ACTA PALAEONTOLOGICA ROMANIAE V. 5 (2005), P. 205-210

DENTAL ERUPTION SEQUENCE IN *MESOPITHECUS PENTELICUS*

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Abstract: Colobines are distinctive among catarrhine primates in showing early molar eruption relative to their incisors. Several hypotheses have been proposed to account for this, including phylogenetic, dietary, size and life history interpretations. This study addresses the phylogenetic hypothesis of dental eruption in colobines by examining the European Late Miocene colobine *Mesopithecus pentelicus*. Early molar eruption is variable among extant colobines, with Asian taxa showing a greater degree of variation than the African genera. Sequences range from extreme early molar eruption (*Presbytis*) to macaque-like late molar eruption (*Nasalis)*. Schultz (1935) suggested that the colobine pattern represents the primitive catarrhine condition. More recently, dietary and life-history hypotheses have been proposed to explain its variability. If the colobine eruption sequence is primitive, it implies that papionins and hominoids converge on the same sequence. Alternatively, if the colobine condition is derived, factors like diet and mortality patterns probably shaped the colobine pattern. Casts of five *Mesopithecus* juveniles were scored following Harvati (2000). They showed early eruption of the second molar relative to the second incisor, a pattern most commonly observed in extant colobines (except *Nasalis*). This finding tentatively supports a primitive colobine, and possibly also catarrhine, status for early molar eruption.

Keywords: primates, colobines, dental growth, *Mesopithecus*, life history

INTRODUCTION

Colobines are distinctive among catarrhine primates in the early eruption of their molars relative to anterior teeth (Schultz 1935; Harvati 2000; see Table 1, Figure 1). Dental development and eruption sequences are often considered useful indicators of life history (Smith 1991, 1994), and early eruption of the molars relative to the replacement dentition has been proposed to indicate a generally accelerated life-history among various mammals (Smith 2000). Their dental eruption sequences therefore indicate that colobines are characterized by 'fast' life history profiles relative to other catarrhines. Very little is known about life history variables in colobines (such as age at first birth, interbirth intervals etc). However, available evidence suggests that they possess small brains relative to other catarrhines of similar body size (Clutton-Brock and Harvey 1980; Harvey *et al.* 1987; Godfrey *et al.* 2001). 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. Furthermore, colobines show faster growth rates both in body size (Leigh 1994) and in their dentition (Dirks 2000, 2003). These findings suggest that colobines may indeed show relatively accelerated life history compared to other catarrhines. This life history profile, in turn, has been interpreted as possibly related to the demands of their highly folivorous diets (Leigh 1994; Dirks 2000, 2003).

Dental eruption sequences have also played a role in the discussion of the evolution of life history in primates, although 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 which he thought it implied) to be primitive for primates, with higher primates showing a more delayed relative molar eruption and 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. If the colobine pattern is derived, however, then the highly variable colobine eruption sequences may be responses to factors such as diet and mortality patterns. They may also indicate that eruption sequences are relatively labile and not good indicators of phylogeny (Smith 1994). In order to shed light on the evolutionary history of colobine dental eruption patterns, we examined well-preserved juvenile specimens of informative dental eruption stages of the Eurasian Late Miocene taxon *Mesopithecus pentelicus.*

MATERIALS AND METHODS

The casts of five juvenile specimens of *Mesopithecus pentelicus* were examined and dental eruption stages were scored (Table 2). *Mesopithecus pentelicus* is the geologically oldest colobine known from Eurasia, and may represent the oldest colobine globally (Szalay and Delson, 1979). It is best known from a large series of material from the Late Miocene locality of Pikermi, Greece, dating to the Middle Turolian (MN 12) or approximately 8 Ma in age (Zapfe, 1991). This date puts *Mesopithecus* close to the divergence time between African and Asian colobines, as estimated by mtDNA (Sterner *et al.* in review). *M. pentelicus* is also known from a number of European and Western Asian localities (Szalay and Delson, 1979; Jablonski, 2002). All of the informative material included here derives from Pikermi, except for one

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Table 1: Eruption sequences established by Harvati (2000) for extant colobines. The last sequence of *Macaca nemestrina*, thought to be typical for catarrhines, is shown for comparison.

