Do mid-crown enamel formation front angles reflect factors linked to the pace of primate growth and development?

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ABSTRACT

Enamel formation front (EFF) angles represent the leading edge of enamel matrix secretion at particular points in time. These angles are influenced by rates of enamel extension (the rates at which tooth crowns grow in height), rates of enamel matrix secretion and the angles that prisms make with the enamel-dentine junction. Previous research suggests, but has not yet established, that these angles reflect aspects of primate biology related to their pace of growth and development, most notably brain and body size. The present study tested this possibility on histological sections using phylogenetically-controlled and Bonferroni-corrected analyses spanning a broad taxonomic range. Ten species were represented in the analysis of anterior teeth; 17 in the analysis of posterior (postcanine) teeth (with varying sample sizes). Also tested was the relationship of EFF angles to striae of Retzius periodicity (long period growth rhythms in enamel) and degree of folivory, as both factors are related to primate developmental rates. Finally, several analyses were conducted to investigate whether tooth size (operationalized as EDJ length) might mediate these relationships. Central results are as follows: (1) Relationships between EFF angles and brain weight (anterior teeth) and between EFF angles and body mass (anterior and posterior teeth) are statistically significant and (2) Mid-crown EFF angles are not statistically significantly related to EDJ lengths. These results suggest that tooth size does not mediate relationships between EFF angles and brain weight/ body mass and are discussed with respect to underlying enamel growth variables (especially rates of enamel extension and secretion).

Tooth enamel grows according to both circadian and longer-period rhythms, each represented by microscopically visible lines in enamel ground sections (Hillson, 2014). Over 24 hour periods, enamel-forming cells, or ameloblasts, oscillate between slower and faster rates of

enamel matrix secretion, forming daily growth lines, or cross-striations. Long-period growth lines, termed striae of Retzius, result from a periodic slowing of enamel formation in all concurrently active ameloblasts, following intervals varying among individuals and species (FitzGerald, 1998; Bromage et al., 2009; 2012). Variation in striae of Retzius periodicity has been linked to differences in body size, brain size, and several life history variables across primate species, in connection with a hypothesized centrally-regulated growth rhythm (Bromage et al., 2009; 2012). The present study investigates variation in the angles at which striae of Retzius meet the enamel-dentine junction (EDJ) (Fig. 1), as these angles have also been suggested to be related to body size (Shellis, 1998), encephalization quotient (EQ) (Hogg and Walker, 2011), and brain mass (Hogg and Walker, 2011) across primate species. This study, therefore, builds on the pioneering work of Shellis (1998) and Hogg and Walker (2011).

[Figure 1]

Shellis (1984) labeled the angle between the EDJ and striae of Retzius "Angle D," while Hogg and Walker (2011) termed it the Enamel Formation Front or "EFF angle." We adopt Hogg and Walker's (2011) term, as it is descriptive of the fact that striae of Retzius represent the enamel forming front at particular points in time. Shellis (1984) included EFF angles in his calculation of enamel extension rates, the rates at which ameloblasts differentiate from the inner enamel epithelium and the crown grows in height (Fig. 1). Specifically, Shellis' (1984) equation (see caption under Fig. 1) related enamel extension rates to three variables: EFF angles (i.e., Shellis' "Angle D"), the angles that enamel prisms make with the EDJ (ibid. "Angle I"), and the daily rates at which ameloblasts secrete enamel matrix. In Shellis' equation enamel extension rates and the tangent of EFF angles are inversely related, such that as EFF angles and their tangents increase, the rate of enamel extension decreases.

Shellis (1984) found that across 16 species of primates (represented by 19 permanent molars), there was a relationship between body size, average enamel extension rates, and average EFF angles; larger-bodied primates had—on average—larger EFF angles and slower rates of enamel extension. In other words, despite the fact that enamel extension rates are related to three variables (i.e., EFF angles, Angle I, and the daily rate of enamel secretion), Shellis found that from smaller to larger-bodied primates, average EFF angles increased and average extension rates decreased, as would be expected by the inverse relationship between EFF angles and enamel extension rates. Shellis did not assess the strength of these relationships nor determine whether they were statistically significant.

Hogg and Walker (2011) incorporated EFF angles as well as daily secretion rates in the mid-crown region of posterior teeth into an analysis of variation in both variables across platyrrhines as they relate to brain size, body size, and aspects of primate life history. For EFF angles, their sample consisted of a mix of posterior teeth from 11 platyrrhine species (species of *Cebidae* and *Alouatta*). They assessed the strength of relationship between EFF angles and body mass, brain mass, encephalization quotient (EQ), weaning age, age at first female reproduction, interbirth interval, and birth rate. EQ and brain mass were the top two predictors of EFF angles (based on R^2 values) and were the only variables for which regression slopes did not include zero, yet *p*-values were not reported for their PGLS regression results. Assuming EFF angles were proxies for enamel extension rates, these authors suggested their results were consistent with the "foraging independence hypothesis" (Godfrey et al., 2001). According to this hypothesis, species with omnivorous/frugivorous diets require prolonged periods of juvenile growth to master complex feeding skills before they can become independent foragers. In contrast, more folivorous species, however, with presumably less cognitively-demanding diets,

can grow up more quickly. Assuming that juveniles have an elevated risk of predation, reaching adult size more rapidly would be an advantage. Thus, folivorous species tend to grow more quickly, erupting their teeth and achieving foraging independence at earlier ages than other primates.

An association between EFF angles and folivory would also be expected on the basis of the Juvenile Risk Aversion Hypothesis as well (Janson and van Schaik, 1993). According to this hypothesis, slow rates of growth are selectively advantageous when there is greater feeding competition within the group. Species that have a greater dependence on fruit experience greater intra-group feeding competition relative to species that have a greater dependence on leaves, which tend to be more evenly distributed in space and time. By reducing metabolic demand, slower growth rates would lessen the high degree of feeding competition that more frugivorous species experience.

Taken together, the Shellis (1998) and Hogg and Walker (2011) studies suggest relationships across primate species between EFF angles and body size (Shellis 1998), brain mass (Hogg and Walker, 2011) and EQ (Hogg and Walker, 2011), although the statistical significance of these relationships has not yet been established. Whether robust and/or statistically significant relationships with EFF angles should be expected *a priori* however, is unclear, as EFF angles are influenced not only by extension rates but also by variation in daily secretion rates and by Angle I. Furthermore, whether extension rates themselves should be expected to correlate with body size, brain size, or elements of life history, is also unclear because what is under selection, presumably, is a functional dentition at a given age, and enamel extension rates are simply one aspect of dental growth and development that may be altered to achieve that functionality. Other such aspects include, but are not limited to, rates of enamel

secretion, signaling involved in the termination of crown and root formation, and the coordinated set of mechanisms responsible for the timing of tooth eruption. Finally, as no quantitative assessment of measurement error in EFF angles has yet been reported in the literature, it is not clear how much noise to expect in EFF angle measurements.

The present study conservatively investigates the statistical strength of these relationships across a diverse set of primate species using both phylogenetically controlled regressions and alpha values corrected for multiple comparisons. Tested here are mid-crown EFF angle relationships to brain weight, body mass, periodicity, and degree of folivory. Following Hogg and Walker (2011), mid-crown EFF angles were used in statistical analyses in order to "…limit the impact [on EFF angles] of gross anatomical differences in enamel" across tooth types and regions (2011:2197). Brain weight, body mass, and degree of folivory were included in statistical analyses as relationships of EFF angles to these variables are implied by the studies of Shellis (1984) and Hogg and Walker (2011). Periodicity is also considered, as it reflects an underlying growth rhythm that controls the "…pace, patterning, and co-variation of life history traits" (Bromage et al., 2012). To the extent that EFF angles are influenced by variation in enamel extension rates across taxa and variation in enamel extension rates are related to the pace of dental growth and development, positive relationships between EFF angles and body mass, brain weight, and periodicity are expected. We predict, in a similar fashion, a negative relationship between EFF angles and degree of folivory according to either the "foraging independence hypothesis" or the "juvenile risk aversion hypothesis." Also reported here is a quantitative assessment of measurement error in EFF angles.

