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ORIGINAL ARTICLE

# Craniometry of the Slovak northeastern beavers (*Castor fiber*) in comparison with the Ukrainian and Polish populations and contribution to the knowledge of the enamel thickness of beaver's incisors

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## Abstract

Like in most European countries, the population of the European beaver *(Castor fiber)* in Slovakia became extinct in the nineteenth century. Thanks to reintroduction of beavers in neighboring states, after a long break the beaver returns also to the territory of Slovakia. This has particularly affected the present distribution of beavers in the Slovak Republic. The first aim of the work was to find phylogenetic similarities of the northeastern Slovak population with the Ukrainian and Polish ones comparing their adult skulls and mandibles on the basis of craniometric measurements. A total of 28 measurements were taken on each skull and mandible. The statistical evaluation showed that the most similar were the Slovak and Ukrainian skulls, while in 8 cranial parameters the Ukrainian and Polish populations were found to be significantly different. The second aim was related to their ability to fell trees. The enamel thickness of incisors in the jaw and mandible were compared within the Slovak sample by measuring for 18 teeth, which were previously scanned by the X-Ray Computer Tomography. The results showed that the average thickness of incisors enamel in the mandible was 0.34 mm, while the incisors of the maxilla had enamel approximately 0.29 mm thick.

**Keywords** *Castor fiber* · European beaver · Skull morphometrics · Craniometry · Enamel thickness · Incisors

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## Introduction

The European beaver *(Castor fiber* Linnaeus, 1758*)* is an original representative of the European fauna. It became extinct in England as early as in the thirteenth century. During the 18th and 19th centuries it was hunted to extinction in almost all Europe and did survive only in small colonies on the Rhône River in France, the Elbe River in Germany, in the south of Norway, and in the inflows of the Dnieper River. Thanks to reintroduction at the beginning of the twentieth century, stabile populations have developed in Finland, Switzerland, Poland and Austria.

The beaver attracted attention of the Slovak scientific community at the time of its return into the landscape of Slovakia after about 120 years. It returned to the country that had been significantly affected by man and raised a new hope that it can contribute to the recovery of the natural environment in relevant areas (Valachovič et al. 2008). In Slovakia beavers are protected by the Act No. 543/2002 of the Code and are mostly found in the Záhorská lowland as this region is rich in the aquatic ecosystems with many streams (Baláž et al. 2013). Interestingly, a large beaver population has permanently settled in Bratislava, the capital of Slovakia (Benčič 2009). Another area occupied by beavers in the Slovak territory is eastern Slovakia, near the Polish border, where they came by natural migration from Poland (Foltan 2011).

As an ecosystem engineer, the beaver plays an important role in the natural environment. Its activity is able to significantly change the character of the landscape (Rosell et al. 2005). For this purpose, beavers need to have strong incisors (Hardisky 2011). The incisors are approximately 10 cm long, prominent, (Żurowski and Krzywiński 1974) curved in shape with a characteristic orange-coloured enamel restricted to the labial surface, and dentine to the lingual surface. This distribution of materials ensures that, as the dentine will wear away more quickly than enamel, a sharp incisor tip is constantly maintained (Cox and Baverstock 2015). The incisors grow continuously throughout the life and are very important for the animal. Gnawing on trees not only provides food and lots of building material, but also keeps their teeth short and sharp (Baker and Hill 2003). Their length and the fact that they are deeply implanted into the supporting bone tissue are an indication of the enormous strength of this type of teeth (Rouas et al. 2006).

This study had two main objectives. The first objective was to use the craniological measurements of an original Slovak sample as a basis for comparison of skulls of the northeastern Slovak population with those from Ukraine and Poland with respect to their similarities or differences. If grinding of the mandibular incisors is specific to beavers (Rouas et al. 2006), the second objective was aimed at the Slovak population and it was intended to verify whether there is a difference in the thickness of the enamel on the incisors between the upper and lower jaws.

## Materials and methods

### Craniometry

We studied 20 skulls and mandibles of `C. fiber` originating from the northeast of Slovakia, which are part of the collection of the Department of Anatomy of the University of Veterinary Medicine and Pharmacy in Košice. We also measured 20 Ukrainian beaver skull specimens from the collection of the Department of Animal Anatomy of the National University of Life and Environmental Sciences of Ukraine, Kiev, and 14 Polish skulls and 10 mandibles, which originated from the area around the town Lublin and are in the depository of the Faculty of Animal Bioengineering of the University of Warmia and Mazury in Olsztyn. Some parts of 14 Polish skulls were damaged, therefore we could not measure all 22 parameters (Table 1).

Only adult specimens were selected, identified by the presence of complete fusion between the basioccipital and basisphenoid (Roberston and Shadle 1954). The skulls were X – ray scanned for the purpose of estimating the age using the Piechocki (1986) method. The ages of the specimens range from about 3 to 7 years and this was determined using the tooth root closure (Fig. 1).

