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Biological variation in a large sample of mouse lemurs from Amboasary, Madagascar: Implications for interpreting variation in primate biology and paleobiology

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ABSTRACT

A thorough knowledge of biological variation in extant primates is imperative for interpreting variation, and for delineating species in primate biology and paleobiology. This is especially the case given the recent, rapid taxonomic expansion in many primate groups, notably among small-bodied nocturnal forms. Here we present data on dental, cranial, and pelage variation in a single-locality museum sample of mouse lemurs from Amboasary, Madagascar. To interpret these data, we include comparative information from other museum samples, and from a newly collected mouse lemur skeletal sample from the Beza Mahafaly Special Reserve (BMSR), Madagascar. We scored forty dental traits ($n = 126$) and three pelage variants ($n = 19$), and collected 21 cranial/dental measures. Most dental traits exhibit variable frequencies, with some only rarely present. Individual dental variants include misshapen and supernumerary teeth. All Amboasary pelage specimens display a "reversed V" on the cap, and a distinct dorsal median stripe on the back. All but two displayed the dominant gray–brown pelage coloration typical of *Microcebus griseorufus*. Cranial and dental metric variability are each quite low, and craniometric variation does not illustrate heteroscedasticity. To assess whether this sample represents a single species, we compared dental and pelage variation to a documented, single-species *M. griseorufus* sample from BMSR. As at Amboasary, BMSR mouse lemurs display limited odontometric variation and wide variation in nonmetric dental traits. In contrast, BMSR mouse lemurs display diverse pelage, despite reported genetic homogeneity. Ranges of dental and pelage variation at BMSR and Amboasary overlap. Thus, we conclude that the Amboasary mouse lemurs represent a single species – most likely (in the absence of genetic data to the contrary) *M. griseorufus*, and we reject their previous allocation to *Microcebus murinus*. Patterns of variation in the Amboasary sample provide a comparative template for recognizing the degree of variation manifested in a single primate population, and by implication, they provide minimum values for this species' intraspecific variation. Finally, discordance between different biological systems in our mouse lemur samples illustrates the need to examine multiple systems when conducting taxonomic analyses among living or fossil primates.

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Introduction

Mammalian teeth are diagnostic morphologically, often identifiable to the level of species (e.g., Roth, 2005). As such, patterns of dental variation provide important information for understanding the taxonomy of living and extinct primates (e.g., Schwarz, 1931; Schuman and Brace, 1954; Swindler et al., 1963; Greene, 1973; Gingerich, 1974; Johanson, 1974; Swindler and Orlosky, 1974; Gingerich and Schoeninger, 1979; Cope, 1989, 1993; Vitzhum, 1990; Cope and Lacy, 1992, 1995; Plavcan, 1993; Uchida, 1998a,b; Sauther et al., 2001; Cuozzo, 2002, 2008; Tornow et al., 2006; Scott et al., 2009; Pilbrow, 2010). Plavcan and Cope (2001: 206) emphasized that comparative analyses of biological variation should be based on data from "restricted geographic localities and time horizons".

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Kieser (1994) made a similar suggestion, addressing the importance of choosing an appropriate reference population. Tornow et al. (2006) noted that there are few such samples of extant primates available for comparison. To date, most studies of dental variation within extant species have focused on anthropoid and/or haplorhine primates, or even more narrowly, on hominoids, which hold keys for ascribing hominin fossils to particular taxa (e.g., Schuman and Brace, 1954; Swindler et al., 1963; Greene, 1973; Johanson, 1974; Swindler and Orlosky, 1974; Cope, 1989, 1993; Vitzhum, 1990; Rosenberger et al., 1991; Wood et al., 1991; Plavcan, 1993; Swindler et al., 1998; Uchida, 1998a,b; Pan and Oxnard, 2003; Tornow et al., 2006; Hlusko and Mahaney, 2007; Scott et al., 2009; Pilbrow, 2010).

By contrast, most previous studies of dental variation in strepsirrhine primates have focused on *inter*specific variation, with an emphasis on species descriptions and phylogenetic relationships (e.g., Schwarz, 1931; Hill, 1953; James, 1960; Swindler, 1976, 2002; Schwartz and Tattersall, 1985; Tattersall and Schwartz, 1991; Tattersall, 1993; Groves and Helgen, 2007). Fewer studies have addressed patterns of intraspecific dental variation in strepsirrhines (Eaglen, 1986; Kieser and Groeneveld, 1989; Schwartz and Beutel, 1995; Sauther et al., 2001; Cuozzo, 2008). Given the primary role of variation as the target of natural selection (e.g., Darwin, 1859; Simpson, 1944; see; Bowler, 2005), understanding the ranges of variation in populations and/or species can provide insights into the amount of variation available for selection and/or drift. Assuming morphological variation correlates with reproductive isolation, the central component of the Biological Species Concept (Mayr, 1940, 1942, 1988; see review in Tattersall, 2007), individual variants can be important for assessing species boundaries in the mammalian fossil record (e.g., Goodwin, 1998). Yet, such variation in strepsirrhine primates remains underexplored (Sauther and Cuozzo, 2008; see summary data in Miles and Grigson, 1990).

Mouse lemurs (*Microcebus*) have been the focus of increased attention in recent years, but their intraspecific patterns of biological variation (i.e., dental, cranial, and pelage) remain poorly documented, and taxonomic inferences are often drawn on the basis of limited information and small samples (see critiques in Tattersall, 2007; Godfrey, 2011). Mouse lemurs are the smallest living primates (Rasoloarison et al., 2000), and traditionally, only two mouse lemur species have been recognized – the western gray mouse lemur (*Microcebus murinus*) and the eastern reddish-brown form (*Microcebus rufus*) (Hill, 1953; Tattersall, 1982; Atsalis et al., 1996; Rasoloarison et al., 2000; Yoder et al., 2000a,b, 2002; Heckman et al., 2006; Gligor et al., 2009). However, the taxonomy of mouse lemurs, as with many of the smaller nocturnal strepsirrhine forms (e.g., the dwarf galagos of continental Africa [Bearder et al., 1995; Honess, 1996; Wickings et al., 1998; Bearder, 1999; Nekaris and Bearder, 2007]), has recently undergone revision, with the two long-standing species now divided into as many as 19 distinct species on the basis of morphological, biogeographic, and/or genetic data (e.g., Yoder et al., 2000a,b; Rasoloarison et al., 2000; Radespiel et al., 2003, 2008, 2012; Andriantompohavana et al., 2006; Louis et al., 2006, 2008; Olivieri et al., 2007; Mittermeier et al., 2010; Weisrock et al., 2010; see Table 1), although this dramatic increase in the number of described species has been contested (e.g., Tattersall, 2007). Recent years have also witnessed a growth in mouse lemur behavioral and/or ecological studies (e.g., Atsalis, 1998, 2007; Rasoazanabary, 2004, 2006; Lahann et al., 2006; Eberle and Kappeler, 2008; Dammhahn and Kappeler, 2008; Génin, 2008, 2010; see review in Atsalis, 2007), as well as expanded genetic analyses capable of recognizing instances of incomplete lineage sorting (Heckman et al., 2007).

Table 1
Currently recognized extant mouse lemur species.[a]

Microcebus berthae	(Madame Berthe's mouse lemur)
Microcebus gerpi	(Gerp's mouse lemur)
Microcebus griseorufus	(Reddish-gray mouse lemur)
Microcebus jollyae	(Jolly's mouse lemur)
Microcebus lehilahytsara	(Goodman's mouse lemur)
Microcebus margotmarshae	(Margot Marshes mouse lemur)
Microcebus mittermeieri	(Mittermeier's mouse lemur)
Microcebus murinus	(Gray mouse lemur)
Microcebus myoxinus	(Pygmy mouse lemur)
Microcebus ravelobensis	(Golden-brown mouse lemur)
Microcebus rufus	(Brown mouse lemur)
Microcebus sambiranensis	(Sambirano mouse lemur)
Microcebus simmonsi	(Simmons' mouse lemur)
Microcebus tavaratra	(Northern brown mouse lemur)
Microcebus mamiratra	(Claire's mouse lemur)
Microcebus lokobensis[b]	(Lokoben mouse lemur)
Microcebus danfossi	(Danfoss's mouse lemur)
Microcebus bongolavensis	(Bongolava mouse lemur)
Microcebus macarthurii	(MacArthur's mouse lemur)

[a] Data compiled from Yoder et al. (2000a,b), Rasoloarison et al. (2000), Louis et al. (2006), Andriantompohavana et al. (2006), Mittermeier et al. (2008), Olivieri et al. (2007), and Radespiel et al. (2008, 2012).
[b] *M. lokobensis* is apparently a synonym for *M. mamiratra*.

Heckman et al. (2006) concluded that, despite substantial variation in pelage characters, individuals belonging to a sample of mouse lemurs, collected across multiple habitats in and around the Beza Mahafaly Special Reserve (BMSR) in southern Madagascar exhibit identical mitochondrial haplotypes (cytochrome *b*), and thus appear to represent a single species. These observations contravened the hypothesis originally posited on the basis of three distinct color variants (e.g., Rasoazanabary, 2004), that at least two and perhaps three species are represented in the sample. Thus, Heckman et al. (2006) made a plea for a careful consideration of the degree to which observed variation can be contained in a single population or species. A parallel case can be made for dental variation (see review of lemur dental variation in Cuozzo and Yamashita, 2006), which becomes critical if dental variants are to be used in diagnosing species boundaries within the fossil record (e.g., Tattersall, 1992; Goodwin, 1998; Cuozzo, 2008). At the very least, we need to examine variation in multiple biological systems when contemplating extant or fossil taxonomic boundaries.

Research questions

The American Museum of Natural History (AMNH) (New York) houses one of the largest single-locality skeletal and soft tissue samples of mouse lemurs available for study ($n = 181$ [Buettner-Janusch and Tattersall, 1985]). These specimens were collected in October and November 1931 by Hans Bluntschli at Amboasary, southern Madagascar. As noted above, at the time, most workers viewed *Microcebus* as comprising two species, the western gray mouse lemur (*M. murinus*) and the eastern reddish-brown form (*M. rufus*), common to the more humid forests that mark the eastern mountains of Madagascar. Amboasary is located in the far southeastern part of Madagascar, below the Tropic of Capricorn, and outside of the humid forest zones. Thus, this sample was initially assigned to *M. murinus* (Buettner-Janusch and Tattersall, 1985). The AMNH collection represents only a portion of the mouse lemur material amassed by Bluntschli at Amboasary, with specimens distributed across institutions in the United States and Europe, including Harvard's Museum of Comparative Zoology, the Museum für Naturkunde (Berlin) and the Muséum National d'Histoire Naturelle (Paris) (Buettner-Janusch and Tattersall, 1985). Bluntschli's collection strategies, which included the collection of

as many as 50 mouse lemurs in a single day (Bluntschli, 1933, 1951), would be anathema to contemporary conservation ideals. Thus, we do not support further collection of such samples, but the collection he assembled does provide a unique opportunity to examine biological variation in a single primate population, and makes use of these sacrificed lemurs. As noted by Yoder et al. (2005), such older samples may be of critical importance for taxonomic analyses of Malagasy vertebrates.

Recent study of mouse lemurs in the southeastern region of Madagascar indicates the presence of both *M. murinus* and *Microcebus griseorufus* (Yoder et al., 2002; Génin, 2008; Gligor et al., 2009). For example, in and around the Berenty Private Reserve (Yoder et al., 2002; Génin, 2008) less than 20 km from Amboasary, *M. murinus* is described from the gallery forest and *M. griseorufus* in the dry, spiny forest areas. Gligor et al. (2009) also note the presence of *M. griseorufus* in dry, spiny forests, as well as *M. murinus* in the littoral and eastern humid forests, 25–30 km east of Amboasary. They also recognize the presence of "intermediate" morphotypes of the two species in the small, remaining transitional forests between the dry western and humid eastern forests. Hapke et al. (2011) suggest that these intermediate morphotypes may represent true hybrids, a by-product of recent, short-term climatic fluctuations, a potentially important process in the diversification of Madagascar's lemurs.

