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Review

Progress in understanding hominoid dental development

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ABSTRACT

Teeth preserve a record of the way they grow in the form of incremental markings in enamel, dentine and cementum. These make it possible to reconstruct cellular activity and the timing of dental development in living and fossil primates, including hominids. They also provide a way of exploring the mechanisms that underlie morphological change during evolution and the nature of the relationship between ontogeny and phylogeny. All living great apes are dentally mature by about 11 y, irrespective of their body mass. While the early period of root formation in living great apes is shorter than in modern humans, enamel takes approximately the same time to form, irrespective of how thick it is. In general, differences in the total time taken to form enamel seem not to be due to differences in the rate at which enamel and dentine are secreted, but rather to faster or slower rates of differentiation of ameloblasts and odontoblasts and therefore to the number of secretory cells active at any one time during tooth formation. Tooth size, especially height, may influence the sequence of appearance of tooth mineralisation stages. The space available in the jaws may also have an influence on both the timing of tooth bud/crypt appearance and the sequence of gingival emergence. When each of these potential influences on dental development are carefully considered, and incremental markings used to calibrate key events, the developing dentition can provide an estimate of the period of dental maturation in fossil hominoids. However, the influence of body mass on the period of dental development among primates remains unclear. The earliest hominoids, dated at around 18 Mya, may still have had modern monkey-like maturational profiles, and the earliest hominids, dated between 1.8 and 3.7 Mya, modern great ape-like maturational profiles. Exactly when the extended or prolonged modern human-like maturational profile first appeared remains debatable, but the most secure suggestion might be at the time of the appearance of the earliest archaic *Homo sapiens*, when brain size and body mass were finally both within the ranges known for modern humans. But at present we should not reject the hypothesis that an extended, modern human-like, maturational profile arose more than once during human evolution in parallel with an increase in brain size.

Key words: Teeth; enamel; dentine; incremental markings; primates.

INTRODUCTION

Those who study human evolution do so for a variety of reasons. For many, the primary goal is to define phylogenetic relationships between species of fossil hominids. For others, the fossil record puts human and primate biology into an evolutionary context and so provides us with a broader perspective and understanding of living primates. The fossil record also provides the means for piecing together the evolutionary history of human growth and development because, fortuitously, the very tissues that preserve their growth histories are also found in relatively large numbers in the fossil record. The fossil record therefore represents one way in which we can begin to understand the processes and mechanisms that underlie morphological change during evolution. Evolutionary biology and developmental biology are

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now more closely allied disciplines than for over a hundred years. At the 125th anniversary meeting of the journal *Nature* in November 1994 this was heralded as one of the most important developments of the decade in science. An editorial in *Nature* (**372**: 31–32, 1994) suggested that because of this close relationship is it now possible to ask much sharper questions about the nature and molecular basis of morphological change during human and primate evolution. Weiss (1993) and Schwartz (1999) have recently reviewed many of these ideas and have provided examples of evolutionary changes for which we can postdict the nature of the developmental mechanism involved. Geneticists and developmental biologists have answered many questions about how animals are basically similar and they have defined many shared processes and mechanisms. For example, embryonic studies of individual rhombomeric crest populations have begun to establish ultimate homologies between cranial elements and to elucidate which molecular pathways have changed during vertebrate evolution (Kontges & Lumsden, 1996). Nonetheless, the questions paleontologists ask are if anything rather harder since it is knowing how animals come to be different, rather than similar, that eventually reaveals how, for example, one species of early hominid is related to another.

With regard to teeth and jaws, there has been an explosion of knowledge about their embryonic development and about morphogenesis of different tooth types as well as about the control of dental patterns at the molecular level (see Thesleff & Aberg, 1997; Thesleff & Sharpe, 1997; Ferguson et al. 2000 for good reviews). Besides the patterning of development across the dentition as a whole, more is now known about the control of cusp development within individual teeth. The enamel knot, a small mass of nonproliferating cells, produces growth factors (e.g. *Fgf-4*) that stimulate mitotic activity in the inner enamel epithelium. The primary enamel knot controls both the first buckling of the inner enamel epithelium in the position of the future first formed cusps as well as the induction of subsequent enamel knots, one for each cusp of the adult tooth (Jernvall et al. 1994, 1998; Jernvall, 1995; Thesleff & Sahlberg, 1996).

For the most part, studies of tooth development focus on events before hard tissues are formed and build on earlier observations (Butler, 1939, 1956) of how tooth germs develop. Some recent studies have come tantalisingly close to linking older theories about, for example, fields of dental development, with the spatial domains of specific gene products (Sharpe, 1995). But a lot less is known about the nature and control of growth processes that, for instance, determine enamel thickness or regulate the rates of proliferation of newly differentiated ameloblasts and odontoblasts in teeth of different shapes and sizes in different species. We understand something of what controls the morphogenesis of a molar tooth or an incisor tooth (Kollar & Baird, 1969) but not yet what controls how one hominoid molar comes to look different from another. Obsorn (1993) has drawn attention to, and attempted to address, aspects of this issue with a computer simulation of tooth morphogenesis that specifically concentrates on the physical interaction of dividing cells at the inner enamel epithelium with each other and with the basement membrane and stellate reticulum. However, more about how cells move, the rate at which they secrete enamel and dentine matrix and the time they are active in their secretory phase can be discerned from studying incremental markings in teeth. Since incremental markings are preserved in fossil teeth they offer a way of studying evolutionary processes in extinct taxa. They can provide a timescale for dental development events even, for example, in long extinct dinosaurs (Erickson, 1996).

Over the past 20 y or so a strong research theme has emerged in hominid paleontology that exploits the link between developmental and evolutionary processes and which seeks to discover more about aspects human evolution that have hitherto been considered inaccessible. This review traces the sequence of questions that have been raised in that time and attempts to show how some of the answers have in turn posed new questions. The first obvious question was, is there a difference in the period of time it takes the modern human and great ape dentitions to develop?

Development of the great ape dentition

Some of the earliest studies to document details of dental development in apes focused on chimpanzees (Keith, 1895, 1899; Zuckerman, 1928; Krogman, 1930; Schultz, 1935; Bennejeant, 1940). Zuckerman (1928) in particular had a keen interest in trying to place the Taung child into a sound comparative developmental perspective. Zuckerman compiled data on the ages of eruption of teeth in chimpanzees in European zoos and even took radiographs of chimpanzees in the London Zoo in order to document the sequence of mineralisation of chimpanzee teeth and thereby determine the period of dental development. Unfortunately, Zuckerman (1928) con-

cluded, quite wrongly, that 'all the available data indicate that the duration of the chimpanzee stages of tooth-development are the same as in Man'. It followed for Zuckerman therefore, that the 'Taungs ape must have been in its sixth or seventh year' and that there was no difference between it and an ape of the same age (or for that matter a modern human by his argument). This erroneous conclusion seeded a long held misconception about early hominid growth and development.

Subsequent studies on chimpanzees have concentrated either on the emergence times of teeth or on the sequence of mineralisation stages of the teeth (as revealed from radiographs or from dissections), or less successfully on both at the same time. The studies of Nissen & Riesen (1945, 1964) are classic longitudinal studies on the emergence times of the deciduous and permanent teeth of chimpanzees. It was clear from these studies on dental emergence that great apes completed dental development in around 11 or 12 y, a much shorter time than modern humans. Newer studies, often on larger numbers of animals (Kraemer et al. 1982; Conroy & Mahoney, 1991; Kuykendall et al. 1992) have confirmed the median emergence ages suggested by these initial studies. Kuykendall et al. (1992) have subsequently provided excellent data on the variability of emergence times in chimpanzees and furthermore, demonstrated statistically significant differences in the emergence times between some male and female teeth (but notably not of the permanent canines which differ so greatly in size, but this may be because of the small sample size for this tooth type). In addition Smith (1994*a*) has provided an excellent analysis of the sequence polymorphisms of tooth emergence in chimpanzees in the context of a comparison with modern humans, macaques and *Australopithecus*.

Gingival emergence of a tooth is, however, just one stage in a continuous process of tooth movement within the jaws towards functional occlusion. Molars emerge through the gingival tissues at approximately the time they come into functional occlusion. Anterior teeth (incisors and canines) emerge through the gingivae at the level of the cervix, or neck, of deciduous teeth and take longer to move from this position into full functional occlusion. Since gingival emergence cannot be recorded in a fossil, there are good reasons for relying less on observations of emergence or eruption sequences and more on sequences of mineralisation stages of teeth in fossils. The lack of any comparative data about mineralisation stages, combined with the reasonably good data on tooth emergence in great apes, resulted in some confusion when researchers attempted to describe and assess the significance of differences between the developing dentitions of early fossil hominids.

These days, more is known about chimpanzee dental development than for any other great or lesser ape. This, however, is simply a reflection of how little we know in contrast about dental development in the gorilla, the orang utan and especially the gibbon (see Smith et al. 1994). There are still huge gaps in our knowledge and we have next to no idea how either dental emergence or mineralisation sequences vary between great apes let alone among the subspecies of great apes. Nonetheless, in a broad comparative context, Swindler (1985) has drawn attention to the more or less common sequence of tooth mineralisation in the deciduous and permanent dentitions of monkeys, apes and humans, to the similar sequence of tooth emergence (excepting the sequential plasticity of the canine and premolar teeth with respect to the second molar tooth; Schultz, 1935; Clements & Zuckerman, 1953; Smith, 1994*a*, *b*) and to the common sequence of cusp initiation (but not coalescence where humans differ) in the permanent molar teeth of hominoids, that probably relates to a common functional molar morphology (Swindler, 1985). Swindler (1985) and others have also drawn attention to the similarities in the circumnatal dental development of teeth among hominoids (Kraus & Jordan, 1965; Oka & Kraus, 1969; Tarrant and Swindler, 1972; Moxham & Berkovitz, 1974; Siebert & Swindler, 1991).

Early studies on the sequence and timing of stages of mineralisation of chimpanzee teeth, therefore, came some time after good data were available for several New and Old World monkey species (see Swindler, 1985; Swindler & Beynon, 1993, for good reviews and discussion on this). The first attempt to establish a chart or atlas of mineralisation stages of great ape teeth (Dean & Wood, 1981) purposely minimised within-group variation and sought to portray a modal, or generalised, pattern of dental development in great apes by excluding teeth whose developmental stages were intermediate between the 9 defined stages (see Anemone et al. 1996). Anemone et al. (1991), Simpson et al. (1992), Kuykendall (1996, 2000), Kuykendall & Conroy (1996), Anemone et al. (1996) and most recently Reid et al. (1998) have all subsequently refined or proposed revisions to the findings of this study using longitudinal or mixed longitudinal samples of known age chimpanzees. Beynon et al. (1991*b*), Chandrasekera et al. (1993) and Winkler (1995) have provided some additional evidence for dental development in chimpanzees, orang utans and

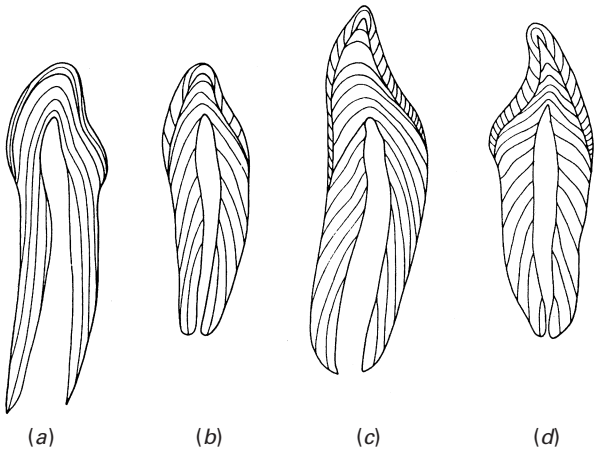

Fig. 1. Drawings made from ground sections of canine teeth belonging to *Homo sapiens* and *Pongo pygmaeus* reduced to approximately the same size for ease of comparison. Section A is a deciduous *Pongo pygmaeus* canine. Section B is a human deciduous canine. Section C is a permanent *Pongo pygmaeus* canine and section D is of a modern human permanent canine. The tooth that takes the least time to form is A; D takes the longest time. Despite substantial differences in the size the smaller human tooth takes longer to form. After Dean & Wood (1981).

gorillas, but data for great apes other than for the common chimpanzee remain scant.

