Measures of maturation in early fossil hominins: Events at the first transition from australopiths to early *Homo*.

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An important question in palaeoanthropology is whether, among the australopiths and the first fossil hominins attributed to early *Homo,* there was a shift towards a more prolonged period of growth that can be distinguished from that of the living great apes and whether between the end of weaning and the beginning of puberty there was a slow period of growth as there is in modern humans. Evidence for the pace of growth in early fossil hominins comes from preserved tooth microstructure. A record of incremental growth in enamel and dentine persists that allows us to reconstruct tooth growth and compare key measures of dental maturation with modern humans and living great apes. Despite their diverse diets and way of life it is currently difficult to identify any clear differences in the timing of dental development among living great apes, australopiths and the earliest hominins attributed to the genus *Homo*. There is, however, limited evidence that some early hominins may have attained a greater proportion of their body mass and stature relatively earlier in the growth period than is typical of modern humans today.

Keywords: hominin evolution; life history; dental development; incremental markings; enamel; dentine.

How modern humans came to be what we are today is a question all anthropologists continue to ask, all be it in a variety of ways. A component question, but one that is focused enough to address in its own right, is why, when and where modern humans evolved a prolonged ~20 year growth period compared with the ~12 year growth period of living (and presumably fossil) great apes? This question is important if we want to explain the origins of the period and pattern of modern human growth because we assume that a general great ape-like period of growth would have most closely resembled that of the last common ancestor of all early hominins. However, modern human growth today is comprised of many complex events and processes and it seems unlikely all of these would have evolved together at one time. Schultz [1,2] wrote that the study of human evolution involves, among other things, investigating the processes that helped shape changes. To ask why, when and where the modern human growth period evolved requires that we think of ways to retrieve information about growth from the hominin fossil record as well as how we can access the processes that underlie change.

1. The biological basis of growing up slowly

In the end, explaining most things in biology comes down to food, sex and the environment. Explaining how the period of growth and the lifespan of organisms differ is no exception. There is great diversity in the way living great apes and modern humans grow and this is best interpreted as a reflection of habitat, food availability, diet and reproductive scheduling. In a general sense, the energy animals acquire from food is apportioned between growth, reproductive effort, movement, maintenance and repair but animals also save energy and store energy in different ways [3,4]. There can be advantages both to growing up quickly and slowly [4]. Growing up quickly increases the probability of reaching reproductive age and is favoured in a risk-filled environment [4-6]. When the risks of growing up are reduced, it can, however, be advantageous to grow up over a longer period of time if as a result fecundity is greater at a later age of first reproduction and if fertility overall is increased over a lifetime [4,7-10]. Two major driving forces play a key role in defining life history schedules, food availability and extrinsic mortality rates [4,5,11]. Given this general framework it then becomes possible to consider why early australopiths and or early *Homo* would or would not be expected to differ from living and fossil great apes in their period of growth. Without some explanation to account for reduced extrinsic mortality rates among australopiths and early *Homo* it is hard to argue that prolongation of the growth period could have been advantageous in any way.

(a) Why would early hominins have a prolonged period of growth?

Neither increased body size nor increased brain size necessarily depend upon a prolonged period of growth as the energetic costs of both could in theory be offset by a plentiful and/or rich food resource [12-17]. The modest increase in mean australopith brain size [18] compared with great apes of similar body mass might be explained almost entirely as the result of expansion and reorganisation of the cognitive and motor components of the brain involved with the planning and execution of tool making and tool use [19-25]. What sets this apart from other explanations for brain expansion that are concerned more with the increasing complexities of coping with larger social group sizes is that the latter take more time to learn to use. The expanding components of the brain concerned with social cognition, theory of mind and the so-called social brain [26-30] not only cost more to grow and maintain in energetic terms but also cost more in terms of time to learn to use them, and for the most part the crucial period of social learning happens during the period of growth [29,31] long before there is any pay-back through greater reproductive success during adulthood. Indeed without sufficient time to learn to use the larger brain components involved in enabling complex social interaction there would seem to be little advantage investing energy to grow and maintain them.

