

A Fine Line: A Comparison of Methods for Estimating Ages of Linear Enamel Hypoplasia Formation

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ABSTRACT It is accepted that linear enamel hypoplasias (LEHs), a specific type of enamel thickness deficiency, are related to periodic physiological disruptions to enamel matrix secretion during times that teeth are developing. Thus, LEHs are treated as general indicators of metabolic stress. Because the disruptions that cause LEHs affect only the portion of the crown that is in the process of forming, determining their locations allows researchers to reconstruct chronologies of stressful events. It is widely held that the many of the commonly used macroscopic methods for estimating the timing of LEHs are imprecise and do not conform to our current understanding of the process of enamel formation. The goal of the present study is to compare estimated ages of LEH formation produced by two of the most commonly used macroscopic methods to those derived from data in

recent histological studies that include more precise information about the timing of crown formation across diverse human populations. These approaches are compared in two ways: 1) by creating a theoretical model using simulated LEHs and 2) empirically, by analyzing data collected on a sample of ancient Nubians from Semna South (present-day Sudan). Results indicate that the approach derived from histological studies provides significantly higher age estimates than the commonly used methods and this difference is particularly marked in early forming LEHs. The magnitude of this difference is large enough to produce divergent interpretation of bioarchaeological datasets and suggests that reevaluation of the methods used to estimate ages of LEH formation may be justified. *Am J Phys Anthropol* 135:348–361, 2008. © 2007 Wiley-Liss, Inc.

Dental enamel hypoplasias are deficiencies of enamel thickness that disrupt the normal contour of the crown surface of a tooth and are formed during the secretion of enamel matrix (Sarnat and Schour, 1941; Goodman and Rose, 1990; Hillson, 1996). Most dental enamel hypoplasias are evident as bands around the circumference of a tooth's crown and are roughly parallel to the cemento-enamel junction (CEJ) and perpendicular to the tooth's long axis (e.g., Hillson, 1996; Goodman and Song, 1999). Although their precise etiology is not well understood, it is accepted that dental enamel hypoplasias are related to periodic physiological disruptions to matrix secretion during times that teeth are developing; therefore, these defects are treated as general indicators of metabolic stress (e.g., Goodman and Rose, 1990, 1991; Hillson, 1996; Hillson and Bond, 1997; Larsen, 1997; Goodman and Song, 1999; Guatelli-Steinberg, 2001). Many forms of enamel hypoplasia exist (see, e.g., Hillson, 1996; Hillson and Bond, 1997); however, linear enamel hypoplasias (LEHs)—which are characterized by a marked horizontal or nearly horizontal area of decreased enamel thickness (Goodman et al., 1980)—have been particularly important to bioarchaeological, paleopathological, and paleoanthropological research. Because the physiological disruptions that cause LEHs affect only the portion of the crown that is in the process of forming, determining the location of these defects (and how these locations correspond to the ages at which the defects formed) allows researchers to reconstruct chronologies of metabolically stressful events in individuals and, by extension, in living or archaeological populations (Goodman and Rose, 1990; Larsen, 1997; Goodman and Song, 1999; Guatelli-Steinberg, 2001; Guatelli-Steinberg et al., 2004). Many

of the macroscopic methods that have been used to estimate the timing of LEHs, however, do not conform to our current understanding of the nonlinear rate at which tooth crowns form and inadequately account for the time during which cuspal enamel develops (Hillson, 1992a,c; Skinner and Goodman, 1992; Hillson and Bond, 1997; Goodman and Song, 1999; Reid and Dean, 2000). Researchers generally agree that these commonly used methods produce age estimates that are considerably younger than the actual ages at which LEHs occurred (Skinner and Goodman, 1992; Hillson and Bond, 1997; Goodman and Song, 1999; Reid and Dean, 2000; King et al., 2002, 2005), although this assumption has never been tested directly.

The goal of the present study is to conduct such a test by comparing estimated ages of LEH formation produced by two macroscopic methods that are commonly used [Goodman et al.'s (1980) chart method and Goodman and Rose's (1990) regression-based method] to age estimates derived from data presented in Reid and Dean's (2006) study, which uses histology to examine variation in both the rate and timing of enamel formation. In addition to

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testing the broadly accepted idea that age estimates produced using the commonly used macroscopic methods systematically underestimate the timing of LEH formation, this study quantifies any apparent differences in age estimates and provides a foundation on which the bioarchaeological implications of these differences are discussed.

BACKGROUND

Summary of enamel formation

To understand how LEHs develop and how their locations on tooth crowns correspond to the ages at which they form, it is necessary to review briefly the process by which tooth crowns grow (see Aiello and Dean, 1990; Hillson, 1996; Schwartz and Dean, 2000). Enamel formation begins when enamel-forming cells (ameloblasts) line up opposite the dentin-forming cells (odontoblasts) along the inner enamel epithelium. Shortly after the odontoblasts lay down a platform of dentin matrix, ameloblasts begin to secrete enamel. This process begins at the dentine horn and continues cervically.

Enamel is laid down in a series of layers. The first layers make up the cusps and are laid down in a series of dome-like layers of increasing size that are deposited atop preceding layers (see Fig. 1). After the deposition of “cuspal enamel,” ameloblasts lined along the cusp’s occlusal surface cease their secretory phase and have a role in the maturation process of the enamel matrix. Subsequently, ameloblasts continue to form enamel down the walls of the crown (“lateral enamel”) where they are arranged in a tile-like, or imbricational, manner.

LEHs are formed when the enamel matrix-secreting function of ameloblasts is temporarily disrupted (Shawashy and Yaeger, 1986). An enamel defect, however, will only be visible on the surface of the crown if the metabolically stressful event that causes it is temporally linked to lateral, not cuspal, enamel formation (Skinner and Goodman, 1992; Goodman and Song, 1999; Reid and Dean, 2000; King et al., 2002). Stressful events that occur during the formation of cuspal enamel will only be visible in histological sections of teeth (Hillson and Bond, 1997).

History of studies on the timing of LEH formation

Previous research aimed at determining the timing of LEH formation has employed both macroscopic and microscopic methods. The foundation of contemporary macroscopic methods was established in two articles published by Schour and coworkers in the early 1940s (Massler et al., 1941; Sarnat and Schour, 1941). Specifically, Massler et al. (1941) reported results of an examination of over 1,000 teeth of normal, healthy children collected by the University of Illinois College of Dentistry.¹ Using information gleaned from histological examination of these teeth and data from Logan and Kron-

¹These teeth were collected from sources in the Chicago area, including dental clinics and private practitioners (Massler et al., 1941), and it is reasonable to assume that the majority of these teeth were from American children of European decent (Goodman and Song, 1999).

