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THE ROLE OF LARGE CANIDS:

PRELIMINARY VARIABILITIES FORMING THE POPULATION STRUCTURE IN MORAVIA

Angela Perri and Sandra Sázelová

Introduction

In general, large numbers of carnivores are characteristic of Central European Upper Paleolithic sites (Soffer 2000), including many Moravian sites (Musil 1997, 2001, 2005, 2014; Wojtal and Wiłczyński 2015). The extensive utilization of carnivores, including cut marks which suggest subsistence processing, has been proposed to reflect either seasonal food stress or ritual consumption (Musil 1994; Soffer and Kozlowski 2003; Wojtal *et al*. 2012; Germonpré *et al*. 2015), though fur production was probably the main reason for targeting most of the canid species (Musil 1958a; West 2001). Particular attention has been paid to the wolves from Gravettian sites in Moravia, although they do not appear to be treated any differently than other fur-bearing species, such as foxes or wolverines (e.g. Pokorný 1951; Fladerer 2001, 2010; Wojtal and Wiłczyński 2015). Interest in Moravian wolves recently increased due to the identification of purported domestic dogs from the site of Předmostí (c. 32,500-29,000 cal BP) in the Moravian Corridor, based on morphological and dietary isotopic variation (Germonpré et al. 2012, 2015; Bocherens *et al*. 2015). However, these identifications lead to a wider discussion with researchers who argue there is not enough information available to make a convincing identification of domesticated dog, or that the remains simply represent different wolf morphs within a broader population (Crockford and Kuzmin 2012; Morey 2014; Boudadi-Maligne and Escarguel 2014; Perri *et al*. 2015). Moreover, the possibility of initial domestication, or at least human-driven genetic isolation, had previously been discussed by various authors who explained morphological variation in the Předmostí canids as the result of natural variation (e.g. Pokorný 1951; Benecke 1994; Musil 2000) or sexual dimorphism (Musil 2000; Wojtal pers. comm.). For this purpose, we would like to discuss here first the historical context of this debate, which has been ongoing in the Czech literature for more than 100 years.

Historical approach to large canid variations in Moravia

During the excavations held by Karel Jaroslav Maška, at the end of the 19th century, more than 100 individual wolves (NISP = 4143) were discovered at the Předmostí Ia site (estimations by Pokorný 1951, p. 34). The most important accumulation of wolf skeletons was found in the period from 17th to 19th May, 1894 in the northern zone of site. An extensive burnt area was discovered, containing separate accumulations of mammoth bones, such as tusks, limb bones, vertebrae and ribs, with little other human activity apparent. Maška describes that next to it within an area of 10 m^2 *"... seven wolf skeletons were laid, their individual parts were found mostly in a natural position. We have observed that the skulls were in some cases intentionally smashed in their frontal part, although the other remains were not damaged.*" (1894, p. 91; translated from Czech). Another note in his diaries concerns the find from 16th August, 1894 within a distance of 13 meters northwest of the main human burial accumulation, when "… *a whole skeleton of a small wolf (or dog)*" was found (Maška 2008, 185; translated from Czech). The German transcription of his diary (Absolon and Klíma 1977, p.48) does not label this find as a dog, nor is there any other mention of a dog presented in his diaries from 1890-1893, published in the same book. Maška was aware of intrusive younger finds at the Předmostí I site, for example in 1893 (p. 112) when he describes two younger prehistoric pits intruding into the Pleistocene layers, containing several bones of a smaller dog (Maška 1893, p. 112), among other finds. Moreover, he must have been aware of variability in the Pleistocene wolf population at the Předmostí Ia site, as he identified three wolf groups according to their general size: *Canis lupus major*, *Canis lupus medius*, and *Canis lupus minor* (Pokorný 1951, p.36). Maška also documented in his field notes the stage of preservation and excavation damage to the wolf skulls.

