Dental Maturation, Eruption, and Gingival Emergence in the Upper Jaw of Newborn Primates

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ABSTRACT

In this report we provide data on dental eruption and tooth germ maturation at birth in a large sample constituting the broadest array of non-human primates studied to date. Over 100 perinatal primates, obtained from natural captive deaths, were screened for characteristics indicating premature birth, and were subsequently studied using a combination of histology and micro-CT. Results reveal one probable unifying characteristic of living primates: relatively advanced maturation of deciduous teeth and M1 at birth. Beyond this, there is great diversity in the status of tooth eruption and maturation (dental stage) in the newborn primate. Contrasting strategies in producing a masticatory battery are already apparent at birth in strepsirrhines and anthropoids. Results show that dental maturation and eruption schedules are potentially independently co-opted as different strategies for attaining feeding independence. The most common strategy in strepsirrhines is accelerating eruption and the maturation of the permanent dentition, including replacement teeth. Anthropoids, with only few exceptions, accelerate mineralization of the deciduous teeth, while delaying development of all permanent teeth except M1. These results also show that no living primate resembles the altricial tree shrew (*Tupaia*) in dental development. Our preliminary observations suggest that ecological explanations, such

as diet, provide an explanation for certain morphological variations at birth. These results confirm previous work on perinatal indriids indicating that these and other primates telegraph their feeding adaptations well before masticatory anatomy is functional. Quantitative analyses are required to decipher specific dietary and other influences on dental size and maturation in the newborn primate. Anat Rec, 298:2098–2131, 2015. © 2015 Wiley Periodicals, Inc.

INTRODUCTION

Modern life history theory posits a link between natural selection and the pace at which an animal develops (Promislow and Harvey, 1990; Charnov and Berrigan, 1993; Janson and Van Schaik, 1993). Comparative studies of nonhuman primates have revealed that primates vary in relative gestation length, relative weaning age, and relative life span (Schultz, 1969; Martin, 1990; Harvey et al., 1987; Ross, 2003). Both morphology (e.g., musculoskeletal system) and behavior (e.g., locomotor development) covary with these longitudinal measurements. Primates are so diverse in the pace of somatic maturation and locomotor development that some are referred to as precocial and others altricial, depending on the context (Crompton, 1983; Nicolson, 1984; Derrickson, 1992; Grand, 1992; Smith et al., 1994; Starck and Ricklefs, 1998; Atzeva et al., 2007; Rosenberg and Trevathan, 2015). Many studies of subadult primates assess morphological or behavioral indicators to determine how quickly a primate achieves independence (Fairbanks, 1993; Ross, 2001; and see Bolter and Zihlman, 2007). In the past two decades, a renewed focus has centered on the schedule of dental development, with a particular focus on the rate at which the teeth erupt from the alveolar bone and emerge through the gingiva (Smith et al., 1994; Godfrey et al., 2001; Henderson, 2007; Guthrie and Frost, 2011).

A particular emphasis of recent dental studies has been to determine if tooth development follows the pace at which the animal grows and attains adulthood. A rather complex picture has been revealed, indicating that dental development appears to correlate more strongly to brain growth than body growth (Smith et al., 1994; Godfrey et al., 2001), and that morphological measurements that are presumed to relate to an independent lifestyle in primates (rate of ossification, attaining muscular mass, pace of dental eruption) are not always predictably in synchrony (Guthrie and Frost, 2011).

Whenever samples were sufficient, previous studies have focused on links between the eruption status and some significant developmental milestone of life, such as weaning age. Because many nonhuman primates are rare in captivity and reproduce relatively slowly, there are numerous species that remain unstudied or poorly understood. In particular, our knowledge of the eruption of deciduous dentition remains poor, especially compared with what is known about permanent tooth eruption

(Smith et al., 1994). For example, in 2002 Swindler presented a broad comparative account of primate dental anatomy. This reference has only one significant omission, the deciduous dentition of prosimian primates. Accordingly, the goal of this report is to present the status of dental eruption of the upper jaw at the perinatal stage from a broad sample of captive-born primates.

Gingival Emergence and Eruption of the Maxillary Dentition at Birth: Previous Studies

In 1935, Schultz undertook a study of the eruption of permanent teeth based on large numbers of primate skulls, with an emphasis on catarrhines. This considerably expanded knowledge of postnatal dental development, but a far greater dearth of information on deciduous teeth remained. Reviewing the literature, again primarily on catarrhines, Schultz observed that eruption of the deciduous teeth occurred postnatally in all species examined at that time, but that gingival emergence was delayed further in apes and humans relative to monkeys. For decades, information accumulated on captive primates, particularly in laboratory settings. These observations generally confirmed that the pace of eruption is relatively rapid in monkeys, beginning within days or weeks of birth (e.g., Long and Cooper, 1968; Chase and Cooper, 1969; Johnston et al., 1970; Trotter et al., 1977; Glassman, 1983), compared with slower rates of eruption in apes and humans (Enlow, 1990; Mooney et al., 1991; and Anemone et al., 1996, regarding lower molars). These studies also confirmed that gingival emergence may be particularly rapid in some platyrrhines, as suggested by Schultz (1935). The greater delay in dental development from platyrrhines to cercopithecoids to hominoids also applies to the age at which the full set of deciduous dentition emerge (Hershkovitz, 1977). Hominoids take longer to erupt a full set of deciduous dentition, and subsequently take longer to replace these teeth (Schultz, 1935). They prolong infancy, defined as the stage prior to eruption of permanent teeth (Bolter and Zihlman, 2007); this slow pace is especially pronounced in humans.

This idea of a phylogenetic continuum of pace, with small platyrrhines having rapid dental development and humans having the slowest pace, was the prevailing view for decades. Still, certain platyrrhines (especially callithrichines) stood apart as having particularly early gingival emergence. And in 1985, Eaglen provided the first detailed information on strepsirrhines, revealing

variation in the timing of eruption within a sample that included six species. Thus, other possible influences on the eruption of deciduous dentition, such as dietary specialization, body size, or phylogeny, loomed large but remained difficult to test because no studies had considered a diverse enough sample.

The most ambitious effort to establish comparative knowledge of the pace of development beginning at birth was by B. Holly Smith and colleagues, who compiled data from decades of studies on captive primates (Smith, 1989; Smith et al., 1994). Later, Godfrey et al. (2001, 2003) and Henderson (2007) analyzed alveolar eruption based on museum samples. Additionally, Godfrey et al. (2004), added to our knowledge of early (fetal and newborn) sifaka dentition, revealing that the precocious state is detectable at these early ages. This rapid pace of dental development has also been noted in tarsiers (Guthrie and Frost, 2011). In a synthesis of existing data, Smith (2000) sorted mammals into two groups: those that grow rapidly and erupt their molars prior to replacement teeth, and those that grow more slowly and instead have relatively earlier erupting replacement teeth.

This "fast" and "slow" growing concept, called "Schultz's rule" by Smith (2000), posits a relationship between pattern of development and pace of growth in a region. Surely factors such as the number or size of teeth can influence upper limits in terms of the midface and lower jaw size. However, some strepsirrhines present clear exceptions to Schultz's rule, with certain folivorous species having especially rapid dental development that would not be predicted based on other somatic growth patterns (Godfrey et al., 2001, 2003, 2004, 2005). Clearly, dental development can be targeted by selection independently of other somatic growth patterns. In addition, it has been observed that brain size (rather than overall body size) is strongly correlated with the pace of dental development (Smith, 1989; Godfrey et al., 2001). Brain development, in turn, strongly correlates with certain life history variables, such as age at weaning. Dental development is likewise correlated (negatively) with age at weaning: earlier weaning is linked with a more precocious dental arcade (Godfrey et al., 2001). These studies suggest, unsurprisingly, that diet is a primary influence on dental development. In addition, metabolic factors may be at work on the brain and teeth simultaneously.

While the pace and chronology of dental development is becoming increasingly well-studied across diverse taxa, there has been little emphasis on the newborn age. The compendium by Smith et al. (1994) clearly reveals earlier gingival emergence in strepsirrhines, but information is limited to lemuroids. The lack of knowledge on the newborn status of dentition is a significant gap, because any adaptations detected at this stage presage their function. They certainly have no immediate significance to mastication, and are of far less importance before weaning than after.

Previous Studies of Perinatal Tooth Mineralization

Existing literature on the perinatal primate dentition is heavily biased toward catarrhine primates, especially hominoids. The order of tooth mineralization is the same in Old World monkeys, the great apes, and humans with some intraspecific variation. The pattern is as follows: di1, dp3, di2, dc, dp4 for deciduous teeth and M1, I1, I2, C, P3, [P4/M2], M3 for permanent dentition (see Swindler, 2002, for original references). In all of these species M1 is mineralized at birth (1 to 3 cusps). This latter point is significant because the eventual eruption of this tooth is closely correlated with timing of weaning in primates (Smith, 1992). Whether this pattern of early mineralization of M1 typifies all primates is not known, since maturational state of the dentition at birth in platyrrhines and strepsirrhines has been poorly documented. In 1973, Tarrant and Swindler (1973) added some details on deciduous tooth development in a single platyrrhine species (*Alouatta caraya*).The precise order of deciduous tooth mineralization could not be determined in *Alouatta*, but the order of cusp mineralization for dp4 is the same as in catarrhines (paracone-protocone-metacone-hypocone).

In part, this lack of data relates to the challenges of studying specimens at this early age. Unmineralized teeth cannot be studied using traditional radiographic techniques (Winkler, 1995), and on the other hand, some species are large and challenging to study using histological methods. Kraus and Jordan (1965) studied numerous fetal and neonatal humans, using whole mount preparations to demonstrate mineralization. They established that M1 cusp mineralization is initiated at birth, but has not extended to the tooth basin. Kraus and Jordan (1965) also discussed the challenges in studying newborn and earlier ages, noting that preceding studies had provided varying accounts on mineralization by age. Garn et al. (1959) noted that results of radiographic studies do not match findings of histological studies of tooth development. This is presumably a problem of resolution and the extent of mineralization, each of which can require different radiographic parameters. In addition, radiographic means of study have a limited capacity to detect detail in poorly mineralized tissues. Histological methods do not have these limitations. Staining options exist to demonstrate any connective tissue, regardless of degree of mineralization, making it the best option, at present, for identifying stages of tooth germs prior to mineralization. The present study entails histology of a large sample of nonhuman primates, precisely in order to detect maturation of all teeth at any stage.

The objectives of this report are twofold. First, the novel data are intended to aid future life history studies in primates by providing researchers with a database of dental eruption and maturation at birth. The perinatal dentition of a large sample of strepsirrhines and platyrrhines are studied here for the first time, allowing a new synthesis of data on the teeth of newborn primates. Second, because our sample includes folivorous and non-folivorous species, we investigate whether the folivorous primates have an advanced state of dental eruption and maturation at birth, as has been observed in newborn *Propithecu*s (Godfrey et al., 2004).

MATERIALS AND METHODS

Sample Composition

In sum, the sample comprises a heterogeneous sample of captive animals that died before or within six days of

parturition. This age range is selected to target the "neonatal" state, that is, the primate within the first postnatal week. This time period is a necessarily reduced range in days compared with that used for the human neonate (28 days). Our maximum age in days is similar to that used in a previous study of neonates in non-human primates (Godfrey et al., 2004). The specimens studied here are referred to at the outset as "perinatal" in age (Table 1). This initial designation of samples acquired from natural deaths acknowledges a degree of uncertainty about their precise stage of development. In a broad sense, the issue is further complicated because not all primates develop at a similar pace. Stillbirths can present particular challenges, since they may not represent the maturation typical of a complete gestational length. Because primates vary in the rate of somatic maturation, including odontogenesis (Schultz, 1935; Godfrey et al., 2003; Pereira and Leigh, 2003), the neonatal stage presents a "moving target" when looking across taxa. In other words, birth is not necessarily tightly correlated with somatic development when looking across taxonomic groups.

Given that fetal and early postnatal dental ontogeny is poorly known for most primate species, we examined numerous representatives of "perinates" for species whenever possible. In sum, 105 individuals were studied (including 104 primates and one specimen of *Tupaia belangeri*; Table 1). These represent specimens histologically processed over the course of nearly two decades. All were obtained following perinatal mortality in captive settings (Appendix) with IACUC approval at Slippery Rock University. Because they were previously used to study midfacial development (e.g., Smith et al., 2001, 2003, 2005, 2010, 2011, 2014; Shimp et al., 2003; Rossie and Smith, 2007; Carmody et al., 2008), each of the histological series included the maxillary and premaxillary dentition. When possible, recorded age was obtained from the source institutions (Appendix; and see Zehr et al., 2014). Because specimens that were stillborn, or even those that died shortly following parturition, might be premature in gestational age, each specimen was examined for external features indicating state of somatic maturity. The following characteristics were noted in particular: (1) presence/absence of body fur, (2) presence of fetal membranes, (3) head and body proportions compared with other perinatal specimens of the species, and (4) overall body length (sitting height) compared with other perinatal specimens of the species. Fetal membranes indicated stillborn animals that may have been aborted or removed for veterinary reasons prior to full gestation. The absence of body fur provided a similar indication, although it was noted that cheirogaleids had less body fur than other primates. Even in such cases, the specimens were compared in size with others of the same species, or to published accounts of neonatal body size. According to these criteria, we were able to exclude certain specimens that were clearly collected well before full gestation length. In addition, several specimens were clearly "near term," or "late fetal" by comparison with other specimens (Appendix). These specimens were examined to draw inferences on the sequence of tooth maturation. Because many species were available in samples of two or more, we have confidence that the samples studied are accurate representatives of the neonatal age. Whenever possible, both male

and female specimens were included, since some somatic sex differences have been observed in primates as early as birth (Williams et al., 1994; Smith and Leigh, 1998). Henceforth, we refer to our samples as either neonates or fetuses.

One final consideration concerning our sample is the "captive effect." The possible effects of captivity on growth and development have long been debated (e.g., Leigh, 1994). It is generally believed that the "captive effect" influences body weight more than the hard tissues of the body (Smith et al., 1994; Swindler, 2002). However, it has been suggested that even the pace of dental eruption differs between captive and wild chimpanzees (Zihlman et al., 2004). While captive and wild chimpanzees may differ in the pace of dental development (but see opposing views in Smith et al., 2010), the effects on other non-human primates have not been conclusively demonstrated. We use captive specimens for practical and ethical reasons (most taxa are rare and endangered). We understand that our finding may not represent "normal" development under natural conditions in all cases. In the end, we assume that any effects of captivity do not mask phylogenetic patterns or dietary adaptations of primates at birth. Indeed, previous studies on large samples of subadult primates have detected certain dietary adaptations and phylogenetic patterns regardless of whether captive or wild samples were studied (Smith et al., 1994; Godfrey et al., 2003).

Specimen Preparation

Most specimens were saved in formalin by the source institution, but in many other cases frozen cadavers were acquired. In such cases, the cadavers were allowed to thaw gradually, in some cases immersed in a phosphate buffered saline solution, and then transferred to formalin. Most specimens were radiographed or CT scanned prior to histology. All specimens were prepared similarly for histological study. First, sitting height was measured. This was the linear distance from the crown to rump, with calipers positioned at the ischial tuberosities, thus excluding the tail. Although sitting height is often used as a synonym for "crown-rump length" (Streeter, 1920), the measurement was taken after straightening the thoracic vertebral region in any individuals that were in a state of extreme vertebral flexion. This is similar to the manner in which sitting height is measured in human newborns or advanced fetuses (Streeter, 1920), as a means of correcting for variability in posture (especially vertebral curvature) among different specimens. Subsequently, the skin was removed from the zygomatic and occipital regions of the skull in order to obtain cranial width (byzygomatic distance) and length (Prosthion-inion). Inion was indistinct in many specimens, but could be positioned as the midline point along the superior nuchal line or as the superior-most midline attachment of the nuchal fascia. In several specimens that were not dissected, it was necessary to take cranial measurements using CT reconstructions. In such cases, inion was located according to the approximate position in which the nuchal fascia inserted in other neonates, at the angular change in contour between the squamous and supraoccipital parts of the occipital. For histology, the head was removed (in the smallest specimens) or one-half of the face above the mandible was dissected

TABLE 1. Primate Sample.

N	Taxa	sex	age(s)	CT only	CL
	Semiorder Strepsirrhini				
	Infraorder Lemuriformes				
	Superfamily Lemuroidea				
	Family Cheirogaleidae				
4	*Cheirogaleus medius*	f, m?	P1		23.2
2	*Microcebus murinus*	m	P1		18.7
2	*Mirza coquereli*	f, m	P0-2		26.3
	Family Lemuridae				
3	*Eulemur collaris*	f, m	Pr.; P0		44.37
1	*E. coronatus*	m	P0		43.7
3	*E. flavifrons*	f, m	P0-1		44.6
2	*E. mongoz*	m,?	P0		43.3
1	*E. rubriventer*	f	P0		48.5
2	*Hapalemur griseus*	m	P0		38.1
3	*Lemur catta*	m,?	fetal; P1-5		41.8
2	*Varecia rubra*	f, m	P0-1		49.4
2	*V. variegata*	f, m	P0-1		47.1
	Family Indriidae				
3	*Propithecus coquereli*	f, m	fetal; P0		46.4
	Infraorder Lorisiformes				
	Family Galagidae				
4	*Otolemur crassicaudatus*	f, m	fetal; P0-6		37.9
3	*O. garnettii*	f, m	P0		35.5
1	*Galagoides demidovii*	f, m	P2		21.1
4	*Galago moholi*	f, m	Pr.; P0-1		24.6
3	*G. senegalensis*	?	P0	X(2)	25.8
	Lorisidae				
2	*Loris tardigradus*	f,?	fetal	X(1)	18.73, 25.1
2	*Nycticebus pygmaeus*	?	P0		28.1
	Semiorder Haplorhini				
	Suborder Anthropoidea				
	Infraorder Platyrrhini				
	Family Cebidae				
3	*Alouatta seniculus*	?	fetal; P0?		58.4
6	*Callithrix jacchus*	f, m	P0-2		29.67
4	*Cebuella pygmaea*	f, m	P0-5		25.4
6	*Leontopithecus rosalia*	f, m	P0-5		36.3
2	*Saguinus bicolor*	f, m	P0		31.84
6	*S. geoffroyi*	f, m	P0-4		34.4
3	*S. midas*	?	P0 or P0?	X(3)	33.98
6	*S. oedipus*	f, m	P0-1		33.5
7	*Saimiri boliviensis*	f, m	P0-2	X(1)	47.9
	Family Pitheciidae				
1	*Pithecia pithecia*	?	P0		47.21
1	*Callicebus cupreus*	?	P0?	X	36.5
1	*Aotus nancymaae*	?	P0?		42.8
	Infraorder Catarrhini				
	Family Cercopithecidae				
1	*Allenopithecus nigroviridis*	?	P0		
1	*Colobus guereza*	f	P2		59.78
1	*Macaca mulatta*	?	P0		
1	*Trachypithecus francoisi*	f	P2		68.79
	Infraorder Tarsiiformes				
1	*Tarsius bancanus*	m	P1	X	31.7
4	*T. syrichta*	f, m	Fetal; P0-6		28.96
	Order Scandentia				
1	*Tupaia belangeri*	?	P1		22.35

CL, cranial length (if different age specimens are represented in the sample, this column is average of neonates only); CT only, no histology for these specimens; f, female; m, male; N, number of specimens; P, postnatal age in days; Pr., likely premature birth;?, sex or precise age not recorded.

away from the head. The tissues were decalcified using a sodium citrate-formic acid solution, testing each week for completion, as described in DeLeon and Smith (2014). After completion, the tissues were returned to formalin for at least 2 h and then dehydrated using a graded ethanol series as follows: (1) 50% ethanol, 1 h;

TABLE 2. Stages of tooth development

Thickening of dental lamina[a]		The dental lamina initially appears as a thin, elongated line of cells. Prior to formation of a bud, the dental lamina thickens at its deepest side (in the maxilla, this is its superior limit).
Bud[b]		The bud is a spherical or ovoid mass, still bearing a connection to the dental lamina, which is surrounded by condensed mesenchyme.
Cap[b]		The mass is now "cap-shaped," due to an indentation on its deep surface by mesenchyme forming the dental papilla.
		Later, the cap-shaped mass now bears a more distinct internal enamel epithelium of columnar cells; stellate reticulum first appears.
Bell[b]	Early	The developing tooth now has a "bell-shaped" appearance; the tooth germ now has 4 identifiable layers surrounding the dental papilla: (1) external enamel epithelium, (2) stellate reticulum, (3) stratum intermedium, (4) internal enamel epithelium.
	Late[c]	Associated with formation of dental hard tissues; extension of dental lamina into permanent buds

[a]From descriptions in van Nievelt and Smith (2005).
[b]From description in Osborn (1981).
[c]Teeth in the late bell stage varied in the amount of stellate reticulum. Since this portion of the tooth germ is lost as the tooth matures and approaches eruption, some unerupted teeth that had little or no stellate reticulum are indicated in Table 4.