The first goal of our project was to assess 1) whether the AMNH Amboasary mouse lemur sample represents a single species, and 2) the taxonomic affinity of this sample, previously recognized as *M. murinus*. To do this, we compared patterns of dental and pelage variation with those from a known, single-species population of *M. griseorufus* from Beza Mahafaly, including a newly collected sample of dental remains from a cache of owl pellets recovered by authors FPC, MLS, IAYJ, and MML in 2008. Our second goal was to gain new insights into the biological variation within a single primate species, and to explore the implications of such variation for understanding primate biology and for diagnosing primate taxa, particularly in paleobiology.

Materials and methods

Cranial and dental metric analyses

A total of 126 mouse lemur cranial and/or dental specimens at the American Museum of Natural History AMNH were studied. Only adult specimens were analyzed, with adult status determined by a fully erupted permanent dentition. Twenty-one cranial and/or dental measures were collected (measure to the nearest 0.01 mm) using Fowler digital needle-point calipers, (see Table 2 for definition of each measure). All dental measurements were taken using a Nikon SMZ-1 binocular scope, and were collected by one person (FPC), thereby eliminating the potential for inter-observer error. Measurements were collected from left tooth positions when possible, and from right teeth only when measurements of left teeth were not available due to damage or pathology. A measurement reliability analysis was conducted by taking measurements on a subset of the sample several months after taking the original measurements. This analysis revealed average measurement errors of 0.03 mm for M_1 length ($n = 25$), 0.04 mm for cranial length ($n = 25$), and 0.04 mm for M^1 width ($n = 25$).

A comparable set of odontometric data was collected from a sample of mouse lemurs from the Beza Mahafaly Special Reserve (BMSR), southern Madagascar (also by FPC). This sample ($n = 32$) includes nine cranial/dental specimens collected previously from naturally deceased individuals at two separate locations, and twenty-three new craniodental specimens recovered in July 2008 in a cache of owl pellets from the gallery forest area of BMSR. Owl pellets and loose skeletal remains were collected at a large regurgitation site. The site encompassed an approximate 3 m radius surrounding a large felled dead tree stump. Pellets were weighed, measured and photographed before being immersed in water to loosen compacted material (about two days). Loose bones were soaked overnight in water if they had dirt, hair, chitin, or other matter attached. After rinsing and drying for one day, bones were separated and categorized, using the Beza Mahafaly Special Reserve Museum's comparative osteology collection (BMOC). Bones were identified as bird, reptile, rodent or primate. The rodent genera included both *Rattus* and *Mus*, while *Microcebus* was the sole primate genus. As with the Amboasary sample, measurements were collected from left tooth positions when possible, and from right teeth only when measurements of left teeth were not available due to damage or pathology.

Table 2
Definition of cranial and dental measurements.

1. **Cranial length**: Distance from the anterior border of the nasals to the posterior boundary of the occiput.
2. **Bizygomatic breadth**: Distance between the outer margins of the zygomatic arches, along the inferior border of the cranium.
3. **Biorbital breadth**: Maximum distance between the outer margins of the orbits, measured horizontally across the orbits.
4. **Palate breadth**: Distance between the buccal edges of the third upper molars.
5. **Maxillary toothrow length**: Measured from the mesial edge of the canine to the distal edge of the third upper molar, parallel to the toothrow.
6. **Mandibular toothrow length**: Measured from the mesial edge of the second (caniniform) premolar to the distal edge of the third lower molar, parallel to the toothrow.
7. **First and second mandibular molar length**: Measured parallel to the toothrow, from the mesial edge of the paracristid to the distal border of the postentocristid.
8. **Third mandibular molar length**: Measured parallel to the toothrow, from the mesial border of the paracristid to the distal edge of the tooth.
9. **Mandibular molar trigonid width**: Measured as maximum width, perpendicular to the toothrow.
10. **Mandibular molar talonid width**: Measured as maximum width, perpendicular to the toothrow.
11. **Maxillary molar length**: Measured parallel to the toothrow, across the paracone and metacone.
12. **First and second maxillary molar width**: Measured perpendicular to the toothrow, across the metacone and hypocone.
13. **Maxillary third molar width**: Perpendicular to the toothrow, across the paracone and protocone.

Quantitative assessment of cranial and dental metric variation

Summary statistics (mean, standard deviation, and coefficient of variation) were calculated for each cranial and dental variable, from both samples. All coefficients of variation (CVs) were corrected for sample size following Sokal and Rohlf (1995) and Plavcan and Cope (2001), as CVs are known to vary dramatically in small samples (see discussion below). Odontometric data for the two samples were compared using the Student's *t*-test, with a significance level of 0.05. All metric data were analyzed using Statview statistical and data analysis software (Haycock et al., 1992).

The coefficient of variation has long been used as an analytical tool in mammalian biology and paleobiology to assess specific boundaries. The use of metric variation to assess taxonomic boundaries in fossil forms, often based on odontometry, stems from the expectation that, as noted by Cope and Lacy (1994), there is little to suggest that patterns of dental variation would dramatically differ between living and fossil mammals. The coefficient of variation is a numerical index defined as the standard deviation divided by the mean, usually multiplied by 100 (e.g., Simpson et al., 1960;

Carrasco, 1998; Plavcan and Cope, 2001; Van Valen, 2005). Use of this statistic has received significant attention over the years (e.g., Simpson, 1937; Simpson and Roe, 1939). Initially, a CV of greater than 10 was interpreted as indicating a taxonomically diverse sample (Simpson and Roe, 1939; Simpson et al., 1960; see review in Plavcan and Cope, 2001). More recently, researchers have refined this idea, noting that premolars generally exhibit more metric variation than do molars (Gingerich, 1974; Gingerich and Schoeninger, 1979), that third molars generally vary more than first and second molars (e.g., Gingerich, 1974; Sauther et al., 2001), and that a contrast in metric variation between anterior and posterior teeth (i.e., greater variability in canines vs. molars) indicates sexual dimorphism rather than taxonomic diversity (Gingerich, 1995).

The CV has remained an important measure with which to assess taxonomic boundaries in primates and other mammals, extant and extinct (e.g., Gingerich, 1974, 1995; Cope, 1989, 1993; Cope and Lacy, 1992, 1995; Carrasco, 1998; Plavcan and Cope, 2001; Cuozzo, 2002, 2008; Tornow et al., 2006). Its use continues, despite some limitations and critiques (e.g., Lande, 1977; Soulé, 1982; Kelley and Plavcan, 1998; Polly, 1998; Plavcan and Cope, 2001; see debate on the efficacy of CVs between; Kieser, 1994 and Cope and Lacy, 1994). First, CVs are known to vary greatly in small samples (e.g., Plavcan and Cope, 2001). Thus, use of the correction factor CV $[1 + 1/4(n)]$ is often required (e.g., Sokal and Rohlf, 1995; Plavcan and Cope, 2001). Also, as noted by Lande (1977), CVs produced from a set of correlated data, for example, measurement of a series of cranial variables, or multiple measures from a single tooth, will likely result in lower values than those collected from unrelated variables. CVs can also only show the presence of multiple species in an assemblage, but cannot generally illustrate that only one species is present (Cope and Lacy, 1992; Carrasco, 1998). In addition, Polly (1998) noted that under certain circumstances CVs can be size-dependent. For example, when comparing variables of dissimilar size, CVs will vary according to size, with larger measures displaying higher CVs. Because of these limitations, the CV is best used as a "first approximation" when assessing taxonomic boundaries, especially in the fossil record, to eliminate the possibility of multiple species (e.g., Carrasco, 1998; Cuozzo, 2008). Still, when combined with analyses of dental morphology, and assessed in the context of adequate data from appropriate comparative samples, the CV can be a crucial first approximation in assessing taxonomic diversity among extinct forms (Kieser, 1994; Plavcan and Cope, 2001; Tornow et al., 2006; Cuozzo, 2008). When identifying species among living forms, additional measures and data analyses (e.g., pelage and/or molecular information) are essential, as described herein.

Dental morphology

A total of forty non-metric dental traits (Table 3) were scored for both right and left dentitions (whenever possible) for all specimens in both the Amboasary and Beza Mahafaly samples. Traits scored came from prior studies of mouse lemur dentition (e.g., Forbes, 1894; Elliot, 1913; Hill, 1953; James, 1960; Swindler, 1976; Schwartz and Tattersall, 1985; Rasoloarison et al., 2000), as well as initial, preliminary analyses of the AMNH sample by FPC. The majority (28) of the forty scored traits have binary conditions: these features were scored as "present" whenever they could be discerned, or "absent". For these binary traits, the "degree" of presence was not scored (i.e., strong, weak, etc.), resulting in a very conservative (i.e., confident) measure of trait presence. The remaining 12 traits represent tripartite conditions, with each trait appropriately scored. Individual variants (i.e., supernumerary, abbreviated, and/or connate teeth) were also recorded.

Table 3
Dental traits examined.[a]

# Trait	Conditions scored
1. C w/distal style	Absent, present
2. P^2 paracone only	Absent, present
3. P^3 w/protocone	Absent, present
4. P^4 w/protocone	Absent, present
5. M^1 pericone	Absent, present
6. M^1 hypocone	Absent, present
7. M^1 lingual extension/style	Absent, present
8. M^1 parastyle	Absent, present
9. M^1 metastyle	Absent, present
10. M^1 shape	Square, buccal–lingual elongation
11. M^1 buccal cingulum	Strong, weak, absent
12. M^2 pericone	Absent, present
13. M^2 hypocone	Absent, present
14. M^2 lingual extension/style	Absent, present
15. M^2 parastyle	Absent, present
16. M^2 metastyle	Absent, present
17. M^2 shape	Square, buccal–lingual elongation
18. M^2 buccal cingulum	Strong, weak, absent
19. M^3 pericone	Absent, present
20. M^3 hypocone	Absent, present
21. M^3 parastyle	Absent, present
22. M^3 metastyle	Absent, present
23. M^3 buccal cingulum	Strong, weak, absent
24. P_2 caniniform	Absent, present
25. P_2 buccal cingulum	Strong, weak, absent
26. P_3 buccal cingulum	Strong, weak, absent
27. P_4 thick buccal cingulum	Absent, present
28. P_4 w/talonid	Absent, present
29. P_4 entoconid position	Central, lingual
30. M_1 shape	Square, rectangular, parallelogram
31. M_1 buccal cingulum	Strong, weak, absent
32. M_1 distal cingular shelf	Strong, weak, absent
33. M_2 shape	Square, rectangular, parallelogram
34. M_2 buccal cingulum	Strong, weak, absent
35. M_2 distal cingular shelf	Strong, weak, absent
36. M_3 buccal cingulum	Strong, weak, absent
37. M_3 w/hypoconulid	Absent, present
38. M_3 w/notch between hypoconid/hypoconulid	Absent, present
39. M_3 w/cingulum in notch	Absent, present
40. M_3 w/entoconid and hypoconulid	Distinct, not distinct

[a] See text for discussion of the identification of morphological traits examined.

Pelage assessment

Pelage data from Amboasary were collected to aid our assessment of the sample's taxonomic affinity and to assess the single-species diagnosis for this sample. Among the mouse lemurs at Beza Mahafaly there exists a discordance between degrees of variation in pelage and genetic traits. Specifically, there is substantial pelage variation but limited diversity in mitochondrial DNA (cytochrome *b*) in this sample, taken by Heckman et al. (2006) to represent a single species.

