Morphology and Systematics of Fossil Vertebrates

Edited by Dariusz Nowakowski

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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

Dental enamel structure in fossil bears *Ursus spelaeus* and *U. wenzensis* (=*minimus*) in comparison to selected representatives of other *Carnivora*

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Abstract

Dental enamel is a very strong mineralized tissue therefore its structure is very well preserved in fossil state. Thanks to that the enamel is a very precious source of information about dietary habits and food processing in extinct species. We analyzed in details the enamel structure in two fossil bears *Ursus wenzensis* from the Early Pliocene and *U. spelaeus* from the Late Pleistocene, which were compared with other ursids and also with selected members of *Carnivora*. The enamel of *U. spelaeus* showed the most distinct features in comparison to other analyzed species, such as: (1) the prism pattern 3 in Hunter-Schreger bands suggesting a faster enamel secretion rate resulting in bigger enamel thickness, (2) larger proportion of radial enamel which is more resistant to attrition, (3) thinner HSB relative to the estimated bite force and (4) more intensive than in other bears waviness of HSB, which led to more effective enamel reinforcement. Although the enamel structure of the cave bear did not show features of typical herbivore, all the above-mentioned modifications can be interpreted as an adaptation to the increase of plant products in cave bear diet. On the other side, *U. wenzensis* showed the enamel structure similar to other representatives of *Carnivora*.

Key words: Hunter-Schreger bands, enamel prisms, cave bear, dietary adaptation, dentine

Mammalian dental enamel is a tissue that can not be substantially remodeled after its formation and mineralization, except by ion exchange within the mouth. Therefore biomechanical adaptations in the enamel must be established first in a genome as a result of natural selection of previous generations and can not be regarded as an immediate onto-genetic reaction to actual needs. Therefore the structure of this tissue should reflect biomechanical and functional constraints inherited during generations.

Since the enamel is the highly mineralized tissue, its structure is altered very little during fossilization process and it is often very well preserved in fossil material. Thanks to that the enamel is a very precious source of information about feeding behavior and functioning of dentition in extinct species. We can also follow changes in the enamel structure in time and use this tissue in different taxonomic and phylogenetic studies. Unlike most other tissues, extant and fossil enamel can be studied with the same methods.

Enamel structure was studied in evolutionary, phylogenetic, taxonomic, dietary and biomechanical aspects in different groups of animals (for the most synthetic reviews see: Carlson 1990; Koenigswald & Clemens 1992; Koenigswald et al. 1993; Pfretzschner 1994; Clemens 1997; Koenigswald 1997a,b,c; Koenigswald & Sander 1997a; Rensberger 1997). The enamel structure shows a complex organization in which five hierarchical levels are distinguished: crystallites, prisms, enamel types, Schmelzmuster and dentition (Koenigswald & Clemens 1992; Koenigswald et al. 1993; Koenigswald & Sander 1997b).

The crystallites of hydroxyapatite are basic elements of enamel. Bundles of the crystallites form the prism and the interprismatic matrix (IPM). There are three basic patterns or types of prisms (named 1, 2 and 3) which are distinguished according to their cross section, shape, size and arrangement (Boyde, 1964, 1965, 1969; Boyde & Martin 1983; Carlson 1990; Koenigswald & Sander 1997b). The prisms can be differently oriented to one another in their course from the enamel-dentine junction (EDJ) toward the outer enamel surface. For example, prism can be parallel to each other (e.g. in radial enamel), or can decussate in an irregular or a regular fashion (e.g. in Hunter-Schreger bands, HSB). Such regions of enamel showing identical or periodic prism orientation are called enamel types. Next, these various enamel types can be arranged in a significant pattern (e.g. in layers) and can be differentially distributed in one tooth. This three-dimensional arrangement and combination of the enamel types is named Schmelzmuster. Finally, the Schmelzmuster can be variously developed throughout the dentition in a given organism. This hierarchical system of classification is very useful in the description and investigation of enamel structure.

Here we compared the enamel structure of two fossil bears *Ursus spelaeus* and *U. wenzensis* with extant bears *U. arctos* and *U. maritimus* and also with other representatives of *Carnivora*. *U. wenzensis* (Stach 1953; Ryziewicz 1969) from the Early Pliocene is considered a synonym of *U. minimus* (Morlo & Kundrát 2001; Wagner *et al.* 2008) and represents the early diverged lineage of *Ursinae* named the *U. minimus-thibetanus* group (Mazza & Rustioni 1994; McLellan & Reiner 1994). Bears of this lineage are thought to be unspecialized omnivores, whereas *U. spelaeus*, known from the Late Pleistocene is considered predominantly a vegetarian (e.g. Kurtén 1976; for recent review see Pacher & Stuart 2008 and also discussion in Mackiewicz *et al.* 2010). That is why it is interesting to compare these species from dietary and evolutionary perspective.

So far, the enamel structure of brown bear was studied in general comparative analyses with other mammals by Shobusawa (1952) and Kawai (1955). More specifically and in more details the enamel structure were described in *Ailuropoda* species (Zhao & Li 1987) and *U. spelaeus* (Breuer 1931; Koenigswald 1992). However, the latter analysis of the cave bear enamel did not reveal any adaptations which are characteristic of typical herbivorous mammals. The lack of these features was explained by a short period of the cave bear lineage evolution.

The enamel structure and thickness of brown and cave bears were also compared with human from a diagnostic point of view to make a taxonomic assessment of fragmentary tooth specimens preserved in cave deposits (Kysela & Vlček, 1977; Vlček, 1978; Gantt *et al.* 1980; Gibert *et al.* 1999). However, detailed and direct comparison of the cave bear with other representatives of *Ursidae* or *Carnivora* was not carried out. The more wide-range survey including bears was focused on searching relationships between bone consumption and the presence of specialized type of Hunter-Schreger bands called zig-zag HSB (Stefen 2001) which independently evolved in different families of *Carnivora*, *Creodonta*, *Condylarthra* and some *Artiodactyla* (e.g. Koenigswald 1997a, Stefen 1997a,b; 1999; 2001; Rensberger 1999; Stefen & Rensberger 1999; Rensberger & Wang 2005; Ferretti 2007).