Obvious questions arise from these studies on great ape dental development about how larger ape teeth might grow in a shorter time period than available in modern humans. Specifically, a key question was is it the period of crown formation, or the period of root formation, or both, that are reduced in apes to reflect the foreshortened growth period?

Crown and root formation times in hominoids

The first study to attempt to estimate the period of crown and root formation in great ape teeth was Dean & Wood (1981). A key finding in this study was that in each of the 3 great apes, crowns appeared to take approximately the same times as modern humans to complete (this was later confirmed by Beynon et al. (1991*b*) using a histological approach). Another key finding was the corollary that root formation clearly took much less time in modern great apes than in modern humans. Dean & Wood (1981) made histological sections of ape and human canines in order to demonstrate how this might occur (Fig. 1). It was obvious that the orientation of the incremental markings in the enamel and the dentine differed between deciduous and permanent teeth in humans and great apes.

Teeth begin to mineralise at the cusp tip and grow in length until the root apex is completed (Dean, 1989). The rate at which a tooth grows in length however, only partly reflects the total growth period of the individual. A shift in the sequence of tooth mineralisation, or an earlier initiation of mineralisation, may alter the time an individual tooth has available to grow, even though the total period of the individual's development may be much shorter. It follows then that there are ways a tooth, or a part of a tooth, may be 'buffered' from the effects of a shorter overall time available for development of an individual. By way of example, human canines begin to mineralise shortly after birth and are complete at 12 or 13 y of age. Great ape canines also begin to mineralise shortly after birth and similarly complete their roots at 12 y or so. However, in the case of great apes this represents the whole of the period of dental growth and development while in modern humans it represents only 2/3rds of the total period. Another important example of this kind is the shift in initiation to an earlier time of M2s and M3s, each with respect to the M1s and M2s, such that crown formation of molar teeth in apes overlaps more than in modern humans. By beginning to mineralise earlier, before the crowns of the preceding molars have finished, enamel formation can continue over the same period of time that it does in humans. The extra time required to grow a molar crown in the same period of time in modern great apes comes in part from initiating mineralisation earlier.

Anemone et al. (1991), Simpson et al. (1992) and Kuykendall (1996, 2000) have all presented data for the time it takes to grow roots in chimpanzee teeth and it is clear that some tooth roots take longer than indicated by Dean & Wood (1981), even approaching the times taken in modern humans. Since crowns take as long to form as they do in modern humans, in order for a permanent tooth to emerge into functional occlusion earlier in great apes than in modern humans it is the portion of root that forms between crown completion and emergence into occlusion that must grow especially quickly in great apes. Subsequent root growth, that results in the long roots of great apes in certain teeth (e.g. canines and M3s) may well continue after the tooth has emerged for as long as it does in modern humans.

For many reasons the first permanent molar tooth is regarded as a key tooth developmentally in primates (Smith 1989, 1991*a*, *b*, 1994*a*, *b*; Smith et al. 1995). Its emergence into the mouth marks the time many primates are weaned. Its emergence also marks the time that brain growth (in volume at least) is 90% complete in all primates (Ashton & Spence, 1958). For

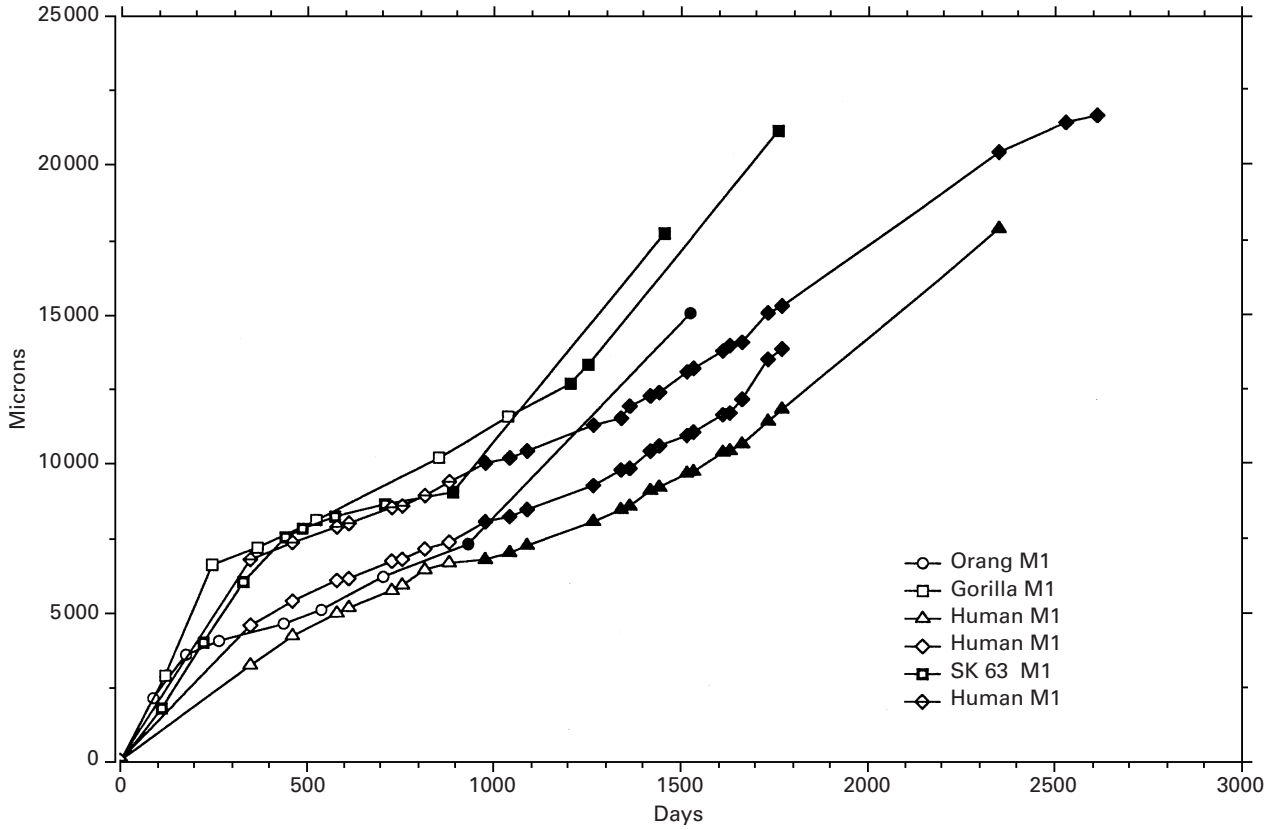

Fig. 2. Line plots of increasing tooth length in μm against age in days for 3 histological sections made from 1 first permanent molar of *Homo sapiens* (each section contains cusps growing at different rates) and 1 section each of first permanent molars belonging to *Gorilla*, *Pongo* and of SK 63 (*Paranthropus robustus*). Solid symbols represent root formation and open symbols enamel formation. Early root formation in the apes and in SK 63 occurs at a faster rate than in modern *Homo sapiens*.

these reasons and others this tooth has often been the focus of studies in humans, fossil hominids and in many living primates. It is a useful tooth to study in order to discover more about rates of root growth. If crown formation times in first permanent molar teeth are indeed broadly comparable in hominoids, as suggested, then because the age at which teeth emerge into occlusion is different among hominoids, the rate at which the first part of the root forms is likely to reflect this. By this argument, if the first half of the first permanent molar roots from 2 different taxa were the same length, then the teeth of one with first molar emergence at 3 or 4 y, will have faster growing roots than the teeth of that with first molar emergence at 6 or 7 y of age. Because the first part of root growth must occur before the tooth can emerge, this is where the greatest differences are likely to be found between modern humans and apes. Some data support this (Fig. 2). By using incremental markings in the teeth to reconstruct longitudinal growth curves, increase in molar tooth crown *and* root height has been plotted against time for apes, humans and a fossil hominid (Dean, 1995*b*).

While these data document important potential differences between apes and humans and fossil hominids they do not explain, at a developmental level, how ape and human roots grow differently. In other words, are there any differences in the daily rates of dentine formation between humans and apes that might underlie the initially faster rates of root elongation (extension rates) in ape permanent molars?

Dentine formation rates in great apes and humans

Enamel, dentine and cementum each grow incrementally. Alternating periods of slow and faster growth during development are evident from incremental markings in each tissue on histological examination (see Dean, 1987*a*, 1995*a*; Lieberman, 1993; FitzGerald, 1995, 1998 for reviews). Very slow growing cementum often contains seasonal bands about a year apart. Odontoblasts and ameloblasts secrete more tissue but over a shorter period of time than do cementoblasts. Enamel and dentine therefore, contain daily increments of growth (and occasionally

even subdaily infradian or ultradian increments of growth) as well as prominent long-period incremental markings (Dean & Scandrett, 1996). In monkeys, apes and humans the periodicity of long-period increments varies between 4 and 5 d to as much as 10 or even 11 or 12 d. All these incremental phenomena in tooth tissues are useful markers of rates of tissue formation and there are many ways in which they can be used together or alone to retrieve information about the ways in which teeth grew in both living and extinct species of hominoids.

The daily incremental markings in dentine are more difficult to see than those in enamel. This means methods other than direct visualisation of incremental markings using transmitted light microscopy have to be used to determine the daily rates of dentine formation in primate teeth. Teeth that have become labelled with tetracycline antibiotic in the dentine and enamel are especially useful. Tetracycline fluoresces in incident ultraviolet light and is easily seen in fluorescence microscopy of tooth tissues. Enamel cross striations can be used to calibrate the time interval between label lines in the enamel and dentine forming at the same time (Dean et al. 1993*a*; Dean & Scandrett, 1995, 1996). Dentine tubules represent the path over which odontoblasts secrete predentine matrix as they pass from the enamel- or cement-dentine junction towards the periphery of the future pulp chamber during dentine formation. Thus the distance along dentine tubules can be measured between label lines at known time intervals from the enamel-dentine junction pulpwards. By repeating this procedure for several 'tracks' in the crown, at the cervix and in the root dentine, it has been possible to identify gross similarities and differences in the way odontoblasts secrete dentine matrix throughout tooth formation in modern humans and great apes (Dean & Scandrett, 1995).

In the following examples ground sections from the first permanent molar of an orang utan and of a modern human were used. The progress of dentine formation was tracked using both tetracycline labelling and long-period markings (Dean, 1995*a*). The latter have the same periodicity as striae of Retzius in the enamel of the same individual (9 d apart in the orang utan and 8 in the modern human). Several 'tracks' were identified along dentine tubules in the crown, at the cervix and in the root of these molar teeth. The distance between successive lines was then measured along the direction of the dentine tubules. Figure 3*a* and *b* illustrates the label lines and the tracks used in the human and orang utan molars. Figure 4*a* and *b* are plots of the cumulative distance travelled by odontoblasts against time. There is a striking similarity between the graphs of human and orang utan teeth. In fact, rates of dentine formation calculated from the slopes of the lines suggest in both teeth, dentine formation begins slowly between 1 and 2 μm per day. They then rise to between 4 and 5 μm per day and fall off again as the pulp is approached. Most are typical 'S-shaped' growth curves and reflect the secretory activity of the odontoblast during dentine formation in the crown and root of both the human and ape molar tooth. Thus there appear to be no significant differences in the rates at which dentine formation occurs between the molar teeth of humans and apes that could account for the way the first portion of ape tooth roots extend at a faster rate than humans. Differences in the daily rate of dentine matrix secretion (or mineralisation) cannot then alone be held responsible for differences in the rates at which tooth roots extend in length.

