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Sympatric Mouse Lemurs in North-West Madagascar: A New Rufous Mouse Lemur Species *(Microcebus ravelobensis)*

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Key Words

Microcebus ravelobensis · Lemur · Taxonomy · Morphology · Ecology · Madagascar

Introduction

The differentiation of species and the mechanisms for their emergence are fairly controversial topics in evolutionary biology [1–4], but species recognition and discrimination are urgently needed as a basis for further research as well as for any conservation programme.

Mouse lemurs (*Microcebus* spp.) are house-mouse-sized nocturnal primates living in a wide range of forest habitats in Madagascar from sea level up to a height of at least 1,300 m above sea level [5–7]. Due to their broad distribution range, we propose that they form an excellent model for getting more insight into mechanisms of the outstanding adaptive radiation of Malagasy lemurs. Repeated speciation and subsequent specialization in such widely distributed genera should generate a great diversity of species and may give hints of the underlying speciation processes.

Schwartz [8] lumped together all lesser mouse lemurs into a single species, *Microcebus murinus.* Later on, two separate species were recognized [9–10], a grey long-eared form *(M. murinus)* typically inhabiting dry forests in west and south-west Madagascar and a brown short-eared form *(M. rufus)* typically inhabiting rain forest areas in east Madagascar. Furthermore, Petter [11] noted that a brown rufous mouse lemur resembling the eastern form occurs in Ankarafantsika in north-west Madagascar sym-

† Deceased in a tragic road accident.

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Fig. 1. **a** Grey mouse lemur of Ampijoroa. **b** Golden-brown mouse lemur of Ampijoroa. **c** Comparison of body profiles of grey and golden-brown mouse lemurs.

patrically with the western grey form. Martin [12] confirmed this by a comparison of skull measurements of both forms. Petter et al. [9] also mentioned the presence of a brown rufous mouse lemur in Morondava. A recent field study in the Kirindy forest in the north-east of Morondava has indeed identified a rufous mouse lemur as a third species *(M. myoxinus)*, differing from the grey long-eared form with which it lives sympatrically by its significantly lower body weight and its shorter ears and longer tail [13].

In October 1994, one of us (E.Z.) captured several golden-brown mouse lemurs in the Réserve forestière d'Ampijoroa in north-west Madagascar. The fur was as dense and short as in the sympatric grey form, but the upper parts were golden-brown, the

Table 1. Comparison between the north-western grey (grey Ampi) and golden-brown (brown Ampi) mouse lemurs and the eastern (brown Anda) and western (brown Kiri) rufous mouse lemurs

Mouse lemur	Grey Ampi (n=57)		Brown Ampi (n=27)		Brown Anda (n=15)		Brown Kiri (n=32)	
	mean	range	mean	range	mean	range	mean	range
Ear length	23.9 (0.26)	18.8–28	23.9 (0.43)	16–26.1	16.9 (0.67)	11.6–20	17 (0.18)	14.4–19
Ear width	15 (0.16)	11.8–17.5	14.9 (0.27)	11.7–18	10.9 (0.26)	9–13	13.5 (0.16)	11.5–15.4
Head length	34.5 (0.28)	29.7–39.3	35.7 (0.29)	32.7–39	33.5 (0.40)	31.5–37.4	31.2 (0.15)	29.6–33
Head width	20.6 (0.25)	17.2–27.5	21.6 (0.31)	19.7–26.3	19.7 (0.50)	16.7–24.4	18.1 (0.1)	17.1–19.7
Tail length	128.4 (1.07)	107–152	157.1 (2.53)	130–175	117.9 (2.63)	100–146.2	136.2 (1.21)	120–148
Tail width	24.5 (0.53)	19–39	18.2 (0.80)	11–25	26 (1.51)	15–35		
Hindfoot length	22.5 (0.18)	19.9–25.5	24.8 (0.25)	22.4–26.9	20 (0.39)	17.8–23.2		
Toe length	9.1 (0.15)	7.2–10.7	10.2 (0.5)	7.1–13	9.5 (0.54)	7.6–11.5		
Body length	83.3 (0.93)	70–100	81.3 (1.85)	60–95	72.7 (1.79)	60–85	61.9	52–71
Weight	53.9 (0.9)	39–69	56.2 (1.76)	38–68	46.2 (2.19)	35–62	30.6 (0.57)	24.5–38

