An examination of dental development in *Graecopithecus freybergi* (=*Ouranopithecus macedoniensis*)

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Abstract

This study examined enamel thickness and dental development in *Graecopithecus freybergi* (=*Ouranopithecus macedoniensis*), a late Miocene hominoid from Greece. Comparative emphasis was placed on *Proconsul*, *Afropithecus*, *Dryopithecus*, *Lufengpithecus*, and *Gigantopithecus*, fossil apes that vary in enamel thickness and patterns of development. In addition, comparisons were made with *Paranthropus* to investigate reported similarities in enamel thickness.

Several sections of a right lower third molar were generated, from which enamel thickness and aspects of the enamel and dentine microstructure were determined. Data from parallel sections shed light on the effects of section obliquity, which may influence determination of both enamel thickness and crown formation time. *Graecopithecus* has relatively thick enamel, greater than any fossil ape but less than *Paranthropus*, with which it does show similarity in prism path and Hunter–Schreger band morphology. Aspects of enamel microstructure, including the periodicity and daily secretion rate, are similar to most extant and fossil apes, especially *Afropithecus*. Total crown formation time was estimated to be 3.5 years, which is greater than published values for modern *Homo*, similar to *Pan*, and less than *Gigantopithecus*. Data on dentine secretion and extension rates suggest that coronal dentine formation was relatively slow, but comparative data are very limited. *Graecopithecus* shares a crown formation pattern with several thick-enamelled hominoids, in which cuspal enamel makes up a very large portion of crown area, is formed by a large cell cohort, and is formed in less than half of the total time of formation. In *Paranthropus*, this pattern appears to be even more extreme,

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which may result in thicker enamel formed in an even shorter time. Developmental similarities between *Paranthropus* and *Graecopithecus* are interpreted to be parallelisms due to similarities in the mechanical demands of their diets.

Introduction

Graecopithecus freybergi (=*Ouranopithecus macedoniensis*) is a hominoid taxon known from several localities in Greece that are biochronologically dated to approximately 9.0–9.5 Ma (Andrews et al., 1996). Only dental and cranial remains have been described to date, including several mandibles and maxillae, and a partial face (de Bonis et al., 1990; de Bonis and Koufos, 1994; Koufos, 1995; de Bonis et al., 1998; Begun, 2002). *Graecopithecus* has been reconstructed as a large-bodied ape that occupied open environments and fed on hard food items such as roots, tubers, seeds, and nuts (de Bonis and Koufos, 1994). Several authors have noted that certain features of the face and dentition of *G. freybergi* are similar to fossil hominids, and are likely parallelisms related to similarities in diet and environment (Andrews, 1990; Andrews and Martin, 1991; Begun, 2002). Ungar and Kay (1995) demonstrated that, based on shearing quotients derived from second molars, *G. freybergi* may have consumed harder foods than all other living or fossil apes. This dietary strategy may explain some of the apparent similarities to hominids, particularly to *Paranthropus,* which is also inferred to have been a hard object feeder (Grine, 1986; Grine and Kay, 1988).

Recent work on a number of Miocene hominoids and Plio-Pleistocene hominids has provided insight into dental development in human and other primate lineages (reviewed in Dean, 2000; Smith et al., 2003a). Incremental features of the enamel in particular have received substantial attention from paleoanthropologists, as they may permit estimates of the age at death (Bromage and Dean, 1985; Dean, 1987; Stringer et al., 1990; Dean et al., 1993a; Dean et al., 2001) and age at M1 emergence in fossil specimens representing juvenile individuals (Dean et al., 1993a; Kelley,

1997, 2002; Kelley and Smith, 2003). In addition, dental growth trajectories determined from daily rates of enamel secretion (e.g., Beynon et al., 1998; Dean, 1998a; Dean et al., 2001) and crown formation times (reviewed in Smith et al., 2003a) provide insight into developmental pathways. This information may help to select between common ancestry and independent functional adaptations as explanations for shared possession of, for example, thick enamel.

The aim of this study was to examine dental development in *G. freybergi* based on a sectioned right lower third molar, which was previously examined by Andrews and Martin (1991). Relative enamel thickness was calculated and incremental features of the enamel and dentine microstructure were quantified, which allowed us to reconstruct the rate and duration of crown formation, as well as the rates of coronal dentine secretion and extension. This information was compared to that extracted from other extant and fossil hominoids, which provided insight into the potential pathways of enamel formation discussed by Grine and Martin (1988). Particular emphasis was given to the development of thick enamel in *Paranthropus* so that the similarity with *Graecopithecus* noted by Andrews and Martin (1991) could be further investigated.

Background

Taxonomy and phylogeny

The type specimen of *G. freybergi* is a fragmentary mandible from Pyrgos, a site near Athens, that was described by von Koenigswald (1972), and prepared further and described by Martin and Andrews (1984). Additional material has been recovered from the northern localities of Ravin de

la Pluie (de Bonis et al., 1974, 1975; de Bonis and Melentis, 1977a,b; de Bonis et al., 1998), Xirochori (de Bonis et al., 1990; de Bonis and Koufos, 1993), and Nikiti (Koufos 1993, 1995). The issue of the taxonomic nomenclature for this material has been the subject of much debate (Martin and Andrews, 1984; de Bonis and Koufos, 1993; Koufos, 1993; Andrews et al., 1996; Cameron, 1997; Begun, 2002). Among the authors of the present paper, there is a difference of opinion on this issue; the nomenclature used here reflects the preference of the first two authors.

A second issue that has been debated is the phylogenetic position of *G. freybergi*. De Bonis and colleagues have suggested that this material is most similar to *Australopithecus afarensis*, representing a member of the Hominidae that was ancestral to *Australopithecus* and *Homo* (de Bonis et al., 1981, 1990; de Bonis and Koufos, 1993; Koufos, 1993; de Bonis and Koufos, 1994; de Bonis et al., 1998). However, Andrews (1990, 1992) argued that the similarities used to support the exclusive relationship between *G. freybergi* and hominids are shared ancestral characters, whereas several shared derived features unite this hominoid with both African apes and hominids (see also Dean and Delson, 1992; Kelley, 2001; Begun, 2002).

Incremental dental development

The development of incremental features in enamel and dentine has been reviewed in numerous sources (Boyde, 1989; Dean et al., 1993b; FitzGerald, 1998; Risnes, 1998; Dean, 2000; Smith et al., 2003a), and will only be briefly summarized here. Enamel and dentine formation are characterized by the production of long- and short-period increments, respectively known as striae of Retzius (in enamel) or Andresen's lines (in dentine), and cross-striations (in enamel) or von Ebner's line (in dentine) (Dean et al. 1993b; Dean, 1995a; Dean and Scandrett, 1996). Cross-striations show a 24-hour frequency, and are used as a standard to determine the periodicity of long-period features in both tissues. Long-period features show a consistent periodicity within all teeth belonging to the same individual, although there is variation among individuals within a species (Beynon, 1992; FitzGerald, 1998; Schwartz et al., 2001). The quantification of these long- and short-period features permits determination of the rate and duration of dental development. Additional incremental features that are referred to in this study include short-period features known as laminations, and sub-daily features known as intradian lines (Smith et al., 2003a).

Studies on incremental features in dentine have yielded important information complementing data derived from the enamel, and have provided additional information on rates of dentine formation and extension. However, recent histological data on dentine secretion and/or extension rate in hominoids have been limited to studies of one or a few teeth each from one gorilla, one orangutan, and one chimpanzee (Beynon et al., 1991a; Dean, 1995a,b, 1998a,b, 2000), two gibbons and one siamang (Dirks, 1998; Dean, 1998b), two individuals each of *Proconsul heseloni* and *Proconsul nyanzae* (Beynon et al., 1998), two individuals of *Dryopithecus laietanus* (Kelley et al., 2001), one individual of *Lufengpithecus hudienensis* (Schwartz et al., 2003), two modern humans, and two fossil hominids (*Homo habilis*: OH 16 and *Paranthropus robustus*: SK 63) (Dean and Beynon, 1991; Dean et al., 1993a,b; Dean, 1995a,b; Dean and Scandrett, 1995, 1996; Dean, 2000). For a review of several older studies on dentine, see Dean (1995a) and Dean and Scandrett (1995). In this study, we will use enamel and dentine microstructure to gain insight into the evolutionary developmental biology of *G. freybergi*, as demonstrated by other studies of hominoid taxonomy, evolutionary relationships, and life history strategies (e.g., Beynon et al., 1998; Dean, 2000; Dean et al., 2001; Kelley and Smith, 2003; Smith et al., 2003a).

Materials and methods

Histological preparation

One isolated right lower third molar from Ravin de la Pluie (RPL 641) was initially prepared according to procedures described in Smith et al. (2003a), which produced a single thin section

approximately 60 μm thick that did not preserve the entire crown, and two embedded block faces (anterior and posterior halves of the mesial cusps). Dean et al. (1992) noted that attempts to cut very thin sections of fossil teeth are often unsuccessful, and they advocated cutting a slightly thicker initial section to minimize the risk of losing data. Therefore, a second thin section approximately 100 μm thick was produced following similar procedures described in Reid et al. (1998a,b), which generated a complete superior section relative to the first. The thin sections and block faces were examined under polarizing light microscopy (PLM), tandem scanning reflected light microscopy (TSRLM), and scanning electron microscopy (SEM). Images were collected using 35 mm film, analog, and digital cameras, and were analyzed with NIH Image software and/or a reticular eyepiece (Smith et al., 2003a).

Enamel thickness and enamel microstructure

Relative enamel thickness (RET) was measured using established methodology (Martin, 1983, 1985; Smith et al., 2003a) from the block faces and the complete thin section. Using measurements of the area of the enamel cap (c), the length of the enamel dentine junction (e), and the area of the dentine under the enamel cap (b), RET was calculated as $[(c/e)/\sqrt{b}]*100$, which provides a dimensionless index that facilitates interspecific comparisons. Small corrections were made to compensate for the cervical tips that were missing in several planes of section.

Data on enamel microstructure were primarily taken from the complete thin section, although both sections were examined; differences between these sections are reported below. Several aspects of the enamel microstructure were quantified: periodicity, daily secretion rate (DSR), angle of intersection of the developing front with the enamel dentine junction (EDJ), total number and spacing of Retzius lines, and crown formation time. The periodicity (number of cross-striations between Retzius lines) was determined in several areas where Retzius lines meet the surface of the enamel and terminate as perikymata. Observations were also made on laminations, which were

defined as closely spaced features that run parallel to the Retzius lines or the position of the developing enamel front (Smith et al., 2003a). The DSR was measured from repeat intervals of thousands of cross-striations grouped into inner and outer zones in the cervical region, and inner, middle, and outer zones in the lateral and cuspal regions using a $50\times$ objective. We defined cross-striations as light and dark *bands* that are perpendicular to the long axis of the prism, in contrast to intradian lines, which were defined as slight subdivisions or *thin lines* that further subdivide cross-striations. The angle of intersection between the developing front and the EDJ was measured in cuspal, lateral, and cervical enamel using a $25\times$ objective. The position of the developing front was represented by (irregularly spaced) accentuated lines in the cuspal enamel and by Retzius lines in the lateral and cervical enamel. The total number of Retzius lines was counted on photomontages and under the microscope; a small correction was made for the missing cervical enamel of the metaconid and protoconid. To determine Retzius line spacing at the enamel surface (perikymata distribution), the distance from the first imbricational stria to the estimated cervix was divided into ten equal intervals, and the number of Retzius lines per interval was counted.

