Lateral Enamel Formation and Life History in New World Monkeys

Allison Clark, Department of Anthropology, The Ohio State University
Edward F. Hayes Graduate Research Forum, 2015

Abstract

The field of anthropology has seen a continuous interest in the human life history evolution. Since the modern human life history pattern is unique when compared to the rest of the primates, the question of when and why the modern human life history arose has become a frequent topic of research. The relationship between dental development and life history profiles within extant and fossil primates has not been systematically tested, especially in the anterior dentition. In order to explore this relationship, this study tests the hypotheses that there is a relationship between life history and estimated lateral enamel formation time as well as percent of perikymata in the cervical half of the crown. This study examined these relationships in incisor replicas of twelve extant species of platyrrhines. The measures of life history and related variables include: encephalization quotient, age at weaning, age at reproductive maturation, and average lifespan in addition to brain size and body size. Platyrrhines were chosen for their wide life history variation and their use in previous studies examining dental development and life history. Results show that there are relationships of differing strengths between all variables for each incisor type. Estimated lateral enamel formation time is strongly related to brain size, body size, age at weaning and age at reproductive maturation. The percent of perikymata in the cervical region of the crown is significantly related to brain size, age at

reproductive maturation, and weaning age, although these relationships are much weaker and are not found in all tooth types. These results suggest that the relationship between dental development, specifically lateral enamel crown formation time, and life history is robust and should be explored further.

Chapter 1: Introduction

The life history of hominins and non-human primates has become a topic of increasing interest in the field of paleoanthropology (e.g., Beynon and Dean, 1986; Dean et al., 2001; Guatelli-Steinberg et al., 2007; Smith, 2008). Modern human growth and development has been a focal point of anthropological research since its inception as a discipline (Boas, 1932). Patterns, variation, and causes of human growth continue to be of interest to researchers (Bromage et al., 2009; Crews and Bogin, 2010; Guatelli-Steinberg et al., 2012). Life history theory defines stages of growth in an evolutionary framework. Life history profiles involve trade-offs between energy allocated to various stages of growth and reproductive output, and can therefore be seen as evolutionary strategies. The modern human life history strategy is a result of millions of years of evolutionary forces (Bogin, 1999). As a result of our evolutionary history, modern humans have a unique pattern of growth unlike that of other living primates (Bogin, 1999). Specifically, modern humans have prolonged periods of growth and development before reaching adulthood (Bogin,1999). Our unique life history pattern has raised three main research questions for anthropologists. First, *when* did the modern human pattern evolve? Secondly, *why* did this pattern evolve? And finally, what evidence can be used to answer the former questions? (Dean, 2006).

Aspects of dental development, such as first molar eruption (Smith, 1989), molar crown formation time (Macho, 2001), and occlusal enamel formation rates (Dean, 2006) have been shown to be associated with brain size, body size, and pace of primate life histories across the order. These aspects of dental development can be instrumental in answering questions about the

pace of life history, specifically, when the prolonged juvenile period arose in the hominin lineage. There are additional aspects of dental development that have not been fully researched that may also further knowledge about the evolution of life history. Aspects of enamel microstructures such as perikymata (incremental growth lines on the enamel surface) may also be related to the pace of life history (e.g. Dean et al., 2001).

Much previous research on dental development and life history focuses on molars (e.g. Smith, 1989), and therefore these relationships need to be tested in the anterior dentition. Studies involving fossil hominins often utilize anterior dentition (Dean et al., 2001; Ramirez-Rozzi and Bermudez de Castro, 2004, Guatelli-Steinberg et al., 2005), but a robust relationship between dental development and life history in these teeth has yet to be established (Guatelli-Steinberg, 2009). In fossil studies where teeth cannot be sectioned, anterior teeth (incisors and canines) provide a benefit over posterior teeth (molars and premolars) in that a larger portion of their enamel formation time is represented by perikymata on the enamel surface. The present investigation focuses on the potential relationships between estimated lateral enamel formation time in anterior teeth and several life history variables as well as associated aspects of primate biology (e.g., brain size). This investigation also examines potential relationships between perikymata distribution on anterior teeth and these same life history and associated variables. Tests of these relationships are performed within platyrrhines, chosen for their wide variation in life history patterns. Platyrrhines were also chosen for this investigation because few studies have focused on the connections between dental development and life history in this infraorder (Henderson, 2007; Hogg and Walker, 2011).

Section 1: Life History

The life history pattern of a particular species involves, "a series of growth and maturational phases ultimately related to the scheduling of reproduction and lifetime reproductive output" (Kelley and Smith, 2003). Phases of growth differ in timing and length between species. In other terms, life history is a "…strategy an organism uses to allocate its energy toward growth, maintenance, reproduction, raising offspring to independence, and avoiding death" (Bogin and Smith, 2012). Similarly, Stearns, (1992) defines life history as, "…demographic traits-birth, age and size at maturity, number and size of offspring, growth and reproductive investment, length of life, and death-connected by constraining relationships tradeoffs…" (Stearns, 1992).

Across the primate order life history variables tend to be correlated, and these variables are connected to brain size, body size, and dental development, specifically eruption timing (Smith, 1989). Research on dental development, brain size, body size, and life history suggests in a general relationship; primates with larger body size tend to have slower dental development (Harvey and Clutton-Brock, 1985; Schwartz et al., 2005). There are some exceptions to these relationships, specifically in lemurs (Schwartz et al., 2005). Brain and body mass have been discovered to be correlated with other life history variables such as age at weaning (Smith, 1991).

However, in comparisons between two, or a few, closely related species, there are often disassociations among life history variables (Guatelli-Steinberg, 2009). This breakdown of life history correlations may pose limitations to primate studies involving lower taxonomic subsets. The connections between life history variables, brain size, and body size may exist for several reasons. First, the driver for life history profiles may be the energetic requirements for brain

growth (Leigh and Blomquist, 2007). Those energetic requirements in turn may be related to gestation length, somatic growth rates, or maternal investment (Martin, 1990). The causes for the connections between life history variables are debated (see Deaner et al., 2003).

Researchers seeking to understand life history patterns in non-human primates and hominins compare data from skeletal and dental remains to data from modern humans. Dental remains provide advantages over skeletal evidence, as dental development is more canalized, i.e., less easily perturbed by environmental influences (Smith, 1991). For this reason, Schultz (1960) first used dental eruption timing and dental eruption sequences as markers of primate life stages. From Schultz's initial divisions of primate life stages based on dental eruption, numerous other studies (Section 3) have explored connections between dental development and primate life history variation. Based on these associations, inferences are made about the pace of life history in fossil species (e.g., Smith, 1991; Dean et al., 2001).

Section 2: Dental Growth and Microstructure

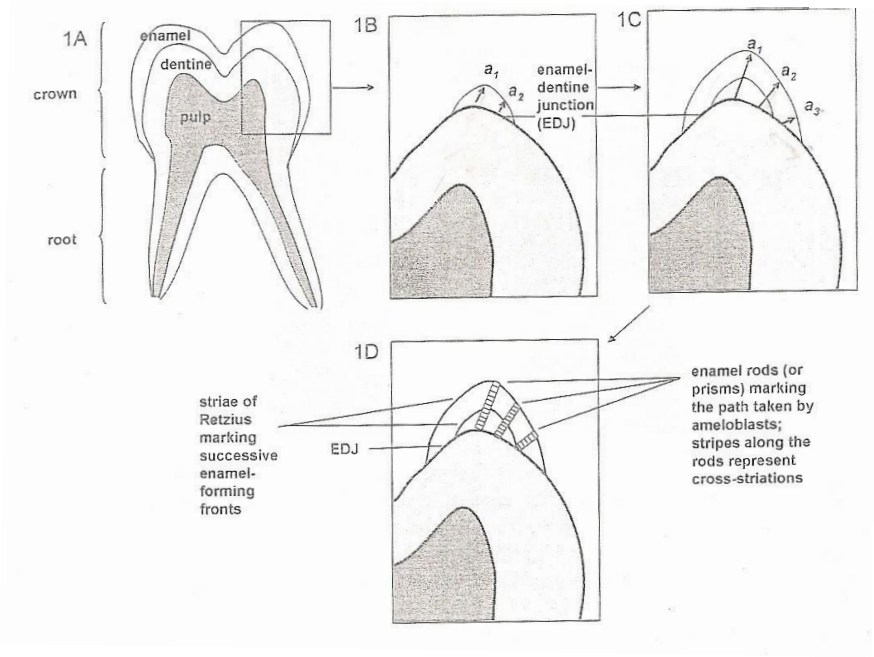
Teeth offer several benefits for studies of growth and development over other skeletal remains. First, teeth provide a permanent record of growth in enamel and dentine (Hillson, 1996). Unlike bone, enamel is not remodeled and replaced throughout life. Incremental growth microstructures in dentine and enamel can be preserved for millions of years (Hillson, 1996). Dental growth also reflects somatic growth to some extent (Smith, 1991). Additionally, dental remains are often preserved better than skeletal remains in the fossil and bioarchaeological record. Some species of fossil primates are only known from their teeth, including hominins (Wolpoff et al., 2006). Research on hominin dental development is possible through non-destructive methods, such as through surface perikymata studies (e.g., Dean et al., 2001) or methods involving synchrotron microCT (Smith et al., 2010).

