

A review of the genus *Scotophilus* (Mammalia, Chiroptera, Vespertilionidae) on Madagascar, with the description of a new species

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ABSTRACT

The bat genus *Scotophilus* Leach, 1821 is poorly known from islands in the western Indian Ocean. *S. borbonicus* (É. Geoffroy, 1803) was originally described in the early 19th century from La Réunion on the basis of two specimens. Its presence on that island has not been subsequently documented. The holotype specimen has been lost and the lectotype is in a very poor state of preservation, further complicating a proper diagnosis of this taxon. *S. borbonicus* has also been reported from Madagascar, but these records are without clear documentation. Little information is available on *S. robustus* A. Milne-Edwards, 1881, a Malagasy endemic. On the basis of recently discovered old specimens and newly collected material from Madagascar we reevaluate the species limits of members of this genus. Three species of *Scotophilus* are documented on Madagascar, one of which is new to science and described herein. This new species, *S. tandrefana* n. sp., is distinguished from the other species occurring on Madagascar and elsewhere in the world by pelage coloration and cranial and dental measurements.

KEY WORDS

Mammalia,
Chiroptera,
Vespertilionidae,
Scotophilus,
Madagascar,
La Réunion,
new species.

RÉSUMÉ

Révision du genre Scotophilus (Mammalia, Chiroptera, Vespertilionidae) de Madagascar et description d'une espèce nouvelle.

Les chauves-souris du genre *Scotophilus* Leach, 1821 sont très mal connues dans les îles de l'ouest de l'océan Indien. *S. borbonicus* (É. Geoffroy, 1803) a été décrit pour la première fois au début du XIX^e siècle à partir de deux spécimens provenant de La Réunion. L'holotype a été perdu et le lectotype est en très mauvais état, ce qui complique la détermination des caractères précis de ce taxon. *S. borbonicus* a été signalé à Madagascar, mais la documentation existante est peu claire. Très peu d'informations sont disponibles sur l'espèce endémique de Madagascar, *S. robustus* A. Milne-Edwards, 1881. Sur la base des découvertes faites aussi bien avec de vieux spécimens qu'avec ceux nouvellement collectés de Madagascar, nous réévaluons les limites des espèces malgaches contenues dans ce genre. Trois espèces de *Scotophilus* sont connues à Madagascar dont une est nouvelle pour la science et décrite ci-dessous. Cette nouvelle espèce, *S. tandrefana* n. sp., se distingue des autres espèces rencontrées à Madagascar et partout dans le monde par la couleur de son pelage et les mesures crâniennes et dentaires.

MOTS CLÉS

Mammalia,
Chiroptera,
Vespertilionidae,
Scotophilus,
Madagascar,
La Réunion,
nouvelle espèce.

INTRODUCTION

The Old World genus *Scotophilus* is currently considered to comprise 12 species (Simmons in press) found from the Philippines, across portions of Asia, to the Middle East, the Mascarene Islands (La Réunion), Madagascar, and much of Africa. The taxonomic distinction of members of this genus, particularly sub-Saharan forms, has been the source of some controversy, as certain species possess few mensural differences for their clear differentiation (Hayman & Hill 1971; Robbins *et al.* 1985). Further, and more specifically for this current paper, specimen records of this genus on western Indian Ocean islands are few (Cheke & Dahl 1981; Moutou 1982; Peterson *et al.* 1995), and confusion exists as to the number of species occurring in this region and their distribution.

Dorst (1947) signaled the occurrence of *S. borbonicus* (É. Geoffroy, 1803) on Madagascar, a moderate-sized species originally named from La Réunion. In their review of Malagasy bats, Peterson *et al.* (1995) noted that amongst the considerable collections of specimens they exam-

ined from Madagascar, there was no material of *S. borbonicus*, and only five individuals of *S. robustus* A. Milne-Edwards, 1881, a large-bodied island endemic. Robbins *et al.* (1985) tentatively concluded that based on specimens in the Muséum national d'Histoire naturelle, Paris (MNHN), perhaps three or four species of *Scotophilus* occur on Madagascar: one corresponding to *S. robustus*, another perhaps to *S. borbonicus*, another close to *S. leucogaster* (Cretzschmar, 1830), and the fourth approaching *S. viridis* (Peters, 1852). However, given that the material of the latter three species was in poor condition, as is the lectotype of *S. borbonicus*, they refrained from positive taxonomic identification of these specimens.

Recent bat surveys on Madagascar have resulted in the capture of several examples of *Scotophilus*, which provides material to reexamine species limits of the island's taxa. Further, in the collections of the MNHN there are three older specimens of relatively small *Scotophilus* from western portions of the island, which were apparently unknown to Peterson *et al.* (1995) and pose some difficulties with their specific identification. In this paper we

use morphological characters to examine the species limits between the different *Scotophilus* taxa occurring on Madagascar and those taken elsewhere in the world.

TAXONOMIC NOTES

There are considerable differences of opinion in the species definitions of *Scotophilus* bats, particularly amongst African and western Indian Ocean Island species (cf. Hayman & Hill 1971; Hill 1980; Koopman 1984, 1994; Robbins *et al.* 1985). *Scotophilus robustus* has been considered by some taxonomists as a subspecies of a widespread sub-Saharan species, *S. leucogaster* (Koopman 1994). Further, three mainland African and the La Réunion forms were considered by Koopman (1994) to be closely related and to represent subspecies of the same taxon. Due to priority associated with the original date of publication these were placed under the name *S. borbonicus* and comprised four subspecies: *S. b. nigrnellus* De Winton, 1899, *S. b. viridis*, *S. b. damarensis* Thomas, 1906, and *S. b. borbonicus*. We follow the conclusions of Simmons (in press), at least in part taken from the study of Robbins *et al.* (1985), that the *Scotophilus* from La Réunion is a separate species from the above listed forms occurring on the mainland, *S. b. damarensis* is a synonym of *S. leucogaster*, and that *S. b. nigrnellus* is a synonym of *S. viridis*. We further abide by the conclusions of Robbins *et al.* (1985) and Schlitter *et al.* (1980) in recognizing the smaller African *S. leucogaster*, *S. dinganii* (A. Smith, 1833), and *S. viridis* as distinct species and that *S. robustus* is restricted to Madagascar.

