

Dental Eruption Sequences in Fossil Colobines and the Evolution of Primate Life Histories

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Abstract Unlike other catarrhines, colobines show early molar eruption relative to that of the anterior dentition. The pattern is variable, with Asian genera (Presbytina) showing a greater variability than the African genera (Colobina). The polarity of early relative molar eruption, as well as the degree to which it is related to phylogeny, are unclear. Schultz (1935) suggested that the trend reflects phylogeny and is primitive for catarrhines. More recently, however, researchers have proposed that life history and dietary hypotheses account for early relative molar eruption. If the colobine eruption pattern is primitive for catarrhines, it implies that cercopithecines and hominoids converged on delayed relative molar eruption. Alternatively, if the colobine condition is derived, factors such as diet and mortality patterns probably shaped colobine eruption patterns. Here we update our knowledge on eruption sequences of living colobines, and explore the evolutionary history of the colobine dental eruption pattern by examining fossil colobine taxa from Eurasia (*Mesopithecus*) and Africa (*Kuseracolobus aramisi* and *Colobus* sp.) and the basal cercopithecoid *Victoriapithecus macinnesi*. We scored specimens per Harvati (2000). The Late Miocene-Early Pliocene *Mesopithecus* erupts the second molar early relative to the incisors, while the Early Pliocene *Kuseracolobus aramisi* does not. These results demonstrate that the common colobine tendency for early molar eruption relative to the anterior dentition had appeared by the Late Miocene, and that some of the diversity observed among living colobines was already established in the Late Miocene/Early Pliocene. We discuss the implications of these results for phylogenetic, life history, and dietary hypotheses of dental development.

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Introduction

Colobines are distinctive among catarrhines in the early eruption of their molars relative to anterior teeth (Schultz 1935; Harvati 2000). Dental development and eruption sequences are often considered useful indicators of life history (Smith 1989, 1994), and researchers have proposed early eruption of the molars relative to the replacement dentition to indicate a generally accelerated life history among various mammals (Smith 2000), a pattern often referred to as Schultz's rule. According to this rule, colobine dental eruption sequences should indicate that these primates are characterized by fast life history profiles relative to other catarrhines.

We know very little about life history variables in colobines, i.e., age at first birth, interbirth intervals, etc. However, available evidence suggests that they possess small brains relative to those of other catarrhines of similar body size (Clutton-Brock and Harvey 1980; Godfrey *et al.* 2001; Harvey *et al.* 1987). As brain size is thought to be highly correlated with other life history parameters, a smaller brain size for colobines would also indicate faster life history. Further, colobines show faster growth rates both in body size (Leigh 1994) and in their dentition (Dirks 2000, 2003), which indicates that colobines may indeed have relatively accelerated life history vs. that of other catarrhines. Researchers have in turn interpreted their presumed fast life history profile as possibly related to their highly folivorous diets (Dirks 2000, 2003; Leigh 1994).

Because of their proposed close relationship with life history profiles, dental eruption sequences have played a role in the discussion of the evolution of life history in primates, though the degree to which they accurately reflect phylogeny is debated (Smith 1994). Schultz (1935, 1960) considered the early eruption of the molars relative to the anterior dentition and the faster life history that he thought it implied to be primitive for primates, with higher primates showing a more delayed relative molar eruption, earlier appearance of replacement teeth and concomitant slower general growth. In this view, the colobine eruption pattern would be primitive for catarrhines, implying that cercopithecines and hominoids independently acquired a similar eruption sequence and slower growth rates. Alternatively, if the colobine pattern is derived then the highly variable colobine eruption sequences may be responses to factors such as diet and mortality patterns, and may also indicate that eruption sequences are relatively labile and not good indicators of phylogeny (Smith 1994).

To further evaluate the evolutionary history of colobine dental eruption patterns, we examined fossil colobines from 3 genera preserving juvenile specimens of informative dental eruption stages to establish their dental eruption sequences: the Eurasian Late Miocene-Early Pliocene taxon *Mesopithecus* (including both *M. pentelicus* and *M. monspesselanus*), African Early Pliocene *Kuseracolobus aramisi*, and Pleistocene and possibly Pliocene specimens of *Colobus* sp. We also examined the basal cercopithecoid *Victoriapithecus macinnesi* (Table I). Furthermore, we report additional eruption sequence data on the extant colobine taxa *Nasalis larvatus*, *Procolobus badius* and *Procolobus verus*, which adds to the known variation of colobines and will help to clarify the relationship between dental eruption and life history patterns in these primates.

Materials

If we were unable to examine original specimens of the 3 fossil colobine taxa and *Victoriapithecus*, we used casts provided by Eric Delson (Table I). We included in the analysis 3 additional specimens that Zapfe (1991) discussed and clearly illustrated. *Mesopithecus* includes 2 species: *M. pentelicus* and *M. monspesselanus*. *Mesopithecus pentelicus* is geologically the oldest colobine from Eurasia, and may represent the oldest colobine globally depending on the provenance of 1 specimen from Wissberg, Germany (Andrews *et al.* 1996). It is best known from a large series of material from the Late Miocene locality of Pikermi, Greece. Pikermi is Middle

Table I Fossil specimens used in this study, presented by taxon, sex, anatomical element, geological age, and locality

Specimen	Institution	Anatomical element	Sex	Geological age	Locality
<i>Mesopithecus</i> spp.					
Unnumbered ^a	MNHN-P	Mand	m		Moloyan, Afghanistan
NHM M8957 ^a	NHM	Mand	u	ca. 8 Ma	Pikermi, Greece
Unnumbered-1 ^a	NHMW	Mand	f	ca. 8 Ma	Pikermi, Greece
UM-4001 ^a	Univ. Montpellier	Mand	f	ca. 4 Ma	Montpellier, France
BSM AS II 15 ^a	BSPHGM	Mand	u	ca. 8 Ma	Pikermi, Greece
1839/3939 ^a	SMNS	Max	m	ca. 8 Ma	Pikermi, Greece
BSM AS II 607 ^b	BSPHGM	Mand	u	ca. 8 Ma	Pikermi, Greece
Unnumbered-2 ^b	NHMW	Mand	m	ca. 8 Ma	Pikermi, Greece
Athens 29 ^b	Univ. Athens	Max	f	ca. 8 Ma	Pikermi, Greece
<i>Kuseracolobus aramisi</i>					
NME ARA-VP-1/2978	NME	Mand	u	4.4 Ma	Aramis, Ethiopia
NME ARA-VP-1/2696	NME	Max	f?	4.4 Ma	Aramis, Ethiopia
<i>Colobus</i> sp.					
BMNH M15911	NHM	Mand	u	ca. 3 or 1.5 Ma	Kanam East, Kenya
NME KL188-3	NME	Mand	m	ca. 0.25 Ma	Andalee, Ethiopia
<i>Victoriapithecus macinesi</i>					
KNM-MB 18815	KMN	Mand	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 315	KMN	Max	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 21020	KMN	Max	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 21033	KMN	Mand	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 21021	KMN	Mand	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 14301	KMN	Mand	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 14314	KMN	Max	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 11647	KMN	Mand	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 18794	KMN	Max	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 31303	KMN	Max	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 31306	KMN	Max	u	>14.7 Ma	Maboko Isl., Kenya
KNM-MB 9444	KMN	Mand	u	>14.7 Ma	Maboko Isl., Kenya

^a Specimens for which casts were used.

