

## **Specific Status of Populations on Madagascar Referred to *Miniopterus fraterculus* (Chiroptera: Vespertilionidae), with Description of a New Species**

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Source: Journal of Mammalogy, 88(5):1216-1229. 2007.

Published By: American Society of Mammalogists

DOI: <http://dx.doi.org/10.1644/06-MAMM-A-285R1.1>

URL: <http://www.bioone.org/doi/full/10.1644/06-MAMM-A-285R1.1>

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# SPECIFIC STATUS OF POPULATIONS ON MADAGASCAR REFERRED TO *MINIOPTERUS FRATERCULUS* (CHIROPTERA: VESPERTILIONIDAE), WITH DESCRIPTION OF A NEW SPECIES

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A new species of bat of the genus *Miniopterus* is described from Madagascar based on a series of specimens taken in the Central Highlands of the island. This new species previously was identified as *M. fraterculus*, which is widespread in portions of eastern and southern Africa. Comparisons between these 2 taxa were further complicated because *M. fraterculus* occurs in portions of its range in sympatry with a morphologically similar species, *M. natalensis*. Based on specimen material and associated tissue samples from near the type localities of *M. natalensis* and *M. fraterculus*, as well as access to some of the critical type specimens, morphological and genetic molecular analyses were used to determine that Malagasy specimens previously assigned to *M. fraterculus* represent a previously unrecognized species of *Miniopterus* endemic to the island. Given that the habitat used by *Miniopterus* sp. nov. is not necessarily associated with native forest, that it has a broad distribution across the Central Highlands, and that it has been found in synanthropic situations, this species is not considered a conservation concern.

Key words: Africa, Chiroptera, Madagascar, *Miniopterus*, new species, Vespertilionidae

The bat genus *Miniopterus* Bonaparte, 1837, is broadly distributed in the Old World. The history of speciation in this genus is complex, because, for example, in several documented cases, based on molecular data, morphologically similar sympatric species are not each other's closet relatives and there are numerous cases of phenotypic convergence. Paraphyly among several "species" is not uncommon and many details of the evolutionary history and systematics of this group remain to be resolved (Appleton et al. 2004; Cardinal and Christidis 2000; Miller-Butterworth et al. 2005); this is certainly the case on Madagascar. Herein we examine the species relationships of 1 taxon known from this island, *M. fraterculus* Thomas and Schwann, 1906, based on morphological and molecular characters. This taxon currently is thought to have a broad distribution in portions of eastern and southern Africa, as well as Madagascar.

Between the compilation of Koopman (1993) and that of Simmons (2005) of bats for 2 different editions of *Mammal Species of the World* (Wilson and Reeder 1993, 2005), the number of species in the genus *Miniopterus* increased from 10 to 17. During the interim only 1 species was described, *M. gleni* Peterson et al. (1995) from Madagascar, and the additional 6 are the result of the division of paraphyletic complexes into separate species. For example, within the *M. schreibersii* (Kuhl, 1817) group, the subspecies *majori* Thomas, 1906 (Madagascar), and *natalensis* (A. Smith, 1834) (portions of sub-Saharan Africa and the Arabian Peninsula) were elevated to full species. Subsequent molecular analyses have shown that even after these taxonomic changes, the remaining *M. schreibersii* complex still remains nonmonophyletic, as do some other broadly distributed species such as *M. australis* Tomes, 1858 (Appleton et al. 2004; Miller-Butterworth et al. 2005).

The taxonomic history of *Miniopterus* on Madagascar is complicated. Researchers have presented diverse numbers of species and species associations for the Malagasy forms (Table 1). Until the early 1990s, generally 2 taxa were recognized, one being the most diminutive form on the island, with the epithet

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**TABLE 1.**—Comparison of the species of *Miniopterus* recognized on Madagascar during past 50 years.

| Dorst (1947)     | Jones et al. (1982)             | Koopman (1993)         | Hill (1993)                   | Koopman (1994)           | Peterson et al. (1995)               | Simmons (2005)        |
|------------------|---------------------------------|------------------------|-------------------------------|--------------------------|--------------------------------------|-----------------------|
| <i>M. manavi</i> | <i>M. minor</i> [manavi]        | <i>M. minor</i>        | <i>M. minor manavi</i>        | <i>M. manavi</i>         | <i>M. manavi</i>                     | <i>M. manavi</i>      |
| <i>M. majori</i> | <i>M. schreibersii</i> [majori] | <i>M. schreibersii</i> | <i>M. schreibersii majori</i> | <i>M. schreibersii</i>   | <i>M. majori majori</i> <sup>a</sup> | <i>M. majori</i>      |
|                  |                                 |                        | <i>M. fraterculus</i>         | <i>M. f. fraterculus</i> | <i>M. fraterculus</i>                | <i>M. fraterculus</i> |
|                  |                                 |                        | <i>M. inflatus</i>            |                          | <i>M. gleni</i>                      | <i>M. gleni</i>       |
|                  |                                 |                        |                               | <i>M. minor</i> ?        |                                      |                       |
|                  |                                 |                        |                               | <i>M. magnater</i> ?     |                                      |                       |

<sup>a</sup> Also separating African *M. natalensis* from *M. schreibersii*.

