

Is dental development an important feature of mammal life history?

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Abstract

A mammal's state of development at birth is a critically important marker of life history. A superficial dichotomy that exists between placental mammals and marsupials attaches an altricial or precocial label to a neonate's developmental maturity. This categorization is limited to external features and physical behaviors observed in the examination of soft tissue. This mode of classification makes the investigation of evidence from the fossil record unproductive due to the hard tissue nature of the preserved specimens. The goal of this paper is to characterize the dental variability within animals that are traditionally considered to be altricial or precocial. This was accomplished through the comparison of neonatal dentition in two small-bodied primate species, *Callimico goeldii* and *Galago senegalensis*. The contribution of fossil evidence is indispensable to the construction of life history schemes, particularly in assessing normal development in species that cease to exist. Hard tissues, such as bones and mineralized teeth, may also serve as important determinants of a neonate's altricial or precocial development. Therefore, studying the eruption of teeth could be an important tool in determining the maturation level of an individual in comparison to other elements of its life history. Surprisingly, little has been published in terms of detailed imaging of neonatal dentition. Primary research presented in this paper explores the altricial or precocial nature of mammalian neonates by engaging in comparative morphology and offering three-dimensional images of neonatal dentition. Investigational research is included in the interest of determining whether soft tissue examination alone is a reliable marker for the categorization of newborn mammals as altricial or precocial. The application of this research is an exploration of the differences in development of

soft and hard tissues at birth, which could contribute a more accurate representation of a neonate's developmental state and schedule of life history events.

Introduction

The human condition has been studied for millennia, yet, the life history scheme of *Homo sapiens* is still a puzzling mosaic. The study of life history lends an enormous volume of insight into an organism's evolutionary past, insight that may be essential to the continued existence of its species in the future. Life history itself is a catalogue of synchronized events that occur over an organism's lifetime, assembled by natural selection to favor increased fitness. Improving our understanding of how this sequence of developmental events reflects the evolution of a species might allow us to disentangle some of the perplexities of human evolution. Our fragmented understanding of the evolution of life histories is a consequence of an incomplete fossil record. The known fossil record is not exact in time or place of origin for many mammalian species (Lillegraven et al., 1987). Reconstructing the timeline of events in human evolution requires information regarding an evolutionary past that is not fully understood, or is simply missing. The absence of a dense continuum of fossil specimens required to thoroughly study the evolution of the human species necessitates a comparison and analysis of evidence collected from closely related species. Humans belong to the class Mammalia, which affirms the importance of having a clear understanding of the life histories of other mammals.

The introduction of teeth into the fossil record and documentation of landmarks observed in the dentition could provide a more complete history of multiple species. The dentition of humans and other primates alike maintains a record of diet and behavior as well as growth and development (Molnar, 1971). Dental development is highly hereditary and less modified than

other tissues by variance in environmental conditions. The record of maturation preserved in dentition is a valuable source of information. Documentation of dental growth markers could extend this resource to extant and extinct species. Ultimately, data gained from teeth on age of maturity can to fill in a fossil record of life history (Smith, 1989). Progress toward a more complete fossil record will give researchers more room to extrapolate information and substantiate claims made regarding life histories. Exploring the life histories of species that are similar to humans may reveal elements of human evolution that were previously neglected. This study strives to create a new link to human development by using primates as a proxy and assessing the range of conditions in the dental development of primate species.

Life History Theory

The concept of life history maps out a path of evolution that has enabled the continued survival of an extant species. Life history theory explains that energy is not unlimited, and thus, strategies must evolve in order to ensure a species' perpetuation. Natural selection plays a role in life history by arranging a timeline of events in an organism's lifecycle that will maximize its fitness, or ability to produce the greatest quantity of surviving offspring (Kappeler, 1996). Life history is composed of units such as energy budgeting, reproductive strategy and maternal investment, length of gestation, as well as senescence and death. The life history of a species can be understood by examining events that occur throughout the duration of an individual's lifetime. Because species are perpetuated by reproduction, exploring reproductive processes and the condition of newborn offspring is central to understanding life history. Offspring body size and level of maturation as well as postnatal growth patterns are all a part of life history strategy.

Examining Teeth to Understand Life History

A considerable amount of information regarding the biology of extinct taxa originates from the examination of teeth. Learning about an organism's biology or life history from teeth is advantageous because both bones and teeth tend to fossilize well. Teeth provide insight into growth and maturation in mammals because their development is tightly linked to the mammalian lifecycle (Smith, 1991). Similar to tree rings, certain lines and bands in dentition preserve an enormous amount of information about an individual's life. The information recorded in teeth includes, but is not limited to: birth, trauma, better or worse times, and age at death in organisms that died while teeth were still developing. The neonatal line—a landmark demarcating birth—provides valuable insight regarding life history. It is possible that mammals could be sorted into altricial and precocial categories based on the location of the line.

Advanced imaging software can reveal the developing deciduous and permanent dentition even in the tiniest mammal. Imaging makes it possible to expose this distinction in beautiful detail. Observing developmental landmarks in newborn morphology provides a novel way to decipher life history details. For example, the width and location of the neonatal line could supply information about the birthing process (Eli, Sarnat and Talmi, 1989), while the total dental development of a neonate would indicate birth status. Examining and assessing developmental landmarks in dentition could contribute to our ability to make a more accurate prediction of a specimen's position in the fossil record. Recently, it has been suggested that a record of the mammal's development preserved by the teeth can then be used to designate altriciality or precociality (Gingerich et al., 2009). This characterization affords a more detailed picture of development that could subsequently be incorporated into the species' life history.

Previously, determining which postnatal category a species belonged to was limited to the examination of soft tissue or behavior of a newborn. Specimens obtained from the fossil record or teeth from extant species may strengthen the accuracy regarding the use of these labels. The dental component of the variability between altricial and precocial mammals has not fully been explored (Smith et al., 1994). The examination of the neonatal dentition provides a portrait of an animal's dental development at birth, unscathed by destruction from wear. Additionally, patterns of tooth eruption parallel rates of maturation. Exploring differences in neonatal dentition between species could ultimately redefine the characteristics involved in determining the degree of altriciality or precociality. This result would call for the implementation of a new system that allows for a spectrum of altriciality-to-precociality rather than limiting the classification of species to one category or the other. New parallels drawn between species based on their relative degree of altriciality versus precociality could build new phylogenetic links and strengthen presumed evolutionary relationships.

Energy Budgeting

Energy reserves are limited by biotic and abiotic factors. Specifically, animal physiology and environmental conditions operate as principal energetic constraints (Gittleman and Thompson, 1988). Along the course of evolution, a system of resource distribution evolved in response to the unique energetic requirements of different species. Natural selection shaped budgeting strategies that support species survival. What we see as an animal's life history timetable is evolved strategy of where and when to best distribute available energy resources.

