

Molar crown formation in the Late Miocene Asian hominoids, *Sivapithecus parvada* and *Sivapithecus indicus*

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Abstract

During the past decade, studies of enamel development have provided a broad temporal and geographic perspective on evolutionary developmental biology in Miocene hominoids. Here we report some of the first data for molar crown development in one hominoid genus, *Sivapithecus*. The data are compared to a range of extant and extinct hominoids.

Crown formation times (CFTs), daily rates of enamel secretion (DSR), Retzius line number and periodicity, and relative enamel thickness (RET) were calculated in a mandibular first molar of *Sivapithecus parvada* and a maxillary first molar of *Sivapithecus indicus* from the Siwalik sequence of Pakistan. A CFT of 2.40 years for the protoconid of *S. parvada* and 2.25 years for the protocone of *S. indicus* lie within the range of first molar (M1) formation times for the majority of Miocene hominoids (1.96–2.40 years, excluding *Proconsul heseloni*), and are similar to an M₁ from *Gorilla* (2.31 years) and M₁s from *Pan* (2.22–2.39 years). This is unlike the longer CFTs in modern humans, which appear to be linked with their extended growth period. In contrast to extant great apes and humans, daily rates of enamel secretion are rapid in the *Sivapithecus* M1s during the early stages of growth, which seems to be a common pattern for most Miocene apes. The rapid accumulation of cuspal enamel in the *Sivapithecus* molars produced thicker enamel than either *Pan* or *Gorilla* in a comparable period of time. Future studies on larger samples of living and fossil hominoids are needed to clarify trends in crown development, which may be better understood in the context of life history strategies coupled with good data on body mass and brain size.

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Introduction

Fossil remains assigned to the extinct hominoid genus *Sivapithecus* include three species that date between 12.7 and 8.5 Ma: *Sivapithecus indicus*, *Sivapithecus parvada*, and

Sivapithecus sivalensis (Kelley, 2005). The largest of these, *S. parvada* (ca. 10 Ma), has an estimated body mass range of roughly 50–90 kg based on postcranial remains, with presumed female remains comparable in size to chimpanzees and presumed male remains comparable to female gorillas (Rose, 1986; Kelley, 1988; Pilbeam et al., 1991; Spoor et al., 1991). The other two species are smaller, and estimates of their body mass are less certain because of limited postcranial remains. What remains there are range in size between those of large macaques and baboons on the one hand and small chimpanzees on the other (Pilbeam et al., 1980; Rose,

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1984; Madar et al., 2002), suggesting that *S. indicus* and *S. siwalensis* were roughly half the size of *S. parvada*.

While there have been numerous studies of both the craniodental and postcranial morphology of *Sivapithecus*, little is known about dental development in any of these species. Martin (1983) carried out the only examination of molar enamel histology in *Sivapithecus* (*S. indicus*) and provided information on relative enamel thickness as well as preliminary results on rates of enamel secretion. Using incisor perikymata to determine growth duration, Kelley (1997, 2002) provided an estimate of the age at first molar emergence in *S. parvada* that was similar to that for chimpanzees. Aspects of molar crown formation, as well as measures of enamel thickness, have also been reported for a range of other Miocene hominoids (Beynon et al., 1998; Kelley et al., 2001; Dean and Schrenk, 2003; Schwartz et al., 2003; Smith et al., 2003a, 2003b, 2004).

The aim of this study is to provide data on dental development in two species of *Sivapithecus*, and to consider this in the context of dental development for Miocene and extant hominoids. Crown formation times, rates of enamel secretion, Retzius line numbers and periodicities, and relative enamel thickness are reported based on histological sections from two *Sivapithecus* molars.

Materials and methods

One mandibular first molar (M_1) attributed to *S. parvada* (GSP 47585) and one maxillary first molar (M^1) attributed to *S. indicus* (NHM M13365) were examined. Standard histological procedures were followed as described in Schwartz et al. (2003) and Smith et al. (2004) to produce a single ground section from each tooth. Each molar was molded prior to sectioning and an epoxy cast was prepared. The molars were embedded in polyester resin or methyl methacrylate to reduce the risk of splintering while sectioning. A single coronal section measuring between 180–500 μm in thickness was taken through the mesial cusp tips and dentine horns of each tooth using a diamond-wafering blade saw (Buehler[®] Isomet 5000) or annular saw (Logitech). The sections were mounted on microscope slides, lapped to 100–120 μm thickness using a graded series of grinding pads (Buehler[®] EcoMet 4000), polished with a 0.3 μm aluminum-oxide powder, placed in an ultrasonic bath to remove surface debris, dehydrated through a series of alcohol baths, cleared (using Histoclear[®]), and mounted with cover slips using a xylene-based mounting medium (DPX[®]).

