International Journal of Primatology, Vol. 21, No. 6, 2000

Taxonomic Revision of Mouse Lemurs (*Microcebus*) in the Western Portions of Madagascar

Rodin M. Rasoloarison,[1] Steven M. Goodman,[2] and Jörg U. Ganzhorn[3]

Received October 28, 1999; revised February 8, 2000; accepted April 17, 2000

The genus Microcebus *(mouse lemurs) are the smallest extant primates. Until recently, they were considered to comprise two different species:* Microcebus murinus, *confined largely to dry forests on the western portion of Madagascar, and* M. rufus, *occurring in humid forest formations of eastern Madagascar. Specimens and recent field observations document rufous individuals in the west. However, the current taxonomy is entangled due to a lack of comparative material to quantify intrapopulation and intraspecific morphological variation. On the basis of recently collected specimens of* Microcebus *from 12 localities in portions of western Madagascar, from Ankarana in the north to Beza Mahafaly in the south, we present a revision using external, cranial, and dental characters. We recognize seven species of* Microcebus *from western Madagascar. We name and describe 3 spp., resurrect a previously synonymized species, and amend diagnoses for* Microcebus murinus *(J. F. Miller, 1777),* M. myoxinus *Peters, 1852, and* M. ravelobensis *Zimmermann et al., 1998.*

KEY WORDS: mouse lemurs; *Microcebus*; taxonomy; revision; new species.

[1]Département de Paléontologie et d'Anthropologie Biologique, B.P. 906, Université d'Antananarivo (101), Madagascar and Deutsches Primantenzentrum, Kellnerweg 4, D-37077 Göttingen, Germany.

[2]To whom correspondence should be addressed at Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, Illinois 60605, USA and WWF, B.P. 738, Antananarivo (101), Madagascar.

[3]Deutsches Primantenzentrum, Kellnerweg 4, D-37077 Göttingen, Germany. Current address: Zoologisches Institut und Zoologisches Museum, Martin Luther King Platz 3, 20146 Hamburg, Germany.

INTRODUCTION

The mouse lemurs of Madagascar, *Microcebus*, are small nocturnal prosimians that are broadly distributed across much of the vegetated portions of the island. They occur in primary, secondary, and heavily disturbed forest habitats and often at densities reaching 360–400 individuals per km^2 (Hladik *et al.,* 1980, 1998; Harcourt and Thornback, 1990). Until a few decades ago, only one species, *Microcebus murinus* with two distinct subspecies, was recognized (Schwarz, 1931; Hill, 1953; Petter, 1962; Napier and Napier, 1967). Largely on the basis of Martin's (1972) ecological studies in the Tolagnaro area, it become clear that two different morphotypes (gray and rufous) lived in near sympatry, but in different habitats. Petter *et al.* (1977), Tattersall (1982), and most subsequent authors distinguished two species: gray (*Microcebus murinus*) occurring in western dry forests and rufous (*M. rufus*) in eastern humid forests. Groves (1993) and most other authors have followed this schema.

Further field work in areas of Madagascar that had been previously unexplored or poorly known by zoologists revealed that the simple arrangement of *Microcebus murinus* in the west and *M. rufus* in the east was insufficient to explain the patterns of morphological variation and the distribution of members of the genus. For example, reports of rufous individuals from areas of the west (Petter, 1962; Petter *et al*., 1971, 1977; Petter and Andriatsarafara, 1987; Tattersall, 1982; Rakotoarison *et al*., 1993), had been known for some time (Peters, 1852; Schwarz, 1931). Many of these records were from the Ankarafantsika and Morondava regions and indicated that gray and rufous morphotypes lived sympatrically.

Recent field studies in the Kirindy/CFPF (Centre de Formation Professionnelle Forestière) Forest near Morondava on the life history of mouse lemurs involved the capture of over 80 individuals (Schmid and Kappeler, 1994; Atsalis *et al.,* 1996; Schmid, 1997, 1999; Fietz, 1998; Ganzhorn and Schmid, 1998). Two species of *Microcebus* occur syntopically there; pelage coloration and measurements distinguish them: Schmid and Kappeler (1994) concluded that the small rufous mouse lemurs in the Kirindy/CFPF Forest is referable to *M. myoxinus*, a form that had been considered a synonym of *M. murinus*, and the larger gray mouse lemurs are *M. murinus.* Soon after the discoveries near Morondava, another study commenced on mouse lemur ecology in the Ankarafantsika region to the east of Mahajanga. Here too, Zimmerman *et al.* (1998) realized that there are two different sympatric species of *Microcebus*; they concluded that one is *M. murinus* and named the other *M. ravelobensis.*

Thus, records of mixed populations of rufous and gray mouse lemurs living in sympatry in western Madagascar were confirmed. This vast region

includes an array of vegetational formations and climatic zones: the dry forests of the Ankarana, Mahajanga, and Morondava regions, the humid forests of the Sambirano, the transitional humid/dry forests near Sakaraha, and the spiny bush of the extreme southwest. The region shows considerable variation in habitat and soil types (Bourgeat, 1972; Du Puy and Moat, 1996). Further, in recent geological times the region experienced considerable change in vegetational cover (Burney, 1997). Given that these variables often play an important role in isolation of mammalian populations and subsequent differentiation, a detailed analysis of patterns of geographic variation in western populations of mouse lemurs is warranted. Accordingly, we provide a taxonomic revision of *Microcebus* based on morphology of individuals from 12 localities in western Madagascar. In conjunction with our study is a phylogeographic analysis using molecular data, the results of which will be presented separately and were derived independently of the morphometric data (Yoder *et al*., in press).

Materials and Methods

An initial survey of *Microcebus* from western Madagascar in several major museum collections revealed that most sites were represented by one or few specimens, insufficient to quantify intrapopulation variation in morphological and other phenotypic characters. Without further collections from several sites little progress could be made in revising the taxonomy of mouse lemurs. To obtain material to address the question of the specific limits of *Microcebus*, Madame Berthe Rakotosamimanana, Chef du Département de Paléontologie et d'Anthropologie Biologique, Université d'Antananarivo, submitted a research proposal to the Malagasy authorities for the collection of limited samples from western populations associated with the Ph.D. thesis of Rasoloarison. Permission was granted by the Commission Tripartite (Authorization no. 153-MADR/DEF/SEFLFB/FF, dated 30 July 1996 and no. 49-MINENV/SG/DGE/DEF/SEFLFB/BIOD, dated 15 April 1997).

The majority of specimens used in this project were prepared as standard museum skins with associated skulls and postcranial skeletons. Tissue samples, ectoparasites, and stomach contents were also saved. Voucher specimens have been catalogued at the Field Museum of Natural History (FMNH), Chicago, and will be divided between the FMNH and the Université d'Antananarivo. Locality information is generally presented as written on the original specimen labels. Collection sites and other localities are in Fig. 1.

Rasoloarison made all of the osteological and most of the external

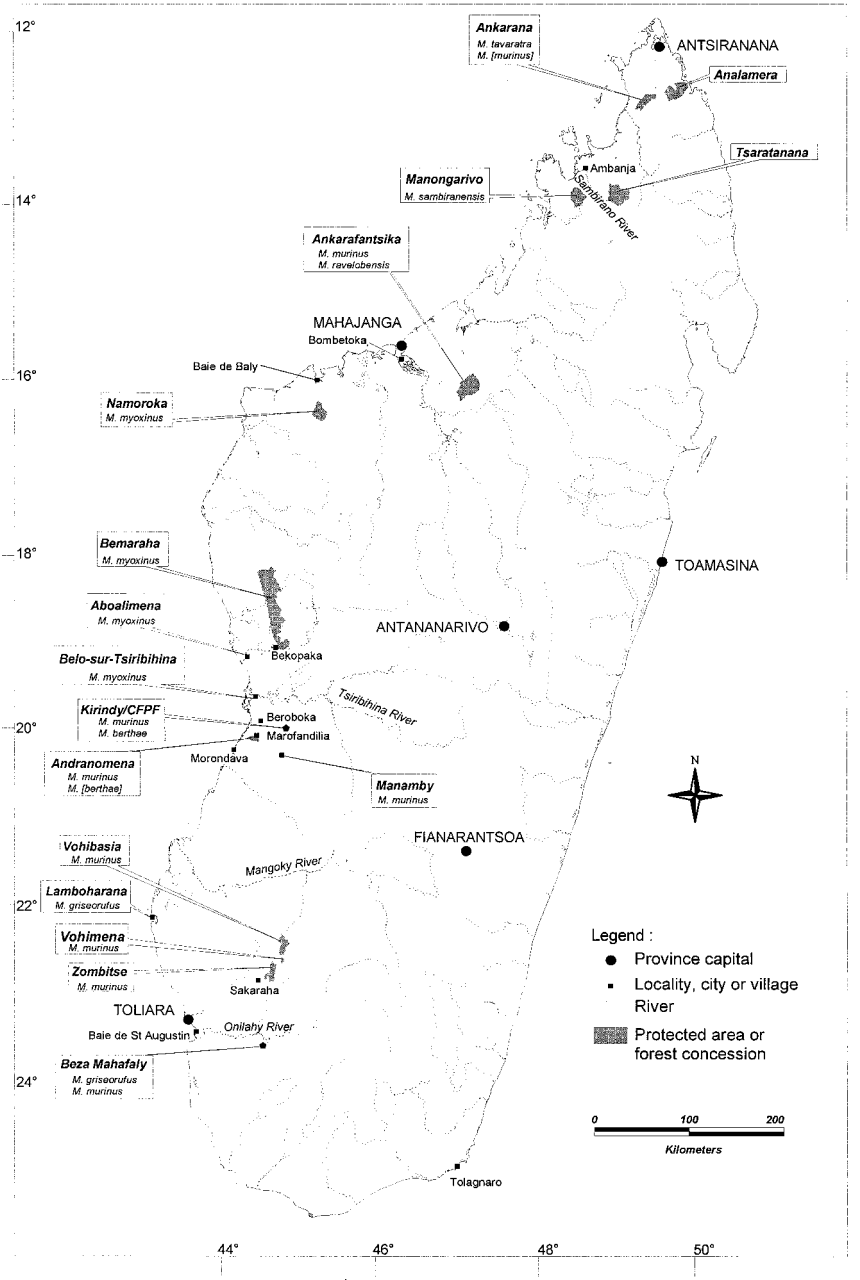

Fig. 1. Map showing our study sites and other geographic localities mentioned in the text. The *Microcebus* spp. recorded at each site is listed. Species names in brackets indicate unverified records.

measurements of the specimens. Different field workers measure animals in various ways, and comparisons are often unreliable. This problem becomes even more confounded when comparisons are made between live animals and cadavers. It is in part for this reason that we have generally refrained from including measurements, particularly external, made by other scientists in our comparisons.

External Measurements (Table I)

The following measurements were made of specimens in the flesh. (We present only measurements from adults):

- Ear length: from the notch at the base of the ear to the distalmost edge of the pinna ±0.5 mm.
- Head and body length: from the tip of the nose to the distalmost point of the body (at base of tail) ±1 mm.
- Hindfoot length: from the back edge of the heel to the tip of the longest toe (not including claw) ±0.5 mm.
- Length of toe IV: from base of the digit to the tip of the toe (not including claw) ±1 mm from dried specimens. The digits were pinned out while the specimens were drying.
- Length toe III: from base of the digit to the tip of the toe (not including claw) ±1 mm from dried specimens. The digits were pinned out while the specimens were drying.
- Tail length: from the base of the tail (at right angles to the body) to the end of the distalmost vertebra, excluding terminal hair tufts, ±1mm.
- Total length: from the tip of the nose to the end of the last caudal vertebra, excluding terminal hair tuft, ±1 mm.
- Mass: measured with Pesola spring scales to ±0.5 g for individuals <100 gm and to ± 1 g for those >100 gm.
- Width of digital pad: greatest width of digital pad on digit I of hindfoot (from dried specimens) ±1 mm.
- Width of grooming claw: greatest width of grooming claw on digit II of hindfoot (from dried specimens) ±1 mm.

Cranial and Dental Measurements (±0.1 mm; Table II)

We took cranial measurements via digital calipers to an accuracy of ±0.1 mm. Dental nomenclature is based on Swindler (1976) and Hershkov-

Table I. Descriptive statistics of external measurements of adult specimens of *Microcebus* spp. collected at different localities in the western half of Madagascar[a]

	M. ravelobensis Ankarafantsika (includes Ampijoroa)	*M. tavaratra* Ankarana	*M. griseorufus* Beza Mahafaly	*M. berthae* Kirindy/CFPF	*M. sambiranensis* Manongarivo	*M. myoxinus* Aboalimena and Bemaraha	*M. murinus* Andranomena, Vohimena, and Manamby
Total length (mm)	285.6 ± 17.52 (260–313; $n = 9$)	285.2 ± 6.49 (276–296; $n = 6$)	267.0 ± 9.88 (253–280; $n = 6$)	226.0 ± 3.60 (223–230; $n = 3$)	258.5 ± 9.27 (247–271; $n = 6$)	272.9 ± 10.42 (246–286; $n = 14$)	266.6 ± 14.38 (249–289; $n = 11$)
Tail length (mm)	160.3 ± 8.54 (144–172; $n = 9$)	154.8 ± 7.63 (145–167; $n = 6$)	142.8 ± 5.85 (136–153; $n = 6$)	135.3 ± 2.31 (134–138; $n = 3$)	140.8 ± 5.64 (134–148; $n = 6$)	147.0 ± 6.70 (132–155; $n = 14$)	136.8 ± 7.77 (126–152; $n = 11$)
Hindfoot length (mm)	34.9 ± 0.93 (33.0–36.0; $n = 9$)	34.8 ± 1.26 (33.0–36.0; $n = 6$)	32.3 ± 0.82 (31.0–33.0; $n = 6$)	29.3 ± 0.58 (29.0–30.0; $n = 3$)	32.0 ± 0.63 (31.0–33.0; $n = 6$)	34.2 ± 1.21 (32.0–36.0; $n = 15$)	32.5 ± 1.37 (30.0–34.0; $n = 11$)
Ear length (mm)	24.1 ± 0.93 (22.5–25.0; $n = 9$)	22.3 ± 0.88 (21.0–23.5; $n = 6$)	23.7 ± 0.81 (23.0–25.0; $n = 6$)	17.5 ± 0.50 (17.0–18.0; $n = 3$)	18.0 ± 0.71 (17.0–19.0; $n = 6$)	21.2 ± 1.24 (18.0–23.0; $n = 15$)	25.0 ± 0.81 (23.0–26.0; $n = 11$)
Mass (gm)	71.7 ± 15.63 (59.0–110.0; $n = 9$)	61.1 ± 15.65 (48.0–83.5; $n = 6$)	62.6 ± 16.36 (50.0–85.0; $n = 6$)	30.6 ± 0.57 (24.5–38.0; $n = 32$)[b]	44.1 ± 5.91 (38.0–51.5; $n = 6$)	49.0 ± 6.32 (36.5–64.0; $n = 15$)	62.3 ± 4.70 (54.0–69.0; $n = 11$)
Head and body length (mm)	127.3 ± 6.67 (120–139; $n = 9$)	126.3 ± 9.51 (113–139; $n = 6$)	123.3 ± 6.38 (113–132; $n = 6$)	92.0 ± 2.65 (90–95; $n = 3$)	116.5 ± 4.14 (113–123; $n = 6$)	123.7 ± 4.76 (113–131; $n = 15$)	129.4 ± 7.89 (120–141; $n = 11$)
Length 4th toe (mm)	11.1 ± 0.33 (11–12, $n = 9$)	10.8 ± 0.41 (10–11, $n = 6$)	10.0 ± 0.0 ($n = 6$)	9.0, 9.0 ($n = 2$)	10.2 ± 0.41 (10–11, $n = 6$)	10.7 ± 0.70 (10–12, $n = 15$)	10.5 ± 0.52 (10–11, $n = 11$)
Length 3rd toe (mm)	10.1 ± 0.33 (10–11, $n = 9$)	10.0 ± 0.0 ($n = 6$)	9.0 ± 0.0 ($n = 6$)	9.0, 9.0 ($n = 2$)	9.2 ± 0.41 (9–10, $n = 6$)	9.7 ± 0.62 (9–11, $n = 15$)	9.6 ± 0.51 (9–10, $n = 11$)
Width digital pad (mm)	3.3 ± 0.13 (3.1–3.5, $n = 9$)	3.0 ± 0.16 (2.7–3.1, $n = 6$)	2.7 ± 0.11 (2.5–2.8, $n = 6$)	2.1, 2.6 ($n = 2$)	3.0 ± 0.13 (2.8–3.1, $n = 6$)	3.0 ± 0.16 (2.8–3.3, $n = 15$)	3.1 ± 0.16 (2.9–3.3, $n = 11$)
Width (mm) grooming claw	1.3 ± 0.14 (1.2–1.6, $n = 9$)	1.0 ± 0.8 (0.9–1.1, $n = 6$)	1.0 ± 0.05 (1.0–1.1, $n = 6$)	0.9, 1.1 ($n = 2$)	1.1 ± 0.75 (1.0–1.2, $n = 6$)	1.1 ± 0.70 (1.0–1.2, $n = 15$)	1.1 ± 0.60 (1.0–1.2, $n = 11$)

[a]If ≤2 specimens are available, only the individual measurements are given.
[b]Based on Schmid and Kappeler (1994).

itz (1977). We use the following dental notations: premaxillary and maxillary teeth are denoted by upper case and mandibular teeth by lower case. The following abbreviations are used: incisor (I/i), canine (C/c), premolar (P/p), molar (M/m).

- Basal skull length: from the anterior edge of the premaxillae to the anteriormost point on the lower border of the foramen magnum.
- Condylobasal axis: distance between the basal mandibular plane to the condylar projection.
- Condylobasal length: from the anterior edge of premaxillae to the posteriormost projection of occipital condyles.
- Coronoidbasal axis: distance between the basal mandibular plane to the coronoid process.
- Frontal length: greatest length from fusion with the nasal bone to the fusion with the parietal bone.
- Greatest orbital diameter: greatest diameter of the orbit from the malar fossa.
- Greatest skull length: from the rostrum to the back of braincase.
- Least orbital breadth: smallest distance dorsally between the orbits.
- Lower postcanine tooth row: distance between p_3 and m_3 at level of cusp.
- Mandibular length: greatest length of the mandible from the anteriormost point of the symphysis to the condyle.
- Nasal length: greatest length of nasal bone (rostral end to fusion with frontal).
- Nasal width: greatest width across nasal bone anteriormost.
- Occipital length: greatest dimension following the nasal–frontal–parietal line.
- Occipital width: greatest dimension of the occipital bone, perpendicular to skull length.
- Orbital transverse diameter: diameter of the orbit from lachrymal bone to level of zygomatic bridge fusion.
- Palatal length: from anterior edge of premaxillae to anteriormost point on posterior edge of the palate.
- Palatal width: between alveoli of second upper molars.
- Parietal length: greatest length from the fusion with the frontal to occipital bones.
- Parietal width: greatest width of the parietal bone at the fusion of the temporal line with the occipital complex.
- Skull height: from bullae to parietal bone, perpendicular to skull length.
- Skull width: greatest skull width perpendicular to the greatest skull length, above bullae.

