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Dental eruption sequence and eruption times in *Erythrocebus patas*

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Abstract *Erythrocebus patas* has a short inter-birth interval, juveniles become independent from their mother early, females are young at first birth, and adult females have a high mortality rate. According to Schultz's rule, the molars of fast-growing and shorter-lived primate species erupt early relative to the replacement teeth. Based on the life history of *E. patas*, we hypothesized that the molars would erupt before the replacement teeth and/or that the eruption time of its molars would be early. The purpose of the present study was to determine the dental eruption sequence and eruption times for *E. patas* and to test our hypothesis. The eruption sequence for the permanent teeth of *E. patas* is $\frac{\text{M1 I1 I2 M2 P3 P4 [C M3]}}{\text{M1 I1 I2 M2 P4 [P3 C]M3}}$ in males and $\frac{\text{M1 I1 I2 [M2 P4 P3 C]M3}}{\text{M1 I1 I2 [M2 P4 P3 C]M3}}$ in females. Because these sequences constitute the general pattern seen in cercopithecines, Schultz's rule could not be applied to *E. patas*. The emergence time of upper and lower first molar (M1) is earlier in *E. patas* than in macaques, baboons, and mandrills and is similar to that in *Chlorocebus aethiops*. The emergence time of deciduous upper and lower fourth premolar (dp4) is similar to that in the above-mentioned cercopithecines but is later than that in *Ch. aethiops*. The emergence times of upper and lower second molar (M2) and upper and lower third molar (M3) in *E. patas* are earlier than those in the above-mentioned cercopithecines but later than those in *Ch. aethiops*. However, the intervals of the emergence time between each permanent molar in *E. patas* are similar to those of the above-mentioned cercopithecines. The early appearance of M2 and M3 in *E. patas* is related to the short interval of emergence time between dp4 and M1.

Keywords *Erythrocebus patas* · Dental eruption sequence · Dental eruption times · Schultz's rule

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Introduction

The habitat of *Erythrocebus patas* covers a broad area across central Africa, from the Sahara in the north to the equatorial rain forest in the south (Chism and Rowell 1988). This monkey is classified within the Cercopithecinae along with guenons, mangabeys, macaques, and baboons, among others (Groves 2005) and is most closely related to *Chlorocebus aethiops* (Tosi et al. 2005). The uniqueness of *E. patas* among the Cercopithecinae has been reported with regard to certain aspects of its life history. The juvenile *E. patas* develops rapidly, soon gaining independence from its mother (Chism 1986). The female *E. patas* is younger at first birth and has a shorter inter-birth interval than the closely related forest guenons (Nakagawa et al. 2003). Mortality rates in the adult females are higher than those in *Ch. aethiops* (Isbell et al. 2009).

Schultz (1935) proposed that early molar eruption was the most primitive trait in primates and that the eruption of molars was delayed in higher forms. The dental eruption sequence correlates with life history in primates, although not necessarily indicating phylogenetic relationships (Smith 1994, 2000). Smith (2000) reconstructed Schultz's rule as "the tendency for replacing teeth to come in relatively early in slow-growing, longer-lived species." Taking the opposite view, fast-growing and shorter-lived species have molars that erupt early relative to the replacement teeth (incisors, canines, and premolars) (see Smith 2000, p. 225). The life history of *E. patas* suggests that the molars erupt before the replacement teeth. In addition to the dental eruption sequence, *E. patas* would have molars erupt early relative to the replacement teeth in response to their life history. However, there is little information on the dental eruption sequence in *E. patas*; only one study, by Bolwig (1963), reported the dental eruption sequence and eruption times of deciduous teeth, based on one living individual. The purpose of the present study was to reveal the dental eruption sequences and eruption times for *E. patas*. In addition, we tested the hypothesis that the molars of *E. patas* erupt before the replacement teeth and/or that the eruption time of its molars is early.

Methods

The present study was based on 107 specimens of *E. patas* (43 males and 64 females). We selected 95 specimens (38 males and 57 females) from the Japan Monkey Centre (JMC), and 12 specimens (5 males and 7 females) from the Primate Research Institute, Kyoto University (PRIKU). Although the specimens used for the present study were bred in captivity, almost all the individuals from the JMC were bred not in cages but in open enclosures called "patas grassland." This "patas grassland" was located in Inuyama, Aichi, Japan, on a site within the JMC, from February 1965 to February 1990. The plot size was 7000 m^2, and the *E. patas* were free-range. The colony of "patas grassland" was started with 15 animals in 1965. Three animals (1 male and 2 females) were added in 1986, two (1 male and 1 female) in 1970, and four (2 males and 2 females) in 1990. The colony had a maximum of 25 animals including new born babies. The colony usually kept 10 to 20 animals for mating at the JMC. None of the specimens used in the present study had any skeletal abnormalities. In addition, none of the specimens at the JMC had growth impediment either in their medical history or as a cause of death.

In living mammals, tooth eruption is defined as the point when any part of the crown has pierced the gingiva (Smith 1994). Research on skeletal materials, however, has led some researchers to recognize tooth eruption as the point when the tip of the dental crown is above the alveolar margin (Schultz 1935; Thorington and Vorek 1976), whereas other researchers have restricted this term to the stage of full eruption (Cheverud 1981). Thus, there is no consensus among researchers on the definition of dental eruption with regard to skeletal materials. In the present study, tooth eruption was defined as "emergence" when any part of the dental crown had risen above the alveolar margin, and "full eruption" when the alveolar margin was closed around the base of the dental crown. In each jaw, a tooth was scored as "0" when it was completely buried within the socket or absent, and the score was "1" for full eruption. The dental emergence of a tooth was scored as "1/4", "1/2", or "3/4" based on the proportion of dental crown relative to total crown height above the alveolar margin (Schultz 1935). The eruption order was also recognized in accordance with the method of Schultz (1935). For example, if one tooth is scored as "1/2" has erupted and another is scored as "1/4", it is assumed that the former has appeared before the latter. When the two sides of the dental arcade show different stages of eruption, following Harvati (2000), the most advanced condition for each tooth is scored.

