Teeth and Human Life-History Evolution*

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Abstract

Modern humans differ from wild great apes in gestation length, weaning age, interbirth interval, sexual maturity, and longevity, but evolutionary anthropologists do not know when these distinctive life-history conditions evolved. Dental tissues contain faithful records of birth and incremental growth, and scholars suggest that molar eruption age, tooth wear, growth disturbances, tooth chemistry, and/or tooth calcification may provide insight into the evolution of human life history. However, recent comparative approaches and empirical evidence demonstrate that caution is warranted when inferring hominin weaning ages or interbirth intervals from first molar eruption, tooth wear, or growth disturbances. Fine-scaled studies of tooth chemistry provide direct evidence of weaning. Early hominin tooth calcification is more ape-like than human-like, and fully modern patterns appear only after Neanderthals and *Homo sapiens* diverged, concurrent with changes in cranial and postcranial development. Additional studies are needed to relate these novel calcification patterns to specific changes in life-history variables.

INTRODUCTION

M1: first molar

Dental development: continuous process of cellular differentiation, matrix secretion, calcification/ mineralization, eruption, and root completion of deciduous (primary) and permanent (secondary) teeth during childhood

Humans are rather unusual great apes. We have long gestations but helpless offspring, our infants wean early but have long childhoods, females reproduce at late ages but have short interbirth intervals, and females cease reproducing long before their death (Schultz 1960, Harvey & Clutton-Brock 1985, Bogin 1990). Evolutionary biologists and anthropologists have wrangled with these paradoxes over the past century, particularly as discoveries of juveniles such as the Taung child (*Australopithecus africanus*) evoked intense debate about the origins of humanity (e.g., Dart 1925, Keith 1925). These debates have given rise to formal studies of how primates and other mammals allocate energy to growth, reproduction, and maintenance over the course of life (reviewed in Bogin 1990, Smith & Tompkins 1995, Kaplan et al. 2000, Hawkes & Paine 2006, Schwartz 2012). This framework, known as life-history theory, refers to hypotheses posited to explain interactions among an organism's energy investment, environment, and ecology, as well as the relationships among aspects of the life cycle and related variables such as brain and body mass (Harvey & Clutton-Brock 1985, Charnov 1991, Sterns 1992).

Numerous scholars have proposed theories to explain why human life history evolved to be so unique (e.g., Bogin 1990, Smith 1992, Hawkes et al. 1998, Kaplan et al. 2000, Bock & Sellen 2002, Hawkes & Paine 2006, Robson & Wood 2008, Kramer et al. 2009, Konner 2010, Lee 2012), although many of these ideas are difficult to test owing to the nature of the fossil record. Kaplan et al. (2000) argue that our elongated childhood and life span resulted from a dietary shift to large sources of nutrient-dense food that required sophisticated acquisition skills such as coordination, knowledge, and strength. Kramer et al. (2009) and Lee (2012) emphasize how shifts in juvenile energetics due to nonmaternal provisioning or communal resource pooling may lead to changes in ages at first reproduction or weaning. In addition to ethnographic studies of traditional human societies and comparative studies of nonhuman primates, hominin fossil bones and teeth yield the primary evidence for testing these theories. In the following review I explore five ways that teeth have been employed to refine and test these ideas: first molar (M1) eruption age, tooth wear, developmental stress, tooth chemistry, and tooth calcification patterns. I place particular emphasis on the utility of each approach for understanding the evolution of human life history.

FIRST MOLAR ERUPTION AND PRIMATE LIFE HISTORY

Several widely cited studies of life-history evolution derive from the important work of B.H. Smith, who tests Adolf Schultz's (1935, 1960) observations about the relationship between primate dental development and life history in a comparative study of 21 primate species (Smith 1989, Smith et al. 1994). Smith (1989) reports that the age of mandibular M1 eruption into the oral cavity correlates ($r > 0.9$) with age at weaning and age at sexual maturity, as well as with somatic measurements (neonatal body mass, neonatal brain mass, adult brain mass). She notes similar correlations for third molar (M3) eruption ages and life history and somatic variables, particularly for the ages of M3 eruption and sexual maturity. These relationships were then extended to infer life history from the human fossil record (Smith 1991a, 1992; Smith et al. 1995; Smith & Tompkins 1995), where they continue to influence reconstructions of hominin life history (e.g., Bogin 2010, Thompson & Nelson 2011, Kelley & Schwartz 2012, Lee 2012). For example, Kelley & Schwartz (2012) suggest that differences in M1 eruption ages may imply that early hominin life histories were more rapid than those of wild great apes. However, others have questioned the predictive value of certain correlations because exceptions are known to occur when closely related hominoids are compared (Dirks & Bowman 2007, Robson & Wood 2008, Guatelli-Steinberg 2009, Humphrey 2010).
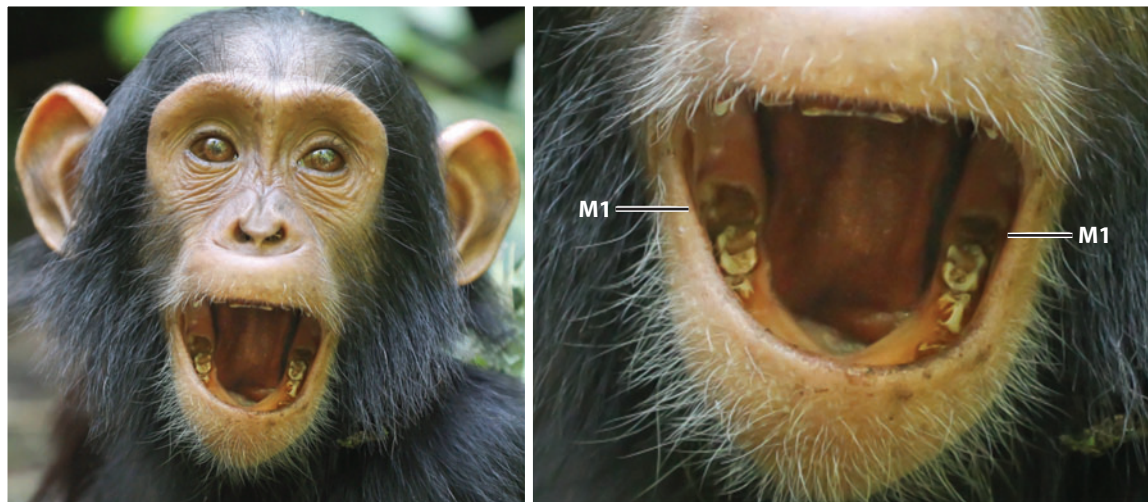
Figure 1