For whatever reason, fossil hominin specimens attributed to early *Homo* have larger brains than living great apes of similar body mass [32]. This begs an obvious question; did the general period of growth first show signs of prolongation at this early transitional stage of human evolution? If so, this has implications for *why* their brains were bigger. Or alternatively, were australopiths, early *Homo* and great apes, while clearly all very diverse in their body size and brain size, not actually significantly different from one another in their general period and/or pattern of growth? Given a *plentiful* food resource, something different to the *quality* of food as judged, for example, by percentage fibre or meat content [15], this alone would have been sufficient to account for the observed diversity in body size and brain size among the various australopith and early *Homo* species [14,15]. Moreover, new and novel ways of tool-enabled food acquisition [15] and of extra-oral food preparation would likely have added calorific value to food consumed in a given time [15,33].

There is, however, an alternative argument that would imply *all* early hominins might be expected to have had slightly longer periods of growth compared with what we know of living and fossil great apes. All early hominins show evidence of reduced canine size and canine dimorphism which implies greater male male tolerance, and hence perhaps fewer intra-species conflicts, so enabling larger social group size and promoting longer bouts of co-operative scavenging, gathering and foraging [17]. It can be argued that the combination of larger group sizes with increased body size might well have had a significant effect on extrinsic mortality rates among early hominins. Under these circumstances prolonging growth and spreading reproductive effort further into adulthood would have been an advantage. Then, investing, or redistributing, energy resources towards growing aspects of the brain involved primarily in maintaining social cohesion, collaboration and cooperation would pay off. So far, however, there is little hard evidence to support this alternative scenario [34,35]. But simply seeking to determine the period of dental and/or skeletal growth in early hominins may fall short of being able to resolve this issue. In many ways age at first reproduction is a better biological definition of adulthood than the end of tooth and/or bone development. One way forward for the future then is to look for evidence of age at first reproduction through parturition lines in the late forming teeth of early hominins [36] and so attempt to bring aspects of reproductive biology into context with the timing of dento-skeletal maturation [37]. However, until such time as this becomes feasible we still need to focus on maturational events that are more accessible in the hominin fossil record.

(b) What makes modern human growth different?

The number of maturational process that can be studied in the fossil record is currently limited but skeletal and dental development as well as occasional estimates of stature and body mass and of endocranial volume can be informative. It is important to recognise the great diversity in the way living great apes grow and to put the human pattern of growth into a bigger perspective.

Body mass attainment in male and female great apes is not only an important measure of maturation but also determines how adult sexual dimorphism arises [38]. Orangutan males appear to continue to grow well into adulthood far beyond the age that female growth slows markedly. *Pongo pygmaeus* males show apparently unlimited (or indeterminate) growth [38]. *Gorilla* males also continue to gain body mass for longer than females, however growth clearly ceases in both sexes but much earlier in female gorillas ~9.5 years compared with males ~12-15 years. Both sexes also show a spurt in weight attainment with females peaking considerably earlier ~5 years than males ~13 years [38]. Interestingly, the growth weight curves for *Pan paniscus* resemble those for *Gorilla* more closely than *Pan troglodytes*. Female adult body mass is attained ~8-10 years and males ~11-12 years with both sexes showing a spurt and then a peak in growth between 5-7 years [38]. In *Pan troglodytes*, female weight attainment is near complete ~11-12 years but with little evidence of a spurt in growth, while males in contrast show a marked spurt that peaks at ~8.5 years with growth completion at ~12-13 years. Gavan [39] showed that human children are heavier than *Pan troglodytes* at birth and adulthood but are smaller between the ages of 4 and 12 years. Willoughby [40] noted that gorillas do not show the same postnatal rate of weight attainment as humans and chimpanzees but gain weight more uniformly during the first few years. If it were possible to estimate body mass in infant fossil hominins, such as Dikika (Dik-1-1), the Taung child and, for example, Laetoli hominin 21 (LH 21) and others, for example, from Drimolen, South Africa, we would gain significant insights into their early life history biology. The clear message is that we should expect diversity in the way early fossil hominins grew and attained body mass and not assume that what we observe in one taxon necessarily applies to all.

The contrasting body proportions between humans and great apes make comparisons of stature, trunk height and limb growth difficult but recent studies and reviews of epiphyseal fusion in *Pan troglodytes* relative to dental development confirm earlier observations that mid to complete fusion of all skeletal elements is occurring by, or from, about 9.5 years of age [41-43] and in captive chimpanzees the last of the epiphyses to fuse, complete union of distal radius, was at 14.5 years. There are, however, reports [44] of later fusion ages in some free-living chimpanzees aged between 14.5 and 17 years of age. Hence Zihlman et al. [44] have made the important point that while M3 eruption reportedly occurs at ~12.5 years of age in free-living chimpanzees, proximal humeral head fusion occurs after M3 emergence, between 13.4 and 16.5 years of age. Clearly, different measures of maturation tell different stories and may well, in a comparative sense, be independent of one another to some degree.