Most of the mouse lemur skulls and/or skeletons from Amboasary in the AMNH Bluntschli collection lack skins. The population is represented by 126 cranial specimens (most without associated postcrania), and only 16 skins. These specimens were collected during a 10 day period, in late October, 1931. No more than three skins were kept during any given day during the collection period. Thus, although derived from a small sample, these specimens appear to have been randomly collected. Given the small number of Amboasary *Microcebus* pelage specimens, we compiled a comparative pelage database from a total of 72 dried skins scored at three museums (Chicago Field Museum [FMNH], American Museum of Natural History [AMNH], and the Museum of Comparative Zoology at Harvard University [MCZ]). This database includes the 16 AMNH Amboasary pelage specimens plus three specimens from Amboasary housed at MCZ. In addition to the 72 museum pelage samples,

ER collected field data on pelage from a total of 196 live-caught individuals at Beza Mahafaly between 2003 and 2004. Mouse lemurs were captured using Sherman live animal traps (Sherman Traps, Inc., Tallahassee, FL, USA), hand-sedated, and released in their original capture area, with University of Massachusetts-Amherst IACUC approval. All captured individuals at BMSR were microchipped (Trovan, Identify UK, Ltd., East Yorkshire, HU13 0RD, United Kingdom), so that recaptured individuals could be distinguished from first captures, making it easy to eliminate any duplication of individuals in the sample. Individuals were sampled from three forests: the gallery and spiny forests within the Beza Mahafaly Special Reserve, and a nearby mixed dry forest (Ihazoara). Despite marked variation in coat coloration, these individuals have been shown to belong to a single species; their DNA (cytochrome *b*) matched reference samples of *M. griseorufus* from Berenty, while diverging from reference samples of *M. murinus* from a variety of locations (Heckman et al., 2006). In all, comparative pelage data include samples from 19 sites (counting the three Beza locations as a single site), and from individuals that have been attributed to eight separate species (Table 4).

A Munsell (GretagMacbeth; New Windsor, New York) soil color book was used as a reference in collecting the data on dried skins. Colors in the Munsell book are coded by hue (i.e., specific color), value (i.e., lightness or darkness), and chroma (i.e., color intensity), and arranged on sheets of color chips that are perforated, so that any sample can be matched easily to individual color chips. Similar chips are assigned the same color names (e.g., strong brown, yellowish brown). Although preservation of pelage specimens can vary, thus possibly impacting their color, we assigned hue scores allowing for a range of more and less faded shades of the same color hues (i.e., not scoring obviously faded skins as a different hue), thus controlling for some possible pelage degradation. ER used this system to record the closest matching pelage colors for the following regions on each specimen: interorbital, orbital ring, nasals, cheeks, cap, shoulder and dorsal neck, middle back, rump, throat, chest, middle belly, groin, proximal tail (dorsal and ventral), distal tail (dorsal and ventral), dorsal thigh, dorsal leg, dorsal upper arm, and dorsal forearm. Two additional pattern variables were scored: the presence or absence of a distinct "reversed V" on the cap, and the presence or absence of a distinct dorsal median stripe. The "reversed V" is a fork-like mark, which is darker (usually browner or redder) than the surrounding fur; the lines begin just above the eyes and converge to an apex at the back of the cap. For any particular variable, not all individuals could be scored due to damage on specimens.

Table 4
Total comparative sample – pelage analyses.

Comparative sample	*N*	Sample field locations	Condition
M. griseorufus	196	Beza Mahafaly (Gallery, Spiny forest, Ihazoara)	Live
M. griseorufus	16	Beza Mahafaly, Tabiky	Dried skins
M. griseorufus	19	Amboasary	Dried skins
M. murinus	7	Andranomena (Kirindy), Toliara, Vohimena, Manamby	Dried skins
M. myoxinus	6	Aboalimena, Bemaraha, Ambararatabe, Namoroka	Dried skins
M. ravelobensis	6	Ankarafantsika	Dried skins
M. berthae	1	Kirindy	Dried skins
M. rufus	9	Antsihanaka, Andampy, Didy, Ivondro, Tampina, Analamazaotra	Dried skins
M. tavaratra	5	Ankarana	Dried skins
M. sambiranensis	3	Manongarivo	Dried skins

For live-caught individuals, coat color was scored for the dorsal region only, and the presence or absence of a reversed V and a dorsal median stripe was also recorded. Dorsal fur color was grouped into three categories: 1) gray (corresponding mainly to Gray or Dark gray on the Munsell chart), 2) gray–brown (corresponding mainly to Grayish brown, Dark grayish brown, or Dark yellowish brown on the Munsell chart), and 3) "red" or dark brown (corresponding mainly to Dark brown or Very dark brown on the Munsell chart). Fur color varies on the dorsum of single individuals, thus "categories" designate the dominant color of the dorsal pelage (excluding the median stripe which, when distinct, is always darker or browner than the surrounding fur).

We used StatXact (Cytel Studios) to test the null hypothesis of no differences across taxa in the frequencies of the reversed V, dorsal median stripe, and dorsal fur coloration (gray, gray–brown, or "red"). This program allows one to calculate Fisher's exact test for the relationship between two variables in a row-by-column frequency table of any size. We prefer this to the traditional Pearson's Chi-square or the maximum likelihood test for independence, because the Chi-square estimates of the true probability value may not be very accurate when the marginal values are strikingly uneven or when one or more expected values are very small, particularly when there are small expected values (less than five) in one or more of the cells. Fisher's exact test provides the exact probability of finding any given result (or more extreme differences) by chance alone (Agresti, 1990).

We first tested the significance of differences in frequency distributions of coat characteristics for Amboasary and Beza Mahafaly alone. We then used StatXact to assess the significance of frequency differences across the living and museum samples studied herein. For these tests, the specimens from Amboasary were treated as a distinct, unassigned population. For the purpose of these broader statistical comparisons, we also omitted *Microcebus berthae* and *Microcebus sambiranensis*, both of which were too poorly sampled to capture meaningful patterns of variation.

Results

Cranial and dental metrics

Metric data for the 21 cranial and/or dental measures at Amboasary are presented in Table 5a. Metric variation in the six cranial measures is quite limited, with Coefficients of Variation

Table 5a
Amboasary craniometric and odontometric summary statistics.

Measure	*N*	Mean	SD	Range	CV
Skull length	122	31.47	0.77	29.68–33.88	2.4
Biorbital breadth	120	19.90	0.61	18.56–21.70	3.1
Zygomatic breadth	117	20.12	0.67	18.60–21.59	3.3
Palate breadth at M^3	123	9.59	0.27	9.02–10.36	2.8
Maxillary toothrow	105	10.08	0.25	9.23–10.64	2.5
Mandibular toothrow	103	9.27	0.26	8.34–9.85	2.8
M_1 length	124	1.58	0.06	1.37–1.78	4.0
M_1 trigonid width	123	1.20	0.06	1.07–1.35	4.7
M_1 talonid width	123	1.27	0.06	1.17–1.40	4.3
M_2 length	124	1.59	0.06	1.40–1.82	4.0
M_2 trigonid width	124	1.32	0.06	1.16–1.49	4.9
M_2 talonid width	124	1.33	0.06	1.20–1.48	4.7
M_3 length	124	2.05	0.09	1.73–2.30	4.5
M_3 trigonid width	121	1.24	0.07	1.09–1.43	5.5
M_3 talonid width	122	1.16	0.07	1.00–1.32	5.7
M^1 length	123	1.59	0.06	1.42–1.77	3.7
M^1 width	123	2.08	0.10	1.80–2.35	4.6
M^2 length	123	1.59	0.06	1.40–1.75	3.6
M^2 width	123	2.10	0.10	1.84–2.39	4.9
M^3 length	123	1.48	0.05	1.35–1.66	3.7
M^3 width	123	1.95	0.11	1.70–2.26	5.5

(CVs) ranging from 2.4 for cranial length ($n = 122$) to 3.3 for bizygomatic breadth ($n = 117$). We also examined the Amboasary cranial sample for the presence of heteroscedasticity, as a trend toward greater variation in smaller or larger individuals would be informative for interpreting variation, and thus species boundaries, in living and fossil primates. Fig. 1a, b and c, present bivariate scatterplots and linear regressions of skull length compared with each of the three cranial measures we collected (biorbital breadth, bizygomatic breadth, and palate breadth). The linear relationship between cranial length and each of these variables is significant ($p < 0.05$), with cranial length and biorbital breadth ($n = 119$, $R^2 = 0.210$, $p = < 0.0001$), cranial length and bizygomatic breadth ($n = 117$, $R^2 = 0.276$, $p = < 0.0001$), and cranial length and palate breadth ($n = 122$, $R^2 = 0.204$, $p = < 0.0001$), all exhibiting distinct linear patterns. This illustrates that neither larger nor smaller specimens exhibit greater variability, and provides a potential framework for interpreting how an individual cranial specimen, either extant or fossil, fits within a broader data set.

Dental measures also exhibit a limited range of variation (Table 5a), with M^1 length being the least variable (CV = 3.7, $n = 123$), and M_3 talonid width being the most variable (CV = 5.7, $n = 122$). CVs for both tooth rows are also low, with the maxillary toothrow having a CV of 2.5 ($n = 105$), and the mandibular toothrow having a CV of 2.8 ($n = 103$). Samples sizes for both toothrows are somewhat smaller than for other measures due to damage of the maxillary canines or caniniform P_2, the mesial boundaries of toothrow length (in mouse lemurs, as in most strepsirrhine primates, the mandibular canine is incorporated into the toothcomb [see review in Cuozzo and Yamashita, 2006]).

Metric data for the Beza Mahafaly sample are presented in Table 5b. Only dental data are available (maxillary and mandibular first molars), as the majority of the 32 BMSR specimens represent partial remains recovered from owl pellets. Patterns of variation at BMSR are similar to those for Amboasary, with all M^1 and M_1 CVs less than 5.0. The two samples are also similar in having lower CVs for M^1 and M_1 lengths than for corresponding widths at BMSR. In addition, the overall ranges of dental measures at BMSR fall within the range of variation at Amboasary (Table 5a and b).

Table 5b
Beza Mahafaly odontometric summary statistics.

Measure	*N*	Mean	SD	Range	CV
M_1 length	15	1.62	0.05	1.55–1.73	3.2
M_1 trigonid width	15	1.25	0.04	1.18–1.32	3.4
M_1 talonid width	15	1.31	0.05	1.22–1.38	3.8
M^1 length	14	1.60	0.05	1.51–1.67	2.9
M^1 width	14	2.09	0.09	1.93–2.25	4.2

Table 5c presents a statistical comparison of Amboasary and BMSR samples for the five first molar measures. Measures for each of the three mandibular molar measures are significantly larger at BMSR than at Amboasary (M_1 length, $p = 0.0269$; M_1 trigonid width, $p = 0.0018$; M_1 talonid width, $p = 0.0133$). In contrast, measures for the first maxillary molar do not significantly differ. Table 5d provides comparative CV data for BMSR, Amboasary, two subfossil mouse lemur assemblages (Andrahomona Cave and Ankilitelo Cave), and the samples described by Rasoloarison et al. (2000) of *M. murinus* and *M. griseorufus*, respectively, which include the neotypes for both species. First maxillary and mandibular molar variation at BMSR is lower than that seen at Amboasary (M^1 length CV 2.90 and 3.70, respectively; M_1 length CV 3.20 and 4.00, respectively). Both BMSR and the Amboasary samples display less first molar variation than either of the two subfossil cave samples, as well as both of the extant mouse lemur samples reported by Rasoloarison et al. (2000). Of note,

Table 5c
Amboasary and Beza Mahafaly odontometric comparisons.

