

## ARTICLE

# Costly teeth? Gestation length in primates suggests that neonate dentition is not expensive to produce

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## Abstract

Variation in the relationship between gestation length and body mass can arise because different types of tissue require varying amounts of energy to build, and not all species build such tissues in the same proportions. Given that a pregnant female has a finite amount of energy, trade-offs between investment in different tissues may occur. Here we examine if dental precocity accounts for variation in primate gestation length. If true, this could explain why folivorous species with precocial dentition have longer gestation lengths than predicted by neonatal brain and body mass. We compiled data on gestation length, neonate and adult female body and brain mass from the literature. We used published postcanine eruption schedules at 4 months of age and measured the total occlusal area as dental endowment to approximate dental precocity at birth. Species with embryonic delay in growth or altricial neonates were not considered because they represent grade shifts regarding gestation length. Consequently, our data were biased toward Simiiformes and Old World monkeys, specifically. We performed a phylogenetic generalized least squares regression (pGLS) of neonate brain mass in relation to neonate body mass, and a second pGLS with dental endowment as an additional predictor variable. Including dental endowment in the pGLS did not improve the model. Dental endowment did not systematically impact primate gestation length. Concordant with results from previous studies, this indicates that the energetically expensive period of tooth mineralization may occur postnatally. More data are required to examine if the results are typical across primates.

## KEYWORDS

dental endowment, development, expensive tissues, fetal tissue, folivores, life history, maternal energy, mineralization

## 1 | INTRODUCTION

Gestation (i.e., prenatal growth) is the first period of development in placental mammals. Because the production of neonate tissue during gestation is directly dependent on the energetic contributions of the mother (Martin, 1996), the length of gestation is often used as a proxy for the total maternal energy expenditure required to produce a

neonate. As such, and because gestation length can be measured relatively precisely and noninvasively (Strier & Ziegler, 1997), cross-species comparisons provide a window into the factors affecting the pace of prenatal growth and development.

Gestation length is often considered as the least flexible of all life history variables, being tightly correlated with maternal body mass (Clutton-Brock, 2016; Lee, 2012). Theoretically,

this is because larger mothers give birth to larger neonates, and correspondingly larger neonates take longer to build (Ross, 1998). Well-established, systematic deviations from this body mass allometry relate to differences in life history strategies (Harvey, Promislow, & Read, 1989). For example, species that give birth to underdeveloped young (i.e., altricial, rather than precocial, Martin, 1983) have a gestation length that is short for body mass (Martin & MacLarnon, 1985). At the other end of the spectrum, species with periods of delayed embryonic growth (i.e., diapause) have a gestation length that is much longer than predicted by body mass (Oerke, Heistermann, Kuederling, Martin, & Hodges, 2002).

Additional variation in the relationship between gestation length and body mass can arise because different types of tissue require varying amounts of energy to build, and different species build such tissues in different proportions (Aiello & Wheeler, 1995). These differences are most pronounced when considering the brain. For example, in primates, gestation length is more strongly correlated with neonate brain mass than with either neonate or maternal body mass (Harvey, Martin, & Clutton-Brock, 1987; Martin & Isler, 2010; Sacher & Staffeldt, 1974). This is likely because brain tissue is metabolically expensive to produce and maintain compared to muscle or bone (Kuzawa et al., 2014; Mink, Blumenschine, & Adams, 1981).

Given that a mother has a finite amount of energy to allocate towards producing different fetal tissues, it has been suggested that trade-offs in maternal energy allocated to building different tissues may occur during gestation (Godfrey, Samonds, & Jungers, 2001; Godfrey, Samonds, Jungers, & Sutherland, 2003; Isler & van Schaik, 2009). This can be accomplished either by mediating energy allocations to different types of tissue or by modifying gestation length. For example, a neonate with a well-developed gut (i.e., gastrointestinal tract) would be predicted to have a relatively smaller brain if gestation length remained constant (all other things being equal). While this type of tissue trade-off has been demonstrated in adult primates (e.g., the Expensive Tissue Hypothesis, Aiello & Wheeler, 1995; but see Navarrete, van Schaik, & Isler, 2011), the current lack of data on neonate gut mass prevents this potential influence on gestation length from being tested directly.

