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A Faithful Record of Stressful Life Events Preserved in the Dental Developmental Record of a Juvenile Gorilla

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The pattern and rate of dental development are critical components of the life history of primates. Much recent research has focused on dental development in chimpanzees and other hominoids, but comparatively little is known about dental development in *Gorilla*. To date, dental chronologies for *Gorilla* are based on a sample of 1 and information about variations in the time and timing of crown initiation and completion is lacking. We provide data on dental development in 1 captive, juvenile, female, western lowland *Gorilla gorilla gorilla* of known age, sex, life events, and date of death (carefully documented as part of zoo records) that experienced various physical insults during her first year of life. The perfect natural experiment allowed us to test the association of the timing of accentuated stress lines in teeth with significant physiological and psychological events during ontogeny of this juvenile gorilla. We analyzed histological sections from 14 permanent teeth (maxillary and mandibular I1-M2) and assessed crown initiation (CI) and crown formation times (CFT) using short- and long-period incremental lines in both enamel and dentine; they are advanced for all teeth compared to previously published chronology. The data suggest a relatively accelerated pace of dental development in gorillas compared to chimpanzees and fit an emerging

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pattern of an accelerated life history schedule in gorillas. Data on the timing of major accentuated lines in the developing dentition are tightly associated with exact dates of surgical procedures and follow-up hospital visits as recorded on zoo medical records. Our data highlight the importance of captive individuals with well-documented medical records for studying life history.

KEY WORDS: enamel formation; *Gorilla gorilla gorilla*; growth and development; hominoids; life history; stress; tooth growth.

INTRODUCTION

Teeth grow such that information about the pace and pattern of dental development, certain life history attributes (gestation length, weaning age, etc.), and important developmental milestones in an individual's life are faithfully preserved. From early in the 20th century, anthropologists noted that the overall pace of life and certain life history events are highly correlated with the eruption schedules of teeth (Schultz, 1935; Mann, 1974; Smith, 1986, 1989a,b, 1992, 2000; Smith *et al.*, 1994; Godfrey *et al.*, 2001, 2004). New techniques have emerged to map the growth of individual teeth and entire dentitions that researchers can apply to fossils and complement and clarify life history inferences derived from studies of dental eruption, body mass, skeletal dimensions, etc. Cells that secrete dental hard tissues leave a record of their activity in short- and long-period incremental lines. Over the last 2 decades, analyses of them have facilitated fascinating insights into the evolutionary history of primate growth and development (Beynon and Dean, 1988; Beynon *et al.*, 1991a,b, 1998; Dean, 1987, 1998; Dean and Reid, 2001; Dean *et al.*, 1993, 2001; Dirks, 1998; Dirks *et al.*, 2002; Kelley and Smith, 2003; Ramirez Rozzi and Bermudez de Castro 2004; Reid *et al.*, 1998; Schwartz *et al.*, 2002, 2005; Smith *et al.*, 2003).

Given the close relationship of African apes to humans, comparative dental data highlight the uniquely modern human pattern of growth and development. Much more is known about chimpanzees because they are better represented in captive situations and in museum collections. In fact, large data sets on variation in nearly all aspects of chimpanzee dental development are readily available (Anemone *et al.*, 1991, 1996; Conroy and Mahoney, 1991; Kraemer *et al.*, 1982; Kuykendall, 1996; Kuykendall and Conroy, 1996; Kuykendall *et al.*, 1992; Mooney *et al.*, 1991; Nissen and Riesen, 1964; Reid *et al.*, 1998; Schwartz and Dean, 2001; Smith *et al.*, 1994; Zihlman *et al.*, 2004).

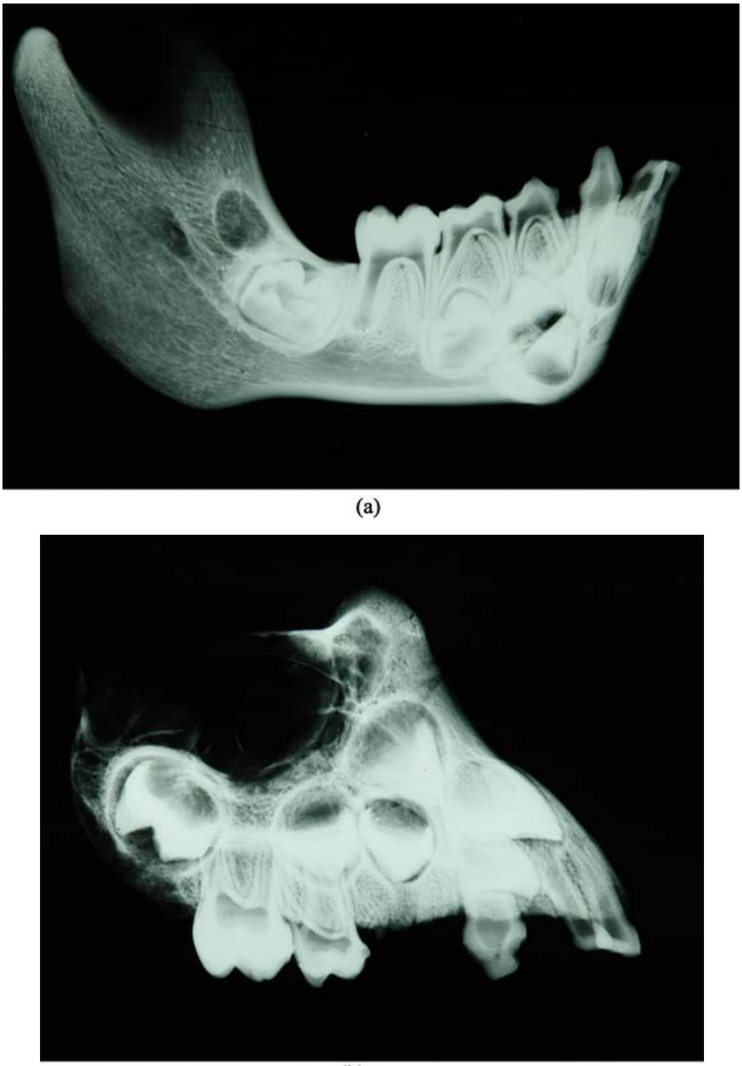
Though closely related, gorillas differ from chimpanzees in many aspects of biology, behavior, diet, and ecology, and we know comparatively little about gorilla growth and development. Gorillas are of considerable interest because they are closely related to humans and chimpanzees and form part of an African hominoid radiation. A few studies are available on certain aspects of growth in gorillas, including skeletal growth, body mass, and body composition (Bellisari *et al.*, 2001; Bolter and Zihlman, 2002; Leigh and Shea, 1995, 1996; McFarland and Zihlman, 2001; Randall, 1943a,b; 1944; Taylor, 1997). Insights into permanent tooth development in gorillas are more limited and based on much smaller samples (Beynon *et al.,* 1991b; Willoughby, 1978) or focus exclusively on the deciduous dentition (Bellisari *et al.*, 2005; Keiter, 1991).

