



## The enigma of the Předmostí protodogs. A comment on Prassack et al. 2020

Luc A.A. Janssens<sup>a,b,\*</sup>, Myriam Boudadi-Maligne<sup>c</sup>, L. David Mech<sup>d</sup>, Dennis F. Lawler<sup>e,f,g</sup>

<sup>a</sup> Ghent University, Department of Archaeology, UFO, Sint Pietersnieuwstraat 35, 9000, Ghent, Belgium

<sup>b</sup> Department of Archaeology, University of Leiden, Einsteinweg 2, 2333 CC, Leiden, the Netherlands

<sup>c</sup> PACEA UMR 5199, CNRS, Université de Bordeaux, B2, Allée G St Hilaire CS 50023, 33615, Pessac cedex, France

<sup>d</sup> Northern Prairie Wildlife Research Center, U. S. Geological Survey, Jamestown, ND, 58401, USA

<sup>e</sup> Center for American Archaeology, Kampsville, IL, 62053, USA

<sup>f</sup> Illinois State Museum, Springfield, IL, 62703, USA

<sup>g</sup> Pacific Marine Mammal Center, Laguna Beach, CA, 92651, USA

### ARTICLE INFO

#### Keywords:

Microwear  
Dog  
Domestication  
Wolf  
*Canis lupus*

### ABSTRACT

Prassack et al. (2020) analyzed dental microwear in a sample of canids from the Gravettian site of Předmostí that had been identified as either Paleolithic dogs or Pleistocene wolves ( $n = 10$  in each group), accepting that the morphological differences between the groups validly distinguished the (self-domesticating) protodogs from wolves. The authors then concluded that differences in one m2 microwear pattern separated those groups and indicated enhanced anthropogenic based durophagy in the putative protodogs. The study also inferred protodog diets from another isotope study.

We disagree with this report for several reasons. First morphological criteria (skull and mandible) accepted here to distinguish the groups have been challenged based on robust research and can be explained by variability within wolves. Thus, we reject that one of the groups represents protodogs. We also question why only ten specimens were examined in each group, while about 130 were available in the original study, and why no specimen-selection criteria were reported. The study accepts the self-domestication hypothesis, which we reject based on solid knowledge of wolf behavior and inferences about what prey remains would be available, and where, in a hunter-gatherer setting. In summary, we can neither accept the existence of protodogs, nor the proposed difference in m2 microwear as being related to anthropogenic durophagy.

### 1. Introduction

In a recent article (JAS 115, 105092), Prassack and colleagues report on microwear of two mandibular molars among 20 Předmostí canids; “Gravettian;  $\pm 28.5$  kya”. These 20 specimens were divided in two morphological groups (Germonpré et al., 2015) based on an earlier study, with Předmostí protodogs defined as having nine shorter mandibular measurements (defined as leading to more robustness), including: shorter mandibles, shorter mandibular tooth rows for molars and premolars, and shorter mesio-distal diameter of m1), compared to Předmostí wolves (*Canis lupus*) (Germonpré et al., 2015).

Protodogs (Prassack et al., 2020, Table 1), were already reported in earlier publications (Camarós et al., 2016; Germonpré et al., 2009, 2012; Sablin and Khlopachev, 2002), and defined as having mainly shorter and wider snouts and shorter skulls.

Microwear of one parameter in m2, was significantly different between the groups, leading the authors to suggest that a more-gentle subgroup of wolves, called protodogs, were in contact with hunter-gatherers and feeding on anthropogenic bones. Based on this durophagy more robust mandibles originated in order “consistent with selection, to generate, transmit, and dissipate the forces necessary to break bone”.

Prassack et al. (2020) built the division between protodogs and wolves, on a wider series of specimens (Table 1 in Prassack et al. (2020)) and on a number of wolf-dog morphological differences: “dental crowding, carnassial size reduction, shorter and wider snouts, sagittal crest reduction, differences in mandibular shape orientation and robustness, pedomorphosis, and higher prevalence of dentognathic pathologies” (Germonpré et al., 2009, 2012, 2015) even though these differences are controversial (Boudadi-Maligne and Escarguel, 2014;

\* Corresponding author. Ghent University, Department of Archaeology, UFO, Sint Pietersnieuwstraat 35, 9000 Ghent, Belgium.

