ANTHROPOLOGIE • XXXVIII/1 • pp. 51–62 • 2000

MICHELLE LAMPL, ALAN MANN, JANET MONGE

A COMPARISON OF CALCIFICATION STAGING AND HISTOLOGICAL METHODS FOR AGEING IMMATURE MODERN HUMAN SPECIMENS

ABSTRACT: The past fifteen years have been a time of controversy regarding how to interpret dental development and chronological ages at death from skeletal specimens. A central focus of some of these debates concerns the comparison of ages derived from traditional radiological studies that identify calcification stages of developing dentition to ages derived from histological study of enamel microstructure.

This study provides a detailed description of two unaged children from an archaeological context in the Middle East. These individuals are assessed according to previously published methods for the ageing of incremental growth in crowns and roots of different teeth. Scanning electron micrographs were taken to count the perikymata on enamel surfaces and histological sections of teeth were prepared and analysed for counts of internal striae of Retzius and cross striations. In line with previously published methods, total crown formation times were derived and root formation rates established in order to establish ages at death.

With the exception of first incisor crown formation, the results found here are in line with other studies for crown formation. The ages at death assessed by the histological methods are significantly shorter than those derived from radiological references standards and provoke questions: one child with first molar erupted is aged at 3.4 years of age and a second child, at second molar alveolar eruption, is aged at 5. 8 years. These early ages are hypothesised to result from methodological flaws in the proposed method. By comparison with the other extant study of root extension rate, the human children studied here overlap ranges previously reported for non-human primates. The notions concerning distinctive differences are considered within this context. The present data extend the descriptive data base on population variability in perikymata counts and striae of Retzius observations for comparative studies of dental development in modern humans. The ages at death resulting from these methods are questioned, and some reconsiderations of the validity of these approaches are suggested.

KEY WORDS: Skeletal ageing – Dental calcification – Dental histology – Age-at-death – Immature human skeletons

INTRODUCTION

A number of palaeoanthropological studies have focussed on the determination of the pattern and rate of tooth development in modern humans, apes and in extinct hominines[1)], with the aims of investigating the significance that these may have in furthering our understanding of the development of maturational processes during the course of human evolution (e.g. Kuykendall, Conroy 1996, Macho, Wood 1995, Mann, Lampl, Monge 1991, Smith, Tompkins 1995). The goal of these studies is to provide insight into the evolution of the unique qualities that may characterise modern human growth and development and when these

[1)] In this paper, we follow Weiss (1987) in employing the subfamily Homininae, rather than the family Hominidae, to describe humans and our close immediate ancestors and relatives.

occurred in evolution, with particular interest directed to better understanding the prolongation in the developmental period leading to the attainment of physical adulthood and the cessation of skeletal and dental development in modern human growth patterns.

One of the seminal features of these studies is a careful focus on the differences between the *pattern* vs the *rate* of dental development. While it is clear that the pattern of tooth development can be determined on both living and extinct species through the examination of the maturational state of the individual teeth in immature specimens, the rate of development in all skeletal samples has been more difficult to ascertain by traditional approaches. This is because rate assessments are time-dependent and require real time markers such as chronological age. This cannot be reliably identified in skeletal samples (Lampl, Johnston 1996) because of both genetic and environmental influences that manifest as individual and population differences in the chronological age of attainment of maturational events. The only well documented and generally acceptable way of assessing the rate of development in real time is with living individuals at specific moments in the course of their maturation, and sometimes, on samples of known age at death.

A number of research efforts have focussed on observations of dental development patterns in human, ape and fossil juveniles, investigating calcification stages and eruption patterns in immature fossil specimens, or individuals whose dentitions are not yet completely adult (Anemone *et al.* 1996, Conroy, Vannier 1987, 1988, 1991a,b, Dean 1987a,b, Lampl, Monge, Mann 1993, Mann 1975, Simpson *et al.* 1990, 1991, Smith 1986, 1989, 1991, 1992, 1994).

The framework for establishing the pattern of ape dental development is founded on the work of Dean and Wood (1981) who studied a mixed museum skeletal sample of *Pongo* and African apes of unknown age. Recent radiographic analysis of the permanent dentition of a sample of known age *Pan troglodytes* (Anemone *et al.* 1991, Kuykendall 1996) and eruption data accumulated on a mixed longitudinal sample of this species (Conroy, Mahoney 1991), have revised our understanding of the pattern of development in this African ape. Additionally, studies have been carried out on the microstructural ageing of an unknown age-at-death specimen of *Gorilla gorilla* and one specimen of *Pongo pygmaeus* (Beynon *et al.* 1991) which may contribute to a reconsideration of the established pattern of dental development in these two species, as originally published by Beynon and Dean (1991). More recently, work has been conducted on histological reconstruction of rates and patterns of ape dentition, provoking serious reconsideration of our ideas as reflected by the earlier radiological studies (Beynon *et al.* 1998, Reid *et al.* 1998).

For humans, while population data on dental eruption patterns exist (collated, for example, in Eveleth, Tanner 1976, 1990), less work has been done comparing populations in terms of dental calcification patterns. The most commonly cited reference in calcification based ageing studies is the work of Moorrees *et al.* (1963), which describes percentiles of aged stages achieved by chronological ages for 100 to 300 children from the Fels and Boston growth studies in the United States.

In the past 15 years, a number of studies included comparisons of dental patterns found in the fossil juvenile specimens to developmental patterns observed in living humans and the non-human primates (Kuykendall, Conroy 1995, Smith, 1989, 1991, 1992, 1994), other studies have been more concerned with the reconstruction of the rate of dental maturation from the patterns themselves. For example, Smith (1992, Smith, Tompkins 1994) used the research of Sacher (1975), who calculated relationships between maturation rate and brain weight in extant mammals, in her exploration of the theoretical bases of rates of dental maturation in the Homininae, and constructed a model of hominine dental maturation rates.

The possibility of direct assessment of dental development rates based on hard tissue remains has also been explored. Using external and internal features of enamel and dentin, Dean (1987b), Beynon and Dean (1991) and Bromage and Dean (1985) suggested that a time ordered and time-delimited sequence of enamel developmental events provides an accurate clock from which to infer dental development. This work is based primarily on limited experimental evidence that structures observed in the enamel of humans, or cross striations, are deposited in regular 24 hour increments (reviewed in Risnes 1998). Internally on the enamel, lines of Retzius can be found, which usually encompass 2 to 12 cross striations and are often said to mark weekly amounts of enamel deposition (Yilmaz *et al.* 1977, Schour, Poncher 1937, Ramirez, Rozzi 1991, 1992). Many, but not all, striae of Retzius reach the enamel surface, where they leave a horizontal indentation, or perikymata, which have been used as indirect measures of enamel development. When counted directly on the enamel surface of teeth, these have been used to age individual specimens and infer developmental rate (Bromage, Dean 1985).

