The growth and development of *Pachylemur*, a large-bodied lemurid

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Abstract

As the largest-bodied member of the family Lemuridae and the presumed primary disperser of large seeds, *Pachylemur*, now extinct, was a critical member of Madagascar's primate communities. Material of this genus has been found at almost all subfossil sites across Madagascar, but extensive samples of this taxon are known from very few. It has been one of the more historically neglected of the "giant" extinct lemurs, as it is not very different in morphology from its nearest extant relative, *Varecia*, except in body size.

The flooded cave called Vintany at the Tsimanampesotse National Park in southwestern Madagascar has yielded numerous specimens of *P. insignis*, including whole skulls and mandibles, many isolated postcranial elements, and, importantly, partial associated skeletons of immature individuals. This material allows us to address previously unanswered questions regarding its paleobiology, including questions concerning its growth and development. This article focuses specifically on its life history profile (especially developmental sequences and life-history-related traits such as Retzius line periodicity of the teeth and endocranial volume in adults). We ask to what extent, despite its larger size, did *Pachylemur* "grow" like its smaller-bodied relatives? Did its dental eruption sequence and index of Relative Retardation of the Replacement teeth resemble those of its closest relatives? Did it, like other lemurs, have a Retzius line periodicity that is lower than "expected" for a primate of its body size, and if so, what is the likely significance of this? Was its brain smaller than expected for a primate of its body size? For these and other questions, we evaluate how large-bodied lemurs differ from anthropoids of comparable body size.

Key words: sequence heterochrony, Retzius line periodicity, index of Relative Retardation of Replacement teeth, endocranial volume, life history analysis, Tsimanampesotse, Madagascar

Résumé détaillé

En tant l'un des plus grands lémuridés et un présumé principal disséminateur des grosses graines, *Pachylemur* était un membre essentiel des communautés de primates de Madagascar. Des spécimens de ce genre ont été trouvés dans presque tous les sites subfossilifères de Madagascar, mais la plupart des échantillons de ce taxon n'est connue que dans quelques sites. Il était l'un des lémuriens « géants » éteints les plus historiquement négligés, car il n'était pas très différent de son plus proche parent existant, *Varecia*, sauf par sa taille corporelle.

La grotte inondée appelée Vintany du Parc National de Tsimanampesotse dans le Sud-ouest de Madagascar a contenu de nombreux spécimens de *P. insignis*, y compris des crânes et des mandibules entières, de nombreux éléments post-crâniens isolés et, surtout, des squelettes partiels associés à des individus immatures. Ces matériaux ont permis d'aborder des questions jusqu'alors sans réponse, sur sa paléobiologie, incluant sa croissance et son développement. Ainsi, cet article se concentre spécifiquement sur le profil de son histoire de vie, en particulier les séquences de son développement, la périodicité de la ligne de Retzius de ses dents et le volume endocrânien chez les adultes. Nous nous demandons dans quelle mesure, malgré sa plus grande taille, *Pachylemur* a-t-il « grandi » comme ses parents de plus petite taille ? Est-ce que la séquence d'éruption dentaire et l'indice de retard relatif de remplacement dentaire (RRR) ressemblaient-ils à ceux de ses plus proches parents ? A-t-il, comme les autres lémuriens, une périodicité de ligne de Retzius inférieure à celle « attendue » pour un primate de même taille ; et si oui, quelle en est la signification probable ? Son cerveau était-il plus

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petit que prévu pour un primate de taille identique ? Pour ces questions et d'autres encore, nous avons évalué dans quelle mesure les lémuriens de grande taille diffèrent-ils des anthropoïdes de taille corporelle comparable ?

Les résultats ont alors montré que le profil de développement de *Pachylemur* ressemble davantage à celui des lémuriens de plus petite taille, en particulier les lémuridés, qu'à celui des anthropoïdes de taille corporelle comparable. Sa séquence d'éruption dentaire et son indice de retard relatif des dents de remplacement ressemblent à ceux de ses plus proches parents. Son volume endocrânien et la périodicité de la ligne de Retzius sont plus faibles que prévus pour un primate de sa taille corporelle. Des différences entre les lémuridés (y compris *Pachylemur*) et les indriidés ont été également trouvées. Les lémuridés présentent une éruption relativement tardive des prémolaires permanentes et donc des valeurs élevées de RRR, ainsi qu'une croissance et une maturation postcrânienne relativement rapides, alors que les indriidés présentent le contraire. Cependant, les différences entre les lémuridés et les anthropoïdes sont plus importantes et plus fondamentales que celles entre les familles de lémuriens. Ces différences peuvent être corrélées à celles de dépense énergétique globale chez ces animaux, elles-mêmes liées à des contraintes environnementales, y compris les ressources disponibles (comme les protéines apportées par les fruits), qui peuvent influencer les stratégies de cycle de vie des lémuriens. Elles peuvent nous aider à comprendre pourquoi les lémuriens ne parviennent pas à se conformer aux « attentes » de l'histoire de la vie qui sont basées sur les normes anthropoïdes.

Mots clés : hétérochronie de séquence, périodicité de la ligne de Retzius, indice de retard relatif de remplacement dentaire, volume endocrânien, analyse de l'histoire de la vie, Tsimanampesotse, Madagascar

Introduction

Pachylemur is a member of the lemur family Lemuridae that went extinct during the late Holocene. Its closest extant relative, *Varecia*, is represented by two species (*V. rubra* and *V. variegata*), both of which are Critically Endangered according to the International Union for Conservation of Nature's (IUCN) "Red List of Threatened Species". Most of the island's living lemurs are threatened with extinction. Madagascar also had around 17 lemur species that are part of a "megafaunal" community (including elephant birds, large-bodied euplerids, pygmy hippopotamuses, horned crocodiles, etc.) that more-or-less simultaneously went extinct. As a large-seed disperser, *Pachylemur* was presumably a critical member of Madagascar's primate community. Based on postcranial morphology, *Pachylemur* has been reconstructed as slow and careful in its locomotion (Jungers *et al*., 2002; Shapiro *et al*., 2005). As in extant lemurs, it likely had a more restricted home range and was less mobile than anthropoid primates of similar size (Crowley & Godfrey, 2019). Molecular-based phylogenies of lemurids suggest that *Varecia* forms a clade with *Pachylemur*, which is in turn the sister clade to all other lemurids (including *Lemur*, *Prolemur*, *Hapalemur*, and *Eulemur*) (Crovella *et al*., 1994; Kistler *et al*., 2015). Among the recently extinct subfossil lemurs, the Lemuridae is believed to be more closely related to the Megaladapidae than to the Indriidae (Kistler *et al*., 2015; Marciniak *et al*., 2021).

A species' life history is the pattern, sequence, and pace of growth for individuals. A body of theory, termed life history theory, allows researchers to understand how a particular life history schedule results from the ways in which natural selection has operated on a series of trade-offs in the allocation of that species' energetic budget. Any organism's total energetic budget is distributed across three basic domains: growth, maintenance, and reproduction. As a result, a "life history analysis" for any species focuses principally on aspects of a species' growth rate and reproductive scheduling including key attributes such as gestation length, weaning age, age at sexual maturation, age at first birth, interbirth intervals, and longevity. Species are often characterized as having "fast" or "slow" life histories, depending on how rapidly individuals grow, develop, and reproduce. Assessing life histories in extinct animals is not easy because one cannot measure individuals as they grow, directly documenting developmental milestones such as age at weaning, age at first birth, and interbirth intervals. Paleontologists have discovered ways to reconstruct some of these traits using proxies that can be measured in teeth or bones. Most easily estimated are what are called "life-history related" traits, including brain and body size. Brain volume, for example, is estimated in fossils by the volume of the neurocranium that houses the brain. Other tools are available to paleontologists, including sequence heterochrony and some histological techniques.

Sequence heterochrony allows researchers to describe the sequence of developmental events and compare the relative pace of growth and development of different body parts in different taxa. As it relates to dental development, it was proposed that dental eruption sequences could be used as proxies for the absolute pace of dental eruption. In other words, relative developmental timing might reflect absolute developmental timing. This relationship between the sequence and pace of dental development was called Schultz's Rule (Smith, 2000).

As mammals, primates possess two sets of teeth throughout their lives: the deciduous and the permanent dentitions. Primate deciduous teeth consist of deciduous incisors, canines, and premolars and emerge prior to the eruption of any of the permanent teeth (comprising permanent incisors, canines, and premolars, as well as an additional set, permanent molars). These two dentitions (deciduous and permanent teeth) can be subdivided into a series of three sequentially-emerging sets of teeth: all of the deciduous teeth (set 1), the permanent molars (set 2), and the permanent replacement teeth (set 3). Schultz's Rule postulates that species with "fast" life histories (that is, rapid dental development, rapid body growth, early sexual maturation, and short life spans) will erupt their permanent molars (set 2) before the replacement teeth (permanent premolars, canines, incisors; set 3). Schultz's Rule also predicts that the opposite would be the case for species with "slow" life histories (that is, slow dental development, slow body growth, late sexual maturation, and long lifespans) who would be characterized by set 3 (the permanent replacement teeth) emerging into the oral cavity in advance of the teeth within set 2 (the permanent molars). An index to quantify this degree of overlap between the emergence of these two sets of teeth (permanent replacement teeth and permanent molars) was created by Smith (2000) and is called the index of *Relative Retardation of the Replacement* teeth, or RRR. It was constructed in such a manner that species with different total numbers of permanent teeth could be compared. Species with high values (wherein the permanent replacement teeth, i.e., the incisors and premolars, erupt late relative to the permanent molars) were presumed to erupt their teeth quickly and have "fast" life history trajectories. Relatively early eruption of the permanent replacement teeth was presumed to indicate late dental eruption (in absolute time) and a "slow" life history.

