

## Somatic Variation in Living, Wild Ring-Tailed Lemurs (*Lemur catta*)

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### Key Words

Dental variation · Plasticity · Growth and development · Teeth · Mammal · Beza Mahafaly Special Reserve · Tsimanampesotse

### Abstract

While understanding somatic variability among wild primates can provide insight into natural patterns of developmental plasticity, published data for living populations are rare. Here we provide such information for two distinct wild populations of *Lemur catta*. Variants observed include microtia, athelia, and female virilization. Dental variants observed include individuals with supernumerary teeth, rotated teeth, maxillary incisor agenesis, and severe malocclusion. There was a sex bias in incisor agenesis, with 5 of 7 examples (71%) found in males. The frequency of dental variants in our sample is lower than that seen in many other lemuriformes, as well as other primates. This may be a product of their less derived dental formula and/or their relatively fast dental development. Amassing such data is a critical first step to assess if wild primate populations are exhibiting normal variability or are being affected by potential inbreeding and/or environmental effects.

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### Introduction

Understanding the range of natural phenotypic variability in wild populations is obviously important, as it provides us with insight into the process of evolution. Ranges of population variation also provide important points of comparison for interpreting taxonomic affinities in fossil assemblages, including among fossil humans [Jacob et al., 2006]. All variation is not equivalent as some occurs outside the norm in terms of survival and/or reproduction. Norms of variation (those not at odds with survival and/or reproduction) are thus important in elucidating the inter-

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play between environment and genetics. However, to date there is a paucity of data on the ranges of biological variability in wild primate populations. In studies of variation in the wild it is perhaps useful to go back to Darwinian basics and contemplate variation outside the norm in terms of survival and reproduction, as these variants or varieties might be the relevant measures of normal, absolute ranges of somatic variation in natural populations. This is especially important given variation's role as the raw material for natural selection and, thereby, evolution [Darwin, 1859; Simpson, 1944]. In this paper, we document the range of such variation, emphasizing varieties as the 'edges' of variation, among two wild populations of ring-tailed lemurs.

## Methods

Ring-tailed lemurs, *Lemur catta*, living within the gallery forest portion of the Beza Mahafaly Special Reserve, Madagascar (23°30'S, 44°40'E), have been the focus of ecological, behavioral and biological studies since 1987 [see summary in Sauther et al., 1999]. Much more recently, research has been expanded outside this protected reserve to focus on how anthropogenic factors are affecting the behavior and biology of this species [Sauther et al., 2006]. This is a seasonal habitat with both dry (June to September) and wet (October to May) seasons [Sauther et al., 1999; Ratsirarson, 2003]. As of 2006, there were approximately 225 individuals in the study area, which included Beza Mahafaly Special Reserve and a 9 km<sup>2</sup> area of fragmented forest south and west of the reserve [Sauther and Cuozzo, unpubl. data]. Groups within three habitats were studied: reserve, degraded, and marginal. The reserve habitat is within the Beza Mahafaly Special Reserve, and is 80 ha of intact gallery forest that has not been affected by human disturbance for over 20 years. The degraded habitat is next to the reserve, it includes a camp for the researchers and, throughout 2004, a number of local Mahafaly families also lived on the site. The adjoining forest has been highly impacted by members of local villages, with portions of the riverine forest now removed for the planting of local crops, and grazing by goats and cattle is a common occurrence [Whitelaw et al., 2005]. Lemurs within this habitat commonly encounter humans and domestic animals and these lemurs readily exploit human resources such as crops, water sources, and cattle forage. It should be noted that the Mahafaly who live there do not hunt lemurs, and it is a cultural taboo to kill them [Ratsirarson, 2003]. The marginal habitat is located in a dry spiny forest approximately 3 km from the gallery forest reserve. Lemurs there live within an area dramatically impacted by grazing and the destruction and/or removal of forest products.

Prior to our research, comprehensive data on ring-tailed lemur biology, ecology, and behavior have only been collected from riverine gallery forests [Sauther et al., 1999]. During May and June 2006, we collected comparative biological data (and preliminary information on feeding ecology and behavior) from the ring-tailed lemurs at the Tsimanampesotse National Park, on the southwestern coast of Madagascar. Although there is some overlap with Beza Mahafaly in terms of plant species [Sauther et al., in preparation], the habitat at Tsimanampesotse differs substantially from that of the riverine gallery forest at Beza Mahafaly, consisting of (1) a dry limestone spiny forest along the escarpment forming the edge of the Mahafaly Plateau and (2) a mixed deciduous forest with few tamarind trees adjacent to an alkaline carbonate playa lake. Unlike Beza Mahafaly, this park has only minimal human disturbance. The only previous data reported for the ring-tailed lemurs at Tsimanampesotse focused on biomedical values from a sample of 20 individuals [Dutton et al., 2003].

### *Lemur Sampling Protocol*

All methods and materials followed animal handling guidelines (Institutional Animal Care and Use Committee, University of Colorado and University of North Dakota). The research team included trained veterinarians as well as two members of the Beza Mahafaly eco-

logical monitoring group, Enafa (who has over 15 years of darting experience) and Ehandidy Ellis (who has 5 years of darting experience). Darting was done with a Telinject and/or Daninject blowgun system and either ketamine hydrochloride or Telazol, using doses that have been worked out over the past 18 years of captures [see summary in Cuzzo and Sauter, 2006]. All captures occurred in the morning to allow lemurs time to recover in order to be released before nightfall on the same day. The captured individuals were transported to the camp's laboratory. Biological data were collected while the lemurs were under general anesthesia, based on protocols developed by Drs. Randy Junge, DVM and R. Eric Miller, DVM of the St. Louis Zoo, and Dave Miller, DVM of the Colorado State University Veterinary Teaching Hospital. A basic medical evaluation of each sedated lemur included heart rate, respiratory rate, temperature, and a physical examination of the whole body. All individuals successfully integrated back into their groups, and maintained their previous social ranks. Biological and morphological data were collected from a total of 250 individual lemurs (111 females and 139 males) from three separate time periods at Beza Mahafaly: 1987, 1995 and 2003–2006. Dental data from Beza Mahafaly are presented only for the 161 individuals captured between 2003 and 2006. Morphological, biological, and dental data from Tsimanampesotse are based on a sample of 25 individuals (10 females and 15 males) captured during May and June of 2006, following the same protocol used at Beza Mahafaly.

