Evolutionary Anthropology 15:142–154 (2006)

The Secrets of Lemur Teeth

LAURIE R. GODFREY,[1] GARY T. SCHWARTZ,[2] KAREN E. SAMONDS,[3,4] WILLIAM L. JUNGERS,[4] AND KIERSTIN K. CATLETT[2]

New tools are available for teasing out aspects of life-history variation among extinct species. Here we summarize research on the life histories of the extinct lemurs of Madagascar. There is a wide range of variation in dental developmental timing among these species, from among the most accelerated (*Palaeopropithecus*) to among the most prolonged (*Hadropithecus*) within the Order Primates. Rather than reflecting variation in body size, this diversity appears to relate to niche characteristics and encephalization.

Beginning three-quarters of a century ago with the pioneering work of Adolf Schultz, primatologists have shown a sustained interest in the skeletal developmental correlates of primate life-history variation and their implications for understanding the evolution of life history. More recently, the fossil record has been the direct focus of such comparative work.[1–6] Most fossil studies to date, constrained by the fragmentary nature of the fossil record and the difficulty in obtaining an adequate growth series even for extant species, are based on limited cross-sectional samples. However, because teeth preserve a permanent record of their development, dental microstructural analysis allows researchers to retrieve longitudinal developmental data from single adult specimens. Such work has proven useful for exploring life histories of extinct species. It also promises to revolutionize our understanding of some aspects of the life histories of extant species.[7–11]

We have begun to apply these tools of analysis to extinct lemurs.[12–16] Dental microstructural data are now available for members of three families: the Palaeopropithecidae (*Palaeopropithecus ingens*), Archaeolemuridae (especially *Archaeolemur majori*), and Megaladapidae (*Megaladapis edwardsi*). We have also examined other attributes of their enamel crowns, including relative enamel thickness and the degree of enamel prism decussation, both possible indicators of crack resistance and correlates of diet. By combining analysis of single individuals with analysis of growth and dental wear across ontogenetic series, we have been able to address questions never before asked of extinct lemurs or, indeed, most extinct primates: How rapidly did their molar crowns form? How dentally precocious were they at birth? At what age did their first permanent molars erupt? At what age did weaning likely occur? How long was gestation? We have also begun to chronicle the relationships among crown formation time (CFT), adult brain size, and adult body size in extinct lemurs and other primates, and to test current hypotheses regarding the evolution of life history in one of the world's most unusual adaptive radiations.[14]

LIFE-HISTORY RECONSTRUCTION IN EXTINCT SPECIES: TOOLS OF ANALYSIS

To build a chronology of dental developmental "events" from which life-history profiles can be inferred, one must document the position and timing of accentuated lines in the enamel and dentine for each analyzed tooth. These lines usually correspond to "stressful events." They are simultaneously recorded in all developing teeth and therefore can be used to register the relative degree of crown and root formation in each tooth at the moment the stressful event occurred. This technique yields a dental chronology for each specimen, and can be used to assess age at death of dentally immature individuals.[12,14,17–19] Death is taken to have occurred at the time development was terminated, as indicated by the last-formed portion of tooth crown or root. Age-at-death es-

[1]Department of Anthropology, 240 Hicks Way, University of Massachusetts, Amherst, MA 01003
[2]Institute for Human Origins, School of Human Evolution and Social Change, Arizona State University, Tempe, AZ 85287-2402
[3]Redpath Museum, McGill University, 859 Sherbrooke St. West, Montreal, Quebec, H3A 2K6 Canada
[4]Department of Anatomical Sciences, School of Medicine, Stony Brook University, Stony Brook, NY 11974
Laurie Godfrey and William Jungers have studied Madagascar's extinct lemurs for over three decades and have conducted paleontological fieldwork with Elwyn Simons and David Burney. Gary Schwartz studies the incremental nature of dental tissue formation in extant and extinct Primates. Karen Samonds studies the origin and evolutionary history of Madagascar's modern fauna, especially bats. Kierstin Catlett is a doctoral student at Arizona State University interested in comparative primate root development.
Email addresses: lgodfrey@anthro.umass.edu (Laurie R. Godfrey), garys.iho@asu.edu (Gary T. Schwartz), Karen.Samonds@mail.mcgill.ca. (Karen E. Samonds), william.jungers@sunysb.edu (William L. Jungers), and Kierstin.Catlett@asu.edu (Kierstin K. Catlett).

Key words: dental microstructure, subfossil lemurs, life history

DOI 10.1002/evan.20102

timates generated in this manner provide a measure of "age for stage"; that is, the pattern, sequence, and amount of tooth crown and root formation achieved at a particular age.

Dental developmental chronologies can be used to compare the degrees of molar crown formation of different taxa at different life-history events such as birth or weaning. For example, the position of the neonatal line, the prominent incremental feature that coincides with birth,[19–21] can be used to calculate the proportional amounts of tooth crown formed prenatally and postnatally, and to assess dental precocity at birth. The time of emergence of the first molar (M1) is of special interest, given its purported correlation with other life-history variables.[22] The best way to obtain age at M1 emergence in extinct lemurs is to target immature individuals with M1 erupting or just erupted and relatively unworn. Lacking that, and assuming we can identify a neonatal line on M1, we can use postnatal CFT plus information on root extension rates and the amount of root present at emergence to estimate age at M1 gingival eruption. Postnatal ages at crown completion, coupled with estimates for root extension, can be used to estimate emergence ages for second and third molars as well.

Minimum gestation length can also be determined from the dental chronologies of fossil taxa if they have a high percentage of M1 crown formation occurring prenatally. If it is assumed that calcification of the permanent M1 cannot begin before the end of the first trimester, the normal transition from embryological to fetal growth phase, then the duration of prenatal M1 CFT as determined by the position of the neonatal line provides a minimum value for gestation length. More compelling estimates of gestation length in a fossil taxon can be made using gestation lengths for that taxon's closest living relatives, coupled with knowledge of exactly when, within those gestation periods, M1 crown mineralization begins. In anthropoid primates, mineralization of the permanent M1 crown normally begins late in the third trimester; in living lemurs, it can begin much earlier.

The teeth provide clues to dietary proclivity, which in turn may correlate with life-history variation. Two such indicators are relative enamel thickness (RET) and the degree of enamel prism decussation. RET is a dimensionless index commonly used to compare enamel thickness across taxa that differ in tooth size. It is calculated using the formula $([c/e]/\sqrt{b}) * 100$, where "c" is the enamel cap cross-sectional area (or area of enamel exposed in the section), "e" is the length of the enamel-dentine junction (EDJ) in the exposed section, and "b" is the exposed dentine area. Relatively thicker enamel increases the functional longevity of teeth. Species subjecting their teeth to high occlusal loads resulting from hard food trituration should possess thicker enamel than species with softer diets.

Enamel prism decussation, the 3-dimensional undulation of enamel prisms in and out of the plane of section as they make their way from the EDJ toward the future enamel surface,[23–26] is difficult to quantify. It can vary qualitatively in terms of the presence and morphology of Hunter-Schreger bands, the optical manifestations of enamel prisms undulating and crossing over one another; it can also vary regionally across both cuspal and imbricational enamel. Heavy decussation is thought to enhance structural resistance to crack propagation.[27] Animals subsisting on harder, coarser diets exhibit a greater degree of decussation, particularly in the cuspal portions of their crowns.[27] As yet, no means of quantifying the precise degree of decussation exists, but broad levels of decussation (heavy, moderate, and slight) are easily recognizable and are used here to characterize a sample of primate molars. Heavy decussation is a high degree of enamel prism undulation throughout the full thickness of enamel. Decussation is only moderate if prism undulation is not severe and occurs only throughout one-half of the thickness of enamel. Slight decussation occurs when the enamel primarily comprises radial prisms running fairly straight from the EDJ to the outer enamel surface or decussates marginally close to the EDJ.

THE CASE OF THE SUBFOSSIL LEMURS

The results reported here depend largely on chronologies developed for three individuals: *Palaeopropithecus ingens* (UA AM-PPH1) from Ankazoabo Grotte in Southwest Madagascar; *Megaladapis edwardsi* (UA 4620/AM 6567) from Beloha Anavoha in Southwest Madagascar; and *Archaeolemur majori* (uncatalogued hemi-mandible) from Taolambiby, Southwest Madagascar.

The *Palaeopropithecus* specimen is a cranium of a juvenile individual, originally figured by Lamberton in 1938.[28] All but two of the permanent teeth were fully erupted at the time of death; the exceptions are the canine, which is in its crypt, and the M^3, which is nearly fully erupted. The deciduous canines are missing, but small alveoli located just mesial to the buccal edge of P^3 bear testimony to their former presence. Lingual to each is the gubernacular canal accommodating the tip of the permanent canine. The apices of the roots of P^4, M^1, and M^2 are closed, and M^3 has substantial root development. All three maxillary molars of this immature individual were sectioned. Aspects of the chronology derived from those sections have been published.[12,13] Additional details are provided here.