Table II. Descriptive statistics for cranial measurements of adult specimens of *Microcebus* spp. collected at different localities in the western half of Madagascar

	M. ravelobensis Ankarafantsika (includes Ampijoroa)	*M. tavaratra* Ankarana	*M. griseorufus* Beza Mahafaly	*M. berthae* Kirindy/CFPF	*M. sambiranensis* Manongarivo	*M. myoxinus* Aboalimena and Bemaraha	*M. murinus* Andranomena, Vohimena, and Manamby
Greatest skull length (mm)	34.2 ± 1.09 (33.1–36.1; n = 9)	32.9 ± 0.61 (31.8–33.6; n = 6)	30.9 ± 0.75 (29.9–31.7; n = 6)	29.4 ± 0.47 (29.0–29.9; n = 3)	32.1 ± 0.46 (31.5–32.8; n = 6)	32.3 ± 0.63 (31.2–33.3; n = 15)	32.4 ± 0.60 (31.5–33.0; n = 11)
Greatest skull width (mm)	17.8 ± 0.40 (17.2–18.4; n = 9)	17.4 ± 0.10 (17.2–17.5; n = 6)	16.3 ± 0.46 (15.5–16.9; n = 6)	16.0 ± 0.20 (15.7–16.1; n = 3)	17.3 ± 0.39 (16.6–17.7; n = 6)	17.0 ± 0.31 (16.3–17.4; n = 15)	16.7 ± 0.46 (15.9–17.3; n = 10)
Skull height (mm)	15.7 ± 0.63 (14.4–16.2; n = 9)	15.3 ± 0.51 (14.6–15.8; n = 6)	14.4 ± 0.44 (13.8–15.0; n = 6)	13.8 ± 0.12 (13.7–14.0; n = 3)	15.1 ± 0.29 (14.8–15.4; n = 6)	14.6 ± 0.58 (13.3–15.7; n = 15)	14.6 ± 0.42 (14.2–15.3; n = 10)
Palatal length (mm)	14.3 ± 0.59 (13.3–15.2; n = 9)	13.8 ± 0.42 (13.3–14.3; n = 6)	11.8 ± 0.26 (11.5–12.1; n = 6)	11.5 ± 0.43 (11.3–12.0; n = 3)	13.5 ± 0.28 (13.3–14.0; n = 6)	13.3 ± 0.33 (12.8–14.3; n = 15)	12.3 ± 0.16 (12.1–12.6; n = 11)
Palatal width (mm)	n = 6.0 ± 0.32 (5.5–6.5; n = 9)	5.7 ± 0.23 (5.4–5.9; n = 6)	5.1 ± 0.15 (4.9–5.3; n = 6)	5.4 ± 0.23 (5.2–5.6; n = 3)	6.3 ± 0.25 (5.8–6.5; n = 6)	5.9 ± 0.24 (5.5–6.3; n = 15)	5.4 ± 0.28 (5.0–6.0; n = 11)
Basal skull length (mm)	27.4 ± 0.83 (25.9–28.7; n = 9)	26.1 ± 0.74 (25.3–26.9; n = 6)	24.9 ± 0.67 (24.2–25.9; n = 6)	23.3 ± 0.56 (22.9–23.9; n = 3)	25.3 ± 0.24 (25.2–25.6; n = 6)	26.0 ± 0.80 (24.9–28.2; n = 15)	26.6 ± 0.54 (25.7–27.4; n = 11)
Condylobasal length (mm)	30.5 ± 0.86 (29.1–31.8; n = 9)	29.2 ± 0.65 (28.4–29.9; n = 6)	27.7 ± 0.71 (26.8–28.6; n = 6)	26.1 ± 0.48 (25.8–26.7; n = 3)	28.3 ± 0.43 (27.7–29.0; n = 6)	28.8 ± 0.57 (27.8–29.9; n = 15)	29.4 ± 0.51 (28.5–30.2; n = 11)
Temporal fossa greatest length (mm)	7.7 ± 0.52 (7.0–8.8; n = 9)	7.2 ± 0.32 (6.8–7.6; n = 6)	7.4 ± 0.45 (6.7–8.1; n = 6)	6.4 ± 0.20 (6.3–6.5; n = 3)	7.3 ± 0.21 (7.0–7.7; n = 6)	7.2 ± 0.29 (6.5–7.7; n = 15)	7.6 ± 0.40 (6.9–8.3; n = 11)
Zygomatic breadth (mm)	21.6 ± 0.65 (20.4–22.8; n = 9)	20.3 ± 0.90 (19.3–21.6; n = 6)	19.6 ± 0.55 (18.9–20.2; n = 6)	17.8 ± 0.75 (17.3–18.7; n = 3)	20.3 ± 0.54 (19.6–21.1; n = 6)	19.9 ± 0.51 (18.9–20.8; n = 15)	20.7 ± 0.58 (19.9–21.6; n = 10)
Nasal length (mm)	9.7 ± 0.54 (9.1–10.7; n = 9)	9.9 ± 0.51 (9.3–10.7; n = 6)	8.9 ± 0.23 (8.7–9.3; n = 6)	7.9 ± 0.64 (7.5–8.6; n = 3)	10.0–0.41 (9.6–10.8; n = 6)	9.8 ± 0.53 (9.0–10.7; n = 15)	9.6 ± 0.74 (8.6–10.8; n = 10)
Nasal width (mm)	2.3 ± 0.16 (2.2–2.7; n = 9)	2.3 ± 0.13 (2.1–2.4; n = 6)	2.1 ± 0.22 (1.8–2.4; n = 6)	2.2 ± 0.13 (2.1–2.4; n = 3)	2.0 ± 0.14 (1.8–2.2; n = 6)	2.3 ± 0.15 (2.1–2.6; n = 15)	2.4 ± 0.14 (2.2–2.6; n = 10)
Frontal length (mm)	13.3 ± 0.64 (12.5–14.5; n = 9)	12.0 ± 0.73 (11.1–13.0; n = 6)	12.7 ± 0.41 (11.9–13.0; n = 6)	11.1 ± 0.62 (10.4–11.6; n = 3)	11.6 ± 0.24 (11.3–12.0; n = 6)	11.6 ± 0.59 (10.1–12.7; n = 15)	11.9 ± 0.90 (10.4–13.6; n = 10)
Parietal length (mm)	11.9 ± 0.70 (10.9–12.9; n = 9)	11.3 ± 0.94 (10.0–12.5; n = 6)	9.0 ± 0.78 (8.5–10.6; n = 6)	10.3 ± 0.87 (9.3–10.8; n = 3)	10.3 ± 0.32 (10.0–10.8; n = 6)	10.9 ± 0.48 (10.0–11.5; n = 15)	10.2 ± 0.76 (9.0–11.4; n = 11)
Parietal width (mm)	11.9 ± 0.55 (10.5–12.3; n = 9)	10.3 ± 1.31 (8.7–11.8; n = 6)	6.8 ± 1.37 (5.4–9.3; n = 6)	11.7 ± 0.11 (11.6–11.8; n = 3)	11.1 ± 0.79 (10.0–12.2; n = 6)	10.7 ± 0.62 (9.6–11.8; n = 15)	7.2 ± 1.19 (6.1–10.4; n = 11)

Occipital length (mm)	4.1 ± 0.55 (2.9–4.9; $n = 9$)	4.5 ± 0.37 (4.2–5.2; $n = 6$)	4.2 ± 0.31 (4.0–4.8; $n = 6$)	3.8 ± 0.27 (3.6–4.1; $n = 3$)	4.3 ± 0.14 (4.1–4.5; $n = 6$)	3.8 ± 0.29 (3.3–4.2; $n = 15$)	4.6 ± 0.50 (3.5–5.4; $n = 11$)
Occipital width (mm)	11.7 ± 0.42 (10.9–12.3; $n = 9$)	10.9 ± 0.45 (10.5–11.8; $n = 6$)	10.7–0.29 (10.4–11.0; $n = 6$)	10.7 ± 0.15 (10.5–10.8; $n = 3$)	10.6–0.39 (10.0–11.1; $n = 6$)	11.0 ± 0.29 (10.5–11.5; $n = 15$)	10.8 ± 0.44 (9.9–11.5; $n = 11$)
Temporal line (mm)	6.5 ± 0.37 (6.0–7.0; $n = 8$)	5.5 ± 0.68 (4.5–6.4; $n = 6$)	4.3 ± 0.79 (3.3–5.2; $n = 6$)	5.9 ± 0.20 (5.8–6.1; $n = 3$)	6.3 ± 0.42 (5.5–6.7; $n = 6$)	5.9 ± 0.58 (5.0–6.6; $n = 15$)	3.8 ± 0.80 (3.2–5.9; $n = 11$)
Greatest orbital diameter (mm)	10.7 ± 0.27 (10.1–11.0; $n = 9$)	10.6 ± 0.44 (10.0–11.2; $n = 6$)	9.9 ± 0.33 (9.4–10.3; $n = 6$)	9.7 ± 0.40 (9.3–10.1; $n = 3$)	10.4 ± 0.22 (10.4–10.6; $n = 6$)	10.2 ± 0.25 (9.8–10.6; $n = 15$)	10.0 ± 0.22 (9.6–10.4; $n = 11$)
Orbital transverse diameter (mm)	10.5 ± 0.30 (9.9–10.9; $n = 9$)	10.4 ± 0.43 (9.9–11.2; $n = 6$)	9.9 ± 0.31 (9.3–10.2; $n = 6$)	9.3 ± 0.48 (8.8–9.8; $n = 3$)	10.2 ± 0.22 (9.8–10.4; $n = 6$)	10.1 ± 0.23 (9.4–10.4; $n = 15$)	10.0 ± 0.20 (9.7–10.3; $n = 11$)
Least orbital breadth (mm)	3.5 ± 0.20 (3.3–3.9; $n = 9$)	3.5 ± 0.23 (3.3–3.8; $n = 6$)	3.1 ± 0.27 (2.8–3.5; $n = 6$)	3.2 ± 0.16 (3.0–3.3; $n = 3$)	3.6 ± 0.22 (3.4–3.9; $n = 6$)	3.4 ± 0.22 (3.0–4.0; $n = 15$)	3.5 ± 0.26 (3.1–3.9; $n = 11$)
I^1 height (mm)	1.4 ± 0.20 (1.1–1.7; $n = 9$)	1.3 ± 0.04 (1.3–1.4; $n = 6$)	1.2 ± 0.09 (1.2–1.4; $n = 6$)	0.9 ± 0.15 (0.8–1.1; $n = 3$)	1.1 ± 0.12 (0.9–1.2; $n = 6$)	1.2 ± 0.12 (0.9–1.4; $n = 15$)	1.3 ± 0.12 (1.1–1.5; $n = 11$)
I^2 height (mm)	1.0 ± 0.09 (1.0–1.3; $n = 9$)	1.0 ± 0.08 (0.9–1.1; $n = 6$)	1.0 ± 0.08 (0.9–1.1; $n = 6$)	0.7 ± 0.04 (0.6–0.7; $n = 3$)	0.8 ± 0.05 (0.7–0.9; $n = 6$)	1.0 ± 0.09 (0.8–1.1; $n = 15$)	1.1 ± 0.10 (0.9–1.2; $n = 11$)
C height (mm)	2.7 ± 0.19 (2.4–3.0; $n = 9$)	2.4 ± 0.10 (2.2–2.5; $n = 6$)	2.3 ± 0.08 (2.2–2.4; $n = 6$)	1.8 ± 0.16 (1.6–1.9; $n = 3$)	2.2 ± 0.11 (2.0–2.4; $n = 6$)	2.2 ± 0.15 (2.0–2.6; $n = 15$)	2.6 ± 0.07 (2.5–2.8; $n = 11$)
P^2 height (mm)	1.6 ± 0.09 (1.6–1.8; $n = 9$)	1.5 ± 0.05 (1.4–1.6; $n = 6$)	1.5–0.10 (1.3–1.6; $n = 6$)	1.1 ± 0.15 (0.9–1.2; $n = 3$)	1.3 ± 0.13 (1.1–1.4; $n = 6$)	1.4 ± 0.07 (1.2–1.5; $n = 15$)	1.6 ± 0.13 (1.3–1.8; $n = 11$)
P^3 height (mm)	1.5 ± 0.14 (1.4–1.8; $n = 9$)	1.5 ± 0.06 (1.4–1.6; $n = 6$)	1.3 ± 0.11 (1.1–1.4; $n = 6$)	1.1–0.07 (1.0–1.2; $n = 3$)	1.3 ± 0.08 (1.2–1.4; $n = 6$)	1.4 ± 0.08 (1.3–1.6; $n = 15$)	1.4 ± 0.11 (1.2–1.6; $n = 11$)
P^4 height (mm)	1.4 ± 0.12 (1.3–1.8; $n = 9$)	1.4 ± 0.12 (1.3–1.6; $n = 6$)	1.2 ± 0.09 (1.1–1.3; $n = 6$)	1.1 ± 0.00 ($n = 3$)	1.3 ± 0.06 (1.2–1.4; $n = 6$)	1.3 ± 0.09 (1.1–1.5; $n = 15$)	1.3 ± 0.07 (1.2–1.4; $n = 10$)
M^1 length (mm)	1.9 ± 0.09 (1.8–2.0; $n = 9$)	1.9 ± 0.06 (1.8–1.9; $n = 6$)	1.6 ± 0.11 (1.4–1.7; $n = 6$)	1.5 ± 0.03 (1.4–1.5; $n = 3$)	1.8 ± 0.11 (1.6–1.8; $n = 6$)	1.7 ± 0.08 (1.6–1.9; $n = 15$)	1.7 ± 0.08 (1.6–1.8; $n = 11$)
M^2 length (mm)	1.8 ± 0.09 (1.7–1.9; $n = 9$)	1.8 ± 0.06 (1.8–1.9; $n = 6$)	1.5 ± 0.06 (1.4–1.6; $n = 6$)	1.4 ± 0.00 ($n = 3$)	1.7 ± 0.09 (1.6–1.8; $n = 6$)	1.6 ± 0.09 (1.5–1.9; $n = 15$)	1.6 ± 0.07 (1.5–1.7; $n = 11$)
M^3 length (mm)	1.7 ± 0.07 (1.5–1.8; $n = 9$)	1.7 ± 0.04 (1.6–1.7; $n = 6$)	1.4 ± 0.07 (1.3–1.5; $n = 6$)	1.4 ± 0.05 (1.3–1.4; $n = 3$)	1.5 ± 0.08 (1.4–1.6; $n = 6$)	1.6 ± 0.09 (1.4–1.7; $n = 15$)	1.5 ± 0.09 (1.4–1.6; $n = 11$)
Mandibular length (mm)	20.2 ± 0.46 (19.6–20.9; $n = 9$)	19.4 ± 0.51 (18.8–20.0; $n = 6$)	18.3 ± 0.60 (17.7–19.1; $n = 6$)	16.9 ± 0.38 (16.6–17.3; $n = 3$)	18.7 ± 0.42 (18.3–19.5; $n = 6$)	19.0 ± 0.43 (18.5–20.0; $n = 15$)	19.6 ± 0.47 (18.6–20.1; $n = 10$)
Condylobasal axis (mm)	5.8 ± 0.40 (5.3–6.5; $n = 9$)	5.6–0.44 (5.1–6.2; $n = 6$)	5.3 ± 0.27 (5.0–5.8; $n = 6$)	4.8 ± 0.26 (4.6–5.0; $n = 3$)	5.1 ± 0.31 (4.6–5.4; $n = 6$)	5.3 ± 0.36 (4.5–5.8; $n = 15$)	5.9–0.33 (5.4–6.5; $n = 11$)
Coronoidobasal axis (mm)	9.9 ± 0.53 (9.1–10.7; $n = 9$)	10.1 ± 0.51 (9.5–10.8; $n = 6$)	9.7 ± 0.51 (8.8–10.2; $n = 6$)	8.2 ± 0.18 (8.0–8.3; $n = 3$)	8.9 ± 0.44 (8.6–9.7; $n = 6$)	9.4 ± 0.30 (8.9–9.9; $n = 15$)	10.5 ± 0.53 (9.8–11.5; $n = 11$)
Lower postcanine tooth row (mm)	8.9 ± 0.34 (8.3–9.3; $n = 9$)	8.8 ± 0.32 (8.4–9.3; $n = 6$)	7.7 ± 0.14 (7.5–7.9; $n = 6$)	7.3 ± 0.07 (7.2–7.4; $n = 3$)	8.5 ± 0.26 (8.1–8.9; $n = 6$)	8.3 ± 0.24 (8.0–8.8; $n = 15$)	8.3 ± 0.17 (8.0–8.6; $n = 10$)

- Greatest width of temporal fossa: from the posteriormost point of the zygomatiotemporal suture to the posteriormost point of the maxilla posterior to M^3.
- Temporal line: distance between parietal line and temporal line, perpendicular to the former at its origin.
- Zygomatic breadth: greatest breadth across the zygomatic process, perpendicular to skull length at the junction of the zygomaticoorbital suture.

- C: height of the canine from the mesial edge of the alveolus to the distalmost point of the crown.
- I^1: height of the upper first incisor from the anterior border of alveolus to the distalmost point of the crown.
- I^2: height of upper second incisor from the anterior border of alveolus to the distalmost point of the crown.
- M^1: length of the upper first molar at greatest width of the cusp.
- M^2: length of the upper second molar at greatest width of the cusp.
- M^3: length of the upper third molar at greatest width of the cusp.
- P^2: height of the upper second premolar from the mesial edge of alveolus to the distalmost point of the crown.
- P^3: height of the upper third premolar from the mesial edge of alveolus to the distalmost point of the crown.
- P^4: height of the upper fourth premolar from the mesial edge of alveolus to the distalmost point of the crown.

Postcranial (± 0.1 mm; Table III)

- Caudals: number of caudal vertebrae (whole number).
- Femoral length: greatest length of femur.
- Femoral width distal: greatest width of distal part of femur, from medial condyle to lateral epicondyle.
- Femoral width proximal: greatest dimension from the femoral head to the greater trochanter.
- Humeral length: greatest length of the humerus.
- Humeral width distal: greatest width of the distal part of the humerus, from the medial epicondyle to the lateral epicondyle.
- Humeral width proximal: greatest dimension of the humeral head.
- Pelvic length: greatest length of the pelvis from the anteriormost point of the ilium (anterior superior iliac process) to the posteriormost point of the ischium.
- Tibial width proximal: greatest width of the tibia proximally from the laterale condyle to medial condyle.

Table III. Descriptive statistics for postcranial skeletal measurements of adult specimens of *Microcebus* spp. collected at different localities in the western half of Madagascar

	M. ravelobensis Ankarafantsika (includes Ampijoroa)	*M. tavaratra* Ankarana	*M. griseorufus* Beza Mahafaly	*M. berthae* Kirindy/CFPF	*M. sambiranensis* Manongarivo	*M. myoxinus* Aboalimena and Bemaraha	*M. murinus* Andranomena, Vohimena, and Manamby
Humeral length (mm)	22.2 ± 0.67 (21.4–23.4; $n = 9$)	21.5 ± 1.19 (19.0–22.5; $n = 6$)	20.8 ± 1.19 (19.1–22.0; $n = 6$)	19.0 ± 1.01 (18.0–20.0; $n = 3$)	19.8 ± 0.75 (18.9–20.7; $n = 6$)	20.9 ± 0.59 (20.1–22.3; $n = 15$)	21.3 ± 0.65 (20.1–22.4; $n = 11$)
Humeral width proximal (mm)	3.6 ± 0.14 (3.4–3.8; $n = 9$)	3.4 ± 0.18 (3.2–3.7; $n = 6$)	3.4 ± 0.23 (3.1–3.6; $n = 6$)	3.1 ± 0.07 (3.1–3.2; $n = 3$)	3.2 ± 0.06 (3.2–3.3; $n = 6$)	3.4 ± 0.09 (3.2–3.6; $n = 15$)	3.6 ± 0.09 (3.5–3.8; $n = 11$)
Humeral width distal (mm)	5.3 ± 0.16 (5.1–5.6; $n = 9$)	5.2 ± 0.20 (4.9–5.4; $n = 6$)	5.0 ± 0.25 (4.7–7.4; $n = 6$)	4.3 ± 0.09 (4.2–4.4; $n = 3$)	4.9 ± 0.18 (4.6–5.1; $n = 6$)	4.9 ± 0.22 (4.3–5.1; $n = 15$)	5.3 ± 0.27 (5.0–5.8; $n = 11$)
Femoral length (mm)	31.2 ± 0.75 (30.2–32.6; $n = 9$)	30.6 ± 1.53 (28.3–32.3; $n = 6$)	29.2 ± 1.15 (27.6–30.4; $n = 6$)	27.4 ± 1.69 (25.6–28.9; $n = 3$)	27.7 ± 1.20 (26.4–29.6; $n = 6$)	30.2 ± 0.72 (29.0–31.5; $n = 15$)	29.4 ± 0.51 (28.5–30.2; $n = 11$)
Femoral width proximal (mm)	5.9 ± 0.28 (5.4–6.2; $n = 9$)	5.4 ± 0.24 (5.0–5.6; $n = 6$)	5.5 ± 0.20 (5.2–5.7; $n = 6$)	4.9 ± 0.17 (4.7–5.1; $n = 3$)	5.2 ± 0.24 (4.8–5.4; $n = 6$)	5.5 ± 0.19 (5.1–5.9; $n = 15$)	5.7 ± 0.28 (5.0–6.1; $n = 11$)
Femoral width distal (mm)	4.7 ± 0.12 (4.6–4.9; $n = 9$)	4.6 ± 0.28 (4.4–5.1; $n = 6$)	4.4 ± 0.29 (3.9–4.6; $n = 6$)	4.0 ± 0.00 ($n = 3$)	4.1 ± 0.18 (4.0–4.5; $n = 6$)	4.5 ± 0.11 (4.2–4.7; $n = 15$)	4.6 ± 0.18 (4.4–4.9; $n = 11$)
Trochanteric height (mm)	5.4 ± 0.20 (5.1–5.7; $n = 9$)	5.2 ± 0.10 (5.1–5.4; $n = 6$)	5.0 ± 0.36 (4.5–5.4; $n = 6$)	4.7 ± 0.25 (4.5–5.0; $n = 3$)	4.7 ± 0.19 (4.5–5.0; $n = 6$)	5.2 ± 0.27 (4.8–5.7; $n = 15$)	5.4 ± 0.33 (5.1–6.0; $n = 11$)
Tibial width proximal (mm)	4.7 ± 0.19 (4.4–5.0; $n = 9$)	4.6 ± 0.20 (4.4–5.0; $n = 6$)	4.4 ± 0.21 (4.0–4.6; $n = 6$)	4.0 ± 0.09 (4.0–4.1; $n = 3$)	4.2 ± 0.09 (4.1–4.3; $n = 6$)	4.5 ± 0.12 (4.3–4.7; $n = 15$)	4.5 ± 0.17 (4.3–4.9; $n = 11$)
Pelvic length (mm)	24.7 ± 0.84 (23.6–26.0; $n = 9$)	23.7 ± 1.59 (21.8–26.3; $n = 6$)	23.5 ± 1.56 (21.7–24.9; $n = 6$)	20.5 ± 0.40 (20.3–20.8; $n = 3$)	21.8 ± 1.22 (20.2–23.6; $n = 6$)	23.2 ± 0.87 (22.2–25.0; $n = 15$)	24.1 ± 1.06 (22.8–25.8; $n = 11$)
Number of caudal vertebrae	28.0 ± 1.21 (27–30; $n = 9$)	28.4 ± 0.55 (28–29; $n = 5$)	27.5 ± 1.55 (27–28; $n = 6$)	27.0 ± 0.00 ($n = 3$)	28.0 ± 0.63 (27–29; $n = 6$)	27.5 ± 0.66 (27–29; $n = 13$)	26.7 ± 0.79 (25–28; $n = 11$)

- Trochanteric height: distance between the trochanteric fossa to the lesser trochanter.