E-mail addresses: [coati1@icloud.com](mailto:coati1@icloud.com) (L.A.A. Janssens), [myriam.boudadi-maligne@u-bordeaux.fr](mailto:myriam.boudadi-maligne@u-bordeaux.fr) (M. Boudadi-Maligne), [mechx002@umn.edu](mailto:mechx002@umn.edu) (L.D. Mech), [dlawler122@gmail.com](mailto:dlawler122@gmail.com) (D.F. Lawler).

<https://doi.org/10.1016/j.jas.2020.105160>

Received 19 March 2020; Received in revised form 27 April 2020; Accepted 27 April 2020

Available online 4 March 2021

0305-4403/© 2020 Elsevier Ltd. All rights reserved.

Crockford and Kuzmin, 2012; Janssens et al., 2016c, 2019; Morey, 2010; Perri, 2016).

As a result, we have several concerns we want to discuss.

## 2. Microwear differences and related parameters

In Předmostí protodogs the grinding and shearing area is shorter than in Předmostí wolves (Germonpré et al., 2015). This contradicts the results from other publications in which durophagy resulted specifically in an expanded premolar row (shearing-arcade) (Meachen et al., 2014) and reduced grinding area (molars) (Meachen et al., 2014; Van Valkenburgh and Koepfli, 1993). The lack of a reduced grinding area undermines the inference of enhanced durophagy in the Předmostí protodogs.

Also, the specific area responsible for bone crushing is the talonid basin of m1 (Tanis and DeSantis, 2018), a location where no difference is recorded in the study of Prassack et al. (2020). This makes the argument that one of two groups consumed more bone less convincing.

Only two groups of 10 mandibles each were examined, yet a great number of mandibles from this site have been published before (about 130) with about 30–40 specimens defined as protodogs and about as many as wolves (Germonpré et al., 2015). Thus, it is puzzling why not many more were examined. Nor is it clear on which selection criteria only ten of each group were examined. Such a case selection reduces sample size and statistical robustness, and additionally questions possible directional selection.

A last, powerful, argument to doubt the existence of protodogs (and thus the theory that self-domesticating, durophagic, wolves existed), is that all nine morphometric differences observed in the Germonpré et al. (2015) study were also observed in a group of 75 recent German shepherd dogs (Janssens et al., 2019). Two morphological mandibular subgroups, different in the same nine morphological parameters as measured in the Předmostí canids, thus were observed in one recent dog breed, solely as the result of group variability. In support of the latter, we note that great morphological differences have also been proved to exist in a wild population of wolves (Boudadi-Maligne and Escarguel, 2014). And if they did not exist, the anthropogenic durophagy theory is a void structure.

## 3. Microwear difference related to the protodog theory

If durophagy was the result of an anthropogenic bone-rich diet in protodogs, Prassack et al. (2020) follow the self-domestication scavenging hypothesis (Coppinger and Coppinger, 2001) with contact seeking wolves being attracted to waste dumps (including bones) present at human camps, and on humans offering bones; in both cases the remains of the human diet. Wild wolves in the same area would not show such behavior, and thus consume less bones.

We see problems with this theory. We elaborate on these points in response.

### 3.1. Were there nutritious bones available nearby humans?

Hunter gatherers are, and were, nomadic and highly mobile (Binford, 1982; Kelly, 1995; 78–104; Lee, 2009; Sherwood et al., 2009), and occupied camps only for limited periods, so camp waste dumps would have been meagre. A study on Předmostí suggests year-round occupation, based on dental analysis of seven specimens of which four died during summer (Nyvltova-Fisakova, 2013). Year round can be but not necessarily permanently but repetitively. It can thus be that the three carnivores that died during winter (two wolves, one fox) were starving individuals that searched an empty camp for bone remains and died locally.