Crown formation time was calculated as the sum of cuspal and imbricational enamel formation times. These two regions were differentiated by the position of the first imbricational stria to meet the surface of the tooth. Cuspal formation time was estimated for each cusp by dividing the linear cuspal enamel thickness by the average cuspal DSR. Linear thickness measurements were taken from the most anterior block face, as this face showed the least section obliquity. The average DSR was determined from measurements of cross-striations from the EDJ to the surface of both cusps. (Due to the relatively straight course of the prisms, we did not feel that it was necessary to apply a correction factor to linear cuspal thickness, as Risnes [1986] has suggested for human premolars.) Imbricational formation time was determined by multiplying the total number of Retzius lines by the periodicity. Total crown formation time was determined by combining these two times

in the protoconid and adding an estimate of 0.1 years to correct for the final period of (non-overlapping) hypoconid formation (Reid et al., 1998a,b; Smith et al., 2003a). In addition, the areas of cuspal and imbricational enamel were measured from an overview, which facilitated integration of data on crown formation time and crown area. Finally, counts of Retzius lines were made between a well-defined pair of accentuated lines (E_0 and E_1) in the imbricational enamel of both cusps, which permitted registration of the stages of enamel formation between cusps.

Dentine microstructure

In an ideal section, counts of long-period Andresen's lines in the dentine provide an independent check of the crown formation time determined from enamel. This was done separately for the dentine corresponding to cuspal and imbricational enamel formation. Eleven accentuated lines were identified in the dentine (D_1–D_{11}), several of which were related to diffuse accentuated bands in the cuspal enamel or to the approximate ends of cuspal and imbricational enamel formation. The angle of intersection between each accentuated band and the EDJ was measured. Counts and measurements were made of the Andresen's lines between each pair of accentuated lines, which yielded the timing between accentuations and the local rate of dentine secretion. Because dentine secretion rate varies, separate values are given where possible for axial dentine (along a line from the tip of the dentine horn to the projected pulpal tip) and coronal dentine near the EDJ (lateral dentine). In addition, the extension rate was determined by dividing the distance along the EDJ between accentuated features by the time of formation. Finally, several dentine accentuations were related to accentuated bands in the cuspal enamel to construct a chronology of developmental stresses during crown formation.

Results

Enamel thickness and enamel microstructure

Table 1 shows the RET values of the four cross-sectional planes of the mesial cusps. Fig. 1 shows overviews of the planes from anterior to posterior. The value of the most anterior face (25.5) differs from the value of the most posterior face (29.0) by about 12%. We consider the former face to be closest to a plane passing through the tips of the dentine horns, and the higher value of the latter face to be an artifact resulting from an oblique plane of section.

The overviews show that the decussation pattern in this tooth is unusual for hominoids in the relative lack of "gnarled enamel" over the dentine horns. Narrow Hunter–Schreger bands (HSB) run from the EDJ to the surface of the enamel with little deviation from a straight path, although they show differences in width and length from anterior to posterior planes, suggesting that the plane of section may affect assessment of the degree of development of HSB.

The periodicity in this tooth is eight cross-striations between Retzius lines (Fig. 2). In some areas, laminations complicate the determination of this value, as they range in appearance from 6–8 evenly spaced features between Retzius lines (Fig. 2c). In contrast to Retzius lines, individual cross-striations cannot be seen in areas where laminations are expressed (although intradian lines are infrequently seen), nor are the laminations expressed as perikymata where they intersect the surface of the tooth (Fig. 3). Laminations are

Table 1
Relative enamel thickness (RET) values for *Graecopithecus freybergi*

Face	b	c	e	c/e	RET
Anterior	53.98	38.55	20.55	1.88	25.53
Middle	n/a	n/a	n/a	n/a	28.11
Thin section	53.47	42.50	20.54	2.07	28.30
Posterior	49.83	40.04	19.56	2.05	29.00