It had been obvious from the orientation of the incremental markings in different canine teeth illustrated by Dean & Wood (1981), and from a study of root cone angles in modern humans and fossil hominids (Dean, 1985*a*), that part of the reason for the faster extending roots in apes and early hominids was the result of a larger numbers of odontoblasts becoming active at any one time as differentiation proceeds at the cervical loop. However, without information about daily rates of dentine formation and about the inclination of dentine tubules to the enamel- or cement-dentine junction it was not possible to quantify rates of root extension. The obviously important question was whether it was possible to make estimates of root extension rates in fossil hominoids and hominids from fractured and/or histological sections of their teeth.

Estimating root extension rates in fossil hominoids and hominids

Three factors determine the rate at which tooth roots grow in length: (1) the daily rate at which odontogenic cells produce matrix; (2) the direction of cell movement; and (3) the number of mature secretory cells active at any one time (their rate of differentiation) Shellis (1984) has expressed the 'extension rate' of teeth at the enamel dentine junction in the crown or at the cement dentine junction in the root, mathematically. In the equation $c = d\{(\sin I/\tan D) - \cos I\}$, c is the extension rate, d the daily rate of dentine secretion, angle I is the angle the dentine tubules make with the root surface, and angle D is the angle between an incremental or accentuated line and the root surface.

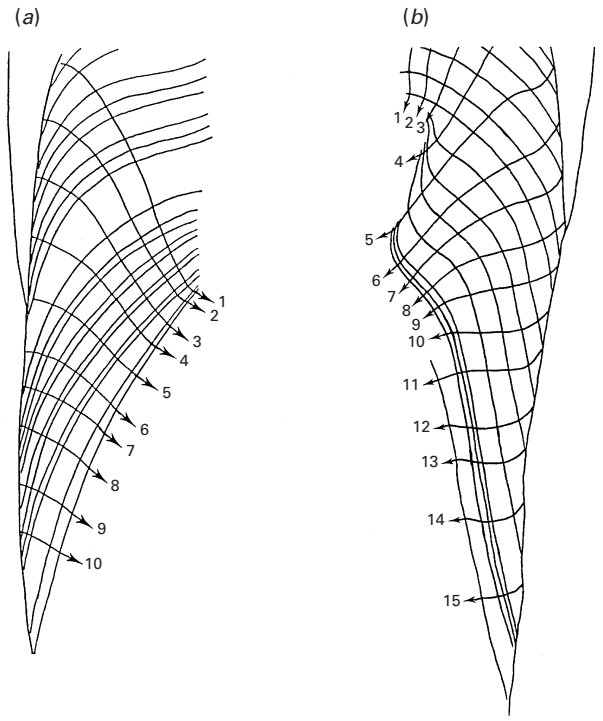

Fig. 3. The left-hand drawing from a ground section (*a*) represents the dentine and enamel of the modern human M1 used in this study. Tetracycline lines that fluoresce in incident UV light in the dentine are drawn in and represent successive (but irregular) positions of the mineralising front during dentine formation. Drawn across these and following the direction of dentine tubules from the first formed dentine towards the pulp chamber are 10 'tracks'. The first begins high in the cervical region and the last low in the cervical root. Cumulative measurements were made between successive tetracycline lines along each 'track'. The right hand drawing (*b*) is of the ground section of the orang utan M1 used in this study. In this drawing fluorescing tetracycline lines and long period lines were used to calibrate dentine formation and are drawn in. 'Tracks' 4 to 15 in Fig. 3*b* are equivalent to 'tracks' 1–10 in the modern human M1 and it is only these appear in Fig. 4.

The equation defines the contribution of each of the 3 variables to the rate of tooth root extension. In order to calculate the rate of extension of tooth crowns and roots from living or fossil species 3 things need to be measured from high power reflected or transmitted light images of teeth: (1) the amount of tissue secreted in a day; (2) the direction of travel of the ameloblast or odontoblast relative to the EDJ or CEJ (which can be inferred from the alignment of an enamel prism or dentine tubule); and (3) the angle that the active cell sheet subtends to the EDJ (a reflection of the number of active secretory cells).

Incremental lines in the dentine of the crowns and roots are exquisitely preserved in ground sections made from 13 teeth belonging to 3 individuals of the early Miocene fossil hominoids *Proconsul heseloni* and *Proconsul nyanzae* (Beynon et al. 1998). By calculating the rates of root extension along tooth roots at several locations and then by dividing the length of the tooth root by the rate of root extension it was possible to estimate root formation times for both permanent and deciduous teeth belonging to these fossils. Extension rates in the cervical third of permanent tooth roots of *Proconsul heseloni* were on average 6.5 μm per day. In the apical third of the root they were on average 14.5 μm per day and close to the apex 21.5 μm per day. A 7–8 mm long root probably took around 2.5 y to form (Beynon et al. 1998). Root extension rates in a deciduous tooth, which one would expect to form much faster, were estimated at 35 μm per day. One potentially important point to come out of this is the apparent similarity among hominoids of root extension rates increasing towards the root apex in permanent teeth. However, the early root extension rates in *Proconsul* are not as fast as those estimated for modern great apes. We need, therefore, to be alert to the possibility that there may be several combinations of initial mineralisation time, crown formation time, and root extension rates among primates that would each result in a tooth having sufficient root formed 'in time' for gingival emergence. Dean (1993) reported a fairly consistent rate of daily dentine deposition in macaque tooth roots as well as a constant extension rate in permanent tooth roots as judged from labelled incremental markings of known time intervals in the dentine. It will be interesting to see if these observations hold true for other monkey species. Importantly, we need to be aware that *Proconsul*, which many would regard as the earliest known hominoid, might have achieved M1 emergence at relatively later times than monkeys of the same body weight by a combination of fast crown formation and slow root formation times. In other words, we should not assume that what we now know of modern great apes was true for all fossil apes.

The same approach has been used to estimate the time taken to grow tooth roots in *Homo habilis* (Dean, 1995*a*). Figure 5*a* and *b* shows 2 sieving fragments selected from many belonging to Olduvai Hominid 16 (Tobias, 1991). Figure 5*a* is a photomicrograph of a portion of naturally-fractured crown and root. The tooth is most probably of a permanent molar, fractured axially and is viewed here under ethyl alcohol and in incident polarised light to eliminate unwanted reflectance from the unpolished tooth surface, and in order to highlight long-period incremental markings. Direct visualisation of the second sieving fragment (Fig. 5*b*) under alcohol reveals the angle the accentuated incremental markings in the dentine make with the cement-dentine junction (close to the granular layer of Tomes) as well as the angle the

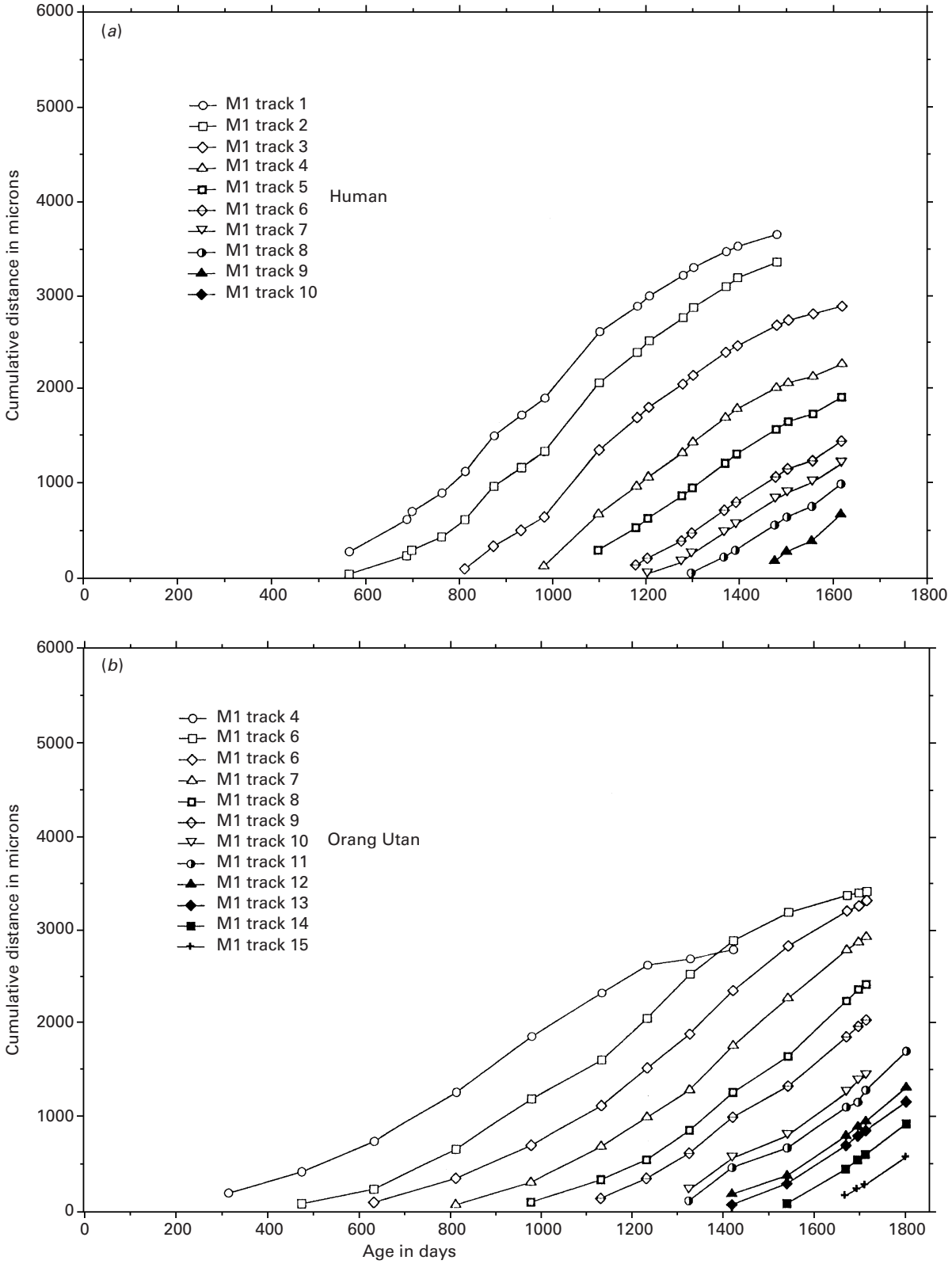

Fig. 4. (*a*, *b*) Line charts showing cumulative distances travelled by odontoblasts along each 'track' (previously shown in Fig. 3*a*, *b*), representing the distances (μm) odontoblasts travel over time (in d) during dentine formation along each 'track'. Importantly, there is no sudden change to the general pattern at the end of enamel formation at the cervix (tracks 5 and 8 respectively in each graph) in either ape or human tooth as root formation begins. If anything, the rates of dentine formation as indicated by the slopes of the lines in each graph rise to higher levels in the human teeth, but the discrepancy is no more than 1 μm or so per day in the inner dentine. The broad equivalence of these plots confirms that fast rates of root extension in great apes do not result from fast daily rates of dentine secretion. It is the combination of faster rates of cell differentiation at the growing apex of the tooth and differences in direction of travel of the odontoblasts with similar daily rates of dentine formation that result in increased rates of root extension in the apes.