Camps would also be relatively poor in bones, as kills are typically not near camps (Lee, 2009; Sherwood et al., 2009), because prey avoid humans and camps. After kills, larger prey is butchered locally (Kelly,

1995; 63–64; Lee, 2009), and mainly high-quality meat pieces, with rather few bones attached are brought to camp (Dupont, 1872; Kelly, 1995; 77–92; Lee, 2009; Sherwood et al., 2009). And large prey was the main prey in Předmostí (Bocherens et al., 2015), being reindeer (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*) and mammoth (*Mammuthus primigenius*).

Kill sites, away from humans (geographical wolf-human isolation), would be more attractive feeding places for wolves. There, canids could consume entrails, organs, tendons, skin, bones and muscle remains (low quality and abundant: mammoths, e.g.); a more nutritious choice than a bony waste dump.

Even if bone remains were available in camps, humans would leave few with an interest for wolves, as humans are eager consumers of bone marrow and ground epi- and metaphyses (Blasco et al., 2019; Burchell, 1824; Van Kolfshoten et al., 2015), leaving mainly diaphyseal cortical fragments. Such remains are unattractive and contain no energetic value.

Next, if protodogs showed durophagy, they must have consumed a diet identical to humans, as it were the bony remains of their diet that these animals consumed. As thus their stable isotope values must have been comparable to those of humans, as shown in several comparative isotope studies on humans and dogs (Burleigh and Brothwell, 1978; Ewersen et al., 2018; Guiry, 2012, 2013; Kays and Feranec, 2011; Fisher, 2019). In Předmostí however human and protodog isotopes differ greatly, demonstrating that protodogs did not feed on bones from human diets (Bocherens et al., 2015).

Last, if wolves would search for opportunistic and anthropogenic dietary advantage, it would not be while humans were nearby (Mech and Hertel, 1983; Fritts et al., 2003) a prerequisite for self-domestication (temporary wolf-human isolation). Also, it would routinely not be for bones, as wolves rely on bones only in exceptional circumstances of starvation (Boitani, 1982; DeSantis et al., 2015; Mech and Hertel, 1983; Mech, 1966; Van Valkenburgh, 1996).

In conclusion, wolves would be only minimally motivated to approach humans and their camps to feed on bones, a prerequisite to explain the origin of protodogs and their durophagy. In addition, those specimens defined as protodogs, that is animals that sought human contact and were given bones or scavenged on human leftovers, do not show any evidence of having done so (isotopes).

### 3.2. Other possible reasons to explain microwear difference

We propose that other etiologies might explain durophagy. These include wolf diet difference based on habit, preference, sex, social hierarchy, season and climate.

Difference in prey choice, based on **preference** by individuals or packs, may have existed naturally in contemporary wolf subgroups living in the same geographical region (Perri, 2016). Such differences in diet have been reported to give rise to morphological differences (O'Keefe et al., 2013) and might be one explanation for mandibular morphometric variability.

Another reason might be **sex** and **hierarchy**, with more dominant animals eating first, leaving more boney prey to subordinates (Mech and Boitani, 2003).

**Season-of-death**, may explain differences in microwear, as the latter reflects to a certain degree the diet during the last months of life (Calandra and Merceron, 2016; Grine, 1986). As diets undergo seasonal alterations, canids dying in winter might show quite a different microwear pattern than those dying in summer when prey is abundant. One problem is that, while seasonal differences may explain microwear differences, mandibular differences can only be explained by longer lasting phenomena such as climate.

**Climate differences** might have affected the Předmostí canids. Indeed, the approximate dating of 28.5 kya BP by Prassack et al. (2020) is, based on several available <sup>14</sup>C datings, (Weninger and Jöris, 2008), the full-occupation phase thus being 31.900–29.600 ka cal BP Hulu

(Jöris et al., 2010). This period covers cold Greenland Stadial 5.2 (32.0–30.8 kya BPcal) and 5.1 (30.6–28.9 kya BPcal) with a warmer interstadial (30.8–30.6 kya BPcal) in between (Rasmussen et al., 2014; Weninger and Jöris, 2008) (Fig. 1). Microwear differences, might thus be the result of scarcer or different diet during the cold and warm periods, with more bone consumption during cold periods (Van Valkenburgh et al., 2019).