Finally, a series of additional statistical tests was performed to explore the possibility that any relationships between EFF angles and these life-history related variables might be mediated

by an association with tooth size. We use the length of the EDJ as a measure of tooth size that is most closely related to enamel extension rates, which can be defined as the length of the EDJ over which ameloblasts differentiate during a particular period of time. We first determine whether a statistically significant correlation between mid-crown EFF angles and EDJ length exists. We then determine if a scaled measure of EFF angles to tooth size --a ratio of mid-crown EFF angle to EDJ length--yields any significant correlations to body mass, brain weight, periodicity, or degree of folivory. If EFF angles themselves correlate with these variables, *and* if mid-crown EFF angles bear a consistent relationship to EDJ length, then correlations between this scaled measure and these life-history related variables would also be expected. This would not be the case, however, if any relationship between mid-crown EFF angles and EDJ length is perfectly isometric. In the case of isometry, this scaled measure (a ratio of mid-crown EFF angles to EDJ length) would be constant across species and would therefore have no correlation with any of the life-history related variables.

All of that said, however, we predict a different outcome for this final set of analyses. Non-human primate teeth may achieve larger tooth sizes by speeding up rates of enamel extension in shorter periods of time, or by prolonging their growth periods while maintaining relatively slow rates of enamel extension (Dean, 2009; Guatelli-Steinberg et al., 2012). Furthermore, variation in crown formation times and enamel extension rates both may contribute to variation in tooth size (Guatelli-Steinberg et al., 2012). Within modern humans, for example, taller teeth of a particular tooth type have both elevated rates of enamel extension early on in crown formation *and* grow over longer periods of time (Guatelli-Steinberg et al., 2012). Because mechanisms for achieving teeth of particular sizes can and do vary, we predict that mid-crown EFF angles will *not* be significantly correlated with EDJ lengths. We further predict that if mid-

crown EFF angles do not correlate with EDJ length, then scaling mid-crown EFF angles to EDJ

length as a ratio will result in inconsistent values across species that will negate any relationships

between EFF angles and life-history related variables.

Combined, these analyses provide a means to more thoroughly assess whether mid-crown

EFF angles reflect aspects of primate biology associated with the pace of primate growth and

development, and whether such relationships might be mediated by tooth size.

MATERIALS AND METHODS

Sample and measurements

Histological sections used for measuring EFF angles are listed in Table 1. The total

sample from which data were collected consists of ground sections from Donald J. Reid's and

Wendy Dirk's laboratory at the University of Newcastle upon Tyne, from the late Phillip

Walker's collection (made by Steven Molnar and David Gantt and currently housed at The Ohio

State University). Supplementing this sample is one tooth section from Scott McGraw's Tai

Forest monkey skeletal collection (*C. diana*). Samples consisted of anterior (incisors and

canines) and posterior (premolars and molars) teeth; these were analyzed separately owing to

evidence that in humans, anterior and posterior teeth differ in extension rate patterns along the

EDJ (Shellis, 1984; Guatelli-Steinberg et al., 2012). We also perform one set of analysis on the

incisors only, removing the canines, because large canine teeth might differ from incisors in their

extension rate patterns along the EDJ. The opportunistic nature of the sample left by-tooth type

sample sizes too small to further subdivide within anterior and posterior tooth groups for

statistical analysis. The potential impact of tooth type variation on these results is considered in

the discussion. Overall, 10 taxa are represented in the sample of anterior teeth (with sample sizes

ranging from one to 15 per taxon); 17 taxa in the sample of posterior teeth (with sample sizes

ranging from one to four per taxon).

[Table 1]

To be included in the total sample, sections had to be from completely formed tooth

crowns with 80% or more of the reconstructed crown height present. Sections were also assessed

for obliquity, and those with more than moderate obliquity (e.g., diffuse enamel-dentine junction,

plane of section far from the tip of the dentine horn) were eliminated from the sample.

Digital images of each section were made by using one of three microscope-camera

suites (Newcastle: Zeiss microscope and Canon 350D EOS camera/software; Washington DC:

Olympus BX51 microscope and DP71 camera/software, and Columbus: Olympus BX51

microscope and Spot camera/software) and montaged and resized for optimal angle measurement

in Adobe Photoshop CS3. Total monitor-view magnifications ranged from 25X to 100X when

images were viewed at 100% zoom. Crown height reconstructions were performed using the

method established by Saunders et al. (2007), after which deciles of crown height were marked

on each image. To measure EFF angles, images were opened in the ImageJ freeware program

(Abramoff et al., 2004). For each decile of crown height, a Retzius line that intersected the EDJ

near the center of the decile was selected and the angle of that line with the EDJ was measured.

The direction of the EDJ was established with the first arm of the angle tool, and then the Retzius

line itself was aligned with the second arm (Fig. 1, far right). Deciles that included visible

(moderate to severe) linear enamel hypoplasia, which can change the angle of the Retzius lines to

the EDJ, were excluded from all analyses. Not all angles were measurable because striae may not

have been visible in particular deciles.

EFF angles were measured by either RJF or DGS. Both intra-observer measurement error (for RJF) and inter-observer measurement were assessed on a sub-sample of 15 slides spanning teeth from strepsirrhines through hominoids (though not all specimens could be measured for each decile). RJF's duplicate measurements were made more than one year after the original data were collected, and were performed on a different computer screen. DGS measured EFF angles on the same sample of 15 specimens on a third computer screen.

Table 2 summarizes the assessment of measurement error results by decile. First and second measurements were compared for Observer 1 (RJF). Average absolute intra-observer error ranged from a low of 0.8 degrees for Decile 7 to a high of 2.3 degrees for Decile 8. While absolute measurement error is low, percentage error (calculated as absolute error over the average of measurements one and two) is high, ranging from 4.7 % for Decile 7 to 21.9% for Decile 2.

[Table 2]

Inter-observer error was somewhat higher. Two sets of interobserver error calculations were performed. The first set compares the measurements of Observer 2 (DGS) to the first measurement made by Observer 1. The second set compares the measurements of Observer 2 to the second measurement made by Observer 1. Across both sets, absolute error ranges from a low of 1.2 degrees (Decile 4) to a high of 2.9 degrees (Decile 2). Percent error, across both sets, ranges from a low of 7.2 percent Decile 8) to a high of 25.3% (Decile 3). Of the mid-crown decile angles (Deciles: 4, 5, 6, and 7), Decile 6 appears to have been measured most consistently, and this decile was therefore chosen for statistical analysis. As Shellis (1984) first pointed out, smaller angles seem to be subject to greater measurement error than larger angles. It is not

necessarily the case that smaller angels are more difficult to measure, but a one to two-degree difference in measurement constitutes a relatively larger percent error on small angles.

To consider the potential relationship of EFF angles to tooth size, EDJ lengths were measured. Measurements were performed using the segmented line tool in ImageJ along the length of the EDJ (Figure 2), from the cemento-enamel junction (CEJ) to the tip of the dentine horn. The shape and length of the EDJ could not be reconstructed in some specimens (even though the overall crown height could be). Figure 2b shows an example of a *P. anubis* canine on which the crown height could be reconstructed, but for which the exact path of the EDJ could not be. In such cases, we did not measure EDJ length. For this reason, the sample of teeth on which we could measure EDJ length is a subset of the overall sample. Asterisks mark the tooth sections in Table 1 on which both EFF angles and EDJ lengths were measured.