Measure	Amboasary mean	BMSR mean	*P*-Value[a]
M_1 length	1.58	1.62	**0.0269**
M_1 trigonid width	1.20	1.25	**0.0018**
M_1 talonid width	1.27	1.31	**0.0133**
M^1 length	1.59	1.60	0.4188
M^1 width	2.08	2.09	0.4966

[a] Bold values (student's *t*-test) represent significant differences ($p < 0.05$).

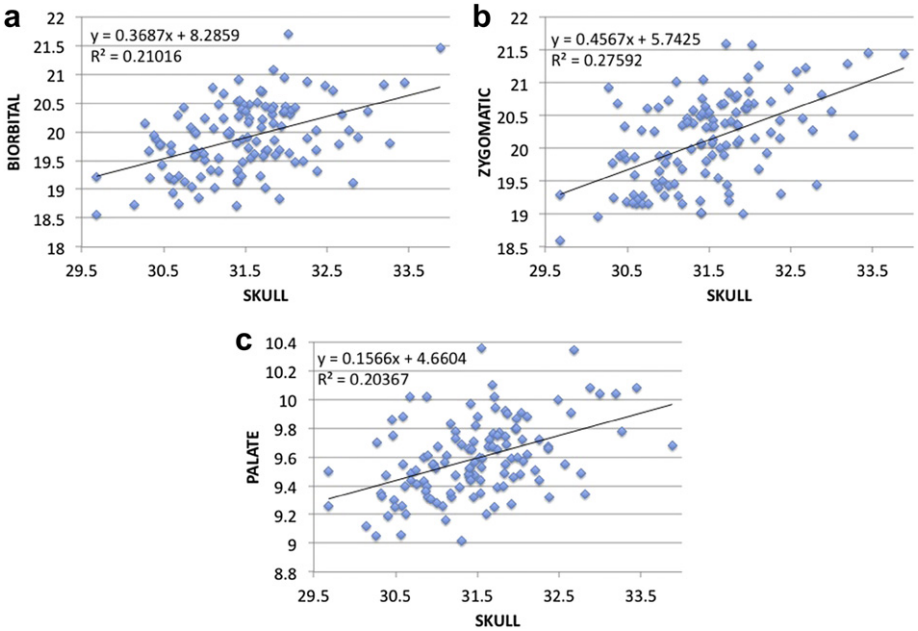

Figure 1. Bivariate scatterplots and linear regressions of cranial measurements in the Amboasary mouse lemur sample. (a) Comparison of skull length and biorbital breadth; (b) comparsion of skull length and zygomatic breadth; (c) comparison of skull length and palate breadth.

Table 5d
Microcebus cranial and odontometric variation comparisons.

Locality	M^1 length CV[a]	*N*	M_1 length CV[a]	*N*	Skull length CV[a]	*N*
Amboasary[b]	3.70	123	4.00	124	2.40	122
BMSR[b]	2.90	14	3.20	15	–	–
Andrahomana Cave[c]	5.33	45	6.83	47	–	–
Ankilitelo[d]	–	–	7.69	21	–	–
Microcebus murinus[e]	4.82	11	–	–	1.89	11
Microcebus griseorufus[e]	7.17	6	–	–	2.53	6

[a] All CVs corrected for sample size following Sokal and Rohlf (1995) and Plavcan and Cope (2001).
[b] Data from current study.
[c] Data from Rasoazanabary (unpublished).
[d] Data from Muldoon et al. (2009).
[e] Data on *M. murinus* and *M. griseorufus* samples from Rasoloarison et al. (2000) – *M. murinus* represents three localities; *M. griseorufus* represents a single locality.

Rasoazanabary (unpublished data) has concluded that the Andrahomana Cave sample may represent a single species assemblage, based on patterns of metric and morphological variation, while Muldoon et al. (2009) argue that the Ankilitelo sample contains both *M. murinus* and *M. griseorufus*, based on two distinct dental morphs. The M^1 and M_1 CVs for the fossil sites are approximately twice as large as those of the samples at Amboasary and BMSR. The *M. murinus* sample described by Rasoloarison et al. (2000) represents three localities, across a wide geographic range. On the other hand, the Rasoloarison et al. (2000) sample for *M. griseorufus* near BMSR includes only 6 individuals, which may account for its relatively high CV (7.17).

Dental morphology

Frequencies for each condition of the 40 traits (Appendix A [right teeth] and Appendix B [left teeth]) show that eight (20%) exhibit 100% presence for both left and right teeth in the Amboasary sample. Included among these are traits characteristic of all mouse lemurs, such as a single cusped P^2 and P_2, a distinct protocone on P^4, and P_4 with a thick buccal cingulid and centrally placed entoconid. Other traits exhibiting 100% presence for both left and right tooth positions are M^1 hypocones, and metastyles on M^1 and M^2. The remaining traits exhibit a wide range of variation, with several exhibiting a nearly dichotomous distribution in the sample, and others exhibiting low frequencies. Traits exhibiting a dichotomous distribution include lower molar cingular development (Appendices A and B, traits 11, 18, and 23: nearly equal frequencies of individuals with weak and strong buccal cingula on left and right M^1, M^2, and M^3), and P_3 buccal cingulids (Appendices A and B, trait 26) with nearly equal frequencies of weak and strong rims on both left and right teeth. Also of note is the low, but distinct, presence of variable secondary cusps on the maxillary teeth: protocones on P^3 (Appendices A and B, trait 3; 4.0% in right teeth, 2.4% in left teeth), an accessory ridge and/or cusp distolingual to the hypocone on M^1 (Appendices A and B, trait 7; 6.5% of right M^1, 5.7% of left M^1), and M^3 hypocones. These traits are similar to ones often assigned taxonomic significance, particularly in cladistic analyses, among both living and especially fossil primates and other mammals (see discussions in Krishtalka and Stucky, 1985 and Simons, 2003).

One example of the range of dental morphology seen in this sample is variation in the lingual morphology on M^1, which results in the existence of very dissimilar teeth within the sample. The lingual portion of M^1 may or may not exhibit pericones, accessory ridges, or a cusp distolingual to the hypocone. Furthermore, the overall shape of M^1 can be squared, when a pericone equal in size to the hypocone is present (Fig. 2a), squared with a distolingual extension when the post-hypocone accessory ridge and/or cusp is present, or triangular (i.e., tribosphenic) when the pericone is absent, or greatly reduced. The latter triangular shape can also be accentuated if the post-hypocone area is well-developed (Fig. 2b). As a result of these traits, the morphology of M^1 varies tremendously in this sample.

Patterns of variation at BMSR are similar to those described for Amboasary. Of the 40 traits scored for right and left teeth (Appendices C and D), approximately half display 100% presence or absence of specific traits. This percentage is higher than that at Amboasary, but is largely a product of the smaller sample sizes at BMSR, as a number of the traits not present in 100% of the specimens at Amboasary occur at low frequencies. Of those traits representing dichotomous distributions at BMSR, many are also dichotomous at Amboasary. This includes traits 25 and 26 (P_2 and P_3 buccal cingulum strength), and trait 31 (M_1 buccal cingulum strength). Certain traits show low frequencies of occurrence in both samples; this includes trait 7, a lingual extension/style on M^1, which occurs in 6.5% of the Amboasary right teeth (Appendix A) and 5.6% of the left (Appendix B). At BMSR (Appendices C and D) this trait is seen in only one tooth, a left M^1 (Appendix D, $n = 12$). The one specimen at BMSR displaying this feature is one of six from Ihazoara Canyon, approximately 5 km from the protected BMSR parcel where the majority of the new mouse lemur specimens were recovered in 2008. However, this specimen does not exhibit an M^2 pericone, similar to the majority of individuals in both the BMSR and Amboasary samples. In contrast, a second BMSR specimen from Ihazoara Canyon possesses an M^2 pericone, but does not exhibit the M^1 lingual extension. This illustrates that even in a small subset of a large sample, traits associated with lingual dental development can vary widely, and are likely of limited taxonomic and/or phylogenetic value among living or fossil primates.

Individual dental variants

In addition to the above patterns of intraspecific dental variation, some interesting variants characterize single individuals in the AMNH sample. For example, one specimen (AMNH 174496) displays a single cusped, connate M^3 (Fig. 3a). This tooth differs substantially from the regular M^3 pattern (Fig. 3b), and out of context, would be impossible

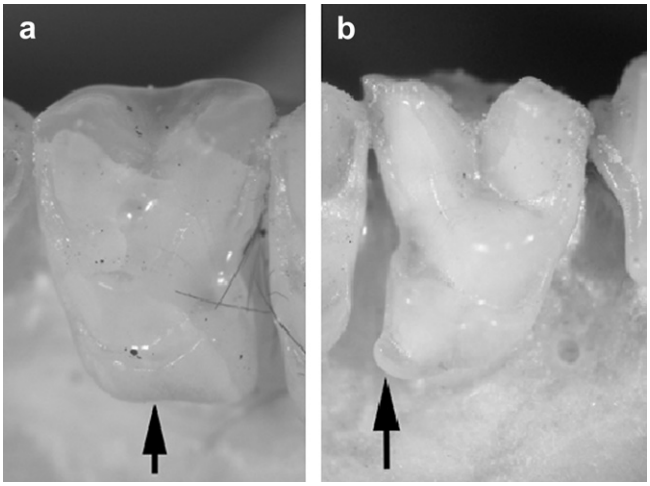

Figure 2. Variation in AMNH mouse lemur (*Microcebus griseorufus*) maxillary molar morphology. (a). "Squared" left M^1 with thick cingulum, equal pericone and hypocone, and no distolingual extension (black arrow); (b). "Triangular" right M^1 with small pericone, large hypocone, and distinct distolingual extension (black arrow). [Photos by Frank Cuozzo].

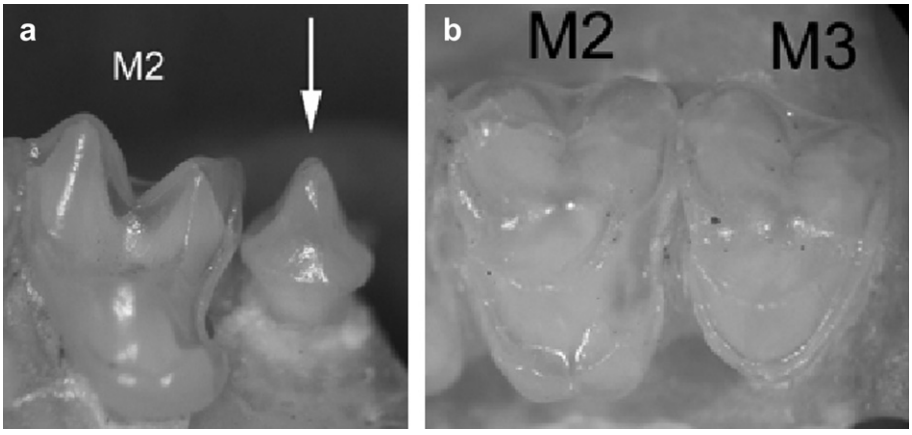

Figure 3. (a). Connate M^3 (white arrow) in AMNH 174496 (*Microcebus griseorufus*). (b) "Regular" triangular M^3 shape in AMNH *Microcebus griseorufus*. [Photos by Frank Cuozzo].

to identify either as an M^3, or as a mouse lemur tooth. Another individual specimen has a significantly shortened M_3 (AMNH 174523), with the typically extended hypoconulid absent (Fig. 4a and b). These variants are quite different from the standard mouse lemur pattern, and again illustrate the possible range of variation that can exist in a likely breeding population. Two specimens (AMNH 174499 and AMNH 174515) exhibit supernumerary teeth. Individual AMNH 174499 has supernumerary lower molars on both the left and right mandibles (Fig. 5), and AMNH 174515 has an extra left maxillary incisor (Fig. 6). These individual variants often result from disruptions during odontogenesis (Miles and Grigson, 1990; Swindler, 2002), although supernumerary teeth may be polymorphisms in the lemur genome – i.e., artifacts of the ancestral mammalian dental formula, which included three incisors in each quadrant (see discussion in Sauther and Cuozzo, 2008). Kangas et al. (2004) note that increase in the expression of a single gene can lead to an increased number of teeth in mice, thus supernumerary teeth may also reflect a rapid genetic change. These traits, as well as the traits discussed previously, have implications for interpreting mammalian paleotaxonomic diversity based on dental morphology (Goodwin, 1998).

