Incremental dental development: Methods and applications in hominoid evolutionary studies

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Abstract

This survey of dental microstructure studies reviews recent methods used to quantify developmental variables (daily secretion rate, periodicity of long-period lines, extension rate, formation time) and applications to the study of hominoid evolution. While requisite preparative and analytical methods are time consuming, benefits include more precise identification of tooth crown initiation and completion than conventional radiographic approaches. Furthermore, incremental features facilitate highly accurate estimates of the speed and duration of crown and root formation, stress experienced during development (including birth), and age at death. These approaches have provided insight into fossil hominin and Miocene hominoid life histories, and have also been applied to ontogenetic and taxonomic studies of fossil apes and humans. It is shown here that, due to the rapidly evolving nature of dental microstructure studies, numerous methods have been applied over the past few decades to characterize the rate and duration of dental development. Yet, it is often unclear whether data derived from different methods are comparable or which methods are the most accurate. Areas for future research are identified, including the need for validation and standardization of certain methods, and new methods for integrating nondestructive structural and developmental studies are highlighted.

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Keywords: Age at death; Dentine formation; Enamel formation; Incremental features; Life history

Introduction

Dental remains represent a well-established means of reconstructing the evolution of humans and their Miocene hominoid predecessors. Commonly noted reasons for this include their relative abundance in the fossil record, lack of remodeling (other than attrition), relatively strong genetic component, evidence for dietary preferences, and taxonomic utility. Less commonly noted is the temporal record of development preserved in teeth. In a process similar to the production of many biological hard tissues, dental tissues are formed in an accretional manner that permanently captures the rate and duration of their formation. Incremental manifestations of biological rhythms in teeth range from a subdaily to an annual periodicity, and have been documented by microscopists and oral biologists for several centuries (reviewed in Boyde, 1964, 1990; Dean, 1987a,b, 1995a; Smith, 2006). Anthropologists have only recently turned their attention to incremental dental development after early reports of incremental features (perikymata) on the surface of fossil hominin teeth (e.g., Robinson, 1956) and studies of internal enamel and dentine microstructure in living primates (e.g., Fukuhara, 1959; Boyde, 1963; Shellis and Poole, 1977; Dean and Wood, 1981). Subsequent research by Beynon, Boyde, Bromage, Dean, Martin, Reid, and Shellis ushered in a new field of dental microstructure studies in living and fossil apes and humans (Table 1). Research on incremental development during the past few decades has grown quite rapidly (Smith and Hublin, 2008); active areas of inquiry span the primate order and extend back to the fossil record of the earliest primates (e.g., Schwartz et al., 2002, 2005).

Following Dean and Wood’s (1981) landmark radiographic study of hominoid dentitions, histological studies during the 1980s and 1990s began to provide a new understanding of
Table 1
Studies of incremental development in hominoid primates (1983–2007)*

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<tr>
<th>Taxon</th>
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<td><em>Homo erectus</em></td>
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<td>Early <em>Homo sapiens</em></td>
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<td>Smith et al., 2007c</td>
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<td><em>MSA Homo sapiens</em></td>
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<td>UP <em>Homo sapiens</em></td>
<td>E,D</td>
<td>Dean, 1985; Ramirez Rozzi and Bermudez de Castro, 2004</td>
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* Includes reports of novel data in full-length papers/dissertations only; E = data on enamel formation; D = data on dentine formation.
hominoid dental development, driven, in part, by the goal of characterizing fossil hominin development. Beynon and Dean (1987) noted that, prior to the 1980s, fossil hominin dental development had been assessed by comparing human and ape eruption sequences, which yielded only relative ages. It was not until studies by Bromage and Dean (1985), Dean et al. (1986), Beynon and Wood (1987), and Beynon and Dean (1987) that hominin crown formation times were directly estimated from incremental features. Subsequent studies in the 1990s began to establish a framework for nonhuman primate dental development, although both sample sizes and the number of reports were smaller than those for hominins. Research conducted in the past decade has reported on aspects of incremental development in larger samples, as well as in a greater diversity of fossil hominoid taxa. This expanding database provides critical insight into developmental variation within and among hominoids, leading to more refined comparisons of dental development and better assessment of the evolutionary utility of these approaches.

Paleoanthropological studies of incremental development generally aim to increase knowledge of hominoid ontogeny, life history, and/or taxonomy. During the past few decades numerous methods have been developed to quantify tooth growth, especially the daily secretion rate, extension rate, and/or formation time. These variables are critical to assessments of crown formation time, root formation time, and age at death. Studies of incremental dental development are also used for a broader spectrum of anthropological applications (reviewed in Smith, 2004), including forensic science, paleodemography, paleoprimatology, and reconstruction of past diets (via isotopic studies; e.g., Humphrey et al., 2007; Tafforeau et al., 2007). Furthermore, due to the well-established relationship between dental development and life history, studies of tooth growth (especially molar eruption) in immature individuals provide important evidence of the evolution of hominin and hominoid developmental biology (e.g., Smith and Tompkins, 1995; Kelley, 1997, 2002; Dean, 2000, 2006; Kelley and Smith, 2003; Skinner and Wood, 2006).

While many studies have focused on establishing the consistent temporal nature of incremental features (reviewed in FitzGerald, 1998; Smith, 2006), less attention has been paid to establishing the precision or accuracy of methods that quantify developmental rate or time (but see exceptions in Beynon et al., 1991a, 1998a,b; Dean et al., 1993a; Ramirez Rozzi, 1997; Reid et al., 1998a; Dean, 1998a; Antoine et al., 1999; Kelley et al., 2001; Smith et al., 2004; FitzGerald and Saunders, 2005; Smith et al., 2006a). As a result, little methodological standardization exists, and the comparability of some data is unclear. This issue has been compounded by recent information on variation within and among teeth. For example, histological studies have demonstrated that all cusps within a molar and all molars within a row do not develop identically (e.g., Reid et al., 1998a,b; Reid and Dean, 2006; Smith et al., 2007a,b), implying that interspecific comparisons of formation time should be limited to equivalent cusp and molar types (Smith et al., 2007a). In the following sections, recent methods for quantifying incremental features are reviewed, and evolutionary applications to hominin and hominoid cases are examined. Avenues for future study are suggested, including the need for standardization and validation of particular methods. Finally, a new approach to the integration of structural and histological data using high-resolution micro-computed tomography (μCT) is outlined.

**Background**

Incremental enamel and dentine microstructure features are defined in this review as structural phenomena that are formed with a consistent periodic repeat interval (in contrast to aperiodic structural features such as enamel prisms, dentine tubules, and Hunter-Schreger bands). Traditionally, this includes the following enamel features: (1) cross-striations and (2) Retzius lines and their surface manifestation, known as perikymata (Fig. 1). (See Smith [2006] and Tafforeau et al. [2007] for investigations of intradian lines and laminations, enamel incremental features that are not typically used for the quantification of hominoid enamel development.) Cross-striations and Retzius lines are also frequently referred to as short- and long-period structures due to their respective 24-hour and >24-hour rhythms. They are also distinguished from growth disturbances that may manifest as marked accentuations or disruptions of the developing enamel front, features referred to as accentuated lines (also sometimes termed pathological lines or Wilson bands) and enamel hypoplasias, which have an irregular periodicity that is thought to conform to an extrinsic form of stress (reviewed in Hillson and Bond, 1997; Skinner and Hopwood, 2004; Schwartz et al., 2006).

Short- and long-period features of dentine microstructure are known as (1) von Ebner’s lines and (2) Andresen lines, which have been shown to correspond to cross-striations and Retzius lines in enamel, respectively (Bromage, 1991; Dean et al., 1993b; Dean, 1995a; Dean and Scandrett, 1996). There is evidence to suggest that Andresen lines may manifest on the root surface of juvenile individuals as periradicular bands (Fig. 1) (Dean, 1995a; Smith et al., in press-a), which may be equivalent to perikymata on the enamel surface. Finally, tooth cementum is believed to show an annual rhythm manifest as cementum annulations in tooth roots (e.g., Kay et al., 1984; Wittwer-Backofen et al., 2004), but due to the difficulty of accurately identifying these lines sequentially (Renz and Radlanski, 2006), they have not been used in hominoid evolutionary studies, and will not be discussed further. Given that the great majority of studies of incremental development focus on permanent teeth, as enamel microstructure is more difficult to image in deciduous teeth, the following review will be limited to studies of permanent teeth. (See FitzGerald et al. [1999] and Macchiarelli et al. [2006] for recent data on incremental development in deciduous teeth.)