The skulls subjected to our study were of both sexes. On the basis of information provided by Kitchener and Lynch (2000) and Korablev et al. (2011) we ignored the effects of sex because it was assumed that the degree of sexual dimorphism was similar. In total, we measured 54 beaver

**Table 1** The measurements taken from the Polish beaver skulls and mandibles

| Skulls from Poland | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Parameters | 1. | 2. | 3. | 4. | 5. | 6. | 7. | 8. | 9. | 10. | 11. | 12. | 13. | 14. |
| AP | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| CbasLen | + | + | + | + | + | + | – | + | + | + | + | + | + | + |
| BasLen | + | + | + | + | + | + | – | + | + | + | + | + | + | + |
| BSt | + | + | + | + | + | + | – | + | + | + | + | + | + | + |
| StP | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| NasRh | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| ZygZyg | + | + | + | – | + | + | + | – | + | + | + | – | + | + |
| SupProc | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| PorbBrea | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| EntEnt | + | + | + | + | + | + | + | + | + | + | – | + | + | + |
| MxtLen | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| SagCrest | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| NuchCrest | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| EuEu | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| OccCond | + | + | + | + | + | + | – | + | + | + | + | + | + | + |
| ParaOcc | + | + | + | + | + | + | – | + | + | + | + | + | + | + |
| MxBrea | + | + | + | + | + | + | + | + | + | + | + | – | + | + |
| Anas | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| NasP | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| PremP | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| IncisBrea | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| PalaBrea | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| DM | + | + | + | + | + | + | + | + | + | + | – | – | – | – |
| M + D | + | + | + | + | + | + | + | + | + | + | – | – | – | – |
| D | + | + | + | + | + | + | + | + | + | + | – | – | – | – |
| CDS | + | + | + | + | + | + | + | + | + | + | – | – | – | – |
| VSkPCd | + | + | + | + | + | + | + | + | + | + | – | – | – | – |
| VSkPCn | + | + | + | + | + | + | + | + | + | + | – | – | – | – |

For abbreviations and descriptions see Materials and methods

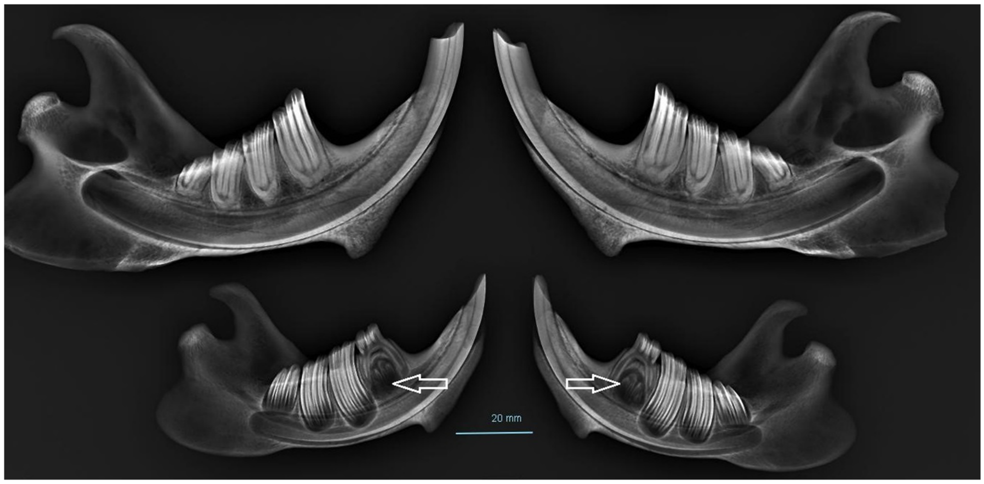


**Fig. 1** The X-ray image of adult beaver mandible (upper) – tooth root openings are closed and juvenile (lower) – tooth root openings are open: permanent premolar seen in a bone (arrows)

skulls and 50 mandibles of *C. fiber* (Fig. 2) to the nearest 0.01 mm, using digital calipers, following the von den Driesch (1976) measuring method. All measurements are given in millimeters.

22 metric parameters were taken on skulls (Fig. 2)

1. AP – total length of the skull
2. CbasLen – condylobasal length
3. BasLen – total length of the cranial base
4. BSt - basal – palatal length
5. StP – median palatal length
6. ANas– median frontal length
7. NasP – length of the viscerocranium
8. NasRh – length of nasals
9. ZygZyg – zygomatic breadth
10. SupProc – breadth across the supraorbital processes
11. PorbBrea – postorbital breadth
12. EntEnt – interorbital breadth
13. MxtLen – length of maxillary toothrow
14. PremP – length between the first premolar tooth and Prosthion
15. SagCrest – length of the external sagittal crest
16. NuchCrest – length of the nuchal crest
17. EuEu – neurocranium breadth
18. ParaOcc – breadth at the bases of the paracondylar processes
19. OccCond – breadth of the occipital condyles
20. IncisBrea – width of the incisive bone
21. MxBrea – width across infraorbital foramen
22. PalaBrea– width of palate at M3

6 metric parameters were taken on mandibles (Fig. 2)

23. DM – mandibular molar tooth row length
24. M + D – mandibular molar tooth row + diastema length
25. D– length of mandibular diastema
26. CDS– length of mandible
27. VSkPCd – height of condyloid process
28. VSkPCn – height of coronoid process

Abbreviations of cranial measurements were derived from Komosa et al. (2007).

