

Molar development in common chimpanzees (*Pan troglodytes*)

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Abstract

Numerous studies have reported on enamel and dentine development in hominoid molars, although little is known about intraspecific incremental feature variation. Furthermore, a recent histological study suggested that there is little or no time between age at chimpanzee crown completion and age at molar eruption, which is unlikely given that root growth is necessary for tooth eruption. The study presented here redefines growth standards for chimpanzee molar teeth and examines variation in incremental features. The periodicity of Retzius lines in a relatively large sample was found to be 6 or 7 days. The number of Retzius lines and cuspal enamel thickness both vary within a cusp type, among cusps, and among molars, resulting in marked variation in formation time. Daily secretion rate is consistent within analogous cuspal zones (inner, middle, and outer enamel) within and among cusp types and among molar types. Significantly increasing trends are found from inner to outer cuspal enamel (3 to 5 microns/day). Cuspal initiation and completion sequences also vary, although sequences for mandibular molar cusps are more consistent. Cusp-specific formation time ranges from approximately 2 to 3 years, increasing from M1 to M2, and often decreasing from M2 to M3. These times are intermediate between radiographic studies and a previous histological study, although both formation time within cusps and overlap between molars vary considerably. Cusp-specific (coronal) extension rates range from approximately 4 to 9 microns/day, and root extension rates in the first 5 mm of roots range from 3 to 9 microns/day. These rates are greater in M1 than in M2 or M3, and they are greater in mandibular molars than in respective maxillary molars. This significant enlargement of comparative data on non-human primate incremental development demonstrates that developmental variation among cusp and molar types should be considered during interpretations and comparisons of small samples of fossil hominins and hominoids.

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Introduction

Assessments of the skeletal and dental development of chimpanzees have been underway since before the beginning of the twentieth century (Keith, 1899; Selenka, 1899), continuing today

in both captive and natural environments (e.g., Kraemer et al., 1982; Goodall, 1986; Anemone et al., 1991, 1996; Kuykendall, 1996; Marzke et al., 1996; Zihlman et al., 2004). Hominoid dental development and tooth emergence have historically been valued because they offer insight into theories of life history and phylogeny (Zuckerman, 1928; Krogman, 1930; Schultz, 1935; Bennejeant, 1940; Clements and Zuckerman, 1953; Gavan and Swindler, 1966; Gavan, 1967), as well as the absolute ages of individuals that are still developing their dentitions (e.g., Garn et al., 1959; Bailit, 1976; Dean and Wood, 1981; Smith et al., 1994).

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Recent histological studies of dental development have been conducted for each of the extant hominoid genera (e.g., Dirks, 1998; Reid et al., 1998a,b; Schwartz et al., 2001; Reid and Dean, 2006; Schwartz et al., in press). Among numerous studies of anterior and posterior teeth, however, only Reid and Dean (2006) included a sample of molars from more than a few (human) individuals. Clearly, more data on the posterior teeth of nonhuman primates are needed to assess intraspecific variation, particularly given reports suggesting that environmental factors may influence the timing of dental development (e.g., Phillips-Conroy and Jolly, 1988; Kahumbu and Eley, 1991; Zihlman et al., 2004). Additionally, a recent study of chimpanzee molar development implied that there is little or no time between age at crown completion and age at molar eruption (Reid et al., 1998a), which is unlikely given the amount of root present at eruption (Kelley and Smith, 2003).

In this study, we address this particular discrepancy, and offer a re-evaluation of previously examined chimpanzee molar histological sections. This study also aims to increase the available data on molar crown formation time and to document developmental variation among cusp and molar types. Several aspects of molar development are quantified, including the timing and order of cuspal initiation, completion, and the

degree of molar overlap. Additionally, root length, root extension rate, and dentine secretion rate were calculated in developing molars to assess age at death and the duration of root formation prior to eruption. Little is known about species-level variation in the rate and time of formation within molar crowns or roots. In the absence of data on variation at this fundamental taxonomic level, interpretations of developmental differences in small samples of fossil and living hominoids are necessarily speculative. Data on chimpanzee molars presented in this study thus provide additional insight into the developmental biology of tooth growth in the closest living relative of humans, demonstrating that comparative analyses must consider variation among cusps and molars, and showing the need for additional data on molar overlap, root growth, and molar eruption in captive and wild individuals of known provenance.

Incremental development

Enamel development is characterized by the production of long- and short-period incremental lines that are formed in the enamel, representing rhythmic changes or disturbances in enamel secretion (Fig. 1). Long-period lines are known as *Retzius lines*. The first-formed enamel over the dentine horns,

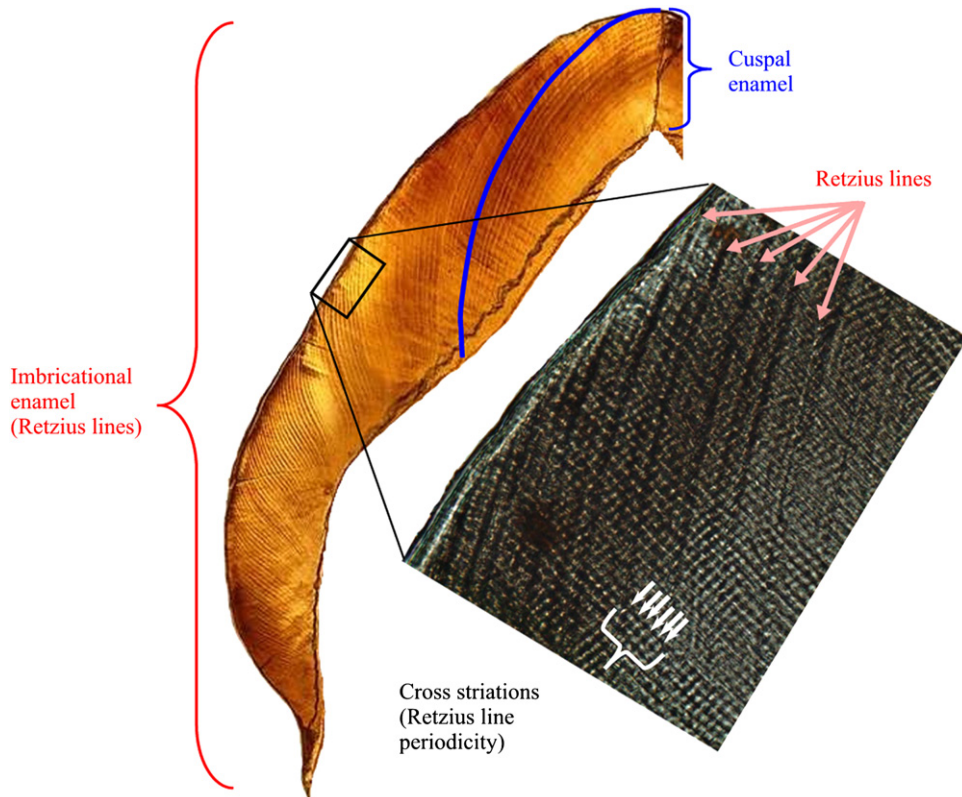


Fig. 1. Illustration of enamel developmental features in a chimpanzee M^3 mesiolingual cusp (protocone). Enamel is secreted by cells known as ameloblasts, which differentiate at the enamel-dentine junction (EDJ) and migrate outward towards what becomes the surface of the enamel, producing **cuspal enamel** (defined by the blue line) followed by **imbricational enamel** (red bracket). The tracks left by these individual cells are known as enamel prisms, which show daily features known as **cross striations** (white arrows) that result from the circadian rhythm of enamel secretion. The position of the advancing front of forming enamel is preserved as long-period incremental structures termed **Retzius lines** (pink arrows). In this study, the linear thickness of cuspal enamel was measured, the spacing of cross striations in the cuspal enamel was determined, the total number of Retzius lines was counted from the cusp tip to the cervix, and the Retzius line **periodicity** (white brackets), or number of cross striations between Retzius lines, was established for each cusp. This information was used to determine the crown formation time.

the *cuspal enamel*, does not display Retzius lines that meet the enamel surface. Later-formed Retzius lines extend to the surface of the tooth and form perikymata. This region is referred to as *imbricational enamel*. Short-period lines, known as *cross striations*, show a circadian repeat interval, and may be used to determine the daily secretion rate (DSR) (reviewed in Smith, 2006). These features show a consistent number along enamel prisms between Retzius lines, known as the *periodicity* of Retzius lines (reviewed in FitzGerald, 1998).

Crown formation time is the sum of the formation times of cuspal and imbricational enamel. Cuspal formation is often assessed by dividing the cuspal enamel thickness by the average daily secretion rate (or cross striation spacing). In several previous studies, cuspal thickness has first been multiplied by a correction factor (1.15) to account for the three-dimensional curvature of prism paths (e.g., Risnes, 1986; but see Dean, 1998a; Smith et al., 2004). Formation time of imbricational enamel is assessed by counting Retzius lines from the cusp tip to the cervix, and multiplying this number by the periodicity of Retzius lines. When combined, this yields a cusp-specific crown formation time. Because molar crown formation generally begins and ends at different times in different cusps, crown formation times derived from different cusps should not be directly compared. Examination and registration of the first- and last-formed cusps are required to assess total crown formation time accurately (Reid et al., 1998a,b). To register cusps (or teeth) forming at the same time, accentuated lines in the enamel or dentine are usually identified and matched between cusps (or teeth). Alternatively, cessation of formation at death in developing teeth also allows cusps to be registered with one another (e.g., Dirks, 1998; Reid et al., 1998a; Smith et al., 2006).