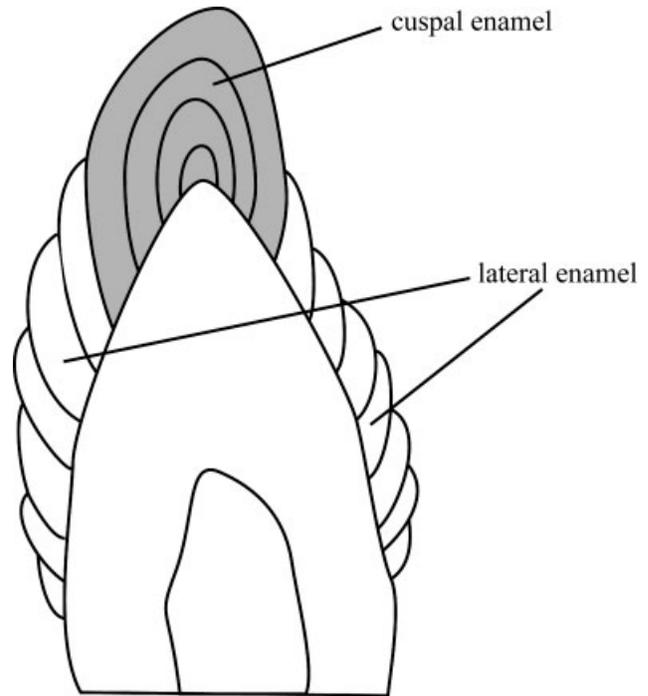


Fig. 1. Depiction of incisor crown illustrating cuspal and lateral enamel. Redrawn and adapted from Aiello and Dean (1990).

feld’s (1933) study, they developed a standard of dental development (their Figs. 6 and 7) that depicted ages of formation for increasing portions of crown height. Building on this developmental standard, Swärdstedt (1966) developed an explicit method that used the location of LEHs to estimate an individual’s age when the defect formed. Swärdstedt (1966) divided each tooth into six-month intervals and produced a diagrammatic model that illustrated these increments. Using this diagram, Swärdstedt (1966) was able to convert the location of LEHs, as measured from the CEJ, into six-month developmental zones. This method was revised by Goodman et al. (1980), although the basic form of the Swärdstedt’s (1966) diagram was retained: for each tooth, linear distances from the CEJ were matched to six-month intervals that were based on Massler et al.’s (1941) dental development standard. This method (hereafter referred to as the “chart method”) is the one most commonly used by bioarchaeologists today (see later).

In an effort to provide more precise age estimates, Goodman and Rose (1990, 1991) asserted that methods aimed at reconstructing chronologies of LEH formation could be refined by the application of regression equations. This argument was based on the contention that the variation in growth velocity of enamel within teeth is negligible, contrary to the implication conveyed by the varying distances between six-month intervals in individual teeth in the chart method. Their regression equations (Table 1) were based on mean crown heights from Swärdstedt’s (1966) study and Massler et al.’s (1941) dental development standards and took the following form:

$$\text{Age at LEH formation} = -[(1/\text{velocity}) \times \text{distance of LEH from CEJ}] + \text{age at crown completion}$$

TABLE 1. Regression equations from Goodman and Rose (1990)

Tooth type	Formula ^a
Maxillary teeth	
I1	Age (in years) = $-(0.454 \times H) + 4.5$
I2	Age (in years) = $-(0.402 \times H) + 4.5$
C	Age (in years) = $-(0.625 \times H) + 6.0$
P3	Age (in years) = $-(0.494 \times H) + 6.0$
P4	Age (in years) = $-(0.467 \times H) + 6.0$
M1	Age (in years) = $-(0.448 \times H) + 3.5$
M2	Age (in years) = $-(0.625 \times H) + 7.5$
Mandibular teeth	
I1	Age (in years) = $-(0.460 \times H) + 4.0$
I2	Age (in years) = $-(0.417 \times H) + 4.0$
C	Age (in years) = $-(0.588 \times H) + 6.5$
P3	Age (in years) = $-(0.641 \times H) + 6.0$
P4	Age (in years) = $-(0.641 \times H) + 7.0$
M1	Age (in years) = $-(0.449 \times H) + 3.5$
M2	Age (in years) = $-(0.580 \times H) + 7.0$

^a Where H equals the distance between LEH and the CEJ in mm.

Considerable attention has been paid to identifying possible sources of bias inherent in the chart method and regression equations (e.g., Goodman and Rose, 1990, 1991; Hillson, 1992a,c; Skinner and Goodman, 1992; Katzenberg et al., 1996; Goodman and Song, 1999; King et al., 2002). One of the most evident limitations of the chart method and Goodman and Rose's (1990) regression equations is that they do not account for cuspal enamel formation time and, therefore, are likely to produce ages that significantly underestimate the true timing of LEH formation (Skinner and Goodman, 1992; Goodman and Song, 1999; King et al., 2002, 2005). Goodman and Song (1999), however, argue that including cuspal enamel formation time increases age estimates by no more than six months. The chart method and Goodman and Rose's (1990) regression equations also assume that tooth crowns grow at a constant rate, an assumption that has been demonstrated repeatedly to be spurious (e.g., Hillson, 1992a,c; Skinner and Goodman, 1992; Goodman and Song, 1999; King et al., 2002, 2005). It is presently unclear how using nonlinear models of crown growth would affect age estimates. Finally, because they are based on a population whose crowns have been shown to be small, Goodman and Rose's (1990) regression equations may not provide accurate age estimates for populations with larger crowns (Goodman and Song, 1999). Hodges and Wilkinson (1990) and Goodman and Song (1999), however, found that employing a population's own crown heights had little effect on population distributions of LEH age estimates.

Despite discussions of how the biases inherent in the chart method and regression equations may result in inaccurate age estimates, these methods have been applied frequently in contemporary bioarchaeological research. For instance, studies of medieval Danes (Ben-nike et al., 2005), Native South Americans (Santos and Coimbra, 1999), medieval Slavic people (Obertová, 2005), colonial era Canadians (Wood, 1996), and late medieval/early modern Lithuanians and Danes (Palubeckaitė et al., 2002) all employed the chart method, while studies of ancient Egyptians (Lovell and Whyte, 1999) and

Classic Period Lowland Maya (Wright, 1997) used regression equations.² In addition, the chart method is the suggested means for estimating ages of LEH formation in Buikstra and Ubelaker's (1994) widely used standards for data collected from human skeletal samples.

Other researchers (e.g., Hillson, 1992a,b,c; Hillson and Bond, 1997; King et al., 2002, 2005) have used microscopic methods for estimating the ages at which LEHs formed. The approach employed by Hillson et al. entails making coated replicas of teeth that are then examined using scanning electron microscopy (SEM). SEM is used to quantify the spacing between adjacent perikymata. These data are used to identify possible LEHs, which are verified with SEM and binocular microscopy. LEHs are matched across at least two teeth to ensure that the recorded lesions represent "systemic growth disruptions" rather than enamel defects that could have been caused by localized trauma on individual teeth (King et al., 2005; p 550). The age of the earliest forming defect in each individual is determined by adding the estimated time formation for the completion of cuspal enamel in the tooth on which the defect appears to the age at which the tooth initiates growth and the time required for the completion of lateral enamel formation between the cusp tip and the defect. The latter is calculated by counting the number of perikymata between the cusp tip and the defect and multiplying this number by the periodicity (i.e., the estimated number of days of enamel secretion between adjacent perikymata).

Unlike the chart method and the regression equations, Hillson et al.'s microscopic approach does not assume that tooth crowns grow at a constant rate and explicitly includes the time for cuspal enamel formation in determining the ages at which LEHs form. This approach also does not rely on crown height data from a single reference population, so it is unaffected by errors that may be introduced using the chart method or regression equations (see earlier). Cuspal enamel formation time and perikymata periodicity, however, have been shown to vary between individuals (Hillson, 1996; Reid and Dean, 2000) and between populations (Reid and Dean, 2006). The accuracy of the ages determined using this microscopic method, therefore, is contingent on the degree to which the assumptions about these aspects of crown formation hold in the sample being measured. Assumptions of this nature are required whenever the population from which the measured sample of teeth is drawn and the sample used to establish periodicity and cuspal enamel formation time are not identical. Intra-population variability in these measures cannot be accounted for unless the specimens on which LEHs are aged are also sectioned.

²These authors employed regression equations that varied slightly from those developed by Goodman and Rose's (1990). Lovell and Whyte (1999) employed equations independently developed by Phillip Walker based on Massler et al.'s (1941) developmental standard, while Wright (1997) used regression equations that incorporated population-specific data on crown height (see below). The basic form of the equations, however, was identical to those presented by Goodman and Rose (1990). Regardless of their specific parameters, equations that take this form assume the process of crown growth is linear and do not account for the fact that enamel defects that develop while cuspal enamel is being laid down are not apparent at the crown's surface.