SPECIMENS AND MEASUREMENTS

To investigate the taxonomic identity of *Scotophilus* species from Madagascar and La Réunion we have consulted specimens taken from a variety of localities and housed in several natural history museums: Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology,

Harvard University, Cambridge, Massachusetts (MCZ); Muséum national d'Histoire naturelle, Paris (MNHN); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Université d'Antananarivo, Département de Biologie animale, Antananarivo (UADBA).

When available six external measurements (in mm) were taken from the specimen labels or associated field catalogs of collected specimens and included: total length, tail length, hind foot length, tragus length, ear length, and forearm length. In some cases these measurements were made directly from the museum specimens. Measurements taken from museum labels were made by a variety of collectors using possibly different techniques. Further, weight measures (in g) are available for some individuals. Six wing measurements were also taken from specimens: 1) 3rd digit-metacarpal; 2) 3rd digit-1st phalange; 3) 3rd digit-2nd phalange; 4) 4th digit-metacarpal; 5) 4th digit-1st phalange; and 6) 4th digit-2nd phalange. Further, the tibia length was also measured.

Six cranial and five dental or mandible measurements were made using digital calipers, accurate to the nearest 0.1 mm:

- anterior palatal width (C^1-C^1): taken across the outer alveolar borders of the canines;
- braincase width (BCW): greatest width across skull at mastoid processes;
- complete mandibular tooththrow ($I-M_3$): length from anterior alveolar border of incisors to posterior alveolar border of M_3 ;
- condyloincisive length (CBL): from occipital condyles to anterior-most point of upper incisors;
- greatest skull length (GSKL): from posterior-most part of occipital to anterior-most point of upper incisors;
- greatest zygomatic breadth (ZYGO): width taken across zygomatic arches at the widest point;
- interorbital width (IOW): dorsal width at most constricted portion of skull;
- mandible length (MAND): from the posterior-most portion of the condyles to anterior-most point of upper incisors;
- maxillary tooththrow ($C-M^3$): length from anterior alveolar border of canine to posterior alveolar border of M^3 ;

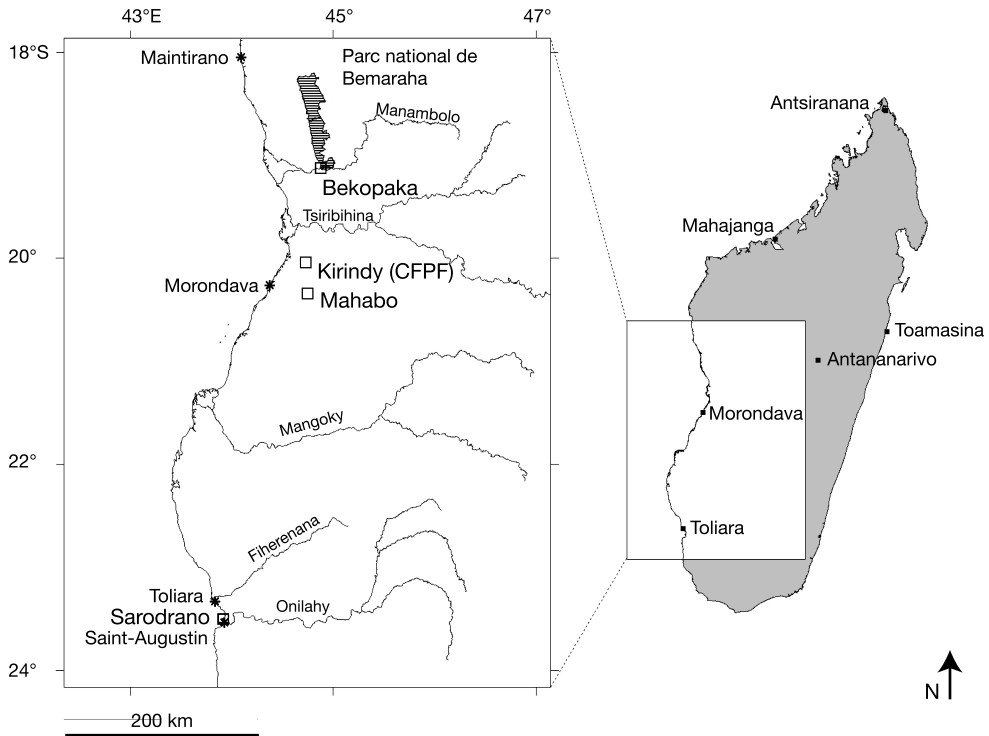


FIG. 1. — Map of Madagascar with localities mentioned in the text. Symbols: □, collection site; *, other localities.

– palatal length (PAL): from posterior border of hard palate to anterior edge of premaxillary bone;
– posterior palatal width (M^3 - M^3): taken across the outer alveolar borders of the third molars.

SPECIMENS OF SMALL *SCOTOPHILUS* FROM MADAGASCAR

We have been able to examine four specimens of moderate to small *Scotophilus* collected on Madagascar. In the MNHN there are two specimens (MNHN 1912.48 and 1976.420) that were obtained by Alphonse Grandidier and catalogued as *S. borbonicus*. On the associated specimen labels the collection locality is noted as “Grottes de Saroundrava”. This is a transcription error from the original specimen labels, which are no longer associated with the specimens, to modern rewritten labels for the locality Grotte de

Sarodrano, a region that A. Grandidier visited during his third trip to Madagascar in 1868 (Vérin & Mantaux 1971). A number of other bat specimens, which are part of the same accession, have original collector’s labels and the site is clearly noted as “Grotte de Sarondrano”, which is the same locality as Sarodrano (Fig. 1). These two specimens were originally preserved in liquid, presumably formalin, and subsequently transferred to ethanol and the skulls extracted and cleaned.