A synthesis of all available data makes it clear that one of the major differences in dental development between chimpanzees and gorillas is the rate of increase in crown height and root length. A recent examination of the ontogeny of canine dimorphism provided clear evidence for differences in both the rate of attainment of canine crown height and the overall duration of canine growth between African ape species (Schwartz and Dean, 2001; Schwartz *et al.*, 2001). To date, however, only 1 study specifically focused on charting the chronology of the entire developing dentition in this *Gorilla* (Beynon *et al.*, 1991b). For more than a decade, the study has served as a benchmark for our understanding of dental development in gorillas (i.e., crown initiation and completion times as well as eruption times); as a result, we know very little about variation in the pace and overall pattern of dental development.

The incremental lines preserved as dental tissues develop appear in 2 forms: short- and long-period lines, both of which occur in both enamel and dentine. A fascinating detail about the growth lines is that the long-period incremental markings in enamel (also referred to as striae of Retzius) manifest on the tooth crown surface as perikymata (Fig. 1). Metabolic and physiological disturbances during growth are recorded in developing teeth as accentuated striae of Retzius (or sometimes as Wilson bands[6]) occasionally surfacing as upsets in the regular spacing and appearance of external perikymata, and are referred to as hypoplastic lesions. Researchers have viewed such lesions, i.e., enamel defects, as reliable markers of overall health and lie at the core of population studies on nutrition and disease patterns in humans and nonhuman primates (Guatelli-Steinberg, 2001).

To date, it is unknown whether certain types of lesions (and the degree to which they are expressed) correlate with particular types of developmental perturbations. For instance, such disturbances could be the result of seasonal fluctuations in food or water availability (Dirks *et al.*, 2002; Macho *et al.*, 1996), an animal's position within the dominance hierarchy,

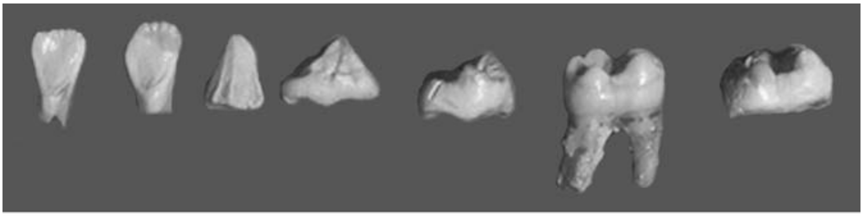
[6]Accentuated striae differ from normal striae in their optical properties when viewed under polarized light. Wilson bands are a special subset of accentuated striae that correspond to hypoplastic lesions on the external crown surface. Accentuated striae can occur between 2 successive, or be coincident with, normal striae.



(a)

(b)

Fig. 1. (a, b) X-ray films of the hemimandible and hemimaxilla from the captive juvenile gorilla showing the permanent incisors and canines in crypt, as well as the permanent M2 nearly crown complete in its crypt. Note the presence of a crypt for the M_3, but no evidence of crown initiation. (c) I_1-M_2, after extraction (from left to right: I_1, I_2, C, P_3, P_4, M_1, M_2). Note the similar state of crown development of P_4 and M_2. (d) The hemimandible after restoration of the corpus including acrylic replicas of teeth placed back into corpus.



(c)

(d)

Fig. 1. Continued.

or perhaps the stress associated with the process of weaning (Dirks, 1998). Analyses of accentuated striae and "stress" in fossil or isolated museum specimens are limited in their ability to attribute developmental disruptions and disturbances in tooth formation to particular types of stressors. Studies in which known events in the lives of captive primates can be correlated with the time of stressful events have a great deal to reveal about when, how often, and under what conditions primates experience metabolic or physiological disruptions or both.

We studied a captive, female, western gorilla (*Gorilla gorilla gorilla*) with detailed life history data recorded by zoo personnel. Her unfortunate early accidental death provides a natural experiment and an opportunity to test the strength of association between physiological stress and disturbances in the developing dentition.

Our goals were to 1) augment available data on the gorilla by providing chronological details of dental development in an additional gorilla specimen; 2) compare and contrast our findings with previously published data on dental development in *Gorilla*; 3) chart the timing of stress during her early ontogeny; and 4) examine the relationship, if any, between the timing of stress in developing dental hard tissues by comparing stressful events in the dentition in *real time* with those occurring during her life.

MATERIALS AND METHODS

Subject

A healthy, captive juvenile western lowland gorilla (*Gorilla gorilla gorilla*; studbook no. 1268/650; studbook name OKLA 13/G) died suddenly in an accident (at 3 yr 3 mo; 26.8 kg), not from a chronic or acute illness. The individual was shipped frozen to the University of California, Santa Cruz for quantitative anatomical study. Detailed zoo documents contain date of birth, body masses, and health status during life, which provide a record of her overall normal development (McFarland and Zihlman, 2001).

