

A new species of *Scotophilus* (Chiroptera: Vespertilionidae) from western Madagascar

STEVEN M. GOODMAN^{1, 2}, FANJA H. RATRIMOMANARIVO^{2, 3}, and
FÉLICIEN H. RANDRIANANDRIANINA^{3, 4}

¹*Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA*
E-mail: goodman@fieldmuseum.org

²*WWF, B.P. 738, Antananarivo (101), Madagascar*

³*Département de Biologie Animale, Faculté des Sciences, Université d'Antananarivo, B.P. 906,
Antananarivo (101), Madagascar*

⁴*Madagasikara Voakajy, B.P. 5181, Antananarivo (101), Madagascar*

We describe a new species of *Scotophilus* (Vespertilionidae) from western Madagascar. This bat differs from the other members of this genus known from the island, Africa, and Asia based on its notably diminutive size, pelage coloration, and tragus shape and length. *Scotophilus* sp. nov. is known from seven different specimens taken at three different sites in the central western portion of the island, in zones with anthropogenic savanna dominated by palms (*Bismarckia nobilis*) and dry deciduous forest. The holotype was collected in the palm leaf roof of a thatched dwelling, which is the first evidence of the synanthropic occurrence of a member of this genus on Madagascar. Four species of *Scotophilus* are now known to occur on Madagascar of which three are endemic.

Key words: *Scotophilus*, Vespertilionidae, new species, western Madagascar

INTRODUCTION

On going biological inventories of Madagascar continue to reveal new information on the island's chiropteran fauna, including species previously unknown to science (e.g., Goodman and Cardiff, 2004; Goodman *et al.*, 2005a), resolution of taxonomic issues (e.g., Goodman and Ranivo, 2004; Yoder *et al.*, 2005), and insight into ecological and biogeographical aspects (Goodman *et al.*, 2005b). Several families or genera of bats remain poorly sampled, and new specimen material helps to resolve some of the remaining taxonomic issues.

The Old World genus *Scotophilus* comprises 13 species (Goodman *et al.*, 2005a; Simmons, 2005) found from the Philippines, across portions of Asia, to the Middle East, La Réunion, Madagascar, and much of Africa. Species limits in members of this genus, particularly sub-Saharan animals, have been difficult to resolve, as certain forms possess few clear mensural differences and there is considerable intraspecific variation in pelage coloration (e.g., Hayman and Hill, 1971; Robbins *et al.*, 1985). The genus was previously poorly known on Madagascar, with only a handful of specimens available of one or two recognized

forms (e.g., Dorst, 1947; Peterson *et al.*, 1995). Goodman *et al.* (2005a) recently reviewed the available specimen material of this genus from the island, including specimens collected up until 2003, and concluded that three species occur locally (arranged from largest to smallest): *S. robustus* A. Milne-Edwards, 1881; *S. cf. borbonicus* (E. Geoffroy, 1803); and *S. tandrefana* Goodman, Jenkins, and Ratrimomanarivo, 2005. Because of the poor state of the *S. borbonicus* holotype collected on La Réunion, the only known specimen clearly referable to this taxon, the occurrence of this species on Madagascar could not be confirmed. Since the completion of that study, other *Scotophilus* specimens have become available, including a fourth species from the island, which is the subject of this paper.

MATERIALS AND METHODS

To investigate the taxonomic identity of *Scotophilus* species from Madagascar we have consulted specimens taken from a variety of localities and housed in several natural history museums. The acronyms of these institutions are: BMNH — The Natural History Museum, London (formerly The British Museum of Natural History); FMNH — Field Museum of Natural History, Chicago; MCZ — Museum of Comparative Zoology, Cambridge, MA; MNHN — Muséum National d'Histoire Naturelle, Paris; RMNH — Naturalis, Leiden (formerly Rijksmuseum van Natuurlijke Historie); and UADBA — Université d'Antananarivo, Département de Biologie Animale, Antananarivo.

We recorded six external measurements in millimeters using a ruler from collected specimens before preparation. These included: total length, tail length, hind foot length (excluding claws), tragus length, ear length, and forearm length. Further, we measured body mass in grams using a spring balance. For certain taxa, these data were obtained directly from specimen labels or field catalogs in museum collections. SMG also took six wing measurements using a dial calipers from liquid preserved specimens: 3rd digit-metacarpal, 3rd digit-1st phalanx, 3rd digit-2nd phalanx, 4th digit-metacarpal, 4th digit-1st phalanx, and 4th digit-2nd phalanx.

Seven cranial or mandible and four dental measurements were made using digital calipers, accurate to

the nearest 0.1 mm: greatest skull length (GSL): from posterior-most part of occipital to anterior-most point of upper incisors; condyloincisive length (CIL): from occipital condyles to anterior-most point of upper incisors; zygomatic breadth (ZYG): width taken across zygomatic arches at the widest point; interorbital width (IOW): dorsal width at most constricted part of skull; braincase width (BCW): greatest width across skull at mastoid processes; palatal length (PAL): from posterior border of hard palate to anterior edge of premaxillary bone; width across upper canines (C^1-C^1): taken across the outer alveolar borders of the upper canines; width across posterior upper molars (M^3-M^3): taken across the outer alveolar borders of the third upper molars; maxillary toothrow (C– M^3): length from anterior alveolar border of upper canine to posterior alveolar border of the third upper molar; complete mandibular toothrow (I_1-M_3): length from anterior alveolar border of lower incisors to posterior alveolar border of the third lower molar; and mandible length (MAND): from the posterior-most portion of the condyles to anterior-most point of upper incisors.

SYSTEMATIC DESCRIPTION

As currently recognized the genus *Scotophilus* is composed of 13 species, three of which occur on Madagascar (Robbins *et al.*, 1985; Goodman *et al.*, 2005a; Simmons, 2005). In the latter portion of 2004 and first third of 2005, six specimens were captured in western Madagascar of a notably small species of *Scotophilus* with forearm length ranging from 41 to 45 mm. These six individuals are different from any species known from the island. Using the recent study of Goodman *et al.* (2005a) for comparative data, four diminutive species across the worldwide range of this genus were identified with forearm lengths less than 50 mm. These include *S. tandrefana*, restricted to the western lowland portions of Madagascar; *S. leucogaster* (Cretzschmar, 1830), found in Africa from Mauritania south to a zone running from western to eastern portions of the continent; *S. viridis* (Peters, 1852), known from sub-Saharan Africa from Senegal east to Ethiopia and south to South Africa; and *S. kuhlii* Leach,

1821, recorded from Indonesia and the Philippines west across mainland Asia to Pakistan. After detailed comparisons of external morphology and pelage coloration, cranial and dental measurements and characteristics, as well as tragus shape, these six recently captured individuals, as well as a specimen collected in 1869, could not be assigned to any existing species and are here described as new to science.