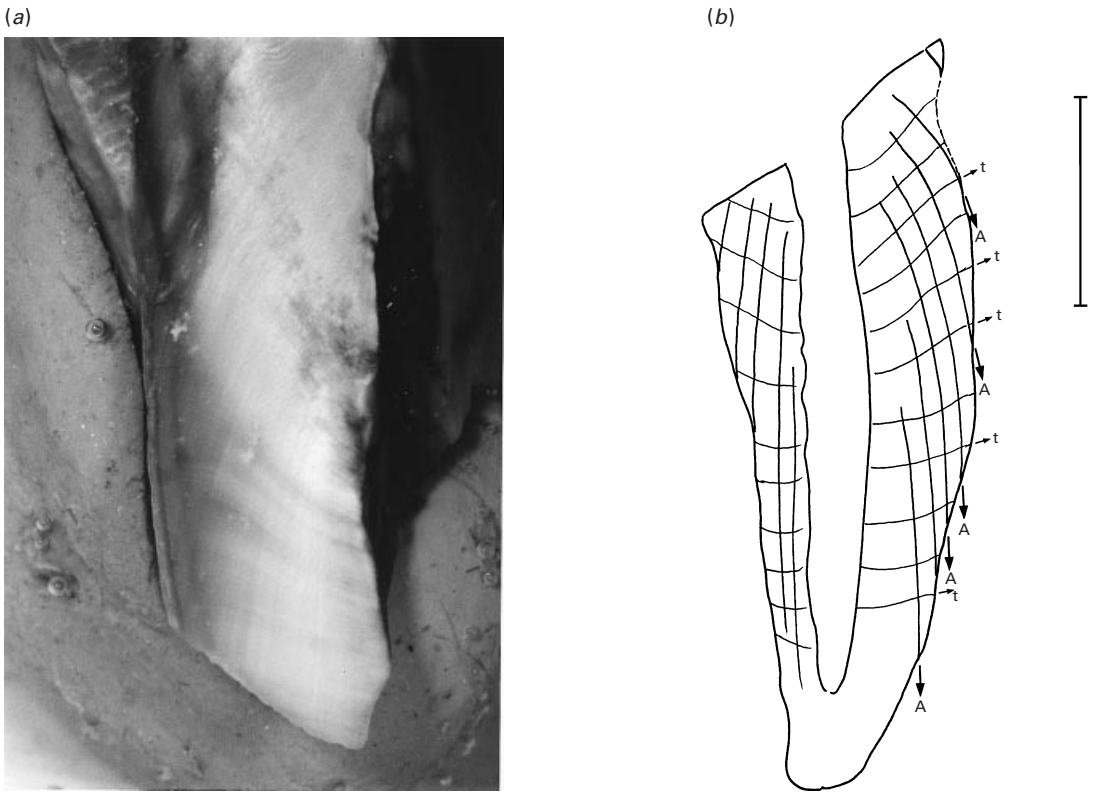

Fig. 5. (*a*, *b*). Two sieving fragments selected from a collection of many that cannot be matched to any other fragments nor to any of the more completely preserved teeth, but which undoubtedly belong to permanent posterior teeth of OH 16 (Tobias, 1991). Figure 5*a* is photomicrograph of a naturally fractured crown and root. Here it is viewed under alcohol with a Wild binocular microscope at $\sim \times 80$ magnification. The specimen was illuminated with polarised incident light. Strong accentuated lines in the dentine show the direction of the incremental lines. The direction of dentine tubules is also visible. Note the cementum at the root surface and the position of the granular layer of Tomes just deep to this which looks like a dark band in this micrograph. (*b*) Drawing of second fragment viewed in the same way and made using a drawing tube attachment on the same microscope. The scale bar is 5 mm long and the whole fragment 18 mm long. Arrows (A) show the inclination of accentuated incremental lines at the root surface. The smaller arrows (t) indicate the inclination of dentine tubules to the root surface. Measurements (defined in the text) on this second fragment were made just deep to the granular layer of Tomes and in the cervical third of the tooth root using a goniometer eyepiece and at as high a power as possible. The measurements appear in Table 1.

dentine tubules make to the dentine at the root surface. The change in direction of the tubules from the cement-dentine junction towards the pulp chamber can also be tracked quite clearly in both panels *a* and *b* of Figure 5. Given that it is likely the daily rates of dentine secretion, close to the root surface, are similar in apes and humans (Dean, 1998*b*) and, therefore, more than likely the same in this and other fossil hominids, we can surmise it to be in the range of 2 to 3 μm per day in this position in OH 16. It is likely that 2.5 μm per day is a good average value for rates of dentine formation close to the granular layer of Tomes which is found adjacent to the first formed root dentine in hominoids (Dean, 1998*b*).

A range of measurements for angle D and angle I made in the cervical third of the second tooth fragment together with values for daily rates of dentine formation common to hominoids in this location (Dean, 1998*b*), give an estimated extension rate of between 9.6 and 15.7 μm per day (Table 1). This extension rate is greater than that expected in modern human teeth close to the end of crown formation

Table 1. *Data from OH 16 for* '*angle I*' *and* '*angle D*'

Angle I	Angle D	Daily rate 'd'	Extension rate 'c'
115	11	2.5	12.7
115	11	2.5	12.7
130	10	2.5	12.5
109	9	2.5	15.7
117	11	2.5	12.6
122	13.5	2.5	10.2
133	14.5	2.5	9.6

d, daily rate of dentine formation; c, extension rate calculated from these variables using the formula described in the text (Shellis, 1984). Data for d were derived from measurements made between 50 and 100 μm from the granular layer of Tomes in humans and apes (Dean, 1998*b*).

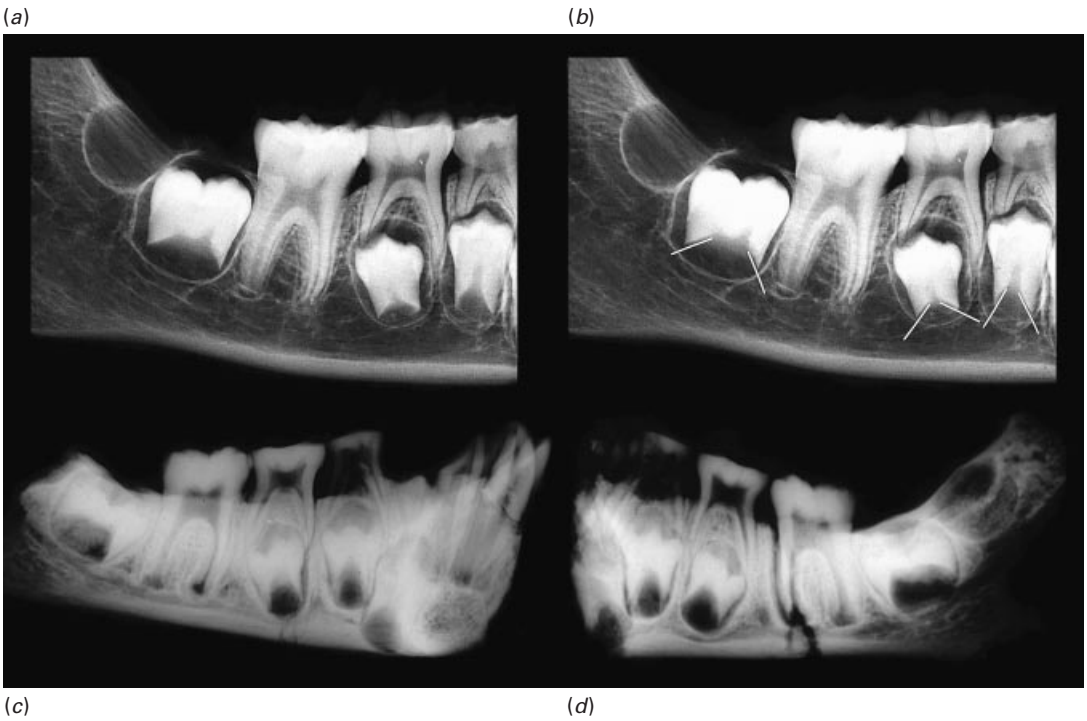

Fig. 6. The top 2 radiographs (*a*, *b*) are of a modern human child ~ 10 y of age. Both radiographs are identical except the one of the right has developing root cone angles highlighted by white lines drawn along the forming dentine front of the premolar and second permanent molar roots. This radiograph can be compared with the identical but 'unaltered' radiograph on the left. In modern humans the first stages of root formation are associated with large root cone angles (Dean, 1985*a*) but these reduce towards the apex as the extension rate increases. The lower two radiographs (*c*, *d*) are of the right and left sides of a fossil mandible (KNM-ER 820) attributed to early African *Homo erectus* (Wood, 1991). They show clearly that the forming roots of the premolars and the second permanent molar on both left and right are quite different from those typical of a modern human of the same relative dental developmental age. There is much less dentine formed along the root margins in the fossil specimen. If daily rates of dentine formation are identical in modern humans and early *Homo*, and if the direction of travel of odontoblasts is the same then extension rates in this specimen were greater during the first stages of root formation than in modern humans (after Dean, 1985*a*).

(Dean & Beynon, 1991*b*; Dean et al. 1992; Liversidge et al. 1993; Simpson & Kunos, 1998) and it fits with other observations on this specimen that suggest a comparatively fast rate of tooth root extension in *Homo habilis* at the root cervix (Dean, 1995*a*). Given more data of this kind and a secure estimate for the age of emergence of M1 in several individuals it is likely one could say more confidently whether tooth development in *Homo habilis* simply resembled that in *Australopithecus* and *Paranthropus* (Bromage & Dean, 1985; Beynon & Dean, 1988; Dean et al. 1993*b*) or whether it had shifted towards the prolonged period of growth and development we associate with modern *Homo sapiens*. At present, in the light of the data presented here and elsewhere (Dean, 1995*a*) this seems highly unlikely.

There are no good data about rates of early root formation in early African *Homo erectus*. Even if there were this alone would not be the best way of establishing for sure that the total period of dental formation occurred in an early hominid-like, modern human-like or intermediate-like period of time. Nonetheless, radiographs of a juvenile specimen, KNM-ER 820 (Wood, 1991), show clearly that the forming roots of the premolars and the second permanent molar are quite different from those typical of modern humans (Fig. 6). The root cone angles in these teeth (Dean, 1985*a*) are smaller than in modern humans for this portion of root growth and if the daily rates of dentine formation were 2.5 μm per day and if the angulation of the dentine tubules to the cement-dentine junction were as in OH 16, then it would be hard to argue that first part of root formation in early African *Homo erectus* was not as fast as that in modern great apes and other earlier hominids. The null hypothesis should be that it was, and until this has been falsified with further and more extensive histological analysis it would be unwise to assume a modern period of dental development for early African *Homo erectus*. One other fossil specimen attributed to early African *Homo erectus*, KNM-ER 1507 (Dean, 1985*a*; Wood, 1991), is dentally younger than KNM-ER 820 and has minimal root formation on M2 and Pm3 but unfortunately radiographic images of the roots are