Materials

Analyses were performed on teeth or their fragments coming from 9 taxa which were listed in Tab. 1. Fossil teeth and other animal remains found in Niedźwiedzia Cave in Kletno were described by Wiszniowska (1970, 1976, 1989a) and were dated to the Late Pleistocene, between > 40 ka and ~22 ka (Bieroński *et al.* 2007). The remains of *U. wenzensis* from a bone breccia at Węże I near Działoszyn dated to the Early Pliocene,

4.2 - 3.4 Ma (GŁAZEK *et al.* 1976*a*; FEJFAR *et al.* 1997) were characterized by STACH (1953) and RYZIEWICZ (1969). The analyzed M_1 from *Vulpes vulpes* was excavated from the Late Pleistocene deposits in Raj Cave near Kielce (KOWALSKI 1972) whereas the M_1 from *U. deningeri* was studied by WISZNIOWSKA (1989b) and came from cave sediments at Kozi Grzbiet near Chęciny dated to the Middle Pleistocene, 700-555 ka and 685-615 ka (GŁAZEK *et al.* 1976*b*, LINDNER *et al.* 1995). This specimen was loaned from the collection of the Institute of Systematics and Evolution of Animals at the Polish Academy of Sciences in Kraków. The other fossil teeth came from collections housed in the Department of Palaeozoology at the University of Wrocław. Recent teeth were selected from collections at the Department of Palaeozoology and the Department of Vertebrate Zoology at the University of Wrocław, as well as from the private collection of PM.

Methods

The course of Hunter-Schreger bands (HSB) on tooth surfaces was examined under a stereo microscope with obliquely directed light. Measurements of HSB width were taken under light or stereo microscopes in the middle of enamel layer on vertical sections of teeth. The sections were perpendicular to the enamel-dentine junction (EDJ) and usually crossed the main cusps and/or the widest region of tooth crown.

Specimens of bear teeth appropriated to the observation in scanning electron microscopy, after sectioning and polishing in various planes (i.e. horizontal, vertical and tangential) were cleaned in an ultrasonic bath and etched with 2N HCl for several seconds or 0.074M H_3PO_4 for one minute. After sputtercoating with carbon and gold in the Electron Microscopy Laboratory of Institute of Microbiology at Wrocław University, the specimens were examined in SEM Tesla BS 300 at 20 kV under supervision of dr Jerzy Kassner and with assistance of Marek Chmielewski.

Table. 1. List of taxa analyzed in this study.

Taxon	Age	Locality for fossil specimens
Canis lupus familiaris Linne, 1758	recent	
Canis lupus lupus Linne, 1758	Late Pleistocene	Niedźwiedzia Cave in Kletno
Felis catus Linne, 1758	recent	
Ursus arctos Linne, 1758	recent	
	Late Pleistocene	Niedźwiedzia Cave in Kletno
Ursus deningeri Reichenau, 1906	Middle Pleistocene	Kozi Grzbiet near Chęciny
Ursus maritimus Phipps, 1774	recent	
Ursus spelaeus Rosenmüller et Heinroth, 1794	Late Pleistocene	Niedźwiedzia Cave in Kletno
Ursus wenzensis Stach, 1953	Early Pliocene	Węże near Działoszyn
Vulpes vulpes Linne, 1758	recent	
	Late Pleistocene	Raj Cave near Kielce

Results

Enamel prisms

The enamel structure of analyzed extinct and extant bear species show a typical prismatic organization and consists of clear visible enamel prisms (rods) surrounded by interprismatic matrix (IPM). Studying enamel of *U. spelaeus* on different tangential sections, we have found a relation between prism patterns and their occurrence in different enamel types. In the outer enamel layer occupied by the radial enamel, we observed only the pattern 1 according to Boyde's terminology (BOYDE 1964, 1965, 1969; BOYDE & MARTIN 1983) (Fig. 1A). These prisms were pentagonal and hexagonal and had thick complete prism sheaths. However, the pattern 3 of prisms occurred in the inner enamel layer filled with HSB (Fig. 1B). These prisms had an arcade arrangement and were ovoid, trapezoidal to irregular in shape while their sheaths were always incomplete and open basally. In some regions, they also resembled the "key-hole pattern" (the prisms of type 3B). Some prism showed the "seam", a minor crystalite convergence bisecting the basal opening of prism sheath (Fig. 1B).
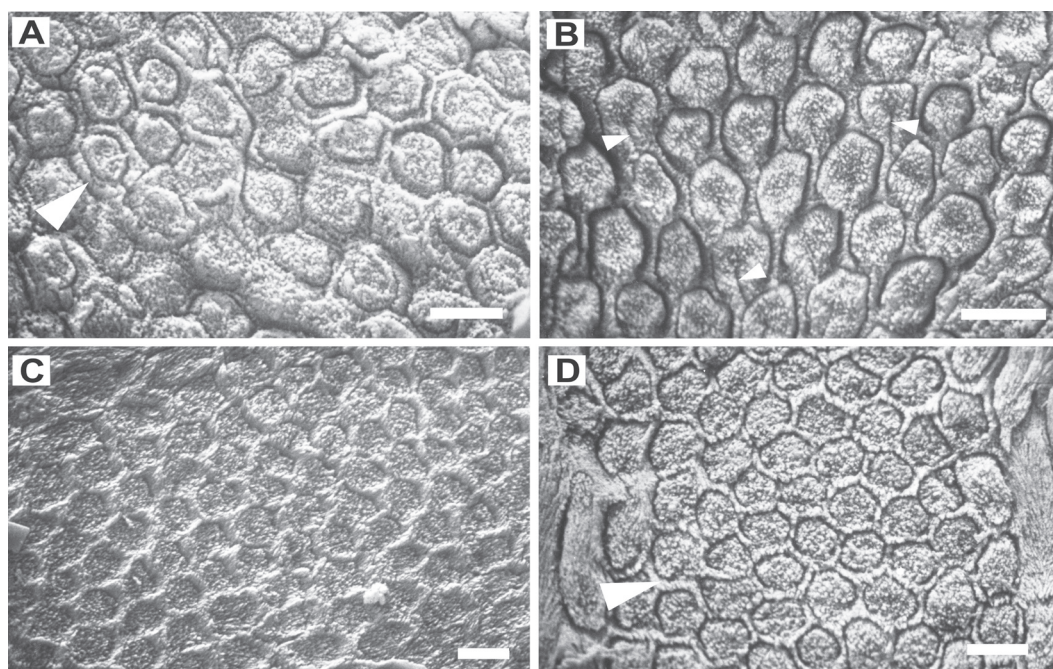
Figure 1. Types of enamel prisms in cross-section in analyzed bears. (A) Type 1 in the radial enamel in *U. spelaeus*; the arrow head indicates the sheath of IPM. (B) Type 3 in the layer of HSB in *U. spelaeus*; arrow heads indicate the seam in some prisms. Type 1 in the layer of HSB in *U. arctos* (C) and in *U. wenzensis* (D); the arrow head indicates the sheath of IPM. Scale bar = 5 μm.
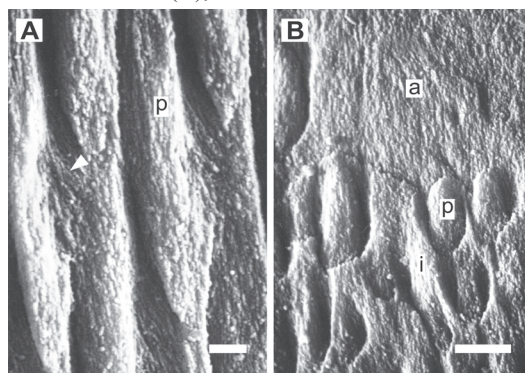

Figure 2. High magnification of *U. spelaeus* enamel in vertical section through M². (A) Crystallites of IPM (indicated by the arrow head) inclined to prisms (p). (B) Boundary between the outer aprismatic enamel (a) and prismatic enamel consisted of prisms (p) which are surrounded by the inter prismtic matrix (i).
Scale bar = 2 μm in (A) 5 μm in (B).