Later, from 1946-1951, the large canid material from Předmostí Ia was studied by Miloslav Pokorný (1951), who made a complex description of the wolf population based on the osteometric analysis of skulls and mandibles, including notes on aging and pathology. He concluded then that Maška's *Canis lupus medius* might be classified as the smaller "type" of *Canis lupus*, but he also states that (1951, p. 47-48; translated from Czech): " *…it is possible to observe some variability, although the measuring of bone fragments does not always provide accurate values. In our case, the preserved material does not display enough characteristic markers necessary to decide safely about the difference of varieties. Most of the markers, possibly measurable, are under the influence of changes in their function and could not therefore be convincing in their distinguishing… Further study will be necessary to select fossil material, if possible, of the same geological age, because the closer study of fossil material from Předmostí shows that, on some skeletal remains belonging to Canis lupus L, the markers leading to older forms (Cuon) as well as to younger forms (Canis familiaris) are preserved."* Additionally, we should mention the work of Norbert Benecke (1987, 1994) who studied morphoscopically the crowding of premolars and molars in wolf mandibles from Předmostí Ia and stressed the higher occurrence of oligodontism (natural absence of teeth) or polydontism (redundant presence of teeth) in comparison to recent wild wolves. He suggested that this crowding might indicate a first genetic isolation of captured or semi-captured canids from the Pleistocene wolf population (Benecke 1995, 82-84).

Another accumulation of wolf skeletons was found in 1952 by Bohuslav Klíma at Pavlov I, southeast of the Pálava hills. The osteological material from this and excavations in 1953 was first studied by Rudolf Musil (1958a), where he reported that during the 1952 season the smallest wolf mandible (with a crowded "zig-zag" form of teeth) was found, in comparison to other known Gravettian canids from Dolní Věstonice I and Předmostí Ia. He did not observe any similar examples in the assemblage from 1953, but in his later work (1994) another example of a crowded zig-zag form mandible is described from the 1957 season of Pavlov I – northwest. Although he noted that tooth crowding is typically a domestication marker, he did not propose that the canids were dogs, only that future complex population analysis is needed (1997; 2005). Moreover, in 1955 he had suggested that, "*... Dimensions of our recent wolves and certainly of the diluvial ones are, beside other things, influenced by landscape, where they live. The mountain wolves are commonly stronger and robust if compared to swamp and lowlands wolves, which are gracile and weak. At Pavlov, mainly the smaller "type" of wolves occurs. It is possible that it is related to the position of Pavlov within the lowlands and flatlands of Southern Moravia. Contrary to Předmostí, where both types occurred in approximately the same proportion. Perhaps, their presence at this site might be affected by the neighboring location of Beskydy and Jeseníky Mountains, which are occupied by wolves with bigger and robust stature running down to lowlands in the winter* " (pp. 284-285; translated from Czech). Musil also later said of the two crowded "zig-zag" mandibles, "*In two cases the teeth were closely packed against each other. I'm sure that this was due to much variability in the size of the wolves rather than to attempts at domestication*" (2005, p. 197). Additionally, the most recent analysis of the wolf population of Pavlov I (southeastern part) estimated 57 individuals (NISP = 6190) with cut marks related to dismembering and filleting (Wojtal et al. 2012; Wojtal and Wiłczyński 2015).

Large canids at Dolní Věstonice II sites

Our preliminary analysis of *Canis* followed the previously mentioned importance of focusing on populations, not individuals, when examining the possibility of domesticated dogs from Gravettian sites. Here we present the canid material recovered at a complex of sites, Dolní Věstonice (DVII), repeatedly occupied by Gravettian hunter-gatherers between c. 36,000-29,000 cal. BP (Svoboda *et al*. 2014; see chapter in this volume). The canids originate from the 1958-2015 excavations or surface collections by Bohuslav Klíma and Jiří Svoboda at several parts of DVII sub-sites – northern slope, western slope, southern edge, site-top, and DVIIa (or closely indeterminate DVII). The faunal remains from individual parts have previously been discussed by Svoboda (1991), Seitl (1995), West (2001), Nývltová Fišáková (2001) and Wojtal and Wiłczyński (2015), see also Wojtal and Wiłczyński and Sázelová, this volume. The most highly represented carnivore species at Dolní Věstonice II sites are polar and red foxes (*Vulpes lagopus/V. vulpes*), occurring as 14.9-7.8% of all taxonomically identified material, followed by grey wolves (*Canis lupus*) with an interval between 12.1-5.3%. Other carnivore species are presented with an interval lower than 2%, such as wolverine (*Gulo gulo*) at 1.99-0.1%; cave lion (*Panthera leo spelaea*) at 0.07%; brown and cave bears (*Ursus arctos/U. spelaeus*) at 0.4-0.1%, lynx (*Lynx lynx*) at 0.03% and wild cat (*Felis sylvestris*) at 0.01%.

