Chapter 6

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HISTOLOGICAL STUDY OF AN UPPER INCISOR AND MOLAR OF A BONOBO (*PAN PANISCUS*) INDIVIDUAL

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Abstract

Work based on ground sections of teeth has provided accurate information on dental development in extant and extinct hominoid species. In contrast to radiographic studies, histological work is usually carried out using relatively small sample sizes. However, incremental lines in enamel and dentine enable us to interpret stages of crown formation and to establish patterns of dental development. Although these kinds of studies have been carried out in modern humans, common chimpanzees, gorillas, orangutans, gibbons as well as in some extinct hominoids, almost nothing is known about the bonobo (*Pan paniscus*). We present here some aspects of dental development of a young female with the I^1 crown just completed. Ground sections were obtained for right I^1 and M^1. The spacing between successive cross striations was measured in the outer, middle and inner portions of occlusal, lateral and cervical thirds of the enamel. Periodicity of striae of Retzius was obtained and the number of striae/perikymata was used to calculate the imbricational formation time. Prism length and the average distance between cross striations were used to determine the appositional formation time. Spacing between cross striations, similar to the situation in modern humans and great apes, shows a gradual increase from inner to outer portions and a decrease from cuspal to cervical region. It is noteworthy that average values in this *P. paniscus* individual appear to be high. Crown formation of the *P. paniscus* I^1 is short. The perikymata packing pattern in *P. paniscus* is also different from that of *G. gorilla* and *P. troglodytes* in that the number of perikymata increases towards the cervix.

Keywords: Striae of Retzius, appositional rate, perikymata, bonobo, *P. paniscus, P. troglodytes*

Running title: Dental development in bonobo

Introduction

Recent studies on the tooth histology of the common chimpanzee (*Pan troglodytes*) have provided useful data for comparing the variation of microstructural features expressed among the three great ape genera (Beynon *et al*.;1991a, Reid *et al*.; 1998, Smith 2004). Additionally, these studies have increased the reliability of data on dental development of *P. troglodytes*, elucidating some differences between histological and radiological methods (Reid *et al*.; 1998). As a result, a clearer picture has emerged that allows correlations between developmental time and cuspal function in molars (Reid *et al.*; 1998).

Most histological studies on great apes have focused attention on comparisons between genera (e.g. Beynon *et al.*; 1991a, b, Dean 1998). Little attention has been paid to understanding the variation among closely related species from a histological perspective. These studies are necessary for assessments of species differences in the fossil record.

The pygmy chimpanzee or bonobo (*Pan paniscus*) is distinguished from its closest relative the common chimpanzee (*P. troglodytes*) on the bases of social behavior, morphological and genetic differences (Johanson 1974; Shea 1984; Uchida 1992; Ruvolo 1994; Uchida 1996; White 1996; Braga 1998). Body size differences have been recorded between these taxa, *P. troglodytes* being slightly larger-bodied and showing more marked sexual dimorphism, even when the smallest of the *P. troglodytes* subspecies is considered (Jungers & Susman 1984; Shea 1984). There are some metrical and morphological differences in the dentitions of *P. paniscus* and *P. troglodytes* (Kinzey 1984; Uchida 1992). However, the greatest morphological differences appear to be the paedomorphic skull of *P. paniscus* (Shea 1983).

The aim of this research was to provide preliminary histological data on crown formation time, age at death, variation of appositional rates and perikymata packing

pattern for various tooth types of a young female *P. paniscus.* This information was then compared with data for the better known *P. troglodytes.* Although only one individual was available for this study, it marks the beginning of an investigation into intraspecific hominoid variation.

Materials and Methods

The specimen was a young female that was brought to a zoo in South Africa from the Democratic Republic of Congo and died before reaching maturity. It was buried within the zoo premises and has been recently exhumed due to re-structuring of the premises some four years after the death of the individual. The remains were donated to the Palaeontology Dept. at the University of the Witwatersrand.

Most of the post-cranial skeleton and part of the skull and face were preserved. The facial region consists of a right and left maxillary fragment with deciduous dc, dm^1, dm^2 and an erupting permanent M^1. The permanent I^1, I^2, C, P^3, P^4, crowns and one incomplete M^2 crown were encrypted in the maxilla. The roots of the first permanent molars were almost complete but lacked apical closure (stage 6 of Demirjian *et al.*; 1973). The protocone is the only cusp showing minimal wear. Crown formation had just been completed on the right I^1, where only a tiny fragment of root had developed. The crowns of the remaining teeth (I^2, C, P^3, and P^4) had not yet completed their formation.

The central right incisor and the first permanent right molar were removed from the specimen and embedded in cyano-acrylate. They were then sectioned (150 µm in thickness) along the mesial and distal cusps on the molar, and the incisor was cut labio-lingually. All sections were polished from both sides to a final thickness of about 100 µm. The sections were studied using polarized and transmitted light (Zeiss Universal Photomicroscope).

Daily appositional rate of ameloblasts corresponds to the cross striation repeat interval. The buccal face of the incisor and of the M^1 protocone was divided in three

equal parts (thirds), cuspal, central, and cervical (Figure 1). In each third, three regions of enamel were identified, outer, middle, and inner. In each region, distance between cross striations was measured several times and an average value for the cross striation repeat interval was obtained.

The arrangement of the striae allows the division of the enamel crown into two parts (Figure 2): cuspal or appositional enamel where the striae do not reach the enamel surface and involves successive layers of enamel, and lateral or imbricational enamel where the striae emerges at the tooth surface and forms perikymata (Beynon & Wood 1986, 1987; Dean 1987a; Risnes 1985). Crown formation time (CFT) is thus the sum of both cuspal and lateral formation time. Cuspal formation time was calculated as follows: First, the tip of the protocone cusp of the right M^1 was reconstructed and the first lateral stria estimated (Figure 3). Second, the length of a prism running from the dentine horn to the estimated first lateral stria was measured. Close to the dentine horn, prisms' course undulate whereas in the outer part of the enamel, prisms run straight; thus prisms course can be followed in an accurately manner on the reconstructed region of the protocone. Prism length was then divided by the mean of cross striation repeat interval in outer, middle and inner regions of the cuspal third of the enamel, giving an approximate value of cuspal formation time. The same method was used to obtain the cuspal formation time on the right I^1. Lateral formation time was obtained in both teeth by direct counts of striae which were then multiplied by the cross striation periodicity, which is the number of cross striations between striae.