[Figure 2]

Phylogenetically Controlled Analyses

A variety of phylogenetic methods (Nunn, 2011) has been developed since Felsenstein's seminal paper (1985), but the most widely accepted and employed technique is the phylogenetically controlled generalized linear model (PGLS) (Pagel 1999), which is built into the R package 'caper' (Orme et al. 2012). A consensus phylogenetic tree for non-independence correction was downloaded from the 10k trees website (http://10ktrees.fas.harvard.edu/; Arnold et al. 2010) and employed in the regression analyses. Two sets of regression analyses were performed: one in which the dependent variable was the EFF angle of Decile 6 and another in which the dependent variable was the ratio of Decile 6 EFF angle to EDJ length. Independent variables for Decile 6 EFF angle included EDJ length, as well as the four life history related

variables: Natural log-transformed measures of female adult brain size, female adult body size, periodicity (log-transformed where appropriate) and logit-transformed degree of folivory. For the scaled measure of Decile 6 EFF angle (the ratio of the angle to the tooth's EDJ length), the life-history related independent variables were the same. Nearly all of the data used for the life-history related variables were taken from the literature, although in one case (periodicity for *Cercopithecus diana*) the data derive from the present study. To determine periodicity for *Cercopithecus diana*, cross-striations were counted between adjacent Retzius lines in several regions of the crown, and these were consistently 4 days. Folivory was quantified as the percentage of time dedicated to consuming leaves. Values for the independent variables (and sources) are given in Table 3. Table 4 provides greater detail on the folivory "average" values, breaking them down into the values reported in specific studies. For each species, an effort was made to search the literature for as many independent sources describing as many different sites as could be found. The folivory values included in Table 3 and used in the regression analysis are averages of these values.

Because multiple comparisons were made, adjusted alpha values were produced using a modified Bonferroni correction developed by Cheverud (2001). The modified correction accounts for the fact that in highly co-linear data sets, such as the one presented here with a number of correlated variables, the separate iterations of the PGLS are not truly independent analyses (Cheverud 2001; García 2004). The target alpha value for significance varied by the number of tests performed, and the collinearity of the data.

[Tables 3 and 4]

RESULTS

Table 5 gives the ranges and means of Decile 6 angle measurements for each taxon for anterior and posterior dentitions. Table 6 gives this information for EDJ lengths and for the ratio of Decile 6 EFF angle to EDJ length.

[Tables 5 and 6]

Table 7 gives the results of the PGLS regression analyses. Where the Shapiro-Wilk test revealed significant departures from normality variables were transformed (either by log or logit- see Table for specifics).

For the anterior dentition, the regression of Decile 6 EFF angle on brain weight was statistically significant ($r^2 = 0.745$, $p<0.001$) as was the regression of Decile 6 EFF angle on body mass ($r^2 = 0.597$, $p<0.008$), both falling below the Bonferroni-adjusted alpha value of 0.009. Regressions of Decile 6 EFF angle on periodicity and of Decile 6 EFF angle on degree of folivory exceeded the required alpha values. Similar results were found when canine teeth were removed from the analysis, with the exception that the relationship of Decile 6 EFF angle to body mass was no longer significant ($r^2 = 0.426$, $p<0.056$) at the Bonferroni-adjusted alpha value of 0.010.

Also for the anterior dentition, the ratio between Decile 6 EFF angles and EDJ lengths was not constant, varying between 0.75 (*Papio anubis*) and 3.0 (*Hylobates spp.*). There was no statistically significant relationship between Decile 6 EFF angle and EDJ length, nor were there any statistically significant relationships between the Ratio value (ratio of Decile 6 to EDJ length) and any of the independent variables.

[Table 7]

[Figure 3]

For the posterior dentition, the regression of Decile 6 on body mass was statistically significant ($r^2 = 0.369$, $p<0.009$), falling below the Bonferroni-adjusted alpha value of 0.014. Regressions for Decile 6 on periodicity, brain weight and folivory-- exceeded the required alpha value.

Also for the posterior dentition, the ratio between Decile 6 EFF angles and EDJ lengths varied greatly, from 1.4 (*Cercocebus atys*) to 7.1 (*Pongo* spp.). There was no statistically significant relationship between Decile 6 and EDJ length, nor were there any statistically significant relationships between the Ratio value (ratio of Decile 6 EFF angle to EDJ length) and any of the independent variables.

Note that the value of Pagel's lambda (λ) ranges between 0 (no phylogenetic signal) to 1 (strong phylogenetic signal), depending on the relationship tested.

DISCUSSION

The aim of this study was to assess the relationship of EFF angles to four aspects of primate biology related to the pace of their life histories: brain weight, body mass, periodicity and degree of folivory (measured as the percent of time spent eating leaves). As discussed in the introduction, the relationships of EFF angles to rates of dental growth and development are complex. First, EFF angles are not truly "proxies" of enamel extension rates as Hogg and Walker (2011) suggested, but are simply related variables. Second, enamel extension rates themselves are an aspect of dental growth and development that can achieve independence from other such aspects (e.g., Dean, 2009; Guatelli-Steinberg et al., 2012). The question this study sought to address is whether, despite these facts, EFF angles *are* related to additional aspects of primate

biology that are correlated with the pace of growth and development, as suggested by the work of Shellis (1984) and Hogg and Walker (2011). The present study explored these relationships by using phylogenetically controlled analyses, Bonferroni-corrected alpha values, species sampled across a wide taxonomic span, and both anterior and posterior teeth.

The positive relationships of mid-crown EFF angles of anterior teeth to brain weight and body weight were statistically significant; brain weight, however, had the largest r^2 value. When canines were removed, only the relationship to brain weight remained statistically significant at the Bonferroni-corrected alpha value. It is not clear why the relationship to body mass became statistically insignificant when canines were removed: this result could indicate either that canines drove the relationship in the combined set of anterior teeth or that the removal of canines reduced the power of the analysis because it reduced the number of species in the anterior tooth sample from ten to nine. There was also a statistically significant positive relationship between the EFF angles of posterior teeth and body mass. Other relationships trended in the anticipated direction, but were not statistically significant. For anterior teeth, these were the positive relationships of EFF angles to periodicity and the negative relationship between EFF angles and degree of folivory. For posterior teeth, the positive relationships of EFF angles to brain weight and periodicity were in the expected direction. The positive (though non-significant) relationship of EFF angles to degree of folivory in posterior teeth was not expected.

Statistically significant relationships between mid-crown EFF angles and EDJ length were not found for either anterior nor posterior teeth, though the relationships were positive, with low coefficients that ranged from 0.028 (anterior teeth without canines) to 0.867 (anterior teeth with canines). The fact that there is no clear relationship between mid-crown EFF angles and EDJ length across the species sampled in this study results in values for EFF angles-scaled-to-

EDJ lengths that are highly variable across species (Table 6) and that show no statistically significant correlations with any of the life-history related variables tested. These results suggest that, as predicted, mid-crown EFF angles and tooth size interact across species in an unpredictable manner and that the relationships of mid-crown EFF angles to brain and body mass found here are not mediated by tooth size.

When many species are compared across the primate order, brain size, body size, and the pace of growth and development tend to be positively correlated with one another (e.g., Harvey and Clutton-Brock 1985; Bromage et al., 2012). Yet, there is also evidence that body size, brain size, and the pace of growth of development can evolve independently in primates. For example, large-bodied sub-fossil lemurs had rapid rates of dental development (Schwartz et al., 2002). Although several examples of dissociations between these inter-correlated aspects of primate biology exist (e.g., Schwartz et al., 2002; Godfrey et al., 2003; Dirks and Bowman, 2007; Leigh and Blomquist, 2007), it remains the case that across a wide primate spectrum, species with larger brains tend to have larger bodies, slower rates of skeletal growth, and slower metabolic rates (Bromage et al., 2009; 2012). Thus, the correlations between EFF angles and brain size (present in anterior teeth) and body size (present in the combined sample of anterior teeth and in the posterior teeth) identified here may simply reflect that the variable in question is a stronger indicator of growth rates, growth periods, or metabolic rates than the other variables within the particular set of species being compared. The fact that, in this study, a signal of these life history related variables is present in the mid-crown EFF angles of both the anterior and posterior dentition suggests that variation in developmental rates across the primate order may affect the entire dentition. Given the relationships Bromage et al. (2009; 2012) found between periodicity

and body mass, it is surprising that periodicity did not emerge as a statistically significant predictor in either set of analyses (for anterior or posterior teeth).