In contrast to *U. spelaeus*, in the layer of HSB in *U. arctos* (Fig. 1C), *U. wenzensis* (Fig. 1D) and *U. maritimus* we found only prisms of type 1. These prisms were arranged in a hexagonal closest packing, were circular, hexagonal or polygonal in transverse section and were surrounded by distinct sheaths of IPM. These sheaths, however, were thinner (0.57 μm in *U. wenzensis*) than sheaths enclosing prisms of type 1 in *U. spelaeus* (0.65 μm). Prisms of *U. spelaeus* were also slightly bigger in cross section than prisms in *U. wenzensis* (Tab. 2). Crystallites of IPM were oriented parallel to prism crystallites although in *U. arctos*, *U. spelaeus* and *U. wenzensis* we also observed some inclination up to about 45° (Fig. 2A).

Table 2. Measurements of prism in *U. wenzensis* and *U. spelaeus*.

Species	Prism feature	Prism pattern	Number of measurements	Mean (μm)	SD (μm)
U. wenzensis	diameter	1	38	3,7	0,4
U. spelaeus	diameter	1	53	3,9	0,6
U. spelaeus	length of head	3	71	4,4	0,6
U. spelaeus	width of head	3	84	3,0	0,4

General enamel organization (Schmelzmuster and enamel types)

The enamel of analyzed members of *Carnivora* was characterized by a quite simple organization composed of two enamel types: the outer, thinner layer of radial enamel and the inner, thicker layer of Hunter-Schreger bands (HSB) (Fig. 3). The radial enamel
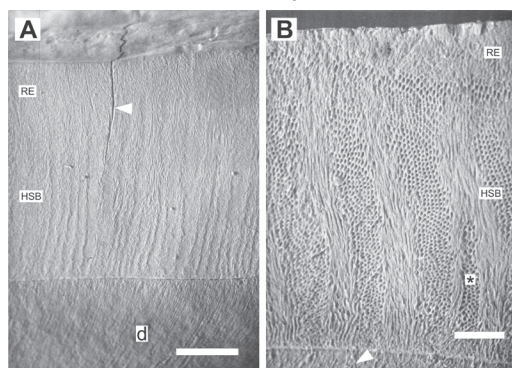

Figure 3. Vertical sections through the whole enamel layer and fragment of dentine (d) in the M² of *U. spelaeus* (A) and *U. wenzensis* (B). Two enamel types create two distinct layers: the inner, thicker layer of Hunter Schreger bands (HSB) and the outer, thinner layer of radial enamel (RE). The arrow head in (A) indicates an artificial crack which continues from the outer enamel layer and stops in the region of HSB. In (B), the asterisk shows a smaller HS band that does not reach the outer enamel layer. The arrow head indicates dentine tubules that penetrate the enamel layer. Scale bar = 200 μm in (A) and 50 μm in (B)
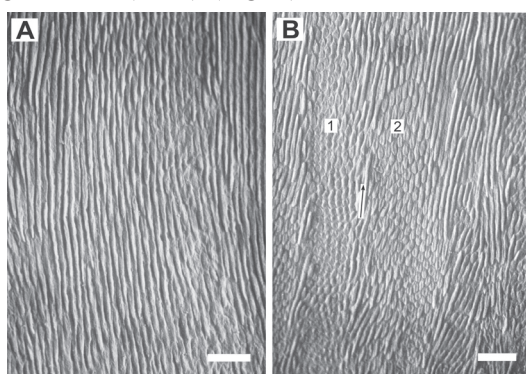

Figure 4. Enlarged regions of Fig. 3A showing two enamel types. (A) Radial enamel with parallel prisms. (B) Hunter-Schreger bands with decussating prisms in two adjacent bands (1 and 2) which are separated by the transition zone (indicated by the arrow). Scale bar = 25 μm.

Figure. 5. Incremental features of dental enamel in *U. spelaeus*. (A) Retzius lines in the radial enamel of M². (B) Perikymata on the surface of P⁴. Scale bar=50 μm in (A) and 200 μm in (B).

(Fig. 4A) consisted of almost straight and parallel prisms which were at right angles to the outer enamel surface. In HSB, prisms (Fig. 4B) were arranged in layers. Prisms within one layer (band) were oriented parallel to each other, but were placed at distinct angles (up to 90°) to the prisms in the adjacent layers. Very thin layer of aprismatic enamel was found in some areas close to the outer enamel surface in *U. spelaeus* teeth (Fig. 2B).

Retzius lines (Fig. 5A) were clearly visible in the radial enamel of *U. spelaeus*, while cross-strations in the enamel of *U. wenzensis*. The distance between the successive Retzius lines was on average 15.5 μm and the distance between the cross-strations equalled 3 μm. The Retzius lines manifested in tooth surfaces as perikymata (Fig. 5B). The distance between two perikymata measured in the same tooth region (i.e. anterior edge of P⁴) equaled 132 ± 22 SD μm (n= 50) and 184 ± 33 SD μm (n = 54) in *U. spelaeus* and *U. wenzensis*, respectively.