Scotophilus marovaza sp. nov.

Holotype

FMNH 184050, an adult male (Figs. 1–4; Tables 1–2), collected on 11 December 2004 by S. M. Goodman and F. H. Ratrimomanarivo, field No. SMG 14474. The specimen was conserved in formalin and the skull extracted and cleaned. Both the specimen and skull are in good condition. Tissue samples are preserved in EDTA.

Etymology

The name of the type locality (Marovaza) is placed in apposition to the generic name.

Type locality

Madagascar, Province de Mahajanga, Marovaza, 14°56'S, 47°16'E, 5 m above sea level (see Fig. 1).

Habitat

The type specimen was collected roosting during the day in dry palm leaves (*Bismarckia nobilis*) forming the roof soffit of a building in a remote coastal area of central western Madagascar. The principal habitats surrounding the village and to the north and east is degraded dry deciduous forest with anthropogenic savanna dominated by the same palm species, and to the west the Mozambique Canal. Within 100 m south of the collection site are extensive limestone outcrops, many eroded into pinnacle forms, which are known as tsingy in Malagasy.

Diagnosis

A member of the genus *Scotophilus* based on a number of characters (Hayman and Hill 1971; Robbins *et al.*, 1985; Koopman, 1994), including the long tapering tragus, no notable inflation of rostrum near the lacrymal, anterior palatal emargination, single pair of upper incisors, I_3 not reduced in size, M^1 and M^2 with reduced mesostyle and indistinct W-shaped pattern, and M^3 notably small. Adult dental formula 1/3-1/1-1/2-3/3.

Scotophilus marovaza is distinguished from other described members of this genus by its diminutive body size with, for example, an average forearm length of 43.8 mm (range 41–45 mm, $n = 6$), which is notably smaller than any other described species of this genus (see Table 1). Muzzle is notably broad and short, giving a pug-like appearance. There is a distinct rostral swelling anterior to each eye. The nostril openings are crescent in shape and are pointed in an outward direction. Tragus notably long, sickle-shaped, and tapering to a fine point at the apex (Fig. 2). The outer margin of the tragus is convex and with a circular lobe at its base. Dorsal pelage is relatively short, reddish-brown in color with the exception of a distinctly lighter brownish-red band extended across central back (Fig. 3). Ventrum and throat a uniform shiny light brownish-yellow. Wing membranes dark brown. Sagittal crest is well developed, particularly in males, and bifurcates at the level of the interorbital region and extends as a weak crest to the front of the orbits. Lambdoid crests are not well developed.

Paratypes

MNHN 1984.433 collected at Mahabo (20°23'S, 44°38'E) on 29 April 1869; UADBA 46965 (R. B. Jenkins [RBJ] 215) obtained at Antafinimihakatra, Parc National d'Ankarafantsika (16°16'S, 46°48'E) on 24 November 2004 by Félicien H.

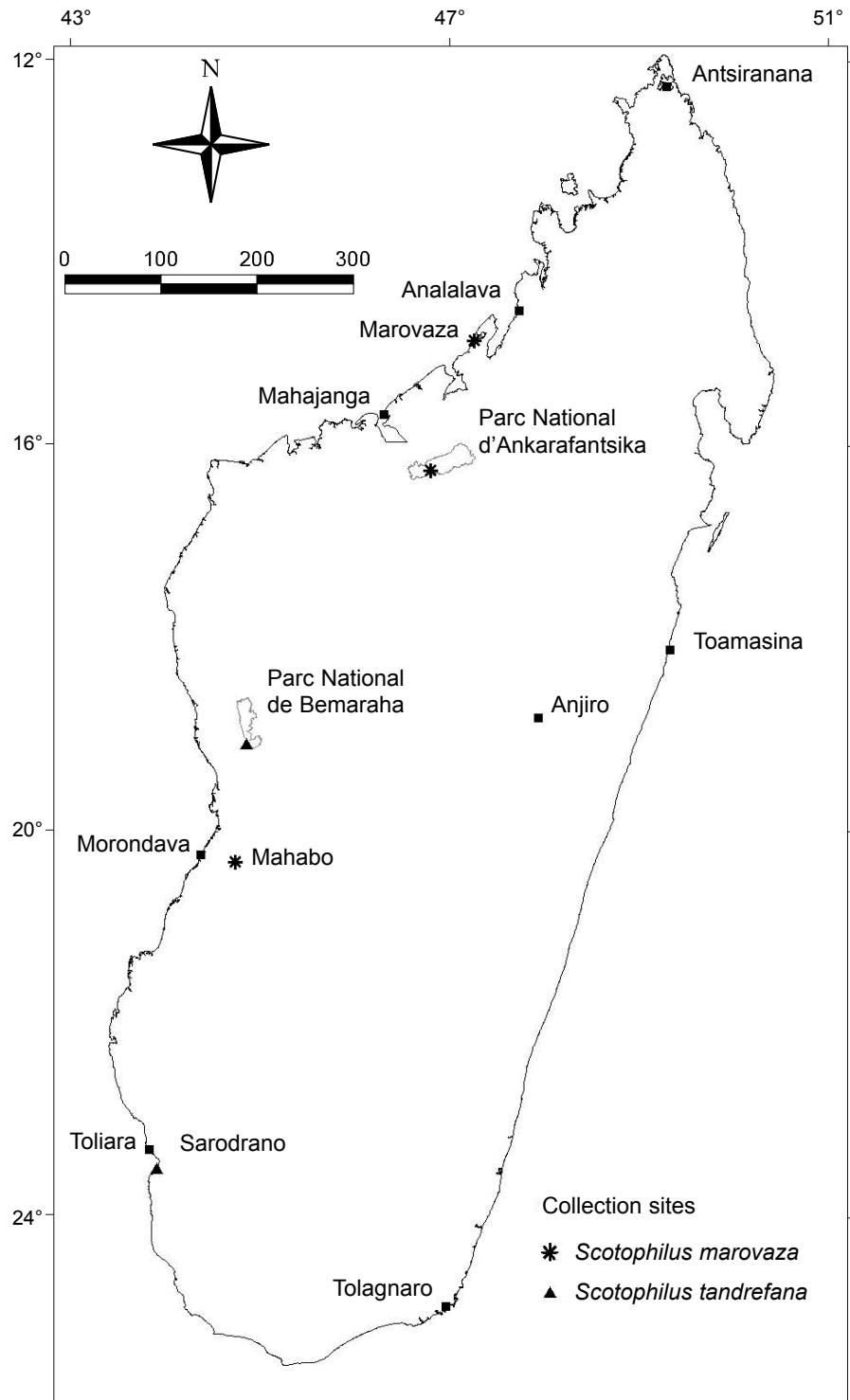


FIG. 1. Map showing sites at which *Scotophilus marovaza* and *S. tandrefana* have been collected, as well as other localities

Randrianandrianina and Hanta Julie Razafimanahaka; and FMNH 184051, 184052, 184085, 184086 obtained at the holotype locality between 21 and 22 April 2005 by Steven M. Goodman and Mamy Ravokatra. The specimen label of the Mahabo specimen is without the collector's name. This date conforms to the period Alphonse Grandier visited the village of Mahabo (Vérin and Mantaux, 1971: 22) and there can be little doubt that the specimen was obtained by him.