Methods

Without access to the medical and zoo records for the subject, Schwartz and Reid extracted and analyzed 14 teeth (maxillary and mandibular I1-M2) from the permanent dentition (Table I; Figs. 1a–d). Only after we collected data on the timing and sequence of tooth initiation and the position of accentuated striae did we compare the results to the available records; in essence, we determined the timing of accentuated striae, or stress lines, via a blind study protocol.

We carefully extracted cleaned each tooth from a hemimandible and hemimaxilla (Fig. 1c). We prepared molds via Coltene™ silicon medium body putty and replicated each tooth in a colored acrylic resin before carrying out histology. We also prepared an acrylic replica cast of the mandible that allowed the tooth germ casts to be replaced, in the same anatomical position before extraction, to make future studies of the developing dentition possible (Fig. 1d).

Before sectioning, we embedded each specimen in polyester resin or coated it with cyanoacrylate to reduce the risk of splintering. Using a Logitech™ PM30 annular blade saw, we prepared 180–200 μm ground

Table I. Major life events in the juvenile *Gorilla* specimen associated with accentuated stress lines in the developing dentition

Life events	Week of life	Days	Years
D.O.B. December 15, 1992	0	0	0
D.O.D. February 25, 1996	166.7	1168	3.20
Traumatic events			
Birth	0		
Eye injury and surgery	5		0.10
Follow-up hospital visits	20		0.39
	25		0.48
	28		0.54
	46		0.89
Enclosure transfers	54		1.04
	72		1.39
	79		1.51
	143		2.75
Death	166.7	1168	3.20

Note. Other enclosure transfers are included in zoo records but are not associated with accentuated markings and so are not included in the table.

sections from the midline axial plane for anterior teeth and from both the mesial and distal cusp planes for posterior teeth such that each section traversed both cusp tips and dentine horns. We mounted sections on microscope slides, lapped with 3 μm aluminum oxide powder to a final thickness of 90–110 μm, polished with a 0.1-μm diamond suspension paste, placed in an ultrasonic bath to remove surface debris, dehydrated through a graded series of alcohol baths, cleared in xylene, mounted with cover slips in DPX™ mounting medium, and analyzed via polarized light microscopy. We prepared and analyzed a total of 34 thin sections from the individual.

Short-period (i.e., daily cross-striations) and long-period (i.e., striae of Retzius) lines were clearly visible throughout the enamel. We used both types of incremental markings to measure daily enamel secretion rates (DSRs) and total crown formation times (CFTs) for each tooth. We determined CFTs by summing the time to form the cuspal (appositional) and lateral (imbricational) components of each tooth. We defined the transition between cuspal and lateral enamel as the point where successive domes of enamel formation are no longer completely buried within the cusp by subsequently formed enamel, but instead outcrop on the enamel surface of the tooth as perikymata (Fig. 2). (In most ape anterior teeth, Retzius lines do not reach the surface as perikymata because of the presence of a thin layer of aprismatic enamel. This is not problematic in histological studies because Retzius lines are clearly visible, but it hampers attempts to determine CFT by counting perikymata on the labial surface of most anterior teeth.)

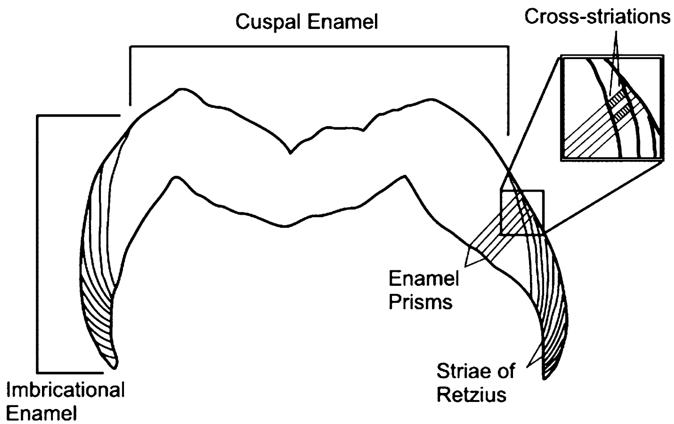


Fig. 2. Schematic representation of a cross section of a molar illustrating cuspal and imbricational (lateral) components of the crown and the major incremental features associated with enamel growth. Enamel prisms run from the enamel-dentine junction out toward the crown surface and contain short-period lines, or daily cross striations. Each stria of Retzius (long-period line) runs obliquely to the direction of prisms and is separated from adjacent striae by a certain number of days (the periodicity) which remains constant in all the teeth of 1 individual. One can determine imbricational enamel formation time by multiplying the number of striae by the periodicity. In posterior teeth, such as the molar here, each internal striae in the imbricational enamel is continuous with an external perikyma (see text). (From Smith *et al.*, 2003.)

Lateral enamel formation time in days is the total number of imbricational striae multiplied by the striae periodicity (number of days between adjacent striae). We repeatedly determined CFT in this way for each tooth to calculate both the rate and duration of growth and the total amounts of pre- and postnatal tooth growth.

To create a chronology of dental development, one needs to register the first molar in time-at-zero-days development (i.e., the day of birth), and then each tooth can be registered to one another. We accomplished the former by charting the position of the neonatal line while the latter required information on the timing of accentuated striae of Retzius throughout the dentition (Figs. 2 and 3). The neonatal line is a prominent accentuated line that coincides with birth (Fig. 3). Accentuated striae of Retzius mark brief periods of disruption in enamel and dentine matrix secretion and are often the result of physiological insults of one kind or another. As these events occur at a particular point in development, they are recorded in all teeth developing at that particular moment in time. Thus, accentuated striae facilitate the calibration of dental development across teeth; i.e., each stria