Histological techniques have provided researchers with additional proxies for life history traits; in particular, they allow researchers to quantify traits that reflect internal biological clocks. One such trait is the Retzius line periodicity (RP), which is the result of how a system-wide neuroendocrine rhythm manifests in developing teeth. As dental crowns grow, enamel is deposited in an incremental manner according to a circadian (or daily) rhythm and a second longer-period rhythm. As a result, within tooth enamel there are two different types of temporal markers preserved: daily lines called cross striations and longer period lines called striae of Retzius. RP reflects the duration (in number of days) of enamel secretion between adjacent striae of Retzius. RP values are thought to be invariant within individuals (both within and between teeth) but are known to show some variance both within and between species. In primates, they are usually longer than one day but are usually less than two weeks. Homologous growth structures are also present in dentine: von Ebner lines are daily while Andresen lines represent the longer period rhythm. These short- and long-term rhythms must reflect some biological function – some aspect of growth – but at present it is uncertain what that function might be. Among anthropoid primates, RP values tend to correlate significantly with body size and other aspects of a species' life history. Large-bodied anthropoids tend to have, in addition to high values for RP: (1) low reproductive rates; (2) slow craniodental maturation and dental eruption; (3) slow postcranial growth and development; (4) a large brain; and (5) low values for the index of RRR.

Bromage *et al*. (2012) proposed a hypothesis regarding the function of RP, tying RP to the life history schedule of a species. They noted that RP intervals in extant anthropoids are correlated with rates of cell proliferation, growth rates, basal metabolic rates, and body mass. They hypothesized that RP intervals reflect the underlying Havers-Halberg Oscillation (HHO), a neuroendocrine rhythm tied to the pituitary gland that appears to regulate aspects of growth, development, and metabolism in animals. The HHO is believed to modulate (or control) aspects of the life histories and life-history related traits such as brain and body size, age at first reproduction, and activity levels of vertebrates, including primates. According to the HHO hypothesis, species with low RP intervals should have short HHO rhythms, accelerated cell proliferation, fast growth rates, small adult body (and brain) mass, and broadly speaking, "fast" life histories. In contrast, species

with high RP intervals have long HHO rhythms, slow rates of cell proliferation, slow growth rates, large adult body (and brain) mass, and broadly speaking, "slow," more protracted, life histories (i.e., wean late, reproduce late, live longer). In addition, species with low RP intervals should be less mobile and less active (and therefore have smaller home ranges) than species with high RP intervals, a product of the link to metabolic rate.

What is interesting, however, is the fact that, among lemurs, reproductive rates and other life history parameters are not necessarily correlated with any of the other variables that are typical predictors in other primate taxa. Among lemurs, for example, having a high RRR does not necessarily mean having a fast life history and having a low RRR does not necessarily mean having a slow life history (Schwartz *et al*., 2005). Furthermore, no extinct lemur, no matter how large in body size, has a very high value for RP (Hogg *et al*., 2015), and RP does not correlate with reproductive parameters in extant lemurs. There are also, among lemurs, odd combinations of variables describing the absolute pace of growth and development. For example, indriids exhibit extremely rapid dental development and eruption, but they do not live life in the "fast lane" (Richard *et al*., 2002; Schwartz *et al*., 2002; Godfrey *et al*., 2004). Indeed, Richard *et al*. (2002) described the extant indriid, *Propithecus*, as a "bet hedger" *par excellence*, with exceptionally delayed age at first reproduction and low reproductive rate. In contrast, lemurids exhibit much slower dental development and eruption (Schwartz *et al*., 2002), but they begin reproducing at an earlier age and have higher reproductive rates, with twinning or triplets far more common than in indriids (Godfrey *et al*., 2004; Baden *et al.*, 2013; Vasey *et al*., 2018). Members of these two extant families differ in their relationship between dental and postcranial growth and development. Indriids have fast dental and slow postcranial growth and development; lemurids have the opposite (Godfrey *et al*., 2004). Godfrey *et al*. (2004) explore diet as a variable that may influence these life history patterns. These authors suggested that the differing developmental schedules of folivorous indriids and frugivorous lemurids reflect different solutions to the ecological problem of environmental instability, with the former depending on low maternal input and slow returns, and the latter on high maternal input and fast returns. Dependency on large fruiting trees (which are often highly vulnerable to environmental catastrophes such as cyclones and droughts) places juveniles and adults under greater risk of mortality under environmental stress. Lemurids compensate for this increased population risk by being able to rebound quickly through early reproductive maturation and through bearing litters of multiple offspring. In contrast, indriids lower juvenile mortality risk by endowing young individuals with the dental equipment needed to process tough herbivorous foods. Populations are maintained through bet hedging rather than rapid reproductive resilience.

All lemurs measured thus far have cranial capacities that are lower than expected for anthropoids of similar body mass; the same is true of RP values. Among lemurs, including extinct species, endocranial volume (ECV) correlates with RP values far better than body size (Hogg *et al*., 2015). Other variables, perhaps related to energy constraints and energy procurement, may be important in understanding variation in RP among lemurs (Hogg *et al*., 2015). Body size does not predict the pace of dental development, or reproductive rates, in lemurs.

To strengthen our understanding of these relationships in lemurids, we need more data. To date, information on development of the largest-bodied lemurid, the extinct *Pachylemur*, has not been available for dental eruption sequence, RRR, sequence heterochrony, RP, the relationship between cranial and postcranial development, and even ECV. Only its body mass, estimated by Jungers *et al*. (2008), has been published; *Pachylemur* was approximately three times the size of the next largest lemurid, members of the extant genus *Varecia*. Here, we report new data from recently collected subfossils of *Pachylemur* on each of the above developmental and anatomical attributes and evaluate each within the broader context of other lemurs and anthropoid primates.

Our primary goal is to determine whether *Pachylemur* "behaves" like other lemurids, like members of other lemur families (such as indriids), or like anthropoids of comparable body size. Does it differ from other lemurids in a manner that might be expected if large-bodied lemurids conformed to expectations about development and life history based on anthropoids? If we can show that *Pachylemur* had a developmental trajectory similar to those of other lemurids such as *Varecia* or *Lemur catta* (and unlike those of indriids such as *Propithecus* or *Avahi*), then this may also imply that we can use extant lemurids as models to retrodict *Pachylemur*'s life history profile and reproductive strategy. Most importantly, if *Pachylemur* closely resembled smaller-

bodied lemurids, it would become another example of a large-bodied animal that does not conform to "expectations" for large-bodied animals based on large-bodied anthropoids. Finally, if *Pachylemur* "behaves" like other lemurids, we can ask whether those characteristics make sense in terms of what we know about other aspects of the biology of *Pachylemur*, including its diet, activity levels, and other aspects of its behavior. We also evaluate our results to help us understand the constraints that may influence the growth and development of the lemurs in general and of lemurids in particular.

Materials and methods

Samples

Data were collected on 14 crania of *Pachylemur* (nine immature and five adult), 23 mandibles (nine immature and 14 adult), 36 humeri (14 immature and 22 adult), and 37 femora (five immature and 32 adult). All specimens were recovered in flooded deposits in the Vintany Cave (Tsimanampesotse National Park, southwest Madagascar) by a team of professional divers. Some were collected from the floor of the cave, others from sediments in selected and mapped excavated locations. Field expeditions were conducted under a collaborative accord and with permission from Madagascar National Parks to collect a specified number of fossils during the 2015, 2016, 2018, and 2019 field seasons. All are housed at the Université d'Antananarivo, Mention Bassins Sédimentaires, Evolution, Conservation (UABEC) and have UABEC catalogue numbers.

Sequence heterochrony: establishing dental developmental and other maturational sequences

To determine the dental eruption sequence, as well as cranial suture closure and postcranial epiphyseal fusion developmental sequences in *Pachylemur*, we adopted the sequence heterochrony methods of King (2004). Dental development was scored on eight hemi-mandibles of immature *Pachylemur*. A ninth hemi-mandible was microCT-scanned (Bruker Skyscan 1173) at the Institute of Human Origins' Visualization Lab in the School of Human Evolution and Social Change, Arizona State University, Tempe, and the dental developmental sequence reconstructed directly from the scan.

