Uneven distribution of enamel in the tooth crown of the hypsodont Plains Zebra *Equus quagga*

Daniela E Winkler, Thomas M Kaiser

Unworn teeth of herbivorous mammals are not immediately functional. They have to get in wear to expose enamel ridges which can then act as shear-cutting blades to disintegrate the food. We use the Plains Zebra (*Equus quagga*) as a hypsodont, herbivorous model organism to investigate how initial wear of the tooth crown is controlled by underlying structures. We find that the enamel proportion is smaller at the apical part of the tooth crown in all upper tooth positions. Measurements of enamel thickness on the first molar show that the outer enamel band is widest in the lower half of the tooth crown, where enamel content is also highest. We therefore find evidence that the distribution of enamel within the tooth crown is uneven and lower enamel content at the apex promotes early wear. This gradient in enamel distribution is less pronounced in the last molar (txM3), which has also a higher overall enamel content. The M3 is thus hypothesised to have a slightly different functional trait in mastication, resisting highest bite forces along the tooth row and maintaining functionality while anterior teeth are already worn down.

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Introduction

Hypsodonty is a common evolutionary strategy by herbivorous mammals to counter large abrasive loads in the food consumed, which result in high dental wear. Hypsodonty can be easily achieved in all tooth positions by extending specific ontogenetic phases during tooth development (von Koenigswald, 2011). Newly erupted hypsodont cheek teeth share a feature between all taxa: they are not immediately functional. To disintegrate tough plant matter, the relatively rounded apex of the (pre)molar tooth crowns has to wear down slightly, exposing the enamel ridges which may then act as shearing blades during mastication. The rapid wear of the topmost tooth crown has been noted in selenodont molars (Osborn and Lumsden, 1978) and several authors have hypothesised how this initial wear is facilitated. One theory is that empty chewing movements (thegosis) sharpen teeth in adults and helps to bring the teeth in wear in young due to pure attritional contacts (Every, 1972; Every et al. 1998). More often, however, such empty chewing is considered a behavioural anomaly (termed bruxism or pathological thegosis) which appears in livestock, other domestic or captive animals (eg. Murray et al., 1998; Troxler, 2007; 2012) and also in man.

We propose that the top of the tooth crown should be less resistant to both attritional and abrasional contacts in order to promote early wear and henceexpose functional enamel ridges quickly. This could be accomplished by either building the top of the tooth crown from less and/or thinner enamel or by building a less resistant enamel microstructure. Both hypotheses suggest that the top of the tooth crown is structurally different from the rest of the tooth. Analysis of enamel microstructure at different tooth crown heights is a destructive and time consuming method, therefore we chose to study enamel distribution within the tooth crown of a subadult Plains Zebra (*Equus quagga* sp.) using micro CT-scanning. The Plains Zebra is an ideal model organism for large, hypsodont herbivores, because it is adapted to grazing in both arid and savannah climates and therefore needs to have a high tolerance of abrasional tooth wear. Amongst extant large herbivore species, the Equidae exhibit the highest degree of hypsodonty, only equalled by a few Bovidae like *Bison bison* (compare hypsodonty indices in Janis, 1988).

Material and Methods

The selected individual is a loan from Museum für Naturkunde (Berlin). It shows very low or no wear on the premolar and molar teeth and is therefore in the optimal stage to investigate enamel distribution within all tooth positions of the same individual. The tooth eruption sequence for upper permanent teeth in *Equus burchelli* (which is synonymous to *E. quagga*) is M1, M2, I1, P2, P3, P4, I2, C, M3, I3 (Erz, 1964). Hence we see small amounts of material loss in the earlier erupting teeth M1, M2, P2, and P3 compared to the unworn P4 and M3. However, we chose not to use unworn premolars and molars of several individuals in order to exclude inter-individual variation in enamel distribution. We focus on the upper permanent dentition, because upper teeth are employed as the standard in studying dental characteristics (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002; Archer and Sanson, 2002) and functional traits should be more pronounced as compared to lower teeth (Kaiser and Fortelius, 2003) due to the lack of gravity impact. High resolution computed tomography (microCT) scans with an x-y-z resolution between 0.075 and 1.0 mm were obtained at Steinmann-Institut für Geologie, Mineralogie und Paläontologie (Universität Bonn, Germany) on the CT scanner v|tome|× s (GE phoenix|x-ray). The software VG StudioMax 2.1 (Volume Graphics, Heidelberg) was used for reconstruction of virtual models and further processing. First, each tooth was recreated with all dental tissues (enamel, dentin and cementum) as a voxel model using manual and automatic segmentation tools. Next the mineralised enamel was selected and pure enamel voxel models were created (Fig.1). We then cut both, the enamel and the full tooth model at approx. 75%, 50% and 25% of the initial crown height and created individual models of four tooth sections: Section 1 from 100-75% crown height, Section 2 from 75-50% crown height, Section 3 from 50-25% crown height and Section 4 from 25% down to the base of the crown (Fig.2). Volumes of the enamel sections and full tooth sections were taken directly from these models using VG StudioMax. We further measured thickness of enamel ridges on virtual cross sections through txM1. Measurements were taken at approximately the same position at the metacone for the outer enamel ridge and the inner enamel ridge (Fig.3.A) at the apical and basal part of each section. The approximate height of measurements is indicated in Fig.4.B.