## Results

Of the 275 individuals evaluated, 7 (2.6% of the entire sample) were found to exhibit some form of nondental somatic variation not related to trauma or injury, based on veterinary and a range of other biological assessments (table 1). Six of the 7 individuals were observed at Beza Mahafaly. A total of 12 (6.5%) of the 186 individuals for which dental data were collected (8 of 161 at Beza Mahafaly, 4 of 25 at Tsimanampesotse National Park) exhibit some form of dental variant (table 2). Hence, a total of 19 somatic and/or dental examples were identified across 17 individuals, with 2 individuals exhibiting multiple variants (male 166 of the orange troop at Beza Mahafaly Special Reserve displays both a somatic and a dental variant, and an adult male at Tsimanampesotse National Park possesses two dental variants).

### *Microtia*

Microtia refers to a congenital maldevelopment of the external ear, with or without absence or narrowing of the external auditory canal [Stach, 1998]. Figure 1a shows male 136 of blue troop, a ring-tailed lemur, who exhibits microtia. The atypical right ear of this individual is shown in figure 1b, and the normal left ear is illustrated in figure 1c. A close examination by the authors and our field veterinarian indicates no evidence of trauma; in fact all parts of the ear are present but are reduced in size.

### *Digital Deformities*

Two individuals were observed with fleshy growths on the sides of what are otherwise normal-appearing fingertips (fig. 2). One old adult female, 156 (18 years old in 2006), has a large preaxial fleshy growth on the side of the fingertip of the third digit of her right hand. One adult male, 166, exhibits a similar large preaxial fleshy growth on the side of the second digit of the right hand. Both individuals were from the same group (orange troop).

**Table 1.** Spontaneous somatic variability in selected captive and wild mammals including humans<sup>1</sup>

	Number of cases	Comments	References
<b>Microtia</b>			
Ring-tailed lemur ( <i>L. catta</i> )	1	Wild, adult male, Beza Mahafaly; percentage in this wild population over time is 0.4% (1/250)	Sauther and Cuozzo [this volume]
Humans	–	Percentage is 0.01% (1/7,000)	Stach [1998]
<b>Digital deformity</b>			
Ring-tailed lemur ( <i>L. catta</i> )	2	Wild, 1 old adult female with a large preaxial fleshy growth on the side of the fingertip of the right hand; 1 adult male with a large preaxial fleshy growth on the side of the second digit of the right hand; both individuals exploit areas influenced by anthropogenic change (see text); percentage in this wild population over time is 0.8% (2/250)	Sauther and Cuozzo [this volume]
Red ruffed lemur ( <i>Varecia rubra</i> )	1	Captive, Duke Primate Center; a female born with a deformed right arm (very small, misshapen, and underdeveloped); this female has reproduced and given birth to normal infants	C. Williams [pers. commun.]
Potto ( <i>Perodicticus potto</i> )	1	Captive, microdactyly	Schultz [1956]
Black-mantled tamarin ( <i>Saguinus nigricollis</i> )	1	Captive, syndactyly	Hetherington et al. [1975]
Common marmoset ( <i>Callithrix jacchus</i> )	1	Syndactyly/ectrodactyly, hand/foot	French [1986]
Spider monkey ( <i>Ateles</i> sp.)	1	Captive, microdactyly	Schultz [1956]
Mandrill ( <i>Mandrillus</i> sp.)	2	Captive, brachydactyly/oligodactyly (n = 1), split food (n = 1)	Hill [1962]; Schultz [1972]
Anubis-Hamadryas hybrids	?	Wild, from the Awash; fleshy growths on the sides of fingers, similar to that described for wild ring-tailed lemurs	J. Phillips-Conroy [pers. commun.]
Rhesus macaques ( <i>Macaca mulatta</i> )	15	Captive, polydactyly (n = 8), syndactyly (n = 3), split hand/foot (n = 3), oligodactyly (n = 1)	Valerio [1969]; Primack et al. [1972]; Schultz [1972]; Petersen et al. [1997]; Brignolo [2002]
Japanese macaques ( <i>Macaca fuscata</i> )	variable, depending on troop	Wild, fluctuates over time; ranges from 4 to 40%	Furuya [1966]; Homma [1980]; Iwamoto [1967]; Yoshihiro et al. [1979]; Newell [1971]
Proboscis monkeys ( <i>Nasalis larvatus</i> )	1 of 31 (3.2%)	Polydactyly	Schultz [1972]
Langurs ( <i>Presbytis</i> sp.)	1 of 83 (1.2%)	Polydactyly	Schultz [1972]
Gibbons ( <i>Hylobates</i> sp.)	18 wild, 11 skeletal	Wild; 18 of 113 (16%) had postaxial polydactyly of hands or feet; skeletal population, wild shot; 9.2% (11 of 120) exhibited various digital anomalies	Schultz [1944, 1972]
Bonobos ( <i>Pan paniscus</i> )	–	Wild; brachydactyly (2 cases); abnormal digit enlargement (16 digits); dwarfing of digit (2 cases); zygodactyly (85 cases); 49% (96 of 47) showed webbing in at least one foot	Kano [1984]
Chimpanzee ( <i>Pan troglodytes</i> )	4	Wild, captive; polydactyly, foot (n = 1); split foot (n = 1); monodactyly (n = 1); adactyly, hand (n = 1)	Goldschmidt [1910]; Pearson [1931]; Rahm [1967]; Schultz [1972]
Orangutan ( <i>Pongo</i> sp.)	2	Polydactyly (n = 1); oligodactyly, foot (n = 1)	Bolau [1877]; Schultz [1956]

