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Spondylosis deformans in three large canids from the Gravettian Předmostí site: Comparison with other canid populations

Mietje Germonpré[a,*], Robert Losey[b], Martina Lázničková-Galetová[c], Patrik Galeta[c], Mikhail V. Sablin[d], Katherine Latham[b], Jannikke Räikkönen[e]

[a] Operational Direction "Earth and History of Life", Royal Belgian Institute of Natural Sciences, Vautierstraat 29, 1000 Brussel, Belgium
[b] Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada
[c] Department of Anthropology, Faculty of Philosophy and Arts, University of West Bohemia, Sedláčkova 15, 306 14 Pilsen, Czech Republic
[d] Zoological Institute RAS, Universitetskaya nab. 1, 199034 Saint-Petersburg, Russia
[e] Swedish Museum of Natural History, Department of Environmental Research and Monitoring, P.O. Box 50007, S-104 05 Stockholm, Sweden

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ABSTRACT

Spondylosis deformans is a common degenerative condition of the spinal column, especially in modern domestic dogs. The presence and severity of lesions are related to age and physical activity, but they can be influenced by genetics, with some modern breeds being particularly predisposed. Spondylosis deformans also has been reported in prehistoric dogs. Here, we describe three affected vertebrae, likely from three individuals, in a large canid assemblage from the Gravettian Předmostí site, Czech Republic. We compare the proportion of affected individuals from the Předmostí assemblage with that of affected individuals among recent wild Northern wolves, inbred wolves, captive wolves, and recent Northern dogs. The proportion of affected individuals among the captive wolves differs significantly from the other wolf groups. The proportion in the Předmostí assemblage does not differ significantly from that of the wild wolf groups.

1. Introduction

1.1. Disease description

Spondylosis deformans (SD) is a degenerative response to spinal inter-vertebral disk disease. It is characterized by bony spurs or bridges that form around cranial and caudal vertebral end-plates, possibly as a stabilizing response (Morgan, 1967; Morgan and Biery, 1985; Morgan et al., 1989; Thomas and Fingeroth, 2015). The osteophyte formations can develop into extensive lesions resembling an "Elizabethan" collar (Read and Smith, 1968), resulting in stiffening of the spinal column (Weidl, 1998). SD has been observed in many mammal and bird species (Hultgren et al., 1987) and in general occurs with higher frequency and greater severity in older individuals (Read and Smith, 1968; LeCouteur and Child, 1995).

SD is likely to develop in all domestic dogs that live sufficiently long (Morgan and Biery, 1985). Furthermore, certain recent dog breeds, such as German shepherd dog, Boxer, Cocker Spaniel, Airedale Terrier, and Flat-coated Retriever, have higher genetic risk for the condition (Hoerlein, 1978; Langeland et al., 1995; Carnier et al., 2004; Levine et al., 2006; Kranenburg et al., 2011).

An association may exist between type II inter-vertebral disc disease and SD (Levine et al., 2006). Bony bridges and spurs also may form secondary to instability between adjacent vertebrae due to congenital vertebral deformities, trauma, or discospondylitis (Morgan et al., 1989; LeCouteur and Child, 1995). Three SD cases have been reported in recent wild wolves (Cross, 1940; Fritts and Caywood, 1980; Zeira et al., 2013).

Here we describe three SD-affected vertebrae from three Pleistocene large canids, recovered at the Gravettian Předmostí site in the Czech Republic. We compare the proportion of affected individuals in this assemblage with specimens from modern canids, including outbred wild Northern wolves, Scandinavian inbred wolves, captive wolves, and recent Northern dogs. To our knowledge, this is the first report that includes data from wild and captive wolves in a study of SD.

1.2. Site description

Předmostí is part of a series of large Gravettian sites located in Central Europe (Fig. 1). These sites are characterized by large

* Corresponding author.
E-mail addresses: mietje.germonpre@naturalsciences.be (M. Germonpré), robert.losey@ualberta.ca (R. Losey), laznicko@yahoo.fr (M. Lázničková-Galetová), galeta@ksa.zcu.cz (P. Galeta), msablin@yandex.ru (M.V. Sablin), jannikke.raikkonen@nrm.se (J. Räikkönen).

