Chapter 11

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ENAMEL MICROSTRUCTURE OF THE HOMINID KB 5223 FROM KROMDRAAI, SOUTH AFRICA

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ABSTRACT

The Plio-Pleistocene site of Kromdraai, South Africa, is well known for the recovery of the holotype of *Paranthropus robustus*, one of nine individual hominids recovered from this site to date. Among the Kromdraai sample, the specimen KB 5223 comprises several isolated deciduous and permanent lower teeth assigned to Paranthropus, the only recognized genus at this site. However, a more recent analysis of this specimen suggested that it should be classified as *Homo*. The lower right first permanent molar of KB 5223 had been previously sectioned along the tips of the mesial cusps, exposing its enamel microstructure. Previous studies had indicated differences between Homo and Paranthropus at the microstructural level. A portable confocal scanning microscope was used to describe details of the enamel microstructure of the M_1 and I_1 of this specimen. Angles formed between the striae of Retzius and the enamel dentine junction (EDJ), daily secretion rates in cuspal enamel of the protoconid and metaconid and crown formation time of the RM₁ are provided. The number of perikymata on the right I_1 was counted. Results indicate that some features recorded in the KB 5223 molar differ from those of *Paranthropus*. However, the number of perikymata on the I_1 is lower than values so far reported for early Homo but similar to Paranthropus. Crown formation time of KB 5223 M_1 was markedly lower than mean values of M_1 in *H. sapiens* but similar to other early hominids. Daily secretion rates in the cuspal enamel of KB 5223 M_1 were higher than in modern humans.

INTRODUCTION

The Kromdraai hominid site is located some 1.5 km east of the Sterkfontein cave and has yielded 27 hominid specimens representing a minimum of nine individuals (Thackeray *et al.*; 2001), including the holotype of *Paranthropus robustus* (TM 1517) (Broom 1938). Among the Kromdraai sample, the specimen KB 5223/4 consists of several isolated permanent and deciduous teeth all representing a single juvenile individual. Both the holotype and KB 5223/4 derive from Member 3 of the Kromdraai B Formation (Grine 1982). Until recently, only a single taxon, *P. robustus*, had been recognized from this site. However, in a more recent analysis of the lower dentition of KB 5223 (Braga & Thackeray 2003), it was suggested that this specimen belongs to the genus *Homo*. Thus, Kromdraai would become the third Plio-Pleistocene South African site with Swartkrans (e.g. Brain 1993) and Drimolen (Keyser *et al.*; 2000) where *Paranthropus* and *Homo* appear to be contemporaneous. The age of Kromdraai B has been estimated to be about 1.9 my (Thackeray *et al.*; 2002), which is within the age range for the presence of *Homo* in Southern Africa (Hughes & Tobias 1977; Kuman & Clarke 2000).

It is noteworthy that some authors found differences between the *Paranthropus* specimens from the better known site of Swartkrans, and those recovered from Kromdraai (Broom 1950; Howell 1978; Grine 1981, 1982). It is also fortuitous that part of the information provided by Grine and Martin (1988) in support of the differences between the Swartkrans and Kromdraai hominids included the analysis of some aspects of the enamel microstructure of the Kromdraai specimen KB 5223 (RM₁). This is the same specimen that the recent study of Braga and Thackeray (2003) used to suggest the presence of *Homo* at this site.

Most studies on enamel microstructure of fossil hominids are based on the analysis of samples derived from East African sites, and little information is available for

South African fossils. These works on the East African material have indicated that early hominid molars formed in less time than those of modern humans (Beynon & Wood 1987; Ramirez Rozzi 1993). To test this hypothesis and to further investigate enamel development in South African fossil hominids, the enamel microstructure of the Kromdraai specimen KB 5223 was analyzed using newly developed non-invasive portable confocal microscopy (Bromage *et al.*; 2003, 2005, in press).