**Table 1** (continued)

	Number of cases	Comments	References
Lowland gorilla ( <i>Gorilla gorilla gorilla</i> )	1	Anomaly of the hallux	Hill and Sabater [1971]
Human	–	Polydactyly: 0.05–0.19% (5–9 per 10,000 live births in different populations)	Zguricas et al. [1999]
<b>Virilization<sup>2</sup></b>			
Ring-tailed lemur ( <i>L. catta</i> )	2	Wild; 1 female with a male carpal spur on the right wrist, female type carpal spur on the left; 1 female with male-like labia, clitoris appears functionless, with vaginal opening in an atypical position above the clitoris; percentage in this wild population over time is 1.8% (2/111 females)	Sauter et al. [2006]; Sauter and Cuozzo [this volume]
Ring-tailed lemur ( <i>L. catta</i> )	2	Captive (Indianapolis Zoo); mother-daughter exhibited large male carpal spurs on both wrists, accompanied by male-like stink fighting; the mother continued to reproduce, the daughter was recommended not to breed; percentage in this captive population over time is 5% (2/40 females)	C. Lent and L. Villers [pers. commun.]
Tufted capuchins ( <i>Cebus apella</i> )	9	Clitoral length of juvenile females significantly longer than adult females	Carosi et al. [2001]
Polar bear ( <i>Ursus maritimus</i> )	4	Wild; female intersexuality, no male Y chromosome DNA present; 1.5% (4/269)	Wiig et al. [1998]
Polar bear ( <i>Ursus maritimus</i> )	11	Wild; female intersexuality; chromosomal abnormalities, male Y chromosome DNA present in only 1 bear; other possible causes for the remaining 10 are fetal exposure to androgens, tumors, freemartinism and exposure to environmental contaminants	Carmichael et al. [2005]
Black bear ( <i>Ursus americanus</i> )	4	Wild; female intersexuality; chromosomal abnormalities, male Y chromosome DNA present	Cattet [1988]
Brown bear ( <i>Ursus arctos</i> )	1	Wild; female intersexuality; chromosomal abnormalities; male Y chromosome DNA present	Cattet [1988]
Fossa ( <i>Cryptoprocta ferox</i> )	8 juvenile females	Wild; each possessed several masculine features including an enlarged clitoris, an enlarged os clitoridis and penile spines, when compared to adult females; all of these traits appear transient, as they are not seen in adults	Hawkins et al. [2002]
Humans	–	Male intersexuality between 3 and 15 per 100,000; female intersexuality between 1 and 8 per 100,000 people	Rappaport [2000]
<b>Polythelia</b>			
Ring-tailed lemur ( <i>L. catta</i> )	1	Wild; contrary to prior reports, the usual complement of nipples in adult ring-tailed lemur females is two pairs; 1 individual at Tsimanampesotse in 2006 displayed a third pair of pectoral nipples; percentage in this total wild sample is 4% (1/24); only females were regularly evaluated for polythelia	Sauter and Cuozzo [this volume]
Ring-tailed lemur ( <i>L. catta</i> )	3	Captive (Indianapolis Zoo); 3 females had three pairs of pectoral nipples; percentage in this captive samples is 33% (3/9)	Sauter and Cuozzo [this volume]
Mouse lemurs ( <i>Microcebus</i> sp.)	–	Wild (Ranomafana); ‘several’	P. Wright [pers. commun.]
Formosan macaque ( <i>Macaca cyclopis</i> )	109	Wild; 1–6 extra nipples; found in 33% of population; 42.2% (89/211) of females and 17% (20/117) of males show this; there is also a high rate of twinning (1%); may be related to founder effect and/or inbreeding in an isolated population	Hsu et al. [2000]
Rhesus macaque ( <i>Macaca mulatta</i> )	1	From a sample of 89 individuals, with a frequency of 1.1%, noted by the author as being similar to modern humans	Schultz [1948]
Rhesus macaque ( <i>Macaca mulatta</i> )	14	From approximately 1,000 individuals examined in several laboratories (approximately 1.4%)	Speert [1942] (cited in Schultz [1948])

**Table 1** (continued)

	Number of cases	Comments	References
Red howler monkeys ( <i>Alouatta seniculus</i> )	5	Wild; 5 of 13 immobilized males exhibited supernumerary nipples	Thorington et al. [1979]
Anubis baboon ( <i>Papio anubis</i> )	1	Wild	J. Phillips-Conroy [pers. commun.]
Yellow baboon ( <i>Papio cynocephalus</i> )	–	Wild	Buss and Hamner [1971]
Patas monkey ( <i>Erythrocebus patas</i> )	1	Captivity; male	Bland-Sutton [1890]
Humans	–	1–5%	Grossl [2000]; Rudolph et al. [2003]
<b>Athelia</b>			
Ring-tailed lemur ( <i>L. catta</i> )	1	Wild; adult female; examined both as a subadult and as an adult; no observable nipples; percentage in this wild population over time is 0.9% (1/111 females)	Sauther and Cuozzo [this volume]; R. Bauer [pers. commun.]; L. Gould [pers. commun.]
Human	43	Either bilateral or unilateral absence of the breast associated with or without congenital ectodermal defects	Trier [1965]
Human	1	Bilateral absence of the breast not associated with other congenital defects; may be related to failure of parathyroid hormone-related protein production	Ishida et al. [2005]

<sup>1</sup> None of these variations have been reported for captive lemurs at the Duke Primate Center [C. Williams, pers. commun.] or the St. Louis Zoo [R. Junge, pers. commun.].

<sup>2</sup> We have listed here only cases of naturally occurring virilization beyond what is normal for the species. Thus, we have not included data on naturally masculinized females such as the spotted hyena or the European mole.

**Table 2.** Dental variants in wild ring-tailed lemurs

Variant	Beza Mahafaly <sup>1</sup>	Tsimanampetse <sup>1</sup>
Supernumerary teeth	1 (1 male)	0
Rotated teeth	2 (1 male, 1 female)	1 (1 male)
Agenesis	4 (3 males, 1 female)	3 (2 males, 1 female)
Malocclusion	1 (1 male)	0
Total	8 (n = 161) <sup>2</sup>	4 (n = 25) <sup>2</sup>

<sup>1</sup> Number of individuals in the sample with this trait.

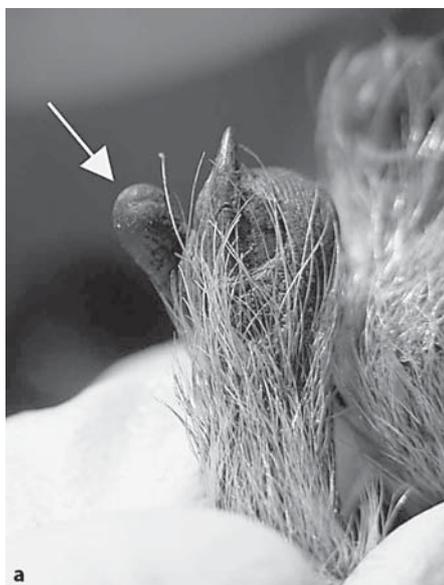
<sup>2</sup> n = Total sample size.