Lack of statistical significance in this study may occur for other reasons. First of all, this study demonstrated that EFF angles are subject to relatively high measurement error. Even in the decile chosen for analysis (decile 6), percent intra-and inter-observer error was about 10%. The most likely impact of measurement error on this study would be to create noise, making relationships difficult to detect. There is further noise in this study owing to variation in EFF angles within each taxon, which in turn is a function of individual variation in EFF angles and tooth-type variation in EFF angles. The present study was limited by the primate material available for sectioning. As a consequence, single specimens represented some species, as was also the case in the studies of Shellis (1984) and Hogg and Walker (2012). Given the level of measurement error and natural variation in EFF angles by individual and tooth- type, such single specimens may not necessarily be representative of the species from which they were derived. Nevertheless, the present study suggests statistically significant relationships between EFF angles and brain size (anterior teeth) and body size (anterior and posterior teeth) in the expected direction. Lack of significance to degree of folivory may be additionally influenced by the high degree of variability some species exhibit in the time they spend eating leaves at different sites (see Table 4). The use of average values does not reflect that variation, and we lack dental samples from specific sites that might reflect local adaptation.

Additional patterns in the data are worth noting. Of all the great apes, *Gorilla* had the smallest EFF angles, both for anterior and posterior teeth. This finding is line with other studies that find more accelerated rates of dental growth and development in gorillas than in *Pan* or *Pongo* (Schwartz and Dean, 2001; Kelley and Schwartz 2010), and in turn are in agreement with

the overall pace of growth and development in these great apes (Kelley and Schwartz, 2010). It is also interesting that the signal is similar for both the anterior and posterior teeth in the great apes sampled here, suggesting a systemic effect on the dentition. Secretion rates close to the EDJ in the lateral enamel of *Gorilla* and *Pongo* canine teeth are nearly equal, with a mean of 2.83 micrometers per day in 206 measurements for *Gorilla* and 2.85 micrometers per day in 102 measurements for *Pongo* (Schwartz et al., 2001). Thus, the EFF angle difference between *Pongo* and *Gorilla* is unlikely to be related to enamel secretion rate differences between them. Note also that anterior tooth EDJ lengths in *Gorilla* are comparable to those of *Pongo* in this study, while they exceed those of *Pongo* for posterior teeth. This point in turn suggests that gorillas are growing teeth that are similar or greater in size to those of orangutans at a faster rate. We speculate that with shorter overall developmental periods, gorillas must speed up their rates of enamel growth in order to achieve their final large tooth sizes.

Enamel secretion rates close to the EDJ in the lateral enamel of canine teeth are statistically significantly greater in *Pan* (3.03 micrometers per day in 120 measurements; Schwartz et al., 2001) than they are in *Gorilla* or *Pongo*. By Shellis' (1984) equation, higher rates of enamel secretion would be expected to push striae to more oblique angles; thus, *Pan's* large EFF angles may be in part be influenced by its faster rates of enamel secretion.

One anomalous finding is the very low EFF angle found in the single *Cebus apella* molar included here (10.7 degrees). Consistent with the large brain size of this species, its relatively slow pace of growth and development, and the much larger mid-crown EFF angles Hogg and Walker (2011) reported (average 22.35 for 5 *Cebus apella* teeth), this value seems atypical. In the present study, specimens with obvious obliquity were removed from analysis, but they were originally measured. It is worth mentioning that the original sample included two additional

(oblique) specimens and these had greater decile 6 angle measurements (17.5 and 22.4, respectively), more consistent with the measurements of Hogg and Walker (2011). Thus, the single *Cebus apella* specimen retained in the sample may not have been representative of this species. Given Hogg and Walker's (2011) results, this seems most likely.

There are several next steps that could be taken to further explore the relationship between EFF angles and other aspects of primate biology. Beyond the obvious need to increase sample sizes, it would be useful to clarify to what extent these angles actually represent extension rate differences among taxa. It would be especially helpful to know the degree to which variation in daily rates of enamel secretion across taxa influences EFF angles. Hogg and Walker (2011) argued there exists a positive relationship between daily secretion rates and brain size across 17 platyrrhine species. If faster rates of enamel secretion are associated with larger brain size across the broader primate spectrum, they would be expected to augment the effect of enamel extension rates on EFF angles; i.e., they would be expected to push striae to even larger angles in species with larger brain sizes. So, one question to explore would be the extent to which larger EFF angles in species with larger brain sizes is related to faster rates of enamel secretion vs. slower rates of enamel extension.

In summation, the present study provides support for the contention of Shellis (1984) and Hogg and Walker (2011) that EFF angles are related to aspects of primate biology associated with the pace of their growth and development. However, further exploration is needed with larger samples, diverse tooth types, and with independent measurements of enamel extension rates and enamel secretion rates, as well as measurements of the angle that enamel prisms make with the enamel-dentine junction (Shellis' Angle I). The relationships found in the present study suggest that such further investigation is warranted.

ACKNOWLEDGMENTS

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FIGURE LEGENDS

Figure 1: Relationship between EFF angles and extension rates. The image on the far left is a portion of a modern human incisor (taken with Olympus BX51 with a 2x objective in non-polarized light) that shows two areas, outlined in boxes where striae of Retzius (marked by arrows) make different angles with the EDJ. Next this image are two boxes, highlighting the relationships between EFF angles and the variables in Shellis' equation (below). In the upper box, the striae of Retzius, which mark the former enamel formation front (EFF) at a particular point in time, make more acute angles with the EDJ than they do in the lower box, where the angles are more obtuse. These boxed areas are enlarged and diagramed on the right, using labels from Shellis' equation relating enamel extension rates to EFF angles: $\mathbf{c = d[(\sin I/\tan D) - \cos I]}$, where d = the length of prism formed in one day, c = the distance over which ameloblasts have differentiated over the course of a single day, angle I is the angle that enamel prisms make with the EDJ, and angle D is the angle that the EFF makes with EDJ, synonymous with what is

termed the "EFF angle" in the present study. In these diagrams, "d" and "c" are labeled. Enamel

prisms are indicated by alternating white and grey stripes. Angle I is represented by the angle

that these stripes make with the EDJ, and Angle D is represented by the angle that the EFF

makes with the EDJ. Additionally, in these diagrams, the prior EFF (from one day earlier) is

indicated with a dotted line, while the current EFF occurs along the line of ameloblasts

symbolized by stippled boxes at the end of each prism. The newly differentiated ameloblasts

(those that differentiated within the last day) are indicated with lighter stippling, and the hatched

area indicates inner enamel epithelium that has not yet differentiated to form ameloblasts.

Note that in the top box, representing more acute EFFs in the incisal region of the tooth, c

is longer than it is in the bottom box, where c is shorter. In other words, where the EFF angle is

more acute, more ameloblasts have differentiated over the course of a day, such that the

extension rate is faster. Also note that if Shellis' equation were rearranged to solve for angle D

(see text), then the value of D would be shown to depend not just on "c" (the length of EDJ over

which ameloblasts have differentiated in one day) but also on "d" (the length of the enamel prism

secreted by an ameloblast in one day) and on "I" (the angle that the enamel prisms make with the

EDJ).

At the far right is an example of angle measurements taken with Olympus BX51 with 2x

objective). The EFF angle measurement was made between a line tangent to the EDJ and a

straight line best representing the Retzius line at the EDJ.

Figure 2: A) EDJ length was measured along the red dotted line from the CEJ to tip of the dentine horn (red arrows) using the segmented line tool in ImageJ (scale not shown). The grey shaded area represents the reconstructed crown tip which was used to establish deciles (black bars). B) For some teeth, like this *P. anubis* canine, it was possible to reconstruct the crown height and therefore the deciles, but the exact path of the EDJ could not be reconstructed, so EDJ length was not measured.

Figure 3: Anterior teeth: Statistically significant relationships between log EFF angle and brain size, body size. Posterior teeth: Statistically significant relationship between log EFF angle and body size.