Table 1 provides a list of traits scores and the system we used for each (e.g., 0 to 2, or 0 to 4). We scored eruption stage for all mandibular teeth (deciduous and permanent); closure for cranial sutures (basioccipital, occipital, metopic, coronal, sagittal, squamosal, lambdoidal, frontonasal, zygo/maxillary, and zygo/temporal); fusion for humeral epiphyses (humeral head-tubercles, humeral head-diaphysis, capitulum-trochlea, medial epicondyle-diaphysis, and distal humerus-diaphysis); and fusion for femoral epiphyses (femoral head-diaphysis, lesser trochanter-diaphysis, third trochanter-diaphysis, and distal femur-diaphysis). We also measured diaphyseal lengths on the anterior faces of each humerus and femur. Adult diaphyseal lengths exclude the portions of the adult long bone shafts that belong to the epiphyses.

Developmental sequences were established following the methods of King (2004). Table 2 provides the scoring for the permanent dentition of eight

Table 1. List of craniodental and postcranial traits and measurements.

Trait	Scoring or description
Dental eruption stage	For each tooth, 0 = unerupted, 1 = erupting, 2 = erupted
Dental developmental stage	For each individual, from 0 to 1, where 1 = full adult: sum of eruption stage scores for each tooth ÷ (total # of teeth x 2)
Cranial suture closure stage	For each cranial suture, 1 = unfused, 2 = fusing, 3 = fused, but visible, and 4 = fused and invisible
Cranial maturational stage	For each cranium, from 0 to 1, where 1 = full adult: sum of suture closure stage scores ÷ (total number of sutures x 4)
Epiphyseal fusion stage	For each humeral or femoral epiphysis, 1 = unfused, open, 2 = fusing (i.e., can see bridging from bone to bone), 3 = completely fused, but visible, 4 = completely fused, invisible
Humeral or femoral maturational stage	For each humerus or femur, from 0 to 1, where 1 = full adult: sum of epiphysis fusion scores ÷ (total number of epiphyses x 4)
Diaphyseal length	For each humerus or femur, length of diaphysis (excluding proximal and distal epiphyses) measured along midline of the anterior face of the bone
Humeral or femoral growth stage	For each humerus or femur, from 0 to 1, where 1 = full adult: diaphyseal length ÷ mean adult length of the diaphysis for the species

Table 2. Scores for permanent mandibular teeth, for 10 specimens (eight immature and two adults) of *Pachylemur* (i: incisor, c: canine, p: premolar, m: molar). Inferred sequence: m1 [m2 i1 i2 c1] m3 p4 p3 p2.

Specimen number	i1	i2	c1	p2	p3	p4	m1	m2	m3
UABEC 0314	2	2	2	1	2	2	2	2	2
UABEC 0312	2	2	2	2	2	2	2	2	2
UABEC 0447	2	2	2	0	0	0	2	2	0
UABEC 0318	2	2	2	2	2	2	2	2	2
UABEC 0608	2	2	2	1	2	2	2	2	2
UABEC 0833	2	2	2	0	0	1	2	2	2
UABEC 0532a	0	0	0	0	0	0	1	0	0
UABEC 0532b	0	0	0	0	0	0	2	0	0
UABEC 0813	2	2	2	0	2	2	2	2	2
UABEC 0889	2	2	2	0	0	0	2	2	0
Sum	**16**	**16**	**16**	**6**	**10**	**11**	**19**	**16**	**12**

immature and two adult mandibles of *Pachylemur* and serves as an example for how we determined heterochronic sequences. For each mandible (rows), we scored eruption state for each tooth (row cells on Table 2). The sums of these scores provide the data needed to calculate maturational stages for individuals, that is to say, the sum of the individual's scores for each trait divided by the total maximum maturational score (in this case, each tooth, including the replaced deciduous teeth, fully erupted). Dental developmental "stage" for any individual mandible ranges in value from 0 to 1.0, where 0 represents no erupted teeth (including the deciduous teeth) and 1.0 represents full adult development, with all permanent teeth erupted. Finally, to derive developmental sequences, we summed the scores for each column. The column sums indicate how early or late each tooth erupts relative to the others in this species. High column sums represent early eruption, and low column sums represent late eruption. The developmental sequence is determined by ordering these sums.

Relative growth was assessed by comparing diaphyseal lengths of the humerus and femur of immature individuals to the means for adults of the same species, as defined by King (2004). One immature individual found underwater at Vintany Cave had most of its skeleton preserved (UABEC 0889). We used the first mandibular molar of this individual for dental histological analysis. We also scored maturational stages for this individual's mandibular dental eruption stage, cranial suture closure, humeral and femoral maturation stage, and humeral and femoral growth.

Index of Relative Retardation of Replacement teeth (RRR)

Evaluating variation across species in dental eruption sequences can be challenging because different taxa have different species-typical numbers of teeth. Also, when two or more teeth erupt more-or-less simultaneously, there can be notable intraspecific or population variation in dental eruption sequences. Particular teeth can assume very different functions in different species. For example, canines that belong to tooth combs, as in most strepsirrhine primates, have very different functions than canines that play a role in social display or agonistic behavior, as in many anthropoid primates. Such variation strongly impacts not merely canine form, but when they erupt. Mandibular canines that are part of the tooth comb of many lemur species tend to erupt with the mandibular incisors, whereas canines in male-dominant, sexually dimorphic species may erupt only with sexual maturation. When Smith (2000) proposed a simple formula to capture the relative pace of eruption of molars vs. replacement teeth, she deliberately excluded the canine so that such differences would not affect the comparison among taxa. The formula was designed merely to focus on this relationship, and to allow comparison of taxa with different numbers of replacement teeth.

To calculate the index of Relative Retardation of Replacement teeth (RRR), one divides the mandibular replacement teeth (ignoring the canine) into three groups: teeth that erupt after the third molar; teeth that erupt after the second molar but before the third; and teeth that erupt after the first molar but before the second. The numbers of teeth in each group are given different weights: the total erupting after the third molar is multiplied by 3, the total erupting after the second molar but before the third is multiplied by 2, and the total erupting after the first molar but before the second is multiplied by 1. These quantities are then summed, and that sum is divided by the species-typical number of replacement teeth (ignoring the canine). The result is an RRR value that will be high in species with relatively late eruption of the replacement teeth, and low in species with relatively early eruption of the replacement teeth.

Retzius line periodicity (RP)

We measured Retzius line periodicity for *Pachylemur* using standard techniques of dental microstructural analysis (Schwartz *et al.*, 2002, 2005). We sectioned the first permanent molar of a mandible of a young

Pachylemur (UABEC 0889) from Vintany Cave (Figure 1). Retzius line periodicity was determined by counting the number of daily cross striations (red arrows) between adjacent Retzius lines (double white arrows) along an enamel prism (white dotted lines) (Figure 2). This was repeated in several areas of the sectioned tooth to confirm results.

Endocranial volume (ECV)

Endocranial volume was measured on nine fully adult *Pachylemur* skulls. The foramina were plugged using modeling clay, and then the endocranial cavity was filled using black mustard seeds poured into the foramen magnum. The seed contents of the neurocranium were then poured into a graduated cylinder and the volume recorded to the nearest ml.

Comparative analyses

We folded our new data for *Pachylemur* into a sequence heterochrony database generated by King (2004) that included 929 individual primates belonging to the following superfamilies: Hominoidea, Cercopithecoidea, Ceboidea, Lorisoidea, and Lemuroidea. Taxa and sample sizes are listed in King

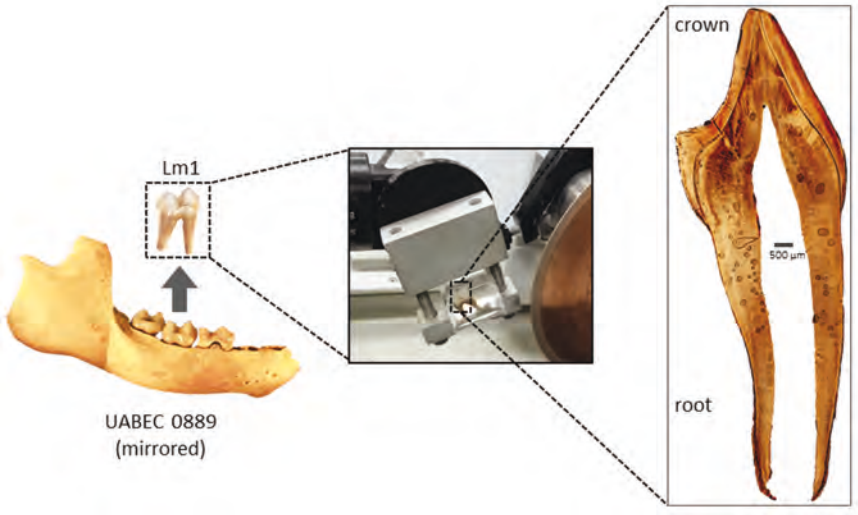

Figure 1. Left: composite (mirrored) photograph of the hemimandible of UABEC 0889, *Pachylemur insignis* from Vintany Cave, Tsimanampesotse National Park. The inset shows the extracted left m1 prior to embedding and sectioning. Middle: Lm1 of UABEC 0889 embedded in an epoxy resin block and mounted to a chuck in preparation for sectioning with a diamond wafering blade. Right: Photomontage of the section through the Lm1 protoconid.