In the same institution there is a third specimen (MNHN 1984.433) of a small *Scotophilus* collected at Mahabo (Fig. 1) on 29 April 1869, and lacking the collector’s name. This date conforms exactly to the period Alphonse Grandidier visited the village of Mahabo (Verin & Mantaux 1971: 22) and there can be little doubt that the specimen was obtained by him. This animal was conserved in liquid and the skull extracted and

cleaned for the current study. The specimen was originally catalogued as “*Eptesicus hottentotus*”, a species unknown from the island, and had apparently escaped the attention of various researchers studying Malagasy bats.

The fourth Malagasy specimen of a small *Scotophilus* was obtained on 27 July 2003 by members of the project “Lamin’asa Fiarovana Ramanavy” or “Bat Conservation Madagascar” just outside the limit of the Parc national de Bemaraha (19°08.454’S, 44°48.524’E; Fig. 1) in an ecotonal area between the forest edge and an agricultural zone. The specimen holds the UADBA number 46923.

The only other record of a small *Scotophilus* on Madagascar that we are aware of is a male specimen netted at Kirindy (CFPF), north of Morondava (Fig. 1), in January 1993 that was deposited in the Université d’Antananarivo, Département de Paléontologie collection. We have been unable to locate this specimen in that collection. External measurements and a description of the pelage coloration of this individual were kindly sent to us by Martin Göpfert.

SYSTEMATICS

Family VESPERTILIONIDAE Gray, 1821

Genus *Scotophilus* Leach, 1821

Scotophilus borbonicus (É. Geoffroy, 1803)

Vespertilio borbonicus É. Geoffroy, 1803: 55.

Scotophilus borbonicus – Jentink 1888: 184.

REMARKS

This species was described by Geoffroy (1803) from the “île de Bourbon” (La Réunion) based on two individuals sent to Paris by a M. Macé. Hill (1980) discusses the historical details of this material. The two specimens were apparently divided between the MNHN and the Musée des Pays-Bas in Leiden, which would be later called the Rijksmuseum van Natuurlijke Historie. Neither of these specimens has been located in the MNHN, nor are they referred to by Rode

(1941) in his catalogue of type specimens in that collection. However, one of the specimens was registered in the museum’s catalog (Moutou 1982). In Jentink’s (1888: 184, entry c) catalogue of bats in the Leiden Museum it is mentioned under the heading *Scotophilus borbonicus* Geoffroy, “Individu adulte monté, figuré dans la Mammalogie de Temminck, T. II, Pl. XLVII, fig. 7. Bourbon. Du voyage de M. Macé”. It is almost without question that this specimen (RMNH 28508) is one of the two animals É. Geoffroy used in the original description of this species, and, based on this logic, Hill (1980) designated it as the lectotype of *S. borbonicus*.

After the inspection of collections and queries at numerous natural history museums, including the MNHN and Muséum d’Histoire naturelle of Saint-Denis (La Réunion), as well as literature citations (e.g., Hill 1980; Moutou 1982; Robbins *et al.* 1985), the lectotype in the RMNH appears to be the only known extant specimen in the world of *S. borbonicus* from La Réunion. It is in very poor condition. The mounted skin has partially extended wings and associated membranes are brittle, partially broken, and the distal portions frayed. An incision made in the lower abdomen, presumably when it was prepared as a mounted skin, is only partially closed. Further, the pelage is foxed, but certain aspects of the original coloration can still be clearly discerned. The dorsum of the specimen is a reddish-brown and the ventrum a dull whitish (Table 1). In Geoffroy’s (1803: 55) original description it is noted, “pelage marron en dessus, blanchâtre en dessous”, which closely fits with our judgment of this specimen’s current coloration. The associated skull is partially broken, with the cranium largely shattered – rendering it impossible to make numerous measurements.

As mentioned earlier, Dorst (1947) noted the occurrence of *S. borbonicus* on Madagascar, presumably based on the Grandidier material in the MNHN. Of the three small Malagasy *Scotophilus* specimens in that collection, one (MNHN 1976.420) from Sarodrano has a distinctly reddish-brown dorsum and light-colored ventrum. This specimen was collected in 1868

TABLE 1. — Patterns of pelage coloration and forearm length in small species of African, western Indian Ocean, and Asian *Scotophilus* (Rosevear 1965; Kingdon 1974; Hill 1980; Robbins *et al.* 1985; Ingle & Heaney 1992; Bates & Harrison 1997; Taylor 2000; specimens in FMNH). The other two species of *Scotophilus* known from Madagascar, *S. cf. borbonicus* and *S. robustus* A. Milne-Edwards, 1881, are also included. **1**, lectotype (RMNH 28508) in very poor condition and precise coloration of specimen is difficult to discern; **2**, there is considerable variation in the pelage coloration of this species, particularly the venter; **3**, pelage coloration and measurements after Robbins (1984).

Species	Dorsum	Throat	Ventrum	Forearm length
<i>S. borbonicus</i>¹	reddish-brown	whitish	whitish	51-52 mm
<i>S. dinganii</i>	olive to grayish-brown	white to yellowish-orange	white to yellowish-orange	50-57 mm
<i>S. kuhlii</i>	chestnut-brown	pale brown	pale brown	50-52 mm
<i>S. leucogaster</i>²	light to medium brown	white to dirty-brown	white to dirty brown	44-53 mm
<i>S. nucella</i>³	dark brown	medium brown	medium brown	50-53 mm
<i>S. nux</i>	dark brown	medium brown	medium brown	53-58 mm
<i>S. robustus</i>	medium brown	medium brown	medium brown	62-65 mm
<i>S. tandrefana</i> n. sp.	dark brown	medium brown	medium brown	44-47 mm
<i>S. viridis</i>	yellowish-brown	white, grayish-white to yellowish	white, grayish-white to yellowish	44-53 mm

and has been stored in alcohol over the intervening years, and thus it is not unexpected that the natural pelage coloration has become washed-out. Even given the poor condition of the lectotype, these two specimens (RMNH 28508 and MNHN 1976.420) showed considerable resemblance in basic pelage coloration and comparable cranial and dental structures (Tables 1-5), and we are inclined to identify MNHN 1976.420 as *S. borbonicus*. However, until new material from La Réunion of *S. borbonicus* is uncovered in museum collections or collected in the wild, final determination of MNHN 1976.420 will not be possible. At the present time we refer this specimen to *S. cf. borbonicus*. The tragus of the MNHN specimen is rounded towards the apex and has a simple peduncle attachment (Fig. 2). In Figure 3 we have illustrated the skull and mandible of MNHN 1976.420 for future comparative purposes.

