

The background of the cover is a detailed photograph of fossilized vertebrate bones. The bones are light brown to tan in color, with some darker, possibly mineralized areas. They are arranged in a complex, overlapping manner, showing various shapes and sizes, including what appear to be vertebrae and long, slender bones. The texture of the bones is visible, showing some pitting and irregularities. The overall composition is dense and fills the entire frame.

Morphology and Systematics of Fossil Vertebrates

Edited by Dariusz Nowakowski

MORPHOLOGY
AND SYSTEMATICS
OF FOSSIL VERTEBRATES

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Preface

In 2009, the scientific world celebrated important anniversaries - bicentenary of the birth of Charles Darwin, and 150 anniversary of his work “The Origin of Species by Means of Natural Selection”. It was a jubilee year for the evolution and paleontology, but the celebration was held in the shadow of the numerous contradictions and scientific discussions, resulting, inter alia, from the controversy surrounding the latest developments of biological sciences. Perhaps Charles Darwin himself would not be surprised, because 150 years ago, he created a paradigm in biology, based on a constant and ever deeper discussion, which fully absorbed the achievements of the historical nature and the essence of the first theory of evolution created by Jean-Baptiste de Lamarck. Life sciences are the realization of this paradigm, mainly through the historically established areas such as paleontology, anthropology, morphology, comparative and evolutionary embryology, genetics, genomics and molecular biology.

Amongst the most important evidence of evolution, priority should be given to paleontology studies, which provide original material and convincing evidence of macroevolution and phylogenetics. In these studies the taxonomy and systematics problems are dealt also with modern research methods, including the analysis of proteins and DNA of extinct forms, which allows the determination of relative age and relationships between taxa.

Topics covered in this monograph reflect the chosen, but a very wide range of palaeontological research in Poland and Central Europe, both in relation to geological time (from the Precambrian to the present), research methods and relative to taxonomic diversity (from Pisces to Mammalia).

Dariusz Nowakowski

Analysis of dental enamel thickness in bears with special attention to *Ursus spelaeus* and *U. wenzensis* (= *minimus*) in comparison to selected representatives of mammals

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Abstract

Dental enamel thickness carries precious information about dietary habits and functioning of dentition in fossil species. In the present study we analyzed enamel thickness in ursids, including three fossil taxa: *Ursus wenzensis* (Early Pliocene), *U. deningeri* (Middle Pleistocene) and *U. spelaeus* (Late Pleistocene). Enamel of typical meat-eating carnivorans, artiodactyls, chiropterans and primates was also considered for comparison. Enamel thickness was measured using a planar method, and was scaled by body mass. Analyses showed a clear relationship between the enamel thickness and diet of the bear taxa analyzed. Observed differences in enamel thickness followed a general evolutionary tendency in ursids, relating to the transition from carnivory to omnivory and the increase in tough and abrasive plant products in their diet, especially in cave bears. Among large-bodied ursids, *U. spelaeus* showed the thickest enamel while *U. maritimus* was characterized by very thin enamel layer to its body mass, which can be related to its exclusive carnivorous diet. A significant increase in enamel thickness from anterior to posterior teeth was found in *U. spelaeus* and *U. arctos*, but not in the domestic dog and *U. wenzensis*. This is concordant with the progressive increase in the contribution of posterior molars to tough food processing in the evolution of ursids.

Key words: cave bear, dietary adaptation, bear evolution, body mass, allometry

Teeth are the most frequently preserved fossil remains of mammals, mainly because the dental enamel cap is one of the most mineralized tissues in these organisms. The thickness of dental enamel, together with its shape and microstructure carry an important adaptive signal in relation to diet and dental function (LUCAS *et al.* 2008). An increase in enamel thickness may enhance enamel's resistance to fracture from biting on hard objects and may prolong a tooth's lifetime where mastication causes substantial loss of the enamel surface.

The majority of enamel thickness studies were devoted to primates and considered many different aspects of enamel thickness, such as: functional implications (e.g. MOLNAR & GANTT 1977, MACHO & BERNER 1994, GANTT & RAFTER 1998, SCHWARTZ 2000a,b, SHIMIZU 2002, KONO 2004, GRINE 2005, GRINE *et al.* 2005, SMITH *et al.* 2005), relation to dietary habits (e.g. KAY 1981, 1985, NAGATOSHI 1990, DUMONT 1995, SHELLIS & HIEMAE 1998, ULHAAS *et al.* 1999, SHIMIZU 2002, MARTIN *et al.* 2003, OLEJNICZAK *et al.* 2008c, VOGEL *et al.* 2008), differences between deciduous and permanent teeth (GRINE 2005), variation with respect to tooth position (e.g. MACHO & BERNER 1993; Grine *et al.* 2005, SMITH *et al.* 2005, 2006a, 2008), relation to development rate of tooth crown formation (see for review SMITH 2008), sexual dimorphism (SCHWARTZ & DEAN 2005; SMITH *et al.* 2006a), differences among human populations (SMITH *et al.* 2006a), taxonomic variation (e.g. SHELLIS *et al.* 1998, ULHAAS *et al.* 1999, MARTIN *et al.* 2003, KONO 2004, SMITH *et al.*

2005, OLEJNICZAK *et al.* 2008a,b) and implications for the phylogeny and evolution of apes and humans (e.g. KAY 1980, MARTIN 1985, ANDREWS & MARTIN 1991, BEYNON *et al.* 1991, GANTT & RAFTER 1998, KONO 2004, SMITH *et al.* 2006b, OLEJNICZAK *et al.* 2008d).

Enamel thickness in rodent teeth was also analyzed from functional and evolutionary perspective (e.g. KORVENKONTIO 1934, RENSBERGER 1975, FLYNN *et al.* 1987, GRAYSON *et al.* 1990, MARTIN 1993, MÖINICHEN *et al.* 1996, SANDER *et al.* 2008). However, quantitative analyses of enamel thickness of other mammalian groups were restricted to some chiropterans (DUMONT 1995) and horses (KILIC *et al.* 1997), and only a preliminary study was carried out on teeth of the domestic dog and cat (CROSSLEY 1995).