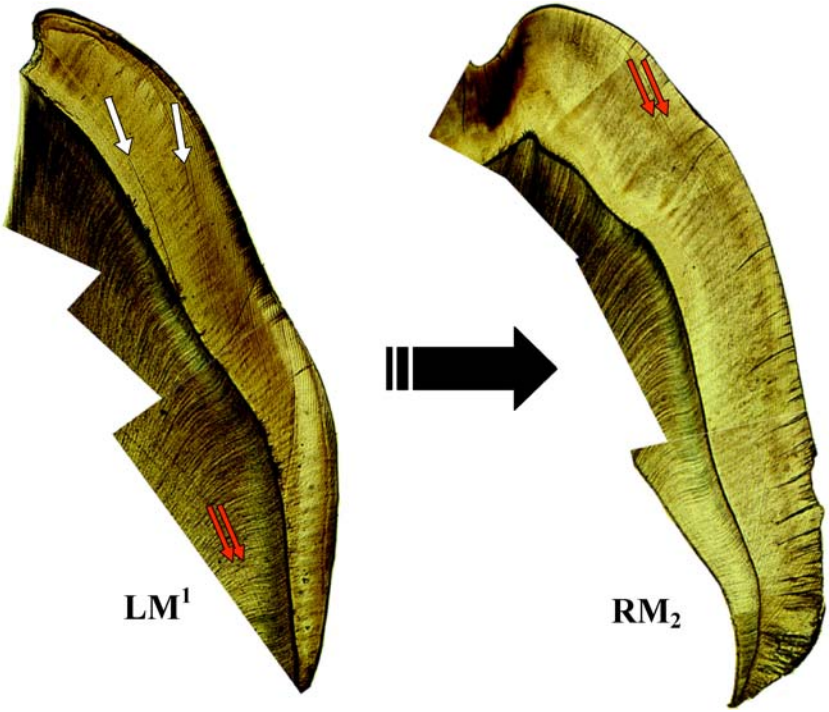


Fig. 3. LM^1 and RM_2 of *Gorilla gorilla gorilla* illustrating the technique of registering 1 tooth to another during development. Several accentuated lines appear throughout crown development (white and red arrows). A doublet (2 red arrows), representing the 2 stress events close in time, is visible in both teeth and enables tying in the proportion of crown developed in the RM_2 with that in LM^1; nearly two-thirds of the RM_2 crown is completed at the same time that the entire LM^1 crown formed.

provides a temporal benchmark for registering all teeth developing at the same time to one another (Fig. 2). We determined the timing of accentuated striae from the dental histology and mapped it onto a chronology of gorilla dental development (Figs. 4 and 5).

RESULTS

Data on date of birth, date of death, and other important episodes during development in our juvenile gorilla specimen are in Table I. Results of the dental chronology including ages at initiation, total crown and root formation times, age at completion, etc., are in Table II. Comparative data on

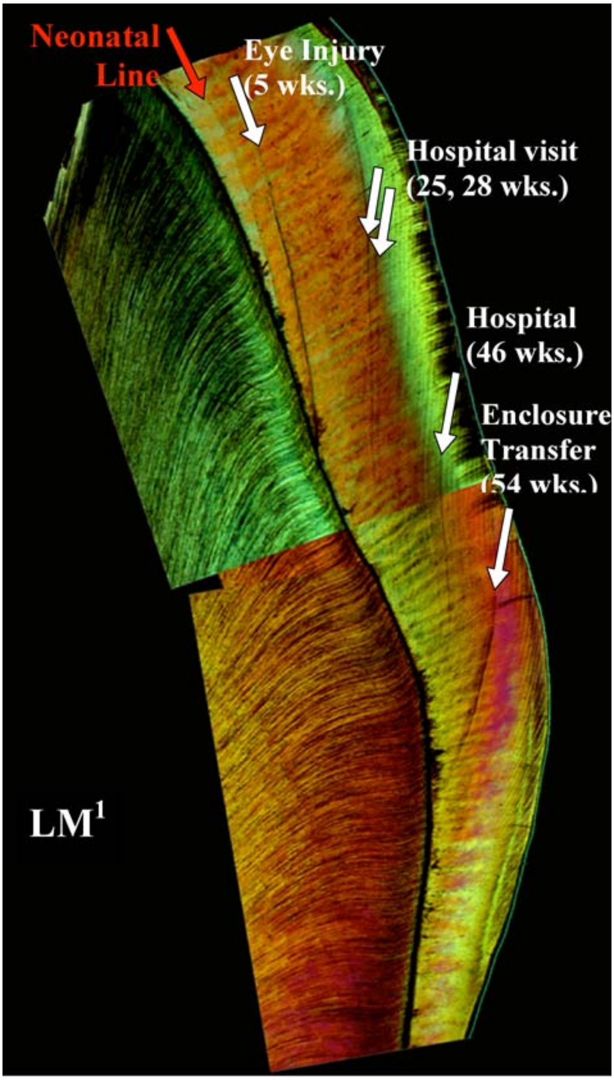


Fig. 4. Polarized light montage of the LM1 crown (lingual cusp) illustrating the position of the accentuated lines associated with the major life events in our gorilla specimen.

crown formation times in the 2 gorilla specimens for which dental developmental data are available are in Table III.

