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The Role of Time and Timing in Hominid Dental Evolution

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Exactly when during evolution hominids acquired their extended extra-uterine growth period is a contentious issue. In order to shed light on the tempo and mode of ontogenetic changes during hominid evolution, research has focused on the pattern and, to a lesser extent, the rate of growth observed in the developing dentition of extant and extinct hominoid taxa. From these data, the absolute timing of events has often been inferred, either implicitly or explicitly. Differences in patterns of growth, especially of the eruption of teeth, are reasonably well documented among hominoids. However, data on the absolute timing of dental developmental events are much more scarce, rendering tentative all inferences about timing from patterns alone. Such inferences are even more tentative when they involve interpreting ontogenetic trajectories in extinct species such as Plio-Pleistocene hominids, which almost certainly had unique patterns of maturation. In order to contribute to the debate about possible relations between pattern and timing in the developing dentition, we have collated information that specifically relates to the absolute timing of developmental events in extant and extinct hominoids and, hence, also to the rate at which processes occur. In doing so, we have attempted to identify both developmental constraints and possible heterochronic processes that may have led to the extended growth period characteristic of humans. There appears to be growing evidence that evolution toward an extended hominid ontogeny did not follow a path that can be described as a simple heterochronic event.

Time and the relative timing of events are important factors in biological studies, for they have the potential to permit inferences about the evolution of both morphology and life history. The best known category of study that invokes time as an influence on morphology is allometry.¹ In an earlier issue of *Evolutionary Anthropology*, Smith² demonstrated the importance of time and the timing of dental developmental events as tools to help us understand changes in life-history variables that have occurred during hominid evolution. These vari-

ables include, for example, gestation length, age at weaning, and sexual maturity. Such inferences are possible only because evidence suggests that dental eruption sequence is correlated with significant life history parameters among mammals and that the absolute timing of events can be reasonably deduced from eruption patterns. A case in point is that, at one extreme, rapidly growing, short-lived mammals such as insectivores erupt all their molars before their deciduous dentition has been shed, whereas slowly growing mammals such as humans generally delay the eruption of their molars. However, differences between closely related species or genera are often subtle. As Harvey and Clutton-Brock³ pointed out, "...it is desirable that analyses should be carried out at a higher level than the species" (p. 561).³⁻⁸ The difficulty of describing life history precisely enough, and of de-

termining the timing of developmental events from patterns is compounded when one is dealing with extinct taxa. It is a virtual certainty that the ontogenetic trajectories of those taxa are not exactly paralleled by those of extant species. Demonstrably, that is the case with regard to Plio-Pleistocene hominids and modern humans.⁴ Most researchers would probably agree that even early African *Homo erectus* did not yet exhibit an extended infancy precisely like that seen in modern humans. Thus it comes as little surprise that there is an ongoing debate about the nature of the ontogeny of early hominid taxa.

Many discussions about the development and life history of early hominid taxa have centered around the conceptual framework within which to interpret the data rather than focusing on the data. An example is the disagreement between Alan Mann and Holly Smith. Both have studied development in early hominid taxa. Mann and his colleagues⁹⁻¹² maintain that the pattern of dental development is within the limits of modern human variation and therefore implies a "modern human" timing of developmental events. On the other hand, Smith's interpretations^{2,7,13-19} favor the conclusion that the early hominid pattern is more like that of apes than modern humans, thus suggesting a more pongid-like rate of development for these early hominid species. This debate has not only highlighted the problem of inferring time from pattern, but has also led researchers to investigate variations in dental development within and between species, as well as between sexes.²⁰⁻²² Such studies are invaluable for establishing the extent of intraspecific plasticity during development, but they have

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also been used to validate other studies that have proposed that species are characterized by a typical sequence of eruption, despite a considerable amount of variation.¹⁸ In order to extract information about any species-specific pattern from the fragmented remains of fossil taxa, however, some combinations of teeth within the developing dentition lend themselves more readily than others to characterizing and thus deciphering this typical pattern.¹⁹ Disregard of this constraint has reduced the value of many discussions about the development and life history of early hominids. Even so, it still remains to be determined to what extent tooth development and eruption in extinct species are taxonomically valent variables. To make this determination, we require not only a better understanding of differences in the sequence, or pattern, but also data about the absolute timing of different events during dental development. It is only through combining both data sets that we will be able to identify developmental constraints, as well as to make inferences about which changes in developmental pathways may have occurred during hominid evolution.

Heterochronic changes are the predominant means by which evolutionary change occurs within members of smaller taxonomic units, such as the family, genus, or species.^{23–27} Heterochrony refers to changes in the timing of events. These changes during growth and development can be either global or local. In the former, the relative growth relationships are preserved and the whole of growth is extended to a longer period or reduced, concertina fashion, to a shorter absolute period. Local heterochronic events result from a dissociation of developmental processes, so that growth of one or more parts of an organism is advanced or retarded relative to the growth of the rest of the organism. There are, however, only three aspects of a developmental process that can be changed: the time when it is initiated, the rate at which it occurs, and the time when it is terminated.

Evolutionary modifications are theoretically possible at any point during ontogeny.²⁸ Moreover, change can result from more than one kind of het-

erochronic modification during development. For example, early eruption of a tooth may result from early initiation of formation, a fast rate of growth, an early termination of the growth period, or a combination of these processes. Our aims in this paper are to determine which processes might have operated to bring about the extended period of dental development in modern humans and to ask to what extent the heterochronic changes that occur within the developing dentition are correlated with each other. Throughout the paper, the initiation times and growth periods of teeth are generally given as mean values. No confidence limits are provided because, in many cases, the data are too scarce. Although this means of presentation suggests a higher level of precision and accuracy than the evidence allows, we have adopted it for simplicity for, in this review, we are mainly concerned with general trends.

ARE THERE SPECIES DIFFERENCES IN THE TIME OF ONSET OF DENTAL DEVELOPMENT IN HOMINIDS?

Data available on the timing of the initiation of crown formation are scarce owing to the difficulties of obtaining histological samples, or, alternatively, because of the problem of determining satisfactory criteria for radiographic definition of this event [Box 1]. Some trends, however, are apparent. Based on the interference in the development of enamel and dentine referred to as the neonatal line,²⁹ there is general agreement that first permanent molars in hominoids start calcifying shortly before or around birth.^{30, 31} In gibbons, which appear to be an exception to this rule, first permanent molar calcification is apparently somewhat more advanced at birth than that of other hominoids.³²

The initiation of central incisor crown formation occurs shortly after the onset of first molar development in all hominoids.^{33–38} Although many publications have presented developmental charts indicating the approximate time of initiation of crown formation, at present good species data are available only for *Pan troglodytes*,^{21, 33} *Homo sapiens*,^{36, 37} and

Pongo.^{20, 34} (Table 1). In modern humans, incisors start calcifying in swift succession from anterior to posterior; the times reported for one individual are around 0.3 years for central incisors and about 0.7 years for lateral incisors.³⁶ Data graphically presented by Liversidge and colleagues³⁸ suggest a similar timing for the onset of incisor calcification. This concurs with observations made in great apes.^{21, 33, 34} Canine crown formation also commences at about 0.38–0.5 years in humans and chimpanzees.^{33, 36–38} In orangutans, it may occur somewhat earlier.²⁰ Hence, crown initiation times of anterior teeth and the first permanent molars appear to conform to a common developmental chronology and sequence in modern humans and living great apes.