The main object of this study was thickness of dental enamel in two fossil bears: *Ursus spelaeus* from the Late Pleistocene and *U. wenzensis* (= *U. minimus*) from the Early Pliocene, which were compared with the fossil bear *U. deningeri* (Middle Pleistocene) and three extant species: brown bear (*U. arctos*), sun bear (*U. malayanus*) and polar bear (*U. maritimus*). Bears show remarkable variation in their dietary habits, therefore offering interesting possibilities to analyze their enamel thickness in the context of different feeding strategies and adaptations (SACCO & VAN VALKENBURGH 2004; CHRISTIANSEN 2007). Among the *Ursus* genus there exist opportunistic omnivores (e.g. *U. arctos*), extreme carnivores (*U. maritimus*) and nearly exclusive herbivores (e.g. *U. spelaeus*). Enamel thickness in these species can also be considered in an evolutionary context because *U. deningeri* is an ancestor of *U. spelaeus* (MAZZA & RUSTIONI 1994), while *U. maritimus* is a recent descendent of *U. arctos* (KURTÉN 1964; LINDQVIST *et al.* 2010). Furthermore, *U. minimus* represents an early diverged unspecialized lineage of *Ursinae* (MAZZA & RUSTIONI 1994).

To evaluate enamel thickness within a broader framework, representatives of typical meat-eating carnivorans (*Canis lupus familiaris*, *C. l. lupus*, *Felis catus*, *Vulpes vulpes*) were included in the study. We also analyzed omnivorous (*Sus scrofa domestica*) and herbivorous (*Bos taurus*, *Cervus elaphus*, *Ovis aries*) artiodactyls. In addition, data about the enamel thickness of primates and chiropterans available in the literature were taken into account.

Knowledge about the enamel thickness of bears compared to humans may also be interesting from a diagnostic point of view. Fossil teeth of humans and bears (such as *U. deningeri*, *U. spelaeus* and also *U. arctos*) are often found in Pleistocene cave deposits, mainly as a result of their common interest in natural shelters. Although bear teeth are larger than human ones, they both show bunodont morphology and are adapted to an omnivorous diet. Many of these remains are too fragmentary to make any conclusive diagnosis about taxonomic affiliations. Very often, however, tooth fragments are the only human remains at interesting evolutionary and anthropologically important localities, and their accurate taxonomic assessment is therefore desirable. Nonetheless, comparisons of dental enamel structure and thickness have facilitated decisive diagnoses in some cases, attributing dental fragments to either bears or humans (KYSELA & VLČEK 1977, VLČEK 1978, GANTT *et al.* 1980, GIBERT *et al.* 1999).

Materials

The total sample of original material consisted of 102 unworn or very lightly worn teeth with a fully developed enamel cup. In the analyses, both whole teeth and large fragments were utilized. Most of the teeth were permanent premolars and molars. The teeth of *U. spelaeus* were additionally represented by canines and incisors, and also by deciduous canines and molars. Deciduous teeth were also analyzed in humans, and canine teeth were examined in two canids and four other bear species. In sum, the teeth represented 15 taxa which are listed in Tab. 1.

All teeth of *U. spelaeus*, the P⁴ (A-0009 Kletno) from *C. lupus lupus* and a P³

ascribed to *U. arctos* were excavated from the Late Pleistocene deposits in Niedźwiedzia Cave in Kletno. The animal remains from this cave were studied by WISZNIOWSKA (1970, 1976, 1989a) and were dated recently to between > 40 ka and ~22 ka (BIEROŃSKI *et al.* 2007). Teeth of *U. wenzensis* were recovered from a bone breccia at Węże I near Działoszyn dated to the Early Pliocene, about 4.2 - 3.4 Ma (GŁĄZEK *et al.* 1976a; FEJFAR *et al.* 1997). The remains of *U. wenzensis* were described by STACH (1953) & RYZIEWICZ (1969). The M_1 (MF/1249/74) of *V. vulpes* came from Late Pleistocene deposits from Raj Cave near Kielce (KOWALSKI 1972). All these teeth were selected from collections at the Department of Palaeozoology, University of Wrocław. The M_1 (MF/1346/148) attributed to *U. deningeri* by WISZNIOWSKA (1989b) was excavated from cave deposits at Kozi Grzbiet near Chęciny dated to the Middle Pleistocene, 700-555 ka and 685-615 ka (GŁĄZEK *et al.* 1976b, LINDNER *et al.* 1995). This specimen belongs to the collection from the Institute of Systematics and Evolution of Animals at the Polish Academy of Sciences in Kraków. Two molars from *U. maritimus* (ZMB18700 and ZMB43701) came from the Berlin Museum für Naturkunde, and other recent teeth were selected from collections housed at the Department of Palaeozoology, the Department of Vertebrate Zoology and the Museum of Natural History at the University of Wrocław, as well as from the private collection of PM.

Methods

Specimen preparation

To expose the enamel layer for measurements, vertical sections of teeth were prepared or selected from naturally fractured specimens. The sections for almost all of the premolars, molars and some canines were in a buccolingual plane; in the case of incisors the sections were in a labiolingual plane. The other canines and one incisor were also represented by a mesiodistal plane of section. The sections were prepared to cross the main cusps and/or the widest region of tooth crown. The choice of section plane in some instances (especially fossil specimens) was determined by the manner in which they were naturally fractured. Finally, the specimens were polished to obtain the desired optimum plane. Pictures of sections taken from light or stereo microscopes were digitalized and analyzed using AutoCad software. Additionally, sections of two *U. maritimus* molars were obtained via microtomography (microCT) (Olejniczak 2006). Differences between the traditional and microCT methods for polar bear molars of the same type were less than 1.4 %.