**Fig. 1.** Microtia in a wild ring-tailed lemur, blue 136 (a). Close-up (b) and comparison with a normal ear (c).

#### *Virilization*

Virilization refers to the development of male secondary sexual traits in a female. While ring-tailed lemurs are not sexually dimorphic in terms of body size, they do have specialized morphology that relates to scent marking. In ring-tailed lemurs, there is an antebrachial gland which in males is accompanied by a horny epidermal spur that develops on the wrist area [Montagna and Yun, 1962]. This is used to gouge

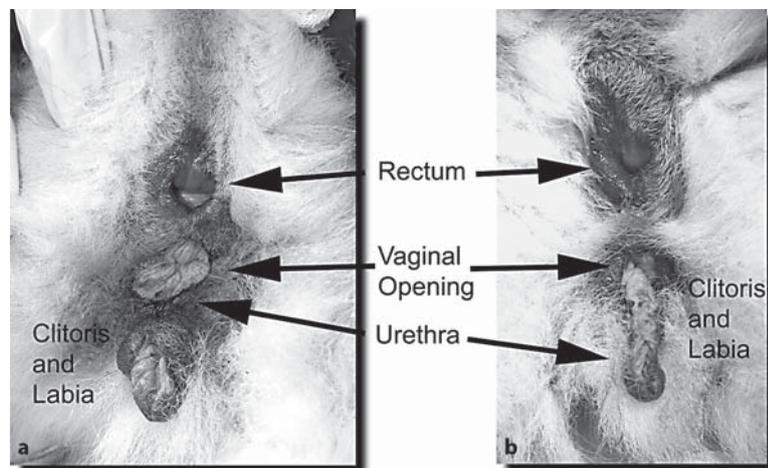


**Fig. 2.** Digital deformities in two wild ring-tailed lemurs. Both have large preaxial growths on the side of the fingertip.

and embed scent into the surface of trees and onto their tails during fights with other males (called 'stink fights' [Jolly, 1966]). In females, this area is smooth, without such spurs. A young adult female, 167 (green troop), exhibits a male-like carpal spur on her left wrist, but a carpal area that shows the usual female morphology on the right wrist (fig. 3). Another adult female, 100 (hot pink II troop), not only has scrotum-like labia, but a hypertrophied clitoris with the vaginal opening located above the clitoris (fig. 4). The labia were hard upon palpation. The urethral opening appears to be located at the base of the vaginal opening as urine was expressed here. The clitoris has no openings.



**Fig. 3.** Male-like carpal development in a wild female ring-tailed lemur, green 167. **a** Male carpal area. **b** Left wrist showing male morphology. **c** Right wrist showing a typical female carpal area.



**Fig. 4.** Unusual reproductive morphology in a wild female ring-tailed lemur, hot pink II 100. **a** Clitoris and labia. **b** Typical clitoris and labia morphology for female ring-tailed lemurs. Female 100 not only has scrotum-like labia, but the vaginal opening is located above the clitoris.

#### *Variation in Nipple Number*

In 2006, we recorded the total pairs of pectoral nipples for all adult females ( $n = 24$ ; Beza Mahafaly: 16 adults; Tsimanampesotse: 8 adults). All adult females at Beza Mahafaly had 2 pairs of nipples. At Tsimanampesotse, 6 of the 8 adults had 2 pairs of nipples, 1 adult female had only 1 pair and 1 adult had 3 pairs of nipples. In all cases, the lower pair was much smaller in length than the primary pair (e.g. female 54, tan east troop at Beza Mahafaly: primary pair right = 1.3 cm, left = 0.8 cm, lower pair right = 0.5 cm, left = 0.1 cm).

Athelia is a rare condition in which there is a complete absence of nipples/areolae [Ishida et al., 2005]. It appears to be a congenital defect that is usually associated with a variety of other conditions, but can also occur without other alterations. There has been 1 case of athelia in a female lemur at Beza Mahafaly. Female 34 (green troop), was captured twice, once as a subadult (2003) and once as a 4-year-old adult (2005). She has been examined by our field veterinarian and no identifiable nipples have ever been located. This individual exhibits no other somatic or dental variants.

#### *Dental Variation*

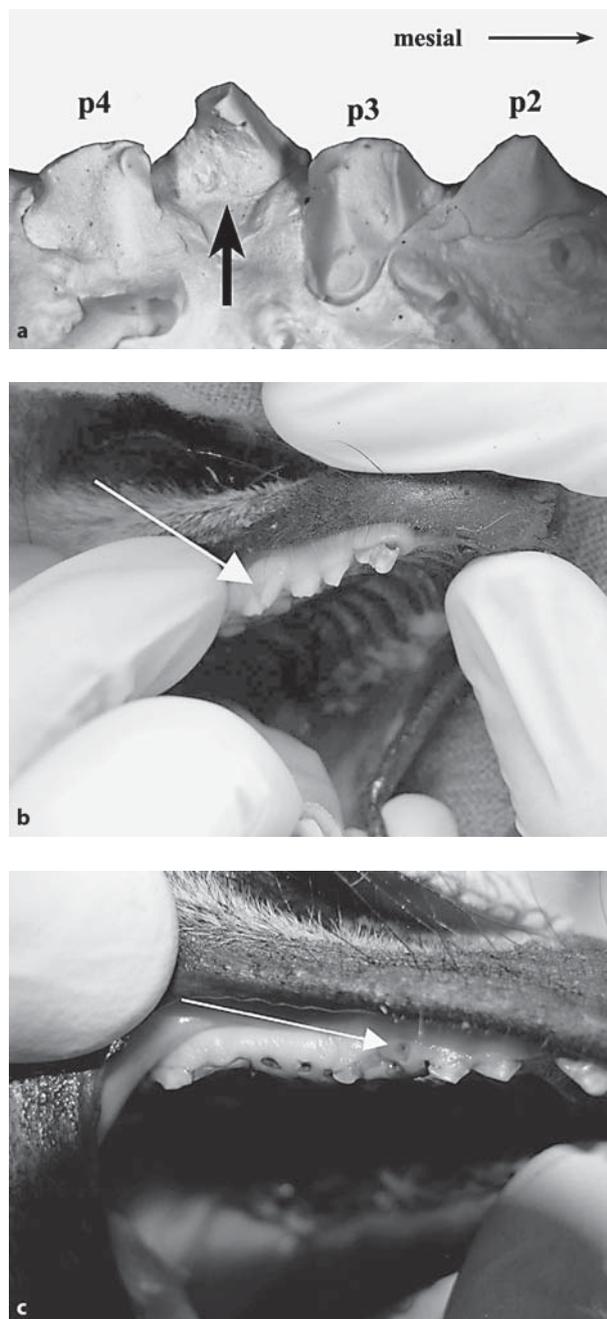
The lemurs at both sites exhibit several cases of individual dental variants. In 2005, a subadult male (light blue 253) was identified with severe dental malocclusion (fig. 5a, b). The toothcomb of this individual occludes with the left anterior maxillary dentition, including the deciduous maxillary canine, which has been worn to the root. In addition to the maloccluding toothcomb, neither of the mandibular tooth rows makes direct contact with the corresponding maxillary dentition. Malocclusion can result from a number of causes, including heredity [see reviews in Hillson, 1996; Mossey, 1999a, b]. This example appears congenital, resulting from a dis-