Age Classes

We recognize the following age classes:

- Subadult: individuals in which the molars are not fully erupted. The initial eruption of permanent teeth follows the sequence (Schwartz, 1974):

$$\frac{(M^1\ I^2\ I^3)\ M^2 \quad C\ P^2\ M^3\ P^4\ P^3}{m_1\ m_2\ i_2\ i_3 \quad c\ p_2\ m_3\ p_4\ p_3}$$

- Adult: individuals with a fully erupted permanent dentition; cranial sutures generally fused. The dental formula of adult *Microcebus* is:

$$\frac{2\text{-}1\text{-}3\text{-}3}{2\text{-}1\text{-}3\text{-}3} = 36$$

Color

We used the guide of Smithe (1975) as a standard for terminology associated with pelage color. The color names commence in capital letters and the associated color numbers from Smithe (1975) are also included. The guide's palette is limited with regard to pale tones so sometimes we had to use our own combinations naming colors not given by Smithe in lower case. We compared and described pelage color in natural light. In many cases the fur of older museum specimens shows signs of foxing and did not fit the descriptions presented below in the taxonomic evaluations.

Statistical Tests

We used two statistical packages: StatView (version 4.51) for descriptive statistics and a variety of tests including ANOVA, t-tests, regression, and principal component analysis, and SPSS (1997) exclusively for discriminate function analysis based on log transformed data. We used KnowledgeSEEKER to distinguish between different populations of *Microcebus.* We consider probabilities at the 95% level to be statistically significant.

Taxonomic Perspective

The taxonomic history of *Microcebus* is complex. Because several reviews on *Microcebus* have appeared over the past 140 years (Mivart, 1867; Major, 1894; Schwarz, 1931; Tattersall, 1982; Martin, 1995), we will not summarize details, but point out that numerous synonyms exist in the literature for gray and rufous mouse lemurs (Schwarz, 1931; Tattersall, 1982). Most nomina lack associated holotypes in the form of skins and skulls and are based on designated lectotype illustrations. In deriving our taxonomic conclusions, we compared our specimens to earlier published lectotype illustrations to determine if any of the older names were applicable for species defined herein. There is no implied phylogenetic relationship in the order of the various mouse lemur taxa that we discuss; they are arranged per geographic ranges from north to south. Phylogenic aspects of *Microcebus* are addressed by Yoder *et al.* (in press).

TAXONOMIC EVALUATIONS

We do not describe in detail the dental and cranial characters that define *Microcebus*, but instead refer to Mivart (1867), Major (1894), Swindler (1976) and Tattersall (1982). Little variation in cranial and dental structure, other than differences in measurements, occurs among the different populations of western *Microcebus.* When such characters exist, we generally mention them in the description of the species. We found few differences in caudal vertebral counts or measurements of postcranial elements.

Some populations of *Microcebus murinus* exhibit sexually dimorphic traits, notably greatest skull length and body mass (Kappeler, 1990; Jenkins and Albrecht, 1991). The latter trait varies differently between the sexes due to augmentation of female mass during reproduction (Randrianambinina, 1997; Schmid, 1997, 1999; Fietz, 1998). Other than presumed type II errors, we found little evidence to support that adult mouse lemurs from the same populations in western Madagascar display morphological differences between the sexes. Accordingly, in all analyses we combined them.

On the basis of a series of external morphological characters—pelage coloration and measurements—and cranial and postcranial skeletal measurements, we define 7 species that are concordant with an independent phylogenetic analysis based on molecular data obtained from many of the same individuals (Yoder *et al*., in press).

There is a north-south cline in decreasing body size among the specimens (Fig. 2). The first major separation between populations is on the basis of palatal length: the group of taxa that form the northern assemblage

Variables	Location	Species
➸ Palate length ≤ 12.6 mm		
➸ Canine height < 1.9 mm	Kirindy/CFPF (3/3)	*M. berthae*
➸ Canine height 2.2 – 2.4 mm	Beza Mahafaly (6/6)	*M. griseorufus*
➸ Canine height > 2.5 mm	Andranomena (6/6)	*M. murinus*
	Manamby (2/2)	*M. murinus*
	Vohimena (3/3)	*M. murinus*
➸ Palate length ≥ 12.8 mm		
➸ Ear length ≤ 19 mm	Manongarivo (6/6)	*M. sambiranensis*
➸ Ear length ≥ 20 mm		
➸ M^1 length ≤ 1.74 mm	Aboalimena (4/4)	*M. myoxinus*
	Bemaraha (8/10)	*M. myoxinus*
➸ M^1 length ≥ 1.75 mm		
➸ Condylobasal axis < 4.9 mm	Bemaraha (2/10)	*M. myoxinus*
➸ Condylobasal axis > 5.0 mm		
➸ Canine height < 2.5 mm	Ankarana (5/5)	*M. tavaratra*
	Ankarafantsika (1/9)	*M. ravelobensis*
➸ Canine height ≥ 2.5 mm	Ankarafantsika (8/9)	*M. ravelobensis*

Fig. 2. Determination key based on single morphological characters for western *Microcebus* spp. Values in parentheses are the number of specimens from a given locality that fall within the specified measurement range, followed by the total number within the sample. Decision tree developed with the KnowledgeSEEKER program.

has palatal length ≥12.8 mm and the southern assemblage of ≤12.6 mm. The geographic divide between them appears to be the Tsiribihina River. Within the northern group the Manongarivo population has ear length ≤19 mm, while all of the others, excluding a single specimen from Belo-sur-Tsiribihina, measure ≥20 mm. Thereafter, the length of M^1 separates most individuals from Aboalimena and Bemaraha from the other northern populations: individuals from the former areas measure <1.74 mm on average and from the latter >1.75 mm on average. The remaining northern populations can be distinguished by several characters, for example, the C height of most individuals from Ankarafantsika/Ampijoroa is >2.5 mm versus those from Ankarana (<2.5 mm). Within the southern region, C height separates three different species groups: individuals from Kirindy/CFPF Forest measure <1.9 mm, Beza Mahafaly between 2.2 and 2.4 mm, and the Vohimena and Andranomena >2.5 mm. In virtually all cases, patterns of intrapopulation and interpopulation variation in pelage coloration independently corroborate the results of the morphometric comparisons.

Microcebus tavaratra, New Species (Fig. 3, color plate)

Holotype. FMNH 161630; adult female; skin, skull, partial skeleton, and preserved tissues; original number RMR 71; collected 5 May 1997 by R. M. Rasoloarison.

Standard measurements (in mm, except for mass) recorded in the original field catalog and on the skin tag of the type include total length, 284; head and body length, 130; tail length, 153; hindfoot length, 35.0; ear length, 23.5; and mass, 78 gm. Selected cranial measurements (in mm) are: greatest skull length, 33.7; skull width, 17.3; skull height, 14.7; palate length, 14.1; condylobasal length, 29.9; zygomatic breadth, 21.6; nasal length, 10.7; occipital length, 4.7; C height, 2.5; and M^1 length, 1.8.

The skin, skull, and associated skeleton are in good shape. The vagina was perforated and teats large.

Type Locality. Madagascar: Province d'Antsiranana, Réserve Spéciale (RS) de l'Ankarana, Campement des Anglais, 9 km NO de Mahamasina, 13°05′S, 49°06′E, about 180 m above sea-level.

Diagnosis. A large mouse lemur (total length 276–296 mm, tail length 145–167 mm, hindfoot length 33.0–36.0 mm) with dark brownish back, distinctly rufous head markings, and a distinct middorsal line. Venter with a mixture of whitish-beige and dark gray underfur. M^1 length >1.8 mm and condylobasal axis length averages 5.6 mm. The fourth toe is longer than the third toe.

Referred Specimens. Province d'Antsiranana, RS de l'Ankarana, Forêt d'Analamahitsy, 12 km SE d'Anivorano Nord, 12°52′S, 49°14′E, 200 m above sea level (FMNH 161629); Province d'Antsiranana, RS de l'Ankarana, Campement des Anglais, 9 km NO de Mahamasina, 13°05′S, 49°06′E, about 180 m above sea-level (FMNH 161631, 161632); Province d'Antsiranana, RS de l'Ankarana, Campement des Américains, 9.5 km ONO de Mahamasina, 13°04′S, 49°03′E, about 180 m above sea level (FMNH 161633-637).

Distribution. Currently only known from the RS de l'Ankarana.

Description. The dense and long cover hairs of the dorsum are bicolored to tricolored—Raw Umber (123), Clay Color (123b) and Yellow Ochre (123c). There is considerable variability in the middorsal stripe. In some individuals the line, which varies in coloration from Raw Umber (123) to Verona Brown (223b), is continuous from the crown to the base of the tail and in others it commences behind the shoulders and terminates at the base of the tail. The midventral fur is a soft toned whitish-beige with irregular patches that towards the flanks become distinctly bicolored—whitish-beige and a pigment falling between Light Neutral Gray (85) and Pale Neutral Gray (86). The underfur on both the dorsal and ventral sur-

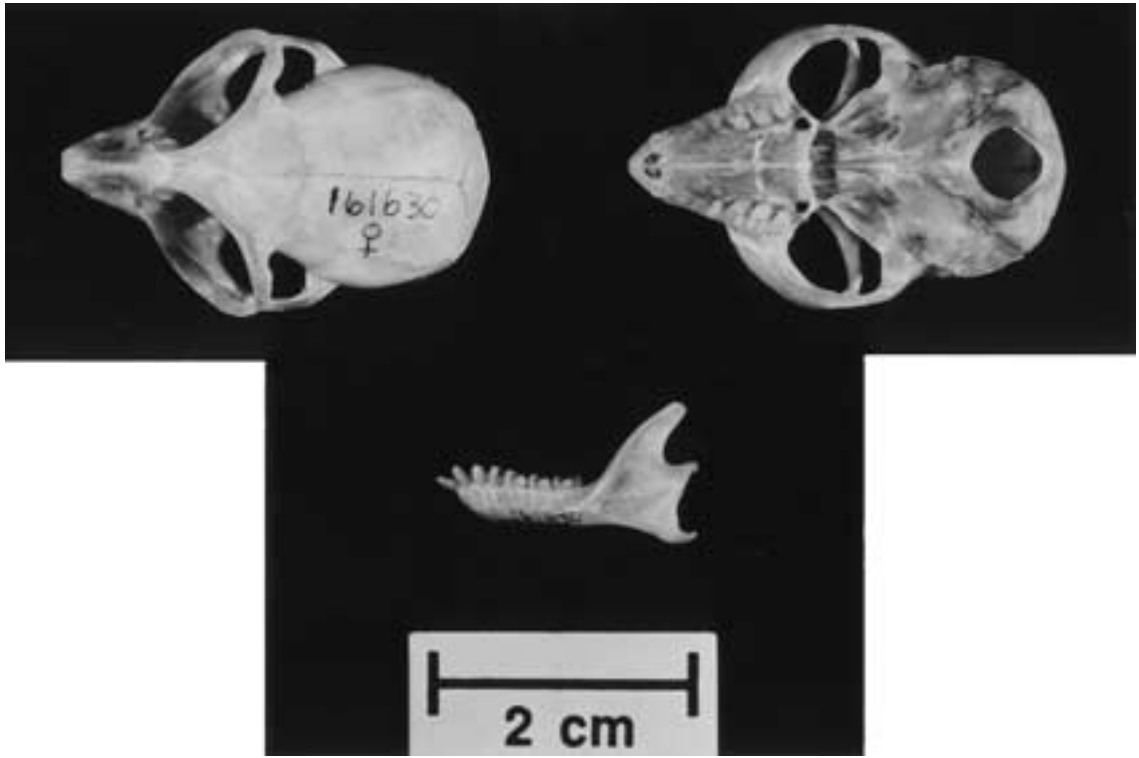

Fig. 3. Three views of *Microcebus tavaratra* nov. sp. (FMNH 161630). (**Upper left**) dorsal view of cranium (FMNH neg. Z 94262); (**upper right**) ventral view of cranium (FMNH neg. Z 94263); (**lower center**) lateral view of mandible (FMNH neg. Z 94252).

Color plate. The species of *Microcebus* in western Madagascar (clockwise from extreme upper left-hand corner): *Microcebus ravelobensis*, *M. tavaratra*, *M. sambiranensis*, *M. murinus*, *M. griseorufus*, *M. berthae* (middle center), *M. murinus* (lower center), and *M. myoxinus.* Painting by Peggy MacNamara.

faces of the body is Vandyke Brown (221). This latter color continues posterior to the eyes. Crown and ears are Robin Rufous (340). The region between the eyes is grayish-white (holotype is more reddish than in the majority of specimens from the reserve). The orbital region and crown are Raw Umber (123) and Cinnamon (123b). There are distinct black markings around the anterior portions of the orbits.

The pied tail pelage is relatively long, particularly distally; the proximal 60–70% is bicolored Raw Umber (123) and Cinnamon (123b) and the remaining distal portion is Cinnamon Brown (33) and Raw Umber (123). The furred portion of the hands and feet are whitish-gray. Vibrissae are dark. The single subadult in the collection (FMNH 161633) fits the description for this species.

Of the species, those from Ankarana show the greatest amount of variation in pelage coloration. The specimen from Analamahitsy is particularly pale. The pelage variation is generally associated with the cover hairs of the dorsum and seems to be related to the proportion of the different hair colors. On the basis of morphometric (Tables I–III) and biochemical studies (Yoder *et al.*, in press), we suggest that all of these individuals represent a single species.

The skull is distinctly stout and heavily built (Fig. 3), with proportionately short and squared rostrum. No clear concavity in the rostrum when viewed laterally. Prosthion projection prominent. One pair of palatal fenestrae. Temporal lines fit the pattern of *Microcebus murinus* (Martin, 1995, p. 554). Small diastema separating P^2 from C and P^3. C is long (2.2–2.5 mm), and the distal stylid of lingual cingulum is distinctly pointed. Upper premolars are all approximately the same height. On M^{1-3} the buccal cingulum is well developed, like the parastyles and metastyles on M^{1-2}. In general the postcanine maxillary teeth are among the widest and longest of the western species of *Microcebus*, particularly M^1, which is long (1.8–1.9 mm). The protoconid of p_2 is caniform and is at about a 45° relative to the mandibular axis. There is a stylar rim on p_2, but it is not well developed, while it is well-defined on p_3 and p_4; m_1 and m_2 are rectangular.

In all of the individuals within our series from Ankarana the fourth toe measures 11 mm and the third toe 10 mm. The width of the digital pad on the first toe measures, on average, 3.0 mm (range 2.7–3.1 mm), and the width of the grooming claw on the second hind toe is, on average, 1.0 mm (range 0.9–1.1 mm).

Comparisons and Remarks. The species is well differentiated from other *Microcebus* in western Madagascar. The only other species that shows notable overlap in measurements and pelage coloration is *Microcebus ravelobensis* from the Ankarafantsika region, about 450 km to the southwest of Ankarana. *Microcebus ravelobensis* is larger in body size and mass (Table

I), and has a proportionately and absolutely more massive skull than that of *M. tavaratra* (Table II). For example, greatest skull length in the specimens from Ankarana varies from 31.8 to 33.6 mm (x = 32.9 mm, n = 6) and from the Ankarafantsika/Ampijoroa area from 33.1 to 36.1 mm (x = 34.2 mm, n = 9)–the difference is statistically significant (Anova-Scheffé comparisons between these two populations, critical difference = 1.1414, P = 0.03). Other significant cranial and dental differences between the two species are condylobasal length, frontal length, occipital width, and C height. The average ear length of *Microcebus ravelobensis* is longer (22.5–25.0 mm, x = 24.1 mm, n = 9) than that of *M. tavaratra* (21.0–23.5 mm, x = 22.3 mm, n = 6); but the difference is not statistically significant. *Microcebus tavaratra* has a shorter tail than that of *M. ravelobensis* (Table I). The two species show consistent genetic differences from one another, but are part of the same clade (Yoder *et al*., in press). Thus, the apparent similarity in pelage coloration, body size and proportions, and cranial and osteological measurements is due to convergence.

Notes on Natural History. The Ankarana Reserve is composed principally of dry deciduous forest with areas of gallery forest. A portion of the reserve includes a labyrinth of deep canyons with limestone pinnacles or cliffs (= *tsingy*). Of the three sites that we visited, Campement des Américains is in an ecotone of open savanna with widely scattered trees and the base of *tsingy* cliffs. The site is degraded by human activities, namely cattle and associated fires to stimulate pasture growth. Forêt d'Analamahitsy and Campement des Anglais are in natural forests, the former growing directly from limestone and the latter sitting on soil in the valleys between deep canyons.

In an inventory of the primate fauna in the RS d'Ankarana, Hawkins *et al.* (1990) noted that the local mouse lemur, which they considered to be closer to a rufous form, occurred sporadically at different surveyed sites with densities ranging from 67 ± 57 to 220 ± 204 individuals per km^2. Two species have been previously noted to exist within the reserve (*Microcebus murinus* and *M. rufus*) by Nicoll and Langrand (1989) and Mittermeier *et al.* (1994). There is little doubt that the previous reports of *Microcebus rufus* are actually of *M. tavaratra.* We have not examined any specimen of *Microcebus murinus* from the site. In the collection of the Parc Botanique et Zoologique de Tsimbazaza (PBZT), Antananarivo, there is a specimen (PBZT 1250) collected in the Forêt de l'Ankarana in January 1969 by R. Albignac and G. Randrianasolo that is referable to *Microcebus tavaratra.*

Etymology. The name *tavaratra* is derived from Malagasy and means "from the north."

Vernacular Names. Northern rufous mouse lemur or Microcèbe roux du nord.

Microcebus sambiranensis, New Species (Fig. 4, color plate)

Holotype. FMNH 161624; adult female; skin, skull, partial skeleton, and preserved tissues; original number RMR 38; collected 22 November 1996 by R. M. Rasoloarison.

Standard measurements (in mm, except for mass) recorded in the original field catalog and on the skin tag of the type include total length, 262; head and body length, 120; tail length, 141; hindfoot length, 32.0; ear length, 17.0; and mass, 51.5 gm. Selected cranial measurements (in mm) are: greatest skull length, 31.9; skull width, 16.6; skull height, 14.8; palate length, 13.3; condylobasal length, 28.3; zygomatic breadth, 20.0; nasal length, 9.6; occipital length, 4.4; C height, 2.2; and M^1 length, 1.8.

The skin, skull, and associated skeleton are in good shape. This specimen had the vagina perforated, pubic symphysis open, and was lactating.

Type Locality. Madagascar: Province de Mahajanga, Réserve Spéciale (RS) de Manongarivo, Forêt de Bekolosy, 2.3 km E de Beraty, 14°02′S, 48°16′E, about 360 m above sea level.