## Incisor enamel thickness

The total number of investigated incisors of adult *C. fiber* originating from Slovakia was 18, 10 of the mandible (5 pairs) and 6 of the maxilla (2 pairs and two single teeth). There were 2 isolated incisors, identified as mandibular because they were less bent than the maxillary ones. The teeth inside the skull and mandible were scanned by the Computer Tomography (CT) using Metrotom 1500 from Carl Zeiss, with scanning distance of 500 mm and voxel value of 133 μm, U = 180 kV, $I$ = 350 μA. This allowed us to carry out a non-destructive measurement of the enamel thickness. Using CT, a comprehensive image of the tooth from any angle and in any cross-section is obtained. Since the density of the tooth layers differs, the thickness of the incisors`- enamel is measurable. The measurements were carried out from the tip of *corpus dentis* to the *apex dentis* in many points. We have created our own methodology. We decided to measure the enamel thickness in the middle of the labial surface of the tooth. The specific points may vary depending on the length of the tooth, approximately 9 measurements per tooth and the measuring points were determined by the software. The enamel was measured in a labio-lingual direction, at a right angle to the transversal plane. All measurements are given in millimeters. The enamel thickness of incisors was evaluated using software Volume Graphics VG Studio MAX 2.2.

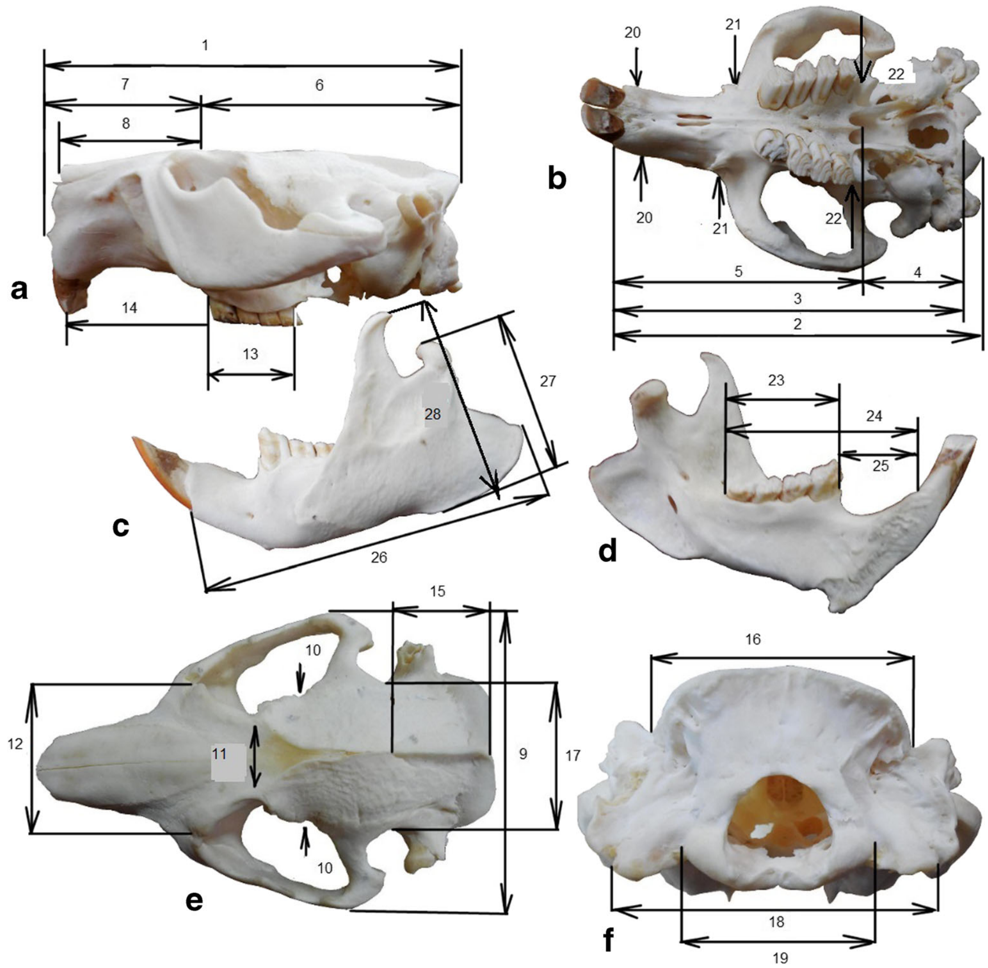


**Fig. 2** The measurements taken from the beaver skulls in the study. **a** Lateral view of the cranium. **b** Basal view of the cranium. **c** Lateral view of the mandible. **d** Medial view of the mandible. **e** Dorsal view of the cranium. **f** Caudal view of the cranium. For abbreviations and descriptions see Materials and methods

### Statistical analysis

All values measured on the skulls and mandibles were compared using a one-way analysis of variance and Tukey's multiple comparison test. The results were evaluated by means of software Graph Pad Prism 5 (GPP). The coefficient of variation (CV), was calculated using the following formula: $CV\% = \frac{a}{x}$ (a – standard deviation, x – mean value).