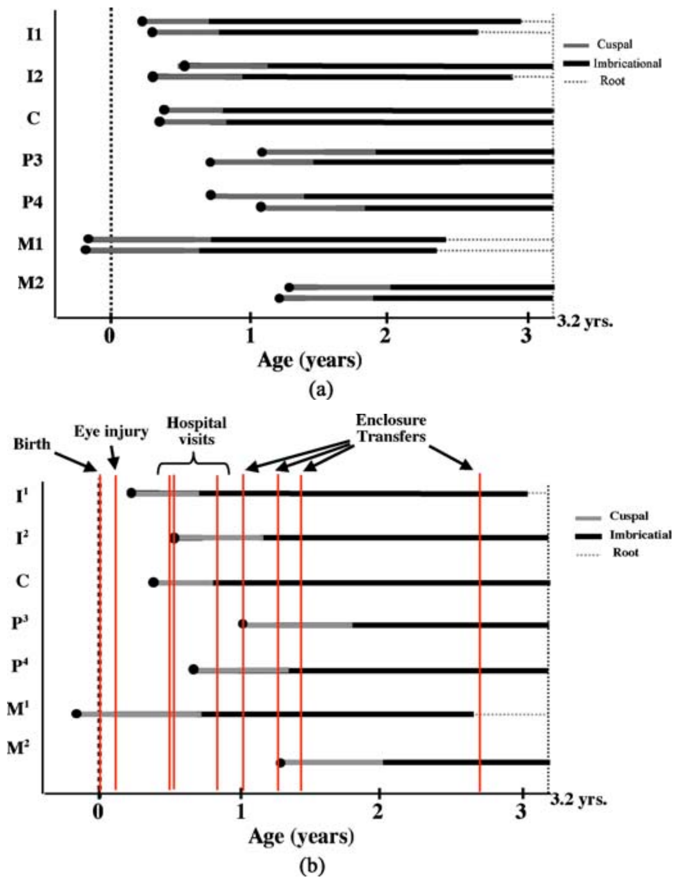


Fig. 5. (a) Dental chronology for the western lowland gorilla (*Gorilla gorilla gorilla*). For each tooth type, the top bar represents the maxillary tooth and the bottom bar represents the mandibular tooth. (b) A composite dental chronology (averaging the initiation times of the mandibular and maxillary teeth within each tooth type) showing the timing of the major accentuated lines cutting across all teeth developing at a particular point in time (Table I and text).

Age at Death, Crown Initiation, and Crown Formation Times

Histologically derived dates of birth and death for the specimen yielded an age at death of 166.7 wk, or 1168 d, or 3.2 yr, which matched exactly the known age at death of the specimen from autopsy records (Table I; Fig. 4). As in all anthropoids for which data exist, first permanent molars initiate before birth. In the juvenile gorilla, M1 begin calcification

5–12 wk prenatally (Table II). Death occurred before completion of most teeth so that complete CFT are available only for I1, I_2, and M1. CFT for these teeth are markedly shorter in the individual studied here compared to the only such data available in the literature, in particular for the maxillary and mandibular first molars (Table III). For instance, crown initiation (CI) times and CFT are advanced for all teeth compared to the previously published chronology. CI for I1 and I2 are 0.5–0.8 yr earlier than in precedent data and complete 1.13 yr ahead of schedule. CFT for M^1 and M_1 are advanced by 0.5 and 0.8–1.1 yr, respectively. Values for sequential molar overlap between M1 and M2 are 0.99 yr for maxillary molars and 0.94 yr for mandibular molars.

Canine growth seems only slightly accelerated, if at all: based on longitudinal study of canine growth in a sample of female gorilla canines (polynomial regression models: Schwartz and Dean, 2000), crown formation times predicted for maxillary and mandibular canines (of the crown height in our specimen) are 3.05 and 2.48 yr, respectively. Adding on the time from birth to canine crown initiation adds 0.33 and 0.29 yr, yielding an age at death of 3.38 and 2.77 yr, for maxillary and mandibular canines, respectively.

A composite dental chronology for maxillary and mandibular teeth is in Fig. 4. Not only are CFT accelerated compared to data in the literature, but crown initiation times are advanced in all teeth, in particular the premolars and molars. For the previously published specimen, incisor crowns are 1/2 complete at just over 3 yr, compared to incisors already being crown complete with some root growth having occurred (Beynon *et al.*, 1991b). The first molar is the only tooth that shares a similar developmental history between study individuals, initiating just before birth and completing its crown just before 3 yr of age. M2 shows the greatest acceleration initiating at *ca.* 1.3 yr postnatally (compared to *ca.* 2.5 yr of age; Beynon *et al.*, 1991a,b); >1 yr in advance (Table II; Fig. 4).

Timing of Stress Events

After completing the dental chronology, we determined and mapped the timing of each accentuated stria onto the chronology. After working out the timing of the developmental lesions (or accentuated striae or stress lines as they are referred to in the dental growth literature), we examined the medical records for this juvenile gorilla that revealed several severe physiological insults. The first major traumatic event was birth, which is recorded in the developing permanent teeth of all individuals as a clearly visible accentuated growth line. The second major traumatic event, at 5 wk postnatal age, was the result of an attack by the silverback male resulting in several injuries to the orbit necessitating immediate surgery and a series of follow-

Table II. Timing of crown initiation, crown formation time (CFT), and completion

	Initiation	Cuspal enamel	Imbricational enamel	Root	CFT (wk)	CFT (yr)	Total crown formation (yr)	Crown initiation (yr)
I^1	9	28	121	8 +	149		2.86	0.17
I^2	26	29	111 +		140 +			0.50
C	17	28	121 +		149 +			0.33
P^3mb	56	41	69 +		110 +			1.08
P^3mp	66	42	58 +		100 +			1.27
P^4mb	34	36	96 +		132 +			0.65
P^4mp	50	25	91 +		116 +			0.96
M^1mb	–5	42	85	44 +	127	2.44	2.53	–0.10
M^1mp	–10	37	75	64 +	112	2.15		–0.19
M^2mb	70	37	59 +		96 +			1.35
M^2mp	66	40	60 +		100 +			1.27
I_1	11	28	110	17	138		2.65	0.21
I_2	12	26	115	13	141		2.70	0.23
C	15	32	119 +		151 +			0.29
P_3	34	35	63 +		132 +			0.65
P_4mb	55	40	71 +		111 +			1.06
P_4ml	70	28	68 +		96 +			1.35
M_1mb	–12	36	84	58 +	120	2.31	2.30	–0.23
M_1ml	–10	33	69	74 +	102	1.96		–0.19
M_2mb	59	38	69 +		107 +			1.13
M_2ml	68	36	62 +		98 +			1.31

Note. All data are in weeks unless otherwise noted. mb, mesiobuccal; mp, mesiopalatal; ml, mesiolingual; + indicates tooth crown was incomplete at time of death.

