



Distribution and Geographic Variation in the Western Woolly Lemur (*Avahi occidentalis*) with Description of a New Species (*A. unicolor*)*

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Received July 28, 1999; revision November 29, 1999; 2nd revision March 3, 2000; accepted March 14, 2000

The western woolly lemur is distributed through central western, northwestern and possibly northern Madagascar and is traditionally viewed as a monotypic species (*Avahi occidentalis*) or as a subspecies of *A. laniger*. We present new data on body weights of *Avahi* which, together with previously available body weights, provide additional evidence for recognizing eastern and western woolly lemurs as two distinct species. We then reexamine the distributions of, and chromatic variation within and between, populations of western woolly lemurs. A comparative study of wild subjects and museum skins reveals that several geographically discrete morphs exist in western *Avahi*, which is clearly polytypic. Marked differences between populations in fur coloration suggest that ≥ 3 distinct taxa should be recognized. The populations differ considerably in their habitat structure. In addition, field observations suggest clear differences in population density between ≥ 2 of the populations. We describe and name one new species.

KEY WORDS: systematics; *Avahi occidentalis*; western woolly lemur; Madagascar; new species.

*This paper was submitted independently by the authors and was placed here by R. H. Tuttle, Editor.

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INTRODUCTION

Two new large-bodied cathemeral or diurnal lemur species have been described by Meier *et al.*, (1987: *Hapalemur aureus*) and Simons (1988: *Propithecus tattersalli*), and a new high altitude population of the diurnal *Lemur catta* has been discovered (Goodman and Langrand, 1996). Moreover, new discoveries and distribution refinements have also been reported for nocturnal lemurs. Groves and Tattersall (1991) noted that fewer species per genus, and subspecies per species have been recognized among nocturnal lemurs, though they are geographically and ecologically equally widespread as their diurnal or cathemeral counterparts. They attribute this to the less obvious variety in coloration in nocturnal forms and the difficulties of nocturnal field surveys.

Groves and Tattersall's (1991) detailed examination of museum specimens of the fork-marked lemur *Phaner furcifer* revealed several subspecies. Intensified field surveys also led to the rediscovery of the rare *Allocebus trichotis* (Meier and Albignac, 1990) and evidence for this species in other regions (Rakotoarison *et al.*, 1996; Schütz and Goodman, 1998). Long-standing inferences on the sympatric existence of two distinct forms of *Microcebus* in western Madagascar (Petter, 1962; Petter *et al.*, 1977; Tattersall, 1982; Martin, 1995) have been substantiated (Schmid and Kappeler, 1994; Zimmermann *et al.*, 1998), and other distinct populations may be present in other regions of Madagascar (Rakotoarison *et al.*, 1993; Thalmann and Rakotoarison, 1994a; Hawkins *et al.*, 1998). For most nocturnal lemurs that were at some time believed to be extremely rare, such as the aye-aye, new evidence for their continued existence and a wider distribution than expected has been found. Even populations that had been deleted from recent distribution maps, e.g. the form of the greater dwarf lemur in the Bongolava region in central western Madagascar (Petter *et al.*, 1977), were rediscovered by Thalmann and Rakotoarison (1994b).

Accordingly, we expect that our knowledge of Malagasy lemurs in natural habitats is limited. At the same time, natural habitat—various types of forests—continues to disappear at a disastrous rate. Entire lemur populations may disappear with the loss of small patches of forest, some of which may be completely unknown because they are rare, occur in remote regions, or have an inconspicuous appearance.

For a long time, *Avahi laniger* was considered to be the only species of *Avahi*. The distinction of two subspecies based on differences in coloration and body size—*Avahi laniger laniger* and *A. laniger occidentalis*—was widely accepted (von Lorenz-Liburnau, 1898; Schwarz, 1931; Hill, 1953; Petter *et al.*, 1977; Tattersall, 1982). On the basis of cytogenetic evidence, Rumpler *et al.* (1990) convincingly demonstrated that the western popula-

tion of *Avahi* from Ampijoroa differed from the southeastern population in Ranomafana in karyotype, and inferred that meiotic chromosomal pairing of hypothetical hybrids would probably result in markedly reduced fertility. They concluded that western and eastern populations should be distinguished at the specific level: *Avahi laniger* and *A. occidentalis*.

The western woolly lemur (*Avahi occidentalis*) occurs in at least three discontinuous areas (Petter *et al.*, 1977; Tattersall, 1982; Harcourt and Thornback, 1990; Rakotoarison *et al.*, 1993; Mittermeier *et al.*, 1994). The largest area extends from north and east of the Betsiboka River to the Bay of Narinda (Tattersall, 1982) and includes the Ankarafantsika Strict Nature Reserve and the Forestry Reserve of Ampijoroa (Fig. 1; Appendix).

A second area is situated well to the north, including the Ampasindava peninsula (Milne-Edwards and Grandidier, 1875a,b) and the Manongarivo Special Reserve (Raxworthy and Rakotondraparany, 1988). Hawkins *et al.* (1990) also report *Avahi* from the Ankarana Special Reserve in northern Madagascar. Evidence for the latter population is scarce, and *Avahi* seem to be at best exceedingly rare in this reserve. The affinities of the Ankarana population are unknown, but Mittermeier *et al.* (1994) allocate it to the eastern form.

A previously unknown population of *Avahi* was discovered in the Strict Nature Reserve Bemaraha in western Madagascar in 1990 and was tentatively classified as *Avahi* cf. *occidentalis* by Mutschler and Thalmann (1990) and Rakotoarison *et al.* (1993). Subsequent surveys in the region suggested that the distribution of this population is limited to the south by the Manambolo River, and that *Avahi* is either generally rare in this region or that considerable differences in local densities occur, because *Avahi* is apparently limited to certain forest types (Thalmann and Rakotoarison, 1994a).

We present data from several field surveys of western woolly lemurs, including the regions of Bemaraha, Ampijoroa and various other localities where *Avahi* might potentially occur. In addition, we describe characteristics of fur coloration for each population based on our field observations together with examination of several museum collections.

Although the western woolly lemur (*Avahi occidentalis*) occurs in ≥ 3 distinct geographic zones, current classifications of the Malagasy primates treat the western *Avahi* as a monotypic species (Mittermeier *et al.*, 1994) or continue to regard it as one subspecies of *A. laniger* (Groves, 1993; Rowe, 1996). Conversely, our comparative study suggests that the eastern woolly lemurs not only constitutes a distinct species but also that western woolly lemurs can further be divided into three distinct morphs, probably representing two species, one of which comprises two subspecies.

