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Schultz's Unruly Rule: Dental Developmental Sequences and Schedules in Small-Bodied, Folivorous Lemurs

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Key Words
Dental eruption · Schultz's rule · *Avahi* · *Lepilemur* · Sequence heterochrony

Abstract

Schultz's rule (as reconstructed by Smith) states that there is a relationship between the *pattern* (or relative order) of eruption of molar versus secondary (replacement) teeth and the overall *pace* (or absolute timing) of growth and maturation. Species with 'fast' life histories (rapid dental development, rapid growth, early sexual maturation, short life spans) are said to exhibit relatively early eruption of the molars and late eruption of the secondary replacement teeth (premolars, canines, incisors), whereas species with 'slow' life histories are said to exhibit relatively late eruption of the molars and early eruption of the secondary dentition. In a recent review, B.H. Smith noted that primates with tooth combs might violate this rule because tooth combs tend to erupt early, regardless of the pace of life history. We show that exceptions to Schultz's rule among lemurs are not limited to the relative timing of eruption of the tooth comb. Rather, among lemurs, some species with extremely accelerated dental development exhibit a pattern of eruption of molars and of secondary teeth in direct opposition to the expectations of Schultz's rule. We focus particularly on the pattern (order) and pace (absolute timing) of dental development and eruption in *Avahi* and *Lepilemur* – two relatively small, nocturnal folivores with rapid dental development. These taxa differ markedly in their eruption sequences (the premolars erupt after M2 and M3 in *Lepilemur* but not *Avahi*). We offer an ex-

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planation for the failure of Schultz's rule to predict these differences. Schultz's rule presumes that eruption timing is dependent on the size of the jaw and that, therefore, molar crown formation and eruption will be delayed in species with slow-growing jaws. We show that a variety of processes (including developmental imbrication) allows the crowns of permanent teeth to form and to erupt into jaws that might appear to be too small to accommodate them.

Introduction

On the basis of the work of Adolph H. Schultz [1935, 1960], B.H. Smith [2000] defined 'Schultz's rule' as the tendency of replacement teeth (incisors, canines and premolars) to erupt relatively early (cf. the molars) in slow-growing, long-lived species. Early eruption of the second and third molars relative to the replacement teeth, expressed in many strepsirrhines and some New World monkeys, is considered a consequence of rapid growth and dental eruption, and thus indicative of a 'fast' (or short) life history. Relatively early eruption of the *replacement* teeth, present in Old World monkeys and other catarrhines, is considered a 'slow (life history) signature' [Smith, 2000]. *Homo* represents the extreme example of a primate with a slow dental eruption signature – with the replacement teeth erupting in succession after the eruption of the first permanent molar, and in many cases, with all replacement teeth erupting prior to the emergence of the second molar. If indeed the *sequence* or order of dental eruption is a reliable predictor of dental eruption *schedule* or pace [Schultz, 1935, 1960; Della Serra, 1952; Smith, 2000; Harvati, 2000], the utility of Schultz's rule as a tool for drawing life history inferences for fossil taxa is apparent. Dental eruption order has been used to predict whether certain extinct species likely exhibited 'fast' or 'slow' life history strategies [Smith, 1994, 2000; King et al., 2001; Hogg et al., 2003].

Smith [2000] conceptualizes Schultz's rule as a shift in the eruption relationship between three 'sets' of teeth: the deciduous teeth (set 1), the permanent molars (set 2) and the replacement teeth (set 3; fig. 1). In species that reach their adult size rapidly, the jaw grows quickly, allowing it to accommodate the first, second and third molars (set 2) while the deciduous teeth (set 1) are still functional. In species that reach their adult size slowly, the jaw grows slowly, and eruption of the second and third molars is delayed. The replacement teeth (set 3) emerge as the deciduous teeth lose their functionality – often before there is sufficient space in the jaw to accommodate the second and third molars. Thus, sequence implies schedule. Schultz's empirical rule can be explained by the relationship between the rate of jaw growth and the functional lifetime of the deciduous teeth.

Smith [2000] also notes that lemurs appear to violate Schultz's rule because their mandibular canines and incisors erupt relatively early. She took this as evidence not for the failure of Schultz's rule, but for a functional imperative for early eruption of the tooth comb. The implication is that, with the exception of the teeth comprising the tooth comb, the dentitions of lemurs and other species with rapid dental eruption should exhibit a 'fast' sequence signature. We examine whether two relatively small-bodied lemurs with rapid dental eruption conform to the expectations of Schultz's rule. *Avahi* and *Lepilemur* are both nocturnal and highly folivo-

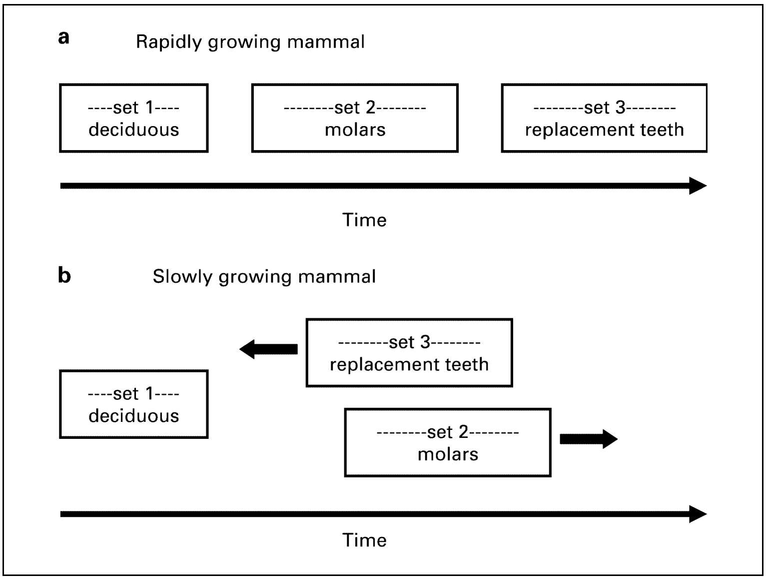

Fig. 1. Model of Schultz's rule, adapted from Smith [2000]. **a** According to Schultz's rule, rapidly growing mammals have molars that erupt early relative to the replacement teeth. **b** In slowly growing mammals, the replacement teeth erupt relatively early.

rous [Petter, 1962; Petter et al., 1977; Ganzhorn et al., 1985; Harcourt, 1991; Thalmann, 2001, 2002]. Both typically give birth to singletons and can be compared directly to anthropoids that give birth to single young. *Lepilemur* (family Megaladapidae) comprises 7 species, each of which weighs less than 2 kg.[1] *Avahi* (family Indriidae) includes at least 3 species (*A. laniger*, *A. occidentalis* and a recently named third species *A. unicolor* [Thalmann and Geissmann, 2000]). Like *Lepilemur*, all members of this genus are small-bodied forms. The highest recorded weights are 1.4–1.6 kg for adult *Avahi laniger* from Ranomafana National Park [Glander et al., 1992; Roth, 1996]. Unpublished adult weights collected by Mireya Mayor at Anjanaharibe-Sud and Betampona average 1.25 kg. Thalmann and Geissmann [2000] have recently summarized the published data.

Both *Avahi* and *Lepilemur* exhibit rapid dental eruption. Year-old *Avahi* and *Lepilemur* have their full adult postcanine dentitions [Godfrey et al., 2001] (see below). Similarly sized New World monkeys do not. Year-old *Aotus* (<1 kg) lack their anteriormost permanent premolars. Year-old *Saimiri* (<1 kg) still have full sets of deciduous premolars, although M1 and M2 have erupted. Nevertheless, in comparison to catarrhines, even *Saimiri* exhibits rapid dental eruption [Smith et al., 1994; Godfrey et al., 2001]. These monkeys appear to conform to the expectations

[1] Most *Lepilemur,* with the exception of Milne-Edwards' sportive lemur, *L. edwardsi,* weigh less than 1,000 g [Rowe, 1996; Smith and Jungers, 1997]. Ed Louis [unpubl. data] recorded masses of *Lepilemur* sp. at Kalambatritra of up to 2 kg; these animals are described in Irwin and Samonds [2001].