BACKGROUND TO THE STUDY

Teeth probably best represent the natural history of species (Jernvall 1995) and therefore it is not surprising that in the hominid fossil record, teeth commonly form the basis to interpret adaptation, development and taxonomy. Tooth enamel preserves in its microstructure, mineralized records of its development which allow for assessments of rates of growth (Boyde 1964). In addition, enamel microstructural features enable us to make inferences about aspects of life history in extant and extinct taxa (Bromage & Dean 1985; Beynon & Dean 1988; Dean et al.; 2001; Macho 2001; Kelley & Smith 2003; Kuykendall 2003). Two structural markers in enamel, cross striations and striae of Retzius, are commonly used in such studies (Boyde 1989). The latter form troughs at the lateral enamel surface known as perikymata. Cross striations represent the daily linear secretion rates of enamel by specific cells known as ameloblasts (Boyde 1964; Bromage 1991), and can be identified as lines running perpendicular to the cell's main secretory path. Striae of Retzius represent the position of the enamel forming front as it moves from the enamel dentine junction (EDJ) to the outer enamel surface (OES) (Shellis 1984). The number of cross striations between striae, or periodicity, indicates the number of days between striae or perikymata, which is an important feature in assessments of crown formation time (Reid & Ferrell 2006). In modern humans, periodicities range between 6 and 12 days (Reid & Dean 2006), with a mean value of 9

days (Dean & Reid 2001). In the chimpanzee, the range is 6 to 8 (Reid *et al.*; 1998; Smith 2004) with a mean value of 7 days (Smith 2004). In fossil hominids, Dean (1987) and Beynon and Dean (1987) reported a periodicity of 7 cross striations in a premolar and a molar of *P. boisei*, Dean *et al.*; (1993a) reported 9 days in a canine of *P. robustus*. More recently, Bromage *et al.*; (in press) and Lacruz *et al.*; (2006) provided periodicities for 14 teeth attributed to *Australopithecus africanus* and *P. robustus*, which ranged between 6 and 9 days in *A. africanus* and 6-8 days in *P. robustus*.

It is generally accepted that the angles of intersection between the striae and the EDJ are informative about the rate of ameloblast differentiation along the EDJ as the growth of the crown proceeds in the cervical direction (Boyde 1964; Shellis 1984). Several studies have been carried out using these enamel markers to interpret variation in fossil hominids. In general, it has been shown that *Paranthropus* taxa have low angle values of striae/EDJ (Beynon & Wood 1986; Ramirez Rozzi 1993, 2002, Lacruz *et al.*; 2006), lower than values reported for *Homo* (Beynon & Wood 1986; Ramirez Rozzi *et al.*; 1997) and *A. africanus* (Bromage *et al.*; in press; Lacruz *et al.*; 2006). The values in the cervical aspect of the crown tend to show more clearly differences on the striae/EDJ angles between taxa (Ramirez Rozzi 2002; Lacruz *et al.*; 2006). Additionally, daily secretion rates are greater in *Paranthropus* than in *Homo* (Beynon & Wood 1986; Lacruz & Bromage 2006).

To further investigate the enamel microstructure of KB 5223, perikymata counts were made on the I_1 , and measurements of the angles striae/EDJ, cuspal daily rates, and crown formation time is provided for the M_1 . This information is compared with data on other early hominids and modern humans.

MATERIALS AND METHODS

The operating principles of the PCSOM, summarized here but described in detail in Bromage *et al.*; (2003, 2005, in press), are based on the Nipkow disk technique which, in this case, employs a confocal module configured to a custom stand. This arrangement facilitates vertical height adjustments suitable for all imaging needs. Image acquisition for the PCSOM is performed with a high resolution 12 bit monochrome camera. Images are transferred in real-time to a laptop computer and are then imported into software that montages in-focus image content through Z- series. The microscope returns image detail from a very thin optical plane at and immediately below the object surface (1-50 micrometers, depending upon specimen characteristics). A range of lenses (5x, 10x, 20x and 50x) and adapters (0.5; 1:1) provide width of fields from 190 microns to about 3.65 mm. The images reported here are confocal circularly polarized light images of enamel microstructure.

One of the molars of KB 5223 was originally sectioned along the apices of the mesial cusps in Grine and Martin's (1988) study of enamel thickness and development in hominids (Figure 1). The specimen does not preserve roots and the dentinal area is missing as a result of diagenesis. The loss of dentine hampers the study of certain aspects of the microstructure and enamel thickness as the contour of the EDJ is irregular (Grine & Martin 1988). In places, the most cervical aspect of the enamel crown is also missing.