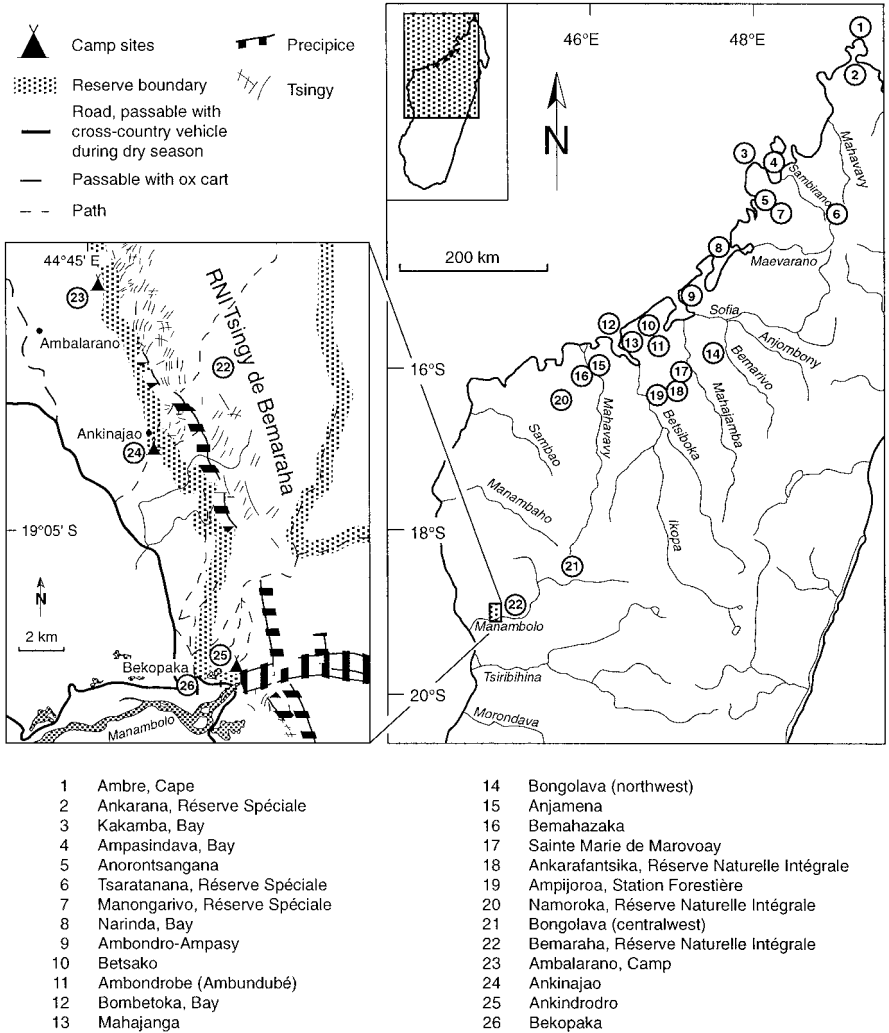


Fig. 1. Maps of the study regions and numbers referring to localities. Locality coordinates, are in Appendix.

MATERIAL AND METHODS

In Bemaraha, we conducted night surveys (two local guides and Thalmann) between 28 June and 7 July 1994 in the forest of Ankindrodro (2.5 km west of Bekopaka) for 13 h 24 min and near Ankinajao for 5

h 5 min (Fig. 1). We designed surveys to cover a maximal forest area, thereby detecting as many *Avahi* as possible, and used small existing forest trails established by humans or other animals: zebu cattle, boars. We also include unpublished data from surveys carried out in 1991 at Ambalarano.

We conducted additional short surveys to refine distribution limits of the different populations of *Avahi* at Anjamena on the northern riverbank (one local guide and Thalmann; 1–3 December 1994), at Bemahazaka on the south bank of the Mahavavy du Sud River (one local guide and Thalmann, 8–9 December 1994), in the Strict Nature Reserve of Namoroka (Thalmann *et al.*, 1999; 28–30 September 1997), and at Ambondro–Ampasy close to the Bay of Narinda, i.e. north of the Mahajamba and Sofia Rivers (Thalmann and Alexandra Müller; 11–14 November 1997).

We used headlamps to locate the subjects by their eye reflections. Then we firmly identified them with a strong flashlight and binoculars. We paid special attention to sportive lemurs as well, because they have about the same body size and may potentially be confounded with *Avahi* and because they are under considerable hunting pressure in some regions of Madagascar (Favre, 1989). *Lepilemur* are among the most frequently encountered nocturnal lemurs in western Madagascar, and the sighting relationship between *Lepilemur* and *Avahi* permits inferences with regard to habitat and hunting pressure.

We saw more than 43 individuals in the field. In order to compare external characteristics of *Avahi* from different populations, we also photographed wild animals (5 in Bemaraha, 9 in Ampijoroa), and videotaped them (1 in Bemaraha, >2 in Ampijoroa). Field observations also include detailed physical examination of anaesthetized animals (1 from Bemaraha and 5 from Ampijoroa).

We examined museum specimens in the following institutions (cited by the abbreviation given in parentheses): the American Museum of Natural History, New York (AMNH); the British Museum (Natural History), London (BMNH); the Zoology Laboratory of the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo (PBZT); the Muséum National d'Histoire Naturelle, Paris (MNHN); the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); the Naturhistorisches Museum, Vienna (NHMW); the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). Examined skins of museum specimens are listed in Table I, representing the entire collection of localized specimens of western *Avahi* known to us. Specimens examined include 16 museum specimens, of which 13 are adults.