TABLE 1: TOTAL SAMPLE*

Taxon	Individual	Tooth Types	Totals
Pan troglodytes	88-89	UI1	1
Pan troglodytes	901-2	UI1*, UI2*, UM1*, UM2*	4
Pan troglodytes	HT04-01	LI1*, LI2*	2
Pan troglodytes	HT10-02	LI1*, LC*, LI2*	3
Pan troglodytes	HT15-00	LI1*, LI2*, LC	3
Pan troglodytes	HT43-87	LI1*, LI2*,LC*	3
Pan troglodytes	930-1	LI2, UP1*, UP2*	3
Total Pan troglodytes			**19**
Gorilla gorilla	HT-12-00	UI1*	1
Gorilla gorilla	HT76-89	UI1*, UI2*, LI1*, LI2*	4
Gorilla gorilla	901-1	UI2*, LP2*	2
Gorilla gorilla	932-1	LI1	1
Gorilla gorilla	6896	LC*	1
Gorilla gorilla	932-4	UM2*	1
Gorilla gorilla	932-5	LM2*	1
Total Gorilla gorilla			**11**
Pongo spp.	9-02	UI1, UM1*, UM3*	3
Pongo spp.	162-88	UI1, UI2,	2
Pongo spp.	166-88	LI2*	1
Pongo spp.	170-88	LC*	1
Total Pongo spp.			**7**
Symphalangus syndactylus	1993	LI2	1
Total Symphalangus			**1**
Hylobates spp.	24-91	LC	1
Hylobates spp.	43-95	UI1*, LI2*	2
Total Hylobates			**3**
Papio anubis	17	LC	1
Papio anubis	18	LC	1
Papio anubis hybrid	19	LC *	1
Total Papio			**3**
Colobus polykomos	935-10	UI1*	1
Colobus polykomos	935-11	LI1*	1
Colobus polykomos	932-26	UM3*	1
Colobus polykomos	932-27	LM2*	1
Colobus polykomos	935-9	LM1*	1
Total Colobus polykomos			**5**
Cercocebus atys	43-97	LI1*, LI2*	2
Total Cercocebus atys			**2**
Chlorocebus aethiops	920-1	LM1*	1
Chlorocebus aethiops	920-2	UP1*, UM1*	2
Total Chlorocebus aethiops			**3**

Species	Specimen	Teeth	Count
Erythrocebus patas	905-7	UM3*	1
Total *Erythrocebus patas*			**1**
Cercopithecus diana	2117	UP*	
Total *Cercopithecus diana*			**1**
Macaca mulatta	904-8	UM1*	1
Total *Macaca mulatta*			**1**
Macaca fascicularis	921-1	LI1*, LI2*, LP2*	3
Total *Macaca fascicularis*			**3**
Macaca nemestrina	905-4	LI1*	1
Macaca nemestrina	905-3	UP2*	1
Macaca nemestrina	905-5	UM2*	1
Macaca nemestrina	913-4	LM1*	1
Total *Macaca nemestrina*			**4**
Ateles fusciceps	906-1	UM2*, UM4*	2
Ateles spp.	HT40-90	UM2*	1
Total *Ateles*			**3**
Alouatta pigra	HT61-89	LM1*	1
Alouatta spp.	906-9	UM2*	1
Total *Alouatta*			**2**
Cebus apella	906-5	LM1	1
Total *Cebus apella*			**1**
Propithecus diadema	HT16-90	LM2	1
Propithecus diadema	HT 15-89	LM2*	1
Total *Propithecus diadema*			**2**
Otolemur crassicaudatus	HT12-90	LM1, UM2	2
Total *Otolemur crassicaudatus*			**2**
Perodicticus potto	Unk1	UM1	1
Perodicticus potto	Unk2	UM2*	1
Total *Perodicticus potto*			**2**

* Asterisks denote teeth that were measured for both EFF angles and EDJ lengths.

TABLE 2: MEASUREMENT ERROR

| Decile | N (Observer 1/ Observer 2) | Intra-Observer | | Inter-Observer | | | |
| | | | | Measurement 1 | | Measurement 2 | |
		Average Absolute Error	Average Percent Error	Average Absolute Error	Average Percent Error	Average Absolute Error	Average Percent Error
1	(2/0)	1.2°	8.7	-	-	-	-
2	(10/8)	1.6°	21.9	2.5°	23.4	2.4°	19.5
3	(13/11)	2.1°	18.9	2.1°	17.4	2.9°	25.3
4	(15/13)	2.1°	15.2	1.2°	8.9	2.1°	15.3
5	(14/14)	1.2°	6.9	2.2°	13.6	1.6°	10.4
6	(15/15)	1.6°	9.0	2.1°	10.4	2.0°	10.8
7	(14/13)	0.8°	4.7	1.9°	13.4	2.0°	14.1
8	(14/14)	2.3°	12.1	2.3°	11.8	1.4°	7.2
9	(12/10)	1.8°	9.0	1.8°	10.0	1.4°	8.4
10	(10/10)	2.0°	11.5	2.3°	13.3	1.9°	11.6

TABLE 3: INDEPENDENT VARIALBES USED IN PHYLOGETIALLY CONTROLLED ANALYSES

Taxon	Average Periodicity[a]	Female Body Mass (kg)[b]	Female Brain Weight (g)[c]	% Time Eating Leaves[d]
Pan troglodytes	6	40.4	351.27	17.47
Gorilla gorilla	9.5	80	395.03*	28.5
Pongo spp.	10	35.7	350.87	15.65
Symphalangus syndactylus	4.5	10.7	104**	40.7
Hylobates spp.	4	5.34	97.86*	21.25
Papio anubis	7	13.3	148*	22.9
Colobus polykomos	.	8.4	76.7**	52.75
Cercocebus atys	.	5.5	102.77*	1.25
Chlorocebus aethiops		2.98	66.1**	14.85
Cercopithecus diana	4		77.3**	9.5
Erythrocebus pata	4	4.8	84.42	4.18
Macaca fascicularis	4	3.59	63.16	16.5
Macaca mulatta	4	5.18	89.1	49.49
Macaca nemestrina	4	6.5	96.2**	7
Ateles fusciceps	4	8.8	108.8*	
Ateles spp.	4	6.6	104.28*	20.95
Alouatta pigra	6	6.4	.	45.1
Alouatta spp.	6	5.34	51.05	45.9
Cebus apella	4.5	2.6	68.81	0
Propithecus diadema	2	6.26	37**	42.1
Otolemur crassicaudatus	.	1.21	.	0
Perodicticus potto	.	1.08	14.3**	0

[a] Periodicities based on taxon averages (or single observations per taxon) as given in Bromage et al. (2012), with the exception of the periodicity for *A. fusciceps* (Guatelli-Steinberg et al., 2009), *Cercopithecus diana* (this study) and the periodicity for *P. verrauxi* (Schwartz et al., 2002) used for *P. diadema*. Periodicities from Bromage et al. (2012) for *A. palliata* were substituted for both *Alloutta pigra* and *Alouatta spp.*, and *H. lar* for *Hylobates* spp.
[b] Female body masses are from Godfrey et al. (2001) with the following exceptions: *S. syndactylus* (Dirks and Bowman, 2007); *C. polykomos* (Harvey and Clutton-Brock, 1985), *C. atys* (Harvey and Clutton-Brock, 1985) *A. fusciceps* (Ford, 1994), *Ateles* spp. (average for *Ateles* species in Harvey and Clutton-Brock, 1985), *A. pigra* (Ford, 1994), *Alouatta* spp. (average for *Alouatta* species in Ford, 1994), and *O. crassicaudatus* (Jones et al.2009; for "adult body mass."), *Perodicticus potto* (Harvey and Clutton-Brock, 1985).
[c] Female brain weights: Those with no asterisk are from Barickman et al. (2008); those with an asterisk are from Boddy et al. (2012); and those with a double asterisk from Harvey and Clutton-Brock (1985).
[d] Percent of time eating leaves: Averages based on values from studies listed in Table 4.