There is debate about the precise nature of these enamel structures. While they continue to be employed to calculate the rate of tooth development in earlier hominines (e.g. Ramirez-Rossi 1993 a,b, 1995, 1996), there is evidence indicating a greater range of variation than previously appreciated in crown formation times when this method is applied to teeth of known age at death individuals (Stringer *et al.* 1990). There are also suggestions that these features may be closely related to the structural integrity of enamel (Mann, Lampl, Monge in prep.).

Previous research on modern humans aiming to determine the rate and pattern of dental development, employing histological methods, is limited and includes two specimens of unknown population affinity (Boyde 1963, 1990), one Anglo-Saxon archaeological specimen

(Miles 1963), a specimen from the 19th century Christ Church cemetery at Spitalfields, London (Dean, Beynon 1991), four individuals from Picardie, France (Reid *et al.* 1998a), one adult male "African" (Dean *et al.* 1993) and eight children from St. Bride's Church, London (Huda, Bowman 1995). Only one immature fossil specimen has been likewise assessed, in terms of a comparison between histological, radiographic and CT assessment (Dean *et al.*1993b).

PRESENT STUDY

This research assesses the age-at-death estimates of two skeletal juvenile specimens from an Iron Age archaeological collection whose provenance is modern day north-west Iran by both a pattern-based method and a rate-based method. Specifically, the histological methods as outlined by Dean and Beynon (1991) are employed and the results are compared to chronological age-based estimates based on the calcification stages published by Moorrees *et al.* (1963).

SAMPLE

Juvenile skeletal specimens No. 703-5-508 and No. 60-20-226 are curated at the University of Pennsylvania Museum as part of the collection from excavations at the early Iron Age fortified settlement at Hasanlu in the Solduz-Ushnu Valley in north-western Iran (Muscarella 1989). These are two of the 246 skeletons excavated from Hasanlu period IVB, which represents the final destruction of the settlement by conflagration in the 9th century BC. In general, the preservation of skeletal materials from this site is excellent. These two young individuals apparently were inhabitants of the city who were either executed by the invaders or killed by falling debris that followed the burning and destruction of the central part of the town (Muscarella 1989).

These two specimens were chosen for this analysis because they are relatively complete dental specimens who died at gross maturation ages of significance for traditional skeletal ageing studies: first and second molar eruption. Further, both specimens preserve right and left antimeres and, thus, the destructive sectioning required for this study involved only one side of the dentition and was considered conservative in terms of skeletal preservation.

Specimen 73-5-508 died at the time of first molar eruption. The dentition is partially isolated and only the maxillary left M^1 and mandibular right P_3 and M_2 are embedded in bone. Excavation records document that these teeth belong to the same individual. On the basis of the extensive damage to the skull and the fragmentary condition of the postcranial bones, this child was apparently crushed by falling debris during destruction of the citadel. However, the isolated teeth are intact and in excellent

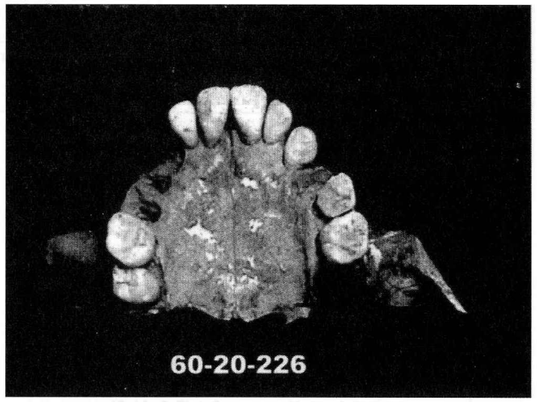

FIGURE 1. Occlusal view of an immature maxilla from the site of Hasanlu (University of Pennsylvania Museum catalogue number 60-20-226).

condition, with even the very recently calcified roots well preserved and without cracks or chips.

Specimen 60-20-226 (*Figure 1*) died at a time just after bone eruption of the M2 with the permanent I1, I2 and M1 at the occlusal plane. Alveolar bone of the maxilla has been broken and repaired, which permitted the removal of the erupted left I^1, I^2, M^1, the partially erupted M^2 as well as the erupting C.

The general range of ages for these two specimens, based on dental eruption, estimates that the younger child (No. 73-5-508) with first molar eruption was between 4.5 and 7.5 years of age, and the older child (No. 60-20-226), with erupting second molar, between 9 and 13 years of age at death (Eveleth, Tanner 1977, 1990).

METHODS

For each of the specimens, the age at death, when assessed by calcification stage based ageing according to modern reference standards, is compared to the age at death as assessed by histological methods. In order to exclude errors associated with the use of different methods of assessment (Liversidge 1994), all calcification stages reported here are based on examination of the teeth themselves and do not include radiographic assessment of teeth that remain in alveolar bone.

For the histological ageing, the method employed follows that outlined in Dean and Beynon (1991). The crown formation times are assessed from direct counts of striae in imbricational enamel added to the count of cross-striations in appositional enamel as outlined below. In this study, imbricational striae of Retzius counts are compared to external perikymata counts for cross validity of the structures and their identification. Root formation time estimates also follow Dean and Beynon (1991) for assessment of age at death.

TABLE 1. Calcification ages and histological counts for the present study.

	Calcification stage ages[a]		Perikymata counts*	Striae of Retzius*	Cross striations*
	female	male			
Specimen 73-5-508					
I^1	NA	NA	137	130	217
I^2	NA	NA	143	145	
C	3.0 (2.0-3.8)	2.8 (2.0–3.8)	97	99	
M^1	5.0 (4.0–6.5)	5.25 (4.0–6.5)	83	90	370
M^2	6.0 (4.75–7.75)	6.5 (5.5–8.25)			
Specimen 60-20-226					
I^1	8.6 (7.75–11.75)	8.2 (6.5–10.0)	90	85	210
I^2	8.7 (7.0–10.5)	8.25 (6.75–10.25)	110	105	
C	7.0 (5.5–8.8)	8.0 (6.5–10.0)	101	107	
M^1	5.5 (4.8–7.0)	6.0 (5.0–7.25)		51	330
M^2	9.25 (7.3–11.0)	9.4 (7.5–11.5)	47	54	

[a] Calcification stage ages from Moorrees *et al.* (1963). It is noted that these data are mandibular references for all but incisor teeth and the second specimen here consists of maxillary teeth.
* All counts presented represent the average of three raters with standard deviations ranging from 1 to 5.

External enamel structures: Perikymata

All isolated or extracted teeth were moulded and epoxy casts were made. These casts replaced the original teeth in the specimens, and served as replicas for microscopic analysis of enamel surface features. Moulding and casting techniques follow those described in Mann and Monge (1987). Moulds were made using *Reprosil* brand of polysiloxane and the replicas cast in epoxy resin (*Hysol* RE6345NA/HD0111). Casts were coated with gold-palladium and imaged using a Phillips 500 scanning electron microscope (SEM). Perikymata were counted on montages of each tooth magnified to 80×. Only buccal or labial surfaces were counted.