Table 1. Samples

Taxon	Immatures	Dental adults	Total
Lepilemur sp.	(1 near-term fetus)	–	1
Lepilemur dorsalis	4	7	11
Lepilemur edwardsi	5 (plus 7 fetuses)	23	35
Lepilemur leucopus	2	21	23
Lepilemur mustelinus	2	4	6
Lepilemur microdon	7	15	22
Lepilemur ruficaudatus	12 (plus 3 fetuses)	31	46
Lepilemur septentrionalis	1	3	4
Avahi laniger	11	31	42
Avahi unicolor	1	1	2
Avahi occidentalis	1	7	8
Total	46 (plus 11 fetuses)	143	200

of Schultz's rule, as *Aotus* has a 'fast' sequence signature, and *Saimiri* exhibits a somewhat 'slower' sequence signature, but not as slow as that of catarrhines [Smith, 2000].

If small-bodied lemurs with rapid dental eruption schedules conform to the predictions of Schultz's rule, we can expect the following of both *Avahi* and *Lepilemur*:

(1) both should exhibit a 'fast' dental eruption signature – i.e. relatively early eruption of the second and third molars and late eruption of the replacement teeth;

(2) because both have tooth combs, these expectations may be confounded by early eruption of teeth that contribute to the tooth comb; other teeth, however, should not be affected;

(3) any differences in the pattern of dental eruption should reflect differences in the pace of dental eruption; the species with the 'faster' eruption signatures should also exhibit faster eruption of the permanent dentition.

This paper evaluates the evidence relating to each of the above predictions.

Materials and Methods

We collected cranial measurements (bizygomatic breadth, maximum cranial length, palate length and breadth) and stage of dental eruption for 200 individuals belonging to all 7 species of *Lepilemur* (including 44 dentally immature individuals and 104 dental adults) and 3 species of *Avahi* (including 13 dentally immature individuals and 39 dental adults; table 1). Eleven of the *Lepilemur* immatures were fetuses. All alcohol specimens were examined radiographically. For each individual, we measured maximum cranial length, palate length and bizygomatic breadth. Mesiodistal and buccolingual diameters of all cheek teeth (maxillary and mandibular) were measured for subsamples of *Avahi laniger* and *Lepilemur ruficaudatus*. For skeletons, the degree of cranial suture closure was recorded, and postcrania were examined, when available, for state of growth (bone lengths) and development (including epiphyseal fusion).

Dental eruption *sequences* were assessed as described in King [2003, 2004; see also Washburn, 1943; Tappen and Severson, 1971]. Essentially, a species' tooth eruption sequence is implicit in the raw developmental scores of individuals for all teeth. For each skull and mandible, each tooth (including those that have been replaced) was scored as 0 (unerupted), 1 (erupting) or 2 (eruption complete). Eruption order can be inferred by summing the scores for individual teeth across all individuals; teeth that erupt relatively early will tend to have high scores even in young individuals, whereas late-erupting teeth will tend to have low scores even in older individuals. The sum of the scores of all individuals for a tooth is an indication of how early or late that tooth erupts during ontogeny. By sorting those sums (from highest to lowest), the species-typical order of tooth eruption (from earliest to latest) is revealed. The dental developmental stage of individuals was calculated as the percentage of teeth (deciduous and permanent) that have erupted relative to the species-typical total number of primary and secondary teeth. Using this proxy for dental development, we have been able to compare the pace of dental development to that of growth in skull size [Samonds et al., 1999, Schwartz et al., 2002; Godfrey et al., 2001, 2004].

Dental eruption *schedules* for *Lepilemur* and *Avahi* were assessed as described in Godfrey et al. [2001]. Normally, measuring the absolute timing of dental eruption requires that individuals of known age, often in captivity, be available. Because neither *Lepilemur* nor *Avahi* thrives in captivity, there are few known-aged specimens of either taxon in museum collections. However, most lemurs (including *Lepilemur* and *Avahi*) exhibit pronounced reproductive synchrony (that is females tend to enter estrus simultaneously, and infants are born within a few weeks of one another). Individuals grow in cohorts that are easily distinguishable from one another in museum collections and that can be aged (within some margin of error) when capture dates are recorded.

We used capture dates to estimate ages for wild-caught immature individuals. When capture dates were not available, we were sometimes able to reconstruct them from collector travel itineraries specifying dates at particular localities. Finally, maternal capture dates could be used to infer capture dates for dependent infants (presumably the same), when the former (but not the latter) were recorded.

Birth seasonality was derived from published and unpublished field observations, including those available in museum archives. For example, during the years 1906, 1911 and 1912, W. Kaudern documented the pregnancies of the adult females as well as states of development of the lemur fetuses he collected at Sainte Marie de Marovoay in northwestern Madagascar [Kaudern, 1914]. In his fetal collection (now at the Stockholm Natural History Museum) were 9 *Lepilemur edwardsi*, including 2 well-developed fetuses collected on August 22 and September 9. All other fetuses (collected between June 19 and September 4) are less well developed. Using this information, we could infer ages for all infant *Lepilemur* in Kaudern's Stockholm collection. An infant male *Lepilemur edwardsi* collected by Kaudern on October 24, 1906 (NRM 534232), for example, was unlikely to have been older than 2 months at death.

Results

Table 2 shows eruption sequence data for immature *Lepilemur* and *Avahi* ordered (in rows) by their dental developmental stages. Table 3 shows the eruption order inferred on the basis of these data for both species, along with eruption sequences for other taxa published by Smith [2002]. *Lepilemur* does exhibit a classic 'fast' signature in its eruption of the replacement versus permanent teeth. It appears to conform to Schultz's rule. Indeed, in *Lepilemur*, the tooth comb does not erupt relatively early. As in classic 'fast' species (such as *Eulemur*, other lemurids and small-bodied New World monkeys such as *Saimiri*, see table 3), the mandibular incisors erupt after the second molar but before M3.

However, *Avahi* exhibits a classic 'slow' dental eruption sequence signature. In *Avahi*, the tooth comb does erupt early. In addition, at least one premolar erupts

Table 2. Eruption sequence data

a Permanent-dentition eruption sequence in *Lepilemur*

Species and specimen No.	C	P2	P3	P4	M1	M2	M3
Maxillae							
Lepilemur sp. BMNH 95.303 (fetus)	0	0	0	0	0	0	0
Lepilemur ruficaudatus MNHN 1962.2721	0	0	0	0	0	0	0
Lepilemur dorsalis RVNH 23120	0	0	0	0	0	0	0
Lepilemur leucopus AMNH 174357	0	0	0	0	1	0	0
Lepilemur leucopus AMNH 170797	0	0	0	0	1	1	0
Lepilemur dorsalis RVNH 23119	0	0	0	0	1	0	0
Lepilemur edwardsi NRM 534232	0	0	0	0	1	0	0
Lepilemur mustelinus BMNH 1870.5.5.26	0	0	0	0	1	1	0
Lepilemur ruficaudatus MNHN 1961.267	0	0	0	0	2	1	0
Lepilemur ruficaudatus MNHN 1962.2716	0	0	0	0	2	1	0
Lepilemur ruficaudatus MNHN 1962.2717	0	0	0	0	2	2	0
Lepilemur mustelinus NRM A611474	0	0	0	0	2	1	1
Lepilemur dorsalis RVNH 23117	0	0	0	0	2	2	1
Lepilemur ruficaudatus? MNHN 1962.85	0	0	0	0	2	2	2
Lepilemur ruficaudatus MNHN 1962.2718	0	0	0	1	2	2	1
Lepilemur microdon NRM A622248	0	0	1	2	2	2	2
Lepilemur ruficaudatus MNHN 1962.2733	1	0	1	2	2	2	2
Lepilemur microdon BMNH 1958.3.4.7	0	1	2	2	2	2	2
Lepilemur microdon BMNH 1897.9.1.17	0	2	2	2	2	2	2
Lepilemur microdon BMNH 1897.9.1.18	1	2	2	2	2	2	2
Lepilemur microdon BMNH 1881.760	1	2	2	2	2	2	2
Lepilemur septentrionalis MNHN 1974.77	1	2	2	2	2	2	2
Lepilemur ruficaudatus MNHN 1962.2728	1	2	2	2	2	2	2
Lepilemur microdon BMNH 1881.785	1	2	2	2	2	2	2
Lepilemur ruficaudatus BMNH 1892.11.6.1	1	2	2	2	2	2	2
Lepilemur microdon BMNH 1881.763	1	2	2	2	2	2	2
Lepilemur edwardsi NRM A615895	1	2	2	2	2	2	2
Lepilemur edwardsi NRM A615899	1	2	2	2	2	2	2
Lepilemur ruficaudatus BMNH 1948.151	1	2	2	2	2	2	2
Lepilemur edwardsi NRM A615207	1	2	2	2	2	2	2
Lepilemur ruficaudatus MNHN 134b	1	2	2	2	2	2	2
Lepilemur ruficaudatus AMNH 100612	1	2	2	2	2	2	2
Lepilemur dorsalis BMNH 1935.1.8.139	1	2	2	2	2	2	2
Lepilemur edwardsi RVNH 23124	1	2	2	2	2	2	2

