Variation in enamel development of South African fossil hominids

Rodrigo S. Lacruz a,*, Fernando Ramirez Rozzi b, c, Timothy G. Bromage d

Abstract

Dental tissues provide important insights into aspects of hominin 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 called striae of Retzius. These enamel features were studied in the molars of two well known South African hominin 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 periodicity of seven days in these small-bodied hominids. Important differences were observed in the inferred mechanisms of enamel development between 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 a much shorter 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 suggest the presence of different mechanisms of amelogenesis, and thus tooth development, in these taxa.

Keywords: Plio-Pleistocene hominids; Crown formation time; Portable confocal microscopy; Australopithecus; Paranthropus

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 and 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 hominin 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 hominin pelvic, facial, and dental architectures (Lovejoy et al., 1999; McCollum, 1999; McCollum and 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 hominin postcranial morphology.

Teeth are also appropriate for the study of developmental mechanisms because 1) “combined within one organ system...
Some differences in crown development of the anterior dentition have been previously described between the South African hominids *Australopithecus africanus* and *Paranthropus robustus* (Bromage and Dean, 1985; Dean and Reid, 2001a), but no data on molar crown formation time have been reported. Additionally, angles formed between the striae of Retzius and the enamel dentine junction (EDJ), which relate to ameloblast rate of differentiation (Boyd, 1964), have not been quantified. Recently, Lacruz and Bromage (2006) have recorded daily ap- positional 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 nine days (Dean et al., 1993). In the East African fossil sample, the periodicity is known for a single individual of *P. boisei*, the specimen KNM ER-733, for which a premolar and a molar both showed a seven day rhythm (Beynon and Dean, 1987; Dean, 1987); and for two *A. anamensis* molars for which a peri- ocity of seven days was reported (Ward et al., 2001). Dean et al. (2001) determined the periodicity for a single sectioned Neanderthal molar to be nine days. The paucity of striae peri- ocity studies in fossil hominids indicates the great difficulty in obtaining such information in this 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 instru- ment was purposefully designed for paleoanthropological 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 (Beynon and Dean, 1988; Dean, 1988), but these features are more readily observed with the PCSOM, which also allows observation and measurement of cross striation intervals (Lacruz and Bromage, 2006). Therefore, PCSOM 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 as- pects 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 lit- erature for other fossil hominid taxa and modern humans.

**Enamel development**

Two main microstructural markers may be identified in hominin enamel: cross striations and striae of Retzius, the lat- ter 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 are 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 because more cuspal cells become active before 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 in an 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 of 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 (Boyd, 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 Ma (Vrba, 1995) and ten *P. robustus* from Swartkrans Members 1–3 dated between 1.8 and 1.5 Ma (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 scanning optical microscopy (Bromage et al., 2005, in press). Figure 1 shows imaged striae in the Swartkrans specimen SKX 21841 using both incident light (Fig. 1B) and PCSOM (Fig. 1A). 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.

Following Schwartz et al. (2003), striae/EDJ angles were measured at the point of contact between these two features. Three equal lengths of the EDJ (cuspal, lateral, and cervical) were measured, 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 15.3: 326). 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.

It was possible to obtain crown formation time 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 and 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., Fig. 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 10 equal divisions, in a similar manner to that described by Dean and Reid (2001a).

Because developmental time varies from mesial to distal cusps (e.g., Kraus and 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