Diagnosis. Except the *Microcebus* species in the Kirindy/CFPF Forest, *M. sambiranensis* is the smallest mouse lemur from western Madagascar. The dorsal pelage is rufous, with a poorly defined middorsal stripe, and short ears (17.0–19.0 mm). The underside is a dull whitish-beige with dark gray underfur. Short C (2.0–2.4 mm). Fourth toe longer than third toe.

Referred Specimens. Province de Mahajanga, RS de Manongarivo, Forêt de Bekolosy, 2.3 km E de Beraty, 14°02′S, 48°16′E, about 360 m above sea level (FMNH 161623, 161625-628).

Distribution. Microcebus sambiranensis is currently only known from the RS de Manongarivo.

Description. The dense and long dorsal cover hairs are a brightly bicolored Cinnamon Rufous (40) and Cinnamon (39). The poorly defined Amber (36) middorsal stripe starts just behind the shoulders and continues to the terminus of the tail. The proximal half of the belly, particularly along the midventral area, is composed of Chamois (123d) cover hairs, while the flanks and more distal portions are a mixture of pale Chamois (123d) and light Pale Neutral Gray (86). The dorsal and ventral underfur is Blackish Neutral Gray (82).

The tail has long dense fur, particularly towards the terminus, and the proximal two-thirds of the dorsal surface is Amber (36) and ventral surface Yellow Ochre (123c). The terminal one-third is distinctly darker than the proximal portion and composed of a dorsally bicolored Raw Umber (233) and Sayal Brown (223c) and ventrally bicolored Chamois (123d) and Pale Neutral Gray (86) fur.

The pale patch between the eyes starts anteriorly as dull white, changes

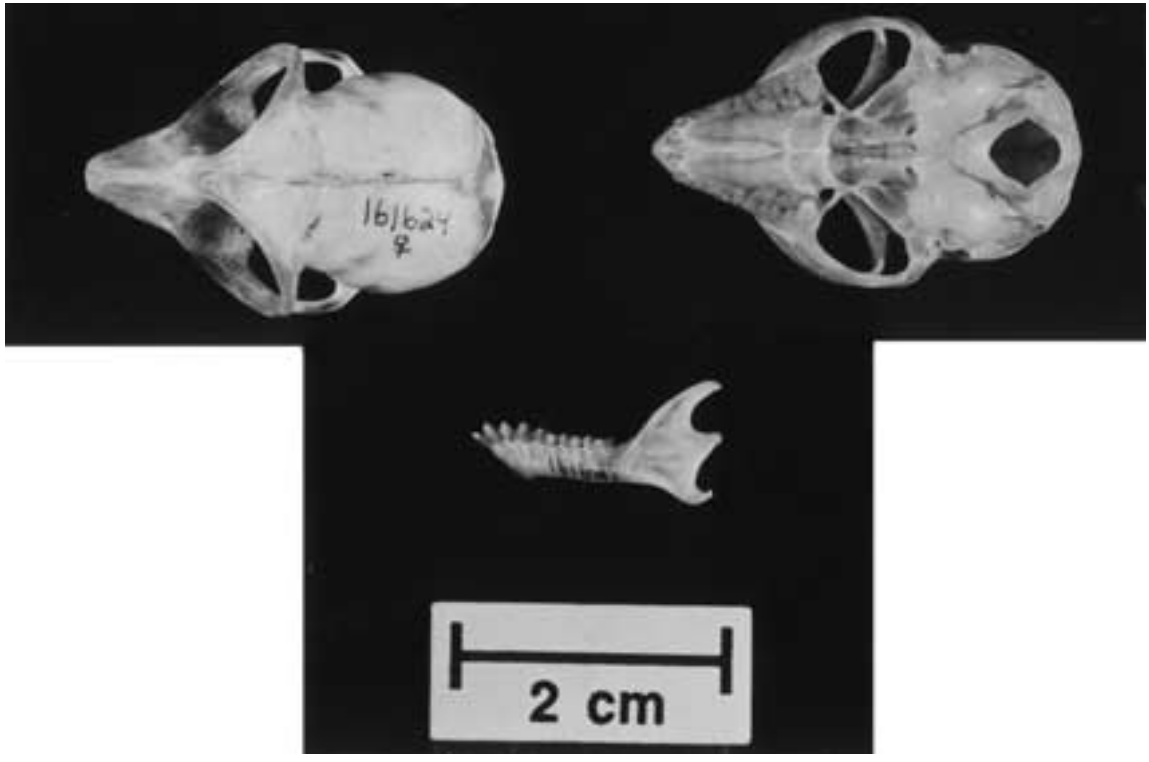

Fig. 4. Three views of *Microcebus sambiranensis* nov. sp. (FMNH 161624). (**Upper left**) dorsal view of cranium (FMNH neg. Z 94264); (**upper right**) ventral view of cranium (FMNH neg. Z 94265); (**lower center**) lateral view of mandible (FMNH neg. Z 94253).

posteriorly to Cinnamon (39), which then merges to Cinnamon Rufous (40) between the eyes. There is a dark, nearly blackish, orbital ring. The crown and ears are Amber (36). The fur on the hands and feet is generally dull rufous, sometimes mixed with a trace of whitish-beige; although in some individuals dull whitish-beige is the dominant tone. Vibrissae are generally dark.

The skull is small and delicate (Fig. 4). The rostrum is relatively short and blunt, giving a squared appearance in dorsal view. There is no clear concavity in the rostrum when viewed laterally. Prosthion projection prominent. One pair of palatal fenestrae. Temporal lines fit the pattern of *Microcebus rufus* (Martin, 1995, p. 554). Upper premolars all approximately the same height. Diastema separating P^2 from C, and P^3 present but not well-developed. C is not particularly prominent (2.0–2.4 mm), and the distal stylid of lingual cingulum is relatively blunt. Among the diminutive mouse lemur species in western Madagascar, *Microcebus sambiranensis* has a long palate (13.3–14.0 mm) as compared to individuals from Kirindy/CFPF Forest (11.3–12.0 mm) and Beza Mahafaly (11.5–12.1 mm). Several other cranial and dental characters show a parallel to palatal length in completely or nearly separating individuals from Manongarivo, Kirindy/CFPF, and Beza Mahafaly (in each case the Manongarivo population is larger): palatal width, nasal length, least orbital breadth, M^1 length, M^2 length, and lower postcanine tooth row length. The shape of the rostrum in *Microcebus sambiranensis* is more elongated and pointed than in individuals from Kirindy/CFPF and Beza Mahafaly. The frontoparietal suture in *Microcebus sambiranensis* is posteriorly more shallow, with a distinct U-shape rather than a V-shape in the Kirindy/CFPF and Beza Mahafaly specimens. The protoconid of p_2 is caniform and is at approximately 45° relative to the mandibular axis. Stylar rim on p_2 and p_3 present but not well-developed. Distinct basins below protostylids of m_1, m_1 and m_2 are rectangular in shape.

The fourth toe on the hindfoot measures between 10 and 11 mm and the third toe between 9 and 10 mm; for each individual the fourth toe is about 1 mm longer than the third toe. The mean value for the width of the grooming claw on the second toe is 1.1 mm (range 1.0–1.2 mm) and the width of the digital pad averages 3.0 mm (range 2.8–3.1 mm).

Notes on Natural History. The lowland forest formations of Manongarivo and surrounding areas, a region known as the Sambirano, have been separated by phytogeographers due to a unique combination of botanical elements of eastern (humid) and western (dry) forests (Humbert, 1965; Koechlin *et al.,* 1974). We collected specimens in the Forêt de Bekolosy, in the western foothills of the Manongarivo Massif. Most of them are from degraded lowland forest at the edge of slash-and-burn agricultural sites (= *tavy*) and a few are from slightly disturbed forest.

During a field trip to the northeastern portions of the RS de Manongarivo in late 1998 and early 1999, Goodman and Schütz (in press) found a *Microcebus* sp. to be uncommon on the northeastern slopes. Only a few individuals were observed within study sites at 800, 1250, and 1600 m. On the basis of the phenotypic characters of specimens of *Microcebus sambiranensis* taken on the western side of the massif and close observations of the mouse lemurs occurring on the northeastern slopes, we conclude that they are referable to the same species.

The species of *Microcebus* that has been previously reported from the reserve and the Sambirano in general is *Microcebus rufus* (Tattersall, 1982; Raxworthy and Rakotondraparany, 1988; Nicoll and Langrand, 1989; Mittermeier *et al.,* 1994); however, we believe that these earlier records from at least Manongarivo are referable to *Microcebus sambiranensis.* Recent fieldwork on the Ambato Massif, 30 km north of Ambanja, found no evidence of *Microcebus* (Colquhoun, 1998), and apparently *M. sambiranensis* does not occur that far north. Specimens from Manongarivo have a mean tail length of 140.8 mm (Table I), which is distinctly longer than the mean of 121.7 mm ($n = 41$) for individuals of *Microcebus rufus* from the Parc National de Ranomafana in the central eastern humid forest (Atsalis *et al.,* 1996).

Etymology. The area of northwestern Madagascar, specifically the coastal zone surrounding Ambanja, inland areas (including the Manongarivo Massif), and nearby offshore islands is referred to as the Sambirano, from which the specific name of this new species is derived. The Sambirano River forms the major watershed of this region.

Vernacular Name. Sambirano mouse lemur or Microcèbe de Sambirano.

Microcebus ravelobensis, Zimmerman *et al.,* 1998 (Fig. 5, color plate)

Zimmermann *et al.* (1998) conducted fieldwork on *Microcebus* in the Jardin Botanique B of the Réserve Forestière d'Ampijoroa, to the east of Mahajanga. On the basis of external morphology and vocalizations, they concluded that two distinct species live sympatrically within the reserve. One of them fits the description of the widespread western species *Microcebus murinus,* and they described a second new species *M. ravelobensis.*

Two live individuals of the new *Microcebus* were transported to the Parc Botanique et Zoologique de Tsimbazaza (PBZT), Antananarivo, where they were held captive. Zimmermann *et al.* (1998) designated one of them, a female, the holotype (PBZT 1421) and the second individual, a male, as the paratype (PBZT 1422). Their original intention was that,

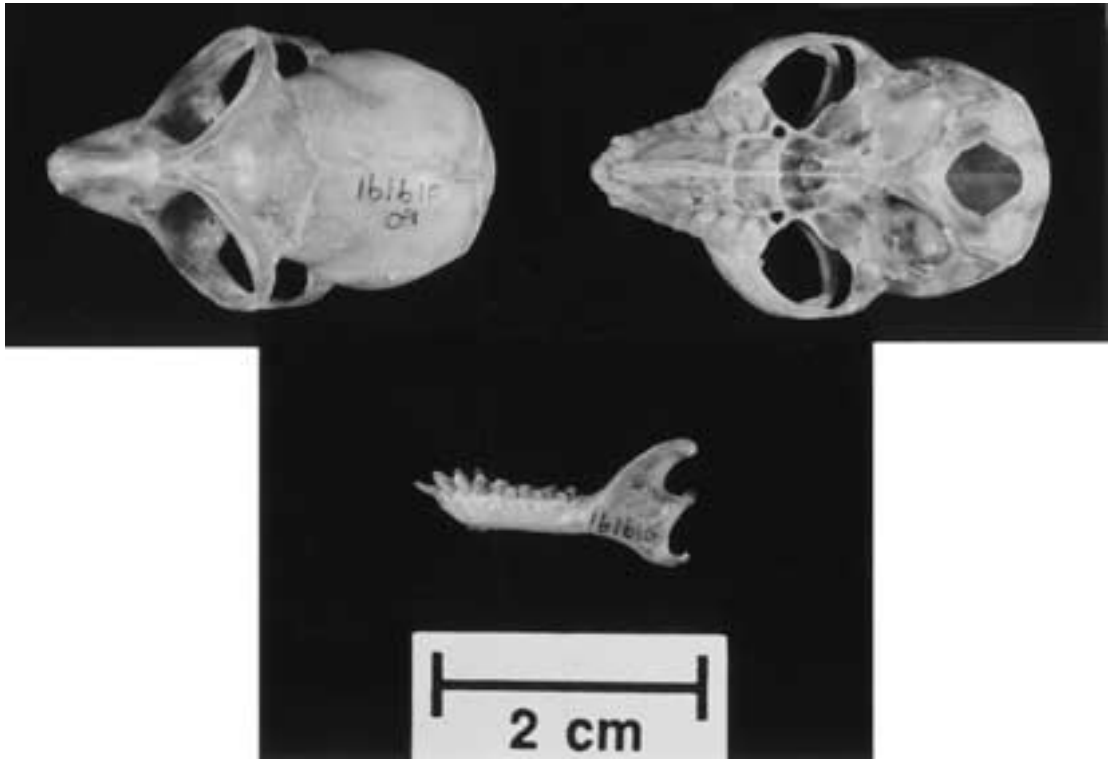

Fig. 5. Three views of *Microcebus ravelobensis* (FMNH 161610). (**Upper left**) dorsal view of cranium (FMNH neg. Z 94268); (**upper right**) ventral view of cranium (FMNH neg. Z 94269); (**lower center**) lateral view of mandible (FMNH neg. Z 94255).

after their deaths the captive lemurs would be prepared as specimens for the PBZT museum collection. The two lemurs died, but no portion of them remains in the PBZT (F. Rakotondraparany, pers. comm.). No holotype (living or a museum) specimen exists associated with the nomen *Microcebus ravelobensis.*

The lack of a type impedes detailed taxonomic conclusions on the relationships among mouse lemur populations in the vicinity of Ampijoroa and Ankarafantsika. Following the rules of the International Code of Zoological Nomenclature (1985), article 75, the designation of a neotype is essential in order to solve a detailed taxonomical problem. We have chosen a neotype that comes from the same forest as the individuals that used in the original description of *Microcebus ravelobensis.*

Designation of Neotype. FMNH 161610; adult male; skin, skull, partial skeleton, and preserved tissues; original number RMR 57; collected 12 March 1997 by R. M. Rasoloarison.

Standard measurements (in mm, except for mass) recorded in the original field catalog and on the skin tag of the neotype include total length, 293; head and body length, 128; tail length, 164; hindfoot length, 35.0; ear length, 24.5; and mass, 67.5 gm. Selected cranial measurements (in mm) are: greatest skull length, 34.4; skull width, 18.1; skull height, 16.0; palate length, 14.3; condylobasal length, 30.2; zygomatic breadth, 21.1; nasal length, 9.8; occipital length, 4.2; C height, 2.8; and M^1 length, 1.9.

The skin, skull, and associated skeleton are in good shape. The testes measured 7.7 × 5 mm and the epididymis is convoluted.

Neotype Locality. Madagascar: Province de Mahajanga, Réserve Forestière (RF) d'Ankarafantsika, Station Forestière d'Ampijoroa, Jardin Botanique B, 16°35′S, 46°52′E, about 200 m above sea level (as given by collector). The incorrect coordinates 16°35′S, 46°82′E given by Zimmermann *et al.* (1998) for the collection site of their live individuals is presumably the result of a typographical error.

Emended Diagnosis. Zimmermann *et al.* (1998) provided the original description of this species. On the basis of the specimens in our possession we add the following details to the diagnosis of *Microcebus ravelobensis.* This species has a distinctly mottled rufous dorsal pelage, with a poorly marked middorsal stripe. It is distinguished from most of its congeners, with the exception of *Microcebus tavaratra,* by its long tail (144–172 mm), long ears (22.5–25.0 mm), and a wide variety of cranial features such as greatest skull length (33.1–36.1 mm), M^1 length (1.8–2.0 mm), and lower postcanine tooth row length (8.3–9.3 mm). The fourth toe is consistently longer than the third toe.

Referred Specimens. Province de Mahajanga, RF d'Ankarafantsika, 5 km SSO d'Ampijoroa, Ankarokaroka, 16°20.3′S, 46°47.6′E, 160 m above

sea-level (FMNH 161605-609); Province de Mahajanga, RF d'Ankarafantsika, Station Forestière d'Ampijoroa, Jardin Botanique B, 16°35′S, 46°52′E, about 200 m above sea-level (FMNH 161611–616).

Distribution. Microcebus ravelobensis is currently only known from the region of Ankarafantsika.

Description. Cover hairs of the dorsum are largely fine, dense, short, and slightly variable from a bicolored to tricolored pattern and are composed of cinnamon (123a), Clay Color (123b), and Drab (27). The middorsal Raw Umber (223) stripe is poorly delineated and runs posteriorly from behind the shoulders to the base of the tail. In some adults and subadults the back stripe is faint. The ventrum shows variable coloration from small irregularly shaped Clay Color (123c) patches, particularly towards the midventral line, to bicoloration along the flanks consisting of Clay Color (123c) and Chamois (123d) cover hairs. Dorsal and ventral underfur Dusky Brown (19). One (FMNH 161616) of the 10 adult specimens is distinctly paler in pelage coloration: the dorsal cover hair is tricolored Clay Color (123b), Chamois (123d), and Buff (124), while the venter is slightly paler than the neotype.

The pelage posterior to the nose and between the eyes is a pale grayish that merges to Cinnamon (39) behind the eyes. The crown and ears have the same coloration as the dorsum. The dorsal and ventral portions of the tail are uniformly bicolored—Raw Umber (223) and Cinnamon (123a). There is a slight tendency for the tail to become gradually darker towards the terminal tip. The pilosity of the tail changes from being short proximally to long and feathery 10 mm hairs at the distal tip. The distal furred portion of the hands and feet are grayish-white. Vibrissae are dark. Three subadults (FMNH 161612, 161614, and 161615) have the same coloration as adults.

The skull of *Microcebus ravelobensis* is robust (Fig. 5). The long rostrum tapers anteriorly to a blunt and squared nasal area. When viewed laterally the frontal and nasal areas are concave. Prosthion projection is prominent. One pair of palatal fenestrae. Temporal lines fit the pattern of *Microcebus rufus* (Martin, 1995, p. 554). The frontal bones are elongated and on average the longest among western *Microcebus* spp. (12.5–14.5 mm). A small diastema separates P^2 from C and P^3. C is well-developed and long (2.4–3.0 mm), and the distal stylid of the lingual cingulum is pointed. Upper premolars approximately the same height. Buccal cingulum on M^{1-3} is well-developed, like the parastyles and metastyles on M^{1-2}. The protoconid of p_2 is caniform and at about a 45° relative to the mandibular axis. Stylar rims on p_2 and p_3 are well-developed; m_1 and m_2 are rectangular. There is a distinct basin below the protostylid of m_1. The lower postcanine tooth row is, on average, the longest of any of the western mouse lemurs, (though broadly overlapping with that of *Microcebus tavaratra*).

Microcebus ravelobensis is the largest species of the 7 western mouse lemur species. Average adult mass is 71.7 g (range 59.0–110.0 g), versus 61.1 g (range 48.0–83.5 g) in *Microcebus tavaratra*, 62.6 g (range 50.0–85.0 g) in individuals from Beza Mahafaly, and 62.3 g (54.0–69.0 g) in typical *M. murinus* (Table I). For the mean values of three of the five external measurements from cadavers, *M. ravelobensis* is the largest western *Microcebus.* The means of ear length and head and body length for populations of *Microcebus murinus* are at most a few mm greater than values for *M. ravelobensis.* Further, for the vast majority of cranial, postcranial, and dental characters, mean values for *Microcebus ravelobensis* are larger than those of other *Microcebus.* In some cases there is overlap in measurements of the similarly colored *Microcebus tavaratra.*

In *Microcebus ravelobensis* the fourth toe is 11 and 12 mm and the third toe between 10 and 11 mm long; for the 12 individuals in our series from Ankarafantsika, the fourth toe is consistently about 1 mm longer than the third toe. The mean value for the width of the grooming claw on the second toe is 1.3 mm (range 1.2–1.6 mm) and the width of the digital pad averages 3.3 mm (range 3.1–3.5 mm).

Taxonomic Comments. The first use of the name *Microcebus ravelobensis* was by Randrianambinina (1997), who included a detailed morphological description as well as color photographs of the new species. However, on the basis of article 9 of the International Code of Zoological Nomenclature (1985) a thesis does not constitute a valid publication of a new name.

In October 1997, Zimmermann *et al.* published an abstract associated with the description of this new species. They used the new name, *Microcebus ravelobensis*, and gave some details on how the species differs from *M. rufus* and *M. murinus.* However, their diagnosis of *Microcebus ravelobensis* is rather vague and insufficient to properly characterize it; we consider Zimmermann *et al.* (1998) as the formal description of this species.