Recent analyses of enamel and dentine microstructure have sought to characterize several developmental variables using short- and long-period incremental features: (1) daily secretion rate; (2) periodicity of long-period lines (number of short-period increments between successive long-period lines); (3) number and distribution of long-period lines (or their external...
manifestation as perikymata/periradicular bands); and (4) extension rate of crown and/or root growth. The quantification of these variables may be used to determine rate and duration of crown and/or root formation, as well as the age at death (in developing dentitions) and stress experienced during development. Several researchers have noted that histological methods provide more accurate estimates of crown formation time than radiographic methods (Beynon et al., 1991a; Winkler, 1995; Beynon et al., 1998a; Reid et al., 1998a,b). Due to the nature of crown formation, radiographs tend to overestimate the age at crown initiation, underestimate the age at crown completion, and therefore underestimate the duration of crown formation. Due to the time-consuming and partially destructive nature of traditional histological studies, studies of internal development have been limited to a small number of fossils, and only slightly greater numbers of nonhuman primate. Although nondestructive studies of external development (e.g., Bromage and Dean, 1985; Ramirez-Rozzi, 1998; Lacruz et al., 2005) may be the most practical when considering valuable fossil material, data obtained by direct sectioning methods (e.g., Dean et al., 1993a; Reid et al., 1998a; Smith et al., 2004; Schwartz et al., 2006) or virtual sectioning (Smith et al., 2006b, 2007c; Tafforeau and Smith, 2008) are potentially more accurate due to the smaller number of necessary assumptions (discussed below).

Methods and applications

Quantification of daily secretion rate

Assessment of daily secretion rate (DSR) is based on the theory that cross-striations in enamel and von Ebner's lines in dentine are formed every 24 hours (Schour and Poncher, 1937; Mimura, 1939; Schour and Hoffman, 1939; Okada, 1943; Bromage, 1991; Antoine, 2000; Smith, 2006). Determination of rate is generally accomplished by dividing an empirical quantity, such as distance, by a known time; in enamel, the distance between two cross-striations is divided by one day (for greater accuracy, a series of cross-striations is typically measured and divided by the same number of days). Enamel DSR has been conventionally quantified and reported in four primary ways: (1) measurements of cross-striation spacing derived from a single area or a number of unspecified areas within the crown (e.g., Shellis and Poole, 1977; Martin, 1983); (2) measurements averaged in specific regions of the crown (Beynon et al., 1991b); (3) the quotient of prism length divided by (experimentally known) time between intervals (e.g., Dean et al., 1993b); and (4) direct counts of cross-striations between fixed-distance points (e.g., Beynon et al., 1998b; Dean, 1998a; Dean et al., 2001). In dentine, because successive daily lines are difficult to image without demineralization (Dean, 1998b), DSR is often quantified by dividing the spacing of long-period Andersen lines by their periodicity, which is determined from enamel cross-striations and Retzius lines (e.g., Dirks, 1998; Smith et al., 2004, 2007b). A number of experimental studies have also used fluorescent-labeled material to calculate rates of dentine DSR (e.g., Dean, 1993; Dean and Scandrett, 1995), and in material of exceptional quality, DSR has been calculated directly from the spacing of daily lines in dentine (Dean, 1998b, 1999, 2007b).

Initial reports of hominoid enamel DSR were made without reference to the location of measurements (e.g., Shellis and Poole, 1977; Martin, 1983). As subsequent work began to demonstrate that secretion rate was not constant throughout the crown, Beynon et al. (1991b) proposed a method of data collection that divided the enamel crown into eight areas: cuspal inner, middle, and outer; lateral inner, middle, and outer; and cervical inner and outer (see Fig. 2 in Beynon et al., 1991b). This model was an attempt to organize the crown into zones that represented successive stages of development. However, Dean (1998a) noted that defining rates as inner, middle, and outer averages may mask variation, leading to a simplified categorization of this complex developmental process. Furthermore, because secretion and extension rates change throughout development, the equally spaced divisions proposed by Beynon et al. (1991b) are not likely to correspond to equivalent temporal divisions.

Dean et al. (1993b) presented a method for quantifying DSR by measuring the increase in crown height over a known period of time and then plotting this length against time to yield DSR (as the slope) (e.g., see Fig. 5 in Dean et al., 1993b). These types of graphs have included data on both enamel and dentine DSR (Dean, 1993, 1995a,b; Dean et al., 1993b; Dean and Scandrett, 1995) and may include information from a series of successive teeth, provided that they are registered with one another (Dean and Scandrett, 1996). The advantages of this approach are that it may provide insight into changes in rate throughout the continuous development of the enamel (and/or dentine), and extreme rates at the beginning and end of crown formation may be apparent. However, for accurate and continuous assessment of local DSR, many successive intervals must be utilized. Additionally, this method requires either teeth that have been experimentally labeled or identification of a series of accentuations that can be registered with one another in different tissues, cusps, and/or teeth (discussed further below).

Beynon et al. (1998b) and Dean (1998a, 2000) presented DSR data as monthly box-and-whisker plots of cuspal enamel formation based on counts of cross-striations from the beginning to the end of cuspal formation. Dean et al. (2001) illustrated a similar application of this method, where growth...
trajectories of cuspal enamel were determined from counts of cuspal cross-striations in 100-μm intervals from the dentine horn to the tooth surface, and the number of days was plotted against increasing enamel thickness (see also Dean, 2006). A noteworthy limitation of this method is that it requires exceptionally high-quality sections, and sections of such quality are rare (e.g., Schwartz and Dean [2001] reported being able to do this in only 12 of 115 sectioned canines). Furthermore, Smith et al. (2003a, 2004) noted that, even in excellent-quality material, enamel DSR may be difficult to assess along entire prism paths due to high proportions of subdaily features (intradian lines).

Given that these different methods illuminate crown growth in different regions and over different periods of development, it is likely that certain results are not directly comparable. Additionally, Smith et al. (2003a) noted that different researchers do not agree on the implementation of these methods. Beynon et al. (1991b), Dirks (1998), and Reid et al. (1998a,b) suggested that measurements of cross-striations should not be made in the first 100 μm of enamel at the enamel-dentine junction (EDJ) or in the last 100 μm at the surface because aprismatic enamel in these regions and the convergence of Retzius lines at the tooth surface may obscure or complicate measurements of daily lines. When comparing chimpanzee cuspal DSR data from Reid et al. (1998a) and Dean (1998a), reported values in the former do not show the relatively wide range of values reported by the latter (summarized in Table 5.15 of Smith, 2004). Dean’s (1998a) inclusion of the first and last month of cuspal enamel formation (corresponding approximately to the first and last 100 μm) often increases the range of reported DSR values (Dean, 1998a; Beynon et al., 1998b). A similar problem exists between studies that quantify cuspal secretion rates lateral to the cusp tip (e.g., see Fig. 4 in Dean, 1998a) rather than directly over the dentine horn (e.g., Smith et al., 2007b); DSR is often higher on the side of the cusp where the same cohort of cells produces a greater thickness of enamel (relative to the cusp tip, which often shows a slightly “compressed and gnarled” pattern) (e.g., see Fig. 5.5c–d in Smith, 2004). In summary, a consistent and accurate methodology is needed for determining DSR that reflects the underlying process of accretion, that does not substantially mask variation, and that may be applied to a maximal number of sectioned teeth.

Hominoid daily secretion rates

Two general trends have emerged from recent studies: (1) DSR increases from the EDJ to the tooth surface and (2) DSR decreases (at equivalent depths) from the cusp to the cervix. The most commonly studied region of the crown is the cuspal enamel (see reviews in Schwartz et al., 2003; Mahoney et al., 2007), as cuspal secretion rates are important for estimates of crown formation time. Although Smith et al. (2007b) recently concluded that DSR is consistent among cusps within Pan molars, and may be consistent among molar types, additional data are needed to assess trends in DSR through the dentition. Recent work on daily secretion rates in hominoid enamel suggests a lower limit of 2–3 μm/day and an upper limit of 6–7 μm/day (reviewed in Smith, 2004). Beynon et al. (1991b) found that average molar DSR values were fairly similar among hominoids, with Homo and Pan showing the lowest average values, and Gorilla showing higher averages (also see tables in Dirks, 1998; Reid et al., 1998a; Smith et al., 2003a, 2004; Lacruz and Bromage, 2006). Mean cuspal DSR values among Miocene and living apes appear to be fairly similar, although the inner cuspal rates show some variation, particularly when compared to living humans (see Table 2 and Fig. 6 in Mahoney et al., 2007). When fossil hominins are considered, australopiths appear to show the highest cuspal secretion rates, followed by early Homo, which shows similarities with African apes (Dean et al., 2001; Lacruz and Bromage, 2006). Modern humans and Neandertals show lower cuspal rates than other hominins (Dean et al., 2001; Macchiarelli et al., 2006).