It is in the other postcanine teeth that differences between taxa occur with regard to the time of initiation of crown formation. In modern humans, the reported time for the initiation of P3 crown formation is 1.67–1.8 years and, for P4, 2.41–3.00 years.³⁶ These are similar to the times derived from radiographic studies, which, respectively, are approximately 1.8 and 3.0 years.³⁷ In *Pan* and *Pongo*, the initiation of premolar development occurs almost simultaneously in upper and lower P3 and P4 at about 1.5–1.9 years of age.^{20, 21, 33, 34} There are also differences between apes and humans in the timing of the initiation of second and third molar development. Human second molars initiate crown formation at about 2.5–3.7 years of age.^{36, 37} (See Smith¹⁷ for a summary of earlier studies.) Third molar initiation is delayed until 6.42–9.6 years.^{36, 37} Some studies suggest, however, that these ranges are too narrow and that the amount of variation and, hence, the amount of overlap between stages of molar formation is greater when other, non-European populations are included.^{17, 37, 39–41} In other hominoids, the initiation of molar crown formation is less widely spaced, resulting in a marked overlap between stages of molar crown mineralization. For chimpanzees, initiation of second molar formation has been reported to vary from 1.1–1.6 years,^{21, 22, 33} whereas an average age of 2.9–4.0 has been given for the initiation of third molar formation.^{3, 21, 22} (Ta-

Radiographic Studies of Dental Development

Radiographic studies have substantially contributed to our understanding of dental development sequences. However, problems arise when one wishes to determine the time and timing of dental developmental events precisely.

- Since the amount of time a living animal can be anesthetized and exposed to radiation must be kept to a minimum, most studies have relied on routine lateral radiographs. Although lateral radiographs allow reasonably good assessment of the developing stages of molars and, to a lesser extent, premolars, they do not allow accuracy in determining crown stages of anterior teeth.^{22,33,38}
- Detection of early stages of crown formation from radiographs is particularly problematic. For example, Winkler and colleagues²⁹ have recently extracted the tooth bud of a first permanent orangutan molar of which there was no radiographic evidence. Although all hominoids start molar calcification around birth, the earliest radiographic indication of M1 having started to form was found in a specimen nearly 3 weeks of age.²⁹ This problem applies equally to other teeth. Initiation of crown formation cannot be reliably determined from radiographs.
- Determination of cessation of crown formation is difficult because the tapering enamel toward the cervix is too small to be clearly visible. This difficulty and the underestimation of early stages of calcification have led to estimates of crown formation times that are lower than those based on histological studies.
- Assessment of attainment of stages of crown and root formation from radiographs must rely on a priori knowledge of the morphology of the fully formed tooth. For example, it is necessary to assess whether a tooth crown is half or two-thirds complete.²⁰ This is especially problematic with regard to fossils of extinct species, for which we have little knowledge about the range of variation in tooth size or about sexual differences.
- Developing crowns and roots cannot always be matched with the "idealized" stages of development, but are often visualized when they are between stages. Therefore, an absolute time scale cannot be put to various stages.
- Recent histological studies have shown that crown completion is not an abrupt process, but that some parts or cusps of a tooth may grow for a longer time than others. For example, Liversidge and colleagues³⁶ drew attention to the fact that in incisors and canines enamel extends further down the buccal and lingual root surface, so that the cemento-enamel junction may be difficult to identify in radiographs. A similar situation is found in molars, although to a lesser extent.⁷²
- Tooth development does not occur in a regular linear manner.³⁵ There is a slowing of the rate of enamel and dentine extension toward the cervix, which is most marked in modern humans and least marked in robust australopithecines (see text). Differences in this slowing need to be taken into account when determining developmental stages of tooth formation and, in particular, crown completion.⁴ Moreover, enamel and dentine secretion and extension rates are insufficiently documented for some tooth types in extant and extinct species.
- Interpretation of developmental stages from radiographs may be further confounded by differences in patterns of secondary mineralization (maturation) between teeth and between species.⁴

In summary, although radiographic studies have provided useful information about the sequence of developmental events, information about the time and timing derived from radiographs must be interpreted cautiously. The reader is therefore reminded that throughout the text we place more emphasis on histological and morphological studies than on radiographic findings. The latter are mainly used to provide a more complete picture of dental developmental events.

ble 1). Beynon, Dean, and Reid,³⁴ in their study of the initiation of the second molar in *Pongo* and *Gorilla*, have shown that although this occurs somewhat later than in *Pan*, the estimated age of M2 initiation is just under 2 years, resulting in a developmental overlap between molar crowns in these taxa.²⁰

Although few detailed data are available on other extant or extinct hominoids, two general trends can be discerned from the reported ages of the initiation of permanent crown formation. First, the time of initiation of the stem progenitor within a tooth

class⁴²—specifically, the central incisor, canine, P3, and the first permanent molar—varies relatively little among hominoid taxa. (See Osborn⁴³ for an alternative interpretation of the premolar clone.) Second, the initiation times of central and lateral incisors do not vary significantly among hominoids, whereas there are differences between modern humans and apes in the initiation times of P4, M2, and M3. Although the timing of the initiation of human premolars extends over a longer period than it does in other hominoids, delays in initiation are most marked within the molar

class, with the third molar experiencing the greatest absolute and relative shift when the extant apes are compared to living modern humans.

DOES THE RATE OF TOOTH TISSUE FORMATION DIFFER AMONG HOMINOIDS?

The development of teeth is permanently recorded within their microstructure. Both tooth crowns and roots grow in an incremental manner. But even though the rate and mode of enamel formation has been relatively well documented, good data for rates of dentine formation in the roots of

TABLE 1. Crown Formation Time (Years)

	I1	I2	C	P3	P4	M1	M2	M3
Maxilla								
<i>Pan troglodytes</i> ⁷⁵	5.47 ± 0.24	4.61 ± 0.15		4.54 ± 0.34	3.66 ± 0.06	2.83 ± 0.21	3.45 ± 0.16	3.33 ± 0.21
<i>Gorilla gorilla</i> ³⁴	4.0 (4.1)	4.2 (4.0)	>5.5 (5.0)	>4.7 (5.1)	3.4 (3.5)	2.9 (2.8)	2.6 (3.1)	>1.1
<i>Pongo pygmaeus</i> ³⁴	4.88	5.38	7.79	5.85	4.29	2.81	3.47	
<i>Homo sapiens</i> ^{37a}			3.5	3.1–3.4	3.1–3.4	2.1	2.8	2.8
<i>Homo sapiens</i> ³⁶	3.15	3.72	4.37	2.85	3.11	2.41	3.13	
Mandible								
<i>Pan troglodytes</i> ⁷⁵	4.86 ± 0.37	5.56 ± 0.39	7.78 ± 0.96	5.54 ± 0.79	4.04 ± 0.40	2.90 ± 0.19	3.77 ± 0.24	4.10 ± 0.40
<i>Pan troglodytes</i> ^{33a}	2.5	2.33	6.0	3.5	3.5	2.0	2.5	3.5
<i>Pan troglodytes</i> ^{22a}						1.4 ± 0.25	2.16 ± 0.38	
<i>Pan troglodytes</i> ^{21a}								
males:	3.95 ± 0.65	3.50 ± 0.65	6.83 ± 1.29	3.19 ± 0.45	4.56 ± 0.59	1.6 ± 0.22		3.57 ± 1.09
females:	3.00 ± 0.89	3.00 ± 0.89	5.96 ± 0.64	3.26 ± 0.24	3.30 ± 0.24		3.71	4.14 ± 0.88
<i>Gorilla gorilla</i> ³⁴	3.6 (3.8)	4.2 (4.5)	>5.3 (5.0)	>4.6 (>4.6)	3.8 (3.5)	2.7 (3.1)	3.2 (3.3)	>1.1
<i>Pongo pygmaeus</i> ³⁴	4.72	5.70	8.73	7.08	4.31	3.12	2.87	
<i>Homo sapiens</i> ⁴⁵	4.45	4.96				3.12		
<i>Homo sapiens</i> ^{37a}			3.5	3.1–3.4	3.1–3.4	2.1	2.8	2.8
<i>Homo sapiens</i> ³⁶	3.10	3.72	4.37	2.85	3.11	2.67		3.16
Maxilla and mandible combined								
<i>Homo sapiens</i> ⁵⁵	4.21	4.21		3.34		2.35	2.75	2.74
range	3.71–4.71	3.71–4.71		2.71–3.97		2.20–2.50	1.95–3.53	1.17–4.31

^a Radiographic studies (see Box).

primate teeth are scarce.^{36,44–47} Hence, this study will place somewhat more emphasis on enamel formation within and between tooth types, while root formation will be dealt with within a broader framework only.