First molar (M1) eruption in a three-year-old female wild chimpanzee (*Pan troglodytes schweinfurthii*) from Kanyawara (Kibale National Park, Uganda). Modified from Smith et al. (2013).

Smith (1992) reports that M1 eruption and weaning occurred at the same age in a sample of 14 primate species, but recent work demonstrates problems with using M1 eruption age as a proxy for weaning age in great apes (Robson & Wood 2008, Bogin 2010, Humphrey 2010, Smith et al. 2013). Robson & Wood (2008) note that orangutans, gorillas, and chimpanzees erupt M1s prior to their respective weaning ages, whereas humans erupt M1s several years after weaning. My colleagues and I recently conducted a longitudinal study of subadult chimpanzees in the Kanyawara community (Kibale National Park, Uganda) that sheds further light on this relationship (Smith et al. 2013). High-resolution photography was used to precisely assess tooth emergence (**Figure 1**), which was compared with behavioral data and maternal life history. Five infant chimpanzees erupted their mandibular M1s by or before they were 3.3 years old, which did not coincide with weaning events such as the introduction of solid foods, resumption of maternal estrous cycling, or termination of nursing. These results do not support Smith's (1992) finding of equivalence between M1 eruption age and weaning age, nor a hypothetical relationship between "duration of lactation" (interbirth interval minus gestation length) and hominoid molar eruption ages (contra Lee 2012). Thus caution is warranted when inferring particular life-history traits from M1 emergence in juvenile hominins given the complex interplay between ecology, energy balance, somatic development, and life history within chimpanzees and modern humans.

Little is known about the impact of evolutionary relationships on correlations between M1 emergence age and primate life-history variables, although methods that employ phylogenetic relationships to estimate the degree of phylogenetic signal are well established (e.g., Nunn 2011). Investigations are currently in progress that incorporate phylogeny, use updated comparative data, and control for potentially confounding variables such as body mass (C. Lane, J. DeSilva, C.L. Nunn & T.M. Smith, manuscript in preparation). These analyses reveal evidence for strong phylogenetic signals in a number of comparisons between M1 emergence age and life-history variables, suggesting that high correlations may be partially driven by shared evolutionary history. Controlling for phylogeny leads to marked decreases in correlations between M1 eruption age and gestation length and between M1 eruption age and interbirth interval. However, certain

Emergence: tooth crown movement past the jaw bone margin (alveolar eruption) and the gum (gingival eruption) to emerge into functional occlusion

conclusions from Smith's original (1989) data set remain consistent in these new analyses, especially the primate-wide correlations between M1 eruption age and weaning age and between M1 eruption age and age at sexual maturity. These results imply that reconstructions of certain life-history variables based on M1 eruption ages underestimate the confidence intervals of predicted values when investigators do not control for phylogeny and/or body mass (e.g., Smith 1991a, 1992; Smith & Tompkins 1995). Multivariate phylogenetic approaches may improve the accuracy of hominin life-history reconstruction.

TOOTH WEAR AND LIFE-HISTORY RECONSTRUCTION

Aiello et al. (1991) propose a novel approach to infer life-history variables from hominoid deciduous tooth wear (attrition) in wild-shot juvenile great apes. They contrast patterns of dental attrition in lowland gorillas with that of chimpanzees and orangutans, noting that the teeth of gorillas appear more worn at equivalent developmental stages. Aiello and colleagues suggest that these patterns reflect earlier weaning and a shorter interbirth interval, a supposition extended to Plio-Pleistocene juvenile hominins with heavily worn deciduous teeth. However, when the work by Aiello et al. was published, information on gorilla weaning and interbirth intervals was available only for mountain gorillas, which are now believed to show more rapid life histories than do lowland gorillas (Pusey 1983, Watts 1991, Knott 2001, Robbins et al. 2004, Nowell & Fletcher 2007, Breuer et al. 2009, Emery Thompson 2013). Current evidence suggests that lowland gorilla life histories may be more similar to those of chimpanzees, and therefore differences in tooth attrition between lowland gorillas and chimpanzees reported by Aiello et al. (1991) are likely due to other factors.

Hominoid dentitions vary in size and absolute enamel thickness (Martin 1985, Aiello et al. 1991, Smith et al. 2005), and their diets are known to vary markedly (Harrison & Marshall 2011). Kelley & Schwartz (2010) demonstrate that the M1s of lowland gorillas erupt earlier than do those of orangutans, which may also be true for the deciduous dentition (Smith et al. 1994). These factors likely influence the progression and assessment of tooth wear. Given that the individuals studied by Aiello et al. (1991) are of unknown age at death, comparisons across similarly staged animals may be problematic because we do not know whether individuals within a particular wear stage are the same age. Examination of known-aged wild chimpanzees (discussed further below) reveals that this model of progressive attrition underestimates actual age in certain cases. For example, a 3.8-year-old chimpanzee (Piment, illustrated in Smith et al. 2010a, figure 6, p. 371) would have been aged at 2.5–3.0 years following the standards in Aiello et al. (1991).