It is known that there are individual variations in the eruption sequences of many primates (Swindler 2002). In the present study, following Harvati (2000), brackets ([]) simply indicate any sequence polymorphism, although these have been used to denote a high level of variation by other workers (Smith 1994). In addition, the equal sign (=) is used when the emergence time of each tooth is identical in all the individuals.

The samples included 22 males and 36 females whose ages were known. Only age in years was inscribed on labels [quotation marks ("and") are used for such specimens here] for most specimens. Because several teeth erupt within a year in many primates (see Smith 1994), age measured in months should be provided to detect eruption time; however, it is quite difficult to determine the emergence time. The age was provided in years at the JMC. It is meant that both one year and two months animals and one year and ten months animals are counted as one year. Therefore, in this study we calculated "averages of the ranges" with regard to tooth emergence.

Results

Deciduous teeth

Eruption sequence

Specimen JMC 1562(2) had emerging deciduous incisors (Fig. 1). JMC 1565 had fully erupted deciduous incisors, and emerging deciduous canines and deciduous upper and lower third premolar (dp3). JMC 4324 showed full eruption of deciduous incisors, dc and dp3, and emergence of deciduous upper and lower fourth premolar (dp4). Therefore, it appears that the emergence of the deciduous dentition begins with the incisors, followed by the posterior teeth (Tables 1, 2). The eruption sequence of the deciduous dentition is therefore $\frac{\text{di1=di2 dc=dp3 dp4}}{\text{di1=di2 dc=dp3 dp4}}$.

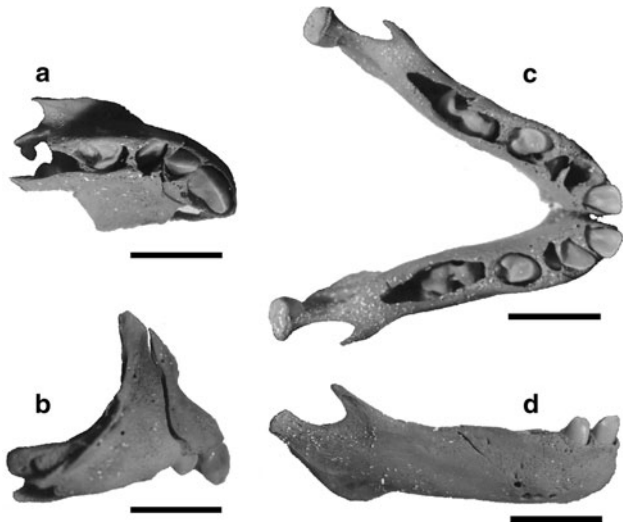

Fig. 1 Upper and lower jaws of a 3-day-old *Erythrocebus patas* [JMC 1562(2)]. **a**, **b** In the upper jaw: deciduous upper first incisor (di^1) and deciduous upper first incisor (di^2) emerge. **c**, **d** In the upper jaw: deciduous lower first incisor (di_1) and deciduous lower first incisor (di_2) emerge. *Scale bar* 1 cm

Table 1 Specimens number, dental formula and age of deciduous teeth in males

Specimen Number		Dental Formula di1	di2	dc	dp3	dp4	Age
JMC1562(2)	upper	1/2	1/2	0	0	0	0.008 years (3 days)
	lower	1/2	1/2	0	0	0	
JMC1565	upper	1	1	1/2	1/2	0	0.42 years
	lower	1	1	1/2	1/2	0	
JMC 4324	upper	1	1	1	1	3/4	0.42 years
	lower	1	1	1	1	3/4	
JMC 2384	upper	×[a]	×	×	×	×	0.5 years
	lower	1	1	1	1	1	
JMC 3454	upper	1	1	1	1	1	"0 years"
	lower	1	1	1	1	1	
JMC 2430	upper	1	1	1	1	1	"0 years"
	lower	1	1	1	1	1	
JMC 2689	upper	×	×	×	×	×	"1 year"
	lower	1	1	1	1	1	
JMC 1402	upper	1	1	1	1	1	
	lower	1	1	1	1	1	
JMC 2300	upper	1	1	1	1	1	
	lower	1	1	1	1	1	

Quotation marks around ages ("and") shows only age in years was known

[a] "×" shows there was no the tooth.

Eruption time

One newborn individual (PRIKU 7299) had no teeth. JMC 1562(2), with emerging deciduous incisors was 3 days old. Bolwig (1963) reported that living *E. patas*, 5–12 days old, had emerging deciduous incisors apart from deciduous lower second incisor (di_2), a finding comparable to ours.