^b Indicates specimens described and illustrated in Zapfe (1991), pp. 34–36.

NHM = Natural History Museum, London; BSPHGM = Bayerisches Staatssammlung für Historische Geologie und Paläontologie, München; KNM = Kenya National Museums; NHMW = Naturhistorisches Museum Wien; NME = National Museum of Ethiopia; SMNS = Städtisches Museum der Naturkunde, Stuttgart.

Turolian (MN 12) or *ca.* 8 Ma in age (Zapfe 1991; Andrews *et al.* 1996). The date puts *Mesopithecus* close to the divergence time between African and Asian colobines, as recently estimated by mtDNA (Sterner *et al.* 2006). *Mesopithecus pentelicus* is from European and Western Asian localities (Andrews *et al.* 1996; Jablonski 2002; Szalay and Delson 1979). *Mesopithecus monspesselanus* is from a series of Early to Middle Pliocene (MN 14–16) localities in Europe. All of the informative material included in our study derives from Pikermi, with 2 exceptions: a mandible from Moloyan Afghanistan assigned to *Mesopithecus pentelicus* (Heintz *et al.* 1981), and UM 4001, which represents *M. monspesselanus*, from the Early Pliocene site of Montpellier, France. Because the eruption sequence data preserved in the latter specimens, albeit incompletely, is consistent with that from the Pikermi series, we pooled the 2 taxa.

Researchers have assessed aspects of the paleobiology of *Mesopithecus pentelicus* on the basis of the large series from Pikermi. Delson *et al.* (2000) estimated population means for body mass for the series utilizing cranial, dental, and post-cranial material. They calculated mean body masses of 13 (range 10–15 kg) and 9 (range 7–11 kg) for males and females, respectively. Several authors have considered *Mesopithecus pentelicus* to be more semiterrestrial in locomotor behavior than most extant colobines—perhaps more similar to extant *Semnopithecus entellus*—on the basis of limb proportions, elbow, calcaneal, and phalangeal morphology (Szalay and Delson 1979; Youlatos 2003; *cf.* Escarguel 2005). Reitz (2001; see also Reitz and Benefit 2001) estimated paleodiets for *Mesopithecus pentelicus* from molar morphology and microwear, both of which indicate that fruit may have predominated over leaves in the diet.

Kuseracolobus aramisi is from the Middle Awash and Gona areas of the Afar Depression in Ethiopia (Frost 2001a; Frost *et al.* in press; Semaw *et al.* 2005). It derives from stratigraphic intervals ranging from 5.2 to 4.4 Ma, with more fragmentary material possibly extending the range to 5.7–4.2 Ma. Frost (2001a) estimated mean male and female body masses of 18 (range 14–22 kg) and 12 (range 10–14 kg), respectively, via the equations of Delson *et al.* (2000) on the basis of dental material from the Aramis Member of the Sagantole Formation. This is where the largest sample, including the informative juvenile material used here, derives from. Two distal humeral fragments and an astragalus have been tentatively allocated to *Kuseracolobus* from the late Miocene deposits. Elbow morphology suggests that they may have been comparable to most extant colobines in the use of arboreal positional behaviors (Frost *et al.* in press). Paleodiet has not been estimated for this taxon.

We included 2 fossil specimens that can be allocated to the extant genus *Colobus*—to the exclusion of *Procolobus*—in our analysis (Table 1). Neither can be definitively diagnosed to species, nor is there any indication that they are conspecific. NME KL188-3 is from Middle Pleistocene sediments in the Middle Awash (Kalb *et al.* 1982). Morphologically, it is unlikely to represent *Colobus guereza*, but it is otherwise unclear whether it represents another extant species such as *C. angolensis* or an extinct form (Frost 2001b). NHM M15911 is from Kanam East, Kenya and is also of uncertain specific affinity (Harrison and Harris 1996). In addition, it is of uncertain provenance within the strata at Kanam. It may be either Middle Pliocene age, perhaps as early as 3 Ma, or may date to the Early Pleistocene (Plummer *pers. comm.*).

Victoriapithecus macinnesi is a basal cercopithecoid from the Middle Miocene deposits at Maboko, Kenya, dated to *ca.* 14.7 Ma (Benefit 1999). Other taxa assigned to the Victoriapithecinae are from Early and Middle Miocene localities in eastern and northern Africa (Benefit and McCrossin 2002; Szalay and Delson 1979). Researchers have estimated several aspects of the paleobiology of *Victoriapithecus macinnesi*. Delson *et al.* (2000) produced a combined-sex estimate of 8.5 kg (range 6.5–11.5) on the basis of the taxon's dentition, and an estimate of 6 kg on the basis of the only known male cranium. Harrison (1989) estimated a combined-sex specific mean similar to extant *Cercopithecus* spp., *ca.* 3.5–5 kg based on rough comparison of postcranial elements to extant taxa. Delson *et al.* (2000) concurred with previous assessments that the species is relatively megadont (Benefit and McCrossin 1997), and that an overall combined-sex mean of *ca.* 7 kg is reasonable.

An analysis of several, mostly fragmentary, elements of the postcranium estimated the positional and locomotor behavior of *Victoriapithecus macinnesi* to be similar to that of other semiterrestrial cercopithecoids, perhaps not unlike the comparably-sized *Chlorocebus aethiops* (Harrison 1989). Analysis of functional aspects of the molar tooth morphology suggested that the annual diet of *Victoriapithecus macinnesi* consisted primarily of fruits (Benefit 1999, 2000). Microwear data are most similar to those of hard-object feeders and frugivores (Benefit 1999; Palmer *et al.* 1998; Ungar and Teaford 1996).

We also report additional data for 3 extant colobine species: *Nasalis larvatus*, *Procolobus verus* and *Procolobus badius* (Table II). Harvati (2000) established an incomplete sequence for *Nasalis* based on a small number of specimens. The reported sequence suggested an eruption pattern for them that differs markedly from that of other colobines and that resembles a cercopithecine pattern. Because this was one of the most intriguing results of Harvati (2000), we expanded the sample of *Nasalis* to include 2 specimens from the Natural History Museum London (NHM), which helped to complete the eruption sequence and confirmed the previous result. Harvati (2000) also pooled *Procolobus badius* and *P. verus* in her analysis owing to the very small sample for the latter taxon (only 2 specimens). However, the 2 taxa are different in body size. *Procolobus verus* is the smallest living colobine at 4.4 kg for males and 4 kg for females, whereas averages for male and female *P. badius* are 8.7 and 7.2 kg, respectively (Delson *et al.* 2000; Godfrey *et al.* 2001). Some authors have separated the taxa subgenerically (Delson 2000; Grubb *et al.* 2003) and others generically (Fleagle 1999). To evaluate better the relationship between body size and dental eruption sequence we expanded the sample of *Procolobus verus* to include 4

Table II Numbers of specimens of extant colobines for which expanded sequences are reported

	Females	Males	Unknown sex	Total	Institution
<i>Nasalis larvatus</i>	6	9		15	AMNH, NMNH, NHM
<i>Procolobus badius</i>	15	8	4	27	AMNH, NMNH
<i>Procolobus verus</i>	5	1		6	NMNH, NHM

Abbreviations as in Table I and AMNH = American Museum of Natural History, New York, NMNH = National Museum of Natural History, Washington, DC.

specimens from the NHM and established separate eruption sequences for the 2 *Procolobus* spp.