The *Megaladapis* specimen comprises a partial mandible with dp_4 and M_1 fully erupted and M_2 unerupted. The first and second molars of this individual have been sectioned and their chronology has been reported.[14] The *Archaeolemur* specimen is a mandible with full adult dentition; it was figured by its discoverer[29] and aspects of its molar microstructure have been described.[15] All three molars have now been sectioned. The full chronology is reported here for the first time.

Limited microstructural data were also collected for the extinct lemur, *Hadropithecus stenognathus,* on the basis of an isolated second molar recovered in 2003 at Andrahomana Cave in Southeast Madagascar by David Burney and his co-workers.[15] Comparative microstructural data on extant lemurs were collected for molars (M1–3) of *Propithecus verreauxi* (BMOC #88), *Lemur catta* (DPC 6530F), and *Varecia variegata* (DPC

TABLE 1. CROWN FORMATION TIME, IN DAYS, IN EXTINCT LEMURS AND OTHER PRIMATES

Taxon	M1 CFT	M2 CFT	M3 CFT	Sources (reference numbers)
Palaeopropithecus ingens	221	246	133	12, 13
Megaladapis edwardsi	380	517	(No data)	14, 16
Archaeolemur majori	522	460	408	15
Pongo pygmaeus	993	1267	(No data)	17
Pan troglodytes	1004	1333	(No data)	16, 19
Gorilla gorilla	1237	>1200	(No data)	Schwartz, Dean, & Reid, unpublished
Papio hamadryas	529	559	715	31
Papio cynocephalus	642	555	708	10

5870F). Comparative microstructural data for anthropoids were taken from the literature or personal observations (GTS), as indicated. It goes without saying that data on CFT are sparse, not merely for extinct primate species but also for most extant ones, and that intraspecific variance in CFT is poorly understood. It is only with this caveat made explicit that we take our measured values of CFT in single individuals as "representative" for the taxa in question.

Molar Crown Formation Time in Subfossil Lemurs

Table 1 shows molar CFTs for three species of extinct lemur and several selected anthropoids (roughly comparable in body mass to our extinct lemur taxa).[30] Table 2 compares their molar dimensions. At ca. 40–50 kg, *Palaeopropithecus ingens* was slightly heavier than the largest female *Pongo pygmaeus,* but had considerably larger first and second molars. At ca. 80–90 kg, *Megaladapis edwardsi* approximated the mass of adult female *Gorilla gorilla;* its first molars were somewhat larger than those of female gorillas and its second and third molars were substantially so. At ca. 15–20 kg, *Archaeolemur majori* roughly matched the body mass of some adult male baboons, but had slightly smaller first and second molars and considerably smaller third molars. Figure 1 displays our data on the molar crown developmental chronologies for extinct lemurs and for *Papio,* the anthropoid in our comparative database with the least protracted dental developmental chronology.

Crown formation time tends to vary intraspecifically but not interspecifically with molar size. Thus, CFT is roughly equal for the like-sized M1 and M2 in both *Palaeopropithecus* and *Archaeolemur,* and far longer in the much larger M_2 than M_1 of *Megaladapis.* But M1 CFT is much shorter in *Palaeopropithecus* (221 days) and *Megaladapis* (380 days) than in the much smaller-toothed *Archaeolemur* (522 days). Our only datum for the 30–35 kg archaeolemurid, *Hadropithecus stenognathus,* reveals an extremely long M^2 CFT (2.59 years or 945 days).[15] This is close to recorded M2 CFTs in *Pan troglodytes* and *Pongo pygmaeus.* M1 CFT is roughly similar in *Archaeolemur* and *Papio.* For all other giant lemur molars examined thus far, CFTs are much shorter than in like-sized anthropoids, regardless of molar size.

Age at Death of Immature Individuals, with Implications for the Pace of Dental Development

Box 1 illustrates how, by constructing a complete chronology, including root formation, for M_1 and M_2, we determined the age at death, to the day, of our immature *Megaladapis edwardsi.* M_2 was crown complete 442 days after birth. The individual died 66 days later (at 508 days, or 17 months, after presumptive birth), with its M_2 root partially developed but its M_2 crown unerupted. The M_1 CFT is 380 days and the first molar was crown-complete at 248 days after birth. In contrast, M_1 of a recently analyzed female gorilla was crown-complete at 1,212 days (3.3 years) af-

TABLE 2. MAXILLARY AND MANDIBULAR MOLAR MESIODISTAL AND BUCCOLINGUAL DIMENSIONS (MM) IN EXTINCT LEMURS AND LIKE-SIZED ANTHROPOID PRIMATES; MEAN IN MM (STANDARD DEVIATION)[a]

Taxon	Jaw	M1 md/bl	M2 md/bl	M3 md/bl
Palaeopropithecus ingens	Upper	17.9 (0.7)/13.7 (1.1)	17.7 (0.9)/13.5 (1.3)	9.1 (0.5)/8.8 (0.5)
Palaeopropithecus ingens	Lower	18.0 (1.0)/10.3 (1.1)	17.0 (0.9)/9.5 (.7)	14.0 (0.8)/8.7 (0.7)
Pongo pygmaeus, female	Upper	11.9 (0.8)/12.2 (0.9)	12.1 (0.8)/12.9 (1.1)	11.5 (0.5)/12.6 (0.4)
Pongo pygmaeus, female	Lower	11.4 (2.7)/11.3 (0.6)	13.3 (0.6)/12.1 (0.7)	12.9 (.8)/11.8 (0.6)
Megaladapis edwardsi	Upper	18.2 (1.0)/16.1 (0.6)	23.0 (1.1)/20.6 (0.8)	25.9 (1.4)/21.7 (1.0)
Megaladapis edwardsi	Lower	17.2 (0.6)/12.0 (0.6)	22.0 (0.9)/14.7 (0.8)	34.8 (1.5)/15.8 (0.8)
Gorilla gorilla, female	Upper	14.8 (0.9)/15.0 (1.1)	16.0 (0.9)/15.8 (0.8)	14.6 (0.7)/14.5 (1.2)
Gorilla gorilla, female	Lower	15.4 (0.8)/13.2 (0.6)	17.0 (0.9)/15.1 (0.8)	15.6 (0.6)/14.4 (0.6)
Archaeolemur majori	Upper	7.8 (0.5)/9.6 (0.6)	6.8 (0.5)/8.6 (0.6)	5.8 (0.4)/7.0 (0.5)
Archaeolemur majori	Lower	8.0 (0.5)/8.1 (0.6)	7.6 (0.5)/8.0 (0.5)	6.6 (0.4)/7.1 (0.5)
Papio cynocephalus, female	Upper	10.3 (0.3)/9.3 (0.4)	11.7 (0.4)/10.9 (0.6)	11.8 (0.6)/11.2 (1.0)
Papio cynocephalus, female	Lower	10.1 (0.4)/8.1 (0.4)	11.6 (0.5)/9.5 (0.5)	14.3 (0.8)/10.2 (0.5)

[a] Molar dimensions for extinct lemurs were collected by Godfrey; molar dimensions for anthropoids (means for samples of females) are taken from Swindler.[32]

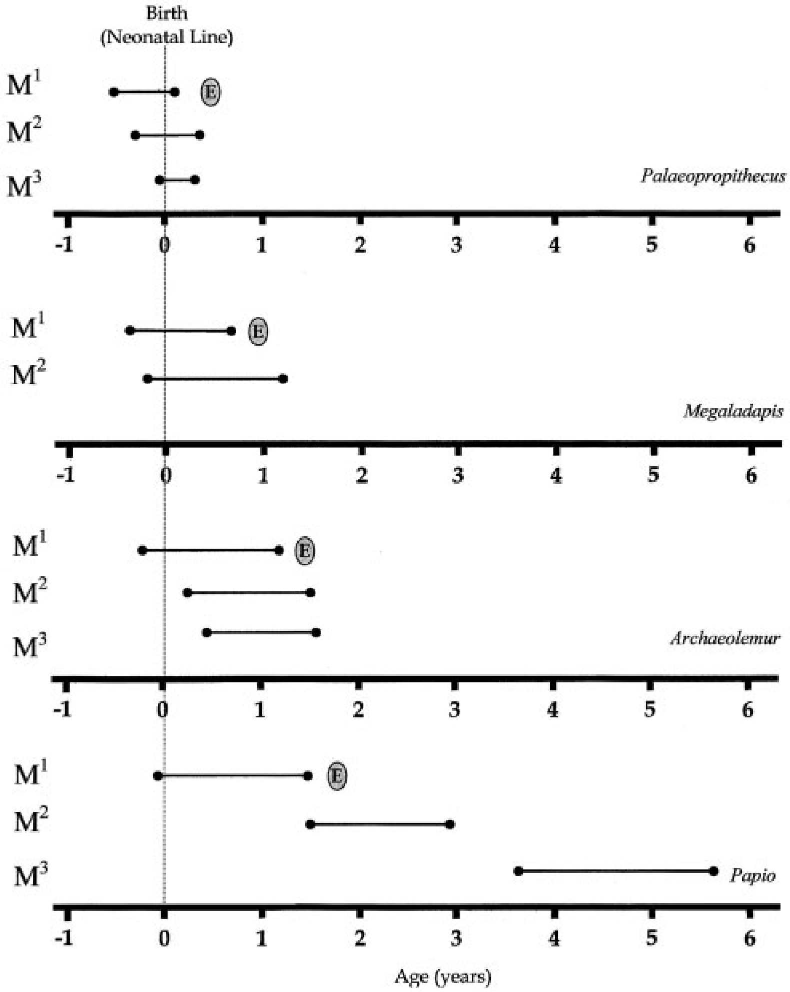


Figure 1. Molar crown chronologies for *Palaeopropithecus, Megaladapis, Archaeolemur,* and *Papio.* The M_1 CFT of *Archaeolemur* resembles that of *Papio;* both *Palaeopropithecus* and *Megaladapis* have shorter M_1 CFTs.