Pelage variation

The pattern of pelage variation exhibited by the Amboasary specimens and those of *M. griseorufus* from other sites is not shared by most other mouse lemurs, including other recognized species from the west (Table 6). This is confirmed by Fisher's exact test of significance of differences in frequency distributions across taxa (Tables 7 and 8); all are highly significant. However, a comparison of coat characteristics of individuals from Amboasary and from Beza Mahafaly affirms their similarity, in which the limited variation in Amboasary pelage (all individuals display a "reversed V" on the cap and a dorsal median stripe, and all but two exhibit a gray–brown coat), falls within the range of pelage variation at BMSR (Table 6). When assessed quantitatively, frequency differences in these traits are not significant between Amboasary and BMSR, suggesting that the populations at these two sites likely belong to the same species (Tables 7 and 8). The match was poor for Amboasary specimens with those belonging to *M. murinus* or to *M. rufus* (Table 6).

Qualitative data also point to a good match between Amboasary specimens and *M. griseorufus* at Beza Mahafaly. Individuals captured at BMSR generally display what may be called the "typical" *M. griseorufus* pattern (Table 6), consisting of a red–brown tail, shades of gray and brown on the back, a red–brown stripe of varying intensity along the dorsal midline, that generally matches the color of the tail, a white underside, a white stripe between the eyes, and reddish-brown markings above the eyes converging in an apex (the "reversed V") on an otherwise gray or yellowish-brown cap (Fig. 7a and b). However, variants included some that are more similar to *M. murinus* at the Kirindy forest (a red–brown tail, a gray back lacking a contrasting dorsal midline stripe, a cream

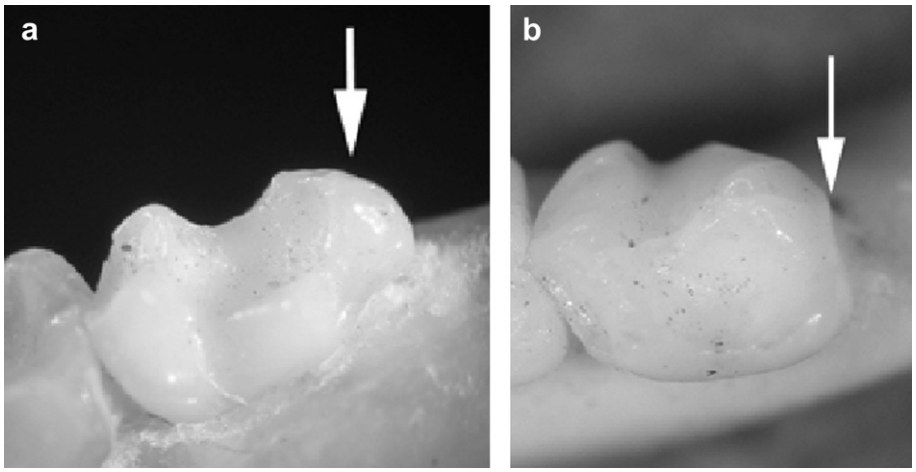

Figure 4. Variation in AMNH mouse lemur (*Microcebus griseorufus*) mandibular third molars. (a). The "typical" M_3 morphology, with distal extension and hypoconulid, marked by a white arrow (buccal view); (b). M_3 without distal "heel" and hypoconulid (AMNH 174523), with white arrow marking the "squared" distal border rather than the distal extension seen in 3a (occlusal view). [Photos by Frank Cuozzo].

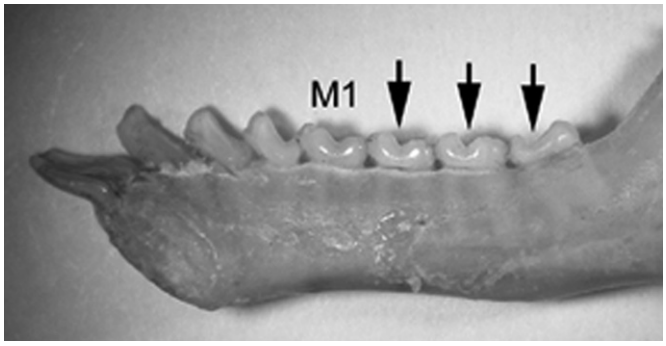

Figure 5. Supernumerary molar in a right mandible of AMNH 174499 (*Microcebus griseorufus*). Black arrows mark the three molars distal to M_1. [Photo by Frank Cuozzo].

underside, and no reverse V on the cap) (Fig. 7c). Additional individuals are all "red" (a red–brown tail, a red–brown back lacking a dorsal midline stripe, a cream underside, a red–brown face and cap but with a creamy white stripe between the eyes). A dorsal median stripe is most distinct in individuals with relatively light coats; it becomes less distinct, or disappears entirely, as the coat darkens. As seen in Fig. 7a–c, and in Table 6, the BMSR mouse lemurs display a wider range of pelage variation than at Amboasary, where all individuals display at least two of the "typical" *M. griseorufus* traits (two of the 19 Amboasary pelage specimens display a "red/dark brown" overall color, compared to the typical gray–brown of *M. griseorufus* [Table 6]). This wide range of pelage characteristics at BMSR is especially notable, as this population has been shown to illustrate genetic homogeneity (Heckman et al., 2006). Thus, the BMSR mouse lemurs exhibit clear discordance between mitochondrial DNA and pelage.

Qualitatively, the coats of individuals from Amboasary in the AMNH Bluntschli collection resemble the majority from Beza Mahafaly in the tendency to have light fur between the eyes and on the nasal region (white, pale yellow, or pale brownish gray), pale cheeks, a yellowish brown cap with a dark reversed V, a white, pale yellow, or pale yellowish brown throat and ventrum; dark yellowish brown pelage on the dorsal surfaces of the arm and upper arm, and a dorsal median stripe. The color of the tail and the dorsal median stripe is more uniform across mouse lemurs; it tends to be dark yellowish brown or dark brown. *M. rufus* from Antsihanaka, Andampy, Didy, Ivondro, Tampina, and Analamazaotra have consistently darker pelage, with brown, dark brown, or very dark brown faces and dorsal pelage, and light yellowish brown fur or yellowish brown fur on the throat and ventrum. Sometimes the tail is very dark brown. *M. murinus* from Andranomena, Toliara, Vohimena, and Manamby is characterized by more gray or yellowish brown fur on the cheeks, more gray, brown, or dark brown fur on the dorsum, and mostly yellowish brown fur on the throat and ventrum.

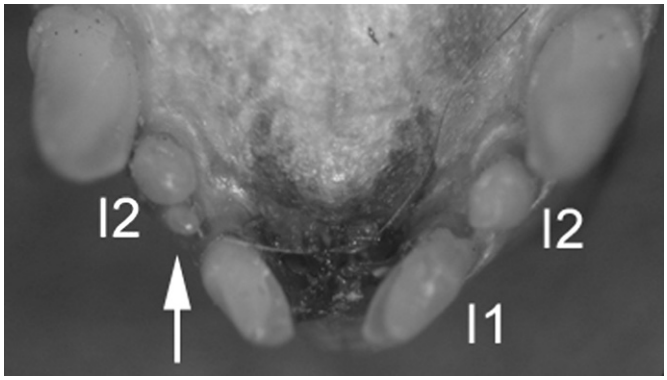

Figure 6. Supernumerary left incisor in AMNH 174499 (*Microcebus griseorufus*) [Photo by Frank Cuozzo].

Discussion

Taxonomic affinity of the AMNH Amboasary mouse lemur sample

The immediate goal of our project was to assess the single-species status of the Amboasary mouse lemur sample housed at AMNH. We were also interested in establishing the specific affinity of this sample, given the dramatic recent changes in mouse lemur taxonomy (see earlier references). We recognize that pelage can vary significantly among related, morphologically similar primate species (e.g., African guenons, genus *Cercopithecus* [Enstam and Isbell, 2007]). However, we are confident that the BMSR mouse lemur population provides an accurate point of reference for assessing specific variability in southern Madagascar's mouse lemurs. Specifically, mitochondrial DNA and a consensus phylogeny derived from a combination of mtDNA and nDNA markers supports a single species designation for BMSR mouse lemurs (Heckman et al., 2006, 2007), despite notable variation in pelage characters (Table 6, Fig. 7a–c). Although occurring in a small area (all specimens were collected within five km of the reserve headquarters), mouse lemur habitats at BMSR range from an open, dry, xerophytic forest, to an area of closed-canopy tamarind-dominated gallery forest along the Sakamena River, to the mixed dry forest at Ihazoara Canyon. Heckman et al. (2006) suggested that the pelage variation observed, which is independent of habitat, is inconsequential, and likely plays no role in mate recognition in these nocturnal, solitary animals, as mouse lemurs frequently depend on olfaction and vocalizations in social encounters (e.g., Yoder et al., 2002). However, this deserves further study, as recent, dramatic habitat fragmentation in the Beza Mahafaly area, and southern Madagascar as a whole, may also impact current patterns of pelage variation within single lemur species. Of note, a previous sample of mouse lemur jaws collected from owl pellets by Goodman in the early 1990s, across the Sakamena River from the eastern edge of the Beza Mahafaly reserve near the village of Ambinda, has been identified as being made up almost entirely (all but one specimen) of *M. griseorufus* material (Rasoloarison et al., 2000). Furthermore, when single nDNA markers are analyzed alone, they show patterns of paraphyly consistent with incomplete lineage sorting (Heckman et al., 2007; see also Hapke et al., 2011). However, genetic evidence as a whole (with nDNA and mtDNA considered in combination) firmly establishes *M. griseorufus* and *M. murinus* as sister taxa and independent species despite the existence of pockets of hybridization.

As we have seen, pelage characteristics (color and patterning) of individual mouse lemurs from Amboasary in the Bluntschli collection housed at the AMNH and MCZ generally match "typical" *M. griseorufus* from Beza Mahafaly (Table 6), and there are no significant differences in trait frequencies when the two samples are compared (Table 8). Furthermore, the distribution of trait variants at Amboasary is not unlike that seen in living *M. griseorufus* from Beza Mahafaly, albeit displaying far less variation than at BMSR (Table 6). This limited variation in pelage characteristics at Amboasary when compared to BMSR, in which each trait scored at BMSR shows some variation, while those at Amboasary vary in only two of the three traits, may be a product of the smaller sample sizes at Amboasary. However, it is noteworthy to again emphasize that pelage characteristics of individuals at Beza Mahafaly, a population shown to be genetically homogenous (cytochrome *b*) and

Table 6
Frequency data, scores on dried and live-animal coats for three variables.