The modern human pace and pattern of growth differs from other primate species. There are several components of modern human maturation that together define it as distinct [45-48]. One is the length of the growth period (~20 years) judged by the time body mass, stature and skeletal development (epiphyseal fusion) are all usually completed. But besides this Tanner [45] drew attention to the prolongation of time between weaning and puberty in modern humans and to the slow pace of attainment of both stature and body mass during this period. Human growth is also characterised by a marked spurt of growth in weight and stature at the beginning of adolescence and by the fact that these spurts occurs earlier on average in girls than in boys [46].

Traditionally, this overall pattern of human growth has been considered advantageous for learning, especially for learning the co-operative skills required for social life prior to an individual becoming sexually mature and coming into competition with others [45]. Equally important are the energetic savings for the individual and for the mother during the slow period of growth between weaning and puberty. Brain growth and maintenance are costly and, it has been argued, there is a tight inverse relationship between brain metabolism and body growth rate from infancy until puberty [49] so that staying small for longer offsets this cost. Staying small between weaning and the onset of puberty also reduces the energetic demands on mothers who are primarily responsible for providing food for all their infants and children [50]. Energy saved in this way is one of several factors that enable surprisingly short inter birth intervals in modern humans. What lies behind the early origins of the remarkably prolonged period of growth and the unique pattern of growth in modern humans must have been an event or accumulation of events with fundamental biological consequences for growth.

2. Measuring maturation in fossil hominins

Maturation is the process of progress towards maturity. Three classic maturational processes (skeletal, sexual and dental) that underpin human growth studies have been described using maturity events such as menarche, spermarche, voice change, peak height velocity and attainment of 95% mature height [51]. Individuals have their own 'maturational clocks' and 1 year of maturational time is not equivalent to 1 year of chronological time so that at a given chronological age there is variation in maturational, or biological, age. Even within different maturational systems there is 'uneven' progress of different marker events [52]. To be reliable, maturity indicators must occur regularly in all individuals of both sexes and should progress through well-defined and irreversible stages. They must also reflect real maturational change and not just variation in size [51]. Measuring maturation in anything other than a relative sense requires knowledge of, or some estimate of, chronological age.

The early hominin fossil record is spread thinly but it contains many teeth and developing dentitions as well as cranial and postcranial remains. This does, however, limit the maturational processes that can be studied. Until sufficient is known about the process and timescale of maturation in individual fossil hominin species we are limited to making comparisons with maturational standards available for modern humans and other primates. Even then, so little comparative data for dental and skeletal development exists for living great ape species a number of potential lines of enquiry are currently impossible.

Being able to estimate the age at death of immature individuals is fundamental to the study of maturation in fossil hominins. This has become possible in a few cases by studying the incremental structure of tooth enamel and dentine [53-56]. The evidence that growth markings in enamel and dentine have a daily periodicity [57-59] has recently strengthened with new studies documenting the control of enamel matrix protein secretion by various clock-genes [60-62]. The ages at death cited in this study and the ages for defined stages of tooth development used here have all previously been published [34,35,63-70] and are based on the daily incremental record preserved within fossil tooth enamel and dentine. The measures, or indicators, of maturation used in this study are limited to dental eruption, a few defined stages of dental development and to one or two estimates of stature and body mass in subadult fossil hominins. Estimates of ages of attainment of these stages are again based on the observed or estimated cumulative total of daily incremental markings in the teeth of the fossils studied.

(a) Dental eruption as a measure of maturity

Molar eruption ages have come to represent an important comparative measure of maturity in primate biology [3,56,71-77]. Gingival eruption data for molars exist for many primate species, and are relatively easy to collect compared with the stages of formation of teeth within the jaws that usually require radiographs or other imaging techniques to visualise them. Unfortunately, there are no secure estimates of age at eruption of M2 and M3 for any early fossil hominins but there are now several estimates for age at M1 eruption. Nonetheless, there are serious problems in interpreting these data. Tooth eruption is a process and not a specific event (and the gingival tissues through which teeth emerge do not fossilise). What we have for a few fossil specimens is a snap-shot of ages at death for specimens where M1 eruption is well underway or in many cases nearing completion [35,69]. There is also a general paucity of good comparative data for living great ape species. Data for *Gorilla* and *Pongo* are very sparse but data for *Pan* are better and improving.