ter birth, and her total M_1 CFT was 1,237 days. The contrast in dental developmental between *Megaladapis* and *Gorilla* is striking.[16]

Whereas we cannot directly measure age at death for the other subfossils in our database, we can assess the ages at which their third molars reached crown completion (Table 1). For *Palaeopropithecus ingens,* this was an astounding 135 days (4.2 months) after birth. For *Archaeolemur majori,* it was 576 days (1.6 years) after birth. For *Palaeopropithecus,* the third molar is one of the last teeth to erupt, with only the upper canine and perhaps the anterior-most upper premolar erupting later. In *Archaeolemur,* several replacement teeth erupt after the third molar, including some premolars and incisors, as well as the upper canine, depending on the species. It is clear that there was tremendous variation within the giant lemurs in age at dental maturity.

Dental Developmental Stage at Birth

Table 3 shows prenatal crown formation and the state of molar development at birth for our three extinct species, with comparative data for both extant lemurs and selected anthropoids. Both the timing of crown initiation and overall CFT contribute to making crown completion relatively early in *Palaeopropithecus* and relatively late in *Archaeolemur.* In *Palaeopropithecus,* M^1 CFT is short (7 months total) and M^1 initiates the earliest (6 months before birth), so that M^1 is crown-complete at a very young age. In *Megaladapis,* M_1 has a longer CFT (12.5 months) and initiates 4.5 months before birth. In *Archaeolemur,* M1 CFT is longer yet (17 months), and it initiates less than 3 months prior to birth. Of these three taxa, *Archaeolemur* is the last to complete M1 crown formation. Also, there is an apparent phylogenetic signal, with *Palaeopropithecus* exhibiting a pattern common in indriids, wherein all three molars initiate crown formation before birth, and contrasting with that of the more distantly related Archaeolemuridae.

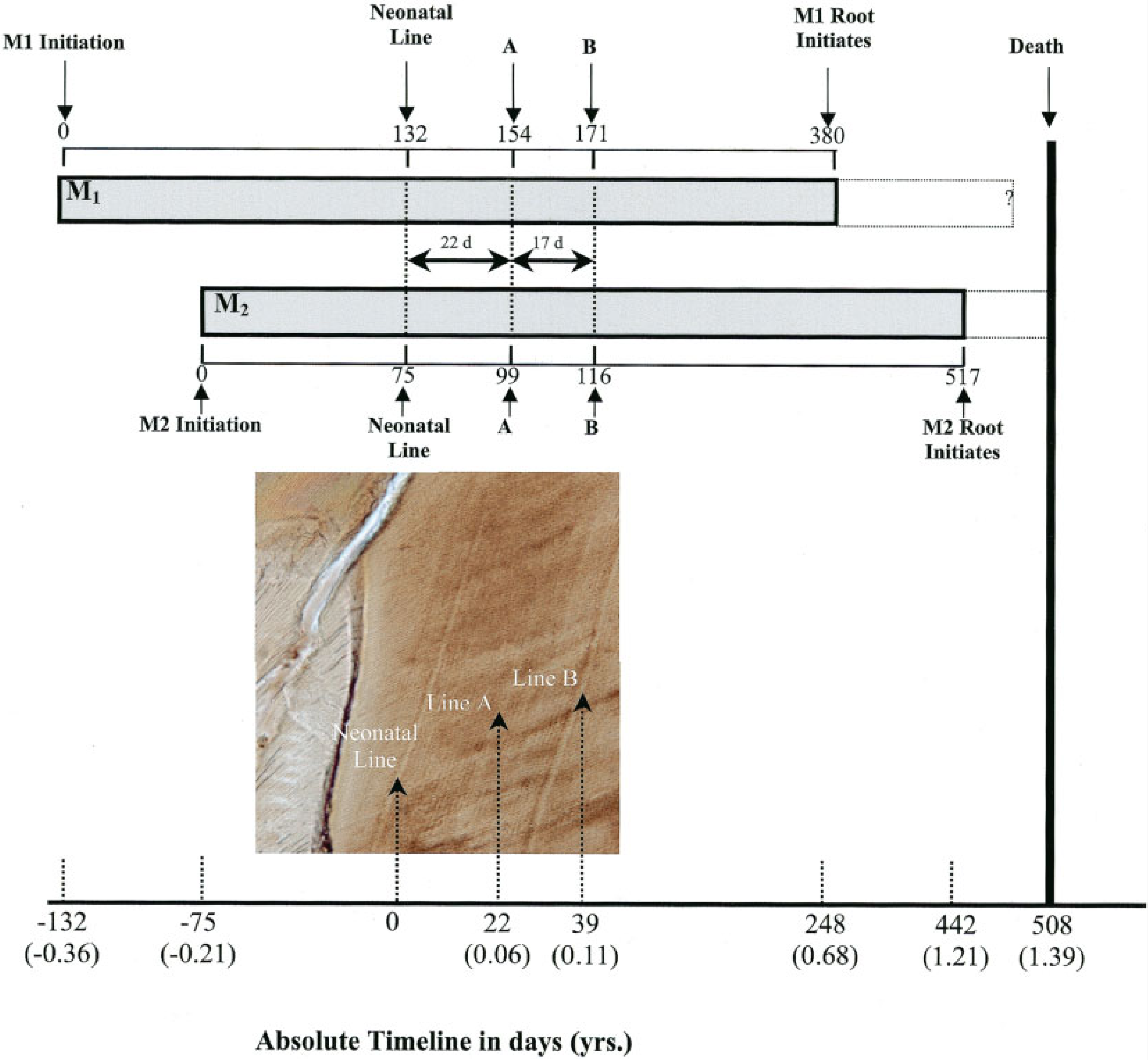
Age at Molar Crown Completion and M1 Gingival Eruption

Table 4 provides age at M1 crown completion and estimates for the age at M1 gingival emergence for each of the three extinct lemurs. Gingival emergence, the initial appearance of the occlusal surface as it passes through the gumline,[35] occurs after crown completion but before the roots are fully formed. Roots continue to form during eruption and, indeed, after the teeth have attained full occlusion, as the jaws continue to grow in height or depth.

Data on ages at M1 crown completion and gingival emergence in anthropoids reveal a lag of between five months and a year.[35] Preliminary data for lemurs suggest a shorter lag, associated with extremely rapid root extension rates (Box 2). In extant lemurs, gingival emergence often occurs within a month of crown completion. Cusps initiate and finish at different times, as do their corresponding roots; therefore, roots associated with cusps that complete first will begin to form before the very last portion of crown is formed. The overlap can be great. In *Propithecus verreauxi,* for example, M_1 root formation begins only a few weeks after birth. M^1 root formation initiates several weeks later, but the first molar crowns are not fully formed until ca. 3 months.[14] M_1 begins erupting shortly thereafter, certainly by 4 months, when the mandibular corpus height is only slightly greater than half its total

Box 1. Mapping Out Growth

G.T. Schwartz



Box 1 Figure.

Life-history reconstruction for extinct species depends on our ability to decipher when teeth initiate their formation, how long they take to complete their crowns and roots, and when they emerge into the oral cavity. Building dental developmental chronologies allows us to answer questions such as: Did permanent teeth begin their formation *in utero?* At what age do particular teeth, such as the M1, erupt? And how much root is present at the time of eruption?

Using incremental growth lines, both short- and long-period, in enamel and dentine, we can readily pinpoint when crowns initiate and complete formation. To chart the chronology of molar development, for example, one must know when each molar initiated and completed its crown formation relative to the timing for each other molar; that is, it is necessary to register all developing crowns to one another. Doing so requires the use of a special class of incremental features, accentuated lines.