## Results and discusssion

### Craniometry

On the basis of GPP, 28 measured craniometric parameters of the Slovak, Ukrainian and Polish skulls and mandibles were statistically evaluated and compared.

It was found that three dimensions (SupProc, OccCond, EuEu) of the skulls differed significantly ($p < 0.05$). The breadth across the supraorbital processes (SupProc) and breadth of the occipital condyles (OccCond) exhibited variability on the cranium among the Ukrainian and Polish populations. It was exactly the neurocranium breadth (EuEu) that differed significantly between the Slovak and Polish skulls. One metric parameter of the mandible, the mandibular molar tooth row length together and diastema length (M + D), showed a significant difference ($p < 0.05$) between both Slovak and Ukrainian mandibles and Ukrainian and Polish mandibles (Fig. 3). Highly significant differences ($p < 0.01$), ($p < 0.001$) were noted between the Ukrainian and Polish skulls in four craniometric parameters: median frontal length – ANas; breadth at the bases of the paracondylar processes – ParaOcc; length of the viscerocranium – NasP; length between the first premolar tooth and prosthion – PremP. When comparing the Polish and Slovak populations, three dimensions (ANas, NasP, PremP) on the skulls differed significantly (Fig. 3), but only one morphological difference was detected at the same level of significance (ParaOcc) between the Ukrainian and Slovak skulls. The measurements of the mandibles revealed highly significant difference ($p < 0.001$) in one parameter (D – length of mandibular diastema) among all three studied populations. The mean values of the other 19 craniometric dimensions presented similar results for the Slovak, Ukrainian and Polish collections of skulls.

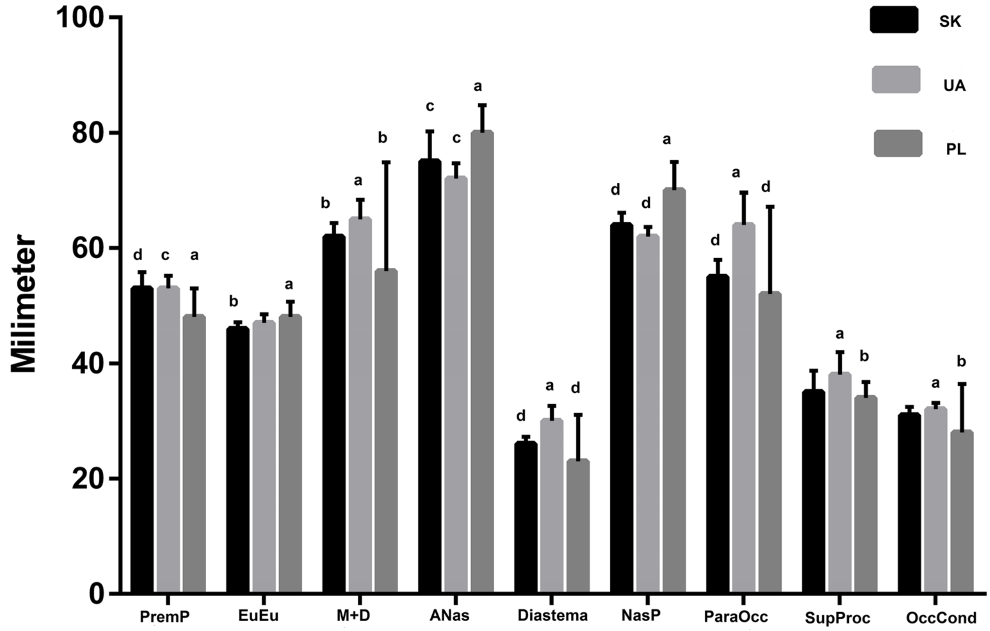


**Fig. 3** The bar graph shows the 9 craniometric parameters, which were different between the three studied beaver populations. Means with different superscripts are significantly different [ab] $p < 0.05$, [ac] $p < 0.01$, [ad] $p < 0.001$ (SK- Slovak specimens, UA-Ukrainian specimens, PL-Polish specimens) The statistical method applied in this study was One-way analysis of variance and Tukey's multiple comparison test

The calculation of the CV focused on the detection of intraspecific variability of the studied beaver skulls. It was observed that except for one case, the intrapopulation variability of the Slovak skulls was within the range (0.2–12.0%) of the total variability of basic craniomorphological characters, as concluded by Jablokov (1966) in his compilation about variability in mammals.