We identified the neonatal line on the paracone of the M^1 (Figure 4). This marked stria corresponds to the moment of birth. The length of a prism running between the neonatal line and one imbricational stria was followed and the formation time determined in the same way that the cuspal formation time.

Marked striae of Retzius were identified on the four cusps of the M^1, and these lines were also observed on the I^1 (Figure 5). These marked striae enable to reconstruct dental formation from the M^1 to the I^1. It is worth noting that the death of the individual occurred when crown formation of I^1 had just completed and no root had developed. Therefore, the age at death of the individual was obtained by summing the formation time of the prism to the number of imbricational striae (in the paracone first and later in the incisor) multiplied by periodicity.

For each cusp, the crown was divided into ten equal zones or deciles, where counts of lateral striae were made to assess the perikymata packing pattern along the outer surface of the enamel (Figure 6).

Results

Tables 1 and 2 show the appositional rates in the incisor and molar protocone of the *P. paniscus* and other hominoid taxa (Figures 7, 8, and 9).

The length of prisms in the cuspal enamel of I^1 was 848 microns and in the protocone of the M^1 was estimated to be 830 microns. When these values are divided by appositional rates corresponding to the three regions of the cuspal third of the enamel (Tables 1 & 2), a cuspal formation time of 0.41 and 0.45 years respectively was obtained (Table 3). The incisor and the first molar were used to obtain striae periodicity. Periodicity could not be precisely determined for this individual. Although the most likely periodicity is 8 days, given the uncertainty in determining the exact value, CFT was calculated assuming a 7 and 9 day intervals, which, given our observations, appeared to be the lowest and highest possible values. Lateral enamel striae counts and crown formation times are shown in Table 3.

Accentuated lines in dentine and enamel allow the reconstruction of the timing of developmental events by comparing the chronology of these events in different cusps of the same tooth, and across tooth types of the same individual (Boyde 1964, 1990). Two

accentuated lines labeled A and B were identified in the four cusps of the M^1 and in the I^1 (Figure 5). These can be easily matched from one cusp to another and they are associated with marked lines in the dentine which cross the crown.

Lines A and B correspond to the 8th and 10th lateral stria (counting from cusp to cervix) in the protocone and to the 18th and 20th lateral striae in the paracone. Line A is about the 12th-13th lateral striae in the metacone and is cuspal in the hypocone, line B corresponding to the first lateral stria in this last cusp. Comparisons between the positions of lines A and B on the lateral enamel suggests that this part of the crown was more developmentally advanced in the paracone than in the protocone. The imbricational part of the hypocone is the last to be formed.

Lines A and B were also observed in cuspal enamel of the central incisor. Line B was formed at 0.25 years in the incisor whereas it appears at 0.62-0.67 years in the protocone. In the paracone, the prism length between the neonatal line and the first lateral striae is 697 microns. Cross striation repeat interval measured in the cuspal third of the paracone show similar values to those obtained in the protocone. Thus, average cross striation repeat interval of the protocone were used to calculate period of prism formation. The first lateral stria in the paracone was formed 129 days (0.35 years) after the neonatal line. Line B corresponds to the 20th imbricational stria in the paracone, thus assuming a 8 day periodicity, line B was formed at 0.79 years (0.35 yrs + 20 x 8). In the I^1, the cuspal enamel formed after 0.16 years of line B. The lateral enamel of I^1 was formed in 3.77 years. Therefore, this individual died approximately at the age of 4.72 years (0.79 yrs + 0.16 yrs + 3.77 yrs).

The perikymata packing patterns follows the same outline in all teeth studied of this individual, with the number of perikymata increasing while the space between perikymata decreases towards the cervix (Figure 10, Table 4).

Discussion

Results presented in this work are preliminary as they are based on only one individual. The cross striation appositional rates measured in the incisor and molar of the *P. paniscus* individual studied here are higher than values observed in *P. troglodytes* (Beynon *et al.*; 1991b, Reid *et al*.; 1998; Smith 2004). Reid *et al*.; (1998) and Smith (2004) showed values for each tooth type (1^{st}, 2^{nd} or 3^{rd} molar) while Beynon *et al.*; (1991a) averaged values for molars. In general, the values for this *P. paniscus* individual are among the highest in great apes for both tooth types (Tables 1, 2, Figures 7, 8, 9). Differences between our values and those presented by Reid *et al*.; (1998) and Smith (2004) could be the result of using different measurement schemes Indeed, appositional rates in *P. paniscus* for inner, middle, and outer areas shown here represent average values of measurements taken across the whole area of each third (Figure 1C); in other words, average values do not result from measurements along an imaginary line crossing a particular area of the enamel, as it has been the case in previous studies (Figure 1 B) (Beynon *et al*.; 1991b, Reid *et al*.; 1998). However, it is worth noting that high values, even higher than those reported here for *P. paniscus* were observed in some *P. troglodytes* teeth. For example, Dean (1998) measured daily increments following prisms from the EDJ to the outer enamel to obtain cuspal crown formation; it means that daily increments correspond exactly to the appositional rate in cuspal enamel of other works (Beynon *et al*.; 1991b, Reid *et al*.; 1998). In the outer cuspal enamel of this *P. troglodyte* individual, appositional rates were 6.5 microns and higher (Dean 1998, Figure 2). Therefore, the use of different methods could in part explain the differences in appositional rates among the great apes shown in Tables 1 and 2, but it may also be due to intraspecific variation.