Internal structures: Striae of Retzius and cross-striations

The original teeth were embedded in methylmethacrylate and sectioned either bucco-lingually or labio-lingually using an Isomet low speed diamond saw. Only left side teeth were sectioned. The molars were sectioned through the apex of the protocone, the incisors through the mid-point of the crown and the canines through the tip of the cusp. Sections were etched for 30 seconds using a 0.5% solution of HCl and then carbon coated. Each tooth was imaged using either the Phillips 500 SEM at the University of Pennsylvania Museum, or the Joel SEM at the Material Science Engineering Facility at the University of Pennsylvania. Montages were made at 160× for analysis of the striae of Retzius and 320× for identification of the cross-striations. All counts are made on the buccal or labial surfaces. Cross striations are counted by following the course of several enamel prisms and counting the cross-striations from the tip of the dentin horn to the tip of the enamel, as previously outlined by Dean and Beynon (1991).

Crown formation times

For each individual, total crown formation time is calculated from the observed counts of these enamel structures. First, the internal line corresponding to the neonatal line is identified in the first molars of both specimens. Appositional enamel completion reflects the total number of cross-striations counted, minus those found under the neonatal line, and imbricational enamel completion time is calculated from the striae of Retzius lines and an average cross striation periodicity.

Root formation times and age at death

For each tooth, the amount of root present is identified visually and measured. Root lengths and thus root formation times on the molars are derived from the mesial lingual root. The methods developed by Dean and Beynon (1991) and employed by them on an unaged, unsexed child from Christ Church Spitalfields are repeated here: Common unique hypoplastic striae are located on the adjacent incisors for these specimens. Perikymata subsequent to these hypoplastic bands become the clock for root formation as follows: The lateral incisor lags in development behind the central incisor. As the central incisor is completing its development and continuing to develop root, the lateral incisor is still in the process of crown formation. Theoretically, according to Dean and Beynon (1991), the time for root formation on the more rapidly developing central incisor can be indirectly identified. If it is assumed that incisor and root development are continuous, then the root formation time on the central incisor can be calibrated by the remaining crown formation time on the lateral incisor that exceeds that on the central incisor. The assumption underlying this approach is that root formation immediately follows calcification and

occurs at a continuous rate. Thus, calculation of the continuing crown formation time on the lagging lateral incisor provides a clock for the root formation on the central incisor.

Histological ages at death are calculated as the sum of crown formation time assessed from appositional and imbricational enamel, together with root formation time. These are then compared to results from radiologically-based developmental ages according to Moorrees *et al.* (1963).

RESULTS

Pattern-based method of assessment: Calcification staging

Both of these immature Hasanlu individuals can be assigned an age at death with a broad range using the standards of Moorrees *et al.* (1963) *(Table 1)*.

For the younger specimen at first molar eruption, the age at death based on calcification stages encompasses a total range from 2.0 to 8.25 years of age when all teeth are considered, with an overall mean age of about 4.8 years (female, male reference respectively). It should be noted that the mean ages are heavily influenced by the relatively young ages assessed for canine teeth by comparison with the remainder of the dentition. As the canines are known to have been difficult to assess in the original study (Hunt: pers. comm.), and have often been noted to be very young when compared to other studies, it may be appropriate to exercise caution in interpreting these calculations.

The older specimen, at second molar eruption, is more difficult to interpret: The standards of Moorrees *et al.* (1963) consist of maxillary ages only for the incisors; the remaining dental reference ages are determined based on mandibular dental No. 6–2-development. As the teeth under consideration are maxillary, the ages of the incisors from the maxillary reference range between 6.5 and 11.75, with a mean age of about 8.5 years. The mandibular reference applied to these maxillary specimens provides ages that range from 5 to 11.5, with a mean age of 7.3 to 7.8 (female, male respectively). By contrast with modern population data for second molar eruption (9 to 13 years) (Eveleth, Tanner, 1976,1990), these averages would put this individual at quite a young age. Thus, it is likely that perhaps the specimen falls at the later end of the distribution of the Moorrees *et al.* sample calcification ranges and/or the differences between mandibular and maxillary development are emphasised. Considering the population difference between these individuals and the reference standards, it is quite possible that they are being underaged to this extent, in view of the significant differences found merely within regions of the United States (Mappes *et al.* 1992).

Rate of development methods

Enamel structures: Perikymata and striae of Retzius

All enamel structure counts represent the average of three raters with a standard deviation of between 1 and 5. Perikymata and striae of Retzius counts for these specimens are presented in *Table 1*. The amount of abrasion on the first molar from 60-20-226 obscured clear visualisation of the perikymata and no counts were taken on this tooth. In general, there was good correspondence between the external perikymata counts and the internal striae of Retzius numbers and there is no statistically significant difference between the counts. There is no systematic error evident in the direction of estimation and the differences in the two estimates are within one standard deviation inter-observer error (only the molars are slightly greater).

Cross-striation counts were determined between the beginning of enamel formation at the tip of the dentine horn and the surface of the teeth. This was most clearly identified in the outer cervical enamel. In contrast to previous reports, finding consistent cross striations between striae of Retzius within individuals (Fitzgerald 1998), a range of between 3 and 10 appear between adjacent striae of Retzius are found here, results in line with variability in cross striation counts reported by others (Huda, Bowman 1995, Risnes 1998). In some cases, several cross-striations were present within the structure of the striae themselves. While the complexity of the counts is not illustrated by the means shown, the ages derived and presented here are based on the use of a mean count of 7 cross-striations between striae of Retzius, for comparison with previous reports.

Crown formation times

Specimen 60-20-226. A distinct neonatal line is evident in the first molar of this specimen, present just over the tip of the dentin horn in some of the very first layers of enamel. The age at death of this child is guaged from this point, as it marks the beginning development of the dentition since birth. Appositional enamel in the first molar *(Figure 2)*, calculated from the cross-striations that extend from the tip of the dentin horn to the tip of the enamel (less those under the neonatal line), total 370 cross-striations. This is said to reflect 370 days of enamel formation time for the appositional enamel in the protocone, or 53 weeks.

Imbricational enamel in the first maxillary molar for this individual is estimated by the total number of striae of Retzius *(Figure 3)*, and an average of seven cross-striations separating these markers. Thus, a total count of 51 striae of Retzius times 7 provides an estimated crown formation time of the imbricational enamel of the protocone of the first molar at 357 days, or 51 weeks. Taken together, these enamel microstructures identify an estimated 727 days (370+357 days) as the total time for crown formation of the first molar, or about 2 years.