One striking aspect of the history of moderate to small *Scotophilus* species on Madagascar is that two different sea caves near the village of Sarodrano, presumably exactly at or close to where Grandidier collected his specimens, and the nearby village of Saint-Augustin have been extensively surveyed over the past few years by our field teams and no example of this genus has

been found. While it is true that much of our capture work has been conducted at cave entrances, a site type *Scotophilus* rarely use for their day-roosts, we have surveyed synanthropically-living bat species in the village of Saint-Augustin. Further, the late R. L. Peterson also captured bats in the sea caves of Sarodrano in 1967 and no *Scotophilus* was collected. Even more exceptional is that amongst the two specimens of *Scotophilus* obtained by Grandidier in the Sarodrano region are two different species — *S. cf. borbonicus* and a second species that is new to science and described below. Although the specimen labels indicate that these individuals were captured in caves, it is possible that they were obtained in the nearby village of Sarodrano, which would have been a series of thatched houses during the period of Grandidier's visit, a construction style *Scotophilus* frequently inhabit (Kingdon 1974).

Considerable work has been conducted over the past century of the bats of the Mascarene Islands, particularly La Réunion. The reputed presence of *S. borbonicus* on Mauritius Island is erroneous (Cheke & Dahl 1981), and there is no evidence of a *Scotophilus* on the Comoro Islands (Louette *et al.* 2004). Given that members of this genus are often associated with man-made shelters and are relatively easy to catch, the absence of any

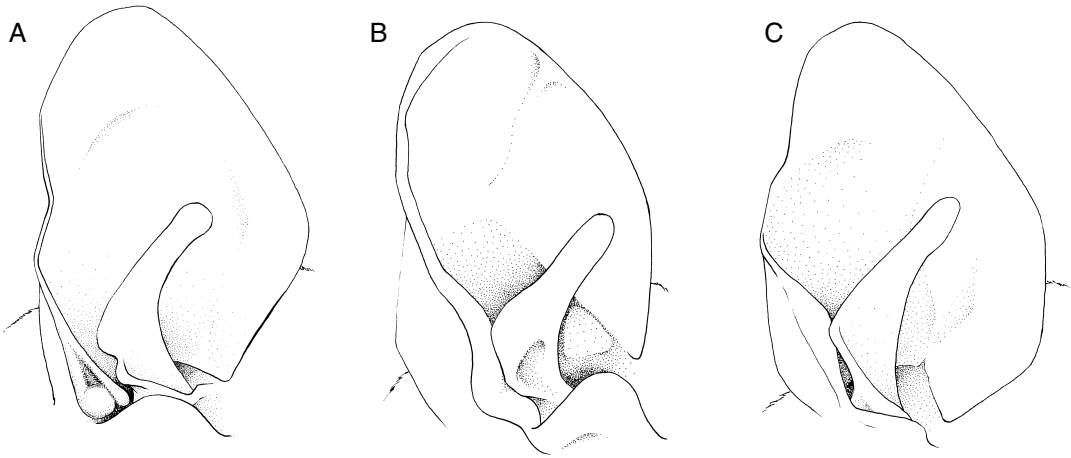


FIG. 2. — Right ear and tragus of *Scotophilus* from Madagascar; **A**, holotype of *S. tandrefana* n. sp. (UADBA 46923); **B**, *S. cf. borbonicus* (MNHN 1976.420); **C**, paratype of *S. tandrefana* n. sp. (MNHN 1984.433). There is some variation in the sickle-shaped tragus of *S. tandrefana* n. sp., but the attachment peduncle of the tragus is a slightly complex structure, rather than a simple attachment stalk as in *S. borbonicus* (É. Geoffroy, 1803).

subsequent records of *S. borbonicus* on La Réunion is rather notable (Cheke & Dahl 1981; Moutou 1982). This would imply that this species is exceptionally rare, difficult to capture, part of an extralimital migratory population, or even extinct. Given that currently available material is insufficient to properly diagnose *S. borbonicus*, the possibility cannot be completely eliminated that the provenance of the two Macé specimens is incorrect or that these captured individuals were vagrants to La Réunion. It has been suggested that *borbonicus* might be conspecific with African *leucogaster* (Hill in Cheke & Dahl 1981). The same point might hold for MNHN 1976.420 in that it may not be a representative of a resident population on Madagascar. In a recent action plan for microchiropteran bats, Hutson *et al.* (2001) listed *S. borbonicus* as occurring on La Réunion and Madagascar and considered it to be critically endangered.

Scotophilus robustus A. Milne-Edwards, 1881

Scotophilus robustus A. Milne-Edwards, 1881: 1035.

REMARKS

The holotype of this species (MNHN 218) was obtained by M. Humblot “entre Foulpointe et le lac d’Alaoutre” in the central portion of the eastern humid forest and was described by Milne-Edwards (1881). The animal was preserved in fluid and the skull has never been extracted. We have examined the holotype specimen in the MNHN, which, together with a second specimen of this taxon, is in a jar labeled “holotype 218, paratype 218a” (in accordance with Rode [1941]) and with two modern catalogue numbers – 1997.1883a and 1997.1883b. There is no MNHN numbered tag on either specimen and it is not possible to differentiate which of the two specimens is the holotype.

S. robustus is characterized by its large size, short rostrum, and well developed sagittal crest (Peterson *et al.* 1995: fig. 57; Tables 2-5). Peterson *et al.* (1995) had five specimens of this species, several without locality data, available to them during their studies of Malagasy bats, and came to the tentative conclusion that *S. robustus* might be limited to the northern portion of the island. Subsequently, it has been captured at a variety of more southerly sites: the Parc national de



FIG. 3. — Dorsal, ventral and lateral views of adult crania and mandible of *Scotophilus cf. borbonicus* (MNHN 1976.420; greatest skull length = 19.0 mm) from Sarodrano.