Box 1. Mapping Out Growth (continued)

The etiology of the striae of Retzius is largely unknown. Superimposed on these striae are lines that appear more marked under transmitted polarized light. These can be coincident with striae, but often occur between successive Retzius lines. The etiology of accentuated lines is even less clear; however, we do know that these lines chart the temporal position of stressful episodes.[33] Any single "stressful" event, which may be nutritional, physiological, or even psychological,[34] will affect the cells of all developing teeth and will therefore mark the same moment in time. To build a precise chronology requires cross-matching accentuated striae that correspond to the same "stressful" event across all of the developing teeth. One special kind of accentuated line, the neonatal line, allows us to root that chronology to day 0 in the life of that individual; that is, to the day of birth. In the figure, we provide an example of this technique using the developing dentition of the giant subfossil lemur *Megaladapis edwardsi.*

Incremental lines in enamel (daily cross striations and striae of Retzius) were used to determine the time of initiation and completion for the M_1 and M_2 of a juvenile specimen of *M. edwardsi,*[14] indicated by the two horizontal gray bars in the figure. At the termination of crown formation, root development begins (open horizontal box). The absolute timeline on the bottom reveals total crown formation times of 380 days and 517 days for M_1 and M_2, respectively. But at what point during M_1 development did M_2 initiate? To answer that, we found a set of three accentuated lines, one of which is the neonatal line. We determined that these same three lines, labeled Neonatal Line, Line A, and Line B, appear in both molars by counting the number of daily lines between each. The first line, the Neonatal Line, occurred 22 days before the second line, Line A, which occurred 17 days before the third line, Line B, in both molars. The position of these lines relative to the first- and last-formed enamel for each molar enabled us to determine the total amounts of prenatal and postnatal molar development, and thus to derive a chronology, rooted in real time, from 132 days before birth until this individual died 640 days later, at 508 days old.

adult value, and the longest roots have attained a corresponding proportion of their full adult length. Eruption itself proceeds rapidly, and individuals with fully erupted first molars (at five months in *Propithecus verreauxi*) can exhibit an advanced stage of first molar root formation (more than three quarters complete). At 8 months in *Propithecus,* all of the postcanine cheek teeth have erupted, although root formation is not complete.[38,39]

The only giant lemur for which we have directly measured root formation time is *Megaladapis edwardsi*. The roots of the M_1 in this individual are long, but their apices are not fully closed; we infer that the root was in its terminal phase of growth when this individual died. This occurred 260 days (or eight-and-a-half months) after M_1 crown completion at 248 days postnatal. Assuming a constant root extension rate and no overlap between crown and root formation, this implies an upper limit of just over 4 months for the first 50% of root formation, and thus the time between crown completion and gingival emergence, assuming a similar amount of root formation at emergence as in *Propithecus*. Bracketing this further to account for the likelihood of variable root extension rates, overlapping root and crown formation, and variable degrees of root formation at gingival eruption, we estimate M_1 gingival eruption at not less than one and not more than five months after crown completion (thus, between the ages of 9 and 13 months in *Megaladapis edwardsi;* Table 4). Here, the timing of root extension was empirically determined as part of the process of determining the age at death of this immature individual.[14] The M_2 root formed at a slower rate than did M_1. After 66 days of root formation, little root was present and the second molar was unerupted.

Given its accelerated dental development, it is not unreasonable to assume that the M^1 root extension rate for *Palaeopropithecus ingens* was at least as rapid as that of *Megaladapis edwardsi*. Using the same estimate for time from crown completion to gingival emergence, and given M^1 age at crown completion of 1.1 months after birth, we estimate M^1 gingival emergence at between the ages of 2–6 months, and probably closer to the early end of this range (Table 4). This is on a par with M^1 emergence in the much smaller-bodied *Propithecus* and considerably earlier than in like-sized anthropoids. For example, in *Pan troglodytes,* the M_1 crown is complete at 985 days (2.7 years) on average,[19] and does not erupt until ca. 3.5–4.0 years.

First-molar root extension may have been slower in *Archaeolemur majori* than in *Megaladapis*. However, it was probably faster than in like-sized baboons. M_1 crown completion oc-

TABLE 3. PRENATAL CROWN FORMATION (DAYS) IN EXTINCT AND EXTANT LEMURS AND OTHER PRIMATES[a]

Taxon	Prenatal M1 CFT	Prenatal M2 CFT	Prenatal M3 CFT
Palaeopropithecus ingens	187 days (6 months)	111 days	24 days
Megaladapis edwardsi	132 days (4.5 months)	75 days	—
Archaeolemur majori	85 days (3 months)	None	None
Propithecus verreauxi	94 days	56 days	16 days
Lemur catta	67 days	None	None
Varecia variegata	55 days	None	None
Pongo pygmaeus	24 days (<1 month)	None	None
Gorilla gorilla	25 days (<1 month)	None	None
Papio hamadyras	36 days (1 month)	None	None

[a] Sources for data are given in Table 1.

TABLE 4. ESTIMATED AGE AT M1 ERUPTION FOR EXTINCT LEMURS

Taxon	Age at M1 Crown Completion	Age at M1 Eruption[a]
Palaeopropithecus ingens	34 days (1.1 months)	~2–6 months
Megaladapis edwardsi	248 days (8.3 months)	~9–13 months
Archaeolemur majori	437 days (14.6 months)	~15–19 months

[a] Estimated as age at M1 crown completion plus 1–5 months.

curs in the *Archaeolemur majori* individual at 437 days (14.6 months) after birth. It occurs in like-sized baboons about two months later; for example, 493 days, 511 days. In baboons, the first molar erupts at around 20 months.[35] We project a slightly earlier eruption in *Archaeolemur* (Table 4). Whereas age at M_1 emergence is similar in the two, the whole dental eruption chronology was certainly less protracted in *Archaeolemur* than in *Papio,* given that M_3 is crown-complete in the former at 19 months, but not until 5.71 years in *Papio.*[31] Nevertheless, the contrast is not as strong here as it is between other giant lemur species and like-sized anthropoids. At least for M1 emergence, the difference between *Archaeolemur* and baboons appears to have been minimal.

Given the rapidity of root formation in extant lemurs for which we have data, it is reasonable to assume that gingival emergence occurs within a few months of crown completion, and that age at gingival emergence is correlated with age at crown completion. It follows that, in comparison to like-sized anthropoids, giant lemurs exhibited relatively early gingival emergence, and that this was particularly the case for *Palaeopropithecus* and *Megaladapis,* the largest-bodied of extinct lemurs in our sample.

Age at Weaning, Juvenile Foraging, and Acquisition of Adult Diet

There is no simple way to infer age at weaning in extinct species. Smith[22] noted a correlation among Primates between age at weaning and age at M1 eruption. This relationship holds poorly, however, for lemurs.[38,39] There may be a trace element or isotopic signal of weaning,[40–44] but research along these lines for subfossil lemurs is very preliminary.

Another strategy is to examine tooth wear across ontogenetic series. Flanagan[15,45] examined microwear under low magnification for ontogenetic series of *Macaca fascicularis* and *Archaeolemur* spp. For *Macaca fascicularis,* she could map life-history landmarks such as weaning and sexual maturation on the microwear ontogeny, as the schedule for dental eruption is well known for this species. Flanagan observed an increase in pit and scratch counts per unit area from early to later infancy, leveling off after M1 comes into occlusion. This is followed by a prolonged period during which feature counts remain relatively stable. This is apparently a post-weaning juvenile foraging phase. Microwear feature counts do not increase until around sexual maturation, at which time adult values for their range and frequencies are manifested. Interestingly, *Archaeolemur* shows the same pattern, including a prolonged phase before dental adulthood during which scratch counts, particularly hypercoarse scratch counts, remain relatively low.[15] Microwear feature counts and variabilities are higher for individuals with full adult dentitions than for dentally immature individuals. Nevertheless, whereas *Archaeolemur* youngsters with only M1 erupted do not exhibit a full adult signal for scratches and pits, they do show moderately high frequencies of both. It may be reasonable to assume that weaning occurred in *Archaeolemur,* as in macaques, at around the age of M1 eruption at ca. 15–19 months, and that youngsters experienced a prolonged period thereafter during which they slowly acquired full adult foraging skills.

In contrast, in *Megaladapis,* by the time M1 comes into full occlusion and begins to wear, which certainly is before 17 months and likely before 13 months of age, the microwear signal cannot be distinguished from that of full adults. This suggests an earlier age for acquisition of adult foraging skills.[16] We project an even earlier age for acquisition of adult foraging skills in *Palaeopropithecus* on the basis of its extremely rapid dental development. As in *Propithecus,* it is likely that *Palaeopropithecus* was dentally precocious at weaning and, shortly thereafter, was handling tough, fibrous foods. Half-year old *Propithecus* have full permanent teeth and are weaned; weaning generally begins at between 4 and 5 months. New weanlings may subsist largely on young leaves and other foods that are available during the season of plenty, but the full adult repertoire is acquired within a few months, during the season of scarce resources.

In summary, relatively early weaning can be inferred for larger-bodied species, even if we assume that weaning did not occur until after youngsters had erupted many of their permanent teeth. There is evidence of prolonged acquisition of adult foraging skills in *Archaeolemur* and of rapid acquisition of adult foraging skills in *Megaladapis* and especially *Palaeopropithecus.*

Brain Growth in Giant Lemurs

With some reconstruction of the posterior portion of the neurocranium, we were able to estimate the cranial capacity of our immature *Palaeopropithecus ingens* at 65–70 cc. Full adult *Palaeopropithecus ingens* average a capacity of 101 cc. There is little question that individuals at the stage of dental development represented by the *Palaeopropithecus* individual described here, which has full adult dentition except the upper canine, would have been weaned. Cranial capacity at weaning was perhaps well under 65% of the adult value.