Species and specimen No.	I1	I2	C	P2	P3	P4	M1	M2	M3
Mandibles									
Lepilemur sp. BMNH 95.303	0	0	0	0	0	0	0	0	0
Lepilemur ruficaudatus MNHN 1962.2721	0	0	0	0	0	0	0	0	0
Lepilemur dorsalis RVNH 23120	0	0	0	0	0	0	0	0	0
Lepilemur leucopus AMNH 174357	0	0	0	0	0	0	1	0	0
Lepilemur leucopus AMNH 170797	0	0	0	0	0	0	1	0	0
Lepilemur dorsalis RVNH 23119	0	0	0	0	0	0	1	1	0
Lepilemur edwardsi NRM 534232	0	0	0	0	0	0	1	1	0
Lepilemur mustelinus BMNH 1870.5.5.26	1	1	1	0	0	0	1	1	0
Lepilemur ruficaudatus MNHN 1961.267	1	1	1	0	0	0	2	1	0
Lepilemur ruficaudatus MNHN 1962.2716	1	1	1	0	0	0	2	1	0
Lepilemur ruficaudatus MNHN 1962.2717	1	1	1	0	0	0	2	2	1
Lepilemur mustelinus NRM A611474	2	2	2	0	0	0	2	1	1
Lepilemur dorsalis RVNH 23117	1	1	1	0	0	0	2	2	1
Lepilemur ruficaudatus? MNHN 1962.85	2	2	1	0	0	0	2	2	2
Lepilemur ruficaudatus MNHN 1962.2718	2	2	1	0	0	1	2	2	2
Lepilemur microdon NRM A622248	2	2	2	1	0	2	2	2	2
Lepilemur ruficaudatus MNHN 1962.2733	2	2	2	0	0	2	2	2	2
Lepilemur microdon BMNH 1958.3.4.7	2	2	2	1	1	2	2	2	2
Lepilemur microdon BMNH 1897.9.1.17	2	2	2	2	2	2	2	2	2
Lepilemur microdon BMNH 1897.9.1.18	2	2	2	2	2	2	2	2	2

Table 2 (continued)

Species and specimen No.	I1	I2	C	P2	P3	P4	M1	M2	M3
Lepilemur microdon BMNH 1881.760	2	2	2	2	2	2	2	2	2
Lepilemur septentrionalis MNHN 1974.77	2	2	2	2	2	2	2	2	2
Lepilemur ruficaudatus MNHN 1962.2728	2	2	2	2	2	2	2	2	2
Lepilemur microdon BMNH 1881.785	2	2	2	2	2	2	2	2	2
Lepilemur ruficaudatus BMNH 1892.11.6.1	2	2	2	2	2	2	2	2	2
Lepilemur microdon BMNH 1881.763	2	2	2	2	2	2	2	2	2
Lepilemur edwardsi NRM A615895	2	2	2	2	2	2	2	2	2
Lepilemur edwardsi NRM A615899	2	2	2	2	2	2	2	2	2
Lepilemur ruficaudatus BMNH 1948.151	2	2	2	2	2	2	2	2	2
Lepilemur edwardsi NRM A615207	2	2	2	2	2	2	2	2	2
Lepilemur ruficaudatus MNHN 134b	2	2	2	2	2	2	2	2	2
Lepilemur ruficaudatus AMNH 100612	2	2	2	2	2	2	2	2	2
Lepilemur dorsalis BMNH 1935.1.8.139	2	2	2	2	2	2	2	2	2
Lepilemur edwardsi RVNH 23124	2	2	2	2	2	2	2	2	2

b Permanent-dentition eruption sequence in *Avahi*

Species and specimen No.	I1	I2	C	P3	P4	M1	M2	M3
Maxillae								
Avahi laniger MNHN 1882.1500	0	0	0	0	0	0	0	0
Avahi laniger MNHN 1882.1499	0	0	0	0	0	0	0	0
Avahi laniger MCZ 16454	0	0	0	0	0	0	0	0
Avahi laniger MNHN 1871.229	0	0	0	0	0	0	0	0
Avahi unicolor RVNH 23118	0	1	0	0	1	2	0	0
Avahi laniger AMNH 170500	1	1	0	1	1	2	1	0
Avahi laniger MNHN 1871.228	2	2	0	1	1	2	1	0
Avahi laniger NRM 621306	2	2	0	1	2	2	1	0
Avahi laniger (Manombo raptor capture)	2	2	0	2	2	2	2	0
Avahi laniger MNHN A2853	2	2	1	2	2	2	2	0
Avahi occidentalis NRM 534214	2	2	1	2	2	2	2	0
Avahi laniger MNHN 1986.435	2	2	1	2	2	2	2	0
Avahi laniger (wild caught, Ranomafana)	2	2	1	2	2	2	2	2
Avahi laniger USNM 83650	2	2	2	2	2	2	2	2
Avahi laniger MNHN 1882.1489	2	2	2	2	2	2	2	2
Avahi laniger MNHN 1882.1492	2	2	2	2	2	2	2	2

Species and specimen No.	I1	I2	P2	P4	M1	M2	M3
Mandibles							
Avahi laniger MNHN 1882.1500	0	0	0	0	0	0	0
Avahi laniger MNHN 1882.1499	0	0	0	0	0	0	0
Avahi laniger MCZ 16454	0	0	0	0	1	0	0
Avahi laniger MNHN 1871.229	0	1	0	0	1	0	0
Avahi unicolor RVNH 23118	1	1	0	1	2	0	0
Avahi laniger AMNH 170500	1	1	0	1	2	1	0
Avahi laniger MNHN 1871.228	2	2	1	2	2	1	0
Avahi laniger NRM 621306	2	2	1	2	2	1	0
Avahi laniger (Manombo raptor capture)	2	2	1	2	2	2	0
Avahi laniger MNHN A2853	2	2	1	2	2	2	0
Avahi occidentalis NRM 534214	2	2	1	2	2	2	1
Avahi laniger MNHN 1986.435	2	2	2	2	2	2	0
Avahi laniger (wild caught, Ranomafana)	2	2	2	2	2	2	1
Avahi laniger USNM 83650	2	2	2	2	2	2	2
Avahi laniger MNHN 1882.1489	2	2	2	2	2	2	2
Avahi laniger MNHN 1882.1492	2	2	2	2	2	2	2

BMNH = British Museum of Natural History; MNHN = Muséum national d'histoire naturelle, Paris; RVNH = Nationaal Natuurhistorisch Museum, Leiden; AMNH = American Museum of Natural History; NRM = Naturhistoriska Riksmuseet, Stockholm; MCZ = Museum of Comparative Zoology, Harvard University; USNM = United States National Museum, Smithsonian Institution.