TABLE 4: DEGREE OF FOLIVORY

Taxon	% time eating leaves of total time eating	Basis of values
Pan troglodytes	**17.47***	**Rabenold and Pearson (2011); Data from five study sites included in average**
Gorilla gorilla	***28.5**	**Average**
	26	Remis (1997) (Bai Hokou, Central African Republic)
	31	Doran-Sheehy et al. (2009) (Mondika Resaerch Center, Central African Republic and Republic of Congo) (Average for males and females)
Pongo pygmaeus	**15.65***	**Rabenold and Pearson (2011): Data from four study sites included in average**
Symphalangus syndactylus	**40.7***	**Average**
S. syndactylus	17	Palombit (1997) (Ketambe, Sumatra)
S. syndactylus	58	Chivers and Raemaekers (1986); one study site in Malaya
S. syndactylus	47	Chivers and Raemaekers (1986); second study site in Malaya
Hylobates spp	**21.25***	**Average**
H. lar	4	Palombit (1997) (Ketambe, Sumatra)
H. lar	26	Chivers and Raemaekers (1986); Malaya
H. agilis	31	Chivers and Raemaekers (1986); Malaya
H. moloch	24	Kim et al. (2011): Java
Papio anubis	**22.9***	**Average**
P. anubis	17	Okecha and Newton-Fisher (2006): Budongo, Uganda
P. anubis	41	Hill and Dunbar (2002): Bole, Ethiopia
P. anubis	27	Hill and Dunbar (2002): Chololo, Kenya
P. anubis	53	Hill and Dunbar (2002): Gilgil, Kenya
P. anubis	14	Hill and Dunbar (2002): Gombe, Tanzania
P. anubis	44	Hill and Dunbar (2002): Masai Mara, Kenya
P. anubis	8	Hill and Dunbar (2002): Shai Hills, Ghana
P. anubis	15	Hill and Dunbar (2002): Amboseli, Kenya
P. anubis	14	Hill and Dunbar (2002): Mikumi, Tanzania
P. anubis	19	Hill and Dunbar (2002): Ruaha, Tanzania
Colobus polykomos	**52.75***	**Average**
C. polykomos	57	Davies et al.(1999): Tiwai, Sierra Leone
C. polykomos	48.5	Korstjens and Dunbar (2007): Tai Forest, Ivory coast
Cercocebus atys	**1.25***	**Pampush et al. (2013): Taï Forest, Ivory coast**
Chlorocebus aethiops	**14.85***	**Average**
C. aethiops	18.7	Dunbar and Dunbar (1974): Ethiopia, various sites
C. aethiops	11	Harrison (1983): Senegal (combined category of leaves, grass, herbs, gun, fungi)
Cercopithecus diana	**9.5***	**Average**

C. diana	3.5	Wachter et al. (1997) Taï Forest; Ivory Coast
C. diana	11	Oates and Whitesides (1990): Sierra Leone (one group)
C. diana	14.1	Oates and Whitesides (1990): Sierra Leone (second group)
Erythrocebus patas	**4.18***	**Average**
E. patas	2.85	Isbell (1998): Laikipia, Kenya
E. patas	5.5	Nakagawa (1989): Kala Maloue, Cameroon
Macaca fascicularis	**16.5***	**Average**
M. fascicularis	17.2	Richter et al. (2013): Data from table on different unprovisioned groups
M. fascicularis	24	"
M. fascicularis	16.1	"
M. fascicularis	8.4	"
M. fascicularis	10.5	"
M. fascicularis	9	"
M. fascicularis	5.5	"
M. fascicularis	41	"
Macaca mulatta	**49.49***	**Average**
M. mulatta	22.5	Leigh (1994); North India
M. mulatta	78.37	Pampush et al. (2013); Pakistan
M. mulatta	47	Zhou et al. (2014): Nonggang, China (estimated from graph);
Macaca nemestrina	**7***	**Richter et al. (2013): Malayasia**
Ateles spp.	**20.95***	**Average**
Ateles fusciceps	.	.
Ateles spp.	55	Gonzalez-Zamora et al.(2008): Data from summary table on multiple study sites (*Ateles geoffroyi*)
Ateles spp.	31	"
Ateles spp.	10.5	"
Ateles spp.	13.7	"
Ateles spp.	16.1	"
Ateles spp.	26	"
Ateles spp.	15.6	"
Ateles spp.	23.7	"
Ateles spp.	28.7	"
Ateles spp.	15.5	"
Ateles spp.	6	"
Ateles spp.	11.7	"
Ateles spp.	12.5	"
Ateles spp.	14	"
Ateles spp.	22	"
Ateles spp.	37	"
Ateles spp.	17.2	"
Alouatta pigra	**45.1***	**Silver et al. (1998) Northern Belize**

Alouatta spp.	**45.985***	**Average**
Alouatta spp.	53.3	Estrada et al. (1999): Los Tuxtlas, Mexico (*Alouatta palliata*)
Alouatta spp.	57.06	Asensio et al. (2007): Forest fragment, Mexico
Alouatta spp.	36.65	"
Alouatta spp.	36.93	"
Cebus apella	**0***	**Rabenold and Pearson (2011): Data from five study sites included in average**
Propithecus diadema	**42.1***	**Powzyk and Mowry (2003): Mantadia Park, Madagascar**
Otolemur crassicaudatus	**0***	**Hladik (1979): No leaves in diet noted**
Perodicticus potto	**0***	**Hladik (1979): No leaves in diet noted**

* Value used for regressions.

TABLE 5: SUMMARY DATA FOR EFF ANGLE MEASUREMENTS

Taxon	Anterior vs. Posterior (N)	Range	Mean
Pan troglodytes	Ant. (15)	24.6 - 42.7°	32.5°
	Post (4)	22.6 - 38.4°	32.1°
Gorilla gorilla	Ant. (7)	14.3 - 33.3°	20.0°
	Post. (3)	18.2 - 25.4°	20.1°
Pongo spp.	Ant. (5)	23.9 - 40.0°	31.4°
	Post. (2)	30.1 - 65.4°	47.8°
Symphalangus syndactylus	Ant. (1)	17.8°	17.8°
Hylobates spp.	Ant. (2)	16.1 - 25.0°	20.5°
Papio anubis & P.a. hybrid	Ant. (3)	14.6 - 16.3°	15.6°
Colobus polykomos	Ant. (2)	14.0 - 15.5°	14.8°
	Post. (3)	14.1 - 21.1°	17.4°
Cercocebus atys	Ant. (2)	16.3 - 21.1°	18.7°
Erythrocebus patas	Post. (1)	13.6°	13.6°
Chlorocebus aethiops	Post. (3)	21.0 - 28.9°	23.8°
Cercopithecus diana	Post. (1)	25.3°	25.3°
Macaca fascicularis	Ant. (2)	10.1 - 13.9°	12.0°
	Post. (1)	13.9°	13.9°
Macaca mulatta	Post. (1)	14.0°	14.0°
Macaca nemestrina	Ant. (1)	11.5°	11.5°
	Post. (3)	17.1 - 22.2°	19.0°
Ateles fusciceps	Post. (2)	18.0 - 25.8°	21.9°
Ateles	Post. (1)	13.0°	13.0°
Alouatta pigra	Post. (1)	10.8°	10.8°
Alouatta spp.	Post. (1)	16.6°	16.6°
Cebus apella	Post. (1)	10.9°	10.9°
Propithecus diadema	Post. (2)	22.9 - 25.0°	24.0°
Otolemur crassicaudatus	Post. (2)	13.6 - 15.8°	14.7°
Perodicticus potto	Post. (2)	10.5 - 19.6°	15.1°

TABLE 6: SUMMARY DATA FOR EDJ LEGNTHS AND EFF/EDJ LENGTH RATIOS (scaled EFF angles)

