Relative tooth size at birth in primates: Life history correlates

Timothy D. Smith[1,2], **Magdalena N. Muchlinski**[3], **Wade R. Bucher**[1], **Christopher J. Vinyard**[4], **Christopher J. Bonar**[5], **Sian Evans**[6,7], **Lawrence Williams**[8], and **Valerie B. DeLeon**[9]

[1]School of Physical Therapy, Slippery Rock University, Slippery Rock PA, 16057

[2]Department of Anthropology, University of Pittsburgh, Pittsburgh PA

[3]Center for Anatomical Sciences, University of North Texas, Health Science Center, Fort Worth Texas 76107

[4]Department of Anatomy and Neurobiology, NEOMED, Rootstown, Ohio 44272

[5]Dallas Zoo, Dallas TX, 75203 USA

[6]Dumond Conservancy, Miami, Florida 33170

[7]Department of Biological Sciences, Florida International University, Miami Fl 33199

[8]Michale E. Keeling Center for Comparative Medicine and Research, Department of Veterinary Sciences. UT MD Anderson Cancer Center

[9]Department of Anthropology, University of Florida, Gainesville, FL.

Abstract

Objectives—Dental eruption schedules have been closely linked to life history variables. Here we examine a sample of 50 perinatal primates (28 species) to determine whether life history traits correlate with relative tooth size at birth.

Materials and Methods—Newborn primates were studied using serial histological sectioning. Volumes of deciduous premolars (dp^2-dp^4), replacement teeth (if any), and permanent molars ($M^{1-2/3}$) of the upper jaw were measured and residuals from cranial length were calculated with least squares regressions to obtain relative dental volumes.

Results—Relative dental volumes (RDVs) of deciduous or permanent teeth have an unclear relationship with relative neonatal mass in all primates. Relative palatal length (RPL), used as a proxy for midfacial size, is significantly, positively correlated with larger deciduous and permanent postcanine teeth. However, when strepsirrhines alone are examined, larger RPL is correlated with *smaller* RDV of permanent teeth. In the full sample, RDVs of deciduous premolars are significantly negatively correlated with relative gestation length (RGL), but have no clear relationship with relative weaning age. RDVs of molars lack a clear relationship with RGL; later weaning is associated with larger molar RDV, although correlations are not significant. When strepsirrhines alone are analyzed, clearer trends are present: longer gestations or later weaning are

Corresponding author: Timothy D. Smith, Ph.D., School of Physical Therapy, Slippery Rock University, Slippery Rock, PA 16057; timothy.smith@sru.edu; phone: 724-738-2885; fax: 724-738-2113.

associated with smaller deciduous and larger permanent postcanine teeth (only gestational length correlations are significant).

Discussion—Our results indicate a broad trend that primates with the shortest RGLs precociously develop deciduous teeth; in strepsirrhines, the opposite trend is seen for permanent molars. Anthropoids delay growth of permanent teeth, while strepsirrhines with short RGLs are growing replacement teeth concurrently. A comparison of neonatal volumes with existing information on extent of cusp mineralization indicates that growth of tooth germs and cusp mineralization may be selected for independently.

Keywords

anthropoid; dental; growth; odontogenesis

INTRODUCTION

Our species' unique ontogenetic trajectory has long been a subject of fascination. Early in the 20th century, cranial characteristics of adult humans were regarded as a retention of subadult characteristics in the adult, paedomorphosis. This can be (and was) discussed both in terms of evolutionary and strictly ontogenetic perspectives. The flexed cranial base and reduced projection of the face (orthognathy) of adult humans were each recognized to resemble juvenile (even prenatal) form more so than in other mammals (Geoffroy Saint-Hillaire, 1836; and see Gould (1977) for a discussion of works by Louis Bolk and others). Research that ensued focused heavily on humans and our closest extant and extinct ancestors (e.g., Weidenreich, 1941), or used non-primate animal models to elucidate the basis for basicranial and facial characteristics (e.g., Dubrul, 1950; Moss, 1961). Early efforts to understand cranial and dental development in a comparative context focused on hominoids. It was clear to most researchers that pongids develop their dentofacial form at a faster pace than humans (Keith, 1931; Krogman, 1930; Schultz, 1935), and this information was brought to bear in interpretation of subadult fossil hominid remains (Zuckerman, 1928). However, this limited comparative scope may have yielded a distorted perspective. As Gould (1977) noted, there is no firm basis to expect that ontogeny of our hominid ancestors matches those of extant pongids. Secondly, a relatively limited focus on non-hominoids in turn limits our ability to identify broader patterns of dentofacial growth across primates.

Schultz (1960) was the first to gather a comparative data set on the duration of life stages in primates. His classic comparison of "life period" among primates illustrated proportions of prenatal, infant, juvenile and adult (including reproductive and post-reproductive) periods in a lemur, monkey and hominoids. Subsequent work has emphasized the great degree of dependency in subadult primates compared to other mammals, as well as the risks and benefits of prolonged juvenility (Altmann, Altmann & Hausfater et al., 1977; Walters, 1987; Zihlman, Morbeck & Goodall 1990). However, dependency does not reflect the state of somatic maturity. Altricial mammals are born poorly developed and completely dependent. Most primates are actually highly precocial in neurosensory development (Grand, 1992; Schaal, Marlier & Soussignan 2000). Although some strepsirrhines are nest bound for a short duration, many primates quickly develop the capacity to cling to their mothers (Ross, 2001), and some are able to leap within weeks (Crompton, 1983; and see Atzeva, Demes,

Demes, Kirkbride et al., 2007). Thus, although primates are regarded as precocial in a broad sense (Martin, 1990), there is variation in the duration of their dependency on maternal care.