Material Description

The large canid skeletal remains deposited at the Centre for Research of Paleolithic and Paleoethnology in Dolní Věstonice (Institute of Archeology Brno, Academy of Sciences of the Czech Republic) were solely studied in this paper. Some additional canid material from the DVII sites is held at the Moravian Museum (Brno, Czech Republic) and was not included here. The wolf material was identified with assistance from virtual databases (ArchéoZoo or Virtual Zooarcheology of the Arctic Project), 3D models from the Max Planck Institute for Evolutionary Anthropology (Niven et al. 2009), and comparative atlases (Kolda 1951; Schmid 1972; Hillson 2005; France 2009). The frequencies of skeletal elements and number of individuals were studied in terms of number of identified specimens (NISP), minimum number of elements (MNE), and minimum number of individuals (MNI) when in some cases the side matching was possible (Klein and Cruz-Uribe 1984; Lyman 1994, 2008; Reitz and Wing 2008). However, the total number of remains estimated in this paper differs slightly from previously published papers (West 2001; Nývltová Fišáková 2001; Wojtal and Wilczyński 2015), because highly weathered or extremely fragmented material with a high probability of incorrect taxonomic determination were excluded, affecting namely the underestimation of vertebrae (for a comparison, see Wojtal and Wiłczyński, this volume).

Figure 1: Detail of large canid metapodia in anatomic position from the excavations in 1987, Dolní Věstonice II – Western Slope (courtesy of J. Svoboda).

Table 1: General distribution of wolf (*Canis lupus*) skeletal remains at Dolní Věstonice II sites. Abbreviations: NISP = number of identified specimens, MNE = minimum number of elements.

Skeletal element	NISP	NISP%	MNE	MNE%
cranium	2	0.26	2	0.28
maxilla	20	2.59	20	2.83
dentes superiores	41	5.31	28	3.96
mandibula	49	6.35	45	6.37
dentes inferiores	78	10.10	65	9.21
dentes indet.	77	9.97	57	8.07
vertebrae cervicales	37	4.79	31	4.39
vertebrae thoracicae	1	0.13	1	0.14
vertebrae lumbales	3	0.39	3	0.42
vertebrae caudales	6	0.78	6	0.85
vertebrae indet.	1	0.13	1	0.14
scapula	17	2.20	16	2.26
humerus	25	3.24	24	3.39
radius	25	3.24	22	3.12
ulna	24	3.11	24	3.39
carpals	9	1.16	9	1.27
metacarpals	84	10.88	82	11.61
pelvis	11	1.42	11	1.56
femur	10	1.29	10	1.42
patela	2	0.26	2	0.28
tibia	16	2.07	16	2.27
fibula	1	0.13	1	0.14
tarsals	48	6.22	48	6.79
metatarsals	48	6.22	45	6.37
metapodia indet.	36	4.66	36	5.09
phalanges	99	12.89	99	14.02
ossa sesamoidea	2	0.26	2	0.28
Total	**772**	**100.00**	**706**	**100.00**