Table 2 Specimens number, dental formula and age of deciduous teeth in females

Specimen Number		Dental Formular di1	di2	dc	dp3	dp4	Age
PRIKU 7299	upper	no eruption					new born
	lower						
JMC 4934	upper	×[a]	×	×	×	×	0.399 years
	lower	1	1	1	1	1	
JMC 2302	upper	1	1	1	1	1	"0 years"
	lower	1	1	1	1	1	
JMC 2519	upper	1	1	1	1	1	"0 years"
	lower	1	1	1	1	1	
JMC 1314	upper	1	1	1	1	1	"1 year"
	lower	1	1	1	1	1	
JMC 1402	upper	1	1	1	1	1	"1 year"
	lower	1	1	1	1	1	
JMC 1405	upper	1	1	1	1	1	"1 year"
	lower	1	1	1	1	1	
JMC 1406	upper	1	1	1	1	1	"1 year"
	lower	1	1	1	1	1	
JMC 1556	upper	1	1	1	1	1	0.5 years
	lower	1	1	1	1	1	
JMC 3358	upper	1	1	1	1	1	1.5 years
	lower	1	1	1	1	1	
JMC 1904	upper	1	1	1	1	1	
	lower	1	1	1	1	1	
JMC 2513	upper	×	×	1	1	1	"1 year"
	lower	1	1	1	1	1	
JMC 2515	upper	1	1	1	1	1	"0 years"
	lower	1	1	1	1	1	
PRIKU 1314	upper	×	×	1	1	1	
	lower	1	1	1	1	1	
PRIKU 1557	upper	1	1	1	1	1	
	lower	1	1	1	1	1	

Quotation marks around ages ("and") shows only age in years was known

[a] "×" shows there was no the tooth

JMC 4324, with emerging dp4, was 0.42 years old (5 months), while JMC 2384 (0.5 years old) had fully erupted deciduous dentition in the lower jaw (upper dentition was absent). JMC 4934 at 0.399 years old (4 months and 24 days) showed full eruption in the lower jaw (upper dentition was absent). Thus, all deciduous teeth emerged at 0.42 years; and full eruption of deciduous teeth occurred at 0.5 years or even less (Tables 1, 2).

Permanent teeth

Eruption sequence

In both sexes, permanent teeth emerge after full eruption of the deciduous teeth. The timing of tooth emergence is identical in the upper and lower jaws, and full eruption of upper and lower first molar (M1) is achieved before the

Table 3 Specimens number, dental formula and age of permanent teeth in males

Specimen Number		Dental Formula								Age
		I1	I2	C	P3	P4	M1	M2	M3	
JMC 1719	upper	0	0	0	0	0	1/4	0	0	
	lower	0	0	0	0	0	0	0	0	
JMC 3350		0	0	0	0	0	×	0	0	
		0	0	0	0	0	1/4	0	0	
JMC 2610		×	×	×	×	×	×	×	×	"0 years"
		0	0	0	0	0	1/4	0	0	
JMC 2711		0	0	0	0	0	1/4	0	0	"0 years"
		0	0	0	0	0	1/4	0	0	
JMC 2160		0	0	0	0	0	1/4	0	0	"0 years"
		0	0	0	0	0	1/4	0	0	
JMC 1903		0	0	0	0	0	1/4	0	0	"1 year"
		0	0	0	0	0	1/4	0	0	
JMC 2139		0	0	0	0	0	1/4	0	0	
		0	0	0	0	0	1/4	0	0	
JMC 4126		0	0	0	0	0	1/4	0	0	
		0	0	0	0	0	1/4	0	0	
JMC 3456		×[a]	×	×	×	×	×	×	×	0.5 years
		0	0	0	0	0	1/2	0	0	
JMC 2716		0	0	0	0	0	1/2	0	0	"0 years"
		0	0	0	0	0	1/2	0	0	
JMC 2893		0	0	0	0	0	1/4	0	0	
		0	0	0	0	0	1/2	0	0	
JMC 3618		0	0	0	0	0	3/4	0	0	"1 year"
		0	0	0	0	0	3/4	0	0	
JMC 2138		0	0	0	0	0	1	0	0	1.5 years
		0	0	0	0	0	1	0	0	
JMC 2298		1/2	1/4	0	0	0	1	0	0	"2 years"
		1/2	1/4	0	0	0	1	0	0	
JMC 3853		1	1	0	0	0	1	0	0	"2 years"
		1	1	0	0	0	1	0	0	
JMC 2916		1	1	0	0	0	1	3/4	0	"3 years"
		1	1	0	0	0	1	3/4	0	
PRIKU 3682		1	1	0	0	0	1	1/2	0	
		1	1	0	0	0	1	1	0	
JMC 3280		1	1	0	1	3/4	1	1	0	young
		1	1	1/2	1/2	1	1	1	0	

emergence of other teeth. Among the males, upper and lower first incisor (I1) emerged earlier than upper and lower second incisor (I2) in JMC 2298. Upper and lower second molar (M2) emerged after full eruption of the incisors but before full eruption of the premolars. Upper and lower fourth premolar (P4) emerged later than upper and lower third premolar (P3) in the upper jaw of one specimen and earlier than P3 in the lower jaw of four. Emergence of the upper canines was followed by the upper premolars. Full eruption of the lower canines was followed by the lower premolars. However, the emergence of the lower canines was coincident with that of lower third premolar (P_3) in two individuals, with some specimens showing emergence of the lower canines before P_3 and others after. Upper third molar (M^3) emerged earlier than the canines in two specimens, but later in four. In two