Methods

We scored specimens per Harvati (2000). We scored a tooth as emerging when any part of the crown had risen above the alveolar margin. We further scored teeth showing an intermediate level of eruption—between emerging and full occlusion—to 1/3, 1/2, and 2/3 of the way to full occlusion. When the 2 sides showed different stages of eruption, we scored the most advanced condition for each tooth. Finally, we determined precedence in the sequence as follows. We considered that one tooth preceded another if either: 1) one was present and the other absent or 2) both teeth had emerged but there was a difference of at least a half step to full occlusion between them. Because we did not know the sex of the specimens in most cases owing to their youth, we pooled males and females. Upper and lower jaws from the same individual did not occur for any of the fossil material. It was therefore not possible to estimate the eruption sequence of the upper relative to the lower permanent teeth.

Owing to the small number of informative juvenile specimens, we were not able to determine the full sequence of eruption for the fossil species. In the case of *Victoriapithecus macinnesi* and *Colobus* sp., no juvenile specimen preserved permanent anterior dentition in combination with molars in intermediate stages of eruption, or vice versa. It was therefore impossible to determine whether the taxa exhibited a trend for early molar eruption relative to the anterior teeth. For the 2 remaining species, it was possible to determine the relative sequence of the molars and the incisors, even if their eruption sequence remains incomplete. Some parts of the eruption sequences for which no specimen was available are very stable among catarrhines including colobines, e.g., the position of the first molar, which is always the first permanent tooth to emerge in nonhuman catarrhines (Harvati 2000; Smith 1994, 2000; Swindler 2005). The position of the molars relative to each other is also always in sequence (M1 M2 M3), as is that of the central and lateral incisors (I1 I2) (Harvati 2000; Smith 1994, 2000; Swindler 2005). If not known from the specimens examined, we filled out these parts of the sequence based on the invariable catarrhine patterns and report them in italics. The sequence of the premolars relative to each other is highly variable within catarrhines, including colobines (Harvati 2000; Smith 1994, 2000), and we could not determine it for any of the fossil taxa or for upper jaws of *Nasalis* and *Procolobus verus*. When their relative sequence was unknown, we represented premolars in the sequences as a unit: PP. We left parts of the sequence that are unknown from the fossil evidence and are variable in catarrhines/colobines empty. When possible, we present the sequences in the form of augmented sequences (Harvati 2000; Smith 1994, 2000), which indicate variability among specimens of the same taxon: the order in which a sequence is presented is the most common, and brackets indicate sequence polymorphisms. Finally, for the 3 living colobine samples, we also present eruption sequence data in the form of matrices showing the frequency of both alternative sequences for any 2 teeth, i.e., A before B or B before A, and sample sizes for any given position and polymorphism

per Harvati (2000) and [Smith (1994) Appendix]. Because the number of fossil specimens is very small, we compiled no matrix for fossil taxa.

Table III Expanded eruption sequences for *Nasalis larvatus*, *Procolobus verus*, and *Procolobus badius* and tentative eruption sequences established for the 4 fossil primate taxa examined (marked *)

<i>Nasalis larvatus</i>	<u>M¹ I¹ I² M² PP C M³</u>
	M ₁ I ₁ I ₂ M ₂ [PP C] M ₃
<i>Procolobus verus</i>	<u>M¹ I¹ M² I² PP C M³</u>
	M ₁ I ₁ M ₂ I ₂ P ₃ P ₄ C M ₃
<i>Procolobus badius</i>	<u>M¹ [I¹ M²] I² [P³P⁴] [C M³]</u>
	M ₁ [I ₁ I ₂ M ₂] [P ₄ P ₃] [C M ₃]
* <i>Mesopithecus</i>	<u>M¹ I¹ M² PP I² C M³</u>
	M ₁ I ₁ M ₂ I ₂ PP C M ₃
* <i>Kuseracolobus</i>	<u>M¹ I¹ I² M² M³</u>
	M ₁ I ₁ I ₂ M ₂ M ₃
* <i>Colobus</i>	<u>M₁ M₂ PP C M₃</u>
	M ₁ M ₂ PP
* <i>Victoriapithecus</i>	<u>M¹ M² PP M³</u>
	M ₁ M ₂ PP

See text for further explanation.

Results

Nasalis larvatus

The 2 specimens from the Natural History Museum, London (NHM) confirmed Harvati's (2000) previous finding of no early eruption of the second molar relative to the incisors in either upper or lower jaw for *Nasalis*. They also provided information on some previously uncertain parts of the sequence. The updated sequence is in Table III, and the updated sequence matrix is in the Appendix.

Procolobus (Procolobus) verus

Though still very small, the new sample of 6 specimens was enough to allow us to determine an eruption sequence for *Procolobus verus* (Table III). M2 erupted before the second incisor in both jaws in 3 maxillae and 1 mandible. No specimen was informative for the relative sequence of I1 and M2. The most common catarrhine condition of I1 precedence for this position in both jaws (as indicated by italics) is therefore shown in Table III. We could establish no precedence for the upper premolars. In the only informative lower jaw, P₃ erupted before P₄. Finally, no tendency was present for the M3 to erupt before the canine in either jaw. However, there were only 2 female upper and 1 lower jaw for the position.

Procolobus (Piliocolobus) badius

Procolobus badius has a very similar sequence to the combined generic sequence reported by Harvati (2000). The position of the second molar is variable in both jaws. The tendency for early M2 eruption is more pronounced in the maxilla, with M² sometimes erupting before the I¹ (1 out of 5 specimens) and always before the I² (2 specimens). In the mandible, M₂ most frequently erupted after both incisors (4 of 5 specimens), but sometimes before both (1 of 5). The relative sequence of the premolars is variable, with P3 erupting before the P4 most often in the upper jaw (2 of 3 specimens) and vice versa in the mandible (3 of 4 specimens). The position of the canine is also polymorphic, especially in the mandible. The lower canine erupted before either premolar and before M₂ in one specimen. Both upper and lower canines erupted after the M3 in some individuals (3 of 11 in the maxilla, 4 of 7 in the mandible). Finally, the lower M₃ erupted before P₃ in 2 (of 6) specimens.