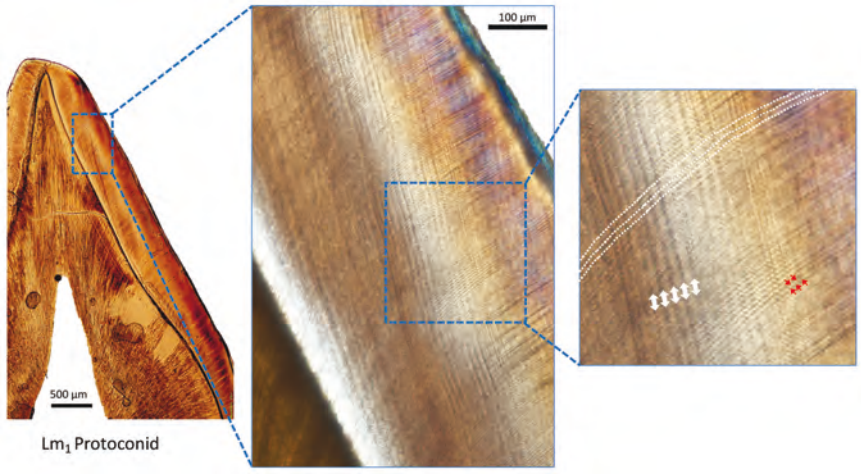

Figure 2. Left: close-up of cuspal region of the m1 protoconid of UABEC 0889, *Pachylemur insignis.* Middle: inset of the cuspal enamel region. Right: close-up of the enamel from the middle panel showing the path of enamel prisms (white dotted lines), a series of striae of Retzius (double white arrows), and a set of daily cross striations (red arrows).

(2004). We supplemented the King (2004) extant strepsirrhine database with a database compiled by one of us (LRG) targeting extant lemurs. This included 44 *Lepilemur ruficaudatus*, 38 *Varecia variegata*, 73 *Lemur catta*, 34 *Hapalemur griseus*, 31 *Eulemur mongoz*, 26 *Eulemur macaco*, 22 *E. collaris*, 46 *E. albifrons*, 26 *Indri indri*, 127 *Propithecus verreauxi*, 35 *P. edwardsi*, 54 *P. coquereli*, and 39 *Avahi laniger*. Additional data on dental histology and mandibular dental eruption sequences of extinct lemurs were taken from King *et al*. (2001), Schwartz *et al*. (2002, 2005), and Catlett *et al*. (2010). These include data for the megaladapid *Megaladapis edwardsi*, palaeopropithecids *Palaeopropithecus ingens*, *Mesopropithecus globiceps*, and *Babakotia radofilai*, and archaeolemurids *Archaeolemur majori* and *Hadropithecus stenognathus*. Estimated body masses for extinct lemurs were taken from Jungers *et al*. (2008). Finally, comparative data on endocranial volume, body mass, and RP of primates were taken from Hogg *et al*. (2015).

We followed Hogg *et al.* (2015) in plotting the natural logarithm of Retzius line periodicity against the natural logarithms of body mass and ECV. We then used Discriminant Function Analysis (DFA) to determine whether variation in traits (i.e., the sequences of dental eruption, cranial suture maturation, humeral and femoral epiphyseal fusion, postcranial growth, RP, ECV, and body mass) distinguish lemuriform families from each other, and distinguish lemuriforms (suborder Strepsirrhini) as a group from anthropoids (suborder Haplorhini). We determined the degree to which *Pachylemur* resembles other Lemuridae in the relationships among these variables. Each DFA was based on correlation matrices and for each analysis, we grouped all individuals, with the exception of *Pachylemur*, by family. We treated *Pachylemur*'s familial affiliation as unknown and allowed its scores on Functions 1 and 2 to reveal its similarity to members of different primate families, and, thus, to determine whether this taxon "behaves" like a lemurid. We examined the correlation matrices for relationships between the scores of individuals on original variables and on Functions 1 and 2 for each analysis. This allowed us to interpret each discriminant function as a contrast vector, i.e., with some original variables strongly positively correlated and others strongly negatively correlated with the function scores of specimens. In this manner we could determine which traits are most important in distinguishing individuals with high and low scores on each function axis.

To determine the relationship in *Pachylemur* between postcranial and cranial maturation, and how this relates to patterns in other primate taxa, we entered the scores for immature skeleton UABEC 0889 into a discriminant function analysis. We restricted this analysis to this individual and individuals belonging to other primate taxa that were at roughly the same dental developmental stage. By effectively holding dental developmental stage constant, we could determine how far along the developmental trajectories for cranial maturation and for both postcranial growth and maturation individuals of roughly equivalent dental development but belonging to different taxa had progressed. We could then assess differences in relative growth and development of various body parts across taxa, including *Pachylemur*. All statistical analyses were conducted using the "Statistical Package for the Social Sciences" (SPSS 26 and 27).

Results

Dental eruption sequence

When immature specimens of mammals are microCT-scanned, the sequence of dental eruption can be reconstructed to a large degree from a single specimen. From our 3D scan of a mandible of immature *Pachylemur* (UABEC 0456), well-developed crowns of all permanent teeth are evident (Figure 3). This figure also shows the last deciduous premolar (dp_4) and first permanent molar (m_1) fully erupted; the other deciduous teeth are missing but were clearly fully erupted, as evidenced by the presence of deeply-rooted alveoli. Judging from the stage of development of the unerupted teeth, in particular the roots, this specimen suggests that the tooth comb (the lower canine and two incisors) would erupt prior to the eruption of m_2, followed by p_4, followed quickly by the third molar, p_2, and p_3. This sequence is common in members of the family Lemuridae; essentially four teeth (the three permanent replacement teeth and the last molar) erupt in close succession, with one of the permanent premolars variably preceding the last molar. Using the methods of King (2004) for our full series of *Pachylemur* at different dental developmental stages yielded a slightly different order; we found that the three replacement premolars (part of set 3) erupt after the third molar in the order p_4, p_3, and p_2 (see Table 2). In Table 3 we present inferences regarding the mandibular dental eruption order for *Pachylemur* based on sequence heterochrony,

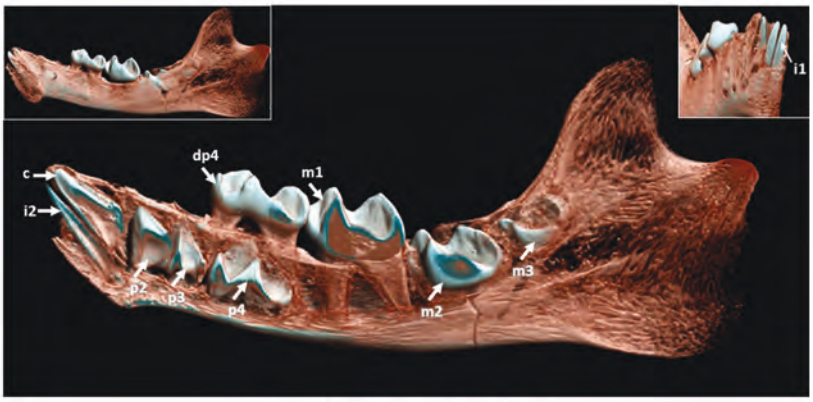

Figure 3. Internal view of a 3D-scanned right hemimandible of an immature *Pachylemur insignis* (UABEC 0456) from Vintany Cave, Tsimanampesotse National Park. A reconstruction of the dental eruption sequence is provided below the scan; teeth in brackets are at essentially identical developmental stages.

Table 3. Comparison of the mandibular eruption sequences of lemurs, canines excluded, derived using King's (2004) methods of sequence heterochrony (i: incisor, p: premolar, m: molar).

Species	Dental eruption order							
Lepilemur ruficaudatus	m1		m2	ii	m3	p4	p2	p3
Archaeolemur majori	m1		m2	ii	m3	p4	p3	p2
Archaeolemur edwardsi	m1		m2	p4	m3	p3	ii	p2
Hadropithecus stenognathus	m1		m2	ii	m3	p4	p3	p2
Lemur catta	m1		m2	ii	m3	p4	p2	p3
Varecia variegata	m1		m2	iip4	m3	p3	p2	
Pachylemur insignis	**m1**	**ii**	**m2**		**m3**	**p4**	**p3**	**p2**
Hapalemur griseus	m1	ii	m2		m3	p4	p3	p2
Eulemur mongoz	m1	ii	m2		m3	p2	p4	p3
Eulemur macaco	m1	ii	m2	p2	m3	p4	p3	
Eulemur rufus	m1	ii	m2	p2	m3	p4	p3	
Eulemur collaris	m1	ii	m2	p4	m3	p3	p2	
Eulemur albifrons	m1	ii	m2	p4	m3	p3	p2	
Indri indri	m1	ii	m2	p4p2	m3			
Avahi laniger	m1	iip4	m2	p2	m3			
Propithecus verreauxi	m1	ii	m2	p4p2	m3			
Propithecus edwardsi	m1	ii	m2	p4p2	m3			
Propithecus coquereli	m1	ii	m2	p4p2	m3			

along with comparative data for other extinct and extant lemurs.

