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A radiographic study of the development of the human mandibular dentition

This paper presents new data on the absolute timing of the growth of the mandibular permanent teeth, with an emphasis on the timing of the completion of the enamel crown. Two collections of cranio-dental radiographs were analyzed: (1) 267 juveniles from a contemporary pediatric dental clinic (Case Western Reserve University School of Dentistry, Cleveland, Ohio), and (2) 36 individuals sampled longitudinally from the Bolton-Brush Growth Study Center. The ages of the individuals span from three months to 18 years of age and the study includes both cross-sectional and longitudinal data. Comparisons of the ages of attainment of the Cleveland samples with other schedules of dental development are made. The relative contribution of the multiple underlying sources of variation producing the differences between the radiographically based developmental schedules remain elusive.

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Introduction

A number of longitudinal and cross-sectional studies of human dental development now exist (Cattell, 1928; Hess *et al.*, 1932; Schour & Massler, 1941; Gleiser & Hunt, 1955; Demisch & Wartmann, 1956; Garn *et al.*, 1959; Nolla, 1960; Fanning, 1961; Moorrees *et al.*, 1963*a*,*b*; Nanda & Chawla, 1966; Fanning & Brown, 1971; Liliequist & Lundberg, 1971; Nielsen & Ravn, 1976; Demirjian & Levesque, 1980; Trodden, 1982; Nichols *et al.*, 1983; Nystrom *et al.*, 1986; Demirjian, 1980; Diato *et al.*, 1989, 1990; Harris & McKee, 1990; Ochollo, 1990; Diaz *et al.*, 1993). Although these studies rely on different sampling procedures, analytic techniques, and media, many, especially those most commonly used, are based on broadly similar populations (primarily healthy middle-class children of European ancestry). Although populational and regional differences in the timing of dental development have been identified (Nanda & Chawla, 1966; Fanning & Moorrees, 1969; Nielsen & Ravn, 1976; Chertkow, 1980; Nichols *et al.*, 1983; Owsley & Jantz, 1983; Nystrom *et al.*, 1986, 1988; Ochollo, 1990; Harris & McKee, 1990; Mappes *et al.*, 1992; Diaz *et al.*, 1993; Tompkins, 1996; Speechly & Liversidge, 1997), their significance and cause are uncertain. Differences in the timing of developmental events between these studies

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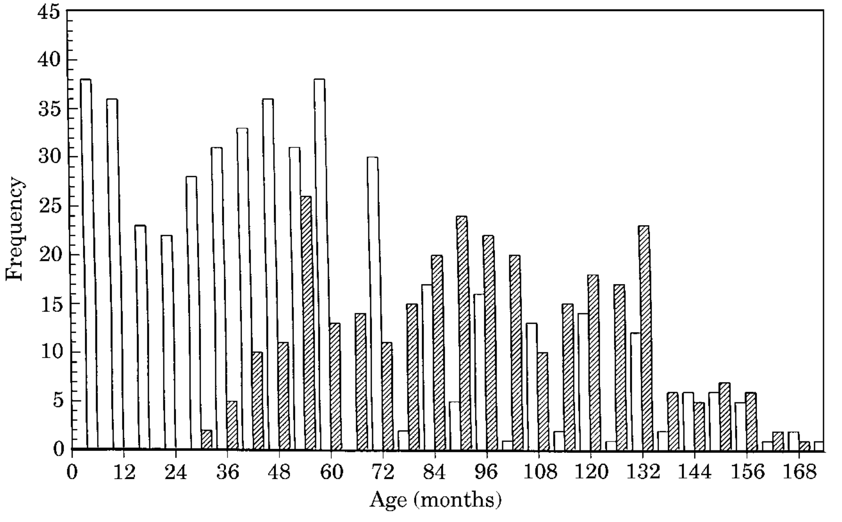

Figure 1. Age distribution of the radiographs used in this study. Observational data are calculated to nearest month. Total number of radiographs examined is 774. Total number of individuals included in this study is 303. The cases are coalesced into six month intervals for this figure. Figure truncated at 168 months although cases included in this study extend up to 220 months. Pediatric Dental Clinic: filled bars; Bolton-Brush Growth Study: open bars.

can be marked and nonbiological factors (e.g., methodology, choice of morphological standard, differences in analytic approach and sample age distribution) have been identified as a potential source of variation (Harris & McKee, 1990; Smith, 1991). This study will examine dental growth from cross-sectional and longitudinal radiographs of contemporary urban children ranging in age from 3 months to 18 years. These data are then compared with existing schedules of the growth of the mineralized dental tissues. Although both maxillary and mandibular data were collected and analyzed, only the growth of the mandibular dentition will be presented here.

Samples: PDC and BBGS

The radiographs were derived from the Case Western Reserve University School of Dentistry Pediatric Dental Clinic (PDC) and the Bolton-Brush Growth Study Center (BBGS) which is curated by the CWRU School of Dentistry. Both samples are derived from individuals residing in the area of Cleveland, Ohio, U.S.A. The PDC sample included 134 girls and 133 boys (231 individuals with one radiograph and 36 individuals with 2–5 radiographs) from a contemporary teaching pediatric dental clinic examined between 1993 and 1996. These radiographs included intraoral and panoramic radiographs. The anterior teeth were examined in the labio-lingual plane. Age of the individuals is reported to the nearest month and the mean age of the sample of radiographs was $95{\cdot}2 \pm 37{\cdot}2$ months with a range between 26 and 216 months (Figure 1). This truncated age sample is a consequence of the difficulty in radiographing very young children as well as the infrequency of dental pathology in this cohort. The longitudinal PDC data are individuals that have multiple (2–5) plates separated by at least three months. The PDC population is biologically diverse and reflects the local urban and suburban populational composition of the Cleveland, Ohio area. Specific populational affiliation is not possible because these data are not a part of the personal histories collected for the patients. Some health data are available (e.g., history of febrile diseases, ear infections, Sickle-cell anemia/trait) but these were not rigorously collected so a health profile of this population is not possible.

The BBGS collection is a longitudinal growth study which includes anthropometric, radiographic, and behavioral data on a sample of over 4000 healthy, primarily middle-class individuals mainly of European descent residing in the Cleveland, Ohio area (Behrents & Broadbent, 1984). The study began in the 1920s and the radiographs used here were taken in the 1930s and 1940s. The patient's head was fixed in a frame (cephalometer) which standardized cranial orientation while lateral and antero-posterior radiographs were taken. Some very young children (usually less than 18 months) were held manually in place. Subjects were expected to appear for mensuration following a very strict schedule and most of the visits adhered to this schedule. The testing was to occur every three months in the first year, every six months until five years, and then annually on the birthday. The age of examination was calculated to the nearest month and these scheduled visits are clearly reflected in the age distribution (Figure 1). Although many individuals continued in the study into their third decade (and beyond—the BBGS is still active after more than 60 years), we collected limited data after the thirteenth year. The radiographs of the 36 individuals (19 males, 17 females) have a mean age of $56{\cdot}2 \pm 42{\cdot}1$ months with a range between three and 220 months. The number of radiographs per case ranged between four and 24 (mean = 12·7 plates per child). The age structure and composition of the BBGS and PDC samples is markedly different.

The BBGS radiographic plates showed virtually no deterioration although the intense use of the collection is evident. The images were generated not to maximize resolution of the dental tissues but to identify cranial landmarks. Lateral and AP cranial radiographs are not the optimal views for evaluating dental maturity because of the overlapping structures. However, the two views of the anterior teeth allowed us to maximize accuracy of their morphological scoring. Nonetheless, the BBGS is an extremely valuable resource that will continue to provide excellent, fine-grained, rigorously normalized longitudinal data on a large sample of healthy individuals.

Data collection

The resolution of any growth study is a product of both sampling interval and number of morphological increments of the changing anatomy. Accurate identification of subtle morphological change in the growing dentition can be improved by reducing the interval between radiographic sampling and/or increasing the number of morphological scoring categories. Long time intervals and broad scoring categories impose a saltatory appearance onto the maturation of the teeth where it does not exist. Attainment of defined stages must be then made by both chronological and morphological interpolation (Tanner, 1962). For example, the yearly sampling schedule of the BBGS after five years of age means the vast majority of the annual growth remains unsampled during this very dynamic period. Shortening the sampling interval may expose individuals to a potentially excessive dose of radiation. In addition to the BBGS data, we have included the more randomly aged PDC children. They present a flat and more even distribution of ages which complements well the serrated distribution of the BBGS, especially after 30 months (Figure 1).

An additional approach to improving the description of dental growth is to increase the number of morphological increments. Virtually all of the studies of human dental development in the past 50 years have adopted some variant of the stage system of dental scoring (Gleiser & Hunt, 1955; Demisch & Wartmann, 1956; Garn *et al.*, 1959; Nolla, 1960; Fanning, 1961; Moorrees *et al.*, 1963*a*,*b*; Demirjian *et al.*, 1973; Demirjian & Levesque, 1980; Fanning & Brown, 1971; Liliequist & Lundberg, 1971; Anderson *et al.*, 1976; Nielsen & Ravn, 1976; Harris & McKee, 1990; although see Israel & Lewis 1971; Shellis, 1984; Beynon & Reid, 1987; Dean & Beynon, 1991; Beynon & Dean, 1991; Liversidge *et al.*, 1993; Liversidge, 1995). Growth of the teeth in each of these studies has been divided into a series of morphological classes or stages. The definition of the stages is arbitrary and depends on the sample composition, research questions, and required degree of precision. Consequently some researchers have found as few as eight stages useful (Demirjian & Levesque, 1980) whereas others have defined as many as 20 (Gleiser & Hunt, 1955; Fanning, 1961). Many have adopted the 13/14 stage system (or a variant) used by Moorrees and coworkers (1963*a*) [hereafter referred to as MFHp] for the permanent teeth (e.g., Anderson *et al.*, 1976; Harris & McKee, 1990). This MFHp system is a modification of the 15 stage system originally described by Gleiser & Hunt (1955). As Moorrees *et al.* (1963*a*) noted, the stages are arbitrarily defined and not necessarily the only scoring approach possible. The MFHp system combines ease of application with replicability, yet is still capable of identifying subtle differences in morphology. On the other hand, a stage system can force the teeth into one of a limited number of stages which are not necessarily equivalent in degree of morphological breadth. It also has the potential of condensing a great degree of morphological change into too broad a category.

