

Dental microstructure and life history in subfossil Malagasy lemurs

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Edited by David Pilbeam, Harvard University, Cambridge, MA, and approved March 18, 2002 (received for review December 19, 2001)

When compared with their recently extinct relatives, living lemurs represent a mere fraction of a broad radiation that occupied unique niches in the recent past. Among living lemurs, indrids exhibit the fastest rates of dental development. This dental precocity is tightly correlated with rapid pace of postnatal dental eruption, early replacement of the deciduous teeth, high dental endowment at weaning, and relatively slow somatic growth. This pattern is in stark contrast to that seen in extant lemurids, where somatic development is highly accelerated and dental development is relatively slow. We report on the pace of dental development in one species of palaeopropithecids, the sister group to extant indrids. Like much smaller modern indrids, the chimpanzee-sized *Palaeopropithecus ingens* was dentally precocious at birth as evidenced by the advanced state of molar crown formation. This finding implies a pattern characteristic of *Propithecus* and other indrids—rapid dental development despite relatively prolonged gestation. Gestation length in this one species of subfossil lemur was likely greater than 9 months. Our results demonstrate that large body size in primates does not preclude exceedingly rapid dental development.

body size | *Palaeopropithecus* | dental development | incremental markings | gestation length

The extant lemurs represent only a fraction of the lemur species that occupied Madagascar in the recent past. Skeletal remains of 17 recently extinct (or “subfossil”) lemur species are common in Quaternary deposits across most of the island (1). As a group, subfossil lemurs exhibit diverse ecological, behavioral, and anatomical adaptations, many of which are not represented in extant lemurs (2). One way in which extinct lemurs are strikingly unlike their living relatives is in their larger body size. Body masses of several of the extinct lemurs rivaled those of chimpanzees and orangutans (≈40–75 kg), and the largest, *Archaeoindris fontoyntonii* (≈200 kg), equaled or exceeded that of adult male gorillas (≈175 kg). None of the giant lemurs was smaller than the largest-bodied of living lemurs (*Propithecus diadema* and *Indri indri*, 6–7 kg).

Life history parameters—such as growth rates, age at first reproduction, lifespan, and birth rate—generally scale allometrically with size (3–6). Presumably, the large-bodied subfossil lemurs possessed prolonged growth (and slower rates of development), relatively longer life spans, and lower reproductive rates than do their still-extant relatives. It might be posited that slow growth and development, late age at first reproduction, and poor reproductive resilience put large-bodied species at a distinct disadvantage in increasingly disturbed ecological regimes after the arrival of humans on Madagascar (see ref. 7 for a review).

For extinct species, life-history pace must be inferred indirectly from skeletal and dental correlates (8–11). Here, we examine the pace of dental development in *Palaeopropithecus ingens*, a chimpanzee-sized lemur (and member of the family Palaeopropithecidae, which includes the largest of the extinct lemur species). We ask two questions: First, was the pace of dental development in *Palaeopropithecus* slow, as one might

expect of a large-bodied primate if indeed the pace of life history is strongly affected by body size? Our goal here is to quantify the dental growth rates in a giant lemur by using incremental markers preserved in developing dental hard tissues. Second, to what extent can we draw inferences regarding reproductive parameters such as gestation length in extinct taxa from their pace of dental development? We also look briefly at other indicators of the pace of the life history of *Palaeopropithecus* and comment on the relationships among the absolute timing of dental development, somatic growth rates, body mass, and gestation length in this remarkable radiation of primates.

Lemur Dental Development

Lemurs can be grouped into seven or eight families, at least two of which are comprised solely of extinct taxa. One of these extinct families, the Palaeopropithecidae (or “sloth lemurs”, including *Mesopropithecus*, *Babakotia*, *Palaeopropithecus*, and *Archaeoindris*) is the likely sister taxon to extant Indridae (*Indri*, *Propithecus*, and *Avahi*) among Lemuriformes (12, 13).