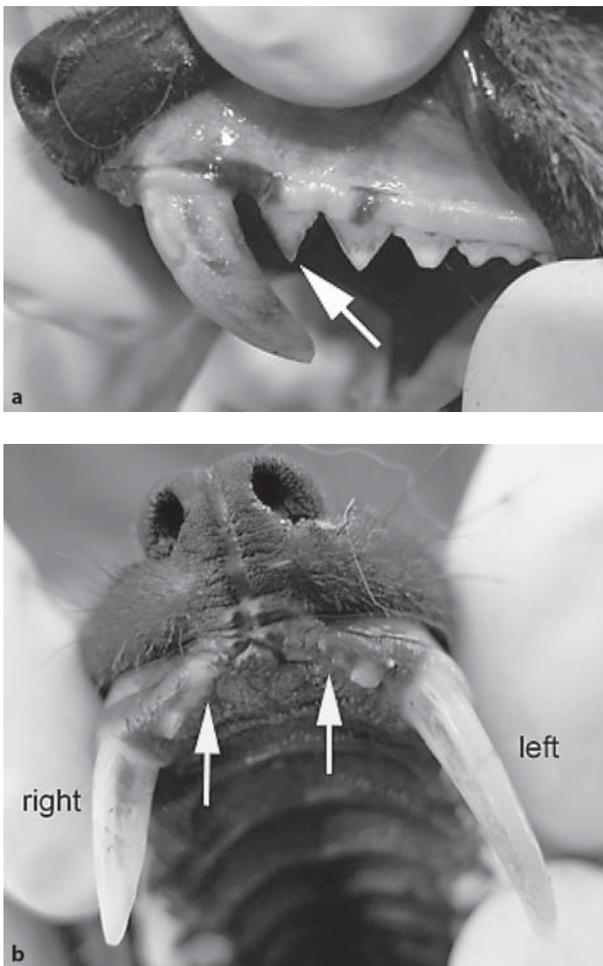
**Fig. 5.** Dental malocclusion in a wild male ring-tailed lemur, light blue 253. **a** A gap between p2 and p3 in the right tooth row indicates differential growth in the mandible, with the right ramus being 'longer' than the left, which has shifted the occlusion to the left. **b** The tooth-comb occludes with the left maxillary teeth.

ruption during development, rather than the result of injury: the left and right rami are of different lengths, with no evidence of trauma or illness. There is also a gap between p2 and p3 in the right tooth row, suggesting differential growth in the mandible, with the right ramus being 'longer' than the left. This has shifted the occlusion to the left (fig. 5b).

In 2003, we documented the presence of a supernumerary tooth in an adult male, 166 (orange troop), that also exhibits the digital deformation (see above). This individual had an extra maxillary premolar (fig. 6). The supernumerary premolar in the male 166 (fig. 6a is from a cast made in 2003) showed some wear and damage when first observed (note the heavy wear to the adjacent teeth). By 2004, this tooth had been



**Fig. 6.** Supernumerary tooth in a wild male ring-tailed lemur, orange 166. **a** Extra premolar (photo from a cast made in 2003) showing wear and damage (note the heavy wear to the adjacent teeth). **b** Extra premolar in 2004. **c** By 2005, there is only the root of this tooth remaining.



**Fig. 7.** Rotated left maxillary canine in an adult male ring-tailed lemur from Tsimanampesotse National Park. **a** Note the position of the canine and its orientation overlapping left P<sup>2</sup>. Its position precludes occlusion of the left P<sup>2</sup> with the mandibular teeth (note the unworn primary cusp of the left P<sup>2</sup> indicated by the arrow). **b** Compare the elongation of the left maxillary canine with the right tooth; also note the areas of maxillary incisor agenesia (white arrows).

worn down extensively (fig. 6b), and when examined in 2005, no trace of the tooth remained except one root (fig. 6c). This type of rapid tooth wear is not uncommon among the Beza Mahafaly ring-tailed lemurs [Cuozzo and Sauter, 2004, 2006]. We also documented 4 examples (blue 127 and blue 136, green 459 and green 209) of dental agenesia (the congenital absence of a tooth [Lavelle and Moore, 1973]) in the Beza Mahafaly population. At Tsimanampesotse National Park, 3 of 25 individuals exhibited agenesia. Each case of agenesia across both populations was an absent first maxillary incisor, with 3 of the 7 individuals (2 at Beza Mahafaly, 1 at Tsimanampesotse

National Park) missing both left and right I<sup>1</sup>. Although maxillary incisors are often lost in ring-tailed lemurs at Beza Mahafaly due to use and excessive wear [Cuozzo and Sauter, 2006], an absent maxillary incisor not associated with severe wear and tooth loss in other tooth positions is easily identified as a case of agenesis.

At Beza Mahafaly, we identified 2 individuals (yellow 221 and light blue 271) with rotated left fourth maxillary premolars. These teeth, although fully erupted, were each oriented with their occlusal surface facing distally, towards the back of the mouth. The right P<sup>4</sup> of both individuals was fully erupted, and in normal occlusion. At Tsimanampesotse National Park, an adult male was captured that displayed a severe case of maxillary canine rotation (fig. 7a). This tooth (fig. 7b) was dramatically elongated when compared to the right maxillary canine (left canine height = 13.5 mm, right canine height = 10.0 mm), and was oriented distally. The orientation of the tooth has resulted in severe damage to LP<sub>2</sub>, which has been broken off at the root, likely caused by occlusion with the abnormally oriented maxillary canine. This individual also exhibits agenesis of both maxillary first incisors (fig. 7b), the only individual with more than one dental variant in either population.

## Discussion

### *Microtia*

In table 1, we list the conditions observed in the two study populations along with examples from relevant wild and captive primate and mammal populations. We were unable to locate examples of spontaneous microtia among wild mammals. However, this condition also occurs in humans, and may be congenital in origin. The percentage in humans is 1/7,000 or 0.01%. Among the Beza Mahafaly lemurs, the percentage is higher, at 0.4% (1/250). This type of variation does not have obvious reproductive or survival implications in and of itself, and the affected male appears behaviorally normal.