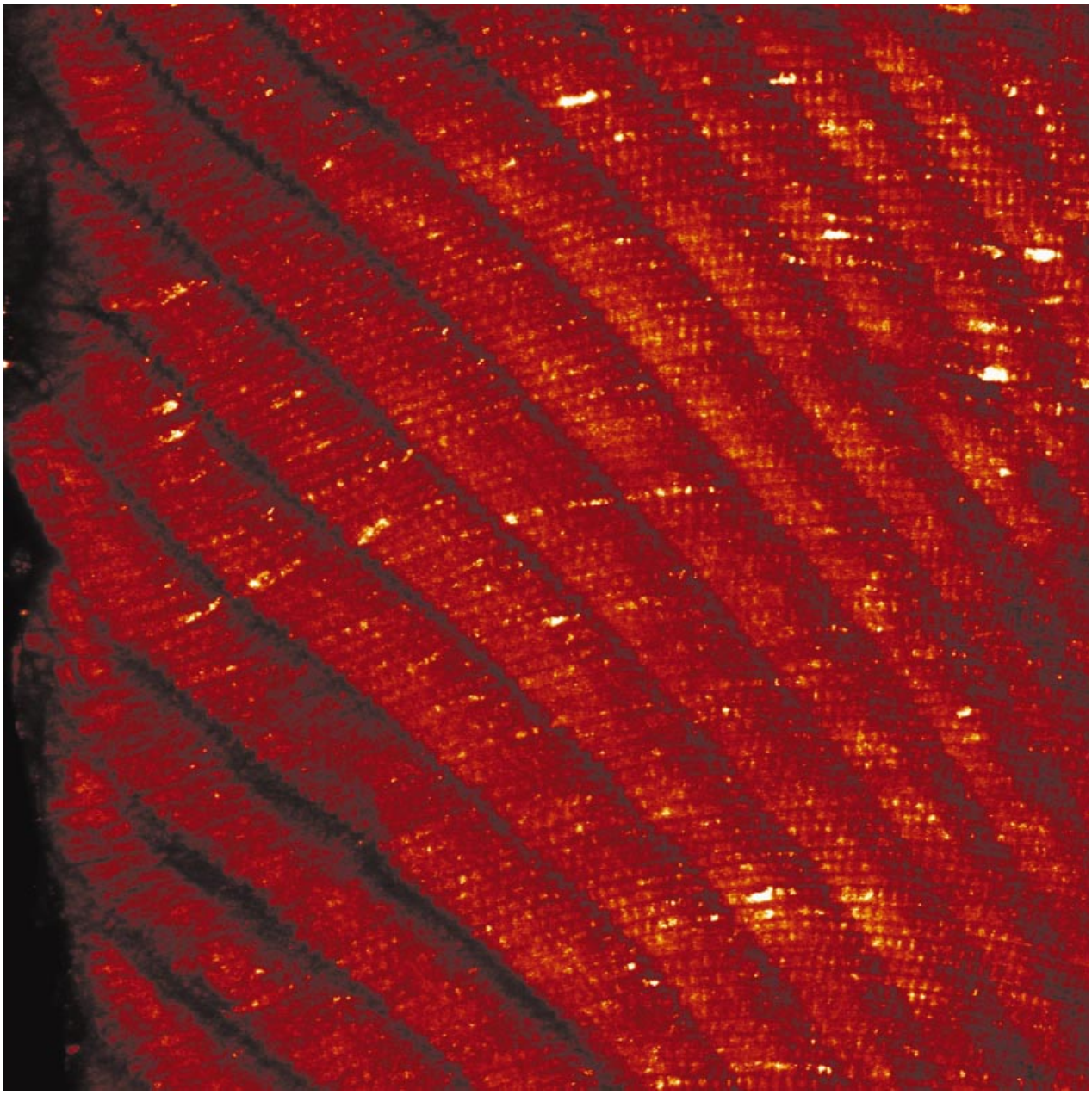

Fig. 7. Confocal micrograph of lateral enamel in an orang utan molar tooth sectioned longitudinally. Coarse oblique long-period striae run diagonally from the bottom right of the micrograph to the surface at the top left. The surface enamel appears along the left margin and each long-period stria is associated with a perikyma at the surface. Perikymata create regular ridges and troughs that run around the circumference of the tooth surface. Rod-like enamel prisms are finer structures that, in this micrograph, run from the right margin of the field of view towards the surface. In this section they turn cervically (towards the bottom of the field of view) as they approach the outer enamel. Cross striations (daily increments of enamel formation) are fine dark lines that run across the prisms. In this individual there are 9 daily increments between adjacent long-period striae (and therefore between adjacent perikymata on the tooth surface). Each cross striation is spaced approximately 5–6 μm apart in this micrograph. Equivalent daily and long-period incremental markings exist in dentine forming at the same time.

obscured by matrix such that no root cone angles can be reliably measured at the cervical root margin. In any case, root cone angles are a less acurate way of saying something about rates of root extension than are estimates made from histological evidence.

An obvious question that arises from what we now know about the comparative development of dentine formation and its role in regulating the rate of root growth relates to enamel. If daily rates of dentine formation are the same in humans, apes and fossil hominids and if the orientation of the long-period lines in dentine are a direct reflection of extension rates, then how in enamel, where long-period lines also vary greatly in their orientation among homi-

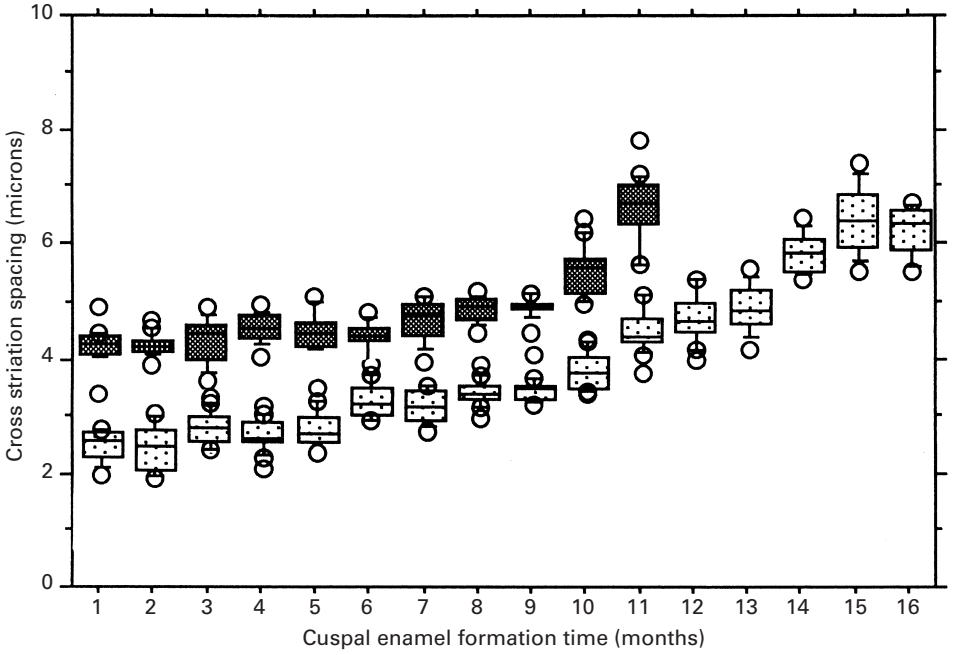

Fig. 8. Box plots of cross striation spacings in the second permanent molar cusps of *Proconsul nyanzae* (dark infill) and *Homo sapiens* (light infill) both demonstrate a clear gradient of increasing rate of enamel matrix secretion from the enamel dentine junction to the cusp tip. Cuspal enamel in both *Proconsul nyanzae* and *Homo sapiens* second permanent molars is thick. Cuspal enamel in *Homo sapiens* takes approximately 16 mo to form but only 11 mo in *Proconsul nyanzae*. Within the shorter period of time available to form a *Proconsul* molar crown, cuspal ameloblasts secrete enamel matrix at a consistently faster rate than in the *Homo sapiens* molar and in this way form similarly thick enamel in less time.

noids, can one account for crown formation times being equal in modern hominoids? In other words, are daily rates of enamel formation, like those of dentine, the same in modern great apes, humans and fossil hominids?

Rates of enamel formation in humans, apes and fossils

There is considerable experimental and circumstantial evidence to suggest that enamel cross striations reflect daily, or circadian, growth increments along the length of enamel prisms. The literature on this is extensive, and has been reviewed by Dean (1987*a*, 1995*a*) and FitzGerald (1995, 1998) as well as by others. While there is no place for yet another review to document what is now well known it is worth stating that a series of key experimental studies were carried out by Okada and colleagues (see Okada, 1943), and by Schour & Poncher (1937), Schour & Hoffman (1939) and Bromage (1991). All the available evidence suggests that so called enamel cross striations are circadian (around a day) incremental markings. Enamel cross striations are short-period markings which appear as fine dark lines that mark prisms across their long axis in a regular manner (Fig. 7). They may result from shifts in acid base balance and/or from changes in carbonate concentration that occur in a regular circadian manner which alter the refractive index of enamel as seen in transmitted light (Boyde, 1979, 1989; Shinoda, 1984). Whatever the mechanism whereby they form they are crucial markings for reconstructing the timing of tooth tissue formation in fossils.

The role that the daily secretory rate of ameloblasts plays in the control of enamel thickness during growth of the crowns of teeth is complex. In contrast to dentine, it is possible to make measurements of the spacing between enamel cross striations reasonably easily using routine microscopy of ground sections of teeth. It is also possible to make many more measurements in a single region or zone of enamel than one can in the majority of ground sections of dentine. When enamel cross striations are tracked through the cuspal enamel of ape and human second permanent molars, just lateral to the maximally decussating (so called gnarled) enamel under the cusp tip, a clear gradient of increasing rate of enamel secretion becomes obvious (Fig. 8). Clearly, prisms weave in and out of the plane of section but many can be followed for long distances in 2 dimensions. What is clear from the box plots in Figure 8 is that the ameloblasts that secrete enamel matrix in the human molar tooth cusp do so at a slow rate for many

months before increasing in rate towards the outer cuspal enamel. For the first 5 mo in human cuspal enamel the mean rate of enamel secretion is below 3 μm per day. Only after 10 mo in this human tooth cusp does the rate increase above 4 μm per day. Similar data for *Proconsul* (Fig. 8) show how cuspal enamel was secreted more rapidly in this early hominoid, but in the same well-organised manner and with a similar gradient of secretory activity through the cusp. These results provide a clue about how cuspal enamel thickness may be achieved in different ways in different primates (Beynon et al. 1998; Dean, 1998*a*). In other primates, molar enamel thickness appears to be achieved in yet other ways, for example, in *Pongo* the gradient of increase is greater initially, but fails to rise to the very high rates measured in *Pan* and *Homo*.

Unfortunately, simplistic measures of enamel thickness among primates are unlikely to reveal the developmental and evolutionary mechanisms that control for different thicknesses of enamel in teeth. It is clear that there are differences in both the gradient of change and in the daily rates of enamel formation in cuspal enamel despite similar overall crown formation times among modern humans and modern great apes. What is obviously required is a large scale survey of different tooth types across a range of primates which integrates information about cuspal and lateral enamel secretory rates with measurements of enamel thickness. It is also clear that there is a gradient of increasing cuspal and lateral enamel thickness from the front of the mouth to the back (Aiello et al. 1991; Macho & Berner, 1993, 1994; Macho, 1994; Macho & Wood, 1995). This also needs to be documented more carefully and the developmental mechanisms that account for this gradient traced through both deciduous and permanent dentitions. While gradients of enamel secretion over time must relate to function (Beynon & Wood, 1986, 1987; Shellis et al. 1998; Schwartz, 2000) the determination of the relative influences of function and taxonomy on this system will be a considerable challenge.

The changes in secretory rate in cuspal enamel contrast with what one finds in the axial dentine. Odontoblasts that differentiate at the same time as the cuspal ameloblasts move from the dentine horn to the pulp horn during primary dentine formation. When rates of dentine formation are tracked towards the pulp chamber in this direction, the rates of secretion seem to remain maximal and constant, with the exception of the very early and the very late stages of dentine formation (Dean & Scandrett, 1995). Odontoblasts and ameloblasts may become mature secretory cells at the same time, but thereafter their direction of travel and their rate of secretion differ, demonstrating that there are clearly different signals controlling their activity during cusp formation.

Once differentiated, ameloblasts that form lateral enamel do not contribute to the height of the crown while they secrete enamel matrix. There is nonetheless a regular shift in the gradient of enamel secretory rates from slow to faster rates as ameloblasts move from inner, to middle and finally to outer lateral enamel. Beynon et al. (1991*a*), Dean & Shellis (1998) and Shellis (1984, 1998) have provided comprehensive data to show that this is so and in addition demonstrated a reduction in rates towards the cervix that occurs in all living hominoids. When the secretory rates of ameloblasts and odontoblasts that differentiate together in the lateral part of the tooth are compared through their secretory lifespans, the gradient of increase in enamel secretion resembles that for the plots of dentine more closely in some ways than in cuspal enamel. A key difference, however, is that there is no gradual slowing down of lateral enamel in the way there is of dentine formation that is approaching the pulp cavity.