The HSB were well developed in all analyzed species. However, the examined species differed in the proportion of radial enamel layer to the whole enamel thickness. This proportion in cheek teeth was the largest in *U. spelaeus* (up to 27%), smaller (up to 22%) in *U. wenzensis* and *C. lupus familiaris*, and the smallest in *F. catus* (up to 19%). This enamel type was not observed at all in many tooth regions in *U. wenzensis*, canids and the domestic cat. In other *Ursus* species it was also very weak constituted. The contribu-

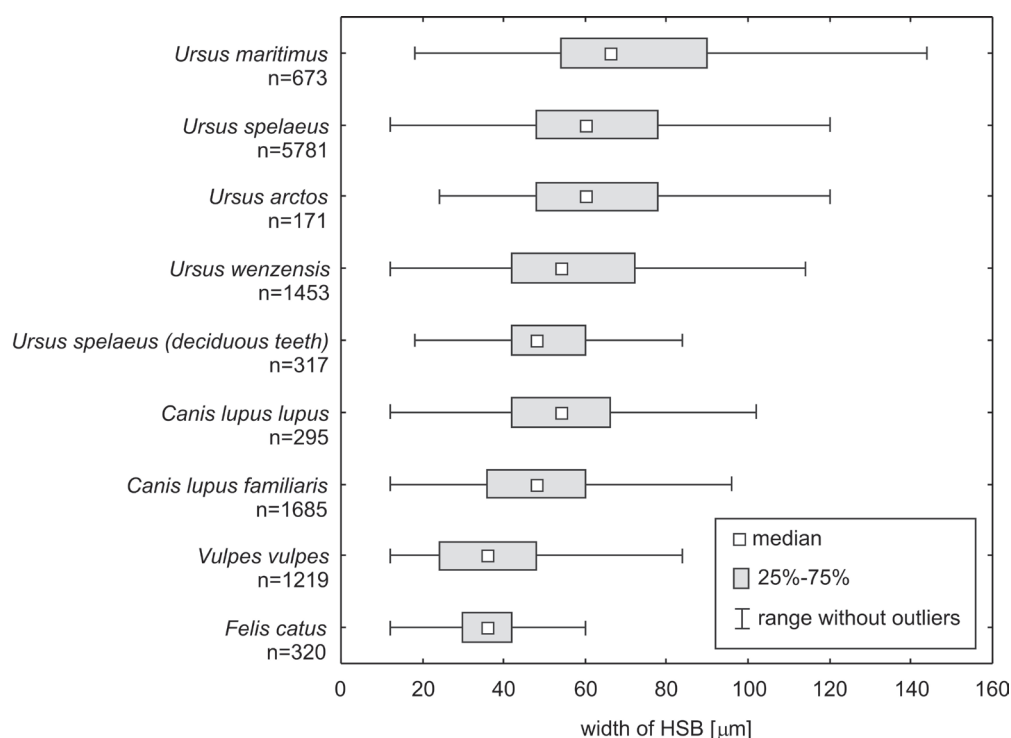Figure 6. Width of Hunter-Schreger bands (HSB) in studied species of carnivores; n denotes number of measurements.

tion of the radial enamel increased toward the occlusal surface, especially in *U. spelaeus* and dominated on the wrinkled occlusal surface of multicuspid molars where HSB were less pronounced. The radial enamel layer was much thinner in canines and constituted 17%, 9% and 5% in *U. spelaeus*, *U. wenzensis* and *C. lupus familiaris*, respectively.

The HSB layers were inclined or were perpendicular to the enamel-dentine junction. However, we observed some variation among the HSB inclination in a *U. spelaeus* M^1. This inclination was measured as the angle between the HSB and the line perpendicular to the EDJ in vertical section. This inclination on the lingual surface was positive (i.e. HSB were directed toward the tooth apex) and decreased from 26° after cingulum to 11° at the tooth apex. However, on the buccal surface, the inclination was negative and changed from -34° to -22° toward the apex. On the occlusal surface, the HSB were inclined at the angle 11° and 16° in the lingual and buccal side of occlusal basin, respectively.
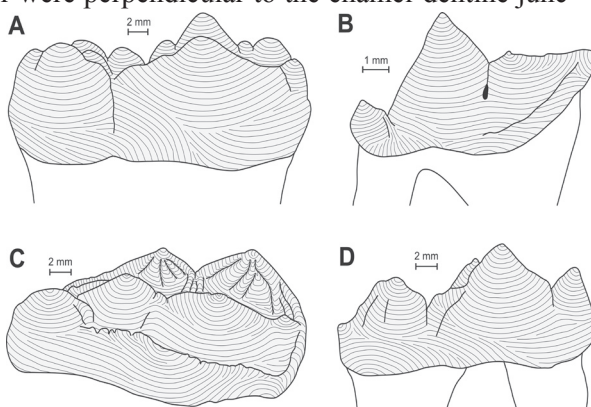
Figure 7. Course of Hunter-Schreger bands (HSB) on: the buccal side of M_2 from *Ursus spelaeus* (A), the buccal side of P^4 from *Felis catus* (B), the *U. wenzensis* M^2 viewed from the lingual and occlusal side (C) and the buccal side of M_1 from *U. wenzensis*.

Thickness of Hunter-Schreger bands

We found significant differences in the width of HSB between various representatives of *Carnivora* (Fig. 6) but did not record substantial variation among different tooth types (i.e. incisors, canines, premolars and molars) and among regions of a given tooth.

However, we noticed that bands at the very tips of M_1 from *U. spelaeus* were thinner (mean = 60.1, n = 27) than bands on the side of tooth crown (mean = 70.2, n = 21). HSB were poorly developed in some deciduous teeth and in highly reduced P_2 from *U. wenzensis*.

The teeth of *F. catus* and *V. vulpes* had the narrowest HSB, the representatives of genus *Canis* - wider, and the members of genus *Ursus* - the widest. Among bears the thinnest HSB were in *U. wenzensis* and the thickest in *U. maritimus*. Width of HSB in *U. spelaeus* and *U. arctos* were placed between the former species. HSB of deciduous teeth of *U. spelaeus* were much thinner than those of permanent teeth. The differences in the HSB width were not statistically significant (p > 0.05) only between pairs (Kruskal-Wallis test): *V. vulpes* vs. *F. catus*; *U. spelaeus* (deciduous teeth) vs. two *C. lupus* subspecies, *U. wenzensis* vs. *C. lupus lupus*, and *U. arctos* compared with other *Ursus* species. The thickness expressed in the number of prisms per one HSB was on average 11 in *U. spelaeus* and 8 in *U. wenzensis*.

These results clearly indicate an increasing trend in the width of HSB from smaller to bigger carnivorans. Actually, we have found a significant positive correlation (r = 0.964; p = 0.0001) between the median of HSB width and body mass in log-log scale (Data on body mass were taken from MACKIEWICZ *et al.* (2010). However, the slope of the regression line equaled 0.123 and was significantly lower from 1.0, i.e. value expected in the case of isometric scaling (95% confidence interval for the slope was from 0.089 to 0.157). It indicates a negative allometry scaling in this relationship.