In lieu of this approach, a different scoring system was adopted (Figure 2) (Simpson *et al.*, 1990; Simpson, 1992). Each tooth was scored on a scale of 0·00 to 2·00 in increments of 0·01 where 0·00 indicates no radiographic evidence of crown formation, 1·00 equals a complete enamel crown, and 2·00 equals apical closure of the root. This morphological definition was originally developed by seriating radiographs of maxillary and mandibular dentitions from the Hamann-Todd Osteological collection (Cleveland Museum of Natural History, Cleveland, Ohio) and by direct examination of teeth from the late Woodland Libben population (Department of Anthropology, Kent State University, Kent, Ohio) in comparison with the MFHp stages (1963a: Figures 1 & 2). This system is comparable and can be translated into the stage scores assigned by other researchers (e.g., Nolla, 1960; Fanning, 1961; Moorrees *et al.*, 1963a; Demirjian, 1980). For example, an MFHp score of crown one-half complete is equal to a score of 0·50 in this study or a Nolla (1960) score of root two-thirds complete is broadly equivalent to a score of 1·67 here. The MFHp system identified a series of morphological changes in the root apex. These are consistent with a score of greater than 1·90 in this study. When scoring the longitudinal BBGS radiographs continual reference between sequential radiographs for an individual produced an internally consistent scoring (also noted by Moorrees *et al.*, 1963*a*).

This approach recognizes and accounts for the continuous change that occurs in dental development as opposed to the saltatory growth that a stage system can impose. Although Nolla (1960: 257) noted that a finer-grained scoring system of the dentition from radiographs may not be feasible, the goals of this research differs from that of clinical practice where a rapid approximation of the dental status of a single case is paramount. The rate of morphological change in the tooth crown is nonlinear, and teeth show slowed growth in the cervical

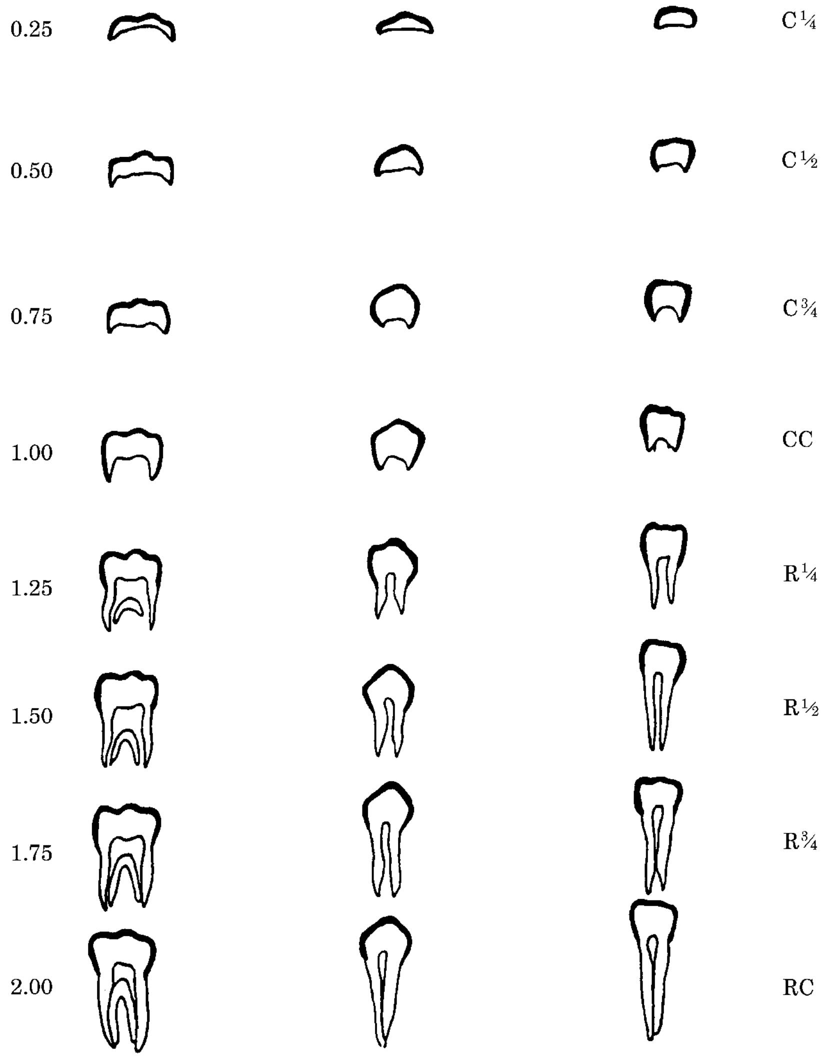

Figure 2. Schematic illustration of dental scoring method. Modified from Dean & Wood (1981). C½ = Crown one-half complete, CC = crown complete with no root, R½ = root one-half complete, RC = root complete or apical closure.

region and during apical closure. Minor changes in shape, which may develop over a protracted period of time, may not be clearly described by a system that has stages that are too broad and inclusive. Here, we are attempting to identify fine morphological changes for comparative purposes. Broader categories may combine teeth identifiably different into a single group and reduce the resolution of the comparison. Conversely, the morphological intervals in this study can be coalesced into larger stages. For example, summary data for the completion of the enamel crown in the anterior teeth were calculated by combining individuals having a score between 0·95 and 1·03 based on morphological criteria (see below). Finally, each increment is approximately equivalent in degree of morphological change (although not necessarily in duration) and is more amenable to parametric statistical analyses.

The PDC incisors were examined from panoramic and intraoral plates viewed along the labio-lingual plane. Teeth with sinusoidal cervices (especially incisors and canines) begin root formation before the enamel crown is complete (Beynon & Reid, 1987; Liversidge, 1995). As such, we identified a completed crown in the anterior teeth only when the labial and lingual enamel margins developed their characteristic cervical extension. Teeth with a truncated cervical enamel edge, even if the mesial and distal surfaces showed evidence of root formation, were considered to have an incomplete crown. The BBGS lateral radiographs allowed viewing of the completed crown and initial root elongating on the labial and lingual surfaces. Then these were compared with the AP views of the same individual to maximize congruence of scoring for the different views. Therefore, consistent types of data were collected for the two samples.

Like the incisors, the canines were viewed labio-lingually in the PDC sample while in the BBGS sample they were seen in both the sagittal and coronal planes. As above, only when a sinusoidal enamel cervical outline was apparent was the crown identified as complete. The premolars and molars in both studies were viewed and scored along the bucco-lingual plane and similar criteria of dental completion were applied.

Ages of attainment were calculated in two ways. First, a simple mean age of attainment was calculated for all cases within a defined scoring range (e.g., crown completion [canine: 0·95–1·03]). Second, the median age of attainment is calculated from a cumulative frequency score of cases for a morphological range. This latter value tends to be less biased by asymmetry in the distribution. Bivariate representations of dental development with age are also presented for each mandibular tooth.

The goals of this paper are: (1) to present new data on the developmental timing of the mandibular dentition in humans from oral radiographs and (2) to compare these data with previously published schedules.

Results

Mandibular central incisor

Data for the first two years of development are limited to the BBGS collection. The sample size increases considerably by the fourth year with the inclusion of the PDC radiographs (Figures 1 & 3). Not unexpectedly, the formation of the I1 precedes the I2. The earliest radiographic evidence of the central incisor appears in the first half of the first year. This is consistent with the other radiographic estimates of the onset of mineralization. Histologic observations indicate that the mandibular central incisor initiates crown formation perinatally or postnatally (Logan & Kronfeld, 1933; Dean & Beynon, 1991; Liversidge, 1995; Reid, personal communication). Radiographic assessments of any tooth's maturity will always be biased towards a later age because of the low degree of mineralization of the most recently formed enamel and dentine and by the absence of radiographic data on prenatal dentitions. Histologic estimates of formation using complete, unworn teeth seem to overcome both of these problems. Although there are topographic and imaging reasons why radiographic observations should underestimate the age of crown formation and overestimate the time of initial crown mineralization (Gleiser & Hunt, 1955), future research should continue to attempt to reconcile the radiographic and histologic approaches in determining the absolute schedule of crown and root formation (Winkler, 1995).

The radiographs included both coronal and sagittal views (BBGS) and panoramic or intraoral plates (PDC). The panoramic and intraoral plates view the anterior teeth in the

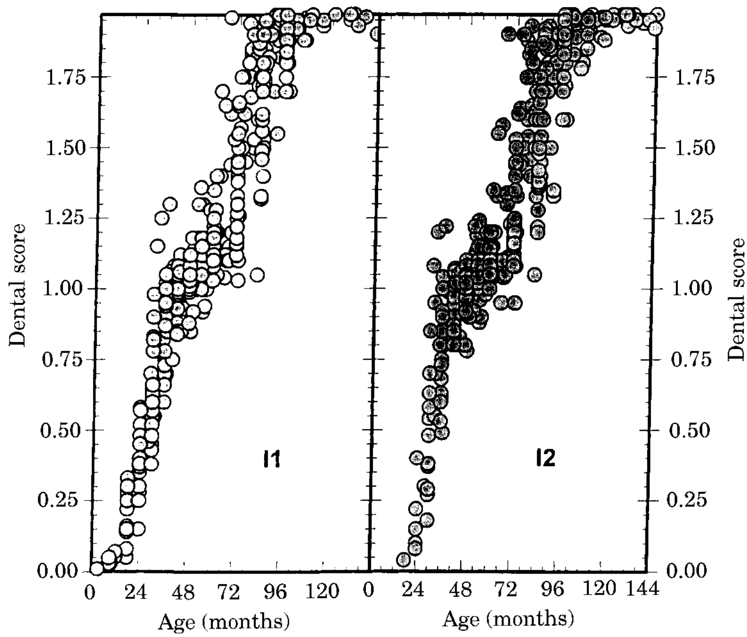

Figure 3. Bivariate comparison of dental development of the mandibular incisors with age in months. Dental score is measured between 0·00 and 2·00 (see Figure 2 and text). Each circle represents a single observation (i.e., radiograph).

labio-lingual dimension. In incisors, the labial and lingual margins of the crown extend more apically than the mesial or distal borders. Consequently, as others have noted (Beynon *et al.*, 1991; Beynon & Reid, 1987; Liversidge, 1995) the forming root can be visible on the mesial and distal margins of an incompletely formed crown giving the mistaken impression that the crown has completed growth. Consequently, teeth imaged in the labio-lingual view may be assigned an inappropriately higher score. Imaging orientation may result in aging biases but it does not appear to be a significant factor here.

Crown formation of the I1 is estimated to be completed in the most precocial individuals by about 36–39 months, with the longest duration about four and a quarter years, and a mean of about 44–46 months (Table 1). This value is consistent with other radiographic (Table 2) and histology-based estimates. Using a careful accounting of surface developmental increments (perikymata), Beynon & Dean (1991) estimated the age of crown completion to be 39–44 months ($n=10$). Reid (personal communication) calculated the period of crown formation based on enamel microstructural increments to be about 41 months with an age of crown completion of 44 months. Some histologic estimates of crown formation have yielded longer developmental durations (59 months [Shellis, 1984], 53·4 months, $n=1$ [Dean & Beynon, 1991], between 54 and 72 months [Liversidge, 1995]).

