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Paleoneurological Studies in Honor of Ralph L. Holloway
Douglas Broadfield, Michael Yuan, Kathy Schick and Nicholas Toth, editors

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THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies
in Honor of Ralph L. Holloway



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FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway.

Upper left: A modern human brain.

Upper right: Ralph measuring landmarks on an endocast ca. 1976.

Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).

Lower left: Ralph with an endocast of the Flores "hobbit" cranium.

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CHAPTER 15

DENTAL MATURATION, MIDDLE CHILDHOOD AND THE PATTERN OF GROWTH AND DEVELOPMENT IN EARLIER HOMININS

JANET MONGE AND ALAN MANN

The direction of research outlined in this paper owes a great deal to the life-long research and publications of Ralph Holloway. His amassing and interpretation of large comparative data sets of hominin and hominid brain endocasts have provided science with a normative basis for the collection and analysis of many other human biological complexes, including the dentition. In this research, he moved into uncharted areas: not only to identify those unique aspects of the brain that developed in our lineage, but also to employ knowledge gleaned from studies in brain research to integrate these morphological changes with behavior. As with dental development studies, diverse data sets need to be synthesized in order to fully understand the nature of “humanness”. For all his contributions to our understanding of the evolution of the human neurological system and the emergence of human cognition, our discipline is deeply in his debt; we are very pleased to have this paper included in a volume honoring Professor Holloway.

ABSTRACT

Recent research indicates that human dental development and eruption are much more variable than had been previously thought. Data collected on wild chimpanzees shows their eruption patterns are significantly retarded in comparison to that of captive animals. These data imply that considerable caution must be exercised in using modern dental standards to reconstruct growth and development in extinct hominins. There is, however, one aspect of human development that may have significant implications for our understanding of the emergence of human cognition. Between the eruption of the initial permanent teeth, the two incisors and first

molar, there is a time of about three years, from about seven to ten years of age, when no teeth erupt. This time, termed the ‘Quiescent period’ is followed by the eruption of the two premolars, canine and second molar. The Quiescent period in dental maturation appears to be coincident with the developmental age known as middle childhood, a time when a youngster’s ability to utilize the cultural norms of its society emerges. Examination of the dentition of immature fossil hominin specimens, including australopithecines and members of *Homo*, reveals the presence of the Quiescent period, whereas dental development in chimpanzees lacks this time. Using the models of neurological reorganization, especially of the inferior parietal cortex, described by Holloway in a series of publications, it is suggested that middle childhood evolved very early in hominin evolution, perhaps prompted by the need for enhanced foraging abilities in seasonally variable mosaic environments.

VARIATION IN HUMAN DENTAL DEVELOPMENT

Over the last twenty years, a number of original research projects dealing with aspects of human dental growth and development have been published (see, for example Thompson et al., 2003; Bogin, 1999; Minugh-Purvis and McNamara, 2002; Hawkes and Paine, 2006; Robson and Wood, 2008). These have vastly increased our knowledge of many parts of dental development that were not known before this. For example, by the beginning of 2009, over 200 genes had been identified that are expressed during the complex processes involved in tooth development (De Coster et al., 2009). Considering the potential complexity and interactions of these gene

pathways, including possible cascading effects of each, it is no wonder that variation occurs at both the histologic and developmental levels. For example, on the microstructural level, Smith and Tafforeau (2008) summarized recent research and concluded that human variation in dental histologic development is substantial. Finally, in this context, Liversidge (2003 and 2008) reviewed developmental dental studies primarily employing x-rays, emphasizing the degree of developmental variation that exists in living *Homo sapiens*.

One of the major problems with these studies is that it is difficult or impossible to resolve or integrate the results of these analyses to each other. Further, it is troublesome to assign recognized variations to the level of the individual, population, sub-species, or species. While it does appear that a certain amount of variation is patterned, given the limitations inherent in each data set, it is not currently possible to determine at which level these patterns are significant.

In order to move beyond the purely descriptive or comparative nature of studies it is necessary to more precisely focus on those specific features that identify the dental development correlates of the period of prolonged growth and maturation that has often been described as a unique characteristic of our species (see, for example, Bogin 1999). There are several sources of data for this analysis including dental development in wild chimpanzees (Zihlman et al., 2004) and the much larger data sets produced in the last decade on human dental development (summarized in Liversidge, 2003). After delineating the possible species specific pattern of maturation as displayed in the dentition, we apply the very same identifiers to a sample of extinct fossil hominin forms.

Finally, we attempt to understand the human dental development pattern in terms of unique aspects of human behavior and biology. Assuming that dental development is tied to other aspects of growth and development, not only can differences in dental development be tied to issues of population or taxonomic distinctiveness, but to fundamental growth trajectory changes that perhaps are associated with lineages.

This work is informed by the life-long research of Ralph Holloway. He set the bar in the collection and interpretation of large comparative data sets on human brain evolution. In this research, he moved into uncharted areas: to identify unique aspects of the brain in our lineage, but more importantly, to the translation of these morphological changes to behavior as associated with state of the knowledge in brain research. As with dental development studies, very diverse types of data need to be synthesized in order to fully understand the nature of “humanness”.