Root formation begins as the dentine-forming front extends beyond the enamel cervix, which simultaneously grows inwards toward the pulp in an appositional manner (Fig. 2). Long-period increments are known as *Andresen lines*, which are analogous to Retzius lines in the enamel. Short-period daily lines called *von Ebner's lines* are also present, although they are often more difficult to image than Andresen lines. Root formation is often assessed by measuring and counting a series of Andresen lines, multiplying the number of Andresen lines by the periodicity (derived from Retzius lines and cross striations in enamel), and dividing the distance by the time. When applied to the surface of the root, this yields the extension rate; when applied to the increments along dentine tubules, this yields the secretion rate. These rates allow the duration of root formation to be estimated, particularly for individuals with incomplete root formation. When added to the period of postnatal enamel formation, root development in incomplete teeth may also accurately yield the age at death (Smith et al., 2006).

In the past two decades, several studies have reported on incremental development in chimpanzee molar teeth (Martin, 1983; Beynon et al., 1991; Beynon and Reid, 1995; Beynon et al., 1998a; Dean, 1998a; Reid et al., 1998a; Shellis, 1998). However, most of these studies were exploratory, and did not examine variation within and between individuals.

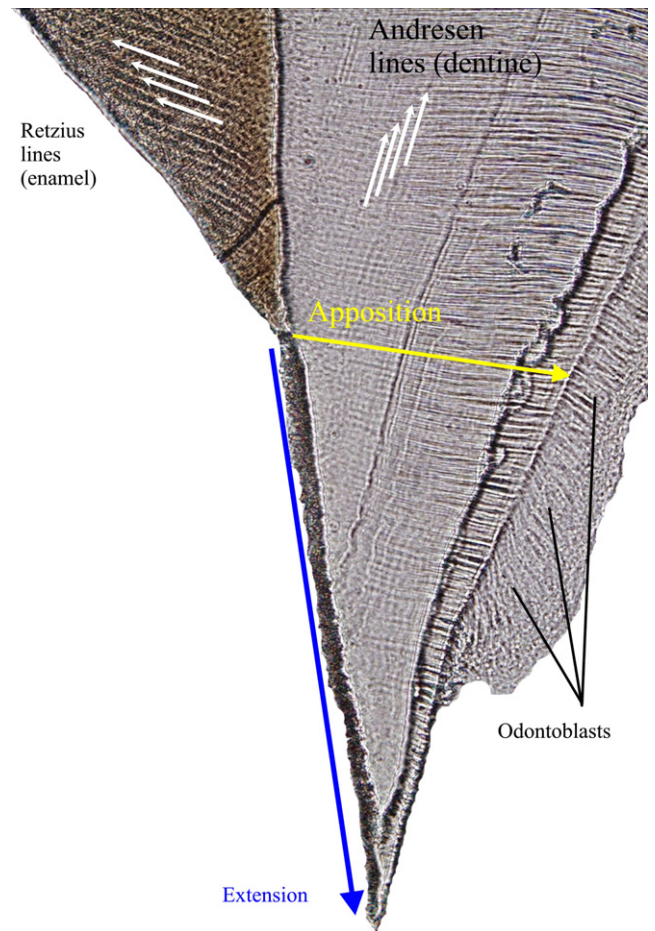


Fig. 2. Dentine formation in a developing root of the distolingual cusp (entocoid) from an unerupted M₁. Dentine is secreted by cells known as **odontoblasts**, which differentiate at the enamel-dentine junction (EDJ) and migrate inward towards what becomes the pulp chamber, producing dentine via **apposition** and **extension**. The tracks left by these individual cells are known as dentine tubules, which show daily features known as von Ebner's lines that result from the circadian rhythm of dentine secretion (not illustrated). The position of the advancing front of forming dentine is preserved as long-period incremental structures termed **Andresen lines** (white arrows in dentine), which correspond to **Retzius lines** (white arrows in enamel). In this study, the linear thickness of dentine was measured along a tubule (yellow line), the length of root formed was measured along the surface (blue line), and the spacing of Andresen lines was determined and divided by the periodicity (formation time in days) to yield the secretion and extension rates. This information was used to determine the duration of root formation prior to death. For example, this individual died at approximately 2.42 years of age, and the 770 microns of root extension (blue arrow) represents approximately 239 days of growth prior to death (detailed in the text below).

Reid et al. (1998a) presented data on partial and full dentitions of four individuals and three isolated teeth of unknown origin. At the time, their study represented the largest data set on incremental development in nonhuman hominoids, providing the first histological estimates of total crown formation time and age at crown completion in chimpanzees. Recent work by Reid, Schwartz, and Dean (Dean and Reid, 2001; Schwartz and Dean, 2001; Schwartz et al., 2001) has provided insight into the development of a large sample of chimpanzee anterior teeth, as well as variation in aspects of the enamel microstructure. Dean and Reid (2001) demonstrated that chimpanzee

anterior teeth are characterized by a large number of closely packed perikymata (surface manifestations of Retzius lines) and are formed over a longer period than equivalent human teeth. Schwartz and Dean (2001) and Schwartz et al. (2001) examined sex differences in canine development in 12–20 chimpanzee teeth, which showed significant differences in crown formation time and DSR between male and females.

Despite these studies, several questions remain regarding variation within and between species, particularly for post-canine teeth. For example, it is unclear whether and how developmental variables (i.e., incremental features and formation times) differ among cusp types or tooth types. It is also unknown to what extent the timing and sequence of molar cusp formation may vary, and to what degree sequential molar crowns show variation in developmental overlap with one another. For example, there appears to be some disagreement between radiographic/dissection-based studies (Oka and Kraus, 1969; Tarrant and Swindler, 1972; Moxham and Berkovitz, 1974; Siebert and Swindler, 1991; Winkler, 1995) and the histological study of Reid et al. (1998a) concerning the order of cuspal initiation in chimpanzee maxillary teeth. Dissection-based studies have reported that the first cusp to calcify in both mandibular and maxillary molars is the mesiobuccal cusp (protoconid or paracone), which is generally followed by the mesiolingual cusp (metaconid or protocone), followed by the distobuccal cusp (hypoconid or metacone). The distolingual cusp (entoconid or hypocone) is consistently reported to be the fourth cusp to begin calcification (followed by the hypoconulid in mandibular molars). Reid et al. (1998a), however, presented histological data on a single M¹ that suggested an order of mesiolingual, mesiobuccal, distolingual, and distobuccal, which they related to the fact that “principal maxillary cusps” (mesiolingual and distolingual) are generally larger, rounder, and have thicker enamel, and therefore initiate earlier than the respective mesio- and distobuccal cusps. Even less is known about the sequence or timing of cusp completion, partially due to the difficulty of assessing this from radiographic studies, and the time-consuming nature of histological studies. Reid et al. (1998a) reported a completion sequence for a single M¹ of distobuccal, mesiobuccal, distolingual, and finally mesiolingual. This suggests that the mesiolingual cusp of maxillary molars may represent the total crown formation time, but

more data are needed to confirm this and to assess the pattern in lower molars.

Finally, it has been suggested that nonhuman primates that are born and raised in captivity show more rapid skeletal, dental, and sexual development than wild animals (e.g., Phillips-Conroy and Jolly, 1988; Kahumbu and Eley, 1991; Marzke et al., 1996; Kelley and Smith, 2003; Zihlman et al., 2004). Zihlman et al. (2004) demonstrated this for ages at maxillary molar eruption in chimpanzees, and Phillips-Conroy and Jolly (1988) found the same results for maxillary and mandibular teeth in wild and captive baboon populations. Given these findings, crown and/or root formation must be advanced in captive populations, but this has yet to be examined directly. In short, despite recent publications on dental development in extant hominoids, additional data are necessary to understand intraspecific developmental variation. This will allow for more appropriate comparative analyses, and will clarify the relationship between crown completion time and age at molar eruption.

Materials and methods

Sample

Several collections of wild-born, captive, and unknown-provenance individuals were studied, including *Pan troglodytes verus* and *Pan troglodytes* ssp. (Table 1) (described in detail in Smith, 2004). A total of 272 histological sections of mesial and distal cusps of 135 molars from 75 individuals were prepared according to several histological procedures, which have been detailed in previous studies (Reid et al., 1998a; Smith, 2004) and are only briefly reviewed below. Little is known about the majority of this material, including sex or subspecific affiliation, but it is likely that some individuals were from research facilities and/or zoos (NCL/UCL Collection). The material ranges in developmental stage from infants with unerupted, crown-complete M1s to adult individuals with erupted M3s showing heavy wear.

