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## EVOLUTION OF MODERN HUMAN DENTAL ONTOGENY REVISITED

**ABSTRACT:** *Modern humans are characterised by an extended growth period, and this delay in maturation is also reflected in their delayed eruption of permanent teeth. This, as well as the fact that teeth and jaws are abundant in the fossil record, has led many researchers to study hominid dental remains in order to elucidate the evolution of modern human ontogeny. Advances in the methods which allow the processes of tooth formation to be related to absolute time, together with conclusions of recent studies of dental growth in apes, now provide a better understanding of the unique features of modern human dental development. Differences in tooth formation times alone cannot account for the delayed eruption of modern human teeth. Instead, within the hominid clade the nature of the links between tooth eruption, facial growth, dental function and life history seems to be more complex than previously thought, whereby the extended ontogeny cannot be described by a simple heterochronic event.*

A cardinal feature of modern humans is our greatly prolonged growth period, and one of the expressions of this general somatic retardation is the time it takes to erupt our teeth (Schultz, 1924). Although this delay is well-documented, the developmental basis for it is poorly understood. Refinements in the methods which allow the processes of tooth formation to be related to absolute time (Dean, 1987a, 1989), together with the conclusions of recent studies of dental growth in apes (Anemone et al., 1996; Kuykendall et al., 1992, 1996; Winkler et al., 1996), now allow researchers to identify more precisely the unique features of modern human dental development. This contribution integrates the new evidence, presents hypotheses for the mechanisms which underlie the delayed dental development of modern humans, and appraises these hypotheses in the wider context of overall somatic development.

The genetic similarities between modern humans and the chimpanzee (Ruvolo, 1994; Ruvolo et al., 1994), together with the chimpanzee-like dental morphology of the earliest hominids (Leakey et al., 1995; White et al., 1994), suggest that the chimpanzee is the most appropriate extant model we have for the type of dental developmental system possessed by the common hominid ancestor. By focusing on the developmental pathways that are held in common, especially between *Pan* and *Homo sapiens*, as well as on those aspects that apparently differ between

higher primates, it is possible to specify the unique features of the modern human pattern of dental ontogeny.

The dentition might appear to be an unusual system to use to investigate the evolution of human ontogeny, but there are good reasons for focusing upon it. Firstly, the material properties of tooth crowns make them particularly resistant to physical damage and to chemical erosion. These factors, along with their compact shape, mean that teeth are unusually well-represented in the fossil record. Secondly, and importantly for the issue at hand, is the regular manner in which teeth grow. Enamel and the underlying dentine are formed incrementally. Circadian growth markings are preserved within the microstructure of both tissues (Beynon & Dean, 1988; Bromage, 1991; Dean, 1987a, 1989; Dean et al., 1993a; Massler & Schour, 1946; Schour & Hoffman, 1939a, 1939b), but they are more easily discerned in the enamel of tooth crowns than in the dentine of the roots (Dean, 1995a). Enamel growth markings, which occur at a near-weekly interval, can also be discerned along the unworn sides of the teeth. They are particularly prominent on the labial surface of incisors, and have been used to estimate the ages of death of individuals (Bromage & Dean, 1985; Dean, 1987b; Mann et al., 1990, 1991). It is for these reasons that dental development is often the only means to track evolutionary changes in somatic development. Lastly, the eruption time of teeth is not only correlated with general somatic matu-



ality, but it is also linked with brain size and with several aspects of life history (Clutton-Brock & Harvey, 1980; Schultz, 1960; Smith, 1989a, 1989b, 1991a, 1992). The developing dentition is therefore unique, for not only does it provide evidence for researchers who seek to establish the developmental basis for evolutionary change, but it also provides access to otherwise unavailable information about the evolutionary biology of extinct species.

## TEETH AND THE DENTITION AS A WHOLE

In order to identify the developmental constraints and evolutionary pathways that have resulted in the human pattern of dental development, it is important to clearly distinguish between the development of individual teeth and that of the dentition as a whole. Although both teeth and the dentition carry information about functional adaptation and taxonomy, differences exist in what each can tell us about growth and development. Whereas the incremental nature of enamel and dentine development (Dean, 1989) permits the rate and time of formation of a single tooth to be determined, it is the eruption of teeth within the dentition which allows assessment of the maturation of the individual in relation to its life history. For example, eruption of first permanent molars marks the end of infancy, and is highly correlated with adult brain size (Clutton-Brock & Harvey, 1980; Schultz, 1960; Smith, 1989a, 1989b, 1991a, 1992). Hence, if we were able to determine the age of eruption of first permanent molars in fossil hominid species this would provide researchers with a powerful heuristic tool. However, the complex nature of the development of individual teeth, and the many factors which influence the growth of the dentition as a whole, combine to make it difficult to obtain such information.