b=area of dentine under the enamel cap, c=area of enamel, e=length of enamel dentine junction. Values of b and c are in mm^2, e is in mm. The final column, relative enamel thickness (RET), is dimensionless. RET is calculated as $[(c/e)/\sqrt{b}]*100$. Absolute values for the middle face were not available as it was used in the generation of the thin section and was not photographed in the same manner as the other three faces prior to thin section preparation.
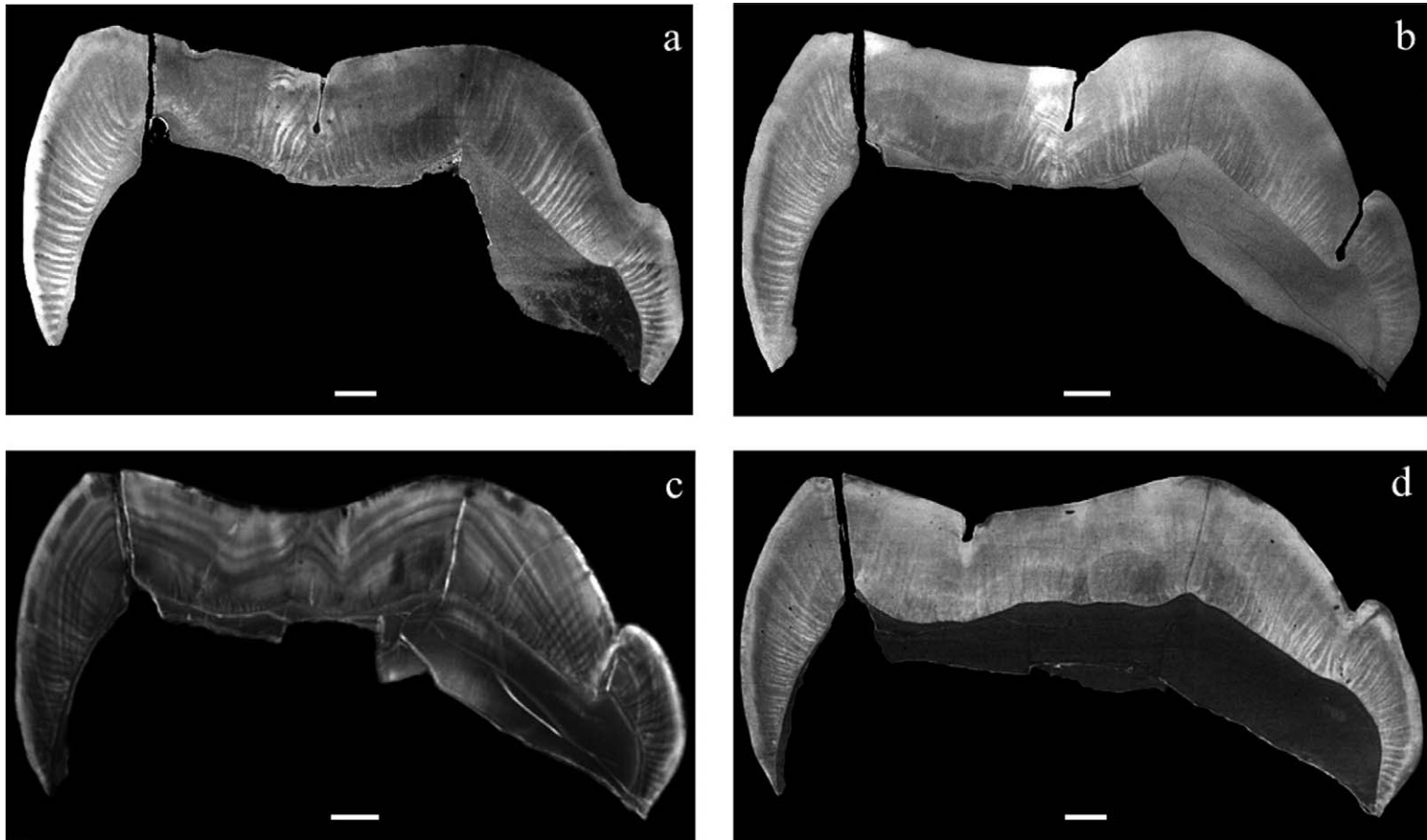
Fig. 1. Cross-sectional planes of the mesial cusps of a right lower third molar of *Graecopithecus freybergi*. The images represent the (a) most anterior section, (b) middle section, (c) thin section (posterior to b), and (d) most posterior section. The distance between the most anterior and the most posterior faces is estimated to be 1–1.5 mm. In each photo, the metaconid is on the left and the protoconid is on the right, and the scale bar at the bottom represents 1 mm.
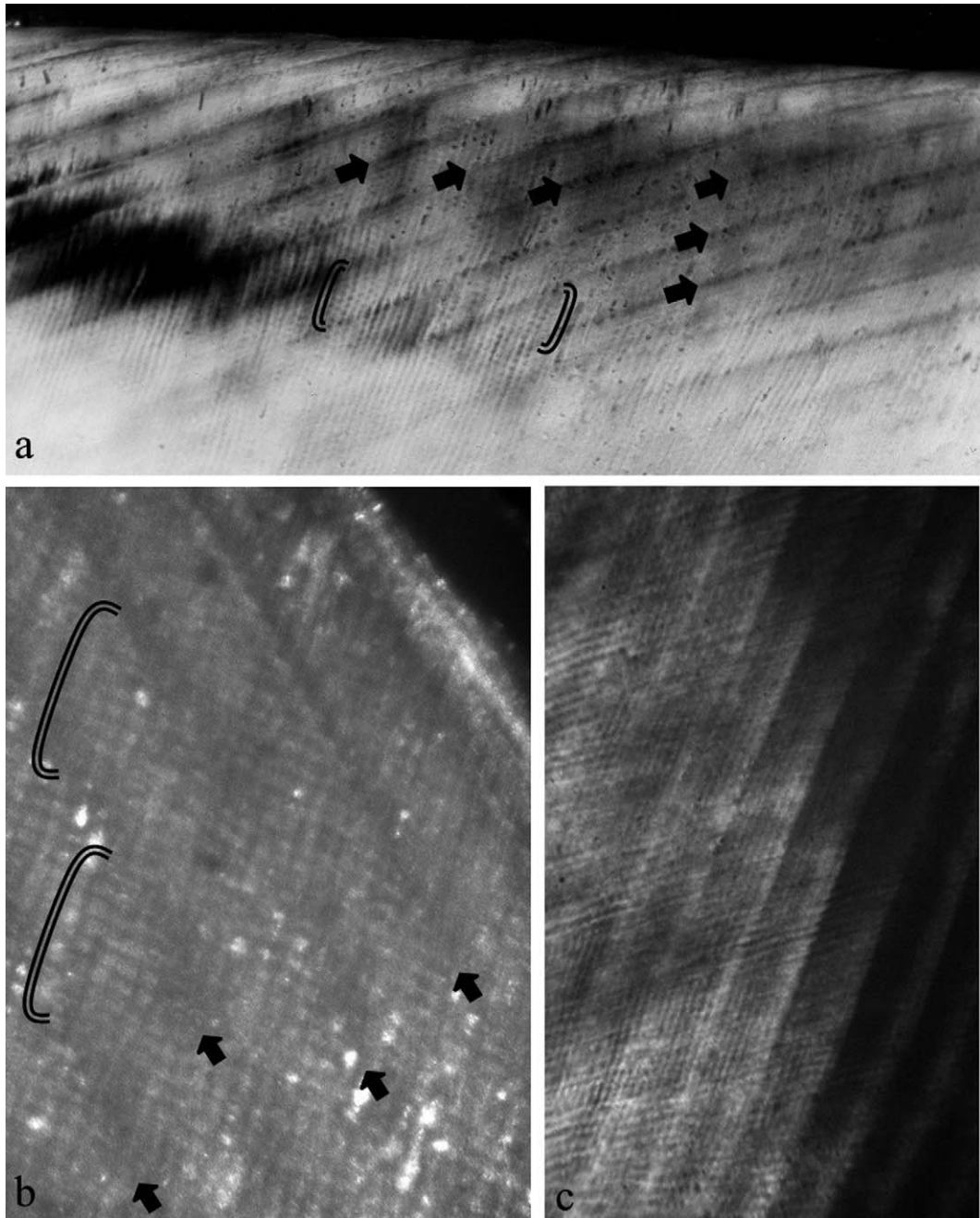
Fig. 2. The periodicity, or number of cross-striations between Retzius lines, in a right lower third molar of *Graecopithecus freybergi*. (a) PLM image showing Retzius lines (black arrows) running towards the surface of the tooth, and eight cross-striations between pairs of lines (bracketed). The field width is 630 μm. (b) TSRLM (confocal) image showing Retzius lines (black arrows) running to the surface of the tooth (not pictured) with eight cross-striations between lines (bracketed). (c) PLM image of Retzius lines running towards the surface of the tooth (to the right of the field) with six to eight laminations running between and parallel to each Retzius line. This illustrates a region where the periodicity was intentionally not determined. The field width is 200 μm.
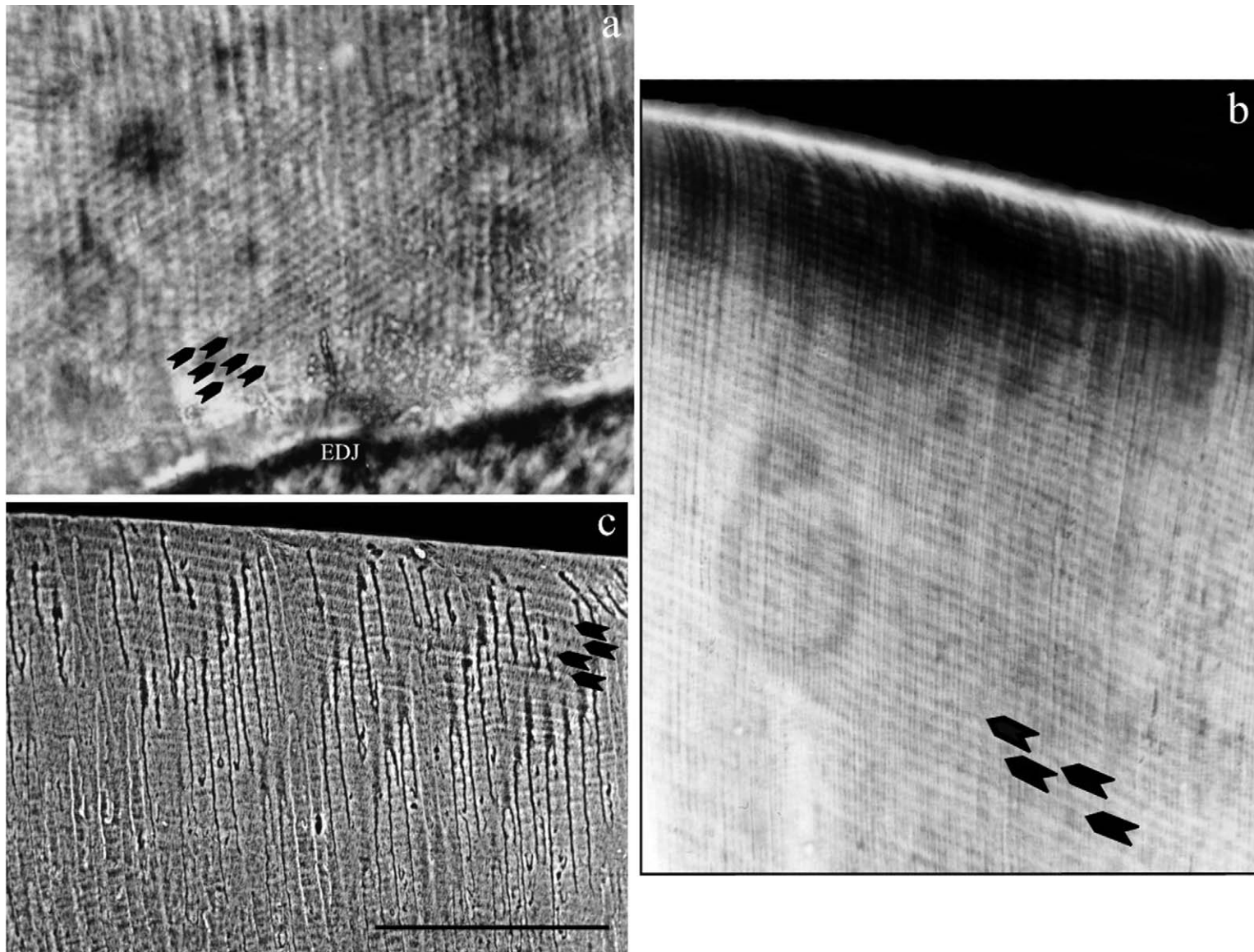
Fig. 3. Laminations (indicated by black bullets) in several areas of the crown of a right lower third molar of *Graecopithecus freybergi*. (a) PLM image of laminations at the EDJ (labeled) in the cuspal enamel, which have a spacing of approximately 3.7 μm between lines (measured along prisms). The field width is 170 μm. (b) PLM image of laminations deep to the surface of the enamel in the later-formed cuspal enamel, which have a spacing of up to 7.4 μm. The first few Retzius lines reach the surface of the protoconid at the top of the image. The field width is 375 μm. (c) SEM image of laminations in a region nearby to Figure 3b, showing a transition of prismatic to aprismatic enamel at the surface of the tooth. The laminations are spaced 6.6 μm apart just below the surface. The scale bar equals 100 μm.

Table 2
Average daily secretion rate (DSR) in *Graecopithecus freybergi*

Cusp	Region	Inner zone	Middle zone	Outer zone
Metaconid				
	Cuspal[a]	4.08 ± 0.68 (12)	4.38 ± 0.57 (12)	4.56 ± 0.51 (12)
	Lateral	3.71 ± 0.38 (19)	4.78 ± 0.50 (21)	3.99 ± 0.43 (15)
	Cervical	3.24 ± 0.33 (11)	–	4.52 ± 0.47 (12)
Protoconid				
	Cuspal	4.21 ± 0.51 (15)	4.53 ± 0.32 (15)	4.06 ± 0.20 (13)
	Lateral	3.89 ± 0.44 (18)	4.83 ± 0.44 (15)	4.87 ± 1.20 (21)
	Cervical	3.42 ± 0.62 (18)	–	3.85 ± 0.57 (17)
Overall				
	Cuspal	4.15 ± 0.59 (27)	4.46 ± 0.44 (27)	4.30 ± 0.45 (25)
	Lateral	3.80 ± 0.41 (37)	4.80 ± 0.47 (36)	4.50 ± 1.05 (36)
	Cervical	3.35 ± 0.53 (29)	–	4.13 ± 0.62 (29)

Data derived from polarized light microscopy using a 50× objective. Three equal divisions made along the EDJ from the dentine horn to cervix define regions. Zones represent enamel depth within a particular region. In the cervical enamel, zones were divided into inner and outer only. Values in μm represent the average of all cross-striations measured from prisms within each region, standard deviation is reported as ±1 deviation, and number of prisms is in parentheses.
[a] Data for the cuspal region of the metaconid is reported here for the first thin section as it is considered less oblique (see text).

found most frequently near the EDJ, near the tooth surface, and also in association with accentuated cuspal bands. They are closely spaced at the EDJ and more widely spaced at the tooth surface, similar to patterns of cross-striations and Retzius lines, which result from a progressive increase in secretion rate from the EDJ to the tooth surface.

Table 2 shows the average daily secretion rate (DSR) for each of the eight crown areas, which range from 3.2–4.9 μm/day. (Single measurements on individual prisms range from 2.4–6.6 μm/day.) Rates generally increase from inner to outer zones and from cervical to cuspal regions, with two exceptions. In the metaconid, the average rate in middle lateral enamel is greater than outer lateral enamel. In the protoconid, the middle cuspal rate is greater than the outer cuspal rate. These trends are sufficiently robust to hold when the two cusps are combined into an overall value. Differences between equivalent areas in the two cusps are generally minor, save for differences of 0.5–0.9 μm/day in outer cervical, lateral, and cuspal areas.

In terms of more local cuspal secretion rates (required for determination of the cuspal enamel formation time), the metaconid cuspal DSR begins at approximately 3.1 μm/day near the EDJ, rises briefly to about 5.6 μm/day in the middle/outer

enamel, and ends at about 4.3 μm/day just below the surface (average 4.3 μm/day). The protoconid cuspal enamel begins at 3.7 μm/day, rises briefly to just over 5.3 μm/day in the inner/middle enamel, and ends at about 4.5 μm/day, showing a more uniform pattern of DSR than in the metaconid (average 4.3 μm/day). Average rates vary slightly depending on the area of cuspal enamel sampled, as well as the thin section examined. In the metaconid, the initial rate near the EDJ is approximately 0.5 μm/day lower in the first thin section than in the second thin section. The former was used in the determination of metaconid cuspal DSR as it appears to preserve a less oblique plane of section for this cusp, and the higher rate in the latter appears to be an artifact of obliquity.