Reid *et al*.; (1998) have reported that crown initiation in upper first incisors of *P. troglodytes* starts at 0.21-0.26 years and M^1 at 0.15 years before birth (-0.15). The same

relationship between I^1 and M^1 crown formation is found in *P. paniscus* where crown formation in M^1 is advanced by about 0.4 years with regard to the I^1. The two most recent studies on the histology of *P. troglodytes* in which the same specimens were analyzed, reported different periodicities (Reid *et al*.; 1998; Smith 2004). The first study reported values of 7 and 8 for four individuals and included all tooth types, while Smith (2004) reported 6 and 7 as the most common values in molars only (n = 75). If the values of Reid and co-workers are correct, an intriguing pattern emerges when molar and incisor crown formation times in the *P. paniscus* specimen are compared to data on *P. troglodytes* (Reid *et al*.; 1998). Molar crown formation is similar or slightly less in *P. paniscus* (depending on the periodicity used), whereas incisor crown formation is not, being 20%-37% shorter in the former depending on striae periodicity. However, Smith (2004) reported lower periodicities which in the case of the specimen 88/89 were 7 instead of 8. Therefore, if this value is correct, given the number of lateral striae on the I^1 reported by Reid *et al*.; (1998) on that specimen (mean of left and right I^1 is 218 striae), then the differences between both specimens are less marked in molar/incisor comparisons (only about 10%). The lowest value of lateral striae counts reported by Smith (2004) on anterior cusps of M^1 was 91 (n=2) and similar values were obtained by Reid *et al*.; (1998), only slightly higher than the values reported here for *P. paniscus*. Dean and Reid (2001) did not report values of perikymata or striae counts in their sample of *P. troglodytes* (n = 11). However, extrapolating information from their Figure 1, it appears that when a larger sample of *P. troglodytes* I^1 is considered, the *P. paniscus* specimen studied here falls markedly below the mean values of I^1 in *P. troglodytes*.

The different positions of lines A and B in the molar cusps reflect differences in the onset of enamel formation. Kronfeld (1954) has suggested that in modern humans the sequence of cusp formation in upper molars is paracone, protocone, metacone, and hypocone. Thus it would be expected to find lines A and B situated in a more cuspal

position in the metacone than in the protocone. However, the position of these lines in the metacone is more cervical than in the protocone. The lack of knowledge about appositional formation in each cusp does not allow inferring accurately the sequence of cusp formation in the right M^1, but it is not possible to confirm at moment the same sequence of cusp formation in *P. paniscus* than in modern humans

The perikymata packing pattern in *P. paniscus* is different from that in *G. gorilla* and *P. troglodytes* shown in Dean and Reid (2001). In the anterior teeth of *G. gorilla* and *P. troglodytes*, the number of perikymata increases towards the second third of the crown and from about the 7^{th} division, perikymata markedly decrease in number towards the cervix. In contrast, the number of perikymata in *P. paniscus* increases towards the cervix, where the highest number of perikymata is found (Figure 11). It is noteworthy that the number of perikymata decrease slightly from the 8^{th} to the 9^{th} decile in the *P. paniscus* teeth studied here. Different perikymata packing patterns do not always reflect differences in the extension rate of the enamel (Ramirez Rozzi in prep). Indeed, variation in the number of perikymata in each decile does not seem to reflect changes in the extension rate. However, when perikymata spacing is considered in the 1^{st}, 5^{th}, and 10th decile the general pattern of perikymata spacing reflects the variation reported for the extension rate of the enamel (Ramirez Rozzi in prep). *P. paniscus* shows a pattern different from that in *G. gorilla* and *P. troglodytes*. When the 1^{st}, 5^{th}, and 10^{th} deciles are considered, the pattern is always different between *P. paniscus* and African great apes suggesting differences in the variation of the extension rate of the enamel between them. The perikymata packing pattern observed in *P. paniscus* is similar to extant and extinct *Homo* and australopiths (e.g. Dean & Reid 2001). The number of perikymata increases towards the cervix and the space between them reduces.

Conclusion

We have presented some preliminary results on dental growth of *P. paniscus* based on a single individual. These results need to be confirmed using larger sample sizes. Although there maybe some differences in methodology between our study and others, it appear that the *P. paniscus* individual studied here shows high appositional rates. Molar crown formation is similar or slightly shorter than values reported for *P. troglodytes* depending on the periodicity used. Incisor formation of the *P. paniscus* studied here appears to be shorter than *P. troglodytes* regardless of the periodicity obtained in the studies of Reid *et al.*; (1998) and Smith (2004). Differently to other African great apes, *P. paniscus* presents a perikymata packing pattern characterized by an increase in the number of perikymata towards the cervix.

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Figure captions

Figure 1: Divisions of the lateral crown faces. A: Beynon et al*.; (1991, Fig. 2) proposed the division of the crown into occlusal, lateral and cervical areas. In the occlusal area , striae of Retzius do not reach the enamel surface. The lateral part is formed by the lateral striae in the upper half of the crown whereas the lateral striae in the lower half form the cervical region. B: Following these divisions, the appositional rate was measured in previous works in three limited area for inner (I), middle (M), and outer (O) enamel. C: In the present work, the lateral crown face was divided in three equal thirds (cuspal, central, and cervical) where three regions are distinguished, outer, middle, and inner. Average appositional rate is given for each of these regions in each third.*

Figure 2: two parts

Figure 3: M^1, protocone. The protocone shows very minimal wear on the cusp tip. It is the only cusp showing signs of wear. The number of perikymata STRIAE around the cusp tip is very low and thus it is easy to estimate the number of perikymata/STRIAE lacking due to wear. In our case, we know the stria's course which does even more easily an accurate estimation of the number of striae affected by wear and even to reconstruct the few microns worn on the cusp tip. The reconstruction of the original cusp can be done by following the buccal and the occlusal enamel surface. The first striae to reach the enamel surface (first imbricational stria) can be thus identified.