Schultz's work on life periods was the first attempt to understand the timing and pace at which maturational and reproductive events occur throughout the lifetime of primates, or their life history. Life history studies on primates have since been conducted using field observations (e.g., Altmann et al., 1977; Zihlman et al., 1990), metrics of growth and development (e.g., Tanner, 1978; Bogin, 1988), and in recent years, comparative studies of non-human primates (e.g., Harvey, Martin & Clutton-Brock, 1987; Charnov & Berrigan, 1993; Janson & Van Schaik, 1993; Ross, 2003).

The limits of Schultz's life periods were devised based on dental eruption data. In the decades since, data on dental eruption have accumulated in literature based on rearing captive primates. Smith et al., (1994) consolidated this literature to produce a new synthesis, and found the dental eruption patterns correlate with primate life history. For example, age at M1 eruption is highly correlated with adult brain weight in primates (Smith 1989; Smith Crummett, & Brandt 1994). She cited this as evidence that brain size and maturation rate are closely tied in mammals. Some significant developmental milestones, such as age at weaning are correlated with dental development: earlier weaning is linked with a more precocious dental arcade (Godfrey, Samonds & Jungers, 2001).

Phylogenetic, adaptive, and structural influences may all play a role in determining dental eruption patterns. The adaptive influences on developing teeth have traditionally been investigated while controlling for the effect of phylogeny (e.g., Scott, 2012; Winchester, Boyer & St. Clair 2014; Terhune, Cooke & Otárola-Castillo 2015). Smith (2000) categorized life history as an important adaptive factor affecting dental eruption. Facial architecture may also have a structural influence on dental eruption, morphology, or even tooth size, due to spatial constraint related to facial dimensions or covariance of jaw/dental growth (Boughner & Dean, 2004; Scott, 2012; Vinyard & Hanna, 2005).

Here, we examine the size of the tooth germ at birth. Birth represents an important point of transition in the type of maternal investment (gestational development to lactational investment of the prenatal placental mammal). Tooth germ size may be directly assessed for correlation with other body metrics, including measurements of facial dimensions. We can also compare dental measurements to gestational length or weaning age to draw inferences about the nature of parental investment.

Rationale and hypotheses

All primates are born completely dependent on maternal care, at least initially, and then are provisioned by the mother for a variable duration. The maturational state of the teeth at birth is strictly a result of prenatal growth and development, and an indirect reflection of maternal investment. However, the study of dental characteristics at this age is difficult due to the partially mineralized state of all teeth. Tooth mineralization is an independent process from overall tooth growth in the sense that teeth of differing maturational classes have differing rates of mineralization (Butler, 1967). Few tooth roots are formed at birth in most primates, with some exceptions (e.g., indriids – Godfrey, Samonds, Jungers et al., 2004). Thus, using

radiographic methods or even whole mount preparations the majority of the tooth germ is impossible to measure in most species. In the present study, we examine the volume of postcanine tooth germs using serial histology. Here, we use relative volume of the developing teeth to measure the extent of prenatal growth of the future tooth crown.

Because variation in primate dental eruption status and crown mineralization has been related to many somatic and life history variables (e.g., Godfrey et al., 2001; Schwartz, Samonds, Godfrey, et al., 2002), we test the hypothesis that the extent of prenatal dental growth is under similar influences. Because primates with relatively shorter gestations and/or earlier independence have accelerated eruption of deciduous and permanent dentition, we predict the same relationship exists with postcanine tooth size. Alternatively, it is possible that the growth of the developing teeth may be dictated by factors influencing overall body or midfacial dimensions. If this alternative hypothesis is correct, we predict that relative tooth size at birth is positively correlated with relative neonatal mass and/or relative palatal length, as a proxy for midfacial length.

MATERIALS AND METHODS

Fifty cadaveric primates were studied from 28 species (Table 1). The specimens studied here are all aged from 0 to 6 days of age, and were previously examined in terms of crown-rump length, cranial length, and dental cusp formation to exclude infants that were born preterm (Smith, Muchlinski, Jankord et al., 2015). These were the most pristine specimens from a larger sample of serially sectioned partial heads studied by Smith et al. (2015). Specifically, we selected specimens from this larger sample where the histological cross-sections were not damaged or distorted, which allowed us to measure the perimeter of the dental follicles.

Volumes of deciduous premolars (dp2/dp3 to dp4), premolars (if present) and permanent molars (M1 to 2/3) of the upper jaw were calculated based on serial cross-sectional areas of postcanine tooth follicles. First, at least every fifth section (an interval of 50 to 60 μm) was photographed using a Leica stereomicroscope at 10 to 12.5X, or at 25X using a Leica DMLB photomicroscope (Leica Microsystems: Wetzlar, Germany). Erupted teeth were excluded from analysis because the largest volumetric component of the tooth germ (stellate reticulum) as well as the outer lining (external enamel epithelium) are completely regressed at eruption. In cases where stained sections near the end points of dental follicles were unusable (e.g., due to folding or tearing), unstained sections were retrieved as a replacement. In cases where distortion was too severe throughout the teeth, the tooth was omitted from the analysis. In some cases, absence of individual teeth prevented analysis of a group of teeth (e.g., total deciduous postcanine tooth volume) for a species.

To measure the tooth volumes, the inner perimeter of dental follicle was traced in each section using ImageJ software (NIH). This margin was selected because of its relative stability during histological processing; that is, it was subject to relatively little distortion. In contract, the outer enamel epithelium, which lies inside the follicle, tends to separate and shrink in some cases (Fig. 1). Thus, the follicle is taken to provide a more reliable approximation of overall tooth germ volume. After calibrating to a digital image of a stage micrometer photographed at the same magnification, each traced dental follicle was

measured in mm^2 in every section in which it was present. Each cross-section was multiplied by the distance in millimeters to the next section, yielding a segmental volume of the dental follicle between sections. All segmental volumes were then summed and recorded as dental follicle volume. All postcanine teeth were measured, including replacement teeth, if they were at least at the cap stage of development (see Smith et al., 2015, for tooth stages). Tooth buds were of such minute size that they make little change to summed volumes, and were thus excluded.