Taxon (N)	Reversed V		Dorsal median stripe		Dominant color of the dorsal fur		
	Absent or indistinct	Present	Absent or indistinct	Present	Gray	Gray–brown	"Red" (dark brown)
M. berthae (1)	0	1	0	1	0	1	0
M. sambiranensis (3)	3	0	3	0	0	0	3
M. ravelobensis (6)	6	0	6	0	0	6	0
M. murinus (7)	7	0	7	0	1	0	6
M. myoxinus (6)	6	0	0	6	0	5	1
M. tavaratra (5)	5	0	5	0	0	2	3
M. rufus (9)	9	0	9	0	0	2	7
M. griseorufus (212)	39	173	37	175	16	170	26
Amboasary (19)	0	11	0	19	0	17	2

suggested to belong to *M. griseorufus*, are quite variable (Heckman et al., 2006). Although we have not surveyed variation in coat characteristics of living mouse lemurs from other sites, it is apparent that similar variation may exist elsewhere. *M. murinus* is one such variable species; for example, the skins (including the neotype from Andranomena, south of Kirindy) of *M. murinus* at the Field Museum of Natural History, Chicago (Rasoloarison et al., 2000) differ strikingly from the grayer *M. murinus* skins that occur in the Kirindy forest (ER, pers. obs.). Evidently, it is not pelage coloration *per se* but the frequency distribution of pelage traits that can be described as characterizing any particular species. This implies that coat characteristics must be well sampled before species can be properly described, and before pelage variation can be assessed in relation to patterns of dental variation.

Patterns of dental variation in the Amboasary sample, similar to pelage variants, are consistent with those seen in the BMSR mouse lemurs, a known, single-species sample (Heckman et al., 2006). This includes overlapping ranges of dental measurements, similar degrees of odontometric variation, and low CVs for all dental measures (Table 5a–d). The Amboasary sample also exhibits a very low degree of craniometric variation (Fig. 1a–c; Table 5a–d). Although mandibular first molar measures are significantly larger at BMSR than Amboasary, maxillary molar size does not differ (Table 5c). Therefore, these metric data do not appear to indicate a meaningful biological difference between the two samples. In addition, patterns of dental morphology are also consistent across the two mouse lemur samples, with the same dental features in each sample displaying 100%, dichotomous, and infrequent occurrences. Given the limited metric variation in cranial and dental measures, and the overlap of similar, variable, non-metric dental traits, in the mouse lemurs at Amboasary and BMSR – combined with pelage patterns that overlap, and that match traits of established *M. griseorufus* at BMSR, it seems to be highly unlikely that the Amboasary sample comprises more than one species. We therefore conclude that the AMNH Amboasary sample represents a single species – *M. griseorufus*.

Table 7
Fisher's exact test of significance of differences in frequency distributions of coat characteristics.[a]

Trait tested	*N*	Fisher's statistic	Significance (two-sided)
Reversed V (present or absent)	256	88.3	$p < 0.001$
Dorsal median stripe (present or absent)	264	82.8	$p < 0.001$
Dorsal fur dominant color (gray, gray–brown, or "red")	264	241.6	$p < 0.001$

[a] Included taxa are: *M. ravelobensis*, *M. murinus*, *M. myoxinus*, *M. tavaratra*, *M. rufus*, *M. griseorufus*, and "Amboasary."

Interpreting primate biological variation

The presence of diverse pelage (BMSR) and substantial variation in dental morphology (i.e., non-metric traits [BMSR and Amboasary]), combined with limited cranial and/or dental metric variation in each of our two single-locality, single-species *Microcebus* samples, provides a strong point of comparison for interpreting variation, and thus species boundaries, in primate biology. Most notably, our data indicate that different biological systems can be discordant in a single species, thus drawing attention to the efficacy of identifying primate species on the basis of single biological traits, whether genetic markers, pelage variants, dental morphology, or cranial/dental metric variation.

This point is further illustrated when we compare our mouse lemur data to that of sympatric ring-tailed lemurs (*Lemur catta*). The Beza Mahafaly ring-tailed lemurs comprise an important comparative database for assessing biological variation among primates, particularly because dental variation in this unequivocal, single-species primate population has been so well documented (Sauther et al., 2001; Cuozzo and Sauther, 2004, 2006a,b; see reviews in Cuozzo and Yamashita, 2006, and Cuozzo, 2008). As noted by Plavcan and Cope (2001) and Tornow et al. (2006), such samples for extant species are rare. In this population, a number of dental traits vary (Table 6; Sauther et al., 2001; Cuozzo and Yamashita, 2006; Cuozzo, 2008). Variable traits include P^4 metaconids and upper molar lingual cusps (Table 9), the absence of which have been suggested as diagnostic of ring-tailed lemurs (Tattersall and Schwartz, 1991; Tattersall, 1993). At Beza Mahafaly, two individuals display pronounced lingual cusps on M^1 and M^2, and 24 individuals (45.3%, $n = 53$; Table 9) exhibit distinct metaconids on P_4. The presence of upper molar lingual cusps (albeit at a low frequency) is especially notable, as these distinct cusps are viewed as diagnostic of *Eulemur* (i.e., *Eulemur fulvus*) in contrast to *Lemur catta* (Tattersall and Schwartz, 1991; Tattersall, 1993; Swindler, 2002; see discussion in Cuozzo and Yamashita, 2006). The pattern of lingual dental morphological variability in *L. catta* at the Beza Mahafaly Special Reserve thus parallels that in each of our mouse lemur samples. This is an especially interesting point of comparison, as ring-tailed lemurs have been reported to exhibit

Table 8
Fisher's exact test of significance of differences in frequency distributions of coat characteristics for Beza Mahafaly and Amboasary.

Trait tested	*N*	Fisher's statistic	Significance (two-sided)
Reversed V (present or absent)	212	1.18	$p = 0.37$
Dorsal median stripe (present or absent)	220	1.14	$p = 0.56$
Dorsal fur dominant color (gray, gray–brown, or "red")	220	2.6	$p = 0.14$

Figure 7. Coat color variation within *Microcebus griseorufus* at Beza Mahafaly. (a). The typical "griseorufus" morph; (b) The "gray" morph; (c) The "red" morph. [Photo credits: Emilienne Rasoazanabary]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pelage variation, with a higher altitude population in the northernmost area of their natural range exhibiting differences in tail ring number and overall darker pelage color (Goodman and Langrand, 1996), yet are not genetically distinct from other populations (e.g., cytochrome *b* [Yoder et al., 2000b]).

The recognition of substantial intraspecific dental morphological variation in extant primates is not new (e.g., Schwarz, 1931; Schuman and Brace, 1954; Swindler and Orlosky, 1974; Schwartz and Beutel, 1995). However, many scholars have failed to fully appreciate the degree to which such variation can exist in extant species, or even within populations. This is especially true among paleontologists, who sometimes assign taxonomic and/or phylogenetic significance to even slight variations among the specimens in a fossil assemblage and/or when conducting cladistic and other taxonomic analyses (see discussions in Krishtalka and Stucky, 1985; Jernvall, 2000; Cuozzo, 2002, 2008; Simons, 2003; Kangas et al., 2004; see also chapters in Kimbel and Martin, 2003).

One complicating factor in the use of nonmetric dental variation to diagnose primate (and other mammalian) species, in either living or fossil forms, is the apparent rapidity in which slight developmental differences can generate surprising amounts of variation in dental morphology (e.g., Jernvall, 2000; Kangas et al., 2004). For example, Kangas et al. (2004) report that increased expression in a single gene in mice leads to changes in the number, shape, and position of cusps. Thus, in effect, failure to appreciate the developmental component of the generation of variation can "obscure phylogenetic history" (Kangas et al., 2004: 211). Also, recent work illustrates differences in the degree of heritability for different dental features, and that tooth size and discrete traits are not necessarily linked (e.g., Hlusko and Mahaney, 2003, 2007; Hlusko et al., 2007). For instance, certain traits of the lingual cingulum in a large sample of pedigreed baboons show high heritability within the arcade (e.g., between left and right teeth of either the maxilla or mandible), but less so between arcades (Hlusko and Mahaney, 2003).

Our lemur data suggest that notable variation in nonmetric dental traits can occur in populations exhibiting limited odontometric variation. Most notably in our two extant mouse lemur samples, the M^1 post-hypocone ridge and/or cusp (Fig. 2b) is variable in appearance, ranging from a small ridge, to a ridge with an accessory cusp, and it can also vary within the arcade, with either left or right teeth, or sometimes both, displaying the trait. In contrast, the lingual cingulum traits discussed by Hlusko and Mahaney (2003) show a strong correspondence within an arcade. This trait also appears in a single M^2 from Amboasary (Appendix B). In addition, several Amboasary specimens displayed an inflation of the area of M^1 distolingual to the hypocone without any true manifestation of a post-hypocone ridge or cusp. This trait, with its various manifestations along a gradient ranging from a slight lingual inflation to a ridge with a distinct cusp, corresponds with Jernvall's (2000) observation that various trait conditions are present, albeit at low frequencies, within geographically-restricted samples of a single mammal species. Under selective pressure (or due to genetic drift), any of these variants could become more

Table 9
Variation in dental traits among ring-tailed lemurs (*Lemur catta*) from Beza Mahafaly Special Reserve, Madagascar.

Trait	*N*	# with trait	% with trait
M^{1-2} ledge-like cingulum	58	56	96.5
P_3 metaconid absent	57	57	100.0
P_4 metaconid absent	53	29	54.7
M_1 lingual notch: narrow/pinched	48	48	100.0

frequent in the population. The same applies to other dental variants we describe. For example, protocones on P^3 could hold a selective advantage over time, given their potential for aiding in the processing of certain, perhaps novel foods. Butler (2000), in describing the evolution of primate teeth notes the potential "crushing" benefit of the development of a protocone on P^3, when combined with corresponding changes in the mandibular molars. Jernvall et al. (2008) also discuss the "molarization" of premolars (e.g., development of lingual cusps) in *Hapalemur simus*, as a benefit to processing more fibrous foods. Thus, the development of this premolar feature in mouse lemurs could be beneficial in a changing environment, and could quite rapidly become frequent in a population. Kangas et al. (2004) suggest that the potential for changes in a single gene to cause quite dramatic morphological variation, could lead to such rapid changes in dental morphology in response to environmental change. Thus, changes in the frequency of lingual dental traits over time in the fossil record *might* prove useful in delineating species (e.g., Rose and Bown, 1984; Cuozzo, 2008) if viewed in the context of environmental change. Given the potential for dramatic variation in nonmetric dental traits that we document, it would be prudent, when conducting taxonomic analyses, to heed the advice of Strauss (1954: 308) who, citing Schuman and Brace's (1954) seminal paper on chimpanzee dental variation, wrote that the demonstration of high dental variation within a homogeneous population of chimpanzees should "serve as a rein upon unbridled odontological speculation".