There is a distinct change in the rate of tooth formation near crown completion. The rate of morphological change drops drastically as the cervical portion of the crown is formed (Fanning, 1961; Shellis, 1984; Beynon & Reid, 1987; Dean & Beynon, 1991; Huda & Bowman, 1995). This is consistent with the evidence from perikymata distribution and breadth

Table 1 Summary data for age of mandibular tooth crown completion for the BBGS/PDC samples

Tooth type	Median	Mean	S.D.	Minimum	Maximum	25%	75%	*N*
I1	42	44·6	8·17	30	73	42	48	44
I2	48	48·8	7·22	32	73	42	54	55
C	60	65·7	11·36	48	96	58·5	72	64
P3	85·5	85·0	10·84	67	108	74·5	92·5	28
P4	85·5	87·2	13·75	67	132	77	94	38
M1	42	42·3	5·62	30	55	37	48	50
M2	96	92·4	11·09	72	111	84	97·8	39

Sexes are combined. All ages in months. All crowns calculated as complete by combining a range of scores. Anterior teeth include values between 0·95 and 1·03. Post canine teeth combine values between 0·95 and 1·01. Mean values are unweighted means of all cases within this range. Median age is determined by a survival function of cases within this range.

(Figure 4) (Beynon & Reid, 1987; Dean & Beynon, 1991; Hillson & Bond, 1997). As shown in Figure 4, there is a marked increase in the density of perikymata at the cervix of the I1 crown. This indicates that a substantial period of time elapsed with only minor changes in crown morphology (i.e., many narrow perikymata are formed).

The rate of morphological change increases after the root is about 15% complete. The rate of root elongation remains high until about 90% of the root is completed. As expected the rate of root elongation is greatest in the period accompanying emergence (Carlson, 1944; Marks & Schroeder, 1996). Root extension slows as the apical opening becomes smaller. This pattern of root formation has been identified in all studies. It is very difficult to determine from radiographs when apical closure is completed. However, the full functional length of the root is attained between the ages of seven and eight and a quarter years. This occurs about 1–2 years following emergence.

Mandibular lateral incisor

The lateral incisor follows a very similar period and pattern of growth as the first incisor except for two minor differences (Figure 3). First, there is an offset in the attainment of the various stages of development (e.g., onset, crown completion, and attainment of full root length) of about 4–12 months. Second, the period of growth deceleration at crown completion is shorter. If a bivariate plot comparing the relative growth of the first and second incisors is made, these differences can be clearly seen (Figure 5). The diagonal line represents morphological identity. Cases which lie to the left or above the line have a relatively advanced central incisor. Throughout the entire sequence of development from onset to root completion the central incisor is developmentally advanced relative to the lateral incisor. The closest overlap between the two teeth occurs around crown completion when the more slowly growing central incisor is overtaken slightly by the lateral incisor with its shorter period of crown completion delay.

Again, the age of I2 crown completion (49 months) in the BBGS/PDC sample (Table 1) is concordant with the other radiographic standards with the exception of Nielsen & Ravn (1976) who record an age of I2 crown completion over a year earlier (females: 34·5 months; males: 36 months) than the Cleveland sample. Little histological research has been done on the duration of the lateral incisor crown formation. Dean & Beynon (1991) report an archaeological specimen that began enamel matrix

Table 2 A comparison of some commonly used dental developmental schedules for mandibular teeth for the stage of crown completion

Tooth type	G&H 1955	GLP 1959	Nolla 1960	Fanning 1961	MFHp 1963*a*	Fass 1969	F&B 1971	N&R 1976	ATP 1976	D&L 1980	H&M 1990	PDC/BBGS
I1	ND	ND	44/42*	ND	ND	40	ND	37/33·5	43/43	ND	**44/47 48/41	45
I2	ND	ND	52/48	ND	ND	47	ND	36/34·5	48/44	ND	49/54 53/49	49
C	ND	ND	72/68	50/49	53/48	55	54/53	52/49·5	58/49	40/35	67/60 66/59	66
P3	ND	85/83	84/78	53/63	67/65	72	69/63	69/56·5	67/60	54/50	82/77 76/74	85
P4	ND	95/92	92/86	80/74	79/78	84	78/79	80·5/77·5	76/71	71/67	91/88 86/79	87
M1	42/39	48/44	48/46	ND	30/29	35	29/29	39/35·5	44/ND	ND	42/42 36/38	42
M2	ND	102/101	98/84	78/74	82/78	ND	80/81	ND	80/76	76/71	96/89 88/82	92

All ages rounded to nearest month. PDC/BBGS scores of 0·95–1·03 constituted crown completion for the anterior teeth and 0·95–1·01 for the postcanine teeth (see Table 1). G&H 1955 = Gleiser & Hunt, 1955. GLP 1959 = Garn *et al.*, 1959. MFHp 1963*a* = Moorrees *et al.*, 1963*a*. ATP 1976 = Anderson *et al.*, 1976. N&R 1976 = Nielsen & Ravn, 1976. D&L 1980 = Demirjian & Levesque, 1980. H&M 1990 = Harris & McKee, 1990. PDC/BBGS = this study.

* = The first number of each pair is male, the second female. Where only one number is given, the sexes are combined. ** = First row are white males and females and the second row is black males and females. ND = No Data.

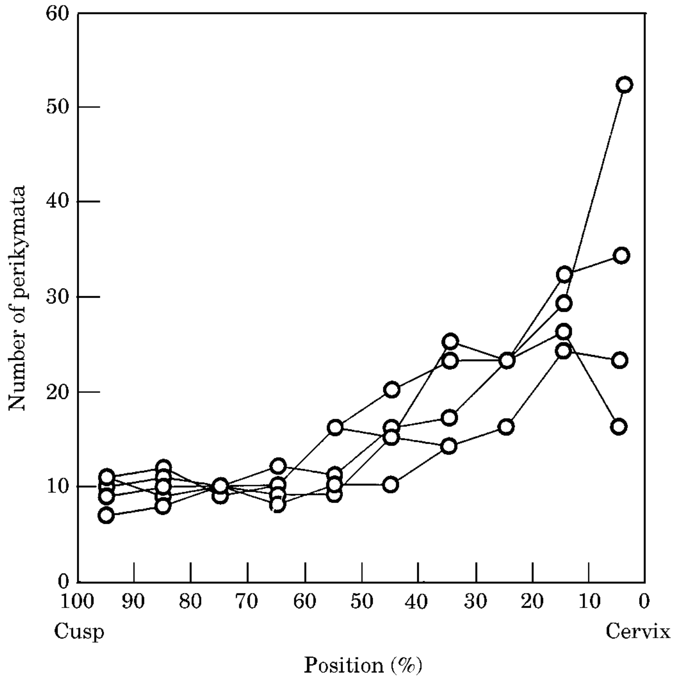

Figure 4. Position specific density of perikymata on the mandibular central incisor ($n=5$). The number of perikymata per 10% interval of crown height is given. Perikymata were counted from scanning electron microscope montages (40–50 ×). Perikymata are incremental features continuous with the underlying striae of Retzius. Each increment is considered to represent approximately 7–10 days of growth (Dean, 1987; Beynon & Reid, 1987; Beynon & Dean, 1991; Dean & Beynon, 1991). Note that the density of the perikymata increases in the cervical region of the tooth indicating that a substantial period of time has elapsed without a concomitant large change in crown morphology.

deposition perinatally and had a crown formation duration of 4·96 years (59·5 months) based on an accounting of enamel microstructural increments. Shellis (1984) recorded a period of 3·91 years (47 months) for a lateral incisor crown formation period. Liversidge and coworkers (1993) record an age of 4·5 years (54 months) as the earliest age of crown formation in their known-age archaeological sample from Spitalfields.

Mandibular canine

The lower canine crown appears to begin mineralizing late in the first year of life and into the second year (Figure 6). This is about nine months later than described in other radiographic studies. Histological evidence of mineralization is present between the third and sixth months (Logan & Kronfeld, 1933; Liversidge, 1995). Although the canine and lateral incisor appear to begin forming at about the same time, the rate of crown growth differed markedly between the two teeth. The canine crown grows at a much slower rate. This may be an actual difference in the rate of growth of the crown height (Liversidge, 1995) and/or a consequence of the larger size of the canine crown.

Crown completion in the canine was defined as the cervical enamel margin having a sinusoidal profile. Neither maximum breadth nor first appearance of the root was sufficient for identification of a completed canine crown. The crown was completed between 54 and 75 months (mean = 65 months [Table 1]).

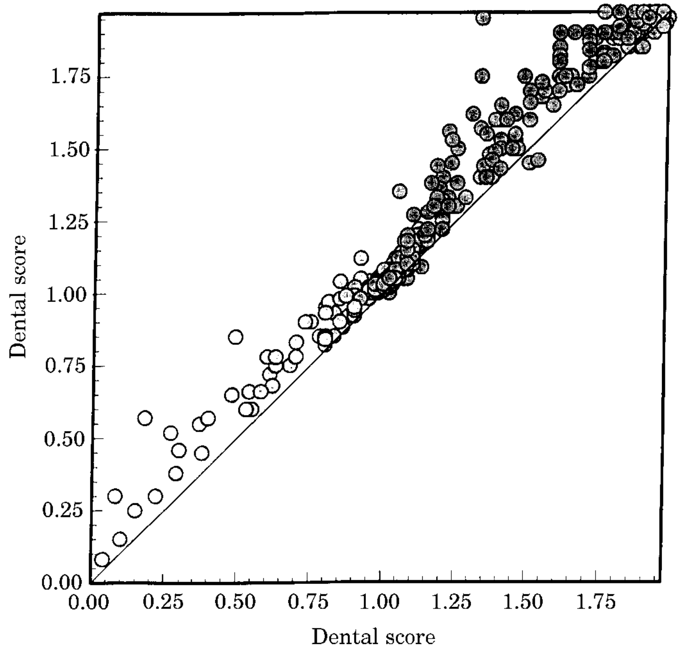

Figure 5. Bivariate comparison of the mandibular central and mandibular lateral incisors. The I1 is on the *y*-axis and the I2 on the *x*-axis. The diagonal line represents unity (I1 is morphologically equal to I2). The I1 is advanced (above the diagonal) relative to the I2. The greatest similarity in morphology occurs in the area of early root formation (~1·00–1·15).

Following crown completion, root elongation begins at a very slow rate. The rate of root elongation, once initiated, is generally constant. There does not appear to be a change in the rate of root formation associated with emergence. The mandibular canine root attains full length at about 11–13 years. The high variance in this value is a product of sex specific differences in root formation.

Examination of the development of the PDC and BBGS mandibular canine shows minor differences in distribution (Figure 7). Although there is an almost complete overlap between the samples at any stage of development, the PDC is somewhat more accelerated in development. No other tooth shows differences between the two samples in the timing of development. This tooth specific sensitivity may stem from a variety of interacting factors including populational composition and health, environmental effects, or dietary quality.

