Chapter 10

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VARIATION IN ENAMEL DEVELOPMENT OF SOUTH AFRICAN FOSSIL HOMINIDS

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ABSTRACT

Dental tissues provide important insights into aspects of hominid palaeobiology that are otherwise difficult to obtain from studies of the bony skeleton. Tooth enamel is formed by ameloblasts, which demonstrate daily secretory rhythms developing tissue-specific structures known as cross striations, and longer period markings or striae of Retzius. These enamel features were studied in the molars of two well known South African hominid species, *Australopithecus africanus* and *Paranthropus robustus.* Using newly developed portable confocal microscopy, we have obtained cross striation periodicities (number of cross striations between adjacent striae) for the largest sample of hominid teeth reported to date. These data indicate a mean value of seven days in these small-bodied hominids. Important differences were observed in the inferred mechanisms of enamel development in these taxa. Ameloblasts maintain high rates of differentiation throughout cervical enamel development in *P. robustus* but not in *A*. *africanus*. In our sample, there were fewer lateral striae of Retzius in *P. robustus* than in *A. africanus*. In a molar of *P. robustus*, lateral enamel formed in much less time than cuspal enamel, and the opposite was observed in two molars of *A. africanus*. In spite of the greater occlusal area and enamel thickness of the molars of both fossil species compared with modern humans, the total crown formation time of these three fossil molars was shorter than the corresponding tooth type in modern humans. Our results provide support for previous conclusions that molar crown formation time was short in Plio-Pleistocene hominids, and strongly suggests the presence of different mechanisms of amelogenesis and thus tooth development in these taxa.

Introduction

An understanding of the biological processes involved in generating morphology can be fully appreciated only when the underlying mechanisms controlling final form are known (Butler 1956; Atchley & Hall 1991). In some ways, understanding how these mechanisms operate implies that hard tissues need to be studied at the cellular level. This approach was originally applied to the hominid fossil record in studies of bone remodeling patterns of the face and mandibles of *Paranthropus*, *Australopithecus* and *Homo* (Bromage 1985; 1990). More recently, several authors have re-introduced this morphogenetic approach in studies of evolutionary changes of hominid pelvic, facial, and dental architectures (Lovejoy *et al.*; 1999; McCollum 1999; McCollum & Sharpe, 2001). In particular, Lovejoy and co-workers (Lovejoy *et al*.; 1999, 2002, 2003) appear to be inspired by Wolpert's (1969) concept of cell positional information to pursue a developmental biology approach that explains changes in hominid post-cranial morphology.

Teeth are also appropriate for the study of developmental mechanisms because 1) "combined within one organ system are spatial organization, symmetry, acquisition of complex form and organ specific cytodifferentiation" (Lumsden 1988); 2) the control mechanisms of their development are relatively well known (Jernvall & Thesleff 2000; Kangas *et al*.; 2004); 3) alterations of the enamel once the crown has erupted can only be attributed to wear and not remodeling, as may occur in bone; and 4) enamel preserves growth markers with a circadian periodicity that allows one to obtain chronological data related to the life of the organism (Boyde 1964; Dean 1987; Boyde 1989; Bromage 1991). Cross striations, or short term growth markers, represent variations in ameloblast secretory activity that correspond to daily cell secretions and can be observed as lines perpendicular to the main prism direction (Boyde 1989). Long term growth markers, or striae of Retzius, are oblique bands running from the enamel dentine junction (EDJ) to the outer surface of enamel where they form troughs known as perikymata in the lateral portion of the crown. The number of cross striations between striae determines the periodicity of this long term marker and hence, the periodicity of perikymata. Understanding variation in these microstructural features elucidates several aspects of enamel growth and tooth formation (Beynon & Wood 1986, 1987; Ramirez Rozzi 1993, 1998, 2002).

Since Bromage and Dean's (1985) pioneering study on human and early hominid perikymata, this and subsequent studies have revealed a series of differences, primarily

of the anterior dentition, among the early hominid genera *Australopithecus*, *Paranthropus*, and early *Homo.* Additionally, it has been shown that these three taxa completed the development of their anterior teeth in a shorter time than do modern humans (Bromage & Dean 1985; Dean & Reid 2001a; Dean *et al.*; 2001). Alternatively, molar crown formation time is either similar (Ramirez Rozzi 1994) or shorter (Beynon & Wood 1987) in Plio-Pleistocene hominids than in modern humans. That larger *Paranthropus* and early *Homo* molars take a similar or lesser amount of time to form than do those of *Homo sapiens*, has been explained by differences in growth mechanisms governing amelogenesis. These mechanisms include high numbers of cells actively secreting enamel at any given time during crown formation as well as high daily secretion rates (measured in 2-D) (Beynon & Wood 1987; Beynon & Dean 1988; Ramirez Rozzi 2002; Lacruz & Bromage 2006). When this morphogenetic approach is employed in a wider taxonomic range that includes *Australopithecus*, *Pan*, *Pongo*, *Proconsul,* and *Homo erectus* molars, it becomes clear that enamel thickness can be achieved through variations in both of these mechanisms (Dean 1998; Dean 2000; Dean *et al*.; 20001; Dean & Reid 2001a; Dean 2004). Investigations of enamel tissue at this level, therefore, yield significant biological information for more accurate interpretation of hominid palaeobiology (Wood 1996; Kuykendall 2003).

Most studies of Plio-Pleistocene hominid molar development have been undertaken on East African material (n ≈ 70 molars and premolars; Beynon & Wood 1986, 1987; Dean 1987; Beynon & Dean 1987; Ramirez Rozzi 1993, 1995, 1998, 2002; Dean *et al*.; 2001), whereas much less information is available for South African taxa (Grine & Martin 1988; Beynon 1992; Moggi-Cecchi *et al*.; 1998).

Some differences in crown development of the anterior dentition have been previously described between the South African hominids *Australopithecus africanus* and *Paranthropus robustus* (Bromage & Dean 1985; Dean & Reid 2001a), but no data on molar crown formation time have been reported. Additionally, angles formed between the striae of Retzius and the EDJ, which relate to ameloblast rate of differentiation (Boyde 1964), have not been quantified. Recently, Lacruz and Bromage (in press) have recorded daily appositional growth in molars of these taxa, suggesting greater daily rates in *P. robustus* than in *A. africanus*.

A critical aspect in estimating crown formation time is the periodicity of the striae. Periodicity has been reported for only a single South African *P. robustus* specimen, the canine SK 63; using classical histological methods the periodicity is 9 days (Dean et al.;

1993a). In the East African fossil sample, the only periodicity is known for only a single individual, the *P. boisei* specimen KNM ER- 733 for which a premolar and a molar both showed a 7 day rhythm (Dean 1987; Beynon & Dean 1987). The paucity of striae periodicity studies in fossil hominids indicates the great difficulty in obtaining such information in fossil hominid material.