Notes on Natural History. Ankarafantsika, which includes the Station Forestière d'Ampijoroa, is composed of dry deciduous forest. Some areas of the reserve have been heavily disturbed by humans. The new material of *Microcebus ravelobensis* presented here was collected at two different sites. The first locality is along the southern limit of the reserve at Ankarokaroka, a forest with an extremely open understory and growing on sandy soils without much humus. The average canopy height is between 10 and 15 m, and the forest was degraded by cattle and probable occasional burning. The second site, the Jardin Botanique B, is in the central portion of the reserve, just to the north of Lake Ravelobe (= Lake Ampijoroabe). The collection site is degraded forest, largely due to cattle activity, with an average canopy height of 15–20 m, and growing on sandy soil. The Ankaro-

karoka and Jardin Botanique B sites are separated by a direct linear distance of about 6 km.

On the basis of morphology and pelage coloration, all of our material from the Ankarafantsika region is referable to *Microcebus ravelobensis.* Randrianambinina (1997), Zimmermann *et al.* (1998), Nicoll and Langrand (1989), and Mittermeier *et al.* (1994), reported that *Microcebus murinus* also occurs in the reserve. At Ankarokoraka we saw two different types of *Microcebus* and we assume that the non-collected species is *M. murinus* (RMR and SMG, pers. obs). Evidence that the two species occur sympatrically within the reserve comes from two specimens held in the Muséum National d'Histoire Naturelle (MNHN 1964.61 and 1964.62) and one in the PBZT (1246), which are referable to *Microcebus murinus* based on pelage coloration, external measurements, and cranial measurements.

Microcebus murinus (J. F. Miller, 1777) (Fig. 6, color plate)

- *Lemur prehensilis* Kerr, 1792
- *Lemur pusillus* E. Geoffroy, 1795
- *Galago madgascariensis* E. Geoffroy, 1812
- *Myscebus palmarum* Lesson, 1840
- *Galago minor* Gray, 1842
- *Chirogaleus gliroides* A. Grandidier, 1868

The taxonomic history of *Microcebus murinus* is entangled, but it has been excellently outlined and discussed in detail by Tattersall (1982, p. 119). An understanding of the taxonomic complexity of this species is made more difficult because the designated type (Schwarz, 1931) is a plate in Shaw (1796). It does not help to define the morphological attributes of the species or the site where the type material was obtained. Following the rules of the International Code of Zoological Nomenclature (1985), article 75, the designation of a neotype in this case is essential in order to solve a detailed taxonomic problem.

Designation of Neotype. FMNH 161618; adult female; skin, skull, partial skeleton, and preserved tissues; original number RMR 45; collected 26 December 1996 by R. M. Rasoloarison.

Standard measurements (in mm, except for mass) recorded in the original field catalog and on the skin tag of the neotype include total length, 289; head and body length, 136; tail length, 152; hindfoot length, 34.0; ear length, 26.0; and mass, 69.0 gm. Selected cranial measurements (in mm) are: greatest skull length, 33.1; skull width, 16.9; skull height, 14.6; palatal length, 12.5; condylobasal length, 29.9; zygomatic breadth, 21.4; nasal length, 9.9; occipital length, 4.8; C height, 2.6; and M^1 length, 1.6.

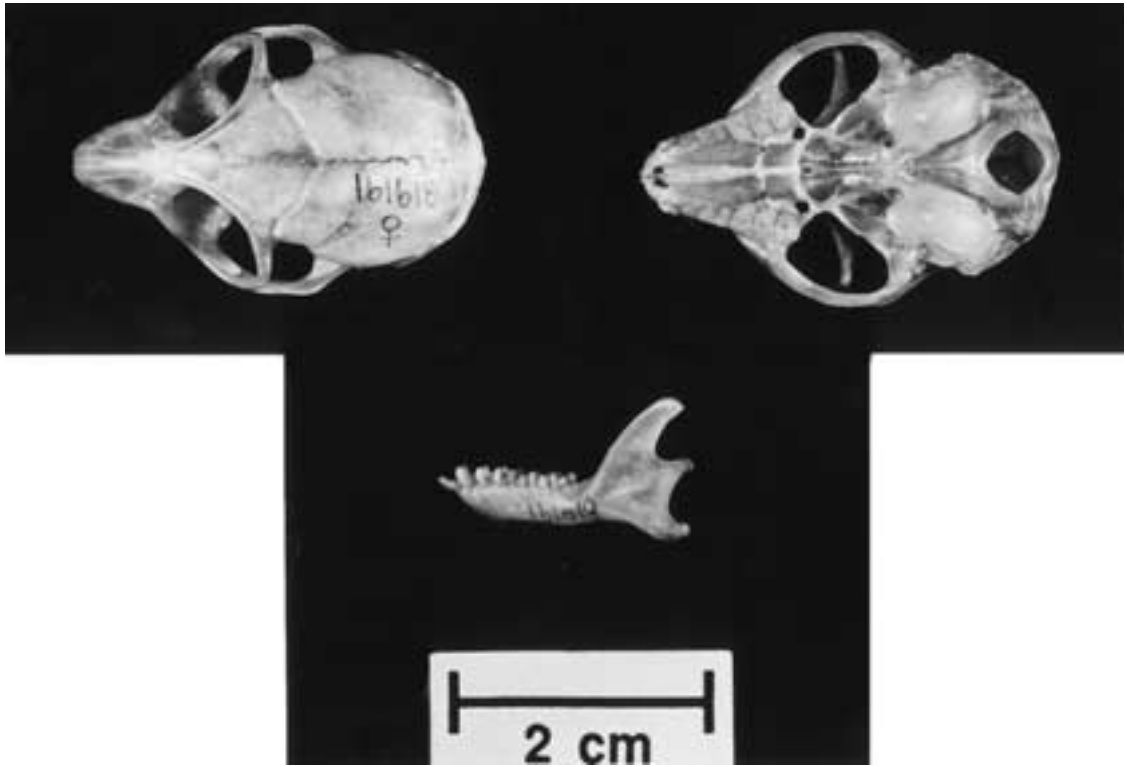

Fig. 6. Three views of *Microcebus murinus* (FMNH 161618). (**Upper left**) dorsal view of cranium (FMNH neg. Z 94256); (**upper right**) ventral view of cranium (FMNH neg. Z 94257); (**lower center**) lateral view of mandible (FMNH neg. Z 94249).

The skin, skull, and associated skeleton are in good shape. The vagina was perforated and mammae large.

Designated Neotype Locality. Madagascar: Province de Toliara, Réserve Spéciale (RS) d'Andranomena, 20 km NNE de Morondava, 20°09′S, 44°33′E, 40 m above sea level (as given by collector).

Emended Diagnosis. This large mouse lemur has a variable grayish-brown to brownish-gray back and tail, dull reddish-brown or cinnamon diffused middorsal stripe, and mixed dull beige and gray underside. Palatal length is <12.6 mm. C height is >2.5 mm, and hindfoot length is between 30.0 and 34.0 mm. The fourth toe generally longer than the third toe.

Referred Material. Province de Toliara, RS d'Andranomena, 20 km NNE de Morondava, 20°09′S, 44°33′E, 40 m above sea-level (FMNH 161617, 161619-622); Province de Toliara, Forêt de Manamby, 60 km E de Morondava, 20°22′S, 44°51′E, 180 m above sea-level (FMNH 161654-658); Province de Toliara, Forêt de Vohimena, 35 km NE de Sakaraha, 22°41.0′S, 44°49.8′E, 780 m above sea level (FMNH 161660-668).

Distribution. Poorly known, but on the basis of literature references the species lives in the region from near Tolagnaro west to the southwestern portion of the island and then north to the Sambirano region (Tattersall, 1982). However, in light of this current revision of western mouse lemurs it is clear that many of the previous reported records of the species from western Madagascar need to be reassessed.

Description. The soft, relatively short and dense dorsal cover hairs are bicolored Raw Umber (123) and Cinnamon (123a) or Pale Pinkish Buff (121d). In a few cases the anterior two-thirds of the dorsal pelage is Clay Color (123b) and Yellow Ochre (123c) underfur, while the posterior portion is slightly lighter consisting of Yellow Ochre (123c) and Chamois (123d) hairs. The Cinnamon (123a) back stripe is diffused, and is largely visible along the midportion of the middorsal area to the base of the tail. In some individuals this line is better defined than in others. The ventrum has small discrete dull beige or whitish-beige patches along the central and upper portions of the belly and bicolored dull beige and Light Neutral Gray (85) flanks. Dorsal and ventral underfur Dusky Brown (19) or Vandyke Brown (221). The proximal 80–90% of the bicolored tail is Cinnamon (123a) or Clay Color (123b) and Yellow Ochre (123c) and the distal 10–20% is bicolored Raw Umber (223) and Cinnamon (123a). The tail fur is short and does not change markedly in pilosity towards the distal tip.

The head has a uniform pale white patch above the nose and between the eyes, clear Clay Color (123b) area posterior to the eyes, and the crown and ears are generally the same color as the upper dorsum. In some individuals there are dark, nearly blackish, orbital markings. The furred portion of

the hands and feet are a whitish-beige or grayish-white. Vibrissae are generally dark, but some in the mental region are lightly colored. Subadults tend to be distinctly darker, particularly the dorsal cover hairs and dorsal and ventral portions of the tail. Among a few of the younger individuals, the lateral back stripe is poorly defined, and on some specimens it is indiscernible.

Skulls of *Microcebus murinus* are robust and stout; the rostrum is rather short and slightly blunt (Fig. 6). When viewed laterally the frontal and nasal area shows no distinct concavity. There is no prosthion projection. One pair of palatal fenestrae. C is long (2.5–2.8 mm) and the distal stylid of the lingual cingulum is pointed. A distinct diastemata separate P^2 from C and P^3. P^3 is longer than P^4 and P^5. P^4 is longer than P^5. The buccal cingulum on M^{1-3} is well-developed, including parastyles and metastyles on M^{1-2}. The protoconid of p_2 is caniform, distinctly procumbent, blade-shaped, and at about a 75° relative to the mandibular axis. The stylar rim on p_2 and p_3 is well-developed; m_1 and m_2 are rectangular.

The fourth toe on the hind foot is between 10 and 11 mm and the third toe is between 9 and 10 mm long. In most of our specimens from Andranomena, Vohimena, and Manamby the fourth toe is consistently 1 mm longer than the third toe. The only exceptions are three specimens for which these two toes are the same length. The mean value for the width of the grooming claw on the second toe is 1.1 mm (range 1.0–1.2 mm) and the width of the digital pad averages 3.1 mm (range 2.9–3.3 mm).

Comparison and Remarks. Several external, cranial, and dental characters are statistically significantly different (ANOVA Scheffé tests) between *Microcebus murinus* and *M. ravelobensis.* In all cases the mean values for the former species are smaller than those of the latter species (Table I): tail length ($P < 0.001$); greatest skull length ($P < 0.0001$); skull width ($P < 0.0001$); skull height ($P = 0.001$); palatal length ($P < 0.0001$); palatal width ($P = 0.001$); frontal length ($P < 0.0001$); parietal length ($P = 0.002$); parietal width ($P < 0.0001$); occipital width ($P = 0.003$); temporal line ($P < 0.0001$); greatest orbital diameter ($P = 0.005$); M^1 ($P = 0.007$); M^2 ($P = 0.007$); M^3 ($P = 0.002$); and lower postcanine tooth row ($P = 0.0004$). Further, there are statistical differences between measurements of populations of *Microcebus murinus* and *M. tavaratra* (*mean values are lower in *M. tavaratra*): tail length ($P = 0.05$); hindfoot length ($P = 0.04$); *ear length ($P = 0.0008$); skull width ($P = 0.05$); palatal length ($P < 0.0001$); parietal width ($P < 0.0001$); temporal line ($P = 0.001$); *C height ($P = 0.04$); M^1 ($P = 0.03$); M^2 ($P = 0.0008$); M^3 ($P = 0.03$); and lower postcanine tooth row ($P = 0.01$).

There are several ways to distinguish *Microcebus murinus* from the other western *Microcebus.* The dorsal pelage of *Microcebus murinus* is generally grayish or bicolored and lacks the distinctive rufous or reddish appearance of *M. tavaratra* and *M. ravelobensis.* Further, within the western grayish *Microcebus*, *M. murinus* can be separated by its longer C height (x = 2.6 mm, range 2.5–2.8 mm, n = 11), while measurements of C in gray individuals from sites further south are shorter (Kirindy/CFPF − x = 1.8 mm, range 1.6–1.9 mm, n = 3; Beza Mahafaly − x = 2.3 mm, range 2.2–2.4 mm, n = 6).

Within our samples of *Microcebus* from western Madagascar there are several localities from which the collected specimens possess very similar phenotypic, cranial, and osteological characters, and we consider all of them to be typical of *M. murinus*, with respect to the designated neotype. Their placement in a single species is further supported by genetic data (Yoder *et al.,* in press).

The type specimen of *Chirogaleus gliroides* A. Grandidier, 1868 (MNHN 1868-1441, type no 172) in the Paris Museum, is extremely foxed in coloration, and based on cranial ossification is a subadult. Contrary to the statement of Rode (1939), the skull of the specimen is in the MNHN. The provenance of this specimen is simply Madagascar.

Notes on Natural History. The specimens we report here of *Microcebus murinus* come from several localities. The first site, the RS d'Andranomena, is a dry deciduous forest that has been heavily degraded by human activities. We collected the specimens near the northern limit of the reserve, within a few hundred meters of the village of Marofandilia. The second site is the Forêt de Manamby, which has a similar forest structure to that at Andranomena. The third site is the Forêt de Vohimena, to the east of Sakaraha. The forests of this region are more transitional between dry deciduous formations and humid forests to the east (Morat, 1973; Du Puy *et al.,* 1994).

Previous reports on the primate fauna of Andranomena only include records of *Microcebus murinus* (Nicoll and Langrand, 1989). The forests near Sakaraha, including Vohimena, Zombitse, and Vohibasia, were inventoried recently by Ganzhorn (1994) and Goodman *et al.* (1997): *Microcebus murinus* occurs at all of them, and there was no evidence of a rufous species (Ganzhorn, 1994; Goodman *et al.,* 1997). Specimens collected near Beroboka [19°58′S, 44°37′E] by F. Petter (MNHN 1961.266) and by C. S. Webb (BMNH 48.182, 48.183, and 48.185) possess the external pelage characters, bodily measurements, and cranial measurements typical of *Microcebus murinus.* This site is south of the Tsiribihina River and not far north of the Kirindy/CFPF Forest. A specimen from Tsiombe [25.3° S, 45.5° E] (BMNH 48.186) is referable to *Microcebus murinus.*

Microcebus myoxinus Peters, 1852 (Fig. 7, color plate)

After a zoological collecting expedition to the eastern coast of Africa, with a brief side trip to Madagascar, Peters (1852) described several new species of mammals. Among them were three small rufous *Microcebus* from the western coast of Madagascar that he named *M. myoxinus.* One of them was from the coastal site of Bombatoka [= Bombetoka] (16° S) and the other two from Baie de St. Augustin (23.5° S). When describing *Microcebus myoxinus,* Peters did not designate a holotype.

In 1931 Schwarz published an important revision of the genera and species of Malagasy lemurs and concluded that *Microcebus myoxinus* is a synonym of *M. murinus.* Further, Schwarz (1931) designated one of Peters' specimens in the Berlin Museum [not the British Museum as mentioned by Hill (1953, p. 333)] as the lectotype—no. 319 (mounted skin), 14655 (skull); ♀, St. Augustine's Bay, S. W. Madagascar. It is still in the Zoologisches Museum, Berlin, but Rasoloarison and P. M. Kappeler (pers. comm.) could not find the associated skull during recent visits to the museum. Other material from Peters' collection in the Berlin Museum include a fluid preserved specimen catalogued as 5634, from which the skull had been extracted and cleaned, and a skin and skull bearing the number 14763 (P. M. Kappeler, pers. com.). Apparently, the original collection localities for these specimens are no longer associated with the specimens.

Elliot (1912, pp. 106–107) examined the material in Berlin and noted that "it has evidently faded considerably, for now the sides of the head, lips, entire under parts and inner sides of the arms are white; upper part of back is whitish brown, and only the dorsal stripe on lower back is reddish brown; tail ochraceous buff above, yellowish white beneath. . . . The type is now practically useless for determining the species, as it does not resemble at all Peters' published colored figure, nor agree with his description."

Researchers working over the past decade in the Kirindy/CFPF Forest, 60 km NE of Morondava, found that two species of *Microcebus* occurred sympatrically at the site (Schmid and Kappeler, 1994). After capturing and measuring over 80 live individuals of *Microcebus* in the Kirindy/CFPF Forest, they concluded that the larger and grayer species is referable to *Microcebus murinus* and the smaller and more rufous animal was not assignable to any recognized species. Given that the name *Microcebus myoxinus* was available for a western population of *Microcebus* and that the pelage description of this form appeared to fit their rufous animals, they decided to resurrect that name for the distinct Kirindy/CFPF population.

Subsequent work on the taxonomy of western mouse lemurs, including the opportunity to reevaluate the material collected by Peters, has shown that the Kirindy/CFPF Forest mouse lemurs are not referable to *Microcebus*

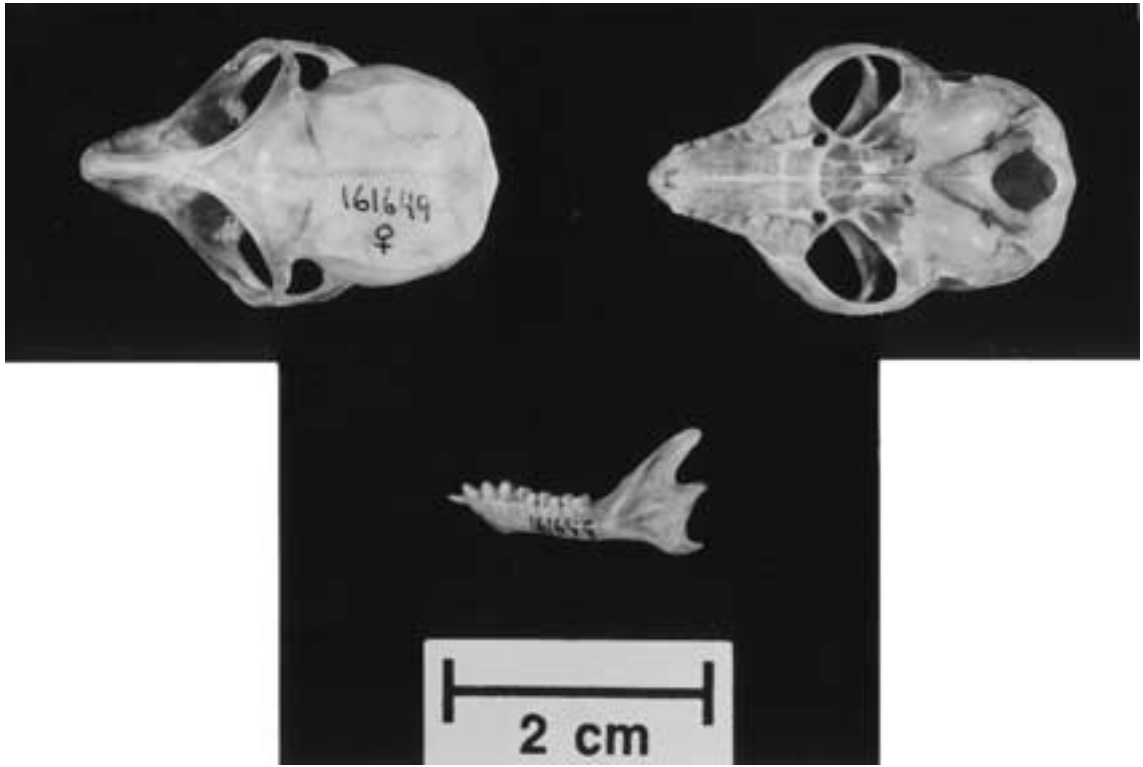

Fig. 7. Three views of *Microcebus myoxinus* (FMNH 161649). (**Upper left**) dorsal view of cranium (FMNH neg. Z 94260); (**upper right**) ventral view of cranium (FMNH neg. Z 94261); (**lower center**) lateral view of mandible (FMNH neg. Z 94251).

myoxinus, but instead to a previously unrecognized species. All of the measurements of Peters' *Microcebus myoxinus* (Table IV) fall within the 95% confidence interval of the measurements of individuals from the Aboalimena and Bemaraha. Further, none of the 95% confidence intervals of the measurements of the three individuals from Kirindy/CFPF Forest include the values of Peters' specimen, which strongly indicates that his specimens show greater similarity to the Aboalimena and Bemaraha populations versus the Kirindy samples.