During the early weeks of development, deciduous and permanent teeth begin to form. In the bud stage, the dental lamina, a thickened layer of epithelium, extends down into the ectomesenchyme, which is derived from neural crest cells (Hillson, 1996). In the next stage, the cap stage, the dental lamina that has extended into the ectomesenchyme forms a cap and it now called the dental or enamel organ (Hillson, 1996). At the bottom tip of the organ the ectomesenchyme condenses into the dental papilla. The cells then begin to differentiate in the bell stage (Hillson, 1996). The stellate reticulum forms from star-shaped cells that draw in water. Below this layer of cells, the inner epithelium forms, followed by the papilla, and the dental sac or follicle. The inner epithelium layer of the dental organ will become the ameloblasts, which produce enamel; the papilla will become the odontoblasts, dentin, and pulp; and the dental sac will become the cementum and periodontal ligament (Hillson, 1996). Later in the bell stage, the inner epithelial cells cluster to form enamel knots which mark future cusp tips. Enamel knots produce a chemical signal to the papilla to differentiate into odontoblasts which induce them to produce dentine. When the pre-dentine begins forming it sends a signal back to the inner epithelium to induce these cells to differentiate into ameloblasts. The crown stage then begins during which the dentine and enamel are formed. Finally, the root, cementum, and periodontal ligament form from the dental sac (Hillson, 1996).

Enamel is an inorganic material that covers the crown. Enamel is formed by matrix-secreting cells called ameloblasts. The matrix is one-third organic and two-thirds mineralized (Hillson, 1996). When matrix secretion is complete ameloblasts lose their functional ability and the organic portion of the matrix dies. The secretion of the enamel matrix follows a consistent rhythm. This rhythm can be seen through long period increments, the striae of Retzius, and through short period increments, the cross striations. Cross striations cut perpendicularly across

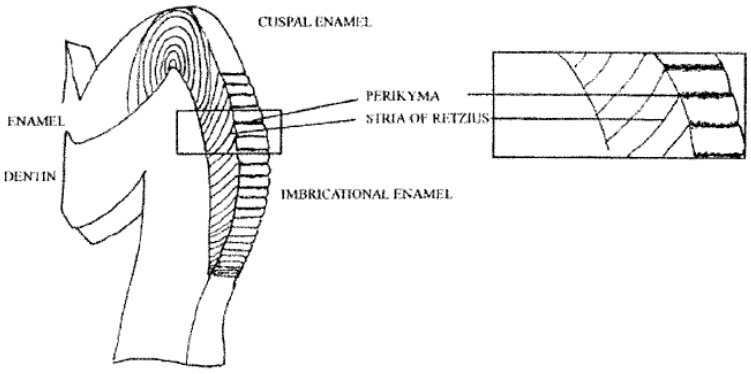
enamel prisms. The striae of Retzius represent the *enamel forming front* of the ameloblasts at a given time in development (Hogg and Walker, 2011). The rate at which the ameloblasts differentiate is called the *enamel extension rate* (Guatelli-Steinberg, 2010). The number of cross striations between the sequential striae of Retzius represents the *periodicity*, or how many days it took to form the enamel between each stria (Hillson, 1996). Cross striations manifest as alternating bands that appear as constrictions and expansions under scanning electron microscopes (Aiello and Dean, 2001). Cross striations appear to represent a circadian rhythm (Bromage, 1991; Hillson, 1996). The rate at which ameloblasts secrete enamel is known as the *daily secretion rate*. The number of striae in humans varies per tooth type and varies between individuals. However the periodicity of the striae is the same for all of the teeth of an individual (FitzGerald, 1998). Within humans, average periodicity is 8 or 9 days, depending on the population, with a range of 6-12 days (Hillson, 1996; Dean and Reid, 2001). The secretion of enamel by ameloblasts can be seen in Figure 1 below.

Figure 1. The secretion of enamel, showing striae of Retzius and cross striations. (Taken from Guatelli-Steinberg, 2010)



Perikymata are the manifestations of the striae on the surface of the enamel (Dean, 1987). Therefore *lateral enamel formation time* for a tooth can be estimated by counting perikymata and multiplying by the average periodicity for that species. Overall *crown formation time* consists of lateral enamel formation time and cuspal enamel formation time. The striae in cuspal enamel are not visible on the surface of the tooth, and therefore these striae are called "buried increments" (Guatelli-Steinberg, 2010). Cuspal and lateral perikymata are shown in Figure 2 below. In order to view the cuspal striae, often destructive techniques must be used, and therefore many fossil studies focus on lateral enamel formation time.

Figure 2. Cuspal and lateral (imbricational) perikymata (Taken from Guatelli-Steinberg, 2001, modified from Ten Cate, 1994)



Section 3: Previous Research on the Relationship between Dental Development and Life History

The following section reviews the relationship between various aspects of dental development and primate life history, integrating studies of fossil hominins. All of this work in non-human primates relies on posterior teeth. It is unclear whether dental development in anterior teeth is related to primate life history variation, even though anterior teeth have been used to make inferences about the pace of life history in fossil hominins (Dean et al., 2001; Ramirez-Rozzi and Bermudez de Castro, 2004; Guatelli-Steinberg et al., 2005).

Dental Eruption

Schultz (1960) defined somatic developmental stages of primates (infantile, juvenile and adult) by dental eruption timing of permanent teeth. Smith (1989) showed the relationship between dental eruption periods to life history variables in a sample of twenty-one primate species including humans. These variables include age at weaning, age at sexual maturation, and

gestation length. First molar eruption is most strongly correlated with age at weaning, which is most likely due to the need to feed on solid foods (Smith, 1989; Guatelli-Steinberg, 2009).

First molar eruption in *Homo erectus* appears to have been intermediate between that of early hominins and modern humans (Dean et al., 2001). Neanderthal first molar eruption time is suggested to be earlier than that of most modern humans (Smith et al., 2010), but a reassessment by Shackelford et al. (2012) suggests that Neanderthal dental development is encompassed within the modern human range.

Total Crown Formation Time: Cuspal and Lateral

Macho (2001) examined published data on primate life history variables, brain mass, and female body mass in relation to molar crown formation times. The sample included extant and extinct primates. Crown formation time of molars was found to be correlated to all life history variables, but most significantly to weaning age, brain mass, and female body mass.

Dean and colleagues., (2001) used a large sample of *Australopithecus, Paranthropus*, early *Homo,* one Neanderthal and a stem hominoid, *Proconsul* to assess the dental growth of these species. These growth rates were compared to modern humans and living great apes. This sample relied on canines and incisors from the hominins and all tooth types for the modern *Homo* sample (Dean et al., 2001). These researchers used cross striations in the occlusal enamel to determine enamel formation times, as well as perikymata counts. The results show the modern *Homo* trajectory is the slowest, with none of the other groups being similar to this pattern (Dean et al., 2001). The Nariokotome boy anterior dentition was compared to modern humans. In order to calculate crown completion time, lateral enamel perikymata counts were added to the buried increments of the occlusal enamel, using a periodicity of nine days. These results showed that the

Homo erectus specimen's enamel formation time fell within the *Australopithecus* range and was thus faster than that of modern humans (Dean et al., 2001).

Ramirez Rozzi and Bermudez de Castro (2004) estimated crown formation time for a sample including *Homo antecessor*, *Homo heidelbergensis, Homo neanderthalensis,* Upper Paleolithic/Mesolithic *Homo sapiens*, and modern humans (Ramirez Rozzi and Bermudez de Castro, 2004). Using lateral perikymata counts and an average periodicity of nine days, crown formation times were estimated. Ramirez Rozzi and Bermudez de Castro concluded that Neanderthals crown formation time was 15% faster than that of modern humans. These authors further conclude that dental growth can be used as a proxy for overall growth rates, and thus the somatic development of Neanderthals would be expected to be faster in Neanderthals than modern humans (Ramirez Rozzi and Bermudez de Castro, 2004).

However, not all studies on Neanderthal crown formation time show the same results as Ramirez Rozzi and Bermudez de Castro (2004). Guatelli-Steinberg and colleagues (2005) reexamined Neanderthal lateral enamel formation. This study compared Neanderthal dentition with a wide range of modern human teeth from Alaska, England, and South Africa. The results showed that Neanderthals do not differ from some of these modern human groups in estimated anterior tooth lateral enamel formation time. However Guatelli-Steinberg at al., (2007) also found that Neanderthals differed from all of these modern human groups more so than modern human groups do from one another in terms of the percentage of total perikymata in the cervical half of the teeth. Therefore, these studies suggested that Neanderthals may not have differed in the overall time they took for form their lateral enamel but only in the "way they achieved this growth" (Guatelli-Steinberg et al., 2007).

Smith and colleagues (2010) once again re-examined Neanderthal and modern human dental development. Using synchrotron virtual histology, periodicity for each specimen was determined. A geographically diverse sample of modern humans, Middle Paleolithic juveniles, and Neanderthals were examined. Using striae of Retzius and periodicity, as well as cuspal enamel formation time, total crown formation times and rates were established. In the Neanderthals included in this study, total crown formation times were generally shorter than they were in the modern human comparative samples.

Enamel Microstructures

Bromage and colleagues (2009) found that in a large sample of mammals, the periodicity of striae of Retzius is positively correlated with body mass. Further, Bromage and colleagues (2012) examine the relationship between primate periodicities and life history variables. A model was created to test the metabolic mechanisms associated with life history profiles. Periodicity was tested against a variety of life history variables and found to be correlated with all of these variables, as well as with basal metabolic rates. Body mass appears to be the key variable, having strong correlations with the rest of the life history variables (Bromage et al., 2012).