However, the recent development of a portable confocal scanning optical microscope (PCSOM) (Bromage *et al.*; 2005, in press) has made possible the study of dental development and crown formation time (CFT) in a relatively large sample of *A. africanus* and *P. robustus* molars. This instrument was purposefully designed for palaeoanthropological studies (Bromage *et al.*; 2005; in press), to allow imaging of hard tissue microstructure on, for instance, natural fractures of bones and teeth when destructive histological sampling is not an option. Striae can be seen only rarely by scanning electron microscopy (Dean 1988; Beynon & Dean 1988), but these features are more readily observed with the PSCOM, which also allows observation and measurement of cross striation intervals (Lacruz & Bromage 2006). Therefore, PSCOM provides a unique opportunity to obtain striae of Retzius periodicities (and hence perikymata) providing strong bases for estimating the duration of crown development.

The aim of this study is to provide information on several aspects of the enamel microstructure of molars of the well known Plio-Pleistocene South African hominid taxa, *A. africanus* and *P. robustus*. We report striae periodicity for a relatively large sample of molars of each taxon, the angles formed between the striae and the EDJ, and molar crown formation time. This information is then compared with values obtained from the literature for other fossil hominid taxa as well as modern humans.

Enamel development

Two main microstructural markers may be identified in hominid enamel: cross striations and striae of Retzius, the latter of which manifest at the enamel surface as perikymata in the lateral, or imbricational, portion of the crown.

Tooth crown formation is a continuous process initiated at the dentine horns. Proliferation of the basal membrane, which separates enamel and dentine forming cells, proceeds towards the cervical margin of the forming crown as ameloblasts become differentiated along the enamel-dentine junction (EDJ). A pre-determined number of cell cycles, which are dependent on genetic programs, are necessary to acquire cell competence (Amar *et al*.; 1989; Ruch 1990). There is a slight time delay in competence such that the more cuspal cells become active before more cervical cells in response to

reciprocal induction, based upon a cuspal-to-cervical wave of dentine production. Cells are tightly bound by cell- cell communication mechanisms that coordinate their movement and secretory activity (Sasaki 1990). Once ameloblasts mature and begin to secrete matrix they move in cell cohorts (or enamel forming front) away from the EDJ and toward the outer enamel surface (OES) whilst forming enamel prisms, or rods. When the first secreting cells reach the cusp tips and OES, the enamel forming front at that moment contains cells at all stages in cusp development, including newly differentiating ameloblasts at the EDJ. At any given time during enamel development, every secretory cell is rhythmically subjected to a physiological perturbation of unknown etiology but which is observed to occur on a 24 hour, or circadian, timescale. These "disruptions" have an effect on a cell's secretory product, giving rise to cross-striations that appear as linear contrasts across and perpendicular to each prism in transmitted light microscopy. Another, but more marked disturbance induces the formation of striae of Retzius which are identified as dark brown lines in transmitted light microscopy. Striae cross the prisms and represent the position of the advancing enamel front (Shellis 1998). Additionally, the angles formed between the striae and the EDJ have been suggested to indicate broad differences in the rate of ameloblast differentiation along the EDJ (Boyde 1964; Shellis 1984). More acute angles are associated with higher rates.

Materials and Methods

Fifteen molars of *A. africanus* from Sterkfontein Member 4 dated to about 2.5 my (Vrba 1995) and ten of *P. robustus* from Swartkrans Members 1-3 dated between 1.8 and 1.5 my (Brain 1993) were used in this study (Table 1). Cross striation periodicity, angles of striae incidence at the EDJ, and counts of striae of Retzius were recorded for as many specimens as possible. These features were observed, with a few exceptions, in natural occluso-cervical fractures, which occurred during post-depositional processes. Two specimens (Stw 284, SKX 21841) were previously sectioned (Table 1) in a plane connecting the apices of the mesial cusps and one specimen (Stw 402) was sectioned along the distal cusps (Grine and Martin, 1988). Counts of striae of Retzius and measurements of striae/EDJ angles were made using incident light stereo zoom microscopy on specimens immersed in ethanol at a magnification of 25 times and by portable confocal microscopy (Bromage *et al*.; 2005; in press). Figures 1a and 1b show imaged striae in the Swartkrans specimen SKX 21841 using both incident light and PCSOM. Figures 2-4 show striae in the Swartkrans specimen Skw 37 in both incident light and under the PCSOM showing some detail of striae at higher magnification. The

striae imaged with the PCSOM are indistinguishable from striae imaged with incident light microscopy.

Striae/EDJ angles were measured at the point of contact between these two features, as shown in Schwartz *et al*.; (2003: Fig. 2A), along three equal lengths of the EDJ (cuspal, lateral and cervical), which permits the analysis of crown development at each stage. Angle values of the South African hominids were compared with data available for East African *Paranthropus* derived from Ramirez Rozzi (2002; Table 15.2). The non-parametric Mann-Whitney *U* test was used to compare striae/EDJ angle values between taxa. Wilcoxon Signed-Rank test, also non-parametric, was used to assess differences between different regions of the cusps in the same specimens.

Crown formation time was obtained for two molars of *A*. *africanus* (Stw 284, Stw 402) and one of *P*. *robustus* (SKX 21841) because these teeth had been previously sectioned in a plane that passed at or near the dentine horn (i.e., minimal obliquity) and showed minimal cuspal wear (Grine & Martin 1988). Counts of striae of Retzius were made on a number of other molars for each taxon. These teeth were selected because striae could be observed along the entire face and the crowns showed minimal wear (e.g. Figure 5), or if they showed some wear, striae could be confidently estimated. To assess differences in the distribution of the striae, the crowns of a molar of each taxon were divided into ten equal divisions, in a similar manner to that described by Dean and Reid (2001).

Because developmental time varies from mesial to distal cusps (e.g. Kraus & Jordan 1965; Reid *et al*.; 1998b), corrected lateral formation times were obtained by counting striae made directly on naturally broken surfaces and then, after following the last identified cervical stria to its corresponding perikyma, adding cervical perikymata on the distal cusps, as detailed in Ramirez Rozzi (1993). The duration of cuspal enamel was obtained by first measuring cuspal thickness at the point where cuspal and lateral enamel meet; that is, the point at which striae do not reach the enamel surface. Because prism decussation was observed near the EDJ in the *A. africanus* specimens, cuspal thickness was then multiplied by a correction factor of 1.15 (Risnes 1986) which adjusts the length of prisms, and thus in this case linear enamel thickness, by taking into account prism decussation in a similar manner to that described by Reid *et al*.; (1998b). The result was then divided by the mean value of cuspal appositional rate; these values were obtained by averaging groups of three to five cross striations (Bromage *et al*.; in press). This process was repeated for as many fields as possible. In all cases, the

closest values measured in the inner enamel were taken at about 100 μm from the EDJ, which may overestimate the innermost appositional rate. Cuspal enamel formation for the *P. robustus* specimen was calculated following the same method, but the Risnes (1986) correction factor was not employed as decussation was minimal.