In cases where more than one specimen of a species was measured, data were averaged. Cube roots of volumes were used for comparison to the linear cranial length (CL, prosthion-inion), and palatal length (PL, prosthion-posterior midpalatal point). Log_{10} transformations were made of all variables to ensure normality. Plots were generated using JMP 13 to qualitatively examine the data. A life history profile was created for each species, including neonatal body mass (grams), female adult body mass (grams), gestation length (days) and age at weaning (days). Most life history variables were obtained from the compiled life history data base assembled by Kappeler and Pereira (2003), with updates from body masses and life history data collected by LEW and Zehr et al. (2014).

Somatic metric data have been collected and published for all of the specimens used in this study (Smith et al., 2015), and CL was examined for its relationship to our dental volumes. Our CL data are highly correlated (Pearson correlation coefficient: $R^2 = 0.96$; $p < 0.05$) with previous data on neonatal body mass (Table 2). In addition, palatal length (prosthion-posterior midpalatal point) was routinely measured (e.g., Smith et al., 2007), and this was used as a proxy for midfacial length in our analysis. This allows us to draw inferences about the relationship between midfacial length and developing teeth. Most variables were strongly correlated with CL (Table 2; and see Cummings, Muchlinski, Kirk et al., 2012). Therefore, residuals were calculated from a least-squares regression of dental and life history variables versus CL (e.g., relative dental volume). Henceforth, these residuals are referred to as the "relative" value for the dependent variable in question. To provide a size-adjusted metric of neonatal body size, we also calculated "relative neonatal body mass" for each species as the residual from a least-squares regression of neonatal body mass (dependent variable) on adult female body mass (independent variable).

The relationship between life history variables and relative tooth volume was assessed using Pearson correlation tests. Tests were run twice, once for the full sample of primates, and once for strepsirrhines. The sample of anthropoids was considerably smaller and was not analyzed separately. However, a post hoc comparison of the groups was done to assess how relative tooth volume is correlated to relative gestational length in strepsirrhines versus anthropoids. Significance was assessed at $p < 0.05$.

Because closely related species are more likely to share anatomical similarities than more distantly related species, phylogenetic information was considered in morphological analyses. For this analysis we used a dated consensus phylogeny obtained from 10kTrees version 3 (http://10ktrees.fas.harvard.edu/). To examine the effect phylogeny may have on our statistical models, we estimated the parameter lambda (λ), which serves as a measure of phylogenetic signal (Frechleton Harvey PH & Pagel 2002). Non-phylogenetic signals are not

statistically different from a lambda of zero, while values statistically greater than zero indicate that the given tree topology and branch lengths may account for some of the variation in the trait under a Brownian motion model of evolution. We used GEIGER to generate the maximum likelihood estimates of lambda for each variable. A χ^2 distribution was used to evaluate if the maximum likelihood estimate of lambda is significantly greater than 0 and not significantly different from 1. All lambda values were equal to or not statistically different from zero. Therefore a phylogenetic generalized least squares (PGLS) model was not used to examine the relationship between morphometric and ontogenetic variables while controlling for phylogenetic non-independence.

RESULTS

Our head measurements, CL and PL, are significantly and highly correlated with each other and with previous data on neonatal body mass (Table 2). CL and PL have significant and strong correlations with weaning age, with somewhat weaker correlations to gestation age (non-significant between PL and gestation age in the whole sample). CL and PL are significantly correlated with all individual or summed dental volumes; the correlation is notably stronger for deciduous compared to permanent teeth (Table 2). Weaning age has a stronger correlation with individual or summed dental volumes than does gestational length. Among tooth volumes, deciduous teeth are more highly correlated with one another than any is to M1. When the strepsirrhine sample is analyzed separately nearly all correlations are at least slightly stronger (Table 2).

The distribution of log10 transformed data implies a grade shift between strepsirrhines and anthropoids for the deciduous premolars. This is especially salient for dp4, in which most strepsirrhines are distributed above the regression line for all primates, and anthropoids are all distributed below the line (Fig. 2). This separation is similar for data on molars. *Tarsius* is an outlier among haplorhines for M1 (Fig. 2; the deciduous premolars of *Tarsius* were erupted and not measured).

Of all teeth, only the RDV of dp4 is significantly and negatively correlated with relative neonatal body mass (Table 3). However, no other RDVs has a significant correlation with relative neonatal body mass (Tables 3, 4).

All relative dental volumes (RDV) are significantly correlated with relative PL (Table 3). However, when strepsirrhines are analyzed separately, only permanent tooth volumes are significantly, negatively correlated with relative PL; deciduous teeth are poorly correlated, especially dp4 (Table 4). Relative neonatal mass has only one significant (negative) correlation, to the RDV of dp4 (Table 3). However, even this tooth is not significantly correlated to body mass in the strepsirrhine sample, and there is instead a trend of positive correlations of relative neonatal mass and RDVs (Table 4).

In the full primate sample, RDV of deciduous premolars are significantly, negatively correlated with relative gestation length, but M1 or summed permanent tooth volumes are not correlated (Table 3). However, in the strepsirrhine sample RDV of dp4 is not significantly correlated with relative gestation length, and the permanent teeth have stronger

and positive correlations to this life history character (significantly so in the case of the summed molars; Table 4). Plots of these results (Fig. 3) indicate different trends may exist for anthropoids and strepsirrhines. However, our anthropoid sample is small and not cohesive in the case of deciduous teeth. There is a great cohesiveness of data points to the regression lines in the case of permanent tooth volumes. In this case data on the anthropoid sample suggest a negative relationship between gestation length and relative molar volume; in strepsirrhines there is a positive relationship between the same variables (Fig. 4). RDVs of the molars in *Tarsius*, which has the longest relative gestational length, scale along the regression line for strepsirrhines.