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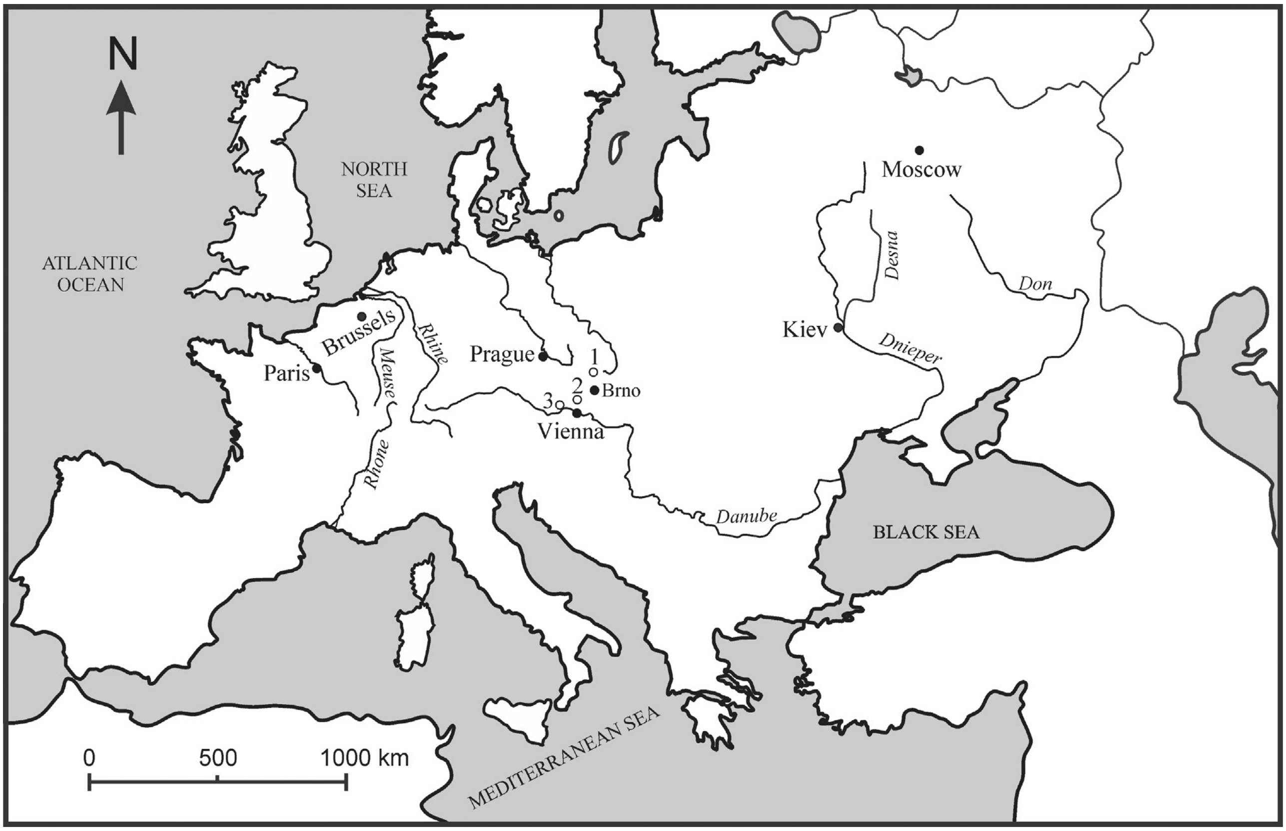

Fig. 1. Map showing the most important Gravettian sites from Central Europe with human burials covered by mammoth scapulae: 1, Předmostí I (Czech Republic); 2: Dolní Věstonice I and Pavlov I (Czech Republic), 3: Krems-Wachtberg (Austria).

accumulations of mammoth bones; distinctive lithic tools (backed bladelets and shouldered points); ivory implements and ornaments; and human female representations. Human burials at these sites often are associated with mammoth scapulae (Oliva, 1997; Svoboda, 2008; Lázničková-Galetová, 2015; Wojtal and Wilczyński, 2015). Large canids are the second most abundant animal group at Předmostí, after mammoths, based on Minimum Number of Individuals (MNI) calculations (Pokorný, 1951).

Two morphotypes are present among the large canid material: palaeolithic dogs that have estimated mean body weight c. 36 kg, and Pleistocene wolves with estimated mean body weight c. 42 kg (Germonpré et al., 2015a,b). The vertebrae we describe cannot be diagnosed definitively as Pleistocene wolf or palaeolithic dog because the morphology for the two species is insufficiently distinctive. With this in mind, the null hypothesis of this study is that the proportions of individuals affected by SD are the same across the Předmostí canids and a series of modern comparative wolf and domestic dog specimens.