The sections were examined under polarized light microscopy to record the presence of both short-period and long-period incremental growth lines in enamel. Short-period lines, or cross-striations, represent daily increments of enamel deposition. Long-period lines, referred to as Retzius lines or striae of Retzius, represent periodic disruptions in enamel deposition that occur every six to twelve days in extant great apes and humans, although the periodicity is constant within any given individual (see Dean, 1987, 1998, 2000; FitzGerald, 1998; for fuller descriptions of enamel incremental growth lines and their use in reconstructing dental ontogeny). The presence of a neonatal growth line formed in response to stress during

and immediately after birth was also recorded. Lastly, measurements were made to calculate an index of relative enamel thickness (Martin, 1983, 1985). These approaches are described in detail in the following sections.

Enamel secretion rates, Retzius line number and periodicity, crown formation times, and pre- and postnatal crown formation times

The enamel cap is divided into two portions for the purpose of calculating crown formation time: cuspal enamel, in which successive increments of enamel are buried under subsequently formed enamel; and lateral enamel, in which Retzius lines reach the tooth surface and outcrop as perikymata. The first line to reach the surface of the tooth divides the crown into cuspal and lateral regions (see Ramirez Rozzi, 1994). Total enamel formation time is calculated differently in these two crown portions.

The cuspal enamel was divided into three regions of equal thickness (inner, middle, and outer). For each region, average daily enamel secretion rates (DSR) were calculated by measuring the distance corresponding to five days of secretion along the long axis of an enamel prism. This procedure was repeated a minimum of six times in different areas in each region to produce a mean value and standard deviation. The means for each region were then averaged to produce a grand mean DSR for cuspal enamel. The cuspal enamel thickness was measured from the tip of the dentine horn to the position of the first Retzius line at the tooth surface, reduced by 50 μm for each cusp due to slight obliquity, and was then divided by the overall mean cuspal DSR to yield the time taken to form the cuspal enamel.

Lateral (buccal or lingual) enamel formation times were calculated by multiplying the number of Retzius lines by their periodicity. Periodicity was determined by counting the number of cross-striations between adjacent long-period lines. Where long-period lines were indistinct in the *S. parvada* molar, enamel prism lengths were divided by secretion rates to estimate formation time in the affected area (Fig. 1; Boyde, 1963). In this procedure, the last clearly visible long-period line at the surface of the enamel was followed cervically to the enamel-dentine junction (EDJ). Prisms originating at the boundary between the EDJ and this long-period line were traced toward the enamel surface, thereby by passing the area of indistinct striae. The time taken to form these prisms was included in the estimate of buccal or lingual lateral enamel formation time.

Prenatal crown formation time was calculated by locating the position of the neonatal line—the first accentuated growth line over the dentine horn. The thickness of the enamel between this line and the dentine horn was measured and divided by the local DSR to yield a formation time in days.

Enamel thickness

Relative enamel thickness was calculated following Martin (1985; also see Fig. 2). The area of the enamel cap (c) was

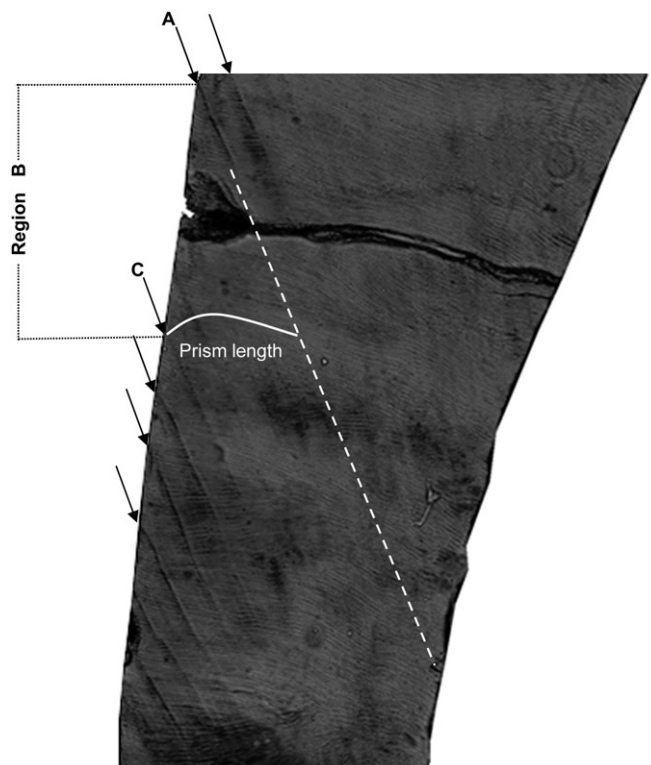


Fig. 1. Enamel formation time estimated from prism lengths. The image shows Retzius lines in the metaconid lateral enamel of the *S. parvada* M₁. Black arrows point to Retzius lines that are clearly visible on the thin section. Two clearly visible Retzius lines, (A) and (C), are separated by a region of indistinct Retzius lines, region (B). The clearly visible Retzius lines form part of the estimate of lateral enamel formation time, calculated by multiplying the number of lines by the Retzius periodicity. In order to navigate from Retzius line (A) through region (B) to Retzius line (C), an estimate of enamel formation time for region (B) is taken from a prism length. In this procedure, Retzius line (A) represents the position of the forming enamel front. Anywhere along this front, which is indicated by the white dashed line, represents the same point in time. A prism traveling from the white dashed line outward to Retzius line (C) is identified. The length of the prism is measured and divided by a local DSR to give an estimate of the formation time for region (B). The formation time for the prism is summed with the estimate derived from the Retzius lines to give lateral formation time.