The highest CV (13.2%) was recorded in the width of the incisive bone (IncisBrea), while the lowest 2.41% was found for neurocranium breadth (EuEu), as seen in Table 2. In the case of the Ukrainian population the CV was higher than 12% with four variables (Table 3). The highest value of the CV (33.83%) was calculated for Polish skulls (Table 4). The above mentioned results indicate that the greatest intrapopulation variability was detected for the skulls originating from Ukraine.

A similar study was done by Kitchener and Lynch (2000). They mentioned that the biggest variation among the beaver populations in Europe was found in Germany compared with the French, English and Scandinavian populations. The German specimens were characterised as having large mandibles with relatively large tooth rows. Their results also confirmed that the skulls of British fossil beavers are morphologically closest to those of the extant Scandinavian beavers.

Comparison of the Slovak population with the Ukrainian and Polish ones conducted in our study revealed that the Polish population had the longest skulls (AP), the longest maxillary (MxtLen) and mandibulary toothrow (DM) and elongated viscerocranium (NasP). The Ukrainian specimens had wider skulls (ZygZyg), longer nasals (NasRh) and mandibular diastema (D). On the other hand, they had the highest mandibles (VSkPCn). The characteristic features of the Slovak skulls were a wider rostrum (MxBrea) and the longest mandibles (CDS).

Frahnert and Heidecke (1992) reported preliminary results of their morphometric study involving the variability of 400 beaver skulls from the Elbe population as well as limited numbers of skulls from other populations. On the basis of 24 measured parameters, the above authors concluded that four studied populations originating from the same geographical area differ in two parameters, the length of nasals and interorbital breadth. They also noticed, that the most obvious was the trend to smaller measurements from the largest Elbe individuals eastwards to the Sibirian and further to the Canadian populations. Freye (1959) also studied the cranium of European beavers from the Elbe and he found a major intrapopulation variability between the length of nasals and condylobasal length. Frahnert (2000) described skull proportions during the ontogenetic growth. She carried out measurements of 72 parameters of skulls from beavers of the German population that were used for taxonomic differentiation of this species. The author concluded that it is not relevant to classify the representative examples metrically.

The study by Korablev et al. (2011) focused on cranium proportions in the aboriginal relict population, and the reintroduced daughter population of the European beaver in the Upper Volga Basin and showed that these populations differed significantly ($P < 0.01$) in all cranial parameters. They also found out that for the decades after reintroduction (about 20 generations) the skulls of reintroduced beavers were characterized by a longer and narrow rostrum, shorter maxilla length, larger zygomatic width, and a short and high mandible in comparison with the maternal population. The mean CV for integrative

**Table 2** The values of the coefficient of variation (CV) in the Slovak beaver population. The highest value of CV is in bold

| Variable | n[a] | x[b] | SD[c] | CV % |
|---|---|---|---|---|
| AP | 20 | 140.84 | 8.36 | 5.94 |
| CbasLen | 20 | 134.64 | 8.45 | 6.28 |
| BasLen | 20 | 129.56 | 8.36 | 6.45 |
| BSt | 20 | 38.43 | 2.51 | 6.53 |
| StP | 20 | 90.5 | 5.85 | 6.46 |
| NasRh | 20 | 57.63 | 4.28 | 7.43 |
| ZygZyg | 20 | 98.91 | 4.78 | 4.83 |
| SupProc | 20 | 35.2 | 3.73 | 10.6 |
| PorbBrea | 20 | 27.58 | 1.9 | 6.9 |
| EntEnt | 20 | 43.8 | 3.05 | 6.96 |
| MxtLen | 20 | 32.79 | 1.69 | 5.15 |
| SagCrest | 20 | 30.95 | 3.12 | 10.08 |
| NuchCrest | 20 | 47.82 | 4.65 | 9.72 |
| EuEu | 20 | 46.81 | 1.13 | 2.41 |
| OccCond | 20 | 31.62 | 1.44 | 4.55 |
| ParaOcc | 20 | 55.16 | 2.95 | 5.35 |
| MxBrea | 20 | 34.26 | 2.39 | 6.98 |
| Anas | 20 | 75.24 | 5.2 | 6.9 |
| NasP | 20 | 64.66 | 2.16 | 3.34 |
| PremP | 20 | 53.91 | 2.78 | 5.16 |
| IncisBrea | 20 | 26.96 | 3.56 | **13.2** |
| PalaBrea | 20 | 37.59 | 2.48 | 6.6 |
| DM | 20 | 36.08 | 1.45 | 4.02 |
| M + D | 20 | 62.49 | 2.33 | 3.73 |
| D | 20 | 26.41 | 1.2 | 4.54 |
| CDS | 20 | 108.91 | 6.33 | 5.81 |
| VSkPCd | 20 | 47.19 | 2.44 | 5.17 |
| VSkPCn | 20 | 61.93 | 2.51 | 4.05 |

