



A wolf from Gravettian site Pavlov I, Czech Republic: Approach to skull pathology

Sandra Sazelová, Dennis Lawler, Šárka Hladilová, Soňa Boriová, Soňa Šáliová,
Tomáš Janoušek, Angela Perri, Jean-Jacques Hublin, Jiří Svoboda

► To cite this version:

Sandra Sazelová, Dennis Lawler, Šárka Hladilová, Soňa Boriová, Soňa Šáliová, et al.. A wolf from Gravettian site Pavlov I, Czech Republic: Approach to skull pathology. International Journal of Paleopathology, 2020, 31, pp.7-13. <10.1016/j.ijpp.2020.07.001>. <hal-04044650>

HAL Id: hal-04044650

<https://hal.science/hal-04044650v1>

Submitted on 5 Jun 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization



A wolf from Gravettian site Pavlov I, Czech Republic: Approach to skull pathology

Sandra Sazelová^{a,*}, Dennis Lawler^{b,c,d}, Šárka Hladilová^e, Soňa Boriová^{a,f}, Soňa Šáliová^{a,g},
Tomáš Janoušek^a, Angela Perri^h, Jean-Jacques Hublin^{i,j}, Jiří Svoboda^{a,g}

^a Czech Academy of Sciences, Institute of Archeology, Brno, Center for Paleolithic and Paleoanthropology Dolní Věstonice, Čechyňská 19, CZ - 602 00 Brno, Czech Republic

^b Center for American Archeology, Rt. 100, Kampsville IL 62053 USA

^c Illinois State Museum, 1011 E. Ash St., Springfield IL 62703 USA

^d Pacific Marine Mammal Center, 20612 Laguna Canyon Rd., Laguna Beach CA 92561 USA

^e Masaryk University, Faculty of Science, Department of Geological Sciences, Kotlářská 2, CZ - 611 37 Brno, Czech Republic

^f University of Hradec Králové, Faculty of Arts, Department of Archeology, Rokitanského 62, CZ - 500 03 Hradec Králové, Czech Republic

^g Masaryk University, Faculty of Science, Department of Anthropology, Kotlářská 2, CZ - 611 37 Brno, Czech Republic

^h University of Durham, Department of Archeology, Stockton Road, Durham, DH1 3LE United Kingdom

ⁱ Max Planck Institute for Evolutionary Anthropology, Department of Human Evolution, Deutscher Platz 6, 04103 Leipzig, Germany

^j Collège de France, 11 place M. Berthelot, 75005 Paris, France

ARTICLE INFO

Keywords:

Archeozoology

Differential diagnosis

Grey wolf

Mid-Upper Paleolithic

Osteomyelitis

ABSTRACT

Objective: Describe pathological features on internal and external aspects of the skull of an ancient grey wolf.

Materials: Wolf remains that were found at the southwestern settlement Area A of Gravettian site Pavlov I.

Methods: Visual observation and description; microcomputed tomography; porosity and fragmentation indices for internal and external skull features; histological section of the fourth upper premolar tooth.

Results: Dorsally, the sagittal crest revealed bone healing and remodeling. The sagittal lesion differential diagnosis was blunt trauma with or without fracture. Ventrally, otic region pathology included severe proliferation and lysis (osteomyelitis). The pathology was not resolvable among differential (microbial) causes of osteomyelitis, although other potential etiologies were ruled out.

Conclusions: Probable first report of otic region osteomyelitis in an ancient grey wolf.

Significance: The proximity of the wolf remains to human-related findings, and presence of red ochre and shells, suggest human involvement in the burial.

Limitations: This is a single specimen with differential diagnoses that were not resolvable to a single definitive diagnosis.

Suggestions for Further Research: Further investigation of the possible anthropological significance of the burial circumstances.

1. Introduction

1.1. Overview

Since the 19th century, excavations at Moravian Gravettian archaeological sites have yielded multiple sizes of wolves. At sites that we are studying, three groups of wolves can be observed, having large, intermediate, and small statures. The stature differences exceed criteria for sexual dimorphism, possibly by 20 % or more (Perri and Sazelová,

2016), and it seems likely that these remains represent ecologically-driven morphotypes (Larson et al., 2012; Thalmann et al., 2013; Morey, 2014; Boudadi-Maligne and Escarguel, 2014; Perri, 2016; Lupo, 2017; Pitulko and Kasparov, 2017). However, some authors suggest secondary human-driven genetic isolation as the reason for the observed morphological and dietary variation (Germonpré et al., 2012, 2015, 2016; Bocherens et al., 2015, 2019).

The Pavlov I site is an extensive Gravettian mammoth hunters' campsite with a main cultural layer dated between 30–34 ky cal BP

* Corresponding author.

E-mail addresses: sazelova@arub.cz (S. Sazelová), dlawler122@gmail.com (D. Lawler), sarka@sci.muni.cz (Š. Hladilová), boriova@arub.cz (S. Boriová), saliova@arub.cz (S. Šáliová), janousek.t@seznam.cz (T. Janoušek), angela.r.perri@durham.ac.uk (A. Perri), hublin@eva.mpg.de (J.-J. Hublin), sekretariat@arub.cz (J. Svoboda).

<https://doi.org/10.1016/j.ijpp.2020.07.001>

Received 9 December 2019; Received in revised form 17 July 2020; Accepted 30 July 2020

Available online 28 August 2020

1879-9817/ © 2020 Elsevier Inc. All rights reserved.

(Svoboda, 2016a,b). The site was excavated by two researchers in two phases: a) Bohuslav Klíma in 1952–1972 (Klíma, 1954, 1987; Svoboda et al., 1994, 1997, 2005); and b) Jiří Svoboda in 2013–2015 (Svoboda et al., 2016a, 2016b). Skeletal remains from a single wolf (*Canis lupus*) were recovered from Southwestern Area A. The analysis of this specimen, found alongside remnants of human cultural activity, suggests that interaction between humans and wolves may have occurred. The goal of this study is to evaluate the pathological conditions present on the wolf skeleton, as a means to explore the life of this wolf and its possible interaction with humans.

2. Material and methods

2.1. Relevant site description

During 2013–2015, rescue excavations at Southwestern Area A involved opening a trench with 9.0×5.5 m sides (Svoboda et al., 2016a, 2016b). An identified cultural layer had its uppermost depth at 2.5–3.4 m, and was deepest at 3.0–3.9 m. Recovered charcoal from the cultural layers yielded radiocarbon dates ranging from 30,495–29,564 cal BP (Beta 359288; deviation 95.4) to 33,561–32,524 cal BP (Beta 359286; deviation 95.4).