It is also now clear from studies of *Proconsul* teeth (Beynon et al. 1998) that rates of dentine formation in this early hominoid are very much less than the rates of enamel formation (a third slower in some teeth). In contrast, the daily rate of secretion of enamel in cuspal enamel is faster in *Proconsul* than in other hominoids. Yet again this is clear evidence that even though cells differentiate at approximately the same time and become active secretory ameloblasts and odontoblasts at more or less the same time, they must be influenced by an independent set of control mechanisms. This in turn suggests there are very many ways that selection may operate to alter tooth morphology and that it will be necessary to tease apart the processes that take place in each dental tissue before shared and derived developmental processes can be identified between living and fossil primate taxa with confidence.

Long-period lines in enamel reveal information about extension rates which can then be compared with information about the daily secretory rates of ameloblasts. Fast extension rates in the cuspal enamel give way to slower extension rates towards the cervix in all hominoid teeth (Shellis, 1998). However, all the evidence from naturally-fractured surfaces suggests that some molar teeth, belonging to thick-enamelled fossil hominids, maintain a high rate of extension even into cervical enamel (Beynon & Wood, 1986, 1987; Ramirez Rozzi, 1993, 1995, 1998). However, no histological sections of early hominid molar teeth have

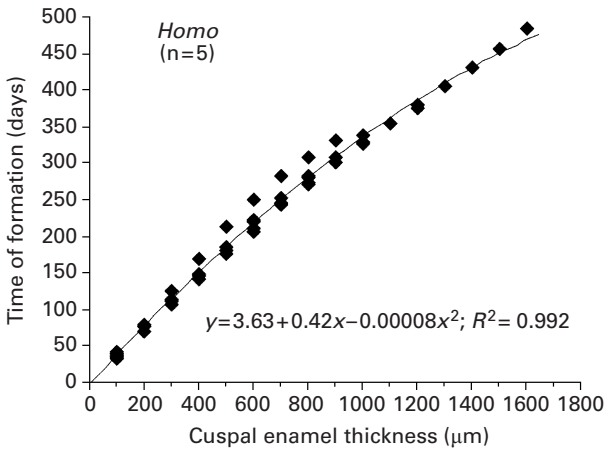

Fig. 9. Daily cross striations were counted along prisms in canine teeth through successive 100 μm zones of enamel starting from the enamel dentine junction (EDJ) to the cusp surface. Counts were made along groups of prisms that decussated minimally and travelled to the surface in the same direction. Enamel close to the EDJ forms slowly (2–3 μm per day). Enamel secretion rates rise increasingly towards the surface (5–6 μm per day). The relationship between time taken to form enamel for increasing thicknesses of enamel in the cusp can be described by a polynomial regression equation. Regression equations for predicting the time taken to form any given thickness of cuspal enamel in modern human canines and great apes canines are as follows: *Homo* (n = 5), $y = -3.63 + 0.42x - 0.00008x^2$, $R^2 = 0.992$; *Pan* (n = 2), $y = 0.41 + 0.31x - 0.00007x^2$, $R^2 = 0.991$; *Gorilla* (n = 3), $y = 1.44 + 0.29x - 0.00005x^2$, $R^2 = 0.983$; and *Pongo* (n = 2), $y = 11.3 + 0.37x - 0.0001x^2$, $R^2 = 0.962$.

ever been made in a way that rigorously controls for plane of section and tooth aspect. The evidence so far (Dean & Shellis, 1998; Ramirez Rozzi, 1993, 1995, 1998) points to there being many complex and variable ways of maintaining a high rate of enamel extension into cervical regions. But further exploration of these mechanisms may yet yield more taxonomic information about the evolution of early hominid teeth.

The net effect of changing daily rates of enamel secretion and of changing rates of enamel extension is that some parts of hominoid tooth crowns grow fast in their heights and others more slowly. While the different components of a tooth crown vary in the time they take to form between species of primates the overall regulatory effect of these shifting variables has been to keep the total time of crown formation fairly constant between modern humans and modern great apes, and in all probability, early fossil hominids. Other hominoids, *Proconsul* and *Hylobates*, for example, grow their tooth crowns in a shorter period of time than hominids and modern great apes and achieve their adult crown heights at different rates. The challenge is to understand how the regulatory processes that control for this both reflect, and are tied into life history variables and in particular to the period of growth and development in primates.

It emerges from these studies and from those on modern great ape dental development that virtually no information exists on sex differences between hominoids. The most dimorphic tooth in the mouth is the canine and among living and fossil great apes this a key tooth for sorting and sexing mixed samples. Only recently is information about emergence of canine teeth and about the way male and female canine crowns grow differently coming to light.

Sex differences in emergence and mineralisation stages of hominoid canines

One of the most intriguing themes in primate and human evolution is the nature of sexual dimorphism. This goes well beyond the simple observation that males are often bigger than females. It raises sociological and behavioural issues that Darwin recognised must underlie the nature of sexual selection in evolution. Now, more than ever, it begs questions about the nature of the developmental and evolutionary mechanisms that bring about morphological differences between males and females, both within the same species and between different species.

Kuykendall et al. (1992) have provided excellent data on the variability of emergence times in chimpanzees and have demonstrated statistically-significant differences in the emergence times between some male and female teeth. Notably, this is not true for the permanent canines even though they differ most in size between the sexes, but the canine sample size is small. Kuykendall (1996) has in addition documented differences between sexes in some tooth mineralisation stages but, oddly in the light of the differences documented by Kuykendall et al. (1992), only those relating to the canine were statistically significant. With respect to the permanent canine, where Bonferoni tests show stage 6 (defined as the stage where the 'root length is equal to or greater than the crown height') to be statistically significant, the mean age attainment of this stage was 1.4 y different between males and females. Thus male canine crown and root formation time, judged at this stage, was prolonged with respect to females. Other stages of canine development also showed smaller, but less significant, differences between the sexes. This study is the first to clearly document biologically meaningful sex differences between developing mineralisation stages of male and female chimpanzee teeth in a large sample (n = 118) of known age. Despite this, and as noted earlier this review, Kuykendall (1996) also concluded that in absolute terms human and chim-

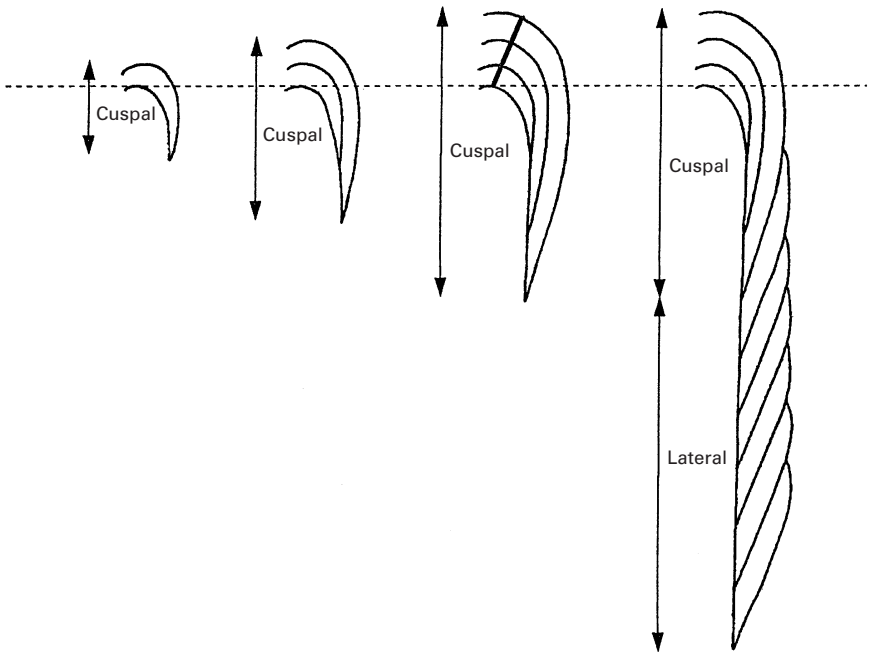

Fig. 10. Diagram of a series of longitudinal sections through the buccal aspect of a tooth germ at 4 stages of development. The dotted line is drawn through the dentine horns. Cuspal appositional enamel increases the thickness of enamel here and as a result the tooth germ grows in height above this line. Proliferation of ameloblasts at the cervical loop of the inner enamel epithelium also contribute to an increase in the cuspal height of the developing tooth below the dotted line. This proliferation of ameloblasts continues also in lateral enamel formation after cuspal enamel is complete. Long-period incremental markings are represented in the enamel and show how appositional enamel formation below the cuspal portion contributes only to thickness of the buccal enamel but not to the height of the growing tooth.

panzee canines take an equivalent time to form, but that relatively less of that time is devoted to root formation in the chimpanzee.

Given that sexual dimorphism is marked in great ape canines it is surprising that no radiographic, or other studies, have provided a clearer idea about how these differences in crown height developed. Histological studies suffer from being limited by the number of individuals it is possible to include in any one study (Kuykendall, 2000). They do however, provide a clearer picture of the processes involved in tooth growth and are able to define the sequence of developmental events between teeth in the same individual more precisely. A step forward in being able to process more material, and thereby include more individuals in comparative histological studies on tooth development, has been to develop reliable statistical models of cuspal growth that do not require the labour intensive methods relied on so far (Boyde, 1963, 1990; Dean, 1998*a*). Gradients of increasing rates of enamel secretion in hominoid tooth cusps clearly follow a curvilinear trajectory (Fig. 8). When the number of daily cross striations are counted for every 100 μm of cuspal enamel thickness in permanent canines, from the enamel dentine junction to the cusp surface, a plot of time in days against increasing enamel thickness reveals a well-defined growth curve. This curve is slightly different in each of the 3 modern great ape genera and different again in modern humans. The relationship of cusp thickness to time can be described by a polynomial regression equation (Fig. 9). In the case of 5 humans, for example, this is $y = -3.63 + 0.42x - 0.0008x^2$ ($R^2 = 0.992$). This demonstrates a very close relationship between time and cuspal thickness (as is also the case for modern great ape genera and other primates studied so far), and that it is quite feasible to make predictions about cuspal enamel formation time based on careful measurements of cuspal thickness at any stage of crown formation (Schwartz et al. 1999; Schwartz & Dean, 2000).

Cuspal enamel grows in height by enamel apposition but also by extension of newly-differentiated ameloblasts at the cervical loop. Increase in tooth height of lateral enamel is, however, by enamel extension at the cervical loop only. Even though lateral enamel matrix is secreted appositionally in the same way as cuspal enamel, growth is in a lateral direction only and so does not contribute to increase in tooth height. The cumulative sum of the increase in height of cuspal and lateral enamel, with respect to time reveals how canines growth in height (Fig. 10).