(2) 70% ethanol, overnight; (3) 80% ethanol, 30 min; (4) 95% ethanol, 1 h (2×); (5) 100% ethanol, 1/2 h; (6) 100% ethanol, 1 h (2×). Tissues were then cleared using xylenes, and embedded in paraffin in a vacuum oven.

Using a rotary microtome, paraffin blocks were sectioned at 10 or 12 μm thickness through the midfacial region. Sectioning was accomplished in the coronal plane in all specimens; in selected cases, half the head was prepared in the sagittal cutting plane. Every 5th to 10th section was mounted on labeled glass slides and alternate slides were stained using hematoxylin and eosin or Gomori trichrome procedures. Serial sections were photographed using an Axiocam MRc 5 Firewire camera attached to either a Zeiss stereo microscope (0.64× to 1.6× magnification) or a Leica DMLB photomicroscope (25×), depending on the size of the specimen. Selected sections were photographed at higher magnifications for detailed comparisons.

Micro-CT scanning of selected specimens was done at Northeast Ohio Medical University (NEOMED) using the Scanco viva-CT scanner (scan parameters: 70 kVp; 114 μA.). The volumes were reconstructed using 20.5μm cubic voxels (see DeLeon and Smith, 2014; Smith et al., 2014). Three-dimensional digital reconstructions from the micro-CT volume for selected specimens were rendered using Amira® software (Visage Imaging GmbH).

Dental Eruption and Staging Criteria

We followed the practice of Smith et al. (1994) in using the term "emergence" to denote that a tooth pierced the gingiva. "Eruption" refers to teeth that are protruding beyond the margins of the alveolar bone. Our sample differs from most previous studies in that emergence and eruption are determined using histology sections. Emergence was detected when the tooth cusp tip pierced through the gingiva. A cusp was considered erupted if the tip extended past a straight line drawn between the lowest point of the medial and lateral margins of the alveolar bone in cross-section. Some dental eruption data were completed by making reference to CT slices, and these are indicated in Appendix.

Histology introduces some distortion such as tearing, folding, or shrinkage (DeLeon and Smith, 2014). It is possible that tearing of the gingiva during preparation could yield a false rating of emergence. To minimize this possibility, the gingiva was carefully examined to ensure the margins were not torn. It is also possible that a cusp could be emergent between two mounted histologic sections. However, the intersection distance was merely 50 μm for most specimens, and the tooth cusps almost always created larger apertures through the gingiva (see below). Additional distortion can be detected by comparing histology sections to CT slices of the same specimen. To assess the effect of histological distortion on tooth position, we examined two specimens with deciduous teeth that were not completely mineralized, *Eulemur collaris* and *Tupaia belangeri* neonates. By comparing CT slices with histology of each specimen, it was possible to examine the position of the teeth before and after histological processing. The plane of the CT slices of each specimen were reoriented by rotating the three-dimensional (3D) volume until slice planes matched that of the histology, as explained in detail previously (Smith et al., 2014; DeLeon and Smith, 2014). Then, using CT and histology, the deciduous teeth were examined for evidence that they protruded beyond the rim of their alveolar sockets in the maxillary bone. By comparing teeth in CT and histology at similar sectional levels, some artifactual distortion of tooth was observed in the histological sections. Specifically, the position of the tooth cusps shifted slightly superiorly, especially in more posterior teeth, which tended to be less mineralized. This positional shift is best explained by differential shrinkage of the dental germ follicles, with the dental papilla more affected than the mineralized crown. Whereas this can affect the position of the cusp tip, the margin where the dental follicle (the fibrous capsule at the outer perimeter of the tooth germ) meets outer enamel epithelium was not shifted upward with the cusp. In other words, the shrinkage affected the position of the cusp in less mineralized teeth, but not the outer boundary of the developing tooth. Therefore, histology is not expected to affect the assessment of tooth eruption,

TABLE 3. Dental eruption and gingival emergence of maxillary deciduous teeth in primates at birth

TAXA[a]	di1[b]		di2		dc		dp2		dp3		dp4	
	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.
Strepsirrhini												
Cheirogaleids												
Microcebus murinus	X	X	X	U	X	X	X	U	X	U	X	U
Cheirogaleus medius	X	X	X	U	X	U	X	X/U	X	U	X	U
Mirza coquereli	X	X/U	X	U	X	U	X	U	X	U	X	U
Lemurids												
Lemur catta	X	U	X	U	X	U	X	U	X	U	X	U
Eulemur macaco	X	U	X	U	X	U	X	U	X	U	U	U
E. collaris	X	U	X	U	X	U	X	U	X	U	U	U
E. coronatus	X	U	X	U	X	U	X	U	X	U	X	U
E. mongoz	X	U	X	U	X	U	X	U	X	U	X	?
E. rubriventer	X	U	X	U	X	U	X	U	X	U	?	?
Varecia variegata	X	U	X	U	X	U	X	U	X	U	X	U
Hapalemur griseus	X	U	X	U	X	U	X	U	X	U	U	U
Indriids												
Propithecus coquereli	X	X	X	X	X	X	Shed	Shed	X	X	X	X
Galagids												
Otolemur crassicaudatus	X	U	X	X/U	X	X	X	U	X	U	X	U
O. garnettii	X	X/U	X	X/U	X	X/U	X	U	X	U	X	U
Galago moholi	X	U	X	X/U	X	U	X	X/U	X	U	X	U
G. senegalensis	X	U	X	X	X	X	X	U	X	U	X	X?[c]
Galagoides demidovii	X	U	X	U	X	X	X	X	X	U	X	U
Lorisids												
Nycticebus pygmaeus	X	U	X	U	X	X?	X	X?	X	U	X	U
Haplorhini												
Platyrrhini												
Cebids												
Cebuella pygmaea	X	X	X	X	X	U	X	U	X	U	X	U
Callithrix jacchus	X	U	X	U	X	U	X	U	X	U	X	U
Leontopithecus rosalia	X	X	X	X	X	X/U	X	U	X	U	X	U
Saguinus oedipus	X	X/U	X	U	X	U	X	U	X	U	X	U
S. bicolor	X	X/U	X	X/U	X	U	X	U	X	U	X	U
S. geoffroyi	X	X/U	X	X/U	X	U	X	U	X	U	X	U
Saimiri boliviensis	X	X/U	X	U	X	U	X	U	X	U	U	U
Alouatta seniculus	X	U	X	U	U	U	X	U	U	U	U	U
Pitheciids												
Pithecia pithecia	X	U	X	U	X	U	X	U	X	U	U	U
Aotus nancymaae	X	U	X	U	X	U	X	U	X	U	X	U
Catarrhini												
Allenopithecus nigroviridis	X	U	X	U	U	U	–	–	X	U	U	U
Colobus guereza	X	U	X	U	X		–	–	U	U	U	U
Macaca mulatta	X	U	X	U	Damaged		–	–	U	U	U	U

TABLE 3. (continued).

TAXA[a]	di1[b]		di2		dc		dp2		dp3		dp4	
	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.	Alveolar eruption	Gingival emerg.
Trachypithecus francoisi	X	X	X	U	X	U	–	–	X	U	U	U
Tarsiiformes												
Tarsius bancanus[d]	X		X		X		Shed		X		X	
T. syrichta	X	X	X	X	X	X	Shed		X	X	X	X
Scandentia												
Tupaia belangeri	X	U	X	U	X	U	U	U	X	U	X	U

[a]Primate systematics are arranged according to Fleagle (2013) except for Platyrrhini, which are arranged according to Rosenberger (2011).
[b]Abbreviations for teeth: di, deciduous incisor; dc, deciduous canine; dp, deciduous premolar; I, permanent incisor; C, permanent canine; P, permanent premolar; M, molars.
[c]The paracone of the right dp4 in one specimen appeared to pierce the gingiva, however, artifactual breakage of the thin gingiva cannot be completely ruled out.
[d]Alveolar eruption for this species determined using μCT slices; ?, uncertain due to artifactual distortion; U, unerupted; X, erupted.

as long as eruption is defined as protrusion of the outer boundary of the dental sac, rather than cusp position.

Identification of teeth was accomplished by examination of serial histology (or CT slices, in several cases). The premaxillary teeth were considered incisors and the maxillary teeth commenced with the canines. Histological series were initially studied using a Zeiss Steromicroscope and a Leica DMLB compound microscope was used for final identification of dental stages (magnifications ranging from $1\times$ to $25\times$ were used). Teeth were identified based on previous reports for the number of each deciduous tooth category (compiled in Smith et al., 1994). The stage of each tooth was also noted in every instance. We assume dental stages will be more similar within ontogenetic tooth cohorts (i.e., deciduous or replacement teeth). Using this information, we verified previous reports concerning teeth that are shed before or near birth. Throughout the text, lower case abbreviations are used to denote deciduous teeth, with numbers indicating position as follows: di1, di2, dc, dp2, dp3, dp4 (Tables 3 and 4). Upper case abbreviations are used to denote permanent teeth, with the numbers denoting position as follows: I1, I2, C, P2, P3, P4, M1, M2, M3 (Tables 3 and 4).

Staging of teeth was done based on descriptions by Osborn (1981) (Table 2). A stage preceding the tooth bud, called thickened dental lamina, was also noted (see van Nievelt and Smith, 2005). Here we do not distinguish early versus late cap stages. However, because our sample includes many teeth that are considerably advanced toward eruption, we made notations on whether mineralization was initiated (beginning with dentine along cusp tips) and the extent of stellate reticulum. Stellate reticulum is identifiable as a loose mesenchymal tissue between the inner and outer enamel epithelia (Nanci, 2007). If not well preserved, its absence can be inferred if the two enamel epithelia are fused (as occurs when the stellate reticulum disappears—Nanci, 2007). By assessing the extent of remaining stellate reticulum, we extended observations of the late bell stage. The late bell stage begins with cusp mineralization. Later, prior to eruption, the stellate reticulum disappears, ending the earliest phase of amelogenesis, and bringing the inner enamel epithelium in closer proximity to blood supply (Nanci, 2007). More advanced characteristics of the tooth prior to eruption, including development of roots or thinning of the enamel epithelia, so-called "pre-eruption phases" (Avery, 2002), were also noted. Whenever possible, all staging criteria were gleaned from histology. In some cases histology was unavailable at more posterior locations, and CT was useful for detecting tooth mineralization (see below). "Erupted" or "shed" were the most advanced stages.

To characterize the extent of mineralization of the developing teeth, two maturation indices were calculated. Maturation index 1 is used as an indicator of the relative extent to which dentition has at least initiated mineralization of cusps. The number of teeth with at least one cusp tip mineralized, combined with those that were advanced farther, were divided by the total number of teeth on one side. Maturation index 2 is used as an indicator of the relative extent to which dentition has advanced beyond the first phase of amelogenesis. The number of teeth in which the stellate reticulum has nearly or completely regressed, combined with those
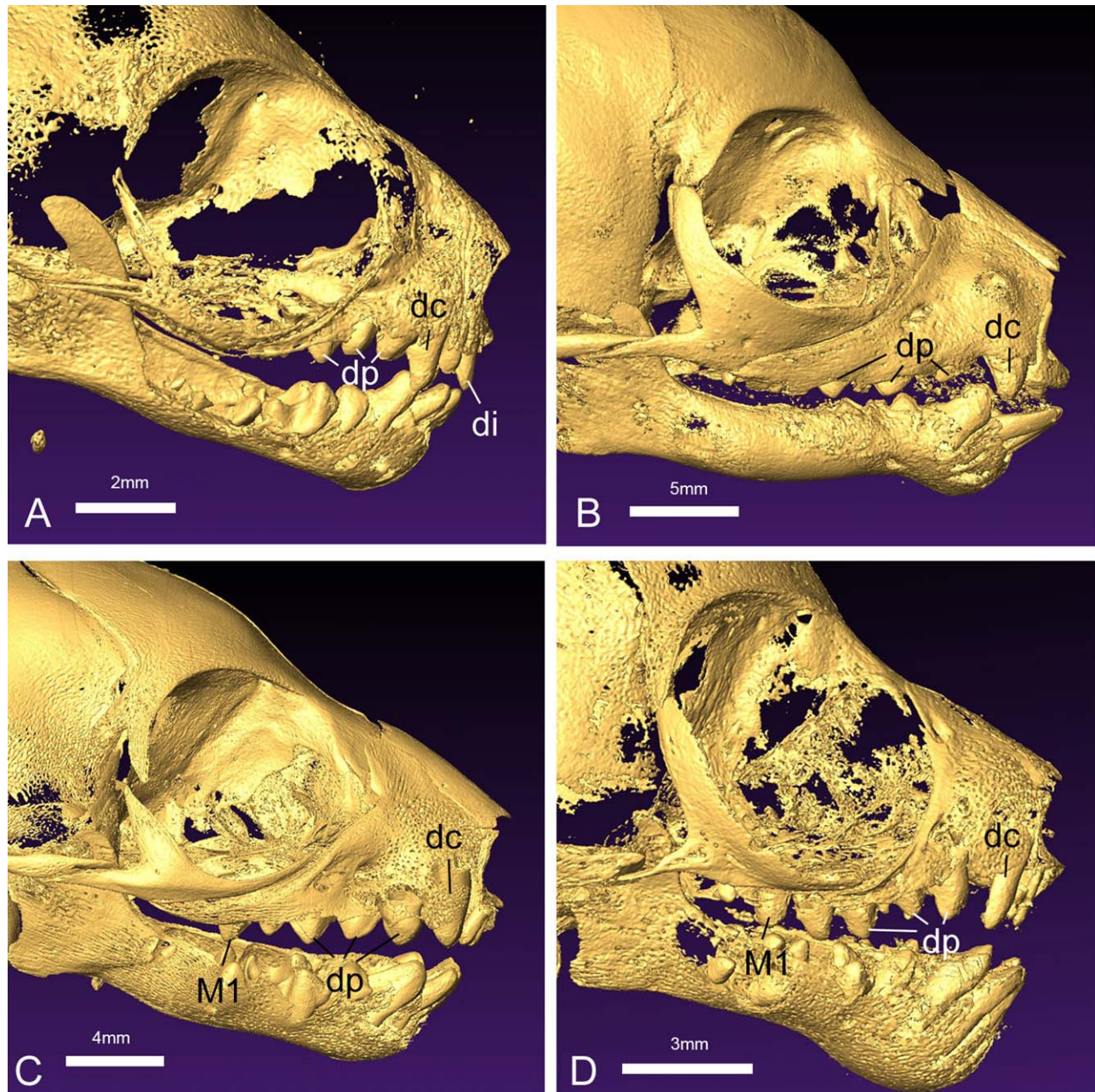
Fig. 1. Lateral view of *Microcebus murinus* (top left), *Eulemur mongoz* (top right), *Otolemur crassicaudatus* (bottom left), and *Nycticebus pygmaeus* (bottom right) showing extent of alveolar eruption at birth. Most or all deciduous teeth (di, dc, dp) are in a prominent state of eruption in strepsirrhines. M1 is incompletely surrounded by bone compared with deciduous teeth, and has not reached the same occlusal plane as the deciduous premolars (dp) in some lemuroids (**A**, **B**). Correspondingly, the thinness of mandibular bone in *Microcebus* allows visualization of lower M1, which is nested deep within the crypt. In lorisoids (**C**, **D**), M1 has reached the same occlusal plane as dp4.

that were advanced farther, were divided by the total number of teeth on one side. These indices were calculated separately for all teeth, deciduous teeth, permanent teeth and replacement teeth.

CT assessment of tooth mineralization. Some specimens that were not histologically sectioned were micro-CT scanned, and were used to verify which teeth had entered the late bell stage. These specimens were excluded from maturation index calculations, because it is unclear whether micro-CT can detect the earliest phase of cusp mineralization as reliably as histology. Nonetheless it was possible to categorize teeth according to the degree of cusp mineralization of the crown as well as the number of mineralized cusps. Thus, teeth were
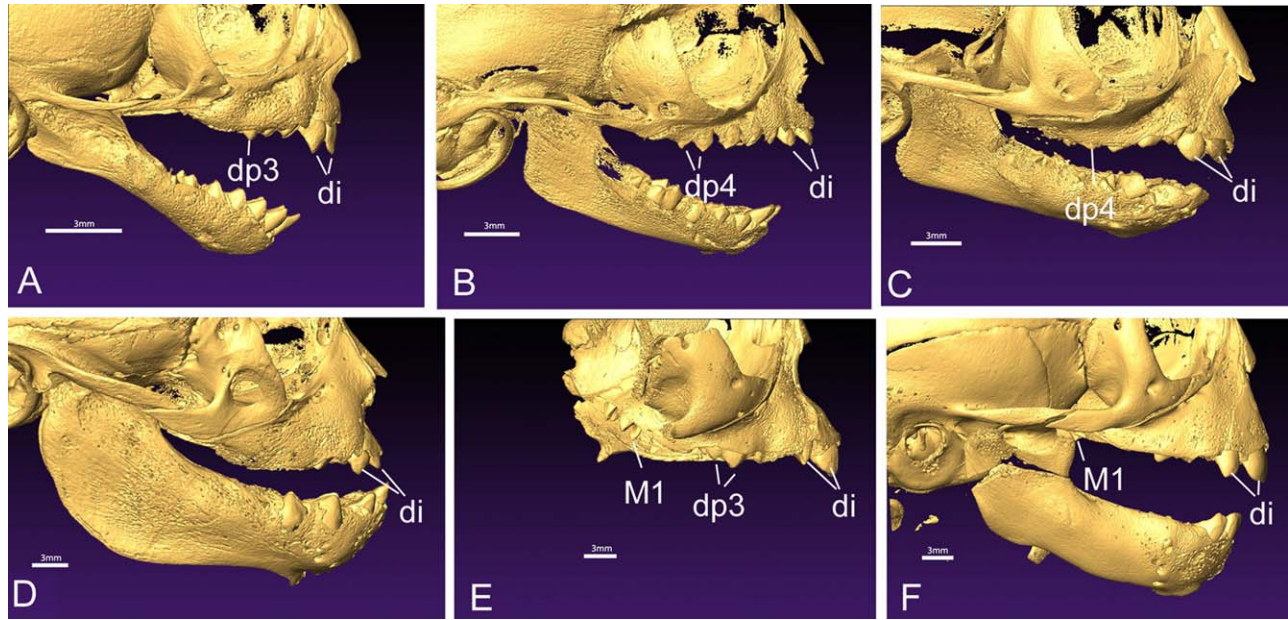
Fig. 2. Lateral views of *Cebuella pygmaea* (**A**), *Callicebus cupreus* (**B**), *Aotus nancymaae* (**C**), *Alouatta seniculus* (**D**), *Allenopithecus nigroviridis* (**E**), and *Trachypithecus francoisi* (**F**) showing extent of alveolar eruption at birth. Deciduous incisors (di) are prominent in all species, but the deciduous canines (not arrowed) and premolars are less advanced in eruption. Deciduous premolars (e.g., dp3, dp4) are more exposed in smaller platyrrhines (see A, B, C) than *Alouatta* or the catarrhines.

categorized as having cusps and crowns mineralized (CrCu), partial crowns and cusps (PCrCu), or cusps only (Cu) (see Appendix).