Evolution of HSB is considered as a structural adaptation to enamel reinforcement against loading and crack propagation (KOENIGSWALD *et al.* 1987, PFRETZSCHNER 1988, RENSBERGER 1997). Therefore in the case of higher loading we should expect a decrease in thickness of HSB. To check how the HSB thickness is related to the bite force of analyzed species, we used calculated bite forces at carnasial eocone for extant ursids from Christiansen (2007), for the domestic cat and canids from Christiansen & Wroe (2007) and for *U. spelaeus* from GRANDAL-D'ANGLADE (2010). A significant positive corre-
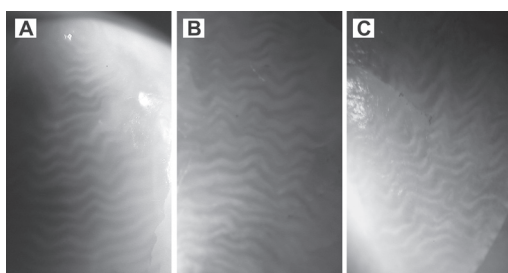
Figure 8. Acute-angled Hunter-Schreger bands in *Ursus spelaeus* teeth. (A) M_1, (B) M_2, (C) I^2.
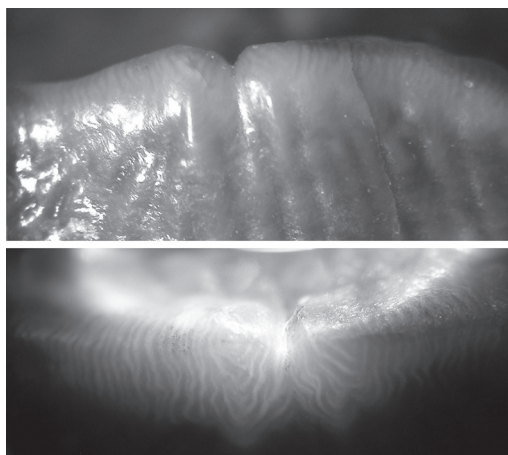
Figure 9. Vertical orientation of Hunter-Schreger bands on the ridge of protocone in *Ursus wenzensis* M^2.
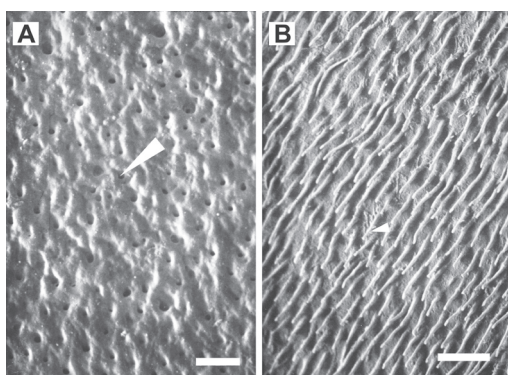
Figure 10. Dentine structure in *Ursus wenzensis* (A) and *U. spelaeus* (B). Notice in (A) that dentinal tubules in *U. wenzensis* are very distinct and protrude from the intertubular dentine. They have also short lateral branches which are indicated by the arrow head. In (B), the arrow head shows a hole of dentine tubule. Scale bar = 20 μm in (A) and 10 μm in (B).

lation was found between the HSB width and the bite force in log-log scale (r = 0.958; p = 0.0007). The slope 0.250 found for the regression of $\log_{10}$(median HSB width) to $\log_{10}$(bite force) had the 95% confidence interval from 0.164 to 0.336 and was significantly lower from 1.0 (i.e. value expected in the case of isometric scaling). This also indicates a negative allometry between HSB thickness and bite force. Interestingly, point for *U. spelaeaus* lay below the regression line.

Course of Hunter-Schreger bands on tooth surface

All analyzed teeth of bears, similarly to other carnivorans showed typical undulating HSB (Fig. 7) according to the terminology proposed by STEFEN (1997 *a,b*). They resembled flat sinusoids, were widespread horizontally around the tooth crown and bifurcated locally in one direction. However, we observed a transition from the undulating HSB to acute-angled bands at the tooth tips in two cave bears and also in some tooth sides in *U. spelaeus*. The acute-angled HSB were characterized by higher wave crest and troughs than the undulating HSB (Fig. 8). Interestingly, we found that *U. spelaeus* showed a higher degree of HSB waviness than its ancestor, *U. deningeri*. The average folding angle at wave crests and troughs measured on the acute-angled bands in the protoconid of M_1 was $113° \pm 10$ SD (n=31) and $130° \pm 5$ SD (n=22) in *U. spelaeus* and *U. deningeri*, respectively (t-test, p = 6×10^{-9}). This angle for the undulating HSB is assumed to be higher than $140°$ (Stefen 1997*a,b*). The acute-angled HSB were observed in all tooth types (incisors, canines, premolars and molars) in *U. spelaeus*. The average folding angle measured for all teeth was $97° \pm 14$ SD (n=729). Interestingly, 3% of measurements were lower than $70°$ which is the folding angle typical of the zig-zag HSB.

We did not notice any acute-angled HSB in brown and polar bears. In *U. wenzensis* we found these bands only on two teeth in restricted regions. The average folding angle for these bands reached $112° \pm 12$ SD (n=35) and was significantly higher than in *U. spelaeus* (t-test, p = 3×10^{-9}).

Although the HSB had generally horizontal course, some bending from the horizontal to some vertical orientation was observed, especially in crests and ridges of *U. wenzensis* molars and metastyle of P^4 in *F. catus* (Fig. 7, 9).

Dentine structure

Analyzing tooth specimens under SEM we noticed also some interesting difference in the dentine structure of *U. wenzensis* and *U. spelaeus*. In *U. wenzensis* (Fig. 10A) dentinal tubules were very distinct and protruded from the intertubular dentine. They had often short lateral branches. However, in the cave bear (Fig. 10B), we observed only holes of tubules which were inherent in the dentine bulk. It is not out of question that these differences result from various conditions of tooth mineralization.

Discussion

Enamel prisms

Analyses of *U. spelaeus* enamel at the prism level showed that the prism pattern 1 occurred in the radial enamel while the pattern 3 in the deeper layer of HSB. Some prism in *U. spelaeus* showed the "key-hole pattern" (the prism type 3B) typical of higher primates and also found in elephants and sirenias (KOENIGSWALD & SANDER 1997*b*). Similar distribution of the prism types was observed by BREUER (1931) who noticed the presence of hexagonal and polygonal prisms near the outer enamel surface whereas an arcade arrangement of prisms in regions close to the EDJ, which are usually occupied by HSB. Both types of prisms were also found by KOENIGSWALD (1992) in the cave bear. Interestingly, in other analyzed bears in the HSB enamel type, only the pattern 1 was observed. In the cave bear

U. deningeri were described hexagonal/polygonal prisms (Stefen 2001) but in the figures published by Gantt *et al.* (1980) many prisms with incomplete sheaths are also visible. Stefen (2001) also reported closed hexagonal to polygonal prisms in brown and polar bear, and round to oval prism in *Cephalogale*, a bear-like hemicyonid carnivore considered as an ancestor of all bears (Mclellan & Reiner 1994). Other carnivores in general also showed round to hexagonal prisms (Shobusawa 1952; Stefen 1997*a*, 1999, 2001).