*manavi* Thomas, 1906, and assumed belonging to the African *M. minor* Peters, 1867, group, and the other with the name *majori* and generally placed as a subspecies of the broadly distributed *M. schreibersii* (Dorst 1947; Jones et al. 1982). Hill (1993) listed 4 taxa for the island, all belonging to African species; the 2 cases mentioned above, as well as the African species *M. fraterculus* and *M. inflatus* Thomas, 1903. In her recent treatment of bats of the world, Simmons (2005) included 4 taxa of *Miniopterus* on Madagascar: *manavi*, *majori*, *gleni*, and *fraterculus*—all endemic to the island except the last species, which also occurs in portions of sub-Saharan Africa. These varied taxonomic treatments of Malagasy *Miniopterus* are the result of at least 2 factors: the meager collections of certain forms from the island were not sufficient to properly assess inter- and intraspecific variation, and the difficulties in differentiating species. Over the past few decades, bat surveys have been conducted across much of Madagascar and voucher specimens, with associated tissue samples, have been collected. We are now in the position to better evaluate the systematics of Malagasy *Miniopterus* based on morphological and molecular studies.

In Africa, *M. fraterculus*, which was named from specimens collected at Knysna in the southern Cape Province, South Africa (Thomas and Schwann, 1906), generally is characterized as a species of lower elevations (e.g., Taylor 2000). The type series was collected in a sea cave. Based on published information, this low-elevation range is in notable contrast to records of this species on Madagascar, where it is restricted to moderate to relatively high elevations from 500 to 2,000 m above sea level (Eger and Mitchell 2003). The rather divergent habitats used by *M. fraterculus* in its southern African and Madagascar ranges called into question the determination of the Malagasy animals as *M. fraterculus*. Within this paper, the 1st of a series on Malagasy members of this genus, we examine this query using both morphological and molecular data sets.

## MATERIALS AND METHODS

*Morphological comparisons and analyses.*—To ensure the appropriate comparisons of specimens from African populations of *M. fraterculus* with the Malagasy animals, we used only specimens referable to *M. fraterculus* that were collected in the general vicinity of its terra typica, the Cape Province of South Africa. Further, we examined the holotype of *M. fraterculus* from Knysna, South Africa (BMNH 5.5.7.18), and we used a topotype from the same locality (BMNH

5.5.7.22) in comparisons to the Malagasy material. This analysis is complicated by the fact that *M. natalensis* occurs in sympatry with *M. fraterculus* across the southern portion of South Africa. Morphologically, the 2 species are very similar to one another (Stoffberg et al. 2004), and numerous museum specimens of these 2 taxa are misidentified. However, several external, cranial, and dental characteristics have been identified that distinguish these species (Stoffberg et al. 2004; see “Comparisons” section below).

To understand the taxonomic relationships of bats referred to *M. fraterculus* from Madagascar and those taken in southern and eastern South Africa, we examined specimens from several different natural history museums, including AMNH—American Museum of Natural History, New York; BMNH—The Natural History Museum, London (formerly British Museum of Natural History); DM—Durban Natural Science Museum, Durban; FMNH—Field Museum of Natural History, Chicago; ROM—Royal Ontario Museum, Toronto; TM—Transvaal Museum, Pretoria; and USNM—The National Museum of Natural History (formerly The United States National Museum), Washington, D.C.

Six standard external measurements (in millimeters) were taken from Malagasy specimens before preparation: total length, tail length, hind-foot length (not including claw), tragus length, ear length, and forearm length (FA). Most of the recent specimens from Madagascar were collected by SMG and the external measurements of these animals were consistent. Mass was measured with the use of a spring balance and recorded in grams. Unless otherwise specified, measurements are reported for adults only (defined by presence of a fully erupted permanent dentition and fused basisphenoid–basisoccipital suture). Tooth abbreviations include: I = incisor, C = canine, P = premolar, and M = molar. Uppercase abbreviations are used for upper teeth and lowercase abbreviations for lower teeth.

