DENTAL MICROSTRUCTURE AND GROWTH IN THE CEBID PRIMATES

by

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This manuscript has been read and accepted for the
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ABSTRACT

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by

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This dissertation is an analysis of growth rates in the teeth of the Cebidae, a family of New World monkeys (Platyrrhini, Primates) which includes capuchins, squirrel monkeys, tamarins, and marmosets. The dissertation is motivated by the need to: 1) further catalogue information on dental microanatomy within this group and analyze it as it relates to dietary adaptations; 2) catalogue dental growth rates in New World primates, a large group which has gone largely unstudied in this regard; 3) assess the impact which body mass, brain mass, and ecology have upon the evolution of growth patterns within primates and mammals in general; 4) better understand how physiologies (metabolism, reproduction, etc.) evolve to meet environmental demands, and 5) better understand the evolution of mating behaviors in primates. Teeth provide an excellent means to answer these questions, because they preserve permanent records of their own growth within their microscopic anatomy, in a similar manner to tree rings; therefore, we can compare growth lines (increments) within teeth of different species to better understand the evolution of growth across major groups. In order to access microanatomical data from teeth of cebid primates, this dissertation uses microscopic imaging and measurement of all eight genera within this family, focusing on circularly polarized light as an imaging modality.

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Chapter 1:

Introduction

Rationale for the Dissertation

Primate life history and dental ontogeny

Life history can be defined as the entire sequence of changes through which an organism passes from its conception to its death (Lande 1982). This includes developmental and growth events as well as reproduction (e.g., fecundity) and death (mortality; e.g., Cole 1954; Charnov 1973, 1991; Lande 1982; Calder 1984; Harvey and Clutton-Brock 1985; Stearns 1992; Brown and Sibly 2006; Sibly and Brown 2007). Over the last three decades, studies of teeth have greatly expanded our understanding of life history evolution in mammals (especially primates), and teeth have proven to be an excellent test bed for hypotheses on the interactions between ontogeny, ecology, and evolution. For example, researchers have used information from developmental genetics of teeth, dental eruption patterns, and dental tissue growth to learn about: ontogenetic constraints upon evolution, relationships between body mass and dental growth, the evolution of life histories in fossil hominins, and the evolution of growth in response to environmental forces (e.g., Bromage and Dean 1985; Macho et al. 1996; Godfrey et al. 2001, 2003, 2004, 2005, 2006; Jernvall 2000; Jernvall and Jung 2000; Jernvall and Thesleff 2000; Thesleff et al. 2001; Dirks et al. 2002; Ramirez-Rozzi

2002; Schwartz et al. 2005a, 2005b, 2007; Dirks and Bowman 2007; Lacruz et al. 2008; Leigh 2008; Smith 2008; Bromage et al. 2009).

There are several reasons that ontogenetic information from teeth has proven so useful in the study of primate life histories, ecology, and evolution. First, teeth incorporate fewer organs and tissue types than structures such as limbs (e.g., they do not have moving components such as synovial joints, musculoskeletal interactions, or complex networks of nerves such as the brachial plexus), and are relatively simple systems to understand in terms of the developmental processes which underlie their anatomy (e.g., Jernvall 2000; Jernvall and Jung 2000; Jernvall and Thesleff 2000; Thesleff et al. 2001).

Second, teeth have long been recognized as an important interface between organisms and their environment. In turn, they have been intensely studied by those interested in the evolution of diet across species. As early as the studies of Cuvier (1817) and Osborn (1840-1845), we have seen that gross dental morphology of mammals is determined in large part by mechanical needs of food breakdown. More recent studies have demonstrated that the microstructure of mammal teeth is also reflective of a species' diet (e.g., Koenigswald et al. 1987; Pfretzschner 1988; Lucas and Peters 2001; Rensberger 2000; Popowics et al. 2004).

The relationship between dental morphology and diet is well-established, but our understanding of dental ontogeny and how it evolves according to a species' ecology is less well-known. Cole (1954) and Lack (1954) were the first to put forth

the idea that ontogeny and ecology are connected. This notion was later codified in the theory of *r* vs. K selection by MacArthur and Wilson (1967). Originally, these researchers focused on ontogenetic responses to population density. However, their theories were later expanded to take into account the effects that additional variables, such as predation, have upon ontogeny and general life history (e.g., Gadgil and Bossert 1970; Pianka 1970; Wilbur et al. 1974; Stearns 1976, 1977). Wilbur and colleagues (1974) summarize the overall concept eloquently: "The life history of organisms, *like all other phenotypic attributes*, represents a series of selective compromises to a suite of environmental variables" (p. 805, emphasis mine). Therefore, we should expect dental ontogeny to respond adaptively to changing environmental conditions. As a consequence, we should be able to use analyses of dental ontogeny to make inferences about ecology and adaptation.

A third reason why teeth have received special attention in studies exploring the ties between ecology and ontogeny is that dental growth is at least *in part* independent of the growth of other components of the body (Pereira and Leigh 2003), and in turn, comparative anatomical studies across regions help us understand how selective forces act differently on separate anatomical complexes. Needham (1933) first developed the concept that discrete components of an organism might act as dissociable developmental elements. Studies in developmental genetics and primate life histories have since shown that there is a complex

web of epigenetic, ontogenetic, and functional factors governing the semi-independent growth of different suites of features (for discussion see Gould 1977; Raff 1996; Pereira and Leigh 2003). These dissociable parts must accommodate each other as well as meet external ecological demands to contribute to the functioning of a whole, viable organism (e.g., Cheverud 1982, 1989; Raff 1996; Raff and Raff 2001; Pereira and Leigh 2003; Leigh 2005). There is abundant observational evidence in support of the idea that although dental ontogeny is indeed timed within the overall framework of a growing organism, it can still respond semi-independently to specific selective factors (e.g., Godfrey et al. 2001; Schwartz and Dean 2001, Schwartz et al. 2002; Godfrey et al. 2004, 2005); therefore, it is worthwhile to explore primate dental ontogeny as a distinct entity that is separate from the ontogeny of other organs and organ systems.

One other major reason why dental ontogeny has received a great deal of focus is that teeth are the only structures in primates (and mammals in general) that preserve a permanent record of their own growth within their anatomy. Unlike bone, which is subject to remodeling over the life of an organism, the enamel of teeth is never remodeled endogenously, though they do experience abrasive wear (e.g., Boyde 1989; Ferguson et al. 2000). Due to this lack of remodelling, as well as the fact that dental tissues have appositional, periodic growth and an incremental histological structure, one can examine the microstructure of dental enamel (as well as dentine and, to a

lesser extent, cementum) to obtain absolute chronologies of dental growth (e.g., Boyde 1989; Dean 2000). Sometimes referred to as odontochronology, this process by which microstructural dental increments are used to reconstruct the growth histories of teeth is often compared to dendrochronology. However, dendrochronology is a method useful for examining spans of years, decades, and centuries, whereas dental incremental analysis is a method useful for studying shorter time spans such as days, weeks, months, and at most, years (Smith 2004).

In his landmark study of anthropoid dental eruption patterns and dental senescence, Schultz (1935) was perhaps the first researcher who sought to understand the relationship between overall life history patterns and dental growth rates within the primate order. Specifically, he postulated a connection between dental eruption sequence and the relative speed of life history, so that species with slower life histories delay the eruption of their molars relative to their permanent incisors, canines, and premolars (Schultz 1935; see also Smith 2000). Since this work, primatologists have devoted more and more attention to the types of questions that Schultz asked, using an ever-expanding dental ontogenetic dataset. We have also been able to formulate increasingly detailed hypotheses pertaining to the interactions among ecology, ontogeny, and evolution as evidenced in primate teeth, as we have come to better appreciate the implications of the four concepts discussed above (i.e., developmental biology, importance of ecology in

driving dental ontogeny, developmental independence of anatomical regions, and preservation of growth records within teeth).

For example, a growing body of research has focused on the biomechanical properties and adaptive significance of enamel microanatomy across different primates (e.g., Gantt et al. 1977; Maas 1994; Maas and Dumont 1999; Macho et al. 2003; Martin et al. 2003; Dean 2004; Lucas et al. 2008b). Other researchers have catalogued the growth records available in cercopithecoid, hominoid, and lemuroid teeth in detail (e.g., Boyde 1963; Bromage and Dean 1985; Beynon et al. 1991; Dean and Beynon 1991; Dirks 1998; Reid et al. 1998; Macho et al. 1996; Schwartz and Dean 2001; Schwartz et al. 2002; Schwartz and Dean 2005; Smith 2006; Lacruz et al. 2008), and have sought ecological explanations for the dental growth patterns in these taxa (e.g., Macho et al. 1996; Macho 2001; Dirks et al. 2002; Dirks 2003; Godfrey et al. 2006; Schwartz et al. 2006; Dirks and Bowman 2007). Other studies have used analyses of dental eruption patterns to explore the relationships between dental ontogeny and overall life history, body mass and brain mass, as well as ecological variables (e.g., Smith 1989, Smith et al. 1994; Smith 2000; Godfrey et al. 2001, 2003, 2004, 2005). The evolution of canine dimorphism among primates, and therefore the evolution of primate mating behaviors, is another topic to which dental growth data have been applied (Schwartz and Dean 2001; Schwartz et al. 2001, 2005b, Guatelli-Steinberg et al. 2009).

The histological sampling techniques used in many of these studies were first established in the 1960's, and are now well-tried and tested (see Chapters 2 and 3). Moreover, we now have relatively complete dental growth data for many extant catarrhine species (e.g., Boyde 1963, Beynon et al. 1991; Dean and Beynon 1991; Dean 1998; Dirks 1998; Reid et al. 1998; Macho et al. 1996; Schwartz and Dean 2001; Schwartz et al. 2001; Dirks et al. 2002; Dirks and Bowman 2007; Smith 2008), a number of extant strepsirhines (e.g., Schwartz et al. 2002), as well as multiple extinct members of both of these groups (e.g., Bromage and Dean 1985; Schwartz et al. 2002; Smith et al. 2003, 2004; Schwartz and Dean 2005a, 2005b; Godfrey et al. 2006; Schwartz et al. 2007; Lacruz et al. 2008). Therefore, at first glance it would seem that we have reached a relatively good point in our sampling of the dental histology of different primate taxa.

However, several large gaps still exist in our sample of primate dental growth, which prevent us from properly assessing the effect which diet, mating behavior, size, metabolism, and other factors may have on dental microstructure and growth. For example, with the exception of the Hominoidea, there have been no extensive surveys which focus on family-level patterns of dental growth, largely because no primate families (or superfamilies) have been as completely sampled as this group. Moreover, there are virtually no published data on microstructural growth records within the teeth of Lorisoidea, Tarsioidea, or Platyrrhini. Though there are a few studies of enamel architecture and dental

eruption in platyrrhines (Chase and Cooper 1968; Long and Cooper 1968; Gantt 1980; Fleagle and Schaffler 1982; Nogami and Yoneda 1983; Nogami and Natori 1986; Henderson 2007), the lack of histological growth studies of platyrrhines means that we have no absolute growth data from this group which we can incorporate into broader comparative contexts.

It is important to sample the dental growth of platyrrhines in particular because they are a large and diverse group of extant primates with a wide range of diets, body mass, and social/mating behaviors (e.g., Hershkovitz 1977; Ross 1991; Ford and Davis 1992; Rosenberger 1992; Anapol and Lee 1994; DiFiore and Rendall 1994; Kinzey 1997; Rosenberger et al. 2009). The range of platyrrhine diets and body mass is different from that of catarrhines (e.g., Schultz 1970; Eisenberg 1977; Harvey and Clutton-Brock 1985; Harvey et al. 1987; Ford and Davis 1992; Rosenberger 1992; Fleagle and Kay 1997; Fleagle 1999; Rosenberger et al. 2009), and therefore platyrrhines may provide important insight into the impact which diet and mass have on dental ontogeny within anthropoids. In addition, platyrrhines are variable in terms of mating behavior and canine dimorphism, unlike other large groups such as the cercopithecoids (Kay et al. 1988; Plavcan and Kay 1988; DiFiore and Rendall 1994; Ford 1994; Masterson and Hartwig 1998). In turn, platyrrhines provide a comparative sample with which we can test prior models on the evolution of canine dimorphism among anthropoids and primates in general (e.g., Schwartz et al. 2005b). The Platyrrhini also

include families that are relatively speciose, such as the Cebidae (e.g., Kinzey 1997), which provide unique evolutionary scenarios for study, and which are potentially important to developing an understanding of the evolution of dental microstructure and ontogeny at lower taxonomic levels within the primate order.

Cebid phylogeny and systematics

The platyrrhine Family Cebidae has a relatively high number of species, good available samples, and high diversity among platyrrhines in terms of body mass, ecology, and behavior; therefore, I chose to focus on the dental microstructure of this family for the dissertation (for further discussion of these reasons, see the next section). In order to be able to discuss the specifics of this family, I will first outline their systematics; discussions of cebid phylogeny in this section refer specifically to cladistic relationships.

The Family Cebidae consists of seven or eight extant genera depending on the inclusion of *Aotus* (e.g., Rosenberger 1984; Rosenberger et al. 1989; Rosenberger et al. 1990; Rosenberger 1992; Kinzey 1997; Schneider 2001; Ray et al. 2005, 2007; Osterholtz et al. 2009; Rosenberger et al. 2009). Interpretations based on both morphological and molecular datasets generally support the idea that Cebidae can be divided into two subfamilies, the Cebinae and Callitrichinae. Cebinae is

comprised of *Cebus* and *Saimiri*, the capuchins and squirrel monkeys, respectively. Callitrichinae includes the marmosets (*Callithrix* and *Cebuella*), tamarins (*Saguinus*), lion tamarins (*Leontopithecus*), as well as Goeldi's monkey, *Callimico* (e.g., Rosenberger 1984; Rosenberger et al. 1989; Rosenberger et al. 1990; Rosenberger 1992; Kinzey 1997; Schneider 2001; Ray et al. 2005, 2007; Osterholtz et al. 2009; Rosenberger et al. 2009). For examples of morphological and molecular cladograms for Cebidae, see Fig. 1-1.

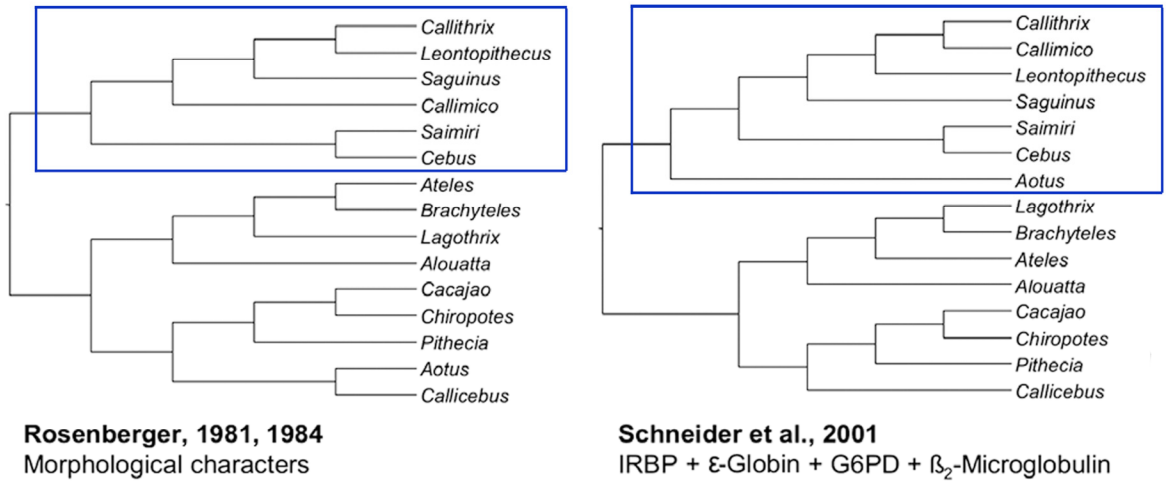


Fig. 1-1. Sample morphological (**A**) and molecular (**B**) cladograms for the Cebidae, adapted from Osterholz et al. (2009). Both trees also include genera from other platyrrhine families in order to highlight differing interpretations of *Aotus*. In both trees, Cebidae is indicated by the box. In the morphological tree **A**, Cebidae consists of Callitrichinae (*Callithrix*, *Leontopithecus*, *Saguinus*, and *Callimico*) and Cebinae (*Cebus* and *Saimiri*) only. Also observe that *Callimico* falls as a sister taxon to the remaining callitrichine genera. *Aotus* is interpreted as a sister taxon to *Callicebus*, falling outside of Cebidae. In the molecular tree **B**, *Callimico* is interpreted as a sister taxon to *Callithrix* (and *Cebuella*, not shown), while *Aotus* is grouped within Cebidae as a third family, Aotinae. Although *Cebuella* is not depicted in either tree, it is generally accepted to be the closest relative of *Callithrix*.

A third possible subfamily of the Cebidae, the Aotinae, has been suggested based on molecular data, and its extant members include only the owl monkeys of the genus *Aotus* (Schneider 2001; Ray et al. 2005, 2007; Osterholtz et al. 2009). However, Rosenberger and colleagues (e.g., Rosenberger 1981, 1984; Rosenberger et al. 1989; Rosenberger et al. 1990) have argued based on morphological grounds that *Aotus* is a sister taxon to *Callicebus* within the family Atelidae (subfamily Pitheciinae). Rosenberger and colleagues have also argued more recently that previously published molecular trees do not accurately represent the true phylogenetic relationships of *Aotus* (Rosenberger et al. 2009; Rosenberger and Tejedor in press).

Another disagreement between molecular and morphological phylogenetic studies concerns the placement of *Callimico* within the Callitrichinae. Whereas several molecular studies have argued that *Callimico* is a sister group to the *Callithrix/ Cebuella* clade (e.g. Sarich and Cronin 1980; Schneider 2000; Seuanez et al. 2005; Osterholtz et al. 2009), morphological phylogenies have most often placed *Callimico* as an outgroup to all of the other genera based on potentially primitive features such as lack of twinning and presence of a third molar, for which the other callitrichine genera exhibit more derived states (Rosenberger 1984; Ford 1986; Kay 1990; Horovitz et al. 1998).

Even though molecular and morphological phylogenies for the cebids are largely concordant, the contested statuses of *Aotus*

and *Callimico* present a clear taxonomic problem. However, these conflicting interpretations are not highly problematic for this dissertation because the project is not intended to assess phylogenetic patterns of dental microstructure and growth *per se*, but is instead interested in more general cebid and primate questions tied to factors such as diet and body size. Even though its exact position within the Callitrichinae is disputed, no one argues that *Callimico* is not a member of this subfamily; therefore, since I do not examine the differences among the callitrichines a precise phylogenetic placement of *Callimico* is not needed. The dispute over *Aotus* presents a greater problem than *Callimico*, because the taxonomic status of *Aotus* as cebid or non-cebid (see Rosenberger et al. 2009; Rosenberger and Tejedor in press) has a more direct influence of how data from this genus are interpreted. In order to be the most inclusive for the present purpose, I include *Aotus*. Accordingly, all future discussion will treat *Aotus* as a member of Cebidae, with the implicit understanding that the phylogenetic status of this genus is still under debate.

The importance of the Cebidae in primate dental ontogeny

As discussed above, the Cebidae are a diverse family with a relatively high range of variation in body sizes and dietary preferences (e.g., Rosenberger 1992). Therefore, within the Platyrrhini, the Cebidae are an ideal group to help us further

understand the interrelationships among dental development, life history, and ecology.

Regarding body mass, the different species of *Saimiri* can weigh between around 0.6 and 1.3 kg, while *Cebus* is considerably larger, with individuals of some species exceeding 3 kg in mass (e.g., Ford and Davis 1992, Rosenberger 1992). The callitrichines, in comparison, are well-characterized as the smallest extant anthropoid group (e.g., Ford and Davis 1992, Rosenberger 1992). In fact, the callitrichine genus *Cebuella,* at around 0.11 to 0.12 kg, is the smallest extant primate genus with the exception of the mouse lemur, *Microcebus* (e.g., Ford and Davis 1992, Rosenberger 1992; Harvey and Clutton-Brock 1985; Smith and Cheverud 2001). *Callithrix, Saguinus,* and *Callimico* are somewhat larger, ranging roughly between 0.2 to 0.55 kg. *Leontopithecus* is larger than these genera and slightly smaller than *Saimiri,* at around 0.5 to 0.7 kg (e.g., Ford and Davis 1992; Rosenberger 1992; Smith and Cheverud 2001; Porter and Garber 2004).

Members of the Cebidae live in primary, secondary, and edge forest habitats in Central and South America (Ross 1991). In general they have been characterized as "frugivores-insectivores" in terms of diet, though this an oversimplification (e.g., Rosenberger 1992; Anapol and Lee 1994; Wright 1996; Dietz et al. 1997; Porter 2001; Porter and Garber 2004; Wolovich et al. 2008). While *Saimiri* certainly does seem to fit a generic frugivore-insectivore model, eating mostly soft fruits, arthropods, and

small vertebrates (e.g., Boinski 1999), all of the other cebid genera have modified this regime to some degree. For example, *Aotus* includes a substantial amount of leaves in its diet (e.g., Wright 1985; Wright 1996; Wolovich et al. 2008), while *Cebus* (especially *C. apella*) has developed a range of hard-object feeding behaviors that includes seeds and tough, pithy fruits as well as softer fruits and animal matter (e.g., Struhsaker and Leland 1977; Teaford 1985; Brown and Zunino 1990; Fragaszy et al. 1990; Fernandes 1991; Janson and Boinksi 1992; Galetti and Pedroni 1994; Fragaszy and Boinski 1995; Kinzey 1997; Fragaszy et al. 2004; Wright 2005; Addessi 2008). In fact, *Cebus* is perhaps best considered an omnivore (Rosenberger 1992).

The callitrichines, meanwhile, include varying degrees of exudate feeding in their dietary regime, which provides them with a relatively reliable source of extra energy and minerals such as calcium (Ramirez et al. 1977; Sussman and Kinzey 1984; Rosenberger 1992; Power 1996; Power and Oftedal 1996; Dietz et al. 1997; Kinzey 1997; DiBitetti and Janson 2000). *Callithrix* and *Cebuella* rely on this resource to a considerably greater degree than the three other callitrichine genera, actively gouging tree bark to obtain gums and saps (e.g., Kinzey et al. 1975; Ramirez et al. 1977; Sussman and Kinzey 1984; Ferrari 1993). Moreover, *Callimico* is also known to consume a substantial amount of fungi (Porter 2001; Porter and Garber 2004).

These differing dietary emphases should result in differences in the structure of enamel prisms (fundamental units of mammalian tooth enamel) among the teeth of different genera, because this feature seems to be closely governed by the mechanical needs imposed by differing diets (Lucas et al. 2008b). Although some studies have already assessed such enamel patterns for the cebids (Nogami and Yoneda 1983; Nogami and Natori 1986), they have not taken into account variation across or within teeth, and so further analyses of cebid microstructure may provide interesting insights. For example, comparisons of prism patterns among different tooth regions may provide further insight into functional adaptations to tree-gouging within *Callithrix* and *Cebuella* (e.g., Rosenberger 1978; Rosenberger, 1992; Maas and Dumont 1999; Vinyard et al. 2003; Vinyard et al., 2009). Moreover, such analyses may also provide further insight into the ways in which *Cebus* uses its teeth during extractive foraging and hard-object feeding, by highlighting differences in functional adaptations among tooth types.

The variation in cebid diets and body sizes also makes them a good group to study the effect of ecology and mass upon dental growth. For example, although body mass and brain mass have been considered as variables correlated to dental growth rates (e.g., Schwartz et al. 2002) and dental increment periodicities (e.g., Dean and Scandrett 1995; Smith 2008), the relationships between dental tissue growth rates and body mass or brain mass have not been statistically tested. Dental growth rate data for species

in the lower end of the range of primate size variation (e.g., *Cebuella*) are also not available. Furthermore, analyses of the statistical relationships between eruption sequences, ages of primate tooth eruption, and ecological variables have been conducted (Smith et al. 1994; Godfrey et al. 2001), but there is still little published tissue growth *rate* data. With their substantial body mass diversity (including some of the smallest primates) and ecological diversity, data from the Cebidae should hopefully serve to fill in some of these gaps.

In addition to daily lines deposited by ameloblast cells, mammalian tooth enamel also contains lines deposited at regular time intervals which are specific to different taxa, known as striae of Retzius (see Boyde 1989 for review, and Chapter 2). Several primate-focused studies have suggested that the periodicity of these Striae of Retzius is tied to body mass (Dean and Scandrett 1995; LaCruz et al. 2008; Smith 2008). However, there is a still a substantial lack of data regarding the variation in primate Retzius periods, especially regarding smaller bodied taxa. In fact, our lack of knowledge regarding overall variation in Retzius periodicities is a major reason why the physiology underlying this microstructural phenomenon has so far gone unexplained. Although researchers have speculated on the cause of the Retzius phenomenon over the years (e.g., Newman and Poole 1974, 1993), the data available have not allowed these specific hypotheses to be tested (Bromage et al. 2009). Therefore, we have had little insight regarding the evolutionary

importance of this biological rhythm, though a new hypothesis has recently been advanced which argues that oscillations within the autonomic nervous system of mammals may be responsible for variation within Retzius periodicities (Appenzeller et al. 2005; Bromage et al. 2009). As a result of their smaller body sizes, the cebids can help us fill in a major gap in our understanding of overall primate variation in Retzius periodicity by allowing us to test this hypothesis.

Lastly, the cebids may provide important details pertaining to the evolution of canine dimorphism in anthropoids and in primates in general. Schwartz and colleagues (2005b) reasoned that differences in growth patterns underlying canine dimorphism among taxa (i.e., faster growth rates in males vs. longer growth periods in males) are homoplastic. These authors used dental growth rate data from catarrhines and the notharctine genus *Cantius* to infer that anthropoids and notharctines evolved their dimorphism independently of one another. This study has major implications for our understanding of social evolution in primates; however, our models of anthropoid social evolution still contain a large gap because we have no absolute ontogenetic data on canine dimorphism within the platyrrhines. Dental ontogenetic data from *Cebus* and *Saimiri* may be of importance to filling that gap, because they are two of the most dimorphic platyrrhine genera with regard to canine size (along with *Alouatta*; see Kay et al. 1988; Plavcan and Kay 1988; Ford 1994; Masterson and Hartwig 1998). Specifically, canine growth data

from these two genera may be compared to prior growth data from other dimorphic primates in order to investigate patterns of homoplasy and homology.

Therefore, the major goal of this dissertation is to catalogue the dental microstructure of cebid platyrrhines and provide information on the variations within a primate group at a lower taxonomic level (i.e., at the level of the family), as well as to initiate a broader platyrrhine dental growth dataset. Furthermore, based on the patterns exhibited by the cebids discussed above, my analyses focus on: 1) the patterns of enamel microstructure within the cebids as they relate to possible dietary adaptations; 2) the potential influence/effect which body mass, brain mass, and ecology have upon dental growth rates; 3) the relationship between body mass, brain mass, and long-term biorhythms (i.e., Retzius periodicity); and, 4) the ontogeny of canine dimorphism.

Structure of the Dissertation

This dissertation is organized into three distinct sections. The first section (Chapters 2 and 3) provides a brief history of dental tissue research and methodology. Chapter 2 provides an in-depth review of dental structure, growth, and evolution, and presents a history of research into these areas as they pertain to understanding the enamel of the platyrrhines. It

also presents a brief review of prior dental growth studies in primates. Chapter 3 follows with a commentary on enamel's varying structural, chemical, and optical properties, and the implications these properties have for choosing methods of microscopic analysis. This chapter also discusses the evidence behind the periodicity of dental increments in more detail. Chapter 3 also describes the specific materials and methods used herein, including sampling, preparation, imaging, and analysis. Lastly, the chapter details new preparation and imaging protocols for hard tissue histology which I developed during the course of the project.

The second portion of the dissertation includes four data and analysis chapters (4-7), which correspond to the four major foci of the dissertation as discussed at the end of the section above. Chapter 4 catalogues and describes the range of variation in daily enamel increments across the cebid species sampled in the dissertation and describes the variation in their enamel extension rates (e.g., Ramirez-Rozzi 2002). This chapter also expands upon prior analyses of enamel prism patterns within the Cebidae (e.g., Nogami and Yoneda 1983; Nogami and Natori 1986) by discussing patterns of variation in enamel microanatomy within teeth and across tooth types, made possible by the method of circularly polarized imaging used in this study (see Chapter 3 for discussion of the advantages of this protocol). It also discusses the potential functional and ecological importance of the enamel prism patterns seen.

Chapter 5 assesses cebid enamel growth rate data in the context of other adaptational variables. It seeks to explain variation in cebid enamel growth rates by focusing on the statistical relationships that dental growth exhibits with regard to brain mass, body mass, age at foraging independence, environmental risk, and maternal investment. These analyses are largely modeled on prior studies of dental eruption patterns (Smith 1989, Smith et al. 1994; Godfrey et al. 2001), which were designed to determine whether enamel growth rates and dental eruption patterns respond to similar selective forces.

Chapter 6 examines the evolution of organism-wide physiological patterns among primates, using striae of Retzius data for cebids and other primates to help test whether a central mechanism in the autonomic nervous system might be responsible for the evolution of physiological processes such as metabolism, growth, and reproduction, which largely comprise species' life history patterns. This chapter is part of the framework for analyses recently published by Bromage and colleagues (2009), who postulated that such a mechanism, known as the Havers-Halberg Oscillation (HHO), could help control species' long term responses to shifting energetic limits imposed upon them by their environments.

Chapter 7 explicitly addresses the evolution of canine dimorphism in the platyrrhine primates from an ontogenetic perspective, operating under the assumption that differing ontogenetic patterns suggest differing evolutionary origins of

specific features such as dimorphism. The chapter compares differences in growth rates between the canines of males and females in dimorphic platyrrhine species, to test whether dimorphic platyrrhine males achieve their larger teeth via faster growth rates or longer growth periods (bimaturism), as is the case in catarrhines (Schwartz and Dean 2001; Schwartz et al. 2001; Leigh et al. 2005; Schwartz et al. 2005b). By comparing this platyrrhine dataset to prior analyses of catarrhines, one would expect to gain further insight into the evolution of canine dimorphism within the anthropoid primates.

The final part of the dissertation, Chapter 8, summarizes the results of the preceding chapters, offers concluding remarks on the various topics, and reviews promising areas for future analysis. The appendices then provide tables of specific data used in the dissertation, including samples, measurements, and data taken from the literature.

Chapter 2:

Dental microstructure, development, and evolution

Dental Anatomy and Microstructure, With a Focus on Enamel

Mammal teeth are composed of four primary substructures or tissue types: enamel, dentine, cementum, and pulp (Fig. 2-1). The first three of these are composed of tissues that have been mineralized to various degrees, with enamel containing the least organic material (e.g., Noyes and Thomas 1921; Scott and Dixon 1966; Boyde 1989; Goldberg et al. 1995; Maas and Dumont 1999). Enamel is acellular, avascular, and unmodifiable in its morphology past its initial deposition, except through abrasive wear (Boyde 1989; Maas and Dumont 1999). Dentine, which is composed of dentine tubules laid down by odontoblast cells, can be remodeled to some extent through an organism's lifespan as the odontoblasts themselves persist throughout the life of the tooth (e.g., Noyes and Thomas 1921; A.J. Smith 2000; Smith and Sansom 2000). Cementum, which is commonly described as a bone-like tissue, acts as a thin coating over the dentine of the tooth root and provides anchorage for the periodontal ligaments, but is rarely incremental in primates (Boyde 1989). The pulp, which is the only non-mineralized dental component, is a highly vascularized tissue which also contains the nerve endings for the individual teeth (e.g., Noyes and Thomas 1921; Scott and Dixon

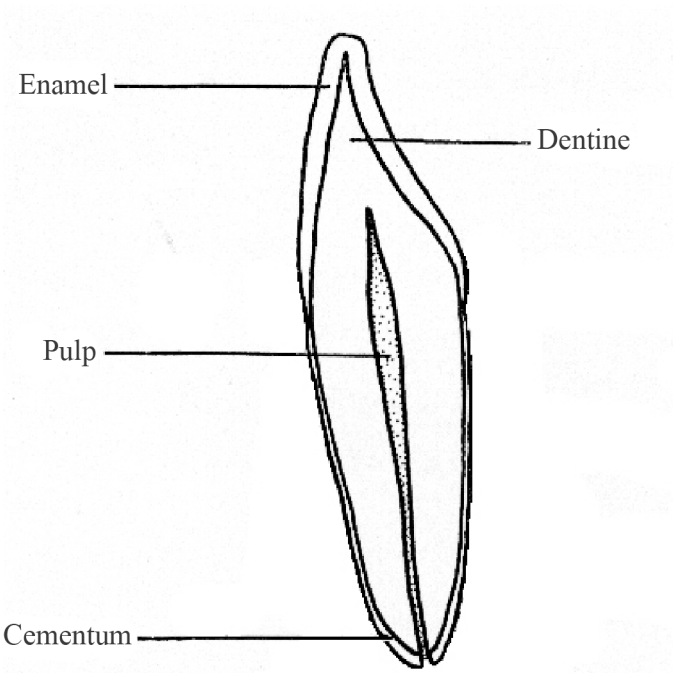


Fig. 2-1. A diagram of stereotypical mammalian tooth structure at the gross anatomical level. Note that the region consisting of dentine and enamel is considered the crown, while the regions consisting of dentine and cementum is the root. Modified from Scott and Dixon (1966).

1966). These four primary tissue types, combine to form the crown (primarily enamel and dentine) and root (primarily cementum and dentine) of the tooth, functioning to process food and anchor the tooth to its alveolus, respectively.

Enamel itself is composed mostly (96%-98%) of crystallites of the mineral apatite, which consists of calcium phosphate with an attached ion. In teeth and bone, the apatite primarily occurs in carbonate hydroxide form (carbonate hydroxyapatite), though fluoride and other ions can replace the hydroxides in the chemical structure of apatite throughout the lifetime of the tooth (creating fluoroapatite, etc.; see Lowenstam and Weiner

1989; Driessens and Verbeeck 1990; Maas and Dumont 1999; Hoppe et al. 2004; Hillson 1996). The remaining 2%-4% of the enamel is composed of water and organic chemicals such as amelogenin, enamelin, and lipoproteins, which form a compound material when combined with the mineral crystallites to improve the enamel's properties of fracture resistance and crack propagation (Scheinmann et al. 1961; Lowenstam and Weiner 1989; Maas and Dumont 1999).

Enamel crystallites are much longer than apatite crystallites in bone, reaching up to a hundred microns (Diekwisch et al. 1995; Smith 2004). Their widths can be expressed in small fractions of a micron, with width tending to increase away from the enamel-dentine junction, or EDJ (Palamara et al. 1980). Enamel crystallites are bound by organic matrix and can be arranged in one of two ways: as *prismatic* or *aprismatic* enamel. In prismatic enamel, which occurs only in mammals, crystallites are bundled in long, solid cylindrical structures that run from the dentine to the surface of the tooth (Maas and Dumont 1999; Line and Novaes 2005). These cylindrical structures are commonly referred to as enamel prisms, though in the clinical literature they are often referred to as enamel rods. Within enamel prisms, crystallites run largely parallel to one another and to the long axis of the prism (Waters 1980; Maas and Dumont 1999; Sander 2000; Habelitz et al. 2001; Line and Novaes 2005; Wood and Rougier 2005). These prisms are separated from each other and from the inter-prismatic crystallites among them by divergent

paths in the crystallites themselves. That is, within the prism crystallites run mostly parallel, but outside the prism they are oriented in tangential directions. The location where abrupt discontinuities occur is visible in SEM micrographs as a line surrounding the prism, the "prism sheath" (Waters 1980; Maas and Dumont 1999; Sander 2000; Habelitz et al. 2001; Line and Novaes 2005; Wood and Rougier 2005; see Figs. 2-2 and 2-3). These discontinuities most likely evolved to help reduce the risk of crack propagation (Line and Novaes 2005).

The structure of aprismatic enamel is much less complex than that of prismatic enamel (Fig. 2-4). In the simplest type of aprismatic enamel, crystallites are oriented with their long axes roughly perpendicular to the tooth surface; this can be seen in both mammals and reptiles such as archosaurs (Maas and Dumont 1999; Line 2000). Aprismatic enamel can also take a form known as *columnar* or *columnar unit enamel*, in which prisms slightly diverge away from one another to give the appearance of parallel columns in the microstructure (Koenigswald and Sander 1997; Sander 2000; Line 2005). Generally speaking, aprismatic enamel is much less common in mammalian teeth, often occurring at tooth surfaces and toward the cervix of teeth where Tomes' processes (see below) tend to break down as ameloblasts age (Maas and Dumont 1999; Smith 2006). Toothed cetaceans are an exception to this overall mammalian pattern, as they have reverted to the primitive aprismatic state entirely (Maas and Thewissen 1995).

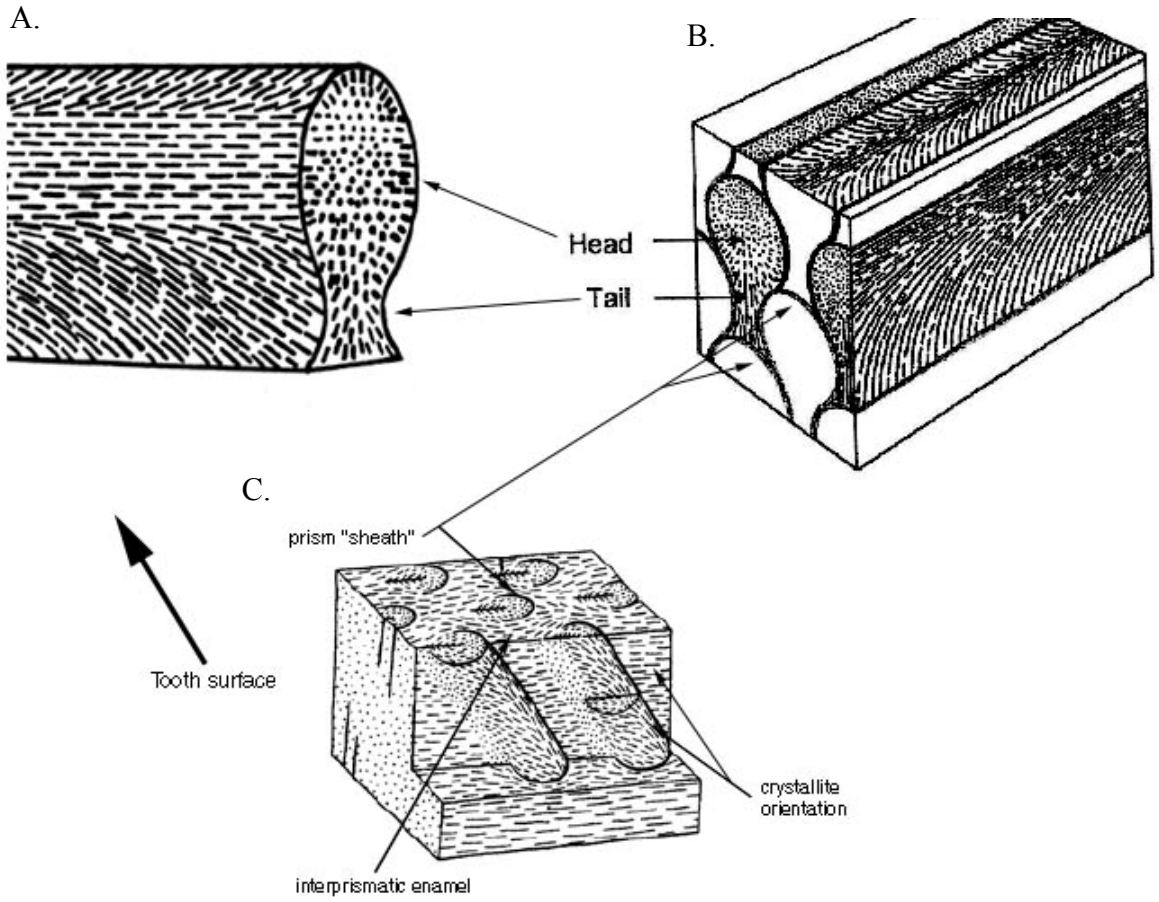


Fig. 2-2. Different components of enamel, such as individual prisms result from differing orientations of these crystallites, as seen here. **A.** Crystallite orientation in an isolated prism, from Waters (1980). Observe that the crystallites in the head of the prism run parallel to the course of the prism itself, whereas in the tail (and the very top of the head) the crystallites begin to diverge; **B.** A series of prisms from *Habelitz and colleagues* (2001). Here, at the top of the sectioned block, one can see differing orientations of crystallites among prisms. The point where differing orientations converge is the boundary of the prism, or prism "sheath"; **C.** an illustration of a similar pattern modified from Wood and Rougier (2005). Here prism boundaries can also be seen clearly as semicircular prism sheaths. On the section cut away from the front of the block, which exposes two prisms, one can see within the prism how the crystallites have a gradually shifting orientation from top to bottom (i.e., right to left in this image). Immediately to the right of each prism sheath, one can also see a rapid transition in orientation between those above the prism (running right to left) versus those in the prism head itself, which run more in line with the direction of the prism's course. Thus sudden transition, again, marks the boundary between the prism and the enamel outside that particular prism.

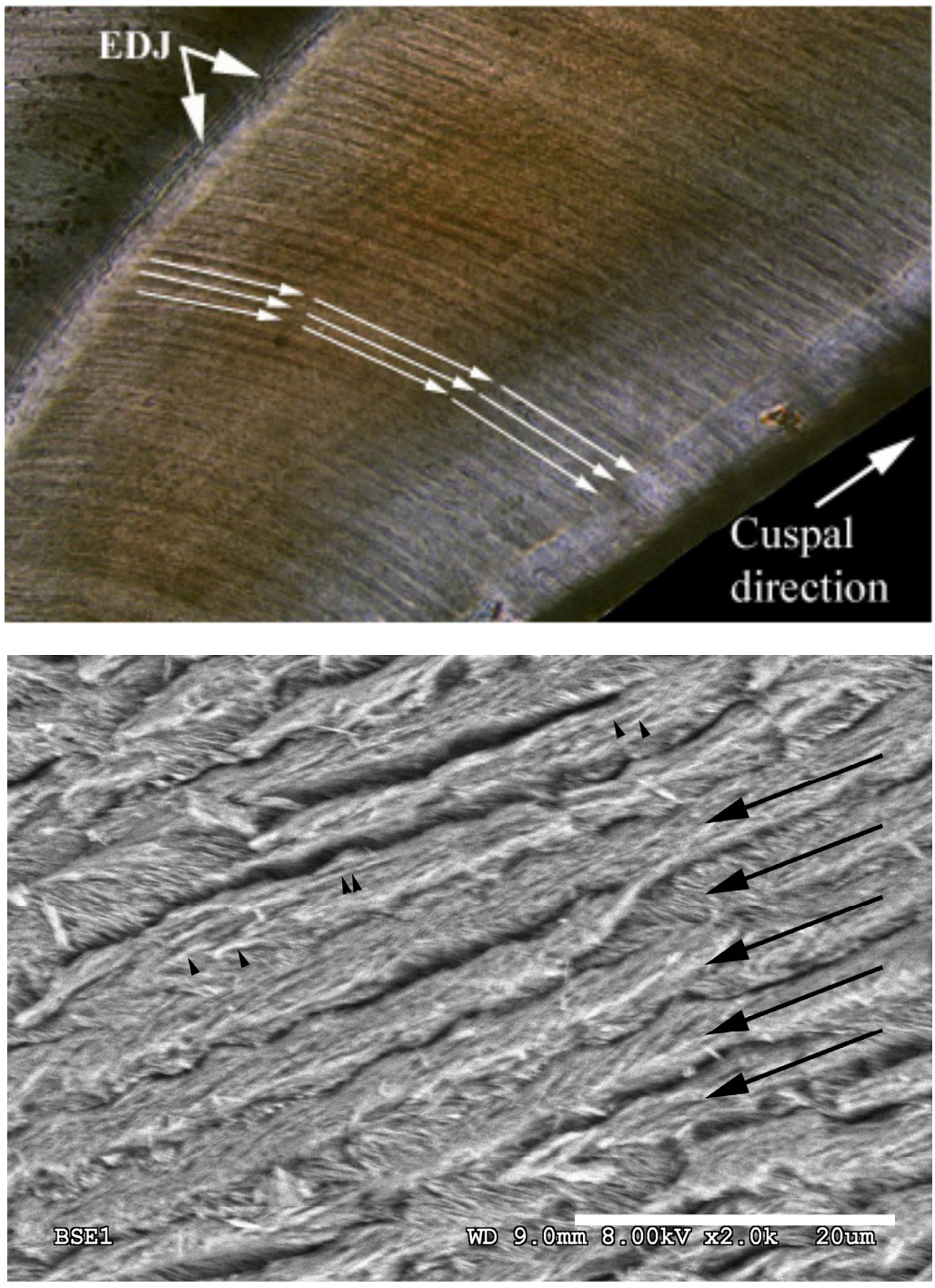


Fig. 2-3. A. Light micrograph of a *Saimiri sciureus* premolar, showing enamel prisms (large arrows). **Field width = 134 microns. B.** SEM micrograph of enamel prisms in longitudinal section in a *Cebus apella* molar. Enamel crystallites can clearly be seen as tiny linear structures (small arrows) making up the larger prisms (large arrows), running from upper right to lower left. "Prism sheaths" can be seen as large black lines between prisms. Scale bar represents 20 microns.

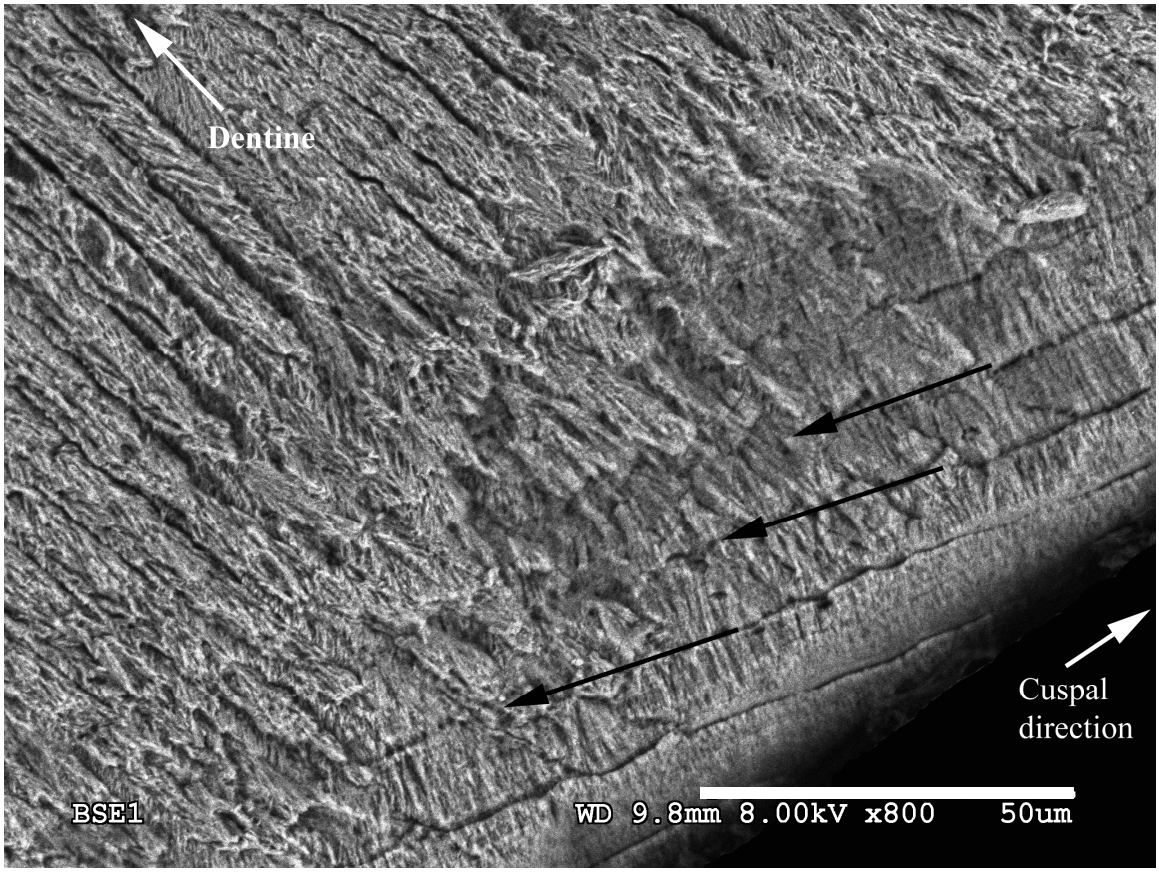


Fig. 2-4. Two types of enamel patterns, shown at high magnification in an SEM micrograph of a *Cebus albifrons* molar. Toward the top left of the photo, one can clearly see enamel prisms as self-contained linear structures aligned slightly less than perpendicular to the tooth surface at lower right. Nearer the surface, however, the prisms break down, giving way to aprismatic (parallel crystallite) enamel (arrows). Scale bar represents 50 microns.

In both prismatic and aprismatic enamel, crystallites and prisms are punctuated by both short and long period increments: cross-striations and striae of Retzius, respectively (e.g., Asper 1916; Boyde 1963; see Figs. 2-5 and 2-6). Boyde (1964) suggested that enamel increments result from chemical differences in the mineral matrix which affect the optical properties of the tissues, as acid-etching of prepared specimens generally enhances the optical contrast between the light and dark bands that represent these regions. Thus there seem to be different pH properties of different regions in enamel. Okada (1943) showed that daily cross-striations probably result from differing acid-base chemistries in the blood that are driven by daily wake/sleep cycles, which suggests a physiological explanation for this phenomenon. In addition to this study, there is extensive observational evidence to support the idea that cross-striations are deposited with a daily periodicity (e.g., Asper 1916; Gysi 1931; Bromage 1991; Fitzgerald 1998; Shellis 1998). For an in-depth discussion of this evidence, see Chapter 3.

Retzius lines, on the other hand, appear to represent a disturbance of enamel secretion which affects the orientation/ orderliness of enamel crystallites from all actively secreting ameloblasts at once and thus creates a discontinuity (Boyde 1989; Risnes 1998). This discontinuity seems to be of a different chemical nature than cross-striations, as acid-etching tends to make Retzius lines less, rather than more, visible (Risnes 1998).

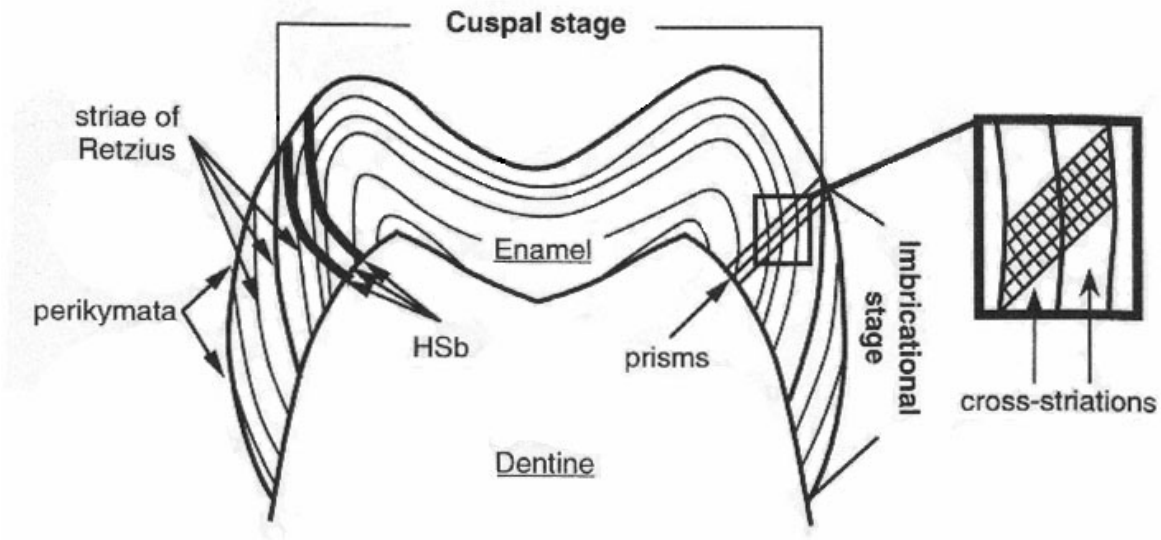


Fig. 2-5. Model of typical mammalian enamel microanatomy. Enamel prisms can be seen with small lines running perpendicular to their long axis, known as cross-striations. Moreover, prisms are also intersected by larger periodic lines known as striae of Retzius. HSb = Hunter-Schreger bands, which are regions where bundles of enamel prisms have alternating orientations (see below and Chapter 4). From Ramirez-Rozzi (2002)

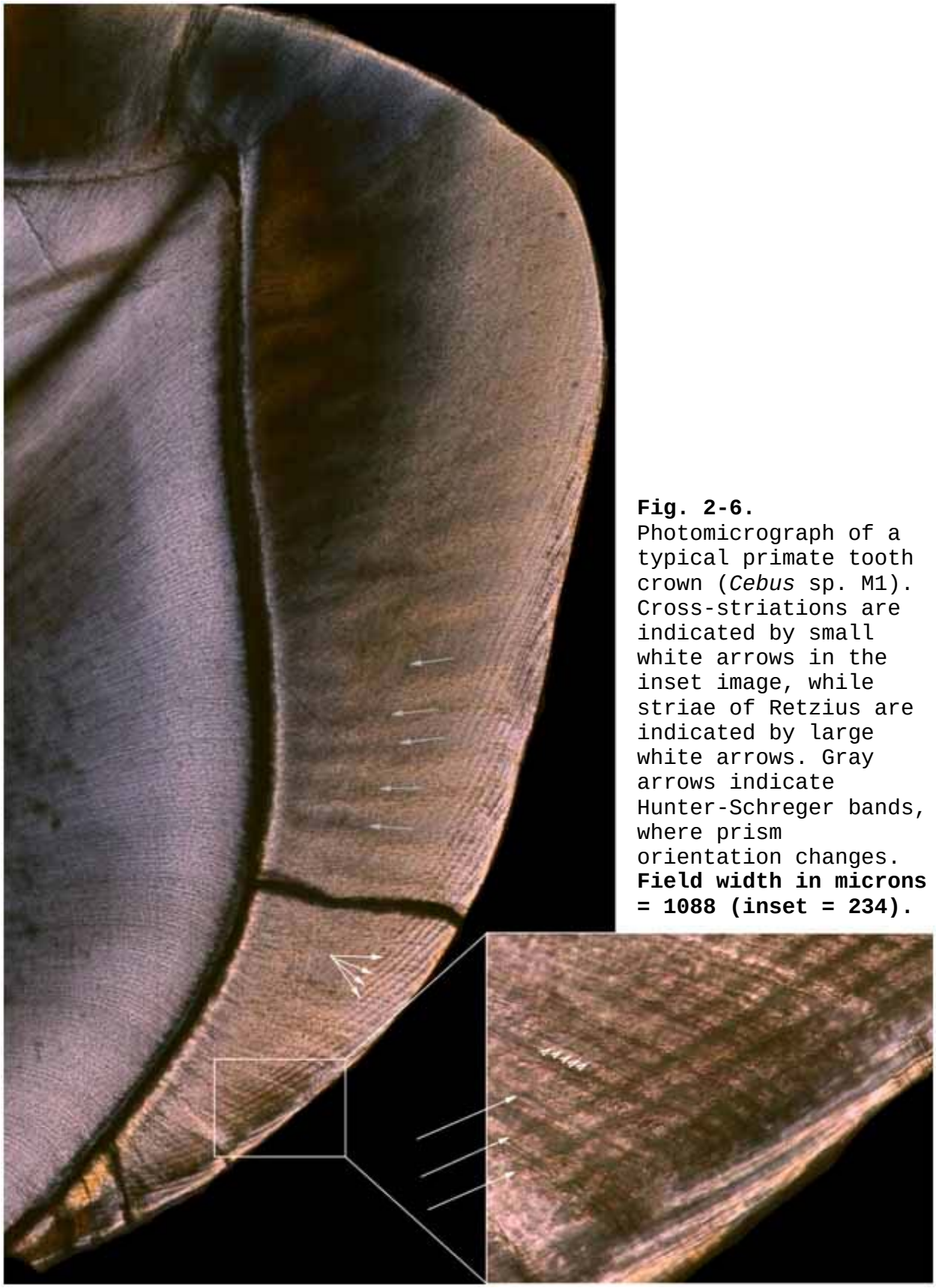


Fig. 2-6. Photomicrograph of a typical primate tooth crown (*Cebus* sp. M1). Cross-striations are indicated by small white arrows in the inset image, while striae of Retzius are indicated by large white arrows. Gray arrows indicate Hunter-Schreger bands, where prism orientation changes. **Field width in microns = 1088 (inset = 234).**

Striae of Retzius are also periodic structures deposited at specific time intervals, but unlike the period of cross-striations, the length of this rhythm varies across taxa and even to some degree among individuals of the same species (e.g., Boyde 1963; Boyde 1989; Risnes 1998. Within individuals, however, the period is consistent (Dirks 1998; Fitzgerald 1998; Shellis 1998). More on the periodicity and physiology of cross-striations and striae of Retzius is discussed in Chapters 3 and 6.

Where Retzius lines reach the surface of the enamel, they appear as a series of bands or lines running around the circumference of the tooth, known as perikymata (Bromage and Dean 1985; Fig. 2-7). Wherever ameloblast function is affected by stress (whether nutritional, social, infectious, etc.) across several Retzius periods, insufficient enamel will be deposited and a shelf of arrested growth known as a hypoplasia will appear (Guatelli-Steinberg 2001).

In addition to the two enamel increments mentioned above, Smith (2004) has also recently emphasized two other incremental types. The first, "intradian lines," are a much less regular banding of prisms, which appear to occur at intervals of less than a day. Their reliability for odontochronology is undetermined at this point, and so for the purpose of this project they have been excluded. The second type, called "laminations," are in fact the expression of the circadian enamel rhythm in aprismatic enamel, as shown by Smith (2004). In my opinion, the term "cross-striation" should be taken to mean a

daily increment visible on groups of enamel crystallites (or even individual crystallites, where possible), which runs perpendicular to the long axis of those crystallites. This is a more inclusive definition than the traditional one, which refers to the cross-striation as an increment visible on enamel prisms (e.g., Smith 2004). I feel that a change in the definition is warranted so that a common terminology can be applied to daily increments across different types of enamel and different taxa, including those which do not exhibit prisms. Therefore, this eliminates the need for the term "lamination."

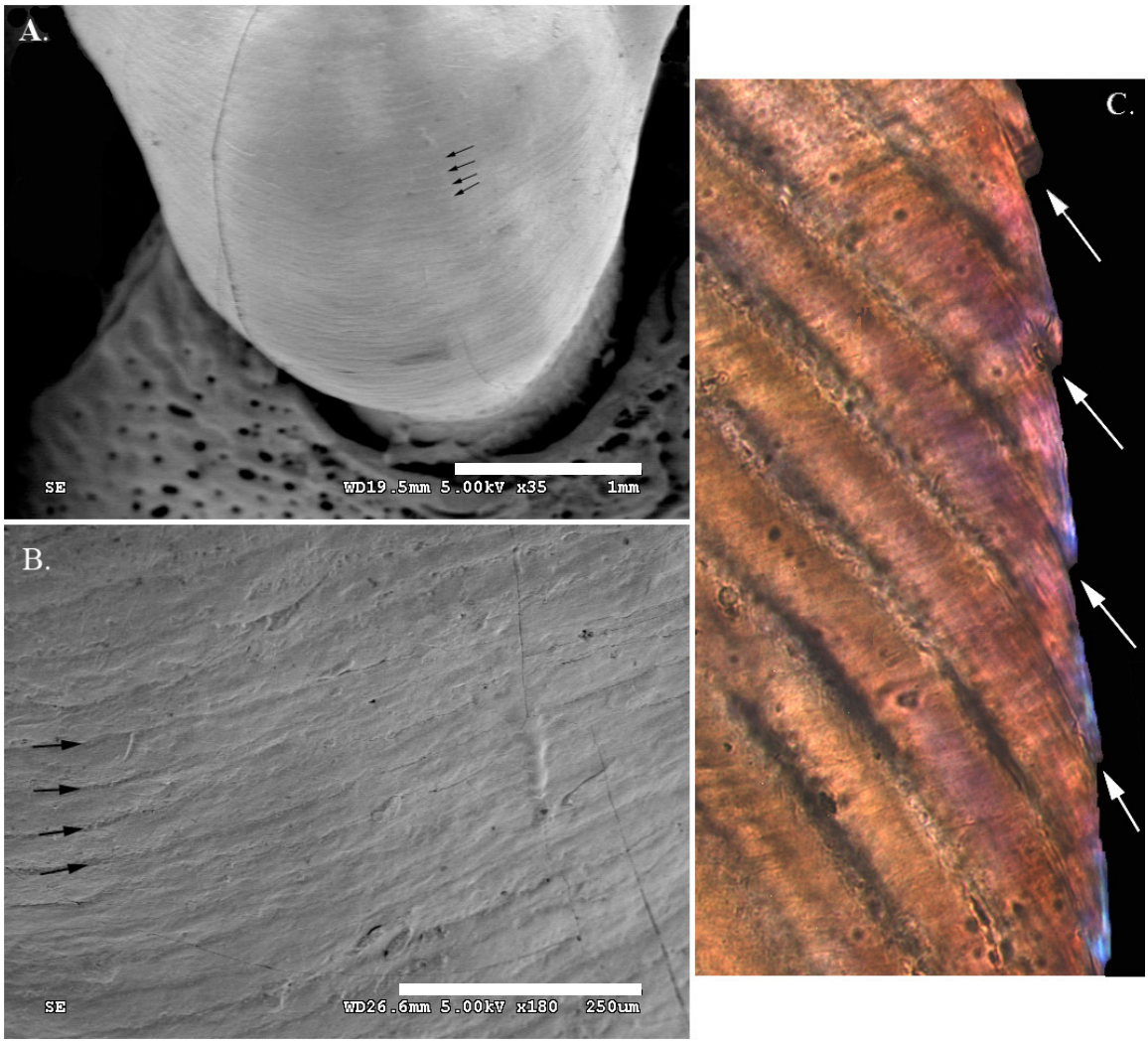


Fig. 2-7. **A.** SEM micrograph of perikymata on the surface of a *Cebus* sp. P2 (indicated by black arrows). Scale bar = 1mm. **B.** Close-up view of perikymata on the same premolar. Scale bar = 250 microns. **C.** Light micrograph of a P3 from the same individual, with white arrows indicating the manifestation of striae of Retzius as perikymata on the tooth surface. Tooth surface is to the right; dark bands running from upper left to lower right are striae of Retzius. **Field width = 66 microns.**

Schmeltzmuster, or enamel pattern, is used to describe the next level of dental organization. This term refers specifically to the ways in which aprismatic and prismatic enamel are arranged within a tooth, overall. In other words, it refers to the types of aprismatic and prismatic enamel which are present, how they run in patterns relative to one another, and where these patterns are located in relation to the overall structure of the tooth.

Aprismatic enamel can occur in a parallel crystallite, wavy, or columnar form throughout any tooth or in specific regions of a tooth (Maas and Dumont 1999; Sander 2000). In primates, aprismatic enamel tends to be located near the EDJ, the tooth surface, or the cervix of the tooth (Maas and Dumont 1999; Smith 2004, 2006). This most likely has to do with ameloblast life cycles, and will be addressed in more detail in the next section. Prismatic enamel, in its simplest form, consists of prisms running directly from the EDJ to the tooth surface with minimal deviation. This is known as *radial enamel* or *radial prismatic enamel* (Boyde 1989; Risnes 1998; Maas and Dumont 1999). In addition to being structurally the simplest form, it is also the most common and the most primitive form of prismatic enamel for mammals (Koenigswald et al. 1987). It frequently occurs in small mammals – including small primates (Maas and Dumont 1999; Koenigswald 2000; Line and Novaes 2005). However, radial enamel has a mechanical disadvantage with respect to crack propagation, as an initial crack can easily travel down the relatively linear

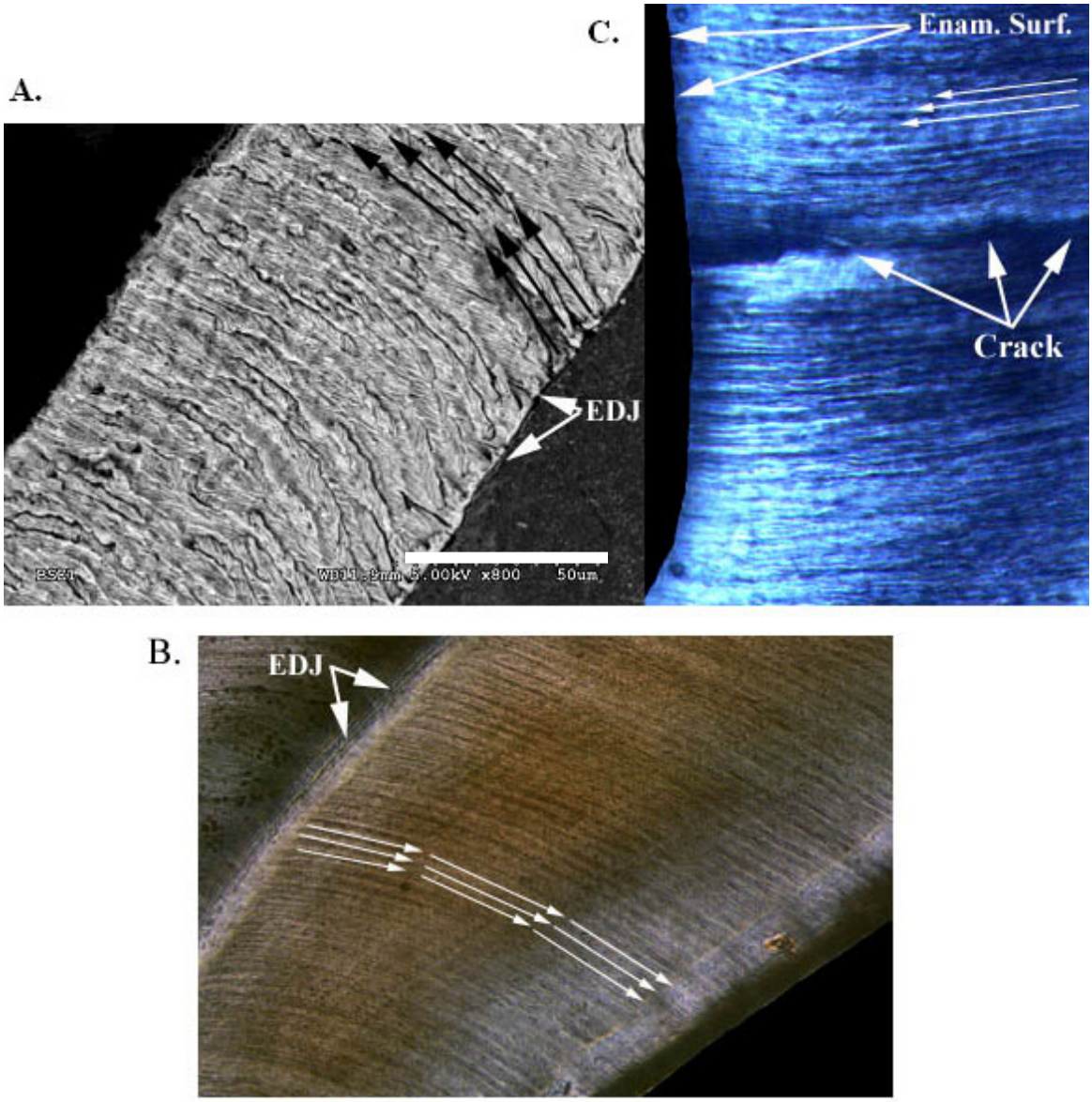


Fig. 2-8. Radial prismatic enamel. **A.** SEM micrograph of a *Saguinus* premolar. Scale bar = 50 microns. **B.** Light micrograph of a *Saimiri sciureus* premolar. **Field width = 134 microns. C.** Light micrograph of crack propagation in radial enamel, where a crack can be seen moving from the tooth surface at the left, all the way to the EDJ (*Saimiri sciureus*). **Field width = 110 microns,** arrows indicate prism paths.

borders between prisms all the way to the EDJ (Rensberger 2000; see Fig. 2-8 and Chapter 4). Thus, in larger mammals and mammals whose diets require the teeth to withstand more loading, other patterns have evolved to help dissipate these loads more effectively (Koenigswald et al. 1987; Maas and Dumont 1999; Rensberger 2000; Popowics et al. 2004; Line and Novaes 2005).

The first alternative is *decussating enamel*, in which prisms are arranged together in groups that have a distinctive orientation significantly different from the orientations of their neighbors, so that successive groups of prisms can be seen to "cross" each other (Tomes 1850; Boyde 1989; Risnes 1998; Maas and Dumont 1999; see Figs. 2-9 and 2-10). In section, this pattern is visible as alternating longitudinal- and cross-sections of prisms in the same cut, or in polarized light as different colored bands (different prism orientations refract the transmitted light differently, see Fig. 2-11 and Chapter 3). Decussation is most extreme in the phenomenon known as *Hunter-Schreger bands*, which are distinct alternating bands of prisms that are often visible in tooth sections even with the naked eye (Noyes and Thomas 1921; Boyde 1989; Risnes 1998; Maas and Dumont 1999). Hunter-Schreger bands are quite common in primates and result from sinusoidal variations in prism direction (Risnes 1998). With decussation, any crack traveling along prism boundaries will be interrupted by a sudden change of prism orientation, and thus be less able to propagate (Pfretzschner 1988; Rensberger 2000; Popowics et al. 2004; see also Chapter 4).

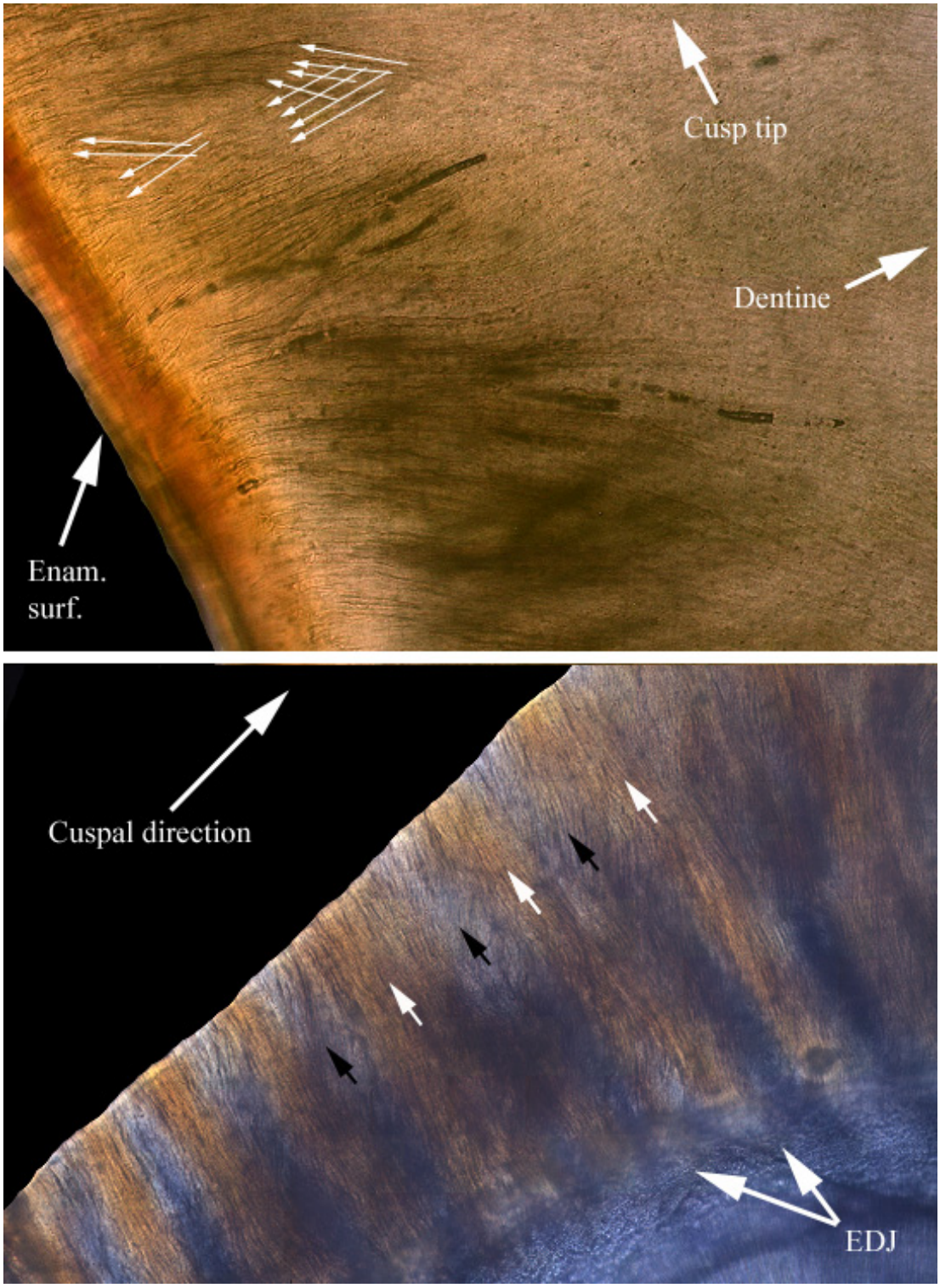


Fig 2-9. A. Decussating prisms in cuspal enamel of a *Cebus* molar. Arrows indicate crossing prism paths. **Field width = 437 microns. B.** Hunter-Schreger bands in a *Cebus* molar, showing an example of color differences between diazones and parazones (alternating color arrows) in polarized light. **Field width = 974 microns.**

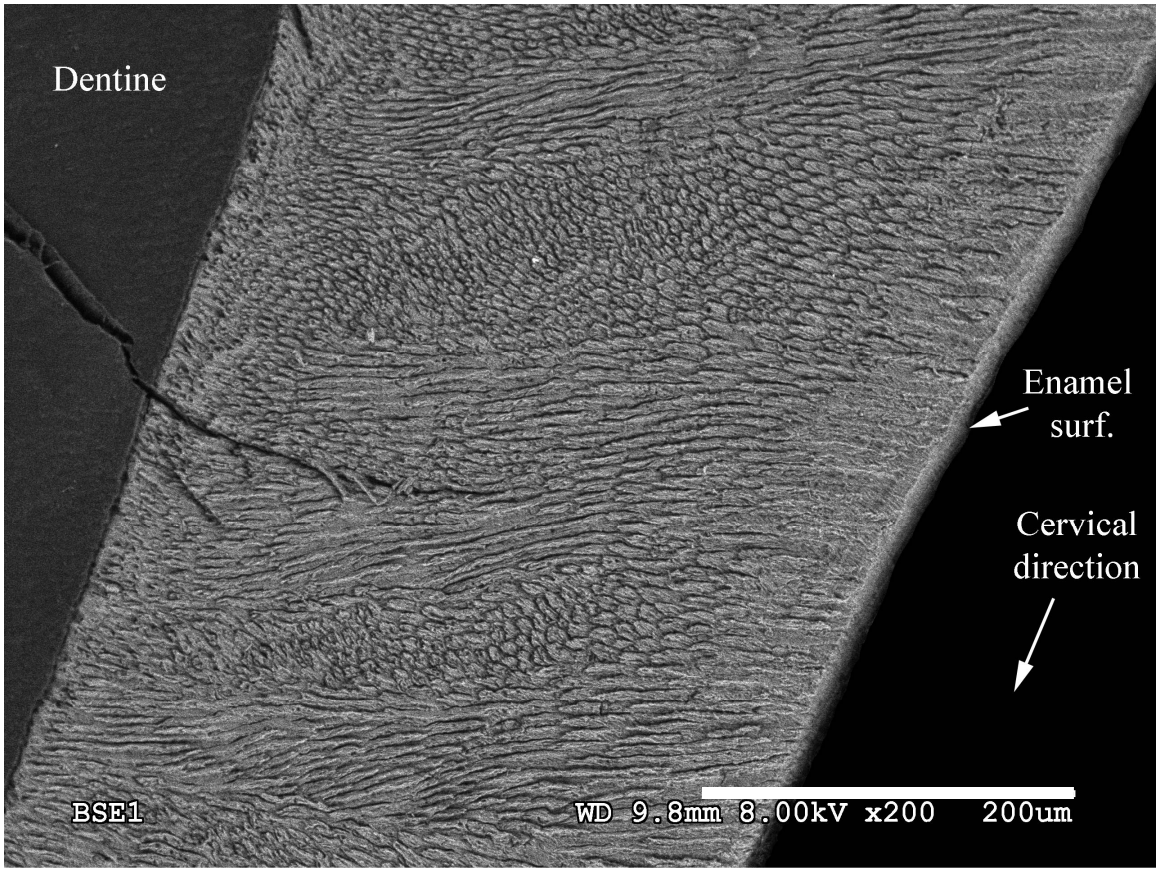


Fig. 2-10. SEM micrograph of Hunter-Schreger bands, revealing details of alternating prism orientation. Note the differing zones in which prisms are longitudinally oriented toward the viewer, versus those where they approach the viewer more directly (more circular in appearance). Also note the crack moving into the enamel from the dentine on the left, whose propagation has been arrested in the enamel. Scale bar = 200 microns.

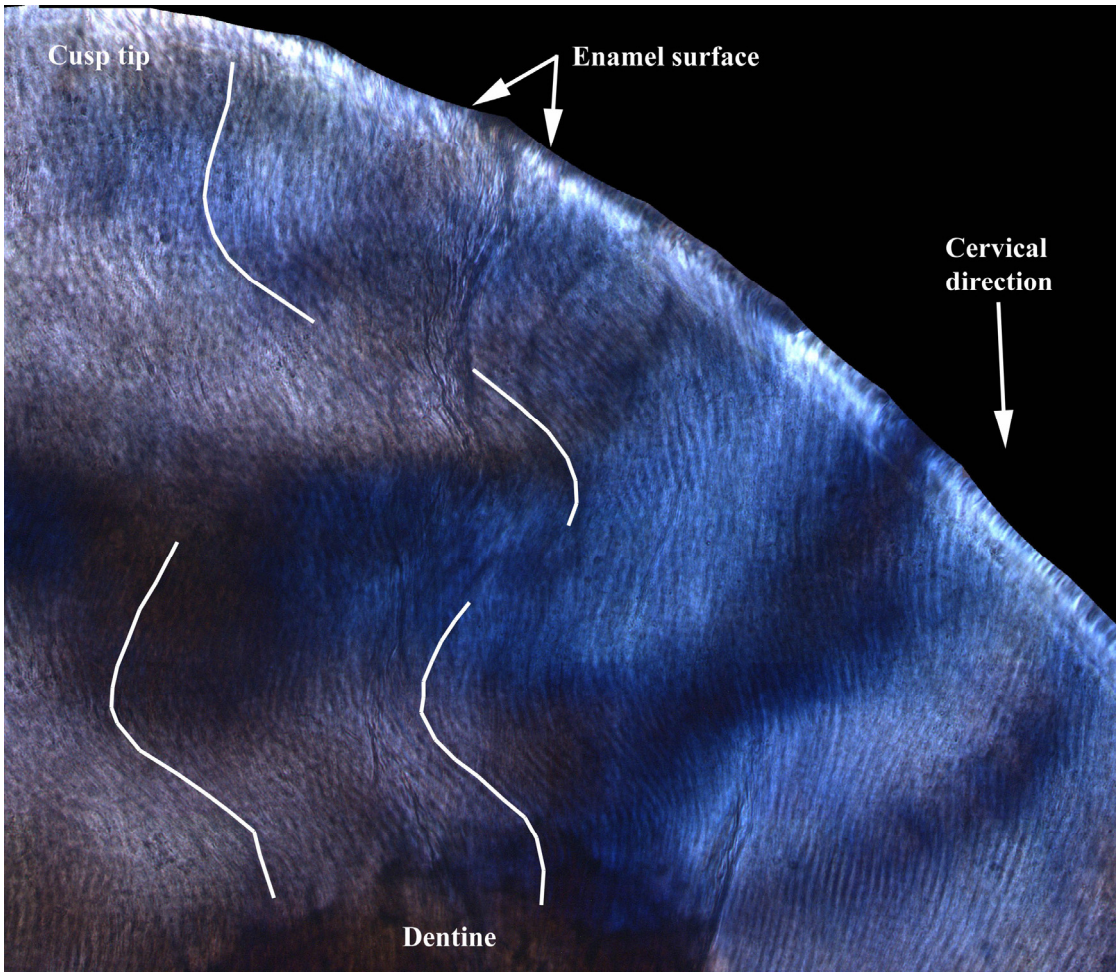


Fig. 2-11. Gnarled enamel in the cusp of a *Cebus apella* canine. Note "waviness" in prism paths, highlighted by white lines. **Field width = 445 microns.**

Gnarled prismatic enamel (Fig. 2-11) forms the third basic prismatic pattern. In this type, the prisms themselves follow complicated, meandering paths (e.g., Noyes and Thomas 1921; Weber 1973; Dean 1998). Most often found in cuspal enamel, gnarled prisms tend to become more radial at the surface of the tooth in cebids (pers. obs.).

Dentine is similar to enamel in many ways, though its structure will be described here only briefly as it is less

important to this particular project; Goldberg and colleagues (1995) provide a more detailed treatment, as do Smith and Sansom (2000). Like enamel, dentine is a compound material composed mostly of mineral apatites, though unlike enamel it has a much higher percentage of organic matrix (around 30%, as opposed to the 2-4% of enamel). Dentine is more similar to bone in that the organic matrix of dentine is composed mostly of collagen, whereas the enamel contains no collagen whatsoever (Scheinmann et al. 1961; Lowenstam and Weiner 1989; Goldberg et al. 1995; Maas and Dumont 1999. The higher organic content of dentine means that it is much softer than enamel, but also more resistant to cracking and brittle fracture (e.g., Noyes and Thomas 1921; Goldberg et al. 1995; Smith and Sansom 2000). Also like bone (and unlike enamel), dentine can be modified somewhat during the lifespan of an individual (e.g., Noyes and Thomas 1921; A.J. Smith 2000; Smith and Sansom 2000). This is because the odontoblasts which secrete dentine remain in place at the border between dentine and pulp throughout the life of an individual, and reach up into the dentine via numerous fibrous processes (Smith and Sansom 2000). In mammals, these odontoblasts initially deposit the dentine in structured tubules which look similar to enamel prisms in longitudinal section, and which extend from the EDJ inward toward the pulp in a radial fashion (e.g., Noyes and Thomas 1921; Boyde 1989; Smith and Sansom 2000; Fig. 2-12). Again like enamel, dentine exhibits two types of incremental lines – von Ebner's and

Andresen's lines – which are laid down by the odontoblasts at a circadian and a taxon-specific periodicity, respectively (e.g., Kawasaki et al. 1973; Dean 1993; Dean 1995).

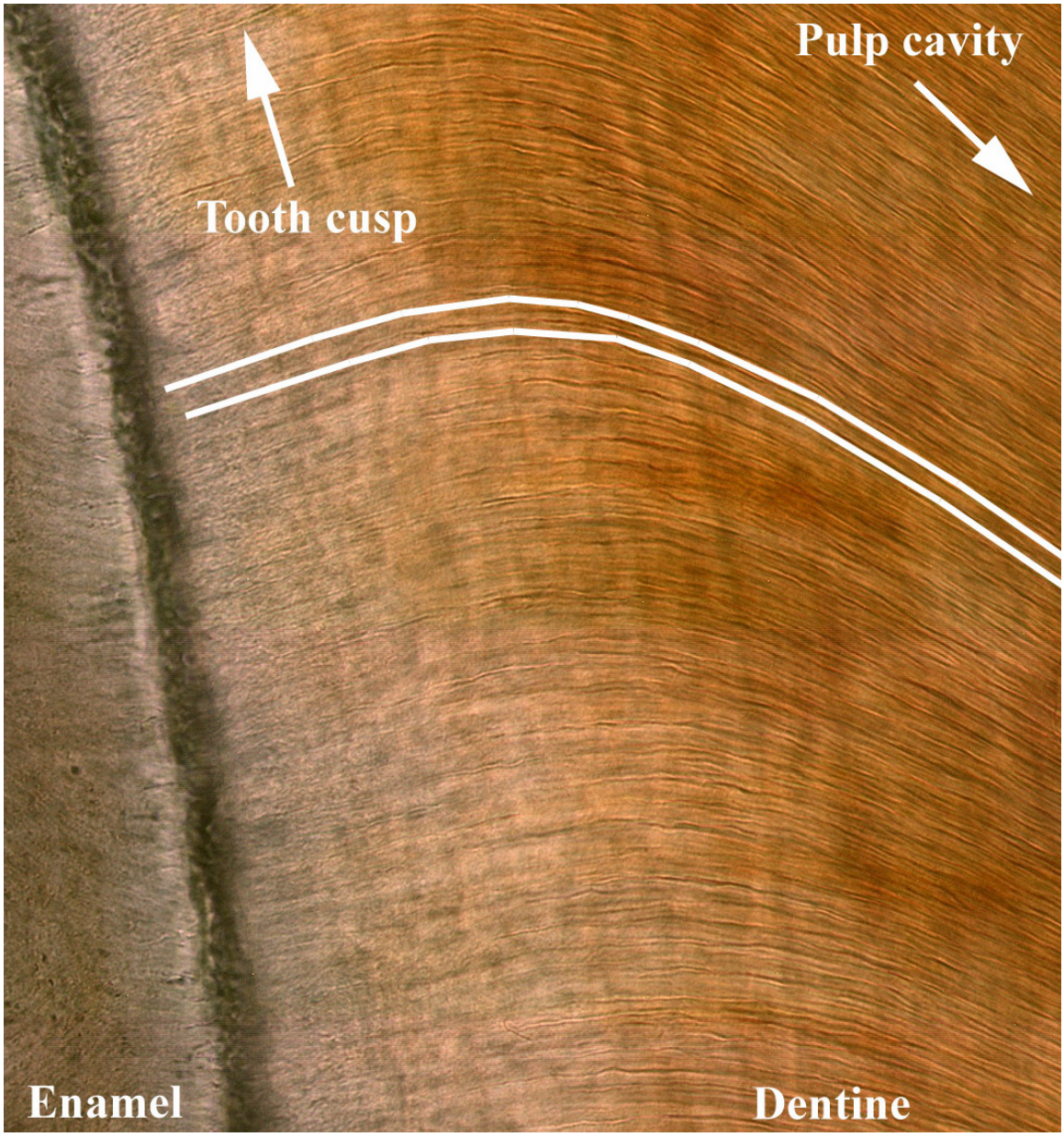


Fig. 2-12. Light micrograph of dentine tubules in a *Cebus capucinus* M1. White lines highlight the paths of two example tubules. Dark vertical line to the left represents the EDJ. **Field width = 324 microns.**

Dental Growth and Mineralization

Embryologically speaking, a tooth is built by a tooth bud which is made from ectoderm-derived epithelium (the eventual enamel organ), and from mesoderm-derived mesenchyme (the eventual dental papilla). Both of these tissues are in intimate proximity in the developing mandible and maxilla (Maas and Bei 1997; Sharpe 2000; Smith 2003). Both proper dental initiation and final dental formation are dependent upon a complex set of reciprocal interactions ("inter-inductions") between these two tissues. Ultimately, enamel is developmentally derived from epithelium, while dentine, pulp, and cementum are derived from mesenchyme (Hertwig 1892; Stohr and Lewis 1906; Noyes and Thomas 1921; Ferguson et al. 2000); however, without its partner present, neither oral epithelium nor mesenchyme cells can progress to form their part of a tooth bud or their proper tooth-secreting cells (Maas and Bei 1997). In this way, teeth are developmentally similar to a number of structures associated with the integument, such as hair follicles and mammary glands in mammals, and denticles in sharks (Smith and Coates 2000). In fact teratomas (tumors) in mammalian ovaries can often be found with morphologically "normal" teeth and hairs within them, as these tumors are composed of epithelium- and mesenchyme-derived tissues together (Sharpe 2000).

Where the epithelium and mesenchyme come together in the developing oral cavity, an epithelial tissue thickening, or

dental lamina, forms (e.g., Maas and Bei 1997). Usually this lamina is limited to the alveolar portions of the mandible/ maxilla, but this is not always the case. In some bony fish and amphibians, odontogenic tissues and teeth can also arise on the roof of the mouth, the pharynx, and the tongue (Slavkin and Diekwisch 1996). Again, without both epithelium and mesenchyme inducting each other, no tooth will form. The epithelium triggers the initial formation of the dental papilla, and the mesenchyme in turn inducts the epithelium to differentiate and fold for proper enamel secretion (Thesleff and Sharpe 1997).

The cells in the dental lamina and the mesenchyme grow into a mature enamel organ and dental papilla, respectively, through *bud*, *cap*, and *bell* stages before cytodifferentiation and hard tissue secretion occur (Diekwisch et al. 1995; Slavkin and Diekwisch 1996; Maas and Bei 1997; Smith 1998). After the dental lamina stage is reached, the cells of the dental epithelium continue to thicken and invade the space of the mesenchyme, forming a sort of extended pocket known as the bud. This bud proceeds to invaginate into a slightly concave structure, the cap, and as the invagination continues to deepen, reaches the bell stage, where the final folding and shape of the mature crown becomes evident (Fig. 2-13).

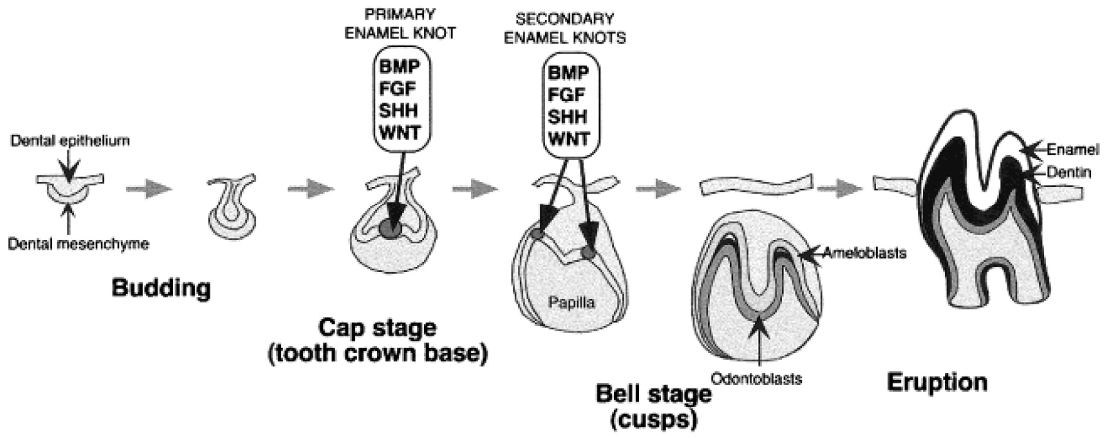


Fig. 2-13. The stages of tooth crown formation. From left to right: 1) lamina stage: dental epithelium and mesenchyme combine; 2) bud stage: dental epithelium invades mesenchyme to form tooth bud; 3) cap stage: primary enamel knot forms in epithelium and induces folding by controlled proliferation of epithelium, through expression of developmental genes; 4) bell stage: primary enamel knot has disappeared, replaced by secondary enamel knots which express the same genes to stimulate further proliferation and folding 5) late bell stage: cytodifferentiation and secretion: ameloblasts and odontoblasts form and begin laying down their mineral products; 6) mineral maturation and tooth eruption. Note the dark gray layer of odontoblasts remains extant in the adult tooth. BMP, FGF, SHH, and WNT refer to gene products which are known to control enamel organ folding and cusp formation (see text below). From Jernvall and Jung (2000).

During the cap stage of dental formation, a densely packed region of non-proliferating cells appears in the epithelium, the *primary enamel knot* (PEK). The PEK was first identified in histological section more than a hundred years ago, but its vital role in programming the shape of the final tooth was not fully appreciated until recent developmental genetics studies of Jernvall, Thesleff and colleagues (Jernvall and Thesleff 2000, Thesleff et al. 2001). The PEK is an inductive region which causes cells in the tooth bud to proliferate in such a manner

that they fold the bud into a shape that resembles a tooth crown. In teeth that have only one cusp this first folding is sufficient to determine the final form of the tooth.

The PEK is a transient structure lasting only a few days, being most likely eliminated by rapid apoptosis (Tucker and Sharpe 1999; Jernvall and Thesleff 2000). However, in multicusped teeth, when the PEK disappears it is followed by the appearance of *secondary enamel knots* (SEK's) at specific points in the tooth bud. These cause secondary folds that will become future cusps (Jernvall et al. 1994; Jernvall 2000; Jernvall and Jung 2000; Jernvall and Thesleff 2000; see Fig. 2-13 and 14). These SEK's do not appear in locations that are determined by any specific gene, but develop instead according to a patterning cascade that follows the expression and diffusion of inductive and inhibitory proteins such as *Shh*, *Fgf*'s and *Bmp*'s, which are generally important as controlling signals in developing mammal teeth. This cascade also seems to affect the apoptotic disappearance of the SEK's, as it does for the PEK (Maas and Bei 1997; Jernvall 2000; Jernvall and Thesleff 2000; Thesleff et al. 2001).