Further, on the basis of numerous external pelage characters clearly evident in Peters' (1852, pl. III) color illustration of *Microcebus myoxinus* and his measurements, his specimens from St. Augustin are rather close to ones from Aboalimena and Bemaraha, north of the Tsiribihina River. Instead of designating a neotype for the nomen *Microcebus myoxinus* based on a specimen collected north of the Tsiribihina River, we prefer to maintain the lectotype designated by Schwarz (1931). We restrict the range of *Microcebus myoxinus* to the region from the northern banks of the Tsiribihina River north at least to the Soalala Peninsula.

We are still faced with the question of the published distribution of *Microcebus myoxinus.* Peters (1852, p. 18) mentioned that the captain of another ship gave him the specimen from Bombetoka. Implicit this statement is the possibility that it was not collected at that site, but instead had been transported from another area of Madagascar. During this period there was a major trading center at Bombetoka (Okoth, 1993). Further, Peters (1852, p. 18) stated that the two specimens from St. Augustin were obtained via trading during his short stay at the site (''die beiden anderen erhandelte ich während meines kurzen Aufenthalts in der Bahia de S. Agostinho''). Accordingly, the specimens that Peters obtained in St. Augustin also might have been transported from another region of the island. St. Augustin is nearly 450 km south of the Tsiribihina River; there is no evidence that *Microcebus myoxinus* occurs south of it.

Martin (1995) mentioned that two specimens of mouse lemur collected at Namoroka and held in the Paris Museum (MNHN 1932.3370 and 1932.3373) are distinctly rufous in pelage. We have examined them. One is young without an associated skull, and the other is an adult with a damaged skull. On the basis of pelage coloration and certain cranial measurements the latter is referable to *Microcebus myoxinus.* There is another specimen from this locality in the American Museum of Natural History (AMNH 100665; Buettner-Janusch and Tattersall [1985]). A specimen held in The Natural History Museum, London, (BMNH 35.1.8.157) and taken at Ambararatabe [16°11′S, 45°58′E; *fide* Jenkins, 1987], Soalala Peninsula, is an example of *Microcebus myoxinus.*

Lectotype. Zoologisches Museum, Berlin, no. 319 (mounted skin), 14655 (skull); collected by W. Peters; as designated by Schwarz (1931).

Lectotype Locality. Given by Schwarz (1931) as Bahia de S. Agostinho (= Baie de St. Augustin), S. W. Madagascar. Here restricted to the region north of the Tsiribihina River, including the RNI de Bemaraha, and north to the Soalala Peninsula.

Emended Diagnosis. Medium-sized *Microcebus* with distinct rufous-brown dorsum, well-defined reddish-brown mid-dorsal stripe, and distinctly rufous-red markings on the head. Relatively short ears (18.0–23.0 mm) and M^1 (1.6–1.9 mm) as compared to the other species of western *Microcebus* with rufous backs. The fourth toe longer than third toe.

Referred Specimens. Province de Toliara, RNI de Bemaraha, 5 km E de Bekopaka, 19°06′S, 44°49′E, about 140 m above sea level (FMNH 161644-648, 161650-653); Province de Toliara, S du fleuve de Manambolo (Aboalimena), 19°15′S, 44°27′E, about 50 m above sea level (FMNH 165576-579); Province de Toliara, near Belo-sur-Tsiribihina, north side of river (FMNH 161669).

Distribution. Microcebus myoxinus is currently known from the northern banks of the Tsiribihina River north to the Soalala Peninsula.

Description. The proximal two-thirds of the dorsum of *Microcebus myoxinus* has bicolored, short, and dense Mikado Brown (121c) or Antique Brown (37) and Yellow Ochre (123c) or Cinnamon (39) fur–while the distal third tends to be slightly lighter Yellow Ochre (123c) and Chamois (123d). The well-delineated dorsal Tawny (38) stripe commences behind the shoulders and continues to the base of the tail. The anterior half of the belly, largely the midventral area has Chamois (123d) cover hairs, while the flanks and more distal portions are a mixture of pale Chamois (123d) and light Pale Neutral Gray (86). The dorsum and ventrum underfur is similarly colored Blackish Neutral Gray (82) or Plumbeous (78).

Microcebus myoxinus has a dull white and Cinnamon (39) patch between the eyes, reddish Buff (124) region posterior to the orbits, distinct dark eyebrows, and Tawny (38) crown and ears. The tail has short fur to the distal tip; the proximal 60–75 % has a bicolored dorsal surface of Tawny (38) and Cinnamon (39) and the ventral portion is Pale Horn (92) to Yellow Ochre (123c). The darker tail tip has a largely monocolored dorsal surface of Raw Umber (223) or bicolored Raw Umber (223) and Tawny (38) and a variable bicolored ventral pattern with the darker fur being Chamois (123d) or Antique Brown (37) and the lighter fur being Cinnamon (39) or Pale Neutral Gray (86). The furred portion of the hands and feet are whitish-gray or whitish-beige. Vibrissae are generally dark, though some of them in the mental region are light.

The skull of *Microcebus myoxinus* is slightly gracile with a tapered

and somewhat rounded rostrum (Fig. 7). When viewed laterally the frontal and nasal areas show no distinct concavity. Prosthion projection is not prominent. There is one pair of palatal fenestrae. Temporal lines fit the pattern of *Microcebus rufus* (Martin, 1995, p. 554). C height is short (2.0–2.6 mm) and blunt. The distal stylid of lingual cingulum is present but not well-developed. There is no diastema separating P^2 from C and P^3. P^5 is longer than P^3 and P^4. The protoconid of p_2 is caniform and at 45° relative to the mandibular axis. A stylar rim on p_2 and p_3 is present but not well-developed. There is a distinct basin below the protostylid of m_1; m_1 and m_2 are rectangular.

The fourth toe on the hindfoot is 10–12 mm and the third toe is 9–11 mm long; in our series the fourth toe is consistently 1–2 mm longer than the third toe. The mean value for the width of the grooming claw on the second toe is 1.1 mm (range 1.0–1.2 mm) and the width of the digital pad averages 3.0 mm (range 2.8–3.3 mm).

Comparisons and Remarks. Most of our specimens of *Microcebus myoxinus* are from two separate localities—near Aboalimena and the RNI de Bemaraha. On the basis of a series of ANOVA tests (Scheffé comparisons) there is no statistical difference found for any of the 49 variables, which include external, cranial, and postcranial measurements among individuals from the two sites. There is some variation in pelage coloration within the species that is continuous among specimens from Aboalimena and Bemaraha.

Individuals of *Microcebus ravelobensis* are differentiated from *M. myoxinus* on the basis of several characters. The tail length of *Microcebus myoxinus* averages 147.0 mm (range 132–155 mm, $n = 14$) versus 160.3 mm (range 144–172 mm, $n = 9$; ANOVA Scheffé test, P= 0.01) in *M. ravelobensis.* Ear length in *Microcebus myoxinus* is on average 21.2 mm (range 18.0–23.0 mm, $n = 15$), which is significantly shorter than that of *M. ravelobensis* (24.1 mm; range 22.5–25.0 mm, $n = 9$; ANOVA Scheffé test, $P < 0.0001$). Further, *Microcebus myoxinus* weighs less ($x = 49.0$ g, range 36.5–64.0 g, $n = 15$) than *M. ravelobensis* ($x = 71.7$ g, range 59.0–110 g, $n = 9$; ANOVA Scheffé tests, $P = 0.003$). Cranially and dentally *Microcebus myoxinus* is significantly smaller than *M. ravelobensis* in numerous measures (Table II). All of the humeral measurements in *Microcebus myoxinus* are smaller than those of *M. ravelobensis* (Table III). They are the only postcranial variables that are statistically significantly different between the two species.

Several characters separate *Microcebus myoxinus* from *M. tavaratra.* For example, in *Microcebus tavaratra* occipital length ranges from 4.2 to 5.2 mm and in *M. myoxinus* from 3.3 to 4.2 mm. Differences in other variables are statistically significance between them (ANOVA, based on

Scheffé comparisons), and in all cases *Microcebus myoxinus* is smaller than *M. tavaratra*: occipital length ($P = 0.04$), M^1 ($P = 0.02$), M^2 ($P = 0.004$), and lower postcanine tooth row ($P = 0.009$). Further, on the basis of genetic data the two species are well-differentiated (Yoder *et al.,* in press).

Mivart (1867) noted that "*Microcebus myoxinus* differs from *M. pusillus* [a synonym of *M. murinus* (Schwarz, 1931; Tattersall, 1982)] . . . in the greater production forwards of the premaxillae, the larger size of the openings in the palate, and also, possibly, in the somewhat longer symphysis of the mandible." A comparison of *Microcebus myoxinus* from north of the Tsiribihina River to *M. murinus* shows none of these characters to be consistent between the two species.

Notes on Natural History. Specimens collected in the RNI de Bemaraha, not far from Bekopaka, are from two different habitats within dry deciduous forest: the first site is on soil with little organic material and the second grows directly on rock outcrops. At Aboalimena we obtained specimens in the ecotone between savanna and heavily degraded dry deciduous forest. The third locality, close to the village of Andramasay (19°28′S, 44°29′E), north of Belo-sur-Tsiribihina, is 1–2 km inland and composed of dry deciduous forest.

There are recent observations of *Microcebus* in mangrove habitat in the Baly Bay area (Hawkins *et al.,* 1998), just to the north of Namoroka; we suspect that they are referable to *Microcebus myoxinus.* However, the Baly Bay area is directly west of Ankarafantsika, and it is possible that *Microcebus ravelobensis* is represented at the former site. Mouse lemurs observed in the Namoroka area were identified as *Microcebus murinus* by Hawkins *et al.* (1998), thus it appears that two different *Microcebus* occur at the site. There are reports from Bemaraha of two locally occurring species of *Microcebus* (Rakotoarison *et al.,* 1993; Thalmann and Rakotoarison, 1994; Ausilio and Raveloanrinoro, 1998), one of them *Microcebus murinus* and the other smaller and more rufous. The latter taxon is probably *M. myoxinus.* There is no specimen or photographic evidence for *Microcebus myoxinus* in the regions of Ankarafantsika or Analamera as suggested by Garbutt (1999).

Recent field research in the Kirindy/CFPF Forest revealed two species of syntopically occurring species of *Microcebus: M. murinus* and *M. myoxinus,* a name Schmid and Kappeler (1994) resurrected from synonymy. After comparison of the Kirindy/CFPF Forest specimens to other samples of *Microcebus* from western Madagascar, it is clear that the name *M. myoxinus* is applicable to the population of rufous mouse lemurs north of the Tsiribihina River (Table IV). In turn, no available name seems applicable to the Kirindy/CFPF population. Consequently, we propose to call it *Microcebus berthae.*

Microcebus berthae, new species (Fig. 8, color plate)

Holotype. FMNH 165580; adult female; skin, skull, partial skeleton; original number RMR 93; taken from the wild in 1995 or 1996 by Dorothea Schwab, died in captivity, and was prepared in January 1997 by R. M. Rasoloarison.

Standard measurements (in mm) recorded in the original field catalog and on the skin tag of the type: total length, 223; head and body length, 90; tail length, 134; hindfoot length, 29.0; and ear length, 17.0. Selected cranial measurements (in mm) are: greatest skull length, 29.3; skull width, 15.7; skull height, 13.8; palatal length, 11.3; condylobasal length, 25.9; zygomatic breadth, 17.3; nasal length, 7.5; occipital length, 3.6; C height, 1.6; and M^1 length, 1.5.

The skin, skull, and associated skeleton are generally in good condition. The specimen had been stored in a freezer for several months before it was prepared. A substantial patch of fur is missing from one of its flanks, and the pelage is matted in a few places. It is an adult female.

Type Locality. Madagascar: Province de Toliara, Forêt de Kirindy/CFPF, 60 km NE de Morondava, 20°04′S, 44°39′E, about 40 m above sea level.

Diagnosis. A diminutive rufous lemur with a well defined middorsal line. The region around the head is distinctly brighter rufous than the dorsum. Total length from 223–230 mm, hindfoot length 29.0–30.0 mm, and head-and-body length 90–95 mm. Greatest skull length (29.0–29.9 mm), condylobasal length (25.8–26.7 mm), zygomatic breadth (17.3–18.7 mm), C height (1.6–1.9 mm), as well as many other cranial and dental measurements

Table IV. Comparison of measurements (means ± standard deviations in mm) of the type of *Microcebus myoxinus,* the small rufous mouse lemur from Kirindy/CFPF, and specimens from north of the Tsiribihina River in the areas of Aboalimena and Bemaraha[a]

	Holotype of *myoxinus*	Kirindy/CFPF (n = 3)	Aboalimena and Bemaraha (n = 14)
Total length	About 300[b]	226.0 ± 3.60	272.9 ± 10.42
Tail length	150[b,c]	135.3 ± 2.31	147.0 ± 6.70
Ear length	24[d]	17.5 ± 0.50	21.2 ± 1.24
Greatest skull length	33[d]	29.4 ± 0.47	32.3 ± 0.63
Zygomatic breadth	21[d]	17.8 ± 0.75	19.9 ± 0.51
Nasal length	10[d]	7.9 ± 0.64	9.8 ± 0.53
Mandibular length	20[d]	16.9 ± 0.38	19.0 ± 0.43

[a]Measurements presented in the last two columns are from Tables I and II.
[b]Based on Elliot (1912).
[c]Given as 160 mm by Peters (1852).
[d]Based on Peters (1852).

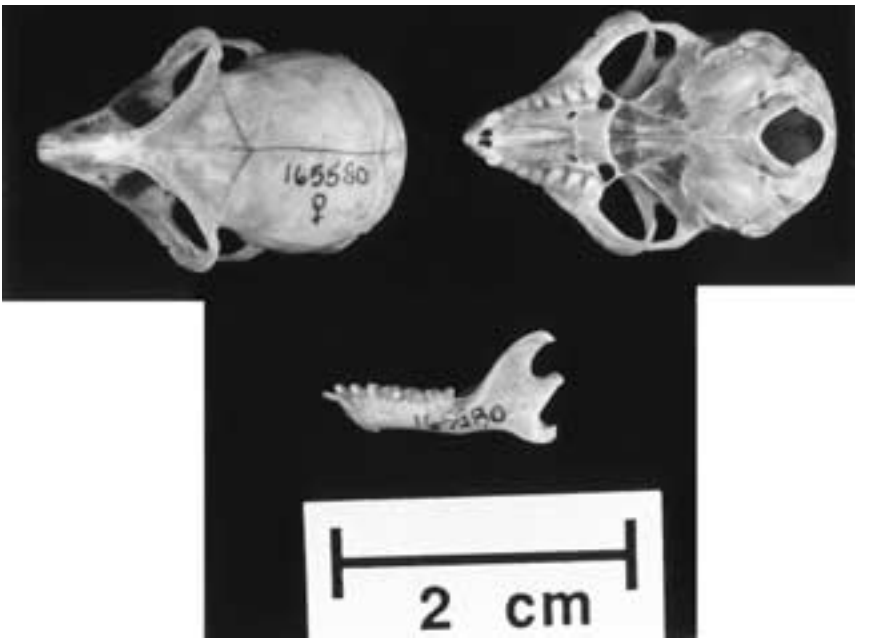

Fig. 8. Three views of *Microcebus berthae* nov. sp. (FMNH 165580). (**Upper left**) dorsal view of cranium (FMNH neg. Z 94292); (**upper right**) ventral view of cranium (FMNH neg. Z 94291); (**lower center**) lateral view of mandible (FMNH neg. Z 94293).

show no overlap with other *Microcebus* spp. The fourth and third toes of the hindfoot are equal in length.

Referred Specimens. Province de Toliara, Forêt de Kirindy/CFPF, 60 km NE de Morondava, 20°04′S, 44°39′E, about 40 m above sea level (FMNH 165581; RMR 92 housed in the Département de Paléontologie et d'Anthropologie Biologique, Université d'Antananarivo).

Distribution. Microcebus berthae is currently only known from the region surrounding the Kirindy/CFPF Forest and perhaps south to the RS d'Andranomena and north to the region of Analabe.

Description. The dorsal pelage of the species is dense and short and has a distinct bicolored appearance—composed of Cinnamon (123a) and Yellow Ochre (123c) fur. The middorsal Tawny (38) line is well defined and starts just behind the shoulders and descends to the tail tip. The anterior portion of the underside, particularly along the midventral area, is composed of Chamois (123d) cover hairs, while the flanks and other portions of the venter are a mixture of pale Chamois (123d) and light Pale Neutral Gray (86). The underfur of the lower and upper surfaces of the body is

Blackish Neutral Gray (82). The patch above the nose is dull white, the region around the eyes is Cinnamon (39), and the crown and ears are Tawny (38). A narrow black band surrounds the orbits. The tail is uniformly Tawny (38) with proximally short hair that becomes a bit more pilose posteriorly. The hands and feet are dull beige.

The coloration in the photo of "*Microcebus myoxinus*" [= *M. berthae*] published in Schmid and Kappeler (1994, Fig. 2b) is taken with a flash, and the back of the animal appears too reddish. Further, the light underside is bleached out. The color photograph printed in Mittermeier *et al.* (1994, plate 5a) of an animal at Analabe, north of Kirindy/CFPF Forest, is much closer to the natural coloration of *Microcebus berthae,* as is the color photo in Garbutt (1999, figure 87) from Kirindy/CFPF Forest.

None of the other *Microcebus* spp. that we describe possess as diminutive and gracile a skull as *M. berthae* (Fig. 8). The rostrum is relatively short and tapers to a slightly rounded tip. In lateral view the outline of the frontal and nasal area is distinctly concave. The prosthion projection is distinct. There is one pair of palatal fenestrae. The temporal lines fit the pattern of *Microcebus murinus* (Martin, 1995, p. 554). C is the shortest of any known *Microcebus* (1.6–1.9 mm) and distinctly blunt. The distal stylid of the lingual cingulum is present but not well-developed. All maxillary postcanine teeth are evenly spaced with no diastema and more-or-less the same length. The lower postcanine tooth row is the shortest (7.2–7.4 mm) of all known mouse lemur dentitions and does not overlap with the minimum measurement in any other species. The toothcomb is distinctly finer in shape and length than in other *Microcebus* spp. The protoconid of p_2 is caniform and at about 45° relative to the mandibular axis. Stylar rim on p_2 and p_3 present but not well developed; m_1 and m_2 are rectangular in shape.

Although our sample size is limited, the fourth and third toe on the hind foot measures consistently 9 mm. The values for the width of the digital pad are 2.1 mm and 2.6 mm and for the width of the grooming claw 0.9 mm and 1.1 mm.

Taxonomic Comments. The name *Lemur pusillus,* which Schwarz (1931) placed as a synonym of *Microcebus murinus,* could be an appropriate name for the Kirindy/CFPF Forest population of *Microcebus.* Schwarz (1931) designated a color plate in Audebert (1800, p. 19, pl. VIII) as the type of the species. One noticeable aspect of this illustration is the distinctly short ears; the Kirindy/CFPF Forest population has the shortest ears among western *Microcebus* (Table I). However, Audebert mentioned nothing about ear length in the text associated with the plate, and it is impossible to determine if the specimen from which the illustration was made, had distinctly short ears or this is the result of artistic license. Further, the pelage coloration presented in Audebert's plate shows none of the salient

characters of *Microcebus berthae.* Thus, we concluded that the name *pusillus* is not appropriate for this species.

The nomen *Prosimia minima* Boddaert 1784, was considered by Schwarz (1931) to be a synonym of *Microcebus murinus.* The type was designated by Schwarz (1931) as a plate in Brown (1776, pl. XLIV). Neither the coloration of the individual in the plate nor the accompanying text show or describe any of the distinguishing phenotypic characters of the Kirindy/CFPF Forest mouse lemur; the name is inappropriate to resurrect for them.

Recently Rumpler *et al.* (1998) published on the cytogenetics of *Microcebus myoxinus.* Their samples were from the Kirindy/CFPF Forest: they are referable to *Microcebus berthae.* Like *Microcebus murinus,* they have 66 chromosomes.

Notes on Natural History. The Kirindy/CFPF Forest is a well-studied region of dry deciduous forest (Ganzhorn and Sorg, 1996). Currently, *Microcebus berthae* is only known from the general Kirindy/CFPF region, where they occur sympatrically with *M. murinus* (Schmid and Kappeler, 1994). A *Microcebus* was captured in the RS d'Andranomena that closely fits the phenotypic characters of *Microcebus berthae,* and it probably occurs in forested areas to the south of the Kirindy/CFPF Forest (J. Ganzhorn, unpublished). A photograph of a small rufous mouse lemur from Analabe, a few km NW of Kirindy/CFPF (Mittermeier *et al.,* 1994, pl. 5a) seems to be *Microcebus berthae.* Specimens of *Microcebus murinus* have been identified from Beroboka (see p. 994), which is adjacent to the Analabe Forest.