Dentine DSR in hominoid permanent teeth is similar to enamel DSR values, with mean values of axial (coronal) dentine ranging from 2 to 4 μm/day in hominoid molars (reviewed in Table 6 of Smith et al., 2004), close to 5 μm/day in the I1 of Proconsul (Beynon et al., 1998b), and between 5 and 6 μm/day in the axial dentine of human anterior teeth (Dean and Scandrett, 1995). Dentine DSR near the enamel cervix and near the root surface (zone 1 in Dean, 1998b) has been reported to range from approximately 1 to 2 μm/day (Dean and Scandrett, 1995; Beynon et al., 1998b; Dean, 1998b; Smith et al., 2004, 2007b), and from 2 to 3 μm/day in slightly deeper dentine (Dean, 2007b). Unlike the situation for enamel, few studies have systematically assessed variation in dentine DSR within a tooth, within a dentition, or among nonhuman hominoids (but see Dean, 1998b, and references therein).

Periodicity of long-period lines

The determination of the periodicity of long-period Retzius lines and Andresen lines is based on the theory that a consistent number of daily increments (cross-striations or von Ebner’s lines) is expressed between successive long-period lines in all teeth of an individual’s dentition. This has been reviewed and tested by Fitzgerald (1995, 1998) and Smith (2004, 2006). Periodicity has been determined traditionally by counting a series of cross-striations between Retzius lines in areas that preserve them clearly, which is often difficult to do with certainty (Fig. 2). Two main complications are the ability to unambiguously identify long-period lines (discussed in the following section) and the precise identification of a complete series of daily lines between successive long-period lines. The periodicity of long-period lines is very rarely assessed in dentine due to the difficulty of imaging successive daily increments (e.g., see Fig. 7 in Dean, 1998b).

In addition to direct counts of cross-striations between successive Retzius lines, Dean et al. (1993b) and Swindler and Beynon (1993) suggested that this variable could also be determined by dividing the spacing between Retzius lines by the average (local) DSR. However, Smith et al. (2003a) noted...
that this method does not necessarily produce periodicity values that are equivalent to direct counts of cross-striations, as DSR is not always constant between pairs of Retzius lines. Local variation, most commonly resulting from the convergence of Retzius lines at the tooth surface (e.g., see Fig. 2.3b in Smith, 2004), may influence DSR when cross-striations from only a portion of the interval are measured. It is suggested that this method for periodicity determination should be applied only in areas that show no evidence of changes in secretion rate (spacing of Retzius lines), and should ideally be used only to verify direct counts. Although it is rare to find areas with clear cross-striations across multiple Retzius line intervals (e.g., see Fig. 7 in Dean, 2000), averaging counts across two or more such intervals may be the most reliable method for accurately determining the periodicity of long-period lines (Fig. 2c) (see Smith [2004, 2006] for additional discussion of confounding factors in periodicity determination).

Smith et al. (2003a) reviewed periodicity values of hominoid long-period lines, which are known to range from 4 to 12 days (see Table 3 in Smith et al., 2003a). Studies of large numbers of modern humans have demonstrated a wide range of Retzius line periodicities (e.g., Beynon, 1992; FitzGerald, 1995, 1998; Smith et al. (2007a) recently reported periodicity in 365 modern humans, which ranged from 6 to 12 days with a mean and mode of 8 days. Few studies of fossil hominins have directly established the periodicity of the material under study (but see Dean, 1987a; Dean et al., 1993a; Ward et al., 2001; Lacruz et al., 2006; Macchiarelli et al., 2006; Smith et al., 2007c; Smith et al., in press-a). Studies of fossil hominins by Bromage and Dean (1985), Dean et al. (1986), Beynon and Dean (1987), and Dean (1987b) used periodicity estimates of 7–9 days, which are the most common values for modern human teeth. Others have used an estimate of 9 days to calculate formation time (e.g., Dean and Reid, 2001; Dean et al., 2001; Cunha et al., 2004; Ramirez Rozzi and Bermudez de Castro, 2004; Ramirez Rozzi, 2005), as a periodicity of 9 days was reported as the mean and modal value of a large study of great apes and humans (reviewed in Dean and Reid, 2001). However, when single-integer estimates are used instead of range data, the accuracy of these nondestructive methods may be in question. It is clear that nondestructive techniques are needed to determine ranges, means, and modes of long-period line periodicities in additional fossil hominins (e.g., Lacruz et al., 2006; Smith et al., 2007c; Tafforeau and Smith, 2008), which may clarify debates over differences in perikymata numbers and formation times between taxa.

Long-period line number and distribution

Long-period line number is typically determined from either histological sections or crown/root surfaces (Fig. 1a–d); given their relatively distinct appearance, this often proves to be the most straightforward aspect of incremental-feature quantification. However, other features such as accentuated lines or enamel laminations found within intervals or coincident with long-period lines may make identification more difficult (FitzGerald, 1995; see Figs. 2.5b and 3.16 in Smith,

2004). Dean (1987a) proposed what has become a paradigm for many histological studies of enamel long-period lines; he suggested that Retzius lines should be identified as those lines that reach the surface as perikymata (see Fig. 4 in Kelley and Smith, 2003; see Fig. 3 in Taforeau and Smith, 2008) in contrast to other lines that may be superimposed on this pattern. Although identification of corresponding perikymata may often represent a reliable means of discriminating Retzius lines, convergence of these lines may sometimes result in a smooth enamel surface without obvious terminal points (Beynon and Dean, 1991; see Fig. 2.5b in Smith, 2004). This is partially due to the production of aprismatic subsurface enamel, which varies within a tooth crown (Whittaker, 1982). The most reliable method of defining and counting Retzius lines may involve the assessment of several characteristics together, including their consistent appearance from the EDJ to the enamel surface, the regular spacing of successive lines, and their terminal manifestation as perikymata on the tooth surface.

Perikymata (Fig. 1a) are often visualized on high-resolution impressions of tooth crowns, and counts are typically made from the cervix to the cusp tip (or vice versa). Studies mapping the distribution of long-period lines have typically used one of two approaches: (1) counts of long-period lines in each millimeter of crown height (e.g., Dean, 1987b; Beynon et al., 1998b; Moggi-Cecchi et al., 1998; Reid et al., 1998a,b), or (2) counts of long-period lines in each decile of crown height (e.g., Reid and Dean, 2000; Dean and Reid, 2001). The latter method has been more commonly applied in the past few years, as it allows for comparisons of the distribution of long-period lines across teeth of differing sizes.

The distribution of perikymata has often been noted as one of the more taxonomically diagnostic features of hominin enamel microstructure. Robinson’s (1956) comparison of perikymata patterns in fossil hominins and modern humans revealed that fossil hominins showed more “regular” spacing of cervical perikymata when compared to a modern sample of postcanine teeth, but that Paranthropus and Australopithecus did not differ. However, Bromage and Dean (1985) suggested that perikymata spacing on incisors does distinguish Paranthropus from Australopithecus, early Homo, and modern humans. They noted that Paranthropus does not show a marked trend of perikymata “narrowing and condensation” cervically as shown in these other taxa, implying a more uniform pattern of cervical enamel formation and possibly a more rapid period of completion (see Fig. 5 in Beynon and Dean, 1988; also see Dean, 1987b; Beynon, 1992; Dean and Reid, 2001; Dean et al., 2001; Lacruz et al., 2006). A few studies have reported developmental differences among Paranthropus species (Dean, 1987b; Ramirez-Rozzi, 1993a, 1998; Dean and Reid, 2001; but see Lacruz et al., 2006). Dean (1987b) and Dean and Reid (2001) reported that Paranthropus boisei shows a different pattern of perikymata distribution than P. robustus; this extremely uniform cervical perikymata distribution in P. robustus may represent a derived condition relative to other hominins. However, Ramirez-Rozzi (1998) questioned the use of perikymata spacing or counts for taxonomic distinction, as he found that patterns of perikymata spacing did not group the Omo hominin teeth in any fashion that agreed with the taxonomic attribution based on macrostructure. More recently, Ramirez Rozzi and Bermudez de Castro (2004) and Guatelli-Steinberg et al. (2007a) reported that perikymata distribution in the cervical aspect of anterior teeth differs between Neandertals and modern humans, with Neandertals showing a more uniform pattern from the cusp to the cervix (somewhat similar to reported differences between Paranthropus and Australopithecus), Guatelli-Steinberg et al. (2007a) found that the degree of surface curvature in modern humans and Neandertals did not explain the apparent taxonomic differences.