DENTAL DEVELOPMENT - THE STATE OF IT ALL

An overview of studies on dental development must include a discussion of both histological dental develop-

ment as well as measures of developmental chronologic events usually performed with imaging techniques (x-ray or CT analyses) or, on a less refined level, using dental eruption timing. In all but a few cases (see, for example, Kuykendall, 2003 and Skinner and Wood, 2006), most studies ultimately direct discussion of the overarching issues concerning growth and development to comparison within the confines of each data set. It has become increasingly difficult to bring these sometimes conflicting data sets into a kind of synchrony in the evaluation of both living *Homo sapiens* and species of the common chimpanzee, for which we have the most complete information. Adding more complexity, are the resolution of issues surrounding dental growth and development of fossil hominins. A full review of the literature is not necessary to highlight some of the emerging difficulties in the application of these methods to living and extinct forms.

It has become increasingly clear that histological studies of enamel formation in modern humans indicate that there is substantial variation in all detailed parameters (cuspal, cervical enamel, enamel extension rates and periodicity) associated with enamel formation. The recent expansion of histological findings on the composition and structure of Neandertal molar enamel highlights some of the interpretive difficulties. In a discussion of the enamel thickness and histology on the fossil from Lakonis, Greece, Smith and colleagues (2009) summarize the information accumulated from several studies undertaken on Neandertal enamel. In some aspects of molar and incisor enamel histology including projections to enamel formation timing, Neandertals appear to overlap the known modern human range. In other aspects, this fossil form appears unique (summarized in Guatelli-Steinberg, 2009). The question becomes: what, if any of these differences, are significant in projections to growth and development patterning? For example, does the conclusion based on microstructure that Neandertals formed molar enamel in something like 100 days shorter (approximately 3 months) than a limited sample of modern humans, have any meaning in the extrapolation to life history variables? Are these representations of population or taxon differences? Certainly some of these differences are a reflection of enamel thickness, cusp morphology, and even crown height (Dean, 2000).

As critically and importantly, certain enigmas emerge as these histological studies move away from description to extrapolations of time frames of dental development. Some of these problems could certainly be resolved with more information on root formation timing since a much larger proportion of overall dental development depends on this portion of the tooth. For example, Beynon et al. (1998) completed a study of incisor histology in the chimpanzee in relation to the timing of development. These authors concluded that in the genus *Pan* incisor enamel is formed in 4.5 to 5.6 years. Since chimpanzees, based on radiographic studies, erupt the incisors at just under 6 years, and with what appears

to be approximately 3 years of root formation (root 3/4th complete), it is hard to reconcile these two pieces of data. While it is true that radiography is notoriously variable in its ability to resolve fine details of tooth mineralization, it is difficult to imagine how a radiograph could both underestimate crown formation times by half while at the same time overestimating root formation by a magnitude of well over double. This same inconsistency, resulting from histologic versus radiographic data for the molar teeth (Reid et al., 1998) which led to a re-evaluation of histologic methods to bring crown formation times more into line with radiographic studies (Smith et al., 2007).

In the end, the power of growth and development studies depends increasingly on an understanding of the developmental timing of individual teeth in conjunction with the order and time frame of initial enamel differentiation. The relative order of dental development still relies entirely on radiographs with comparative standards based on a broad range of populations and species. While the time frame of development of individual teeth can be obtained from radiographic data on dental development of children, it can be used in conjunction with histologically derived time frames. Based on multiple studies of histologically derived time frames, it seems clear that there is a remarkable amount of overlap in the time frame of molar development among hominoids including many extinct hominin species (summarized in Kuykendall, 2003). In addition, this synchrony of results appears to well match the data derived from radiographic analyses. It is probably fair to say that hominoids appear to develop molar tooth crowns in approximately 2 to 3 years (not including the M3 with longer crown formation times). The differences in incisor formation appears broader (Smith and Tafforeau, 2008).

As interpretive and methodological problems exist in histological studies, so too do difficulties arise in the extraction of data from radiographs (cross sectional and mixed longitudinal) of the developing dentition of both modern humans and other primates. Many of these problems are outlined in (Liversidge, 2003 and 2006) and include:

- methods used to score the individual teeth
- variation in the x-ray equipment and ability to judge relative opacity or translucency of regions of the teeth
- statistical methods used to analyze the data.

Based on the population sample including sample size and methodological variation in assessment presented in the literature, it is almost impossible to compare studies to each other.

In her critical assessment of the literature, Liversidge (2008) does report on population-based differences as a well documented phenomenon in the crown and root formation timing of the M3, the only tooth in the radiographic sequence that can be fully evaluated from crown initiation to apex closure. She concludes that the population-based differences may result differences in the

architecture of the face including the mandible between populations, an aspect of dental development explored earlier by Simpson et al. (1990) on fossil hominin forms. De Coster et al. (2009), in a similar way, speculate that some of the differences observed in dental development in modern human samples especially in reference to the permanent premolar sequence may be a consequence of more effective preventive dentistry and the longer retention of healthy deciduous molars. Finally, Liversidge (2008) argues that dental development is minimally influenced by environmental factors and under strong genetic control in comparison to other growth and development systems.

These complex data sets, from histologic and radiographic analyses of the developing dentition, have together forced a newer synthesis of dental development and to ask the question: What do we know about dental development in living *Homo sapiens* and in the common chimpanzee? Can this be applied to fossil forms and what are the limits and limitations?