Table 3 continued

Specimen Number		Dental Formula								Age
		I1	I2	C	P3	P4	M1	M2	M3	
JMC 4450	upper	1	1	1/4	1	1	1	1	0	2.71 years
	lower	1	1	1/2	1/4	3/4	1	1	0	
JMC 3012		1	1	1/4	1	1	1	1	0	young
		1	1	1/2	1/2	1	1	1	0	
JMC 3013		1	1	1/4	1	1	1	1	0	young
		1	1	1/4	1/2	1	1	1	0	
JMC 4362		1	1	1/4	1	1	1	1	0	3.03 years
		1	1	1/2	1	1	1	1	0	
JMC 2091		1	1	1/2	1	1	1	1	1/2	
		1	1	3/4	1	1	1	1	1/4	
JMC 2084		1	1	1/2	1	1	1	1	3/4	adult
		1	1	3/4	1	1	1	1	3/4	
JMC 5889		1	1	3/4	1	1	1	1	3/4	
		1	1	1	1	1	1	1	1	
JMC 4922		1	1	3/4	1	1	1	1	1	8-9 years
		1	1	1	1	1	1	1	1	
JMC 4187		1	1	1	1	1	1	1	1	4.95 years
		1	1	1	1	1	1	1	1	
JMC 2388		1	1	1	1	1	1	1	1	adult
		1	1	1	1	1	1	1	1	
JMC 4413		1	1	1	1	1	1	1	1	adult
		1	1	1	1	1	1	1	1	
JMC 2604		1	1	1	1	1	1	1	1	adult
		1	1	1	1	1	1	1	1	
JMC 1713		1	1	1	1	1	1	1	1	adult
		1	1	1	1	1	1	1	1	
PRIKU 76		1	1	1	1	1	1	1	1	
		1	1	1	1	1	1	1	1	
PRIKU 5399		1	1	1	1	1	1	1	1	
		1	1	1	1	1	1	1	1	
PRIKU 6448		1	1	1	1	1	1	1	1	adult
		1	1	1	1	1	1	1	1	
PRIKU 7145		1	1	1	1	1	1	1	1	
		1	1	1	1	1	1	1	1	

Quotation marks around ages (“and”) shows only age in years was known

[a] “×” shows there was no the tooth

specimens, M^3 and the upper canines emerged at similar timing. Lower third molar (M_3) emerged after the other teeth in the lower jaw (Table 3). In females, I1 either emerged before I2 or fully erupted simultaneously. The emergence of the incisors occurred ahead of or was coincident with that of M2. P4 emerged earlier than P3. The order of emergence of the canines, premolars, and M2 was uncertain, but M2 tended to fully erupt before the canines erupted (six of nine individuals for the upper jaw; six of seven individuals for the lower jaw). Upper and lower third molar (M3) was the last permanent tooth to erupt (Table 4). The eruption sequences of the permanent teeth of *E. patas*

Table 4 Specimens number, dental formula and age of permanent teeth in females

Specimen Number		I1	I2	C	P3	P4	M1	M2	M3	Age
JMC 1474	upper	0	0	0	0	0	1/4	0	0	
	lower	0	0	0	0	0	0	0	0	
JMC 2304		0	0	0	0	0	1/4	0	0	"0 years"
		0	0	0	0	0	0	0	0	
JMC 2299		0	0	0	0	0	1/4	0	0	"1 years"
		0	0	0	0	0	0	0	0	
JMC 3748		0	0	0	0	0	0	0	0	0.5 years
		0	0	0	0	0	1/4	0	0	
JMC 2306		0	0	0	0	0	1/4	0	0	"0 years"
		0	0	0	0	0	1/4	0	0	
JMC 1910		0	0	0	0	0	1/4	0	0	"1 years"
		0	0	0	0	0	1/4	0	0	
JMC 3362		0	0	0	0	0	1/4	0	0	"0 years"
		0	0	0	0	0	1/2	0	0	
JMC 2609		0	0	0	0	0	1/2	0	0	"0 years"
		0	0	0	0	0	1/4	0	0	
JMC 2521		0	0	0	0	0	1/2	0	0	"0 years"
		0	0	0	0	0	1/2	0	0	
JMC 4192		0	0	0	0	0	1/2	0	0	0.91 years
		0	0	0	0	0	1/2	0	0	
PRIKU 3685		0	0	0	0	0	1/4	0	0	
		0	0	0	0	0	3/4	0	0	
JMC 2145		0	0	0	0	0	1/2	0	0	
		0	0	0	0	0	1	0	0	
JMC 2432		0	0	0	0	0	3/4	0	0	"0 years"
		0	0	0	0	0	1	0	0	
JMC 5443		0	0	0	0	0	1	0	0	1.70 years
		0	0	0	0	0	1	0	0	
JMC 3755		0	0	0	0	0	1	0	0	"1 years"
		0	0	0	0	0	1	0	0	
JMC 2503		0	0	0	0	0	1	0	0	"1 years"
		0	0	0	0	0	1	0	0	
JMC 2600		0	0	0	0	0	1	0	0	"1 years"
		0	0	0	0	0	1	0	0	
JMC 1347		0	0	0	0	0	1	0	0	"2 years"
		0	0	0	0	0	1	0	0	
JMC 2884		0	0	0	0	0	1	0	0	young
		0	0	0	0	0	1	0	0	

were determined as $\frac{\text{M1 I1 I2 M2 P3 P4 [C M3]}}{\text{M1 I1 I2 M2 P4 [P3 C]M3}}$ for males, and $\frac{\text{M1 I1 I2 [M2 P4 P3 C]M3}}{\text{M1 I1 I2 [M2 P4 P3 C]M3}}$ for females.