Reproduction is central to the continued existence of any species. Therefore, an elevated provision of energy resources is essential to ensuring reproductive success. Total metabolic

expenditure must be regulated to maintain fecundity (Clutton-Brock, 1991:131). Yet, living mammals show that there are many different life plans that work and have worked for millions of years and mammals demonstrate substantial variation in the cost of a reproductive event. Differences in energy expenditure are observed in the length of gestation, placentation, fetal growth patterns, energy content of milk, duration of lactation, as well as size and the developmental state of offspring at birth. Preservation of health in a reproductive female and her offspring is contingent on the proper allocation of energy resources.

Large-brained species, such as humans and primates, need increased energy consumption to support fetal brain growth and development. The high cost involved may even require modification of metabolic processes. Increased distribution of energy resources to the brain could compel other energy resources to be reapportioned, limiting energy for other developing systems (Isler and Schaik, 2009). It is conceivable that compensation for elevated reproductive costs, in general, could be achieved by reducing energy consumption for nonreproductive activities and thermoregulatory expenditures. The heightened energy supply could then be allocated toward gestation (Gittleman and Thompson, 1988). Gestation takes a huge toll on maternal energy reserves. Thus, length of the gestation period is relative to how long the pregnant female can support the energetic demands of the growing fetus. Gestation duration and litter size dictates differences in the developmental state of the neonate and varies widely among species.

Categorization of Birth Status

Status of newborn eutherians was originally restricted to two narrow categories. Lower organization—the primary type—consisted of animals with reproductive events involving a short

gestation period, great number of progeny, and altricial young that were kept in a nest for some time, the “Nesthocker.” Insectivores and rodents fell into this primary category, while hoofed animals, whales, and primates exhibited characteristics of the secondary category. Higher organization—the secondary type—was composed of animals that experienced long gestation, limited progeny numbers, and precocial young that might get up and walk early, thus the “Nestfluechter” (Portmann, 1938). Many species, namely humans, were not a perfect fit for either of these categories. Human babies may be at an extreme, but all primate babies are poor in motor coordination at birth, when compared to the hoofed mammals. Langer (2008) suggested that birth status of mammalian young should be divided into four categories to accommodate major variations (see Table 1). The following categories account for differentiations in birth status including intermediate cases.

Table 1. Categories of Birth Status*	
Birth Status	Birth Status Number
Altricial, nidicolous	I
Precocial, nidicolous	II
Precocial, transported	III
Precocial, nidifugous	IV

Altricial: closed eyes, hairless

Precocial: open eyes, haired

Nidicolous: remains nested for short time

Transported: mother carries young

Nidifugous: leaves site of birth shortly after birth

*Table from (Langer, 2008)

Newborn mammals, like birds, present in one of two ways: altricial (less developed) or precocial (more fully developed). The criteria for the classification of birth status involve four types of developmental independence: locomotory, sensory, thermoregulatory, and nutritional (Derrickson, 1992). Altricial animals have been described as being born with one or more of the following characteristics: closed eyes, sealed ears, lack of hair and low muscular development. These animals may experience difficulty in independent movement and temperature regulation

of their bodies. They may be kept in a nest for some time after birth where they are highly dependent on further parental care. Panda neonates, a species of altricial mammals, are particularly small and helpless. They require transportation and protective care from their mothers until they grow large enough to become independently mobile (Hoff, Nadler, and Maple, 1983). Animals that are precocial in development assume this postnatal distinction based on good motor coordination—demonstrating locomotory independence—and possess features that are almost fully developed, which may include hair on the body—indicating thermoregulatory independence. Precocial animals can open their eyes freely—representing sensory independence—and do not have sealed ears. Additionally, the more mature anatomy of precocial animals can tolerate solid foods—a step on the way to nutritional independence (Derrickson, 1992). For example, newborn foals, fully haired with eyes and ears open, are able to stand up and walk around independently shortly after exiting the birthing canal. Thus, horses embody the precocial category.

Birth status of newborns tends to characterize whole orders or suborders of mammals—seemingly a very conservative feature of life history—although the parameters of altriciality and precociality permit limited flexibility in their interpretation (Langer, 2008). The panda and horse newborn represent clear opposites in birth status, however, other cases are not so clear and fixed definitions are called into question.

Although the Primate order as a whole is considered precocial, humans bear a mosaic of characteristics. Human newborns do not have sealed ears or closed eyes and are born with hair. However, their neuromuscular control is limited (e.g. they cannot grasp) and they are born toothless. These characteristics do not allow for a definite postnatal distinction of altricial or

precocial. Rather, the observed features of newborn babies fall into a third category that labels humans as *secondarily altricial* (Portmann, 1941). Humans demonstrate characteristics from both sides of the spectrum ranging from the helplessness observed in altricial mammals to the precociality of primates. In contrast to other primates, human neonates have an altriciality of neurological processes and behaviors (Dunsworth et al., 2012). Humans exhibit precocial characteristics in other respects such as sensory and thermoregulatory independence. Examining certain elements of the fossil record could potentially clarify how the unique human condition evolved.

Reproductive Strategies and Maternal Investment

Distinct reproductive strategies have evolved through natural selection to favor increased fitness in mammals. The class Mammalia is divided into two subclasses of Monotremata and Theria. Only five species of monotremes, or egg-laying mammals, have survived to the present day as oviparous species. The evolution of internal fertilization and viviparity, or live birth, made hard-shelled protection in parturition obsolete for the two infraclasses of Theria: Eutheria (placental mammals) and Metatheria (marsupials). The development of the corpus luteum and allantois placenta reproductive structures made it possible to substitute a feto-placental unit for an egg in the delivery of placental mammal and marsupial offspring (Weir and Rowlands, 1973). A further division of reproductive strategies results in the birth status of young. Such adaptations presumably evolve to accommodate environmental pressures and requirements of distinct species niches. Maternal investment functions to support offspring survival (Trivers, 1972). In turn, the degree and causes of neonatal mortality shape maternal investment and reproductive strategy. One approach taken by mammals in response to selection on infant survival is the variation of

litter size and neonate maturity (Lillegraven et al., 1987). Energetic commitment during pregnancy is reflected in the state of development of the offspring at birth. Maternal investment in eutherian mammals can be divided into three phases: gestation, milk-only feeding, and mixed feeding. The mixed feeding phase involves ingestion of both milk and solid foods (Langer, 2008). Species evolve investment strategies that maximize fitness in response to environmental conditions (Dunsworth et al., 2012). Pressures from the environment such as predation risk favor a decline in the length of the early developmental period a fetus spends in the womb, or gestation. The clearest, most consistent difference between marsupials and placental mammals is the mechanism of reproduction (Pond, 1977). Reproductive strategies that evolved for marsupials favored altricial development. Eutherian mammals, in contrast, vary in their degree of altriciality or precociality at birth (Dunsworth et al., 2012).