SYNTHESIS OF DENTAL DEVELOPMENT DATA

It is likely that lengthened molar crown formation times, in the range of 2.5 to 3 years, is the primitive condition for all hominoids. These assumptions appear to be supported by both histologic and radiographic studies and appears to be the case for Miocene fossil hominoids (Keeley, 2002). This appears to be confirmed from the limited histologic studies on australopithecine molar crown formation time (summarized in Kuykendall, 2003).

In addition, it is reasonable to infer that increase in crown formation time occurs in the sequence from M1 to M3 (Dean, 2000) except perhaps in the genus *Pan* where crown formation time in the M3 appears to decrease from CFT in the M2 (Smith et al., 2007).

What remains are the discussions of the time frames of full dental development since by all measures, virtually all of these analyses attempt to resolve issues of unique features of either individual tooth growth (which may be applied to issues of taxonomy or taxonomic affinity) or unique features in total patterns of growth and development. Newer data sets on the developing dentition in both humans (for example, Monge et al., 2007; Nadler, 1998; and Rousset et al., 2003) and wild chimpanzees (Zihlman et al., 2004) and have blurred the chronologic age differences representing distinctive growth and development patterns between these two living forms. Thus, the question may be raised: are there growth and development differences in the dentition that can uniquely identify unique patterns in humans and chimpanzees? And can these be applied to the fossil record of human evolution?

We previously published information on a large data set derived from US populations living within the city confines of Philadelphia (preliminary details of this

	<i>WILD CHIMPANZEES</i>	<i>CAPTIVE CHIMPANZEES</i> 10–90% range
dC	</– 1.5	0.8–1.4
M1	4.1 (2.6 < x </– 4.9)	2.7–4.1
I1	6.3–8.4 (5.7 < x </– 10.2)	4.7–6.5
I2	7.4–8.6 (6.5 < x </– 10.2)	5.3–6.9
M2	8.2–8.4 (8.2 x </– 10.2)	5.3–7.3
C	10.1–10.8 (8.5 < x </– 14.2)	7.9
M3	12.4 (10.8 < x </– 14.2)	10.5

Table 1. All information on wild chimpanzees is from Zihlman et. al. (2004). For a further summary of data on captive chimpanzees, see Kuykendall et al. (1992). For the most part, wild chimpanzees appear to show a delayed pattern of dental maturation over their captive counterparts. In some cases, wild animal emergence timing is outside the maximum limit of the recorded range of emergence in captive animals. Clearly environmental factors have an influence on dental development both in humans and non-human primates.

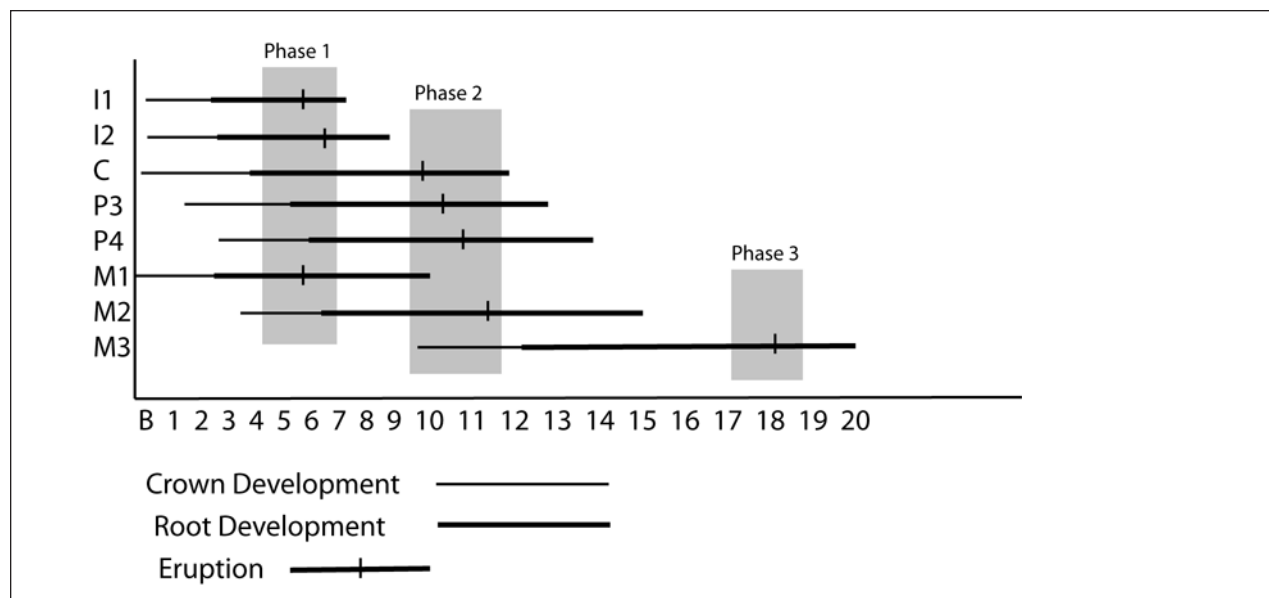


Figure 1. The three major Phases of human dental emergence. Tanner and Eveleth outlined three Phases based on the eruptive cycles of the human dentition. Phase 1 includes the Is and M1s; Phase 2, the Cs, Ps, and M2s. In Phase 3, the most varied in eruptive times, includes only the M3s, standing alone and thus marking the end of dental maturation. On the other hand, chimpanzees (both captive and wild born and raised) have no distinct phases of dental emergence and presumed calcification. In fact, based on the work in sequence polymorphisms by Conroy and Mahoney (1991), what clearly are Phase 1 teeth in humans, mix in with eruption of Phase 2 teeth in the genus *Pan*. (See TABLE 2 for sequence polymorphisms from Conroy and Mahoney 1991.)