C. guereza	M1 I1 M2 I2 [P3 5 P4] [M3 C] M1 I1 I2 M2 P4 [P3 M3 C]
C. angolensis	M1 [M2 I1] [I2 P3 5P4] C M3 M1 M2 I1 I2 P4 [P3 M3 C]
Procolobus	M1 [I1 M2] I2 [P3 P4] [C M3] M1 [I1 I2 M2] P4 [P3 C M3]
Nasalis	M1? I1? I2 M2 P3? P4 C M3 M1? I1? I2 M2 [P3? P4 C] M3
Trachypithecus	M1 I1 M2 I2 [P3? P4 C] M3 M1 I1 [I2 M2] P4 P3 [C M3]
Presbytis	M1 M2 I1 I2 [M3 P4 P3 C] M1 M2 I1 I2 [M3 P4 P3] C
Pygathrix	M1 [I1 M2] I2 P3? P4 C M3 M1 I1 M2 I2 C P3? P4 M3
M. nemestrina	M1 I1 I2 M2 P3 P4 C M3 M1 I1 I2 M2 P3 P4 C M3

Brackets indicate variability in that part of the sequence, with the reported sequence being the most common one. Question marks indicate portions of the sequences that were not known from the specimens examined by Harvati (2000).

mandible from Moloyan Afghanistan (Heintz *et al.*, 1981).

A number of aspects of the paleobiology of this fossil taxon have been assessed. Delson *et al.* (2000) estimated population means for body weight for the Pikermi series utilizing cranial, dental, and postcranial material. They calculated mean body weights of 13 (range 10-15) and 9 (range 7-11) Kg for males and females respectively. *M. pentelicus* has been argued to be more semi-terrestrial in its locomotor behavior than most extant colobines, perhaps more similar to extant *Semnopithecus entellus* based on limb proportions, elbow, calcaneal, and phalangeal morphology (Szalay and Delson, 1979; Youlatos, 2003; but see Escarguel, 2005). Paleodiets for *M. pentelicus* have been estimated based on relative shear-crest length and microwear (Reitz, 2001; Reitz and Benefit, 2001). Both of these indicate that fruit may have predominated over leaves in the diet.

Specimens were scored following the methods described in Harvati (2000). A tooth was scored as "emerging" when any part of the crown had risen above the alveolar margin. Teeth showing an intermediate level of eruption (between "emerging" and "full occlusion") were further scored to 1/3, 1/2, and 2/3 of the way to full occlusion. When the two

Fig. 1. Stage of eruption of the maxillary anterior dentition relative to the molars in A: *Nasalis larvatus,* B: *Colobus guereza*, and C: *Presbytis frontata* (from Harvati 2000).

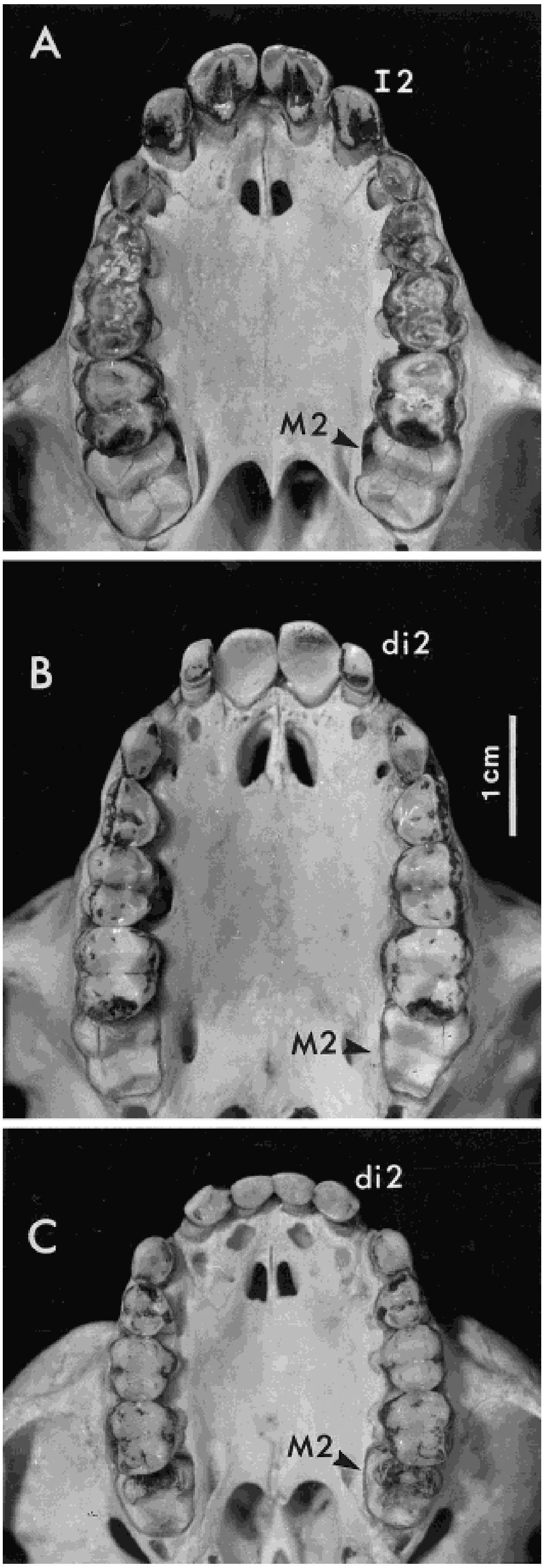

Table 2: *M. pentelicus* specimens used in this study.