Altricial species experience short generation times and tend to produce large litters. Maternal investment is dispersed among all of the offspring. Altricial animals have relatively smaller body sizes in comparison to animals of precocial development. Early maturity, short lifespans, and high fecundity, or potential reproductive capacity, are also characteristic of altricial species (Derrickson, 1992). Generally, this reproductive strategy is thought to be advantageous in unstable environments that favor rapid reproduction.

Precocial species, such as primates, tend to produce litters as small as one progeny. Animals of a precocial character are frequently larger in body size, live longer, and experience dependency on parental investment until maturity is achieved. Precocial neonates are more frequently born to large mammals than small-bodied mammals. Relative to their smaller-bodied counterparts, the offspring of large mammals spend more time achieving any fraction of adult

mass (Derrickson, 1992). The reproductive strategy demonstrated by precocial species enables distribution of a higher level of parental investment to each individual offspring. This strategy is favored in environments that are stable, with relatively constant population numbers and occurs in habitats with competition for limited resources. Additionally, the newborn offspring may require a specialized diet from the parent that differs from the diet of an adult animal (Clutton-Brock, 1991:23).

Commitment made to offspring during gestation varies based on stability of the environment into which progeny will be reared. The value of the offspring may be significantly reduced in conditions that compromise the mother's overall fitness contribution. This is especially pertinent to species that expect high fecundity through the reproductive lifespan of an individual. Unstable conditions, such as those that limit access to resources or require evasion of predators, impose the need for a capacity to easily shed a fetus to ensure survival of the mother. Strategically, making a small investment in marsupial gestation is advantageous, because when conditions are bad—as in times of famine—a joey can easily be brushed from the teat. Conversely, a human female would experience huge loss if resources became depleted during pregnancy. The human reproductive system does not allow for voluntary expulsion of a growing fetus. Thus, poor conditions endanger both the mother and offspring in human reproduction.

Maternal investment in offspring involves gestation, lactation, protection, and transportation for some species. Gestation and lactation are considered to be greatest consumers of energy in this group (Gittleman and Thompson, 1988). Lactation is unique to mammalian reproduction and is quite advantageous for young offspring (Pond, 1977). Producing nutrient-rich milk, however, is extremely energetically expensive for reproductive females (Langer,

2008). Eutherian mammals are not well equipped to process adult foods at birth. Thus, young offspring experience many benefits of maternal milk ingestion. Not only does lactation provide nourishment for offspring, it acts as a source of energy transfer (Gittleman and Thompson, 1988). Additionally, feeding exclusively on maternal milk resources protects the vulnerable young from the inconstancy of the adult food supply (Pond, 1997). The consumption of maternal milk affords a certain level of immunity to infection for the young. Once weaned, the offspring can no longer tap into the maternal supply of immunoglobulin A antibodies (Berthon et al., 1999). Weaning is initiated when the mother is no longer energetically capable of supporting offspring growth through maternal milk. At this stage, in order to obtain sufficient energy resources, solid foods must be integrated into the infant's diet (Lee et al., 1991). The weaning process is a difficult transition for infants. Many eutherian mothers weaken the blow by gradually introducing their offspring to nutritional independence through a mixed feeding phase. The infant continues to ingest maternal milk at decreasing quantities, while solid food intake is increased. The offspring's immune system becomes more developed as nutritional independence approaches, decreasing susceptibility to health hazards brought about by the adult diet. Birth status is defined by the state of morphological and functional differentiation. The three phases of maternal investment—gestation, milk-only feeding, and mixed feeding—may influence birth status of offspring (Langer, 2008). Both length of gestation and lactation influence the birth status (Gittleman and Thompson, 1988).

Maternal investment in rearing a primate infant to independence presents a considerable cost. Energetically, these costs include lactation and infant transport. Infant care also impacts a mother's ability to forage and avoid predation (Hoff, Nadler, and Maple, 1983). Primate species

give birth to offspring that exhibit varying degrees of precocial characteristics. Precociality requires enormous maternal investment from conception through a long gestational period and lactation to nutritional independence. While all extant marine mammals are precocial and experience mainly in utero development (Gingerich et al., 2009), mammals of the order Primates are complex creatures and experience much of growth and development postnatally. In general, the primate order is referred to as precocial. However, there is an apparent range of neonatal development among primates (Smith et al., 1994). Some primate neonates demonstrate low muscular development at birth, and as a result, require transport for protection and locomotion. In accordance, the birth status observed in many primate species is “precocial, transported.” The infant remains reliant on maternal transport, until its own motor system is developed enough to locomote unaided. Different modes of maternal transport correspond to the motor coordination development of the infant. As the infant matures, different transport positions can be employed. Energy expended in transporting infants is directly proportional to the infant’s mass and the carrier’s lean body mass (Hoff, Nadler, and Maple, 1983).

In some species such as *Galago senegalensis* and *Callimico goeldii*, paternal and helper transport is common, which decreases the energetic burden on the mother (Schradin and Anzenberger, 2001). *Callimico* mothers carry infants on their own until postnatal week 3-5 and then fathers begin to share some of the transportation responsibilities (Ross, Porter, Power, and Sodaro, 2010). However, in order to increase infant safety from predation and accident risks mothers may delay assistance from others (Schradin and Anzenberger, 2003). *Callimicos* have not been observed attempting to leave their carriers until postnatal week 10 (Ross, Porter, Power, and Sodaro, 2010), and only exhibit complete independence from transport at roughly 12 weeks

after birth (Shradin and Anzenberger, 2001). *Galago senegalensis* neonates begin to resist assisted transport when they reach four weeks of age (Sauer, 1967). Earlier independence suggests that galagos are more precocial than callimicos. This inference may have important implications for birth status classification. Further elaboration of this concept will be included in the Discussion and Analysis (found on page 34).

Comparative studies of the closest primate relatives of humans have been used to gain insight into how humans fit in as primates. Human babies, like other primate species, require maternal transport during early postnatal development. Newborn humans are essentially helpless at birth and likely to die if left unattended.

With flexible marsupial-like reproduction, effort lost in the support of new, and potentially less viable offspring can be redirected toward the mother's own endurance and the survival of extant offspring. Longevity of young progeny is considerably diminished by maternal mortality in humans and other mammalian species. Poorly developed motorneuronal skills and slow maturation of human babies demand increased parental attention subsequent to birth. In infancy, feebleness puts newborns in peril without proper parental investment in protection and transportation of the offspring. Human progeny require maternal investment to support their survival for some 25% of their lifetime (Lachmann, 2011). Species that are not born in such immature forms do not require the same level of parental investment to reach independence.