Reid and Dean (2000, 2006) data

Reid and Dean's (2000) study clarified some of the issues relating to the timing of LEH formation. Using histological data derived from a relatively small sample of anterior teeth, Reid and Dean (2000) divided each tooth's crown into equal tenths (i.e., "deciles" of crown height). They calculated the number of days it takes for each of these deciles to grow and, by summing all deciles and adding an estimate of the number of days required for cuspal enamel formation and the number of days between birth and crown initiation, calculated ages at crown completion. Using the same methods, Reid and Dean (2006) analyzed much larger samples in additional tooth types, including two samples (northern Europeans and southern Africans) from which 12 teeth (I_1 , I^1 , I_2 , I^2 , maxillary C, mandibular C, M_{1-3} , M^{1-3}) were measured.³ Reid and Dean (2000) did not suggest that these data alone represent a new standard with which timing of LEH formation can be estimated. They noted, however, that a more accurate estimate of the average timing of metabolically stressful episodes in an individual could be calculated if these data were used to age all LEHs in the dentition and these ages were then averaged.

Although Reid and Dean's (2000) data have been applied to bioarchaeological research aimed at estimating the ages at which LEHs form (e.g., Cucina, 2002; Cucina et al., 2006; Palubeckaitė et al., 2006), no studies to date have evaluated the differences between ages of LEH formation estimated using methods derived from these data and age estimates that employed the more commonly used macroscopic methods.

RESEARCH OBJECTIVES

The present study has two main components, each of which compares ages of LEH formation derived from two commonly used macroscopic methods [i.e., the chart method and Goodman and Rose's (1990) regression equations] to those derived from Reid and Dean's (2006) data (see later). The first component is a theoretical comparison of the formation ages produced for hypothetical LEHs. This component is aimed at identifying the extent to which estimated ages of LEH formation derived from the commonly used methods differ from those produced using Reid and Dean's (2006) data and describes the pattern of these differences in terms of the location of the hypothetical LEHs on tooth crowns.

The second component is an empirical analysis of differences in estimated ages of LEH formation produced by the commonly used methods and the Reid and Dean (2006) data. As such, this component compares the ages of LEHs provided by each of the approaches for a sample of teeth drawn from an archaeological population. The goal of this component is to examine explicitly how the choice of method for determining the age of LEH formation impacts the interpretation of the possible sources of stresses on this archaeological population. In addition, because the Reid and Dean (2006) model also includes geographically diverse human reference samples, this

component also evaluates the effect of choice of reference sample on such interpretations.

MATERIALS AND METHODS

Theoretical analysis

To compare theoretically the differences between the commonly used macroscopic methods and ages estimated on the basis of Reid and Dean's (2006) data, the ages of 10 hypothetical LEHs (representing each of the 10 deciles of crown height) on a mandibular canine were evaluated. The mandibular canine was chosen for the theoretical analysis because this tooth had the largest sample size in the empirical analysis (see later). For each hypothetical LEH, four ages were calculated: 1) using the chart method, 2) using the Goodman and Rose (1990) regression equations, 3) using the comparative data for the northern European sample in Reid and Dean (2006), and 4) using the comparative data for the southern African sample in Reid and Dean (2006). The specific methods that were used to determine ages using the data from Reid and Dean (2006) are outlined in the next section.

Empirical analysis

Metric analyses. To compare methods of determining ages at which LEHs formed, Nubian specimens ($n = 62$ individuals; total of 125 teeth) from the Semna South collection housed at Arizona State University were measured. Semna South is located on the west bank of the Nile River, 15 miles south of Wadi Halfa in present-day Sudan, in a rugged region between the Second and Dal cataracts known as the Batn el Hajar or "Belly of the Rocks" (see Fig. 2). This skeletal collection was excavated by the University of Chicago's Oriental Institute between 1966 and 1968 (Žabkar and Žabkar, 1983) and consists of remains from the cemetery north of the fort at Semna South (Alvrus, 1996, 1999). Skeletal material in the collection dates to three time periods: the Meroitic period (350 B.C.–A.D. 350), X-group or Ballana culture (A.D. 350–A.D. 550), and Christian period (A.D. 550–1400); the vast majority of the sample is Meroitic. Forty-six individuals from the Meroitic period (90 teeth), 10 individuals from the Ballana period (22 teeth), two individuals from the Christian period (four teeth) and four individuals from unknown temporal context (nine teeth) were included in the present study.

A total of 72 LEHs were measured (across 63 teeth of 37 individuals; Tables 2 and 3). Specimens were selected for inclusion if they had at least one easily observable LEH (see Fig. 3) on one of the following permanent teeth from either side of the dental arcade: I_1 , I^1 , I_2 , I^2 , mandibular C, maxillary C, M_1 , M^1 , M_2 , M^2 . When antimeres possessed LEHs, only the side that was more easily observed was measured. Most teeth (55.6%) that were measured were canines (30.2% mandibular C and 25.4% maxillary C); no M^3 s with easily observable LEHs were found.

The distance from the middle of the LEH to the CEJ was measured in the midline to the nearest hundredth of a millimeter using Mitutoyo Absolute Digimatic digital sliding calipers. LEHs were measured on protoconids on mandibular molars and protocones on maxillary molars. Measurements on 10 LEHs were repeated on three different days to assess intra-observer error. A repeated measures ANOVA indicates no significant dif-

³Reid and Dean (2006) also measured three other samples (North American "Caucasian," North American "mixed," and medieval Danish). The two North American samples, however, included only maxillary third molars and the medieval Danish sample included only maxillary and mandibular canines, rendering them of little utility in the present study.

ferences among repeated measures ($F = 1.715$; $P = 0.208$) and the mean measurement error was two percent.

To accommodate the methods of estimating timing of LEHs derived from the Reid and Dean (2006) model of enamel formation, the crown heights of 71 unworn teeth representing 32 individuals were measured (Table 4). Crown heights were measured from the CEJ to the cuspid tip and were taken in the midline on incisors and canines, on the protoconid of mandibular molars and on the protocone of maxillary molars. Table 4 lists descrip-

tive statistics for crown height in unworn teeth used in the present study as well as in three comparative samples. A comparison of these statistics indicates that the Semna South dental sample used here is not substantially more variable than other archaeological samples and justifies the use of mean crown height in estimating ages of LEH formation using Reid and Dean's (2006) data. Measurements of crown height for 10 unworn teeth were repeated on three different days to assess intra-observer error. A repeated measures ANOVA indicates no significant differences among repeated measures ($F = 0.020$; $P = 0.980$).

Four age estimates were calculated using these measurements. One estimate was derived from the regression equations published by Goodman and Rose (1990) and another, using the chart method, which estimates the six-month interval in which a LEH formed. Two age estimates were calculated using the data from Reid and Dean (2006): one using the data from their northern European sample (hereafter, the "RDNE model") and one using the data from their southern African sample (hereafter, the "RDSA model").

To employ the RDNE and RDSA models, distances from the hypoplasia to the CEJ were subtracted from the mean crown height of the appropriate tooth (calculated using data for unworn teeth, Table 4), thus reconstructing the distance of the LEH from the occlusal tip. For each LEH, this reconstructed distance was assigned to a decile of crown height. LEHs were assigned to the last decile that had completed growth before the formation of the defect. The age of occurrence for each LEH was then calculated by adding the number of days required to form the assigned decile of crown height to the number of days required for cuspal enamel formation. Because all of the teeth measured in the present study except M1s initiate formation after birth, the number of days between birth and initiation of formation for these teeth was also added to the age estimates. To facilitate comparison to the chart method, the absolute ages from both the RDNE and RDSA models were also converted into six-month intervals.