Dean (2010) suggests that deciduous tooth attrition indicates the consumption of solid (supplemental) foods but does not necessarily indicate the cessation of nursing. Behavioral observations on the Kanyawara chimpanzees reveal that infants begin supplementing mothers' milk by ∼6 months of age, consume the same percentage of fibrous foods as do adults shortly after 1 year, and spend the same time feeding as do adults by ∼3.5 years of age, but they do not cease nursing until after age 4 (Smith et al. 2013). I have examined high-resolution photographs of eight Kanyawara juveniles and nine Taï forest juvenile skeletons (Smith et al. 2010a) and have found that wild chimpanzee deciduous anterior teeth do not show dentine exposure until ∼2–3 years of age, which is ∼2–3 years before the cessation of nursing (Pusey 1983, Boesch & Boesch-Achermann 2000, Smith et al. 2013). First molars in this sample do not show dentine exposure until ∼6–7 years of age. Thus the gradual and progressive attrition of deciduous teeth and the M1 does not provide a clear indication of when chimpanzees begin or complete the process of weaning.

Research on hominin tooth wear and life history has met with similar challenges. Skinner (1997) compares Middle and Upper Paleolithic hominin dentitions to determine whether these groups showed differences in life history. He first estimates age at death of 82 juvenile hominins using

modern human developmental standards and then estimates the "functional age" and degree of attrition of each tooth, which permits comparisons of wear between teeth of equivalent functional ages. Skinner concludes that dietary supplementation began one year earlier in Upper Paleolithic hominins (fossil *Homo sapiens*) than in Middle Paleolithic hominins (Neanderthals), which may have led to shorter interbirth intervals in *H. sapiens*. However, this conclusion is questionable because variables that affect attrition are not equivalent in these groups. Enamel thickness differs between Neanderthals and fossil *H. sapiens* (Olejniczak et al. 2008, Benazzi et al. 2011, Smith et al. 2012), as do eruption ages (Smith et al. 2007a,b, 2010b; but see Macchiarelli et al. 2006) and dietary breadth (Richards & Trinkaus 2009; but see Fiorenza et al. 2011). Moreover, Neanderthal age at death is overestimated when based on human developmental standards (Smith et al. 2010b, Thompson & Nelson 2011). Three juvenile ages in Skinner's (1997) sample are overestimated by ~0.5 years on average when compared with histologically derived ages (Smith et al. 2010b; method detailed in **Supplemental Figure 1**. Follow the **Supplemental Material** link from the Annual Reviews home page at **http://www.annualreviews.org**). Precise comparisons of attrition in juvenile hominins would be more conclusive with information on specific dietary items and food material properties, independent age-at-death estimates, and data on the species-specific timing of tooth emergence.

Others have used tooth wear patterns in adult individuals to explore demographic differences between fossil hominin groups (Vallois 1937; Caspari & Lee 2004, 2006; Wolpoff & Caspari 2006; Trinkaus 2011). Caspari & Lee (2004) report the frequencies of young versus old hominins in a sample of 768 dental individuals. They find that survivorship (% of old adults) was low in australopithecines, increased slightly in early *Homo* and in Neanderthals, and increased markedly in Upper Paleolithic *H. sapiens*. These results appear to be unrelated to the practice of intentional burial in the Middle and Upper Paleolithic, and they imply a substantial shift in human paleodemography after *H. sapiens* diverged from the common ancestor shared with Neanderthals (but see Hawkes & O'Connell 2005). In contrast, Trinkaus (2011) does not find differences in mortality profiles in a smaller sample of Middle and Upper Paleolithic individuals. However, these studies employ fundamentally different aging methods; Caspari & Lee (2004) apply intrataxon seriation to divide individuals into old and young categories, whereas Trinkaus (2011) estimates age from modern human wear standards for both groups. As noted above, interspecific comparisons of occlusal wear incorporating variables that differ between Neanderthals and modern humans (such as the approaches of Skinner or Trinkaus) are likely to be biased (Smith et al. 2012).

GROWTH DISTURBANCES IN TEETH AND WEANING

Studies of human health and life history frequently examine developmental disturbances during tooth formation. Certain defects manifest externally as circumferential rings known as linear enamel hypoplasias (LEH) (reviewed in Hillson & Bond 1997, Guatelli-Steinberg 2001), which may also be found on tooth roots (**Figure 2**). The timing of LEH formation may be precisely assessed from counts of incremental features (**Supplemental Figures 1** and **2**). Documented causes of LEH include childhood illnesses, vitamin deficiency, and malnutrition (reviewed in Goodman & Rose 1990, Hillson 1996, Guatelli-Steinberg & Benderlioglu 2006). Numerous studies also invoke aspects of the weaning process as a cause of LEH formation, although evidence from populations with historic records or behavioral histories is often contradictory (e.g., Goodman et al. 1987, Blakey et al. 1994, Moggi-Cecchi et al. 1994, Katzenberg et al. 1996, Wood 1996, Humphrey 2008).

Despite the lack of direct evidence for a relationship between LEH and weaning in living humans, several studies of the human fossil record invoke this association (e.g., Ogilvie et al.