Thin sections were cut from either embedded methylmethacrylate blocks or teeth coated with cyanoacrylate using an annular saw, which produces approximately 200–500- μ m-thick sections. Each section was mounted to a microscope slide

Table 1
Composition of the *Pan troglodytes* molar sample

Taxon	Provenance	Indiv.	Molars	Collection	Primary references
<i>P. t. v.</i>	Liberian (wild)	47	72	37 M ¹ , 33 M ³ , 2 M ₁	Peabody Schuman and Brace, 1954 Schuman and Sognaes, 1956
<i>P. t. ssp.</i>	Unknown (wild)	5	15	3 M ¹ , 3 M ² , 1 M ³ 2 M ₁ , 4 M ₂ , 2 M ₃	BMNH Martin, 1983
<i>P. t. ssp.</i>	Unknown (wild)	10	19	10 M ₁ , 7 M ₂ , 2 M ₃	BMNH Smith, 2004
<i>P. t. ssp.</i>	Unknown (captive?)	13	29	2 M ¹ , 1 M ² , 2 M ³ 9 M ₁ , 8 M ₂ , 7 M ₃	NCL/UCL Reid et al., 1998a
	Totals	75	135		

P. t. v. = *Pan troglodytes verus*; *P. t. ssp.* = *Pan troglodytes* subspecies unknown; Indiv. = number of individuals; Peabody = Peabody Museum, Harvard University; BMNH = Natural History Museum, London; NCL/UCL = histological collections of Newcastle University and University College London.

with dental sticky wax, and the more ideal (less oblique) face was lapped on a lapping machine with 3- μm alumina, ultrasonicated, and finished with a 1- μm diamond or alumina suspension. This face was then fixed to a microscope slide with Logitech ultraviolet curing resin under pressure. After curing, the section was lapped to an approximate 100- μm thickness, ultrasonicated, and finished with a 1- μm polishing suspension. The section was then ultrasonicated, dehydrated in an alcohol series, cleared in xylene, and a cover slip was mounted with DPX mounting media.

It should be noted that this sample is characterized by an uneven distribution of molar types from different collections. The least-represented tooth positions overall are M^1 , M^2 , and M_3 . Despite the large number of molars available, relatively few unworn/lightly worn cusps were suitable for assessment of formation time. The approach taken in this study was intentionally conservative; worn or missing enamel was generally not estimated, which considerably reduced the sample sizes. Sections that were clearly oblique or moderately-to-heavily worn were only used for periodicity determination.

Data collection and analysis

Each section was examined with polarized light microscopy. Several aspects of the enamel and dentine microstructure were quantified and are detailed below: (1) enamel daily secretion rate (DSR), (2) periodicity of Retzius lines (number of cross striations between), (3) total number of Retzius lines, and (4) cuspal enamel thickness. From these data, (5) cusp-specific crown formation time and (6) cusp-specific extension rate were established. Aspects of root formation were also quantified: (7) root dentine DSR, (8) root extension rate, and (9) duration of root formation prior to death (in developing molars).

(1) The enamel DSR was determined from mean cross-striation spacing in each unworn cusp measured with a 40 \times or 50 \times objective. Measurements were made along an axis that approximated the path of a prism from the tip of the dentine horn to the position of the first imbricational Retzius line at the tooth surface, which was divided into inner, middle, and outer zones. A minimum of three daily cross striations along a single prism were measured in each area (field of view), and a minimum of two areas were measured per zone. Cross striations were defined as light and dark bands that crossed enamel prisms perpendicularly, and intradian lines [closely spaced, fine bands dividing cross striations (see Smith, 2006)] were avoided. Means, ranges, and standard deviations were computed for inner, middle, and outer cuspal enamel zones, as well as for the overall average of each individual cusp and molar type.

Rank-based statistical methods were used to test for differences, given the relatively small sample sizes for specific cusps and molar positions; such samples likely do not meet the assumptions inherent in parametric testing (see Conover, 1999). Tests were performed using SPSS software (v13.0, SPSS Science, Inc.). Kruskal–Wallis tests for DSR differences

among samples were performed using both cusp type and molar type as factors, with all six tooth types and all eight cusp types tested separately. When significant differences were achieved, the multiple-comparisons technique described by Conover (1999) was performed to determine which cusp or molar types differed from one another. The Mann–Whitney *U*-test was employed to test for differences between buccal and lingual analogues (within mesial or distal pairs) and between maxillary and mandibular molar analogues for each cuspal zone and for the overall average cuspal value. Conover's (1999) recommended adaptation of the Jonckheere–Terpstra test for trends was used to test for a gradient in rate from inner to outer cuspal enamel. Spearman's rho is the statistic of choice for assessing the level of significance of the Jonckheere–Terpstra test statistic, and it is a more appropriate test for trends than the parametric ANOVA model, which does not explicitly test for directional differences (discussed further in Smith et al., 2005).

(2) Periodicity was determined between Retzius lines that clearly met the tooth surface. Where possible, cross striations were counted over multiple Retzius-line intervals and average periodicities were determined, as this technique may give a more accurate estimate than counts within single intervals. In some instances, when a single integer could not be determined with confidence, the range was recorded.

(3) The total number of Retzius lines that met the surface of the enamel was counted from the enamel cervix to the cusp tip. Slight corrections (<5%) were made when cervical tips were broken or when light wear obscured the first-formed Retzius line in cusp tips. For each cusp, Retzius lines were counted three times, and the average was calculated.

(4) The linear thickness of cuspal enamel was measured from the tip of the dentine horn to the approximate point where the first imbricational Retzius line was identified at the tooth surface (in unworn teeth only). A visual estimate of the degree of prism decussation (deviation from a straight line) was also made for each cusp based on the prism path from the dentine horn to the tooth surface, which was scored from 1.05 to 1.30 for slight to marked decussation, respectively. [Smith et al. (2003) traced enamel prism paths in the cuspal enamel of *Afropithecus turkanensis* molars and found light to moderate decussation may represent 1.06–1.11 times the prism path length, while Dean (1998a) calculated that the difference in a single chimpanzee molar represented 1.2 times the prism path length.]

(5) As illustrated above, total crown formation time represents the development of two regions of the crown: cuspal and imbricational enamel. Cuspal enamel formation was determined using three methods, minimum and maximum estimates were determined, and the average of these two values was used to calculate crown formation time. First, the linear cuspal enamel thickness was divided by the average cuspal DSR to yield an “uncorrected” (conservative) estimate of cuspal formation time (in days). This value was multiplied by an estimated correction factor (1.05–1.30), based on the degree of decussation observed, to compensate for the three-dimensional curvature of enamel prisms, yielding a second “corrected”

estimate. Finally, enamel thickness was entered into a regression equation that predicts the time of cuspal formation in days (Dean et al., 2001), yielding a “regressed” estimate. This equation was also used as the only method of assessing cuspal enamel formation in three cusps where DSR could not be determined due to poor cross-striation quality. In addition to sections for which total formation time was determined, cuspal enamel thickness and formation time were also determined in 23 additional cusps where it was not possible to determine imbricational enamel formation due to missing cervices or incomplete development.

The imbricational formation time, or lateral plus cervical enamel, was determined by multiplying the total number of Retzius lines for each cusp by the periodicity. Cusp-specific crown formation was determined from the sum of cuspal and imbricational enamel. In nine instances, a modified approach was taken due to light wear or missing cuspal enamel; Retzius lines were counted to the edge of the wear facet or break, the enamel thickness was measured from this point to the dentine horn (along a prism path), DSR was determined along this measurement, and the thickness was divided by the average rate for this region. Additionally, the degree of prism decussation was approximated, a corrected estimate of cuspal formation was determined, the uncorrected and corrected estimates were averaged, and the cuspal and imbricational regions were combined to yield total crown formation time. Smith et al. (2006) applied a similar approach to estimate crown formation in several macaque molar cusps, and because it yielded fairly accurate estimates, it was assumed to be appropriate for these lightly worn cusps.

(6) Additional data were recorded on the length of the enamel-dentine junction (EDJ) from the dentine horn to the cervix of each cusp using stereo microscope overviews and Sigma Scan Pro 5 software (SPSS Software, Inc.). The length of the EDJ was then divided by its cusp-specific crown formation time to determine a mean rate of crown extension (Smith, 2004; Smith et al., 2004).

When a neonatal line was identified in the cuspal enamel of M1, the prenatal DSR was quantified from measurements of a minimum of three cross striations in three areas between the dentine horn and the farthest point on the line (maximum thickness). Prenatal formation time was determined by dividing the prenatal thickness by the mean DSR.

Additionally, pairs of accentuated lines representing the same points in time were identified and mapped between cusps (or roots), and the sequence, timing, and age of cusp initiation and completion were determined when possible (illustrated in Reid et al., 1998a,b). For example, a pair of accentuated lines followed by 7 and 13 Retzius lines before cervical completion in respective mandibular mesiobuccal and distobuccal cusps demonstrates that the mesiobuccal cusp finished before the distobuccal cusp [by 6 times the periodicity (in days)]. By comparing the period of crown formation before these accentuated lines in each cusp, the initiation sequence and timing may also be determined. In this example, the total crown formation time would then be determined by adding the time of nonoverlapping formation

in the distobuccal (last-forming) cusp to the duration of formation of the mesiobuccal (first-forming) cusp. Patterns of accentuated lines were also similarly examined in the enamel and dentine to assess the degree of formation-time overlap in mandibular molars, which were matched between the distobuccal (last-forming) cusp of the more anterior molar (M_1 or M_2) and the mesiobuccal (first-forming) cusp of the successive molar (M_2 or M_3).