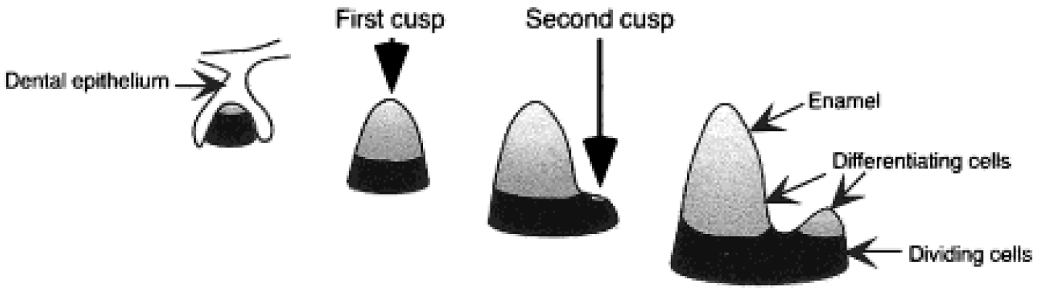


Fig. 2-14. Diagram detailing cusp formation in a multi-cusped tooth. Dental epithelium is assumed to be present over the three drawings to the right, as it is on the 1st drawing; the appearance and growth of the second cusp here is within the folding of that epithelium and the dental papilla below it, so that the "cusps" in the figure actually represent the folding that will produce the future dentine horns; the stage of formation at this point is prior to actual ameloblast differentiation and enamel secretion. From Jernvall and Jung (2000).

During the cap stage, while epithelium and mesenchyme cells proliferate, inner enamel epithelial cells differentiate somewhat from the outer cells and become more columnar, while their nuclei move to the end of the cell facing away from the mesenchyme (Moss-Salentijn et al. 1997; Thesleff et al. 2001). By the point of the early bell stage, the epithelial cells of the enamel organ have differentiated into four distinct layers: outer enamel epithelium, stellate reticulum, stratum intermedium, and inner enamel epithelium (Hillson 1996; Ferguson et al. 2000; see Fig. 2-15). Berkovitz and Moxham (1981) have suggested that the former two layers may serve a supportive and nutritive role, respectively, for the enamel-forming cells.

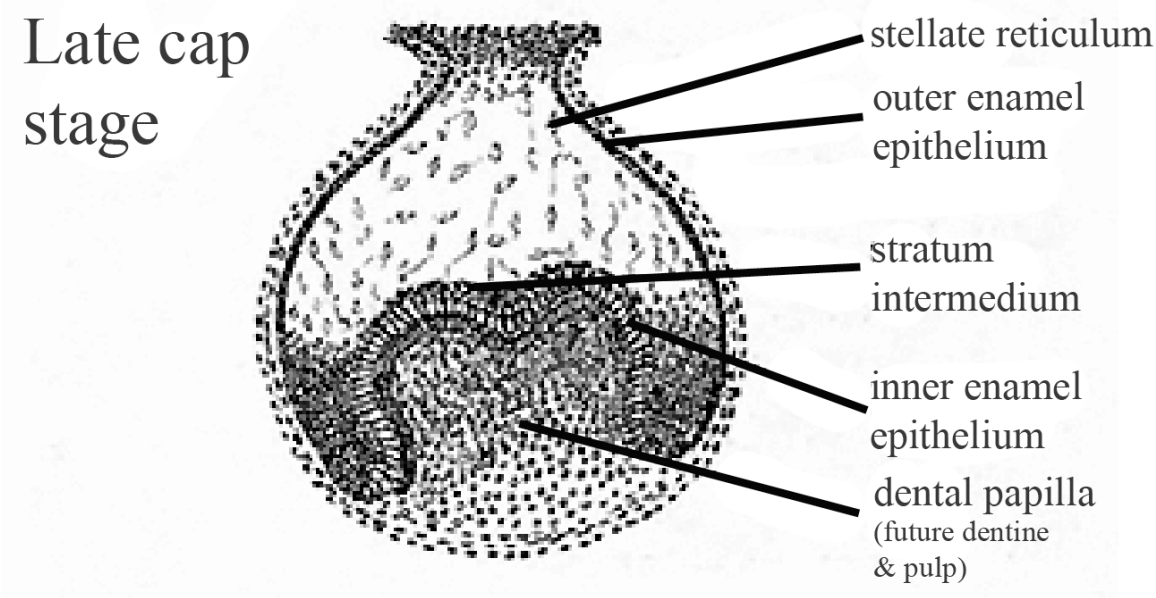


Fig. 2-15. A diagram of a mature tooth bud within its crypt. All four layers of the epithelium-derived enamel organ can be seen, including the mesenchyme-derived dental papilla which will eventually become the dentine and pulp cavity of the tooth. Modified from Ferguson et al.(2000).

When the dental papilla has folded into its proper shape, the outer layer of mesenchyme-derived dental papilla cells mature into odontoblasts and begin secreting dentine (Furguson et al. 2000). Soon afterward, when a base of dentine has formed, the columnar cells of the inner enamel epithelium finally differentiate into a layer of mature ameloblasts, which begin secreting their own mineral product, enamel. Both sets of secretory cells proceed away from the EDJ, pushed forward by their secretory action, lined up together to form a single formation front for each tissue (enamel and dentine formation fronts, respectively; Ferguson et al. 2000). Remnants of these fronts can be seen in striae of Retzius and Andresen lines, which

permanently record the position of cells when their secretory activity is disturbed by the metabolic perturbations that cause these increments (e.g., Noyes and Thomas 1921; Boyde 1963, 1989; Dean 1995; Risnes 1998). All cells in the formation front must act together in response to a disturbance in order to preserve a sign of the formation front in the anatomy of the tooth (e.g., Noyes and Thomas 1921; Boyde 1989; Ferguson et al. 2000). Odontoblasts march inward to the future pulp cavity and proliferate downward toward the root, whereas ameloblasts march outward to the tooth surface and proliferate downward toward the future cervix of the tooth (Noyes and Thomas 1921; Ferguson et al. 2000). Thus the enamel formation front, or EFF (and hence the striae of Retzius), continually advances outward and downward (Schwartz and Dean 2001; Schwartz et al. 2005b; Fig. 2-16); the outward progression of ameloblasts is known as the enamel secretion rate (or daily enamel secretion rate, DESR), whereas the downward addition of active ameloblast is known as enamel extension rate (Ramirez-Rozzi 2002; Fig. 2-17).

Using enamel increments, we can track the progress of the EFF all the way from the dentine horn underlying the cusp to the tooth cervix (e.g., Schwartz and Dean 2001). DESR can be quantified by measuring the breadths of daily cross-striations, whereas enamel extension rate can be quantified using striae of Retzius (Ramirez-Rozzi 2002; Lacruz et al. 2008). In this case, the periodicity of striae of Retzius is less important than their geometry, because striae of Retzius represent the position

of all active ameloblasts along the EFF during the time at which individual striations are formed (e.g., Noyes and Thomas 1921). A narrower angle between EFFs and the EDJ signifies a relatively longer EFF, a relatively higher number of active ameloblasts, and in turn indicates that the enamel extension rate is faster. Therefore, by measuring the angle between striae of Retzius (i.e., successive EFFs) and the EDJ, we can compare enamel extension rates in different teeth, individuals, and taxa (Ramirez-Rozzi 2002; Lacruz et al. 2008). See Chapters 3 and 4 for further discussion.

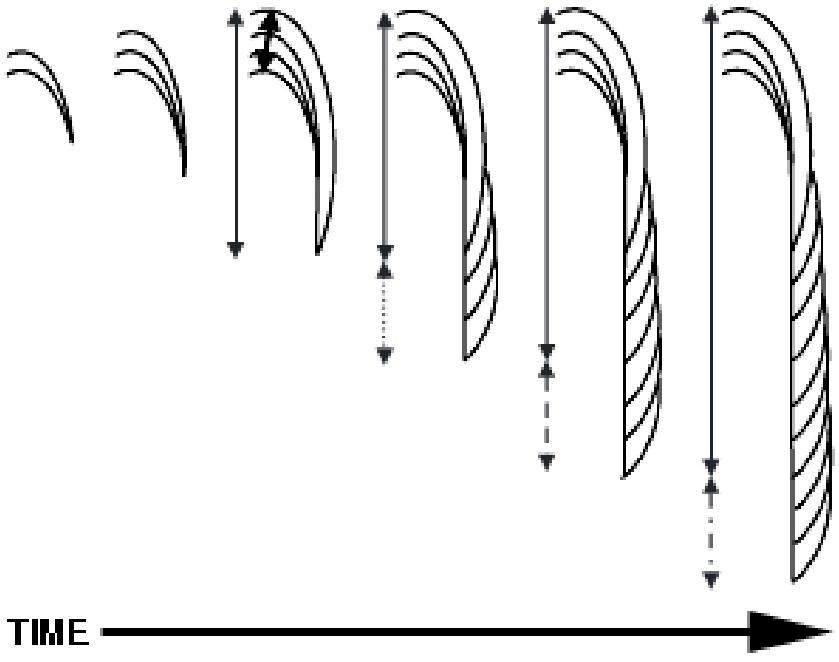


Fig. 2-16. Diagram of an idealized tooth crown's enamel growth, proceeding from the cusp (top) to the cervix (bottom). Taking advantage of the increments that ameloblasts deposit along their way, we can track this growth in a very detailed manner. Modified from Schwartz et al. (2005b).

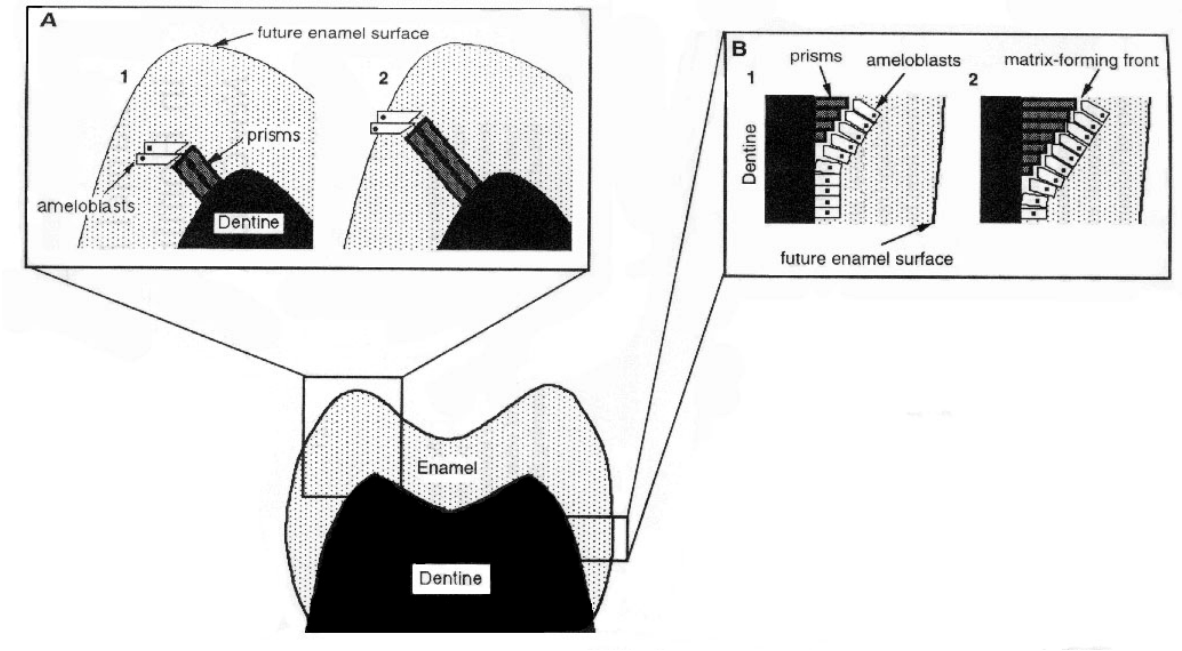


Fig. 2-17. Two measurements of enamel growth: **A.** Enamel secretion rate. **B.** Enamel extension rate. The narrower the angle between the enamel formation front and the EDJ, the more ameloblasts are secreting at once and hence the quicker the crown will form. Enamel secretion rate can be quantified using cross-striations, whereas enamel extension can be quantified using the angle between striae of Retzius and the EDJ. From Ramirez-Rozzi (2002).

Enamel secretion and maturation is a process that has been gradually revealed over the last few decades, through work that began in the 1950's and 1960's and eventually flourished as a result of advances in electron microscopy. Although Hunter (1771) seems to have been the first researcher to report that enamel had a soft, immature form prior to its final hard, mature form, the notion that enamel formation has two separate stages, secretion and maturation, is mostly based on the histological and histochemical examinations of the 1950's and 1960's (e.g., Marsland 1951, 1952; Symons 1955, 1956; Fearnhead and Watson

1960; Avery et al. 1961; Reith 1961; Rönnholm 1961, 1962a, 1962b; Boyde 1964, 1965).

As explained by Slavkin and Diekwisch (1996), the current consensus is that this two-step process of enamel formation begins in ameloblasts, with the transcription and translation of genes coding for the various enamel matrix proteins such as amelogenin, enamelin, ameloblastin, and tuftelin (unlike dentine matrix, which is mostly collagen-based; see Goldberg et al. 1995; Slavkin and Diekwisch 1996; Fincham et al. 2000). When secreted by the ameloblasts, these proteins lay down the framework for the growth of the hydroxyapatite crystals that will eventually form some 96%-98% of the final, mature enamel. To begin with, however, these proteins form the primary enamel constituent. Mineral components are the minor part of early enamel matrix makeup (Diekwisch et al. 1995; Goldberg et al. 1995; Wöltgens et al. 1995). These initial calcium hydroxyapatite crystallites generally form with an orientation that is perpendicular to that of the secretory surface of the ameloblast (in mammals, most often a Tomes' process). These crystallites may be initially seeded by apatite within the dentine, though enamel matrix proteins have also been implicated in this role (Simmons 1979; Diekwisch et al. 1995; Goldberg et al. 1995; Robinson et al. 1995).

This secretion phase of amelogenesis is essentially a "mapping out" of the overall final morphology of the enamel, in which the crystallite orientations, prism patterns, and thickness

of the final enamel are laid out for final mineralization using a protein scaffold, with the organic enamel matrix also guiding crystallite geometry (Smith 1998; Fincham et al. 2000). Specifically, Fincham and colleagues (2000) recently advanced a model whereby enamel crystallites form between and are aligned by nanospheres of amelogenin proteins, which inhibit lateral crystallite growth as long as they are present (Fig. 2-18).

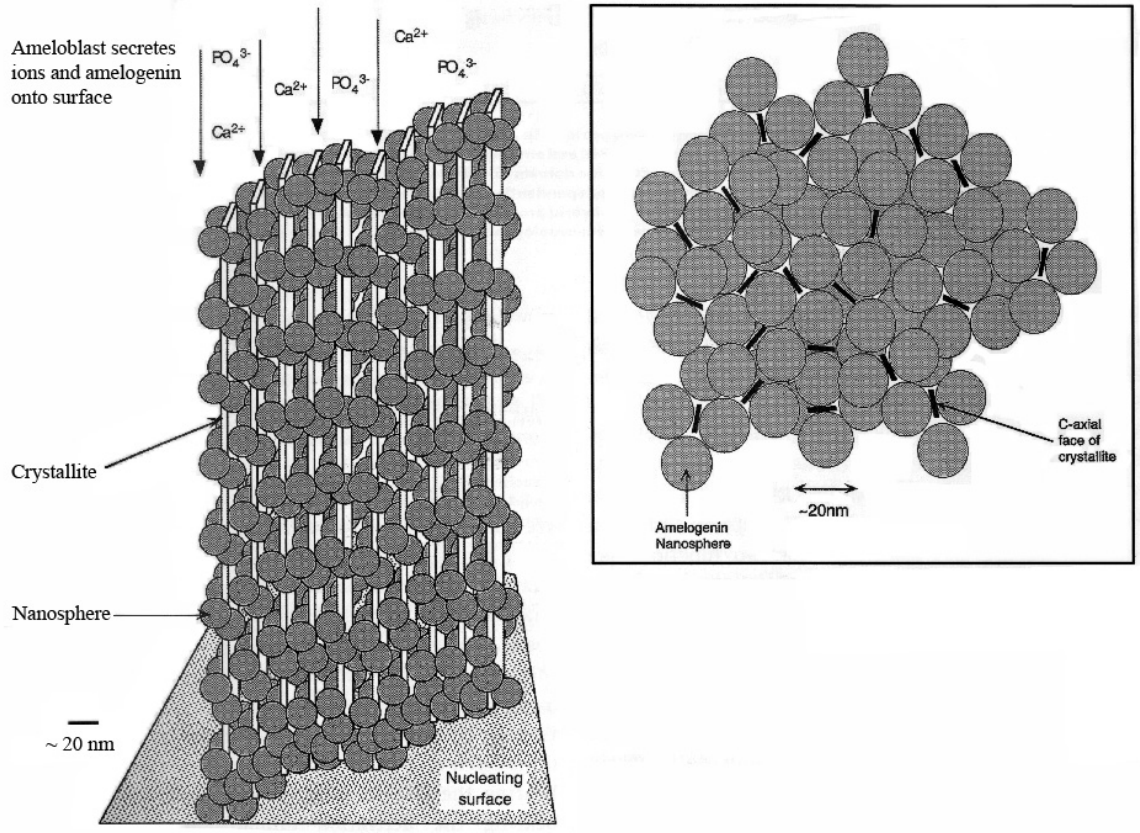


Fig. 2-18. Model of amelogenin and calcium hydroxyapatite crystallite interactions in the secretion stage of enamel formation. Gray circles represent amelogenin nanospheres, whose geometry determines the alignment of the mineral crystals. From Fincham et al. (2000).

Once ameloblasts finish secreting their matrix (i.e., once they have reached the surface of the tooth and have resorbed their Tomes' processes, if present), the next phase of enamel formation begins: maturation. Post-secretory ameloblasts increase their mineral charge and cycle the overall pH balance of the enamel, while most of the enamel matrix proteins are destroyed via enzymatic action (Goldberg et al. 1995; Slavkin and Diekwisch 1995, C.E. Smith 1998, Fincham et al. 2000). Although matrix-degrading enzymes function throughout amelogenesis, their action is drastically increased in the maturation phase (Smith 1998). Thus, enamel crystallites increase in length and width and most likely multiply (Palamara et al. 1980), steadily increasing in mass and density (in terms of the number of crystallites per unit volume of enamel) until, in the mature enamel, they comprise the overwhelming majority of the final material. Because enamel is not an impermeable substance, mineralization and maturation continue throughout the life of the individual even after the ameloblasts are shed, with new ions such as fluoride joining the hydroxyapatite matrix while organic content continues to decline (Glimcher et al. 1977).

In mammals generally, ameloblasts begin their secretion at the EDJ by depositing a short layer of aprismatic enamel, because they begin with more or less "flat" secretory faces. This is the primitive amniote ameloblast morphology, as inferred from the evolution of enamel crystallite patterns (Sander 2000; Line and Novaes 2005; Wood and Rougier 2005). However, soon afterward

mammalian ameloblasts develop extensions known as *Tomes' processes* (Figs. 2-19 and 2-20). As mentioned above, enamel crystallites tend to run perpendicular to the cellular face which secreted them (though see Risnes 1999 for a counterexample), so it is the morphology of the Tomes' process which allows for the different crystallite orientations that are responsible for the appearance of enamel prisms. Therefore, it is the evolution of modern Tomes' processes that is responsible for much of the structure of modern mammalian tooth enamel (e.g., Sander 2000; Line and Novaes 2005; Wood and Rougier 2005).

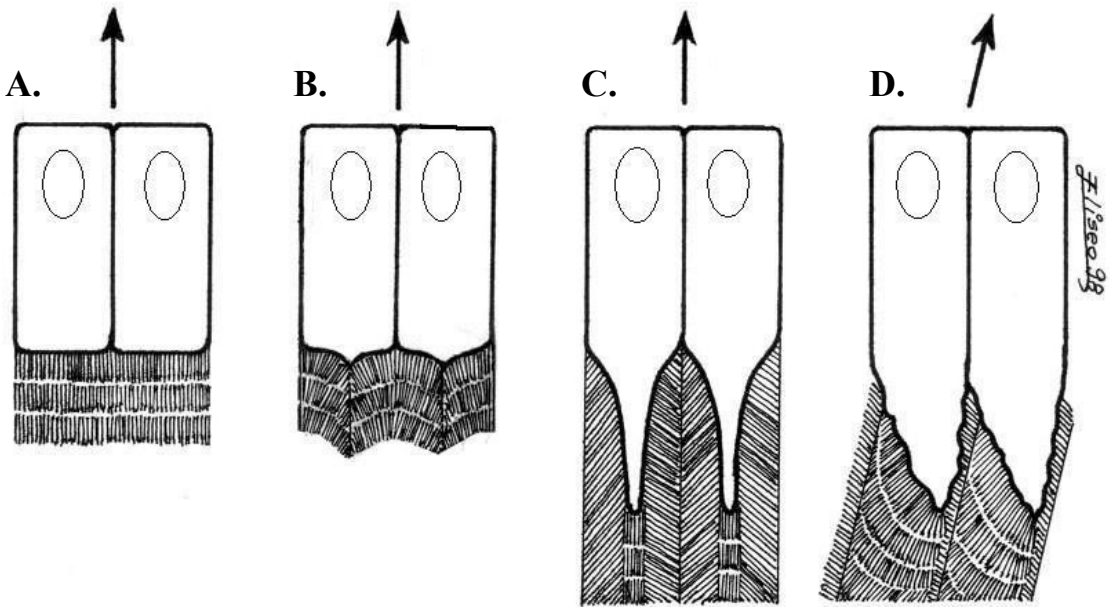


Fig. 2-19. Enamel crystallite orientation in relation to ameloblast morphology. **A.** Flat secretory faces, yielding aprismatic enamel (primitive amniote condition, still found in some regions of mammalian teeth). **B.** Slightly modified secretory face, creating a sort of columnar enamel. **C and D.** Ameloblasts with Tomes' processes, secreting distinctive enamel prisms which are identifiable by the sharp demarcations in crystallite orientation. From Line and Novaes (2005).

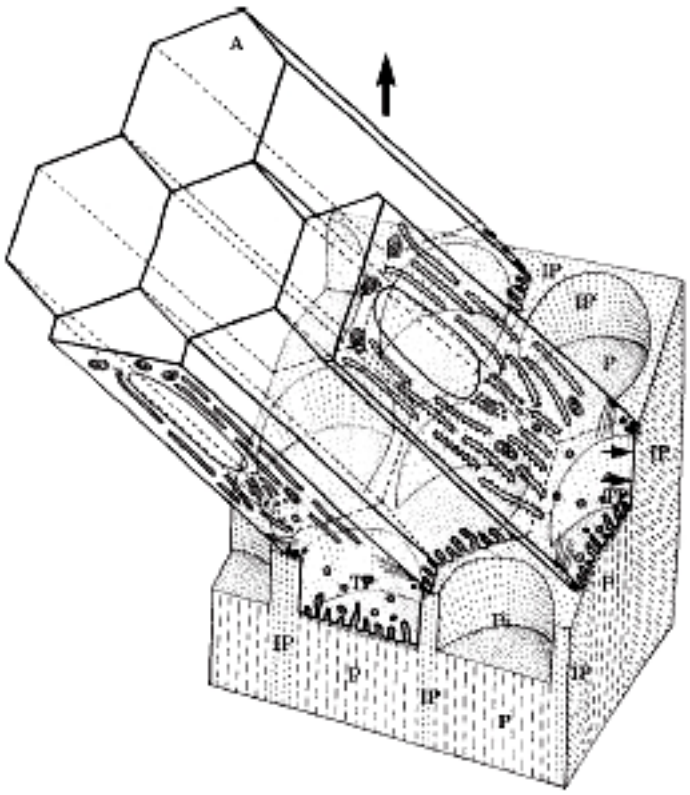


Fig. 2-20. 3-D model showing relationship between ameloblast morphology, packing, and enamel prism morphology. Hexagonal structures are ameloblasts, some of which have been sectioned longitudinally to show interior structure. Hash marks represent crystallite orientations; "P" stands for prismatic enamel, "IP" stands for interprismatic enamel (or prism tail). The semi-cylindrical depressions that can be seen in the developing face are filled by Tomes' processes. From Risnes (1998).

Once odontoblasts cease their primary secretory activity, they take up residence at the dentine-pulp boundary (Noyes and Thomas 1921). Meanwhile, ameloblasts form a protective layer, or capsule, around the maturing enamel once they finish their secretory phase. When the tooth begins to erupt through the gingiva, they are sloughed off to leave the enamel exposed for use (e.g., Noyes and Thomas 1921; Boyde 1964). Without ameloblasts, therefore, no new enamel can be formed and the crown

cannot be modified. In organisms with ever-growing crowns, such as rodents and some ungulates, an ameloblast front remains within the periodontal tissues to produce enamel continuously as the tooth progressively erupts throughout its lifespan (e.g., Smith and Warshawsky 1975).

Because the mammalian lifestyle generally requires that food be processed to a high degree by teeth, and because proper dental morphology and occlusion are thus highly important to acquiring energy and nutrients, the genetic programs that govern these developmental processes tend to be relatively constrained and controlled (e.g., Jernvall 2000; Jernvall and Jung 2000; Jernvall and Thesleff 2000; Thesleff et al. 2001). As with most developmental systems, however, this must be tempered with some degree of evolvability, and Jernvall (2000) has shown that mammal teeth seem to have come to a good compromise between these two needs. According to Jernvall's model, the largest cusps, being arguably the most important to an overall mechanical design, are the least evolvable, and their design and expression will tend to affect the formation of smaller cusps. These cusps, then, can undergo size increase or decrease as necessary. The larger they become, the earlier relative to other cusps they will begin to appear, and the more they will tend to dominate the positioning of other cusps around them through the developmental cascade of inducting and inhibiting gene products. The smaller they become, the less this will be true. Likewise, a small shift in the position of one early-forming and therefore large cusp will shift

patterns of gene expression, and therefore alter the overall relative positions of the other cusps. Shape, meanwhile, seems to be controlled across the board by genes which affect the folding of the enamel organ across the tooth (Jernvall and Jung 2000).

The early stages of formation in teeth seem to be under the tightest canalization (Ferguson et al. 2000; Miletich and Sharpe 2003). When the oral epithelium and mesenchyme (which is derived from neural crest mesenchyme) come together in the dental lamina, the oral epithelium expresses a combination of the activator *BmP4* and inhibitor *Fgf8* at varying amounts across the potential tooth germ, which encourage and suppress expression of *Msx-1* in varying amounts across corresponding regions of the mesenchyme (Ferguson et al. 2000; Miletich and Sharpe 2003). This seems to be a mechanism for determining where, exactly, the tooth buds will form, and seems to be the initial induction mechanism in the reciprocal epithelium-mesenchyme relationship described above. *Wnt* proteins and Sonic hedgehog (*Shh*) also seem to act as early epithelial inducers (Ferguson et al. 2000; Miletich and Sharpe 2003). At the bud stage, the mesenchyme takes its turn as the inducer, expressing a combination of *Bmp* and *Fgf* along with signals such as *activin*β*A* and *Pax9*, which take their effect in the epithelium to drive formation of the bud (see Miletich and Sharpe 2003 for a more detailed description of mesenchyme gene expression).

The formation of the PEK also seems to be part of this tightly canalized developmental process, as everything up to this point is vital to the creation of a basic, functional tooth. Any change in the epigenetics could potentially cause an across-the-board breakdown of the odontogenic system (Ferguson et al. 2000; Jernvall 2000; Jernvall and Jung 2000; Jernvall and Thesleff 2000; Thesleff et al. 2001; Miletich and Sharpe 2003). But as development proceeds past the PEK stage we would hypothesize that the system must be more flexible (though not too flexible) to allow for fine-tuning of the final cusp morphology in the tooth (Jernvall 2000; Jernvall and Jung 2000; Jernvall and Thesleff 2000; Thesleff et al. 2001). This fine-tuning or adjustment allows the completed organ to function according to its own specific dietary demands (both across taxa and across different types of teeth in the same jaws), and also allows the crown morphology to evolve along with changes in those demands. As we have seen, this seems to be the precisely the case. The patterning cascade that governs SEK timing and positioning is well-controlled so that single-gene mutations (in a one-gene-per-character sense) will not be able to "interrupt" any part of the crown's layout to a great degree. That is, random cusp formation is less likely to obstruct functional occlusion, because any mutation that affects the layout will operate across the dentition (Jernvall 2000; Jernvall and Jung 2000). Thus the need for mechanical conservativism is met. But the system also meets the need for evolvability, as this cascade is flexible enough to

allow for new cusps to form, for cusps to grow larger in a phyletic sense, and for overall tooth morphologies to shift to reflect changing specializations in such feeding types as folivory, carnivory, etc. (Jernvall 2000; Jernvall and Jung 2000).

History of Research in Primate Enamel

Since the 1980's, primates have become the test bed for studies in enamel microstructure and odontochronology as they relate to life history, ecology, and adaptation for mammals and vertebrates. The earliest extensive work on enamel microstructure occurred with human specimens, excepting Leeuwenhoek's (e.g., 1665-1678) early work on elephant teeth (e.g., Havers 1691; Hunter 1771; see also Leeuwenhoek 1800). Though Sir John Tomes performed extensive studies of dental microanatomy in marsupials and rodents in the mid-1800's (Tomes 1849, 1850), which was followed up by others such as Mummery (1914), by the 1930's much of the interest in such studies had apparently waned. Perhaps this was due to perceptions of the limited effectiveness of such studies in generating good phylogenetic or adaptive information; where one researcher may have attempted to hypothesize a good phylogenetic character within dental microanatomy, the next researcher would find the same character in distantly related taxa such as marsupials, insectivores, and primates (e.g., Tomes 1849; Tomes 1906; Mummery

1914; Carter 1922). Regardless of the reasons, few studies in dental microanatomy during the middle of the twentieth century seem to have been focused on evolutionary questions.

However, the usefulness of dental increments and the biomechanical importance of microanatomy were rediscovered by primatologists toward the end of the century, and dental histology was again applied to broad comparative analyses for primates. Research into other animal taxa has followed this lead and has greatly benefited from the methodologies, theories, and observations that have resulted from several decades of close primate study.

Carter (1922) serves as the earliest major example of dental microstructural analyses for primates. Sampling from a wide variety of Eocene and extant taxa, he made ground sections and analyzed them microscopically as a first-stage effort in a grand survey of the mammals. For the most part, his study was performed in a similar manner to those of John and Charles Tomes (1849, 1850; 1906), the father and son who did so much for the description of enamel structure in mammals. Indeed, the Carter study is directly intended to operate in a comparative context with those studies, searching for salient homologies that could be used to group taxa based on their dental microanatomy. Specifically, he focused on the extension of dentine tubules into the enamel proper, and described the general character of the prisms as had the studies mentioned above. Carter seems to have been especially interested in the then-contested relationships of

Tarsius (he mentions Pocock, who established the Haplorhini, in his acknowledgements for donating a *Tarsius* mandible), stating that its microanatomy is almost indistinguishable from *Galago.* This serves as an emphasis on the notion that enamel microstructure can and does modify along a fairly flexible set of guidelines to meet its functional demands (e.g., Lucas et al. 2008b), and that any perceived homologies in the enamel matrix must be treated extremely carefully.

Past Carter, however, comparative primate dental microanatomy virtually disappears for some sixty years. This is not to say that primatologists lost all interest in dental growth, though indeed such interest seems to have declined. Eruption schedules were still seen as important for aging animals and specimens, and Adolphe Schultz's landmark 1935 study made a careful analysis of primate eruption schedules and dental senescence for a wide variety of taxa, as well as advancing some implications of tooth eruption sequence for life history study.

However, since the 1980's, with a steadily emerging new paradigm on the importance of life history and ecology to the study of primates (e.g., Shea 1983, 1985, 1986; Bromage and Dean 1985; Harvey and Clutton-Brock 198), dental development began to be viewed as a specific tool to analyze evolutionary changes in growth trajectory. For example, radiographic imaging of primate tooth development and eruption has seen increased use as a means to access dental life history information (e.g., Luckett and Maier 1982; Conroy and Vannier 1991; Simpson et al. 1991; Godfrey

et al. 2002). Such analyses as these are especially useful where sections cannot be made, as in the case of rare fossil material. These studies have occurred alongside gross dental eruption studies unaided by visualization techniques, which expanded upon earlier eruption work to correlate timing of dental growth with life history variables and track evolutionary change (e.g., Smith 1989, 1991; Smith et al. 1994; Harvati 2000; Godfrey et al. 2001; Henderson 2007).

However, radiographic and gross eruption studies are usually incapable of establishing absolute chronologies, due to a lack of precise age information about specimens being studied. This is especially limiting when dealing with fossils (Mann 1975). Therefore, such studies need to be paired with histological analysis, which came into maturity alongside both radiographic and gross eruption analysis.

The reintegration of dental microanatomy (especially the study of dental growth increments) with zoology and more specifically primatology was in large part initiated by the work of Alan Boyde, beginning in the 1960's. Seeing first hand the usefulness of increments as periodic structures, as already established by both descriptive and experimental studies, Boyde applied their analysis to the archaeological record – and hence to anthropology – for the first time in 1963, in a study of a human child from the site at Dinas Powys. Through the 1970's Boyde continued to focus most of his attention on studying enamel as a tissue (e.g., Boyde 1979). His work, however, became more

widely known in the anthropological community when he joined Lawrence Martin to describe hominoid enamel structure in 1982. Thus, not only did Boyde provide (or expand upon) much of the theoretical and methodological foundation for the study of dental increments, he also performed some of the first forays into primate enamel microanatomy since Carter's work some sixty years before. The studies of Gantt and colleagues (1977) and Vrba and Grine (1978) also serve as important early landmark analyses of prism structure in hominoids, perhaps inspiring the 1982 work of Boyde and Martin – and others – that began to follow. Gantt (1980) also examined prism structure in platyrrhines as it related to their evolutionary origins, concluding that platyrrhine and catarrhine prism structure indicated a common origin for the two groups, to the exclusion of adapid and omomyid primates.

These papers focus primarily upon *schmeltzmuster* and prism packing as opposed to increments, as does Martin's 1983 dissertation work on extant and extinct hominoid enamel. Bromage and Dean (1985) took the next landmark step in their comparison of australopith perikymata breadths to those of modern humans and apes, for the purpose of determining whether the fossil hominins had a more human- or ape-like growth schedule. This represented a first attempt to study the evolution of life histories in a fossil mammal in the context of extant relatives, and the first example of microstructural odontochronology in a nonhuman primate. It was soon followed up by further studies such as Beynon and

Dean (1987) and Beynon and Wood (1987), which examined crown formation times in detail for these organisms. The Bromage and Dean (1985) study was also followed up by radiographic and gross studies such as Conroy and Vannier (1991) and Smith (1991).

The research of Boyde, Martin, Bromage, Dean, and Beynon, then, set the stage for a boom of microstructural odontochronology in the 1990's and 2000's. In fact, much of this early research occurred within Alan Bodye's laboratory, which fostered a productive research environment involving all of these researchers with the exception of Beynon, who worked in a nearby facility (Bromage, pers. comm.). In order to answer lingering doubts on the validity of enamel increments as periodic structures, Bromage (1991) provided additional experimental evidence that cross-striations do indeed have a circadian rhythm. Other authors such as Fitzgerald (1998) and Shellis (1998) generated and compiled even more evidence in favor of the periodic hypothesis, and it is now considered well-proven (see Chapter 3 for further discussion). Beynon, Dean, Reid, Dirks, Ramirez Rozzi, Schwartz, and colleagues documented the microanatomy of hominoid and human enamel in detail during the 1990's (e.g. Beynon et al. 1991, 1998; Dean and Beynon 1991; Dean 1998; Dirks 1998; Reid et al. 1998a, 1998b; Dean 2000; Schwartz and Dean 2001), and this work has expanded to include cercopithecoids and other fossil hominoids (e.g., Beynon et al. 1998b; Dean and Leakey 2004; Macho et al. 1996; Martin et al. 2003; Smith 2003; Smith et al. 2003; Smith et al. 2006). Maas

(1994), Maas and O'Leary (1996), and Schwartz and colleagues (2002, 2004, 2005aandb) have also expanded the sample to include strepsirhine taxa. These studies have all created detailed comparisons of Retzius periodicity, enamel secretion rates, *schmeltzmuster*, crown formation times, and ecological impact upon dental growth. Schwartz and colleagues (e.g. Schwartz and Dean 2001, Schwartz et al. 2001; Schwartz et al. 2005a) have also examined canine dimorphism in hominoids and compared it to that of extinct notharctines. Smith and colleagues (2007) have more recently shown that synchrotron particle accelerators form a viable alternative to thin-sectioning teeth in order to acquire incremental or other microstructural data.

In sum, the primate dental microstructure literature is just now becoming prolific. But apart from a few analyses of prism structure (Carter 1922; Gantt 1980; Nogami and Yoneda 1983; Nogami and Natori 1986), the platyrrhines have been largely unsampled in the study of primate dental microstructure as an indicator of life history. As noted in the introduction, this is a major gap considering the ecological and social diversity of the platyrrhines.

Chapter 3:

Methodological Commentary and Description

This chapter has two main objectives. First, it will highlight the physics (i.e., optics) and biology which are relevant to the methodology of the dissertation as a whole. Specifically, it will focus on the optical properties of enamel which are relevant to the microscopic imaging modalities used in the dissertation, and will also discuss the biology of enamel as it relates to enamel increments and the quantification of enamel growth rates, in order to provide justification for their use. Second, this chapter will review the materials and methods used in the dissertation. This review will include the preparation, imaging, and analytical protocols followed throughout the course of the project, including any novel techniques employed.

Optical Properties of Enamel, and Enamel Microscopy

As explained in Chapter 2, enamel is a compound material made from both mineral and organic components in combination with water. It consists mostly of mineral apatite crystallites, which in mammalian teeth are generally arranged in bundles known as enamel prisms (illustrated in Figs. 2-2 and 2-3; see Scheinmann et al. 1961; Koenigswald et al. 1987; Boyde 1989; Lowenstam and Weiner 1989; Driessens and Verbeeck 1990; Risnes 1998; Maas and

Dumont 1999; Hoppe et al. 2004; Hillson 2006). These crystallites are framed by a sort of "latticework" of proteins that act as the scaffold for the final enamel structure, and which make the enamel tougher and more resilient (e.g., Scheinmann et al. 1961; Boyde 1989; Lowenstam and Weiner 1989; Diekwisch et al. 1995; Slavkin and Diekwisch 1996; Maas and Dumont 1999; Fincham et al. 2000; Sander 2000). These enamel prisms and associated structures are not visible to the naked eye, and require microscopic analysis.

The inherent chemical and physical properties of these microscopic enamel structures affect the way light interacts with the enamel overall. Therefore, they will affect the way we view enamel under a microscope as well as the information we are able to glean from it (e.g., Slayter and Slayter 1992; Rochow and Tucker 1994; Espirito Santo et al. 2006; Sousa et al. 2006). Methods of microscopic visualization must be chosen with these properties in mind, so that the best possible images, and in turn data, are obtained.

In general, beams of light can be divided into two categories: unpolarized and polarized (Slayter and Slayter 1992). In unpolarized light, individual light waves do not travel in any specific orientation with respect to one another. In a beam of polarized light, however, the troughs and crests of light waves are aligned with a given order (Slayter and Slayter 1992; Rochow and Tucker 1994). We can further subdivide polarized light into two categories: linearly polarized light (LPL) and

elliptically polarized light (EPL). In LPL, all waves are polarized along one axis only, much as individual waves of water all have their crests and troughs aligned in one direction. In EPL, each wave is polarized along two axes. This has the effect of giving the light wave a helical structure, rather than the sinusoidal contour usually depicted for light (Slayter and Slayter 1992; Rochow and Tucker 1994). In other words, LPL has crests and troughs in only two dimensions, while EPL has crests and troughs in three dimensions, giving its waves the appearance of a coiled spring. If the two axes in EPL are perpendicular to each other, the helix becomes strictly circular, rather than elliptical, in cross section. This specific type of EPL is known as circularly polarized light, or CPL (Slayter and Slayter 1992). CPL can reveal much more detail about variations in enamel structure than is possible with other forms of light microscopy, as explained below, and so was the primary imaging modality used in this project.

This special property of CPL results from the fact that all types of light, including unpolarized and polarized light, have specific electromagnetic interactions with materials based on the chemical composition and physical structure of those materials, which influences their properties of refraction and reflection (Slayter and Slayter 1992; Rochow and Tucker 1994). With regard to polarized light specifically, certain materials will refract light waves with a certain orientation (i.e., polarization) differently than light waves of other orientations. This

property of a material is called *birefringence*, and results when the molecules of a material are arranged in an orderly manner (Slayter and Slayter 1992). The light waves of a certain orientation will be refracted more or less than light of other orientations as they pass through a birefringent material (Slayter and Slayter 1992; Rochow and Tucker 1994). Birefringence is exhibited by most crystalline materials and also many biological structures, such as collagen (Slayter and Slayter 1992; Espirito Santo et al. 2006; Sousa et al. 2006).

When birefringent materials are imaged with polarized light, one can see variations in structure because separate regions will have different effects on the light waves (Rochow and Tucker 1994). Regions with differing structural properties will cause corresponding color variations to appear in the final image. These color patterns appear because the birefringent material refracts some wavelengths (colors) so that they will be out of phase and will thus interact to decrease overall amplitude, while others will be in phase and tend to increase in amplitude (Rochow and Tucker 1994). Thus some colors from the original white light will undergo an increase in intensity as they are refracted out and reassembled in the final image, and others will undergo a decrease in intensity, based on the properties of the specific region through which they are passing. Therefore, color differences in a polarized light image indicate differential refraction and hence variation in underlying structure.

The apatite crystals and organic material within enamel are orderly and birefringent (Espirito Santo et al 2006; Sousa et al 2006). Therefore, when examining enamel (and dentine) microstructure via light microscopy, polarized light reveals variations in microstructure. Polarized light reveals differences in crystallite and prism orientations as well as chemical composition across tooth components by producing color variations. This color variation allows the examination of prism orientations (see Chapters 2 and 4 for discussion). It also enhances contrast in such features as cross-striations and striae of Retzius (see Chapter 2, and below).

Valentin (1861, cited in Thewlis 1939) was perhaps the first to note the birefringence of enamel in polarized light, and many studies since have used polarized light to image teeth because of its usefulness in determining microanatomy. The vast majority of such studies have used LPL to produce images. However, LPL can only reveal changes in organization along one polarization axis (see above), and thus is less advantageous when visualizing hard tissues. Mineral and organic components of bone and teeth change their orientation across regions in complex three-dimensional patterns based on functional need (e.g., Lucas et al. 2008b). Therefore, LPL is somewhat more limited than CPL in terms of the detail and contrast it can provide. CPL, by adding another polarization axis, reveals more information about shifting crystallite orientations because it reveals refractive interference across 360 degrees (Rochow and Tucker 1994). Therefore, it allows the full range of variations in

birefringence to be seen in any given specimen (see Figs. 3-1 through 3-3).

CPL is sometimes limited in use because some institutions restrict or prohibit thin-sectioning of teeth, which permanently alters a specimen. Another limit upon the use of CPL is that, as with other types of light microscopy, CPL cannot provide images of sufficient resolution at narrow fieldwidths (e.g, <50 microns). With these restrictions, alternate forms of microscopy must be used, including (but not necessarily limited to) confocal microscopy and scanning electron microscopy (SEM). Both have the advantage of allowing specimens to be studied with little permanent alteration. Confocal microscopy has an additional advantage in that it captures an image just under the enamel surface, reducing artifacts of preparation and wear (e.g., Lacruz et al. 2006). SEM, on the other hand, allows high-resolution images to be made at extremely high magnifications. Therefore, confocal microscopy and SEM were also used in this study as a complement to CPL images, most often for purposes of visualization. All measurements of cross-striations and striae of Retzius were drawn from CPL images (see below), whereas perikymata of *Saimiri* teeth were measured using SEM due to sampling constraints (see below).

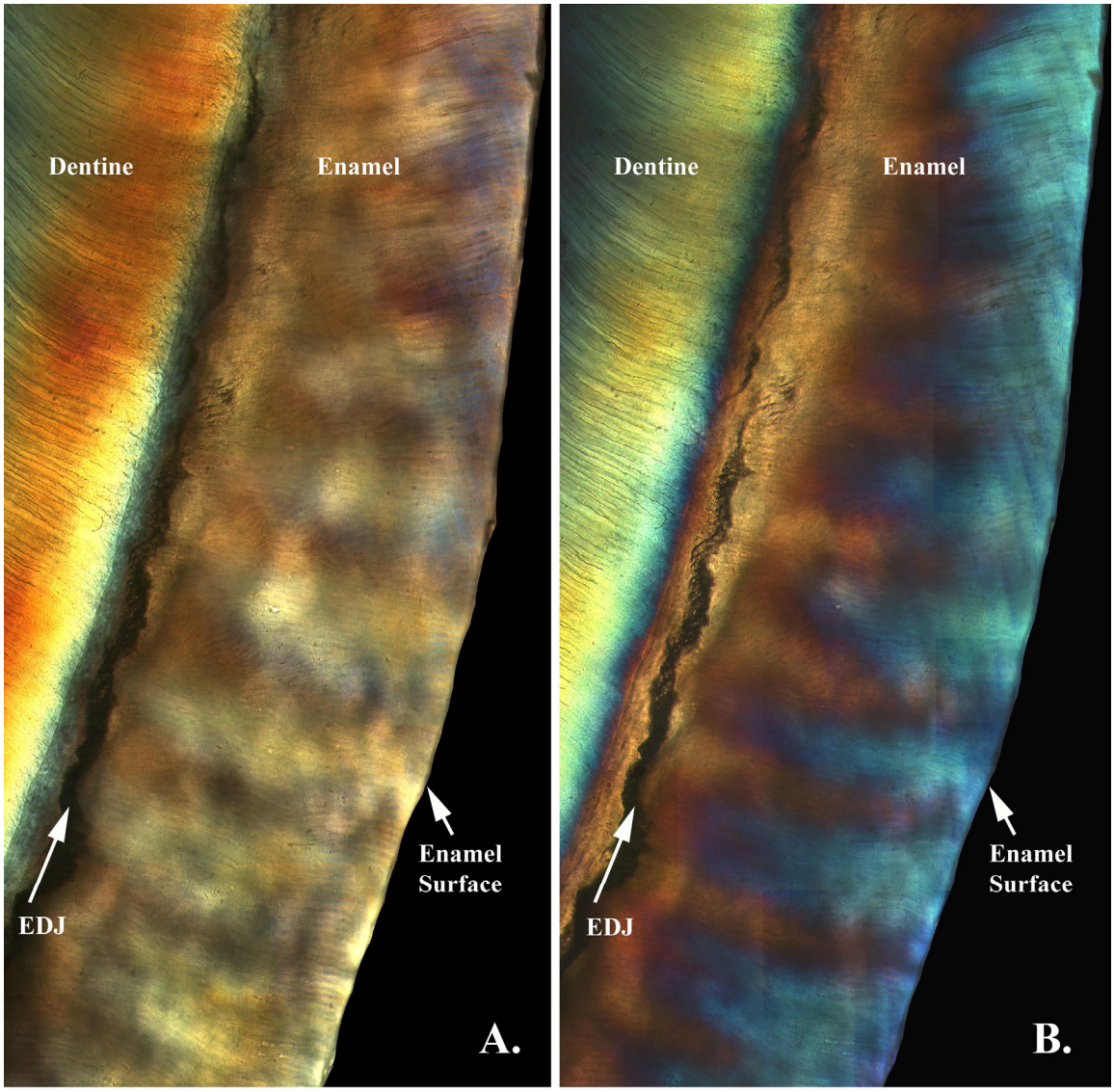


Fig. 3-1. Linearly polarized (**A**) vs. circularly polarized (**B**) light (LPL vs. CPL) in a *Cebus* premolar. Banding as a result of decussation (Hunter-Schreger bands) can be seen in both images in terms of color contrast. Note, however, that in the CPL image the bands are much more readily seen and are much better delineated. CPL also reveals a major difference in structure between the EDJ and the tooth surface (a much higher extent of orange at the EDJ versus blue at the surface), even where banding is less obvious toward the image top. **Field width of each image = 486 microns.**

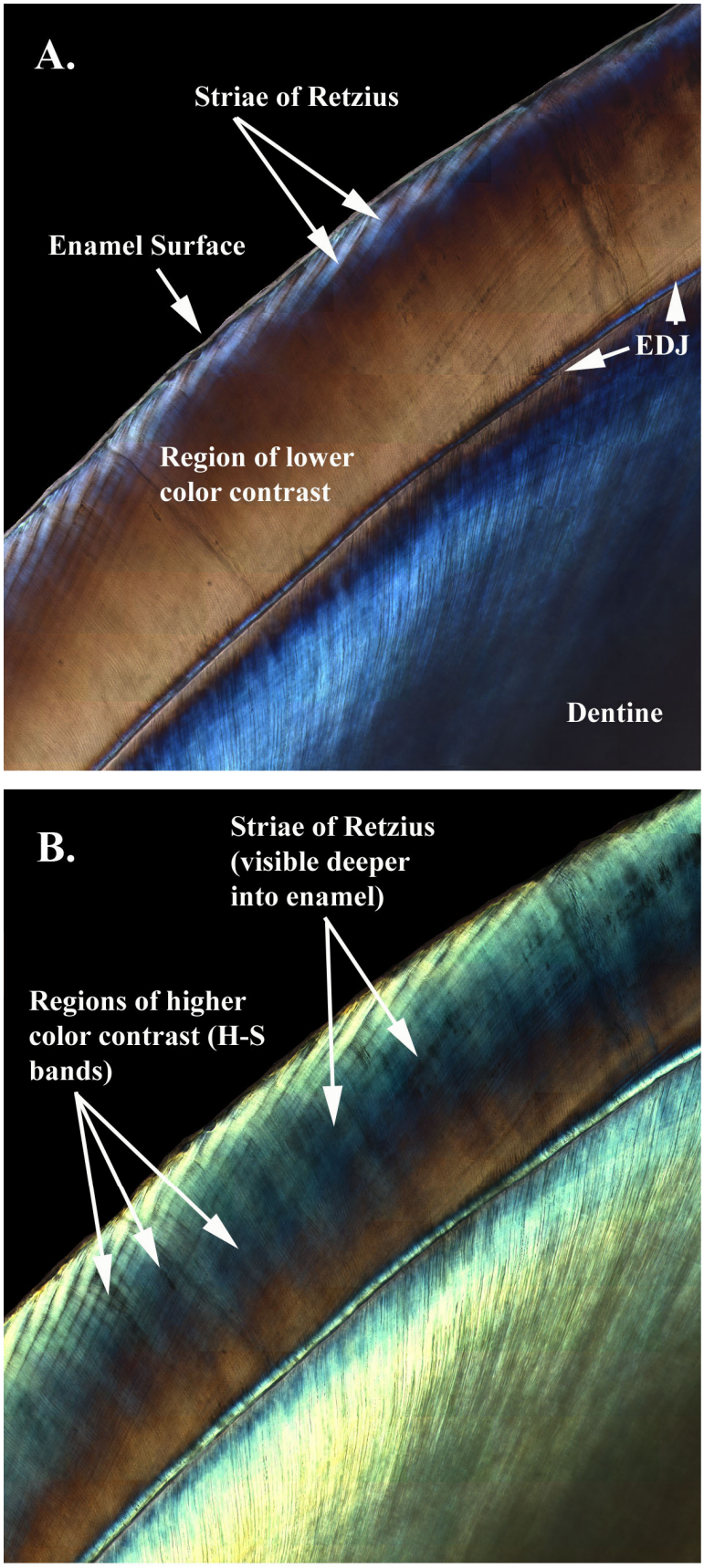


Fig. 3-2. LPL (**A**) vs. CPL (**B**) images of a *Lagothrix* canine. In **A**, light orange can be seen extending through about half of the enamel, yielding to dark orange and then blue as structure changes. In **B**, however, we have many more color changes occurring, revealing much greater detail of prism orientation changes throughout the tooth. Note also that in the CPL image there is more contrast in terms of striae of Retzius, allowing them to be tracked deeper into the enamel. The CPL image also reveals Hunter-Schreger banding which is very difficult to discern in **A**. **Field width of each image = 384 microns.**

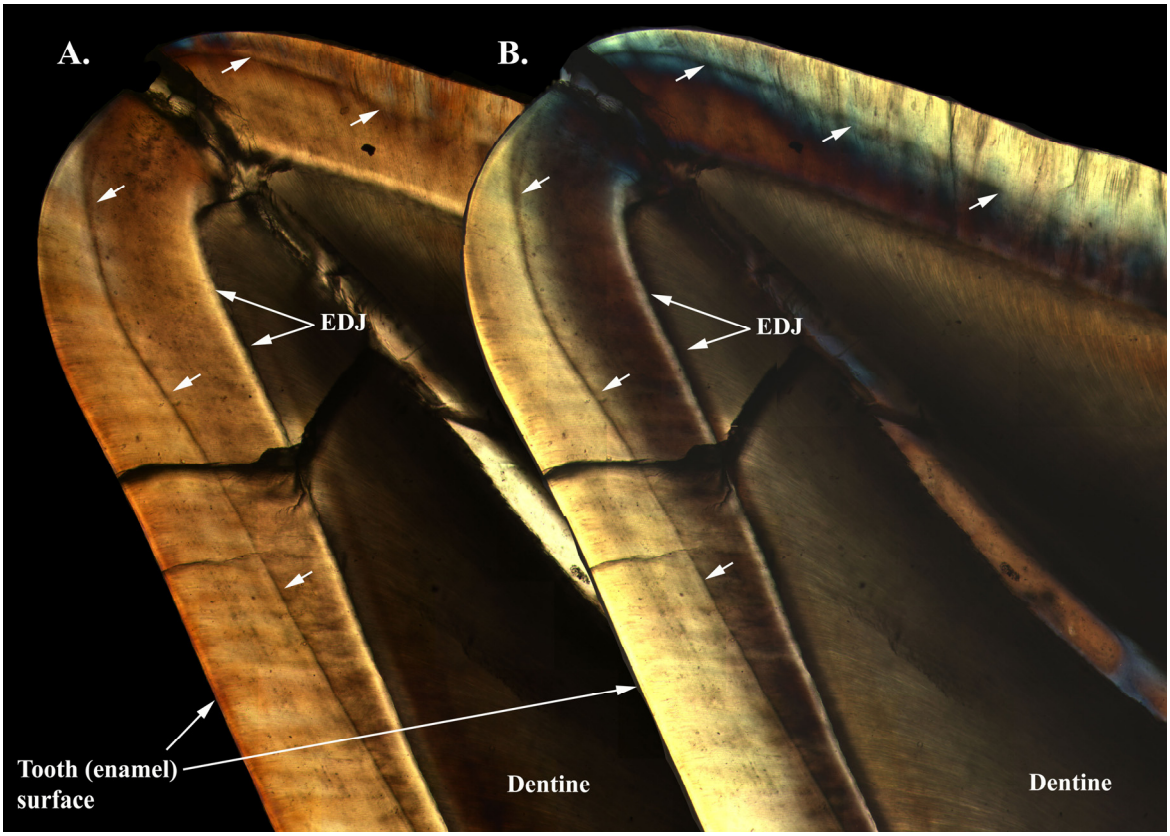


Fig. 3-3. LPL (**A**) vs. CPL (**B**)images of a *Cebus* canine. The strong, dark line running around the cusp in mid-enamel is an accentuated stria of Retzius, most likely a neonatal line (small white arrows; see Boyde 1989). In **A**, there is little observable difference in prism/crystallite structure evident on either side of this structure because the enamel is a relatively uniform orange. In **B**, however, underlying structural differences become apparent. Most noticeably, enamel deep to the neonatal line appears generally much darker than other enamel. Subregions which alternate between yellow and blue also suggest complex microstructural differences. Cusp tips are to upper left. **Field height is 1127 microns.**

Justification of Odontochronology as a Method

Since most of this dissertation involves the use of enamel increments to learn about the life history of cebid primates, it is worthwhile to discuss the evidence which supports the theory that such increments reflect regular, periodic intervals of time. This is especially the case because, as late as 1998, there was still argument against the validity of enamel increments as periodic structures (see Fitzgerald 1998).

General ideas of periodicity in enamel go back to the observations of Leeuwenhoek and Havers in the late 1600's (e.g., Leeuwenhoek 1665-1678, 1800; Havers 1691). Circumstantial evidence regarding periodicity, specifically that cross-striations represent a daily rhythm, was first suggested by Asper (1916); in 1963, Boyde also suggested that striae of Retzius represent a circaseptan (7 day) biorhythm in humans. Since the 1960's, numerous researchers have operated under circumstantial evidence to analyze enamel and dentine periodicity (Bromage 1991).

However, several groups of researchers have criticized these ideas. For example, some have suggested that cross-striations may actually be an optical artifact generated by aligned rows of cross-sectioned prisms. Others have argued that cross-striations are caused by knife- or saw-chatter during the sectioning process (e.g., Weber and Glick 1975; Warshawsky 1983). Moreover, the range of values for Andresen's lines in dentine (4.19 to 5.83 days) obtained from an analysis of rhesus macaques

led other researchers to argue that dentine increments do not follow a given periodicity (Molnar et al. 1981). Furthermore, Mann and colleagues (1991) called into question the validity of using perikymata counts to assess tooth formation times, as their perikymata-based estimates did not match up with their data on known crown formation times of modern humans.

However, the overwhelming majority of evidence gathered over the past century has countered these criticisms in support of dental periodicity. In terms of experimental studies, the primary means of verifying circadian periodicity have been chemical labeling procedures, in which animals are injected at certain intervals with a fluorescent chemical marker which will embed itself in forming hard tissues. This marker, injected at known time intervals, can therefore serve as the basis for direct comparison of dental increments to specific time intervals. For example, Schour and Poncher (1937) first showed a correspondence between cross-striation counts and the number of days between injection events in a study of a human child. Mimura (1939) injected dogs, rabbits, and pigs with lead acetate and sodium fluoride markers and demonstrated the same number of cross-striations between acetate and fluoride lines as the number of days between injections. Also with the use of a labeling procedure, Okada (1943) demonstrated that Von Ebner's lines in dentine correspond chemically to sleeping and waking cycles based on the amount of calcium in the matrix. In addition, Okada also showed that changing pH levels of blood between waking and

sleeping correspond with this changing calcium composition of dentine matrix, revealing a circadian physiological link to dental increments (Okada 1943). Other research has also found a correspondence between labeling times and increment counts for dentine in human teeth (Kawasaki et al. 1980).

More recently, Bromage (1991) used macaque teeth labeled with polychrome fluorescent dyes to further verify the hypothesis of regular periodicity. In this study, counts of cross-striations (enamel) and von Ebner's lines (dentine) corresponded with the number of days between labeling injections. Dean and Scandrett (Dean 1993, 1995; Dean and Scandrett 1995, 1996) performed similar labeling analyses of *Macaca*, *Pongo*, as well as in a human forensic case, and produced similar results.

In terms of observational evidence, Boyde (1963, 1964) showed that age at death for a juvenile human calculated from cross-striation counts corresponded with eruption sequence patterns of the same individual. Risnes (1986) calculated an expected secretion rate for enamel prisms and this rate corresponded with the observed cross-striation measurements in the same teeth. Research using SEM imaging also clearly reveals that the basis for criticisms against the validity of cross-striations are unfounded. For the optical artifact criticism (Weber and Glick 1975), high magnification SEM images of longitudinal tooth sections reveal cross-striations along the lengths of individual prisms, rather than as an alignment of prisms seen in cross section (e.g., Smith 2004). For the knife-

chatter criticism (Warshawsky 1983), the extremely high magnification of SEM images allows a visual distinction between superficial knife artifacts and cross-striations throughout the entire tooth enamel. At this high magnification, the cut surface of the tooth can be prepared to remove the knife artifacts by polishing with or without acid-etching (Shellis 1998). One must also verify that all significant artifacts are removed by examining the section at a high magnification in SEM. As a final counter to these criticisms, Boyde and Martin (1987) showed that enamel increments can be viewed deep to any prepared surface using confocal microscopy, which allows the microscopist to exclude any surface information.

Since cross-striations are daily periodic structures, if we can find consistent cross-striation counts between long-period increments in teeth (e.g., striae of Retzius in enamel), we can also verify a given periodicity. Schour and Hoffman (1939) showed that the breadth between Retzius lines is a multiple of the cross-striation breadth in the mammal species they examined; for example, if the cross-striation interval was five microns, then the Retzius interval would be in multiples of five microns (10, 15, 20, or more). Moreover, numerous primate studies have offered a consistent interval for Retzius lines across teeth and within individuals (e.g., Beynon and Reid 1987; Beynon 1992; Beynon and Reid 1995; Fitzgerald 1998). Thus, for the purposes of this research, we can take the periodicity of both cross-striations and striae of Retzius as a reliable biological feature.

Methods of Preparation, Imaging, and Analysis Used Throughout the Dissertation

All procedures listed in this section are common protocols for the entire dissertation. Measurements and statistical analyses that are specific to individual chapters in this dissertation are described in separate sections below.

Materials

Seventeen species of eight cebid genera were sampled. The non-cebids *Alouatta* and *Callicebus personatus* were also sampled; species designations were not available for *Alouatta* samples. Only canine and postcanine mandibular teeth were studied in order to limit the amount of destructive sampling. In all, 19 canines, 38 premolars, and 43 molars were prepared and examined. See Appendix A for a listing of all specimens and their sources, as well as specific teeth sampled for each species.

Preparation

The preparation of teeth mostly followed the protocols of the Hard Tissue Research Unit (HTRU) at NYU College of Dentistry (Department of Biomaterials and Biomimetics; e.g., Goldman et al. 1999; McFarlin 2006; Warshaw 2007). I will discuss the

dissertation protocol as a whole and then highlight the novel techniques specific to this study.

All specimens were first cleaned to remove organic material and other debris. This was performed through incubation in a 5% enzyme detergent solution (Terg-a-zyme®, Alconox, Inc.) at 50^0C until fully cleaned (a minimum of one week), with daily solution changes. Teeth from preserved or frozen specimens were carefully dissected out, and were also treated with the detergent solution.

The teeth prepared for thin-section were first embedded in a matrix of polymethyl-methacrylate (PMMA), an acrylic resin which undergoes a polymerization process under ultraviolet light and/or heat, transitioning from a low-viscosity liquid to a rigid transparent plastic. PMMA functions to protect teeth from splintering and cracking during the processes of sectioning and mounting onto microscope slides, and also continues to protect the teeth thereafter.

In order to embed teeth in PMMA, they were first dehydrated using a graded series of ethanol/water solutions (50% ethanol, 75% ethanol, 100% ethanol), which were placed in a vacuum chamber for fifteen minutes at each solution change. Subsequently, teeth were put through a series of graded solutions of acetone (used as a vehicle) and PMMA, with each stage under a vacuum as described above. With each change the amount of acetone in the solution was reduced (50%, 25%, and 5% acetone) until a final 100% PMMA embedding solution was achieved. Teeth were then placed in small glass jars (2-5 mL) along with 100% liquid PMMA. A chunk of

cured (solid) PMMA acrylic, which was prepared in advance, was also placed in each tooth-containing jar in order to accelerate curing time of the liquid PMMA in that jar (see below). Before the containers were capped and sealed with parafilm, the ambient air within them was replaced with argon to remove water vapor, which can slow PMMA curing time. To cure the specimens, the sealed jars were then placed under indirect sunlight with two hours under an ultraviolet lamp per day to accelerate curing time (see below).

Once cured, PMMA blocks containing the embedded teeth were removed from their glass containers. A 200-500 micron-thick section (depending on tooth size) was cut from each embedded tooth using an Isomet® (Buehler, Ltd.) slow-speed diamond wafering saw with a three-inch diameter blade. Sections for molars were taken in the mesiodistal plane through the apex of the highest cusp as a reference point; sections for premolars and canines were taken in the buccolingual plane (also through the apex of the highest cusp) due to differences in tooth shapes.

Sections were next mounted onto glass microscope slides using Permatex® Windshield Repair Kit (Permatex, Inc.), a methacrylate-based adhesive designed to bond to glass. Sections were ground and polished to a thickness of around 100 microns using a graded series of emery papers, though this final thickness varied depending on the unique optical properties of each tooth; image quality, rather than a precise measurement, was the primary determinant of final section thickness. Final

polishing was achieved with a 1 micron diamond polish (in water suspension) on a nylon pad, using an Ecomet® (Buehler, Ltd.) drum polisher at 500 rpm.

For SEM imaging, whole teeth were cleaned and dehydrated as described above and were subsequently sputter-coated with gold. For backscattered SEM imaging of tooth thin sections, specimens were also polished using the 1 micron diamond abrasive, then acid-etched using a 30% phosphoric acid solution for fifteen seconds. Following this, they were rinsed with distilled water for one minute and air-dried. Subsequently, they were sputter-coated with carbon.

Imaging

All SEM images were taken on a Hitachi S3500-N scanning electron microscope; both standard and backscattered SEM modalities were used.

All sectioned and mounted teeth were imaged using a Leica PL Fluotar 40/0.70 objective lens, mounted on a Leica-Leitz DMRX/E Universal Microscope configured with a Marzhauser motorized stage, phase contrast, and circularly polarizing filters. Images were acquired via Syncroscopy Montage Explorer (Synoptics, Ltd.), using a JVC KYF55B color video camera.

Novel preparation techniques

Several novel protocols of tooth preparation were developed which greatly affect the time in which a good thin section can be

obtained. These protocols have important implications for other studies of this kind, allowing an increased laboratory efficiency and decreased project turnaround time.

The standard protocol seals teeth in glass containers with liquid PMMA and places the specimens under indirect ultraviolet light (sunlight), where the liquid resin cures into a hard, clear acrylic over a period of several weeks to months as the methacrylate molecules polymerize. I modified the protocol in several ways in order to accelerate the polymerization process. For example, after experimentation I discovered that placing chunks of cleaned, solid, pre-cured PMMA in specimen jars along with teeth and liquid PMMA greatly speeded curing time. Moreover, I also replaced ambient air in the jars with 100% argon gas to remove water vapor, which acts to slow or impede PMMA polymerization (Bromage, pers. comm.). Lastly, I supplemented indirect, natural UV light for two hours a day with direct exposure under an ultraviolet lamp. With this method it was possible to produce an embedded specimen ready for cutting in one to two weeks, rather than one to two months as was the case with the original protocols used in developing this project.

The section-mounting protocol used here is also novel. Standard HTRU protocol uses a series of non-toxic dental adhesives to mount sectioned teeth/bones onto glass microscope slides for visualization (e.g., Goldman et al. 1999; McFarlin 2006; Warshaw 2007). Though effective, this procedure is a complicated process that is time consuming, especially when many

slides must be prepared. Instead, I used a methacrylate-based adhesive to bond specimens to slide glass. This adhesive is sold commercially as Permatex® Windshield Repair Kit (Permatex, Inc.). It bonds readily to glass, with which it shares the same refractive index, and also bonds well with PMMA, thus making an ideal adhesive for mounting PMMA-embedded specimens on glass with minimal optical consequences. One drop of adhesive is placed on the glass microscope slide, and the PMMA-embedded specimen is pressed against the adhesive and glass to remove any air bubbles. Nearly all of my sections were smaller than two centimeters in diameter; therefore, if research involved larger sections, additional drops of adhesive would be required based on the size of the specimen.

Next, the slide assembly is placed under an ultraviolet lamp for a period of one hour. Although this curing time is substantially longer than the curing time for dental adhesives, the simplicity of the new procedure allows multiple slides to be prepared at once in much less time than it takes to go through the several steps of the dental adhesive protocol.

During the course of my dissertation research, I also discovered a new application of an established imaging preparation method. Visualization of dental thin-sections in SEM requires that specimens be finely polished and acid-etched to remove preparation artifacts and accentuate microanatomy. Thin-sections must also be carbon-coated so that the specimen will properly carry an electron charge within the electron microscope.

In order to compare conclusions reached with the SEM with those of polarized light, I visualized some specimens which were prepared in such a manner in CPL after having taken my SEM images. Although acid-etching reduced the visibility of striae of Retzius, carbon-coating greatly enhanced contrast so that individual prism boundaries could be much more easily distinguished. This preparation also seems to reveal microcracks between individual crystallite bundles within the prisms themselves (Fig. 3-4). This provides a novel method for visualizing individual enamel structures at the micron and sub-micron scale, which could be used as a complement to SEM images.

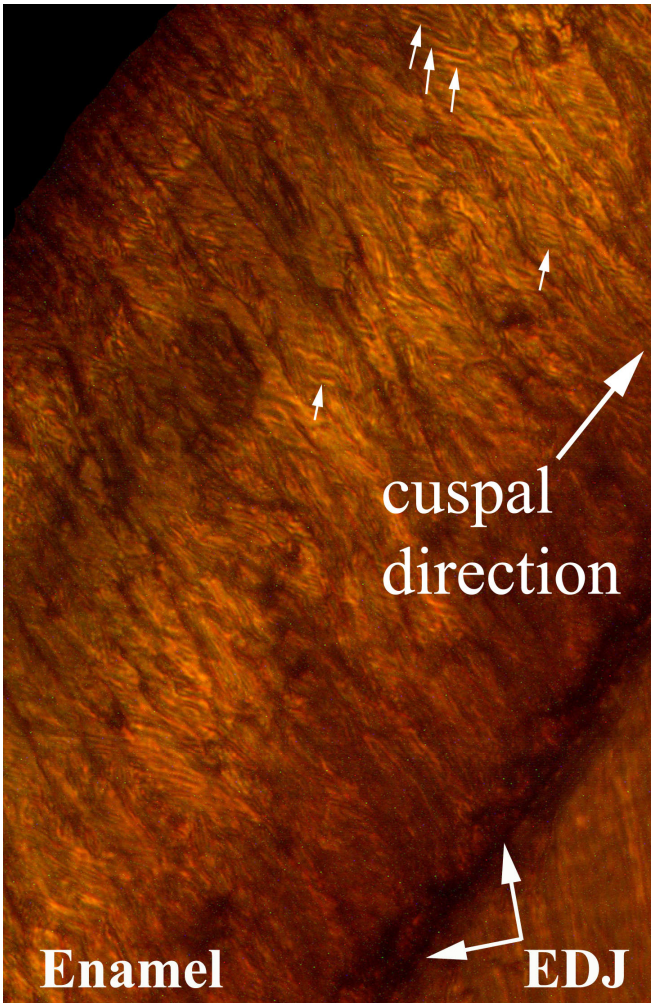


Fig. 3-4. Image demonstrating the results of acid-etching and carbon-coating in a CPL image (M1, *Callithrix jacchus*). Unlike non-coated sections, structural details can be seen within enamel prisms in the form of darkened lines (examples indicated by small white arrows). **Field width = 132 microns.**

Measurements

Measurements of cross-striation breadths were taken in order to obtain daily enamel secretion rates for each individual (DESRs; see Fig. 3-5). One cross-striation (i.e., 24 hours of growth) consists of one light and one dark alternating band on an enamel prism when viewed in polarized light. To obtain a more precise measurement of a cross-striation, breadths were taken

from the middle of successive dark bands within individual prisms. Averages of cross-striation breadths were computed for nine regions within each postcanine tooth. Each tooth crown was divided into three main regions: cuspal, midcrown imbricational (hereafter referred to as "imbricational") and cervical imbricational (hereafter referred to as "cervical"). Each of these three regions has three subsets: inner (closer to dentine), middle, and outer (closer to the enamel surface). Generally, a minimum of fifty measurements was collected for each of these nine regions; however, in a few cases only twenty to thirty measurements were obtained due to a lack of visible anatomy.

For most individuals, multiple postcanine teeth were available for sampling (see Appendix A). Therefore, mean cross-striation breadth for each individual (i.e., mean DESR) was calculated as the mean of all regional averages for all teeth for that individual; species means were then calculated as a grand mean of individual means. This step-by-step approach prevents a high number of measurements in any one tooth or region from skewing the final mean for each individual and species. Whenever a tooth did not display an adequate number of cross-striations in all nine regions, the data for regions that were available were still included in analyses.

Canines were excluded from general cross-striation averages and analyses, except for the analyses of sexual dimorphism (see Chapter 7 methods below), due to concerns that sexual dimorphism

and the overall large size of canine crowns might skew the DESR averages in different ways in different species.

In order to verify the accuracy of this method as well as the degree to which any group of cross-striation measurements is reflective of the entire population of cross-striations within any tooth region, an intra-observer error study was conducted in two parts. First, a single cross-striation was measured repeatedly over a one week period (n = 35) to provide an idea of the accuracy of any one cross-striation measurement within the study. In this test, all measurements were in close accord with one another (mean = 3.69 microns, median = 3.65, mode = 3.64, variance = 0.023, standard error of mean = 0.026). Second, samples of imbricational cross-striation measurements from one tooth were separated into three groups for two individuals of *Saimiri* (AMNH 208075 canine, MNRJ 433 M2) as well as *Cebus* (MNRJ 449 M3, MNRJ 446 M2) (i.e., one tooth per individual). One-way ANOVAs were then conducted for each individual, to determine whether there was any statistically significant difference among subsets from the same tooth. With the exception of AMNH 208075 ($p = 0.011$, n = 78 cross-striations), there was no statistically significant difference among any of the grouped samples from any tooth (MNRJ 433, $p = 0.198$, n = 60 cross-striations; MNRJ 449, $p = 0.635$, n = 74; MNRJ 446, $p = .165$, n = 75). However, when the sample from AMNH 208075 was divided in two (rather than three) and subjected to a standard student t-test, the statistical difference between samples disappeared ($p = 0.104$). In the ANOVA,

the respective samples include 26 measurements apiece, whereas in the t-test, the two samples number 39 measurements apiece. Since no statistical difference was noted ANOVAs from the other three individuals, whose samples range from 20 to 25 measurements, this suggests that in most cases an n of 25 measurements from any one tooth region will accurately reflect the whole population for that region. As evidenced by AMNH 208075, however, this does not always apply. Increasing the sample to around 40 seems to eliminate the problem. As all whole-tooth mean DESRs were calculated using grand means of cross-striation measurements for separate tooth regions, and as 50 was used as the standard minimum number of cross-striation measurements taken from each region, any error due to sampling issues should be minimized for the majority of individuals.

All statistical tests in this dissertation were performed using Statistica 6.0 statistical software (Statsoft, Ltd.). These will be discussed in more detail in following sections, since they pertain specifically to the objectives of specific chapters. For all tests, a 95% confidence interval was used as the benchmark for statistical significance.

Methods specific to Chapter 5

For Chapter 5 as well as 4, enamel extension rate was quantified by measuring angles between successive enamel

formation fronts (EFFs; see Fig 3-5 and Chapters 2 and 5) and the enamel-dentine junction (EDJ) (Beynon and Wood 1986). EFF angles [also termed "D degrees" angle by Beynon and Wood (1986; see also Bromage et al. (1995)] reflect the number of ameloblasts actively secreting enamel along the EFF at any one point in time. Since the EFF *is* the enamel surface throughout growth, an increase in the number of active ameloblasts will lengthen the EFF and in turn, decrease the angle between the EFF and the EDJ. Therefore, as illustrated in Fig. 3-5, a smaller EFF angle reflects a greater amount of enamel being secreted during a specific unit of time (= higher extension rate).

EFF position was quantified using striae of Retzius (Fig. 3-5), while the plane of the EDJ was easily observed in thin-sections as a line separating enamel from the dentine structures underneath. In order to limit the impact of gross anatomical differences in enamel among different tooth types and tooth regions, all EFF angles were taken only from imbricational enamel in M1 and M2 teeth. EFF angles were then averaged together across individuals to create a species mean angle, which was included in regression analyses. As with cross-striations, all angular measurements were calibrated to the optical system used to provide the image data, and were taken in Syncroscopy Automontage (Synoptics, Ltd.).

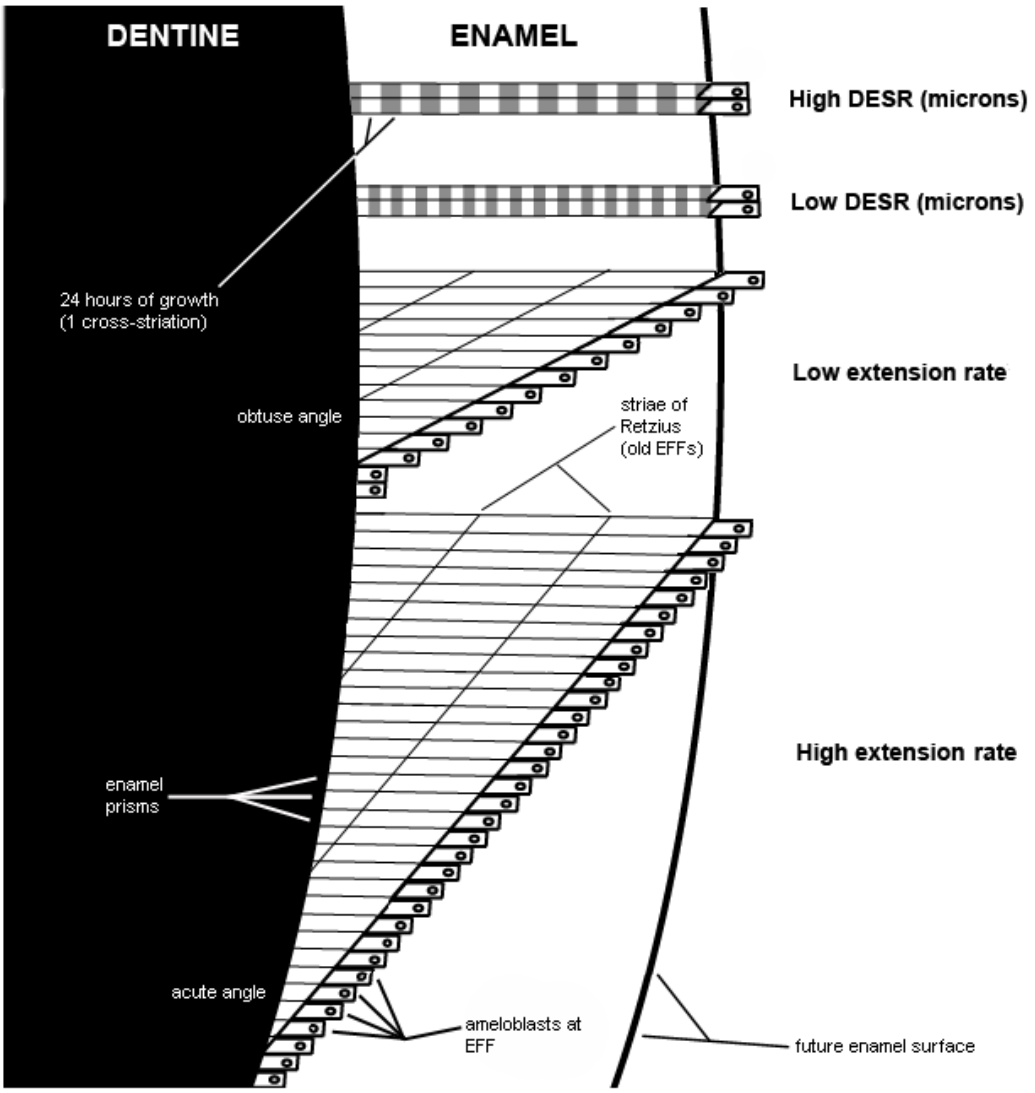
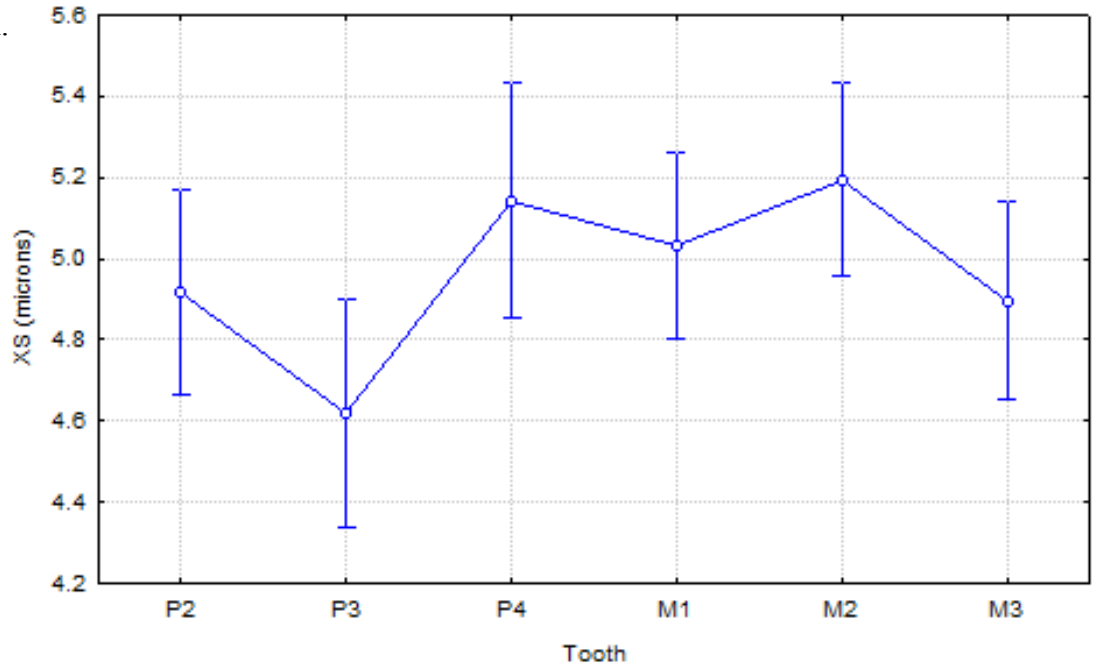


Fig. 3-5. The two components of enamel growth, showing ameloblasts as they progress from the enamel-dentine junction (EDJ) to the enamel formation front (EFF), which represents the change in position of the enamel surface as the enamel thickens. **Top:** Individual ameloblasts can increase enamel growth rate by increasing daily enamel secretion rate (DESR), represented by thicker alternating gray-and-white bands. **Below:** Also, by increasing the number of ameloblasts, the same amount of work will be performed in less time. For the same final enamel thickness, an increase in the number of active ameloblasts (=high extension rate) will cause the angle between the EFF and the EDJ to become more acute. Therefore, the group of ameloblasts with the more obtuse EFF angle has deposited relatively less enamel (=low extension rate) in the same amount of time and in turn has a slower growth rate. Striae of Retzius demarcate the position of ameloblasts along the EFF at earlier growth times. The slope between striae and the EDJ is measured to compare the enamel extension rate across species.

In addition to EFF angles, data on DESR were also included in analyses for this chapter. Mean DESR data from all postcanine teeth were incorporated into the statistical analyses, in order to include all the data available for each individual and to cover the longest possible period of growth (due to the fact that primate tooth types do not all grow at the same time within the same individual). In order to ensure that measurements from differing tooth types would not skew results, a one-way analysis of variance (ANOVA) was performed to compare DESR variation across the different tooth types for all cebids (see Fig. 3-6). This analysis showed that P3 mean DESR seems to differ from other tooth types; when P3 is removed, cebid teeth are not statistically different in terms of cross-striation breadths ($p = 0.37$). However, because P3 does represent an important part of cebid dental growth schedules, I included it in all subsequent analyses.

For statistical analyses in this chapter, mean DESR (i.e., cross-striation breadth) and mean EFF angle for each species were regressed against species mean values for body mass, brain mass, age at weaning, age at first female reproduction, and interbirth interval. Values for these variables were acquired from Ford and Davis (1992; body mass), Harvey and Clutton-Brock (1985; brain mass, weaning age and interbirth interval), Ross (1991; age at

A.



B.

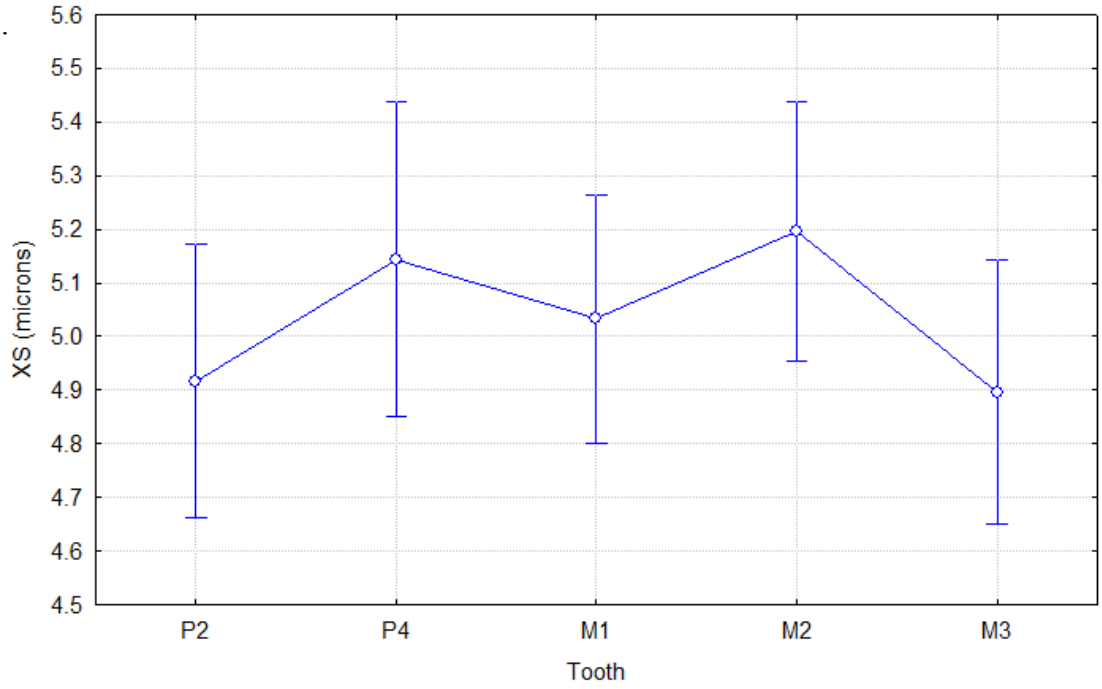


Fig. 3-6. A. ANOVA comparing cross-striation (XS) breadths across teeth within Cebidae, combining all species examined in this study ($p = 0.04$). **B.** ANOVA excluding P3, which differed the most from other tooth types as shown in A. Without P3, there is no significant difference among tooth types ($p = 0.37$). In both graphs, vertical bars denote 95% confidence intervals.

first female reproduction), Hartwig (1996; brain mass), Godfrey and colleagues (2001; weaning age and age at first female reproduction), and Lindenfors (2002; brain mass, age at weaning, age at first female reproduction). See Table 3-1 for specific details of data sources for each species. To verify accuracy of cebid body mass data, values from Ford and Davis (1992) were compared against values from Rosenberger (1992); all body mass analyses yielded similar results for both datasets. Data from Ford and Davis (1992), however, were used in this dissertation because they include separate sex estimates, which are important to analyses of Retzius periodicity in Chapter 6. To verify accuracy of brain mass data, values for all species were compared against cranial capacity estimates from Kirk (2006).

Values for encephalization quotient (EQ) were generated by entering brain and body mass data into the standard EQ equation (Jerison 1973) as modified for primates by Martin (1990), who gives 0.68 as the best allometric exponent in this group: EQ = observed brain mass/expected brain mass = brain mass/body mass$^{0.68}$.

Species	Body mass	Brain mass	Age at weaning	Age at 1st fem repr	Interbirth Interval
Alouatta spp.	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al. (2001)	Godfrey et al. (2001)	Harvey and Clutton-Brock (1985)
Aotus spp.	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al. (2001)	Ross (1991)	Harvey and Clutton-Brock (1985)
Callimico goeldii	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Callithrix humeralifer	Ford and Davis (1992)	Hartwig (1996)	Lindenfors (2002)	Lindenfors (2002)	-
Callithrix jacchus	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Godfrey et al. (2001)	Harvey and Clutton-Brock (1985)
Cebuella pygmaea	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Cebus albifrons	Ford and Davis (1992)	Harvey and Clutton-Brock (1985), Hartwig (1996)	Godfrey et al. (2001)	Ross (1991)	Harvey and Clutton-Brock (1985)
Cebus apella	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al. (2001)	Godfrey et al. (2001)	Harvey and Clutton-Brock (1985)
Cebus capucinus	Ford and Davis (1992)	Harvey and Clutton-Brock (1985)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Cebus olivaceus	Ford and Davis (1992)	Harvey and Clutton-Brock (1985)	Lindenfors (2002)	Lindenfors (2001)	Harvey and Clutton-Brock (1985)
Leontopithecus rosalia	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Saguinus fuscicollis	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al. (2001)	Godfrey et al. (2001)	Harvey and Clutton-Brock (1985)
Saguinus midas	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Saguinus nigricollis	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al. (2001)	Godfrey et al. (2001)	Harvey and Clutton-Brock (1985)
Saguinus oedipus	Ford and Davis (1992)	Hartwig (1996)	Harvey and Clutton-Brock (1985)	Ross (1991)	Harvey and Clutton-Brock (1985)
Saimiri boliviensis	Ford and Davis (1992)	-	-	-	-
Saimiri oerstedii	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al. (2001)	-	-
Saimiri sciureus	Ford and Davis (1992)	Hartwig (1996)	Godfrey et al. (2001)	Ross (1991)	Harvey and Clutton-Brock (1985)

Table 3-1. Specific sources of data for the variables analyzed in Chapter 5. The same body mass and brain mass data sources were also used in analyses for Chapter 6.

Methods specific to Chapter 6

Retzius periodicities were acquired directly from CPL images of cebid teeth (as well as *Alouatta* and *Callicebus;* see below), counting the number of successive cross-striations on individual enamel prisms between adjacent Retzius lines. This enabled a record of the number of days between Retzius events, which has been shown to be consistent within teeth and within individual animals (Fitzgerald 1998). In order to verify all direct counts from the images, average breadth between Retzius lines for each tooth was also divided against average cross-striation breadth for that tooth to estimate periodicity. In all cases, estimates acquired with this method corresponded to those gained by a direct count.

In addition to the same cebid specimens used throughout (see Appendix A), this chapter also includes data from *Alouatta* spp. and *Callicebus personatus* teeth. I included these two genera due to the fact that analyses of Retzius periodicities in this study are directed at uncovering physiological processes that operate across taxa, via a broad sampling of primate variation. Therefore, since *Alouatta* and *Callicebus* teeth were available, it was important to include them as additional platyrrhine data points. I was also able to process and image one patas monkey (*Erythrocebus patas)* female courtesy of Dr. Shannon McFarlin; however, Retzius periodicities for all other

non-platyrrhine primates were obtained from the literature (see Chapter 6 for citations).

For statistical analyses, Retzius periodicities acquired directly from specimens as well as from the literature were regressed against body and brain mass values for each species (see Table 3-1). Male and female values were kept separate in statistical analyses in order to highlight Retzius variation both within and across species. If separate male and female mass averages could not be found, or if the sex of a specimen was unknown, one combined-sex species estimate was used.

Specifically, body mass estimates for platyrrhines are derived from Ford and Davis (1992), whereas body mass estimates for non-platyrrhines and brain mass estimates for all groups are derived from Harvey and Clutton-Brock (1985), Hartwig (1996), and Lindenfors (2002), unless otherwise noted in Table 6-1. Brain mass and body mass values were checked against the same alternate data sources mentioned for Chapter 5 in order to verify their accuracy (i.e., Rosenberger 1992; Kirk 2006). See Table 3-1 for specific information on data sources for platyrrhine species.

Methods specific to Chapter 7

The total number of species and specimens in the sexual dimorphism analyses is reduced because not all cebid species are sexually dimorphic. In addition, canines were not as readily

available for study. Therefore, Table 3-2 gives a complete listing of specimens and sources whose canine data were included in the analyses of sexual dimorphism. Also note that the non-cebid *Alouatta* was included for comparison in these analyses.

As stated above, to determine growth rates for species of *Cebus* and *Alouatta,* cross-striation/DESR measurements were compared using images obtained in CPL. However, since the *Saimiri* females in my sample could not be sectioned due to restrictions of the institutions from which they were borrowed, growth rates of *Saimiri* canines were determined using perikymata breadth measurements obtained in SEM. As demonstrated in Chapter 2, perikymata are external manifestations of striae of Retzius and can therefore provide information about growth rates.
For SEM measurements of perikymata, teeth were aligned so that the planes of measurement were perpendicular to the electron sensor. In the few instances where this was not possible (such as on surfaces with changing angles), trigonometric functions were used to extrapolate an estimated length (hypotenuse) of perikymata from the two-dimensional image, using a manual measurement of the approximate angle of that portion of the tooth surface away from the perpendicular. Using the calibration bars specific to the individual images, measurements of perikymata breadth were taken using Adobe Photoshop CS2 (Adobe Systems, Inc.).