Some incremental markings in teeth, which are visible as cross-striae, result from the approximately 24-hour periodic oscillations in the rate of secretion of enamel matrix by ameloblasts. Similar daily markings also occur in dentine.⁴⁷ Superimposed on this circadian rhythm is a second rhythm having a periodicity of 6–10 days, which produces the so-called striae of Retzius in enamel (for review, see Dean^{48,49}) and the analogous lines of Andresen in dentine (Fig. 1). Schour and Poncher,⁵⁰ in a pioneering *in vivo* labeling experiment on a human infant with inoperable hydrocephalus and meningocele, were the first to demonstrate unequivocally the periodicity of incremental markings in teeth. Schour and colleagues^{51–53} then validated their findings in subsequent experiments. These and other studies

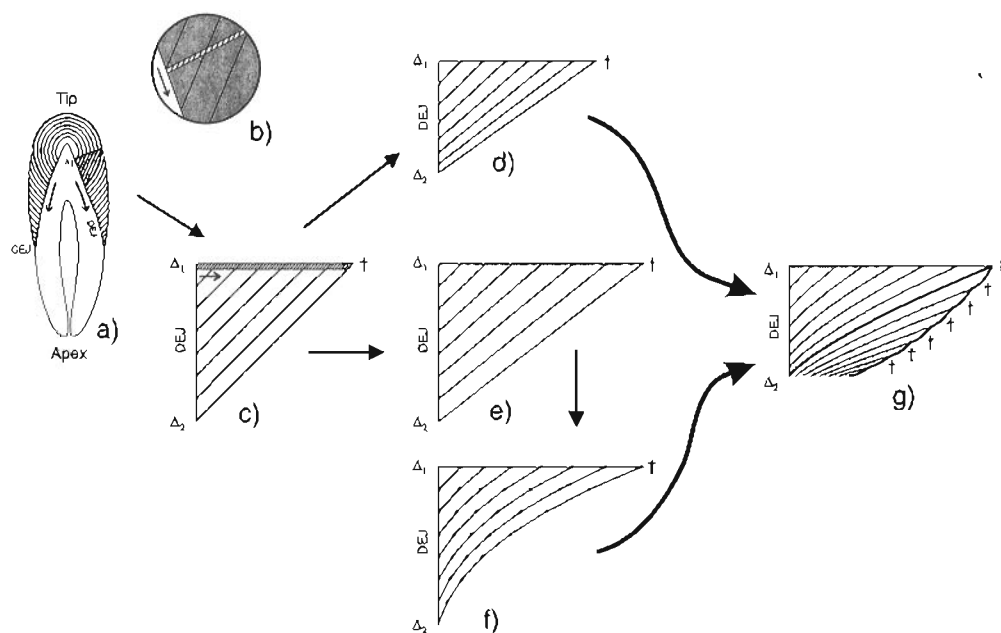
have now provided a solid understanding of the daily incremental nature of tooth formation⁵⁴ (see Dean⁴⁷ for review). It is the shorter periodic markings that permit estimates of daily rates of enamel secretion and crown formation times in fossil hominids.

Schour and colleagues^{50–53} first showed that human deciduous teeth exhibit a far higher secretion rate than do permanent teeth; the average figures given range from 3.6 μm to 8.0 μm per day for the deciduous teeth and from 2.4 to 4.5 μm for first permanent molars. Moreover, enamel secretion varies not only between and within individual teeth, but also between species, although there is apparently a common pattern of enamel matrix secretion within permanent teeth in extant primates^{34,40,45,54–57} and extinct hominids.^{58–60}

Two trends characterize changes in ameloblast activity during the growth of individual teeth in the primates studied. First, there appears to be an overall slowing of enamel matrix se-

cretion toward the cervical margin, a trend that is most pronounced in human permanent teeth⁵³ (Fig. 1). In human postcanine teeth, the enamel secretion rate toward the cervix is about 60% of that at the outer enamel surface at the cuspal part.⁵⁷ Among great apes, the relatively high-crowned *Gorilla* teeth show the greatest (71%) and *Pan* the least (86%) change; *Pongo* is intermediate (78%). Second, ameloblasts tend to increase their daily secretion rates from the dentino-enamel junction (DEJ) toward the surface of the tooth crown, a phenomenon that apparently is widespread within higher primates⁵⁷ (Fig. 1). In *Homo* and all great apes, the average increase in the rate of enamel matrix secretion from the DEJ to the surface is 2.3 to 6.0 μm/day in cuspal enamel and from 2.0 to 4.0 μm/day in the cervical region.⁵⁷ These values may be consistent across an even wider taxonomic group. Bromage⁵⁴ has given an average mid-cuspal value of 4.9 μm for *Macaca nemestrina*, a value that falls within the ranges given for homi-

Figure 1. Enamel Formation Among Hominoids



(a) Vertical section through a stylized single-rooted tooth showing the appearance of the advancing front of enamel formation. Enamel is produced by ameloblasts, cells that begin their active life at the interface between enamel and dentine and what will become the dentino-enamel junction (DEJ). Ameloblasts are not all activated at once, but start enamel secretion in order, beginning with the cells at the tip of the cusp. The "wave" of activation then spreads down the DEJ toward the cemento-enamel junction (CEJ). The rate of progress of this wave is called the extension rate. Enamel secretion continues until the ameloblasts die. The thick line marks the boundary between the last wave of ameloblasts that contribute exclusively to enamel forming the cuspal part of the enamel and those that contribute to formation of the tooth walls. The former is referred to as the appositional enamel, where complete layer is built upon complete layer, whereas the sides of the tooth are laid down in a file-like fashion, and thus are referred to as "Imbricational" enamel. Where the imbricational enamel comes to the surface, the cycles of enamel formation form grooves called perikymata, from the Greek "peri," meaning "around," and "kyma," meaning "wave."

(b) The best analogy for the process of enamel secretion is to liken the ameloblasts to old-fashioned toothpaste tubes. The "paste," in this case the enamel matrix, apparently is squeezed out of the tube continuously, but not always at the same rate. Two periodicities occur, a short one and a long one. The short ones have a period of about 24 hours and are known as cross-striae; the long ones, called the striae of Retzius, may be the result of regular interferences of various circadian rhythms, which occur approximately every 6–10 days. It is noteworthy that the number of cross-striae between striae do not vary between teeth of an individual and even appear to be relatively stable within a species, although differences may occur between genera or families. It is these striae of Retzius that produce the "waves" of enamel formation shown in (a) and represented by the solid continuous lines in (b)–(g). To illustrate how enamel is secreted, the small inset diagram (b) shows a close-up of the DEJ indicating the movement of a single ameloblast and the column of enamel formed by that ameloblast. The more frequent shorter lines correspond to the cross-striae, with their approximately 24-hour periodicity, the long lines represent the striae of Retzius. The arrow indicates the progress of the wave of activation.

(c) This diagram, a close-up of the triangle shown in (a), represents the enamel that is secreted during the active life of the ameloblast that began to secrete enamel at Δ_1 . During the life of this ameloblast, which spanned just seven of the longer cycles during the interval between Δ_1 and its death (t), its secretion rate was constant. In that time, the wave of activation had spread down the DEJ, from Δ_1 to Δ_2 , at a regular rate. Thus, when the ameloblast died, the cell at Δ_2 was just beginning its period of enamel matrix secretion. The hypotenuse of the triangle represents the advancing front of enamel at the time of death

of the first ameloblast.

This diagram illustrates in a simplified way how enamel forms but, in reality, hominoid teeth modify the rate of enamel formation in a systematic manner from the cusp tip toward the CEJ and from the DEJ toward the outer enamel surface. These variations from the steady state are shown in diagrams (d)–(f).

(d) The enamel extension rate along the DEJ is not constant, but reduces from the cusp tip downward. Diagram (d) shows the effect of gradually reducing the extension rate while maintaining a steady secretion rate. Thus, at the time of the death of the individual ameloblast, and compared with (c), the wave of activation has not progressed as far down the DEJ at time Δ_2 . Although all hominoids show a similar pattern of reducing the enamel extension rate toward the CEJ, this slowing of cell activation is most marked in modern humans. However, changes also occur in the enamel secretion rate, as illustrated in diagrams (e) and (f).