Mesopithecus

Of the fossils, *Mesopithecus* preserved the highest number of informative juvenile individuals. It was therefore possible to determine the eruption sequence almost completely. We determined the position of the second molar relative to the lateral incisor on 2 specimens: a mandible (NHM M8957) and a maxilla (SMNS unnumbered specimen). The former has M₁ and M₂ in full occlusion and I₂ emerging, while the central permanent incisor is not preserved (Fig. 1a). The latter has M¹, M², and I¹ in full occlusion and I² halfway to occlusion (Fig. 1b). The only specimen preserving both permanent incisors had M2 already in full occlusion, and it was

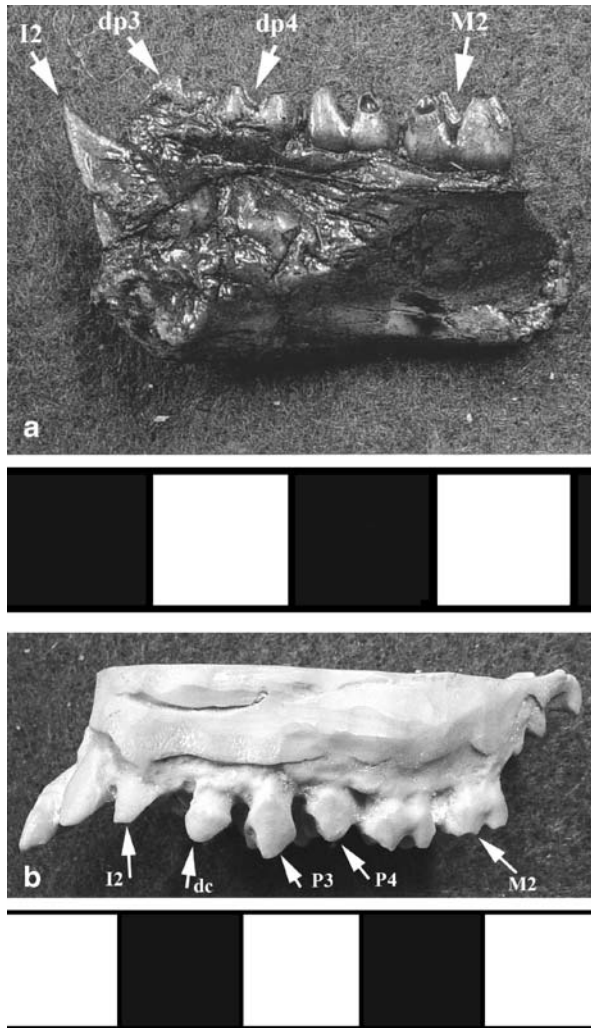


Fig. 1 *Mesopithecus pentelicus* NHM M8957 (a) and SMNS 1839/3939 maxilla (b) showing M2 in full occlusion and I2 in the process of erupting.

therefore not possible to determine whether M2 erupted before I1. Koufos *et al.* (2004) recently published an additional juvenile specimen of *Mesopithecus pentelicus* (VTK-78) from Macedonia, Greece, which preserves both the cranium and the mandible, and is described as showing upper and lower M2 and dI^1 in place and lower incisors erupting. We were not able to score VTK-78 based on the published drawings, but the specimen could provide evidence of precedence of the second molar over both incisors, a condition present variably in several colobine taxa (Harvati 2000). However, in the absence of conclusive data, we assumed that the common catarrhine sequence of precedence of the central incisor to the second molar.

No specimen informed the sequence of the premolars relative to each other. The premolars appeared to erupt after the second molar in 5 specimens: the mandibles

NHM M8957, BSM AS II 15, and 607 and NHMW unnumbered specimen and the Athens 29 maxilla. They appeared before the lateral incisor in maxilla SMNS 1839/3939, but after it in mandible BMNH M8957. The canine erupted after the premolars in 2, the Moloyan mandible and maxilla SMNS 1839/3939. However, mandible NHMW [unnumbered-2], a male, had the canine in a very similar stage of eruption as the third premolar, both at emergence. Four individuals informed the relative position of the third molar, the premolars, and the canine. Two mandibles had the canine in full occlusion (NHMW [unnumbered-1]) or one-third of the way to occlusion (Moloyan) and the third molar emerging. The SMNS maxilla 1839/3939 and mandible NHMW (unnumbered-2) both showed the canine emerging and the third molar still in the crypt. Four individuals (Moloyan, SMNS 1839/3939 and both NMHW specimens) showed either 1 or both of the premolars preceding the third molar in the eruption sequence, which suggests that the third molar was the last tooth to erupt. BSM AS II 607 is described in Zapfe (1991) as having a dp_4 still in place and M_3 erupting. However, the third molar of the specimen is loose. Though its crown appears formed, it is not possible from the illustration to determine whether the tooth would have already erupted or was still be in the crypt. We therefore do not consider that to provide evidence for a polymorphic position of the M_3 in *Mesopithecus*. The sequence presented here for *Mesopithecus* is very similar to a preliminary sequence that we published previously (Harvati and Frost 2005).

Kuseracolobus aramisi

Two juvenile specimens were available for *Kuseracolobus aramisi*, both informative on the position of the molars relative to the incisors in the eruption sequence.

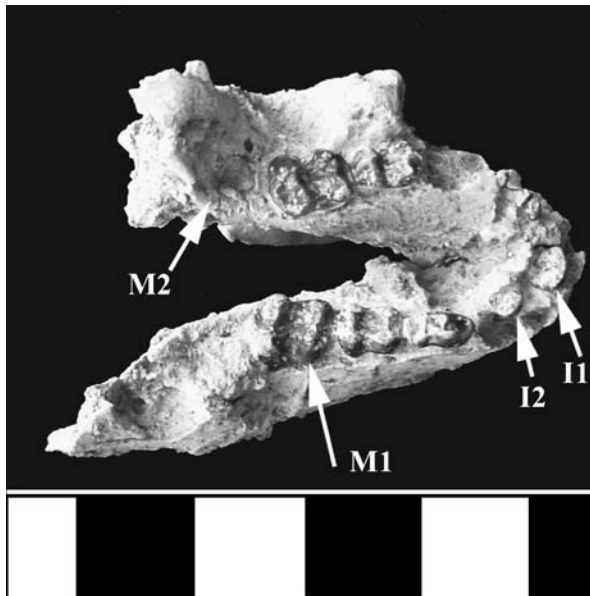


Fig. 2 *Kuseracolobus aramisi* specimen ARA-VP-1/2978, showing both central and lateral incisors erupting and M2 still in crypt.

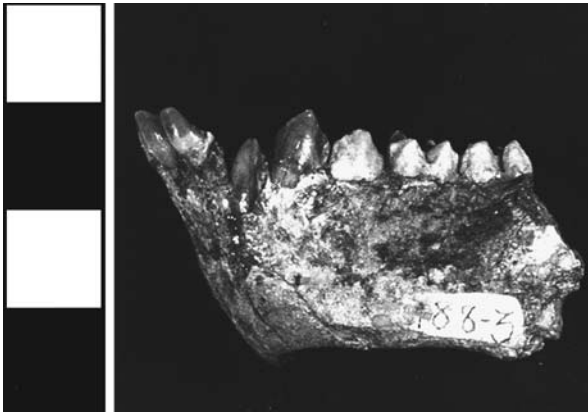


Fig. 3 *Colobus* sp. specimen NME KL 188-3, showing I₁-I₂, P₃-M₂ in place and the canine erupting. The M₃ is still in the crypt.