Similar caution should also be used when assessing species diversity using biological systems other than teeth. For example, many new species of living mouse lemur have been defined on the basis of single systems, frequently molecular data (e.g., Yoder et al., 2000a,b; Louis et al., 2006, 2008; Weisrock et al., 2010). However, the use of DNA characters in taxonomy has been critiqued by some as having no more weight than other biological characters (see comments by Lipscomb et al., 2003). Tattersall (2007) has argued against what he perceives as a dramatic and unwarranted proliferation of recognized extant lemur species, many of which have been diagnosed from small samples, and with limited knowledge of hard-tissue variation, and/or ecological and reproductive behavior. Markolf et al. (2011) follow this theme, suggesting that genetic markers from several loci should be combined with other biological data, such as behavioral, ecological, and morphological information, for interpreting species boundaries in lemurs. For the BMSR mouse lemurs we document notable variation in pelage (Table 6) and non-metric dental traits (Appendices C and D), yet limited dental metric variation (Table 5b). Heckman et al. (2006) report homogeneity in cytochrome *b* in a sample of 70 mouse lemurs at BMSR, collected across multiple habitats, which refuted their earlier hypothesis that multiple species were present at BMSR. The distinction between *M. griseorufus* and *M. murinus* is also further explored in their later work (Heckman et al., 2007), using both nDNA and mNDA markers. In the Amboasary sample, we show that limited cranial variation (Table 5a) and no evidence of heteroscedasticity (i.e., neither larger nor smaller values are more variable, Fig. 1a–c), corresponds to low levels of dental metric variation (Table 5a), notable variation in non-metric dental traits (Appendices A and B), and variation in one of three pelage characters (Table 6). This parallels the findings in the BMSR mouse lemurs, where for the markers assessed, a single species designation is supported, across habitats and pelage variants (Heckman et al., 2006). We thus argue that substantial variation in pelage and non-metric dental traits can occur in a single primate species, but that this species diagnosis rests upon tandem interpretations of limited metric variation of hard-tissue traits (e.g., cranial and/or dental measures) and molecular data showing distinct differences between species for certain genetic markers. From our mouse lemur example, it is clear that careful consideration of multiple biological systems is needed when interpreting variation, and subsequently, species boundaries in contemporary primate biology.

Implications for primate paleotaxonomy

Species diagnosis in paleobiology necessarily differs from the diagnosis of extant taxa, as paleotaxonomy must depend to a greater degree on morphological data (e.g. Tattersall, 1992). However, in addition to qualitative analyses of teeth, patterns of metric variation, when adequate samples are available, also provide an important point of comparison for interpreting and identifying species in the primate fossil record. Recall earlier comments by Kieser (1994), Plavcan and Cope (2001), and Tornow et al. (2006) on the importance, but rarity, of characterizing variation in geographically restricted samples. Our data do just that – provide data on patterns of biological variation in a large, geographically restricted primate sample. Thus, this work provides a useful reference for assessing the degrees of similarity and/or difference in other taxa, providing a template for confident assessment and interpretation of biological variation in the primate fossil record.

Of all our results, discordance between different traits, notably, consistent patterns of limited cranial and dental metric variation corresponding to marked variation in non-metric dental traits, is most relevant for questions of interpreting paleobiology. One especially relevant aspect of our data for interpreting the fossil record is the absence of heteroscedasticity in cranial variation in the large ($n = 126$) Amboasary sample. One of the challenges in interpreting fossil specimens, especially in the absence of large samples (e.g., in many hominin taxa), centers on the ability to accurately assess single specimens. For example, Trinkaus (2003) notes the impact that a single "large" Neandertal specimen has had on descriptions of Neandertal biology, especially when compared to modern humans. Dayan et al. (2002) note that there is substantial heteroscedasticity in cranial and dental measures in wolves (*Canis lupus*) and wild cats (*Felis silvestris*), which they suggest as cautionary for interpreting the relationships between dental and cranial variation, most specifically in the context of interpreting taxonomic diversity in the carnivoran fossil record. They attribute this pattern, in part, to the derived dentition of extant carnivores, not an issue for many early primates (e.g., Rasmussen, 2007), or many extant lemurs (e.g., Cuozzo and Yamashita, 2006), given their retention of a number of ancestral dental traits. As we illustrate in Fig. 1a, b and c, the relationships between skull length and biorbital breadth, zygomatic breadth, and palate breadth, respectively, there is a significant linear relationship between skull length and each of these other variables ($p < 0.0001$), thus indicating that this sample does not exhibit greater variation in larger or smaller cranial measures. These data provide a template for interpreting the taxonomic placement/identification of single fossils, when cranial specimens are available, especially among early primates, as extant mouse lemurs are among the analogs for the small-bodied extinct primates of the Eocene Epoch (Covert, 1995, 1997; Cuozzo, 2008).

As we briefly note earlier, the patterns of morphological variation we describe in the dentition of our lemur samples also provide a point of reference for interpreting variation in primate fossils. For example, the importance of acknowledging the potential for substantial variation in dental traits is seen in Szalay's critiques (1982, 1993) of several Eocene omomyid species. In developing these critiques, Szalay argued that species sharing similar, although not identical, morphologies, as well as temporal congruence, may not represent distinct species, but may instead represent a single, highly variable species. Similarly, Albrecht and Miller (1993) argue that the morphological variation seen in fossil primates may largely

represent intraspecific geographic variation, rather than species differences. Our data support these assertions; for example, the absence of a distinct, extended hypoconulid in AMNH 174523 is analogous to the Eocene adapid *Smilodectes* missing its "talonid heel", the shape of which is considered by many as a diagnostic trait of this genus (e.g., Covert, 1990). Also, the parallel patterns of lingual dental cusp variation in each of our mouse lemur samples, and in our comparative ring-tailed lemur sample, provide further support that dental morphology varies in single-species samples.

Evaluating more subtle non-metric dental variation has even greater importance than the above example for assessing fossil assemblages and interpreting individual specimens. Maxillary molar lingual traits, and premolar secondary cusps, vary widely among the mouse lemurs at Amboasary and BMSR (recall these traits also vary among the ring-tailed lemurs at BMSR), often exhibiting dichotomous characters states. While these traits can prove important in delineating species boundaries, when viewed over time in the geologic record, as seen in several small-bodied Eocene omomyid primates from North America (e.g., Rose and Bown, 1984; Cuozzo, 2008), their significance in single locality assemblages are likely of limited taxonomic importance. Rose et al. (2009) recognized the importance of such patterns of dental variation (e.g., premolar cusps) in their analysis of Eocene primates from southern Asia. They argue that two forms previously identified from the same stratum on the basis of subtle premolar differences, *Suratius robustus* and *Asiadapis cambayensis*, should be synonymized. Cuozzo (2002) made a similar argument for synonymizing two small omomyids from the early Eocene of Wyoming (see Tornow, 2008 for a contrasting view).

Conclusions

We encourage the integration of dental, cranial, pelage, and ecological data, combined with information, when available, from genetic samples, when diagnosing primate species among living, and when appropriate, among fossil forms. We also strongly discourage the sacrifice of living, wild primates solely for taxonomic purposes. Our collaborative, long-term work at the Beza Mahafaly Special Reserve, Madagascar, illustrates the power of sustained research on living individuals and populations, for example, the collection of dental, linear, and pelage data during exams of sedated, living primates, as well as the importance of collecting data from those individuals who die natural deaths, including from predation.

Knowledge of variation in multiple biological systems, as we describe herein for established single-species samples, their discordance, and their role in assigning specific status, also transcends interpretation of the fossil record. For example, Stanford (2001: 310) notes that taxonomic status "often dictates conservation priorities" among primates, illustrating the need to understand the range of variation within species. Hey et al. (2003: 600) note that species "living in nature must be part of evolving populations", thus acknowledging the link between contemporary conservation concerns and evolutionary biology. Among Madagascar's lemurs, the past three decades have witnessed a dramatic increase in the number of recognized species, from 36 species (Tattersall, 1982) to 97–99 species (Mittermeier et al., 2008, 2010). The new data that we present provide an important reference for interpreting primate intraspecific variability, which is directly relevant to the efficacy of recent, rapid increases in named lemur species (e.g., Tattersall, 2007; Markolf et al., 2011), as well as other primate groups (e.g., Stanford, 2001).

Finally, as Tattersall (1992: 343) noted in reference to hominin paleontology, species in the fossil record "are, and will continue to be, categorized and ranked…at least primarily on the basis of morphological attributes." This is not to say that paleotaxonomy should be trapped in a world of typology, but rather, that assessing the fossil record will remain dominated by morphology, regardless of how much we appreciate the importance of spatial, temporal, and behavioral variables in addressing the theoretical question, "What is a species?" Our new data provide a template to begin to address this question in living and fossil primates.

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Appendix A. Variation in Amboasary dental traits: right teeth

#	Trait	*n*	Condition	%	*n*	Condition	%	*n*	Condition	%	*n*
1	C w/distal style	118	Absent	11.9	14	Present	88.1	104			
2	P^2 paracone only	125	Absent	0.0	0	Present	100.0	125			
3	P^3 w/protocone	125	Absent	96.0	120	Present	04.0	5			
4	P^4 w/protocone	125	Absent	0.0	0	Present	100.0	125			
5	M^1 pericone	116	Absent	87.1	101	Present	12.9	15			
6	M^1 hypocone	123	Absent	0.0	0	Present	100.0	123			
7	M^1 lingual extension/style	124	Absent	93.5	116	Present	06.5	8			
8	M^1 parastyle	118	Absent	10.2	12	Present	89.8	106			
9	M^1 metastyle	121	Absent	0.0	0	Present	100.0	121			
10	M^1 shape	125	Square	0.8	1	Elongated	99.2	124			
11	M^1 buccal cingulum	125	Strong	49.6	62	Weak	50.4	63	Absent	0.0	0
12	M^2 pericone	115	Absent	89.6	103	Present	10.4	12			
13	M^2 hypocone	120	Absent	03.3	4	Present	96.7	116			
14	M^2 lingual extension/style	120	Absent	100.0	120	Present	0.0	0			
15	M^2 parastyle	120	Absent	06.7	8	Present	93.3	112			
16	M^2 metastyle	124	Absent	0.0	0	Present	100.0	124			
17	M^2 shape	122	Square	0.0	0	Elongated	100.0	122			
18	M^2 buccal cingulum	124	Strong	56.5	70	Weak	42.7	53	Absent	0.8	1
19	M^3 pericone	120	Absent	98.3	119	Present	0.8	1			
20	M^3 hypocone	106	Absent	95.3	101	Present	04.7	5			
21	M^3 parastyle	120	Absent	10.8	13	Present	89.2	107			
22	M^3 metastyle	121	Absent	05.0	6	Present	95.0	115			
23	M^3 buccal cingulum	125	Strong	62.4	78	Weak	37.6	47	Absent	0.0	0
24	P_2 caniniform	125	Absent	0.0	0	Present	100.0	125			
25	P_2 buccal cingulum	124	Strong	26.6	33	Weak	72.6	90	Absent	0.8	1
26	P_3 buccal cingulum	126	Strong	48.4	61	Weak	51.6	65	Absent	0.0	0
27	P_4 thick buccal cingulum	125	Absent	0.0	0	Present	100.0	125			
28	P_4 w/talonid	125	Absent	0.8	1	Present	99.2	124			
29	P_4 entoconid position	125	Central	100.0	125	Lingual	0.0	0			
30	M_1 shape	124	Square	0.0	0	Rectangular	01.6	2	Parrallelogram	98.4	122
31	M_1 buccal cingulum	126	Strong	27.0	34	Weak	72.2	91	Absent	0.8	1
32	M_1 distal cingular shelf	123	Strong	11.4	14	Weak	74.0	91	Absent	14.6	18
33	M_2 shape	123	Square	27.6	34	Rectangular	05.7	7	Parrallelogram	66.7	82
34	M_2 buccal cingulum	126	Strong	29.4	37	Weak	69.8	88	Absent	0.8	1
35	M_2 distal cingular shelf	124	Strong	32.3	40	Weak	60.5	75	Absent	07.3	9
36	M_3 buccal cingulum	125	Strong	31.2	39	Weak	68.0	85	Absent	0.8	1
37	M_3 w/hypoconulid	123	Absent	01.6	2	Present	98.4	121			
38	M_3 w/notch between hypoconid/hypoconulid	124	Absent	01.6	2	Present	98.4	122			
39	M_3 w/cingulum in notch	118	Absent	11.0	13	Present	89.0	105			
40	M_3 w/entoconid and hypoconulid	108	Distinct	86.1	93	Not distinct	13.9	15			