Table 3. Mandibular sequence comparisons

Tupaia	M1		M2		M3	PIPIPI
Aotus	M1		M2	I	M3	IPPP
Lepilemur	M1		M2	tc	M3	PPP
Eulemur	M1	tc	M2	P	M3	PP
Saimiri	M1		M2	IIPPP	M3	
Chlorocebus	M1	II	M2	PP	M3	
Macaca	M1	II	M2	PP	M3	
Pan	M1	II	M2	PP	M3	
Avahi	M1	tc P	M2	P	M3	
Homo	M1	IIP	M2	P	M3	

From Smith [2000], figure 15.4, modified – *Lepilemur* and *Avahi* added. tc = Tooth comb.

prior to M2, and all of the replacement teeth erupt before the emergence of M3. Such a signature would appear to be that of an animal with extremely *slow* dental eruption (table 3). It suggests a dental developmental *pace* that is slower than that of macaques or chimpanzees. In fact, at least in terms of the relative timing of eruption of the permanent versus the replacement teeth in the mandible, this eruption sequence suggests a human-like pace of dental eruption, as the *Avahi* sequence is like that of *Homo sapiens*.

If Schultz's rule has any explanatory power for lemurs, we might expect consistency of the sequence/schedule relationship *among these species*, even when broader taxonomic comparisons do not yield results that conform to Schultz's expectations. Given its 'slower' eruption signature, we might expect *Avahi* to exhibit a slower *pace* of dental eruption than *Lepilemur*.

Tables 4 and 5 show data bearing on the absolute pace of dental eruption in *Lepilemur* and *Avahi*. Highlighted are those individuals whose first permanent molars are erupting. Table 6 shows our inferred ages at M1 eruption for *Lepilemur* and *Avahi*. Comparative data for other taxa are taken from Smith et al. [1994].

Our data provide no reason to believe that *Avahi* exhibits slower dental development than does *Lepilemur*. To the contrary, the opposite may be true. Field data on birth seasonality for both taxa are summarized below. Using these to determine the age of museum specimens, we infer that the first molar erupts during the first month (and certainly before 2 months) in both *Lepilemur* and *Avahi*. Eruption of the *permanent* dentition is complete by 4 months in *Avahi* and, with the exception of the upper canine which erupts slowly over a prolonged period, by 6 months (or less) in *Lepilemur*. Weanlings (3- to 4-month-olds) are dentally well endowed in both taxa; in *Avahi*, they have full-adult dentitions!

The birth season is apparently more variable in *Lepilemur* than in *Avahi*. It is also more difficult to track, as newborns are hidden and raised in tree holes, from which they emerge only after a period of uncertain duration. Thus, the young may be sighted in the field for the first time well after their actual births. New infants have been reported between September and November, and even later [Ganzhorn, 2002]. However, there is some consistency across species in that gravid females captured in early and mid-June have young fetuses, whereas those captured in Sep-

Table 4. Growth and dental development in *Lepilemur*, highlighting individuals with their first permanent molars erupting

Species and specimen No.	Dental development stage	Bizygomatic breadth mm	Cranial length mm	Capture date and inferred age months
Lepilemur sp. BMNH 95.303	0.278	18.6 (50.2)	34 (58.1)	near-term fetus
Lepilemur ruficaudatus MNHN 1962.2721	0.333	19.4 (53.1)	35.6 (62.2)	neonate?
Lepilemur dorsalis RVNH 23120	0.407	15.0 (42.9)	31.9 (59.8)	neonate?
Lepilemur leucopus AMNH 174357	0.444	17.9 (54.1)	35.9 (71.1)	November 24; <2 months
Lepilemur leucopus AMNH 170797	0.463	–	–	late October to late November; <2 months
Lepilemur dorsalis RVNH 23119	0.463	22.5 (64.4)	38.0 (71.2)	–
Lepilemur edwardsi NRM 534232	0.463	22.5 (60.0)	39.7 (67.2)	October 24; 1 month?
Lepilemur mustelinus BMNH 1870.5.5.26	0.537	26 (70.2)	45 (76.9)	–
Lepilemur ruficaudatus MNHN 1961.267	0.574	24.5 (64.3)	42.2 (73.7)	–
Lepilemur ruficaudatus MNHN 1962.2716	0.574	25.3 (67.2)	43.0 (75.1)	–
Lepilemur ruficaudatus MNHN 1962.2717	0.630	28.1 (74.7)	46 (80.4)	–
Lepilemur mustelinus NRM A611474	0.648	27.5 (74.2)	47 (80.3)	–
Lepilemur dorsalis RVNH 23117	0.648	25.7 (73.5)	46.8 (87.7)	November to December; <3 months
Lepilemur ruficaudatus? MNHN 1962.85	0.722	29.9 (79.5)	48.1 (84.0)	–
Lepilemur ruficaudatus MNHN 1962.2718	0.741	28.7 (76.3)	46.3 (80.9)	–
Lepilemur microdon NRM A622248	0.852	30.6 (81.6)	50.1 (85.3)	December 2; 2–3 months
Lepilemur ruficaudatus MNHN 1962.2733	0.852	32.5 (86.4)	52.9 (92.4)	–
Lepilemur microdon BMNH 1958.3.4.7	0.907	32.3 (86.1)	52.1 (88.7)	January 6; 3–4 months
Lepilemur microdon BMNH 1897.9.1.17	0.963	35.2 (93.9)	56.3 (95.9)	–
Lepilemur microdon BMNH 1897.9.1.18	0.981	32.5 (86.7)	54.7 (93.2)	March 16; 6 months
Lepilemur microdon BMNH 1881.760	0.981	34.6 (92.3)	55.9 (95.2)	March 16; 6 months
Lepilemur septentrionalis MNHN 1974.77	0.981	31.5 (89.9)	49.7 (91.4)	–
Lepilemur ruficaudatus MNHN 1962.2728	0.981	32.5 (86.4)	49.3 (86.1)	–
Lepilemur microdon BMNH 1881.785	0.981	34.5 (92.0)	56.3 (95.9)	March 19; 6 months
Lepilemur ruficaudatus BMNH 1892.11.6.1	0.981	35.6 (94.6)	50 (87.4)	–
Lepilemur microdon BMNH 1881.763	0.981	35.9 (95.7)	57.8 (98.5)	May 18; 8 months
Lepilemur edwardsi NRM A615895	0.981	32.8 (87.5)	53.0 (89.7)	August 16; 11 months
Lepilemur edwardsi NRM A615899	0.981	32.8 (87.5)	56.1 (95.0)	September 4; 12 months
Lepilemur ruficaudatus BMNH 1948.151	0.981	36.2 (96.2)	52.3 (91.4)	September 9; 12 months
Lepilemur edwardsi NRM A615207	0.981	34.2 (91.2)	54.7 (92.6)	September 26; 12 months
Lepilemur ruficaudatus MNHN 134b	0.981	34.7 (92.2)	55 (96.1)	–
Lepilemur ruficaudatus AMNH 100612	0.981	38 (101.0)	54.8 (95.7)	November 14; 14 months
Lepilemur dorsalis BMNH 1935.1.8.139	0.981	32.5 (92.9)	52.5 (98.4)	November 26; 14 months
Lepilemur edwardsi RVNH 23124	0.981	36.2 (96.6)	57.9 (98.0)	–

Figures in parentheses indicate percent adult size. For a key to collection abbreviations, see table 2.

tember are near term.[2] The youngest infants in museum collections have October or November capture records (table 4). It is possible that there is a latitudinal gradient to birth seasonality, as suggested by Rasmussen [1985] for lemurids, but our data are not sufficiently rich to allow us to test this hypothesis.

More specifically, *Lepilemur leucopus* was observed at Beza Mahafaly (southwest) by Charles Dominique and Hladik [1971] and by Nash [1998]. Charles Dominique and Hladik [1971] noted that in September, females were at the end of their period of gestation. Nash [1998, pers. commun.] saw one copulation in early June and young infants in November and December. *L. ruficaudatus* was studied in western Madagascar by Petter et al. [1977], Drack et al. [1999] and Ganzhorn [2002]. Petter et al. [1977] reported that all adult female red-tailed sportive lemurs captured in August and September were pregnant. They saw mating from May to July, and births from September through November. Drack et al. [1999] studied *L. ruficaudatus* at Kirindy Forest during July and August 1996. All were adults save 2 youngsters (perhaps 9 months old), weighing on average slightly over 60% of adult female mass. Ganzhorn [2002] observed mating between June and August. Infants were seen in December and January.

