Review

Retrieving chronological age from dental remains of early fossil hominins to reconstruct human growth in the past

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A chronology of dental development in *Pan troglodytes* is arguably the best available model with which to compare and contrast reconstructed dental chronologies of the earliest fossil hominins. Establishing a time scale for growth is a requirement for being able to make further comparative observations about timing and rate during both dento-skeletal growth and brain growth. The absolute timing of anterior tooth crown and root formation appears not to reflect the period of somatic growth. In contrast, the molar dentition best reflects changes to the total growth period. Earlier initiation of molar mineralization, shorter crown formation times, less root length formed at gingival emergence into functional occlusion are cumulatively expressed as earlier ages at molar eruption. Things that are similar in modern humans and *Pan*, such as the total length of time taken to form individual teeth, raise expectations that these would also have been the same in fossil hominins. The best evidence there is from the youngest fossil hominin specimens suggests a close resemblance to the model for *Pan* but also hints that *Gorilla* may be a better developmental model for some. A mosaic of great ape-like features currently best describes the timing of early hominin dental development.

Keywords: hominin evolution; dental development; incremental markings; tooth root growth; enamel; dentine

1. BACKGROUND

The lives of all living organisms can be divided into stages. This allows comparisons to be made between them. There are many reasons for studying the stage or period of growth in primates in a comparative context, which include identifying those ontogenetic changes shared by all primates and those that are unique to modern humans (Schultz 1937). Relative comparisons of the stages of skeletal or dental growth have proved to be a useful way of defining similarities and differences between both living and fossil primates. When chronological age is known, then the length of the phases of growth as well as the rates of growth of individuals can be compared. Dental development is just one measure of biological maturity, but is arguably the most stable, and it occurs over an unusually long period of time from before birth to maturity. Besides enabling us to discover things about the evolutionary history of our own growth period, studies of comparative dental development provide us with an opportunity for investigating the biological processes that govern tooth formation from the initial mineralization of teeth to the completion of their roots (Swindler 1985).

Smith (1989) has shown that certain key marker events during dental development actually correlate better with important variables that describe life-history variation than any of these life-history variables do with each other. Because of this, some tentative inferences can be made about the way fossil primates lived their lives compared with living primates that go beyond simple relative dento-skeletal comparisons. A powerful aspect of dental biology is that tooth tissues preserve an incremental record of their growth, which remains literally embodied within the microstructure of enamel and dentine. This offers an opportunity to reconstruct the period of maturation in fossil primates and compare them in real time with living primates. Even if it may never be possible to retrieve information about many life-history variables from the fossil record, it should be possible to reconstruct a time scale for growth in the past.

2. INCREMENTAL GROWTH OF ENAMEL AND DENTINE

The cells that form enamel and dentine (ameloblasts and odontoblasts) secrete their matrix in a rhythmic manner (Bromage 1991; Smith 2006; Bromage *et al.* 2009). A circadian rhythm in cell function is expressed as a daily slowing of secretion during enamel and dentine formation and is still manifest in the enamel and dentine microstructure of fully formed teeth as a

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Figure 1. Scanning electron micrograph showing perikymata on the upper lateral incisor of MLD 11 (*Au. africanus*) from Makapansgat, South Africa (a). Their spacing becomes closer towards the cervix. Two or three regions of enamel hypoplasia are evident indicating periods of slowed enamel growth during tooth formation. (b) Transmitted polarized light micrograph of enamel incremental markings seen in a longitudinal ground section of a probable second molar fragment (Ward *et al.* 2001) attributed to *Au. anamensis* (KNMER 30748) from Allia Bay, Kenya. Coarse oblique long period incremental markings (approx. 35 μm apart) run from bottom left to top right and emerge at the surface within perikymata troughs. Along prisms, that run left to right in this image, are short period daily increments marked by fine cross striations approximately 5 μm apart. In this specimen, there are seven daily increments between adjacent long period striae.

daily incremental marking (Boyde 1976, 1979, 1989, 1990a; Shinoda 1984). Thin sections of teeth prepared for histological analysis, or even polished or naturally fractured surfaces of fossil teeth that are suitable for examination with various kinds of microscopy (figure 1) can be used to reveal these markings in enamel and dentine (Boyde 1989, 1990b; Dean 2000, 2006; Lacruz *et al.* 2006, 2008). Counts of daily incremental markings in the teeth of individuals with known dates of birth and death match very closely with the number of days of life (Antoine *et al.* 2009). The daily increments of enamel secretion in great ape and fossil hominin teeth cumulate at a faster rate than they do in modern human tooth enamel (Dean *et al.* 2001). Enamel measuring 200 μm thick over the cusp of a great ape tooth, takes on average between 55 and 65 days to form, whereas in modern humans this takes 70–80 days (Dean *et al.* 2001; Dean 2009; Smith *et al.* 2006). Daily rates of dentine formation, however, are more similar in great apes and humans and take between 80 and 100 days to form 200 μm close to the root surface (Dean 2009, *in press*).

Another, but longer period rhythm, that also slows dental hard tissue formation in a regular way is superimposed upon this daily rhythm (figure 1). In modern humans this coarser more prominent marking usually occurs every 7, 8, 9 or 10 days with a modal value of 8 days (Smith *et al.* 2006). Long-period incremental markings are aligned along the original mineralizing tissue front in both enamel and dentine. The slope of these incremental markings, with respect to the

junction between enamel and dentine, provides a way of estimating past rates of differentiation of new secretory cells during tooth formation (Boyde 1963, 1964, 1990b; Shellis 1984; Dean 1985; Risnes 1986). The rate of increase in both tooth crown height and root height can be reconstructed by dividing increments of tooth crown length along the enamel dentine junction (EDJ), or cement dentine junction (CDJ) by the time intervals taken to form them (Boyde 1963; Risnes 1986; Dean 2006, 2009). In figure 2, consecutive 200 μm -thick increments of enamel and dentine have been used to plot increasing tooth height against time from the dentine horn to a point as close to completion of the root as possible (Dean 2009).