2. Materials and methods

2.1. Specimens and curation

The Předmostí canid skeletal remains described here are housed at the Moravian Museum, in Brno, Czech Republic. This material was excavated primarily by K. J. Maška (1882–83, 1886–91, 1893–94); M. Kříž (1893–97); J. Knies (1882, 1884, 1925); and K. Absolon (1922–25, 1927). A detailed review can be found in Svoboda (2008). In the Moravian Museum, all canid material is stored according to skeletal element. No information is available on the context of the finds. It is not known if the Předmostí vertebrae were discovered as part of associated skeletons or as dispersed and isolated elements.

The canid cervical, thoracic, and lumbar vertebrae from this collection were evaluated for pathologies. In total, 383 vertebrae from the site were studied (Supporting Table 1). The MNI used here is estimated from this vertebral material. The axis is the most frequently found, among the vertebrae (48 specimens). The axis-derived MNI estimate is smaller than the MNI based on mandibles (120 specimens) (Germonpré et al., 2015a,b) and postcranial material (106 specimens) (Germonpré, unpublished data). The MNI based on the axis is larger than that based on thoracic vertebrae (2 specimens) and lumbar vertebrae (9 specimens).

2.2. Species-related data

The three pathological Předmostí specimens were photographed, radiographed, and described. Their relative sizes indicate derivation from three different canids. The normal and SD-affected specimens from the Předmostí assemblage were compared with normal and affected wild Northern wolves from Canada, Alaska, Russia, and Scandinavia (Table 1).

The Scandinavian wolf material consists of one historical collection dating prior to 1980. A second group of Scandinavian wolves post-dates 1984. This second group was established by a wolf pair in 1983 (Liberg et al., 2005) and represents an inbred population of 51 individuals. Age at death is known for a large portion of this assemblage. A third group is formed by captive wolves from various locations. No information is available on the types and sizes of these captive wolves' enclosures. Knowledge of their longevity is limited and there is no information about familial relationships.

We also examined the spines of ten 19th and 20th century Northern domestic dogs. These were indigenous dogs from

Table 1
List of the large canids used in this study; BM: University of Bergen, Museum of Zoology, Norway; GNM: The Gothenburg Museum of Natural History, Gothenburg, Sweden; MZM: Moravian Museum, Anthropos Institute, Brno, Czech Republic; NRM: Swedish Museum of Natural History, Stockholm, Sweden; RAM: Royal Alberta Museum, Edmonton, Canada; RBINS: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; SNM: Natural History Museum of Denmark, Copenhagen, Denmark; UAA: University of Anchorage, Alaska; UAM: University of Alaska Museum of the North, Fairbanks, Alaska; ZIN RAS: Zoological Institute of the Russian Academy of Science, Saint-Petersburg, Russia; ZMO: University of Oslo, Museum of Zoology, Norway; c.: century; MNI: Minimum Number of Individuals.

	Age	Institute	MNI
Předmostí	Gravettian	MZM	48
Reference Groups			
Wild Northern wolves			143
Canada	19th & 20th c.	RAM	39
Alaska	19th & 20th c.	UAM	54
Russia	19th & 20th c.	ZIN RAS	20
Scandinavia Historical	19th & 20th c.	BM, GNM, NRM, SNM, ZMO	30
Contemporary inbred wolves			
Scandinavia	20th & 21st c.	NRM	51
Captive (zoo) wolves			11
Canada	20th & 21st c.	UAA	2
Alaska	20th & 21st c.	UAM	1
Russia	20th & 21st c.	ZIN RAS	1
Sweden	20th & 21st c.	NRM	3
Belgium	20th & 21st c.	RBINS	4
recent Northern dogs			10
Greenland	19th & 20th c.	NRM, SNM	8
Sakhalin	20th c.	SNM	1
Siberia	19th & 20th c.	ZIN RAS	1
Grand Total			263

Greenland, Sakhalin, and Siberia (Table 1). Genetic admixture between recent Northern dogs and modern European dogs is limited because of geographic and cultural isolation of the former group (cf. Larson et al., 2012; Brown et al., 2013; van Asch et al., 2013). Furthermore, Siberian huskies and Greenland sled dogs, all presumably directly related to our recent Northern dogs, share an important ancestry with East Asian dog lineages (Frantz et al., 2016).

Three of the canids in our recent Northern dog group suffered trauma, as shown by broken and healed bones (Germonpré, unpublished data). Age at death was estimated for some recent Northern dogs, based on tooth wear of the associated skull, using the method of Gipson et al. (2000). Survival to advanced age is unlikely for wild wolves because of high-risk for stochastic events (see discussion in Lawler et al., in press). By contrast, captive wolves often enjoy much greater longevity (Lawler et al., in press).