Index of Relative Retardation of the Replacement teeth (RRR)

According to our data, *Pachylemur* has a moderately high value for the index of RRR, whether calculated on the basis of sequence heterochrony (2.2) or our microCT-scan (2.0) (Table 4). Its developmental sequence is like those of other extant Lemuridae (especially *Varecia variegata* and *Hapalemur griseus*). The possession of a high (≥ 2.0) index of RRR is also shared with the families Lepilemuridae, Archaeolemuridae, and Megaladapidae. This dental developmental pattern differs from that of the Indriidae (*Indri*, *Avahi*, *Propithecus*) and most anthropoids, wherein the permanent premolars erupt mainly if not entirely prior to the eruption of the third molar. Data for the Palaeopropithecidae are sparse but they suggest that these animals displayed the dental eruption pattern of extant indriids (their sister taxon) (Godfrey *et al*., 2002; Schwartz *et al*., 2002).

Retzius line periodicity (RP)

Pachylemur has an RP of 3, which falls within the range of variation for all Malagasy lemurs, extinct

Table 4. Relative Retardation of the Replacement teeth (RRR) values for lemurs and other primates, as well as the tree shrew, *Tupaia*.

Taxon	Family	Dental eruption order (mandibular)						RRR
Tupaia	Tupaiidae	m1		m2		m3	pipipi	3.0
Aotus	Aotidae	m1		m2	i	m3	ippp	2.8
Archaeolemur edwardsi	Archaeolemuridae	m1		m2	p	m3	piip	2.8
Hadropithecus stenognathus	Archaeolemuridae	m1		m2	ii	m3	ppp	2.6
Archaeolemur majori	Archaeolemuridae	m1		m2	ii	m3	ppp	2.6
Lepilemur ruficaudatus	Lepilemuridae	m1		m2	ii	m3	ppp	2.6
Lemur catta	Lemuridae	m1		m2	ii	m3	ppp	2.6
Hapalemur griseus	Lemuridae	m1	ii	m2		m3	ppp	2.2
Pachylemur insignis	**Lemuridae**	**m1**	**ii**	**m2**		**m3**	**ppp**	**2.2**
Pachylemur insignis	**Lemuridae**	**m1**	**ii**	**m2**	**p**	**m3**	**pp**	**2.0**
Varecia variegata	Lemuridae	m1	ii	m2	p	m3	pp	2.0
Megaladapis edwardsi	Megaladapidae	m1	ii	m2	p	m3	pp	2.0
Saimiri	Cebidae	m1		m2	iippp	m3		2.0
Pongo	Pongidae	m1		m2	ipip	m3		2.0
Eulemur collaris	Lemuridae	m1	ii	m2	pp	m3	p	1.8
Eulemur rubriventer	Lemuridae	m1	ii	m2	pp	m3	p	1.8
Semnopithecus	Cercopithecidae	m1	ii	m2	p	m3	p	1.75
Indri indri	Indriidae	m1	ii	m2	pp	m3		1.5
Propithecus verreauxi	Indriidae	m1	ii	m2	pp	m3		1.5
Propithecus edwardsi	Indriidae	m1	ii	m2	pp	m3		1.5
Papio	Cercopithecidae	m1	ii	m2	pp	m3		1.5
Chlorocebus	Cercopithecidae	m1	ii	m2	pp	m3		1.5
Macaca	Cercopithecidae	m1	ii	m2	pp	m3		1.5
Gorilla	Hominidae	m1	ii	m2	pp	m3		1.5
Pan	Hominidae	m1	ii	m2	pp	m3		1.5
Avahi laniger	Indriidae	m1	iip	m2	p	m3		1.25
Hylobates	Hylobatidae	m1	iip	m2	p	m3		1.25
Homo	Hominidae	m1	iip	m2	p	m3		1.25

and extant. All indriids, lemurids, megaladapids, and palaeopropithecids measured to date have RP values of 2 or 3. The families with the lowest mean RP values are the Palaeopropithecidae ($\bar{x}$ = 2.33) and the Indriidae ($\bar{x}$ = 2.43). The mean for the Lemuridae (including *Pachylemur*) is 2.75 and for the Megaladapidae is 3.0. The lemur families with the highest mean values are the Archaeolemuridae ($\bar{x}$ = 4.0) and the Daubentoniidae ($\bar{x}$ = 3.5).

Endocranial volume

Values of endocranial volume for nine skulls of fully adult *Pachylemur* ranged from 40 to 46 cc, with a mean of 42.7 cc (Table 5). This mean value is in line with expectations for a member of the family Lemuridae of its body size (Figure 4). In general, among Lemuriformes, the Palaeopropithecidae and Indriidae have the lowest expected brain size given their body size, the Daubentoniidae and Archaeolemuridae have the highest, and the Lemuridae and Megaladapidae are intermediate. This pattern parallels that for variation in RP.

Table 5. Average cranial capacity for adult *Pachylemur*.

Specimen number	Cranial capacity (ml)
UABEC 0311	43
UABEC 0815	44
UABEC 0321	40
UABEC 0307	41
UABEC 0814	40
UABEC 0308	44
UABEC 0767	45
UABEC 0531	41
UABEC 0753	46
Mean	**42.7**

Comparative analyses

Given our new observations for RP and ECV (as well as estimated body mass) for *Pachylemur*, we can revisit how ECV and body mass correlate with RP in strepsirrhines and haplorhines, with an emphasis on how these aspects of *Pachylemur*'s biology are related. In Figures 5 and 6 we reproduce analyses presented in Hogg *et al*. (2015) but update them to include *Pachylemur*.

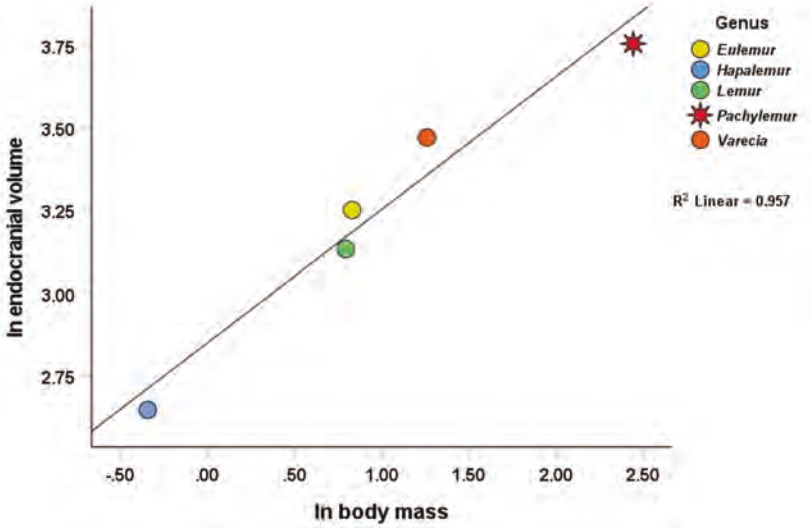

Figure 4. Relationship between ln endocranial volume in cc (ECV) and ln body mass (kg) in Lemuridae. *Pachylemur* has an ECV as expected of a lemurid of its reconstructed body mass.

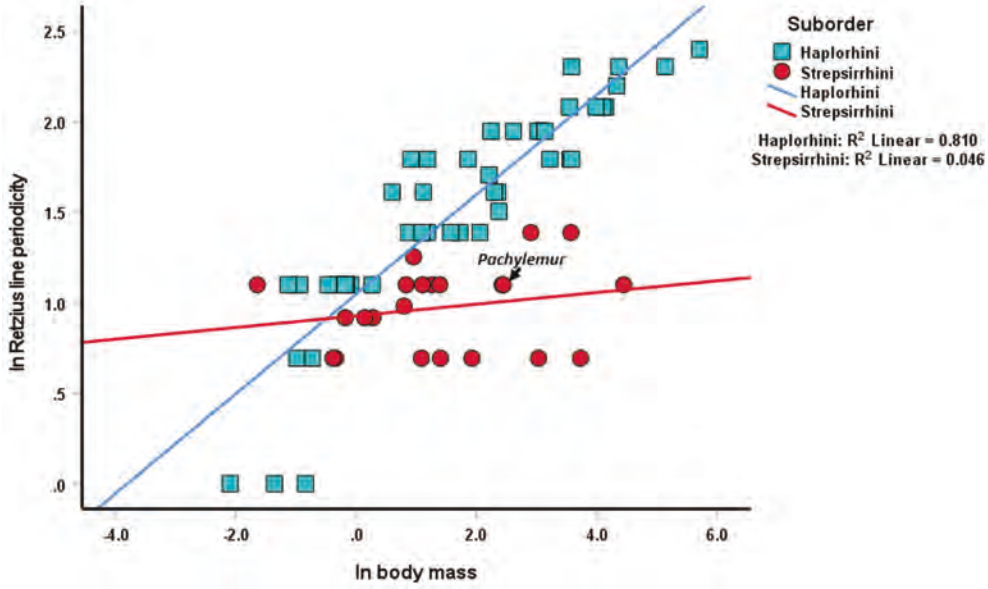

Figure 5. Linear regression of ln Retzius line periodicity (Y) on ln body mass (X), with separate regression lines calculated for anthropoids (Haplorhini) and lemurs/lorises (Strepsirrhini). The RP value for *Pachylemur* is below the regression line for anthropoids of its body mass.