Hogg and Walker (2011) tested patterns of enamel microstructure against life history variables in *Ceboidea*. Several life history variables were tested, each corresponding to a life history hypothesis. Variables tested include brain and body mass, encephalization, age at weaning, interbirth interval, birthrate, and age at first female reproduction. The hypotheses are; “foraging independence”, “risk aversion”, and “maternal investment”. The foraging independence hypothesis predicts that primates with foraging strategies that do not require advanced cognitive abilities do not require as much energy for brain growth and instead devote more energy to body mass (Godfrey et al., 2005; Hogg and Walker, 2011). Primates that require

high cognitive functioning in order to successfully forage should devote more energy to brain growth, have a longer juvenile period, and a later weaning and reproductive maturation age (Hogg and Walker, 2011). The risk aversion hypothesis assumes that primates living in risky and unpredictable environments will grow slowly to avoid starvation (Janson and van Shaik, 1993; Hogg and Walker, 2011). The maternal investment hypothesis assumes that primates with more maternal investment will have slower growth and longer juvenile periods (Hogg and Walker, 2011).

In Hogg and Walker's (2010) study, enamel extension rates (via EFF angle proxy) and daily secretion rates were measured. The authors also employed a "crown formation index, " defined as mean daily secretion rate divided by the mean enamel forming front angle in order to examine the effect of both variables simultaneously (Hogg and Walker, 2011). The results showed that the angles striae of Retzius form with the enamel-dentine junction, EFF angles, are statistically significantly associated with brain size and encephalization quotient. These angles are used as proxies for enamel extension rates (Hogg and Walker, 2011). In addition, daily enamel secretion rates, the rates at which enamel forming cells secrete the enamel matrix, were found to be related to weaning age and interbirth intervals. The results indicate that foraging independence has an important role in enamel development, suggesting that dental growth is timed to correspond to the age at which these primates need to forage on their own, which is related to weaning age (Hogg and Walker, 2011).

Shellis (1998) found that in 16 diverse species of non-human primates, enamel extension rate varied. In small, fast-growing teeth, the extension rate remained fairly constant, however in larger teeth that take longer to form, the extensions rate is fast in the beginning and then slows, suggesting a different pattern of growth. Tooth size is correlated with body size (Shellis, 1998),

and thus this study suggests a relationship between patterns of change in enamel extension rates during crown formation and body size.

Perikymata Distribution

No research has examined the potential relationship between the distribution of perikymata along the tooth crown and life history variables. Before the relationship between perikymata distribution and life history can be understood, the underlying causes of variation in perikymata distribution need to be determined (Guatelli-Steinberg, 2010). Several causative factors have been proposed as being potentially relevant including enamel extension rates, daily enamel secretion rates, enamel thickness, and the course of the striae (Shellis, 1998; Schwartz and Dean, 2001; Guatelli-Steinberg et al., 2012). It is possible that it is not only one of these mechanisms causing the distribution of perikymata, but perhaps a combination of factors. Additionally, it is possible that similar patterns in perikymata in different species may not be the result of the same processes.

One hypothesis proposes that perikymata spacing is a function of the enamel extension rate, or the rate at which the ameloblasts differentiate (Shellis, 1998). While some researchers have proposed this as the main factor causing the spacing and pattern of perikymata (Ramirez Rozzi and del Castro, 2004), other researchers propose that this mechanism is only responsible for part of the patterning (Guatelli-Steinberg et al., 2012). The general hypothesis about enamel extension is that a faster extension rate over a region of the tooth will produce fewer perikymata than a slower extension rate over the same length of the tooth crown (Aiello and Dean, 1990; Guatelli-Steinberg, 2010). In order to better understand the effects of enamel extension rates Guatelli-Steinberg and colleagues (2012) examined the variation of enamel extension rates that exists within a large sample of modern humans. The results of this study show that initial enamel

extension rates and the pattern of enamel extension rates change along the enamel-dentine junction and vary in relation to the length of the enamel-dentine junction (Guatelli-Steinberg et al., 2012). The results also show that enamel formation times vary in relation to the length of the enamel-dentine junction, although this varies independently of initial enamel extension rates (Guatelli-Steinberg et al., 2012). The study also examined the enamel extension rate patterns only in the lateral enamel to determine how the changes relate to perikymata distribution. The results of this part of the study confirm previous hypotheses that a decline in the enamel extension rate is associated with increased perikymata density in those regions of the tooth. The sample used in this population is from diverse geographical regions and thus the results would suggest that there is a universal cause for perikymata distribution in modern humans (Guatelli-Steinberg et al., 2012). These results hold for modern humans, however they may not hold for comparisons among species (Guatelli-Steinberg et al., 2012).

The course at which the prisms and striae run through the enamel can also affect the striae angles and thus the perikymata distribution over the course of the tooth (e.g., Schwartz and Dean 2001; Guatelli-Steinberg et al., 2007). However, the effect of the linearity of the pathway of these enamel structures remains to be researched in detail. It has also been suggested that tooth growth and enamel formation rates and times may be connected to jaw and facial growth (Beynon and Dean, 1988). It is unknown to what extent the growth of those bones and features affects tooth growth (Beynon and Dean, 1988).

Section 4: Hypotheses

The purpose of the present study is to investigate possible links between key life history variables and estimated lateral enamel formation time, as well as the potential link between these variables and perikymata distribution.

Hypothesis 1: There is a statistically significant connection between platyrrhine life history variables and estimates of lateral incisor enamel formation times, calculated from total perikymata counts multiplied by a species average periodicity.

Null hypothesis 1: There is no statistically significant association between estimated lateral enamel formation in time platyrrhine incisors and the life history variables tested in this study.

This connection is hypothesized for several reasons. Smith's (1989) data on non-human primate eruption ages for incisors shows a trend across the order which could be related to the pace of life history. Dean et al. (2001) show a shorter lateral enamel formation time in the anterior teeth of earlier hominins, possibly suggesting a relation to lateral enamel formation time and certain life history events, assuming a faster maturation of the early hominins.

Hypothesis 2: The distribution of perikymata in the lateral enamel of platyrrhine incisors is statistically significantly associated with life history variables.

Null hypothesis 2: There is no statistically significant link between perikymata distribution of lateral enamel of platyrrhine incisors and the life history variables chosen in this study.

Many fossil studies rely on perikymata, which represent a longer portion of total enamel formation time in anterior teeth than in premolars and molars (Dean et al., 2001; Ramirez-Rozzi and Bermudez de Castro, 2004, Guatelli-Steinberg et al. 2005). Shellis and colleagues (1998) suggested that in teeth with thicker enamel, enamel extension rates slow as tooth formation progresses, providing time for enamel to mature before the tooth erupts. Given that there is also an association between enamel thickness and body size (Shellis et al., 1998) as well as longevity (Pampush et al., 2013), a relationship between the slowing of enamel extension rates and life

history might be expected. This slowing appears to be reflected in the distribution of perikymata on the enamel surface in modern humans (Guatelli-Steinberg et al., 2012). For these reasons, platyrrhines with slower life histories and thicker enamel are hypothesized to exhibit a steeper gradient in perikymata distribution from cusp to cervix, reflecting a slowing of enamel formation as the crown forms. Preliminary examination of platyrrhine perikymata spacing (Newell et al., 2006) suggests that this may be the case. This previous research is the basis for hypothesis two. However, as mentioned, perikymata distribution is not identical to enamel extension rates and therefore this connection is a more tenuous possibility.

Chapter 2: Materials and Methods

Section 1: Replica Sample

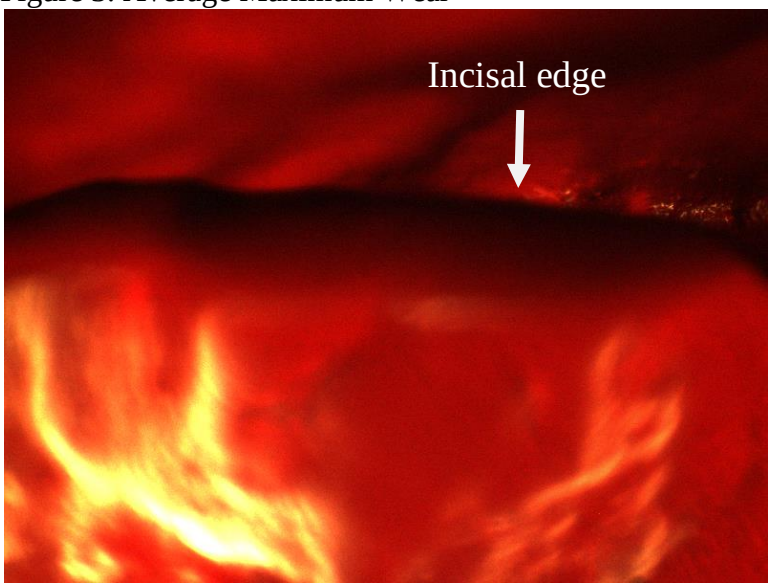
The sample used in this study consists of lower and upper incisors surface replicas. The replicas were made from specimens at the American Museum of Natural History and the National Museum of Natural History. Twelve species of platyrrhines were included. These species are shown in Table 1 represented by their scientific name and their common name. Each tooth type, upper and lower first and second incisors consisted of ten specimens for each species, thus a total of 480 teeth is included in this sample. Efforts were made to include replicas with complete crowns and visible perikymata, therefore there are uneven numbers of male and females represented in each sample, as an equal number of the sexes was not the focus of producing the sample. The museums assigned the genus and species designations and these names were updated by Debbie Guatelli-Steinberg using Groves (2001).