The number of daily increments between long-period markings appears always to be the same in each of the teeth of an individual but it varies between individuals. In large samples of individuals there are also outliers with a long-period rhythm of 6 or 11 or even perhaps 12 days. We now know that these long-period markings (first described by Anders Retzius (1837) and, therefore, also referred to as Retzius lines) occur in the enamel of other primates including early fossil hominins (figure 1). Of 29 australopithecids examined so far, 17 (59%) showed a mean periodicity of 7 days and of seven early *Homo* specimens examined so far, two had long-period lines 7 days apart, four were 8 days apart and one was 9 days apart (Lacruz *et al.* 2008). Fossil teeth, however, are precious and it is only rarely possible to employ partially destructive techniques to retrieve data about their growth. Nevertheless, long-period markings also create a furrow or trough on the external surface of permanent tooth enamel. These so-called perikymata (waves around the tooth) first defined by Preiswerk (1895) in ungulate enamel are well preserved on many early hominin teeth and they can be counted with scanning electron microscopy (figure 1) or even in oblique-reflected light. They can be used to estimate enamel formation times in fossil teeth since counts of perikymata are equivalent to counts of long-period striae within the tooth but their periodicity may not be known unless the internal structure of the enamel can be visualized.

3. CONSTRUCTING A COMPARATIVE MODEL FOR EARLY HOMININ MATURATION

Recent evidence about DNA sequence analysis and from molecular biology suggests that modern humans and chimpanzees are more closely related to each other than to any other living ape (Goodman *et al.* 1994; Ruvolo 1994; Bradley 2008). It is, therefore, not an unreasonable assumption that the last common ancestor of the *Pan–Homo* clade had a life history more like that of modern chimpanzees than modern humans (Robson & Wood 2008). It is nonetheless equally likely that among the species of early hominins there were many different life-history strategies that spanned what we know today about life history in modern orangutans, chimpanzees, bonobos and gorillas. One key question that we can then ask is whether there is any evidence among early hominins

Figure 2. Plots of M1, M2 and M3 formation time (years) against increasing tooth height (μm) along the mesiobuccal (protoconid) EDJ (red open circles), continued along the CDJ (open blue circles) for (a) *Pan troglodytes* and (b) modern human molars. The mean length (± 1 s.d.) of mesiobuccal root formed at gingival emergence in free-living *Pan* specimens given in Kelley *et al.* (2009), M1, 4.2 mm; M2, 5.2 mm; M3, 6.8 mm has been used to generate a likely range of root lengths (and thereby corresponding ages) where molars in *Pan* might have emerged into the mouth (yellow filled circles). Arrows denote the median ages of gingival emergence. The rates of crown and root growth, as well as the total tooth formation times in modern humans and *Pan*, are similar but earlier initiation times compress *Pan* molar development into approximately 12 years rather than approximately 18 years. Distance curves for a single *Gorilla* M1, a short M1 fragment of KNM-ER 30749 and a longer M2 fragment of KNM-ER 30748 (both attributed to *Au. anamensis*, Ward *et al.* 2001) are superimposed over the *Pan* M1 and M2 molars (filled black circles, crown; filled blue circles, root). Rates of root extension in *Gorilla* and *Au. anamensis* are faster than in *Pan*.

for a period of maturation that differs from that known today for modern chimpanzees. Another feasible question is whether there is evidence among the various species of early hominins for any differences between them in the timing of dental development that might point to the presence of different life-history strategies existing together during the first four million years of human evolution. If this were so it might point to interesting links with climate change or diet. To answer these questions requires a detailed knowledge of the chronology of dental development in modern great apes and an assessment of how early fossil hominins do or do not compare with this. Since this is realistically only presently possible for *Pan troglodytes*, it makes sense to try and construct a model that brings together everything that is known about the timing of dental development in *P. troglodytes* and use this to examine the timing of dental development in early hominins.

4. THE CHRONOLOGY OF DENTAL DEVELOPMENT IN *PAN TROGLODYTES*

Early studies of dental development in great apes were made on single individuals or on samples of animals brought to zoos or acquired for comparative skeletal collections (Keith 1899; Schultz 1924, 1935, 1940; Zuckerman 1928; Krogman 1930; Bennejeant 1940; Clements & Zuckerman 1953). Few of the living animals studied were actually born in captivity and so their chronological age was rarely known. While some early studies identified differences in the sequence of dental eruption between great apes and humans and also noted earlier ages for the eruption of certain teeth, others found no differences in the timing of dental development between great apes and

modern humans (Zuckerman 1928). In recent years many issues have been clarified through studies on samples of captive animals of known chronological age. Parallel histological studies of enamel and dentine growth in great apes have also helped to build a better picture of the chronology of dental development in a comparative context. What follows is a synthesis of those studies.¹

(a) *Permanent tooth eruption times in Pan*

In two classic longitudinal studies on chimpanzee dental emergence, Nissen & Riesen (1945, 1964) presented the first reliable data for ages of gingival emergence (eruption) in captive chimpanzees. They showed that the deciduous dentition was fully emerged into functional occlusion by approximately one year of age (Nissen & Riesen 1945) and that for eight males and seven females combined (Nissen & Riesen 1964), the mean ages of emergence for M1 were 3.3 years (range, 2.6–3.8); M2, 6.7 years (range, 5.6–7.8); and M3, 10.8 years (range, 9.0–13.6). All of these molar eruption ages are much earlier than those known for modern humans. Interestingly, however, the equivalent data for incisors and canines are indistinguishable from those known for modern humans. Mean gingival emergence ages for those teeth are, respectively, I1: 5.7 years (range, 4.5–7.0); I2: 6.4 years (range, 5.0–8.3); C: 9.0 years (range, 7.6–10.1). Kuykendall *et al.* (1992) in a study of 22 male and 36 female laboratory born and raised chimpanzees aged between 1 and 10 years observed median emergence times for permanent teeth that were rarely more than a month or two different from the data of Nissen & Riesen (1964). One exception was the permanent canine that in both the mandible and maxilla erupted a year earlier at approximately

8 years (range 6.5–8.7). Unfortunately, the age sample of Kuykendall *et al.* (1992) did not extend to individuals with emerging M3s, but the general consistency for dental emergence ages between these samples of laboratory-raised chimpanzees is remarkable. However, these data are not so closely reflected by those derived from a much smaller sample of free-living chimpanzees of known chronological age originally described by Zihlman *et al.* (2004) but subsequently revisited by Smith *et al.* (2009, 2010).