In a similar manner, calculations are made for the upper first incisor. Appositional enamel formation is estimated

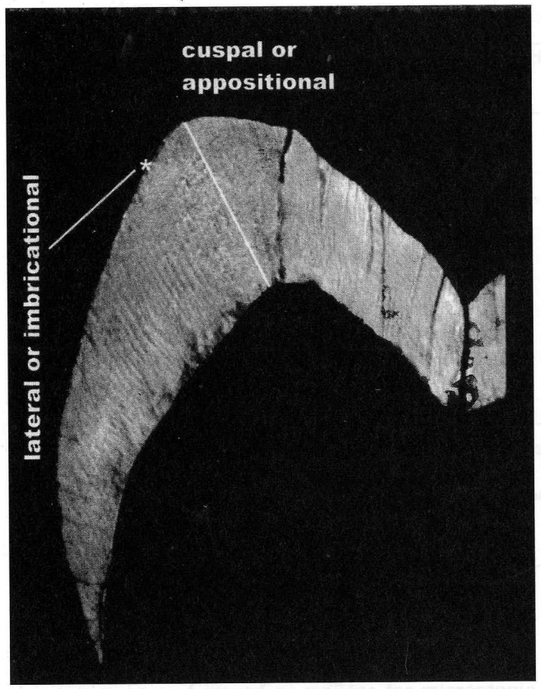

FIGURE 2. Scanning electron micrograph at 40× of a section through the protocone of the upper left first molar from Hasanlu specimen 60-20-226, illustrating the pattern of appositional and imbricational enamel.

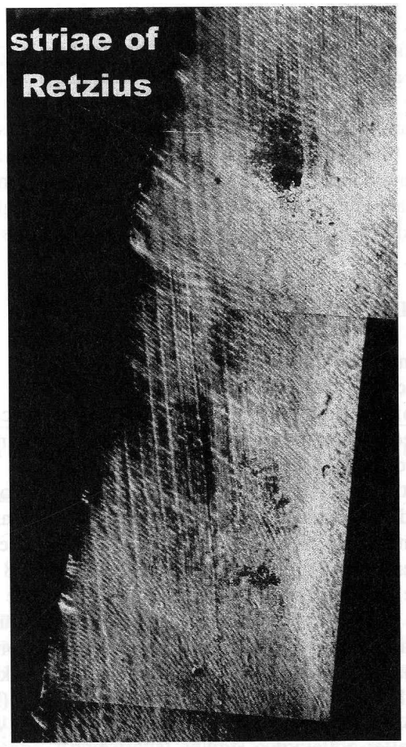

FIGURE 3. Scanning electron micrograph at 120× of a montage of the protocone section shown in *Figure 2*, illustrating the pattern of striae of Retzius and cross striations. Actual counts of the striae were done on montages at 160×, and of the cross striations at 320×.

at 217 days (217 cross-striations), or 31 weeks. Imbricational enamel formation is estimated as taking 595 days (85 striae of Retzius × 7 days). The total crown formation time estimated for this individual's incisor is 812 days, or 2.23 years.

Root formation time and age at death: Employing the method outlined by Dean and Beynon (1991) gives the following results: The lateral incisors lag behind the central incisors in both of these specimens, and thus, root formation on the central incisor precedes that on the lateral. The difference between the amount of enamel formed after the distinctive shared striae to the end of crown calcification on the lateral incisor is said to provide a time estimate for the development of the root formation on the central incisor. A 28 perikymata difference between the central and lateral incisor (lateral exceeding central) is found beyond this unique structure, or 196 days. Following Dean and Beynon (1991), this calculation provides the basis for an estimate of root formation rate for this tooth in this child and, thus, the total time of tooth formation for this child can be estimated and an age at death can be derived. The central incisor contains 1.5 mm of root more than the lateral incisor. If this took 196 days to form, as per the enamel structure counts, then it can be estimated that the root formation rate in this incisor is 7.6 µm per day. At this rate, the total root formation time for the first incisor was 1,315 days (10 mm at 7.6 µm per day). Taken together, this provides an estimated age at death of 5.8 years.

According to Dean and Beynon (1991), the root formation time of the first molar can be calculated as follows: The largest estimate for crown formation time for the first permanent molar was 1.99 years. If the age at death according to the first incisor is 5.8 years, the 9.0 mm of first molar root may have taken as long as 3.81 years to form, at a calculated rate of 6.5 µm per day. Thus, the root formation rates for this individual are estimated at 7.6 µm per day for the incisors and 6.5 µm per day for the molar.

The age at death as assessed from histological methods puts this individual at between 5.8 years of age based on a replication of the methods of Dean and Beynon (1991).

Specimen 73-5-508. The same method was applied to the forming incisors and first molar for this second specimen. After identification of the neonatal line, appositional enamel in the first molar was calculated from the cross-striations that extend from the tip of the dentin horn to the tip of the enamel. The total, less those under

the neonatal line, is 330 cross-striations. This is said to reflect 330 days of enamel formation time for the appositional enamel in the protocone, or 47 weeks (0.91 year).

Imbricational enamel in the first mandibular molar for this individual is estimated by the total number of striae of Retzius, and an average of seven cross-striations separating these markers. A total count of 90 striae of Retzius times 7 provides an estimated crown formation time of the imbricational enamel of the protocone of the first molar at 630 days, or 90 weeks (1.73 years). Taken together, these enamel microstructures identify an estimated 960 days as the total time for crown formation of this mandibular first molar, or about 2.63 years.

For the lower first incisor, appositional enamel formation is estimated at 210 days (210 cross-striations), 30 weeks, or 0.58 year. Imbricational enamel formation is estimated as taking 910 days (130 striae of Retzius × 7 days). The total crown formation time estimated for this individual's incisor is 1120 days, or 3.07 years. Similar analysis was performed on the lower lateral incisor (*Table 1, Figure 4*).

Root formation time and age at death: As this individual is younger than the first one, and less root formation is present on the dentition, the time taken for root formation is shorter than in the older specimen. By a comparison of unique enamel characteristics on both of the incisors, 9 more perikymata occur on the lateral incisor than the central incisor after the common prominent enamel band. Calculating the root formation rate from the 0.5 mm difference in root length between the two teeth reflects a 7.9 µm per day root extension rate and the age at death of this specimen is estimated at 3.42 years.

According to the methods of Dean and Beynon (1991), it can be proposed that root formation time for the first molar required 0.79 year, or 288 days (derived from 3.42 years age at death based on incisor histology less the 2.63 years calculated years for enamel formation on the first molar). This provides a root extension rate of 14.6 µm per day (4.2 mm / 288 days) for the molar tooth.

DISCUSSION

A comparison of the age at death estimates derived by two alternative methods identifies significantly younger ages resulting from histological methods than those derived from calcification stage references. This is contrary to recent observations from a similar study employing non-human primate comparisons (Reid *et al.* 1998b).