Table 1. Species scientific names and common names

Scientific Name	Common Name
Ateles geoffroyi	Spider monkey
Cebus apella	Tufted capuchin
Cebus albifrons	White-fronted capuchin
Aotus trivirgatus	Owl monkey
Aotus azare	Night monkey
Pithecia pithecia	White-faced saki
Callithrix jacchus	Common marmoset
Callicebus cupreus	Coppery titi
Callicebus torquatus	Collared titi
Saguinas midas	Red-handed tamarin
Saguinas fuscicollis	Brown-mantled tamarin
Saimiri boliviensis	Black-capped squirrel monkey

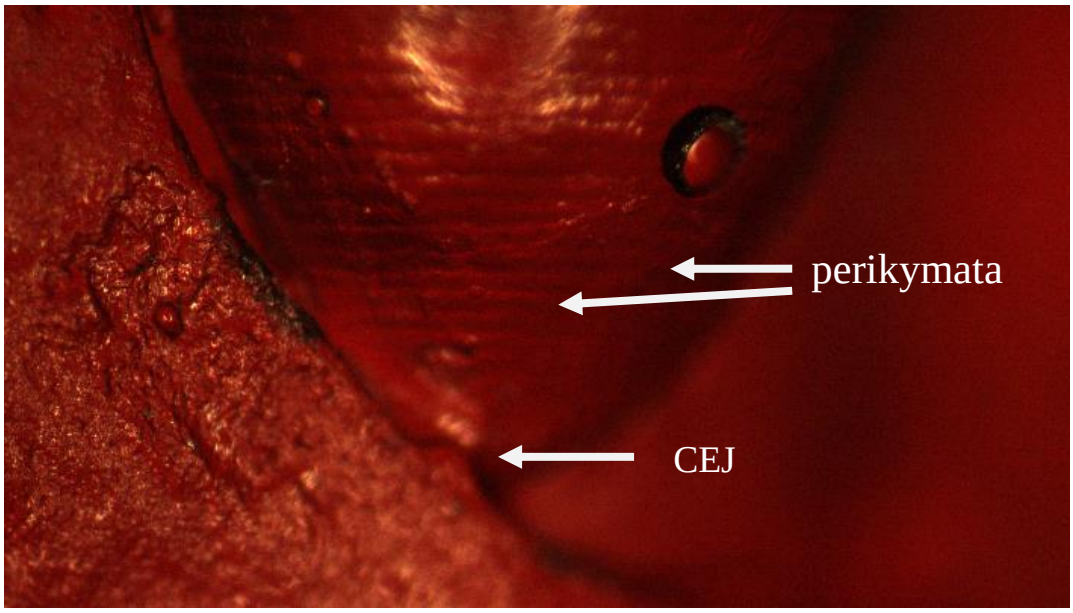
Replicas were made by Debbie Guatelli-Steinberg for previous research projects and are housed at The Ohio State University Department of Anthropology. Before molding the replicas, the incisors were cleaned with acetone. Using Coltene's President Jet regular Body, impressions were made that were then used to create the replicas. Replicas were made using Struers' Epofix epoxy and red dye. The dye was used for easier viewing of the perikymata under the microscope. Some specimens were further enhanced with a gold palladium coating. Specimens were selected for replication if the perikymata were visible over most of the surface. Replicas were only included in this study if there was very minimal wear or no wear. Therefore, selection for little or no wear twice over from a larger sample allowed for complete perikymata counts to be made. The maximum amount of wear is shown below in Figure 3. Crown height was determined to be complete by the presence of mammelons (three shallow cusps on the incisal edge). Replicas also needed to have visible cemento-enamel junctions (CEJ) in order for perikymata to be accurately counted, as this is where the counts started.

Figure 3. Average Maximum Wear



Perikymata were counted, by the author, under a measuring microscope using VisionGauge software. Each click by the user logs the X, Y and Z position of each perikyma. 5x magnification was used in this study in order to clearly view and differentiate among perikymata. Placed under the microscope, the middle of the CEJ was set at position (0,0,0) and perikymata were counted from the CEJ to the cusp. Each perikyma was counted and its position logged. Some teeth required a movement away from the midline of the tooth in order to find visible perikymata. Most teeth required no movement from the center line; however the largest deviation from an x of zero was 0.12 μm. An image from the software of perikymata is shown below in Figure 4.

Figure 4. Screen capture of perikymata on URI2 of a *Cebus albifrons* specimen under 5x



The crown height of each incisor was divided by two and perikymata were counted within each half in order to plot the distribution of perikymata. The percent of perikymata in the cervical half of the crown surface was recorded. Lateral enamel formation time was calculated by multiplying the total number of perikymata by the periodicities for each species. Periodicities were taken from published literature (Bromage, 2009; Bromage et al., 2012). Some species have a range of published periodicities and therefore the average periodicity is used in these cases.

Section 2: Life History Variables

Life history variables were taken from previously published literature (Napier and Napier, 1967; Harvey and Clutton-Brock, 1985; Ross, 1991; Bromage et al., 2009; Hogg, 2010;

Hogg and Walker, 2011; Bromage et al., 2012) as well as the PanTHERIA database (Jones et al., 2009), a database of life history, geographical, and ecological variables. Variables are given only as one value for both sexes (an average of both sexes or average for one sex) based on the available published data. These six variables and their species values are given in Table 2. PD represents the species average periodicity, EQ represents the encephalization quotient, BrM is the brain mass, BdM is the body mass, W is weaning age, RM is age at reproductive maturation, and L is average lifespan. These specific variables were chosen based on their presence in previously published literature as well as their previously published relationships with dental development. Body size and brain size have been shown in many studies to be related to aspects of dental development such as overall crown formation time, periodicities, and eruption (Smith, 1989; Shellis et al., 1998; Macho, 2001). Weaning age was chosen from its correlation to dental eruption, crown formation time, and daily enamel secretion rates (Smith, 1989; Macho, 2001; Hogg and Walker, 2011). Age at sexual maturation is also included in this study due to its relationship to crown formation time and eruption (Smith, 1989; Macho, 2001). This study further tests these relationships using perikymata.

Table 2. Species specific life history variables in sample

Species	n	PD	EQ	BrM	BdM	W	RM	L
Ateles geoffroyi	40	4□	0.26◦	110.9◦	7.58◦	2.23◦	5.7◦	27.3◦
Cebus apella	40	4.5*	0.34◊	72◊	2.6◊	1.14◊	5.78◊	40▪
Cebus albifrons	40	5.5*	0.39◊	74.4◊	2.27◊	0.75◊	4◊	44◦
Aotus trivirgatus	40	3*	0.18◊	18.2◊	0.91◊	0.49◊	2.42◊	18.2◦
Aotus azare	40	3*	0.18◊	18.2◊	0.91◊	0.49◊	2.42◊	18.2◦
Pithecia pithecia	40		0.24◦	31.7◦	1.67◦	0.31◦	2.08◦	13.7◦
Callithrix jacchus	40	1*	0.18◊	7.9◊	0.26◊	0.17◊	1.67◊	12▪
Callicebus torquatus	40	3•	0.18◦	19◦	1.17◦	0.55◦	3◦	26.4+
Callicebus cupreus	40	3•	0.16◦	22◦.4	1.21◦	0.38◦	4+	12◦

Saguinas midas	40	2•	0.15◊	10.4◊	0.55◊	0.19◊	2◊	13▪
Saguinas fuscicollis	40	2*	0.17◊	9.3◊	0.37◊	0.25◊	2.33◊	24.5
Saimiri boliviensis	40	3*	0.28•	24.4•	0.7◊	0.32±	2.77±	17˚

PD: Average periodicity in days, EQ: Average encephalization quotient (measured from the standard equation-Jerison 1973, as modified for primate by Martin 1990, BrM: Average brain mass in grams, BdM: Average body mass in kg, W:Average age at weaning in years, RM: Average age at reproductive maturity in years, L: Average lifespan in years
*Bromage et al., 2009, 2012
□ Bromage et al., 2012
• Hogg, 2010
◊ Hogg and Walker, 2011
˚Jones et al., 2009
▪Harvey and Clutton-Brock, 1985
+ Ross, 1991
±Napier and Napier, 1967

Section 3: Statistical Methods

Principal Components Analysis

A principal components analysis was run in *IBM SPSS Statistics 21* using all six life history variables, including brain and body mass. Each species is represented by their species average values. This analysis was run in order to visualize the relationships between species based on the life history variables, as well as to create a new, meaningful variable with the life history variables that are driving the relationships shown in the principal components plot. Based on the graphs given in the appendix, there is evidence that most of the variables are strongly correlated to lateral enamel formation. These variables are also correlated with each other, as all reflect an aspect of life history. Therefore, in order to reduce the amount of regressions, and thus reduce the possibility of statistical significance due to error, this PC was run to identify the variables that are driving species differences in lateral enamel formation and create an new life history variable. This plot is shown below in the results section in Figure 5. This analysis was run a second time without *Cebus albifrons*, *Cebus apella*, and *Ateles geoffroyi*, as these are

outliers. These three species are outliers in this sample due to their large body size. Body size is an important variable, however the principal component analysis was run again to determine if the trends among species still hold true in the smaller bodied primates. Thus, a clearer picture of the relationships among the remaining species is shown in the results section in Figure 6.

Linear Regressions

Linear regressions using the first two principal components scores were run in *IBM SPSS Statistics 21,* against the two independent variables; estimated lateral enamel formation time and percent of perikymata in the cervical half of tooth. These regressions were run a second time using the principal component scores from the analysis excluding the three outlier species. Therefore a total of eight different regressions were run. These regressions were also run separately for each of the four tooth types.

Multiple Linear Regressions

Multiple regressions were run in *IBM SPSS Statistics 21* with all six life history variables for each of the two independent variables; estimated lateral enamel formation time and percent of perikymata in the cervical half of the tooth. These regressions were also run a second time, excluding the three outlier species.