However, fetal guts and brains may not be the only expensive tissues that mothers produce during gestation. Godfrey et al. (2001) hypothesized that accelerated production of mineralized tissues, such as teeth, would also require additional maternal energy. While there are currently no data available to quantify the metabolic costs of tooth production in utero, it is well established that many folivorous primates have accelerated rates of dental development, with an emphasis on erupting large

postcanine (i.e., food processing) teeth at an early age (Godfrey et al., 2001; Godfrey et al., 2003; Harvati, 2000). This is in line with evidence that several folivorous primates have longer gestation lengths than expected for their brain and body mass (e.g., Asian Colobines, Borries, Lu, Ossi-Lupo, Larney, & Koenig, 2011; Malagasy lemurs, Godfrey et al., 2001; Godfrey et al., 2003; Godfrey, Samonds, Jungers, Sutherland, & Irwin, 2004). However, it remains unclear if dental precocity affects gestation length across primates.

The objective of this study was to examine the relationship between dental precocity and gestation length in primates. Specifically, we tested the hypothesis that the dental material produced in utero accounts for a significant proportion of the variance in primate gestation length. Based on evidence from previous studies, we predicted that advanced neonatal dental development will account for extended gestational periods in our models. This effect should be largest in more folivorous primates.

## 2 | MATERIALS AND METHODS

### 2.1 | Data selection

With the exception of occlusal area (a measure we took; see below) we compiled the remaining data from the literature following criteria explained below. To ensure appropriate data quality, we proceeded from published compilations and then relocated all data in their primary reference, or we used specific, vetted compilations (Borries et al., 2016).

We compiled data for primate species for which reliable information on gestation length, adult female body mass, neonate body mass, adult female brain mass, neonate brain mass, and dental eruption schedules were available (Table 1, additional information on sample sizes, primary references, etc. in Table S1). Only species which typically give birth to precocial singletons and without delayed embryonic growth (diapause) were considered to eliminate the well-established effects of neonatal state, litter size, and diapause on gestation length (see above). Consequently, many species, especially strepsirrhines, could not be considered because no comparable gestation length values exist. Other excluded species either did not bear singletons (most callitrichids, cheirogaleids, and *Varecia*), had a diapause (callitrichids, some lorises, galagids, and perhaps tarsiids and *Saimiri*), had a modal litter size that exceeds one (several callitrichids, *Varecia*), or the neonates were altricial (cheirogaleids), or semi-altricial (*Varecia*). Because the remaining sample is biased toward Simiiformes, our results may not extend to all primates.