Mandible NME ARA-VP-1-2978 (Fig. 2) has M₁ in full occlusion, M₂ still in the crypt, and both permanent incisors emerging, indicating that the first permanent tooth to erupt is the first molar, followed by the 2 incisors. Maxilla NME ARA-VP-1-2696 has a similar pattern wherein M¹ is in full occlusion, but is nearly unworn. Based on the preserved alveolar area I¹ and I² are either in full occlusion or nearly so. The alveolar area in the region of M² is damaged, and the bone is broken away to reveal parts of 2 buccal roots and perhaps part of the rim of the lingual alveolus. From the breadth of the buccal roots it is clear that the crown was not far above them. Based on this, we estimate that M² was somewhere between just emerging and < 1/2 erupted. The specimens are not informative on any other part of the eruption sequence.

Colobus sp.

Only 2 juvenile specimens were available for *Colobus*, both mandibles. NME KL 188-3 (Fig. 3) preserved both anterior and posterior permanent dentition and had both permanent incisors, the first and second molars, and the 2 premolars in full occlusion, the canine erupting and the third molar still in the crypt. It was thus not possible to determine the relative position of the molars and the incisors in the eruption sequence. However, the canine is the second to last permanent tooth to emerge, and M₃ the last one. The less complete specimen NHM M15911 (Harrison and Harris 1996) informs the position of the premolars relative to the molars, but not on the P₃/P₄ sequence. The 2 teeth are in the same stage of eruption (1/3 to occlusion), while both M₁ and M₂ are in occlusion and M₃ is in the crypt.

Victoriapithecus macinnesi

Though *Victoriapithecus macinnesi* was represented by the largest number of juvenile specimens, none of them preserved the anterior permanent dentition. Two specimens inform the position of M₂ relative to the premolars: maxilla KNM-MB 21020 has M² at 1/3 to occlusion and dp⁴ in place, and mandible KNM-MB 21033 has M₂ in occlusion, dp₄ in place and P₃ in the crypt. One specimen, maxilla KNM-MB 31303,

informs the position of the third molar relative to the premolars, showing M^3 halfway to occlusion and both premolars in full occlusion.

Discussion

The updated sequences for 3 extant colobine taxa augment previous reports of colobine variability. The tendency for late molar eruption in *Nasalis* reported by Harvati (2000) was confirmed, and some variability between the subgenera of *Procolobus* (*P. [Procolobus]* and *P. [Piliocolobus]*) was also established based on the increased samples. *Procolobus verus* is of special interest, because it is the smallest extant colobine. Its sequence therefore allows us to evaluate better the hypotheses about the relationship between body size and eruption patterns.

More importantly, we showed that the tendency among colobines for early molar eruption relative to the anterior teeth was already present in Late Miocene Eurasian *Mesopithecus pentelicus*. The taxon had early eruption of the second molar relative to the second incisor. It was not possible to determine whether *Mesopithecus* also had the more extreme condition of the second molar erupting before the first incisor, which exists among living colobines: always in *Presbytis* and variably in *Pygathrix*, *Procolobus*, and *Colobus angolensis* (Harvati 2000). The only informative maxilla on the position of the I^2 relative to the premolars has an unusual pattern of the permanent premolars erupting before the lateral incisor. This is a rare polymorphism, but it occurs in the upper jaws of *Colobus angolensis* (Harvati 2000). Finally, early eruption of the third molar relative to the premolars and the canine, an extreme condition variably found in *Presbytis* (Harvati 2000). The third molar appeared after the canine in all specimens (male: $n=3$ and female: $n=1$), and we documented no sexually dimorphic delay of the appearance of the canine in males: present in *Colobus guereza* and suggested for several other colobine taxa (Harvati 2000) from the available data.

Among the African fossil colobines, only Pliocene *Kuseracolobus aramisi* was informative on the relative position of the molars and the incisors. The taxon did not exhibit early eruption of the second molar. Instead, the first molar was followed by the close eruption of the 2 permanent incisors. The pattern is uncommon in colobines. Harvati (2000; also this study) found it to be the predominant sequence in both mandibles and maxillae only in *Nasalis*. However, it is the predominant sequence among cercopithecines and hominoids, and it variably occurs in the lower—but never in the upper—jaws of *Colobus guereza*, *Procolobus*, and *Trachypithecus* (Harvati 2000). The fossil specimens of *Colobus* were not informative on the eruption sequence of the second molar relative to the incisors. However, both mandibles showed M_3 appearing last. Though the sample of *Colobus* sp. is very small, there is no evidence suggesting a tendency for the tooth to appear before the canine or even before either premolar, as is common in the lower jaws of extant *Colobus*, as well as *Procolobus*, *Trachypithecus*, *Presbytis*, and *Semnopithecus* (Harvati 2000). Finally, the eruption sequence of *Victoriapithecus macinnesi* was too incomplete to shed light on the position of its molars relative to the anterior dentition.

Our results demonstrate that the common colobine tendency for early molar eruption relative to the anterior dentition was already established in the Late Miocene

in *Mesopithecus*. They also show that a substantial part of the variability observed among colobine primates today was also in place by the Early Pliocene of Africa, as represented by the uncommon sequence for colobines in *Kuseracolobus*. Whether the variability was at the individual or the taxonomic level is unknown.

Dental Eruption Sequences, Life History, and Diet

Whether early molar eruption relative to the anterior dentition is a good indicator of rate of growth and life history is difficult to address. Smith (2000) tied the eruption sequence of the permanent molars relative to the replacement teeth to rates of jaw growth, and hence general growth (Schultz's rule). In her view, slow-growing species will delay the eruption of the molars because their jaws cannot accommodate them until later in age. At the same time, as the deciduous dentition loses functionality, it is replaced by permanent teeth before the molars erupt. Therefore, slow growing species have the incisors (and replacement dentition in general) erupting before the molars. Fast growing taxa, grow their jaws quickly enough to accommodate the molars before the deciduous dentition loses functionality and is replaced. They therefore have molars erupting early relative to the incisors, and to replacement teeth in general. Smith (2000) found evidence supporting this hypothesis in primates, tree shrews, and ungulates, but pointed out that individual taxa may not always follow Schultz's rule. Based on the limited information available on colobine life history variables, Harvati (2000) suggested that the early relative molar eruption in many colobines may be related to relatively fast life history, in accordance with Schultz's rule.