We also measured the cranial capacity of an immature *Megaladapis edwardsi* (AM-MGH2/UA 5491) at a dental developmental stage slightly more advanced than that of the 17-month old individual from which we derived our dental developmental chronology (Fig. 2). At death, AM-MGH2 had an erupting M^2; in all other features (fully erupted M^1, unreplaced deciduous teeth) the dental development of the two was comparable. The mea-

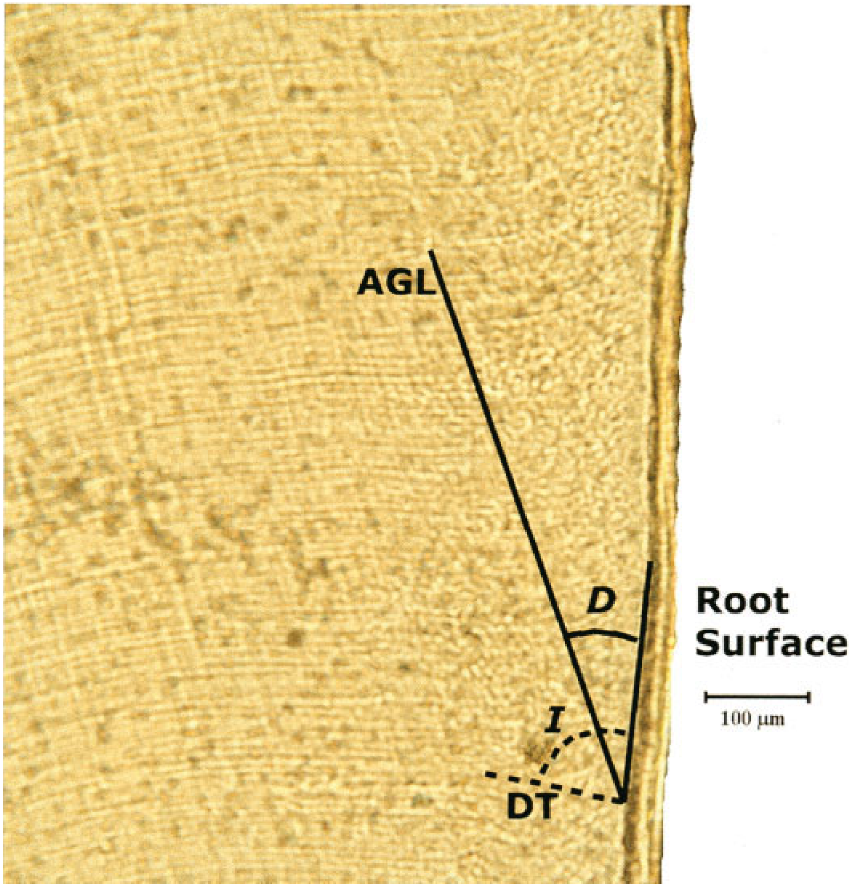
Box 2. Getting to the Root of the Matter

K.K. Catlett and K.E. Samonds

Whereas recent histological research on molar crown formation times has greatly aided reconstructions of extinct lemur life histories, these studies have largely ignored the incremental data preserved within developing roots. Long and short incremental lines preserved in dentine enable researchers to reconstruct the timing and sequence of root development, just as similar lines preserved in enamel allow the reconstruction of crown development. Because root extension continues well after crown completion, the daily incremental lines preserved in roots allow the interpolation of aspects of growth that occur during eruption and even much later in an individual's life. Roots also provide researchers with increased opportunities to correlate "events" histologically recorded in different teeth, which is crucial for constructing comprehensive dental chronologies. We have begun to use such histological techniques, along with dissection and radiographic analysis, to expand our knowledge of lemur development.

Shellis[36] developed a geometric formula, $c = d[(\sin I/\tan D) - \cos I)]$, using the cell secretion rate (d) and prism direction to calculate the extension rate, c, of imbricational enamel. The similar nature of enamel and dentine secretion makes Shellis' equation also appropriate for estimating root extension rates (RERs) for any length of root.[18] To determine d, the daily dentine secretion rates (DSRs), one must take several measurements across long-period dentine lines and divide by the periodicity.

Using these techniques, we calculated the average RER for the M_1 in a *Propithecus verreauxi* (BMOC #88) to be approximately 29.8 μm/day with an average DSR of 3.0 μm/day. These rates suggest that approximately 175 days were required to grow 4.8 mm of measurable root. The calculated M1 RERs for both extant and extinct anthropoid species (other than humans) range from 5.20 μm/day in *Hylobates lar*[37] to 19.40 μm/day in *Proconsul.*[18] Regardless of body size, it is clear that *Propithecus* has not only accelerated enamel development,[14] but also extremely rapid root development.



Box 2 Figure. Image of *Hadropithecus stenognathus* RM^2 illustrating variables used to obtain RERs (see text). Angle I (dotted line) is formed between the developing root surface and a dentine tubule (DT) where they intersect an accentuated growth line (AGL). Angle D (solid line) formed by the intersection of AGL with the root surface.

We also devised a scoring technique to compare measurements from radiographs and from extracted teeth of the same individuals to attain stages of root formation for an ontogenetic series of known-aged specimens. The stages correspond to percentages of developing root lengths calculated against adult root lengths, determined by direct measurement of extracted teeth. Using this technique, we scored mandibular molars for a series of *Varecia variegata* and *Propithecus verreauxi* ranging from newborn individuals to dental adults. Results indicate that in *Propithecus,* M_1 roots reach 29% of adult root length at only 2.5 months of age, while *Varecia* requires an additional 100 days to reach a comparable stage of M_1 root development. In *Propithecus,* M_1 gingival emergence, estimated to occur at ~3–4 months, closely follows the initiation of M_1 root formation. The amount of root formation at M_1 alveolar emergence is relatively consistent between species, with mesial roots at ~35% of adult length and distal roots at ~45% of adult length by the time M_1 has started to cross the alveolar plane.

These results suggest that charting root extension rates and formation times will enhance our ability to glean dental developmental information from an individual's entire dentition. Histological research on root dentine provides longitudinal data that can assist in refining our understanding of the amount of daily root growth, information not captured in radiographs from a cross-sectional sample. Such analyses will enable us to compare the pace of lemur and similarly sized anthropoid tooth root development to determine how much root is present at the time of eruption and how much time is required for lemur tooth roots to achieve apical closure.

Figure 2. Specimens of *Megaladapis edwardsi* used in analysis of dental microstructure and endocranial growth. A. Buccal view of the left hemi-mandible of a juvenile specimen (UA 4620/AM 6567) illustrating the erupted dp_4 and M_1, and the M_2 in crypt. B. Buccal view of the unerupted M_2 after removal from the crypt. The arrow points to the few millimeters of initial root formation. C. Lingual view of hemi-mandible showing dp_4 and M_1. D. Cranium of *Megaladapis edwardsi* (AM-MGH2). Scale bar = 10 cm.

sured cranial capacity, 90 cc, was ca. 65% of the adult value of 137 cc for *Megaladapis edwardsi*. If we are correct in inferring that individuals at this stage of dental development had been weaned, this implies a small cranial capacity for *Megaladapis edwardsi* at weaning as well.

Both *Palaeopropithecus* and *Megaladapis* bear testimony to a phenomenon that is not manifested in anthropoids: relatively slow acquisition of adult cranial capacity with respect to dental development and weaning. Typically among anthropoids, cranial capacity is at 90%–95% of the adult value at weaning.[46–51] Clearly, this was not the case for *Palaeopropithecus* or *Megaladapis*.

To better understand this phenomenon, we collected cranial capacity growth trajectories for living strepsirrhines. Between 4 and 6 months, the cranial capacities of *Propithecus* increase from 65% to 75% of their adult value. This is far less than the 90%–95% of adult cranial capacity typical of anthropoid weanlings. This phenomenon in sifakas is part of the "fast teeth-slow growth" pattern described by Godfrey and colleagues,[39] and was evidently shared, to varying degrees, by *Palaeopropithecus* and *Megaladapis*.

In contrast, *Varecia variegata* attains 65% of adult cranial capacity at less than 3 months. At 6 months, after weaning but before any permanent teeth, including M1, have erupted, its brain measures ~95% of the adult value. *Varecia* weanlings may not have 90% of their adult cranial capacity quite yet, but their brain growth trajectory is well ahead of their dental developmental trajectory. In other words, *Varecia* exhibits, in stark contrast to *Propithecus,* slow teeth-fast growth.