The specimen, which had been re-fitted after Grine and Martin's (1988) study, was carefully prepared by separating the mesial from distal blocks which were cleaned with acetone. The exposed faces were subsequently immersed in ethanol and imaged at a magnification of 25x using a stereoscopic microscope following protocols detailed in Beynon and Wood (1986). Striae/EDJ angles were measured on the metaconid using this magnification at the cervical third of the EDJ, which showed regular contours. The

values obtained were then compared to values reported for *Homo* (Beynon & Wood 1986; Ramirez Rozzi *et al.*; 1997); *A. africanus* (Bromage *et al.*; 2005; Lacruz *et al.*; 2006) and *Paranthropus* (Ramirez Rozzi 1993, 2002; Lacruz *et al.*; 2006). Daily secretion rates were measured on the cuspal area of the protoconid and metaconid using the PCSOM at a magnification of 50x. The average secretion rates were calculated by measuring the length of groups of 3 to 5 cross striations, which was then divided by the number of cross striations in each group, and this process was repeated in as many places as possible within each field of view. Using the 50x lens and 1:1 adapter, and with the doubling effect of magnification of the confocal unit, the width of field measures approximately 190 microns, although seldom were cross striations clearly visible across the entire field. Cross striations were visible in inner, mid and outer cuspal enamel, and in outer lateral enamel. It is noteworthy that cuspal cross striations could not be measured close to the EDJ, but some 100 µm away, which probably overestimated the appositional rate and may have slightly underestimated cuspal formation time (see below).

To calculate the number of perikymata on the I_1 , the labial surface of this specimen was imaged by simply placing it with the long axis perpendicular to the observer. The 5x lens with the 0.5 adapter was used in this case, which provides a width of field of 3.65 mm.

The formation time of the protoconid and metaconid was calculated by adding the duration of the lateral and cuspal enamel respectively, following the division of the crown by Beynon and Wood (1987). In this scheme, the portion of the cusp where striae reach the outer enamel surface is referred to as the lateral enamel and the part of the crown where striae do not reach the outer enamel surface is referred to as cuspal enamel (Beynon & Wood 1987). Using the PCSOM, counts were made of the lateral striae on the protoconid and metaconid cusps. In the protoconid, the most cervical 0.9

mm were missing and the number of striae for that portion of the crown had to be estimated by projecting the contours of the outer enamel and the EDJ (Figure 2).

Although daily secretion rates could be measured in certain places, the periodicity could not be confidently determined because cross striations and striae of Retzius were not clearly visible simultaneously in this specimen when using the 50x lens. Therefore, to assess lateral enamel formation, a range of periodicities reported for other fossil hominids was used, which was 6 to 9 days (Beynon & Dean 1987; Dean 1987; Dean *et al.*; 1993a; Dean *et al.*; 2001; Bromage *et al.*; in press; Lacruz *et al.*; 2006). Cuspal enamel development was calculated by measuring the enamel thickness of the protoconid and metaconid at the point where the first lateral stria surfaced. Prism decussation, or the deviation of prisms from a straight line (e.g. Dean 2004), influences the relationship between true prism length and enamel thickness. The work of Risnes (1986) represents an important attempt to quantify prism decussation in modern humans, suggesting the use of a correction factor which has been employed in studies of primate crown formation time (e.g. Reid *et al.*; 1998a; Smith *et al.*; 2003). This correction factor was used here in an attempt to correct for the observed prism decussation in KB 5223.

RESULTS

Table 1 shows the angles measured in the Kromdraai specimen compared to values reported for other fossil hominid taxa at the cervical third, also represented in Figure 3. Table 2 shows values of cuspal appositional rates reported for South African *Paranthropus* (Lacruz & Bromage 2006). Cuspal values obtained for the Kromdraai specimen KB 5223 in the protoconid and metaconid were very similar, and in both cases below those reported for a sample of *P. robustus* (Lacruz & Bromage 2006) (Table 2).