Figure 4: M^1, paracone cusp. Close to the apparent dentine horn and near the enamel dentine junction (EDJ), the distance between 5 cross striations is 19 microns, the cross striation repeat interval measures thus 3.8 microns. The neonatal line is easily observable. X indicates the possible first imbricational stria. The prism's course from the neonatal line to the first imbricational stria was followed and measured to calculate number of days and deduce the cuspal formation time after birth in order to obtain the age at death. It maybe possible

that our identification of the first imbricational stria in the paracone may not be completely accurate. However, this has very little effect on estimations of the age at death because the crown formation time was followed from neonatal line till lines A and B, and from there to the end of formation of the upper first incisor, the time at which the animal died.

Figure 5: Section of four cusps of the M^1 and of the I^1 showing marked striae of Retzius labelled as A and B. These marked striae of Retzius correspond to accentuated lines in dentine which run through dentine from one cusp to the other. The matching of lines A and B in M^1 and in I^1 enables to reconstruct dental formation from one tooth to the other and since individuals died at the time when I^1 crown formation had finished, the age at death can been obtained. X indicates the contact between the first imbricational stria and the enamel surface in each cusp.

Figure 6: Perikymata packing pattern. A measure of the buccal enamel height was taken using a vernier micrometer eye-piece connected to a digital ocular measure linked, in turn, to a calculator-meter-printer RZD-DO (Leica). Buccal enamel height was divided into 10 equal divisions (deciles) from the first formed enamel at the cusp to the last formed at the cervix (Dean and Reid, 2001). Perikymata (Pk) counts were made in each of the divisions of the crown height.

Figure 7: I^1, buccal face, decile 6th close to the enamel surface (ES). Only some few cross striations (white arrows) are indicated but they can be seen throughout this image as well as striae of Retzius (black arrows). Seven cross striation were marked which measured 38 microns, thus average distance between cross striations is equal to 5.43 microns. The distance between two adjacent striae of Retzius along the prism axis (white dots) is equal to 96 microns. If we assume a periodicity of 8 cross striations between striae, the average distance between cross striations is 6 microns; if a periodicity of 9 is assumed, the mean distance between cross striations would be 5.33 microns. The lower average value for the outer lateral third presented in table 3 results for a reduction of the distance between cross striations towards the EDJ and the cervix

(see Dean 1998). Cervix is upper right. Although average values presented in this work are difficult to compare with appositional rates measured in a very limited area of the enamel from other studies (Beynon *et al*.; 1991, Reid *et al*.; 1998), values for the 6th decile closely correspond to the lateral enamel values from previous studies. The appositional rate in *P. paniscus* is higher than those reported for *P. troglodytes*, even when a periodicity of 9 is assumed.

Figure 8: M^1, protocone. The first imbricational stria is indicated with an X (see figure 5). Cross striations are seen in the cuspal enamel. One group of 6 cross striations and another of 4 cross striations are shown in the detailed picture. In the main picture only the limits of each group are identified. The distance measured for 6 cross striations is 32 microns, indicating a cross striation repeat interval of 5.33 microns. The distance measured for 4 cross striations closer to the enamel surface is 25 microns, equivalent to 6.25 microns for each cross striations. Prism width measured from 10 prisms corresponds to 5.3 and 5.5 microns respectively.

Figure 9: M^1, protocone, buccal face, 8th decile. Striae of Retzius (black arrows) are visible next to the enamel surface. Seven cross striations are marked (white arrows), the total distance is 34 microns, indicating that the average distance between them is 4.86 microns. The distance between three striae of Retzius along prism's axis (white dots on the left) measures 100 microns. If we assume a periodicity of 8, the average distance between cross striations corresponds to 4.17 microns.

Figure 10: Perikymata packing pattern in the molar and incisor of P. paniscus *studied here. The number of perikymata (N°Pk) increases towards the cervix.*

Figure 11: Left plot shows the perikymata packing pattern in the I^1 of *P. paniscus* compared with that in anterior teeth in *P. troglodytes* and *G. gorilla*. The pattern in *P. paniscus* is different than in other great apes, with the highest number of perikymata found in the last decile. The diagram on the right represents imbricational formation time (days) and it is clearly noticeable the shorter time of CFT in *P. paniscus*, even when a 9-day periodicity is considered as it was the case in this figure. However, the higher values in *P. troglodytes* and *G. gorilla* can result to plot all types on anterior teeth altogether. Modified after Dean and Reid (2001).

Figure 1.

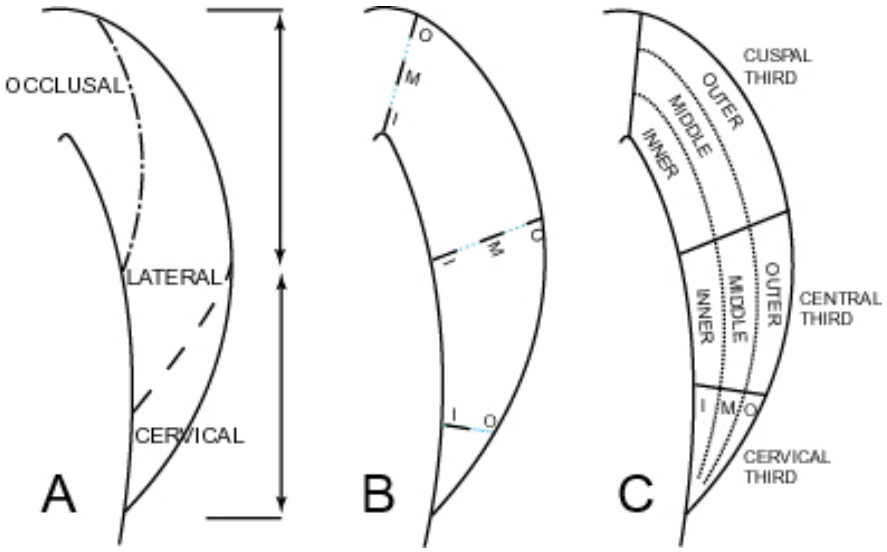


Figure 2.