In two cases, it was possible to use micro-CT to approximate missing information due to histological artifact. M1 was assessed in *Allenopithecus* and *Eulemur mongoz* based on CT slices of the contralateral side or a different specimen, respectively. In both cases, M1 was advanced to the late bell stage but not approaching "pre-eruption" phase. Based on mineralization of isolated M1 cusps, it was thus surmised to be in the late bell stage (see Appendix, specimens Alleno1; P6426).

RESULTS

Alveolar Eruption

The three cheirogaleids have fully erupted deciduous maxillary dentition at birth (Table 3; Fig. 1a). Among larger lemuroids, di1 through dp3 are erupted in all species, although in some cases only one cusp is partially projecting (Fig. 1b). dp4 was erupted in *Lemur catta, Eulemur coronatus*, and *E. rubriventer*. Neonatal *Propithecus* and all lorisoids (Fig. 1c,d) have a full complement of deciduous teeth that are at least partially erupted from the upper jaw bones.

In anthropoids, fewer teeth were erupted for most species, and in many cases only the tip of a cusp was exposed below the level of the alveolar socket margin. Generally, the deciduous incisors are most fully erupted (Fig. 2). The platyrrhines with the most erupted maxillary teeth are callitrichines (especially *Cebuella*—Fig. 2a). *Callicebus* (Fig. 2b) and *Aotus* (Fig. 2c) also have full eruption of deciduous teeth, though with less of the

crowns exposed compared with *Cebuella*. *Alouatta* has the least extent of alveolar eruption of the deciduous crowns (Fig. 2d). Aside from *Alouatta*, di1, di2, dp2, and dp3 are erupted in all platyrrhines (Table 3; Fig. 2). dc, dp3 and dp4 have not grown beyond the alveolar margins in *Alouatta* (Fig. 2). *Saimiri* and *Pithecia* have unerupted dp4 (Table 3).

In the catarrhines, both incisors are erupted. Both premolars are unerupted in *Macaca*, and dp4 is unerupted in all species. None of the catarrhines exhibit more than a small portion of dp3 or 4 cusps in eruption. In addition, dc is unerupted in *Allenopithecus*.

In tarsier specimens, all deciduous teeth have erupted. There remains no trace of dp2 in our specimens. P2 is also erupted (Figs. 3 and 4). di2 is shed in some of the specimens (see below).

Eruption of permanent molars is not considered here, because in all cases, M1 is incompletely enclosed by bone. For example, in large lemurs alveolar bone near M1 is restricted to the level of the most mesial cusps (Fig. 5a). *Tarsius* has the greatest extent of alveolar bone surrounding M1, although there is no "roof" to the socket (Fig. 5b). In all species, alveolar bone is far more robust at deciduous levels compared with M1 (Figs. 6–10).

In *Tupaia*, all deciduous teeth are erupted except dp2.

Gingival Emergence

In *Tarsius syrichta* (Fig. 4) and *Propithecus* (Fig. 7) all deciduous teeth have emerged. Aside from *Propithecus*, in all other strepsirrhines except *Galago moholi* (dp2 in one specimen), *Galagoides* (dp2), one of the four *Cheirogaleus* specimens (dp2), and possibly *Nycticebus* (dp2?), the only
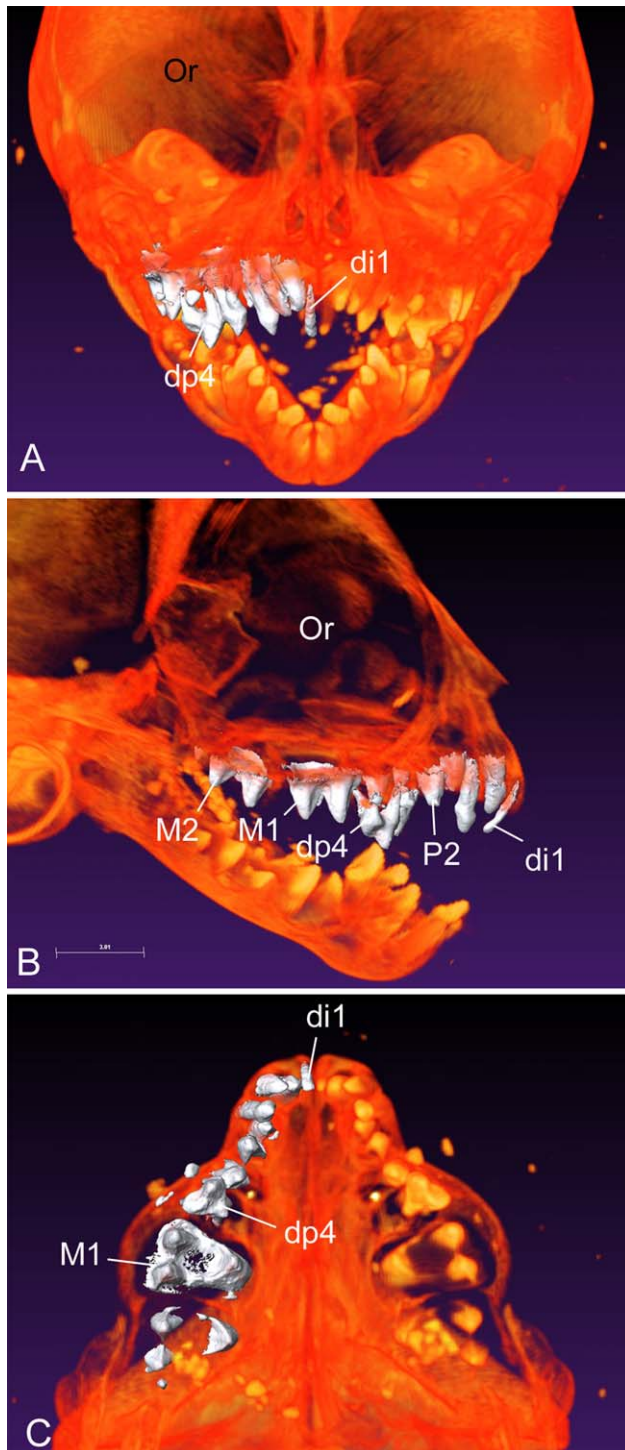
Fig. 3. Three-dimensional reconstructions of the dentition of neonatal *Tarsius syrichta* in three perspectives, frontal (**A**), lateral (**B**), and occlusal (**C**). Tarsiers have the greatest extent of eruption of both deciduous (e.g., di, dp) and permanent teeth (e.g., M1; P2) of any primate for this age.

teeth to have pierced the gingiva at birth are di1, di2, and/or dc (Table 3). A single postcanine of *Galago senegalensis* appeared to pierce the gingiva on the right (but not left) side of the palate, but this seems equivocal because artifactual damage due to freezing was seen elsewhere in the specimen (Table 3). All cheirogaleids have di1 emerged or at a pre-eruptive stage (enamel epithelia fusing to oral epithelium), and dc has emerged in *Microcebus*. No teeth have emerged through the gingiva in lemurids. Galagids vary in whether just one or all three of these teeth have emerged (Table 4). It should be noted, in regard to Table 4, most teeth that are identified as having restricted (or loss of) stellate reticulum are also in a pre-eruptive state.

Few anthropoids in our sample have gingival emergence of any tooth. Deciduous incisors are emergent in at least some specimens of each callitrichine species. One of the *Leontopithecus* specimens had an emergent dc. *Saimiri* was the only other platyrrhine with emerged teeth (di1 in one specimen). Among the four catarrhines studied, only *Trachypithecus* had an emerged tooth (Table 3).

None of the dentition has pierced the gingiva in *Tupaia*.

Tooth Germ Stages and Mineralization

In most primates at birth, few aside from the deciduous teeth have reached the late bell stage (Table 4). Among permanent teeth, M1 has commenced mineralization of at least one cusp with few exceptions. Qualitatively, M1 appears particularly well mineralized in folivorous primates (Figs. 9 and 10), as well as galagids and cheirogaleids (Fig. 11). Callitrichines (excluding *Cebuella*) and *Varecia* are least advanced in M1 maturation (Table 4, Fig. 11). The slow pace of dental development continues postnatally in *Varecia* (Godfrey et al., 2003). Lemurids have mineralization of one or more cusps of M1 (Figs. 5a and 11b). M1 is most mineralized in *Propithecus* (Fig. 11c), *Galagoides* (Fig. 11d), and *Hapalemur* (Fig. 10) in that enamel has bridged the tooth basin. M1 is unmineralized in all tamarins (Fig. 11e), but well mineralized in most anthropoids (Fig. 11f–h).

A dichotomy exists between strepsirrhines and anthropoids in that replacement teeth are generally less advanced in the latter. Callitrichines are the only anthropoids in which replacement teeth have reached or passed the early bell stage (di1). Maturation indices (below) provide more detailed contrasts by tooth class. Galagids and *Nycticebus* are notable for the advanced state of maturity of the permanent incisors compared with all other strepsirrhines (Fig. 12). In particular, I2 is further matured than in any species other than *Tarsius* spp.

Among all primates, dental maturation is most progressed in *Propithecus* and *Tarsius*. If the maturity of the complete dental arcade is expressed as the percentage of all teeth that have reached the late bell stage or have matured further (e.g., to eruption), in these species approximately 92% (*Propithecus*) and 93% (*Tarsius*) of the teeth have begun or completed mineralization (excluding teeth which are shed in each species). In light of previous work on the dentition of subadult tarsiers (see, e.g., Luckett and Maier, 1982; Schwartz, 2003), additional observations are merited concerning our tarsier sample. In one *T. syrichta* neonate, we easily located two premaxillary teeth that are erupted through the gingiva. Both are in a nearly identical advanced state of mineralization based on trichrome preparations (Fig.
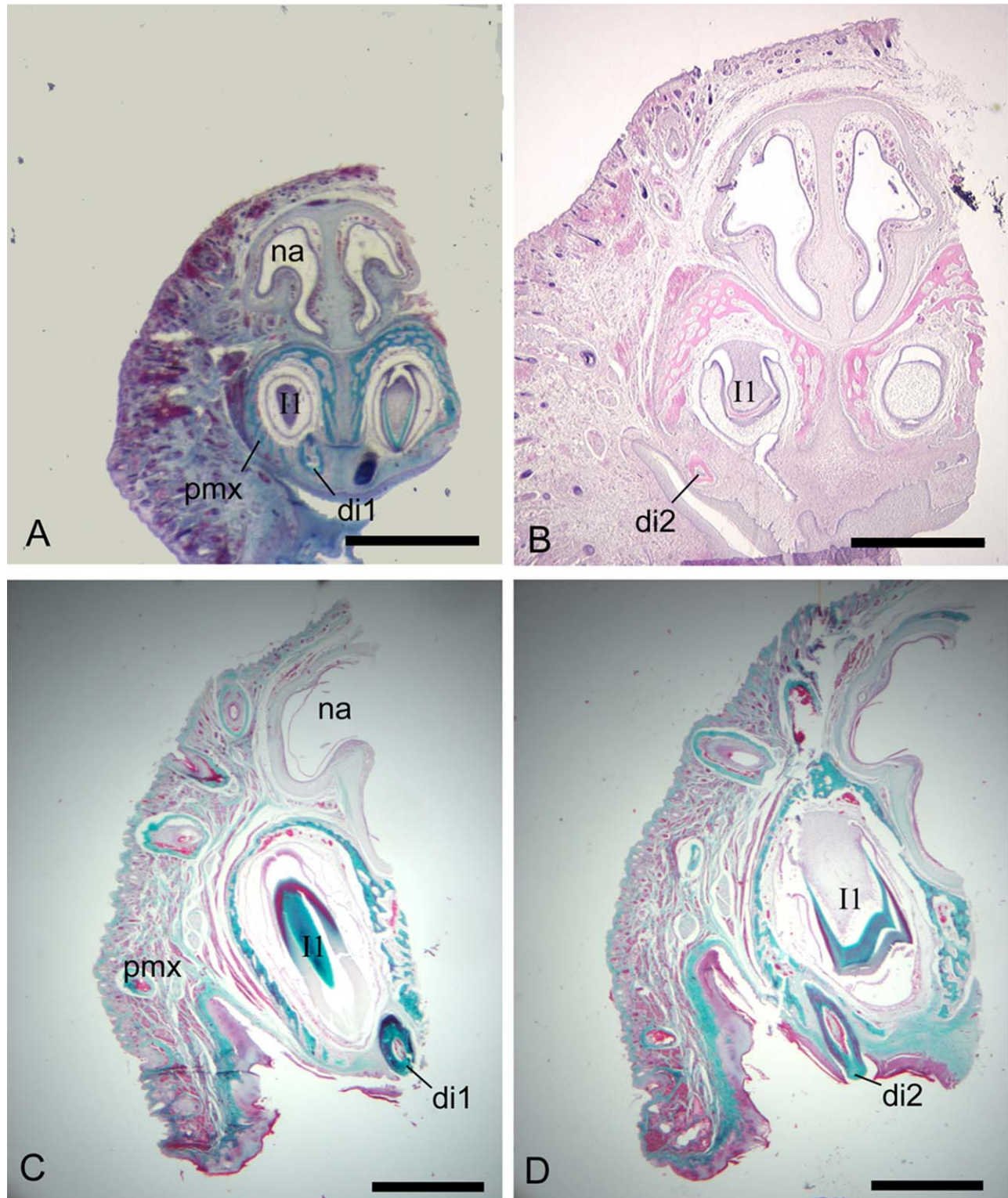
Fig. 4. Premaxillary teeth in late fetal (**A**, **B**) and neonatal (**C**, **D**) *Tarsius syrichta*. The largest tooth in the premaxilla is I1, at the late bell stage. In both of these specimens, two erupted deciduous teeth could be found near this tooth. The presumptive di1 is anteroinferior to I1 (A, C) and the presumptive di2 could be found inferolateral to it (C, D). Scale bars, 1 mm; na, nasal airway; pmx, premaxillary bone.
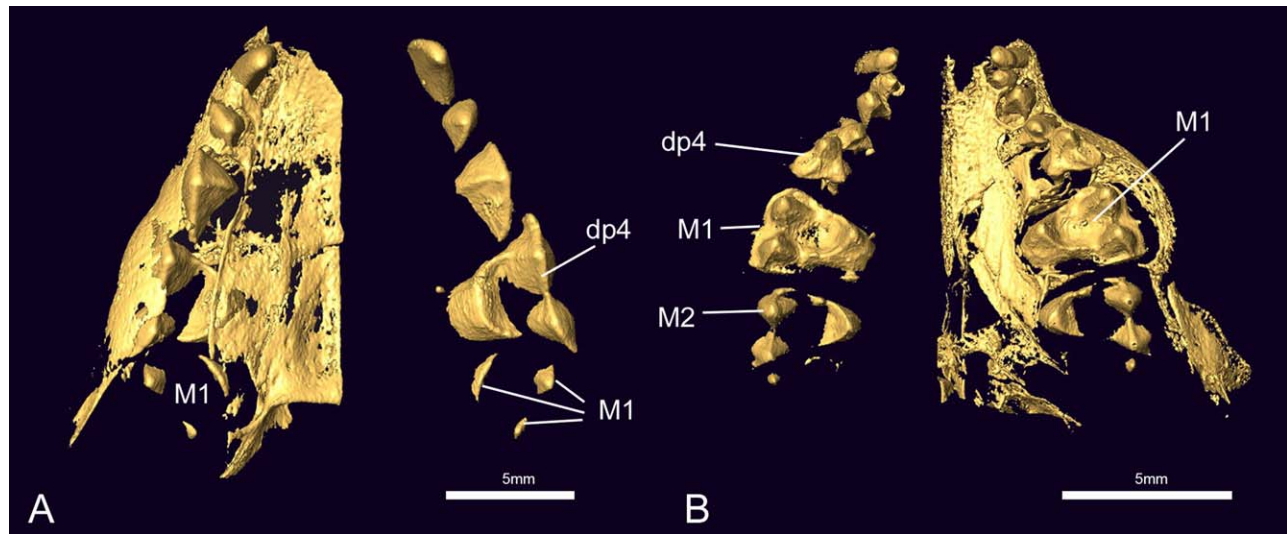
Fig. 5. In most primates M1 is poorly encased by bone at birth, as in *Eulemur fulvus* (**A**). *Tarsius syrichta* (**B**) has an exceptional amount of alveolar bone, extending around and posterior to M1. In these bilateral occlusal views, each panel includes the isolated maxilla and palatine bones from one side. dp. deciduous premolar; M, permanent molars.

4c,d), thus being consistent with deciduous incisors. These are also present in the late fetus. In addition, both of these teeth are accompanied by a successional tooth germ at the bell stage in the late fetus. I2 could not be located in the sectioned 0-day-old *T. syrichta*, although both di1 and di2 were present. In one of the 0-day-olds and the 6-day *T. syrichta*, di2 was absent. With the exception of I2, permanent teeth were at the late bell stage, and the stellate reticulum is mostly regressed in P2. Mineralization of M1 is advanced, reaching the basin of the tooth (Figs. 4 and 5).

The two maturation indices (Tables 5 and 6), tracking the mineralization of teeth, reveal inter- and intrafamily level variation in primates. Maturation index 1 (Table 5) reveals, on average, more teeth have initiated mineralization in all cheirogaleids and galagids compared with any lemurid, though neither family rivals *Propithecus*. The disparity remains for all tooth classes, although maturation of replacement teeth was variable (Table 5). Among all primates, only galagids, cheirogaleids, *Tarsius* and *Propithecus* have mineralization extending to the level of M2 (Tables 4 and 5). With the exception of the singularly advanced *Propithecus*, large lemuroids have mineralization limited mainly to deciduous teeth and M1. Anthropoids are rather uniform in regard to which teeth have initiated mineralization, including all deciduous and one or two permanent teeth in all cases. Replacement teeth at birth are rarely mineralized (only observed in *Cebuella*—Table 5). In terms of the number of teeth that have at least initiated mineralization, the pattern in *Tupaia* resembles anthropoids more than strepsirrhines (Tables 4 and 5).

Maturation index 2 (Table 6), indicating the completion of the first phase of amelogenesis, shows less disparity among strepsirrhines. Among lemuroids, *Propithecus* is the most advanced in this index, and *Varecia* has no teeth progressed to this stage of maturation.

All other strepsirrhines have indices between 0.2 and 0.33 (between 3 and 5 teeth). Anthropoids show an entirely different pattern of dentition that had reached this stage of maturation. While the overall number of teeth at this index 2 overlaps that seen in strepsirrhines, a great contrast is seen in the deciduous dentition. The average maturation index 2 of the deciduous teeth in anthropoids exceeds that seen in strepsirrhines, and also exceeds most individual species with the exception of *Propithecus, Lemur*, and *Hapalemur* (Table 6). The sifaka and tarsier have the highest maturation index 2 for deciduous teeth (1.0). *Tupaia*, in contrast to all primates, has the lowest index 2 (0).