Striae periodicity was examined by PCSOM (Bromage *et al*.; 2005; in press) and, generally, observations were made on the outer enamel surface in regions located at the boundary between the cervical and lateral enamel, as the striae tended to be more prominent. Cross striations were observed and counted directly on specimens using the PCSOM (Figures 6-9).

Results

The pattern of ameloblast differentiation based on the angles formed between striae of Retzius and the EDJ distinguishes the South African taxa (Figure 10; Table 2). South African *Paranthropus* shows only a slight increase from the lateral to cervical enamel, which is not statistically significant ($p > 0.05$). In contrast, *A. africanus* shows a marked increase in stria/EDJ angles from the cusp to the cervix (Figure 10), a difference that is statistically significant ($p< 0.05$). In addition, comparisons of the cervical values with East African *Paranthropus* show that East and South African *Paranthropus* show no statistical differences between them ($p > 0.05$). However, when these two groups are compared with *A*. *africanus*, differences in the cervical values are statistically significant ($p< 0.05$). In our sample (n=15), the mean striae periodicity for both *A*. *africanus* and *P. robustus* is 7 (Table 4). In some cases cross striations were less easily resolved, in which case two equally likely periodicities were considered (Table 4).

An important feature characterizing molar formation is the number of lateral striae (Ramirez Rozzi 1998; Reid & Ferrell 2006). In our study, *A*. *africanus* molars (n = 4) have a greater number of lateral striae than do those of *P. robustus* (n = 5) (Table 3). The values obtained for *P. robustus* are similar to values reported for *P. aethiopicus* (Ramirez Rozzi 1993). The disposition of the striae along the outer enamel of SKX 21841 and Stw 284 shows a similar pattern to that observed by Dean and Reid (2001) in the anterior dentition and suggests a decrease in striae number towards the end of crown formation (Figure 11).

In our effort to obtain crown formation time, eighty two striae were counted on the protocone of the *A*. *africanus* specimen Stw 284 (M^2). Twelve additional perikymata on the hypocone (last cusp to be formed) were added, following the criteria of Ramirez Rozzi (1993) to include in the CFT the difference in developmental time between mesial

and distal cusps, giving a total of 94 striae/perikymata. As the cross striation periodicity in this specimen was 6 or 7 days, this gives a total of 1.5 to 1.7 years for the formation of the lateral enamel. Cuspal enamel formation was estimated to be 1.5 years based on enamel thickness (2.67 mm), average cuspal appositional rate (5.6 microns; Bromage *et al*.; in press), and a correction factor, which gives a total of 3.0 to 3.2 years for the formation of the Stw 284 molar.

Similarly, 75 striae were counted on the metacone of the *A*. *africanus* specimen Stw 402 (M^1). The most cervical aspect of the enamel of this tooth did not show distinct perikymata that could be confidently followed to other cusps and thus it was assumed, by using Stw 284, that 12 perikymata had to be added to calculate duration of lateral enamel of this tooth. Metacone enamel thickness was 1.89 mm, which was then multiplied by Risnes (1986) correction factor. It was not possible to measure the cuspal appositional rate or the cross striation periodicity in this specimen, but using the mean of appositional rates of six *A. africanus* molars (Lacruz & Bromage 2006) which was 5.5 microns and presuming a 7 day periodicity (this study), a period of 1.08 years for cuspal and 1.66 for lateral enamel was established, giving a total of 2.74 years for the development of the enamel crown of Stw 402. As enamel thickness is usually greater in functional cusps of maxillary molars (protocone and hypocone) than in non-functional cusps (paracone and metacone) (Reid *et al*.; 1998b), it may be possible that the cuspal formation time of Stw 402 has been slightly underestimated.

Fifty striae were counted on the paracone of the *P*. *robustus* specimen SKX 21841 (M^3), to which an additional 14 perikymata were added from the hypocone. The cross striation periodicity was 6 days, giving a total of 1.05 years for imbricational enamel. Cuspal enamel thickness was 3.48 mm, which was divided by the mean cuspal appositional rate of 5.7 microns calculated for this specimen; a value of 1.67 years was obtained, giving a total of 2.72 years for the formation of the SKX 21841 molar.

Discussion

This study used naturally fractured teeth to access enamel microstructural features in *P*. *robustus* and *A. africanus*. This implies that there is little or no control over the observed plane of section, and thus a number of problems arise that need to be addressed. First, striae/EDJ angles may partly depend upon the plane of fracture, or they may be related to differences between cusps (e.g. Smith *et al*.; 2004). In our study of a relatively large sample of teeth of each taxon, a characteristic pattern could be sought from the many values obtained. The differences illustrated in Figure 10 are thus

unlikely to represent the effects of opportunistic natural breaks which favor, for instance, greater angles in *A*. *africanus* rather, Figure 10 indicates biological differences. A second problem concerns variation in developmental times of different cusps from the same tooth. However, by taking into consideration perikymata additional to the last cervical stria as detailed in (Ramirez Rozzi 1993); this problem can be addressed in assessments of CFT.

The present study has greatly increased our knowledge of aspects of the enamel microstructure of molars of *P*. *robustus* and *A. africanus* for which only very limited information was previously available. Of special importance is the periodicity of the striae of Retzius, which until recently (Bromage *et al*.; in press), was limited to only four studies of Plio-Pleistocene hominid enamel representing a total of three individuals (Dean 1987; Beynon & Dean 1987; Dean *et al*.; 1993; Dean *et al*.; 2001). Knowledge of cross striation periodicity is critical to assess variability in crown formation time in hominids and other primates, and also provides the basis for important insights into life history variation (Schwartz *et al*.; 2002). The mean striae periodicity in molars of both species, which probably represent 15 individuals, is equal and, in both cases, are 7 days, with ranges of 6 to 8 in this sample (Table 4). Therefore, previous interpretations of CFT on posterior teeth which had assumed a periodicity of 7 days should be considered correct. The modal values are 7 days in *Paranthropus* and 6 or 7 days in *A. africanus* (Table 4).