(b) Environmental effects on dental development in great apes

An important issue that is still not well understood is the effect on great ape dental development of being born and raised in captivity and perhaps more significantly, the effect of being nursed and raised by the mother in captivity or being hand-nursed and bottle-fed by humans. Zihlman *et al.* (2004, 2007) have presented a range of data for free-living chimpanzees that demonstrate a slower rate of behavioural, somatic and dental development than for captive animals. They place M1 emergence at approximately 4 years, M2 between 6 and 8 years, canine emergence between 10 and 11 years and M3 emergence at approximately 12.5 years. Smith *et al.* (2006) have also illustrated a wild-born chimpanzee aged 4.4 years (fig. 6 in Smith *et al.* 2006), where M1 is still far from functional occlusion. Phillips-Conroy & Jolly (1988) and Kahumbu & Ely (1991) also recorded later eruption times in free-living than in captive baboons. Even if the degree of difference is both population- and sample size-sensitive, some degree of difference is certainly real. Kelley *et al.* (2009) used the extrinsic staining on newly emerged cusps of molar teeth to indicate gingival emergence in wild-collected great ape skulls. In figure 2, the mean lengths for mesiobuccal roots (± 1 s.d.) measured at gingival emergence in that study are plotted individually onto each *Pan* molar root (M1, $n = 14$; M2, $n = 10$; M3, $n = 8$). The age ranges generated for these root lengths have been used to simulate a likely range and median age of attainment for gingival emergence in the predominantly wild-collected *Pan* specimens represented in figure 3. The results are a close match with those of Zihlman *et al.* (2004) for M1 and to some extent for M2 with simulated median age of attainment of M1 at approximately 4.0 years, M2 at approximately 7.0 years and M3 at approximately 10 years. Interestingly, they also fall close to the 32.6, 59.4 and 86 per cent of the total time to complete dental development that Swindler (1985) calculated for modern human molar eruption times, assuming that this total time is approximately 12 years in *P. troglodytes*. However, with the exception of M1, these simulated median ages of attainment for molar gingival emergence still fall within the ranges reported for captive chimpanzees. Kelley & Schwartz (2009) have drawn attention to the wide range of ages likely for gingival emergence in free-living great apes but Smith *et al.* (2010) have suggested that ages for gingival emergence may be influenced more by free-living or captive rearing than crown or root formation are.

Figure 3. Predicted median ages of attainment (50th percentile) for molar gingival emergence ages in *Pan* (M1, 4.1 years; M2, 6.9 years; M3, 10.1 years). These are derived from the times corresponding to root lengths formed at gingival emergence shown as yellow filled circles in figure 2. The interquartile age ranges (vertical lines) of attainment were simulated by using 1 s.d. of root formed at gingival emergence. The median values are represented by central vertical lines. A spread of initiation times over a lower age range, which in reality seems likely, would, reduce these estimates slightly.

What lies behind this difference is likely to be multifactorial but certainly to a large extent nutritional. Lippert (1977) showed that captive hand-reared infant apes double their birth weight by three months, whereas mother-nursed infants do not do so until six months. This difference persists until at least 21 months and probably continues as a trend into adulthood (Nissen & Riesen 1945; Fooden & Izor 1983). Nissen & Riesen (1945), Marzke *et al.* (1996) and Winkler *et al.* (1991) have all noted advanced deciduous tooth emergence ages between mother-nursed and formula-fed infant great apes. Marzke *et al.* (1996) specifically made the point that data from mother-nursed captive animals are likely to be more directly relevant to free-living conditions than data for hand-reared great apes. The available data for great ape dental development needs, therefore, to be considered carefully in this light if a model for dental development in fossil hominins is to be realistic.

(c) Tooth initiation times, sequences and overlaps

Swindler (1985), Anemone *et al.* (1991), Anemone & Watts (1992), Kuykendall (1996) and Reid *et al.* (1998) have all noted that the times for initial mineralization of the permanent incisors and canines in *Pan* are very similar to those described for humans (Kronfeld 1935) and that the sequence of mineralization is identical. Lower permanent incisors initiate at approximately 3–4 m after birth and canines at 4–5 m although both earlier and later times have been recorded (Kronfeld 1935; Anemone *et al.* 1991; Kuykendall 1996; Winkler 1996; Schwartz *et al.* 2006). Winkler (1995) demonstrated that direct observations of tooth germs can pick up earlier initiation

times than radiography as Hess *et al.* (1932) and Beynon *et al.* (1998) also observed. Reid *et al.* (1998) have nonetheless noted generally similar initiation times in *Pan* from histological studies for lower I1 (range, 1.8–5.6 m), lower I2 (range, 2.3–8.5 m) lower canines (range, 4.6–6.9 m) as well as for P3 and P4 initiation (range, 1.1–1.95 years) something also observed by Anemone *et al.* (1991) and Kuykendall (1996) to between 1.4 and 1.8 years in *Pan*.

Understanding the differences in dental development that exist between great apes that take approximately 12 years to grow up and modern humans that take approximately 18 years to grow up is fundamental to our being able to interpret juvenile fossil hominin material. It is molar development that reflects these somatic growth differences most closely. While the sequence of molar initiation is also always identical in great apes and humans (M1, M2, M3), the timing of molar initiation has been much debated. Molar formation is drawn out in modern humans between birth and approximately 18 years. Initiation of M1 around birth is followed by M2 initiation at approximately 3 years and M3 initiation at approximately 8 years with each molar then taking about 10 years to form.