Considerably less attention has been paid to the number and distribution of long-period lines in dentine (Dean et al., 1993b; Dean, 1995a; Dean and Scandrett, 1996; Smith et al., 2004) relative to the many studies of long-period lines in enamel. This is partially due to the difficulty of imaging Andresen lines from the beginning to the end of crown/root formation, as well as the historically ambiguous nature of periradicular bands (Fig. 1b), which may represent external circumferential manifestations of long-period lines on the surface of tooth roots (Newman and Poole, 1974; Dean, 1995a, 1999; 2000; Berkovitz et al., 1998; Smith et al., in press-a). In a comprehensive review of dentine incremental features, Dean (1995a) inferred the periodicity of periradicular bands in the roots of OH 16 based on their distribution and the expected rates of root extension, and he suggested that periradicular bands were equivalent to other long-period lines (however, Dean [2007a] recently suggested that these features should be regarded with caution). Smith et al. (in press-a) provided both indirect and direct evidence for the incremental nature of periradicular bands. This was done by identifying similar numbers of long-period lines between stress events across crowns and roots of the anterior teeth of a single individual, and by demonstrating equal numbers of internal and external features between accentuated lines in a single tooth root.

Correlations between periodicity and number of long-period lines and body mass

In a large sample of human canines, Reid and Ferrell (2006) demonstrated that there is a significant negative correlation between long-period line periodicity and Retzius line number (for similar results for all human tooth types, see Guatelli-Steinberg et al., 2005; Smith et al., 2007a; Reid et al., 2008). Apparently, in populations of living Homo, where there is substantial variation in periodicity, the growth period of imbricational enamel may be constrained to produce teeth within a certain period of time, although it remains to be seen if the relationship exists in other hominoids.

Dean (1995a) and Dean and Scandrett (1996) suggested that there may be a link between long-period line periodicity and body size based on evidence from monkeys, apes, humans, and elephants. Smith et al. (2003b) examined this in 18 living and fossil apes and found a significant positive relationship between average periodicity and body mass (tested with separate
Table 2

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Age (Ma)</th>
<th>Mass (kg)</th>
<th>Periodicity</th>
</tr>
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<tr>
<td>Proconsul major</td>
<td>19–20</td>
<td>63.5</td>
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<td>Proconsul africenus</td>
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<td>31.9</td>
<td>2</td>
</tr>
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<td>34.5</td>
<td>2</td>
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<tr>
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<td>1</td>
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<tr>
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</tr>
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<td>76.8</td>
<td>1</td>
</tr>
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<tr>
<td>Homo sapiens</td>
<td>Extant</td>
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<td>365</td>
</tr>
</tbody>
</table>

1 Age = ranges in millions of years (Ma) from Klein (1999) and Hartwig (2002).
2 Mass = average body mass estimates from dental and postcranial estimates (for fossils) when possible in kilograms (kg). Dental estimates were calculated from Conroy’s (1987) dental regressions rounded to nearest 0.5 kg (tooth-size data from Pilbeam, 1969; Swindler, 1976; Koufos, 1993; Kelley and Plavcan, 1998; Kelley et al., 2002), or are from Leaky and Walker (1997). Values derived from cranial and postcranial regressions were taken from Rafferty et al. (1995), Moya-Sola and Kohler (1996), Leaky and Walker (1997), McHenry and Caffin (2000), and Kelley (2001). Extant ape body masses were taken from Smith and Jungers (1997), as an average of both sexes for all subspecies of each species.
3 For periodicity, number of individuals (n), range of long-period line values taken from sources in Table 1, and mean of individual long-period line values are given (“~” represents uncertainty).

Quantification of dental microstructure depends on the fact that growth in tissue thickness and height occurs in two ways: in an appositional manner as ameloblasts/odontoblasts move away from the EDJ (represented by the number and spacing of short-period lines), and by extension of newly differentiated ameloblasts/odontoblasts along the EDJ from the dentine horn to the future cervix (coronal extension) or from the cervix to root apex (root extension) (Fig. 4). Extension rate has been quantified using several indirect and direct methods: (1) measurement of the angle of intersection between the developing front and the EDJ (e.g., Fukuhara, 1959; Boyde, 1964; Beynon and Wood, 1986; Ramirez Rozzi, 1997) or the developing front and root surface (Dean, 1985); (2) calculation based on trigonometric developmental models (Gohdo, 1982; Shellis, 1984a,b); (3) calculation based on a geometric relationship of secretion and extension rates (Dean, 2006, 2007b, in press; Macchiarelli et al., 2006; Dean and Vesey, 2008); (4) direct measurements based on fluorescent labels or long-period lines along the EDJ or root surface (e.g., Schwartz and Dean, 2001; Smith, 2004; Smith et al., 2004, 2007b); and (5) measurement of the overall rate of crown/root extension based on the height of the crown, length of the EDJ, or length of the root divided by the time of formation (e.g., Beynon et al., 1991a; Dean et al., 1993b; Dean, 1995b; Dirks, 1998; Smith et al., 2004, 2006a, 2007c).

Boyde (1964) suggested that the angle of intersection between the developing enamel front and the EDJ provides evidence of the differentiation rate of new enamel-forming cells, with smaller angles indicating faster rates (see Fig. 6.3 in Boyde, 1964). Ramirez Rozzi (1997) attempted to validate this approach by comparing angle of intersection in cuspal, lateral, and cervical regions with the average spacing between dental and skeletal body-mass estimates, and between first molar crown formation time and body mass. The former analysis is expanded here to include hominin taxa (for a total of n = 26 species; see Table 2). A highly significant correlation was found between mean periodicity and body mass among hominoids (Spearman’s ρ = 0.794, p < 0.001) (Fig. 3). This remains highly significant when hominins are excluded (Spearman’s ρ = 0.830, p < 0.001), but is not significant when only hominins are considered (Spearman’s ρ = 0.778, p = 0.069).

However, when considering primates as a whole, this trend may not hold, as large-bodied lemurs show very low values (Schwartz et al., 2002). Furthermore, it is difficult to explain the range of variation in long-period lines within humans and other well-documented hominoids. Additional work is necessary to assess relationships among dental development variables and biological variation (i.e., body mass, brain size, life span), particularly among known-mass individuals and in a broader taxonomic sample of primates.
Retzius lines at the EDJ (although the periodicity of Retzius lines was unknown in this material). His results showed a general agreement between the pattern of increasing angles and decreasing spacing of Retzius lines from the cuspal to cervical regions, suggesting that trends in the angles of intersection represent trends in the extension rate. Smith et al. (2004) also found that low angles between the developing enamel front and the EDJ represent rapid extension, provided that DSR remains constant along the EDJ. However, because enamel secretion rates have been shown to decrease from the inner cuspal to the inner cervical enamel (near the EDJ), angular values may not be directly comparable among regions. Smith et al. (2004) illustrated this in a fossil hominoid molar by showing an area of enamel (underlying the cingulum) with high angles of intersection formed via rapid extension and secretion. In this instance, Boyde’s (1964) model would have predicted a low extension rate from the high angles in this area. This possibility should be considered when making comparisons among primates that have different rates of enamel secretion (also see Smith [2004] for a review of additional factors that influence assessment of extension rate from angles of intersection).