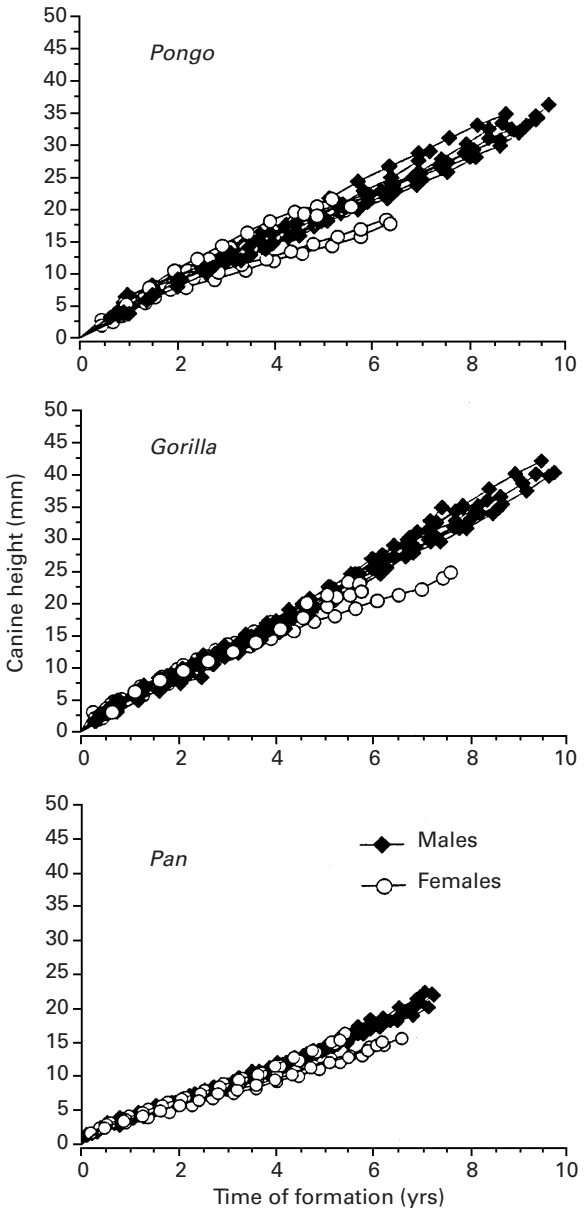

Fig. 11. A longitudinal record of increasing crown height has been retrieved from histological sections of *Pongo*, *Gorilla* and *Pan* canines of known sex. Plots of canine height for males and females over time reveals that males take longer to form taller crowns. This time difference is more marked in great apes where the degree of sexual dimorphism is greater than in *Pan* (after Schwartz et al. 1999; Schwartz & Dean, 2000).

Time in lateral enamel must be calibrated in some way from a knowledge of the periodicity of the long-period striae and this is easily done when good daily cross striations can be counted between adjacent striae and total counts of striae in a tooth made along the length of the crown. Figure 11 is a plot of growth in canine crown height for male and female great apes (after Schwartz et al. 1999; Schwartz & Dean, 2000). It is clear from this that male canines take longer to form than female canines. They achieve their greater heights primarily through time hypermorphosis (Shea, 1983). Mean crown formation times were 5.8 y in female chimpanzees and 6.8 y in male chimpanzees. Similar data for *Gorilla* and *Pongo* show the same clear pattern of males growing for longer than females with an average crown formation time 3 y, or so, in excess of females. Some male gorillas and orangs take close to 10 y to grow enamel on their canines, almost twice that of some females (Schwartz et al. 1999; Schwartz & Dean, 2000).

Some modern human canine crowns may take as long as 5 or 6 y to form enamel; none ever take as long as 9 or 10 y, and most are complete between 4 and 5 y. Given the substantial differences in crown completion times, why in male and female modern great apes, are there not clearer differences in the times of canine gingival emergence into the mouth (Conroy & Mahoney, 1991; Smith et al. 1994)? Do male canines emerge into the mouth with hardly any root formed, and do female canines emerge with considerably more root formed? Each of these questions still begs a satisfactory answer.

With some idea of how long it takes to form sexually dimorphic great ape canine crowns and of how this is achieved it is now reasonable to start to look for developmental information to help sort and sex samples of fossil ape teeth. Human canine crowns follow a different growth trajectory to chimpanzees. Even female gorilla and male chimpanzee canines that are roughly the same height can be distinguished by their growth curves (Schwartz & Dean, 2000). This raises several more questions. Is there a characteristic growth curve for a hominid canine crown that might better distinguish a hominid from a hominoid than the simple linear measurement of crown height? Indeed, are characters based on developmental processes more reliable than metric characters alone for phylogenetic analysis?

Out of these studies on sexual dimorphism come further questions. If male canine teeth are so much bigger than female canine teeth, and take so much longer to form, are the jaws of great apes proportionately bigger to accommodate them while they grow? It is also obvious from a cursory look at the fossil record that Neanderthal mandibles have a large amount of space in the retromolar area, distal to the third permanent molars, and that australopithecines in contrast commonly have third permanent molars that are virtually hidden behind the ascending ramus of the the mandible. What factors ensure that there is sufficient space in the jaws for the developing dentition?

Sequences of tooth formation and the relation of tooth growth to space available in the jaws

Early observations about the sequence of tooth emergence in australopithecines (Broom & Robinson, 1951) pointed to probable differences in the timing of incisor emergence as judged against emergence of the first permanent molar. As we have seen previously, it is not possible to document the sequence of gingival emergence in a fossil as soft tissues are not preserved, although alveolar emergence can be recorded and a probable order of the teeth that come into functional occlusion can be worked out. The problem is that comparative data from great apes and modern humans relates to gingival emergence, yet the fossil data comprise observations about wear, distance of a tooth above the alveolar crest, distance from the occlusal plane, and the amount of root formed on the tooth. The solution is to compare only the mineralisation stages of teeth in living and fossil taxa, but good comparative data of this kind have been lacking.

Subsequent studies of the sequences of tooth emergence (Dean, 1985*b*; Grine 1987; Conroy, 1988) supported the observations of Broom & Robinsion (1951), but they either confused information about mineralisation stages and tooth emergence in fossils or allocated gross patterns of incisor and molar mineralisation stages to an 'ape-like' or 'human-like' mode of development (Broom & Robinson, 1951; Dean, 1985*a*; Smith, 1986, 1994*a*; Conroy & Vannier, 1987, 1991*a*, *b*; Conroy & Kuykendall, 1995). It is now clear, especially since we know so much more about dental development in modern chimpanzees, that these gross categories are an inappropriate way of describing dental developmental sequences in fossils that may each have a unique sequence of dental development (Mann, 1975; Mann et al. 1990). Recently Moggi-Cecchi et al. (1998) have carefully documented the sequence of tooth mineralisation and emergence in a hominid fossil (Stw 151) from Sterkfontein, South Africa, whose development was neither obviously *Australopithecus*-like nor *Homo*-like.

These studies provide support for the hypothesis that the developing jaws may influence the timing and rate of tooth emergence. At the heart of this debate is the realisation that the space available in the jaws, while teeth are growing in them, may have some effect on both the time of initiation of tooth mineralisation and on the speed at which the various stages of tooth mineralisation are achieved. Obviously, a tooth that completes a crown more quickly may then be able to emerge into the mouth sooner, although the apparent link between earlier crown completion and earlier gingival emergence is a tenuous one, since a great deal may depend upon the rate of root growth and the length of the path over which a tooth must erupt. Dean & Beynon (1991*a*) drew attention to the contrasting anteriorly narrow 'V-shaped' mandibles of great apes and *Australopithecus* and the more rounded 'U-shaped' mandibles of *Paranthropus* and modern humans. Paradoxically, the mandibles with the least amount of space anteriorly contain the largest anterior teeth that appear to emerge into the mouth later in time; those mandibles that are wide anteriorly have smaller incisor teeth that apparently erupt relatively earlier. This apparent crowding (in a nonclinical sense) of larger teeth in great apes and *Australopithecus* and of comparative spaciousness of smaller teeth in *Paranthropus* and modern humans might underlie differences in the relative timing of tooth mineralisation stages. This in turn might be reflected in the timing or sequence of tooth emergence. With respect to the posterior dentition, it certainly seems that second and third permanent molar tooth germs may appear earlier in the jaws when there is more space available in the alveolar bone for them to grow. The contrasting sequences of molar initiation seen in australopithecines and Neanderthals may simply be a function of the space available in the jaws (Wolpoff, 1979; Dean et al. 1993*b*; Tompkins, 1996).

What we know of tooth embryology offers some support for this idea. Embryological theory holds that teeth in a series develop from a progress zone (specifically a molar series in the experiments that support this theory). The progenitor theory or clone theory was proposed by Osborn (1978). The cells of the progress zone are said to divide and proliferate distally while all the molar teeth develop. As the cells emerge distally from an area of inhibition surrounding the previously formed molar tooth, a new tooth bud appears from which the second and subsequently the third molar teeth develop. When a clone reaches a critical size, a tooth bud is initiated at its centre. A zone of inhibition is said to surround the tooth bud and the next tooth bud is not initiated until the progress zone of the clone has escaped its influence. Essentially the clone theory holds that the dental papilla might develop by division from different populations (clones) of mesenchymal cells. The molar clone would start first with dm1 or dm2, then M1, M2, and M3. Successive teeth in the series would involve more cell divisions leading to an accumulation of variability along the series.

If the hypothesis that proposes a zone of inhibition around each tooth germ is correct, then space

available in the jaws would be likely to influence the time at which a new tooth bud can initiate. An obvious problem with this idea is that it has been possible to grow a whole molar series of teeth within the confined space of the anterior chamber of the eye in experimental animals (Lumsden, 1987). This rather complicates the notion of an inhibitory zone that is space dependent, but not necessarily one where the zone of inhibition is extrinsic to the progress zone and not intrinsic to it, but rather defined by a some gene product, say, that inhibits further tooth bud formation and which may diffuse though the jaws in the sense that Butler (1939, 1956) envisaged.

The first cusp mineralises in *Pan* molars before the previous molar tooth has completed crown formation (Reid et al. 1998); the converse is true in *Papio* (Reid & Dirks, 1997). Only after the crown of the preceding molar tooth is complete does the next molar begin to mineralise its cusps. However, we do not know anything about the first appearance of the tooth crypts in the bone, as this is really the first stage of discernible tooth formation closest to the bud stage of development. There may be a false impression about when these teeth actually begin to form resulting from huge differences in the time it takes to form the mineralised phase of molar teeth in *Pan* and *Papio*. We need to look not only for the first mineralising stages of tooth formation but also for the earliest signs of crypt formation if we are to account for tooth formation sequences in terms of space available in the alveolar bone. The true space available in the jaws at the time the first suggestion of a crypt appears is equal to the ratio of space taken up by teeth and crypts, to the total length (or breadth or volume) of alveolar bone in the jaws at the time the observation is being made. *Pan* and *Papio* are both prognathic primates, but they have very different sized and shaped teeth and we do not know if there are any differences in 'space availability' as each tooth crypt begins to appear in each taxon. However, this hypothesis is testable and the aim of current studies is to try to shed more light on the relationship between space in the jaws and the sequence of dental developmental events in primates.

Perhaps the most fundametal question of all we can ask about fossil hominoids is 'what can dental development tell us about growth and maturation?' Much of the research reviewed up to this point has served to demonstrate how complex dental development is and how it is necessary to ask ever simpler questions in order to better understand the processes that underlie tooth development. In fact much of this research has been driven by bigger questions about the whole animal biology of hominoids and early hominids. It was the realisation that tooth histology could provide a timescale for measuring key developmental events in the lives of early hominids that provoked closer scrutiny of their enamel and dentine histology in the first place.

Life history in hominoids

Life history traits are a package of interrelated events and attributes that together reflect the reproductive effort an animal expends over a lifetime. They include the timing of key maturational events such as weaning, age at first reproduction, general reproductive strategy with respect to the number of offspring and longevity. They are essentially what every biologist wants to know about an organism in order to understand it fully. A host of variables that in some way reflect these traits correlate with each other tightly. Body size in particular and brian size as well as dental maturation have all been suggested as measures of life history strategy. The full spectrum of life history profiles extends from animals that develop, mature and reproduce rapidly and die young to others that develop over a long period of time, mature late, reproduce more slowly and live a very long time. It is now clear that adult mortality rates in particular play a key role in driving the evolution of life history profiles. While not to do with primates, a vivid illustration of this is the more than tenfold difference in life expectancy between the queens of eusocial insects, such as ants, termites and bees that are so well protected in nests, and those of adult solitary insects of identical body mass (Keller & Genoud, 1997).