Enamel thickness measurements

To measure enamel thickness we applied the planar method developed by MARTIN (1983, 1985). In this method, three measurements are calculated in each cross-section: the area of the enamel cap (c), the length of the enamel-dentine junction (e) and the area of coronal dentine and pulp cavity enclosed by the enamel cap (b), as shown in Fig. 1. Next, the average enamel thickness (AET) is calculated as c/e , yielding the average linear distance (usually in mm units) from the enamel-dentine junction to the outer enamel surface.

The other index, relative enamel thickness is expressed by $RET_b = 100 \cdot AET/b^{1/2}$ and is a unitless measure of enamel thickness. It is assumed that it allows comparison of enamel thickness among species of different body size when the b is used as the surrogate for body size (e.g. SHELLIS *et al.* 1998). However, this index appears to be most useful when it is applied to teeth with generally the same crown morphology and to section planes crossing the same tooth regions. The teeth used in this study came from different groups of mammals with very different tooth shapes and crown morphologies (e.g. secodont teeth in canids vs.

buonodont teeth in bears). Moreover, it was difficult to locate section planes going through homologous cusps or corresponding tooth regions even for the same tooth types because the cusps were not present or were outside the desired section plane. Moreover, the same tooth types in different species showed various level of macroevolutionary development (e.g. P^4 is reduced in bears but is very large and functions as carnassial in canids and felids; the opposite is true for posterior molars, which are enlarged in bears but reduced in canids and felids). In these cases, the RET_b index is influenced not only by body size but also by tooth shape and crown morphology (see also DUMONT 1995). Therefore, we used the average enamel thickness (AET) and scaled this directly by the body mass as an alternative index of relative enamel thickness to that proposed by MARTIN (1983, 1985): $RET_m = 100 \cdot AET / m^{1/3}$, where m is a body mass.

In total, 120 cross sections were measured. Bear species were represented in sum by 84 sections, of which 46 were of *U. spelaeus* and 15 were of *U. wenzensis*. All raw values of measurements for particular sections will be made available in electronic form at the website: www.smorfland.uni.wroc.pl/~pamac/enamel, so they may be used by researchers who would like to include them in comparative analyses.

Data regarding enamel thickness for chiropterans were taken from DUMONT (1999) and data for different primate species were taken from: MARTIN (1983), DUMONT (1995), BEYNON *et al.* (1998), SHELLIS *et al.* (1998), ULHAAS *et al.* (1999), DEAN & SCHRENK (2003), MARTIN *et al.* (2003), SMITH *et al.* (2003, 2004, 2005, 2006b, 2008, 2009a,b), KONO (2004), SCHWARTZ & DEAN (2005), OLEJNICZAK (2006), MAHONEY *et al.* (2007) and OLEJNICZAK *et al.* (2008b,c,d). These data were recorded using the planar method and represent 67 taxa in total.

Body mass estimation

Data regarding body mass of the analyzed taxa were carefully selected from the literature. The body mass for a particular taxon was averaged for male and female, and for values coming from different references. For some primates, where a taxon was identified to only the genus, the body mass for that genus was taken as the average of values for its constituent species. Data for extant non-primate species were taken from: ALEXANDROWICZ & MAZARAKI (1981), NOWICKI *et al.* (1995), HENDRIKS *et al.* (1997), FELISA *et al.* (2003), MEIRI & DAYAN (2003), ANDERSSON (2004), WEBSTER *et al.* (2004), ANYONGE & ROMAN (2006), CHRISTIANSEN (2007), CHRISTIANSEN & WROE (2007) and references therein. Data for both extant and extinct primate taxa came from: KAPPELMAN (1996), Smith and Jungers (1997), GEOBO (2004), WARD *et al.* (2004), SMITH (2008) and references therein.

Mean body mass for *U. spelaeus* $\sim 330 \pm 35$ (SD) kg was obtained from estimates by KURTÉN (1967, 1976), VIRANTA (1994), CHRISTIANSEN (1999) and GRANDAL-D'ANGLADE (2010). Mean body mass for *U. wenzensis* predicted as $\sim 136 \pm 5$ (SD) kg, resulted from

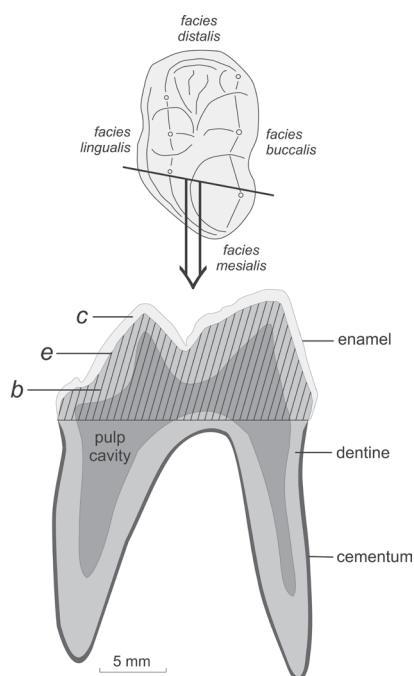


Figure 1. Cross-section through the right M^1 of the cave bear *U. spelaeus* showing measurements used in the qualitative assessment of enamel thickness: the area of the enamel cap (c), the length of the enamel-dentine junction (e) and the area of coronal dentine and pulp cavity enclosed by the enamel cap (b).