Although there is a tremendous degree of overlap in the development of the mandibular canine by sex, characteristic differences do exist. These data do not identify pattern differences between the sexes in the earliest phases of canine crown development, showing a great degree of overlap until a score of ~1·10 (Figure 8). After this time, males begin to lag behind females. However, throughout subsequent development, the male and female distributions overlap substantially. The most precocial individuals are female and the most delayed are generally male. When the two samples are compared separately, the PDC shows very little difference in canine development by sex although the BBGS does. Overall, it is the BBGS males that are most dissimilar in growth presenting a delay (especially in

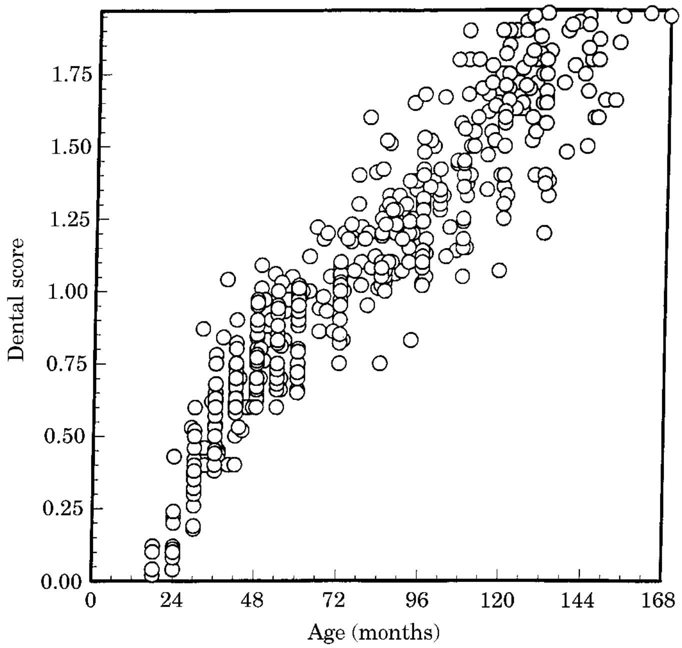

Figure 6. Bivariate comparison of the mandibular canine with age. Each circle represents a single observation (i.e., radiograph).

canine root formation) from the rest of the sample. The factors which cause the canine to develop earlier in the contemporary sample may be differentially affecting the sexes with males having a greater degree of developmental plasticity in the canine root formation. Hurme (1949), Garn *et al.* (1958), Moorrees *et al.* (1963*a*), and Harris & McKee (1990) all noted that it was the difference in the timing of mandibular canine root formation which was the greatest difference between the sexes especially after 25% of the root is formed. Demirjian & Levesque (1980) noted a similar increase in the degree of differences in development after the age of five years. Other radiographic studies (Anderson *et al.*, 1976) have identified the timing of apical closure to be among the greatest differences of dental development between the sexes. The sexes may differ by as much as 25 months in the modal time of apical closure (Ten Cate, 1985). In retrospective or interspecific studies, we should be sensitive to these gender-based differences when exploring growth in the canine where the sex of the specimen is not known *a priori*.

Mandibular third premolar

The crown of this tooth begins to be recognized radiographically by 30 months (Figure 9). Although no individuals had an identifiable P3 crown at 24 months, the degree of development of the 30-month specimens indicates that crown formation must have initiated about the end of the second or beginning of the third year, with some individuals initiating formation towards the end of the third year. This is about 3–6 months later than seen in other radiographic studies (Garn *et al.*, 1959) and 6–12 months later than histologic analyses (Logan & Kronfeld, 1933).

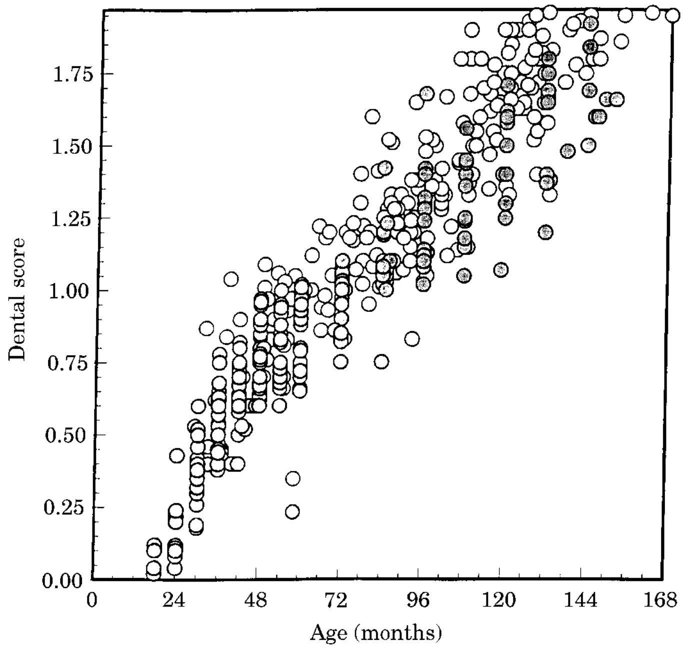

Figure 7. Bivariate comparison of the mandibular canine with age for the PDC and BBGS samples. Open circles: BBGS; filled circles: PDC.

Crown completion occurs at about the end of the seventh year. This is a markedly older age of attainment than reported in most other studies, which report crown completion by 67 months or younger (Table 2), although see data from Garn and coworkers (Garn *et al.*, 1959; Lewis & Garn, 1960; Nolla, 1960; and Harris & McKee, 1990. When the P3 ontogeny data are compared with the MFHp (1963a) schedule, it is clear that the same pattern of dental development is obtained, but that the MFHp mean age of attainment data set are found at the most precocial end of the developmental range seen here. It is uncertain which factors contribute to this discrepancy although differences in the definition of crown completion between the studies may be important.

Mandibular fourth premolar

Overall, the two premolars show a very similar pattern of development, the main difference being a delay by the fourth premolar in attaining the various stages (Figure 9). This difference is most marked at the time of crown onset with the P4 crown first visible in the fourth and as late as the fifth year. The mean age of crown formation is 87 months or about two months later than the P3. This is from six months to one year later than reported in other studies (Table 2). A bivariate plot of the relative growth of the third with the fourth premolar shows (Figure 10) a linear relationship with the P3 presenting a crown approximately 20% at about the time the P4 crown is mineralized visibly for the first time. The rates of crown formation differ, with the P3 having a slower rate for a longer period than the P4. As in the P3, the rate of root formation is initially slow but becomes more rapid in the middle three-quarters of development (the time of emergence) and attainment of final position. The differences in stage attainment are least around crown

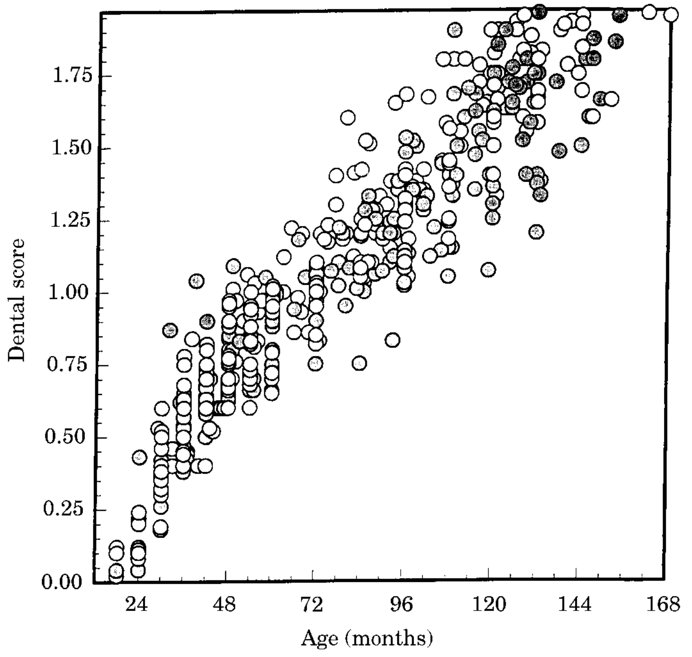

Figure 8. Bivariate comparison of the mandibular canine with age by sex for the complete sample. Open circles: females, closed circles: males.

completion and early root formation. The P4 root is completing its development in the period between 11–14 years. Overall, both teeth seem to display a similar degree of developmental variation.

Mandibular first molar

The mandibular first molar is consistently identifiable in the youngest age cohort (three months) (Figure 11). Although it is impossible to estimate with these data, it is widely reported that the first molar initiates development perinatally. This is supported by histological research (Schour, 1936; Krauss & Jordan, 1965) which demonstrates that crown calcification initiates about 32 weeks *in utero*. Gleiser & Hunt (1955) report that females more often show prenatal evidence of crown formation than males. The growth of the crown is initially slow although once the cusps coalesce and the outline is completed, the margins of the tooth elongate rapidly and the crown is completed during the middle of the fourth year (39–47 months). This is longer than some radiographic studies (e.g., MFHp; Fanning & Brown, 1971; Fass, 1969) although consistent with others (Gleiser & Hunt, 1955; Garn *et al.*, 1959; Lewis & Garn, 1960; Nolla, 1960; Anderson *et al.*, 1976; Harris & McKee, 1990) (Table 2). Shellis (1984) reports a slightly longer period of crown formation (47 ± 6 months, $n=2$) using an histologic approach. By contrast, Liversidge and coworkers (1993), in their study of the known age Spitalfields collection, identified their youngest individual with a completed crown at 35 months (range: 35–43 months [Liversidge, 1995]) and a similar value was recorded (36 months) by Reid (personal communication) using a quantitative histologic approach for completion of the lower M1 crown.

There is a slight reduction in the rate of morphological change at crown completion. The rate of root elongation accelerates

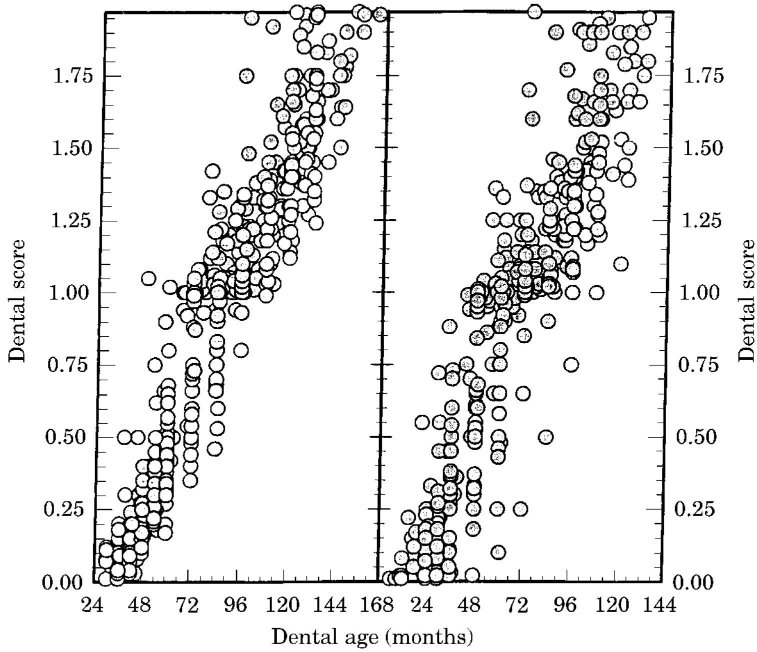

Figure 9. Bivariate comparison of the mandibular premolars with age. The mandibular P3 plot is on the left and the mandibular P4 plot is on the right.

during emergence. These observations in rate changes in crown and root formation are similar with those identified in other studies (Gleiser & Hunt, 1955; Moorrees *et al.*, 1963*a*; Anderson *et al.*, 1976). Complete root length is attained during the eighth and ninth years.