LEH: linear enamel hypoplasia

Incremental features: microscopic markers in dental hard tissues representing intrinsic biological clocks. Range from subdaily to annual rhythms
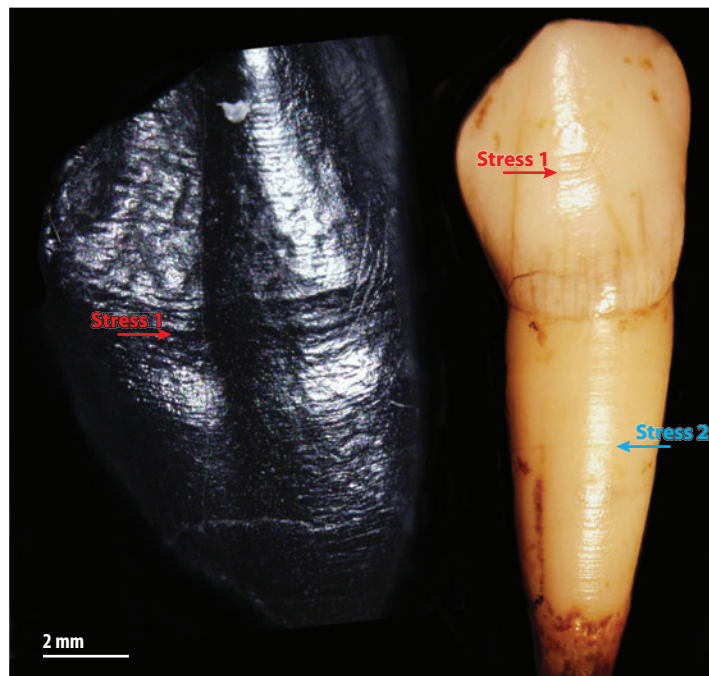
Figure 2

Developmental defects (hypoplasias) on the Scladina Neanderthal's lower canine crown and root.
Left: magnified replica of tooth crown; *right*: actual tooth. Stress 1 (*red arrow*) was identified and dated to
2.4 years of age in a histological section of this individual, and stress 2 (*blue arrow*) was determined to have
occurred at 4.9 years of age (Smith et al. 2007b). Regular long-period incremental growth lines horizontally
encircle the tooth crown and root.

1989, Cunha et al. 2004, Dean & Smith 2009; but see Lacruz et al. 2005). Ogilvie and colleagues
(1989) argue that the many hypoplasias on Neanderthal teeth from ∼2–5 years of age represent
nutritional stress at the initiation of weaning (also see Skinner 1996, 1997). However, these results
should be reconsidered in light of developmental differences between Neanderthals and living and
fossil *H. sapiens* (Guatelli-Steinberg & Reid 2010, Smith et al. 2010b), as well as direct evidence
for weaning in Neanderthals (Austin et al. 2013; discussed below). Lacruz et al. (2005) reject
the possibility that LEH at ∼2.5 years of age in the *A. africanus* Taung child is due to weaning
because 21 other *A. africanus* M1s do not show LEH. Dean & Smith (2009) suggest that hypoplasias
in the *Homo erectus* Nariokotome juvenile at ∼3.5 and ∼4 years of age may indicate the end of
weaning or postweaning illness. This interpretation would be strengthened with information about
the timing and frequency of developmental defects in other *H. erectus* individuals.

Skinner et al. (2012) detail a new possible defect termed "coronal waisting," or localized
narrowing of the middle of anterior tooth crowns, which was observed in permanent canine
teeth from 7 of 9 Taï Forest chimpanzees. These defects occurred between ∼2.0–6.8 years of
age, leading the authors to suggest an association with events during the weaning process (al-
though the dietary histories of these animals are not available for confirmation). Few published
data exist on weaning in this community; Gagneux et al. (1999) note that maternal lactation
lasts for up to 4 years, and Boesch & Boesch-Achermann (2000) report that weaning occurs at
∼5 years of age. Eastern chimpanzees from Gombe cease nursing at 5.2 years of age on average

Hypoplasia:
depression (furrow,
band, or pit) on crown
or root surfaces
formed when hard
tissue formation has
been disrupted

Stress events (age in days)
B 0: birth
1 25
2 142–151
3 183–185
4 223–231
5 293–301 (8-day event)
6 363
D 403: death