The incomplete skeleton of an adult wolf (*Canis lupus*) was found centrally in Area A (Fig. 1). The thorax was articulated, with a skull close by (approximately 0.4–0.5 m), arguably belonging to the same individual. The area around the skeleton was delimited spatially by several mammoth ribs. An accumulation (diameter of 0.5 m) of 14 dentalia shells (*Fissidentium badense*) was found approximately 0.6–1.0 m northwest of the wolf skeleton; some were filled by charcoal matrix or covered with ochre, and a few displayed artificial markings.

Approximately 1.2 m south of the skeleton, an oval-shaped hearth (0.8×0.6 m with depth up to 15.0 cm) was discovered, together with small pits at its base. The immediate surroundings included 984 bones-teeth fragments, of which 262 belong to the wolf skeleton. Other

species recovered included bones of raven, hare, and fox, along with fragments of mammoth tusk and molar lamellae. From the girdle of the fore- and hind limbs of the wolf, only the right scapula and left pelvic bones are preserved. All growth zones are fused completely. The partially-preserved axial skeleton consists of vertebrae from cervical to upper coccygeal, and includes ribs. The postcranial skeleton is without pathological changes, except two lumbar vertebrae (SI Fig. 1) that have mild osteophytes on the caudal aspect of the vertebral plates (up to 2.9×4.3 mm). Additional visible porosity on cranial (20.4×10.8 mm) and caudal (5.5×6.4 mm) articular surfaces of a lumbar vertebra appear to represent taphonomic demineralizing.

2.2. Virtual reconstructions of skull

Micro-CT scanning of the wolf skull was done by the Department of Human Evolution, Max Planck Institute, Leipzig, using a transportable industrial scanner (Diondo d3 high-resolution micro-CT system, Diondo, Henderson, Nevada). A virtual model was constructed from separate micro-CT scans at voxel resolution 0.1 mm. Visualization and model processing were completed using the program Avizo 9.7.0 (FEI Visualization Sciences Group, ThermoFisher Scientific, Hillsboro, Oregon) (Fig. 2a-c). Bone irregularities were observed on the skull external sagittal crest and recovered parietal bones, on both temporal bones, and on the occipital bone; these were marked manually. The porosity index (PI) and fragmentation index (FI) were calculated using Avizo 9.7.0. The PI expresses void spaces in materials as the ratio of void space to total volume. In this instance, high PI indicates greater occurrence of isolated cavities in the otherwise more compact bone structure of the sagittal crest, whereas low PI indicates a more uniform porous bone without isolated cavities. The FI offers an indication of connectivity, calculated on the relative surface convexity and concavity; negative values indicate a high prevalence of surface irregularities.

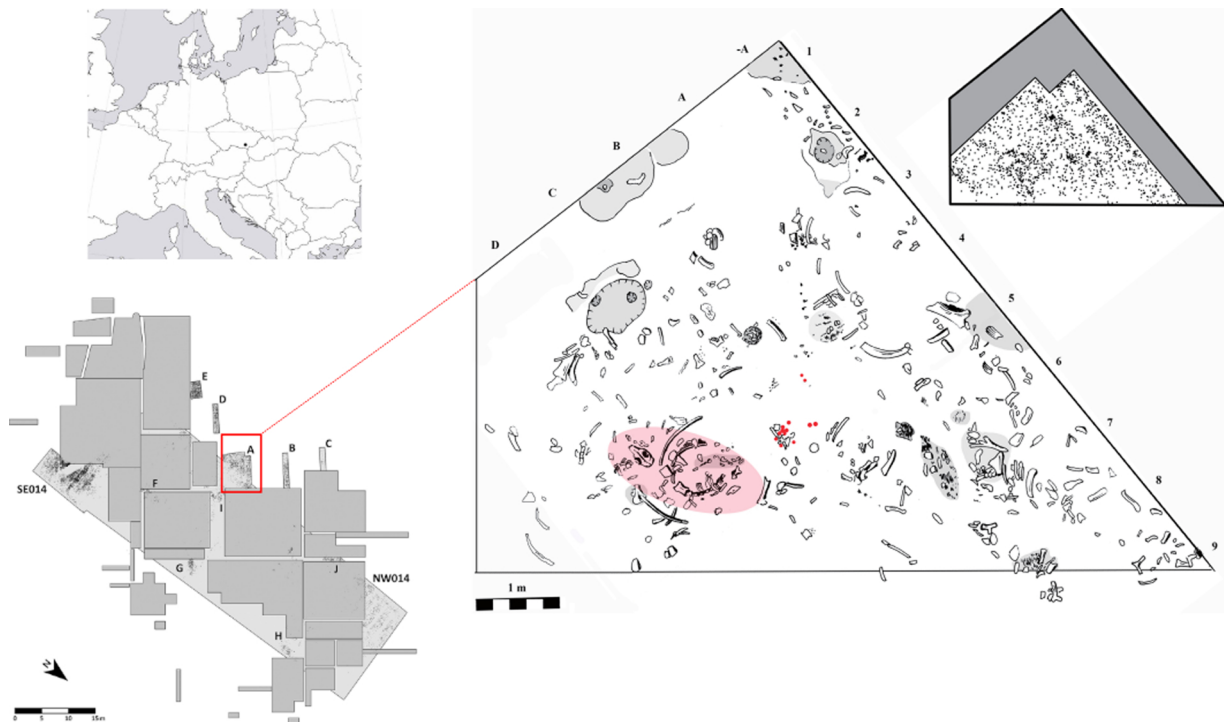


Fig. 1. Left: Site plan of the Pavlov I in which the contour of the Archeopark Pavlov building is inserted. The dark grey shows the areas excavated by B. Klíma, while the light grey is connected to excavations by J. Svoboda. Right: Plan of the southwestern area A. The wolf skeleton marked with a red oval and the Dentalium shells by red dots. Scales: 15 m and 1 m in detail. Modified after Svoboda 2016a,b (Figure by SS) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