Statistical analyses. Before comparisons of the different methods for estimating the timing of LEH formation were made, a set of statistical procedures (using SPSS 11.0) was used to test the validity of the measurement protocols employed here. First, because previous authors (e.g., Hillson, 1992a,c; Reid and Dean, 2000; King et al., 2002, 2005) have stressed the importance of matching enamel defects across different teeth in single dentitions,

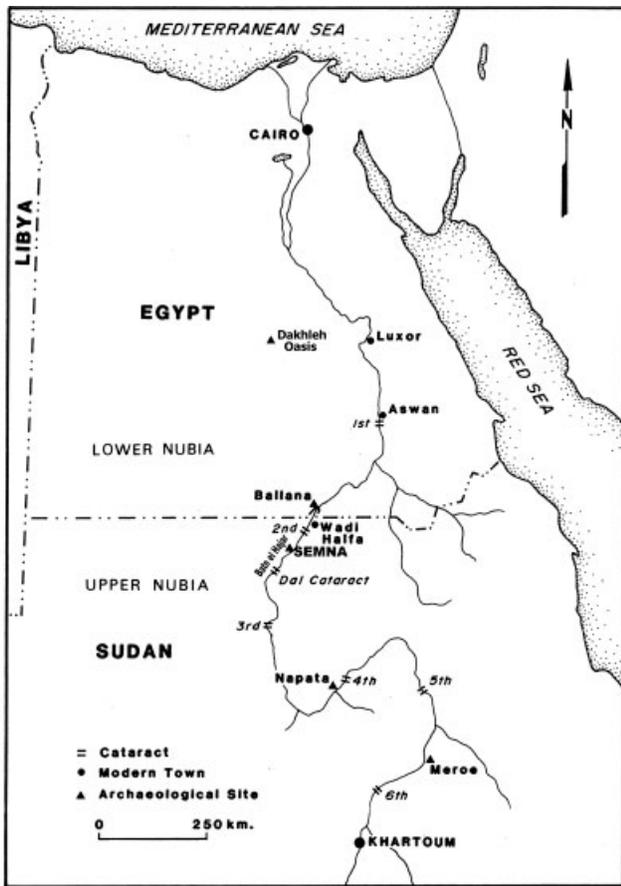


Fig. 2. Map of the Nile Valley showing the location of Semna South. Adapted from Baker (1992).

TABLE 2. Number of hypoplastic teeth in sample and the number of teeth with one, two, three, and four LEHs separated by tooth type^a

Tooth type	No. of hypoplastic teeth	No. of teeth with 1 LEH	No. of teeth with 2 LEHs	No. of teeth with 3 LEHs	No. of teeth with 4 LEHs	Total no. of LEHs
LC	19	17	1	0	1	23
UC	16	15	1	0	0	17
I ₁	2	1	1	0	0	3
I ₁ ⁺	7	7	0	0	0	7
I ₂	4	3	1	0	0	5
I ₂ ⁺	4	4	0	0	0	4
M ₁	7	7	0	0	0	7
M ₂	3	2	0	1	0	5
M ₂ ⁺	1	1	0	0	0	1

^a No teeth with more than four LEHs was included in the present study.

TABLE 3. Number of individuals with one, two, three and four hypoplastic teeth^a

	Number of hypoplastic teeth			
	1	2	3	4
Number of individuals	19	11	6	1

^a No individuals with more than four LEHs was included in the present study.

the effect of treating all LEHs individually was evaluated. Specifically, using an independent samples *t*-test, the mean age from a sample that included all LEHs was compared to the mean age of systemic growth disruptions. The ages of these systemic growth disruptions were derived by averaging the ages of groups of LEHs that could be matched between tooth types with overlapping developmental schedules. Student's *t*-tests were performed using the RDNE and RDSA models and the regression equations to determine if, in each case, the means of matched and unmatched LEHs were significantly different. A *t*-test was not performed using the chart method because LEHs were assigned to six-month intervals rather than absolute ages; thus, averaging the ages of matched LEHs was not possible. Second, because Reid and Dean (2006) divided tooth crowns into deciles by measuring the tooth lengths along the curved length (instead of using crown height, as was employed in the present study), LEHs on anterior teeth used in this study were reassigned to deciles after correcting for the difference between crown height and surface curvature; this correction was performed using comparative data from Table 8 in Guatelli-Steinberg et al. (2007).

A series of statistical procedures was also designed to determine if significant differences exist between the commonly used macroscopic methods of determining the age at which LEHs formed [i.e., Goodman and Rose's (1990) regression equations and the chart method] and the RDNE and RDSA models. Ages estimated using Goodman and Rose's (1990) regression equation, the RDSA model, and the RDNE model were compared using a repeated measure ANOVA. Paired *t*-tests were also used to make two pairwise post-hoc comparisons: 1) a comparison of ages produced using the RDNE model and those produced using the Goodman and Rose (1990) regression equations and 2) a comparison of ages produced using the RDNE model and those produced using the RDSA model. ANOVAs and paired *t*-tests were performed using all tooth types pooled.

A Friedman test was used to compare the median ages calculated using the Goodman et al. (1980) chart method, the RDSA model (converted to six-month intervals), and the RDNE model (converted to six-month intervals). Two post-hoc pairwise tests were performed using Wilcoxon signed rank tests: 1) a comparison of ages produced using the chart method and those using the RDNE model (converted to six-month intervals) and 2) a comparison of ages produced using the RDNE and RDSA models (converted to six-month intervals). Friedman tests and Wilcoxon signed rank tests were carried out with all tooth types pooled.

As outlined earlier, the RDNE model, the Goodman and Rose (1990) regression equations and the chart method are based on similar sample populations (i.e., European populations or populations of European descent). Thus, comparing ages estimated using the RDNE model to ages estimated using either of the com-

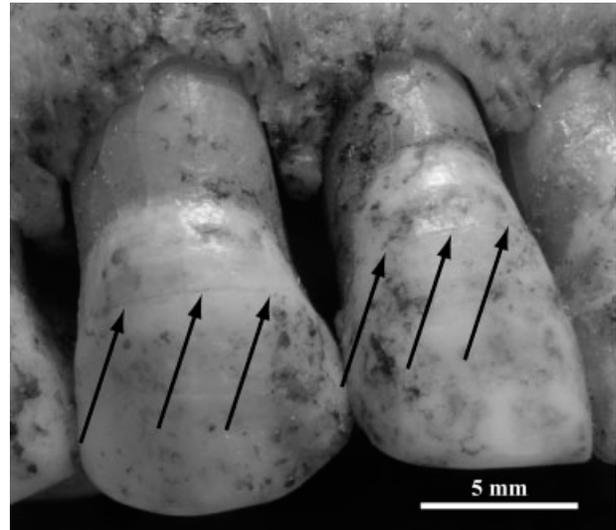


Fig. 3. Example of LEHs (arrows) measured in the present study.

monly used methods essentially controls for population variation in enamel formation time.⁴ Thus, statistical procedures that compare the RDNE model to the chart method and the regression equations respectively, permit an assessment of differences between ages of LEH formation derived from the commonly used methods and those produced using Reid and Dean's (2006) data. Comparisons of the RDSA and RDNE models, on the other hand, hold constant the method for determining the age at which LEHs form. Consequently, these comparisons approximate the amount of variation that might be expected if different population models are used to estimate the age at which LEHs formed and provide a baseline of population variation against which the differences between the ages estimates calculated using the commonly used methods and those calculated using the RDNE model can be judged.