four calculations made by formulas based on: the lower carnassial crown area for ursids (LEGENDRE & ROTH 1988), the length of the lower carnassial for ursids (VAN VALKENBURGH 1990), and the skull length for all carnivores and for ursids (VAN VALKENBURGH 1990). Data on *U. wenzensis* teeth and skull measurements required for these estimations were taken from RYZIEWICZ (1969). In estimation of mean body mass for *U. deningeri* of $\sim 248 \pm 85$ (SD) kg we used eight formulas specific to ursids and based on: the lower carnassial crown area (LEGENDRE & ROTH 1988), the length of the lower carnassial (VAN VALKENBURGH 1990), the length of the femur (ANYONGE 1993, VIRANTA 1994, CHRISTIANSEN 1999), the length of the humerus (VIRANTA 1994, CHRISTIANSEN 1999) and the distal epiphysial width of the humerus (CHRISTIANSEN 1999). Data on *U. deningeri* long bones measurements were taken from ATHEN (2007) and teeth measurements came from WISZNIOWSKA (1989b), STINER *et al.* (1998), GRANDAL-D'ANGLADE & LÓPEZ GONZÁLEZ (2004) and BARYSHNIKOV (2006). In the case of VAN VALKENBURGH'S (1990) methods for ursids we updated bear body sizes according to CHRISTIANSEN (2007) because the former did not take into account differences between sexes.

Results

Comparison of enamel thickness between different taxa

To evaluate the average enamel thickness (*AET*) for a particular taxon we calculated a mean from *AET* values averaged for a given tooth type. In these calculations we included only permanent cheek teeth, excluding some reduced premolars measured in carnivorans and domestic pigs. Nonetheless, calculations based on the full set of permanent premolars and molars gave only slightly smaller values.

The average enamel thickness for carnivoran species is presented in Fig. 2. In absolute terms, the enamel cap is the thinnest in domestic cat teeth. Teeth of canids are

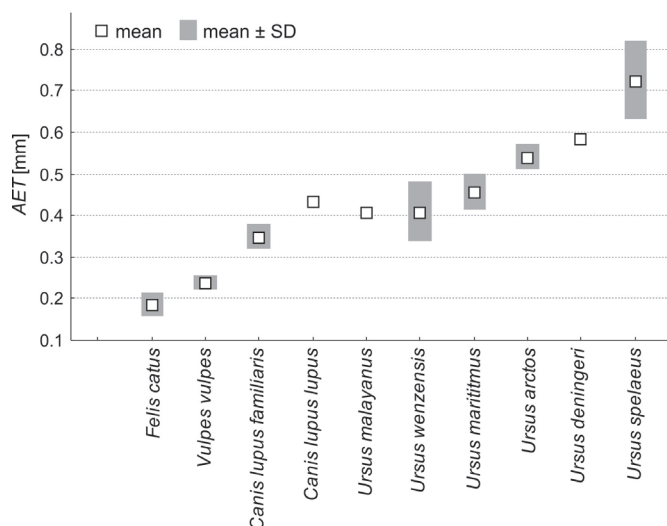


Figure 2. Average enamel thickness (*AET*) of the Carnivora species studied.

covered by thicker enamel, and ursids have the thickest enamel.

Among bears, the thinnest enamel was found in *U. malayanus* and *U. wenzensis*, and the thickest one in *U. spelaeus*. Polar bear have thinner enamel than brown bears. It is clear that the observed differences in enamel thickness are influenced by variation in body size among the species analyzed. The cat is the smallest and has the absolutely thinnest enamel, whereas bears are large carnivorans with absolutely thick enamel. Interestingly, the largest among the species analyzed, *U. maritimus*, does not show the thickest enamel, as would be

expected if absolute enamel thickness related to body size alone. Therefore, we analyzed enamel thickness in relation to body mass. Fig. 3 presents the relationship between *AET* and body mass in log-log scale to evaluate allometry in carnivorans and three other groups of mammals included for comparison. The relationships for all of these groups are a statistically significant positive correlation. Chiropterans have absolutely the thinnest enamel, however, relative to their body mass, it is thicker

than in some primates. Considering species with similar body mass, *AET* in primate taxa is considerably higher than in artiodactyls and carnivorans, the latter having the thinnest enamel among analyzed mammalian groups in relation to their body mass.

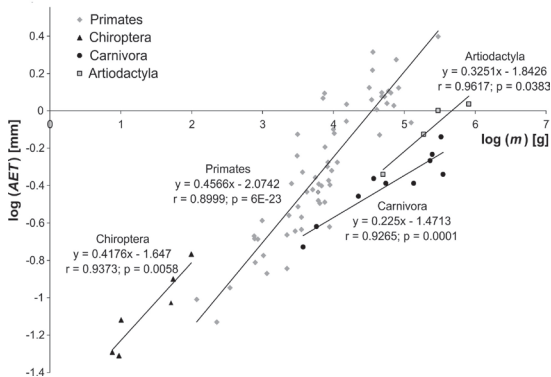


Figure 3. Relationship between average enamel thickness (AET) and body mass (m) shown in log-log scale for four groups of mammals.

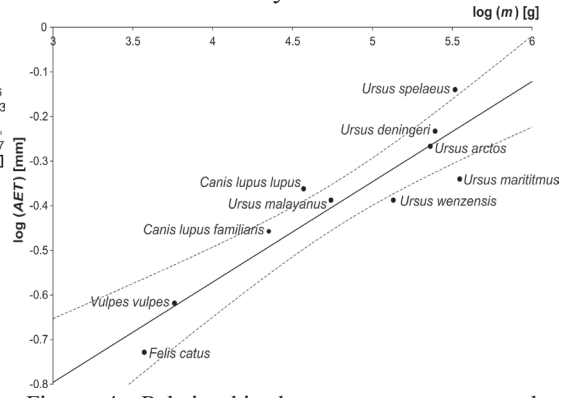


Figure 4. Relationship between average enamel thickness (AET) and body mass (m) shown in log-log scale for carnivorans. Dashed lines indicate 95% confidence intervals.