Kaudern [1914, 1915] captured pregnant female *L. edwardsi* at Sainte Marie de Marovoay over a several-year period, between mid-June and mid-September. The youngest fetus (found in mid-June) was poorly developed (14.5 mm long) and impossible to sex. Near-term fetuses (approx. 65 mm long and close in cranial dimensions to neonates) were found in late August and mid-September. Young infants were captured in October. More recently, *L. edwardsi* was studied at Ankarafantsika by Rasoloharijaona et al. [2000]. All infants were born in late September and early October. A month-old, nursing infant fell victim to infanticide in early November.

During the 1860s, Pollen and van Dam collected *Lepilemur dorsalis* at Anorontsangana in northwest Madagascar. Detailed records of many of their collection dates are lost; however, we know that 'very young' individuals were captured in late 1868 [Jentink, 1887].

Some data are available for *Lepilemur sp.* (originally incorrectly identified as *L. microdon*) at Ranomafana; here, infants typically emerge from their nests in tree holes, fairly well-developed, in late September [P.C.W., pers. observation]. During the months of June and July 1995, Porter [1998] followed a juvenile (non-nursing) female and 2 associated individuals of unknown age and sex, one of whom shared her sleeping site and was presumed to be her mother. The juvenile had a body mass about 70% that of adults; she was perhaps 8–10 months old.

The birth season for *Avahi* is best known for populations in the eastern rain forest. At Andasibe, Ganzhorn et al. [1985] recorded 4 births of *A. laniger* in August and September. Harcourt [1991] similarly observed the birth of an infant *A. laniger* in August. Births have been recorded at Ranomafana from August 18 through late September [P.C.W., pers. observation]. In 1993, an infant was born in Roth's [1996, p. 25] study group at Ranomafana 'between September 29 and October 7.' To our knowledge, this is the latest birth record for *A. laniger*. Weaning

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[2] On the basis of his extensive fetal collection, Kaudern [1914] thought that gestation length in *L. edwardsi* could not exceed 3 months. Longer gestations have been presumed by field workers since then [e.g. Petter et al., 1977].

Table 5. Growth and dental development in *Avahi*, highlighting individuals with their first permanent molars erupting

Species and specimen No.	Dental development stage	Bizygomatic breadth, mm	Cranial length mm	Capture date and inferred age months
Avahi laniger MNHN 1882.1500	0.423	16.5 (44.2)	32.5 (60.44)	September 21; <1 month
Avahi laniger MNHN 1882.1499	0.423	18.0 (48.3)	32.7 (60.8)	September 18; <1 month
Avahi laniger MCZ 16454	0.442	21.3 (57.1)	37.6 (69.9)	September 29; 1 month
Avahi laniger MNHN 1871.229	0.462	19.1 (51.2)	36.9 (68.6)	October 9; 1 month
Avahi unicolor VNH 23118	0.596	21.6 (60.6)	39.2 (76.5)	–
Avahi laniger AMNH 170500	0.673	27.4 (73.5)	46.0 (85.6)	mid-October; 1–2 months
Avahi laniger MNHN 1871.228	0.788	25.9 (69.4)	41.2 (76.6)	October 26; 2 months
Avahi laniger NRM 621306	0.808	26.9 (72.1)	43.4 (80.7)	–
Avahi laniger (raptor kill, Manombo)	0.865	29.4 (78.8)	–	November 14; 2.5 months
Avahi laniger MNHN A2853	0.885	27.2 (72.9)	45.0 (83.7)	–
Avahi occidentalis NRM 534214	0.904	29.6 (83.0)	44.6 (87.1)	November 22; 3 months
Avahi laniger MNHN 1986.435	0.904	–	–	November 25; 3 months
Avahi laniger (wild caught, Ranomafana)	0.962	–	–	December 16; 3.5 months
Avahi laniger USNM 83650	1.00	37.2 (99.7)	54.3 (101.0)	February; 5.5 months
Avahi laniger MNHN 1882.1489	1.00	35.4 (94.9)	52.3 (97.3)	September 15; 12 months
Avahi laniger MNHN 1882.1492	1.00	33.8 (90.6)	51.6 (96.0)	September 17; 12 months

Figures in parentheses indicate percent adult size. For a key to collection abbreviations, see table 2.

occurs in late November or December, when immature as well as mature *A. laniger* become easy raptor targets at Ranomafana [Sarah Karpanty, unpubl. data]. In January, the new weanlings are no longer carried by their mothers [Roth, 1996]. The same pattern appears to apply throughout the geographic range of this species – perhaps for all *Avahi*. An adult female *A. laniger* with a nursing infant was observed in the vicinity of Maroantsetra (in the northeast) toward the beginning of the austral summer – i.e. between September and November 1994 [N. Vasey, pers. commun.].

A stunning ontogenetic series of museum specimens underscores the precocity of dental development in *Avahi*. Milne-Edwards and Grandidier [1875, plate 44, fig. 5, 6] illustrate an *A. laniger* 'fetus'. The specimen is preserved in the osteological collection of Mammifères et oiseaux at the Muséum national d'histoire naturelle, Paris (MNHN 1871.229), where a collection date of October 9, 1870, can

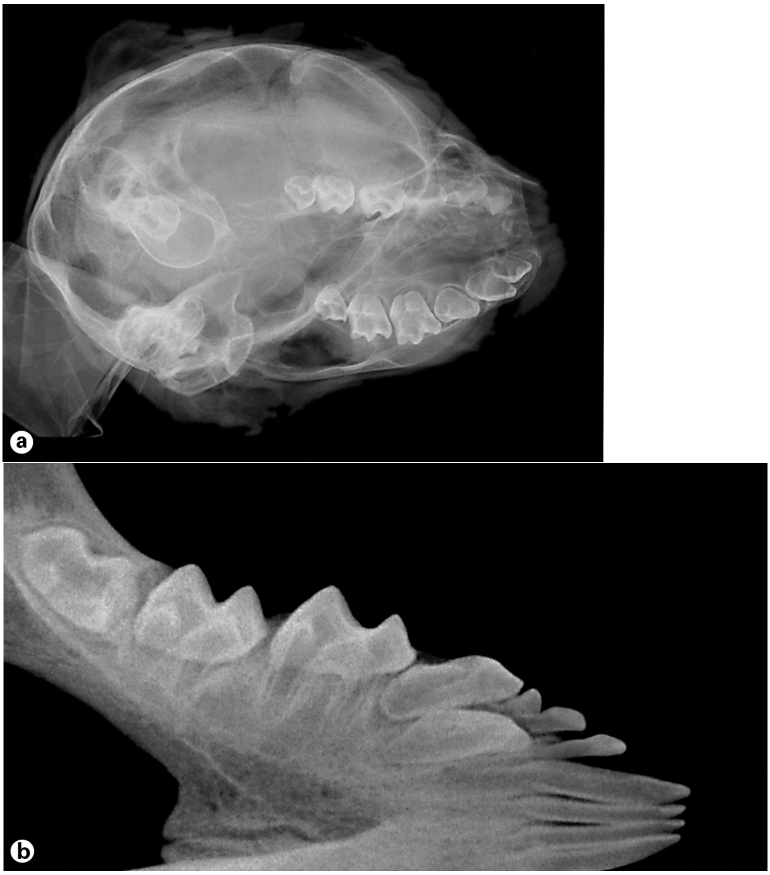

Fig. 2. Radiograph of approximately 2-month-old *A. laniger* (AMNH170500) from Eminiminy. **a** In the maxilla: adult incisors are barely erupting, dc, dp^3, P^3 beginning to erupt, P^4 erupting (already displaced dp^4), M^1 in place, M^2 beginning to erupt and M^3 in crypt. **b** In the mandible: permanent tooth comb erupting, dc, dp_2, dp_3, P_4 erupting, M_1 erupted, M_2 erupting, M_3 in crypt. The unerupted crown of P_2 is located lingual and slightly anterior to the erupting P_4, in the fashion of overlapping scales.