Description

In the fresh material of *S. marovaza* available to us the reddish-brown dorsal pelage is similar in all individuals. Some dorsal hairs are lighter in color towards their tips and give a slightly shiny appearance to the pelage. In a few of the individuals there is a distinctly lighter brownish-red band extended across the central portion of the back. The brownish-yellow throat and underside are generally similar in coloration and with no clear demarcation between these two regions, although some specimens show a slightly progressive darkening ventrally. One specimen (UADBA 46965), an adult female, shows a distinctly lighter yellowish-brown ventrum. The wing

membrane and uropatagium are dark brownish-black and show no notable change in coloration. Dorsally, particularly close to the humerus head, and ventrally there is a slight extension of the corporal body fur on to the wing membranes.

The ear length in *S. marovaza* is relatively consistent and does not differ markedly from the other diminutive members of this genus, with the exception of the larger bodied *S. kuhlii* in which ear length is notably smaller (Table 1). The antitragus in *S. marovaza* is a well-formed slightly asymmetric semi-round structure measuring 3 mm in width × 2 mm in height and is separated from the ear by a distinct notch. The tragus is more elongated and sickle-shaped in *S. marovaza* than in any other species of *Scotophilus* occurring on Madagascar (Fig. 2). At the base of the tragus there is a distinct elongated ridge that extends posteriorly along slightly less than one half the tragus length.

The skull of *S. marovaza* is notably small for a species of *Scotophilus* (Tables 1 and 2). The braincase is relatively narrow and when seen in profile the sagittal crest extends posteriorly as a sort of helmet-shaped structure (Fig. 4). The bifurcation of the sagittal crest over the edge of the orbital

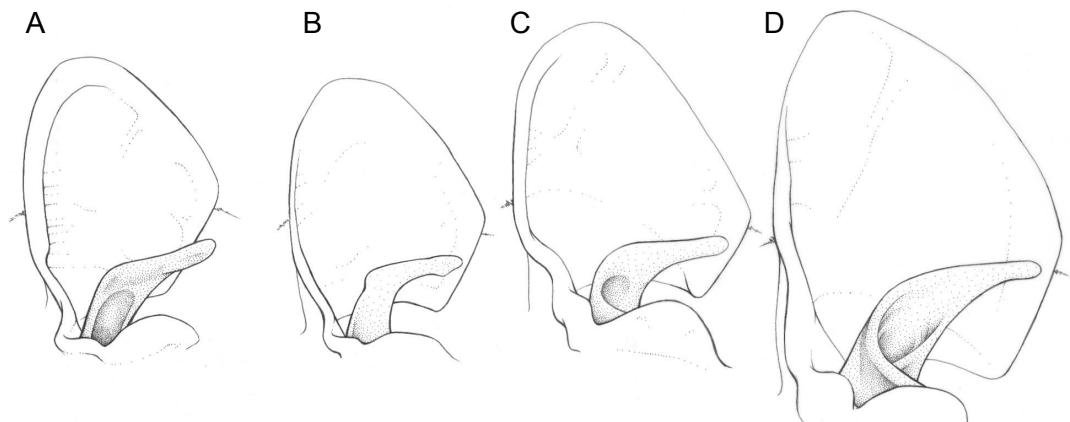


FIG. 2. Right ear and tragus of *Scotophilus* spp. from Madagascar: A — holotype of *S. marovaza* (FMNH 184050), B — *S. tandrefana* (UADBA 51344), C — *S. cf. borbonicus* (MNHN 1976.420), D — *S. robustus* (FMNH 166186)



FIG. 3. Photograph views of holotype of *S. marovaza* (FMNH 184050; SMG 14474). Upper — dorsal view, and lower — ventral view. (Photographs taken by S. M. Goodman)

region forms a distinct brow. The rostrum is relatively short and broad, without any notable expansion or swelling in the lacrymal region. Slight ovoid flaring to the zygomatic arches. The interorbital constriction is not pronounced. Anterior emargination of palate is relatively deep and broad. Posterior palatal extension terminates as a small acute spine.

The tooth formula and structure is characteristic of other species of *Scotophilus* (Koopman, 1994: 128). The single upper pair of incisors is trifid and the upper and lower canines well developed and seemingly powerful for a bat of this size. M^1 and M^2 have reduced mesostyles and in the former the cusps form a distorted ‘W-shape’ and in the latter a distinct ‘W-shape’ M^3 is notably reduced in size. The second lower premolar (PM_1) and fourth lower premolar (PM_2) have the trigonid distinctly more developed than the talanid. There is a conspicuous swollen gland in the interior of the mouth at the base of the toothrows.

Distribution

This species is known from three sites in the western portion of Madagascar (north to south): Marovaza, Ankrafantsika, and Mahabo (see Fig. 1). Given the different habitat types, including synanthropic settings, this species has been recorded, we suspect that it has a broad range across much of western lowland Madagascar.

COMPARISONS

When describing *S. tandrefana*, Goodman *et al.* (2005a) had access to three specimens that they referred to this taxon. One of these, MNHN 1984.433 collected at Mahabo in 1869, was smaller in most external, cranial, dental, and wing measurements than the other two specimens. Although pelage coloration was one of the diagnostic characteristics to differentiate *S. tandrefana*

from other diminutive members of the genus, particularly the holotype that was recently collected, the Mahabo specimen was notably faded in coloration after being stored in alcohol for nearly 140 years. A re-evaluation of the identification of this specimen (MNHN 1984.433), based on a variety of characters and measurements, indicates that it falls within the range of *S. marovaza*, rather than *S. tandrefana*.

The reddish-brown dorsal and uniform shiny light brownish-yellow ventral pelage distinguishes *S. marovaza* from other diminutive members of this genus including *S. kuhlii* — chestnut-brown dorsally and pale brown ventrally; *S. leucogaster* — light to medium brown dorsally and white to dirty-brown ventrally; *S. tandrefana* — dark brown dorsally and medium brown ventrally; and *S. viridis* — yellowish-brown dorsally and white, grayish-brown to yellowish dorsally (Goodman *et al.*, 2005a).