Dean & Wood (1981) suggested that molar initiation times were compressed together in great apes (M1 close to birth, M2 at 2.5 years and M3 at 5 years) and that total molar formation times were shorter, with M3 root formation completing between 11 and 12 years. Certainly, studies of dissected M1 germs in great apes have usually, but not always, demonstrated three or four mineralizing cusps at birth (Oka & Kraus 1969; Tarrant & Swindler 1972; Moxham & Berkovitz 1974; Winkler 1996). Schwartz *et al.* (2006) have described an extreme case of M1 initiation in a captive hand-raised gorilla as early as 90 days before birth. However, Anemone *et al.* (1991) and Anemone (1995) in the first longitudinal radiographic studies of dental development in captive *P. troglodytes*, showed that for 16 individuals, the proposal of Dean & Wood (1981) for M2 and M3 initiation in *Pan* was incorrect. They demonstrated even earlier initiation times for M2 at 1.5 years and M3 at 3.5–4.0 years.

Subsequently, Kuykendall (1996) in an extensive cross-sectional radiographic study imaged stages of tooth formation in 118 captive chimps and reported even younger median ages of molar initiation: M2, 1.3 years (range, 1.15–1.48) and M3, 3.2 years (range, 3.0–4.6). Despite the supposed advantage of picking up initial mineralization of tooth germs earlier in histological studies, Reid *et al.* (1998) estimated M2 initiation in *Pan* at between 1.7 and 1.9 years and M3 initiation between 3.6 and 3.8 years. In figure 2, for consistency, and because for isolated teeth initiation times can never be known, histological estimates for molar initiation times have been used and fixed at the average age for molar tooth types estimated in Reid *et al.* (1998): M1, birth; M2, 1.75 years; M3, 3.69 years.

The issue of early molar initiation in great apes has become confused with observations about the degree of overlap in crown formation periods between sequential molars. Overlap of crown formation periods

has as much to do with how long or short the crown formation period of the earlier forming molar is as it has to do with the early or late initiation of the subsequent forming molar. Smith *et al.* (2006) noted the potential effect earlier or later molar initiation might have on eruption timing and highlighted the need to document the degree of molar overlap in free-living versus captive animals and in hand-reared versus mother-nursed animals. Indeed in figure 2, a spread of molar initiation times towards earlier ages would reduce the simulated estimates for median emergence times in figure 3. Winkler *et al.* (1996) studied a much larger originally free-living sample of 89 orangutans and concluded that sequential molars in orangutans had usually begun to mineralize by the time a previous molar had reached crown completion but that variability was too high to consistently predict that crown initiation had always commenced prior to crown completion of a preceding molar. Smith *et al.* (2006) in a histological study of *Pan* molars from the same individuals again noted variability in the degree of molar overlap but that more often than not this was considerable. The effects of captive rearing, therefore, cannot yet be resolved.

(d) Total tooth and root formation times

Kuykendall (1996) made the important observation that the overall duration of crown and root formation in chimpanzee permanent incisors and canines is comparable with that in modern humans. Some of the best summary data for mean age at entering a formation stage for modern humans (Liversidge 2009) places apex closure for mandibular I1 (8.04 years), I2 (8.69 years), canines (12.2 years) and M1 (9.38 years) at very close to the recorded ranges reported for *Pan* (Anemone *et al.* 1991; Anemone 1995; Kuykendall 1996). The median values and ranges of ages for root apex completion in *Pan* are: I1, 9.55 years (range, 7.99–10.75); I2, 9.69 years (range 8.35–10.75); C, approximately 12 years.

When initiation times are taken into account, total molar formation times in *Pan* appear to come close to those for modern human molars (approx. 10 years). Data for 30 observations of mean M1 apex closure (M1, 8.14 years, range 6.47–10.75 years) given in Kuykendall (1996) and data for M2 and M3 from Anemone *et al.* (1991) and Anemone (1995) also suggest overlap in total M2 and M3 formation times with modern humans (M2, 6.5–9.8 years; M3, 11–13 years). Kuykendall (1996), however, concluded that, unlike incisors and canines, total molar formation times in *Pan* were in fact slightly shorter than those known for modern humans but since no longitudinal studies exist with sufficient samples of older animals this remains speculative. Nevertheless, the wide range of ages reported for molar apex closure in great apes is noteworthy. Beynon *et al.* (1991) illustrated a gorilla with an open M1 apex at approximately 6 years with a little more root growth to come (see also the additional gorilla M1 in figure 2) and Schwartz *et al.* (2006) yet another gorilla at the same stage but aged only 3.2 years. These data suggest that total molar formation times in *Gorilla* may be shorter than

Figure 4. Anterior crown formation times in *Pan troglodytes*. Crown heights are divided into deciles and an average chronological age of attainment for each decile of height has been calculated from estimates of enamel formation time made from counts of daily cross striations and long period striae in longitudinal ground sections of teeth. (Data from Reid *et al.* 1998, 2000; Schwartz & Dean 2001; Schwartz *et al.* 2001.)

those reported for *Pan* but sample size and these data for captive animals may be misleading.

(e) *Crown formation times*

Perhaps, the most debated aspect of great ape dental development is the time taken to form enamel, or crown formation time. The reason for this is that it bears heavily on whether early fossil hominins can be judged 'ape-like' or 'human-like' with respect to this formation time. However, enamel formation time may be defined differently in radiographic studies and histological studies of tooth development (Beynon *et al.* 1998; Kuykendall 2001) and an added complication is that in histological studies, different enamel formation times are often estimated for each cusp of a molar tooth (Smith *et al.* 2006). For these reasons and others many comparisons of enamel formation times between modern humans and great apes have often been either unconvincing or incomparable (Kuykendall 2001).

With the exception of lower canines (Schwartz & Dean 2001; Schwartz *et al.* 2001), the data for anterior crown formation times in great apes is very poor. Figure 4 summarizes what is known for a few

specimens of *Pan* with data taken from Reid *et al.* (1998, 2000), Schwartz & Dean (2001) and Schwartz *et al.* (2001). However, the data for one or two specimens of *Gorilla* published by Beynon *et al.* (1991) and Schwartz *et al.* (2006) suggest crown formation times for incisors may sometimes be as short as 2.7 years suggesting that *Pan* may be atypical in this sense. Once again this raises the question of potentially advanced dental development in captive animals or perhaps of significant differences between *Pan* and *Gorilla* that are currently unappreciated and in addition, whether a *Pan*-like model for dental development is actually the most appropriate for early hominins.