### *Digital Deformities*

Existing data on primate morphological variation indicate that congenital limb and digital malformations are found in a number of primate species and within all major primate infraorders (table 1). There is a high incidence among Japanese macaques and gibbons [see review in Brignolo, 2002]. Similar finger deformities as those reported here for ring-tailed lemurs are also found among Anubis-Hamadryas baboons [J. Phillips-Conroy, pers. commun.].

### *Virilization*

As previously noted, virilization is the presence of male secondary sexual traits in a female. In humans, this may include an increase in body hair, facial hair, a deepening of the voice, male pattern baldness, and clitoral enlargement. Virilization may result from excessive testosterone production in the endocrine glands [Bagatell and Bremner, 2003]. In many lemur species, females naturally exhibit both female dominance as well as masculine-appearing genitalia [Dixson, 1998] making it a challenge to understand virilization among lemurs. In wild ring-tailed lemurs, females have an elongated clitoris as well as large labia. During the brief mating season, both become swollen which increases the male-like appearance [Van Horn and Resko, 1977].

Ring-tailed lemurs are not sexually dimorphic in terms of body size, yet they do have specialized morphologies, such as a horny wrist spur that is used for scent marking. Females typically do not have this male trait.

In our wild population at Beza Mahafaly, female 167 (green troop) exhibits both the male carpal morphology as well as the typical female morphology. This has not been reported among ring-tailed lemurs of the Duke Primate Center [C. Williams, pers. commun.] nor the St. Louis Zoo [R. Junge, pers. commun.], but it has been noted among ring-tailed lemurs of the Indianapolis Zoo. Here a mother-daughter pair each exhibited male carpal spurs on both of their wrists, and both would engage in male-like bouts of stink fighting [C. Lent, L. Villers, pers. commun.]. Similar male-like bouts of stink fighting, directed at potential predators, have been observed among Beza Mahafaly Special Reserve females who had the usual female carpal morphology [Sauther, 1989], so this behavior does occur without male-like carpal morphology. Female 167 successfully gave birth to her first infant in 2005 and, although she subsequently lost her infant, she appears reproductively normal. Given that younger female ring-tailed lemurs (3–4 years of age) experience high frequencies of infant mortality [Sauther, 1991; Sussman, 1991; Parga and Lessnau, 2005], it is unlikely her infant's death was related to this variation.

Female 100 (hot pink II) is more difficult to evaluate. Overall the labia and clitoris appear very male-like. In addition, she was captured in July, while the mating season, which normally lasts for only several weeks, occurs in May. Given that any one female is in estrus for only a short, approximately 24-hour period [van Horn and Resko, 1977; Sauther, 1991], this suggests the labia are not simply swollen as a result of estrus. The abnormal placement of the vaginal opening and urethra suggests a developmental component. It is not known if this female has reproduced as she lives in an unhabituated group that is far from the reserve. As nipples elongate over time in response to nursing behavior in ring-tailed lemurs, nipple length is a good marker of whether a female has recently had an infant, and young females who have not yet reproduced have small but clearly identifiable nipples [Sauther, pers. obs.]. This adult female's nipple length was similar to young females who have not yet had an infant.

Some studies indicate that prenatal hormones may play an important role in the development of masculinized genitalia in this species [Drea, 2007]. It is possible that such hormones may also be responsible for the occasional occurrence of male secondary traits in female ring-tailed lemurs, such as the development of male carpal spurs, but this requires further study. Virilization among other primates has rarely been reported. Recent research on *Cebus apella* indicates that female tufted capuchins have an elongated clitoris, which can be made turgid. This makes young female capuchins difficult to distinguish from males [Carosi et al., 2001]. Among nonprimates, bears appear highly susceptible to virilization (see citations in table 1). Pseudohermaphroditism has been reported among three bear species, and is especially high among wild polar bears (table 1). The latter may be related to environmental contaminants such as polychlorinated biphenyls [Haave et al., 2003].

#### *Variation in Nipple Number*

Ectopic clusters of breast cells along the milk line may result in polythelia (supernumerary nipples) [Hultman, 2003], which is relatively common among primates, especially among macaques and humans (table 1). The number of nipples varies widely among placental mammals, including across the primate radiation

[Schultz, 1948]. Schultz [1948] noted that nipple number also varies intraspecifically. For the genus *Lemur*, Schultz [1948, p. 12] did not differentiate between *L. catta* and the other members then recognized as belonging to the genus *Lemur* (i.e., *Eulemur* and *Varecia*), noting that 'one finds most frequently only 1 pair of mammae, being situated on the chest'. For *L. catta*, a single pair of nipples has been reported [Hill, 1953; Jolly, 1966; Sauther et al., 2002], although there are examples of individuals with more than one pair [Montagna and Yun, 1962; Sauther et al., 2002]. Three pairs have also been reported as typical for ring-tailed lemurs [Kappeler, 1998].

During our regular examination of ring-tailed lemurs at both Beza Mahafaly and Tsimanampesotse National Park in 2006, we observed that, in contrast to earlier reports [Hill, 1953; Jolly, 1966; Kappeler, 1998; Sauther et al., 2002], female ring-tailed lemurs typically have two pairs of nipples. We have also noted this in captivity, where 6 of 9 (67%) adult female ring-tailed lemurs examined at the Indianapolis Zoo had two pairs of nipples [Sauther, unpubl. data]. Combining the two wild populations and the captive group ( $n = 33$  adult females), we recorded 1 wild female (Tsimanampesotse National Park) (3%) with only one pair of pectoral nipples, and 1 wild female (Tsimanampesotse National Park) and 3 captive females (Indianapolis Zoo) (12%) [Sauther, unpubl. data] with a third pair of nipples. The number of pairs of pectoral nipples (and potentially mammae) appears to be a polymorphism in this species, varying from one to three pairs. A second or third pair of nipples could facilitate nursing twins, although wild ring-tailed lemurs usually give birth to only 1 infant [Koyama et al., 2001; Jolly et al., 2002; Gould et al., 2003]. In semicaptive conditions, twins are frequent, and even triplets occur, but usually only 1 of the infants survives [Parga and Lessnau, 2005].

Athelia is very rare and is usually associated with a variety of other conditions. Ishida et al. [2005] report a case in a 17-year-old woman, with no other conditions. In modern human populations, such a condition does not preclude reproduction. However, athelia in the wild has obvious negative consequences, and female 34 with athelia has never been observed with a dependent infant [L. Gould, D. Whitelaw, pers. commun.; Sauther, pers. obs.].