The DSR is sometimes difficult to determine in areas that show high frequencies of intradian lines, such as in the middle and outer lateral and cuspal enamel, because they obscure cross-striation boundaries (Fig. 4). Cross-striations are frequently identified by "focusing through" layers of prisms under PLM and TSRLM, which helps to distinguish between cross-striations and intradian lines. Intradian lines are closely spaced (less than 3–4 μm), although this is not a sufficient criterion to distinguish sub-daily from daily features, since
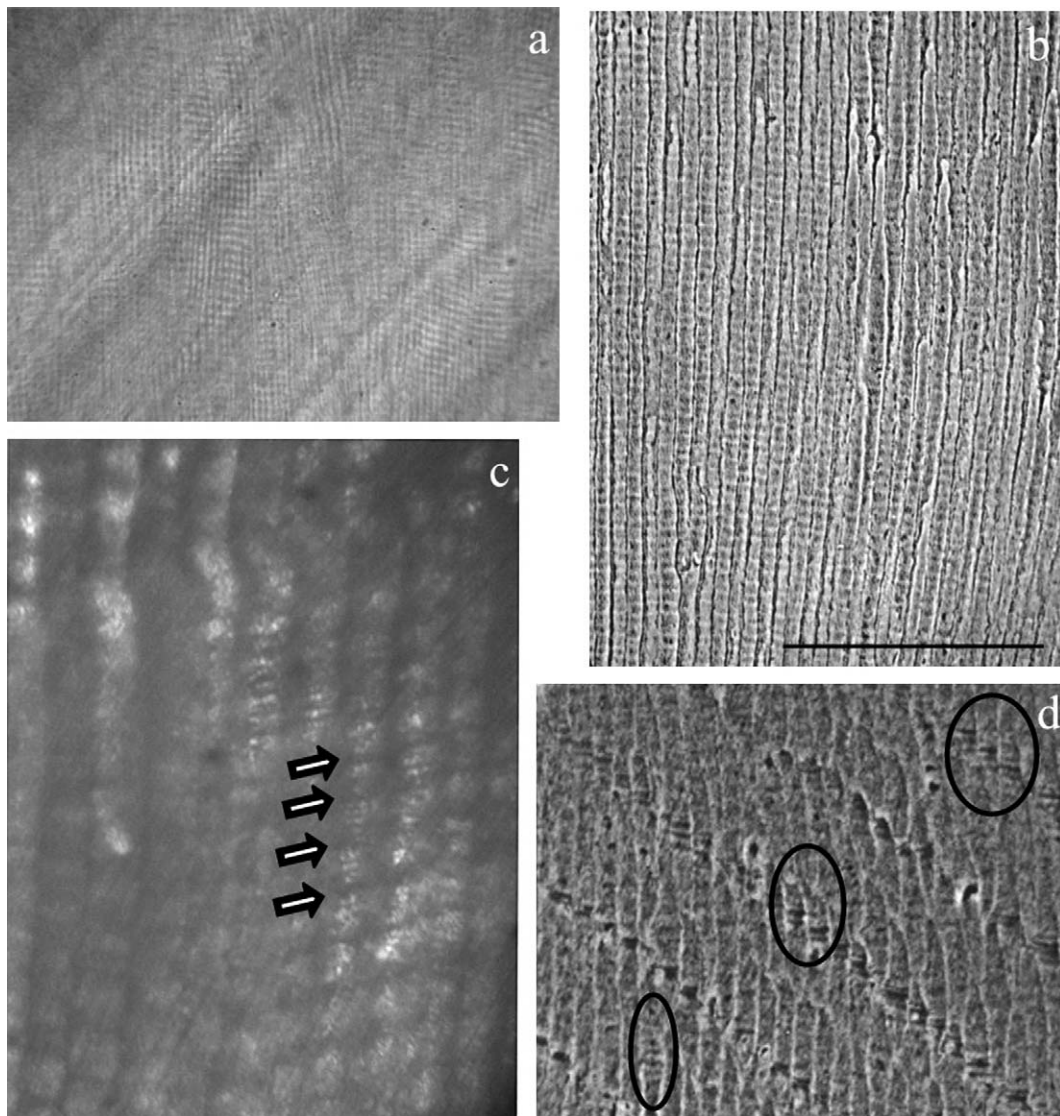
Fig. 4. Cross-striations and intradian lines in a right lower third molar of *Graecopithecus freybergi*. (a) PLM image of cross-striations in the cuspal enamel, which are perpendicular to the prisms that run vertically toward the surface of the tooth, and have an average spacing of 5.4 μm in this area. (Dark bands running from the lower left to the upper right are diffuse, irregularly-spaced, accentuated features of the cuspal enamel noted in the text). The field width is 345 μm. (b) SEM image of closely spaced cross-striations in the middle/outer cuspal enamel, (oriented similar to those in a), and spaced 4.1 μm apart on average in this area. Note the relatively straight course of prisms from the bottom of the image toward the tooth surface (beyond the top of field), characteristic of the majority of cuspal enamel in this tooth. The scale bar equals 100 μm. (c) TSRLM (confocal) image of intradian lines between cross-striations. Enamel prisms run toward the top of the image, cross-striations are the light and dark bands that bisect prisms almost perpendicularly (arrows), and intradian lines are the finer lines between cross-striations. (d) SEM image showing prisms running vertically and Retzius lines running from the lower right towards the tooth surface (beyond top of the image), with fine intradian lines (circled) in the prisms near the Retzius lines, which are 3.0–3.5 μm apart. The field width is 145 μm. (Note: cross-striations are difficult to discern here clearly, and are not indicated.)

Table 3
Angle of intersection of the developing front with the enamel dentine junction (EDJ)

Cusp	Cuspal[a]	Lateral	Cervical
Metaconid	28.3 ± 5.7 (11)	39.4 ± 5.4 (8)	39.1 ± 7.3 (9)
Protoconid	22.5 ± 5.1 (7)	37.9 ± 2.7 (8)	46.3 ± 6.0 (6)

Angles are presented as average degrees ±1 standard deviation. The number of angles measured is in parentheses. Individual values range from 15–46 degrees in the metaconid and 15–55 degrees in the protoconid. Combined overall values are not reported, as it appears there may be developmental differences between cusps.

[a]It was not possible to sample the initial period of cuspal crown extension, as there are no measurable features for the first 100–150 days of formation in either cusp.

these values are within the range of cross-striation widths in some areas.

Table 3 shows the average angle of intersection between the developing enamel front and the EDJ, which generally increases from cuspal to cervical regions and may imply a decrease in extension rate. Differences between cusps are apparent: the protoconid shows lower angles than the metaconid in the cuspal and lateral regions, suggesting that the protoconid may initially extend more rapidly. It appears that where accentuated cuspal bands are found initiating at the EDJ in both cusps, the angles of these features are higher than features in the adjacent enamel, suggesting a potential decrease in extension rate (or increase in secretion rate) that may be related to the stressors registered by the accentuated band.

The total numbers of Retzius lines in the metaconid and protoconid are 63–64 and 83–84, respectively, which includes estimations of 3–4 and 6–7 missing striae at the respective cervical tips. The first thin section shows 61–63 Retzius lines in the metaconid, which also includes 7–9 estimated striae at the tip. Fig. 5 shows the distribution of these lines at the surface in the metaconid and protoconid of the second section.

The crown formation time is shown in Table 4. Formation times of the metaconid and protoconid are estimated to be 2.74–2.76 and 3.35–3.38 years, respectively. Total crown formation time is estimated by adding an estimate of 0.1 years for the

final (non-overlapping) period of hypoconid formation to the protoconid time, which yields 3.45–3.48 years. Fig. 6 shows that the proportions of cuspal and imbricational cross-sectional area are 85% and 15% of the total crown area, respectively. The relative timing of initiation and completion of cuspal and imbricational enamel is shown in Fig. 7. Based on the position of the two accentuated lines (E_0 and E_1), it is clear that the metaconid initiated calcification after the protoconid and completed both cuspal and imbricational enamel formation earlier than the protoconid.

Dentine microstructure

Although both thin sections show numerous long-period Andresen's lines, the second thin section was analyzed because it preserves much more dentine than the first, particularly under the protoconid. However, when the protoconid profiles of the most anterior block face and second thin section are compared, the most anterior face shows a lower absolute thickness of enamel and a higher dentine horn, indicating that the thin section is missing the tip of the dentine horn (Fig. 8). Despite the thin section not being an ideal plane of section, the Andresen's lines in the remaining dentine corresponding to the cuspal and imbricational regions of the enamel were mapped, counted, and measured (Figs. 9 and 10).

Table 5 shows the angle of intersection of the eleven accentuated dentine lines with the EDJ, as well as the number of Andresen's lines between accentuations, the maximum and minimum measured secretion rates, and the extension rate of each interval. The dentine based estimates of the cuspal and imbricational enamel formation times are 544 days and 616–696 days, respectively (68 and 77–87 total lines multiplied by the eight day periodicity), which yields an overall estimate of 1160–1240 days, or 3.2–3.4 years, for the protoconid. The number of lines equivalent to the imbricational enamel is presented as a range, as it is not possible to discern the exact Andresen's line that corresponds to the end of enamel formation because of missing cervical enamel. In addition, interglobular dentine and calcospherites obscure
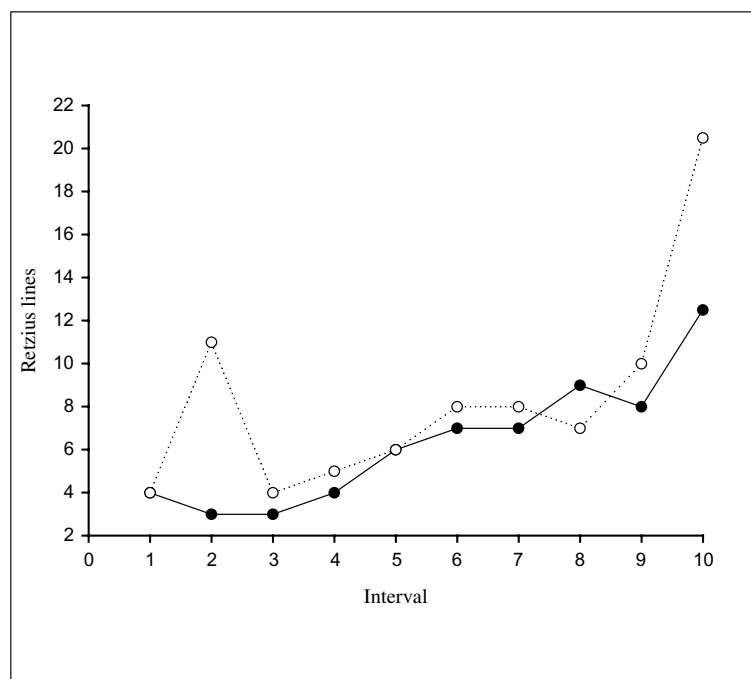
Fig. 5. Retzius line/perikymata distribution in the mesial cusps of a right lower third molar of *Graecopithecus freybergi*, shown in ten intervals from cuspal to cervical surfaces. In the metaconid (closed circles), Retzius lines are distributed over 5.8 mm (each interval represents 0.58 mm), and in the protoconid (open circles), these lines were distributed over 7.2 mm (each interval represents 0.72 mm). Several areas in the protoconid showed varying degrees of curvature, such as the fissure of the cingulum and the cervical tip (intervals 2 and 10, respectively), which displayed very closely spaced Retzius lines. The tenth interval of both cusps represents an average of the estimated number of lines due to the missing cervices; values for these regions should be regarded as estimates only.