Table 1. List of museum skin specimens of western *Avahi* that we examined^a

Catalogue No.	Date	Sex	Age	Locality	Coordinates	Remarks
Antananarivo, PBZT						
1271	Aug. 1956	m	ad	Ampijoroa	16°19'S 46°49'E	—
1281	4 Oct. 1954	m	ad	Ambavanimarovoany (Prov. Mahajanga)	nd	Collected by R.M.
1284	6 Feb. 1955	m	juv	Ankarafantsika	16°15'S 46°55'E	Collected by R.M.
Harvard, MCZ						
44877	10 Feb. 1930	f	ad	140 km SE Majunga (Ankarafantsika)	16°15'S 46°55'E	Sent to Grandidier by M. Lavauden
London, BM(NH)						
ZD.1868.9.7.2	1868	f	ad	N.W. Madagascar	nd	Voyage Van Dam, N.O. Madagascar
Leiden, RMNH						
23118	1868	f	inf	Mourountsang (Anorontsangana)	13°55'S 47°55'E	Pollen and van Dam, leg.
40031	1868	m	ad	Cacamba (Kakamba)	13°45'S 47°57'E	D.C. van Dam, leg.
40032	1868	f	ad	Cacamba (Kakamba)	13°45'S 47°57'E	D.C. van Dam, leg.
40033	1868	f	inf/juv	Baie de Passandava (Ampasindava Bay)	13°40'S 48°15'E	D.C. van Dam, leg.
New York, AMNH						
41266	nd	nd	ad?	Betsako	15°36'S 46°31'E	—

Table I. (Continued)

Catalogue No.	Date	Sex	Age	Locality	Coordinates	Remarks
Paris, MNHN CG1964 No. 71	13 Nov. 1962	m	ad	Ampijoroa	16°19'S 46°49'E	Mission Bauchot, M103. "Avahi occidentalis, néotype provisoire" Mission Bauchot, M108
CG1964 No. 68	14 Nov. 1962	m	ad	Ampijoroa	16°19'S 46°49'E	Mission Bauchot, M108
CG1964 No. 69	7 Nov. 1962	f	ad	Ampijoroa	16°19'S 46°49'E	Mission Bauchot, M69
Vienna, NHMW B3773	March 1868	m	ad	nd	nd	F.P.L. Pollen and D.C. van Dam, leg AV1870/III/1
4400/B3997	Jan. 1892	f	ad	Ambundubé	15°38'S, 46°24'E	A. Voeltzkow AV1899/II and AV92 "Avahi laniger occidentalis" Lorenz 1898, Holotypus"

^aNot listed, because specimen consists of skeleton and skull without skin: RMNH 40034, ad., NW-Madagascar, D.C. van Dam, leg., Cat. ostéol. *Avahi* "a." Abbreviations: f = female, m = male, ad = adult, inf = infant, juv = juvenile, nd = no data.

RESULTS

Surveys

Survey data from the Bemaraha region, including data from 1991 for Ambalarano, are summarized in Table II, together with information from a single short survey in the Ankarafantsika region (Ampijoroa) for comparative purposes. In the forest of Ankindrodro, we detected 5 individual *Avahi* representing 2 groups, and 55 *Lepilemur*. In the forest of Ankinajao, we detected 10 *Avahi* representing 5 groups, and only 6 *Lepilemur*. In 1991, we saw 2 *Avahi* and 14 *Lepilemur* during 3 h 35 min of survey in the forest near Ambalarano. In Bemaraha, the relative density and encounter rate for *Avahi* obviously differs between forests: In the forests of Ankindrodro and Ambalarano, *Avahi* is markedly (7–11 times) less common than *Lepilemur* (Table II). Conversely, in the forest of Ankinajao we encountered *Avahi* more often than *Lepilemur*, and *Avahi* encounters per hour were 3–5 times higher, whereas *Lepilemur* encounters were 3 times fewer than in the other forests in the Bemaraha area.

During a single 1 h 50 min walk in Ampijoroa, we detected 16 *Avahi* (6 groups) and 6 *Lepilemur*. This very high encounter rate for *Avahi* is 4–22 times higher than in forests in Bemaraha. The encounter rate for *Lepilemur* is comparable to that in the forests of Ankindrodro and Ambalarano, but considerably higher than in the forest of Ankinajao.

At the other localities (Ambondro-Ampasy, Anjamena, Bemahazaka, Namoroka), we neither saw nor heard *Avahi*, and interviews revealed no evidence for the presence of *Avahi* there. We saw *Lepilemur* in all these localities with the exception of the heavily disturbed forests near Bemahazaka, where we saw none.

Table II. Survey results for western *Avahi* and *Lepilemur* spp. at three different localities in the Bemaraha area and one locality in the Ankarafantsika area^a

Locality	Survey time (h:min)	<i>Avahi</i>		<i>Lepilemur</i>		Proportion Le/Av
		N	Per hour	N	Per hour	
Ankindrodro	13:24	5(2)	0.4	55	4.1	11.0
Ankinajao	5:05	10(5)	2.0	6	1.2	0.6
Ambalarano	3:35	2(1)	0.6	14	3.9	7.0
Ampijoroa	1:50	16(6)	8.7	6	3.3	0.4

Abbreviation: Av = *Avahi occidentalis*; Le = *Lepilemur* spp.

^aNumbers of groups are indicated in brackets. Localities are in Fig. 1.

Comparisons

We found no obvious difference in basic body dimensions or body mass between western woolly lemurs from Bemaraha and Ampijoroa. The single captured male in Bemaraha weighed 830 g, which is within the range of woolly lemurs from Ampijoroa (mean 815 g, range 698–1005 g, $n = 13$; Table III). Body weights of western woolly lemurs have not usually been recorded for museum specimens, but the body weights published by Bauchot and Stephan (1966) are most probably those of the specimens stored in the MNHN. The average value from our combined sample of body weights from western woolly lemurs is much lower than that of eastern woolly lemurs (mean and standard deviation: 816 ± 80 g vs. 1207 ± 211 , Table III). The difference is highly significant (Mann-Whitney U test, $p < 0.0001$).

All three populations from the west differ from one another in fur

Table III. Body weights (g) of adult eastern and western *Avahi* compared

Locality	Date	Sex	Body weight	References
Ranomafana	8/87	m	880	Glander <i>et al.</i> (1992)
Ranomafana	5/88	m	900	Glander <i>et al.</i> (1992)
Ranomafana	6/89	m	1150	Glander <i>et al.</i> (1992)
Ranomafana	5/87	f	1200	Glander <i>et al.</i> (1992)
Ranomafana	5/87	m	1200	Glander <i>et al.</i> (1992)
Ranomafana	5/89	f	1225	Glander <i>et al.</i> (1992)
Ranomafana	6/89	f	1240	Glander <i>et al.</i> (1992)
?Perinet/Andasibe	?/62	f	1270	Bauchot and Stephan (1966)
Ranomafana	1/93	m	1400	Roth (1996)
Ranomafana	5/88	f	1600	Glander <i>et al.</i> (1992)
Eastern <i>Avahi</i> ($n = 10$): Mean \pm standard deviation (range)			1207 \pm 211 (880–1600)	
Ampijoroa	10/92	f	698	Warren (1994)
Ampijoroa	9/92	m	708	Warren (1994)
Ampijoroa	11/95	f	735	This study
Ampijoroa	6/92	f	758	Warren (1994)
Ampijoroa	8/94	m	780	This study
Ampijoroa	6/92	m	807	Warren (1994)
Ampijoroa	9/92	m	808	Warren (1994)
Bemaraha	9/91	m	830	This study
Ampijoroa	11/62	m	845	Bauchot and Stephan (1966)
Ampijoroa	11/62	m	855	Bauchot and Stephan (1966)
Ampijoroa	11/62	m	860	Bauchot and Stephan (1966)
Ampijoroa	10/96	m	865	This study
Ampijoroa	11/62	f	875	Bauchot and Stephan (1966)
Ampijoroa	1/96	m	1005	This study
Western <i>Avahi</i> ($n = 14$): Mean \pm standard deviation (range)			816 \pm 80 (698–1005)	