Table III. Comparison of crown formation times in our specimen with those reported in literature

Tooth	CFT (years)		
	Beynon *et al.* (1991b)	This study	Percentage diff.[a]
I^1	4.05	2.86	70.6
I_1	3.60	2.65	73.6
I^2	4.10	>2.70	—
I_2	4.35	2.70	62.1
$\underline{C}$	>5.25	>2.87	—
$\overline{C}$	>5.15	>2.91	—
P^3	5.10	>2.12	—
P_3	>4.60	>2.55	—
P^4	3.45	>2.55	—
P_4	3.65	>2.14	—
M^1	2.85	2.53	88.8
M_1	2.90	2.30	79.3
M^2	2.85	>1.93	—
M_2	3.25	>2.07	—

Note. >indicates crowns are incomplete and so represent a minimum CFT at the very most.
[a]CFT of specimen used here as a proportion of CFT from the Beynon *et al.* study.

up hospital visits. The surgery occurred at 5 wk, and hospital visits took place at wk 20, 25, 27, and 46. Subsequent to the hospital visits, the juvenile gorilla also underwent a series of enclosure transfers, 1 at wk 54 (Table I).[7] Each of these episodes was recorded as an accentuated stria (stress line) in all of the teeth developing at the time of each event, matching up exactly, to within the same week. Thus, major accentuated striae in the enamel and dentine are associated with major physiological traumas (i.e., birth, injuries) as well as psychologically stressful situations (follow-up hospital visits and enclosure transfers).

DISCUSSION

Dental developmental data for the juvenile *Gorilla gorilla gorilla* vary in both the time and timing of tooth formation compared to that in the literature. The source of the variation, however, is unclear and could be attributed to differences in sex, subspecies, tooth size, etc., or some

[7]Other enclosure transfers were in the zoo records but were not associated with accentuated striae.

combination thereof, between the previously published specimen (Beynon *et al.*, 1991b) and our data.

While the *rate* of development for particular teeth is advanced, the *sequence* of tooth development is what is expected for a juvenile gorilla. Compared to a composite dental developmental record based on 60 wild-shot juvenile gorillas (Fig. 3 in Dean and Wood, 1981) our juvenile gorilla fits with a generalized ape of *ca.* 4-yr-old: there is a hint of I1 root development, an incomplete M2 crown, and only the early stages (in the mandible) of a crypt for M3, but no M3 tooth germ.

Captive individuals exhibit measurable differences in many aspects of biology compared to free-ranging individuals. Wild populations of baboons grow more slowly than their captive counterparts (Phillips-Conroy and Jolly, 1988). Accelerated somatic development in captive individuals is by far better documented in hominoids, in particular for the African apes. Leigh (1994) found that captive adult female gorillas weigh more than free-ranging females. Several other studies demonstrate differences in growth schedules, e.g., for body mass, limb lengths, age at maturity, with development being prolonged in wild populations (Boesch and Boesch-Achermann, 2000; Hamada *et al.*, 1996; Kimura and Hamada, 1996). Zihlman *et al.* (2004) recently suggested that dental development in wild chimpanzees is consistently delayed compared to captive individuals, with the important developmental marker of M1 emergence occurring closer to 4 yr of age, rather than 3–3.5 yr suggested previously (Anemone *et al.*, 1991, 1996; Kuykendall *et al.*, 1992; Kuykendall, 1996; Kuykendall and Conroy, 1996). In our juvenile gorilla, the M1 showed evidence of slight attrition and was therefore in functional occlusion, indicating that M1 eruption occurred just before 3.2 yr at the very latest. This is near the eruption age for captive chimpanzees and slightly younger than that for wild chimpanzees (Zihlman *et al.*, 2004). Age at M1 emergence is an important life history marker because it indicates the transition from the childhood to the juvenile stage of development. Surprisingly few data exist on age at M1 eruption in gorillas and orangutans (Kelley and Schwartz, 2005; Schultz, 1935; Willoughby, 1978). The only data available for age at M1 emergence in gorillas is 3.5 yr (mean) with a range of 3–4 yr (Willoughby, 1978, in B. H. Smith, 1986, 1989a,b). To date, dental development and eruption schedules for all of the gorilla specimens published are based on captive individuals, so we are unable to comment on the impact on dental growth rates of being reared in artificial environments.

All available data on M1 eruption in gorillas (including our data) suggest the important developmental milestone occurs at 3–3.5 yr (*cf. ca.* 4 in wild chimpanzee populations). Given the tight correlation between age at M1 eruption and overall pace of life in anthropoids, the earlier eruption of M1 in gorillas (relative to chimpanzees) suggests the presence of a slightly faster life history schedule. If true, it is expected that other aspects of gorilla dental development and eruption (e.g., the deciduous dentition) would be equally accelerated—as appears to be the case for the deciduous incisors, though not for the deciduous molars (Keiter, 1981; Smith *et al.*, 1994). Such accelerated dental growth would most likely be tied to accelerations of other important components of life history profiles, such as age at weaning in gorillas, age at sexual maturity and first reproduction, interbirth interval and longevity. Evidence that gorillas mature faster than chimpanzees is available, e.g., certain gorilla populations possess shorter interbirth intervals than those of chimpanzees (median of 3.9 yr compared to 5.1–6.2 yr, respectively) and an earlier age at first reproduction (8.7–12.8 yr compared to 11.1–20 yr) (Boesch and Boesch-Achermann, 2000; Knott, 2001; Nishida *et al.*, 1990; Sugiyama, 1994; Watts, 1991; Zihlman, 1997). Likewise, Bolter and Zihlman (2000) found that gorillas accumulate muscle tissue and limb mass early, and thus display a more advanced locomotor anatomy than chimpanzees of similar age. Leigh and Shea (1995, 1996) and Taylor (1997) suggested folivory as an ecological basis for the apparent accelerated growth trajectory they observed in gorillas compared to chimpanzees, and in mountain gorillas compared to lowland gorillas, respectively. The emerging picture suggests that gorillas possess faster life history schedules than chimpanzees, despite large differences in size, forcing us to rethink the scaling relationship between body mass and life history profiles in hominoids.

Whatever the source of accelerated dental growth schedules in gorilla and its implications for our understanding of life history variation within the hominoids, our data clearly document the accuracy with which data on life events are recorded in the developing dentition and how they are readily retrieved via histological ground sections. They also highlight the value of tracking individuals through life stages and the important contribution of zoo personnel who record life events of animals in their care.