An additional debate has focused on how appropriate comparative data for tooth eruption collected on captive animals are compared with data for free-living great apes. Smith & Boesch [78] have indicated that free-living chimpanzees might well erupt lower M1s on average at 3.6 or 3.75 years. Studies of captive chimpanzees, however, have reported M1 eruption at earlier ages between 32 and 45 months, mean 39.2 months, [78] and between 2.14 and 3.99 years, probit median, 3.05 and 3.24

years for left and right mandible respectively, [80,81]. Kelley & Schwartz [74], however, reported individual M1 eruption ages of 4.6 years in a free-living orangutan and of 3.8 years in a free-living gorilla. Overall, the known range of eruption ages for lower M1 in living great apes currently spans 2.14 to 4.6 years with a grand mean age close to 3.5 years. Figure 1 is a representation of that summary data for M1 eruption for living great apes alongside data recorded for 160 Japanese children who had dental impressions and casts taken at two-month intervals between 8 months and 12 years of age [82]. M1s in these children erupted between 4 and 8 years of age (2% of children erupted lower M1s in their 5th year and 2% in their 7th year) and the whole eruption process averaged 17 months (range 5-36 months). Machanda et al. [83], however, recently reported the duration of M1 eruption to be shorter than this in free-living chimpanzees, between 2-6 months, contra Zuckerman [84] who supposed it to take about 1 year.

Superimposed onto this summary data for living great apes and modern human M1 eruption are published data for six fossil hominins [34,5,63]. The general impression is that M1 eruption ages in fossil hominins fall within the range reported for living great apes but some also overlap with the most advanced of the modern humans. There is no question, however, that some of these fossils had passed the initial stage of M1 gingival eruption. Unfortunately, there are no data for M1 eruption in any early *Homo* specimens. However, there is no evidence that the pattern seen for M1 eruption in early australopiths (or early *Homo*) would necessarily have been the same for M2 and M3 eruption ages later on in the growth period. A tantalising age at death of 1.7 years for a specimen from Drimolen, South Africa (DNH 44) is also a reminder that the deciduous dentition may also tell a different story, Table 3 in Smith et al. [35] and Dean & Liversidge [70], than the data for permanent M1 eruption do. In this specimen dm_2 appears still to be erupting at 1.7 years of age, beyond the age range known for living great apes [80,81,85] but well within the modern human range for dm_2 eruption today [86].

(b) Dental development as a measure of maturity

Three specimens, two from Africa and one from Java, each attributed to early *Homo*, allow us first to ask whether their estimated chronological age at death, or at defined stages of dental development, would fall within or beyond the ranges observed in a large modern human sample of children today. Then for P4 crown completion we can compare their estimated ages for this stage of maturation with those known for modern humans and *Pan troglodytes* [87]. The first specimen is an adult but several precise past stages of tooth development have been retrieved from thin ground sections of two permanent teeth. The other two specimens are subadult and contain one or two developing teeth where the precise stages of formation can be aged. These stages are equivalent to the stages defined in dental radiographic studies of modern humans and chimpanzees [70,88].

The first specimen, Sangiran S7-37, is a right maxillary fragment attributed to *Homo erectus* containing an M^1 and P^4 from the Pucangan formation of the Sangiran Dome, Java, Indonesia, which may date to ~1 Mya. The second, StW 151, is a juvenile fossil hominin recovered in 1983 from a single solution pocket at Member 4, Sterkfontein, South Africa, dated to ~2 Mya. This has been considered on balance to be an early *Homo* specimen by Moggi-Cecchi et al. [65] and others. The third, KNM-WT 15000, is a near-complete 1.5 Mya partial skeleton of a sub-adult male *Homo erectus* recovered from Nariokotome, West Turkana, Kenya [89]. Something of the microstructure of the teeth of all these specimens is known and by using this it has been possible to estimate either how old they would have been at death (StW 151 and KNM WT 15000) or at what chronological age various clearly defined stages of tooth formation would have occurred (S7-37).