Therefore, it seems that the pattern 1 can be considered an ancestral state for ursids while the pattern 3 a derived character for cave bears. The evolution of type 3 in the cave bear lineage may be related with an increase of enamel thickness because Martin (1983, 1985) and Grine *et al.* (1986) found that prisms of type 3 are secreted with higher rate than prisms of type 1, which probably results from the different shape of Tomes' process in ameloblasts. Actually, the thicker enamel was observed in the cave bears in comparison to other ursids and was considered as an adaptation to herbivorous way of life (Mackiewicz *et al.* 2010).

General enamel organization (Schmelzmuster and enamel types)

Although the enamel of analyzed members of *Carnivora* shows the same mode of organization: the outer radial enamel and the inner layer of HSB, we noticed some quantitative difference related to the significant increase in thickness of radial enamel layer in *U. spelaeus* by comparison with other carnivorans. The radial enamel was very weakly developed in many tooth regions of other bears. Stefen (2001) did not observe the radial enamel in *Cephalogale* and *U. maritimus*, either.

The radial enamel is more resistant to attrition than other enamel types because its prisms are normal to the enamel surface (Rensberger & Koenigswald 1980; Boyde 1984; Fortelius 1985; Boyde & Fortelius 1986; Koenigswald 1988). Then, the increase in proportion of this enamel type in *U. spelaeus*, especially on the occlusal surface could be associated with the adaptation to a higher abrasion of teeth and a vegetable diet containing many hard elements.

The observed higher proportion of the radial enamel on molars than on canines in studied species reflects specializations of dentition in different food processing. Molars are usually used in shearing, crushing and grinding, and are subjected to more abrasive forces than canines. The observed differences in the HSB inclination in various tooth surfaces in *U. spelaeus* may be related to some different biomechanical constraints superimposed on these surfaces during mastication. However, additional studies are required to prove such relationship.

Thickness of Hunter-Schreger bands

It is commonly assumed, that HSB evolved in response to increased chewing stresses in Cenozoic mammals associated with their larger body size and thus greater chewing muscles (Koenigswald *et al.* 1987; Pfretzschner 1988; Rensberger 1997). Such prism decussation reinforces the enamel against propagation of cracks which are stopped by the alternating orientation of prisms in adjacent HSB (See Fig. 3A for an artificial crack which continues from the outer enamel layer but stops in the region of HSB). This protective mechanism is the more efficient, the thinner HSB are. Actually, the decrease in HSB thickness was found, where occlusal stresses were very high: in incisors of the primate *Daubentonia madagascarensis* (Pfretzschner 1988) and in rodents with extremely reduced HSB thickness to layers composed of only one prism (e.g. Koenigswald 1982; 1985; Martin 1993, 1997). In agreement with that the narrower HSB that were observed in the cave bear at the very tips of tooth may reflect some adaptation to a higher load on tooth cusps.

The analyzed species showed differed significantly in HSB width which clearly increased with body mass of these animals. Our calculations showed the negative allometry for the relationship between the HSB width with the body mass and the estimated bite force. This indicates that bigger species with absolutely more powerful bite force (i.e. ursids, especially *U. spelaeus*) had a relatively thinner HSB than smaller species (i.e. typical meat-eating carnivorans). In other words, the increase in the bite force was larger than in the width of HSB. Although *U. spelaeus* had absolutely wide HSB, these bands were relatively thin in relation to the estimated bite force. This feature may be interpreted as an adaptation to reinforcement of enamel due to stronger chewing and more powerful bite forces related to a vegetarian diet of this species.

Course of Hunter-Schreger bands on tooth surface

The undulating HSB are the most common type of bands observed in *Carnivora* and are regarded as a plesiomorphic condition (STEFEN 1997*a*, 1999, 2001). However, in carnivorans also acute-angled and zig-zag bands were found. In contrast to other HSB types, the acute-angled HSB were never observed alone but only in tips of teeth or in the transition zone between the undulating and zig-zag HSB. The latter type has such exaggerated waviness that some vertical orientation of bands appears. The presence of this type well correlates with ossiphagous feeding habits and was reported in different families of carnivorans, especially in haenids and borophagine canids, and also in creodonts, condylarths and some artiodactyls (e.g. KOENIGSWALD 1997*a*, STEFEN 1997*a,b*; 1999; 2001; RENSBERGER 1999; STEFEN & RENSBERGER 1999; RENSBERGER & WANG 2005; FERRETTI 2007). The zig-zag HSB thanks to its complex three-dimensional structure plays an important role in a reinforcement of enamel against formation and propagation of cracks under varying loading conditions during bone crushing.

The presence of undulating HSB is an ancestral state also for *Ursidae* because only this type of bands was found in the early representatives of main bear lineages, such as: *Cephalogale*, *Ursavus* and *Plionarctos* (STEFEN 2001). In agreement with that, we also observed that many teeth of *U. wenzensis* (=*minimus*), an early member of *Ursinae* had the undulating HSB and only in two teeth we noticed the acute-angled bands in restricted areas. From the undulating HSB, the zig-zag bands evolved independently in *Ailuropoda*, *Arctodus*, *Hemicyon*, *Agriotherium* and *Indarctos* (STEFEN 2001). In these genera, with exception to the herbivorous panda the presence of the zig-zag HSB is also correlated with the frequent bone consumption but in the panda this type of bands is probably related with a reinforcement of its enamel because of biomechanical constraints on bamboo chewing.

However, in subfamily *Ursinae* only some transitions from the undulating to acute-angled bands were observed at tooth tips in *U. thibetanus*, *U. americanus*, *U. deningeri* and *U. spelaeus* whereas *U. arctos*, *U. maritimus* and *U. malayanus* showed only the undulating type of bands (STEFEN 2001). Our results are in agreement with these findings although we observed a clear increasing trend in the waviness of bands from *U. deningeri* to its descendent *U. spelaeus*. It may reflect some biomechanical constraints on the enamel structure due to multidirectional occlusal loading and higher occlusal forces found in *U. spelaeus* (GRANDAL-D'ANGLADE 2010), which were likely related with the increasing tendency towards herbivory in the cave bear lineage. The acute-angled bands can reinforce the enamel better than the undulating HSB but less than the zig-zag HSB.

Taken into account our findings and results obtained by STEFEN (2001) about the distribution of HSB types in *Ursinae*, and superimposing them on the phylogeny of analyzed ursids (Fig. 11) we can assume an independent evolution of acute-angled bands in the black bear and the cave bear lineages. In their sister taxa only the undulating bands were observed. *U. minimus* was a polymorphic species (MORLO & KUNDRÁT 2001) thus addi-

tional studies on broadened and diverse samples are necessary to asses a variation among enamel structure in this taxon. It would be also interesting to analyze the enamel structure in *U. etruscus* which is thought to be related to the arctoid and spelaeoid lineages.