Measurements (mm and g) of the western mouse lemurs are taken from Schmid and Kappeler [13], means (standard errors in parentheses) and ranges are displayed.

ventral parts yellowish-white. Body and ear size appeared to be similar in both colour forms but the tail was much longer and thinner and the tip more densely furred in the golden-brown form (fig.1). During our subsequent field study in this area we captured and observed many more mouse lemurs of both forms.

Within this paper, we present first quantitative morphometric data on the two mouse lemur forms of this area and compare them with our own and published data on mouse lemurs occurring in west and east Madagascar. Our results suggest that the north-western golden-brown mouse lemurs are (1) quite distinct from the sympatric grey mouse lemurs in Ampijoroa, (2) different from the rufous mouse lemurs of east Madagascar *(M. rufus)*, (3) different from the rufous mouse lemur of west Madagascar *(M. myoxinus)* and (4) therefore form a distinct new species of the genus *Microcebus.*

Methods

The study was conducted in the western Malagasy deciduous dry forest [14] in the Réserve forestière d'Ampijoroa (16°35′ S, 46°82′ E, approx. 200 m above sea level), about 110 km south-east of the town Mahajanga in north-west Madagascar. The vegetation profile of this forest was analyzed by Razafy [15]. The climate is characterized by a very hot and humid rainy season from November to March with about 1,200 mm rainfall and a cool dry season from April to October (ANGAP, Fiche technique 1994). Sites were located in a 70,000-ha forest reserve of the Département des Eaux et Forêts, near the forestry station of Ampijoroa, around and in the 'Jardin botanique A' and around the lake of Ravelobe.

In October 1994 and from August to October 1995, Sherman traps baited with bananas were set in the late afternoon at distances of about 25 m in trees and bushes, 1–2 m above ground along roads, trails and in a grid system. Early in the morning, the traps were checked and the locality of captured mouse lemurs was noted. Mouse lemurs were sexed, measured according to Hafen et al. [16] (tail width = circumference of tail at its basal end and toe length = length of the 3rd digit without nail were measured additionally) and individually marked by a Trovan Small Animal Marking System (Telinject®). Kruskal-Wallis ANOVA was used to check for differences between the populations. Variables that differed significantly ($p \leq 0.005$) in the Kruskal-Wallis test were included in further multivariate analysis. Measurements of body proportions were then compared between sexes and two different populations, respectively, using the Mann-Whitney U test. A cluster analysis (complete linkage, squared Euclidean distance) was performed on standardized values of the variables to reveal potential group structures. Finally a discriminant function analysis was used to establish a classification matrix on the basis of the 3 most discriminative variables [17]. Included were all cases for which the values for the 3 selected variables were complete.

Results

Our comparison is based on 84 adult and healthy mouse lemurs of Ampijoroa and 15 rufous mouse lemurs (9 males, 6 females) *(M. rufus)* of the area of Andasibe in central eastern Madagascar. Fifty-seven (35 males and 22 females) individuals of Ampijoroa belonged to the grey colour form *M. murinus*, 27 animals (10 males, 17 females) to the new, golden-brown colour form described as *M. ravelobensis.* Tables 1 and 2 show similarities and divergences between the two sympatric populations of Ampijoroa and the distinct eastern rufous form of Andasibe.