Eruption time

In males, M1 began to emerge in five specimens at age "0 years" and in two individuals at age "1 year". In JMC 3456, M_1 emerged at 0.5 years of age (upper dentition was absent). JMC 2138 showed full eruption of M1 at 1.5 years of age (Table 3). In females, M1 began to emerge at "0 years" in the upper jaw in six specimens and in the lower jaw in seven specimens. One specimen at age "1 year" had an emerging M1 in the upper jaw, and two specimens had an emerging M1 in the lower jaw. In JMC 3746, M_1 emerged at 0.5 years of age. In JMC 4192, M1

Table 4 continued

Specimen Number	Dental Formula								Age
	I1	I2	C	P3	P4	M1	M2	M3	
JMC 3389	×[a]	×	0	0	0	1	0	0	
	0	0	0	0	0	1	0	0	
JMC 2673	1/4	0	0	0	0	1	0	0	
	0	0	0	0	0	1	0	0	
JMC 2674	1/4	1/4	0	0	0	1	0	0	
	1/4	1/4	0	0	0	1	0	0	
JMC 2510	1/2	1/4	0	0	0	1	0	0	"2 years"
	1	1/4	0	0	0	1	0	0	
PRIKU 2469	1	1/2	0	0	0	1	0	0	
	1	1/2	0	0	0	1	0	0	
JMC 1712	1/2	1/2	0	0	0	1	1/2	0	"2 years"
	1	1	0	0	0	1	1/4	0	
JMC 2512	×	1/4	0	0	0	1	1/4	0	
	1	1	0	0	0	1	1/4	0	
JMC 2511	1	1	0	0	0	1	1/2	0	"2 years"
	1	1	0	0	0	1	1/2	0	
JMC 1896	×	×	1/4	0	0	1	0	0	
	×	×	×	×	×	×	×	×	
JMC 1439	1	×	1/2	0	0	1	0	0	
	×	×	0	0	0	1	1/4	0	
PRIKU 3684	1	1	1/4	0	0	1	1/4	0	
	1	1	1/2	0	0	1	1/4	0	
JMC 1322	1	1	0	1/2	3/4	1	1	0	adult
	1	1	0	0	1/4	1	1	0	
PRIKU 3683	1	1	1/2	3/4	3/4	1	1	0	
	1	1	1/2	1/2	3/4	1	1	0	
JMC 3015	1	1	3/4	1	1	1	1	0	"2 years"
	1	1	1	1	1	1	1	0	
JMC 3092	1	1	1	1	1	1	1	0	"4 years"
	1	1	1	1	1	1	1	1/4	
JMC 3202	1	1	1	1	1	1	1	1/2	"4 years"
	1	1	1	1	1	1	1	1	
JMC 4104	1	1	1	1	1	1	1	1	old
	1	1	1	1	1	1	1	1	
JMC 2707	1	1	1	1	1	1	1	1	adult
	1	1	1	1	1	1	1	1	
JMC 3364	1	1	1	1	1	1	1	1	adult
	1	1	1	1	1	1	1	1	

emerged at age 0.91 years (47 weeks and 4 days) (Table 4). Ranges of averages of dental emergence times were as follows: $0.40 <$ upper first molar (M^1) < 1.40 and $0.29 <$ lower first molar (M_1) < 1.29 in males; $0.22 < M^1 < 1.22$ and $0.14 < M_1 < 1.14$ in females (Table 5).

A male that was "2 years" old had an emerging M2, whereas a male that was 2.67 years old (2 years 8 months) had a fully erupted set of M2 (Table 3). In females, two specimens showed M2 emerging at age 2 years, with M2 in one specimen of the same age showing full eruption (Table 4). The emergence times of M2 occurred at age 2 years, i.e., from just 2 years old to the end of age 2 years, in both sexes.

In males, no specimens whose ages were known had emerging M3. The individuals that were 3 years old and

Table 4 continued

Specimen Number	I1	I2	C	P3	P4	M1	M2	M3	Age
JMC 1346	1	1	1	1	1	1	1	1	adult
	1	1	1	1	1	1	1	1	
JMC 4772	1	1	1	1	1	1	1	1	old
	1	1	1	1	1	1	1	1	
JMC 4538	1	1	1	1	1	1	1	1	over 24 years
	1	1	1	1	1	1	1	1	
JMC 5138	1	1	1	1	1	1	1	1	adult
	1	1	1	1	1	1	1	1	
JMC 5241	1	1	1	1	1	1	1	1	"27 years"
	1	1	1	1	1	1	1	1	
JMC 1441	1	1	1	1	1	1	1	1	
	1	1	1	1	1	1	1	1	
JMC 1733	1	1	1	1	1	1	1	1	
	1	1	1	1	1	1	1	1	
JMC 1839	1	1	1	1	1	1	1	1	adult
	1	1	1	1	1	1	1	1	
JMC 3818	1	1	1	1	1	1	1	1	adult
	1	1	1	1	1	1	1	1	
JMC 4270	1	1	1	1	1	1	1	1	old
	1	1	1	1	1	1	1	1	
PRIKU 551	1	1	1	1	1	1	1	1	
	1	1	1	1	1	1	1	1	
PRIKU 4237	1	1	1	1	1	1	1	1	
	1	1	1	1	1	1	1	1	
PRIKU 6447	1	1	1	1	1	1	1	1	
	1	1	1	1	1	1	1	1	

Quotation marks around ages (“and”) shows only age in years was known

[a] “×” shows that there was no the tooth

aged 3.03 years had no emerging M3, but M3 had fully erupted by age “4 years”. The emergence time of M3 was about 3–4 years in males (Table 5). One female specimen that was “4 years” old (JMC 3092) showed emerging M3, while another of the same age (JMC 3202) had emerging M^3 and fully erupted M_3. The emergence time of M3 was at age 4 years in females (Table 5).