Genus/Species	Sex	Source/Designation
Cebus apella	M	AMNH 133091
Cebus apella	M	MNRJ 447
Cebus apella	F	NYU
Cebus apella	F	MNRJ 446
Cebus albifrons	M	AMNH 62838
Cebus albifrons	F	AMNH 78504
Saimiri oerstedii	M	AMNH 19212
Saimiri sciureus	M	AMNH 94206
Saimiri sp.	F	AMNH 14003
Saimiri sp.	M	AMNH 17116
Alouatta sp.	M	MNRJ 2756
Alouatta sp.	F	MNRJ 484
Alouatta sp.	F	MNRJ 499

Table 3-2. Listing of specimens included in Chapter 7.

Statistical comparisons (standard student t-tests) were made for both cross-striation breadths (DESRs) and perikymata breadths to analyze patterns of growth rates between males and females of each species and genus included. Analyses which examined DESRs only included measurements of cross-striations from the imbricational region of the tooth, because this region

provided the most complete measurement sample in all canines included. In the case of *Cebus*, only measurements from the middle third (in terms of distance from EDJ to enamel surface) of the imbricational region (mid-imbricational) was used in analyses, because a number of specimens lacked sufficient incremental anatomy in either surface or deep enamel for statistical analyses including all three regions. Due to the fact that all specimens of *Alouatta* presented adequate detail in surface, middle, and deep imbricational enamel, all three enamel-depth regions were included in analyses of this genus.

For the t-tests comparing males and females of *Saimiri*, all specimens from the genus were grouped in order to boost sample size. This option was deemed appropriate because *S. oerstedii* and *S. sciureus* are not statistically distinguishable from one another in terms of DESR (see Fig. 3-7), or Retzius periodicity (see Table 6-1) in their postcanine dentition. The single female *S. boliviensis* specimen was not included in analyses for Chapter 7, as its overall (postcanine) DESR significantly differs from that of all other *Saimiri* sampled (see Chapter 4).

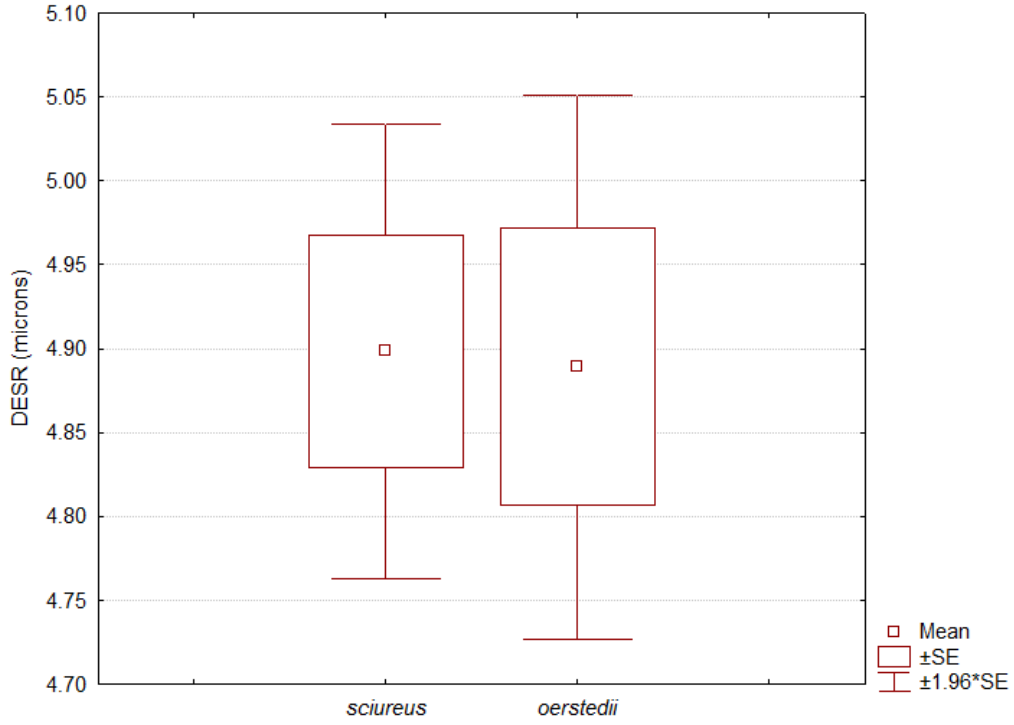


Fig. 3-7. Box-plot comparison of DESR in *S. sciureus* and *S. oerstedii*, which do not differ significantly (p = 0.94).

It is important to note here that any comparison of perikymata (male versus female *Saimiri* in this study) is only reliable as an estimator of growth rate if the Retzius periodicity (i.e., number of cross-striations between perikymata) is known. This is especially true in dimorphic taxa where males will tend to have an overall longer Retzius periodicity than females due to their larger body size (see Chapter 6). This difference will be reflected in a relative increase in perikymata breadth for males that is unrelated to actual growth rates, which could be misinterpreted as a signal of faster growth rate in males versus females. However, due to the fact that all members

of *Saimiri* which have been analyzed histologically in this study have a Retzius period of three days regardless of sex or even species, perikymata are viable indicators of growth rate dimorphism in this genus. *Cebus* and *Alouatta*, on the other hand, are sexually dimorphic in their Retzius periodicity, probably because they have more body mass dimorphism than *Saimiri* (Plavcan and Van Schaik 1997).

In order to make direct comparisons to previous histological studies of canine dimorphism in non-platyrrhine taxa (e.g., Schwartz et al. 2005), I also estimated canine crown formation times. Overall canine formation times for males and females were estimated using striae of Retzius and DESRs to calculate the total number of days taken to deposit the enamel of the entire tooth crown. This method traces the progression of the enamel formation front of the tooth during growth, adding the number of days required to form individual enamel prisms at successive, non-overlapping striae of Retzius along the crown length. By using non-overlapping Retzius lines as landmarks, it is possible to track the progress of individual ameloblasts whose activity does not overlap in time so that an accurate estimate of crown formation time can be achieved (Fig. 3-8).

In locations where Retzius lines were not clearly visible, an estimate of their angle and EDJ intersection were extrapolated from the nearest available Retzius lines in the tooth. This technique provides only a rough estimate of crown formation time. In order to determine the consistency of my estimates for the

position of these striae, I independently repeated the estimation process on two separate tooth images four times over the course of several months. The estimate was very similar all four times for each image and suggests repeatability. Unfortunately, for some teeth there was not sufficient Retzius anatomy for such large portions of the enamel (due to decussation, etc.) that reasonable estimates of crown formation time were not possible. Because of this, crown formation times in this study should be seen as auxiliary data to DESRs.

Materials and Methods specific to the four data chapters (4-7) are further discussed in each of these chapters.

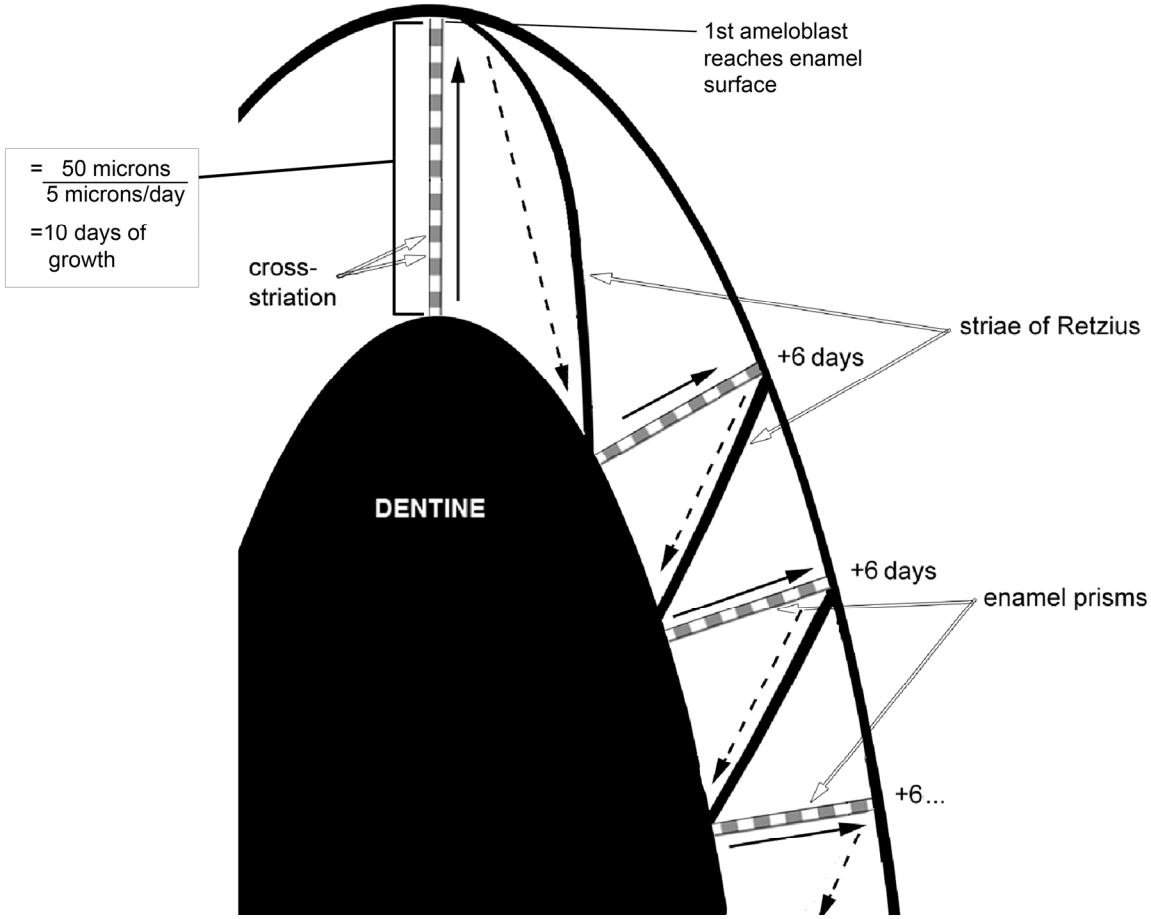


Fig. 3-8. Method used to estimate total crown formation time (CFT) in this study. First, an estimate of cuspal enamel formation time was calculated (=10 days in illustration) by measuring the greatest distance between the dentine and enamel surface at the cusp tips parallel to enamel prism paths (50 microns in illustration), and dividing this by the known DESR for this hypothetical species (i.e., 5 microns/day). When the first cuspal ameloblast reaches the enamel surface, it is finished secreting. The solid arrows proceed out along prisms and represent the number of days it took to form that segment of enamel (i.e., 10). From this cuspal point, I traced the nearest stria of Retzius down to the EDJ (see dashed arrows); at this new location, a new ameloblast starts working when the first cuspal ameloblast is finished and starts a successive prism (i.e., growth time does not overlap). Therefore, I continued this process of counting days and proceeding along striae of Retzius to the next block of time down (prism segment) until I reached the cervix of the tooth. Then I calculated the total number of days it took to complete all successive prism segments of enamel formation to provide a CFT estimate.

Chapter 4:

A General Description of Microanatomy in Cebid Teeth

Introduction

Although gross morphology and eruption patterns of cebid teeth have been described in detail (e.g., Schultz 1960b; Kinzey 1974; Rosenberger and Kinzey 1976; Hershkovitz 1977; Rosenberger 1979; for eruption patterns, see Chase and Cooper 1968; Long and Cooper 1968; Hershkovitz 1977; Fleagle and Schaffler 1982; Henderson 2007), their enamel microanatomy has received much less attention, with the exception of a few studies (i.e., Gantt 1980; Nogami and Yoneda 1983; Nogami and Natori 1986). However, none of these studies examines enamel growth or function. Gantt (1980), which only examines individual prism anatomy, does demonstrate homology in prisms between platyrrhines and catarrhines when compared to other primates such as the adapids. The other two studies (Nogami and Yoneda 1983; Nogami and Natori 1986) focus on the *schmeltzmusters* (overall prism patterns; see Chapter 2) of the platyrrhines. While these two studies provide important information regarding the presence or absence of specific patterns (e.g., radial enamel) in a tooth of a species, they do not address how these *schmeltzmusters* vary within a tooth or across tooth types and they also give little attention to the evolutionary significance of their findings. Therefore, the mechanical structure, function and microstructural evolution of

platyrrhine teeth are still poorly understood. And again, as none of these studies examines dental increments (Retzius lines and cross-striations) of the teeth, knowledge regarding the development of platyrrhine teeth is also limited. Thus, although a few other papers and abstracts have included some platyrrhine genera in their analyses of enamel increments and function (e.g., Maas 1986; Dirks et al. 2004; Martin et al. 2003), there is still little comprehensive analysis of microstructure within platyrrhine taxa such as the cebids.

Overall, therefore, more information is still needed in order to better understand the intricacies and patterns of variation in the dental microstructure of cebids. The three main goals of this chapter, then, are: 1) to increase the known sample by further describing and cataloguing the enamel microstructure of the cebids, and to provide additional data regarding dental increments and *schmeltzmusters* within a tooth crown and across tooth types; 2) to understand how the *schmeltzmusters* of teeth reflect the mechanical demands of food breakdown as well as phylogeny/evolution; and 3) to provide the framework for later chapters which examine and discuss the life histories of cebid genera based on analysis of enamel increments.

First, I will describe the overall cebid patterns of enamel microstructure (dental increments and *schmeltzmusters*), and then will describe the specific *schmeltzmusters* of each cebid genus.

Brief Description of Cebid Enamel Increments

Cebid Retzius repeat intervals range between 1 and 6 days; that is, a stria of Retzius is laid down every 1 to 6 days depending on the species (Table 4-1). Striae of Retzius do not appear below the neonatal line in any cebids sampled. Cross-striation breadths (i.e., daily enamel secretion rates or DESR's) for cebids range between approximately 3.4 to 5.3 microns, with means of 3.9 to 5.2 microns for individual genera (Fig. 4-1). See Chapters 5 and 6 for specific analyses and discussion on enamel increments.

Genus	Species (N)	Retzius interval average (days)	Genus average (days)
Aotus	sp. (2)	3	**3**
Cebus	*albifrons* (2)	6.5	**5**
	apella (2)	4.5	
	capucinus (2)	5	
	olivaceus (1)	4	
Saimiri	*boliviensis* (1)	3	**3**
	oerstedii (1)	3	
	sciureus (1)	3	
Callimico	*goeldii* (1)	3	**3**
Callithrix	*jacchus* (1)	1	**2**
	humeralifer (1)	3	
Cebuella	*pygmaea* (1)	1	**1**
Leontopithecus	*rosalia* (1)	3	**3**
Saguinus	*fuscicollis* (1)	2	**1.667**
	midas (1)		
	nigricollis (1)	2	
	oedipus (1)	1	

Table 4-1. Average Retzius repeat interval (in days) for each cebid species analyzed in this dissertation, as well as average Retzius intervals for each genus.

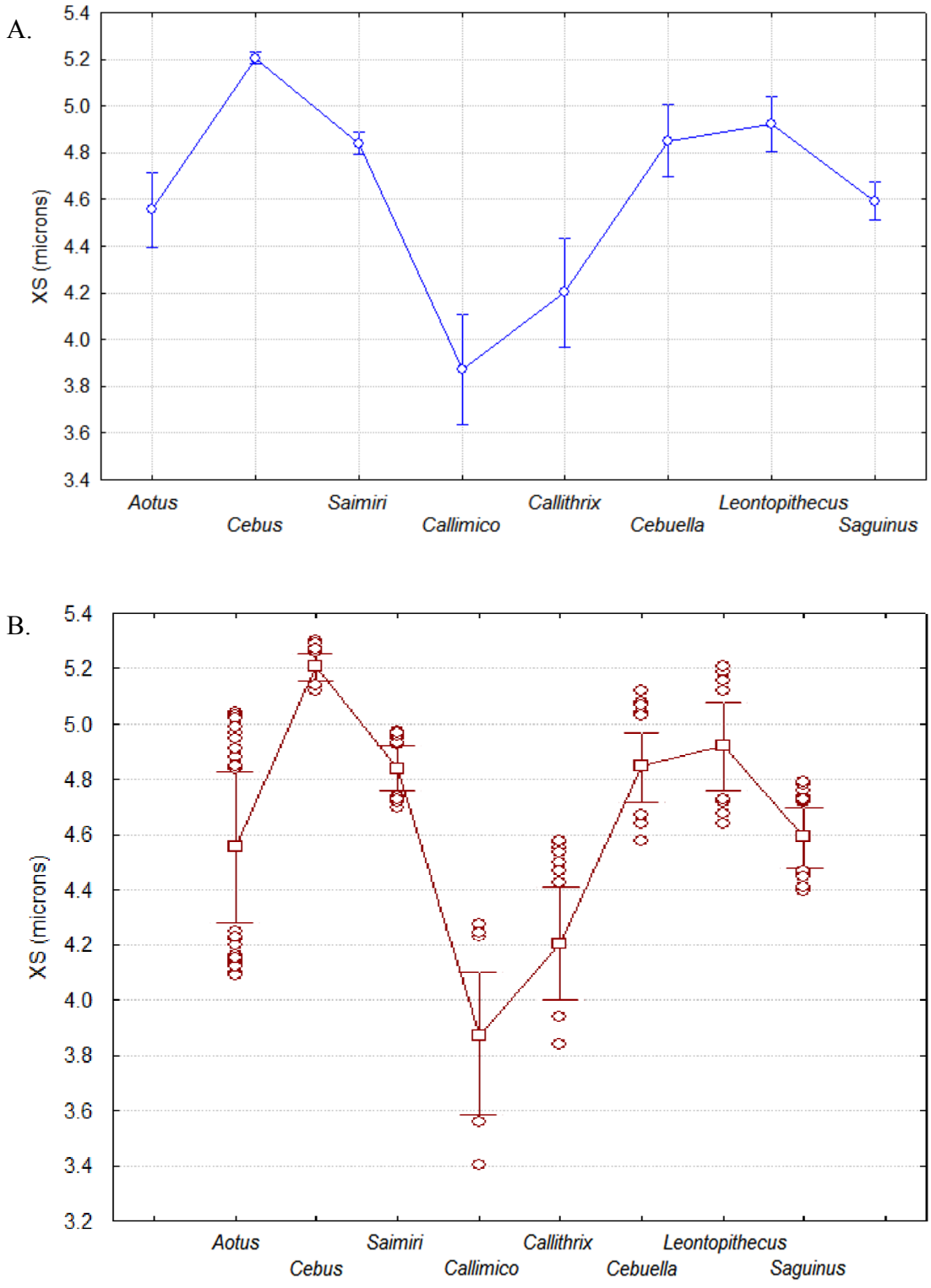


Fig. 4-1. Variation in the cross-striation breadths, or DESRs (XS, in microns) of the Cebidae. **A.** Diagram showing mean cross-striation breadth and 95% confidence intervals for each genus (whiskers); **B.** Diagram showing means and non-outlier range (whiskers), with outliers included (circles).

Striae of Retzius in cebids are most readily apparent near the surface of imbricational enamel, and also are more visible toward the cervix of the tooth. In other words, they appear less often as clear structures in cuspal and deep enamel (e.g., Figs. 4-2 and 4-3). This pattern is observed in some cercopithecoids and hominoids as well, and so is not unusual for anthropoids (e.g., Smith et al. 2003b, 2006). Retzius lines are also more clear in areas where prism structure has broken down and the enamel is aprismatic. Since aprismatic enamel is most often found near the enamel surface and/or cervix, it makes sense that the striae of Retzius in cebids were the most apparent in these locations (Figs. 4-2 to 4-5). However, I must highlight that aprismatic enamel in cebids did not always feature emphasized striae of Retzius or cross-striations[1] (Fig. 4-6) and that striae of Retzius are found in prismatic enamel, but are usually not as strongly developed (see again Figs. 4-3 to 4-5).

[1] Smith (2004) uses the term 'laminations' for the cross-striations between Retzius lines in aprismatic enamel. She has shown that 'laminations' carry the circadian rhythm of cross-striations, and appear to be a manifestation of the same phenomenon in aprismatic enamel that cross-striations are in prismatic enamel; therefore, I believe the term 'lamination' should be subsumed into 'cross-striation'.

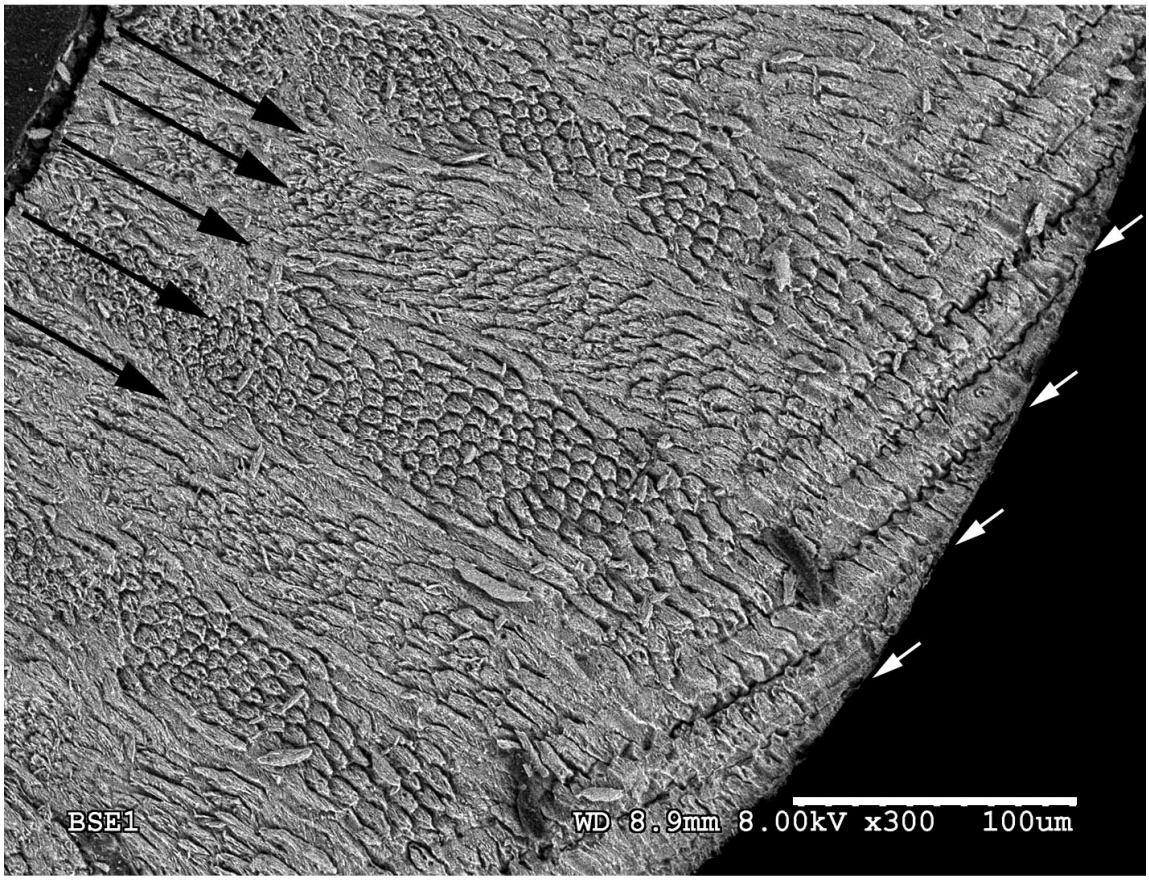


Fig. 4-2. SEM micrograph of a *Cebus albifrons* P2 taken near mid-crown on the lingual side of the tooth. Note the appearance of Retzius lines (white arrows) near the enamel surface (lower right corner of picture). The top right of the picture is in the direction of the tooth cusp, whereas the lower left is closer to the cervix. Also, note the black arrows near the dentine (upper left corner), which indicate the clear Hunter-Schreger bands, discussed later in this chapter. The white bar in the lower right corner indicates a scale of 100 microns.

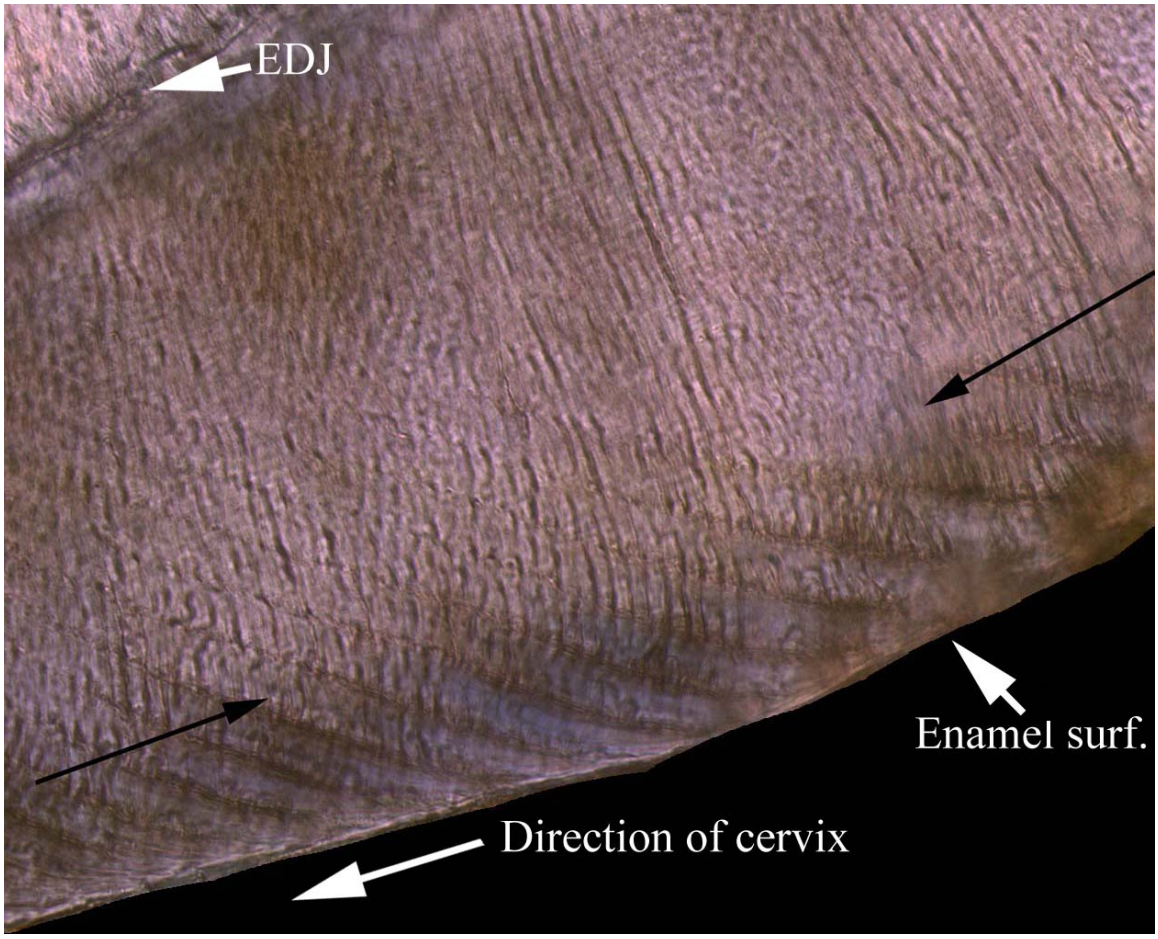


Fig. 4-3. An image of a *Cebus albifrons* P2 taken in CPL; the specimen and tooth region are the same as in Fig. 4-2, and the orientation is similar. Black arrows indicate the plane near which prism morphology breaks down and Retzius morphology becomes more apparent (near the enamel surface). **Field width = 396 microns.**

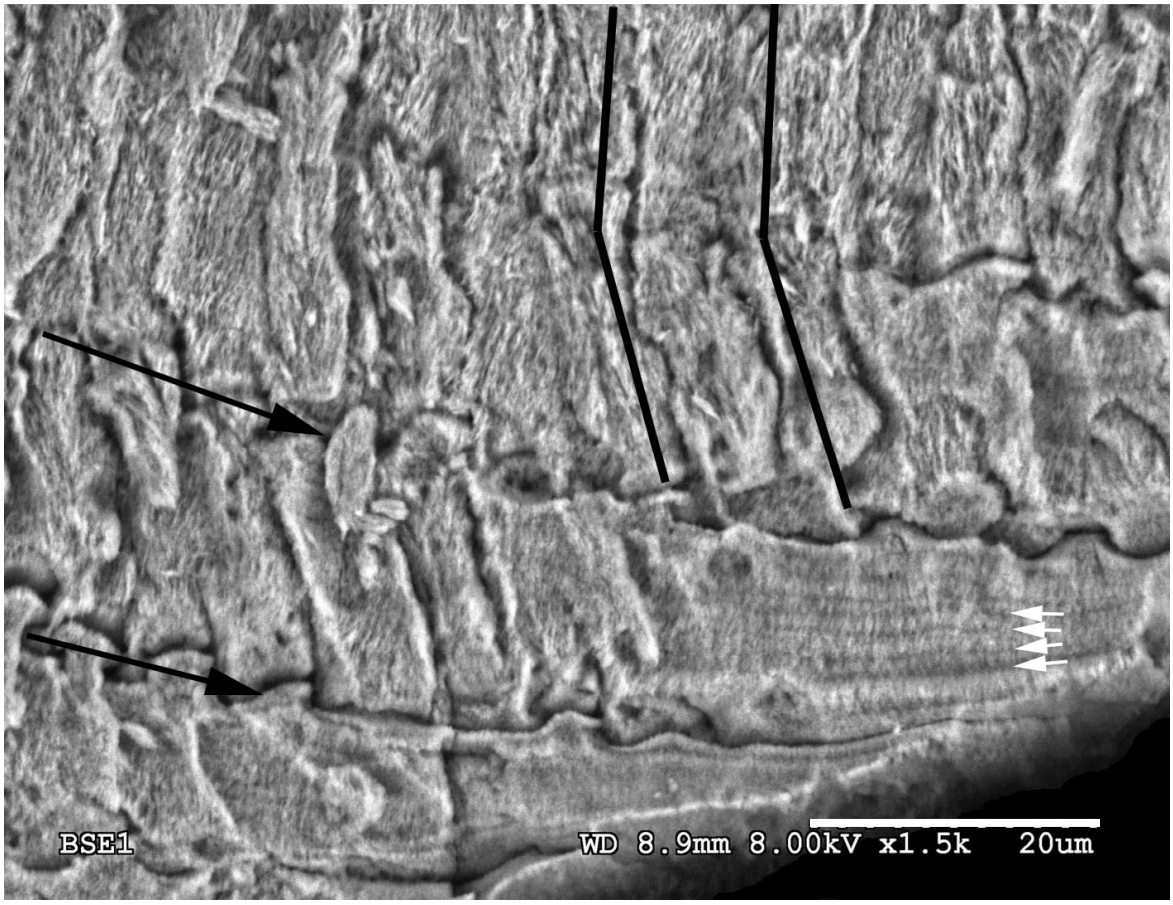


Fig. 4-4. Magnified image of the same specimen shown in Fig. 4-2, near the tooth surface (*C. albifrons*, P2). Tooth surface is indicated by the black space in the lower right corner, while the dentine is located in the direction of upper left. The left and right sides of the image represent the cervical and cuspal directions, respectively. This image demonstrates that cross-striations (white arrows) and striae of Retzius (black arrows) are more apparent closer to the enamel surface where there is dissolution of the enamel prisms (e.g., a prism is between the parallel black lines). The white line in lower right corner indicates a scale of 20 microns.

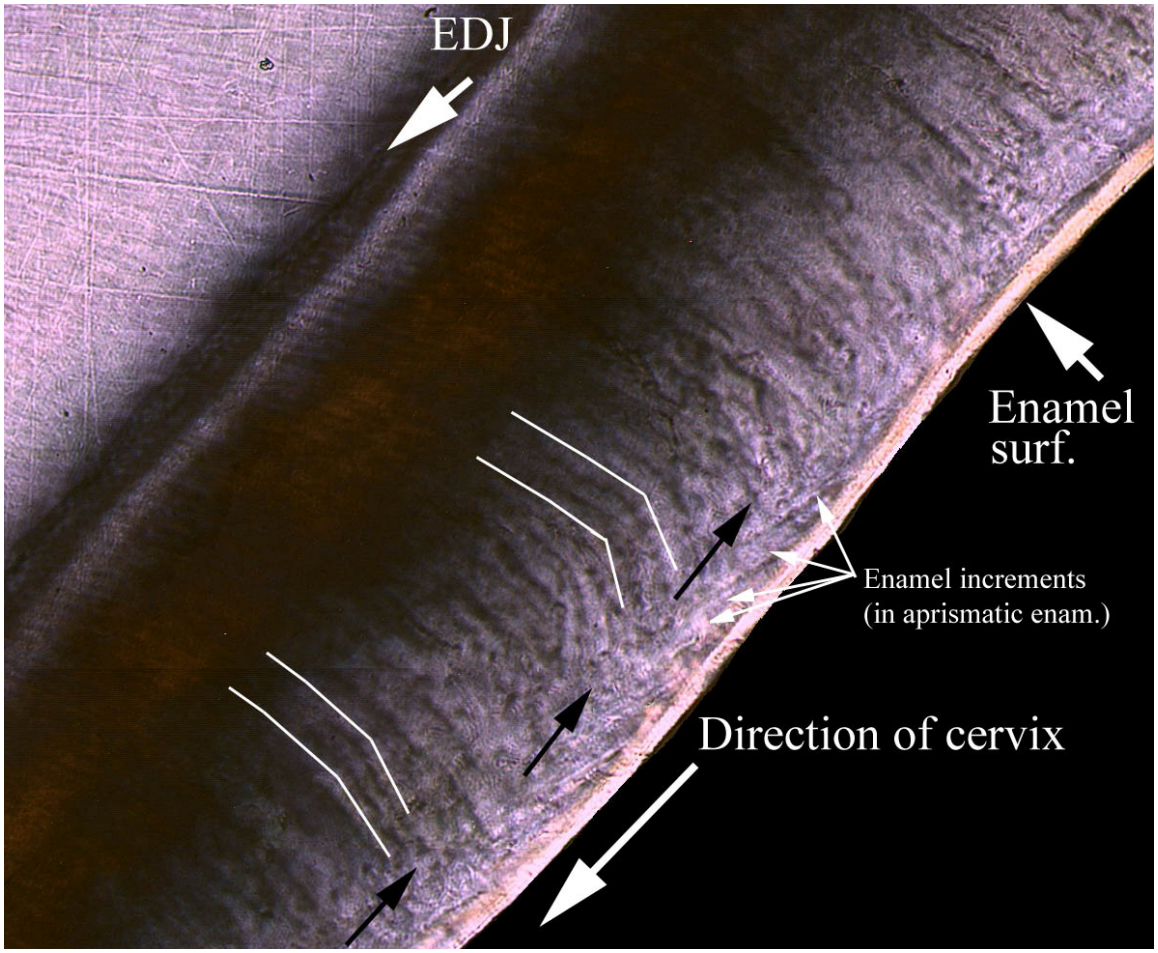


Fig. 4-5. CPL image of a *Saimiri sciureus* P3, taken in mid-crown on the buccal side of the tooth. Enamel prisms (e.g., between white lines) can be seen as alternating gray and black bands traveling from the dentine to the tooth surface. Note that toward the tooth surface, at the area indicated by the black arrows, individual prisms become indistinct as aprismatic enamel appears. Note also that incremental lines become more distinct. **Field width = 373 microns.**

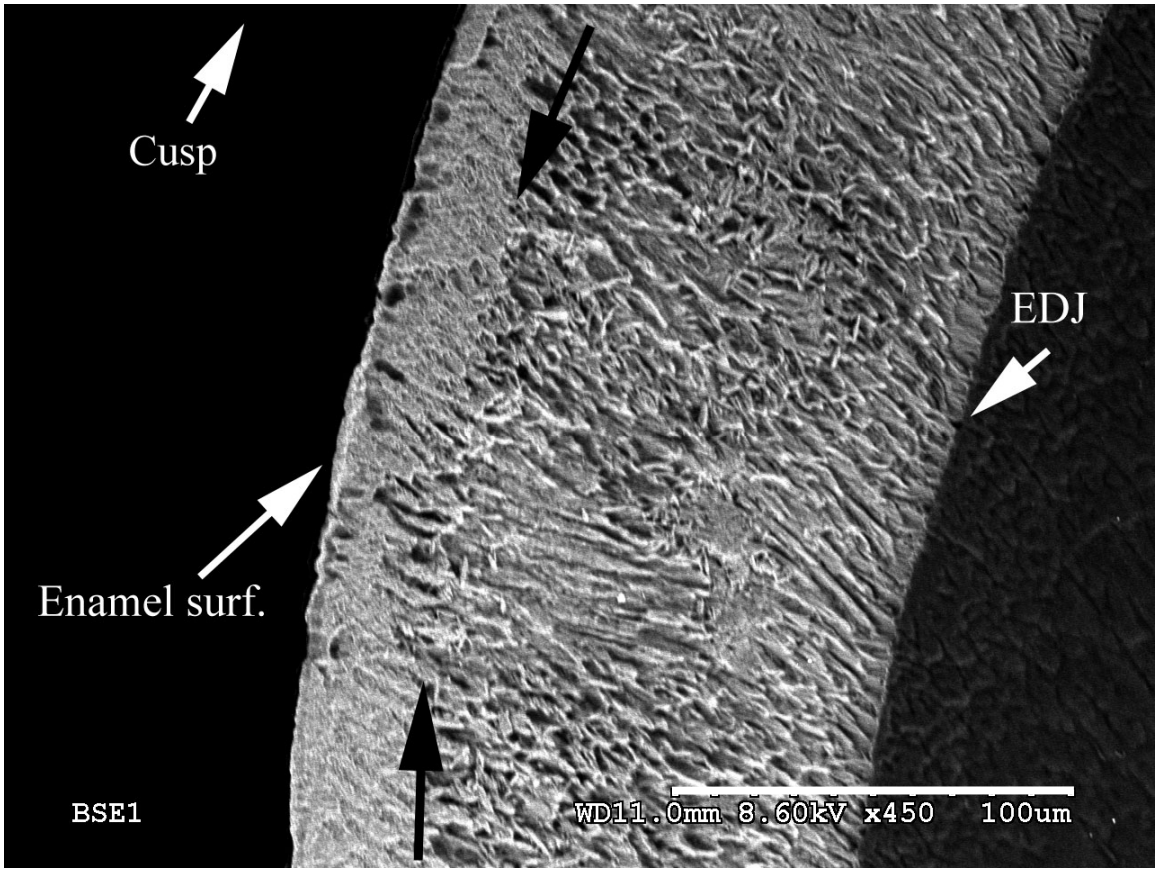


Fig. 4-6. SEM image of imbricational enamel near the cusp of a P4 from *Callimico goeldii*, on the lingual side of the cusp. Area to the right of the black arrows shows distinct prism anatomy, whereas toward the enamel surface the enamel becomes aprismatic. However, in this case striae of Retzius are not apparent in either prismatic or aprismatic enamel. The white line in lower right represents a scale of 100 microns.

In mammals, aprismatic enamel usually occurs near the enamel surface and/or the cervix of the tooth. Since the geometry of the Tomes' process determines enamel crystallite orientations, and in turn, the presence of prisms (e.g., Risnes 1998; see Chapter 2 for an explanation), the transition from prismatic to aprismatic enamel probably occurs because ameloblast cells undergo a 'regression' of their Tomes' processes as they come to the end of their secretory phase near the surface of the tooth (Risnes 1998). The cebids, then, seem to reflect a general mammalian pattern in this case.

As discussed in Chapters 2 and 3, striae of Retzius not only record biological rhythms, they also record the position of all actively secreting ameloblasts at the time when an individial stria is formed. Therefore, they act as a "fossilized" remnant of the position of enamel formation fronts (EFFs; see Chapter 3). Due to this, their morphology can provide information about crown formation rates. A narrower angle between striae of Retzius/EFFs and the enamel-dentine junction (EDJ) reflects an increased number of active ameloblasts along the EFF (illustrated in Fig. 3-5). This enables a faster enamel extension rate, which translates into a faster crown growth rate. Therefore, one way to assess and compare crown growth rates across different taxa is to use these EFF/EDJ angles. Accordingly, measurements of these angles were taken for this dissertation (see Chapter 3). Fig. 4-7 presents general comparative data on EFF/EDJ angles for each cebid genus which I was able to measure for this study (data were

not available for *Callithrix* or *Cebuella*), while Table 4-2 presents mean EFF/EDJ angles for each species and tooth sampled. For more detailed analysis of these EFF/EDJ angles and their relationship to life history variables in the cebids, see Chapter 5. The remainder of this chapter will focus on cebid *schmeltzmusters* specifically.

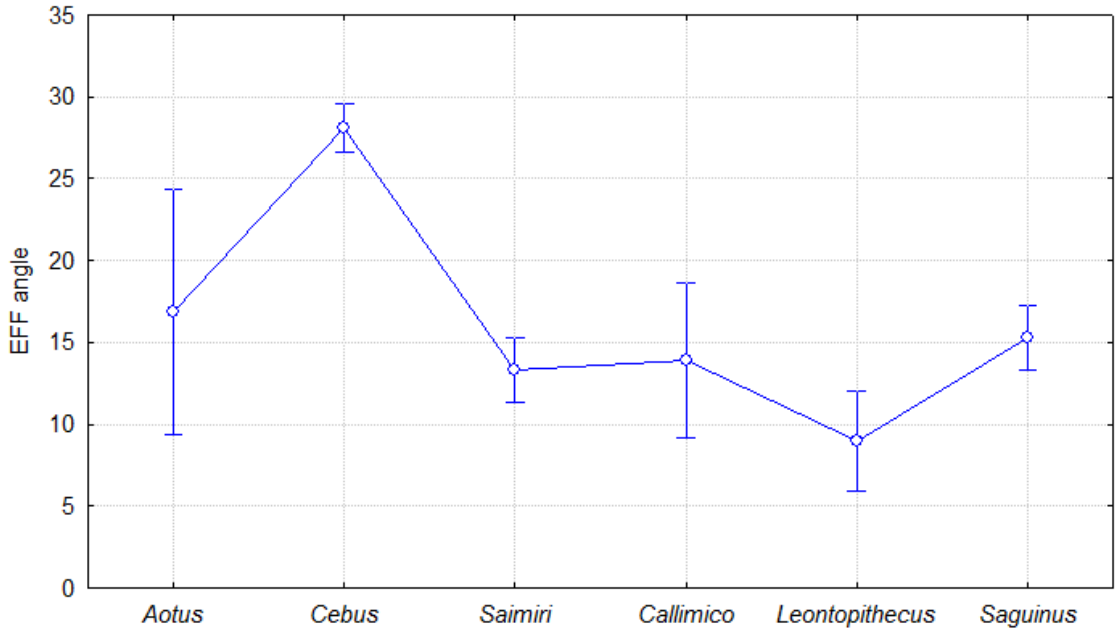


Fig. 4-7. Plot showing mean angles between EFFs (striae of Retzius) and EDJs, in degrees, for the different cebid genera. Whiskers denote 95% confidence intervals. As illustrated in Fig. 3-5, *lower* angle values reflect *faster* crown extension rates; therefore, *Cebus* has the slowest extension rate shown here.

Genus	Species (N)	Tooth	Tooth average (degrees)	Species average (degrees)
Aotus	sp. (1)	M1	16.868	16.868
Callimico	*goeldii* (1)	M1	13.905	13.905
Cebus	*albifrons* (1)	M1	36.743	36.74
Cebus	*apella* (1)	M1	19.56	
		M2	23.951	22.355
Cebus	*capucinus* (2)	M1	24.578	
		M2	24.124	24.36
Leontopithecus	*rosalia* (1)	M1	8.961	8.96
Saguinus	*fuscicollis* (1)	M2	16.763	16.763
Saguinus	*nigricollis* (1)	M1	13.938	
		M2	15.815	14.791
Saimiri	*oerstedii* (1)	M1	14.176	14.176
Saimiri	*sciureus* (1)	M1	12.601	
		M2	13.801	13.001

Table 4-2. Enamel formation front angles (angle between striae of Retzius/EFF and EDJ) for species sampled in this study. Averages of angle measurements are given for each tooth sampled (M1's and M2's), as well as an average across both teeth for each species. Values for standard deviations, etc. are not given, due to low sample sizes for most species (raw data for EFF angle measurements are available in Appendix B). Note that only two Retzius lines were clear enough to provide a measurable angle in available *Aotus* molars.

General Cebid *Schmeltzmuster* Description

With regard to enamel microanatomy, this study confirms that, like all other primates and the majority of mammals, cebids primarily exhibit a prismatic-type of enamel (e.g., Nogami and Natori 1986; Koenigswald et al. 1987, Koenigswald 2000; Maas and Dumont 1999; see Chapter 2). This study also corroborates and builds on prior observations that Cebidae is characterized by a high degree of variation in *schmeltzmusters*; some genera exhibit purely radial enamel while others exhibit high gnarling, decussation, and varying degrees of Hunter-Schreger band organization (see Nogami and Yoneda 1983; Nogami and Natori 1986).

This study has specifically found an arc-shaped path of individual enamel prisms in some teeth that has not been discussed in previous studies. This arc-shaped path was only found in some of the *Cebus, Saimiri, Callimico, Leontopithecus,* and *Saguinus* teeth sampled; not all teeth and not all individuals of these genera exhibited this arc-shaped path. This condition was not observed in any of the teeth from the *Aotus*, *Callithrix* and *Cebuella* individuals. In areas where this arc-shaped path is present, the enamel is radial as opposed to decussating. The convex side of the arc was always observed to be oriented in a cuspal (vs. cervical) direction (Fig. 4-8).

In some cebid genera such as *Saimiri*, *Cebus*, *Leontopithecus*, and *Cebuella*, enamel prism orientation is relatively perpendicular to the EDJ initially, but in some teeth it makes a turn in the cervical direction (Fig. 4-9; see also section on *Leontopithecus* below). This direction-shift occurs as prisms approach the enamel surface in the lower half of the

imbricational and the cervical portions of the tooth. This downward angulation of prisms is often associated with the breakdown of prism structure and increased visibility of the striae of Retzius (mentioned above; see also Fig. 4-9B and C). This pattern also appears in a *Callicebus torquatus* (i.e., a non-cebid) molar imaged during the course of this study.

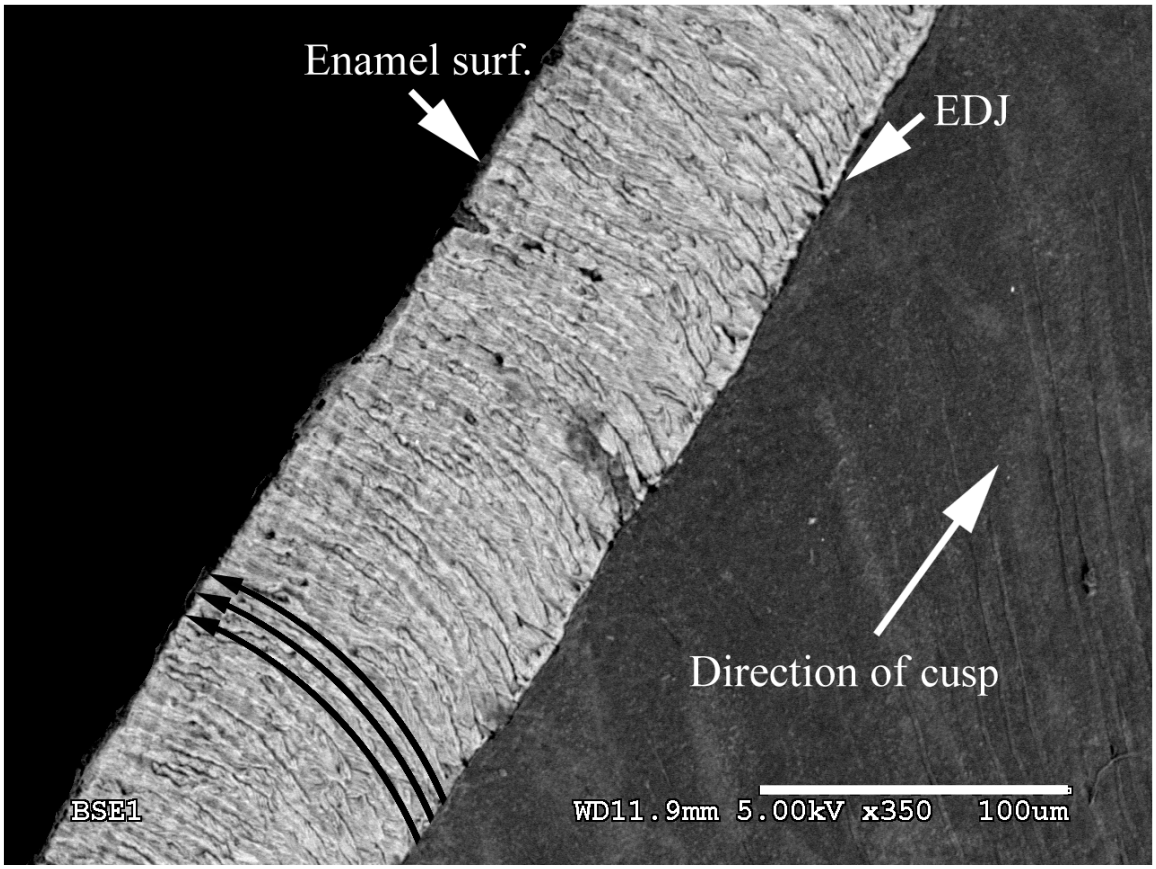


Fig. 4-8. An example of the prism arcing seen sometimes in cebids, specifically from mid-crown (imbricational) enamel on the lingual side of a *Saguinus oedipus* premolar. Curved black arrows moving away from dentine (dark gray in lower right corner of picture) diagram the arced prism paths, which can be seen along the light-gray enamel band. Cross-striations are also visible. The white line indicates a scale of 100 microns.

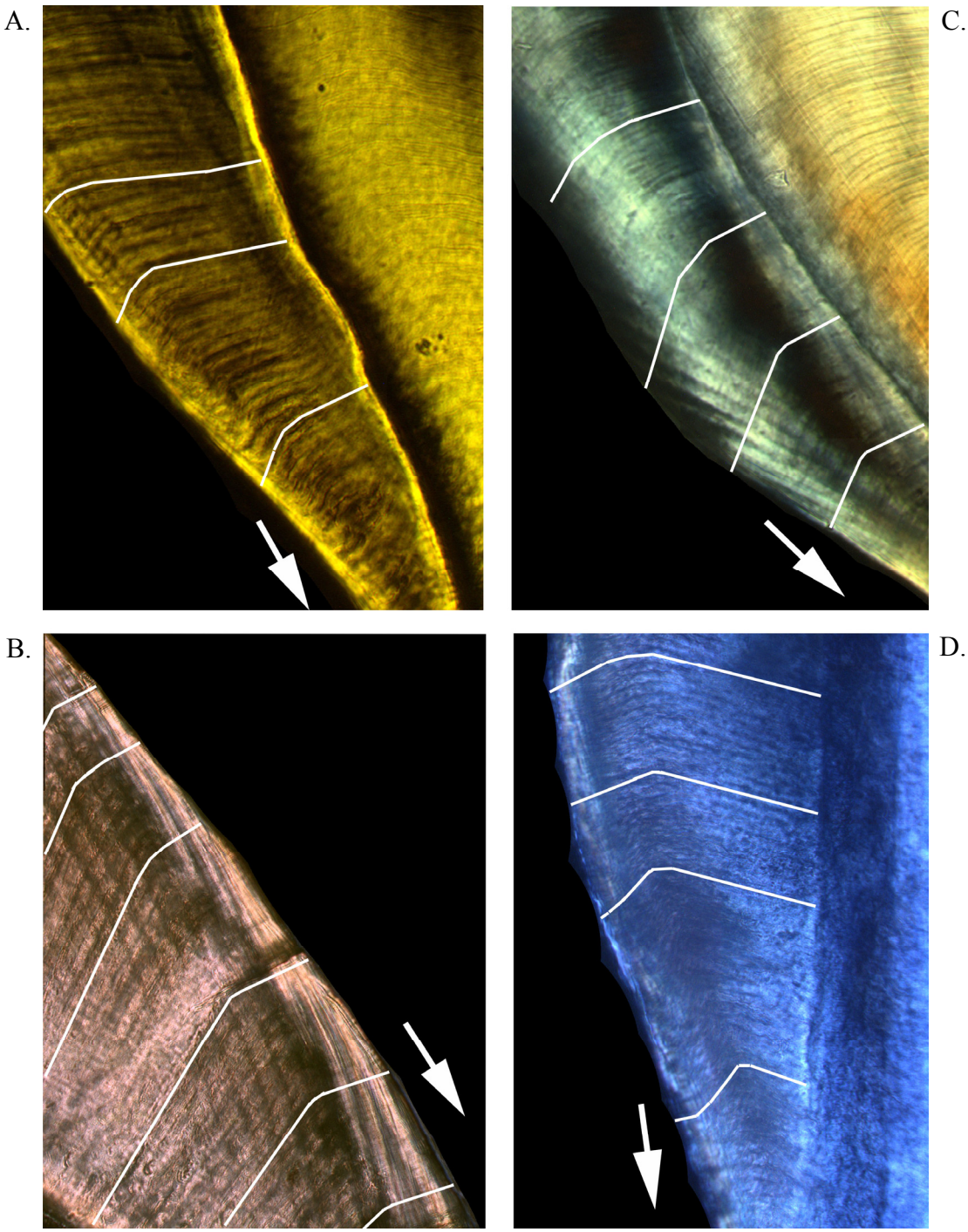


Fig. 4-9. Cervical bending of prisms close to the cervix in three different cebid genera, as well as *Callicebus*. **A.** *S. oerstedii* M1, **B.** *C. albifrons* M3, **C.** *L. rosalia* P2, **D.** *C. torquatus* M3. White arrows indicate direction of tooth cervix, just out of view. Angled white lines follow the paths of a few example prisms to show changes in orientation. The prisms are initially roughly perpendicular to the EDJ and switch their orientation toward the cervix as they approach the enamel surface. **Field width in microns: A = 211; B = 239; C = 281; D = 224.**

Microanatomy: Genus Descriptions

In comparing patterns of prism microstructure among genera, the *schmeltzmusters* of *Saimiri* and *Aotus* will be discussed first to provide a comparative standard for the rest of Cebidae. Even though these two genera are most likely not members of the same subfamily (see Chapter 1), I have chosen them as the first baseline because they both exhibit a common, simple enamel pattern. In other words, these two genera do not differ enough in their *schmeltzmusters* to warrant individual discussion here. All of the other cebid genera exhibit enamel patterns that are different from this shared pattern of *Saimiri* and *Aotus*. See Table 4-3 for a summary of enamel characters seen among the cebid taxa.

Cebines/Aotines

Saimiri and *Aotus*

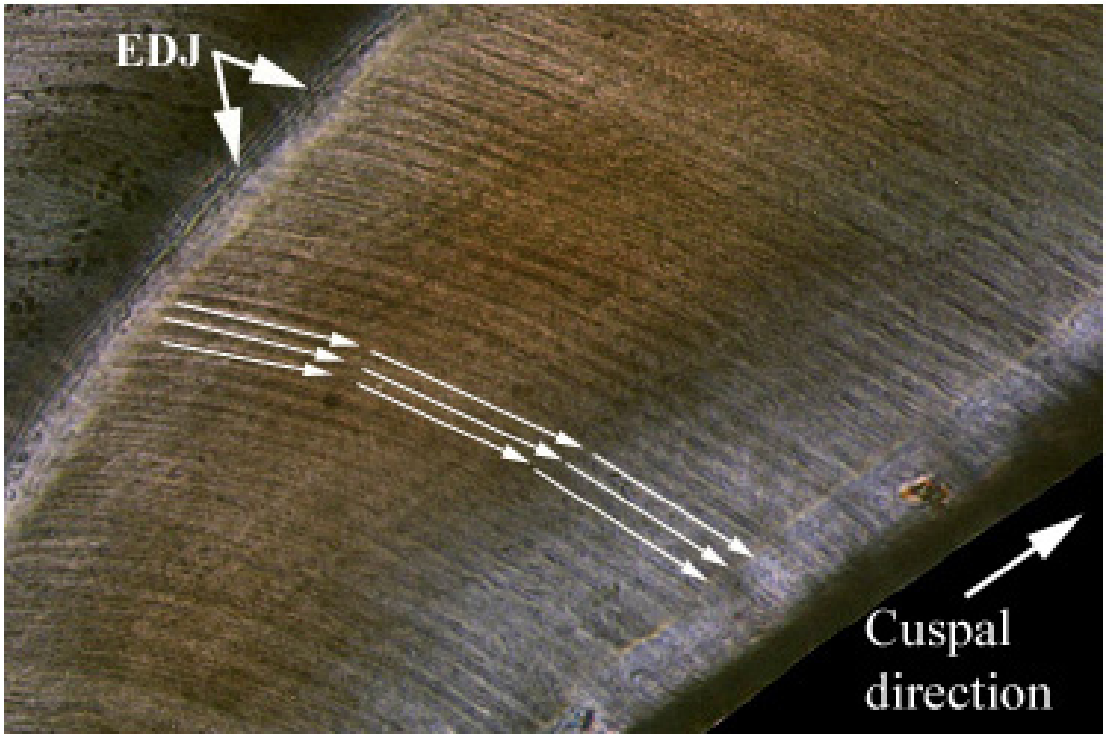
As just mentioned, *Saimiri* and *Aotus* have the simplest *schmeltzmuster* of the cebids, and most closely resemble the primitive therian condition as interpreted by Koenigswald and colleagues (1987). None of the three *Saimiri* species or the *Aotus* specimens examined in this study showed any degree of decussation. Instead, all of the enamel patterns observed in

Genus (N)	Radial enamel	Decussating enamel	H-S bands	Prism arcing	Cervical downturn in prisms	Aprismatic enamel observed
Aotus (2)	Y	N	N	Y	N	?
Saimiri (4)	Y	N	N	Y	Y	Y
Cebus (12)	Y	Y	Y	Y	Y	Y
Callimico (1)	Y	Y	Y (No - N&N)	Y	?	Y
Callithrix (2)	?	Y	Y	N	?	?
Cebuella (1)	?	Y	? (Yes - N&N)	?	Y	?
Leontopithecus (1)	Y	Y (No – N&N)	? (No - N&N)	Y	Y	?
Saguinus (4)	Y	Y (No – N&N)	Y (No - N&N)	Y	Y	Y

Table 4-3. Chart of *schmeltzmuster* characters in cebid genera, as seen in this dissertation. "Y" indicates that a character was observed whereas "N" indicates that it was not observed. A question mark (?) indicates that the sample size and/or image quality for this character was too poor to provide a reliable observation. The first three columns corroborate the results of previous studies (see Nogami and Yoneda 1983; Nogami and Natori 1986) with the exception of a few cases which specifically disagree with the findings of Nogami and Natori (see N&N). The data in the last three columns are fully original data and have not been examined in previous studies.

these two genera were radial (see also Nogami and Yoneda 1983 and Fig. 4-10). This completely radial enamel pattern suggests that the teeth of these two genera have not needed to adapt to resist high bite forces or mechanically demanding diets (see discussion below). Once again, the only variation to this pattern is the occasional appearance of arc-shaped prisms (both *Saimiri* and *Aotus*) and cervical prism bending (*Saimiri* only); see Table 4-3.

A.



B.

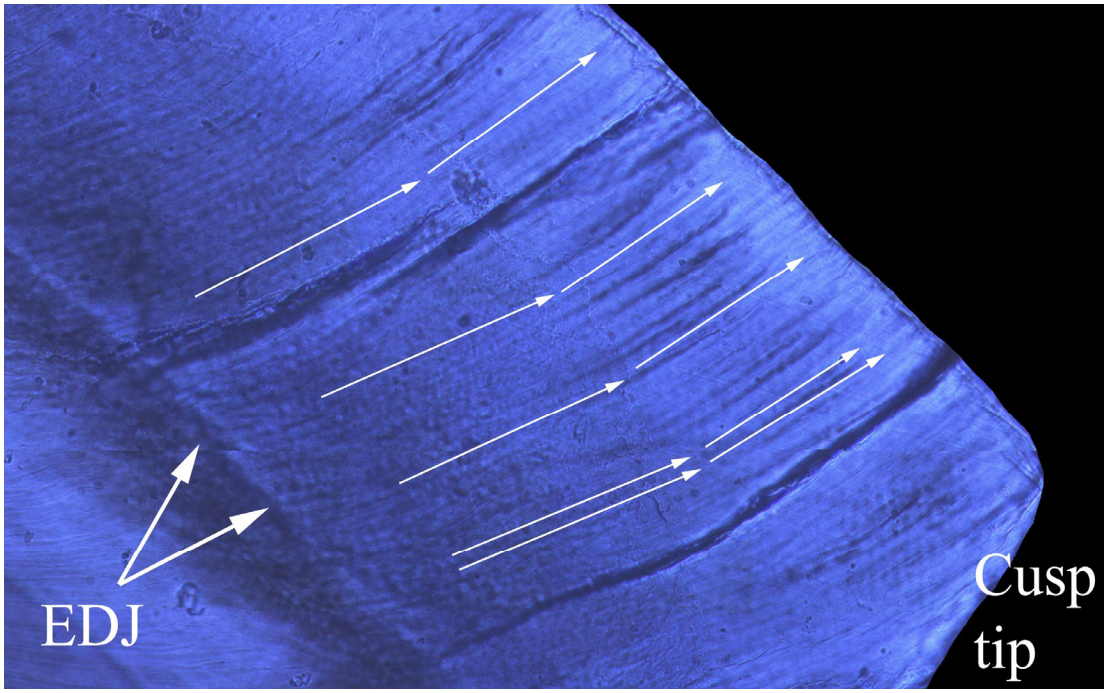


Fig. 4-10. Radial enamel in *Saimiri* and *Aotus*. Narrow white arrows indicate prism paths. **A.** Cuspal enamel from a *S. sciureus* M2. **B.** Cuspal enamel on the buccal side of an *Aotus* sp. mandibular canine. **Field width in microns: A = 134; B = 432.**

Cebus

There were substantially more specimens of *Cebus* available for study in this project than any other genus, and so more detail is available for the *schmeltzmuster* of *Cebus*. In general, *Cebus* exhibits the highest degree of gnarled and decussating prism patterns for the cebids, and possesses only a small amount of radial enamel. In general, all *Cebus* teeth examined in this study exhibited extensive Hunter-Schreger banding especially in their imbricational enamel (e.g., Fig. 4-11; see also Fig. 4-2). There are two main reasons it is not surprising that *Cebus* teeth are highly decussated. First, *Cebus* is an omnivore and hard-object feeder to varying degrees, with *C. apella* standing out as the species with the most mechanically demanding suite of foods in its diet (e.g., Kinzey 1974; Struhsaker and Leland 1977; Teaford 1985; Brown and Zunino 1990; Fragaszy et al. 1990; Fernandes 1991; Janson and Boinksi 1992; Galetti and Pedroni 1994; Fragaszy and Boinski 1995; Kinzey 1997; Fragaszy et al. 2004; Wright 2005; Addessi 2008). *Cebus*, especially *C. apella*, is also well outside the relative enamel thickness values of other platyrrhines (e.g., Martin et al. 2003). Therefore, *schmeltzmuster* data for *Cebus* seem to fit in well with prior interpretations that *Cebus* teeth are adapted to a high-force feeding regime, based on diverse datasets such as enamel thickness, gross morphology, and microwear (e.g., Kinzey 1974;

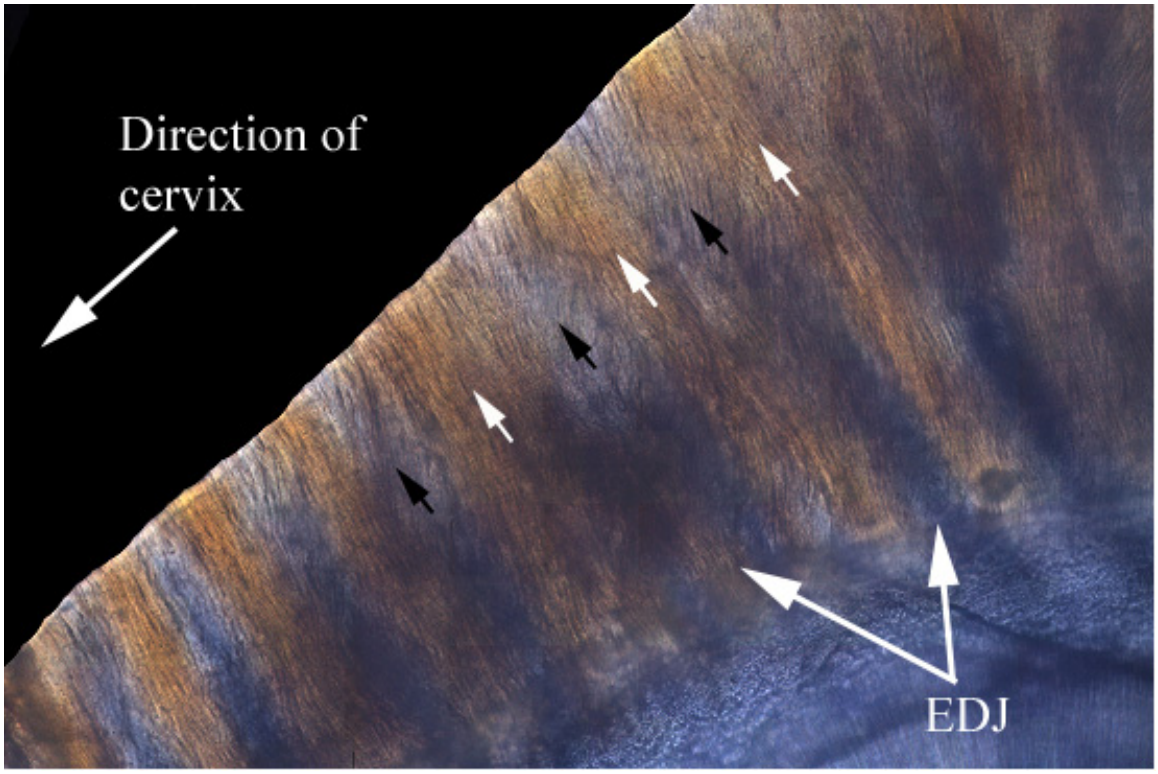


Fig 4-11. Image of Hunter-Schreger bands in a *Cebus* sp. M3, showing an example of color differences between alternating prism bundles) in circularly polarized light (alternating black and white arrows; see Chapter 3 for discussion of CPL imaging). The photo was taken just cervical to the cusp tip on the mesial side of the tooth. **Field width = 974 microns.**

Fig. 4-12. Image of decussation and enamel gnarling in the cusp (see right) of a *C. albifrons* canine. Alternating bands of color represent Hunter-Schreger bands, which are located throughout the canine (i.e., in the cusp tip and imbricational enamel in this image). White box depicts inset area for Fig. 4-13. **Field width = 1,612 microns.**

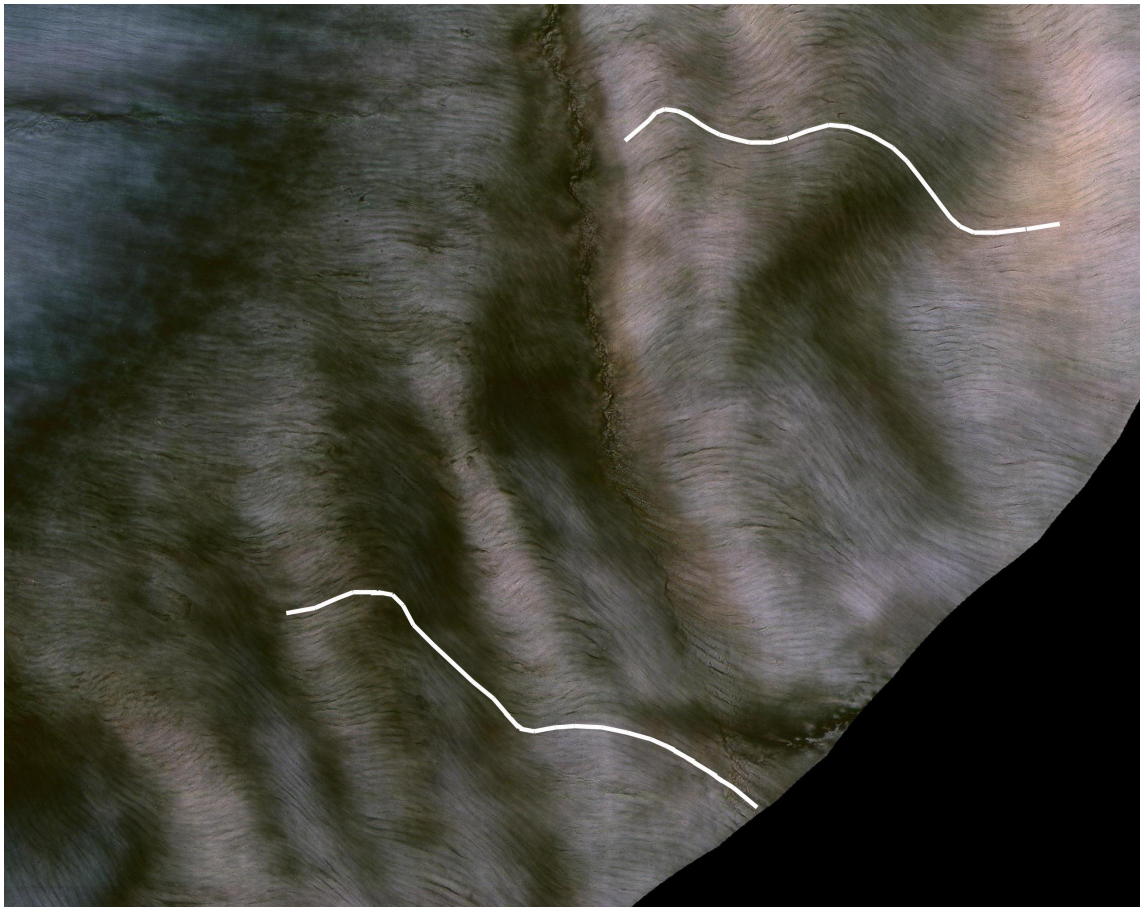


Fig. 4-13. Enlarged image of inset from Fig. 4-12. In this image individual prism paths can be seen in addition to Hunter-Schreger banding. The paths of two individual prisms are traced here with white lines, showing a highly gnarled pattern. **Field width = 839 microns.**

Teaford 1985; Rosenberger 1992; Lucas and Peters 2001; Rensberger 2000; Lucas et al. 2008b; see also behavioral papers cited above, and see Cole 1992; Anapol and Lee 1994; Wright 2005 for discussion of craniomandibular adaptation to similar forces). Second, *Cebus* is the largest genus of its family (e.g., Ford and Davis 1992; Rosenberger 1992), and larger mammals generally tend to have more decussating enamel than smaller ones since they can generate more bite force (Koenigswald et al. 1987; Koenigswald

2000; Rensberger 2000). For example, referring primarily to eutherians, Koenigswald (2000) observes that "only very few mammals of large body size have radial enamel as the dominant enamel type…" (p. 110). As the largest extant cebid, we should expect *Cebus* to exhibit the most decussation within its group. In support of this argument, all relatively large platyrrhines (e.g., *Ateles* and *Lagothrix*) seem to exhibit decussation, with the exception of *Alouatta* (Nogami and Yoneda 1983), and in turn reflect this general mammalian pattern. *Alouatta* probably does not exhibit strong decussation, despite its size, due to selection for resisting abrasive wear as opposed to resisting crack propogation (e.g., Rensberger 2000; see section on enamel function below). This may also suggest that diet is more of a driving force for *schmeltzmuster* evolution than body size (also see below).

In accordance with Martin and colleagues' (2003) paper on enamel thickness, this study confirms that *Cebus* does possess a vertical deviation in prism paths from the EDJ to the surface in Hunter-Schreger bands, in addition to the usual horizontal deviation seem in primates. However, by increasing the *Cebus* sampled in this study, I have discovered that this vertical pattern is not ubiquitous within *Cebus*. It did not appear in every tooth or even every individual. In addition, of the four species sampled only *C. apella* and *C. albifrons* exhibited vertical deviation in imbricational prisms (Fig. 4-14).

There are distinct differences between the patterns of decussation seen in *Cebus* canines versus in their postcanine

teeth. Both male and female *Cebus* canines showed significant decussation, with Hunter-Schreger bands appearing throughout the crown, including the entire cusp tip (see Figs. 4-12 to 4-14). Enamel in canine tips also appears highly gnarled (Fig. 4-12, 4-13). In postcanine teeth, however, Hunter-Schreger bands did not appear in the entire cusp tip, specifically they were not found in the apex of the cusp (i.e., directly over the dentine horns). Banding was also not found in the enamel of basins.

However, in postcanine teeth, fully developed Hunter-Schreger bands were found throughout most of the imbricational, cervical, and cuspal enamel and along the sides of the cusp tip (Figs. 4-15 to 4-17). The decussation which does occur in post-canine cusp tips is not organized in distinct bands, and the angles between alternating prisms are usually relatively narrow (Figs. 4-15 to 4-17). Not only do postcanine cusp tips lack Hunter-Schreger bands, the paths of individual prisms in the tips (and basins) are less sinuous than those seen in canines (e.g., compare Figs. 4-15 through 4-17 to Figs 4-12 and 4-13).

Despite the prevalence of decussating enamel in *Cebus* teeth, radial and aprismatic enamel do appear near the cervix in most of the *Cebus* teeth sampled in this study (Figs. 4-18 and 4-19).

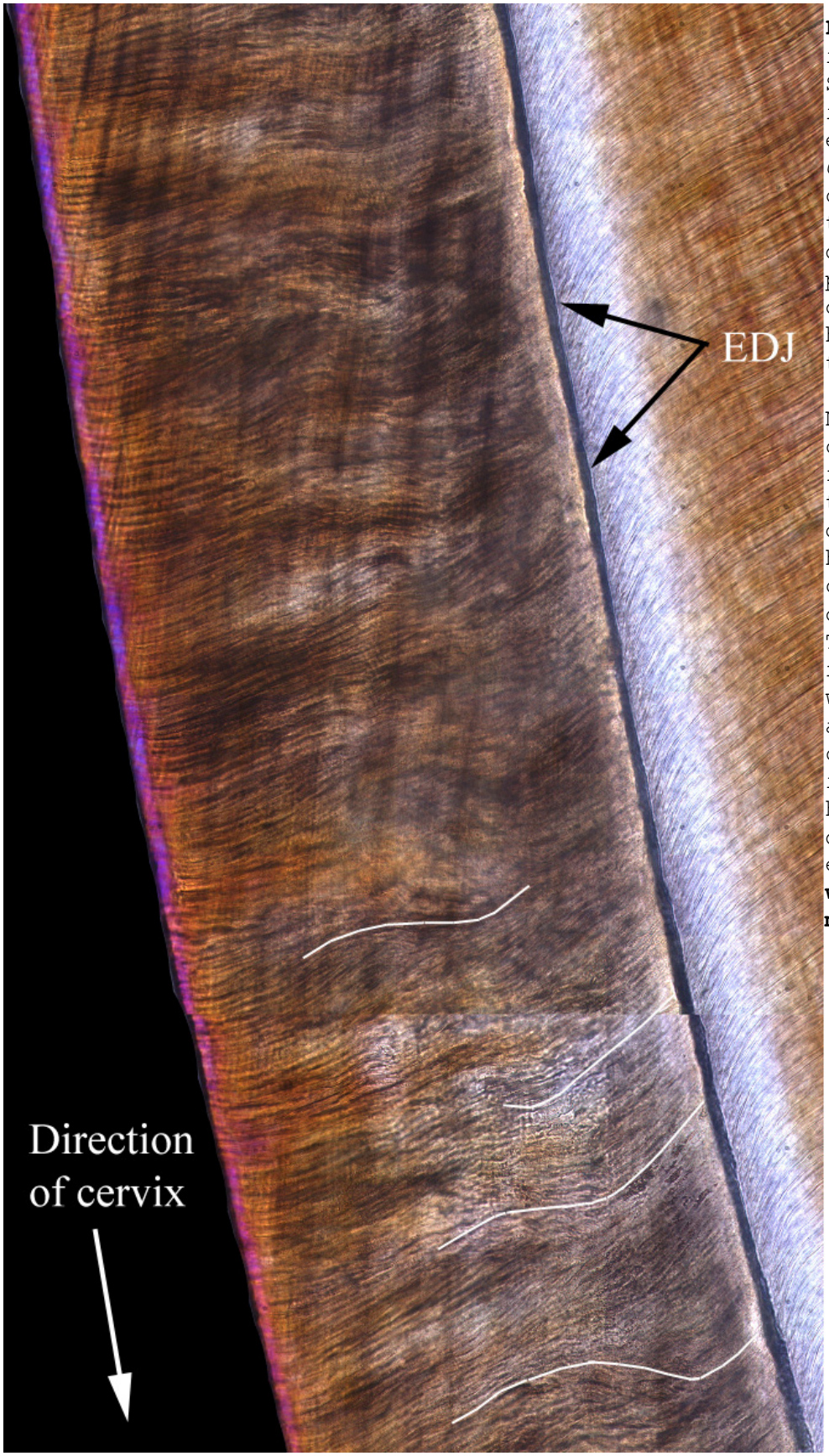


Fig. 4-14. CPL image of Hunter-Schreger bands in imbricational enamel of a *Cebus* sp. canine. Note the vertical deviation of the prisms, examples of which are highlighted by the white lines.

Note also the color changes from gray-brown to orange which denote horizontal changes in prism orientation. This is also a rare example where Retzius anatomy is clearly visible in a region of highly decussating enamel. **Field width = 624 microns.**

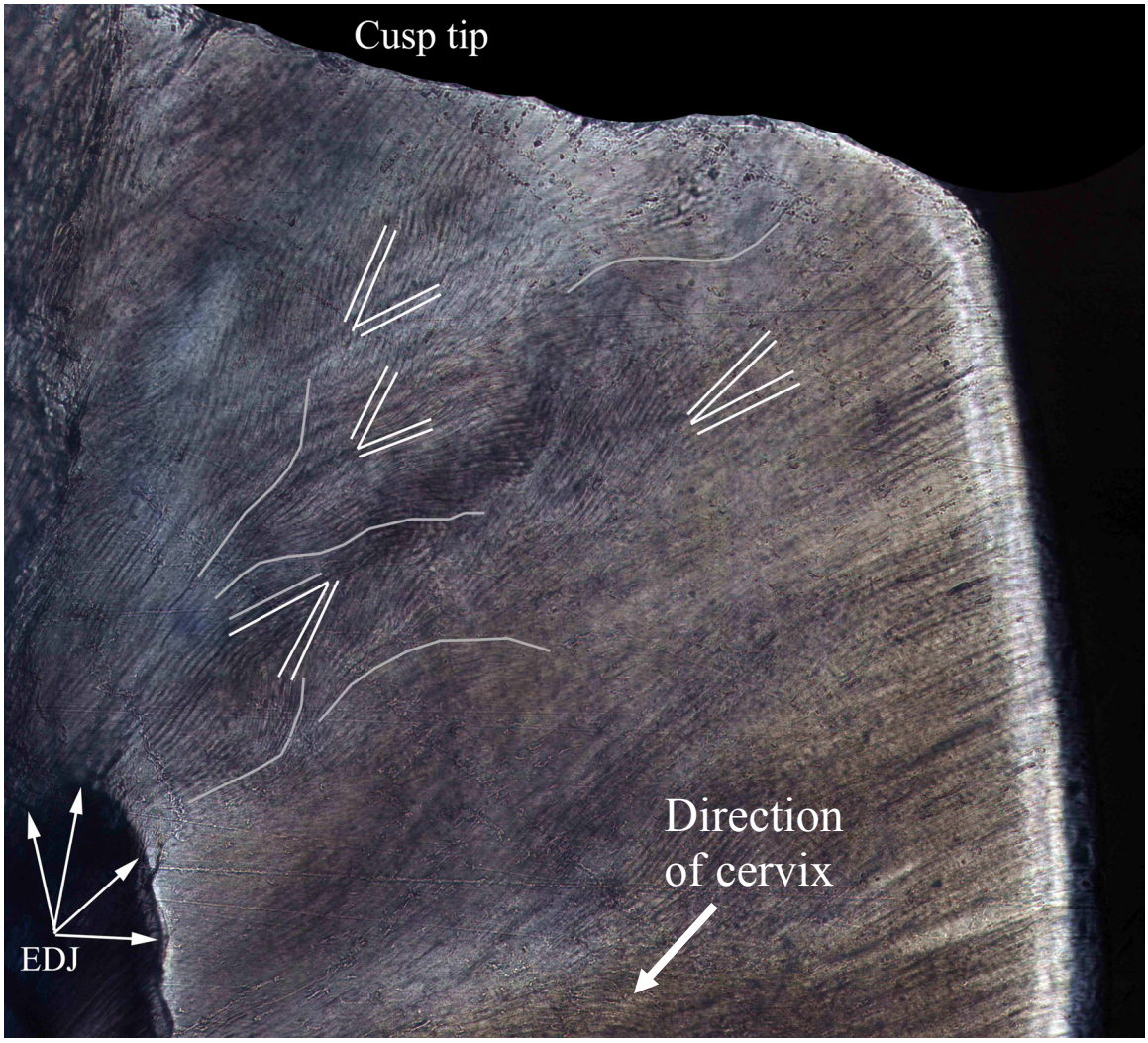


Fig. 4-15. Cuspal enamel from a *Cebus* sp. M2. Cervical direction is toward the bottom and slightly left. Notice the lack of strong color contrast above the dentine horn (toward upper right), indicating lack of strong Hunter-Schreger banding. However, enamel decussation can be seen by tracking individual prisms, whose crossing paths are denoted by white lines. Gray lines follow individual prisms to display their somewhat sinuous paths. **Field width = 673 microns.**

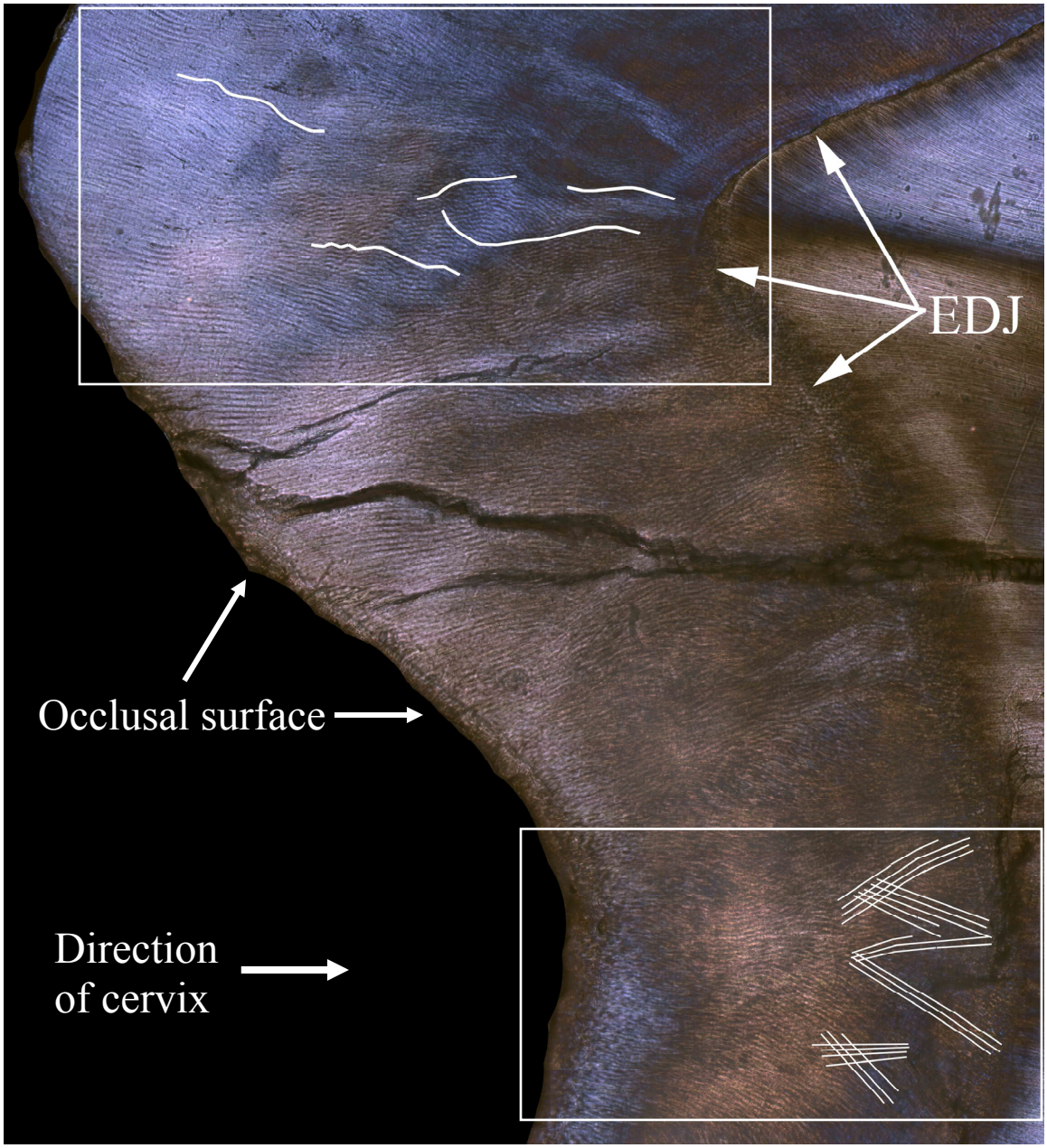


Fig. 4-16. Prism patterns in cuspal enamel of a *C. albifrons* P3. Apical surface of the tooth is located toward the left of the image. White lines in top inset depict sinuous prism paths above the dentine horn (just right of center). Crossing white lines in bottom inset display prism decussation seen in the tooth basin. See Fig. 4-17 for increased magnification. **Field width = 1181 microns.**

A.

B.

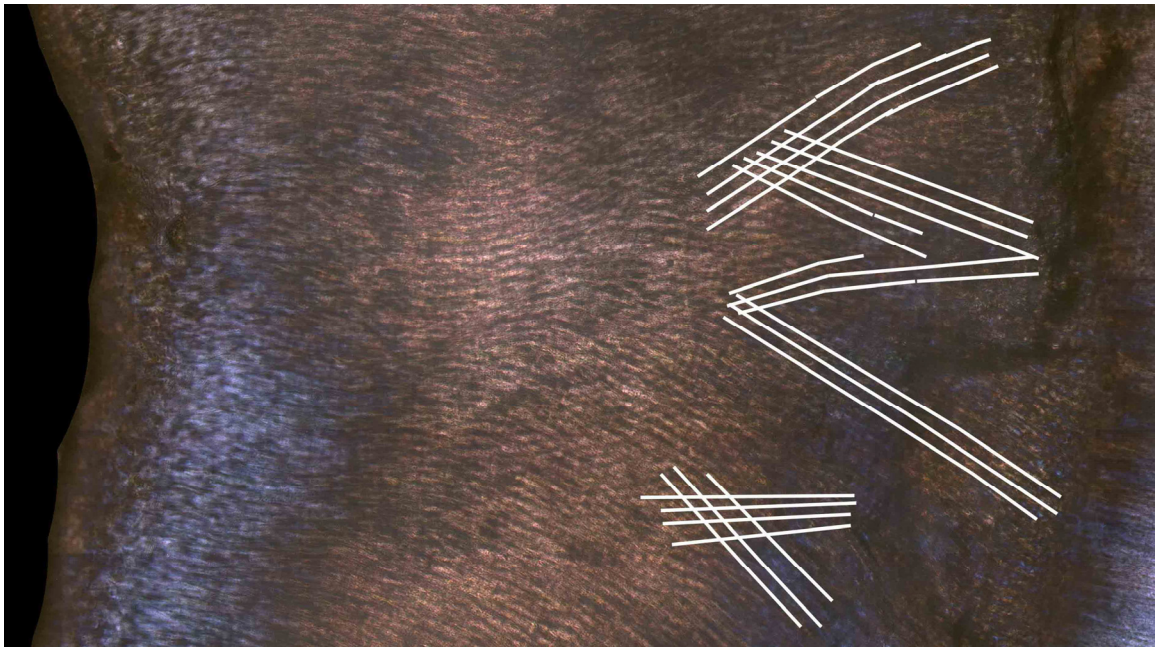


Fig. 4-17. A. Increased magnification of top inset from Fig. 4-16, showing more detail on decussation and sinuous prism paths (highlighted by white lines). **B.** Increased magnification of bottom inset from Fig. 4-16, showing decussation in basin prisms (highlighted by white lines). **Field width in microns: A = 764; B = 590.**

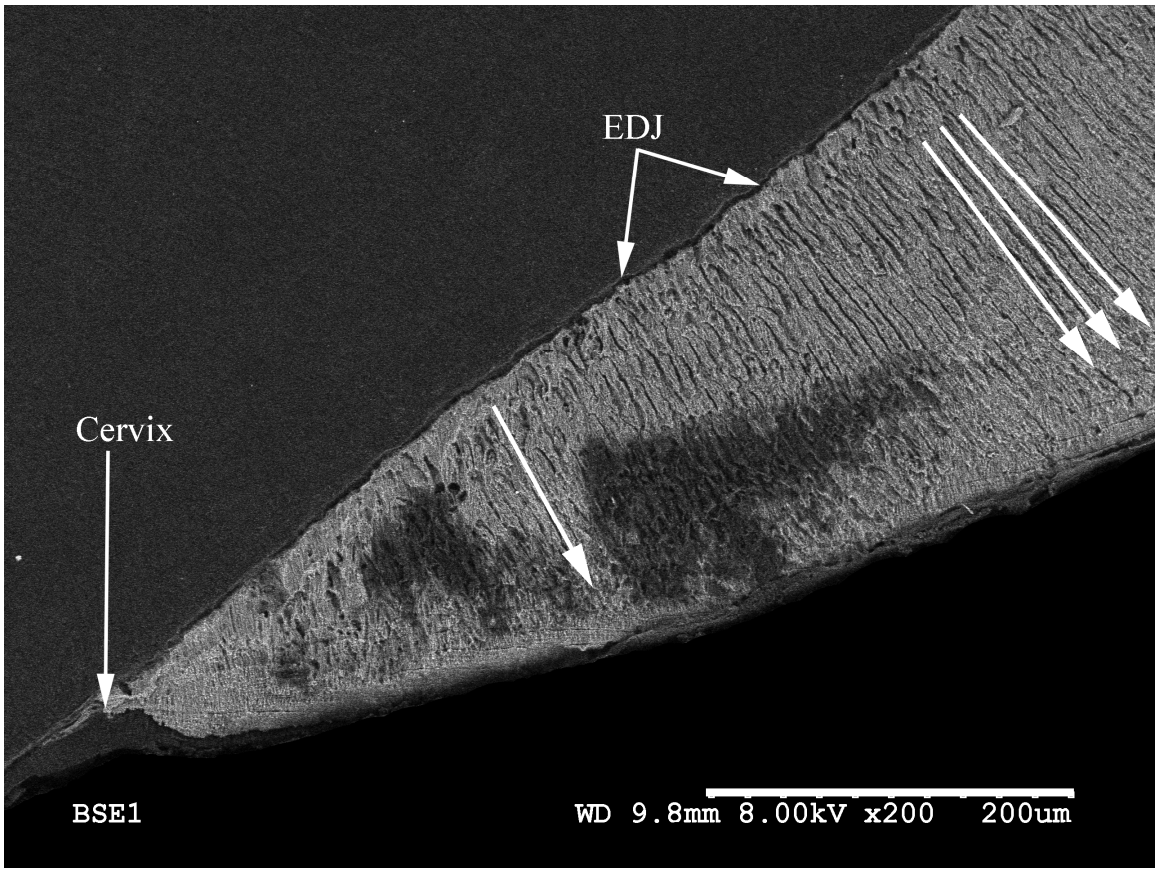


Fig. 4-18. Cervical enamel on the lingual side of a *C. albifrons* P2, revealing the radial nature of enamel prisms in this location. Unlabeled white arrows highlight prism direction. The scale bar denotes 200 microns.