coloration, especially in the facial area (Figs. 2, 3). The Ankarafantsika population shows a contrasting whitish face mask with relatively broad dark eye rings (Figs. 2b, 3b). The ventrum is light beige, the tail is gray-beige. The northern population shows only a slightly paler facial area and almost no trace of black eye rings (Figs. 2c, 3c). These individuals generally have darker fur than that of other western *Avahi*. The ventrum is light gray and the tail is dark gray brown. In the southern population, the whitish face mask and the dark eye rings are also absent. These individuals have a dark chevron pattern on the forehead (Figs. 2a, 3a). The ventrum is light gray; the tail is beige.

All western *Avahi* clearly differ from their eastern counterparts in the museums: Eastern *Avahi* not only tend to be bigger (Table III) but also are darker and more reddish colored and usually exhibit a thin pale band or two distinct pale patches above the eyes. The tail is rusty red and also darker than in the western populations.

Systematics

Before proceeding to a revision, clarification of the present situation is necessary. Although the eastern woolly lemur (*Avahi laniger*) was first described in the 18th century, western woolly lemurs were recorded and figured for the first time by Milne-Edwards and Grandidier (1875a,b). The importance of their work is that, for the first time, they proposed that there are two races of *Avahi*, an eastern one and a northwestern one. Of the northwestern form, they illustrate an individual in plate 10 (Milne-Edwards and Grandidier, 1875a) and state in the legend (Milne-Edwards and Grandidier, 1875b: p. 346): “*Avahis* (sic) *laniger* (Gmelin), variété septentrionale, tué à la baie de Pasandava (côte N. O. de Madagascar).” In plates 45 (Figs. 8–10) and 46 (Figs. 1–2), they figure a skull (probably the same specimen each time) in different views (Milne-Edwards and Grandidier, 1875a) under the designation of “*Avahis laineux occidental*” (Milne-Edwards and Grandidier, 1875b: p. 357). Unfortunately, Milne-Edwards and Grandidier’s use of terms is inconsistent: “septentrionale” (p. 327); “*Avahi du Nord-Est*” (*lapsus*, p. 329); “variété septentrionale” (p. 346); “*Avahis laineux occidental*” (p. 357). In the text, they consider *Avahi laniger* to be monospecific (“espèce unique,” p. 325) with two “races” (p. 327). They use the term race in the preceding section on *Propithecus* as the equivalent of what is now a subspecies (e.g. “Deuxième Race. *Propithecus verreauxii*, var. *Deckenii*, Peters”; p. 312). There is no doubt that they actually meant that there are two subspecies of *Avahi* (p. 327): “Les *Avahis* ne se subdivisent pas en races aussi nombreuses ni aussi tranchées que les diverses



Fig. 2. Faces of western woolly lemurs: (a) Bemaraha form, (b) *Avahi occidentalis* from Ampijoroa, and (c) *A. unicolor* from Ampasindava.



Fig. 3. Photographs of *Avahi* from Bemaraha (a); *Avahi occidentalis* at Ampijoroa (b); type specimen for *Avahi unicolor* (new species, RMNH 40031) (c); and type specimen (lectotype) for *Avahi occidentalis* (NHMW No. 4400/B3997) (d, top) and a specimen of *Avahi unicolor* (NHMW No. 3773) (d, bottom).

espèces de Propithèques; on en reconnaît cependant deux, l'une orientale qui est le type de l'espèce, l'autre septentrionale [. . .]” Unfortunately, they did not provide a full Latin name for the newly discovered northwestern form.

They specify the distribution of the northwestern form as the region between the Montagne d'Ambre and Anorontsangana and explain that individuals from Pasandava (= Ampasindava) are “constamment” smaller and differ in other characters from those from the east (Milne-Edwards and Grandidier 1875b: p. 328), making clear that they saw more than one specimen from that locality.

It was not until Voeltzkow collected lemurs in the region of Mahajanga that the best known population of western *Avahi* was discovered. Von Lorenz-Liburnau (1898: p. 452) had access to one *Avahi* (skin and skull) collected by Voeltzkow in Ambundubé (= Ambondrobe) and declared it to be identical to the specimens of Milne-Edwards and Grandidier (1875a,b), though it is not clear whether he actually saw them or merely consulted Milne-Edwards' and Grandidier's (1875a,b) publication. In addition, von Lorenz-Liburnau (1898) translated the French components of the name used by Milne-Edwards and Grandidier (“*Avahis laineux occidental*”) into Latin resulting in *Avahis laniger occidentalis*. Thus, he provided the first proper trinomial and has since been cited as author for the taxon (Schwarz, 1931; Hill, 1953; Petter *et al.*, 1977; Tattersall, 1982). Von Lorenz-Liburnau (1898) did not explicitly designate a type specimen. He simply stated that *Avahis laniger occidentalis* is the name of the western form of *Avahi* described by Milne-Edwards and Grandidier (1875a,b) and that the specimen later collected by Voeltzkow belonged to the same subspecies.

Schwarz (1931) reversed the generic name from *Avahis* to *Avahi*, following Jourdan's (1834, p. 231) original orthography for the generic name (Schwarz, 1931: p. 427). In his list of synonyms for *Avahi laniger occidentalis*, Schwarz (1931: p. 427) listed *Avahis laniger variété septentrionale* and *Avahi laineux occidental* and annotated the latter with “*type* from Ampasindava” (sic). This potential lectotype designation has no nomenclatural status because the synonym has no adequate base in nomenclature (Tattersall, 1982; ICZN, 1999), i.e. is not a scientific name. No later designation of a lectotype in the sense of the International Code of Zoological Nomenclature (ICZN, 1999: Art. 74) was undertaken.