Table 4
Third molar crown formation time in *Graecopithecus freybergi*

Cusp	Cuspal			Imbricational			Combined	
	Thick	DSR	Days	Ret	Per	Days	Days	Years
Metaconid	2150	4.34	495	63–64	8	504–512	999–1007	2.74–2.76
Protoconid	2390	4.27	560	83–84	8	664–672	1224–1232	3.35–3.38

Thick=Maximum cuspal enamel thickness in μm determined from the least oblique plane of section. DSR=Average cuspal daily secretion rate in μm/day, determined from measurements of cross-striations made from the EDJ to the cusp tip. Days=Cuspal formation time, determined by dividing the thickness by the rate. Ret=Number of Retzius lines. Per=Periodicity (number of cross-striations between Retzius lines). Days=Imbricational enamel formation, determined by multiplying the number of Retzius lines by the periodicity. The value for total crown formation time reported in the text reflects the protoconid formation time added to a correction of 0.1 years for the period of non-overlapping hypoconid formation.

the Andresen's lines in a few areas, making exact counts difficult.

Dentine DSR appears to increase slightly in the axial dentine from the EDJ to the projected pulpal horn, save for the interval of the "incipient dentine horn" (D_5–D_6) corresponding to the enamel cingulum, which shows the highest DSR. The average secretion rate is 2.3 μm/day for the first year and a half of axial dentine formation, which is equivalent to the cuspal enamel formation period.
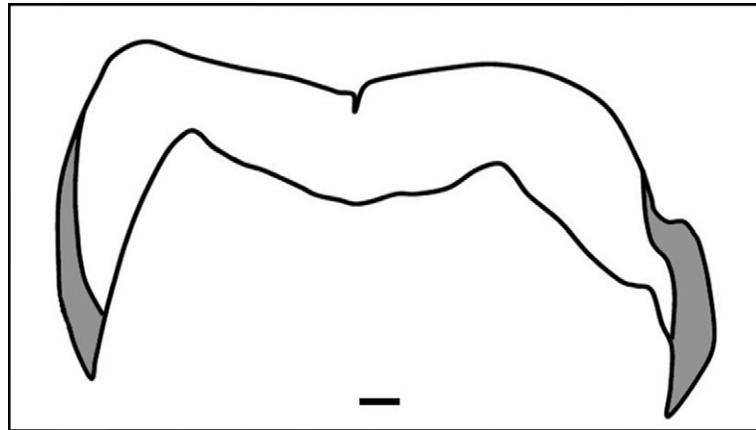
Fig. 6. Overview of the most anterior section of the mesial cusps in a right lower third molar of *Graecopithecus freybergi*. Cuspal enamel (not shaded), is defined by the position of the first Retzius line at the tooth surface, and represents 85% of the total crown area, while imbricational enamel (shaded) makes up the remaining 15%. The scale bar at the bottom represents 1 mm.

The ratio of dentine area to corresponding cuspal enamel area is 1:3, suggesting higher rates of secretion in the enamel. The extension rate of both tissues begins at a high initial rate and decreases towards the end of coronal dentine/enamel formation, excepting the area including the cingulum, which shows the highest local extension rate. Unfortunately, no root is preserved, which would provide rates of dentine secretion and extension corresponding to the periods of tooth emergence and root completion.

Fig. 11 shows a number of diffuse accentuated bands in the cuspal enamel that illustrate the position of the developing enamel front across both cusps, as well as the two accentuated lines in the imbricational enamel. Because the cuspal bands are composed of numerous irregularly spaced accentuations, it is not possible to determine an exact chronology of developmental stressors from the enamel. However, the presence of accentuated lines in both enamel and dentine permits registry between the two so that the dentine can be used to develop a chronology of events in the enamel. This tooth shows several irregularly timed periods of developmental stress for just over the first two years of formation, but does not show any signs of stress over the final 16 months of crown formation.

Discussion

Enamel thickness and enamel microstructure

The RET of 25.5 is less than the "hyper-thick" value of 28.34 reported for the same tooth by Andrews and Martin (1991). We feel that this new value is more accurate, as several planes of section have been measured in this study, and the most anterior face appears to have the highest dentine horns, the thinnest absolute enamel, and the lowest RET. This value is still greater than that of any other Miocene hominoid or extant primate. It is also greater than those of *Homo* and *Australopithecus africanus*, but is less than the value of 29.6 for *P. robustus* (Grine and Martin, 1988; Martin et al., 2003; Smith et al., 2003a). Fossil hominoids that appear to show a RET similar to *G. freybergi* include *Proconsul nyanzae* at 22.4 (Beynon et al., 1998), *Gigantopithecus blacki* at ∼23 (Dean and Schrenk, 2003), and *L. lufengensis* at 24.1 (Schwartz et al., 2003). *Paranthropus* has the absolutely thickest enamel of any known hominoid, with linear cuspal thickness ranging between 2.2–3.9 mm for molars (Beynon and Wood, 1986; Grine and Martin, 1988; Dean et al., 1993b; Dean and Schrenk, 2003). Only *G. blacki* shows an absolute cuspal thickness value (3.6–3.75 mm)
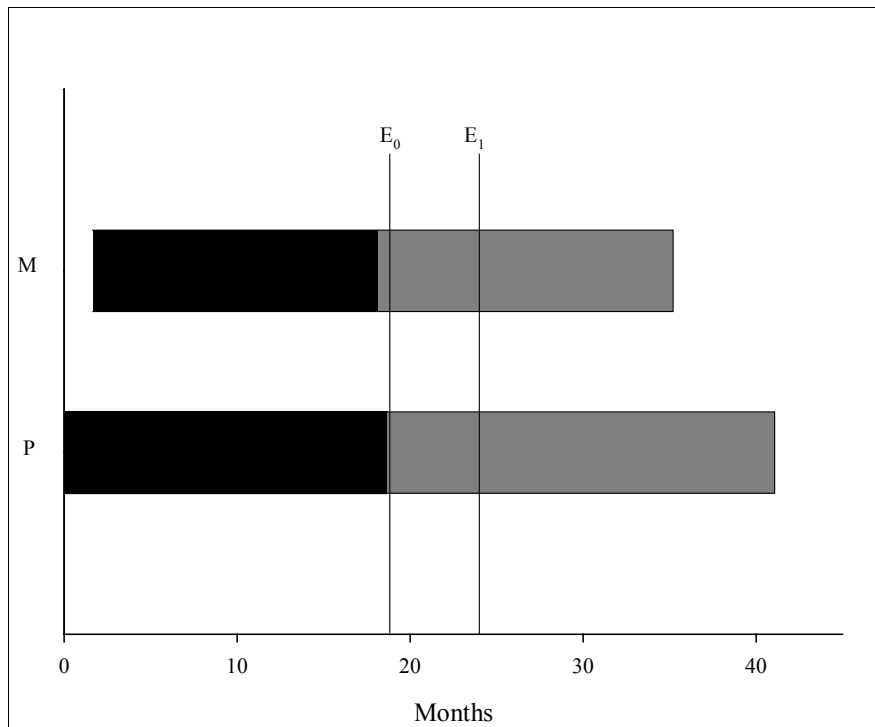
Fig. 7. Bar chart of mesial cusp development in a right lower third molar of *Graecopithecus freybergi*. The upper and lower bars represent the metaconid (M) and protoconid (P), respectively. Cuspal development is shown in black and imbricational enamel is shown in gray. In the metaconid, a dramatic accentuation (E_0) appeared between the second and third Retzius lines in the imbricational enamel, and a second accentuation (E_1) appeared between the eighteenth and nineteenth Retzius lines. In the protoconid, the first equivalent line (E_0) appeared at the beginning of imbricational formation (within the first Retzius interval), and the second line (E_1) appeared between the sixteenth and the seventeenth Retzius lines (illustrated in Fig. 11). This suggests 16 lines, or approximately 128 days between events. It appears that the metaconid initiated cuspal formation approximately 49 days after the protoconid, completed cuspal enamel formation two to three weeks earlier, and completed imbricational formation about 176 days earlier.

closer to the *Paranthropus* range than *G. freybergi* (2.15–2.39 mm), which may simply be a function of its large size (Dean and Schrenk, 2003).

The periodicity of eight cross-striations between Retzius lines in *G. freybergi* is within the known hominoid range of 5 to 12 (reviewed in Smith et al., 2003a: Table 3). Known periodicities range from 5 to 9 in Miocene apes, 6 to 11 in extant apes, 6 to 12 in modern humans, and 7 to 9 in *Paranthropus*. Recently, Smith et al. (2003b) demonstrated that, within hominoids, periodicity is significantly correlated with body mass, although this relationship does not explain low periodicity values found in large-bodied extant and subfossil lemurs (Schwartz et al., 2002). The daily secretion rates in *G. freybergi* are also similar to rates reported for

other extant and fossil apes, particularly *Afropithecus turkanensis* (Beynon et al., 1991a,b, 1998; Reid et al., 1998a; Kelley et al., 2001; Dean and Schrenk, 2003; Smith et al., 2003a), but are less than in *Paranthropus* (Beynon and Dean, 1987; Beynon and Wood, 1987; Dean et al., 1993a; but see Dean and Schrenk, 2003). The pattern of rate change through the crown of *G. freybergi* is similar to that seen in one of two teeth of *A. turkanensis*, which also decreased from the middle to outer cuspal enamel (Smith et al., 2003a). The latter study noted that published values for other primates also sometimes show a leveling off or decrease in DSR from the middle to outer cuspal enamel.