The association between striae periodicity and body size (Dean & Scandrett 1995; Dean 2000; Smith *et al*.; 2003) appears to hold true in light of observations made in this study. Gracile and robust australopithecines are generally considered small-bodied hominids, although *P. robustus* has a somewhat larger body size estimate than *A. africanus* (McHenry 1994). However, both taxa have similar body size as *Pan troglodytes* (Smith & Jungers 1997), for which a periodicity of 6-8 days in molars has been observed (Reid *et al*.; 1998b; Smith 2004). The values obtained for the fossil taxa fall within the highly variable ranges reported for modern humans, which is 6-11 days (Dean & Reid 2001a; Reid & Dean 2006).

The tooth types and duration of the entire enamel crowns considered here for the fossil taxa are: M^1 (2.74 years), M^2 (3.0 to 3.2 years), and M^3 (2.72 years). Reid and Dean's (2006) most recent study on crown formation times in the largest histological sample of modern human molars to date, observed that South African specimens showed slightly shorter crown formation times than did samples of European descent. The mean values reported by Reid and Dean (2006) for modern South Africans were:

3.0 years for the M^1 protocone (n=37), 3.38 years for the M^2 protocone (n=18), and 3.28 years for the M^3 paracone (n=20). When we compare the values obtained for the fossil taxa with the means of modern South Africans, the fossil hominids molar crowns formed in less time, specially the Swartkrans specimen SKX 21841. Additionally, given that Reid and Dean's study did not consider the values of total crown formation time but only values of individual mesial cusps, it is likely that the values for the whole crown would increase, thus increasing the differences between modern humans and the fossil taxa for which we report values for total crown formation times.

Recently, Dean *et al*.; (2001) provided regression equations to calculate cuspal enamel formation in early hominids and other primates. The equation for *Australopithecus* and *Paranthropus* (including *A. anamensis* and *P. boisei*) is $y= 6.64 + 0.21x – 0.00001x^2$, where "x" is enamel thickness in microns. We compared our cuspal values with those derived from the use of the Dean *et al*.; (2001) regression equation. The cuspal enamel values obtained using this method were: Stw 402 (1.10 years); Stw 284 (1.53 years), and SKX 21841 (2.02 years), whereas our cuspal values were 1.08 (Stw 402), 1.50 (Stw 284), and 1.67 (SKX 21841) years. The values for *A. africanus* compare well between both methods, but the value obtained for the *P. robustus* molar in our estimations is less than the value obtained using the Dean et al.; (2001) equation. It maybe possible that the cuspal values reported here for SKX 21841, especially in the inner enamel, had been slightly overestimated thus yielding low cuspal values. It is also possible that given the inclusion of different tooth types and different taxa with different cuspal enamel thickness (e.g., *A. anamensis* and *P. boisei*), that the Dean *et al*'s.; (2001) regression equations may overestimate the values of the thick-enameled *P. robustus*.

In our sample, *P. robustus* appear to have fewer striae than do *A. africanus.* However, it maybe possible that these differences derive from sampling different tooth types or cusps. There is only limited data on modern humans of the striae numbers for different tooth classes. In Table 2 of Reid *et al*.; (1998a), the largest number of striae in four medieval French individuals was recorded in an M_1 metaconid, whereas the largest values in the maxilla were recorded in M^1 and M^2 protocones. This study, however, was limited to the mesio-buccal cusps. In the common chimpanzee, Reid *et al*.; (1998b) recorded higher values in the protocone and hypoconid of maxillary and mandibular M2s respectively. Smith's (2004) study of chimpanzees found a similar pattern; M2s (maxillary and mandibular) showed greater number of striae than the other molars types

(M2 >M3> M1). Importantly, Reid *et al*.; (1998b) and Smith (2004) found differences between cusps, although these were variable according to the tooth type considered. For example, the largest striae number on the M^2 was recorded on the metacone, but on the M^1 was the paracone.

Based on the studies of Reid *et al*.; (1998a,b) and Smith (2004), it is difficult to contextualize our results. In the fossil sample studied here, the largest number of striae in *A. africanus* is recorded in an M^2 protocone and in *P. robustus* in the M^3 paracone, whereas the lowest values in each taxon are found in M^3 (*A. africanus*) and M^2 (*P. robustus*) hypocones; that is no clear pattern can be discerned. In addition, we could not sample the same cusps on the same tooth type and no M1s were sampled in *P. robustus*. However, taking into consideration that the anterior teeth of both taxa have shown differences in the number of perikymata, with *P. robustus* having markedly fewer perikymata than do *A. africanus* (Bromage & Dean 1985; Beynon & Dean 1988; Dean & Reid 2001a,b), it is very likely that these differences can also be inferred for the posterior teeth, as our sample of molars appears to indicate. However, this requires further confirmation and investigation.

Several studies have observed differences in enamel incremental lines among fossil hominid taxa (Bromage & Dean 1985; Beynon & Wood 1986; Beynon & Dean 1988; Beynon 1992; Ramirez Rozzi 1993; Dean & Reid 2001a; Dean *et al.*; 2001). Nevertheless, caution has been suggested in the use of enamel microstructure as a taxonomic indicator (Ramirez Rozzi 1998; Dean *et al*.; 2001). While we concur, in this study we have sought to evaluate differences in molar microstructure observed between *P. robustus* and *A. africanus*, which provide some indication on differences in enamel development.

Our interpretations of differences in hominid molar development can be summarized as follows: The striae/EDJ angles are more acute in *P*. *robustus* than *A*. *africanus*, particularly at the cervical third; the acute angles also characterize eastern African *Paranthropus*. This indicates that the development of the cervical area of the crown developed faster in *Paranthropus* than in *A*. *africanus*. This difference has already been noted in other studies based on perikymata distributions on anterior teeth (Bromage & Dean 1985; Dean 1987; Beynon & Dean 1988) and in a small sample of molars (Bromage *et al*.; in press). In addition, the time dedicated to lateral and cuspal enamel formation differs between taxa; cuspal enamel takes more than 60% of the total formation time in the *Paranthropus* molar studied, whereas the two *A. africanus* molars

formed this area of the crown in less than 50% of the total crown formation time. A similar pattern to that found in *P*. *robustus* has been described for East African *Paranthropus* (Beynon & Wood 1987). This may be associated with differences in enamel thickness whereby *Paranthropus* has thicker enamel than *A. africanus* (Robinson 1956; Martin 1985; Grine & Martin 1988; Macho & Thackeray 1992).

Given that *A*. *africanus* and *P*. *robustus* share the same mean value of striae periodicity, the differences in the number of lateral striae (*A*. *africanus* more than *P*. *robustus*) observed in our molar sample, points to differences in the pattern of enamel formation, as previously indicated for the anterior dentition (Bromage & Dean 1985; Dean & Reid 2001a,b).