Chapter 3: Results

Section 1: Descriptive Statistics

The descriptive statistics for species and tooth specific total perikymata counts, estimated lateral enamel formation time, and percent of perikymata in cervical half are shown in Table 3 below. The averages plus and minus one standard deviation are presented. Species average periodicities are also shown.

Table 3. Descriptive Statistics (No published periodicity data for *Pithecia pithecia)*

Species	Tooth Type	Pk Count Average +/- 1 SD (10)	Periodicity Average (10)	Estimated Lateral Enamel Formation Time +/- 1 SD in days(10)	Percent Pk in cervical half +/- 1 SD (10)
Ateles geoffroyi	LI1	73.4±9.45	4 °	239.6±37.81	58.7±5.14
	LI2	73.4±15.98	4 °	293.6±63.9	59.6±5.04
	UI1	72±10.35	4 °	288±41.40	61.9±3.9
	UI2	53.5±15.64	4 °	213.2±62.6	65±7.47
Cebus apella	LI1	58.9±15.74	4.5*	265.05±71.73	58.1±11.11
	LI2	69.8±9.077	4.5*	314.1±40.85	60.7±4.35
	UI1	74.7±17.14	4.5*	336.15±77.13	56.2±10.54
	UI2	70.3±11.126	4.5*	316.35±50.1	57.7±7.945
Cebus albifrons	LI1	56.8±13.56	5.5*	312.4±74.6	63.6±2.75
	LI2	63.6±13.87	5.5*	349.8±76.31	62.5±3.923
	UI1	58.3±8.934	5.5*	320.65±49.27	63.2±5.53
	UI2	61.7±7.35	5.5*	339.35±40.43	65.7±7.543
Callithrix jacchus	LI1	51.4±9.143	1*	51.4±9.143	50.3±10.23
	LI2	40.6±9.74	1*	40.6±9.74	43.1±5.46
	UI1	41.1±11.52	1*	41.1±11.52	47.5±4.625
	UI2	37.3±4.6	1*	37.3±4.6	48±2.21
Callicebus cupreus	LI1	40.4±7.76	3•	121.2±23.9	47.4±5.58
	LI2	39.5+6.55	3•	118.5±19.66	48.5±2.8
	UI1	36±7.73	3•	108±23.19	47.2±8.14
	UI2	30.9±4.04	3•	92.7±12.12	50.1±4.89
Callicebus torquatus	LI1	54.6±19.08	3•	163.8±42.26	50±5.41
	LI2	55.3±20.6	3•	165.9±61.89	49±17.11
	UI1	44.7±13.31	3•	134.1±39.42	47.9±7.58
	UI2	35.6±9.45	3•	106.8±28.36	48.3±3.26
Aotus azare	LI1	36.3±8.77	3*	108.9±26.31	50.7±9.15
	LI2	30.4±6.328	3*	91.2±18.98	48.4±6.38
	UI1	32±5.63	3*	96±16.91	49±3.27
	UI2	30.7±2.91	3*	92±8.723	47.5±1.43
Aotus trivirgatus	LI1	53.9±10.94	3*	161.7±32.81	49.4±3.5
	LI2	49.5±8.61	3*	148.5±25.86	51.5±2.41
	UI1	50.7±11.03	3*	152.1±33.07	47±4.7
	UI2	42±4.77	3*	126±14.28	48.6±3.92
Saguinas midas	LI1	36.8±7.56	2•	73.6±15.1	48.7±3.16
	LI2	35±6.34	2•	70±12.79	43.2±7.7
	UI1	41.8±8.56	2•	83.6±17.12	45.6±6.88

Table 3: Continued (Continued)

	UI2	34.9±5.02	2•	69.8±1004	45.5±5.74
Saguinas fuscicollis	LI1	31.3±5.42	2*	62.6±10.84	49.7±8.28
	LI2	31.4±5.68	2*	62.8±11.36	48.5±2.76
	UI1	29±5.19	2*	58±10.37	48.2±2.2
	UI2	31.2±5.39	2*	62.4±10.78	48±4.58
Saimiri boliviensis	LI1	50.5±8.21	3*	151.5±24.62	59.6±8.34
	LI2	59.5±16.2	3*	178.5±48.9	51.3±4.6
	UI1	53.8±16.23	3*	161±48.67	53.6±5.23
	UI2	50.9±10.53	3*	152.7±31.6	53.8±5.18
Pithecia pithecia	LI1	74.3±18.53			49±3.53
	LI2	73.9±14.84			51.7±4.52
	UI1	55.1±15.04			50.8±4.13
	UI2	45.1±9.52			45.1±9.52

*Bromage et al., 2009, 2012
˚ Bromage et al., 2012
• Hogg, 2010

Section 2: Principal Components Analysis

The plot of the principal components analysis including all twelve species is shown below in Figure 5. This plot is a simple transformation of the data to understand the variation between species. The variance explained by the first two components is shown below in Table 4. The loadings of each variable within the first two components are also shown below in Table 5. The important variables influencing the spacing between species in principal component 1 are brain size, age at reproductive maturation, body size, and age at weaning. The second principal component reflects variation mainly due to EQ, lifespan, and body size. The second analysis without *Cebus apella*, *Cebus albifrons*, and *Ateles geoffroyi* is represented below with a plot in Figure 6, the variance explained by components in Table 6, and the loadings of the life history variables in each component in Table 7. The variables driving the spacing of species along

principal component 1 are brain size and body size, while principal component 2 largely reflects differences in life span, age at reproductive maturation, and age at weaning.

Figure 5. Plot of principal component score 1 versus principal component score 2

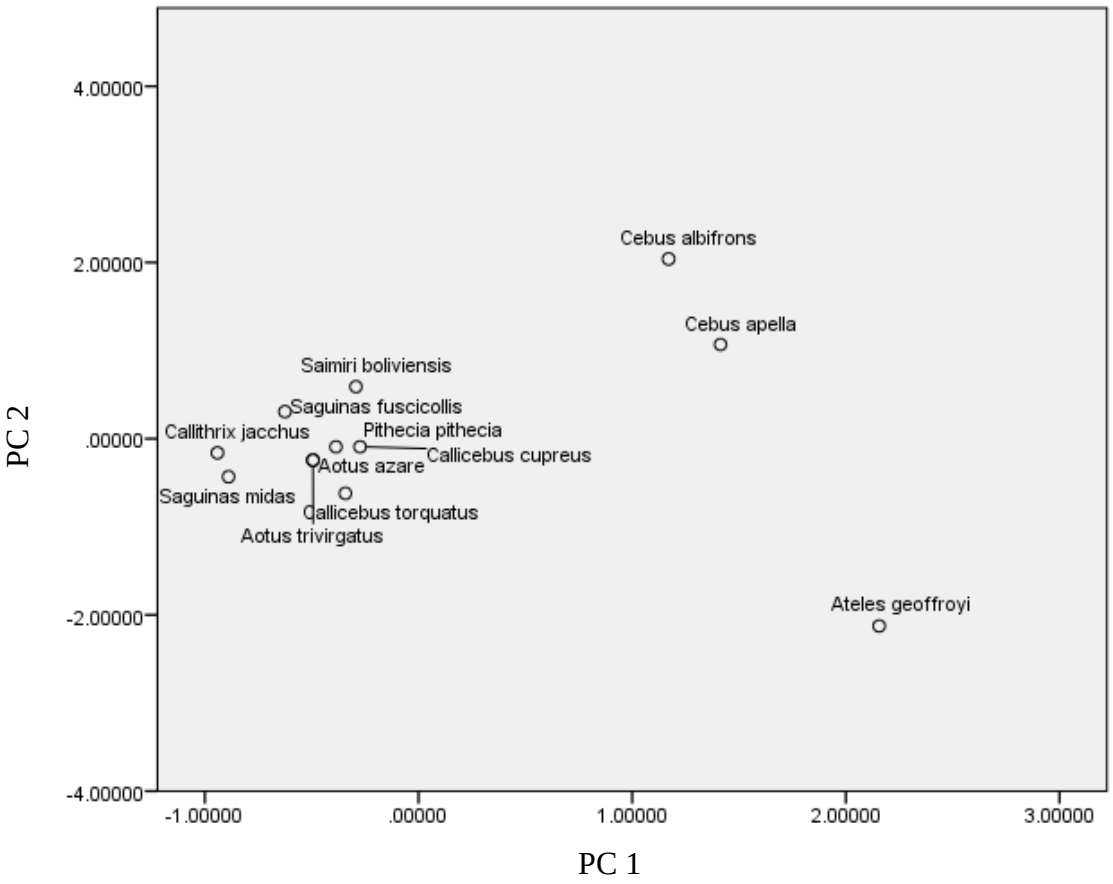


Table 4. Variance Explained by Principal Components Analysis

Component	% of Variance Explained
1	75.834
2	16.476

Table 5. Component Matrix of Principal Components Analysis

Variable	Component1	Component 2
EQ Avg	0.740	0.581

Brain Size Avg	0.987	-0.063
Body Size Avg	0.877	-0.452
Weaning Age Avg	0.916	-0.375
Repro Mat Age Avg	0.921	-0.045
Lifespan Avg	0.755	0.548

Figure 6. Plot of principal component score 1 versus principal component score 2. Cebus *apella, Cebus albifrons,* and *Ateles geoffroyi* excluded.