Godfrey *et al.* (2005a) recently challenged Schultz's rule because it does not always hold true among lemurs. They examined the eruption sequence and rate of growth in 2 small folivorous and nocturnal lemurs: *Avahi* and *Lepilemur*. Their findings show, though *Avahi* had late relative molar eruption, strongly indicating slow-growth, it did not grow at slower rates than *Lepilemur*, which had molars erupting early relative to replacement teeth. Based on dental microstructure of the subfossil lemur *Archaeolemur*, Godfrey *et al.* (2005b) estimated a much later age at M1 eruption—generally considered to correlate tightly with other life history variables—than had been predicted on the basis of its early molar eruption relative to the incisors (King *et al.* 2001; Smith 2000). However, even the new estimate of M1 eruption at *ca.* 15 mo, as opposed to the 2.5–8 mo Smith (2000) predicted, is earlier than in similarly-sized anthropoids, e.g., baboons, lending some support to Smith's (2000) hypothesis. Further, Schwartz *et al.* (2005) recently found *Megaladapis edwardsi*, one of the largest extinct primates, to have M1 eruption at a very early age. Because this taxon shows early relative molar eruption, the life history profile is consistent with its eruption sequence and with Schultz's rule, but not with its large body size, estimated at 88 kg.

These results paint a rather complicated picture of dental development and life history in lemurs, because dental schedules, body size, and dental eruption sequences do not seem to be correlated with one another (Schwartz 2005). Though the situation may be particular to lemurs, e.g., lemur eruption sequences may be complicated by possible functional imperatives for early eruption of the toothcomb (Smith 2000), the results of Godfrey *et al.* (2005a, b) cast doubt on the relationship between dental growth pattern and growth rate in general.

Other factors thought to affect dental growth and eruption sequences include diet, environmental stability and mortality patterns, and brain and body size. The latter 2 variables themselves are generally thought to be tightly correlated with growth rates. Godfrey *et al.* (2001; *cf.* Schwartz *et al.* 2005) evaluated several of these hypothesis. They found that fast rates of dental development—as represented by high dental precocity (the percentage of total postcanine teeth present at selected ages) and large dental endowment at weaning (the percentage of adult postcanine occlusal area at weaning)—correlate closely with small cranial capacity. However, folivorous species showed even faster dental development than predicted based on body or brain size alone, suggesting that a folivorous diet substantially affects the rate of dental growth. If dental precocity and endowment at weaning can be related to earlier molar eruption relative to the anterior dentition, then our study suggests that the colobine trend for early relative molar eruption is related to their folivorous adaptation. The interpretation is supported by findings of faster dental growth rates based on dental histology and faster body weight growth rates in folivorous relative to frugivorous primates (Dirks 2000, 2003; Leigh 1994).

Though the results are suggestive, within colobines the taxa with earliest molar appearance are not necessarily the most folivorous. Folivory is difficult to quantify and there is no variable that can accurately describe diet. However, given this caveat, one may consider estimates of total annual leaf intake to indicate the relative degree of folivory (Table IV). Accordingly, *Presbytis*, which has the earliest relative eruption of the molars, is less folivorous than *Trachypithecus* or *Colobus guereza* (Bennet and Davies 1994; Lucas and Teaford 1994; Table IV), both of which show a less pronounced tendency for early molar appearance. Conversely, *Nasalis*, which shows no tendency for early molar eruption, subsists mainly on fruit, seeds, young leaves, and a very small component of mature leaves (Bennett and Davies 1994). Among fossil colobines, *Mesopithecus* exhibits early molar eruption but is thought to be predominantly frugivorous (Reitz 2001; Reitz and Benefit 2001). Further, among papionins, *Theropithecus gelada*, the sister taxon to *Papio*, does not show early relative molar eruption (Swindler and Beynon 1993), even though they subsist mainly on grass (Iwamoto 1993).

It is also unclear how dental eruption sequences among colobines are related to body and brain size (Table IV). Within colobines, the large *Nasalis* and similarly-sized *Kuseracolobus* do not show early molar eruption, while small-bodied *Presbytis* is the most extreme in this respect. Further, the estimated body size for *Mesopithecus* places them within the range of mid-size colobines such as *Colobus guereza* or *Procolobus badius oustaletti*. Both of them, like *Mesopithecus*, have early relative molar eruption. Though this may suggest a relationship between body size and early molar eruption, large-bodied *Pygathrix (Rhinopithecus) roxellanae* also exhibits early molar appearance, unlike *Nasalis* and *Kuseracolobus*. In addition, the smallest colobine, *Procolobus verus*, is not as extreme in the relative eruption of the molars as *Presbytis* is. A strong relationship between body size and relative molar eruption is therefore not supported. Further examination of this hypothesis may be provided by examining Northern and Southern populations of *Semnopithecus entellus*, which differ greatly in body size, as well as through the discovery of informative juvenile specimens of the large-bodied Pliocene colobines: *Rhinocolobus*, *Paracolobus*, and *Cercopithecoides*.

Re the relationship of brain-to-body size (Table IV), some, though not all, colobine taxa appear less encephalized than the three cercopithecines included here for comparison (*Papio hamadryas cynocephalus*, *Theropithecus gelada*, and *Macaca mulatta*) are. Based on the estimated cranial capacity for *Mesopithecus* (70–75 cc: Radinsky 1974), its encephalization quotient is comparable to that of similarly-sized *Colobus guereza* and in the low end of the colobine range. Unfortunately, there is no calvaria complete enough to reliably estimate cranial capacity for *Kuseracolobus*. The data in Table IV show that, among colobines, encephalization is not directly related to larger body size or to more frugivorous diets, and that none of these variables predicts the presence (or absence) of a tendency for early relative molar eruption in colobines.

Dental Eruption Sequences and Phylogeny

Dental eruption sequences have long been considered phylogenetically informative (Mann 1972, 1988; Schultz 1935, 1960; Simons and Rasmussen 1996). King *et al.* (2001) found ontogenetic sequences in general to preserve a strong phylogenetic signal. Schultz (1935) saw the early eruption of the molars relative to the anterior dentition—a pattern common in lemurs, platyrrhines, and colobines—as an indicator of faster life history, a condition he thought was primitive for primates. In his view, higher primates show a derived trend toward prolonged life history, directly resulting in their delayed molar eruption. The trend was considered to be taken to extremes in humans, who have very slow life history and late eruption of the molars, both in absolute time and relative to the anterior dentition. If the colobine eruption pattern is primitive for catarrhines, it signifies that cercopithecines and hominoids converged on a similar eruption sequence, and, if we accept that eruption sequence reflects life history in most cases, probably also slower growth rates. Alternatively, if the colobine pattern is derived, the highly variable colobine eruption sequences may reflect responses to dietary factors, environmental instability, and mortality patterns.