The slope of the regression lines varies according to the groups of mammals analyzed. The slope of the chiropteran lines, 0.418, is higher than 0.333 (i.e. value expected in the case of isometric scaling), although its wide 95% confidence interval (0.202-0.633) does not allow the rejection of the hypothesis of isometric scaling. Isometry is also characteristic of artiodactyls (slope: 0.325, 95% confidence interval: 0.043-0.607). Primates show a significant tendency toward positive allometry (slope: 0.457, 95% confidence interval: 0.399-0.514), whereas carnivorans tend towards negative allometry (slope: 0.225, 95% confidence interval: 0.150-0.300). This indicates that the enamel thickness of primate species increases more with their body mass than is expected from the isometric scaling, while in carnivorans this increase is smaller than expected.

The regression analysis of *AET* versus body mass for *Carnivora* is presented in greater detail in Fig. 4. The largest deviation from the regression line shows points for two biggest bears: *U. spelaeus* and *U. maritimus*. The mean *AET* for the cave bear lies above the line while that for the polar bear falls under this line. It indicates that *U. spelaeus* had much thicker enamel than is expected based on the global trend, while *U. maritimus* enamel is much thinner than expected. In agreement with this finding, the same

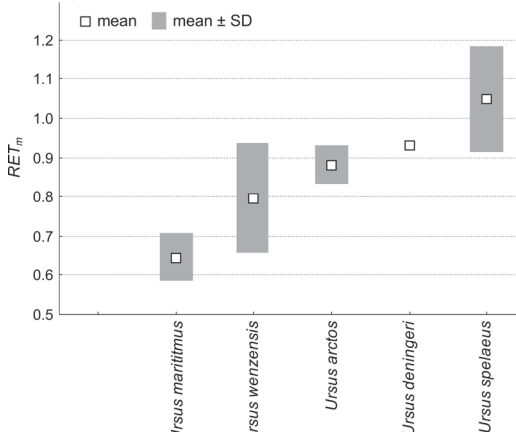


Figure 5. Relative enamel thickness scaled by body mass for bears heavier than 100 kg.

results were obtained when we compared large-bodied bears in terms of relative enamel thickness scaled by body mass (Fig. 5). The RET_m index is the lowest for polar bears and gradually increases from *U. wenzensis*, brown bear to cave bears, from which *U. spelaeus* shows the highest value.

As discussed in the introduction of this contribution, bear and human teeth are often found in the same cave sediments and their fragments are usually morphologically indistinguishable, so the description of diagnostic features is very desirable. One such feature could be enamel thickness. In Fig. 6 we compared the average enamel thickness

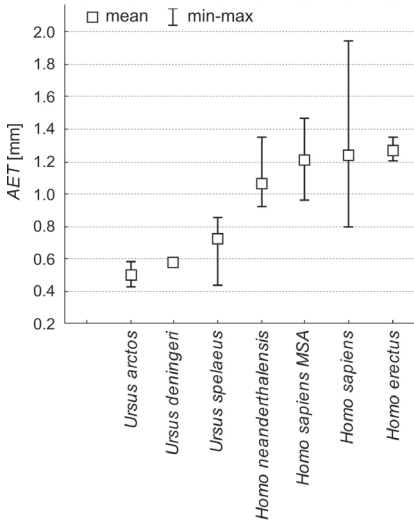


Figure 6. Comparison of average enamel thickness and its range between cheek teeth for three bears and molars from four hominin taxa. MSA denotes Middle Stone Age humans from South Africa.

between cheek teeth from three bear species with molars from four hominin taxa which could have coexisted with bears. It is evident that human teeth have much thicker enamel than bears, and the ranges of *AET* show nearly no overlap.

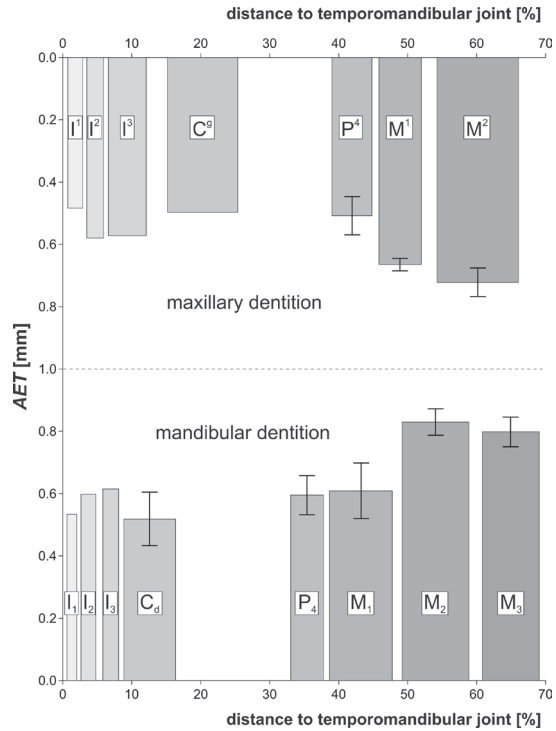


Figure 7. Mean values of average enamel thickness (*AET*) and standard deviation for particular tooth types in respect to their distance to temporomandibular joint in *U. spelaeus*. Width of bars representing teeth corresponds to the distance between dental alveoli for a particular tooth.