No tooth volume has a significant correlation to relative weaning age. However, correlation coefficients are negative for deciduous teeth and positive for permanent teeth (Tables 3, 4).

DISCUSSION

Primate parents may ensure that their young have the means to survive independently during two time intervals. During gestation, the developing primate is solely dependent on the mother for nutrition. Postnatally, the young primate is provisioned by the mother, potentially with some alloparental help, until weaning. The pre-weaning interval may include education by the mother and other adults that may give the juvenile the skills needed for independent feeding, including appropriate food choice strategies or means of acquiring food (see review by Rapaport & Brown, 2008). The relationship of the pace of dental development to these two time intervals is of interest because on the one hand, selection may influence preparatory measures to ensure survival, long before they are actually needed. A relatively long gestation presumably buffers the developing primate from many selective pressures (e.g., dietary). On the other hand, a relatively shorter gestation may delay metabolic investment in dental growth until closer to the time at which teeth are required for independent feeding.

Previous reports reveal primates vary in the overall pace of eruption (Godfrey et al., 2001), and the extent of cusp mineralization, alveolar eruption, and gingival emergence achieved at birth (Smith et al., 1994; Smith et al., 2015). The present study is the first attempt to determine if somatic or life history traits influence tooth size at birth.

Neonatal body mass and midfacial length

Our criteria for specimen selection (based on recorded age and somatic characteristics) was described previously (Smith et al., 2015). The high correlation coefficients between the CL and PL measurements, averaged from our larger sample, and neonatal body mass derived from the literature (Table 2), suggests all three variables are closely associated in terms of the extent of prenatal growth. The somewhat smaller coefficients for PL in the pooled sample likely reflects the great variation in midfacial length across all primates. The significant correlation of CL with all somatic and life history variables is the basis for our size adjustment of dental and life history variables. As an aside, our Pearson's correlation tests on log transformed data suggest a closer relationship of deciduous tooth volume with PL, our proxy for midfacial length. This is consistent with both the greater variability in

presence/absence of permanent tooth germs that are present at birth and the varied extent to which M1-M3 are housed in bone at this age (Smith et al., 2015).

In absolute size, there is a close correlation between neonatal mass and deciduous tooth volumes (less so for permanent teeth – Table 2). However, once the variables are expressed as residuals, the close correlation disappears. The lack of a clear association of RDVs with relative neonatal mass, particularly as compared to gestational length, suggests the teeth do not grow closely in tandem with body size. The findings suggest that relatively undersized infants (small relative to adult female size) do not typically have relatively smaller teeth as a function of altriciality. For example, *Microcebus* and *Aotus* are born with some altricial characteristics, but each has large postcanine RDVs. Conversely, relatively big infants do not consistently have relatively big teeth.

The potential for dissociation of developmental growth rates of body organs or regions is arguably great in primates due to their long lifespan, which also includes prolonged care of juveniles (Leigh & Blomquist 2007). When organ growth patterns are poorly correlated with body mass, we may expect other factors (phylogenetic, or adaptive) are influential. Relative palatal length has straightforward relationship with the RDV when the whole sample is considered: relatively longer midfaces house relatively large teeth. Facial architecture, it seems, is related to tooth size. Interestingly, when strepsirrhines are examined alone, only permanent teeth RDV are significantly correlated, but *negatively* so. This negative relationship is a reflection of early growth of M1-M2/3 and replacement teeth in smaller lemurs and lorises.

Postcanine Tooth Size and Life History

Our results indicate primates with the shortest gestations have large deciduous RDV. However, plots clearly indicate this relationship is strongly driven by strepsirrhines, with the small anthropoid sample being quite variable (Fig. 3). Among strepsirrhines, two cheirogaleids and two lemurids (both *Varecia* spp.) possess large deciduous RDVs for their short gestation lengths. As relative gestation length increases, strepsirrhines have smaller deciduous RDV with the exception of *Hapalemur griseus*, which has the largest RDV of all deciduous teeth, for any primate.

The correlations of gestational length with permanent teeth in strepsirrhines is nearly as strong (though only significant for summed molar RDV), and yet it is a positive correlation. This implies that strepsirrhines with relatively long gestational times use this extended period to increase size of the permanent teeth. In smaller bodied strepsirrhines, this occurs in tandem with rapid development of replacement teeth (Smith et al., 2015): these animals rapidly ready the permanent dentition for use. With the exception of indriids, larger bodied strepsirrhines grow permanent teeth for a long interval (extending past weaning) in which mixed dentition is used for mastication (Godfrey et al., 2001). The plots suggest that anthropoid RDVs of permanent tooth are negatively related to relative gestational length. Our sample of anthropoids may be too small to draw firm conclusions, but the results are consistent with previous descriptive findings (Smith et al., 2015). Permanent molars are notably underdeveloped in certain callitrichines, which represent anthropoids with the greatest relative gestation lengths in our sample. The anthropoid with the smallest relative

gestation (*Aotus nancymaae*) had the largest relative molar size. Results also verify that *T. syrichta*, which has the greatest relative gestation length of any primate, is atypical among extant haplorhines and scale similarly to strepsirrhines. This is in agreement with previous results on the pace of its tooth eruption and gingival emergence (Luckett & Maier, 1982; Guthrie & Frost, 2011) as well as the extent to which the crowns of permanent teeth are mineralized (Smith et al., 2015).

The relationship of relative weaning age to RDVs at birth, if any, is difficult to detect. The lack of any significant correlations may be due to the variable time schedule for weaning (e.g., Rapaport & Brown, 2008; and see discussions in Godfrey et al., 2001, 2003; Bolter & Zihlman 2007). However, the correlations suggest different trends according to tooth class. For the entire sample and for the strepsirrhines, greater relative weaning ages might be associated with larger relative permanent molar tooth volumes. For deciduous teeth, there is a negative relationship, although the relationships are very weak. Further work is required to verify whether these trends reflect actual developmental patterns.