**TABLE 1** Data used in the present study

|                  | Species                          | Gestation Length (days) | AF Body Mass (g) | Neo Body Mass (g) | AF Brain Mass (g) <sup>‡</sup> | Neo Brain Mass (g)       | Dental Endowment (mm <sup>2</sup> ) |
|------------------|----------------------------------|-------------------------|------------------|-------------------|--------------------------------|--------------------------|-------------------------------------|
| Lemuroidea       | <i>Lemur catta</i>               | 138.7                   | 2,210            | 66.1              | 20.46                          | 8.8                      | 104.96                              |
|                  | <i>Eulemur fulvus</i>            | 122.7                   | 2,333            | 70                | 26.3                           | 10.7                     | 97.7                                |
| Platyrrhini      | <i>Sapajus apella</i>            | 156.3                   | 2,520            | 208.9             | 66.64                          | 35.7                     | 71.46                               |
|                  | <i>Cebus albifrons</i>           | 162                     | 2,290            | 232.6             | 65.52                          | 33.65                    | 51.92                               |
|                  | <i>Aotus trivirgatus</i>         | 133                     | 736              | 91                | 16.71                          | 10.1                     | 32.6                                |
|                  | <i>Ateles geoffroyi</i>          | 210                     | 7,290            | 512               | 113.54                         | 64                       | 32.53                               |
|                  | <i>Alouatta caraya</i>           | 187                     | 4,330            | 262               | 49.52                          | <b>26.31</b><br>(0.021)  | 126.49                              |
|                  | <i>Alouatta palliata</i>         | 186                     | 5,350            | 480               | 49.77                          | 30.8                     | 120.3                               |
| Hominoidea       | <i>Symphalangus syndactylus</i>  | <b>201.0</b><br>(0.005) | 10,700           | 553.5             | 126.86                         | <b>62</b><br>(-0.034)    | 36.75                               |
|                  | <i>Hylobates lar</i>             | 189.5                   | 5,381            | 403.5             | 104.11                         | 50.1                     | 27.13                               |
| Colobinae        | <i>Trachypithecus obscurus</i>   | <b>196.6</b><br>(0.002) | 6,765            | 383               | 62.13                          | 43                       | 124.5                               |
|                  | <i>Semnopithecus vetulus</i>     | 197.6                   | 5,900            | 360               | 62.57                          | <b>44.15</b><br>(0.050)  | 83.01                               |
|                  | <i>Semnopithecus schistaceus</i> | 211.6                   | 12,320           | 500               | 133                            | <b>68.1</b><br>(-0.05)   | 55.23                               |
|                  | <i>Colobus guereza</i>           | 152.3                   | 7,506            | 572.5             | 72.28                          | 38                       | 102.29                              |
| Cercopithecoinae | <i>Macaca mulatta</i>            | 166.5                   | 5,670            | 478.3             | 87.29                          | 54.5                     | 50.94                               |
|                  | <i>Macaca fascicularis</i>       | 163                     | 3,590            | 339.6             | 64.38                          | <b>43.12</b><br>(-0.022) | 41.95                               |
|                  | <i>Macaca nemestrina</i>         | 172.5                   | 6,500            | 463.65            | 104.27                         | 60.9                     | 60.11                               |
|                  | <i>Papio cynocephalus</i>        | 177                     | 12,300           | 770               | 161.75                         | 73.5                     | 36.41                               |
|                  | <i>Papio anubis</i>              | 180                     | 13,300           | 947.5             | 157.94                         | <b>78.71</b><br>(-0.006) | 43.99                               |
|                  | <i>Chlorocebus pygerythrus</i>   | 163.2                   | 3,576            | 335.4             | 61.56                          | 33.5                     | 75.3                                |

Note: Mean imputed values in bold font with the variance for each estimate given in parentheses. Primary sources, sample sizes, alternate species names, comments and other information as well as the data for additional species used to impute are provided as Table S1.

Abbreviations: AF, adult female; Neo, neonate.

We considered only those primate species for which adult female body mass, adult female brain mass, dental schedules, tooth measurements, and at least one of the two neonate measures, either neonate body mass or neonate brain mass, were available. Our goal was to cover as many taxonomic groups as possible while imputing the minimum number of values. Seven of the 33 species for which we had dental data were not considered in the analysis: (a) *Trachypithecus francoisi* no adult female brain mass; (b) *Nasalis larvatus* no gestation length, or neonate measures; (c) *Trachypithecus cristatus* and

*Ptilocolobus badius* no neonate measures; (d) *Varecia variegata* bears litters of semi-altricial neonates; and (e) *Callithrix jacchus* has a diapause (see also above) and bears litters; (f) *Saimiri sciureus* has a large published range of mean gestation length values (147–171 days depending on the study, Goss, Popejoy II, Fusiler, & Smith, 1968; Kerber, Conaway, & Moore, 1977), and the species may have a diapause (McKim Jr., Hutchinson, & Gavan, 1972). We also added 16 species for a total of 45 species (listed in Table S1) to impute neonate data for other species. Because phylogenetically imputed values

are calculated as the predicted values from a phylogenetic generalized least squares multiple regression, we chose the mean values of species closely related to those already in the dataset to avoid estimating values for taxonomically isolated species. The mean imputed values were used in analyses and the variance for each of these estimates is provided in Table 1. All phylogenetic imputations were performed using the R package “Rphylopars” (Bruggeman, Heringa, & Brandt, 2009).