## DEVELOPMENT OF CLASSES OF TEETH

Neural crest cells migrate into the developing jaws, where they interact with the ectodermally-derived oral epithelium to initiate tooth morphogenesis, i.e. formation of the dental lamina and subsequent bud, cap, bell and crown stage formation. Extensive reciprocal epithelial-mesenchymal interactions result in the cytodifferentiation of ameloblasts, which synthesise and secrete enamel matrix, and of odontoblasts, which secrete dentine (Lumsden, 1988). In higher primates, as in mammals generally, the neural crest cells involved in tooth formation are derived from discrete primordia, or clones, and it is from these that the morphologically distinct incisors, canines, (premolars) and molars develop (Osborn, 1977, 1978), although tooth classes could also be a function of a pre-patterning in the oral epithelium (Lumsden, 1988).

Although the dentition as a whole is under selective pressure, its development is hierarchically organised such that some modifications can be made more easily than others. Some aspects of dental development seem to be

remarkably conserved, such as the time of initiation of the stem progenitor of each tooth class and the sequence of tooth calcification of permanent incisors and molars from anterior to posterior (Osborn, 1977); apparently the sequence of premolar calcification is similarly conserved (Macho & Wood, 1995). It is noteworthy that differences in the timing of the initiation of tooth formation between hominoid species almost always involves teeth other than the stem progenitor of a tooth class. In the course of evolution towards modern human dental ontogeny, the growth rate of the molar clone, and to a lesser extent that of the premolar clone, has slowed down such that the onset of tooth mineralisation of the posterior members within these tooth classes has become progressively delayed (e.g., Dean et al., 1993b; Moorrees et al., 1963; Smith, 1991b). The time of initiation of later-developing teeth varies within as well as between hominoid species (Kuykendall, 1996; Winkler et al., 1996), and the range and nature of the variation of this feature in fossil hominids is not well understood.

Thus, for any attempt to reconstruct the evolutionary history of modern human dental ontogeny, the events occurring within the development of the stem progenitor of each tooth class make the most appropriate reference framework. The onset of calcification of the stem progenitor of the incisor and molar classes are particularly significant events, because in hominoids, and perhaps in all primates (e.g., Swindler & Meekins, 1991), the first permanent molars (M1) and central incisors (I1), respectively, start calcifying around, or shortly after, birth (Anemone et al., 1991; Beynon et al., 1991b; Dean & Wood, 1981; Dean et al., 1993b; Moorrees et al., 1963; Liversidge et al., 1993). Hence, any differences in the timing and sequence of M1 and I1 eruption must involve processes which operate after enamel and dentine formation have been initiated. However, it should be noted that a similar eruption sequence does not necessarily indicate similarities in the underlying developmental processes. As a case in point, in both *Paranthropus* and *Homo sapiens* M1 and I1 erupt close together (e.g., Broom & Robinson, 1951; Conroy, 1991, 1991a, 1991b; Smith, 1986; Beynon & Dean, 1988); yet whereas the former has a short growth period (Dean et al., 1993a), that of the latter species is prolonged. In all extant and extinct hominoids other than modern humans, molars not only erupt before the central incisors but do so even before the central incisor crowns have been fully formed.