Indrids possess many craniodental features that are unique among extant lemurs, most of which are correlated with an advanced state of dental development at weaning (14, 15). In indrids, all of the deciduous teeth are very small relative to the size of the first permanent molars (ref. 15; Fig. 1A). Moreover, indrids are born with their milk dentition virtually fully erupted and with their M1 and M2 crowns in an advanced state of calcification (Fig. 1B). This early and rapid growth of molar crowns in conjunction with developmentally small jaws results in the confinement and crowding of the deciduous teeth to the front of the neonatal jaw. Thus, molar megadonty is achieved at the expense of the deciduous dentition. Accelerated tooth crown formation in indrid fetuses is associated with an accelerated postnatal dental eruption schedule (14, 15). In sifakas (*Propithecus* spp.), for example, the first permanent molars begin to erupt around 3 to 4 months of age, and the second molars and first replacement teeth (incisors and posterior premolars) erupt at around 5 months of age, just before weaning. In contrast, the first molars in like-sized macaques erupt at ≈1.5–1.75 years, and the first replacement teeth may erupt up to a year later (see ref. 16 for a compendium). All of the permanent teeth with the exception of the upper canine erupt in *Propithecus* by around 8 months, whereas a comparable stage of dental development (i.e., with the last of the permanent teeth erupting) is not attained in lemurids until 15 months or older. Without exception, indrids are far ahead of like-sized and smaller-bodied lemurids in their dental developmental and eruption schedule (Fig. 2; refs. 14 and

This paper was submitted directly (Track II) to the PNAS office.

Abbreviation: CFT, crown formation time.

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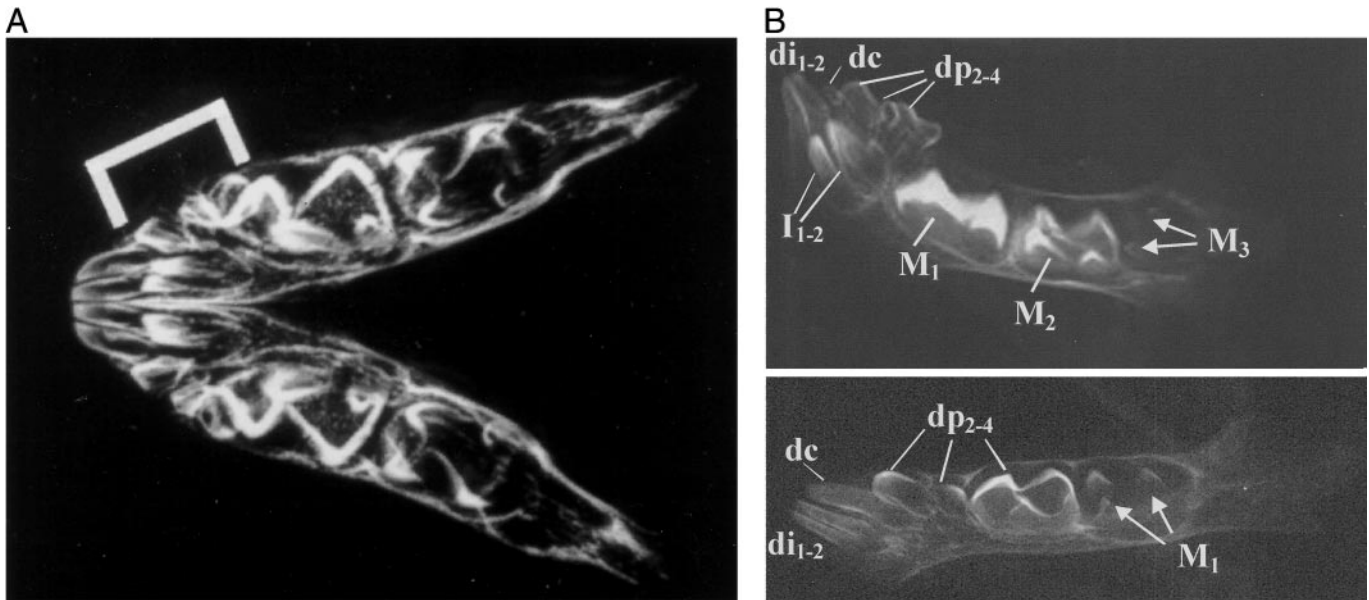