(e) In this diagram, the extension rate is kept constant but the secretion rate is increased steadily. Thus, the rate of enamel matrix secretion by the ameloblast just before its death at t is greater than its initial rate. However, changes in enamel matrix secretion not only occur from the DEJ outward, but also toward the CEJ.

(f) This diagram shows a more elaborate version of the incremental increase in the secretion rate shown in (e). In this scheme, there is not only an incremental increase in the secretion rate during the active life of each ameloblast, but there is also an incremental reduction in the initial secretion rate as the wave of cell activation moves toward the CEJ. The dots represent ameloblasts that have been active for the same length of time, but because of the gradual reduction of the initial rate of enamel secretion as the CEJ is approached, ameloblasts move smaller and smaller distances away from the DEJ per unit of time. This results in striae of Retzius that are curved rather than straight. The extent of the reduction in the initial rate of enamel secretion can be judged by the slope of the lines that connect the equivalent dots in each of the seven striae of Retzius.

(g) This diagram illustrates the developmental scenario that occurs when the changes in (d) are combined with those in (f). All ameloblast shown in (g) have the same life span. The effects of changes in enamel secretion rates combined with reduction in enamel extension rates result in a pattern that resembles a section through the enamel cap. The bold line through the diagram marks the advancing enamel front at time Δ_2 , which corresponds to the death of the first ameloblast.

In summary, the thickness of the enamel and the shape of the surface of a completed tooth crown are reflections of the numbers of active ameloblasts, the amount of enamel each ameloblast secretes per unit of time, and the active life of each cell.

noids. Other monkeys and *Proconsul* range from about 4 to 6 $\mu\text{m}/\text{day}$ (Dean, personal communication).

Enamel matrix secretion rates from inner to outer enamel in Plio-Pleistocene hominids are comparable to that reported for the primate species listed above.^{58–60} As regards the increase of secretion from the DEJ to the crown surface, the cross-striation repeat interval of the cuspal enamel of a *P. boisei* premolar was found to be 4.0 μm at the innermost enamel; increasing to 6.5 μm at the crown surface.⁵⁸ Mid-cuspal daily secretion in a robust australopithecine canine from Swartkrans, southern Africa, was 5 μm . The figures given for early *Homo* and *P. boisei* molars from East Africa are 5.8 μm and 7.3 μm , respectively.⁶⁰ Although the average values of ameloblast secretion for Plio-Pleistocene hominids appear to be relatively high, they nonetheless lie within the range observed for the deciduous and permanent teeth of modern humans.⁵³ Despite differences in the average enamel secretion rates among species, there is sufficient evidence to suggest that the amount of variation in daily enamel matrix secretion rates is as great, if not greater, between anatomical regions of an individual tooth than between primate species. Therefore, a simple distinction between fast-forming and slow-forming enamel^{62,63} cannot be sustained for taxonomic purposes.

The enamel-forming cells, the ameloblasts, successively acquire their competence—that is, the ability to secrete enamel matrix actively—from the cusp tip. Once “switched on,” these cells secrete enamel from the DEJ outward. In modern humans the rate of differentiation of ameloblasts, defined by Shellis as the “enamel extension rate,”⁵⁵ differs for deciduous and permanent teeth (Fig. 1 legend). The extension rate is nearly constant in deciduous teeth, but in permanent teeth it falls from an initially higher level to a constant rate of about 4 μm per day.⁵⁵ The differential between the faster extension rate at the cusp tip and the slower rate toward the cervix is greater in high-crowned than in lower-crowned teeth.⁵⁵ Also, the initial extension rate, as well as the daily rate of secretion, is greater on the longer, labial, surface of upper and lower hu-

man incisors than it is on the shorter, lingual surface.^{56,64}

In early hominids, the slowing of secretion rate toward the cervix apparently is less marked than it is in modern humans.^{58–60} Judging from the angles between the striae of Retzius and the DEJ⁵⁵ some Plio-Pleistocene hominids

Except for maxillary incisors in *Pan*, all extant hominoids exhibit the same trend: the more posterior teeth within each tooth type (e.g., lateral incisors, second and third molars) take longer to form than do their more mesially positioned counterparts. Although available data on permanent incisor formation times indicate that there is considerable overlap among great apes and humans, it appears that *Gorilla*, take the least time to form these teeth, whereas *Pan* and *Pongo* take the longest time to do so.

also exhibit relatively rapid enamel extension rates,^{58,65} with *Paranthropus boisei* specimens apparently having a rate and pattern similar to that in human deciduous teeth.^{59,60} Incremental markers on the surface of the tooth, called perikymata, suggest that progressive slowing of the enamel extension rate toward the cervix may have occurred in *Australopithecus* incisors as compared to *Paranthropus* inci-

sors.⁴ In early *Homo*, on the other hand, this slowing of the enamel extension rate is unequivocal,^{59,60} although it appears to be less marked than in modern humans. Bearing in mind the proportionally lower tooth crowns of robust australopithecines⁶⁶ and their reportedly earlier eruption, the similarities in enamel extension rates between these Plio-Pleistocene hominid teeth and human deciduous teeth are not surprising.

Although good data for daily rates of dentine formation and for the extension rates of primate tooth roots are scarce, some general trends emerge from the available studies.^{36,44,46,47,67,68} Like enamel matrix formation, dentine formation in the cuspal region is initially high in primates but slows to a constant rate of about 4 μm toward the apex. Changes in dentine extension rates toward the cervix are comparable to changes observed in enamel extension rates during tooth crown formation, but uncertainty remains about the exact nature of the dentine extension rate after crown completion. Dean^{35,69} proposed a method, which involved analyzing the geometry of the growing root front, the “root cone angle,” as a proxy for root extension and, hence, root formation, to assess the rate of root extension from radiographs (see Box 1). Simpson⁷⁰ has challenged this proposal. Using a large sample of *Pan*, *Gorilla*, and *Homo* he has found variations in root cone angles within species to be greater than between species and therefore has suggested that all hominoids share a common pattern of root development. Until this impasse is resolved, caution should be exercised when employing Dean’s method to assess the developmental status of fossil hominids. Whether any clear species-specific trends have also been masked by paying too little attention to various tooth types, however, needs to be established.

To summarize, it appears that overall tooth size, especially crown height and enamel thickness, together with the time available to form a particular tooth crown determine the enamel extension rate as well as the average daily enamel secretion rate. Thus, large teeth and thick enameled teeth,

as in robust australopithecines, or fast-forming teeth, such as ape and human deciduous teeth, have on average both greater extension rates and higher secretion rates. This is consistent with the pattern observed in other mammalian species.⁷¹

DOES CROWN FORMATION TIME DIFFER AMONG HOMINOIDS?

Studies have determined the rate of enamel secretion among hominoid species by using either specially prepared sections of teeth^{34,58,61} or the exposed enamel of naturally broken teeth.^{59,60,72} These studies have also estimated crown formation times. Traditionally, crown formation times have been assessed from routine lateral skull radiographs (see Box 1). In addition, anthropologists have used the surface manifestations of the striae of Retzius, the perikymata, as a nondestructive technique to determine crown formation times in fossil material.⁶ This method, however, is not without pitfalls, which has led some researchers to question its usefulness for taxonomic interpretations.^{10,11}

Problems can arise at various levels. During the cuspal, or appositional, stage of enamel formation, striae do not reach the tooth surface. Only striae of Retzius formed at the later, imbricational stage, become manifest as perikymata on the enamel of the side of the tooth crown. Hence, the amount of appositional enamel, directly assessed by counts of daily increments, needs to be taken into account when comparing crown formation times using perikymata counts. In those cases in which crown formation time has been calculated, it transpires that each tooth type in each taxon, and even each cusp of posterior teeth, has consistent but different appositional enamel formation times.^{36,45,61} Recently, evidence has come to light that suggests that previous assessments of crown formation times in Plio-Pleistocene hominids⁶ may have underestimated the time required to form this early deposited enamel.⁶¹ Consequently, the upper limits of crown formation times listed in earlier studies⁶ probably provide more accurate estimates of crown formation times. The second potential problem is that, although striae of Retzius occur at a regular interval with

a near-weekly periodicity, an exact assessment of that periodicity, which usually is on the order of 7–9 days, cannot be made on intact teeth. This, again, can lead to underestimation or overestimation of crown formation times. In addition, perikymata are variably expressed at the cervix of teeth.^{73,74}

For all these reasons, estimates of crown formation times from perikymata counts should be interpreted with caution. Nevertheless, despite these potential sources of error and the general presumption that estimates made in this way may be too low, a substantial body of comparative data using these and other approaches is now available to assess differences in crown formation times among extant hominoids. This has made it possible to compare average crown formation times of fossil hominid and extant hominoid teeth.