## 2.2 | Variables

For gestation length (given in days) we used Martin's (2007) compilation as the starting point, and verified that conceptions (i.e., the beginning of gestation) were determined with reliable methods for every value (see above). This information is given as Table S1. For two species (*Symphalangus syndactylus* and *Trachypithecus obscurus*), gestation length was phylogenetically imputed using adult female body mass, brain mass, and gestation length from the other 43 species.

Adult female body mass values (given in grams) were available for all species considered. Values were taken from Smith and Jungers (1997) and from Isler et al. (2008), both of which are vetted, comprehensive compilations that provide new values and the primary sources for compiled values. Four additional values were taken from other primary sources (Table S1).

The compilation by Smith and Leigh (1998) was our main source for neonate body mass data (given in grams). Three additional values were taken from other primary sources (Table S1). Data for male and female neonates were combined into a species mean.

Adult female brain mass values (given in grams) were available for all species considered. Most values were taken from Isler et al. (2008), and three values we took from other primary sources (Table S1). Values given as endocranial volume (ECV) were converted to grams using the equation ( $[\text{Mass} = \text{ECV} * 1.036]$ ; Isler et al., 2008).

The compilations by Sacher and Staffeldt (1974) and Harvey and Clutton-Brock (1985) served as starting points for neonate brain mass data (given in grams). Every value we subsequently traced back to its original reference. We combined data for male and female neonates, if available. Values for six species (*Alouatta caraya*, *Macaca fascicularis*, *Papio anubis*, *Semnopithecus schistaceus*, *Semnopithecus vetulus*, *Symphalangus syndactylus*) were phylogenetically imputed.

While an abundance of primate life history data can be gleaned from the literature, there remain serious limitations on the number of species for which both reliable life history variables and neonatal dental histology data

are available. Therefore, dental eruption schedules were taken from a compilation of published material recorded by Godfrey et al. (2001), and used to calculate the total number of erupted deciduous and permanent postcanine teeth at 4 months of age as an approximation for the amount of dental material available at birth. This assumption is supported by prior histological data suggesting a tight relationship between the dentition that has erupted at 4 months, and the dentition that was present in the crypt of the mandible at birth (i.e., more teeth at birth = more teeth at 4 months, Smith et al., 2015). However, we caution that this coarse-grained approach does not account for postnatal differences in rates of dental development.

We took the dental measurements of the mesiodistal (md) and buccolingual (bl) diameters from both deciduous and permanent postcanine teeth erupted at 4 months for a given species to estimate a species mean value for the occlusal area of each tooth using the formula (occlusal area =  $\text{mean}(\text{md}) * \text{mean}(\text{bl})$ ). Occlusal areas ( $\text{mm}^2$ ) of all erupted teeth were then summed up to reach the total area of postcanine teeth erupted at 4 months. In the following, we refer to this summed surface area measurement as “dental endowment.”

## 2.3 | Value standardizations

In our dataset, the proportion of brain tissue relative to neonate body mass ranged from 6.4% in *Alouatta palliata* to 17.1% of neonate body mass in *Sapajus apella*. Accordingly, because brain tissue is, in itself, thought to be an expensive tissue, we subtracted neonate brain mass from neonate body mass and used this measure of neonate body mass in the analysis. This adjustment did not impact the distribution of neonate mass data and led to similar results. We report only the results of the analyses which were conducted using the adjusted variable.

We transformed variables to the same dimension (Smith, 2005) by calculating the square root of dental endowment (a square dimension) and the cube root of neonate body mass (a cubic dimension). Gestation lengths were log-transformed.