Although minor differences between the sexes in the timing of M1 dental development have been observed by others (Gleiser & Hunt, 1955; Garn *et al.*, 1959), we were unable to identify different developmental paths between males and females (Figure 12). Nor were differences between the PDC and BBGS samples apparent.

Mandibular second molar

The crown of the second molar begins mineralization near the end of the third year (Figure 13). Like the first molar, the crown has an initially slow rate of change which increases towards the latter half of crown formation. Crown completion in the BBGS/PDC samples was calculated to occur between 88 and 96 months (mean 92 months). Radiographic estimates of the age of crown completion of the M2 vary markedly, spanning between about 72 months of age (Demirjian & Levesque, 1980) and 102 months (Garn *et al.*, 1959) (Table 2). There is a substantial slowing of growth rate following crown completion and it takes approximately three years for the first one-quarter of the root to form. The rate of root elongation increases markedly again coinciding with emergence. Root length is completed by about age 12–13.

Mandibular third molar

The crown begins to mineralize at about eight years of age and the crown is completed during the 12th year (Figure 13). The initial rate of root elongation is slow (similar

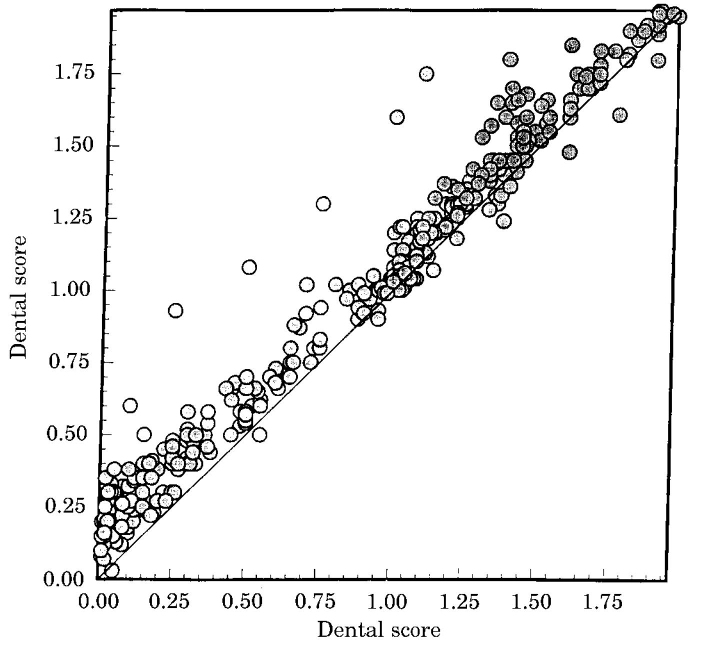

Figure 10. Bivariate comparison of the mandibular third and mandibular fourth premolars. The P3 is on the *y*-axis and the P4 on the *x*-axis. The diagonal line represents unity (P3 = P4). The P3 is advanced (above the diagonal) relative to the P4. The greatest coincidence of morphology occurs in the area of a completed crown ($\sim$1·00) and the early stages of root development where a similar pattern of growth is evident although the P4 lags about 0·10 behind the P3.

in rate to the M2). The paucity of cases older than 168 months prevents a fine-grained description of the formation of the M3 root.

It is clear that the degree in variation in formation increases markedly between the first, second, and third molars. Where the first molar shows little variance in time of formation, the second and third molars demonstrate an increasing absolute and relative dispersion in the timing of formation (Schultz, 1935; Garn *et al.*, 1959; Hurme & Van Wagenen, 1961; Anderson *et al.*, 1976). Another difference in the development of the molars is the rate of morphological change in the earliest stage of root formation. The M2 and M3 roots elongate at slower rates than the M1.

The M2 crown initiates mineralization when the M1 crown is nearing completion (Figure 14). A similar developmental relationship between the M2 and M3 is also seen. Therefore, the human M3 does not differ in its growth parameters from the other molars and is not a developmentally specialized tooth. Although it can exhibit interpopulational variation (Tompkins, 1996), it shares a similar pattern of growth with the African great apes (Schultz, 1935) and fossil hominids (Simpson *et al.*, 1992; Simpson, 1992).

Comparisons with other dental maturation studies

Smith (1991) reviewed a number of commonly used dental developmental and emergence studies and concluded that the Moorrees and coworkers studies (1963*a*,*b*) were the most useful in terms of both sample

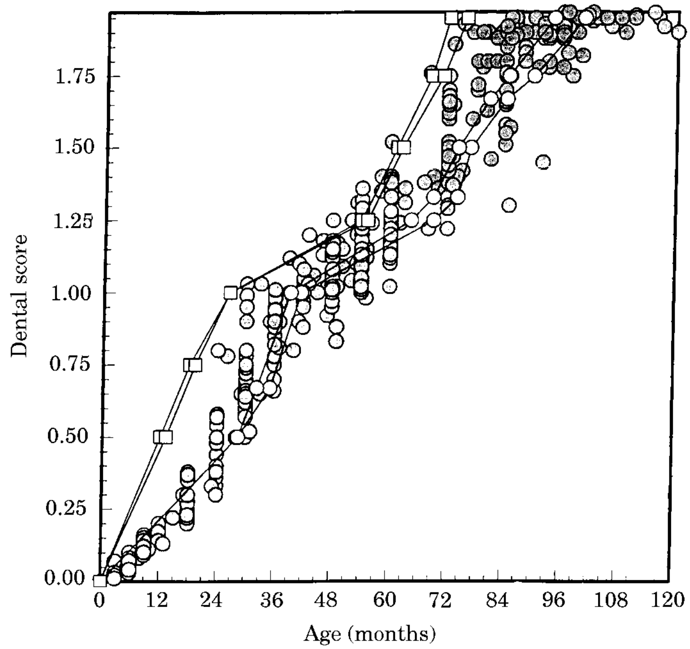

Figure 11. Bivariate comparison of the mandibular M1 with age. The times of attainment of crown and root formation from Gleiser & Hunt (1955) (squares) and Moorrees *et al.* (1963a) (circles) have been added. The Gleiser and Hunt schedule differs markedly in time and rate from the MFHp schedule but is very similar to the BBGS/PDC data.

size, age distribution, and statistical analyses. Support for the quality of the MFH standards was echoed by Saunders and coworkers (1993) who calculated age at death using the MFHp (1963a), MFH deciduous (1963b), and Anderson and coworkers (1976) standards for a skeletal sample (a subset of known age) and noted that the age of estimates using the MFH schedules of permanent and deciduous tooth formation were consistent with known age. However, they recommend that the estimates derived from the maxillary incisors be omitted in the final calculation of age. In addition, use of the MFH standards (a visual and not tabular representation) was noted to be difficult to visually interpolate ages and could be a source of error in age estimation.

As noted above, there are marked differences in the timing of dental development between the various dental schedules. These differences, due to statistical analysis of the data or sample composition (Smith, 1991) in addition to population variation, have implications for their use in clinical or retrospective studies. To illustrate these points, the BBGS/PDC data are compared with the Moorrees and coworkers standard for the permanent dentition (1963a).

Although we adopted a fine-grained scoring system which allows for identification of subtle changes in shape with time, we combined a range of scores to identify various threshold stages such as crown completion. The summing of values across a narrow range allows comparison with other schedules which have fewer, broader stages and recognizes the natural variability in our ability to score the teeth. Crown completion was incrementally defined as a combination of scores between 0·95 and 1·05. Overall, the mean and median ages changed little but, not unexpectedly, the more truncated the definition of crown completion, the lower

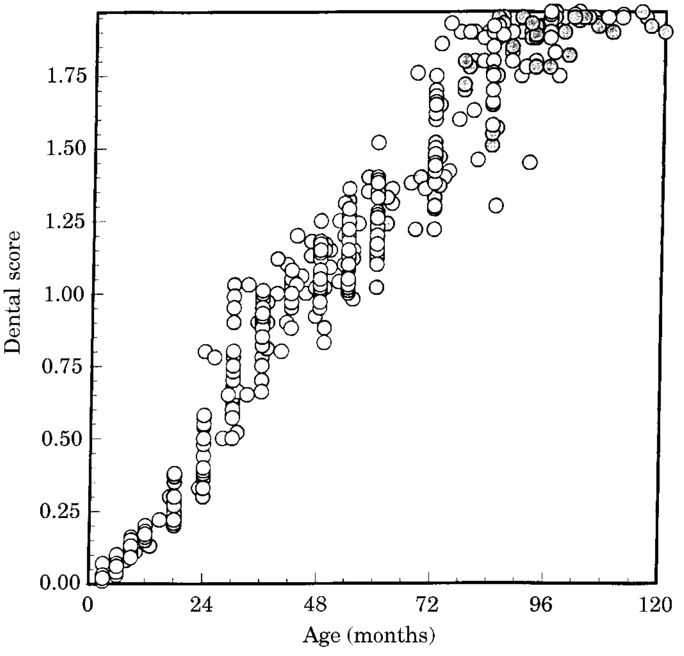

Figure 12. Bivariate comparison of the mandibular M1 with age by sex for both sexes. Note that the male and female distributions overlap completely. No differences in the growth of this tooth between the sexes is evident.

the variance. Also, as the higher scores were omitted (greater than 1·00), the distribution became more symmetrical and the age of attainment lessened. Both the mean and median age of attainment of crown completion were reduced by six months when the range was truncated from 1·05 to 1·00. Based on a review of the radiographic anatomy, we adopted here the convention that incisors and canines with a score of between 0·95 and 1·03 and molars and premolars with a score between 0·95 and 1·01 were identified as having a complete enamel crown.