DISCUSSION

The perinatal stage of life has an inherent level of interest regarding life history because the dentition at or near birth are not yet functional. The characteristics of newborn dentition, to the extent that they correlate with specializations of the adult primate (e.g., dietary or communication), reveal the extent of adaptation to a niche in an animal prior to any behavioral requirements. The neonatal primate is, after all, completely dependent on maternal (and sometimes alloparental) provisioning. However, by as early as four months of age, primates are already known to have distinct patterns of dental eruption that reflect both phylogeny and diet (Godfrey et al., 2001, 2003). Patterns at four months beg the question: to what extent are phylogenetic and/or dietary signals evident at birth?

Perinatal Dental Eruption and Maturation in Light of Phylogeny

Alveolar eruption. Godfrey et al. (2001, 2003) measured the progression toward a functional and fully
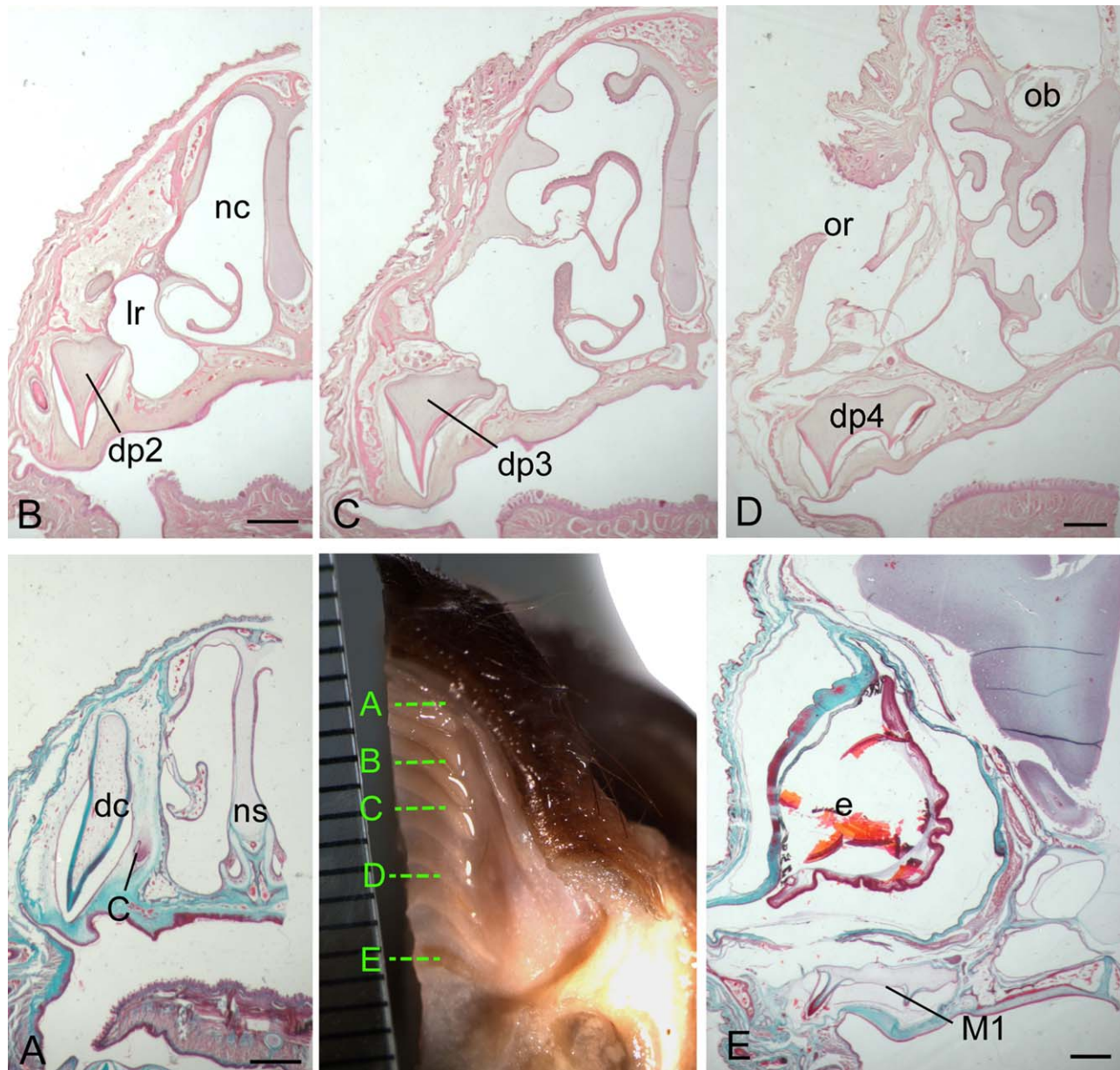
Fig. 6. Lack of gingival emergence in *Lemur catta*. Scale bars, 1 mm. C, permanent canine; dc, deciduous canine; dp2, dp3, dp4, deciduous premolars; e, eye; lr lateral recess; M1, first permanent molars; nc, nasal cavity; ns, nasal septum; ob, olfactory bulb; or, orbit.

erupted dental arcade. The variable "dental precocity" is the proportion of erupted postcanine teeth (at a given age) to the total number of deciduous and permanent teeth in each species. By family, primates have remarkably little variability in precocity (Godfrey et al., 2003). Indriids, galagids, and lepilemurids have high dental precocity at 4 months, weaning, and 1 year of age. Among anthropoids, callitrichines have high dental precocity at 4 months and 1 year of age, but are not distinguished from other anthropoids at weaning. This distinction reflects their early weaning age (all weaned <4 months; Kappeler and Periera, 2003).

The pattern of dental eruption in our perinatal sample generally agrees with the scenario apparent at four months of age for larger lemuroids (Godfrey et al., 2001, 2003). Larger lemuroids had incomplete eruption or no eruption of dp4 and lag behind other strepsirrhines at birth, as is the case at four months of age (Godfrey et al., 2001, 2003).

At birth, eruption of the permanent molars is nearly an irrelevant concept for many primate species, because the dental follicles are not yet surrounded by bone in most species. Larger lemuroids, and to a lesser extent the cheirogaleids, had incomplete enclosure of M1 by
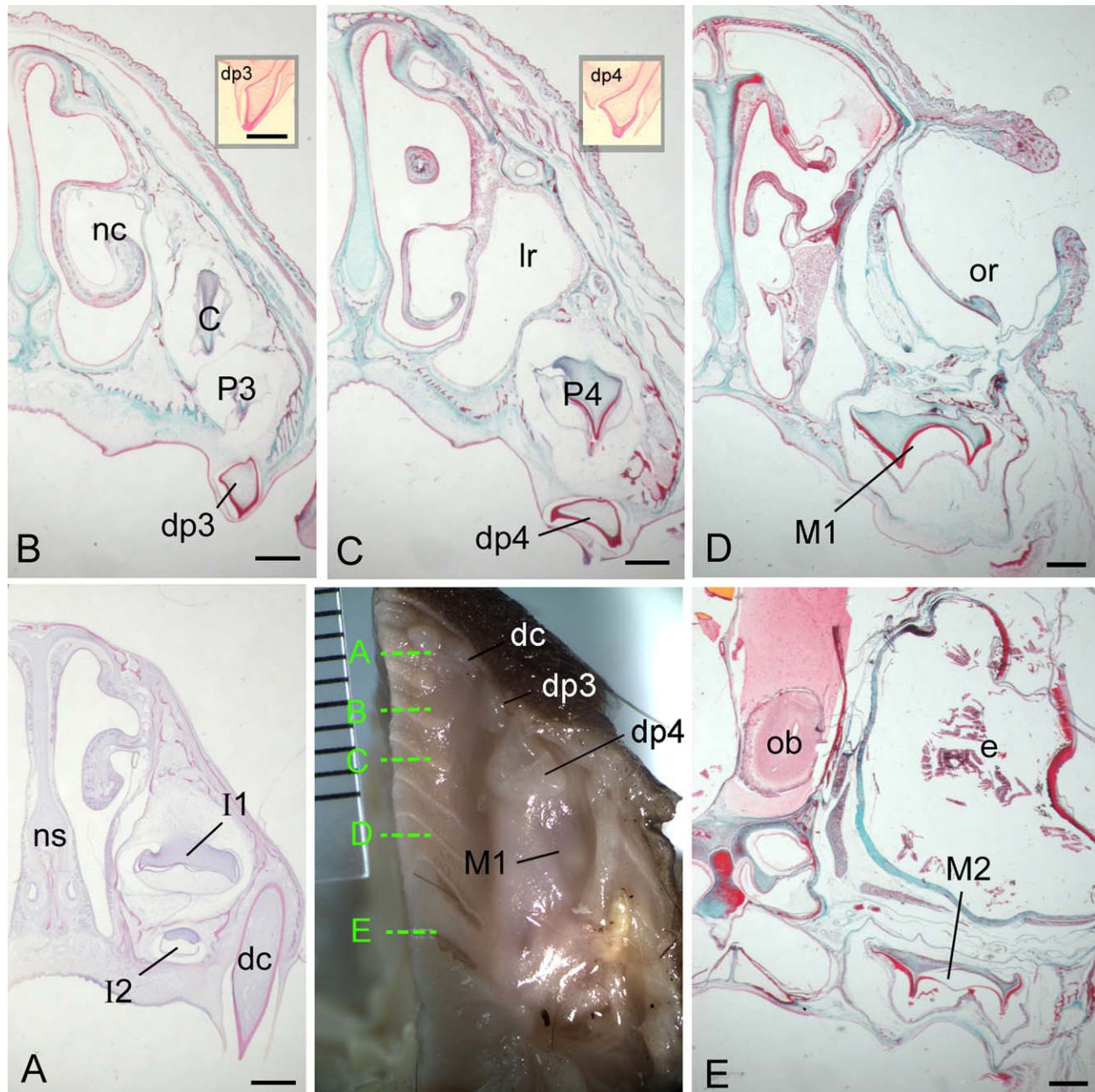
Fig. 7. Gingival emergence in *Propithecus coquereli* at birth. Note gingival emergence of the deciduous canine (**A**) and deciduous premolars (level of emergence is shown in insets). Scale bars, 1 mm. C, permanent canine; dc, deciduous canine; dp3, dp4, deciduous premolars; e, eye; lr lateral recess; M1, M2, first and second permanent molars; nc, nasal cavity; ns, nasal septum; ob, olfactory bulb; or, orbit; P3, P4, permanent (replacement) premolars.

bone. The tooth follicles themselves likely regulate alveolar bone resorption and deposition (Marks and Cahill, 1987); thus, the advanced maturation of M1 in galagids and the sifaka may be directly correlated to the well-formed alveolar portion of the maxilla in these primates. Conversely, delayed dental maturation in other species may relate to poor enclosure of M1 by alveolar bone.

Small-bodied species stand out as having highly erupted deciduous dentition, with the exception of *Saimiri* (in which the state of eruption resembles larger anthropoids). As in the case with gingival eruption (below), this suggests a possible influence of body size on the state of alveolar eruption at birth. However, all galagids have advanced alveolar eruption at birth, regardless of body size. Thus, a thorough quantitative analysis
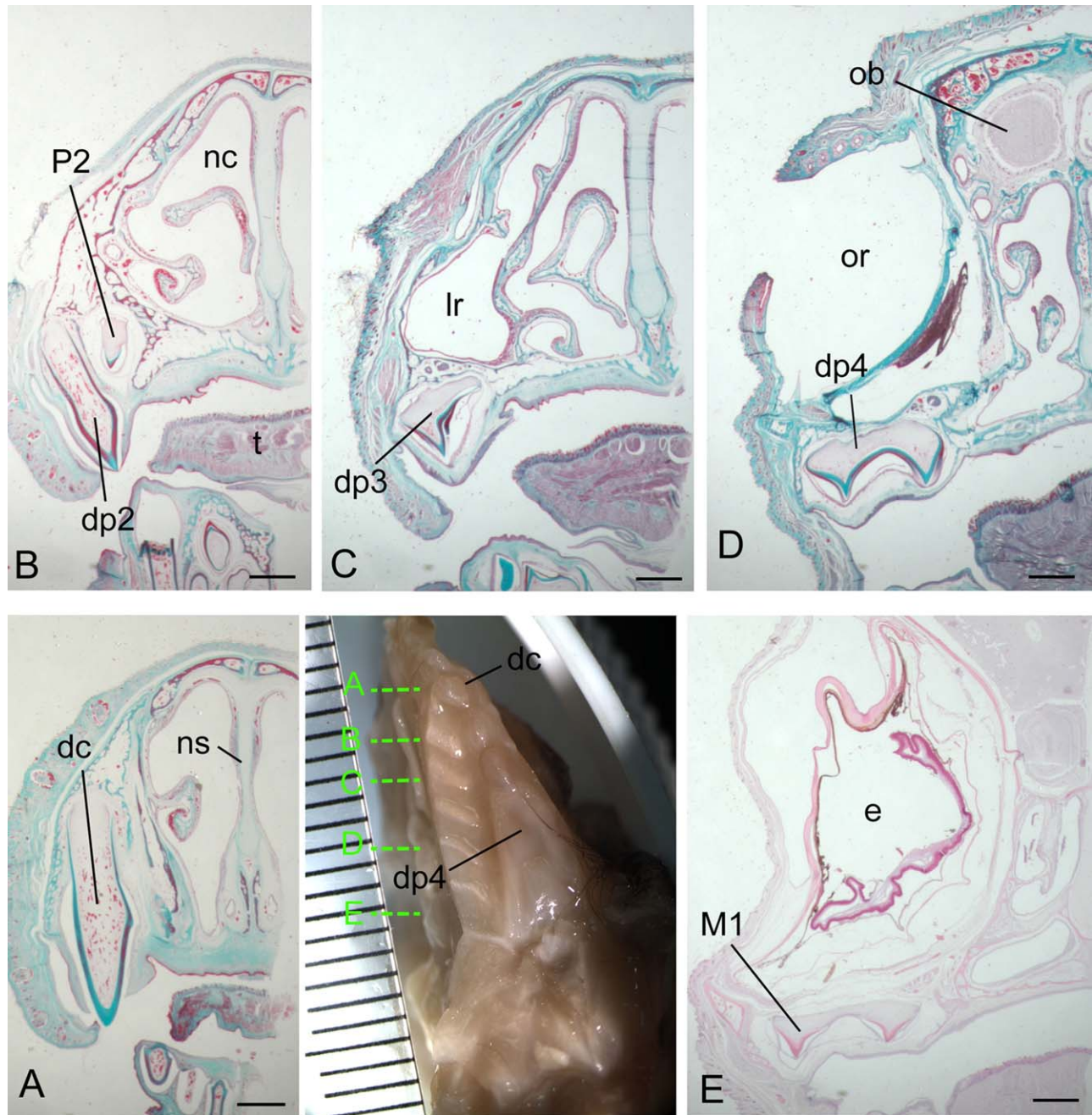
Fig. 8. Gingival emergence in *Otolemur crassicaudatus* at birth. Note emergence of the deciduous canine (**A**). Scale bars, 1 mm. C, permanent canine; dc, deciduous canine; dp2, dp3, dp4, deciduous premolars; e, eye; lr lateral recess; M1, first permanent molar; nc, nasal cavity; ns, nasal septum; ob, olfactory bulb; or, orbit; P2, permanent (replacement) premolar.

of tooth size in light of body size and phylogeny is needed.

The observations on dental eruption have some bearing on the hypothesis that callitrichines are phyletic dwarfs (Ford, 1980), in that eruption patterns broadly correlate with body size across all primates. In other words, callitrichines are not unusual in their eruption patterns at birth relative to other primates. Yet, the importance of the deciduous postcanine teeth (all of which are more erupted in smaller primates) to the dwarf hypothesis may be inversely related to the permanent teeth, as their early eruption relates in part to earlier replacement. The bearing of the permanent dentition at birth to this hypothesis can be evaluated
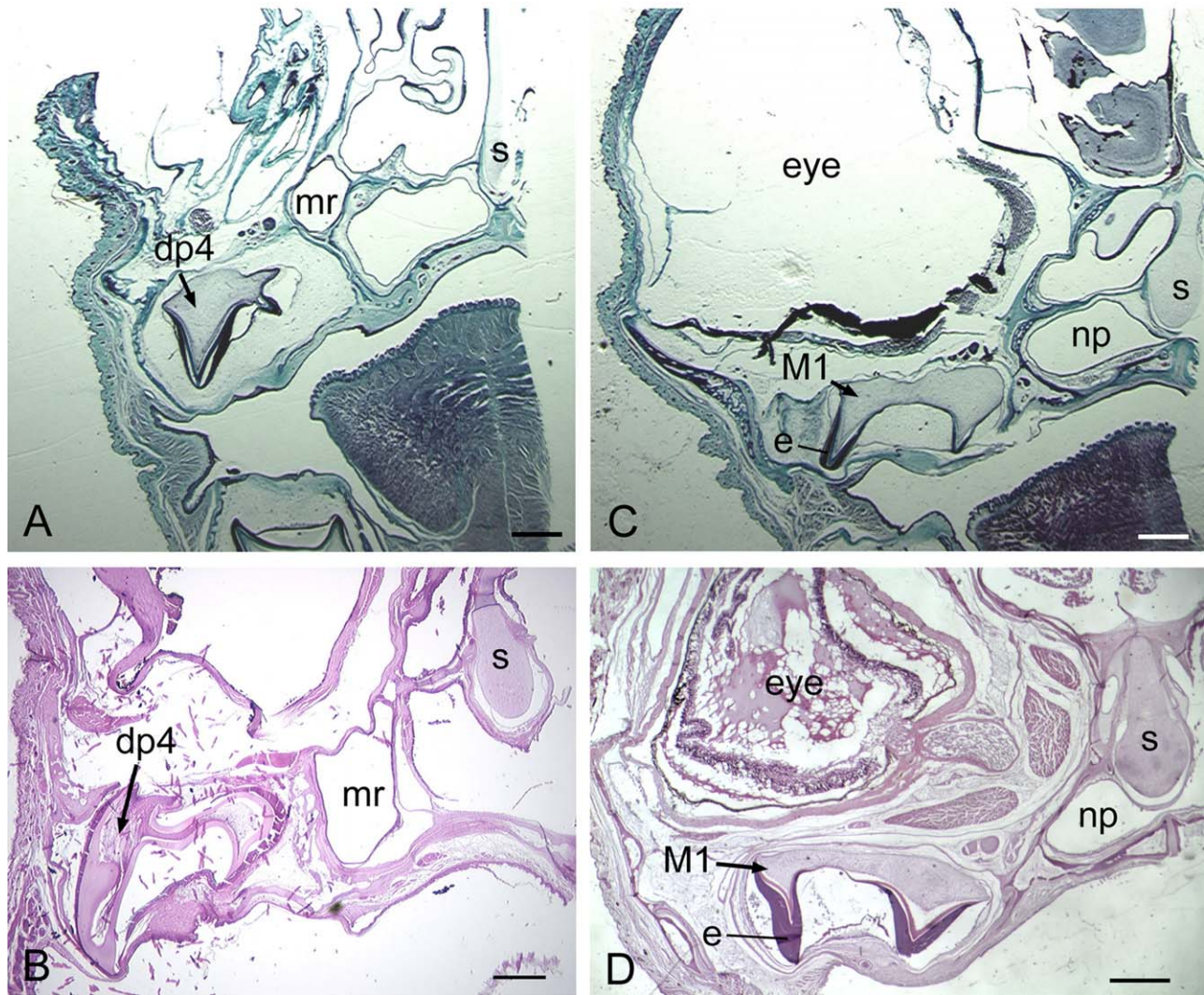
Fig. 9. Comparison of histological sections of the frugivorous *Eulemur macaco* (**A**, **C**), and the folivorous *Hapalemur griseus* (**B**, **D**) at dp4 and M1 levels. Note thicker mineralized cusps in *Hapalemur* at both levels, including thicker enamel (e). Scale bars, 1 mm. dp4, deciduous premolar; e, enamel; mr, maxillary recess; M1, first permanent molar; nc, nasal cavity; np, nasopharyngeal ducts; or, orbit; S, nasal septum.

in terms of tooth maturation. As will be discussed further below, callitrichines as a group do not stand out as having more rapidly developing permanent teeth than other anthropoids. However, we can infer that there is a variable rate of prenatal mineralization among the genera, resulting in marked differences in the extent of maturation of M1 in particular (see below). Plavcan and Gomez (1993), found three of the four callitrichine genera have relatively small teeth for body size. Only *Leontopithecus* stands out in their analysis as having relatively large postcanine teeth, and yet they have a less mineralized M1 than other callitrichines suggesting variable rates of postnatal growth and maturation of these teeth in this group. Thus, the dental status (i.e., eruption and tooth maturation) at birth show no evidence for especially well-developed postcanine teeth, as might be predicted by the dwarf hypothesis (Ford, 1980; Plavcan and Gomez, 1993). Since callitrichines follow general anthropoid patterns at birth, we hypothesize that if they are dwarfed, it likely involved only postnatal changes in growth rate that affect size. Further evaluation must await quantification of tooth size and hydroxyapatite density at early ages.