Finally, all variables were individually regressed against neonate body mass (neonate brain mass subtracted) with the residuals of these regressions representing *relative* gestation length, *relative* neonate brain mass, and *relative* dental endowment, respectively.

## 2.4 | Analysis

All analyses were conducted within a phylogenetic comparative framework using the molecular consensus

phylogeny from the 10K trees project (Arnold, Matthews, & Nunn, 2010).

We performed two phylogenetic generalized least squares regressions (“pGLS”). In these linear models a dependent variable is predicted by an independent variable in a least squares framework. A pGLS is a generalized least squares regression (GLS) using the expected covariance due to shared phylogenetic history as weights among observations. Notably, pGLS does not treat phylogenetic relatedness as a covariate that is “corrected” for, but rather accounts for expected covariance in the calculation of regression parameters using standard GLS procedures (Rohlf, 2001). Specifically, a pGLS accounts for the phylogenetic nonindependence by using the expected covariance due to shared phylogenetic history (i.e., the variance–covariance matrix of the tree) as part of the structure of the error term when calculating the slope and intercept of a GLS regression (Rohlf, 2001). pGLS thus differs from standard GLS only in accounting for species dependence due to phylogenetic relatedness (i.e., the tendency for species which are more closely related to be more phenotypically similar to one another) by weighting the data accordingly.

As with GLS models, competing pGLS models can be compared using log-likelihood ratios, as well as information criteria, such as the traditional Akaike’s information criterion (AIC). These model comparisons are interpreted in the same way as GLS model comparisons, with a smaller AIC value indicating a better fitting model. While there are several different versions of AIC (with slightly different penalties employed by each), it is conventionally accepted that, when comparing two models, a difference in AIC values of  $>2$  indicates relatively strong support for choosing one model over the other (Burnham & Anderson, 2002; Wagenmakers & Farrell, 2004).

The particular strength and type of phylogenetic signal in the data can be accounted for by including a model of evolution in the pGLS calculation. The most frequently used models of evolution use branch length transformations that can be directly translated to the variance–covariance matrix of the tree. Here we use the standard lambda model of evolution (Freckleton, Harvey, & Pagel, 2002; Pagel, 1999). pGLS models were carried out using the packages “nlme,” “caper,” “geiger,” “phytools,” and “APE” in R v3.4.3 (Harmon, Weir, Brock, Glor, & Challenger, 2008; Orme et al., 2013; Paradis, Claude, & Strimmer, 2004; Pinheiro et al., 2014; R Core Team, 2014; Revell, 2012).

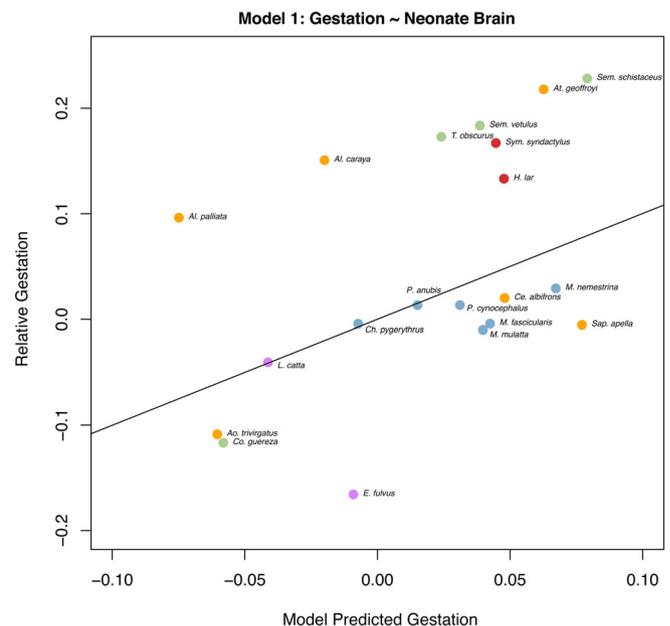
The first pGLS analysis modeled a standard hypothesized predictor of primate gestation length, that is, relative neonate brain mass (Model 1: relative gestation length  $\sim$  relative neonate brain). In the second pGLS analysis, we incorporated relative dental endowment as an additional predictor variable for gestation length