divided by the length of the enamel-dentine junction (e). This figure was divided by the square root of the area of dentine enclosed by the enamel cap (b) and multiplied by 100 ($RET = [(c/e)/\sqrt{b}]$). This provided a dimensionless index of relative enamel thickness that is adjusted for differences in overall tooth size.

Results

Table 1 shows maxillary and mandibular first molar crown formation times. Thin sections showing long-period lines and daily cross striations are illustrated for the M₁ of *S. parvada* (Figs. 3–4) and the M¹ of *S. indicus* (Fig. 5).

Sivapithecus parvada

The mean DSR for the M₁ protoconid is $5.01 \pm 0.55 \mu\text{m}$ and $5.12 \pm 0.47 \mu\text{m}$ for the metaconid. Dividing enamel

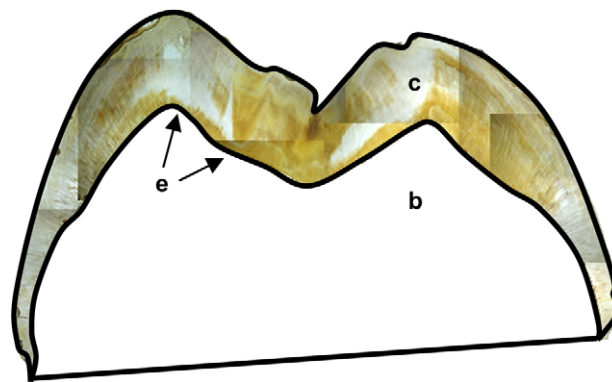


Fig. 2. Calculating relative enamel thickness: (c) is the area of the enamel cap, (b) is the area of dentine enclosed by the enamel cap, and (e) is the length of the enamel dentine junction. $RET = [(c/e)/\sqrt{b}]$.

thickness by the mean DSR yields M₁ cuspal formation times of 399 days for the protoconid and 383 days for the metaconid.

The periodicity in this individual is 9, and the number of striae in the lateral enamel of the metaconid is 54, yielding a formation time of 486 days. There are 35 distinct striae in the lateral enamel of the protoconid. An additional five lines were added to account for a small amount of missing cervical enamel. The 35 actual and five estimated striae were multiplied by the periodicity of 9, to which was added 101 days calculated from prism lengths in the region where striae are indistinct, yielding a lateral enamel formation time in the protoconid of 461 days. Re-calculating the protoconid lateral enamel formation time using just prism lengths, from the cuspal/lateral transitional striae to the reconstructed cervical margin, yields 496 days. An average of the two figures produces a lateral enamel formation time for the protoconid of 478 days. Summing the lateral and cuspal formation times gives a CFT of 877 days (2.40 years) for the protoconid and 869 days (2.38 years) for the metaconid.

Dividing prenatal enamel thickness by the mean rate of enamel secretion for the inner enamel gives a minimum prenatal crown formation time of 19 days. No evidence was found for prenatal enamel formation in the metaconid. The enamel cap and dentine areas are 26.8 mm^2 and 49.4 mm^2 , respectively, and the EDJ length is 20.2 mm, yielding an RET of 18.9.

Sivapithecus indicus

The mean DSRs for the M¹ paracone and protocone are $4.70 \pm 0.73 \mu\text{m}$ and $5.12 \pm 0.60 \mu\text{m}$, respectively, giving cuspal formation times of 223 days for the paracone and 264 days for the protocone.

The number of striae is 65 in the paracone and 70 in the protocone, and multiplying these by the periodicity of 8 yields lateral formation times of 520 days and 560 days, respectively. Summing the cuspal and lateral formation times results in a CFT of 743 days for the paracone (2.04 years) and 824 days for the protocone (2.25 years).

The mean prenatal enamel secretion rates for the paracone and protocone are $3.67 \pm 0.38 \mu\text{m}$ and $3.57 \pm 0.38 \mu\text{m}$.

