on the tibial crest are visible, for the metrics of this bone see Table 12.



Text-fig. 9. Defleshing marks on ulna 98-596-D on the olecranon related to the cutting of caput longum and the caput laterale of the m. triceps, for the metrics of this bone see Table 12.

Text-fig. 10. Defleshing marks on femur 98-601a-D to cut loose the quadriceps femoris muscle, for the metrics of this bone see Table 12.

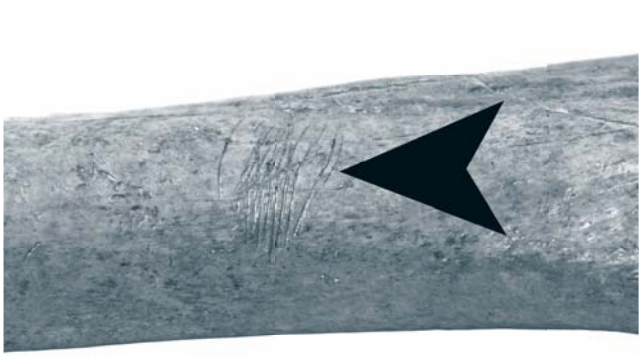
Plant root traces

Three hundred and fifty long bones (30% $NISP_{long\ bones}$) in the large canid assemblage from Předmostí bear a sinuous shaped pattern of grooves that were made by plant roots (Tabs 10–11). Table 12 indicates which of the long bones modified by humans and carnivores also carry root traces.

Discussion

The mean lengths of the skull and mandible of the large canids assigned to the Palaeolithic dog morphotype and the Pleistocene wolf morphotype differ significantly, although the observed ranges (OR) of these measurements overlap to a certain extent (Germonpré et al. 2012, 2015a). Their body mass estimations, calculated on the basis of the length of the mandible (cf. Losey et al. 2015), also overlap: the observed range for the Palaeolithic dogs is from 26 kg to 49 kg and for the Pleistocene wolves from 36 to 56 kg. Nevertheless their means clearly differ: the mean BMe for Palaeolithic dogs is 37 kg and for Pleistocene wolves is 44 kg. Furthermore, the BMe for the smallest Palaeolithic dogs falls outside the OR of the Pleistocene wolves and inside the OR (19–32 kg) of the archaic dogs, a group composed of recent northern dogs with the addition of two prehistoric dogs (Germonpré et al. 2015a: tab. 8). Therefore, we presume that although the sizes of the long bones from the Palaeolithic dogs most likely overlap with the sizes of the long bones of the northern wolves, it is possible that the smaller Palaeolithic dogs could have long bones that are shorter and narrower

Text-fig. 11. Longitudinal defleshing marks on ochre-stained tibia 98-601a-F to extract the meat of m. fibularis longus and part of m. flexor digitorum, fossilised rootlets visible on the shaft.



Text-fig. 12. "Repetitive" marks on humerus P12404 Předmostí 1928, root traces visible on the shaft, for the metrics of this bone see Table 12.

Text-fig. 13. "Repetive" marks on femur P12403 Předmostí 1928, for the metrics of this bone see Table 12.

than the long bones from northern wolves, and that these bones could have dimensions that are comparable to the dimensions of the recent northern dogs. The lower limits of the dimensions of the long bones and the SHe and BMe, calculated on these measurements, for the Předmostí canids fall inside the OR of the recent northern dogs in our data set (Tabs 3–9). These smaller Předmostí canids can be described as "dog-like in size". Nevertheless, the means and upper limits of the dimensions of the Předmostí long bones concur mostly with these values of the wolf groups in our data set (Tabs 3–9). Some Předmostí bones are larger however than the means of the northern wolves in our data set. These latter canids can be termed "wolf-like in size". It should be stressed that these terms do not imply that the "dog-like in size" canids are Palaeolithic dogs and the "wolf-like in size" canids are Pleistocene wolves. However, we propose that these remains would be interesting to analyse in more detail in the future.