The pattern of average angle of intersection between the developing enamel front and the EDJ
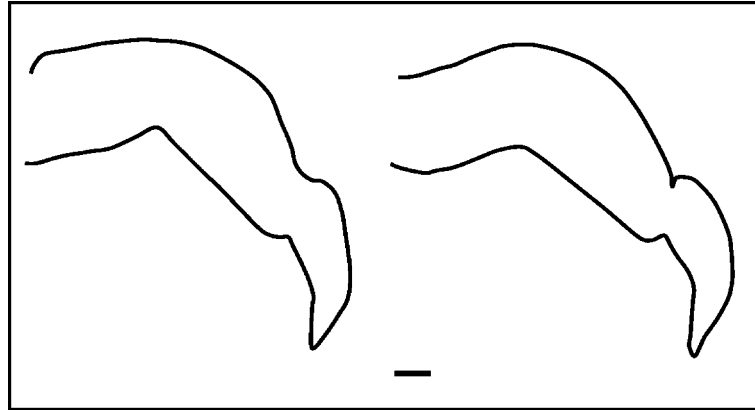
Fig. 8. The effect of obliquity on the profile of the protoconid in the most anterior face and thin section of a right lower third molar of *Graecopithecus freybergi* (planes a and c in Fig. 1). The most anterior profile on the left has thinner cuspal enamel and a higher dentine horn, in contrast to the profile of the thin section on the right, which has an exaggerated thickness of enamel and a dentine horn with artificially low relief. The scale bar at the bottom represents 1 mm.
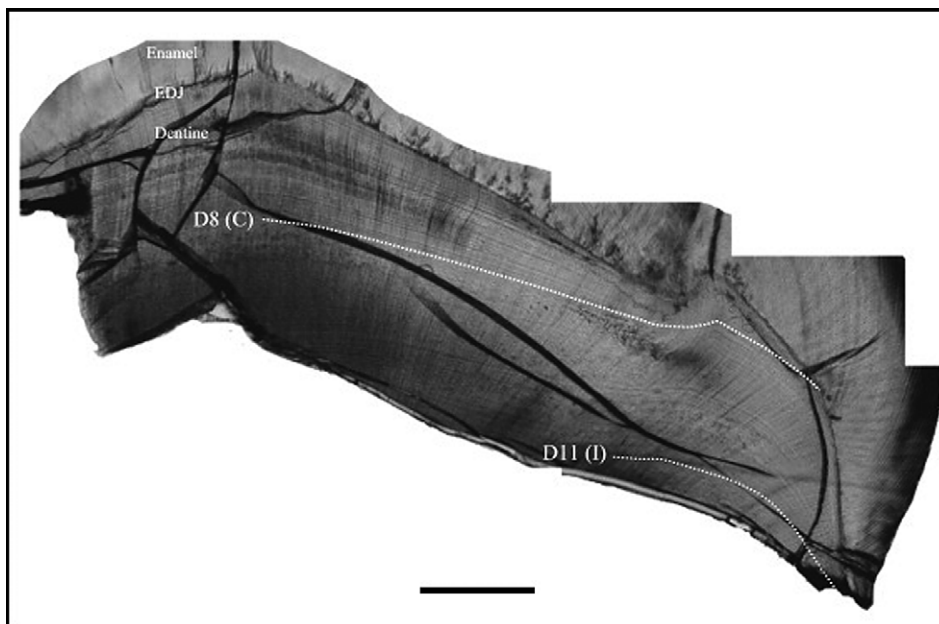

Fig. 9. Transmitted light montage of the dentine of a right lower third molar of *Graecopithecus freybergi*. Two accentuated lines in the dentine are highlighted, which correspond to the approximate end of cuspal (D_8) and imbricational enamel formation (D_{11}). Note that dentine in the axial region (dentine horn tip to projected pulpal horn tip) was preserved for the area corresponding to cuspal enamel and the beginning of imbricational enamel only. The scale bar at the bottom represents 1 mm.

from cuspal to cervical regions in *G. freybergi* is relatively uniform compared to some hominoids (Beynon et al., 1998; but see Ramirez Rozzi, 1993, 1997; Smith et al., 2003a). However, had the earliest-formed cuspal enamel contained more measurable features, it is likely that the average
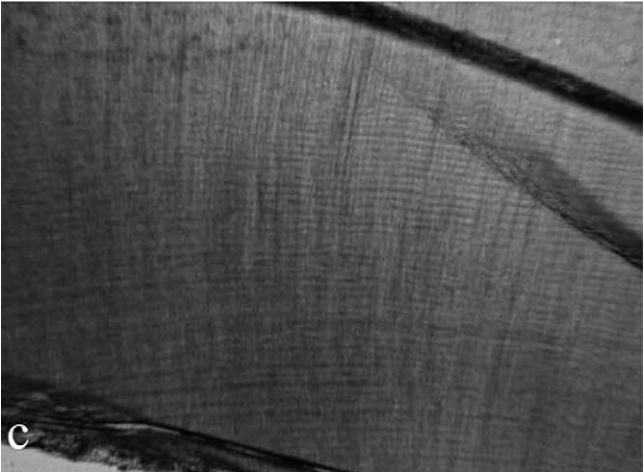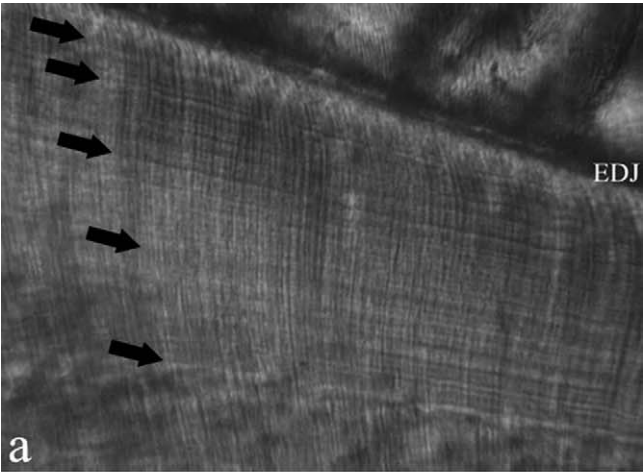
angle in the cuspal region would be somewhat lower, as this area typically shows the lowest angles. In addition, individual measurements suggest that the earliest- and last-formed enamel may be briefly characterized by lower and higher angles that are not apparent when data are reported as average regional values for each third of the crown. The implications of the absolute value and pattern of these angles for crown extension are further discussed in the section on methodological considerations (see below), where they are placed in the context of extension rate data derived from dentine.

The number of Retzius lines in the protoconid of *Graecopithecus* is in the middle of reported ranges of other fossil hominoids, except for *Lufengpithecus lufengensis* (Schwartz et al., 2003), which tends to have fewer than 100 Retzius lines in the longest-forming mesial cusp of its molar teeth (Beynon et al., 1998; Kelley et al., 2001; Dean and Schrenk, 2003; Smith et al., 2003a). Modern humans also frequently appear to show fewer than 100 Retzius lines in molars (Dean et al., 1992; Reid et al., 1998b). Reid et al. (1998a) reported much higher ranges of Retzius lines in chimpanzees (127–168 Retzius lines in three mandibular third molars), which have the longest crown formation times known among hominoids. Comparative data on the spacing or distribution of Retzius lines in hominoid posterior teeth are rare, and few studies report the distribution of lines in equivalent intervals (as in this study and in Dean and Reid [2001]). Of the two studies of human and chimpanzee molars by Reid et al. (1998a,b) that are somewhat comparable to this study, *Graecopithecus* appears to be more similar to the human pattern than the chimpanzee pattern, as both of the former show more uniform distributions of Retzius lines per mm than the chimpanzee pattern.

Crown formation

Crown formation time in *G. freybergi* is longer than in most hominoids, although this may be due to a limited comparative sample, particularly of third molars (reviewed in Smith et al., 2003a: Table 7). Reported third molar formation times range from 1.7 years in *Proconsul heseloni* (Beynon et al., 1998) to 2.1–2.6 years in *Paranthropus boisei* (Beynon and Wood, 1987), 3.1–3.4 years in modern humans (Reid et al., 1998b), 3.5–4.0 years in *Pan troglodytes* (Reid et al., 1998a), and 4.1 years in *Gigantopithecus blacki* (Dean and Schrenk, 2003). Several studies have looked at the relationships between crown formation time (including the individual cuspal and imbricational components) and relative and absolute enamel thickness (Grine and Martin, 1988; Dean and Schrenk, 2003; Smith et al., 2003a,b). Smith et al. (2003b) failed to find a significant association between crown formation time and RET in a sample of ten hominoid teeth. These authors showed that Miocene hominoid crowns with relatively thick enamel often formed in an equivalent or shorter period of time than those of extant taxa with relatively thin enamel, such as *P. troglodytes*. However, when cuspal formation time was evaluated relative to RET, a significant positive relationship was found ($P<0.05$) (which indicated a lack of association between cuspal and imbricational formation times).

Grine and Martin (1988) suggested that three factors influence (cuspal) enamel thickness: daily secretion rate, duration of secretion, and the number of cells secreting enamel. Certain Miocene hominoids secreted cuspal enamel at a higher rate than extant apes and humans, which resulted in thick enamel (e.g., *Proconsul nyanzae*, *Afropithecus*

Fig. 10. Transmitted light images of dentine accentuations and long-period lines in a right lower third molar of *Graecopithecus freybergi*. (a) Long-period Andresen's lines in the dentine near the EDJ (labeled). The arrows indicate accentuated lines D_1–D_5 from top to bottom (see Table 5). The average dentine DSR in this region is 1.1–1.3 μm/day. The field width is 680 μm. (b) Andresen's lines in the dentine under the enamel cingulum. The arrows indicate accentuated lines D_5–D_9 from top to bottom, and the D_8 arrow is outlined as it corresponds to the end of cuspal enamel formation. The average DSR in this region is 1.9–2.2 μm/day. This image also shows an area of interglobular dentine (circled), which is a defect of mineralization. The field width is 1330 μm. (c) Andresen's lines near the axial dentine with an average DSR of 2.1–2.3 μm/day. Note that these lines, which correspond to imbricational enamel formation, are more distinct and uniformly spaced than those in the earlier-formed dentine. The broad dark bands in the upper right are cracks in the dentine. The field width is 1330 μm.