[a] number of specimens
[b] mean value
[c] standard deviation
For abbreviations and descriptions see Materials and methods

**Table 3** The values of the coefficient of variation (CV) in the Ukrainian beaver population. The highest value of CV is in bold

| Variable | n[a] | x[b] | SD[c] | CV % |
|---|---|---|---|---|
| AP | 20 | 136.4 | 2.96 | 2.17 |
| CbasLen | 20 | 132.63 | 6.19 | 4.67 |
| BasLen | 20 | 127.56 | 6.18 | 4.84 |
| BSt | 20 | 36.39 | 3.72 | 10.22 |
| StP | 20 | 91.58 | 5.81 | 6.34 |
| NasRh | 20 | 60.14 | 3.03 | 5.04 |
| ZygZyg | 20 | 102.13 | 5.62 | 5.5 |
| SupProc | 20 | 38.49 | 3.97 | 10.3 |
| PorbBrea | 20 | 29.03 | 4.48 | **15.4** |
| EntEnt | 20 | 44.59 | 3.32 | 7.45 |
| MxtLen | 20 | 31.78 | 0.78 | 2.45 |
| SagCrest | 20 | 30.59 | 7.04 | **23.01** |
| NuchCrest | 20 | 48.84 | 9.71 | **19.88** |
| EuEu | 20 | 47.81 | 1.48 | 3.09 |
| OccCond | 20 | 32.96 | 1.14 | 3.46 |
| ParaOcc | 20 | 64.41 | 5.59 | 8.68 |
| MxBrea | 20 | 32.65 | 3.85 | 11.8 |
| Anas | 20 | 72.91 | 2.69 | 3.7 |
| NasP | 20 | 62.96 | 1.65 | 2.62 |
| PremP | 20 | 53.5 | 2.16 | 4.04 |
| IncisBrea | 20 | 24.88 | 2.55 | 10.25 |
| PalaBrea | 20 | 39.7 | 6.92 | **17.43** |
| DM | 20 | 35.38 | 1.42 | 4.01 |
| M + D | 20 | 65.43 | 3.41 | 5.21 |
| D | 20 | 30.61 | 2.59 | 8.46 |
| CDS | 20 | 106.58 | 4.62 | 4.33 |
| VSkPCd | 20 | 45.56 | 2.22 | 4.87 |
| VSkPCn | 20 | 62.54 | 3.48 | 5.56 |

[a] number of specimens
[b] mean value
[c] standard deviation
For abbreviations and descriptions see Materials and methods

characteristics of intra-population variability for all signs were calculated in accordance with Jablokov (1966). The CV in the reintroduced population was greater, but not significantly, considering standard error.

We could not overlook the study by Komosa et al. (2007) who described differences in morphological distance of a cranium between the Neolithic and contemporary beavers. Comparison of the mean values of the northeastern Slovak population with those from the Wielkopolska region showed that the data obtained in the group of 3-year old and 4–5 year old contemporary Polish beavers and in Slovak specimens were almost identical in 5 parameters. The remaining 17 characters were very similar metrically which indicates morphological closeness of these skulls.

## Incisor enamel thickness

The results of measurements of enamel thickness of mandibular incisors and maxillary incisors are presented in Tables 5 and 6. The mean value of enamel thickness calculated from 93 measured values carried out on 5 pairs of incisors of the mandible reached 0.34 mm. The mean thickness of incisor enamel of the maxilla calculated from 49 measurements was 0.29 mm. Interestingly, the highest values in the mandible incisors` enamel were measured in the first third of the *corpus dentis* and the thickness of the enamel incisors in maxilla was the highest at the tip of the tooth. When the enamel of two isolated teeth (they were considered as teeth coming from the mandible) was

**Table 4** The values of the coefficient of variation (CV) in the Polish beaver population. The highest value of CV is in bold

| Variable | n[a] | x[b] | SD[c] | CV % |
|---|---|---|---|---|
| AP | 14 | 141.14 | 8.62 | 6.11 |
| CbasLen | 13 | 138.25 | 7.94 | 5.74 |
| BasLen | 13 | 132.2 | 7.98 | 6.04 |
| BSt | 13 | 38.41 | 2.73 | 7.11 |
| StP | 14 | 94.1 | 5.46 | 5.8 |
| NasRh | 14 | 58.77 | 4.27 | 7.26 |
| ZygZyg | 11 | 101.91 | 6.09 | 5.98 |
| SupProc | 14 | 34.4 | 2.74 | 7.96 |
| PorbBrea | 14 | 28.43 | 2.36 | 8.3 |
| EntEnt | 13 | 45.71 | 3.81 | 8.34 |
| MxtLen | 14 | 33.23 | 1.7 | 5.12 |
| SagCrest | 14 | 36.33 | 12.29 | **33.83** |
| NuchCrest | 14 | 46.72 | 3.29 | 7.04 |
| EuEu | 14 | 48.74 | 2.64 | 5.42 |
| OccCond | 13 | 31.15 | 1.31 | 4.21 |
| ParaOcc | 13 | 56.04 | 2.73 | 4.87 |
| MxBrea | 13 | 34.0 | 2.13 | 6.26 |
| Anas | 14 | 80.63 | 4.78 | 5.93 |
| NasP | 14 | 70.9 | 4.89 | 6.9 |
| PremP | 14 | 48.26 | 4.98 | 10.32 |
| IncisBrea | 14 | 25.76 | 1.94 | 7.53 |
| PalaBrea | 14 | 36.5 | 1.62 | 4.44 |
| DM | 10 | 36.23 | 1.45 | 4.0 |
| M + D | 10 | 62.13 | 2.51 | 4.04 |
| D | 10 | 26.04 | 1.74 | 6.68 |
| CDS | 10 | 105.46 | 4.78 | 4.53 |
| VSkPCd | 10 | 45.64 | 2.98 | 6.53 |
| VSkPCn | 10 | 60.52 | 3.03 | 5.0 |