be inferred from capture records for its mother. All of its deciduous teeth have erupted, and the tips of the mandibular M1 as well as the lateral lower incisor (part of the tooth comb) are above the alveolar margin. Bone cutaways reveal fully or nearly fully formed crowns of all replacement teeth as well as the first 2 molars; the crown of the third molar is also at a relatively advanced state of mineralization. The skull has a small coronal fontanelle; skulls of apparently neonatal *Avahi* with September capture dates (table 5) have larger coronal as well as lambdoidal fontanelles. But even if Milne-Edwards' and Grandidier's 'fetus' was mislabeled as such, this individual could not have been more than a month old. All *Avahi* neonates in museum collections have fully erupted deciduous teeth and advanced min-

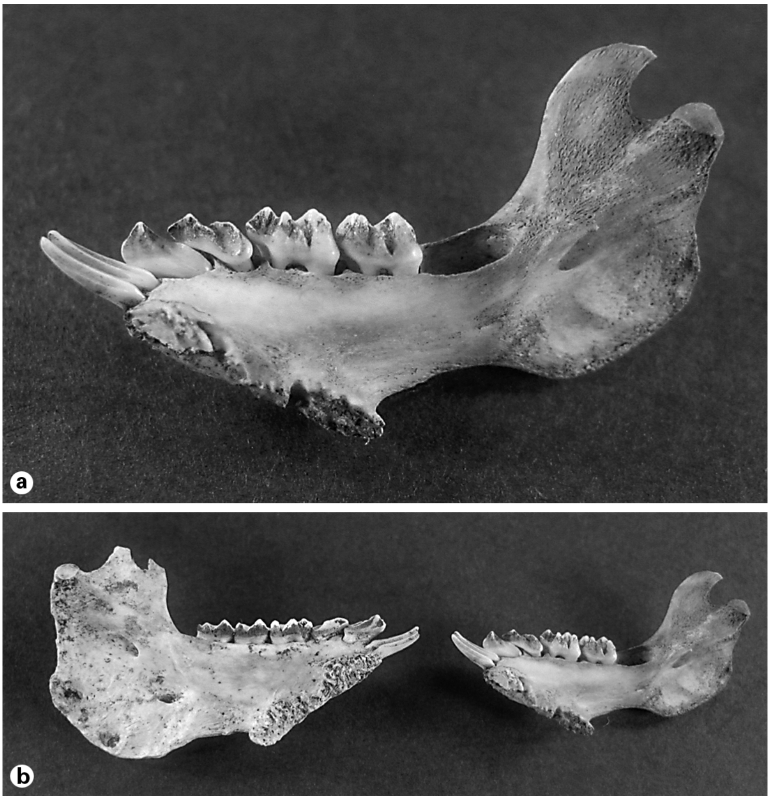

Fig. 3. a Mandible of a 2.5-month-old *A. laniger* who was killed by a raptor in mid-November 1998 at Manombo, southeast Madagascar. This specimen illustrates imbrication of P_2 and P_4 upon eruption. The long axis of P_4 is oriented obliquely (mesiobuccally to distolingually) such that the anterior moiety of its lingual face borders the distal moiety of the buccal face of the crown of P_2. This imbrication can exceed 50% of the total premolar crown length even after these teeth have erupted fully. (Note: there is no P_3 in indriids.) **b** Mandible of the same 2.5-month-old *Avahi* compared to that of a full adult from Ranomafana National Park (collected by Sarah Karpanty).

eralization of the permanent dentition, and the first molar is erupting (or has erupted) in all individuals with collection dates of late September or after.

Figure 2 shows a radiograph of the mandible of an *A. laniger* from Eminiminy in southeast Madagascar (AMNH 170500); eruption of the replacement dentition is well under way. This individual was collected in October and could not have been older than 2 months at death. Figure 3 shows the mandible of a slightly older individual, found by Jonah Ratsimbazafy and others in a regurgitated raptor pellet at Manombo (southeast Madagascar) on November 14, 1998. By 2.5 months, eruption of the permanent dentition is almost complete.

Kaudern [1915] described a young *Avahi occidentalis* (NRM 534214, in alcohol, from Sainte Marie de Marovoay) that was brought to him on November 22,

Fig. 4. Photograph of fully-weaned, 3.5-month-old *A. laniger*, captured on December 16, 2002. This individual has its full adult dentition (although the third molars are not in full occlusion). Photograph by Désiré Randrianarisata.

Table 6. Inferred and documented ages (years) at M1 emergence in *Avahi*, *Lepilemur* and other primates

Taxon	Maxillary M1	Mandibular M1
Avahi spp.	<0.125	0.083
Lepilemur spp.	0.125	0.125
Aotus trivirgatus	0.40	0.36
Saimiri sciureus	0.40	0.37
Eulemur macaco	0.37	0.43
Eulemur fulvus	0.42	0.42
Chlorocebus aethiops	0.88	0.83
Macaca fascicularis	1.63	1.38
Pan troglodytes	3.33	3.26
Homo sapiens	6.38	6.24

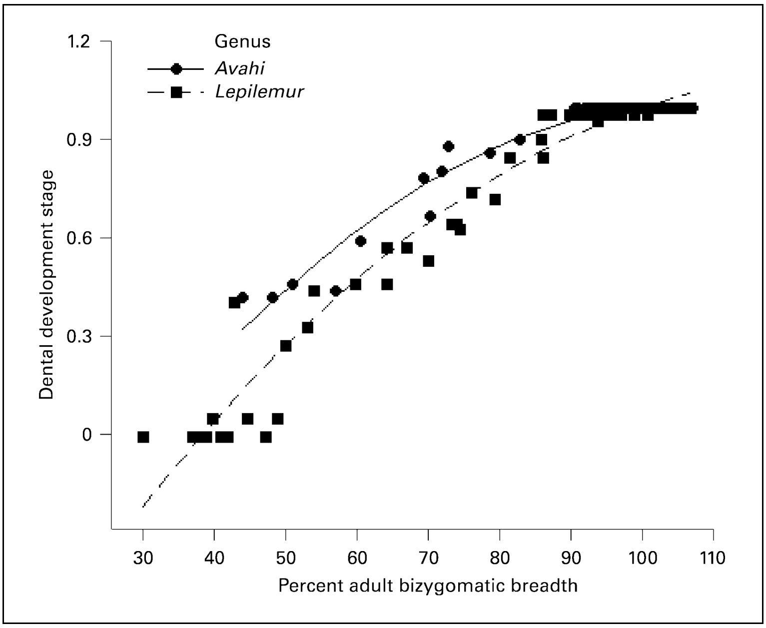

Fig. 5. Dental developmental stage plotted against percent completion of growth in skull width (bizygomatic breadth) in *Avahi* and *Lepilemur*. Quadratic functions were fitted to the data for *Avahi* and for *Lepilemur*. Note that these curves must converge at a dental developmental stage of 1.0 and 100% bizygomatic growth. Prior to adulthood, at every stage of skull growth, the predicted value for dental development in *Avahi* is higher than that for *Lepilemur*. It is clear that Schultz's rule (which would predict more rapid dental development in *Lepilemur* because of its much 'faster' eruption signature) is not supported by these data.

1906, by a Sakalava who had killed its mother. He noted the excellent development of what he mistakenly took to be this individual's milk teeth. In actuality, this individual already had most of its permanent teeth. On the basis of the infant's death date, we surmise that this individual was probably 3 months old at death. It has its maxillary adult incisors, C^1 erupting, P^3, P^4, M^1 and M^2 erupted, and M^3 unerupted but well formed in its crypt. In the mandible are the erupted adult tooth comb, P_2 almost fully erupted, P_4, M_1 and M_2 erupted, and M_3 erupting.