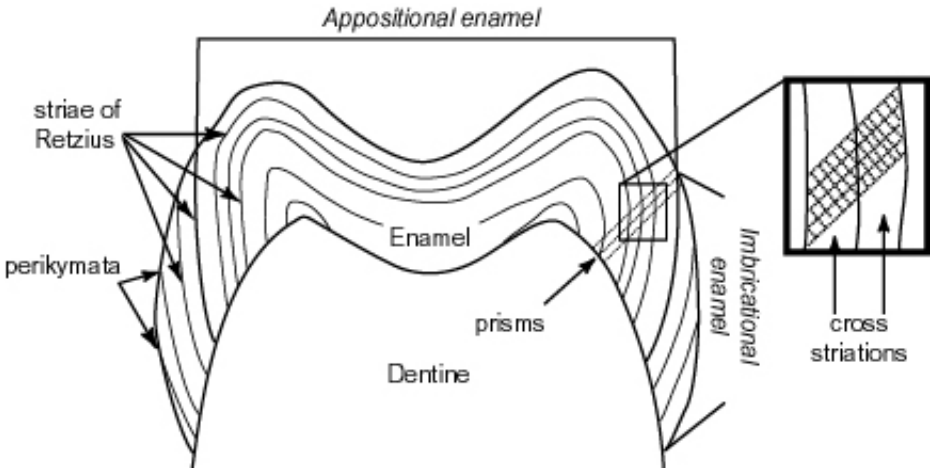


Figure 3.

Figure 4.

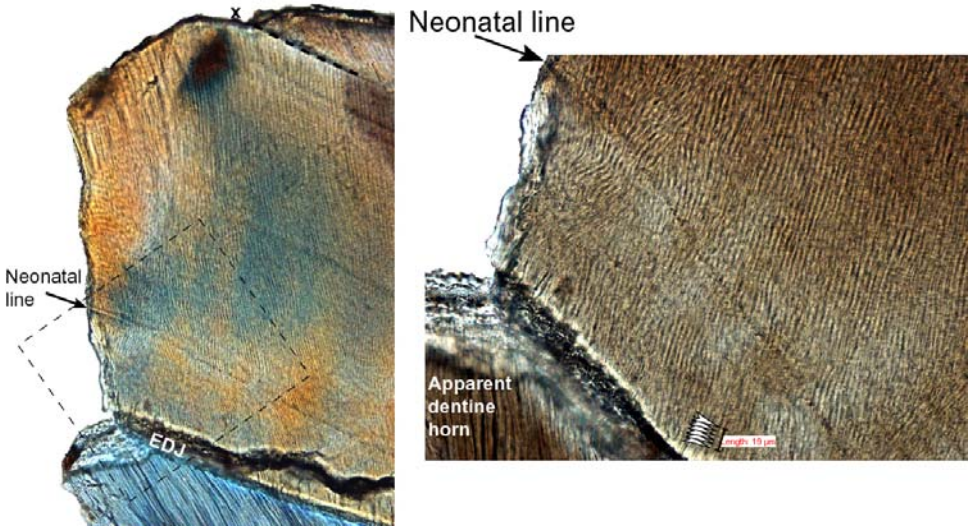


Figure 5.

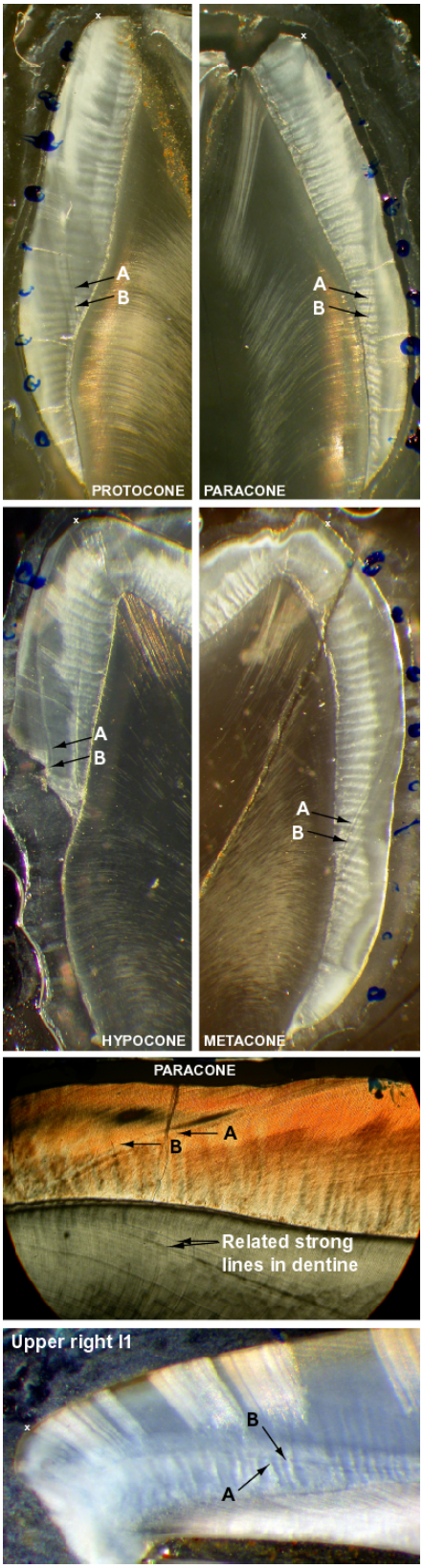

A
B
PROTOCONE
A
B
PARACONE
A
B
HYPOCONE
A
B
METACONE
PARACONE
A
B
Related strong
lines in dentine
Upper right I1
B
A

Figure 6.