(7) The root dentine DSR was determined along dentine tubules running from the tip of the enamel cervix to the edge of the forming dentine (apposition line in Fig. 2). When long-period Andresen lines were visible, a series of lines was counted and multiplied by the periodicity (determined from enamel), and this was divided by the length of the Andresen lines along the dentine tubule, which yields the rate of secretion in $\mu\text{m}/\text{day}$.

(8) The root extension rate was determined by one of two methods. In developing roots where a series of Andresen lines could be clearly identified and traced to the root surface, the distance between Andresen lines at the surface was measured, and this value was divided by the number of lines multiplied by the periodicity to yield the rate of extension in $\mu\text{m}/\text{day}$. In the second method, the orientation of Andresen lines or accentuated lines was used to identify a position 200 μm deep to the surface, which was assumed to represent 80 days of formation time traced along a dentine tubule [using the 2.5 $\mu\text{m}/\text{day}$ secretion rate reported in Dean (1998b)]. The length along the root surface corresponding to this interval was then divided by 80 days to yield the rate of extension in $\mu\text{m}/\text{day}$. This was done at fixed distances along the root surface (100 μm , 200 μm , 500 μm , 1000 μm , 2000 μm , 3000 μm , 4000 μm , and 5000 μm).

(9) Root formation time was only calculated in sections that showed clear incremental features (developing teeth), and were not cut in a markedly oblique orientation across the developing roots. This was calculated by one of three methods: (1) counting the number of Andresen lines between crown completion and death and multiplying this by the periodicity, (2) dividing the thickness of the dentine (measured along a tubule) by the average DSR, or (3) by dividing the length of the root by the average extension rate. It was found that the second method may be prone to overestimation due to section-plane obliquity (inflated thickness), while the third method may be prone to underestimation due to obliquity (underestimated length).

Once the period of root formation was determined, it was possible to iteratively determine or confirm the sequence of enamel cuspal completion and initiation (when cusp-specific crown formation time was known for the respective cusp), as well as the degree of molar overlap when the successive molar was incomplete. This was possible because the cessation of formation at death permits registration of all developing material (illustrated in Fig. 5 of Smith et al., 2006: 133), which is similar to the identification and use of accentuated lines described above. In M1 cusps that showed a clearly identifiable neonatal line, postnatal crown formation was added to root formation to determine the age at death.

Results

The enamel daily secretion rate (DSR) was quantified for the molar enamel of 75 unworn cusps, and the grand mean of 225 average regional cuspal measurements was 4.15 $\mu\text{m}/\text{day}$ (range = 2.78–5.77 $\mu\text{m}/\text{day}$, s.d. = 0.35 $\mu\text{m}/\text{day}$). No significant differences in inner, middle, outer, or overall rates were found among cusps within a molar type, within cusps among molar types, between buccal and lingual analogues, or between mandibular and maxillary analogues (mean values are given in Table 5.3 of Smith, 2004: 259). Table 2 shows the lumped values for each zone; differences were tested using the Jonckheere–Terpstra test for trends, which revealed a significant increase in rate from inner to outer enamel ($p < 0.001$, $n = 225$) (Fig. 3) despite considerable overlap between middle and outer zones.

The periodicity was found to range from 6 to 7 (days between pairs of Retzius lines) in 61 chimpanzees (Table 3). The average value was 6.4 days, and the mode was 6 days. Values of either 5 or 8 could not be ruled out in three individuals, as cross striations were unclear between Retzius lines. No conclusive evidence was found to suggest that periodicity varied within or among teeth of the same dentition.

The average number of Retzius lines for each cusp and molar type, which ranged from 67 to 187, are shown in Table 4. In general, the number of Retzius lines appeared to be greater in mesial cusps than in distal cusps within a tooth type, and greater in M2 relative to M1 and M3. In mandibular molars, buccal cusps consistently showed a greater number of Retzius lines than lingual cusps, while maxillary molars showed more similarity between buccal and lingual cusps. Cuspal enamel thickness ranged from 190 to 1095 μm (Table 5). In general, distal cusps were thicker than or equal to mesial cusps, and M1 tended to have thinner enamel than M2 and M3. On the mandibular molars, the buccal cusps were equal to or thicker than the lingual cusps, while the opposite pattern was found in maxillary molars.

The mean cusp-specific crown formation times, representing summed cuspal and imbricational enamel formation times, are shown in Table 6 (individual cuspal and imbricational times are given in Table 5.8 of Smith, 2004: 266). Mean cusp-specific crown formation times in chimpanzees generally ranged from 2 to 3 years. Individual values ranged from 1.52 to 4.14 years and were dependent on cusp and molar type. The

Table 2
Inner, middle, and outer chimpanzee cuspal enamel daily secretion rates (in microns/day)

Position	<i>n</i>	Min	Max	Mean	Std. Dev
Inner	75	2.78	4.72	3.62	0.42
Middle	75	3.01	5.38	4.23	0.50
Outer	75	3.64	5.77	4.60	0.51

Position indicates the zone within the cuspal enamel where measurements of cross striations were derived from; *n* indicates the total number of cusps sampled; min and max indicate the minimum and maximum average values, respectively; mean indicates the average of all 75 cusps; the standard deviation is also in $\mu\text{m}/\text{day}$.

Table 3
Retzius line periodicities of 75 individual chimpanzees

	Unknown	5/6	6	6/7	7	7/8
Frequency	7	2	41	4	20	1

Values are number of cross striations (days) between successive Retzius lines.

lowest value was from an M₁ distolingual cusp, and the highest value was from an M² distolingual cusp (although other cusps of this individual's molar could not be compared). In general, mandibular molar buccal cusps consistently showed longer crown formation times than lingual cusps, while upper buccal and lingual cusps showed similar crown formation times. Average cusp-specific crown formation time generally increased from M1 to M2, and decreased from M2 to M3. Mean cusp-specific crown extension rates, which typically ranged from 4 to 9 $\mu\text{m}/\text{day}$, are shown in Table 7. Crown extension rates were generally greater in M1 than in M2 or M3 and were greater in mandibular molars than in respective maxillary molars.

Prenatal secretion rates ranged from 2.64 to 4.31 $\mu\text{m}/\text{day}$, with a mean of 3.53 $\mu\text{m}/\text{day}$. Prenatal crown formation times, which ranged from 14 to 70 days depending on cusp type, are shown in Table 8. For two maxillary molars, the order of prenatal initiation was variable; the mesiobuccal cusp initiated 11 days before the mesiolingual cusp in one individual, while the opposite pattern was found in a second individual (20-day

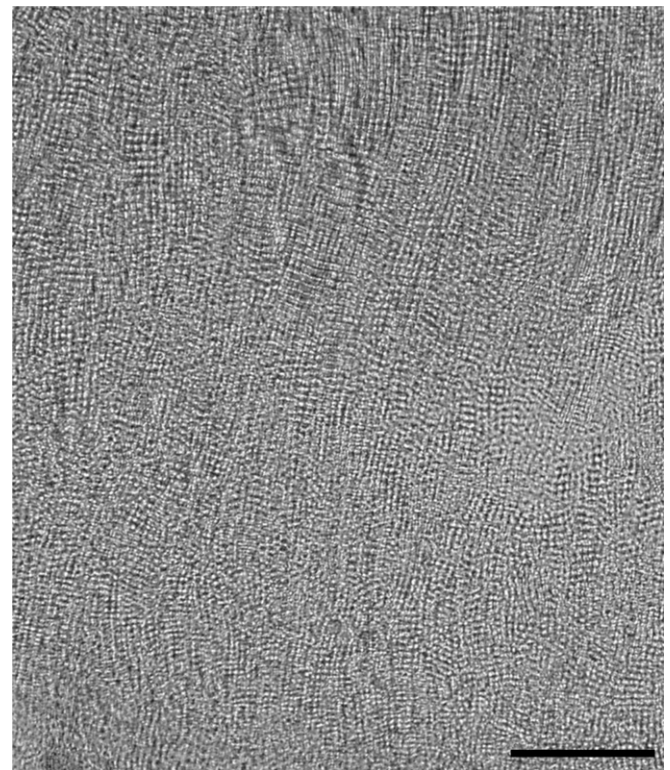


Fig. 3. Cross striations (light and dark bands crossing vertically oriented enamel prisms) in chimpanzee occlusal molar enamel showing the progressive increase in spacing (secretion rate) from the inner enamel (bottom) towards the surface of the tooth (top). The scale bar in the bottom right is equal to 200 microns.

difference). The distobuccal cusp was observed to be the third cusp to begin calcification prenatally. No evidence was found for prenatal enamel formation in the distolingual cusp of these two M^1 s. In most of the comparisons among M_1 s, the mesiobuccal cusp initiated before the mesiolingual cusp. The distobuccal cusp typically initiated after the mesiobuccal cusp and was closely followed by the mesiolingual cusp, but the order of the second- and third-forming cusps was variable. No evidence was found for prenatal formation in the distolingual cusp.

Among all molar types, patterns of cuspal initiation and completion showed more variation than previously reported (Table 9). When maxillary molar types are lumped, the order of initiation varied between the first- and second-forming mesial cusps, which were generally followed by the distobuccal cusp, although the order of initiation between distal cusps was also variable. Among mandibular molars, the mesiobuccal cusp was almost always the first cusp to initiate, often followed by the distobuccal cusp and then the mesiolingual cusp, but this also showed some variation. The distolingual cusp was consistently the last cusp to initiate. Overall, within mesial or distal pairs, maxillary molar cusps were more similar in the timing of initiation, which may have led to more variable sequences. In contrast, mandibular molars show a more consistent initiation sequence of first and last cusps with several months in between, and variation occurred most often between the second and third positions.