Distribution of skeletal elements at the DV II complex of sites

In total, 772 skeletal fragments belonging to a minimum of 20 canid individuals were identified (Table 1), with most of the anatomical parts preserved (except hyoid bones documented, for example, at Pavlov I; Musil 1958a,b, 1994, or *sternebrae* and *baculum* as from Předmostí Ia by Pokorný 1951). The material was mainly post-depositionally fragmented within the index 1.09 (NISP/MNE), although various parts were found still in their anatomic position (Figure 1), such as a series of vertebrae or apical parts of limbs. Furthermore, neither Dolní Věstonice site (DVI and DVII) displays large wolf skeleton accumulations as seen at Pavlov I and Předmostí Ia. A side disproportion (prevalence of left side) was observed for the scapula, radius and carpals, and tibia and tarsals. Also, there was a prevalence of complete mandibles from the right side, although the total number from both sides, including fragments, was almost equal. However, similar side-patterns were not documented at Pavlov I or Předmostí Ia, so we suggest here accidental taphonomic selection at DVII sites, rather than intentional human activities. When considering the distribution of wolf skeletal elements from within the site area, perhaps the clearest observations can be made with the material from 1987 excavation. Within Klíma's section, the individual bones and teeth of canids were highly accumulated within features K1, K5 and K6, and within approximately 3 meters of K4 was a concentration of individual bones and teeth (3 x 5 m). Svoboda's 1987 area displays several concentrations – the first, with a diameter of 3 x 4 m, laid within 13 m from feature S1; the second laid in the western part of the hearth, and the third was accumulated above feature S1 with male burial DV16 (in its southeastern part). The distribution of wolf remains outside the dwelling is greater than inside the dwelling, so it seems that wolves do not play any special role within this burial context (as was previously suggested by Nývltová Fišáková and Sázelová 2008). The occurrence of wolf remains and gnawing marks is rare within the mammoth bone depository (see Wojtal and Wiłczyński, this volume). Additionally, the distribution of wolf skeletal elements originating from new excavations in 1991-2015 at DVII -recess and DVIIa are extremely random, thus we were not able to observe any spatial patterns.

Morphological and age structure of population

Most of the research concerning the morphological or morphometric descriptions of large prehistoric canid populations describes mainly the skulls and mandibles. Similarly, the DVII material will be analyzed as part of an ongoing dog domestication project, *Deciphering dog domestication through a combined aDNA and geometric morphometric approach*, led by Greger Larson (University of Oxford) and Keith Dobney (University of Aberdeen). For the purpose of this project, 2D measurements, 3D geometric morphometric photogrammetry, and ancient DNA sampling of the DVII material was involved. Because most of these analyses are still ongoing and metric descriptions of variability in DVII skulls and lower jaws will be discussed in a separate paper (Perri and Sázelová in prep.), we would like to demonstrate here only the preliminary variability of selected postcranial parts, namely the metapodials. Metapodials are generally one of the most variable elements in mammal skeletons, however they have two dimensions which are recommended for analysis according to von den Driesch (1976) – greatest length (GL) and greatest breadth of the distal end (Bd). As shown in Figures 2a-c, the variability within each metapodial group is high and in many cases exceeds the differences suggested as relevant for sexual dimorphism noted as a standard for recent wolf populations (Hillis and Mallory 1996; Morris and Brandt 2014).

Moreover, if we look at the age structure of the large canid population from DVII sites (Figure 3), it is clear that our 20+ individuals do not represent a data set with a uniform distribution. The population is imbalanced, with an absence of newborns and puppies up to 6 months and subadults aged between 1-1.5 years, which is important given previous suggestions that human groups at Moravian sites may have been breeding these canids (Germonpré *et al.* 2012). Taphonomic explanations for missing young canids can be excluded, as newborns or young animals from other species are present at DVII sites. On the other hand, this age imbalance is similar to the age structures of large canids documented at Předmostí Ia and Pavlov I sites (Pokorný, 1951; Musil 1955, 1958a, 1994), where both authors note that young individuals are present, but the prevalence of older animals is obvious. Additionally, it is possible that previous researchers mistook wolverine (*Gulo gulo*) bones, which can look similar, for wolf bones, especially when fragmented. For example, West (2001, p. 113) published a photographic example of an 'immature wolf' maxilla from the Western Slope at Dolní Věstonice, which is actually a wolverine.