Preliminary data for *Archaeolemur* suggest a pattern more similar to that of *Varecia* than *Propithecus*. This matches expectations derived from studies of other aspects of craniofacial growth.[5,6] *Archaeolemur* exhibits a relatively rapid pace of craniofacial growth when benchmarked against dental development. Thus, it appears that *Megaladapis* and especially *Paleopropithecus,* giant lemurs with relatively rapid dental development, experienced relatively slow brain growth, while the opposite applied to species with relatively slow dental development such as *Archaeolemur*. It also is interesting to note that the archaeolemurids are the only larger-bodied lemurs that even approach anthropoid-like brain-body relationships.[14] *Palaeopropithecus* and *Megaladapis* have very small brains for their adult body size.

Gestation Length

Schwartz and colleagues[12] used the position of the neonatal line, and thus the inferred time *in utero* that M1 began forming, to estimate gestation length for *Palaeopropithecus ingens*. Their estimate of over 9 months must be regarded as a theoretical minimum; it is based on the assumption that no part of M1 crown formation can occur during the embryonic phase of gestation—essentially the first third. Table 5 shows estimates of gestation length for *Megaladapis, Archaeolemur,* and *Palaeopropithecus,* using this theoretical minimum method as well as models based on extant-lemur analogs. For example, a model based on *Propithecus verreauxi*

TABLE 5. RECONSTRUCTING GESTATION LENGTH, IN DAYS, IN EXTINCT LEMURS

Taxon	Prenatal M1 CFT	Minimum Model	*Propithecus* Model	*Varecia* Model	*Lemur* Model
Palaeopropithecus ingens	187	279	317	346	381
Megaladapis edwardsi	132	197	224	244	269
Archaeolemur majori	85	127	144	157	173

TABLE 6. MACRO- AND MICROSTRUCTURAL INDICATORS OF TROPHIC ADAPTATIONS IN EXTINCT LEMURS AND OTHER PRIMATES

Taxon	Cuspal Decussation[a]	Imbricational Decussation[a]	R.E.T. (Means and Range, When Available)[b]
Varecia variegata	1	1	5.7
Lemur catta	1	1	7.3 (6.7–8.1)
Gorilla gorilla	1	1	10.0 (6.8–13.4)
Pan troglodytes	1	1	10.1 (7.0–13.3)
Propithecus verreauxi	1	1	10.7
Palaeopropithecus ingens	1	1	11.3
Megaladapis edwardsi	1	1	13.7 (10.6–16.0)
Papio cynocephalus	1	1	15.4 (12.4–18.6)
Pongo pygmaeus	1–2	1	15.9 (11.3–20.5)
Hadropithecus stenognathus	2	1	14.4 (13.9–15.2)
Cebus apella	2	2	19.2
Archaeolemur majori	3	3	28.3 (24.9–35.2)
Archaeolemur sp. cf. *edwardsi*	3	3	30.6 (25.7–35.2)
Paranthropus boisei	3	3	34.9 (31.0–38.6)

[a] Decussation 1 = slight or none, 2 = moderate, 3 = heavy

[b] Relative enamel thickness: $((c/e)/\sqrt{\ }\, b) * 100$. See text for explanation. RET data for *Palaeopropithecus, Archaeolemur,* and *Hadropithecus* are taken from Godfrey and coworkers.[15] Data for *Megaladapis* are new, and are combined for M^1 and M^2. All other data are taken from references Schwartz, Liu, and Zheng[56] and Smith, Martin, and Leakey[57] and are means based on RET values for M1–M3. Recent work[68] documents metameric variation in enamel thickness in hominoids. However, these differences are trivial in comparison to the variation in subfossil and extant strepsirrhines.

begins with the observation that gestation averages 158 days in this species[38,52] and that molar crown formation begins ~94 days prior to birth (our data for BMOC #088, *Propithecus verreauxi* from Beza Mahafaly). A *Propithecus* model assumes that M1 crown formation occupies the same proportion of overall gestation in the extinct taxon as it does in *Propithecus.* This proportion is calculated as the observed prenatal crown formation time divided by the observed gestation length (in *Propithecus,* 94/158 = 0.59). To calculate the estimated gestation time in the extinct species, the observed prenatal CFT is divided by this ratio; for example, for *Palaeopropithecus ingens,* 187 days/0.59 = 317 days or, 10.5 months. Gestation lengths in extant lemurids are much shorter than in *Propithecus,* ca. 102–136 days for the largest-bodied lemurids.[53–55] Also, the proportion of the gestation period during which M1s are developing is smaller. A *Varecia* model (gestation length of 102 days and prenatal crown formation time of 55 days) yields a ratio of 0.54; a *Lemur catta* model (gestation length of 136 days and a prenatal crown formation time of 67 days) yields a ratio of 0.49.

M1 crown formation time in *Palaeopropithecus ingens* is 221 days, with 187 prenatal days of crown forming. Even if M1 crown mineralization in *P. ingens* began at the end of the first trimester, our theoretical minimum, gestation length would have had to be longer than 9 months. Using a *Propithecus* model, gestation in *Palaeopropithecus* is estimated at 10.5 months. Using extant lemurids as a model for *P. ingens* would result in far longer and probably unrealistic estimates of gestation length (12.5 months), underscoring the importance of using the appropriate modern analog in our analyses. We take a model based on the theoretical minimum or the *Propithecus* model as the most appropriate for *Palaeopropithecus* and therefore estimate gestation length as 9–11 months (Table 5).

The theoretical minimum is much shorter for *Megaladapis edwardsi* (6.5 months) and *Archaeolemur majori* (4.2 months) (Table 5). Applying a lemurid model to these species, we derive gestation estimates of 8–9 months for *Megaladapis* and 5–6 months for *Archaeolemur*. Gestation would have been longer in *Archaeolemur* only if its dental developmental trajectory was more similar to those of anthropoids, which initiate M1 crown formation closer to birth.[14]

In summary, gestation was not short in giant lemurs, a phenomenon that may reflect their early initiation of molar crown formation. Indeed, there is credible evidence that the gestation period was longer in *Palaeopropithecus ingens* than in humans, which is all the more remarkable given that this is a species with one of the most rapid dental developmental trajectories of all primates.

Dental Structural Indicators of Trophic Adaptations

Enamel prism morphology and the relative thickness of the enamel vary widely across extant and extinct lemurs (Table 6). They provide strong evidence of a coarse diet with hard-object processing in *Archaeolemur,* but not in *Megaladapis* or *Palaeopropithecus.*[15,58] For these two indicators of diet, nearly all extant lemurs are similar to *Megaladapis* and *Palaeopropithecus,* with only *Daubentonia madagascariensis* exhibiting relatively thick enamel (RET = 21.7).[59] In *Archaeolemur,* molar enamel prism decussation and relative enamel thickness are no less than remarkable (Fig. 3; Table 6). Only a few extant primates, including the omnivorous hard-object processor *Cebus apella,* have molars that combine thick enamel and well-defined Hunter-Schreger bands, suggesting enhanced resistance to high occlusal loads and

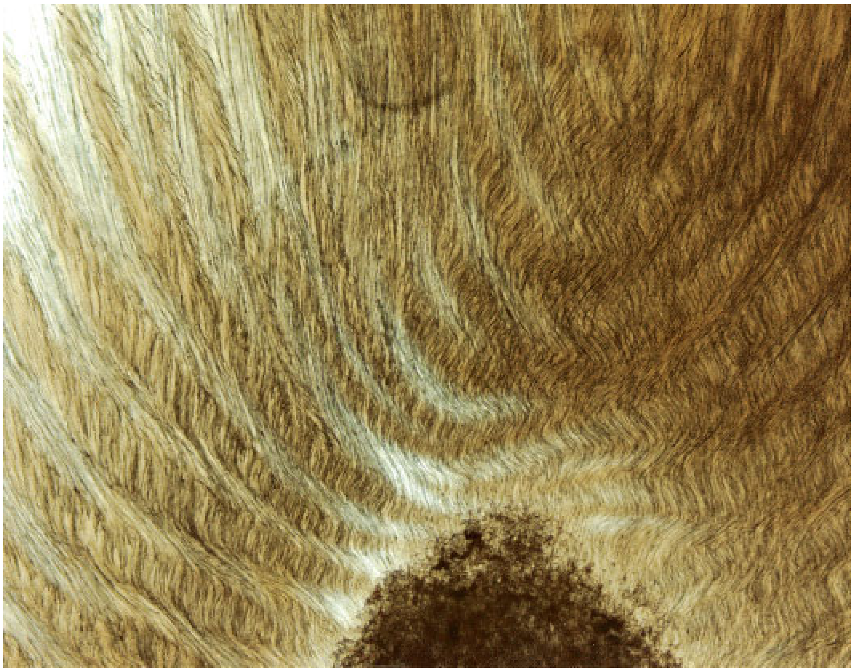


Figure 3. Heavy enamel prism decussation in *Archaeolemur.*

crack propogation. Pitheciins (*Cacajao, Chiropotes,* and *Pithecia*) have well-defined Hunter-Schreger bands but relatively thinner enamel and are, in this manner, more like *Hadropithecus.*[60] Certain extinct anthropoids have striking microstructural similarities to *Archaeolemur,* including *Graecopithecus freybergi* and *Paranthropus* spp.[61]