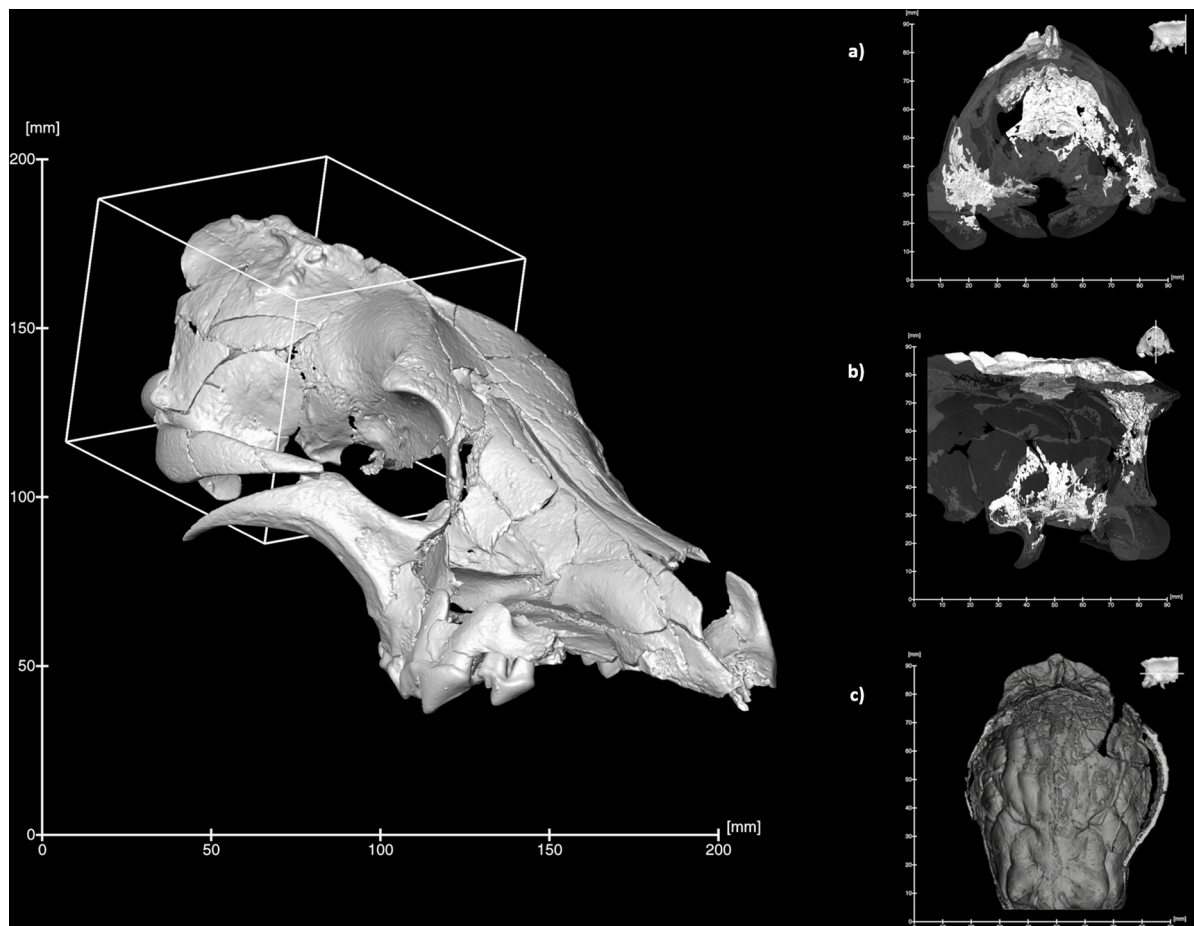


Fig. 2. 3-D models of the wolf in transversal plane with range of osteomyelitis changes in frontal (a), lateral (b), and basal (c) planes. In collaboration with EVA MPG in Leipzig (Figure by TJ and SS).

2.3. Tooth enamel development

Thin histological sections were obtained from the permanent upper fourth premolar tooth in the bucco-palatinal plane through the mesial and distal cusps. These were evaluated to document age- and stress-related changes in the enamel increments (Dean, 2000; Hillson, 2014; Kierdorf et al., 2019). Methodologically, we focused on crown formation over a period of weeks to months, daily secretion rate of enamel formation, and Retzius periodicity (Dean, 2000; Hillson, 2014). This approach would yield information regarding stress events during puppyhood and pre-adult development (Fig. 3a,b). The most suitable teeth for histological evaluation usually are permanent incisors or a 1st premolar (Hillson, 2005). However, given the taphonomic circumstances, it was necessary to use an upper 4th premolar. The daily secretion rate (DSR) was calculated by measuring the distance between daily lines that followed the course of enamel prisms photographed at different areas of the buccal side of the crown, including in all 30 measurements taken in the interval of $250\ \mu\text{m} \times 155\ \mu\text{m}$. The Retzius periodicity was determined by counting cross-striations (daily increments) between successive striae of Retzius at several locations in a tooth (Hogg et al., 2015).

3. Results

The remains are those of an adult *Canis lupus* that died at an undetermined age. The nearly-complete skull (Fig. 2) reveals asymmetric torsion. The skull is matured fully, with all permanent teeth erupted. There are visual pathological changes dorsally, involving the sagittal crest, and ventrally, involving the entire otic region.

3.1. Pathological features of the sagittal crest

The sagittal crest and occipital bone are attachment sites of strong neck and temporal muscles (*m. sternooccipitalis*, *m. cleidooccipitalis*, *m. splenius*, and *m. temporalis*; Miller et al., 1964; König and Liebich, 2014). The dorsal aspect of the sagittal crest reveals a 30 mm boney callus (Fig. 4a). A length $> 20.0\ \text{mm}$ of the crest length is displaced approximately $5.0\ \text{mm}$ from the sagittal plane, toward the right side of the skull. This feature is composed of thick bone (up to $3.0\ \text{mm}$) having a greatest axis length $23.5\ \text{mm}$ and greatest axis width $20.4\ \text{mm}$. Based on micro-CT analysis, the external sagittal crest feature represents earlier remodeling that yielded the observed compact external new bone. Histologically, boney changes are observed at the level of *diploë* and do not penetrate to the inner level of the bone. The feature is healed fully.

The internal aspect of the dorsal cranium reveals lytic and proliferative lesions with predominance of bone resorption, based on relative porosity and fragmentation indices (Table 1). These features are noted on the internal occipital bone, both parietal bones, and right temporal bone. Their proximity to *diploë* precludes measuring exact depth, but they are $< 5.0\ \text{mm}$ at the deepest point of the occipital bone. Pathologically, the skull dorsum lesions are focally-disseminated-to-diffuse, chronic, and of moderate severity (Fig. 4b-d). Also observed are foci of color change from dark ochre to brown, mainly at porotic foci. The latter appear to be taphonomic changes.