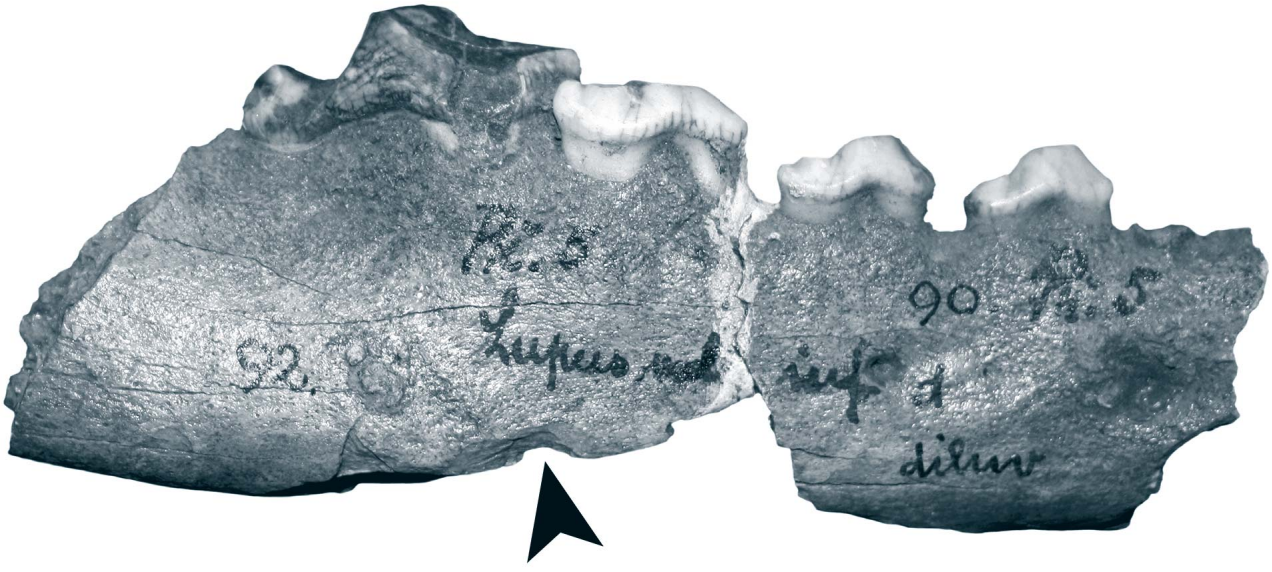
At Předmostí, cut marks occur on 16 large canid bones (0.4% $NISP_{all}$) from at least six individual canids (5% MNI_{all}) (Tabs 10, 11). Although no skinning marks were discerned, the animals most likely were skinned as a first step in the butchering process. Since all skeletal elements are represented at Předmostí and since the excavators noted in their diaries that complete wolf skeletons were regularly found (see Svoboda 2008 and references therein), it can be assumed that the butchering of the bodies of the large canids took place at the site. Four of the cut-marked long bones correspond to at least two individuals that were "wolf-like in size" canids; a bone bearing cut marks related to tool manufacturing is from a "dog-like in size" canid (Tabs 3–6, 12). This suggests, in combination with the identification of human modified canid skulls as from Palaeolithic dogs and Pleistocene wolves (Germonpré et al. 2012), that the bodies of both morphotypes were manipulated by Gravettian peoples.

Text-fig. 14. Longitudinal scraping marks on radius 98-595-B, root traces visible on the shaft.

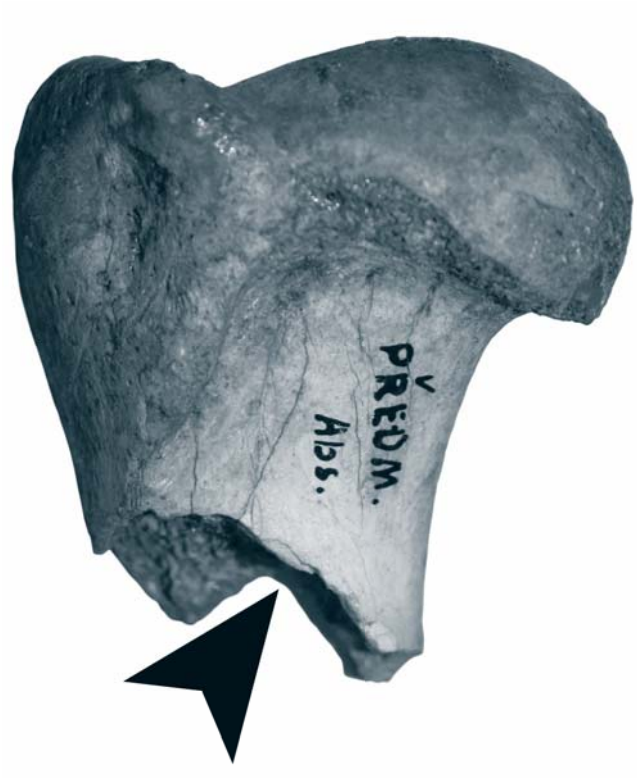
Text-fig. 15. Oblique cut marks on the mid-shaft of tibia 98-596-B (1) Př15/5 83, root traces visible on the shaft, for the metrics of this bone see Table 12.