Table 1
Mesial crown formation time for two species of *Sivapithecus*

| | <i>Sivapithecus parvada</i> | | <i>Sivapithecus indicus</i> | |
|---------------------------------------|-----------------------------|--------------------------|-----------------------------|-------------|
| | M ₁ | | M ¹ | |
| | Protoconid | Metaconid | Paracone | Protocone |
| Cuspal | | | | |
| Daily Secretion Rates (µm/day): Inner | 4.48 ± 0.41 | 4.48 ± 0.41 ¹ | 4.03 ± 0.37 | 4.73 ± 0.21 |
| Middle | 5.16 ± 0.59 | 5.30 ± 0.49 | 4.97 ± 0.54 | 5.44 ± 0.54 |
| Outer | 5.40 ± 0.66 | 5.60 ± 0.51 | 5.11 ± 0.75 | 5.20 ± 0.73 |
| Mean | 5.01 ± 0.55 | 5.12 ± 0.47 | 4.70 ± 0.73 | 5.12 ± 0.60 |
| Cuspal Enamel Thickness (µm) | 2048 | 2014 | 1100 | 1400 |
| Adjustment for obliquity ² | 1998 | 1964 | 1050 | 1350 |
| Cuspal Enamel Formation Time (days) | 399 ³ | 383 | 223 | 264 |
| Prenatal | | | | |
| Daily Secretion Rates (µm/day) | — | — | 3.67 ± 0.38 | 3.57 ± 0.38 |
| Enamel Thickness (µm) | 86 | — | 135 | 110 |
| Enamel Formation Time (days) | 19.1 ⁴ | — | 37 | 31 |
| Lateral | | | | |
| No. striae | 40 ⁵ | 54 | 65 | 70 |
| Periodicity (days) | 9 | 9 | 8 | 8 |
| Formation time from striae (days) | 360 | 486 | 520 | 560 |
| Prism lengths (days) | 101 (496) ⁶ | — | — | — |
| Imbricational formation time (days) | 478 ⁷ | 486 | 520 | 560 |
| Crown formation time (days) | 877 | 869 | 743 | 824 |
| Maximum mesial crown formation time | 877 days (2.40 years) | | 824 days (2.25 years) | |

¹ An inner enamel rate was not available for the metaconid. Given the similarity in DSRs between cusps of the same tooth type (Smith et al., 2007), inner DSR for the protoconid was used for the metaconid.

² Minus an estimate of 50 µm due to the obliquity of the protoconid, metaconid, paracone, and protocone dentine horn. The sections were oblique because they were taken slightly mesial or distal to the apex of the dentine horn, thus producing slightly thicker enamel, which could lead to an overestimation of appositional formation time.

³ A count of cross striations along continuous prism tracks gave an estimate of 380 days, similar to the above estimate.

⁴ The prenatal enamel formation time is calculated from the inner enamel DSR (4.48 ± 0.41) because of indistinct prenatal cross-striations, which may slightly underestimate the actual value due to the higher rate of secretion.

⁵ Includes estimate for missing protoconid cervical region enamel.

⁶ The first figure was calculated from prism lengths in a region where striae were indistinct (see Materials and methods). The second figure in brackets, was derived using only prism lengths, from the cuspal/lateral transitional striae to the reconstructed cervical margin.

⁷ The lateral formation time for the protoconid is an average of 461 days (prism lengths and Retzius lines combined) and 496 days (prism lengths only).

Dividing prenatal enamel thickness by these secretion rates gives a prenatal crown formation time of 37 days for the paracone and 31 days for the protocone. The areas of the enamel cap and dentine are 19.1 mm² and 37.9 mm², respectively, while the length of the EDJ is 18.8 mm, yielding an RET of 16.5.

Discussion

Daily rates of enamel secretion

There were no marked differences in the rates of enamel secretion between the two *Sivapithecus* molars. In both, there is a progressive increase in the secretion rate from the inner enamel to the outer, a phenomenon that characterizes extinct and extant hominoids (e.g., Beynon et al., 1991, 1998; Reid et al., 1998; Kelley et al., 2001; Schwartz et al., 2001, 2003; Dean and Schrenk, 2003; Smith et al., 2003a; Smith et al., 2007).

Secretion rates during the early stages of enamel growth in the *Sivapithecus* molars are higher than in some other species

(Table 2; Fig. 6). The DSRs in the inner enamel of both *Sivapithecus* species are above the known ranges for M₁ in *Gorilla*, M₂ in *Pongo* and humans, and overlap only the upper end of the range for M₁ in *Pan*. The *Sivapithecus* DSRs do, however, completely or substantially overlap the ranges recorded for *P. nyanzae* and *A. turkanensis* M₂s, as well as *G. freybergi* and *G. blacki* M₃s. The rates of inner enamel secretion for *Sivapithecus* seem to support the idea that some fossil hominoids shared a common pattern of higher initial average cuspal DSRs than extant apes and humans (Beynon et al., 1998; Dean, 2000; Smith et al., 2003a).