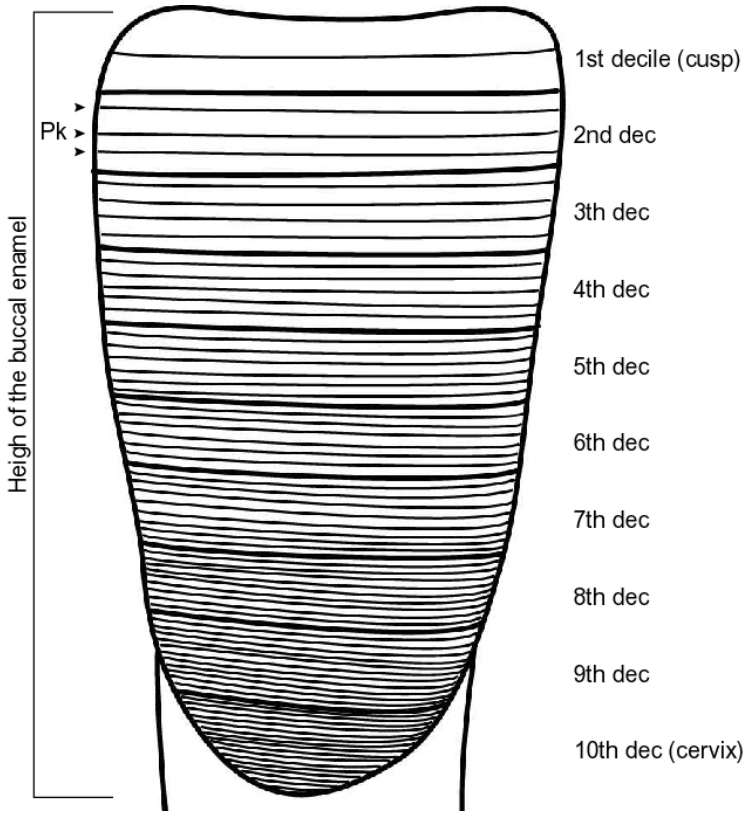
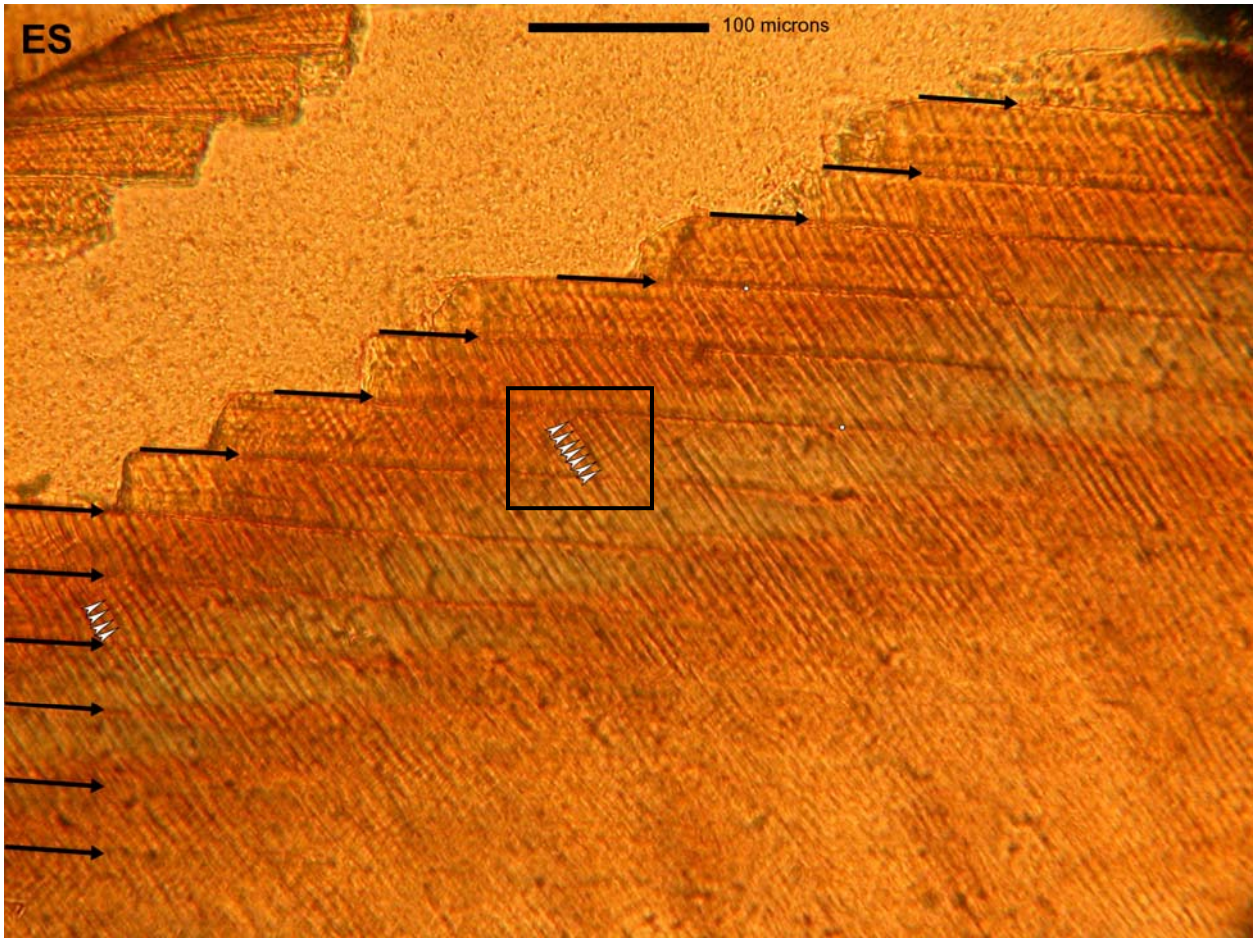

Heigh of the buccal enamel
Pk
1st decile (cusp)
2nd dec
3th dec
4th dec
5th dec
6th dec
7th dec
8th dec
9th dec
10th dec (cervix)

Figure 7.