Little is known about dental eruption patterns of fossil primates. However, recent findings made possible in large part by advances in the field of dental histology have complicated the early interpretations of life history evolution. Analysis of enamel microstructure in fossil hominoids has suggested that the modern ape-like dental development appeared earlier than previously expected. Kelley and Smith (2003) estimated *Afropithecus turkanensis*, dated at 17.5 ma, to have an age at M1 eruption of 28.2–43.5 mo, well within the chimpanzee range of 25.7–48 mo. Because age of M1 eruption tightly correlates with life history variables, they interpreted this finding to indicate an ape-like life history pattern for *Afropithecus turkanensis*. Similarly, the later Miocene apes *Sivapithecus parvada*, dated to 10 ma, and *Dryopithecus laietanus*, dated to 9.5–10 Ma, show an ape-like age at M1 emergence (Kelley 1997, 2002; Kelley *et al.* 2001), while *Graecopithecus freybergi*, dated to ca. 9 ma, may also have had ape-like prolonged life history (Smith *et al.* 2005). Beynon *et al.* (1998) found the older Early Miocene basal hominoid *Proconsul heseloni* to have a total period of dental development intermediate between that of chimpanzees and baboons. However, the authors did not exclude the possibility of a more apelike prolonged maturation period in the taxon relative to cercopithecoids of similar body size. Based on the early appearance of apelike life history in fossil hominoids and on limited evidence for more prolonged growth in some

Table IV Body mass, brain mass (g), encephalization quotients (EQ), and diet of cercopithecoïd taxa, including the fossils *Mesopithecus* and *Kaiseracolobus*

	Female body mass (g)	Observed brain mass (g)	Expected brain mass (g)	EQ	Diet	Early relative molar eruption ⁹	Age at MI eruption
<i>Colobus guereza</i>	7508 ²	69.00 ¹	95.1	1.33	75% leaves ⁶	Yes	—
<i>Sennopithecus entellus</i>	11,516 ²	98.20 ¹	51.9	1.37	51% leaves ⁷	—	—
<i>Trachypithecus cristatus</i>	5699 ²	54.5 ¹	71.9	1.29	91% leaves ⁶	Yes	—
<i>Nasalis larvatus</i>	9767 ²	82.80 ¹	42.1	1.31	52% leaves ⁷ 40–50% fruit and seeds ⁹	No	—
<i>Pygathrix roxellanae</i>	12,300 ²	121.70 ³	63.4	1.61	Leaves, fruit, lichen, bark ⁸	Yes	—
<i>Pygathrix nemeaus</i>	8064 ²	108.50 ³	75.6	1.98	63–82% leaves ⁸	Yes	—
<i>Procolobus verus</i>	4023 ²	57.80 ³	54.8	1.79	68–91% leaves ¹³	Yes	—
<i>Procolobus badius</i>	8250 ¹	64.80 ¹	32.3	1.16	50–52% leaves ¹³ High seed intake ⁸	Yes	—
<i>Presbytis melalophos</i>	6600 ³	80 ³	55.8	1.70	33% leaves ⁷	Yes, extreme	—
<i>Papio hamadryas cynocephalus</i>	12,657 ²	145.50 ¹	47.1	1.88	21% leaves ⁶	No	2 yr (F) 1.92 (M) ¹⁴

<i>Theropithecus gelada</i>	11,920 ²	131.9 ³	77.2	1.79	90% grass, seeds/herbs seasonally ^{1,5}	No ^{1,5}	1.7
<i>Macaca mulatta</i>	7970 ¹	81.30 ¹	54.3	1.50	84%, leaves, stems, grass, clover ¹⁷	No	1.44 yr (F) 1.49 (M) ¹⁴
* <i>Mesopithecus pentelicus</i>	9000 ²	72.50–77.60 ⁴	59.6	1.22–1.30	Fruit ¹⁸	Yes	–
* <i>Kuseracolobus aramisi</i>	12,000 ⁵	–	74.2	–	–	No	–
* <i>Anapithecus hemyaki</i>	15,000 ¹¹	110 ¹¹	87.9	1.25	Soft fruit ¹²	Yes ¹¹	17.4 mo ¹¹ (1.45 yr)

EQ calculated as observed brain mass/expected brain mass. Expected brain weight calculated according to the method described by Martin (1990) based on the relationship between brain and body mass in a large sample of mammals ($\log_{10}[\text{expected brain mass}] = .76 \times \log_{10}[\text{body mass}] + 1.77$). Brain mass for *Mesopithecus* calculated from its estimated cranial capacity of 70–75 cc (Radinsky 1974) based on the formula given in Ruff *et al.* (1998; brain mass = $1.147 \times \text{cranial capacity}^{.976}$). Data from: ¹ Godfrey *et al.*, 2001; ² Delson *et al.*, 2000; ³ Harvey *et al.*, 1987; ⁴ Radinsky 1974; ⁵ Frost 2001a; ⁶ Yeager and Kool, 2000; ⁷ Unpublished database from Nunn 2002; ⁸ Lippold 1998; Pham 1993; ⁹ Bennet and Davies 1994; ¹⁰ Harvati 2000, this study; Smith *et al.* 1994; ¹¹ Nargowalla *et al.* 2005; Ungar and Kay 1995; ¹² Kay and Ungar 1997; ¹³ Davies *et al.* 1999; Korsjiens, *pers. comm.*; Oates and Korsjiens *in press*; Korsjiens *et al.*, *in review*; ¹⁴ Smith *et al.* 1994; ¹⁵ Iwamoto 1993; ¹⁶ Swindler and Beynon 1993; ¹⁷ Goldstein and Richard 1989; Wenyuan *et al.* 1993; ¹⁸ Reitz 2001; Reitz and Benefit 2001.

platyrrhines than previously thought, Kelley and Smith (2003), contrary to Schultz's earlier interpretation, suggested that the primitive catarrhine condition was characterized by relatively prolonged growth periods—occurring today in hominoids and perhaps platyrrhines—and that cercopithecoids are derived in having a comparatively accelerated life history.

Researchers have conducted much less work on fossil cercopithecoids. Dean and Leakey (2004) assessed the dental development of *Victoriapithecus* from dental microstructure to be similar to that of small-bodied macaques based on C and M2 crown formation times, and hence slower than expected if its body mass were the *ca.* 3–5 kg that they used. If its body mass was *ca.* 7 kg, Delson *et al.* (2000) estimated that rate might be as expected. Dean and Leakey (2004) were not able to estimate ages at emergence of either the first or the second molar. Nargolwalla *et al.* (2005) examined the dental histology of the stem catarrhine *Anapithecus hernyaki* from Late Miocene Europe. This taxon is particularly interesting not only owing to its phylogenetic position as a basal catarrhine, but also because its dental eruption sequence is known. *Anapithecus* erupts the second molar after the central but before the lateral incisors, a sequence typical of most colobines. Further, third molars of *Anapithecus* are not always the last teeth to erupt, but appear before the canines in males. The sexually dimorphic pattern also occurs in *Colobus guereza* and is suggested for several other colobine taxa, but differs from the sexually dimorphic position of the canine in macaques, in which the canine appears after the premolars but before M3 in males and before the premolars and M3 in females (Harvati 2000). Nargolwalla *et al.* (2005) interpreted the dental histological evidence in the taxon to indicate rapid dental development and early second and third molar deployment. However, they found the age at M1 eruption to be equivalent to those of similarly-sized Old World monkeys, presumably indicating similar life histories. Based on the body mass and brain mass in Nargolwalla *et al.* (2005), we calculated the encephalization quotient of *Anapithecus* (Table IV). *Anapithecus* show a mid-range EQ, a diet of soft fruits (Kay and Ungar 1997; Ungar and Kay 1995; estimated from shearing crest quotients and microwear), and eruption of the first molar at a younger age than similarly-sized *Papio cynocephalus* and equivalent to the smaller *Macaca mulatta* (Table IV). From these data, it appears that early relative molar eruption in *Anapithecus*, as in modern colobines, is not related to a folivorous diet, nor is it associated with particularly low encephalization. Its life history, as indicated by age at M1 emergence, is cercopithecoid-like, though it may be somewhat accelerated