Crown formation

Like extant hominoids, the sequence of enamel initiation differed between the mesial molar cusps of *S. parvada*. The protoconid is generally the first cusp to mineralize prior to birth in humans (at -0.05 years), gorillas (at -0.23 years), and chimpanzees (at -0.13 years) (Reid et al., 1998; Schwartz et al., 2006; Smith et al., 2007). Calcification in the *S. parvada* M₁ commenced with the protoconid, also prenatally, suggesting

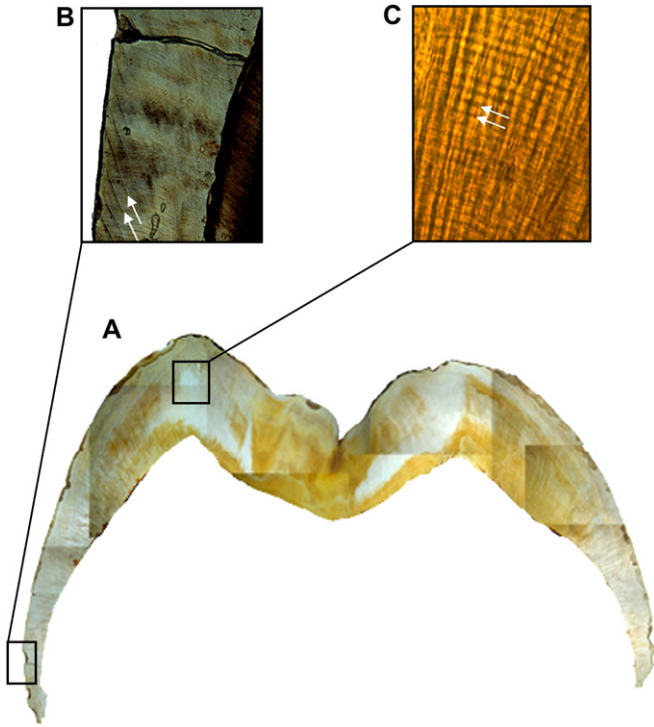


Fig. 3. Thin section of *S. parvada* M₁. (A) Thin section through the metaconid (left) and protoconid (right), imaged using polarized microscopy at a magnification of $\times 10$. (B) Close-up of inset, $\times 20$. White arrows point to Retzius lines. (C) Close-up of inset, $\times 60$. White arrows point to cross-striations.

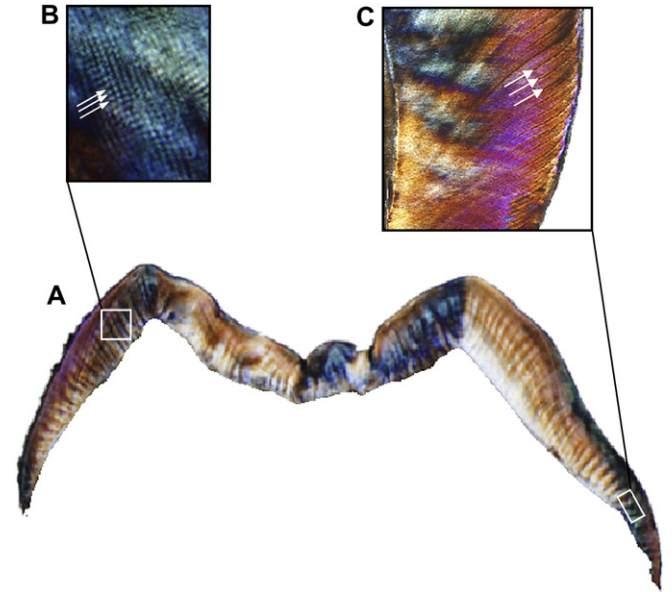


Fig. 5. Thin section of *S. indicus* M₁. (A) Paracone (left) and protocone (right), imaged using polarized light microscopy at a magnification of $\times 10$. (B) Close-up of inset, $\times 40$. White arrows point to cross-striations. (C) Close-up of inset, $\times 20$. White arrows point to Retzius lines.

an enamel initiation sequence in the mesial cusps similar to the extant hominoids, which is further supported by a lack of evidence of prenatal mineralization in the metaconid. The order of initiation of the mesial cusps of M₁s can vary within extant apes (Smith et al., 2007), which makes it difficult to compare prenatal calcification between *S. indicus* and the extant species.

First molar CFTs for Miocene hominoids range between approximately 1.96 years and 2.43 years, with only *P. heseloni* showing a substantially shorter formation time (Table 3). The mesial crown formation times for *Sivapithecus* fall within the range of CFTs for the Miocene hominoids. The values for *Sivapithecus* also follow an extant great ape-like formation time, similar to an M₁ from *Gorilla* and M₁s from *Pan*, rather than M₁s in modern humans, where longer CFTs may be associated with an extended growth period (Table 3; Reid and Dean, 2006).

The development of thick enamel in some of the fossil hominoids corresponds to a longer period of cuspal enamel growth (Smith et al., 2003a). The data for *Sivapithecus* supports this idea. Cuspal formation in the thick-enamelled *S. parvada* molar (discussed below) required 45% of the CFT; cuspal enamel on the slightly thinner-enamelled *S. indicus* molar formed in 32% of the cuspal formation period (Table 1). This trend contrasts with cuspal formation in first molars from extant great apes, which requires between 14% (*Pongo*) and 21% (*Pan*) of the total cuspal formation time (Smith et al., 2003a: Table 7).