S7-37: Viewed in polarized transmitted light, two thin ground sections of M^1 and P^4 belonging to S7-37 show well-preserved enamel and dentine with daily incremental markings visible in both tissues. A birth line (or neonatal line) was not visible in the M^1 over the dentine horn in the first formed enamel but if it is assumed this tooth began to mineralise at birth then the enamel took 2.5 years to form (Fig. 2). At 4.6 years half the length of the root was formed and the whole length of the root was completed at 7.3 years. Within the M^1 root dentine at 3.3 years two strong hypoplastic or accentuated markings are visible and these can also be seen in the enamel of the P^4 allowing the growth of these two teeth to be linked and cross-matched in time. Enamel in the P^4 completed formation at 5.2 years, half the length of the root was formed at 8.0 years, three quarters at 9.4 years and root completion would have occurred at approximately 10.7 years of age. Unfortunately, no M3 exists in this specimen that would have allowed the age at dental maturity (M3 root completion) to be tracked beyond the age at P^4 root completion but it would have likely been 3 or 4 years more.

Liversidge and colleagues have now published several large data-bases of chronological ages of children with teeth at many fractional stages of development [70,90-95]. These dental radiographic data are especially valuable because they include many populations worldwide. Moreover, the very broad age range of children studied ensures the very earliest and latest ages that a stage of tooth development first appears is recorded. Figure 3 show the distribution of ages of children, drawn from a large sample of 6,540 children worldwide, at stages of crown completion (Cc), root a quarter (R1/4) and root three quarters complete (R3/4) as defined by Moorrees et al. [96]. Superimposed onto these distributions for modern human M1 and P4 are the age estimates for identical stages of tooth development in S7-37. For all stages the age estimates for the *Homo erectus* fossil fall within the known human age distribution but among the more advanced modern human children.

StW 151: This specimen died with the enamel crowns of the P4 and M2 just completed and with the crypt for the M_3 just starting to develop in the jaw. Moggi-Cecchi et al. [65] used counts of surface enamel growth increments (perikymata) on the lower right permanent canine of StW 151 together with estimates of the hidden cuspal enamel formation within this tooth to provide a range of ages at death, preferring a final estimate of 5.2-5.3 years of age. Since this time remarkable advances in imaging techniques using non-destructive synchrotron 3D virtual histology have made it possible to visualise and quantify rates of enamel formation in many fossil hominin specimens. Three such synchrotron studies have provided new data for StW 151 [35,68,69] that now makes it an invaluable specimen. Two of these studies estimated the age at death to be between 4.63 and 4.7 years of age but used estimates for the hidden cuspal enamel formation time of the canine derived from observed daily enamel increments in the cusp of a lower M3 attributed to another early *Homo* specimen, KNM ER 1802, [97]. Subsequently, it has been possible to refine this estimate with actual measurements made on the cuspal enamel of the lower canine of StW 151 itself [69]. This potentially adds 148 to 166 days to the estimated age at death. Nonetheless, many of the original calculations of Moggi-Cecchi et al. [65] appear to have been cautious over-estimates such that now the best estimate for age at death in this specimen hovers just below rather than just above 5 years of age. Figure 4 shows StW 151 superimposed on a modern human sample for age at M2 crown completion. While the probability that a child of 4.75 years less would be sampled from this distribution is low (*P*=0.01) it does not fall beyond the observed range, all be it among the most advanced children today. The same is true for the stage of M_3 crypt formation (Fig. 4) that is just visible in StW 151, although among modern human children first appearance of M3 crypt at 4.75 years would be considered unusually advanced if not exceptional.

KNM-WT 15000: At the time of death, the upper right M3 crown of this specimen was ¾ completed and the roots of the M2 approximately half their final estimated fully-grown length (~20 mm). Other stages of dental development (the ages at P4 and M2 crown completion) have been estimated previously [67] using what is known of the internal and external enamel microstructure of this specimen. KNM-WT 15000 has a naturally fractured lower central incisor crown. Scanning electron micrographs (SEMs) of this fractured surface show the angle the internal striae of Retzius within the enamel make to the surface enamel as they crop out at perikymata, see Fig 8.8 in [98]. New SEMs of the same fractured surfaces clearly show enamel prisms with daily incremental markings (alternating varicosities and constrictions) along their length (Fig. 5). These measure on average 4.8-5.2 µm apart and match similar measurements in other early *Homo* specimens in the same relative position within the enamel crown [97]. In addition the angle these prisms make to the enamel surface can be measured such that using two angles, a given prism length and the daily rate of enamel secretion, the number of days between adjacent striae of Retzius (the periodicity) can be calculated. This estimate varies between 8.8-9.3 days in several such calculations made from these SEMs and rounds to 9 days – since periodicities are only ever observed to be whole numbers of days. However, the periodicity has not actually been observed directly in this specimen and it may well be more or less than 9 days (a range of 8-10 days [67] is easily possible). But using a 9 day periodicity and estimates for hidden cuspal enamel in the upper canine tooth (0.57-0.88 years) and a generous time interval between birth and the initial mineralisation of the canine (0.25-0.75 years) the crown completion of the canine can be estimated as having occurred at ~3.95 years (range 3.7-4.2 years using 8-10 day periodicity).