#### 4. Protodogs?

##### 4.1. Rejected criteria from the Prassack et al. (2020) list

**Dental crowding** formerly was thought to be present in dogs, but not in wolves (Benecke, 1987; Stockhaus, 1965; Wolfgram, 1894). However, dental crowding now is recognized as an unreliable domestication marker, since it occurs in a large percentage of wolves (Ameen et al., 2017). Additionally, some dog groups (Pfahlbauten Swiss Alpine Neolithic dogs) (Janssens et al., 2019) or breeds (Shiba Inu) (Esaka, 1982) do not evince tooth crowding. As a result, tooth crowding, or the lack thereof, cannot be used alone, or among grouped measures, to assign a specimen phylogenetically.

Three studies, involving more than 1700 measurements, reject **snout shortening** as a characteristic that defines dogs (Janssens et al., 2019; Morey, 2010; Wayne, 1986). There is convincing evidence that **sagittal-crest reduction** also is not an indicator of domestication (Lawrence and Bossert, 1967; Rizk, 2012). A further robust study revealed no difference in **mandibular coronoid process orientation** between dogs and wolves (Janssens et al., 2016a). Furthermore, **mandible robustness** (Clutton-Brock, 1962; Dimitrijević, 2006; Dimitrijević and Vuković, 2012; Lawrence and Reed, 1983; Tchernov and Valla, 1997) is a subjective assessment that lacks a sound morphometric foundation and cannot be used (Janssens et al., 2019). Several high-quality studies involving large numbers of specimens have proven that dogs are not **paedomorphic** wolves (Drake, 2011). Last, wild wolves exhibit the same types and frequencies of **dental pathology** as do domesticated dogs (Janssens et al., 2016c).

##### 4.2. Acceptable criteria to distinguish dogs from wolves

Acceptable wolf-dog distinguishing metrics include **in dogs**: important size reduction; as most measured by skull size reduction of 25% or more, a larger mean orbital angle (Janssens et al., 2016b), a higher mean skull ratio (Janssens et al., 2019; Pitulko and Kasparov, 2017), a wider mean snout ratio (Janssens et al., 2019; Morey, 2010; Wayne, 1986), maxillary P4 mesio-distal diameter under 21.9 mm (Janssens et al., 2019), and mandibular M1 mesio-distal diameter size difference in extreme cases (dogs small, wolves large) (Janssens et al., 2019).

In conclusion, from the list that Prassack et al. (2020) report, only snout width and carnassial size reduction are retained. However, none of these criteria differ in the Předmostí protodogs (Germonpré et al., 2009, 2012, 2015), compared to Pleistocene wolves (Boudadi-Maligne and Escarguel, 2014; Janssens et al., 2019), questioning -again- the reality of the existence of two separate groups in the Prassack et al. (2020) study.

#### 5. Conclusions

The microwear difference, in the Prassack et al. (2020) study, of only one parameter in m2 only, could be the result of, among others, natural variability and climatological difference during stadial and interstadial phases of the Předmostí occupation phase. We thus question the suggested diet of these canids. Also, the small sample used for the microwear analysis, and the lack of their selection criteria, invite doubt.