#### *Dental Variation*

##### Supernumerary Teeth and Agenesis

Supernumerary teeth are exceedingly rare in ring-tailed lemurs (0.5% in our sample). The only example of ring-tailed lemur supernumerary teeth known to us from outside our study populations is a cranial specimen in the collection of the American Museum of Natural History (AMNH 170740), which possesses a small, misshapen fourth molar at the distal end of each maxillary tooth row. Relative to other living lemurs, the incidence of supernumerary teeth in ring-tailed lemurs is also low (table 3). Among extinct lemurs, Lamberton [1939] reported supernumerary molars in three specimens of *Archaeolemur*.

Supernumerary teeth can be caused by 'twinning' of the tooth buds or by excessive growth of the dental lamina during odontogenesis [Jungers and Gingerich, 1980; Scheiner and Sampson, 1997; Garvey et al., 1999; Swindler, 2002]. Heredity may also play a role, as supernumerary teeth are more common in relatives of affected individuals in humans [Scheiner and Sampson, 1997; Garvey et al., 1999]. Among non-human primates, the highest frequencies of supernumerary teeth are concentrated within a single group (the hominoids), suggesting a phylogenetic (and thus a hered-

itary) influence. Supernumerary teeth are generally less common in eutherian mammals retaining less derived dental formulae [Feldhamer and McCann, 2004; Gisburne and Feldhamer, 2005], for example pigs and wild canids (table 3). Among primates, supernumerary teeth are most common in the large-bodied nonhuman hominoids (ranging from 2.9 to 7.9%; table 3), which have a more derived dental formula compared to most prosimians [Cuzzo and Yamashita, 2006]. Among lemurs, those with a more derived dental formula (e.g. *Lepilemur*) [Tattersall, 1982; Swindler, 2002; Cuzzo and Yamashita, 2006] (table 3) also have higher frequencies of supernumerary teeth. The retention of a less derived dental formula in ring-tailed lemurs may account, in part, for the low frequency of supernumerary teeth.

An additional factor is the rate of dental development. Lemurs, including the large-bodied subfossil forms, display rapid dental development [Eaglen, 1985; Schwartz et al., 2005], and there are likely few opportunities for localized (i.e., non-hereditary) causes of supernumerary teeth to occur, such as twinning of the tooth bud. This may also account for the low frequency of supernumerary teeth in *L. catta* (0.5%) and most other lemurs, when compared to the slow-developing, long-lived nonhuman hominoids. The rapid dental development exhibited by *Propithecus verreauxi* [Eaglen, 1985; Schwartz et al., 2002], which displays no supernumerary teeth at Beza Mahafaly, also supports this idea.

Agensis is relatively common in some primate taxa. For example, Lavelle and Moore [1973] reported an 11.1% frequency of agensis in modern humans, and a 7.9% frequency in *Colobus*. Jablonski [1992] reported a 33.3% frequency of premolar agensis in a sample of *Rhinopithecus roxellana*. Agensis is also common among other mammals (gray foxes and wild pigs), with frequencies approaching or even exceeding 20% in some samples [Feldhamer and McCann, 2004; Gisburne and Feldhamer, 2005]. In modern humans, agensis primarily occurs at the third molar position, with most examples of congenitally missing teeth across both the cercopithecoids and hominoids being molars [Lavelle and Moore, 1973]. In contrast, all cases of agensis in *L. catta* (3.8% of the sample) are maxillary incisors (incisor agensis is rare in Old World anthropoids [Lavelle and Morre, 1973]). Agensis generally shows a female bias in modern humans [Mattheeuws et al., 2004; Polder et al., 2004]; in contrast, our sample exhibits a male bias (table 2). The high frequency of agensis in some primate samples (including modern humans) likely results from genetic isolation [Jablonski, 1992]. Incisor number varies in lemuriformes [Cuzzo and Yamashita, 2006]. For example, reduction in maxillary incisor number has occurred in two lemur genera (reduction to one pair in *Daubentonia*, and none in *Lepilemur* [Cuzzo and Yamashita, 2006]). The absence of only first maxillary incisors in 7 individuals across the two *L. catta* study populations, including bilateral agensis in 3 of 7 individuals, may therefore reflect natural variability (i.e., a genetic polymorphism).

#### Malocclusion and Disruptions of Eruption

Although the etiology of malocclusion is complex, and includes genetic, environmental, and even dietary influences [Corrucini and Beecher, 1982; Fitch and Fagan, 1982; Hillson, 1996; Mossey, 1999a, b; Jena et al., 2005], the example in our study appears to have resulted from a disruption during growth and development, seen in the difference in rami lengths. When discussed in humans, malocclusion most often refers to the 'abnormal' occlusion (i.e., failure to meet normal occlusion [Hillson, 2005]) of specific corresponding teeth [Hillson, 1996; Behbehani et al.,

**Table 3.** Frequency of supernumerary teeth in ring-tailed lemurs compared with selected extant primates and other mammals

Genus	Sample size	% with supernumerary teeth <sup>a</sup>
Primates		
<i>Homo</i> <sup>b</sup>	5,000	1.9% (94)
<i>Gorilla</i> <sup>b</sup>	190	7.9% (15)
<i>Gorilla</i> <sup>c</sup>	245	4.9% (12)
<i>Gorilla</i> <sup>d</sup>	675	4.4% (30)
<i>Pan</i> <sup>b</sup>	100	3.0% (3)
<i>Pan</i> <sup>c</sup>	126	3.2% (4)
<i>Pan</i> <sup>d</sup>	560	2.9% (16)
<i>Pongo</i> <sup>b</sup>	100	6.0% (6)
<i>Pongo</i> <sup>c</sup>	67	6.0% (4)
<i>Pongo</i> <sup>d</sup>	295	6.8% (20)
<i>Hylobates</i> <sup>b</sup>	150	0.0% (0)
<i>Hylobates</i> <sup>d</sup>	306	0.7% (2)
<i>Symphalangus</i> <sup>b</sup>	44	9.1% (4)
<i>Symphalangus</i> <sup>d</sup>	85	4.7% (4)
<i>Colobus</i> <sup>b</sup>	140	0.0% (0)
<i>Colobus</i> <sup>d</sup>	1,485	1.1% (16)
<i>Presbytis</i> <sup>b</sup>	100	1.0% (1)
<i>Presbytis</i> <sup>d</sup>	985	0.6% (6)
<i>Cercopithecus</i> <sup>b</sup>	350	1.1% (4)
<i>Cercopithecus</i> <sup>d</sup>	1,823	0.8% (14)
<i>Macaca</i> <sup>b</sup>	350	0.5% (1)
<i>Macaca</i> <sup>d</sup>	901	0.1% (1)
<i>Papio</i> <sup>b</sup>	38	2.6% (1)
<i>Papio</i> <sup>d</sup>	410	0.7% (3)
<i>Alouatta</i> <sup>d</sup>	787	0.9% (7)
<i>Alouatta</i> <sup>e</sup>	137	0.7% (1)