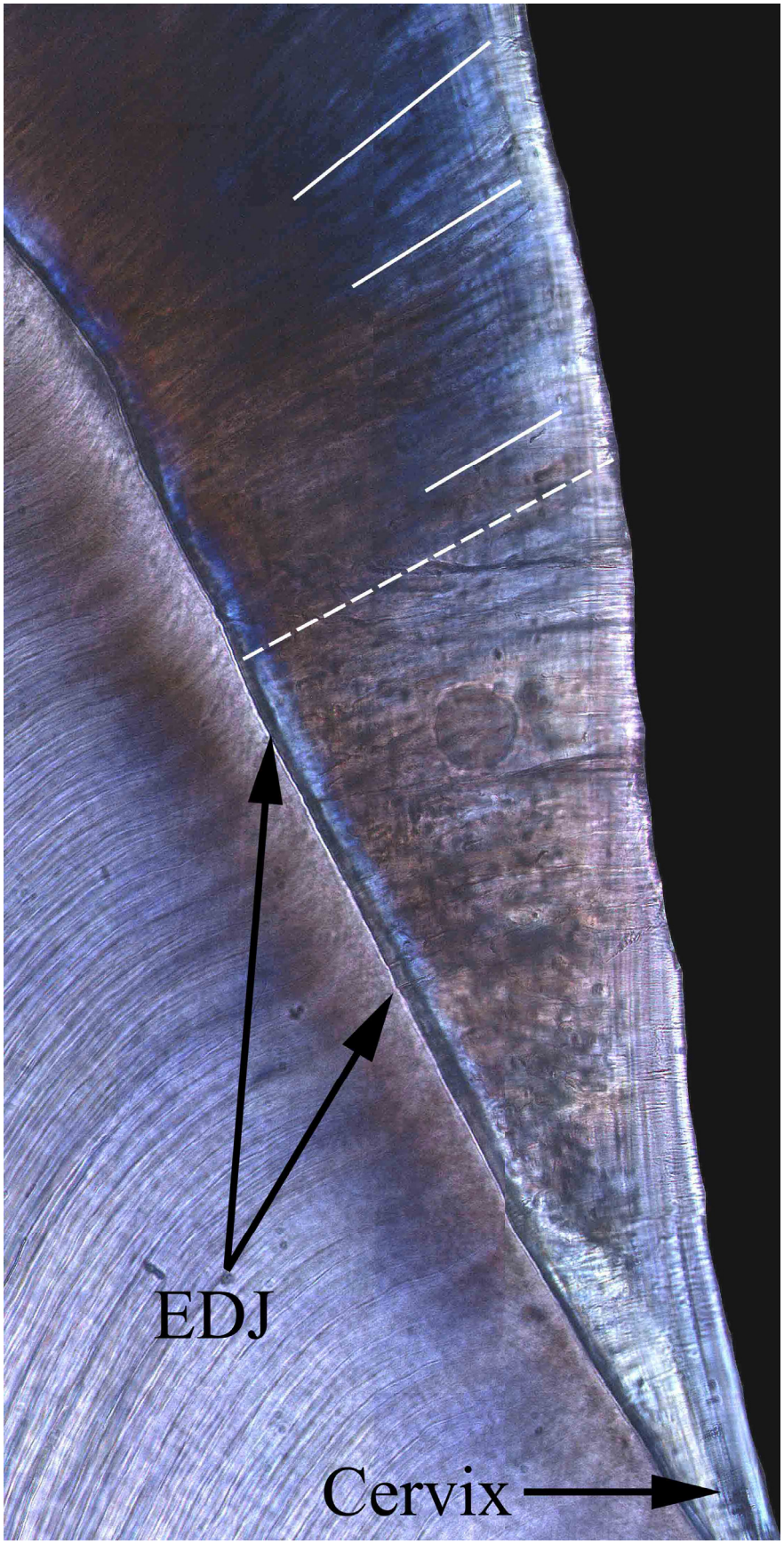


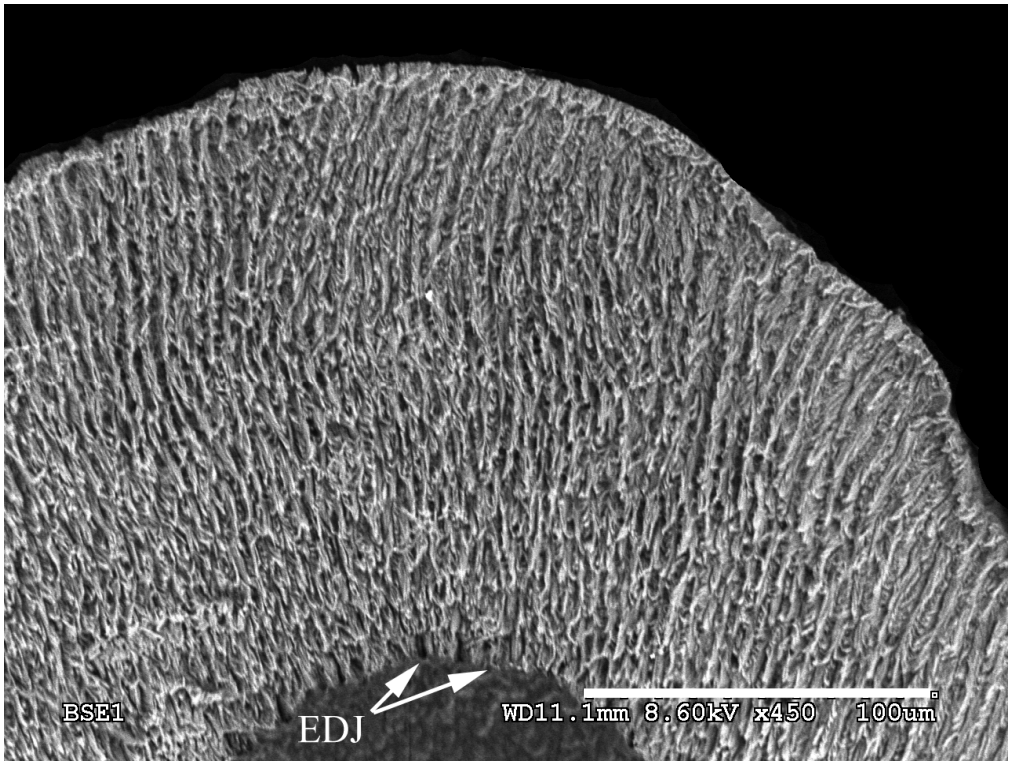
Fig. 4-19. CPL image of imbricational enamel from an M1 of *C. apella*, showing aprismatic enamel toward the cervix. Solid white lines denote paths of visible prisms. Note alternating blue and brown colors, indicative of decussation. Below the dotted line, however, lack of clearly visible prisms and reduced color contrast indicate lack of prism structure and decussation. This is due to enamel becoming increasingly aprismatic toward the cervix (bottom). **Field width = 350 microns.**

Callitrichines

Callimico

The premolars of the *Callimico* specimen examined here possess a different *schmeltzmuster* in the cusp versus the imbricational enamel. The premolar cusps are largely composed of radial enamel, with some degree of sinuosity, but not enough to consider it "gnarled". Instead, the pattern is a minor deviation from being purely radial (Fig. 4-20). However, the imbricational enamel contains decussation in the form of Hunter-Schreger bands and a high degree of sinuosity in the prisms (Fig. 4-20). The pattern observed here differs from the observations of Nogami and Natori (1986), which state that the *schmeltzmuster* of *Callimico* is purely radial. However, these authors sampled *Callimico* incisors versus the premolars sampled in this study. Therefore, the differing results may be a consequence of inherent differences among tooth types (i.e., anterior versus postcanine teeth) as is seen in *Cebus*. In addition, relative to the other cebids examined, the imbricational enamel in this *Callimico* becomes aprismatic at an unusually deep point relative to the tooth surface. However, the unusual location of aprismatic enamel may be unique to this particular specimen (see Fig. 4-6).

A.



B.

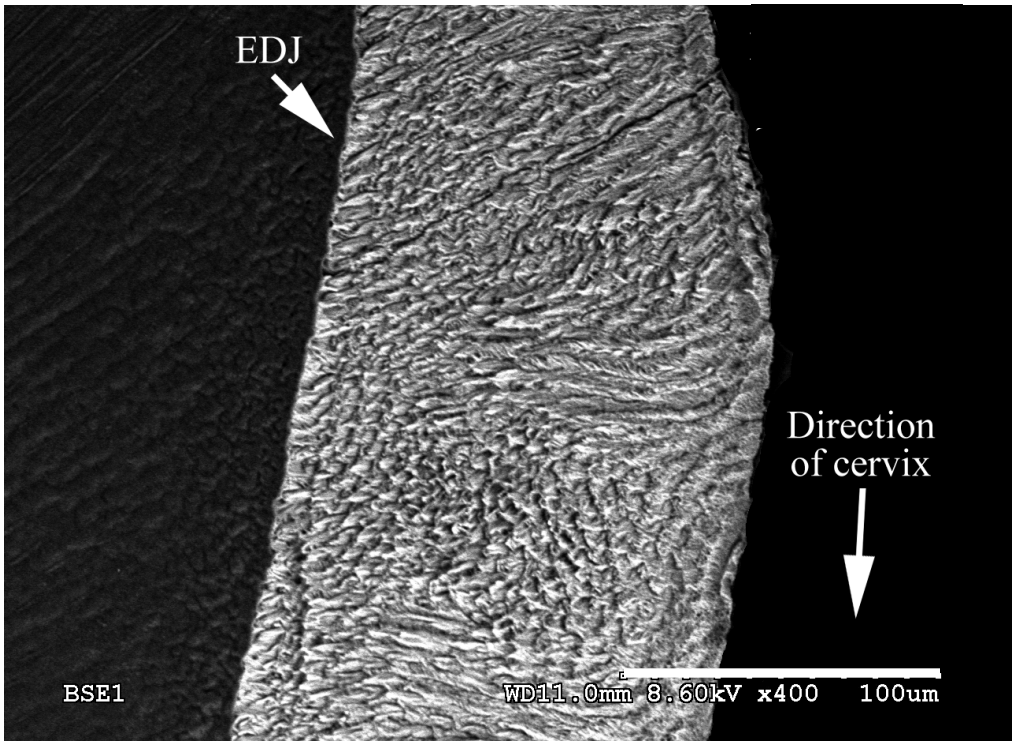


Fig. 4-20. Decussation in a *Callimico* P4. **A.** Cusp tip, with relatively straight (radial) enamel prisms. **B.** Imbricational enamel in mid-crown from the same tooth, with sinuous enamel prisms. Alternating longitudinal- and cross-sections can be seen as well. In both images, scale bar indicates 100 microns.

Callithrix

For postcanine teeth, *Callithrix* follows a prism decussation pattern similar to that of *Callimico;* however, the *Callithrix jacchus* and *humeralifer* teeth sampled do not possess sinuosity in their prisms. As with *Callimico*, the cuspal enamel is relatively radial, while the imbricational enamel is decussated in these teeth (Fig. 4-21). It is also important to note that the anterior teeth of *Callithrix* do not resemble those of *Callimico*. In other words, the incisors of *Callithrix jacchus* have Hunter-Schreger banding whereas the incisors of *Callimico* do not (Nogami and Natori 1986). In addition, the canine of *Callithrix humeralifer* imaged in this study also displays a well-organized and extensive pattern of Hunter-Schreger banding throughout the tooth. The difference in anterior versus posterior teeth is most likely tied to the tree-gouging behavior in *Callithrix* (for discussion, see the "Adaptation to tree gouging in anterior teeth of marmosets" section below).

Cebuella

The limited sample of *Cebuella* in this study shows some imbricational decussation in the postcanine teeth. The prisms in Fig. 4-22 have differing orientations, but are not bundled to form the discrete Hunter-Schreger bands as is seen in *Callithrix* and *Callimico*. However, the larger sample of Nogami and Natori (1986) shows that anterior and postcanine teeth both have

discrete bundles of decussating prisms. They do not discuss these as Hunter-Schreger bands, but their published microphotographs show that clear Hunter-Schreger banding is present. Therefore, based on the combined sample of this study and the Nogami and Natori study (1986), *Callithrix* and *Cebuella* exhibit Hunter-Schreger bands in anterior and postcanine teeth, whereas *Callimico* has only been observed to possess them in their postcanine teeth.

Interestingly, one specimen of *Cebuella* analyzed in this study also exhibits a drastic cervical turn in prism orientation near the tooth surface in its cervical imbricational enamel (image unavailable; however, confirmed by observation of Dr. Timothy Bromage as well). This seems to be an exaggeration of the cervical downturn in prism orientation sometimes seen in other cebids as well as in other platyrrhines (e.g., *Callicebus*; see above).

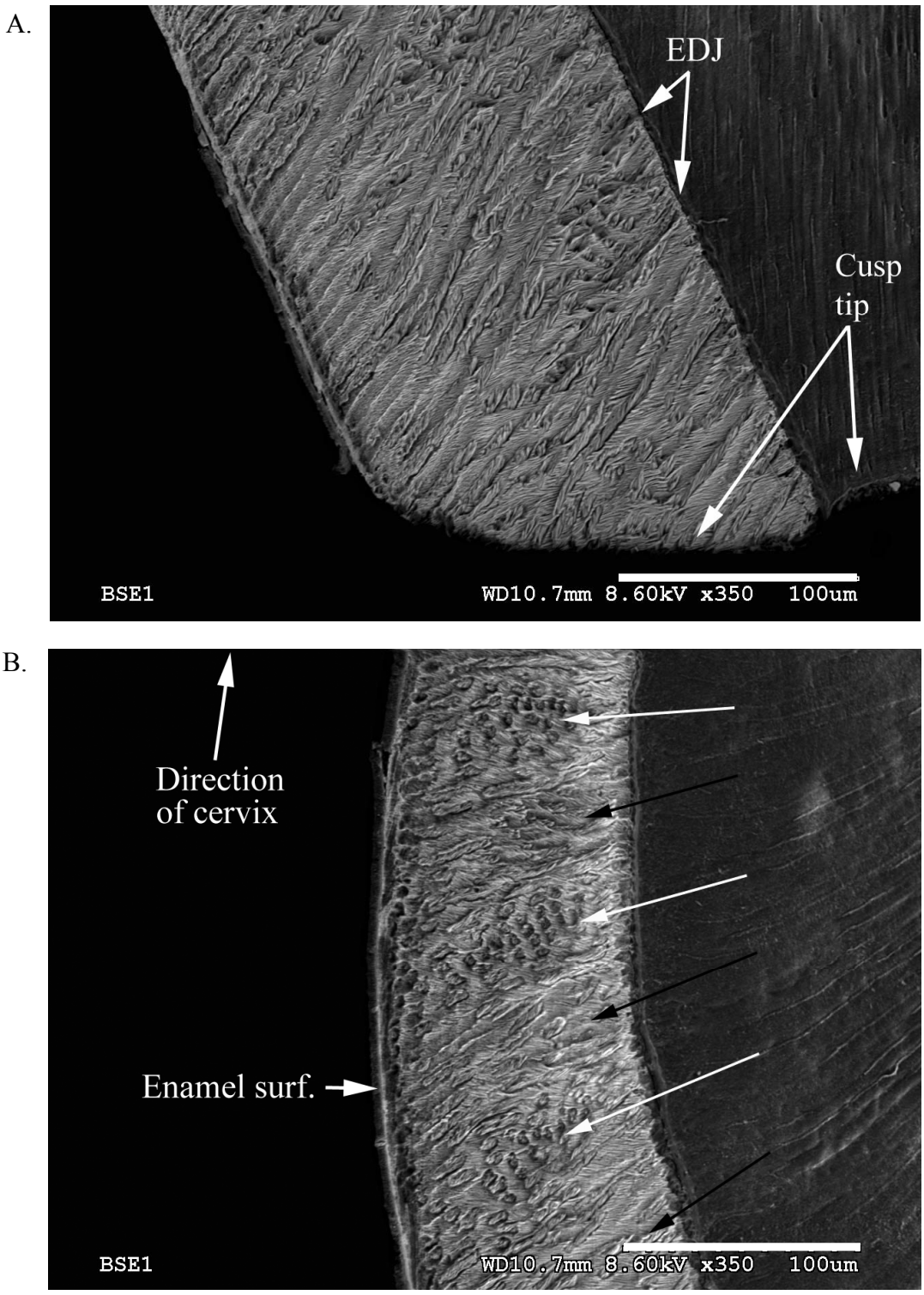


Fig. 4-21. Prism patterns in a *Callithrix jacchus* M1. **A.** Image of cusp tip showing radial prisms. **B.** Buccal imbricational enamel, taken around mid-crown, with decussation appearing in the form of Hunter-Schreger bands. Alternating black and white arrows point to the alternating regions of prism orientation. In both images, scale bar indicates 100 microns.

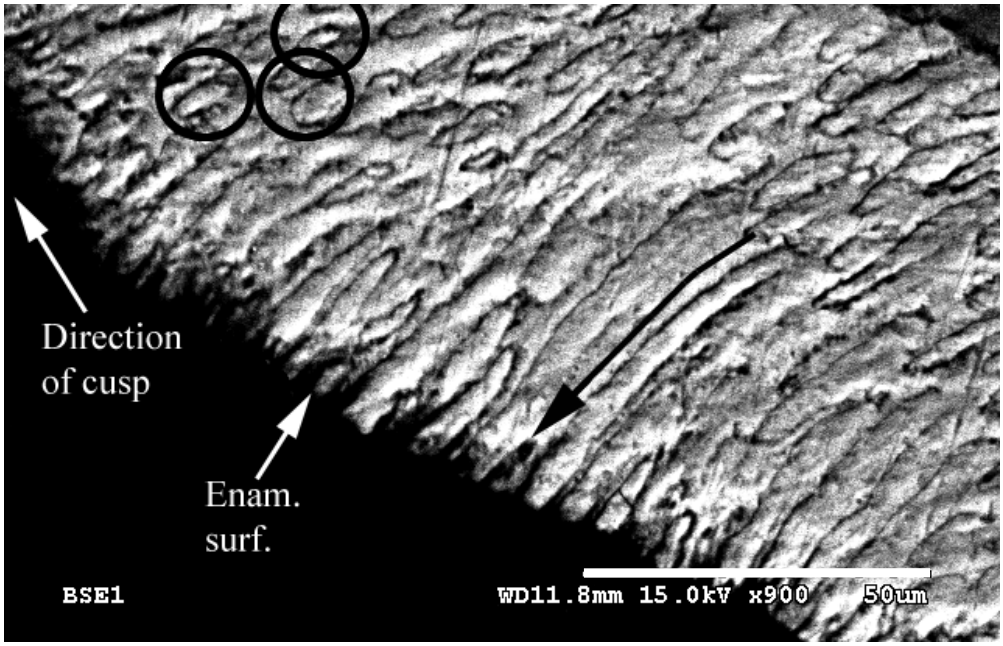


Fig. 4-22. Enamel prisms in imbricational enamel of *Cebuella* (postcanine, tooth number unknown). In the upper left, prisms can be seen traveling perpendicular to this page (black circles), whereas toward the middle of the image, prisms can be seen running parallel to the page and toward the enamel surface (black arrow highlights their direction). Scale bar indicates 50 microns.

Leontopithecus

Images reveal alternating dark patches in M1 cervical and imbricational enamel of *Leontopithecus,* but these alternating patches do not appear in cuspal enamel. This suggests that imbricational enamel in *Leontopithecus* is probably also decussated to some degree since different colors in CPL represent differential birefringence and in turn alternating orientations (Fig. 4-23 and 4-24; see Chapter 3 for discussion of CPL methodology). However, the incisors of *Leontopithecus* have been described as purely radial in previous studies (Nogami and Yoneda

1983; Nogami and Natori 1986). Therefore, *Leontopithecus* seems to have a different *schmeltzmuster* for its anterior teeth compared to its postcanine teeth as is seen in *Callimico* (see above).

Leontopithecus was the only cebid genus which exhibited cervical downturn in its prisms in all postcanine teeth (i.e., P2 through M2). Moreover, the P3 examined here exhibited an exaggerated version of the cervical downturn, although it is not as exaggerated as is seen in the *Cebuella* specimen mentioned above (Fig. 4-24).

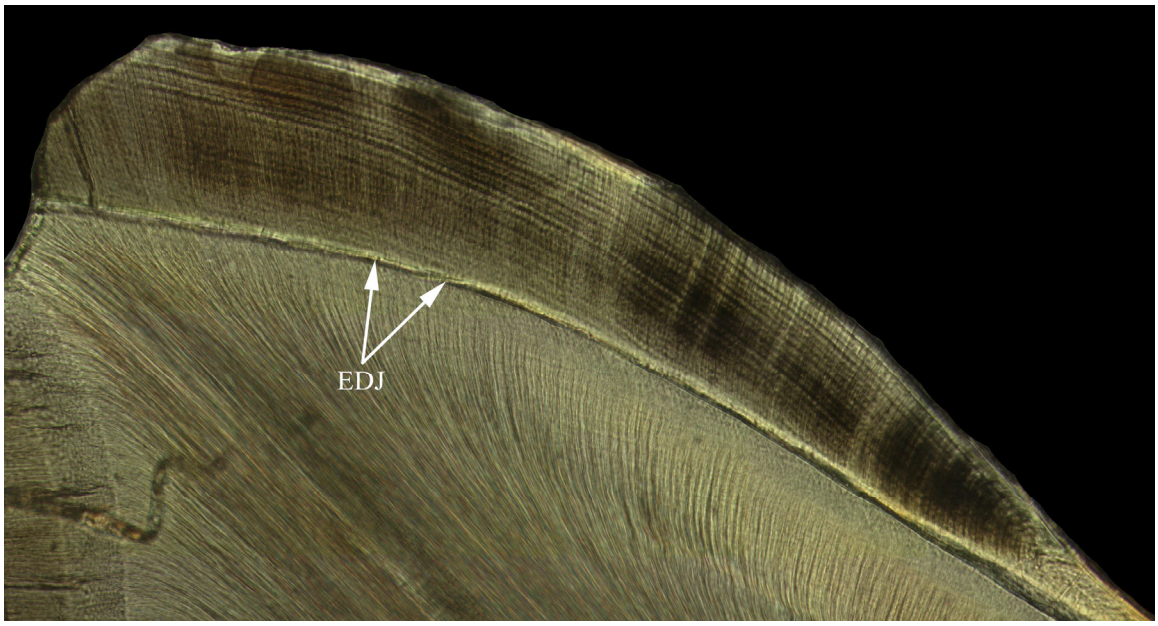


Fig. 4-23. Enamel pattern in the mesial enamel of a *Leontopithecus rosalia* M1. Dark patches toward cervix (right) represent probable areas of decussation. However, the three dark patches near the cusp (upper left) are most likely breakage artifacts due to their circular nature and evidence of enamel surface breakage. **Field width = 965 microns.**

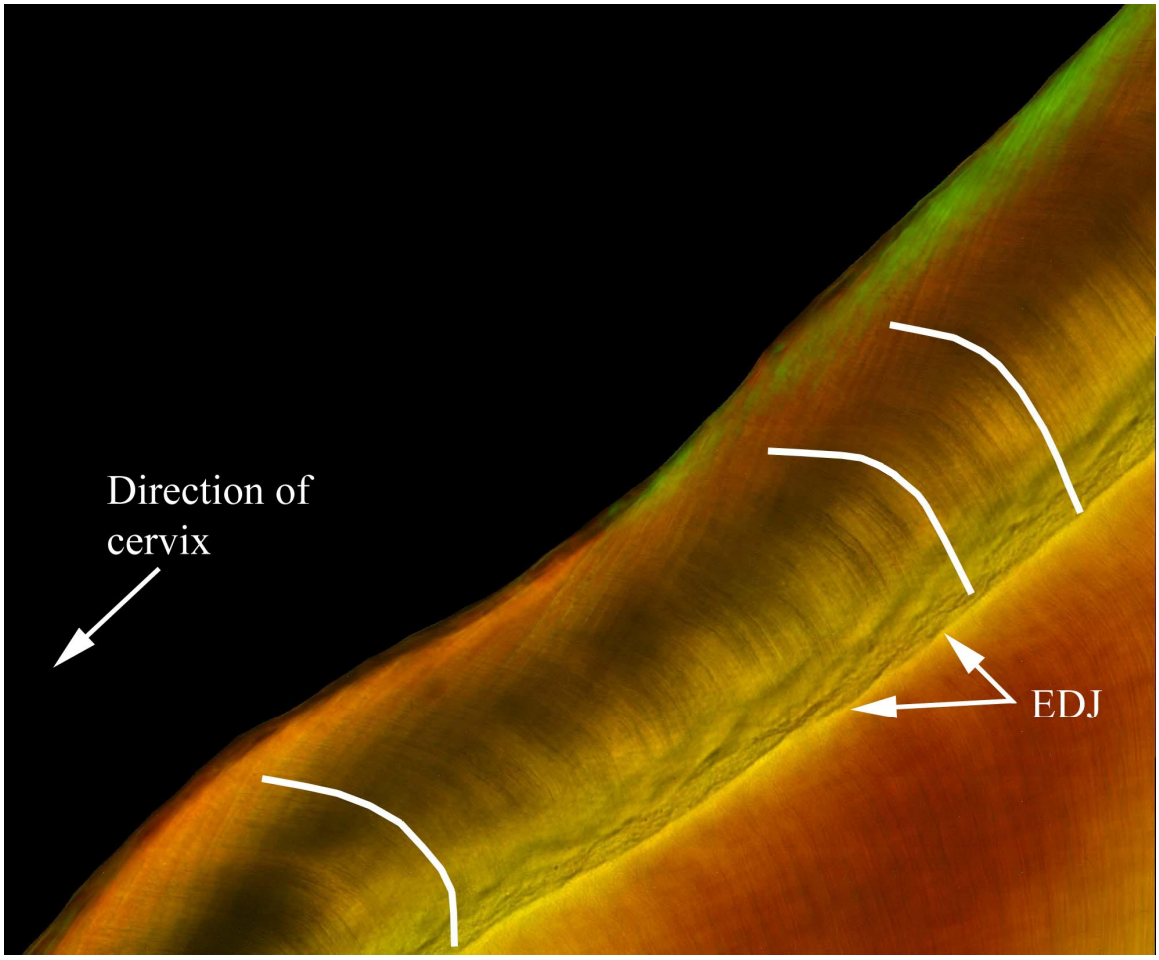


Fig. 4-24. Prism bending in lingual imbricational enamel of a *L. rosalia* P3. White lines trace the paths of sample prisms in the tooth. Prisms begin their bend approximately halfway to the enamel surface (closer to the EDJ than any other genus), so that the effect of the bend is greater. Bending also appears closer to the cusp here than any other cebid genus sampled. **Field width = 623 microns.**

Saguinus

Previous studies (Nogami and Yoneda 1983; Nogami and Natori 1986) classify all tooth types for *Saguinus* as "nonserial" (i.e., non-decussating), whereas this study reveals that the postcanine teeth of *Saguinus* do contain decussating enamel. The patterns of decussation seem to vary among *Saguinus* species. One *Saguinus* pattern, for example seen in S*. nigricollis*, follows the general pattern of other callitrichines. That is, the enamel prisms are radial in the cusp tips, but are decussating in the imbricational enamel. A second pattern, for example seen in the P4 of *S. oedipus*, shows decussating enamel all along the buccal tooth surface and radial enamel along the lingual surface; these buccal and lingual patterns extend from cervix to cusp tip (Figs. 4-25 and 4-26). At this point, it is not possible to say if this is unique to *S. oedipus* or if it appears in other *Saguinus* or callitrichines as well. If further sampling demonstrates that this buccal-lingual pattern is unique to *S. oedipus,* then this species may be loading its teeth differently than other callitrichines.

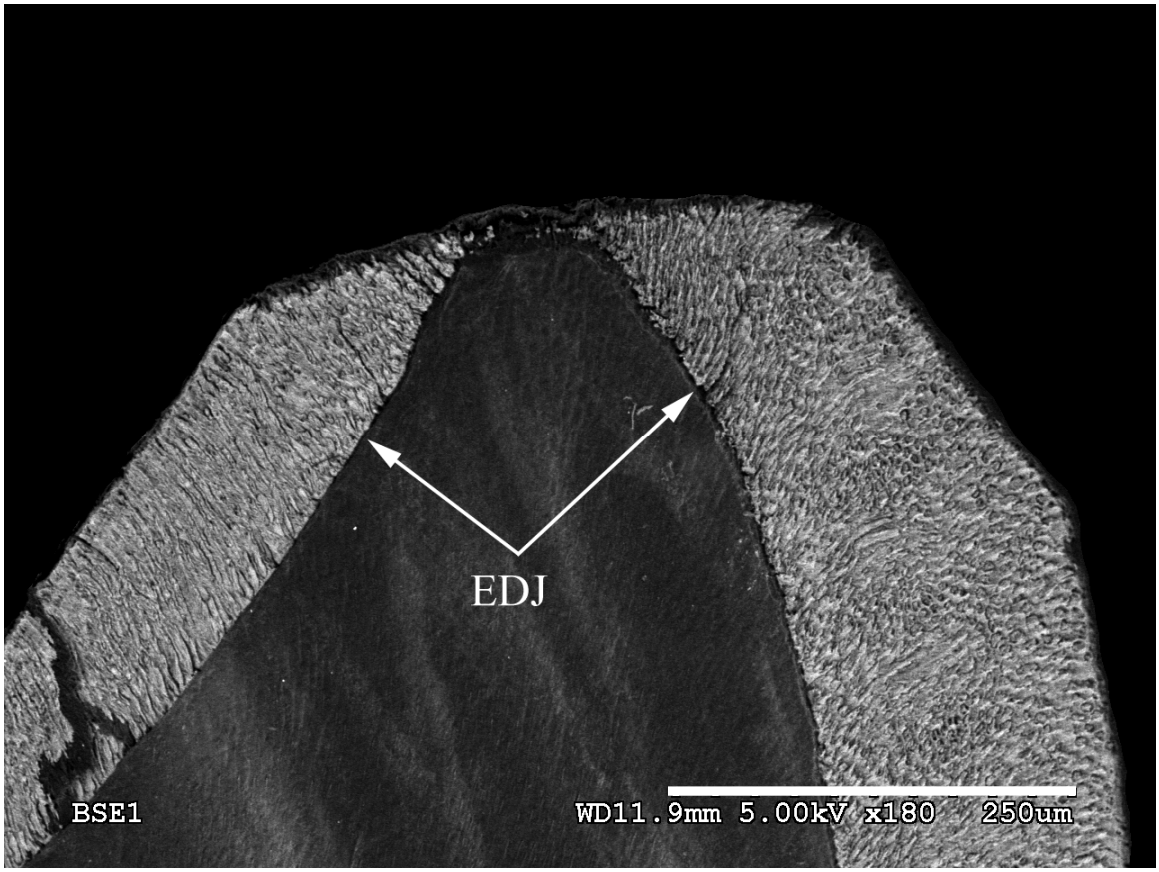
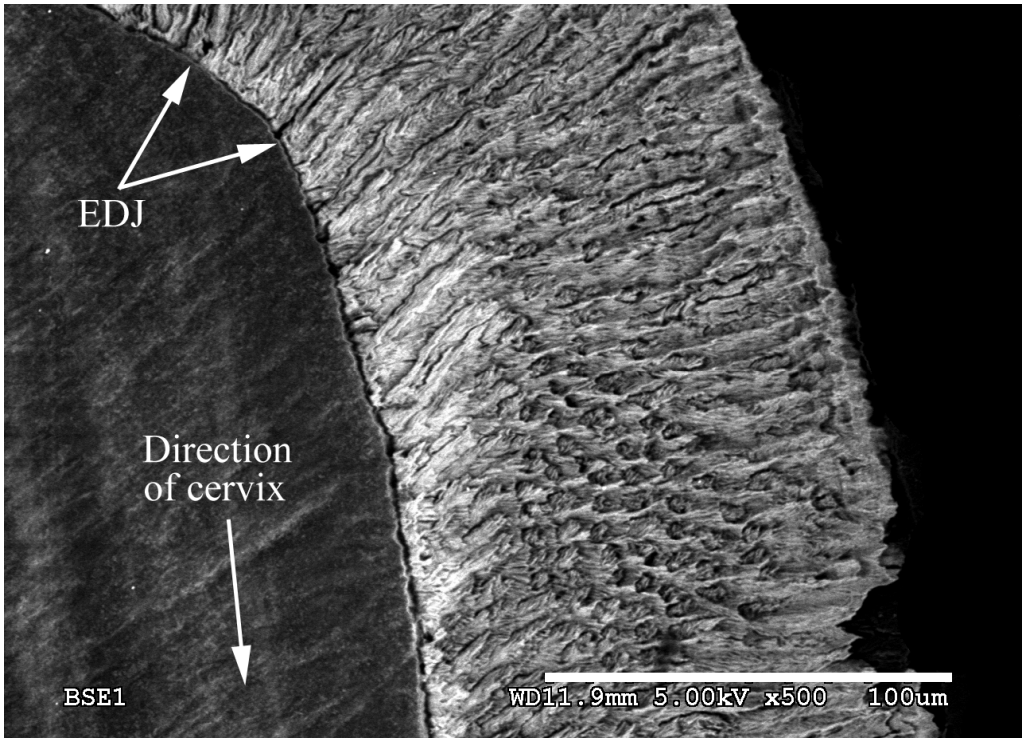


Fig. 4-25. Enamel decussation in the worn cusp of a *Saguinus oedipus* P4. Buccal enamel (right) is composed of alternating Hunter-Schreger bands even in the cusp tip, whereas the lingual surface (left) consists of radial enamel. Scale bar denotes 250 microns.

A.



B.

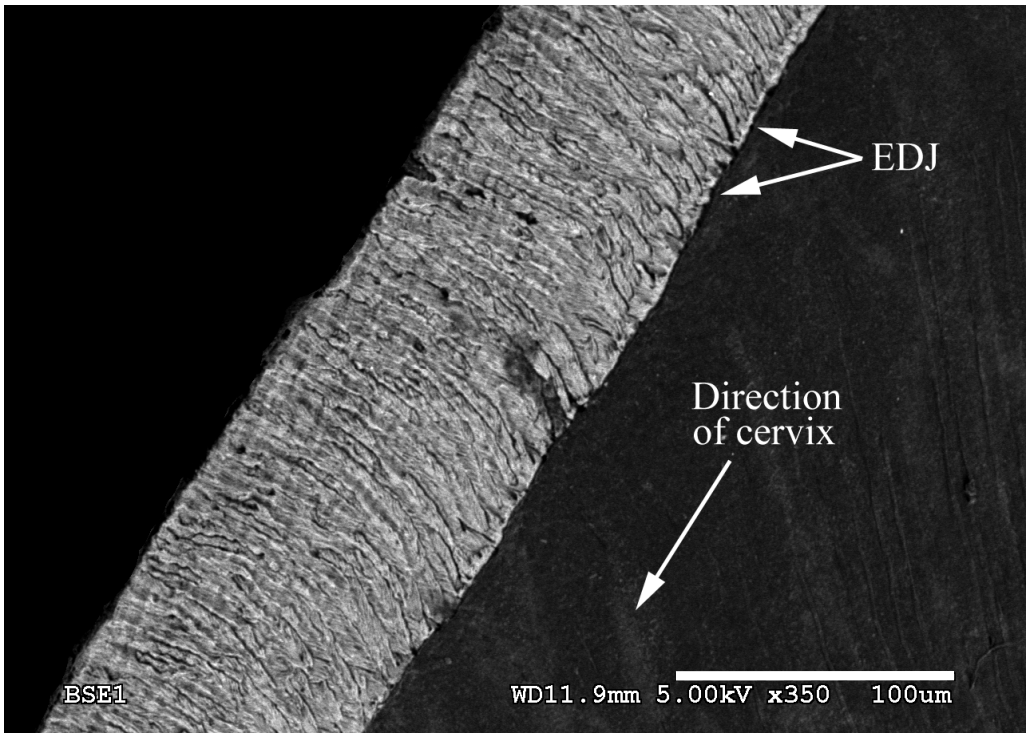


Fig. 4-26. Images of the same specimen in Fig. 4-25, showing buccal and lingual regions at higher magnification. **A.** Buccal enamel is decussated, with different prisms presenting both longitudinal as well as cross-sections to the page. **B.** Lingual enamel in this specimen is radial, though slightly arcuate. Scale bars denote 100 microns.

General Evolutionary Patterns Based on Cebid Enamel

Phylogenetics

In terms of phylogenetic signal, we can make two confident statements regarding cebid microstructure. The first of these is that radial enamel should be considered most likely primitive for Cebidae, whereas decussating enamel should be considered derived for the family. Decussating enamel is rare among small mammals (Koenigswald et al. 1987; Maas and Dumont 1999; Koenigswald 2000; Rensberger 2000), and it is most likely that primitive cebids were small monkeys since most fossil and extant cebid genera are substantially smaller than *Cebus* (e.g., Szalay and Delson 1979; Rosenberger 1992; Fleagle and Kay 1997; Fleagle and Tejedor 2002; Tejedor et al. 2006; Rosenberger et al. 2009). Currently, the only exception to this rule is a fossil taxon, *Acrecebus,* which based on its molars exceeds the size of *Cebus* (Kay and Cozzuol 2006). However, *Acrecebus* seems to be most closely related to *Cebus* to the exclusion of *Saimiri* and other known fossil cebines (Kay and Cozzuol 2006). Therefore, *Acrecebus* is not a primitive cebine and does not contradict the hypothesis that primitive cebids were small. Taken in this context, the fact that both *Aotus* and *Saimiri* have purely radial enamel suggests that primitive cebids most likely shared this condition. Thus, the primitive cebids, which were small, were not unusual for mammals and probably had radial enamel. Therefore, decussation in *Cebus* and the callitrichines is most likely a homoplasy.

However, it is important to note that the callitrichines are the source of the major counterargument to radial enamel being primitive for cebids. The callitrichines are unusual because they are very small platyrrhines which have decussating enamel, and are actually more similar to the relatively larger *Cebus* than they are to the more similarly-sized *Saimiri* and *Aotus*. Therefore, the counterargument is that decussating enamel is primitive for Cebidae, and is maintained as such in callitrichines and *Cebus*. In this case, *Saimiri* and *Aotus* would be expressing the derived, homoplastic condition.

However, this is unlikely for several reasons. First, decussating enamel does not appear in any other small primates sampled to date [e.g., *Callicebus, Aotus, Saimiri* (Nogami and Yoneda 1983; this study), small extant strepsirhines and small adapiforms (Maas and Dumont 1999), and tarsiiforms (Maas and Dumont 1999)]. Moreover, the only other platyrrhines which exhibit decussation either possess a relatively large body size or are known to have mechanically demanding diets or a combination of the two (see Nogami and Natori 1983 for data on non-cebid platyrrhines). Thus, with the exception of the callitrichines, platyrrhines seem to fall in line with general mammalian predictions regarding the appearance of decussation (Koenigswald et al. 1987; Maas and Dumont 1999; Rensberger 2000).

Therefore, the most likely interpretation is that these small callitrichines present an unusual derived condition which is driven by an unusual adaptive need among primates (see below).

As a consequence of this, we come to our second major conclusion: the presence of significant decussation in a fossil platyrrhine of small body size should be considered as a good indicator that it is a member of the Callitrichinae. All callitrichines have decussating enamel; therefore, these complex enamel patterns are likely a synapomorphy for the crown group. Once again, it must be noted that previous studies did not find decussation in the dentition of some callitrichine genera (e.g., *Saguinus*; Nogami and Yoneda 1983 and Nogami and Natori 1986), but this study found decussation in the postcanine teeth of every callitrichine genus. Moreover, since decussation is so unusual for small primates, it is not likely that any small platyrrhines outside of the callitrichine adaptive and evolutionary sphere would exhibit this feature. Therefore, enamel decussation may be included as a valuable character for phylogenetic analysis in fossil platyrrhines, when treated as a complement to more traditional gross morphological characters.

Function

Overall, the Cebidae possess a heterogeneous array of microstructural arrangements across species. The presence/absence of prismatic enamel as well as the orientation and grouping of enamel prisms have a direct relationship with the mechanical function of enamel, specifically its ability to withstand abrasive wear and crack propagation (e.g., Koenigswald

et al. 1987; Pfretzschner 1988; Koenigswald 2000; Rensberger 2000; Popowics et al. 2004; see also Chapter 2). Accordingly, the variation seen in cebid *schmeltzmusters* reflects variable mechanical properties of enamel among the different cebid genera. Enamel mechanics are most likely under high selection, especially in cases where fallback foods must be relied upon (e.g., Lambert et al. 2004; Lucas et al. 2008b). Even though cebid *schmeltzmusters* do seem to show some phylogenetic patterns (as seen above), enamel patterns are mostly likely responding strongly to the specific adaptive needs of different taxa (Lucas et al. 2008b). Therefore, we should be able to tie the enamel prism patterns we see within cebids to mechanical function and ultimately to diet, even though making such adaptive connections for dental enamel (i.e., connecting structure to function to role) is a complex exercise as previous researchers have shown (e.g., Popowics et al. 2004; Lucas et al. 2008b).

This section will discuss the functional implications of the three main overarching enamel patterns seen in the cebids: 1) *radial enamel*, which is seen in *Saimiri* and *Aotus*; 2) the *moderately decussating enamel* of the callitrichines; and 3) the *highly decussating enamel* of *Cebus.* I will briefly describe each of the three enamel categories in terms of functional advantages and disadvantages mandated by the structural design of the enamel. Where possible, I will attempt to link this functionality to a dietary context.

Radial enamel

As mentioned in Chapter 2, previous studies on the mechanical properties of enamel have shown that decussating enamel limits crack propagation by increasing the energy necessary for a crack to spread (e.g., Koenigswald et al. 1987; Pfretzschner 1988; Koenigswald 2000; Rensberger 2000; Popowics et al. 2004; Lucas et al. 2008a, 2008b;). Therefore, decussating enamel reflects a functional need for teeth to dissipate high forces.

Enamel crystallites are more able to resist wear vectors parallel to their long axis, and because decussating enamel by definition cannot uniformly orient its crystallites along this vector, it is more subject to wear. Radial enamel, on the other hand, does orient its crystallites in a relatively uniform manner, and so better resists abrasive wear although it provides poorer protection against crack propagation (Koenigswald et al. 1987; Pfretzschner 1988; Koenigswald 2000; Rensberger 2000; Popowics et al. 2004; Lucas et al. 2008a, 2008b). Therefore, as stated by Rensberger (2000), there is a functional trade-off with resisting fracture (decussating enamel) versus resisting wear (radial enamel).

Saimiri and *Aotus*, as discussed above, exhibit a radial type of enamel in every specimen observed in this study, as well as in the study by Nogami and Yoneda (1983). The ubiquitous presence of radial enamel in these two genera most likely

indicates that abrasive wear is the primary mechanical factor governing their *schmeltzmusters.* Although *Aotus* does ingest leaves, these two genera do fall fairly well into the generalized "frugivore-insectivore" dietary category (e.g., Rosenberger 1992; Wright 1996; Boinski 1999; Wolovich et al. 2008). Therefore, *Aotus and Saimiri* are not hard or tough object feeders and their diets do not seem to mandate the kind of high force generation which would jeopardize the structural integrity of their enamel at any one point. Given their diet and the fact that their small body size also limits the maximum force they can generate with their masticatory apparatus, the presence of radial enamel in these genera is what we would expect.

Moderately decussating enamel

Tough objects (such as fibrous foods) spread their load around crown surfaces, loading imbricational areas and hence causing cracking closer to the cervix of the tooth (Pfretzschner 1988; Rensberger 2000; Popowics et al. 2004; Lucas et al. 2008a, 2008b). In other words, tough objects exert a compressive force on the cusp tips, with the force vector oriented toward the roots of the teeth. As this force is transmitted downward it creates lateral *tensile* stresses on the side of the tooth as they attempt to spread under the force (Rensberger 2000; Popowics et al. 2004). An analogy for this is a cone made of soft wax or clay, sitting

on a table: if you push down on the apex of the cone, the sides of the cone will spread out and possibly fracture, especially near the base. Just as with this wax cone, teeth experiencing these lateral tensile forces will tend to initially crack on the outside (enamel surface) and propagate inward toward the dentine (Pfretzschner 1988; Rensberger 2000; Popowics et al. 2004). Harder objects, on the other hand, pinpoint their forces and cause *bending* stresses in enamel, initiating deep radial cracks which then propagate from the dentine outward toward the enamel surface (Lucas et al. 2008a, 2008b). Foods of different consistencies, in other words, localize stresses differently within teeth. Therefore, dental enamel should adapt so that it maximizes the energy required to propagate cracks in those regions of the tooth which receive the most loading and are at the greatest risk of failure based on the diet of the animal (Lucas et al. 2008b). Thus, decussation in imbricational enamel occurs where mechanical resistance to forces created by tough, fibrous objects is required. Decussation around cusp tips, on the other hand, is designed to accommodate the direct pressure of hard food items (such as seeds and nuts), which tend to produce radial cracking in enamel near the EDJ over the dentine horns (Pfretzschner 1988; Rensberger 2000; Popowics et al. 2004; Lucas et al. 2008a, 2008b). Moreover, due to the functional tradeoff between abrasive wear and crack propagation, areas which are not at great risk of either type of fracture should exhibit radial enamel in order to limit abrasion (Rensberger 2000).

Therefore, when we examine the extent and location of decussation, we can gain an overall idea about the degree to which fracture resistance is influencing the microstructural anatomy as well as infer information about the mechanical demands of the diet (e.g., hard versus tough versus soft).

The presence of postcanine decussation in the callitrichines (Nogami and Yoneda 1983; Nogami and Natori 1986; this study) comes as a surprise because one would expect that small mammals cannot easily generate the large loading forces that would crack enamel as is seen in the larger *Cebus.* To the contrary, based on their small body size and more importantly their "frugivorous-insectivorous" diet (see Chapter 1), we should expect the callitrichine genera to resemble the enamel pattern of *Saimiri* and *Aotus*. However, it is important to point out that degree and type of frugivory and insectivory varies across animals and in turn, will require different forces for breakdown (Sussman and Kinzey 1984; Rosenberger 1992). Therefore, we need to discuss the specifics regarding the mechanical characteristics of foods eaten by callitrichines versus those eaten by *Saimiri* to possibly explain this unusual callitrichine enamel pattern (see Chapter 8).

Data from this study suggest that most callitrichine decussation appears to occur in imbricational enamel [the positioning of decussation is not discussed by Nogami and colleagues (Nogami and Yoneda 1983; Nogami and Natori 1986)]; therefore, it does seem that the callitrichines are adapted to

breakdown tougher (as opposed to soft or hard) food resources than we might have otherwise predicted. Moreover, since callitrichine cusp tips seem to be more radial in their prism patterns, there appears to be selection in favor of a mechanical design that also limits abrasive wear in the cusps and in turn maintains cusp relief through time. For example, this enamel pattern would be well-adapted to maintain the high shearing surfaces which are optimal for breaking down insect exoskeletons (e.g., Kay 1975). *Saguinus oedipus* provides another unexpected pattern, with its decussating and radial prism patterns separated into the buccal and lingual enamel of its P4, respectively (see above). Unless this individual is idiosyncratic, this pattern would suggest that *S. oedipus* may transmit dental loading from tough foods through its buccal enamel, however there is little to no published data on the masticatory loads of this species which would provide insight into this pattern.

Highly decussating enamel

Cebus is a mid-sized primate omnivore which is known to consume mechanically demanding foodstuffs and to act as an extractive forager (e.g., Struhsaker and Leland 1977; Teaford 1985; Brown and Zunino 1990; Fragaszy et al. 1990; Fernandes 1991; Janson and Boinksi 1992; Galetti and Pedroni 1994; Fragaszy and Boinski 1995; Kinzey 1997; Fragaszy et al. 2004; Wright 2005;

Addessi 2008). Unlike the callitrichines, *Cebus* presents a set of prism patterns which is reflective of what we would expect based on their size and diet. That is, a hard or tough food diet (even as fallback foods) will require a greater force to breakdown foodstuffs and a larger body size will result in a greater potential to exert that force. In turn, a greater risk of internal structural failure will result, and therefore, we would expect to see a greater degree of decussation to lessen this risk. In addition to the strong decussating enamel of *Cebus*, the genus posseses very thick enamel, which also seems designed to accommodate a high-stress diet (Dumont 1995a; Shellis et al. 1998; Martin et al. 2003). The mechanical demands of extractive foraging (e.g., Janson and Boinski 1992; Fragaszy and Boinski 1995; Fragaszy et al. 2004) probably also play a role in driving enamel microanatomy in *Cebus*. For example, the canines of *Cebus* are the most highly decussated tooth examined in this study, and this is most likely tied to their use of canines (as well as incisors) when tearing apart woody substrates and tough fruit husks (e.g., Janson and Boinski 1992; Fragaszy and Boinski 1995; Fragaszy et al. 2004). Biomechanical data support this idea, as research has shown that masseter and temporalis lever arms in *Cebus* seem optimized for producing high bite forces with the anterior teeth (Anapol and Lee 1994; Wright 2005).

Also not surprisingly, the microanatomy of *Cebus* teeth seem well-adapted adapted to the forces generated by breakdown of both hard and tough food objects, as decussation occurs in both cuspal

and imbricational regions of *Cebus* teeth, respectively. The presence of decussation in *Cebus* was first noted by Nogami and Yoneda (1983) for an incisor of *C. apella.* This study expands our knowledge of the location of decussation within an individual Cebus tooth as well as observes that strong decussation is also present in the canines and postcanine dentition of all four extant species. The *Cebus schmeltzmuster* appears well-designed to limit crack propagation from hard objects which create pinpointed bending forces on cuspal enamel as well as tough objects which create tensile forces along the sides of a tooth. Moreover, the vertical as well as horizontal deviation of prism paths first noted by Martin and colleagues (2003) seem to indicate that *Cebus* teeth are designed to dissipate force vectors with a variety of angles relative to the tooth.

Adaptation to tree-gouging in marmoset anterior teeth

Callithrix and *Cebuella* (the marmosets) seem to exhibit differences in their enamel structure when compared to the other callitrichines, due to the fact that they emphasize exudativory to a much greater degree than *Leontopithecus* and *Saguinus* (the tamarins) as well as *Callimico* (e.g., Ramirez et al. 1977; Coimbra-Filho and Mittermeier 1977; Sussman and Kinzey 1984; Rosenberger 1992; Power and Oftedal 1996). Marmosets are well-known to actively modify tree bark to gain access to exudates,

using their lower teeth as a gouge or chisel to make holes through which exudates will flow (see, e.g., Coimbra-Filho and Mittermeier 1977; Ramirez et al. 1977; Sussman and Kinzey 1984; Rosenberger 1992; Power and Oftedal 1996; Taylor and Vinyard 2004). *Saguinus*, *Leontopithecus* and *Callimico*, on the other hand, feed on tree exudates only through pre-existing wounds, which sometimes have been previously made by marmosets (Soini 1987; Ferrari and Martins 1992; Kinzey 1997).

With this behavior, marmosets have modified the gross anatomy of their anterior dentition to facilitate its role as a tree-gouging tool. The incisors have thickened labial enamel and lack lingual enamel, presumably so that they maintain sharp edges with wear (Rosenberger 1978; see also Rosenberger 1992 and Vinyard et al. 2009). Moreover, the incisors have increased in size so that they are able to function with the canines in gouging (Rosenberger 1992; see Fig. 4-27). Rosenberger (1992) has argued that this anterior dental morphology "is conditioned by mechanical consequences related to bark prizing," (p. 554) in contrast to the other callitrichines, all of whom maintain large, tusk-like canines and lingual enamel on their incisors (Fig. 4-27); these features are much more similar to non-callitrichine relatives such as *Saimiri*.

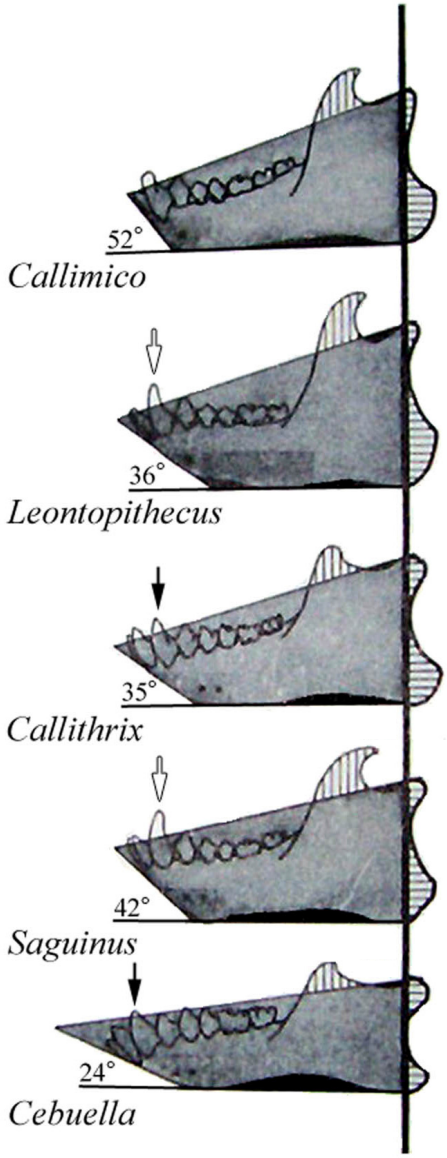


Fig. 4-27. Comparison of anterior dental morphology in gouging and non-gouging callitrichines (*Callithrix* and *Cebuella* vs. *Callimico*, *Leontopithecus*, and *Saguinus*, respectively). Notice the tusk-like canines of non-gougers (open arrows) versus those of the gougers (black arrows), which are brought in line with the incisor row. Also notice that *Callithrix* and especially *Cebuella* have procumbent anterior teeth, associated with a more horizontally oriented mandibular symphysis. This is highlighted by a more acute ramus/symphysis angle; mean angles for gougers and non-gougers in this figure are 29.5 degrees versus 43.3 degrees, respectively. Modified from Hershkovitz (1977); not to scale.

One would predict that marmosets have altered their masticatory apparatus in other ways to accommodate the mechanical demands placed upon the teeth and skull by tough tree bark. For example, one might expect to see morphological adaptations to resist increased bite forces and allow for an increased gape (e.g., Szalay and Seligsohn 1977; Vinyard et al. 2003). These predictions have been examined in a series of papers by Vinyard and colleagues (e.g., Vinyard et al. 2003; Taylor and Vinyard 2004; Vinyard and Ryan 2006), who have shown that the lowered position of the mandibular condyle relative to the tooth row and alteration of masseter fibers (i.e., greater stretch properties) have allowed marmosets to possess a significantly expanded gape. However, Vinyard and colleagues have argued that there is currently no biomechanical reason to believe that marmosets have a relatively more powerful bite than other callitrichines. (Vinyard et al. 2003; Taylor and Vinyard 2004; Vinyard and Ryan 2006; Vinyard et al. 2009). The derived marmoset location of the condyle may actually result in a loss of masseter bite force due to a decrease in the length of the masseter lever arm (e.g., Greaves 1974; Herring and Herring 1974; Hylander 1978, 1979; Ravosa 1990; Vinyard et al. 2003). Furthermore, when marmosets do gouge, they do not even seem to generate *their own* maximum possible bite force (Vinyard et al. 2009).

Despite the lack of evidence for increased bite force, we can clearly see from even a cursory examination that the anterior dentition of marmosets has undergone evolutionary change.

Therefore, I predict that even if marmosets cannot produce higher bite forces, tree-gouging is still an activity that should place higher stresses on the teeth themselves relative to the forces placed on the anterior teeth of other callitrichines (see also Ravosa et al. in press; Hogg et al. in prep.).

Therefore, even if the total amount of loading has not increased, the type and location of loading is different and seems to have increased the decussation in the anterior dentition of marmosets. For example, this study shows that *Callithrix* possesses a much higher degree of decussation in its canines when compared to *Saguinus*, a non-gouging callitrichine (see Figs. 4-28 and 4-29), while Nogami and Natori (1986) reached similar conclusions for the incisors of *Callithrix* and *Cebuella* versus *Saguinus*. This study is better able to highlight the extent of decussation based on its use of CPL imaging of the entire crown, however. In this case, the decussation seen in *Callithrix* canines is expressed as a highly distinct array of Hunter-Schreger bands which run from the cusp tip all the way to the cervix (see Figs. 4-28 and 4-29). In addition, these bands in the canines are also more pervasive and appear more organized than the bands in the postcanine teeth of *Callithrix* examined in this study (see Fig. 4-21). Given the array of derived anterior dental features in marmosets which are related to tree-gouging, (e.g., Rosenberger 1978), this behavior does seem the best explanation for the high decussation seen in anterior teeth of marmosets. In other words, tree-gouging does seem to place high

stresses on the enamel of anterior teeth, subjecting it to possible failure through cracking. Therefore, the high decussation seen in the anterior teeth of marmosets appears to be part of an evolutionary strategy to minimize crack propagation.

The next chapters will discuss relations between enamel increments and life history as well as ecological variables, the relationship between long period increments and biological rhythms, as well as the relationship between incremental indicators of sexual dimorphism.

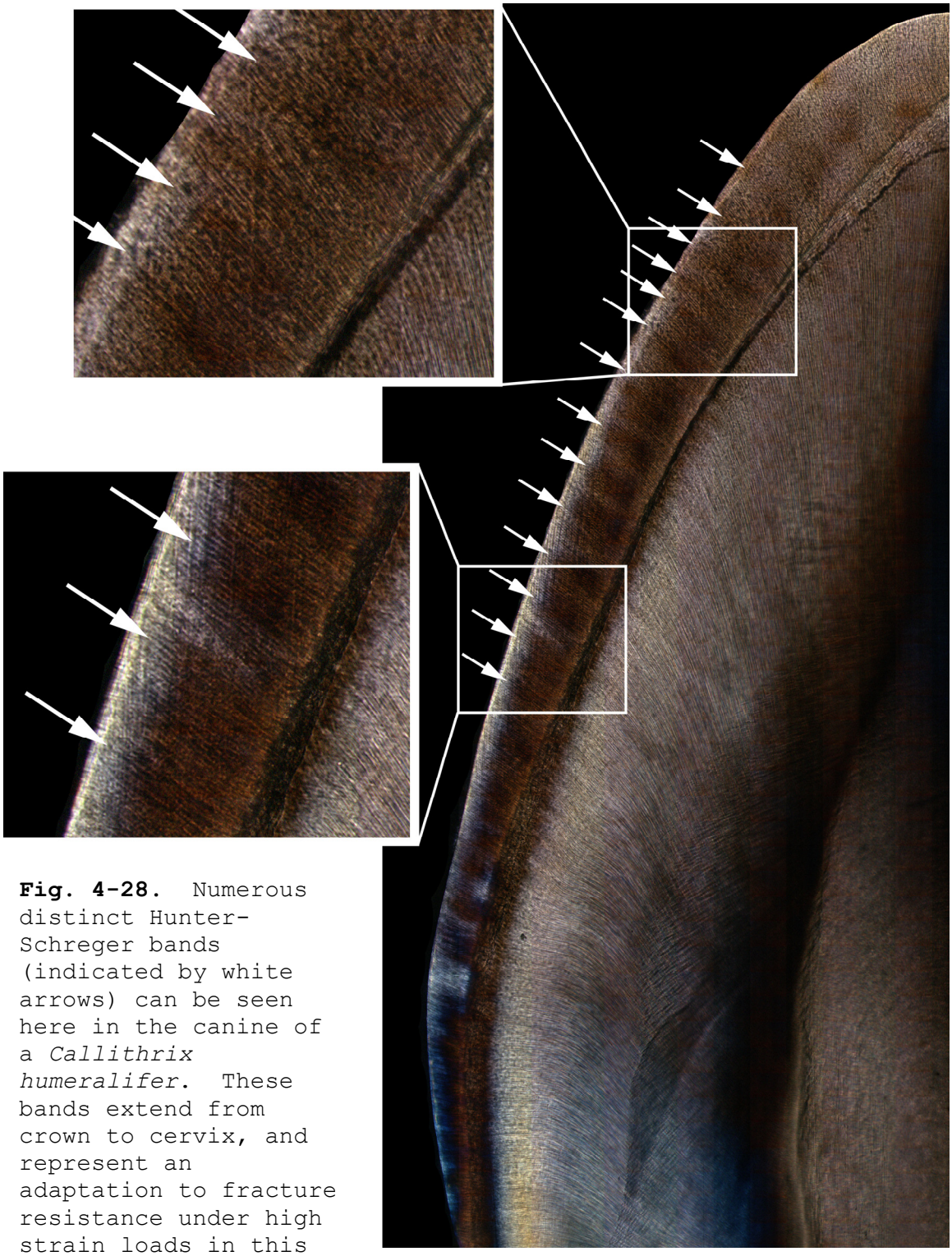


Fig. 4-28. Numerous distinct Hunter-Schreger bands (indicated by white arrows) can be seen here in the canine of a *Callithrix humeralifer*. These bands extend from crown to cervix, and represent an adaptation to fracture resistance under high strain loads in this type of tooth. **Field width in microns = 1,336; top inset = 380; bottom inset = 384.**

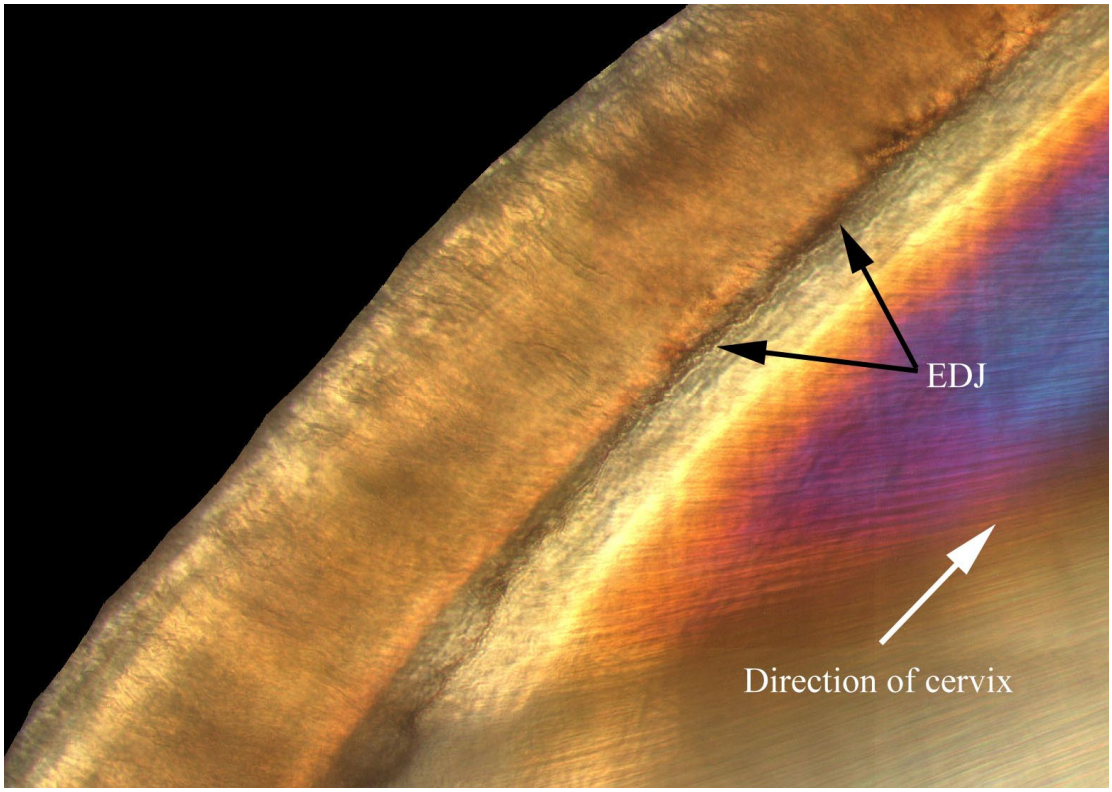


Fig. 4-29. Canine prism paths in *Saguinus fuscicollis.* Although the prisms are not strictly radial (one can see slight variations in their paths), they still are arranged into a relatively simple *schmeltzmuster.* **Field width = 489 microns.**

Chapter 5:

Description and Analysis of Enamel Growth Rates in Cebidae

Introduction

Over the last few decades, numerous papers have been published on how life history (e.g., growth rates; see Chapter 1) is linked to body and brain mass as well as socioecological variables such as dietary availability (e.g., Harvey and Clutton-Brock 1985; Harvey et al. 1987; Smith 1989; Charnov 1991; Ross 1991; Janson and Van Schaik 1993; Leigh 1994; Smith et al. 1994; Hartwig 1996; Joffe 1997; Godfrey et al. 2001, 2004, 2005, 2006; Schwartz et al. 2007). These studies are part of the wave of ontogenetic research (see Godfrey and Sutherland 1995) performed since the seminal work of Gould (1977), and have greatly increased our knowledge of life history by examining large-scale morphological changes throughout ontogeny (e.g., dental eruption sequences). However, previous research has not adequately assessed the effect of the above-mentioned variables on tissue-level ontogenetic processes; for example, does body mass have an effect on *tissue* growth rates, such as in enamel? Due to the fact that ontogenetic processes ultimately begin at the level of cells and tissues (e.g., Enlow and Hans 1996; Raff 1996), a major gap remains in the understanding of ontogenetic evolution.

In other words, since cells and tissues cause the growth of organs and organisms, knowledge regarding physiology at this microscopic level is needed to further understand the correlations between ontogeny and variables such as body mass and diet (Enlow and

Hans 1996; Ramirez-Rozzi 2002; Bromage et al. 2009). Therefore, to continue to obtain more information about ontogeny, researchers are looking at the different underlying and interacting subcomponents which are influencing this process (e.g., Curry 1999; Ramirez-Rozzi 2002; Schwartz et al. 2002, 2007; McFarlin 2006; LaCruz and Bromage 2006; Karsenty 2006; Warshaw 2007; Bromage et al. 2009). Dental ontogeny is an overarching process which results from the interaction of different subcomponents such as mandibular and maxillary growth, periodontal ligament activity, dental eruption, and dental tissue growth rates, each of which may be differentially driven or limited by genetics, selection, etc. (e.g., Enlow and Hans 1996; Raff 1996; Daegling and Hylander 2000; Jernvall 2000; Raff and Raff 2001; Miletich and Sharpe 2003). By understanding these subcomponents, we gain important information about the forces that drive dental ontogeny.

As discussed in previous chapters, vertebrate dental tissues and bone provide an excellent window into underlying ontogenetic processes since these tissues preserve a permanent record of the cellular activities which create them. Dental increments in particular provide a powerful tool for analyzing tissue-level ontogenetic processes, due to their regular periodicity (see Chapter 3 for details). Therefore, it is not surprising that there has been a recent increase in dental increment research focused on understanding life history evolution (e.g., Bromage and Dean 1985; Beynon and Dean 1987; Beynon and Wood 1987; Beynon et al. 1991, 1998; Dean and Beynon 1991; Dean 1998; Dirks 1998; Reid et al. 1998a, 1998b; Dean 2000; Macho 2001; Schwartz and

Dean 2001; Schwartz et al. 2002, 2005b, 2007; Godfrey et al. 2006; see Chapter 2 for discussion).

To date, there have not been any broad taxonomic interpretations on the interaction between body mass, brain mass, and especially socioecological variables and dental microstructural growth rates, with the exception of a few recent studies on subfossil Malagasy strepsirhines (e.g., Schwartz et al. 2002, 2007; Godfrey et al. 2006). These studies specifically examine the differences in dental microstructural growth rates between the subfossil Malagasy strepsirhines and other primates and are able to suggest underlying ecological reasons for these differences (e.g., age at foraging independence; see Macho 2001; Schwartz et al. 2002, 2007; Godfrey et al. 2006, Catlett et al. 2010). However, due to the limitations of sampling in these studies, addressing potential statistical correlations between growth rates and other variables has not been possible.

The primary aim of this chapter is to analyze the growth response of dental tissues to body and brain mass as well as specific socioecological variables (i.e., age at foraging independence, dietary availability/risk, and maternal investment) within the Cebidae. The Cebidae provide an ideal group for such analyses since they exhibit a high degree of diversity in their body mass and ecological adaptations within a narrow phylogenetic space. As a group, the Cebidae should not be as subject to phylogenetic noise when compared to analyses across primates (e.g., Harvey and Clutton-Brock 1985; Godfrey et al. 2001), yet they contain enough diversity to hopefully reveal interesting patterns (e.g., Rosenberger 1992; see Chapters 1 and 4). They may

provide further insight into the differences and similarities between anthropoids and the previously studied strepsirhines (e.g., Schwartz et al. 2002, 2007; Godfrey et al. 2006).

To accomplish this goal, I examine daily enamel secretion rates (DESRs) and enamel formation front (EFF) angles as direct indicators of enamel growth rate (described in Chapters 2, 3, and 4, and illustrated in Fig. 3-5; see also Lacruz et al. 2008),and how the microstructural growth indicators correlate with brain and body mass as well as the other socioecological variables mentioned above. I also specifically compare my results regarding the statistical effect of these variables on enamel growth rates to previous studies examining the effect of brain and body mass (Smith 1989; Smith et al. 1994) and ecological variables (Godfrey et al. 2001) on dental eruption patterns. First, I provide some historical context regarding brain/body mass and socioecology as they relate to dental ontogeny (i.e., dental eruption sequence, overall pace of dental eruption, and enamel growth rates) across primates.

Body Mass, Brain Mass, and Dental Ontogeny

Primate research has repeatedly shown that body and brain mass are strongly correlated with many life history variables, such as age at weaning and somatic growth rates (e.g., Schultz 1960; Harvey and Clutton-Brock 1985; Harvey et al. 1987; Ross 1991; Ford and Davis 1992; Charnov and Berrigan 1993). Therefore, it is not surprising

that the length of time it takes to complete overall dental eruption is also significantly correlated with brain and body mass across primates (e.g., Smith 1989; Smith et al. 1994; Godfrey et al. 2001). Moreover, the different patterns of tooth eruption sequences in anthropoids have also been shown to be correlated with body mass specifically (Schultz 1935; Smith 2000). In other words, larger, slower-growing anthropoids tend to delay the eruption of their molars relative to their permanent premolars, possibly due to limitations of available space in the posterior aspect of their dental arcades during growth (Schultz 1935; Smith 2000). In contrast, Godfrey and colleagues (2005) show that while this correlation between body mass and eruption sequence does characterize the lemuroid genus *Lepilemur,* it does not characterize the lemuroid *Avahi*. Therefore, the lemuroids and perhaps even the strepsirhines in general seem to exhibit a pattern of variation which is not seen within the anthropoids. This suggests that a greater understanding of the influences on eruption sequence in the two primate suborders is needed (see Chapter 8 for a discussion).

The discrepancy between lemuroids and anthropoids regarding eruption sequence and body mass is also present when examining the relationship of body mass to enamel growth rates (Schwartz et al. 2002, 2005, 2007; Godfrey et al. 2006). Studies of dental increments have shown that the large subfossil lemurs, *Megaladapis* and *Palaeopropithecus,* possessed a rapid dental growth similar to their much smaller extant strepsirhine relatives. This similarity exists despite the fact that *Megaladapis* and *Palaeopropithecus* are more

similar to *Gorilla* and *Pan* in terms of body mass, respectively (Schwartz et al. 2002, 2005, 2007; Godfrey et al. 2006). This is evidence that factors beyond body mass, such as diet and phylogeny, do play a role in dental growth and eruption in primates.

As mentioned above, tooth eruption is a complex process which is itself the result of multiple physiological processes such as mandibular/maxillary bone growth, growth rates of tooth crown (enamel and dentine) tissues, growth rates of tooth root tissues, gingival tissue resorption, and periodontal membrane activity (Enlow and Hans 1996; Ramirez-Rozzi 2002; Schwartz et al. 2002). Moreover, research has shown that tooth crown growth and tooth eruption are not strongly correlated among primates (e.g., Godfrey et al. 2006). Therefore, it is possible that growth rates of dental tissues are evolutionarily driven or constrained by a variety of forces. This difference between growth and eruption could be a major reason why patterns seen for anthropoids and strepsirhines in prior studies are so different (e.g., Smith 1989, 2000; Smith et al. 1994; Schwartz et al. 2002, 2005, 2007; Godfrey et al. 2004, 2005, 2006).

Whether tissue growth rates of teeth and tooth eruption show important differences with respect to their relationships to body and brain mass is unknown, primarily because previous studies have not analyzed the relationships between dental tissue growth rates and body/brain mass. By performing such an analysis, we can hopefully provide some insight into the forces which are driving dental growth versus eruption among the primate suborders.

Socioecological Variables and Dental Ontogeny

It is important to note here that even if body mass and/or brain mass prove to be correlated with enamel growth rates within cebids (and within primates in general), prior studies suggest that they are nevertheless insufficient to completely explain the patterns of dental growth across primates (Godfrey et al. 2001, 2004, 2005, 2006; Schwartz et al. 2002, 2005a, 2007). For example, the differences in dental growth between the large-bodied hominoids and subfossil lemurs, as well as the similarities between these subfossil lemurs and their much smaller extant relatives, cannot be explained by body and/or brain mass alone (Schwartz et al. 2002, 2005, 2007; Godfrey et al. 2006). Furthermore, Godfrey and colleagues (2001, 2004, 2005) have specifically shown that phylogeny and ecology are strongly tied to dental ontogeny both within strepsirhines and across primates.

Considering the functional importance of teeth in the evolutionary history of mammals, it is logical that ecology should have such an effect on dental ontogeny. As discussed in Chapters 1 and 2, teeth are a crucial point of interaction between a mammal and its environment, and so the growth of teeth (as well as their morphology) should be closely tied to ecological demands in terms of the timing of food availability and mechanical consistency of food resources (e.g., Kay 1975; Godfrey et al. 2001; Ramirez-Rozzi 2002). Therefore, it is important to assess the interaction of specific socioecological variables with dental growth in addition to the statistical effects of brain and body mass.

Godfrey and colleagues (2001) performed the first major study examining the relationship between dental ontogeny and socioecological variables. Specifically, they developed and tested an array of hypotheses regarding the effects of these variables on the pace (absolute timing) of tooth eruption in different primate taxa. Among these variables, age at foraging independence seems to be the most important predictor of dental eruption (see also Gibson 1986; Dunbar 1992, 1995; Byrne 1995; Joffe 1997; Ross and Jones 1999); non-statistical studies of subfossil strepsirhines have suggested it may be important to enamel growth rates as well (e.g., Godfrey et al. 2006). Therefore, species whose young are adapted to foraging independently at earlier ages seem to be selected for faster dental ontogeny relative to species with delayed independence (see below). Other ecological variables, such as environmental risk (*sensu* Janson and Van Schaik 1993; see explanation below), seem to have less of a statistical effect on dental eruption timing (Godfrey et al. 2001; see below for details).

These socioecological hypotheses should be applied to enamel growth rates as well, since these two ontogenetic processes for teeth are not correlated in primates and may reflect different selective forces (Godfrey et al. 2006; see above). More importantly, enamel growth rates should give us insight into tissue-level issues of physiology and metabolism which may be obscured in gross eruption studies. With these ideas in mind, this study will test two of the dietary hypotheses put forth by Godfrey and colleagues (2001) because they are especially pertinent to cebids: the foraging independence

hypothesis and the risk aversion hypothesis. It will also examine the statistical interaction of maternal investment strategies with dental growth rate. Specifically, this chapter will examine the relationships between enamel growth rates, as reflected in DESR's and EFF angles, and quantifiable proxy variables which are tied to age at foraging independence and risk aversion, as outlined in the study of Godfrey and colleagues (2001; see also Janson and Van Schaik 1993), as well as proxy variables tied to maternal investment (see below). The three hypotheses that I am testing in this chapter regarding socioecological variables and enamel growth rates are outlined below:

1) Foraging independence hypothesis – Primates are assumed to vary in the cognitive and learning capabilities which underlie their foraging behavior. It has been argued that primate species whose feeding regimes require relatively low cognitive abilities (e.g., folivores) have less to learn for successful foraging, and therefore, do not need to devote as many resources to brain growth (Gibson 1986; Dunbar 1992, 1995; Byrne 1995; Joffe 1997; Ross and Jones 1999; Godfrey et al. 2001). Because larger (i.e., more fully grown) animals should be less subject to predation, these species should devote most of their energy to body mass growth so that they can grow more quickly and be less subject to predation pressure (Godfrey et al. 2001). In contrast, primate species whose feeding regimes are more cognitively demanding (e.g., requiring advanced mapping or problem-solving abilities), undergo selection for lengthened juvenile learning periods,

delayed weaning and reproduction, larger brains, and should devote relatively more energy to brain growth to facilitate the acquisition of complex foraging skills (Gibson 1986; Dunbar 1992, 1995; Byrne 1995; Joffe 1997; Ross and Jones 1999; Godfrey et al. 2001). Although the delayed body mass growth which results should put them at increased predation risk relative to their less encephalized relatives, it is hypothesized that the fitness benefits of the lengthened juvenile period outweigh these costs (Gibson 1986; Dunbar 1992, 1995; Byrne 1995; Joffe 1997; Ross and Jones 1999; Godfrey et al. 2001).

Coincident with their faster body mass growth, species that obtain foraging independence at relatively younger ages should exhibit faster enamel growth due to their need to process an adult diet at an earlier age (Godfrey et al. 2001). Species with delayed ages at foraging independence will wean later, will therefore not need full adult dentitions as quickly, and in turn should exhibit overall slower dental ontogenies (Godfrey et al. 2001). Overall, we can derive the following from the predictions of Godfrey and colleagues (2001): 1) species with larger brains relative to body mass (i.e., species with a higher encephalization quotient, or EQ) should exhibit slower enamel growth rates than species with relatively smaller brains; and 2) species with delayed weaning should exhibit slower enamel growth rates.

2) Risk aversion hypothesis – This hypothesis, originally put forward by Janson and Van Schaik (1993; see also Leigh 1994), suggests that species which live in a riskier environment and have a more unstable dietary supply should have slower overall growth rates to reduce the risk of starvation at any one point in time. That is, in environments where resource availability may fluctuate highly, species with lower energy expenditure in terms of metabolism and growth will be less likely to suffer from malnutrition (Janson and Van Schaik 1993; Leigh 1994; Godfrey et al. 2001). Where environmental resources are relatively stable, species should be better able to afford higher growth rates and metabolism. Research has shown that this hypothesis does seem to hold true with regard to body mass growth in the anthropoids studied so far (Leigh 1994). However, dental eruption data have not supported it; specifically, the time it takes to complete dental eruption is not significantly correlated to age at first female reproduction (Godfrey et al. 2001). Therefore, I will test the risk aversion hypothesis using enamel growth rates.

3) Maternal investment hypothesis – Based on the idea that mothers and infants may have slightly different fitness needs (e.g., Trivers 1972, 1974; Nicolson 1987), I hypothesize that an increase in maternal investment will result in slower infant dental growth rates. Lee (1999) has argued that increased maternal investment (reflected by prolonged interbirth intervals) is tied to greater brain growth during the period of lactation.

Given this, it seems likely that the statistical effect of maternal investment upon growth rates may extend to teeth as well, especially considering that the state of dental growth is important to a young primate's ability to fend for itself (e.g., Smith et al. 1994).

Therefore, I predict that when it is in the interest of both mother and offspring to have a high maternal investment and delay juvenile independence, juveniles should experience relatively slower dental growth. This slower growth should result because the continued allocation of maternal resources allows the juveniles to complete dental ontogeny at a later stage of their overall development. However, for species where mothers need to conserve resources for future infants at the cost of current ones (Trivers 1972, 1974; Nicolson 1987), the juveniles of that species should exhibit faster dental growth rates.

Age at weaning and interbirth interval should be good proxy variables for assessing maternal investment (e.g., Trivers 1972, 1974; Nicolson 1987; DiBitetti and Janson 2000; Lee 1999). Relatively higher values for these proxies should reflect a relatively higher maternal investment in individual offspring. Based on the above-mentioned prediction, species with delayed weaning and relatively longer interbirth intervals should have relatively slower enamel growth rates.

Overall, in this chapter, I test these socioecological hypotheses as well as whether brain and body mass affect enamel growth rates.

See Chapter 3 for details of specimen preparation, imaging and measurement techniques, data sources and statistical software used. See also Appendices A and B for further detail on specimens included and raw data. I have included data from *Alouatta* spp., a noncebid platyrrhine, in these analyses since *Alouatta* is relatively larger than the cebids, but has a relatively small brain size. Also note that body mass data for *Leontopithecus rosalia* were obtained from captive individuals; to reflect this *L. rosalia* will be highlighted in red in analyses examining body mass. Body mass data for all other species are from wild-caught individuals (see Chapter 3 for details).

Results

Table 5-1 provides descriptive statistics on DESR, EFF angle, and crown formation index (CFI = mean DESR/mean EFF angle) for each species included in the analyses. Note that EFF angles were used in the statistical analyses; however, with regard to enamel growth, these angles will often be discussed in terms of their reflection of enamel extension rates (i.e., the number of ameloblasts operating at a specific point in developmental time). Specifically, a greater EFF angle reflects a slower enamel extension rate and vice-versa (see Chapter 3, specifically Fig 3-5, and Chapter 4 for discussion of the relationship between EFF angles and enamel extension rates). In other words, more obtuse EFF angles signify a slower enamel growth rate. Due to the preservation of some teeth, I was unable to obtain a

measurable EFF angle for some cebid taxa (see Table 5-1). For figures showing general distributions of DESR and EFF values, see Chapter 4.

Genus	Species (N)	DESR mean	DESR range	DESR stand. dev.	DESR CV	EFF angle mean	EFF angle range	EFF angle stand. dev.	EFF angle CV	CFI
Alouatta	spp. (3)	**5.11**	6.67	1.27	0.25	**19.64**	6.92	2.08	0.11	**0.26**
Aotus	spp. (2)	**4.67**	6.28	1.05	0.22	**16.87**	5.43	3.84	0.23	**0.28**
Callimico	*goeldii* (1)	**4.31**	4.35	0.76	0.17	**13.91**	3.78	1.43	0.1	**0.31**
Callithrix	*humeralifer* (1)	**4.13**	2.41	0.62	0.15	**-**	-	-	-	**-**
Callithrix	*jacchus* (1)	**4.3**	2.73	0.53	0.12	**-**	-	-	-	**-**
Cebuella	*pygmaea* (1)	**4.8**	3.93	0.61	0.13	**-**	-	-	-	**-**
Cebus	*albifrons* (2)	**4.87**	9.07	1.4	0.29	**36.74**	19.63	4.61	0.13	**0.13**
Cebus	*apella* (5)	**5.14**	9	1.31	0.25	**22.35**	14.37	4.07	0.18	**0.23**
Cebus	*capucinus* (2)	**5.72**	8.34	1.31	0.23	**24.36**	14.86	3.45	0.14	**0.23**
Cebus	*olivaceus* (1)	**4.47**	6.4	0.88	0.2	**-**	-	-	-	**-**
Leontop.	*rosalia* (1)	**4.93**	4.49	0.83	0.91	**8.96**	13.83	4.3	0.5	**0.55**
Saguinus	*fuscicollis* (1)	**4.66**	5.11	0.8	0.17	**16.76**	7.6	2.61	0.16	**0.28**
Saguinus	*midas* (1)	**4.29**	5.08	0.86	0.2	**-**	-	-	-	**-**
Saguinus	*nigricollis* (1)	**4.73**	4.83	1.02	0.21	**14.79**	12.17	3.0	0.2	**0.31**
Saguinus	*oedipus* (1)	**4.44**	3.85	0.69	0.16	**-**	-	-	-	**-**
Saimiri	*boliviensis* (1)	**5.7**	4.99	0.8	0.14	**-**	-	-	-	**-**
Saimiri	*oerstedii* (1)	**4.78**	3.86	0.83	0.17	**14.18**	12.15	4.38	0.31	**0.34**
Saimiri	*sciureus* (2)	**4.7**	7.38	1.01	0.21	**13.0**	8.64	2.54	0.2	**0.36**

Table 5-1. Descriptive statistics for enamel increment data obtained in this study. These mean DESR and EFF angle values (in bold) were used in the regression analyses (see below). The values used for brain and body mass as well as the four ecological proxy variables are in Appendix B. DESR values are given in microns, EFF angle values are given in degrees. CV = coefficient of variation. CFI (crown formation index = mean DESR/mean EFF angle).

Bivariate analyses: body mass and brain mass

See Table 5-2 for a summary of all bivariate regression statistics for this section.

In the bivariate linear regression analyses, both DESR and EFF angle were moderately to strongly correlated with body and brain mass. However, the correlations of DESR were weaker (r = 0.5 for body mass and 0.58 for brain mass) than the correlations of EFF angle (r = 0.61 for body mass and 0.71 for brain mass). All correlations listed here were statistically significant at a 95% confidence interval (see Table 5-2; Figs. 5-1 through 5-4).

These results are in concordance with those of prior studies which suggest that body and brain mass are both linked to programs controlling dental ontogeny in anthropoids (e.g., Schultz 1935; Smith 1989; Smith et al. 1994; Smith 2001). Moreover, they also show that for the cebids, brain mass is the better predictor of enamel growth. However, it is important to note that the relationships observed for DESR and EFF angle are in fact *opposite* one another in these analyses. In other words, in the cebids, DESR increases with body and brain mass (positive relationship) whereas enamel extension rates decrease (i.e., a more obtuse EFF angles) for species with larger bodies and brains (negative relationship; see Figs. 5-3 and 5-4). Therefore, EFF angles show a relationship between dental ontogeny and body/brain mass which is similar to that of previous studies based on tooth eruption (Smith 1989; Smith et al. 1994), whereas DESR shows the opposite pattern.

Predictor (X)	Dependent (Y)	r^2	r	p	Figure
LN body mass	DESR	0.25	0.5	0.03	5-1
	EFF angle	0.37	0.61	0.045	5-3
	CFI	0.25	-0.5	0.12	5-6
LN brain mass	DESR	0.33	0.58	0.02	5-2
	EFF angle	0.5	0.71	0.014	5-4
	CFI	0.33	-0.57	0.07	5-7
Weaning age	DESR	0.63	0.79	0.0002	5-8
	EFF angle	0.39	0.63	0.04	5-12
	CFI	0.33	-0.57	0.07	5-16
EQ	DESR	0.17	0.42	0.09	5-9
	EFF angle	0.48	0.69	0.02	5-13
	CFI	0.27	-0.52	0.1	5-17
Age at 1st female reprod.	DESR	0.27	0.52	0.04	5-10
	EFF angle	0.39	0.62	0.05	5-14
	CFI	0.25	-0.5	0.14	5-18
Interbirth interval	DESR	0.35	0.59	0.02	5-11
	EFF angle	0.38	0.61	0.06	5-15
	CFI	0.19	-0.43	0.21	5-19

Table 5-2. Summary of linear regression statistics for DESR (cross-striation breadths, EFF angles and CFI relative to brain and body mass as well as the four proxy socioecological variables (EQ = Encephalization Quotient). The EFF angles were obtained from mandibular M1s and M2s only (see Chapter 3). The last column indicates the figure of each specific bivariate plot/analysis.

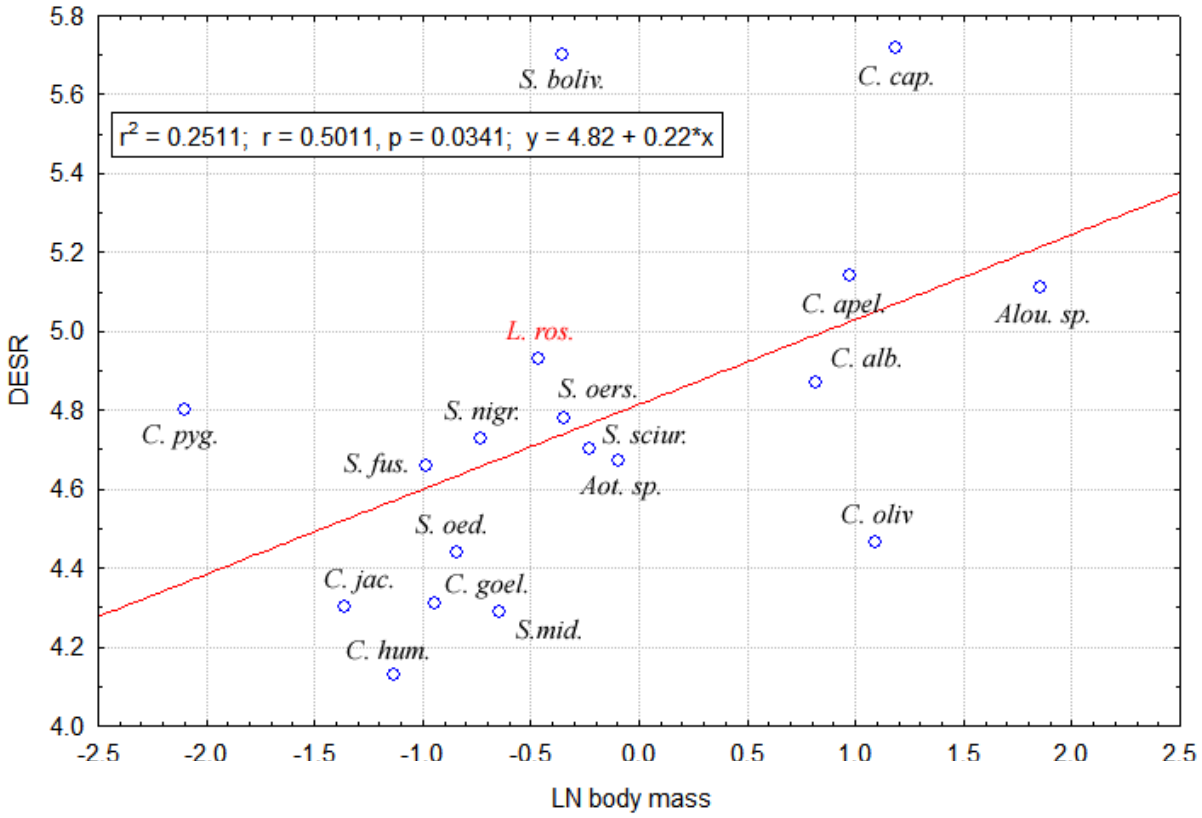


Fig. 5-1. Mean DESR (in microns) for each species regressed against the natural log (LN) of mean body mass. Note that as body mass increases, DESR also increases. This can also be seen in *Alouatta*, the larger-bodied, noncebid platyrrhine which has a relatively higher DESR. However, note that several species (e.g., *Cebus capucinus*) do not plot close to the regression line, demonstrating that body mass is not the best predictor of DESR for the cebids. Body mass data are from Ford and Davis (1992); body mass data for *L. ros.* (in red) is from captive individuals.

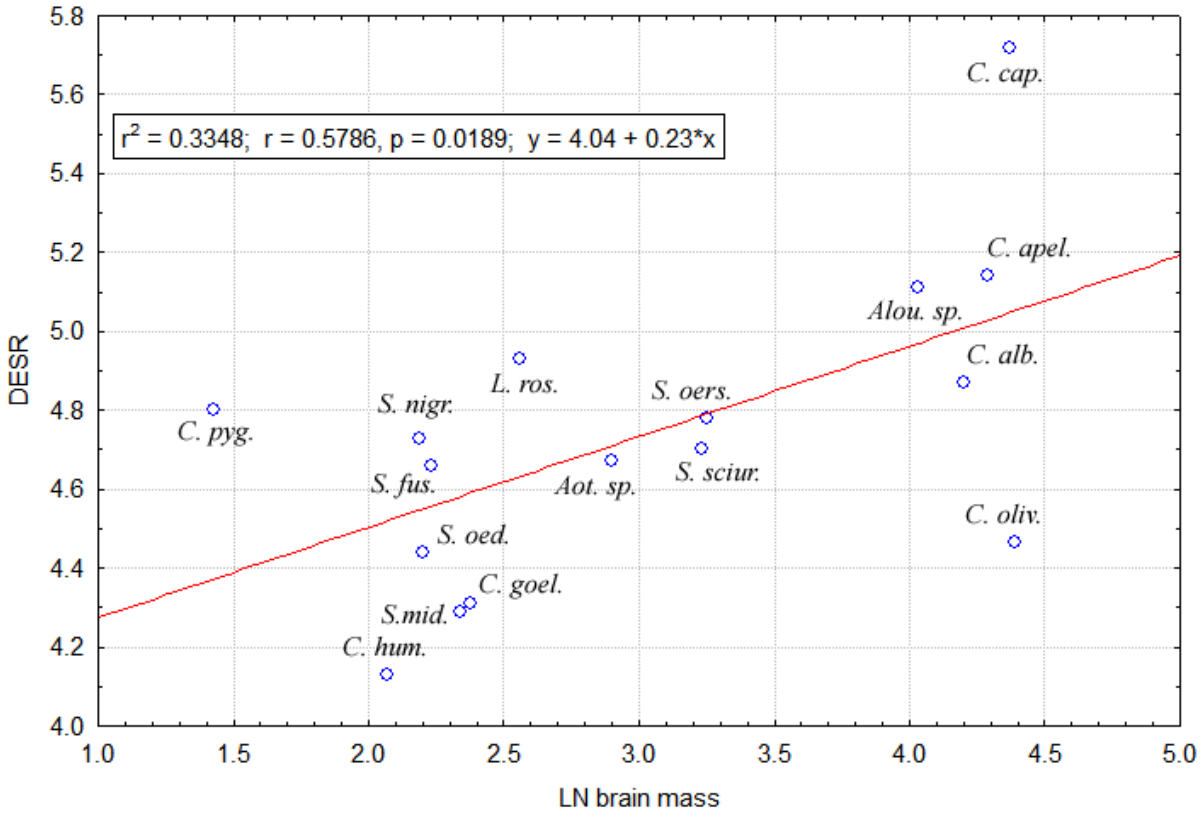


Fig. 5-2. Mean DESR for each species regressed against the natural log (LN) of mean brain mass. Again, as brain mass increases, DESR also increases, with a stronger and more significant correlation than is seen for body mass (see Fig. 5-1). See Table 3-1 in Chapter 3 for data sources on brain mass.