Table V *Nasalis larvatus*—Upper

	M1	I1	I2	M2	P3	P4	C	M3
M1		1/1	1/1	4/4	10/10	10/10	12/12	14/14
I1	0		1/1	4/4	10/10	10/10	12/12	14/14
I2	0	0		3/3	9/9	9/9	11/11	13/13
M2	0	0	0		9/9	9/9	11/11	13/13
P3	0	0	0	0		–	2/2	4/4
P4	0	0	0	0	–		2/2	4/4
C	0	0	0	0	0	0		2/2
M3	0	0	0	0	0	0	0	

Table VI Lower

	M1	I1	I2	M2	P3	P4	C	M3
M1		1/1	1/1	3/3	10/10	10/10	10/10	13/13
I1	0		–	3/3	10/10	10/10	10/10	13/13
I2	0	0		3/3	10/10	10/10	10/10	13/13
M2	0	0	0		9/9	9/9	9/9	13/13
P3	0	0	0	0		–	2/4	3/3
P4	0	0	0	0	–		2/4	3/3
C	0	0	0	0	2/4	2/4		5/5
M3	0	0	0	0	0	0	0	

Table VII *Procolobus verus*—Upper

	M1	I1	I2	M2	P3	P4	C	M3
M1		1/1	4/4	2/2	5/5	5/5	6/6	6/6
I1	0		3/3	–	4/4	4/4	5/5	5/5
I2	0	0		0	4/4	4/4	5/5	5/5
M2	0	–	3/3		4/4	4/4	5/5	5/5
P3	0	0	0	0		–	2/2	2/2
P4	0	0	0	0	–		2/2	2/2
C	0	0	0	0	0	0		1/1
M3	0	0	0	0	0	0	0	

Table VIII Lower

	M1	I1	I2	M2	P3	P4	C	M3
M1		1/1	4/4	1/1	4/4	5/5	6/6	6/6
I1	0		–	–	2/2	3/3	3/3	4/4
I2	0	–		0	3/3	4/4	4/4	5/5
M2	0	–	1/1		3/3	4/4	4/4	5/5
P3	0	0	0	0		1/1	1/1	2/2
P4	0	0	0	0	0		1/1	2/2
C	0	0	0	0	0	0		2/2
M3	0	0	0	0	0	0	0	

Table IX *Procolobus badius*—Upper

	M1	I1	I2	M2	P3	P4	C	M3
M1		6/6	11/11	10/10	14/14	14/14	20/20	25/25
I1	0		5/5	4/5	8/8	8/8	14/14	19/19
I2	0	0		0	4/4	4/4	10/10	15/15
M2	0	1/5	2/2		6/6	6/6	12/12	17/17
P3	0	0	0	0		2/3	8/8	13/13
P4	0	0	0	0	1/3		7/7	12/12
C	0	0	0	0	0	0		8/11
M3	0	0	0	0	0	0	3/11	

Table X Lower

	M1	I1	I2	M2	P3	P4	C	M3
M1		5/5	7/7	10/10	16/16	15/15	17/17	16/16
I1	0		2/2	4/5	11/11	10/10	12/12	13/13
I2	0	0		4/5	10/10	9/9	11/11	12/12
M2	0	1/5	1/5		9/10	8/9	10/11	11/11
P3	0	0	0	1/10		1/4	3/4	4/6
P4	0	0	0	1/9	3/4		4/5	4/4
C	0	0	0	1/11	1/4	1/5		4/7
M3	0	0	0	0	2/6	0	3/7	

relative to cercopithecines of similar body size. If this is the case, the taxon also follows Schultz's rule in its relatively early molar eruption. However, regardless of its ability to predict life history the presence of early molar eruption in the basal catarrhine and in the Late Miocene colobine *Mesopithecus* lends some support to the idea that this sequence is primitive for colobines and perhaps also for catarrhines.

Conclusions

The tendency for early eruption of the molars relative to the incisors common among extant colobines was already present in Late Miocene *Mesopithecus pentelicus*. In addition, much of the variability in eruption sequences in extant colobines was established by the Early Pliocene, as evidenced by *Kuseracolobus aramisi*. Previous conclusions on the diversity of eruption sequences in living colobines were strengthened by our incorporating additional specimens with the original samples. Within colobines, early molar eruption has no simple relationship with folivory, small body size, or low levels of encephalization. As life history data are all but unknown for extant colobines, it is not possible to determine whether the tendency for early molar eruption in these taxa is the result of short life history profiles, as would be expected according to Schultz's rule.

The polarity of early relative molar eruption is also difficult to establish. Its presence in *Mesopithecus* supports the idea that it is primitive for colobines, and that a macaque-like late molar eruption (*Nasalis*, *Kuseracolobus*) or more extreme early molar eruption (*Presbytis*) represents later divergences. Early molar eruption in *Anapithecus* lends support to the hypothesis that this eruption sequence is primitive for catarrhines. However, we cannot exclude the possibility that the fossil taxa we examined are derived in their own right, and that early relative molar eruption is a response to factors not incorporated in our study, such as environmental stability, adult and infant mortality levels, and maternal investment. In Primates, the relationships among life history variables is more complicated than once thought; each taxon may arrive at unique solutions to environmental challenges (Godfrey *et al.* 2004, 2005a, b; Leigh 2004; Schwartz 2005; Schwartz *et al.* 2005). Further research on the life history profiles of extant colobines, whether from long-term observations of living individuals in the wild or from histological studies of their dentitions, would help resolve the issues and greatly increase our understanding of the evolution of primate life history.

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Appendix

The sequences across the top and down the left side of the matrices is the eruption sequence of *Macaca nemestrina* (Smith 1994), also present in several other cercopithecines and hominoids (Smith 1994; Smith *et al.* 1994; Swindler 2005) and thought to characterize most catarrhines (Schultz 1935). We used it as a baseline to illustrate the differences between this common catarrhine sequence and colobine taxa. Specimens that conform to the common catarrhine sequence (M1 before I1, I1 before I2, etc.) lie above the diagonal; specimens that deviate from it (I1 before M1, I2 before I2, etc.) lie below the diagonal. Numbers in each cell represent the number of specimens showing a particular pairwise sequence/total number of specimens informative for that sequence. Tables V, VI, VII, VIII, IX, X

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