Milne-Edwards and Grandidier (1875b: pp. 328–329) mention only few localities for northwestern *Avahi* (“Pasandava” and “entre la montagne d'Ambre and Anorontsangana”). Because D. C. van Dam collected *Avahi* in Cacamba and Pasandava, the original material described and illustrated by Milne-Edwards and Grandidier (1875a,b) may have been collected by Van Dam, though they do not say so. Milne-Edwards and Grandidier

(1875b: p. 2) only mention that specimens in Madagascar were collected by “l’un de nous, d’une part, MM. Lantz, Pollen, Van Dam, Crossley, d’autre part.”

Most of Van Dam’s collection is in the RMNH, but evidently some of the specimens also went to the BMNH (Jenkins, 1987; label of BMNH ZD.1868.9.7.2; archival information; Table I), the NHMW (Table I), and the MNHN (Milne-Edwards and Grandidier, 1875b: p. III of the Preface). We were unable to identify Milne-Edwards and Grandidier’s type material in any of these collections. If it was in Paris at any time, it probably disappeared relatively early, because Rode (1939) did not list it in his catalogue of type specimens. The NHMW specimen donated by Pollen and Van Dam (Table I) has no locality record; it is also not mentioned by von Lorenz-Liburnau (1898). Five *Avahi* collected by Van Dam went to the RMNH; four are listed as such by Schlegel (1876: pp. 299–300) and Jentink (1887: pp. 56–57; 1892: p. 64), the fifth, a very young infant, was mistakenly identified as a *Lepilemur*. We examined all of them. None of the five specimens appears to be the one figured by Milne-Edwards and Grandidier (1875a,b). For instance, no skull had been cut into halves, like the one shown by Milne-Edwards and Grandidier (1875a: pl. 46).

Two specimens of *Avahi* collected by Van Dam were purchased by the BMNH from a dealer (Mr. G. A. Frank). One of them—the mounted skin of BMNH 1868.9.7.3—is no longer in the collection (P. Jenkins, pers. com., 22 Jul 1999). We found no evidence identifying the remaining specimen as the one figured by Milne-Edwards and Grandidier (1875a,b).

In any event, it is very clear that the first discovered western *Avahi* came from the most northwestern population. Von Lorenz-Liburnau (1898) allocated specimens from the Mahajanga region collected by A. Voeltzkow in 1892 at Ambundubé (= Ambondrobe, NE of the Bombetoka Bay) explicitly to the northwestern population. This allocation was apparently accepted by Schwarz (1931) and by all subsequent authors. Although no formal holotype or lectotype designation valid in the sense of the International Code of Zoological Nomenclature has been made, all authors after Schwarz (1931) thought that the specimen described by von Lorenz-Liburnau (1898) is the type and cite Ambundubé (= Ambondrobe) as the type locality.

The type collection of the MNHN includes a specimen of *Avahi* (MNHN CG 1964 No. 71) annotated on the label by J.-J. Petter in 1984 as a “neotype” of *Avahi occidentalis*, apparently because the specimen from von Lorenz-Liburnau (1898) was believed to have disappeared (Rumpler *et al.*, 1990: pp. 314–315). The specimen from MNHN has no nomenclatural status (ICZN, 1999: Art. 8, 9, 75). The specimen from von Lorenz-Liburnau (1898) is in the collection of the NHMW (No. 4400/B3997), and a museum label does not constitute published work.

The nomen *Avahis laniger occidentalis* was created by von Lorenz-Liburnau (1898) for the specimen described and illustrated by Milne-Edwards and Grandidier (1875a,b). It has disappeared or cannot reliably be identified among museum specimens. Moreover, von Lorenz-Liburnau (1898) added a specimen of *Avahi* (NHMW 4400/B3997) from Ambundubé (= Amondrobe) to Milne-Edwards and Grandidier's specimens that he had identified as *Avahis laniger occidentalis*. Because no specimen was ever formally designated as holotype or lectotype, all specimens identified by von Lorenz-Liburnau (1898) as *Avahis laniger occidentalis* are syntypes of equal value in nomenclature. Because one of these syntypes (NHMW 4400/B3997) is still available, we here define it as lectotype (ICZN, 1999: Art. 74). We take into account the facts that other potential type specimens have disappeared or are ambiguous, and that the first formally correct description was based on the available syntype.

The designation of a lectotype is all the more important if the type material is not homogenous and includes more than one species or subspecies, as in the present case. By choosing a lectotype, we decide to which form the nomen *occidentalis* should be confined. The other form needs to be described and named, and a new (holo)type needs to be designated for it, which we do below.

Any of the specimens originally available to Milne-Edwards and Grandidier (1875a,b) is a syntype and would have been an equally good candidate for the designation of a lectotype. If we had selected one of their specimens, the name *Avahi occidentalis* would now apply to the northwestern population. Because none of their specimens is still extant or reliably identifiable, we chose the syntype from Ambundube (= Ambondrobe) instead, i.e. an *Avahi* from the Ankaranfantsika population. Moreover, this is the population well known for decades under the name of *Avahi occidentalis*.

DISCUSSION

Survey

Western woolly lemurs are generally rare in Bemaraha, and occur in locally different densities. All forests with *Avahi* have a relatively high proportion of evergreen trees due to a prolonged water supply from the calcareous massif and local soil conditions. The forest of Ankinajao is the greenest; it is situated in a basin of rich soil with a small rivulet and yielded the highest encounter rate for *Avahi*. This forest is severely threatened and was actually partially cut and burned during our presence. The exceptionally

low relative density of *Lepilemur* in this forest, and the low encounter rate for *Avahi* and *Lepilemur* combined suggest that at least *Lepilemur* is under extremely high human-induced pressure, probably partially through hunting by the local land-clearing population. Conversely, the forests of Ankindrodro and those near Ambalarano are less frequented by humans, and *Lepilemur* are readily encountered there. Nevertheless, *Avahi* are relatively rare in these forests, whereas they were comparatively abundant in the heavily disturbed forests around Ankinajao. There is no evidence for *Avahi* in other forests in the wider region of Bemaraha, notably in the deciduous, seasonally dry forests of the western type (Ausilio and Raveloanrinoro, 1998; Sterling, 1998; personal observations).