2.3. Specimen grading

A grading system for SD has been proposed, based on degree of osteophyte development (DOD) (Langeland and Lingaas, 1995; Carnier et al., 2004): DOD 0-no osteophytes; DOD 1-small osteophytes on the epiphyseal margin that do not exceed the vertebral edge; DOD 2- osteophytes enlarged beyond the epiphyseal margin, but not connected to osteophytes on the adjacent vertebra; DOD 3- osteophytes on adjoining vertebrae are connected, establishing a bridge. Small osteophytes could have been broken off during the taphonomic history, obscuring mild SD. Therefore, we excluded DOD 1 and grouped all specimens with SD in stages DOD 2, DOD 3, and DOD 2/3.

2.4. Statistical analysis

We compared proportions of normal and affected specimens among the study groups. The recent Northern dogs were not included in the statistical analysis, since no dogs had vertebrae classified as DOD 2/3. Differences in proportions of affected vertebrae were tested by analysis of contingency tables that cross-tabulated the grouped normal and affected specimens. To test the general 2×4 contingency table, we used the ordinary Pearson chi-square test. For pair-wise comparison of two groups (i.e., 2×2 table), we applied Barnard's test using Z-pooled statistics. Barnard's test belongs to the family of unconditional exact tests that are recommended for testing association in 2×2 contingency tables. These generally are more powerful than ordinary Pearson chi-square test or Fisher's exact test for moderate to small sample sizes (Lydersen et al., 2009). The significance level was set at <0.05. All statistical tests were done in JMP 12.0.1., except Barnard's tests, which were conducted in using R 3.1.2 Exact package (R Core Team, 2014).

3. Results

3.1. Předmostí pathological vertebrae

Three pathological vertebrae from Předmostí large canids are described: one thoracic (98-590-F (20742)) and two lumbar (97-588-A (1), 97-588-A (2)) (Figs. 2–10). The thoracic vertebra 98-590-F (20742) is incomplete, having a broken spinous process. Lipping is present on the caudal surface of the vertebra body, extending beyond the epiphysis (Figs. 2 and 3), consistent with SD stage DOD 2/3. The spinous processes of the two lumbar vertebrae also are broken. Lumbar vertebra 97-588-A (1) reveals a very well-developed "Elizabethan" collar on the cranioventral and craniolateral aspects of its body. Caudal surface osteophytes are partly broken off; remaining osteophytes extend just beyond the margin of the epiphysis. These well-developed osteophytes are consistent with SD stage DOD 2/3 (Figs. 4–7). Lumbar vertebra 97-588-A (2) has osteophytes on cranial and caudal body surfaces. The caudal surface osteophytes are very large and extend beyond the epiphyseal margin, consistent with SD stage DOD 2/3 (Figs. 8–10).

3.2. Comparison vertebrae

All recent wolf groups include vertebrae in SD stage DOD 2/3. The Canadian wild wolf group includes two affected individuals; the Alaskan group has seven affected individuals; the Russian group has two affected individuals; the Historical Scandinavian group has four affected individuals (total affected N = 15; Table 2).

Table 2
Total Minimum Number of Individuals (MNI) and MNI of affected individuals with vertebrae in spondylosis DOD2/3 in the Předmostí assemblage and in the comparative data sets of wild Northern wolves, Scandinavian contemporary (inbred) wolves, captive (zoo) wolves and recent Northern dogs.