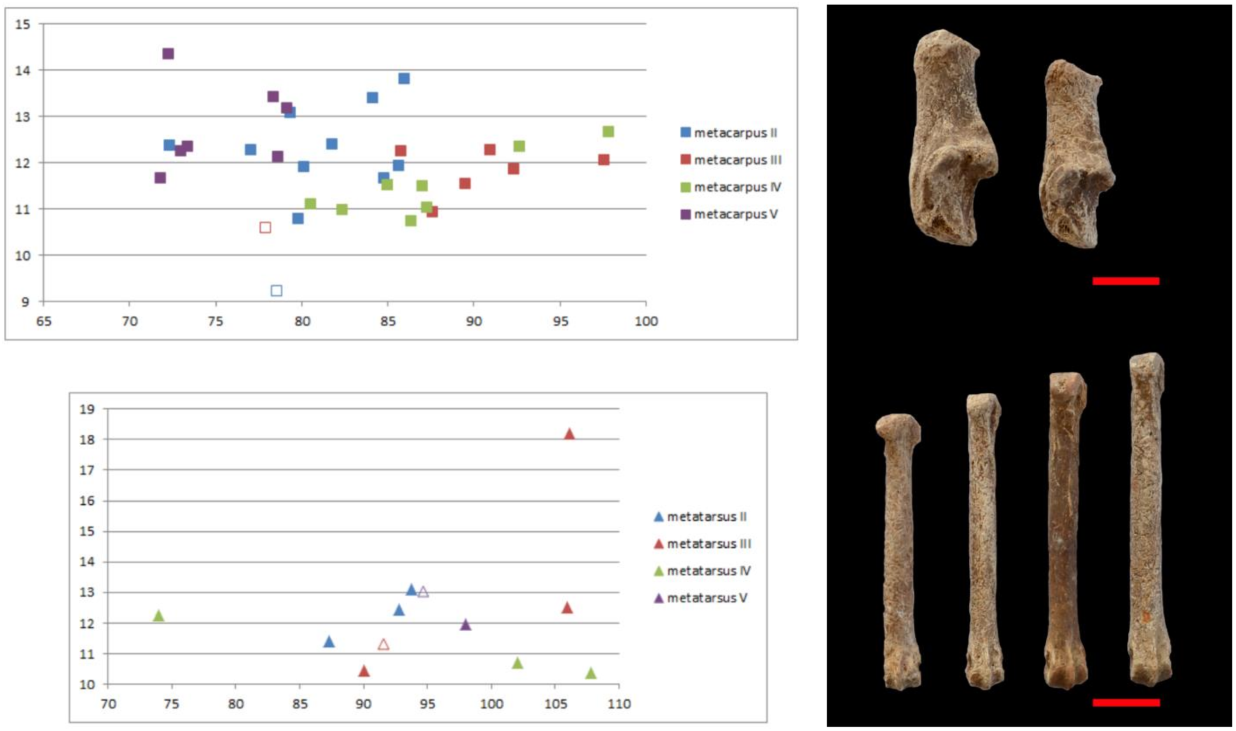

Figure 2a-c: Distribution of metric data on metapodials within the wolf population from Dolní Věstonice II sites. The greatest length (GL) is given on the X axis and the greatest breadth (Bd) of the distal end is given on the Y axis. (a) (upper): metacarpals; (b) (lower): metatarsals. The absence of color infilling indicates estimated measurement. The closest overlap of metapodial measurements signals the presence of the left and right side from the same individual; (c) Morphological variation in the left calcaneous and right 4th metacarpals of Dolní Věstonice II wolves (scale=2cm)