study are published in Monge et al., 2007). This data set, along with internal comparisons of the European-American and African-American subsamples, appear to suggest that there is a trend towards reduction in the chronological time frames associated with M1 and M2 development (Blankenstein et al., 1990; Harris and McKee, 1990; Liversidge et al., 1999; Liversidge and Speechly, 2001; Olze et al., 2004). Thus, this data set appears to reflect 2 distinct patterns:

1. there are significant population differences in the chronology of dental developmental events, and 2. there

appears to be a significant reduction overall in the time frame of dental development since the original dental standards were established (Liversidge, 2008 and Nadler, 1998; for a comprehensive listing of dental calcification and emergence studies, see Liversidge, 2003). Others (for example Rousset et al., 2003; many studies summarized in Liversidge, 2003) have also noted this developmental timing shift but the bulk of this data centers on eruption rather than calcification staging of the dentition.

Similarly, dental development schedules derived from radiographs, show variation between 2 captive

common chimpanzee groups (Kuykendall, 1996 and 2002; in comparison to Anemone et al., 1991 and 1996). More remarkably are derived data on chimpanzee dental eruption showing clear and significant differences between captive and wild animals (Nissen and Riesen, 1964 in conjunction with eruption schedules from Kuykendall et al., 1992 in comparison to Zihlman et al., 2004) (Table 1). This captive/wild distinction has also been demonstrated in baboons (Kahumbu and Eley, 1991 and Phillips-Conroy and Jolly, 1988).

Within the context of human growth and development and life history studies (Hawkes and Paine, 2006), research in many fields, including psychology, anthropology and auxology, have focussed on an understanding of unique features of humans. One such developmental hallmark of humanness appears to be in the much speculated upon frame termed middle childhood (often times labelled as the “juvenile” phase). Eveleth and Tanner (1990) not only described this phase of childhood but in their analyses of dental growth and development proposed that one unique feature of the human dentition, occurring in concert with other developmental changes, is the disjuncting of early dental events (including the calcification of the I1s, I2s, and M1s) from a secondary phase of the developing dentition (including the calcification of the Ps and M2s) (Figure 1). This developmental gap may manifest in the human dentition either by a delay in the initial calcification of the second phase teeth or by a slowing down of dentogenic processes (either in enamel or dentin formation or both). This developmental gap in Phase 1 versus Phase 2 teeth is visible in virtually every population studied and is reproduced in one such visual representation in Figure 2. Given the proposed reduction in chronologic years based on recent human dental development standards, in conjunction with the expansion of chronological years of wild chimpanzee dental development, we asked the question: Does this reduction in human dental developmental years serve to blur the distinction between Phase 1 and Phase 2 teeth? Based on our sample of Philadelphia children (Figure 3), this phase developmental shift is still present and extends upwards of 2 to 3 years. Qualification of this phase shift, and easily applied to dental developmental sequences, is the staging gap between any of the Phase 1 versus Phase 2 teeth. We chose to reproduce this between the latest Phase 1 tooth, the I2, in comparison to the middle Phase 2 tooth, the M2. Using the 14 calcification staging of Moorrees (1963), this calcification gap of at least 2 to 3 stages, occurs in both of the Philadelphia subsamples.

Although no such phase gap exists in reproduced information from captive chimpanzee dental development (Figure 4), it is not possible to determine if elongated maturation patterns of wild chimps results in a phase gap since only eruption data is presented in Zihlman. However, reproduced photos and line drawings clearly show that I2s and M2s are erupting in synchrony - a feature that never occurs in humans and has been well documented in captive chimps by Conroy and Mahoney (1991) (Table 2).

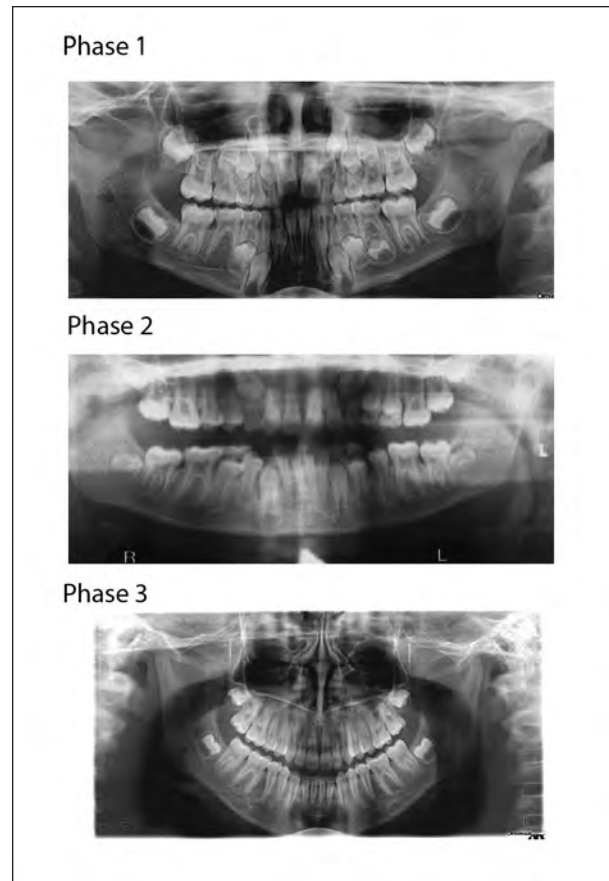


Figure 2. Sample panoramic radiographs of 3 Philadelphia school children in each of the phases of dental maturation.