Nine cranial or mandibular and 7 dental measurements were taken using a digital caliper to the nearest 0.1 mm. Cranial measurements include: greatest skull length (GSKL)—from posteriormost part of occipital to anteriormost point of upper incisors; condyloincisive length (CIL)—from occipital condyles to anteriormost point of upper incisors; greatest zygomatic breadth (ZYGO)—width taken across zygomatic arches at the widest point; postorbital breadth (POB)—dorsal width at most constricted part of skull; mastoid breadth (MAST)—maximum width of skull across mastoid processes; greatest braincase width (GBW)—breadth at widest portion of braincase; palatal length (PAL)—from posterior edge of palatal

emargination to anterior edge of mesopterygoid fossa; lachrymal width (LW)—greatest width across rostrum at lachrymal projections; and mandible length (MAND)—from the posteriormost portion of the condyles to anteriormost point of upper incisors.

The dental measurements include: complete cranial toothrow (I1–M3)—length from anterior alveolar border of incisors to posterior alveolar border of 3rd molar (M3); complete canine–molar toothrow (C–M3)—length from anterior alveolar border of canine to posterior alveolar border of 3rd molar (M3); width across upper canines (C1–C1)—taken across the outer alveolar borders of the canines; width across 3rd upper molars (M3–M3)—taken across the outer alveolar borders of the 3rd molars; upper molar toothrow length (UPMOLS)—length of upper postcanine molariform toothrow; complete mandibular toothrow (i1–m3)—length from anterior alveolar border of incisors to posterior alveolar border of 3rd molar (m3); and lower molar toothrow length (LWMOLS)—length of lower postcanine molariform toothrow.

On the basis of a series of univariate statistical analyses, no evidence of sexual dimorphism was found in the measured specimens of *Miniopterus* from Madagascar and, therefore, adults of both sexes are combined in subsequent analyses presented herein. In order to distinguish Malagasy animals assigned to *M. fraterculus* from African taxa in this same genus, a principal component analysis was conducted using the statistical package Statistica (version 7.0; Statsoft, Tulsa, Oklahoma); data were not log-transformed and the unrotated option was used. Separate analyses were conducted for cranial and dental measurements. Herein we follow the classification for members of the genus *Miniopterus* proposed by Simmons (2005).

When making comparisons to material of *M. fraterculus*, we have limited these to specimens collected in the southern and eastern portions of South Africa, near the type locality of this species. Using a series of characters, discussed in the “Comparisons” section below, this allowed us to differentiate between specimens of *M. fraterculus* and *M. natalensis*. This aspect was critical in providing confidence that comparisons were correctly made to Malagasy animals, without complications associated with misidentified museum specimens or paraphyly in either *M. fraterculus* or *M. natalensis*.

**Molecular analysis.**—Further clarification of the species status of the Malagasy animals referred to *M. fraterculus* was sought using molecular analyses. The 5' end of the cytochrome-*b* gene was chosen because it has been shown previously to be informative at the species level in the study of miniopterine bats (Cardinal and Christidis 2000; Miller-Butterworth et al. 2005). Researchers who were unaware of the results of morphological analyses conducted the molecular analyses. Data sets were only compared once they were completed. The genetic data set includes new sequences obtained from specimens of *M. “fraterculus”* from Madagascar, *M. fraterculus*, *M. natalensis*, *M. gleni*, *M. manavi*, and *M. majori*. The specimens of *M. “fraterculus”* from Madagascar used for genetic analysis originated from 2 localities in the Central Highlands. Tissue samples were not available from other Malagasy collection localities from which specimens have been

identified as *M. “fraterculus”*; these are referred to as *Miniopterus* sp. in Figure 1.

In line with the morphological portion of this study, the genetic analyses have included sequences of African *M. fraterculus* from the vicinity of its terra typica to ensure that appropriate comparisons were made with Malagasy animals. Because of the complicating fact that *M. natalensis* occurs in sympatry with and is difficult to distinguish from African populations of *M. fraterculus*, we included sequences of *M. natalensis*. The similarity in the morphology of *M. “fraterculus”* from Madagascar and *M. majori* prompted us to also include sequences of the latter in the genetic analysis. Where possible, sequences were obtained from individuals that were included in the morphological analyses. New sequences from Malagasy *M. gleni* and *M. manavi* also were included. These extra species were incorporated in the genetic analyses to ensure that the phylogenetic relationships between the species of interest would be revealed. A GenBank sequence of *M. schreibersii pallidus* (AY614736) was included for comparison, as were sequences from Asian “*M. australis*” (AY614735) and Australian “*M. schreibersii*” (AY614733).