Furthermore, it has been shown that the first lateral stria in *Paranthropus* tends to be longer than in *A*. *africanus* and *Homo*, because of their high striae/EDJ angles and thus larger number of secreting cells involved in enamel formation (Beynon & Dean 1988; Grine & Martin 1988; Ramirez Rozzi 1993). Additionally, daily ameloblast secretion rates are faster in *P. robustus* than in *A. africanus* (Lacruz & Bromage 2006), and are similar to the limited data on secretion rates available of East African *Paranthropus* (Beynon & Wood 1987).

The parallels observed in the enamel microstructure of both eastern and southern African *Paranthropus* suggest that the underlying mechanisms governing enamel development are very similar and are directed to the rapid formation of large and thick-enameled molar teeth. This supports a previous hypothesis (Grine & Martin 1988) that suggested that the paranthropines share a number of features in the enamel microstructure which are not present in *A*. *africanus.*

Conclusion

This study has provided the largest account of striae periodicity for any fossil hominid taxa, and these data indicate that the mean periodicity value was 7 days in the small-bodied hominids *A. africanus* and *P. robustus*. The CFT reported for three hominid molars (Stw 402 (M^1) 2.74 years; Stw 284 (M^2) 3.0 to 3.2 years and SKX 21841 (M^3) 2.72 years) is lower than mean values reported for molar crown development in modern humans (Reid *et al*.; 1998a; Reid & Dean 2006) in spite of the fact that both *P. robustus* and *A*. *africanus* molars have much greater occlusal areas and thicker enamel. The pattern recorded here for South African hominids corroborates a more generalized

pattern of relatively rapid growth of fossil hominid molars in relation to modern humans (Beynon & Wood 1987), suggesting clear differences during amelogenesis between the extinct and extant hominid taxa (Lacruz & Bromage 2006). However, important differences were found in patterns of crown development between *A*. *africanus* and *P*. *robustus.*

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Table captions:

Table 1. Samples of *A. africanus* and *P. robustus* molars used in this study indicating the tooth type and the face studied.

Table 2. Values of striae/EDJ angles on the samples of molars derived from Sterkfontein and Swartkrans compared with data on East African *Paranthropus* (taken from Ramirez Rozzi, 2002). In *Paranthropus*, the mean values striae/EDJ is lower than in *A. africanus.*

Table 3. Counts of lateral striae of Retzius on the *P. robustus* and *A. africanus* samples studied.

Table 4. Striae periodicity on a sample of molars of *A. africanus* and *P. robustus*. In the case of Stw 40 and Stw 284, the periodicity could not be clearly discerned and thus we have included the two possible periodicities, which we identified as being 6 or 7 days (indicated in parenthesis). Both fossil taxa showed a mean periodicity of 7 days. Modal values in *A. africanus* are given depending on the periodicities of the two specimens mentioned above.

Figure captions:

Figures 1A and 1B. Figure 1A (left) shows the cervical region of a *P. robustus* molar imaged with the PCSOM using 5x lens and 0.5 adapter. A clearing medium (immersion oil) and a cover slip were placed on the surface of this specimen. A marked stria has been arrowed as well as two small cracks in the enamel running from the EDJ to the outer surface. Figure 1B (right) is the same specimen as Figure 1A now immersed in ethanol and imaged using incident stereoscopic microscopy. The markings in Fig. 1A are easily identifiable on Fig. 1B.

Figure 2. Swartkrans specimen SK 37 imaged using incident light at low magnification after immersing the specimen in ethanol. The highlighted area at the cervix has been enlarged on Figures 3A and 3B.

Figures 3A and 3B. Figure 3A shows the area near the cervix enlarged from Figure 2 of the Swartkrans specimen SK 37 using incident light microscopy. Figure 3B represents the cervix of this specimen imaged using 10x and 0.5 adapter using a clearing medium but no cover slip. The white arrows indicate the same areas on both images.

Figure 4. Detail of the striae of Retzius on the outer part of the lateral enamel of the Swartkrans specimen SK 37. To image this specimen we used the PCSOM with 10x lens and 1:1 adapter using a clearing medium but no cover slip.

Figure 5. Sterkfontein specimen Stw 37 immersed in ethanol at low magnification showing lateral striae along the hypocone.

Figure 6. Swartkrans specimen SK 875 immersed in ethanol and imaged using stereoscopic microscopy. Striae of Retzius can be seen reaching the outer enamel surface. The area highlighted in this image has been enlarged on Figures 7 and 8.

Figure 7. Detail of striae (arrowed) reaching the outer enamel surface on SK 875 imaged using PCSOM with 20x and 1:1 adapter. A cover slip and a drop of immersion oil were placed over the specimen. Prisms and cross striations can be recognized in this image running broadly from right to left. The highlighted area has been enlarged on Figure 8.

Figure 8. Striae (long white arrows) and cross striation can be easily recognized in the specimen SK 875 near the outer surface of lateral enamel. Seven cross striations could be counted in this specimen.

Figure 9. *P. robustus* molar SKW 4769. Eight cross striations were identified between Retzius lines in this specimen. A marked stria can be observed between the first and second cross striations on the left side.

Figure 10. Graphical representation of the angles formed between the striae/EDJ derived from our samples and from data of Ramirez Rozzi (2002). The EDJ was divided in three equal divisions and the angles were measured as in Schwartz et al., (2003).

Figure 11. Pattern of striae distribution on the *P. robustus* specimen SKX 21841, and the *A. africanus* specimen Stw 284. Striae numbers decrease toward the cervical end of the crown, as similarly observed in the anterior dentition of both taxa by Dean and Reid (2001a).

Table 1.

A. africanus			***P. robustus***		
Specimen	**Tooth**	**Cusp**	**Specimen**	**Tooth**	**Cusp**
Stw 402	M^1	protocone	SK 849	M^1	paracone
Stw 252 K	M^1	mes-grooves	SKW 11	M^2	metacone
Stw 217	M^1	metacone	SKW 4768	M^2	hypocone
Stw 284	M^2	protocone	SK 35	M_2	metaconid
Stw 71	M^2	protocone	SK 37	M_2	hypoconid
Stw 37	M^3	hypocone	SK 55	M_2	hypoconid
Stw 252 H	M^3	mes cusps	SKW 4769	M_2	protoconid
Stw 11	M^3	metacone	SKX 21841	M^3	paracone
Stw 285	M_2	entoconid	SK 875	frg	
Stw 96	M_3	metaconid	SKW 4771	frg	
Stw 90	M_3	protoconid			
Stw 93	?	?			
Stw 190	frg	hypocone			
Stw 325	?	?			
Stw 590	frg	?			