Table 5
Dentine formation in the protoconid of *Graecopithecus freybergi*

Band	Angle	Andresen	Max DSR	Min DSR	Ex Rate
Cuspal					
D_1	5.7	14[a] (112)	1.3[a]	n/a	12.2[a]
D_2	4.7	4 (32)	1.3	1.3	12.7
D_3	6.3	7 (56)	1.8	1.3	11.9
D_4	9.8	9 (72)	1.4	1.2	7.1
D_5	11.0[b]	12 (96)	1.9	1.1	6.7[b]
D_6	14.8	12 (96)	3.8	2.2	14.4
D_7	17.5	6 (48)	2.3	1.9	6.5
D_8	23.7[b]	4 (32)	2.3	1.1	5.9[b]
Overall		68 (544)	2.3		9.6[b]
Imbricational					
D_9	28.4[b]	10 (80)	1.4	0.9	4.5[b]
D_{10}	18.7[b]	38–43 (304–344)	2.1–2.3	1.7–1.9	3.5–4.0[b]
D_{11}	n/a	29–34[c] (232–272)	2.6–3.0	1.2–1.4	2.3–2.7[c]
Overall		77–87[c] (616–696)	2.3–2.6		3.2–3.6[c]
Total		145–155[c] (1160–1240)			6.0–6.4[c]

Band=Eleven accentuated dentine features that are identified, mapped, and divided into areas corresponding to cuspal and imbricational enamel formation (see Figs. 9 and 10). Angle=Intersection of the accentuated band with the EDJ in degrees. Andresen=Number of long-period lines in the interval preceding the band, with the equivalent number of days in parentheses, determined by multiplying the number of Andresen's lines by the periodicity of eight. Max DSR=Maximum measured distance between successive bands divided by the number of days within an interval (axial dentine when possible) in μm/day. Min DSR=Minimum distance between successive bands divided by the number of days within an interval (lateral dentine near EDJ) in μm/day. Ex Rate=Distance along the EDJ between successive bands divided by the number of days within an interval in μm/day. Overall values for Andresen represents the sum of lines in the region corresponding to cuspal or imbricational enamel formation. Overall values for dentine DSR corresponding to cuspal enamel determined by dividing axial thickness of 1250 μm by the formation time of 544 days. Dentine extension in this region was calculated by dividing the corresponding EDJ of 5250 μm by 544 days. Overall values for the dentine corresponding to imbricational enamel were determined in the same manner using a maximum lateral thickness of 1575 μm and an estimated EDJ length of 2200 μm. Total Andresen value was determined by combining the overall values of cuspal and imbricational regions. It was not possible to determine an average axial rate for the entire period of crown formation as the corresponding dentine was not preserved. The total extension rate represents the length of the EDJ in the cuspal and imbricational regions divided by the range of formation times.

[a]Estimated from adjacent dentine beneath this region. Because it was not possible to identify lines in the indistinct, earliest-formed dentine, the first 150 μm of axial dentine was divided by the local rate of 1.3 μm/day in the adjacent dentine to yield an estimate of 14 lines.

[b]Estimated due to lack of clarity of intersection with EDJ.

[c]Estimated due to missing cervical tip.

Note: the interval D_5–D_6 contains the dentine making up the "incipient horn" underlying the cingulum. D_9–D_{10} contains marked interglobular dentine and the beginning of the calcospheritic dentine formation.

turkanensis) (Beynon et al., 1998; Dean, 2000; Smith et al., 2003a). The duration of cuspal enamel secretion ranges between 0.5–1.5 years in known Miocene hominoids, which encompasses the entire extant ape range, with *G. freybergi, P. nyanzae,* and *A. turkanensis* displaying the longest times (see also Dean and Schrenk [2003] for a discussion of *G. blacki* and *Homo*). It is more difficult to determine the number of cells secreting enamel, and as noted above, reported values of the angle of intersection between the developing enamel front and the EDJ suggested that this factor was variable in Miocene hominoids.

Smith et al. (2003a) reviewed the proportions of cuspal and imbricational enamel formation times in hominoids. *Graecopithecus*, with cuspal time

Fig. 11. PLM montage of a thin section of a right lower third molar of *Graecopithecus freybergi*. Approximately nine months after initiation of the protoconid, a series of accentuations was produced over the next six to seven months (corresponding to some marked calcospheritic dentine), followed by approximately two to three months of formation without stress, at which point the cuspal enamel was completed and the imbricational enamel began. Just after the beginning of imbricational enamel formation, a series of accentuated lines was produced for approximately five to six months (beginning with the accentuated line referred to as E_0 [solid line] and including E_1 [dotted line]), during which time the fissure of the cingulum in the protoconid was formed. This correlates with the production of a wide band of interglobular dentine and marked calcospherites (Fig. 10b). The final 16 months of lateral and cervical enamel formation does not show any notable accentuations. The scale bar at the bottom represents 1 mm.

representing 40–45% of the total formation time, is most similar to *A. turkanensis*, *P. nyanzae*, and modern *Homo* (Smith et al., 2003a; Reid, unpublished data). This proportion is lower than in *Paranthropus*, where cuspal time may comprise up to 60% of the total formation time. Although cuspal enamel in *G. freybergi* is formed in less than half of the total time, it represents 85% of the total enamel area. Cuspal area in *Paranthropus* may constitute an even greater proportion, up to 90% of the total, which is broadly similar to the pattern of modern human deciduous teeth (Beynon and Wood, 1987; Grine and Martin, 1988). These authors suggest that this is the result of high numbers of ameloblasts actively secreting enamel (which is compatible with the reported low angles of intersection of the developing enamel front with the EDJ). Based on the pattern of cuspal accentuations that demonstrate a continuous cohort of enamel-forming cells across the occlusal basin (shown in Fig. 11), the possession of a

large, active, cuspal cell cohort appears to be another similarity between *G. freybergi* and *Paranthropus*.

When cuspal and imbricational enamel are considered together, five factors appear to determine total crown formation time: 1) rate of cuspal enamel secretion, 2) duration of cuspal enamel secretion, 3) number of cells secreting enamel, 4) number of imbricational striae, and 5) the periodicity of striae. These variables exhibit a complicated pattern of variation in the apes. Differences may serve to distinguish some fossil from extant taxa, but additional work is necessary before we will know to what extent these variables distinguish fossil ape taxa from one another.

Dentine microstructure

Data on dentine secretion and extension rates in this third molar show that coronal dentine development was relatively slow in *G. freybergi*. The

Table 6
Average axial dentine secretion rates in hominoid molar teeth

Taxon	Tooth	DSR	Reference
Proconsul heseloni	M1 (2)	2.5–3.3	Beynon et al. (1998)
	M2 (2)	2.4–2.5	Beynon et al. (1998)
	M3	2.1	Beynon et al. (1998)
Graecopithecus freybergi	M3	2.3[a]	This study
Proconsul nyanzae	M1	2.75	Beynon et al. (1998)
	M2	2.75	Beynon et al. (1998)
Lufengpithecus hudienensis	M1	3.4	Schwartz et al. (2003)
Homo sapiens	M1	3.8	Dean and Scandrett (1995)
	M2	2.8[a]	Dean (1998a)
Pongo pygmaeus	M2	3.0[a]	Dean (1998a)
Hylobates lar	M2	3.3	Dirks (1998)
Pan troglodytes	M2	3.3[a]	Dean (1998a)
Dryopithecus laietanus	M1	3.8	Kelley et al. (2001)
	M2 (2)	3.8–3.9	Kelley et al. (2001)

Tooth type samples sizes are one unless otherwise noted in parenthesis. DSR=Daily secretion rate in μm/day.
[a] Values for axial dentine corresponding to cuspal crown formation only. Average values may have been slightly higher had the entire distance from dentine horn to pulpal horn been measured. Several other published rates may be for cuspal areas only, but the authors were not explicit about the location where axial rates were determined.

DSR in the axial dentine is lower than most values reported for extant and fossil taxa (Table 6). *Graecopithecus* appears most similar to *Proconsul heseloni*, although this is the only other hominoid for which values on third molars are available. Given the current data, it is not clear if there is a decreasing trend of average axial rate from first to third molars. However, if it is the case, values reported for *G. freybergi* may not be unusually low.

When considering extension rates comparatively, it is worth noting that rates of coronal dentine are rarely reported separately from rates of root dentine (formed after crown completion). Since extension rate varies within and between teeth, comparisons should ideally be limited to homologous regions of the same tooth type. However, extension rates are only reported for dentine near the cervix of a *P. heseloni* M2 (Beynon et al., 1998), and for the subsequent earliest-formed root dentine in several other studies (Beynon et al., 1991a; Dean and Beynon, 1991; Dean 1995a; Beynon et al., 1998; Dirks, 1998; Kelley et al., 2001). These data on root formation show higher rates than those at the end of coronal dentine formation for *Graecopithecus*. Extension rates are

lowest in modern *Homo*; values of 2.9–3.8 μm/day have been reported for the first few years after crown completion in first molars (Dean and Beynon, 1991). Simpson and Kunos (1998) reported that the rate of root extension increases markedly after emergence, and extension rates in first molars are higher than in second and third molars in a large sample of developing human mandibular dentitions (see also Dirks, 1998). Investigation of additional extant and fossil material is necessary to determine the pattern of extension rates changes within and between successive molars.

Finally, it is not clear what may have caused the irregular accentuations seen in this tooth. Numerous studies have examined the surface manifestations of developmental stressors, known as enamel hypoplasias, in a number of hominoid taxa. Several studies have recently examined the patterns of accentuations within the enamel in archaeological populations (Antoine et al., 1999; Ferrell, 2002) and in fossil and living baboons (Macho et al., 1996; Dirks et al., 2002). Macho et al. (1996) suggested that the pattern of accentuated lines in the enamel of several individuals of fossil *Theropithecus* resulted from environmental

stressors relating to annual and seasonal events. Dirks et al. (2002) related a series of accentuated increments in several extant baboon dentitions to records of rainfall, as well as life history traits such as weaning and the onset of menarche. However, without additional data on paleoecology and life history in *G. freybergi*, interpretations of the pattern of accentuations in this tooth would be purely speculative.

Methodological considerations

Several methodological considerations have become apparent during the course of this study. These warrant brief discussion, particularly as analyses of incremental features continue to become more refined. Our study provides an opportunity to examine differences in the plane of section, which influences the morphology of the enamel/dentine profiles, and the assessment of prism decussation, enamel thickness, and crown formation time. In addition, data derived from multiple forms of microscopy in our study are shown to shed light on features such as laminations and intradian lines, which have generally been overlooked in previous analyses. Finally, the exceptional quality of coronal dentine in *G. freybergi* permits an independent means of checking results derived from the enamel, and provides information on rates and patterns of extension in both tissues.

The morphology of the sectioned faces provides insight into the development of the cingulum and HSB. Butler (1956) suggested that the cingulum originates from a local thickening of the enamel rather than from the underlying morphology of the dentine (Butler, 1956: Figure 2). However, it is clear from several planes of section of *G. freybergi* that the cingulum is derived from ameloblasts that begin on an "incipient horn" in the dentine. This also appears to be the case for sections of *Proconsul* teeth (Beynon et al., 1998: Figure 4). Our study is the first to show histologically that this morphology may result from changes in the local rates of odontoblast secretion and extension at the developing EDJ (Table 5: intervals D_5–D_7). Since enamel is secreted on top of a predentine layer, these depositional changes influence the

morphology of the future EDJ, and ultimately the topography of the enamel surface.

The pattern of prism decussation, manifested in low magnification cross-sections as HSB, appears to vary from one face to another, as the most anterior face shows wider bands that extend almost to the surface of the tooth. The pattern of long, thin HSB with little angular change in *G. freybergi* is most similar to that reported for *P. boisei* (Beynon and Wood, 1986). However, if it is the case that these features vary from one plane to another, as the current study suggests, reported differences in HSB or prism path between taxa may be at least partially explained by differences in section plane rather than by biological variation (contra Beynon and Wood, 1986 and Macho et al., 2003).