Zombitse-Vohibasia (22°51'S, 44°43'E, 870 m; FMNH 151939); Parc national de Bemaraha (19°08.287'S, 44°49.618'E, 120 m and 19°07.869'S, 44°48.524'E, 60 m; UADBA uncatalogued); and Andakandava River, St Luce Forest, Tolagnaro (24°59.2'S, 46°57.9'E, 10 m; netted individual that was released). Other new localities this species has been obtained include the Tsinjoarivo Forest (19°42'23"S, 47°50'6"E, 1400 m; FMNH 166186) and Antsahabe Forest, Anjozorobe (18°24.342'S, 47°56.385'E, c. 1400 m; UADBA 46726, 46727, 46734). Thus, *S. robustus* has a broad distribution across much of the island, including all of the distinct biomes with the exception of spiny bush, and has a considerable elevational range. In all cases these new records are of individuals not captured in a synanthropic context.

Scotophilus tandrefana n. sp.
(Figs 3-5; Tables 1-5)

HOLOTYPE. — Adult ♂, 27.VII.2003, R. K. B. Jenkins and F. H. Ratrimomanarivo coll., field number RBJ 161 (UADBA 46923).

The specimen was preserved in formalin and the skull extracted and subsequently cleaned. The specimen is in a good state of preservation, except that the skull has a cut mark across ventral posterior portion. Muscle tissue samples taken from the upper breast were preserved in EDTA, resulting in small cuts across both sides of the chest.

PARATYPES. — Mahabo, 20°23'S, 44°38'E, 29.IV.1869, A. Grandidier, 1 ♀ (MNHN 1984.433); Grotte de Sarodrano, 1868, A. Grandidier, 1 ♀ (MNHN 1912.48).

Both specimens were preserved in fluid and the skulls have been extracted and cleaned.

TYPE LOCALITY. — Madagascar, Province de Mahajanga, just outside the limit of the Parc national de Bemaraha, 1.8 km SE from Bekopaka and 0.6 km NE from Andadoany, 19°08.454'S, 44°48.732'E, about 50 m above sea-level (Fig. 1).

ETYMOLOGY. — The name *tandrefana* is derived from the Malagasy meaning "from the west".

MEASUREMENTS. — Measurements taken directly from the fluid preserved specimen are noted with an asterisk.

External: total length 111 mm, tail length *46 mm, hind foot *7 mm, tragus length 7 mm, ear length *13 mm, forearm length *47 mm.

Weight: 14.2 g.

Skull and teeth: GSKL 17.9 mm, CBL 16.7 mm, ZYGO 12.3 mm, IOW 4.2 mm, BCW 10.5 mm, PAL 8.2 mm, C¹-C¹ 5.9 mm, M³-M³ 7.8 mm, C-M³ 5.8 mm, I-M³ 7.1 mm, and MAND 11.6 mm (Tables 2-4).

DISTRIBUTION. — *Scotophilus tandrefana* n. sp. is currently known from three localities in western Madagascar: Bemaraha, Mahabo, and Sarodrano (Fig. 1) — all below 100 m elevation. On the basis of current information there is no evidence that this species is strictly forest dwelling or synanthropic.

In January 1993 Martin Göpfert and colleagues captured a small *Scotophilus* in the Kirindy (CFPF) Forest to the northeast of Morondava (20°04.6'S, 44°40.5'E, 30 m; Fig. 1). The pelage coloration of this individual was noted as "ventrum being uniformly brown and hair on upper side light brown with dark brown tips" (M. Göpfert pers. comm., 25 May 2004). The forearm was measured as 45.5 mm. On the basis of these characters this individual is probably referable to *S. tandrefana* n. sp.

HABITAT. — The type specimen was captured in a 9 m mist-net placed in an open grassy clearing adjacent to rice fields and disturbed deciduous forest and within 100 m of a limestone outcrop. The original natural habitat of this region is dry semi-deciduous forest and the capture site is about 200 m from the relatively intact natural forest formations of the Parc national de Bemaraha.

DIAGNOSIS. — A member of the genus *Scotophilus* of small size with average forearm length of 44-47 mm. Muzzle is pronounced, relatively short, and pug-like. Slightly elongated crescent-shaped nostrils opening slightly antero-laterally (Fig. 4). Distinctly long forward projecting tragus with a slightly complex peduncle (Fig. 2). Dorsal fur is relatively long, soft, and a uniform dark brown, while the throat and ventral pelage is shorter and finer, and a lighter medium-brown (Fig. 4). Wing membranes and uropatagium dark. Relatively well developed lamboidal and sagittal crests. Dental formula 1/3-1/1-1/2-3/3.

DESCRIPTION

Amongst the three specimens available for study (holotype and two paratypes) there is not a marked difference in fur coloration between the dorsal and ventral surfaces. In the recently collected holotype specimen the dorsal pelage is a dense and rich dark chocolate brown and the basal portions are distinctly lighter brown. The ventrum pelage coloration, including the throat and upper breast, is a medium-brown, that appears to become lighter posteriorly, and basally

TABLE 2. — External measurements (mm) and weights (g) of small *Scotophilus* species. Measurements followed by an asterisk were made by S. M. Goodman from dried or alcohol preserved specimens. Descriptive statistics are presented as mean \pm standard deviation, minimum-maximum, number of specimens. 1, measurements derived from Robbins (1984) and no standard deviations are available for his descriptive statistics.