Smith has championed the study of life history among primates and hominoids as pivotal for our attempts to understand the evolution of human growth and development (Smith, 1989, 1990, 1991*a*, *b*, 1992; Smith & Tompkins, 1995). Kelley (1997) has also drawn attention to the fact that major shifts in life history strategy exist between monkeys, apes and humans. These so-called grade shifts in life history strategy must have an evolutionary history, and Kelley (1997) has proposed that one way of enquiring about the ape-like or monkey-like nature of an extinct primate is to determine something of its life history strategy from examination of its fossil dental tissues. Excellent reviews of life history theory as it relates to primates and to hominoids in particular can be found in Smith & Tompkins (1995) and in Kelley (1997, 2000). Dental development and in particular the ability to put a timescale to key events during growth and development has been fundamental in being able

to say something about the biology of the whole organism. Without teeth, it is hard to see how we would ever have been able to know such things about fossil primates and hominoids in particular.

As noted previously, the first permanent molar is a good overall indicator of several life history variables in regression analyses that include large numbers of primate species. Importantly, Smith & Tompkins (1995) and Smith et al. (1995) have drawn attention to the fact that interspecific regressions are, nonetheless, often poor predictors of small subspecific differences. It would be dangerous to raise too many generalisations about life history parameters among early hominids based on what we know about general primate trends. For example, it is quite clear that robust australopithecines were weaned before they erupted M1 from the tooth wear present on deciduous molars at the time of M1 crown completion only (Aiello et al. 1991), even though age at weaning apparently correlates well with age at M1 emergence among primates (Smith, 1991*b*). We know also that first reproduction in macaques may occur while they are still growing their M3 roots for Bowman (1991) has observed parturition lines of known history in macaques, yet gibbons do not reproduce until well after third molar root development is complete. It follows there are many observations about life history that cannot be tightly predicted from a specific dental developmental event. Even skeletal development and epiphyseal fusion do not follow a common sequence with dental development across primates (Watts, 1985; Winkler, 1996). Nonetheless, a knowledge of dental development provides a broadly accurate maturational profile for fossil primates. Comparative work on the nature of longitudinal growth curves in primates points to important differences in the relative length of the early postnatal and later periods of development (Leigh & Park, 1998). It seems unlikely now that each may simply increase or decrease in proportion as the total length of the growth period changes and more probable that each may vary independently. Leigh & Park (1998) concluded that the prolonged human growth period results from an extension of the early postnatal years rather than the later years, and that this most likely relates to a pattern of neural development in humans that facilitates an extended plasticity in learning ability.

Kelley (1993, 1997, 2000) has concluded, on the basis of perikymata counts on a developing central incisor associated with a juvenile mandible, that the age of M1 emergence in the fossil ape *Sivapithecus parvada* (10 Mya) was within the ranges known for extant great apes. It follows that the modern chimpanzee to female gorilla sized *S. paravada* would have had a maturational profile that approached those of modern great apes. Kelley (1999, 2000) has also provided provisional developmental evidence for a similar modern ape-like maturational profile in *Afropithecus turkanensis* dated at 17 Mya (Leakey & Walker, 1997). This is important since with a male body weight estimate of 34 kg, close to that of modern female chimpanzees and near the middle of the *Proconsul nyanzae* size range estimates (Leakey & Walker, 1997) it appears to show clearer evidence of a modern great ape-like growth period than *P. nyanzae* does. However, the danger of this particular comparison lies in the quite different kinds of information we have, so far, about *Proconsul* and *Afropithecus*. On the one hand we have data for molar crown formation times in *P. nyanzae*, which were short compared with modern chimpanzees but know nothing about early root extension rates. We only know these were slow in the smaller *P. heseloni* individuals (that probably took only around 6 y to mature dentally) but do not yet know if this was also the case in *P. nyanzae*. On the other hand we have data derived from a permanent incisor tooth in *Afropithecus turkanensis* about the age of M1 emergence.

Kelley (1997) has cautiously suggested that the very first evidence for a more prolonged life history might be found in what is perhaps the earliest hominoid, *Proconsul heseloni* (10–11 kg), from Rusinga Island, Kenya, dated at around 18 Mya. Kelley (1997) estimated M1 emergence, from brain size estimates, at around 20–21 mo, which is at the upper end of the baboon range, but relatively long for an animal of this size (if it is indeed close to the species mean). Other estimates of M1 emergence times in *Procosnul heseloni* are not incompatible with this suggestion (Beynon et al. 1998), but beg the obvious question about how body size might influence the timing of dental development, something we still know very little about and which hinders the interpretation of much comparative data. Dirks has provided the first important evidence for dental development in gibbons (Dirks et al. 1995; Dirks, 1998) which may turn out to be a good test case for what to expect in a small bodied hominoid (the body mass of siamangs matches that estimated for *P. heseloni* closely) but as yet it is still not totally clear at what age M1 emerges either in gibbons or siamangs. It remains likely, however, that postcranial, masticatory and life history traits evolved in a mosaic fashion among the earliest hominoids (Rae, 1997). Of these traits it may be that those such as locomotor and masticatory adaptations (that relate directly to the advantages of a new ecological niche)

evolved first. A subsequent reduction in adult mortality rates may then have triggered an increase in brain size. It remains likely that a prolonged developmental period in primates is, at least in part, a requirement to grow a bigger brain (Dean, 1987*c*) even though a special contributary factor in modern humans may be extention of the fetal brain growth rate beyond birth (Martin, 1983). If this is true, then a prolonged period of growth and develpment may well have appeared alongside brain size enlargement, some while after the primary adaptive shift to a new ecological niche.

Developmental evidence from enamel and dentine in early fossil hominids comes from data for specimens dated between 3.7 Mya (*A. afarensis* at Laitoli) and 1.5–1.8 Mya (*P. robustus* at Swartkrans). These data suggest they may not have had maturational profiles as Zuckerman (1928), and others after him (Mann, 1975), imagined. The first evidence to suggest this came from a study of the surface perikymata visible with scanning electron microscopy on replicas of unworn anterior teeth (Bromage & Dean, 1985). Each perikyma is associated with a long-period stria within the enamel (the striae of Retzius) and total counts of perikymata, when there is no root formed on the tooth, together with small estimates for the time it takes to form cuspal enamel and the period between birth and initiation of the incisor teeth, allow one to make estimates of the age at death.

Early hominids with M1s close to, or just in, functional occlusion all appeared to be aged between 3 and 4 y using this technique (Bromage & Dean, 1985; Dean, 1987*b*). Another test of the hypothesis, that the earliest hominids had periods of dental development similar to modern great apes, has been to make a ground section of a canine tooth of a robust australopithecine where enamel formation had spanned almost the total period between birth and death. In the individual studied, death occurred when the M1s were worn in excess of a millimetre and functional occlusion was well established (Dean et al. 1993*b*). Daily incremental markings, cross striations, were counted to estimate an age at death for this individual. An age at death of close to 4 y was estimated which is totally compatible with an age of M1 emergence within the same range (broadly between 3 and 4 y) as occurs in modern great apes (Dean et al. 1993*b*). Further evidence for this conclusion was provided by Smith (1989), who used brain weight estimates to predict the age of emergence of M1 in early hominids and who also concluded for a second time (Smith, 1986, 1989) that all the available evidence points to an australopithecine life history profile that is most similar to modern great apes. Naturally, the big question still remains, 'when did the more prolonged modern human life history profile first evolve?' It remains something of a paradox at present that the earliest hominids appear to have had a period of dental development similar to modern great apes. At first sight these observations about life history and periods of dental maturation offer little support for the morphologically-based diagnoses of what a hominid (or even a hominoid) might be. However, data about body size and brain size and their effects on dental development are badly needed to help us to refine this view.

A view has recently been put forward that proposes only fossils with a growth period and with body proportions more like that seen in modern humans, and with a brain that is considerably expanded with respect to body mass, over and above that of great apes and australopithecines, should be included in the genus *Homo* (Wood & Collard, 1999). If relative brain size, and in particular the time required to grow a large brain, are anything to go by (Smith, 1989, 1990; Dean, 1987*c*) the first candidates worthy of the genus *Homo* in this view of things might well be fossils belonging to so-called archaic *Homo sapiens* (see Aiello & Dean, 1990, fig. 10.17). Smith (1993) and Smith & Tompkins (1995) have used an estimate of brain size in African *Homo erectus* (826 cc based on KNM-WT 15000) to predict an age of M1 gingival emergence of 4.5 y. This falls short of the modern human mean age of M1 gingival emergence by 1.5 y in the crucial childhood period that is supposedly especially prolonged in humans (Bogin, 1990; Leigh & Park, 1998). These authors also noted that a relative dental age estimate for this specimen based on modern human data is in conflict with other age estimates based on ossification status and on stature for this individual. Importantly, however, all 3 would be in near perfect agreement if judged against data for a chimpanzee aged 7 y. The large stature of this individual at this dental age would be more explicable on a chimpanzee schedule of development since a chimpanzee at this age has attained 88% of adult body weight whereas a human at 11 y has attained only 81% (Smith & Tompkins, 1995). These data warn us yet again that dental development, bone development and stature are not inextricably linked, just as growth curves are made up of components that can vary independently of each other (Leigh & Park, 1998). Indeed, Clegg & Aiello (1999) have recently demonstrated that in modern human children, where the age at death is known from good records, attempts to estimate age at death based on stature, dental

development and skeletal development give conflicting results. Clegg & Aiello (1999) point out, therefore, that such conflicting estimates as these are no basis for proposing a non-modern human pattern of growth for early African *Homo erectus*. We must therefore, be careful when we use dental developmental periods alone to make predictions about other physiological systems. Nonetheless, Smith & Tompkins (1995) conclude that the true chronological age of KNM WT 15000 was probably something in between 7–11 y and based on relative brain size and stature did not yet have a distinct modern human-like growth pattern. This conclusion of course would accord with the slim but nevertheless important evidence of fast dentine extension rates reported for premolars and second permanent molars in the juvenile early African *Homo erectus* specimen KNM ER 820 (Fig. 8). An obvious solution to this debate would be to carry out a histological analysis of certain key juvenile *Homo erectus* specimens and thereby determine their age at death based on incremental markings in enamel and dentine.

If early African *Homo erectus* was not fully modern human-like in its maturational pattern then what of archaic *Homo sapiens* and of the first anatomically modern *Homo sapiens*? Arsuaga et al. (1999) noted that fossils classified as ancestors to Neanderthals from Sima de los Huesos in the Sierra de Atapuerca, Spain and dated in excess of 200000 y ago probably had encephalisation quotients well below those for modern humans and Neanderthals. This was largely because of their estimated body weight range of 93.1–95.4 kg (absolute values of cranial capacity appear to have been within the modern human range). The mean value of several cranial capacities in these fossils is given as 1390 cc (Arsuaga et al. 1999). But if other hominid fossils dating between 100000 to 200000 y ago and attributed either to archaic or anatomically modern *Homo sapiens* (in the Middle East, Far East and Africa, for example) also had body weights and large cranial capacities well within the modern human range, then there is a real prospect that an absolutely large cranial capacity and an accompanying prolonged period of maturation already existed with the emergence of anatomically modern *Homo sapiens*, most probably in Africa. Older fossils from the TD6 level (Aurora stratum) of the Gran Dolina site in Sierra de Atapuerca, dated perhaps at 0.8 Mya, appear to have had both cranial capacities in excess of 1000 cc and a modern human sequence of dental development. Bermudez de Castro et al. (1999) have suggested on the basis of this that at least one species of *Homo* (*Homo antecessor*) shared a prolonged modern human-like period of maturation as early as 0.8 Mya.

There remains a possibility, which should not be overlooked, that a prolonged period of maturation developed more than once during hominid evolution and that Neanderthals and modern *Homo sapiens*, for example, evolved large brains and an extended growth period in parallel. After all, few would question the idea that brain size might itself might have increased in parallel during hominoid and hominid evolution. This possibility should raise a cautionary note for the way in which life history variables are incorporated into phylogenetic analyses.

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