RESULTS

Theoretical analysis

The results of the theoretical analysis are summarized in Figures 4 and 5. It is evident that the chart method models crown growth in a nearly linear manner; LEHs located in subsequent deciles of crown height are placed in sequential six-month intervals and there are only two minor gaps in these six-month intervals (i.e., between the sixth and seventh and between the eighth and ninth deciles, as shown in Fig. 4). Likewise, the Goodman and Rose (1990) regression method also depicts crown growth as proceeding in a linear manner (see Fig. 5). The two Reid and Dean models, on the other hand, more accu-

⁴ Although Reid and Dean's (2006) results indicate that the crown formation times in anterior teeth in both the Danish and northern European samples are greater than those of the southern African sample, it should be noted that the difference between the Danish and northern European samples (i.e., 0.54 years) is greater than that between the Danish and southern African samples (i.e., 0.48 years). Thus, populations that share relatively close genetic and/or geographic origins do not necessarily show similar timing of enamel formation.

TABLE 4. Crown height of unworn teeth used in the present study and comparative samples

Tooth type	n	This study		n	Windover ^a	n	Classic Period Lowland Maya ^b		n	Latte Period Guam Islanders ^c	
		Mean ± 1 SD (mm)	No. of unworn teeth with ≥1 LEH ^d				Mean ± 1 SD (mm)	Mean ± 1 SD (mm)		Mean ± 1 SD (mm)	
I ¹	4	11.63 ± 0.82	0	4	11.88 ± 0.55	8	11.14 ± 0.64	18	12.14 ± 0.65		
I ₁	9	10.10 ± 0.57	0	6	9.61 ± 0.83	10	9.86 ± 0.89	14	10.11 ± 0.53		
I ²	10	10.61 ± 0.85	2	6	10.15 ± 1.15	13	10.49 ± 0.82	12	10.49 ± 0.82		
I ₂	9	10.19 ± 0.73	0	5	9.86 ± 0.57	17	9.74 ± 0.77	14	10.85 ± 1.01		
UC	9	10.28 ± 1.19	2	4	11.84 ± 0.77	17	11.18 ± 1.34	12	11.81 ± 0.85		
LC	7	10.99 ± 0.39	1	3	12.36 ± 0.81	11	11.61 ± 1.45	11	11.71 ± 1.12		
M ₁	10	7.57 ± 0.31	1	3	7.68 ± 0.66	9	7.69 ± 0.73	–	–		
M ₂	8	7.08 ± 0.43	0	5	7.55 ± 0.37	12	7.29 ± 0.56	–	–		
M ₂	5	7.23 ± 0.90	1	–	–	8	7.50 ± 0.76	–	–		

^a C. Stojanowski (unpublished data); see also Doran (2002).

^b From Wright (1997).

^c A.L.W. Stodder (unpublished data).

^d These teeth were also included in metric analysis.

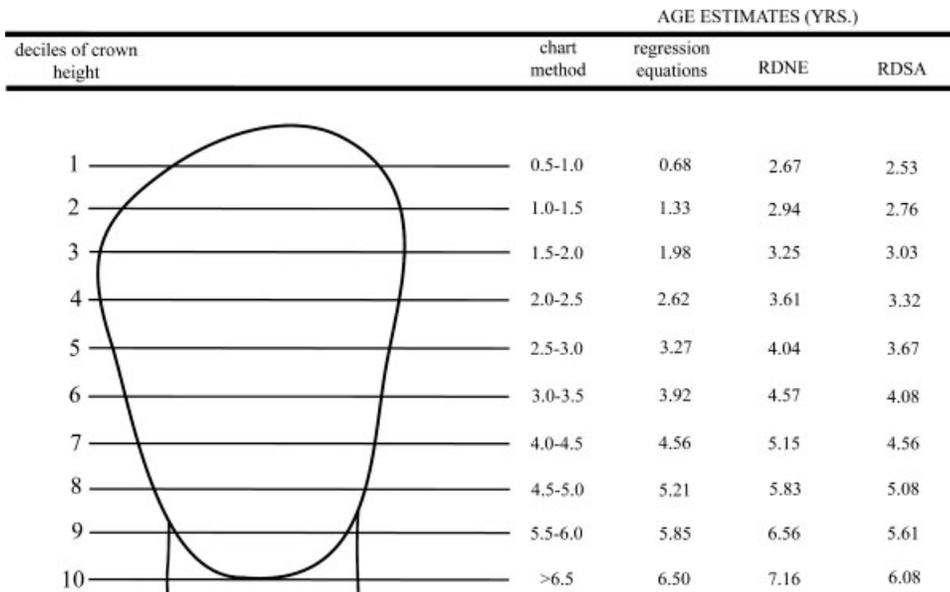


Fig. 4. Theoretical comparison of methods of determining ages at LEH formation: chart method, Goodman and Rose (1990) regression equations; Reid and Dean northern European model (RDNE) and Reid and Dean southern African model (RDSA). The tooth type depicted here is a mandibular canine.

rately represent the nonlinear process by which crowns grow; in both models the rate of growth in crown height is more rapid early on and slows in the later stages, around the fifth decile of crown height.

The most conspicuous difference between the commonly used methods and the Reid and Dean models is the large difference (on the order of 1.5–2.0 years) in age estimates for early forming LEHs. Near the middle of the crown (i.e., the sixth decile) the regression equations and the Reid and Dean models converge on similar ages and the Goodman and Rose (1990) regression equations and the RDNE model, in particular, provide very similar age estimates for the remainder of the crown’s growth. This fact is clear when LEH formation age is plotted as a function of crown height (see Fig. 5). Differences between both Reid and Dean models are also evident and reflect somewhat dissimilar growth trajectories. It is important, however, to note that these differences have only been investigated for the mandibular canine. Major discrepancies between the commonly used methods and the Reid and Dean models, especially for LEHs located in the first five deciles of crown height, are likely to hold for all tooth types because they are due largely to the

effect of including cuspal formation time and a nonlinear model of crown growth in the Reid and Dean models (see discussion later).

Empirical analysis

Tests of measurement protocols. Independent samples *t*-tests comparing mean ages of samples of matched LEHs to unmatched LEHs for each of the methods of estimating the age at LEH occurrence [i.e., the Goodman and Rose (1990) regression equations, the RDNE model, and the RDSA model] reveal that no significant differences exist (regression equations: *t* = 0.685; *P* = 0.455; RDNE model: *t* = 0.855; *P* = 0.395; RDSA model: *t* = 0.871; *P* = 0.386). The results of these tests indicate that the central tendency of age distributions for the models of determining age at LEH formation being compared are the same regardless of whether LEHs are matched or unmatched. For the purposes here, unmatched LEHs were chosen as the unit of analysis because of the difficulty associated with confidently matching LEHs using macroscopic methods.

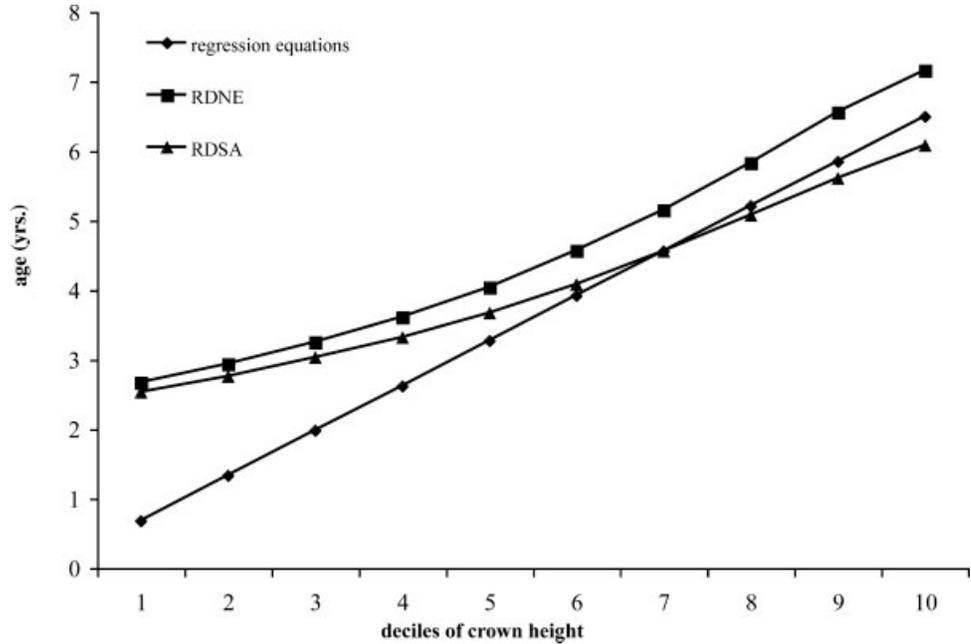


Fig. 5. Age at each of 10 deciles of crown growth for LEH formation ages estimated using the Goodman and Rose (1990) regression equations (diamonds), the Reid and Dean northern European model (RDNE) (squares), and the Reid and Dean southern African model (RDSA) (triangles). The tooth type depicted here is a mandibular canine.