Gestation Period

Gestation is a highly expensive metabolic process. The energetic cost is high for the mother who must maintain her own tissues and those of the growing fetus. It has been posited that a constraint on energy consumption exists in regard to the maximum growth of the fetus and

time spent in the womb (Dunsworth et al., 2012). It is favorable for parturition to occur when the energetic requirements of the offspring are not yet unsustainable. Therefore, the length of gestation is highly variable between species and depends on several factors such as the evolved maternal investment strategy of the species. Body size at full maturity correlates with time spent developing in the mother's womb. There is a positive correlation between the length of gestation and birth status. Birth status 1 is the result of short gestation, while birth status 4 is the product of a long gestation period (Langer, 2008). Altricial species, maturing to relatively smaller adult body sizes, require shorter gestation periods and experience a high degree of postnatal development. In both bird and mammalian species that are precocial, periods of gestation are long. However, the gestation period may be shorter when the mother has to provide for extant offspring (Clutton-Brock 99). In a world of limited energy, it may not be possible to grow, mature and birth an infant that is well developed in all organ systems. Decades ago, work done by Sacher (1959), suggested that building large brains is especially costly. Brain size remains the best predictor of gestation length across mammals (Sacher and Staffeldt, 1974). The rate of growth and aging are dependent on the metabolism and energetics of the brain.

Birth in humans is more difficult than that of other species (Rosenberg, 1992). The complexity of the human brain and central nervous system necessitates a large supply of energy resources. Anthropoid apes with gestation lengths that are similar to humans achieve a level of brain development by birth that shows resemblance to the adult condition. This is not a feasible goal for the immediate postnatal state of development in humans. Even a gestational period of 280 days is not sufficient to support the level of complexity of the central nervous system. Based on the rate of fetal growth in humans, it would take 21 months of gestation to reach a stage of

neurological development that is parallel to other anthropoid apes at birth (Portmann, 1941). The traditional view is that natural selection responded to the energetic demands and locomotive burden of promoting the development of a large brain by evolving a shorter gestation period (Washburn, 1960). Nevertheless, the human 38-week period of gestation is still nearly equal to that of our closest primate relatives, the great apes, despite differences in overall complexity of development. Chimpanzees and gorillas experience 32-week and 37-week periods of gestation, respectively (Rosenberg and Trevathan, 2002). However, humans are born in a much more helpless state than their great ape counterparts.

Secondary altriciality in human infants can be seen as an evolutionary tradeoff. An increase in brain size throughout the evolution of the hominid lineage and the associated difficulties of passing a baby with a larger crown through the birthing canal required modification of the developmental state of a newborn (Kirkwood and Shanley, 2001). The adaptation supported encephalization while maintaining the integrity of the female pelvis. Human neonates are consequently born in a less developed state and demonstrate high dependence on parental investment. The human condition at birth is not proportional to the final level of growth and development achieved in adult humans (Portmann, 1941). As a result, the development of cognitive and motorneuronal skills is heightened during the first year following birth (Dunsworth et al., 2012). In summary, the length of gestation accommodates the anatomical restrictions of a reproductive human female and the maximum level of energy she is capable of supplying to her offspring in utero.

Linking Brain Weight, Neonatal Dentition and Life History

A postnatal examination of dentition can be used to assess the effect of size on the arrangement of events that occur throughout an organism's lifetime. A strong association between brain weight and the age at eruption of the first permanent molar, M_1 , provides solid evidence regarding the influence of size on timing in life history. The connection between size and life history demonstrated in living primates has implications for the history of human evolution. Incorporating the dentition into examination of the fossil record will foster further exploration of this link. It is possible to identify developmental events by studying lines and bands of incremental growth preserved in dentition (Smith, 1991). Landmarks on teeth are well-preserved extending the application of dental examination to extinct species. The ability to point out different stages of development in teeth will enable researchers to draw parallels between species and provide support for potential evolutionary relationships.

The Evolution of Diphyodonty

In many fish and reptiles alike, teeth are expendable. Constant tooth renewal through replacement—as is observed in sharks—eliminates the consequence of tooth damage and loss (Jarvinen et al., 2008). Tooth replacement appears to be requisite in large reptiles due to the nature of their changing diet during development (Pond, 1977). Mammals, in contrast, exhibit a unique dental scheme. The mammalian dentition demonstrates a reduction in the total number of teeth and a limited replacement series. Dental development in humans is generally observed as an early eruption of deciduous teeth in varying order, followed by molars and replacement teeth that are permanent. This pattern is widespread in living mammals today, although not universal. It is possible that the reduction occurred in response to the evolution of lactation (Janis and

Fortelius, 1988). Lactation and parental feeding induce a rapid development of the head and jaws. Rapid growth of the jaws permits diphyodonty: the presence of one set of milk teeth that is subsequently replaced by a set of permanent teeth (Smith, 1991). Diphyodonty establishes permanent integration of the tooth row, which allows for occlusion of interlocking teeth. Occlusion was made possible by the evolutionary change that eliminated continuous replacement and the associated interference caused by frequently losing and adding teeth. Precise occlusion, or controlled contact between the maxillary and mandibular teeth is requisite to processing the non-brittle foods that mammals eat. Mammals have relatively high metabolic rates and require a unique diet composed of foods that are high in energy and enriched with nutrients. Many of the foods vital to the generalized mammal diet require mechanical breakdown in order to be digested. Mastication is far more efficient when performed in cooperation with teeth that occlude. Mammals rely on this mechanical process to breakdown foods that will supply sufficient energy for maintenance and reproductive processes (Janis and Fortelius, 1988).

Dental development parallels the life cycle and is in agreement with several variables of life history. The timing of tooth eruption is crucial for survival. Teeth must emerge in a pattern that promotes functional occlusion and be present in time for babies to be weaned (Smith, 1991). The eruption of deciduous dentition generally begins with the emergence of dI_1 (see Figure 10). The rest of the deciduous teeth follow with eruption in a mesial to distal pattern, with the possible delay of canine emergence. Mandibular dentition tends to erupt before maxillary teeth. However, the last deciduous tooth to emerge is typically dP_4 or dC_1 (Smith et al., 1994). Deciduous teeth serve to maintain dental alignment and spatial arrangement for the future occupation of permanent teeth (Janis and Fortelius, 1988). Permanent teeth replace deciduous

teeth before their function is exhausted, ensuring a sustained capacity to process foods (Smith, 1991). The relatively uniform nature of the mammalian diet from birth to full development diminishes the need for consistent tooth renewal and replacement (Pond, 1977).