Fig. 1. (A) Radiograph of a mandible of a near-term, captive *P. verreauxi* from the Natural History Museum (London), specimen no. BMNH 67.1365. The bracket indicates the position of the entire set of deciduous teeth, which are confined to the anterior-most portion of the mandible. M_1 and M_2 crowns are clearly visible as is the developing crypt for the M_3 s. (B Upper) Radiograph of a mandible of a newborn (0 days) *P. verreauxi coquereli* male (Duke University Primate Center specimen DPC 6620M). At birth, the M_1 is nearly fully formed, M_2 is one-quarter to one-half formed, and the mesial cusps of M_3 are visible in the crypt. The deciduous incisors (di_{1-2}) and premolars (dp_{2-4}) are illustrated as are the developing permanent incisors in the region of the symphysis. (Lower) Radiograph of a mandible of a three-day old male *Eulemur mongoz* (DPC 6537M) showing the deciduous incisors and canine (together comprising the tooth comb) and the anterior deciduous premolars only just erupting. The dp_4 is only just one-half crown complete, and only the cusps of the permanent M_1 have begun to mineralize.

17; L.R.G., K.E.S., W.L.J., and M. R. Sutherland, unpublished results).

Because of their close relationship, the Palaeopropithecidae might be expected to share with the Indridae an accelerated schedule of dental development, despite the size discrepancy between the two. Recent research on subfossil lemur cranial ontogeny hints at the presence of accelerated dental development in the Palaeopropithecidae. Godfrey *et al.* (15) have shown that palaeopropithecids exhibit *relatively* accelerated dental de-

velopment vis-à-vis their craniofacial growth. In other words, very small skulls and jaws of some immature palaeopropithecids have a high percentage of their adult teeth erupted. Confirmation of dental acceleration in *absolute* terms has been elusive, however, because absolute age assessments in fossil specimens are difficult to obtain. Thus, it remains unknown whether *Palaeopropithecus* shares with like-sized anthropoids a pattern of slow dental growth and development, or with indrids a pattern of dental growth that is accelerated in absolute terms. Evidence in support of the latter would be the following: (i) deciduous P_4 s that are very small relative to the size of the M_1 s; (ii) dental precocity at birth; and (iii) short molar crown formation times.

The first criterion is easily recorded from fossils of juveniles preserving mixed deciduous and permanent dentitions. Until very recently, however, no palaeopropithecid fossils preserving deciduous and permanent teeth were known. Several isolated mandibular and maxillary teeth and a fragment of the associated mandible of a *P. ingens* infant were recently found at Ankilitelo Cave in Southwest Madagascar (DPC 17307). This specimen preserves a fully rooted dp_4 , M_1 (with partial roots), M_2 crown (with no roots), P^4 crown (with no roots), and M^1 crown (also with no roots). At death, this individual would have possessed its deciduous dentition, and an erupting mandibular (but not maxillary) first molar. As a result of this discovery, we now know that *Palaeopropithecus* had a low dp_4/M_1 length ratio (57.8)—slightly above the mean for indrids. (Indrid species' mean range = 41.2–45.2; lemurid species' mean range = 96.0–105.3; see ref. 15).

Demonstrating dental precocity at birth and an accelerated molar crown formation schedule requires histological evidence from developing dental tissues. The component hard tissues of teeth (in particular, enamel and dentine) preserve a permanent record of their growth in the form of incremental markings that are clearly seen in histological sections. These histological markers consist of short- (i.e., daily) and long-period lines that can be used to chart with unparalleled accuracy important life history