2005], often based on Angle's classification of 1899 [Hillson, 1996]. Using this definition, malocclusion is quite common in modern human populations, as high as 70% in some studies [Behbehani et al., 2005]. Among nonhuman mammals, the definition of malocclusion is quite varied, especially in domestic forms, for example dogs, in which short-muzzled breeds display traits viewed as normal, but would be described as examples of malocclusion in wild canids [Hillson, 2005]. One case of a wild caught aye-aye exhibiting dental malocclusion of the upper incisors occurs among the Duke Primate Center prosimians [C. Williams, pers. commun.].

The ring-tailed lemur example of malocclusion that we describe (light blue 253) goes far beyond the definition usually applied to humans, and is reminiscent of the degree of malocclusion seen in domestic dogs when compared to wild forms. As noted, this example does not appear to be a result of diet, as suggested for some captive primates [Corrucini and Beecher, 1982] and other captive mammals [Fitch and Fagan, 1982; see review in Young, 1997]. Despite this severe dental impairment, as of 2006, this individual was a normal member of his troop, and had attained a body

**Table 3** (continued)

Genus	Sample size	% with supernumerary teeth <sup>a</sup>
<i>Alouatta</i> <sup>f</sup>	200	1.5% (3)
<i>Ateles</i> <sup>d</sup>	232	4.7% (11)
<i>Ateles</i> <sup>e</sup>	64	1.6% (1)
<i>Cebus</i> <sup>d</sup>	651	0.6% (4)
<i>Cebus</i> <sup>e</sup>	84	1.2% (1)
Marmosets <sup>g</sup>	904	0.7% (7)
<i>Microcebus murinus</i> <sup>h</sup>	126	1.6% (2)
<i>Propithecus verreauxi</i> <sup>i</sup>	78	0.0% (0)
<i>Lemur catta</i> <sup>j</sup>	186	0.5% (1)
<i>Lepilemur</i> <sup>k</sup>	100	3.0% (3)
'Lemurinae' <sup>d, l</sup>	289	1.4% (4)
Other Mammals		
<i>Canis familiaris</i> (domestic dog) <sup>d</sup>	799	8.6% (69)
<i>Canis lupus</i> (wolf) <sup>d</sup>	324	1.8% (6)
<i>Urocyon cinereoargenteus</i> (gray fox) <sup>m</sup>	510	0.6% (3)
<i>Vulpes vulpes</i> (red fox) <sup>m</sup>	150	0.7% (1)
<i>Sus scrofa</i> (domestic and wild pig) <sup>n</sup>	69	0.0% (0)

<sup>a</sup> Number in parentheses = number of cases in each sample. <sup>b</sup> Data from Lavelle and Moore [1973]. <sup>c</sup> Data from Schultz [1935]. <sup>d</sup> Data from Miles and Grigson [1990]. <sup>e</sup> Data from Smith et al. [1977]. <sup>f</sup> Data from DeGusta and Milton [1998]. <sup>g</sup> Data from Hershkovitz [1970] and includes *Cebuella*, *Callithrix*, and *Sanguinus*. <sup>h</sup> Data collected by the authors at the American Museum of Natural History. <sup>i</sup> Data collected by the authors at the Beza Mahafaly Osteological Collection housed at BMSR. <sup>j</sup> Data collected by the authors at Beza Mahafaly and Tsimanampesotse. <sup>k</sup> Data from Miles and Grigson, as cited by Swindler [2002]. <sup>l</sup> Data from Miles and Grigson [1990] not published by genus. <sup>m</sup> Data from Gisburne and Feldhamer [2005]. <sup>n</sup> Data from Feldhamer and McCann [2004].

mass typical for a young adult male at Beza Mahafaly (he was first captured as a sub-adult in 2005), suggesting that he has been able to acquire sufficient nutrition despite his dental abnormality.

Disruptions of eruption (e.g. rotated teeth) are common in nonhuman primates [Miles and Grigson, 1990]. Recently, patterns of dental rotation have also been used in the taxonomic interpretation of hominid fossils recovered on the island of Flores in Indonesia [see discussion in Jacob et al., 2006]. Therefore, understanding the 'normal' occurrence of rotated teeth in extant primate populations has broad implications for understanding questions of hominid and other primate paleobiology and taxonomy. Among hominoids, rotated fourth premolars are quite common [Miles and Grigson, 1990]. In prosimians, Miles and Grigson [1990] reported that most variations of eruption were slight, suggesting that tooth rotations did not significantly compromise normal occlusion, in contrast to the condition frequently seen in anthropoids. Miles and Grigson [1990] also describe two examples of tooth rotation in captive ring-tailed lemurs. In both cases, in keeping with their summary of eruption

disruptions in prosimians, the examples of tooth rotation are slight. This is especially true when compared with the three ring-tailed lemur examples of dental rotation in our study populations (1.6%), which exceed those described by Miles and Grigson [1990] for prosimians in their degree of rotation, and are more reminiscent of the examples described for some anthropoid primates. Miles and Grigson [1990] suggest that, based on Colyer's work, disruptions of eruption may result from crowding of teeth, for example in hominoids. As ring-tailed lemurs (and many other prosimians) retain an elongated muzzle and mandible, the rarity of eruption disruptions, such as rotated teeth (1.6%), may be related to their retention of a prognathic face.

### Conclusion

While researchers are developing a more sophisticated understanding of the mechanism of variation from genetic, congenital or environmental origin, data on the *range* of variation in natural populations are rare. Our ongoing research of the Beza Mahafaly lemurs demonstrates that they exhibit a number of variable traits that can be informative in terms of understanding the pattern and frequency of variation within a wild population. For example, several traits (total pairs of nipples, dental agenesis) appear to be polymorphisms in both the ring-tailed lemur and lemuriforme genomes. Our data from a second population (Tsimanampesotse) allow us to more thoroughly evaluate the patterns seen at Beza Mahafaly. Long-term data on each individual through their life span at Beza Mahafaly will elucidate how such variation may affect their survival, their reproduction, and their life history.

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