Neither mean body weight nor body length and head or ear size differed significantly between the two forms of Ampijoroa. Thus, values do not have to be controlled for differences in body length or body weight but can be compared directly. Besides

Table 2. Differences between the grey and golden-brown mouse lemurs in north-western Madagascar and the rufous mouse lemurs in eastern Madagascar

Mouse lemur	Grey Ampi/ brown Ampi	Brown Ampi/ brown Anda	ANOVA of population comparison
Ear length	0.7538	0.0000	0.0000
Ear width	0.8565	0.0000	0.0000
Head length	0.0134	0.0001	0.0040
Head width	0.0239	0.0006	0.0017
Tail length	0.0000	0.0000	0.0000
Tail width	0.0000	0.0000	0.0000
Hindfoot length	0.0000	0.0000	0.0001
Toe length	0.0214	0.2903	0.0311
Body length	0.9558	0.0026	0.0003
Weight	0.1715	0.0019	0.0013

p values are displayed, $p < 0.005$ was considered as different; Mann-Whitney U test. Ampi = Ampijoroa; Anda = Andasibe.

the obvious and reliable difference in pelage colour, there were significant differences in 3 out of 10 measured morphometric characters: hindfoot length and tail length were significantly longer in the golden-brown colour form than in the grey colour form, but the tail was significantly thicker in the grey colour form. A quantitative comparison of morphometric data between the new golden-brown form of Ampijoroa and the rufous mouse lemurs of Andasibe revealed significant differences in 9 out of 10 measured morphometric characters; only toe length did not differ significantly (tables 1 and 2). We did not find significant sex differences in any of the 10 characters for either form in Ampijoroa nor for the rufous mouse lemur in Andasibe.

Cluster analysis confirmed the results of the univariate statistical analysis (fig. 2a). The mouse lemurs of Ampijoroa were separated into two distinct clusters corresponding to the grey and golden-brown populations based on the measured 10 morphometric characters. Intrapopulation variability was much lower than interpopulation variability. Thus, mouse lemurs could be assigned almost unequivocally to the respective population. The clustering remained consistent, even when the population of the rufous mouse lemurs of Andasibe was included into the analysis (fig. 2b). Three population-specific clusters emerged. The population of the geographically separated rufous mouse lemurs of Andasibe branches first and thus has the same morphometric distance to both, the golden-brown and the grey mouse lemurs of Ampijoroa.

The discriminant function analysis revealed that the combination of 3 significant morphometric characters (tail length, tail width, hindfoot length) was sufficient to assign 97.5% of the individuals to the respective population (table 3).

During capture-recapture studies in the area of Ampijoroa/Ankarafantsika we found that although both colour forms occur syntopically in some parts of the forest, there are areas in which only one form was seen and captured in high numbers. Besides, by observing 2 males and 1 female of each form in a large outdoor enclosure within their habitat, we got the impression that the more gracile golden-brown colour form shows a higher locomotor activity and is more aggressive than the grey one. Furthermore, we found oestrous females of the golden-brown form as early as the end of