The southern population of *Avahi* represents a regional isolate, which may be restricted to the Bemaraha Reserve and adjacent forest types that occur only under certain ecological conditions. The restriction of their presence to certain severely threatened forest types makes woolly lemurs in Bemaraha very vulnerable. There was sign of no woolly lemurs south of the Manambolo River, which probably constitutes the southern barrier of *Avahi* in western Madagascar (Thalmann and Rakotoarison, 1994a).

Further north, we found no *Avahi* in the Réserve Naturelle Intégrale Namoroka (Hawkins *et al.*, 1998; Thalmann *et al.*, 1999), though some forests in Namoroka closely resemble known habitat of *Avahi* in Bemaraha. Likewise, *Avahi* were neither on the southwest bank of the Mahavavy River nor on the southwest bank of the Betsiboka River, which may represent the southern limit for the populations of *Avahi* known from Ampijoroa/Ankarafantsika.

At the Ampijoroa Forestry Station, *Avahi* was very abundant in deciduous seasonally dry western forest on a sandy plateau. This forest is superficially the same as forests in Bemaraha where we recorded no *Avahi*. The northern distribution limit for this population is unclear. Kaudern (1915) reports a specimen from Sainte-Marie de Marovoay, which is close to the southwest bank of the Mahajamba River. Exact locality reports from the opposite riverbank are unknown to us, but distribution maps published by Petter *et al.* (1977) and Tattersall (1982) indicate a range that extends onto the Bongolava plateau and north of the Mahajamba and Sofia rivers, up to the bay of Narinda.

Virtually nothing is known on the population of *Avahi* from Ampasindava. Apparently, they occur in transitional evergreen formations of the Sambirano region, and in the western portion of the Manongarivo Special Reserve (Raxworthy and Rakotondraparany, 1988). However, they have not been detected on the northeastern slopes of the Manongarivo Massif (Goodman and Schütz, in press). Vegetation—evergreen humid formations—is completely different from deciduous formations (Du Puy and

Morat, 1996) associated with other western populations of *Avahi*. Distribution limits of the Ampasindava population remain highly speculative.

Conservation

A recent comparative study of the feeding ecology of *Lepilemur edwardsi* and *Avahi* in the forest at Ampijoroa shows that *Avahi* relies on tree species that are relatively rare and underrepresented in both number of trees and tree crown volume per species and that there is virtually no food niche overlap with *Lepilemur*, if seasonal and size aspects of resources are accounted for. *Lepilemur* feeds on much more common items (Thalmann, in press-a). Ganzhorn (1988, 1993) showed that, where *Avahi* and *Lepilemur* occur in sympatry, *Avahi* feeds on higher-quality items than those eaten by *Lepilemur*. Where *Avahi* is absent, *Lepilemur* feeds on higher-quality items than those eaten by *Lepilemur* that are sympatric with *Avahi*. Petter *et al.* (1977) noted that *Lepilemur* is always present where *Avahi* is found but not *vice versa*. In addition, *Avahi* may occur locally in high numbers (Petter, 1962). *Avahi* does not appear to suffer from food competition with *Lepilemur*, but is strongly dependent on an adequate dietary composition. Adequate forest composition may be very localized, as can be inferred from the low abundance of *Avahi* in the relatively undisturbed forests of Ankindrodro and near Ambalarano, and their greater abundance (at least at the time of this survey) in the highly degraded forest at Ankinajao. Sadly, the latter forest may have disappeared completely in the meantime.

Our findings have major implications regarding distribution, diversity and conservation: (1) It is virtually impossible to predict where additional populations of *Avahi* may be found, as long as key factors of dietary composition and corresponding key species of suitable forests are not known in detail. (2) It has so far been impossible to keep *Avahi* in captivity (Petter *et al.*, 1977; Harcourt and Thornback, 1990), probably because of its highly selective folivorous diet. Conservation of forests *in situ* where *Avahi* occur is the only viable option, if appropriate measures have to be implemented. (3) Because of the local isolation and the reduced genetic exchange between different localized populations, additional genetically discrete morphs of *Avahi* probably exist. In nocturnal lemurs, differences between populations are more likely to be detectable at the genetic level than from patterns of coloration.

Systematics

Western woolly lemurs from the three discontinuous areas of distribution clearly differ in pelage coloration, and their distinctive features

did not overlap among the specimens we examined. These differences and the geographic isolation suggest a classification of the three populations as distinct taxa. We assume for two reasons that at least two of the three populations represent distinct species rather than subspecies, whereas the status of the third population—subspecies or species—is unclear:

1. Among nocturnal primates, variety in pelage coloration is less obvious than among diurnal species. Populations of nocturnal primates that exhibit diagnostically distinct patterns of fur coloration such as those found among western populations of *Avahi* are generally identified as distinct species based on vocal, molecular or chromosomal data (Niemitz *et al.*, 1991; Ishak *et al.*, 1992; Bearder, 1995; Zimmermann *et al.*, 1998; Nietsch, 1999).
2. The distribution areas of the three populations correspond to three distinct zoogeographic regions of Madagascar (Martin, 1972, 1995). A cladistic parsimony analysis of biogeography (Thalmann, in press-b) supports the distinction of three taxa and provides additional support to regard at least the populations from the Ampasindava peninsula and from Ampijoroa as two distinct species. However, that analysis does not predict specific distinction between the populations from Ampijoroa and Bemaraha (Thalmann, unpubl. data). Further study is required in order to decide whether the Bemaraha population represents a subspecies of *Avahi occidentalis*, as suggested by a cladistic parsimony analysis, or a full species, as suggested by fur coloration.

Avahi from each of the three western populations appear to be consistently smaller and more lightly colored than the eastern specimens we examined. This may indicate that the western populations are more closely related to each other than each of them is to the eastern species. This interpretation is very tentative, and needs to be supported by independent information, for instance from molecular data.

The lack of an adequate type specimen prohibits a formally correct description of the southern population as a new subspecies or species. To establish a convincing case that will satisfy most mammalian systematists, a whole specimen (ideally a series of specimens) is required. However, the common procedure of taxonomists to kill one or several animals or to capture and donate them to a zoo in order to obtain type specimens when they die is not an option with such a highly endangered population and with a species that cannot be kept alive in captivity for more than a few days (Petter *et al.*, 1977; Harcourt and Thornback, 1990).

Taxonomic Revision

Avahi occidentalis (von Lorenz-Liburnau, 1898)

- *Avahis laniger occidentalis* von Lorenz-Liburnau, 1898, Abh. Senckenb. Naturf. Ges. 21, p. 452 (ex Milne-Edwards and Grandidier)
- *Avahi laniger occidentalis* Schwarz, 1931, *Proc. Zool. Soc.* 1931, p. 427.
- *Avahi occidentalis* Rumpler *et al.*, 1990, *Am. J. Primatol.* 21, p. 315.