Precociality of Primates

The study of nonhuman primates has the potential to provide information pertinent to the life history of humans, including an understanding of the birth status of our newborns. Primate species demonstrate varying degrees of precociality at birth. Life-history events and growth rates have not been well documented for many species, which makes it difficult to gauge the true range of precociality in primates. Documentation of birth status is especially rare. The lack of comprehensive records may be attributed to the rarity of captive births and difficulty in maintaining records over the long lifespans of some of these species (Smith et al., 1994). An exceptionally small amount of information has been published regarding the development of small-bodied primates. The gradient of precociality that exists in primates is particularly evident in the study of dental development at birth.

The dentition is relatively frequently preserved in the fossil record and provides information regarding species' growth rates to analyze and document. Information that is collected from the teeth of specimens of different ages can be used to organize a chronology of maturation events that occur across a species. Body weight is a useful predictor of dental maturation, with larger species generally maturing more slowly. Patterns of dental maturation can be predicted by body weight to some degree. Many small-bodied primates that develop quickly have teeth at birth. Offspring from larger primates that grow more slowly are less likely to possess teeth when they are born. Literature suggests that most nonhuman primates are born

with erupted teeth and nearly all nonhuman primate species experience the emergence of teeth within the first two weeks of life. A stronger correlation exists between dental development and brain weight. The secondarily altricial condition of human neonates exposes the huge energy expense of encephalization. Additionally, human infants experience a much slower progression of dental development. The emergence of the first tooth does not occur until about 7 months of age and the deciduous dentition does not become complete until approximately 2.3 years of age (Smith et al., 1994). This observation has implications for the human life history scheme. Dental development can act as an indicator of birth status. Therefore, slow dental maturation indicates that humans are developing more slowly in other ways as well, relative to nonhuman primates. The birth status with regard to the dentition indicates the capacity of a neonate to supplement maternal milk with other foods. Mineralization of the teeth at birth has been shown to coincide with the categories of birth status. Specifically, precocial categories II-IV demonstrate a clear association with the mineralization of permanent dentition (Gingerich et al., 2009). Therefore, teeth can be used to create an index of precociality in primates.

Study Introduction

This study was performed to explore the degree of altriciality or precociality observable in the dentition. Generalized mammals uniformly demonstrate a mineralization of the deciduous dentition in utero. However, mineralization of the permanent dentition varies between mammals on a much wider range. Signs of mineralization of the permanent first molars in the fetal skull suggest a precocial birth status (Gingerich et al., 2009).

Primates are heterodonts. The dental formulas of nearly all primate taxa include incisors, canines, premolars, and molars (Swindler, 2002; Tattersall, 1982). This uniformity fosters the

development of networks that establish evolutionary relationships. It is possible that fundamental similarities will be detected and link distinct species, because records of dental maturation are so highly preserved in teeth. A series of investigations of dental development is necessary to organize the position of each primate species in the spectrum of precociality. Identifying the extremes is a useful starting point for this inquiry.

In this paper, the neonatal dental development of two small-bodied primate species, *Callimico goeldii* and *Galago senegalensis*, have been examined and described in detail. These species were chosen to represent primate differences in precociality that are present in the birth spectrum. There has been virtually nothing published regarding dental development at birth for these two species. Only estimations of the timescale for eruption of deciduous teeth exist currently (Smith et al., 1994). Because dental development at birth corresponds to birth status categories (Gingerich et al., 2009), the teeth of a newborn provide insight into different life history. In order to determine the degree of precociality for each of these species, the age of eruption and completion of their deciduous dentition should be investigated and documented as well.

***Callimico goeldii* Background**

The *Callimico goeldii*, or Goeldi's monkey, belongs to the subfamily Callitrichinae in the family Cebidae. Callimicos fall into the suborder Haplorhini of the order Primates. They are South American New World monkeys that are small and transported as infants (Schradin and Anzenberger, 2001). Female callimicos are capable of giving birth to a single offspring twice a year. The length of gestation in this species is 155 days and the offspring are born with low muscular development. Callimico neonates require a high level of investment and experience

much of their development extramaternally (Garber and Leigh, 1997). This species has a dental formula of 2,1,3,3. At birth, callimicos have been reported to show 10 teeth already erupted (Smith et al., 1994). In the present study, a series of *Callimico goeldii* specimens will be studied to evaluate age of tooth emergence and the progression of dental development in neonates ranging from day 0 to day 3 after birth.

***Galago senegalensis* Background**

The *Galago senegalensis*, or Senegal bushbaby, is part of the family Galagidae, which belongs to the suborder Strepsirrhini of the order Primates. The galago is an African strepsirrhine. An adult galago has a 2,1,3,3 dental formula in both the maxilla and mandible. This includes two incisors, one canine, three premolars, and three molars on each respective side. Galagos are more precocial than many other primate species. In 2008, Langer characterized *Galago senegalensis* as a birth status 3 species with an estimated 123.8 day gestation period. The full lactation period documented in Langer's table was 43.5 days, which included both a milk-only and mixed feeding period. Neonates must develop teeth in time for weaning (Smith, 1991), so it is possible that the short lactation period could explain the rapid development of dentition in this species. In order to develop a productive index of precociality among primate species, to begin with, it is important to analyze and document the birth status and development of other closely related species.

Species	Adult body weight (g)	Gestation period (days)	Total lactation (days)	Dental formula	Birth status
Galago senegalensis	145 grams	123.8 days	43.5 days	$I_2^2, C_1^1, P_3^3, M_3^3 / I_2, C_1, P_3, M_3^{**}$	3
Propithecus verreauxi	2290 grams	128.1 days	150 days	$I_2^2, C_1^1, P_2^2, M_3^3 / I_2, C_0, P_2, M_3^{***}$	3

*Data compiled from Langer, 2008 and Cuzzo and Yamashita, 2005

** Dental formula for *Galago senegalensis*

*** Dental formula for *Propithecus v. verreauxi*

The sifaka, for example, is another quite precocious strepsirrhine from Madagascar.

Verreaux's sifaka is the common name for a type of lemuroid from the species *Propithecus v. verreauxi*. Sifakas belong to the family Indriidae. Given the data in Table 2, the galago and sifaka neonates appear to be developmentally similar. However, lemur species experience a 150-day lactation period comprised of 30 milk-only days and 120 mixed feeding days (Langer, 2008). If the length of lactation and dental maturity are associated like many other life history variables, the extended mixed feeding period in lemurs could indicate a difference in the dental development rates of galagos and sifakas. Furthermore, the eruption of the first permanent tooth in *Propithecus v. verreauxi* occurs at 0.22 years of age, while the first permanent tooth emerges at 0.10 years of age for *Galago senegalensis* (Smith et al., 1994). This data suggests that despite various life history traits that indicate a higher degree of precociality in sifakas, the galago's dentition actually matures more rapidly.