In Figures 15 and 16, we plotted the cumulative frequency for dental scores of canine crown two-thirds complete [0·60–0·75; $n=73$], crown 80% complete [0·70–0·90; $n=75$], and crown complete [0·95–1·03 ($n=64$)]. The cumulative frequency of crown two-thirds completed has a mean and median age which are both 48 months and a 50th percentile score of 46 months. Forty-eight months is the mean age of canine crown completion in the Moorrees *et al.* (1963*a*) study. To generate standards compatible with the MFHp ages for canine crown completion, we would have to substantially redefine our morphological criteria of crown completion from 1·00 to 0·75. Other direct analyses of canine crown formation do not support the younger age of canine crown formation (74 months–[Reid, personal communication]; greater than 64 months [Liversidge, 1995]). It is unlikely that such similar biologic and socioeconomic populations can have such a great difference in the timing of attainment of crown completion. A more likely explanation of the differences between the two studies is that it is a product of the different definition and scoring of crown morphology (Demirjian, 1980; Smith, 1991). Similarly, to attain an age of crown completion

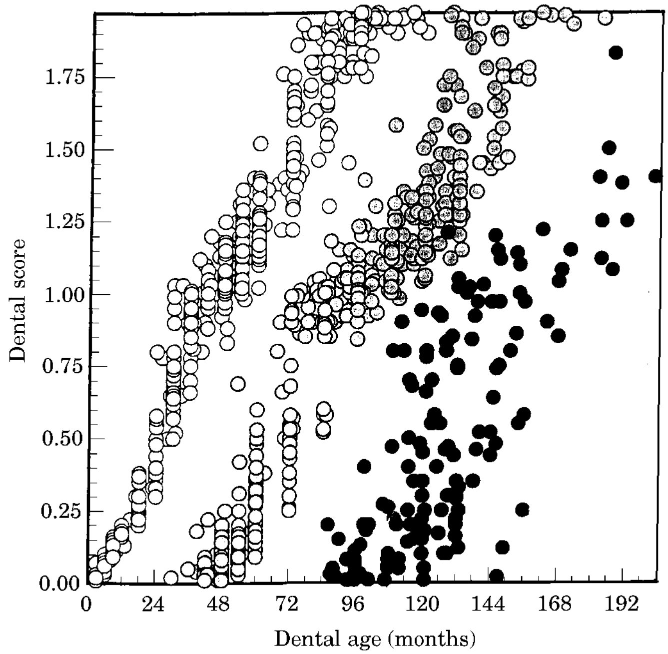

Figure 13. Bivariate comparisons of the mandibular first, second, and third molars with age. Note that the degree of developmental variation increases with age. Also, the rates of initial molar root growth differs markedly from the crown with a progressively slower rate of root elongation in the more distal roots. M1: open circles, M2: gray circles, M3: black circles.

compatible with Demirjian & Levesque (1980) (35–40 months) an even more immature crown would have to be scored as complete. Anderson *et al.* (1976) using the MFHp standards produced times of crown completion of the dentition broadly similar (except the M1) to those of Moorrees, Fanning and Hunt. In contrast, Harris and McKee (1990), also using the MFHp scoring technique produced ages of crown completion greater than both the Moorrees *et al.* (1963*a*) and Anderson *et al.* (1976) studies (about one year later) and very similar to this study (Table 2). It is difficult to resolve whether these differences are a product of actual biological and ecological differences or method of applying the standard.

In our sample of canines with an 80% completed crown, the mean age is 53 months, the median age is 52 months, and the 50th percentile score is 52 months. These ages are compatible with the Fanning & Brown (1971) and the Fass (1969) scores for crown completion. Overall, the age of attainment of canine crown completion in this study (66 months) is most similar to that published by Nolla (1960) and Harris & McKee (1990).

In another example, we observed that the third premolar crown completes formation at about 7–8 years of age (Tables 1 & 2), a full 1·5–2·5 years later than the MFHp standard and as much as 3·5 years later than that published by Demirjian & Levesque (1980). The closest standards for mandibular P3 development are again those of Nolla (1960) (Table 2), Lewis & Garn (1960), Harris & McKee (1990) and the visual standards from the nineteenth century (Pierce, 1884; Black, 1883 [reproduced in Smith, 1991]). The focus populations of the Nolla (1960) (Child Development Laboratories,

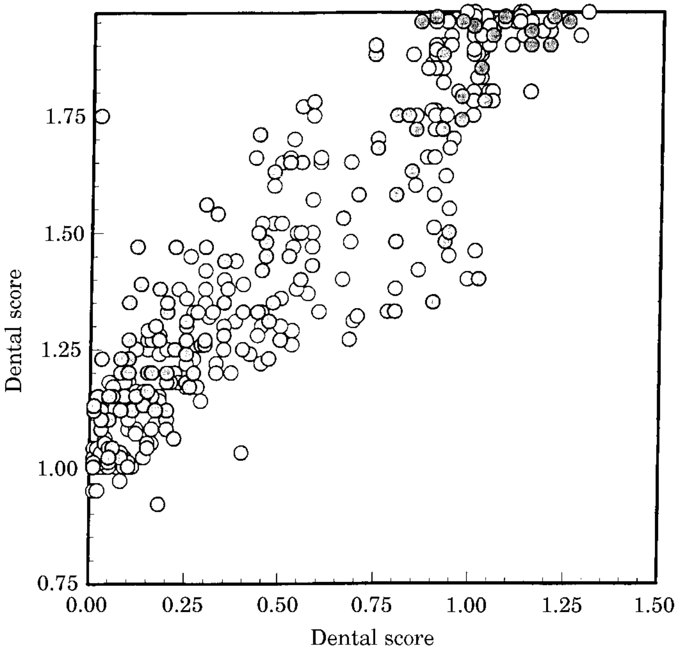

Figure 14. Bivariate comparison of the relative development of the M1 with the M2 and the M2 with the M3. The earlier forming tooth of each pair is on the *y*-axis. The relative timing of the growth of the two teeth is identical. M1–M2 comparison: circles, M2–M3 comparison: circles.

University of Michigan) and Lewis & Garn (1960) (Fels Research Institute, Yellow Springs, Ohio) studies were, like our sample, midwestern American populations with a similar historic and socio-economic profile. Like the PDC sample, the Harris & McKee (1990) sample is a healthy, mostly urban, cross-sectional group collected from the University of Tennessee College of Dentistry records and living in the region of Memphis, Tennessee, U.S.A. However, the MFHp sample was also derived to a great extent from Ohio with a similar biological and economic composition. Therefore, additional sources of variation must be identified.

Additionally, our scores of the first molar, especially during crown formation, are substantially later than the MFHp standard by about 12–18 months (Table 2). In order to make our M1 age of attainment plot (Figure 17) consistent with the MFHp schedule, we would have had to consistently identify an M1 as having a completed crown when we recorded it as being only two-thirds to three-quarters complete. This is unlikely. Smith (1991) showed that age composition of the sample biases the summary statistics of attainment stages. She noted a strong relationship between age of youngest participant in the study and calculated age of M1 crown completion. The MFHp and BBGS/PDC samples are similar by sampling individuals from the first months of life well into the second decade, yet differ markedly on the estimate of M1 crown formation duration. Gleiser & Hunt (1955) also began sampling individuals in their 3rd month and concluded that the crown had completed formation between 39 and 42 months, up to 12 months later than the MFHp standard. The Gleiser and Hunt schedule is very similar to the one presented here (Figure 11). The predicted relationship between age

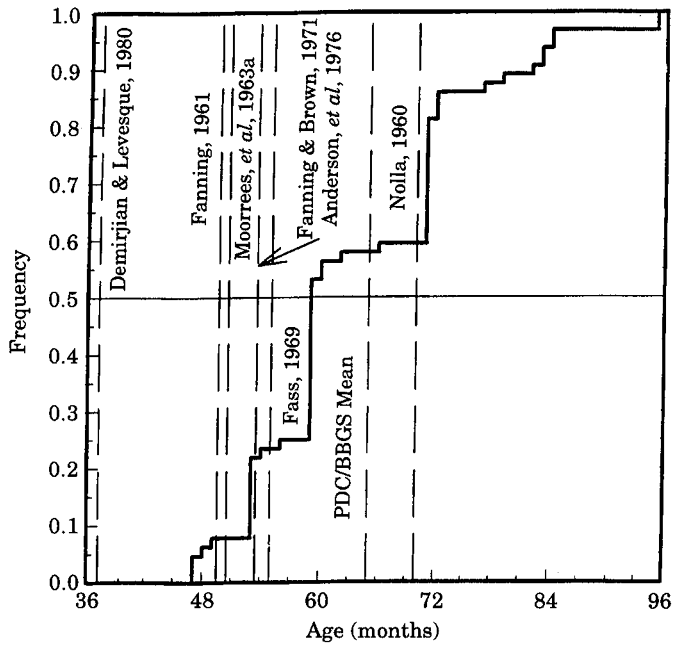

Figure 15. Cumulative frequency of individuals in the sample attaining crown completion of the mandibular canine. Crown completion is identified by a review of the radiographs and morphological criteria to encompass a range of dental scores between 0·95 and 1·03. Mean values (sexes combined) of crown completion for a number of other studies have been included in the figure.

composition and age of attainment is not supported by these data.

By comparison, our schedule of M2 development is similar in pattern to the MFHp standard but again we have a greater age of completion of the crown. Our M3 data show that the BBGS/PDC children are increasingly similar to the published standards. This is an enlightening comparison because the same morphological criteria are used to score crown formation in these three teeth, yet no single pattern of bias is found. For individual molar teeth, the MFHp and BBGS/PDC data become increasingly more concordant following molar crown completion.

Finally, a series of studies involving the same workers (Fanning, 1961; Moorrees *et al.*, 1963*a*,*b*; Fanning & Brown, 1971) are based on the same core of individuals (the 99 School of Public Health, Harvard University study individuals [between four and 11·5 years of age] and a variable amount of Fels Longitudinal studies children [n=246 to 290]). The ages of attainment differ slightly between the various studies, probably as a consequence of both slightly different sample composition and statistical analytic approaches, but they consistently yield the youngest ages of attainment of any study (except Demirjian & Levesque, 1980) especially in the canines and molars. Although it seems intuitive that certain aspects of dental development are unambiguously identifiable and easily recognized between workers (e.g., crown completion), this is not necessarily the case (Liversidge, 1995). Scoring the maturity of teeth is subjective (Moorrees *et al.*, 1963*a*; Nolla, 1960; Nielsen & Ravn, 1976) and must be learned. Researchers working together must agree on a standard definition of morphology. Therefore, it is likely that the similarity in results of these studies is partially a product of a

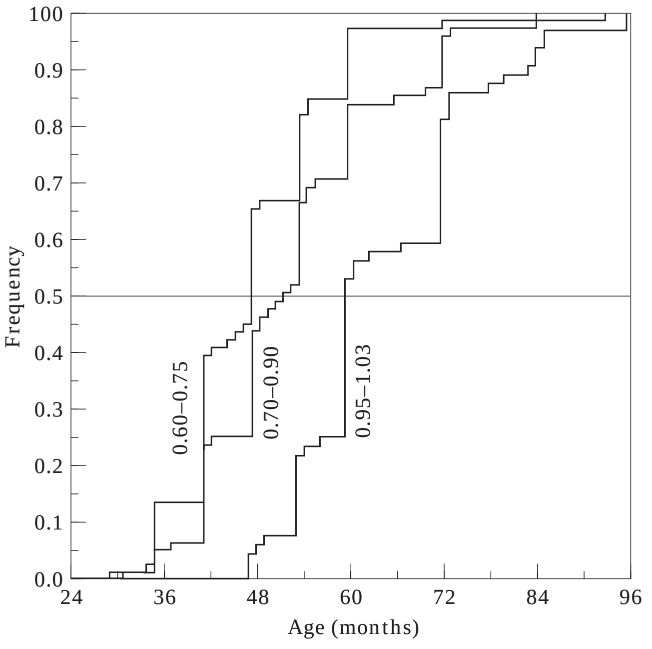

Figure 16. Cumulative frequency of individuals in the sample attaining various stages of completion of the enamel canine crown. Crown completion is identified on morphological criteria to encompass a range between 0·95 and 1·03 (n=64). Crown 80% is equal to 0·70–0·90 (n=73) and crown two-thirds is equal to a range of 0·60 to 0·75 (n=75). Compare with mean values shown in Figure 15.

common definition of stage which is internally consistent but may not be replicable by independent researchers.