Scotophilus marovaza is a notably diminutive *Scotophilus*, with the shortest average forearm length of any known member of this genus from Madagascar (Table 1). The ear is similar in length to the other four diminutive species of *Scotophilus*, with the exception of the generally larger-bodied *S. kuhlii*, in which it is shorter. The tragus is more elongated, sickle-shaped, and finely pointed towards the apex in *S. marovaza* than in any other species of *Scotophilus* occurring on Madagascar (see Fig. 2). Further, the outer margin of the tragus is convex and with a circular lobe at its median base. The most notable difference in tragus shape is that in *S. marovaza* there is a distinct posterior ridge that extends inferiorly as a non-curved structure and in *S. tandrefana* the ridge is not as extensive and curved (Fig. 2). In Figure 2 of Goodman *et al.* (2005a) the ears and tragi of three different individuals of *Scotophilus* are illustrated, including the holotype of *S. tandrefana* (UADBA 46923), an individual identified as *S. cf. borbonicus*

TABLE 1. External measurements (mm), body masses (g), and cranial measurements of small *Scotophilus* species. Descriptive statistics are presented as mean, SD, minimum–maximum, and number of specimens (in parentheses). Measurements followed by an asterisk were made from fluid preserved specimens and are not included in the descriptive statistics. See Materials and Methods section for explanation of acronyms

Species	Total length	Tail length	Hind foot length	Tragus length	Ear length	Forearm length	Tibia length	Body mass
<i>S. marovazae</i> sp. nov.								
FMNH 184085 ♀	113	44	6.0	10	14	45	—	15.5
FMNH 184051 ♀	113	45	6.0	10	14	45	16.7	14.5
FMNH 184052 ♀	112	42	6.0	10	14	45	17.3	14.0
FMNH 184086 ♂	111	44	6.0	11	15	44	—	14.5
FMNH 184050 ♂ holotype	106	40	6.0	9	14	41	17.3	12.5
Ankarafanisika								
UADBA 46965 ♀	100	38	6.5	9	13	43	16.9	16.8
Mahabo								
MNHN 1984.433 ♀	—	—	7.2*	7*	13*	44*	17.3*	—
—, SD	109.2, 5.19	42.2, 2.71	6.1, 0.20	9.8, 0.75	14.0, 0.63	43.8, 1.65	17.1, 0.30	14.6, 1.44
min–max (n)	100–113 (6)	38–45 (6)	6.0–6.5 (6)	9–11 (6)	13–15 (6)	41–45 (6)	16.7–17.3 (4)	12.5–16.8 (6)
<i>S. tandrefana</i>								
111 (1)	43–46 (2)	7–8 (2)	7–7 (2)	7–7 (2)	13–16 (2)	46–47 (2)	17.8–18.9 (2)	14.2 (1)
<i>S. kuhlii</i>								
115.3, 7.43	46.6, 4.83	11.7, 1.11	—	—	12.0	50.5, 1.0	—	—
104–128 (7)	36–51 (7)	10–13 (7)	10–13 (7)	10–13 (7)	12.0–12.0 (4)	50–52 (4)	—	—
<i>S. leucogaster</i>								
122.0, 8.00	48.0, 4.84	10.8, 1.50	—	—	14.1, 0.63	49.8, 3.37	—	—
114–130 (3)	40–52 (5)	10–13 (4)	—	—	13.5–15 (4)	44–53 (6)	—	24 (1)
<i>S. viridis</i>								
116.6, 6.32	47.8, 4.10	10.7, 1.09	—	—	14.4, 1.33	46.7, 5.18	—	17.4, 2.12
105–130 (22)	40–56 (25)	9–12 (24)	9–12 (24)	9–12 (24)	12–17 (25)	44–53 (24)	14–24 (20)	—

TABLE 1. Extended

Species	GSL	CIL	ZYG	IOW	BCW	PAL
<i>S. marovaza</i> sp. nov.						
Marovaza						
FMNH 184085 ♀	16.9	15.9	11.8	4.1	10.4	7.8
FMNH 184051 ♀	16.9	16.1	12.1	4.6	10.3	8.1
FMNH 184052 ♀	16.5	16.0	11.9	4.4	10.4	8.0
FMNH 184086 ♂	16.4	15.9	11.6	4.2	10.2	7.8
FMNH 184050 ♂ holotype	16.9	15.7	11.9	4.6	10.2	7.9
Ankarafanisika						
UADBA 46965 ♀	16.7	15.5	11.2	4.1	10.0	7.8
Mahabo						
MNHN 1984:433 ♀	16.9	15.9	11.5	4.5	10.1	7.9
♂, SD	16.7, 0.21	15.9, 0.20	11.7, 0.30	4.4, 0.22	10.2, 0.15	7.9, 0.12
min-max (n)	16.4–16.9 (7)	15.5–16.1 (7)	11.2–12.1 (7)	4.1–4.6 (7)	10.0–10.4 (7)	7.8–8.0 (7)
<i>S. tandrefana</i>						
17.8–17.9 (2)	16.7–16.8 (2)	11.4–12.3 (2)	4.2–4.3 (2)	10.5–10.5 (2)	8.2–8.5 (2)	
<i>S. kuhlii</i>						
19.4, 0.37	17.9, 0.29	13.2, 0.31	4.7, 0.18	11.2, 0.27	9.1, 0.15	
18.9–19.9 (11)	17.5–18.3 (11)	12.8–13.6 (11)	4.3–4.9 (11)	10.8–11.7 (11)	8.8–9.2 (11)	
<i>S. leucogaster</i>						
19.0, 0.93	17.5, 0.65	13.4, 0.63	4.8, 0.24	11.1, 0.71	9.0, 0.44	
17.1–20.1 (9)	16.2–18.2 (8)	12.0–14.1 (10)	4.2–5.0 (11)	10.0–12.2 (9)	8.3–9.6 (10)	
<i>S. viridis</i>						
18.1, 0.61	16.8, 0.45	12.6, 0.36	4.4, 0.17	10.8, 0.41	8.5, 0.25	
17.0–20.0 (23)	16.0–18.4 (23)	11.9–13.4 (22)	4.1–4.7 (23)	9.8–11.4 (23)	7.8–8.9 (23)	

(MNHN 1976.420), and an individual originally allocated to *S. tandrefana* (MNHN 1984.433) but herein referred to *S. marovaza*. Amongst the six specimens of *S. marovaza* with measurable tragi, the average is 9.8 mm (range 9–11 mm), as compared to two individuals of *S. tandrefana* with lengths of 7 mm. The tibia length in *S. marovaza* is shorter ($\bar{x} = 17.1$, range 16.7–17.3, $n = 4$) than in *S. tandrefana* (17.8 and 18.9, $n = 2$), and there is no overlap in these measures based on the limited available material.