Predictions

Based on the traditional system of classification, the longer gestation length of the *Callimico goeldii* species might lead us to expect that callimico neonates should be more precocial than those of *Galago senegalensis*. Life history traits are tightly associated with dental

development, so corresponding to the longer gestation length in callimicos, we might predict that their dentition should be more mature at birth than that of the galago.

Materials and Methods

A variety of specimens were examined and photographed at the Field Museum of Natural History (FMNH) in Chicago, Illinois. The specimens pictured in Figures 1-7: FMNH153711, FMNH148066, and FMNH150675 are members of the species *Callimico goeldii*. FMNH150676, FMNH140350 and FMNH153713 are *Callimico goeldii* specimens that were also included in the analysis for comparison (not pictured).

The *Galago senegalensis* study specimen, Is1020, comes from a captive colony at Arizona State University supervised by Leanne Nash. Captive galagos that died were frozen and eventually transported to Tim Smith of Slippery Rock University. Professor Smith's laboratory performed a microCT scan of the study specimen that is represented by a three-dimensional image in this paper. The galago was scanned using a vivaCT microscanner at Northeast Ohio Medical University (NEOMED). The scan parameters were 70 kVP with 25 voxels (25 micrometer slice intervals).

The scan was then processed in AMIRA version 5.4.1, a program of advanced imaging software that facilitates the creation of 3-D images produced from a 2-D microCT scan. The microCT scan was divided into several hundred slices. The slices were segmented individually by hand-tracing each tooth on each slice of the microCT scan. The images in Figures 8, 9, 10, and 11 were generated using AMIRA software.

Images of the Dentition of *Callimico*

DAY 0: FMNH153711



Figure 1. Exterior view of callimico skull on day 0.



Figure 2. Occlusal view of callimico mandible on day 0.



Figure 3. Exterior view of callimico skull on day 0.



Figure 4. Occlusal view of callimico mandible on day 0.

DAY 2: FMNH148066

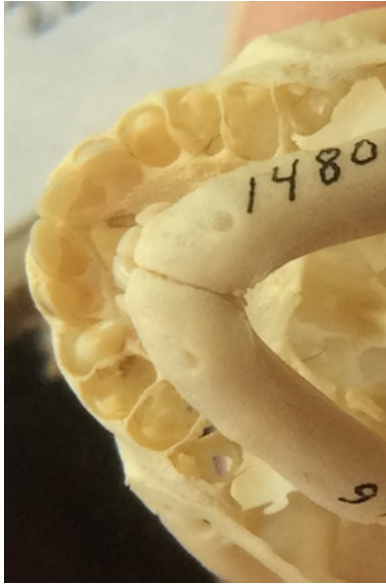


Figure 5. Maxillary dentition of callimico aged 2 days.

DAY 3: FMNH150675



Figure 6. Oblique view of articulated skull and jaw of 3-day-old callimico.

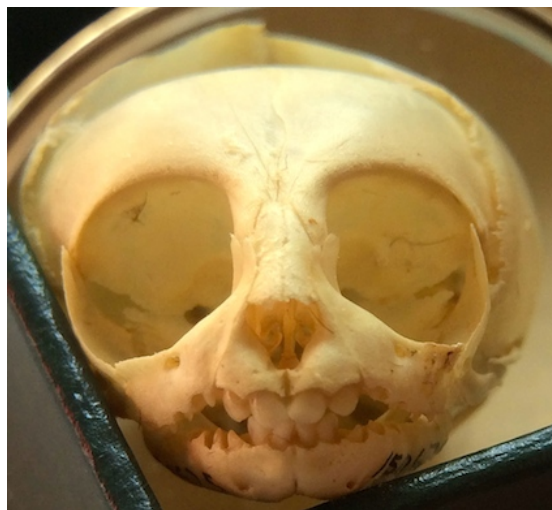


Figure 7. Frontal view of articulated skull and jaw of 3-day-old callimico.

Galago Dentition Images: *G. senegalensis* (Is1020)

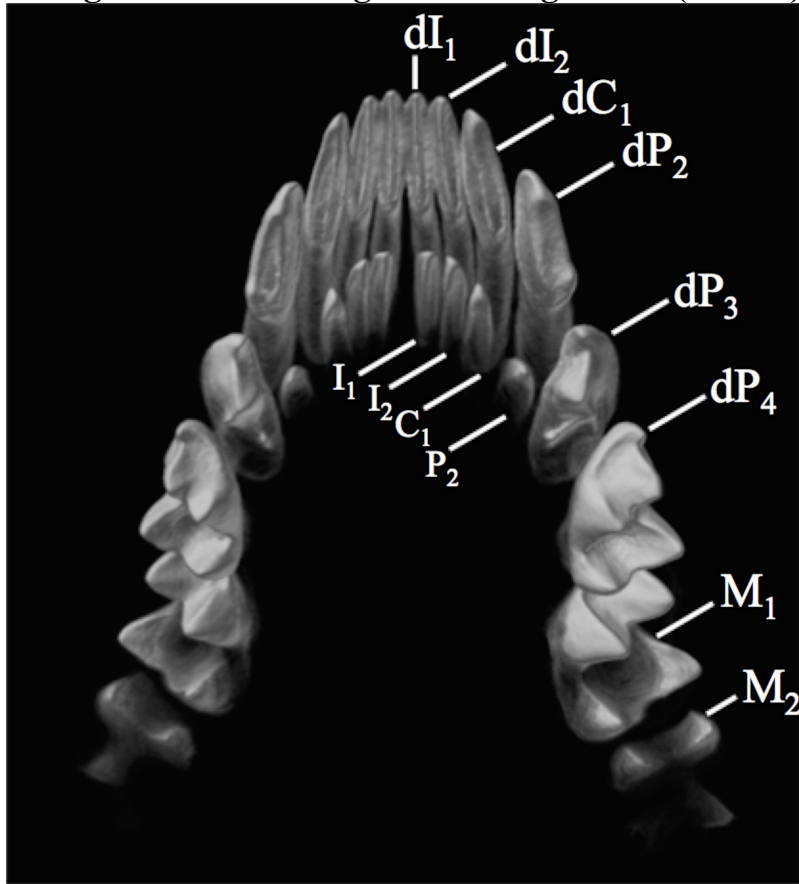


Figure 8. Occlusal view of mandible of 7-day-old galago.



Figure 9. Enlarged view of mandibular premolars and molars.