It is not clear if the two thin sections of *G. freybergi* show actual differences in the number of Retzius lines, as the estimates of 63–64 and 61–63 lines in the metaconid overlap (and it was not possible to compare the protoconid in each section). Even if there are slight differences in number, section obliquity influences estimates of imbricational formation time less than cuspal formation time. Comparisons between two planes of section in this tooth show that obliquity may cause overestimates of linear enamel thickness by up to 260 µm and underestimates of dentine by an unknown amount. Even in slightly oblique sections, this will affect estimates of cuspal formation time that are based on linear enamel or dentine thickness, as obliquity will reduce the apical/coronal dentine (i.e., dentine horn) and inflate the thickness of cuspal enamel relative to the ideal plane of section (Martin, 1983). This may explain why published estimates of crown formation time in fossil hominoids based on enamel are usually higher than those based on dentine (Beynon et al., 1998; Kelley et al., 2001; Schwartz et al., 2003). In our study, using the inflated linear thickness of 2650 µm (from the protoconid of the thin section) and dividing this by average DSR yields a time of 621 days, which is greater than the estimate of 560 days using the thickness derived from the most anterior face, or the estimate of 544 days from the dentine. Correcting for the effects of obliquity is not simply a matter of averaging formation time estimates from enamel and dentine,

as the growth rates are not equivalent and a small amount of missing dentine may represent more time than an equivalent amount of added enamel. Work in progress on parallel sections of extant ape teeth will further clarify this issue.

The high frequency of laminations found at the EDJ, near the tooth surface, and between Retzius lines is unexpected. These features have received very little attention in the literature on enamel microstructure, and it is unclear whether they have been regarded in other studies as a daily feature equivalent to cross-striations. Smith et al. (2003a) discussed the presence of laminations in *Afropithecus turkanensis*, illustrated how these features may complicate determination of the periodicity, and suggested that they may be associated with aprismatic or Pattern 1 enamel. Observation of these features in *G. freybergi*, especially in relation to Retzius lines, suggests either that 1) their periodicity should not be interpreted as daily, or 2) that their variable appearance may prohibit using them to determine the periodicity of Retzius lines if they are daily features. Preliminary work on fluorescent-labeled macaque dentitions suggests that these features are daily, although their resolution near the tooth surface is often complicated by superimposition of features from adjacent layers, resulting in underestimations of the number of laminations between Retzius lines. Thus, we feel that they should not be used for determination of periodicity.

One of the challenges in studies of dentine formation is finding teeth with sufficiently clear incremental features (Dean, 1995a). The study tooth is an excellent specimen in this regard. Data on crown formation time in *G. freybergi* derived from dentine corresponds closely to estimates obtained from enamel. We feel that the similarity of results from dentine long-period lines and linear enamel secretion rates shows that, contra Macho et al. (2003), decussation does not significantly impact estimates of crown formation time. Nor does it necessitate use of a correction factor in taxa with relatively straight prism paths when calculating cuspal crown formation time from linear enamel thickness.

Smith et al. (2003a) discussed several limitations in using the angle between the developing front and the EDJ as a proxy for the extension rate (proposed by Boyde [1964]), as this angle is affected by both local extension and local daily secretion rates. Empirically derived data from dentine in our study show that low angles may be formed when extension rates are fast *and* secretion rates are slow. However, high angles may be formed when the extension rates are slow *or* when secretion rates are fast. For example, the dentine formed just beyond the tip of the "incipient dentine horn" in *G. freybergi* shows a relatively high angle, fast extension rate, and fast secretion rate. Yet, in this instance, a fast extension rate would not have been predicted based solely on the value of this angle.

This study is the first to present a detailed trajectory of dentine secretion and extension rates corresponding to the periods of cuspal and imbricational enamel formation in a fossil ape. We show that the first six to seven months of dentine formation are characterized by the activation of a high number of odontoblasts, which is also shown by the pattern of low angles of intersection of the developing dentine front with the EDJ. Since enamel must extend at a rate identical to that of the dentine, the initial rate of enamel secretion must be greater, as the angles of intersection of the (earliest-formed) developing enamel front at the EDJ are approximately 2–3 times higher than angles in the corresponding dentine. This expected difference in secretion rates is confirmed, as rates are approximately 2–3 times greater in the cuspal enamel, which also explains differences in linear thickness (1250 μm vs. 2390 μm) and the proportion of dentine to cuspal enamel area (1:3).

Following the production of dentine relating to cuspal enamel formation, the imbricational period is characterized by slower extension of dentine and enamel secreting cells, resulting in the production of a smaller volume of dentine and imbricational enamel over a longer period of time. This is generally supported by the pattern of increasing angles of intersection of the developing dentine and enamel fronts at the EDJ towards the cervix. Based on data on hominoid root extension rates reviewed above, we might expect root extension rates to increase after crown completion and tooth emergence.

Implications for phylogeny and life history

Several studies have investigated aspects of enamel thickness and dental development to infer evolutionary relationships or aspects of life history among primates (reviewed in Kelley, 2002; Kelley and Smith, 2003; Smith et al., 2003a). Smith et al. (2003a) suggested that, due to the complicated pattern of enamel thickness within and among Miocene hominoid genera, it was not clear that enamel thickness alone could be used to elucidate evolutionary relationships. Given the extreme degree of enamel thickness in *G. freybergi* and evidence from Ungar and Kay (1995) that it consumed harder food than any known primate, it is likely that the condition of thick enamel was the product of functional demand rather than phylogeny, although these are not mutually exclusive alternatives. Similarities with other taxa possessing very thick enamel, most notably *Paranthropus*, are likely the result of convergence. This conclusion is supported by differences between *G. freybergi* and *Paranthropus* in both rate and duration of crown formation. It is unlikely that closely related taxa would develop a similar trait via such different ontogenetic pathways.

Other studies have used incremental features to determine crown formation time and/or age at M1 emergence as a way of gaining insight into life history traits (Kelley, 1997; Macho, 2001; Kelley et al., 2001; Kelley, 2002; Schwartz et al., 2002; Kelley and Smith, 2003). Macho (2001) reported that histologically derived estimates of crown formation time were positively correlated with several life history traits across primates. However, Kelley and Smith (2003) highlighted similarities in crown formation time between *Pan* and *Homo*, while noting differences in eruption age that result from differential rates of root growth. They cautioned that additional histological data on crown formation time and root formation would be necessary before it was possible to evaluate the relationship between crown formation time and life history variables across primates, including the age of M1 emergence.

Work on Miocene hominoids has shown evidence of several patterns of crown and root formation. Beynon et al. (1998) and Dean (2000) discussed this in relation to the life history of *Proconsul heseloni*, which showed a much shorter period of crown formation than in extant great apes, but a relatively slow rate of root development. Age at first molar emergence is unknown, but has been suggested to be less than two years based on estimates of brain size (Kelley, 1997), which is not incompatible with available histological data (Beynon et al., 1998). Smith et al. (2003a) and Kelley and Smith (2003) demonstrated that *Afropithecus turkanensis* second molar development occurred over a greater period of time than in *Hylobates* or *Proconsul*, and first molar eruption was within the range of ages for *P. troglodytes*. Kelley (1997, 2002) reported an estimated age of first molar emergence for *Sivapithecus parvada* that is even closer to the mean age of eruption in *P. troglodytes*. There are no published data on crown formation time in *Sivapithecus*, or on root development in *A. turkanensis* or *S. parvada*.

Although it was not possible to determine the age of molar eruption in this study, *G. freybergi* may have shown molar eruption ages similar to those of *P. troglodytes*, given similarities in crown formation time. Data on rates of root growth would provide additional support. We suggest that evidence from *G. freybergi* and *S. parvada* reveals that hominoids with dental developmental schedules similar to chimpanzees may have evolved more than 10 myrs ago. Additional evidence from larger samples of fossil and extant hominoid dentitions is required to assess the diversity of dental development over the past 20 myrs.

Summary and conclusions

Based on a mandibular third molar from Ravin de la Pluie, *Graecopithecus freybergi* has the thickest relative and absolute molar enamel of any Miocene hominoid measured to date, but has relatively and absolutely thinner molar enamel than *Paranthropus*, and absolutely thinner molar enamel than *Gigantopithecus blacki*. Incremental features of the enamel, such as the periodicity and daily secretion rate, are similar to those of other Miocene hominoids and, to a lesser degree, to those of extant apes. The daily secretion rates are less than those reported for *Paranthropus*. Crown

formation time in *G. freybergi* is estimated to be 3.5 years, greater than for third molars of *Proconsul heseloni*, *Paranthropus boisei,* and *Homo sapiens*, similar to those of *Pan troglodytes*, but less than that of *G. blacki*.

Cuspal enamel formation in *G. freybergi* resulted from a large number of enamel secreting cells, which generated 85% of the total crown area in less than 50% of the total formation time. During the subsequent imbricational enamel formation, fewer cells secreted enamel over a longer period of time. This pattern of crown formation is similar to that of *Proconsul nyanzae*, which also has thick enamel, but is not as extreme as in *Paranthropus* or in human deciduous teeth. Relative to other hominoids, dentine secretion and extension rates appear to be slow, but comparative material is severely limited. Several periods of developmental stress are apparent in this tooth as accentuations in both the enamel and dentine, which occurred irregularly during the first two years of formation. The causes of this stress are unknown.

Cross-sections of this tooth show that the cingulum developed from an "incipient horn" in the dentine, which was the result of local changes in dentine secretion and extension rates at the enamel dentine junction. Examination of multiple sections suggests that the plane of section influences the width and length of Hunter–Schreger bands. The effects of section obliquity on enamel thickness and crown formation time are illustrated, and are suggested as the basis for differences in previously reported values of crown formation time determined from the enamel and the dentine. Initial developmental differences in enamel secretion and extension rates may exist between the metaconid and protoconid, although the effects of obliquity cannot be ruled out. In this study, estimates of crown formation time from both enamel and dentine are very similar, reconfirming the utility of linear enamel secretion rates (from a non-oblique plane of section) for determination of crown formation time.

In comparison to *Paranthropus*, *G. freybergi* has thinner enamel and similar patterns of prism paths and Hunter–Schreger bands, but may have had slower rates of enamel secretion and extension, and an overall longer period of crown formation

time. *Graecopithecus* shows developmental similarities to several other taxa, including *Proconsul*, *Afropithecus*, and *Homo*. It is suggested that the apparent similarities to these taxa are convergences due to the condition of thick enamel related to similar functional demands, rather than close evolutionary relationships. Although data on root formation are lacking, similarities with *Pan* in crown formation time suggest that *Graecopithecus* displayed a prolonged life history similar to that of other large-bodied fossil hominoids.

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