	total	normal	Spondylosis DOD2/3	
MNI	MNI	MNI	MNI	%
Předmostí				
total	48	45	3	6.25
range cervical vertebrae	48	48	0	0.00
range thoracic vertebrae	2	1	1	50.00
range lumbar vertebrae	9	2	2	22.22
Total wild Northern wolves				
total	143	128	15	10.49
range cervical vertebrae	143	141	2	1.41
range thoracic vertebrae	143	131	12	8.43
range lumbar vertebrae	143	139	4	2.80
Wild wolves Canada				
total	39	37	2	5.13
range cervical vertebrae	39	39	0	0.00
range thoracic vertebrae	39	38	1	2.56
range lumbar vertebrae	39	38	1	2.56
Wild wolves Alaska				
total	54	47	7	12.96
range cervical vertebrae	54	52	2	3.70
range thoracic vertebrae	54	48	6	11.11
range lumbar vertebrae	54	52	2	3.70
Wild wolves Russia				
total	20	18	2	10.00
range cervical vertebrae	20	20	0	0.00
range thoracic vertebrae	20	18	2	10.00
range lumbar vertebrae	20	20	0	0.00
Wild historical wolves Scandinavia				
total	30	26	4	13.33
range cervical vertebrae	30	30	0	0.00
range thoracic vertebrae	30	27	3	10.17
range lumbar vertebrae	30	29	1	3.36
Scandinavian contemporary (inbred) wolves				
total	51	45	6	11.76
range cervical vertebrae	51	51	0	0.00
range thoracic vertebrae	51	46	5	9.90
range lumbar vertebrae	51	49	2	3.98
Captive (zoo) wolves				
total	11	6	5	45.46
range cervical vertebrae	11	9	2	18.18
range thoracic vertebrae	11	7	4	36.36
range lumbar vertebrae	11	8	3	27.27
recent Northern dogs				
total	10	10	0	0.00
range cervical vertebrae	10	10	0	0.00
range thoracic vertebrae	10	10	0	0.00
range lumbar vertebrae	10	10	0	0.00

The Scandinavian inbred wolf group includes six wolf skeletons with evidence of SD stage DOD 2/3. These individuals ranged in age from two to eight years at death (Supporting Table 2). The captive wolf group includes five affected individuals (Table 2), with known age at death for four: 3–4 years, 4–6 years, 10–12 years, and 13 years (Supporting Table 2). The 4–6 year specimen had SD DOD 2/3 over its L1-L6 vertebrae. The 13-year specimen was affected severely, with SD stage DOD 2/3 over T2-T13 and L1-L7. None of the ten recent Northern dogs had SD stage DOD 2/3 (Table 2), and this group was not included in the statistical analyses.

3.3. Statistical results

The affected frequency of Předmostí canids was 6.3% of MNI, lower than that of wild Northern wolves (10.5%) and Scandinavian inbred wolves (11.8%), and much lower than that of captive wolves (45.5%) (Table 2).

Normal and affected individuals are summarized in Table 3, which also shows the expected numbers and the chi-square value of each cell (cf. McHugh, 2013). The difference in proportions of normal and affected individuals among Předmostí, recent wild wolves, inbred wolves, and captive wolves, is statistically significant (Pearson chi-square = 14.6, P = 0.022; Table 3). The chi-square test is not violated because the analysis conforms to both of the two commonly used requirements for sample size. Cochran (1954) assumed that no more than 20% of the cells should have expected cell frequencies <5. Furthermore, according to the less strict rule of Zar (1999), the mean expected frequency should be >10. In the current analysis, only one out of eight cells (12.5%) has expected count <5 (Table 3), and mean expected frequency = 31.6 (253 total specimens divided by the multiple of 2 rows and 4 columns).

The pair-wise comparisons using Barnard's tests indicate that the frequency of affected captive wolf specimens differs significantly from the three remaining groups (Table 4). The affected captive wolf proportion (45.5%) is larger than expected if the

Fig. 2. Ventral view of thoracic vertebra 98-590-F (20742) from the Gravettian Předmostí site with lipping occurring on the caudal end of the vertebra body.

Fig. 4. Caudal view of lumbar vertebra 97-588-A (1) from the Gravettian Předmostí site: with extensive osteophyte growth resembling an "Elizabethan" collar (cf. Read and Smith, 1980). Some of the osteophytes are broken.

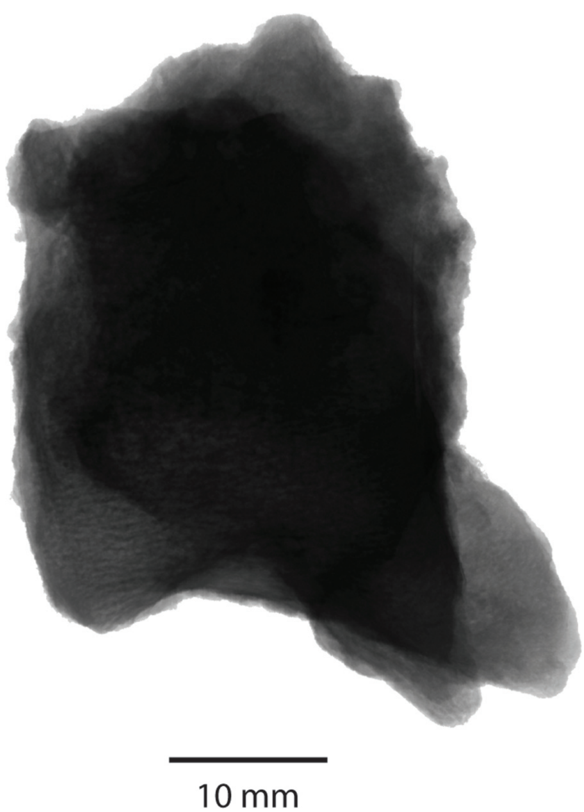

Fig. 3. Radiograph of thoracic vertebra 98-590-F (20742) from the Gravettian Předmostí site, lateral view.