Two hypoplastic markings on the canine crown at the end of enamel formation that represent episodes of slowed growth can also be seen on the P4 and M2 crowns just prior to enamel completion. There are an additional 25 perikymata beyond these two hypoplastic markings in both P4 and M2 to crown completion so this would have occurred at ~4.6 years of age (range 4.2-4.9 years using 8-10 day periodicity). Estimating the age at death of KNM-WT 15000 also involves adding to this to the additional time taken to form 9-10 mm of M2 root formation. At present the best way to estimate this time is to use existing histological data for the same tooth root growth in modern humans and chimpanzees where the rates are very similar, 6.5-7.5 µm/day or 3.4-3.9 years [99]. Adding this M2 root formation time gives 8.0-8.5 years for the age at death (range 7.6-8.8 years using an 8-10 day periodicity). In S7-37 half the P4 root length (6 mm in this case) was also estimated to have completed at 8 years but the average root extension rate was a little slower (5.9 µm/day) in this shorter rooted tooth than in KNM-WT 15000.

Figure 4 shows the distribution of ages for a large sample of modern human children at the stages of M2 root half formed (R1/2) and M3 crown three quarters formed (C3/4) with an age at death of 8 years superimposed to represent KNM-WT 15000. As with the two previous specimens of early *Homo* this individual falls within the known range of ages for children observed at these stages today but among the most advanced of the sample. The lower estimates for age at death of KNM-WT 15000 teeter on the brink of being beyond expectations for any large modern sample of children today, however, the older age estimates fall easily within the modern range. To quantify this Dean and Liversidge [70] calculated that for M2 stage Root ½ the probability of sampling a modern child from this sample would be *P*=0.05 aged 8.51 years and *P*=0.01 at 7.7 years of age.

When the distribution of ages for P4 crown completion in modern humans are compared with the limited data available for chimpanzees of known age [87] the ranges clearly overlap (Fig. 6). Superimposing equivalent data for just these three early *Homo* specimens and a further four australopiths that are close to but not all precisely at this stage (Smith et al. 2015) shows they each fall comfortably within the range reported for *Pan* but are also in some cases among the most advanced modern humans. These data for stages of tooth formation in fossil hominins appear to support the general finding that gingival eruption ages are a better discriminator of differences between great apes and modern humans than are the ages at defined stages of tooth formation. But importantly, all later dental maturational events, both eruption and tooth formation stages, are likely to be far better discriminators than these earlier occurring events [70] and it is these kind of data that are lacking for early hominins.

(c) Body mass and stature as a measure of maturity

Body size is central to the adaptive strategy of all animals [100,101] and putting a time scale to growth allows us to ask how body size and stature were attained during growth in early hominins. Within modern humans different body systems attain adult size in different ways during growth [45] and where good enough data exist it is clear that even different components of the skeleton vary in their proportion of adult size attained during growth [102]. The very nature of the fossil record limits what can be said about body mass and stature as measures of maturity but estimates of age at death of fossil hominins hold the key to understanding how and when the pattern of somatic growth shifted away from something resembling that in living great apes today [38] and towards what we now recognise as a modern human pattern of growth [45-48,103].

Body mass and stature estimates for fossil specimens attributed to *Homo erectus* have been cited as approximately 25% greater than those of australopiths [100,104,105] and the body proportions of *Homo erectus* appear to resemble those of modern humans. This has perhaps led to the expectation that prolongation of the growth period together with a pattern of growth, less like that in australopiths and more like that in modern humans, is something that might have first appeared in the genus *Homo* [106]. However, body mass and stature in other early *Homo* species are hard to estimate and there are now specimens of *Homo erectus* that are smaller

[107,108] suggesting that early *H. erectus* was also unusually variable in both body size and brain size [109].