Furthermore, morphology does not warrant splitting the sample into protodogs and wolves for a number of reasons, so -per definition-a connection between microwear and anthropogenic durophagy is questionable. Apart from the purported distinguishing criteria between dogs

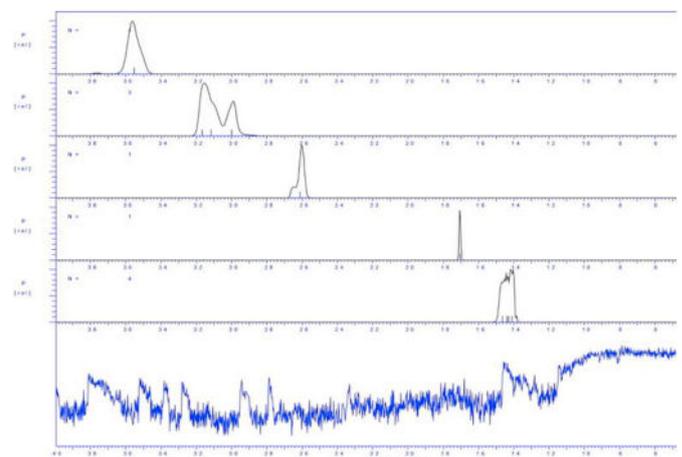


Fig. 1. NGRIP Core adapted to Hulu stalagmite GISP 2 age model, on several archaeological sites with Paleolithic canids. The x-axis relates to time (in kyaBPcal), the y-axis shows site probability dating and duration.

and wolves, mentioned in Prassack et al. (2020), and rejected here, there are more, that can be defined as “historical” but have been proved unreliable.

#### Declaration of competing interest

There are no financial or other or personal relationships that have influenced our work.

#### Acknowledgements

We thank Stefan van Dongen - for advice on statistics, Philippe Crombé and Angela Perri for help with some references, and Olaf Jöris for help with the dates of Předmostí and the making of Fig. 1.

#### References

- Ameen, C., Hulme-Beaman, A., Evin, A., Germonpré, M., Britton, K., Cucchi, T., Larson, G., Dobney, K., 2017. A landmark-based approach for assessing the reliability of mandibular tooth crowding as a marker of dog domestication. *J. Archaeol. Sci.* 85, 41–50.
- Benecke, N., 1987. Studies on early dog remains from Northern Europe. *J. J. Archaeol. Sci.* 14, 31–49.
- Binford, L., 1982. The archaeology of place. *J. Anthropol. Archaeol.* 1, 5–31.
- Blasco, R., Rosell, J., Arilla, M., Margilda, A., Villaba, D., Gopher, A., Barkai, R., 2019. Bone marrow storage and delayed consumption at Middle Pleistocene Qesem Cave, Israel (420 to 200 ka). *Sc. Adv.* 5, 1–13. <https://doi.org/10.1126/sciadv.aav9822>
- Bocherens, H., Drucker, D., Germonpré, M., Laznickova-Galetova, M., Naito, Y.I., Wissing, C., Brůzek, J., Oliva, M., 2015. Reconstruction of the Gravettian food-web at Předmostí I, using multi-isotopic tracking (13C, 15N, 34S) of bone collagen. *Quat. Int.* 359, 211–228. <https://doi.org/10.1016/j.quaint.2014.09.044>.
- Boitani, L., 1982. Wolf management in intensively used area of Italy. In: Harrington, F., Paquet, P. (Eds.), *Wolves of the World: Perspectives of Behavior, Ecology, and Conservation*. Noyes Publications, Park Ridge, New Jersey, USA, pp. 158–172.
- Boudadi-Maligne, M., Escarguel, G., 2014. A biometric re-evaluation of recent claims for Early Upper Palaeolithic wolf domestication in Eurasia. *J. Archaeol. Sci.* 45, 80–89. <https://doi.org/10.1016/j.jas.2014.02.006>.
- Burchell, W., 1824. *Travels into the Interior of Southern Africa*, II. Longman, Hurst, Orme, Brown, and Green. Paternoster row, London.
- Burleigh, R., Brothwell, D., 1978. Studies on amerindian dogs, 1: carbon isotopes in relation to maize in the diet of domestic dogs from early Peru and Ecuador. *J. J. Archaeol. Sci.* 5, 355–362.
- Calandra, I., Merceron, G., 2016. Dental microwear texture analysis in mammalian ecology. *Mamm. Rev.* 46 (3), 215–228.
- Camarós, E., Münzel, S., Cueto, M., Rivals, F., Conard, N., 2016. The evolution of Paleolithic 840 hominin–carnivore interaction written in teeth: stories from the Swabian Jura (Germany). *J. Archaeol. Sci.: For. Rep.* 6, 798–809.
- Clutton-Brock, J., 1962. Near Eastern canids and the affinities of the Natufian dogs. *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 76, 326–333.
- Coppinger, R., Coppinger, L., 2001. *Dogs: A Startling New Understanding of Canine Origin, Behavior, and Evolution*. University of Chicago Press.