	Total length	Tail length	Hind foot length	Tragus length	Ear length	Forearm length	Tibia length	Weight
<i>S. borbonicus</i> (RMNH 28508; lectotype) sex undet.	—	—	—	—	—	51*	20.1*	—
<i>S. cf. borbonicus</i> Sarodrano (MNHN 1976.420) ♀	—	47*	9*	7*	13*	52*	21.2*	—
<i>S. tandrefana</i> n. sp.								
Bemarahia (UADBA 46923; holotype) ♀	111	46*	7	7*	13*	47*	18.9*	14.2
Sarodrano (MNHN 1912.48) ♀	—	43*	7.5*	7*	13*	47*	17.8*	—
Mahabo (MNHN 1984.433) ♀	—	—	7.2*	7*	13*	44*	17.3*	—
	111, n = 1	43-46, n = 2	7.2 \pm 0.25 7-7.5, n = 3	7.0 \pm 0.00 7-7, n = 3	13 \pm 0.00 13-13, n = 3	46.0 \pm 1.73 44-47, n = 3	18.0 \pm 0.82 17.3-18.9, n = 3	14.2, n = 1
<i>S. dinganii</i>	138.4 \pm 6.42 124-152, n = 18	55.2 \pm 5.52 45-65, n = 18	11.3 \pm 1.45 8-13, n = 18	9.9 \pm 1.28 8-11, n = 6	16.9 \pm 0.99 15-19, n = 19	54.0 \pm 2.17 50-57, n = 18	—	24.8 \pm 2.11 22-29, n = 7
<i>S. kuhlii</i>	115.3 \pm 7.43 104-128, n = 7	46.6 \pm 4.83 36-51, n = 7	11.7 \pm 1.11 10-13, n = 7	—	12.0 \pm 0.00 12.0-12.0, n = 4	50.5 \pm 1.00 50-52, n = 4	—	—
<i>S. leucogaster</i>	122.0 \pm 8.00 114-130, n = 3	48.0 \pm 4.84 40-52, n = 5	10.8 \pm 1.50 10-13, n = 4	—	14.1 \pm 0.63 13.5-15, n = 4	49.8 \pm 3.37 44-53, n = 6	—	24 n = 1
<i>S. nucella</i> ¹	121 115-125, n = 7	44 41-47, n = 7	—	—	15 15-16, n = 7	51.3 50-53, n = 7	—	21 15-27, n = 7
<i>S. nux</i>	128.0 \pm 4.00 123-133, n = 5	49.4 \pm 3.05 45-53, n = 5	13.5 \pm 3.26 10.5-19, n = 5	—	15.6 \pm 0.42 15-16, n = 5	56.0 \pm 2.00 53-58, n = 5	—	23.2 \pm 3.33 21-27, n = 3
<i>S. robustus</i>	157.2 \pm 4.21 153-163, n = 5	63.2 \pm 5.36 55-70, n = 5	11.8 \pm 1.10 10-13, n = 5	11.5 \pm 1.73 10-13, n = 4	18.4 \pm 1.52 17-20, n = 5	63.8 \pm 1.07 62-65, n = 7	—	44.5 \pm 3.5 40.5-49, n = 5
<i>S. viridis</i>	116.6 \pm 6.32 105-130, n = 22	47.8 \pm 4.10 40-56, n = 25	10.7 \pm 1.09 9-12, n = 24	—	14.4 \pm 1.33 12-17, n = 25	46.7 \pm 5.18 44-53, n = 24	—	17.4 \pm 2.12 14-24, n = 20



FIG. 4. — Color photograph of anterior portion holotype of *Scotophilus tandrefana* n. sp. (UADBA 46923, field number RBJ 161) obtained near the Parc National de Bemaraha (photograph by R. K. B. Jenkins).

a grayish-brown. The paratypes have been stored in fluid for well over a century and the pelage color is washed-out. Nonetheless, the contrasting dark dorsum and slightly lighter ventrum is clearly discernable in these specimens. The wing membrane and uropatagium are dark brownish-black in the holotype. The muzzle is relatively short and rounded (Fig. 4). Slightly elongated almost tubular nostrils open in a slightly lateral position. The upper lips have a regular, but not dense, covering of hairs.

Scotophilus tandrefana n. sp. is a small species in external measurements, particularly when compared to African and Asian members of this genus (Table 2). The black ears are short (13 mm) and fall outside the range of most African species of *Scotophilus*. There is some variation in the sickle-shaped tragus of *S. tandrefana* n. sp.,

but the attachment peduncle of the tragus is a slightly complex structure, rather than a simple attachment stalk as in *S. borbonicus* (Fig. 2). The apex of the tragus terminates as a slightly round-pointed shape in *S. tandrefana* n. sp.

The skull of *S. tandrefana* n. sp. is relatively diminutive in size, particularly when compared to other species of small *Scotophilus* such as *S. leucogaster* and *S. viridis*. *S. tandrefana* n. sp. has a slightly short and broad rostrum (without expanded lacrimal processes), expanded braincase, and tapered postorbital constriction (Fig. 5). The lambdoidal and sagittal crests are well developed, forming the typical “helmet” of members of this genus, but less prominent than in adults of most other species. Posterior palatal extension terminates as acute spine. Zygomatic arches slightly flared. Anterior emargination of palate is



FIG. 5. — Dorsal, ventral, and lateral views of adult crania and mandible of holotype of *Scotophilus tandrefana* n. sp. (UADBA 46923; greatest skull length = 17.9 mm) from near the Parc national de Bemaraha.

TABLE 3. — Cranial measurements (mm) of small *Scotophilus* species. Descriptive statistics are presented as mean \pm standard deviation, minimum-maximum, number of specimens. See Specimens and measurements section for explanation of acronyms. 1, measurements derived from Robbins (1984) and no standard deviations are available for his descriptive statistics.