Appendix B. Variation in Amboasary dental traits: left teeth

#	Trait	*n*	Condition	%	*n*	Condition	%	*n*	Condition	%	*n*
1	C w/distal style	111	Absent	10.8	12	Present	89.2	99			
2	P^2 paracone only	125	Absent	0.0	0	Present	100.0	125			
3	P^3 w/protocone	124	Absent	97.6	121	Present	02.4	3			
4	P^4 w/protocone	125	Absent	0.0	0	Present	100.0	125			
5	M^1 pericone	115	Absent	87.8	101	Present	12.2	14			
6	M^1 hypocone	122	Absent	0.0	0	Present	100.0	122			
7	M^1 lingual extension/style	124	Absent	94.4	117	Present	05.6	7			
8	M^1 parastyle	115	Absent	08.7	10	Present	91.3	105			
9	M^1 metastyle	119	Absent	0.0	0	Present	100.0	119			
10	M^1 shape	125	Square	0.8	1	Elongated	99.2	124			
11	M^1 buccal cingulum	125	Strong	48.8	61	Weak	51.2	64	Absent	0.0	0
12	M^2 pericone	116	Absent	91.4	106	Present	08.6	10			
13	M^2 hypocone	122	Absent	01.6	2	Present	98.4	120			
14	M^2 lingual extension/style	120	Absent	99.2	119	Present	0.8	1			
15	M^2 parastyle	120	Absent	05.8	7	Present	94.2	113			
16	M^2 metastyle	124	Absent	0.0	0	Present	100.0	124			
17	M^2 shape	122	Square	0.0	0	Elongated	100.0	122			
18	M^2 buccal cingulum	125	Strong	56.8	71	Weak	42.4	53	Absent	0.8	1
19	M^3 pericone	121	Absent	98.4	119	Present	01.6	2			
20	M^3 hypocone	111	Absent	96.4	107	Present	03.6	4			
21	M^3 parastyle	118	Absent	09.3	11	Present	90.7	107			
22	M^3 metastyle	117	Absent	04.3	5	Present	95.7	112			
23	M^3 buccal cingulum	124	Strong	62.1	77	Weak	37.9	47	Absent	0.0	0
24	P_2 caniniform	126	Absent	0.0	0	Present	100.0	126			
25	P_2 buccal cingulum	125	Strong	26.4	33	Weak	72.8	91	Absent	0.8	1
26	P_3 buccal cingulum	124	Strong	51.6	64	Weak	48.4	60	Absent	0.0	0
27	P_4 thick buccal cingulum	125	Absent	0.0	0	Present	100.0	125			
28	P_4 w/talonid	125	Absent	0.0	0	Present	100.0	125			
29	P_4 entoconid position	125	Central	100.0	125	Lingual	0.0	0			
30	M_1 shape	124	Square	0.0	0	Rectangular	01.6	2	Parrallelogram	98.4	122
31	M_1 buccal cingulum	125	Strong	26.4	33	Weak	72.8	91	Absent	0.8	1
32	M_1 distal cingular shelf	123	Strong	11.4	14	Weak	71.5	88	Absent	17.1	21
33	M_2 shape	124	Square	23.4	29	Rectangular	05.6	7	Parrallelogram	71.0	88
34	M_2 buccal cingulum	125	Strong	28.8	36	Weak	70.4	88	Absent	0.8	1
35	M_2 distal cingular shelf	124	Strong	31.5	39	Weak	61.3	76	Absent	07.3	9
36	M_3 buccal cingulum	118	Strong	32.2	38	Weak	66.9	79	Absent	0.8	1
37	M_3 w/hypoconulid	122	Absent	0.8	1	Present	99.2	121			
38	M_3 w/notch between hypoconid/hypoconulid	123	Absent	0.8	1	Present	99.2	122			
39	M_3 w/cingulum in notch	115	Absent	12.2	14	Present	87.8	101			
40	M_3 w/entoconid and hypoconulid	101	Distinct	85.1	86	Not distinct	14.9	15			

Appendix C. Variation in Beza Mahafaly dental traits: right teeth

#	Trait	*n*	Condition	%	*n*	Condition	%	*n*	Condition	%	*n*
1	C w/distal style	5	Absent	0.0	0	Present	100.0	5			
2	P^2 paracone only	5	Absent	0.0	0	Present	100.0	5			
3	P^3 w/protocone	10	Absent	0.0	0	Present	100.0	10			
4	P^4 w/protocone	13	Absent	0.0	0	Present	100.0	13			
5	M^1 pericone	10	Absent	90.0	9	Present	10.0	1			
6	M^1 hypocone	12	Absent	0.0	0	Present	100.0	12			
7	M^1 lingual extension/style	12	Absent	100.0	12	Present	0.0	0			
8	M^1 parastyle	11	Absent	0.0	0	Present	100.0	11			
9	M^1 metastyle	10	Absent	0.0	0	Present	100.0	10			
10	M^1 shape	12	Square	0.0	0	Elongated	100.0	12			
11	M^1 buccal cingulum	11	Strong	9.1	1	Weak	90.0	10	Absent	0.0	0
12	M^2 pericone	9	Absent	77.8	7	Present	22.2	2			
13	M^2 hypocone	10	Absent	10.0	1	Present	90.0	9			
14	M^2 lingual extension/style	10	Absent	100.0	10	Present	0.0	0			
15	M^2 parastyle	10	Absent	20.0	2	Present	80.0	8			
16	M^2 metastyle	10	Absent	0.0	0	Present	100.0	10			
17	M^2 shape	11	Square	0.0	0	Elongated	100.0	11			
18	M^2 buccal cingulum	11	Strong	18.2	2	Weak	81.8	9	Absent	0.0	0
19	M^3 pericone	11	Absent	100.0	10	Present	0.0	0			
20	M^3 hypocone	10	Absent	100.0	10	Present	0.0	0			
21	M^3 parastyle	12	Absent	9.1	1	Present	90.9	11			
22	M^3 metastyle	11	Absent	27.3	3	Present	72.7	8			
23	M^3 buccal cingulum	9	Strong	11.1	1	Weak	88.9	8	Absent	0.0	0
24	P_2 caniniform	6	Absent	0.0	0	Present	100.0	6			
25	P_2 buccal cingulum	6	Strong	33.3	2	Weak	66.7	4	Absent	0.0	0
26	P_3 buccal cingulum	6	Strong	50.0	3	Weak	50.0	3	Absent	0.0	0
27	P_4 thick buccal cingulum	8	Absent	0.0	0	Present	100.0	8			
28	P_4 w/talonid	8	Absent	0.0	0	Present	100.0	8			
29	P_4 entoconid position	8	Central	37.5	3	Lingual	62.5	5			
30	M_1 shape	11	Square	9.1	1	Rectangular	36.4	4	Parrallelogram	54.5	6
31	M_1 buccal cingulum	11	Strong	36.4	4	Weak	54.5	6	Absent	11.1	1
32	M_1 distal cingular shelf	10	Strong	20.0	2	Weak	40.0	4	Absent	40.0	4
33	M_2 shape	13	Square	100.0	13	Rectangular	0.0	0	Parrallelogram	0.0	0
34	M_2 buccal cingulum	12	Strong	25.0	3	Weak	75.0	9	Absent	0.0	0
35	M_2 distal cingular shelf	13	Strong	38.5	5	Weak	38.5	5	Absent	23.0	3
36	M_3 buccal cingulum	10	Strong	30.0	3	Weak	70.0	7	Absent	0.0	0
37	M_3 w/hypoconulid	10	Absent	0.0	0	Present	100.0	10			
38	M_3 w/notch between hypoconid/hypoconulid	9	Absent	0.0	0	Present	100.0	9			
39	M_3 w/cingulum in notch	9	Absent	11.1	1	Present	88.9	8			
40	M_3 w/entoconid and hypoconulid	8	Distinct	100.0	8	Not distinct	0.0	0			

Appendix D. Variation in Beza Mahafaly dental traits: left teeth

#	Trait	*n*	Condition	%	*n*	Condition	%	*n*	Condition	%	*n*
1	C w/distal style	5	Absent	0.0	0	Present	100.0	5			
2	P^2 paracone only	6	Absent	0.0	0	Present	100.0	6			
3	P^3 w/protocone	7	Absent	0.0	0	Present	100.0	7			
4	P^4 w/protocone	9	Absent	0.0	0	Present	100.0	9			
5	M^1 pericone	7	Absent	85.7	6	Present	14.3	1			
6	M^1 hypocone	9	Absent	0.0	0	Present	100.0	9			
7	M^1 lingual extension/stylid	9	Absent	88.9	8	Present	11.1	1			
8	M^1 parastyle	8	Absent	0.0	0	Present	100.0	8			
9	M^1 metastyle	8	Absent	0.0	0	Present	100.0	8			
10	M^1 shape	9	Square	0.0	0	Elongated	100.0	9			
11	M^1 buccal cingulum	9	Strong	11.1	1	Weak	88.9	8	Absent	0.0	0
12	M^2 pericone	7	Absent	71.4	5	Present	28.6	2			
13	M^2 hypocone	9	Absent	0.0	0	Present	100.0	9			
14	M^2 lingual extension/stylid	8	Absent	100.0	8	Present	0.0	0			
15	M^2 parastyle	8	Absent	0.0	0	Present	100.0	8			
16	M^2 metastyle	8	Absent	0.0	0	Present	100.0	8			
17	M^2 shape	9	Square	0.0	0	Elongated	100.0	9			
18	M^2 buccal cingulum	8	Strong	25.0	2	Weak	75.0	6	Absent	0.0	0
19	M^3 pericone	7	Absent	100.0	7	Present	0.0	0			
20	M^3 hypocone	7	Absent	100.0	7	Present	0.0	0			
21	M^3 parastyle	8	Absent	12.5	1	Present	87.5	7			
22	M^3 metastyle	7	Absent	42.9	3	Present	57.1	4			
23	M^3 buccal cingulum	6	Strong	16.7	1	Weak	83.3	5	Absent	0.0	0
24	P_2 caniniform	5	Absent	0.0	0	Present	100.0	5			
25	P_2 buccal cingulum	5	Strong	40.0	2	Weak	60.0	3	Absent	0.0	0
26	P_3 buccal cingulum	6	Strong	50.0	3	Weak	50.0	3	Absent	0.0	0
27	P_4 thick buccal cingulum	8	Absent	0.0	0	Present	100.0	8			
28	P_4 w/talonid	8	Absent	0.0	0	Present	100.0	8			
29	P_4 entoconid position	8	Central	12.5	1	Lingual	87.5	7			
30	M_1 shape	9	Square	11.1	1	Rectangular	33.3	3	Parrallelogram	55.6	5
31	M_1 buccal cingulum	8	Strong	37.5	3	Weak	62.5	5	Absent	0.0	0
32	M_1 distal cingular shelf	7	Strong	14.2	1	Weak	42.9	3	Absent	42.9	3
33	M_2 shape	8	Square	75.0	6	Rectangular	0.0	0	Parrallelogram	25.0	2
34	M_2 buccal cingulum	8	Strong	25.0	2	Weak	75.0	6	Absent	0.0	0
35	M_2 distal cingular shelf	8	Strong	50.0	4	Weak	25.0	2	Absent	25.0	2
36	M_3 buccal cingulum	7	Strong	14.3	1	Weak	85.7	6	Absent	0.0	0
37	M_3 w/hypoconulid	8	Absent	0.0	0	Present	100.0	8			
38	M_3 w/notch between hypoconid/hypoconulid	8	Absent	0.0	0	Present	100.0	8			
39	M_3 w/cingulum in notch	6	Absent	33.3	2	Present	66.74				
40	M_3 w/entoconid and hypoconulid	6	Distinct	83.3	5	Not distinct	16.7	1			

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