When the order of cusp completion is considered, maxillary molars also showed variation in the timing and sequences of cusp completion. In general, the mesiolingual cusp was the latest-forming mesial maxillary cusp, but variation was observed. In one instance, the mesiobuccal cusp completed formation approximately 2 months after the mesiolingual cusp, while in three other instances, the mesiolingual cusp finished 2 to 4 months after the mesiobuccal cusp. Distal maxillary cusps also showed a variable pattern of crown completion order, as they generally complete formation before the mesial cusps, but did not show a consistent sequence. Given the variation in initiation and completion times, it does not appear that any single maxillary cusp consistently represents the total crown formation time. For lower molars, the most common sequence of cuspal completion was: mesiolingual, distolingual, mesiobuccal, and finally the distobuccal cusp. Due to the fact that the distobuccal cusp generally finished after the

mesiobuccal cusp (first to initiate), no single mandibular cusp consistently represented the total crown formation time. By matching accentuated lines (frequently the neonatal line), it was possible to determine the entire range (or duration) of crown formation (2.18–2.64 years), referred to here as the total crown formation time, in six M_1 s. The age at M_1 crown completion in these individuals ranged from 2.01 to 2.58 years, which is less than the total crown formation time due to the fact that M_1 initiates prior to birth.

The degree of overlap in mandibular molar crown formation was determined for ten molar dyads (7: M_1 - M_2 or 3: M_2 - M_3) in nine individuals, which showed marked variation. (Given limited samples of unworn/lightly worn successive maxillary molars, it was not possible to assess maxillary molar overlap). The degree of overlap between M_1 and M_2 ranged from an unknown period of developmental delay to approximately 306 days of overlap (Fig. 4). A single presumably captive individual showed similar overlap (301 days) to the maximum value (306 days) for six wild-born individuals. Three of the seven individuals showed evidence of little or no overlap, while the four others showed a mean overlap of approximately 231 days (range = 70–306 days). In four individuals, it was possible to determine the age at M_2 (mesiobuccal cusp) initiation, which ranged from 1.26 to 2.10 years of age (mean = 1.72 years). Second and third mandibular molar overlap in three individuals ranged from a delay of approximately one year to an overlap of approximately 280 days of formation time. One presumably captive individual showed approximately 70 days longer molar overlap than the wild-born individual with the greatest overlap. When all molar types are considered together, differences in the degree of molar formation overlap likely lead to marked variation in ages at molar eruption.

When dentine microstructure was considered, secretion rates along a dentine tubule near the cervix were found to increase from earlier- to later-formed dentine (ranging from 1 to 2 $\mu\text{m}/\text{day}$ along the first 1.5 mm), and also near the root surface (within approximately 200 μm) from the cervix towards the apex of the tooth for the first 5 mm of root (ranging from 1 to 2 $\mu\text{m}/\text{day}$). Mean dentine extension rates for the lumped sample were also found to increase from the cervix towards the apex of the root, rising from approximately 3.5 $\mu\text{m}/\text{day}$ at 100 μm from the cervix to over 6 $\mu\text{m}/\text{day}$ at 2 mm down the root, and remaining between 6 and 9 $\mu\text{m}/\text{day}$ for the next

Table 4
Average Retzius line number in chimpanzee molars

Tooth	mb	range (n)	ml	range (n)	db	range (n)	dl	range (n)
M^1	113	99–127 (2)	99	91–107 (2)	86	—	77	—
M^2	129	—	131	—	187	—	n/a	—
M^3	119	106–130 (4)	128	125–130 (2)	112	101–126 (6)	108	85–132 (3)
M_1	107	90–139 (5)	83	74–93 (5)	104	89–119 (8)	80	67–94 (4)
M_2	133	110–147 (4)	103	72–130 (4)	128	—	107	98–116 (2)
M_3	123	—	90	73–107 (2)	121	—	90	82–97 (2)

Cusp types are indicated for maxillary molars: mb = mesiobuccal cusp (paracone), ml = mesiolingual cusp (protocone), db = distobuccal cusp (metacone), dl = distolingual cusp (hypocone). For mandibular molars: mb = mesiobuccal cusp (protoconid), ml = mesiolingual cusp (metaconid), db = distobuccal cusp (hypoconid), dl = distolingual cusp (entoconid). Range data indicate the minimum and maximum values, and the number in parenthesis indicates the number of cusps sampled. Sample sizes are one when range data are not indicated. Data were not available for the distolingual cusp of M^2 , indicated by n/a.

Table 5
Average linear cuspal enamel thickness in chimpanzee molars (in microns)

Tooth	mb	range (n)	ml	range (n)	db	range (n)	dl	range (n)
M ¹	445	190–700 (2)	445	—	445	—	475	—
M ²	588	565–610 (2)	670	—	860	—	n/a	—
M ³	705	675–740 (4)	740	685–795 (2)	732	560–1015 (6)	993	855–1095 (3)
M ₁	587	420–750 (5)	554	480–685 (5)	675	615–785 (7)	693	660–750 (5)
M ₂	894	670–1075 (8)	766	635–910 (10)	1002	950–1050 (4)	817	730–895 (3)
M ₃	705	470–920 (3)	697	625–820 (3)	1055	—	700	—

Headings and abbreviations are the same as in Table 4. Values are in μm .

3 mm. Although there was an overall increasing trend in extension rate, the pattern was not linear, and variation was observed both within and between root types. Mean rates were calculated for the first 5 mm of all mandibular molars and for M¹ and M³, which revealed that M1 showed higher initial extension rates than M2 and/or M3. In addition, mean rates were greater for mandibular molars than respective maxillary molars (Fig. 5).

Finally, root lengths of unerupted teeth at the time of death varied as expected; roots associated with cusps that completed crown formation early were typically longer than those for cusps that had completed crown formation relatively late, suggesting a fairly uniform rate of extension among roots. Most unerupted mandibular teeth had maximal root lengths (measured below the cervix of the mesiolingual cusp) less than 6 mm and were from individuals 3.5 years old or younger. Some variation was observed in root formation and age at eruption within a wild population (Fig. 6). One individual (389I) appeared to have just begun M₁ alveolar emergence at 2.78 years of age and showed the following approximate root lengths (given for corresponding cusps): mesiobuccal, 2.345 mm; mesiolingual, 2.865 mm; distobuccal, 1.275 mm; and distolingual, 2.550+ mm. Another individual (389E) with a slightly more advanced M₁ (possibly just beginning gingival emergence) showed the following root lengths: mesiobuccal, 3.700 mm; mesiolingual, 5.120 mm; distobuccal, 3.780 mm; and distolingual, 4.880 mm. This individual was estimated to have died at 4.40 years of age.

Discussion

Variation in incremental development

This study represents the most comprehensive histological examination of molar development in a nonhuman primate

to date. Developmental parameters, such as enamel daily secretion rate (DSR), show little variation within or among cusps, molars, or individuals. Significantly increasing trends were found from inner to outer cuspal enamel, ranging from approximately 3 to 5 $\mu\text{m}/\text{day}$, which is consistent with previous studies (e.g., Beynon et al., 1991; Dean, 1998a; Reid et al., 1998a; see also Table 5.15 of Smith, 2004: 281–282). It is not clear whether DSR values within analogous regions are consistent within an entire dentition, as Reid et al. (1998a) presented values that appeared to decrease from the anterior to the posterior teeth, while the canine cuspal values reported in Schwartz et al. (2001) are within one standard deviation of the molar cuspal values reported here. Additional studies of DSR in full dentitions may assess the relationship between anterior and posterior tooth types and secretion rates.

The periodicity of Retzius lines was also found to be within the values reported by Schwartz et al. (2001), although the range found in this study is smaller. No relationship was found between periodicity and the number of Retzius lines within a cusp type, as Reid and Ferrell (2006) reported for modern humans, which may have been due to low variation in chimpanzee periodicity or limited sample sizes per cusp type (Smith, 2004). The number of Retzius lines and cuspal enamel thickness were both found to be variable among cusp and molar types, which led to variation in cusp-specific crown formation times. Patterns of cuspal enamel thickness are consistent with other studies that have suggested a trend between buccal and lingual analogues, which may be due to functional differences (e.g., Reid et al., 1998a; Spears and Macho, 1998; Schwartz, 2000; Kono, 2004; Smith et al., in press).

Crown formation times in this study generally fall between reported values from radiographic studies and a previous histological study (Table 10). Results of radiographic studies have suggested that chimpanzee M1 formation is completed in 24 months or less, while Reid et al. (1998a) reported crown

Table 6
Average cusp-specific crown formation time in chimpanzee molars (in days)

Tooth	mb	range (n)	ml	range (n)	db	range (n)	dl	range (n)
M ¹	909	753–1065 (2)	840	809–872 (2)	712	—	684	676–692 (2)
M ²	1059	—	1070	—	1511	—	n/a	—
M ³	921	818–993 (4)	1035	966–1104 (2)	821	761–938 (6)	926	777–1049 (3)
M ₁	792	734–952 (5)	633	601–682 (5)	811	709–967 (8)	662	556–746 (4)
M ₂	984	804–1081 (4)	851	712–1086 (5)	1160	—	842	796–888 (2)
M ₃	1001	—	823	697–949 (2)	1120	—	820	776–865 (2)

Headings and abbreviations are the same as for Table 4. Time represents the sum of imbricational and cuspal enamel formation in days.