Crown formation data based on histological studies are now available for the dentition of *Homo sapiens*,^{36,45} *Pan troglodytes*,⁷⁵ *Gorilla gorilla*, and *Pongo pygmaeus*,³⁴ as well as for a maxillary P4 of *P. boisei*⁵⁸ and a mandibular canine of *P. robustus*.⁶¹ Radiographic studies give further information about the range of variation (Table 1, also see Box). Except for maxillary incisors in *Pan*,⁷⁵ all extant hominoids exhibit the same trend: the more posterior teeth within each tooth type (e.g., lateral incisors, second and third molars) take longer to form than do their more mesially positioned counterparts. Although available data on permanent incisor formation times indicate that there is considerable overlap among great apes and humans, it appears that humans, followed by *Gorilla*, take the least time to form these teeth, whereas *Pan* and *Pongo* take the longest time to do so. Canine formation times vary substantially both within and between species, as well as between upper and lower teeth. This variation seems, at least in part, to be associated with sex and size; this suggestion is supported by the fact that canine size not only differs considerably between humans and apes, but also between the sexes within a species. In both instances, moreover, this variation is paralleled by differences in crown formation times.³⁷ Conversely, perikymata

counts of chimpanzee canines suggest that differences in crown height between sexes in that species have not resulted in differences in crown formation times.⁷⁶ However, a recent radiographic study on dental development in *Pan* could not confirm this finding²¹ (Table 1). Overall, available evidence suggests that great apes take eight or more years to form their canines, whereas the smaller modern human canine crowns are formed in less than 4.4 years.³⁶

As regards premolar formation, humans, as compared with other hominoids, appear to exhibit a somewhat foreshortened growth period for the crowns, which is even more marked than it is with regard to human incisors (Table 1). This may, again, be related to differences in overall size between the species, especially where P3 is concerned. On the other hand, the crown formation times of molars are more similar between hominoid species, with all taxa exhibiting a slight increase in crown formation times from first molars to more posterior ones. On average, molar crown formation time is around three years (Table 1).

During the last decade researchers have repeatedly tried to assess crown formation times in hominid fossil teeth, with most of the discussion centered around incisor crown formation time based on perikymata counts. We have already discussed shortcomings of this method and, indeed, recent evidence suggests that appositional enamel formation times may have been consistently underestimated by a few months.⁶¹ Nevertheless, it appears that the average crown formation times of early hominids are all below, or are at, the lower end of the range of the living hominoids. Among early hominid species, *A. afarensis* and *A. africanus* incisor formation times are the longest, with values of 3.0 and 3.1 years for LH 2 and Sts 24a, respectively.⁶ New estimates of timings for *P. robustus* suggest that its lower central incisor crowns formed between 2.35 and 2.68 years, while its lateral incisor crowns took between 2.57 and 2.91 years.⁶¹ The central incisors of *P. boisei* appear to have formed in just over two years,⁷⁷ whereas those of two early *Homo* specimens are reported as hav-

TABLE 2. Age of Eruption^a

	I1	I2	C	P3	P4	M1	M2	M3
Maxilla								
<i>Pan troglodytes</i>								
males: mean	5.62	6.68	8.97	6.93	7.23	3.38	6.82	11.36
range	4.92–6.50	5.83–7.67	8.00–9.83	6.08–7.67	6.33–8.33	3.00–3.75	5.67–7.83	10.00–13.58
females: mean	5.63	6.79	9.03	6.96	7.47	3.27	6.75	11.33
range	4.50–6.75	5.83–8.25	7.58–10.08	6.08–8.08	6.25–8.33	2.75–3.75	5.92–7.58	9.75–13.08
<i>Gorilla gorilla</i> ^b								
mean	6.02	6.50	8.90	7.14	6.95	3.50	6.77	11.40
range	5.3–6.8	5.5–7.5	7.5–10.3	6.0–8.3	5.9–8.0	3.0–4.0	5.9–7.6	9.7–13.1
<i>Homo sapiens</i>								
males: mean/sd	7.34 ± 0.77	8.39 ± 1.01	11.29 ± 1.39	10.64 ± 1.41	11.21 ± 1.48	6.40 ± 0.79	10.52 ± 1.34	20.50
females: mean/sd	6.98 ± 0.75	7.97 ± 0.91	10.62 ± 1.40	10.17 ± 1.38	10.88 ± 1.56	6.35 ± 0.74	11.95 ± 1.22	20.50
Mandible								
<i>Pan troglodytes</i>								
males: mean	5.65	6.22	9.24	7.38	7.39	3.33	6.47	10.27
range	5.17–6.42	5.58–6.92	8.08–10.08	6.33–8.25	6.33–8.25	3.00–3.58	5.58–7.00	9.00–11.08
females: mean	5.84	6.05	8.63	7.32	7.58	3.19	6.45	10.71
range	5.00–7.00	5.00–7.33	7.92–9.08	6.33–8.08	6.08–9.08	2.67–3.75	5.92–7.33	9.00–13.08
<i>Gorilla gorilla</i> ^b								
mean	5.75	6.12	7.70	7.32	7.14	3.50	6.58	10.38
range	4.9–6.6	5.3–7.0	6.4–9.0	6.1–8.6	5.9–8.4	3.0–4.0	5.7–7.5	8.7–12.1
<i>Homo sapiens</i>								
males: mean/sd	6.30 ± 0.81	7.47 ± 0.78	10.52 ± 1.14	10.70 ± 1.37	11.43 ± 1.61	6.33 ± 0.79	12.00 ± 1.38	19.80
females: mean/sd	6.18 ± 0.79	7.13 ± 0.82	9.78 ± 1.26	10.17 ± 1.28	10.97 ± 1.50	6.15 ± 0.76	11.49 ± 1.23	20.40

^a Data are reproduced from Smith et al.,⁸⁰ in which the original sources of the information can be found.

^b Please note that Smith and colleagues⁹³ have recently drawn attention to the inadequately documented data for *Gorilla gorilla* in the original publication⁷⁶ from which these data were taken.

ing formed in 2.52 years in KNM-ER 820 and 2.62 years in SK 74b.⁶ The small canine of *P. robustus* SK 63 formed in less time, 3.18 to 3.48 years,⁶¹ than has been reported for any other hominoid canine (Table 1). The premolar crown formation time in *P. boisei* was similarly truncated to approximately 2.4 years.⁵⁸

Although it could be argued that the small size of the anterior dentition of robust australopithecines may have been responsible for their relatively short crown formation times, this argument cannot be applied to the large molar teeth of these taxa. *Paranthropus aethiopicus* formed its molars between 2 and 2.5 years.⁷² Published crown formation times of *P. boisei* molars suggest that they were formed between 2.12–2.59⁶⁰ years and 2.67–3.43 years.⁷² Unfortunately, little published information is available on differences in crown formation times within the molar series in *Paranthropus*. However, it seems that, at least in *P. boisei*,

although not in *P. aethiopicus*,⁷² there is a trend toward an increase in crown formation time in more posteriorly developing molars. Second molars of *P. boisei* took, on average, 2.88 years to form and M3s completed crown formation in 3.02 years.⁷² This is a modest difference, given the potential errors involved in such calculations. The crown formation time of M1 in *P. robustus* (SK 63) has been estimated to be about 2.40 years.⁶¹