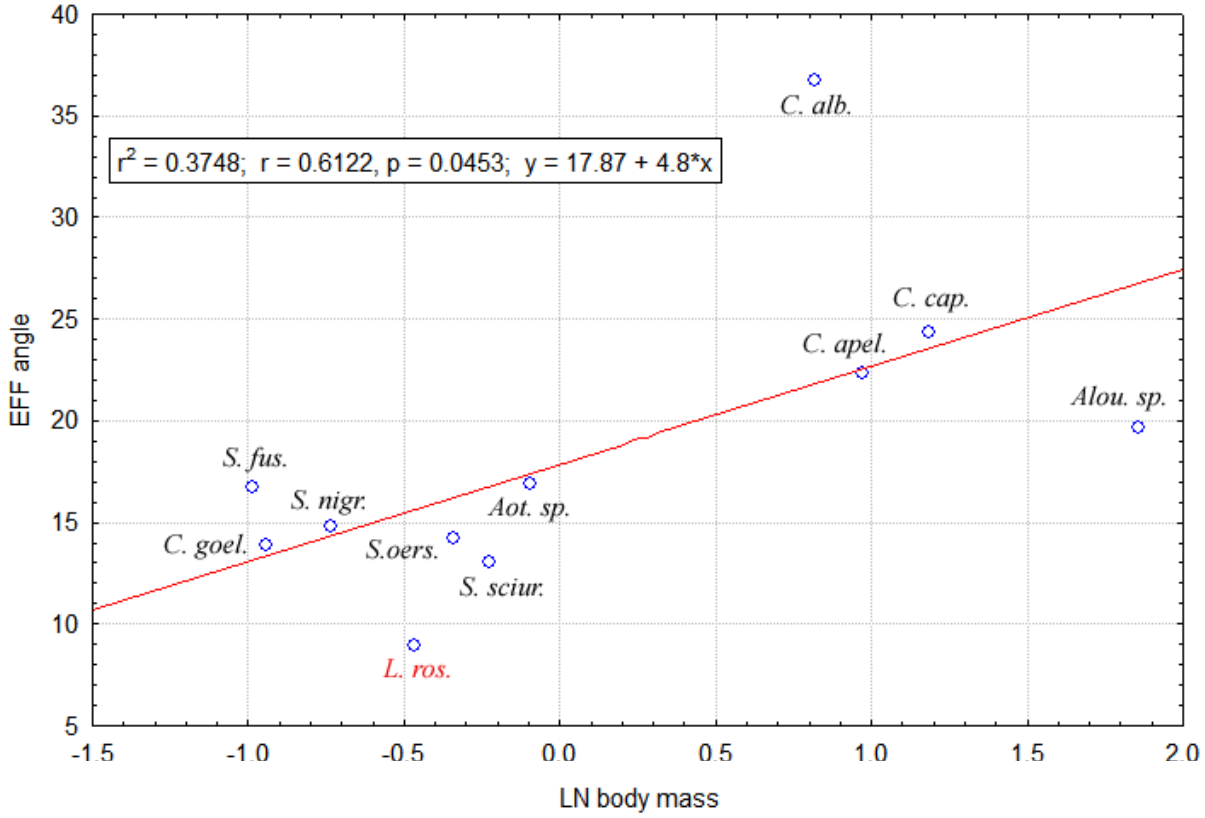


Fig. 5-3. Mean species EFF angle (in degrees) regressed against LN of mean body mass. Observe that the correlation here is higher than the one observed for DESR and body mass (Fig. 5-1). However, it is important to note that increasing values for EFF angle on the Y-axis actually reflect decreasing enamel extension rates. Therefore, this regression actually depicts an inverse relationship in which increasing body mass is correlated with decreasing enamel growth rates (see above and Chapter 3). Body mass data are from Ford and Davis (1992); body mass data for *L. ros.* (in red) is from captive individuals.

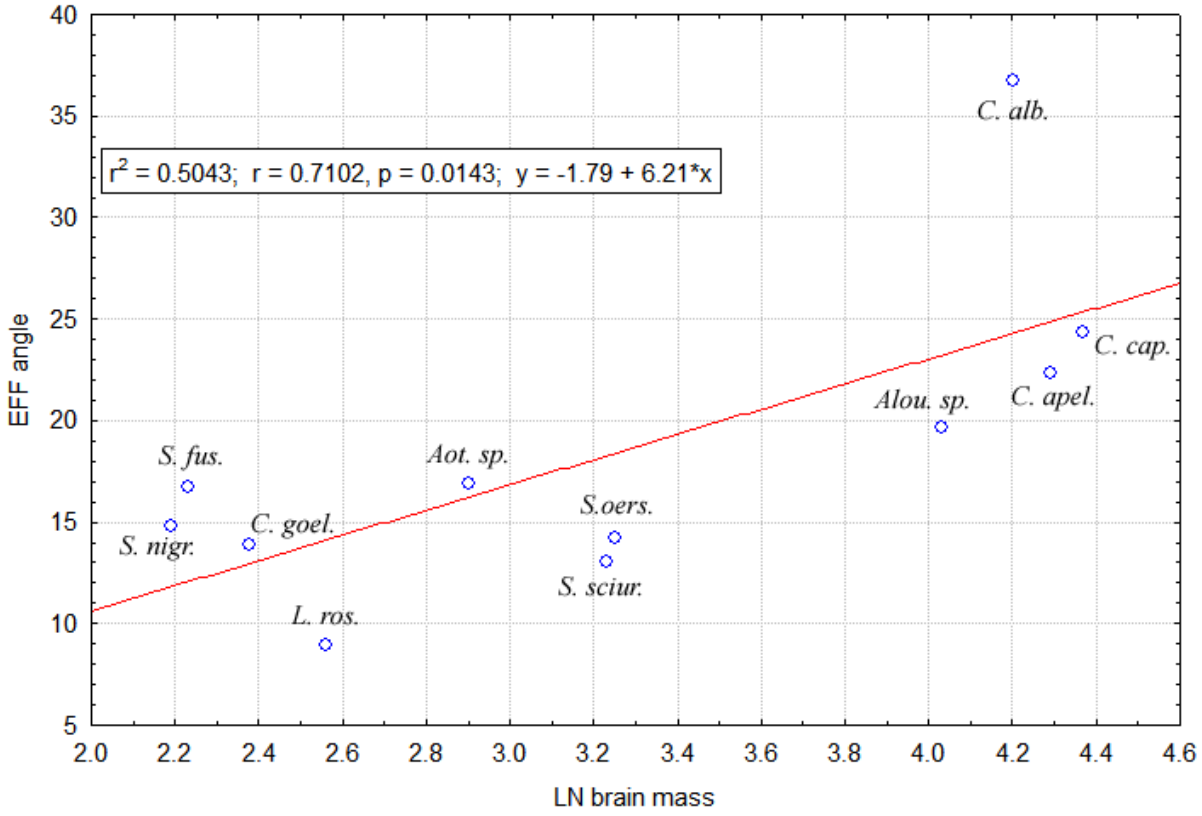


Fig. 5-4. Mean species EFF angle regressed against LN of mean brain mass. Observe that the correlation here is higher than observed for DESR and brain mass (Fig. 5-2). As in Fig. 5-3, however, note that increasing values for EFF angle on the Y-axis actually reflect decreasing enamel extension rates. In other words, enamel extension on this chart is decreasing with a corresponding increase in brain mass. See Table 3-1 in Chapter 3 for data sources on brain mass.

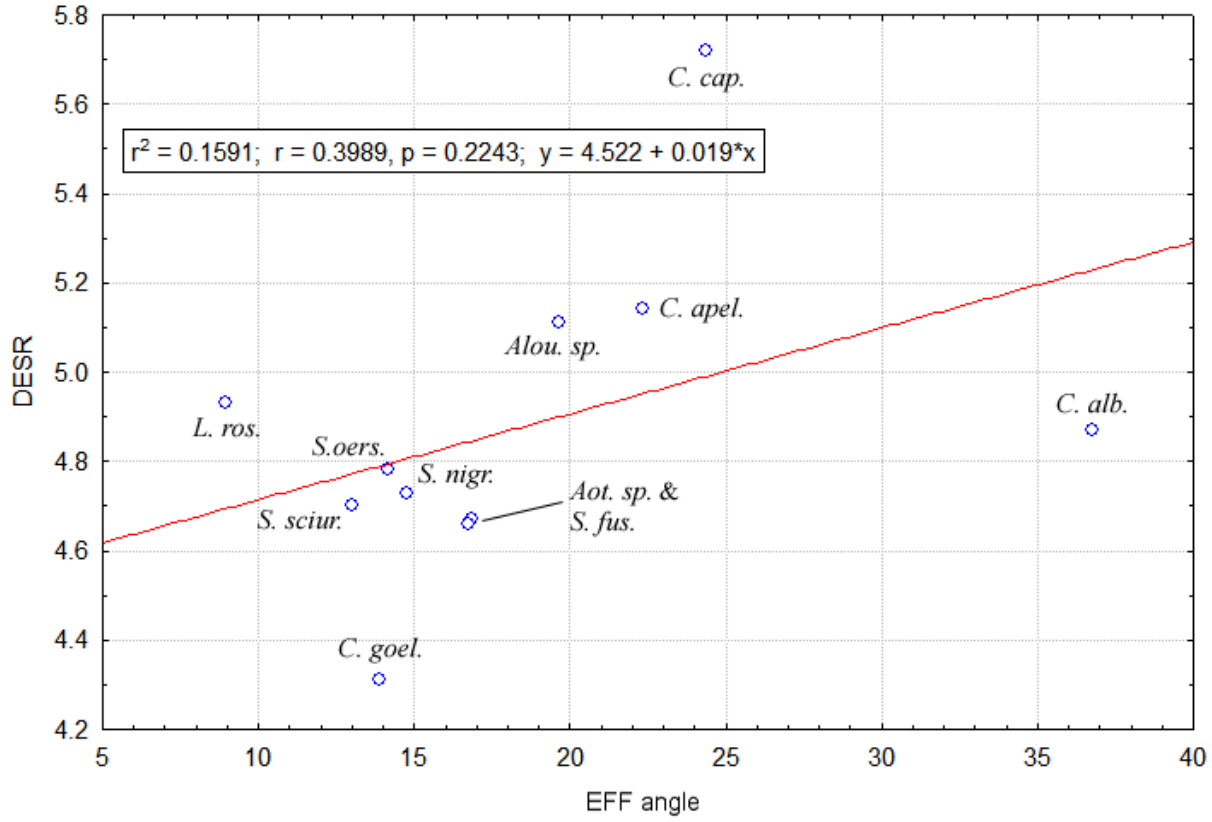


Fig. 5-5. Regression of EFF angle means (degrees) against DESR means (microns), showing that for the cebids (and *Alouatta*), these two components of overall enamel growth rate are not significantly correlated.

When the socioecological proxy variables are regressed against these two aspects of enamel growth, the same contrasting positive versus negative relationship [DESR versus enamel extension (EFF angle), respectively] exists. The biological reason for these opposing patterns is unclear, though it is important to note that DESR and EFF angle are not significantly correlated to one another in cebids (Fig. 5-5). To try and provide some further insight into an overall enamel growth rate pattern, I devised a crown formation index (CFI) to examine the effect of DESR and EFF angle

simultaneously. The CFI for each species divides the mean DESR by the mean EFF angle. Therefore, when both DESR and enamel extension rates (as signified by low EFF angles) are high, the value of the index is high. If either of these values decreases, the value of the index decreases correspondingly. However, an increase in DESR is reflected as a corresponding increase in CFI whereas an increase in the value of EFF angles results in a decrease of the CFI value. This decrease mathematically reflects the fact that increasing EFF angles are tied to slower enamel extension rates (discussed above and in Chapters 3 and 4).

For example, imagine two species with differing mean EFF angles of 10 and 15 degrees, who share a mean DESR of 5 microns. The second species, with the 15 degree EFF angle, will have the slower enamel extension rate because it has fewer ameloblasts operating at one time (see Chapter 3). The CFI for these two species reflects this difference: CFI1 = 5/10 = **0.5**; CFI2 = 5/15 = **0.33**, respectively. See Table 5-1 (above) for CFI values of species in this study.

CFI exhibits a moderate correlation with both body mass and brain mass in the cebids, though brain mass is the better predictor of CFI ($r = -0.5$ and -0.57, respectively). As with EFF angle, the relationships between CFI and brain/body mass are negative. That is, enamel growth rates overall tend to decrease as body and brain mass increase (see Figs. 5-6 and 5-7; see also discussion below). In addition, this is similar to the results of prior studies based on the timing of tooth eruption (Smith 1989; Smith et al. 1994; Godfrey et al. 2001).

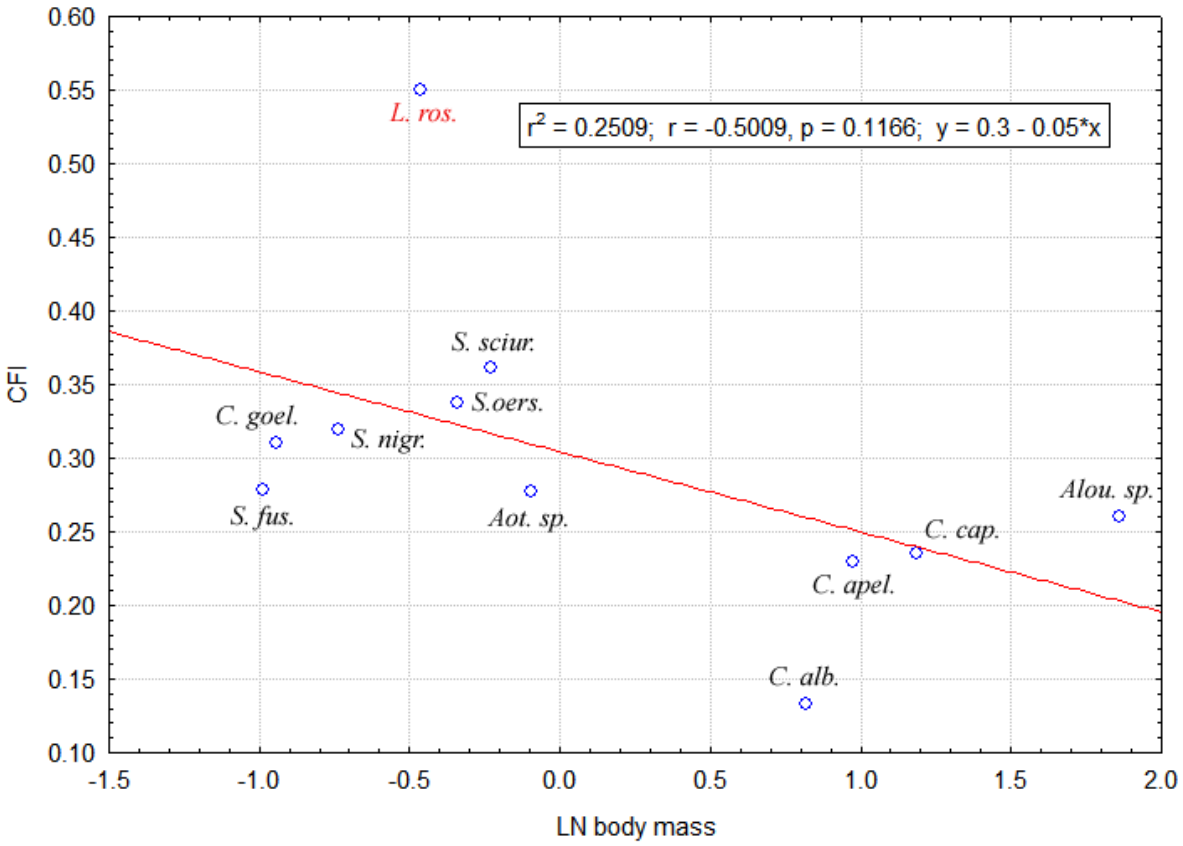


Fig. 5-6. Crown formation index (CFI, = species mean DESR/species mean EFF angle) regressed against LN of mean body mass. As with EFF angle (this study) and dental eruption in prior studies (Smith 1989; Smith et al. 1004; Macho 2001), CFI data reflect a negative relationship between dental ontogeny and body mass. Body mass data are from Ford and Davis (1992); body mass data for *L. ros.* (in red) is from captive individuals.

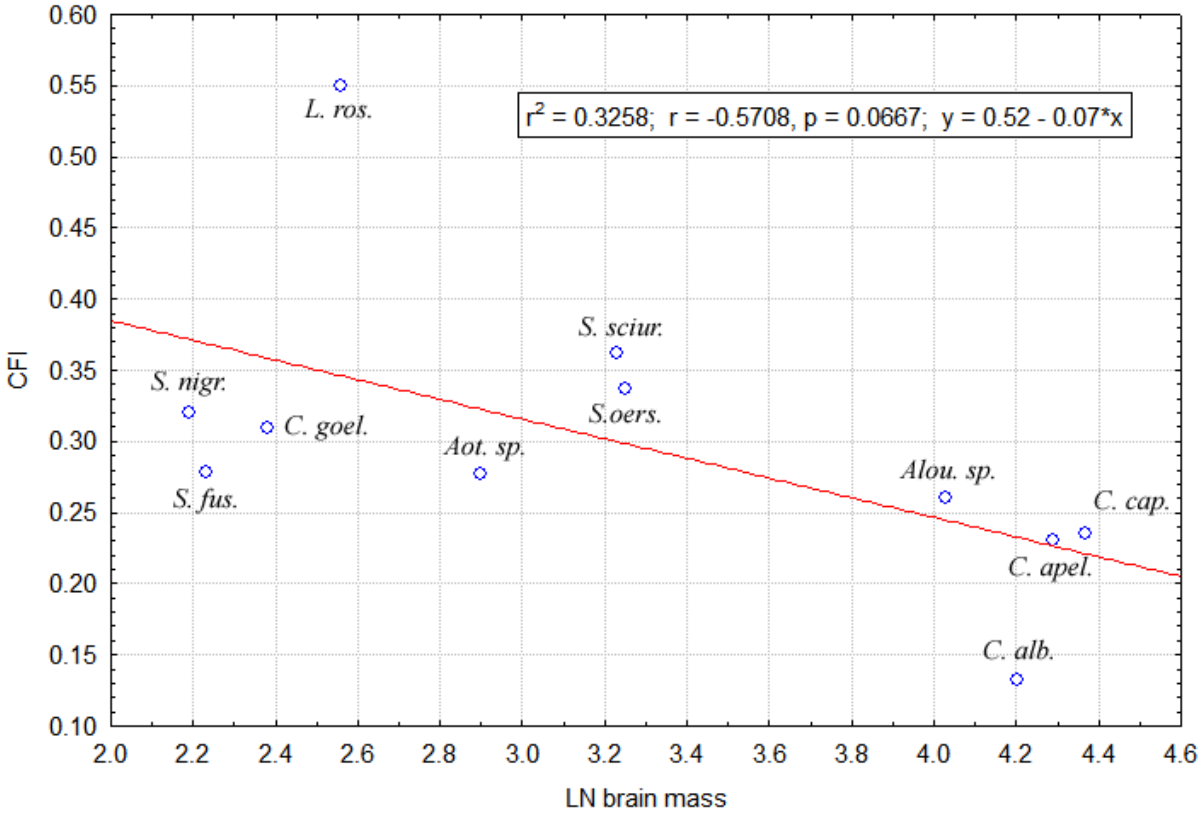


Fig. 5-7. CFI regressed against LN brain mass. CFI data reflect a negative relationship to brain mass, similar to that discussed in Fig. 5-6 for body mass. However, note that the correlation for brain mass is the stronger of the two. See Table 3-1 in Chapter 3 for data sources on brain mass.

Bivariate analyses: ecological hypotheses

See Chapter 3 (Table 3-1) for sources of data for all four ecological proxy variables and an explanation on how encephalization quotients (EQs) were calculated. Specific values for ecological proxy variables can be found in Appendix B.

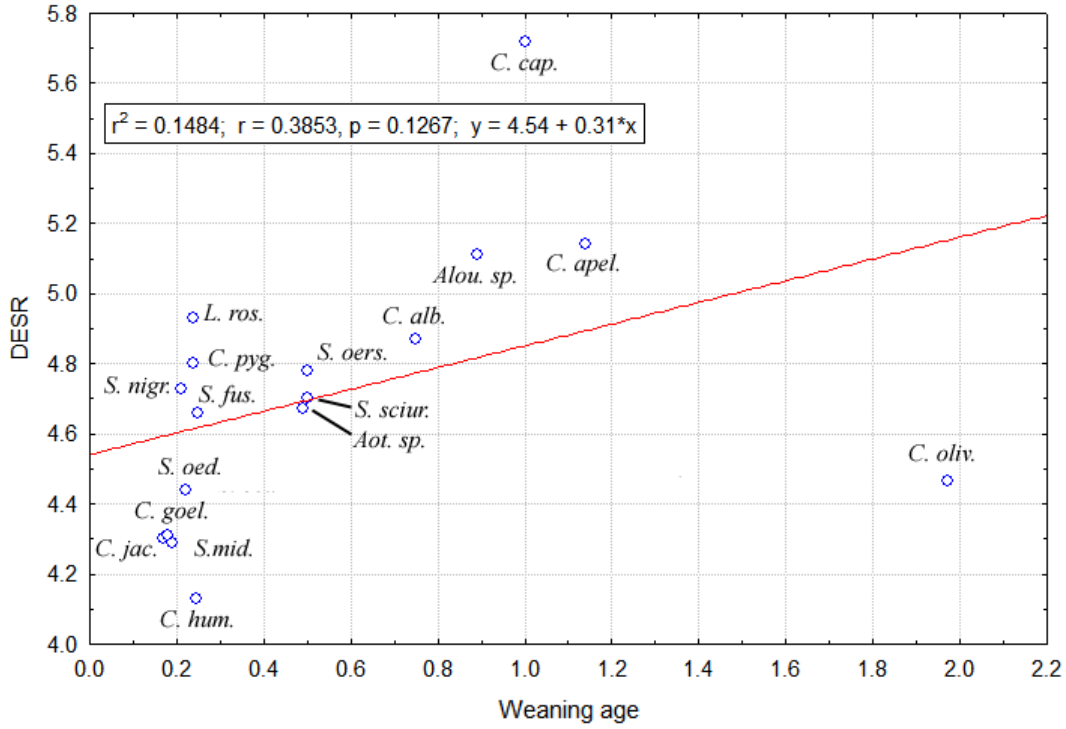
Both DESR and EFF angles were moderately to strongly correlated with encephalization, age at weaning, age at first female reproduction, and interbirth interval (approximately r = 0.5 to 0.8;

for specific values see Table 5-2 and Figs. 5-8 through 5-15). The only exception to this rule was in the relationship between DESR and age at weaning, for which r = 0.39. However, removal of the outlier (*C. olivaceus*) from the analysis yielded an r-value of 0.79 (compare 5-8A and 5-8B). The weaning age value given for this species (around 2 years; see Lindenfors 2002) may be an atypical or incorrect value since all other species of *Cebus* cluster around a weaning age of one year (e.g., Harvey and Clutton-Brock 1985; Godfrey et al. 2001; Lindenfors 2002). Unfortunately, another value for verification of this datum for *C. olivaceus* could not be found in the literature. Due to the extremely large discrepancy between the analyses with and without this one species, I determined that it was best to exclude *C. olivaceus* from further analyses of DESR and weaning age. No EFF angle data were available for *C. olivaceus* in this study, so this species did not affect EFF angle/weaning regressions. Further information is needed to determine whether or not this weaning age is reflective of the behavior of *C. olivaceus.*

DESR

Among the four ecological proxies examined, DESR exhibited the strongest relationship with age at weaning (r = 0.79). DESR was only moderately correlated with the three other proxies (r-values between 0.41 and 0.59; see Figs. 5-8 through 5-11). Of these four socio-ecological proxies, only EQ did not have a statistically significant relationship with DESR (p = 0.09; see Fig. 5-9).

A.



B.

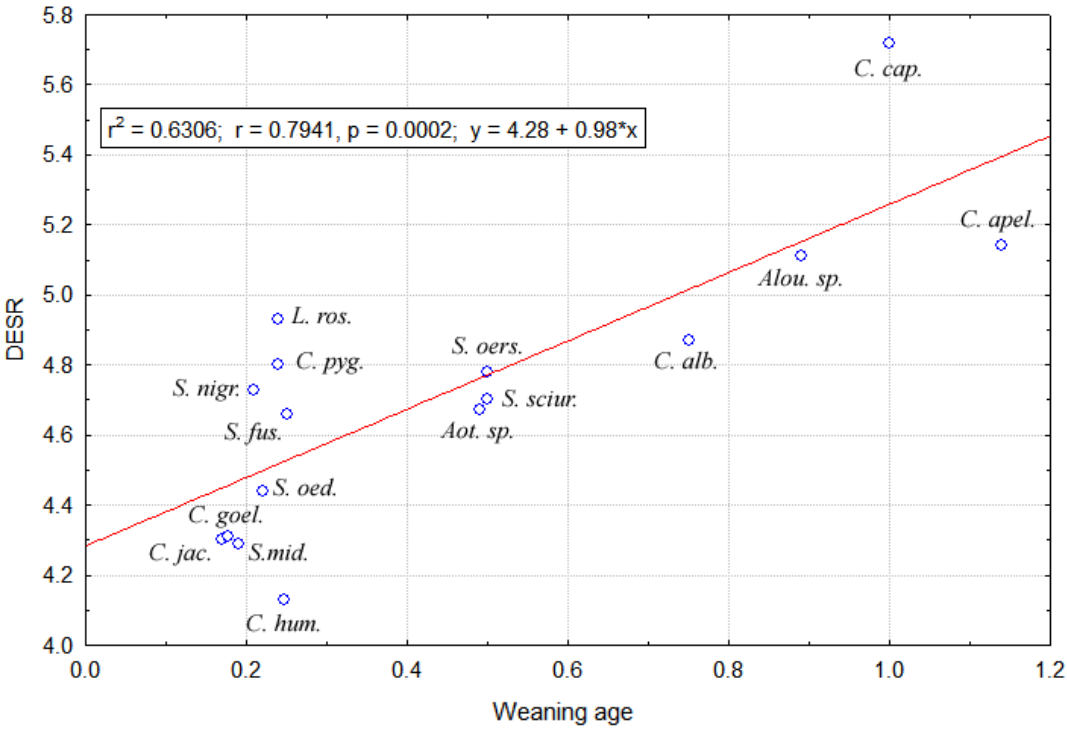


Fig. 5-8. Mean DESR (microns) regressed against species mean for weaning age (in years). **A.** Regression including the outlier *C. olivaceus*. **B.** Regression excluding *C. olivaceus*. All subsequent analyses and discussion on weaning age do not include *C. olivaceus* (see above text for an explanation). See Table 3-1 in Chapter 3 for data sources on weaning age.

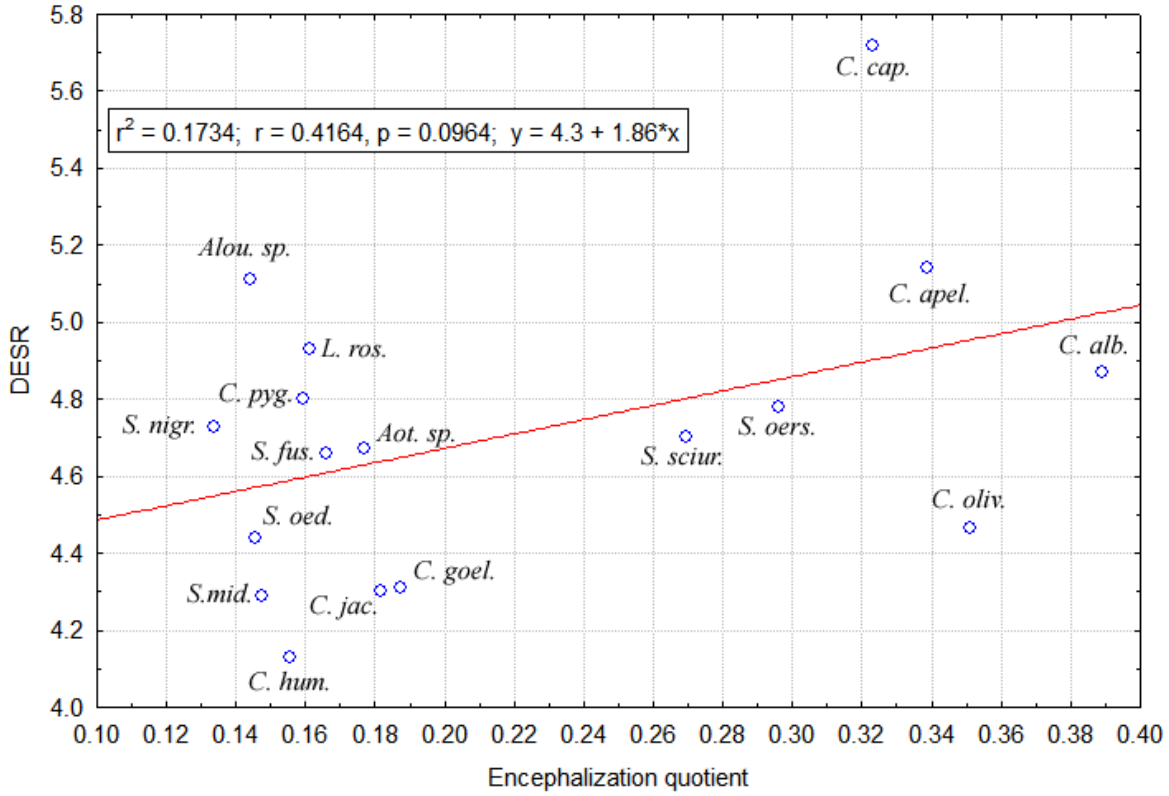


Fig. 5-9. Mean DESR regressed against encephalization quotient (EQ). As with the other socioecological proxies (except age at weaning; Fig 5-8B), EQ is only moderately correlated with DESR. See Table 3-1 in Chapter 3 for data sources on brain mass and body mass used to calculate EQ.

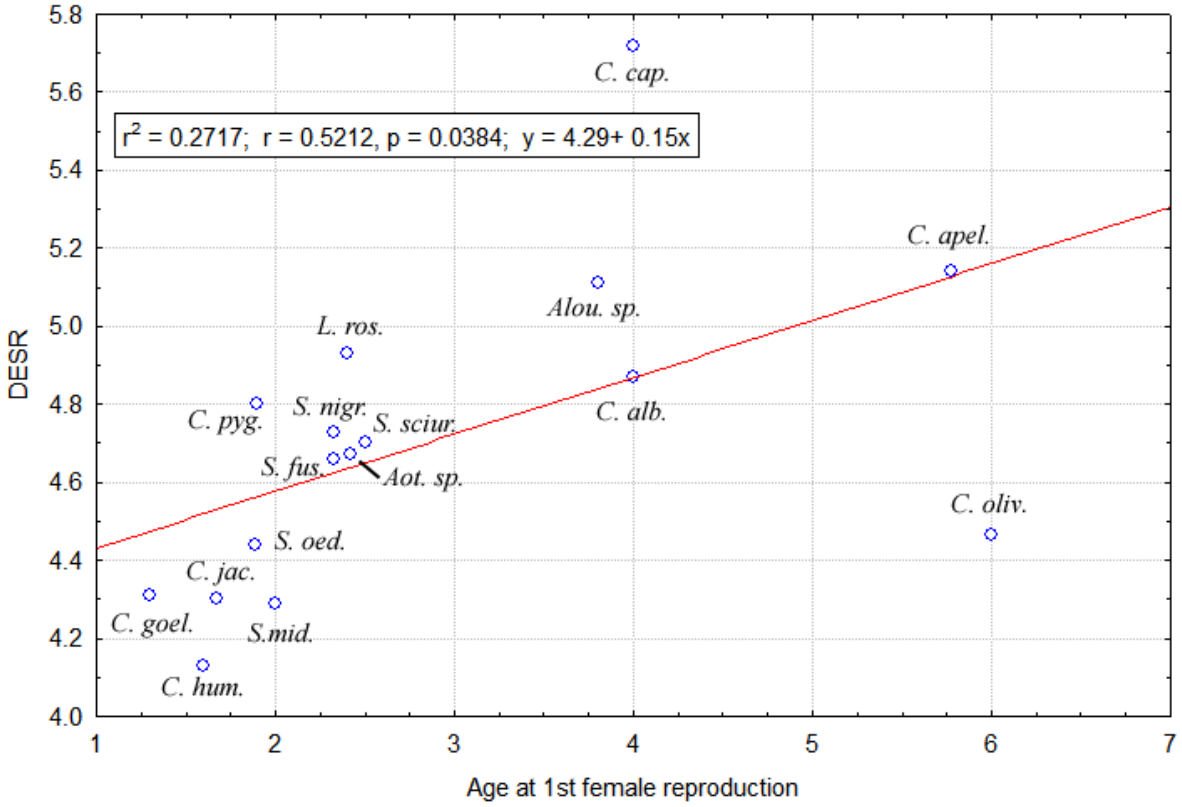


Fig. 5-10. DESR regressed against species mean age at 1st female reproduction (years). As with the other socioecological proxies (except age at weaning; Fig 5-8B), age at 1st female reproduction is only moderately correlated with DESR. See Table 3-1 in Chapter 3 for data sources on age at first female reproduction.

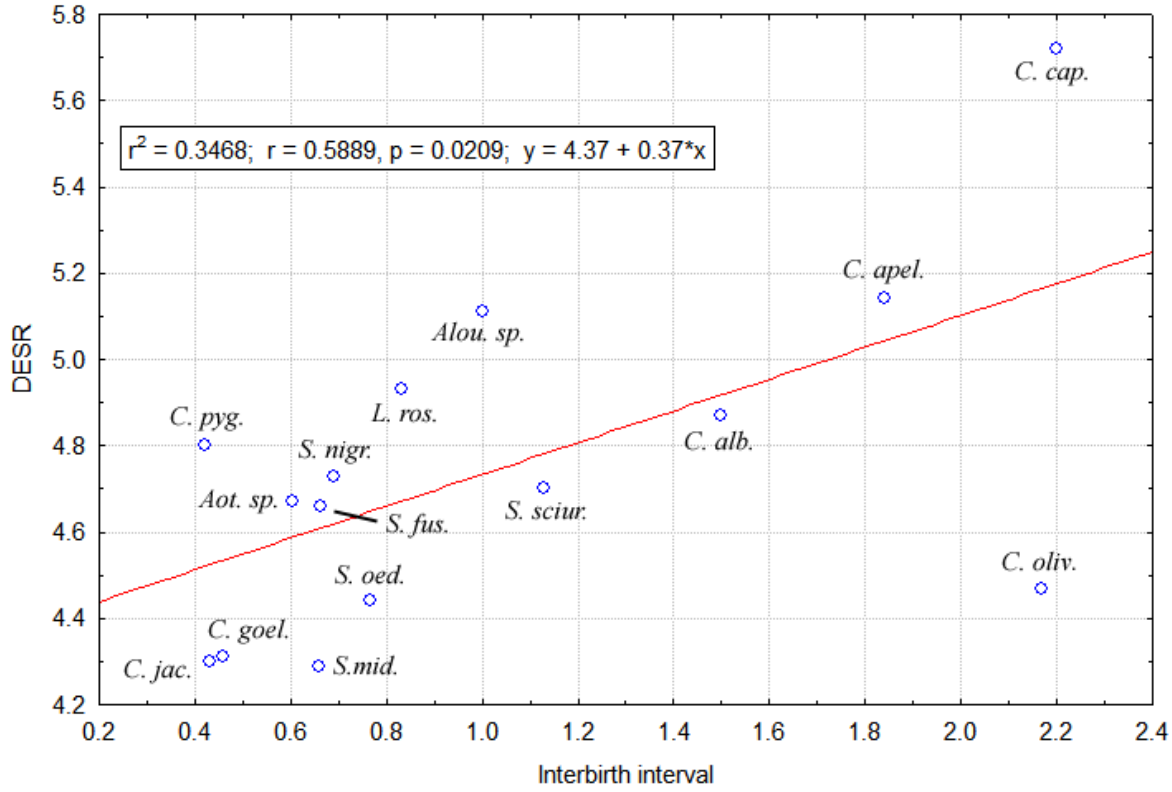


Fig. 5-11. Mean DESR regressed against species mean interbirth interval (years). As with the other socioecological proxies (except age at weaning; Fig 5-8B), interbirth interval is only moderately correlated with DESR. See Table 3-1 in Chapter 3 for data sources on interbirth interval.

EFF angle

Although EFF angle generally shows stronger correlations with all four proxy variables versus DESR, EFF angle is most strongly and significantly correlated with age at weaning (r = 0.63; p = 0.02) and encephalization quotient (r = 0.69 and p = 0.04); see Table 5-2 and Figs. 5-12 and 5-13, respectively). Correlations are only slightly weaker for age at first female reproduction and interbirth interval (r = 0.62 and 0.61, respectively), however they are not statistically significant (p = 0.54 and 0.59, respectively; see Figs. 5-14 and 5-15). Again, DESR and EFF angles show patterns opposite one another,

in that DESR is positively correlated with all four socioecological proxies whereas EFF angles reflect a negative relationship between enamel extension rates and all proxies.

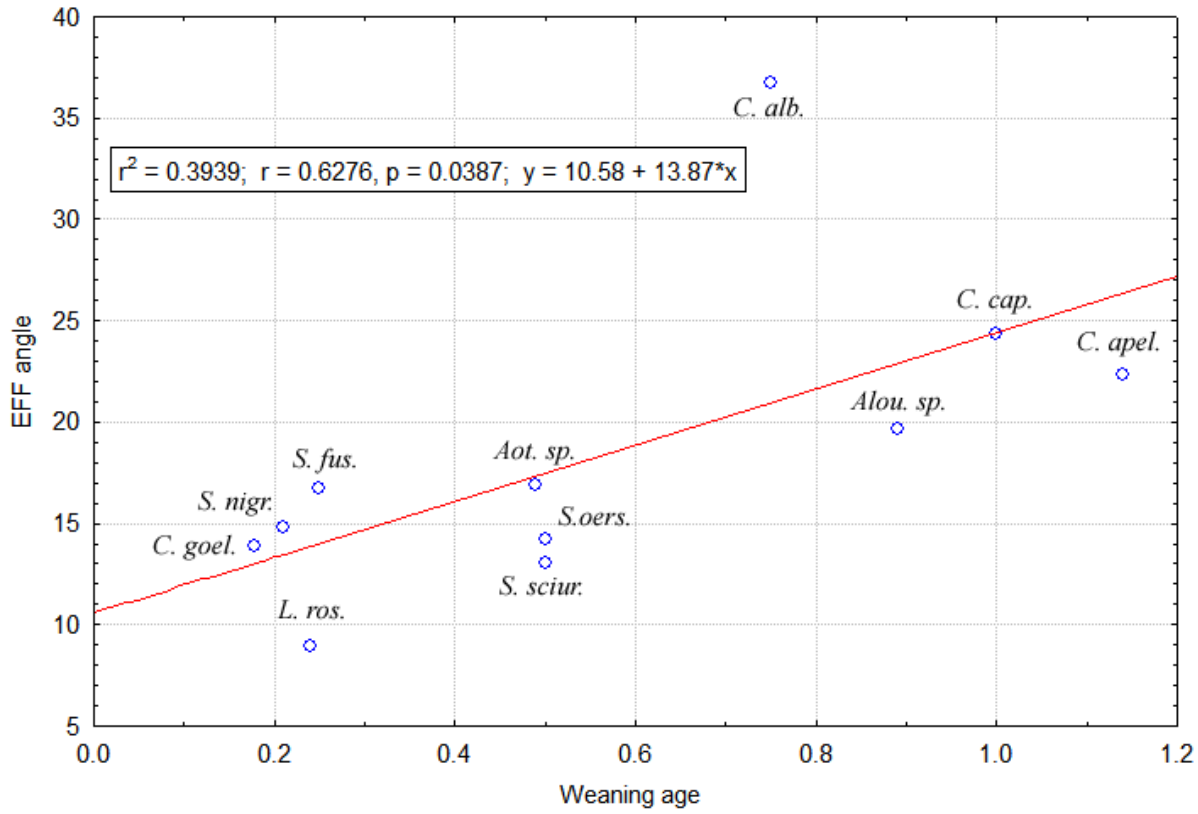


Fig. 5-12. Mean EFF angle (degrees) regressed against weaning age (years). Increased EFF angles are reflecting lower enamel extension rates; therefore, all EFF regressions against socioecological proxies exhibit a negative relationship, which was also seen with the brain and body mass analyses above. See Table 3-1 in Chapter 3 for data sources on weaning age.

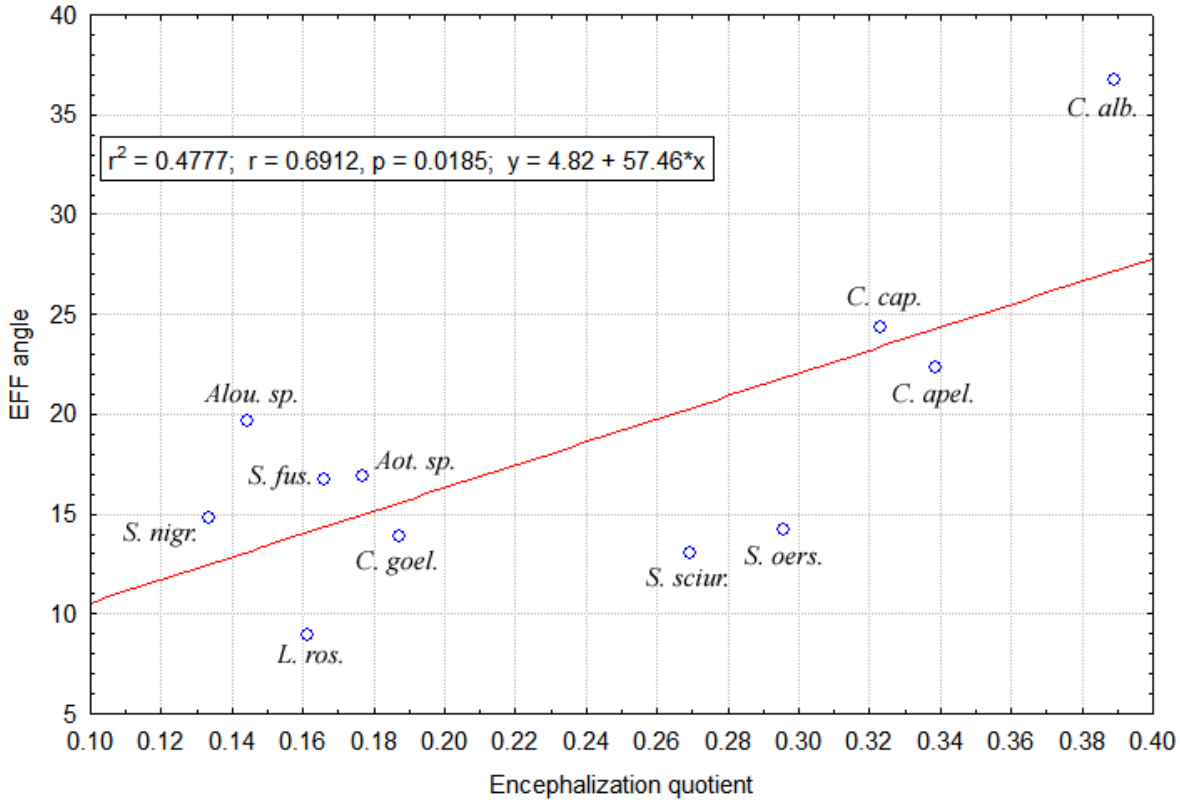


Fig. 5-13. Mean EFF angle regressed against EQ showing a negative relationship between the two. See Table 3-1 in Chapter 3 for data sources on brain mass and body mass used to calculate EQ.

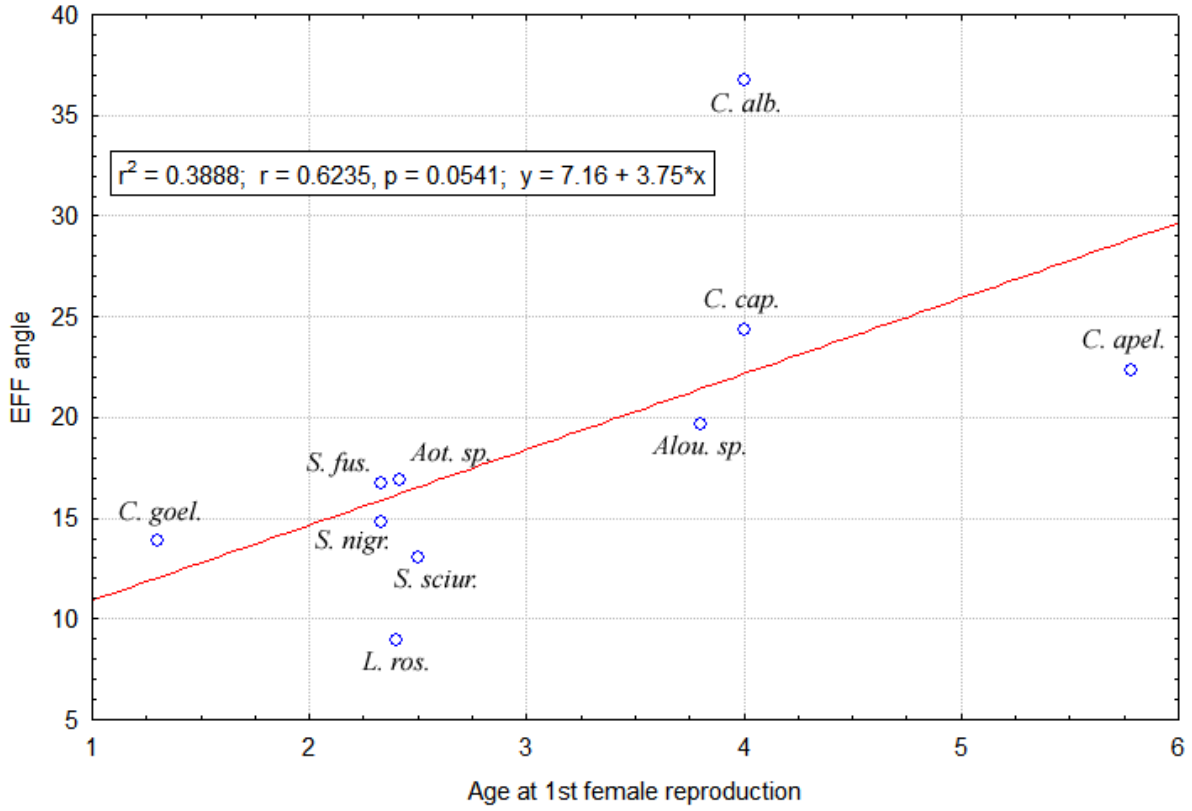


Fig. 5-14. Mean EFF angle regressed against age at 1st female reproduction (years) showing a negative relationship between the two. See Table 3-1 in chapter 3 for data sources on age at first female reproduction.

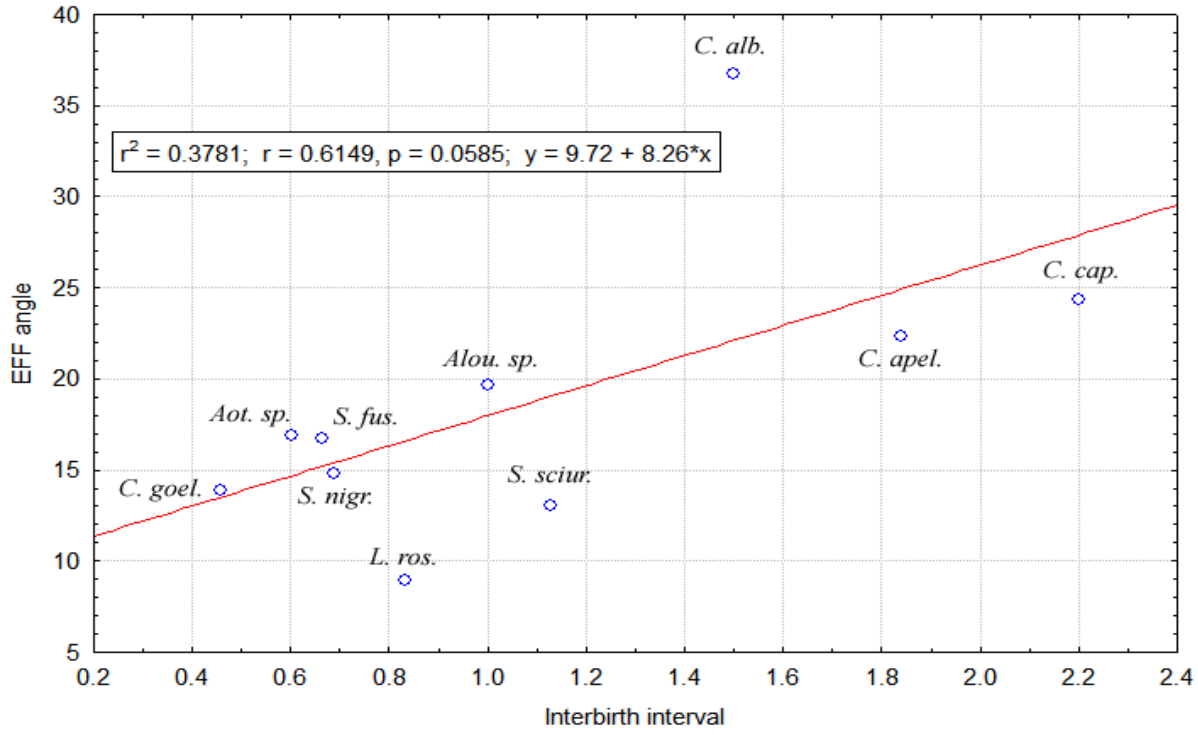


Fig. 5-15. Mean EFF angle regressed against interbirth interval (years) showing a negative relationship between the two. See Table 3-1 in Chapter 3 for data sources on interbirth interval.

CFI

As with EFF angle, CFI exhibits a negative relationship with all four socioecological proxies, and is moderately correlated with each (see Table 5-1, Figs. 5-16 through 5-19). CFI shows the strongest relationships with weaning and encephalization quotient; r = -0.57 and -0.52, respectively (Figs. 5-16 and 5-17). R-values for age at first female reproduction and interbirth interval are -0.5 and -0.43, respectively (Figs. 5-18 and 5-19). None of these proxy variables showed a statistically significant relationship to CFI in bivariate regressions (see Figs 5-16 through 5-19).

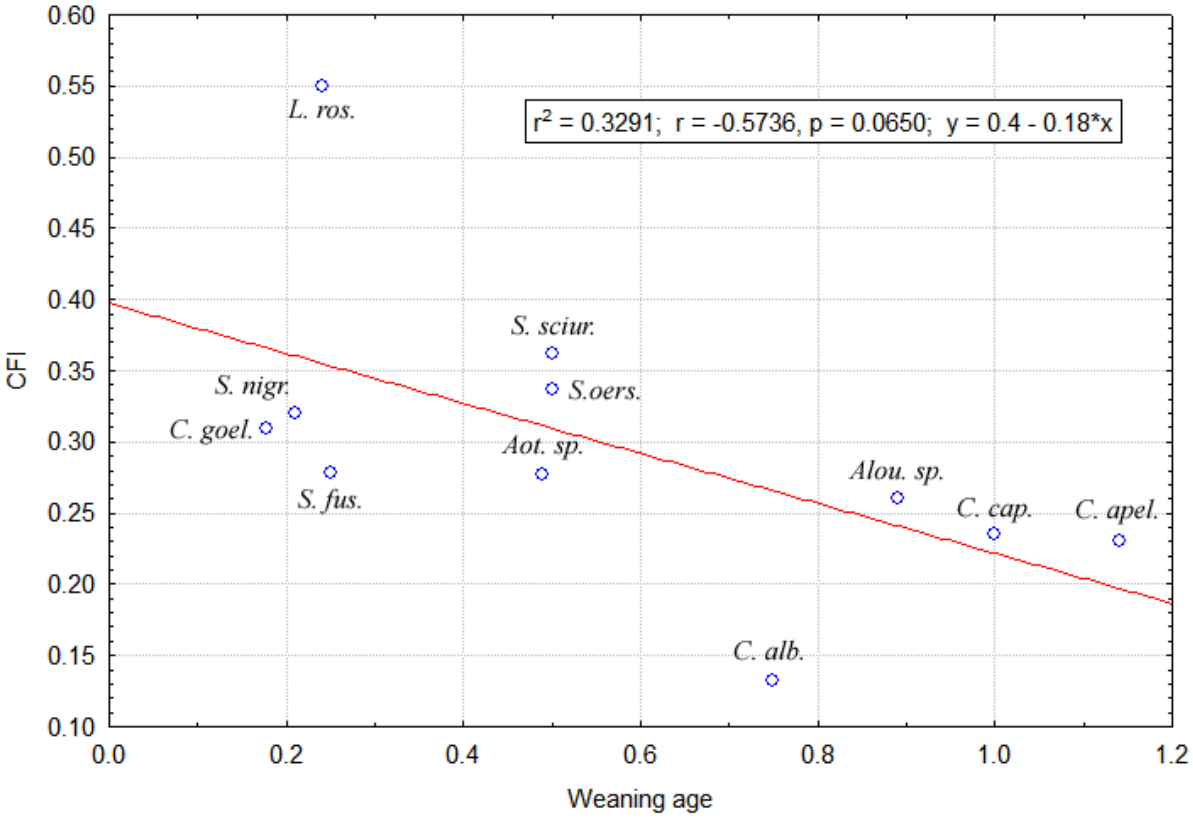


Fig. 5-16. Crown formation index (CFI) regressed against weaning age (years) showing a negative relationship between the two. The correlation of CFI and weaning age is stronger than the correlation of CFI with any other variable except brain mass (Fig 5-7). See Table 3-1 in Chapter 3 for data sources on weaning age.

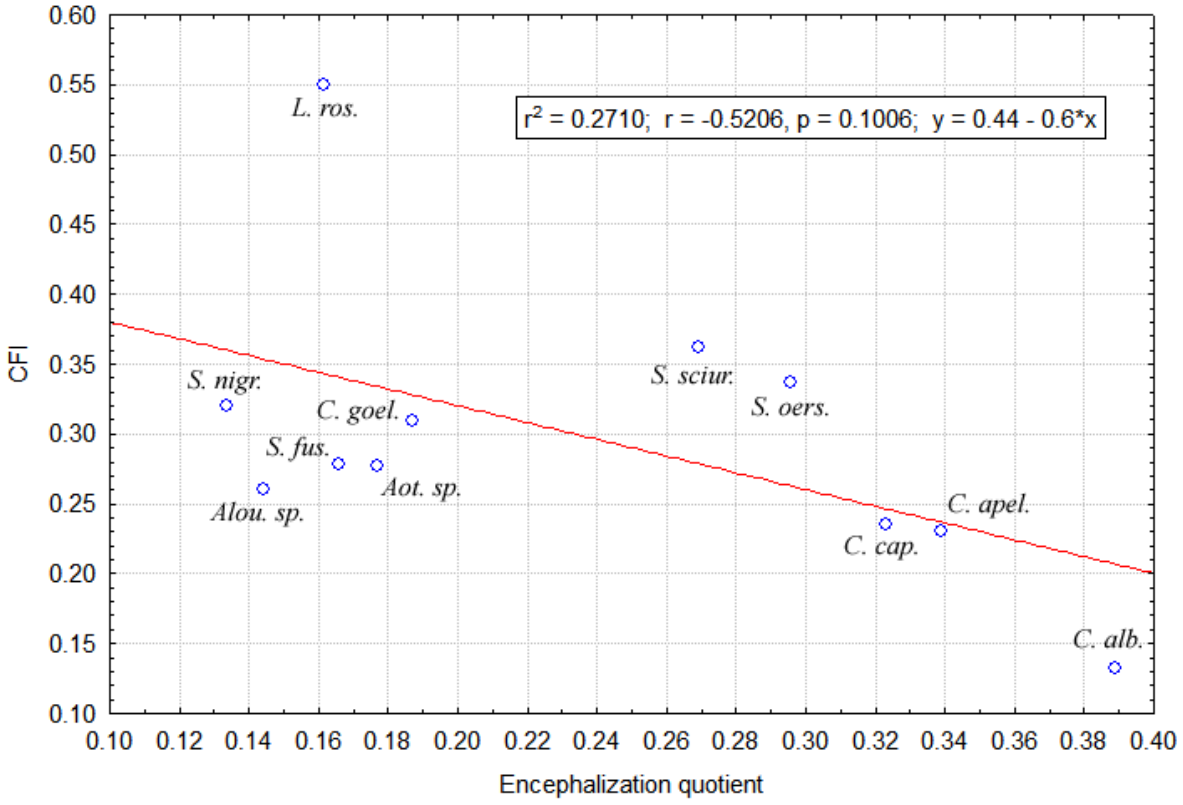


Fig. 5-17. CFI regressed against EQ showing a negative relationship between the two. See Table 3-1 in chapter 3 for data sources on brain mass and body mass used to calculate EQ.

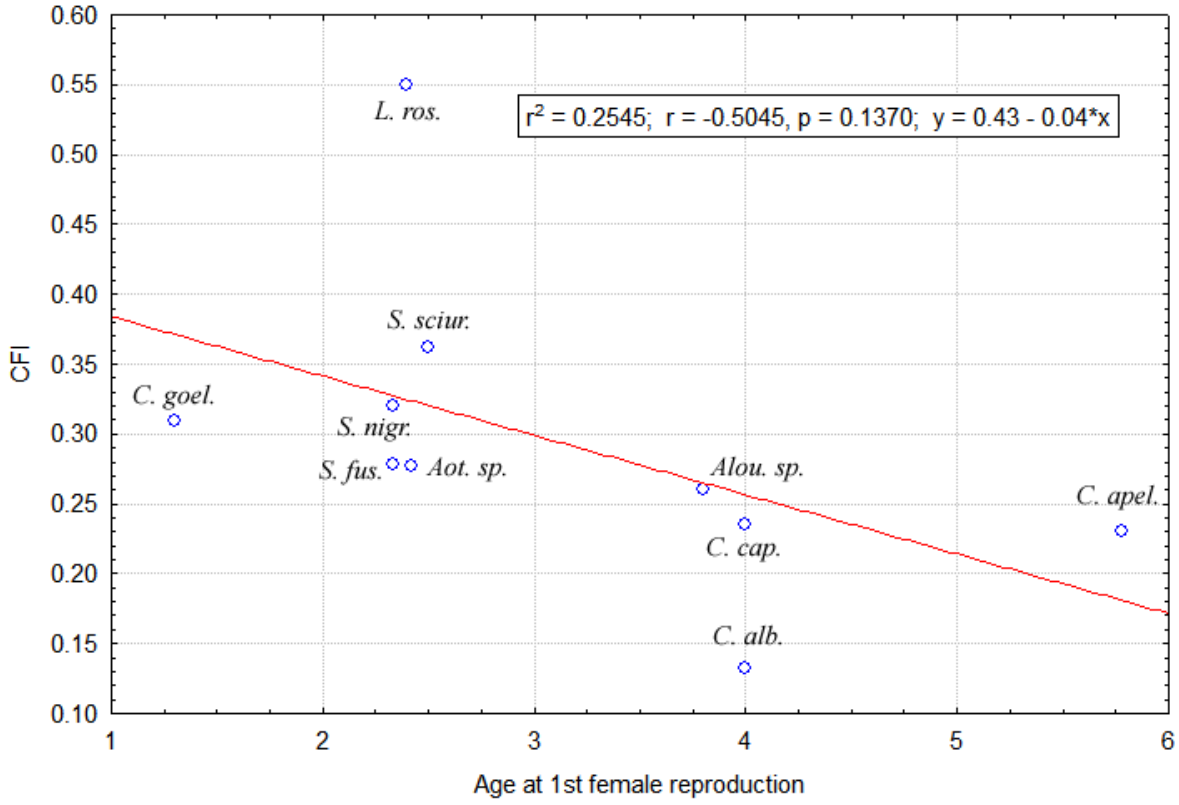


Fig. 5-18. CFI regressed against age at 1st female reproduction (years) showing a negative relationship between the two. See Table 3-1 in Chapter 3 for data sources on age at first female reproduction.

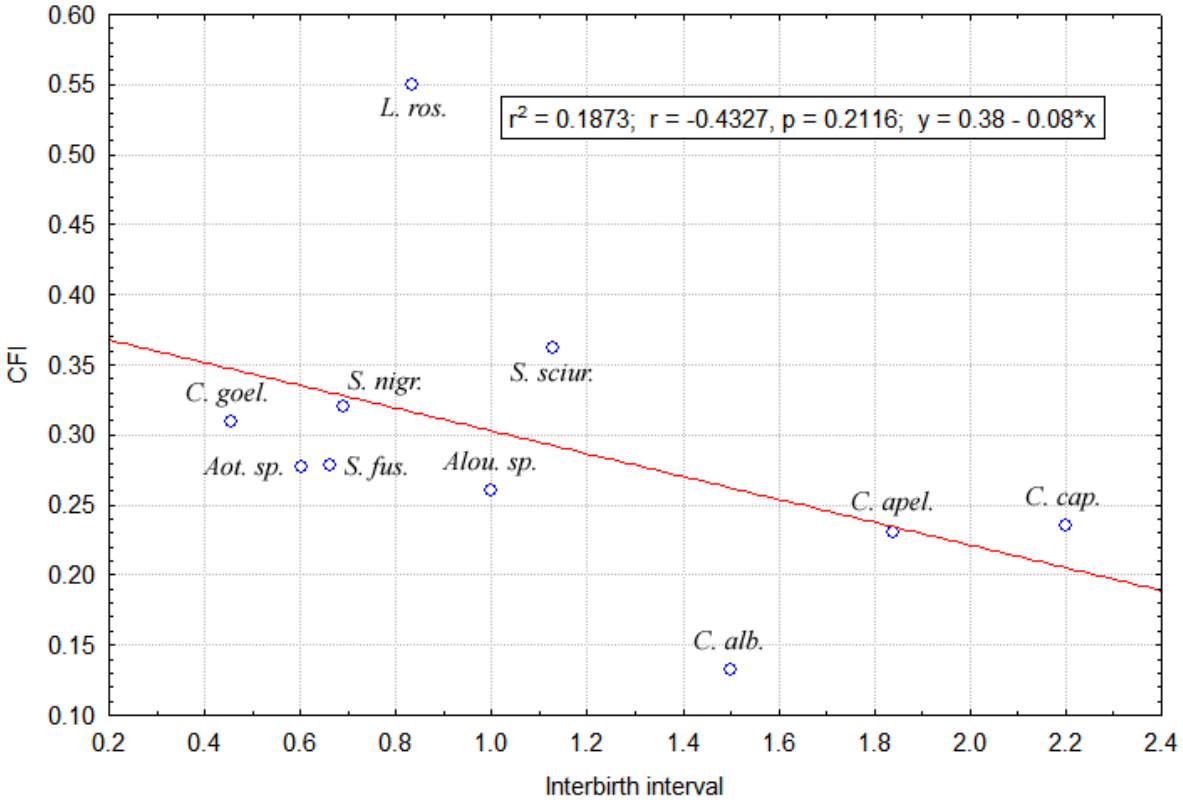


Fig. 5-19. CFI regressed against interbirth interval (years) showing a negative relationship between the two. See Table 3-1 in Chapter 3 for data sources on interbirth interval.

Multivariate analyses: all variables

Due to the fact that most variables showed moderate-to-strong correlations with enamel growth rate (i.e., DESR, EFF angle, and/or CFI), it is necessary also to examine the relationships of these variables to enamel growth rate together to better determine which variables have the greatest interaction with enamel growth. Accordingly, separate multiple regression analyses for DESR, EFF angle, and CFI were performed; each of the three analyses include all of the predictor variables examined in this study (i.e., LN body mass, LN brain mass, encephalization quotient, age at weaning, age at first

female reproduction, and interbirth interval; see Chapter 3). Results show that none of the individual predictor variables examined had a statistically significant relationship to DESR (Table 5-3), and the regression itself was not statistically significant ($p = 0.056$). Since this p value is close to significance, however, as well as the fact that these variables are themselves correlated, separate regressions were run in a stepwise manner, removing the least significant variables until significance was achieved for others. With interbirth interval and weaning age removed, age at first female reproduction becomes significant ($p = 0.049$), however the regression as a whole is not significant ($p = 0.08$, $R = 0.84$). Removing age at first female reproduction, however, causes weaning age to become significant ($p = 0.03$; p for regression $= 0.02$, $R = 0.85$). By themselves, brain mass, body mass, and EQ do not combine to create statistically significant regressions ($p = 0.066$, $R = 0.58$). Taken together, these analyses therefore suggest that weaning age and age at first female reproduction have the greatest statistical effect upon DESR, though the latter seems to have a lesser effect.

However, body mass, brain mass, and encephalization all exhibited a significant relationship to EFF angle; none of the other three ecological proxy variables contributed significantly to variation in EFF angle. Five out of the six predictor variables had a significant relationship with CFI, with interbirth interval being the exception.

Dependent (Y)	Predictor (X)	Beta	p	R-value for test
DESR	LN body mass	1.21	0.67	**0.9**
	LN brain mass	-2.26	0.57	
	Weaning age	1.21	0.21	
	EQ	0.17	0.9	
	1st female repr.	-0.44	0.5	
	Interbirth interval	1.06	0.07	
EFF angle	LN body mass	8.2	0.02	**0.98**
	LN brain mass	-12.35	0.03	
	Weaning age	2.51	0.09	
	EQ	5.44	0.02	
	1st female repr.	-1.09	0.11	
	Interbirth interval	-0.16	0.62	
CFI	LN body mass	-10.22	0.02	**0.96**
	LN brain mass	17.58	0.02	
	Weaning age	-6.06	0.02	
	EQ	-7.01	0.02	
	1st female repr.	2.35	0.03	
	Interbirth interval	0.51	0.27	

Table 5-3. Summary of multiple regression statistics. DESR, EFF angle, and CFI were entered into three separate multiple regression analyses including all six predictor variables listed in the second column. The last column provides the R-value for each of the three regressions.

Discussion

Body mass/brain mass

As is the case for tooth eruption (e.g., Smith 1989; Smith et al. 1994; Godfrey et al. 2001), enamel growth rates do seem to be tied to body mass and brain mass when analyzed separately, with brain mass serving as the better predictor variable of the two. In the previous analysis by Godfrey and colleagues (2001), when body and brain mass

were analyzed together, body mass did not have a significant relationship with tooth eruption. However, in this study, when body and brain mass are analyzed together in multiple regressions of EFF angle and CFI, body mass does seem to play a role in enamel growth rates in cebids, even though brain mass seems more important.

The results of this study also seem to fall in line with the conclusions of prior studies which showed that despite their large role, body and brain mass do not explain dental ontogeny on their own (e.g., Godfrey et al. 2001, 2003; 2006). For example, in bivariate regressions, EFF angle is also strongly correlated with encephalization quotient, DESR is strongly correlated with age at weaning, and CFI has the same r-value for age at weaning that it has for brain mass (see Table 5-2). Multiple regressions also reveal additional correlations with the socioecological proxies such as encephalization, age at weaning, and age at first female reproduction.

Foraging independence hypothesis

As noted above, Godfrey and colleagues (e.g., 2001, 2003, 2006) have found repeated evidence for the importance of foraging independence as a factor affecting dental ontogeny in their analyses across primates and within strepsirhines. For example, encephalization and weaning age are correlated with dental eruption across primates (Godfrey et al. 2001). Moreover, differences in encephalization provide the best explanation for the unusually rapid dental growth of large subfossil strepsirhines; we can only infer that

this is tied to foraging independence in these fossils (Godfrey et al. 2006; see also Schwartz et al. 2002).

Therefore, as predicted, proxy variables linked to foraging independence exhibit the strongest link to enamel growth rates of cebids as well. Further supporting the hypothesis of Godfrey and colleagues (2001), DESR, EFF angles, and CFI all show moderate-to-strong correlations with encephalization and weaning age in bivariate regressions (see Table 5-1). In addition, multiple regressions show that encephalization is negatively correlated with EFF and CFI; age at weaning also has a significant negative correlation with CFI.

In particular, *Cebus* serves as a good example of the foraging independence hypothesis at work within primates. *Cebus* has been identified as the third most encephalized primate genus behind *Homo* and *Pan* (Martin 1990). With regard to weaning age, *Cebus*, in comparison to all of its extant cebid relatives, seems to have extended its juvenile period to a pronounced degree (see Figs. 5-7, 5-11, 5-15). As an extractive forager and omnivore which is known to use tools to access foodstuffs, *Cebus* seems to have adapted to a foraging regime that is cognitively complex (e.g., Visalberghi 1987; Fragaszy et al. 1990; Janson and Boinski 1992; Rosenberger 1992; Fragaszy and Boinski 1995; Fragaszy and Bard 1997; Visalberghi and McGrew 1997; Fragaszy et al. 2004). The lengthened juvenile period of *Cebus*, therefore, seems to be a life history adaptation which is most likely related to this cognitive complexity and demand for prolonged learning (e.g., Gibson 1986; Dunbar 1992, 1995; Byrne 1995; Joffe 1997; Ross and Jones 1999; Godfrey et al. 2001). Just as predicted by

the foraging independence hypothesis, *Cebus* juveniles seem to have not only delayed eruption relative to smaller extant cebids (Smith 1989; Smith et al. 1994; Godfrey et al. 2001), they also have overall "slower" physiologies underlying tooth growth as evidenced in this study.

In contrast to *Cebus*, *Alouatta,* a relatively less-encephalized (Fig. 5-17) and more folivorous genus (e.g. Hladik and Hladik 1969; Milton 1980; Rosenberger and Strier 1989; Ford and Davis 1992; Strier 1992), exhibits somewhat faster or comparable dental growth rates when using EFF angle or CFI as the standard measurement, respectively (see Figs. 5-11 through 5-17). Considering the larger body size of *Alouatta* as well as its lower encephalization (see Table 5-1; see also Ford and Davis 1992; Rosenberger 1992), this genus also seems to fit well within the predictions of the foraging independence hypothesis, albeit on the other side of the spectrum compared to *Cebus*.

Moreover, *Saimiri,* as a relatively encephalized sister-taxon of *Cebus* (e.g., Fig. 5-17), also exhibits slower growth rates relative to similarly sized but less encephalized callitrichine relatives. If increased encephalization is a synapomorphy for cebines as postulated by Tejedor and colleagues (2006), this would suggest that ancestral cebines may have also exhibited delayed foraging independence and decreased dental growth rates relative to their less encephalized ancestors.

Risk aversion hypothesis

In their study of tooth eruption schedules across primates, Godfrey and colleagues (2001) did not find support for the risk aversion hypothesis. That is, they did not find any relationship between age at first female reproduction and dental growth that was not tied to body mass. The results of my study provide some evidence which supports the risk aversion hypothesis, but the statistical support is not strong. In other words, age at first female reproduction is moderately correlated with all enamel variables in the bivariate analyses (see Table 5-1), but this correlation is only significant for DESR. Moreover, the CFI analysis was the only multiple regression which selected age at first female reproduction as a significant predictor variable. However, among the significant predictors of CFI in this analysis, age at first female reproduction had the least important statistical effect. Overall, risk aversion may play some role in driving enamel growth rates in cebids, but given the weakness of the relationships here in conjunction with the analyses of Godfrey and colleagues (2001), it appears to be much less important than foraging independence.

However, somatic growth patterns for anthropoids (both platyrrhines and catarrhines) do appear to be closely tied to environmental risk (Janson and Van Schaik 1993; Leigh 1994). The fact that risk does not show a strong relationship with cebid dental growth (and primate dental ontogeny in general) is therefore somewhat surprising. The different response of anthropoid dental growth and somatic growth to environmental risk probably reflects different

physiological controls acting on the ontogeny of both suites of features (e.g., Schwartz and Dean 2001; Pereira and Leigh 2003). It also further suggests that the ontogenies of these suites are at least in large part able to evolve in response to external selective pressures independently (Pereira and Leigh 2003; see also Chapter 1 and Chapter 7).

Maternal investment hypothesis

Support for the maternal investment hypothesis is somewhat mixed. The hypothesis predicts that relatively lower maternal investment, signified by younger weaning age and shorter interbirth intervals, will result in more rapid enamel growth rates. As noted above, all three enamel growth variables have relatively strong relationships with age at weaning, and as predicted, EFF angle and CFI exhibit a negative correlation with it. Moreover, the multiple regression analysis of CFI also suggests that age at weaning has a significant relationship with enamel growth rates (see Table 5-3). Interbirth interval has moderate correlation to DESR, EFF, and CFI in bivariate regressions (see Table 5-2), but none of the multiple regressions indicate that interbirth interval is a significant predictor.

Ultimately, interbirth interval provides the only unique prediction regarding the maternal investment hypothesis, probably because weaning age seems strongly tied to foraging independence. Therefore, the lack of statistical significance for both bivariate and multiple regressions of interbirth interval detracts from the

hypothesis. Given the moderately high r-value between EFF angle and interbirth interval (r = 0.61), it seems surprising that the correlation between these two variables is not significant. It may be that low sample size is adversely affecting this analysis, and that CFI correlations are also being affected as a result. Therefore, further sampling of platyrrhine EFF angles are needed to provide more insight on this issue.

Overall, it is difficult to separate maternal investment entirely from foraging independence, as the two should be closely related. In other words, foraging independence is in part a consequence of the timing of maternal resource investment, in that foraging independence occurs as maternal resources are increasingly shifted away from individual offspring (see Nicolson 1987 for review). Further implications of the link between foraging independence and maternal investment will be considered in Chapter 8.

In sum, this chapter has shown that enamel growth rates for cebids seem to be most strongly related to brain mass, as is the case for prior studies of dental eruption in primates (Smith 1989; Smith et al. 1994; Godfrey et al. 2001). Body mass also shows a relationship to enamel growth rates, but neither of these two mass variables statistically explains all the variation in enamel growth rates within Cebidae. In other words, enamel growth rate also appears to respond to socioecological variables, with age at foraging independence playing the most significant role as we would predict from prior studies (e.g. Godfrey et al. 2001, 2006). Maternal investment

strategies, which are intimately tied to foraging independence, probably play some role, whereas environmental risk does not. These results in general suggest that enamel growth rates and dental eruption timing seem to respond to similar selective forces within cebids. This is interesting, because they are not correlated with one another across primates and they may be regulated by genetic/ physiological programs which only partly overlap (see above). Therefore, there may be an inherent difference between anthropoids and strepsirhines, since growth rates and tooth eruption seem to be responding to selective forces in a very similar manner for anthropoids but not across primates (e.g., Godfrey et al. 2006; see Chapter 8).

Regarding these anthropoid-strepsirhine differences, this study has increased our knowledge of dental ontogeny by increasing the growth rate dataset of the cebids, and in turn, the anthropoids. There is no evidence from the cebids to suggest that the differences seen between anthropoids and strepsirhines in previous studies (e.g., Smith 1989; Smith et al. 1994; Schwartz et al. 2002; Godfrey et al. 2005) are due to a dichotomy between enamel growth and tooth eruption across primates. Rather, these data suggest that the strepsirhines (specifically the lemuroids) may be different from anthropoids at all levels of dental ontogeny, not just eruption. There are several possible reasons for this difference between the primate suborders. For example, it may be that anthropoid dental ontogeny is highly constrained due to their phylogenetic history, resulting in a highly consistent pattern across taxa, or that the evolutionary and

biogeographic history of the lemuroids has resulted in an unusual diversity of ontogenetic strategies. See Chapter 8 for more discussion.

Chapter 6:

Biological Rhythm, Life History, and Dental Growth

Introduction

Most organisms exhibit regular, periodic fluctuations in biological activity known as biological rhythms, or biorhythms (Roenneberg and Morse 1993). These biological rhythms are presumed to be selective responses to changes in a species' environment that follow one or more predictable cycles, making it advantageous for the species to coordinate its activities with these cycles (e.g., Roenneberg and Morse 1993; Dodd et al. 2005). The daily rotation of the earth is perhaps the most important example of an environmental cycle, though the lunar period (28 days) and the shifting seasons (earth's revolution around the sun) are also known to influence biological activity (e.g., Halberg 1969; Mohr 1975; Pannella 1975; Runcorn 1975; Whyte 1975). Even sunspot cycles (11 years) seem to affect different biological rhythms (Halberg et al. 2000), though it is important to note that not all biorhythms are explicitly linked to external cycles (e.g., Retzius periodicity; see below).

Cross-striations and striae of Retzius within dental enamel are physical manifestations of such regular, periodic biological rhythms within teeth (e.g., Asper 1916; Okada 1943; Boyde 1964; Bromage 1991; see also Chapter 3). The physiology underlying the circadian (24 hour) cross-striation rhythm is relatively well-understood; changes in the pH-balance of blood during waking/sleep cycles (over one earth

rotation) affect enamel chemistry (see Chapters 2 and 3 for details). However, the physiology underlying the periodicity of striae of Retzius has been much more difficult to discern. Every individual has the same number of cross-striations laid down between successive striae throughout development. This phenomenon is referred to as Retzius periodicity, or the repeat interval, and it varies between and sometimes within mammalian species (Fitzgerald 1998).

The most often-cited mechanism for Retzius periodicity is that striae occur in an organism when two or more independent circadian clock systems experience a recalibration and come into phase with one another (Newman and Poole 1974, 1993). This disrupts enamel secretion and causes a line to appear at the enamel formation front (Newman and Poole 1974, 1993). However, there is no direct physiological evidence on clock recalibration to currently support this hypothesis or any evidence of its potential impact on ameloblasts. Moreover, there is a master clock in the suprachiasmatic nucleus of the hypothalamus which tightly regulates the separate circadian clocks in the different tissues/organs of mammals (Reppert and Weaver 2002). This nucleus, or other related hypothalamic structures, may be responsible for longer-term biorhythms such as Retzius periodicity (see below).

A major reason for our inability to access the physiology underlying the Retzius biorhythm is that very few papers have assessed variation in Retzius periodicities in primates or vertebrates in general. Only a few histological studies have analyzed Retzius patterns in primates above the level of the genus (e.g., Lacruz et al. 2008; Smith 2008); however, species-level patterns within the

hominoids, cercopithecoids, and lemurids are well-known (e.g., Beynon et al. 1991, 1998a, 1998b; Dean & Beynon 1991; Maas 1994; Maas & O'Leary 1996; Macho et al. 1996; Dean 1998; Dirks 1998; Reid et al. 1998a, 1998b; Dean 2000; Schwartz & Dean 2001; Schwartz et al. 2002, 2004, 2005a, 2007; Smith et al. 2003; Smith 2004; Dean & Leakey 2004; Smith et al. 2006; Godfrey et al. 2006). The only study which has examined Retzius periodicity across major groups of primates was conducted by Bromage and colleagues (2009). This paper was also the first to use correlations between Retzius periodicity and body mass to address possible underlying physiological mechanisms. Analyses from this chapter contributed to the Bromage et al. (2009) publication.

Therefore, to further develop our understanding of Retzius physiology and its importance for evolution, this chapter will address the variation of Retzius periodicity within primates and examine the influence of body and brain mass on Retzius periodicity. The focus is Retzius period variation within platyrrhines, anthropoids (platyrrhines and catarrhines) as well as across the primate order by including a few strepsirhines.

Body Mass, Metabolism, and Enamel Periodicity: A Potential Mechanism

Prior research has found a significant relationship between Retzius periodicity and body mass in hominoids (Dean and Scandrett 1995; Lacruz et al. 2008; Smith 2008), with larger species having longer Retzius periods. However, Smith (2008) also notes that large

subfossil lemurs do not seem to have this same Retzius/body mass relationship, as they have very short Retzius periodicities despite their large size (e.g., Schwartz et al. 2002, 2005a, 2007; Godfrey et al. 2006). However, the difference in subfossil lemurs should not cause us to dismiss the importance of a possible relationship between body mass and Retzius periodicity across primates, as subfossil lemurs may vary from an overall primate pattern.

The physiological mechanisms connected to body mass differences between taxa provide an important perspective for understanding the relationship between body mass and Retzius periodicity. For example, overall metabolic rate has a well-known inverse relationship with body mass as larger-bodied species have relatively lower metabolic rates; in turn, these two factors affect patterns of cell growth and activity (e.g., Kleiber 1947; McNab 1980; Lindstedt and Calder 1981; Martin 1990; Harvey et al. 1991; West et al. 1997; Sibly and Brown 2007). Body mass is also known to have a strong correlation with biological rhythms that are tied to metabolic rates (e.g., heart rates in mammals; see Stahl 1967). Therefore, it is quite possible that Retzius periodicity represents a biological rhythm which is also tied to body mass and metabolism. If this is true, striae of Retzius would result from a periodic disruption of ameloblast activity tied to a regular physiological shift within the body's physiology as a whole. In turn, the frequency of this shift should differ among taxa with respect to body mass.

If Retzius periods are tied to metabolism and body mass, we should expect to find some other underlying physiological links. The autonomic nervous system provides such a link (Appenzeller et al.

2005; Bromage et al. 2009). Appenzeller and colleagues (2005) were the first to make a qualitative observation that there is an explicit connection between the autonomic nervous system and hard tissues, noting that modern humans have a circaseptan (approximately one week) heart rate period which corresponds with our circaseptan Retzius period.

Research has also shown that the hypothalamus, which regulates the autonomic nervous system, controls osteoblast and osteocyte activity in bones via its sympathetic nerves (e.g., Amling 2001; Karsenty 2001; Takeda et al. 2003; Elefteriou et al. 2004; osteocalcin: Lee et al. 2007). These bone cells directly secrete osteocalcin to regulate the release of leptin, and in turn, these hormones act on the hypothalamus, which completes a physiological neuroendocrine loop (e.g., leptin: Amling 2001; Karsenty 2001; Takeda et al. 2003; Elefteriou et al. 2004; osteocalcin: Lee et al. 2007). In addition to affecting bone mass through osteoblast activity, this neuroendocrine loop is also an integral component in the regulation of cellular proliferation (Ueyama et al. 1999) as well as reproduction via the control of ovulation, estrogen production, etc. (Karsenty 2001). Moreover, and very importantly, this loop is also directly tied to the pituitary gland, therefore control of thyroid hormone levels which regulate basal metabolic rate, or BMR (e.g., Thomas and Burguera 2002).

These links between the autonomic nervous system, metabolism, and hard tissue physiology make it likely that any biorhythms which are expressed in the autonomic nervous system may also be expressed in hard tissues. In humans, a cyclical rise and fall of sympathetic

output occurs predictably over a circaseptan period. As mentioned above, this sympathetic biorhythm has been measured in humans by examining the rise and fall of heart rate (Wu et al. 1990; Rawson et al. 2000; Appenzeller et al. 2005).

Bromage and colleagues (2009) argue that the correspondence of heart rate and Retzius periodicity (Appenzeller et al. 2005) stems from the fact that both periods are different physiological manifestations of a single centrally regulated biorhythm governed in the brain by the hypothalamus, the "Havers-Halberg Oscillation," or HHO (Bromage et al. 2008, 2009). As a potential key motivator of reproductive timing, metabolism (reflected in heart rate and glucose breakdown), and body mass, as well as affecting cellular proliferation, the HHO system has the potential to be a major mechanism involved in life history evolution. This oscillation itself may be the key regulating factor that programs cells to behave and grow as they do, to create a small mouse very quickly or a large elephant much more slowly. In this case, we would find that smaller animals have a shorter oscillation while larger animals have a longer one (Bromage et al. 2009).

The HHO hypothesis predicts that its rhythmic oscillation will be recorded as a permanent anatomical feature in hard tissues. For teeth specifically, ameloblasts are known to record physiological events in terms of daily cross-striations and accentuated non-periodic striae which result from stress events. Therefore, it is likely that ameloblasts will record other physiological shifts as well, and periodic striae of Retzius seem an excellent candidate marker of such an autonomically-mediated rhythm. Therefore, smaller species, which

have faster life histories and presumably a shorter HHO, should exhibit shorter Retzius periods relative to larger species.

To examine relationships between Retzius period and body mass for platyrrhine, anthropoid, and primate samples, separate bivariate linear regressions were performed for each dataset using Statistica 6.0 (Statsoft, Ltd.). Regressions for Retzius period and brain mass were only performed on the platyrrhine and anthropoid datasets, since I was unable to obtain brain mass values for the strepsirhines sampled. If the HHO model is correct, we would expect to see a strong and statistically significant positive correlation between Retzius periodicity and body mass. For details on sampling, raw data and sources, see Chapter 3 and Table 6-1. All specimen preparation, imaging, and measurement protocols are also described in Chapter 3.

Genus	Species	Sex	Retzius period	Body mass in kg (LN)	Brain mass in g (LN)	Specimen Source / Retzius period source
Infraorder Platyrrhini						
Alouatta	sp.	M	6	6.42 (1.86)	56 (4.02)	MNRJ
Callicebus	*personatus*	?	3	1.31 (0.27)	-	MNRJ
Aotus	sp.	F	3	0.91 (-0.09)	18.2 (2.9)	CSHO
Callimico	*goeldii*	F	3	0.39 (-0.94)	10.8 (2.37)	Rose Primate Collection
Callithrix	*humeralifer*	F	3	0.323 (-1.13)	-	AMNH
Callithrix	*jacchus*	?	1	0.26 (-1.35)	7.9 (2.07)	AMNH
Cebuella	*pygmaea*	F	1	0.12 (-2.1)	4.2 (1.43)	MNRJ
Cebus	*albifrons*	M	6	2.48 (0.91)	82 (4.41)	AMNH
Cebus	*albifrons*	F	5	1.81 (0.59)	66.8 (4.2)	AMNH
Cebus	*apella*	M	5	3.05 (1.12)	71 (4.26)	AMNH
Cebus	*apella*	F	4	2.39 (0.86)	73 (4.29)	CSHO
Cebus	*capucinus*	M	6	3.87 (1.35)	-	Rose Primate Collection
Cebus	*capucinus*	F	4	3.27 (1.18)	79.2 (4.37)	NMNH
Cebus	*olivaceus*	M	4	2.97 (1.08)	80.8 (4.39)	AMNH
Leontopithecus	*rosalia*	?	3	0.63 (-0.47)	12.9 (2.56)	AMNH
Saguinus	*oedipus*	F	1	0.43 (-0.84)	9 (2.19)	NMNH
Saguinus	*nigricollis*	F	2	0.48 (-0.74)	8.9 (2.19)	NMNH
Saguinus	*fuscicollis*	?	2	0.37 (-0.99)	9.3 (2.23)	AMNH
Saimiri	*boliviensis*	F	3	0.7 (-0.35)	-	AMNH
Saimiri	*sciureus*	M	3	0.85 (-0.16)	25.3 (3.23)	AMNH
Saimiri	*oerstedii*	M	3	0.829 (-0.19)	25.7 (3.24)	AMNH

Genus	Species	Sex	Retzius period	Body mass (LN)	Brain mass (LN)	Source
Afropithecus†	*turkanensis*	?	8	34.5 (3.54)	-	Smith et al. 2004
Dryopithecus†	*laietanus*	?	7	23 (3.13)	-	Kelley et al. 2001
Erythrocebus	*patas*	F	4	4.8 (1.56)	-	CNAR
Gigantopithecus†	*blacki*	?	11	300 (5.7)	-	Dean and Schrenk 2003
Gorilla	*gorilla* (mode)	F	9*	75.7 (4.33)	505.9** (6.23)	Schwartz et al. 2001
Gorilla	*gorilla* (mode)	M	10*	169.3 (5.13)		Schwartz et al. 2001
Graecopithecus†	*freybergi*	M	8	63 (4.14)	-	Smith et al. 2003
Homo	*sapiens*	F	8*	53.6 (3.98)	1250** (7.13)	Schwartz et al. 2001
Homo	*sapiens*	M	8*	60.2 (4.09)		Schwartz et al. 2001
Hylobates	*lar*	?	4	5.6 (1.72)	107.7 (4.67)	Dirks 1998, 2001
Hylobates	*syndactylus*	F	4.5	10.7 (2.37)	121.7 (4.8)	Dirks 2001
Macaca	*nemestrina*	?	4	7.8 (2.05)	106 (4.66)	Smith et al. 2006
Pan	*troglodytes*	F	7	31.1 (3.43)	410.3 (6.01)	Reid et al. 1998
Pan	*troglodytes*	M	7	40.5 (3.7)	410.3 (6.01)	Reid et al. 1998
Papio	*hamadryas hamadryas*	F	7	9.4 (2.24)	142.5 (5)	Dirks et al. 2002
Papio	*hamadryas anubis*	M	7	21 (3.04)	175.1 (5.17)	Dirks et al. 2002
Pongo	*pygmaeus* (mode)	F	10*	35.8 (3.58)		Schwartz et al. 2001
Pongo	*pygmaeus* (mode)	M	10*	78.3 (4.36)	413.3 (6.02)	Schwartz et al. 2001
Proconsul†	*nyanzae*	?	6	35 (3.55)	-	Beynon et al. 1998
Proconsul†	*heseloni*	?	5	10.5 (2.35)	-	Beynon et al. 1998
Semnopithecus	*entellus*	F	5	9.9 (2.29)	135.2 (4.91)	Dirks and Bowman 2007
Theropithecus	*gelada*	F	7	13.6 (2.61)	131.9** (4.88)	Macho et al. 1996
Theropithecus	*gelada*	M	7	20.5 (3.02)	-	Macho et al. 1996

Genus	Species	Sex	Retzius period	Body mass (LN)	Brain mass (LN)	Source
Suborder Strepsirhini						
Megaladapis†	*edwardsi*	?	3	85.1 (4.44)	-	Schwartz et al. 2005
Nycticebus	sp.	?	2	0.679 (-0.39)	-	Rosenberger's lab
Palaeopropithecus†	*ingens*	?	2	41.5 (3.73)	-	Schwartz et al. 2002

Table 6-1. Raw data on Retzius period, body mass and brain mass for the species used in this study. All platyrrhine Retzius data are original and institutions from which specimens were obtained are noted in the last column (see Appendix A for acronyms). For non-platyrrhines, the last column provides citations from which the Retzius data were obtained. Most Retzius period data were obtained from a single individual, unless noted (*), which indicates a species mean or mode estimate from the literature (last column). LN = natural logarithm.

Body mass and brain mass estimates are obtained from Harvey and Clutton-Brock (1985), Ford and Davis (1992), Hartwig (1996), and Smith and Cheverud (2002); see Chapter 3 for specifics. Mass estimates for the fossils (denoted with a **†**) are obtained from sources listed below. If sex for a specimen could not be determined (denoted with a **?**), combined-sex species averages for brain and body mass were used. If only a species brain mass average was available when Retzius data were available for both sexes, only the female value was included in regressions (denoted with a **).

†Body mass estimates from auxiliary sources: *Afropithecus* = Leakey and Walker (1997); *Dryopithecus, Graecopithecus* = Andrews and Martin (1991); *Gigantopithecus* = Dean and Schrenk (2003); *Proconsul* = Rafferty et al. (1995), Beynon et al. (1998); *Megaladapis, Palaeopropithecus* = Jungers et al. (2008).

Results

Retzius periodicity showed a strong correlation with body mass for the platyrrhine, anthropoid and primate datasets. Retzius period was also strongly correlated with brain mass for the platyrrhine and anthropoid datasets. In all five cases, the r-values exceed 0.8. Moreover, all regressions performed showed that the correlation between Retzius period and body or brain mass is significant (i.e., all p-values are well below 0.01; see Table 6-2). The regression slopes for body mass are very similar between platyrrhine analyses and analyses which include both catarrhines and platyrrhines, suggesting that Retzius periodicity scales similarly across extant anthropoids (Figs. 6-1 and 6-2). The strepsirhine *Nycticebus* falls near the regression line in the primate body mass analysis. However, the subfossil lemurs *Palaeopropithecus* and *Megaladapis* have an unusually low Retzius period for their body size (Fig. 6-3; see also discussion below). Platyrrhine and catarrhine Retzius periods also seem to scale in a similar manner when brain mass is used as the predictor variable (Figs. 6-4 and 6-5).

Predictor (X)	Independent (Y)	Sample	r^2	r	p	Figure
LN body mass	Retzius period	Platyrrhini	0.79	0.89	< 0.0001	6-1
LN body mass	Retzius period	Anthropoidea	0.88	0.94	< 0.0001	6-2
LN body mass	Retzius period	Anthropoidea + Strepsirhini	0.7	0.83	< 0.0001	6-3
LN brain mass	Retzius period	Platyrrhini	0.79	0.89	< 0.0001	6-4
LN brain mass	Retzius period	Anthropoidea	0.82	0.9	< 0.0001	6-5

Table 6-2. Summary of regression statistics. Additional values (e.g., slope) are provided in Figures 6-1 to 6-5, which are referenced in the last column.