Table 7
Average crown extension rate in chimpanzee molars (in microns/day)

Tooth	mb	range (n)	ml	range (n)	db	range (n)	dl	range (n)
M ¹	6.71	5.81–7.61 (2)	7.71	7.66–7.75 (2)	8.67	—	7.27	6.83–7.70 (2)
M ²	5.54	—	6.05	—	4.58	—	n/a	—
M ³	5.91	5.30–6.53 (4)	5.48	4.98–5.98 (2)	5.80	4.77–8.47 (6)	4.99	3.73–6.22 (3)
M ₁	7.94	7.07–8.88 (5)	8.82	8.00–9.43 (5)	8.08	6.47–9.28 (8)	7.88	7.18–8.72 (4)
M ₂	6.61	5.77–7.85 (4)	6.64	5.41–7.27 (5)	5.91	—	6.33	5.95–6.71 (2)
M ₃	7.23	—	6.60	5.44–7.76 (2)	5.10	—	6.22	5.40–7.04 (2)

Headings and abbreviations are the same as for Table 4. Crown extension rate calculated as cusp-specific enamel-dentine junction length divided by cusp-specific crown formation time.

formation times of approximately 29–37 months using histological methods. Similarly, the radiographic studies suggest that M2 formation requires approximately 26–39 months, while Reid et al. (1998a) reported approximately 41–48 months. For M3 formation, radiographic methods suggest between 36 and 54 months, while Reid et al. (1998a) reported 42–54 months. Differences between radiographic and histological results are partially due to the fact that radiographic determination underestimates the actual duration of development, as the initial period of crown formation is not visible in radiographs for several months after initiation, and the end of cervical crown formation appears to be completed on a radiograph prematurely (Hess et al., 1932; Winkler, 1995; Beynon et al., 1998b). Differences between the current and the former histological studies are largely due to reinterpretations of the periodicity of Retzius lines (which was reduced in two of the four main individuals included in Reid et al.'s sample), although the present study also includes more data on molar formation in additional individuals.

The inclusion of crown extension rates is a relatively recent addition to the developmental variables typically reported. Dean (1998a) reported extension rates for the cuspal portion of crown formation in a chimpanzee M2 (approximately 280 days of formation), as well as for a single human and orangutan molar. Smith et al. (2004) reported crown extension rates for a single M₃ mesiobuccal cusp (protoconid) of *Graecopithecus freybergi*, which is similar to the values reported here for chimpanzees. In contrast, cusp-specific extension rates for macaques (*Macaca nemestrina*) are two to four times higher than hominoid values (Smith, 2004; Smith et al., 2006). It appears that, among extant and fossil great apes and humans, extension begins at a rather high rate in the crown, which progressively slows towards the cervix (Dean, 1998a; Smith et al., 2004), and then speeds up after the first or second millimeter of root formation. Future studies are needed to investigate the relationship between rates of coronal extension and subsequent

Table 8
Average prenatal crown formation time in chimpanzee M1s (in days)

Tooth	mb	range (n)	ml	range (n)	db	range (n)	dl	range (n)
M ¹	33	29–36 (2)	37	25–49 (2)	14	—	n/a	—
M ₁	49	26–70 (8)	36	23–44 (5)	35	22–49 (4)	n/a	—

Headings and abbreviations are the same as for Table 4. No evidence was found for prenatal formation in either the upper distolingual cusp (hypocone) or the lower distolingual cusp (entoconid).

root extension within and among cusp and molar types, and among different primate taxa.

Sources of developmental variation found in this study may result from differences between captive and wild populations, differences between subspecies, differences between sexes, or differences related to variation in absolute tooth size. Very little is known about the effects of these factors on incremental development or crown formation time. As noted above, Phillips-Conroy and Jolly (1988) and Zihlman et al. (2004) reported that wild populations of baboons and chimpanzees, respectively, showed later ages at molar eruption than captive populations, but it is not clear if these differences result from differences in crown or root growth. Although samples in the present study were limited, a wide range of crown formation times was found in individuals from one of the three known wild-born populations (BMNH), as well as within one that was believed to be mainly captive (NCL/UCL). When mean values and ranges of developmental variables are compared between the three wild collections versus the likely captive collection, there are no consistent trends in differences, and the majority of values overlap. This result suggests that reported differences in the age at molar eruption between captive and wild populations may be due to differences in the degree of molar overlap and/or rates of root growth rather than the duration of crown formation.

Because the majority of individuals in the current study were of unknown sex, it was not possible to test for sex differences in this sample (although it should be noted that the individual with the longest formation time was a large wild-born male). Schwartz and Dean (2001) and Schwartz et al. (2001) found sex differences in enamel DSR, cuspal enamel thickness, and crown formation times in some extant hominoid canines. *Pan* females showed significantly higher inner cuspal DSR than males, but did not show sex differences in cuspal enamel thickness or periodicity. Smith et al. (in press) examined sex differences in molar developmental variables in two known-sex human populations and found few differences. Only the periodicity of Retzius lines in one of the two populations showed a significant difference, with females showing a higher periodicity than males. Even less is known about subspecific and interpopulation variation in hominoid dental development. Due to the nature of the samples in this study, it was not possible to assess this potential source of variation. Future studies of known-provenance, known-sex, and known-subspecies material are needed to assess the degree of variation seen in chimpanzee molar development.

Table 9
Initiation/completion sequences and cusp formation duration in chimpanzee molars

Individual	Tooth	Initiation sequence	Duration				Completion sequence
			mb	ml	db	dl	
88.89	M ¹	ml > mb, db > dl	—	809	—	676	mb > ml
89.89	M ¹	mb > ml > db > dl	753	872	712	692	db > mb > dl > ml
10.88	M ¹	—	—	—	—	—	db > dl
3387	M ²	mb > ml > db	—	—	1511	—	ml > db
6909	M ³	ml > mb	993	1104	—	—	mb > ml
7038	M ³	—	974	—	—	—	ml > mb
7119	M ³	dl ≥ db	—	—	791	777	dl > db
389A	M ₁	mb > db > dl	772	—	709	556	ml > dl > mb > db
389B	M ₁	mb > ml ≥ db > dl	—	—	766	—	ml > dl > mb > db
389C	M ₁	mb > db > dl	—	—	—	—	—
	M ₂	mb ≥ ml	—	—	—	—	ml > dl > mb > db
	M ₃	mb > ml ≥ db > dl	—	—	—	—	—
389D	M ₁	mb ≥ db > ml ≥ dl	—	—	781	—	dl > db
	M ₂	mb > ml	1015	792	—	—	dl > db
	M ₃	mb > ml > db > dl	—	—	—	—	—
389E	M ₁	mb > ml > db > dl	952	682	904	746	dl ≥ ml > mb > db
	M ₂	mb > db > ml > dl	—	—	—	—	—
389F	M ₁	mb > db > ml > dl	—	660	773	654	dl > ml > mb > db
	M ₂	mb > ml	—	—	—	—	—
389G	M ₁	—	746	601	718	—	ml > db ≥ mb
389I	M ₁	mb > ml, db > dl	734	—	—	—	ml > mb > db
	M ₂	mb > ml > dl	—	—	—	—	—
389J	M ₁	mb > db ≥ ml > dl	758	610	—	—	ml > mb > db
	M ₂	mb > ml > db	—	—	—	—	—
389K	M ₁	mb > ml, db > dl	—	—	—	692	dl > db
	M ₂	mb > ml	—	—	—	—	—
15.00	M ₃	mb > ml	—	949	—	—	ml > mb
28.90	M ₁	mb > db > ml > dl	—	613	869	—	ml > mb, dl > db
	M ₂	mb > ml ≥ db > dl	1037	—	1152+	888	ml > dl > mb > db
4.01	M ₁	mb > ml	—	—	967	—	dl ≥ ml > mb > db
	M ₂	mb > ml > dl	804	—	—	—	ml > mb, dl > db
88.89	M ₁	mb > ml	—	—	—	—	ml > mb, dl > db
	M ₂	—	—	850	1160	—	ml > mb, dl > db
	M ₃	db > dl	—	—	1120	865	ml > dl > db
59.89	M ₂	mb > ml > dl	1081	816	—	796	dl > ml > db ≥ mb

Individual chimpanzees are indicated by accession codes. Tooth types are for maxillary molars followed by mandibular molars. Initiation sequence refers to the order of cusp calcification, with the first cusp to calcify indicated on the left, followed by cusps calcifying in order after or at the same time, > or ≥, respectively (see Table 4 for explanation of cusp codes). Duration is the cusp-specific crown formation time for each cusp indicated (see text for methods), and completion sequence refers to the order of cusp completion, with the first cusp to finish formation indicated on the left, followed by cusps calcifying after or at the same time, > or ≥, respectively.