Other potential influences on Tooth Volume at Birth

Previous studies have shown the pace of dental development is faster in folivorous strepsirrhines (Godfrey et al., 2001; Godfrey, Samonds, Wright et al., 2005), based on their relatively large crowns and perhaps advanced mineralization rates (Godfrey et al., 2004; Smith et al., 2015). Do folivores have relatively larger dental volumes at birth? Our sample size of folivores is too small to say for certain; furthermore, some of the folivores in our sample are not obligate folivores and rely heavily on other tough food items like seeds and/or bamboo. These food items have unique mechanical properties, which may have contributed to a mixed signal with regards to dental development and diet. For example, the folivorous *Propithecus coquereli* has a relatively large M1 for CL, but a relatively small dp4 volume. Conversely, in *Hapalemur griseus* dp4 volume is higher than in any other primate relative to CL, while M1 volume fall well within strepsirrhines of similar CL (Fig. 2). If dietary adaptations are apparent at birth, one phenomenon may make it hard to detect: folivores make use of two strategies of dental development: 1) to enlarge the deciduous tooth for relatively prolonged function and/or, 2) to rapidly develop permanent teeth (Godfrey et al., 2004).

Modularity Within Odontogenesis

Leigh & Blomquist (2007) discussed variation in the pace of development of primate body mass, brain size, and other organ systems. They suggested that "…because of their extended lifespans…" primates have "…flexibility as to when to grow different structures…" (p 402). Our findings offer more support for this assertion of modularity of development, but at the tissue level. Just as development of organs may be prioritized, the same is so for different phases of odontogenesis. Our finding of a link between gestational length and certain tooth volumes implies prioritization of one set of teeth, either deciduous or permanent, during gestation.

Another aspect of odontogenesis has not been directly considered in this study – crown mineralization. Does mineralization proceed in tandem with volumetric growth? New

insights may be available by placing dental volume within the context of a recent descriptive account of cusp mineralization in newborn primates (Smith et al., 2015). First, with reference to absolute volume, it may be said more complete mineralization of deciduous teeth are found in cheirogaleids and galagids compared to most (not all) large-bodied lemuroids. The larger bodied folivorous *Propithecus* and *Hapalemur* possess more mineralized teeth than other large bodied lemuroids. Galagids are among the smallest (*Galagoides*) and largest (*Otolemur*) strepsirrhines. Thus, at least based on descriptive knowledge of crown mineralization in newborns (Smith et al., 2015), dental volume and extent of mineralization do not appear to covary. One generalization may be made: the deciduous premolars of all strepsirrhines are well-mineralized (all cusps and basins mineralized), but M1 is far more variable.

The smallest anthropoids, the callitrichines have poorly mineralized deciduous premolars, whereas all other anthropoids have relatively more mineralized deciduous premolars. Anthropoids develop permanent teeth quite differently than strepsirrhines and tarsiers. At birth, no anthropoids are known to possess any mineralization of M2, and in most anthropoids M1 has only commenced mineralization of one to three cusps. Anthropoids delay mineralization of permanent dentition, regardless of M1 volume. Although quantitative study of tooth mineral density is still needed, the results of this study strongly imply that dental volume at birth is independent of degree of mineralization (as asserted by Butler, 1967). If so, selection may act separately on different tooth classes as well as the rate of dental tissue maturation.

Conclusions

The perinatal RDV of postcanine teeth in primates is independent of relative infant size, as reported for the postnatal pace of dental eruption (Godfrey et al., 2003). This indicates that selection on dental eruption is relatively independent of overall somatic patterns. In primates generally, relatively larger midfaces may house larger dentition, but if so this relationship may be more apparent in anthropoids. In contrast, in strepsirrhines relatively longer midfaces house relatively smaller permanent teeth. This negative relationship is owed to the propensity of smaller lemurs and lorises to develop permanent teeth earlier during ontogeny.

Our results indicate strepsirrhines with the shortest gestations have the largest deciduous RDV. Strepsirrhines with relatively long gestational times have larger permanent teeth. Our results on anthropoids are more tentative, but indicate that anthropoids may differ from strepsirrhines and tarsiers: anthropoids with long relative gestation have the smallest RDV of permanent molars. Whereas our findings on the relationship to relative weaning age are not conclusive, our results imply primates have differing strategies for dental growth, wherein the subadult is supplemented maternally during gestational or postnatal (preweaning) periods.

Mineralization is likely selected for independently of dental growth. The timing of dental mineralization would seem to be of special significance for primate mothers, since dental enamel is the most mineralized tissue in the body. We presume investment in mineralization of fetal tissues, enamel in particular, is metabolically costly for primate mothers, as suggested by Godfrey et al. (2004) and more recently by Mongle et al. (2016). While the

cost is ultimately unavoidable, it may be deferred until postnatal development. At that time, the cost for growing specialized tissues may be gradually shifted to the subadult primate, and perhaps to other adults. We hypothesize that mineralization is a more costly investment than growth of overall tooth size, and is more likely deferred than volumetric growth. Further study quantifying the extent and timing of dental mineralization is required.