3.2. Features of the ventral skull

The ventral skull features are bilateral, involving and essentially obliterating middle and inner ears, tympanic bullae, and immediately

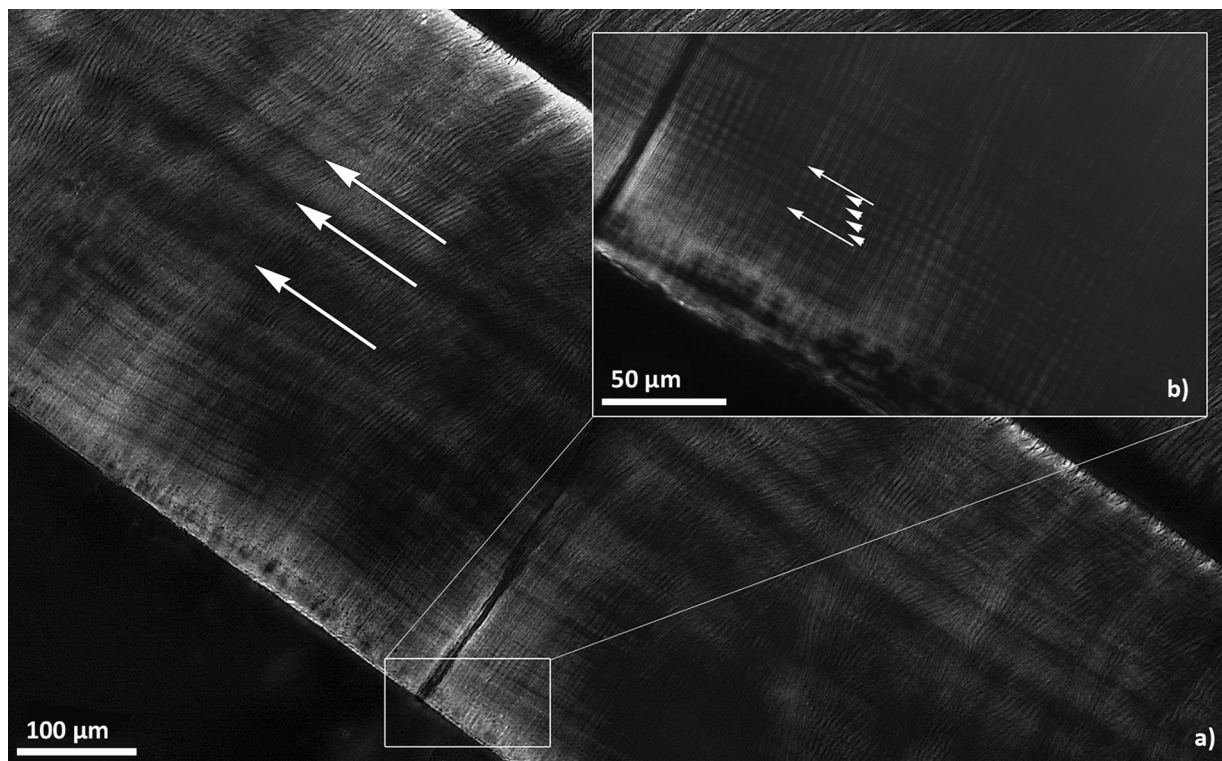


Fig. 3. Enamel increments of the fourth upper premolar. Buccal side of the crown, approximately first third of the tooth. The tooth cusp points to the upper left corner of the figure. White arrows on the part (a) indicate accentuated stress lines in the lateral part of the enamel. The part (b) represents daily increments in detail. Long arrows point to Retzius lines, whereas the short arrows represent the daily increments in between them. Microscale: 1000 microns (Figure by SŠ).

surrounding boney structure (Fig. 2a-c). The feature is very rough-surfaced and reveals mixed bone proliferation and porosity. It is severe, focally-disseminated-to-diffuse by visual assessment, and very likely chronic-active to chronic. The proliferative-lytic pattern indicates osteomyelitis. However, lack of living cellular content for histological evaluation, and lack of microbiological data, limit further observations.

3.3. Dental observations

The alveoli around P^2-M^2 on the right side, and P^3-M^2 on the left side, display taphonomic changes on their labial aspects. The structure of the enamel surface of the sectioned P^4 does not show hypoplastic defects, hypomineralizing, or dental caries (Hillson, 2005). The changes in color of the enamel, and the cracks in enamel microstructure, probably resulted from taphonomic processes. The average value for the secretion rate of enamel formation is $4.1 \mu\text{m}$ per day, and the Retzius periodicity is 4 daily increments between two Retzius lines (Fig. 3b). The crown formation time was calculated at the locus with the best track of the accentuated stress lines, with an outcome of 361 days.

Some of the alveoli on the lingual maxillary side reveal loss of margin bone that likely was caused by periodontal disease. Similar patterns are observed in other canids (Page and Schroeder, 1982).

4. Discussion

4.1. Differential diagnosis of cranial lesions

The differential diagnosis for the morphological changes noted along the sagittal crest of the skull includes trauma or taphonomic change. Differential diagnosis of trauma would be limited here to blunt force with or without fracture, with cause unknown. The healed trauma was documented by micro-CT. Given the advanced state of healing, the event clearly preceded the otic region features by a considerable time, also precluding taphonomic cause (absence of proliferative living cells).

Several etiologic agents could have caused the boney changes noted on the ventral skull. Most probable among these is infection (Wilcock, 1991). *Otitis externa* is common in dogs, as is bilateral involvement. The causal infections may be primary or secondary, and progression is variable (Wilcock, 1991; Rosychuk and Luttgen, 2000; Greene and Budsberg, 2006). A broad field of offending microbes and events can include many bacteria, fungi, parasites, immune disorders, allergies, vasculitis, endocrine dysfunctions, and tumors (Rosychuk and Luttgen, 2000). Within each of the foregoing categories many causes and influences can be identified definitively (during life) by clinical and laboratory methods.

Anatomically, infectious *otitis media* and *otitis interna* can occur via hematogenous or lymphatic dissemination from a distant soft tissue site, although direct inward extension from aggressive *otitis externa*, via the auditory tube from the pharynx or across a ruptured tympanic membrane, is most probable (Rosychuk and Luttgen, 2000). Relative to associated microbiology, it has been reported that the canine middle ear is not sterile under normal circumstances, and is known to harbor members of *Corynebacterium*, *Klebsiella*, *Staphylococcus*, *Streptococcus*, *Escherichia*, and *Branhamella* (Tojo et al., 1985).

By comparison, the most frequent microbial isolates reported from diseased middle ear structures include *Pseudomonas*, *Staphylococcus*, *Malassezia*, *Streptococcus*, *Corynebacterium*, *Enterococcus*, *Proteus*, and *Escherichia* species. Anaerobic microbes also have been identified, as have migrating foreign bodies such as some grass awns (Cole et al., 1998). The inner ear most often becomes involved secondarily, by direct extension from the middle ear and external ear canal (Strain et al., 1995; Rosychuk and Luttgen, 2000).