Periodicity

The known range of long-period stria periodicities in extant large- and small-bodied hominoids is four to twelve days

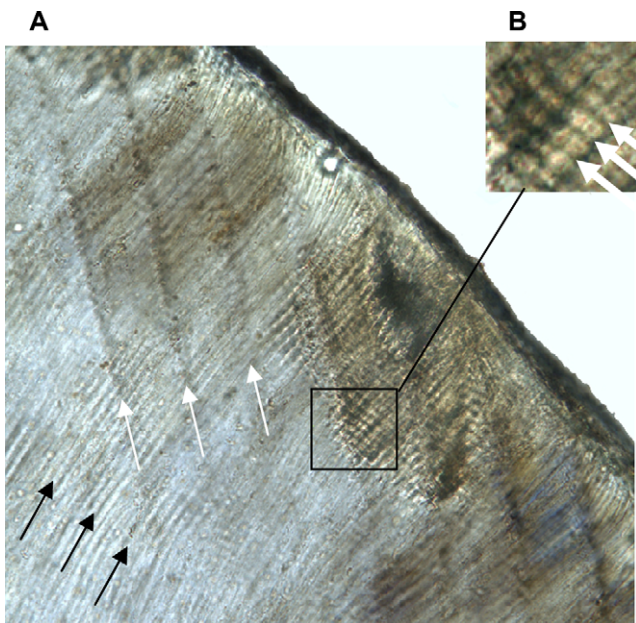


Fig. 4. Calculating periodicity. (A) Retzius lines (white arrows) in the *S. parvada* protoconid, $\times 40$. Black arrows show the direction of enamel prisms, which run towards the outer enamel surface. (B) Cross striations, $\times 60$. White arrows point to cross striations appearing along enamel prisms between two adjacent Retzius lines. Periodicity is determined by counting the number of cross-striations between adjacent Retzius lines.

Table 2
Molar cuspal daily enamel secretion rates in hominoids (in microns/day)

| Species | n-Cusp | Inner | Mid | Outer | Mean |
|---|----------|--------------------|--------------------|--------------------|--------------------|
| Extant | | | | | |
| <i>Homo sapiens</i> ¹ | 1 | 2.66 ± 0.15 | 3.44 ± 0.25 | 5.50 ± 0.85 | 4.00 ± 0.42 |
| <i>Pongo pygmaeus</i> ¹ | 1 | 3.27 ± 0.50 | 4.65 ± 0.45 | 5.20 ± 0.15 | 4.37 ± 0.36 |
| <i>Gorilla gorilla</i> ² | 1 | 3.37 ± 0.49 | 5.37 ± 0.08 | 5.47 ± 0.08 | 4.74 ± 0.69 |
| <i>Pan troglodytes</i> ³ | 73 | 3.62 ± 0.42 | 4.24 ± 0.50 | 4.62 ± 0.49 | 4.16 ± 0.47 |
| Extinct | | | | | |
| <i>Lufengpithecus huiensis</i> ⁴ | 1 | 3.00 ± 0.60 | | 5.60 ± 0.55 | 4.30 ± 0.57 |
| <i>Dryopithecus laietanus</i> ⁵ | 1 | 3.25 ± 0.50 | 5.05 ± 0.30 | 5.50 ± 0.20 | 4.60 ± 0.33 |
| <i>Afropithecus turkanensis</i> ⁶ | 2 | 3.97 ± 0.62 | 4.34 ± 0.71 | 4.85 ± 1.08 | 4.38 ± 0.80 |
| <i>Gigantopithecus blacki</i> ⁷ | 1 | 4.10 ± 0.30 | 4.50 | 6.00 | 4.86 ± 0.30 |
| <i>Graecopithecus freybergi</i> ⁸ | 2 | 4.15 ± 0.59 | 4.46 ± 0.44 | 4.30 ± 0.45 | 4.31 ± 0.49 |
| <i>Sivapithecus indicus</i> ⁹ | 2 | 4.38 ± 0.29 | 5.20 ± 0.54 | 5.15 ± 0.74 | 4.91 ± 0.66 |
| <i>Proconsul nyanzae</i> ¹⁰ | 1 | 4.40 ± 0.15 | 4.80 ± 0.20 | 5.40 ± 0.60 | 4.87 ± 0.31 |
| <i>Sivapithecus parvada</i> ⁹ | 2 | 4.48 ± 0.41 | 5.23 ± 0.54 | 5.50 ± 0.58 | 5.07 ± 0.52 |

The bold identifies the two species that are the focus of the research.

¹ Dean (1998: Table 1); data for M₂ divided into inner, mid and outer regions, with an average and standard deviation calculated for each region. Overall mean from Dean (1998).

² Schwartz et al. (2006).

³ Smith et al. (2007). Data for M1–M3 combined.

⁴ Schwartz et al. (2003); data for M₁. Outer region value is for outer- and mid-cuspal enamel combined.