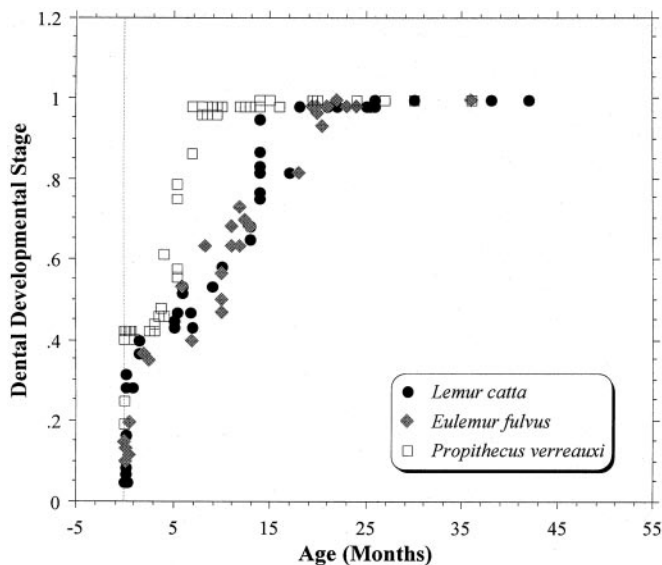


Fig. 2. Dental developmental stage, which is an index of dental maturity and represents the percentage of teeth (deciduous and permanent) that have erupted at each age relative to the species-specific total number of teeth, vs. age in months.