A 3.5-month-old *A. laniger* (weighing 400 g – about one third of adult mass) was captured by one of the authors (P.C.W.), with its mother, at Ranomafana National Park on December 16, 2002 (fig. 4). No milk could be expressed from its mother, and it can be presumed that this youngster had already been weaned. Only the third molars were not in full occlusion.

In summary, it is clear that Schultz's rule does not accurately predict differences in the pace of dental development among small-bodied, folivorous lemurs. Dental eruption does not proceed at a slower pace in *Avahi* than in *Lepilemur*, as expected under Schultz's rule. Indeed, the opposite may be true (fig. 5).

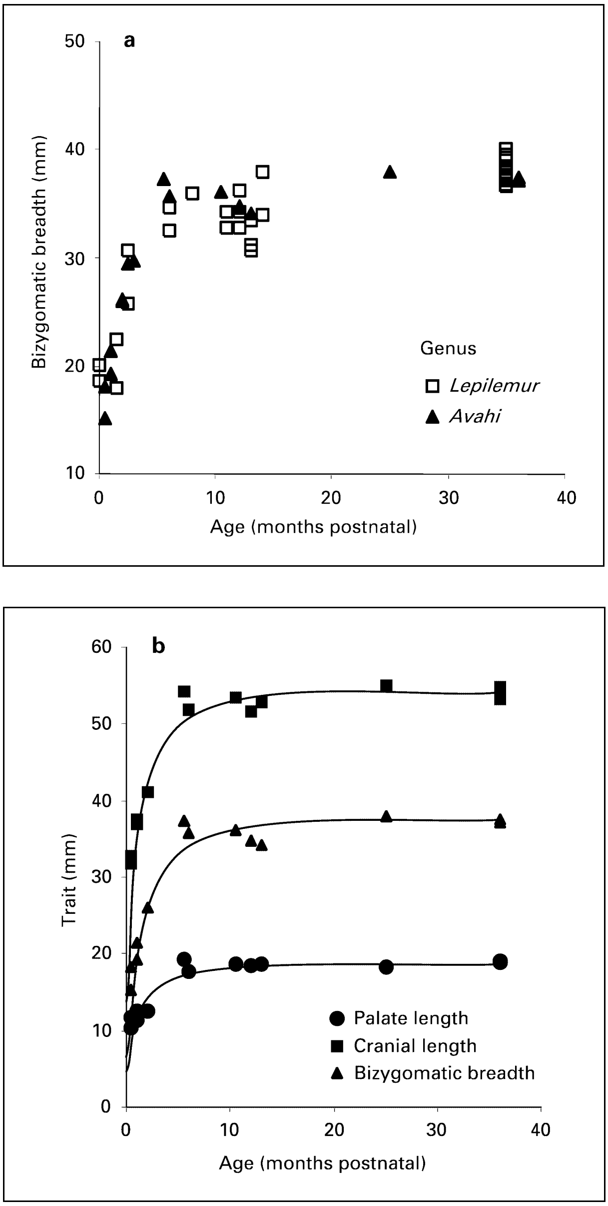

Fig. 6. a Bizygomatic breadth plotted against age (in months) for *Lepilemur* and *Avahi*. **b** Skull growth (but not postcranial growth) is complete prior to 1 year in both taxa. Note the similar ages at maturation of palate length, cranial length and bizygomatic breadth in *Avahi*.

Table 7. Results of t test for the significance of differences in dental dimensions for *A. laniger* and *L. ruficaudatus*

Trait	*A. laniger* mean, mm	*L. ruficaudatus* mean, mm	Independent sample t value	Significance p
P^2md	–	4.16	–	– (*L. ruficaudatus*)
P^2bl	–	1.97	–	– (*L. ruficaudatus*)
P^3md	4.37	3.37	7.56	0.000 (*A. laniger*)
P^3bl	2.32	2.68	–5.23	0.000 (*L. ruficaudatus*)
P^4md	3.86	3.49	2.47	0.019 (*A. laniger*)
P^4bl	2.78	3.28	–7.86	0.000 (*L. ruficaudatus*)
M^1md	4.17	3.88	3.07	0.004 (*A. laniger*)
M^1bl	3.90	3.89	0.09	NS
M^2md	3.82	3.69	1.61	NS
M^2bl	3.83	3.99	–1.45	NS
M^3md	3.07	3.27	–1.94	NS
M^3bl	3.20	3.55	–4.09	0.000 (*L. ruficaudatus*)
P_2md	4.39	4.48	–0.80	NS
P_2bl	1.77	2.14	–7.85	0.000 (*L. ruficaudatus*)
P_3md	–	4.07	–	– (*L. ruficaudatus*)
P_3bl	–	1.89	–	– (*L. ruficaudatus*)
P_4md	4.34	3.76	4.8	0.000 (*A. laniger*)
P_4bl	1.96	2.20	–2.8	0.008 (*L. ruficaudatus*)
M_1md	4.39	4.24	1.56	NS
M_1bl	2.84	2.71	2.58	0.014 (*A. laniger*)
M_2md	3.84	4.12	–3.01	0.005 (*L. ruficaudatus*)
M_2bl	2.95	2.80	2.66	0.012 (*A. laniger*)
M_3md	4.09	4.51	–4.73	0.000 (*L. ruficaudatus*)
M_3bl	2.84	2.50	4.78	0.000 (*A. laniger*)

The species with the significantly larger value is given in parentheses. NS = Not significant.

According to Schultz's rule [Smith, 2000], the *relative* timing of molar eruption is related to the *absolute* rate of growth of the jaws. It is presumed that the molar teeth cannot erupt *relatively* late if they also erupt at an early age. It is also presumed that the first molars will not erupt when the jaws are very small. All of these assumptions are violated in *Avahi*. Molar eruption is accelerated in *Avahi*, but the eruption of the replacement teeth is even more accelerated.

The teeth of mammals are essentially dysfunctional before they come into occlusion. Early replacement (i.e. prior to weaning) probably reduces the negative impact of the temporary loss of masticatory function that occurs when pairs of deciduous teeth are shed, but before their replacements come into occlusion. Furthermore, the sequence of eruption of permanent teeth is probably of little functional import when the eruption of the entire dentition is accelerated. Effectively, eruption occurs nearly simultaneously. When infants can no longer depend on their mothers to satisfy their nutritional needs, an operational battery of teeth, capable of meeting the mechanical demands imposed by the foods to be processed, must be available.

Table 8. Mean occlusal areas (mm^2) for the maxillary and mandibular dentitions

Genus and tooth row examined	Total premolar occlusal area	Total molar occlusal area	P2	P3	P4	M1	M2	M3
Avahi maxilla	20.89	40.89	–	10.16	10.73	16.26	14.59	10.04
Lepilemur maxilla	28.68	41.42	8.20	9.03	11.45	15.09	14.72	11.61
Avahi mandible	16.28	35.42	7.77	–	8.51	12.47	11.33	11.62
Lepilemur mandible	25.55	34.42	9.59	7.69	8.27	11.56	11.56	11.30

Mesiodistal × buccolingual diameters are summed for premolars and for molars independently to yield totals.

Both *Avahi* and *Lepilemur* have highly fibrous diets and are dentally precocious at weaning [Godfrey et al., 2001, 2003, 2004]. What is surprising is the degree to which they achieve that precocity via different routes.

Avahi and *Lepilemur* have similar rates of growth of the skull and jaws; skull growth is virtually complete at approximately 6 months in both (fig. 6). Their different eruption sequences cannot stem from differences in rates of skull or jaw growth. Nor does *Avahi* achieve rapid dental development by decreasing the sizes of its permanent teeth (table 7).