ACKNOWLEDGEMENTS

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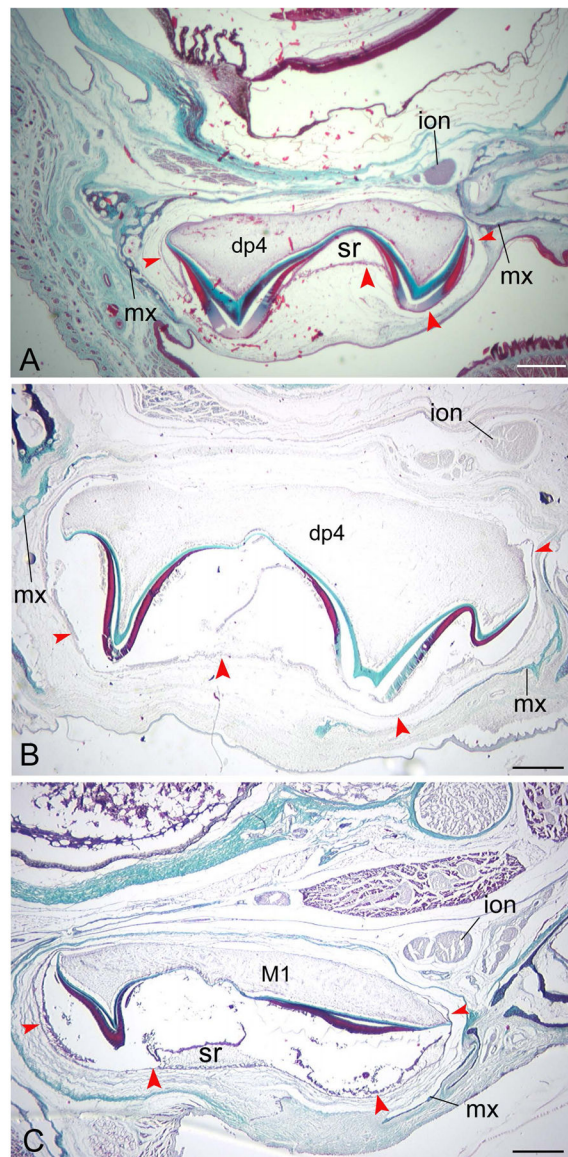
Figure 1:
Coronal sections of tooth germs in neonatal primates, demonstrating measurement site. The amout of the distortion within the follice varies. Without distortion, the developing enamel is close to the follicle at the cusps, or separated by stellate reticulum (Fig. 1A, dp4 of *Otolemur garnettii*). The stellate reticulum (sr) may not preserve as well in some specimens (Fig. 1B, *Eulemur rubriventer*) or may become detached from the developing crown (Fig. 1C, *Hapalemur griseus*). Regardless of the amount of internally distortion, the inner perimeter of the dental follice (red arrowheads), was usually attached to the surrounding maxillary bone (mx) by connective tissue. Thus, as long as the internal perimeter of the follicle was intact, it was used to trace cross-sectional area of the tooth germ in serial sections. ion, infraorbital nerve. Scale: 0.5 mm.
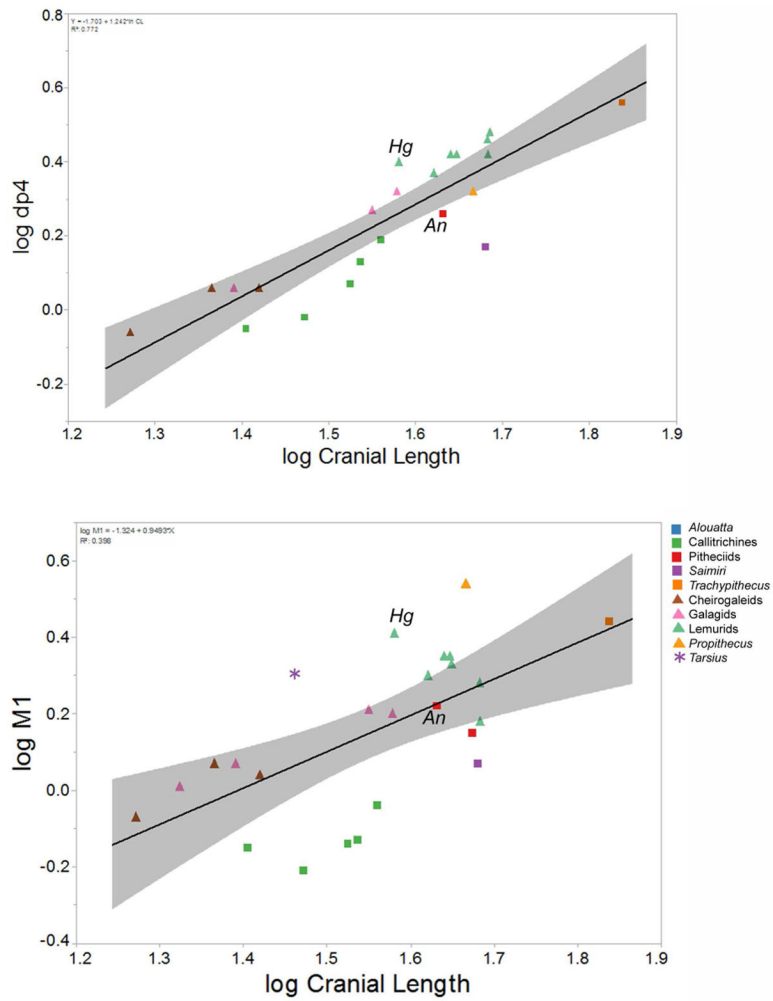
Figure 2:
Graphs showing log10 transformed data of cube root of tooth volumes (dp4 and M1) plotted against log10 cranial length. Squares are anthropoids; triangles are strepsirrhines; * indicates *Tarsius*. An, *Aotus nancymaae*; Hg, *Hapalemur griseus*.
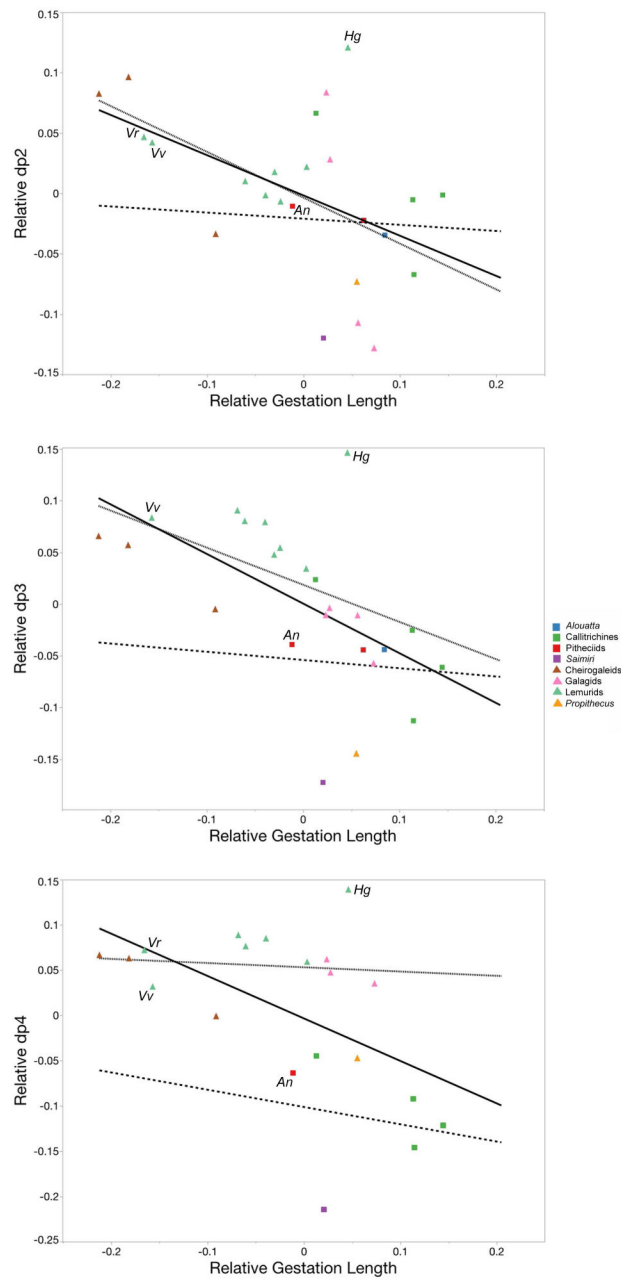
Figure 3:

Relationship between relative deciduous tooth volume and relative gestational length. Solid line indicate linear regression line for all primates; short dashed lines, strepsirrhines; long dashed line, anthropoids. Squares are anthropoids; triangles are strepsirrhines; * indicates *Tarsius*. An, *Aotus nancymaae*; Hg, *Hapalemur griseus*; Vr, *Varecia rubra*; Vv, *Varecia variegata*.

Figure 4:

Relationship between relative permanent tooth volume and relative gestational length. Solid line indicate linear regression line for all primates. Squares are anthropoids; triangles are strepsirrhines; * indicates *Tarsius*. An, *Aotus nancymaae*; Hg, *Hapalemur griseus*; Vr, *Varecia ru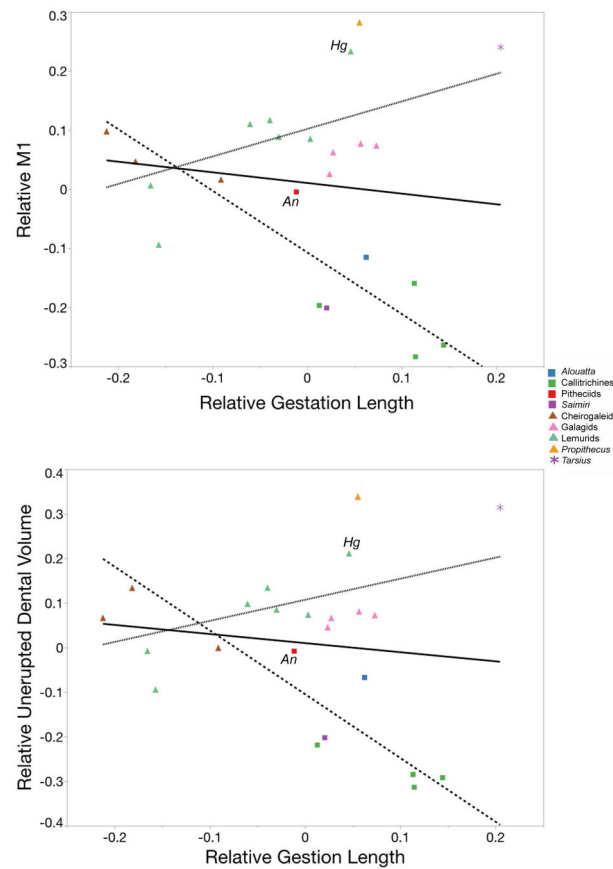bra*; Vv, *Varecia variegata*. Note the relationship to relative gestational length is opposite in strepsirrhines (short dashed line), compared to anthropoids (long dashed line).

TABLE 1:

Primate life history data

Species (n)	neo BM	maternal BM	gestation	weaning	life history sources
Cheirogaleus medius (1)	14.3	156	62.0	61	1,2
Eulemur collaris (1)	50.4	2369	120.0	159	1,2
Eulemur coronatus (1)	46.6	1129	125.0		1,2
Eulemur flavifrons (2)	88.8	2522	129.0	135	1,2
Eulemur mongoz (1)	61.7	1644	129.0	152	1,2
Eulemur rubriventer (1)	89.0	1948	123.0	126	1,2
Galago moholi (2)	12.0	180	123.0	92	1,2
Galagoides demidovii (1)	8.0	63	110.0	45	1,2
Hapalemur griseus (1)	51.8	723	142.5	132	1,2
Lemur catta (2)	65.7	2250	135.0	142	1,2
Microcebus murinus (1)	9.4	68	60.0	40	1,2
Mirza coquereli (1)	15.6	308	87	86	1,2
Otolemur crassicaudatus (1)	46.0	1115	135	135	2
Otolemur garnettii (3)	48. 0	731	132	140	1,2
Propithecus coquereli (2)	106.7	3762	160	182	1,2
Varecia rubra (1)	110.9	3612	98	105	1,2
Varecia variegata (1)	111.4	3543	100	108	1,2
Tarsius syrichta (2)	26.2	120	180	82	2
Alouatta seniculus (1)	295	5427	191	372	2
Aotus nancymaae (1)	94	780	132		2, 3, 4
Callithrix jaccus (4)	28.6	334	148	76	2
Cebuella pygmaea (2)	13.1	101	137	90	2
Leontopithecus rosalia (4)	56.2	579	129	90	2
Pithecia pithecia (1)		1592	164		2
Saguinus geoffroyi (1)	48.1	502			2
Saguinus oedipus (4)	43.1	415	168	50	2
Saimiri boliviensis (6)	104	711	150		2, 3
Trachypithecus francoisi (1)	457	7325		394	2