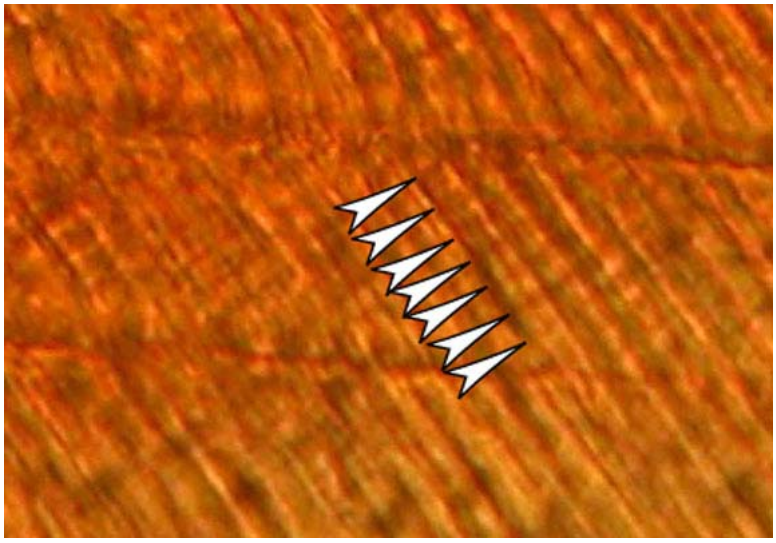


Figure 8

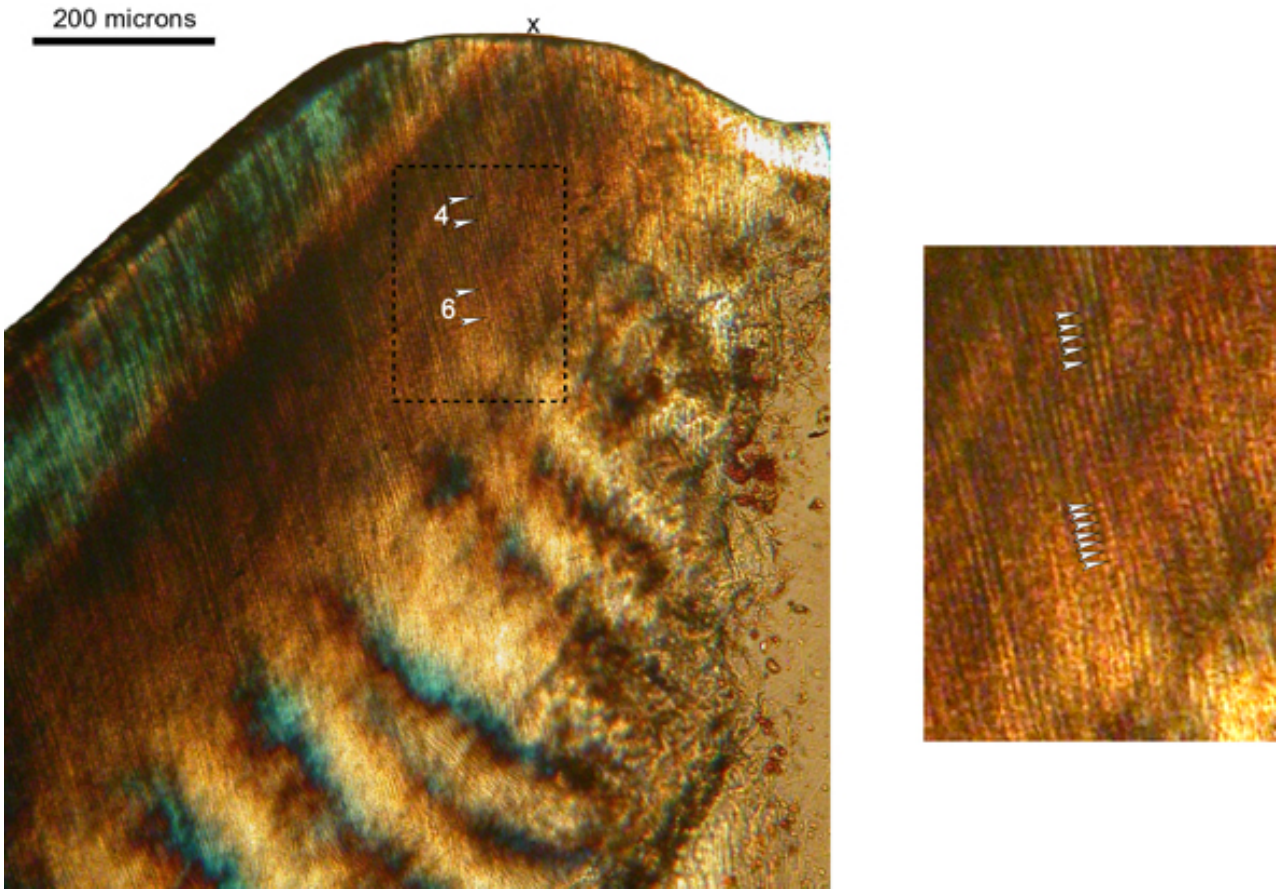


Figure 9

Figure 10

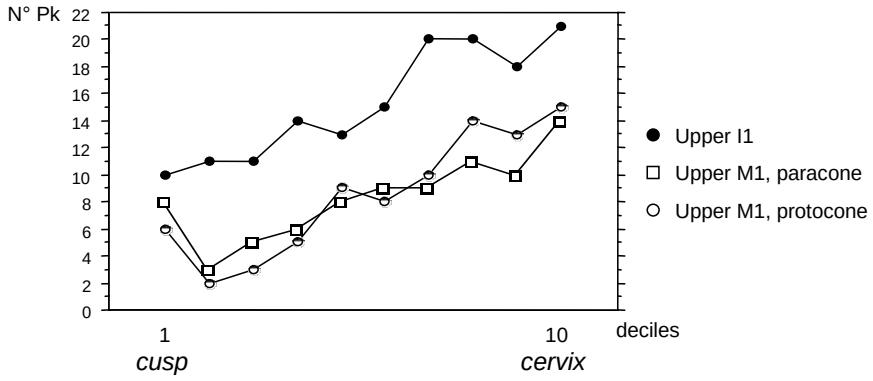

N° Pk
22
20
18
16
14
12
10
8
6
4
2
0
1
cusp
10
cervix
deciles
Upper I1
Upper M1, paracone
Upper M1, protocone