Results

Data on enamel content are given in Fig.4. Though distribution of enamel content per section was variable between teeth, it was consistently smallest in Section 1 (the most apical section) for all tooth positions. Section 2 contained 2.5-5.5% more enamel than Section 1, Section 3 even 4.5 -9.0% more enamel. The largest ontogenetic increase in enamel content was found for txM1 and txM2, where Section 4 contained more than 9.6% more enamel. The highest enamel contents were found either in Section 3 (txP2, txP4, txM3) or Section 4 (txP3, txM1, txM2). It is notable that txM3 was composed of more enamel than all other tooth positions and also showed the lowest differences in enamel content between sections. Results for enamel thickness measurements are given in Table 1. The thickness of the inner enamel ridge is largest in Section 2, but very similar in all other sections. The outer enamel ridge is getting thinner from the apical part of Section 1 to the apical part of Section 2, but then increases in thickness from the basal part of Section 2 down to the crown base (compare Fig.3.A and 3.B for location of measurements).

Discussion

The results of this study support our hypothesis that the top of the tooth crown is structurally different from the remainder of the tooth. We have shown that the overall enamel content is lowest at the crown top and highest in the lower half of the crown. Our measurements of enamel thickness indicate that both thickness and distribution of enamel vary along the tooth crown. The thinnest enamel ridges were not found at the top of the crown; however the overall amount of enamel was lowest at this level.

There are relatively more soft dental tissues (dentin and cementum) at the top of the crown and therefore this part of the tooth is prone to fast wear. We further note that the base of each tooth seems to be structurally “enhanced”, as the larger content of enamel should strengthen it and help resist high pressure and stress loads. This interpretation is consistent with our enamel thickness measurements at the base of the crown (Section 4 basal). There the greatest thickness of the outer enamel ridge is recorded, but the inner enamel bands are no longer present, because the two fossettes are worn out.

In *Equus quagga*, we find the third upper molar to be structurally different from all other upper teeth, as it has the highest proportion of enamel and the least variation of enamel distribution along the tooth crown. We relate this phenomenon to adaptive pressures related to generally two phenomenona:

1. Mechanical constraint: As the upper M3 is closest to the temporomandibular joint, the highest masticatory forces can be generated here (Greaves, 2012). The high enamel content will then prevent excessive wear and maintain chewing evenly distributed forces induced.
2. Biogenetic constraints: The M3is the last tooth to erupt in most mammals, so in the Zebra. Therefore it is also the tooth position maintaining function when anterior teeth have already been worn out..

In general, by being more resistant to wear, txM3 can thus compensate for the functional loss of anterior teeth. Because it comes in occlusion while shear-cutting functionality in anterior teeth is well established, there is no need for a weakened crown top as in other cheek teeth.

Though *Equus quagga* is an appropriate model organism, these observations are still singular and restricted to this very taxon. They can, however, help us to understand how mechanical and ontogenetic constraints of wear and resistance may be solved in a biological system, by slight modifications of common structures. The findings also illustrate, that at least the Zebra as a hypsodont herbivore has undergone severe need of optimisation of its chewing system and that the acquisition of hypsodonty does not mean, that basic constraints are rendered insignificant in terms of functional optimisation. As these constraints are universal for all mammals feeding on abrasive diets, we expect to find similar adaptations in other herbivorous species, including bovids.