Fifty four striae of Retzius were counted on the metaconid and 49 striae were estimated on the protoconid of KB 5223 (Figures 2, 4). The periodicity could not be

assessed in this specimen, but using a range of periodicities of 6, 7, 8 and 9 days; an estimated time of 0.88, 1.03, 1.18 and 1.33 years was obtained for the development of the lateral portion of the metaconid; and 0.80, 0.93, 1.07 and 1.20 years for the protoconid. Enamel thickness was 1669 microns on the metaconid and 1890 microns on the protoconid. Given the irregular contour of the EDJ and loss of the innermost enamel of the metaconid in that region, enamel thickness may have been slightly underestimated. The measured thickness was then multiplied by Risnes (1986) correction factor, and this value was divided by the average cuspal appositional rate measured in the protoconid and metaconid. This value was similar in both cusps with a mean of 5.05 μ m (Table 2). Using this method, the development of the cuspal enamel of the metaconid was approximately 1.04 years and 1.18 years for the protoconid, which for this cusp is taken as a minimum value. The sum of lateral and cuspal enamel growth considering the range of periodicities yields 1.92, 2.07, 2.22, 2.37 years for the development of metaconid, and 1.98, 2.11, 2.25, 2.38 years for the protoconid.

Three perikymata counts were made on the RI₁ of KB 5223, yielding a mean value of 86± 3 perikymata, which is identical to the value reported by Dean and Reid (2001a) using light microscopy on high resolution replicas of this specimen.

DISCUSSION

In a sample of 10 molars attributed to *Paranthropus* from Swartkrans, it was found that the mean value of striae/EDJ angle at the cervix was 30 (sd = 3.6) (Lacruz *et al.*; 2006) while in a sample of 12 East African *Paranthropus* the mean value was 26 (sd = 6.5) (Ramirez Rozzi 2002). The mean value of 42.4 (sd = 2.6) obtained here for the cervical region of KB 5223 does not overlap with values of East and South African *Paranthropus*, but falls within the values obtained for *A. africanus* (Table 1, Figure 3) and are similar to those of the *H. rudolfensis* specimen UR 501 (Ramirez Rozzi *et al.*; 1997). The striae/EDJ angles are high in KB 5223, which indicates that the rate of ameloblast

recruitment was low in this region of the crown of KB 5223 and thus it was presumably formed slowly. In *Paranthropus*, this region of the crown is formed at a faster rate (Ramirez Rozzi 1993; Lacruz *et al.*; 2006). Grine and Martin (1988) had already noted, although only qualitatively, the higher angles of striae/EDJ in KB 5223 than in other specimens from Swartkrans.

Daily secretion rates in a sample of *P. robustus* molars from Swartkrans and Kromdraai, showed that the mean values in outer cuspal enamel were 7.25 microns (n = 5; sd = 0.44), and about 6.12 microns for the mid cuspal enamel (n = 4; sd = 0.56) (Lacruz & Bromage 2006). The values obtained for KB 5223 (Table 2) are about 8-12% lower than these values. Values reported in mid cuspal enamel of east African early *Homo* and *Paranthropus* by Beynon & Wood (1987) were 5.8 microns and 7.3 microns respectively, thus indicating that KB 5223 values are more similar to those of early *Homo* in that region. The values of KB 5223 in the outer cuspal and lateral areas are about 20-25% higher than values reported for the same crown areas in modern humans (Beynon *et al.*; 1991).

Fifty four lateral striae were counted on the metaconid of KB 5223, and 49 were estimated on the protoconid. These values are higher than the mean of a sample of five *P. robustus* molars from Swartkrans (mean = 42, sd = 9.2), where 50 striae was the highest value recorded (Lacruz *et al.*; 2006). A summary of striae/perikymata on fossil hominid molars is shown in Table 3. On the right M₁ of SK 63, attributed to *P. robustus*, 50 perikymata were counted on the protoconid of this tooth, and the same number was reported for SK 834 (Dean *et al.*; 1993a). Slightly higher values were recorded in the *H. rudolfensis* specimen UR 501, where 60 striae were counted on the distal face of the right M₂ (Ramirez Rozz*i et al.*; 1997). On the specimen Stw 151 from Sterkfontein, 62 perikymata were counted on the hypoconid of the right M₁ (Moggi-Cecchi *et al.*; 1998). The taxonomic attribution of this specimen was ambiguous as it showed a dental

developmental pattern similar to *A. africanus* but also showed some cranio-facial features that linked this specimen with *Homo* (Moggi-Cecchi *et al.*; 1998). The number of striae of KB 5223 is higher than the mean in a sample of *P. aethiopicus* molars (n = 4) and lower than the mean in *P. boisei* (n = 4) (Ramirez Rozzi 1993). In a large sample of molars from the Omo Formation, Ramirez Rozzi (1995) documented a wide range of striae counts that encompassed his previously reported values as well as those of KB 5223.