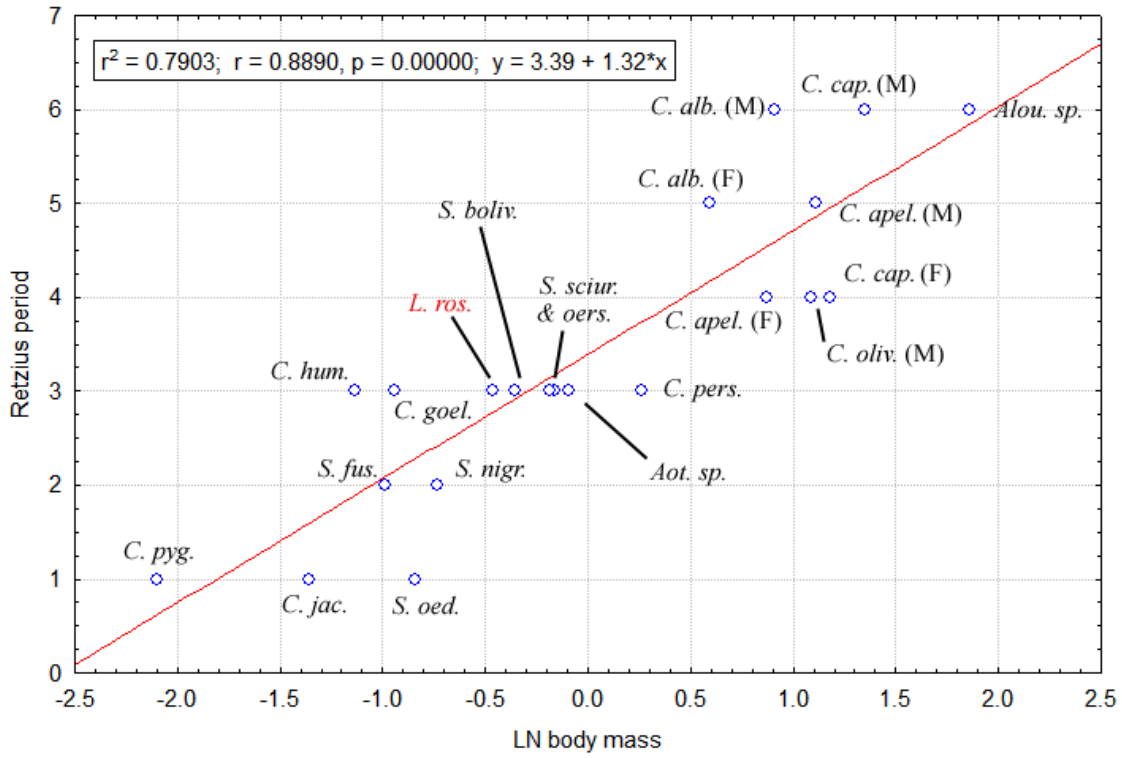


Fig. 6-1. Regression of the natural log (LN) for body mass against Retzius period for platyrrhines. Note: *Leontopithecus rosalia* (*L. ros.*) is highlighted red to indicate the body mass measurements are derived from captive animals; all other data are from wild animals.

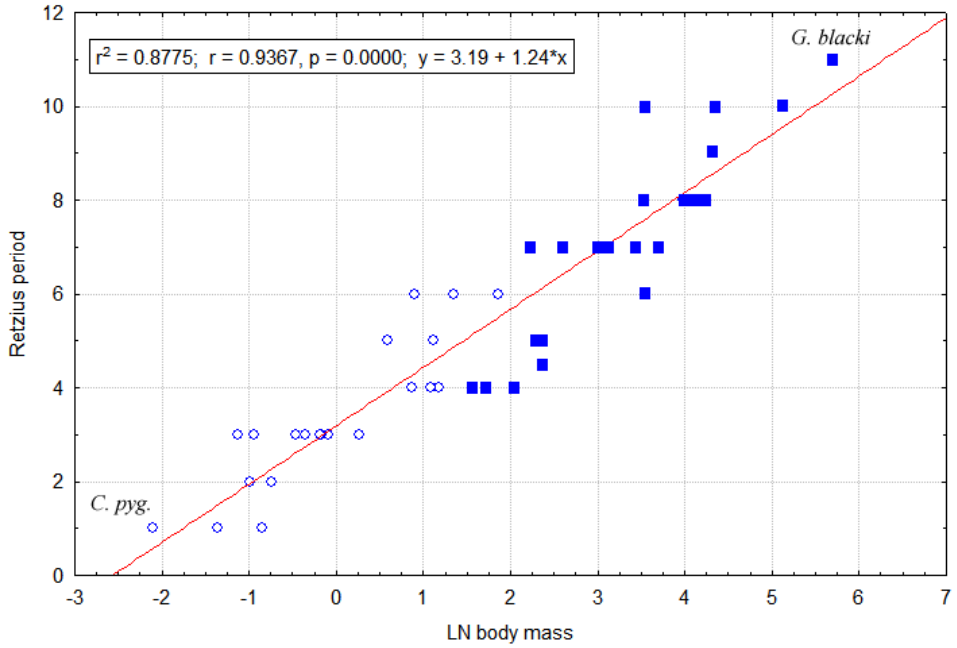


Fig. 6-2. Regression of LN body mass against Retzius period for platyrrhines and catarrhines (anthropoids). Circles = platyrrhines, squares = catarrhines. Note that the regression slope seen here is similar to that seen for just the platyrrhines in Fig. 6-1.

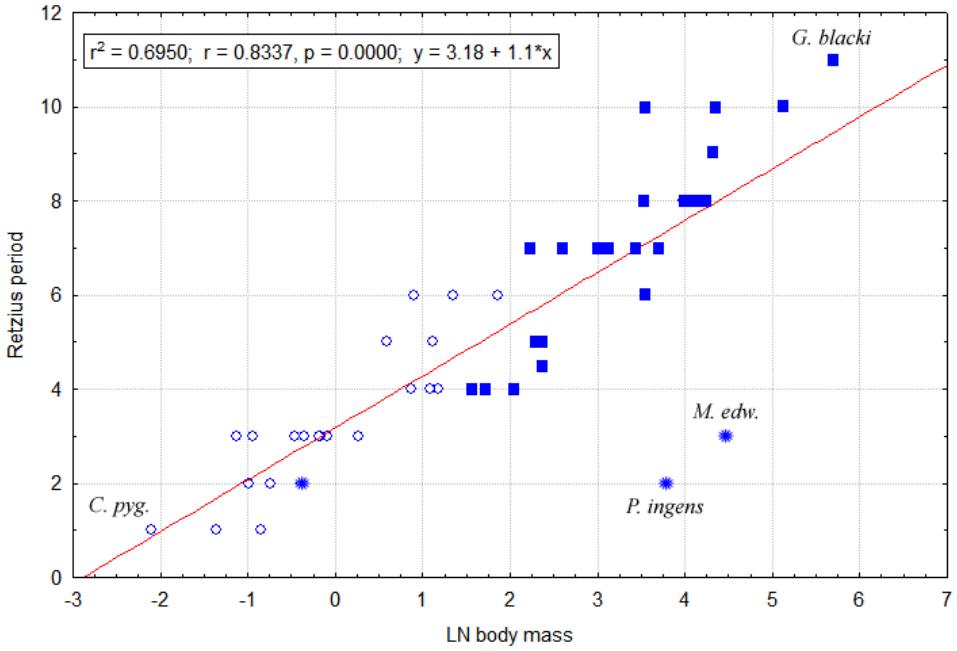


Fig. 6-3. Regression of LN body mass against Retzius period for platyrrhines, catarrhines, and strepsirhines (primate dataset). Hollow circles = platyrrhines, squares = catarrhines, closed circles = strepsirhines. The subfossil lemurs *Palaeopropithecus ingens* and *Megaladapis edwardsi* plot well below the regression line in the lower right quadrant of the graph, whereas the extant strepsirhine *Nycticebus* plots closer to the other primates.

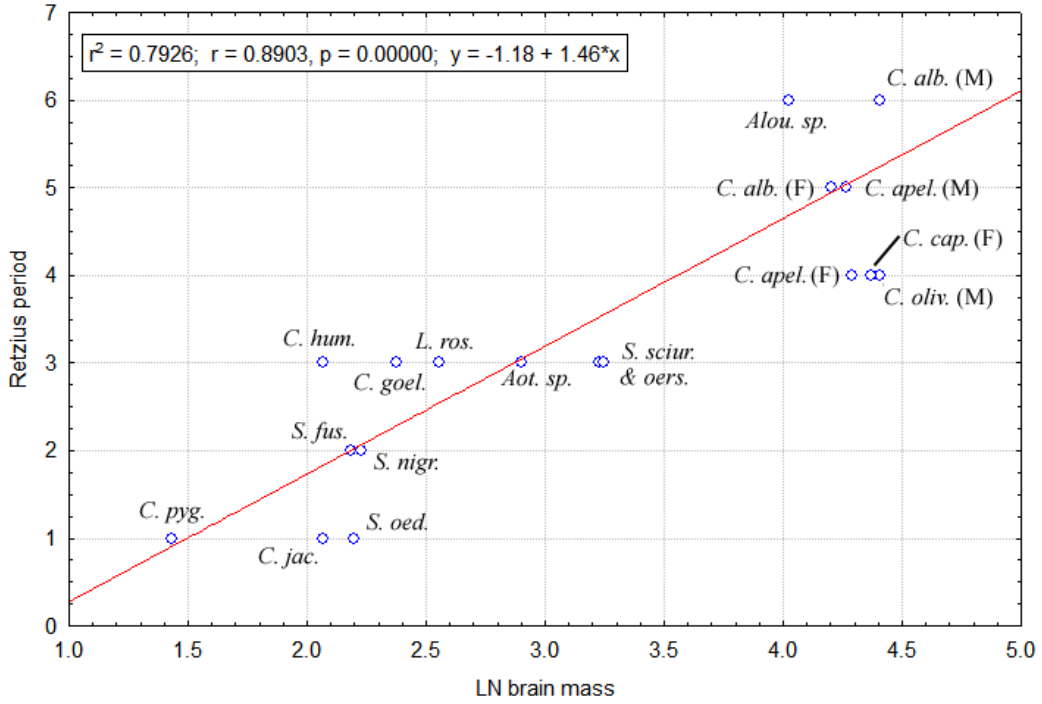


Fig. 6-4. Regression of LN brain mass against Retzius period for platyrrhines.

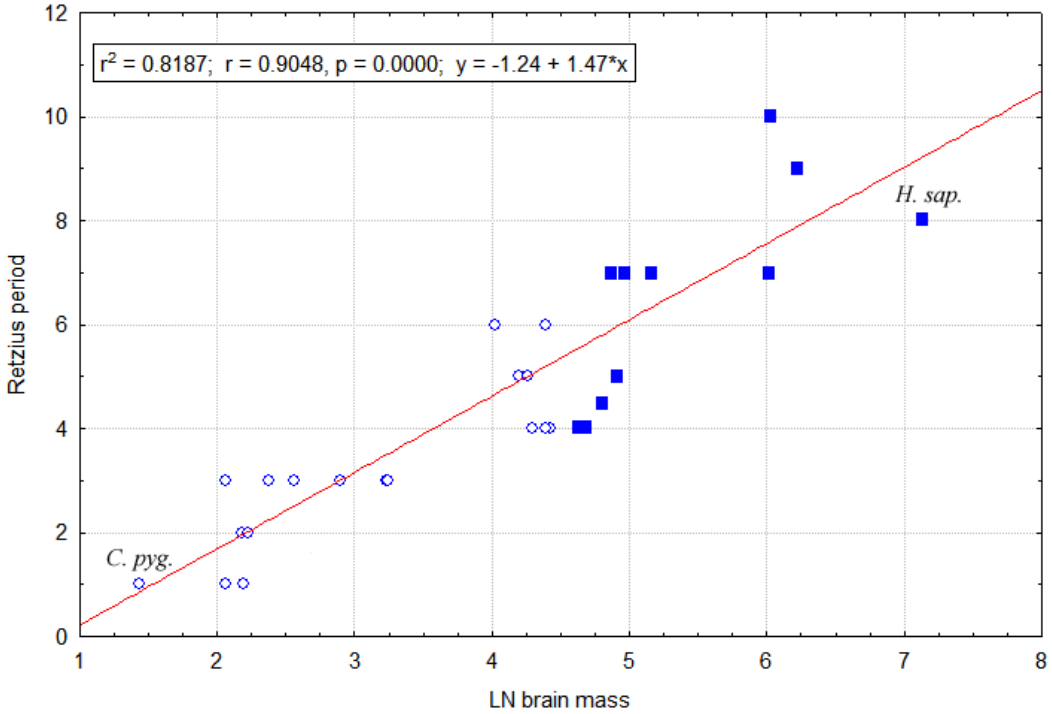


Fig. 6-5. Regression of LN brain mass against Retzius period for platyrrhines and catarrhines (anthropoids). Circles = platyrrhines, squares = catarrhines. Note that, as for body mass, the regression slope for platyrrhines and catarrhines seen here is similar to that seen for platyrrhines alone (Fig. 6-4).

Discussion

The strength of the relationships between body mass, brain mass, and Retzius periodicity in primates corroborates the HHO model of Bromage and colleagues (2009). As predicted, the relationships are positive so that, in general, larger-bodied and larger-brained primates possess a longer Retzius period, with the exception of the two subfossil lemurs. Interestingly, brain and body mass variables are much more strongly and significantly correlated to Retzius periodicity than to enamel growth rates (see Chapter 5). Moreover, the strength of the relationships for Retzius periodicity are much greater than the strength of the relationships seen in *any* bivariate regressions of enamel growth rates performed in Chapter 5. That is, r-values for Retzius period range between 0.83 and 0.94, whereas r-values for DESR and EFF angles range between approximately 0.45 and 0.75. In fact, to produce correlation values greater than 0.9 for enamel growth rates, multiple regression analyses which include the interaction of <u>many</u> variables (i.e., brain mass, body mass, encephalization quotient, weaning age, etc.) must be performed. This suggests that while enamel growth <u>rate</u> is influenced by a complex interaction of variables, Retzius period variation is almost entirely explained (statistically speaking) by body and/or brain mass. This evidence further supports the HHO hypothesis (see Bromage et al. 2009).

Within lower taxonomic levels (e.g., at the generic level), the HHO relationship also seems to hold. For example, all *Cebus* males in

this study exhibit longer Retzius periods than conspecific females (Table 6-1), most likely because of body mass dimorphism. Due to the small sample size available, the differences between sexes of a species/genus seen here constitute a qualitative observation. Further data and analyses focusing on sexual dimorphism are needed to quantitatively corroborate or falsify this observation. Further data are also needed on intrageneric and intraspecific patterns in general.

There also appears to be some taxonomic difference in the scaling of Retzius periodicities, which suggests that there may be some phylogenetic or trophic variables which affect variation of the HHO across different primate groups. For example, the platyrrhines exhibit a strong correlation between Retzius periodicity and body mass when analyzed on their own. When the catarrhines are added to the analysis, they do not seem to alter the correlation in a pronounced way because the r-values, p-values, and the slope of the regression change only a little. In other words, the anthropoids in general all seem to follow a highly similar pattern of scaling (Figs. 6-1 and 6-2). However, when all primate taxa are included in the body mass regression, both of the subfossil strepsirhines plot together well below the regression line (Fig. 6-3). It is clear that the inclusion of the subfossil strepsirhines reduces the strength of the correlation between body mass and Retzius period, as was previously discussed by Smith (2008). However, the only extant strepsirhine sampled in this study, *Nycticebus,* falls close to the line along with the anthropoids. Therefore, the strepsirhines as a whole, or the lemurs, may have a completely different relationship between body mass and Retzius period

(i.e., a less steep slope) relative to the anthropoids; analyses of currently available lemuroid data support this argument (Godfrey, unpublished data). This is possible because scaling relationships between body mass and metabolic rate are known to differ among different mammalian groups (e.g., Harvey et al. 1991), and recent studies have argued that strepsirhines, including large subfossil species, are hypometabolic (Snodgrass et al. 2007). Further analysis of the strepsirhines is needed to tease apart the reason for this difference between anthropoids and strepsirhines.

To summarize, striae of Retzius are known to occur with a regular periodicity which varies across taxa (see Chapters 2 and 3). Moreover, the Retzius period of humans has been shown to correspond with oscillations in heart rate (Appenzeller et al. 2005). Since the autonomic nervous system is known to drive heart rate oscillation and is also known to control body mass, growth rates, reproduction, and metabolism, it seems likely that Retzius period and heart rate oscillations are linked in a common autonomic biorhythm which may act as a central regulator of life history. This link can be seen in the close statistical relationship exhibited between body mass and Retzius periodicity among primates.

The separate physiological pathways of the hypothesized HHO system have been thoroughly researched in the clinical literature as individual mechanisms, and their interconnections (Bromage et al. 2009) potentially represent a significant advance in understanding a mechanism behind evolutionary change. Although more data are needed to provide a better understanding of variation in the HHO both across

and within vertebrate taxa, this model provides a new means to assess how natural selection can modify populations in regard to life history. Evolutionary modification of a species' HHO may result in a centrally-controlled alteration of many of the physiological traits selected in response to an environmental or biogeographic shift. Rather than just changing body size in such cases, for example, HHO would simultaneously change BMR, growth rates, and alter reproductive patterns, all of which can change in environmental and biogeographic shifts (for recent reviews, see Brown and Sibly 2006; Raia and Meiri 2006; Sibly and Brown 2007). With this in mind, the exploration of HHO patterns across taxa as well as experimental data are needed to help us understand the evolutionary response of life history to such phenomena.

Chapter 7:

The Ontogeny of Canine Sexual Dimorphism in Platyrrhines

Introduction

Sexual dimorphism in mammals is often used as a morphological proxy for specific mating behaviors such as intermale competition in polygynous groups, and plays an important role in evolutionary studies (Huxley 1938; Kay et al. 1988; Plavcan and Kay 1988; Plavcan 2001). Traditional studies of sexual dimorphism in primates tend to focus upon the quantification of dimorphism in adult forms (Shea 1986; Corner and Richtsmeier 1991; Anderson 1994; German and Stewart 2001. See Ralls 1977; Leutenegger and Kelley 1977; Leutenegger and Cheverud 1982; Gaulin and Sailer 1984; Kay et al. 1988; and Ford 1994 for examples). However, morphological features are the result of specific ontogenetic trajectories (e.g., Wilbur et al. 1974; Shea 1986; Anderson 1994; Bromage et al. 1995; Raff 1996). Therefore, with regard to dimorphic characters such as body mass, cranial shape, and canine size, the adult morphology results from selection throughout ontogeny with an explicit difference in adaptive need between males and females (e.g., Gaulin and Sailer 1984; Shea 1986, Kay et al. 1988; Plavcan and Kay 1988; Anderson 1994; Ford 1994; German and Stewart 2001; Plavcan 2001).

Adaptive needs change throughout the duration of an individual's ontogeny (e.g., Wilbur et al. 1974; Shea 1986;

Bromage et al. 1995). Therefore, the way in which adult dimorphism is achieved can be just as important as the final amount of dimorphism for an organism's overall fitness (Wilbur et al. 1974; Shea 1986; Bromage et al. 1995). Accordingly, different species and populations will likely have different ontogenetic ways of achieving similar dimorphic ends according to their own evolutionary constraints and specific socioecological needs (e.g., Corner and Richtsmeier 1991, 1992; Taylor 1997; O'Higgins and Collard 2002).

Closely related species within the New World monkeys, Old World monkeys, and apes exhibit highly variable patterns of growth rate and duration between males and females in body mass and craniofacial dimorphism (e.g., Corner and Richtsmeier 1991, 1992; Taylor 1997; O'Higgins and Collard 2002). For example, within the Cebinae, *Cebus* and *Saimiri* share morphological similarities of dimorphism in adult basicranial shape. However, *Cebus* males attain this pattern via *faster* growth *rates* while *Saimiri* males achieve their pattern via a *longer* growth *period* (Corner and Richtsmeier 1991, 1992). The ontogenetic underpinnings of dimorphism can very greatly even at the subspecific level as is seen in *Gorilla gorilla* (Taylor 1997). Therefore, these studies show that within primate taxa (even down to alpha-taxonomic levels), there are a host of epigenetic, environmental, and reproductive cues interacting to produce adult patterns which may seem superficially quite similar.

Ontogenetic studies have played an increasingly important role since the revolution in developmental biology and reexaminations of heterochrony (e.g., Gould 1977; Shea 1983, 1985, 1986). Following Shea's initial analysis of the ontogeny of sexual dimorphism in African hominoids (1985), numerous studies have thoroughly documented the ontogenetic patterns of dimorphism in body mass and craniofacial morphology across primates (e.g., Corner & Richstmeier 1991, 1992, 1993;, Corner et al. 1993; Leigh 1992, 1995; Leigh and Shea 1995; Taylor 1997; Leigh and Terranova 1998; German and Stewart 2002; O'Higgins and Collard 2002; Blanco and Godfrey 2006; Cobb and O'Higgins 2007). The overall complexity and variability in morphology and behavior across primate taxa, including the intricacies of their underlying genetics, provides a significant challenge for interpreting the evolutionary history of dimorphism.

When we consider the evolutionary implications of ontogeny in canine dimorphism, the above-mentioned complexities may not be as confounding if teeth are subject to fewer variables controlling their growth relative to the body as a whole (Schwartz and Dean 2001). Given that the morphological and developmental complexity of a single tooth is far less than that of the entire craniofacial apparatus or the body in general, this assumption is reasonable (see Chapter 2 for discussion of dental developmental genetics). Thus, an ontogenetic analysis of canine dimorphism is less subject to interfering variables, and in turn will make the determination of character polarities easier. In

addition, since each tooth captures its entire growth history in its microstructure, the dentition is an ideal dataset for approaching evolutionary problems regarding dimorphism.

This growth record has particular pertinence to reconstructing evolutionary histories and mating behavior in fossil and extant taxa, since dental increments allow one to circumvent issues of preservation and sampling. To obtain a detailed understanding of the ontogeny of body mass or craniofacial dimorphism in a species, longitudinal studies or large sample sizes are needed to provide a reasonable cross-sectional understanding of the different growth phases between the sexes (e.g., Leigh et al. 2005). In comparison, the required data are much easier to obtain for canine dimorphism because of their preserved microscopic growth record as well as the fact that teeth are the most commonly preserved skeletal element (see Chapter 2).

Despite these advantages, the ontogeny of canine dimorphism has received a lesser degree of attention than that of body mass or the craniofacial apparatus, with the exception of a few recent studies on the hominoids and cercopithecoids (e.g., Schwartz and Dean 2001, 2005; Schwartz et al. 2001; Leigh et al. 2005). Schwartz and colleagues (2005) have also examined the homology of canine dimorphism between catarrhines and notharctines using enamel microstructure. However, our understanding of the evolution of dimorphism and mating behavior for primates is still relatively fragmentary, and one reason for this is that the

dental microstructure of platyrrhines has not been sufficiently examined. Specifically, Cebidae is a key taxon for canine dimorphism research since it includes some of the most dimorphic platyrrhines (see below).

Canine Dimorphism: Building a Phylogenetic History

There are some inherent difficulties in using gross morphological characters to formulate hypotheses on the homology of dimorphism. To the best of my knowledge it has not been shown that dimorphism is tightly linked to features such as canine shape and occlusal patterns. In other words, I believe it is possible that such features may evolve as a result of dietary and behavioral changes while still retaining their pattern of sexual dimorphism due to the presence of consistent sexual selective forces. Therefore, it is not the shape of the gross morphology but the magnitude of sexual dimorphisms that exist which is important to this study. In other words, the magnitude of the ontogenetic or morphological difference between male and female canines provides the most reliable source of data regarding the evolution of dimorphism (e.g., Plavcan 2001).

Previous research has provided a great deal of information on the presence and magnitude of canine dimorphism across primate species. I will provide a brief discussion of the research history of canine dimorphism across primates to demonstrate the

foundation upon which this study of the homology in platyrrhine canine dimorphism was constructed as well as how and why the questions asked were formulated.

Although extant lemuriform strepsirhines exhibit little to no dimorphism between the sexes (e.g., Leigh & Terranova 1998), the extinct adapiforms in North America and Eurasia do exhibit a strong degree of canine dimorphism similar to that of the anthropoids (Stehlin 1912, cited in Gingerich 1980; Gregory 1920; Gingerich 1980). The genera of adapiforms which have been shown to exhibit dimorphism include: *Adapis*, *Leptadapis*, *Sivaladapis*, *Notharctus*, *Pelycodus*, *Cantius*, and *Smilodectes* (Gregory 1920; Gingerich 1979; Gingerich 1981; Gingerich and Martin 1981; Gingerich and Sahni 1984; Krishtalka et al. 1990; Alexander 1994; Gingerich 1995). The presence of canine dimorphism across both North American and Eurasian adapiform genera suggests that canine dimorphism in these primates is homologous.

Even though, as haplorhines, the tarsiiforms (omomyids and tarsiids) are more closely related to anthropoids than adapiforms, they do not exhibit canine dimorphism (Gingerich 1980). However, the tarsiiform pattern of monomorphism is not necessarily the primitive condition for haplorhines, and I believe we need more information about the early haplorhine fossil record to provide a clear picture of the evolution of monomorphism in this group. Given this, as well as the degree of dimorphism in the morphology of adapiforms and most anthropoids, I feel the two hypotheses put forward by Krishtalka and

colleagues (1990) must still be considered and tested: 1) that dimorphism must be a primitive character for the euprimates; or 2) dimorphism has evolved at least twice in two major primate clades (i.e., the adapiforms and anthropoids).

Unlike in the early strepsirhines and haplorhines, the evolutionary patterns of catarrhine sexual dimorphism are relatively well-understood. Among stem catarrhines, Fleagle and colleagues (1980) first noted a high degree of canine dimorphism in *Aegyptopithecus* (=*Propliopithecus*). With regard to extant catarrhines, males have canines that are generally at least 1.5 times longer than those of females. Eleven out of fourteen genera in Manning and Chamberlain (1993) and fifteen out of seventeen genera in Plavcan and Van Schaik (1997) equal or surpass this 1.5 M/F canine height ratio. R*hinopithecus*, *Semnopithecus*, *Trachypithecus*, and *Allenopithecus* were also examined by Plavcan (2001) and identified as having "strong" canine dimorphism. However, quantification of the sex ratio in canine size was not described in this paper. Overall, minus the overlap in genera studied, these three papers identify twenty dimorphic extant catarrhine genera out of a total of twenty-three examined. The only exceptions are *Hylobates*, *Homo*, and *Pan*. Studies also suggest that canine dimorphism is present in the majority of extinct hominoid and cercopithecoid genera, including *Proconsul*, *Limnopithecus*, and *Dryopithecus* (e.g., Pickford 1986; Kelley 1995). Thus, canine dimorphism appears in most catarrhine genera, including extant and extinct members of both stem and

crown taxa. In addition to this morphological evidence, comparison of catarrhine behavior across members of the clade also suggests that this group is characterized by sexual dimorphism as a well-canalized part of its phylogenetic, behavioral/adaptive, and ontogenetic sphere (DiFiore and Rendall 1994). On the other hand, species such as *Hylobates*, *Homo*, and *Pan* are a rare exception to the catarrhine rule, and most likely have secondarily reduced their canine dimorphism and intra-sexual competition (Plavcan and Van Schaik 1992; DiFiore and Rendall 1994; Plavcan and Van Schaik 1997; Plavcan 2001).

The platyrrhines have a social evolution whose history is more difficult to parse since they have a much more diverse array of mating behaviors relative to the catarrhines. In parsimony-based analyses which phenetically link different primate genera from all major extant groups, the catarrhines all cluster together whereas the platyrrhine genera are dispersed throughout the tree (DiFiore and Rendall 1994; see Fig. 7-1). This diversity is not surprising given the deep ages of extant platyrrhine lineages and the history of biogeographic change on the South American continent (e.g., Rosenberger et al. 2009).

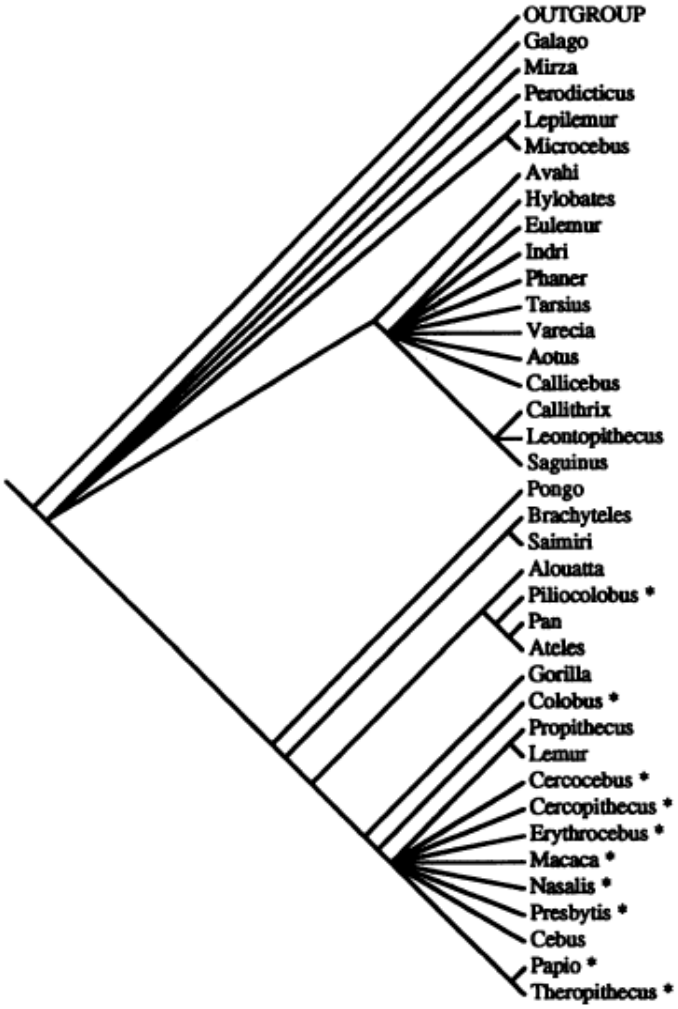


Fig. 7-1. Parsimony tree of social and mating behavior patterns among extant primate genera. "Clades" on the tree represent behavioral similarity and not phylogenetic relationships. The platyrrhines are spread through the tree, with the more dimorphic platyrrhine genera clustering with the highly dimorphic catarrhines. Asterisks denote cercopithecoids. From DiFiore and Rendall (1994).

Even though platyrrhines are commonly seen as less dimorphic than their Old World counterparts, the group does include species with a relatively high degree of canine dimorphism (Kay et al. 1988; Masterson and Hartwig 1998; Hartwig

and Rosenberger 2005). *Cebus* and *Saimiri* (cebines) as well as *Alouatta* and *Lagothrix* (atelines), for example, have all been observed to have male-to-female canine height ratios ≥ 1.5 (Kay et al. 1988). However, the extreme dimorphism seen in *Mandrillus* canines is not found in the Platyrrhini (Kay et al. 1988; Plavcan and Van Schaik 1992). As discussed above, the catarrhines most likely exhibit dimorphism as a homology. However, because major platyrrhine clades (i.e., Atelinae, Cebidae, and Pitheciinae) include monomorphic and dimorphic forms, dimorphism and its associated mating behavior in the platyrrhines was either independently gained or lost multiple times and it is difficult to determine their character polarity.

Even though the atelines are most likely primitively dimorphic (see Rosenberger and Strier 1989), the cebids and pitheciines do not give such a clear picture of their primitive condition in my opinion due to their diversity. With regard to the cebids, the cebines (*Cebus* and *Saimiri*) are dimorphic whereas the callitrichines generally are not (Kay et al. 1988). However, some callitrichines exhibit slight "reverse" dimorphism in which females are larger than males (e.g., *Cebuella*; see Plavcan and Van Schaik 1992). Most pitheciines, with the exception of the monomorphic *Callicebus*, are also dimorphic albeit with a lower male/female ratio in canine length (e.g. a 1.32 ratio is found in *Pithecia*; see Kay et al. 1988). *Aotus*, which like the callitrichines and pitheciines is highly derived

(e.g., Rosenberger 1992) is another monomorphic exception (Kay et al. 1988; Plavcan and Van Schaik 1992).

The fossil record does not readily clarify the platyrrhine picture, since direct quantitative assessment of canine dimorphism is seldom possible based on the samples available. For example, *Branisella* (including *Szalatavus*) is the only primitive or stem platyrrhine which has been recovered that is not closely related to an extant taxon; therefore, it could provide insight into the evolutionary history of dimorphism among the earliest platyrrhines. However, the canine sample of *Branisella* is not sufficient to make a clear determination of dimorphism. The relatively few canine specimens available are highly worn or broken (for reviews of the current sample, see Takai et al. 2000; Fleagle and Tejedor 2001; Kay et al. 2001). Takai and colleagues (2000) attempt to circumvent this sampling problem based on the differences in p2 size among recovered specimens, and posit that *Branisella* may have possessed canine dimorphism. However, Plavcan (2001) has demonstrated that non-canine tooth size should only be used as an indicator of *body mass* dimorphism, and does not directly reflect canine dimorphism. Takai and colleagues' paper anticipates this argument by showing that the p2 size differences are greater than those for p4 teeth in *Branisella*. However, the four teeth they sample are from four different individuals with little if any other associated material. Given this sampling issue, the p2 size differential cannot be taken as strong evidence of dimorphism in my opinion.

There are several fossil pitheciine genera available; however, the information from these taxa is insufficient to fully understand dimorphism in this group. If the canines are present for these genera, they are either highly worn or broken. For example, the Patagonian genera *Homunculus*, *Soriacebus,* and *Carlocebus* are thought to be primitive pitheciines (e.g., Fleagle et al. 1988; Rosenberger et al. 1990; Tejedor 1996; Fleagle and Kay 1997; Fleagle and Tejedor 2002; Tejedor 2002; Tejedor and Rosenberger 2008). If one of these genera or a near relative were shown to be dimorphic this would in my opinion be best interpreted as a shared primitive character for the pitheciines in general. In turn, monomorphism in *Callicebus* would then represent a derived condition for pitheciines.

Fleagle and Kay (1997) have suggested that *Homunculus* most likely possesses canine dimorphism whereas Tejedor (2002) generally believes these three genera are monomorphic based on their anterior dental morphology. Tejedor does entertain the possibility of dimorphism in *Soriacebus* based on size differences between individuals which are established members of *Soriacebus* and some smaller canines which have a possible attribution to this genus (Tejedor 2002). However, as stated above, the hypodigms for these three genera do not currently allow direct quantitative assessment of male versus female canine size.

The few fossil genera which do present intact canines are generally cebines and too closely related to extant taxa to be of much assistance regarding primitive platyrrhine patterns. For

example, the probable cebine *Killikaike* (Tejedor et al. 2006) appears to be dimorphic (Tejedor, pers. comm.) and corroborates the idea that dimorphism is primitive for cebines. However, due to its phylogenetic position as a cebine, *Killikaike* gives little insight into broader cebid and platyrrhine patterns. Other fossils are closely related enough to modern genera that we can reasonably infer the presence of dimorphism, even though poor canine samples preclude direct quantification of this (e.g., *Dolichocebus*, another probable cebine; see Rosenberger 1979, 1992; Reeser 1984; Fleagle and Kay 1989, 1997; Kay et al. 2008).

Aotus dindensis has also been described as possessing canine dimorphism (Takai et al. 2009) but is also closely related to extant taxa (i.e., extant *Aotus* spp.; see Setoguchi and Rosenberger 1987). The pattern of *A. dindensis* may be different from that of its extant relatives and could provide significant insight into the evolution of platyrrhine dimorphism. If this species is shown to be dimorphic, it would suggest that dimorphism is primitive for either Cebidae or Pitheciinae (depending on the phylogenetic affinities of *Aotus*; see Chapter 1). However, as in the *Branisella* study by Takai and colleagues (2000), the interpretation of dimorphism in *A. dindensis* (Takai et al. 2009) is not based on quantitative comparison of canines between the sexes in members of the same species (or even genus). Therefore, the status of *A. dindensis* must still be considered uncertain.

In sum, due to the presence of mono- and dimorphism in the extant taxa as well as poor preservation and/or the phylogenetic position of the taxa from the fossil record, we currently cannot make strong determinations about evolution of dimorphism in primitive platyrrhines or even in primitive cebids and pitheciines (e.g., Delson and Rosenberger 1984; Rosenberger 1984; Schneider and Rosenberger 1996; Schneider 2000; Corruccini 2001; Hartwig and Meldrum 2001; Rosenberger 2001; Rosenberger et al. 2009). Therefore, several questions still need to be answered regarding the polarity of platyrrhine dimorphism and I will use ontogenetic data to provide insight into some of these questions. First, is canine mono- or dimorphism the primitive condition for platyrrhines? In other words, is dimorphism a homoplasy which evolved independently in the atelines and cebines (and to a lesser extent in pitheciines) or is it a homology among these groups? Second, if dimorphism is homoplastic in the platyrrhines, in which taxa did it evolve and how many times? Lastly, can platyrrhine ontogenetic data help resolve the question of canine dimorphism as a synapomorphy for extant anthropoids?

Ontogeny, Dental Increments, and Dimorphism

Before the current wave of research on dental increments, few studies of primate canines related dimorphism to ontogeny

(e.g., Zingeser 1968). Dean and Beynon (1991) were the first to assess the ontogeny of canine dimorphism using dental increments, focusing specifically on *Pan troglodytes*. Expounding upon these data, Schwartz and colleagues were able to examine all genera of the extant great apes to understand canine dimorphism in the hominoids (see Schwartz and Dean 2001 and Schwartz et al. 2001). By comparing canine growth rates against growth times (quantified as crown formation time) in male and female hominoids, these studies showed that hominoid males tend to achieve their larger canine sizes via bimaturism; that is, males achieve their larger size via a longer growth period (time). Moreover, the growth rates of males and females do not significantly differ (see Figs. 5-2 and 5-3).

As first put forward by Wiley (1974), the term "bimaturism" signifies a difference between the ages at which males and females achieve full adult reproductive physiology. However, considering the arguments on life history modes from Pereira and Leigh (2003), it is possible on theoretical grounds to make the term more inclusive. In other words, bimaturism can indicate timing differences between males and females for the completion of growth and/or development in any character (e.g., the end points of canine growth in male versus female hominoids as is seen in Schwartz et al. 2001). The expansion of the definition of "bimaturism" is important for ontogenetic studies, since different suites of morphological characters may exhibit different growth patterns due to the intricacies of adaptive

needs. These characters may or may not be fully formed even though the individual has reached adult reproductive status (see above; see also Chapters 1 and 4).

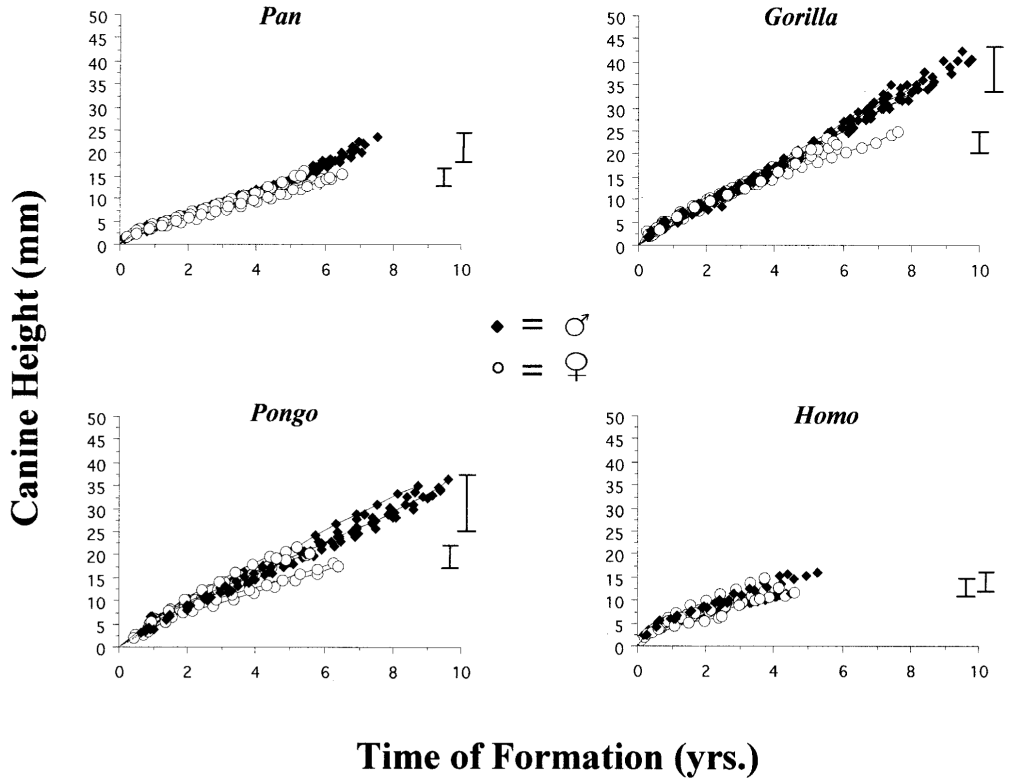


Fig. 7-2. Longitudinal canine growth trajectories for male and female hominoids. Note the indications of bimaturism: male trajectories are extended further in time than those of females (most markedly in *Gorilla* and *Pongo*, the most dimorphic hominoids). Male and female slopes show little difference from one another, indicating that growth rates for male and female canines are similar. From Schwartz and Dean (2001).

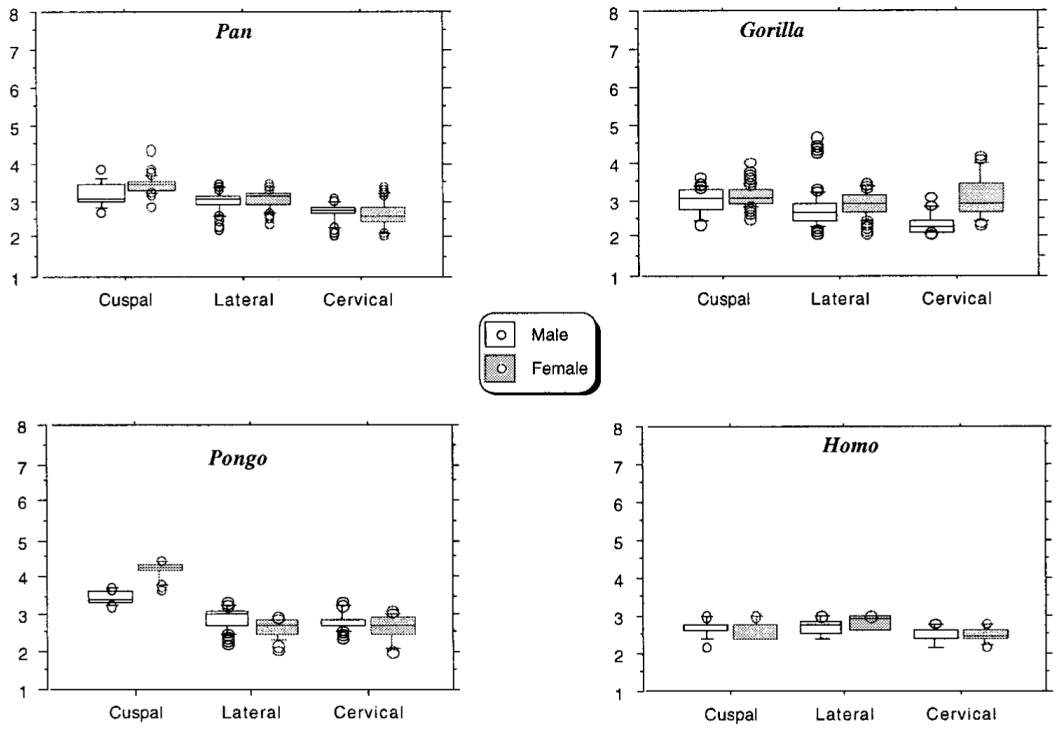


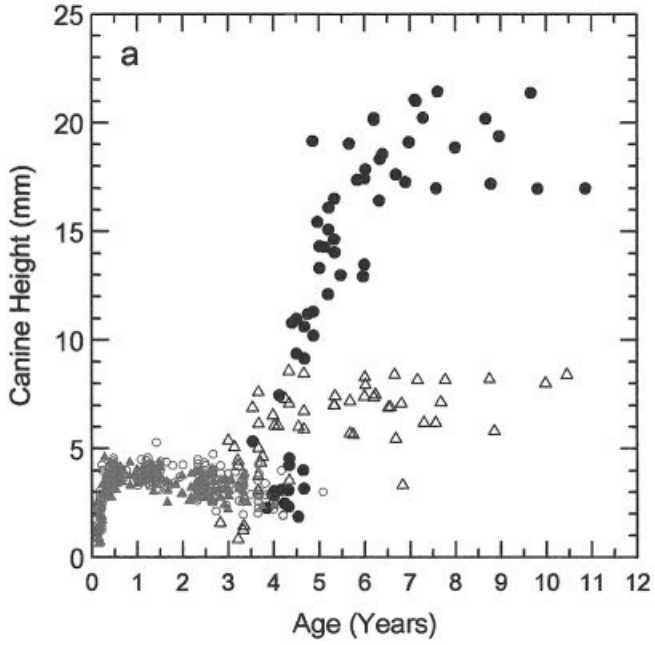
Fig. 7-3. Box-and-whisker plots which compare canine daily enamel secretion rates (DESRs) of male and females of hominoid genera, grouped across cuspal, lateral, and cervical regions of canine teeth for each genus. DESR represents the average amount of enamel secreted each day by individual ameloblast cells within a tooth bud, and so is an indicator of growth rate (versus length of growth period). These data consistently show that males have similar secretion rates to females, corroborating results of crown formation data shown in Fig. 7-2. From Schwartz et al. (2001)

It is currently unknown why dimorphic hominoid canines uniformly exhibit bimaturism. There may be some adaptive significance to the extended growth period, such as delaying contest competition for mates until males have grown larger and stronger (Jarman 1983). However, it may also be possible for bimaturism to persist as a byproduct of phylogenetic inertia, without necessarily having a strong adaptive significance.

Regardless of the reason for the uniform occurrence of canine bimaturism in hominoids, the dichotomy between ontogeny of body mass dimorphism and canine dimorphism in the great apes prompted Schwartz and Dean (2001) to argue that different ontogenetic processes regulate these two features. They note that dental growth is generally seen as more evolutionarily conservative relative to general somatic growth. Considering the consistency of canine growth patterns in hominoids versus the variation in somatic growth trajectories, the most plausible scenario seems to be that different ontogenetic processes are influencing somatic versus dental growth. If this was not the case, one would predict more variation in the ontogeny of canine dimorphism among hominoids.

Data from cross-sectional and longitudinal sampling of cercopithecine canines (Leigh et al. 2005) corroborate the argument of Schwartz and colleagues (2001). Again, despite ecological diversity, the canines of dimorphic papionin species from this group follow a very similar pattern of bimaturism. In *Macaca*, *Cercocebus*, *Mandrillus*, and *Papio*, males have a significantly longer duration for canine growth; *Mandrillus*, which is extraordinarily dimorphic, has modified this pattern to some degree (Leigh et al. 2005, 2008; see below). *Saguinus*, a non-dimorphic platyrrhine that serves as the outgroup in Leigh and colleagues' (2005) analysis, has no significant differences in either rate or duration of canine growth between males and females (see Fig. 7-4).

A.



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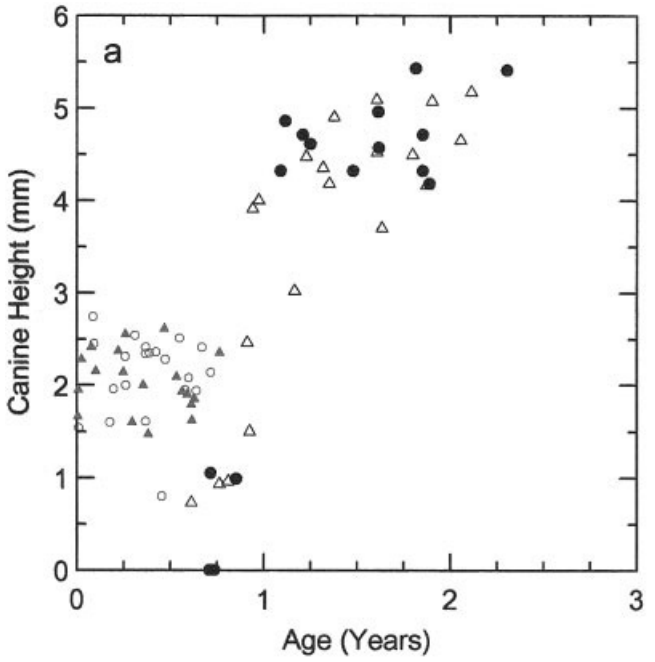


Fig. 7-4. Canine height plotted against age for *Macaca mulatta* (A) and *Saguinus fuscicollis* (B). All triangles represent females (open triangles = adults, gray triangles = juveniles), while all circles represent males (closed circles = adults, open circles = juveniles). Note that male *Macaca* canines cease to add crown height at around age 6-7, while females cease at around age 4. In *Saguinus*, there is no significant difference between male and female patterns. From Leigh et al. (2005).

These ontogenetic data for both hominoids and papionins corroborate the interpretations of above-cited studies, suggesting that canine dimorphism is primitive for catarrhines. Operating under the assumption that this catarrhine-type of sexual dimorphism is a primitive character for anthropoids in general, Schwartz and colleagues (2005) used microstructural data to determine whether or not canine dimorphism evolved independently in anthropoids and adapiforms. Using increments in enamel and dentine, Schwartz and colleagues computed growth trajectories for male and female *Cantius* (the notharctid genus sampled to represent adapiforms), and compared this to catarrhine trajectories. Their results show that *Cantius* achieved its canine dimorphism via faster growth rates in males rather than via bimaturism. Schwartz and colleagues (2005) interpret this ontogenetic difference as a suggestion that dimorphism evolved independently in notharctids and anthropoids (Fig. 7-5).

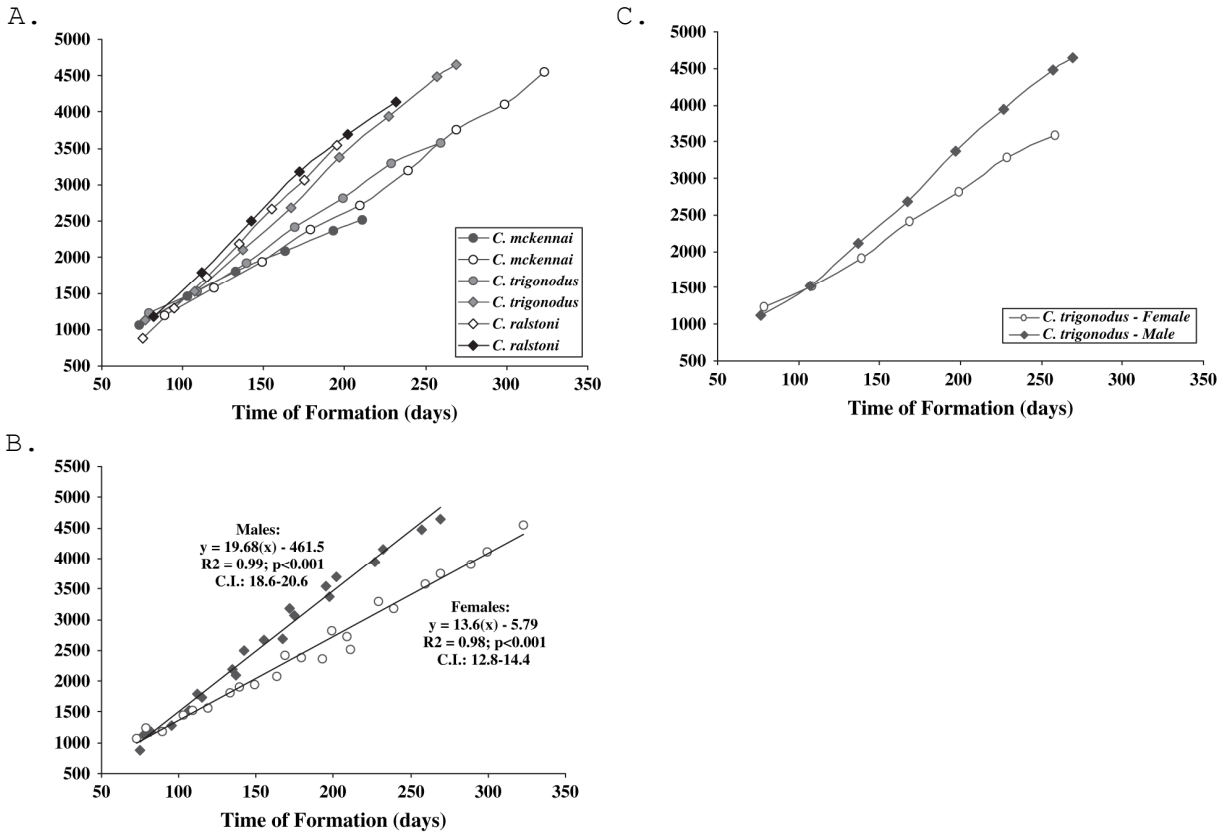


Fig. 7-5. Canine growth trajectories for adult males (diamonds) and females (circles) of *Cantius* spp. Canine crown height is regressed against crown formation time. All teeth included were fully formed, and so crown height data for given intervals were assessed using enamel and dentine increments. Crown formation time was also calculated using dental increments. Teeth were sexed prior to the study "based on differential canine height and canine base dimensions" (p. 98; see Schwartz et al. 2005 for details). Units for the Y axis are not given in the paper, but are assumed to be microns as this is the standard unit used in incremental analyses. **A.** Regression plot with species analyzed separately. **B.** Regression plot and statistics which include all 6 species. **C.** Plot comparing growth profiles of only *C. trigonodus*. All plots show that unlike the hominoids, male growth trajectories for *Cantius* do not extend significantly further in time than those of females (and sometimes even appear shorter; see graphs A and B). Instead, the males do have a significantly steeper growth trajectory, indicating a faster growth rate. From Schwartz et al. (2005).

However, there are problems with this labeling of "anthropoid" versus notharctid patterns, as the anthropoid data used in the Schwartz study are drawn entirely from catarrhine specimens. Again, given the range of platyrrhine mating behaviors relative to the conserved nature of mating behavior in catarrhines, we cannot safely assume that dimorphism is a homologous feature of the two extant anthropoid groups. To the contrary, it is entirely possible that dimorphism has evolved and/or disappeared more than once within anthropoids, as the polarity of canine dimorphism for primitive platyrrhines is unknown. By analyzing ontogenetic data from platyrrhines (in the form of dental increments) and placing them in the context of behavioral and gross morphological data, I hope to be able to help pinpoint whether dimorphism is homologous or homoplastic across the extant anthropoids.

Sampling

All preparation, imaging, and measurements for light microscopy and SEM were performed as described in Chapter 3, which also contains a description of statistical methods used. For all t-tests, a 95% confidence interval was used as the benchmark for statistical significance.

This study examines enamel increments of right or left mandibular canines of thirteen individuals. Three genera of

platyrrhines were sampled: *Cebus*, *Saimiri* and *Alouatta*. The canines were on loan from the following institutions: AMNH, NYU/CSHO, and MNRJ (see Chapter 3 and Table 3-1 for a list of specimens used and their institutional sources).

The study primarily examines the dimorphism of two cebid genera, *Cebus* and *Saimiri*, specifically *Cebus apella, C. albifrons, Saimiri oerstedii,* and *S. sciureus*. The focus on these two genera stems from the fact that they are the most dimorphic cebids and more importantly, they are two of the most dimorphic platyrrhines in general (e.g., Kay et al. 1988). *Cebus* and *Saimiri* have male-to-female canine height ratios approaching or exceeding 1.5 for mandibular and maxillary canines. Note that different studies give slightly different values for some of these species, but the males have significantly larger canines approaching a 1.5 M/F ratio in all of the studies [see Kay et al. 1988; Plavcan and Van Schaik 1992; Masterson 2003; see Table 7-1 for a compilation of platyrrhine dimorphism data (Masterson and Hartwig 1998), and Table 7-2 for more detailed data specifically for *Cebus* (Masterson 2003)].

Any data generated from the cebines alone, however, cannot explicitly address larger platyrrhine or anthropoid social evolution issues. As suggested above, even though the fossil evidence indicates that dimorphism is most likely primitive for cebines, it is possible that cebines secondarily evolved dimorphism from a primitive pattern of monomorphism for either cebids or platyrrhines.

Taxon	Body weight dimorphism (Leigh, 1994) Wild	Captive	Body weight dimorphism (wild) (Ford and Davis, 1992)	Body weight dimorphism (wild) (Smith and Jungers, 1997)	Body weight dimorphism (wild) (Plavcan and van Schaik, 1997)	Canine height dimorphism (Plavcan and Kay, 1988)	Canine diameter dimorphism (Kay et al., 1988)
Atelinae							
Alouatta caraya	1.41	1.85	1.48	1.48	1.53	1.48	1.34
Alouatta palliata			1.34	1.34	1.28	1.51	1.28
Alouatta fusca			1.36	1.55	1.37	1.52	1.40
Alouatta belzebul			1.32	1.32	1.39	1.81	1.42
Alouatta seniculus			1.28	1.28	1.26	1.50	1.31
Ateles geoffroyi	1.20	1.34	1.10	1.07	1.25	1.52	1.11
Ateles paniscus			0.85	1.08	1.10	1.57	1.10
Lagothrix lagotricha	1.35		1.45	1.04	1.20	1.88	1.22
Pitheciinae						1.26	1.19
Cacajao calvus			1.20	1.20	1.20		
Pithecia pithecia	1.27		1.14	1.23	1.19	1.32	1.18
Aotus nancymai			0.98	1.02			
Aotus trivirgatus	1.07	0.98	0.97	1.10	0.99	1.08	1.04
Callicebus cupreus			0.90	0.91			
Callicebus moloch	1.03	1.08	1.16	1.07	1.09	1.08	0.99
Cebinae							
Cebus albifrons	1.22		1.37	1.39			
Cebus apella	1.42	1.91	1.28	1.45	1.38	1.41	1.22
Cebus capucinus			1.45	1.45			1.16
Cebus olivaceus			1.24	1.30	1.40		
Saimiri sciureus	1.25	1.47	1.26	1.18	1.22	1.61	1.17
Callitrichinae							
Saguinus fuscicollis	1.19	0.98	0.96	0.96	1.00	1.03	0.98

Table 7-1. Indices of sexual dimorphism in platyrrhines (from Masterson and Hartwig 1998, canine height data originally from Kay et al. 1988, *contra* the table heading). A higher index value indicates larger male body weight or canines relative to those of females. All species or genera included in this study which are listed in this table exceed an M/F canine height ratio of 1.5, except *C. apella*. However, this species does exceed this value in Masterson (2003); see Table 7-2.

Variables	*C. albifrons*	*C. apella*	*C. capucinus*	*C. olivaceus*
Max. canine M/D length	1.236***	1.203***	1.215***	1.276***
Max. canine B/L width	1.133***	1.169***	1.147***	1.173***
Max. canine height	1.680***	1.582***	1.597***	1.668***
Mand. canine M/D length	1.206***	1.226***	1.199***	1.237***
Mand. canine B/L width	1.210***	1.257***	1.266***	1.205***
Mand. canine height	1.473***	1.443***	1.481***	1.484***

*** $P < 0.001$.

Table 7-2. Indices of canine dimorphism for the four species of *Cebus* (from Masterson 2003). Asterisks denote a statistically significant difference in canine metrics between males and females (*P* is less than 0.001).

Therefore, in order to establish broader evolutionary comparisons for platyrrhines and anthropoids, this study also includes the dimorphic ateline *Alouatta*. *Alouatta* contains the most dimorphic platyrrhine species in terms of canine size (Kay et al. 1988; Plavcan and Van Schaik 1992). Across different species *Alouatta* has a M/F height ratio between 1.35 and the extremely high value of 2.78 in mandibular canines (Plavcan and Van Schaik 1992) and between 1.48 and 1.81 for maxillary canines (Kay et al. 1988; Plavcan and Van Schaik 1992). However, most species cluster around a 1.5 M/F canine height ratio. No other platyrrhine species approaches the 2.78 M/F height ratio for mandibular canines that is seen in *Alouatta belzebul*. In addition, *Lagothrix* (M/F ratio of 1.77 or 1.88, depending on the source; see Plavcan and Van Schaik 1992 vs. Kay et al. 1988, respectively) is the only taxon that approaches or exceeds the 1.81 ratio for maxillary canines that is seen in *A. belzebul* (Kay et al. 1988; see also Table 7-1). As *Alouatta* is only distantly related to the cebines within Platyrrhini (see "Systematics" section of Chapter 1), its inclusion in this study allows a somewhat broader platyrrhine interpretation. Unfortunately, the only *Alouatta* available had no known species or locality information, so all three specimens were analyzed together. The individuals used in this analysis were sexed based on a comparative study of the *Alouatta* collection at AMNH.

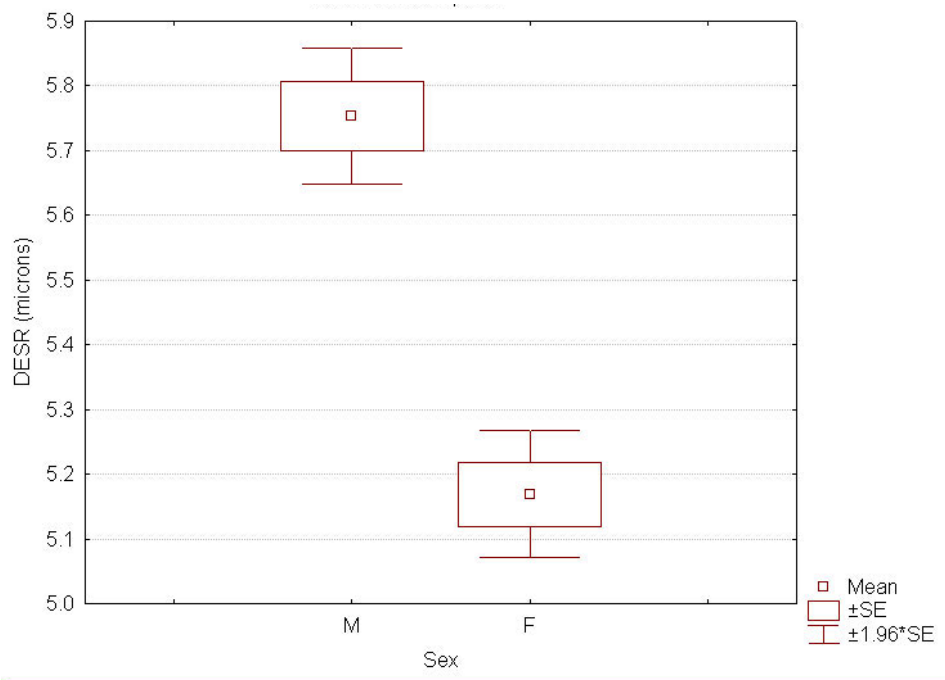
Results

Growth RATE analyses

Based on standard t-tests, the males in both species of *Cebus* (*apella and albifrons)* have a higher canine growth rate in terms of the daily enamel secretion rate (more microns/day in mid-imbricational DESR; see Chapters 2 & 3) relative to females. This difference is highly significant for both species ($p = 2.09*10^{-14}$ for *C. apella*, $p = 2.2*10^{-16}$ for *C. albifrons*; see Fig. 7-6 A & B). This significantly higher canine growth rate in males occurs despite a slightly higher mean growth rate for females in all post-canine teeth within these species, though the difference between the sexes in postcanine teeth is not statistically significant ($p = 0.35$; see Fig. 7-7).

To understand the canine growth rates of *Saimiri*, I was unable to measure DESR due to sample limitations. However, similar growth rate data can be obtained from perikymata breadth measurements (see Chapter 3 for an explanation of perikymata breadth as a substitute for DESR). In a standard t-test comparing perikymata breadth measurements acquired from SEM images, male *Saimiri* have a significantly higher growth rate than females ($p = 0.02$; Fig. 7-8). Therefore, males of both *Saimiri* and *Cebus* have a higher growth rate relative to females in their genus/species. Understanding that the Retzius period has been established as 3 days for both males and females across all

A.



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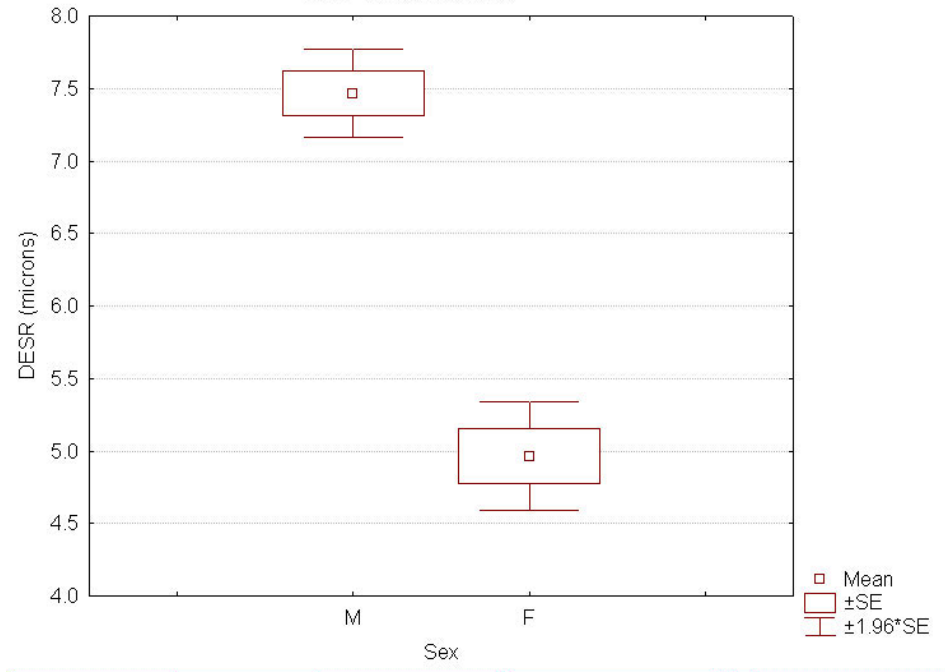


Fig. 7-6. A. Box-plots of canine mid-imbricational DESR in *Cebus apella* and **B.** *Cebus albifrons*. Both plots show that males of *Cebus* have a significantly higher canine growth rate than females ($p = 2.09*10^{-14}$ for *C. apella*, $p = 2.2*10^{-16}$ for *C. albifrons*). For *C. apella* (A), the number of cross striations measured to obtain mean DESRs for the sexes was: males $n = 209$, and females $n = 1344$. For *C. albifrons* (B), the number of cross striations measured was $n = 62$ for males and $n = 35$ for females. See Table 3-1 for specimens included.

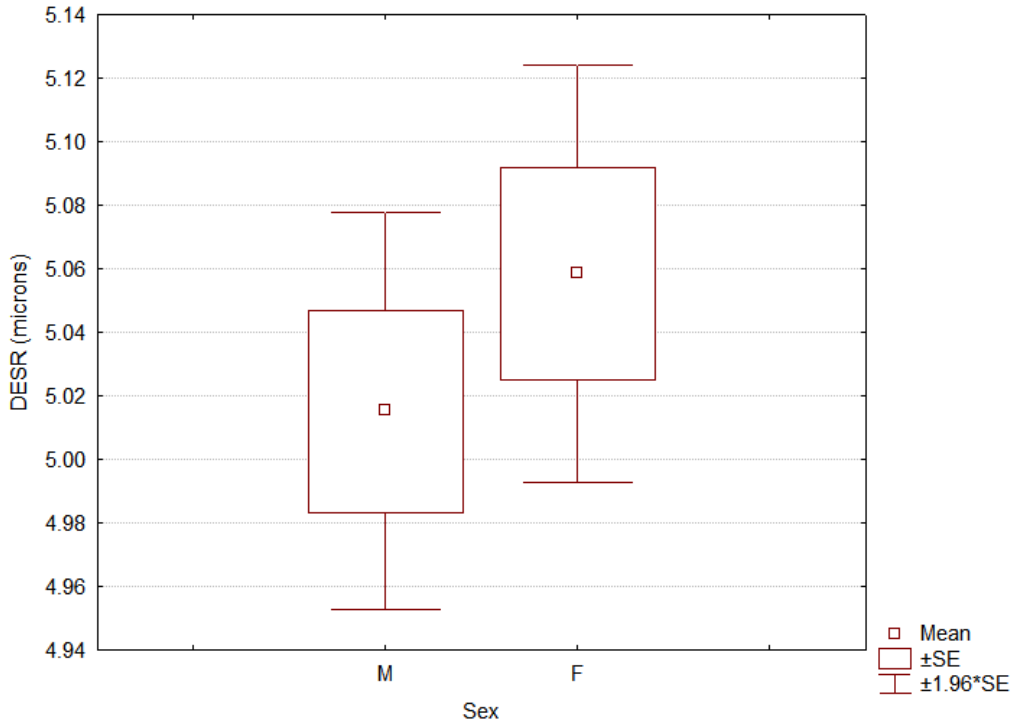


Fig. 7-7. Box-plots comparing DESRs of all post-canine teeth in males and females of *Cebus apella* and *C. albifrons*, combined to increase sample size. The female mean DESR is slightly higher than that of males; however, the difference is not statistically significant ($p = 0.35$, males $n = 1599$ cross striations, females $n = 1458$).

species and individuals of *Saimiri* sampled in this dissertation (see Chapters 3 and 6), I am confident that perikymata breadths are a valid source of data for growth rate comparisons between the sexes of *Saimiri*. Note that the two species of *Saimiri* were combined in this analysis also due to sampling limitations (See Chapter 3).

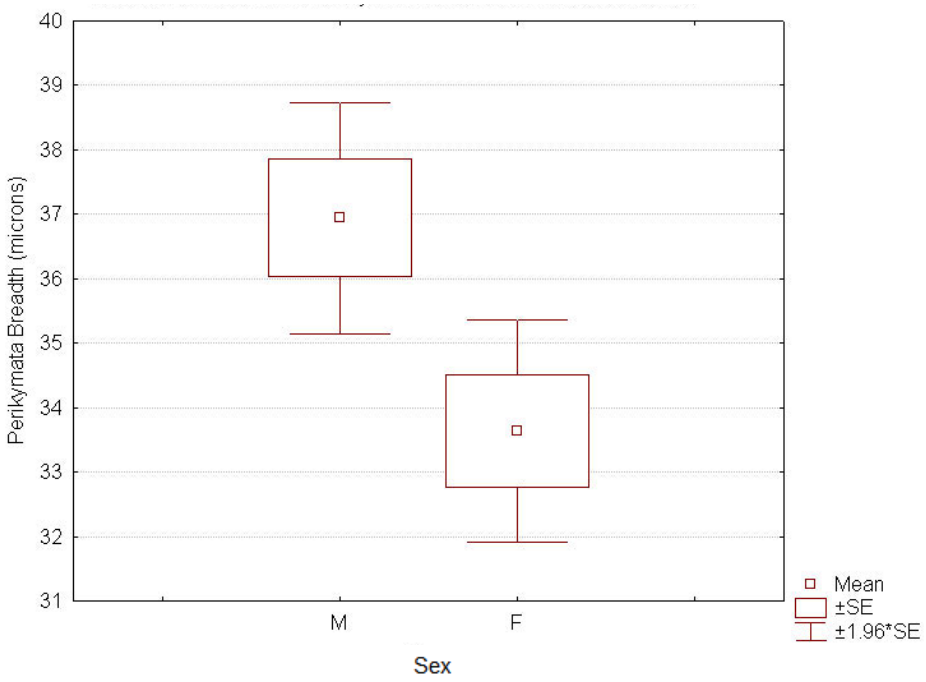
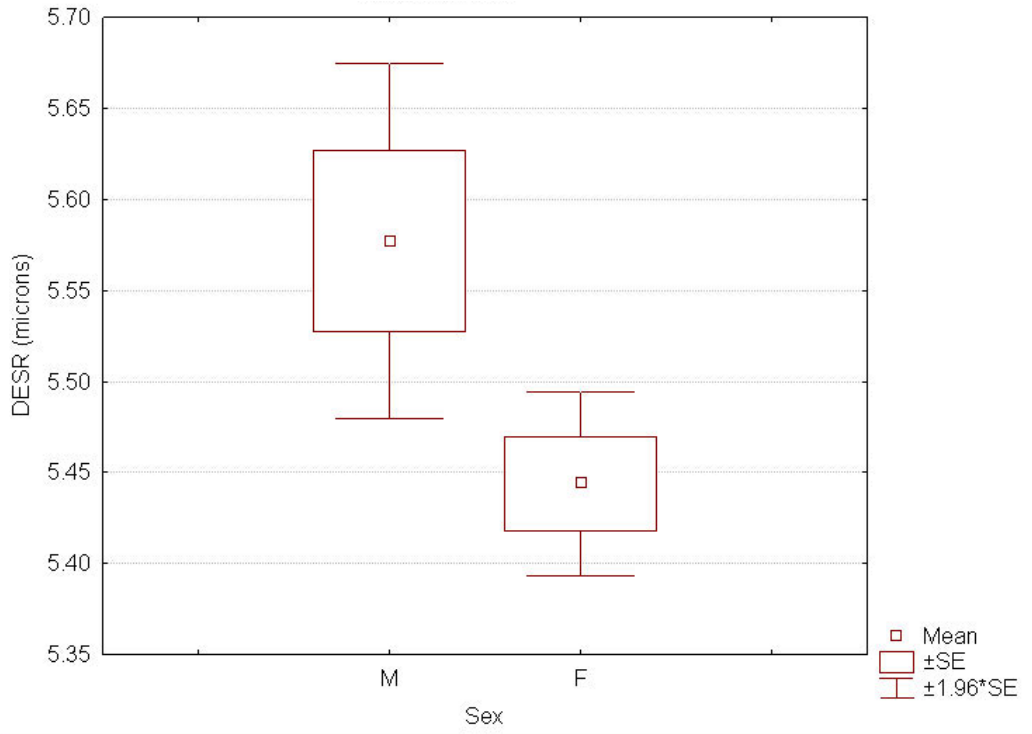


Fig. 7-8. Box-plot of male canine perikymata breadths relative to females in *Saimiri oerstedii* and *S. sciureus* (see Chapter 3). Males have a higher growth rate than females (p = 0.024; males *n* = 58 perikymata, females *n* = 28). See Table 3-1 for specimens included.

For *Alouatta*, since the inner and outer regions of imbricational enamel preserved adequate incremental anatomy in all three individuals, cross striation breadths were collected from the EDJ to the tooth surface. The results of the t-test comparing this data between male and female specimens showed the same pattern as *Cebus* and *Saimiri*; in other words, the male *Alouatta* has a significantly higher mean DESR than the two females (p = 0.0099; see Fig. 7-9 A).

To be consistent with the analyses of *Cebus*, a second t-test was conducted on *Alouatta* which limited the data to mid-imbricational cross striations (see Chapter 3 for an explanation of method choice). For mid-imbricational enamel, comparison of

A.



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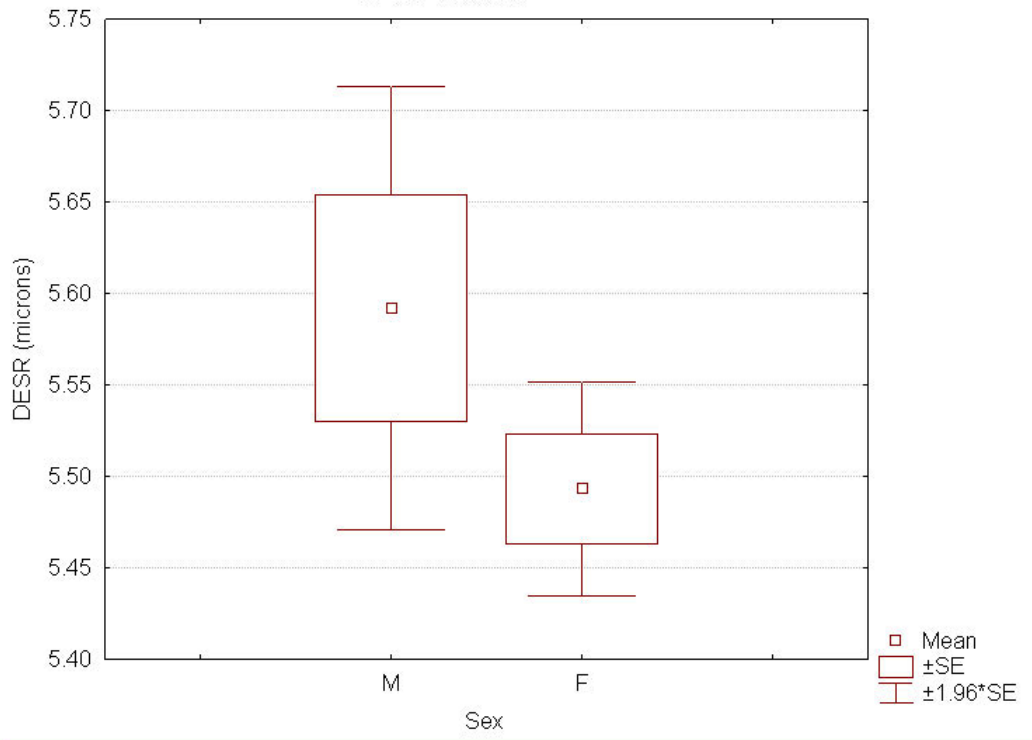

Fig. 7-9. Box-plots of all male vs. female *Alouatta* spp. **A.** DESR data gathered from EDJ to tooth surface in imbricational enamel. p = 0.0099, males *n* = 306 cross striations, females *n* = 771. **B.** DESR estimated from mid-imbricational enamel only. p = 0.105, males *n* = 201 cross striations, females *n* = 467.

the single male (MNRJ 2756) against both females (MNRJ 484 & 494) yielded no statistically significant difference ($p = 0.105$) in DESR. However, when comparing the male with just the MNRJ 484 female, a significant difference is seen ($p = 0.04$; Fig. 7-9 B). In addition, when the male is compared with just the MNRJ 494 female, the results are not significant ($p = 0.728$) and MNRJ 494 only has a slightly lower DESR than the male. Therefore, it is clear that when all three specimens are included in this mid-imbricational analysis of *Alouatta*, the MNRJ 494 female is the reason that a significant difference does not exist between males and females. Since the species designation for the *Alouatta* specimens is unknown, a possible reason that the MNRJ 494 female is exhibiting a slightly different pattern from the other female is that it belongs to a different species, making the genus *Alouatta* highly variable. The other possibilities are that this female individual is an outlier and the mid-imbricational data obtained are the result of idiosyncracy, that the DESR ranges of males and females overlap, or that MNRJ 494 is a very small male. Although I believe that the first explanation is the most likely, further samples of *Alouatta* are needed to determine which of these factors is driving the pattern seen here.

See Table 7-3 for a summary of statistical data.

Sample	Female Mean	Female SD	Male Mean	Male SD	t-value	df	p-value
*C. albifrons** (1F, 1M)	4.96	1.13	7.47	1.22	9.94	95	$2.09*10^{-14}$
*C. apella** (2F, 2M)	5.16	0.91	5.75	1.22	8.55	1551	$2.2*10^{-16}$
*Saimiri*** † (1F, 3M)	33.63	4.72	36.94	6.96	2.3	84	0.024
Alouatta all F(2) vs. M(1)‡	5.44	0.71	5.58	0.88	2.58	1075	0.0099
Alouatta all F v. M*	5.49	0.64	5.59	0.88	1.623	666	0.105
Alouatta 484 v. 2756*	5.46	0.61	5.59	0.88	1.993	520	0.04
Alouatta 494 v. 2756*	5.56	0.71	5.59	0.88	0.35	345	0.728

Table 7-3: Statistical summary.
Mean = mean DESR, given in microns; SD = standard deviation
* = Cross-striation data from mid-imbricational sample only
** = perikymata in microns, rather than DESR
† = *Saimiri oerstedii* + *S. sciureus*
‡ = Cross-striation data taken from EDJ to tooth surface in imbricational region

Growth PERIOD analyses

The following analyses examine the amount of time that it takes an individual canine crown to form. Unfortunately, direct comparisons of crown formation time within *C. apella* and *C. albifrons* were not possible with the samples available. Some teeth were too worn to be good indicators, while others lacked sufficient Retzius anatomy to produce reliable estimates of enamel crown formation time (see Chapter 3). However, I was able to obtain reliable estimates for two individual *Cebus* specimens, and in turn, compare a male *C. apella* to a female *C. albifrons.* It is interesting to note that the male *C. apella* (AMNH 133091)

has a somewhat *shorter* crown formation time than the female *C. albifrons* (AMNH 78504), which has a much shorter and more narrow canine crown; the male crown formation time is around 700 days while the female time is around 770. Thus, the male has produced a *greater* quantity of enamel in a shorter amount of time than the female, resembling some members of the Notharctidae in this regard (i.e., *Cantius*; see above).

In *Alouatta*, crown formation time of the MNRJ 2756 male is around 659-667 days while the MNRJ 484 female is around 632-640 and the MNRJ 494 female ranges from 815-860 days. Therefore, the male has a slightly longer crown formation time than the 484 female but is much shorter than the 494 female. The first comparison between 484 and the male shows a superficially similar pattern to catarrhines with males having longer crown formation times than females. However, the difference between this male and female is only around 20-40 days whereas the differences between the sexes within species of catarrhines is often around a year or more (e.g., Schwartz and Dean 2001; Leigh et al. 2005). Therefore, given the significantly higher DESR for the male *Alouatta* (MNRJ 2756), the most reasonable interpretation is that crown formation time is not driving the size difference between this male and female.

If the MNRJ 494 female is the same species of *Alouatta* as the other two specimens, the range of variation within and between males and females would be very large. This is a possibility, since we do not know for certain if this type of

intraspecific variation exists within primate canines; however dental data up to this point do not provide evidence for such variation (e.g., Schwartz and Dean 2001; Leigh et al. 2005). To the contrary, such major differences between congeneric primate individuals have only been shown to appear *between* species (e.g., Schwartz et al. 2005). Therefore, as stated previously, it is likely that this female specimen represents a different species than the other two. In addition, due to the preservation of anatomy, the estimate for the MNRJ 494 female is admittedly less reliable than the other two *Alouatta* specimens. Regardless of these two issues, the female 494 canine is smaller than the male 2756 canine yet it does not exhibit a shorter crown formation time.

Therefore, the crown formation data for both *Cebus* and *Alouatta* suggest that the crown formation times in males of both genera are not longer relative to the females of the same genus. When there is any notable difference, males seem to have shorter, rather than longer crown formation times.

Discussion

These findings are in conflict with those of a recent study, which did not find evidence for faster growth rates in male *Cebus* (or *Ateles*) based on measurements of perikymata breadths in lateral canine enamel (Guatelli-Steinberg et al.

2009). There are several weaknesses in this prior study, including the fact that only one species of *Cebus* was sampled, and that the difference they find in the mean time periods of canine growth between male and female *Cebus* and *Ateles* are much less than the differences seen between male and female catarrhines. For example, in this study *Cebus* males and females differ in perikymata counts by about 36 perikymata (in this study, a higher difference in perikymata counts within a canine is interpreted to represent differences in time period taken to form a tooth crown), whereas different dimorphic catarrhine genera in the study exhibit differences of between 58 and 115 perikymata. This suggests that if there is a time difference in the growth of canines between male and female *Cebus*, this time difference is not nearly as important as it is in catarhines.

The most important weakness in the analyses of Guatelli-Steinberg and colleagues (2009), however, is that this study rests on the assumption that Retzius periodicities in platyrrhines do not differ between males and females of a given species. It also does not take into account the possible range of variation in Retzius periodicities for the species which they examined. My study has shown that for *Cebus*, males and females do differ with respect to their Retzius periodicity (see Chapter 6). Even if they did not, the range of variation for Retzius periodicity for *Cebus* is four to six days, which was not accounted for in the analyses of Guatelli-Steinberg and colleagues (2009). Analyses of perikymata breadth that do not

verify Retzius periodicity for the specimens which are being measured, or do not at least address the possible range of Retzius variation, cannot provide accurate indications of growth rates. This is because, without knowledge of Retzius periodicity, one cannot be certain that the growth increments represented by perikymata in different specimens represent equal amounts of time. Therefore, the perikymata data of this study are of uncertain nature.

The most reliable way to be certain of the time of crown formation for a tooth, as well as its growth rates, is to image its internal structure. The DESR and crown formation time data on canine dimorphism in this dissertation is more reliable than data from perikymata-based studies because of the fact that internal data reflect an absolute, rather than a relative, measure of dental growth. Perikymata breadth measurements from *Saimiri* specimens were only included in my study because I was able to verify that the Retzius periodicity of multiple individuals of three *Saimiri* species, including both sexes, had a consistent value of three days, as mentioned above and in Chapter 3. It is true that my intraspecific samples are more limited than those of Guatelli-Steinberg and colleagues (2009), and therefore it is still possible that an expansion of *Cebus* samples (especially *C. apella*) could reveal a pattern like that seen in the other study.

However, the platyrrhine data collected in the present study show that two major platyrrhine clades, the Cebidae and

Atelidae, have members which differ from the catarrhines in the same way, with regard to canine ontogeny and dimorphism. Unlike the catarrhines, the cebines and *Alouatta* do not achieve their dimorphism via bimaturism, but rather males have faster canine growth rates. Out of all the other primates that have been analyzed thus far, the cebines and *Alouatta* most resemble the notharctids (specifically *Cantius*). In turn, based on these major differences in ontogenetic data, the presence of dimorphism in the platyrrhines and catarrhines is not a synapomorphy and is most likely the result of homoplasy.

With regard to the questions of polarity *within* the platyrrhines, the enamel data suggest that dimorphism may be the primitive state for crown platyrrhines assuming that ontogenetic similarities most often result from common descent. In this case, monomorphism would be independently derived in the callitrichines, *Brachyteles, Aotus,* and *Callicebus*. The latter two genera may share monomorphism through common descent assuming that they are closely related (see Chapter 1). However, without further ontogenetic data from additional dimorphic platyrrhine taxa such as *Pithecia*, it is still possible that the genera examined here independently engaged a common ontogenetic mechanism to evolve dimorphism.

Overall, however, the most likely explanation is that dimorphism is primitive for the crown platyrrhines based on the following reasons: 1) the ontogenetic underpinnings for canine dimorphism between cebines and *Alouatta* are similar, 2)

dimorphism is probably primitive for atelines in general (Rosenberger and Strier 1989), and 3) the Cebidae and Atelidae, which most likely diverged sometime before 23-25 Ma, have had a great deal of evolutionary time to alter these similar ontogenetic patterns of dimorphism (e.g., Rosenberger 1984; Schneider et al. 2000). Therefore, the dimorphic platyrrhine taxa have maintained continuous selection for a set of mating behaviors and morphological correlates which they share from a common ancestor. Even though pitheciine ontogenetic data and better fossils are needed to verify the hypothesis of primitive platyrrhine dimorphism, and even though we cannot currently comment on the polarity of canine dimorphism in stem platyrrhines, it would seem that in extant platyrrhines dimorphism is primitive and monomorphism (e.g., in callitrichines) is more likely to be a secondarily evolved feature.

Chapter 8:

Summary, Conclusions, and Future Work

This dissertation is the first in-depth examination of cebid enamel microstructure, and provides a foundation for understanding the platyrrhines as a whole and how they compare to the other primates which have been studied more thoroughly in this respect. The main goal of this dissertation has been to analyze cebid enamel microstructure in order to better understand the following: 1) the relationship between prism patterns, enamel function, and diet within the Cebidae; 2) the impact of body mass and ecological variables upon cebid dental growth rates; 3) the physiological underpinnings and significance of the Retzius biorhythm; and 4) the ontogenetic factors underlying canine dimorphism in this primate family and platyrrhines in general.

Even though this is a small study with a sample limited by the constraints of whole-specimen histological research, analyses of the cebids have provided insight into the structure and growth of primate teeth. For example, the microstructural patterns of decussation within cebids seem to follow a general mammalian pattern (e.g., Koenigswald et al. 1987; Koenigswald 2000); however, they also present a few surprises which reveal that dental microstructure evolution and its relationship to size and diet among mammals has important subtleties. Moreover, the analyses of the cebids have helped to understand the impact of differing factors, such as brain mass and physiological processes,

upon ontogeny and life history evolution. Specifically, these microstructural growth rate analyses have shown that within anthropoids small-scale ontogenetic processes are responding to similar selective forces as the large-scale processes, such as tooth eruption. This highlights a major difference in the dental ontogenies of anthropoids and strepsirhines. Lastly, the project has provided evidence that the evolution of sexual dimorphism in anthropoids is more complex than previously thought.

Enamel Structure and Function in Cebids

Prior studies of enamel microstructure within mammals have shown that relatively larger species and/or species with more mechanically demanding diets generally have more complicated enamel anatomy (e.g., Koenigswald et al. 1987; Koenigswald 2000). Enamel prisms within these species decussate (crisscross one another), and are often grouped into Hunter-Schreger bands (bundles of prisms with alternating orientations). These complex enamel patterns serve in the dissipation of forces, helping to prevent tooth enamel from breaking under high masticatory loads (e.g., Koenigswald et al. 1987; Pfretzchner 1988; Boyde 1989; Maas and Dumont 1999; Rensberger 2000; Popowics et al. 2004).

In some cases, cebids clearly follow this general pattern. For example, *Cebus* is an extractive forager and hard-object feeder which uses its teeth to break open a variety of

mechanically resistant objects (e.g., Struhsaker and Leland 1977; Teaford 1985; Brown and Zunino 1990; Fragaszy et al. 1990; Fernandes 1991; Janson and Boinksi 1992; Galetti and Pedroni 1994; Fragaszy and Boinski 1995; Kinzey 1997; Fragaszy et al. 2004; Wright 2005; Addessi 2008). It has much more complicated enamel than its smaller relatives *Saimiri* and *Aotus*. These two genera are usually classified as more general "frugivore-insectivores" though *Aotus* is also known to eat leaves (e.g., Rosenberger 1992; Wright 1996; Boinski 1999; Wolovich et al. 2008). *Cebus* has a high degree of Hunter-Schreger banding and prism decussation, whereas the latter two genera have purely radial enamel (i.e., have only parallel enamel prisms; see also Nogami and Yoneda 1983).

Another example that clearly follows the mechanical rule is the pattern in the anterior teeth of some callitrichines. *Callithrix* canines and incisors possess distinct Hunter-Schreger banding, whereas *Saguinus* has much less complex enamel in their anterior teeth (Nogami and Natori 1986; this study). Although these two genera are similar in size, *Callithrix* is known to use its anterior teeth during tree-gouging behavior, whereas *Saguinus* does not. This behavioral difference seems to explain the microstructural disparity in these two genera (for further discussion of tree-gouging morphology in callitrichines, see: Kinzey et al. 1975; Rosenberger 1978; Nash 1986; Rosenberger 1992; Vinyard et al. 2003; Taylor and Vinyard 2004; Vinyard and

Ryan 2006; Taylor et al. 2009; Vinyard et al. 2009; Hogg et al. in press).

However, the presence of decussation in callitrichine postcanine teeth does not fit within this framework at first glance. Callitrichines are on the smaller end of the primate body size continuum and as a group are often generally classified as "frugivore-insectivores" (like *Saimiri*), even though there are some major differences in feeding strategies among them (e.g., Coimbra-Filho and Mittermeier 1977; Sussman and Kinzey 1984; Soini 1987; Ford and Davis 1992; Rosenberger 1992; Anapol and Lee 1994; Power and Oftedal 1996; Dietz et al. 1997; Porter 2001). Species within this group have a diet consisting of fruits, flowers, nectar, exudates, fungi, insects, and small vertebrates (e.g., Sussman and Kinzey 1984; Rosenberger 1992; Ferrari 1993; Kinzey 1997; Porter 2001). With the exception of tree-gouging, this diet does not seem mechanically demanding at first glance. Therefore, based on diet and body size, we would predict that callitrichines would mostly exhibit radial enamel in order to minimize tooth wear (e.g., Rensberger 2000).

Therefore, the reason for decussation in callitrichine post-canine enamel is not readily apparent based on the hypothesis that size and mechanics are the primary selective influences concerning ultrastructure. Other factors are likely involved. First, body size is not an absolute barometer of bite forces to which enamel must routinely respond. Larger species may be physically capable of producing more force overall, but

may only be adapted to use a greater force if their dietary context demands it. For example, *Alouatta* is considerably larger in body mass than *Cebus* (see Chapter 5); however, *Alouatta* has relatively simple enamel (Nogami and Yoneda 1983; pers. obs.), probably due to a dietary regime that places less strain on its teeth. On the other hand, *Cebus*, even though it is smaller, is specially adapted in craniodental morphology for operation under a high bite-force regime (e.g., Wright 2005).

Second, the cebids suggest that it is important to avoid overly-generalized terms in relation to dietary descriptions when speaking about functional adaptations. Although the terms "frugivore-insectivore" and "frugivore-folivore" can be useful terms for general discussion, they overlook substantial dietary variation (Rosenberger 1992). For example, within their frugivore-insectivore category, different callitrichine genera and species are known to place differing emphases on resources such as exudates and fungi (e.g., Coimbra-Filho and Mittermeier 1977; Sussman and Kinzey 1984; Soini 1987; Ford and Davis 1992; Rosenberger 1992; Anapol and Lee 1994; Power and Oftedal 1996; Dietz et al. 1997; Porter 2001). Moreover, fruits and insects have a variety of sizes, shapes, and morphologies, which can demand a range of mechanical solutions within teeth and jaws (e.g., Freeman 1979; Sussman and Kinzey 1984; Lucas and Corlett 1991; Kinzey 1992; Rosenberger 1992; Kinzey and Norconk 1993; Dumont 1995a; Strait and Vincent 1998; Dumont 1999; Lucas 2004; Evans and Sanson 2005; Lucas et al. 2008b). If enamel

microstructure is highly responsive to functional-adaptive need as proposed by Lucas and colleagues (2008b), the decussation in callitrichine postcanine teeth suggests they must have some specific feeding difference that makes them functionally distinct from their close relative *Saimiri*, for example.