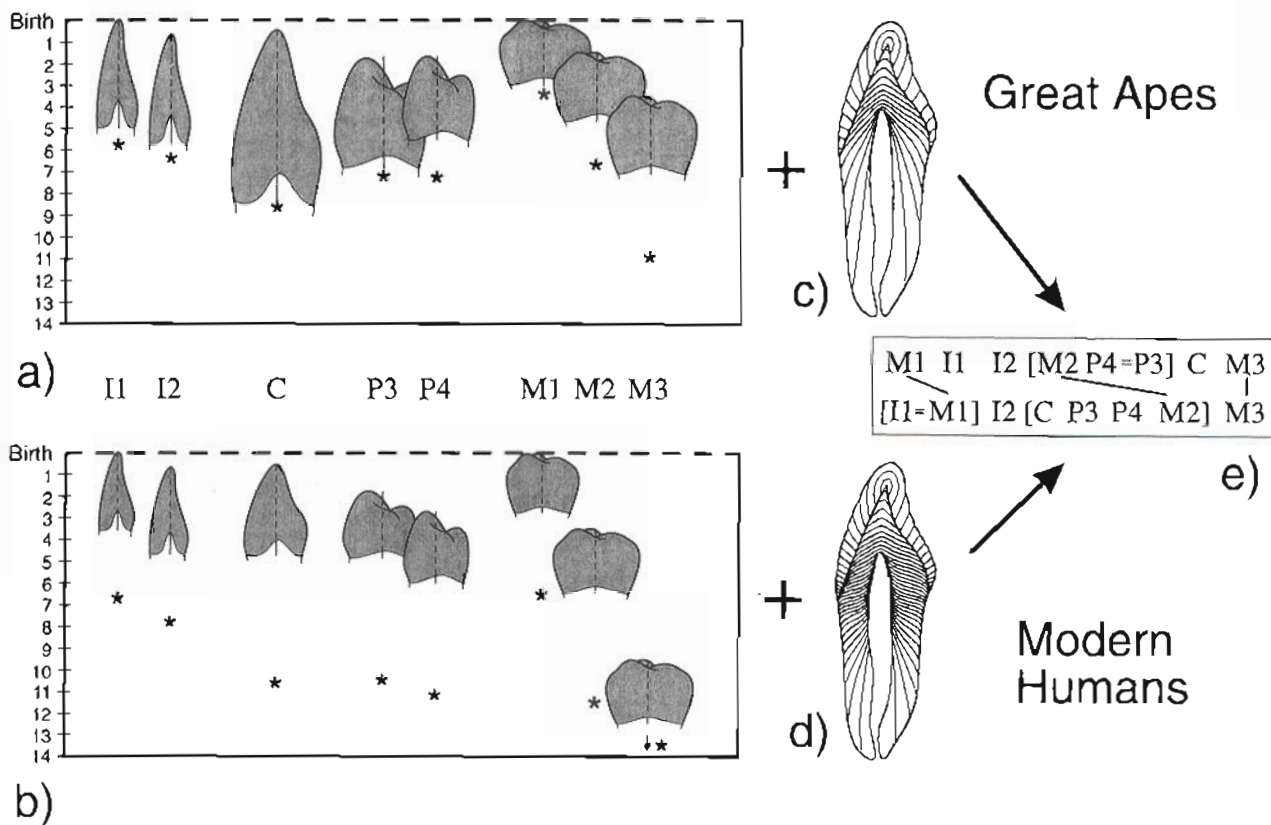
These data indicate that Plio-Pleistocene hominids may, in general, have had somewhat foreshortened anterior tooth crown formation times. What evidence there is suggests that crown formation times of postcanine teeth may also have been abbreviated. As regards anterior teeth, it should be noted that such short formation times are not only rarely observed in modern humans, but also clearly are distinct from the observed ranges in extant nonhuman hominoids (Table 1). Great

apes differ most from fossil hominids and modern humans in canine formation times, a fact that commonly has been associated with absolute differences in canine size.^{5,6,18} However, while size may account for differences in crown formation times in incisors, canines, and third premolars, the different formation times of the other postcanine teeth cannot be so easily explained (Fig. 2). Although all living great apes have similar molar crown formation times, values given for modern human and *P. boisei* premolars, despite the discrepancy in overall size, are all below those reported for *Pan*, *Pongo*, and *Gorilla*.

DO ROOT FORMATION TIMES DIFFER AMONG HOMINIDS?

Root formation times in hominoids are less well documented than are crown formation times.^{21,22,33,35,37,78} In effect, comparable data are available

Figure 2. Heterochronic Changes That Have Occurred During Hominid Evolution, Which May Account for the Unique Eruption Pattern and the Delay in Tooth Eruption in Modern Humans



The diagram is an attempt to show how the timing of initiation of crown formation, the time crowns take to form, and the rate of root development combine to produce the differences between great apes and modern humans with regard to the time and sequence of tooth eruptions. These average data are almost exclusively derived from histological and morphological studies (see Box 1). In (a) and (b), respectively, each tooth type is given the same basic image for the great apes and modern humans. The highest point on the crown of each tooth image represents the average time of the initiation of crown formation; the height of the tooth represents the average time taken for that particular tooth to form. Crown formation is completed at the time corresponding to the bottom of the vertical line that runs through each tooth image. Thus, the height of each image is a reflection of the crown formation time and not necessarily of the shape of the tooth crown. However, it is noteworthy that there is an approximate correspondence between the shapes of the images in the diagram and the relative crown heights in the two groups. The differences in the size of the images of the three molars of modern humans in (b), on the other hand, do not reflect observed crown size, but rather the major differences in crown formation between first and third molars. Crown formation times in (a) are the composite of the crown formation times given for the maxillary and mandibular dentition for *Gorilla* and *Pan* in Table 2. The crown formation times in (b) are average times given for the maxillary and mandibular dentition for modern humans (Table 2). Initiation of crown formation of the central tooth within a tooth class varies little between the two

groups. Conversely, initiation of later forming members of the premolar and molar tooth class are delayed in modern humans as compared to the great apes. Asterisks refer to average eruption times.

The diagrams (c) and (d) are stylized sections of a single-rooted tooth. They illustrate the differences in the tempo and mode of tooth formation around the CEJ. In modern humans, the rate of enamel formation and extension slows toward the CEJ. Also, there is a corresponding slow-down of the root extension rate around the CEJ and extending beyond I1, although changes in dentine secretion rates are not marked. The slowing of enamel and root extension rate affects each tooth type differently, as is reflected in the discrepancies between the completion of crown formation and eruption.

These different mechanisms combine to produce the differences in the timing of eruption in great apes and modern humans, which are shown in (e) and documented in Tables 2 and 3. The sequence of eruption shown in (e) is based on Smith's findings,¹⁷ whereby "=" indicates polymorphisms of eruption in more than 40% within each group. The brackets point to waves of eruption within each species whereby sequence reversals may occur in 15% or more of the sample. The asterisks in (a) and (b) mark the average times of tooth eruption and emphasize, in diagrammatic form, the discrepancies between great apes and modern humans with respect to the cessation of crown formation and the timing of tooth eruption.

for *Homo* and *Pan troglodytes* only, and all estimates are derived from radiographs (see Box). Except for inci-

sors, chimpanzee tooth roots generally are formed in a shorter time^{21,22,33} than are the equivalent roots of mod-

ern human teeth.^{37,78} Modern human incisor roots form in 4.4–5.2 years,⁷⁸ but those of chimpanzees take be-

tween 5 and 6 years.²¹ Conversely, the roots of *Pan* premolars take about 4 to 6 years to form, whereas those of modern humans take up to 7 years. Although published data are scarce and do not provide a clear picture, modern humans nonetheless seem to form their molar roots in 4.6–7.2 years,^{37,38} whereas *Pan* does so in 3–6.5 years.^{21,22,33} Available data also suggest that, with the exception of modern humans, there may be an increase in root formation time from anterior to posterior molars; this pattern seems to be common among primates.⁷⁹