Gingival emergence. The status of gingival emergence in our sample has some general agreement with the consolidated data that were analyzed by Smith et al. (1994). Gingival emergence does generally occur more rapidly in smaller primates (e.g., cheirogaleids, callithrichines, and lorises) than it does in larger primates. Larger strepsirrhines and larger
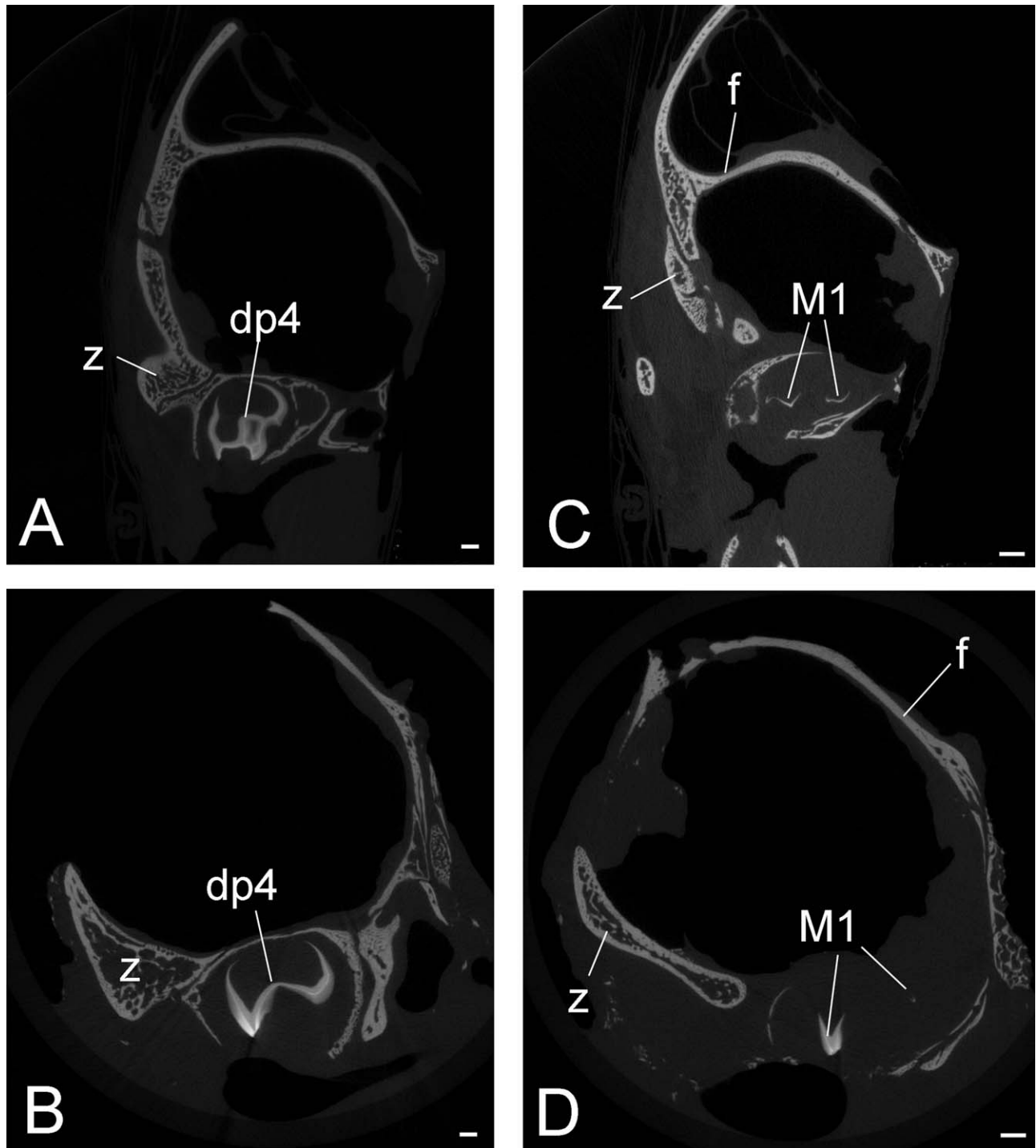
Fig. 10. Comparison of CT slices of the frugivorous *Allenopithecus nivergatus* (**A**, **C**), and the folivorous *Trachypithecus francoisi* (**B**, **D**) at dp4 and M1 levels. Note thicker mineralized cusps in *Trachypithecus* at both levels. Scale bars, 1 mm. dp4, deciduous premolar; f, frontal bone; M1, first permanent molar; z zygomatic bone.

anthropoids in our sample, with the exception of *Propithecus* and *Trachypithecus* (di1 only), exhibit no gingival emergence at birth. Our data also agree with findings that *Propithecus* spp. have an advanced state of gingival emergence at birth (Smith et al., 1994), which is presumably related to rapid growth of permanent teeth (Godfrey et al., 2004), and perhaps other factors that require further study (e.g., absolute

TABLE 4. Maturational stage of maxillary teeth

TAXA[a]	di1	di2	dc	dp2	dp3	dp4	M1	M2	M3	I1	I2	C	P2	P3	P4
Strepsirrhini															
Cheirogaleids															
Microcebus murinus	E	RSR	E	RSR	Late bell	Late bell[c]	Late bell	Late bell	NO	late bell[d]	early bell	late bell	early bell	bud	bud
Cheirogaleus medius	E/RSR	RSR	RSR	RSR/E	Late bell[c]	Late bell[c]	Late bell	Early/late bell	bud	late bell	early/late bell	late bell	late bell	bud	bud
Mirza coquereli	RSR/E	RSR	RSR	RSR	Late bell	Late bell	Late bell	Early/late bell	TDL	Cap/early bell	cap	early/late bell	cap	no	TDL
Lemurids															
Lemur catta	RSR	RSR	RSR	Late bell[c]/RSR	RSR	Late bell	Late bell	NO	NO	bud	bud	early bell	TDL	TDL	TDL
Eulemur macaco	RSR	RSR	RSR	Late bell[c]/RSR	Late bell	Late bell	Late bell	Cap/TDL	NO	cap?	bud?	late bell	Bud/cap	TDL	NO
E. collaris	RSR	RSR	RSR	Late bell[c]	Late bell	Late bell	Late bell	Cap	NO	cap?(dam.)	bud?(dam.)	late bell	bud(dam.)	bud(dam.)	bud(dam.)
E. coronatus	RSR	RSR	RSR	Late bell[c]	Late bell	Late bell	Late bell	Cap	NO	cap?(dam.)	cap?(dam.)	late bell[d]	bud(dam.)	bud?(dam.)	Bud(dam.)
E. mongoz	RSR	RSR	RSR	Late bell[c]	Late bell	Late bell	Late bell	NA	NO	cap	cap	late bell[d]	bud	NO	NO
E. rubriventer	RSR	RSR	RSR	late bell	Late bell	Late bell	Late bell[d]	NO	NO	cap?(dam.)	bud?(dam.)	early bell	TDL?(dam.)	NO	TDL
Varecia rubra	Late bell	Late bell	Late bell[c]	Late bell	Late bell	Late bell	Late bell[d]	NO	NO	cap?(dam.)	TDL	early bell	TDL/cap	TDL	TDL
V. variegata	Late bell	Late bell	Late bell[c]	Late bell	Late bell	Late bell	Late bell	NO	NO	cap	TDL	early bell	TDL	NO	TDL
Indriids															
Hapalemur griseus	RSR	RSR	RSR	Late bell	Late bell	RSR	Late bell	Cap	NO	bud	early bell	early bell	TDL	TDL/NO	TDL
Propithecus coquereli	RSR	E	E	shed	E	E	Late bell	late bell	Late bell	late bell	late bell	late bell	–	Late bell	Late bell
Galagids															
Otolemur crassicaudatus	RSR	RSR	E	RSR	Late bell	Late bell[c]	Late bell	late bell	NO	early bell	late bell	late bell	late bell	bud(dam.)	TDL
O. garnettii	E	E	E	RSR	Late bell	Late bell[c]	Late bell[c]	Late bell	NO	late bell	late bell	late bell	late bell	TDL	bud
Galago mohoii	RSR	RSR	RSR	E/RSR	Late bell	Late bell[c]	late bell	late bell	cap	early bell	late bell[d]	late bell	late bell	bud/cap	bud/cap
Galago senegalensis	RSR	RSR	E	RSR	Late bell?	Late bell[c] (dam.)	late bell	late bell	bud?	? (dam.)	? (dam.)	late bell	early bell (dam.)	? (dam.)	? (dam.)
Lorisids															
Galagoides demidovii	RSR	RSR	RSR	RSR	Late bell	Late bell[c]	Late bell	late bell	cap (dam.)	bud	Cap	late bell	early bell	bud	cap
Nycticebus pygmaeus	E	RSR	E	E	Late bell or RSR (dam.)	Late bell or RSR (dam.)	Late bell (dam.)	late bell (dam.)	? (dam.)	late bell[c]	early bell?(dam.)	late bell	Late bell	? (dam.)	? (dam.)
Haplorhini	di1	di2	dc	dp2	dp3	dp4	M1	M2	M3	I1	I2	C	P2	P3	P4
Platyrrhini															
Cebids															
Cebuella pygmaea	E	E	RSR	RSR	RSR	RSR	late bell	NO/TDL	NO	Early bell/late bell[d]	cap	Cap	TDL	TDL	TDL/bud
Callithrix jacchus	RSR	RSR	RSR	late bell[c]/RSR	Late bell[c]	Late bell	Early/late bell[d]	TDL/NO	NO	cap/early bell	TDL	TDL/bud	TDL or NO	NO	NO
Leontopithecus rosalia	E	E	RSR	RSR	Late bell[c]/RSR	Late bell[c]	Early/late bell[d]	NO/TDL	NO	early bud	BUD	TDL	TDL	NO/TDL	NO/TDL
Saguinus oedipus	E/RSR	RSR	Late bell	RSR	Late bell	Late bell	Early bell/late bell[d]	NO	NO	cap	TDL	TDL	NO/TDL	NO/cap	NO/cap
S. geoffroyi	E/RSR	E/RSR	Late bell	Late bell	Late bell	Late bell	Early bell	NO	NO	cap/early bell	NO/TDL	TDL	NO	? (dam.)	NO
S. bicolor	RSR	RSR	Late bell[c]	Late bell	Late bell	?	?	?	?	Cap	TDL	TDL(dam.)	?	?	?
Saimiri boliviensis	E/RSR	E/RSR	RSR	Late bell[c]/RSR	Late bell[c]/RSR	Late bell[c]	Late bell	NO/bud/cap	?	Cap	TDL	TDL	NO/TDL/cap	NO/TDL	TDL
Atelids															
Alouatta seniculus	RSR	RSR	RSR	RSR	RSR	Late bell	Late bell	(dam.)	(dam.)	Cap	bud	(dam.)	TDL	NO	NO
Pitheciids															
Pithecia pithecia	RSR	RSR	Late bell	RSR	RSR	RSR	Late bell	Early bell	NO	Cap	TDL	TDL	NO	TDL	TDL
Aotus nancymaae	RSR	RSR	RSR	RSR	RSR	RSR	Late bell	Early bell	NO	Cap	NO	TDL	TDL	TDL	NO
Catarrhini															
Macaca mulatta	RSR	RSR	(dam.)	–	Late bell[c] (dam.)	Late bell[c] (dam.)	Late bell (dam.)	? (dam.)	NO		NO		–	? (dam.)	? (dam.)
Colobus guereza	RSR	RSR	late bell[c]	–	RSR	RSR	Early bell	NO	NO	Cap	NO	cap	–	NO	NO
Allenopithecus nigroviridis	RSR	RSR	RSR	–	RSR(dam.)	Late bell[c] (dam.)	Late bell	NO	NO	Cap	(dam.)	TDL	–	?(dam.)	?(dam.)
Trachypithecus francoisi	RSR	RSR	RSR	–	RSR	Late bell[c]	Late bell	NO	NO	Cap	NO	TDL	–	NO	NO
Tarsiiformes															
Tarsius syrichta	E	E	E	shed	E	E	Late bell[c]	Late bell	Late bell	Late bell	early bell	late bell	late bell	late bell	late bell[d]
Scandentia															
Tupaia belangeri	Late bell	Late bell	Late bell	Late bell	Late bell	Late bell	Late bell	Cap	Bud	Bud	NO	TDL	TDL	NO	TDL

[a] Primate systematics are arranged according to Fleagle (2013) except for Platyrrhini, which are arranged according to Rosenberger (2011).

[b] Abbreviations for teeth: di, deciduous incisor; dc, deciduous canine; dp, deciduous premolar; I, permanent incisor; C, permanent canine; P, permanent premolar; M, molars.

[c] In one or more specimens the SR (stellate reticulum) is restricted to approximately the distal half of tooth germ.

[d] Initial mineralization of a cusp (beginning late bell stage).

RSR, stellate reticulum is nearly or completely regressed; TDL, thickened dental lamina; NA, material not available; NO, not observed; E, gingival emergence; dam, damage due to artifact or poor preservation prevented determination.
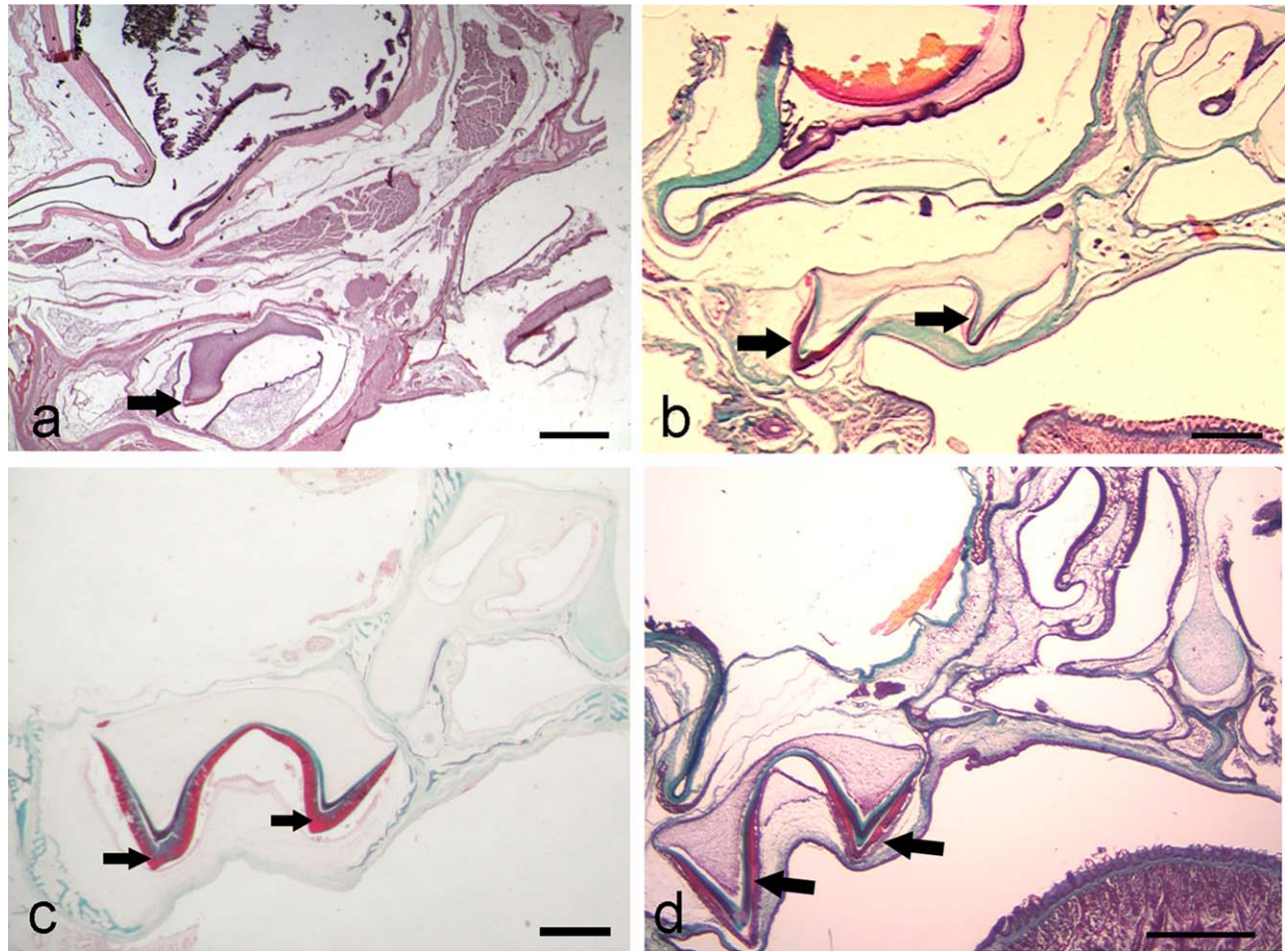
Fig. 11. Variations of M1 mineralization across primates at birth. Mineralized cusps are indicated with large arrows. Among strepsirrhines, *Varecia variegata* (**A**) had the least mineralization of M1, limited to one cusp. *Lemur catta* (**B**) has mineralization of the cusps but not the tooth basin. By comparison, a late fetal *Propithecus coquereli* is far more advanced (**C**). Nocturnal strepsirrhines, such as *Galagoides demidovii*, have a well-mineralized M1 (**D**). Tamarins, such as *Leontopithecus rosalia* (**E**), have the least advanced development of M1, here in the early bell stage, adjacent to the last cusp of dp4. In all other anthropoids, M1 is well advanced in the late bell stage: f, *Aotus nancymaae*; g, *Alouatta seniculus*; h, *Pithecia pithecia*. Scale bars, 1 mm.

face size, as hypothesized by Vinyard and Hanna, 2005).