The almost concomitant onset of crown formation of M1 and I1 around the time of birth, together with the incremental nature of tooth development, permit estimates to be made of the eruption time of the first permanent molars of fossil specimens (Bromage & Dean, 1985; Beynon & Dean, 1988; Dean, 1987b) (Figure 1). The fact that crown formation times of incisors and the overall length of dental ontogeny have apparently been truncated in *Paranthropus* when compared with *Homo sapiens* seems to have led to two assumptions, namely, that (A) crown formation can serve as a surrogate for the whole of dental



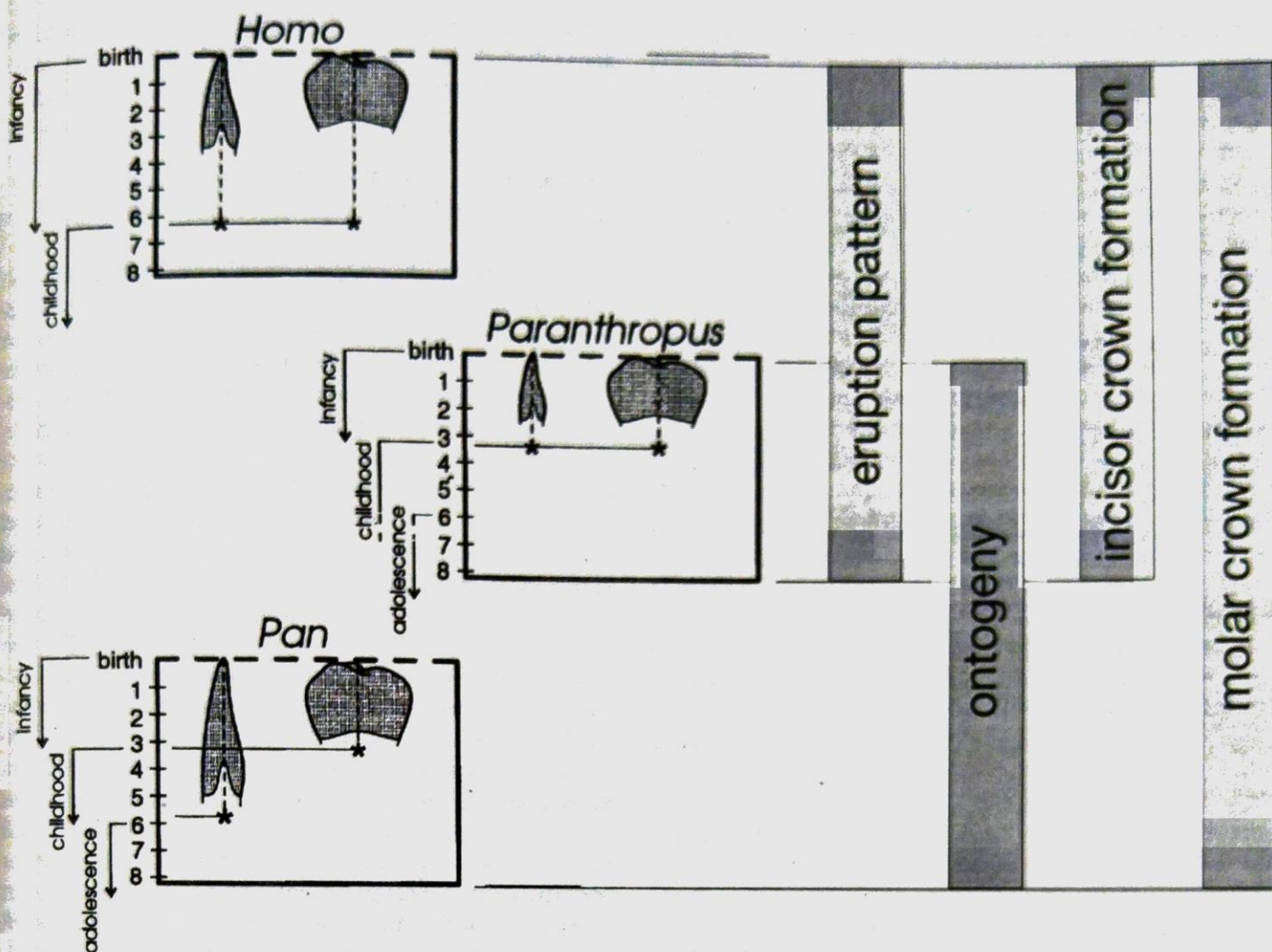


FIGURE 1. Diagram showing the crown formation and eruption times of a lower central incisor (I1) and a first molar (M1) of *Homo*, *Pan troglodytes* and *Paranthropus*. The times are based on data from several studies, details of which are given elsewhere (MACHO & WOOD, 1995). In all three taxa crown formation begins around the time of birth (M1), or shortly afterwards (I1). Crown formation begins at the cusp tips and proceeds towards the cemento-enamel junction. The height of the images of the teeth in the diagram are thus a reflection of the crown formation times.