Table 2.

		N	Min	Max	Mean	SE	SD
P. robustus	cervical	10	25.25	37.8	30	1.15	3.6
	lateral	10	17.4	29.3	26. 1	1.1	3.4
	cuspal	5	10.5	18.4	13.9	1.7	3.8
A. africanus	cervical	15	33.8	51.4	38	1.1	4.3
	lateral	13	23	35	27.9	0.9	3.5
	cuspal	5	12	19.5	16.4	1.37	3.1
E. A. *Paranthropus*	cervical	12	15	36	26	1.8	6.5
	lateral	12	17	38	26.7	2.0	6.9
	cuspal	12	7	25	13.2	1.5	5.1

Table 3.

Taxa	Spec. number	N. striae
A. africanus	Stw 402 (M^1)	75
	Stw 284 (M^2)	82
	Stw 37 (M^3)	57
	Stw 285 (M_2)	62
P. robustus	SKW 4768 (M^2)	33
	SKW 4769 (M_2)	41
	SK 35 (M_2)	37
	SK 875 (?)	49
	SKX 21841 (M^3)	56

Table 4.

	Specimen	**Periodicity**	**Specimen**	**Periodicity**
A. africanus			***P. robustus***	
	Stw 40	6; 7	SKX 21841	6
	Stw 284	6; 7	SK 4769	8
	Stw 11	6	SK 4771	7
	Stw 285	7	SKW 35	6
	Stw 252k	8	SK 1524	7
	Stw 90	7	SK 875	6
	Stw 188	6	SKW 37	7
	Taung	8		
Mean		**6.6** (6) **6.8** (7)		**6.9** (7) **7** (8)
SD		0.78 or 0.69		0.69 or 0.81
Range		6 to 8		6 to 8
Mode		**6** (6) **7**(7)		**7**

Figures 1A and 1B

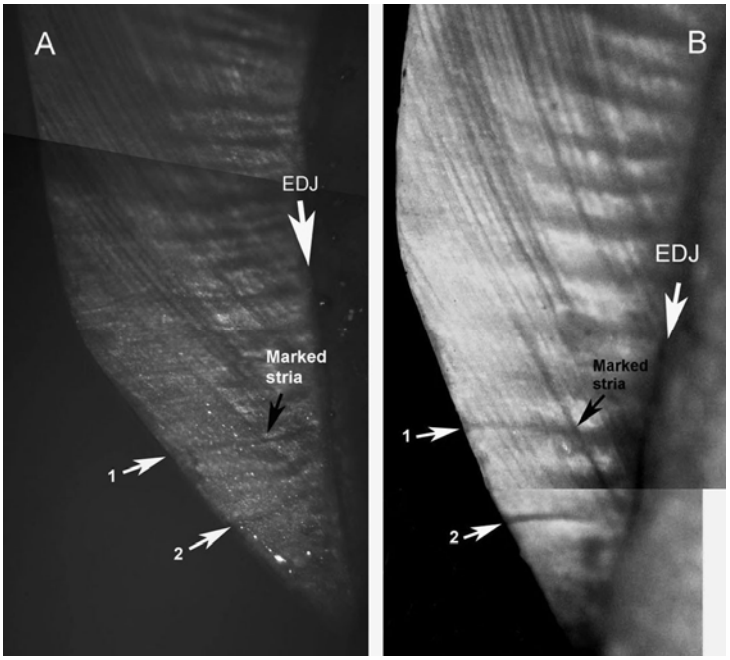
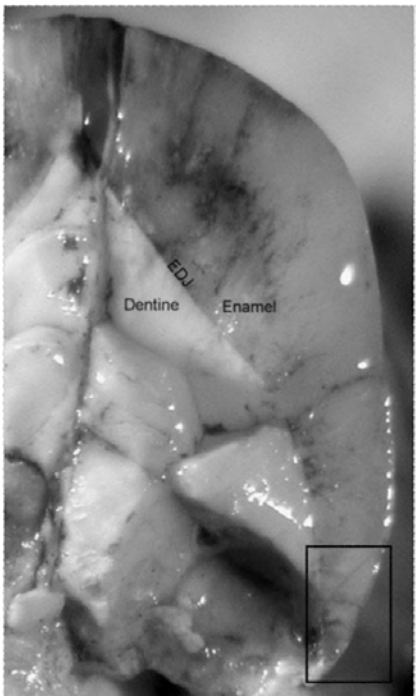


Figure 2.



Figures 3A and 3B.

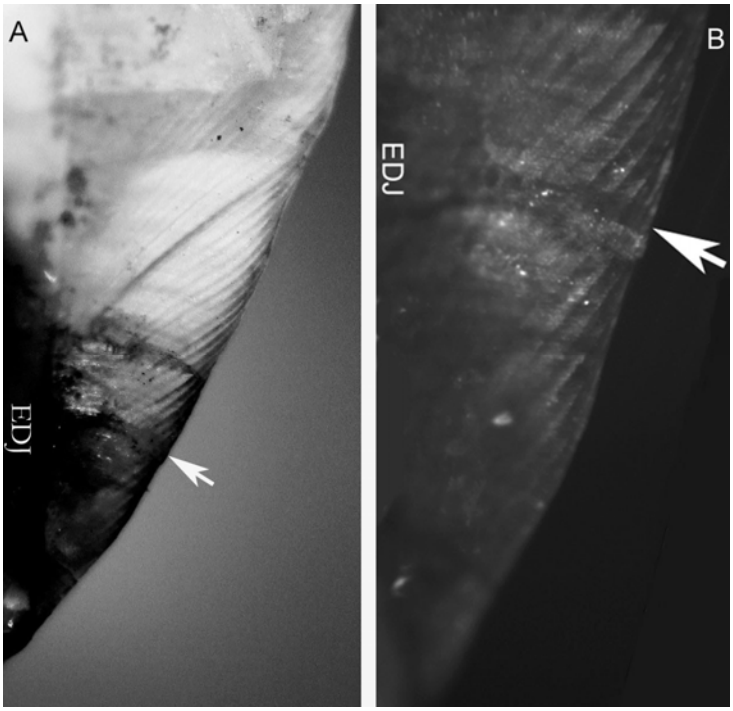
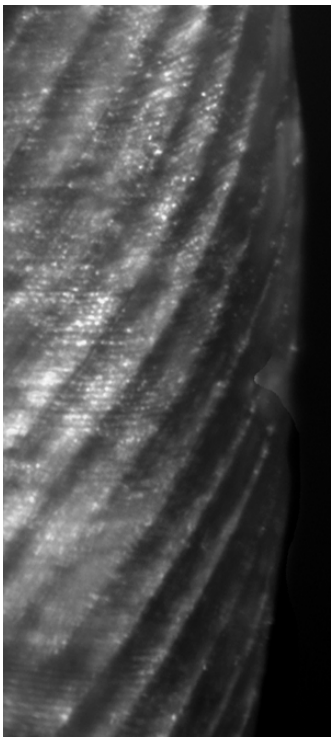


Figure 4.