Neurologically, the facial nerve (7th cranial) emerges from the brain stem and associates physically with the vestibulocochlear nerve (8th cranial). Their pathway passes into the internal auditory meatus, whereupon the facial nerve diverges into the facial canal to continue its course (Miller et al., 1964). The vestibulocochlear nerve has two bundles, vestibular and cochlear. The former serves tissues that govern the

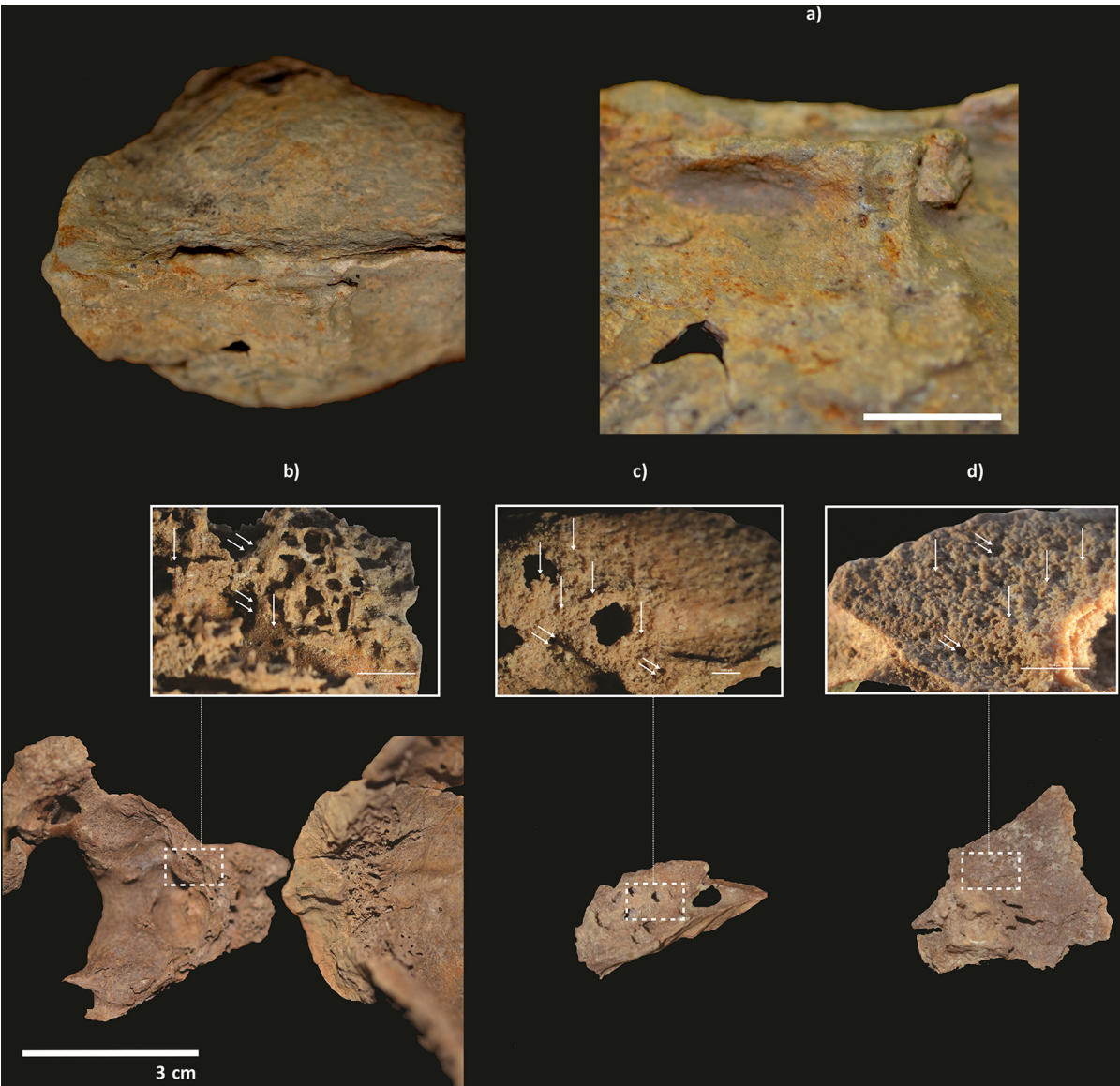


Fig. 4. Lytic (double transverse arrows) and proliferative (single vertical arrow) changes on the selected internal skull fragments: external plane of the sagittal crest and detail in lateral view (a), basal view on the occipital bone (b), medial view on the petrous bone (c), internal plane of the temporal bone (d). Scale: 3 cm (1 cm in detail), microscale: 1000 microns (Figure by SS and SB).

sense of balance, and the latter serves the cochlea (hearing). There are sympathetic and parasympathetic nerves in this small region as well (Miller et al., 1964). *Otitis media* and *interna* thus are likely to be accompanied by clinical signs involving at least these two cranial nerves, possibly with autonomic complications.

Clinically, outwardly visible symptoms of external, middle, and inner ear disease include pain, ataxia, head tilt, circling, nystagmus of the eyes, facial nerve paralysis, and proprioceptive abnormalities. Bilateral disease may or may not produce a head tilt, and crouched posture may be observed (Rosychuk and Luttgen, 2000). A severely

affected individual would have significant pain and ataxia, with near inability to walk, to pursue prey, or to defend itself. Additionally, microbial movement via the 8th cranial nerve has been suggested as a physical pathway to meningeal and brain tissue. Such extension into the brain stem or systemic sepsis would represent very serious complications (Wilcock, 1991).

Concerning outcome, given their locations and severity, each of the above-described ventral skull pathological processes and avenues would have been fatal in the absence of aggressive and specifically-directed treatment (Rosychuk and Luttgen, 2000). For so-affected wild

Table 1
Measurements of pathologically changed areas in virtual model of the wolf skull done in Avizo 9.7.0 software (FEI Visualization Sciences Group).

Skeletal component	Changed areas (mm ²)	Porosity index (PI)	Fragmentation index (FI)
Cerebral aspect of occipital bone	2269	1.132	−0.413
Sagittal crest	1661	3.646	−1.755
Cerebral aspect of left and right parietal bone	1428	0.394	−0.456
Cerebral aspect of right temporal bone	1583	0.660	0.118
Cerebral aspect of left temporal bone	740	0.213	0.088

carnivores, a further risk would be predation by pack members or other carnivores. The time course of the osteomyelitis near the end of life would have been no more than a few weeks.