MANDIBLE	MAXILLA
M1 I1 I2 M2 (P3/P4)	M1 I1 M2 I2 P4 P3 C
M1 I1 I2 M2 (P3/P4)	M1 I1 I2 M2 (P3/P4) C
M1 M2 I1 I2 (P3/P4)	M1 I1 I2 (M2/P3/P4)
M1 I1 I2 M2 P4	M1 I1 I2 (M2/P3/P4)
M1 (I1/I2) M2 (P3/P4)	M1 I1 M2 I2 P3 P4
M1 I1 I2 M2 P4	M1 I1 (I2/M2) P3 P4
M1 I1 I2 (M2/P3/P4)	M1 M2 I1 (I2/P3/P4)
M1 (I1/M2) I2	M1 I1 M2 P4 (I2/P3)

Table 2. Various eruption sequences for both the mandible and maxilla of the common chimpanzee. **BOLD** type face indicates situations where the eruption of the M2 actually precedes the eruption of the I2. This array of erupting teeth also characterizes wild chimpanzee populations as summarized by Zihlman (2004). Thus, from eruption data alone, there is no phase distinction between the teeth in either wild or captive chimpanzees.
Data From: Conroy and Mahoney 1991

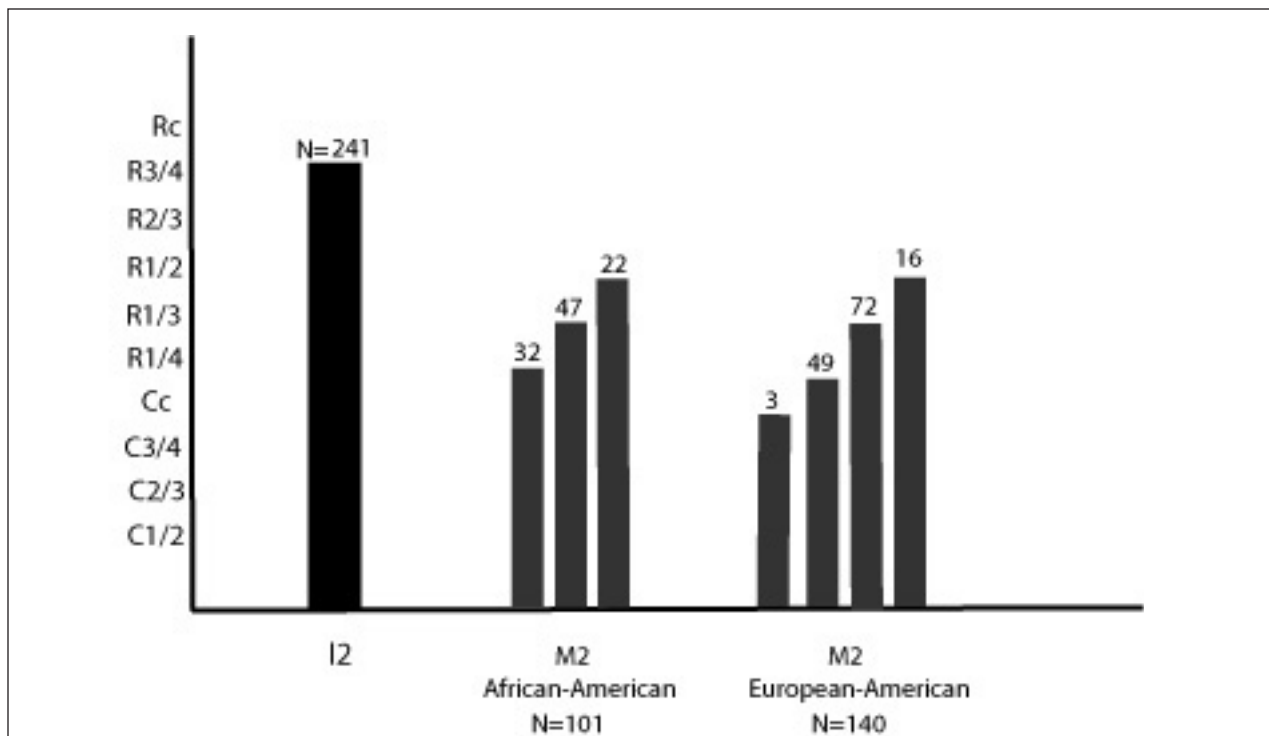


Figure 3. Relationship of the I2 Phase I tooth development to the M2, a Phase 2 tooth. In a sample of 1,245 Philadelphia school children, a total of 241 show the stage of development of the I2 (a first Phase tooth and the last in most cases to develop and erupt in that stage) at R3/4th. Although there are difference in the chronological time frame of development of the teeth between the subsamples, both populations of children show at least a 2 staging delay in development of the Phase 2 tooth - the M2. This delay between the developmental stage of these 2 teeth clearly shows evidence of the Quiescent phase in the developing human dentition. Although there is a clear trend for an earlier maturation of all teeth in comparison to many samples previously published, the retention of the delay between each phase is clearly retained.