Smith et al. (1994) noted that to some extent, the body size differences in gingival emergence break down within families, and we can confirm this observation. Among cheirogaleids, *Mirza coquereli* has the fewest exposed teeth while the most are observed in the smaller cheirogaleid, *Microcebus*. Among lorisoids, galagids are variable in emergence of the anterior teeth (di1 through dc), and in emergence of dp2. However, given that multiple specimens were present for most galagids, and there are differences among specimens for each species, one might infer that gingival emergence of di1 through dp2 is occurring in all species *near* birth. The extent to which the cusps were embedded in gingival mucosa is consistent with this reasoning: in all lorisoids, the tip of the cusps for di1 through dp2 were covered by only a thin membrane (pre-eruptive phase—Avery, 2002). This small barrier from gingival emergence supports the idea that eruption of these teeth can be expected to occur early in these primates, perhaps as a perinatal event. We thus suggest lorisoids are likely precocious in gingival emergence, and the variability indicated by Table 2 reflects the tight perinatal window of gingival emergence.

Larger-bodied lemurids are cohesive in the reduced degree of gingival emergence at birth, relative to lorisoids. This includes the folivorous *Hapalemur*, which resembles all other lemurids, as shown for the overall pace of dental eruption by Godfrey et al. (2003).

Among anthropoids, variation is seen in the callitrichines, as previously noted for *Saguinus* and *Callithrix* (Smith et al., 1994). Our findings suggest that *Saguinus oedipus* and *S. geoffroyi* may be in a somewhat less precocious state than reported for two other *Saguinus* spp. by Glassman (1983) and Chase and Cooper (1969). The anterior teeth are not always emergent in either species studied here, and no dc has emerged through the gingiva. It should be noted that the gingival covering of the anterior teeth is membranous in both
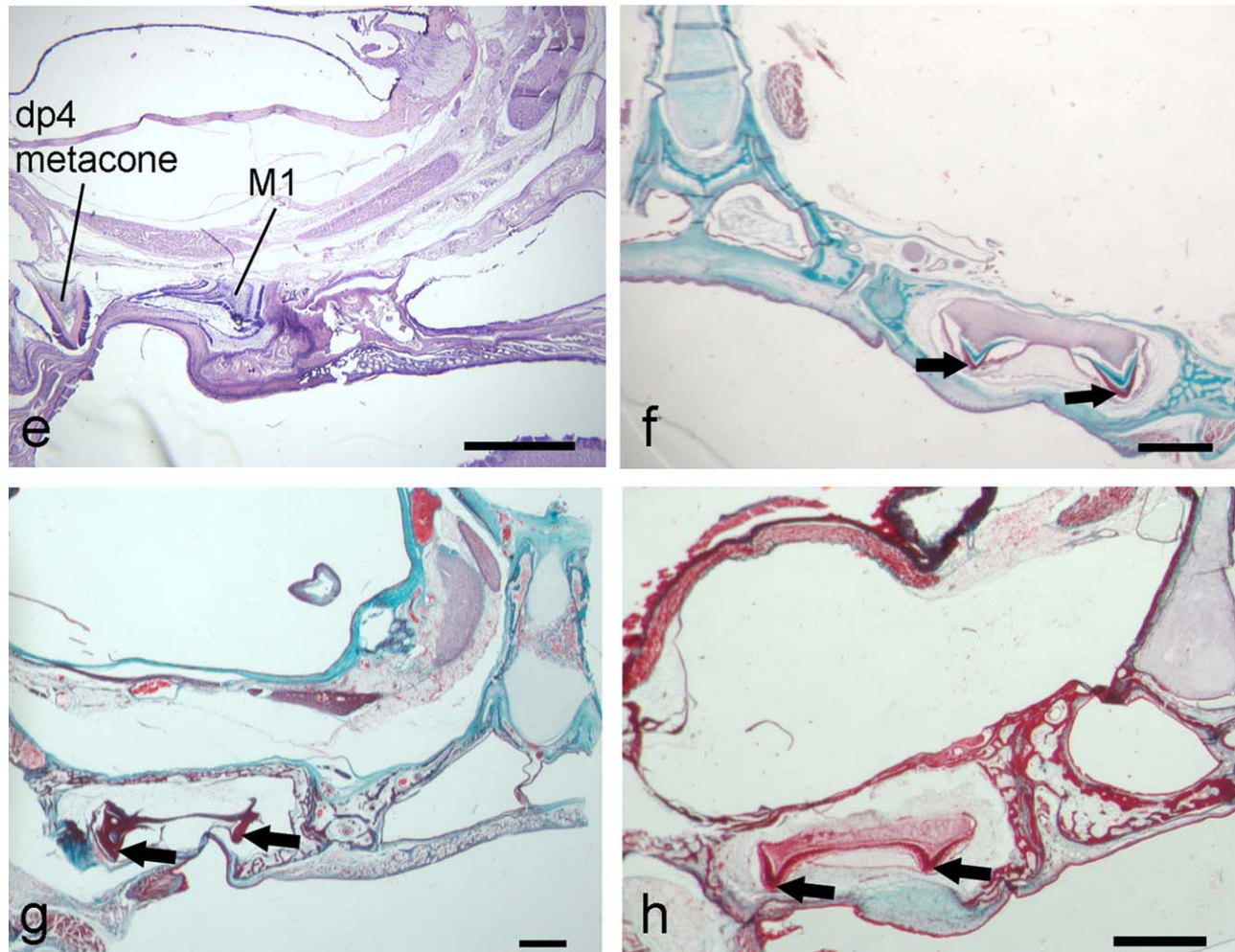
Fig. 11. Continued

species, and eruption was therefore possibly imminent. *Leontopithecus* has di1/di2 emergence in all specimens examined, and dc emergence in most cases. Our findings agree with the data summarized by Smith et al. (1994) regarding *Callithrix jacchus*, which has no emergent cusps in any specimen. Only two *Cebuella pygmaea* neonates were studied histologically, but in both cases, they were the most precocious of any callitrichine in extent of eruption (Fig. 2a) and gingival emergence (Table 3). Evidence from CT scans of similar sized specimens also indicates that this is the most precocious anthropoid.

The remainder of the anthropoids consistently lack gingival emergence of any teeth, with one exception. The di1 of *Trachypithecus* pierces the gingiva. Although the dc was damaged in *Macaca* and could not be assessed, the remaining teeth are covered with gingiva, as known for several other *Macaca* spp (Smith et al., 1994). Our results are entirely consistent with the compiled database presented on anthropoids by Smith et al. (1994). Gingival eruption of upper teeth at birth is rare in anthropoids, and most common in callitrichines. Our data and those summarized by Smith et al. (1994) suggest that eruption of premaxillary incisors is incipient at birth in platyrrhines and many catarrhines; if not emergent, the teeth pierce the gingiva within days (or several weeks at most). This increases the contrast with great apes, all of which delay emergence of any teeth for months (Robinow et al., 1942; Gavin, 1967; Neugebauer, 1980; Keiter, 1981; Fooden and Izor, 1983; Kuykendall et al., 1992; Kuykendall, 1996).

The advanced rate of development of the dentition in tarsiers has been well described (Luckett and Maier, 1982) and complete gingival emergence of upper deciduous dentition is observed in *T. syrichta*. The dp2 is shed and P2 is seen prominently in a state of alveolar eruption, as in perinatal *T. bancanus* (Luckett and Maier, 1982). Given that M1 is nearing the same occlusal plane as dp4 (Fig. 3b), *Tarsius* has the most advanced state of alveolar eruption and gingival emergence of any primate at birth.

Dental stages. Some clear phylogenetic patterns in tooth germ maturation are discernible in strepsirrhines
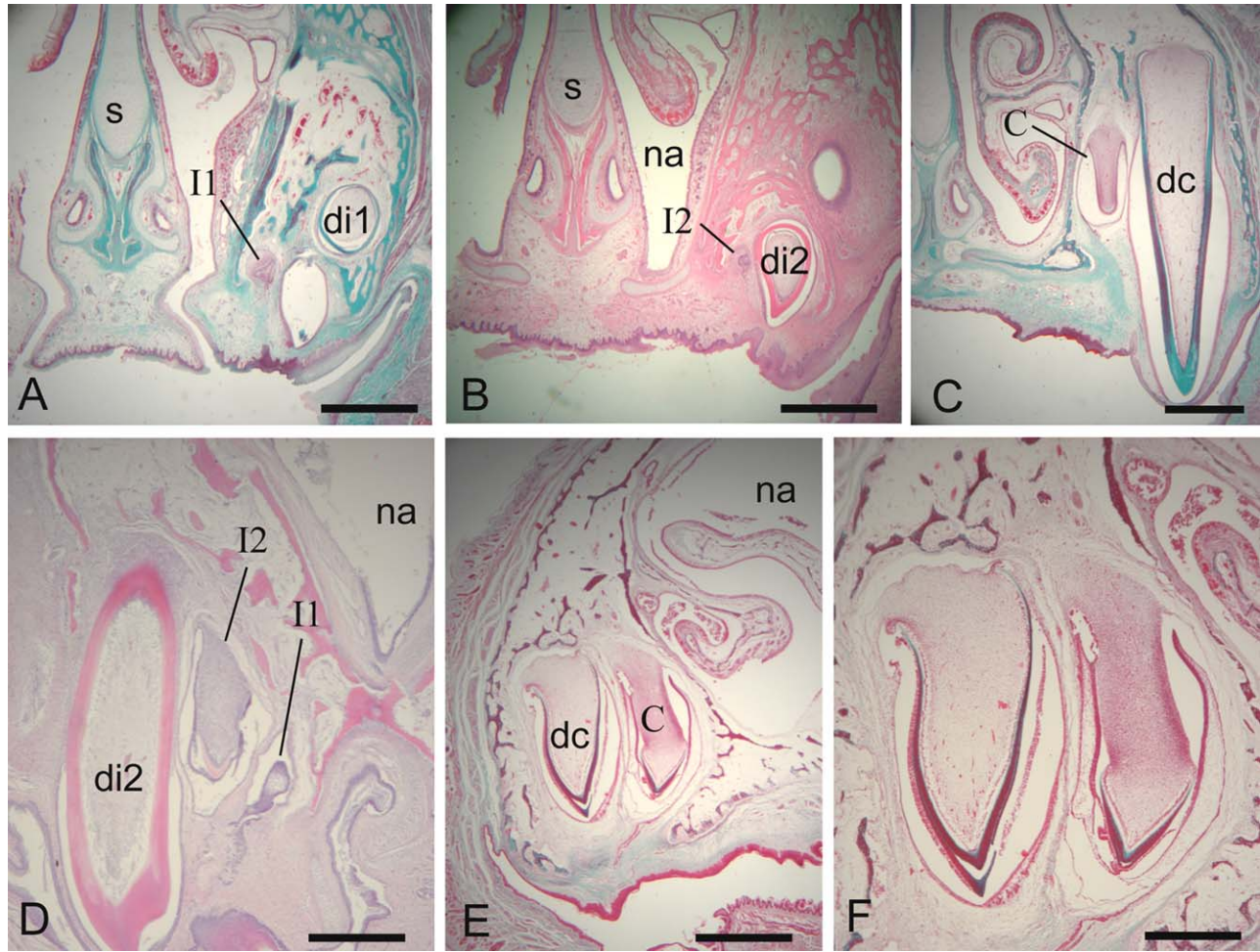
Fig. 12. The anterior teeth in *Eulemur mongoz* (top row) compared with *Otolemur crassicaudatus* (bottom row). In *Eulemur*, as in most primates, I1 (**A**, cap stage) is more advanced than I2 (**B**, bud stage). In galagids, these teeth are at similar stages at birth, or I2 is more advanced, as in **D** (I2: late bell; I1: early bell). The permanent canines are at more advanced stages than I1/I2 at birth (**C**: early bell stage; **E**, enlarged in **F**, late bell stage). Scale bars, 1 mm; na, nasal airways; s, septum.

at the family level. In galagids, M2 is progressed to the late bell stage, and M3 is present in the smaller species (cap stage). They are the closest to rival *Propithecus* and *Tarsius* in terms of overall dental maturation. Due to poor preservation, it is unclear whether *Nycticebus* follows this trend, but it appears at least as advanced as cheirogaleids, in which M1 and M2 have each reached the bell stage. *Nycticebus* is similar to galagids in advanced maturation of the anterior teeth at birth. Missing from our sample is *Lepilemur*, which was previously shown to have rapid dental eruption (Godfrey et al., 2005), and presumably has advanced stages of tooth germ development at birth.

The lemurids as a group have the least advanced dental maturation at birth among strepsirrhines. As might be predicted based on our knowledge of the eruption schedule (Godfrey et al., 2001, 2003), *Varecia* has the least precocious dental arcade. Perhaps most notably, M1 has little or no cusp mineralization. Among the remainder of species studied, no lemurid stands out as

being far more advanced than any other. M2 is often not present (i.e., it has not even proliferated to a bud stage via the dental lamina). Most permanent premolars are yet to reach the cap or bud stage.

In some species, the rapid eruption and shedding of deciduous teeth may relate to precocious development of permanent tooth buds. This is clearly the case across ontogeny in *Propithecus* (Godfrey et al., 2004), for it has advanced maturation of permanent teeth at birth (Table 4), and even before (Godfrey et al., 2004). The state of maturation of teeth and tooth germs in *Propithecus* exceeds every other primate studied. *Propithecus* and *Tarsius* are all the more notable regarding the maturational state of permanent molars. Cheirogaleids and lorisoids are the only other primates to possess M2 at a stage of maturation at the early bell stage or beyond.

The replacement teeth present an even more stark contrast when one compares *Propithecus coquereli* and *Tarsius syrichta* to most other primates. At birth, P2 is

TABLE 5. Maturation indices for newborns of nonhuman primates: Early stage of mineralization

| | Maturation index 1 (late bell) | | | | | | | | | | | |
| | All teeth | | | Deciduous | | | Permanent | | | Replacement | | |
	LB stage	Total no.	IND	LB stage	total no.	IND	LB stage	total no.	IND	LB stage	total no.	IND
Strepsirrhini												
Cheirogaleids												
Microcebus murinus	10	15	0.667	6	6	1	4	9	0.444	2	6	0.333
Cheirogalues medius	12	15	0.800	6	6	1	6	9	0.667	4	6	0.667
Mirza coquereli	9	15	0.600	6	6	1	3	9	0.333	1	6	0.167
Lemurids												
Lemur catta	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Eulemur macaco	8	15	0.533	6	6	1	2	9	0.222	1	6	0.167
E. collaris	8	15	0.533	6	6	1	2	9	0.222	1	6	0.167
E. coronatus	8	15	0.533	6	6	1	2	9	0.222	1	6	0.167
E. mongoz												
E. rubriventer	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Varecia spp	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Hapalemur griseus	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Indriids												
Propithecus coquereli	12	13	0.923	5	5	1	7	8	0.875	4	5	0.800
Galagids												
Otolemur crassicaudatus	11	15	0.733	6	6	1	5	9	0.556	3	6	0.500
O. garnettii	12	15	0.800	6	6	1	6	9	0.667	4	6	0.667
Galago moholi	11	15	0.733	6	6	1	5	9	0.556	3	6	0.500
Galagoides demidovii	9	15	0.600	6	6	1	3	9	0.333	1	6	0.167
Lorisids												
Nycticebus pygmaeus	11	15	0.733	6	6	1	5	9	0.556	3	6	0.500
Strepsirrhine average			**0.629**			**1**			**0.374**			**0.300**
Haplorhini												
Platyrrhini												
Cebids												
Cebuella pygmaeus	8	15	0.533	6	6	1	2	9	0.222	1	6	0.167
Callithrix jacchus	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Leontopithecus rosalia	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Saguinus oedipus	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
S. geoffroyi	6	15	0.400	6	6	1	0	9	0.000	0	6	0.000
Saimiri boliviensis	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Atelids												
Alouatta seniculus	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Pithecids												
Pithecia pithecia	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Aotus nancymaae	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000
Catarrhini												
Colobus geureza	6	13	0.385	5	5	1	1	8	0.125	0	5	0.000
Allenopithecus nigroviridis	6	13	0.385	5	5	1	1	8	0.125	0	5	0.000
Trachypithecus francoisi	6	13	0.385	5	5	1	1	8	0.125	0	5	0.000
Anthropoid average			**0.448**			**1**			**0.114**			**0.015**
Tarsiiformes												
Tarsius syrichta	13	14	0.929	5	5	1	8	9	0.889	5	6	0.833
Scandentia												
Tupaia belangeri	7	15	0.467	6	6	1	1	9	0.111	0	6	0.000

LB, late bell (i.e., mineralization has commenced in at least one cusp).

at the early or late bell stage in two of the cheirogaleids we studied, and is at the early or late bell stage in all lorisoids we studied. Aside from *G. moholi*, in which P3 was at an early bell stage, P3 and P4 are markedly underdeveloped in all primates studied when compared with *Propithecus* and *Tarsius*.

In all anthropoids studied here, maturation of the deciduous dentition is nearly on a par with cheirogaleids, in that most or all deciduous teeth have pro-gressed beyond the late bell stage. The stellate reticulum has completely or mostly disappeared, and in some cases the teeth have erupted through the gingiva. This places dental maturation of deciduous teeth in platyrrhines and catarrhines at a more advanced state than lemurids. On the other hand, M2 is observed in most strepsirrhines, and has developed into a tooth germ in only two anthropoids (*Aotus* and *Saimiri*). With few exceptions, the pace of maturation of deciduous teeth

TABLE 6. Maturation indices for newborns of nonhuman primates: advanced stage of mineralization

	Maturation index 2 (RSR)							
	All teeth			Deciduous			Permanent	Replacement
	RSR	Total no.	IND	RSR	Total no.	IND		
Strepsirrhini								
Cheirogaleids								
Microcebus murinus	4	15	0.267	4	6	0.667	No permanent teeth in any species are at RSR stage	No replacement teeth in any species are at RSR stage
Cheirogalues medius	4	15	0.267	4	6	0.667		
Mirza coquereli	4	15	0.267	4	6	0.667		
Lemurids								
Lemur catta	5	15	0.333	5	6	0.833		
Eulemur collaris	3	15	0.200	3	6	0.500		
E. coronatus	3	15	0.200	3	6	0.500		
E. flavifrons	3	15	0.200	3	6	0.500		
E. rubriventer	3	15	0.200	3	6	0.500		
Varecia spp	0	15	0.000	0	6	0.000		
Hapalemur griseus	6	15	0.333	6	6	0.833		
Indrids								
Propithecus coquereli	5	13	0.385	5	5	1.000		
Galagids								
Otolemur crassicaudatus	4	15	0.267	4	6	0.667		
O. garnettii	4	15	0.267	4	6	0.667		
Galago moholi	4	15	0.267	4	6	0.667		
Galagoides demidovii	4	15	0.267	4	6	0.667		
Strepsirrhine average			**0.254**			**0.632**		
Haplorhini								
Platyrrhini								
Cebids								
Cebuella pygmaea	6	15	0.400	6	6	1.000		
Callithrix jacchus	4	15	0.267	4	6	0.667		
Leontopithecus rosalia	5	15	0.333	5	6	0.833		
Saguinus oedipus	2	15	0.133	2	6	0.333		
S. geoffroyi	2	15	0.133	2	6	0.333		
Saimiri boliviensis	5	15	0.333	5	6	0.833		
Atelids								
Alouatta seniculus	5	15	0.333	5	6	0.833		
Pitheciids								
Pithecia pithecia	5	15	0.333	5	6	0.833		
Aotus nancymaae	6	15	0.400	6	6	1.000		
Catarrhini								
Allenopithecus nigroviridis	4	14	0.286	4	5	0.800		
Colobus geureza	4	14	0.286	4	5	0.800		
Trachypithecus francoisi	4	14	0.286	4	5	0.800		
Anthropoid average			**0.291**			**0.742**		
Tarsiiformes								
Tarsius syrichta	5	14	0.357	5	5	1.000		
Scandentia								
Tupaia belangeri	0	15	0.000	0	6	0.000		

RSR, stellate reticulum is nearly or completely regressed.

appears to be greatest in callitrichines. In the order of deciduous cusp mineralization, dp3 is reported to precede di2 and dc in cercopithecoids, hominoids, and *Alouatta* (Swindler, 2002). Among all anthropoids studied here, tooth maturation of the incisors and the dc tend to be more advanced than postcanine teeth, with few exceptions (*Aotus* and *Saimiri*). This suggests the pace of mineralization of individual teeth diverges, with di2 and dc accelerating at some point during fetal growth. Similar divergent rates of maturation may occur among the permanent teeth of anthropoids (see below).