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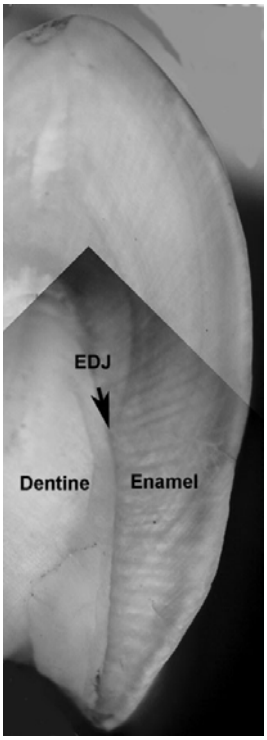

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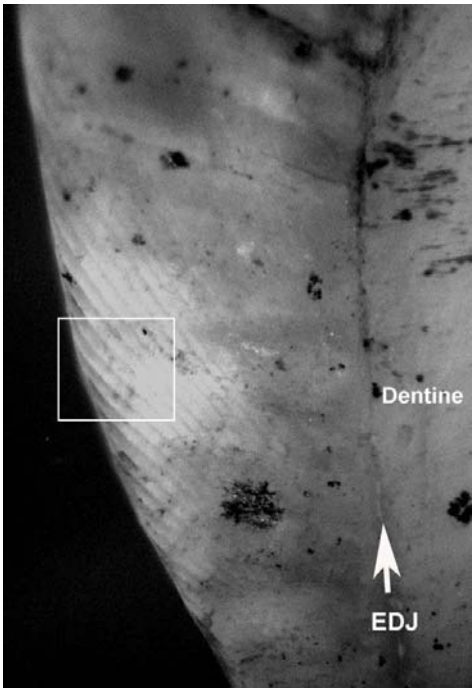
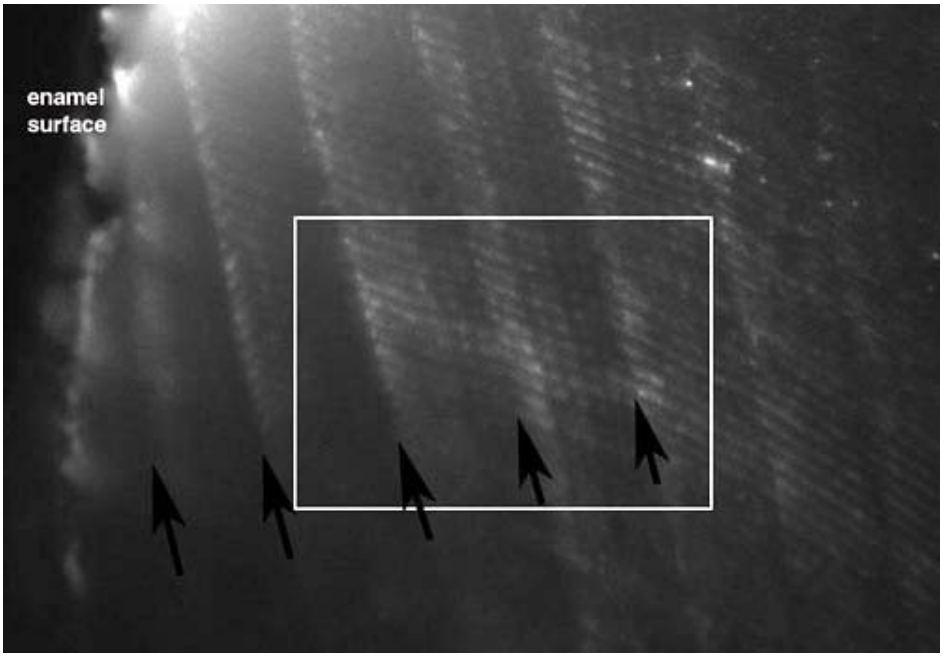


Figure 7.



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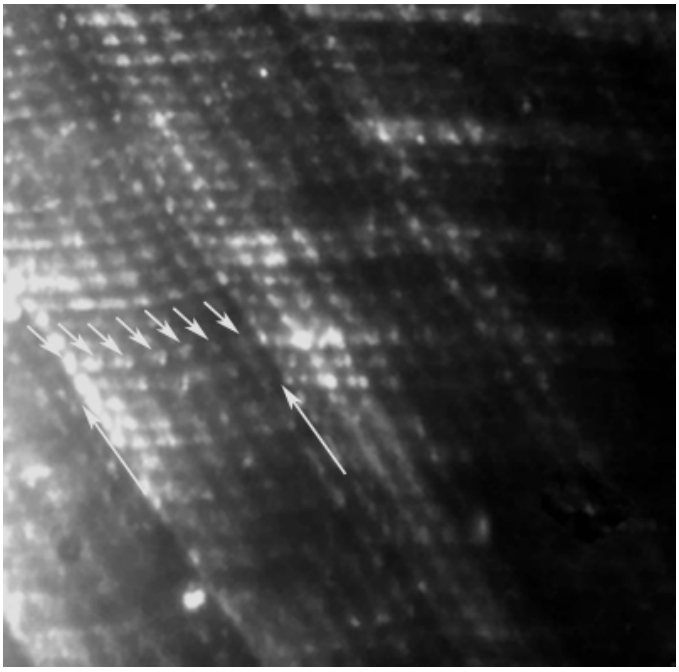

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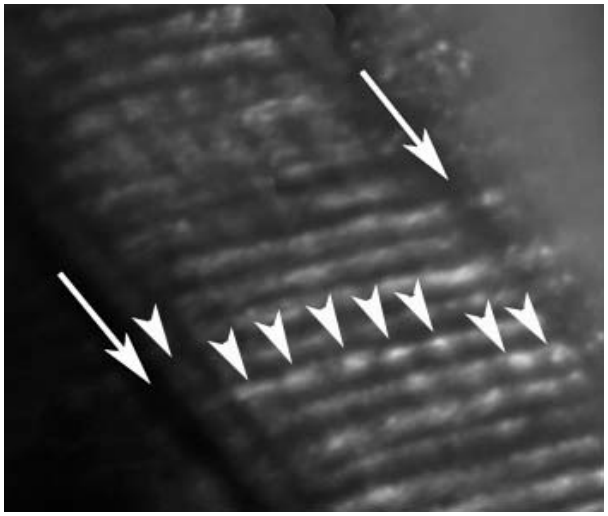


Figure 10.