SOURCES: 1, Zehr et al. (2014); 2, Kappeler PM, Pereira ME (2003); 3, Gestation based on timed matings and trans-abdominal palpations at the Michale E. Keeling Center for Comparative Medicine and Research, Department of Veterinary Sciences. UT MD Anderson Cancer Center; 4, note that an alternative method estimates gestation at 117 days, based PdG levels in urine samples at Dumond Conservancy (Wolovich et al., 2008). Note: either method reveals that *Aotus* has a relatively short gestation compared to most anthropoids, even controlling for body size.

TABLE 2:

Pearson correlation coefficients between life history variable and neonatal metrics for body and tooth size

	PL	NM	GEST	WEAN	dp2 vol.	dp3 vol.	dp4 vol.	M1 vol.	UE vol.	SM vol.
ALL PRIMATES										
CL	**0.87**	**0.96**	**0.51**	**0.86**	**0.93**	**0.91**	**0.87**	**0.61**	**0.48**	**0.55**
PL		**0.83**	0.26	**0.72**	**0.9**	**0.92**	**0.95**	**0.75**	**0.64**	**0.69**
NM			**0.5**	**0.84**	**0.91**	**0.87**	**0.82**	**0.58**	**0.46**	**0.51**
GEST				**0.53**	**0.41**	**0.41**	0.24	0.21	0.13	0.2
WEAN					**0.73**	**0.8**	**0.81**	**0.76**	**0.65**	**0.71**
dp2 vol.						**0.96**	**0.9**	**0.63**	**0.53**	**0.56**
dp3 vol.							**0.97**	**0.73**	**0.63**	**0.67**
dp4 vol.								**0.86**	**0.77**	**0.98**
M1 vol.									**0.98**	**0.99**
UE vol.										**0.99**
STREPSIRRHINES ONLY										
CL	**0.99**	**0.98**	**0.61**	**0.85**	**0.95**	**0.94**	**0.97**	**0.84**	**0.74**	**0.78**
PL		**0.97**	**0.58**	**0.82**	**0.94**	**0.94**	**0.96**	**0.78**	**0.66**	**0.72**
NM			**0.57**	**0.82**	**0.94**	**0.91**	**0.93**	**0.82**	**0.74**	**0.77**
GEST				**0.8**	0.46	**0.54**	**0.6**	**0.75**	**0.69**	**0.77**
WEAN					**0.77**	**0.78**	**0.81**	**0.87**	**0.78**	**0.84**
dp2 vol.						**0.96**	**0.95**	**0.77**	**0.68**	**0.69**
dp3 vol.							**0.98**	**0.77**	**0.64**	**0.68**
dp4 vol.								**0.82**	**0.7**	**0.75**
M1 vol.									**0.96**	**0.99**
UE vol.										**0.98**

CL, cranial length; PL, palatal length; NM, neonatal mass; GEST, gestation length; WEAN, weaning age; vol., volume; UE, unerupted tooth volume (includes P2-P4, if present); SM, summed volume of permanent molars; **bolded** values indicate significant ($0 < 0.05$) correlations.

TABLE 3:

Pearson Correlation Coefficients of Relative Tooth Volumes with Life History Variables : All Primates

Size/Life history variable	dp2 volume	dp3 volume	dp4 volume	M1 volume	Total unerupted dental volume	Total molar volume
Relative palatal length	0.415[*] (25)	0.552[***] (26)	0.752[***] (22)	0.529[**] (25)	0.502[*] (25)	0.503[*] (25)
Relative neonatal mass	-0.098 (24)	-0.362 (25)	-0.590[***] (22)	-0.333 (24)	-0.268 (24)	-0.300 (24)
Relative gestation length	-0.485[*] (25)	-0.567[***] (24)	-0.520[*] (20)	-0.124 (23)	-0.123 (23)	-0.073 (23)
Relative weaning age	-0.244 (20)	-0.182 (21)	0.122 (18)	0.438 (20)	0.376 (20)	0.424 (20)

[*] $P < 0.05$ (2-tailed);

[**] $P < 0.01$;

[***] $P < 0.005$;

sample size in parenthesis. Unerupted dental volume included tooth germs for replacement teeth and permanent molars, when present.

TABLE 4:

Pearson Correlation Coefficients (and sample size) of Relative Tooth Volumes with Life History Variables in Strepsirrhine Primates

Size/Life history variable	dp2 volume	dp3 volume	dp4 volume	M1 volume	unerupted dental volume	Total molar volume
Relative palatal length	0.358 (16)	0.164 (16)	0.054 (14)	-0.613 [*] (15)	-0.596 [**] (15)	-0.583 [*] (15)
Relative neonatal mass	0.477 (16)	0.280 (16)	0.346 (14)	0.130 (15)	0.202 (15)	0.106 (15)
Relative gestation length	-0.529 [*] (16)	-0.508 [*] (16)	-0.124 (14)	0.500 (15)	0.424 (15)	0.549 [*] (15)
Relative weaning age	-0.254 (14)	-0.465 (14)	-0.230 (13)	0.513 (13)	0.419 (13)	0.493 (13)

[*] $P < 0.05$ (2-tailed);

[**] $P < 0.01$. Unerupted dental volume included tooth germs for replacement teeth and permanent molars, when present.