Smith [103] first pointed out that skeletal age in KNM-WT 15000, based on human standards for epiphyseal fusion of the distal humerus, was advanced relative to dental age and that it was possible a greater proportion of adult stature and body mass had been attained in this individual than is typical for modern human children with erupting M2s today. The stature of this individual has been estimated [110-112] to have been 159 cm (± 7) and the body mass 49.2 kg (±10).

Besides KNM-WT 15000 there are now other fossil hominins with postcranial remains at broadly the same maturational stage of dental development. At Dmanisi, Georgia, postcranial remains (including 2 humeri, D2715, D2680, and a femoral shaft fragment, D3160) are associated with a subadult skull D2700 / D2735. The M3 root is described as 30% formed and so slightly older but still comparable in age to KNM-WT 15000. Based on the associated postcrania of D 2700 / D2735, stature was estimated [107] at 153 cm (95% CI=145-161 cm) and body mass at 41 kg (95% CI=40.0-42.5 kg). This specimen and three further adult *Homo erectus* specimens have yielded overall estimates for adult stature and body mass of between 145-166 cm and 40-50 kg [107] and so less than but overlapping with those from East Africa, which appear to be especially large [101,113]. Fossil hominins attributed to *Homo antecessor* from the Gran Dolina-TD6 at Atapuerca, Spain, also have adult stature estimates between 168-173 cm [114,115] that overlap with individuals from Koobi Fora <1.7 Myr [101] but are greater than the average adult stature estimates (145-166 cm) from Dmanisi [101]. The Gran Dolina-TD6 *Homo antecessor* fossils are particularly interesting because they show perhaps the earliest evidence of a modern human-like pace and pattern of dental development, evidently not linked to a trend in body mass or stature increase [116].

The adolescent specimen from Malapa Cave, South Africa, (MH1) attributed to *Australopithecus sediba* and dated to between 1.78 and 1.95 Mya again shows a pattern of dental maturation and humeral epiphyseal fusion that suggests its age at death was 12-13 years by human standards [117]. Interestingly, in this sense, it yet again compares well to the Nariokotome boy, KNM-WT 15000, from West Turkana, Kenya [103] and also to the adolescent, D2700 / D2735, from Dmanisi, Georgia [107] and indeed in its dental development to the type specimen of *Homo habilis*, OH7, from Olduvai Gorge, Tanzania [32]. However, MH1, while australopith-like in size, is reported already to have had a bigger skeleton and mandible than another presumed adult female specimen, MH2, from Malapa [117].

Unfortunately, there are no published estimates of body mass, stature or age at death for MH1. Neither is there a published chronological age at death estimate for the Dmanisi adolescent specimen but it seems reasonable to assume, given the histological data now available for StW 151, S7-37 and KNM-WT 15000, that each of these was aged somewhere within the broad chronological age-span of 7-10 years at death. Figure 7 illustrates the heights and weights of a sample of 438 children aged 7-10 years of age from Sudan [118] alongside the estimates for KNM-WT 15000 and the Dmanisi adolescent. Both fossil *Homo* specimens exceed the heights and weights of the modern children aged 7-10 years who do not achieve such average values in this population until they are 14 or more years of age [88].

3. Conclusions

In this study the fossils available for study and the data obtained from them are not identical for australopiths and early *Homo* species but what data there are fail to demonstrate that the timing of dental development in early fossil hominins differed significantly from what we know of dental development in living great apes today. Neither do these data identify any obvious differences between australopiths and early *Homo,* although these may well exist but simply not resolve well with the age range of the fossils available for study. Part of the problem lies not with the lack of evidence available in the fossil record but with the lack of information about dental development and general growth in living great apes species. Wood [119] has previously observed that we should redouble our efforts to ensure that we understand the living before we try and interpret the dead.

A pattern appears to exist where both within and between developing dentitions the estimated ages for clearly definable tooth formation stages of three early *Homo* specimens fall within the distributions known for modern human children but consistently among the most advanced individuals. As yet, no reliable ages for M1 eruption exist for any early *Homo* specimens but those estimated for australopiths appear to fall comfortably within the range now reported for living great apes. Future studies of later erupting permanent molar teeth (M2 and M3) and of earlier erupting deciduous molars (dm1 and dm2) may improve our understanding of dental eruption as a measure of maturation among hominins.