Figure 11

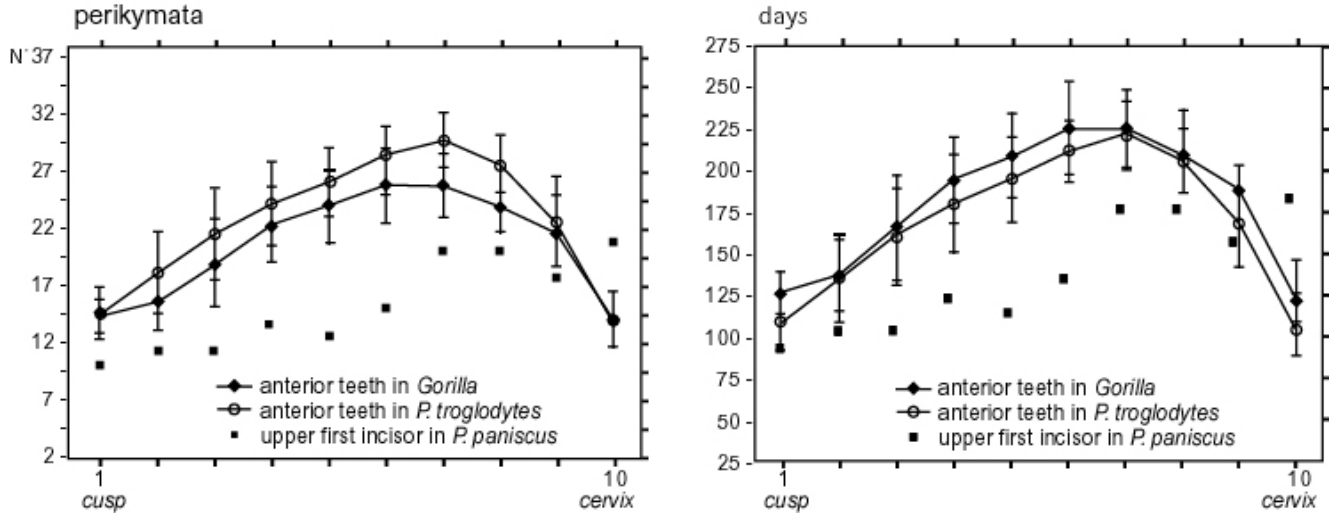

perikymata
N˚37
32
27
22
17
12
7
2
1
10
cusp
cervix
anterior teeth in Gorilla
anterior teeth in P. troglodytes
upper first incisor in P. paniscus
days
275
250
225
200
175
150
125
100
75
50
25
1
10
cusp
cervix
anterior teeth in Gorilla
anterior teeth in P. troglodytes
upper first incisor in P. paniscus

Table 1: Appositional rates in I^1 in microns

	Cuspal			Lateral			Cervical		
	outer	*middle*	*inner*	*outer*	*middle*	*inner*	*outer*	*middle*	*inner*
*P. troglodytes**	4.9	4.5	3.5	4.6	4.1	3.5	3.5		3.0
P. paniscus	5.8	5.9	5.1	5.1	5.6		4.9	4.6	4.0

* From Beynon et al. (1991b).

Table 2: Appositional rates in molars in microns

	Cuspal			Lateral			Cervical		
	outer	*middle*	*inner*	*outer*	*middle*	*inner*	*outer*	*middle*	*inner*
H. sapiens†	5.1	4.3	2.7	5.0	4.0	2.6	2.8		2.3
P. troglodytes†	5.0	4.4	3.1	4.1	4.1	3.1	3.8		2.8
*P. troglodytes**	4.8	4.0	3.5	4.8	4.4	3.3	3.2		2.9
P. troglodytes°	4.6	4.3	3.6						
Gorilla†	6.1	5.2	3.2	6.1	4.9	3.3	4.4		3.2
Pongo†	5.3	4.7	3.3	5.1	4.0	3.4	3.7		2.9
P. paniscus	6.2	5.7	4.4	5.2	5.3	4.8	4.6	4.4	3.9

† From Beynon *et al.* 1991b. * From Reid *et al*. 1998. ° From Smith 2004.

Table 3: Crown formation time

Pan paniscus	ImbSr	CH	IFT (7)	IFT (8)	IFT (9)	AppFT	CFT (7)(8)(9)
I^1	153	1221	2.9	3.35	3.78	0.41	3.34/3.76/ 4.18
M^1 protocone	85	624	1.63	1.86	2.09	0.45	2.08/2.31/ 2.54
M^1 paracone	83	549	1.59	1.81	2.0		
Pan troglodytes							T-CFT
Mean I1*	218	1410					4.18
Mean M^1 proto (N=2) †	99	650				0.32	2.30§
Mean M^1 para (N=2) †	113	625				0.4	2.49§

ImbSr: number of imbricational striae, CH: crown height in microns, IFT: imbricational formation time calculated with 7-8 and 9-day periodicity in years, AppFT: cuspal or appositional formation time in years, CFT: crown formation time in years. * From Reid *et al*. (1998). CFT for this specimen (88/89) was re-calculated using a periodicity of 7 instead of 8 as originally proposed by Reid *et al*., (1998). † Smith (2004). § Average cusp CFT reported in Smith (2004: Table 5.10).

Table 4: Perikymata packing pattern in *P. paniscus*

	deciles									
	1 (cuspal)	***2***	***3***	***4***	***5***	***6***	***7***	***8***	***9***	***10 (cervix)***
I^1	10	11	11	14	13	15	20	20	18	21
M^1 paracone	8	3	5	6	8	9	9	11	10	14
M^1 protocone	6	2	3	5	9	8	10	14	13	15