On the basis of Boyde’s (1964) model of extension, Shellis (1984a,b) proposed a formula to quantify coronal extension rate using cross-striation repeat interval (DSR), the angle between prisms and the EDJ, and the angle between the developing enamel front and the EDJ. Shellis (1984a,b) applied this formula to determine crown formation time by summing the time of extension along the EDJ (discussed below). Smith et al. (2006a) tested the accuracy of Shellis’s formula in experimentally labeled macaque teeth and found that this formula typically overestimated extension rate (and therefore underestimated crown formation time) in fast-forming teeth. They concluded that additional research should be conducted prior to the continued use of this formula for either extension rate or formation time estimation.

Dean (2006, 2007b) described a novel method for calculating root extension rates based on identification of accentuated lines in dentine (Owen’s lines) and estimation of the mean DSR (typically assumed to be 2.5 μm/day) in the root dentine below the granular layer of Tomes (see Fig. 1 in Dean, 2007b). The advantages of this approach are that it does not rely on information from crown growth (e.g., long-period line periodicity), and that it may be applied in areas where incremental features are indistinct (Dean, 2007b). Successive applications along the root surface of modern human first molars yield longitudinal records of root extension rates that are similar to those calculated by other methods (Dean, 2007b). However, this method requires knowledge of the mean dentine DSR, and makes the assumption that this rate is constant from the cemento-enamel junction to the root apex. Dentine DSRs of less than 2.0 μm/day have been recorded in hominoid enamel near the cemento-enamel junction/root surface (Dean, 1995a; Dean and Scandrett, 1995; Dean, 1998b; Smith et al., 2004, 2007b), and it was found that chimpanzee root extension rates for the first 1–2 mm were overestimated by this method when compared to rates calculated directly from the number and spacing of Andresen lines (Smith et al., 2007b). Additional systematic data on dentine DSR within and among hominoid roots would help to establish the accuracy of this approach for additional taxa.

Another approach to assess extension rates involves tracing either experimentally introduced labels or long-period increments to the EDJ or root surface, and measuring the distance between labels or long-period lines (Schwartz and Dean, 2001; Smith et al., 2004, 2006a, 2007b). Schwartz and Dean (2001) measured the length of EDJ formed for every 20 Retzius lines, and plotted cumulative crown height against formation time, yielding extension rates as the slope of these graphs (see Fig. 4 in Schwartz and Dean, 2001). They also noted that, in contrast to Retzius lines at the EDJ, measurements of corresponding perikymata (at the tooth surface) do not yield direct information on extension rates. Perikymata spacing is influenced by both local appositional growth and by the extension of the advancing enamel-forming front. While these methods using known intervals of time may be the most accurate,
measurements are limited to labeled samples or sections with clear expression of long-period lines, which are quite rare for the later stages of root formation.

Finally, several studies have quantified overall extension rates from the length of the EDJ or root surface divided by the respective crown or root formation time (determined independently). Smith et al. (2004) used data on cusp-specific crown-formation time to empirically derive an overall coronal extension rate for the Miocene hominoid Graecopithecus freybergi and subsequently applied this approach to other primates (Smith et al., 2006a, 2007b, in press-a). Beynon et al. (1991a) worked iteratively from the age at death to determine root extension rates for several developing Gorilla teeth (also see Dean and Beynon, 1991; Dirks, 1998). A disadvantage of quantifying overall extension rates in this manner is the lack of information on rate variation; molar coronal extension begins rapidly and slows down (Dean, 1998a; Smith et al., 2004), while molar root extension begins slowly, speeds up, and may fluctuate before apical closure (Dean, 1985, 2000, 2006, 2007b; Macchiarelli et al., 2006; Smith et al., 2007b). Therefore, overall extension rates derived from developing EDJs or roots of different lengths (or developmental stages) may not be comparable. As is the case for secretion rate, numerous methods have been developed to quantify extension rate; a number of these approaches would benefit from validation, particularly to assess if data derived from different methods are comparable.

**Hominoid crown and root extension rates**

Fukuhara (1959) presented some of the earliest data on the angle of intersection between the developing enamel front and the EDJ, which was greatest in anthropoids and hominoids relative to other primates. A number of subsequent studies have presented similar data for living and fossil apes and humans (e.g., Beynon and Wood, 1986; Beynon and Reid, 1995; Beynon et al., 1998b; Ramirez Rozzi, 1997; Ramirez-Rozzi, 1998; Ramirez Rozzi, 2002; Smith et al., 2003a, 2004; Lacruz et al., 2006). Beynon and Reid (1995) reported similar patterns among extant hominoids; angles show an increase from the cuspal enamel to the cervical enamel. This may imply a decrease in extension rate (but not necessarily), which also corresponds to the pattern of decreasing DSR towards the cervix. Among fossil hominins and hominoids, variation in angular trends has been seen from the cuspal to cervical enamel (e.g., Ramirez-Rozzi, 1998; Smith et al., 2003a; Lacruz et al., 2006). A comparison of average angles in two Miocene hominoids suggested that differences exist between buccal and lingual cusps within regions (cuspal, lateral, and cervical thirds of the crown) (Smith et al., 2003a, 2004). Additional information is necessary on extension-rate variation among cusp and molar types before differences in these angles may be fully understood among hominoid taxa.

Empirically derived rates of crown and root extension are known for few hominoids. Crown extension in the M₃ protoconid of G. freybergi ranged from 14 μm/day to less than 3 μm/day, with an overall value of 6 μm/day (Smith et al., 2004). Smith et al. (2007b) presented overall values for chimpanzee molars in their Table 7, which ranged from 4 to 9 μm/day and were higher in lower molars than in respective upper molars. Smith et al. (in press-a) presented similar data for two Neandertal molars, which showed values more similar to chimpanzees than to humans. More data are available on hominoid root extension rates (e.g., Beynon et al., 1991a; Dean and Beynon, 1991; Dean, 1995a, 2006; Liversidge, 1995; Dirks, 1998, 2003; Moggi-Cecchi et al., 1998; Dean et al., 2001; Kelley et al., 2001; Macchiarelli et al., 2006; Smith et al., 2007b; Dean and Vesey, 2008). It appears that anterior teeth typically show higher rates than posterior teeth (Beynon et al., 1991a; Liversidge, 1995; Dirks, 1998; Simpson and Kunos, 1998), and that great apes and most fossil hominins show higher values than living humans (e.g., Beynon et al., 1991a; Dean et al., 2001; Dean, 2006; Smith et al., 2007c, in press-a,b). Additional data on crown and root extension rates are needed from the beginning to the end of formation, particularly as this may facilitate nondestructive estimates of crown and/or root formation time from high-resolution μCT scans of developing material, or possibly from knowledge of tooth crown height (Dean, 2006, 2007b).

**Estimation of crown formation time**

Analyses of incremental features may permit accurate estimation of crown and/or root formation time, as well as age at death in developing material (Antoine et al., 1999; Antoine, 2000; Smith, 2004; Smith et al., 2006a). Enamel formation is often divided into cuspal and imbricational components of the crown, while dentine may be quantified in the coronal region and/or root (Fig. 4). Several primary methods have been employed to estimate crown formation: (1) counts of successive cross-striations (cuspal and/or total crown formation time); (2) application of extension rate along the EDJ (cuspal and/or total time); (3) division of the prism path length by the DSR (cuspal, imbricational, and/or total time); and (4) estimation of cuspal enamel time added to counts of long-period lines multiplied by their periodicity (imbricational time), which is summed for total time. In the following sections, methods will be reviewed for quantification of the entire crown, cuspal, and imbricational formation times.