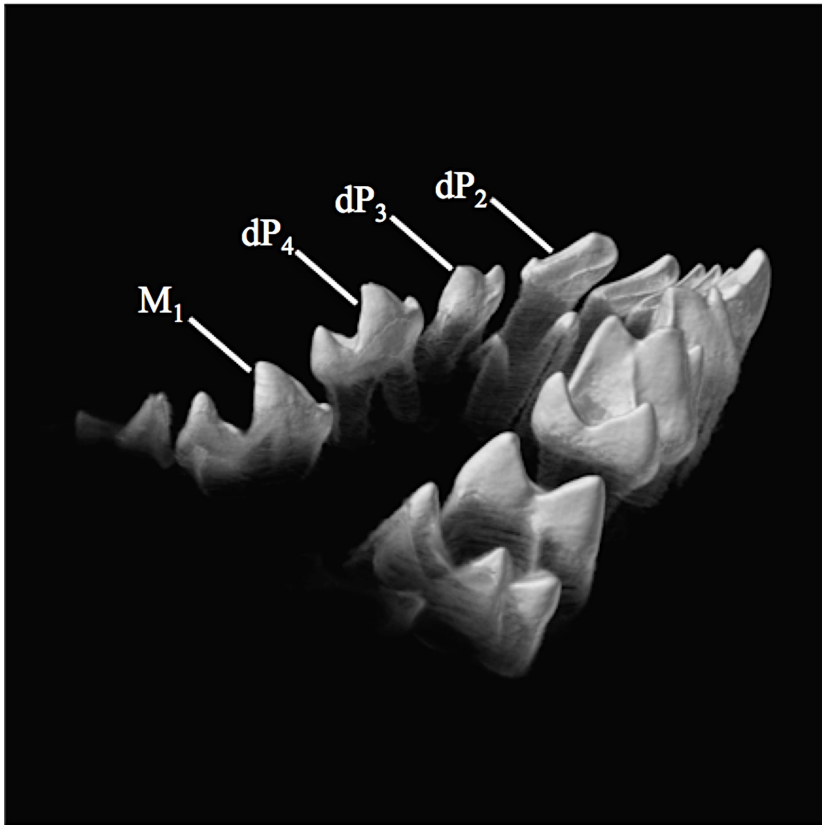


Figure 10. Left medial view of roots of mandibular dentition.



Figure 11. Aerial perspective of mandibular dentition.

Results

Age & Specimen(s)	Deciduous incisors	Deciduous canines	Deciduous premolars	Permanent canines	Permanent premolars	Permanent molars
FMNH153711 Day 0 <i>Callimico</i>	Erupted	Partial tooth emergence	Unerupted, developing	Not visible	Not visible	Not visible
FMNH148066, FMNH150676 Day 2 <i>Callimico</i>	Erupted, roots unfinished	Partial tooth emergence	Unerupted, developing	Not visible	Not visible	Not visible
FMNH150675 Day 3 <i>Callimico</i>	Erupted	Partial tooth emergence	Partial tooth emergence	Not visible	Not visible	Not visible
FMNH140350 4 mos. <i>Callimico</i>	Erupted	Erupted	Erupted	Not visible	Not visible	Partial tooth emergence
FMNH153713 11 mos. <i>Callimico</i>	Replaced	Erupted, not replaced	Replaced	Not visible	Erupted	Erupted
Is2010 Day 7 <i>Galago</i>	Erupted, Calcified	Erupted, calcified	Erupted, calcified	Unerupted, crowns near completion	Unerupted, crowns near completion	Possibly erupted, approaching coalescence

Specimen FMNH153711 is a male *Callimico goeldii* (Figures 1-4). The day of birth and death for this individual took place on September 5, 1982 (day 0). The maxilla and mandible of this specimen are each pictured twice in order to achieve maximum resolution of different sections of the image. All 8 deciduous incisors appear to be erupted. In the mandible, dP_2 , dP_3 , and dP_4 are somewhat developed, but have likely not pierced the gingiva.

Specimen FMNH148066 is a male *Callimico goeldii* (Figure 5). This male lived from December 30, 1986 until January 1, 1987, dying on day 2. Only the maxillary dentition is fully pictured for this specimen. Both the maxillary and mandibular deciduous incisors can be observed, indicating that all 8 deciduous incisors had emerged. Mineralization of the cusps of deciduous premolars dP^2 , dP^3 , and dP^4 is visible. The tooth sockets of the maxilla show progress of development of the remaining unerupted deciduous teeth. The sockets for the first permanent molars are broken away in this specimen.

Loose teeth from another male *Callimico goeldii* (FMNH150676), also aged day 2, were examined and compared to the specimen that is pictured above (FMNH153711). The roots of the deciduous incisors are unfinished. The premolars present with some finished crowns and root initiation, which is especially apparent in dP₄.

Specimen FMNH150675 is a male *Callimico goeldii*. Its life began on February 21, 1984 and ended on postnatal day 3, February 24, 1984. This specimen has an articulated skull and jaw, which is useful in determining which teeth have emerged through the gingiva. The ability to observe where contact is made between the upper and lower dentition allows us to more accurately determine which teeth have erupted into the oral cavity. The progress of emergence is demonstrated by the contact between the maxillary incisors and mandibular incisors (Figures 6,7). The deciduous incisors have erupted. Deciduous mandibular canine and premolar, dC₁ and dP₂, appear to be partially erupted. The rest of the deciduous dentition is likely still developing in the alveolar processes of the maxilla and mandible.

Two additional *Callimico goeldii* specimens of known age were examined in order to follow the progress of dental development to nearly one year of age. At 4 months old, specimen FMNH140350 demonstrates eruption of the crowns of the first permanent mandibular molars, M₁. The next specimen, FMNH153713, is just over 11 months old. The maxilla of this specimen demonstrates eruption of all permanent teeth with the exception of the permanent canines. The upper deciduous canines are still in place. Similarly, the mandible has all of its permanent teeth with the permanent mandibular canines unemerged but likely approaching the piercing of the gingiva.

The mandibular dentition of the *Galago senegalensis* fetal skull (Is1020) is mapped in detail (Figure 8). The 7-day-old galago presents with a set of highly developed deciduous teeth. The deciduous toothcomb is erupted and composed of a total of four incisors and two canines. The deciduous incisors have good long roots, indicating that their development is almost complete. The deciduous premolar of the galago, dP₂, is caniniform; it is developed and calcified in the seven-day old. The deciduous premolars, dP₃ and dP₄ are both visible. The molariform fourth deciduous premolars have long roots (Figure 10), which suggests that their development is near completion. The first molar, M₁, has a mineralized crown; root formation has started, but is incomplete. The lacuna visible between the cusps of each M₁ raise the possibility of incomplete calcification across the molar. Mineralized metaconid, protoconid, and hypoconid cusps of M₂ are visible, but the crown has not coalesced yet. In the front of the jaw, permanent replacement teeth can be seen developing beneath deciduous precursors. For example, images clearly show that mineralization of the crowns of the permanent incisors is well underway (Figures 8 and 11). A diastema is present between the central permanent incisors at this stage of development. The crowns of the permanent mandibular canines are also visible (Figure 8); these will eventually form a part of the permanent tooth comb. From anterior to posterior, the anterior permanent teeth are more developed than the posterior permanent teeth. However, more minimal crown mineralization is observed in C₁. On either side of the permanent mandibular canines, permanent premolars (P₂) are developing, showing about two-thirds crown completion.