TABLE 5. Comparison of age estimates between the Goodman and Rose (1990) regression equations and the Reid and Dean northern European (RDNE) model when all tooth types are pooled^a

Descriptive statistic	Goodman and Rose (1990) regression (years)	RDNE (years)	Difference (years) ^b
<i>n</i>	72	—	—
Mean	3.76	4.83	1.06 ^c
SD	1.13	0.97	

^a Comparisons were also made with the sample separated by tooth type. For all tooth types, the means using the RDNE model are larger than those using the regression equations. Differences in all tooth types, except M₂ (for which the small sample size precluded statistical comparison) are significant at the *P* < 0.05 level. All of these differences except I¹ remain significant using a Bonferroni adjusted alpha level.

^b Difference computed as age from RDNE model minus that from Goodman and Rose (1990) regression equation.

^c Difference significant using Bonferroni adjusted alpha level.

None of the decile assignments changed when Guatelli-Steinberg et al.'s (2007) data were applied to the anterior teeth used in the present study. This finding validates the use of measures of crown height for assigning LEHs to deciles of crown growth and confirms that the ages produced using this technique would not differ from those that used curvilinear measures of crown height [as employed by Reid and Dean (2006)].

Repeated-measures ANOVA. The results of the repeated measures ANOVA indicates that, when all tooth types are pooled, there is a significant difference among the means of the ages determined using the regression equations, the RDNE model, and the RDSA model (*F* = 370.97; *P* < 0.001).⁵

⁵ Repeated measures ANOVAs were also performed for each tooth type separately. For every tooth type, except M₂ (for which small sample size precluded statistical comparison), the differences between the means are significant at the *P* < 0.05 level.

TABLE 6. Comparison of age estimates between the Reid and Dean northern European model (RDNE) and the Reid and Dean southern African model (RDSA) when all tooth types are pooled^a

Descriptive statistic	RDSA (years)	RDNE (years)	Difference (years) ^b
<i>n</i>	72	—	—
Mean	4.44	4.83	0.39 ^c
SD	1.00	0.97	

^a Comparisons were also made with the sample separated by tooth type. For all tooth types, the means using the RDNE model are larger than those RDSA model. Differences in all tooth types, except M₂ (for which the small sample size precluded statistical comparison) are significant at the *P* < 0.05 level. All of these differences except I¹ remain significant using a Bonferroni adjusted alpha level.

^b Difference computed as age from RDNE model minus that from RDSA model.

^c Difference significant using Bonferroni adjusted alpha level.

Paired *t*-tests. Table 5 presents the descriptive statistics comparing the results of age estimates using the Goodman and Rose (1990) regression equations and the RDNE model. When all tooth types are pooled, the mean age using the RDNE model is 1.06 years greater than that calculated using the regression equations. This difference is significant at the *P* < 0.05 level.

Table 6 presents the descriptive statistics comparing the results of age estimates using the RDNE and RDSA models. When all tooth types are pooled, mean ages estimated using the RDNE model are 0.39 years greater than those estimated using the RDSA model. This difference is significant at the *P* < 0.05 level.

The differences described earlier are also significant when the alpha level is adjusted using a Bonferroni correction for two comparisons (i.e., α < 0.025).

Friedman test. The results of the Friedman test indicate that, when all tooth types are pooled, there is a significant difference among the median of the ages determined using the chart method, the RDNE model (converted to six-month intervals), and the RDSA model

TABLE 7. Results of Wilcoxon signed-rank tests with all tooth types pooled^a: chart method v. Reid and Dean northern European method (RDNE); RDNE v. Reid and Dean southern African method (RDSA)

Comparison	Z Score	P-value
Chart method vs. RDNE	-7.522	<0.001
RDNE vs. RDSA	-6.416	<0.001

^a Comparisons were also made with the sample separated by tooth type. For all tooth types, the medians using the RDNE model are larger than those using the chart method. In both pair wise comparisons, differences in mandibular C, maxillary C, I¹, and M₁ are significant at the $P < 0.05$ level and these differences remain significant using a Bonferroni adjusted alpha level. When the chart method and RDNE models are compared, differences in I₂ are significant at $P < 0.05$ level, but not significant using a Bonferroni adjusted alpha level and the difference in I² is not significant. When the RDNE and RDSA models are compared, there is no difference in I₂ or I¹. The Friedman test for I₁ did not show significant differences and small sample size precluded statistical comparisons for M₂.

(converted to six-month intervals) ($\chi^2 = 129.32$; $P < 0.001$).⁶

Wilcoxon signed rank. The median age provided by the RDNE model is larger than that provided by the chart method. The Wilcoxon signed rank test (Table 7) reveals that this difference is statistically significant at the $P < 0.001$ level when all tooth types are pooled. Figure 6 compares the age distributions calculated using the chart method and RDNE model (converted to six-month intervals) when all tooth types are pooled. The modal interval for the chart method is 3.5–4.0 years, compared to 5.0–5.5 years for the RDNE model.

The median age provided by the RDNE model is larger than that provided by the RDSA model and the Wilcoxon signed rank test (Table 7) reveals that this difference is statistically significant at the $P < 0.05$ level when all tooth types are pooled. Figure 7 illustrates the comparison between ages estimated using the RDSA and RDNE models (converted to six-month intervals) when all tooth types are pooled. The modal interval for the RDSA model is 4.0–4.5 years (compared to 5.0–5.5 years for the RDNE model; see earlier).

The differences described earlier are also significant when the alpha level is adjusted using a Bonferroni correction for two comparisons (i.e., $\alpha < 0.025$).

DISCUSSION

The theoretical analysis demonstrates major discrepancies between the commonly used macroscopic methods of estimating age of LEH formation and the Reid and Dean models: for the latter, higher age estimates predominate in the early phases of crown growth. This difference is almost certainly due to the fact that, unlike the commonly used methods, the Reid and Dean models include time for cuspal enamel formation. This explanation was presaged by previous authors (e.g., Skinner and Goodman, 1992; Goodman and Song, 1999). Age estimates of LEHs in later forming deciles are much more congruent for the commonly used methods and the Reid

and Dean models (Figs. 4 and 5). These observations suggest that discrepancies between age estimates are more substantial when samples dominated by LEHs that form early in life are measured.

The differences between the RDNE and RDSA models in the theoretical analysis emphasize the effect of choice of reference population variation in estimating the ages of LEH formation. While these differences are noteworthy, it is clear that age estimates provided by the two Reid and Dean models are much more similar to each other than either is to age estimates produced using the standard methods. In both cases, both Reid and Dean models provide higher age estimates than the commonly used methods.