‘‘Whole-crown approaches.’’ Asper (1916) suggested that counts of cross-striations provide an accurate determination of the period of crown formation, which was employed first by Gygi (1931; see also Boyd, 1963, 1990; Antoine, 2000). However, this method requires sections of exceptional quality (such as the Spitalfields archaeological material used by Antoine), as it is quite rare that successive cross-striations can be counted from the dentine horn to the tip of the cuspal enamel (Schwartz and Dean, 2001) and along prisms throughout the entire crown. A second ‘‘whole-crown approach’’ was proposed by Shellis (1984a,b, 1998), who applied his extension-rate formula to determine the duration of enamel formation, where crown formation time is equal to the sum of times derived from segments of the EDJ divided by corresponding extension rates (but see discussion above and Smith et al., 2006a).
Massler and Schour (1941, 1946) suggested that prism length could be divided by the “characteristic rate of apposition,” or DSR, to determine the time of formation. Beynon et al. (1991a) and Reid et al. (1998a) applied this approach to calculate crown formation times of extant ape teeth (see Fig. 1 in Reid et al., 1998a) and compared these results to those derived from the more common “cuspal plus imbricational approach.” Reid et al. (1998a) found differences ranging from an 8.6% underestimate to a 20.9% overestimate for the “rate of apposition approach” relative to the alternative method. A related method used in recent studies of fossil apes involved division of axial dentine thickness (coronal dentine directly beneath the dentine horn) by the mean axial dentine DSR (e.g., Beynon et al., 1998b; Kelley et al., 2001). The main advantage of this latter method is that it may be applied to slightly worn teeth, and it is based on dentine tubule paths, which are straighter than cuspal enamel prisms. When compared to estimates derived from enamel, this method may yield similar or slightly lower values (Kelley et al., 2001; Smith et al., 2004). Smith et al. (2004) noted that, although this method is promising, it is prone to error in oblique sections that do not preserve the actual tip of the dentine horn. Furthermore, it is difficult to calculate dentine DSR in the earliest-formed dentine due to the lack of clearly defined incremental features.

Risnes’s (1986) commonly cited research on enamel prism path lengths suggests that, due to the three-dimensional (3D) nature of prism paths, formation-time calculation requires an adjustment of the linear enamel thickness with a correction factor. Although several early studies applied Risnes’s correction factor to estimations of cuspal enamel formation time, several others have noted that this factor may not be appropriate for all hominids (reviewed in Smith et al., 2003a; see also Macho et al., 2003). Hominins or hominoids with fairly straight prisms paths, such as *Paranthropus* or *G. freybergi*, may not require a correction factor (Smith et al., 2004), while other hominoids may show more marked prism deviation (Dean, 1998a). Additionally, little is known about the variation of prism paths in different regions of the crown, different cusps in the same tooth, or different tooth types and positions (Shimizu et al., 2005). More work is needed to better understand the relationship between the 3D course of a prism and the linear thickness of enamel (Macho et al., 2003), which may be possible with phase contrast X-ray synchrotron microtomography (Tafforeau and Smith, 2008).

**Cuspal formation time.** Cuspal formation time is typically more difficult to assess than imbricational formation time, partially due to the lack of developmental features expressed externally. This difficulty is underscored by the number of quantitative approaches developed in the past two decades: (1) counts of cross-striations in the cuspal enamel (e.g., Beynon and Dean, 1987; Dean et al., 1993a; Dean, 1998a); (2) counts of Retzius lines in the cuspal enamel (e.g., Bullion, 1987; Dirks, 1998; Ramirez Rozzi, 1998); (3) counts of Andresen’s lines in the corresponding coronal dentine (Smith et al., 2004); (4) cuspal prism path length divided by average cuspal DSR (e.g., Dean et al., 1993a; Dean, 1998a; FitzGerald et al., 1999); (5) cuspal enamel thickness divided by average cuspal DSR (e.g., Reid et al., 1998a,b); (6) axial dentine length divided by dentine DSR (e.g., Dean, 1998a; Schwartz et al., 2003); and (7) cumulative length of the cuspal EDJ divided by the local extension rate (Dean, 1998a).

In addition to these methods, Schwartz and Dean (2001) and Dean et al. (2001) presented regression equations of enamel thickness against DSR, which have been used to predict cuspal enamel formation time (from cuspal enamel thickness). This method can be applied to sectioned teeth with poor cross-striation visibility or to virtually sectioned material using high-resolution μCT (Smith et al., 2006b, 2007c, in press-a), which may yield accurate linear measurements non-destructively (Olejniczak and Grine, 2006). Given the wide range of linear-thickness values reported for humans and chimpanzees (e.g., Suwa and Kono, 2005; Smith et al., 2007b), this approach yields more precise estimates of cuspal formation time in material that may not be physically sectioned.

In an important test of four methods for estimating cuspal enamel formation time, Dean (1998a) compared results from (1) direct counts of cross-striations, (2) axial dentine length divided by average dentine DSR, (3) prism length divided by average enamel DSR, and (4) division of cuspal EDJ length by the estimated extension rate. The results of all four methods were within 5—10% of one another; however, because actual cuspal formation times were unknown, it is not clear which method is the most accurate. In a subsequent test of the accuracy of crown formation time and age at death estimation, Smith et al. (2006a) found that section obliquity confounded estimation of cuspal formation time due to inflated thickness and potentially inflated secretion rates (see also Dean et al., 1993a; Smith et al., 2004). Careful section preparation is essential for accurate assessment of cuspal formation time using any of the methods described above.

**Imbricational enamel formation.** Numerous studies of fossil hominins have estimated the imbricational aspect of crown formation time from counts of perikymata at the enamel surface or from Retzius lines in naturally fractured teeth, as these are nondestructive analytical methods. One of the major limitations of this approach is that an individual’s long-period line periodicity must be determined from an internal surface, or an estimated value must be used. A small error in the total number of long-period lines may affect estimates by a few weeks, but an error in the determination of the periodicity by a single day (cross-striation) may result in a difference of a few months to more than half a year (depending on tooth type). This difference may be seen when comparing data on chimpanzee molar crown formation times from Reid et al. (1998a) with revised values from Smith et al. (2007b); misidentification of Retzius line periodicity in the former study resulted in overestimated molar formation times. Due to limitations in imaging, equivalent long-period lines in coronal dentine are rarely counted to assess corresponding enamel formation (but see Smith et al., 2004).
Hominoid crown formation times

Crown formation times are most commonly reported for extant hominoid canines and molar enamel thickness. Aside from studies of great ape incisors and canines (Dean and Reid, 2001; Schwartz and Dean, 2001; Schwartz et al., 2001) and chimpanzee molars (Smith et al., 2007b), histologically derived crown formation times have been described for a maximum of four dentitions per ape species (Beynon et al., 1991a; Dirks, 1998, 2003; Reid et al., 1998a; Schwartz et al., 2006; Ramirez Rozzi and Lacruz, 2007). Schwartz et al. (2006) recently demonstrated a wide range of crown formation times in two Gorilla dentitions, and Smith et al. (2007b) found even greater variation among common chimpanzee molars. Crown formation times in most fossil and living ape molars fall within chimpanzee ranges, except for Proconsul heseloni and Hyllobates lar, which are at the low end, and Gigantopithecus blacki, which is at the high end (reviewed in Table 7 of Smith et al., 2003a; also see Dean and Schrenk, 2003; Mahoney et al., 2007). The proportion of cuspal to imbricate formation time may yield better distinction among hominoids than total molar formation times (Smith et al., 2003a, 2004), although this would benefit from further study.

Several researchers have recently established crown formation times for modern humans using histological methods, noting that variation exists among populations. Reid and Dean (2006) and Reid et al. (2008) reported crown formation times in South African and northern European teeth, which showed fairly consistent population differences in anterior teeth and premolars, but less differences among molars. Smith et al. (2007a) examined only unworn and lightly worn molar sections in a more diverse sample (including that used by Reid and Dean, 2006) and found a number of differences among human populations, emphasizing the need for data from additional modern human populations. When human molars were compared to equivalent chimpanzee molar and cusp types, Smith et al. (2007a) found that crown formation times were greater in humans, although some overlap was found. Limited data exist for fossil hominin crown formation times; estimates for early hominins suggest shorter periods than respective modern human teeth (e.g., Bromage and Dean, 1985; Beynon and Dean, 1987; Beynon and Wood, 1987; Dean, 1987b; Dean et al., 1993a; Dean and Reid, 2001; Dean et al., 2001; Lacruz, 2007). Beynon and Wood (1987) reconstructed crown formation times in Paranthropus boisei and early Homo, and concluded that enamel development in P. boisei shows a pattern similar to that seen in modern human deciduous teeth, which may imply that there was strong selective pressure to grow teeth rapidly with very thick enamel (see also Beynon and Dean, 1987; Grine and Martin, 1988). Dean et al. (2001) suggested that early fossil Homo formation times fall between australopiths and living Homo. Limited data on Neandertals appear to indicate greater similarity with modern human crown formation times than with earlier hominins (e.g., Mann et al., 1991; Dean et al., 2001; Guatelli-Steinberg et al., 2005; Macchiarelli et al., 2006; Guatelli-Steinberg and Reid, 2008; but see Ramirez Rozzi and Bermudez de Castro, 2004; Smith et al., in press-a). Small samples of Early and Middle Stone Age Homo sapiens show crown formation times similar to modern humans (Smith et al., 2006b, 2007c). In short, there appears to be a trend for hominin crown formation times to increase over the past several million years, as is the case for hominin brain and body size (e.g., Ruff et al., 1997; McHenry and Coffing, 2000; Skinner and Wood, 2006).