Spec. No	Instit.	Anat. Elem.	Sex	Geol. Age	Locality
Un-numbered	MNHMP	mand	m		Moloyan, Afgan.
NHM M8957	NHM	mand	u	~8 Ma	Pikermi, Greece
Un-numbered	NHMW	mand	f	~8 Ma	Pikermi, Greece
BSM AS II 15	BSPHGM	mand	u	~8 Ma	Pikermi, Greece
1839 / 3939	SMNS	max	m	~8 Ma	Pikermi, Greece

Abbreviations: NHM: Natural History Museum, London; BSPHGM: Bayerisches Staatssammlung für Historische Geologie und Paläontologie, München; MNHMP: Muséum National d'Histoire Naturelle, Paris; NHMW: Naturhistorisches Museum Wien; SMNS: Stadtliches Museum der Naturkunde, Stuttgart.

sides showed different stages of eruption, the most advanced condition for each tooth was scored. Finally, precedence in the sequence was determined as follows. One tooth was considered to precede another if either: a) one was present and the other absent, or b) both teeth had emerged but there was a difference of at least a half step to full occlusion between the two. As the sex of the specimens used was in most cases not known due to their young age, male and female fossil specimens were pooled. Upper and lower jaws from the same individual did not occur for any of this material. It was therefore not possible to estimate the eruption sequence of the upper relative to the lower permanent teeth.

Due to the small number of informative juvenile specimens we were not able to determine the full sequence of eruption. Some parts of the eruption sequence for which no informative specimens were available are very stable among catarrhines including colobines. Such is the position of the first molar, which is always the first permanent tooth to emerge in non-human catarrhines (Smith 1994; Harvati 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) (Smith 1994; Harvati 2000; Swindler 2005). The position of the first molar was not known from the specimens examined, but was assumed to be the first tooth in the sequence (reported in italics) based on these invariable catarrhine patterns. The position of the first incisor was also not known. For this tooth (also reported in italics) we chose the most conservative catarrhine position of second tooth in the eruption sequence, although I1 can also erupt after M2 in some colobines. The sequence of the premolars relative to each other is highly variable within catarrhines, including colobines (Smith 1994; Harvati 2000; see also Smith 2000), and could not be determined for *M. pentelicus*. Premolars were therefore represented in the sequence as a unit: PP.

Fig. 2. *M. pentelicus* MNH M8957 (top) and SMNS 1839/3939 (bottom) showing M2 in full occlusion and I2 in the process of erupting.

RESULTS

Based on the five informative specimens examined here, we were able to determine the eruption sequence of *M. pentelicus* almost completely. The tentative eruption sequence for this taxon is:

$$\frac{M^1\quad I^1\quad \mathbf{M^2}\quad \mathbf{PP}\quad \mathbf{I^2}\quad \mathbf{C}\quad \mathbf{M^3}}{M_1\quad I_1\quad \mathbf{M_2}\quad \mathbf{I_2}\quad \mathbf{PP}\quad \mathbf{C}\quad \mathbf{M_3}}$$

The position of the second molar relative to the lateral incisor was determined on two specimens, a mandible and the single maxilla included here for this species (NHM M8957 and SMNS 1839/3939 specimen respectively; see Figure 2). The former individual shows M_1 and M_2 in full occlusion and I_2 emerging, while the central permanent incisor is not preserved (Figure 1a). The latter individual shows M^1, M^2 and I^1 in full occlusion and I^2 halfway to occlusion (Figure 1b). The only specimen preserving both permanent incisors had M2 already in full occlusion, and it was therefore not possible to determine whether M2 erupted before I1. In the absence of relevant data we assumed the common catarrhine sequence of precedence of the central incisor to the second molar.

No specimens were informative of the sequence of the premolars relative to each other. The two premolars appear to erupt after the second molar in both informative specimens (MNH M8957 and BSM AS II 15, both mandibles). They appear before the lateral incisor in the SMNS 1839/3939 maxilla, but after it in the MNH M8957 mandible. The canine erupts after the premolars in both informative specimens (Moloyan mandible and SMNS maxilla). Three individuals were informative on the relative position of the third molar, the premolars and the canine. Two specimens showed the canine in full occlusion (NHMW unnumbered mandible) or one third of the way to occlusion (Moloyan mandible) and the third molar emerging. The SMNS maxilla showed the canine emerging and the third molar still in the crypt. This suggests that the third molar was the last tooth to erupt.