The asterisks indicate the time of eruption of the two teeth. While eruption times for the extant species are mainly based on direct observations (Smith et al., 1994), the estimates of eruption times for *Paranthropus* are based on extrapolations made as part of a histological study (Dean et al., 1993). The eruption of M1 is taken to be the onset of childhood, and generally corresponds with the achievement of a brain size, which is approximately 95% of the adult size.

With respect to incisor development, the differences in crown formation times between *Homo* and *Pan* are a reflection of their crown heights. First molar crown formation times are similar in *Homo* and *Pan*. The main developmental contrast is in their time of eruption, which is delayed in *Homo* and which is reflected in a different pattern of eruption.

*Paranthropus* and *Homo* share the same eruption pattern, but the length of their ontogeny is apparently different, with *Paranthropus* and *Pan* sharing a short infancy as defined by the eruption of M1 (e.g., Smith, 1993). The differences in the crown formation and eruption times between the incisors of *Pan* and *Paranthropus* are merely a reflection of crown height differences and have no obvious bearing on the life histories of these two species.

Ranges of variation of first molar crown formation times overlap considerably among the three taxa illustrated, and do not contribute significantly, if at all, to the dental developmental differences between *Pan* and *Homo*.

development (Beynon & Dean, 1987; Beynon & Wood, 1986, 1987; Mann et al., 1990, 1991; Ramirez Rozzi, 1993), and that (B) the study of enamel and dentine development within a single tooth will reveal useful information about the evolution of modern human dental ontogeny (Beynon & Dean, 1987; Beynon & Wood, 1986, 1987; Mann et al., 1990, 1991; Ramirez Rozzi, 1993) (Figure 1). Although evidence from comparisons between *Paranthropus* and *Homo sapiens* refute such a generalisation, it is, nonetheless, legitimate to explore whether there

are systematic trends in the time and mode of crown formation during hominid evolution.

#### TOOTH FORMATION AND THE EVOLUTION OF ONTOGENY

Evolutionary changes in hominid crown formation times have apparently not followed a simple sequence. Differences in crown formation times between teeth in the same



dentition and between the same teeth in different extant and extinct species, although related to overall growth velocity, appear to be more closely-related to crown size/height than previously thought (Macho & Wood, 1995); but research into the details of the relationship between crown height and crown formation time is still in its early stages (Dean & Beynon, 1991a; Liversidge et al., 1993). Furthermore, once enamel matrix formation and mineralisation are initiated, they apparently proceed in a manner that is common to all higher primates (Beynon et al., 1991a). The pattern is such that in all the species investigated the daily rate of enamel secretion increases from the dentino-enamel junction towards the outer enamel, but decreases from the cusp tip towards the cervix. Likewise, the enamel extension rate is fastest immediately after the first ameloblasts are activated at the cusp tip, but thereafter it slows as the wave of activation moves towards the cervix. This latter trend is seen in a range of higher primates (Beynon et al., 1991a), but it is most pronounced in modern humans (e.g., Beynon & Dean, 1988; Dean, 1987b). However, differences in both the enamel secretion rates of fully-differentiated ameloblasts and of enamel extension rates also exist between teeth, and even cusps, within a species, although details of these differences are not yet available.

Given the role of tooth size and morphology in food processing and social display, it is evident that teeth and the dentition are under strong selection pressures; yet the processes, whose modifications result in these different morphologies seem to show a substantial amount of plasticity. It would appear that the dominant influence on the enamel secretion rate and the enamel extension rate is the morphology of the tooth. Species with thick enamel, such as *Paranthropus*, generally have higher average enamel secretion rates (Beynon & Wood, 1986, 1987), while high-crowned teeth, like the canines of *Pan*, have higher enamel and dentine extension rates (Shellis, 1984). However, once tooth size and morphology have been properly accounted for, differences in the patterns of tooth crown and root formation may become apparent, and promise to reveal taxonomic information, although probably not about developmental changes in the timing of ontogenetic events. Furthermore, except for canines, there is no clear-cut relationship between crown formation time and eruption. For example, despite the generally foreshortened dental ontogeny in *Pan*, the relatively late-erupting incisor crowns actually take longer to form than do those of modern humans (Chandrasedekera et al., 1993) (Figure 1). Conversely, the small incisors of *Paranthropus*, which various evidence suggests has a short ontogeny similar to that of *Pan* (Dean et al., 1993a), form more quickly than those of *Homo sapiens* (Dean, 1993b; Dean & Beynon, 1991b; Moorrees et al., 1963) (Figure 1). Thus, a knowledge of crown formation times *per se* can only make a limited contribution to our understanding of the evolution of hominid ontogeny (Macho & Wood, 1995). As is the case with tooth crowns, the absolute time it takes to form a particular tooth root appears to provide limited information about overall