The young specimen in this study parallels one that was previously published in discussions surrounding the usefulness of perikymata-based age at death estimates (Mann *et al.* 1990b). Dean and Beynon (1991) contested these observations and stated that they doubted such a specimen would stand up to "histological scrutiny" (Dean, Beynon 1991: 227). As in our earlier publication, the specimen in the present study has incisor perikymata counts

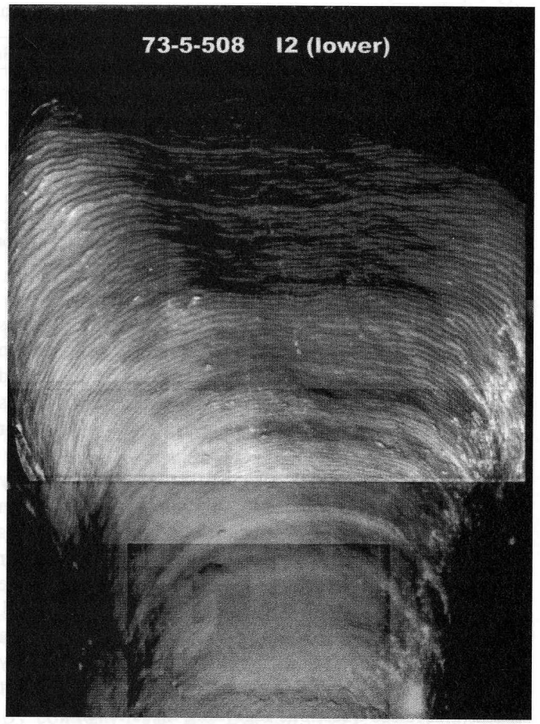

FIGURE 4. Scanning electron micrograph at 40× of the labial surface of a mandibular lateral incisor from an immature specimen from the site of Hasanlu (University of Pennsylvania Museum catalogue number 73-5-508) illustrating the pattern of perikymata. Actual counts of the perikymata were done on montages at 80×.

(137) quite similar to those found on Sts 24 (135) as published by Bromage and Dean (1985) and, thus, seemed a good candidate for histological scrutiny with the criteria and techniques set out in Dean and Beynon (1991), in terms of detailed assessment of crown formation and root growth.

The histological investigation reported here provides an estimated age at death at about 3.4 years of age using the Dean, Beynon (1991) methods. These are estimates that overlap an age at death based only on perikymata counts. In fact, this child is the predicted age of Sts 24 (Bromage, Dean 1985). These results provoke questions: Is it likely that this child, with first molar erupted, was indeed about 3.4 years of age at death?

The older individual studied here was aged, according to these histological methods, at 5.8 years of age. Again, these results raise the question of how likely it is that these ages are accurate and valid. For individuals at their respective dental maturity levels, first and second molar eruption, these are remarkably young ages by modern human standards. Indeed, it may be that our concepts and present descriptive data sets are not yet broad enough to accommodate such individuals. However, by contrast with

TABLE 2. A comparison of histologically-derived crown formation times.

	Present study	Reid *et al.* 1998a	Reid *et al.* 1998a	Dean *et al.* 1991	Dean *et al.* 1993
Upper I1	1.99	3.63–4.21			3.15
Lower I1	3.07	3.38–3.59			3.10
Lower I2		4.03–4.24		4.45	3.72
Upper M1	2.63	2.61–3.16	*2.83+/–0.29	3.09–3.12	2.41
Lower M1	2.23	3.06–3.59	*3.39+/–0.22		2.67

* Molar cusp formation calculated for the mesiobuccal cusp (protoconid), the counts in the present study and those of Dean *et al.* 1991, 1993.

conclusions one might reach on fossil specimens, there is no uncertainty in this study as to species growth pattern affinity of these two individuals and it cannot be concluded that they reached dental eruption at these very early ages by an accelerated growth pattern without further investigation.

When the ages at death deriving from the histologically based methods are compared to ages based on calcification stages, it is evident that the microstructural analysis consistently yields results that are either very young, or frankly outside of the range of variation for the respective tooth stages according to the reference of Moorrees *et al.* (1963) *(Table 1)*. This was also the case with perikymata counts (Mann *et al.* 1990a). While conceivable based only on calcification ages, it is the presence of the erupted first molar that raises questions regarding these results.

The older child exhibits a similar pattern of underageing by the histological method by comparison with radiologically derived calcification ages. This child, like the one previously discussed, is most curious in terms of the young assigned age at death in view of the developmental stage of the second molar. Taking into consideration the likely underageing that the radiographic approach may also reflect (Liversidge 1994), these specimens may be chronologically even somewhat older than this approach as well.

Differences between histological method based calculations of age at death and radiographically derived ages based on calcification staging have been the object of other recent investigations. However, these researchers conclude that radiographic methods consistently underestimate the ages of calcification, and, thus, age at death (Beynon *et al.* 1998, Reid *et al.* 1998), with data documenting crown formation times determined from histology longer than those identified by radiography by as much as two years (recently reviewed by Beynon *et al.* 1998). These explanations do not apply to the specimens studied here. We point out again that all histological counts were taken on the long developing buccal/labial surface on these specimens, and, thus, our results are not confounded by differential enamel surface deposition (Beynon *et al.* 1998).

A consideration of the present results requires careful consideration of the various aspects of the methods employed.

Crown formation times

A comparison of the crown formation times found here with those reported previously on other samples points out that with the exception of the maxillary incisor, they are close to those reported by Dean and Beynon (1991) for an English child from Spitalfields, and somewhat shorter than Reid *et al.* (1998a) report for incisor and molar crown formation times assessed in four French skeletal specimens *(Table 2)*. A consideration of methodological differences between these studies includes both the methods of calculating both appositional and imbricational enamel formation.

Appositional enamel methods: While the approach employed here parallels that of Dean and Beynon (1991), an alternative approach to the calculation of appositional enamel formation is used by Reid *et al.* (1998a). The latter study calculates crown formation times employing estimates of cumulative prism length (measures of enamel thickness corrected for prism decussation) divided by the average cross striation measurement. These alternative methods have been compared by Reid *et al.* (1998b) who document significant differences in crown formation times based on these two approaches, with overestimations of 2.5 to 21%, primarily in the anterior dentition, and underestimations ranging from about 4 to 8 percent, primarily in the molars, when the enamel thickness method is employed vs the striae count method. Thus, shorter crown formation times are predicted for the method employed by ourselves and Dean and Beynon (1991). Indeed, our results are less than those reported by Reid *et al.* (1998a) on the French specimens for the anterior dentition, although this is more pronounced in the maxillary incisor studied here. However, the molar crown formation times in our study are also lower than the range reported by Reid *et al.* (1998a), but in line with those reported by Dean *et al.* (1993a) for an African skeleton.

The results we report here contribute to the data base that is developing on crown formation times derived from histological methods. The known population affinity of our specimens also contributes to a perspective on what may be either population and/or individual differences in these developmental processes.

Imbricational enamel methods: In our calculation of imbricational enamel we employ the number of striae of Retzius (as do Reid *et al.* 1998a), whereas Dean and

Beynon (1991) used perikymata numbers. This should not influence our results as we document that there is high correspondence between our visualised striae of Retzius and the counted perikymata. In all of these histological studies, the time for crown formation is achieved by multiplying the visible line counts (perikymata or striae of Retzius) by the intervening number of cross striations to achieve the number of days of imbricational enamel formation.

In this study, we employ a seven day cross-striation repeat interval for calculating imbricational enamel. The number seven was adopted in the early studies of histological age reconstruction, from the original hominine studies (Bromage, Dean 1985), where seven cross striations between perikymata were employed on theoretical grounds, to the study of Beynon and Dean (1991), who identified seven cross striations between striae of Retzius in their specimen. While Reid *et al.* (1998a) review a number of studies by their colleagues who find that the number of cross striations between adjacent striae is always the same for an individual, we did not find this in our specimens. Whether this is due to population or individual differences unique to these specimens is unknown. Other studies have likewise observed variability in inter-striae cross striation counts, ranging from 4 to 11 (Huda, Bowman 1995, Risnes 1998).