There was some similarity in morphology between *M. “fraterculus”* from Madagascar and *M. australis*; however, previous studies have shown that *M. australis* is unrelated to lineages found on the African continent (Appleton et al. 2004; Miller-Butterworth et al. 2005). The phylogenetic position of miniopterine bats within the larger phylogeny of bats is unclear: according to traditional taxonomy, they represent a subfamily within the Vespertilionidae, but examination of recent data suggests that they might warrant recognition as a separate family (Hooper and Van Den Bussche 2003; Kawai et al. 2002). Thus, it is difficult to select an appropriate outgroup for the genus. In agreement with the study by Miller-Butterworth et al. (2005), use of outgroup taxa from other vespertilionid genera or from Asian *Miniopterus* did not alter the tree topology significantly (data not shown).

Genomic DNA was extracted using a lithium chloride and chloroform extraction method as described by Gemmel and Akiyama (1996). Mitochondrial DNA-enriched extractions also were performed on representatives according to the alkaline lysis procedure described by Tamura and Aotsuka (1988). A fragment of the mitochondrial cytochrome-*b* gene was amplified and sequenced using the primers L14115 and H14542 (Smith and Patton 1991). Template DNA was amplified by polymerase chain reaction in 25- $\mu$ l reaction volume containing the following: 1X reaction buffer (Promega, Madison, Wisconsin), 2.5 mM MgCl<sub>2</sub>, 0.2  $\mu$ M of each deoxynucleoside triphosphate, 0.28  $\mu$ M of each primer, 1 unit of Taq polymerase (Promega), and approximately 100 ng of template DNA. Cycling consisted of an initial denaturation at 94°C for 3 min, followed by 30 cycles at 94°C for 30 s, 45°C for 30 s, and 72°C for 40 s, and a final extension of 72°C for 3 min. The single polymerase chain reaction product was directly sequenced using the ABI Prism BigDye Cycle Sequencing kit (Applied Biosystems, Perkin-Elmer, Melbourne, Australia) according to the manufacturer's instructions. Sequencing products were visualized on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems, Perkin-Elmer). The

**TABLE 2.**—External measurements (in millimeters) and mass (in grams) of *Miniopterus sororculus*, *M. fraterculus*, and *M. natalensis* (both from the eastern and southern portion of South Africa), and *M. majori*. Measurements presented as mean  $\pm$  SD, minimum and maximum measurements, and number of specimens. Figures in bold are of specimens collected and measured by SMG and those marked with a lowercase letter (a) were made from fluid-preserved specimens.

|                               | Total length  | Tail length  | Hind-foot length  | Tragus length   | Ear length   | Forearm length   | Body mass  |
|-------------------------------|---|--|---|---|--|--|--|
| <i>Miniopterus sororculus</i> |   |  |   |   |  |  |  |
| Holotype FMNH 177259 ♀        | <b>108</b>  | <b>53</b>  | <b>7</b>  | <b>8</b>  | <b>11</b>  | <b>43</b>  | <b>7.4</b>   |
| Other adults                  | <b>110.7 <math>\pm</math> 2.83,</b><br><b>105–115,</b><br><b>n = 21</b> | <b>54.5 <math>\pm</math> 1.83,</b><br><b>51–58,</b><br><b>n = 21</b> | <b>6.7 <math>\pm</math> 0.64,</b><br><b>6–8,</b><br><b>n = 21</b> | <b>6.7 <math>\pm</math> 0.66,</b><br><b>6–8,</b><br><b>n = 21</b> | <b>10.7 <math>\pm</math> 0.64,</b><br><b>10–12,</b><br><b>n = 21</b> | <b>43.5 <math>\pm</math> 0.87,</b><br><b>42–45,</b><br><b>n = 21</b> | <b>8.0 <math>\pm</math> 0.66,</b><br><b>7.0–9.1,</b><br><b>n = 20</b>  |
| <i>M. fraterculus</i>         |   |  |   |   |  |  |  |
| Holotype BMNH 5.5.7.18 ♂      | —   | 52   | —   | 4   | 9  | 43.3 <sup>a</sup>  | —  |
| Topotype BMNH 5.5.7.22 ♂      | —   | 53   | —   | 4   | 12   | 42.7 <sup>a</sup>  | —  |
| Adults                        | 102.9 $\pm$ 6.2,<br>97–118,<br>n = 11                                   | 49.8 $\pm$ 5.23,<br>42–57,<br>n = 11                                 | 8.9 $\pm$ 1.06,<br>7–10,<br>n = 10                                | 5.3 $\pm$ 2.31,<br>4–8,<br>n = 3                                  | 9.2 $\pm$ 0.74,<br>7–10,<br>n = 9                                    | 43.5 $\pm$ 0.69,<br>41.8–44.1,<br>n = 12                             | 8.4 $\pm$ 0.87,<br>6.8–9.2,<br>n = 6                                   |
| <i>M. majori</i>              |   |  |   |   |  |  |  |
| Holotype BMNH 97.9.1.38 ♀     | —   | —  | —   | —   | —  | 45.2 <sup>a</sup>  | —  |
| Adults                        | <b>115.6 <math>\pm</math> 2.43,</b><br><b>112–120,</b><br><b>n = 40</b> | <b>55.5 <math>\pm</math> 1.89,</b><br><b>51–60,</b><br><b>n = 40</b> | <b>7.7 <math>\pm</math> 0.53,</b><br><b>7–9,</b><br><b>n = 38</b> | <b>7.3 <math>\pm</math> 0.45,</b><br><b>7–8,</b><br><b>n = 40</b> | <b>11.9 <math>\pm</math> 0.46,</b><br><b>11–13,</b><br><b>n = 40</b> | <b>45.4 <math>\pm</math> 0.91,</b><br><b>43–47,</b><br><b>n = 39</b> | <b>9.7 <math>\pm</math> 0.94,</b><br><b>8.4–12.5,</b><br><b>n = 39</b> |
| <i>M. natalensis</i>          |   |  |   |   |  |  |  |
| Adults                        | 105.5 $\pm$ 6.13,<br>95–116,<br>n = 16                                  | 50.7 $\pm$ 4.66,<br>41–57,<br>n = 16                                 | 9.9 $\pm$ 0.98,<br>9–11,<br>n = 14                                | 5.0 $\pm$ 0.82,<br>4–6,<br>n = 4                                  | 10.6 $\pm$ 1.15,<br>9–13,<br>n = 16                                  | 44.7 $\pm$ 1.38,<br>43–47,<br>n = 12                                 | 10.6 $\pm$ 2.14,<br>6.5–13.9,<br>n = 11                                |