The skull is notably smaller in *S. marovaza* than any of the other diminutive members of this genus, including *S. tandrefana* (Table 1), and there is no overlap between these two species in greatest skull length and condyloincisive length. Principal components analyses of cranial measurements indicate heavy loadings for these two variables in separating out the five species of small *Scotophilus* compared in this study (Table 3). The cumulative percentage of cranial variation explained in the first two components is 90.2%, of which the first component accounts for 80.0% of the variation, and *S. marovaza* forms a separate group from the other small congeneric species (Fig. 5A). On the basis of this analysis and the grouping within the diagram, it is the smallest and morphologically discrete member of this genus.

Of the various dental measurements made there are few variables that allow clear separation of the examined species, particularly in this case between *S. marovaza* and *S. tandrefana* (Table 2). These two species are notably similar in most dental measurements, but smaller than the other three species (*S. kuhlii*, *S. leucogaster*, and *S. viridis*) they were compared to. In the three larger species there is considerable intraspecific variation in dental measurements. Although C–M³ and I₁–M₃ had high principal components loadings (Table 3),

these variables did not allow for the clear separation of *S. marovaza* from *S. tandrefana* (Fig. 5B). Further, within the scatter of points of *S. marovaza*, there are also individuals of *S. leucogaster* and *S. viridis*.

NATURAL HISTORY

Scotophilus marovaza is currently known from three sites spanning a considerable area of the western portion of Madagascar (Fig. 1). The direct line distance from the northern-most locality, Marovaza, to the southern-most site, Mahabo, is about 660 km. The holotype and other specimens from Marovaza were collected in a village setting 5 m a.s.l. and within 50 m of the sea; the specimen from Ankrafantsika at the ecotone between savanna and disturbed dry deciduous forest at approximately 65 m altitude and 90 km inland; and the third specimen from Mahabo, assumed to have been collected by A. Grandier in 1869, in a presumed synanthropic setting at about 60 m a.s.l. and about 40 km inland. Based on direct and in direct evidence five of the six specimens were collected in and around villages and one individual in an open area close to natural forest.

The holotype of *S. marovaza* was obtained in December 2004 within several dense layers of palm leaves (*B. nobilis*) that were attached to the roof soffit of a building, where it was roosting within the thatching (Fig. 6). In late April 2005, when the site was revisited, three individuals were found roosting together in the same exact place as the December specimen. These included two females and a third unsexed individual that escaped before it could be captured, but was pursued to three different sites associated with palm thatching. At all of these three day-roost sites, within 30 m of one another, there was a well-defined opening amongst the palm leaves, as well as the distinct musky odor of this *Scotophilus*, and

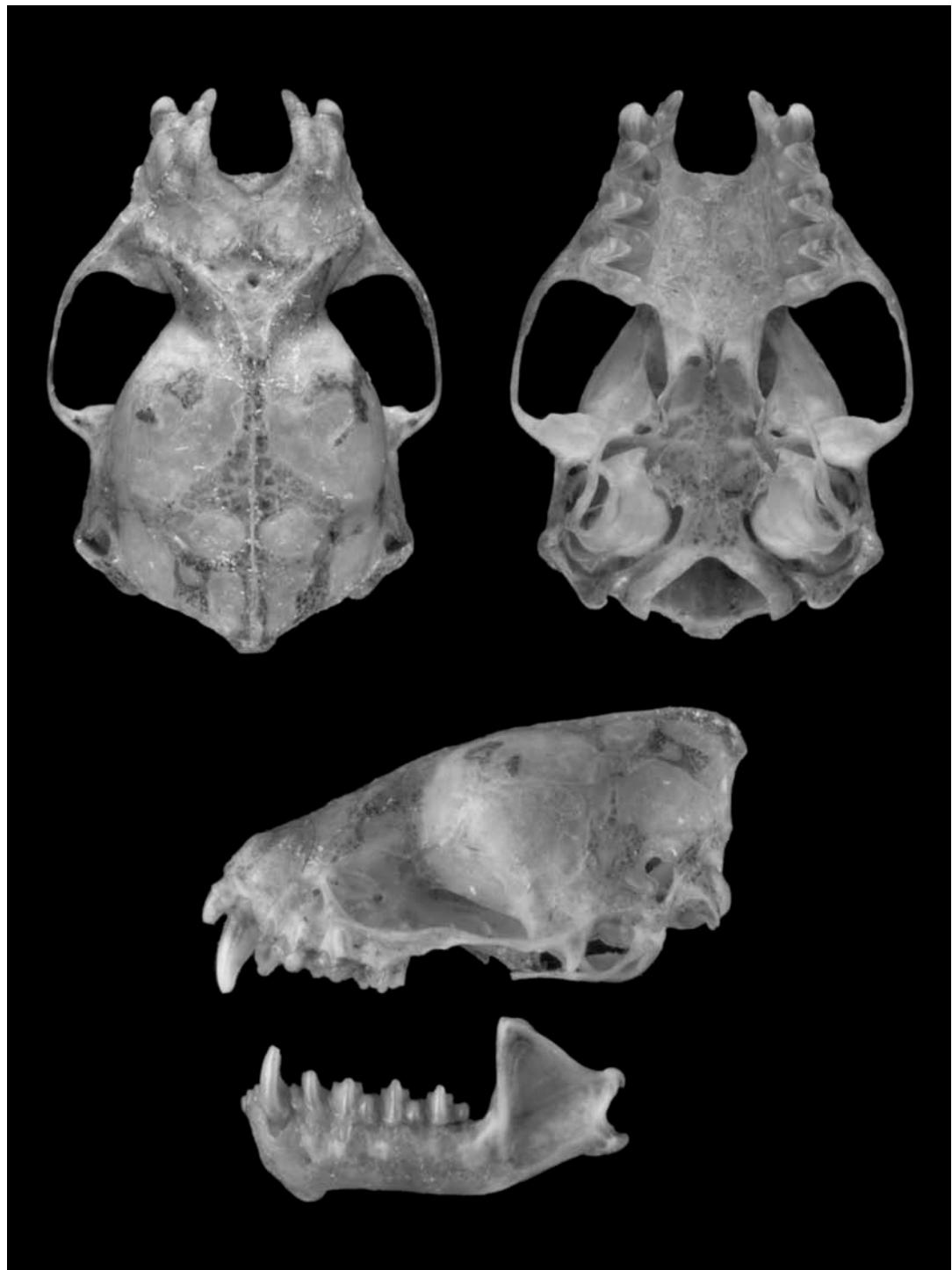


FIG. 4. Different views of the skull of *S. marovaza* (holotype FMNH 184050, SMG 14474). Upper left — dorsal view of cranium, upper right — ventral view of cranium, and lower — lateral view of cranium and mandible. The greatest skull length of this specimen is 16.9 mm. (Photograph taken by John Weinstein, FMNH image No. Z94430-05d)