Variation of enamel thickness in different tooth types and categories

Mean values of *AET* for the full set of all tooth types from *U. spelaeus* with respect to their distance to the temporomandibular joint are presented in Fig. 7. Canines show

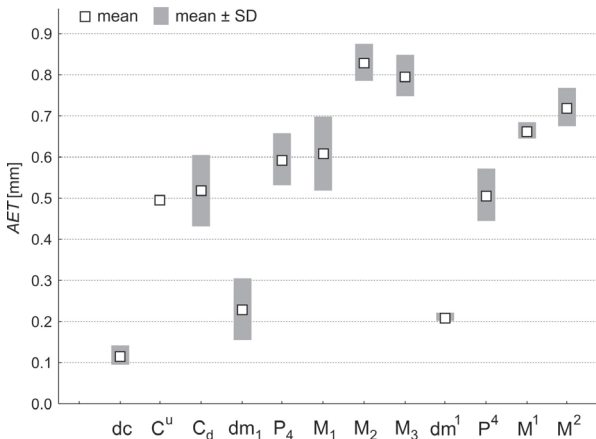


Figure 8. Comparison of average enamel thickness between deciduous and permanent teeth in *U. spelaeus*.

the lowest average enamel thickness. Incisors, premolars and M₁ have generally higher *AET* than canines, and the thickest enamel is observed on posterior molars. The increasing trend in *AET* from anterior to posterior teeth is significant both for maxillary and mandibular dentitions, regardless of which tooth sets are considered (Tab. 2). The significant trend is also present in *U. arctos*, but not in *U. wenzensis*, although the correlation coefficients are moderately high with p-values close to the assumed statistically significant limit of 0.05. No statistically significant correlations were found for tooth rows in the domestic dog.

The abundance of *U. spelaeus* teeth in cave deposits allowed us also to select deciduous teeth and compare their average enamel thickness with the permanent dentition (Fig. 8). Enamel on deciduous canines is more than four times thinner than on permanent canines, whereas deciduous molars have on average three times thinner enamel than permanent cheek teeth.

Table 1. List of taxa analyzed in this study

Taxon	Age	Locality for fossil specimens
Artiodactyla		
<i>Bos taurus</i> Linne, 1758	recent	
<i>Ovis aries</i> Linne, 1758	recent	
<i>Cervus elaphus</i> Linne, 1758	recent	
<i>Sus scrofa domestica</i> Linne, 1758	recent	
Carnivora		
Canidae		
<i>Canis lupus familiaris</i> Linne, 1758	recent	
<i>Canis lupus lupus</i> Linne, 1758	Late Pleistocene	Niedźwiedzia Cave in Kletno
<i>Vulpes vulpes</i> Linne, 1758	recent	
	Late Pleistocene	Raj Cave near Kielce
Felidae		
<i>Felis catus</i> Linne, 1758	recent	
Ursidae		
<i>Ursus arctos</i> Linne, 1758	recent	
	Late Pleistocene	Niedźwiedzia Cave in Kletno
<i>Ursus deningeri</i> Reichenau, 1906	Middle Pleistocene	Kozi Grzbiet near Chęciny
<i>Ursus malayanus</i> Raffles, 1821	recent	
<i>Ursus maritimus</i> Phipps, 1774	recent	
<i>Ursus spelaeus</i> Rosenmüller et Heinroth, 1794	Late Pleistocene	Niedźwiedzia Cave in Kletno
<i>Ursus wenzensis</i> Stach, 1953	Early Pliocene	Węże near Działoszyn
Primates		
<i>Homo sapiens</i> Linne, 1758	recent	

Table 2. Spearman correlation coefficient and its significance for trends in average enamel thickness from anterior to posterior teeth. Statistically significant correlations (with $p < 0.05$) are denoted in **bold**

Taxon	Considered tooth row	Spearman correlation coefficient	P-value
<i>Canis lupus familiaris</i>	mandibular CPM	-0.036	0.933
	mandibular PM	0.234	0.613
<i>Ursus arctos</i>	maxillary CPM	0.727	0.027
	maxillary PM	0.954	8.E-04
<i>Ursus spelaeus</i>	maxillary ICPM	0.851	3E-05
	maxillary CPM	0.889	5E-05
	maxillary PM	0.872	2E-04
	mandibular ICPM	0.676	8E-04
	mandibular CPM	0.811	4E-05
	mandibular PM	0.734	0.007
<i>Ursus wenzensis</i>	mandibular PM	0.685	0.061
	maxillary CPM	0.730	0.063
	maxillary PM	0.555	0.252

I- incisors; C- canines; P - premolars; M - molars

Discussion and conclusions

Comparative analyses of enamel thickness revealed that *U. spelaeus* had the thickest enamel cap among the bear species analyzed, both in absolute terms and when body mass is considered as scaling factor. The thick enamel on this species' teeth could be considered an adaptation to an herbivorous diet which is more abundant in hard and abrasive food items than an omnivorous or carnivorous one. This is in agreement with a generally held viewpoint that the cave bear was a vegetarian species (see for recent review: PACHER & STUART 2008). This view is based on many craniodental features (e.g. KURTÉN 1976; MATTSO 1998; RABEDER *et al.* 2000; GRANDAL-D'ANGLADE & LÓPEZ GONZÁLEZ 2004, 2005), extremely worn teeth (KURTÉN 1958), massive blunt claws (HILDEBRAND 1985) and powerful front limbs and shoulder architecture well-suited to scratch digging (ERDBRINK 1953, KURTÉN 1976). The herbivory of the cave bear is also firmly confirmed by numerous stable isotope studies (e.g. BOCHERENS, 1990, BOCHERENS *et al.* 1994, 2006, NELSON *et al.* 1998, VILA *et al.* 1999, FERNÁNDEZ-MOSQUERA *et al.* 2001) and by estimation of very high bite forces in this species (GRANDAL-D'ANGLADE 2010). Recently, WISZNIOWSKA *et al.* (2010) found several adaptations in enamel structure of *U. spelaeus* which also indicate an increase of plant products in a diet of this species. The observed large proportion of radial enamel made the enamel cap more resistant to attrition, and the thinner HSB relative to the estimated bite force and more intensive than in other bears waviness of HSB led to more effective enamel reinforcement. Moreover, the enamel of the cave bear was build of prisms with pattern 3 characterizing by a fast secretion rate. This would explain the bigger enamel thickness found in *U. spelaeus*.