Disarticulation marks indicate that the humerus was detached proximally from the scapula (Text-figs 3, 5–6) and distally from the ulna. Marks on the distal part of a humerus suggest that the butcher started carving on the medial side of the distal end of this element. Once the lateral side of the epicondyle was reached, the disarticulation was advanced enough to allow sufficient space for easier manipulation, so cutting of the bone at the lateral epicondyle could be avoided. The femur was disarticulated from the hip joint (Text-figs 3, 7) and the tibia from the knee (Text-figs 3, 8). At least five large canid individuals were dismembered, corresponding to 4% of the total MNI (Tabs 10, 11). At least two of those individuals are "wolf-like in size".

Defleshing marks occur on an ulna, a femur and three tibiae from at least two individuals (Text-figs 3, 9–11). The marks on the proximal ulna indicate that the m. triceps was cut. If the m.



Text-fig. 16. Impact marks on the ventral edge of mandible 98-583-C-Př5-90-92, for the metrics of this bone see Table 12.



Text-fig. 17. Percussion marks on the diaphysis of humerus 98-594-A-Předm, for the metrics of this bone see Table 12.

Text-fig. 18. Carnivore chewing traces on medial trochlear ridge of humerus 98-594-A-Př (2), for the metrics of this bone see Table 12.

triceps was also cut on the medial face of the olecranon and at its proximal attachment site on the humerus and scapula, then the whole meaty muscle group could have been filleted. In recent greyhound dogs, with a mean of body mass 31.8 kg, the mean weight of this muscle is about 600 g (Williams et al. 2008). The defleshing marks on the proximal femur imply that the meat of the quadriceps femoris muscle was sought after. In recent greyhound dogs the mean mass of this muscle is about 577 g (Williams et al. 2008). The defleshing marks on

Text-fig. 19. Carnivore chewing traces on the olecranon process of ulna 98-599-B.

Text-fig. 20. Carnivore puncture mark on tibia 97-597-C-Př82, for the metrics of this bone see Table 12.

the three tibiae point to removal of the meat from the laterally located muscles (m. tibialis cranialis, m. extensor digitorum longus, m. fibularis longus, m. extensor digitorum lateralis, m. flexor digitorum lateralis). In recent greyhounds these muscles have a mean mass of about 114 g (Williams et al. 2008). The defleshing marks on the long bones suggest that the meat of at least two large canids was consumed. Probably each canid could have produced at least 2.6 kg meat.

Marks on two other modified canid bones suggest that occasionally marrow was also eaten. Marrow was seemingly obtained from the mandibular canal of a lower jaw, likely from a Pleistocene wolf (Text-figs 2, 16) with a BMe of 51 kg. An impact mark also occurs on a proximal humerus with the aim of accessing the medullary cavity (Text-figs 3, 17). This mark is probably the result of direct impact on the humerus after the meat had been removed.

It cannot be totally excluded that the canids were butchered to feed the Palaeolithic dogs. However, the results