Root formation time, age at death, life history, and developmental chronology

In a similar approach to the calculation of root extension rates, root formation times have been typically quantified by (1) counts of Andresen lines (Smith et al., 2006a, 2007b); (2) application of extension rate along the root surface (e.g., Beynon et al., 1998b; Dean, 2006; Macchiarelli et al., 2006); (3) division of tubule length by dentine DSR along successive root segments (Smith et al., 2007b); and (4) subtraction of the age at crown completion from the age at death (in developing roots) (e.g., Beynon et al., 1991a; Dirks, 1998; Smith et al., 2007c). Several early histological estimates of hominoid root formation time came from studies of juvenile dentitions (e.g., Beynon et al., 1991a; Dean and Beynon, 1991; Dean et al., 1992; Dirks, 1998). When an individual dies prior to root completion, formation is halted (and registered) across the dentition, allowing rates and times to be determined iteratively with knowledge of age at death, crown formation, and initiation age. Other studies have used accentuated lines, hypoplasias, or fluorescent labels to register teeth and estimate the duration of root formation between events (e.g., Dean et al., 1993b; Reid et al., 1998a). As noted above, few studies have quantified root formation time directly from incremental growth due to the difficulty of imaging successive incremental features in dentine, representing one of the more challenging areas of histological research on teeth.

Boyd (1963, 1990) suggested that histological assessments of dental development are more reliable than assessments of skeletal development for determining the age at death of young individuals, as dental development is less variable. However, he speculated in 1963 that this time-consuming method was not likely to find widespread application, which proved true until the 1980s. In order to accurately assess chronological age in hominoids, an accentuated line formed at birth, known as the neonatal line (Rushton, 1933; Schour, 1936), is identified in the first molar, which begins formation approximately 15–60 days before birth (Beynon et al., 1991a; Dirks, 1998; Reid et al., 1998a,b; Schwartz et al., 2006; Smith et al., 2007b). Chronological age is calculated as the developmental time of enamel and root dentine formed after the neonatal line (provided that the individual has not completed root formation). An alternative approach to reconstruct age at death is to estimate the amount of postnatal delay prior to initiation of a specific tooth, adding subsequent crown and root formation time (e.g., Bromage and Dean, 1985; Kelley and Smith, 2003; Smith et al., 2007c). Dean (1987a) noted that using modern human estimates for initiation ages is likely to lead
to overestimation when applied to fossil hominins that demonstrate a faster period of overall dental development. However, Smith et al. (2007c) noted that this may be less of a problem for early-forming teeth than for later-forming teeth, as there is less variation among living great apes and humans in the former case. New histological data on crown-initiation ages from diverse human populations would be particularly valuable, as these data have been reported for very few individuals to date (Dean et al., 1997b; Reid et al., 1998b; Antoine, 2000), yet are crucial to nondestructive studies of fossil hominins.

Bromage and Dean (1985) were the first to apply incremental-feature quantification to assess age at death for several fossil hominins, suggesting that juvenile Australopithecus afarensis, A. africanus, Paranthropus robustus, and early Homo individuals demonstrated developmental stages more similar to extant great apes than to modern humans. A number of studies have subsequently estimated age at death for fossil material (Table 3), as well as for recent human and ape individuals (e.g., Beynon et al., 1991a; Dean and Beynon, 1991; Reid et al., 1998a; Dirks, 1998; Antoine, 2000; Schwartz et al., 2006; Smith et al., 2007b). The results of these investigations have led to a dramatic reinterpretation of the timing of growth and development in hominin evolution (e.g., Bromage and Dean, 1985; Beynon and Dean, 1988; Dean et al., 1993a, 2001; Dean, 1995a, 2000, 2006; Smith and Tompkins, 1995; Smith et al., 2007c). Dean et al. (2001) demonstrated that early hominins showed a more rapid developmental profile (of cuspal enamel growth) than great apes, and early Homo showed a very similar profile to great apes, suggesting that slow, prolonged developmental processes are a relatively recent evolutionary development in human evolution. As noted above, studies of Neandertals are equivocal, and more data are needed to assess if there are differences in mean crown formation times or ages at molar eruption (Kelley, 2004). Crown calcification stages and dental eruption patterns in an early Moroccan H. sapiens juvenile from 160,000 years ago suggests that modern human life history may have originated with the advent of H. sapiens (Smith et al., 2007c), although more data are needed on incremental development in middle Pleistocene hominins (e.g., Bermudez de Castro et al., 2003; Ramirez Rozzi and Bermudez de Castro, 2004).

A number of studies have also used incremental features to provide insight into life history trends among nonhuman hominoids (e.g., Kelley, 1997, 2002; Dirks, 2001; Kelley et al., 2001; Macho, 2001; Kelley and Smith, 2003; Schwartz et al., 2006; Zhao et al., 2008). Macho (2001) suggested that crown formation time is positively correlated with several life-history traits across primates, although there is some uncertainty about the accuracy of the crown-formation and life-history data used in this study (Kelley and Smith, 2003). Limited data on age at M1 emergence in Proconsul nyanzae, Afropithecus turkanensis, Sivapithecus parvada, and Lufengpithecus lufengensis suggest that hominoids with dental developmental schedules similar to those of chimpanzees may have evolved as long ago as the early Miocene (Kelley, 1997, 2002; Kelley and Smith, 2003; Zhao and He, 2005; Dean, 2006; Zhao et al., 2008).

Beynon et al. (1991a) presented the first use of enamel microstructure for inferring the overall chronology of tooth development in individual Pongo and Gorilla specimens. This was possible due to the developmental arrest at death, as well as the presence of hypoplasias and/or tetracycline labels in all of the teeth. Gustafson (1955) demonstrated that patterns of (nonincremental) accentuated lines in enamel are remarkably similar in related teeth of the same type (contralateral pairs), allowing identification of an equivalent point in developmental time across the dentition (see also Boyd, 1963,

Table 3

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Specimen</th>
<th>Age (yrs)*</th>
<th>Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Afropithecus turkanensis</td>
<td>KNM–MO 26</td>
<td>2.2–3.3</td>
<td>Kelley and Smith, 2003</td>
</tr>
<tr>
<td>Sivapithecus parvada</td>
<td>GSP 11536</td>
<td>2.5–4.8</td>
<td>Kelley, 1997</td>
</tr>
<tr>
<td>Lufengpithecus lufengensis</td>
<td>PA 868</td>
<td>2.4–4.7</td>
<td>Zhao and He, 2005; Zhao et al., 2008</td>
</tr>
<tr>
<td>Australopithecus afarensis</td>
<td>LH2</td>
<td>3.3–3.5</td>
<td>Bromage and Dean, 1985; Beynon and Dean, 1988</td>
</tr>
<tr>
<td>Australopithecus africanus</td>
<td>Taung</td>
<td>3.3–3.9</td>
<td>Bromage and Dean, 1985; Lacruz et al., 2005</td>
</tr>
<tr>
<td></td>
<td>Sis24a</td>
<td>3.3</td>
<td>Bromage and Dean, 1985</td>
</tr>
<tr>
<td></td>
<td>Sis151</td>
<td>5.2–5.3</td>
<td>Moggi-Cecchi et al., 1998</td>
</tr>
<tr>
<td>Paranthropus robustus</td>
<td>SK 62</td>
<td>3.3–3.5</td>
<td>Bromage and Dean, 1985</td>
</tr>
<tr>
<td></td>
<td>SK 63</td>
<td>3.1–4.5</td>
<td>Bromage and Dean, 1985; Dean et al., 1993a; Dean, 1999</td>
</tr>
<tr>
<td>Paranthropus boisei</td>
<td>KNM-ER 1477</td>
<td>2.5–3.0</td>
<td>Dean, 1987b</td>
</tr>
<tr>
<td></td>
<td>KNM-ER 812</td>
<td>2.5–3.0</td>
<td>Dean, 1987b</td>
</tr>
<tr>
<td></td>
<td>KNM-ER 1820</td>
<td>2.5–3.1</td>
<td>Dean, 1987b</td>
</tr>
<tr>
<td></td>
<td>OH 30</td>
<td>2.7–3.2</td>
<td>Dean, 1987b</td>
</tr>
<tr>
<td>Early Homo</td>
<td>KNM-ER 820</td>
<td>5.3</td>
<td>Bromage and Dean, 1985</td>
</tr>
<tr>
<td>Homo erectus</td>
<td>KNM-WT 15000</td>
<td>&gt;8, &lt;12</td>
<td>Dean et al., 2001</td>
</tr>
<tr>
<td>Homo neanderthalensis</td>
<td>Dederiye1</td>
<td>1.4–1.5</td>
<td>Sasaki et al., 2002</td>
</tr>
<tr>
<td></td>
<td>Devil’s Tower</td>
<td>3.1–4.4</td>
<td>Dean et al., 1986; Stringer et al., 1990; Stringer and Dean, 1997</td>
</tr>
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<td></td>
<td>Hortus II-III</td>
<td>6.5–7.9</td>
<td>Ramirez Rozzi, 2005</td>
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<td></td>
<td>Scladina</td>
<td>8.0</td>
<td>Smith et al., in press-a</td>
</tr>
<tr>
<td></td>
<td>Obi-Rakhmat</td>
<td>7.2–8.6</td>
<td>Smith et al., in press-b</td>
</tr>
<tr>
<td>Homo sapiens</td>
<td>Irhoud 3</td>
<td>7.8</td>
<td>Smith et al., 2007c</td>
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</table>