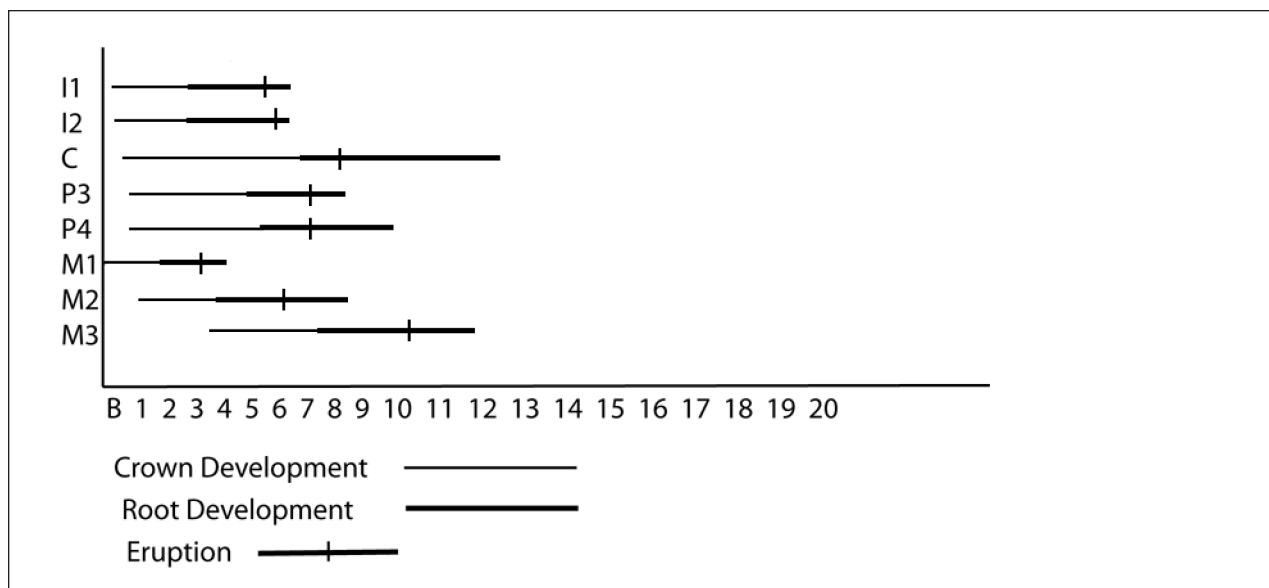


Figure 4. Dental development chart adapted from Smith (1986) and including the data on chimpanzee from Anemone et al. 1991 and 1996. Both captive and wild chimpanzees show a direct overlap in the development of the I2 and the M2. In the wild version of chimps, eruption data indicates that the overall time frame of dental development is shifted to the right along with an assumed eschew of each of the calcification stages. For example, the I2 erupts between 7.4 and 8.6 years; the M2 between 8.2 and 8.4 years (Zihlman et al. 2004).