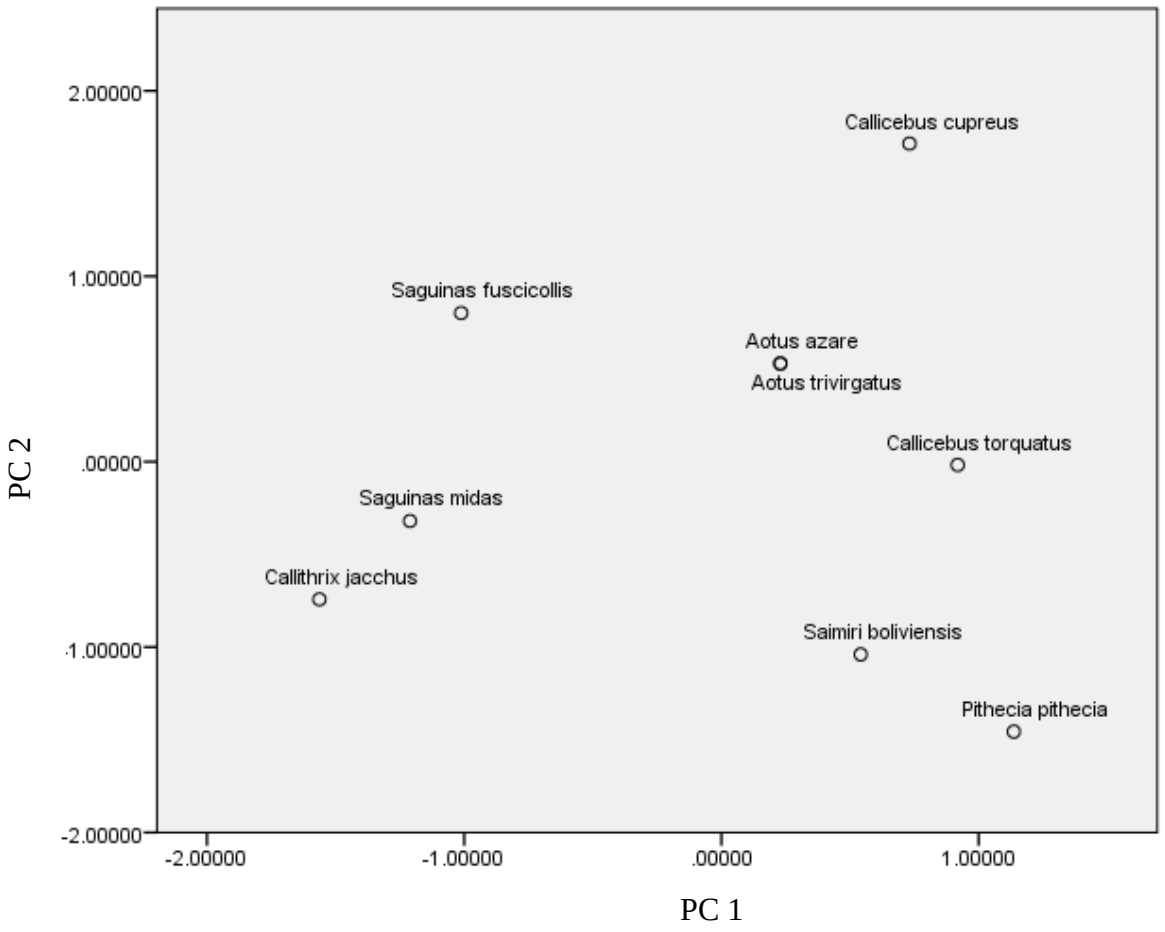


Table 6. Variance Explained by Principal Components Analysis (*Cebus apella, Cebus albifrons, Ateles geoffroyi* excluded)

Component	% of Variance Explained
1	45.932
2	28.169

Table 7. Component Matrix of Principal Components Analysis (*Cebus apella, Cebus albifrons, Ateles geoffroyi* excluded)

Variable	Component1	Component 2
EQ Avg	0.462	-0.672
Brain Size Avg	0.927	-0.350
Body Size Avg	0.898	-0.079
Weaning Age Avg	0.685	0.624
Repro Mat Age Avg	0.631	0.319
Lifespan Avg	0.098	0.787

Section 3: Linear Regressions

Each life history variable is plotted against estimated lateral enamel formation time in the Appendix in order to illustrate relationships to individual life history variables. These graphs are separated by tooth type. Each life history variable is also plotted against percent of perikymata in the cervical half of the crown in Appendix A in order to illustration relationships to individual life history variables. These graphs are also separated by tooth type. However, the following linear regression tests used the new independent variables created by the principal components analyses; in order reduce the number of regressions and error, while using only two variables that sufficiently summarize the important life history variables between species.

The results of the linear regressions between the first two principal component scores and the two independent variables are shown below in Tables 8 through 15. Tables are separated by variables and results within each table are separated by tooth type. R squared and significance

values are presented. Statistically significant results are bolded. Statistical significant was determined at a p value < 0.05 level.

Table 8. Linear regressions results of lateral formation time and PC1 (no *Pithecia pithecia*). Significant results in bold

Tooth Type	R Square	Sig.
LI1	**0.728**	**.000**
LI2	**0.722**	**.000**
UI1	**0.754**	**.000**
UI2	**0.658**	**.000**

Table 9. Linear regressions results of lateral formation time and PC2 (no *Pithecia*

Tooth Type	R Square	Sig.
LI1	0.027	0.087
LI2	**0.073**	**0.004**
UI1	**0.067**	**0.006**
UI2	**0.210**	**0.000**

Table 10. Linear regressions results of %Pk in cervical half and PC1. Significant results in bold

Tooth Type	R Square	Sig.
LI1	**0.217**	**0.000**
LI2	**0.530**	**0.000**
UI1	**0.411**	**0.000**
UI2	**0.508**	**0.000**

Table 11. Linear regressions results of %Pk in cervical half and PC2. Significant results in bold

Tooth Type	R Square	Sig.
LI1	**0.062**	**0.006**
LI2	**0.059**	**0.008**
UI1	0.025	0.085
UI2	0.021	0.112

Table 12. Linear regressions results of lateral formation time and PC1 (no *Pithecia pithecia. Cebus apella, Cebus albifrons, Ateles geoffroyi excluded*). Significant results in bold

Tooth Type	R Square	Sig.
LI1	**0.618**	**0.000**

LI2	**0.549**	**0.000**
UI1	**0.469**	**0.000**
UI2	**0.513**	**0.000**

Table 13. Linear regressions results of lateral formation time and PC2 (no *Pithecia pithecia. Cebus apella, Cebus albifrons, Ateles geoffroyi excluded*) Significant results in bold

Tooth Type	R Square	Sig.
LI1	0.003	0.658
LI2	0.003	0.643
UI1	0.002	0.662
UI2	0.007	0.473

Table 14. Linear regressions results of %Pk in cervical half and PC1. (*Cebus apella, Cebus albifrons, Ateles geoffroyi excluded)* Significant results in bold

Tooth Type	R Square	Sig.
LI1	0.003	0.587
LI2	**0.171**	**0.000**
UI1	0.035	0.078
UI2	0.011	0.331

Table 15. Linear regressions results of %Pk in cervical half and PC2. (*Cebus apella, Cebus albifrons, Ateles geoffroyi excluded)* Significant results in bold

Tooth Type	R Square	Sig.
LI1	**0.044**	**0.048**
LI2	0.000	0.840
UI1	0.043	0.051
UI2	0.003	0.586

Section 4: Multiple Linear Regressions

The results of the four multiple linear regressions are shown below in Tables 16 through 19. Results are presented through R square, significance, zero-order correlations, and partial correlation values. Significant results are bolded.

Table 16. Multiple regression results of lateral enamel formation time with life history variables (*no Pithecia pithecia*). Significant results in bold.

Model	Adjusted R Square	Sig.		
	0.815	**0.000**		
Coefficients			Zero-Order Correlations	Partial Correlation
EQ Avg		0.429	0.834	0.038
Brain Size Avg		**0.000**	**0.824**	**0.204**
Body Size Avg		**0.001**	**0.607**	**-0.158**
Weaning Age Avg		0.515	0.648	0.031
Repro Mat Age Avg		**0.000**	**0.791**	**0.174**
Lifespan Avg		0.332	0.754	-0.047

Table 17. Multiple regression results of % Pk in cervical half with life history variables Significant results in bold.

Model	Adjusted R Square	Sig.		
	0.548	**0.000**		
Coefficients			Zeo-Order Correlations	Partial Correlation
EQ Avg		**0.001**	**0.624**	**0.147**
Brain Size Avg		0.512	0.627	-0.030
Body Size Avg		0.370	0.482	0.041
Weaning Age Avg		0.488	0.503	0.032
Repro Mat Age Avg		0.792	0.536	-0.021
Lifespan Avg		0.122	0.552	0.071

Table 18. Multiple regression results of lateral enamel formation time in with life history variables (*Pithecia pithecia, Cebus apella, Cebus albifrons, Ateles geoffroyi* excluded) Significant results in bold.

Model	Adjusted R Square	Sig.		
	0.612	**0.000**		
Coefficients			Zero-Order Correlations	Partial Correlation
EQ Avg		**0.001**	**0.469**	**-0.189**
Brain Size Avg		**0.000**	**0.776**	**0.285**
Body Size Avg		**0.002**	**0.585**	**-0.177**
Weaning Age Avg		0.998	0.482	0.000

Repro Mat Age Avg	0.687	0.560	-0.023
Lifespan Avg	0.910	0.006	0.006

Table 19. Multiple regression results of % Pk in cervical half with life history variables (*Cebus apella, Cebus albifrons, Ateles geoffroyi* excluded) Significant results in bold.