Cusp completion at 195 days

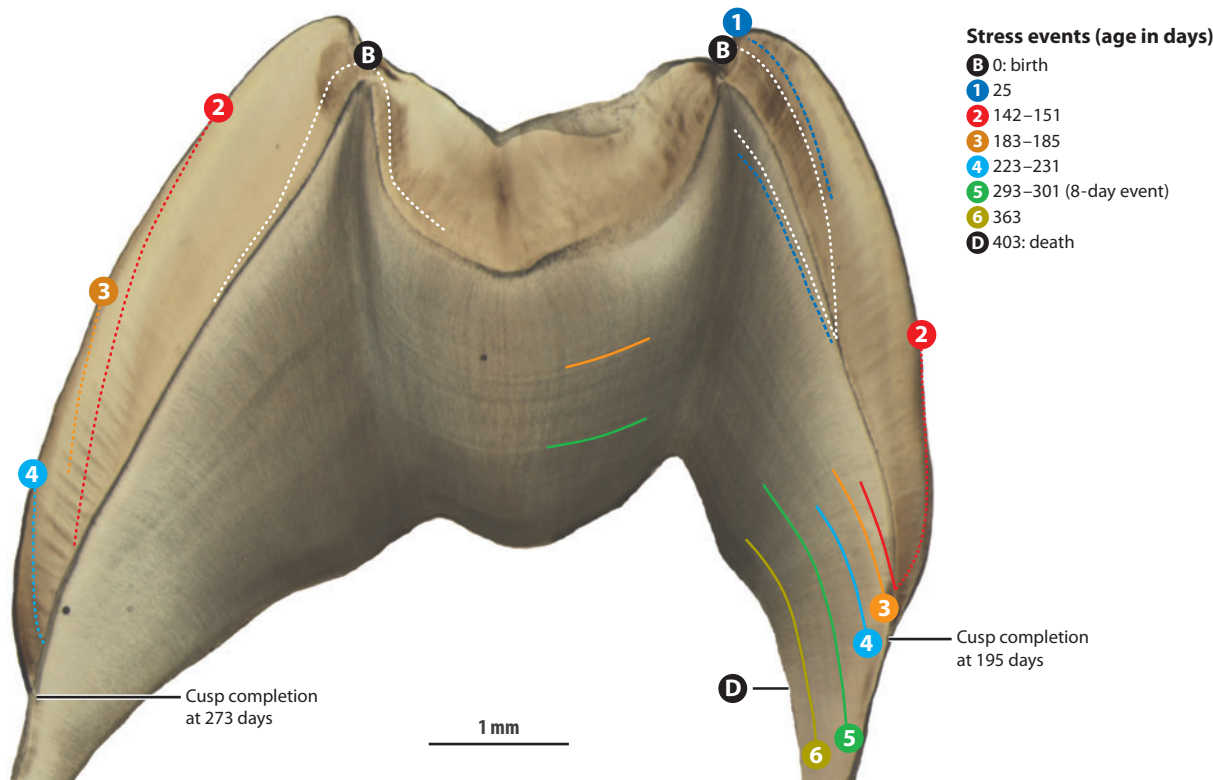Cusp completion at 273 days

1 mm

Figure 3

Growth disturbances (accentuated lines) in a captive rhesus macaque M1 (first molar). The timing of accentuated line formation and age at death shown in the image were determined without knowledge of this individual's developmental history or actual age at death. The cusp on the left began forming 51 days before birth (B), and the cusp on the right began 72 days before birth. Subsequent review of colony records indicates that this individual experienced potential stress at the following ages: 19, 20, and 33 days (enclosure transfers); 166–194 days (hospitalization without mother because of a leg abscess, leading to abrupt weaning at 166 days of age); tail amputation at 217 days of age; and hospitalization due to dehydration/diarrhea at 217–232 days, 267–292 days, 306–313 days, and 357–376 days of age. The individual was euthanized at 402 days of age. Histological estimates of development stress immediately preceding hospitalizations are likely related to initial infections that led to subsequent treatment. Modified from Austin et al. (2013).

(range = 4.2–7.2 years, n = 11; Pusey 1983), and an individual from Kanyawara was last observed nursing at 4.4 years of age (Smith et al. 2013). Taken together, these studies suggest that developmental defects in chimpanzee teeth that occur after ~4–5 years of age are less likely related to the cessation of nursing than they are to periods of illness or suboptimal nutrition related to inadequate foraging skills (Humphrey 2008). Information on wild chimpanzees with associated dietary and behavioral records would help investigators interpret these enigmatic dental features.

Internal stress lines in enamel or dentine are referred to as accentuated lines (**Figure 3**) (reviewed in Goodman & Rose 1990, Dirks et al. 2010). Less is known about their formation than about LEH, save for the neonatal line (**Figure 3**), which is a microscopic accentuated line created in all teeth developing at birth (Rushton 1933, Schour 1936). Simpson (1999) observes that accentuated lines and LEH have "a different structural and temporal signature, suggesting that they are the products of physiological disruptions with different courses, timings and durations" (p. 259). Although numerous sources have speculated on the etiology of accentuated lines

Accentuated line: pronounced line corresponding to the developing enamel or dentine front that relates to a physiological stressor experienced during tooth development

(Goodman & Rose 1990; Dirks 1998; Simpson 1999; Dirks et al. 2002, 2010), few studies of individuals with documented histories are available (save for Bowman 1991, Schwartz et al. 2006).

Dirks et al. (2010) use an innovative combination of tooth chemistry and histological defect aging in two wild baboons, finding peak stresses at 6 and 11 months of age that may correlate with the reduction and cessation of nursing. However, because the baboons show accentuated lines nearly every month over the ∼1.0–1.5-year period, these authors conclude that additional study is necessary to determine whether these lines may be reliable indicators of weaning stress. Two cases illustrated here may be informative. Elemental analyses of the Scladina Neanderthal (discussed below) demonstrate that this individual ceased nursing abruptly at 1.2 years of age, which corresponds with the presence of an accentuated line in the M1 (Austin et al. 2013). However, hypoplasias are not apparent on the anterior teeth of this individual until 2.4 years of age (**Figure 2**) (Smith et al. 2007b), long after the transition to a solid food diet. In contrast, a captive rhesus macaque that was abruptly weaned at 166 days of age does not appear to show a corresponding stress line in enamel or dentine (**Figure 3**). Although limited in scope, studies of this nature may help to guide the interpretation of developmental defects in hominin dental remains.

TOOTH CHEMISTRY AND WEANING

Anthropologists are increasingly interested in elemental analyses of dental remains for reconstructing the weaning process in humans and nonhuman primates (reviewed in Katzenberg et al. 1996; Wright & Schwarcz 1998; Humphrey 2008; Smith & Tafforeau 2008; Jay 2009; Humphrey 2010). Common elemental isotopes (atomic variants) and trace elements that come from food and water are incorporated during tooth growth in a way that reflects circulating levels in the body. Dental tissues are powerful recorders of childhood diets because elemental distributions can be related to fine-scaled temporal records of enamel and dentine formation (**Supplemental Figure 3**) (Dean 1987; Bromage 1991; Smith 2006). Two main approaches use knowledge of dental development to investigate weaning: serial tooth sectioning and investigation of stable isotope ratios, and laser ablation of internal tooth surfaces for trace element analyses.

Investigators have documented broad dietary shifts in patterns of nitrogen and carbon isotopes across several years of dentine formation (e.g., Fuller et al. 2003, Eerkens et al. 2011, Beaumont et al. 2013). Carbon and nitrogen isotopes are elevated (enriched) in mothers' milk, and these isotopes are recorded in dentine collagen formed during nursing. Changes in nitrogen values appear to correspond with the termination of nursing, whereas subtle differences in carbon isotopes may reveal the incorporation of supplemental foods during nursing (reviewed in Humphrey 2008, Jay 2009). However, this method requires relatively large samples from transversely sectioned teeth, prohibiting precise determination of the timing of dietary transitions. Others employ laser ablation inductively coupled plasma mass spectrometry (ICP-MS) to sample small spots of ∼10–100 microns in diameter (e.g., Dolphin et al. 2005; Sponheimer et al. 2006; Humphrey et al. 2007, 2008a,b; Arora et al. 2011; Hare et al. 2011; Shepherd et al. 2012; Austin et al. 2013). These elemental maps may be registered with incremental features in enamel and dentine, yielding precise estimates of the timing of each sample.