- Crockford, S.J., Kuzmin, Y.V., 2012. Comments on Germonpré et al., *Journal of Archaeological Science* 36, 2009 "Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes", and Germonpré, Lázkicková-Galetová, and Sablin, *Journal of Archaeological Science* 39, 2012 "Palaeolithic dog skulls at the Gravettian Predmostí site, the Czech Republic". *J. Archaeol. Sci.* 39 (8), 2797–2801. <https://doi.org/10.1016/j.jas.2012.04.033>.
- DeSantis, L., Schubert, B., Schmitt-Linville, E., Ungar, P., Donohue, S., Haupt, R., 2015. Dental microwear textures of carnivores from the La Brea Tar Pits, California, and potential extinction implications. *Contrib. Sci. LACMNH* 42, 37–52.
- Dimitrijević, V., 2006. Vertebrate fauna of vinča-belo brdo: excavation campaigns 1998–2003. *Stariinar* 56, 245–269.
- Dimitrijević, V., Vuković, S., 2012. Was the dog locally domesticated in the Danube Gorges? Morphometric study of dog cranial remains from four Mesolithic–Early Neolithic archaeological sites by comparison with contemporary wolves. *Int. J. Osteoarchaeol.* 22, 12–34.
- Drake, A.G., 2011. Dispelling dog dogma: an investigation of heterochrony in dogs using 3D geometric morphometric analysis of skull shape. *Evol. Dev.* 13, 204–213.
- Dupont, E., 1872. Les temps préhistoriques en Belgique: L'Homme pendant les ages de la pierre dans les environs de Dinant-Sur-Meuse. Sec. Ballière et Fils, Paris, p. 250.
- Esaka, S., 1982. Development of rotation of mandibular premolar tooth germs in the dog. *Cells Tissues Organs* 114, 211–227.
- Ewersen, J., Ziegler, S., Schmölcke, U., 2018. Stable isotope ratios from Mesolithic and Neolithic canids as an indicator of human economic and ritual activity. *J. Archaeol. Sci. : For. Rep.* 17, 346–357.
- Fisher, A., 2019. When is a wolf a dog? Combined geometric morphometrics and stable isotope analysis for differentiating wild from domestic canids on the Northern Plains. *Plains Anthropol.* <https://doi.org/10.1080/00320447.2018.1548064>.
- Fritts, S., Stephenson, R., Hayes, R., Boitani, L., 2003. Wolves and humans. In: Mech, L., Boitani, L. (Eds.), *Wolves, Behavior, Ecology, and Conservation*. University of Chicago Press, pp. 289–316.
- Germonpré, M., Sablin, M.V., Stevens, R.E., Hedges, R.E., Hofreiter, M., Stiller, M., Després, V.R., 2009. Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes. *J. Archaeol. Sci.* 36 (2), 473–490. <https://doi.org/10.1016/j.jas.2008.09.033>.
- Germonpré, M., Laznickova-Galetova, M., Sablin, M.V., 2012. Palaeolithic dog skulls at the gravettian predmostí site, the Czech republic. *J. Archaeol. Sci.* 39 (1), 184–202. <https://doi.org/10.1016/j.jas.2011.09.022>.
- Germonpré, M., Laznickova-Galetova, M., Losey, R.J., Raikkonen, J., Sablin, M.V., 2015. Large canids at the gravettian predmostí site, the Czech republic: the mandible. *Quat. Int.* 359, 261–279. <https://doi.org/10.1016/j.quaint.2014.07.012>.
- Grine, F., 1986. Dental evidence for dietary differences in Australopithecus and Paranthropus: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783–822.
- Guiry, E., 2012. Dogs as analogs in stable isotope-based human paleodietary reconstructions: a review and considerations for future use. *J. Archaeol. Method Theor* 19, 351–376.