Model	Adjusted R Square	Sig.		
	0.115	**0.000**		
Coefficients			Zero-Order Correlations	Partial Correlation
EQ Avg		0.933	0.313	0.005
Brain Size Avg		0.442	0.197	0.041
Body Size Avg		0.310	0.046	-0.054
Weaning Age Avg		0.608	0.069	0.027
Repro Mat Age Avg		0.443	0.103	0.041
Lifespan Avg		0.344	0.040	0.050

Chapter 4: Discussion

This study aimed to investigate the relationship between anterior lateral enamel formation and the life histories of twelve species of New World monkeys. Perikymata counts and average periodicities were used to calculate estimated lateral enamel time formation. The percent of perikymata in the cervical half of the crown was also measured. It was hypothesized that there is a connection between estimated lateral enamel formation time and the life history variables, and that there is a connection between percent of perikymata in the cervical half of the crown and life history variables. This discussion is divided into the following sections 1) a discussion of the results for estimated lateral enamel time 2) a discussion of the results for percent of perikymata in the cervical half of the crown 3) a brief discussion of implications for platyrrhine biology and environmental factors 4) limitations of the present study and 5) future research.

Section 1: Estimated Lateral Enamel Formation Time

Linear regressions using the principal component scores show that there is a significant relationship between life history variables, brain size and body size and estimated lateral enamel formation time for most tooth types. Principal component one (PC1) showed the most significant correlations, which is expected, as it explains the most variation among species. Estimated lateral enamel formation time for all tooth types are significantly correlated with PC1. R^2 values for these teeth are high, ranging from 0.658-0.754, suggesting this is a strong relationship. When principal component two (PC 2) is tested with estimated lateral enamel formation time, there are significant results for all tooth types except lower I1. R^2 values for correlations with PC 2 are low, ranging from 0.027-0.210. Thus estimated lateral enamel formation time is highly correlated with brain size, age at reproductive maturation, and weaning age, although body size, lifespan, and encephalization quotient are quite strong as well.

When the three outlier species are removed from analysis, principal component one (PC1) showed the most significant correlations; all tooth types are significantly correlated with PC1. R^2 values for these teeth are high ranging from 0.469-0.618. When principal component two (PC 2) is tested with estimated lateral enamel formation time, there are significant results for all tooth types except lower I1. R^2 values for correlations with PC 2 they are not statistically significant. Thus estimated lateral enamel formation time for this set of species is highly correlated with brain size, body size, and weaning age. The lack of significance for PC 2 when the three outlier species are removed is most likely from the small sample size that remains, as *Pithecia pithecia* is also excluded due to a lack of periodicity data. Therefore, in future work a large number of species should be used.

The results of the multiple regressions allow for the nature of the relationship between the life history variables and estimated lateral enamel formation time to be understood. With all species, excluding *Pithecia pithecia,* the model is significant, with a high adjusted R^2 value of 0.815, therefore explaining much of the variation in estimated lateral enamel formation time. The significant variables in this model are brain size, body size, and age at reproductive maturation. Partial correlations of these variables are 0.204, 0.158, and 0.174 respectively. These results suggest that controlling for the effects of all other variables in the model, brain size and reproductive maturation age are positively correlated with estimated lateral enamel formation time, and body size is negatively correlated. When the three outlier species are removed, the multiple regression model is still significant with an adjusted R^2 value of 0.612. EQ, brain size, and body size are the significant variables in this model. Partial correlations for these variables are -0.189, 0.285, and -0.177, showing that EQ and brain size are positively correlated with estimated lateral enamel formation time, and body size is again negatively correlated with estimated lateral enamel formation time.

It is not surprising that there are significant correlations between anterior dentition estimated lateral enamel formation time and brain size, body size, and other life history variables. Previous research has shown that molar eruption timing is related to body size, brain size, and weaning age, as well as a relation between molar and incisor eruption (Smith, 1989). Lateral and total crown formation times of anterior dentition have been used in hominin studies to predict life histories of fossil hominins; however, until now, this relationship has not been systematically tested (Dean et al., 2001; Dean, 2006). Guatelli-Steinberg (2009) noted this lack of published results demonstrating how anterior estimated lateral enamel formation time or cuspal formation time is related to life history. It has also been noted that male canines do not

follow expected life history trends in comparisons of few species (Guatelli-Steinberg et al., 2009). However, this present study systematically tests these relationships within a range of platyrrhine species. Therefore, when an adequate sample size is used, there are certain specific statistically significant relationships of incisor estimated lateral enamel formation time and life history.

It has been suggested that canine dental development in females follow the expected trends related to life history, however male canines do not (Guatelli-Steinberg et al., 2009). This is understandable given that male canines need to be larger and take more time to grow due to male-male competition (Guatelli-Steinberg et al., 2009). Therefore, patterns of growth in non-sexually dimorphic teeth would be expected to track life history patterns, which they do, in these platyrrhine species. Macho (2001) showed that among primates, total enamel formation time in molars is correlated with brain size, body size, and life history variables. Combined with the results of this study, the overall results suggest a coordination within individuals among tooth types, which may be, at least partly attributed to the fact that periodicity is the same for all of the teeth of an individual (FitzGerald, 1998).

Section 2: Percent of Perikymata in Cervical Half of Tooth

Linear regressions using the principal component scores show that there is a significant relationship for some tooth types. Principal component one (PC1) showed the greatest number of significant correlations, all tooth types are significantly correlated with PC1. R^2 values for these teeth are high but lower than estimated lateral enamel formation time, ranging from 0.217-0.530. When principal component two (PC 2) is tested with estimated lateral enamel formation time, there are significant results for lower incisors only. R^2 values for correlations with PC 2 are low, ranging from 0.021-0.062. Thus percent of perikymata in the cervical half of the crown is highly

correlated with brain size, age at reproductive maturation, and weaning age, although body size, lifespan, and encephalization quotient are quite strong as well.

When the three outlier species are removed from analysis, principal component one (PC1), only lower I2 is significant with a low R^2 value of 0.171. When principal component two (PC 2) is tested with percent of perikymata in the cervical region of the crown, there is only a significant result lower I1, with a low R^2 value of 0.044. Thus percent of perikymata in the cervical region of the tooth for this set of species is highly correlated with brain size, body size, and weaning age. The lack of significance when the three outlier species are removed is most likely from the small sample size that remains, or perhaps because there is not a strong relationship to life history variables.

The results of the multiple regressions allow for the nature of the relationship between the life history variables and percent of perikymata in the cervical half of the crown to be understood with respect to each other. With all species, the model is significant, with an adjusted R^2 value of 0.548. The only significant variable in this model is EQ average, with a partial positive correlation of 0.147. When the three outlier species are removed, the multiple regression model is still significant with an adjusted R square value of 0.115, however no single variable is significant.

Although the factors that cause certain perikymata distributions and spacing are unknown, and what is being reflected in the distribution is still unclear, there are results of previous work that suggest there may be some relation of perikymata distribution to life histories. In modern humans, there is a relationship between the enamel extension rate and perikymata distribution (Guatelli-Steinberg et al., 2012). However, it is not known to what degree this relationship holds across the primate order.

Additionally, Guatelli-Steinberg et al., (in progress) show that the enamel forming front angles are related to perikymata distribution, although not directly. Hogg and Walker (2011) showed that enamel forming front angles are related to brain mass, body mass, and life history variables. The enamel forming front angles are related to the angles of the striae of Retzius, however these are not identical. Therefore, this relationship may underlie the association between perikymata distribution and life history; however, the lack of direct connection between perikymata distribution and enamel extension rates may explain why the results for these analyses were not as significant or numerous.

Section 3: Implications for Platyrrhine Biology and Environment

The connections between anterior lateral enamel formation and brain size, body size and life history in platyrrhines, may reflect potential implications for platyrrhine biology and adaptations. The evolution of dental growth and life history patterns of these taxa may be connected. Thus, as Hogg and Walker (2011) concluded, these connections may require further analysis into the ecological factors of these primates, such as foraging independence and risk aversion. Selective pressures from the environment, diet, and predation may be driving the relationships shown by this study. The results of this study indicate that primates with larger body and brain sizes have slower lateral enamel formation times and more perikymata in the cervical half of their teeth than primate with smaller brains and bodies. The larger bodied primates also have slower life histories than the smaller bodied primates. Thus, there must be environmental factors allowing for the slow growth of the enamel, body, and brain for certain species, while other patterns of growth are reflected in smaller species.

Section 4: Limitations

There are several limitations of the present study. First, there is a small number of species sampled; only twelve New World monkey species, and some of these species are within the same genus. Additionally, statistical analyses are separated into tooth type; however, there are only ten of each tooth type for each species. The results of these analyses may become clearer in larger sample sizes and a larger taxonomic range.

To continue, not all species have recorded periodicity, which is critical in estimating crown completion time. Measures of periodicity for the two *Aotus* species are unclear in the literature, and there is no periodicity data for *Pithecia pithecia.*

Finally, the regressions in this study were not phylogenetically corrected. It is therefore, possible that the significant correlations are not completely suggestive of life history variables, but are a signal of phylogenetic relationships.

Section 5: Future Research

Future research will expand the sample in number of teeth, across the extant primate order, and include canines. With a larger sample, it will be possible to test the differences between male and female anterior dentition. Specifically, it will be possible to test if female canines follow the expected relationships shown from this study, while male canines do not as suggested in Guatelli-Steinberg et al. (2009). The differences in male and female incisors can also be tested, although previous research has not demonstrated expectations of sex differences in incisors. A larger sample size of tooth types will also allow for distinctions between left and right anterior teeth to be tested. Periodicities for all species will be measured or found in the literature to allow for better estimations of lateral enamel formation time. Also mentioned as a

limitation of this study, phylogenetically controlled analyses will be run on these data and on the expanded data set.