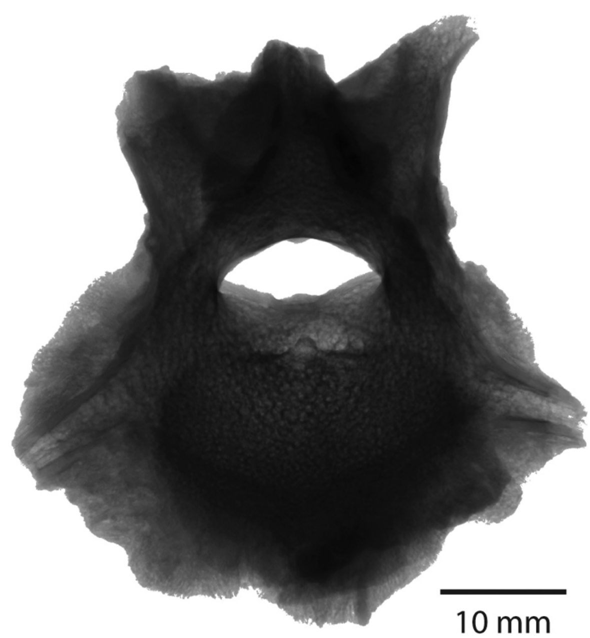

Fig. 5. Radiograph of lumbar vertebra 97-588-A (1) from the Gravettian Předmostí site, caudal view.

proportions of affected specimens were the same across groups (Table 3).

Age at death of individual canids is available for about two thirds of the inbred wolf group, and for only some captive wolves and recent Northern dogs (Supporting Table 2). No statistically significant difference was found (chi-square = 5.11, DF = 2, P = 0.08).

4. Discussion

4.1. Prior SD reports

We found few published reports of SD in wild wolves. Cross (1940) illustrated two thoracic vertebrae with well-developed vertebral lipping in an aged wild Canadian wolf. Based on Fig. 1 in that paper, the vertebrae are SD stage DOD 2. Fritts and Caywood (1980) described an aged male wolf from Minnesota (USA) with osteophytosis of several skeletal elements, including the ventral aspect of several cervical and thoracic vertebrae. Based on Fig. 1c in Fritts and Caywood (1980), two thoracic vertebrae are SD stage DOD 2.

Fig. 6. Lateral view of lumbar vertebra 97-588-A (1) from the Gravettian Předmostí site, with extensive osteophyte growth.

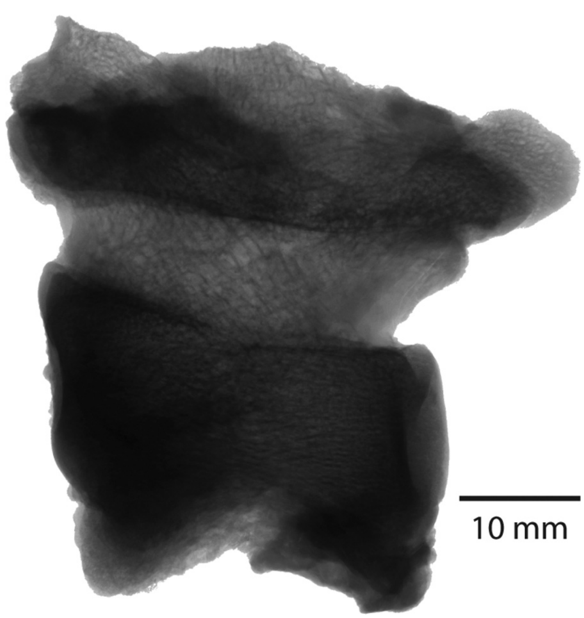

Fig. 7. Radiograph of lumbar vertebra 97-588-A (1) from the Gravettian Předmostí site, lateral view.