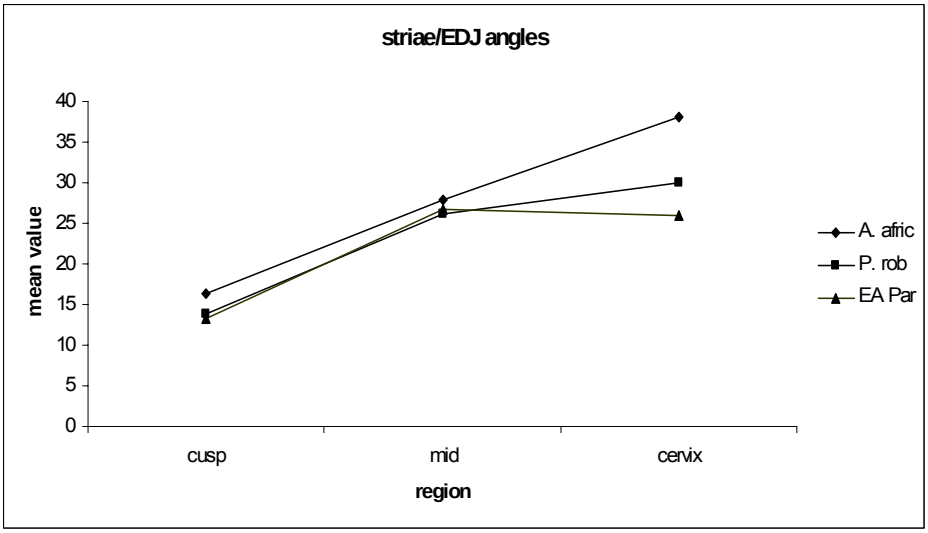
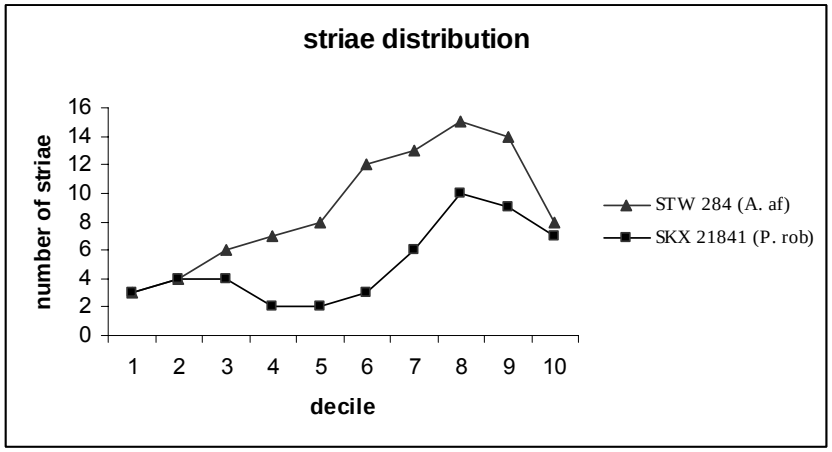

striae/EDJ angles
40
35
30
25
20
15
10
5
0
mean value
cusp
mid
cervix
region
A. afric
P. rob
EA Par

Figure 11.


striae distribution
number of striae
16
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
decile
STW 284 (A. af)
SKX 21841 (P. rob)

ANNEX 10.1 : Supplementary information of striae/EDJ angles in fossil taxa

Table 10. 1. Angles measured for each individual tooth in *A. africanus*.

Specimen number	Area	Mean
Stw 284	Cuspal	20 (2)
	Lateral	31.3 (6)
	Cervical	40.6 (5)
Stw 96	Cuspal	14.6 (3)
	Lateral	28 (5)
	Cervical	39.3 (4)
Stw 90	Cuspal	21 (2)
	Lateral	30.7 (7)
	Cervical	34.7 (7)
Stw 11	Cuspal	16.5 (2)
	Lateral	28.5(7)
	Cervical	51.4 (7)
Stw 37	Cuspal	18.0 (2)
	Lateral	35.0 (5)
	Cervical	38.0 (5)
Stw 93	Cuspal	19.5 (3)
	Lateral	23.0 (4)
	Cervical	37.0 (4)
Stw 190	Cuspal	?
	Lateral	?
	Cervical	36.0 (4)
Stw 71	Cuspal	19.0 (4)
	Lateral	28.2 (5)
	Cervical	35.0 (2)
Stw 402	Cuspal	18.0 (1)
	Lateral	25.5 (4)
	Cervical	33.8 (5)
Stw 252 K	Cuspal	?
	Lateral	?
	Cervical	38.3 (4)
Stw 217	Cuspal	?
	Lateral	23.6 (3)
	Cervical	36.0 (4)
Stw 325	Cuspal	?
	Lateral	25.7 (4)
	Cervical	40.3 (4)
Stw 252 H	Cuspal	14.5 (2)
	Lateral	25.3 (3)
	Cervical	34.0 (4)
Stw 590	Cuspal	?
	Lateral	32.0 (4)
	Cervical	39.4 (5)
Stw 285	Cuspal	12.0 (1)
	Lateral	26.0 (3)

	Cervical	36.0 (7)

Table 10.2. Angles measured in each specimen of *P. robustus.*

Spec number	Area	Mean
SK 55	Cuspal	10.5 (2)
	Lateral	26.1 (5)
	Cervical	27.2 (7)
Sk 35	Cuspal	18.4 (1)
	Lateral	23.9 (5)
	Cervical	27.9 (5)
Sk 37	Cuspal	?
	Lateral	?
	Cervical	37.8 (5)
SKX 21841	Cuspal	16.8 (2)
	Lateral	28.5 (5)
	Cervical	33.8 (6)
SK 849	Cuspal	?
	Lateral	29.3 (3)
	Cervical	30.6 (4)
Sk 875	Cuspal	?
	Lateral	26.3 (4)
	Cervical	27.3 (4)
SK 1524	Cuspal	?
	Lateral	17.4 (3)
	Cervical	17.36 (3)
SKW 11	Cuspal	?
	Lateral	28.6 (4)
	Cervical	25.2 (4)
SKW 4771	Cuspal	12.5 (2)
	Lateral	26.5 (3)
	Cervical	30.1 (4)
SKW 4769	Cuspal	10.7 (2)
	Lateral	28.5 (3)
	Cervical	31.2 (4)
SKW 4768	Cuspal	?
	Lateral	25.6 (4)
	Cervical	29.6 (4)