### Table 1

Specimens of *A. africanus* and *P. robustus* molars used in this study indicating the tooth type and the area studied. mes = mesial; frg = fragment.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Tooth</th>
<th>Cusp</th>
<th>Specimen</th>
<th>Tooth</th>
<th>Cusp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stw 402</td>
<td>M₁</td>
<td>protocone</td>
<td>SK 849</td>
<td>M₁</td>
<td>paracone</td>
</tr>
<tr>
<td>Stw 252 K</td>
<td>M₁</td>
<td>mes-grooves</td>
<td>SKW 11</td>
<td>M₁</td>
<td>metacone</td>
</tr>
<tr>
<td>Stw 217</td>
<td>M₁</td>
<td>metacone</td>
<td>SKW 4768</td>
<td>M₁</td>
<td>hypacon</td>
</tr>
<tr>
<td>Stw 284</td>
<td>M₁</td>
<td>protocone</td>
<td>SK 35</td>
<td>M₁</td>
<td>metacoid</td>
</tr>
<tr>
<td>Stw 71</td>
<td>M₁</td>
<td>protocone</td>
<td>SK 37</td>
<td>M₂</td>
<td>hypacon</td>
</tr>
<tr>
<td>Stw 37</td>
<td>M₁</td>
<td>hypacon</td>
<td>SK 55</td>
<td>M₂</td>
<td>hypacon</td>
</tr>
<tr>
<td>Stw 252 H</td>
<td>M₁</td>
<td>mes cusps</td>
<td>SKW 4769</td>
<td>M₁</td>
<td>protoconid</td>
</tr>
<tr>
<td>Stw 11</td>
<td>M₁</td>
<td>metacone</td>
<td>SKX 21841</td>
<td>M₁</td>
<td>paracone</td>
</tr>
<tr>
<td>Stw 285</td>
<td>M₁</td>
<td>entoconid</td>
<td>SK 875</td>
<td>frg</td>
<td>frg</td>
</tr>
<tr>
<td>Stw 96</td>
<td>M₁</td>
<td>metaconid</td>
<td>SKW 4771</td>
<td>frg</td>
<td>frg</td>
</tr>
<tr>
<td>Stw 90</td>
<td>M₁</td>
<td>protocoon</td>
<td>SK 875</td>
<td>frg</td>
<td>frg</td>
</tr>
<tr>
<td>Stw 93</td>
<td>frg</td>
<td>frg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stw 190</td>
<td>frg</td>
<td>hypacon</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stw 325</td>
<td>frg</td>
<td>frg</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stw 590</td>
<td>frg</td>
<td>frg</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
point at which striae do not reach the enamel surface. Because prism decussation was observed near the EDJ in the *A. africanaus* 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 150 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 observations were made on the outer enamel surface in regions located at the boundary between the cervical and lateral enamel where the striae tended to be more prominent. Cross striations were observed and counted directly on specimens using the PCSOM (Figs. 6–9).

Results

The pattern of ameloblast differentiation based on the angles formed between striae of Retzius and the EDJ...

Fig. 1A (left) shows the cervical region of a *P. robustus* molar imaged with the PCSOM using 5× 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 Figure 1A are easily identifiable on Figure 1B.

Fig. 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.
distinguishes between the South African taxa (Fig. 10; Table 2). South African *Paranthropus* shows only a slight, not significant ($p > 0.05$) increase in angle from the lateral to cervical enamel. In contrast, *A. africanus* shows a marked increase in stria/EDJ angles from the cusp to the cervix (Fig. 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 seven (Table 4). In cases in which cross striations were less easily resolved, two equally likely periodicities were considered (Table 4).

An important feature characterizing molar formation is the number of lateral striae (Ramirez Rozzi, 1998; Reid and 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 pattern similar to that observed by Dean and Reid (2001a) in the anterior dentition and suggests a decrease in striae number towards the end of crown formation (Fig. 11).

In our effort to obtain crown formation time, 82 striae were counted on the protocone of the *A. africanus* specimen Stw 284 (M2). Twelve additional perikymata on the hypocone (the 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. Together these give 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 (M1). 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 impossible 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 ($x = 5.5$ microns; Lacruz and Bromage, 2006) and presuming a 7 day periodicity (this study), a period of 1.08 years for cuspal and 1.66 for lateral enamel was established. Together these yield 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; Reid et al.,...
it is 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 (M3), 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 (3.48 mm) was divided by the mean cuspal appositional rate calculated for this specimen (5.7 microns); a value of 1.67 years was obtained. Together these yield 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 that favor, for instance, greater angles in *A. africanus*. Instead Figure 10 is likely to indicate biological differences. A second problem concerns variation in developmental times of different cusps of the same tooth. However, by taking into consideration perikymata in addition to the last cervical stria, as detailed in Ramirez Rozzi (1993), this problem can be addressed in assessments of CFT.

The present study greatly increases 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 five studies of Plio-Pleistocene hominid enamel representing a total of five individuals (Beynon and Dean, 1987; Dean, 1987; Dean et al., 1993, 2001; Ward 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). Based on about 15...
individuals, the mean striae periodicity in molars of both species is 7 days, with ranges of 6 to 8 days 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 and Scandret, 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). Both taxa are similar in size to *Pan troglodytes* (Smith and 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 and Reid, 2001a; Reid and Dean, 2006).
The tooth types and duration of the entire enamel crown formation considered here for the fossil taxa are: M1 (2.74 years), M2 (3.0 to 3.2 years), and M3 (2.72 years). The largest histological study of modern human molars to date (Reid and Dean, 2006) showed that South African specimens had slightly shorter crown formation times than did those of European descent. The mean values reported by Reid and Dean (2006) for modern South Africans were: 3.00 years for the M1 protocone (n = 20). Compared with the values of modern South Africans, the fossil hominid molar crowns formed more quickly, especially the Swartkrans specimen SKX 21841. Since Reid and Dean (2006) did not consider total crown formation time but only values from individual mesial cusps, it is likely that their values for the whole crown would increase, thus increasing the differences between modern humans and the fossil taxa measured here.