Lectotype. NHMW 4400/B3997, skin and skull of an adult female, collected January 1892 by A. Voeltzkow (AV1899/II and AV92), stored in the Natural History Museum of Vienna (NHMW), Austria. Lectotype designated because type series contains more than one taxon.

Type Locality. Ambundubé (= Ambondrobe), NE of the Bombetoka Bay, northwestern Madagascar, approximately 15°38'S, 46°24'E.

Diagnosis. Distinguished from other *Avahi* by the presence of a contrasting light face mask and relatively broad dark eye rings, and from the Bemaraha form (see below) by lacking the dark chevron pattern on the forehead.

Description (Figs. 2b, 3b). The fur of the face is white, cream or white-gray. It forms a light face mask which strongly contrasts with the surrounding fur in both color and hair consistency. The mask is invaded in most individuals by a small wedge of darker frontal fur above the nose. The light facial hair extends laterally below the ears. The eyes are brown-yellow encircled with a ring of black, hairless skin; the nose is hairless and also black. The fur surrounding the snout is whitish. Head and body with brown-gray or ochreous fur coloration; fur of a woolly (slightly curled) flecked appearance. In some individuals, the upper back may exhibit some slight sagittal darkening. The pygal area has a triangular light patch of cream or pale beige color. The tail is pale gray, gray-beige or cream-beige, but may also have a distinct reddish tinge in some individuals, especially near the base. At least in one specimen (type), the tail has a white tip. The inner dorsal surface of the lower limbs is white. The fur of chest, belly and inner surface of the upper limbs is relatively thin, downy, and very light beige, cream or apricot in color.

Distribution. Southwestern limit Betsiboka River. Northern limit unclear, possibly Mahajamba, Sofia, or even Maevarano rivers. However, no evidence from surveys and interviews between Sofia and Maevarano rivers around Ambondro-Ampasy.

Hypodigm. AMNH 41266; MCZ 44877; MNHN CG1964 No.68, CG1964 No.69, CG1964 No.71; NHMW 4400/B3997; PBZT 1271, 1281, 1284.

Avahi unicolor New Species

- *Avahis laniger occidentalis* von Lorenz-Liburnau, 1898, Abh. Senckenb. Naturf. Ges. 21, p. 452 (ex Milne-Edwards and Grandidier)
- *Avahi laniger occidentalis* Schwarz, 1931, *Proc. Zool. Soc.* 1931, p. 427.

Holotype (Fig. 3c). RMNH 40031 (*Avahi laniger* “d” in Jentink, 1892: p. 64. *Avahi laniger* #4 in Schlegel, 1876: p. 299), mounted adult female, and corresponding skull (*Avahi laniger* “h” in Jentink, 1887: p. 57. *Avahi laniger* #10 in Schlegel, 1876: p. 300). Stored in the Rijksmuseum van Natuurlijke Historie (RMNH) in Leiden, the Netherlands.

Paratypes. RMNH 40032 (*Avahi laniger* “c” in Jentink, 1892: p. 64. *Avahi laniger* #3 in Schlegel, 1876: p. 299), mounted adult male, and corresponding skull (*Avahi laniger* “g” in Jentink, 1887: p. 57. *Avahi laniger* #9 in Schlegel, 1876: p. 300).

RMNH 40033 (*Avahi laniger* “e” in Jentink, 1892: p. 64. *Avahi laniger* #5 in Schlegel, 1876: p. 299), mounted inf./juv. female.

RMNH 40034 (*Avahi laniger* “a” in Jentink, 1887: p. 56. *Avahi laniger* #6 in Schlegel, 1876: p. 299), mounted skeleton.

RMNH 23118 (*Lepilemur mustelinus* “h” in Jentink, 1892: p. 76. *Lepilemur mustelinus* #8 in Schlegel, 1876: p. 318), mounted inf. female, and corresponding skull (*Lepilemur mustelinus* “f” in Jentink, 1887: p. 65. *Lepilemur mustelinus* #31 in Schlegel, 1876: p. 318).

All paratypes are stored in the Rijksmuseum van Natuurlijke Historie (RMNH) in Leiden, the Netherlands.

Type Locality. Cacamba (= Kakamba), on the peninsula of Ampasin-dava, northwestern Madagascar, approximately 13°35'S, 47°57'E.

Etymology. *Unicolor* (Lat.), one-colored, in reference to its absence of contrasting color patterns.

Diagnosis. Distinguished from *Avahi occidentalis* by lacking the white facial mask and broad dark eye-rings, and from the Bemaraha form by lacking the dark chevron pattern on the forehead.

Description (Figs. 2c, 3c). The face is only slightly paler than the upper head. The impression of a face mask is caused mainly by the difference in hair consistency and hair length: The facial hair is short, stiff and not curled at all, in contrast to the surrounding pelage. The facial area is invaded by a wedge of frontal fur above the nose. The facial fur type differs so strongly from the fur on the forehead that the border between the two areas may appear like a dark line, though the fur is not in fact darker there. The eyes are maroon and have black, hairless eyelids. The snout is also black and hairless. The fur surrounding

the corners of the mouth is whitish. Head and body with light sandbrown-gray fur coloration and of a woolly (slightly curled) flecked appearance. The tail may be darker gray-brown or more reddish-brown, the tail base is pale brown-gray or cream. The pygal area has a triangular light patch of cream or light beige color. The back may be slightly darker in the scapular area. The inner dorsal surface of the lower limbs is whitish. The fur of chest, belly and inner surface of the upper limbs is relatively thin, downy, and very light gray or mouse gray in color.

Distribution. Probably restricted to Sambirano region (incl. Ampasin-dava peninsula). Southern limit unclear, possibly Andranomalaza or Maev-arano River. According to Milne-Edwards and Grandidier (1875b) close to Anorontsangana (13°55'S, 47°55'E). Northern limit unclear, possibly Sambirano River. Known to occur on the western slope of the Manongarivo Special Reserve (Raxworthy and Rakondroparany, 1988), but not detected on the northeastern slope of this massif (Goodman and Schütz, in press). Eastern limit unknown, possibly western slope to the Tsaratanana Massif.

Hypodigm. BMNH ZD.1868.9.7.2; NHMW B3773; RMNH 23118, 40031, 40032, 40033, 40034.