[a] number of specimens

[b] mean value

[c] standard deviation

For abbreviations and descriptions see Materials and methods

measured, the mean thickness was 0.32 mm, (teeth 11, 12) see Table 5.

The beavers are characterized by hypsodont teeth, which are extremely important for them (Rouas et al. 2006; Stefen 2009). Their strong incisors are specialized for gnawing. They need this for feeding purposes, but it also provides lots of building material for constructing dams, ponds and canals (Rosell et al. 2005). Zhijiang et al. (2003) and Maul (2003) reported that the upper incisors of beavers moved only slightly when incising wood and were used mainly as an anchor. The lower incisors can perform gnawing movements, because the rodents can move their mandible laterally to some degree (Maul 2003). Hinze (1950), Rybczynski et al. (2010) and Cehláriková (2010) also indicated a similar use of lower and upper incisors. Stefen (2009) named the incisors as the "freest "teeth, because they have a space to increase in size. The author found that within the first 50 months, the length of the incisors in *C. fiber* nearly doubles, from about 4 mm to nearly 8 mm. The mentioned research about intraspecific variability of beaver teeth showed that the overall range of variation in lower incisor length over all studied ages (from about 3 months to 18 years) is about 6 mm.

The morphology of the skull, mandible and jaw-closing muscles enable the beaver to produce a very effective and efficient bite. The incisor bite force calculated for the American beaver (550–740 N) was much higher than it would be predicted from the body mass and incisor dimensions (Cox and Baverstock 2015). Enamel in this type of teeth is only on the labial surface and is normally two-layered. Korvenkontio (1934) called the inner layer *portio interna* (PI) and the outer layer *portio externa* (PE). As reported by von Koenigswald and Mörs (2001), the enamel formation is closely controlled by genetic and epigenetic factors and is devoid of modifications during the use of the tooth. Thus the enamel microstructure contains much phylogenetic information.

Although beaver teeth attracted attention of many scientists, we have not found a publication that would have given a measurement of enamel thickness explicitly.

The only relevant research available was conducted by von Koenigswald and Mörs (2001) who found that enamel of the fossil representative of the family Castoridae – *Steneofiber dehmi* (Freudenberg, 1941) is unusually thin (about 100 μm), but clearly divided into PI and PE. In *Steneofiber eseri* (Meyer, 1838) the incisor enamel was thicker (150 μm), the thickness reaching a value approximately half that of our results.

Rouas et al. (2006) described the incisors from the histological point of view. The colouring helped the authors to determine the structures and tissues. They carried out several horizontal sections perpendicular to the corono-apical axis at different levels. At the occlusal level, they found a blue coloured vestibular enamel, surmounted by a brown layer corresponding to the deposit of ferric oxide on the enamel. At the median level, the enamel was located on the vestibular face. The dark pink dental surface corresponded to the dentine surrounding the pulp tissue which appeared black. They mentioned that because the enamel is the tissue which is the most mineralised and the hardest, the enamel arc is still the portion of the dental tissue that wears least, giving the tooth a bevelled, occlusal surface.

Gordon et al. (2015) were also involved in the research of enamel of beaver's incisors. Their study revealed that beaver teeth have layers of calcium and phosphorus "nanowires" that make up the core structure of the enamel. At this microscopic level, the iron and magnesium in beaver enamel also surrounds the nanowires helping the teeth resist the decaying power of acid. The researchers concluded that one reason for