(Model 2: relative gestation length  $\sim$  relative neonate brain + relative dental endowment). Predictor variables were considered significant at  $p < 0.05$ . Model 1 and Model 2 were compared using AIC scores, as well as a log-likelihood ratio test. Of the 26 species with complete/reconstructed records we used 20 in these two models: six species within Hominoidea were excluded because at 4 months of age no postcanine teeth had erupted (i.e., relative dental endowment = 0).

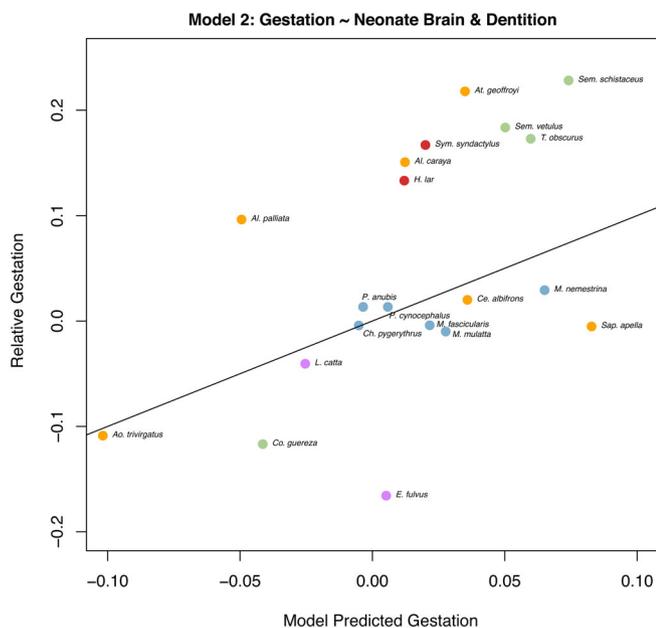
For visual comparisons between Model 1 (a linear regression) and Model 2 (a multiple regression) relative gestation length values were plotted against the relative gestation lengths predicted by each model (Figures 1 and 2). Given the complexity of Model 2, we also plotted the individual model components separately against relative gestation length to visualize the variance that each contributed to the model (Figure 3a,b).

### 3 | RESULTS

The model of gestation length predicted by relative neonate brain mass alone (Model 1, Figure 1) was significant ( $p < 0.05$ ;  $\lambda = 1.02$ ), that is species with larger neonate brains have longer gestations. However, when dental



**FIGURE 1** Comparison between relative gestation length (corrected for neonate body mass) plotted on the y-axis with the values predicted by phylogenetic least-squares regressions of Model 1 (relative gestation length  $\sim$  relative neonate brain) on the x-axis. This model of gestation length predicted by relative neonate brain mass alone was significant ( $p < 0.05$ ;  $\lambda = 1.02$ ). Points are color coded according to taxonomy, with Lemuroidea in purple, Platyrrhini in orange, Hominoidea in red, Colobinae in green, and Cercopithecinae in blue