Taxon	Anterior vs. Posterior (N)	EDJ length (mm.)		EFF/EDJ Length Ratio (degrees/mm.)	
		Range	Mean	Range	Mean
Pan troglodytes	Ant. (12)	11.0-17.3	13.4	1.8-3.3	2.5
	Post (4)	5.2-7.9	6.4	4.2-5.7	5.0
Gorilla gorilla	Ant. (7)	11.0-18.8	15.1	0.9-1.8	1.3
	Post. (3)	5.1-11.2	7.8	1.6-3.6	2.9
Pongo spp.	Ant. (1)	15.5	15.5	1.5	1.5
	Post. (2)	6.4-6.9	6.7	4.7-9.4	7.1
Symphylangus syndactylus	Ant. (0)	-	-	-	-
Hylobates spp.	Ant. (1)	5.4	5.4	3.0	3.0
Papio anubis & P.a. hybrid	Ant. (1)	21.4	21.4	0.75	0.75
Colobus polykomos	Ant. (2)	6.3-8.2	7.3	1.7-2.5	2.1
	Post. (3)	3.5-5.4	4.3	3.2-6.0	4.2
Cercocebus atys	Ant. (2)	12.1-14.8	13.5	1.1-1.8	1.4
Erythrocebus patas	Post. (1)	4.0	4.0	3.4	3.4
Chlorocebus aethiops	Post. (3)	3.2-4.5	3.9	4.6-7.4	6.2
Cercopithecus diana	Post. (1)	4.8	4.8	5.3	5.3
Macaca fascicularis	Ant. (2)	10.3-11.6	11.0	0.9-1.4	1.1
	Post. (1)	5.7	5.7	2.4	2.4
Macaca mulatta	Post. (1)	4.7	4.7	3.0	3.0
Macaca nemestrina	Ant. (1)	11.6	11.6	1.0	1.0
	Post. (3)	4.5-7.2	6.0	2.7-3.9	3.2
Ateles fusciceps	Post. (2)	4.2-4.4	4.3	4.2-5.9	5.1
Ateles	Post. (1)	5.2	5.2	2.5	2.5
Alouatta pigra	Post. (1)	6.6	6.6	1.6	1.6
Alouatta spp.	Post. (1)	4.4	4.4	3.8	3.8
Cebus apella	Post. (0)	-	-	-	-
Propithecus diadema	Post. (1)	4.0	4.0	5.7	5.7
Otolemur crassicaudatus	Post. (0)	-	-	-	-
Perodicticus potto	Post. (1)	2.2	2.2	4.8	4.8

TABLE 7: REGRESSION RESULTS

Model	DF	F-statistic	Coeff.	r^2	λ	p	Bonf. alpha
Anterior Dentition pgls Results (with canines)*							
D6 vs Perio	1,6	0.103	0.0317	0.017	0.00	0.759	0.009
D6 vs BdMa	**1,8**	**11.83**	**5.532**	**0.597**	**0.00**	**0.008**	**0.009**
D6 vs BrW	**1,8**	**23.41**	**9.295**	**0.745**	**0.00**	**0.001**	**0.009**
D6 vs Fol	1,8	1.366	-1.549	0.146	1.00	0.276	0.009
D6 vs EDJL	1,6	1.614	0.867	0.212	0.839	0.251	0.009
Ratio vs Perio	1,4	2.696	-0.150	0.402	1.00	0.176	0.009
Ratio vs BdMa	1,6	0.526	-0.182	0.080	0.95	0.496	0.009
Ratio vs BrW	1,6	0.124	-0.134	0.020	0.73	0.737	0.009
Ratio vs Fol	1,6	1.363	0.194	0.049	0.00	0.287	0.009

*BdMa log-transformed, BrW log-transformed, Fol logit-transformed

Model	DF	F-statistic	Coeff.	r^2	λ	p	Bonf. alpha
Anterior Dentition pgls Results (without canines)**							
D6 vs Perio	1,5	3.694	0.668	0.425	0.00	0.112	0.010
D6 vs BdMa	1,7	5.207	0.224	0.426	0.00	0.056	0.010
D6 vs BrW	**1,7**	**10.45**	**0.398**	**0.599**	**0.00**	**0.014**	**0.010**
D6 vs Fol	1,7	1.383	-0.104	0.045	1.00	0.278	0.010
D6 vs EDJL	1,5	0.301	0.028	0.059	0.42	0.607	0.010
Ratio vs Perio	1,3	1.799	-1.340	0.375	1.00	0.272	0.009
Ratio vs BdMa	1,5	0.091	-0.084	0.018	0.56	0.774	0.009
Ratio vs BrW	1,5	0.165	-0.218	0.031	1.00	0.702	0.009
Ratio vs Fol	1,5	0.858	0.178	0.146	0.00	0.396	0.009

** D6 log-transformed, Perio log-transformed, BdMa log-transformed, BrW log-transformed, Fol logit-transformed

Model	DF	F-statistic	Coeff.	r^2	λ	p	Bonf. alpha
Posterior Dentition pgls Results***							
D6 vs Perio	1,12	1.157	0.311	0.088	0.00	0.303	0.014
D6 vs BdMa	**1,15**	**8.755**	**0.206**	**0.369**	**0.00**	**0.009**	**0.014**
D6 vs BrW	1,14	2.197	0.159	0.136	0.00	0.161	0.014
D6 vs Fol	1,14	0.320	0.044	0.022	0.00	0.580	0.014
D6 vs EDJL	1,14	0.737	0.057	0.050	0.00	0.405	0.014
Ratio vs Perio	1,11	0.000	-0.020	<0.001	0.00	0.985	0.014
Ratio vs BdMa	1,13	0.130	0.139	0.009	0.00	0.724	0.014
Ratio vs BrW	1,13	0.003	0.027	0.000	0.00	0.953	0.014
Ratio vs Fol	1,12	0.389	-0.240	0.031	0.00	0.544	0.014

***D6 log-transformed. Periodicity log-transformed, BdMa log-transformed, BrW log-transformed, Fol logit-transformed.

Shapiro-Wilk Tests for normality

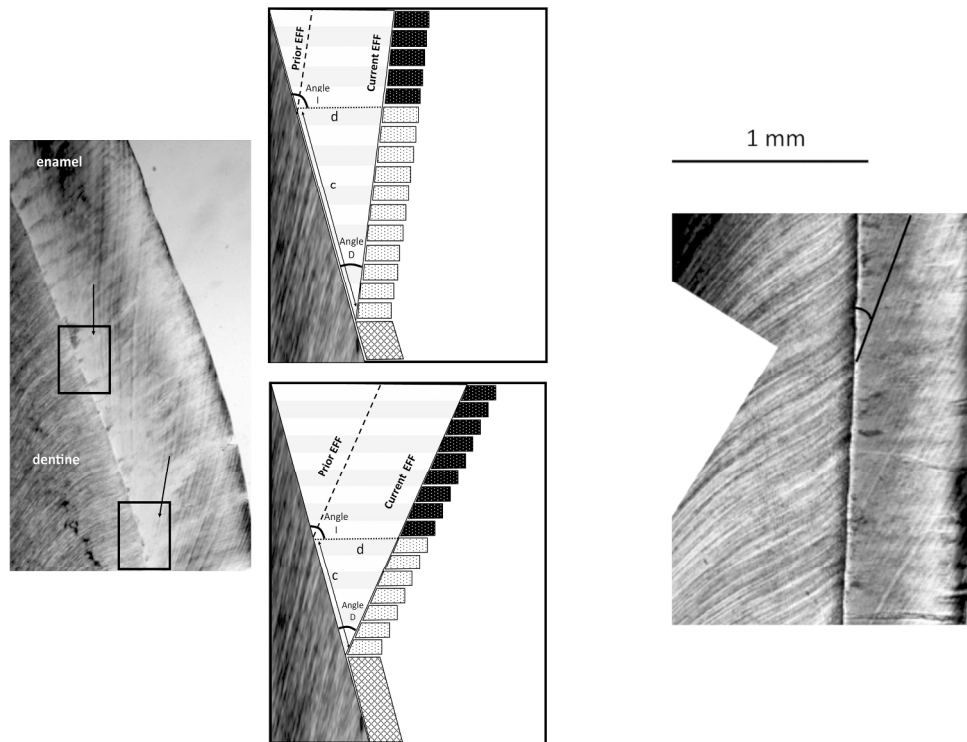| Variable	Dentition	W	p
Decile 6	Anterior(w/Cs)	0.935	0.505
Periodicity	Anterior(w/Cs)	0.824	0.052
Body Mass	Anterior(w/Cs)	0.730	0.002
Brain Mass	Anterior(w/Cs)	0.751	0.003
Percentage Feeding Leaves	Anterior(w/Cs)	0.942	0.584
EDJL	Anterior(w/Cs)	0.889	0.160
Ratio	Anterior(w/Cs)	0.910	0.280
Decile 6	Anterior	0.833	0.049
Periodicity	Anterior	0.761	0.016
Body Mass	Anterior	0.738	0.004
Brain Mass	Anterior	0.730	0.003
Percentage Feeding Leaves	Anterior	0.939	0.576
EDJL	Anterior	0.912	0.327
Ratio	Anterior	0.911	0.327
Decile 6	Posterior	0.803	0.002
Periodicity	Posterior	0.798	0.005
Body Mass	Posterior	0.583	<0.001
Brain Mass	Posterior	0.760	<0.001
Percentage Feeding Leaves	Posterior	0.898	0.074
EDJL	Posterior	0.942	0.340
Ratio	Posterior	0.969	0.825