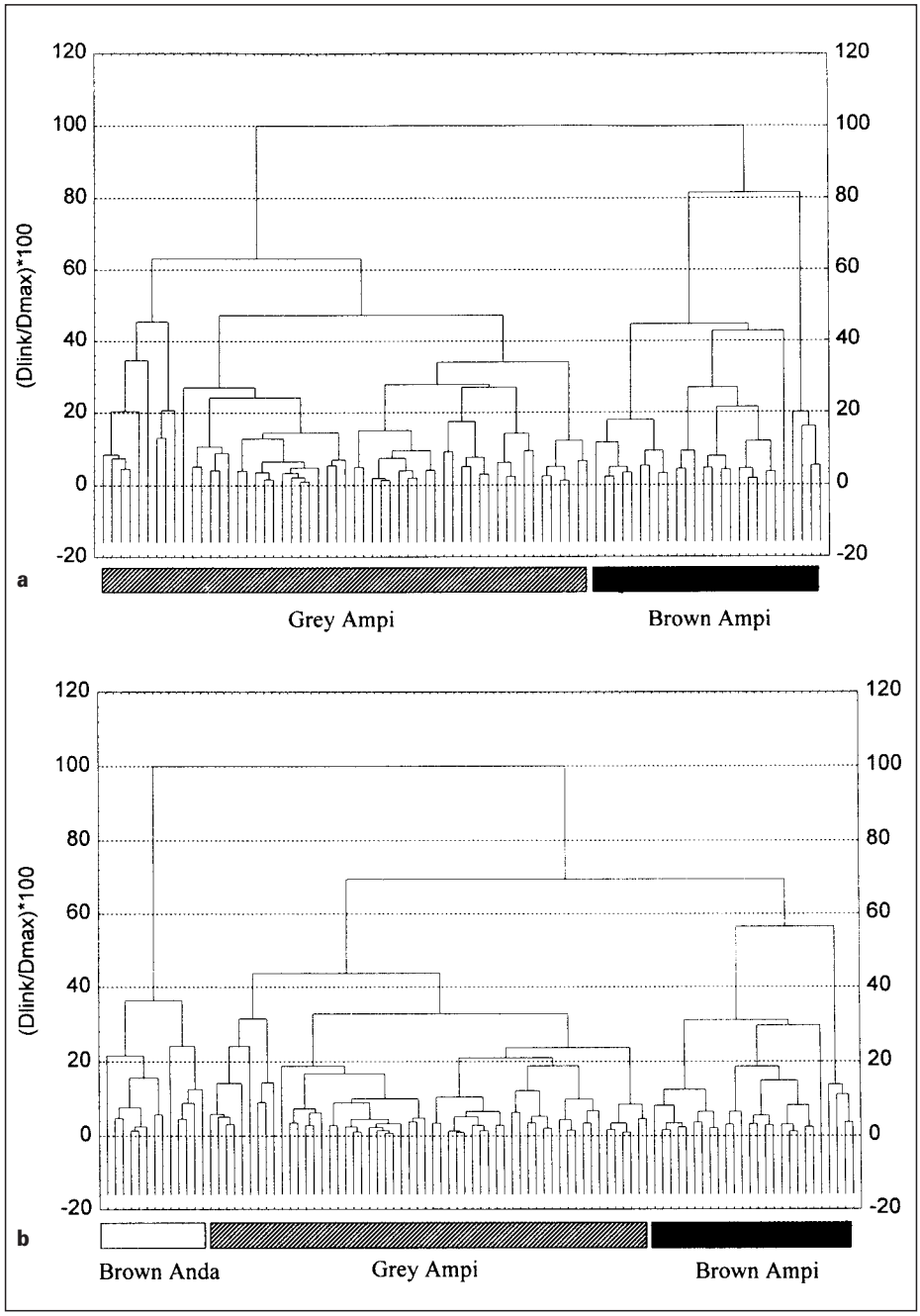

Fig. 2. **a** Dendrogram of the morphometric distances between the golden-brown and grey mouse lemurs of Ampijoroa (Ampi). **b** Dendrogram of the morphometric distances between the golden-brown and grey mouse lemurs of Ampijoroa (Ampi) and the rufous mouse lemurs of Andasibe (Anda).

Table 3. Classification of individuals of the golden-brown mouse lemur and the grey mouse lemur of Ampijoroa, in relation to the two populations, by 3 variables (tail length, tail width, hind-foot length)

Actual membership	Predicted membership		Correct, %
	grey	golden-brown	
Grey	54	0	100
Golden-brown	2	25	92.5
Total			97.5

Table 4. Measurements of the living holotype and paratype of *Microcebus ravelobensis*, August 1995 (values are in mm or g)

	Female No. 22 (PBZT No. 1421)	Male No. 26 (PBZT No. 1422)
Ear length	24	25.8
Ear width	15.6	14.6
Head length	36	39
Head width	24.1	20.5
Tail length	165	175
Tail width	20	22
Hindfoot length	25.4	26.3
Body length	90	85
Weight	67	55

August whereas females of the grey form were in oestrus not before the middle of September.

Because of the revealed divergences in a number of morphologic and behavioural characters between the two sympatrically living populations which are quite distinct from the morphological variation found in neighbouring and isolated populations of the grey mouse lemurs in western Madagascar [16], we suggest that the two colour forms of mouse lemurs in Ampijoroa represent two different species. For the new, golden-brown mouse lemur we propose the name *Microcebus ravelobensis*, new species, because of the locality of the type specimen which was the forest around the sacred lake Ravelobe near the forestry station of Ampijoroa.