- Guiry, E., 2013. A canine surrogacy approach to human paleodietary bone chemistry: past development and future directions. *Archaeological and Anthropological Sc* 5, 275–286.
- Janssens, L., Miller, R., Dongen, S., 2016a. The morphology of the mandibular coronoid process does not indicate that *Canis lupus chanco* is the progenitor to dogs. *Zoomorphol* 135, 269–277.
- Janssens, L., Spanoghe, I., Miller, R., Van Dongen, S., 2016b. Can orbital angle morphology distinguish dogs from wolves? *Zoomorphol* 135, 149–158.
- Janssens, L., Verhaert, L., Berkowic, D., Adriaens, D., 2016c. A standardized framework for examination of oral lesions in wolf skulls (Carnivora: canidae: *Canis lupus*). *J. Mammal.* 97, 1111–1124 gyo058.
- Janssens, L., Perri, A., Crombre, P., Van Dongen, S., Lawler, D., 2019. An evaluation of classical morphologic and morphometric parameters reported to distinguish wolves and dogs. *J. Archaeol. Sci.* 23, 501–533.
- Jöris, O., Neugebauer-Maresch, C., Weninger, B., Street, M., 2010. The radiocarbon chronology of the auriignacian to mid-upper palaeolithic transition along the upper and middle danube. In: Neugebauer-Maresch, C., Owen, L. (Eds.), *New Aspects of the Central and Eastern European Upper Paleolithic – Methods, Chronology, Technology and Subsistence*, vol. 72. Mitteilungen der Prähistorischen Kommission, Vienna, pp. 101–137.
- Kays, R., Feranec, R., 2011. Using stable carbon isotopes to distinguish wild from captive wolves. *Northeast. Nat.* 18, 253–264.
- Kelly, R.J., 1995. *The Foraging Spectrum. Diversity in Hunter-Gatherer Lifeways*. Smithsonian Institution Press, London.
- Lawrence, B., Bossert, W.H., 1967. Multiple character analysis of *Canis lupus*, *latrans*, and *familiaris*, with a discussion of the relationships of *Canis Niger*. *Am. Zool.* 7, 223–232.
- Lawrence, B., Reed, C.A., 1983. *The dogs of Jarmo. Prehistoric Archeology along the Zagros Flanks*. University of Chicago Oriental Institute, Chicago, pp. 485–489.
- Lee, R., 2009. What hunters do for a living, or, how to make out on scarce resources. In: Lee, R., Devore, I. (Eds.), *Man the Hunter*. Aldine Transaction New Brunswick USA Sec, pp. 31–48.
- Meachen, J., Janowicz, A., Avery, J., Sadleir, R., 2014. Ecological changes in coyotes (*Canis latrans*) in response to the Ice Age megafaunal extinctions. *PLoS One* 9 (12), e116041. <https://doi.org/10.1371/journal.pone.0116041>.
- Mech, L., 1966. *The Wolves of Isle Royale*. National Parks Fauna Series, vol. 7. U.S. Government Printing Office, p. 210.
- Mech, L., Hertel, H., 1983. An eight-year demography of a Minnesota wolf pack. *Acta Zool. Fennica* 174, 249–250.
- Mech, L.D., Boitani, L. (Eds.), 2003. *Wolves, Behavior, Ecology, and Conservation*. University of Chicago Press, p. 428.
- Morey, D.F., 2010. *Dogs: Domestication and the Development of a Social Bond*. Cambridge University Press, New York City, p. 210.
- Nyylvtova-Fisakova, M., 2013. Seasonality of gravettian sites in the middle Danube region and adjoining areas of central Europe. *Quat. Int.* 294, 120e134.