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<u>Figures and Tables</u>

Fig.1.A. Cross section through a full virtual tooth model with all dental tissues. B. As Fig. 1.A., enamel only. Scale bar 50mm.

Fig.2. Virtual 3D-model of txP3 with all dental tissues. The tooth is separated in four sections, which are slightly separated from each other for better illustration.

Fig. 3.A. Cross section through the virtual model of txM1. Black bars indicate the approximate position where measurements of enamel thickness were taken on the outer and inner enamel ridge. Scale bar is 50mm. B. Dashed lines show approximate heights where thickness measurements were taken. Solid lines represent borders of each section. The tooth is in anatomically correct position with the top of the crown facing the bottom of the image. Hence, the lower dashed line within one section marks the positions referred to as “apical”, the upper dashed line as “basal” in Tab.1.

Fig.4. Enamel content per section and tooth position. Each bar represents 100% enamel content per tooth position and shows relative enamel content per section. Percentages above bars give the relative enamel content per tooth position.

Tab.1. Measurements of enamel thickness for the outer and inner buccal enamel ridge at two positions (“apical”, “basal”) of each section. For the basal part of Section 4 no thickness could be measured for the inner enamel ridge as it has already ended at another height.

Table 1 (on next page)

Tab.1

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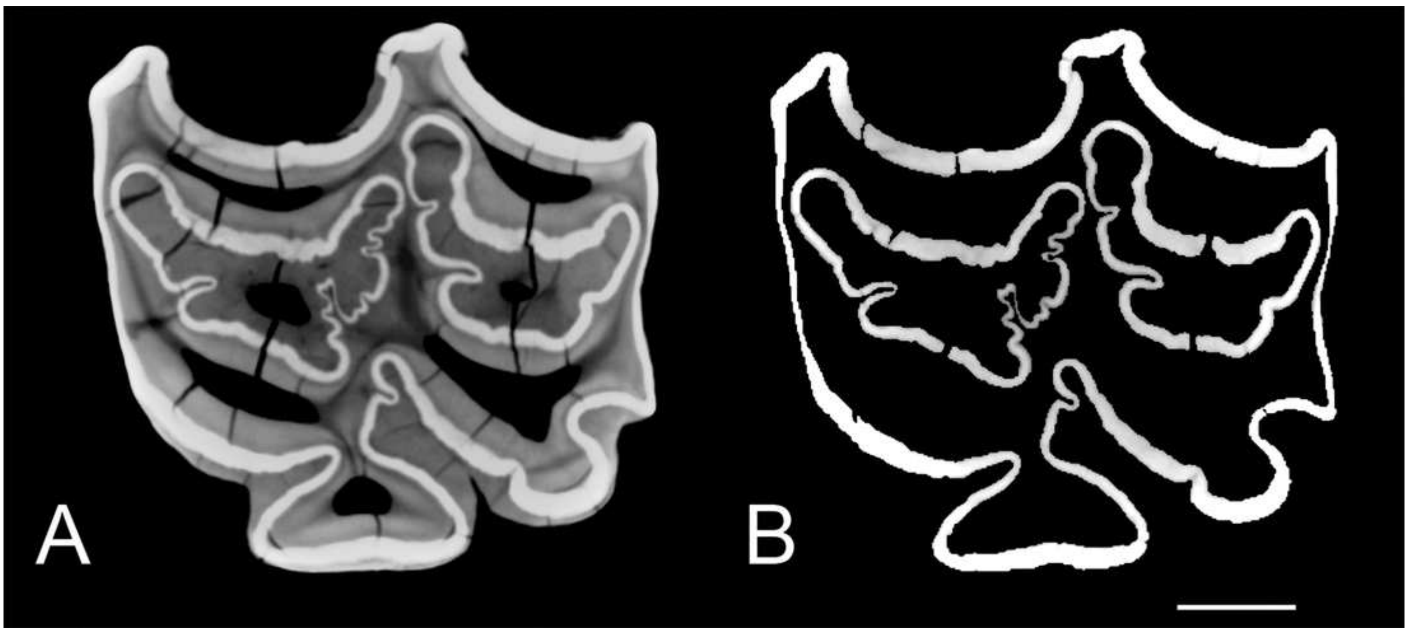
	Position of measurement	
txM1	**Outer enamel ridge [mm]**	**Inner enamel ridge [mm]**
Section 1 apical	12	10
Section 1 basal	11	10
Section 2 apical	11	13
Section 2 basal	14	13
Section 3 apical	14	11
Section 3 basal	13	10
Section 4 apical	15	11
Section 4 basal	16	-