There exist insufficient historical and modern data to estimate the frequency and severity of middle and inner ear disease among ancient or modern wolves. Furthermore, comparing this wolf to modern canine data is hazardous because most existing clinical data have come from tertiary referral centers that by their nature see the most complicated cases (Iwata et al., 2017). Furthermore, Victorian and post-Victorian humans have manipulated the canine gene pool, with often-disastrous effects, including susceptibility to ear diseases (Gough and Thomas, 2004). While we caution in general that directly comparing data from ancient dogs with Victorian-to-modern dogs is tenuous scientifically, it is correct to state that the infection-related information related herein applies broadly to domesticated animals (Wilcock, 1991; Tourigny et al., 2016). In the latter study, the same bones were affected in an ancient dog, with a diagnosis that was most compatible with chronic osteitis (Tourigny et al., 2016), although a plausible listing of possible offending microorganisms would be virtually the same.

Additional possible differential diagnoses are much more distant in this instance, but potentially could include neoplasms. Primary tumors of the middle ear are rare in dogs (Little et al., 1989). In these few instances, the inner ear may become involved secondarily, through extension from the middle ear. Middle and inner ear ototoxicity can result from drugs and environmental chemicals (Little et al., 1989), but these agents would have been absent from the environment of this wolf, thus ruling them out of the differential diagnosis. Other differential diagnoses that might associate with similar outward appearances (in the living individual) include decompensated congenital anomalies, stroke, cerebral vascular hemorrhage, head trauma, severe hypoglycemia, severely deranged acid-base or electrolyte balance, and meningitis or encephalitis (Fenner, 2000; Podell, 2000). All of these disorders can result from multiple possible underlying pathophysiological insults, but would be ruled in or out during life or soon after death by the characteristic bony features of osteomyelitis (with the possible exceptions of originating or accompanying complications of the infection) (Greene and Budsberg, 2006) and the microbiological studies. Summarily, the detailed description of the differential diagnostic list in this section accomplishes two objectives. First, the overt appearance that the subject wolf would have presented to approaching humans is clear. Second, the complexity of diagnosis during life is clear as well.

4.2. Enamel stress

Enamel is formed by daily secretion rhythms that form regular incremental daily markings (cross-striations) and longer periodic markings (striae of Retzius). The record can document early crown mineralization stress events such as malnutrition, pathogen invasion, trauma, weaning, or seasonal changes of resource availability (Macho et al., 1996; Dirks et al., 2002; Birch and Dean, 2014; Lorentz et al., 2019; Skinner and Byra, 2019). Survival of stress is recorded in enamel as stress lines that are accentuated (darker) in microscopic appearance, as compared to daily increments (Fitzgerald and Rose, 2007; Żądzińska et al., 2015; Hogg et al., 2018). This appearance results from disturbance of the physiological secretion of matrix by ameloblasts during the development of tooth enamel. An example is the *neonatal line* that associates with birth stress (Hillson, 2014). The periodicity of Retzius striae of this wolf, if compared to modern dogs, remains at 4 daily increments. This relatively short periodicity indicates faster growth rates, smaller body size, and shorter lifespan for both species (Hogg et al., 2018).

This wolf evidently overcame several separate stress events during its crown mineralization. Early life experiences with malnutrition, serious pathogen invasion, and environment-related stressor events only rarely have no consequences at clinical or subclinical/physiological levels. Thus, this wolf could have been infection-susceptible from

early life. By opposing argument, we suggest that the oral pathology in this instance likely was insufficient to have been involved in the otic region osteomyelitis, unless the invading microorganism was unusually virulent and/or the wolf's immune competence was compromised severely.

4.3. Human-wolf interactions

The skeletal remains of the wolf under investigation here were discovered next to a hearth and an accumulation of dentalia shells covered with ochre that often was used in human burials. The distribution of lithics and other faunal remains recovered within Southwestern Area A was uniform and without significant pattern of accumulation. Thus, based on the context and lacking evidence of other human traces of meat processing such as butchering/skinning or filleting, we suggest that this could have been an intentional burial. We also posit that humans would have recognized that this wolf was ill. If the burial was intentional, its cultural significance remains unresolved, although a similar care pattern regarding unusual individuals is known from Mid-Upper Paleolithic human burials (Trinkaus, 2018).

5. Conclusion

Untreated and barring intervening predation, the consequences of the ventral skull pathology would have been fatal. Several factors in this evaluation provide insight into bridging paleopathology observations with modern diagnostic medicine. Having described the pathological features and considered the bone-related differential diagnosis in context, one next works toward understanding the immediate soft tissue anatomical environment. Mentally linking bone and surrounding soft tissues then provides a pathway to evaluating physical and biochemical consequences that would have affected the wolf's outcome.

Observing basic mammalian morphology and understanding the broad and deep conservation of the fundamental insult responses of bone and the general reactions to infection (Tangredi and Lawler, 2019) allows using the acquired data to construct a more thorough evaluation (Lawler, 2017). Most paleopathology is somewhat less straightforward, and therefore, the learning involves understanding where a well-considered differential diagnosis can be preferred to a less rigorously-derived definitive diagnosis.

Acknowledgements

We are grateful to H. Temming, D. Plotski, and N. Stephens from the EVA MPG, Leipzig; and M. Králík from the Faculty of Science at Masaryk University. The paper was supported with Czech national institutional support [RVO: 68081758 awarded to IA CAS Brno] and Czech Academy of Sciences [Strategy AV 21 Memory in the digital age: Paleolithic site of Pavlov awarded to IA CAS Brno].

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ijpp.2020.07.001>.