Holotype

Adult female currently maintained in captivity at the Parc botanique et zoologique de Tsimbazaza (PBZT), Antananarivo, Madagascar. On its demise, this specimen will be added to the collection of the PBZT (Catalogue of mammal species in the collection of the Parc de Tsimbazaza under PBZT No. 1421). The same will be performed with the male paratype (PBZT No. 1422), actually living together with the female. Colour photographs have been deposited with the catalogue cards in the collection of the PBZT.

Measurements. For measurement, see table 4.

Type Locality. Western Malagasy deciduous dry forest [14, 15]; 16°35′ S, 46°82′ E, approximately 200 m above sea level; about 2 km north of the forestry station of Ampijoroa.

Diagnosis and Comparison to Related Species. A house-mouse-sized nocturnal *Microcebus* of golden-brown colour dorsally; underparts yellow to whitish; white

stripe from lower forehead to the tip of the muzzle; dark brown circumorbital ring; tail brown with dark brown end; long and thin tail; long and naked yellow-brown ears. For a detailed comparison of morphometric characters with related species see tables 1 and 2. The north-western golden-brown mouse lemur represents the largest known rufous form with regard to body length. Besides the colour, it differs by 3 of the 10 measured morphometric characters from the sympatric grey form. Nine significantly different characters separate it from the eastern rufous mouse lemur. A qualitative comparison with its western counterpart reveals obvious differences in 6 of 7 comparable characters. After controlling for differences in body length between the different rufous forms, the north-western form had longer and broader ears, a longer and thinner tail and a longer hindfoot than its eastern counterpart. From its western counterpart it differs by its longer ears and its smaller head. Tail width and toe length of *M. myoxinus* were not measured and hindfoot length was measured differently by Schmid and Kappeler [13]. Thus, these values could not be compared. The obvious weight difference between *M. myoxinus* and the other forms is seasonally dependent (weight in this species was measured from May to August and not from August to October as in this study) and might not be as large as it appears.

Discussion

Two sympatric mouse lemur populations differing in pelage colour and significantly in tail and limb size were detected in the Réserve forestière d'Ampijoroa in the deciduous dry forest of north-west Madagascar. The revealed differences between the two populations might be explained by differences in ecology, although this has to be confirmed by further investigations.

According to our preliminary findings, the golden-brown mouse lemur seems to prefer parts of the forest with a higher canopy height where it moves around by leaping rather than quadrupedally, when compared to the grey mouse lemur. An adaptation to this locomotion mode is its more gracile form with elongated tail/body and limb/body proportions. The difference in the circumference of the tail (tail width) measured during the same time of the year may reflect differences in energy metabolism. It seems as if the north-western rufous form does not have the same capability to store fat in the tail as the sympatric grey form. Altogether these observations imply that these two mouse lemur populations occupy slightly different ecological niches within the same habitat.

Different climate conditions may lead to the pronounced differences in ear and tail length between the north-western and eastern mouse lemurs. According to Allen's rule, taxa inhabiting colder climates should evolve reduced extremity sizes such as nose, ear and tail relative to body length [18]. Both the golden-brown mouse lemurs and the grey mouse lemurs live in the climatically more extreme, dry deciduous forests of north-western Madagascar (temperature range from 16 to 35 °C between night and day, September 1995, end of the dry season). In the eastern rain forest, the habitat of the eastern rufous mouse lemurs, temperatures are lower and differences between night and day are less extreme. Even during the dry season in September it may rain for days with fairly low temperatures and lesser temperature differences between day and night (temperature range 12–24 °C, September 1995, end of the dry season). As predicted by Allen's rule, eastern rufous mouse lemurs have shorter ears and a shorter tail than their north-western counterparts.

In summary, the presented data show that morphologic characters alone are sufficient to discriminate the new form both from the sympatric grey mouse lemur and from the western *(M. myoxinus)* and eastern *(M. rufus)* rufous mouse lemurs. Further comparative studies on the ecology, behaviour, communication, physiology, morphology and genetics of nocturnal lemurs such as mouse lemurs are needed to identify ecological and social determinants of speciation, to clarify the taxonomic status of phenotypically different populations and to illuminate thereby the evolution of the outstanding radiation of the actually highly endangered Malagasy lemurs.

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