sequences were aligned using Sequencher version 4.6 (Gene Codes Corporation, Ann Arbor, Michigan). Newly produced sequences and those collected from GenBank were overlapping but partially offset so sequences were trimmed to match, with a final 414 base pairs (bp) of sequence used in the analysis. All new sequences were deposited in GenBank (accession numbers DQ899760–DQ899780).

Analysis using DNA strider (Marck 1990) showed that sequences did not contain insertions, deletions, or stop codons. Maximum-parsimony and minimum-evolution (neighbor-joining) phylogenetic analyses were conducted using PAUP\* 4.0 (Swofford 2003). Heuristic maximum-parsimony searches were conducted using the random addition option and the tree-bisection-reconnection (TBR) branch-swapping algorithm. The neighbor-joining method used pairwise sequence distances estimated by Kimura's 2-parameter model (Kimura 1980). Nodal support of maximum-parsimony and neighbor-joining trees was estimated by 1,000 bootstrap pseudoreplicates.

Modeltest 3.6 (Posada and Crandall 1998) was used to determine the most appropriate model of molecular evolution before maximum-likelihood analysis was conducted in PAUP\*. The model, HKY+I+G, was estimated under the Akaike information criterion and was incorporated into the heuristic searches and bootstrapping (1,000 pseudoreplicates) for the maximum-likelihood analysis. Modeltest estimated parameters settings with base frequencies = 0.3085, 0.3079, 0.1154, and 0.2682; proportion of invariable sites = 0.6017; and shape parameter of gamma distribution = 1.6861. All characters were equally weighted and unordered. Bayesian analysis was conducted using the program MrBayes version 3.1.2 (Ronquist

and Huelsenbeck 2003). The HKY+I+G model was specified, flat priors were used, and starting trees were random. We ran 4 chains (1 hot and 3 cold) for 1,000,000 generations, sampling trees every 100 generations. We ensured that our Bayesian runs achieved sufficient convergence by ascertaining that the average standard deviation of split frequencies between chains had reached below 0.01 at the end of the run and that the potential scale reduction factor (PSRF) of each parameter stayed within  $0.997 < \text{PSRF} < 1.003$ . Plots of generation versus the log probabilities of observing actual data did not reveal any trends for the last 75% of generations. We excluded the first 250,000 generations from the calculation of posterior probabilities.

## DESCRIPTION OF THE NEW SPECIES

### *Miniopterus sororculus* sp. nov.

*Holotype*.—FMNH 177259 (field number SMG 13560) collected 23 March 2003 by Steven M. Goodman. The specimen was prepared in formaldehyde and subsequently transferred to 70% ethanol. Before preservation, the skull, which is in fine condition, was removed, conserved in dilute ethanol, and then cleaned using dermestid beetles (Dermestidae). During the extraction of the skull, small incisions were made on either sides of the mouth. Pectoral muscle samples from the individual were collected and saved in lysis buffer. The specimen has a full adult dentition and the basisphenoid–basioccipital sutures are completely fused. External measurements are total length 108 mm, tail length 53 mm, hind-foot length (without claws) 7 mm, tragus length 8 mm, ear length 11 mm, and forearm length 43 mm. Animal weighed 7.4 g (Table 2).