The rate of mineralization of certain teeth differs among primates, especially in the more posterior teeth. This is based on observed variation in M1 and M2. Particularly in anthropoids, M1 is not yet mineralized at birth in all tamarins of either genus studied here (in fact, few samples reached the late bell stage—see Appendix), while it is advanced to a late bell stage in all others. In lemuroids, it appears that folivores have more heavily mineralized dp4s than frugivores, and the contrast is greater still in M1. Advanced mineralization of M1 also appears to be one similarity between *Propithecus* and *Hapalemur* at birth; otherwise, the uniquely different strategies in development of these two taxa (see Godfrey et al., 2003) are already apparent at birth. These suggestions must be verified quantitatively, with appropriate controls for body size.

A final nuance that must be clarified is the basis for advanced eruption at birth. Clearly, advanced eruption could relate to a maxilla that is crowded by erupting deciduous teeth and developing permanent teeth. However, in many cases the array of replacement teeth is not sufficiently large, and sometimes undifferentiated from the dental lamina. Thus, we have a clear picture of certain taxa with erupted teeth soon to be replaced, and others growing their deciduous arcade for early masticatory function. Our comparative sample of primate tooth stages indicates which teeth lack a well-developed replacement at birth: all lemurids lack any well-developed replacement for deciduous premolars. This is unsurprising in that lemurids have a slow schedule for tooth eruption (Godfrey et al., 2001). However, it also may be observed that no primates except *Propithecus* and *Tarsius* telegraph the impending formation of P4 at birth—it does not surpass the bud or cap stage. This broad trend, along with the similar pattern of perinatal tooth maturation in *Tupaia*, suggests it may be primitive to delay investment in growing the replacement for the last deciduous premolar, the deciduous tooth that is most molar-like of all. As discussed by Godfrey et al. (2003), the dietary adaptations regarding the eruption of M1 and the morphology of dp4 are of special significance to subadult primates.

Tarsiers. This study confirms numerous other accounts of the precocious dental arcade in late fetal and early postnatal tarsiers (e.g., Luckett and Maier, 1982; Schwartz, 2003). Our sample provides additional support using captive specimens of known age, thus adding a more certain picture of the neonatal condition. Our specimens appear to be roughly comparable in size to the near-term fetuses and a neonate by Luckett and Maier (1982). The newborn *T. bancanus* has a similar head size to the "infant" in their study.

In most respects, our findings confirm the findings of Luckett and Maier (1982). All deciduous teeth are erupted or already shed at birth. M1 is well enclosed by alveolar bone and in an erupted position. P2 is prominent in eruption, although at a less advanced state of maturation compared with the adjacent (deciduous) erupted teeth. No trace of dp2 could be observed even in the late fetus. The presence of a complete set of deciduous incisors was uncertain given a report of absence of di1 in near-term fetuses and a neonate by Luckett and Maier (1982). However, we were able to find four teeth (two erupted and two bell stage) in some but not all specimens. These results are consistent with the idea that two sets of premaxillary teeth are generated, but the lateral-most deciduous element is lost in the perinatal timeframe. Our results do not refute Luckett and Maier's suggestion that di2 is erupted and lost within the first postnatal week (1982, p 22).

Broader comparisons. As an order, Primates has few discernible trends in dental status at birth, except perhaps that many primates suppress the development of selected deciduous teeth (e.g., dp2 absent or shed prenatally), as seen in some other mammals (Järvínen et al., 2008). Some mammals have unifying evolutionary trends, such as delayed eruption of permanent teeth in Afrotheria (Asher and Lehmann, 2008), or the lack of entire classes of teeth as in Xenarthra (Vizcaíno, 2009). Previous work has shown primates to be more heterogeneous, particularly with regard to development patterns and tooth size (e.g., Smith et al., 1994; Godfrey et al., 2001). The results of this study provide firm evidence that primates vary in patterns of development for dental stage cohorts, with variation in reliance on deciduous versus replacement teeth occurring within suborders. This level of developmental diversity exists in other mammals, such as Chiroptera (e.g., Friant, 1965; Czaplewski, 1987). As with bats, the ultimate explanation of developmental diversity of newborn primates will require further analysis to determine the extent to which the neonatal dentition telegraphs function in adults, or perhaps, is constrained by other somatic developmental trends.

In one respect, all primates have a unifying characteristic, and this is emphasized by their accelerated state of dental maturation at birth. Here we show that the state of dental maturation and eruption for all primates at birth are far in advance of that in *Tupaia*. *Tupaia* has certain morphological and developmental similarities to primates that render it a useful comparative model in some respects (e.g., Collins and Tsang, 1987). Yet, in somatic maturation, *Tupaia* may not be a useful model for ancestral primates. *Tupaia* has extremely altricial neonates (Martin, 1990; Ferner et al., 2010). Although many strepsirrhines primates at birth are nest-bound and do not immediately tend to practice locomotor movements (Ross, 2001), birthing altricial newborns is not regarded as an ancestral strategy for the primate order (Martin, 1990). That stated, the primate position along the "altricial-precocial spectrum" is not firmly at one end. All primates are arguably initially helpless, even though they are well adapted for locomotion at a far earlier age than altricial mammals. In a subtle way, they represent a hybrid condition, with relatively large

brains, but weak musculature (Grand, 1992). In their musculature, it may be a lower percentage of muscle mass that ultimately separates newborns from actively locomoting subadults (Grand, 1992; although muscle mass distribution within segments *is* precocial—Atzeva et al., 2007). The dental status at birth is another area of contrast, and the newborn primate is even more sharply contrasted with *Tupaia* in this regard. The dentition of the *Tupaia* neonate appears to reflect slower maturation compared with primates. In dental eruption status, *Tupaia* is not a contrast to all primates since anthropoids, especially hominoids, are far slower to erupt their teeth compared with strepsirrhines (Mooney et al., 1991; Smith et al., 1994; Anemone et al., 1996). However, all primates are far in advance of *Tupaia* in terms of dental maturation, based on a comparison of dental stages at birth. The most parsimonious conclusion based on extant primates is that early primates also invested in the somatic prenatal development of their young, particularly advancing tooth development. This is not surprising, given the existence of fossil data on ancient deciduous primate teeth (as recently discussed by Franzen et al., 2009). Well preserved fragments would simply not be expected in mammals whose teeth are not progressed to the late bell stage and beyond at birth.

Perinatal Dental Eruption and Maturation in Light of Diet

Godfrey et al. (2003) discussed, in great detail, the different strategies apparent in dental ontogeny of two highly folivorous strepsirrhines, *Propithecus* and *Hapalemur*. The highly accelerated eruption schedule of indriids has been described numerous times (Smith et al., 1994; Godfrey et al., 2001, 2003, 2004). In this strategy, the eruption of permanent dentition is greatly accelerated, and ontogenetic comparisons of indriids to other lemuroids emphasize this (Godfrey et al., 2004). Our histological findings on perinatal *Propithecus* agree with the observations of Godfrey et al. (2004) that the accelerated development of replacement teeth is well underway even before birth. Our findings are also consistent with the notion that *Hapalemur* spp. depend on deciduous premolars (presumably primarily dp4) long into subadulthood (Godfrey et al., 2003). *Hapalemur griseus*, like other lemurids, has little or no maturation of the postcanine replacement teeth at birth. Thus, folivores can invest in development of either deciduous or permanent dentition to make the transition through weaning. Retaining deciduous premolars throughout juvenility is most common for primates, and one would expect that the molariform dp4 is important to most primates for processing food, if only for a finite amount of time. No anthropoid in our sample adopts a strategy similar to indriids.

Our qualitative observations offer some insight into the strategy of *Hapalemur* spp. for mastication of tough foods early in life. Setting aside the smallest primates (which are insectivores or gum specialists) and *Propithecus*, *Hapalemur griseus* has the most advanced development of deciduous premolars at birth for any strepsirrhine. The stellate reticulum has disappeared or regressed to a small isolated patch near the neck of the crown in all teeth. Qualitatively, it would appear that *Hapalemur* has a far more mineralized dp4 and M1 than any other lemurid (Fig. 9), suggesting this tandem of teeth is prepared for earlier functionality. At this time, no other lemurids distinguish themselves in tooth maturation, although quantitative study of cusp mineralization is needed. Among anthropoids, perinatal *Trachypithecus* and *Alouatta* appear to have well mineralized cusps of dp4 and M1 compared with all other anthropoids. These qualitative observations indicate mineralization rates of postcanine teeth may be rapid in folivores compared with frugivores, and detectable as early as birth.

Dental Eruption and Maturation: Two Paths Toward Independence

The present study provides many novel observations on development of the permanent teeth, inaccessible via many conventional radiographic techniques because so many teeth remain unmineralized at birth. When compared with existing knowledge on dental eruption patterns of permanent teeth, our findings on dental stages at birth shed light on the pace of development. Some findings are unsurprising. I1 erupts before I2 in virtually all anthropoids (see data compiled by Smith et al., 1994), and I1 is more advanced at birth, as might be expected, based on previous dental eruption studies (e.g., Byrd, 1981). The disparity is great in many cases, with I1 achieving bell stages even before I2 appears as a bud. According to Eaglen (1985), *Lemur catta* may not follow this pattern of eruption, and our results suggest the pace of development of the permanent incisors is generally more synchronous in strepsirrhines, or even reversed compared with anthropoids. In *Tarsius*, I1 is far more advanced compared with the stage of I2 at birth. Compared with I2, the permanent canine is at a more advanced dental stage at birth in many primates. Yet, this tooth erupts after I2 (Smith et al., 1994), indicating that the pace of maturation of these neighboring teeth varies in early postnatal time.

In measurements that assess the pace of eruption (dental precocity) and the ratio of adult occlusal surface area (dental endowment), Godfrey et al. (2003) revealed that lemurids develop their postcanine dentition at a slower pace than indriids or galagids. The overall state of the perinatal dentition, in terms of eruption and maturation of the permanent tooth germs, agrees with this assessment. That the perinatal dentition is generally more precocious in these same taxa, compared with lemurids, suggests these differences arise in a sustained pace initiated during the fetal period. Cheirogaleids and lorises have not received the same attention as larger strepsirrhines. The state of the perinatal dental arcade suggests they are rapid developers (high deciduous maturation indices, multiple cusps piercing gingiva), and are nearly comparable to galagids at birth.

Overall, the perinatal status of dental development (pace of tooth germ maturation and tooth eruption) presumably reflects the balance of the importance of deciduous versus permanent teeth. On the one hand, the deciduous dentition may be important to feeding during the subadult time period. But this is balanced with the degree to which natural selection can potentially produce an advantageous acceleration of the development of permanent teeth. One possible influence on dental

development is life history. Smaller strepsirrhines have advanced maturation of the permanent dentition. However, these primates vary greatly in variables relating to prenatal differentiation and growth, such as relative gestation length (Harvey et al., 1987). Instead, strepsirrhines show remarkable phylogenetic consistency in dental stages across the maxillary dental arcade. In anthropoids, smaller species are generally more advanced at birth, while larger species delay the development of permanent teeth, especially the replacement teeth. Among the species studied here, cercopithecoids present the extreme in delay of maturation of the replacement teeth. Though the sample is limited, it is consistent with previous reports that M1 alone, among permanent teeth, is mineralized at birth in Old World monkeys, apes, and humans (Kraus and Jordan, 1965; Reid et al., 1998; Swindler, 2002).

Our results on *Tarsius* concur with the previous assessment of a precociously developed dentition at birth (Luckett and Maier, 1982). In terms of dental eruption, staging, and mineralization (per maturation indices), their status at birth is nearly as progressed as in *Propithecus*. However, indriids and tarsiers appear exceptional in this perinatal condition, as well as in their continued rapid pace of dental growth and eruption (Godfrey et al., 2001, 2003; Guthrie and Frost, 2011). The variations noted for the remainder of primates, described above, require a more nuanced interpretation of maturation and eruption together. One interpretation of these patterns is that each is a distinct strategy for feeding. Broadly, strepsirrhines have more erupted deciduous teeth at birth, and shed them more quickly than most anthropoids (Godfrey et al., 2001, 2003). Conversely, newborn anthropoids have posterior teeth (dp3 and dp4) that, though generally unerupted, are further progressed in maturation compared with most strepsirrhines. The stellate reticulum of most deciduous teeth is regressed or absent in many anthropoids (excluding some callitrichines, as well as hominoids).

While strepsirrhines vary in their tooth eruption and dental maturation, they differ greatly from anthropoids with respect to maturation, eruption, and emergence of permanent and replacement teeth. The maturation index 1 of strepsirrhines is more than twice that of anthropoids in our sample. This reflects initiation of mineralization of M2 and some of the replacement teeth at birth. Lemurids lag behind other strepsirrhines, with *Lemur, Varecia*, and even *Hapalemur* only mineralizing M1, as in most anthropoids. Yet, in their perinatal dentition, and in their later pace of development (Godfrey et al., 2001), lemurids are atypically slow dental developers. In contrast, mineralization has not extended to any permanent teeth beyond M1 in any anthropoid except *Cebuella*. Conversely, mineralization of deciduous dentition is more progressed, on average, in anthropoids than strepsirrhines (per maturation index 2). Some callitrichines are exceptions, which is unsurprising given the well-known variation in this group at birth (Smith et al., 1994). Yet all other primates have more deciduous teeth in which the first phase of amelogenesis is nearly or entirely complete compared with any of the strepsirrhines except *Propithecus* (and presumably other indriids), *Lemur*, and *Hapalemur*. This suggests that most anthropoids invest heavily in accelerating matura-

tion of deciduous teeth for later use as important transition elements for feeding by subadults.

CONCLUSIONS

In this report we provide data on dental eruption and tooth germ maturation at birth in a broad array of non-human primates. This helps to resolve the bias in the literature as much is known about the dentition of newborn anthropoids and hominoids in particular (Schultz, 1935; Smith et al., 1994; Swindler, 2002), but far less about strepsirrhines or tarsiers.

Results reveal one probable unifying characteristic of living primates: relatively advanced maturation of deciduous teeth and (commonly) M1 at birth. Beyond this, there is great diversity in the status of tooth eruption and maturation (dental stage) in the neonatal primate. When our findings are compared with what is known of postnatal eruption schedules, contrasting strategies in producing a masticatory battery are already apparent at birth in strepsirrhines and anthropoids. The divergent patterns show that accelerating dental maturation or eruption are potentially independent strategies for later feeding independence. The most common strategy in strepsirrhines is accelerating eruption and the maturation of the permanent dentition, including replacement teeth. Anthropoids, with only few exceptions, accelerate mineralization of the deciduous teeth, while delaying development of all permanent teeth except M1.

These results emphasize that no living primate resembles the altricial tree shrew (*Tupaia*) in the pace of dental development. Our preliminary observations suggest that ecological explanations, such as adult diet, may well provide an explanation for certain variations. Some of the dietary adaptations of the teeth, previously noted for folivores, are detectable as early as birth. In particular, this study confirms different patterns of potential adaptations for folivory in *Propithecus* and *Hapalemur* (Godfrey et al., 2003) that are evident by birth. Unlike *Propithecus, Hapalemur* has not initiated development of a replacement premolar at birth, a pattern in keeping with other lemurids. Instead, *Hapalemur* may emphasize early mineralization of cusps, including M1. This pattern may also be shared by folivorous anthropoids. For confirmation, quantitative study of tooth germ size or cusp mineralization in newborn primates is warranted. Ultimately, such quantitative analyses are also needed to detect other potential factors affecting the newborn primate dental arcade, such as phylogenetic influences or constraints relating to overall somatic or regional (e.g., facial) growth patterns.

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APPENDIX 1. Somatic Measurements, Source Information, Preservation, And Postcanine Tooth Maturation for Individuals Specimens Under Study

SN	Species	Source	Pres.	sex	Alt#	AGE (days)	wt	CRL	ST
12-17-01A	*Tupaia belangeri*	DMC	Fl	Sex		1		NA	10
P699	*Cheirogaleus medius*	DLC	Fl	2		1		59.25	10
P1690	*C. medius*	DLC	Fr	1		0		61.54	10
P648	*C. medius*	DLC	Fl	2	CM116656	0		55.11	10
P623	*C. medius*	DLC	Fl	1		0		57.2	10
Ecoll	*Eulemur collaris*	CMZ	Fl	?		prem?		NA	10
P6383	*E. collaris*	DLC	Fl	1	M90308	0		118.99	10
P6799	*E. collaris*	DLC	Fl	2		0	67.5	102.69	10
P6103	*Eulemur coronatus*	DLC	Fl	1		0		98.24	10
P5788	*Eulemur flavifrons*	DLC	Fl	1		0		103.1	10
P6853	*E. flavifrons*	DLC	Fl	2		1		100.6	10
P6778/a	*E. flavifrons*	DLC	Fl	1		1	71g	101.58	12to16
EM1	*Eulemur mongoz*	CMZ	Fl	?		1			10
6426m	*E. mongoz*	DLC	Fr	1		1	58.5g		
P6499	*Eulemur rubriventer*	DLC	Fr	2		2		113.58	10
P3097	*Galagoides demidovii*	DLC	Fr	2		0		51.79	10
P3080	*Galago moholi*	DLC	Fr	1		1		56.84	10
P3148	*G. moholi*	DLC	Fl	2		0		56.05	10
P2046	*G. moholi*	DLC	Fl	1		0		58.63	10
P3077	*G. moholi*	DLC	Fr	1		prem?		43.71	10
LN5006	*Galago senegalensis*	LN	Fr			0		64.03	
LN4010	*G. senegalensis*	LN	Fr			3		55.88	
LN3012	*G. senegalensis*	LN	Fr			0		63.16	
P1308	*Hapalemur griseus*	DLC	Fl	1		0		93.01	10
P1305	*H. griseus*	DLC	Fl	1		0		83.76	10
P2502	*Lemur catta*	DLC	Fl	1		5		106.64	10
P6888	*L. catta*	DLC	Fl	1		1		96.29	10
P2934	*L. catta*	DLC	Fl			late fetal		80.7	10
P2935	*Loris tardigradus*	DLC	Fl			fetal		39.58	10
P384	*Loris tardigradus*	DLC	Fr		CM116670	fetal		46.97	
P385	*Mirza coquereli*	DLC	Fl	2		2		69.4	10
P886	*M. coquereli*	DLC	Fl	1	CM116661	1		60.32	10
P888	*Microcebus murinus*	DLC	Fl	1		1		41.37	10
2918nd	*M. murinus*	DLC	Fr	1	2919nd	0		40.86	
P2919	*Nycticebus pygmaeus*	DLC	Fr	?		0		NA	10
P1478	*N. pygmaeus*	DLC	Fl	?		0		~53	10
P1459	*Otolemur garnettii*	DLC	Fl	2		0		84.64	10
OG101	*O. garnettii*	DLC	Fl	2		0		NA	10 to 12
P2808	*O. garnettii*	DLC	Fl	1		0		82.09	10
P2824	*Otolemur crassicaudatus*	DLC	Fl	1		6		82.55	10
P2822	*O. crassicaudatus*	DLC	Fl	2		0		98.25	10
P2810	*O. crassicaudatus*	DLC	Fl	?		0		NA	10
P6111	*O. crassicaudatus*	DLC	Fl	1		late fetal		84.97	10
P6871	*Propithecus coquereli*	DLC	Fl	1	"P6611"	0		111.18	10
P6154	*P. coquereli*	DLC	Fl	2		late fetal		117.6	10
P6244	*P. coquereli*	DLC	Fl	2	M40501	0		~102.5	10
Vv3	*Varecia rubra*	CMZ	Fl	?		0		127.4	10
P5759	*V. rubra*	DLC	Fl	1		0		NA	10
P2562	*Varecia variegata*	DLC	Fl	2		1		141.07	10
Alleno	*V. variegata*		Fl	?	m81002			113.69	10
Aotus101	*Allenopithecus nigroviridis*	Dumond	Fr	?		0?	58g	78.27	10
Alouatta4	*Aotus nancymaae*	DWA	Fl	?		0?			10
Alouatta3	*Aouatta seniculus*	DWA	Fl	?		fetal		81.49	10
Alouatta2	*A. seniculus*	DWA	Fl	?		fetal	120g	118.47	10
Cc1	*A. seniculus*	Dumond	Fr	?		still	41.5 g	92.03	10
MM0802	*Callicebus cupreus*	CMZ	Fl	2		0			
CJ101	*Colobus guereza*	WRPC	Fl	2		0?			10
CJ102	*Callithrix jacchus*	WRPC	Fl	?		0?			
Cj1155	*C. jacchus*	WRPC	Fl	1	(04c027)	0?			10
Cj1136	*C. jacchus*	WRPC	Fl	2	(04c029)	0			10
Cj1161	*C. jacchus*	WRPC	Fl	1	(04c034)	0			10
Cj1140	*C. jacchus*	WRPC	Fl	2	(04c033)	0			10
Cp1	*Cebuella pygmaea*	PZ	Fl	2	34114	0?	0.05 lbs	?	10
CP9	*C. pygmaea*	DWA	Fl	1		0?			10
CP15	*C. pygmaea*	DWA	Fl	1		5d	25.35	65.6	10
CP17	*C. pygmaea*	DWA	Fl						
lr1	*Leontopithecus rosalia*	CMZ	Fl	2	MM1110	3	48g	60.68	10

APPENDIX 1. (continued).