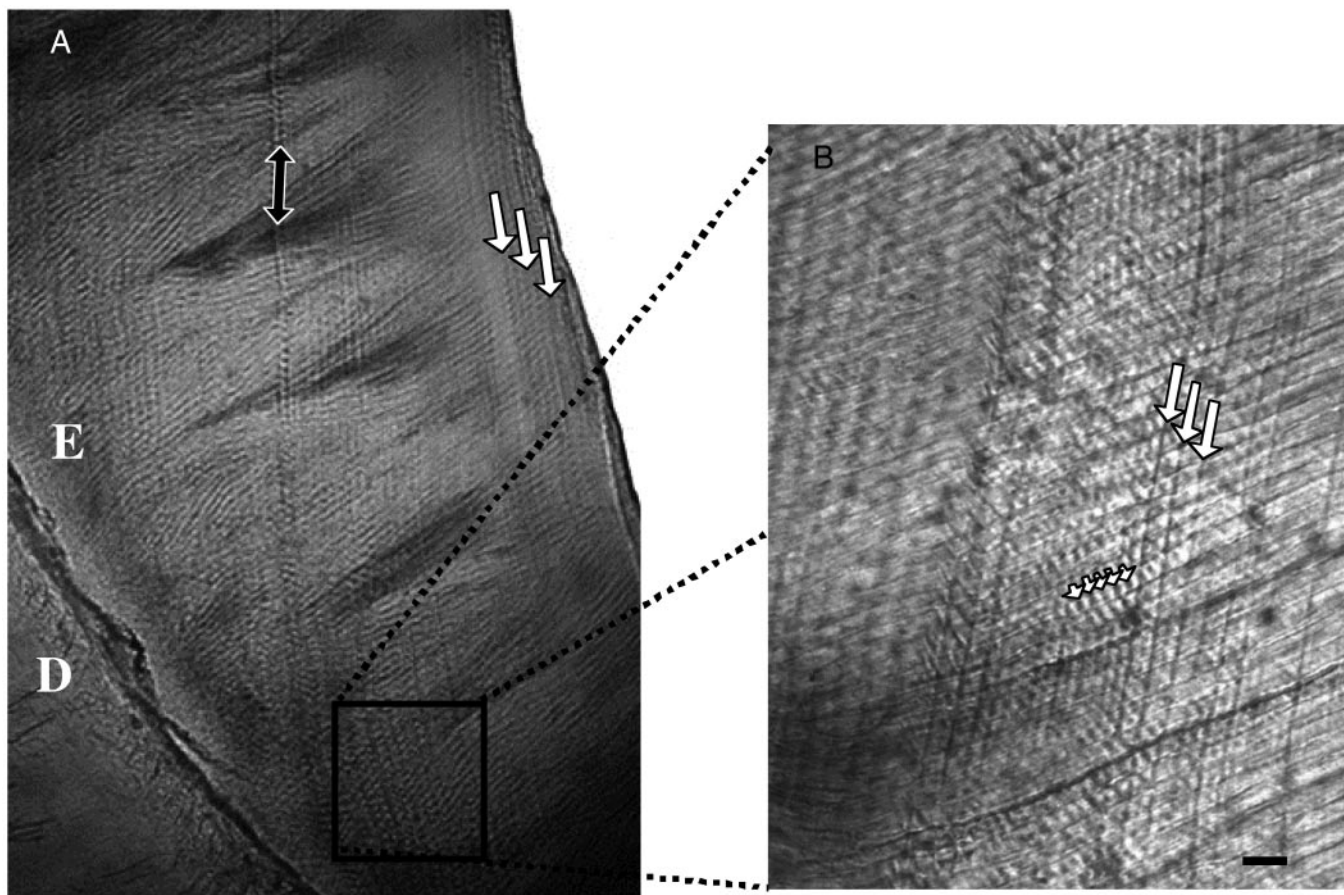


Fig. 3. (A) Long-period lines (striae of Retzius, large white arrows) in lateral enamel of a young *P. ingens* from the cave of Ankazoabo, southwest Madagascar, in the collections of the University of Antananarivo (AM-PPH₁). E, Enamel; D, dentine. Black arrow indicates location of the neonatal line. (B) Daily lines (small white arrowheads) in between adjacent striae (large white arrows) in cervical enamel of *P. ingens* (AM-PPH₁). Enamel prisms run from bottom left to top right. Scale bar = 10 μm .

variables such as the sequence and rate of dental development, the timing of birth, and the age at death in juveniles. Only attrition, abrasion, and erosion can alter teeth once they are formed so that direct evidence for the timing of important developmental events is available from even fragmentary dental remains in the fossil record. Because dental histology provides information on absolute age, it can be used to test aspects of relative dental precocity and dental endowment in subfossil lemurs. In particular, we test the following question: Is *Palaeopropithecus* dentally precocious at birth—i.e., is its M¹ crown virtually complete and is M² only slightly less so at birth, as in extant *Propithecus*? Are molar crown formation times short given body/tooth size reconstructions of *P. ingens*? More generally, what do these data imply about life history (e.g., gestation length) and the relationship between somatic and dental development in a giant strepsirrhine?

Materials and Methods

The molar series, M¹⁻³, of a single juvenile *P. ingens* specimen from Ankazoabo Cave in southwestern Madagascar (University of Antananarivo AM-PPH₁) was chosen for analysis.** Body mass of an adult *P. ingens* has been estimated on the basis of long bone circumferences at approximately 45 kg. The molars of UA-AM-PPH₁ were carefully extracted from their maxillary

alveoli. They were then cleaned, and molds were prepared by using Coltene (Mahwah, NJ) silicon medium body putty. Before sectioning, each specimen was embedded in polyester resin or coated with cyanoacrylate to reduce the risk of splintering. By using a Buehler (Lake Bluff, NY) Isomet diamond wafering blade saw, 180- to 200- μm -thick longitudinal ground sections were prepared. The sections were mounted to microscope slides, lapped to a final thickness of 100–120 μm , polished with a 3 μm aluminum powder, placed in an ultrasonic bath to remove surface debris, dehydrated through a graded series of alcohol baths, cleared in HistoClear (Fisher), and mounted with cover slips in xylene-based DPX (Sigma-Aldrich) mounting medium. A total of 11 sections were taken from planes across, and contiguous to, the principal cusps, including the entire buccal and lingual cervical walls, thereby encompassing the entire period of crown formation.

Short-period (i.e., daily cross striations) and long-period (i.e., striae of Retzius) lines were clearly visible throughout the enamel (Fig. 3). Both types of incremental markings were used to measure daily enamel secretion rates (DSRs) and total crown formation times (CFTs) for each tooth. Daily enamel secretion rate was measured as the linear distance along the long axis of an enamel prism corresponding to 5 days worth of secretion; dividing by 5 yielded the average amount of enamel secreted daily. Total CFT was divided into cuspal enamel formation time plus lateral enamel formation times. Cuspal times were determined directly by counting the number of days it takes for one