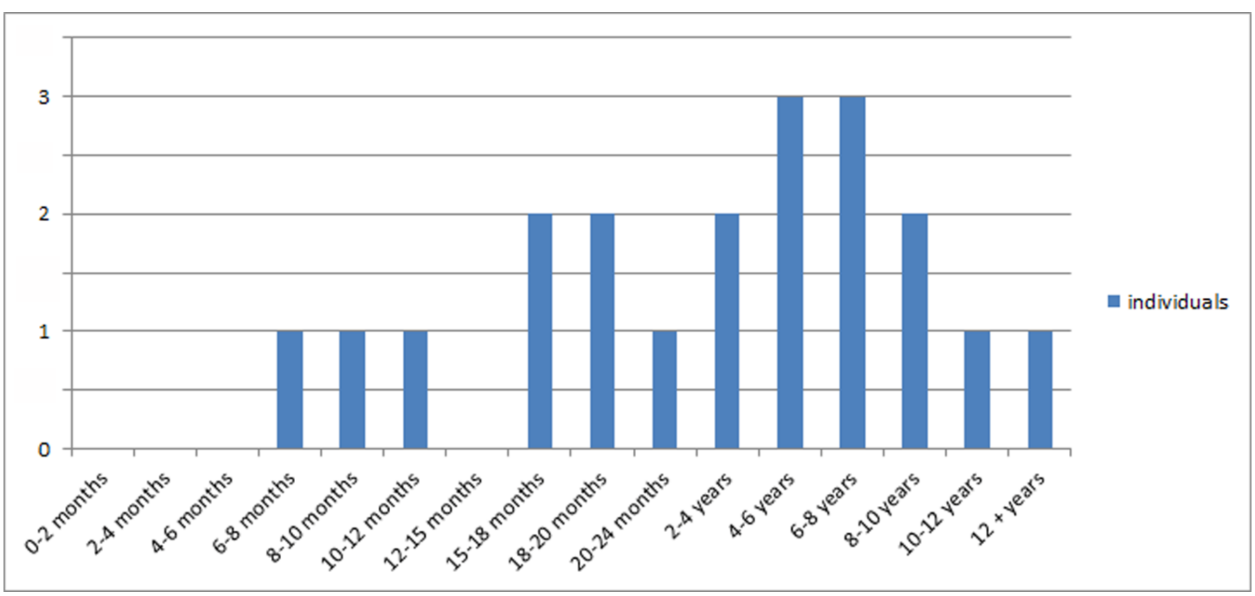

Figure 3: Number of individuals of each age from the large canid population from Dolní Věstonice II sites.

Figure 4a-c: Example of wolf left side mandible with traces of misalignment and *periodontitis* between P_3 and M_2 (a); detail of atypical abrasion on lingual side of canine (scale=5cm) (b); and detail on periodontitic lesions under M_1 causing pathological deformation in alveolar followed by baring of tooth neck and roots (c).

Pathologies and taphonomy

The pathologies observed on our large canid material only include degenerative types, affecting both cranial and postcranial parts of the skeleton. The first type is represented by malocclusions in six instances, causing the misalignment of teeth and atypical abrasions on the lower canines (mainly on the buccal side) or on the P^4-M_1 bite complex, which often preclude further individual age estimation. In four instances of individuals older than 9 years, periodontitis was observed affecting various types of lesions around alveolars (*alveoli dentales*) and expositions of the tooth neck (*collum dentis*) or upper part of roots (*radix dentis*) (Figure 4 a-c). After consultation with Dennis Lawler (DVM, Illinois State Museum), we reached the conclusion that the periodontitis might be caused by a wide variety of bacteria or fungi following the open tissue pathways after primary tooth trauma or gingival trauma with secondary infection. It can also be caused by a softer diet, producing less cleaning of gums and teeth, such as foraging on rotting carcasses, although other factors such as environment or genetics cannot be excluded. Further analyses will be needed in order to determine origin and development of this disease. The second type of postcranial degenerative processes affected mainly limbs, represented by arthritic osteophytes around the *cavitas glenoidalis scapulae*, *incisura trochlearis ulnae*, *caput radii* or on the calcaneus. In one instance, the surface scratches within the elbow (*articulatio cubiti*) suggest the cartilage was thinned enough that the ulnar and radial proximal epiphyses were in direct contact, causing traumatic abrasions.

From the taphonomic point of view, weathering was most frequently observed at I-II stage in 8.80% and III stage in 13.21% (following Behrensmayer 1978, 150-162) and root etching in 11.91%. In several instances both factors were combined together on opposite sides of a bone. For example, root etching on the lingual side and heavy weathering on the buccal side of a mandible. It seems that within its taphonomic history, the phases of exposure on the surface were alternated with bone deposition below the surface, with direct contact to plant roots, but also with an intermediate phase when the bone changed orientation within its layer (for example due to solifluction; chapter in this book). Traces of human activity, such as cut marks or burning, are well described in the chapter by Wojtal and Wiłczyński (this volume), but we would like to mention here a modified wolf upper canine with several traces after enamel removals (Figure 5) which was not previously detected (Sázelová *et al*. in prep.).