**Table 5** The values of the enamel thickness of 12 beaver mandibular incisors in certain points

| Mandibular incisors | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. | 2. | 3. | 4. | 5. | 6. | 7. | 8. | 9. | 10. | 11 | 12. |
| 0.296 | 0.293 | 0.289 | 0.301 | 0.347 | 0.341 | 0.338 | 0.353 | 0.387 | 0.375 | 0.33 | 0.295 |
| 0.3 | 0.295 | 0.258 | 0.301 | 0.363 | 0.352 | 0.336 | 0.347 | 0.391 | 0.384 | 0.325 | 0.312 |
| 0.3 | 0.286 | 0.286 | 0.297 | 0.351 | 0,361 | 0.336 | 0.342 | 0.379 | 0.381 | 0.334 | 0.317 |
| 0.277 | 0.294 | 0.291 | 0.289 | 0.357 | 0.377 | 0.348 | 0.357 | 0.37 | 0.387 | 0.335 | 0.315 |
| **0.326** | **0.32** | **0.31** | **0.313** | **0.429** | 0.38 | **0.375** | **0.386** | **0.394** | **0.396** | **0.337** | **0.32** |
| 0.284 | 0.291 | 0.277 | 0.273 | 0.391 | **0.429** | 0.361 | 0.375 | 0.387 | 0.372 | 0.334 | 0.301 |
| 0.305 | 0.289 | 0.286 | 0.304 | 0.38 | 0.408 | 0.288 | 0.285 | 0.373 | 0.378 | 0.287 | 0.294 |
| 0.283 | 0.318 | 0.302 | 0.307 | 0.397 | 0.385 | 0.329 | – | – | – | 0.321 | 0.309 |
| 0.295 | 0.319 | 0.28 | 0.295 | 0.38 | – | 0.317 | – | – | – | 0.322 | 0.312 |
| – | 0.289 | 0.294 | 0.294 | 0.394 | – | – | – | – | – | 0.327 | 0.288 |
| – | – | 0.294 | 0.297 | – | – | – | – | – | – | – | 0.291 |
| – | – | 0.302 | – | – | – | – | – | – | – | – | 0.31 |
| – | – | 0.29 | – | – | – | – | – | – | – | – | 0.281 |
| – | – | 0.301 | – | – | – | – | – | – | – | – | – |
| – | – | 0.287 | – | – | – | – | – | – | – | – | – |

Thicker enamel (in bold) is in the first third of the *corpus dentis*
The measurements were carried out from tip to root of the tooth
The measurements are given in millimeters

beaver's strong incisors and unusually decay-resistant enamel is the presence of a lot of iron.

Our findings that the mean thickness of the enamel of the upper and lower incisors differs clearly confirms the above-mentioned fact about the cutting technique. The fact that the enamel in the first third of the mandibular incisors is thicker, indirectly confirms the conclusions of Göhre (1954) who described that the lower incisors can cut into the wood to a depth of about 1–2 cm.

**Table 6** Beaver maxillary incisors (13–18) and their values of the enamel thickness in certain points

| Maxillary incisors | | | | | |
|---|---|---|---|---|---|
| 13. | 14. | 15. | 16. | 17. | 18. |
| **0.265** | **0.269** | **0.329** | **0.315** | **0.374** | **0.304** |
| 0.229 | 0.227 | 0.309 | 0.315 | 0.36 | 0.271 |
| 0.232 | 0.247 | 0.317 | 0.313 | 0.349 | 0.303 |
| 0.26 | 0.232 | 0.319 | 0.294 | 0.335 | 0.297 |
| 0.247 | 0.24 | 0.32 | – | 0.354 | 0.298 |
| 0.236 | 0.229 | – | – | 0.34 | 0.302 |
| 0.239 | 0.229 | – | – | 0.335 | 0.263 |
| 0.24 | – | – | – | 0.318 | 0.269 |
| 0.232 | – | – | – | 0.349 | 0.282 |
| – | – | – | – | 0.311 | 0.272 |
| – | – | – | – | 0.351 | 0.283 |
| – | – | – | – | 0.298 | – |
| – | – | – | – | 0.309 | – |

Thicker enamel is at the tip of each tooth (in bold)
The measurements were carried out from tip to root of the tooth
The measurements are given in millimeters

However, the strength of beaver incisors is not related only to the enamel thickness but is affected also by other factors. According to Stefen et al. (2016), the shape and the wedge angle of beaver incisors are also important. They assumed that under the changing conditions the wedge angle of about 23° to 27° is optimal for beavers and is similar to the optimal wedge angle of sharp steel cutting tools. The upper incisors have a slightly larger wedge angle, consistent with their general use as anchors during cutting. From the histological point of view, they reported that the lower incisor in *C. fiber* is fixed by fibres along the complete length within the alveolus.

According Pahlevan et al. (2014), the value of the enamel thickness is 345 μm in a human maxillary central incisor and 235 μm in a lateral incisor, related to the one-third labial cervical area. The maximum thickness in maxillary central and lateral incisors in the one-third labial incisal surface was 1260 μm and 1220 μm, respectively.

Hall et al. (2007) compared enamel thickness between mandibular central and lateral incisors in humans and found that wider teeth were associated with greater enamel thickness ($p < 0.1$), but the thickness varied greatly among subjects (range: 0.44–1.28 mm).

Our research showed that the mean value of enamel thickness in beaver incisors was very similar to that published by Pahlevan et al. (2014).

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This study did not require official or institutional ethical approval.

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