of the stable isotope study of the canids suggest that regular consumption of canid meat by the canids themselves did not take place (Bocherens 2015, Bocherens et al. 2015). On the other hand, the possible consumption of canid meat by people is discernable in the isotopic composition of the bone collagen of the analysed Gravettian human from Předmostí (Bocherens et al. 2015). The isotopic values of the Předmostí human are in accordance with a diet containing no canid meat and about 60% mammoth. However, if canid meat is added to the spectrum of meat potentially consumed by this human, the isotopic values are still consistent with a diet dominated by mammoth meat, with a frequency of about 40%, but with a contribution of about 15% wolf and 5% dog meat (Bocherens et al. 2015: fig. 10). The defleshing marks on the large canid remains from Předmostí point out that canid meat was indeed consumed. Moreover, the isotopic values of the Předmostí human indicate that he consumed wolves in higher quantities than dogs. Interestingly, the vast majority of the large canid bones bearing disarticulation, defleshing or impact marks are "wolf-like" or "wolf-range" in size. Furthermore, we proposed that the Gravettian people of Předmostí opened the braincase of canid skulls (eight neurocrania, from eight individuals, were found perforated) and ate the brain as part of a ritual performance (Germonpré et al. 2012). A perforated canid skull and the impacted jaw are from Pleistocene wolves. Only a minority of the butchered canid bones are "overlapping in size" or are from Palaeolithic dogs (two perforated canid skulls) (Germonpré et al. 2012). The enormous amount of mammoth remains, the growth characteristics of the children and adolescents, and the good physical development of the adults, whose remains were found in the burial zone, suggest that the people from Předmostí were in good health, had ample food (Brůžek and Velemínská 2008) and thus did not need to resort to canid meat regularly (Germonpré et al. 2012). This could suggest that the human consumption of the meat and marrow extracted from the long bones of the canids could be related, just as with the consumption of the canid brain, to ritual events. Taking all the evidence together regarding the consumption of brain, meat and marrow from large canids (0.4% of the $NISP_{all}$ of the large canid remains are bones with defleshing and impact traces produced by human modification), it seems that at Předmostí about 8% of the MNI_{all} of the canid assemblage could have been eaten by the Gravettian inhabitants.

Large canids were also consumed at three other Gravettian sites in Central Europe: at Pavlov I (Wojtal et al. 2012) and Dolní Věstonice I (Wilczyński et al. 2015) in the Czech Republic, and at Krems-Wachtberg in Austria (Fladerer 2001). At Pavlov I, cut marks on large canid bones, occurring at a frequency of 0.6% of the NISP, are related to skinning, dismembering and filleting (Wojtal et al. 2012). Several wolf skeletons were deposited in a complete state at the site and bear indications pointing to the utilisation of their fur (Musil 2003). Not only large canids, but also other carnivores such as foxes, wolverines and bears were eaten. At Dolní Věstonice I, cut marks on the long bones from large canids (2.3% NISP) occur at higher frequencies than at Pavlov I (Wilczyński et al. 2015) and Předmostí. It seems that at Dolní Věstonice I, large canids formed a more important component of the diet. Other carnivores such as lions, bears and wolverines were also eaten. However, not many canid long bones were broken, so marrow from large canids was most likely not commonly consumed (Wilczyński et al. 2015). At Krems-Wachtberg, 20% of the large canid remains bear cut marks. They represent processing for fur utilization as well as for consumption. Here, four percent of the canid bones show impact marks related to marrow consumption (Fladerer 2001).

At the Late Upper Palaeolithic site of Pont-d'Ambon (France), cut marks on dog bones reveal that at least three individuals were consumed (Pionnier-Capitan et al. 2011). From the Mesolithic onwards, clear evidence points to the practice of cynophagy in Europe (e.g. Harcourt 1974, Ewersen and Ramminger 2010, Chrószcz et al. 2015). A recent study by Anthony and Brown (2017) detailed the consumption of dog and wolf within a ritual context at the Bronze Age site of Krasnosamarskoe on the Russian steppes. Moreover, evidence of the consumption of the meat, brain and marrow of wolves can be found in the ethnographic literature. In Mongolia, wolf meat is eaten as a form of medicine (Charlier 2015). Also in Kirgizstan, wolf meat, grease and marrow are used for medicinal purposes (Lescureux 2007).

Not all human-modified canid bones are related to consumption. At Předmostí, three long bones bear marks that can be related to the preparation of tubes, hafts, flutes or beads (cf. Wojtal et al. 2012). Also at the Gravettian Pavlov I site long bones with cut marks for dividing the bone at the mid-shaft were found (Wojtal et al. 2012). The tibia at Předmostí that shows this type of mark can be described as "dog-like in size" (Tab. 12). The "repetitive" marks on the canid bones from Předmostí will be discussed in detail in a forth-coming paper. Femur Předmostí 1928-P12403 is also figured in Valoch (2013: fig. 2.1).