Smith (2004) examined the correlation between developmental variables in this sample, in part to determine if size differences among cusps or molars may explain some of the apparent variation. Bicervical diameter was used as a size scalar, as it has been demonstrated to have a positive relationship with tooth size (and by inference, body mass) (e.g., Martin, 1983; Shellis et al., 1998; Schwartz, 2000; Grine, 2002). Several variables showed positive allometry, including periodicity, number of Retzius lines, and crown formation time. This suggests that variation in molar size (and possibly body mass) may explain some of the developmental variation within this mixed sample. Further, the results for crown formation time trends in successive molars suggest that trends in tooth size may parallel trends in crown formation time [also see Smith et al. (2005) for a related discussion on trends in enamel thickness in this sample].

Individual cusp development and total crown formation time

Although numerous studies have reported the timing and sequence of cuspal calcification (prenatal formation) in human M1s, these data are available for relatively few chimpanzees (Oka and Kraus, 1969; Tarrant and Swindler, 1972; Moxham and Berkovitz, 1974; Siebert and Swindler, 1991; Winkler, 1995; Reid et al., 1998a). Several studies suggest that mandibular and maxillary M1s begin to calcify about one to two months before birth in chimpanzees, which is confirmed in this study. Differences in prenatal enamel initiation times between cusps were found to range from a few weeks to less than two months. The general consensus of previous work is that two to three cusps begin calcification prior to birth, and sometimes a fourth cusp has also begun, which is similar to

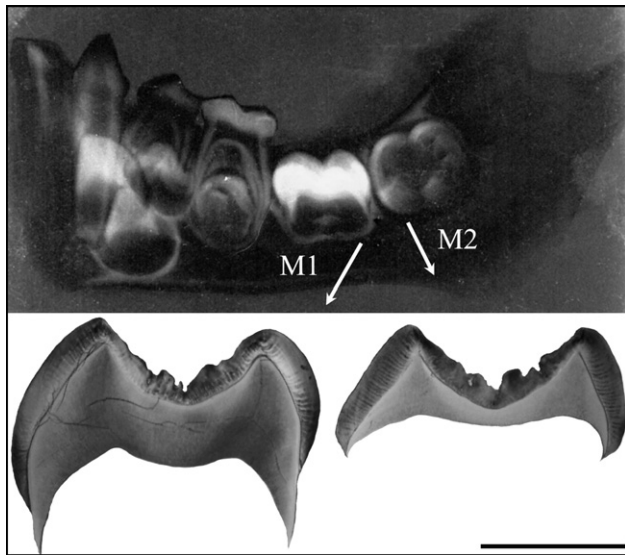


Fig. 4. Mandibular molar overlap in a wild-born infant chimpanzee estimated to have died at 3.22 years of age. The lateral radiograph (above) shows the first molar (M1) prior to alveolar emergence, and the second molar (M2) developing at a 90 degree angle to the occlusal plane. Histological sections of the distal cusps of the M1 (bottom left) and the mesial cusps of the M2 (bottom right) show approximately 8 months of overlapping crown development (M1 distobuccal cusp registered to M2 mesiobuccal cusp). The scale bar for the sections is 5 mm.

the current histological findings, although prenatal initiation in a fourth M1 cusp was not detected in this study.

Several of these studies have also reported variation in the initiation order of cusps from all molar types (Oka and Kraus, 1969; Moxham and Berkovitz, 1974; Winkler, 1995; Reid et al., 1998a), and in this study, variation was found in both mandibular and maxillary cuspal initiation. The sequence of the second and third cusps to initiate was the most variable in mandibular molars, while the first cusp to initiate was variable in the limited sample of maxillary molars. It is likely that assessment of cuspal initiation sequences may be influenced

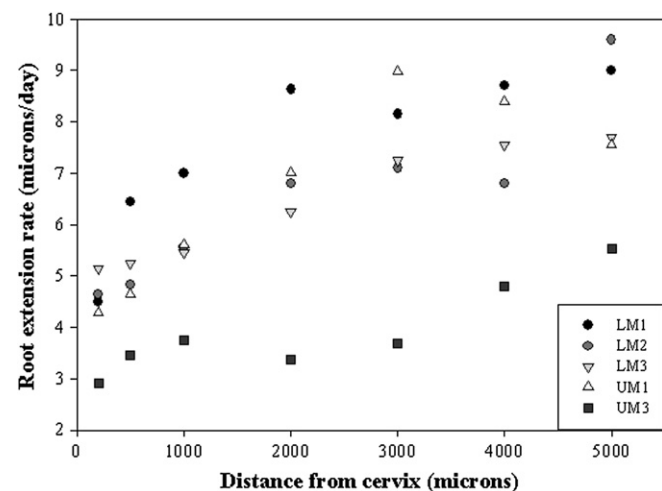


Fig. 5. Mean molar root extension rate (in microns/day) as a function of the distance from the cervix (in microns). Tooth types are specified in the legend in the lower right corner.

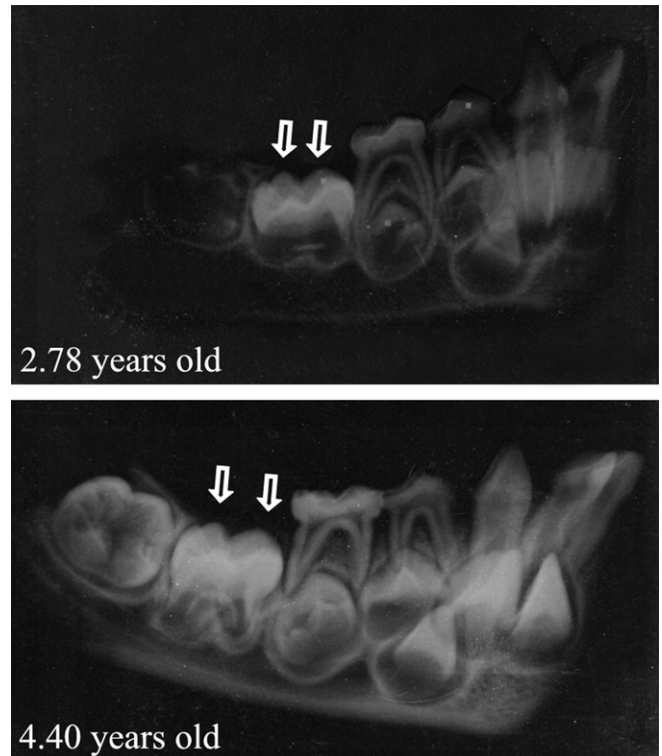


Fig. 6. Developing wild-born chimpanzee mandibular dentitions showing variation in age at M₁ alveolar emergence. The individual on top completed M₁ formation at 2.27 years and died at approximately 2.78 years of age. The individual below completed M₁ formation at 2.64 years of age and died at approximately 4.40 years of age. Note the similarity of the degree of M₁ emergence (white arrows), which is slightly more advanced in the individual on the bottom.

by the study sample; larger samples would be helpful to assess overall trends. When the duration of specific cusp formation in chimpanzees is considered, Reid et al. (1998a) reported that, in maxillary molars, the mesiolingual and mesiobuccal cusps take the longest to form, followed by the distal cusps. They reported that the mesiobuccal and distobuccal cusps in mandibular molars take the longest time to form, followed by the mesiolingual and distolingual cusps. The results of the current study are generally consistent with these findings, although data on maxillary molars are limited in both studies. This trend of longer times in maxillary mesiolingual and mandibular mesiobuccal cusps relative to the other respective mesial cusp has also been confirmed in a large sample of modern human molars from diverse populations (Reid and Dean, 2006; Smith et al., in press). Smith et al. (in press) found a statistically significant difference between mesial cusp analogues (mesiolingual were greater in maxillary and mesiobuccal greater in mandibular), which was due to significantly greater cuspal enamel thickness and also higher numbers of Retzius lines in the respective longer-forming cusp types.

Consideration of cusp initiation, coupled with cusp-specific formation time (or duration), yields the sequence and timing of cuspal completion. As for the other developmental variables, data on maxillary cusps are limited, and they suggest marked variation between mesial analogues, and some variation in

Table 10
Ages at chimpanzee molar calcification, crown formation, and root formation, as well as crown formation duration (in months)

Tooth (<i>n</i>)	Age Calc.	Age C.C.	CFT	Source
Radiographic Studies				
M ₁ (4)	n/a	21–27	~24	Anemone et al., 1991
M ₁ (23)	n/a	20.5 ± 3	<24	Anemone et al., 1996
M ₁ (9)	1.6	20.3 ± 3.6	~18.7	Kuykendall, 1996
M ₂ (3)	15–18	48	30–33	Anemone et al., 1991
M ₂ (14)	15.7 ± 3.3	41.6 ± 4.6	~26	Anemone et al., 1996
M ₂ (7)	16.1 ± 1.6	55.1 ± 7.1	~39	Kuykendall, 1996
M ₃ (2–3)	42–48	84–96	36–54	Anemone et al., 1991
M ₃ (12)	43.7 ± 3.9	n/a	n/a	Anemone et al., 1996
M ₃ (8)	42 ± 7.7	87.4 ± 10.6	45.4	Kuykendall, 1996
Histological Studies				
M ₁ (3)	–1.8––0.6	>28.8–36.6	34.2 ± 3.1*	Reid et al., 1998a
M ₁ (1)	n/a	n/a	17.5	Shellis, 1998
M ₁ (6–8)	–2.3––0.9#	24.0–30.9	26.1–31.6	This study
M ¹ (2)	–1.8	>27–27.6	32.8 ± 3.7*	Reid et al., 1998a
M ¹ (2)	–1.6––1.2	24.9–27.8	26.6–29.0	This study
M ₂ (2–3)	20–23.4	>54.2–>67.3	44.3 ± 3.4*	Reid et al., 1998a
M ₂ (4)	15.3–25.6#	n/a	35.4–>37.8	This study
M ² (1)	16.8	55.2	42.7*	Reid et al., 1998a
M ² (1)	n/a	n/a	>51.7	This study
M ₃ (2)	43.2–43.4	83.2–84	48.5 ± 5.4*	Reid et al., 1998a
M ³ (1)	46.1	n/a	41.8	Reid et al., 1998a
M ³ (1)	n/a	n/a	~36.1	This study