- O'Keefe, F., Meachen, J., Fet, E., Brannick, A., 2013. Ecological determinants of clinical morphological variation in the cranium of the North American gray wolf. *J. Mammal.* 94, 1223–1236. <https://doi.org/10.1644/13-MAMM-A-069>.
- Perri, A., 2016. A wolf in dog's clothing: initial dog domestication and Pleistocene wolf variation. *J. Archaeol. Sci.* 68, 1–4.
- Pitulko, V.V., Kasparov, A.K., 2017. Archaeological dogs from the early holocene zhokhov site in the eastern siberian arctic. *J. Archaeol. Sci. : For. Rep.* 13, 491–515.
- Prassack, K., Dubois, J., Laznickova-Galetova, M., Germonpre, M., Ungar, P., 2020. Dental microwear as a behavioral proxy for distinguishing between canids at the Upper Paleolithic (Gravettian) site of Predmostí, Czech Republic. *J. Archaeol. Sci.* 115, 105092.
- Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W.Z., Lowe, J.J., Pedro, J.B., Popp, T., Seierstad, I.K., Steffensen, J.P., Svensson, A.M., Vallenga, P., Vinther, B.M., Walker, M.J.C., Wheatley, J.J., Winstrup, M., 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. *Quat. Sci. Rev.* 106, 14–28.
- Rizk, O.T., 2012. Insight into the Genetic Basis of Craniofacial Morphological Variation in the Domestic Dog, *Canis familiaris*. University of California Berkeley.
- Sablin, M., Khlopachev, G., 2002. The earliest ice age dogs: evidence from Eliseevichi 11. *Curr. Anthropol.* 43, 795–799. <https://doi.org/10.1086/34>.
- Sherwood, L., Washburn, L., Lancaster, C., 2009. The evolution of hunting. In: Lee, R., Devore, I. (Eds.), *Man the Hunter*. Aldine Transaction New Brunswick USA Sec, pp. 293–303.
- Stockhaus, K., 1965. *Metrische Untersuchungen an Schädeln von Wölfen und Hunden*. *J. Zool. Syst. Evol. Res.* 3, 157–258.
- Tanis, B., DeSantis, L., 2018. Dental microwear textures across check teeth in canids: implications for dietary studies of extant and extinct canids. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* <https://doi.org/10.1016/j.palaeo.2018.07.028>.
- Tchernov, E., Valla, F.F., 1997. Two new dogs, and other Natufian dogs, from the southern Levant. *J. Archaeol. Sci.* 24, 65–95.
- Van Kolfschoten, T., Buhrs, E., Verheijen, I., 2015. The larger mammal fauna from the Lower Paleolithic Schöningen Spear site and its contribution to hominin subsistence. *J. Hum. Evol.* 9, 1–16.
- Van Valkenburgh, B., Koepfli, K., 1993. Cranial and dental adaptations to predation in canids. *Symp. Zool. Soc. Lond.* 65, 15–37.
- Van Valkenburgh, B., 1996. Feeding behavior in free-ranging, large African carnivores. *J. Mammal.* 77, 240–254. <https://doi.org/10.2307/1382725>.
- Van Valkenburgh, B., Peterson, R.O., Smith, D.W., Stahler, D.R., Vucetich, J.A., 2019. Tooth Fracture Frequency in Gray Wolves Reflects Prey Availability. <https://doi.org/10.1101/658468> bioRxiv 658468.
- Wayne, R.K., 1986. Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution* 40, 243–261.
- Weninger, B., Jöris, O., 2008. A 14C age calibration curve for the last 60ka: the Greenland-Hulu U/Th timescale and its impact on understanding the Middle to Upper Paleolithic transition in Western Eurasia. *J. Hum. Evol.* 55, 772–781.
- Wolfgang, A., 1894. Die Einwirkung der Gefangenschaft auf die Gestaltung des Wolfshädelns. *Zool. Jahrbuch (Abt. Systematik)* 7, 773–822.