TABLE 2. Dental and mandibular measurements (in mm) of small *Scotophilus* species. Descriptive statistics are presented as mean, SD, minimum–maximum, and number of specimens (in parentheses). See Materials and Methods section for explanation of acronyms

Species	C ¹ –C ¹	M ³ –M ³	C–M ³	I ₁ –M ₃	MAND
<i>S. marovaza</i> sp. nov.					
Marovaza					
FMNH 184085 ♀	5.6	7.6	5.5	7.1	11.5
FMNH 184051 ♀	6.0	7.5	5.6	7.0	11.7
FMNH 184052 ♀	5.9	7.9	5.6	7.3	11.4
FMNH 184086 ♂	5.7	7.5	5.3	6.9	11.5
FMNH 184050 ♂ holotype	5.7	7.5	5.6	7.1	11.5
Ankarafantsika					
UADBA 46965 ♀	5.7	7.8	5.7	7.1	11.3
Mahabo					
MNHN 1984.433 ♀	5.6	7.2	5.3	—	—
̄, SD	5.7, 0.15	7.6, 0.23	5.5, 0.16	7.1, 0.13	11.5, 0.13
min–max (n)	5.6–6.0 (7)	7.2–7.9 (7)	5.3–5.7 (7)	6.9–7.3 (6)	11.3–11.7 (6)
<i>S. tandrefana</i>					
5.6–5.9 (2)	7.7–7.8 (2)	5.8–5.8 (2)	7.1–7.5 (2)	11.6–12.1 (2)	
<i>S. kuhlii</i>					
6.0, 0.30	8.1, 0.24	6.4, 0.12	8.3, 0.19	13.1, 0.23	
5.7–6.7 (11)	7.6–8.4 (11)	6.2–6.7 (11)	8.0–8.6 (10)	12.8–13.4 (11)	
<i>S. leucogaster</i>					
6.2, 0.28	8.2, 0.41	6.3, 0.30	7.9, 0.57	12.8, 0.51	
5.7–6.6 (11)	7.4–8.6 (10)	5.6–6.6 (11)	6.4–8.4 (11)	12.1–13.4 (9)	
<i>S. viridis</i>					
5.9, 0.24	7.9, 0.31	5.9, 0.19	7.5, 0.30	12.1, 0.44	
5.2–6.5 (23)	7.2–8.4 (23)	5.6–6.5 (23)	6.9–8.3 (23)	11.4–13.6 (21)	

the group probably had several day-roost sites in the same immediate vicinity. Although African and Asian members of the genus *Scotophilus* are known to commonly occur in synanthropic roost sites (e.g., Kingdon, 1974; Bates and Harrison, 1997), this is the first evidence of such a situation for Malagasy species. Subsequently, *S. robustus* has been captured at localities in eastern and southeastern Madagascar in synanthropic settings (Ratrimonanarivo and Goodman, 2005).

The Ankarafantsika specimen of *S. marovaza* was captured in a mist net placed in a slight depression of a dry riverbed and parallel to the banks. This site was at the edge of a slightly disturbed dry deciduous forest. Standing *B. nobilis* trees were not common in the immediate vicinity of the capture site, although about 300 m away several houses had roof thatching made of palm leaves.

No specific details are available on the site A. Grandidier obtained the Mahabo specimen of *S. marovaza* in 1869. However, it is assumed to have been close to or in this village. During the middle of the 19th century the predominant building materials for houses in this portion of Madagascar are presumed to be of wood for the main structure and palm leaves for the roof. We suspect that this specimen was collected in a synanthropic context.

The holotype collected in December 2004 and two of the specimens in April 2005 at Marovaza came from the same exact place within the palm leaf thatching of a building (Fig. 6). Here the palm leaves formed a dense cluster and hung vertically with the opening facing the ground. The precise roosting site of these bats was in a small pocket formed by the curled dried leaves of the palm, just anterior to the leaf stem. A collection of feces was found on

the ground below the roost site. The palm leaves where the bats were found had a pungent odor similar to the animals themselves. The other two specimens collected at Marovaza were netted at the perimeter of a nearby large open building without standing walls. The extensive palm leaf roof had several large aeration openings. These two individuals were captured about 1.5 hrs after sunset and 2 hrs before sunrise, when they passed through the interior of the structure while foraging or entering/exiting roost sites.

The palm *B. nobilis*, known as satrana in Malagasy, has a broad distribution across much of the dry portions of Madagascar and occurs in heavily degraded anthropogenic grassland (Dransfield and Beentje, 1995). The attached lower leaf stems of a standing tree often hang vertically, with respect to the ground, and the dried and collapsed leaves form relatively dense layers. The position and form of these leaves is very similar to the synanthropic setting *S. marovaza* was found roosting in at the holotype locality. We strongly suspect that palm fronds are amongst the natural day roosting sites of this bat species. This style of roost site in collapsed palm fronds has been reported in *S. heathi* in the Philippines (Rickart *et al.*, 1989).

On the basis of the recently collected specimens the following inferences can be made about reproduction in *S. marovaza*. The female captured at Ankrafantsika in late November 2004 had greatly enlarged mammae and appeared to be lactating. Thus, parturition would appear to coincide with the start of the rainy season, as is known in the South African population of *S. viridis* living in a seasonally arid zone (Van der Merwe *et al.*, 1988). The male from Marovaza collected in the first half of December 2004 had enlarged descended testes (8×3 mm) and convoluted epididymes. Of the four individuals obtained at

TABLE 3. Principal components (PC) loadings of cranial and dental variables for *S. marovaza*, *S. tandrefana*, *S. leucogaster*, *S. kuhlii*, and *S. viridis*. Eigenvalues represent the variation among the five species as explained by each axis. Graphic presentations of these comparisons are given in Fig. 5

Variable	PC 1	PC 2
Skull		
Condyloincisive length	0.92	0.27
Greatest skull length	0.90	0.34
Zygomatic breadth	0.89	0.36
Palatal length	0.87	0.28
Braincase width	0.84	0.29
Interorbital width	0.28	0.96
% cumulative variation explained	80.00	90.20
Teeth and mandible		
Maxillary toothrow	0.91	0.35
Mandibular toothrow	0.90	0.34
Mandible length	0.88	0.40
Width across posterior upper molars	0.54	0.70
Width across upper canines	0.31	0.90
% cumulative variation explained	77.80	88.90

Marovaza in late April 2005, three were adult females with large or slightly enlarged mammae, no embryos, and single placental scars in one horn of the uterus and one was an adult male with enlarged descended testes (9×4 mm) and convoluted epididymes. On the basis of this limited information there would appear to be a defined breeding season in females, coinciding with the start of the rainy season (November to February). Males, on the other hand, appear to maintain their reproductive capacity for a distinctly broader portion of the year, as is known in *S. viridis* (Van der Merwe *et al.*, 1988; Van der Merwe and Rautenbach, 1989).