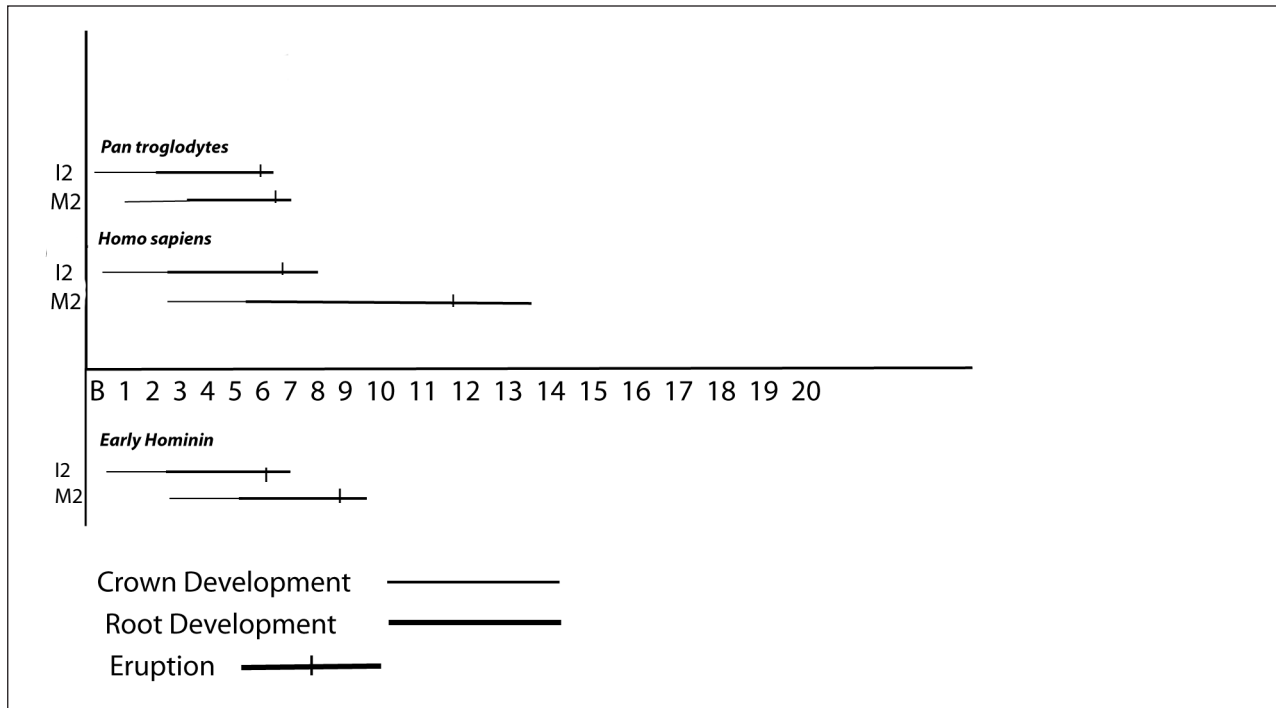


Figure 5. *Pan*, *Homo sapiens* and early hominin dental development of the I2/M2 compared. Using a 2.5 year calcification time for both the I2 and M2 crown, and a root timing developed from radiographic studies of chimpanzees, early hominin specimens would show a developmental delay that is the equivalent of the Phase 2 of modern humans. Although the time frame of dental development is not as elongated as it is in *Homo sapiens*, the initiation of the shift appears relatively early in the evolutionary history of our lineage.

Finally, can Phase 1 and 2 shifts be documented in any fossil forms present in the hominin lineage? Virtually all of the immature fossil hominin specimens where both the developing I2 and M2 are present and imaged, show the identical type of phase delay as shown in all modern humans. This includes members of both the genus *Australopithecus* and non-modern versions of the *Homo* encompassing Neandertals. Table 3 presents the data from various published sources. Although different staging techniques were used, and are explained in the figure caption, clearly this pattern of delay is present. Since virtually all hominoid appear to form molar crowns in approximately the same time frame, the earlier hominin comparison is drawn with crown complete achieved in 2.5 years (average of the variation of 2-3 years). Since more limited information is present for the time frame of root development in these extinct forms, the chart is produced using a rapid root development time frame modeled from the genus *Pan* (Figure 5). With these very conservative estimates of both crown and root formation, coupled with at least a 2 stage lag between the I2 and M2, it is clear that even within the early hominins, there is a developmental delay that corresponds to the Quiescent phase.

THE QUIESCENT PERIOD IN HUMAN DENTAL DEVELOPMENT

In their world wide survey of variation in human

growth, Eveleth and Tanner (1991) describe two active phases in permanent tooth emergence, separated by a period of quiescence (Figure 6). The first active phase lasts one and a half to two years (when we consider the means for populations) M1, I1 and I2 emerge. The second phase lasts slightly longer, M2, C, PM1 and PM2 emerge. The Quiescent phase in between lasts a generally similar time, between two and three years in the male in nearly all populations and between 1.7 and 2.7 years in the female." (Eveleth, P.B. and Tanner, J.M. 1990 *Worldwide Variation in Human Growth*, 2nd ed. page 159)

MIDDLE CHILDHOOD

Developmental psychologists have focused on this period as being a time of crucial importance in the emergence of language based cognitive behaviors as well as the appearance of a greater understanding of, and reliance on, cultural rules.

John Lucy and Suzanne Gaskins (2001:280) have noted that "Regarding the changes in middle childhood, cognitive developmentalists have long recognized this as the period in which the child completes a shift from dependence on more spontaneous, perceptual strategies to reliance on more systematically organized, conceptual ones. In short, the child now enters the world of the adult, which is more heavily guided by systems of shared cultural meaning".

In a review of middle childhood cross culturally,

Hominin		Stage I2	Stage M2
A.robustus	SK 62	5	2 or 3
A.robustus	SK 63	5 or 6	3
A.africanus	Taung	4	2
A.africanus	STS 24	4 or 5	2
Early Homo	KNM-WT 15000	A1/2	R2/3
Neandertal	Devil's Tower	Ri	C1/4

Table 3. Stage delay between the I2/M2 in a sample of earlier hominin forms.

Australopithecine data from Conroy and Vannier 1991 and based on the stages of dental calcification by Demirjian et al. 1973. Early Homo data on KNM-WT 15000 from Smith 1993, and Devil's Tower Neandertal, from Dean et al. 1986 both based on the staging technique from Moorrees et al. 1963.

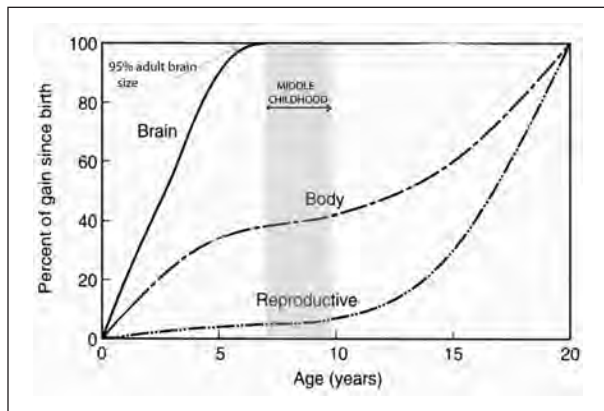


Figure 6. Original Scammon (1930) curves showing the growth of different body tissues (in weight) plotted against chronological age. The Quiescent period corresponds to the age in which brain weight is close to the maximum (95% adult weigh), with body weight gain decelerating and in conjunction with the lengthy attenuation of reproductive organ growth and maturation.