	GSKL	CBL	ZYGO	IOW	BCW	PAL
<i>S. borbonicus</i> (RMNH 28508; lectotype) sex undet.	—	—	—	—	—	—
<i>S. cf. borbonicus</i> Sarodrano (MNHN 1976.420) ♀	19.0	17.5	12.9	4.8	11.8	8.8
<i>S. tandrefana</i> n. sp. Bemaraha (UADBA 46923; holotype) ♀	17.9	16.7	12.3	4.2	10.5	8.2
Sarodrano (MNHN 1912.48) ♀	17.8	16.8	11.4	4.3	10.5	8.5
Mahabo (MNHN 1984.433) ♀	16.9	15.9	11.5	4.5	10.1	7.9
	17.5 \pm 0.55 16.9–17.9, n = 3	16.5 \pm 0.49 15.9–16.8, n = 3	11.7 \pm 0.49 11.4–12.3, n = 3	4.3 \pm 0.15 4.2–4.5, n = 3	10.4 \pm 0.23 10.1–10.5, n = 3	8.2 \pm 0.30 7.9–8.5, n = 3
<i>S. dinganii</i>	21.2 \pm 0.55 20.0–22.2, n = 19	19.5 \pm 0.44 18.5–20.2, n = 19	14.3 \pm 0.43 13.7–15.1, n = 19	4.74 \pm 0.17 4.4–5.1, n = 19	12.2 \pm 0.38 11.3–12.8, n = 18	9.9 \pm 0.34 9.0–10.5, n = 19
<i>S. kuhlii</i>	19.4 \pm 0.37 18.9–19.9, n = 11	17.9 \pm 0.29 17.5–18.3, n = 11	13.2 \pm 0.31 12.8–13.6, n = 11	4.7 \pm 0.18 4.3–4.9, n = 11	11.2 \pm 0.27 10.8–11.7, n = 11	9.1 \pm 0.15 8.8–9.2, n = 11
<i>S. leucogaster</i>	19.0 \pm 0.93 17.1–20.1, n = 9	17.5 \pm 0.65 16.2–18.2, n = 8	13.4 \pm 0.63 12.0–14.1, n = 10	4.8 \pm 0.24 4.2–5.0, n = 11	11.1 \pm 0.71 10.0–12.2, n = 9	9.0 \pm 0.44 8.3–9.6, n = 10
<i>S. nucella</i>¹	—	17.3 17.1–17.5, n = 7	13.6 13.1–14.0, n = 7	4.9 4.7–5.1, n = 7	9.4 9.2–9.6, n = 7	—
<i>S. nux</i>	20.8 \pm 0.52 20.5–21.7, n = 5	18.9 \pm 0.36 18.5–19.3, n = 5	14.1 \pm 0.35 13.6–14.5, n = 5	5.0 \pm 0.11 4.9–5.2, n = 5	12.2 \pm 0.34 11.8–12.6, n = 5	9.7 \pm 0.36 9.3–10.3, n = 5
<i>S. robustus</i>	25.0 \pm 0.43 24.2–25.6, n = 7	21.8 \pm 0.36 21.4–22.3, n = 7	16.1 \pm 0.42 15.6–16.7, n = 7	5.3 \pm 0.21 5.0–5.5, n = 7	14.0 \pm 0.31 13.6–14.5, n = 7	11.3 \pm 0.05 11.3–11.4, n = 7
<i>S. viridis</i>	18.1 \pm 0.61 17–20, n = 23	16.8 \pm 0.45 16–18.4	12.6 \pm 0.36 11.9–13.4, n = 22	4.4 \pm 0.17 4.1–4.7, n = 23	10.8 \pm 0.41 9.8–11.4, n = 23	8.5 \pm 0.25 7.8–8.9, n = 23

deep and broad. Pterygoids expanded posteriorly and wing-shaped.

The dental configuration is typical of other *Scotophilus* species (Koopman 1994: 128). The single upper pair of incisors is trifid and upper and lower canines well developed and powerful. M¹ and M² have a reduced mesostyle, with a dis-

torted W-shaped cusp pattern, and M³ is greatly reduced in size. PM₁ and PM₂ have the trigonid distinctly larger than the talanoid.

REMARKS

Of the 12 species of *Scotophilus* recognized worldwide by Simmons (in press), the following

TABLE 4. — Dental measurements (mm) of small *Scotophilus* species. Descriptive statistics are presented as mean \pm standard deviation, minimum-maximum, number of specimens. See Specimens and measurements section for acronyms. 1, measurements derived from Robbins (1984) and no standard deviations are available for his descriptive statistics.

	C ¹ -C ¹	M ³ -M ³	C-M ³	I-M ₃	MAND
<i>S. borbonicus</i> (RMNH 28508; lectotype) sex undet.	6.3	7.8	6.4	8.0	12.0
<i>S. cf. borbonicus</i> Sarodrano (MNHN 1976.420) ♀	6.4	8.0	6.3	8.0	12.5
<i>S. tandrefana</i> n. sp.					
Bemaraha (UADBA 46923; holotype) ♀	5.9	7.8	5.8	7.1	11.6
Sarodrano (MNHN 1912.48) ♀	5.6	7.7	5.8	7.5	12.1
Mahabo (MNHN 1984.433)	5.6	7.2	5.3	6.7	—
	5.7 \pm 0.17 5.6-5.9, n = 3	7.6 \pm 0.32 7.2-7.8, n = 3	5.6 \pm 0.29 5.3-5.8, n = 3	7.1 \pm 0.40 6.7-7.5, n = 3	11.6-12.1, n = 2
<i>S. dinganii</i>	7.12 \pm 0.25 6.7-7.6, n = 18	9.1 \pm 0.37 8.4-9.7, n = 19	6.9 \pm 0.18 6.6-7.2, n = 18	8.7 \pm 0.23 8.2-9.1, n = 17	14.3 \pm 0.32 13.3-14.8, n = 18
<i>S. kuhlii</i>	6.0 \pm 0.30 5.7-6.7, n = 11	8.1 \pm 0.24 7.6-8.4, n = 11	6.4 \pm 0.12 6.2-6.7, n = 11	8.3 \pm 0.19 8.0-8.6, n = 10	13.1 \pm 0.23 12.8-13.4, n = 11
<i>S. leucogaster</i>	6.2 \pm 0.28 5.7-6.6, n = 11	8.2 \pm 0.41 7.4-8.6, n = 10	6.3 \pm 0.30 5.6-6.6, n = 11	7.9 \pm 0.57 6.4-8.4, n = 11	12.8 \pm 0.51 12.1-13.4, n = 9
<i>S. nucella</i>¹	—	8.3 7.9-8.9, n = 7	6.5 6.5-6.6, n = 7	—	—
<i>S. nux</i>	6.8 \pm 0.04 6.7-6.9, n = 5	8.8 \pm 0.21 8.6-9.1, n = 5	6.8 \pm 0.07 6.7-6.9, n = 5	8.7 \pm 0.05 8.6-8.7, n = 5	14.0 \pm 0.15 13.8-14.1, n = 5
<i>S. robustus</i>	8.2 \pm 0.32 7.8-8.6, n = 7	9.9 \pm 0.30 9.4-10.3, n = 7	8.0 \pm 0.14 7.8-8.2, n = 7	10.0 \pm 0.25 9.6-10.2, n = 5	16.4 \pm 0.13 16.3-16.9, n = 5
<i>S. viridis</i>	5.9 \pm 0.24 5.2-6.5, n = 23	7.9 \pm 0.31 7.2-8.4, n = 23	5.9 \pm 0.19 5.6-6.5, n = 23	7.5 \pm 0.30 6.9-8.3, n = 23	12.1 \pm 0.44 11.4-13.6, n = 21