Scotophilus marovaza is not known to occur in sympatry with *S. tandrefana*, the other notably small Malagasy member of this genus. We suspect with further exploration of lowland western Madagascar, particularly in zones with *B. nobilis* palms, these two diminutive species of Malagasy *Scotophilus* may be found to occur at the same sites. Only two localities are known

on Madagascar where species of *Scotophilus* occur in sympatry — Sarodrano with *S. cf. borbonicus* and *S. tandrefana* and Bemaraha with *S. robustus* and *S. tandrefana* (Goodman *et al.*, 2005a, 2005b).

Scotophilus robustus is also known to occur in eastern humid forest settings.

In their revision of African *Scotophilus*, Robbins *et al.* (1985: 76) noted that amongst the few specimens from

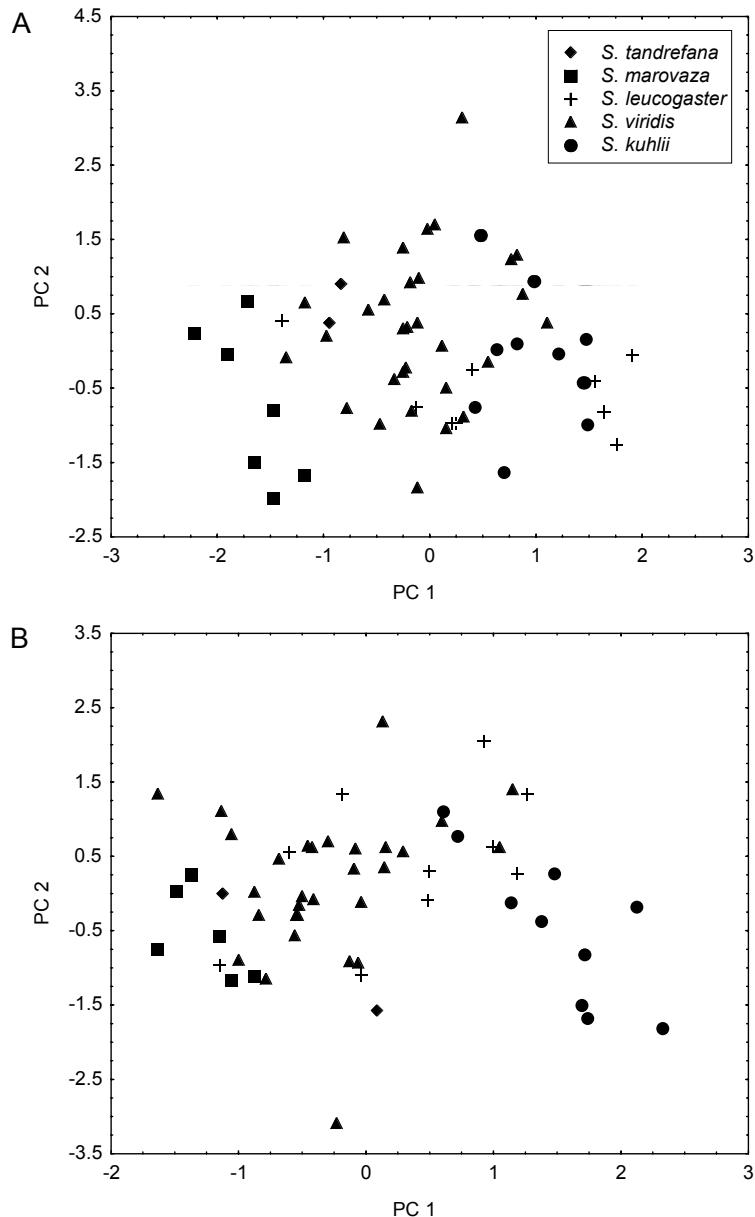


FIG. 5. Scatter plots of principal components (PC) scores for axes 1 and 2 for (A) cranial and (B) dental and mandibular measurements of *Scotophilus* spp. The cumulative contribution of axes 1 and 2 for the cranial variables are 80.0 and 90.2%, respectively, and for the teeth and mandible measurements 77.8 and 88.9%, respectively

Madagascar available to them in the Muséum National d'Histoire Naturelle, Paris, there appeared to be three different species: *S. robustus*, *S. cf. borbonicus*, and *S. cf. viridis*. Thus, there was already an indication that species richness of this genus on the island was higher than the single species concept of Peterson *et al.* (1995). The description of *S. marovaza* brings the number of endemic Madagascar representatives of the genus *Scotophilus* to three, the other two being *S. robustus* and *S. tandrefana*. Given that African *Scotophilus* show considerable variation in pelage and mensural characters, resulting in problems of diagnosing species, the lingering question remains if *S. tandrefana* and *S. marovaza* are conspecific. Additional specimens and data sets, such as vocalizations, should help to



FIG. 6. The specific synanthropic setting where the holotype and a portion of the type series of *S. marovaza* were collected. The arrow indicates the site and the direction bats would have entered into the day roost site within the palm leaves. (Photograph taken by Mamy Ravokatra)

resolve this question. A molecular study is being currently conducted on African and Malagasy *Scotophilus* by R. Trujillo, which will address the question of their phylogenetic relationships and species limits. A similar case of a cryptic species of *Scotophilus* has been recently found in southern Africa and combined morphological, vocalization, and molecular datasets have resolved their differentiation (Jacobs *et al.*, 2006).

The discovery of *S. marovaza*, which lives synanthropically, further highlights how little is known about the mammal fauna of the island, specifically in this case the bats of western Madagascar. Within a short period after the completion of a generic revision of Malagasy members of the genus *Scotophilus* (Goodman *et al.*, 2005a), based on all of the world's known museum holdings of specimens collected on the island of this genus, six other individuals were obtained at two different localities, which represent the new species described herein. Given the considerable range of vegetation types in the western portion of the island, overlaid on significant meteorological clines and a remarkable range of geological formations (de Wit, 2003; Gautier and Goodman, 2003), and that significant portions of the region are zoologically unknown, other species of mammals new to science are certain to be discovered in this region.