⁵ Kelley et al. (2001); data for M¹ with the mean calculated from the three regions and SD calculated from average cross-striation spacings by monthly zones.

⁶ Smith et al. (2003a); data for M₂.

⁷ Dean and Schrenk (2003); data for M₃.

⁸ Smith et al. (2004); data for M₃.

⁹ Average secretion rate calculated from the combined rates for the protoconid and metaconid, and the paracone and protocone.

¹⁰ Beynon et al. (1998); data for M₂ with standard deviations calculated by Kelley et al. (2001).

(Table 4). The 8-day periodicity in the *S. indicus* molar and 9-day periodicity in the *S. parvada* molar both lie in the middle of this range.

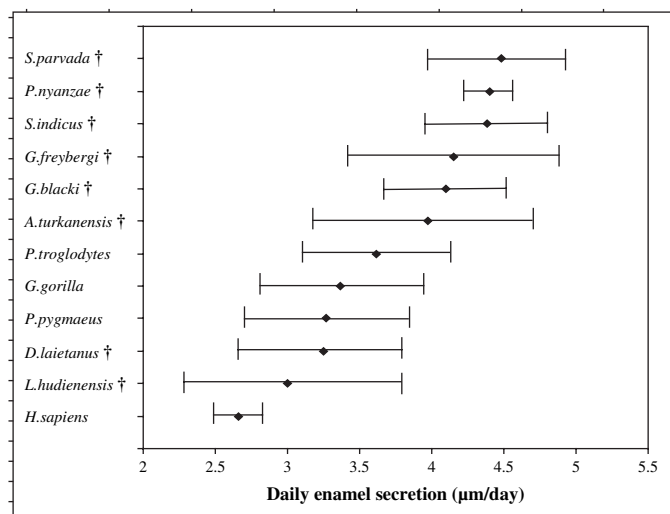
With the exception of *Gorilla* and *Homo*, periodicity differs significantly among extant hominoids (Schwartz et al., 2001), and is correlated with body size in extant and fossil hominoids (Smith et al., 2003b), though this relationship is more complex in non-anthropoid primates (Schwartz et al., 2002, 2005). The data presented here show that another aspect of molar

development, M1 CFT, is positively correlated with periodicity in extant and fossil hominoids (Pearson's $R = 0.927$, $P < 0.001$; data for M1 taken from Table 3, periodicity taken from Table 4). Given these correlations, and others (e.g., CFT and brain size; Schwartz et al., 2005), it seems likely that more comprehensive analyses may reveal more detailed information on the relationship among dental development, brain size, body size, life history strategies, and craniofacial growth across primates.

Enamel thickness

The calculated values of relative enamel thickness place *S. parvada* into a category classified as thick-enamel, and *S. indicus* into a category classified as intermediate-thick enamel (Fig. 2; Martin, 1985).

Comparing just M1s, thus removing any possible variation in enamel thickness due to differences in molar type (Macho and Berner, 1993, 1994; Smith et al., 2005, 2006), *Sivapithecus* and *P. nyanzae* have thicker enamel than *Pan* or *Gorilla*, yet all of these species have broadly similar M1 cusp formation times (Beynon et al., 1998; Smith et al., 2005). Enamel thickness is governed by the rate and duration of enamel secretion, and the number of active cells producing enamel (Grine and Martin, 1988). *Sivapithecus* and *P. nyanzae* have higher daily inner enamel cuspal secretion rates than either *Pan* or *Gorilla*. A higher rate of secretion during the early stages of enamel formation might have contributed towards the thick-enamelled molars of *Sivapithecus* and *P. nyanzae* growing in the same time as thinner-enamelled *Pan* and *Gorilla*.



† Extinct taxa.

Fig. 6. Daily secretion rates in the inner enamel of selected hominoids. Mean value (◆) and range (—). Data taken from Table 2.

Table 3
Crown formation times for hominoid first molars (in years)

| Species | n-Molar | Cusp | CFT (years) | Range |
|---|------------------------|-------------------|-------------|-----------|
| Extant | | | | |
| <i>Hylobates lar</i> ¹ | 1-M ₁ | hypoconid | 1.11 | |
| <i>Gorilla gorilla</i> ² | 1-M ₁ | protoconid | 2.31 | |
| | 1-M ¹ | protocone | 2.15 | |
| <i>Pan troglodytes</i> ³ | 5-M ₁ | protoconid | 2.17 | 2.01–2.61 |
| | 2-M ¹ | protocone | 2.30 | 2.22–2.39 |
| <i>Pongo pygmaeus</i> ⁴ | 2-M ₁ | not given | 2.85 | 2.70–3.00 |
| <i>Homo sapiens</i> ⁵ | 15-M ₁ | protoconid | 3.25 | 3.14–3.36 |
| | 15-M ¹ | protocone | 3.31 | 3.15–3.47 |
| Extinct | | | | |
| <i>Proconsul heseloni</i> ⁶ | 1-M ₁ | protoconid | 1.40 | |
| <i>Dryopithecus laietanus</i> ⁷ | 1-M ¹ | protocone | 1.96 | |
| <i>Proconsul nyanzae</i> ⁶ | 1-M ¹ | protocone | 2.00 | |
| <i>Lufengpithecus huidienensis</i> ⁸ | 1-M ₁ | protoconid | 2.14 | |
| <i>Sivapithecus indicus</i> | 1-M¹ | protocone | 2.25 | |
| <i>Sivapithecus parvada</i> | 1-M₁ | protoconid | 2.40 | |
| <i>Paranthropus robustus</i> ⁹ | 1-M ₁ | not given | 2.43 | |

The bold identifies the two species that are the focus of the research.