1

Fig.1

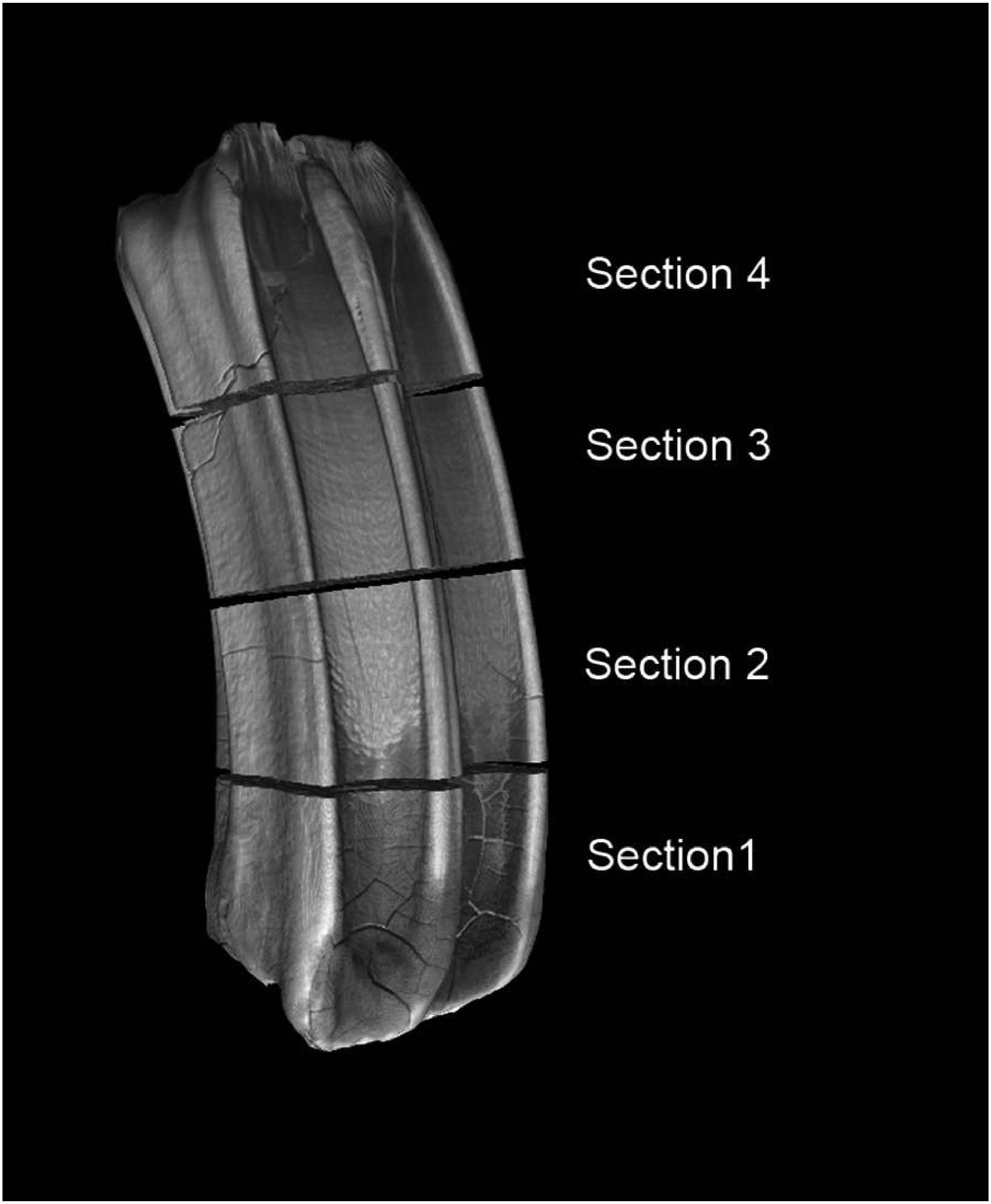
Fig.1.A. Cross section through a full virtual tooth model with all dental tissues. B. As Fig. 1.A., enamel only. Scale bar 50mm.