Etymology. The species is named in honor of Madame Berthe Rakotosamimanana. She has been the Malagasy coordinator of research activities (in collaboration with the Deutsches Primantenzentrum) in the Kirindy/CFPF Forest since 1987. Madame Berthe, as she is known by hundreds of foreign researchers who have worked on Madagascar over the past 25 years and literally thousands of Malagasy students who have sought their degrees at the Université d'Antananarivo, has been one of the major forces in the advancement of Malagasy zoology, and in particular primatology.

Vernacular Names. Berthe's Mouse Lemur or Microcèbe de Berthe.

Microcebus griseorufus Kollman, 1910 (Fig. 9, color plate)

Kollman (1910) described a new subspecies *Microcebus minor griseorufus*, characterized by: "Grandes oreilles [large ears]; dos gris roussâtre [reddish-gray back]; queue également roussâtre, mais *plus claire* [his italics] que le dos" [tail uniformly reddish, but much lighter than the back]. He gave its geographic range as the southeast, south, and southwest of Madagascar.

Fig. 9. Three views of *Microcebus griseorufus* (FMNH 161642). (**Upper left**) dorsal view of cranium (FMNH neg. Z 94266); (**upper right**) ventral view of cranium (FMNH neg. Z 94267); (**lower center**) lateral view of mandible (FMNH neg. Z 94254).

Neither Kollman (1910) nor subsequent revisers of the genus (Schwarz, 1931) listed a holotype.

In the MNHN, Paris, there are five fluid preserved specimens in a jar labeled *Microcebus minor griseorufus*, which bears the museum catalog number 1912.13. There is no locality information on the associated specimen tag. One individual has the skull removed, which could not be located in the collection. We strongly suspect that they are the material that Kollman (1910) used to describe *Microcebus minor griseorufus.* However, given that there is no clear trace connecting Kollman's name to these specimens and all the material lacks locality information, we prefer to designate a neotype. Following the rules of the International Code of Zoological Nomenclature (1985), article 75, the designation of a neotype in this case is essential in order to solve a detailed taxonomic problem. The name *Microcebus minor* is a synonym of *M. murinus* (Tattersall, 1982); therefore, we elevate *Microcebus minor griseorufus* to a full species.

Designation of Neotype. FMNH 161642; adult male; skin, skull, partial skeleton, and preserved tissues; original number RMR 68; collected 6 April 1997 by R. M. Rasoloarison.

Standard measurements (in mm, except for mass) recorded in the original field catalog and on the skin tag of the neotype include total length, 280; head and body length, 126; tail length, 153; hindfoot length, 33.0; ear length, 25.0; and mass, 55.5 gm. Selected cranial measurements (in mm) are: greatest skull length, 31.7; skull width, 16.3; skull height, 14.2; palatal length, 12.1; condylobasal length, 28.1; zygomatic breadth, 20.2; nasal length, 8.7; occipital length, 4.0; C height, 2.3; and M^1 length, 1.6.

The skin, skull, and associated skeleton are in good condition. The testes measured 9.1 × 5.0 mm and the epididymis is convoluted.

Designated Neotype Locality. Madagascar: Province de Toliara, au Nord de la Réserve Spéciale (RS) de Beza Mahafaly, Forêt d'Ihazoara, 7 km SE de Taolambiby, 23°41′S, 44°38′E, about 130 m above sea level.

Emended Diagnosis. A distinctly colored diminutive species with largely gray dorsum contrasting with cinnamon brown middorsal stripe and tail, and rufous washed markings on head. Venter white, including underfur. Easily distinguished from *Microcebus murinus,* the only other grayish mouse lemur in western Madagascar, on the basis of external, cranial, and dental measurements. Numerous characters allow separation of *Microcebus griseorufus* from *M. berthae,* the other diminutive species of western Madagascar. For example, in these two species respective total lengths range from 253 to 280 mm and from 223 to 230 mm, ear lengths from 23.0 to 25.0 mm and from 17.0 to 18.0 mm, and greatest skull length from 29.9 to 31.7 mm and from 29.0 to 29.9. In *Microcebus griseorufus* the fourth hind toe is longer than the third hind toe.

Referred Specimens. Province de Toliara, au Nord de la Réserve Spéciale (RS) de Beza Mahafaly, Forêt d'Ihazoara, 7 km SE de Taolambiby, 23°41′S, 44°38′E, about 130 m above sea level (FMNH 161638-641, 161643).

Distribution. Microcebus griseorufus is currently known from the region around the RS de Beza Mahafaly, near Toliara, and to the north at least to Lamboharana. However, its range may include regions further to the south and southeast of the island.

Description. Microcebus griseorufus from Beza Mahafaly have striking and highly contrasting bicolored or tricolored short and dense dorsal cover hairs—Light Neutral Gray (85), Pale Neutral Gray (86), and light Pale Neutral Gray (86). The Cinnamon (123a) back stripe is laterally diffused and commences in some individuals at the crown and in others at the level of the shoulders and runs to the terminus of the tail. The anterior two-thirds of the venter is a contrasting light grayish-white, and the posterior portion merges towards a bicolored light grayish-white and a light Pale Neutral Gray (86). The change in pelage coloration of the dorsum and ventrum is abrupt and forms a well-demarcated line along the flanks and limbs. The underfur of the dorsal pelage is slightly darker than Dark Neutral Gray (83), while the underfur of the ventral surface is distinctly white, particularly along the midventral area, and laterally a salt and pepper mixture of white and Dark Neutral Gray (83). In a few individuals, e.g., FMNH 161643, the underfur and cover hairs of the ventrum are wholly white. The head of *Microcebus griseorufus* has a strikingly Pale Neutral Gray (86) patch above the nose, Cinnamon (39) area surrounding much of the eyes, excluding the area anterior to the eyes, Clay Color (123b) crown, and light Neutral Gray (86) ears. The upper surface of the tail is a uniform Cinnamon (123a), while approximately two-thirds of the lower portion of the tail is grayish-beige and distal one-third is a Cinnamon (123a) with faint brownish black streaks. The fur at the base of the tail is short and dense and becomes feathery towards the tip. The furred portions of the hands and feet are grayish-white. Vibrissae are largely dark. The subadult pelage is unknown.

The skull of *Microcebus griseorufus* is robust for such a small mouse lemur; the rostrum is broad at the base and tapers to a blunt tip (Fig. 9). In lateral view the outline of the frontal and nasal area is distinctly concave. Prosthion projection is only slightly developed. Most specimens have two pairs of palatal fenestrae; the first pair is medial to M^1 and relatively small, and the second pair (present in all individuals) is medial and posterior to M^3 and at the posterior edge of palate. Temporal lines fit the pattern of *Microcebus rufus* (Martin, 1995, p. 554). C is proportionately long (2.2–2.4 mm) for such a small *Microcebus* and distinctly pointed; the distal stylid of the lingual cingulum is present and well-developed. There is a small diastema separating C and P^3, and the balance of teeth are evenly spaced

and more-or-less the same length. The protoconid of p_2 is caniform and approaching a vertical position relative to the mandibular axis. There is a stylar rim on p_2 and p_3 but it is not well-developed. There is a distinct basin below the protostylid of m_1; m_1 and m_2 are distinctly square versus the typical elongated rectangle.

In our six specimens of *Microcebus griseorufus* from Beza Mahafaly the fourth hind toe consistently measures 10 mm and the third hind toe 9 mm. The width of the digital pad on the first hind toe is on average 2.7 mm (range 2.5–2.8 mm) and width of the grooming claw on the second hind toe 1.0 mm (range 1.0–1.1 mm).

Other Specimens. A specimen in the MNHN, Paris (1986.1213), collected near Lamboharana [22°12′S, 43°14′E] by B. Koechlin, has a distinctly gray back, white underside (including underfur), and reddish markings on the head—all characters that fit closely with *Microcebus griseorufus.* Measurements noted on the specimen label include: head and body length 115 mm; tail length 135 mm, hindfoot length 30.0 mm, and ear length 28.0 mm. Further, on the basis of a principal components analysis of several external and cranial measurements, the specimen falls within the range of *Microcebus griseorufus* from Ihazoara, instead of *M. murinus* (Fig. 10). Lamboharana is approximately 200 km northwest of Beza Mahafaly. Two specimens in The Natural History Museum, London, collected 20 miles

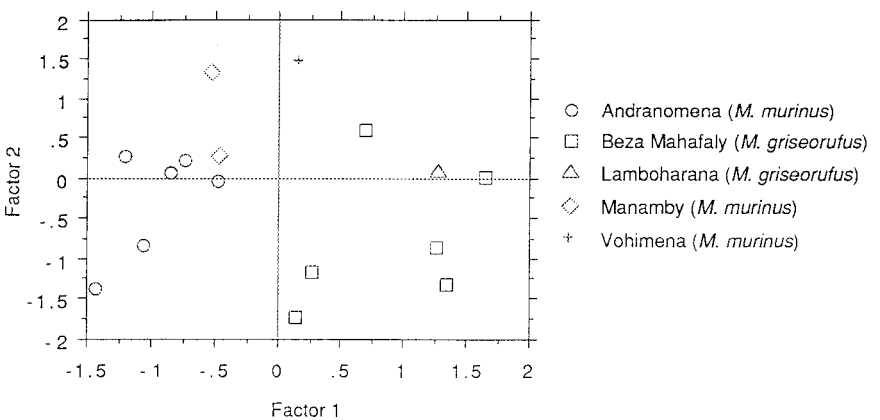

Fig. 10. Plot of factor axis 1 versus factor axis 2 of principal components analysis derived from several external, cranial, and dental measurements of a specimen of *Microcebus* (MNHN 1968.1213) obtained at Lamboharana; *M. murinus* from Andranomena, Vohimena, and Manamby; and *M. griseorufus* from the Beza Mahafaly area. The specimen from Lamboharana groups with *M. griseorufus.*

[= 32 km] SE Tulear (BMNH 48.175 and 48.176) are referable to *Microcebus griseorufus* on the basis of pelage coloration and cranial measurements.

There is no means to associate the 5 fluid preserved specimens of *Microcebus griseorufus* in the single jar labeled MNHN 1912.13. The Catalogue Générale of MNHN, Paris, shows an accession of several mouse lemur specimens in the same lot and identified as "*Microcebus minor griseorufus* M. Koll:" MNHN 1912.2 from Tullear, MNHN 1912.3 with no locality information, MNHN 1912.5 from Manombaro, MNHN 1912.10 from Ankeramena, and MNHN 1912.16 from Ankebo. Since the preserved specimens bear no collection site datum or individual catalog numbers, we can not link them with the catalog entries. However, the sites encompass Kollman's (1910) geographic range for *Microcebus griseorufus.*

On the basis of specimens with locality data, we conclude that *Microcebus griseorufus* occurs in a broad region of southwestern Madagascar from at least Lamboharana, south to the Toliara region, and southeast to Beza Mahafaly. These localities include sites on the opposite sides of the Onilahy and Fiherenana rivers. However, the geographic range of the species may include areas much further south and east.

Notes on Natural History. Our specimens of *Microcebus griseorufus* are from in the Ihazoara Valley, a few km from the limit of the RS de Beza Mahafaly. The habitat of the RS de Beza Mahafaly is typical of subarid thorn scrub of the southern domain (Nicoll and Langrand, 1989; Lowry *et al.,* 1997). The area is composed of two natural forest types: gallery forest and dry thorn scrub (= spiny forest). The Ihazoara region, just across

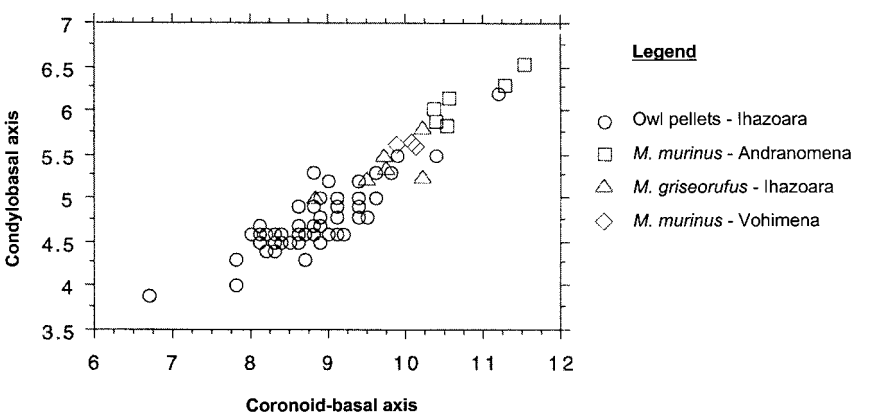

Fig. 11. Plot of coronoid–basal axis versus condylobasal axis mandibular measurements of *Microcebus* obtained from owl pellets in the Beza Mahafaly region, *M. griseorufus* from the Ihazoara Valley, and *M. murinus* from Andranomena and Vohimena.

Table V. Standardized canonical coefficients for four different discriminant function analyses[a]

	A		B		C		D	
	Function 1	Function 2	Function 1	Function 2	Function 1	Function 2	Function 1	Function 2
Ear length	—	—	—	—	—	—	0.897	−0.317
Head and body length	—	—	—	—	—	—	0.545	−0.104
Hindfoot length	—	—	—	—	—	—	0.572	0.605
Tail length	—	—	—	—	—	—	−0.192	0.392
Total length	—	—	—	—	—	—	−0.047	0.034
Basal skull length	2.266	2.356	0.268	0.615	—	—	—	—
Condylobasal length	5.931	−0.018	−0.288	1.715	—	—	—	—
Frontal length	0.793	1.405	0.120	0.955	—	—	—	—
Greatest orbital diameter	4.050	−0.017	0.634	0.634	—	—	—	—
Greatest skull length	−11.172	−2.178	−0.378	−2.473	—	—	—	—
Mandibular length	0.500	−1.390	—	—	—	—	—	—
Nasal length	−0.758	0.316	−0.134	−0.213	—	—	—	—
Nasal width	−1.845	0.779	−0.896	0.576	—	—	—	—
Occipital length	−0.403	−1.373	0.574	0.018	—	—	—	—
Occipital width	−1.499	−0.171	−0.145	−0.404	—	—	—	—
Transverse orbital diameter	−5.092	−1.062	−0.423	−1.145	—	—	—	—
Palatal length	3.988	0.933	1.267	0.569	—	—	—	—
Palatal width	−1.340	−2.057	0.792	−1.606	—	—	—	—
Parietal length	4.364	0.689	1.118	1.063	—	—	—	—
Parietal width	4.444	0.495	0.865	0.585	—	—	—	—
Skull height	−0.324	0.629	−0.648	0.003	—	—	—	—
Skull width	−0.607	−0.569	−0.242	−0.345	—	—	—	—

Temporal fossa greatest length	0.251	−1.368	−0.480	0.030	—	—	—	—
Temporal line	0.175	−1.438	0.610	0.195	—	—	—	—
Zygomatic breadth	2.590	2.496	−0.274	1.931	—	—	—	—
C	2.678	0.828	—	—	—	—	—	—
I^1	−0.632	−0.873	—	—	—	—	—	—
I^2	2.323	1.106	—	—	—	—	—	—
M^1	0.927	0.382	—	—	—	—	—	—
M^2	2.083	1.608	—	—	—	—	—	—
M^3	0.601	0.023	—	—	—	—	—	—
P^2	−1.647	1.264	—	—	—	—	—	—
P^3	0.721	0.462	—	—	—	—	—	—
P^4	0.943	−0.018	—	—	—	—	—	—
Femoral length	—	—	—	—	0.664	−1.223	—	—
Femoral width distal	—	—	—	—	−0.055	−0.220	—	—
Femoral width proximal	—	—	—	—	0.533	−0.054	—	—
Humeral length	—	—	—	—	0.413	0.310	—	—
Humeral width distal	—	—	—	—	0.342	0.858	—	—
Humeral width proximal	—	—	—	—	−0.338	0.575	—	—
Pelvic length	—	—	—	—	−0.974	0.456	—	—
Tibial width proximal	—	—	—	—	0.275	−0.419	—	—
Trochanteric height	—	—	—	—	0.587	0.024	—	—
% variance—factor 1	63.9		69.2		52.8		80.9	
% variance—factor 2[b]	16.4 (80.4)		15.0 (84.1)		24.4 (77.3)		10.2 (91.1)	
% variance—factor 3	14.1 (94.4)		6.2 (90.3)		8.8 (86.1)		7.3 (98.4)	

[a]Column headings refer to plots A—cranial and tooth measurements, B—cranial measurements, C—postcranial measurements, and D—external measurements of Fig. 12. A dash indicates that the variable was not used. Cumulative percentage in parentheses.

the Sakamena River Valley from the reserve, has typical elements of spiny forest habitat, though somewhat degraded through human and cattle activities. The locally occurring species of *Microcebus* that had been previously noted in the RS de Beza Mahafaly is *Microcebus murinus* (Tattersall, 1982; Nicoll and Langrand, 1989; Mittermeier *et al*., 1994).

The two specimens of *Microcebus griseorufus* from near Toliara and now in The Natural History Museum were obtained by C. S. Webb and have associated habitat information. BMNH 48.176 is from dry rocky scrub country and BMNH 48.175 was in thick scrub 6–10 ft [1.9–3.1 m] high: region dry and stony; bushes bare or with tiny leaves; vegetation mainly euphorbias, Didierea, and dwarf mimosas.

The Ihazoara Valley and Beza Mahafaly have been the sites of studies on the food habitats of two different species of owls, *Tyto alba* and *Asio madagascariensis*, both of which feed extensively on *Microcebus* (Goodman *et al*., 1993a, 1993b). We collected a sample of mouse lemur mandibles from owl pellets at these sites. A plot of two different mandibular measurements from these mandibles and specimens collected by Rasoloarison in the Ihazoara Valley (*Microcebus griseorufus*) and Andranomena and Vohimena (*M. murinus*), shows that the vast majority of mouse lemurs taken by the owls fall within the size range of *M. griseorufus* (Fig. 11). Some of the mandibles are smaller than those of typical adult *Microcebus griseorufus*; they probably represent subadults of the species. There is one mandible from the prey samples that fits with *Microcebus murinus.* Thus it appears that *Microcebus griseorufus* and *M. murinus* occur sympatrically in the Ihazoara Valley area, and the former is a more common prey item of owls.

MORPHOLOGICAL VARIATION

On the basis of pelage coloration and external, cranial, dental, and postcranial variables in various combinations, we have characterized and delimited 7 species of *Microcebus* in western Madagascar. The choice of characters used to define the species is not consistent among the different taxa largely because we aimed to simplify the diagnoses of the various species, but also due to the large number of variables associated in our analysis.

We also employed multivariate analysis to determine whether it retains the groupings of our species based on various morphological characters. We conducted four different discriminant function analyses. The first analysis used 29 cranial and tooth variables, the standardized canonical coefficients of which are in Table V (column A). When the first and second

functions are plotted against one another (Fig. 12a) the 7 species form distinct groups. Specimens from Ankarafantsika (*Microcebus ravelobensis*), Beza Mahafaly (*M. griseorufus*), and Kirindy (*M. berthae*) comprise three distinct clouds of points. Specimens of *Microcebus myoxinus* from Aboalimena and Bemaraha form a continuous cluster, and they are distinct from Ankarana *Microcebus tavaratra.* These relationships are also supported by genetic data (Yoder *et al*., in press). Two geographically disjunct populations of *Microcebus murinus* from Andranomena and Vohimena are closer to one another than to any other population of mouse lemur. However, there is some separation between them, which is concordant with genetic data that indicates some geographic variation in this broadly distributed species (Yoder *et al.,* in press). Further, the genetic data shows that within the western populations of mouse lemurs there are two distinct clades: (1) individuals that we defined as *Microcebus murinus* (Andranomena and Vohimena) and those of *M. griseorufus* (Beza Mahafaly), and (2) all of the other populations to the north. The separation is clear within the discriminant function analysis. The first function explained 63.9% of the variance, the second function an additional 16.4%, and third function an additional 14.1% (Table V).

We conducted the second discriminant function analysis with 19 cranial variables—the standardized canonical coefficients are in Table V (column B). In a plot of the first and second functions against one another (Fig. 12b) there is less separation at the level of our defined species as compared to a combination of cranial and dental variables, but most of the species groupings remain clear. Specimens from Aboalimena are completed embedded in those from Bemaraha. Cranial variables show broad separation between the *murinus* clade (composed of *Microcebus murinus* from Andranomena and Vohimena and *M. griseorufus* from Beza Mahafaly) and the *rufus* group composed of numerous species further north. The first function explains 69.2% of the variance, the second function an additional 15.0%, and the third function an additional 6.2%.