Knowing something about anterior crown formation times allows us to link periodic linear hypoplastic banding patterns on anterior teeth that are common in many *Pan* and *Gorilla* specimens collected from locations in West Africa (Gabon, Cameroon) with two rainy seasons each year (Skinner & Hopwood 2003). Besides being generally under the weather in colder wetter conditions, chimpanzees in particular are more susceptible to increased intestinal parasite loads (Lilly *et al.* 2002) since damp soil and sporadic forest floor flooding present perfect conditions for eggs, protozoa and

Figure 5. Extension rates for the same sample of *Pan* M1s shown in figure 2. Rates are high in the cusps of the crown but then quickly fall to values between 4 and 8 $\mu\text{m d}^{-1}$ (see also Dean 2009). These data for 14 teeth are each aligned (arrow) around the mean age (3.8 years) of peak height velocity (PHV) for this sample, which displaces the initiation and completion of tooth formation to earlier or later ages but highlights the root spurt more clearly. The mean chronological age and range of ages at which PHV occurs during early root formation (3.01–4.65 years, s.d. 0.48) broadly mirrors those ages reported for gingival emergence in *Pan* M1s.

helminths to flourish. Seasonal fluctuations such as this increase the likelihood of individuals succumbing to any number of conditions that are known to underlie linear enamel hypoplasias (particularly prolonged bouts of diarrhoea or dysentery) and are a likely explanation for many wild-collected great ape permanent canines having, for example, 15 or so faint bands on canine crowns that took close to 7.5 years to form enamel.

The data presented in figure 2 for molar crown (protoconid) formation times in *Pan* are for slightly bigger sample sizes than previous studies (but comparable to those of Smith *et al.* 2006, 2010) although they are not based on counts or error-prone periodicities of long period incremental markings but only on counts of daily increments close to the EDJ: M1, 2.3 years (range 1.78–2.66); M2, 2.38 years (range 1.72–3.19); M3, 2.71 years (range 2.19–3.34). Mean values for modern human (protoconid) formation times (Reid & Dean 2005) are greater than these: M1 (3.1 years), M2 (3.2 years) and M3 (3.27 years) but there is overlap in the ranges (for example, see Reid & Dean 2005 and Mahoney 2008) such that an individual molar tooth could not always be attributed to *Pan* or *Homo* on the basis of molar crown formation time alone.

(f) Rates of root formation and the timing of gingival emergence

All hominoid teeth show a pattern of change in extension rate that is dominated by an initial high rate in the cusps of the crown but which then quickly reduces to a more constant rate in the lateral enamel (Dean 2009). The transition from cervical enamel formation to cervical root formation in hominoid teeth appears to occur without any abrupt change to the rate of growth in tooth length (figure 5). In many teeth, but

not all, the root extension rate then rises to a peak and falls off again. In very long tooth root, there may again be a rise in root extension rate towards apex completion. In the small sample of *Pan*, M1 mesiobuccal roots plotted in figure 5, the mean age at which this early peak in root extension rate occurs (3.8 years, range = 3.01–4.65 years, s.d. 0.48) is close to that reported for gingival emergence. While this apparent signature for gingival emergence is unlikely to be a simple epigenetic reflection of tooth movement through the bone, it is intuitive that root extension rates should begin to fall off at the time of initial functional occlusion. When the data for extension rates are aligned around this early mean peak height velocity (PHV) rather than plotted with respect to initiation at birth, this small rise in root extension rate is more easily seen and not smoothed out (figure 5). For this sample of *Pan* M1s, PHV is 8.7 $\mu\text{m d}^{-1}$ (range 6.1–10.2 $\mu\text{m d}^{-1}$). The expression of this peak in early root growth becomes weaker distally in M2s and M3s but is still there although it occurs later into root formation. PHV in this sample of M2s was 6.7 $\mu\text{m d}^{-1}$ and occurred at 4.7 years (range 3.4–6.4 years, s.d. 0.85) into tooth formation.

(g) Summary points about dental development in *P. troglodytes*

The sequence and times of initiation as well as total tooth formation times of incisors and canines are little different from modern humans. The ages of gingival emergence of incisors and canines are also little different. Anterior crown formation times (with the exception of male canines crowns which take longer to form) are only slightly longer than average modern human crown formation times. It is the initiation times and eruption times of the molar dentition in modern humans that are drawn out to later ages with prolongation of the growth period. The greatest shift in timing appears to be in eruption times, which can be observed both at later stages of root formation in modern humans as well as at later ages than in *Pan*. This is most marked in M3 that initiates approximately 4.5 years later in modern humans than in *Pan* and which erupts into functional occlusion approximately 8 years later at close to 18 years of age. Average total molar tooth formation times in *Pan* are shorter than those in modern humans, but it only seems by between one and two years, and while molar crown formation times are also shorter on average, this is only by six to nine months with overlapping ranges. It appears (figure 2) that there is little or no difference in the rate of growth in height of the molar crowns or roots between *Pan* and modern humans. Besides these comparisons of timing in tooth formation, it may well be that great ape teeth contain information about seasonality and perhaps even about their own eruptive history.

5. THE EVIDENCE FOR A CHRONOLOGY OF DENTAL DEVELOPMENT IN FOSSIL HOMININS

(a) Molar eruption times

Bromage & Dean (1985) estimated the age at death of four early hominin specimens with M1 just prior to or at functional occlusion (Sts 24, *Australopithecus*

africanus; LH 2, *Au. afarensis*; SK 62 and SK 63, *Paranthropus robustus*) to be 3.2–3.5 years on the basis of perikymata counts on lower permanent incisors. Subsequently, a histological study of SK 63 (Dean *et al.* 1993) placed gingival emergence nearer to 4 years. More recently, Lacruz *et al.* (2005) estimated M1 emergence into occlusion and age at death of the Taung child (*Au. africanus*) to be between 3.73 and 3.93 years on the basis of M1 enamel formation times and length of mesial root formed (5–6 mm: Conroy & Vannier 1991a,b).