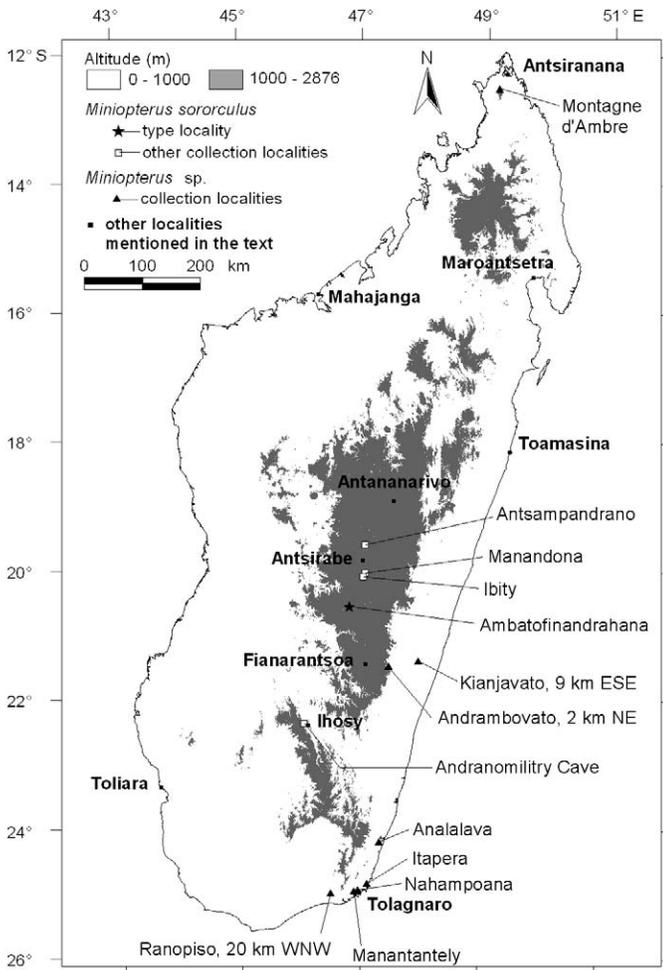


FIG. 1.—Map of Madagascar showing some topographic features, localities mentioned in the text, and sites where specimens of *Miniopterus sororculus*, including the holotype, and the yet unidentified *Miniopterus* were collected.

*Type locality*.—Madagascar: Province de Fianarantsoa, 3 km south of Ambatofinandrahana, in unnamed cave, 20°34.321'S, 46°48.530'E, 1,450 m (Fig. 1).

*Paratypes*.—From same locality as holotype: FMNH 177255–177258, 177260, collected 23 March 2003 (S. M. Goodman).

*Specimens referred to Miniopterus sororculus*.—From north to south, all from Madagascar—FMNH 177261–177274, 177293, collected 26 March 2003 (S. M. Goodman), Province d'Antananarivo, Station Forestière d'Antsampandrano, 26 km SE de Faratsiho, 19°36.720'S, 47°03.770'E, 1,850 m; ROM 42719, 42721, 42723, 42725, 42727, 42729, 42731, 42733, 42735, collected 16 May 1967 (R. L. Peterson, J. Williams, and R. Glen), Province d'Antananarivo, caves of Manandona, high on mountain side, [20°03'S, 47°04'E], 6,600 feet [= 2,200 m]; FMNH 179402, 179403, collected 25 May 2003 (A. Ravoahangy), Province de Fianarantsoa, Ibity Massif, Tombamboanjo, 1,725 m; FMNH 184467, 184468, collected 11 November 2004 (F. Ratriomanarivo and J. Rakotomavo), Province de Fianarantsoa, Ihoay commune rurale, Ankily,

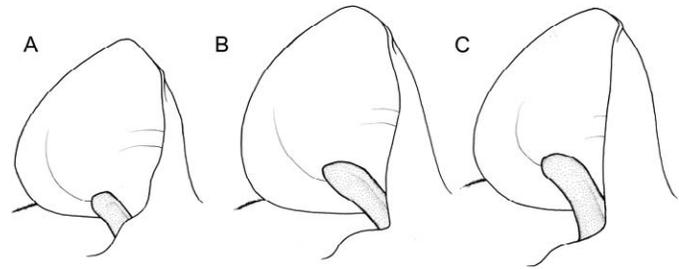


FIG. 2.—Left ear and tragus of *Miniopterus* from Africa and Madagascar. A) *M. fraterculus* (FMNH 96270) from Zambia. B) *M. sororculus* (ROM 42628) from the caves of Manandona near Antsirabe, Madagascar. C) *M. majori* (FMNH 187661) from near Ranomafana, Ifanadiana, Madagascar.