Hence, although average root formation times differ between modern humans and great apes, these differences do not appear to be consistent across tooth types and are not always marked. Kuykendall²¹ also noted that certain periods of tooth formation seem equivalent in *Pan* and *Homo*, and made the interesting suggestion that this may be the result of a shift in proportion between crown and root formation in the two species whereby the absolute time of development remains the same.²¹ Although this may be the case for canines and P3s and, perhaps, P4s, Kuykendall's claim is not borne out for the other teeth (Table 1). Molars of modern humans appear to have extended the period of root growth without reducing crown formation times. More strikingly, both incisor crowns and incisor roots appear to take longer to form in great apes than in modern humans (Table 1).^{37,78}

Lack of detailed data on growth rates and times of root formation have made it difficult to assess the developmental status of fossil hominids, especially because root formation apparently does not proceed linearly.^{36,37,46} Among early hominids, root formation times have been estimated to be between 3 and 5.5 years for one individual of *Homo habilis* (OH 16).⁴⁷ These estimates are based on counts of periradicular bands, which are believed to correspond to long-period incremental markings in the dentine, which are equivalent to perikymata in tooth crowns,⁴⁷ on 8 mandibular teeth of this fossil specimen. This study concluded that the average root formation time in this *Homo habilis* specimen is closer to the range found in chimpanzees than that of modern humans. Al-

though from the available data it appears reasonable to suggest that there is a relationship between root size and formation time, on one hand, and between delayed eruption and root formation time on the other, more comparative data are badly needed to test such a hypothesis.

Great apes differ most from fossil hominids and modern humans in canine formation times, a fact that commonly has been associated with absolute differences in canine size. However, while size may account for differences in crown formation times in incisors, canines, and third premolars, the different formation times of the other postcanine teeth cannot be so easily explained.

DIFFERENCES IN ERUPTION TIMES AND PATTERNS AMONG HOMINIDS

Smith, Crummett, and Brandt⁸⁰ have recently collated data on eruption times for many primate species and the times for extant hominoid permanent teeth are summarized in Table 2. It should be remembered that there are differences among modern humans in the timing of eruption of second and third molars. Specifically, non-European populations, or people living in poor socioeconomic conditions, generally show less of a gap between both formation and eruption of molars⁴⁰ (for review of studies, see Eveleth and Tanner⁸¹). The extent to

which population differences may also exist in nonhuman primates needs to be determined.

It is evident that humans erupt their teeth absolutely and relatively later than do the great apes. However, because the delay in eruption times is not uniform across all teeth, this results in different eruption patterns between modern human and ape species^{2,18,19,35} (Fig. 2). For example, great apes erupt their incisors relatively late, but modern humans tend to erupt theirs at approximately the same time as their first molars. Furthermore, premolar and canine eruption in the apes usually occurs after the second molars have come into occlusion, but in modern humans both tooth types erupt before, or at about the same time as, the second molars. To illustrate this difference further, and to assess it in relation to the absolute timing of events, we computed the average difference in eruption times between the respective ape and human teeth (Table 2). Compared with apes, and using an absolute time scale, central and lateral incisor eruption in humans is delayed by 1 and 1.4 years, respectively, whereas canine eruption is delayed by about 1.8 years. Human postcanine teeth show the greatest delay in absolute eruption times, so that, in increasing order, first permanent molars come into occlusion 2.9 years later than they do in great apes, followed by P3 (3.2 years), P4 (3.8 years), M2 (4.9 years), and M3 (8.7 years) (calculated from Table 2).

Only one study has yet attempted to relate measures of the absolute timing of dental development with the pattern of eruption in the same juvenile fossil specimen.⁶¹ This study confirmed that although the pattern of dental development in this *P. robustus* individual, especially with regard to stages of M1/II development^{4,18,19,82,83} resembles that in modern humans more closely than it does the pattern found in great apes, the absolute timing of its developmental events, as determined by histological methods, was foreshortened.⁶¹ Further studies that directly relate pattern with timing are needed. Presently too much reliance has to be placed on referential and conceptual models (see Smith⁷ for an explanation of the assumptions

TABLE 3. The Average Time Between Completion of Crown Formation and Eruption

	I1	I2	C	P3	P4	M1	M2	M3
Great apes	1.1	0.7	0.2	0.1	1.8	0.4	1.9	3.7
Modern humans	3.2	3.0	5.7	5.8	5.1	3.6	4.9	6.9
Difference	2.1	2.3	5.5	5.7	3.3	3.2	3.3	3.3

underlying each model) to assess the extent to which the patterns of tooth eruption in early hominids suggest an extended period of growth.

DO TEETH THAT GROW FASTER ERUPT EARLIER AND VICE VERSA?

Overall, the answer to this question must be no. Apes erupt their teeth absolutely earlier than humans do (Table 2), yet their canines and P3s—i.e., their sectorial canine complex—and apparently their incisors as well (Table 1), take longer to form than they do in humans. Only for the canines and P3s is it possible to detect a correlation between crown formation and eruption times, although both the extended period of crown formation and the late eruption of the sectorial canine complex in great apes may be linked with their larger overall size.¹⁶ In sexually dimorphic species in which males have much larger canines than do females, formation times vary considerably between the sexes. This may, at least in part, account for polymorphism in canine eruption^{18,21} (but see Dean and Beynon⁷⁶). It has been pointed out^{18,84} that both large size and late eruption of canines and P3s are the result of intermale competition, which allows an animal to attain full adult status before being perceived as a potential reproductive competitor. Although a relationship between overall size, crown formation time, and eruption time may hold for canines and P3, such an arrangement does not apply to the other postcanine teeth. In apes and humans, as well as extinct hominids such as the megadont robust australopithecines, molar teeth take a similar amount of time to form, yet their eruption times appear to differ markedly.

If differences in crown formation times do not account for the differences in eruption times between modern humans and great apes, might the

differences be due to the time of onset of crown formation? Apparently not, for later erupting teeth are not necessarily those in which the initiation of crown formation is delayed. Among hominoids, the time of initiation of the more mesial tooth within a tooth class is relatively invariant, as is the order of tooth initiation within each tooth class from anterior to posterior. Hence, the polymorphism in premolar eruption [$P_3 = P_4$] reported for humans³⁹ results from developmental processes occurring later in ontogeny and that are not manifest during early stages of crown calcification (that is, provided premolars constitute a class of their own, separate from molars).

It appears that developmental changes during evolution have affected each tooth class differently, so that each follows its own developmental pathway. For example, the timing of development of both incisor tooth crowns is relatively stable across taxa and appears to have changed little during hominid evolution, whereas in postcanine teeth the initiation of posterior members has experienced a delay, perhaps gradual, during evolution toward the modern human condition, with the initiation of molar crown formation being more affected than that of premolars.

Given that there is no relationship between the time of crown initiation, crown formation time, and the time of eruption, how is the distinctive rate and pattern of tooth formation and eruption in modern humans to be explained? Do modern human teeth erupt with a greater proportion of their roots formed? Is tooth development in modern humans "retarded" following the completion of crown formation? It would seem that both these mechanisms may operate (Fig. 2). Both humans and great apes erupt their teeth with varying amounts of roots formed,^{20,22,35,85} but there are systematic differences among species

with regard to the absolute and proportional amount of roots formed at eruption (Fig. 2). In modern humans both the crown and, more importantly, the root extension rates slow considerably toward the cervix, thus accounting for their later eruption but similar crown formation times compared to the apes.^{35,45,47}

In order to gain an overall idea about the amount of time that usually elapses between crown completion and eruption in great apes and modern humans, we subtracted the average time of crown completion, plus the time of initiation, from the reported eruption time (Table 3). Although we recognize that such a calculation can provide only a crude measure of how much time elapses, on average, between crown completion and eruption, the figures presented in Table 3 nonetheless offer some insight into the mechanisms that may be operating. As expected from the data presented, it is in modern human canines, third premolars, and third molars, which, however, are notoriously variable among populations, that the longest periods—5.7–5.8 and 6.9 years, respectively—elapse between crown completion and eruption. In great apes, in contrast, fully formed canines and M3s come into occlusion 0.2 and 3.7 years, respectively, after crown completion.