The only evidence for the status of the developing dentition in *Australopithecus* of any species around the age of M2 eruption comes from scans and radiographs of MLD 2 and Stw 327, both of which are described as having M2s recently in functional occlusion (Skinner & Sperber 1982; Conroy & Vannier 1991a). While the M3 crypt of MLD 2 is only partially preserved, CT scans of Stw 327 show a completed M3 crown (Conroy & Vannier 1991a). Skinner & Sperber (1982) have drawn attention to the permanent canines of MLD 2, which are still deep in their crypts and that on CT scans (Conroy & Vannier 1991a) have less root length formed than crown length. However, no histological age estimates are possible for either of these specimens. But if the timing of canine root length formed could be shown to match that known for *Pan*, then the standards defined by Kuykendall (1996) would provide a median age estimate of 7.6 years for MLD 2 (range 6.10–8.75)—but this is speculative. This age range, however, spans the range of histological estimates for age at death of KNM-WT 15000 (attributed to *Homo erectus* at 1.5 Ma), where M2s were also just in functional occlusion and where the one preserved upper M3 crown was also just complete (Dean & Smith 2009).

(b) Molar initiation times

The approximately 3-year-old infant hominin dated to 3.3 Ma from Dikika, Ethiopia (Dik-1-1), and attributed to *Au. afarensis* had M1 crown complete with just 1.6 mm of mesiobuccal root formation (Alemseged *et al.* 2006). The occlusal surface of the M2 crown had already formed. This is clear evidence for early initiation of M2 and of overlap in molar enamel formation. KNM-ER 1477, a juvenile *P. boisei* mandible roughly the same chronological age, preserves the mesial portion of what may have been a well-formed M2 crypt. However, this is the only other potential evidence in any early hominin specimen that M2 may already have been mineralizing at the time of M1 crown completion. The mineralizing P4 in this specimen would be expected to match M2 but this cannot be known. A number of juvenile *P. boisei* or *P. robustus* specimens exist with M1 at or close to crown completion (Skinner & Sperber 1982; Dean 1987; Conroy & Vannier 1991b; Lacruz 2006). Relative to this stage of M1 formation several of the *P. robustus* specimens (SK 438, SK 64, SK 3978) appear to show delayed premolar formation when compared with the *P. boisei* specimens (KNM-ER 1477, KNM-ER 1820) and one explanation for this might be shorter M1 crown formation times in *P. robustus*.

Unlike *Pan* no evidence exists to show early initiation of M3 in fossil hominins. Stw 151, from the late Member 4 breccia deposit at Sterkfontein, is described as a specimen with a dentition ‘not fully distinct from that of *Au. africanus* but with a cranial morphology more derived in some characters’ (Moggi-Cecchi *et al.* 1998). While there is a small mandibular M3 crypt in Stw 151, it is still too small to have accommodated a mineralizing tooth germ, which must, therefore, have initiated after M2 crown completion. Another specimen (SK 63, attributed to *P. robustus*) contains M2 crowns that are not quite completed but at this stage, only incipient M3 crypt depressions in the root of the ascending mandibular rami are present. Certainly, M3 initiation could not have occurred prior to M2 crown completion in this specimen.

(c) Total tooth formation times

The evidence for total anterior tooth formation times in early hominins is lacking but what there is suggests little difference from *Pan*. Median ages for combined sexes in *Pan* for lower incisors at the same developmental stage (Kuykendall 1996) would estimate age at death of Stw 151 at 4.95 years (range 4.61–5.22). This is very close to the histological estimate of 5.2–5.3 years for this specimen (Moggi-Cecchi *et al.* 1998). There is then no evidence to suggest that the timing of root formation in this early hominin was different from that observed in *Pan*. Both standards for lower lateral incisors in modern humans (8.0 years, s.d. 0.99; Liversidge 2009) and *Pan* (8.04 years, inter-quartile range 7.66–8.86; Kuykendall 1996) also each give median age at death estimates that match histological estimates for the *H. erectus* youth from Nariokotome (7.6–8.8 years, Dean & Smith 2009). Again this suggests that there is no evidence for any change in total incisor tooth formation times in early hominins, but histological evidence for ages of hominin specimens with near completed canine roots are needed to show that this also holds true for canines.

Stw 151 is aged histologically to between 5.2 and 5.3 years at death (Moggi-Cecchi *et al.* 1998). It had M1s with one or more incomplete root apex at the time M2, premolar and canine crowns had just completed enamel formation. This age implies that root apex closure of M1 was at the earliest end of the age range reported for *Pan* and occurred close to M2 crown completion. The end of M2 crown completion in KNM-WT 15000 (*H. erectus*) was also estimated to have completed between 4.2 and 4.9 years on the basis of perikymata counts (Dean & Smith 2009).

Other early hominin specimens from Laetoli, LH 3 and LH 6 (attributed to *Au. afarensis*) consist only of isolated teeth (White 1977). However, in both specimens, the upper M1 is at a similar stage of root apex formation as Stw 151 and each have permanent canine and premolar crowns close to or just completed. Close correspondence of the canine crown perikymata counts (Stw 151 = 140 and LH 6 = 134) suggests that LH 6 was close in age with the same pattern of tooth formation and the same early age for

M1 root completion. No M2s are preserved for comparison in either of these specimens from Laetoli.

While speculative, a tooth fragment from Allia Bay, Kenya, attributed to *Au. anamensis* (KNM-ER 30748) may contain information about molar eruption in early hominins. It is plotted in figure 2 as an M2, since it has an enamel formation time (2.7 years) beyond the range of the *Pan* M1s sampled here (see also Ward *et al.* 2001). It contains a marked early root spurt of $9.8 \mu\text{m d}^{-1}$ at 4.2 years into tooth formation that is within the M2 range for *Pan* (3.44–6.38 years). If M2 initiation in *Au. anamensis* was close to 1.75 years, as in *Pan*, and if early root PHV actually reflects the eruptive process, then this would place functional occlusion of this tooth towards the lower end of the range reported for M2 in *Pan* (5.6–7.8 years) (Nissen & Riesen 1964).