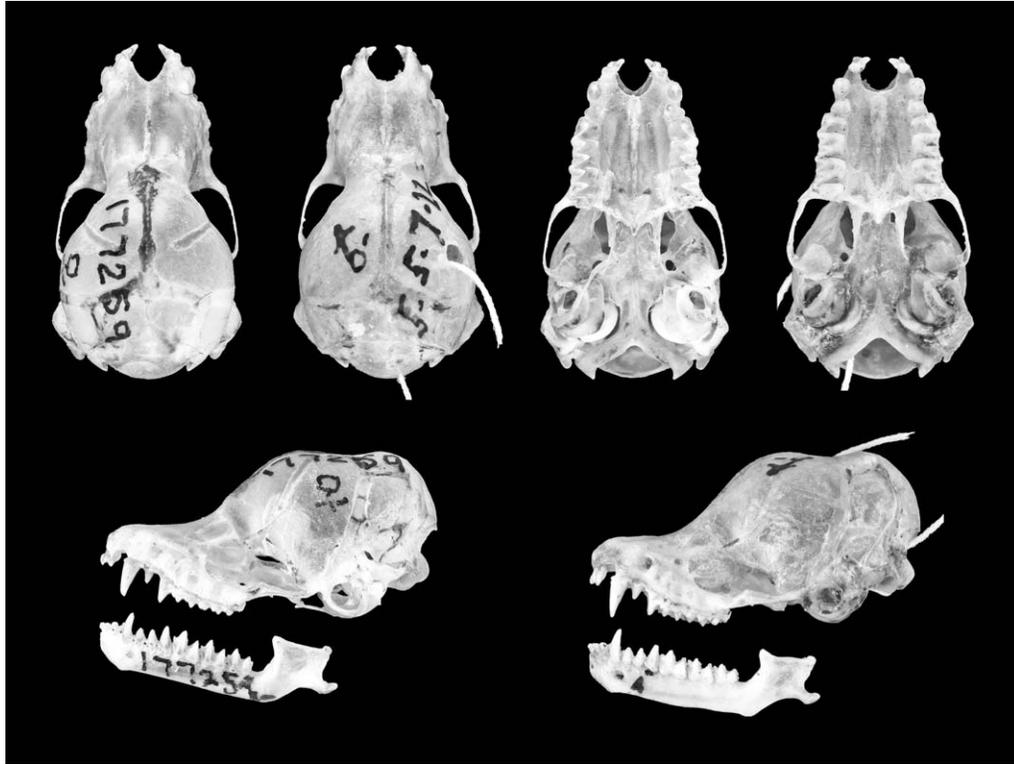
Grotte d'Andranomilitry, 22°23.111'S, 46°03.385'E, 950 m (Fig. 1). Additional specimens from Madagascar previously assigned to *M. fraterculus*, but which are morphologically different from *M. sororculus*, are presented in Appendix I under the name *Miniopterus* cf. *sororculus*.

*Diagnosis*.—A medium-sized species of *Miniopterus* with rich, dark brown-colored pelage and a forearm length of 42–45 mm. Tragus with relatively long, curved projection, 6–8 mm in length, and with laterally thickened base. From dorsal view, cranial palatal emargination with narrow base and distinctly V-shaped. Posterior portion of zygomatic arch slender. Dorsally pointed projection along midportion of zygomatic arch. Well-developed lingual ledge to 1st upper premolar (P2).

*Description*.—A medium-sized *Miniopterus* with a tail approximately one-half of the total body length (Table 2). In the majority of specimens, dorsal pelage is notably dense, relatively long, slightly silky, and with a rich, dark brown color; ventrum is similar in pelage texture, but slightly paler in coloration. In a few individuals, dorsal pelage approaches a medium dark brown. The wing membrane and uropatagium are dark brownish black and show no noticeable change in coloration across their surface area. Dorsally, particularly close to the humerus head, and ventrally, there is a slight extension of the body pelage on to the wing membranes.