The anterior and posterior dentition of *Paranthropus* have lower number of striae/perikymata than *A. africanus* (Bromage & Dean 1985, Beynon & Dean 1988; Dean *et al.*; 1993a; Ramirez Rozzi 1993; Dean & Reid 2001a,b; Lacruz *et al.*; 2006). There are also differences in the number of striae/perikymata in anterior teeth between *P. boisei* and *P. robustus* (Bromage & Dean 1985; Beynon & Dean 1988) in that the former shows higher numbers of striae, and the same can be said for the posterior teeth based on the values reported in Ramirez Rozzi (1993) and Lacruz *et al.*; (2006).

The cuspal formation time of KB 5223 may be influenced by the contour of the EDJ and our measurement of enamel thickness could slightly underestimate cuspal development in the metaconid. The protoconid did not appear to have lost the innermost enamel in that region. In this regard, Braga and Thackeray (2004) noted that linear measurements of cuspal enamel thickness of KB 5223 fall within *Homo* values reported in Beynon and Wood (1986). However, because of the irregular contour of the EDJ and some loss of enamel in the innermost region, Grine and Martin (1988: p 24) corrected the value of cuspal enamel thickness, and this new corrected value was similar to other *Paranthropus* molars. Cuspal enamel was estimated to be 1.04 years on the metaconid and 1.18 years in the protoconid of KB 5223. Recently, Dean *et al.*; (2001) provided several regression equations to calculate cuspal enamel in early hominids. Using these equations for australopiths, early *Homo* and *H. ergaster/H. erectus* respectively, cuspal

development of the metaconid of KB 5223 would be 0.97, 1.19 and 1.24 years. Similarly, the development of cuspal enamel of the protoconid would be 1.10, 1.35 and 1.40 years. The values obtained for the cuspal enamel of KB 5223 are very similar to those obtained using the australopiths and early *Homo* equations. Regardless of which cuspal growth trajectory is employed in KB 5223, it is noteworthy that the results obtained for cuspal development using different methodologies are very similar.

The development of the protoconid and metaconid, the sum of lateral and cuspal enamel, ranged between 1.98 and 2.38 years in the protoconid and between 1.92 and 2.37 years for the metaconid. Ramirez Rozzi (1993) indicated that to more accurately calculate crown formation time, the developmental time of distal cusps had to be considered. In KB 5223, most of the cervical enamel is missing in places making it difficult to follow perikymata between mesial and distal cusps. However, in a sample of *P. robustus* and *A. africanus* (n = 3), a maximum number of 15 additional perikymata were counted when the last mesial cervical perikyma was followed to the distal cusps (Lacruz et al.; 2006). Using a 6, 7, 8 or 9 days periodicities, a further value of 0.24, 0.28, 0.32 or 0.36 years had to be added to the protoconid to obtain a broad estimate of the development of the entire crown of the M_1 of KB 5223. This yields values of 2.22, 2.39, 2.57 or 2.74 years for the RM₁ of KB 5223, which are considerably lower than mean value of about 3.1 years reported in the largest study to date from histological data for the same tooth type in modern *H. sapiens* (n > 35) (Dean & Reid 2006). The values obtained in KB 5223 using the higher end of periodicities (8 and 9 days), are similar to a value reported by Dean et al.; (1993b) in a H. sapiens individual. Values reported P. boisei, P. aethiopicus and early Homo are similar to those of KB 5223 (Beynon & Wood 1987; Dean et al.; 1993a; Ramirez Rozzi 1993; Ramirez Rozzi et al.; 1997; Dean et al.; 2001) which is also comparable to the lower end of values assigned to molars of Stw 151 (Moggi-Cecchi et al.; 1998).