ACKNOWLEDGEMENTS

We are grateful to the Direction des Eaux et Forêts and Association Nationale pour la Gestion des Aires protégées for issuing collection and exportation permits. Funding for a portion of the fieldwork was provided by the John D. and Catherine T. MacArthur Foundation, The Volkswagen Foundation, Darwin Initiative (162/10/024), Fauna and Flora International, and the Conservation, Food and Health Foundation. For access to specimen material under their care, we are indebted to Paulina Jenkins (BMNH), Judith Chupasko (MCZ), Jean-Marc Pons and Ronan Kirsch

(MNHN), Chris Smeenk (RMNH), and Olga Ramiijaona and Daniel Rakotondravony (UADBA). For help in the field, hospitality, and logistic aid we are grateful to the ANGAP team at Parc National Ankarafantsika, Marc Le Groumellec and Rao Manavendra of UNIMA, and Philippe Girard, Thierry Ranaivelo, Mamy Ravokatra, and Abel Nirina. Several friends and colleagues prepared or made available figures: Lucienne Wilmé (Fig. 1), Rebecca Kramer (Fig. 2), John Weinstein (Fig. 4), and Mamy Ravokatra (Fig. 6).

LITERATURE CITED

- BATES, P. J. J., and D. L. HARRISON. 1997. Bats of the Indian subcontinent. Harrison Zoological Museum, Sevenoaks, xvi + 258 pp.
- DE WIT, M. 2003. Madagascar: heads it's a continent, tails it's an island. Annual Review of Earth and Planetary Sciences, 31: 213–248.
- DORST, J. 1947. Les chauves-souris de la faune malgache. Bulletin du Muséum National d'Histoire Naturelle, Paris, 2, 19: 306–313.
- DRANSFIELD, J., and H. J. BEENTJE. 1995. The palms of Madagascar. Royal Botanic Gardens, Kew, xii + 475 pp.
- GAUTIER, L., and S. M. GOODMAN. 2003. Introduction to the flora of Madagascar. Pp. 229–250, in The natural history of Madagascar (S. M. GOODMAN and J. P. BENSTEAD, eds.), The University of Chicago Press, Chicago, xxi + 1709 pp.
- GOODMAN, S. M., and S. G. CARDIFF. 2004. A new species of *Chaerephon* (Molossidae) from Madagascar with notes on other members of the family. Acta Chiropterologica, 6: 227–248.
- GOODMAN, S. M., and J. RANIVO. 2004. The taxonomic status of *Neoromicia somalicus malagasyensis*. Mammal Biology, 69: 434–438.
- GOODMAN, S. M., R. K. B. JENKINS, and F. H. RATRIMOMANARIVO. 2005a. A review of the genus *Scotophilus* (Chiroptera: Vespertilionidae) on Madagascar, with the description of a new species. Zoosystema, 27: 867–882.
- GOODMAN, S. M., D. ANDRIAFIDISON, R. ANDRIANOIVOARIVELO, S. G. CARDIFF, E. IFTICENE, R. K. B. JENKINS, A. KOFOKY, T. MBOHOAHY, D. RAKOTONDRAVONY, J. RANIVO, F. RATRIMOMANARIVO, J. RAZAFIMANAHAKA, and P. A. RACEY. 2005b. The distribution and conservation of bats in the dry regions of Madagascar. Animal Conservation, 8: 153–165.
- HAYMAN, R. W., and J. E. HILL. 1971. The mammals of Africa. An identification manual. Part 2. Order Chiroptera (J. MEESTER and H. W. SETZER, eds.). Smithsonian Institution Press, Washington D.C., 73 pp.
- JACOBS, D. S., G. N. EICK, M. C. SCHOEMAN, and C. A. MATTHEE. 2006. Cryptic species in an insectivorous bat, *Scotophilus dinganii*. Journal of Mammalogy, 87: 161–170.
- KINGDON, J. 1974. East African mammals. An atlas of evolution in Africa. Vol. II, Part A (insectivores and bats). Academic Press, London, xi + 341 pp.
- KOOPMAN, K. F. 1994. Chiroptera: systematics. Pp. 1–217, in Handbuch der Zoologie, Volume VIII, Mammalia, Part 60 (J. NIETHAMMER, H. SCHLIE-MANN, and D. STARCK, eds.) Walter de Gruyter, Berlin, vii + 217 pp.
- PETERSON, R. L., J. L. EGER, and L. MITCHELL. 1995. Chiroptères. Volume 84. Faune de Madagascar. Muséum National d'Histoire Naturelle, Paris, 204 pp.
- RATRIMONANARIVO, F. H., and S. M. GOODMAN. 2005. First records of the synanthropic occurrence of *Scotophilus* spp. on Madagascar. African Bat Conservation News, 6: 3–5.
- RICKART, E. A., P. D. HEIDEMAN, and R. C. B. UTZURUM. 1989. Tent-roosting by *Scotophilus kuhlii* (Chiroptera: Vespertilionidae) in the Philippines. Journal of Tropical Ecology, 5: 433–336.
- ROBBINS, C. B., F. DE VREE, and V. VAN CAKENBERGHE. 1985. A systematic revision of the African bat genus *Scotophilus* (Vespertilionidae). Annales Musée royal de l'Afrique centrale, Sciences Zoologiques, Tervueren, Belgique, 246: 51–84.
- SIMMONS, N. B. 2005. Order Chiroptera. Pp. 312–529, in Mammal species of the World: a taxonomic and geographic reference. 3rd edition (D. E. WILSON and D. M. REEDER, eds.). Johns Hopkins University Press, Baltimore, 2142 pp.
- VAN DER MERWE, N. J., I. L. RAUTENBACH, and B. L. PENZHORN. 1988. A new pattern of early embryonic development in the seasonally breeding non-hibernating lesser yellow house bat, *Scotophilus borbonicus* (E. Geoffroy, 1803) (Chiroptera: Vespertilionidae). Annals of the Transvaal Museum, 34: 551–556.
- VAN DER MERWE, N. J., and I. L. RAUTENBACH. 1989. The male reproductive pattern and histology of the testes of the lesser yellow house bat, *Scotophilus borbonicus* (E. Geoffroy, 1803) (Chiroptera: Vespertilionidae). Journal of the South African Veterinary Association, 60: 83–86.
- VÉRIN, P., and C. G. MANTUAUX. 1971. Souvenirs de voyages d'Alfred Grandidier, 1865–1870. Publication de l'Association malgache d'Archéologie, Tananarive.
- YODER, A. D., C. HANLEY, K. HECKMAN, R. RASOLOARISON, A. RUSSELL, J. RANIVO, L. E. OLSON,

V. SOARIMALALA, K. P. KARANTH, A. P. RASE-LIMANANA, and S. M. GOODMAN. 2005. A multi-dimensional approach for detecting species pat-

terns in Malagasy vertebrates. Proceedings of the National Academy of Sciences, USA, 102: 6587–6594.

Received 30 June 2005, accepted 08 August 2005