Examination of the empirical data from the Semna South sample reflects the patterns of differences among the aging methods that are evident in the theoretical analysis. Specifically, when all tooth types are pooled, the commonly used methods of determining ages at which LEHs form [i.e., the chart method and the Goodman and Rose (1990) regression equations] yield significantly younger ages than the RDNE model. This finding validates the long-held suspicion that age estimates using a method that includes cuspal enamel formation time will be larger than those that do not. The magnitude of this difference, however, is larger than previous authors have posited based on inclusion of cuspal enamel alone.

There is also a significant difference in the empirical analysis between the RDNE and RDSA models, with the age estimates using the RDNE model being older. This pattern persists whether absolute ages or ages converted to six-month intervals are compared. However, these differences are smaller than those between the RDNE model and the chart method as well as those between the RDNE model and the Goodman and Rose (1990) regression equations. Consequently, the results of the present study suggest that the Reid and Dean model provides age estimates that differ more from the commonly used macroscopic methods than would be expected based on population variation alone.

The difference between the two Reid and Dean models is consistent with the results presented by Reid and Dean (2006), which indicated that enamel formation times in the southern African sample were somewhat accelerated (i.e., crown formation times [CFTs] were shorter) relative to the northern European sample. While Reid and Dean (2006) noted that the differences were quite small, they also observed that the most prominent differences were present in anterior teeth. The fact that a large proportion of the teeth measured in the present study are canines might help explain the observed differences between the age estimates generated using the two Reid and Dean models.

Importantly, the differences between the commonly used methods and Reid and Dean models are rather large (i.e., on the order of one year) and could lead to substantially divergent conclusions regarding the timing of metabolically stressful events in archaeological or living populations. Briefly, the differences in peak age of LEH formation found in the present study suggest vastly different interpretations for the biological and cultural factors contributing to LEH formation in the Meroitic to Christian period Nubians of Semna South. The gradual peak in LEH development between ages 2.5 and 4.5 years and modal age interval of 3.5–4.0 years using the chart method corresponds well with other studies of an-

⁶Friedman tests were also performed for each tooth type separately. For all tooth types except I₁ ($P = 0.061$) and M₂ (for which small sample size precluded statistical comparison), the differences between the medians are significant at the $P < 0.05$ level.

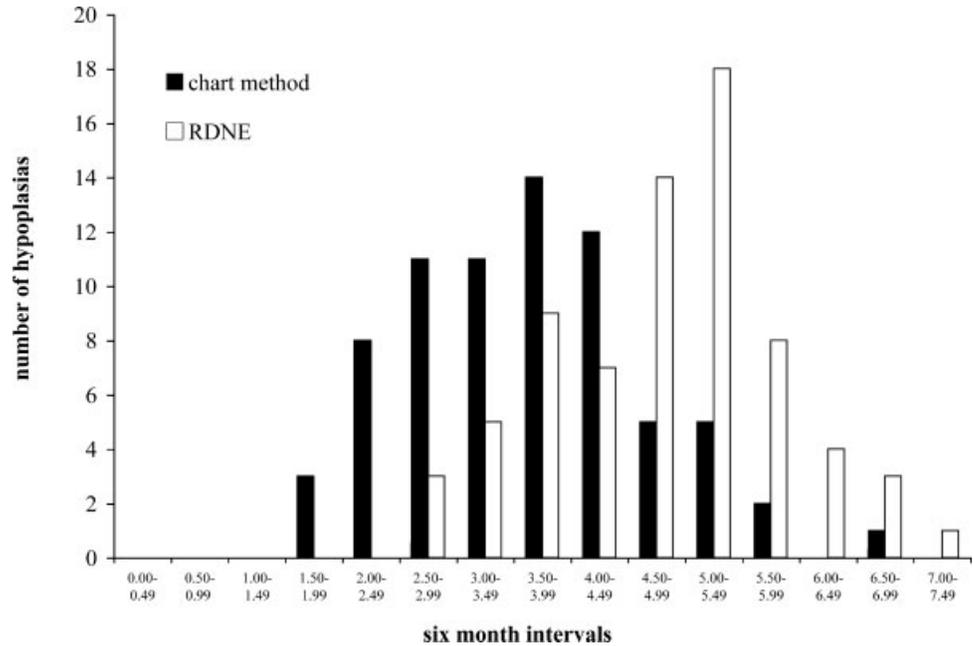


Fig. 6. Number of hypoplasias per six-month interval when all tooth types are pooled: chart method vs. Reid and Dean northern European model (RDNE).

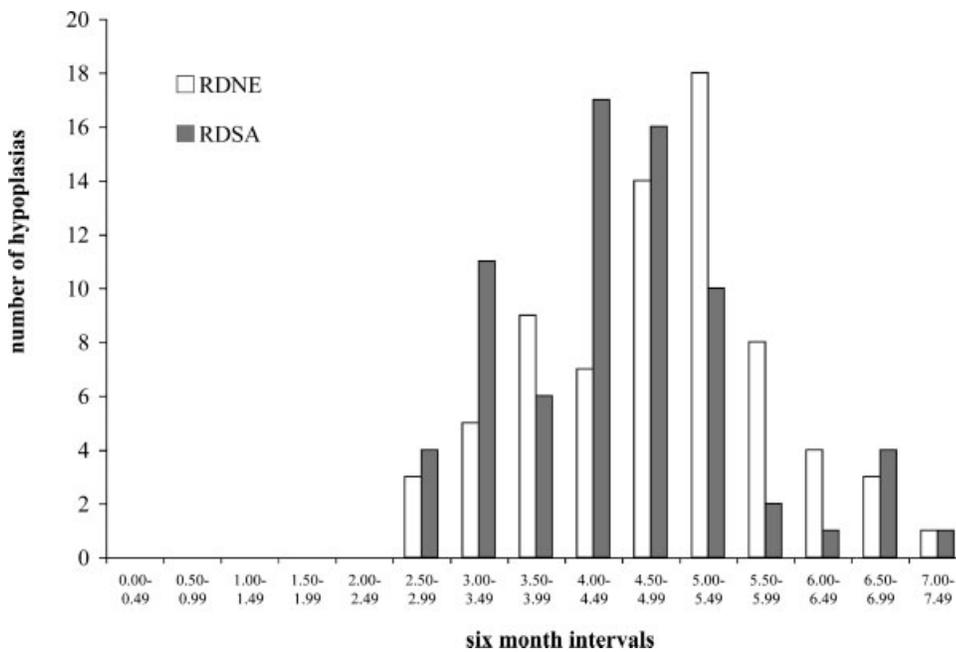


Fig. 7. Number of hypoplasias per six-month interval when all tooth types are pooled: Reid and Dean northern European model (RDNE) vs. Reid and Dean southern African model (RDSA).

cient Nubians (e.g., Van Gerven et al., 1990, 1995) as well as populations outside the Nile Valley (e.g., Swärdstedt, 1966; Hillson, 1979; Corruccini et al., 1985; Goodman, 1988). The timing of this peak is often ascribed to the stressful effects of weaning caused by transition from a diet comprised largely of immunologically protective mother's milk to a diet of gruel made from iron-poor grains that led to malnutrition, infection, and dehydration due to diarrhea (e.g., Goodman et al., 1984a,b; Corruccini et al., 1985; Lanphear, 1990; Ubelaker, 1992; Moggi-Cecchi et al., 1994). Evidence to the contrary has been presented in very few studies of LEH (e.g., Blakey et al., 1994; Wood, 1996). After six months of age, however, breast milk by itself has insufficient nutrients and calories to maintain the growth and development of an

infant (Almedom and de Waal, 1990; Kikafunda et al., 2003).