When compared to a broader sample of strepsirrhines and haplorhines, *Pachylemur* falls where expected for a lemurid of its body mass and ECV (Figures 5 and 6). Figure 5 shows regressions for haplorhines and strepsirrhines (including *Pachylemur*) of ln Retzius line periodicity (Y) on ln body mass (X). For haplorhines, the variance in RP values explained by body mass is 81.0%, while for strepsirrhines, only 4.6% of the variance in RP values is explained by body mass (Figure 5). Virtually all strepsirrhines (red dots) fall below the haplorhine regression line (blue line) for RP on body mass. This is true of *Pachylemur* as well as almost all other strepsirrhines. The RP value for *Pachylemur* is higher than expected for an average strepsirrhine of its body mass, but lower than expected for an average anthropoid of its body mass.

In Figure 6 we show regressions for haplorhines and strepsirrhines (including *Pachylemur*) of ln Retzius line periodicity (Y) on ln endocranial volume or ECV (X). As expected, endocranial volume is a much better predictor of RP in haplorhines (76.4% variance explained) than in strepsirrhines (12.7% variance explained). However, again as expected for strepsirrhines, more variance in RP values is explained by ECV than by body mass. *Pachylemur* has an RP that is below the regression line for haplorhines of its cranial capacity but above the

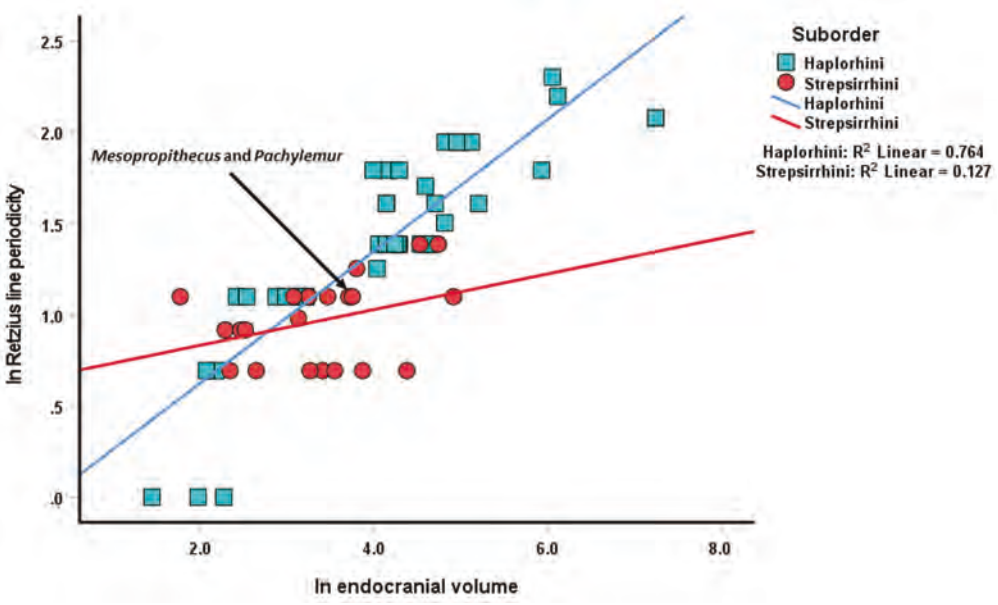

Figure 6. Linear regression of ln Retzius line periodicity (Y) on ln endocranial volume (X), with separate regression lines calculated for anthropoids (Haplorhini) and for lemurs and lorises (Strepsirrhini). The RP value for *Pachylemur* falls below the regression line for anthropoids of its endocranial volume.

regression line for strepsirrhines of its cranial capacity. This is because expected RP values for indriids and palaeopropithecids are very low.

Thus, adding *Pachylemur* to the sample strengthens the fundamental observations made by Hogg *et al*. (2015): 1) that RP values of haplorhines are better explained by body mass than are those of strepsirrhines; 2) that RP values of haplorhines are better explained by ECV than are those of strepsirrhines; and, 3) that ECV does better than body mass in explaining the RP values of strepsirrhines.

A series of discriminant function analyses that depict relationships among families or superfamilies of primates based on parameters reflecting growth and development are shown in Figures 7 to 10. In 100% of the analyses we ran, *Pachylemur* (coded as unknown for family and superfamily) falls with other members of the family Lemuridae, or the superfamily Lemuroidea depending on the DFA, and thus its inclusion in this family is supported by our analyses.

A DFA based on cranial suture closure (which sutures fuse relatively early and which fuse relatively late) nicely separates strepsirrhines (with negative scores on Function 1) from haplorhines (with positive scores on Function 1) (Figure 7). The main difference between strepsirrhines and haplorhines is the relative timing of the fusion of the basioccipital and metopic sutures. Furthermore, lemurs and lorises are distinct from each other on Function 2, indicating that lemurs have relatively later fusion of the squamosal, zygotemporal, and lambdoidal sutures, but earlier fusion of the metopic and frontonasal sutures. Interestingly, this mirrors the way in which cercopithecoids differ from hominoids, with respect to the timing of cranial suture closure.

When a DFA of mandibular dental developmental sequences is used to distinguish among families of primates, the results replicate inferences drawn from analyses of RRR values (Figure 8). The families are distinguished on Function 1 by the relative timing of eruption of the third and fourth premolars and the third molar, with relatively early eruption of the permanent premolars and late eruption of third molars (as seen in Cebidae, Cercopithecidae, Hominidae, and Hylobatidae) differing from taxa possessing relatively late eruption of the premolars and relatively early eruption of the third molar (Galagidae and Lemuridae, the latter including *Pachylemur*). The Lepilemuridae and Indriidae have intermediate values on this function. Function 2 separates the Indriidae from all other families by their relatively earlier eruption of the premolars (including the fourth premolar) and the two permanent incisors.

We also evaluated whether combined variation in RP, ECV, and body mass distinguishes among lemuriform families, and whether *Pachylemur* resembles other lemurids (Figure 9). Function 1 explains the variance in RP that is positively correlated with endocranial volume (particularly) and to some extent body mass. Unsurprisingly, this axis distinguishes the Archaeolemuridae and Daubentoniidae with high RP and ECV values from

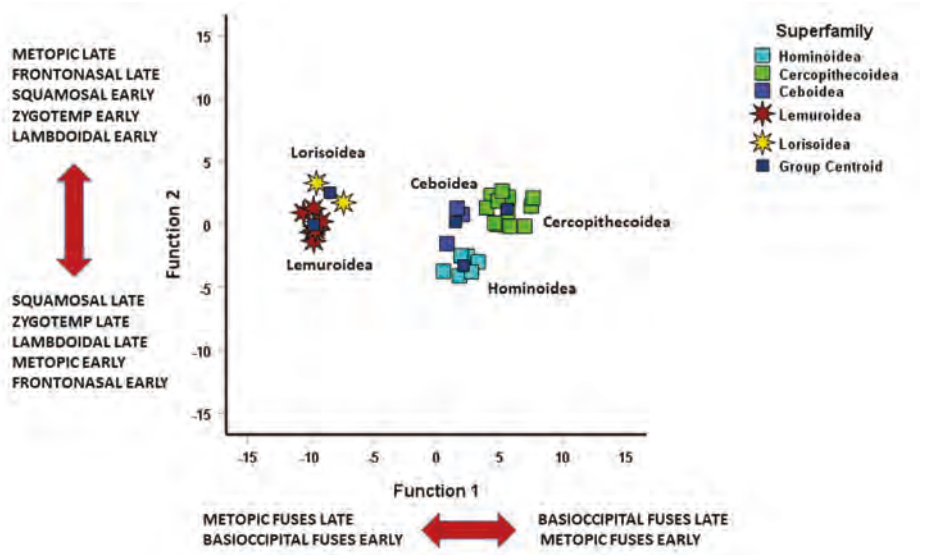

Figure 7. Discriminant function analysis based on the relative timing of cranial suture closure distinguishes strepsirrhine and anthropoid superfamilies.