Figure 1: Relationship between EFF angles and extension rates. The image on the far left is a portion of a modern human incisor (taken with Olympus BX51 with a 2x objective in non-polarized light) that shows two areas, outlined in boxes where striae of Retzius (marked by arrows) make different angles with the EDJ. Next this image are two boxes, highlighting the relationships between EFF angles and the variables in Shellis' equation (below). In the upper box, the striae of Retzius, which mark the former enamel formation front (EFF) at a particular point in time, make more acute angles with the EDJ than they do in the lower box, where the angles are more obtuse. These boxed areas are enlarged and diagramed on the right, using labels from Shellis' equation relating enamel extension rates to EFF angles: c = d[(sin I/tanD) – cos I], where d = the length of prism formed in one day, c = the distance over which ameloblasts have differentiated over the course of a single day, angle I is the angle that enamel prisms make with the EDJ, and angle D is the angle that the EFF makes with EDJ, synonymous with what is termed the "EFF angle" in the present study. In these diagrams, "d" and "c" are labeled. Enamel prisms are indicated by alternating white and grey stripes. Angle I is represented by the angle that these stripes make with the EDJ, and Angle D is represented by the angle that the EFF makes with the EDJ. Additionally, in these diagrams, the prior EFF (from one day earlier) is indicated with a dotted line, while the current EFF occurs along the line of ameloblasts symbolized by stippled boxes at the end of each prism. The newly differentiated ameloblasts (those that differentiated within the last day) are indicated with lighter stippling, and the hatched area indicates inner enamel epithelium that has not yet differentiated to form ameloblasts.

Note that in the top box, representing more acute EFFs in the incisal region of the tooth, c is longer than it is in the bottom box, where c is shorter. In other words, where the EFF angle is more acute, more ameloblasts have differentiated over the course of a day, such that the extension rate is faster. Also note that if Shellis' equation were rearranged to solve for angle D (see text), then the value of D would be shown to depend not just on "c" (the length of EDJ over which ameloblasts have differentiated in one day) but also on "d" (the length of the enamel prism secreted by an ameloblast in one day) and on "I" (the angle that the enamel prisms make with the EDJ).

At the far right is an example of angle measurements taken with Olympus BX51 with 2x objective). The EFF angle measurement was made between a line tangent to the EDJ and a straight line best representing the

Retzius line at the EDJ.
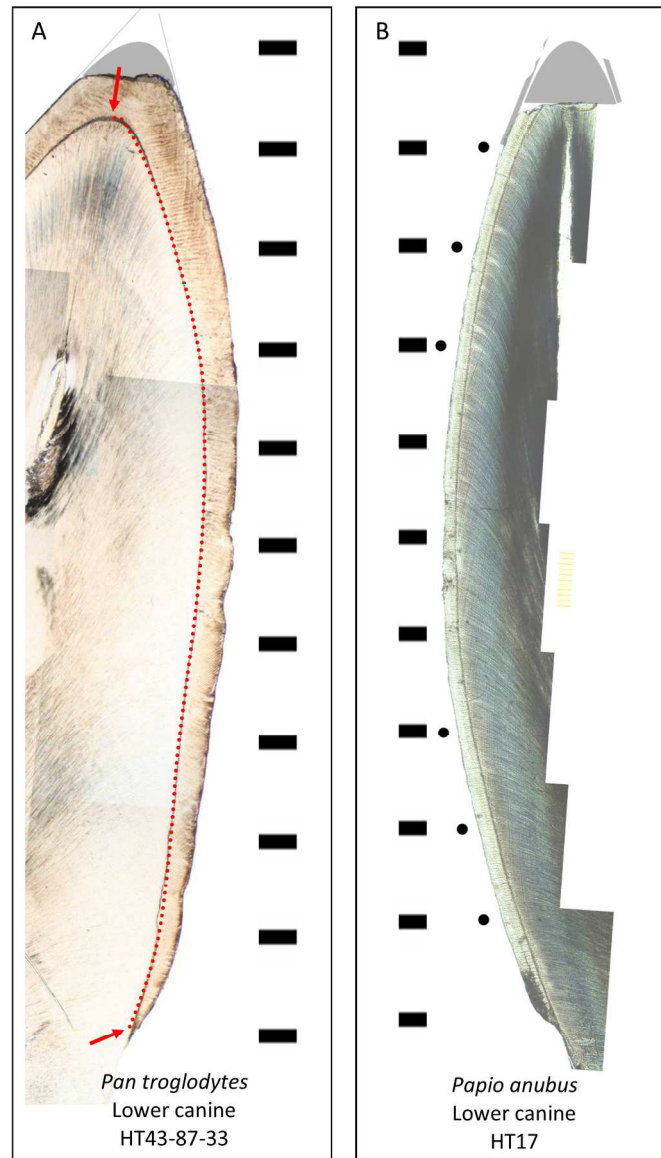
117x89mm (600 x 600 DPI)

Figure 2: A) EDJ length was measured along the red dotted line from the CEJ to tip of the dentine horn (red arrows) using the segmented line tool in ImageJ (scale not shown). The grey shaded area represents the reconstructed crown tip which was used to establish deciles (black bars). B) For some teeth, like this P. anubis canine, it was possible to reconstruct the crown height and therefore the deciles, but the exact path of the EDJ could not be reconstructed, so EDJ length was not measured.
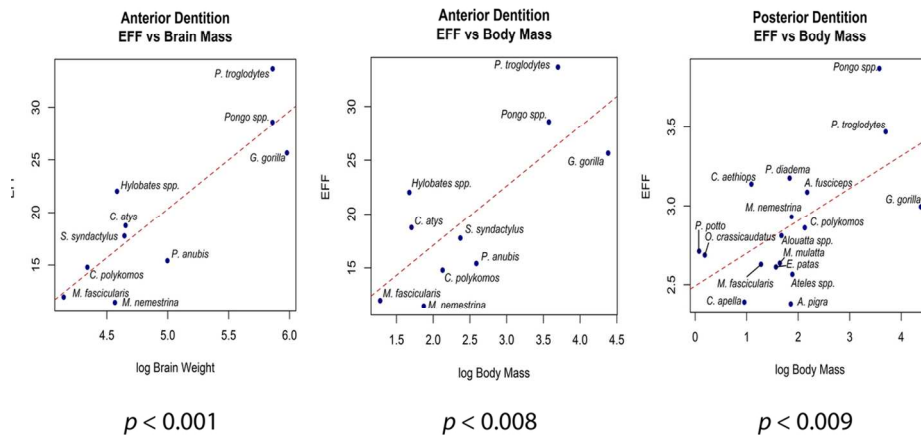
101x172mm (600 x 600 DPI)

Figure 3: Anterior teeth: Statistically significant relationships between log EFF angle and brain size, body size. Posterior teeth: Statistically significant relationship between log EFF angle and body size.

57x31mm (600 x 600 DPI)