species (generalized distribution in parentheses) fall within the approximate size range of *S. tandrefana* n. sp. based on forearm length (Table 1): *S. borbonicus* (La Réunion and possibly Madagascar [see above]), *S. dinganii* (broad range in sub-Saharan Africa), *S. kuhlii* Leach, 1821 (Indonesia to Pakistan), *S. leucogaster* (broad range in sub-Saharan Africa), *S. nucella* Robbins, 1984 (montane zones of western to eastern Africa), *S. nux* Thomas, 1904 (montane zones of western to eastern Africa), and *S. viridis* (broad range in sub-Saharan Africa). Other species not included in these analyses because they are larger

than *S. tandrefana* n. sp. include *S. celebensis* Sody, 1928, *S. heathii* Horsfield, 1831, *S. nigrita* (Schreber, 1774), and *S. robustus* (Koopman 1994; Taylor 2000). One species was excluded because its insular southeastern Asian range is a considerable distance from Madagascar (*S. collinus* Sody, 1936). The other Malagasy members of the genus *Scotophilus* can be easily distinguished from *S. tandrefana* n. sp. These include *S. robustus* based on its notably larger measurements (Tables 2-5) and *S. cf. borbonicus* using pelage coloration and certain cranial measurements (Tables 2; 3).

TABLE 5. — Wing measurements (mm) of small *Scotophilus* species. Descriptive statistics are presented as mean \pm standard deviation, minimum-maximum, number of specimens.

	3rd digit- metacarpal	3rd digit-1st phalange	3rd digit-2nd phalange	4th digit- metacarpal	4th digit-1st phalange	4th digit-2nd phalange
<i>S. borbonicus</i> (RMNH 28508; lectotype) sex undet.	46	—	—	43	—	—
<i>S. cf. borbonicus</i> Sarodrano MNHN 1976.420) ♀	45	18	14	44	13	11
<i>S. tandrefana</i> n. sp. Bemaraha (UADBA 46923; holotype) ♀	41	15	11	40	11	9
Sarodrano (MNHN 1912.48) ♀	42	15	11	41	11	8.5
Mahabo (MNHN 1984.433) ♀	41	14	11	39	11	8.5
	41.3 \pm 0.58 41-42, n = 3	14.7 \pm 0.58 14-15, n = 3	11.0 \pm 0.00 11-11, n = 3	40.0 \pm 1.00 39-41, n = 3	11.0 \pm 0.00 11-11, n = 3	8.7 \pm 0.29 8.5-9, n = 3
<i>S. dinganii</i>	48.1 \pm 1.61 46-50, n = 9	18.9 \pm 1.36 17-22, n = 9	15.4 \pm 0.73 15-17, n = 9	47.9 \pm 1.45 45-50, n = 9	14.6 \pm 0.73 14-16, n = 9	10.9 \pm 0.78 10-12, n = 9
<i>S. kuhlii</i>	42.6 \pm 1.42 41-45, n = 10	15.9 \pm 1.10 41-45, n = 10	11.5 \pm 1.08 10-14, n = 10	42.4 \pm 2.17 39-46, n = 10	13.0 \pm 1.15 11-15, n = 10	9.3 \pm 0.82 8-10, n = 10
<i>S. leucogaster</i>	43.4 \pm 1.77 41-46, n = 10	16.4 \pm 1.51 15-19, n = 10	13.4 \pm 1.17 11-15, n = 10	42.9 \pm 1.91 40-46, n = 10	13.1 \pm 1.10 11-15, n = 10	10.2 \pm 1.14 8-12, n = 10
<i>S. nux</i>	48.5 \pm 0.71 48-49, n = 2	18.0 \pm 1.41 17-19, n = 2	14.0 14-14, n = 2	48.5 \pm 0.71 48-49, n = 2	13.5 \pm 0.71 13-14, n = 2	11.0 11-11, n = 2
<i>S. robustus</i>	56.3 \pm 1.38 54-58, n = 7	20.4 \pm 0.53 20-21, n = 7	14.6 \pm 0.98 13-16, n = 7	55.0 \pm 1.73 53-58, n = 7	15.5 \pm 0.53 15-16, n = 7	11.3 \pm 0.49 11-12, n = 7
<i>S. viridis</i>	36.0 \pm 1.00 35-37, n = 3	14.7 \pm 0.58 14-15, n = 3	12.0 \pm 1.00 11-13, n = 3	36.7 \pm 1.15 36-38, n = 3	12.7 \pm 0.58 12-13, n = 3	10.0 \pm 1.00 9-11, n = 3

S. tandrefana n. sp. can be easily distinguished from several extralimital African and Asiatic members of this genus with approximately the same forearm length (Table 2) by pelage characters. *S. leucogaster*, *S. dinganii*, and *S. viridis* have notably lighter ventrums as compared to their dorsums (Table 1). The remaining three species, *S. nux*, *S. nucella*, and *S. kuhlii* can be differentiated from *S. tandrefana* n. sp. by a variety of external, cranial, and dental measurements (Tables 2-5). Further, the ventral fur coloration of *kuhlii* is notably lighter than the backside. Of the *Scotophilus* species that fall in the same general size-range of *S. tandrefana* n. sp. based on forearm length, *S. nux* and *S. nucella* are the only two that match its basic pelage col-

oration pattern (Table 1), although in both cases these two species are notably larger in numerous cranial measurements (Table 3). The phylogenetic relationships of *S. tandrefana* n. sp. are not addressed here, as R. Trujillo is currently conducting a taxonomic revision of African and Malagasy members of this genus based on morphological and molecular characters. Further, research on the acoustics of members of this genus might provide insight into their phylogenetic relationships.

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