Bemaraha Form

Material. Hair samples AIMZ 13854.a, accompanying photographs (13854.b-n), video tape (13854.o) and audio tape recordings (13854.p). Stored in the Anthropological Institute and Museum of the University of Zurich (AIMZ), Switzerland.

Locality. 18°59'S, 44°45'E, approximately 3 km ENE of the village of Ambalarano, eastern Madagascar.

Description (Figs. 2a, 3a). The face (Fig. 2a) is only slightly paler than the upper head. The facial area above the nose extends up towards the forehead. This upward extension contrasts with the virtually opposite pattern created by the triangle of forehead pelage invading the facial area in other western *Avahi*: *A. occidentalis* and *A. unicolor*. The forehead fur immediately bordering the facial area is blackish, forming a dark chevron pattern above the facial area. The eyes are maroon and have black, hairless eyelids. The snout is also black and hairless. The fur surrounding the corners of mouth is whitish. Head and body with brown-gray fur and of a woolly (slightly curled) flecked appearance. The tail is beige or brown-gray, and slightly reddish only on the dorsal side of the root. The inner dorsal surface of the lower limbs is white. The fur of chest, belly and inner surface of the upper limbs is relatively thin, downy, and of very light gray.

Distribution. Southern limit most probably Manambolo River. Northern limit unclear. No evidence from surveys and interviews for RNI Namoroka (between rivers Sambao and Mahavavy: Hawkins *et al.*, 1998; Thalmann *et al.*, 1999), and no evidence between the Mahavavy and Betsiboka rivers (this study; Curtis, 1997).

Recognition Key

1. Facial area whitish, sharply contrasting with brown-gray forehead; distinct blackish area around eyes: *occidentalis* Facial area light gray brown, only slightly paler than upper head; no distinct dark area around eyes: (2)
2. Facial area narrowed above nose. No dark chevron pattern on forehead: *unicolor* Facial area widened upwards above nose, bordered by dark chevron pattern on forehead: Bemaraha form

CONCLUSIONS

1. The eastern and western woolly lemurs should be separated specifically into *Avahi laniger* and *A. occidentalis*.
2. *Avahi occidentalis* includes at least three distinct taxa: *A. occidentalis*, *A. unicolor*, and (because of lack of adequate type material) an as yet unnamed form from Bemaraha.
3. Because *Avahi* is a highly specialized folivore depending on plants with special characteristics, it is now virtually impossible to predict where further populations of *Avahi* may be found.
4. Conservation of forests *in situ* where *Avahi* occurs is the only viable option for conservation of this genus, if measures have to be implemented.
5. Further distinct populations of *Avahi* may possibly be found. Because *Avahi* is nocturnal, they are likely to differ most in genetic aspects versus coloration patterns.

APPENDIX

Localities mentioned in the text in alphabetical order with coordinates and numbers (ordered from north to south) referring to Fig. 1.

No.	Name	Alternative name	South	East	Remarks	Ref. ^a
23	Ambalarano, Camp		18°59'	44°45'	4 km ENE of village	1
nd	Ambavanimar-ovoany		nd	nd		
9	Ambondro-Ampasy		14°59'	47°14'		1
11	Ambondrobe	Ambundubé	15°38'	46°24'	NE of Betsiboka R.	2
1	Ambre, Cape		11°57'	49°15'		1
4	Ampasindava, Bay	Pasandava, Baie de	13°40'	48°15'		3
19	Ampijoroa, SF		16°19'	46°49'		1
15	Anjamena		16°03'	45°54'		1
18	Ankarafantsika, RNI		16°15'	46°55'		3
2	Ankarana, RS		12°55'	49°06'		4
24	Ankinajao	Kinajao	19°03'	44°47'		1
25	Ankandrodro		19°08'	44°49'		1
5	Anorontsangana	Anorotsangana, Morountsang, Mourountsang	13°55'	47°55'		3
26	Bekopaka		19°09'	44°48'		1
22	Bemarahe, RNI		18°40'	44°46'		4
16	Bemahazaka		16°05'	45°54'		1
10	Betsako		15°36'	46°31'	N Bombetoka-Bai	3
12	Bombetoka, Bay		15°40'	46°16'		5
21	Bongolava (central-west)		18°30'	45°24'		5
14	Bongolava (north-west)		15°48'	47°22'		5
3	Kakamba, Bay	Cacamba	13°35'	47°57'		3
13	Mahajanga		15°43'	46°19'		5
7	Manongarivo, RS		14°00'	48°24'		4
20	Namoroka, RNI		16°28'	45°29'		1
8	Narinda, Bay		14°48'	47°34'		5
17	Sainte Marie de Marovoay		16°08'	46°58'		5
6	Tsaratanana, RS		13°59'	48°52'		4

Abbreviations: RNI = Réserve Naturelle Intégrale, RS = Réserve Spéciale, SF = Station Forestière.

^aReferences: 1 = Thalmann (own data and Global Positioning System); 2 = von Lorenz-Liburnau (1898); 3 = USBGN (1989); 4 = Nicoll and Langrand (1989); 5 = FTM (1979; 1986a, b; 1990).

ACKNOWLEDGMENTS

The research was conducted under an Accord de Coopération between the Universities of Zürich (Switzerland) and Mahajanga (Madagascar), and the governmental institutions of Madagascar (Commission Tripartite) gave research permission. Special thanks go to our guides, M. Lemana and the late M. Felix (Bekopaka). Thalmann thanks Thomas Mutschler for cooperation during field work in 1991, Debbie Curtis for giving permission to visit her camp at Anjamena in 1994, Ian Tattersall for supporting a research proposal, and especially Alexandra Müller for continuous support and cooperation. Without the continuous support of Bob Martin, fieldwork on lemurs would have been far more difficult. We thank Colin Groves, Bob Martin, Chris Smeenk and an anonymous reviewer for reading and commenting upon this manuscript. Steve Goodman and Harald Schütz kindly gave permission to use and cite their unpublished manuscript. We gratefully acknowledge the assistance of the following curators: Antananarivo, the late N. Rakotoarison; Harvard, M. E. Rutzmoser; Leiden, C. Smeenk and L. B. Holthuis; London, P. Jenkins; New York, R. MacPhee and B. Mader; Paris, M. Tranier; Vienna, F. Spitzenberg and F. Bauer. The work of UT was supported by: A. H. Schultz Foundation, G. and A. Claraz Donation, Swiss National Science Foundation (Grant 823A-042920).

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