Discussion

One of the results of this analysis echoes the positions of Brauer & Bahador (1942), Garn and coworkers (Garn *et al.*, 1959; Lewis & Garn, 1960), Moorrees (1965), and Winkler *et al.* (1991) among many others, that there exists a marked degree of normal variation in the timing of dental development. It is tempting to rely on summary mean ages of attainment in evaluating dental development but an appreciation of the variation in formation times demands a broader definition of normative development. Although individual cases with marked pathology were identifiable in the PDC sample, there is no indication that these factors contributed in any systematic way to deviation in the timing of dental maturation.

A possible bias in this analysis towards older ages of attainment is the degree of resolution of the BBGS radiographs. Although they have been maintained in excellent condition, extensive use (including tracing) has scratched some of the plates making ephemeral structures, like poorly mineralized root apices, sometimes difficult to resolve. In addition, the radiographs were not taken to highlight the subtleties of the developing dentition. However, neither of these two reservations are considered to be significant. In contrast to the BBGS, the PDC radiographs were collected recently (1993–1996) for dental diagnosis and high resolution film was used. In addition, if a plate was recognized as inappropriate for diagnosis by the radiologist (movement of patient, incorrect field of view), a second or

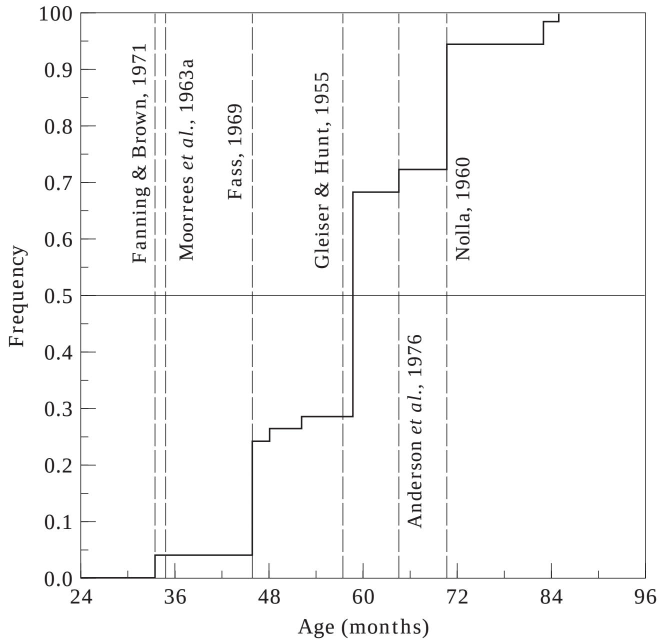

Figure 17. Cumulative frequency of individuals in the sample attaining crown completion of the mandibular first molar. Crown completion is identified by a review of the radiographs and morphological criteria to encompass a range of dental scores between 0·95 and 1·01. Mean values (sexes combined) of crown completion for a number of other studies have been included in this figure.

third plate was taken. Often, radiographic survey of the dentition had overlapping fields allowing multiple views of the same tooth. Scores of teeth taken from these redundant plates yielded similar information and no marked changes in the dental score were noted between plates. Consequently, except for the canine, the schedules of dental formation are insignificantly different between the BBGS and PDC showing that similar phenomena are being sampled. The canine tooth presents a special challenge to describe the sample differences. The BBGS juveniles show a slight delay in root formation relative to the PDC. This difference exceeds the differences seen between the sexes. The canine is the most developmentally labile tooth and is affected by health and hormonal status. Either of these factors can contribute to the precocial development in the contemporary sample. This secular change has implications again for the estimation of individual maturity based on the radiographic appearance of the dentition, especially the canine. The developmental resiliency of the other teeth is notable.

Thus, not only do differences in populational composition, statistical approach, sample age distribution (Smith, 1991), and different environmental factors between studies produce characteristic differences in results, but also the project specific definition of anatomical morphology may be implicated. Stage definition is made subjectively on radiographs. Although it seems unlikely that a tooth at the seemingly unambiguous stage of crown completion can be misidentified, this is in fact easily done (Liversidge, 1995). For example, a crown may be slightly oblique to the plate thus hiding the normal contours of the cervix of the crown and making identification of the morphologic subtleties in this region difficult. Additionally, because of their sinusoidal cervical margins, some teeth may demonstrate initial root formation while the crown is still incomplete (Beynon & Reid, 1987). First appearance of any root, regardless of state of the enamel crown may, in some studies, be sufficient evidence of attainment of crown completion. The best estimates of incisor crown developmental status would be seen in lateral plates where the labial and lingual margins reach their most apical extent. This view can lead to a decision of crown completion of the incisors and canines when there is still substantial enamel formation yet to occur. Ramirez-Rozzi (1993) noted that the enamel cervical margin in the premolar teeth in hominids has a complex topography completing formation about its periphery not in an instant but over a prolonged period. Thus, the enamel crown and root may be forming and elongating concurrently, rendering the definition of crown completion problematic. Practically, the apices of the crown and root growth fronts are poorly mineralized and radiographic observations will always underestimate their maturity (Gleiser & Hunt, 1955; Beynon *et al.*, 1991). Radiographic and histologic definitions of crown completion (or any stage of formation) represent different phenomena. A histologic assessment considers a crown to be completed when the entire enamel matrix has been formed, whereas a radiographic study requires that the matrix be mineralized before it becomes radiopaque and visible using standard radiographic techniques. Radiographic assessments of degree of formation should characteristically underestimate actual maturity when measured in terms of matrix deposition.

A metric approach to aging juvenile dentitions (Israel & Lewis, 1971; Liversidge *et al.*, 1993; Liversidge, 1995) is a useful rapid method of estimating age. However the standards are population and species specific (due to variation in crown height), will overage first appearance of a germ (due to the variable preservation and imaging of poorly mineralized tooth germs in both archaeological and radiological samples), and are susceptible to underscoring crowns where the poorly mineralized margins have been lost in dried specimens. Although the Spitalfields research team addressed these concerns, the broad application of this approach and these standards to other collections must be done with caution. Sample composition and differences in stage identification also may prove to be a significant source of variation between studies as not all aging standards are not equally effective in aging juveniles (Staaf *et al.*, 1991; Hagg & Matsson, 1985; Saunders *et al.*, 1993). Individual variation in dental scoring is also a source of differences both within and between studies. Levesque & Demirjian (1980) evaluated the variation in interobserver scoring of dental radiographs. Even though they relied on only an eight stage system, there were differences between 15% and 30% in the stage assignments of the teeth, especially marked in the premolars and canines. Although most variation was limited to differences of one stage, a small fraction of the scores (1·7%) differed to a greater degree. One of the Demirjian & Levesque (1980) stages equals a score of approximately 0·25 in our study. A rescoring of one stage, then, can translate into a substantial span of morphological change resulting in marked differences in the summary statistics. A finer scale with a greater number of increments should reduce the magnitude of inter- and intraobserver differences. Fanning (1961) likewise noted the variation in scoring the different teeth with the greatest degree of variation found in the premolars and incisors. We echo the sentiments of other researchers (Garn *et al.*, 1967; Demirjian, 1980; Demirjian & Levesque, 1980) regarding the adoption of normative standards of development. In the future, it would be an interesting and important avenue of research to have a single research group examine the different radiographic sample groups which have formed the basis of the different studies and compare the results. Until this concern is addressed, it is difficult to unambiguously identify the biological or ecological sources of variation (e.g., populational affiliation, environmental or geographical factors, diet, or state of health) of the differences in timing of development between the different schedules.

A good schedule of dental development based on radiographs should be internally consistent, have an unbiased and broad age distribution, and use the appropriate analytic statistics. These alone cannot overcome differences in timing between the many studies which sample different geographical and biological populations and where different, often idiosyncratic, morphological criteria, stages, and standards are used to score the teeth. In addition, although radiographic and histologic studies analyze different media for different ends, they ultimately should be reconcilable to produce the best possible description of human dental development, and we should continue working towards that end. Despite the statistical and data collection rigor found in individual radiographic studies, no single schedule based on summary data can be considered the most accurate and representative chronological account of human dental growth. Retrospective studies which rely on knowledge of the absolute growth of the human dentition based on published standards of human dental growth should proceed cautiously.

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References

Anderson, D. L., Thompson, G. W. & Popovich, F. (1976). Age of attainment of mineralization stages of the permanent dentition. *J. forens. Sci.* **21,** 191–200.

Behrents, R. G. & Broadbent, B. H., Jr (1984). A chronological account of the Bolton-Brush growth studies. The Bolton-Brush Growth Study Center. (http://www.cwru.edu/dental/bbgsc/background.html).

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. *Am. J. phys. Anthrop.* **86,** 189–204.

Beynon, A. D. & Reid, D. J. (1987). Relationships between perikymata counts and crown formation times in the human permanent dentition. *J. dent. Res.* **66,** 889–890.

Black, G. V. (1883). Chart showing the lines of contemporaneous calcification of the teeth (frontispiece). Illinois State Dental Society Transactions.

Brauer, J. C. & Bahador, M. A. (1942). Variations in calcification and eruption of the deciduous and permanent teeth. *J. Am. dent. Assoc.* **29,** 1373–1387.

Carlson, H. (1944). Studies on the rate and amount of eruption of certain human teeth. *Am. J. Orthod. and Oral Surg.* **30,** 575–588.

Cattell, P. (1928). *Dentition as a Measure of Maturity*. Cambridge: Harvard University Press.

Chertkow, S. (1980). Tooth mineralization as an indicator of the pubertal growth spurt. *Am. J. Orthod.* **77,** 79–91.

Dean, M. C. (1987). Growth layers and incremental markings in hard tissues: A review of the literature and some preliminary observations about enamel structure in *Paranthropus boisei*. *J. hum. Evol.* **16,** 157–172.

Dean, M. C. & Wood, B. A. (1981). Developing pongid dentition and its use for ageing individual crania in comparative cross-sectional growth studies. *Folia primatol.* **36,** 111–127.