However, a requirement of this method is a constant cross striation repeat interval between striae of Retzius/perikymata for imbricational enamel formation estimation and, thus, if dentition has not a constant cross striation interval, histological age estimation is impossible. We adopt a conservative approach to resolving this problem in employing a seven day periodicity between cross striations for deducing imbricational enamel formation time. We use this number as it is in line with the assumptions underlying the theory of the method. In general, with the exception of the maxillary incisor, the crown formation times found here are in line with previous reports using histological methods. In summary, we posit the cross striation variability between striae as a source of unknown error and agree with the recent statement of Risnes "that the Retzius line periodicity needs to be re-evaluated through further research in order to refine this tool for chronological studies" (Risnes 1998: 343).

Root formation estimation

We believe that a serious problem in this methodology is the method of inference concerning root formation time and that these formation times are having a strong influence on the ages at death of our specimens. Dean and Beynon developed the method used here and initially applied it to a Spitalfields' European child (Dean, Beynon 1991) and one specimen of *Gorilla gorilla* (Beynon *et al.* 1991) reporting 2.85 mm per day growth rates for incisors and 2.9 to 3.8 mm per day growth rates for the molar in this human, and from 5.1 on an upper second incisor to 13.3 on a lower first molar for the gorilla.

The methods posited to identify root formation time are based on an assumption that root formation progresses at a continuous daily rate. This is clearly erroneous: Both radiographic studies (Moorrees *et al.* 1963) and microstructural studies (Molnar *et al.* 1981), completed long before the propositions put forth by Dean and Beynon (1991), documented that there are times of variable velocity in root growth within a single teeth. Thus, it is not surprising that the use of a single rate of growth for the entire root formation time of a tooth would considerably underestimate the overall time frame of tooth development. Employing the identical method, the calculation of root formation time in the first 0.5 mm of one of our subjects' incisors, 7.9 µm per day, is more than twice that found in the earlier study by Dean and Beynon (1991), and the molar root formation rate of 14.6 µm per day found in the young human specimen in the present study, is on the order of that identified for gorilla first molars (13 µm/day), by Beynon *et al.* (1991). Either there is much higher variability in root formation time than previously imagined for humans and non-human primates, or there is a basic flaw in the method of derivation.

Thus, we raise questions about this methodology and the results that derive from it by all authors. When it was documented by Moorrees *et al.* (1963) that "the rate of tooth development is not constant," these authors emphasised that in terms of root growth, the second quarter of development is two to three times longer than the final quarter in their exemplary case of canines and premolars. By contrast, Dean and Beynon (1991) stated that their method likely masks a relatively slow rate of root formation immediately after crown completion, followed by a faster rate as root formation proceeds. They accepted their calculations as demonstrating "that modern human root extension rates may be some three or four times slower for the first portion of root growth than in great apes" (Dean, Beynon 1991:226).

This concept of variable growth rates in root formation is incorporated in more recent work by Dean and colleagues (Dean 1995, Dean, Scandrett 1995) where dentine deposition rates have been further investigated. They propose that the first 500 µm of root formation occur at 1.4 µm per day and the remaining dentine occurs at an average rate of 5.5 µm per day in humans. While these figures do not reflect the radiographic rates, they provide another approach. The validity of this approach awaits further research. We believe that it is highly unlikely that single rates of root formation will be found to be representative of all human children.

Some questions regarding histological age at death estimates

While some researchers find that the histological method works well in predicting age at death of known individuals, others do not come to these conclusions. For example, Stringer *et al.* (1990) used these methods on children of known age at death in their examination of 19 central incisors from the cemetery excavations at Christ Church, Spitalfields (Adams, Reeve 1987). In this study, the ages

at death calculated by the original method outlined by Bromage, Dean (1985) were consistently underestimated, particularly in individuals older than four years. The perikymata-derived age at death was on the average only 75% of the actual age. Stringer *et al.* (1990) employed a revision of the age-estimation method using an 8-day periodicity and a later date for the onset of calcification (6 months for lower central incisors and 9 months for upper central incisors) and produced age estimates that ranged from 85% to 127% of the actual ages in the Spitalfields children. Stringer *et al.* (1990) concluded that no single choice of cross-striation periodicity can reflect a population of individuals, and it is more appropriate to present a range of estimated ages based on a range of initial calcification times and cross-striation repeat intervals. These facts limit the utility of this method on samples of unknown internal dental microstructure.

Huda and Bowman (1995) also tested the histological method of age at death calculation on ten infants aged between 1 and 4 years of age from crypts at St. Bride's Church, London. While this study used a somewhat different methodological approach, one individual is underaged by 95% and three individuals are underaged by 42 to 86% of their actual ages. Thus, only three individuals ages are estimated within error, and two of these are under two years of age, leaving a narrow range for error.

If, in fact, the method is as exact as it is reputed, according to Huda and Bowman, who call it "extremely precise since it ages individuals in days" (Huda, Bowman 1995: 146), why can we not precisely identify the individuals whose ages at death are precisely known as two years, three months, fifteen days vs two years, eight months and twenty-eight days, a difference of 17% for the younger child? Huda, Bowman (1995) conclude that: "The method in itself has been proved to be very accurate; any inaccuracies in age estimation have occurred through practical difficulties, rather than being due to a flaw in the principle of the method" (Huda, Bowman 1995: 145). We believe that further work is necessary to substantiate this viewpoint.

For example, if there were merely methodological problems in carrying out the theoretical aspects of the method, one would expect that the errors in age assignment would be as likely to overestimate as to underestimate the age at death of the specimens, a result in line with statistically expected random error. However, consistently, across researchers and specimens, the greater likelihood is that the method underestimates the age at death of human specimens investigated, regardless of population of origin. It is difficult to applaud the conclusion that "the main argument in favour of the method is that, where it can be tested, it works" (Hillson 1996: 178).

By contrast, the results from non-human primates present an alternative conundrum. In reconstructing the age at death of three juvenile *Pan troglodytes* specimens, two specimens are aged at what appears to be relatively late chronological ages: One specimen (Animal 4, HT 89/89) is aged at 4.24 years at death. This specimen is described as having an unerupted maxillary first molar: "None of the permanent teeth have erupted" (Reid *et al.* 1998b:432-433). A second specimen (Animal 3, HT28/90) is aged at 5.61 years at death. Likewise, this specimen is described as having an unerupted mandibular first molar: "Radiographs showed unerupted I_1, I_2, C, P_3, P_4, M_1 and M_2¼" (Reid *et al.* 1998b: 432). Not only are these ages much later than the often cited ages for first molar eruption published by Nissen and Riesen (1964), but the latter is beyond the 90% confidence interval published by Conroy and Mahoney (1991). Either this analysis immensely extends our understanding of eruption ages in *P. troglodytes*, or further consideration of the methodological validity of histological age derivation needs to be undertaken. If the former is the case, then it is necessary that many often used approaches to differentiating growth patterns in hominines be discarded.