Weisner (1984: 344) notes that “Many cultures also share the belief that between the age of 5 and age 7 children begin to acquire reason or sense, the ability to understand cultural rules and to carry out directions. Rogoff et al. (1975), Super (1981), and J. Whiting and B. Whiting (1960) identified this age period from cross cultural samples, and Nerlove et al. (1974) did so from data from Guatemala.

Sweder (1981) argued that in middle childhood, children begin to acquire self/cultural/moral understandings of their world. He lists a set of ten themes that illustrate this:

1. Personal boundaries: what’s me versus what’s not me.
2. Sex identity: what’s male versus what’s female.

3. Maturity: what’s grownup versus what’s childlike.
4. Cosubstantiality: who is of my kind and thus shares food or blood with me versus who is not of my kind.
5. Ethnicity: what’s our way versus what’s not our way.
6. Hierarchy: the unequal share of life burdens and benefits.
7. Nature versus culture: what’s human versus what’s animal-like.
8. Autonomy: independent, dependent or interdependent.
9. The state: what I want to do versus what the group wants me to do.
10. Personal protection: avoiding the war of all against all.

Clearly these conflicts are part of a child’s increasing socialization and integration into a society. Further, most reflect factors that represent human cultural phenomena. The difference between the younger, pre-Quiescent children and the older post-Quiescent children is in the way by which the cultural rules are recognized and enabled.

Middle childhood is then the time when the norms governing appropriate behavior within the culture are internalized as part of the development of an integrated social member of the group. These cognitive changes coincide with the maturational time frame brain growth in volume is almost complete and body size dimensions are minimally altered.

Interestingly, in his studies of the evolution of the brain in the human lineage, Holloway emphasized organizational rather than volume metric evolution of the brain in the human lineage. He has emphasized that although early hominin endocasts reveal a brain size in the range of the African apes, details of the position of surface anatomical features, such as the lunate sulcus, suggest that these brains had undergone neurological reorganization. Evidence that even early members of the hominin lineage based on dental developmental studies experienced a middle childhood period of would support Holloway’s ideas of reorganization. These data suggest a reevaluation of the ways we view behavior and neurological evolution in early hominin evolution.

MIDDLE CHILDHOOD AND THE EVOLUTION OF HUMAN COGNITION: SUMMARY

1. Collection of a substantial series of panoramic X-rays of American children aged 4-14 indicates that there are significant changes in the timing and variation of human dental maturation since the last major studies were published in the 1960’s and 1970s (Moorrees et al., 1963; Demirjian et al., 1973). This data set, and others that have been collected (i.e. Liversidge 2003, summarized by Guatelli-Steinberg,

2008), indicate there are both changes in the timing of the eruption of many of the permanent teeth as well as an under appreciated level of variation in human dental development that should be considered in reconstructions of earlier hominin development and life history.

2. A recent study by Zihlman and colleagues (2004) has presented data that patterns of dental eruption in a small sample of wild chimpanzees of known age record are significantly retarded compared to dental development in captive animals.
3. While these data sets narrow the timing differences between wild chimpanzee and modern human dental maturation patterns, it may be that when examining and comparing growth and development in humans and chimpanzees, we have failed to appreciate that maturation and growth represent a series of discrete periods. By drawing comparisons across the entire flow of human and chimpanzee maturation and development, shorter episodes in development may have been overlooked.
4. Just such an episode may be present in the dental eruption data that shows consistent differences between chimpanzees and humans in the timing of the eruption of the initial set of permanent teeth (two incisors and first molar) and the second set (canine, both premolars and the second molar). In humans, the time between the eruption of these two permanent teeth sets has been termed the "Quiescent period" (Eveleth and Tanner, 1990); it extends between 1.7 and 3.4 years and occurs at about the same time as a behavioral reordering in children that developmental psychologists term *middle childhood*.
5. It is worth noting that the Quiescent period and middle childhood begin just after the greatest growth of the human brain has been completed.
6. The Quiescent period is clearly marked in the development and eruption patterns of the human dentition but is not present in the dental development of chimpanzees.
7. Immature specimens of hominins of the appropriate dental age, from *Australopithecus* to *Homo sapiens neanderthalensis*, all demonstrate, without exception, the presence of the Quiescent period in their dental development.
8. Numerous publications by Holloway (1969, 1981, 1983a, 1983b, 1996, 2008 and Holloway et al., 2003 and 2004) over the past 40 years have been focused on the evolution of the brain in the human lineage. He has emphasized that although early hominin endocasts reveal a brain size in the range of the African apes, details of the position of surface anatomical features, such as the lunatic sulcus, suggest that these brains had undergone neurological reorganization. Evidence that even early members of the hom-

inin lineage experienced a middle childhood period of would support Holloway's (for example, 1983a, 1983b, 1988, 1996) ideas of reorganization. These data suggest a reevaluation of the ways we view behavior and neurological evolution in early hominin evolution.

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