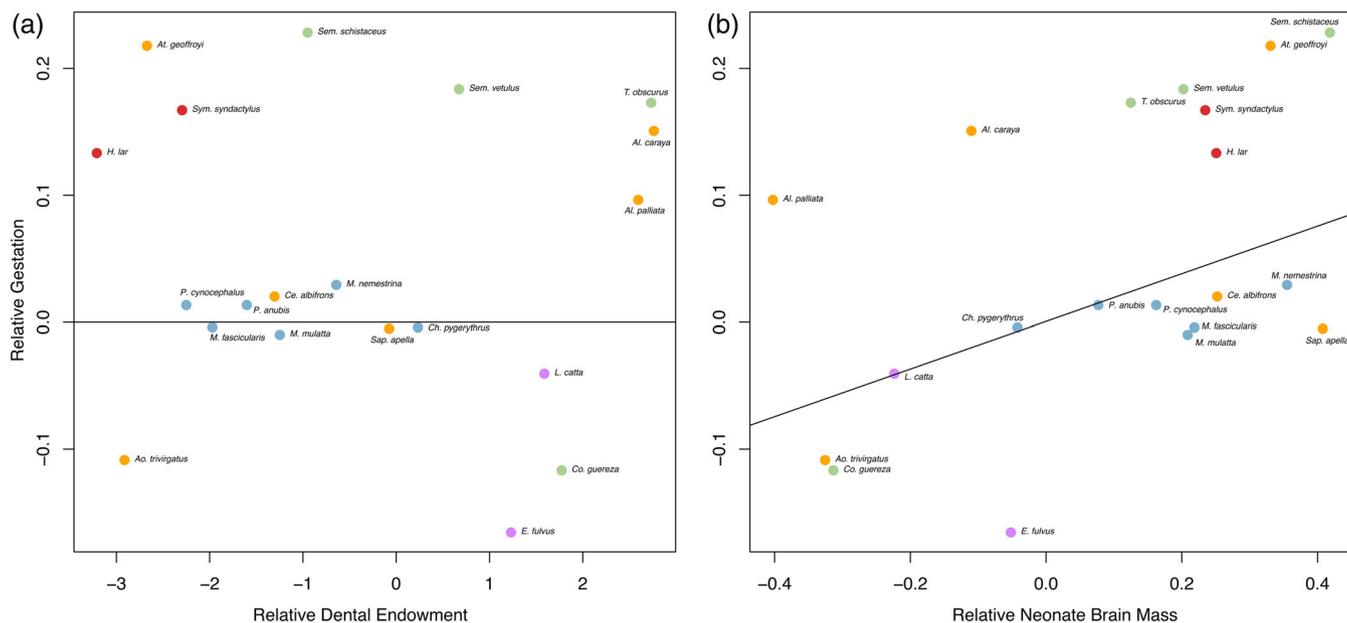
**FIGURE 2** Comparison between relative gestation length (corrected for neonate body mass) plotted on the y-axis with the predicted values from phylogenetic least-squares regressions of Model 2 (relative gestation length  $\sim$  relative neonate brain + relative dental endowment) on the x-axis. The inclusion of dental endowment as a covariate to the pGLS multiple regression did not strengthen the predictive power of the model. Dental endowment was not a significant predictor of gestation length ( $p = 0.24$ ;  $\lambda = 1.03$ ). Points are color coded according to taxonomy, with Lemuroidea in purple, Platyrrhini in orange, Hominoidea in red, Colobinae in green, and Cercopitheciinae in blue

endowment was added as a covariate to the pGLS multiple regression (Model 2, Figure 2) it was not a significant predictor of gestation length ( $p = 0.24$ ;  $\lambda = 1.03$ ). This is further supported by a log-likelihood ratio test which indicates that the model including the degree of dental endowment (Model 2) is not significantly better than the model without it ( $p = 0.27$ ). Moreover, AIC values suggest that the effect of adding dental endowment as a predictor in Model 2 was too weak to justify the inclusion of an additional variable to the model (Model 1 AIC =  $-40.6$ , Model 2 AIC =  $-39.8$ ).

With respect to folivory, there was no clear trend in our data. Of the four folivorous genera included (*Alouatta*, *Colobus*, *Semnopithecus*, and *Trachypithecus*), all but one had positive residuals for dental endowment, with *Semnopithecus schistaceus* as the exception. Three of these four genera also had positive residuals for gestation length, with *Colobus* as the exception (Figure 3b). The remaining two dentally precocious species are characterized as “opportunistic omnivores” (*Lemur catta*) and “highly frugivorous” (*Eulemur fulvus*; Gould, Sauter, & Cameron, 2011) as are three other genera with positive residuals for gestation length (*Ateles*, *Symphalangus*, and *Hylobates*).