2

Fig.2

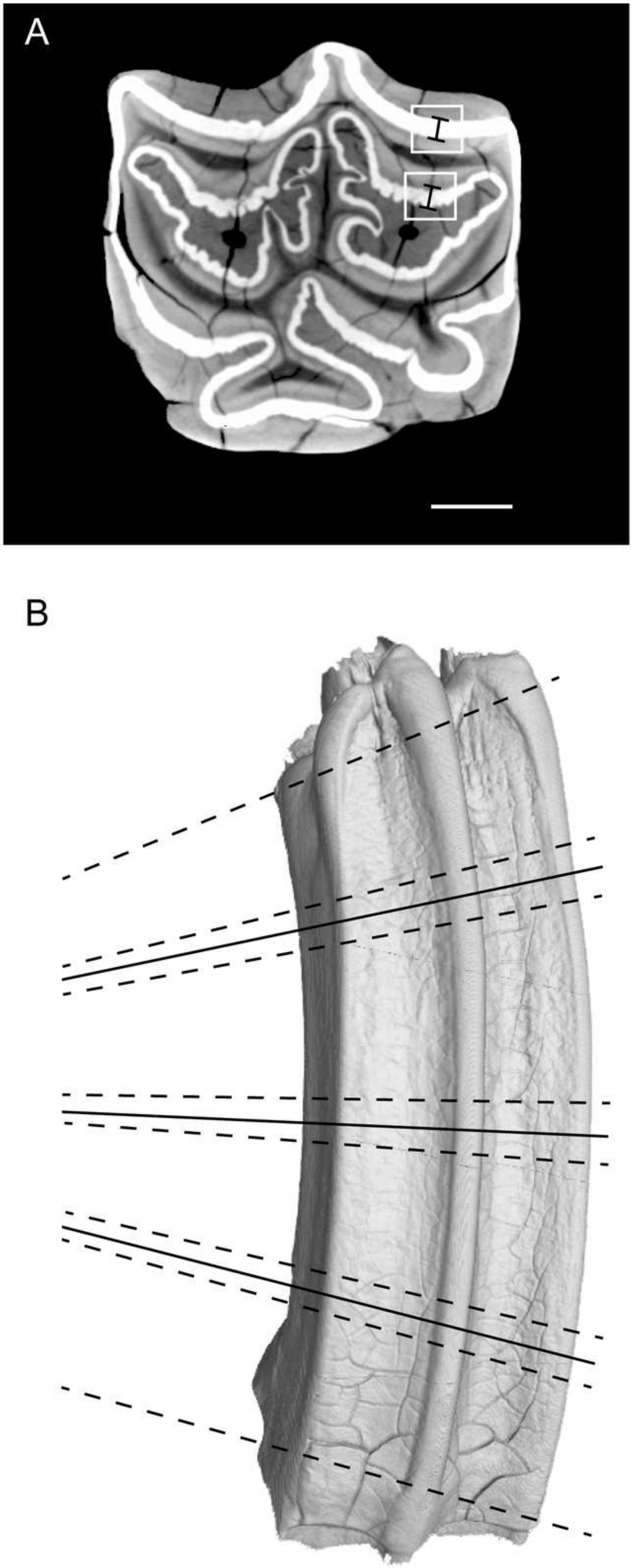
Fig.2. Virtual 3D-model of txP3 with all dental tissues. The tooth is separated in four sections, which are slightly separated from each other for better illustration.


Section 4
Section 3
Section 2
Section1

3

Fig. 3

Fig. 3.A. Cross section through the virtual model of txM1. Black bars indicate the approximate position where measurements of enamel thickness were taken on the outer and inner enamel ridge. Scale bar is 50mm. B. Dashed lines show approximate heights where thickness measurements were taken. Solid lines represent borders of each section. The tooth is in anatomically correct position with the top of the crown facing the bottom of the image. Hence, the lower dashed line within one section marks the positions referred to as “apical”, the upper dashed line as “basal” in Tab.1.


A
B

4

Fig.4

Fig.4. Enamel content per section and tooth position. Each bar represents 100% enamel content per tooth position and shows relative enamel content per section. Percentages above bars give the relative enamel content per tooth position.