**The southwestern variety of this genus is typically somewhat smaller than its congener found on the high plateau (1).

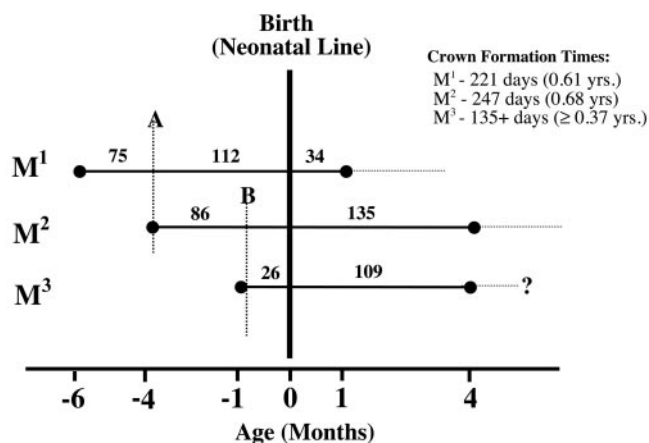


Fig. 4. Bar chart of dental development in *P. ingens*. Solid lines indicate crown formation times, and dashed horizontal lines are estimates of root formation times (not based on data). Vertical dashed lines, A and B, indicate the position of two prominent accentuated striae occurring at 112 days (0.31 yr) and 25 days (0.07 yr) prenatally, respectively. Cervical margin of M^3 slightly broken so that the reported CFT is a slight underestimation.

ameloblast to traverse the distance from the dentine horn to the cusp tip. Lateral enamel formation times were determined by counting the total number of striae of Retzius in the lateral enamel and multiplying by the periodicity, or the number of cross striations between adjacent striae. Retzius lines run obliquely across enamel prism boundaries and thus mark a discontinuity in enamel structure (each stria in the lateral enamel is continuous with one perikyma on the outer enamel surface). Determining total CFTs in this way was repeated for each molar to calculate both the rate and duration of growth for each developing tooth and the total amounts of pre- and postnatal tooth growth (see ref. 18).

To create a chronology (i.e., bar chart) of molar development, each molar had to be registered in time-to-zero-days development, and to one another. The former was accomplished by charting the position of the neonatal line whereas the latter required information on the timing of accentuated striae. The neonatal line is a prominent Retzius line that coincides with birth (19, 20). Accentuated striae of Retzius mark brief periods of disruption in enamel and dentine matrix secretion. As they are recorded in all teeth developing at a particular point in time, they are used to register all teeth developing at the same point in time to one another (18, 21).

Results

Data on daily enamel secretion rates, CFTs, and the timing of accentuated striae were collated to provide an overall chronology of molar development in *Palaeopropithecus*. To our initial surprise, the neonatal line was present in all three molars (see Fig. 3B). By using this line as a starting point and aided by the timing of two prominent accentuated striae (lines A and B in Fig. 4), it was determined that M^1 started formation at 187 days before birth. The periodicity in *P. ingens* is 2; mean values for periodicity range from 6 to 11 in similarly sized extant hominoids (22) and from 2 to 4 in extant lemurs (G.T.S., unpublished data). Crown formation times are as follows: M^1 , 0.61 yr; M^2 , 0.68 yr; M^3 , ≥ 0.37 yr (Fig. 4). These data yield postnatal ages at M^{1-3} crown completion of 0.09, 0.37, and 0.30 yr, respectively. Molar crown development was complete in this specimen by 0.37 yr. The degree of sequential molar overlap is great, given the relatively short overall period devoted to molar crown formation. As a result, all molar teeth are initiated prenatally.

Anterior (M^{1-2}) molar crown formation times are extremely short in *P. ingens* (mean = 0.65 ± 0.05 yr) compared with other primates that possess similar ranges of body and/or molar size (Fig. 5).^{††} Anterior molar CFTs for hominoid taxa are as follows: *Pan*, mean = 3.36 ± 0.41 yr (range = 2.78–4.25 yr); *Gorilla*, mean = 2.86 ± 0.23 yr (range = 2.60–3.21 yr); *Pongo*, mean = 3.00 ± 0.42 yr (range = 2.72–3.30 yr); *Homo*, mean = 3.06 ± 0.33 yr (range = 2.67–3.62 yr). Despite size differences, anterior molar CFTs in *P. ingens* are as fast as that in *Propithecus verreauxi* (0.61 ± 0.04 yrs). *P. ingens* achieves such fast growth in such a relatively short period by possessing some of the highest daily rates of cuspal enamel secretion for all primates (e.g., *Pan*, mean = 4.11 ± 0.49 μm ; *Pongo*, mean = 6.24 ± 1.02 μm ; *P. ingens*, mean = 6.76 ± 1.48 μm). Altogether, these data support the notion that, like modern indrids, certain subfossil lemurs were dentally precocious at birth. In particular, *P. ingens* shares with extant *Propithecus* the same pattern of dental precocity as evidenced by the advanced state of crown formation of permanent molars at birth.