The evidence overall from the developing dentition is that any prolongation of growth in early hominin species is difficult to demonstrate. However, two subadult partial skeletons attributed to *Homo erectus* appear to have estimates for body mass and stature that exceed expectations for modern children aged 7-10 years of age. One explanation for this (and perhaps the best) is that, as in some living great apes, there was no marked period of slow growth between the end of weaning and the beginning of puberty as there is in modern humans. A greater proportion of adult body mass and stature may have been achieved relatively earlier in the growth period in early fossil hominins than is now typical of modern humans. However, if the earliest fossil hominins actually *did* turn out to have patterns of body mass and stature attainment identical to modern humans today (even within a shorter overall period of growth) then we should expect adolescent female fossil hominins of equivalent chronological age to the Turkana boy from West Turkana, Kenya, (KNM-WT 15000) and to the adolescent male from Malapa Cave, South Africa, (MH1), to be larger at this age than the males, as adolescent girls are, on average, than boys today [45,46].

Studies of age estimation in fossil hominins allow us to tease apart changes that have occurred in some of the processes underlying dental development. Potentially, they should also allow us to identify shifts in the timing of skeletal development and in body mass and stature attainment that have occurred with respect to the chronology of dental development. The challenge for now is to be aware that dental development and skeletal development are not in lock-step with each other or with any other maturation processes so there is no reason to believe all early hominins would have expressed the same combinations of skeletal and dental timing during growth. A challenge for the future will be to extract information about age at first reproduction and more about the early nursing history of hominins from the chronological record of tooth growth [36,120-122]. Superimposing aspects of reproductive biology onto the chronological record of dento-skeletal development would throw new light on the question of how, when and where modern humans came to be what we are today. Considering the progress made in the last 10 years the prospects for what will become possible in the future are bright.

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Figure 1 – (page-set ~1.5 columns wide, – centred or even within one column)
Representation of the known ranges of mandibular M1 eruption ages in living great apes and modern humans. Various estimates of M1 eruption ages (which are for the most part towards the end of this process) for six australopiths are represented as vertical dotted lines.

Figure 2– (page-set across ~2 columns wide)
Ground sections of M^1 and P^4 in Sangiran S7-37 annotated with the ages for various fractions of crown and root formation estimated from incremental markings in the enamel and dentine. Matching patterns in regions of hypoplasia (higher power insets) in the M^1 root and P^4 crown allow dental development to be tracked from one tooth to the other from birth to ~10.6 years of age.

Figure 3 – (page-set across ~2 columns wide)
Density curves for three stages each, of M^1 and P^4 in Sangiran, S7-37 (Crown complete, Root ½ and Root complete). Bold vertical lines indicate the age at entering these stages estimated from histology in M^1 and P^4 of S7-37. Shaded light and dark areas indicate *P* values of 0.05 and 0.01 respectively in the modern human distributions.

Figure 4– (page-set across ~2 columns wide)
Density curves for two tooth formation stages each, in StW 151 (M2 Crown complete and M3 Crypt) and KNM-WT 15000 (M2 Root ½ and M3 Crown ¾). Bold vertical lines indicate the age at entering these stages estimated from histology in StW 151 (left) and KNM-WT 15000 (right). Shaded light and dark areas indicate *P* values of 0.05 and 0.01 respectively in the modern human M2 distribution.

Figure 5 – (page-set ~1.5 columns wide, – centred or even within one column)

Scanning electron micrograph of a portion of naturally fractured enamel surface of the lower right central incisor of KNM-WT 15000. Various groups of alternating daily varicosities and constrictions are indicated with arrows. Prisms approach the enamel surface in this location at close to 90 degrees.

Figure 6– (page-set across ~2 columns wide)
Density curves for P4 crown completion in *Pan troglodytes* [87] and modern humans [70; Table 2]. The histologically derived data for StW 151, KNM-WT 15000 and S7-37 are indicated with solid vertical lines (respectively from left to right). Other australopiths close to this stage, observations from Smith et al. [35], are indicated with dotted vertical lines.

Figure 7– (page-set across ~2 columns wide)
Body mass (kg) and stature (cm) for 438 Sudanese children aged between 7.0 and 10.0 years of age [118]. The vertical lines and arrows for KNM-WT 15000 (paler solid and broken lines to the right) represent estimates of the mean, upper and lower 95% confidence limits for body mass based on bi-iliac breadth, and stature (49.2 kg, ±10 kg) and stature (159 cm ± 7 cm) [111]; and for the Dmanisi subadult (darker solid and broken lines to the left) the mean, and 95% confidence limits for body mass (41.2 kg, 47.6-50 kg) and stature (153.1 kg, 144.9-166.2 kg) based on humerus and femur dimensions [107].