## 4 | DISCUSSION

Contrary to our prediction, dental endowment had no systematic effect on primate gestation length. As clear as



**FIGURE 3** Individual model components of Model 2 plotted separately against relative gestation length. Specifically, (a) the relative dental endowment component in comparison to (b) the relative neonate brain component of Model 2 illustrate the limited effect of dental endowment. Points are color coded according to taxonomy, with Lemuroidea in purple, Platyrrhini in orange, Hominoidea in red, Colobinae in green, and Cercopitheciinae in blue

our result is, we need to caution that it is based on a sample biased toward species with prolonged use of deciduous teeth. Our data lack extrema such as obligate folivorous strepsirrhines or the very slowly developing great apes that have no teeth erupted at 4 months of age. In addition, many species could not be included because either gestation length was not determined with reliable methods or essential morphologic measures (mostly for neonates) were lacking. We did also not include species with an embryonic growth delay, because it leads to a grade shift in gestation length (see above), our dependent variable. These restrictions hamper more detailed comparisons with a recent study on tooth development (Smith et al., 2017) in which half of the anthropoid species considered have a confirmed diapause. In light of these caveats the following discussion has to remain preliminary.

Despite these limitations, our results seem to indicate that the mineralization of teeth (the most expensive portion of the process) mainly falls into the postnatal period. This is in line with results from a similar examination of mostly strepsirrhine and platyrrhine neonates (Smith et al., 2017). Although Smith et al. (2017) did find a relationship between relative dental volume at birth and gestation, this pattern was likely driven by strepsirrhines (of which we have very few in our present sample). By comparison, the anthropoids in their study demonstrated a highly variable relationship between the developing dentition and gestation length. This variable relationship may be driven, in part, by the low degree of permanent molar mineralization at birth in most anthropoid primates (Smith et al., 2015). If mineralization is, in fact, the costliest period of dental development, it is possible that anthropoid mothers “delay metabolic investment in dental growth until closer to the time at which teeth are required for independent feeding” (Smith et al., 2017, p. 7), and instead prioritize the development of other somatic tissues during gestation. Interestingly, this carries with it the attendant implication that rates of dental development can be decoupled from other somatic tissue development (Smith et al., 2017).

In light of these results, it may be reasonable to hypothesize that tooth mineralization might be delayed to postnatal development due to the high bioavailability of minerals in milk. At least in humans, milk has a much higher concentration of calcium, along with other components essential for mineralization than blood (Harrington, Young, Essader, Sumner, & Levine, 2014; Klein et al., 2017). Perhaps, then, mammalian females are better able to support mineralization postnatally, rather than during gestation. This could potentially extend the “Metabolic Crossover Hypothesis,” which has previously emphasized the relative ease of postparturition

macronutrient transfer (e.g., fats and simple sugars, Ellison, 2001), to now also include micronutrient transfer. Additional data on the ontogeny of dental mineralization are required to test this hypothesis.

We were not able to consider the gut as another potentially expensive tissue (Aiello & Wheeler, 1995), because quantitative data for primate neonates are not available. However, the colobine species with their large adult gastrointestinal tract (Chivers & Hladik, 1984), displayed opposite patterns: while Asian colobines had longer gestation lengths than predicted by relative neonate brain mass, the African colobine had a much shorter gestation length than predicted (Figure 1). Assuming that gut proportions in primate neonates reflect the morphology found in adults, it seems unlikely that the amount of gastrointestinal tissue explains a significant proportion of the variation in primate gestation length. However, more specialized folivorous species will have to be considered (once data become available) before such conclusions can be drawn.

While it is known that the biorhythm of tooth development is correlated with basal metabolic rates (Bromage, Hogg, Lacruz, & Hou, 2012), more research is needed to directly measure the metabolic costs of producing mineralized tissues both pre- as well as postnatally. As soon as more reliable data become available, these analyses should be repeated to allow for more general conclusions across primates. Currently, however, our results suggest that dental endowment does not impact primate gestation length in a systematic way.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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