Tooth position sample sizes (*n*) may not be equal to the number of individuals, as some radiographic studies combined data on left and right analogous. Age Calc. and Age C.C. are ages at crown calcification and crown completion, respectively, in months, followed by the standard deviation (when reported). CFT is crown formation time, or the period from calcification to completion. * In this source, the age at initiation and crown formation times do not consistently add to age at crown completion; pooled data from their Tables 5 and 6 are not consistent with one another. Determining the sample size and time of crown formation from this source is difficult due to the way the results were presented. # Data from mesiobuccal cusp only.

distal analogues. (Given that it was difficult to relate mesial to distal cusps in maxillary teeth, findings on cusp completion sequences should be investigated in additional samples.) Mandibular molar cusps showed a more consistent pattern of completion sequences, demonstrating that no single cusp consistently encompasses the total crown formation.

Molar eruption and root development

Estimates of crown formation time in the present study are more consistent with previously reported developmental data on age at M1 eruption in chimpanzees, and they suggest that 1–2 years must elapse between M1 crown formation and eruption (Table 11). Several early studies of tooth eruption in chimpanzees utilized small numbers of captive animals or museum specimens of known age (reviewed in Zuckerman, 1928; see also Bingham, 1929; Schultz, 1935; Bennejeant, 1940; Schultz, 1940). It was not until the longitudinal study of Nissen and Riesen (1945, 1964) that data became available on gingival eruption in more than a few individuals. In 1945, they reported eruption age of the deciduous dentition in 16 captive individuals, followed by a 1964 report on the eruption of the permanent dentition in 15 of the original 16 chimpanzees. More recently, Kraemer et al. (1982) and Conroy and Mahoney (1991) reported age at eruption in captive animals. The latter study presented longitudinal data from intraoral exams on 58 chimpanzees over ten years, yielding the largest known data set on age at emergence in captive individuals.

Zihlman et al. (2004) recently reported estimated maxillary eruption ages from dry skulls of wild chimpanzees, which appeared to show later ages than Conroy and Mahoney's captive material, although it is unclear how eruption data from oral examinations or radiographs compare to estimates from museum specimens without soft tissues. Zihlman et al. (2004) suggested that, given differences in eruption ages between captive and wild individuals, previous developmental standards from captive animals may not be the most appropriate comparative material for the interpretation of fossil material. The results of this study also suggest a later age of M1 eruption than previous reports on captive populations; however, it does not appear that this is due to differences in crown formation time.

It is interesting to note that several of the Tāi Forest chimpanzees included in the Zihlman et al. (2004) study show mandibular teeth that are advanced relative to the degree of eruption of the maxillary teeth (Smith, pers. obs.). Maxillary molar eruption advancement has been rarely considered, in particular due to the difficulty of imaging maxillary teeth with conventional radiography. Dean and Wood (1981) did not find developmental differences between mandibular and maxillary teeth in a cross-sectional radiographic hominoid sample. However, Conroy and Mahoney (1991) found that M₁ emerged significantly earlier than M¹ in their large longitudinal sample (also seen in other studies included in Table 11). Mean cusp-specific crown formation times in this study also showed a trend for maxillary molars to form over slightly greater periods of time and to show less root development

Table 11
Published estimates of age at molar emergence in primarily captive chimpanzees (*Pan troglodytes* subsp.)

Tooth (<i>n</i>)	Age	Source
M ₁ (75)	38.4 ± 5.7	Conroy and Mahoney (1991)
M ₁ (30)	32–45	Nissen and Riesen (1964)
M ₁ (4/8)	~33–36*	Bingham (1929)/Schultz (1940)
M ₁ (?)	34–39.6	Kraemer et al. (1982)
M ¹ (74)	40 ± 5.5	Conroy and Mahoney (1991)
M ¹ (30)	33–45	Nissen and Riesen (1964)
M ¹ (4/8)	~33–36*	Bingham (1929)/Schultz (1940)
M ¹ (1)	49.2#	Zihlman et al. (2004)
M ¹ (?)	39.6–48	Kraemer et al. (1982)
M ₁ /M ¹ (2)	> ~42	Oka and Kraus (1969)
M ₁ /M ¹ (2)	≤45	Bennejeant (1940)
Consensus	~32–49	
M ₂ (3/6)	~73–79*	Schultz (1940)
M ₂ (17)	75.8 ± 8.9	Conroy and Mahoney (1991)
M ₂ (30)	67–88	Nissen and Riesen (1964)
M ₂ (?)	70–96	Kraemer et al. (1982)
M ² (3/6)	~73–82*	Schultz (1940)
M ² (16)	74.4 ± 9.7	Conroy and Mahoney (1991)
M ² (30)	68–94	Nissen and Riesen (1964)
M ² (2)	98.4–100.8#	Zihlman et al. (2004)
M ² (?)	70–77	Kraemer et al. (1982)
Consensus	~65–101	
M ₃ (3/6)	~104–121*	Schultz (1940)
M ₃ (28)	108–157	Nissen and Riesen (1964)
M ₃ (?)	96–142	Kraemer et al. (1982)
M ³ (3/6)	~118–134*	Schultz (1940)
M ³ (28)	117–163	Nissen and Riesen (1964)
M ³ (2)	≥148.8–165.6#	Zihlman et al. (2004)
M ³ (?)	126–168	Kraemer et al. (1982)
Consensus	~96–168	

Tooth position sample sizes (*n*) may include right and left analogues from the same individual. Age at eruption is given in months, followed by the standard deviation when reported. *Ages of individuals in Schultz (1940) were not precisely known. # Assessed in dry skulls known to be from a wild population; all other data are from oral examinations of captive individuals.

than respective mandibular molars (although it is unclear which cusps or roots should be compared between molar analogues). A final complication in comparing studies of tooth eruption/emergence is that little is known about the delay from alveolar to gingival emergence. The only published chimpanzee data are from Zuckerman (1928), who reported that two captive chimpanzees showed 4 months of delay between alveolar emergence and the time the tooth was “in place.” The lack of data on nonhuman primates underscores the fact that molar eruption and emergence is a variable and dynamic process that is difficult to characterize as a single age or stage.

Conclusion

This study investigated aspects of incremental development in a relatively large sample of chimpanzee molars. It is clear

that certain developmental variables do not vary among cusps or molars, while others show trends between buccal vs. lingual and/or mesial vs. distal cusps, or among molars. The implication of these findings is that crown formation times derived from different cusps and molars should not be directly compared. Moreover, differences in the timing of initiation and completion, coupled with differences in the duration of individual cusp formation and differences among molars, suggests that comparisons must be made between analogous cusps or analogous molars (or that the total molar crown formation times must be compared). A number of factors should be considered during future studies of dental development in hominoids: sex differences, position in the molar row, tooth size, and/or the developmental environment may affect the timing, duration, and variation of molar crown and/or root development.

The discrepancy between a previous histological study of crown formation time (Reid et al., 1998a) and previous estimates of age at molar eruption has been resolved; crown formation times in these individuals, as well as in a larger sample, are lower on average than previously found. (The standards of developmental timing of the original full dentitions will necessarily be reduced to reflect the new, lower periodicity values.) These new estimates of chimpanzee crown formation time and age at M1 crown completion are consistent with reports of age at M1 eruption, suggesting that 1 to 2 years of root growth occurs prior to eruption. Root growth begins slowly, with extension rates almost doubling within the first few millimeters, but also showing differences among molar types. This study also suggests that reported differences in the age at molar eruption between wild and captive populations may be due to differences in the degree of molar overlap and/or rates of root growth rather than the duration of crown formation. Additional samples will help to clarify this issue, particularly from well-documented environments and subspecific affiliations.

In 1981, Dean and Wood published a radiographic study of great ape dental development based on a large sample of juvenile museum specimens, which has stimulated many studies over the past two decades, including studies examining enamel and dentine microstructure. Given the complete lack of histological data on great ape crown formation at the time, they made several assumptions that have been subsequently revised: they assumed that there was no developmental overlap in crown formation between molars, molar crown formation began at birth, molar crown formation time was equal among molars, and that this time was approximately 2.5 years. It is now becoming possible to fill in some of the gaps in our knowledge of living great apes with histological data from the current study and several recent histological studies. We now know that developmental overlap between molars is variable, that M1 crown formation begins one to two months before birth, and that molar crown formation time varies with position in the molar row. These findings will allow for more precise assessments of dental development among living and fossil hominoids.

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