Weaning is a process that begins with the introduction of supplementary foods and ends with complete cessation of breast-feeding (see Dettwyler and Fishman, 1992; Katzenberg et al., 1996; Van Esterik, 2002; Sellen, 2001, 2007, for a thorough review of literature on infant feeding practices and weaning stress). Cross-cultural research indicates that the modal age at termination of breast-feeding in small-scale societies is ~30 months of age (Sellen, 2007; p 132). Chemical analyses of bone have identified the initiation and cessation of weaning in a variety of archaeological populations (e.g., Sillen and Smith, 1984; Tuross and Fogel, 1994; White and Schwarcz, 1994; Katzenberg and Pfeiffer, 1995; Schurr,

1997, 1998; Herring et al., 1998; Wright and Schwarcz, 1998, 1999; Dupras et al., 2001; Richards et al., 2002; Schurr and Powell, 2005; Fuller et al., 2006; Dupras and Tocheri, 2007). The contribution of weaning stress to the formation of LEHs may, therefore, be evaluated directly in the Semna South sample in the future. To date, stable isotope analyses have not been conducted, although such information is available from a contemporaneous sample in the Wadi Halfa area. For instance, results of a study conducted by White and Schwarcz (1994) showed a decrease in nitrogen enrichment from birth to age six, which the authors interpreted as evidence for a gradual rather than discrete end to breast-feeding. This observation is consistent with the view of weaning as a process rather than an abrupt event, though it suggests that complete cessation of breast-feeding may have occurred as late as age six in at least some of the Meroitic to Christian period children from Lower Nubia. In contrast, stable carbon and nitrogen isotopes from Roman samples (ca. A.D. 100–450) at a cemetery in the Dakhleh Oasis in Egypt, indicate exclusive breast-feeding for the first six months, followed by gradual weaning until age 3 (Dupras et al., 2001; Dupras and Tocheri, 2007). Considerable variation is, therefore, apparent in age of weaning in Egyptian and Nubian samples from the early centuries A.D. and may be only one factor contributing to LEH formation.

Unlike the gradual distribution of LEH formation ages derived from the chart and regression methods, the ages calculated for the Semna South sample using the RDNE model show a dramatic peak in the 4.5–5.5 year age range (see Fig. 6) with a modal interval 1.5 years older than that of the chart method. Investigators who have studied Christian period remains from Kulubnarti (e.g., Rudney, 1983; Van Gerven et al., 1990, 1995) suggest the synergism of nutritional and infectious etiology in the formation enamel defects, including parasitism by helminths (e.g., hookworm, schistosomiasis). Some modern clinical studies, in fact, show a linkage between weaning and parasitic infections (e.g., *Giardia lamblia*, Goto et al., 2002) because of the introduction of contaminated food in a child's diet. Recent research on the Semna South Nubian sample demonstrates that schistosomiasis was prevalent in this population (Alvrus, 2006). Clinical data on modern Nile Valley populations presented by Alvrus (2006) indicate that infection by the parasite commonly occurs around age five, when children begin to play and swim in the slow-moving water of irrigation canals where the intermediate host snail species are found, and are old enough to assist with tasks such as washing dishes or clothes or tending crops in irrigated fields. The correspondence between the peak age of LEH formation based on the RDNE model in this study and the typical age of first infection with schistosomiasis is striking. Weanling stress by itself in children aged 4.5–5.5 years in this society, therefore, is a far less likely explanation for this pattern of LEH development.

It is possible, of course, that the RDSA model is a more appropriate reference population for the Semna South sample measured here, as both samples derive from Africa. An interpretation of weanling stress as the primary causal factor of LEHs in the Semna South Nubians, however, is also unlikely using the RDSA model because the peak age of occurrence is 4.0–5.0 years (see Fig. 7). Like the peak using the RDNE model, the modal interval produced using the RDSA model could be explained by schistosomiasis. The differences

between the modal intervals using the RDNE and RDSA models respectively, underline the differences in CFTs between the two populations. Thus, while choice of population reference may result in slight differences between the peak ages of LEH formation (as evidenced by differences between the RDNE and RDSA models), these differences are much less marked than those between the commonly used methods and either of the Reid and Dean models and, in the case of the Semna South Nubians, do not result in different interpretations of the factors that may have caused LEHs.

One possible source of bias in the present study is the relatively small samples that were used. The small size of the samples no doubt has a large effect on some (if not all) of the comparisons that were made. The small size of the sample of unworn teeth is particularly noteworthy because all of the ages estimated using the Reid and Dean models rely on measures of mean crown height. Although descriptive statistics of the unworn teeth used in the present study (Table 4) indicate that this sample is no more variable than other archaeological samples, it is important to note that, if the mean crown heights from this sample do not accurately represent the true population means, all of the ages estimated using the Reid and Dean model are inaccurate. For instance, it is possible that the crown heights in our sample of hypoplastic teeth differ from those in our sample of unworn teeth simply by chance (i.e., due to small sample sizes) or because the developmental insults that cause LEHs may affect the normal course of crown growth, causing hypoplastic teeth to have shorter crowns than nonhypoplastic teeth. As yet, no data are available to support this claim. One study, however, does suggest that buccolingual widths of teeth are smaller in individuals who have multiple LEHs than those without LEHs (Stodder and Douglas, 2003). Accordingly, despite the fact that the results of the present study indicate important differences between the Reid and Dean models and the methods that are commonly used to estimate ages of LEH formation, this conclusion is tentative and further research with larger sample sizes may produce results contrary to those presented here.

CONCLUSIONS AND FUTURE RESEARCH

The present study indicates that there are significant and biologically important differences between LEH formation ages produced using the commonly used macroscopic methods and those derived from new data based on large comparative samples that more closely conform to our current understanding of dental histology. Specifically, the results of the empirical analysis presented here illustrate that ages estimated using the data from Reid and Dean (2006) are older than those provided by the commonly used macroscopic methods. This conclusion confirms the widely held suspicion that methods that incorporate cuspal enamel formation time and model crown growth as a nonlinear process will produce age estimates that are larger than methods that do not. The present study, however, demonstrates that the difference in age estimates is larger than previously suggested. The results of the theoretical analysis are largely concordant with those of the empirical analysis, but also highlight that the largest difference between the age estimates provided by the commonly used methods and Reid and Dean models is in early forming LEHs.

The explicit goal of the present study was to identify any potential difference between the Reid and Dean models and the commonly used macroscopic methods of estimating ages at which LEHs form. The results presented demonstrate that such a difference does exist. The data, however, do not allow empirical testing of the accuracy of either method. While a facile evaluation of the assumptions of the methods might lead one to believe that the Reid and Dean models provide more reliable age estimates, this supposition requires further testing.

This study identifies a number of avenues for future research that can more fully explicate the differences between methods of estimating the timing of LEH formation. In addition to studies that include larger sample sizes of hypoplastic and unworn teeth, research that compares microscopically derived ages of LEH formation to ages produced employing the commonly used methods would be beneficial. Likewise, theoretical comparisons of other tooth types (like that provided here for the mandibular canine) are also needed to verify the assumption that the pattern of differences between the methods according to vertical location on tooth crowns is also evident when other tooth types are examined. Research aimed at verifying this assumption and identifying additional patterned differences between the commonly used macroscopic methods and Reid and Dean models will provide important new insights into the timing of LEH formation. Finally, further documentation of inter- and intrapopulation variability in crown formation time will be crucial to refining the precision of methods for determining the timing of LEH formation that are based on histological data.

In sum, the present study demonstrates theoretically and empirically that the Reid and Dean models of estimating the ages at which LEHs form yield substantially older ages than those employing the most commonly used macroscopic methods. These differences are most prominent in early forming LEHs. The empirical analysis demonstrates that difference between the age estimates provided by the RDNE model and the commonly used methods are larger than would be expected based on population variation in enamel formation alone and the magnitude of the difference is large, affecting bioarchaeological interpretations of the data. As illustrated in the Semna South sample, the difference found in peak intervals in LEH formation using commonly used methods versus the Reid and Dean models leads to divergent reconstructions of the biocultural factors underlying the metabolic stress.

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