A number of chronologically older hominin specimens exists with incomplete M3 roots. KNM-ER 1802 has a left M3 with just one wear facet on the protoconid and a *ca* 9 mm long mesial root impression in the alveolar bone for the right M3. Sts 52 (attributed to *Au. africanus*), OH5 and KNM-WT 17400 both attributed to *P. boisei*, are specimens closer to dental maturity but there is no histological evidence at all to estimate their chronological age, only a hint from periapical radiographs of the upper canine of OH5 that this root apex may have been recently completed by age at death (Skinner & Sperber 1982).

(d) Crown formation times

Perikymata counts on hominin incisors and canines, especially those attributed to *Paranthropus*, all point to anterior crown formation times having been shorter than those known for modern humans and for *Pan* (Dean *et al.* 1993, 2001; Dean & Reid 2001). One lower canine tooth attributed to *Au. africanus* (Sts 50) has 170 perikymata suggesting a crown formation time of around four years or more (Dean & Reid 2001) but in general the anterior teeth with the greatest crown formation times appear to be those of *Au. anamensis* and *Au. afarensis*. Here, canine enamel formation times come closest to those known for modern humans. Suwa *et al.* (2009a) counted 193 perikymata on the upper canine of ARA-VP-6/1 (the holotype of *Ardipithecus ramidus* and a probable male). This suggests that canine crown formation took between 4.3 and 4.8 years in this specimen (Suwa *et al.* 2009a) and so was potentially within the range recorded for female *Gorilla* and *Pongo*, but below the range so far recorded for female *Pan* canines (Schwartz & Dean 2001). The several clear regularly spaced hypoplastic bands illustrated on this specimen in Suwa *et al.* (2009b) are reminiscent of what are likely to be seasonally related cycles of poor growth on living great ape canines (Skinner & Hopwood 2003). If there were eight or nine such bands on ARA-VP-6/1 and on other *Ar. ramidus* canines, this would strongly suggest that *Ar. ramidus* existed in a seasonal environment with two colder wetter seasons per year.

At least seven juvenile specimens attributed to *P. boisei* (KNM-ER 1477, KNM-ER 812, KNM-ER 1820, OH 30) or *P. robustus* (KB 5223, SK 64,

SK 3978) have M1 at or close to crown completion (Skinner & Sperber 1982; Dean 1987; Conroy & Vannier 1991b; Lacruz 2006). Some have been aged on the basis of perikymata counts on anterior tooth germs at between 2.5 and 3.0 years of age at death (Dean 1987) but with some root formation. This fits well with a histologically derived estimate of 2.4 years for M1 crown formation time in SK 63 (*P. robustus*) from Swartkrans, South Africa (Dean *et al.* 1993). Lacruz & Ramirez Rozzi (2010) have made histological estimates of metaconid as well as total crown formation times of two *Au. afarensis* molar fragments (AL 333-52 and AL 336-1) at between 2.2 and 2.4 years. Beynon & Wood (1987) calculated a range of molar crown formation times of 2.12–2.59 years in *P. boisei*, while Ramirez Rozzi (1993, 1995) found ranges of 1.93–2.49 years for *P. aethiopicus* but a greater range for enamel formation times of *P. boisei* molars of all types (2.67–3.43 years). In *P. robustus* from Kromdraai, Lacruz (2006) calculated protoconid formation times at between 1.98 and 2.38 years and metaconid time to be near identical (1.92–2.37 years) but Lacruz *et al.* (2006) reported protocone formation times in two *Au. africanus* molars to be greater than this (M1, 2.74 years and M2, 3.0–3.2 years). These latter two crown formation times are very close to mean modern human values. In general, molar crown formation times in early hominins are less than those in modern humans and more similar to those of *Pan* but there is considerable overlap in the ranges and still insufficient data to compare sample mean values statistically.

(e) Summary points about dental development in early hominins

The cumulative rates of enamel formation follow a similar trajectory in both *Pan* and early hominins (irrespective of enamel thickness and crown formation times) that is faster than that in modern humans (Dean *et al.* 2001; Lacruz *et al.* 2008). Estimates for gingival emergence times for M1 in several early hominin specimens all fall within the range expected for *Pan*, and in fact are all earlier than the time proposed for free-born, free-living chimpanzees. There is, however, no direct evidence at all for ages of M2 and M3 eruption among the earliest hominins. The evidence for molar initiation times provides only one example (Dikika: Dik-1-1) where there is clear early M2 initiation with respect to M1 and there is no evidence at all for M3 initiation occurring prior to completion of M2 enamel formation in any early hominin specimen. Total molar tooth formation times have only been estimated in three hominin specimens, and appear to fall closest to the earlier ages known for *Pan*. In contrast, those of incisors appear similar to those observed in *Pan*. Anterior crown formation times are almost always consistently less than those known for *Pan* with the shortest crown formation times occurring in *Paranthropus*. Enamel (crown) formation times in molars are generally within the ranges known for *Pan* molars (but occasionally also fall well within modern human ranges).

6. DISCUSSION

Constructing a chronology for dental development in *P. troglodytes* as a comparative model for early hominins is useful for a number of reasons. First, it highlights the processes whereby dental development is likely to have kept pace with prolongation of the period of general growth during hominid evolution. These seem to be confined to the sequence of molar development and to have involved shifts in the timing of initial mineralization, slightly faster crown formation rates and particularly, earlier times of tooth emergence into functional occlusion. The cumulative effects of each of these are most fully expressed in molar emergence times, which appear to be the clearest measure of comparative development than any one of the components that contribute to it. Estimates of M1 emergence times in fossil hominins, as well as observations of early molar initiation, and in some cases shorter crown formation times, resemble *Pan* more closely than modern humans. However, too few specimens exist to provide clear evidence for early initiation or earlier gingival emergence times of M2 or M3 among australopith specimens, although the evidence for this is a little better in early *Homo* (Dean *et al.* 2001; Dean & Smith 2009). The model reveals, however, that the key indicators of a *Pan*-like dental maturation pattern would include early M3 initiation with respect to M2 crown formation time and a lesser proportion of root formed at gingival emergence in all molar tooth types than in modern humans.