An Italian wolf with spondylosis and discospondylitis of the thoracic spine was reported by Zeira et al. (2013). Harris (1977) described 252 wild red foxes (*Vulpes vulpes*) from suburban London, noting an age-related increase in SD. Losey et al. (2011) described SD in a prehistoric dog from Siberia. Additional SD descriptions include a British Bronze Age dog (Baxter, 2007); mulitple ancient Egyptian sacrificed dogs (Ikram et al., 2013); Roman dogs from Tunesia (MacKinnon, 2010) and Turkey (De Cupere, 2001); and pre- and post-European contact North American dogs (Snyder, 1995; Warren, 2000; Tourigny et al., 2015).

Fig. 8. Cranial view of lumbar vertebra 97-588-A (2) from the Gravettian Předmostí site with well-developed osteophytes on the caudal end of the vertebral body.

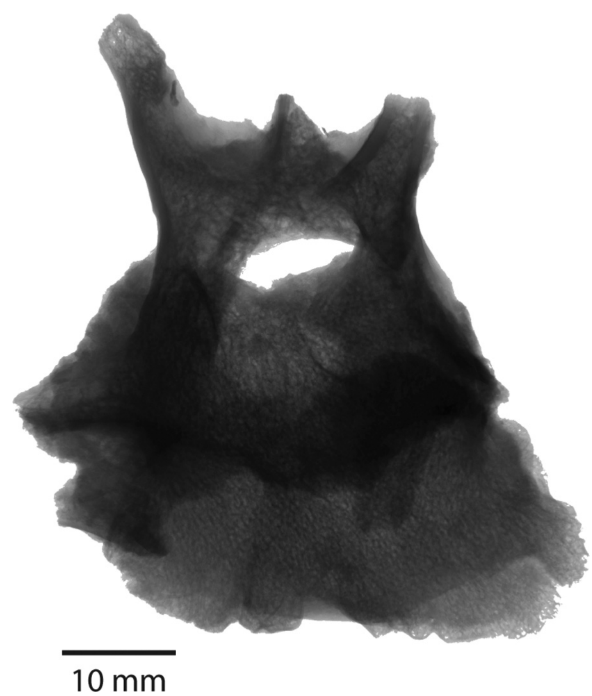

Fig. 9. Radiograph of lumbar vertebra 97-588-A (2) from the Gravettian Předmostí site, cranial view.

4.2. Possible causes and risk factors

Several surveys indicate increasing age-related prevalence of SD. Among English dogs, those aged ≥10 years had recognized SD (Read and Smith, 1968). Some large dog breeds may have increased SD risk, and some European dog breeds, such as the Boxer and German shepherd dog, appear to have a genetic predisposition for SD (Langeland et al., 1995; Weidl, 1998; Carnier et al., 2004; Kranenburg et al., 2011; Daraban et al., 2013).

Spinal traumacould play a causal role in some instances of SD (Weidl, 1998). Pommer (1933) suggested that stresses on vertebral ligaments and periosteum may be causal. Walker (1988) suggested

Table 3
Contingency table of the normal and affected Minimum Number of Individuals (MNI) in the Předmostí assemblage and the comparative data sets from wild Northern wolves, Scandinavian contemporary (inbred) wolves, and captive (zoo) wolves. The count, the expected count and the cell chi-square P value of the healthy and affected individuals are shown, statistically significant results are indicated in bold type.

LR chi-square 14.6, P = 0.022		status	
data set		affected	normal
Předmostí			
	count	3	45
	expected count	5.31	42.69
	cell chi-square P value	0.3158	0.7234
Wild Northern wolves			
	count	14	129
	expected count	15.83	127.17
	cell chi-square P value	0.6462	0.8714
Scandinavian contemporary (inbred) wolves			
	count	6	45
	expected count	5.64	45.36
	cell chi-square P value	0.881	0.9579
Captive (zoo) wolves			
	count	5	6
	expected count	1.22	9.78
	cell chi-square P value	**0.0006**	0.2265

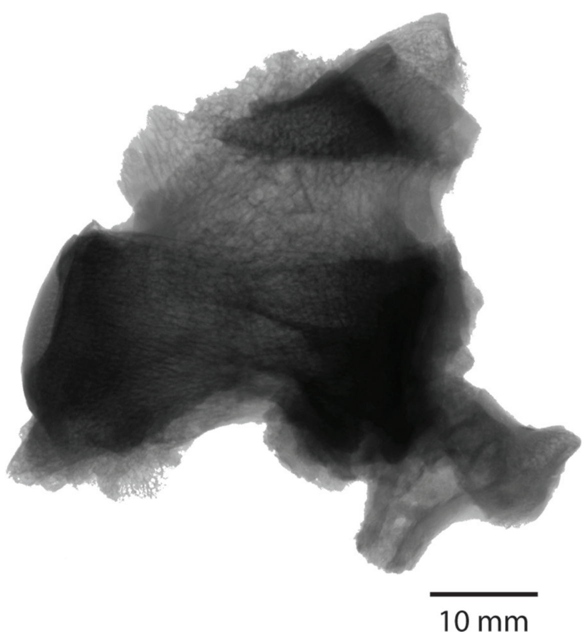

Fig. 10. Radiograph of lumbar vertebra 97-588-A (2) from the Gravettian Předmostí site: well-developed osteophytes present on the caudal end of the vertebral body, lateral view.