CONCLUSIONS

Our study of a juvenile western lowland gorilla illustrates how captive individuals with known life histories can be valuable in investigations of dental development. We also provide support for the use of histological growth markers to assess precise ages at death for skeletal or fossilized specimens. Major accentuated stress lines in teeth were tightly associated with traumatic life events such as birth and injuries. Thus, dental analysis can be an important method for reading the story of an individual's life after its death.

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REFERENCES

Anemone, R. L., Mooney, M. P., and Siegel, M. I. (1996). Longitudinal study of dental development in chimpanzees of known chronological age: Implications for understanding the age at death of Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* 99: 119–134.

Anemone, R. L., Watts, E. S., and Swindler, D. R. (1991). Dental development of known-age chimpanzees, *Pan troglodytes* (Primates: Pongidae). *Am. J. Phys. Anthropol.* 86: 229–241.

Bellisari, A., Duren, D. L., and Sherwood, R. J. (2005). Sex differences in emergence of deciduous dentition in captive lowland gorillas (*Gorilla gorilla gorilla*). *Am. J. Phys. Anthropol.* (Suppl). 40: 72.

Bellisari, A., Newman, T. K., Greenberg, C., Rogers, J., and Towne, B. (2001) Individual variation in the growth of captive infant gorillas. *Am. J. Phys. Anthropol.* 115: 110–132.

Beynon, A. D., and Dean, M. C. (1988). Distinct dental development patterns in early fossil hominids. *Nature* 335: 509–514.

Beynon, A. D., Dean, M. C., Leakey, M. G., Reid, D. J., and Walker, A. C. (1998). Comparative dental development and microstructure of *Proconsul* teeth from Rusinga Island, Kenya. *J. Hum. Evol.* 35: 163–209.

Beynon, A. D, Dean, M. C., and Reid, D. J. (1991a). On thick and thin enamel in hominoids. *Am. J. Phys. Anthropol.* 86: 295–309.

Beynon, A. D, Dean, M. C., and Reid, D. J. (1991b). Histological study on the chronology of the developing dentition in gorilla and orang. *Am. J. Phys. Anthropol.* 86: 189–203.

Boesch, C., and Boesch-Achermann, H. (2000). *The Chimpanzee of the Tai Forest: Behavioral Ecology and Evolution*. Oxford University Press, Oxford.

Bolter, D., and Zihlman, A. L. (2002). Growth and development in body tissues and proportions in African apes (*Gorilla gorilla* and *Pan troglodytes*): A preliminary report. *Am. J. Phys. Anthropol. Suppl*. 34: 26.

Conroy, G. C., and Mahoney, C. J. (1991). Mixed longitudinal study of dental emergence in the chimpanzee, *Pan troglodytes* (Primates, Pongidae). *Am. J. Phys. Anthropol.* 86: 243–254.

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

Dean, M. C. (1989). The developing dentition and tooth structure in primates. *Folia Primatol (Basel)* 53: 160–177.

Dean, M. C. (1998). A comparative study of cross striation spacings in cuspal enamel and of four methods of estimating the time taken to grow molar cuspal enamel in *Pan*, *Pongo* and *Homo*. *J. Hum. Evol*. 35: 449–462.

Dean, M. C, Beynon, A. D, Thackeray, J. F., and Macho, G. A. (1993). Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus spe*cimen, SK 63, from Swartkrans, South Africa. *Am. J. Phys. Anthropol.* 91: 401–419.

Dean, M. C., Leakey, M. G., Reid, D. J., Schrenk, F., Schwartz, G. T., Stringer, C., and Walker, A. C. (2001). Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. *Nature* 414: 628–631.

Dean, M. C., and Reid, D. J. (2001). Perikymata spacing and distribution on hominid anterior teeth. *Am. J. Phys. Anthropol.* 116: 209–215.

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

Dirks, W. (1998). Histological reconstruction of dental development and age at death in a juvenile gibbon (*Hylobates lar*). *J. Hum. Evol*. 35: 411–426.

Dirks, W., Reid, D. J., Jolly, C. J., Phillips-Conroy, J. C., and Brett, F. L. (2002). Out of the mouths of baboons: Stress, life history and dental development in the Awash National Park hybrid zone, Ethiopia. *Am. J. Phys. Anthropol.* 118: 239–252.

Godfrey, L. R., Samonds, K. E., Jungers, W. L., and Sutherland, M. R. (2001). Teeth, brains, and primate life histories. *Am. J. Phys. Anthropol.* 114: 192–214.

Godfrey, L. R., Samonds, K. E., Jungers, W. L., Sutherland, M. R., and Irwin, M. T. (2004). Ontogenetic correlates of diet in Malagasy lemurs. *Am. J. Phys. Anthropol.* 123: 250–276.

Guatelli-Steinberg, D. (2001). What can developmental defects of enamel reveal about physiological stress in non-human primates. *Evol. Anthropol.* 10: 138–151.

Keiter, M. D. (1981). Hand-rearing and development of a lowland gorilla at Woodland Partk Zoo, Seattle. *Int. Zoo Yrbk.* 21: 229–235.

Kelley, J., and Schwartz, G. T. (2005). Histologically-determined age at first molar emergence in *Pongo pygmaeus*. *Am. J. Phys. Anthropol. Suppl*. 40: 132.

Kelley, J., and Smith, T. M. (2003). Age at first molar emergence in early Miocene *Afropithecus turkanensis* and life-history evolution in the Hominoidea. *J. Hum. Evol*. 44: 307–329.

Knott, C. D. (2001). Female reproductive ecology of the apes: Implications for human evolution. In Ellison, P. T. (ed.), Reproductive ecology and human evolution. Walter de Gruyter, New York, pp. 429–463.

Kraemer, H. C., Hovart, J. R., Doering, C., and MaGinnis, P. R. (1982). Male chimpanzee development focusing on adolescence: Integration of behavioural with physiological changes. *Primates* 23: 393–405.