Applying these data to fossil platyrrhine species may be possible. It may be possible to use estimated lateral enamel formation times from this study and apply them to closely related fossil platyrrhines. It may also be possible to calculate estimated lateral enamel formation time from fossil platyrrhine anterior teeth and estimate the nature of their life histories. Finally, these results may have possible implications for fossil hominin research. Anterior tooth estimated lateral enamel formation time may be a useful tool in exploring hominin life history; however, individual species comparisons, or comparisons of a small group of hominin species still may not reflect life history differences among them because the scale of comparison is too narrow (Guatelli-Steinberg, 2009).

Chapter 5: Conclusions

This study adds to the previous research showing a relationship between dental development and life history profiles in primates. Overall, these results suggest that lateral enamel formation time in anterior teeth is an important reflection of life history and a strong measure when predicting life history profiles of fossil platyrrhines. The percent of perikymata in the cervical region of the incisor crowns is also a significant measure of dental development; however, it is not very robust with these specific life history variables. To further explore these relationships, expanded sample sizes, species, and tooth types will be used.

References

Aiello, L., Dean, C. 1990, 2006. An Introduction to Human Evolutionary Anatomy. London: Academic Press.

Beynon, A.D., Dean, M.C. 1986. Crown-formation time of a fossil hominid premolar tooth. Archives of Oral Biology 32: 773-780.

Beynon, A.D., Dean, M.C. 1988. Distinct Dental Development Patterns in Early Fossil Hominins. Nature 326:493-496.

Boas, F. 1932. Race, Language, and Culture. Science N.S. 76:605-613.

Bogin, B. 1999. Patterns of Human Growth, 2nd edn. Cambridge University Press: Cambridge.

Bogin, B. and Smith. 2012. Evolution of the human life cycle. In Stinson, Bogin, O'Rourke (eds). Human Biology. Wiley-Blackwell: Hoboken.

Bromage, T.G.,1991. Enamel incremental periodicity in the pig-tailed macaque-a polychrome fluorescent labeling study of dental hard tissues. AJPA 86:205–214.

Bromage, T., Lacruz, R., Hogg, R., Goldman, H., McFarlin, S., Warshaw, J., Dirks, W., Perez- Ochoa, A., Smolyar, I., Enlow, D., Boyde, A. 2009. Lamellar bone is an incremental tissue reconciling enamel rhythms, body size, and organismal life history. Cell Tissue International 84: 388-404.

Bromage, T., Hogg, R., Lacruz, R., Hou, C. 2012. Primate enamel evinces long period biological timing and regulation of life history. Journal of Theoretical Biology 305: 131-144.

Crews, D. E. and Bogin, B. A. 2010, Growth, development, senescence, and aging: A life history perspective. In C.S. Larsen, (ed). A Companion to Biological Anthropology. Blackwell Publishing: New York.

Dean, M.C., 1987. The dental development status of six East African juvenile fossil hominids. J Hum Evol 16: 197-213.

Dean, M. C., Leakey, M. G., Reid, D., Schrenk, F., Stringer, C., Walker, A. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414: 628-63.

Dean, M.C., 2006. Tooth microstructure tracks the pace of human life-history

evolution. Proc R Soc B 273: 2799-808.

Deaner R.O., Barton RA, Van Shaik CP. 2003. Primate brains and life histories: renewing the connection. In: Kappeler PM, Pereira ME, editors. Primate life histories and socioecology. Chicago: University of Chicago Press.

FitzGerald, CM. 1998. Do enamel microstructures have regular time dependency? J Hum Evol 35: 371-386.

Godfrey LR, Samonds KE, Wright PC, King SJ. 2005. Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. Folia Primatol 76:77–99.

Groves CG. 2001. Primate taxonomy. Washington: Smithsonian Institution Press.

Guatelli-Steinberg D. 2001. What can developmental defects of enamel reveal about physiological stress in non-human primates? Evol Anthropol 10: 138-151.

Guatelli-Steinberg D, Reid DJ, Bishop TA, Larsen CS. 2005. Anterior tooth growth periods in Neandertals were comparable to those of modern humans. Proc Natl Acad Sci 102: 14197-14202.

Guatelli-Steinberg, D., Reid, D.J., Bishop, T.A., 2007a. Did the lateral enamel of Neandertal anterior teeth grow differently from that of modern humans? J Hum Evol 52: 72-84.

Guatelli-Steinberg, D., Ferrell, R.J., Spence, J., Talabere, T., Hubbard, A., Schmidt, S., 2009. Sex differences in anthropoid mandibular canine lateral enamel formation. Am J Phys Anthropol. 140: 216-233.

Guatelli-Steinberg, D.2009. Recent studies of dental development in neanderthals: Implications for neanderthal life histories. Evolutionary Anthropology 8:9-20.

Guatelli-Steinberg, D. 2010. Growing Planes: incremental growth layers in the dental enamel of human ancestors. In Larsen, C. S. (ed.) A Companion to Biological Anthropology. Blackwell Publishing.

Guatelli-Steinberg, D., Floyd., B., Dean, C., Reid, D. 2012. Enamel extension rate patterns in modern human teeth: two approaches designed to establish an integrated comparative context for fossil primates. J Hum Evol 63:475-486.

Guatelli-Steinberg, D. (In Progress). Variation in primate enamel-formation front angles.

Harvey PH, Clutton-Brock TH. 1985. Life history variation in primates. Evolution 39:

559-581.

Henderson, E. 2007. Platyrrhine dental eruption sequences. AJPA 134(2): 226-239.

Hillson, S., 1996. Dental Anthropology. Cambridge Univ. Press, Cambridge.

Hogg RT. 2010. Dental Microstructure and Growth in the Cebid Primates. Ph.D. Dissertation, City University of New York.

Hogg, R. and Walker, R. 2011. Life history correlates of enamel microstructure in *Cebidae (Platyrrhini, Primates)*. Anat Rec 294:2193-2206.

Janson CH, van Schaik C. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. Juvenile primates: Life history, development and behavior. New York: Oxford University Press. p. 57–76.

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MH, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90:2648.

Kelley, J., Smith, T., 2003. Age at first molar emergence in early Miocene *Afropithecus turkanensis* and life-history evolution in the *Hominoidea*. J Hum Evol. 44:307-329.

Leigh SR, Blomquist GE. 2007. Life history. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. New York and Oxford: Oxford University Press. p. 396-407.

Macho, G.A., 2001. Primate molar crown formation times and life history evolution revisited. Am J Primatol 55: 189-201.

Martin RD. 1990. Primate Origins and Evolution: A phylogenetic reconstruction. Princeton: Princeton University Press.

Napier, J., P. Napier. 1967. A handbook of living primates. London: Academic Press.

Newell., E., Guatelli-Steinberg, D., Field, M., Cooke, C., Feeney, R. 2006. Life history, enamel formation, and linear enamel hypoplasia in the Ceboidea. AJPA 131:252-260.

Pampush, J.D., Duque, A.C., Burrows, B.R., Daegling, D.J., Kenney, W.F., and McGraw,

W.S. 2013. Homoplasy and thick enamel in primates. J Hum Evol 64(3):216-224.

Ramirez Rozzi, F.V., Bermudez de Castro, J.M., 2004. Surprisingly rapid growth in Neanderthals. Nature 428: 936-939.

Ross C. 1991. Life history patterns of New World monkeys. Int J Primatol 12:481–502.

Schwartz, G.T., Dean, C., 2001. Ontogeny of canine dimorphism in extant hominoids. Am J Phys Anthropol 115: 269-283.

Schwartz GT, Mahoney P, Godfrey LR, Cuozzo FP, Jungers WL, Randria GFN. 2005. Dental development in Megaladapis edwardsi (Primates, Lemuriformes): Implications for understanding life history variation in subfossil lemurs. J Hum Evol 49: 702-721.

Schultz AH. 1960. Age changes in primates and their modification in man. In: Tanner JM, editor. Human growth. Oxford: Pergamon:1–20.

Shackelford, L., Ashley E Stinespring Harris; Lyle W Konigsberg.2012. AJPA 147(2): 227-253.

Shellis, R. 1998. Utilization of periodic markings in enamel to obtain information on tooth growth. J Hum Evol 35:387-400.

Shellis, R., Beynon, A., Reid, D., Hiiemae, K. 1998. Variations in molar enamel thickness among primates. J Hum Evol 35:507-522.

Smith, H. 1989. Dental development as a measure of life history in primates. Evolution 43:683- 688.

Smith, H. 1991a. Dental development and the evolution of life history in *Hominidae.* Am J Phys Anthropol 86: 157-174.

Smith, B. H. 1991b. Age at Weaning Approximates Age of Emergence of the First Permanent Molar in Non-Human Primates. AJPA Suppl. 12: 163–164.

Smith, T. 2008. Incremental dental development: methods and application in hominoid evolutionary studies. J Hum Evol 54:205-224.

Smith, Tanya, Paul Tafforeau, Donald J. Reid, Joane Pouech, Vincent Lazzari,John P. Zermeno, Debbie Guatelli-Steinberg, Anthony J. Olejniczak, Almut Hoffman, JakovRadovčić, Masrour Makaremi, Michel Toussaint, Chris Stringer, Jean-Jacques Hublin andRichard G. Klein. 2010. Dental evidence for ontogenetic differences between modern humans and Neanderthals. PNAS 49:20923-20928.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford: Oxford University Press.

Ten Cate. 1994. Ten Cate's oral histology: development, structure, and function. 6th ed. St Louis: Mosby.

Wolpoff, M., Hawks, J., Senut, B., Pickford, M., Ahern, J.J. 2006. An ape or the ape : is the Toumaï cranium TM 266 a hominid? Paleoanthropology 36-50.