Important studies by Humphrey and colleagues (2007; 2008a,b) demonstrate the potential of using incremental features and trace elements to document dietary transitions. Trace elements such as strontium (Sr) and barium (Ba) are elevated in certain food sources such as milk, plants, and animal tissue, and the amount available for digestive absorption (bioavailability) differs among these sources. In a study of children with retrospectively recalled dietary histories, Humphrey et al. (2008a) show that strontium/calcium (Sr/Ca) values change at the neonatal line of some deciduous teeth, corresponding to pre- and postnatal dietary shifts. Moreover, a subset of the infants who

Neonatal line:
accentuated line in enamel and dentine of teeth developing during birth, which allows registration of developmental time with chronological age

Supplemental Material

experienced exclusive breastfeeding show different values than do those who were predominantly formula fed. A complementary study of wild-caught baboons (*Papio hamadryas anubis*) reveals changing patterns of Sr/Ca in one individual that appear to match the species-typical timing of periods of exclusive mothers' milk, supplementation, and cessation of nursing (Humphrey et al. 2008b). Results from a second individual are somewhat less conclusive (discussed further in Dirks et al. 2010).

Austin et al. (2013) compare Sr and Ba distributions in the deciduous teeth of human children with prospectively recorded dietary histories and find that Ba is a more effective elemental discriminator of birth and subsequent diet transitions than is Sr. Barium transfer is restricted by the placenta but is heavily enriched in breast milk and most commercial infant formula products. Human children show marked Ba/Ca increases at birth in enamel and dentine, as well as with the introduction of infant formula. Austin et al. (2013) also examined Ba/Ca ratios in captive macaque dentitions and in their mothers' milk. As is the case for humans, Ba/Ca ratios in macaque teeth are enriched after birth, peak during periods of exclusive nursing, and decline during periods of supplementation. In one instance, premature cessation of nursing is apparent in an individual who was separated from its mother for several weeks, appearing as a marked decrease in Ba/Ca at this age (**Figure 4**).
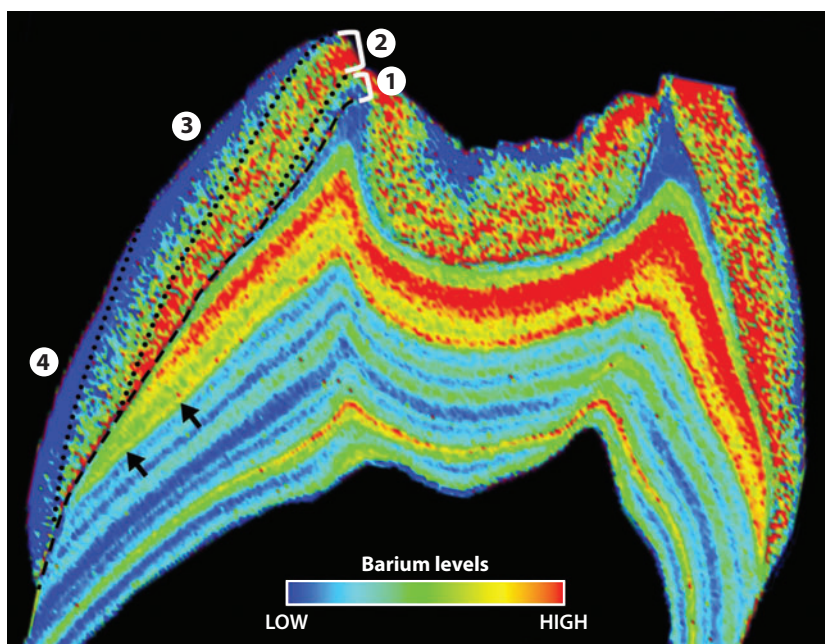
Figure 4

Patterns of barium (Ba) distribution in a captive rhesus macaque M1 (first molar). Four distinct regions are apparent in the enamel and corresponding dentine: (*1*) 51 days of prenatal enamel (low Ba levels due to placental restriction); (*2*) 97 days of exclusive mothers' milk (high Ba levels due to maternal enrichment), (*3*) 69 days of a transition diet (intermediate Ba levels due to a mix of mothers' milk and solid foods), and (*4*) 107 days of exclusive solid food (low Ba levels due to cessation of nursing at 166 days of age). The individual shows an abrupt Ba drop (*black arrows in dentine*), which was independently estimated to have occurred between 151 and 183 days of age from the enamel (see accentuated line map for this tooth in **Figure 3**). Subsequent fluctuations of Ba in the root dentine are likely due to chronic illness. The enamel-dentine junction is indicated with a dashed line. Barium/calcium intensity is displayed as a spectrum that has been normalized to different intensities in the enamel and dentine for clarity. Modified from Austin et al. (2013).

Reconstructing the evolution of human weaning has proven difficult because of the natural processes of organic decay and inorganic modification that occur in bones and teeth after death and during fossilization (diagenesis). Numerous scholars in the isotopic geochemistry community have debated the potential for retrieving the original (biogenic) elemental input signal (reviewed in Smith & Tafforeau 2008, Hinz & Kohn 2010, Kohn & Moses 2013), and researchers generally agree that tooth enamel represents the most promising (although not wholly infallible) paleontological biogenic source. Recent study of a Middle Paleolithic Neanderthal M1 reveals Ba/Ca patterns in the enamel that appear to coincide with periods of placental nutrition, exclusive breast-feeding for 7 months, and supplementation followed by an abrupt cessation of nursing at 1.2 years of age (Austin et al. 2013). This fossil is particularly well preserved and has previously yielded enamel proteins and mitochondrial DNA, and elemental patterns and low levels of diagenetic indicators suggest that Ba/Ca patterns reflect dietary input rather than environmental modification (Austin et al. 2013). Future studies of tooth chemistry and incremental development in well-preserved hominin fossils may be used to directly test theories about changes in the timing of weaning.