Contrary to those studies, recent ecomorphological analyses showed that generalized craniodental morphology of the cave bear is typical of living omnivorous ursids (FIGUEIRIDO *et al.* 2009). However, these analyses may be biased by the lack of a suitable reference model of an herbivorous bear, because the highly specialized and divergent giant panda was used as this reference (GRANDAL-D'ANGLADE 2010). Nonetheless, one stable isotope study also indicated an omnivorous diet for *U. spelaeus* (RICHARDS *et al.* 2008), and there are many other factors that can affect results of such studies (see Pacher & STUART 2008 for discussion). Cave bear omnivory was supported by dental microwear studies (PEIGNÉ *et al.* 2009) and the scavenging habit of this species was suggested by tooth marks on bones found at sites where the cave bear was the only carnivore recorded (e.g. TINTORI & ZANALDA 1992, Pacher 2000, PINTO LLONA & ANDREWS 2004, PINTO LLONA *et al.* 2005, QUILES *et al.* 2006). However, all these findings can be also interpreted as simply occasional changes in preferential herbivorous habits related to hibernation or seasonal resource availability. Since dental enamel is strongly influenced by genetic conditions, the thick enamel observed in cave bears should be interpreted as an adaptation to a long-term herbivorous diet, although this does not exclude the possibility that *U. spelaeus* may have temporarily diversified its dietary habits.

A tendency towards herbivory in the cave bear lineage is also confirmed by comparison of its enamel thickness to that of other ursids. Dental enamel in *U. deningeri*, an ancestor of *U. spelaeus*, is slightly thinner than in its descendant but is thicker than in the omnivorous brown bear. In accordance with this view, isotope analyses support that *U. deningeri* was a vegetarian species (BOCHERENS *et al.* 1994, FERANEC 2008).

On the other hand, *U. maritimus* is characterized by a very thin enamel layer in relation to its body mass, which is likely associated with its exclusive carnivory. Its relative enamel thickness is almost 27% lower than in its ancestor *U. arctos*. This indicates that rapid changes in the *U. maritimus* lineage, since its recent split from the brown bear population about 150 ka (LINDQVIST *et al.* 2010), can be found not only in metabolism, social and feeding behaviors, molar shape and other external morphological features,

but also in this species' dental enamel thickness.

Relative enamel thickness in *U. wenzensis* (= *minimus*), representing an early lineage of ursids, is also relatively thin and occupies an intermediate position between the polar bear and the brown bear. It is consistent both with an assumed omnivorous diet for this primitive member of *Ursinae* (CHRISTIANSEN 2007) and with analyses of dentition, teeth morphology (STACH 1953, RYZIEWICZ 1969) and their function (ŽUK 1985) which indicate a large contribution of meat products to the diet of this species.

Comparisons of enamel thickness between different tooth categories in respect to their distance to temporomandibular joint showed that enamel thickness increased significantly in *U. spelaeus* and *U. arctos* from anterior to posterior teeth, especially molars. Such a tendency was not statistically significant in a typical carnivore, the domestic dog, nor in the primitive bear, *U. wenzensis*, although some increase of enamel thickness in the latter species was observed. The distally increasing gradient in enamel thickness in *U. spelaeus* correlates with a clear growing trend in bite force toward jaw hinge in this species (GRANDAL-D'ANGLADE 2010). Therefore, an increase in enamel thickness in distal molars can be interpreted as an adaptation to higher occlusal load. These results are also consistent with progressive changes in masticatory apparatus, reduction or loss of anterior premolars and increase of posterior molars' size and their contribution to tough food processing, observed in the ursid lineage (MAZZA *et al.* 1995). These changes were most likely a result of transition from carnivory to omnivory, e.g. in brown bear and herbivory in cave bears.

Similarly, a significant increase in enamel thickness from anterior to posterior teeth was observed in hominoid primate taxa (e.g. MACHO & BERNER 1993, SMITH *et al.* 2005, 2006a, 2008) but not in the cercopithecoid primate *Papio ursinus* (GRINE *et al.* 2005). Although it was assumed that this trend may also reflect the magnitude of bite forces, the possibility that greater enamel thickness in posterior human molars results from a reduction in the tooth size and especially, in the dentine component of the tooth crown, cannot be excluded (GRINE 2005, GRINE *et al.* 2005).

Analysis of deciduous and permanent teeth in *U. spelaeus* revealed that absolute enamel thickness in deciduous molars was, on average, three times thinner than in permanent cheek teeth. This difference is higher than those observed in primates. Deciduous teeth in *Proconsul heseloni* have, on average, enamel that is more than two times thinner than in permanent teeth (BEYNON *et al.* 1998), while the enamel of deciduous teeth in humans is about 1.5 times thinner than in permanent teeth (GRINE 2005, this study). Deciduous tooth morphogenesis is more rapid than permanent tooth development, and thinner enamel may be a consequence of this shorter period of odontogenesis, as well as the shorter duration that deciduous teeth are in functional occlusion (presumably, because they will be shed and replaced, deciduous teeth do not require such a substantial layer of enamel as their permanent counterparts). Cave bear cubs likely fed on much softer fruits and plant elements than adults, and differences between deciduous and permanent tooth enamel thickness probably also reflect this large difference in the composition of the diet between adult and young cave bears.