The anterior dentition of this specimen was also investigated. Eighty six perikymata were counted on the right I_1 of KB 5223. This number is identical to the value obtained in a recent study of perikymata counts on anterior hominid teeth for this specimen by Dean and Reid (2001a) using a different technique. This value is within the range of counts reported for Paranthropus incisors but lower and outside the range of early Homo (Bromage & Dean 1985; Dean & Reid 2001b; Dean et al.; 2001). As noted by Dean and Reid (2001b), the patterns of perikymata distribution of H. rudolfensis and *H. erectus* are similar to the *Paranthropus* sample studied, which included KB 5223. However, this observation only provides information on pattern and not rate of growth, and cannot be used on its own to infer direct taxonomic associations between KB 5223 and early Homo. It is noteworthy that Dean and Reid (2001b) indicated that this similarity in the patterns between Paranthropus and early Homo refers only to H. ergaster and H. rudolfensis and not H. habilis. It is also interesting to note that based on the pattern of perikymata distribution observed on the specimen SK 74b originally described as Paranthropus, Bromage and Dean (1985) re-classified this incisor as Homo. Figure 5 shows perikymata distribution on the I_1 of KB 5223 just a few microns from the cervix, displaying a pattern of nearly evenly spaced perikymata near the cervix, which appears to be a feature associated with *Paranthropus* and not with *Homo* (Beynon & Dean 1988). Braga and Thackeray (2003) noted that the mesio-distal index of the lower incisor of KB 5223 is one of the smallest in South African Paranthropus and in the Koobi Fora and Swartkrans Homo samples. The crown height was estimated to be 9.6 mm, which appears to be in mid-range for other P. robustus incisors (Dean & Reid 2001a), although it has been suggested that crown height is not necessarily correlated with number of perikymata (Ramirez Rozzi & Bermudez de Castro 2004).

The picture that emerges from this study is therefore complex. The number of perikymata on the I₁ of KB 5223 is most similar to values reported in East and South

African *Paranthropus*. The angles striae/EDJ are higher and show no overlap with values reported for East and South African *Paranthropus*. Cuspal daily secretion rates of the KB 5223 molar are lower than values reported for *P. robustus*, and appear to be more similar to the very limited information available for East African early *Homo*. The number of lateral striae of KB 5223 is placed in the highest range of *P. robustus* and just slightly lower than in a single specimen of *H. rudolfensis* (UR 501) and the M₁ of the Sterkfontein specimen Stw 151 (Moggi-Cecchi *et al.*; 1998). It is also encompassed within the variation of *P. boisei* (Ramirez Rozzi 1993, 1995).

The study of Braga and Thackeray (2003) on KB 5223 provided strong bases for the inclusion of this specimen within the genus *Homo*. However, the complex pattern of enamel development shown in this study between the anterior and posterior dentition of KB 5223 does not provide clear indications about the presence of *Homo* at Kromdraai using parameters derived from the study of enamel growth. Further discoveries are needed to resolve whether or not there is more than one taxon at this site as well as a better understanding of the taxonomic value of incremental lines in enamel.

CONCLUSIONS

Studies on enamel microstructure are an important source to access mechanisms of development in fossil taxa (Dean 2000; Dean *et al.*; 2001). This study has provided information on enamel incremental lines of a molar and incisor of the Kromdraai specimen KB 5223 using novel imaging technology. The PCSOM, designed by Bromage, Perez-Ochoa and Boyde (2003) is a powerful tool to access details of hard tissue microstructure in fossils when more conventional histological methods are not an option.

Results presented here indicated that the duration of crown formation of the RM₁ of KB 5223 was markedly shorter than the mean value of the corresponding molar type of *H. sapiens*. Cuspal daily secretion rates are about 20-25% higher in this region of the

crown than in molars of modern humans, which is probably one of the mechanisms by which thick enamel was formed in early hominids (Lacruz & Bromage 2006).

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TABLE CAPTIONS:

Table 1. Measurements of striae/EDJ at the cervix of KB 5223 compared to other hominids. The number of specimens studied in the samples of *P. robustus*, EA *Paranthropus* (Ramirez Rozzi 2002; Tables 15.2 and 15.3) and *A. africanus* are noted in the table. The mean of KB 5223 is based on 5 different values measured in the cervical third of the metaconid. The values of UR 501 are combined of mesial and distal faces of the M₂.