TOOTH CALCIFICATION AND OVERALL GROWTH AND DEVELOPMENT

Human biologists have long recognized that the progressive calcification of tooth crowns and roots is related to physical development during childhood, including height, weight, skeletal development, and age at menarche (Lewis & Garn 1960, Anderson et al. 1975, Demirjian et al. 1985, Lewis 1991). Dental calcification is traditionally assessed from flat plate radiographs (e.g., Lewis & Garn 1960, Moorrees et al. 1963, Anderson et al. 1975, Dean & Wood 1981, Skinner & Sperber 1982, Demirjian et al. 1985, Smith 1986) and computed tomography (CT) of skeletal samples (e.g., Conroy & Vannier 1991; Smith et al. 2007a, 2010b). Tooth calcification is less variable than tooth eruption and skeletal development (Lewis & Garn 1960, Demirjian et al. 1985), leading to its frequent use for aging juvenile remains (reviewed in Anderson et al. 1976, Smith 1991b, Hillson 1996).

Skinner & Sperber (1982), Smith (1986), and Conroy & Vannier (1991) report the first large-scale radiographic and CT studies of juvenile fossil hominin dentitions. These and subsequent histological studies have established that calcification patterns in hominins predating Neanderthals show more similarity to those of apes than to those of humans (reviewed in Smith 2008, Lacruz & Ramirez Rozzi 2010). Studies of the *H. erectus* Narikotome individual reach a similar conclusion, and this individual also reveals differences in the patterning of dental and skeletal development (Dean et al. 2001, Dean & Smith 2009). For example, age estimates of Narikotome from modern human tooth calcification standards range from 10.0–10.6, whereas skeletal maturation standards yield estimates of ~13–14 years of age (Dean & Smith 2009). This difference is not entirely surprising because dental and skeletal development are under some degree of independent control (e.g., Garn et al. 1965, Anderson et al. 1975, Demirjian et al. 1985, Lewis 1991, Šešelj 2013).

Considerable efforts have been directed at determining if the life histories of Neanderthals and fossil and living *H. sapiens* differ (e.g., Ramirez Rozzi & Bermudez de Castro 2004; Macchiarelli et al. 2006; Smith et al. 2007a,b, 2010b). Tooth eruption, attrition, developmental stress, crown formation times, and tooth calcification have been examined to address this issue. Histological study of juvenile Neanderthals, fossil *H. sapiens*, and living humans demonstrates differences in the ontogeny of tooth development from early to late childhood (**Figure 5**) (Smith et al. 2010b). Neanderthals show more advanced tooth calcification than does fossil or modern *H. sapiens* for a given chronological age (see also Bayle et al. 2010, Thompson & Nelson 2011, Shackelford et al. 2012) and appear more similar to *H. erectus*. Rapid development in Neanderthals is also supported
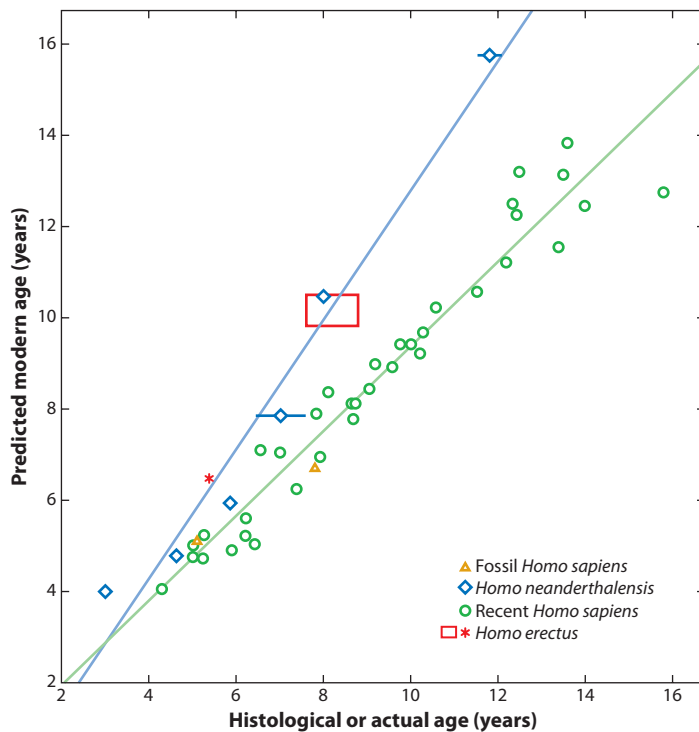
Figure 5

Comparison of fossil hominin ages at death determined from tooth histology versus modern human calcification standards. Fossil *H. sapiens* are represented by Qafzeh 10 and Irhoud 3 (*orange triangles*); Neanderthals (*blue diamonds*) are represented by Engis 2, Gibraltar 2, Krapina Maxilla B, Obi-Rakhmat 1, Scladina, and Le Moustier 1 (*from left to right*). Estimates from two early *Homo* fossils are shown in red (*asterisk*: KNM ER 820: Bromage & Dean 1985, Smith 1986; *box*: KNM WT 15000: ranges in Dean & Smith 2009). Comparisons of known and predicted ages are given for 36 living humans for comparison (*green circles*). Modified from Smith et al. (2010b).

by reports of distinctive Neanderthal cranial ontogeny (reviewed in Smith et al. 2010b, Gunz et al. 2012, Neubauer & Hublin 2012) and postcranial ontogeny (Sasaki et al. 2003, Martín-Gonzáles et al. 2012; but see Thompson & Nelson 2011), which suggests that fully modern growth and development patterns may be unique to our own species. However, given evidence that dental maturation is only moderately correlated with skeletal development, peak height velocity, and age at menarche in living humans (Demirjian et al. 1985, Lewis 1991, Šešelj 2013), specific inferences of general somatic development or life-history variables derived from dental maturation indices should be made with caution.