SUMMARY

The present study provides data that:

(1) Extend perikymata and striae of Retzius counts to non-European populations and emphasise the importance of collecting descriptive data from diverse populations to assist in a general understanding of the nature of dental histological microstructures.
(2) Raise questions about methods previously employed to estimate root formation rates, and suggest reassessments both of these approaches and the data gathered using them that support distinctive human and ape root growth patterns.
(3) Provoke consideration of the accuracy of the dental clock mechanism to identify true chronological ages.
(4) Do not support previous claims that estimates of ages derived from histological methods overlap those from independent methods such as radiography.
(5) Suggest that modern humans are characterised by a much wider range than is presently documented for ages of dental development and eruption.

We do not favour the last conclusion, but it must be considered. It appears from a consideration of the present results that further data collection is required on specimens of known age and diverse population affinities. Most of the present studies that have investigated known age at death individuals have had the greatest success on very young infants. As the margin of error at these ages is small, the most interesting test of the method's accuracy will be with individuals older than four years.

REFERENCES

ADAMS M., REEVE J., 1987: Excavations at Christ Church, Spitalfields 1984–6. *Antiquity* 61: 247–256.

ANEMONE R. L., MOONEY M. P., SIEGAL M. I., 1996: Longitudinal study of dental development in chimpanzees of known chronological age: implications for understanding the age at death of Plio-Pleistocene hominids. *Amer. J. of Phys. Anthrop.* 99: 119–133.

ANEMONE R. L., WATTS E. S., SWINDLER D. R., 1991: Dental development of known-age chimpanzees, *Pan troglodytes* (Primates, Pongidae). *Amer. J. of Phys. Anthrop.* 86: 229–241.

BEYNON A. D., CLAYTON C. B., RAMIREZ ROZZI F. V., REID D. J., 1998: Radiographic and histological methodologies in estimating the chronology of crown development in modern humans and great apes: A review, with some applications for studies on juvenile hominids. *J. of Hum. Evol.* 35: 351–370.

BEYNON A. D., DEAN M. C., 1991 : Hominid dental development. *Nature* 351: 196.

BEYNON A. D., DEAN M. C., REID D. J., 1991: Histological study on the chronology of the developing dentition in gorilla and orang-utan. *Amer. J. of Phys. Anthrop.* 86: 189–203.

BOYDE A.,1963: Developmental interpretations of dental microstructure. Estimation of age at death of young human skeletal remains from incremental lines in the dental enamel. Third International Meeting in Forensic Immunology, Medicine, Pathology and Toxicology, London. In: C. Jean DeRousseau (Ed.): *Primate life history and evolution*. Wiley-Liss, Inc., New York,1990.

BROMAGE T., 1991: Enamel incremental periodicity in the pig-tailed macaque: a polychrome fluorescent labelling study of dental hard tissues. *Amer. J. of Phys. Anthrop.* 86: 205–214.

BROMAGE T., DEAN M. C., 1985: Re-evaluation of the age at death of immature fossil hominids. *Nature* 317: 525–527.

CONROY G. C., MAHONEY C. J., 1991: Mixed longitudinal study of dental emergence in the chimpanzee, *Pan troglodytes* (Primates, Pongidae). *Amer. J. of Phys. Anthrop.* 86: 243–254.

CONROY G. C., VANNIER M. W., 1987: Dental development of the Taung skull from computerized tomography. *Nature* 329: 625–627.

CONROY G. C., VANNIER M. W., 1988: The nature of Taung dental maturation continued. *Nature* 333: 808.

CONROY G. C., VANNIER M. W., 1991a: Dental development in the South African australopithecines. Part I: Problems of pattern and chronology. *Amer. J. of Phys. Anthrop.* 86: 121–136.

CONROY G. C., VANNIER M. W., 1991b: Dental development in the South African australopithecines. Part II: Dental stage assessment. *Amer. J. of Phys. Anthrop.* 86: 137–156.

DEAN M. C., 1987a: The dental developmental status of six East African juvenile fossil hominids. *J. of Hum. Evol.* 16: 197–213.

DEAN M. C., 1987b: Growth layers and incremental markings in hard tissues; a review of the literature and some preliminary observations about enamel structure in *Paranthropus boisei*. *J. of Hum. Evol.* 16: 157–172.

DEAN M. C., 1995: The nature and periodicity of incremental lines in primate dentine and their relationship to perpendicular bands in OH 16 (*Homo habilis*). In: J. Moggi-Cecchi (Ed.): *Aspects of dental biology: Palaeontology, anthropology and evolution*. Pp. 239–265. International Institute for the Study of Man, Florence.

DEAN M. C., BEYNON A. D., 1991: Histological reconstruction of crown formation times and initial root formation times in a modern human child. *Amer. J. of Phys. Anthrop.* 86: 215–228.

DEAN M. C., BEYNON A. D., REID D. J., WHITTAKER D. K., 1993a: A longitudinal study of tooth growth in a single individual based on long and short period incremental markings in dentine and enamel. *Internat. J. of Osteoarchaeology* 3: 249–264.

DEAN M. C., BEYNON A. D., THACKERAY J. F., MACHO G. A., 1993b: Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. *Amer. J. of Phys. Anthrop.* 91: 401–419.

DEAN M. C., SCANDRETT A. E., 1995: Rates of dentine mineralization in permanent human teeth. *Internat. J. of Osteoarchaeology* 5: 349–358.

DEAN M. C., WOOD B. A., 1981: Developing pongid dentition and its use for ageing individual crania in comparative cross-sectional growth studies. *Folia Primatologica* 36: 111–127.

EVELETH P. B., TANNER J. M., 1976: *World wide variation in human growth*. Cambridge University Press, Cambridge.

EVELETH P. B., TANNER J. M., 1990: *World wide variation in human growth*. Cambridge University Press, Cambridge.

FITZGERALD C. M., 1998: Do enamel microstructures have regular time dependency? Conclusions from the literature and a large-scale study. *J. of Hum. Evol.* 35: 371–386.

HILLSON, S., 1996: *Dental anthropology*. Cambridge University Press, Cambridge. 373 pp.

HUDA T. F. J., BOWMAN J. E., 1995: Age determination from dental microstructure in juveniles. *Amer. J. of Phys. Anthrop.* 97: 135–150.

KUYKENDALL K. L., 1996: Dental development in chimpanzees (*Pan troglodytes*): The timing of tooth calcification stages. *Amer. J. of Phys. Anthrop.* 99: 135–157.

KUYKENDALL K. L., CONROY G. C., 1996: Permanent tooth calcification in chimpanzees (*Pan troglodytes*): Patterns and polymorphisms. *Amer. J. of Phys. Anthrop.* 99: 159–174.

LAMPL M., JOHNSTON F. E., 1995: Problems in the ageing of skeletal juveniles: perspectives from the maturational assessment of living children. *Amer. J. of Phys. Anthrop.* 101: 345–355.