Discussion

The region and time period of Dolní Věstonice II sites suggests great variation should be expected in the fauna. Locally, human populations could take advantage of a range of topography, from hills to lowlands and climatic regions, from humid to arid. The chronological range of DVII also covers both a cold event and a warm interstadial, which introduced significant climatic and biotic changes in a short span of time (Musil 2011). This variation across time and space suggests dramatic variation in the wolf subpopulations present at DVII should not be surprising. Skeletal morphological variation, including in skull size and shape, is a known biological response to varying ecological conditions (Thorpe 1991; Eger 1990). For example, within modern North American grey wolves 24 subspecies have been recognized across varying geographical regions (Hall 1981). This suggests *Canis lupus* morphology is highly plastic, based on environmental and ecological conditions. A significant population bottleneck of European grey wolves since the Late Pleistocene suggests grey wolf subspecies may have been even more genetically, morphologically, and ecologically varied in the Gravettian than is known from modern populations (Pilot *et al*. 2014).

Figure 5: The modified wolf upper canine with several traces after enamel removals (scale=2cm)

The variation in Gravettian canids from Moravia (namely Předmostí) has been recently attributed to the identification of Paleolithic dogs (Germonpré *et al*. 2012, 2015), but these determinations rest on the premise that the region was populated by only one identifiable wolf subspecies, with static morphological and dietary parameters. Moreover, within the last century Germonpré is not the first author to suggest a closer social interaction between Gravettian hunters and wolf populations of wolves within the Moravian region (Maška 2008; Pokorný 1951; Benecke 1994; Musil 1955, 1958a, 1994, 1997, 2000), although most of the Czech authors conclude that further systematic analyses are needed. Carnivore gnawing is minimal from south Moravian sites (Wojtal and Wiłczyński 2015), suggesting live carnivores were probably not present alongside humans. Bones that did exhibit carnivore gnawing were primarily those of large mammals, such as mammoth, which would have been scavenged by predators after the sites was abandoned. This idea might be supported by periodontitis observed on several older individuals and if combined with other postcranial degenerative disorders, such individuals might have been disadvantaged in regards to hunting.

Additionally, Soffer (1990) suggested that the wolves from Dolní Věstonice were eaten as a starvation food or for ritual purposes. Others have suggested the eating of canids as a starvation food by Gravettian hunter-gatherers (West 1997; Prestrud and Nilssen 1992) and they have been ethnographically documented as starvation food in many locations (e.g. Lothrop 1928; Nelson 1969), although some recent populations have taboos about eating canids (Bogoras 1904-1909; Jochelson 1905-1908). When looking more closely at the role of wolves at Moravian sites, we should particularly note the large canid accumulations of several individuals at Předmostí Ia and Pavlov I – southeast, which is not mirrored at Dolní Věstonice I or II sites. Furthermore, large canid material within human burial contexts at Předmostí Ia or DVII does not play as important a role as previously suggested (Germonpré *et al*. 2012; Nývltová Fišáková and Sázelová 2008). According to our study of the literature (Maška 2008, Svoboda 2008, Klíma 1954, Musil 2005), we suggest that the smallest wolf remains deposited at Předmostí Ia and Pavlov I-southeast are closely associated with the larger wolf accumulations at both sites. This suggestion cannot be confirmed, as detailed mapping of the material from the original excavations is not available, but notes from Maška's excavation diary of Předmostí Ia (Maška 2008) and Klíma's excavation of Pavlov I-southeast (Klíma 1954), paired with maps of the excavation sites (Klíma 1954, Svoboda 2008), show a close association between the small wolf material and the wolf accumulations.

Thus, according to our preliminary observations, we conclude that human hunters at DVII probably had access to multiple wolf ecomorphs, both geographically and chronologically. The suggestion that similar variation at nearby sites represents early dog domestication events among Moravian hunter-gatherers cannot be supported by the DVII canid material. It is likely that such suggestions of earlier pre-LGM dog domestication are also, in fact, identifying multiple wolf ecomorphs from a single site, especially given our shallow knowledge of Pleistocene wolf populations (Perri, in review). Further analysis of canid material from Gravettian sites in Moravia will help to better characterize the interactions between human hunters and grey wolf subpopulations, assisted by advances in scientific techniques (e.g. stable isotopes, ancient DNA, geometric morphometrics). As our preliminary study here highlights, the analysis of canid populations, in contrast to individuals, is essential to understanding the complex interactions between wolves and humans in the prehistoric past.

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