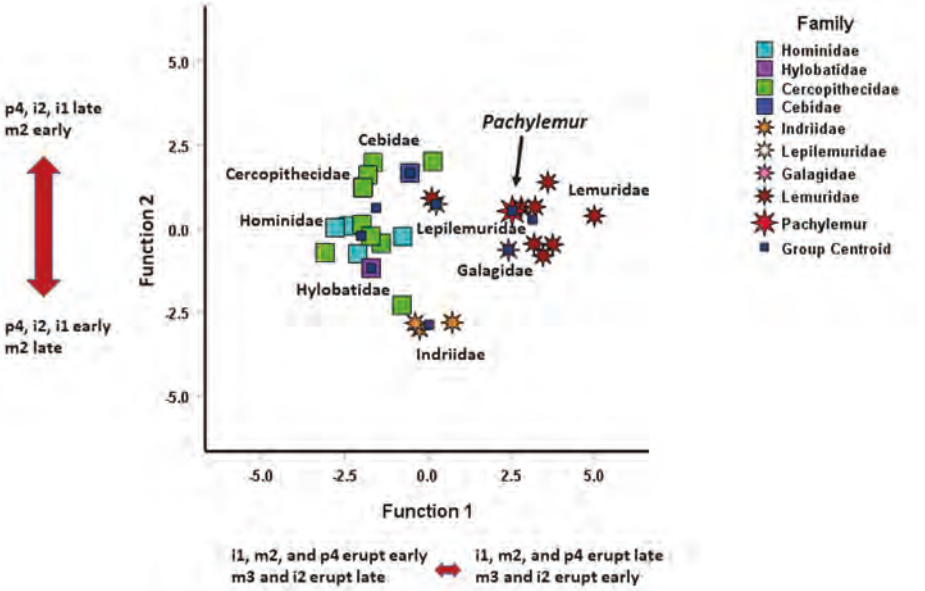

Figure 8. Discriminant function analysis based on the relative timing of mandibular dental eruption distinguishes strepsirrhine and anthropoid families.

the Indriidae and Palaeopropithecidae with low RP and ECV values. Function 2 accounts for the variance in RP that is inversely correlated with body mass. The Palaeopropithecidae and Megaladapidae have large bodies but low RP values, while *Daubentonia* has a relatively small body and high RP value. The Lemuridae and the basal member of the Palaeopropithecidae (i.e., *Mesopropithecus*) fall in the middle of the plot, with intermediate values on both Functions 1 and 2. According to posterior probability values, *Pachylemur* (just below *Mesopropithecus* on Figure 9) is positioned closest to the Lemuridae centroid and is thus classified as a lemurid. We ran another DFA comparing relative maturation (% attainment of full adult epiphyseal fusion and full adult cranial suture closure) in strepsirrhine and haplorhine individuals at dental developmental stages between 0.62 and 0.82 (effectively holding dental developmental stage constant). In effect, this DFA summarizes the relationship between craniodental maturation and postcranial growth and maturation in various primate families (Figure 10). In comparison to anthropoids, all lemurs exhibit relatively rapid postcranial maturation and relatively slow cranial maturation. Within the strepsirrhines, indriids and lorisids differ from lemurids in displaying relatively slow postcranial growth and development. Thus, lemurids have relatively rapid postcranial growth and development not merely in comparison to anthropoids, but also to indriids and lorisids.

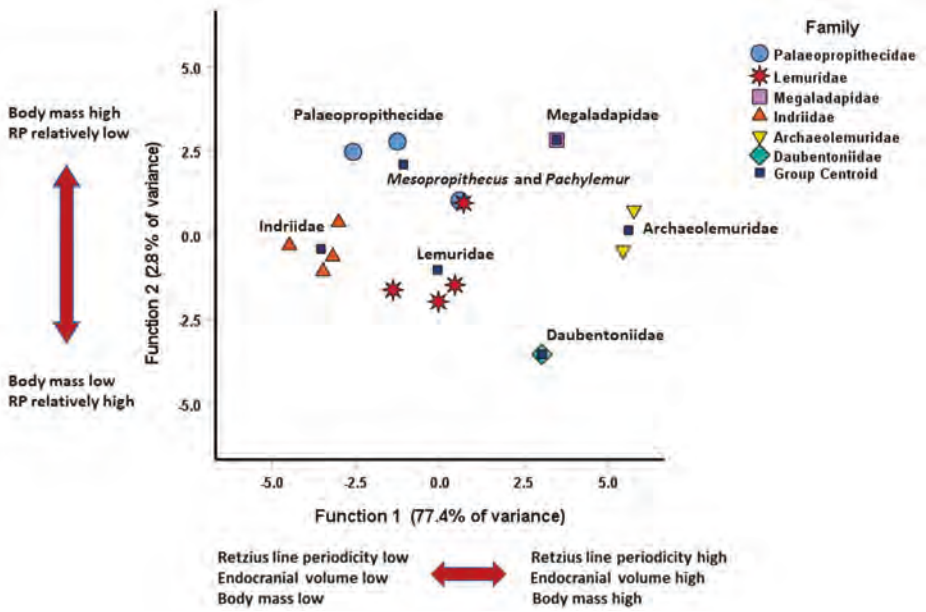

Figure 9. Discriminant function analysis based on RP, ECV, and body mass separates lemur families.

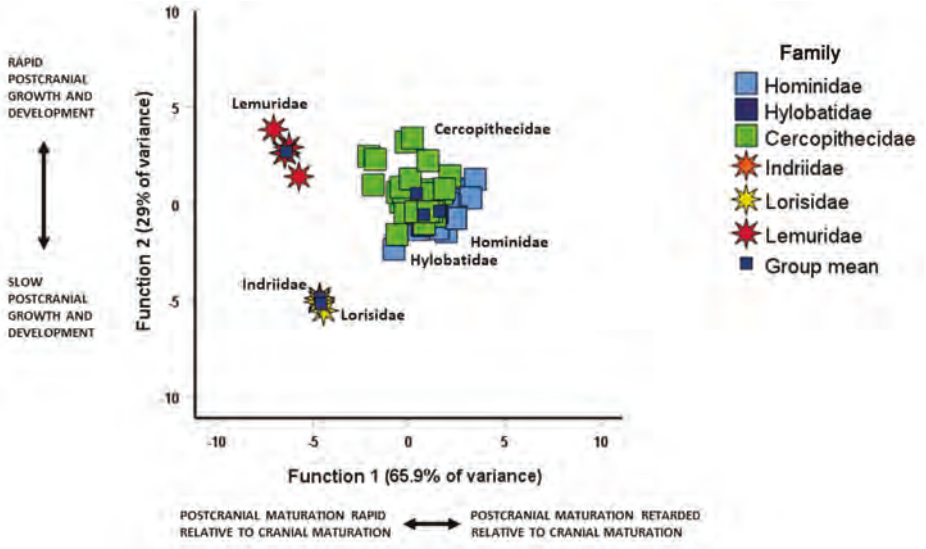

Figure 10. Discriminant function based on the relationship between cranial development, postcranial growth, and postcranial development separates strepsirrhine and anthropoid families.

Discussion

A combined analysis of how skeletal and dental maturation intersect with body and brain size in strepsirrhine taxa, both on their own and in relation to haplorhines, allows us to render several inferences about the overall growth biology of lemuriformes more generally, and of *Pachylemur* specifically.

First, energy expenditure may be critical to understanding RP and ECV in lemurs. It has long been appreciated that lemurs deviate from primate norms of growth and development in unusual ways (Schwartz *et al*., 2002, 2005; Godfrey *et al*., 2006). Among lemurs, as Hogg *et al*. (2015) showed, brain size and activity levels correlate (albeit weakly) with RP values, but body size does not correlate with RP values. Extinct lemurs, like their extant counterparts, have low RP values, and the largest-bodied extinct lemurs have some of the lowest values. Hogg *et al*. (2015) proposed that this may relate to constraints on energy expenditure in lemurs (i.e., selection for risk-averse life histories). They hypothesized that the deviations from the expected correlations in lemurs may relate to low basal metabolic rates and a need to conserve energy in resource-poor environments. Energy expenditure is hypothesized on the basis of their skeletal anatomy to have been extremely low in some of the largest-bodied extinct lemurs, including

the palaeopropithecids and megaladapids (Jungers *et al*., 2002; Shapiro *et al*., 2005; Godfrey *et al*., 2012, 2016). None of the extinct giant lemurs had postcranial characteristics suggesting great agility. Most were arboreal with adaptations for deliberate climbing, and some had adaptations for slow (sloth-like) suspended movement below branches. Extinct lemurs also had small semicircular canals, which are organs of equilibrium in the inner ear, also emphasizing presumed low levels of agility. Again, the palaeopropithecids and megaladapids are the least agile (Walker *et al*., 2008).

If brain size and energy expenditure (but not body size) are the key correlates of RP values in lemurs, then one would expect those animals expending the least energy and with the relatively smallest brains to have the lowest RP values and those expending the most energy and with the relatively largest brains to have the highest RP values. The lack of correlation between body size and RP values in lemurs could perhaps be understood if it is recognized that some of the largest-bodied lemurs (palaeopropithecids and to a lesser extent, the megaladapids) were also some of the least active lemurs. The smaller-bodied archaeolemurids were more active (and had relatively larger brains) than either the megaladapids or the palaeopropithecids (Walker *et al*., 2008), though they were neither as active nor as large-brained as anthropoids of equal body size. The RP of *Archaeolemur* (RP = 4) is low compared to anthropoids of similar size, such as *Theropithecus* (RP = 7), with which *Archaeolemur* has been compared (Jolly, 1970; Tattersall, 1975).