A second point to emerge from the model for *Pan* is that some things appear to be little different between *Pan* and *Homo* and, it follows, might not be expected to differ in early hominins. Total anterior tooth formation times, and maybe also those for molars, fall within the same range, all be it a broad range. Few radiographic studies of molar development in *Pan* have included older animals and few of the individual plots in figure 2 extend all the way to root apex closure and moreover, it is the distobuccal root (not the mesio-buccal root shown in figure 2) in both *Pan* and *Gorilla* that on radiographs completes formation last (Dean & Wood 2003). It is highly likely, therefore, that future studies will show total molar formation times to be equal in *Pan* and *Homo*. In this respect, the evidence for at least three individual australopith specimens suggests that total M1 and M2 formation time may have been at the low end of the range reconstructed for *Pan*. The plot of M2 (figure 2) attributed to *Au. anamensis* (KNM-ER 30748) has a crown formation time at the upper limit of the M2 range for *Pan* (2.66 years) but a total tooth formation time of only 5.5 years (but with a little root still to form) and a faster rate of root formation generally than in *Pan* that might prove to be more typical of *Gorilla*. Shorter anterior crown formation times in many australopiths and earlier times for root completion might also turn out to fit a *Gorilla* model better than a *Pan* model. This mosaic of great ape-like dental development among australopiths is perhaps what one ought to expect given the gorilla-like anatomy of the scapula of Dikika, Dik-1-1 (Alemseged *et al.* 2006) and the gorilla-like mandibular morphology of *Au. afarensis* mandibles (Rak *et al.* 2007).

A third observation about the chronological model of dental development in *Pan* compared with that in early hominins is that anterior tooth growth does not appear to reflect general somatic growth. While total anterior tooth formation times appear to be little different, anterior crown formation times in australopiths are very variable but always shorter than in *Pan* (Dean & Reid 2001; Dean *et al.* 2001). In this respect, the comparative chronological model for anterior tooth crown formation times in *Pan* differs completely from that reconstructed for australopiths. Crown formation time does not relate in any simple way to crown height (Dean 2009) within a tooth type. For example, there is nothing to distinguish the enamel formation times of smaller *P. robustus* canines from taller canines of *H. erectus* (Dean *et al.* 1993, 2001). The fact that both enamel thickness and anterior tooth crown height, characters that can be broadly linked to dietary specialization, are not tightly linked to the time taken to form crowns is interesting. If in fact total anterior tooth formation times are relatively more stable than anterior tooth morphology appears to be, then perhaps crown formation times might be a better candidate for exploring phylogenetic relatedness among closely related species of early hominins than tooth morphology. An interesting case in point worth further consideration is the short time taken to form the reduced canine crown heights of *Ar. ramidus* (Suwa *et al.* 2009a).

All observations made so far on fossil and living apes and on early hominins indicate that M1 eruption times would have fallen within the simulated ranges for free-living *Pan* shown in figure 3 and none appear to fall within the ranges known for modern humans. Interestingly, all predictions so far for M1 emergence in fossil apes (Kelley 1997, 2002; Kelley & Smith 2003; Dean 2006) actually fall below the simulated median age of attainment for M1 emergence predicted in figure 3 as indeed do most estimates for early hominins. This raises questions about how different great ape dental development in the Late Miocene might have been to that known today for modern *P. troglodytes* and how good a model modern *Pan* is for comparisons with the earliest hominins. It also highlights the need to reconstruct a chronology for dental development in *Gorilla* to place that for *Pan* in a better modern comparative perspective. It remains a real possibility that the chronological dental development in the earliest hominins was more similar to that in modern *Gorilla* than to modern *Pan*. Were this the case it would raise very interesting issues about early hominin life-history strategies of the kind discussed by Kelley & Schwartz (2009). The issue of advanced dental maturity in captive hand-reared great apes suggests that even M1 emergence times of approximately 4.5 years predicted for *H. erectus* (Dean *et al.* 2001; Dean & Smith 2009) would still fall comfortably within the simulated range for wild-born chimpanzees (figure 3) as has been suggested by Zihlman *et al.* (2004) but predictions for M2 and M3 eruption of approximately 8 and approximately 14 years, respectively, in *H. erectus* would not.

No convincing evidence exists for any differences in the chronology of molar development and emergence

between early hominin taxa, but estimates of chronological age in specimens around 2.5 years and younger make it clear that tooth wear was excessive in some infant and juvenile late australopiths. Even thicker deciduous dental enamel was insufficient to compensate for this, resulting in extensive islands of dentine exposure on deciduous teeth very early in development (Aiello *et al.* 1991). Moggi-Cecchi *et al.* (2010) describe an infant *P. robustus* hemi-mandible from Drimolen (DNH-44) with an unworn erupting Rdm₂ where islands of dentine are exposed on the Rdc and on four out of five cusps of the Rdm₁, arguably within a year or so of birth. The obvious inference that some early hominin juveniles were taking considerable quantities of supplementary foods at a very early age cannot, at the moment, be extended to assuming they were also weaned early and that interbirth intervals were relatively short in these later australopiths, although this is one interpretation of those observations (Aiello *et al.* 1991; Dean 2006). Once again, there is the tantalizing suggestion that a *Gorilla*-like life-history model may be a better match for some, but not all, early hominins. Many life-history variables in *Gorilla* such as age at weaning (reviewed in Aiello *et al.* 1991) age at first reproduction and interbirth interval (Watts 1991; Robson & Wood 2008; Kelley & Schwartz 2009) are reported to be earlier than in *Pan* and *Pongo* (Wich *et al.* 2004). However, a firm link with these variables and earlier dental development remains illusive (Kelley & Schwartz 2009; Humphrey 2010). In the future, combined studies of tooth microstructure that put a chronological time scale to more sophisticated models of changing infant diets may shed more light on early life-history events such as these during the first four million years of human evolution (Humphrey *et al.* 2008; Humphrey 2010).

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ENDNOTE

¹For consistency and clarity, ages given in the literature are cited here as follows: Prenatal and postnatal ages up to 1 month are given in days, those between 1 month and 1 year in months and those greater than this in years.

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