References

- Birch, W., Dean, M.C., 2014. A method of calculating human deciduous crown formation times and of estimating the chronological ages of stressful events occurring during deciduous enamel formation. *J. Forensic Leg. Med.* 22, 127–144. <https://doi.org/10.1016/j.jflm.2013.12.002>.
- Bocherens, H., Drucker, D., Germonpré, M., Láznicková-Galetová, M., Naito, Y.I., Wissing, C., Brůžek, J., Oliva, M., 2015. Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking (^{13}C , ^{15}N , ^{34}S) of bone collagen. *Quat. Int.* 359–360, 211–228. <https://doi.org/10.1016/j.quaint.2014.09.044>.
- Bocherens, H., Germonpré, M., Drucker, D., Hobson, K.A., Sablin, M., Láznicková-Galetová, M., 2019. Further isotopic insight on dietary partitioning among large canids in Předmostí: Implications for canid-human interactions. In: Wojtal, P.,

- Wilczyński, J. (Eds.), 3rd Conference World of Gravettian Hunters, pp. 6 Kraków, Poland, May 20–24 2019, ISEA PAS, Kraków.
- Boudadi-Maligne, M., Escarguel, G., 2014. A biometric re-evaluation of recent claims for Early Upper Paleolithic wolf domestication in Eurasia. *J. Archaeol. Sci.* 45, 80–89. <https://doi.org/10.1016/j.jas.2014.02.006>.
- Cole, L.K., Kwochka, K.W., Kowalski, J.J., Hillier, A., 1998. Microflora and antimicrobial susceptibility patterns of isolated pathogens from the horizontal ear canal and middle ear in dogs with otitis media. *J. Am. Vet. Med. A.* 212 (4), 534–538. <https://doi.org/10.1046/j.1365-3164.2000.00191.x>.
- Dean, M., 2000. Incremental markings in enamel and dentine: what they can tell us about the way teeth grow. In: Teaford, M., Meredith Smith, M., Ferguson, M. (Eds.), *Development, Function and Evolution of Teeth*. Cambridge University Press, Cambridge, pp. 119–130.
- Dirks, W., Reid, D.J., Jolly, C.J., Phillips-Conroy, J.E., Brett, F.L., 2002. Out of the mouths of baboons: stress, life history, and dental development in the Awash National Park hybrid zone. *Ethiopia. Am. J. Phys. Anthropol.* 118, 239–252. <https://doi.org/10.1002/ajpa.10089>.
- Fenner, W.R., 2000. Diseases of the brain. In: Ettinger, S.J., Feldman, E.C. (Eds.), *Textbook of Veterinary Internal Medicine*, 5th edition. Saunders, Philadelphia, pp. 552–602.
- Fitzgerald, C.M., Rose, J.C., 2007. Reading between the lines: dental development and subadult age assessment using the microstructural growth markers of teeth. *Biological Anthropology of the Human Skeleton*. John Wiley & Sons, Ltd, pp. 237–263.
- Germonpré, M., Láznicková-Galetová, M., Sablin, M.V., 2012. Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. *J. Archaeol. Sci.* 39 (1), 184–202. <https://doi.org/10.1016/j.jas.2011.09.022>.
- Germonpré, M., Láznicková-Galetová, M., Losey, R.J., Rääkkönen, J., Sablin, M.V., 2015. Large canids at the Gravettian Předmostí site, the Czech Republic: the mandible. *Quat. Int.* 359, 261–279. <https://doi.org/10.1016/j.quaint.2014.07.012>.
- Germonpré, M., Losey, R., Láznicková-Galetová, M., Galeta, P., Sablin, M.V., Latham, K., Rääkkönen, J., 2016. Spondylitis deformans in three large canids from the Gravettian Předmostí site: comparison with other canid populations. *Int. J. Paleopathol.* 15, 83–91. <https://doi.org/10.1016/j.ijpp.2016.08.007>.
- Gough, A., Thomas, A., 2004. *Breed Predispositions to Disease in Dogs & Cats*. Blackwell, Oxford, pp. 235.
- Greene, C.E., Budsberg, S.C., 2006. Musculoskeletal infections. In: Greene, C.E. (Ed.), *Infectious Diseases of the Dog and Cat*, 3rd ed. Saunders, Philadelphia, pp. 823–841.
- Hillson, S., 2005. *Teeth*. 2nd edition. Cambridge University Press, New York, pp. 373.
- Hillson, S., 2014. *Tooth Development in Human Evolution and Bioarchaeology*. Cambridge University Press, New York, pp. 307.
- Hogg, R., Godfrey, L., Schwartz, G., Dirks, W., Bromage, T., 2015. Lemur biorhythms and life history evolution. *PLoS One* 10, e0134210. <https://doi.org/10.1371/journal.pone.0134210>.
- Hogg, R., Hu, B., Bromage, T., 2018. Histology of dental long-period biorhythms in *Canis familiaris*. *J. Anat.* 233 (5), 618–624. <https://doi.org/10.1111/joa.12876>.
- Iwata, O., Kawase, A., Iwai, M., Kazuko, W., 2017. Evacuation of a tertiary neonatal centre: lessons from the 2016 Kumamoto earthquakes. *Neonatology* 112 (1), 92–96. <https://doi.org/10.1159/000466681>.
- Kierdorf, H., Breuer, F., Witzel, C., Kierdorf, U., 2019. Pig enamel revisited – incremental markings in enamel of wild boars and domestic pigs. *J. Struct. Biol.* 205, 48–59. <https://doi.org/10.1016/j.jsb.2018.11.009>.
- Klíma, B., 1954. Pavlov, nové paleolitické sídliště na jižní Moravě. *Archeol. rozhledy* 6, 137–142 (In Czech).
- Klíma, B., 1987. Paleolitická parohová industrie z Pavlova. *Pam. archeol.* 78, 289–368 (In Czech).
- König, H.E., Liebich, H.-G., 2014. *Anatomie Der Haussäugetiere*. Schattauer GmbH, pp. 782 (In German).
- Larson, G., Karlsson, E.K., Perri, A., Webster, M.T., Ho, S.Y.W., Peters, J., Stahl, P.W., Piper, P.J., Lingaas, F., Fredholm, M., Comstock, K.E., Modiano, J.F., Schelling, C., Agoulnik, A.I., Leegwater, P.A., Dobney, K., Vigne, J.-D., Vil, C., Andersson, L., Lindblad-Toh, K., 2012. Rethinking dog domestication by integrating genetics, archaeology, and biogeography. *Proc. Natl. Acad. Sci. U. S. A.* 109 (28), 8878–8883. <https://doi.org/10.1073/pnas.1203005109>.
- Lawler, D.F., 2017. Differential diagnosis in archaeology. *Int. J. Paleopathol.* 19, 119–123. <https://doi.org/10.1016/j.ijpp.2016.05.001>.
- Little, C.J., Pearson, G.R., Lane, J.G., 1989. Neoplasia involving the middle cavity of dogs. *Vet. Rec.* 124 (3), 54–57. <https://doi.org/10.1136/vr.124.3.54>.