The subsequent discriminant function analysis was conducted using 9 postcranial osteological measurements—the standardized canonical coefficients are in Table V (column C). In a plot of the first and second functions against one another (Fig. 12c) there is little separation among populations and the 7 species. Further, evidence of distinction between the *murinus* and *rufus* clades collapsed. The first function explains 52.8% of the variance, the second function an additional 24.4%, and the third function an additional 8.8%.

The fourth discriminant function analysis involved five external variables—the standardized canonical coefficients are in Table V (column D). With the exception of specimens from Kirindy (*Microcebus berthae*) and

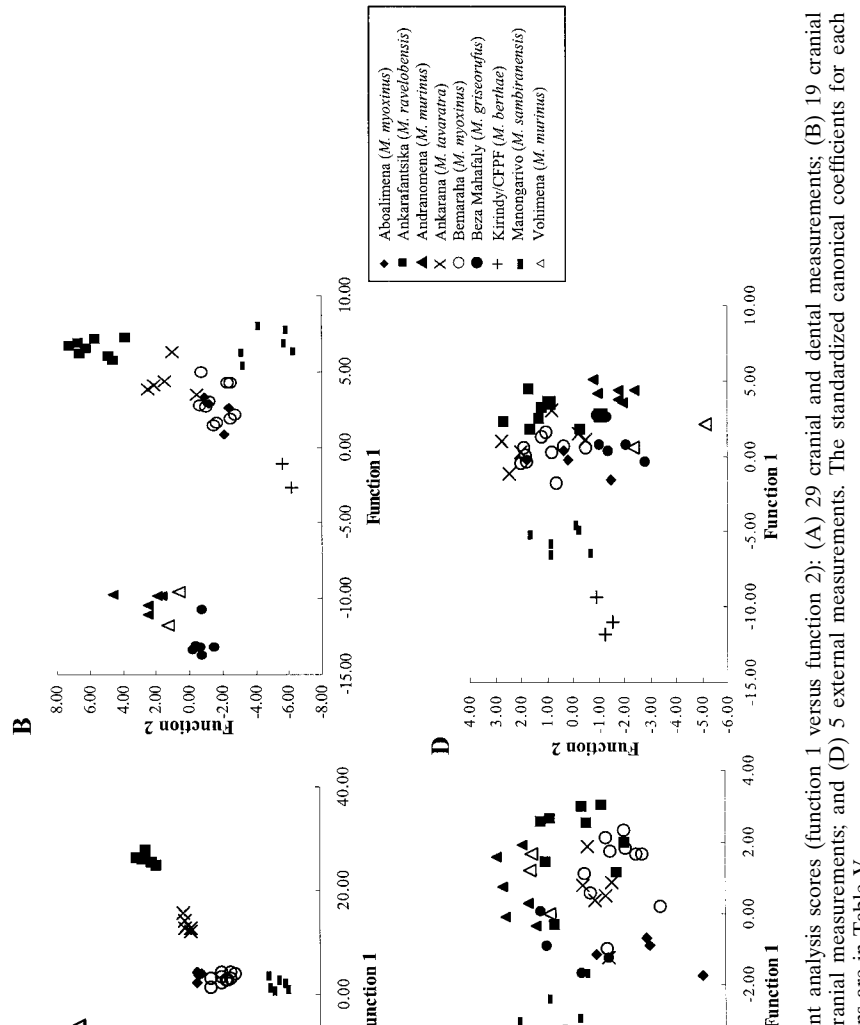

Fig. 12. Plots of discriminant analysis scores (function 1 versus function 2): (A) 29 cranial and dental measurements; (B) 19 cranial measurements; (C) 9 postcranial measurements; and (D) 5 external measurements. The standardized canonical coefficients for each variable in these comparisons are in Table V.

Manongarivo (*M. sambiranensis*), a plot of the scores of the first and second functions shows a more-or-less continuous cloud of points with very little structure associated with the delimitation of the 7 species (Fig. 12d). The first function explains 80.9% of the variance, the second function an additional 10.2%, and the third function an additional 7.3%.

CONCLUSION

Madagascar is the focus of world attention associated with the effects of human related habitat destruction of the island's unique biological diversity. Primates are the most important hallmark for the plight of Madagascar's rapidly dwindling natural forests and the hypothesized wave of extinction that will take place unless the situation is ameliorated. We have reviewed the systematics of mouse lemurs (*Microcebus*) across the western portion of Madagascar. Within this zone there are at least 7 species of mouse lemur. On the basis of preliminary data we strongly suspect that a parallel pattern of several previously unrecognized taxa will also be found along the eastern portion of the island (Yoder *et al*., in press). Numerous researchers have noted remarkable variation between populations of both *Cheirogaleus major* and *C. medius*, and these two species may include other unrecognized taxa (Groves, 2000). The question of how many species of *Lepilemur* should be recognized is still unresolved (Bachmann *et al.,* 2000). These observations in combination with discoveries of other new primate species over the past 15 years (Meier *et al*., 1987; Simons, 1988), show how little is really known about the specific limits and distribution of Malagasy primates. Given the high rates of deforestation on Madagascar, the next few decades may be our last chance to at least partially understand what exists over significant portions of the island. New collections are important to document and archive aspects of the remaining biodiversity of Madagascar.

ACKNOWLEDGMENTS

This study would not have been possible without the assistance and collaboration of several institutions and individuals. Firstly, we are grateful to the Commission Tripartite for issuing the requested research and export permits. Madame Berthe Rakotosamimanana provided guidance and aid during this project. For access to museum specimens we wish to acknowledge Jacques Cuisin, Laurent Granjon and Michel Trainer, Muséum National d'Histoire Naturelle, Paris; Felix Rakotondraparany, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo; Manfred Ade, Zoologisches

Museum, Berlin; and Paula Jenkins, The Natural History Museum, London. Photographs of the prepared skulls were taken by John Weinstein, Photography Department, Field Museum of Natural History. Peggy MacNamara kindly painted the color plate for this publication. Over the course of this project discussions with Sylvia Atsalis, Marion Dagosto, Jack Fooden, Peter Kappeler, Matthew Ravosa, Brian Shea, and Anne Yoder helped to clarify many points. The field and museum work was funded by Conservation International, Deutsche Forschungsgemeinschaft, Deutsches Primantenzentrum, Field Museum of Natural History, The John D. and Catherine T. MacArthur Foundation, Margot Marsh Biodiversity Foundation, Primate Action Fund, and World Wide Fund for Nature. This paper benefited by the comments of two anonymous reviewers.

REFERENCES

Atsalis, S., Schmid, J., and Kappeler, P. M. (1996). Metrical comparisons of three species of mouse lemur. *J. Human Evol.* 31: 61–68.

Audebert, J. (1800). *Histoire naturelle des singes et des makis.* Paris.

Ausilio, E., and Raveloanrinoro, G. (1998). Les Lémuriens de la région de Bemaraha: Forêts de Tsimembo, de l'Antsingy et de la région de Tsiandro. *Lemur News* 3: 4–7.

Bachmann, L., Rumpler, Y., Ganzhorn, J. U., and Tomiuk, J. (2000). Genetic differentiation among natural populations of *Lepilemur ruficaudatus. Int. J. Primat.* 21: 853–864.

Buettner-Janusch, J., and Tattersall, I. (1985). An annotated catalogue of Malagasy primates (Families Lemuridae, Indriidae, Daubentoniidae, Megaladapidae, Cheirogaleidae) in the collections of the American Museum of Natural History. *Am. Mus. Nov.* 2834: 1–45.

Bourgeat, F. (1972). Sols sur socle ancien à Madagascar. *Mémoires ORSTOM* 57: 1–335.

Burney, D. A. (1997). Theories and facts regarding Holocene environmental change before and after human colonization. In Goodman, S. M., and Patterson, B. D. (eds.), *Natural change and human impact in Madagascar,* Smithsonian Institution Press, Washington, DC, pp. 75–89.

Colquhoun, I. C. (1998). The lemur community of Ambato Massif: An example of the species richness of Madagascar's classified forests. *Lemur News* 3: 11–14.

Du Puy, B., Abraham, J. P., and Cooke, A. J. (1994). Les plantes. In Goodman, S. M., and Langrand, O. (eds.), Inventaire biologique, Forêt de Zombitse. *Recherches pour le Développement, série Sciences biologiques, no. spécial.* Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, pp. 15–29.

Du Puy, D. J., and Moat, J. (1996). A refined classification of the primary vegetation of Madagascar based on the underlying geology: using GIS to map its distribution and to assess its conservation status. In Lourenço, W. R. (ed.), *Biogéographie de Madagascar,* ORSTOM Editions, Paris, pp. 205–218.

Elliot, D. G. (1912). *A review of the primates.* American Museum of Natural History, New York.

Fietz, J. (1998) Body mass of wild *Microcebus murinus* over the dry season. *Folia Primatol.* 69 (Suppl. 1): 183–190.

Ganzhorn, J. U. (1994). Les lémuriens. In Goodman, S. M., and Langrand, O. (eds.), Inventaire biologique, Forêt de Zombitse. *Recherches pour le Développement, série Sciences biologiques, no. spécial.* Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, pp. 70–72.

Ganzhorn, J. U., and Schmid, J. (1998). Different population dynamics of *Microcebus murinus* in primary and secondary deciduous dry forests of Madagascar. *Int. J. Primat.* 19: 785–796.

Ganzhorn, J. U., and Sorg, J.-P. (1996). Ecology and economy of a tropical dry forest in Madagascar. *Primate Report* 46–1: 1–382.

Garbutt, N. (1999). *Mammals of Madagascar.* Pica Press, Sussex.

Goodman, S. M., Langrand, O., and Rasoloarison, R. (1997). Les lémuriens. In Langrand, O., and Goodman, S. M. (eds.), Inventaire biologique, Forêt de Vohibasia et d'Isoky-Vohimena. *Recherches pour le Développement, série Sciences biologiques*, no. 12. Centre d'Information et de Documentation Scientifique et Technique, Antananarivo, pp. 156–161.

Goodman, S. M., Langrand, O., and Raxworthy, C. J. (1993a). Food habits of the Madagascar Long-eared Owl *Asio madagascariensis* in two habitats in southern Madagascar. *Ostrich* 64: 79–85.

Goodman, S. M., Langrand, O., and Raxworthy, C. J. (1993b). The food habits of the Barn Owl *Tyto alba* at three sites on Madagascar. *Ostrich* 64: 160–171.

Goodman, S. M., and Schütz, H. (in press). The lemurs of the northeastern slopes of the Réserve Spéciale de Manongarivo. *Lemur News.*

Groves, C. P. (1993). Order Primates. In Wilson, D. E., and Reeder, D. M. (eds.), Mammal species of the world: a taxonomic and geographic reference, 2nd ed., Smithsonian Institution Press, Washington, DC, pp. 243–277.

Groves, C. P. (2000). The genus *Cheirogaleus*: unrecognized biodiversity of dwarf lemurs. *Int. J. Primatol.* 21: 943–962.

Harcourt, C., and Thornback, J. (1990). *Lemurs of Madagascar and the Comoros. The IUCN Red Data Book.* IUCN and The World Conservation Union, Gland, Switzerland and Cambridge.

Hawkins, A. F. A., Chapman, P., Ganzhorn, J. U., Bloxam, Q. M. C., Barlow, S. C., and Tonge, S. J. (1990). Vertebrate conservation in Ankarana Special Reserve, northern Madagascar. *Biol. Conserv.* 54: 83–110.

Hawkins, A. F. A., Durbin. J. C., and Reid, D. B. (1998). The primates of the Baly Bay area, north-western Madagascar. *Folia Primatol.* 69: 337–345.

Hershkovitz, P. (1977). *Living New World Monkeys* (*Platyrrhini*): *With an Introduction to Primates,* Vol. 1. University of Chicago Press, Chicago.

Hill, W. C. O. (1953). *Primates: Comparative Anatomy and Taxonomy. 1. Strepsirhini.* University Press, Edinburgh.

Hladik, C. M., Charles-Dominique, P., and Petter, J.-J. (1980). Feeding strategies of five nocturnal prosimians in the dry forest of the west coast of Madagascar. In Charles-Dominque, P., Cooper, H. M., Hladik, A., Hladik, C. M., Pages, E., Pariente, G. F., Petter-Rousseaux, Petter, J.-J., and Schilling, A. (eds.), *Nocturnal Malagasy Primates: Ecology, Physiology, and Behavior.* Academic Press, New York, pp. 41–73.

Hladik, C. M., Pinte, M., and Simmen, B. (1998). Les densités de population des prosimiens nocturnes du Sud de Madagascar varient-elles à long terme dans les réserves forestiéres accessibles au public? *Rev. Ecol.* (*Tierre Vie*) 53: 181–185.

Humbert, H. (1965). 1965. Description des types de végétation. In Humbert, H. and Cours Darne, G. (eds.), Notice de la carte de Madagascar Vol. 6. *Travaux de la Section Scientifique et Technique de l'Institut Français de Pondichéry* (hors série), pp. 46–78.

International Code of Zoological Nomenclature. (1985). *International Code of Zoological Nomenclature,* third edition. International Trust for Zoological Nomenclature, London.

Jenkins, P. D. (1987). *Catalogue of primates in the British Museum* (*Natural History*) *and elsewhere in the British Isles. Part IV: Suborder Strepsirrhini, including the subfossil Madagascan lemurs and Family Tarsiidae.* British Museum (Natural History), London.

Jenkins, P. D., and Albrecht, G. H. (1991). Sexual dimorphism and sex ratios in Madagascan prosimians. *Am. J. Primat.* 24: 1–14.

Kappeler, P. M. (1990). The evolution of sexual size dimorphism in prosimian primates. *Am. J. Primat.* 21: 201–214.

Koechlin, J., Guillaumet, J.-L., and Morat, P. (1974). *Flore et végétation de Madagascar.* J. Cramer, Vaduz.

Kollman, M. (1910). Note sur les genres *Chirogale* et *Microcebus. Bull. Mus. Nat. d'Hist. Natur., Paris* 16: 301–304.

Lowry, P. P., II, Schatz, G. E., and Phillipson, P. B. (1997). The classification of natural and anthropogenic vegetation in Madagascar. In Goodman, S. M., and Patterson, B. D. (eds.), *Natural change and human impact in Madagascar,* Smithsonian Institution Press, Washington, DC, pp. 93–123.

Major, C. I. F. (1894). Über die malagassischen lemuriden-gattungen *Microcebus, Opolemur,* und *Chirogale. Novit. Zoolog.* 1: 2–39.

Martin, R. D. (1972). A preliminary field-study of the Lesser Mouse Lemur (*Microcebus murinus,* J. F. Miller, 1777). *Zeitschr. Tierpsych.,* Beiheft, 9: 43–89.

Martin, R. D. (1995). Prosimians: from obscurity to extinction? In Alterman, L., Doyle, G. A., and Izard, M. K. (eds.), *Creatures of the Dark: The Nocturnal Prosimians.* Plenum Press, New York, pp. 535–563.

Meier, B., Albignac, R., Peyriéras, A., Rumpler, Y., and Wright, P. (1987). A new species of *Hapalemur* (Primates) from south east Madagascar. *Folia Primatol.* 48: 211–215.

Mittermeier, R. A., Tattersall, I., Konstant, W. R., Meyers, D. M., and Mast, R. B. (1994). *Lemurs of Madagascar.* Conservation International, Washington, DC.

Mivart, St. George. (1867). Additional notes on the osteology of the Lemuridae. *Proc. Zool. Soc. Lond.* 1867: 960–975.

Morat, P. (1973). Les savanes du sud-ouest de Madagascar. *Mémoires ORSTOM* 68: 1–230.

Napier, J. R., and Napier, P. H. (1967). *A Handbook of Living Primates.* Academic Press, London.

Nicoll, M. E., and Langrand, O. (1989). *Madagascar: Revue de la Conservation et des Aires Protégées.* WWF, Gland.

Okoth, P. G. (1993). Nineteenth century food trade in the western Indian Ocean. *Omaly sy Anio* 37-38: 167–180.

Peters, W. C. H. (1852). *Naturwissenschaftliche Reise nach Mossambique.* Georg Reimer Verlag, Berlin.

Petter, J.-J. (1962). Recherches sur l'écologie et l'éthologie des lémuriens malgaches. *Mém. Mus. Nat. d'Hist. Nat., sér.* A (Zoologie) 27: 1–146.

Petter, J.-J., Albignac, R., and Rumpler, Y. (1977). Mammifères lémuriens (Primates Prosimiens). *Faune de Madagascar* 44: 1–513.

Petter, J.-J., Schilling, A., and Pariente, G. (1971). Observations écoéthologiques sur deux Lémuriens malgaches nocturnes, *Phaner furcifer et Microcebus coquereli. La Terre et la Vie* 3: 287–327.

Petter, J.-J., and Andriatsarafara, F. (1987). Conservation status and distribution of lemurs in the west and northwest of Madagascar. *Primate Conservation* 8: 169–171.

Rakotoarison, N., Mutschler, T., and Thalmann, U. (1993). Lemurs in Bemaraha (World Heritage Landscape, western Madagascar). *Oryx* 27: 35–40.

Randrianambinina, B. (1997). Contribution à l'étude biologique de *Microcebus ravelobensis* (Zimmermann *et al.,* in press) dans la région d'Ampijoroa/Ankarafantsika. Mémoire de D.E.A., Faculte des Sciences, Département de Biologie Animale, Université d'Antananarivo, Antananarivo.

Raxworthy, C. J., and Rakotondraparany, F. (1988). Mammals report. In Quansah, N. (ed.), Manongarivo Special Reserve (Madagascar) 1987/88 Expedition report. Madagascar Environmental Research Group, London, pp. 122–130.

Rode, P. (1939). Catalogue des types de mammifères du Muséum National d'Histoire Naturelle. Ordre des primates. B. Sous-ordre des Lémuriens. *Bull. Mus. Natl. d'Hist. Nat., Paris,* sér. 2, 11: 434–449.

Rumpler, Y., Ganzhorn, J. U., Tomiuk, J., Leipoldt, M., and Warter, S. (1998). A cytogenetic study of *Microcebus myoxinus. Folia Primat.* 69: 307–311.

Schmid, J. (1997). Torper beim Grauen Mausmaki (*Microcebus murinus*) in Madagaskar: Energetische Konsequenzen und ökologische Bedeutung. Ph.D. Thesis, Universität Tübingen, Tübingen.

Schmid, J. (1999). Sex-specific differences in the activity pattern and fattening in the gray mouse lemur (*Microcebus murinus*) in Madagascar. *J. Mammalogy* 80: 749–757.

Schmid, J., and Kappeler, P. M. (1994). Sympatric mouse lemurs (*Microcebus* spp.) in western Madagascar. *Folia Primatol.* 63: 162–170.

Schwarz, E. (1931). A revision of the genera and species of Madagascar Lemuridae. *Proc. Zool. Soc. London* 1931: 399–428.
Schwartz, J. H. (1974). Dental development and eruption in the prosimians and its bearing on their evolution. Ph.D. thesis, Columbia University.
Simons, E. L. (1988). A new species of *Propithecus* (Primates) from northeast Madagascar. *Folia Primatol.* 50: 143–151.
Smithe, F. B. (1975). *Naturalist's Color Guide.* Part 1. American Museum of Natural History, New York.
SPSS (1977). *SPSS Base 7.5 for Windows User's Guide.* SPSS Inc., Chicago.
Swindler, D. R. (1976). *Dentition of living primates.* Academic Press, London.
Tattersall, I. (1982). *The Primates of Madagascar.* Columbia University Press, New York.
Thalmann, U., and Rakotoarison, N. (1994). Distribution of lemurs in central western Madagascar, with a regional distribution hypothesis. *Folia Primatol.* 63: 156–161.
Yoder, A. D., Rasoloarison, R. M., Goodman, S. M., Irwin, J. A., Atsalis, S., Ravosa, M. J., and Ganzhorn, J. U. (in press). Remarkable species diversity in Malagasy mouse lemurs (Primates, *Microcebus*). *Proc. Natl. Acad. Sci.*
Zimmermann, E., Ehresmann, P., Zietemann, V., Radespiel, U., Randrianambinina, B., and Rakotoarison, N. (1997). Poster 5—A new primate species in north-western Madagascar: the golden-brown mouse lemur (*Microcebus ravelobensis*). *Primate Eye* 63: 26–27.
Zimmermann, E., Cepok, S., Rakotoarison, N., Zietemann, V., and Radespiel, U. (1998). Sympatric mouse lemurs in north-west Madagascar: A new rufous mouse lemur species (*Microcebus ravelobensis*). *Folia Primatol.* 69: 106–114.