CONCLUSIONS

Our understanding of primate life history and somatic development has progressed since the seminal works of Schultz (1960), Harvey & Clutton-Brock (1985) and Smith (1989). Scholars have proposed new theoretical frameworks for considering variation in life-history traits, as well as the impact of dietary ecology, immune function, and energetics on the expression of these traits (Lee 1996, Godfrey et al. 2001, McDade 2003, Leigh & Blomquist 2007, Kramer et al. 2009, Valeggia & Ellison 2009, Emery Thompson et al. 2012). Leigh & Blomquist (2007) suggest that

developing systems such as teeth, neural tissue, and reproductive organs should be regarded as modular units, or systems that may be variably paced relative to one another. Lee (2012) argues that life-history traits may be more variable than somatic developmental markers, which is supported by studies of great ape life histories (Knott 2001, Emery Thompson 2013, Smith et al. 2013). Comparisons of captive and wild primates and variably provisioned populations also illustrate the plasticity of life-history traits (reviewed in Emery Thompson 2013). Moreover, the commonly held assumption that lactation suppresses ovulation is not supported by studies of humans and some other primates (Lee 1996, Lancaster & Kaplan 2009, Emery Thompson et al. 2012). Thus weaning age (when defined as the cessation of nursing) is not necessarily a reliable or direct proxy for interbirth interval or population growth. In summary, the relationships among life-history variables, as well as variation within these traits, complicate attempts to predict variables from one another as well as from somatic developmental markers.

First molar eruption age is of limited utility for hominin life-history reconstruction (Robson & Wood 2008, Guatelli-Steinberg 2009, Humphrey 2010, Smith et al. 2013). Patterns of variation may not be consistent at different taxonomic levels (e.g., Harvey & Clutton-Brock 1985, Kelley & Smith 2003, Dirks & Bowman 2007), making primate-wide associations unsuitable for interpreting the variation within narrow taxonomic groups such as hominins. Opinions differ regarding whether M1 eruption age, brain mass, or body mass is most appropriate for life-history prediction (Smith et al. 1995; Smith & Tompkins 1995; Robson & Wood 2008; Kelley & Schwartz 2010, 2012). This discrepancy is particularly evident when considering Neanderthals, who have larger estimated body and brain masses than do modern humans (implying later ages of M1 eruption: Smith & Tompkins 1995) but shorter periods of tooth formation (implying earlier ages of M1 eruption: Smith et al. 2010b). R.J. Smith and colleagues (1995) characterize the confidence intervals of the primate regression equation used to predict hominin M1 eruption age from cranial capacity as "undesirably large" (also see Kelley & Schwartz 2012). Larger samples and more rigorous statistical approaches may be necessary to determine the most effective approach for predicting aspects of hominin life history.

Although studies of tooth wear have the advantage of being nondestructive and minimally invasive, they appear to be of limited value for life-history assessments, particularly for juveniles. My observations of known-aged chimpanzees do not support previous suggestions that hominin weaning may be inferred from patterns of tooth wear (Aiello et al. 1991, Kelley & Schwartz 2012). Additional research is needed to untangle potential confounding factors such as variation in enamel thickness, tooth morphology, and eruption schedules. Moreover, as studies of tooth wear and enamel thickness have noted, the material properties of food items, dietary breadth and seasonal variation, and degree of nonmasticatory processing are likely to have significant impacts on the rate and degree of tissue loss (Strait 1997, Constantino et al. 2009, Ungar & Sponheimer 2011).

Developmental defects on tooth surfaces may be assessed from large samples, as is the case for dental attrition studies. However, a noteworthy complication is that the expression of these defects is more continuous than many studies suggest. Hypoplasia quantification is scale dependent; at high magnifications, it can be difficult to distinguish subtle stress-related alterations from the natural variation of regular growth increments (**Figure 2**). This problem applies to internal assessments as well; accentuated lines are not uniform in appearance or degree, and even though they may

be distinguished from regular long-period lines when not coincident (**Supplemental Figure 2**), they may be hard to identify in certain regions of the crown or root. Future studies must address these methodological issues and document defects in individuals with associated physiological and behavioral information in order to accurately interpret developmental defects in hominin teeth.

Studies of tooth chemistry hold the strongest potential for assessing the timing of diet transitions that occur during the weaning process. Direct investigation of weaning in nonhuman

primates, which is notoriously difficult to document in the wild, is now possible for both wild primates and well-preserved hominin fossils. Although it is unclear if these integrated chemical and temporal methods will be widely applied to other hominins (owing to their semidestructive nature), studies of hard-tissue preservation may help inform the judicious selection of suitable material and appropriate elements (e.g., Smith & Tafforeau 2008, Kohn & Moses 2013). Although diagenetic modification will likely remain a limiting factor in particular taphonomic and geological contexts, well-preserved dental remains are particularly valuable sources of direct evidence on diet transitions during infancy.

The evolution of human development has conventionally been modeled from extant reference taxa such as humans and apes, which rely on the assumption that extinct hominins followed similar developmental trajectories (reviewed in Conroy & Vannier 1991, Smith & Tompkins 1995). Recent studies of taxa that do not appear to fit either model, such as *H. erectus* (DeSilva & Lesnik 2008, Dean & Smith 2009), underscore the fact that our understanding of fossil hominin life histories has been rather coarse. Comparisons of calcification patterns in recent *H. sapiens* and Neanderthal dentitions suggest that the characteristically prolonged development of living humans fully evolved after these taxa diverged (Smith et al. 2010b; also see Caspari & Lee 2004), although additional evidence is required to relate these differences to precise changes in characteristics such as interbirth interval, age at reproductive maturity, or life span.

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