LAMPL M., MONGE J. M., MANN A. E., 1993: Further observations on a method for estimating hominoid dental developmental patterns. *Amer. J. of Phys. Anthrop.* 90: 113–127.

LIVERSIDGE H. M., 1994: Accuracy of age estimation from developing teeth of a population of known age (0–5.4 years). *Internat. J. of Osteoarchaeology* 4: 37–45.

LIVERSIDGE H. M., 1995: Crown formation times of the permanent dentition and root extension rate in humans. In: J. Moggi-Cecchi (Ed.): *Aspects of dental biology: Palaeontology, anthropology and evolution*. Pp. 267–275. International Institute for the Study of Man, Florence.

MACHO G. A., WOOD B. A., 1995: The role of time and timing in hominid dental evolution. *Evol. Anthrop.* 4: 17–31.

MANN A. E., 1975: *Some palaeodemographic aspects of the South African Australopithecines*. Philadelphia: University of Pennsylvania Department of Anthropology Publications in Anthropology 1.

MANN A. E., 1988: The nature of Taung dental maturation. *Nature* 333: 123.

MANN A. E., LAMPL M., MONGE J. M., 1990a: Patterns of ontogeny in human evolution: Evidence from dental development. *Yearbook of Phys. Anthrop.* 33: 111–150.

MANN A. E., MONGE J. M., LAMPL M., 1990b: Dental caution. *Nature* 348: 202.

MANN A. E., LAMPL M., MONGE J. M., 1991: Investigation into the relationship between perikymata counts and crown formation times. *Amer. J. of Phys. Anthrop.* 86: 175–188.

MANN A. E., MONGE J. M., 1987: Reproducing our ancestors. *Expedition 29*.
MAPPES M. S., HARRIS E. F., BEHRENTS R. G., 1992: An example of regional variation in the tempos of tooth mineralization and hand-wrist ossification. *Amer. J. of Orthodontics and Dentofacial Orthopedics* 101: 145–151.
MILES A. E. W., 1963: Dentition in the estimation of age. *J. of Dental Research* 42: 255–263.
MOLNAR S., PRZYBECK T. R., GANTT D. R., ELIZONDO R. S., WILKERSON J. E., 1981: Dentin apposition rates and markers of primate growth. *Amer. J. of Phys. Anthrop.* 55: 443–453.
MOORREES C. F. A., FANNING E. A., HUNT E. E., 1963: Age variation of formation stages for ten permanent teeth. *J. of Dental Research* 42: 1490–1502.
MUSCARELLA O. W., 1989: Warfare at Hasanlu in the late 9th century BC. *Expedition* 31: 24–36.
NISSEN H. W., RIESEN A. H., 1964: The eruption of the permanent dentition in the chimpanzee. *Amer. J. of Phys. Anthrop.* 22: 285–294.
RAMIREZ-ROSSI F. V., 1992: Teeth development pathway in 3 Myrs hominids. *Amer. J. of Phys. Anthrop.* 88: 269.
RAMIREZ-ROSSI F. V., 1993a: Tooth development in East African *Paranthropus*. *J. of Hum. Evol.* 24: 429–454.
RAMIREZ-ROSSI F. V., 1993b: Microstructure et dévelopement de l'émail dentaire du néantderthalien de Zafarraya, Espagne. Temps de formation et hypocalcification de l'émail dentaire. *Comptes Rendus de l'Académie des Sciences*, Paris 316, s r. II: 1635–1642.
RAMIREZ-ROSSI F. V., 1995: Time of formation in Plio-Pleistocene hominid teeth. In: J. Moggi-Cecchi (Ed.): *Aspects of dental biology: Palaeontology, anthropology and evolution*. Pp. 267–275. International Institute for the Study of Man, Florence.
REID D. J., BEYNON A. D., RAMIREZ ROZZI F. V.,1998a: Histological reconstruction of dental development in four individuals from a medieval site in Picardie, France. *J. of Hum. Evol.* 35: 464–477.
REID D. J., SCHWARTZ G. T., DEAN C., CHANDRASEKERA M. S., 1998b: A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. *J. of Hum. Evol.* 35: 427–448.
RISNES S., 1998: Growth tracks in dental enamel. *J. of Hum. Evol.* 35: 331–350.
SACHER G. A., 1975: Maturation and longevity in relation to cranial capacity in hominid evolution. In: R. H. Tuttle (Ed.): *Primate functional morphology and evolution*. Pp. 417–442. Mouton, The Hague.
SCHOUR I., PONCHER H. C., 1937: The rate of apposition of human enamel and dentin as measured by the effects of fluorosis. *Amer. J. of Diseases of Childhood* 54: 757–776.
SIMPSON S. W., LOVEJOY C. O., MEINDL R. S., 1990: Hominoid dental maturation. *J. of Hum. Evol.* 19:285–297.
SIMPSON S. W., LOVEJOY C. O., MEINDL R. S., 1991: Relative dental development in hominoids and its failure to predict somatic growth velocity. *Amer. J. of Phys. Anthrop.* 86: 113–120.
SMITH B. H., 1986: Dental development in Australopithecines and early *Homo*. *Nature* 323: 327–330.
SMITH B. H., 1989: Growth and development and its significance for early hominid behaviour. *Ossa* 14: 63–96.
SMITH B. H., 1991: Dental development and the evolution of life history in *Hominidae*. *Amer. J. of Phys. Anthrop.* 86: 157–174.
SMITH B. H., 1992: Life history and the evolution of human maturation. *Evol. Anthrop.* 1: 134–142.
SMITH B. H., 1994: Sequences of eruption of the teeth in *Macaca*, *Pan*, *Australopithecus* and *Homo*. Its evolutionary significance. *Amer. J. of Human Biology* 6: 61–76.
SMITH B. H., TOMPKINS R. L., 1995: Towards a life history of the Hominidae. *Annual Review of Anthropology* 24: 257–279.
STRINGER C. B., DEAN M. C., MARTIN R. D., 1990: A comparative study of cranial and dental development within a recent British sample and among Neanderthals. In: J. de Rousseau (Ed.): *Primate life history and evolution*. Pp. 115–152. Wiley-Liss, New York.
WEISS M. L., 1987: Nucleic acid evidence bearing on hominoid relationships. *Yearbook of Phys. Anthrop.* 30: 41–73.
YILMAZ S., NEWMAN H. N., POOLE D. F. G., 1977: Diurnal periodicity of von Ebner growth lines in pig dentine. *Archives of Oral Biology* 22: 511–513.

Michelle Lampl
Department of Anthropology
Geosciences 219
1557 Pierce Drive
Emory University
Atlanta, Georgia
USA
Tel.: +1- 404-727-2214
Fax: +1-404-727-2860
E-mail: mlampl@emory.edu

Alan Mann
Department of Anthropology
University of Pennsylvania
Philadelphia, Pennsylvania 19104 USA

Janet Monge
Department of Anthropology
Bryn Mawr College
Bryn Mawr, Pennsylvania 19010 USA
and
Department of Anthropology
University Museum
University of Pennsylvania
Philadelphia, Pennsylvania
19104 USA