LESSONS FROM THE LEMURS

The data described here underscore a remarkable diversity of developmental patterns in the lemurs of Madagascar.[6,38,62–64] In many ways, dental development in *Palaeopropithecus* is very like that of indriids: *Palaeopropithecus* is on a par with or even "ahead" of *Propithecus* in its schedule of molar crown formation and dental precocity at birth. As in *Propithecus,* "fast" teeth are apparently accompanied by slow craniofacial growth. Many of the craniofacial correlates of dental precocity in indriids, including diminutive milk teeth, crowding of unerupted and newly erupted teeth, and dissociation of the rates of craniofacial and dental development, are manifested in *Palaeopropithecus.*[6] We add to this list the observation that brain growth was slow in *Palaeopropithecus,* as it is in *Propithecus.*

Only a single deciduous tooth (a dp_4) is known for any individual belonging to a palaeopropithecid species, including *Palaeopropithecus* and its closest relatives *Archaeoindris, Mesopropithecus,* and *Babakotia.* This alone suggests rapid passage through the milk-tooth stage of dental development. The known deciduous tooth, belonging to a very young *Palaeopropithecus ingens* (DPC 17307), was found in association with additional loose teeth, including an M_1 and M_2, P_4, M^1, and P^4. The state of development of the M^1, a crown with no root formation, suggests that this individual was not more than one month old at death. M_1 is crown-complete and has some root formation. The dp_4 has roots and exhibits some macrowear. The M_2 has no roots but is at an advanced stage of crown development, as is P^4. A second, somewhat older, infant *Palaeopropithecus ingens* (DPC 18750) is represented by a left maxilla and associated partial mandible. The maxilla has an erupted M^1, erupting P^4, and full crowns of P^3 and C^1, without roots, in their crypts. The roots of M^1 are not fully formed. The second and third molars are missing. The mandibular molars are missing but their sockets suggest that they had or were erupting and had partial roots.

These specimens establish that the premolars erupt from back to front, as in indriids, that month-old infants were processing solid food, and that the crown of the upper canine, the last tooth to erupt, had fully formed before the precocious first molar had completed its root formation. The eruption sequence manifested in these individuals matches that exhibited by some *Propithecus.* It is possible that the entire chronology of dental development in *Palaeopropithecus* was very like those of extant indriids, and that, as in extant indriids, *Palaeopropithecus* was born with all deciduous teeth erupting or erupted.

Megaladapis also shows rapid dental development, but was not as precocious at birth as was *Palaeopropithecus* or extant indriids. In fact, we know that *Megaladapis,* like lemurids, was born without its deciduous teeth fully erupted. The youngest known *Megaladapis* (DPC 17150) has an unerupted dp_4 lacking roots but a fully erupted dp_3 with roots. The crypt for M_1 is present but broken and the M_1 crown is missing. Because the distal portion of the corpus is also missing, it is impossible to tell the state of development of the second or third molars.

Specimens of *Archaeolemur* spp. and *Hadropithecus stenognathus* suggest very different scheduling of developmental events. Numerous known archaeolemurid specimens bear milk dentitions, which appear to have endured for a prolonged period before they were replaced. There is no diminution of the milk teeth; indeed, the dp4s in both maxilla and mandible are almost as large in the occlusal area as are the M1s.[6] In effect, they serve as functional substitutes for M1 before full eruption of the latter, which we now know did not occur until 15 months or later.[15] Microstructural data confirm a prolonged infancy in *Archaeolemur* prior to the onset of the eruption of the permanent dentition. Microwear data suggest a prolonged period of juvenile foraging following weaning. The pattern of slow growth and fast teeth, manifested so strikingly in *Palaeopropithecus,* does not characterize *Archaeolemur*. Instead, *Archaeolemur* exhibits a growth pattern more like that of lemurids, with relatively rapid somatic growth and slow dental development, but more extreme.[5,39]

We can now draw preliminary inferences regarding the overall pattern of growth and development in large-bodied lemurs. We know that *Palaeopropithecus* and *Megaladapis*, the giant lemur species with the largest molars, do not have the longest CFTs. There is no tendency, as there is among anthropoids, for large-bodied species to exhibit slow growth and development while small-bodied species exhibit rapid growth and development. Instead, there is evidence of an ecological divide, with the hard-object processors, the archaeolemurids, exhibiting relatively slow dental development, while other species (*Palaeopropithecus* especially and *Megaladapis* somewhat) have relatively rapid dental development. The former is associated with relatively rapid acquisition of adult skull and brain size. The former is also associated with relatively high adult encephalization, while the latter is associated with low adult encephalization.[15] The pattern manifested in *Palaeopropithecus* and *Megaladapis* appears to have been associated with early acquisition of food-processing independence. The pattern manifested in *Archaeolemur* appears to have been associated with prolonged acquisition of complex food-processing skills. The parallel here with *Daubentonia madagascariensis* is striking.[65,66] This is the only living lemur with relatively high encephalization, and with a microwear and enamel thickness signature similar to *Archaeolemur*.[56,64,67]

The econiche characteristics of the primate communities of Madagascar have changed dramatically with the disappearance of nearly one-third of their species, including all species greater than 9 kg in body mass. By drawing appropriate comparisons between the extinct lemurs and their much smaller-bodied extant relatives, we will be able to develop a comprehensive understanding of the influence of body size and phylogeny on variation in development and life-history strategies in these species. We can better understand how diet predicts life-history strategy. By comparing the giant lemurs to like-sized anthropoids, we gain a better understanding of the phylogenetic baggage these species carry. Why did the large-bodied species disappear? To separate fact from fiction, we must do a better job than has been done in the past of reconstructing the niche characteristics of these extinct species and, to whatever extent possible, their life-history strategies.

ACKNOWLEDGMENTS

This work was supported by NSF Grants BCS-0237338 to LRG, BCS-0503988 to GTS, and BCS-0129185 to David Burney, LRG, and WLJ. We gratefully acknowledge the help of John Fleagle and three reviewers, and of the many people who contributed to this work, including Frank Cuozzo, Erin Flanagan, Gina Semprebon, Patrick Mahoney and, particularly, our Malagasy hosts (Gisèle Randria, the late Berthe Rakotosamimanana) and colleagues in the field.

REFERENCES

1 Smith BH. 1991. Dental development and the evolution of life history in Hominidae. Am J Phys Anthropol 86:157–174.

2 Smith BH. 1992. Life history and the evolution of human maturation. Evol Anthropol 1:177–231.

3 Conroy GC, Kuykendall K. 1995. Paleopediatrics: or when did human infants really become human? Am J Phys Anthropol 98:121–131.

4 Smith RJ, Gannon PJ, Smith BH. 1995. Ontogeny of australopithecines and early *Homo:* evidence from cranial capacity and dental eruption. J Hum Evol 29:155–168.

5 King SJ, Godfrey LR, Simons EL. 2001. Adaptive and phylogenetic significance of ontogenetic sequences in *Archaeolemur*, subfossil lemur from Madagascar. J Hum Evol 41:545–576.

6 Godfrey LR, Petto AJ, Sutherland MR. 2002. Dental ontogeny and life history strategies: the case of the giant extinct indroids of Madagascar. In: Plavcan JM, Kay RF, Jungers WL, van Schaik CP, editors. Reconstructing behavior in the fossil record. New York: Kluwer Academic/Plenum Publishers. p 113–157.

7 Bromage TG. 1987. The biological and chronological maturation of early hominids. J Hum Evol 16:257–272.

8 Dean MC, Beynon AD, Thackery JF, Macho GA. 1993. Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. Am J Phys Anthropol 91:401–419.

9 Kelley J. 1997. Paleobiological and phylogenetic significance of life history in Miocene hominoids. In: Begun DR, Ward CV, Rose MD, editors. Function, phylogeny, and fossils: Miocene hominoid evolution and adaptations. New York: Plenum Press. p 173–208.

10 Macho GA. 2001. Primate molar crown formation times and life history evolution revisited. Am J Primatol 55:189–201.

11 Dean C, Leakey MG, Reid D, Schrenk F, Schwartz GT, Stringer C, Walker A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominids. Nature 414:628–631.

12 Schwartz GT, Samonds KE, Godfrey LR, Jungers WL, Simons EL. 2002. Dental microstructure and life history in subfossil Malagasy lemurs. Proc Natl Acad Sci 99:6124–6129.

13 Schwartz GT, Godfrey LR. 2003. Box 3. Big bodies, fast teeth. Evol Anthropol 12:259.

14 Schwartz GT, Mahoney P, Godfrey LR, Cuozzo FP, Jungers WL, Randria GFN. 2005. Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): implications for understanding life history variation in subfossil lemurs. J Hum Evol 49:702–721.

15 Godfrey LR, Semprebon GM, Schwartz GT, Burney DA, Jungers WL, Flanagan EK, Cuozzo FP, King SJ. 2005. New insights into old lemurs: the trophic adaptations of the Archaeolemuridae. Int J Primatol 26:825–854.