Along these lines, Sussman and Kinzey (1984) first suggested that callitrichines seem to engage in a different type of insectivory than relatives such as *Saimiri* and *Aotus*. Specifically, the small body size of the callitrichines enables them to be more efficient hunters of orthopteran insects (grasshoppers, locusts, katydids). On the other hand, their relatives tend to eat slower-moving and easier-to-catch insects such as grubs, etc. (Sussman and Kinzey 1984). Research has shown that differences in insect exoskeleton toughness and hardness are related to differences in masticatory architecture in insectivorous bats, such that species which eat insects with more resistant shells have more robust mandibles and teeth (Freeman 1979; see also Strait and Vincent 1998; Evans and Sanson 2005). Moreover, Dumont (1995a) showed that primate and bat species which eat more mechanically demanding insects tend to have thicker dental enamel. Therefore, it seems likely that insect morphology could also drive adaptations in enamel microstructure in primate species. Specifically, the orthopteran exoskeletons encountered by callitrichine enamel may place a significantly more difficult mechanical demand upon their teeth, and may be the driving force behind callitrichine decussation.

Even though some studies have already been conducted on bite-force and the mechanical properties of primate foods (e.g., Strait and Vincent 1998; Lucas et al. 2008b; Vinyard et al. 2009), a major gap remains in our knowledge regarding the callitrichines. In order to provide detailed answers to such questions, specific biomechanical data are needed regarding bite-force generation by callitrichines, as well as the mechanical properties of specific food items consumed by different species.

Enamel Growth Rates, Body Mass, Brain Mass, and Ecology

As with prior research on dental eruption, this study shows that enamel growth rates, in terms of both daily enamel secretion rate (DESR) and enamel extension, are tied to body and brain mass within cebids. Given the homogeneity of anthropoids with regard to dental eruption patterns (e.g., Smith 1989; Smith et al. 1994; Godfrey et al. 2001), it is likely that these enamel growth rate relationships extend to other platyrrhines and catarrhines as well. However, the relationship between body mass and dental ontogeny does not seem to extend to the strepsirhines that have been analyzed thus far (e.g., Schwartz et al. 2002; Godfrey et al. 2006).

This difference between anthropoids and strepsirhines may be an indicator of major differences in the physiology or selective forces underlying dental ontogeny. That such a marked

dichotomy existing within one mammalian order is very intriguing and needs further study. As with tooth eruption, adult body and brain mass are the result of complex ontogenetic processes, and so it is entirely possible that in seeking relationships between dental ontogeny and mass, we are overlooking an underlying ontogenetic variable that acts to control dental growth rates in primates and perhaps mammals in general. For example, somatic growth rates or basal metabolic rate (BMR) may show a relationship with dental ontogeny across primates, and resolve the disparity seen in anthropoid and strepsirhine dental ontogeny patterns thus far. Moreover, major strepsirhine groups such as the lorisoids still have not been adequately sampled, and therefore our knowledge of variation within strepsirhines is still somewhat limited. Therefore, we need taxonomically broader analyses which take somatic growth rate and BMR into account.

Among the three ecological variables examined, age at foraging independence seems to have the greatest impact upon dental growth rates, while environmental risk and maternal investment seem to have a lesser impact. Since species should be timing their dental growth to correspond with the age at which they will need to fully rely upon their teeth (i.e., without the supplement of milk), the strong support for the foraging independence hypothesis makes sense. This result is also consistent with prior analyses based on tooth eruption (Godfrey et al. 2001).

Previous research has shown a strong correlation between somatic growth and environmental risk (Leigh 1994). This study has shown that environmental risk has a different impact upon dental growth than it does on somatic growth. In other words, anthropoid species in riskier environments tend to slow their somatic growth to reduce the risk of malnutrition, but do not seem to slow their dental growth in conjunction. This makes sense, since it seems likely that the energy devoted to dental growth should only comprise a small percentage of an animal's overall energy budget. Moreover, the timing of dental ontogeny seems to be so important for species' fitness that teeth are much less subject to developmental perturbations than bone (Guatelli-Steinberg 2001). Given these two factors, it is likely that a rapid dental ontogeny may not represent a major fitness liability in a risky environment. Instead, a properly-run dental ontogeny is probably of such high fitness value that growth rates and eruption may be tightly canalized despite fluctuations in overall resource availability. This is especially the case considering that fallback foods should be of high importance in a fluctuating environment. In addition, they are often harder or tougher than primary foods, and in turn, fully functional adult teeth are probably better at breaking down such foods (e.g., Rosenberger and Kinzey 1976; Lambert et al. 2004; Lambert 2007; Marshall and Wrangham 2007; Lucas et al 2008b; Marshall et al. 2009). Therefore, it seems likely that dental ontogeny should react differently than general somatic ontogeny under cases of

environmental risk, assuming that teeth are not costly to grow. However, detailed studies on the energetics of dental ontogeny are needed to confirm this idea.

The two variables used to assess maternal investment have differing statistical impacts upon dental growth. Age at weaning is statistically correlated with dental growth rates, but this is mostly likely driven by the fact that age at weaning is a variable related to foraging independence as well. Unlike age at weaning, interbirth interval is not statistically correlated with enamel growth rates. Overall, the two maternal investment variables present differing results, and in turn, unlike foraging independence, maternal investment does not seem the best predictor of enamel growth rates.

However, maternal investment and foraging independence are tied together, because foraging independence begins during the period of a juvenile's life where maternal investment becomes minimal (e.g., Nicolson 1987; Garber and Leigh 1997; Lee 1999). Therefore, with all else being equal, species that attain foraging independence at younger ages should exhibit relatively reduced maternal investment. The results of this study suggest that foraging independence and maternal investment may be dissociable to some degree, at least when discussing dental ontogeny. In turn, maternal investment, as with environmental risk, may have its most significant impact upon the ontogeny of features that are more energetically costly, such as the brain

(Lee 1999). In contrast, the ontogeny of teeth seems more strictly linked to foraging independence *per se*.

Since the timing of tooth growth is very important to fitness, it would be expected that DESR and enamel extension rates would follow similar patterns. However, this project has shown that DESR and enamel extension rate are not significantly correlated with one another and that there are major differences between these two variables when regressed against all of the factors examined in this study (e.g., body mass, brain mass and age at weaning). Not only do the regressions of DESR and enamel extension exhibit opposite correlations with respect to one another, these two variables also have their strongest correlations with different factors.

DESRs have been shown to be relatively high for some catarrhine species with relatively thick enamel (e.g., *Pongo, Theropithecus, Paranthropus, Gigantopithecus*; see Swindler and Beynon 1993; Dean 1998; Dean and Schrenk 2003; Lacruz et al. 2006, 2008), raising the possibility that selection for relative enamel thickness has a significant relationship with DESR. However, several primate genera with relatively thick enamel do not exhibit correspondingly high DESRs (e.g., *Graecopithecus*; see Smith et al. 2004; Lacruz et al. 2008), suggesting that DESR may be driven and constrained by differing factors among separate taxonomic groups. This serves as a caution for broad interpretations of enamel growth rates, and suggests that a taxon-by-taxon approach may provide better insight than sweeping

analyses of large numbers of primate or mammalian taxonomic groups.

These ideas bring us to what is perhaps the most important conclusion we can draw from Chapter 5: enamel growth rates, as with dental eruption, seem to be affected by a complex interaction of variables within the cebids, rather than being dominated by any one factor. As mentioned in Chapter 6, single variables almost always only have a moderate impact on enamel growth rate; however, when all variables are considered together, correlations are very high (i.e., approaching 1). This leaves open the possibility that differing mammalian species may be subject to variations in the constraints and selective factors acting upon their dental ontogeny, based on their specific phylogenetic history and ecological context. Therefore, it may be fruitful to compare the analyses of small taxonomic groups to large-scale taxonomic surveys in order to determine the differences that exist.

Retzius Periodicity and Life History Evolution

Good evidence now exists from teeth and bones to support the idea that an autonomically-mediated biorhythm is important for hard tissue growth. For example, Retzius periodicities have been shown to correspond to known autonomic rhythms such as heart rate (Appenzeller et al. 2005). Bone periodicity has not been

directly tied to autonomic rhythms; however, Retzius lines have been shown to have an interval which corresponds to the periodicity of lamellae in bone (Bromage et al. 2009). As shown in this study (and in Bromage et al. 2009), Retzius periodicity is correlated with body mass and, to a lesser degree, with brain mass.

The evolutionary significance of this autonomic biorhythm, the Havers-Halberg Oscillation (HHO; Bromage et al. 2009), lies in its potential to act as a central coordinator for the body's allocation of energy resources, and hence a coordinator of life history. Physiological research has shown that reproduction, BMR, cellular proliferation, heart rate, body mass, and bone mass are all regulated by the autonomic nervous system in mammals (e.g., Stahl 1967; McNab 1980; Lindstedt and Calder 1981; Martin 1990; Harvey et al. 1991; West et al. 1997; Ueyama et al. 1999; Amling 2001; Karsenty 2001; Thomas and Burguera 2002; Takeda et al. 2003; Elefteriou et al. 2004; Appenzeller 2005; Lee et al. 2007; Brown et al. 2007). In turn, evidence suggests that by altering the HHO, it would be possible for a species to simultaneously adjust all of these seemingly separate variables according to changing adaptive needs (Bromage et al. 2009).

As an example, imagine a species living in an environment that is undergoing a long-term decrease in annual rainfall. Due to this decrease, the availability of resources vital to that species is also in permanent decline. In this hypothetical situation, the available daily energy intake for individuals is

decreasing, and therefore the species is under directional selection to lower its daily, as well as long-term, metabolic costs. Without a central mechanism governing the above-mentioned factors which determine energy usage (e.g., BMR and cellular proliferation rate), each or at least some of these characters would have to have a somewhat independent evolutionary response to this one selective force. However, if these factors were in large part coordinated by a central physiological mechanism, only one mechanism would need to evolve in response to this selective demand. The requisite changes in body mass, metabolism, etc., could then result as a pleiotropic effect. Therefore, the HHO may represent a highly efficient means for mammal species to adjust their physiologies according to changing external demands over time.

This idea is also supported by work in experimental physiology, which has shown that mammal cells from different taxa, which are known to have differing cellular metabolic rates *in vivo*, do not exhibit these differences *in vitro* (Brown et al. 2007). That is, when removed from the overall physiological context of the organism as a whole (e.g., the autonomic nervous system), many metabolic differences between the cells of different mammalian taxa break down, suggesting that overall metabolism and energy usage by cells *are* in fact mediated by a central system.

A great deal more work is necessary to provide more direct physiological data to confirm the HHO model, and also to explain

its variation across different primate and mammalian taxa. For example, experimental manipulation of the autonomic nervous system in laboratory animals would provide the most concrete evidence for the HHO, by revealing how the physiologies (and hard tissue microanatomy) of mammals respond to damage to specific nuclei within the hypothalamus. It is also important to examine Retzius periodicities within species that have a high degree of body mass variation, so we can better understand how the HHO might respond to external selective pressures at low taxonomic levels.

Since within primates we see anomalous taxa such as the subfossil strepsirhines, whose HHO seems to have a much lower value than expected, we need to establish if there are more universal ("better"} predictors of HHO than body mass. BMR may be a key variable in this regard, as it should also be closely regulated by the HHO. For example, it may be that subfossil lemurs have an abnormally high BMR for their body mass among primates, and that their HHO is geared toward maintaining this high BMR. In turn, associated factors within these species such as Retzius period and cellular proliferation will reflect an HHO which is unusually short for large taxa. Considering that enamel growth rates may also tie in to BMR, as suggested above, it is even possible that there is an explicit physiological link between Retzius periodicity and enamel growth rates which is inherent to the operation of ameloblasts themselves.

Evolution of Sexual Dimorphism in Platyrrhines and Catarrhines

Analyses of canine dimorphism for the genera examined in this study (*Cebus, Saimiri, and Alouatta*) all suggest that male specimens of these dimorphic taxa have faster canine growth rates than females, rather than longer growth periods. Specifically, DESRs for males of these genera are higher than in females, and crown formation times for males are either comparable to those of females, or else are shorter. In other words, this study suggests that bimaturism is not responsible for canine dimorphism in the platyrrhines studied, unlike previously studied catarrhines (for catarrhine data see Schwartz and Dean 2001; Schwartz et al. 2001; Leigh et al. 2005; Schwartz et al. 2005. However, see Guatelli-Steinberg et al. 2009 for a different result; see Chapter 7 for reasons why these results may differ).

Therefore, based on my histological data, it currently appears that *Cebus, Saimiri,* and *Alouatta* males share a common pattern of canine growth different from catarrhines. This indicates that canine dimorphism within the platyrrhines and catarrhines evolved convergently. Considering this, in addition to the dimorphism seen in adapiform strepsirhines, it is possible that dimorphism has evolved at least three times within the primate order. Regarding the polarity of dimorphism within the platyrrhines, the shared pattern of the cebines and *Alouatta* suggests that the extant platyrrhines share a distinct process of increasing the relative size of male canines, within taxa that

exhibit canine dimorphism. However, further sampling of dimorphic ateline and pitheciine taxa are still needed to corroborate this suggestion. Moreover, if other factors, such as gross morphology and behavioral patterns among the disparate dimorphic platyrrhine genera also seem to be shared, then the sum of the evidence would seem to suggest that dimorphism is primitive for the extant platyrrhines. Conversely, if other indicators of mating behavior do not match up with the ontogenetic data, this may suggest that canine dimorphism evolved in parallel within different platyrrhine lineages, invoking similar ontogenetic programs to produce similar end results.

Overall, the platyrrhines are a very useful group of primates to help us understand dental ontogeny and evolution, since they contain a number of dimorphic species with varying body sizes and ecological strategies as well as providing a natural phylogenetic control. This initial exploration of dental microstructural growth patterns within the Platyrrhini has therefore opened new questions and avenues for possible research, scratching the surface of issues in life history evolution for which further sampling of teeth in platyrrhines, primates, and mammals will hopefully provide detailed insights.

Appendix A:

Specimens Used in This Study

GENUS	SPECIES	SEX	TEETH	SOURCE	NUMBER
Alouatta	*sp.*	F	c	MNRJ	484
Alouatta	*sp.*	?	m1	MNRJ	490
Alouatta	*sp.*	F	c	MNRJ	494
Alouatta	*sp.*	?	m2	MNRJ	499
Alouatta	*sp.*	M	c, m3	MNRJ	2756
Aotus	*sp.*	F	c, p3	CSHO	
Aotus	*sp.*	F	p3	CSHO	
Callicebus	*personatus*	F	m2	MNRJ	414
Callicebus	*personatus*	F	m3	MNRJ	30183
Callimico	*goeldii*	?	m1, m3	Rose	
Callithrix	*humeralifer*	?	c, m1, m2	AMNH	94926
Callitrhix	*jacchus*	?	p2	HTRU	
Cebuella	*pygmaea*	?	premolar	AMNH	239606
Cebus	*albifrons*	M	c, p2, p3, m2, m3	AMNH	62838
Cebus	*albifrons*	F	c, p3, p4, m1, m2, m3	AMNH	78504
Cebus	*apella*	M	c, p2, p4, m1, m2, m3	AMNH	133091
Cebus	*apella*	?	p3, p4, m1, m2	Rose	Y15
Cebus	*apella*	F	c	CSHO	

GENUS	SPECIES	SEX	TEETH	SOURCE	NUMBER
Cebus	*apella*	M	c, m1, m3	MNRJ	445
Cebus	*apella*	F	c, m2	MNRJ	446
Cebus	*apella*	M	c	MNRJ	447
Cebus	*apella*	M	m3	MNRJ	448
Cebus	*capucinus*	?	p2, p3, m2	Rose	
Cebus	*capucinus*	?	p4, m1	USNM	
Cebus	*olivaceus*	?	p2, p3, p4, m1, m2, m3	AMNH	42419
Cebus	*sp.*	?	c, p2, m1	Rosenberger	
Cebus	*sp.*	?	m2	MNRJ	459
Cebus	*sp.*	?	m1, m2	MNRJ	460
Leontopithecus	*rosalia*	?	p2, p3, p4, m1	AMNH	80244
Saguinus	*fuscicollis*	?	p3, p4, m1, m2	AMNH	182941
Saguinus	*oedipus*	?	p2, p3, p4	USNM	
Saguinus	*midas*	?	p3, p4	AMNH	97280
Saguinus	*nigricollis*	?	p2, p3, p4, m2	USNM	
Saimiri	*boliviensis*	F	c, p2, m1, m3	AMNH	208075
Saimiri	*oerstedii*	M	c	AMNH	19212
Saimiri	*oerstedii*	M	p2, m1	AMNH	139300
Saimiri	*sciureus*	M	p3, p4, m2, m3	AMNH	94206
Saimiri	*sciureus*	F	p2, p4, m1, m2	USNM	397329
Saimiri	*sciureus/ oerstedii*	M	c	MNRJ	433

GENUS	SPECIES	SEX	TEETH	SOURCE	NUMBER
Saimiri	*sciureus/ oerstedii*	F	c	MNRJ	33593
Saimiri	*sp.*	F	c	AMNH	14003
Saimiri	sp.	M	c	AMNH	17116

AMNH = American Museum of Natural History, New York City

HTRU = Hard Tissue Research Unit, New York University College of Dentistry, New York City **CSHO** = Center for the Study of Human Origins, New York University **MNRJ** = Museu Nacional do Rio de Janeiro, Rio de Janeiro **Rose** = Rose Primate Collection, Queensborough Community College, Queens, New York **Rosenberger** = private collection of Dr. Alfred Rosenberger, Brooklyn College, Brooklyn, New York **USNM** = United States National Museum of Natural History, Washington, D.C.

All specimens from CSHO were frozen, predissected cadavers. All specimens from the Rose Primate Collection were cadavers fixed in formaline, except for *Callimico goeldii* (frozen). All other specimens were skeletonized.

Appendix B:

Raw Data for enamel formation front (EFF), Enamel Secretion (DESR), and Ecological Variables

- "EFF angle" represents an individual measurement of angle of enamel formation front (stria of Retzius) to EDJ, taken from imbricational enamel.
- DESR in microns per day is given as a mean for each species (or genus, in the case of *Aotus* and *Alouatta*), as compiled from measurements made in the course of this study. As the data tables containing all individual measurements are too voluminous to present here, the author willing share the relevant spreadsheets electronically with those who are interested.
- Natural logarithms (LN) of body and brain mass are also taken on data from Ford and Davis (1992), Harvey and Clutton-Brock (1985), Hartwig (1996) and Lindenfors (2002), as explained in Chapter 3. Encephalization quotient (EQ) is also calculated from brain and body mass data in these papers, according to the protocols of Jerison (1973) and Martin (1990). See Chapter 3 for the EQ equation.
- Weaning age, age at first female breeding, and interbirth interval are taken from Harvey & Clutton-Brock (1985), Ross (1991), Godfrey et al. (2001), and Lindenfors (2002) as cited in Chapter 3.
- All times are expressed in years.

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Aotus	*sp.*	14.152	M1		4.67	-0.09	2.9	0.18	0.49	2.42	0.603
Aotus	*sp.*	19.584	M1	16.868	4.67	-0.09	2.9	0.18	0.49	2.42	0.603
Saimiri	*boliviensis*				5.7	-0.36					
Saimiri	*oerstedii*	9.36	M1		4.78	-0.34	3.25	0.3	0.5		
Saimiri	*oerstedii*	15.7	M1		4.78	-0.34	3.25	0.3	0.5		
Saimiri	*oerstedii*	14.9	M1		4.78	-0.34	3.25	0.3	0.5		
Saimiri	*oerstedii*	16.9	M1		4.78	-0.34	3.25	0.3	0.5		
Saimiri	*oerstedii*	9.8	M1		4.78	-0.34	3.25	0.3	0.5		
Saimiri	*oerstedii*	8.9	M1		4.78	-0.34	3.25	0.3	0.5		
Saimiri	*oerstedii*	16.8	M1		4.78	-0.34	3.25	0.3	0.5		
Saimiri	*oerstedii*	21.05	M1	14.176	4.78	-0.34	3.25	0.3	0.5		
Saimiri	*sciureus*	9.69	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Saimiri	*sciureus*	13.58	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	10.64	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	13.44	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	9.8	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	10.24	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	12.05	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	13.76	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	18.33	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	14.94	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	13.61	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	14.81	M1		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	15.8	M2		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	16.9	M2		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	12.31	M2		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	15.6	M2		4.7	-0.22	3.23	0.27	0.5	2.5	1.13

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Saimiri	*sciureus*	14.6	M2		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	11.7	M2		4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Saimiri	*sciureus*	9.7	M2	13.001	4.7	-0.22	3.23	0.27	0.5	2.5	1.13
Cebus	*albifrons*	40.34	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	34.61	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	40.95	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	27.13	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	32.04	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	32.81	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	35.62	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	34.63	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	33.26	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	46.76	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	41.1	M1		4.87	0.82	4.2	0.39	0.75	4	1.5

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Cebus	*albifrons*	39.46	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	41.9	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	35.09	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	35.8	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	36.33	M1		4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*albifrons*	36.8	M1	36.74	4.87	0.82	4.2	0.39	0.75	4	1.5
Cebus	*apella*	18.61	M1		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	13.63	M1		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	24	M1		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	22	M1		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	20.15	M2		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	26.02	M2		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	25.55	M2		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	22.54	M2		5.14	0.97	4.29	0.34	1.14	5.78	1.84

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Cebus	*apella*	28	M2	22.354	5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	20.28	M2		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*apella*	25.12	M2		5.14	0.97	4.29	0.34	1.14	5.78	1.84
Cebus	*capucinus*	25.5	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	23.9	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	34.3	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	26.3	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	21.8	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	20.78	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	26.8	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	21.53	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	21.39	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	23.81	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	23.45	M1		5.72	1.18	4.37	0.32	1	4	2.2

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Cebus	*capucinus*	25	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	25.37	M1		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	21.7	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	21.7	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	19.44	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	26.97	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	24.8	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	20.21	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	30	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	28.43	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	23.21	M2		5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*capucinus*	23.9	M2	24.36	5.72	1.18	4.37	0.32	1	4	2.2
Cebus	*olivaceus*				4.47	1.09	4.39	0.35	1.97	6	2.17

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Callithrix	*humeralifer*				4.13	-1.13	2.07	0.16	0.25	1.6	
Callithrix	*jacchus*				4.3	-1.36	2.07	0.18	0.17	1.67	0.43
Cebuella	*pygmaea*				4.8	-2.2	1.43	0.16	0.24	1.9	0.42
Saguinus	*fuscicollis*	15.52	M2		4.66	-0.98	2.23	0.17	0.25	2.33	0.66
Saguinus	*fuscicollis*	16.31	M2		4.66	-0.98	2.23	0.17	0.25	2.33	0.66
Saguinus	*fuscicollis*	13.72	M2		4.66	-0.98	2.23	0.17	0.25	2.33	0.66
Saguinus	*fuscicollis*	16.03	M2		4.66	-0.98	2.23	0.17	0.25	2.33	0.66
Saguinus	*fuscicollis*	21.33	M2		4.66	-0.98	2.23	0.17	0.25	2.33	0.66
Saguinus	*fuscicollis*	15.2	M2		4.66	-0.98	2.23	0.17	0.25	2.33	0.66
Saguinus	*fuscicollis*	19.23	M2	16.763	4.66	-0.98	2.23	0.17	0.25	2.33	0.66

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Saguinus	*nigricollis*	8.86	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	15.72	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	17.03	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	12.02	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	13.15	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	11.11	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	20.72	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	16.69	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	12.55	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	13	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	12.55	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	13.85	M1		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	15.05	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	16.65	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	21.03	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Saguinus	*nigricollis*	17.57	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	11.6	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	14.4	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	13.6	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	17.64	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	15.9	M2		4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*nigricollis*	14.71	M2	14.79	4.73	-0.73	2.19	0.13	0.21	2.33	0.69
Saguinus	*midas*				4.29	-0.65	2.34	0.15	0.19	2	0.66
Saguinus	*oedipus*				4.44	-0.84	2.2	0.15	0.22	1.89	0.77
Leontop.	*rosalia*	10.64	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	17.23	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Leontop.	*rosalia*	8.26	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	12.67	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	5.72	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	3.53	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	5.78	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	6.38	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	10.24	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	14.24	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	3.4	M1		4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Leontop.	*rosalia*	9.44	M1	8.96	4.93	-0.46	2.56	0.16	0.24	2.4	0.83
Callimico	*goeldii*	13.075	M1		4.31	-0.94	2.38	0.18	0.18	1.3	0.46
Callimico	*goeldii*	13.765	M1		4.31	-0.94	2.38	0.18	0.18	1.3	0.46
Callimico	*goeldii*	16.201	M1		4.31	-0.94	2.38	0.18	0.18	1.3	0.46

Genus	Species	EFF angle	Tooth for EFF estimate	EFF: total species average	DESR: total species average	LN body mass	LN brain mass	EQ	Weaning age	Age at first female breeding	Interbirth interval
Callimico	*goeldii*	14.065	M1		4.31	-0.94	2.38	0.18	0.18	1.3	0.46
Callimico	*goeldii*	12.417	M1	13.905	4.31	-0.94	2.38	0.18	0.18	1.3	0.46
Alouatta	*sp.*	18.65	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	19.18	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	15.56	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	19.19	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	20.67	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	22.48	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	17.9	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	17.28	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	20.85	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	21.83	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	18.41	M2		5.11	1.86	4.03	0.01	0.89	3.8	1
Alouatta	*sp.*	22.04	M2		5.11	1.86	4.03	0.01	0.89	3.8	1

Appendix C:

Incremental Data on Canine Dimorphism

Table 1: Perikymata measurements for *Saimiri*

Genus	Species	Specimen	Sex	perikymata breadth (microns)
Saimiri	*sciureus*	94206	M	32.74559
Saimiri	*sciureus*	94206	M	32.74559
Saimiri	*sciureus*	94206	M	32.74559
Saimiri	*sciureus*	94206	M	30.85642
Saimiri	*sciureus*	94206	M	34.94962
Saimiri	*sciureus*	94206	M	37.46851
Saimiri	*sciureus*	94206	M	29.59698
Saimiri	*sciureus*	94206	M	34.63476
Saimiri	*sciureus*	94206	M	23.61461
Saimiri	*sciureus*	94206	M	30.2267
Saimiri	*sciureus*	94206	M	28.02267
Saimiri	*sciureus*	94206	M	36.20907
Saimiri	*sciureus*	94206	M	38.09824
Saimiri	*sciureus*	94206	M	36.62751
Saimiri	*sciureus*	94206	M	35.93642
Saimiri	*sciureus*	94206	M	32.13545
Saimiri	*sciureus*	94206	M	32.13545
Saimiri	*sciureus*	94206	M	31.09883
Saimiri	*sciureus*	94206	M	28.33449
Saimiri	*sciureus*	94206	M	39.73739
Saimiri	*sciureus*	94206	M	32.481
Saimiri	*sciureus*	94206	M	32.481
Saimiri	*sciureus*	94206	M	29.37111
Saimiri	*sciureus*	94206	M	30.75328
Saimiri	*sciureus*	94206	M	33.51762
Saimiri	*sciureus*	94206	M	42.84727
Saimiri	*sciureus*	94206	M	27.29786
Saimiri	*sciureus*	94206	M	32.13545
Saimiri	*sp.*	14003	F	36.62751
Saimiri	*sp.*	14003	F	30.40774
Saimiri	*sp.*	14003	F	34.89979
Saimiri	*sp.*	14003	F	36.62751
Saimiri	*sp.*	14003	F	36.62751
Saimiri	*sp.*	14003	F	34.20871
Saimiri	*sp.*	14003	F	37.66413
Saimiri	*sp.*	14003	F	32.13545
Saimiri	*sp.*	14003	F	29.02557

Genus	Species	Specimen	Sex	perikymata breadth (microns)
Saimiri	*sp.*	14003	F	26.60677
Saimiri	*sp.*	14003	F	31.78991
Saimiri	*sp.*	14003	F	41.4651
Saimiri	*sp.*	14003	F	37.66413
Saimiri	*sp.*	14003	F	38.70076
Saimiri	*sp.*	14003	F	40.42847
Saimiri	*sp.*	14003	F	38.70076
Saimiri	*sp.*	14003	F	34.20871
Saimiri	*sp.*	14003	F	28.33449
Saimiri	*sp.*	14003	F	41.4651
Saimiri	*sp.*	14003	F	23.49689
Saimiri	*sp.*	14003	F	29.71666
Saimiri	*sp.*	14003	F	31.27854
Saimiri	*sp.*	14003	F	34.7032
Saimiri	*sp.*	14003	F	27.16895
Saimiri	*sp.*	14003	F	30.3653
Saimiri	*sp.*	14003	F	34.01826
Saimiri	*sp.*	14003	F	26.94064
Saimiri	*sp.*	14003	F	34.01826
Saimiri	*sp.*	14003	F	36.07306
Saimiri	*sp.*	17116	M	39.318
Saimiri	*sp.*	17116	M	34.1
Saimiri	*sp.*	17116	M	35.0181
Saimiri	*sp.*	17116	M	32.867
Saimiri	*sp.*	17116	M	42.39
Saimiri	*sp.*	17116	M	39.011
Saimiri	*sp.*	17116	M	37.4755
Saimiri	*sp.*	17116	M	38.397
Saimiri	*sp.*	17116	M	36.2468
Saimiri	*sp.*	17116	M	35.325
Saimiri	*sp.*	17116	M	32.868
Saimiri	*sp.*	17116	M	27.34
Saimiri	*oerstedii*	19212	M	33.64
Saimiri	*oerstedii*	19212	M	36.86
Saimiri	*oerstedii*	19212	M	42.857
Saimiri	*oerstedii*	19212	M	38.70968

Table 2: Crown formation data from thin sections (*Cebus* & *Alouatta*)*

Genus	Species	Sex	Specimen	Total CFT (days)
Cebus	non-apella *sp.*	F	Brooklyn skull	568
Cebus	*albifrons*	F	78504	754
Cebus	*apella*	M	133901	696
Saimiri	*sciureus*	M	94206	428
Saimiri	*boliviensis*	F	208075	400
Cebus	*albifrons*	M	62838	n/a
Cebus	*olivaceus*	M	42419	n/a
Cebus	*apella*	F	NYU	n/a
Alouatta	*sp.*	M	2756	657
Alouatta	*sp.*	F	484	632
Alouatta	*sp.*	F	494	838

***** All numbers represent the mean of an error range that extends 17 days above and below the given figure. Given the non-statistical nature of this data (due to extremely low sample sizes), this range is taken from the specimen with the greatest observed variation in magnitude across multiple estimates (#494).

Table 3: DESR data from thin sections (*Cebus & Alouatta*)*

*** Height** refers to the origin of the measurement from cupal, imbricational, or cervical enamel; **depth** refers to the location of the measurement near the EDJ, in the middle of the enamel, or near the exterior. **XS** gives the value of individual cross-striation measurements.

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.59
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.19
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.26
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.52
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.42
Alouatta	*sp.*	MNRJ 494	F	imb	mid	7.1
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.15
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.28
Alouatta	*sp.*	MNRJ 494	F	imb	mid	3.83
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.91
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.73
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.44
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.43
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.74
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.25
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.59
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.76
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.76
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.72
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.5
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.26
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.1
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.93
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.74
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.97
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.51
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.1

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.65
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.97
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.19
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.42
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.71
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.6
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.75
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.51
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.93
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.88
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.51
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.18
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.41
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.98
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.87
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.46
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.82
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.05
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.31
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.19
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.53
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.91
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.83
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.56
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.6
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.79
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.81
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.87
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.68
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.14
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.97
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.16
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.25
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.12
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.56
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.69
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.24

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.48
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.06
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.2
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.02
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.66
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.67
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.9
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.9
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.42
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.93
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.85
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.95
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.76
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.31
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.31
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.68
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.16
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.78
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.02
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.6
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.16
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.51
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.38
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.09
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.38
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.55
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.19
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.57
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.66
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.66
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.92
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.62
Alouatta	*sp.*	MNRJ 494	F	imb	mid	3.97
Alouatta	*sp.*	MNRJ 494	F	imb	mid	3.72
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.15
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.2
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.69

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.07
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.93
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.48
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.58
Alouatta	*sp.*	MNRJ 494	F	imb	mid	3.82
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.18
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.11
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.82
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.42
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.38
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.09
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.53
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.57
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.74
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.5
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6.15
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.4
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.99
Alouatta	*sp.*	MNRJ 494	F	imb	mid	6
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.82
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.9
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.66
Alouatta	*sp.*	MNRJ 494	F	imb	mid	5.51
Alouatta	*sp.*	MNRJ 494	F	imb	mid	4.9
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.77
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.73
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.23
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.23
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.84
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.23
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.82
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.48
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.62
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.14
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.58
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.76
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.66
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.84
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.51
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.24
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.88
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.75
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.31
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.46
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.56
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.7
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.45
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.93
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.2
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.52
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.52

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.89
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.84
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.15
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.82
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.81
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.89
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.42
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.19
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.33
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.14
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.93
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.26
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.1
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.19
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.93
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.87
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.87

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.05
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.72
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.76
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.68
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.34
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.01
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.76
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.27
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.74
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.97
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.78
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.43
Alouatta	*sp.*	MNRJ 484	F	imb	mid	3.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.68
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.92
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.63
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.05
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.15
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.6
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.27
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.69
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.42
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.56
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.05
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.01
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.98
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.5

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.68
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.87
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.68
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.65
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.31
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.24
Alouatta	*sp.*	MNRJ 484	F	imb	mid	7.06
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.69
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.92
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.19
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.56
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.59
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.51
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.24
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.98
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.26
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.99
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.16
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.31
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.07
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.57
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.48
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.49
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.27
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.43
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.49
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.99
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.31
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.77
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.73

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.23
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.23
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.84
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.23
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.82
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.48
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.62
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.14
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.58
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.76
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.66
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.84
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.51
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.24
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.88
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.75
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.31
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.46
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.56
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.61

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.7
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.45
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.93
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.2
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.52
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.52
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.89
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.84
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.15
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.82
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.81
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.89
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.42
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.19
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.33
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.14
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.93
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.26
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.1
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.19
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.93

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.87
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.91
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.87
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.05
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.72
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.76
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.68
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.88
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.44
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.5
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.56
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.48
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.2
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.88
Alouatta	*sp.*	MNRJ 484	F	imb	mid	3.9
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.14
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.16
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.82
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.26
Alouatta	*sp.*	MNRJ 484	F	imb	mid	7.19
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.25
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.82
Alouatta	*sp.*	MNRJ 484	F	imb	mid	3.89

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.99
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.74
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.51
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.49
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.68
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.51
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.35
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.49
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.82
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.79
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.95
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.95
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.26
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.46
Alouatta	*sp.*	MNRJ 484	F	imb	mid	4.43
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.75
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.01
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.1
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.43
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.66
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.75
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.52
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.29
Alouatta	*sp.*	MNRJ 484	F	imb	mid	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	mid	5.11
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.2
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.58
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.52

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.14
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.81
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.76
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.73
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.47
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.58
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.89
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.84
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.31
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.51
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.57
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.61
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.33
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.45
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.1
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.77
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.61
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.57
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.58
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.55
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.77
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.46
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.24
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.11
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.93

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.72
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.82
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.99
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.82
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.42
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.04
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.84
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.94
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.84
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.87
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.92
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.17
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.43
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.88
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.79
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.84
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.13
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.72
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.05
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.2
Alouatta	*sp.*	MNRJ 484	F	imb	edj	3.52
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.29
Alouatta	*sp.*	MNRJ 484	F	imb	edj	3.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.67
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.14
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.82
Alouatta	*sp.*	MNRJ 484	F	imb	edj	3.9
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.51
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.67
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	edj	3.12

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.02
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.73
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.6
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.36
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.65
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.16
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.88
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.28
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.31
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.97
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.46
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.74
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.58
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.4
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.65
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.16
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.53
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.76
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.22
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.46
Alouatta	*sp.*	MNRJ 484	F	imb	edj	7.3
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.85
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.32
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.6
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.26
Alouatta	*sp.*	MNRJ 484	F	imb	edj	7.3
Alouatta	*sp.*	MNRJ 484	F	imb	edj	7.36
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.43
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	edj	7.12

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.38
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.03
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.5
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.51
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.5
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.13
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.03
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.82
Alouatta	*sp.*	MNRJ 484	F	imb	edj	4.79
Alouatta	*sp.*	MNRJ 484	F	imb	edj	7.16
Alouatta	*sp.*	MNRJ 484	F	imb	edj	6.93
Alouatta	*sp.*	MNRJ 484	F	imb	edj	5.56
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.7
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.48
Alouatta	*sp.*	MNRJ 484	F	imb	ext	6.96
Alouatta	*sp.*	MNRJ 484	F	imb	ext	6.2
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.82
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.37
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.84
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.91
Alouatta	*sp.*	MNRJ 484	F	imb	ext	6.02
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.95
Alouatta	*sp.*	MNRJ 484	F	imb	ext	6.02
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.45
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.62
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.68
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.21
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.5
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.09
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.73
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.96
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.33

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.61
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.67
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.61
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.91
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.35
Alouatta	*sp.*	MNRJ 484	F	imb	ext	6.3
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.45
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	ext	6.43
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.57
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.16
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.1
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.35
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.18
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.73
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.01
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.3
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.97
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.91
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.87
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.93
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.65
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.99
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.86
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.64
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.92
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.04
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.41
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.78
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.86
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.46
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.46
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.57
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.86
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.6
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.48

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 484	F	imb	ext	5.38
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.04
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.74
Alouatta	*sp.*	MNRJ 484	F	imb	ext	3.78
Alouatta	*sp.*	MNRJ 484	F	imb	ext	4.16
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.35
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.69
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.91
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.08
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.54
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.35
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.06
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.73
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.54
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.86
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.48
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.35
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	3.78
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.11
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.7
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.86
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.67
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.24
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.51
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.03
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.61
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.3
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.38
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.73
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	8.06
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.19
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.76
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.75
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.82
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.08
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.48
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.15
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.55
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.17

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.03
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.5
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.15
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.82
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.44
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.98
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.66
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.55
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.3
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.73
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.17
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.32
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.71
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.2
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.79
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.13
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.76
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.44
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.46
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.82
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.92
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.26
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.55
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.82
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.91
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.41
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.09
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.5
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.87
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.41
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.5
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.94
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.08
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.47
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.4
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.71
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.41
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.3
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.56

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.92
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.31
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.41
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.03
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.67
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.03
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.77
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.83
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.41
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.76
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.51
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.51
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.75
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.67
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.99
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.9
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.45
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.22
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	8.04
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.67
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.24
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.29
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.52
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.91
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.82
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.82
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.26
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.26
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.09
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.61
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.64
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.99
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.79
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.02
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.56
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.5
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.35
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	7.25
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.73

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.11
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.87
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.73
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.02
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.52
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.93
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.5
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.36
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	3.78
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.54
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.11
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.54
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.31
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.16
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.54
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.48
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.93
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	3.6
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.08
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.44
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.38
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.24
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.93
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.26
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.51
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.86
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.49
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.45
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.48
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.86
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.06
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.86
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.3
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.3
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.67
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.48
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	3.79
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.1
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.54

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.12
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.86
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.73
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.35
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	3.97
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.74
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.1
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.73
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.38
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.27
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.14
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.27
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.54
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.02
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.46
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.3
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.19
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.41
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.52
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.35
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.88
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.98
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.94
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.98
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.13
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.29
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.17
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.51
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.25
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.93
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.56
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.76
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.56
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.32
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.26
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.16
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.86
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.6
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	4.85

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.59
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.09
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.19
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	6.18
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.84
Alouatta	*sp.*	MNRJ 2756	M	imb	mid	5.09
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	7.48
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.94
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	7.01
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.56
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.3
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.06
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.27
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.93
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	7.83
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.35
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.05
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.89
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.44
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.87
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.09
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.24
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.29
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.24
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.1
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.05
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.31
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	7.18
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.91
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.63
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.91
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.91
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.57
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.5
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.91
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.24
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.93
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.28
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.35

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.1
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.42
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.51
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.88
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.37
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.31
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.26
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.99
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.42
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.94
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.31
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.48
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.19
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.16
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.74
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.05
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.34
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.34
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.27
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.44
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.82
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.96
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.82
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.15
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.51
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.75
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.65
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.93
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.74
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.42
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.68
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	6.18
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.57
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.84
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.25
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.57
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	4.76
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	5.56
Alouatta	*sp.*	MNRJ 2756	M	imb	ext	8.03

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.45
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.32
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.5
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.19
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.14
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.85
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.36
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.91
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.69
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	6.53
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.27
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.96
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.85
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.64
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.04
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.82
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.96
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.16
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.8
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	3.72
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.93
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	7.3
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.94
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.41
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.73
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	6.64
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	7.9
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	5.45
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.61
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	4.99
Alouatta	*sp.*	MNRJ 2756	M	imb	edj	6.19
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.44
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.43
Cebus	*albifrons*	AMNH 62838	M	imb	mid	9.48
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.16
Cebus	*albifrons*	AMNH 62838	M	imb	mid	10.78
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.76
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.94
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.39

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.56
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.3
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.6
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.05
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.04
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.21
Cebus	*albifrons*	AMNH 62838	M	imb	mid	9.27
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.45
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.57
Cebus	*albifrons*	AMNH 62838	M	imb	mid	3.79
Cebus	*albifrons*	AMNH 62838	M	imb	mid	4.36
Cebus	*albifrons*	AMNH 62838	M	imb	mid	9.85
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.24
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.96
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.39
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.37
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.76
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.38
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.58
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.77
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.58
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.13
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.56
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.94
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.56
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.88
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.6
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.62
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.65
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.35
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.81
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.62
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.62
Cebus	*albifrons*	AMNH 62838	M	imb	mid	4.73
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.15
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.6
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.56
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.15
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.15

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*albifrons*	AMNH 62838	M	imb	mid	8.89
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.43
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.43
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.82
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.75
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.1
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.86
Cebus	*albifrons*	AMNH 62838	M	imb	mid	7.37
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.43
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.05
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.45
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.99
Cebus	*albifrons*	AMNH 62838	M	imb	mid	6.24
Cebus	*albifrons*	AMNH 78504	F	imb	mid	3.7997
Cebus	*albifrons*	AMNH 78504	F	imb	mid	5.491902
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.50246
Cebus	*albifrons*	AMNH 78504	F	imb	mid	3.889722
Cebus	*albifrons*	AMNH 78504	F	imb	mid	3.283115
Cebus	*albifrons*	AMNH 78504	F	imb	mid	3.473384
Cebus	*albifrons*	AMNH 78504	F	imb	mid	5.966562
Cebus	*albifrons*	AMNH 78504	F	imb	mid	5.966562
Cebus	*albifrons*	AMNH 78504	F	imb	mid	5.428514
Cebus	*albifrons*	AMNH 78504	F	imb	mid	6.56623
Cebus	*albifrons*	AMNH 78504	F	imb	mid	3.283115
Cebus	*albifrons*	AMNH 78504	F	imb	mid	6.56623
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.789794
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.789794
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.379996
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.50246
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.727452
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.413733
Cebus	*albifrons*	AMNH 78504	F	imb	mid	3.51583
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.08805
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.758725
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.413733
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.727452
Cebus	*albifrons*	AMNH 78504	F	imb	mid	5.660378
Cebus	*albifrons*	AMNH 78504	F	imb	mid	3.51583
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.727452

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.195492
Cebus	*albifrons*	AMNH 78504	F	imb	mid	5.738455
Cebus	*albifrons*	AMNH 78504	F	imb	mid	5.119126
Cebus	*albifrons*	AMNH 78504	F	imb	mid	6.633655
Cebus	*albifrons*	AMNH 78504	F	imb	mid	4.674864
Cebus	*albifrons*	AMNH 78504	F	imb	mid	6.868028
Cebus	*albifrons*	AMNH 78504	F	imb	mid	6.868028
Cebus	*albifrons*	AMNH 78504	F	imb	mid	7.651274
Cebus	*apella*	AMNH 133091	M	imb	mid	7.880481
Cebus	*apella*	AMNH 133091	M	imb	mid	7.605904
Cebus	*apella*	AMNH 133091	M	imb	mid	6.202228
Cebus	*apella*	AMNH 133091	M	imb	mid	6.543602
Cebus	*apella*	AMNH 133091	M	imb	mid	7.50117
Cebus	*apella*	AMNH 133091	M	imb	mid	8.302125
Cebus	*apella*	AMNH 133091	M	imb	mid	8.737387
Cebus	*apella*	AMNH 133091	M	imb	mid	3.585457
Cebus	*apella*	AMNH 133091	M	imb	mid	6.105814
Cebus	*apella*	AMNH 133091	M	imb	mid	5.772818
Cebus	*apella*	AMNH 133091	M	imb	mid	5.598897
Cebus	*apella*	AMNH 133091	M	imb	mid	7.42165
Cebus	*apella*	AMNH 133091	M	imb	mid	4.972135
Cebus	*apella*	AMNH 133091	M	imb	mid	5.157616
Cebus	*apella*	AMNH 133091	M	imb	mid	3.401464
Cebus	*apella*	AMNH 133091	M	imb	mid	3.342813
Cebus	*apella*	AMNH 133091	M	imb	mid	4.912107
Cebus	*apella*	AMNH 133091	M	imb	mid	6.367439
Cebus	*apella*	AMNH 133091	M	imb	mid	7.239537
Cebus	*apella*	AMNH 133091	M	imb	mid	5.271401
Cebus	*apella*	AMNH 133091	M	imb	mid	4.922162
Cebus	*apella*	AMNH 133091	M	imb	mid	5.271401
Cebus	*apella*	AMNH 133091	M	imb	mid	4.922162
Cebus	*apella*	AMNH 133091	M	imb	mid	5.572341
Cebus	*apella*	AMNH 133091	M	imb	mid	7.766723
Cebus	*apella*	AMNH 133091	M	imb	mid	4.643026
Cebus	*apella*	AMNH 133091	M	imb	mid	7.454886
Cebus	*apella*	AMNH 133091	M	imb	mid	5.772818
Cebus	*apella*	AMNH 133091	M	imb	mid	6.367439
Cebus	*apella*	AMNH 133091	M	imb	mid	6.289308
Cebus	*apella*	AMNH 133091	M	imb	mid	7.184691

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	AMNH 133091	M	imb	mid	7.066731
Cebus	*apella*	AMNH 133091	M	imb	mid	4.368693
Cebus	*apella*	AMNH 133091	M	imb	mid	7.177806
Cebus	*apella*	AMNH 133091	M	imb	mid	5.373587
Cebus	*apella*	AMNH 133091	M	imb	mid	6.960989
Cebus	*apella*	AMNH 133091	M	imb	mid	5.798456
Cebus	*apella*	AMNH 133091	M	imb	mid	6.19425
Cebus	*apella*	AMNH 133091	M	imb	mid	5.373587
Cebus	*apella*	AMNH 133091	M	imb	mid	5.119126
Cebus	*apella*	AMNH 133091	M	imb	mid	6.788375
Cebus	*apella*	AMNH 133091	M	imb	mid	5.205329
Cebus	*apella*	AMNH 133091	M	imb	mid	5.933321
Cebus	*apella*	AMNH 133091	M	imb	mid	5.205329
Cebus	*apella*	AMNH 133091	M	imb	mid	7.886753
Cebus	*apella*	AMNH 133091	M	imb	mid	8.060381
Cebus	*apella*	AMNH 133091	M	imb	mid	4.50246
Cebus	*apella*	AMNH 133091	M	imb	mid	5.205329
Cebus	*apella*	AMNH 133091	M	imb	mid	5.070602
Cebus	*apella*	AMNH 133091	M	imb	mid	3.283115
Cebus	*apella*	AMNH 133091	M	imb	mid	6.328494
Cebus	*apella*	AMNH 133091	M	imb	mid	4.277192
Cebus	*apella*	AMNH 133091	M	imb	mid	5.669106
Cebus	*apella*	AMNH 133091	M	imb	mid	2.966661
Cebus	*apella*	AMNH 133091	M	imb	mid	3.94024
Cebus	*apella*	AMNH 133091	M	imb	mid	5.080344
Cebus	*apella*	AMNH 133091	M	imb	mid	5.233747
Cebus	*apella*	AMNH 133091	M	imb	mid	4.674864
Cebus	*apella*	AMNH 133091	M	imb	mid	6.265679
Cebus	*apella*	AMNH 133091	M	imb	mid	6.367439
Cebus	*apella*	AMNH 133091	M	imb	mid	3.680723
Cebus	*apella*	AMNH 133091	M	imb	mid	5.345912
Cebus	*apella*	AMNH 133091	M	imb	mid	3.160338
Cebus	*apella*	AMNH 133091	M	imb	mid	4.716981
Cebus	*apella*	AMNH 133091	M	imb	mid	3.773585
Cebus	*apella*	AMNH 133091	M	imb	mid	4.716981
Cebus	*apella*	AMNH 133091	M	imb	mid	4.758725
Cebus	*apella*	AMNH 133091	M	imb	mid	5.345912
Cebus	*apella*	AMNH 133091	M	imb	mid	4.922162
Cebus	*apella*	AMNH 133091	M	imb	mid	5.491902

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	AMNH 133091	M	imb	mid	6.073336
Cebus	*apella*	AMNH 133091	M	imb	mid	6.048863
Cebus	*apella*	AMNH 133091	M	imb	mid	5.205329
Cebus	*apella*	AMNH 133091	M	imb	mid	7.50117
Cebus	*apella*	AMNH 133091	M	imb	mid	5.491902
Cebus	*apella*	NYU	F	imb	mid	5.23
Cebus	*apella*	NYU	F	imb	mid	5.72
Cebus	*apella*	NYU	F	imb	mid	4.93
Cebus	*apella*	NYU	F	imb	mid	3.97
Cebus	*apella*	NYU	F	imb	mid	7.37
Cebus	*apella*	NYU	F	imb	mid	6.05
Cebus	*apella*	NYU	F	imb	mid	5.04
Cebus	*apella*	NYU	F	imb	mid	6.45
Cebus	*apella*	NYU	F	imb	mid	5.75
Cebus	*apella*	NYU	F	imb	mid	4.57
Cebus	*apella*	NYU	F	imb	mid	6.52
Cebus	*apella*	NYU	F	imb	mid	5.1
Cebus	*apella*	NYU	F	imb	mid	4.35
Cebus	*apella*	NYU	F	imb	mid	5.41
Cebus	*apella*	NYU	F	imb	mid	4.36
Cebus	*apella*	NYU	F	imb	mid	4.85
Cebus	*apella*	NYU	F	imb	mid	5.27
Cebus	*apella*	NYU	F	imb	mid	5.82
Cebus	*apella*	NYU	F	imb	mid	5.07
Cebus	*apella*	NYU	F	imb	mid	4.96
Cebus	*apella*	NYU	F	imb	mid	5.1
Cebus	*apella*	NYU	F	imb	mid	5.48
Cebus	*apella*	NYU	F	imb	mid	5.38
Cebus	*apella*	NYU	F	imb	mid	6.28
Cebus	*apella*	NYU	F	imb	mid	4.91
Cebus	*apella*	NYU	F	imb	mid	5.31
Cebus	*apella*	NYU	F	imb	mid	5.92
Cebus	*apella*	NYU	F	imb	mid	5.6
Cebus	*apella*	NYU	F	imb	mid	5.35
Cebus	*apella*	NYU	F	imb	mid	6.71
Cebus	*apella*	NYU	F	imb	mid	4.74
Cebus	*apella*	NYU	F	imb	mid	5.02
Cebus	*apella*	NYU	F	imb	mid	5.2
Cebus	*apella*	NYU	F	imb	mid	4.91

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	NYU	F	imb	mid	6.01
Cebus	*apella*	NYU	F	imb	mid	5.09
Cebus	*apella*	NYU	F	imb	mid	5.62
Cebus	*apella*	NYU	F	imb	mid	4.49
Cebus	*apella*	NYU	F	imb	mid	5.09
Cebus	*apella*	NYU	F	imb	mid	4.97
Cebus	*apella*	NYU	F	imb	mid	6.24
Cebus	*apella*	NYU	F	imb	mid	6.24
Cebus	*apella*	NYU	F	imb	mid	4.93
Cebus	*apella*	NYU	F	imb	mid	5.34
Cebus	*apella*	NYU	F	imb	mid	5.69
Cebus	*apella*	NYU	F	imb	mid	4.99
Cebus	*apella*	NYU	F	imb	mid	5.93
Cebus	*apella*	NYU	F	imb	mid	4.83
Cebus	*apella*	NYU	F	imb	mid	5.1
Cebus	*apella*	NYU	F	imb	mid	4.91
Cebus	*apella*	NYU	F	imb	mid	5.3
Cebus	*apella*	NYU	F	imb	mid	5.09
Cebus	*apella*	NYU	F	imb	mid	5.09
Cebus	*apella*	NYU	F	imb	mid	4.85
Cebus	*apella*	NYU	F	imb	mid	6.93
Cebus	*apella*	NYU	F	imb	mid	5.7
Cebus	*apella*	NYU	F	imb	mid	6.1
Cebus	*apella*	NYU	F	imb	mid	4.54
Cebus	*apella*	NYU	F	imb	mid	5.7
Cebus	*apella*	NYU	F	imb	mid	4.79
Cebus	*apella*	NYU	F	imb	mid	4.01
Cebus	*apella*	NYU	F	imb	mid	4.91
Cebus	*apella*	NYU	F	imb	mid	5.59
Cebus	*apella*	NYU	F	imb	mid	6.88
Cebus	*apella*	NYU	F	imb	mid	4.57
Cebus	*apella*	NYU	F	imb	mid	5.59
Cebus	*apella*	NYU	F	imb	mid	4.35
Cebus	*apella*	NYU	F	imb	mid	4.57
Cebus	*apella*	NYU	F	imb	mid	5.46
Cebus	*apella*	NYU	F	imb	mid	4.96
Cebus	*apella*	NYU	F	imb	mid	5.27
Cebus	*apella*	NYU	F	imb	mid	6.18
Cebus	*apella*	NYU	F	imb	mid	6.18

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	NYU	F	imb	mid	4.9
Cebus	*apella*	NYU	F	imb	mid	5.98
Cebus	*apella*	NYU	F	imb	mid	5.09
Cebus	*apella*	NYU	F	imb	mid	6.52
Cebus	*apella*	NYU	F	imb	mid	4.95
Cebus	*apella*	NYU	F	imb	mid	5.62
Cebus	*apella*	NYU	F	imb	mid	6.34
Cebus	*apella*	NYU	F	imb	mid	7.03
Cebus	*apella*	NYU	F	imb	mid	5.33
Cebus	*apella*	NYU	F	imb	mid	6.01
Cebus	*apella*	NYU	F	imb	mid	5.59
Cebus	*apella*	NYU	F	imb	mid	5.27
Cebus	*apella*	NYU	F	imb	mid	4.99
Cebus	*apella*	NYU	F	imb	mid	6.17
Cebus	*apella*	NYU	F	imb	mid	7.48
Cebus	*apella*	NYU	F	imb	mid	5.75
Cebus	*apella*	NYU	F	imb	mid	5.76
Cebus	*apella*	NYU	F	imb	mid	5.58
Cebus	*apella*	NYU	F	imb	mid	6.53
Cebus	*apella*	NYU	F	imb	mid	4.77
Cebus	*apella*	NYU	F	imb	mid	7.04
Cebus	*apella*	NYU	F	imb	mid	5.84
Cebus	*apella*	NYU	F	imb	mid	5.42
Cebus	*apella*	NYU	F	imb	mid	7.03
Cebus	*apella*	NYU	F	imb	mid	6.32
Cebus	*apella*	NYU	F	imb	mid	5.11
Cebus	*apella*	NYU	F	imb	mid	6.55
Cebus	*apella*	NYU	F	imb	mid	5.56
Cebus	*apella*	NYU	F	imb	mid	6.66
Cebus	*apella*	NYU	F	imb	mid	6.7
Cebus	*apella*	NYU	F	imb	mid	5.14
Cebus	*apella*	NYU	F	imb	mid	6.61
Cebus	*apella*	NYU	F	imb	mid	5.59
Cebus	*apella*	NYU	F	imb	mid	5.75
Cebus	*apella*	NYU	F	imb	mid	5.93
Cebus	*apella*	NYU	F	imb	mid	5.59
Cebus	*apella*	NYU	F	imb	mid	6.04
Cebus	*apella*	NYU	F	imb	mid	5.62
Cebus	*apella*	NYU	F	imb	mid	6.13

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	NYU	F	imb	mid	5.82
Cebus	*apella*	NYU	F	imb	mid	6.05
Cebus	*apella*	NYU	F	imb	mid	4.65
Cebus	*apella*	NYU	F	imb	mid	7.5
Cebus	*apella*	NYU	F	imb	mid	4.91
Cebus	*apella*	NYU	F	imb	mid	5.07
Cebus	*apella*	NYU	F	imb	mid	5.52
Cebus	*apella*	NYU	F	imb	mid	5.25
Cebus	*apella*	NYU	F	imb	mid	4.23
Cebus	*apella*	NYU	F	imb	mid	6.19
Cebus	*apella*	NYU	F	imb	mid	5.69
Cebus	*apella*	NYU	F	imb	mid	6.18
Cebus	*apella*	NYU	F	imb	mid	5.88
Cebus	*apella*	NYU	F	imb	mid	6.28
Cebus	*apella*	NYU	F	imb	mid	4.74
Cebus	*apella*	NYU	F	imb	mid	6.35
Cebus	*apella*	NYU	F	imb	mid	5.41
Cebus	*apella*	NYU	F	imb	mid	6.58
Cebus	*apella*	NYU	F	imb	mid	6.44
Cebus	*apella*	NYU	F	imb	mid	5.35
Cebus	*apella*	NYU	F	imb	mid	5.98
Cebus	*apella*	NYU	F	imb	mid	5.48
Cebus	*apella*	NYU	F	imb	mid	6.96
Cebus	*apella*	NYU	F	imb	mid	6.02
Cebus	*apella*	NYU	F	imb	mid	6.19
Cebus	*apella*	NYU	F	imb	mid	5.42
Cebus	*apella*	NYU	F	imb	mid	5.72
Cebus	*apella*	NYU	F	imb	mid	6.02
Cebus	*apella*	NYU	F	imb	mid	6.68
Cebus	*apella*	NYU	F	imb	mid	6.28
Cebus	*apella*	NYU	F	imb	mid	7.71
Cebus	*apella*	NYU	F	imb	mid	7.02
Cebus	*apella*	NYU	F	imb	mid	6.82
Cebus	*apella*	NYU	F	imb	mid	5.5
Cebus	*apella*	NYU	F	imb	mid	5.41
Cebus	*apella*	NYU	F	imb	mid	6.61
Cebus	*apella*	NYU	F	imb	mid	6.28
Cebus	*apella*	NYU	F	imb	mid	4.82
Cebus	*apella*	NYU	F	imb	mid	5.89

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 447	M	imb	mid	5.21
Cebus	*apella*	MNRJ 447	M	imb	mid	5.26
Cebus	*apella*	MNRJ 447	M	imb	mid	6.68
Cebus	*apella*	MNRJ 447	M	imb	mid	5.93
Cebus	*apella*	MNRJ 447	M	imb	mid	5.26
Cebus	*apella*	MNRJ 447	M	imb	mid	5.5
Cebus	*apella*	MNRJ 447	M	imb	mid	5.91
Cebus	*apella*	MNRJ 447	M	imb	mid	6.02
Cebus	*apella*	MNRJ 447	M	imb	mid	5.48
Cebus	*apella*	MNRJ 447	M	imb	mid	5.08
Cebus	*apella*	MNRJ 447	M	imb	mid	4.73
Cebus	*apella*	MNRJ 447	M	imb	mid	7.45
Cebus	*apella*	MNRJ 447	M	imb	mid	5.23
Cebus	*apella*	MNRJ 447	M	imb	mid	5.48
Cebus	*apella*	MNRJ 447	M	imb	mid	4.54
Cebus	*apella*	MNRJ 447	M	imb	mid	4.95
Cebus	*apella*	MNRJ 447	M	imb	mid	5.5
Cebus	*apella*	MNRJ 447	M	imb	mid	6.82
Cebus	*apella*	MNRJ 447	M	imb	mid	6.56
Cebus	*apella*	MNRJ 447	M	imb	mid	6.55
Cebus	*apella*	MNRJ 447	M	imb	mid	7.12
Cebus	*apella*	MNRJ 447	M	imb	mid	7.65
Cebus	*apella*	MNRJ 447	M	imb	mid	5.62
Cebus	*apella*	MNRJ 447	M	imb	mid	6.32
Cebus	*apella*	MNRJ 447	M	imb	mid	7.09
Cebus	*apella*	MNRJ 447	M	imb	mid	6.03
Cebus	*apella*	MNRJ 447	M	imb	mid	4.05
Cebus	*apella*	MNRJ 447	M	imb	mid	5.89
Cebus	*apella*	MNRJ 447	M	imb	mid	4.43
Cebus	*apella*	MNRJ 447	M	imb	mid	6.09
Cebus	*apella*	MNRJ 447	M	imb	mid	6.05
Cebus	*apella*	MNRJ 447	M	imb	mid	4.88
Cebus	*apella*	MNRJ 447	M	imb	mid	7
Cebus	*apella*	MNRJ 447	M	imb	mid	5.35
Cebus	*apella*	MNRJ 447	M	imb	mid	4.41
Cebus	*apella*	MNRJ 447	M	imb	mid	5.09
Cebus	*apella*	MNRJ 447	M	imb	mid	6.15
Cebus	*apella*	MNRJ 447	M	imb	mid	4.73
Cebus	*apella*	MNRJ 447	M	imb	mid	4.54

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 447	M	imb	mid	4.99
Cebus	*apella*	MNRJ 447	M	imb	mid	5.19
Cebus	*apella*	MNRJ 447	M	imb	mid	5.41
Cebus	*apella*	MNRJ 447	M	imb	mid	5.23
Cebus	*apella*	MNRJ 447	M	imb	mid	6.47
Cebus	*apella*	MNRJ 447	M	imb	mid	5.67
Cebus	*apella*	MNRJ 447	M	imb	mid	5.03
Cebus	*apella*	MNRJ 447	M	imb	mid	5.26
Cebus	*apella*	MNRJ 447	M	imb	mid	4.61
Cebus	*apella*	MNRJ 447	M	imb	mid	4.41
Cebus	*apella*	MNRJ 447	M	imb	mid	5.09
Cebus	*apella*	MNRJ 447	M	imb	mid	4.93
Cebus	*apella*	MNRJ 447	M	imb	mid	5.16
Cebus	*apella*	MNRJ 447	M	imb	mid	4.99
Cebus	*apella*	MNRJ 447	M	imb	mid	5.67
Cebus	*apella*	MNRJ 447	M	imb	mid	5.56
Cebus	*apella*	MNRJ 447	M	imb	mid	2.96
Cebus	*apella*	MNRJ 447	M	imb	mid	5.42
Cebus	*apella*	MNRJ 447	M	imb	mid	4.15
Cebus	*apella*	MNRJ 447	M	imb	mid	4.35
Cebus	*apella*	MNRJ 447	M	imb	mid	5.61
Cebus	*apella*	MNRJ 447	M	imb	mid	5.26
Cebus	*apella*	MNRJ 447	M	imb	mid	4.61
Cebus	*apella*	MNRJ 447	M	imb	mid	5.3
Cebus	*apella*	MNRJ 447	M	imb	mid	4.09
Cebus	*apella*	MNRJ 447	M	imb	mid	6.03
Cebus	*apella*	MNRJ 447	M	imb	mid	5.37
Cebus	*apella*	MNRJ 447	M	imb	mid	7.2
Cebus	*apella*	MNRJ 447	M	imb	mid	5.76
Cebus	*apella*	MNRJ 447	M	imb	mid	7.41
Cebus	*apella*	MNRJ 447	M	imb	mid	6.02
Cebus	*apella*	MNRJ 447	M	imb	mid	6.15
Cebus	*apella*	MNRJ 447	M	imb	mid	6.69
Cebus	*apella*	MNRJ 447	M	imb	mid	5.82
Cebus	*apella*	MNRJ 447	M	imb	mid	6.42
Cebus	*apella*	MNRJ 447	M	imb	mid	6.29
Cebus	*apella*	MNRJ 447	M	imb	mid	5.79
Cebus	*apella*	MNRJ 447	M	imb	mid	6.61
Cebus	*apella*	MNRJ 447	M	imb	mid	5.33

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 447	M	imb	mid	5.92
Cebus	*apella*	MNRJ 447	M	imb	mid	6.26
Cebus	*apella*	MNRJ 447	M	imb	mid	5.27
Cebus	*apella*	MNRJ 447	M	imb	mid	7.12
Cebus	*apella*	MNRJ 447	M	imb	mid	5.5
Cebus	*apella*	MNRJ 447	M	imb	mid	4.78
Cebus	*apella*	MNRJ 447	M	imb	mid	6.06
Cebus	*apella*	MNRJ 447	M	imb	mid	6.88
Cebus	*apella*	MNRJ 447	M	imb	mid	5.27
Cebus	*apella*	MNRJ 447	M	imb	mid	4.73
Cebus	*apella*	MNRJ 447	M	imb	mid	5.27
Cebus	*apella*	MNRJ 447	M	imb	mid	5.62
Cebus	*apella*	MNRJ 447	M	imb	mid	6.28
Cebus	*apella*	MNRJ 447	M	imb	mid	6.6
Cebus	*apella*	MNRJ 447	M	imb	mid	4.13
Cebus	*apella*	MNRJ 447	M	imb	mid	5.67
Cebus	*apella*	MNRJ 447	M	imb	mid	6.12
Cebus	*apella*	MNRJ 447	M	imb	mid	5.14
Cebus	*apella*	MNRJ 447	M	imb	mid	5.48
Cebus	*apella*	MNRJ 447	M	imb	mid	5.53
Cebus	*apella*	MNRJ 447	M	imb	mid	5.38
Cebus	*apella*	MNRJ 447	M	imb	mid	6.56
Cebus	*apella*	MNRJ 447	M	imb	mid	7.06
Cebus	*apella*	MNRJ 447	M	imb	mid	6.15
Cebus	*apella*	MNRJ 447	M	imb	mid	7.34
Cebus	*apella*	MNRJ 447	M	imb	mid	6.44
Cebus	*apella*	MNRJ 447	M	imb	mid	6.34
Cebus	*apella*	MNRJ 447	M	imb	mid	6.01
Cebus	*apella*	MNRJ 447	M	imb	mid	6.46
Cebus	*apella*	MNRJ 447	M	imb	mid	5.86
Cebus	*apella*	MNRJ 447	M	imb	mid	5.33
Cebus	*apella*	MNRJ 447	M	imb	mid	5.23
Cebus	*apella*	MNRJ 447	M	imb	mid	7.6
Cebus	*apella*	MNRJ 447	M	imb	mid	7.12
Cebus	*apella*	MNRJ 447	M	imb	mid	6.24
Cebus	*apella*	MNRJ 447	M	imb	mid	4.93
Cebus	*apella*	MNRJ 447	M	imb	mid	5.98
Cebus	*apella*	MNRJ 447	M	imb	mid	5.27
Cebus	*apella*	MNRJ 447	M	imb	mid	5.34

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 447	M	imb	mid	5.27
Cebus	*apella*	MNRJ 447	M	imb	mid	5.56
Cebus	*apella*	MNRJ 447	M	imb	mid	6.51
Cebus	*apella*	MNRJ 447	M	imb	mid	7.24
Cebus	*apella*	MNRJ 447	M	imb	mid	7.7
Cebus	*apella*	MNRJ 445	M	imb	mid	6.1
Cebus	*apella*	MNRJ 445	M	imb	mid	4.95
Cebus	*apella*	MNRJ 445	M	imb	mid	6.83
Cebus	*apella*	MNRJ 445	M	imb	mid	7.16
Cebus	*apella*	MNRJ 445	M	imb	mid	5.27
Cebus	*apella*	MNRJ 445	M	imb	mid	5.27
Cebus	*apella*	MNRJ 445	M	imb	mid	6.26
Cebus	*apella*	MNRJ 445	M	imb	mid	4.16
Cebus	*apella*	MNRJ 445	M	imb	mid	5.67
Cebus	*apella*	MNRJ 445	M	imb	mid	6.04
Cebus	*apella*	MNRJ 445	M	imb	mid	5.14
Cebus	*apella*	MNRJ 445	M	imb	mid	6.71
Cebus	*apella*	MNRJ 445	M	imb	mid	6.7
Cebus	*apella*	MNRJ 445	M	imb	mid	7.43
Cebus	*apella*	MNRJ 445	M	imb	mid	6.53
Cebus	*apella*	MNRJ 445	M	imb	mid	6.82
Cebus	*apella*	MNRJ 445	M	imb	mid	7.71
Cebus	*apella*	MNRJ 445	M	imb	mid	5.75
Cebus	*apella*	MNRJ 445	M	imb	mid	6.24
Cebus	*apella*	MNRJ 445	M	imb	mid	8.88
Cebus	*apella*	MNRJ 445	M	imb	mid	9.27
Cebus	*apella*	MNRJ 445	M	imb	mid	5.1
Cebus	*apella*	MNRJ 445	M	imb	mid	8.21
Cebus	*apella*	MNRJ 445	M	imb	mid	6.28
Cebus	*apella*	MNRJ 445	M	imb	mid	6.26
Cebus	*apella*	MNRJ 445	M	imb	mid	6.99
Cebus	*apella*	MNRJ 445	M	imb	mid	5.89
Cebus	*apella*	MNRJ 445	M	imb	mid	5.67
Cebus	*apella*	MNRJ 445	M	imb	mid	7.18
Cebus	*apella*	MNRJ 445	M	imb	mid	4.86
Cebus	*apella*	MNRJ 445	M	imb	mid	5.32
Cebus	*apella*	MNRJ 445	M	imb	mid	5.23
Cebus	*apella*	MNRJ 445	M	imb	mid	5.14
Cebus	*apella*	MNRJ 445	M	imb	mid	4.99

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 445	M	imb	mid	6.99
Cebus	*apella*	MNRJ 445	M	imb	mid	6.76
Cebus	*apella*	MNRJ 445	M	imb	mid	5.41
Cebus	*apella*	MNRJ 445	M	imb	mid	6.24
Cebus	*apella*	MNRJ 445	M	imb	mid	7.06
Cebus	*apella*	MNRJ 445	M	imb	mid	5.29
Cebus	*apella*	MNRJ 445	M	imb	mid	6.64
Cebus	*apella*	MNRJ 445	M	imb	mid	4.92
Cebus	*apella*	MNRJ 445	M	imb	mid	6.47
Cebus	*apella*	MNRJ 445	M	imb	mid	5.91
Cebus	*apella*	MNRJ 445	M	imb	mid	4.54
Cebus	*apella*	MNRJ 445	M	imb	mid	5.7
Cebus	*apella*	MNRJ 445	M	imb	mid	6.53
Cebus	*apella*	MNRJ 445	M	imb	mid	6.34
Cebus	*apella*	MNRJ 445	M	imb	mid	5.12
Cebus	*apella*	MNRJ 445	M	imb	mid	5.8
Cebus	*apella*	MNRJ 445	M	imb	mid	6.47
Cebus	*apella*	MNRJ 445	M	imb	mid	6.28
Cebus	*apella*	MNRJ 445	M	imb	mid	5.69
Cebus	*apella*	MNRJ 445	M	imb	mid	7.13
Cebus	*apella*	MNRJ 445	M	imb	mid	6.42
Cebus	*apella*	MNRJ 445	M	imb	mid	4.91
Cebus	*apella*	MNRJ 445	M	imb	mid	5.62
Cebus	*apella*	MNRJ 445	M	imb	mid	6.01
Cebus	*apella*	MNRJ 445	M	imb	mid	5.41
Cebus	*apella*	MNRJ 445	M	imb	mid	5.23
Cebus	*apella*	MNRJ 445	M	imb	mid	5.35
Cebus	*apella*	MNRJ 445	M	imb	mid	6.64
Cebus	*apella*	MNRJ 445	M	imb	mid	4.95
Cebus	*apella*	MNRJ 445	M	imb	mid	5.97
Cebus	*apella*	MNRJ 445	M	imb	mid	6.69
Cebus	*apella*	MNRJ 445	M	imb	mid	6.95
Cebus	*apella*	MNRJ 445	M	imb	mid	4.61
Cebus	*apella*	MNRJ 445	M	imb	mid	5.62
Cebus	*apella*	MNRJ 445	M	imb	mid	6.95
Cebus	*apella*	MNRJ 445	M	imb	mid	5.37
Cebus	*apella*	MNRJ 445	M	imb	mid	6.15
Cebus	*apella*	MNRJ 445	M	imb	mid	5.98
Cebus	*apella*	MNRJ 445	M	imb	mid	6.69

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 445	M	imb	mid	5.11
Cebus	*apella*	MNRJ 445	M	imb	mid	7.78
Cebus	*apella*	MNRJ 445	M	imb	mid	5.56
Cebus	*apella*	MNRJ 445	M	imb	mid	6.44
Cebus	*apella*	MNRJ 445	M	imb	mid	5.45
Cebus	*apella*	MNRJ 445	M	imb	mid	5.52
Cebus	*apella*	MNRJ 445	M	imb	mid	4.68
Cebus	*apella*	MNRJ 445	M	imb	mid	5.11
Cebus	*apella*	MNRJ 445	M	imb	mid	5.41
Cebus	*apella*	MNRJ 445	M	imb	mid	6.35
Cebus	*apella*	MNRJ 445	M	imb	mid	6.62
Cebus	*apella*	MNRJ 445	M	imb	mid	5.94
Cebus	*apella*	MNRJ 445	M	imb	mid	6.44
Cebus	*apella*	MNRJ 445	M	imb	mid	4.2
Cebus	*apella*	MNRJ 445	M	imb	mid	4.35
Cebus	*apella*	MNRJ 445	M	imb	mid	5.56
Cebus	*apella*	MNRJ 445	M	imb	mid	6.15
Cebus	*apella*	MNRJ 445	M	imb	mid	5.48
Cebus	*apella*	MNRJ 445	M	imb	mid	4.95
Cebus	*apella*	MNRJ 445	M	imb	mid	5.84
Cebus	*apella*	MNRJ 445	M	imb	mid	8.75
Cebus	*apella*	MNRJ 445	M	imb	mid	5.31
Cebus	*apella*	MNRJ 445	M	imb	mid	6.7
Cebus	*apella*	MNRJ 445	M	imb	mid	4.95
Cebus	*apella*	MNRJ 445	M	imb	mid	8.3
Cebus	*apella*	MNRJ 445	M	imb	mid	5.97
Cebus	*apella*	MNRJ 445	M	imb	mid	5.38
Cebus	*apella*	MNRJ 445	M	imb	mid	5.19
Cebus	*apella*	MNRJ 445	M	imb	mid	7.06
Cebus	*apella*	MNRJ 445	M	imb	mid	7.06
Cebus	*apella*	MNRJ 445	M	imb	mid	6.38
Cebus	*apella*	MNRJ 445	M	imb	mid	6.28
Cebus	*apella*	MNRJ 445	M	imb	mid	5.27
Cebus	*apella*	MNRJ 445	M	imb	mid	5.64
Cebus	*apella*	MNRJ 445	M	imb	mid	4.2
Cebus	*apella*	MNRJ 445	M	imb	mid	5.82
Cebus	*apella*	MNRJ 445	M	imb	mid	4.49
Cebus	*apella*	MNRJ 445	M	imb	mid	6.52
Cebus	*apella*	MNRJ 445	M	imb	mid	6.9

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 445	M	imb	mid	4.91
Cebus	*apella*	MNRJ 445	M	imb	mid	5.1
Cebus	*apella*	MNRJ 445	M	imb	mid	4.91
Cebus	*apella*	MNRJ 445	M	imb	mid	5.41
Cebus	*apella*	MNRJ 445	M	imb	mid	5.86
Cebus	*apella*	MNRJ 445	M	imb	mid	6.28
Cebus	*apella*	MNRJ 445	M	imb	mid	7.38
Cebus	*apella*	MNRJ 445	M	imb	mid	5.7
Cebus	*apella*	MNRJ 445	M	imb	mid	4.91
Cebus	*apella*	MNRJ 445	M	imb	mid	5.89
Cebus	*apella*	MNRJ 445	M	imb	mid	5.09
Cebus	*apella*	MNRJ 445	M	imb	mid	5.41
Cebus	*apella*	MNRJ 445	M	imb	mid	5.14
Cebus	*apella*	MNRJ 445	M	imb	mid	5.74
Cebus	*apella*	MNRJ 445	M	imb	mid	6.09
Cebus	*apella*	MNRJ 445	M	imb	mid	6.83
Cebus	*apella*	MNRJ 445	M	imb	mid	5.91
Cebus	*apella*	MNRJ 445	M	imb	mid	5.68
Cebus	*apella*	MNRJ 445	M	imb	mid	7.06
Cebus	*apella*	MNRJ 445	M	imb	mid	3.82
Cebus	*apella*	MNRJ 445	M	imb	mid	5.04
Cebus	*apella*	MNRJ 445	M	imb	mid	6.42
Cebus	*apella*	MNRJ 445	M	imb	mid	3.97
Cebus	*apella*	MNRJ 445	M	imb	mid	5.38
Cebus	*apella*	MNRJ 445	M	imb	mid	5.04
Cebus	*apella*	MNRJ 445	M	imb	mid	5.98
Cebus	*apella*	MNRJ 445	M	imb	mid	5.8
Cebus	*apella*	MNRJ 445	M	imb	mid	3.95
Cebus	*apella*	MNRJ 445	M	imb	mid	5.32
Cebus	*apella*	MNRJ 445	M	imb	mid	6.38
Cebus	*apella*	MNRJ 445	M	imb	mid	4.13
Cebus	*apella*	MNRJ 445	M	imb	mid	5.14
Cebus	*apella*	MNRJ 445	M	imb	mid	6.47
Cebus	*apella*	MNRJ 445	M	imb	mid	5.92
Cebus	*apella*	MNRJ 445	M	imb	mid	4.67
Cebus	*apella*	MNRJ 445	M	imb	mid	5.34
Cebus	*apella*	MNRJ 445	M	imb	mid	5.92
Cebus	*apella*	MNRJ 445	M	imb	mid	4.91
Cebus	*apella*	MNRJ 445	M	imb	mid	6.68

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 445	M	imb	mid	5.62
Cebus	*apella*	MNRJ 445	M	imb	mid	4.85
Cebus	*apella*	MNRJ 445	M	imb	mid	5.82
Cebus	*apella*	MNRJ 445	M	imb	mid	4.63
Cebus	*apella*	MNRJ 445	M	imb	mid	5.09
Cebus	*apella*	MNRJ 445	M	imb	mid	3.31
Cebus	*apella*	MNRJ 445	M	imb	mid	4.74
Cebus	*apella*	MNRJ 445	M	imb	mid	5.42
Cebus	*apella*	MNRJ 445	M	imb	mid	5.24
Cebus	*apella*	MNRJ 445	M	imb	mid	5.84
Cebus	*apella*	MNRJ 445	M	imb	mid	4.07
Cebus	*apella*	MNRJ 445	M	imb	mid	5.09
Cebus	*apella*	MNRJ 446	F	imb	mid	5.87
Cebus	*apella*	MNRJ 446	F	imb	mid	4.25
Cebus	*apella*	MNRJ 446	F	imb	mid	4.82
Cebus	*apella*	MNRJ 446	F	imb	mid	3.9
Cebus	*apella*	MNRJ 446	F	imb	mid	3.86
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	5.86
Cebus	*apella*	MNRJ 446	F	imb	mid	3.4
Cebus	*apella*	MNRJ 446	F	imb	mid	4.18
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	5.91
Cebus	*apella*	MNRJ 446	F	imb	mid	3.78
Cebus	*apella*	MNRJ 446	F	imb	mid	4.18
Cebus	*apella*	MNRJ 446	F	imb	mid	5.5
Cebus	*apella*	MNRJ 446	F	imb	mid	4.86
Cebus	*apella*	MNRJ 446	F	imb	mid	3.13
Cebus	*apella*	MNRJ 446	F	imb	mid	3.64
Cebus	*apella*	MNRJ 446	F	imb	mid	4.49
Cebus	*apella*	MNRJ 446	F	imb	mid	4.31
Cebus	*apella*	MNRJ 446	F	imb	mid	3.82
Cebus	*apella*	MNRJ 446	F	imb	mid	5
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	4.93
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35
Cebus	*apella*	MNRJ 446	F	imb	mid	3.95
Cebus	*apella*	MNRJ 446	F	imb	mid	4.79
Cebus	*apella*	MNRJ 446	F	imb	mid	7.17

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	5.86
Cebus	*apella*	MNRJ 446	F	imb	mid	5.87
Cebus	*apella*	MNRJ 446	F	imb	mid	3.82
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	5.12
Cebus	*apella*	MNRJ 446	F	imb	mid	5.51
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	4.74
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35
Cebus	*apella*	MNRJ 446	F	imb	mid	4.16
Cebus	*apella*	MNRJ 446	F	imb	mid	5.14
Cebus	*apella*	MNRJ 446	F	imb	mid	4.76
Cebus	*apella*	MNRJ 446	F	imb	mid	5.49
Cebus	*apella*	MNRJ 446	F	imb	mid	4.38
Cebus	*apella*	MNRJ 446	F	imb	mid	4.79
Cebus	*apella*	MNRJ 446	F	imb	mid	5.2
Cebus	*apella*	MNRJ 446	F	imb	mid	4.25
Cebus	*apella*	MNRJ 446	F	imb	mid	4.92
Cebus	*apella*	MNRJ 446	F	imb	mid	5.12
Cebus	*apella*	MNRJ 446	F	imb	mid	5.35
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35
Cebus	*apella*	MNRJ 446	F	imb	mid	5.51
Cebus	*apella*	MNRJ 446	F	imb	mid	4.16
Cebus	*apella*	MNRJ 446	F	imb	mid	4.57
Cebus	*apella*	MNRJ 446	F	imb	mid	4.16
Cebus	*apella*	MNRJ 446	F	imb	mid	4.16
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	5.49
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	6.28
Cebus	*apella*	MNRJ 446	F	imb	mid	4.16
Cebus	*apella*	MNRJ 446	F	imb	mid	5.49
Cebus	*apella*	MNRJ 446	F	imb	mid	3.59
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 446	F	imb	mid	5.91
Cebus	*apella*	MNRJ 446	F	imb	mid	4.23
Cebus	*apella*	MNRJ 446	F	imb	mid	4.86
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	4.36
Cebus	*apella*	MNRJ 446	F	imb	mid	5.16
Cebus	*apella*	MNRJ 446	F	imb	mid	4.91
Cebus	*apella*	MNRJ 446	F	imb	mid	3.83
Cebus	*apella*	MNRJ 446	F	imb	mid	5.32
Cebus	*apella*	MNRJ 446	F	imb	mid	4.36
Cebus	*apella*	MNRJ 446	F	imb	mid	4.13
Cebus	*apella*	MNRJ 446	F	imb	mid	4.13
Cebus	*apella*	MNRJ 446	F	imb	mid	3.95
Cebus	*apella*	MNRJ 446	F	imb	mid	4.97
Cebus	*apella*	MNRJ 446	F	imb	mid	5.68
Cebus	*apella*	MNRJ 446	F	imb	mid	4.55
Cebus	*apella*	MNRJ 446	F	imb	mid	4.16
Cebus	*apella*	MNRJ 446	F	imb	mid	4.76
Cebus	*apella*	MNRJ 446	F	imb	mid	4.04
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35
Cebus	*apella*	MNRJ 446	F	imb	mid	5.1
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	4.16
Cebus	*apella*	MNRJ 446	F	imb	mid	6.01
Cebus	*apella*	MNRJ 446	F	imb	mid	4.74
Cebus	*apella*	MNRJ 446	F	imb	mid	4.18
Cebus	*apella*	MNRJ 446	F	imb	mid	4.2
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	4.35
Cebus	*apella*	MNRJ 446	F	imb	mid	4.01
Cebus	*apella*	MNRJ 446	F	imb	mid	5.12
Cebus	*apella*	MNRJ 446	F	imb	mid	4.01
Cebus	*apella*	MNRJ 446	F	imb	mid	5.1
Cebus	*apella*	MNRJ 446	F	imb	mid	4.38
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	5.48

Genus	Species	Specimen	Sex	Height	Depth	XS (microns)
Cebus	*apella*	MNRJ 446	F	imb	mid	4.01
Cebus	*apella*	MNRJ 446	F	imb	mid	4.38
Cebus	*apella*	MNRJ 446	F	imb	mid	5.16
Cebus	*apella*	MNRJ 446	F	imb	mid	3.82
Cebus	*apella*	MNRJ 446	F	imb	mid	6.06
Cebus	*apella*	MNRJ 446	F	imb	mid	4.2
Cebus	*apella*	MNRJ 446	F	imb	mid	4.6
Cebus	*apella*	MNRJ 446	F	imb	mid	3.77
Cebus	*apella*	MNRJ 446	F	imb	mid	3.48
Cebus	*apella*	MNRJ 446	F	imb	mid	3.59
Cebus	*apella*	MNRJ 446	F	imb	mid	5
Cebus	*apella*	MNRJ 446	F	imb	mid	4.82
Cebus	*apella*	MNRJ 446	F	imb	mid	3.99
Cebus	*apella*	MNRJ 446	F	imb	mid	5.38
Cebus	*apella*	MNRJ 446	F	imb	mid	5.32
Cebus	*apella*	MNRJ 446	F	imb	mid	4.78
Cebus	*apella*	MNRJ 446	F	imb	mid	4.54
Cebus	*apella*	MNRJ 446	F	imb	mid	4.26
Cebus	*apella*	MNRJ 446	F	imb	mid	3.61
Cebus	*apella*	MNRJ 446	F	imb	mid	4.73
Cebus	*apella*	MNRJ 446	F	imb	mid	4.76
Cebus	*apella*	MNRJ 446	F	imb	mid	3.67
Cebus	*apella*	MNRJ 446	F	imb	mid	3.83
Cebus	*apella*	MNRJ 446	F	imb	mid	4.26
Cebus	*apella*	MNRJ 446	F	imb	mid	6.04
Cebus	*apella*	MNRJ 446	F	imb	mid	4.67
Cebus	*apella*	MNRJ 446	F	imb	mid	4.36
Cebus	*apella*	MNRJ 446	F	imb	mid	3.59
Cebus	*apella*	MNRJ 446	F	imb	mid	4.23
Cebus	*apella*	MNRJ 446	F	imb	mid	4.96
Cebus	*apella*	MNRJ 446	F	imb	mid	4.2
Cebus	*apella*	MNRJ 446	F	imb	mid	4.93
Cebus	*apella*	MNRJ 446	F	imb	mid	5.7
Cebus	*apella*	MNRJ 446	F	imb	mid	5.53
Cebus	*apella*	MNRJ 446	F	imb	mid	4.95
Cebus	*apella*	MNRJ 446	F	imb	mid	5.56
Cebus	*apella*	MNRJ 446	F	imb	mid	4.93
Cebus	*apella*	MNRJ 446	F	imb	mid	6.12

Bibliography

Addessi, E. (2008) Food variety-seeking in tufted capuchin monkeys (*Cebus apella*). *Physiology and Behavior* 93: 304-309.

Alexander, J.P. (1994) Sexual dimorphism in notharctid primates. *Folia Primatologica* 63: 59-62.

Alroy, J. (2001) A multispecies overkill simulation of the End-Pleistocene megafaunal mass extinction. *Science* 292: 1893-1896.

Amling, M., Pogoda, P., Beil, F., Schilling, A., Holzmann, T., Priemel, M., Blicharski, D., Catala-Lehnen, P., Rueger, J., Ducy, P., & Karsenty, G. (2001) Central control of bone mass: brainstorming of the skeleton. *Advances in Experimental Medicine & Biology* 496: 85-94.

Anapol, F., Lee, S. (1994) Morphological adaptation to diet in platyrrhine primates. *American Journal of Physical Anthropology* 94: 239-261.

Anderson, M. (1994) *Sexual Selection*. Princeton: Princeton University Press.

Andresen, V. (1898). Die Querstreifung des Dentins. *Deutsche Monatsschrift fur Zahnheilkunde*. Sechzehnter Jahrgang, Leipzig, 16: 386–389.

Andrews P., Martin, L. (1991) Hominoid dietary evolution. *Philosophical Transactions: Biological Sciences* 334: 199-209.

Aoba, T., Moreno, E.C. (1987) The enamel fluid in the early secretory stage of porcine amelogenesis: chemical composition and saturation with respect to enamel mineral. *Calcified Tissue International* 41: 86-94.

Appenzeller, O., Gunga, H.C., Qualls, C., Furlan, R., Porta, A., Lucas, S., Hecker, A., Kirsch, K., Costa-Junqueira, M., Guillen, S., Sander, M., Schneider, T., & Blottner, B. (2005) A hypothesis: autonomic rhythms are reflected in growth lines of teeth in humans and extinct archosaurs. *Autonomic Neuroscience* 117: 115-119.

Armstrong, H.A., Smith, C.J. (2001) Growth patterns in euconodont crown enamel: implications for life history and mode-of-life reconstruction in the earliest vertebrates. *Proceedings of the Royal Society of London, Series B* 268: 815-820.

Asper, H. (1916) Uber die "Braune Retzius" sche Parallelstreifung im Schmelz der Menschlichen Zahne, Schweiz. *Vierteljahrschrift Zahnheilk* 26: 277-314.

Avery, J.K., Visser, R.L., & Knapp, D.E. (1961) The pattern of the mineralization of enamel. *Journal of Dental Research* 40: 1004-1019.

Badyaev, A.V. (2002) Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution* 17: 369-378.

Berkovitz, B.K. (2000) Tooth replacement patterns in non-mammalian vertebrates. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 186-200.

Berkovitz, B.K., Moxham, B. (1981) Early stages of tooth development. In Osborn, J. (ed.), *Dental Anatomy and Embryology*. Oxford: Blackwell Scientific Publishers, pp. 246-254.

Beynon, A.D. (1992) Circaseptan rhythms in enamel development in modern humans and Plio-Pleistocene hominids. In Smith, P., & Tchernov, E. (eds.), *Structure, Function, and Evolution of Teeth*. London: Freund, pp. 295-310.

Beynon, A.D., Dean, M.C. (1987) Crown-formation time of a fossil hominid premolar tooth. *Archives of Oral Biology* 32: 773-780.

Beynon, A.D., Clayton, C.B., Ramirez Rozzi, F.V., & Reid, D.J. (1998) Radiographic and histological methodologies in estimating the chronology of crown development in modern humans and great apes: a review, with some applications for studies on juvenile hominids. *Journal of Human Evolution* 35: 351-370.

Beynon, A.D., Dean, M.C., Reid, D.J. (1991) Histological study on the chronology of the developing dentition in gorilla and orangutan. *American Journal of Physical Anthropology* 86: 189-203.

Beynon, A.D., Dean, M.C., Leakey, M.G., Reid, D.J., Walker, A. (1998) Comparative dental development and microstructure of *Proconsul* teeth from Rusinga Island, Kenya. *Journal of Human Evolution* 35: 163-209.

Beynon, A.D., Dean, M.C., Leakey, M.G., Reid, D.J., Walker, A. (1998b) Comparative dental development and microstructure of *Proconsul* teeth from Rusinga Island, Kenya. *Journal of Human Evolution* 35: 163-209.

Beynon, A.D., & Reid, D. (1987) Relationships between perikymata counts and crown formation times in the human permanent dentition. *Journal of Dental Research* 66: 889 (abstract).

Beynon, A.D., & Reid, D. (1995) Comparative studies on enamel structure and development in modern hominoids. In Radlanski, R.J., & Renz, H. (eds.), *Proceedings of the 10th International Symposium on Dental Morphology*. Berlin:"M" Marketing-Services, pp. 320-323.

Beynon, A.D., & Wood, B.A. (1986) Variations in enamel thickness and structure in East African hominids. *American Journal of Physical Anthropology* 70: 177-195.

Blanco, M.B., & Godfrey, L.R. (2006) Craniofacial sexual dimorphism in *Alouatta palliata*, the mantled howling monkey. *Journal of Zoology* 270: 268-276.

Boinski, S., & Jacobs Cropp, S. (1999) Disparate data sets resolve squirrel monkey (*Saimiri*) taxonomy: implications for behavioral ecology and biomedical usage. *International Journal of Primatology* 20: 237-256.

Boyde, A. (1963) Appendix on the teeth of the skeletal remains of a child from Dinas Powys. In Alcock, D.J. (ed.), *Dinas Powys*. Cardiff: University of Wales Press.

Boyde, A. (1964) *The structure and development of mammalian enamel.* Ph.D. dissertation, University of London.

Boyde, A. (1965) The structure of developing mammalian dental enamel. In Stack, M.V., & Fearnhead, R.W. (eds.), *Tooth Enamel*. Bristol: John Wright and Sons, pp. 163-167.

Boyde, A. (1969) Correlation of ameloblast size with enamel prism pattern: use of scanning electron microscope to make surface area measurements. *Z. Zellforsch*. 93: 583-593.

Boyde, A. (1979) Carbonate concentration, crystal centers, core dissolution, caries, cross striations, circadian rhythms, and compositional contrasts in the SEM. Journal of Dental Research 58 (special issue B), 981-983.

Boyde, A. (1989) Enamel. In Oksche, A., & Vollrath, L. (eds.), *Handbook of Microscopic Anatomy, Vol. V/6: Teeth*. Berlin: Springer-Verlag, pp. 309-473.