Skeletal evidence supporting the notion that *Pachylemur*, like its lemurid relatives, was less active than anthropoids of equal body mass, is now bolstered by strontium isotopes. These data suggest that the giant lemurs, including *Pachylemur*, had small home ranges (Crowley & Godfrey, 2019). If RP and ECV values are correlated with energy expenditure as was suggested by Hogg *et al*. (2015) for other lemurs, then we would expect *Pachylemur* to have values for RP and ECV that are lower than anthropoids of comparable body mass. This is, in fact, what we observe.

Our second major inference is that RRR and the sequence of dental eruption may have phylogenetic significance. Our data demonstrate family-specific patterns of dental eruption and are thus consistent with other studies that have concluded that dental eruption sequences are phylogenetically conserved in primates (López-Torres *et al*., 2015; Monson & Hlusko, 2018). Monson & Hlusko (2018) argue that the third molar erupted before one or more premolars in the ancestor of primates, and that this pattern is conserved in many descendants. However, within anthropoids, whereas there are several taxa which have a sequence of dental eruption that conforms to the ancestral condition, these may represent secondarily derived sequences (Monson & Hlusko, 2018). The pattern observed in *Pachylemur* and other lemurids manifests itself widely in primitive primates.

Third, our data do not support the notion that RRR values can be used as a proxy for the absolute pace of growth and development. Godfrey *et al*. (2005) showed that Schultz's Rule does not hold for lemurs. Similarities in RRR values in distantly related family groups are not necessarily meaningful indicators of life history parameters. If we compare living lemurids to indriids, we have seen that lemurids (including *Pachylemur*) have relatively early eruption of the molars and late eruption of the premolars, whereas indriids have relatively late eruption of the molars and early eruption of the premolars. RRR values for extant lemurids are considerably higher than those for extant indriids. Based on Schultz's Rule, we would expect that Lemuridae should have faster dental development than Indriidae, but the opposite is actually true (Godfrey *et al*., 2004). Whereas we do not yet know how old *Pachylemur* was at any particular dental developmental stage, we do know that *Pachylemur* behaved like other lemurids in its sequence of dental eruption and in its relationship between cranial and postcranial developmental rates.

It might appear that Schultz's Rule is supported by the fact that RRR values are similar (and low) in indriids and hominids, and these two families are comprised of species that reproduce slowly and have prolonged life histories. However, the dental developmental trajectories of indriids and hominids differ markedly in other ways. In indriids, the permanent mandibular premolar crowns develop in an overlapping manner, forming largely prenatally in a constrained space. The low values of RRR in indriids reflect very accelerated growth and eruption of the permanent replacement teeth. In *Gorilla*, *Pan*, and *Homo*, on the other hand, growth and eruption of the replacement teeth are not accelerated; rather, low values of RRR reflect delayed molar eruption. Among lemurs, the species with the slowest pace (in absolute time) of dental development and eruption (the archaeolemurids) have very high values of RRR, and not the opposite.

Perhaps our most important inference is that *Pachylemur* resembled lemurids, and not like-sized anthropoids, in traits related to life history. As noted above, in addition to having a high RRR, *Pachylemur* resembled lemurids but not indriids in exhibiting relatively accelerated postcranial (cf. craniodental) development. These characteristics distinguish *Pachylemur* not merely from indriids but also from anthropoids. We have documented fundamental differences between lemurs (including *Pachylemur*) and anthropoids in dental development, cranial maturation, postcranial growth and maturation, and "life-history related" characteristics, such as ECV and RP.

There is no overlap between *Pachylemur* and like-sized anthropoids in values for either ECV or RP. *Pachylemur* has an estimated body mass of around 11 kg, an ECV of a little over 40 cc, and an RP of 3. Anthropoids of roughly the same body mass (9 to 13 kg) have ECV values over twice as big (~100 to 150 cc) and RP values approximately twice as large (5 to 7) as those of *Pachylemur*. These anthropoids include New World monkeys such as *Lagothrix lagothricha*, cercopithecoids such as *Semnopithecus entellus*, some baboons, and hominoids such as the *Symphalangus syndactylus*.

Future life history research on *Pachylemur* may elucidate reproductive parameters. For now, inferences regarding reproductive parameters in *Pachylemur* are necessarily speculative. Given the suite of anatomical (dental, cranial, and postcranial) similarities of *Pachylemur* to *Varecia*, as well as their similar developmental trajectories, it is tempting to think they may have had similar reproductive profiles. Dental histology may allow us to test aspects of this hypothesis in the future. A preliminary and ongoing histological analysis of *Pachylemur* dental development reveals the presence of accentuated striae in the cuspal region of the M1 protoconid (see Figure 2, left panel). Operating under the reasonable assumption that the *in utero* environment buffers a developing fetus against 'stress', the presence of a prominent accentuated line, a potential candidate for a neonatal line, early on during M1 formation suggests that the timing of birth fits with an overall chronology of molar development that is more similar to extant lemurids than to extant indriids (Schwartz *et al*., 2002, 2005). Continued histological work, combined with analyses of tooth chemistry, should reveal the exact timing of birth relative to molar development as well as the timing of important life history attributes such as the weaning transition.

In many anthropoid families, there is an inverse correlation between body size and reproductive rates; large-bodied species tend to have low reproductive rates. This is not the case for extant lemurids. This is because the largest-bodied species of extant lemurids, *Varecia* spp., regularly give birth to litters of multiple offspring, with average litter sizes for different study populations of 1.7 to 2.7 offspring (Baden *et al*., 2013). Reproductive rate (the average number of offspring per female per year) depends not merely on average litter size, but on the interbirth interval (IBI). The latter is highly variable in *Varecia*, which may reproduce every year, resulting in a reproductive rate sometimes exceeding 2 (Baden *et al*., 2013). However, an IBI of 4 years was recorded for a population living in a forest at Manombo that had been devastated by a cyclone that hit southeastern Madagascar and killed all fruiting trees, thus eliminating the preferred staples for this population over an extended period of time (Ratsimbazafy, 2002). Dependence on fruit for protein characterizes *Varecia* much more than the more-folivorous lemurs, and the fact that the fruits of Madagascar's fruiting trees tend to be low in protein (Ganzhorn *et al*., 2009) makes their loss all-the-more detrimental to reproduction in this taxon. The reproductive rate for Ratsimbazafy's Manombo population over the recorded four-year period was 0.5. Baden *et al*. (2013) calculated the average reproductive rate for all recorded populations of *Varecia*, including the one devastated by the cyclone, as 1.5 offspring per year, which is nevertheless high.

The point is that larger-bodied lemurid species do not necessarily have lower reproductive rates than smaller-bodied lemurids. Therefore, we cannot assume that *Pachylemur*, by virtue of its larger body size, would have had a low reproductive rate. Vasey & Godfrey (in press) present some indirect evidence (in the form of oral stories) that *Pachylemur* resembled *Varecia* in aspects of its behavior and reproduction: using large fruiting trees for feeding and sleeping; building high-canopy nests for litters of non-clinging altricial young; and foraging at dusk (at least during certain times of year) (see also Vasey *et al*., 2018). If this interpretation is correct, then *Pachylemur* may have had the highest reproductive rates among the extinct lemurs. Ultimately, however, dependency on ripe fruit and large fruiting trees for feeding and nesting could have increased *Pachylemur*'s vulnerability to extinction, as large fruiting trees are vulnerable to fire, logging and habitat fragmentation, all of which are known to have impacted lemur

population viability from the recent past and into the present (Vasey & Godfrey, in press). Future research on the growth and development of *Pachylemur* may help us to better understand these relationships.

Conclusion

We have shown that the developmental profile of *Pachylemur* resembles those of smaller-bodied lemurs, particularly other lemurids, more than those of anthropoids of comparable body size. This is not to say that there are not important developmental differences among lemurs. For example, our data underscore differences between lemurids (including *Pachylemur*) and indriids that may reflect different solutions to the ecological problem of environmental instability. Lemurids exhibit relatively late eruption of the permanent premolars and thus high values for RRR, as well as relatively rapid postcranial growth and maturation, while indriids exhibit the opposite. However, differences between lemurids (including *Pachylemur*) and anthropoids are greater in magnitude and more fundamental than differences among families of lemurs, as they may relate to the fact that, for their body size, lemurs have relatively small endocrania and different biorhythms, as evidenced by their low Retzius line periodicities. These differences may be correlated with dissimilarities in overall energy expenditure in these animals, that are in turn related to environmental constraints, including available resources (such as fruit protein), that may influence the life history strategies of lemurs. They may help us to understand why lemurs, including *Pachylemur*, fail to conform to life history "expectations" that are based on anthropoid norms.

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