* Estimates for all specimens, except for SK 63, Dederiye1, Scladina, and Irhoud 3, are based on estimated periodicity values.
and platyrrhines from catarrhines, or among hominoids (but Dirks, 2003; Thomas, 2003; Smith et al., 2004; Schwartz 1998b; Dirks, 1998; Reid et al., 1998a,b; Antoine, 2000; Dirks, 2003; Thomas, 2003; Smith et al., 2004; Schwartz et al., 2006; Smith et al., 2007b, in press-a). This aspect of hard tissue registry permits more precise estimates of cusp initiation and completion than is possible using conventional dissection or radiographic techniques.

**Taxonomic applications**

Early studies by Fukuhara (1959), Boyde (1963), Shellis and Poole (1977), and Martin (1983) suggested that different combinations of incremental and nonincremental features could distinguish primates from other mammals, prosimians and platyrhines from catarrhines, or among hominoids (but see Beynon et al., 1991b; Risnes, 1998). As detailed in the preceding sections, recent work has pointed to taxonomic differences in hominoid daily secretion rates, average long-period line periodicities, long-period line spacing, extension rates, and crown formation times, in addition to differences in prism paths and Retzius line morphology (e.g., Bromage and Dean, 1985; Beynon and Wood, 1986, 1987; Beynon and Dean, 1988; Grine and Martin, 1988; Dean and Shellis, 1998; Ramirez Rozzi, 1998; Dean et al., 2001; Macho et al., 2003; Smith et al., 2003a; Ramirez Rozzi and Bermudez de Castro, 2004; Lacruz and Bromage, 2006; Lacruz et al., 2006; Guatelli-Steinberg et al., 2007a; Mahoney et al., 2007). The studies reviewed here generally suggest that a combination of features (e.g., secretion rate, perikymata spacing, extension rates, and enamel thickness) may provide the best discrimination between closely related genera, although there are still unresolved questions about the degree of developmental variation found within genera and species (e.g., Ramirez Rozzi, 1998; Smith et al., 2003a; Lacruz, 2007). On going and future studies of developmental variation in living apes and humans may better inform taxonomic studies by documenting developmental variation throughout the dentition at the level of populations, species, and genera.

**Summary and concluding remarks**

This paper presents a comprehensive review of methodology employed for assessment of enamel and dentine incremental development, including daily secretion rate (DSR), long-period line periodicity and number, extension rate, and crown and root formation times. Evolutionary studies have benefited from taxonomic, forensic, and ontogenetic applications of incremental development, although data obtained from different methods are not always comparable. Numerous approaches employed to quantify DSR are reviewed here. It is apparent that enamel daily secretion rate (DSR) differs with crown position, increasing from inner to outer enamel and from cervical to cuspal regions, and ranging from approximately 2 to 7 µm/day among hominoids. This variable is fairly similar among hominoids of differing tooth and/or body size, although cuspal enamel values may distinguish certain hominoids. Known DSR values are also broadly similar between enamel and dentine, although additional data are needed from hominoid roots.

Determination of long-period line periodicity is one of the most difficult aspects of quantifying incremental development, partially due to the requirement of internal feature visualization. Nondestructive applications of confocal microscopy or phase contrast X-ray synchrotron microtomography may allow for periodicity assessment in larger numbers of hominin fossils, leading to greater precision in formation-time estimation. Hominoid periodicity values are known to range from 4 to 12 days, and from 6 to 12 days within humans. It is demonstrated that long-period line periodicity is significantly correlated with hominoid body mass, and in humans the former variable is inversely correlated with long-period line number.

As with DSR, numerous methods of quantifying extension rate have been developed, leading to multiple types of data that are not necessarily comparable. Approaches involving comparisons of angles of intersection of the developing enamel front with the enamel-dentine junction would benefit from assessment of variation within and between cusps, along with consideration of the effects of DSR variation. Both coronal and root extension appear to vary among tooth types; within molars, first molars may show higher rates than posterior molars, and lower molars may have higher rates than respective upper molars. Given variation in root extension rates, it is suggested that rate comparisons should be made between equivalent roots at similar stages of development.

As is the case for long-period line periodicity, estimation of cuspal enamel formation time has also proven to be relatively complicated, and a minimum of eight different approaches have been developed. Although several of these methods have been shown to give consistent results with one another, the accuracy of many of these methods has yet to be demonstrated. For imbricational enamel formation (or root formation time) where it is not possible to assess the long-period line periodicity, it is suggested here that estimates of formation time should be based on a range of periodicity values, rather than upon a single integer. Reports characterizing crown and root formation times have been limited by a paucity of comparative data, although recent studies have provided crown formation times for the entire dentition of two modern human populations. It appears that crown formation time has increased throughout the hominin lineage.

Finally, assessments of age at death, life history, and developmental chronology in developing dentitions are reviewed. Based on estimates of age at death and molar eruption, evidence from Australopithecus, Paranthropus, and early Homo suggests that modern human life history appeared recently. The earliest evidence for modern human developmental patterns is from a juvenile dated to 160,000 years ago, although little is known about hominins from the middle Pleistocene. Additional information on crown initiation ages is needed, which would strengthen estimates of age at death in hominin and hominoid fossils.
A final goal of this review was to identify ways that future work may complement and refine our current understanding of the complex process of tooth formation. Additional research may include experimental studies on long-period line etiologies and defect formation, particularly as accentuated lines and enamel hypoplasias have been the subject of a number of recent studies of living and fossil primates (e.g., Guatelli-Steinberg, 2001; Thomas, 2003; Guatelli-Steinberg, 2004; Skinner and Hopwood, 2004; Fitzgerald and Saunders, 2005). Advances in microscopy and tomography may represent a means to increased knowledge of the three-dimensional paths of ameloblasts and their secretory products (e.g., Radianski et al., 2001; Tafforeau and Smith, 2008). It is anticipated that histological studies may continue to assess variation in daily apposition (Dean, 1998b, 2004) and extension (Smith et al., 2004; Dean, 2007b), which may facilitate more precise nondestructive studies.

Nondestructive micro-computed tomography (μCT) is proving to be an important methodological addition, yielding complementary insight into tooth structure and development (e.g., Avishai et al., 2004; Skinner et al., 2008), linear enamel thickness (e.g., Suwa and Kono, 2005; Smith et al., 2006b, 2007c, in press-a), and extension rates (Smith et al., in press-a). Smith et al. (in press-a) used μCT for virtual orientation of a tooth crown prior to physical sectioning, facilitating precise physical sectioning of rare fossil material. Moreover, advances in X-ray synchrotron microtomographic techniques, which provide a nondestructive means of exploring incremental development (Tafforeau et al., 2007; Smith et al., 2007c; Tafforeau and Smith, 2008), may hold the key to producing accurate three-dimensional models of tooth growth, as well as greater understanding of hominoid evolutionary developmental biology.

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