Our data also demonstrate that gestation length in *Palaeopropithecus* was greater than 187 days (6.23 months or 0.50 yr). In anthropoid primates, the onset of mineralization of deciduous teeth does not occur until the late stages of embryological development, and M_1 crown mineralization normally begins late in the third trimester of gestation. Late mineralization of deciduous and permanent teeth does not characterize extant *Propithecus*. Gestation length in *P. verreauxi* is 158 days, and 179 days in *P. diadema* (cf. 102–136 days for the largest-bodied lemurids), and the state of molar crown formation in both species is advanced at birth (see Fig. 1B; refs. 23–29). In *P. verreauxi*, M_1 erupts at 108–124 days (3.5–4.0 months) of postnatal age. An M_1 CFT of 0.61 yr (221 days) thereby implies an M_1 crown initiation time of at least 98 to 113 days before birth (this result is corroborated by the identification of a neonatal line ≈ 98 –104 days after the initiation of M_1 ; G.T.S., unpublished observations); i.e., molar crown formation begins at the end of the first or beginning of the second trimester in extant *P. verreauxi*. Even if, in *Palaeopropithecus*, M_1 crown mineralization began at the end of the first trimester (as it does in *Propithecus*), gestation length would have had to have been greater than 9 months. This number exceeds gestation length in chimpanzees, orangutans, gorillas, and even humans. Again, *Palaeopropithecus* shows a pattern characteristic of *Propithecus*—rapid dental development despite relatively prolonged gestation.

Discussion

On the basis of their large body size, one might predict that giant extinct lemurs should exhibit slow dental development. One might also expect anthropoid scaling relationships between dental development and reproductive maturation to hold for giant lemurs, thus allowing paleontologists to use the pace of dental development inferred for extinct lemurs to predict other aspects of their life histories (i.e., reproductive characteristics).

Our data support neither supposition. We have shown that *P. ingens* exhibited extremely rapid and early molar crown formation—a pattern that parallels its living indrid relatives and not like-sized anthropoids. Like living indrids, *Palaeopropithecus* exhibited molar megadonty, small deciduous teeth and low dp_4/M_1 occlusal length ratios, a decoupling of the pace of dental and somatic growth with acceleration of dental development relative to somatic growth, and prolonged gestation. Recent field research on living indrids verifies that they reproduce exceedingly slowly (30, 31)—in stark contrast to lemurids. Lemurids tend to grow faster and reach reproductive maturity earlier than

^{††}Values for M^3 not used in determining mean molar CFTs as this molar is very reduced in size in *P. ingens*, as it is in all members of the palaeopropithecoid-indrid clade.

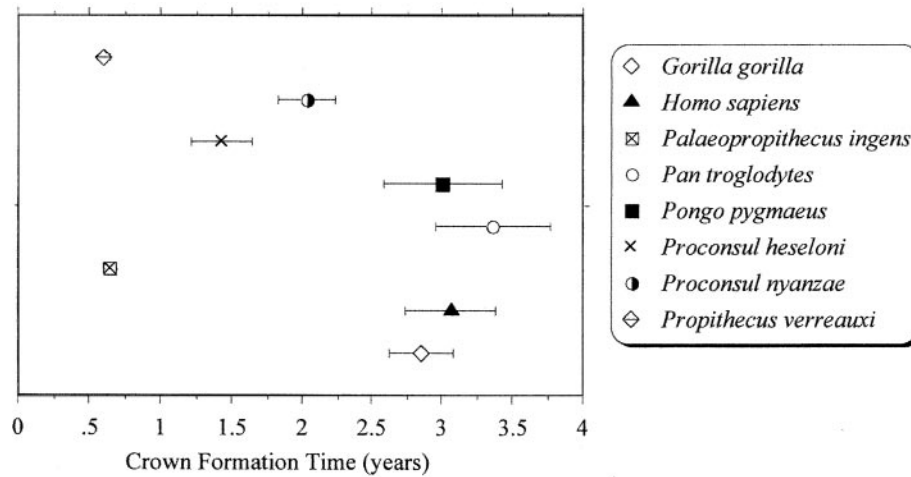


Fig. 5. Anterior molar crown formation times for selected extant and extinct lemurs and hominoids. *P. verreauxi* specimen, BMOC 88, from the Beza Mahafaly Osteological Collection.