¹ Dirks (2003).

² Schwartz et al. (2006).

³ Smith et al. (2007).

⁴ Beynon et al. (1991). Data for M₁ and M¹ combined.

⁵ Reid and Dean (2006). Mean and standard deviation calculated from the northern European and southern African sample combined.

⁶ Beynon et al. (1998); data given for HT2/91C (*P. heseloni*) and RU 1721 (*P. nyanzae*).

⁷ Kelley et al. (2001).

⁸ Schwartz et al. (2003).

⁹ Dean et al. (1993).

Future research

Histological studies of dental development can provide unique insights into growth and development. Daily changes in cellular activity can be quantified and thus provide detailed growth profiles, which can provide insights into primate biology in an evolutionary context (e.g., Bromage, 1991; Beynon et al., 1998; Dean et al., 2001). The pre- and post-natal timing of enamel growth can be tied to accurate estimates of age (e.g., Boyde, 1963), and linked to aspects of life history (e.g., Kelley et al., 2001; Kelley and Smith, 2003; Schwartz et al., 2005; Dean, 2006). Because of this, an increasing number of studies are being undertaken on Miocene apes, as well as continuing work on extant comparative material. Such studies have shown that some aspects of dental development, such as periodicity, vary across primate taxa, while others, such as CFT, are correlated with non-dental measures of growth (e.g., body size) in hominoids (Dean and Scandrett, 1996; Schwartz et al., 2001; Smith et al., 2003b). These findings promise much for the future, though there are still methodological limitations and practical difficulties to overcome. Understanding dental development in living primates is fundamental to understanding primate biology in an evolutionary context, yet work on understanding sources of intraspecific variation in extant samples (*Pan* and *Homo*) has only recently begun (Smith, 2004; Reid and Dean, 2006; Smith et al., 2007). Additionally, little is known about some aspects of dental development for certain extant hominoids (e.g., *Pongo* and *Gorilla*).

Table 4
Periodicity in hominoids

| Species | n | Periodicity |
|---|----------|-------------|
| Extant | | |
| <i>Hylobates lar</i> ¹ | 1 | 4 |
| <i>Pan troglodytes</i> ² | 65 | 6–7 |
| <i>Gorilla gorilla</i> ³ | 36 | 7–10 |
| <i>Pongo pygmaeus</i> ³ | 24 | 8–11 |
| <i>Homo sapiens</i> ³ | 28 | 7–12 |
| Extinct | | |
| <i>Proconsul heseloni</i> ⁴ | 1 | 5 |
| <i>Proconsul nyanzae</i> ⁴ | 1 | 6 |
| <i>Dryopithecus laietanus</i> ⁵ | 1 | 6–7 |
| <i>Lufengpithecus huidienensis</i> ⁶ | 1 | 7 |
| <i>Lufengpithecus lufengensis</i> ⁶ | 2 | 7–9 |
| <i>Paranthropus boisei</i> ⁷ | 1 | 7 |
| <i>Afropithecus turkanensis</i> ⁸ | 2 | 7–8 |
| <i>Sivapithecus indicus</i> | 1 | 8 |
| <i>Graecopithecus freybergi</i> ⁹ | 1 | 8 |
| <i>Sivapithecus parvada</i> | 1 | 9 |
| <i>Paranthropus robustus</i> ¹⁰ | 1 | 9 |
| <i>Gigantopithecus blacki</i> ¹¹ | 1 | 11 |

The bold identifies the two species that are the focus of the research.

¹ Dirks (2003).

² Smith et al. (2007).

³ Schwartz et al. (2001).

⁴ Beynon et al. (1998).

⁵ Kelley et al. (2001).

⁶ Schwartz et al. (2003).

⁷ Dean (1987).

⁸ Smith et al. (2003a).

⁹ Smith et al. (2004).

¹⁰ Dean et al. (1993).

¹¹ Dean and Schrenk (2003).

Conclusion

The *Sivapithecus* molars followed an extant great ape-like formation time. However, they differed in other aspects of crown growth. The enamel is thicker, and, like some other Miocene apes, formed rapidly with comparatively more time devoted to cuspal growth. Future studies on larger samples of living and fossil hominoids are needed to clarify these trends in crown development, which may be better understood in the context of data on body mass, brain size, craniofacial growth, and life history.

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