It was suggested based on tooth marks on bones found at sites where the cave bear was the only carnivoran recorded that cave bears showed the scavenging habit (e.g. TINTORU & ZANALDA 1992; PACHER 2000; PINTO LLONA & ANDREWS 2004; PINTO LLONA *et al.* 2005; QUILES *et al.* 2006). However, no zig-zag HSB so characteristic of typical bone-crushing mammals were observed in *U. spelaeus*. It indicates that this species gnawed on bones only occasionally.

On the other hand, assuming that *U. spelaeus* was an almost exclusive vegetarian, we could expect that a specialized type of HSB, e.g. zig-zag HSB should had evolved in the cave bear as in the herbivorous *Ailuropoda*. However, the panda is a species that is very specialized to the tough fibrous bamboo therefore is not a good reference. Moreover, the panda lineage diverged about 20 million years BP (KRAUSE *et al.* 2008) and its adaptations to the bamboo diet have been evolving at least three million years (JIN *et al.* 2007). On the contrary, the lineage of the cave bear is much younger and appeared just in the Middle Pleistocene, slightly more than one million year BP (MAZZA & RUSTIONI 1994; MCLELLAN & REINER 1994). Moreover, the other predominant herbivore bear *Tremarctos* shows only the undulating HSB (STEFEN 2001) thus vegetarianism in bears in not always related to the zig-zag HSB evolution. Although, GRANDAL-D'ANGLADE (2010) estimated the bite force in the cave bear on very high value, the chewing force was widely dispelled on a large occlusal surface of a grinding character and was not concentrated like in bone-crushing mammals.
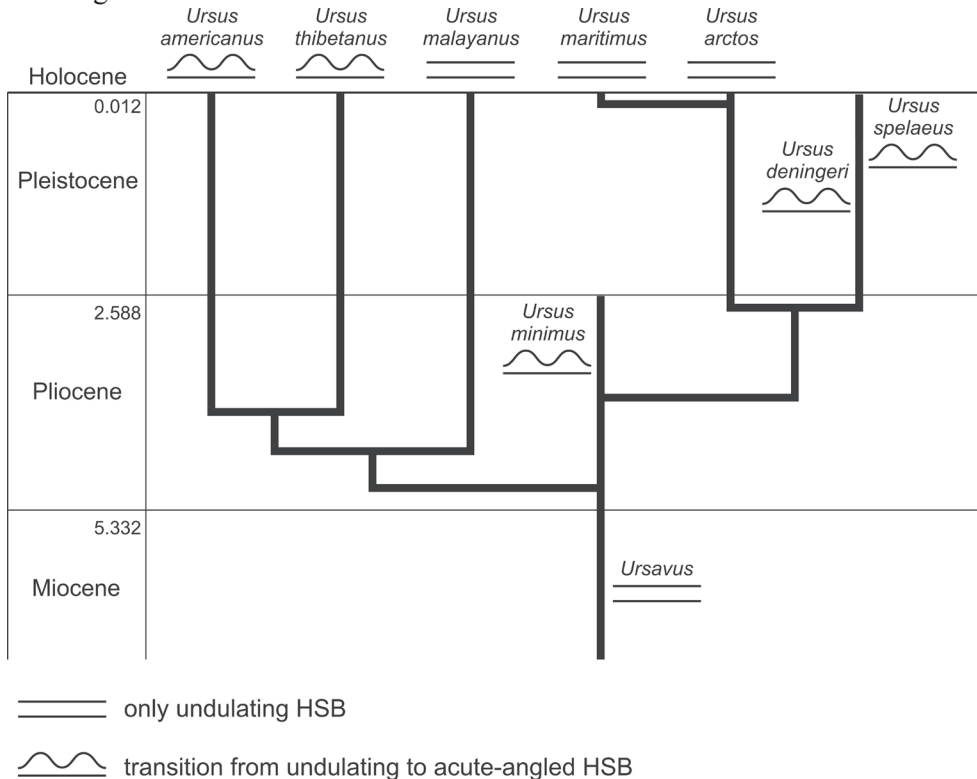

Figure 11. Phylogeny of selected representatives of *Ursinae* for which a type of HSB was determined. The divergence time for brown and polar bears was taken from Lindqvist *et al.* (2010) while for other bear lineages from KRAUSE *et al.* (2008).

We observed some bending of HSB from the horizontal to vertical course on premolars and molars with well pronounced crests and ridges in the domestic cat, canids and *U. wenzensis*, which resembled the U-shaped orientation found in *Brontotheriidae* and *Chalicotheriidae* (KOENIGSWALD 1994). Although these HSB were not the typical vertical decussation known in some ungulates (e.g. RENSBERGER & KOENIGSWALD 1980; FORTELIUS 1985; BOYDE & FORTELIUS 1986; RENSBERGER & PFRETZSCHNER 1992; KOENIGSWALD 1997*c*), carnivores (STEFEN 1997*b*; STEFEN & RENSBERGER 1999) and macropods (BEIER 1983) they may also perform some adaptations to biomechanical constraints. The vertical HSB compensate vertical stresses along the EDJ (PFRETZSCHNER 1994) and reduce abrasion because the bands parallel to abrasive forces are more resistant to wearing than such aligned perpendicular to these forces (RENSBERGER & KOENIGSWALD 1980). The vertical orientation of HSB probably helps to maintain a sharp and slender cutting edge (STEFEN & RENSBERGER 1999). The adaptive meaning of such bending in *U. wenzensis* agrees with analyses of its dentition, teeth morphology (STACH 1953, RYZIEWICZ 1969) and their functioning (ŻUK 1985), which showed a carnivore-like character of its teeth and substantial contribution of vertical jaw movements similarly to typical carnivores.

Concluding remarks

Among analyzed representatives of bears, *U. spelaeus* showed the most different features in the dental enamel structure at the three levels of enamel organization: prism, enamel types and Schmelzmuster. Although enamel of *U. spelaeus* did not reveal characteristics of typical herbivores, such as prisms with "inter-row sheets" or the modified radial enamel with crystallites of IPM oriented at wide angles to prisms (KOENIGSWALD 1992), the observed enamel modifications may indicate some adaptation to the increase of plant products in a diet of this species. The cave bear demonstrated the prism pattern 3 in the HSB layer while in other ursids only pattern 1. The presence of the prisms of type 3 which are secreted with higher rate than the prisms of type 1 may explain greater enamel thickness related to herbivory of this species (MACKIEWICZ *et al.* 2010). The larger proportion of radial enamel in *U. spelaeus* than in other bears and meat-eating carnivorans protected better its enamel against tough and abrasive plant elements during their processing. The HSB of the cave bear were thinner in relation to the estimated bite force than in other carnivores and probably more efficiently reinforced its enamel against crack propagation. Similarly, the pronounced waviness of acute-angled bands found at tooth tips or even in tooth sides in *U. spelaeus* can be also interpreted as more effective reinforcement of enamel subjected to higher and multidirectional occlusal loading during plant food processing.