Discussion

Schultz (1935) noted that the dental eruption sequence was M1, I1, I2, M2, P, P, C, M3 in the cercopithecines *Cercopithecus*, *Macaca*, and *Papio* (individual species were not mentioned, apart from *M. fascicularis*). Since then, the sequences have been reported for several cercopithecine species, in particular *Macaca* and *Papio* (Smith 1994). In the Cercopithecini, although 35 species are classified in the tribe (Groves 2005), there are few reports concerning dental eruption sequences. We are aware of published dental eruption data for *Ch. aethiops* (Ockerse 1959), *Cercopithecus nictitans*, *Cercopithecus diana*, and *Cercopithecus mona* (Lampel 1962). Table 6 shows the dental eruption sequences in cercopithecines based on these studies. The cercopithecine species are identical with regard to the eruption order of incisors, M1 and M2; namely, M1, I1, I2, M2. M3 is the final tooth to emerge in most species, but is fully erupted before the canines in males of some species where the greater height of their canines requires a much longer time for full eruption (Lampel 1962). *E. patas* is identical to the cercopithecine species in sequence patterns, i.e., M1, as the first permanent tooth, is followed in order by I1, I2, and M2, and finally M3 emerges. The order of premolars and canines in the sequence differs among species in various ways. *E. patas* shows sequence polymorphism. Therefore, we could not determine whether any of its sequence patterns of premolars and canines were identical to those of the cercopithecine species.

According to Schultz’s rule, species with a fast life history should exhibit early eruption of molars relative to incisors, canines, and premolars (Smith 2000). *E. patas* is

Table 5 Dental eruption times (in years) in *Erythrocebus patas*

	Males	Females		Males	Females
Upper			*Lower*		
dp4			dp4		
Range of average	0.42		Range of average	0.42	
Range	0.42		Range	0.42	
n	1		*n*	1	
M1			M1		
Range of average	0.40–1.40	0.22–1.22	Range of average	0.29–1.29	0.14–1.14
Range	0.00–2.00	0.00–2.00	Range	0.00–2.00	0.00–2.00
n	5	9	*n*	7	7
M2			M2		
Range of average	3.00–4.00	2.00–3.00	Range of average	3.00–4.00	2.00–3.00
Range	3.00–4.00	2.00–3.00	Range	3.00–4.00	2.00–3.00
n	1	2	*n*	1	2
M3			M3		
Range of average		4.00–5.00	Range of average		4.00–5.00
Range		4.00–5.00	Range		4.00–5.00
n		1	*n*		1

described as a fast-maturing and quick-breeding monkey with a high female mortality rate, in spite of its large body size for a cercopithecine (Chism et al. 1984; Nakagawa et al. 2003; Isbell et al. 2009). These characteristics, which are indicators of a fast-life-history species (Godfrey et al. 2005), would suggest early eruption of the molars related to the eruption of the replacement teeth, based on Schultz's rule. Among the living cercopithecids, *Ch. aethiops* is most closely related to *E. patas* (Tosi et al. 2005), and its inter-birth interval and age of weaning are the same as those of *E. patas* (Cheney 1981). However, its age of giving birth for the first time is later than that of *E. patas* (Cheney 1981), and its body size is smaller (Skinner and Chimimba 2005). Therefore, *Ch. aethiops* is not a fast-life-history species. The life history of *E. patas* would suggest that, based on Schultz's rule, early eruption of the molars would be related to the eruption of the replacement teeth. However, *E. patas* exhibits the sort of eruption order usually seen in the cercopithecine species.

In primates, the age at eruption of M1 is highly correlated with life history variables, such as inter-birth interval, age at first breeding, and age at weaning (Smith 1989, 1992). It is possible to assume that M1 of *E. patas* erupt early, because this guenon is also characterized as a species with short inter-birth interval, young age at first breeding, and early independence from the mother (Chism et al. 1984; Nakagawa et al. 2003). Indeed, *E. patas* shows shorter molar crown formation relative to body size than other primates (Macho 2001). Figures 2 and 3 (and Appendix Table 1) show the averages or the medians of emergence times of dp4 and molars for selected cercopithecines. Emergence times of M1 for *Macaca*, *Papio*, and *Mandrillus* fall outside the upper limits of ranges of averages for *E. patas*, but those for *Ch. aethiops* are in the same range as those for *E. patas*. This indicates that the emergence time of M1 in *E. patas* is earlier than that in the above-mentioned cercopithecines and is similar to that in *Ch. aethiops*. On the other hand, the emergence time of dp4 in *E. patas* is similar to that in *Macaca*, *Papio*, and *Mandrillus* but is later than that in *Ch. aethiops*. Intervals between the emergence of dp4 and M1 are around 1 year in most cercopithecine species, the longest being 1.80 years in the lower jaw of the male *Mandrillus sphinx*, and the shortest being 0.66 years in the upper jaw of *Ch. aethiops*. The interval between dp4 and M1 is less than 0.5 years in *E. patas*, a statistic obtained simply by calculating the difference between the median of ranges of averages for M1 and the emergence time of dp4 (0.42 years). Furthermore, in our study, one specimen showed M1 emerging at 0.5 years (6 months), representing a difference from 0.42 years of only 0.08 years (1 month). The emergence times of M1 of *E. patas* have a large average ranges than those of other cercopithecines. The upper limit of the interval between emergence times of dp4 and M1 were 0.98 years in upper dentition and were 0.87 years in lower dentition of male *E. patas* (Table 5). This time is relatively short. In *E. patas*, therefore, in comparison with other cercopithecines, M1 tends to emerge immediately after the eruption of dp4.