DISCUSSION AND CONCLUSIONS

This study showed that the tendency among colobines for early molar eruption relative to the anterior teeth was already present in the Late Miocene Eurasian colobine *Mesopithecus pentelicus*. This taxon shows early eruption of the second molar relative to the second incisor. It was not possible to determine whether *M. pentelicus* also showed the more extreme condition of the second molar erupting before the first incisor, present among living colobines always in *Presbytis* and variably in *Pygathrix*, *Procolobus* and *C. angolensis* (Harvati 2000). The only informative maxilla on the position of the I^2 relative to the premolars shows an unusual pattern of the permanent premolars erupting before the lateral incisor. This is a rare polymorphism, but it has been observed among living colobines in the upper jaws of *C. angolensis* (Harvati 2000). Finally, early eruption of the third molar relative to the premolars and the canine was not observed, an extreme condition variably found in *Presbytis* (Harvati 2000). The third molar always appeared last in both male (2) and female (1) specimens, and no sexually dimorphic delay of the appearance of the canine in males (present in *C. guereza* and suggested for several other colobine taxa, see Harvati 2000) was evident from the available data.

Dental eruption sequences have been considered phylogenetically informative by many authors (e.g. Schultz 1935, 1960; Mann 1972, 1988; Simons and Rasmussen 1996). Furthermore, ontogenetic sequences in general have been recently found to preserve a strong phylogenetic signal (King *et al.* 2001). 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 a relatively fast life history profile, a condition he thought was primitive for primates. In his view, higher primates show a derived trend toward elongated life history, directly resulting in their delayed molar eruption. This trend was considered to be most derived in humans, who show extremely 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, this signifies that cercopithecines and hominoids independently 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 these early interpretations of life history evolution. Analysis of enamel microstructure in hominoid fossils has suggested that a delayed, modern ape-like dental development had appeared earlier than previously expected. *Afropithecus turkanensis*, dated at 17.5 ma, was found by Kelley and Smith (2003) to show an age at M1 eruption of 28.2-43.5 months, well within the chimpanzee reported range of 25.7 to 48 months. As age of M1 eruption is thought to correlate very tightly with life history variables, the authors interpreted this finding to indicate an ape-like life history. Similarly, the later Miocene apes *Sivapithecus parvada*, dated to 10 ma, and *Dryopithecus laietanus* show an ape-like age at M1 emergence (Kelley 1997, 2002; Kelley *et al.* 2001), while *Greacopithecus freybergi*, dated approximately to 9 ma, may also have shown ape-like prolonged life history (Smith *et al.* 2005). The earlier Early Miocene basal hominoid *Proconsul heseloni* was found by Beynon *et al.* (1998) to show a total period of dental development intermediate to that of chimpanzees and baboons. The possibility of a more-ape like prolonged maturation period in this taxon relative to cercopithecoids of similar body size, however, was not excluded by these authors. Based on this early appearance of ape-like life history in fossil hominoids and on limited evidence for more prolonged growth in some 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 (found today in hominoids and perhaps platyrrhines) and that cercopithecoids are derived in having highly accelerated life history.

Much less work has been conducted on fossil cercopithecoids. The dental development of the basal cercopithecoid *Victoriapithecus macinnesi* was assessed 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 for its body mass of 3-5 kg (Dean and Leakey 2004). However, if its body mass was ca. 7 kg as estimated by Delson *et al.* (2000) then this rate might be as expected. Furthermore, that study was not able to estimate ages at emergence of either the first or the second molar. The dental histology of the stem catarrhine *Anapithecus hernyaki* from the late Miocene of Europe was recently examined by Nargolwalla *et al.* (2005). This taxon is particularly interesting due 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. Furthermore, *Anapithecus* third molars are not always the last teeth to erupt, but appear before the canines in males. This sexually dimorphic pattern is also found in *C. guereza* and is suggested for several other colobine taxa, but differs from the sexually dimorphic position of the canine in macaques (where the canine appears after the premolars but before M3 in males and before the premolars and M3 in females. See Harvati 2000). Nargolwalla *et al.* (2005) interpreted the dental histological evidence in this taxon to indicate rapid dental development and very 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, indicating similar life histories. Therefore its life history as indicated by age at M1 emergence is cercopithecoid-like, though it may be somewhat accelerated relative to cercopithecines of similar body size. The presence of early molar eruption in both this 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.

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