SN	Species	Source	Pres.	sex	Alt#	AGE (days)	wt	CRL	ST
lr2	L. rosalia	CMZ	Fl	1	MM1111	4	50g	~115	10 to 12
LR9	L. rosalia	CMZ	Fl	2	M40202	0	74g	~100	10
LR8	L. rosalia	CMZ	Fl	2	M20402	5	59g	~100	10
LR10	L. rosalia	CMZ	Fl	2	m31001	3	62g	~110	10
LR11	L. rosalia	DWA	Fl	?		0?		98.47	10
YN09-175	Macaca mulatta	YRPC	Fl	1		0?			10
Saki2	Pithecia pithecia	CMZ	Fl	1		2?		121.97	10
Sq101	Saimiri boliviensis	USA	Fl	1		0	126g	132	10
Sq102	S. boliviensis	MK	Fl	1	Ss2672	prem	66g	112	10
Ss2662	S. boliviensis	MK	Fl	1	Ss2671	0	?	128	10
Ss4238	S. boliviensis	MK	Fl	1		0			10
Ss4257	S. boliviensis	MK	Fl	?		0?			10
Ss4269	S. boliviensis	MK	Fl	1		0			10
Ss5021	S. boliviensis	MK	Fl	2		0	91g	125	10
Sb1	Saguinus bicolor	CMZ	Fl	2	M31107	0	38g	90	10
Sb3	S. bicolor	CMZ	Fl	1	10330	0		~110	12
SG4	Saguinus geoffroyi	CMZ	Fl	2	MM0880	0	52g		10 to 14
SG3	S. geoffroyi	CMZ	Fl	?	M10417	0			10
sg5	S. geoffroyi	CMZ	Fl	2	M40308	0	40 g	~100	
SG11	S. geoffroyi	CMZ	Fl	2	M40309	0	59g	~115	10
SG12	S. geoffroyi	CMZ	Fl	2	M30921	4	66g	~100	
SG13	S. geoffroyi	GPZ	Fl	2	10672	0		92.45	
Smid2	Saguinus midas	DWA	Fl	2		0		87.57	
Smid5	S. midas	DWA	Fl	?		0			
Smid7	S. midas	NEPC	Fl	?		0			
So103	Saguinus oedipus	NEPC	Fl	2	A03-642	0			10
So104	S. oedipus	NEPC	Fl	?	A03-644	0			10
So108	S. oedipus	NEPC	Fl	1	A06-355	0		92.1	10
So109	S. oedipus	NEPC	Fl	2	A06-334	0/1 d		84.37	10
So110	S. oedipus	NEPC	Fl	1	A06-356	0		85.11	10
So112	S. oedipus	NEPC	Fl	1	AO3-618	0			10
LM13	Tarsius bancanus	LM	Fr	1	CM116671	1	37.5 g	57.7	
P93	T. syrichta	DLC	Fl	2	Ts4	late fetal		48.53	10
P96	T. syrichta	DLC	Fl	?	P94	0			10
P94R	T. syrichta	DLC	Fl	1		6			right:10; left: 12
P98	T. syrichta	DLC	Fl	2	m80806	2			10
TF1	Trachypithecus francoisi	CMZ	Fl						

SN	dp2 stage	dp3 stage	dp4 stage	M1 stage	M2 stage	P2 stage	P3 stage	P4 stage	Comments
12-17-01A	late bell	late bell	late bell	late bell	cap	TDL	NO	TDL	
P699	RSR	late bell[b]	late bell[b]	late bell	early bell	late bell	bud	bud	
P1690	RSR	late bell[b] (dam.)	late bell[b] (dam.)	late bell	early bell?(dam.)	late bell	(dam.)	(dam.)	
P648	RSR	Late bell[b]	Late bell[b] (dam.)	NA	NA	Late bell	Bud	NA	No age recorded; small compared with P0 specimens; premature?
P623	E	Late bell	Late bell	Late bell	Late bell	Late bell	Bud	Damage	
Ecoll	Late bell	Late bell	Late bell	Late bell	No	No	No	NO	
P6383	Late bell[b]	Late bell	Late bell	Late bell	Cap?(dam.)	Bud(dam.)	Bud(dam.)	Bud(dam.)	
P6799	Late bell[b]	Late bell	Late bell	Late bell	NO	?(Dam.)	TDL(dam.)	NO	
P6103	Late bell[b]	Late bell	Late bell	Late bell	cap	Bud(dam.)	Bud(dam.)	Bud(dam.)	
P5788	Late bell (dam.)	Late bell	Late bell	Late bell	NO	?(Dam.)	?(dam.)	?(dam.)	
P6853	Late bell (dam.)	Late bell	Late bell	Late bell	TDL	Bud	NO	NO	
P6778/a	Late bell[b]	Late bell	Late bell	Late bell	cap	Cap	NO	NO	
EM1	Late bell[b]	Late bell	Late bell	NA	NA	TDL	NO	NO	
6426m	CrCu	CrCu	PC+Cu	Cut(3)	NO	NO	NO	NO	CT-only
P6499	late bell (dam.)	late bell	late bell	late bell	NA	TDL(dam.)	NO	TDL	Facial trauma; teeth intact
P3097	RSR	Late bell	Late bell[b]	Late bell	Late bell	Early bell	Bud	Cap	
P3080	E	Late bell	Late bell[b]	Late bell	Late bell	Late bell	Bud	Bud	

APPENDIX 1. (continued).

SN	Species	Source	Pres.	sex	Alt#	AGE (days)	wt	CRL	ST
P3148	RSR	Late bell[b]	Late bell[b]	(Dam.)	Late bell	Late bell	Bud	Bud	Undersized body compared with other perinatal specimens
P2046	RSR	Late bell	Late bell[b]	Late bell	Late bell	Late bell	Cap	Cap(dam.)	
P3077	RSR	Late bell? (dam.)	Late bell[b] (dam.)	Late bell	NA	late bell	?(dam.)	?(dam.)	CT-only
LN5006	CrCu	CrCu	PCrCu	Cu	Cu	NO	NO	NO	CT-only
LN4010	CrCu	CrCu	PCrCu	Cu	Cu	NO	NO	NO	CT-only
LN3012	RSR	Late bell? (dam.)	Late bell[b] (dam.)	Late bell	Late bell	Early bell? (dam.)	? (dam.)	? (dam.)	SR likely damaged by freezing, but IEE/OEE fused in dp2; gap between IEE and OEE suggests presence of SR in dp3 and dp4 (only in distal half in dp4).
P1308	RSR	RSR	RSR	Late bell	cap	TDL	NO	NO	OEE and IEE are fused throughout most of perimeter of dp2-4
P1305	RSR	RSR	RSR	Late bell		TDL	TDL	NO	OEE and IEE are fused throughout most of perimeter of dp2-4
P6834	RSR	RSR	Late bell[b]	Late bell	NO	TDL	TDL	TDL	
P2502	late bell[b]	RSR	Late bell[b]	Late bell	NO	TDL	TDL	TDL	
P6888	late bell	Late bell	Late bell	Late bell[a]	NO	NO	NO	NO	
P2934	late bell	Late bell	Late bell	Late bell	early bell	early bell	NO	NO	CT only
P2935	CrCu	CrCu	CrCu	Cu	Cu	Cu	NO	TDL	
P384	RSR	Late bell	Late bell	Late bell	Late bell	Cap	NO	TDL	
P385	RSR	Late bell	Late bell	Late bell	Early bell	Cap	NO	Bud	
P886	CrCu	Late bell	Late bell	Late bell	Late bell	Early bell	Bud	NO	
P888	CrCu	CrCu	PCrCu	Cu	Cu	NO	NO	NO	CT only
2918nd	CrCu	CrCu	CrCu	Cut(3)	NO	CrCu	?	?	
P2919	late bell?	Late bell?	Late bell?	Late bell?	NA	Late bell	NO	TDL	
P1478	RSR	Late bell	Late bell	Late bell	Late bell	Late bell	NO	Bud	
P1459	RSR	Late bell	Late bell[b]	Late bell	Late bell	Late bell	NO	Bud	
OG101	RSR	Late bell	Late bell[b]	Late bell	NA	Late bell	TDL	Bud	
P2808	RSR	Late bell	Late bell[b]?(dam.)	Late bell	late bell	late bell	bud(dam.)	TDL	
P2824	RSR	Late bell	Late bell[b]	Late bell	NO	late bell	bud(dam.)	TDL	
P2822	CrCu	CrCu	PCrCu	Cut(3)	NO	PCrCu	NO	NO	CT-only specimen and sibling were still enclosed within fetal membranes
P2810	Late bell[b]	Late bell	Late bell	Late bell	Early bell	early bell	TDL	NO	
P6111	shed	E	E	Late bell	Late bell		late bell	late bell	
P6871	shed	E	E	Late bell	Late bell		late bell?(dam.)	late bell?(dam.)	
P6154	E	RSR	RSR	Late bell[a]	Late bell	cap(dam.)	cap	late bell[a]	
P6244	Late bell	Late bell	Late bell	Late bell[a]	NO	TDL	TDL(dam.)	TDL(dam.)	
Vv3	Late bell	Late bell	Late bell	Late bell[a]	NO	TDL(dam.)	TDL	TDL	
P5759	Late bell	Late bell	NA	NA	NA	NA	NA	NA	
P2562 Allen o	Late bell	RSR	late bell[b] (dam.)	Late bell	NO		NO	NO	SR unclear, but enamel epithelia fused in dp3; CT evidence: M1 has multiple cusps mineralized, but not basin - late bell.
Aotus101	RSR	RSR	RSR	Late bell	early bell	TDL	TDL	NO	stillborn; small for birth size,

APPENDIX 1. (continued).

SN	Species	Source	Pres.	sex	Alt#	AGE (days)	wt	CRL	ST
Alouatta4	RSR	RSR	Late bell	Late bell	NO	TDL	NO	NO	per Dumond conservancy records
Alouatta3	late bell[a]	Early bell	Late bell[a]	Cap	NO	NO	NO	NO	
Alouatta2	late bell	Late bell	Late bell	Late bell[a]	NO	NO	NO	NO	postmortem, fixed weight recorded
Cc1	CrCu	CrCu	PCrCu	Cut(1)	NA	NA	NA	NA	CT-only; small for birth size, per Dumond conservancy records
MM0802		RSR	RSR	late bell	NO		NO	NO	lateral part of dp3 missing from sections, but the portion that is present lacks SR
CJ101	late bell[b]	Late bell	Late bell	Late bell	TDL	TDL	NO	NO	dental only on rt M1 paracone; perhaps first enamel on left M1 para
CJ102	late bell	Late bell	(dam.)	(dam.)	(dam.)	NO	NO	(dam.)	
Cj1155	late bell	Late bell	Late bell	Early bell	(dam.)	NO	NO	NO	
Cj1136	RSR	Late bell[b]	Late bell	Late bell	NO	NO	NO	NO	
Cj1161	late bell	Late bell	Late bell	Early bell	NO	NO	NO	NO	
Cj1140	late bell	Late bell	Late bell	Late bell	TDL	NO	NO	TDL	
Cp1	RSR	RSR	RSR	Late bell	NO	NO	TDL	NO	
CP9	CrCu	CrCu	CrCu	Cut(1)	NO	NO	NO	NO	
CP15	CrCu	CrCu	PCrCu	NO	NO	TDL	TDL	bud	
CP17	RSR	RSR	RSR	late bell	NO	TDL	NO	NO	CT only
lr1	RSR	RSR	late bell	late bell[a] (chk 1060)	NO	TDL	NO	NO	CT only
lr2	RSR	(Dam.)	Late bell	Late bell[a]	TDL	TDL	TDL	TDL	
LR9	late bell[b] (dam.)	Late bell[b] (dam.)	Late bell(dam.)	Late bell[a]	TDL	TDL	TDL	NO	
LR8	RSR	RSR	Late bell[b]	Early bell	NO	TDL	NO	TDL	
LR10	RSR	Late bell[b]	Late bell[b]	Late bell[b]	(dam.)	NO	NO	(dam.)	
LR11	RSR	Late bell[b]	Late bell[b]	Late bell[a]	(dam.)	TDL	TDL	NO	
YN09-175		Late bell[b] (dam.)	Late bell[b] (dam.)	Late bell (dam.)	?	NO	?	?	(Hematoma at occiput may have inflated PrIn)
Saki2	RSR	RSR	RSR	Late bell	early bell	NO	TDL	NO	
Sq101	RSR	RSR	Late bell[b]	Late bell	NO	NO	NO	NO	Necropsy notes: term stillbirth
Sq102	Late bell	Late bell	Late bell	Late bell[a]	NO	NO	NO	NO	Necropsy notes: premature stillbirth
Ss2662	Late bell[b]	Late bell[b]	Late bell	Late bell	bud	TDL	TDL	NO	Necropsy notes: "live birth; rejected"
Ss4238	Late bell[b]	RSR	Late bell[b]	Late bell	(dam.)	TDL	TDL	NO	
Ss4257	Late bell[b]	Late bell[b]	Late bell	Late bell	cap	cap	TDL	TDL	
Ss4269	RSR	RSR	Late bell[b]	Late bell	cap	TDL	NO	NO	
Ss5021	CrCu	CrCu	CrCu	Cut(3)	NO	NO	(dam.)	NO	
Sb1	Late bell	Late bell	(dam.)	(dam.)	(dam.)	(dam.)	(dam.)	(dam.)	
Sb3	Late bell	Late bell	NA	NA	NA	NO	NA	NA	
SG4	Late bell	Late bell	late bell	Early bell	NO	NO	NO	NO	
SG3	Late bell	Late bell	late bell	Early bell	(dam.)	NO	NO	NO	
sg5	Late bell[b]	NA	NA	NA	NA	NA	NA	NA	
SG11	Late bell[b]	Late bell	Late bell	Early bell	NA	NO	NO	(dam.)	
SG12	Late bell	Late bell	Late bell(dam.)	NA	(dam.)	NO	NO	(dam.)	
SG13	Late bell	Late bell	Late bell	(dam.)	NO	NO	NO	(dam.)	
Smid2	CrCu	CrCu	PCrCu	NO	NO	NO	NO	NO	
Smid5	CrCu	CrCu	PCrCu	NO	NO	NO	NO	NO	CT only

APPENDIX 1. (continued).

SN	Species	Source	Pres.	sex	Alt#	AGE (days)	wt	CRL	ST
Smid7	CrCu	CrCu	PCrCu	NO	NO	NO	NO	NO	CT only
So103	Late bell	Late bell	Late bell	Late bell[a]	NO	NO	NO	NO	CT only
So104	Late bell	Late bell	Late bell	Early bell	NO	NO	cap	cap	Necropsy notes:c-section (dam could not deliver); both R & L M1 at early bell stage
So108	Late bell	Late bell	Late bell	Early bell	NO	NO	NO	NO	
So109	Late bell	Late bell	Late bell	Early bell	NO	NO	NO	NO	
So110	Late bell[b] (dam.)	Late bell	Late bell	Early bell	NO	NO	NO	NO	
So112	Late bell[b]	Late bell[b]	Late bell	Late bell[a]	NO	TDL	NO	NO	
LM13	Shed	CrCu	CrCu	PCrCu	Cu	CrCu	PCrCu	PCrCu	CT only
P93	Shed	CrCu	CrCu	PCrCu	Cu	PCrCu	PCrCu	PCrCu	CT only
P96	Shed	RSR	RSR	late bell	Late bell	Late bell	Early bell	Early bell	Specimen stored within fetal membranes
P94R	Shed	E	E	late bell	Late bell	Late bell	Late bell	Late bell	
P98	Shed	E	E	late bell[b]	Late bell	Late bell	late bell	Late bell	
TF1		RSR	late bell[b]	late bell	NO		NO	NO	

[a]Initial mineralization of a cusp (beginning late bell stage):?, unknown or tentative assessment.

[b]In one or more specimens the SR (stellate reticulum) is restricted to approximately the distal half of tooth germ.

SN, specimen number; pres., initial method of preservation; Alt#, alternative specimen name; CRL, crown-rump length; PrIn, cranial length (prosthion-inion); BZW, byzygomatic width. CMZ, Cleveland Metroparks Zoo; DWA, Dallas World Aquarium; DLC, Duke Lemur Center; Dumond, Dumond Conservancy; GPZ, Gladys Porter Zoo; LN, laboratory of Leanne T. Nash; MK, Michale E. Keeling Center for Comparative Medicine and Research; NEPC, New England Primate Research Center; PZ, Philadelphia Zoo; WRPC, Wisconsin National Primate Research Center; YRPC, Yerkes Regional Primate Research Center. CM, Carnegie Museum; IEE, inner enamel epithelium; OEE, outer enamel epithelium; P0, postnatal age at day 0. Tooth stage abbreviations: dam. (damage due to artifact or poor preservation prevented determination); E, gingival emergence; NA, material not available; NO, not observed; RSR, stellate reticulum is nearly or completely regressed; TDL, thickened dental lamina.