In *E. patas*, the emergence times for M2 and M3 were 2 and 4 years, respectively, which is earlier than that for

Table 6 Dental eruption sequences in cercopithecines

Species	Dental eruption sequences	Sources
Erythrocebus patas (male)	$\frac{M^1\ I^1\ I^2\ M^2\ P^3\ P^4\ [\ C\ M^3\ ]}{M_1\ I_1\ I_2\ M_2\ P_4\ P_3\ C\ M_3}$	This study
Erythrocebus patas (female)	$\frac{M^1\ I^1\ I^2\ [\ M^2\ P^4\ P^3\ C\ ]\ M^3}{M_1\ I_1\ I_2\ [\ M_2\ P_4\ P_3\ C\ ]\ M_3}$	This study
Chlorocebus aethiops	$\frac{M^1\ I^1\ I^2\ M^2\ P^4\ P^3\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ P_4\ P_3\ C\ M_3}$	Ockerse (1959)
Cercopithecus diana (male)	$\frac{M^1\ I\ I\ M^2\ P^3\ P^4\ M^3\ C}{M_1\ I\ I\ M_2\ P\ P\ M_3\ C}$	Lampel (1962)
Cercopithecus diana (female)	$\frac{M^1\ I\ I\ M^2\ P^4\ P^3\ C\ M^3}{M_1\ I\ I\ M_2\ P_3\ P_4\ C\ M_3}$	Lampel (1962)
Cercopithecus nictitans (male	$\frac{M^1\ I\ I\ M^2\ P\ P\ [\ C\ M^3\ ]}{M_1\ I\ I\ M_2\ P_4\ P_3\ C\ M_3}$	Lampel (1962)
Cercopithecus mona (male)	$\frac{M^1\ I^1\ I^2\ M^2\ P\ P\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ P\ P\ C\ M_3}$	Lampel (1962)
Cercopithecus mona (female)	$\frac{M^1\ I^1\ I^2\ M^2\ P^4\ P^3\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ P\ P\ C\ M_3}$	Lampel (1962)
Macaca fascicularis (male)	$\frac{M^1\ I^1\ I^2\ C\ P^3\ M^2\ P^4\ M^3}{M_1\ I_1\ I_2\ M_2\ C\ P_3\ P_4\ M_3}$	Honjo and Cho (1977)
Macaca fascicularis (female)	$\frac{M^1\ I^1\ I^2\ C\ P^3\ P^4\ M^2\ M^3}{M_1\ I_1\ I_2\ C\ M_2\ P_3\ P_4\ M_3}$	Honjo and Cho (1977)
Macaca fuscata (male)	$\frac{M^1\ I^1\ I^2\ M^2\ P^3\ P^4\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ P_3\ P_4\ C\ M_3}$	Iwamoto et al. (1987)
Macaca fuscata (female)	$\frac{M^1\ I^1\ I^2\ M^2\ C\ P^3\ P^4\ M^3}{M_1\ I_1\ I_2\ M_2\ C\ P_3\ P_4\ M_3}$	Iwamoto et al. (1987)
Macaca mulatta (male)	$\frac{M^1\ I^1\ I^2\ M^2\ P^3\ P^4\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ P_4\ P_3\ C\ M_3}$	Hurme and van Wagenen (1961)
Macaca mulatta (female)	$\frac{M^1\ I^1\ I^2\ M^2\ P^3\ C\ P^4\ M^3}{M_1\ I_1\ I_2\ M_2\ C\ \mathrm{P3}\ P_4\ M_3}$	Hurme and van Wagenen (1961)
Macaca nemestrina (male)	$\frac{M^1\ I^1\ I^2\ M^2\ P^4\ P^3\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ P_4\ P_3\ C\ M_3}$	Sirianni and Swindler (1985)
Macaca nemestrina (female)	$\frac{M^1\ I^1\ I^2\ M^2\ P^3\ P^4\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ C\ P_3\ P_4\ M_3}$	Sirianni and Swindler (1985)
Papio anubis (male)	$\frac{M^1\ I^1\ I^2\ M^2\ P^3\ C\ P^4\ M^3}{M_1\ I_1\ \mathrm{I2}\ M_2\ C\ P_3\ P_4\ M_3}$	Kahumbu and Eley (1991)
Papio anubis (female)	$\frac{M^1\ I^1\ I^2\ M^2\ C\ P^3\ P^4\ M^3}{M_1\ I_1\ I_2\ C\ M_2\ P_3\ P_4\ M_3}$	Kahumbu and Eley (1991)
Papio cynocephalus (male)	$\frac{M^1\ I^1\ I^2\ M^2\ P^3\ P^4\ C\ M^3}{M_1\ I_1\ I_2\ M_2\ P_4\ C\ \mathrm{P3}\ M_3}$	Phillips-Conroy and Jolly (1988)
Papio cynocephalus (female)	$\frac{M^1\ I^1\ I^2\ M^2\ C\ P^3\ P^4\ M^3}{M_1\ I_1\ I_2\ M_2\ C\ P_3\ P_4\ M_3}$	Phillips-Conroy and Jolly (1988)