Discussion and Analysis

The dentition of the callimico neonates was significantly less developed than the baby galago (see Table 3). The neonatal callimicos that were examined, ranging from ages day 0 to

day 3, demonstrated eruption of all deciduous incisors. Furthermore, development of the deciduous premolars was still taking place within the jaw. In contrast, all of the deciduous teeth of the 7-day-old galago appeared to be erupted and near completion.

The evaluation of additional callimico specimens yielded more data on ages of important developmental events. The age of eruption of the first permanent molar was recorded as shortly before 4 months of age. The age of completion of the permanent dentition (excluding permanent canines) was documented as approximately 11 months old.

We were unable to make an exact comparison of galago and callimico neonatal dentition because we did not have access to a 7-day-old callimico. Additionally, no adult galagos of known age were available to evaluate the rate of dental development firsthand. The age of eruption of the first permanent molar has been documented in galagos at 0.10 years old, or roughly 5 weeks of age (Smith et al., 1994). As indicated by the assessment of specimen FMNH140350, the crowns of the first permanent molar are only beginning to erupt around 4 months of age in callimicos. This demonstrates a much slower rate of dental development in callimicos relative to galagos. It is also important to note the major difference in root development of dp_4 (see Figure 10) of the galago in contrast to the minimal development of dp_4 in the neonatal callimico specimens. On day 7, the deciduous dentition of the galago neonate is well established and nearly ready to be replaced by the developing permanent dentition. The callimico neonates trail behind in their dental development.

Implications for Galago Life History

There is potential for disagreement between soft and hard tissue measurements of altricial-to-precocial neonatal development. Studying hard tissue offers a more progressive

evaluation of neonatal development that can be measured in extant or extinct species unlike the measurements that rely exclusively on soft tissue. The degree of precociality in galagos as compared to callimicos is unexpected given the traditional characterization of an altricial or precocial mammal. Though galagos experience shorter gestation periods and ultimately have lower body weights as adults, they are in fact more precocial than callimicos. This particular circumstance raises questions about species that do not quite fit the mold for the original altricial and precocial categories. The original system did not allow for variance between different species. The distinction was either altricial or precocial with no middle ground. Even now with Langer's birth status categories outlined in Table 1, galagos could be ranked incorrectly in the spectrum of precociality if dental development is ignored. According to positive relationships that relate size to life history, both body weight and length of gestation would indicate that galagos are less precocial than callimicos. Our analysis of dental maturation as well as the pattern of infant transport suggest otherwise. Therefore, including a record and analysis of dental development in the fossil record is imperative to gaining a complete understanding of life histories and evolutionary relationships. Examining both the soft and hard tissues provides a more clear explanation of galago life history.

Conclusion and Future Research

This study facilitated the characterization of dental variability between two precocial species, *Callimico goeldii* and *Galago senegalensis*. It was especially important to accomplish this because little to no data documenting dental development existed for these species prior to this study. In fact, analysis of the data exposed the importance of examining dentition to ascertain the degree of altriciality or precociality in mammals. This demonstrates that dental

development *is* an important feature of mammal life history. The new information presented in the paper will serve to augment the index of precociality in primates.

The evaluation of dental development in the series of *Callimico goeldii* specimens yielded a detailed record of important developmental ages for this species. Preceding this study, minimal data on callimico dentition was available. Now, evidence is offered in an effort to generate a full chronology of events that will be acknowledged as part of callimico life history. More callimicos should be assessed in order to confirm and complete the record of dental maturation for this species. In the future, it would be advantageous to obtain microCT scans of *Callimico goeldii* specimens in an effort to evaluate the development of unerupted teeth that is occurring within the jaw. Hopefully, this research will serve to launch further investigation of dental development. The dentition of more species should be evaluated to increase our knowledge base of primate development.

Teeth contain a wealth of knowledge that could engender an enormous contribution to the interpretation of evolution represented in the fossil record. The information recorded in teeth may bridge the gap for incomplete life histories. This is possible because dental development is tightly correlated to growth patterns that were previously only apparent in soft tissue examinations. Thus, investigations of dentition have the potential to link the past to the future. More primate species need to be studied and their life history characteristics documented. Humans in particular will benefit from new studies of primate dentition. Once a large database of primate dental development is established, it may be possible to employ this information in making connections with events evidenced throughout human evolution. Primate growth can be followed to maturation without difficulty due to the short sixth month postnatal period required

to reach completion of deciduous dentition for many species (Smith et al., 1994). Data that are collected regarding the age of eruption and completion of the deciduous dentition will extend to a variety of life history traits. Additionally, records of age of eruption will enable researchers to extrapolate the growth rate of a species from the data. Examining the teeth of living species, as well as those that are extinct, will allow researchers to validate claims that have been made regarding the life history of a species. Stronger evolutionary relationships can thus be supported on the basis of similarities in dental development.

Creating an accurate life history scheme for *Homo sapiens* is complicated by the absence of a complete collection of specimens that mark each point of development in human evolution. Therefore, attaining a superior understanding of the human condition without definite, tangible evidence demands the integration of productive inferences with information that is already known about other closely related species. Deciphering the web of interrelationships among mammals will enlarge the scope of understanding regarding the evolutionary progress that led to human evolution. The existing collection of data about mammals should be refined to improve the accuracy of connections made between evolutionary events documented in the study of humans and related species. The inclusion of an examination of neonatal dentition serves as an important determinant in the degree of variation in altricial and precocial character experienced by distinct species. The interpretation of the redistribution of species into this spectrum of development has the potential to increase comprehension of evolutionary patterns observed in different species. Understanding these patterns could improve scientists' capacity to decipher the intriguing mosaic of altricial and precocial characteristics displayed by the human species. Thus, further research in this area will allow parallels to be drawn to the evolution of the human

species based on the developmental patterns of various related species. Ultimately, this system could enable the reconstruction of the entire history of human evolution. In doing so, the fund of human knowledge would be enhanced, allowing scientists to peer into the complex nature of the human condition and challenge the etiology of disease.

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