- Lorentz, K.O., Lemmers, S.A.M., Chrysostomou, C., Dirks, W., Zaruri, M.R., Foruzanfar, F., Sajjadi, S.M.S., 2019. Use of dental microstructure to investigate the role of prenatal and early life physiological stress in age at death. *J. Archaeol. Sci.* 104, 85–96. <https://doi.org/10.1016/j.jas.2019.01.007>.
- Lupo, K.D., 2017. When and where do dogs improve hunting productivity? The empirical record and some implications for early Upper Paleolithic prey acquisition. *J. Anthropol. Archaeol.* 47, 139–151. <https://doi.org/10.1016/j.jaa.2017.05.003>.
- Macho, G.A., Reid, D.J., Leakey, M.G., Jablonski, N., Beynon, A.D., 1996. Climatic effects on dental development of *Theropithecus oswardi* from Koobi Fora and Olororgesailie. *J. Hum. Evol.* 30, 57–70. <https://doi.org/10.1006/jhev.1996.0004>.
- Miller, M.E., Christensen, G.C., Evans, H.E., 1964. *Anatomy of the Dog*. WB Saunders, Philadelphia, pp. 558–563.
- Morey, D.F., 2014. In search of Paleolithic dogs: a quest with mixed results. *J. Archaeol. Sci.* 52, 300–307. <https://doi.org/10.1016/j.jas.2014.08.015>.
- Page, R.C., Schroeder, H.E., 1982. Periodontitis in Man and Other Animals: a Comparative Review. The University of Michigan, pp. 330.
- Perri, A., 2016. A wolf in dog's clothing: initial dog domestication and Pleistocene wolf variation. *J. Archaeol. Sci.* 68, 1–4. <https://doi.org/10.1016/j.jas.2016.02.003>.
- Perri, A., Sázelová, S., 2016. The role of large canids. Preliminary assessment of population variabilities in Moravia. In: Svoboda, J. (Ed.), *Dolní Věstonice II: Chronostratigraphy, Paleoethnology, Paleoanthropology, The Dolní Věstonice Studies 21*. Academy of Sciences of the Czech Republic, Institute of Archeology Brno, Brno, pp. 138–146.
- Pitulko, V.V., Kasparov, A.K., 2017. Archaeological dogs from the early Holocene Zhokhov site in the eastern Siberian Arctic. *J. Archaeol. Sci. Rep.* 13, 491–515. <https://doi.org/10.1016/j.jasrep.2017.04.003>.
- Podell, M., 2000. Neurologic manifestations of systemic disease. In: Ettinger, S.J., Feldman, E.C. (Eds.), *Textbook of Veterinary Internal Medicine*, 5th edition. Saunders, Philadelphia, pp. 548–552.
- Rosychuk, R.A.W., Luttgen, P., 2000. Diseases of the ear. In: Ettinger, S.J., Feldman, E.C. (Eds.), *Textbook of Veterinary Internal Medicine*, 5th edition. Saunders, Philadelphia, pp. 986.
- Skinner, M., Byra, C., 2019. Signatures of stress: pilot study of accentuated laminations in porcine enamel. *Am. J. Phys. Anthropol.* 169, 619–631. <https://doi.org/10.1002/ajpa.23854>.
- Strain, G.M., Merchant, S.R., Neer, T.M., Tedford, B.L., 1995. Ototoxicity assessment of a gentamycin sulfate otic preparation in dogs. *Am. J. Vet. Res.* 56 (4), 532–538.
- Svoboda, J. (Ed.), 1994. Pavlov I, Excavations 1952–1953. ERAUL 66/The Dolní Věstonice Studies, vol. 2. Université de Liège, Liège, pp. 215.
- Svoboda, J. (Ed.), 1997. Pavlov I – Northwest. The Upper Paleolithic Burial and Its Settlement Context. The Dolní Věstonice Studies, vol. 4. Institute of Archaeology, Brno, pp. 472.
- Svoboda, J. (Ed.), 2005. Pavlov I – Southeast. A Window into the Gravettian Lifestyles. The Dolní Věstonice Studies, vol. 14. Institute of Archaeology, Brno, pp. 500.
- Svoboda, J., Novák, M., Sázelová, S., Demek, J., 2016a. Pavlov I: a large Gravettian site in space and time. *Quat. Int.* 406, 95–105. <https://doi.org/10.1016/j.quaint.2015.09.015>.
- Svoboda, J., Novák, M., Sázelová, S., 2016b. Pavlov I. Předběžné výsledky výzkumu v letech 2013–2015. *Přehled výzkumů* 57 (1), 9–33 (In Czech).
- Tangredi, B.P., Lawler, D.F., 2019. Osteoarthritis from an evolutionary perspective. *Anat. Rec.* 1–10. <https://doi.org/10.1002/ar.24339>.
- Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V.J., Sawyer, S.K., Greenfield, D.L., Germonpré, M.B., Sablin, M.V., López-339 Giraldez, F., Dominog-Roura, X., Napiwala, H., Uerpmann, H.P., Loponte, D.M., Acosta, A.A., Giemisch, L., Schmitz, R.W., Worthington, B., Buikstra, J.E., Druzhkova, A., Graphodatsky, A.S., Ovodov, N.D., Wahlberg, N., Freedman, A.H., Schweizer, R.M., Koepfli, K.P., Leonard, J.A., Meyer, M., Krause, J., Pääbo, S., Green, R.E., Wayne, R.K., 2013. Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science* 342 (6160), 871–874. <https://doi.org/10.1126/science.1243650>.
- Tojo, M., Matsuda, H., Fukui, K., Sasai, H., Baba, E., 1985. Experimental induction of secretory and purulent otitis media by the surgical obstruction of the eustachian tube in dogs. *J. Small Anim. Pract.* 26, 81–89. <https://doi.org/10.1111/j.1748-5827.1985.tb02088.x>.
- Tourigny, E., Thomas, R., Guiry, E., Earp, R., Allen, A., Rothenburger, J.L., Lawler, D., Nussbaumer, M., 2016. An osteobiography of a 19th-Century dog from Toronto. *Canada. Int. J. Osteoarchaeol.* 26 (5), 818–829. <https://doi.org/10.1002/oa.2483>.
- Trinkaus, E., 2018. An abundance of developmental anomalies and abnormalities in Pleistocene people. *Proc. Natl. Am. U. S. A.* 115 (47), 11941–11946. <https://doi.org/10.1073/pnas.1814989115>.
- Wilcock, B.P., 1991. The eye and ear. In: 4th ed. In: Jubb, K.V.F., Kennedy, P.C., Palmer, B. (Eds.), *Pathology of Domestic Animals Vol. 1*. Academic Press, San Diego, pp. 522–529.
- Żądzińska, E., Lorkiewicz, W., Kurek, M., Borowska-Strugińska, B., 2015. Accentuated lines in the enamel of primary incisors from skeletal remains: a contribution to the explanation of early childhood mortality in a medieval population from Poland. *Am. J. Phys. Anthropol.* 157, 402–410. <https://doi.org/10.1002/ajpa.22731>.