How, then, does *Avahi* achieve an eruption *pace* that is at least as accelerated as that of *Lepilemur*, along with an eruption *sequence* that resembles those of primates with exceedingly slow dental development and eruption? Our data are suggestive on this question. First, *Avahi* has nearly vestigial deciduous teeth that erupt at or before birth, crowding into the anterior portion of the jaw and making room for the developing crowns of the replacement teeth as well as the molars behind them. As in other indriids, several of the deciduous teeth have no replacements. Due to their marked imbrication prior to eruption and bilateral compression, the developing crowns of the replacement teeth require little space. (This is particularly important in the mandible, which is constrained by the horizontally procumbent tooth comb to be shorter than the maxilla.) Protrusion of the mesial portion of the crown of P_2 well beyond the anterior border of its root allows the total (mesiodistal) length of the cheek teeth to exceed the length of the mandibular corpus in immature *Avahi*. Finally, loss of a pair of permanent premolars and the outermost tooth of the tooth comb (the lower canines) reduces the space requirements for the developing replacement teeth. Schultz's rule fails because its assumption (that the pace of eruption of the molars as well as the relationship between the eruption of the molars and replacement teeth are determined by the rate of growth of the jaw) is not always correct. Other factors affect the sequence and schedule of eruption of the permanent teeth.

Many of these traits are not unique to *Avahi* but are shared by its close relatives – the indriids (*Propithecus* and *Indri*) and the larger-bodied, extinct palaeopropithecids. All members of the indriid-palaeopropithecid clade lack a pair of permanent premolars and the adult mandibular canines. All have or appear to have had milk teeth that are essentially vestigial. All have strong shearing crest development [Jungers et al., 2002]. The total occlusal area of the premolars is indeed smaller in *Avahi* than in *Lepilemur* (table 8), but the shearing crest ratio is higher in the former. Accelerated molar crown formation has been confirmed for at least one of the palaeopropithecids as well as *Propithecus* [Schwartz et al., 2002].

Discussion

In this paper, we asked whether or not two folivorous, small-bodied strepsirrhine species with rapid dental eruption also exhibit the 'fast' sequence signature of tooth eruption, as predicted by Schultz's rule. We also asked whether any deviations from the expectations of Schultz's rule might relate to early eruption of the tooth comb in these species. Our expectation was that differences in the *pattern* (or relative order) of dental eruption should reflect differences in the *pace* (or absolute timing) of dental eruption. Finally, we asked whether, among small-bodied folivorous lemurs, the species with the 'faster' eruption signatures also exhibit faster eruption of the permanent dentition (on an absolute scale).

We found that, contrary to expectations based on Schultz's rule, there is little correspondence between the sequence and pace of dental eruption among small-bodied, folivorous lemurs. The eruption *sequences* of *Lepilemur* and *Avahi* are entirely different, despite both having rapid dental development. Indeed, the pace of dental eruption may be *faster* in the lemur with the classic signature of species with *slow* eruption schedules. Furthermore, the tooth comb can erupt before (as in *Avahi*) or after (as in *Lepilemur*) the emergence of the second permanent molar. Our expectations derived from Schultz's rule were not met, not merely with regard to the unique sequence position of tooth combs, but with regard to the relationship between the sequence of dental eruption and the pace (or absolute schedule) of dental eruption.

Three caveats must be interjected at this point. The first is that exceptions to Schultz's rule do not establish its failure as a statistical generalization. Schultz's rule may work for many species without being universal. We would maintain, however, that its failure to predict the pace of dental development in lemurs serves as a cautionary tale and argues against its use for paleontological inference, particularly when dealing with strepsirrhine primates. Furthermore, we would argue that, if Schultz's rule fails under certain circumstances, it is important to understand what those circumstances are.

Secondly, the data presented here have no bearing on the question of whether the pace of dental development is or is not a good proxy for the timing of reproduction. There is good evidence that, at least for strepsirrhines, it is not. A discussion of this is beyond the scope of this paper, but see Godfrey et al. [2004].

Finally, the data presented here have little bearing on Schultz's [1935, p. 540] main argument, which was not that dental eruption *sequence* predicts *pace*, but that relatively early molar eruption may be a primitive mammalian character that reflects a 'fast' (or short) life history. Our data do not contravene this possibility. The 'slow' pattern of dental eruption in *Avahi* is highly unusual in strepsirrhines (although not very different from those of the other indriids, *Propithecus* and *Indri*, both of which exhibit relatively early eruption of the premolars). The 'fast' pattern observed in *Lepilemur* and lemurids is manifested broadly among primitive primates and members of other archontan orders; it may be primitive for primates.[3]

For example, Smith [2000] notes that the replacement incisors and premolars erupt after the appearance of the third molar in *Tupaia*. In *Plesiadapis*, the premolars erupt after M3; in the paromomyid *Acidomomys*, the premolars begin to erupt with the third molar [Bloch et al., 2002]. Hogg et al. [2003] report a similar 'fast' eruption signature for *Notharctus*. The extant and extinct lemurs of Madagascar show variable eruption sequences (particularly with regard to the relative timing of eruption of the incisors [Lamberton, 1938; Schwartz, 1974, 1975; Simons, 1997]), but 'fast' patterns do occur [King et al., 2001]. In *Megaladapis*, the maxillary premolars erupt after M^3 and at least 2 of the 3 mandibular premolars erupt after M_3. In *Hadropithecus*, both mandibular and maxillary premolars erupt after the third molar. *Archaeolemur majori* resembles *Hadropithecus* in its eruption sequence; *Archaeolemur edwardsi* and its northern variant (*A*. sp. cf. *edwardsi*) differ from the former in that only 1 premolar erupts after M_3, 2 of the 3 mandibular premolars erupt before the third but after the second molar. (What is peculiar about *A*. sp. cf. *edwardsi* is the extreme delay in the relative timing of eruption of the incisors, which also erupt after the third molars; see Simons [1997].)

A growing literature in primatology explores the links between dental development, diet and life history patterns [Schultz, 1935, 1960; Smith, 1994, 2000; Leigh, 1994; Harvati, 2000; King et al., 2001; King, 2003; Godfrey et al., 2001, 2003, 2004; Hogg et al., 2003]. Other researchers have focused mainly on the phylogenetic correlates of variation in dental developmental sequences (for strepsirrhines, see especially Schwartz [1974, 1975]). Still others, including proponents of 'sequence heterochrony'[Mabee and Trendler, 1996; Velhagen, 1997; Smith, 2001, 2002; Bininda-Emonds et al., 2002; Bloch et al., 2002; Jeffery et al., 2002a, b], analyze both the phylogenetic as well as potential ecological and life history correlates of developmental patterns and sequences. In fact, we would maintain that one cannot fully understand the variation in dental developmental sequences and rates among lemurs without taking all of these factors into consideration.

Conclusions

Schultz's rule is predicated on the notion that the relative timing of eruption of the molars and the replacement teeth is controlled by the rate of growth of the jaw. This is assumed to be rapid in species with relatively early-erupting (presumably rapidly forming) molars and slow in species with relatively late-erupting (presumably slowly forming) molars. Thus, according to Schultz's rule, a *dental eruption sequence* signal (involving the relationship between the sequence of eruption of the permanent replacement and the primary teeth) can predict the absolute

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[3] Cheirogaleids, bushbabies and lorises tend to share another general pattern (which is typical neither of the fast nor slow signatures described by Schultz), whereby the anteriormost premolar tends to erupt early, but the posterior and middle premolars erupt very late – after the third molar. Schwartz [1974, 1975] argued that the sequence of permanent tooth eruption exhibited by *Lepilemur* cannot be primitive for primates. This inference was based on the apparently unusual sequence of eruption of the premolars in *Lepilemur* (distalmost to mesialmost); it was not based on the relationship between premolar and molar eruption.

timing of dental eruption. Schultz's rule is attractive because it implies that life history signals can be gleaned from patterns easily observed in the fossil record – at least to the extent that the pace of dental development does reflect the overall pace of life histories.

We have shown, however, that the lemurs of Madagascar do not reliably follow Schultz's rule. 'Fast' or 'slow' dental eruption cannot be inferred solely on the basis of the sequence of primary and replacement tooth eruption, as species may exhibit fast dental eruption, but achieve it in different ways. *Lepilemur* displays the classic signature of species with fast eruption schedules and rapid dental eruption. *Avahi* displays the classic signature of species with slow eruption schedules and even faster dental eruption. Schultz's rule must be modified to take into account the various manners in which rapid eruption can be achieved. Within primates, *Avahi* is the most extreme example of dental acceleration in a species with a classic 'slow' sequence of dental eruption.

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