that the pathogenesis of SD relates to biomechanical forces on the spine that produce changes in the disc annulus. Mattoon and Koblik (1993) suggested that frequent microtrauma or a macrotrauma can cause SD, with symptoms including stiffness, discomfort, and reduced mobility.

Morey (2010: pp. 90–99) reviewed use of dogs as pack animals by the Assiniboine, Pawnee, and Hidatsa Native American people, as recorded in the ethnographic literature. Morey suggested that if prehistoric dogs were used in a fashion similar to these Native American dogs, distinct skeletal evidence could be expected in the archaeological record. According to Snyder (1995: Figs. 44–47), dogs from two Missouri (USA) sites, Sommers (1000 years ago) and Larson (occupied during the post-European contact period), were used as pack animals. In both instances, well-developed osteophytes were found on thoracic and lumbar vertebrae, assignable to SD stage DOD 2/3. These SD have been suggested as resulting

Table 4
The P values of pairwise comparisons of the Predmosti data set and the data sets of the wild Northern wolves, the Scandinavian contemporaneaous (inbred) wolves and the captive (zoo) wolves using Barnard's unconditional exact test, statistically significant results are indicated in bold; N: Northern.

Pairwise comparison				
Barnard's test P values	Předmostí	wild N wolves	inbred wolves	captive wolves
Předmostí	–	–	–	–
wild N wolves	0.5699	–	–	–
inbred wolves	0.4274	0.8812	–	–
captive wolves	**0.0057**	**0.0051**	**0.0113**	–

from chronic spinal stress associated with travois pulling (Snyder, 1995: p. 216). Warren (2000) also suggested that well-developed marginal osteophytosis in dog vertebrae at prehistoric Southeastern North American sites could have resulted from use as pack animals. Unfortunately, we are unaware of any study that compares SD prevalence among pack-carrying or travois-pulling dogs with that in dogs of similar types and ages, but having less demanding life activities.

4.3. Morphological summary

The Northern dogs, presumably used as sled dogs, do not present vertebrae in SD stage DOD 2/3; however, trauma is evident in 30%. Among the captive wolf group, the frequency of SD stage DOD 2/3 is much higher than the other groups (Tables 3 and 4). The living conditions of these captive wolves likely were very different from those of the wild wolves (outbred and inbred). The captive wolves spent their lives at zoos and were given proper nutrition and health care. The prevalence of affected individuals in these captive wolves (45.5%) is high. We do not have precise information on any inbreeding in the captive group. However, captive wolves typically experience much greater longevity, thus providing a more likely explanation for their greater SD prevalence (cf. Mech, 2006; Lawler et al., 2016; in press).

The Předmostí canids (6.25%) have lower SD prevalence, compared to the wild Northern wolves (10.5%) and the inbred Scandinavian wolves (11.8%), although these differences are not statistically significant (Tables 2 and 4). In the latter group, full sibling mating and inbreeding depression have accompanied low effective immigration from neighbouring populations (Liberg et al., 2005). Increased prevalence of vertebral and other congenital anomalies has occurred in this population since the 1980s, including several types of congenital vertebral defects (Räikkönen et al., 2013), possibly indicating genetic deterioration.

The low prevalence of SD at the Předmostí assemblage suggests that the large canids from this Gravettian site may have been more outbred and/or did not have great longevity. Indeed, preliminary results from age estimations based on dental wear (cf. Gipson et al., 2000) suggest that most large canids from Předmostí died between ages four and six years, with none surviving beyond eight years of age (Germonpré, unpublished data).

5. Conclusion

Based on the results of this study, limited presence of SD-affected stage DOD 2/3 canids at Předmostí does not support an argument for use of canids from this Gravettian site as pack animals. Such inferences as pack animals, if valid, must be established from other skeletal data, perhaps by analyses of limb elements, including their cross-sectional properties and entheses.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ijpp.2016.08.007.

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