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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.

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