A very intriguing result that we obtained is the negative allometry found for the relationship between average enamel thickness and body mass in *Carnivora*. This means that smaller species represented by typical meat-eating carnivores have relatively thicker enamel for their body mass than larger omnivorous or herbivorous ursids. In this case, we should expect to find the positive allometry that was observed for primate taxa and was explained by an increase of tougher and more abrasive food items in diet of large-bodied and thick-enamelled anthropoids (e.g. KAY 1980, 1981, ANDREWS & MARTIN 1991, SHELLIS *et al.* 1998). Interestingly, CHRISTIANSEN & WROE (2007) also observed negative

allometric scaling between bite force and body mass in *Carnivora*, which indicates that smaller species have more powerful jaws for their body size than large species. Since changes in enamel thickness should correspond to changes in bite forces, we examined how *AET* is related to bite force at the carnassial eocone. This relationship showed a significant positive correlation ($r = 0.937$, $p = 0.00006$) and, interestingly, some tendency to positive allometry, although the assumption on isometric scaling can not be rejected (the slope: 0.451, the interval: 0.315-0.589). In addition, points for three bear species *U. arctos*, *U. deningeri* and *U. spelaeus* lay above the regression line, indicating that their dental enamel is thicker in relation to bite force than expected. This deviation probably results from adaptation of their enamel to abrasion caused by a high proportion of abrasive elements in diet of these species. The negative allometry found for relationships between enamel thickness and bite forces with body mass in carnivorans may result from different factors influencing body mass in ursids more than in smaller, typically meat-eating carnivores. These factors can be, for example, a need to amass a large body weight before hibernation through the accumulation of fat, and requirements for reduction of the ratio of surface area to volume with the increased body size to ensure better thermoregulation in an increasingly seasonal climate at the higher latitude to which bears have adapted (STIRLING & DEROCHE 1990).

Our analyses showed that bear and human teeth differ significantly in enamel thickness, and this parameter may be used for the taxonomic discrimination of small tooth fragments found in cave deposits that were occupied by these two groups in the past. However, our measurements were performed on complete teeth or large fragments. The same analyses based on very small tooth specimens would certainly give higher variation in ranges of the *AET*. Therefore additional analyses based on small tooth fragments should be carried out to increase confidence in taxonomic assessment of small dental remains. Nonetheless, the results presented here can be helpful in preliminary classification.

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Streszczenie

Analiza grubości szkliwa niedźwiedzi ze szczególnym uwzględnieniem *Ursus spelaeus* i *U. wenzensis* (= *U. minimus*) w porównaniu z wybranymi reprezentantami ssaków

Grubość szkliwa dostarcza cennych informacji dotyczących rodzaju spożywanego pokarmu oraz funkcjonowanie uzębienia kopalnych gatunków. Znaczna większość prac dotyczących różnych aspektów grubości szkliwa poświęcona była naczelnym zarówno kopalnym, jak i współczesnym. Natomiast bardzo niewiele wiadomo na temat grubości szkliwa w innych grupach ssaków. Głównym przedmiotem analiz niniejszej pracy była grubość szkliwa kopalnych gatunków niedźwiedzi *Ursus spelaeus* z późnego plejstocenu i *U. wenzensis* (= *U. minimus*) z wczesnego pliocenu, które zostały porównane ze środkowo-plejstocenijskim *U. deningeri* i trzema gatunkami niedźwiedzi współczesnych: *U. arctos*, *U. malayanus* i *U. maritimus* (Tab. 1). W celach porównawczych zbadano dodatkowo grubość szkliwa u typowych mięsożernych przedstawicieli rzędu drapieżnych, parzystokopytnych, nietoperzy i naczelnych. W pomiarach grubości szkliwa zastosowano metodę planimetryczną (Fig. 1), a jako czynnik skalujący wykorzystano masę ciała, która została zebrana z danych literaturowych i oszacowana w przypadku *U. deningeri* i *U. wenzensis* w oparciu o ich szczątki kopalne. Analizując zależność między średnią grubością szkliwa a masą ciała w czterech grupach ssaków stwierdzono izometryczne skalowanie w przypadku nietoperzy i parzystokopytnych, natomiast w przypadku naczelnych allometrię dodatnią, a u drapieżnych allometrię ujemną (Fig. 3). Przeprowadzone analizy wykazały wyraźne związki między grubością szkliwa a zwyczajami żywieniowymi analizowanych gatunków niedźwiedzi. Zaobserwowane różnice w grubości szkliwa są zgodne z ogólnym trendem rozwojowym w ewolucji niedźwiedziowatych związanym z przejściem od mięsożerności do wszystkożerności i wzrostem w pokarmie udziału składników pochodzenia roślinnego, zwłaszcza u niedźwiedzi jaskiniowych. Spośród przeanalizowanych dużych gatunków niedźwiedzi najgrubsze szkliwo stwierdzono u *U. spelaeus*, natomiast najcieńszym szkliwem w porównaniu do swojej masy ciała charakteryzuje się *U. maritimus*, co należy wiązać z jego przejściem do wtórnej mięsożerności (Fig. 2, 4, 5). *U. deningeri*, przodek *U. spelaeus*, posiada nieco cieńsze szkliwo niż jego potomek, natomiast grubość szkliwa *U. wenzensis*, reprezentującego wczesną linię rozwojową *Ursinae*, jest większa niż u *U. maritimus* i mniejsza niż u wszystkożernego *U. arctos*. Wykazano, że szkliwo różnych gatunków rodzaju *Homo* jest dużo grubsze niż szkliwo niedźwiedzi, dlatego grubość szkliwa może być pomocną cechą diagnostyczną w rozpoznawaniu nierozróżnialnych morfologicznie fragmentów zębów tych gatunków często znajdujących się w tych samych osadach jaskiniowych (Fig. 6). Stwierdzono istotny wzrost grubości szkliwa od przednich do tylnych zębów u *U. spelaeus* i *U. arctos*. Taki trend nie był jednak obserwowany u *Canis lupus familiaris* i *U. wenzensis* (Tab. 2, Fig. 7). Jest to zgodne z kierunkową zmianą w aparacie żučiowym i ze wzrostem udziału tylnych trzonowców w obróbce pokarmu u *Ursidae*. Grubość szkliwa na mlecznych kłach *U. spelaeus* jest średnio ponad cztery razy, a na mlecznych trzonowcach średnio trzy razy większa niż na ich stałych odpowiednikach, co wynika z szybszej odontogenezy zębów mlecznych i może świadczyć o różnym typie lub składzie pokarmu młodych i dorosłych niedźwiedzi jaskiniowych (Fig. 8).

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