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. The cuspal enamel values obtained using this equation [Stw 402 (1.10 years), Stw 284 (1.53 years), and SKX 21841 (2.02 years)] compare well with our cuspal values for A. africanus [Stw 402 (1.08 years), Stw 284 (1.50 years), but are substantially more than our value for P. robustus [SKX 21841 (1.67 years)]. It may be possible that the cuspal values reported here for SKX 21841, especially in the inner enamel, have 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 Dean et al.’s (2001) regression equations may overestimate the values of the thick-enamed P. robustus.

In our sample, P. robustus appear to have fewer striae than do A. africanus. However, these differences may 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 a study of mesiobuccal cusps of modern humans, Reid et al. (1998a) found the largest number of striae in the protocone and hypoconid of four medieval French individuals in an M1 metaconid, whereas the largest values in the maxilla were recorded in M1 and M2 protocones. 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

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>
<thead>
<tr>
<th>Taxa</th>
<th>Spec. number</th>
<th>N. striae</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. africanus</td>
<td>Stw 402 (M1)</td>
<td>75</td>
</tr>
<tr>
<td></td>
<td>Stw 284 (M2)</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>Stw 37 (M1)</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>Stw 285 (M2)</td>
<td>62</td>
</tr>
<tr>
<td>P. robustus</td>
<td>SKW 4768 (M2)</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>SKW 4769 (M3)</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>SK 35 (M1)</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>SK 875 (?)</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>SKX 21841 (M3)</td>
<td>56</td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Spec. number</th>
<th>N. striae</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. africanus</td>
<td>Stw 402 (M1)</td>
<td>75</td>
</tr>
<tr>
<td></td>
<td>Stw 284 (M2)</td>
<td>82</td>
</tr>
<tr>
<td></td>
<td>Stw 37 (M1)</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>Stw 285 (M2)</td>
<td>62</td>
</tr>
<tr>
<td>P. robustus</td>
<td>SKW 4768 (M2)</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>SKW 4769 (M3)</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>SK 35 (M1)</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>SK 875 (?)</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>SKX 21841 (M3)</td>
<td>56</td>
</tr>
</tbody>
</table>

Fig. 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).

Fig. 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 is also the case in the anterior dentition of both taxa (Dean and Reid, 2001a).
and mandibular) showed greater numbers of striae than the other molar 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 M2 was recorded on the metacone, but on the paracone of the M1.

Based on these studies 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 M2 protocone and in P. robustus in the M3 paracone, whereas the lowest values in each taxon are found in M1 (A. africanus) and M3 (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 and Dean, 1985; Beynon and Dean, 1988; Dean and 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 and Dean, 1985; Beynon and Dean, 1986; Beynon and Dean, 1988; Beynon, 1992; Ramirez Rozzi, 1993; Dean and 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 of the crown; the acute angles also characterize eastern African Paranthropus. Thus the cervical area of the crown appears to have developed faster in Paranthropus than in A. africanus. These results confirm the differences noted in other studies based on perikymata distributions on anterior teeth (Bromage and Dean, 1985; Dean, 1987; Beynon and 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 and Wood, 1987). This may be associated with differences in enamel thickness whereby Paranthropus has thicker cuspal enamel than A. africanus (Robinson, 1956; Martin, 1985; Grine and Martin, 1988; Macho and 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 has 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 and Dean, 1985; Dean and 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 and Dean, 1988; Grine and Martin, 1988; Ramirez Rozzi, 1993). Additionally, daily ameloblast secretion rates are faster in P. robustus than in A. africanus (Lacruz and Bromage, 2006) and are similar to the limited data on secretion rates available for East African Paranthropus (Beynon and 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 toward the rapid formation of large and thick-enamede molars. This supports a previous hypothesis (Grine and Martin, 1988) that the paranthropines share a number of features in the enamel microstructure which are not present in A. africanus.

Conclusion

This study provides the largest account of striae periodicity for any fossil hominid taxa, and these data indicate that the mean periodicity value was seven days in the small-bodied hominids A. africanus and P. robustus. The CPT reported for three hominid molars [Stw 402 (M1) 2.74 years; Stw 284 (M2) 3.0 to 3.2 years; and SKX 21841 (M3) 2.72 years] is lower than mean values reported for molar crown development in modern humans (Reid et al., 1998a; Reid and 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 and Wood, 1986), suggesting clear differences during amelogenesis between the extinct and extant hominid taxa (Lacruz and Bromage, 2006). However, important differences were found in patterns of crown development between A. africanaus and P. robustus.

Acknowledgements

This research was generously funded by Dr. D. McSherry, the Leakey Foundation, and the Palaeoanthropological Scientific Trust (PAST). Their contributions are greatly appreciated. We would like to thank Mike Raath, Francis Thackeray, and Stephany Potze for making available the materials under their care. M.C. Dean, K. Kuykendall, and B. Wood are thanked for providing very useful suggestions and comments.

References