Dean, M. C. & Beynon, A. D. (1991). Histological reconstruction of crown formation time and initial root formation times in a modern human child. *Am. J. phys. Anthrop.* **86,** 215–228.

Demirjian, A. (1980). Dental development: a measure of physical maturity. In (F. E. Johnson and A. F. Roche, Eds) *Human Physical Growth and Maturation: Methodologies and Factors*, pp. 83–100. New York: Plenum.

Demirjian, A., Goldstein, H. & Tanner, J. M. (1973). A new system of dental age assessment. *Hum. Biol.* **45,** 211–227.

Demirjian, A. & Levesque, G. Y. (1980). Sexual differences in dental development and prediction of emergence. *J. dent. Res.* **59,** 1110–1122.

Demisch, A. & Wartmann, P. (1956). Calcification of the mandibular third molar and its relation to skeletal and chronological age in children. *Child Dev.* **27,** 459–473.

Daito, M. *et al.* (1989). Calcification of the permanent first molars observed in panoramic radiographs. *Journal of the Osaka Dental University* **23,** 45–55.

Diato, M., Kawahara, S., Tanaka, T., Nishihara, G. & Hieda, T. (1990). Calcification of the permanent anterior teeth observed in panoramic radiographs. *Journal of the Osaka Dental University* **24,** 63–85.

Diaz, G., Maccioni, P., Zedda, P., Cabitza, F. & Cortis, I. M. (1993). Dental development in Sardinian children. *J. Craniofac. Genet. Dev. Biol.* **13,** 109–116.

Fanning, E. A. (1961). A longitudinal study of tooth formation and root resorption. *The New Zealand Dental Journal* **57,** 202–217.

Fanning, E. A. & Brown, T. (1971). Primary and permanent tooth development. *Australian Dental Journal* **16,** 41–43.

Fanning, E. A. & Moorrees, C. F. A. (1969). A comparison of permanent mandibular molar formation in Australian Aborigines and Caucasoids. *Archs oral Biol.* **14,** 999–1006.

Fass, E. N. (1969). A chronology of growth of the human dentition. *J. Dent. Child.* **36,** 391–401.

Garn, SM., Lewis, AB., Koski, K. & Polacheck, D. L. (1958). The sex difference in tooth calcification. *J. dent. Res.* **37,** 561–567.

Garn, S. M., Lewis, A. B. & Polacheck, D. L. (1959). Variability in tooth formation. *J. dent. Res.* **38,** 135–148.

Garn, S. M., Rohmann, C. E. & Silverman, F. N. (1967). Radiographic standards for postnatal ossification and tooth calcification. *Med. Radiogr. Photogr.* **43,** 45–66.

Gleiser, I. & Hunt, E. E., Jr (1955). The permanent mandibular first molar: Its calcification, eruption, and decay. *Am. J. phys. Anthrop.* **13,** 253–283.

Hagg, U. & Matsson, L. (1985). Dental maturity as an indicator of chronological age: the accuracy and precision of three methods. *Eur. J. Orthod.* **7,** 25–34.

Harris, E. F. & McKee, J. H. (1990). Tooth mineralization standards for blacks and whites from the middle southern United States. *J. forens. Sci.* **35,** 859–872.

Hess, A. F., Lewis, J. M. & Roman, B. (1932). A radiographic study of calcification of the teeth from birth to adolescence. *Dental Cosmos* **74,** 1053–1061.

Hillson, S. & Bond, S. (1997). Relationship of enamel hypoplasia to the pattern of tooth crown growth: A discussion. *Am. J. phys. Anthrop.* **104,** 89–103.

Huda, T. F. J. & Bowman, J. E. (1995). Age determination from dental microstructure in juveniles. *Am. J. phys. Anthrop.* **97,** 135–150.

Hurme, V. O. (1949). Ranges of normalcy in the eruption of the permanent teeth. *J. Dent. Child.* **16,** 11–15.

Hurme, V. O. & van Wagenen, G. (1961). Basic data on the emergence of permanent teeth in the rhesus monkey (*Macaca mulatta*). *Proc. Am. phil. Soc.* **105,** 105–140.

Israel, H. & Lewis, H. B. (1971). Radiographically determined linear study of permanent tooth growth from age 6 years. *J. dent. Res.* **50,** 334–342.

Krauss, B. & Jordan, R. E. (1965). *The Human Dentition Before Birth*. Philadelphia: Lea & Febiger.

Levesque, G-Y. & Demirjian, A. (1980). The inter-examiner variation in rating dental formation from radiographs. *J. dent. Res.* **59,** 1123–1126.

Lewis, A. B. & Garn, S. M. (1960). The relationship between tooth formation and other maturational factors. *Angle Orthodontist* **30,** 70–77.

Liliequist, B. & Lundberg, M. (1971). Skeletal and tooth development. *Acta Radiol. Diag.* **11,** 97–112.

Liversidge, H. M., Dean, M. C. & Molleson, T. I. (1993). Increasing human tooth length between birth and years. *Am. J. phys. Anthrop.* **90,** 307–313.

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. Florence: International Institute for the Study of Man.

Logan, W. H. G. & Kronfeld, R. (1933). Development of the human jaw and surrounding structures from birth to the age of fifteen years. *J. Am. Dent. Assoc.* **20,** 379–427.

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. *Am. J. Orthod. Dentofac. Orthop.* **101,** 145–151.

Marks, S. C., Jr & Schroeder, H. E. (1996). Tooth eruption: Theories and facts. *Anat. Rec.* **245,** 374–393.

Moorrees, C. F. A. (1965). Normal variation in dental development determined with reference to tooth eruption status. *J. dent. Res. Supplement to Number 1* **44,** 161–173.

Moorrees, C. F. A., Fanning, E. A. & Hunt, E. E., Jr (1963*a*). Age variation of formation stages for ten permanent teeth. *J. dent. Res.* **42,** 1490–1502.

Moorrees, C. F. A., Fanning, E. A. & Hunt, E. E., Jr (1963*b*). Formation and resorption of three deciduous teeth in children. *Am. J. phys. Anthrop.* **21,** 205–213.

Nanda, R. S. & Chawla, T. N. (1966). Growth and development of dentitions in Indian children. I.

Development of permanent teeth. *Am. J. Orthod.* **52,** 837–853.
Nichols, R., Townsend, E. & Malina, R. (1983). Development of permanent dentition in Mexican-American children (abstract). *Am. J. Phys. Anthrop.* **60,** 232.
Nielsen, H. G. & Ravn, J. J. (1976). A radiographic study of mineralization of permanent teeth in a group of children aged 3–7 years. *Scand. J. Dent. Res.* **84,** 109–118.
Nolla, C. M. (1960). The development of the permanent teeth. *J. Dent. Child.* **27,** 254–266.
Nystrom, M., Haataja, J., Kataja, M., Evalahti, E., Peck, L. & Kleemola-Kujala, E. (1986). Dental maturity in Finnish children, estimated from the development of seven permanent mandibular teeth. *Acta Odont. Scand.* **44,** 193–198.
Nystrom, M., Ranta, R., Kataja, M. & Sivola, H. (1988). Comparisons of dental maturity between the rural community of Kuhmo in north-eastern Finland and the city of Helsinki. *Comm. Dent. Oral Epidemiol.* **16,** 215–217.
Ochollo, T. J. O. (1990). The accuracy and reliability of radiographically determined dental age: Observations from two groups of 4–16 year-olds (Abstract). *J. dent. Res.* **69,** 967.
Owsley, D. W. & Jantz, R. L. (1983). Formation of the permanent dentition in Arikara Indians: timing differences that affect dental age estimates. *Am. J. phys. Anthrop.* **61,** 467–471.
Pierce, C. N. (1884). Calcification and development of mandibular teeth. *Dental Cosmos* **26,** 449–455.
Ramirez Rozzi, F. (1993). Tooth development in East African *Paranthropus*. *J. hum. Evol.* **24,** 429–454.
Saunders, S., DeVito, C., Herring, A., Southern, R. & Hoppa, R. (1993). Accuracy tests of tooth formation age estimations for human skeletal remains. *Am. J. phys. Anthrop.* **92,** 173–188.
Schour, I. (1936). The neonatal line in the enamel and dentin of the human deciduous teeth and first permanent molar. *J. Am. dent. Assoc.* **23,** 1946–1955.
Schour, I. & Massler, M. (1941). The development of the human dentition. *J. Am. dent. Assoc.* **28,** 1153–1160.
Schultz, A. H. (1935). Eruption and decay of the permanent teeth in primates. *Am. J. phys. Anthrop.* **19,** 489–581.
Shellis, R. P. (1984). Variations in enamel structure of the enamel crown in human teeth and a possible relationship between growth and enamel structure. *Archs oral Biol.* **29,** 697–705.
Simpson, S. W. (1992). A comparison of dental development among hominoids. PhD Dissertation. School of Biomedical Sciences, Kent State University, Kent, Ohio.
Simpson, S. W., Lovejoy, C. O. & Meindl, R. S. (1990). Hominoid dental maturation. *J. hum. Evol.* **19,** 285–297.
Simpson, S. W., Lovejoy, C. O. & Meindl, R. S. (1992). Further evidence on relative dental maturation and somatic developmental rate in hominoids. *Am. J. phys. Anthrop.* **87,** 29–38.
Smith, B. H. (1991). Standards of human tooth formation and dental age assessment. In (M. Kelley & C. S. Larsen, Eds) *Advances in Dental Anthropology*, pp. 143–168. New York: Wiley-Liss.
Speechly, T. J. & Liversidge, H. M. (1997). Accuracy of Demirjian's method of age determination on British children. (Abstract). *J. dent. Res.* **76,** 247.
Staaf, V., Mornstad, H. & Welander, U. (1991). Age estimation based on tooth development: A test of reliability and validity. *Scand. J. Dent. Res.* **99,** 281–286.
Tanner, J. M. (1962). *Growth at Adolescence*. Oxford, U.K.: Blackwell Scientific Publications.
Ten Cate, A. R. (1985). Physiological tooth movement, eruption, and shedding. In (A. R. Ten Cate, Ed.) *Oral Histology: Development, Structure, and Function* (2nd edition), pp. 264–288. St Louis: The CV Mosby Co.
Tompkins, R. L. (1996). Human population variability in relative dental development. *Am. J. phys. Anthrop.* **99,** 79–102.
Trodden, B. J. (1982). *A Radiographic Study of the Calcification and Eruption of the Permanent Teeth in Inuit and Indian Children*. Ottawa: Museum of Man.
Winkler, L. A., Schwartz, J. H. & Swindler, D. R. (1991). Aspects of dental development in the orang-utan prior to eruption of the permanent dentition. *Am. J. phys. Anthrop.* **86,** 255–271.
Winkler, L. A. (1995). A comparison of radiographic and anatomical evidence of teeth development in infant apes. *Folia primatol.* **65,** 1–13.