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

Kuykendall, K. L., and Conroy, G. C. (1996). Permanent tooth calcification in chimpanzees (*Pan troglodytes*): Patterns and polymorphisms. *Am. J. Phys. Anthropol.* 99: 159–174.

Kuykendall, K. L., Mahoney, C. J., and Conroy, G. C. (1992). Probit and survival analysis of tooth emergence ages in a mixed-longitudinal sample of chimpanzees (*Pan troglodytes)*. *Am. J. Phys. Anthropol.* 89: 379–399.

Leigh, S. R., and Shea, B. T. (1995). Ontogeny and the evolution of adult body size dimorphism in apes. *Am. J. Primatol*. 36: 37–60.

Leigh, S. R., and Shea, B. T. (1996). Ontogeny of body size variation in great apes. *Am. J. Phys. Anthropol.* 99: 43–65.

Macho, G. A., Reid, D. J., Leakey, M. G., Jablonski, N., and Beynon, A. D. (1996). Climatic effects on dental development of *Theropithecus oswaldi* form Koobi Fora and Olorgesailie. *J. Hum. Evol*. 30: 57–70.

Mann, A. E. (1974). *Some Paleodemographic Aspects of the South African Australopithecines*. University of Pennsylvania Press, Philadelphia.

McFarland, R. K,, and Zihlman, A. L. (2001). Body composition in a juvenile gorilla (*Gorilla gorilla gorilla*) compared to adult gorillas. *Am. J. Phys. Anthropol.* 30: 225.

Mooney, M. P., Siegel, M. I., Eichberg, J. W., Lee, D.R., and Swan, J. (1991). Deciduous dentition eruption sequence of the laboratory-reared chimpanzee (*Pan troglodytes*). *J. Med. Primatol*. 20: 138–139.

Nichols, K. A. (1999). Comparative linear skeletal dimensions of captive vs. wild western lowland gorillas. *Am. J. Phys. Anthropol.* (Suppl) 28: 211.

Nishida, T., Takasaki, H., and Takahata, Y. (1990). Demography and reproductive profiles. In Nishida, T. (ed.), *The Chimpanzee of the Mahale Mountains*. University of Tokyo Press, Tokyo, pp. 63–97.

Nissen, H. W., and Riesen, A. H. (1964). The eruption of the permanent dentition of chimpanzees. *Am. J. phys. Anthrop.* 22: 285–294.

Ramirez Rozzi, F., and Bermudez de Castro, J. M. (2004). Surprisingly rapid growth in Neanderthals. *Nature* 428: 936–939.
Randall, F. E. (1943a). The skeletal and dental development and variability of the gorilla. *Hum. Biol.* 15: 236–254.
Randall, F. E. (1943b). The skeletal and dental development and variability of the gorilla (continued). *Hum. Biol.* 15: 307–337.
Randall, F. E. (1944). The skeletal and dental development and variability of the gorilla (concluded). *Hum. Biol*. 16: 23–76.
Reid, D. J., Schwartz, G. T., Chandrasekera, M. S., and Dean, M. C. (1998). A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. *J. Hum. Evol*. 35: 427–448.
Schultz, A. H. (1935). Eruption and decay of the permanent teeth in primates. *Am. J. Phys. Anthropol.* 19: 489–581.
Schwartz, G. T., and Dean, M. C. (2001). The ontogeny of canine dimorphism in extant hominoids. *Am. J. Phys. Anthropol.* 115: 269–283.
Schwartz, G. T., Miller, E. R., and Gunnell, G. F. (2005). Developmental processes and canine dimorphism in primate evolution. *J. Hum. Evol*. 48: 97–103.
Schwartz, G. T., Reid, D. J., and Dean, M. C. (2001). Developmental aspects of sexual dimorphism in hominoid canines. *Int. J. Primatol*. 22: 837–860.
Smith, B. H. (1986). Dental development in *Australopithecus* and *Homo*. *Nature* 323: 327–330.
Smith, B. H. (1989a). Dental development as a measure of life history in primates. *Evolution* 43: 683–688.
Smith, B. H. (1989b). Growth and development and its significance for early hominid behaviour. *Ossa* 14: 63–96.
Smith, B. H. (1992). Life history and the evolution of human maturation. *Evol. Anthropol.* 1: 134–142.
Smith, B. H. (2000). "Schultz's Rule" and the evolution of tooth replacement patterns in primates and ungulates. In Teaford, M. F., Smith, M. M., and Ferguson, M. W. J. (eds.), *Development, Function and Evolution of Teeth*, Cambridge University Press, Cambridge, pp. 212–227.
Smith, B. H., Crummett, T. L., and Brandt, K. L. (1994). Ages of eruption of primate teeth: A compendium for aging individuals and comparing life histories. *Ybk. Phys. Anthropol.* 37: 177–231.
Smith, T. M., Martin, L. B., and Leakey, M. G. (2003). Enamel thickness, microstructure and development in *Afropithecus turkanensis*. *J. Hum. Evol*. 44: 283–306.
Sugiyama, Y. (1994). Age-specific birth rate and lifetime reproductive success of chimpanzees at Bossou, Guinea. *Am. J. Primatol.* 32: 311–328.
Taylor, A. B. (1997). Relative growth, ontogeny and sexual dimorphism in *Gorilla* (*Gorilla gorilla gorilla* and *G. g. beringei*): Evolutionary and ecological consideration. *Am. J. Primatol*. 43: 1–31.
Watts, D. P. (1991). Mountain gorilla reproduction and sexual behavior. *Am. J. Primatol*. 24: 211–226.
Willoughby, D. P. (1978). *All About Gorillas*. AS Barnes & Co, London, 264 pp.
Zihlman, A. L. (1997). Natural history of the apes: Life-history features in males and females. In Morbeck, M. E., Galloway, A., and Zihlman, A. L. (eds.), *The Evolving Female: A Life-History Perspective*, Princeton University Press, Princeton, pp. 86–103.
Zihlman, A. L., Bolter, D., and Boesch, C. (2004). Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. *Proc. Natl. Acad. Sci. USA* 101: 10541–10543.