indrids, despite their far slower dental development (L.R.G., K.E.S., W.L.J., and M. R. Sutherland, unpublished results). For instance, some lemurids achieve nearly 70% of adult weight by the age of weaning, as opposed to the mere 20% of adult weight attained at weaning for certain indrids (30). Dental precocity in extant indrids is associated with relatively slow somatic growth. This result is in stark contrast to extant lemurids, where somatic development is highly accelerated and dental development is relatively slow.

Eaglen (17) was the first to explore the ecological correlates of variation in the timing of dental eruption among extant lemurids. Because most lemur species grow in cohorts (because of reproductive synchrony), selection can fine-tune the timing of the eruption of particular teeth to coincide with particular phenological events. Weaning itself is timed to correspond to the season of greatest availability of young leaves and other foods (30–32). Selection operates on dental development independently of the development of the rest of the skeleton so as to guarantee masticatory proficiency at weaning and during the first postweaning dry season (refs. 14 and 15; L.R.G., K.E.S., W.L.J., and M. R. Sutherland, unpublished results). At weaning, indrids are equipped with their first and (often) second molars, as well as their adult incisors (including the toothcomb), and, sometimes, their adult posterior premolars. In every indrid species, the posterior premolars erupt shortly after weaning, if not before. Lemurid weanlings, in contrast, may lack their first molars, and have not yet shed any of their deciduous teeth. The summed postcanine occlusal area (expressed as a proportion of adult postcanine occlusal area) is therefore much higher at weaning in indrids than in lemurids (33). The small size of indrid deciduous teeth does not compromise food processing at weaning because these teeth are shed during or just before the process of weaning. Given its extreme dental precocity, it seems probable

that the diminutive deciduous premolars of *Palaeopropithecus* were shed early, as in extant indrids.

It is likely that *Palaeopropithecus* and other giant lemurs of Madagascar did reproduce slowly; this is certainly the case for the largest-bodied living lemurs (*Indri* and *Propithecus*). However, this finding does not imply that all other aspects of their development and life histories parallel those seen in large-bodied anthropoids. Rather, our data demonstrate that large body size in primates does not preclude exceedingly rapid dental development (even if somatic development was slow and gestation was long). Our data reaffirm the importance of extracting real developmental time in extinct primates via incremental lines in dental hard tissues. They show how dental microstructure can provide clues to dissociated aspects of the life histories of extinct species (prolonged gestation, rapid crown formation). Finally, they provide important developmental support for a phylogenetic hypothesis (sister-taxon status for indrids and sloth lemurs) developed on the basis of other anatomical data and ancient DNA.

The authors would like to thank Chris Dean, Mitchell Irwin, Jay Kelley, Lawrence Martin, Stephen Nash, Don Reid, Berthe Rakotosamimanana, Gisèle Francine Noro Randria, and two anonymous reviewers. The University of Antananarivo kindly provided access to the *P. ingens* specimen UA-AM-PPH₁, and Alison Richard kindly loaned us the *P. verreauxi* specimen, BMOC 88. Fig. 1 was produced with the generous assistance of Deryck Jones (Museum of Natural History, London), David Haring (Duke University), Terry Button (Radiology Department, Stony Brook University), Lawrence Martin (Anthropology Department, Stony Brook University), and Luci Betti-Nash (Anatomical Sciences, Stony Brook University). Fred Grady (National Museum of Natural History, Washington, DC) provided assistance with molding and casting. Funding was provided by a Smithsonian Institution Postdoctoral Fellowship (G.T.S.), National Science Foundation (NSF) Grant GER 9450175 (L.R.G.), and NSF Grant SBR-9630350 (E.L.S.). This paper is Duke University Primate Center publication no. 740.

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