On the other hand, the enamel structure of *U. wenzensis* did not differ significantly from other representatives of *Carnivora*, which agrees with the view that this bear was an unspecialized member of early evolved lineage still showing many features in its dentition and teeth morphology typical of meat-eating carnivores (STACH 1953; RYZIEWICZ 1969; ŻUK 1985). The observed some bending HSB from horizontal to vertical orientation on shearing crests may support this opinion.

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Streszczenie

**Struktura szkliwa zębów kopalnych niedźwiedzi
Ursus spelaeus i *U. wenzensis (=minimus)*
w porównaniu z wybranymi przedstawicielami
rzędu drapieżnych (*Carnivora*)**

Szkliwo zębów jest tkanką, która nie ulega istotnej przebudowie po swoim uformowaniu i mineralizacji. Z powodu tej silnej mineralizacji, struktura szkliwa podlega bardzo niewielkim zmianom podczas procesu fosylizacji i bardzo dobrze zachowuje się w stanie kopalnym. Dzięki temu stanowi ono cenne źródło informacji o sposobie odżywiania się gatunków kopalnych i funkcjonowania ich uzębienia, a także pomaga w analizach taksonomicznych i filogenetycznych. W niniejszej pracy szczegółowym analizom poddano szkliwo zębów dwóch kopalnych gatunków niedźwiedzi: *Ursus spelaeus* (późny plejstocen) i *U. wenzensis* (wczesny pliocen), które porównano ze szkliwem niedźwiedzi współczesnych: *U. arctos* i *U. maritimus* oraz innymi gatunkami należącymi do rzędu drapieżnych (*Carnivora*) (Tab. 1). Szkliwo *U. spelaeus* wykazało największą liczbę cech unikalnych w porównaniu do innych gatunków. W obrębie szkliwa radialnego u *U. spelaeus* stwierdzono typ 1 pryzmatów szkliwa (Fig. 1A, Tab. 2), a w obrębie pasm Hunter-Schregera (HSB) typ 3 pryzmatów (Fig. 1B, Tab. 2). Natomiast szkliwo zębów *U. arctos*, *U. wenzensis* oraz *U. maritimus* na obszarze tych pasm posiadało pryzmaty typu 1 (Fig. 1C, D, Tab. 2). Obecność pryzmatów typu 3 sugeruje większe tempo sekrecji szkliwa u *U. spelaeus* i w konsekwencji większą grubość szkliwa, co można wiązać z dużym udziałem pokarmu roślinnego w diecie tego gatunku. Kryształy hydroksyapatytu macierzy miedzypryzmatycznej były zorientowane równolegle lub były nachylone pod kątem (do 45°) względem kryształów tworzących pryzmaty (Fig. 2A). Przeanalizowani przedstawiciele *Carnivora* posiadali stosunkowo prostą organizację szkliwa, zbudowanego z zewnętrznej, cieńszej warstwy szkliwa radialnego i wewnętrznej, grubszej warstwy pasm Hunter-Schregera (Fig. 3, 4). Grubość warstwy szkliwa radialnego najbardziej odpornego na ścieranie była największa na zębach *U. spelaeus* (do 27%) w porównaniu do innych przedstawicieli *Carnivora*. Stwierdzono ponadto, że zęby trzonowe wykazywały większy udział tego typu szkliwa w stosunku do kłów. W niektórych regionach zębów *U. spelaeus* zaobserwowano dodatkowo cienką zewnętrzną warstwę szkliwa apryzmatycznego (Fig. 2B). W obrębie szkliwa radialnego u *U. spelaeus* były wyraźnie widoczne przyrostowe linie Retziusa (Fig. 5A), które objawiały się na powierzchni zęba jako perykimaty (Fig. 5B). Analizowane gatunki istotnie różniły się grubością pasm Hunter-Schregera (Fig. 6). Grubość tych pasm istotnie zwiększała się wraz ze wzrostem ich masy ciała

(od *Felis catus* do przedstawicieli niedźwiedziowatych), jednakże ten wzrost był mniejszy niż należałoby tego oczekiwać w przypadku skalowania izometrycznego. Podobne zjawisko występowało w przypadku zależności między szerokością pasm a oszacowaną siłą nacisku na zęby. W porównaniu tej siły, pasma HS okazały się najcieńsze u *U. spelaeus*. Badane gatunki niedźwiedzi charakteryzowały się typowym dla innych drapieżnych falowanym typem pasm HS poziomo obiegających koronę zęba (Fig. 7), chociaż u niektórych gatunków z rodzaju *Ursus*, niezależnie wykształciło się zwiększone falowanie przebiegu tych pasm (Fig. 11). Było ono szczególnie wyraźne na wielu zębach, zwłaszcza na ich guzkach u *U. spelaeus* (Fig. 8), co razem ze zmniejszoną grubością pasm HS w stosunku do siły nacisku prowadziło do zwiększenia odporności szkliwa poddawanego silnym naprężeniom z różnych kierunków, np. podczas obróbki twardego pokarmu pochodzenia roślinnego. Na niektórych krawędziach i grzbietach guzków zębów ssaków mięsożernych i *U. wenzensis* stwierdzono zmianę orientacji pasm HS z układu poziomego na pionowy (Fig. 7, 9), co może być związane ze wzmocnieniem szkliwa na tych strukturach zęba. *U. wenzensis* i *U. spelaeus* różnią się obrazem dentyny oglądanej w mikroskopie skaningowym zwłaszcza wykształceniem tubul dentyny (Fig. 10). Mimo, że w stosunkowo krótkim czasie ewolucji *U. spelaeus* w jego szkliwie nie wykształciły się cech charakterystyczne dla typowych roślinożerców (np. zmodyfikowane szkliwo radialne, grube osłonki między rzędami pryzmatów), to przeprowadzone analizy wykazały pewne modyfikacje, które mogą być związane z roślinożernym trybem życia niedźwiedzia jaskiniowego. Z kolei struktura szkliwa *U. wenzensis* nie różni się istotnie od szkliwa typowych przedstawicieli *Carnivora*, co jest zgodne z pozycją filogenetyczną tego gatunku reprezentującego wczesną linię ewolucyjną *Ursinae*. Obecność pionowego układu pasm HS sugeruje duży udział pokarmu zwierzęcego w diecie tego gatunku.

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