Table 2. Daily secretion rates measured in different regions of the cuspal enamel of KB 5223 compared to values obtained in Lacruz and Bromage (in press) for a sample of *P*. *robustus*. The values shown in the table are for the metaconid, but very similar values were obtained in the cuspal area of the protoconid. Given that the measurements in the inner enamel were taken at about 100 microns away from the EDJ, it is likely that this value is slightly overestimated and thus also the mean of cuspal appositional rate (CAR). For KB 5223, the lateral outer values were also measured. The numbers in parenthesis indicate the specimens used to calculate each value in *P. robustus*.

Table 3. Counts of striae/perikymata reported for hominid molars. The sample ofRamirez Rozzi is the mean of 45 molars which were attributed to East AfricanParanthropus by this author. See text for details.

Figure captions:

Figure 1. The Kromdraai specimen KB 5223 derives from Member 3 of the Kromdraai B Formation and was originally sectioned long the apices of the mesial cusps (to the right of the image) by Grine and Martin (1988). This RM₁ measures 14.3 mm MD and 12.5 BL. The scale-bar represents 3 mm.

Figure 2. Protoconid of KB 5223. The most cervical 0.9 mm of the lateral enamel was lost and to estimate the number of striae in this area, the contours of the outer enamel and the EDJ were reconstructed. Forty nine striae were estimated on this cusp. Scale bar = $1000 \mu m$.

Figure 3. Error bar plot of the values of angles striae/EDJ in the cervical region of Kromdraai specimen KB 5223 (1), *P. robustus* (2), East African *Paranthropus* (3), and *A. africanus* (4). KB 5223 falls outside the 95% confidence interval of reported for East and South African *Paranthropus*. Data on East African *Paranthropus* derives from Ramirez Rozzi (2002). CI cervical = confidence interval at the cervical area.

Figure 4. Metaconid cusp of KB 5223. On this face, a total of 54 striae of Retzius were counted, but only about 46 are shown in this image as the cuspal-most section could not be imaged. It is noticeable the high angle of incidence of striae on the EDJ. Scale bar = $100 \mu m$.

Figure 5. Perikymata on the KB 5223 lower incisor taken at just a few microns from the cervix. Forty eight perikymata out of a total of 86 on the labial surface of this tooth can be counted on the 3.25 mm of the crown shown here. Crown height was estimated to be 9.6 mm. The pattern of perikymata distribution shows relatively evenly spaced perikymata at the cervix, a pattern commonly found in *Paranthropus* and not in *Homo* (Bromage and Dean 1985; Beynon and Dean 1988). Scale bar 500 µm.

Table 1.

	Ν	max	min	mean	sd
A. africanus	15	51	34	38	4.3
P. robustus	11	38	25	30	3.6
EA Paranthropus	12	36	15	26	6.5
KB 5223	1			42	2.6
UR 501	1			41	

Table 2.

	Cus. Out	Cus. Mid	Cus. Inn	Mean CAR	Lat. Out
P. robustus	7.27±0.52 (5)	6.12±0.82 (4)	4.16(1)	5.8	6.59±0.38 (5)
KB 5523	6.45±0.27 (5)	5.67±0.09 (4)	4.04±0.26 (3)	5.1	6.09±0.23 (6)

Table 3.

Taxon	Specimen	Tooth	Face	SR/Pk	Source
P. robustus/Homo	KB 5223	low M1	metaconid	54	this study
P. robustus/Homo	KB 5223 SKX	low M1	protoconid	49	this study
P. robustus	21841	up M3	paracone	50	Lacruz et al., (in press)
H. rudolfensis A.	UR 501	low M2	?	60	Ramirez Rozzi et al., (1997)
africanus/Homo	STW 151	low M1	hypoconid	62	Moggi-Cecchi et al., (1998)
P. robustus	SK 63	low M1	protoconid	50	Dean et al., (1993)
P.robustus E.A.	SK 834	low M1	protoconid	50	Dean et al., (1993)
Paranthropus				61	Ramirez Rozzi (1995)

Figure 1.











Figure 4.



Figure 5.