Boyde, A., & Martin, L.B. (1982) Enamel microstructure determination in hominoid and cercopithecoid primates. *Anatomy and Embryology* 165: 193-212.

Boyde, A., & Martin, L.B. (1987) Tandem scanning reflected light microscopy of primate enamel. *Scanning Microscopy* 1: 1935-1948.

Bromage, T.G. (1991) Enamel incremental periodicity in the pig-tailed macaque: a polychrome fluorescent labeling study of dental hard tissues. *American Journal of Physical Anthropology* 86: 205-214.

Bromage, T.G., Dean, M.C. (1985) Re-evaluation of the age at death of immature fossil hominids. *Nature* 317: 525-527.

Bromage, T.G., LaCruz, R., Hogg., R., Goldman, H., McFarlin, S.C., Warshaw, J., Dirks, W., Perez Ochoa, A., Smolyar, I., Enlow, D.H., Boyde, A. (2009) Lamellar bone reconciles enamel rhythms, body size, and organismal life history. *Calcified Tissue International* 84: 388-404.

Bromage, T.G., Schrenk, F., & Zonneveld, F.W. (1995) Paleoanthropology of the Malawi Rift: an early hominid mandible from Chiwondo Beds, Northern Malawi. *Journal of Human Evolution* 28: 71-108.

Bromage, T.G., Warshaw, J., Hogg, R., LaCruz, R., McFarlin, S., Goldman, H., Smolyar, I., Enlow, D.H., Boyde, A. (2008) Bone rhythms correspond to enamel periods and reflect life history. *Journal of Dental Research* 87: 1283.

Brown, A.D., & Zunino, G.E. (1990) Dietary variability in *Cebus apella* in extreme habitats: evidence for adaptability. *Folia Primatologica* 54: 187-195.

Brown, J.H., & Sibly, R.M. (2006) Life-history evolution under a production constraint. *Proceedings of the National Academy of Sciences* 103: 17595-17599.

Brown, M.F., Gratton, T.P., & Stuart, J.A. (2007) Metabolic rate does not scale with body mass in cultured mammalian cells. *American Journal of Physiology – Regulatory, Integrative, and Comparative Physiology* 292: R2115-R2121.

Byrne, R.W. (1995) Primate cognition: comparing problems and skills. *American Journal of Primatology* 37:127–141.

Calder, W.A. (1984) Size, Function, and Life History. Cambridge, Mass.: Harvard University Press.

Carroll, R.L. (1988) *Vertebrate Paleontology and Evolution*. New York: W.H. Freeman.

Carter, J.T. (1922) On the structure of the enamel in the primates and some other mammals. *Proceedings of the Zoological Society of London* 1922: 599-608.

Catlett, K.K., Schwartz, G.T., Godfrey, L.R., & Jungers, W.L. (2010) "Life history space": a multivariate analysis of life history variation in extant and extinct Malagasy lemurs. *American Journal of Physical Anthropology*, in press.

Charnov, E.L. (1991) Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences* 88: 1134-1137.

Charnov, E.L., & Berrigan, D. (1993) Why do female primates have such long lifespans and so few babies? or Life in the slow lane. *Evolutionary Anthropology* 1: 191-194.

Charnov, E.L., & Schaffer, W.M. (1973). Life-history consequences of natural selection: Cole's result revisited. *The American Naturalist* 107: 791-793.

Chase, J.E., Cooper, R.W. (1968) *Saguinus nigricollis* – Physical growth and dental eruption in a small population of captive-born individuals. *American Journal of Physical Anthropology* 30: 111-116.

Cheverud, J. (1982) Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36: 499-516.

Cheverud, J. (1989) Evolution of morphological integration. In Splechtna, H., & Helge, H. (eds.), *Trends in Vertebrate Morphology* 35. New York: Fisher, pp. 196-197.

Cheverud, J., Dow, M.M., Leutenegger, W. (1985) The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution* 39: 1335-1351.

Clark., G.R. II (1975) Periodic growth and biological rhythms in experimentally grown bivalves. In Rosenberg, G., & Runcorn, S. (eds.), *Growth Rhythms and the History of the Earth's Rotation*. New York: Wiley, pp. 103-118.

Clutton-Brock, T.H., Harvey, P.H., Rudder, B. (1977) Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature* 269:191–195.

Cobb, S.N., & O'Higgins, P. (2007) The ontogeny of sexual dimorphism in the facial skeleton of the African apes. *Journal of Human Evolution* 53: 176-190.

Coimbra-Filho, A.F., & Mittermeier, R.A. (1977) Tree-gouging, exudate-eating, and the "short-tusked" condition in *Callithrix* and *Cebuella.* In Kleinman, D.G. (ed.), *The biology and conservation of the Callitrichidae.* Washington, D.C.: Smithsonian Institution, pp. 105-115.

Cole, L.C. (1954) The population consequences of life history phenomena. *Quarterly Review of Biology* 29: 103-137.

Cole, T.M. (1992) Postnatal heterochrony of the masticatory apparatus in *Cebus apella* and *Cebus albifrons*. *Journal of Human Evolution* 23: 253-282.

Collard, M., & O'Higgins, P. (2001) Ontogeny and homoplasy in the papionin monkey face. *Evolution and Development* 3: 322-331.

Conroy, G.C., Vannier, M.W. (1991) Dental development in South African australopithecines. Part 1: Problems of pattern and ontogeny. *American Journal of Physical Anthropology* 86: 121-136.

Corner, B.D. Richtsmeier, J.T. (1991) Morphometric analysis of craniofacial growth in *Cebus apella*. *American Journal of Physical Anthropology* 84: 323-342.

Corner, B.D. Richtsmeier, J.T. (1992) Cranial growth in the squirrel monkey (*Saimiri sciureus*): a quantitative analysis using three dimensional coordinate data. *American Journal of Physical Anthropology* 87: 67-81.

Corner, B.D. Richtsmeier, J.T. (1993) Cranial growth and growth dimorphism in *Ateles geoffroyi*. *American Journal of Physical Anthropology* 92: 371-394.

Corruccini, R.S. (2001) Confidence intervals for morphology-based cladistic trees: a platyrrhine phylogeny test case. *International Journal of Primatology* 22: 1007-1019.

Crompton, A.W. (1980) Biology of the earliest mammals. In Schmidt-Nielsen, K., Bolis, L., & Taylor, C., *Comparative Physiology: Primitive Mammals*. Cambridge: Cambridge University Press, pp. 1-12.

Currey, J.D. (1999) The design of mineralised hard tissues for their mechanical functions. *Journal of Experimental Biology* 202: 3285-3294.

Curry, K.A. (1999) Ontogenetic histology of *Apatosaurus* (Dinosauria: Sauropoda): new insights on growth rates and longevity. *Journal of vertebrate paleontology* 19: 654-665.

Cuvier, G. (1817) *La Règne Animal, Distribué d'Après son Organization,* Tome I. Paris: Deterville.

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex.* London: Murray.

Dauphin, Y. (1988) L'émail dentaire des reptiles actuels et fossils: Rèparation de la structure prismatique, son role, ses implications. *Paleontographica* 203: 171-184.

Daegling, D.J., & Hylander, W.L. (2000) Experimental observation, theoretical models, and biomechanical inference in the study of mandibular form. *American Journal of Physical Anthropology* 112: 541-551.

Davies, P., Lister, A.M. (2001) *Paleoloxodon cypriotes*, the dwarf elephant of *Cyprus*: size and scaling comparisons with *P. falconeri* (Sicily – Malta) and mainland *P. antiquus*. Rome: *Proceedings 1st Int Cong "The World of Elephants,"* pp. 479-480.

Dean, M.C. (1993) Daily rates of dentine formation in macaque tooth roots. *International Journal of Osteoarchaeology* 3: 199-206.

Dean, M.C. (1995) The nature and periodicity of incremental lines in primate dentine and their relationship to periradicular bands in OH 16 (*Homo habilis*). In Moggi-Cecchi (ed.), *Aspects of Dental Biology: Paleontology, Anthropology, and Evolution.* Florence: Angelo Pontecorboli, pp. 239-265.

Dean, M.C. (1998) A comparative study of cross striation spacings in cuspal enamel and of four methods of estimating the time taken to grow molar cuspal enamel in *Pan, Pongo,* and *Homo. Journal of Human Evolution* 35: 449-462.

Dean, M.C. (2000) Progress in understanding hominoid dental development. *Journal of Anatomy* 197: 77-101.

Dean, M.C. (2004) 2D or not 2D, and other interesting questions about enamel: reply to Macho et al. (2003). *Journal of Human Evolution* 45: 81-90.

Dean, M.C., Beynon, A.D. (1991) Histological reconstruction of crown formation times and initial root formation times in a modern human child. *American Journal of Physical Anthropology* 86: 215-228.

Dean, M.C., Leakey, M.G. (2004) Enamel and dentine development and the life history profile of *Victoriapithecus macinnesi* from Maboko Island, Kenya. *Annals of Anatomy* 186: 405-412.

Dean, M.C., Scandrett, A.E. (1995) Rates of dentine mineralization in permanent human teeth. *International Journal of Osteoarchaeology* 5: 349-358.

Dean, M.C., Scandrett, A.E. (1996) The relation between long-period incremental markings in dentine and daily cross-striations in enamel in human teeth. *Archives of Oral Biology* 41: 233-241.

Dean, M.C., Schrenk, F. (2003) Enamel thickness and development in a third permanent molar of *Gigantopithecus blacki. Journal of Human Evolution* 45: 381-387.

DeBeer, G.R. (1930) *Embryology and Evolution*. Oxford: Clarendon Press.

DeBeer, G.R. (1940) *Embryos and Ancestors.* Oxford: Clarendon Press.

Delson, E., & Rosenberger, A.L. (1984) Are there any anthropoid primate living fossils? In Eldredge, N., & Stanley, S.M. (eds.), *Living Fossils*. New York: Springer-Verlag, pp. 50-61.

DiBitetti, M.S., Janson, C.H. (2000) When will the stork arrive? Patterns of birth seasonality in neotropical primates. *American Journal of Primatology* 50: 109-130.

Diekwisch, T.G.H., Berman, B.J., Gentner, S., & Slavkin, H.C. (1995) Initial enamel crystals are not spatially associated with mineralized dentine. *Cell & Tissue Research* 279: 149-167.

Dietz, J.M., Baker, A.J., Miglioretti, D. (1994) Seasonal variation in reproduction, juvenile growth, and adult body mass in golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology* 34: 115-132.

Dietz, J.M., Peres, C.A., & Pinder, L. (1997) Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia).* American Journal of Primatology 41: 289-305.

DiFiore, A., & Rendall, D. (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proceedings of the National Academy of Sciences* 91: 9941-9945.

Dirks, W. (1998) Histological reconstruction of dental development and age at death in a juvenile gibbon (*Hylobates lar*). *Journal of Human Evolution* 35: 411-425.

Dirks, W. (2001) *Dental development and life history in catarrhine primates*. PhD Dissertation, New York University.

Dirks, W. (2003) Effect of diet on dental development in four species of catarrhine primates. *American Journal of Primatology* 61: 29-40.

Dirks, W., Bowman, J.E. (2007) Life history theory and dental development in four species of catarrhine primates. *Journal of Human Evolution* 53: 309-320.

Dirks, W., Ramirez-Rozzi, F.V., Reid, D.J., & Anemone, R.L. (2004) Thinking small: a comparative study of dental microstructure in *Cantius, Otolemur, Perodicticus,* and *Saimiri*. *American Journal of Physical Anthropology* 123 Supplement: 88.

Dirks, W., Reid, D.J., Jolly, C.J., Phillips-Conroy, J.E., & Brett, F.L. (2002) Out of the mouths of baboons: stress, life history, and dental development in the Awash National Park hybrid zone, Ethiopia. *American Journal of Physical Anthropology* 118: 239-252.

Disotell, T.R., Honeycutt, R.L., & Ruvolo, M. (1992) Mitochondrial DNA phylogeny of the Old-World monkey tribe Papionini. *Molecular Biology and Evolution* 9: 1-13.

Dodd, A.N., Salathia, N., Hall, A., Kévei, E., Tóth, R., Nagy, F., Hibberd, J., Millar, A.J., & Webb, A.A.R. (2005) Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. *Science* 309: 630-633.

Driessens, F.C.M., & Verbeeck, R.M.H. (1990) *Biominerals*. Boca Raton, FL: CRC Press.

Dumont, E.R. (1995a) Enamel thickness and dietary adaptation among extant primates and chiropterans. *Journal of Mammalogy* 76: 1127-1136.

Dumont, E.R. (1995b) Mammalian enamel prism patterns and enamel deposition rates. *Scanning Microscopy* 9: 429-442.

Dumont, E.R. (1997) Cranial shape in fruit, nectar, and exudate feeders: Implications for interpreting the fossil record. *American Journal of Physical Anthropology* 102: 187-202.

Dumont, E.R. (1999) The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): an experimental study. *Journal of Zoology* 248: 219-229.

Dunbar, R.M. (1992) Neocortex size as a constraint on group size in primates. *Journal of Human Evolution* 22: 469–494.

Dunbar, R.M. (1995) Neocortex size and group size in primates: a test of the hypothesis. *Journal of Human Evolution* 28: 287–296.

Dutrillaux, B. (1988) Chromosome evolution in primates. *Folia Primatologica* 50: 134-135.

Ebner, V. von. (1902). Histologie der Zahne mit Einschluss der Histogenese. In Scheff, J. (ed.), *Handbuch der Zahnheilkunde,* Wien: A. Holder, pp. 243–299.

Elefteriou, F., Takeda., S., Ebihara, K., Magre, J., Patano, N., Kim, C.A., Ogawa, Y., Liu, X., Ware, S.M., Craigen, J., Vinson, R., Nakao, K., Capeau, J., & Karsenty, G. (2004) Serum leptin level is a regulator of bone mass. *Proceedings of the National Academy of Sciences* 101: 3258-3263.

Enlow, D.H., & Hans, M.G. (1996) *Essentials of Facial Growth.* Philadelphia: Saunders.

Espirito Santo, A.R. do, Novaes, P.D., Line, S.R.P. (2006) Anisotropic properties of the enamel organic extracellular matrix. *European Journal of Oral Sciences* 114 Supplement: 333-337.

Evans, A.R., & Sanson, G.D. (2005) Biomechanical properties of insects in relation to insectivory: cuticle thickness as an indicator of 'hardness' and 'intractability.' *American Journal of Zoology* 53: 9-19.

Fauchard, P. (1728) *Le Chirurgien Dentiste*. Paris.

Fearnhead, R.W. (1960) The mineralization of rat enamel. *Nature* 188: 509-510.

Felsenstein, J. (1978) Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology* 27: 401-410.

Ferguson, C.A., Hardcastle, Z., Sharpe, P.T. (2000) Development and patterning of the dentition. In O'Higgins, P., & Cohn, M.J. (eds.), *Development, Growth, and Evolution: Implications for the Study of the Hominid Skeleton.* San Diego: Academic, pp.187-205.

Fernandes, M.E.B. (1991) Tool use and predation of oysters (*Crassostrea rhizophorae*) by the tufted capuchin, *Cebus apella apella*, in brackish water mangrove swamp. *Primates* 32: 529-531.

Fernandez-Duque, E. (2007). Aotinae: Social monogamy in the only nocturnal haplorhines. In Campbell, C.J., Bearder, S., Fuentes, A., MacKinnon, K.C., and Panger, M. (eds.), *Primates in Perspective*. Oxford: Oxford University Press, pp. 139-154.

Ferrari, S.F. (1993) Ecological differentiation in the Callitrichidae. In Rylands, A.B. (ed.), *Marmosets and Tamarins: Systematics, Behaviour and Ecology.* Oxford: Oxford University Press, pp. 314–328.

Ferrari, S.F., & Martins, E.S. (1992). Gummivory and gut morphology in two sympatric callitrichids *(Callithrix emiliae* and *Saguinus fuscicollis weddeUi)* from western Brazilian Amazonia. *American Journal of Physical Anthropology* 88: 97-103.

Fincham, A.G., Luo, W., Moradian-Oldak, J., Paine, M.L., Snead, M.L., & Zeichner-David, M. (2000) Enamel biomineralization: the assembly and disassembly of the protein extracellular organic matrix. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 37-61.

Fisher, D.C. (1996) Extinction of proboscideans in North America. In Shoshani, J., & Tassy, P. (eds.), *The Proboscidea: Evolution and Palaeoecology of Elephants and their Relatives.* Oxford: Oxford University Press, pp. 97-315.

Fisher, R.A. (1930) *The genetical theory of natural selection.* Clarendon, Oxford.

Fitzgerald (1996) *Tooth crown formation and the variation of enamel microstructural growth markers in modern humans*. Ph.D. dissertation, University of Cambridge.

Fitzgerald, C.M. (1998) Do enamel microstructures have regular time dependency? Conclusions from the literature and a large-scale study. *Journal of Human Evolution* 35: 371-386.

Fleagle, J.G. (1999) *Primate Adaptation and Evolution.* New York: Academic.

Fleagle, J.G., Buckley, G.A., & Schloeder, M.E. (1988) New fossil primates from Monte Observacion, Santa Cruz Formation (lower Miocene), Santa Cruz Province, Argentina. *Journal of Vertebrate Paleontology* 8: 14A.

Fleagle, J.G., Kay, R.F., & Simons, E.L. (1980) Sexual dimorphism in early anthropoids. *Nature* 287: 328-330.

Fleagle, J.G., & Kay, R.F. (1989) The dental morphology of *Dolichocebus gaimanensis*, a fossil monkey from Argentina. *American Journal of Physical Anthropology* 78: 221

Fleagle, J.G., & Kay, R.F. (1997) Platyrrhines, catarrhines, and the fossil record. In Kinzey, W.G. (ed.), *New World Primates: Ecology, Evolution, and Behavior*. New York: de Gruyter, pp. 3-23.

Fleagle, J.G., & Schaffler, M.B. (1982) Development and eruption of the mandibular cheek teeth in *Cebus albifrons*. *Folia Primatologica* 38: 158-169.

Fleagle, J.G., & Tejedor, M. (2002) Early platyrrhines in southern South America. In Hartwig, W.C., (ed.), *The Primate Fossil Record.* Cambridge: Cambridge University Press, pp. 161-174.

Ford, S.M. (1986) Systematics of the New World monkeys. In Swindler, D.R., & Erwin, J. (eds.), *Comparative Primate Biology, Volume I: Systematics, Evolution and Anatomy.* New York: Alan R Liss, pp. 73–135.

Ford, S.M. (1994) Evolution of sexual dimorphism in body weight in platyrrhines. *American Journal of Primatology* 34: 221-244.

Ford, S.M., & Davis, L.C. (1992) Systematics and body size: implications for feeding adaptations in New World monkeys. *American Journal of Physical Anthropology* 88: 415-468.

Fragaszy, D.M., & Bard, K. (1997) Comparison of development and life history in *Pan* and *Cebus*. *International Journal of Primatology* 18: 683-701.

Fragaszy, D.M., & Boinski, S. (1995) Patterns of individual diet choice and efficiency of foraging in capuchin monkeys (*Cebus olivaceus*). *Journal of Comparative Psychology* 109: 339-348.

Fragaszy, D.M., Visalberghi, E., & Robinson, J.G. (1990) Variability and adaptability in the genus *Cebus*. *Folia Primatologica* 54: 114-118.

Fragaszy, D.M., Visalberghi, E., & Fedigan, L.M. (2004) *The Complete Capuchin: The Biology of the Genus* Cebus. Cambridge: Cambridge University Press.

Freeman, P.W. (1979) Specialized insectivory: beetle-eating and moth-eating molossid bats. *Journal of Mammalogy* 60: 467-469.

Gadgil, M., Bossert, W.H. (1970) Life historical consequences of natural selection. *The American Naturalist* 104: 1-24.

Gaengler, P. (2000) Evolution of tooth attachment in lower vertebrates to tetrapods. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 173-185.

Galetti, M., & Pedroni, F. (1994) Seasonal diet of capuchin monkeys (*Cebus apella*) in a semideciduous forest in south-east Brazil. *Journal of Tropical Ecology* 10: 27-39.

Gantt, D.G. (1980) Implications of enamel prism patterns for the origin of New World monkeys. In Ciochon, R.L., & Chiarelli, A.B. (eds.), *Evolutionary biology of the New World monkeys and continental drift.* New York: Plenum, pp. 201-217.

Gantt, D.G., Pilbeam, D.R., & Steward, G.P. (1977) Hominoid enamel prism patterns. *Science* 198: 1155-1157.

Garber, P.A., & Leigh, S.R. (1997) Ontogenetic variation in small-bodied New World primates: implications for patterns of reproduction and infant care. *Folia Primatologica* 68: 1-22.

Garber, P.A., Rosenberger, A.L., & Norconk, M.A. (1996) Marmoset misconceptions. In Norconk, M., Garber, P., & Rosenberger, A. (eds.), *Adaptive Radiations of Neotropical Primates*. New York: Springer, pp. 87-96.

Gaulin, S.J.C., & Sailer, L.D. (1984) Sexual dimorphism in weight among the primates: the relative impact of allometry and sexual selection. *International Journal of Primatology* 5: 515-535.

Gibson, K.R. (1986) Cognition, brain size and the extraction of embedded food resources. In Else, J., & Lee, P.C. (eds.), *Primate ontogeny, cogntion and social behavior.* Cambridge: Cambridge University Press, pp. 93–104.

Gingerich, P.D. (1980) Eocene Adapidae, paleobiogeography, and the origin of South American Platyrrhini. In Ciochon, R.L., & Chiarelli, A.B. (eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift*. New York: Plenum, pp. 123-138.

Gingerich, P.D. (1979) Sexual dimorphism in Eocene Adapidae: implications for primate phylogeny and evolution. Abstract. *American Journal of Physical Anthropology* 50: 442.

Gingerich, P.D. (1981) Cranial morphology and adaptations in Eocene Adapidae. I. Sexual dimorphism in *Adapis magnus* and *Adapis parisiensis*. *American Journal of Physical Anthropology* 56: 217-234.

Gingerich, P.D. (1995) Sexual dimorphism in the earliest Eocene *Cantius torresi* (Mammalia, Primates, Adapoidea). *Contributions to the Museum of Paleontology* 29: 185-199.

Gingerich, P.D., & Martin, R.D. (1981) Cranial morphology and adaptations in Eocene Adapidae. II. The Cambridge skull of *Adapis parisiensis. American Journal of Physical Anthropology* 56: 235-257.

Gingerich, P.D., & Sahni, A. (1984) Dentition of *Sivaladapis nagrii* (Adapidae) from the late Miocene of India. *International Journal of Primatology* 21: 201-214.

Glimcher , M.J., Brickley-Parsons, D., & Levine, P.T. (1977) Studies of enamel proteins during maturation. *Calcified Tissue Research* 24: 259-270.

Godfrey, L.R., Petto, A.J., & Sutherland, M.R. (2002) Dental ontogeny and life-history strategies: the case of the giant extinct indroids of Madagascar. In Plavcan, M., Kay, R.F., Jungers, W.L., & Van Schaik, C.P. (eds.), *Reconstructing Behavior in the Primate Fossil Record.* New York: Kluwer Academic, pp. 113-157.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., & Sutherland, M.R. (2001) Teeth, Brains, and Primate Life Histories. *American Journal of Physical Anthropology* 114: 192-214.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., & Sutherland, M.R. (2003) Dental development and primate life histories. In Kappeler, P.M., & Pereira, M.E. (eds.), *Primate Life Histories and Socioecology*. Chicago: University of Chicago Press, pp. 177-203.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R., & Irwin, M.T. (2004) Ontogenetic correlates of diet in Malagasy lemurs. *American Journal of Physical Anthropology* 123: 250-276.

Godfrey, L.R., Samonds, K.E., Wright, P.C., & King, S.J. (2005) Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. *Folia Primatologica* 76: 77-99.

Godfrey, L.R., Schwartz, G.T., Samonds, K.E., Jungers, W.L., & Catlett, K.K. (2006) The secrets of lemur teeth. *Evolutionary Anthropology* 15: 142-154.

Godfrey, L.R., and Sutherland, M.R. (1995) What's growth got to do with it? Process and product in the evolution of ontogeny. *Journal of Human Evolution* 29: 405-431.

Godinot, M. (2006) Lemuriform origins as viewed from the fossil record. *Folia Primatologica* 77: 446-464.

Goldberg, M., Septier, S., Lecolle, S., Chardin, H., Quintana, M.A., Acevedo, A.C., Gafni, G., Dillouya, D., Vermelin, L., Thonemann, B., Schmalz, G., Mapahou, P.B., & Carreau, J.P. (1995) Dental mineralization. *International Journal of Developmental Biology* 39: 93-110.

Goldman, H., Kindsvater, J., & Bromage, T.G. (1999) Correlative light and backscattered electron microscopy of bone – Part 1: Specimen preparation methods. *Scanning* 21: 40-43.

Goodrich, E.S. (1907) On the scales of fish, living and extinct, and their importance in classification. *Proceedings of the Zoological Society of London*: 751-774.

Gould, S.J. (1975) On the scaling of tooth size in mammals. *American Zoology* 15: 351-362.

Gould, S.J. (1977) *Ontogeny and Phylogeny*. Cambidge, Mass: Harvard University Press.

Greaves (1974) Functional implications of mammalian jaw joint position. *Forma Functio* 7: 363-376.

Gregory, W.K. (1920) On the structure and relations of *Notharctus*, an American Eocene primate. *Memoirs of the American Museum of Natural History* 3: 49-243.

Guatelli-Steinberg, D. (2001) What can developmental defects of enamel reveal about physiological stress in nonhuman primates? *Evolutionary Anthropology* 10: 138-151.

Guatelli-Steinberg, D., Ferrell, R.J., Spence, J., Talabere, T., Hubbard, A., & Schmidt, S. (2009) Sex differences in anthropoid mandibular canine lateral enamel formation. *American Journal of Physical Anthropology* 140: 216-233.

Gysi, A. (1931) Metabolism in adult enamel. *Dental Digest* 37:661-668.

Habelitz S., Marshall S.J., Marshall, G.W. Jr, & Balooch, M. (2001) Mechanical properties of human dental enamel on the nanometer scale. *Archives of Oral Biology* 46: 173-183.

Halberg, F. (1969) Chronobiology. *Annual Review of Physiology* 31: 675-726.

Halberg, F., Cornélissen, G., Otsuka, K., Watanabe, Y., Katinas, G.S., Burioka, N., Delyukov, A., Gorgo, Y.,Zhao, Z., Weydahl, A., Sothern, R.B., Siegelova, J., Fiser, B., Dusek, J., Syutkina, E.V., Perfetto, F., Tarquini, R.,Singh, R.B., Rhees, B., Lofstrom, D., Lofstrom, P., William., P, & Johnson, C. (2000) Cross-spectrally coherent ~10.5- and 21-year biological and physical cycles, magnetic storms and myocardial infarctions *Neuroendocrinology Letters*: 21:233–258.

Harada, M.L., Schneider, H., Schneider, M., Sampaio, I., Czelusniak, J., & Goodman, M. (1995) DNA evidence on the phylogenetic systematics of New World monkeys: support for the sister-grouping of *Cebus* and *Saimiri* from two unlinked nuclear genes. *Molecular Phylogenetics and Evolution* 4: 331-349.

Harris, E.E. (2000) Molecular systematic of the Old World monkey tribe Papionini: analysis of the total available genetic sequences. *Journal of Human Evolution* 38: 235-256.

Hartwig, W.C. (1996) Perinatal life history traits in New World monkeys. *American Journal of Primatology* 40: 99-130.

Hartwig, W.C., & Meldrum, D.J. (2001) Miocene platyrrhines of the northern neotropics. In Hartwig, W.C. (ed.), *The Primate Fossil Record.* Cambridge: Cambridge University Press, pp. 175-188.

Hartwig, W.C., & Rosenberger, A.L. (2005) New World monkeys. In *Encyclopedia of Life Sciences.* Chichester: Wiley & Sons.

Harvati, K. (2000) Dental Eruption Sequence Among Colobine Primates. *American Journal of Physical Anthropology* 112: 69-85.

Harvey, P.H., Clutton-Brock, T.H. (1985) Life history variation in primates. *Evolution* 39: 559-581.

Harvey, P.H., Martin, R.D., & Clutton-Brock, T.H. (1987). Life histories in comparative perspective. In Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., & Struhsaker, T.T.. (eds.), *Primate Societies*. Chicago: University of Chicago Press, pp. 181-196.

Harvey, P.H., Pagel, M.D., & Rees, J.A. (1991) Mammalian metabolism and life histories. *American Naturalist* 137: 556-566.

Havers, C. (1691) *Osteologia Nova.* London.

Helmcke, J. G. (1966) Form und Verlauf von zehn Schmelzprismen der Hunter-Schreger-Zone (Rhesus). *Plastischer Reconstz* 21: 1065-1070.

Henderson, E. (2007) Platyrrhine dental eruption sequences. *American Journal of Physical Anthropology* 134: 226-239.

Herring, S.W., & Herring, S.E. (1974) The superficial masseter and gape in mammals. *The American Naturalist* 108: 561-576.

Hershkovitz, P. (1977) *Living New World Monkeys (Platyrrhini), With an Introduction to Primates, Vol. I*. Chicago: University of Chicago Press.

Hertwig, O. (1879) Uber das hautskelet der fische 2: Das hautskelet der Ganoiden (*Lepidosteus* und *Polypterus*). *Morphologisches Jahrbuch* 5: 1-21.

Hertwig, O. (1892). *Text-book of the embryology of man and mammals*. Mark., E.L., trans. New York: MacMillan.

Hillson, S. (1996) *Dental anthropology*, 2nd Edition. Cambridge: Cambridge University Press.

Hladik, A., & Hladik, C.M. (1969) Rapports trophieques entre végétation et primates dans la forêt de Barro Colorado (Panama). *Terre Vie* 1: 25-117.

Hoffman, M.M., & Schour, I. (1938) Rate and gradients of growth in rat molar as demonstrated by injections of alizarin red. *Journal of Dental Research* 17: 307-308.

Hogg, R. (2008). Body mass and Retzius periodicity in New World Primates. Abstract. *American Journal of Physical Anthropology* 135, Supplement 46.

Hogg, R., Alexander J.P., Delman B.N., & Márquez, S. (2003) Computer tomographic analysis of growth and development in juvenile adapiform primates from the Eocene of North America. *American Journal of Physical Anthropology* Supplement 36: 116.

Hogg, R., Ravosa, M., Ryan, T., & Vinyard, C. (in press) The functional morphology of the anterior masticatory apparatus in tree-gouging marmosets (*Callithrix,* Cebidae, Platyrrhini). *Journal of Morphology.*

Horovitz, I., Zardoya, R., Meyer, A. (1998) Platyrrhine systematics: a simultaneous analysis of molecular and morphological data. *American Journal of Physical Anthropology* 106: 261-281.

Hunter, J. (1771) *The Natural History of the Human Teeth, Explaining Their Structure, Use, Formation, Growth, and Diseases.* London: J. Johnson.

Huxley, J.S. (1938) Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research. *American Naturalist* 72: 416-433.

Hylander, W.L. (1978) Incisal bite force direction in humans and the functional significance of mammalian mandibular translation. *American Journal of Physical Anthropology* 48: 1-7.

Hylander, W.L. (1979) The functional significance of primate mandibular form. *Journal of Morphology* 160: 223-240.

Janson, C.H., Boinksi, S. (1992) Morphological and behavioral adaptations for foraging in generalist primates: the case of the cebines. *American Journal of Physical Anthropology* 88: 483-498.

Janson, C.H., van Schaik, C. (1993) Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira M.E., & Fairbanks L.A. (eds.), *Juvenile primates: life history, development and behavior*. New York: Oxford University Press. p 57-76.

Jarman, P. (1983) Mating system and sexual dimorphism in large, terrestrial, mammalian herbivores. *Biological Reviews* 58: 485-520.

Jerison, H.J. (1973) *Evolution of the Brain and Intelligence.* New York: Academic.

Jernvall, J. (2000) Linking development with generation of novelty in mammalian teeth. *Proceedings of the National Academy of Sciences* 97: 2641-2645.

Jernvall, J, & Jung, H.S. (2000) Genotype, phenotype, and developmental biology of molar tooth characters. *Yearbook of Physical Anthropology* 43: 171-190.

Jernvall, J., Kettunen, P., Karavanova, I., Martin, L.B., & Thesleff, I. (1994) Evidence for the role of the enamel knot as a control center in mammalian tooth cusp formation: non-dividing cells express growth stimulating Fgf-4 gene. *International Journal of Developmental Biology* 38: 463-469.

Jernvall, J., & Thesleff, I. (2000) Reiterative signaling and patterning during mammalian tooth morphogenesis. *Mechanisms of Development* 92: 19-29.

Joffe, T.H. (1997) Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution* 32: 593-605.

Johnson, G., & Nudds, J. (1975) Carboniferous coral geochronometers. In Rosenberg, G., & Runcorn, S. (eds.), *Growth Rhythms and the History of the Earth's Rotation*. New York: Wiley, pp.27-42.

Johnston, P.A. (1979) Growth rings in dinosaur teeth. *Nature* 278: 635-636.

Jungers, W., Demes, B., Godfrey, L.R. (2008) How big were the 'giant' extinct lemurs of Madagascar? In Fleagle, J., & Gilbert, C. (eds.), *Elwyn Simons: A Search for Origins*. New York: Springer, pp. 343-360.

Kappeler, P.M. (1996) Causes and consequences of life-history variation among strepsirhine primates. *American Naturalist* 148: 868-891.

Kappeler, P.M., Pereira, M.E., & Van Schaik, C.P. (2003) Primate life histories and socioecology. In Kappeler, P.M. & Pereira, M.E. (eds.), *Primate life histories and socioecology.* Chicago: University of Chicago Press, pp. 1-20.

Karsenty, G. (2001) Central control of bone formation. *Advances in Nephrology* 31: 119-133.

Kawasaki, K., Tanaka, S., Ishikawa, T. (1979) On the daily incremental lines in human dentine. *Archives of Oral Biology* 24: 939-943.

Kay, R.F. (1975) The functional adaptations of primate molar teeth. *American Journal of Physical Anthropology* 43: 195-215.

Kay, R.F. (1990) The phyletic relationships of extant and fossil Pitheciinae (Platyrrhini, Anthropoidea). *Journal of Human Evolution* 19: 175-208.

Kay, R.F., & Cozzuol, M.A. (2006) New platyrrhine monkeys from the Solimões Formation (late Miocene, Acre State, Brazil). *Journal of Human Evolution* 50: 673-686.

Kay, R.F., Fleagle, J.G., Mitchell, T.R., Colbert, M., Bown, T., & Powers, D.W. (2008) The anatomy of *Dolichocebus gaimanensis*, a stem platyrrhine monkey from Argentina. *Journal of Human Evolution* 54: 323-382.

Kay, R.F., Plavcan, J.M., Glander, K.E., Wright, P.C. (1988) Sexual selection and canine dimorphism in New World monkeys. *American Journal of Physical Anthropology* 77: 385-397.

Kay, R.F., Williams, B.A., & Anaya, F. (2001) The adaptations of *Branisella boliviana*, the earliest South American monkey. In Plavcan, M., *et al.* (eds.), *Reconstructing Behavior in the Primate Fossil Record.* New York: Kluwer, pp. 339-370.

Kay, R.F., Williams, B.A., Ross, C.F., Takai, M., & Shigehara, N. (2004) Anthropoid origins: a phylogenetic analysis. In Ross, C.F., & Kay, R.F. (eds.), *Anthropoid Origins: New Visions.* New York: Kluwer/Plenum, pp. 91-135.

Kelley, J. (1995) Sex determination in Miocene catarrhine primates. *American Journal of Physical Anthropology* 96: 391-417.

Kelley J., Dean, M.C., & Reid, D.J. (2001) Molar growth in the late Miocene hominoid, *Dryopithecus laietanus*. In Brook, A. (ed.), *Dental Morphology.* Sheffield, UK: Sheffield Academic, pp 123-134.

Kinzey, W.G. (1974) Ceboid models for the evolution of hominoid dentition. *Journal of Human Evolution* 3: 193-203.

Kinzey, W.G. (1992) Diet and dental adaptations in the Pitheciinae. *American Journal of Physical Anthropology* 88: 499-514.

Kinzey, W.G. (1997) Part II: Synopsis of New World primates. In Kinzey, W.G. (ed.), *New World Primates: Ecology, Evolution, and Behavior.* Edison, NJ: Aldine Transaction, pp. 169-324.

Kinzey, W.G., & Norconk, M.A. (1993) Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. *International Journal of Primatology* 14: 207-227.

Kinzey, W.G., Rosenberger, A.L., Ramirez, M. (1975) Vertical clinging and leaping in a neotropical anthropoid. *Nature* 225: 327-328.

Kirk, E.C. (2006) Visual influences on primate encephalization. *Journal of Human Evolution* 51: 76-90.

Kleiber, M. (1947) Body size and metabolic rate. *Physiological Reviews* 27: 511-541.

Klein, D.C., Moore, R.Y., Reppert, S.M., eds. (1991) *Suprachiasmatic Nucleus: The Mind's Clock*. New York: Oxford University Press.

Koenigswald, W.v., Rensberger, J.M., & Pfretzschner, H.U. (1987) Changes in the tooth enamel of early Paleocene mammals allowing increased diet diversity. *Nature* 328: 150-152.

Koenigswald, W.v., & Clemens,W.A. (1992) Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. *Scanning Microscopy.* 6: 195-218.

Koenigswald, W.v. (2000) Two different strategies in enamel differentiation: Marsupialia versus Eutheria. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 107-118.

Kollar, E.J., & Lumsden, A.G. (1979) Tooth morphogenesis: the role of innervation during induction and pattern formation. *Journal Biologie Buccale* 7: 49-60.

Krishtalka, L., Schwartz, J.H. (1978) Phylogenetic relationships of plesiadapiform-tarsiiform primates. *Annals of the Carnegie Museum* 47: 515-540.

Krishtalka, L., Stucky, R.K., & Beard, K.C. (1990) The earliest fossil evidence for sexual dimorphism in primates. *Proceedings of the National Academy of Sciences* 87: 5223-5226.

Lack, D. (1954) *The Natural Regulation of Animal Numbers*. Oxford: Clarendon.

Lacruz, R.S., & Bromage, T.G. (2006) Appositional enamel growth in molars of South African fossil hominids. *Journal of Anatomy* 209: 13-20.

Lacruz, R.S., Dean., M.C., Ramirez-Rozzi, F., & Bromage, T.G. (2008) Megadontia, striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. *Journal of Anatomy* 213: 148-158.

Lacruz, R.S., Ramirez-Rozzi, F., & Bromage, T.G. (2006) Variation in enamel development of South African fossil hominids. *Journal of Human Evolution* 51: 580-590.

Lambert, J.E. (2007) Seasonality, fallback strategies, and natural selection: A chimpanzee and cercopithecoid model for interpreting the evolution of the hominin diet. In Ungar, P.S. (ed.), *Evolution of the human diet: the known, the unkown, and the unknowable.* Oxford: Oxford University Press, pp. 324-343.

Lambert, J.E., Chapman, C.A., Wrangham, R.W., & Conklin-Brittain, N.L. (2004) Hardness of cercopithecine foods: implications for the critical function of enamel thickness in exploiting fallback foods. *American Journal of Physical Anthropology* 125: 363-368.

Lande, R. (1982) A quantitative genetic theory of life history evolution. *Ecology* 63: 607-615.

Leakey, M., Walker, A. (1997) *Afropithecus* function and phylogeny. In Begun, D., Ward, C., Rose, M. (eds.), *Function, Phylogeny, and Fossils: Miocene Hominoid Evolution.* New York: Plenum, pp. 225-239.

Lee, N.K., Sowa, H., Ferron., M., Ahn, J.D., Confavreaux, C., Dacquin, R., Mee, P., McKee, M., Jung, D., Zhang, Z., Kim, J., Mauvais-Jarvis, F., Ducy, P., & Karsenty, G. (2007) Endocrine regulation of energy metabolism by the skeleton. *Cell* 130: 456-469.

Lee, P.C. (1999) Comparative ecology of postnatal growth and weaning among haplorhine primates. In Lee, P.C. (ed.), *Comparative Primate Socioecology*. Cambridge: Cambridge University Press, pp. 111-139.

Leeuwenhoeck, A. (1665-1678) Microscopical observations of the structure of teeth and other bones: made and communicated, in a letter by Mr. Anthony Leeuwenhoeck. *Philosophical Transactions of the Royal Society of London* 12: 1002-1003.

Leeuwenhoek, A. (1800) *The Select Works of Antoni van Leeuwenhoek*. Hoole, S., trans. London: Sidney.

Leigh, S.R. (1992) Patterns of variation in the ontogeny of primate body size dimorphism. *Journal of Human Evolution* 23: 27-50.

Leigh, S.R. (1994) Ontogenetic correlates of diet in anthropoid primates. *American Journal of Physical Anthropology* 94: 499-522.

Leigh, S.R. (1995) Socioecology and the ontogeny of sexual size dimorphism in anthropoid primates. *American Journal of Physical Anthropology* 97: 339-356.

Leigh, S.R. (2004) Brain growth, life history, and cognition in primate and human evolution. *American Journal of Primatology* 62: 139-164.

Leigh, S.R. (2007) Homoplasy and the evolution of ontogeny in papionin primates. *Journal of Human Evolution* 52: 536-558.

Leigh, S.R., & Bernstein, R.M. (2006) Ontogeny, life history, and maternal investment in baboons. In Swedell, L., & Leigh, S.R. (eds.), *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives.* New York: Springer, pp. 225-255.

Leigh, S.R., & Cheverud, J.M. (1991) Sexual dimorphism in the baboon facial skeleton. *American Journal of Physical Anthropology* 84: 193-208.

Leigh, S.R., Setchell, J.M., & Buchanan, L.S. (2005) Ontogenetic basis of canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology* 127: 296-311.

Leigh, S.R., Setchell, J.M., & Charpentier, M., Knapp, L.A., & Wickings, E.J. (2008) Canine tooth size and fitness in male mandrills (*Mandrillus sphinx*). *Journal of Human Evolution* 55: 75-85.

Leigh, S.R., Shea, B.T. (1995) Ontogeny and the evolution of adult body size dimorphism in apes. *American Journal of Physical Anthropology* 36: 37-60.

Leigh, S.R., Terranova, C.J. (1998) Comparative perspectives on bimaturism, ontogeny, and dimorphism in lemurid primates. *International Journal of Primatology* 19: 723-749.

Leutenegger, W. (1978) Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* 271: 610-611.

Leutenegger, W., & Cheverud, J. (1982) Correlates of sexual dimorphism in primates: ecological and size variables. *International Journal of Primatology* 3: 387-402.

Leutenegger, W., & Kelley, J.T. (1977) Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates* 18: 117-136.

Lindenfors, P. (2002) Sexually antagonistic selection on primate size. *Journal of Evolutionary Biology* 15: 595-607.

Lindstedt, S.L., & Calder, W.A. (1981) Body size, physiological time, and longevity of homeothermic animals. *The Quarterly Review of Biology* 56: 1-16.

Long, J., Cooper, R. (1968) Physical growth and dental eruption in captive-bred squirrel monkeys, *Saimiri sciureus* (Letecia, Colombia). In Rosenblum, L., Cooper, R. (eds.), *The Squirrel Monkey*. New York: Academic, pp. 193-205.

Lowenstam, H.A., & Weiner, S. (1989) *On Biomineralization*. New York: Oxford University Press.

Lowrey, P.L., & Takahashi, J.S. (2001) Mammalian circadian biology: elucidating genome-wide levels of temporal organization. *Annual Review of Genomics and Human Genetics* 5: 407-441.

Lucas, P.W., (2004) Dental functional morphology. Cambridge: Cambridge University Press.

Lucas, P.W., Constantino, P., Wood, B.A., Lawn, B.R. (2008a) How enamel form may provide key information on the properties of fallback foods. Abstract. *American Journal of Physical Anthropology* Supplement 46: 143.

Lucas, P.W., Constantino, P., Wood, B.A., & Lawn, B. (2008b) Dental enamel as a dietary indicator in mammals. *BioEssays* 30: 374-385.

Lucas, P.W., & Corlett, R.T. (1991) Quantitative aspects of the relationship between dentitions and diets. In Vincent, J.F., & Lillford, P. (eds.), *Feeding and the Texture of Food.* Cambridge: Cambridge University Press, pp. 93-121.

Lucas, P.W., & Peters, C.R. (2001) Function of postcanine tooth shape in mammals. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 282-289.

Luckett, W.P., & Maier, W. (1982) Development of deciduous and permanent dentition in Tarsius and its phylogenetic significance. *Folia Primatologica* 37: 1-36.

Lumsden, A.G. (1988) Spatial organization of the epithelium and the role of neural crest cells in the initiation of the mammalian tooth germ. *Development* 103: 155-169.

Maas, M.C. (1986) Function and variation of enamel prism decussation in ceboid primates. Abstract. *American Journal of Physical Anthropology* 69: 233-234.

Maas, M.C. (1994) Enamel microstructure in Lemuridae (Mammalia, Primates): assessment of variability. *American Journal of Physical Anthropology* 95: 221-241.

Maas, M.C., & Dumont, E.R. (1999) Built to last: the structure, function, and evolution of primate dental enamel. *Evolutionary Anthropology* 8: 133-152.

Maas, M.C., & O'Leary, M. (1996) Evolution of molar enamel microstructure in North American Notharctidae (primates). *Journal of Human Evolution* 31: 293-310.

Maas, M.C., & Thewissen, J.G.M (1995) Enamel microstructure of *Pakicetus* (Mammamlia: Archaeoceti). *Journal of Paleontology* 69: 1154-1163.

Maas, R., Bei, M. (1997) The genetic control of early tooth development. *Critical Review of Oral Biology and Medicine* 8: 4-39.

MacArthur, R.H., Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton: Princeton University Press.

Macho, G.A. (2001) Primate molar crown formation times and life history evolution revisited. *American Journal of Primatology* 55: 189-201.

Macho, G.A., Jiang, Y., & Spears, I.R. (2003) Enamel microstructure: a truly three-dimensional structure. *Journal of Human Evolution* 45: 81-90.

Macho, G.A., Reid, D.J., Leakey, M.G., Jablonski, N., & Beynon, A.D. (1996) Climatic effects on dental development of *Theropithecus oswaldi* from Koobi Fora and Olorgesailie. *Journal of Human Evolution* 30:57-70.

Maglio, V.J. (1972) Evolution of mastication in the elephantidae. *Evolution* 26: 638-658.

Mallatt, J. (1996) Ventilation and the origin of jawed vertebrates: a new mouth. *Zoological Journal of the Linnaean Society* 117: 329-404.

Mann, A. (1975) *Some Paleodemographic Aspects of the South African Australopithecines*. Philadelphia: University of Pennsylvania Press.

Mann, A., Monge, J., Lampl, M. (1991) An investigation into the relationship between perikymata counts and crown formation times. *American Journal of Physical Anthropology* 86: 175-188.

Manning, J.T., & Chamberlain, A.T. (1993) Fluctuating asymmetry, sexual selection, and canine teeth in primates. *Proceedings of the Royal Society of London B* 251: 83-87.

Marshall, A.J., Boyko, C.M., Feilen, R.H., Boyko, R.H., & Leighton, M. (2009) Fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology* 140: 603-614.

Marshall, A.J., & Wrangham, R.W. (2007) Evolutionary consequences of fallback foods. *International Journal of Primatology* 28: 1219-1235.

Marsland, E.A. (1951) A histological investigation of amelogenesis in rats. *British Dental Journal* 91: 251-261.

Marsland, E.A. (1952) A histological investigation of amelogenesis in rats II. *British Dental Journal* 92: 109-119.

Martin, L.B. (1983) *The relationships of the later Miocene Hominoidea.* Ph.D. Dissertation, University College London.

Martin, L.B., Olejniczak, A.J., & Maas, M.C. (2003) Enamel thickness and microstructure in pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus*. *Journal of Human Evolution* 45: 351-367.

Martin, R.D. (1990) *Primate Origins and Evolution: a Phylogenetic Reconstruction.* Princeton: Princeton University Press.

Massler, M., Schour, I. (1941) Growth potential and appositional life span of the enamel and dentin forming cells in the human deciduous teeth and first permanent molars. *Journal of Dental Research* 20: 282-283.

Massler, M., Schour, I. (1946) The appositional lifespan of the enamel and dentine forming cells. *Journal of Dental Research* 25: 145-50.

Masterson, T.J. (2003) Canine dimorphism and interspecific canine form in *Cebus*. *International Journal of Primatology* 24: 159-178.

Masterson, T.J., & Hartwig, W.C. (1998) Degrees of sexual dimorphism in *Cebus* and other New World monkeys. *American Journal of Physical Anthropology* 107: 243-256.

McCollum & Sharpe, P.T. (2001) Evolution and development of teeth. *Journal of Anatomy* 199: 153-159.

McFarlin, S. (2006) *Ontogenetic variation in long bone microstructure in catarrhines and its significance for life history.* Ph.D. dissertation, City University of New York.

McNab, B.K. (1980) Food habits, energetic, and population biology of mammals. *American Naturalist* 116: 106-124.

Miletich, I., Sharpe, P.T. (2003) Normal and abnormal dental development. *Human Molecular Genetics* 12: R69-R73.

Mills, J.R.E. (1972) Evolution of mastication. *Proceedings of the Royal Society of Medicine* 65: 392-396.

Milton, K. (1980) *The foraging strategy of howler monkeys: a study in primate economics.* New York: Columbia University Press.

Mimura, F. (1939) The periodicity of growth lines seen in enamel. *Kobyo-shi* 13: 454-455.

Mina, M., & Kollar, E.J. (1987) The induction of odontogenesis in non-dental mesenchyme combined with early murine mandibular arch epithelium. *Archives of Oral Biology* 32:123-127.

Mohr, R.E. (1975) Measured periodicities of the Biwabik (Precambrian) stromatolites and their geophysical significance. In Rosenberg, G., & Runcorn, S. (eds.), *Growth Rhythms and the History of the Earth's Rotation*. New York: Wiley, pp. 43-56.

Molnar, S., Prybeck, T., Gantt, D., Elizondo, R., Wilkerson, J. (1981) Dentin apposition rates as markers of primate growth. *American Journal of Physical Anthropology* 55: 443-453.

Moore, R. Y. & Eichler, V. B. Loss of a circadian adrenal corticosterone rhythm following suprachiasmatic lesions in the rat. *Brain Research* 42, 201–206 (1972).

Moss-Salentijn, L., Moss, M.L., & Yaun, M.S.T. (1997) The ontogeny of mammalian enamel. In Koenigswald, W.v., & Sander, P.M. (eds.), *Tooth Enamel Microstructure*. Rotterdam: Balkema, pp. 5-30.

Mummery, J.H. (1914) On the nature of the tubes in marsupial enamel, and its bearing upon enamel development. *Philosophical Transactions of the Royal Society of London, Series B* 205: 295-313.

Nash, L.T. (1986) Dietary, behavioral, and morphological aspects of gummivory in primates. *Yearbook of Physical Anthropology* 29: 113-137.

Needham, J. (1933) On the dissociability of the fundamental processes in ontogenesis. *Biological Reviews* 8: 180-223.

Newman & Poole (1993) Dental enamel growth. *Journal of the Royal Society of Medicine* 86: 61.

Newman, H., & Poole, D. (1974) Observations with scanning and transmission electron microscopy on the structure of human surface enamel. *Archives of Oral Biology* 19: 1135-1143.

Nicolson, N.A. (1987) Infants, mothers, and other females. In Smuts, B. Cheney, D., Seyfarth, R., Wrangham, R., & Struhsaker, T. (eds.), *Primate Societies*. Chicago: University of Chicago Press, pp. 330-342.

Nogami, Y., & Natori, M. (1986) Fine structure of the dental enamel in the family Callitrichidae (Ceboidea, Primates). *Primates* 27: 245-258.

Nogami, Y., & Yoneda, M. (1983) Structural patterns of enamel in the superfamily Ceboidea. *Primates* 24: 567-575.

Noyes, F.B., & Thomas, N.G. (1921) *A Text-Book of Dental Histology and Embryology, Including Laboratory Directions.* New York: Lea & Febiger.

Okada, M. (1943) Hard tissues of animal body - highly interesting details of Nippon studies in periodic patterns of hard tissue are described. *Shanghai Evening Post, Medical Edition* 43: 15-31.

O'Higgins, P., & Collard, M. (2002) Sexual dimorphism and facial growth in papionin monkeys. *Journal of Zoology* 257: 255-272.

Opazo, J., Wildman, D., Prychitko, T., Johnson, R. (2006) Phylogenetic relationships and divergence times among New World monkeys (Platyrrhini, Primates). *Molecular Phylogenetics and Evolution* 40: 274-280.

Osborn, J.W. (1967) Three-dimensional reconstructions of enamel prisms. *Journal of Dental Research* 46:1412-1419.

Osterholtz, M., Walter, L., & Roos, C. (2009) Retropositional events consolidate the branching order among New World monkey genera. *Molecular Phylogenetics and Evolution* 50: 507-513.

Owen, R. (1845) *Odontography – A Treatise on the Comparative Anatomy of the Teeth*. London: Hippolyte Bailliere.

Palamara, J., Phakey, P.P., Rachinger, W.A., & Orams, H.J. (1980) Electron microscopy of surface enamel of human unerupted and erupted teeth. *Archives of Oral Biology* 25: 715-725.

Panda, S., Hogenesch, J.B., & Kay, S.A. (2002) Circadian rhythms from flies to human. *Nature* 417: 329-335.

Pannella, G. (1975) Paleontological clocks and the history of the earth's rotation. In Rosenberg, G., & Runcorn, S. (eds.), *Growth Rhythms and the History of the Earth's Rotation*. New York: Wiley, pp. 253-284.

Paul, P.T. (1896) Some points of interest in dental histology: the enamel organ. *Dental Record* 16: 493-498.

Pereira & Leigh 2003 Pereira, M.E., & Leigh, S.R. (2003) Modes of primate development. In Kappeler, P.M., & Pereira, E. (eds.), *Primate Life Histories and Socioecology*. Chicago: University of Chicago Press, pp. 149-176.

Peres Line, S.R., & Novaes, P.D. (2005) The development and evolution of mammalian enamel: structural and functional aspects. *Brazilian Journal of Morphological Science* 22: 67-72.

Pfretzschner, H.U. (1988) Structural reinforcement and crack propagation in enamel. In Russell, D.E., Santoro, J.P., & Sigogneau-Russell, D.E. (eds.), *Teeth revisited.* Paris: Memoires du Musée Nationale d'Histoire Naturelle. pp. 133—43.

Pianka, E. (1970) On r and K selection. *The American Naturalist* 104: 592-597.

Pickerill, H.P. (1913) The structure of enamel. *Dental Cosmos* 55:969-988.

Pickford, M. (1986) Sexual dimorphism in *Proconsul*. *Human Evolution* 1: 111-148.

Pittendrigh, C.S. (1981) Circadian systems: entrainment. In Aschoff, J. (ed.), *Handbook of Behavioral Neurobiology: Biological Rhythms*. New York: Plenum, pp. 95–124.

Pittendrigh, C.S., & Minis., D.H. (1964) The entrainment of circadian oscillations by light and their role as photoperiodic clocks. *The American Naturalist* 98: 261-294.

Plavcan, J.M. (2001) Sexual dimorphism in primate evolution. *Yearbook of Physical Anthropology* 44: 25-53.

Plavcan, J.M., & Van Schaik, C.P. (1992) Intrasexual competition and canine dimorphism in anthropoid primates. *American Journal of Physical Anthropology* 87: 461-477.

Plavcan, J.M., & Van Schaik, C.P. (1997) Intrasexual competition and body weight dimorphism in anthropoid primates. *American Journal of Physical Anthropology* 103: 37-68.

Pollock CM, Shadwick RE (1994) Relationship between body mass and biomechanical properties of limb tendons in adult mammals. *American Journal of Physiology* 266: 1016-1021.

Popowics, T.E., Rensberger, J.M., & Herring, S.W. (2004) Enamel microstructure and microstrain in the fracture of human and pig molar cusps. *Archives of Oral Biology* 49: 595-605.

Porter, L.M. (2001) Dietary differences among sympatric Callitrichinae in Northern Bolivia: *Callimico goeldii, Saguinus fuscicollis,* and *S. labiatus. International Journal of Primatology* 22: 961-992.

Porter, L.M., & Garber, P.A. (2004) Goeldi's monkeys: a primate paradox? *Evolutionary Anthropology* 13: 104-115.

Power, M.L. (1996) The other side of callitrichines gummivory: digestibility and nutritional value. In Norconk, M., Garber, P., & Rosenberger, A. (eds.), *Adaptive Radiations of Neotropical Primates*. New York: Springer, pp. 97-110.

Power, M.L., & Oftedal, O.T. (1996) Differences among captive callitrichids in the digestive responses to dietary gum. *American Journal of Primatology* 40: 131-144.

Promislow, D.E.L. (1992) Costs of sexual selection in natural populations of mammals. *Proceedings in the Biological Sciences* 247: 203-210.

Raff, E.C., & Raff, R.A. (2001) Dissociability, modularity, evolvability. *Evolution and Development* 2: 235-237.

Raff, R.A. (1996) *The Shape of Life: Genes, Development, and the Evolution of Animal Form.* Chicago: University of Chicago Press.

Raff, R.A. (2000) Evo-devo: the evolution of a new discipline. *Nature Reviews: Genetics* 1: 74-79.

Raff, R.A., & Sly, B.J. (2001) Modularity and dissociation in the evolution of gene expression territories in development. *Evolution and Development* 2: 102-113.

Rafferty, K.L., Walker, A., Ruff, C.B., Rose, M.D., Andrews, P. (1995) Postcranial estimates of body weight in *Proconsul*, with a note on the distal tibia of *P. major* from Napak, Uganda. *American Journal of Physical Anthropology* 97: 391-402.

Raia, P., & Meiri, S. (2006) The island rule in large mammals: paleontology meets ecology. *Evolution* 60: 1731-1742.

Ralls, K. (1977) Sexual dimorphism in mammals: avian models and unanswered questions. *The American Naturalist* 111: 917-938.

Ramirez, M.F., Freese, C.H., & Revilla, J. (1977) Feeding ecology of the pygmy marmoset, *Cebuella pygmaea*, in Northeastern Peru. In: Kleiman, D.G. (ed.), *The Biology and Conservation of the Callitrichidae*. Washington D.C.: Smithsonian Institution, pp 91-104.

Ramirez-Rozzi, F. (2002) Enamel microstructure in hominids: new characteristics for a new paradigm. In Minugh-Purvis, N., & MacNamara, K.J. (eds.), *Human Evolution Through Developmental Change*. Baltimore: Johns Hopkins, pp. 319-348.

Ravosa, M.J. (1990) Functional assessment of subfamily variation in maxillomandibular morphology among Old World monkeys. *American Journal of Physical Anthropology* 82: 199-212.

Ravosa, M.J., Hogg, R.T., & Vinyard, C.J. (in press) Exudativory and primate skull form. In Burrows, A., & Nash, L.T. (eds.), *Evolution of Exudativory in Primates*. New York: Springer.

Rawson, M.J., Cornelissen, G., Holte, J., Katinas, G., Eckert, E., Siegelova, J., Fiser, B., & Halberg, F. (2000) Circadian and circaseptan components of blood pressure and heart rate during depression. *Scripta Medica* 73: 117-124.

Ray, D., Xing, J., Hedges, D., Hall, M., Laborde, M., Anders, B., White, B., Stoilova, N., Fowlkes, J., Landry, K., Chemnick, L., Ryder, O., Batzer, (2005) *Alu* insertion loci and platyrrhine primate phylogeny. *Molecular Phylogenetics and Evolution* 35: 117-126.

Ray, D., Xing, J., Salem, A., Batzer, M. (2006) SINEs of a nearly perfect character. *Systematic Biology* 55: 928-935.

Ray, D. (2007) SINEs of progress: mobile element applications to molecular ecology. *Molecular ecology* 16: 19-33.

Rees, J.W., Kainer, R.A., & Davis, R.W. (1966) Histology, embryology, and gross morphology of the mandibular dentition in mule deer. *Journal of Mammalogy* 47: 640-654.

Reeser, L.A. (1984) Morphological affinities of new fossil talus of *Dolichocebus gaimanensis*. *American Journal of Physical Anthropology* 63: 206-207.

Reid, D.J., Beynon, A.D., & Ramirez-Rozzi, F.V. (1998a) Histological reconstruction of dental development in four individuals from a medieval site in Picardie, France. *Journal of Human Evolution* 35: 463-477.

Reid, D.J., & Ferrell, R.J. (2006) The relationship between number of striae of Retzius and their periodicity in imbricational enamel formation. *Journal of Human Evolution* 50: 195-202.

Reid, D.J., Schwartz, G.T, Dean, M.C., Chandresakera, M.S. (1998b) A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. *Journal of Human Evolution* 35: 427-448.

Reif, W.E. (1982) Evolution of dermal skeleton and dentition in vertebrates: the odontode regulation theory. New York: Plenum.

Reith, D.J. (1961) The ultrastructure of ameloblasts during matrix formation and the maturation of enamel. *Journal of Biophysical and Biochemical Cytology* 9: 825-839.

Rendall, D., & DiFiore, A. (2007) Homoplasy, homology, and the perceived special status of behavior in evolution. *Journal of Human Evolution* 52: 504-521.

Rensberger, J.M. (2000) Pathways to functional differentiation in mammalian enamel. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 252-269.

Retzius, A. (1837) Bemerkungen uber den innern Bau der Zahne, mit besonderer Rucksicht auf den im Zahnknochen vorkommenden Rohrenbau. In Muller, J (ed.), *Archiv fur Anatomie, Physiologie und Wissenschaftliche Medicin, in Verbindung mit Gelehrten*. Berlin: Verlag von W. Thome, pp. 486-566 + plates.

Richtsmeier, J.T., Cheverud, J.M., Danahey, S.E., Corner, B.D., & Lele, S. (1993) Sexual dimorphism of ontogeny in the crab-eating macaque (*Macaca fascicularis*). *Journal of Human Evolution* 25: 1-30.

Risnes, S. (1986) Enamel apposition rate and the prism periodicity in human teeth. *European Journal of Oral Sciences* 94: 294-404.

Risnes, S. (1998) Growth tracks in dental enamel. *Journal of Human Evolution* 35: 331- 350.

Risnes, S. (1999) Mature enamel morphology and forming enamel dynamics: crystal orientation, crystal continuity, prism diameter, Retzius lines, and prism cross- striations. In Mayhall, J.T., & Heikkinen, T. (eds.), *Dental Morphology '98: Proceedings of the 11th International Symposium on Dental Morphology*. Oulu, Finland: Oulu University Press, pp. 312-322.

Robinson, C., Kirkham, J., Brookes, S.J., Bonass, W.A., & Shore, R.C. (1995) The chemistry of enamel development. *International Journal of Developmental Biology* 39: 145-152.

Robinson, T.J., Ruiz-Herrera, A., & Avise, J.C. (2008) Hemiplasy and homoplasy in the karyotypic phylogenies of mammals. *Proceedings of the National Academy of Sciences* 105: 14477-14481.

Rochow, T.G., & Tucker, P.A. (1994) Introduction to Microscopy by Means of Light, Electrons, X-Rays, or Acoustics, 2nd edition. New York: Springer.

Roenneberg, T., & Morse, D. (1993) Two circadian oscillators in one cell. *Nature* 362: 362-364.

Romer, A.S., & Parsons, T.S. (1977) *The Vertebrate Body*, 5th edition. Philadelphia: Saunders.

Rönnholm, E. (1961) Ultra-structure of developing human enamel electron microscopy of human amelogenesis. *Journal of Dental Research* 40: 668-669.

Rönnholm, E. (1962a) The amelogenesis of human teeth as revealed by electron microscopy. *Journal of Ultrastructure Research* 6: 249-303.

Rönnholm, E. (1962b) An electron microscopic study of the amelogenesis in human teeth. *Journal of Ultrastructure Research* 6: 229-248.

Rosenberger, A.L. (1978) Loss of incisor enamel in marmosets. *Journal of Mammalogy* 59: 207-208.

Rosenberger, A.L. (1979) Cranial anatomy and implications of *Dolichocebus*, a late Oligocene ceboid primate. *Nature* 279: 416-418.

Rosenberger, A.L. (1981) Systematics: the higher taxa. In Coimbra-Filho, A.F., & Mittermeier, R.A. (eds.), *Ecology and Behavior of Neotropical Primates.* Rio de Janeiro: Academia Brasilia de Ciencias, pp. 9-27.

Rosenberger, A.L. (1984) Fossil New World monkeys dispute the molecular clock. *Journal of Human Evolution* 13: 737-742.

Rosenberger, A.L. (1992) Evolution of feeding niches in New World monkeys. *American Journal of Physical Anthropology* 88: 525-562.

Rosenberger, A.L. (2001) Platyrrhine paleontology and systematic: the paradigm shifts. In Hartwig, W. (ed.), *The Primate Fossil Record.* Cambridge: Cambridge University Press, pp. 151-160.

Rosenberger, A.L. (2006) Protoanthropoidea (Primates: Simiiformes): a new primate higher taxon and a solution to the *Rooneyia* problem. *Journal of Mammalian Evolution* 13: 139-146.

Rosenberger, A.L., Hartwig, W.C., & Wolff, R.G. (1991) *Szalatavus attricuspis*, an early platyrrhine primate. *Folia Primatologica* 56: 225-233.

Rosenberger, A.L., Hogg, R.T., & Wong, S.M. (2008) The eyes of *Rooneyia* and the postorbital septum. In Sargis, E.J., & Dagosto, M. (eds.), *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay.* Dordrecht, Netherlands: Springer, pp. 325-346.

Rosenberger, A.L., & Kinzey, W.G. (1976) Functional patterns of molar inclusion in platyrrhine primates. *American Journal of Physical Anthropology* 45: 281-297.

Rosenberger, A.L., Setoguchi., T., & Shigehara, N. (1990) The fossil record of callitrichine primates. *Journal of Human Evolution* 19: 209-236.

Rosenberger, A.L., & Strier, K.B. (1989) Adaptive radiation of the ateline primates. *Journal of Human Evolution* 18: 717-750.

Rosenberger, A.L., & Tejedor, M. (in press) The misbegotten: long lineages, long branches, and the interrelationships of *Aotus, Callicebus*, and the Saki-Uakaris. In Barnett, A.A., Viega, L.M., Ferarri, S.F., & Norconk, M.A. (eds.), *Evolutionary Biology and Conservation of Titis, Sakis, and Uacaris.* Cambridge: Cambridge University Press.

Rosenberger, A.L, Tejedor, M., Cooke, S.B., & Pekar, S. (2009) Platyrrhine ecophylogenetics in space and time. In Garber, P., Estrada, A., Bicca-Marques, J.C., Heymann, E.W., & Strier, K.B. (eds.), *South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation*. New York: Springer, pp. 69-116.

Ross, C. (1991) Life history patterns of New World monkeys. *International Journal of Primatology* 12: 481-502.

Ross. C., & Jones, K.E. (1999) Socioecology and the evolution of primate reproductive rates. In Lee, P.C. (ed.), *Comparative primate socioecology.* Cambridge: Cambridge University Press, pp. 73–110.

Ross, C., Williams, B., & Kay, R.F. (1998) Phylogenetic analysis of anthropoid relationships. *Journal of Human Evolution* 35: 221-306.

Ruch, I.V., & Karcher-Djuricic, V. (1975) On odontogenic tissue interactions. In Slavkin, H.C., & Greulich, R.C. (eds.), *Extracellular matrix influences on gene expressions.* New York: Academic, p. 549.

Runcorn, S.K. (1975) Paleontological and astronomical observations on the rotational history of the earth and the moon. In Rosenberg, G., & Runcorn, S. (eds.), *Growth Rhythms and the History of the Earth's Rotation*. New York: Wiley, pp. 285-292.

Sander , P.M. (1997) Non-mammalian synapsid enamel and the origin of mammalian enamel prisms: the bottom-up perspective. In Koenigswald, W.V., & Sander, P.M. (eds.), *Tooth Enamel Microstructure*. Rotterdam: Balkema, pp. 40-62.

Sander, P.M. (1999) The microstructure of reptilian tooth enamel: terminology, function, and phylogeny. *Munchner Geowissenschaftliche Abhandlungen* 38: 1-102.

Sander, P.M. (2000) Prismless enamel in amniotes: terminology, function, and evolution. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 92-106.

Sansom, I.J., Smith, M.P., Armstrong, H.A., & Smith, M.M. (1992) Presence of the earliest vertebrate hard tissues in conodonts. *Science* 256: 1308-1311.

Sarich, V., Cronin, J. (1980) South American mammal molecular systematics, evolutionary clocks, and continental drift. In Ciochon, R., & Chiarelli, A. (eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift*. New York: Plenum, pp. 399-421.

Schaeffer, B. (1977) The dermal skeleton in fishes. In Andrews, S.M., Miles, R. S., & Walker, A.D. (eds.), *Problems in vertebrate evolution.* New York: Academic, pp. 25-52.

Scheinmann, E., Weinreb, M.M., & Wolman, M. (1961) Histochemical study of the ameloblasts and the enamel matrix in rat molars. *Journal of Dental Research* 41: 1293-1303.

Schlosser, G. (2002) Modularity and the units of evolution. *Theory in Biosciences* 121: 1-80.

Schneider, H. (2000) The current status of New World monkey phylogeny. *Anais da Academia Brasileira de Ciências* 72: 165-172.

Schneider, H., Canavez, F.C., Sampaio, I., Moreira., M.A.M., Tagliaro, C., & Seuanez, H.N. (2001) Can molecular data place each neotropical monkey in its own branch? *Chromosoma* 109: 515-523.

Schneider, H., & Rosenberger, A.L. (1996) Molecules, morphology, and platyrrhine systematic. In Norconk, M.A., Rosenberger. A.L., & Garber, P.A. (eds.), *Adaptive Radiations of Neotropical Primates.* New York: Plenum, pp. 3-19.

Schneider, H., Sampaio, I., Harada, M.L., (1996) Molecular phylogeny of the New World monkeys (Platyrrhini, primates) based on two unlinked nuclear genes: IRBP intron 1 and epsilon-globin sequences. *American Journal of Physical Anthropology* 100: 153-179.

Schour, I. (1936) The neonatal line in the enamel and dentin of human deciduous teeth and first permanent molar. *Journal of the American Dental Association* 23: 1946- 1955.

Schour, I., & Hoffman, M.M. (1939) Studies in tooth development: I: The 16 microns calcification rhythm in the enamel and dentin from fish to man. *Journal of Dental Research* 18: 91-102.

Schour, I., & Poncher, H.G. (1937) Rate of apposition of enamel and dentin, measured by the effect of acute fluorosis. *American Journal of Diseases of Children* 54: 757- 776.

Schultz, A.H. (1935) Eruption and decay of the permanent teeth in primates. *American Journal of Physical Anthropology* 19: 489-581.

Schultz, A.H. (1960a) Age changes in primates and their modification in man. In Tanner, J.M. (ed.), *Human Growth*. New York: Pergamon, pp. 1-20.

Schultz, A.H. (1960b) Age changes in the skulls and teeth of the Central American monkeys *Alouatta, Cebus,* and *Ateles. Proceedings of the Zoological Society of London* 133: 337-399.

Schultz, A.H. (1970) The comparative uniformity of the Cercopithecoidea. In Napier, J.R., & Napier, P.H. (eds.), *Old World Monkeys.* New York: Academic, pp. 41-51.

Schwartz, G.T., & Dean, M.C. (2001) Ontogeny of canine dimorphism in extant hominoids. *American Journal of Physical Anthropology* 115: 259-288.

Schwartz, G.T., Dean, M.C. (2005) Sexual dimorphism in modern human permanent teeth. *American Journal of Physical Anthropology* 128: 312-317.

Schwartz, G.T., Godfrey, L.R., & Mahoney, P. (2007) Inferring primate growth, development, and life history from dental microstructure: the case of the extinct giant Malagasy lemur, *Megaladapis*. In Bailey, S.E., & Hublin, J.J. (eds.), *Dental Perspectives on Human Evolution: State of the Art Research in Dental Paleoanthropology*. Dordrecht: Springer, pp. 147-162.

Schwartz, G.T., Mahoney, P., Godfrey, L.R., Cuozzo, F.P., Jungers, W.L., & Randria, G.F.N. (2005a) Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): implications for understanding life history variation in subfossil lemurs. *Journal of Human Evolution* 49: 702-721.

Schwartz, G.T., Miller, E.R., & Gunnell, G.F. (2005b) Developmental processes and canine dimorphism in primate evolution. *Journal of Human Evolution* 48: 97-103.

Schwartz, G.T., Reid, D.J., & Dean, M.C. (2001) Developmental aspects of sexual dimorphism in hominoid canines. *International Journal of Primatology* 22: 837-860.

Schwartz, G.T., Reid, D.J., Dean, M.C., & Zihlman, A.L. (2006) A faithful record of stressful life events recorded in the dental development record of a juvenile gorilla. *International Journal of Primatology* 27: 1201-1219.

Schwartz, G.T., Samonds, K.E., Godfrey, L.R., Jungers, W.L., & Simons, E.L. (2002) Dental microstructure and life history in subfossil Malagasy lemurs. *Proceedings of the National Academy of Sciences* 99: 6124-6129.

Scott, J.H., & Dixon, A.D. (1966) Anatomy for students of dentistry. Edinburgh: E&S Livingstone.

Seiffert, E.R., Simons, E.L., & Simons, C.V.M. (2004) Phylogenetic, biogeographic, and adaptive implications of new fossil evidence bearing on crown anthropoid origins and early stem catarrhine evolution. In Ross, C., & Kay, R. (eds.), *Anthropoid Origins.* New York: Kluwer/Plenum pp. 157-181.

Setoguchi, T., & Rosenberger, A.L. (1987) A fossil owl monkey from La Venta, Columbia. *Nature* 326: 692-694.

Seuànez, H.N., Forman, L., Matayoshi, T., Fanning, T.G. (1989) The *Callimico goeldii* genome: karyology and middle-repetitive (LINE1) DNA sequences. *Chromosoma* 98: 389-395.

Seuànez, H.N., Bonvicino, C.R., Moreira, M. (2005) The primates of the neotropics: genomes and chromosomes. *Cytogenetic and Genome Research* 108: 38-46.

Shea, B.T. (1983) Allometry and heterochrony in the African apes. *American Journal of Physical Anthropology* 62: 275-289.

Shea, B.T. (1985) The ontogeny of sexual dimorphism in the African apes. *American Journal of Primatology* 8: 183-188.

Shea, B.T. (1986) Ontogenetic approaches to sexual dimorphism in anthropoids. *Human Evolution* 1: 97-110.

Shellis, R.P. (1998) Utilization of periodic markings in enamel to obtain information on tooth growth. *Journal of Human Evolution* 35: 387-400.

Shellis, R.P., Beynon, A.D., Reid, D.J., & Hiiemae, K.M. (1998) Variations in molar enamel thickness among primates. *Journal of Human Evolution* 35: 507-522.

Shigehara, N. (1980) Epiphyseal union, tooth eruption, and sexual maturation in the common tree shrew, with reference to its systematic problem. *Primates* 21: 1-19.

Shubin, N., Tabin, C., & Carroll, S. (1997) Fossils, genes, and the evolution of animal limbs. *Nature* 388: 639-648.

Sibly, R.M., & Brown, J.H. (2007) Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences* 104: 17707-17712.

Simmons, N.S. (1979). Enamel calcification. *Journal of Dental Research* 58(B): 1024.

Simons, E.L., Plavcan, J.M., & Fleagle, J.G. (1999) Canine sexual dimorphism in Egyptian Eocene anthropoid primates: *Catopithecus* and *Proteopithecus*. *Proceedings of the National Academy of Sciences* 96: 2559-2562.

Simpson, S.W., Lovejoy, C.O., & Meindi, R.S. (1991) Relative dental development in hominoids and its failure to predict somatic growth velocity. *American Journal of Physical Anthropology* 86: 113-120.

Singleton, M. (2002) Patterns of cranial shape variation in the Papionini (Primates: Cercopithecinae). *Journal of Human Evolution* 42: 547-578.

Skogland, T. (1988) Tooth wear by food limitation and its life history consequences in wild reindeer. *Oikos* 51: 238-242.

Slavkin, H.C., & Diekwisch, T. (1996) Evolution in tooth and developmental biology: of morphology and molecules. *The Anatomical Record* 245: 131-150.

Slayter, E.M., Slayter, H.S. (1992) *Light and electron microscopy*. Cambridge, UK: Cambridge University Press.

Smith, A.J. (2000) Pulpo-dentinal interactions in development and repair of dentine. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 82-91.

Smith, B.H. (1989) Dental development as a measure of life history in primates. *Evolution* 43: 683-88.

Smith, B.H. (2000) 'Schultz's rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. In Teaford, M.F., Smith, M.M., & Ferguson, M.W.J. (eds.), *Development, Function and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 212–227.

Smith, B.H., Crummett, T.L., & Brandt K.L. (1994) Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. *Yearbook of Physical Anthropology* 37: 177-231.

Smith, C.E. (1998) Cellular and chemical events during enamel maturation. *Critical Review of Oral Biology and Medicine* 9: 128-161.

Smith, C.E., & Warshawsky, H. (1975) Cellular renewal in the enamel organ and the odontoblast layer of the rat incisor as followed by radioautography using 3H-thymidine. *Anatomical Record* 183: 523-562.

Smith, M.M., & Coates, M.I. (2000) Evolutionary origins of teeth and jaws: developmental models and phylogenetic patterns. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 133-151.

Smith, M.M., & Sansom, J. (2000) Evolutionary origin of dentine in the fossil record of early vertebrates: diversity, development, and function. In Teaford, M.,F., Smith, M.M., & Ferguson, W.J. (eds.), *Development, Function, and Evolution of Teeth*. Cambridge: Cambridge University Press, pp. 65-91.

Smith, R.J., Cheverud, J.M. (2002) Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's rule in primates. I*nternational Journal of Primatology* 23: 1095-1135.

Smith, T.M. (2004) *Incremental Development of Primate Dental Enamel*. Ph.D. dissertation, SUNY Stony Brook.

Smith, T.M. (2006) Experimental determination of the periodicity of incremental features in enamel. *Journal of Anatomy* 208: 99-113.

Smith, T.M. (2008) Incremental dental development: methods and applications in hominoid evolutionary studies. *Journal of Human Evolution* 54: 205-224.

Smith, T.M., Martin, L.B., Leakey, M.G. (2003) Enamel thickness, microstructure, and development in *Afropithecus turkanensis*. *Journal of Human Evolution* 44: 283-306.

Smith, T.M., Martin, L.B., Reid, D.J., de Bonis, L., Koufos, G.D. (2004) An examination of dental development in *Graecopithecus freybergi* (=*Ouranopithecus macedoniensis*). *Journal of Human Evolution* 46: 551-577.

Smith, T.M., Tafforeau, P., Reid, D.J., Grun, R., Eggins, S., Boutakiout, M., & Hublin, J. (2007) Earliest evidence of modern human life history in North African early *Homo sapiens*. *Proceedings of the National Academy of Sciences* 104: 6128-6133.

Snodgrass, J.J., Leonard, W.R., & Robertson, M.L. (2007) Primate bioenergetics: an evolutionary perspective. In Ravosa, M.J., and Dagosto, M. (eds.), *Primate Origins: Adaptation and Evolution*. New York: Springer, pp. 703-738.

Soini, P. (1987) Ecology of the saddle-back tamarin *Saguinus fuscicollis illigeri* on the Rio Pacaya, northeastern Peru. *Folia Primatologica* 49: 16-32.

Sondaar, P.Y. (1977) Insularity and its effects on mammal evolution. In Hecht, M.K., Goody, P.C., & Hecht, B.M. (eds.), *Major Patterns of Vertebrate Evolution.* New York: Plenum, pp. 671-707.

Sousa, F.B., Vianna, S., Snatos-Magalhaes, N. (2006) A new approach for improving the birefringence analysis of dental enamel mineral content using polarizing microscopy. *Journal of Microscopy* 221: 79-83.

Stahl, W.R. (1967) Scaling of respiratory variables in mammals. *Journal of Applied Physiology* 22: 453-460.

Stearns, S.C. (1976) Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51: 3-47.

Stearns, S.C. (1977) The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics* 8: 145-171.

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

Stehlin, H.G. (1912) Die säugetiere des schweizerischen Eocaens: *Adapis*. *Schweizerische Paläontologishe Abhandlungen* 38: 1165-1298.

Steiper, M., Ruvolo, M. (2003) New World monkey phylogeny based on X-linked G6PD DNA sequences. *Molecular Phylogenetics and Evolution* 27: 121-130.

Stohr, P., & Lewis, F. (1906) *Stohr's Histology: Arranged Upon an Embryological Basis*. Philadelphia: Blakiston.

Strait, S.G., & Vincent, J.F. (1998) Primate faunivores: physical properties of prey items. *International Journal of Primatology* 19: 867-878.

Struhsaker, T.T., & Leland, L. (1977) Palm-nut smashing by *Cebus a. apella* in Colombia. *Biotropica* 9: 124-126.

Sussman, R.W., Kinzey, W.G. (1984) The ecological role of the callitrichidae: a review. *American Journal of Physical Anthropology* 64: 419-449.

Swindler, D.R., & Beynon, A.D. (1993) The development and microstructure of the dentition of *Theropithecus*. In Jablonksi, N.G. (ed.), *Theropithecus: The Rise and Fall of a Primate Genus.* Cambridge: Cambridge University Press, pp. 351-381.

Symons, N.B.B. (1955) Alkaline phosphatase activity in the developing teeth of the rat. *Journal of Anatomy* 89: 238-245.

Symons,, N.B.B. (1956) Ribonucleic acid-alkaline activity in the developing teeth of the rat. *Journal of Anatomy* 90: 117-122.

Szalay, F.S., & Delson, E. (1979) *Evolutionary History of the Primates.* New York: Academic.

Szalay, F.S., & Seligsohn, D. (1977) Why did the strepsirhine tooth comb evolve? *Folia Primatologica* 27: 75-82.

Takai, M., Anaya, F. (1996) New specimens of the oldest fossil platyrrhine, *Branisella boliviana* from Salla, Bolivia. *American Journal of Physical Anthropology* 99: 301-318.

Takai, M., Anaya, F., Shigehara, N, & Setoguchi, T. (2000) New fossil materials of the earliest New World monkey, *Branisella boliviana*, and the problem of platyrrhine origins. *American Journal of Physical Anthropology* 111: 263-281.

Takai, M., Nishimura, T., Shigehara, N., & Setoguchi, T. (2009) Meaning of the canine sexual dimorphism in fossil owl monkey, *Aotus dindensis* from the Middle Miocene of La Venta, Columbia. In Koppe, T., Meyer, G., Alt, K., Brook, A., Dean, M.C., Kjaer, J., Lukacs, R., Smith, B.H., & Teaford, M. (eds.), *Comparative Dental Morphology*. Basel: Karger, pp. 55-59.

Takeda, S. Elefteriou, F., Karsenty, G. (2003) Common endocrine control of body weight, reproduction, and bone mass. *Annual Review of Nutrition* 23: 403-411.

Tardif., S.D., Power, M., Oftedal, O.T., Power, R.A., & Layne, D.G. (2001) Lactation, maternal behavior, and infant growth in common marmoset monkeys (*Callithrix jacchus*): effects of maternal size and litter size. *Behavioral Ecology and Sociobiology* 51: 17-25.

Taylor, A.B. (1997) Relative growth, ontogeny, and sexual dimorphism in *Gorilla* (*Gorilla gorilla gorilla* and *G. g. beringei*): evolutionary and ecological considerations. *American Journal of Primatology* 43: 1-31.

Taylor, A.B., Eng, C.M., Anapol, F.C., & Vinyard, C.J. (2009) The functional correlates of jaw-muscle fiber architecture in tree-gouging and nongouging callitrichid monkeys. *American Journal of Physical Anthropology* 139: 353-367.

Taylor, A.B., & Vinyard, C.J. (2004) Comparative analysis of masseter fiber architecture in tree-gouging (*Callithrix jacchus*) and nongouging (*Saguinus oedipus*) callitrichids. *Journal of Morphology* 261: 276-285.

Teaford, M. (1985) Molar microwear and diet in the genus *Cebus*. *American Journal of Physical Anthropology* 66: 363-370.

Tejedor, M.F. (1996) The affinities of *Homunculus* and *Carlocebus* (Primates, Platyrrhini), early Miocene platyrrhines from Southern Argentina. *American Journal of Physical Anthropology Supplement* 22: 227-228.

Tejedor, M.F. (2002) Primate canines from the early Miocene Pinturas Formation, Southern Argentina. *Journal of Human Evolution* 43: 127-141.

Tejedor, M.F., & Rosenberger, A.L. (2008) A neotype for *Homunculus patagonicus* Ameghino, 1891, and a new interpretation of the taxon. *Paleoanthropology* 2008: 68-82.

Tejedor, M.F., Tauber, A.A., Rosenberger, A.L., Swisher, C.C., & Palcios, M.E. (2006) New primate genus from the Miocene of Argentina. *Proceedings of the National Academy of Sciences* 103: 5437-5441.

Thesleff, I., Keranen, S., & Jernvall, J. (2001) Enamel knots as signaling centers linking tooth morphogenesis and odontoblast differentiation. *Advances in Dental Research* 15: 14-18.

Thesleff, I., & Sharpe, P. (1997) Signalling networks regulating dental development. *Mechanisms of Development* 67: 111-123.

Thewlis, J. (1939) The examination of dental enamel by X rays and the polarizing microscope. *Proceedings of the Physical Society* 51: 992-1002.

Thomas, T., Burguera, B. (2002) Is leptin the link between fat and bone mass? *Journal of Bone and Mineral Research* 17: 1563-1569.

Thompson, I. (1975) Biological clocks and shell growth in bivalves. In Rosenberg, G., & Runcorn, S. (eds.), *Growth Rhythms and the History of the Earth's Rotation*. New York: Wiley, pp. 149-162.

Tomes, C.S. (1897) On the development of marsupial and other tubular enamels. *Philosophical Transactions of the Royal Society of London, Series B* 189: 107-122.

Tomes, C.S. (1906) On the minute structure of the teeth of creodonts, with especial reference to their suggested resemblance to marsupials. *Proceedings of the Zoological Society of London* i: 45-58.

Tomes, J. (1849) On the structure of the dental tissues of marsupial animals, and more especially of the enamel. *Philosophical Transactions of the Royal Society of London* 139, 403–412.

Tomes, J. (1850) On the structure of the dental tissues of the order Rodentia. *Philosophical Transactions of the Royal Society of London* 140: 529-567.

Trivers, R.L. (1972) Parental investment and sexual selection. In Campbell, B. (ed.), *Sexual Selection and the Descent of Man.* London: Heinemann, pp. 136-179.

Trivers, R.L. (1974) Parent-offspring conflict. *Integrative and Comparative Biology* 14: 249-264.

Tucker, A.S., & Sharpe, P.T. (1999) Molecular genetics of tooth morphogenesis and patterning: the right shape in the right place. *Journal of Dental Research* 78: 826-834.

Ueyama, T., Krout, K., Nguyen, X., Karpitskiy, A. (1999) Suprachiasmatic nucleus: a central autonomic clock. *Nature Neuroscience* 2: 1051-1053.

Valentin, G. (1861) Die Untwsuchung dev Pflanzen- und Thiergewebe in Polasiertm Lichte. Leipzig.

Vinyard, C.J., & Ryan, T.M. (2006) Cross-sectional bone distribution in the mandibles of gouging and non-gouging Platyrrhini. *International Journal of Primatology* 27: 1461-1490.

Vinyard, C.J., Wall, C.E., Williams, S.H., & Hylander, W.L. (2003) Comparative functional analysis of skull morphology in tree-gouging primates. *American Journal of Physical Anthropology* 120: 153-170.

Vinyard, C.J., Wall, C.E., Williams, S.H., Mork, A.L., Garner, B.A., Melo, L., Valenca-Montenegro, M., Valle, Y.B.M., Monteiro da Cruz, M., Lucas, P.W., Schmitt, D., Taylor, A.B., and Hylander, W.L. (2009) The evolutionary morphology of tree gouging in marmosets. In Ford, S.M., Porter, L.M., & Davis, L.C. (eds.), *The Smallest Anthropoids: The Marmoset/Callimico Radiation*. New York: Springer, pp. 395-410.

Visalberghi, E. (1987) Acquisition of nut-cracking behaviour by 2 capuchin monkeys (*Cebus apella*). *Folia Primatologica* 49: 168-181.

Visalberghi, E., & McGrew, W.C. (1997) *Cebus* meets *Pan.* *International Journal of Primatology* 18: 677-681.

Vrba, E.S., & Grine, F.E. (1978) Australopithecine enamel prism patterns. *Science* 202: 890-892.

Warshaw, J. (2007) *Primate bone microstructural variability: relationships to life history, mechanical adaptation and phylogeny.* Ph.D. dissertation, City University of New York.

Warshawsky, H. (1978) A freeze-fracture study of the topographic relationship between inner enamel-secretory ameloblasts in the rat incisor. *American Journal of Anatomy* 152: 153-208.

Warshawsky, H. (1983) Knife chatter during thin sectioning or rat incisor enamel can cause periodicities resembling cross-striations. *Anatomical record* 207: 533-538.

Warshawsky, H. (1985) Ultrastructural studies on amelogenesis. In Butler. W.T. (ed.), *The Chemistry and Biology of Mineralized Tissues*. Birmingham: Ebsco, pp. 33-45.

Warshawsky, H. (1989) Are linear markings on dental enamel valid indicators of time? Paper presented at the annual meetings of the Canadian Association for Physical Anthropology (cited in Fitzgerald 1998).

Waters, N.E. (1980) Some mechanical and physical properties of teeth. *Symposia for the Society of Experimental Biol*ogy 34: 99-135:

Watson, M.L. (1960) The extracellular nature of enamel in the rat. *Journal of Cell Biology* 7: 489-492.

Weber, D.F. (1973) Sheath configurations in human cuspal enamel. *Journal of Morphology* 141: 479-489.

Weber, D.F., Glick P.L. (1975) Correlative Microscopy of enamel prism orientation. *American Journal of Anatomy* 144: 407-419.

Welsh, D.K., Logothetis, D.E., Meister, M., Reppert, S.M.(1995) Individual neurons dissociated from rat suprachiasmatic nucleus express independently phased circadian firing rhythms. *Neuron* 14:697–706.

West, G.B., Brown, J.H., & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* 276: 122-126.

Whyte, M.A. (1975) Time, tide, and the cockle. In Rosenberg, G., & Runcorn, S. (eds.), *Growth Rhythms and the History of the Earth's Rotation*. New York: Wiley, pp. 177-190.

Wilbur, H., Tinkle, D., Collins, J. (1974) Environmental certainty, trophic level, and resource availability in life history evolution. *The American Naturalist* 108: 805-817.

Wiley, R.H. (1974) Evolution of social organization and life-history patterns among grouse. *The Quarterly Review of Biology* 49: 201-227.

Williams, L. (1896) On the formation and structure of dental enamel. *Dental Cosmos* 38: 453.

Williamson, W.C. (1849) On the microscopic structure of the scales and dermal teeth of some ganoid and placoid fish. *Philosophical Transactions of the Royal Society of London* 139: 435-475.

Wolovich, C.K., Perea-Rodriguez, J.P., & Fernandez-Duque, E. (2008) Food transfers to young and mates in wild owl monkeys (*Aotus azarai*). *American Journal of Primatology* 70: 211-221.

Wöltgens, J.H.M., Lyaruu, D.M., Bronckers, A.L., Bervoets, T.J.M., & Van Duin, M. (1995) Biomineralization during early stages of the developing tooth *in vitro* with special reference to secretory stage of amelogenesis. *International Journal of Developmental Biology* 39: 203-212.

Wood, C. B., Dumont, E.R., & Crompton, A.W. (1999) New studies of enamel microstructure in Mesozoic mammals: a review of enamel prisms as a mammalian synapomorphy. *Journal of Mammalian Evolution* 6: 177-213.

Wood, C.B., Rougier, G.W. (2005) Updating and recoding enamel microstructure in Mesozoic mammals: in search of discrete characters for phylogenetic reconstruction. *Journal of Mammalian Evolution* 12: 433-460.

Wright, B.W. (2005) Craniodental biomechanics and dietary toughness in the genus *Cebus*. *Journal of Human Evolution* 48: 473-492.

Wright, P.C. (1985) *The Costs and Benefits of Nocturnality for the Night Monkey* (Aotus). Ph.D. Dissertation, City University of New York.

Wright, P.C. (1996) The neotropical primate adaptation to nocturnality: feeding in the night (*Aotus nigriceps* and *A. azarae*). In Norconk, M.A., Rosenberger. A.L., & Garber, P.A. (eds.), *Adaptive Radiations of Neotropical Primates.* New York: Plenum, pp. 369-382.

Wu, J.Y., Cornelissen, G., Tarquini, B., Mainardi, G., Cagnogni, M., Fernandez, J, Hermida, R., Tamura, K., Kato, J., Kato, K. (1990) Circaseptan and circannual modulation of circadian rhythms in neonatal blood pressure and heart rate. *Progress in Clinical and Biological Research* 341A: 643-652.