16 Schwartz GT, Godfrey LR, Mahoney P. n.d. Inferring primate growth, development, and life history from dental microstructure: the case of the extinct giant Malagasy lemur, *Megaladapis*. In: Bailey S, Hublin J-J, editors. Dental perspectives on human evolution: state of the art research in dental anthropology. New York: Springer-Verlag.

17 Beynon AD, Dean MC, Reid DJ. 1991. Histological study on the chronology of the developing dentition in gorilla and orangutan. Am J Phys Anthropol 86:189–203.

18 Beynon AD, Dean MC, Leakey MG, Reid DJ, Walker AC. 1998. Comparative dental development and microstructure of *Proconsul* teeth from Rusinga Island, Kenya. J Hum Evol 35:163–209.

19 Reid DJ, Schwartz GT, Chandrasekera MS, Dean MC. 1998. A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. J Hum Evol 35:427–448.

20 Rushton MA. 1933. Fine contour-lines of enamel of milk teeth. Dent Rec 53:170.

21 Schour I. 1936. Neonatal line in enamel and dentine of human deciduous teeth and first permanent molar. J Am Dent Assoc 23:1946–1955.

22 Smith BH. 1989. Dental development as a measure of life history in primates. Evolution 4:683–688.

23 Boyde A. 1989. Enamel. In: Berkovitz BKB, editor. Handbook of microscopic anatomy, vol. V/6. Teeth. Berlin: Springer Verlag. p 309–473.

24 Boyde A. 1990. Developmental interpretations of dental microstructure. In: De Rousseau CJ, editor. Primate life history and evolution. New York: Wiley-Liss. p 229–267.

25 Ten Cate AR. 1985. Oral histology: development, structure and function, 2nd ed. Princeton: C.V. Mosby.

26 Schwartz GT, Dean MC. 2000. Interpreting the hominid dentition: Ontogenetic and phylogenetic aspects. In: O'Higgins P, Cohen M, editors. Development, growth and evolution: implications for the study of hominid skeleton. London: Academic Press. p 207–233.

27 Rensberger JM, von Koenigswald W. 1980. Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiology 6:447–495.

28 Lamberton C. 1938. Contribution à la connaissance de la faune subfossile de Madagascar.

Note II. Dentition de lait de quelques lémuriens subfossiles malgaches. Mammalia 2:57–80.

29 Walker AC. 1967. Locomotor adaptation in recent and fossil Madagascar lemurs. Doctoral dissertation. University of London, London.

30 Jungers WL, Demes B, Lamm KS. 2005. New body mass estimates for extinct Malagasy lemurs based on long bone geometry. Am J Phys Anthropol 40(suppl):125.

31 Dirks W. 2003. Effect of diet on dental development in four species of catarrhine primates. Am J Primatol 61:29–40.

32 Swindler DR. 2002. Primate dentition: an introduction to the teeth of non-human primates. Cambridge: Cambridge University Press.

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

34 Schwartz GT, Reid DJ, Dean MC, Zihlman AL. n.d. A faithful record of stressful life events recorded in the dental developmental record of a juvenile gorilla. Int J Primatol. In press.

35 Smith BH, Crummett TL, Brandt KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yearbook Phys Anthropol 37:177–231.

36 Shellis RP. 1984. Variations in growth of the enamel crown in human teeth and a possible relationship between growth and enamel structure. Arch Oral Biol 29:697–705.

37 Dirks W. 1998. Histological reconstruction of dental development and age at death in a juvenile gibbon (*Hylobates* lar). J Hum Evol 35:411–425.

38 Godfrey LR, Samonds KE, Jungers WL, Sutherland MR. 2001. Teeth, brains, and primate life histories. Am J Phys Anthropol 114:192–214.

39 Godfrey LR, Samonds KE, Jungers WL, Sutherland MR. 2004. Ontogenetic correlates of diet in Malagasy primates. Am J Phys Anthropol 123: 250–276.

40 Wright LE, Schwarcz HP. 1998. Stable carbon and oxygen isotopes in human tooth enamel: identifying breastfeeding and weaning in prehistory. Am J Phys Anthropol 106:1–18.

41 Mays SA, Richards MP, Fuller BT. 2002. Bone stable isotope evidence for infant feeding in mediaeval England. Antiquity 76:654–656.

42 Mays SA. 2003. Bone strontium:calcium ratios and duration of breastfeeding in a mediaeval skeletal population. J Archaeol Sci 30:731–741.

43 Richards MP, Pearson JA, Molleson TI, Russell N, Martin L. 2003. Stable isotope evidence of diet at Neolithic Catalhoyuk, Turkey. J Archaeol Sci 30:67–76.

44 Humphrey LT, Jeffries TE, Dean MC. 2004. Investigations of age of weaning using Sr/Ca ratios in human tooth enamel. Am J Phys Anthropol 38(suppl):117.

45 Flanagan E. 2004. The ontogeny of dental use wear in *Archaeolemur* spp. and *Macaca fascicularis.* Master's Thesis, University of Massachusetts, Amherst.

46 Dekaban AS, Sadowsky D. 1978. Changes in brain weights during span of human life: relation of brain weights to body heights and body weights. Annals Neurol 4:345–356.

47 Martin RD. 1983. Human brain evolution in an ecological context. New York: American Museum of Natural History.

48 Martin RD. 1996. Scaling of the mammalian brain: the maternal energy hypothesis. Newslett Physiol Sci 11:149–156.

49 Mahaney MC, Leland MM, Williams-Blangero S, Marinez YN. 1993. Cross-sectional growth standards for captive baboons 1. Organ weight by chronological age. J Med Primatol 22: 400–414.

50 Lee PC. 1999. Comparative ecology of postnatal growth and weaning among haplorhine primates. In: Lee PC, editor. Comparative primate socioecology. Cambridge: Cambridge University Press. p 111–136.

51 Wood HT. 2000. The energetics of weaning: testing primate models of body and brain size ontogeny and evolution. Am J Phys Anthropol 30(suppl):326–327.

52 Kappeler PM, Ganzhorn JU. 1993. The evolution of primate communities and societies in Madagascar. Evol Anthropol 2:159–171.

53 Foerg R. 1982. Reproductive behaviour in *Varecia variegata.* Folia Primatol 38:108–121.

54 Brockman DK, Willis MS, Karesh WB. 1987. Management and husbandry of ruffed lemurs, *Varecia variegata,* at the San Diego Zoo. Zoo Biol 6:341–347.

55 Colquhoun IC. 1993. The socioecology of *Eulemur macaco:* a preliminary report. In: Kappeler PM, Ganzhorn JU, editors. Lemur social systems and their ecological basis. New York: Plenum Press. p 11–24.

56 Schwartz GT, Liu W, Zheng L. 2003. Preliminary investigation of dental microstructure in the Yuanmou hominoid (*Lufengpithecus hudienensis*), Yunnan Province, China. J Hum Evol 44:189–202.

57 Smith TM, Martin LB, Leakey MG. 2003. Enamel thickness, microstructure and development in *Afropithecus turkanensis.* J Hum Evol 44:283–306.

58 Godfrey LR, Semprebon GM, Jungers WL, Sutherland MR, Simons EL, Solounias N. 2004. Dental use wear in extinct lemurs: evidence of diet and niche differentiation. J Hum Evol 47: 145–169.

59 Shellis RP, Beynon AD, Reid DJ, Hiiemae KM. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:507–522.

60 Martin LB, Olejniczak AJ, Maas MC. 2003. Enamel thickness and microstructure in pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus.* J Hum Evol 45:351–367.

61 Smith TM, Martin LB, Reid DJ, de Bonis L, Koufos GD. 2004. An examination of dental development in *Graecopithecus freybergi* (= *Ouranopithecus macedoniensis*). J Hum Evol 46:551–577.

62 Eaglen RH. 1985. Behavioral correlates of tooth eruption in Madagascar lemurs. Am J Phys Anthropol 66:307–315.

63 Godfrey LR, Samonds KE, Jungers WL, Sutherland MR. 2003. Dental development and primate life histories. In: Kappeler P, Pereira M, editors. Primate life histories and socioecology. Chicago: University of Chicago Press. p 177–203.

64 Godfrey LR, Samonds KE, Wright PC, King SJ. 2005. Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. Folia Primatol 76:77–99.

65 Feistner ATC, Ashbourne CJ. 1994. Infant development in a captive-bred aye-aye (*Daubentonia madagascariensis*) over the first year of life. Folia Primatol 62:74–92.

66 Krakauer E, van Schaik CP. 2005. Independent and social learning in the development of aye-aye tap-foraging skills. Am J Phys Anthropol 40(suppl):132–133.

67 Godfrey LR, Jungers WL, Schwartz GT. n.d. Ecology and extinction of Madagascar's subfossil lemurs. In: Gould L, Sauther M, editors. Lemur ecology and adaptation. New York: Springer. In press.

68 Smith TM, Olejniczak AJ, Martin LB, Reid DJ. 2005. Variation in hominoid molar enamel thickness. J Hum Evol 48:575–592.