Humans have experienced a general delay in dental maturation during hominid evolution, but the extent of that delay differs across tooth classes. It is least in the incisors, while the canines and premolars have the longest interval between the end of crown formation and eruption (Table 3).

CAN A SINGLE HETEROCHRONIC CHANGE EXPLAIN THE PROLONGED DENTAL MATURATION IN MODERN HUMANS?

In order to explain the major changes in eruption patterns during hominid evolution, Smith¹⁸ has recently drawn attention to Schultz's initial proposal⁸⁶ in which he identified two "waves of eruption" in primates: molars (wave 1) and antemolar teeth (wave 2). Slow-growing species exhibit a relative acceleration of wave 2 eruption in relation to wave 1 so that

both waves erupt simultaneously, whereas fast-growing species erupt the two waves sequentially. In fact, *Homo* appears to be characterized by three waves, with third molar eruption constituting the additional wave. Although we generally concur with this model, the data on absolute timing of developmental events presented here indicate that tooth classes should be viewed and compared as separate units. Furthermore, the appearance of these waves may be a by-product of changes that have occurred within, and are specifically confined to, a particular tooth class. We propose the following mechanisms to explain the changes that occurred during hominid evolution (these are illustrated in Fig. 2).

First we suggest that within the premolar and molar tooth classes a change in growth rate (activity) of the primordia has resulted in a retardation of the initiation of the later-developing teeth within each class. Although each tooth class initiates tooth formation at about the same time, the delay in the calcification of later-forming teeth constitutes a relatively simple heterochronic change. In a series of experimental studies, Snead and colleagues investigated *de novo* amelogenin gene expression in mice⁸⁷⁻⁸⁹ and suggested that the acquisition of competence by preameloblasts to respond to the epigenetic (i.e., autocrine and paracrine) signals depends on a genetically determined minimal number of cell cycles.⁸⁷ According to these investigators, this dependence would explain why the lingual aspect of the inner dental epithelium of mouse incisors did not synthesize and secrete amelogenin even when it was brought into contact with a permissive microenvironment. If ameloblasts become activated only after a minimum number of cell cycles, the delayed initiation of later-forming teeth within a tooth class may thus be a simple consequence of the overall reduced growth rate of the face.¹⁸ Moreover, if initiation of crown formation and overall growth of the face are linked, then the similarities in developmental patterns between *Homo* and *Paranthropus*, even though the absolute timing of events may be different,^{5,84,90,91} come as little surprise,

given the parallels in overall growth and bone remodeling of the face in both genera. Previous studies have suggested that the development of teeth is determined by the space available in the developing jaw.^{76,92} Although there seems to be a relationship between the two, we contend that it may not be a causal one. Rather, development of both the face and the teeth is determined by a common growth trajectory, whereby space only exerts a secondary influence on the later stages of development.

Modification of the masticatory complex is not the simple process some recent interpretations have suggested. The interplay between selection pressures acting both on dental function and social behavior, together with the highly integrated nature of the development of the masticatory system, precludes simplicity.

Second, the cervical slowing of enamel formation and, particularly, the root extension rate is exaggerated in humans when compared with other hominoids. This may be sufficient to account for most of the delay observed in human eruption patterns. It seems that the proportional decrease in incremental enamel growth toward the cervix, and a similar decrease in root extension rate during early root formation, have affected tooth types differently (Table 3).

In summary, it seems evident that evolution toward an extended ontogeny did not follow a path that could be described by a simple heterochronic event, such as an overall retar-

dation of growth. Developmental changes within the dentition appear to have been complex, involving both crown and root initiation and formation. However, some processes within the developing dentition seem remarkably conserved—that is, developmentally constrained. These processes include the initiation time of the stem progenitor within a tooth class and the average rate of enamel and dentine secretion, i.e., the activity rate of the ameloblasts and odontoblasts. It seems that at least two heterochronic mechanisms must be proposed to explain the delayed dental maturation of modern humans. These are the slowing from anterior to posterior of the growth rates of the primordia and the exaggerated slowing of tooth extension rates at the cervix.

DO THESE CONCLUSIONS AND HYPOTHESES HAVE IMPLICATIONS FOR SYSTEMATIC STUDIES AND THE INTERPRETATION OF LIFE HISTORY?

If this relatively complex heterochronic explanation for the peculiar features of modern human dental development survives refutation, it will suggest that evolution toward extended human infancy is not part of a general prolongation of growth and development. Similarly, the data presented here indicate that species differences for such variables as crown formation times, for example, may not be as unequivocal as was previously thought. Should paleoanthropologists therefore abandon studies of hominid dental growth and development for taxonomic purposes or in order to deduce details of life history? We believe not. However, in order to retrieve information that can be used to improve our understanding of phylogenetic relationships and life history, the dentition as a whole, rather than individual teeth, should be the subject of study. In this review we have collated information on differences in dental development among hominoids and have gone on to identify possible taxon-specific developmental constraints and evolutionary mechanisms, but these proposals must remain tentative until a more integrated analysis has been attempted.

Given the importance of the size of the dentition for both food processing and social display, it is reasonable to assume that it is under strong selection pressure, yet the means by which changes in size can be attained are finite and constrained. Although most paleoanthropologists would regard this statement as a truism, its significance for dental developmental studies has perhaps not been fully recognized. The data presented here suggest that more attention should be paid to the impact of overall size on development, although it may be appropriate to move away from the conventional means of expressing overall size. For example, it appears that crown formation time and, to a certain extent, eruption, may be more closely linked with crown height than with tooth size as reflected in crown base area. It is also likely that the rate of enamel secretion is scaled to enamel thickness and not to more conventional measures of tooth size. In the same vein, different scaling procedures may be indicated for individual tooth components, such as, for example, lingual and buccal cusps. Only when such scaling relationships have been taken into account can we begin to assess the taxonomic and functional implications of the differences in dental development between taxa.

Researchers are still in the early stages of elucidating the nature of the heterochronic changes that occur during development. For example, although it is acknowledged that evolution toward an extended infancy is coupled with a delay in overall dental maturation, the exact mechanisms are still elusive. Among mammals, the timing of eruption of first molars is correlated with life history variables, and interspecific studies indicate that these variables are similarly correlated with body weight.⁹³ Such findings are particularly useful for comparisons between species, but they may not have a high enough resolution to be employed in analyses of closely related taxa with greatly overlapping ranges of body and brain sizes. We must therefore seek to identify common biologically relevant correlations between various developmental processes, specifically between dental and somatic growth. For example, in this

review we have proposed that the growth of the primordia may be closely linked with the growth and development of the entire face. However, this needs to be substantiated. Similarly, Smith,^{7,8} in her study of the developmental status of the early African *Homo erectus* specimen from Nariokotome, related indicators of somatic maturity to dental development. The resulting range of different age estimates suggests that much more needs to be learned about the relationship between "general" versus "localized" heterochronies.

We advocate a more holistic approach to dental development studies. One of our professional colleagues has summarized this review as providing "a depressing prospect for those...who had hoped to track the evolution of the slowed human growth pattern by using teeth." On the contrary, we would argue that comparative dental development has much to contribute to our general understanding of the relationship between evolutionary processes. We add our support to the conclusions of a recent review article:⁹⁴

"The notion of a developmental constraint is important in understanding how development influences evolution; the notion of a developmental pattern is important in understanding the evolution of development." (p 233).

Modification of the masticatory complex is not the simple process some recent interpretations have suggested. The interplay between selection pressures acting on both dental function and social behavior, together with the highly integrated nature of the development of the masticatory system, precludes simplicity. Although it is right and proper to adopt a reductionist strategy for investigating evolutionary history, the study of dental development without proper regard for the wider issues involved in the development of the face and jaw probably means taking the reductionist stratagem a stage too far.

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