Three long bones display ochre traces: a humerus and two tibiae from at least two individuals, one adult and one subadult. The subadult bone also bears defleshing marks (Text-fig. 11). Small ochre fragments were discovered in the fillings of shallow erosional canals during the 2006 excavations at Předmostí II (Svoboda 2008). However no ochre was found at the human burial zone; its presence was not mentioned either by Maška in his diaries (Svoboda 2008). Human skeletons dating from the Gravettian are often stained with ochre (Gamble 1999), however, this seems not to have been the case at Předmostí. Since no detailed analysis of the taphonomy of the complete mammal assemblage from Předmostí has been done, it is not clear how many mammal bones are stained with ochre and if specific skeletal elements were selected. Such an analysis would be helpful to discern whether the ochre staining of the canid remains happened accidentally by spilling ochre on the bones, or whether the bones were deliberately coloured (cf. Germonpré and Hämäilänen 2007). However, since one of these canid bone also displays defleshing marks, it is possible that the red colouring of this element could have a specific meaning.

A canid snout fragment has a rib fragment inserted artificially into its nasal cavity (Text-fig. 4). This setting resembles the Palaeolithic dog skull Předmostí (-) that holds a bone fragment between its front teeth (Germonpré et al. 2012: figs 7, 8). Also at Dolní Věstonice a comparably modified canid skull was discovered: a snout fragment with

a lithic fragment inserted into its nasal cavity (Klíma 1963). The two canid skull fragments with objects in their nasal cavities were probably broken before the objects were put into place. In addition, at Předmostí a mammoth lower jaw was found with a ochre-stained stone slab inserted between the left and right rostral incisive parts of the mandible (Absolon and Klíma 1977). We interpreted this phenomenon of inserting strange objects into body parts using evidence from the ethnographic record (cf. Germonpré et al. 2012). Circumpolar peoples often manipulated the remains of hunted carnivores during specific rituals or ceremonies that are part of an animistic cosmology (e.g. Ingold 1986). The Mistassini Cree, for instance, set skulls of hunted bears in trees; sometimes offerings of tobacco were placed in the nasal cavity of these skulls (Tanner 1979). We suggest that Gravettian peoples at Předmostí manipulated canid bodies as part of ritual performances: perforation of the braincase, insertion of body parts of other mammals inside canid skulls (Germonpré et al. 2012), the consumption of canid meat, brain and marrow, and maybe also the colouring of canid remains with red ochre, could be related to certain rituals. The archaeological record of the Early Upper Palaeolithic from Southwestern Germany has allowed description of human--animal relationships – particularly regarding mammoths and carnivores – as being essentially animistic (Hussain and Floss 2015, Porr and Maria 2015). We proposed that specific carnivore – human relationships most likely formed part of the cultural tradition of certain Upper Palaeolithic societies (Germonpré and Hämäläinen 2007, Germonpré et al. 2012, 2015b) and could even have led to the beginning of the domestication process of the wolf; a process that could have been motivated by several intertwined incentives such as the keeping of captive wolf pups in accordance to an Upper Palaeolithic cosmology, for guaranteed access to wolf skins for producing cold-weather clothing, as pets and sentinels, etc. (Germonpré et al. 2015b, submitted).

The frequency of mammal bones with carnivore gnawing marks is very low in Dolní Věstonice I (Wilczyński et al. 2015), Pavlov I (Wojtal et al. 2012) and Krems-Wachtberg (Fladerer 2001). At Předmostí, a detailed analysis of all carnivore marked bones from the total mammal assemblage is so far not available. However, our study indicates that less than 0.1% of the large canid assemblage displays carnivore gnawing (Tabs 10, 11). The gnawed humerus is from a canid "overlapping in size" between dogs and wolves, the gnawed tibia is from a canid "dog-like in size". Metrics on the gnawed ulna are not available (Tabs 3–6, 12). The generally low level of carnivore damage indicates that carnivores had apparently only limited access to the remains from such large mammals at these sites.

Conclusion

Several long bones from large canids found at the Gravettian Předmostí site were modified by Upper Palaeolithic humans. Some of these bones are "wolf-like in size", and one is "dog--like in size". Most long bones, however, cannot be attributed to a size category. Cut marks are related to the disarticulation and defleshing of canid carcasses and the breaking of bones in order to obtain access to meat and marrow. These manipulations suggest that a portion of the canid assemblage was most likely consumed by the Gravettian people of Předmostí. Other modifications of the canid remains can be related to tool making. The handling of these bodies and bones further allude to the existence of a specific relationship between humans and large canids during the Gravettian, as has been previously shown, based on human modified canid skulls and dentition. Only a few canid bones were impacted by carnivores that apparently did not have regular access to the canid assemblage deposited at the site.

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