growth velocities, for *Pan* takes longer to form its incisor roots than does *Homo sapiens* (Kuykendall, 1996), despite the latter having a generally longer growth regime.

#### THE BASIS OF THE MODERN HUMAN DENTAL ERUPTION PATTERN

Since modifications of the rate of tooth crown and root formation apparently account for only some of the differences in dental eruption times and patterns between the non-human higher primates and modern humans, other mechanisms must be invoked to explain the unique timing and pattern of modern human dental development.

Recent observations suggest that it is a slowing-down of the root extension rate and, to a lesser extent, a reduction in extension rate during the final phases of enamel formation towards the cervix that account for the delayed eruption of modern human teeth (Dean 1995a, 1995b; Dean & Beynon, 1991b). These evolutionary changes appear to have affected tooth classes differently (Macho & Wood, 1995). It is also evident that even within a species, such as *Homo sapiens*, the amount of root formation *per se* is a poor predictor of the time a tooth comes into occlusion (Shumaker & El Hadary, 1960; Grøn, 1962). In modern humans incisors erupt on average about three years after completion of crown formation, while fully-formed permanent canines and premolars remain in the jaws for over five years before eruption, whereas in *Pan* teeth generally erupt shortly after, or within the first year after, crown completion. Only with regard to molars is there a common trend in both species, in that the time elapsed between crown completion and eruption increases from anterior to posterior. However, while the first molars of modern humans erupt about 3.6 years after crown completion, that interval is under six months in chimpanzees. It would seem that it is adjustments to root formation prior to eruption which mainly account for the unique timing and pattern of modern human dental development (Dean & Beynon, 1991b; Dean, 1995b; Smith, 1994a, 1994b; Smith et al., 1994).

It is apparent that the relationships between dental and other aspects of development are only very general, whereby only the eruption status of first molars appears to provide an assessment of the overall maturity of hominoids with regard to their life histories (e.g., Dean 1987b; Smith, 1993; Winkler, 1996). Tooth eruption is a multifactorial process, which is under general and localised control (Marks, 1987; Iuszkka et al., 1992); this may explain a dissociation between overall maturity and tooth eruption. For example, when the somatic and dental development of an 1.5 Myrs.-old, almost complete skeleton of an early African *Homo erectus* specimen from Nariokotome (Smith, 1993) are used as predictors, they result in different age estimates, i.e. between 11 and 15 years of age. In this case, assessments were based on referential models based on modern humans, chimpanzees and macaques. Although it is evidently closer to the mod-



ern human standard of dental development, this early African *Homo erectus* individual apparently does not fit with either a chimpanzee or a modern human model. Instead, it exhibits a unique pattern of development.

## CONCLUSION

It is serendipitous that across higher taxonomic units, such as families, there is a clear relationship between the pattern of eruption and the timing of dental developmental events. However, when dealing with closely-related or extinct species, such as *Paranthropus* and *Homo* for example, such a clear-cut relationship may not hold. Neither is there a strong enough relationship between dental and somatic growth across species to allow the former to be used as a surrogate for the latter, or *vice versa*. Hence, ultimate clarification of the maturation status of the early African *Homo erectus* specimen, and those belonging to other early hominid species, must await further studies which will elucidate the relationships between the timing of dental developmental events and eruption pattern, and between dental growth and somatic growth. It is now clear that enamel formation, which can be tracked in such detail in the fossil record, does not play a major role in the evolution of the unique modern human growth pattern. Instead, attention needs to be focused on the subsequent stages of tooth formation (Dean, 1995a, 1995b), and on the relationships between tooth eruption and function, and life history.

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