I1 first incisor, *I2* second incisor, *C* canine, *P3* third premolar, *P4* fourth premolar, *M1* first molar, *M2* second molar, *M3* third molar

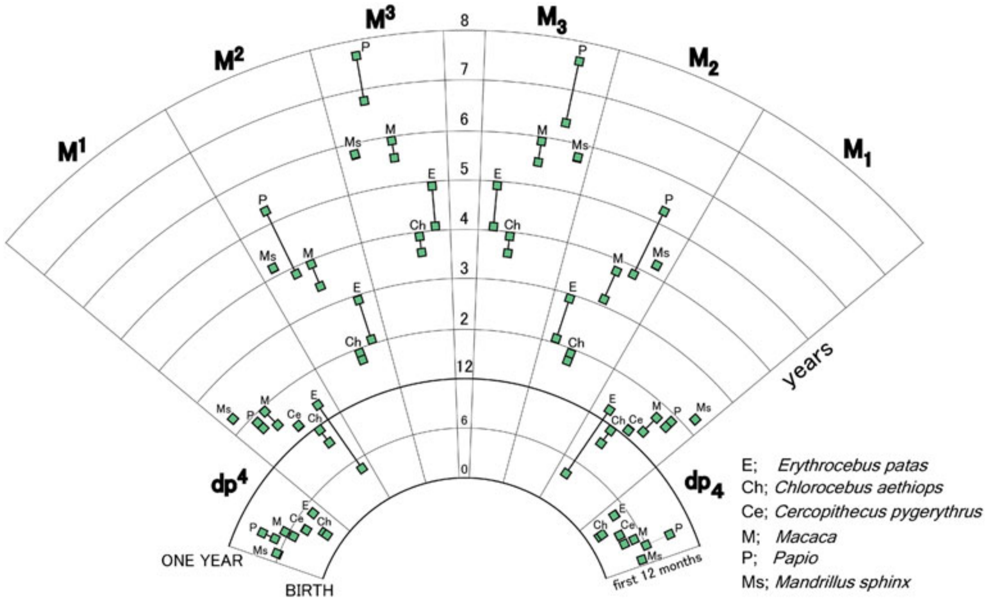

Fig. 2 Dental eruption times (in years) in cercopithecine males. dp^4 deciduous upper fourth premolar, dp_4 deciduous lower fourth premolar, M^1 upper first molar, M_1 lower first molar, M^2 upper second molar, M_2 lower third molar, M^3 upper second molar, M_3 lower third molar

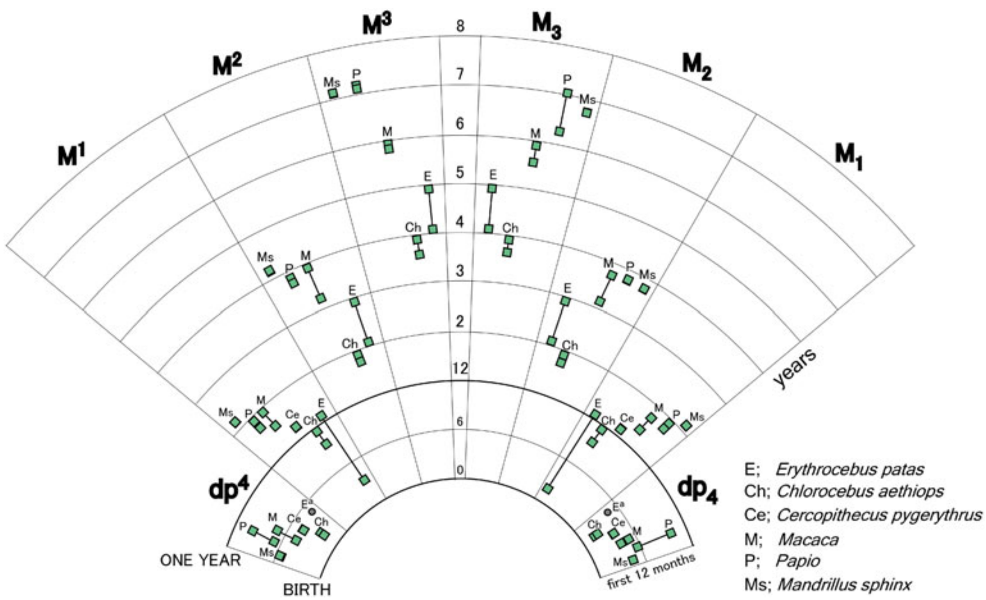

Fig. 3 Dental eruption times (in years) in cercopithecine females. dp^4 deciduous upper fourth premolar, dp_4 deciduous lower fourth premolar, M^1 upper first molar, M_1 lower first molar, M^2 upper second molar, M_2 lower third molar, M^3 upper second molar, M_3 lower third molar

Macaca, *Papio*, and *Mandrillus*, and later than that for *Ch. aetiops* (Figs. 2, 3). However, *E. patas* is similar to the above-mentioned cercopithecines regarding intervals of emergence times between permanent molars (Figs. 2, 3). In *Ch. aethiops*, M1 appears earlier than in other cercopithecines, excluding *E. patas*, and the intervals of eruption time between molars are less than those of the other cercopithecines, including *E. patas*, especially the interval between M1 and M2 (Figs. 2, 3). Thus, all molars erupt early in *Ch. aethiops*, whereas only the interval between dp4 and M1 is short in *E. patas*. The early appearance of M2 and M3 in *E. patas* occurs because of the short interval in emergence times between dp4 and M1.

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