The ear length of *M. sororculus* is on average 10.7 mm (range 10–12 mm,  $n = 21$ ; all measured by the same field collector) and is not markedly different from that of other members of this genus with approximately the same body size as measured by forearm length. The tragus length is relatively long, particularly with respect to African *Miniopterus* of similar body size (Table 2), and measures on average 6.7 mm (range 6–8 mm,  $n = 21$ ; all measured by the same field collector). Along the midportion of the tragus, there is a slight constriction and distally it tapers to an asymmetric rounded point (Fig. 2). There is no notable elongation of the nostrils into tubelike structures.

The skull of *M. sororculus*, as with other members of this genus, has a notably short and broad rostrum and a relatively bulbous braincase (Fig. 3; Table 3). When viewed from above, palatal emargination in *M. sororculus* is distally more closed and proximally more angular, giving a V-shape. This is compared to *M. fraterculus*, for which emargination is distally



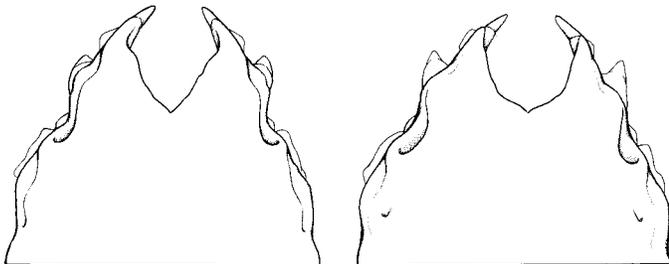
**FIG. 3.**—Different views of skulls and mandibles of *Miniopterus* from Madagascar and Africa. Left) Holotype of *M. sororculus* (FMNH 177259) from near Ambatofinandrahana. Right) Topotype of *M. fraterculus* (BMNH 5.5.7.22) from near Knysna, South Africa. Views include dorsal view of cranium (upper row, left), ventral view of cranium (upper row, right), and lateral view of cranium and mandible (lower row). Photograph taken by J. Weinstein, Field Museum image number Z94450-09d.

more open and proximally more rounded, giving an open U-shape (Fig. 4). The proximal portion of the zygomatic arm in *M. sororculus* tends to be notably narrower and a more fragile structure than in *M. fraterculus* (Fig. 5). Further, along the medial portion of the arm there is a dorsally pointed projection in *M. sororculus*, which is not developed or at all present in the specimens of *M. fraterculus* we have examined. Toothrows in *M. sororculus* are relatively short for an animal of its size, not in parallel, and diverging posteriorly (Table 4).

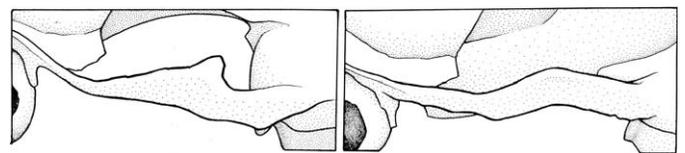
Dental formula is  $i\ 2/3, c\ 1/1, p\ 2/3, m\ 3/3$ , comprising the adult dentition of 36 teeth. First upper premolar (P2) is relatively small and with more simple cusp morphology than

2nd upper premolar (P3), typical of members of this genus (Koopman 1994). In general, the dentition of *M. sororculus* is typical of medium-sized *Miniopterus*. One notable and consistent difference between this taxon and *M. fraterculus* is that in the former the 1st upper premolar (P2) has a distinct lingual ledge that is not well developed in the latter (Fig. 6).

*Habitat.*—The holotype of *M. sororculus* was collected in a small limestone cave surrounded by pseudosteppe at 1,450 m. The region near Ambatofinandrahana, the type locality, has been largely cleared of its natural forest cover and certain zones have been replanted with introduced trees. Numerous rock outcrops occur in the area, being a mixture of marble and calcareous formations, and in some cases contain shallow caves.



**FIG. 4.**—Dorsal view of palatal emargination of *Miniopterus* from Madagascar and Africa. Left) Holotype of *M. sororculus* (FMNH 177259) from near Ambatofinandrahana. Right) Topotype of *M. fraterculus* (BMNH 5.5.7.22) from near Knysna, South Africa.



**FIG. 5.**—Lateral view of the zygomatic arm in *Miniopterus* from Madagascar and Africa. Left) Holotype of *M. sororculus* (FMNH 177259) from near Ambatofinandrahana. Right) Topotype of *M. fraterculus* (BMNH 5.5.7.22) from near Knysna, South Africa.

**TABLE 3.**—Cranial measurements (in millimeters) of adult *Miniopterus sororculus*, *M. fraterculus*, and *M. natalensis* (both from the eastern and southern portion of South Africa), and *M. majori*. Measurements presented as mean  $\pm$  SD, minimum and maximum measurements, and number of specimens. See “Materials and Methods” for an explanation of variable acronyms.

|                           | GSKL                                     | CIL                                      | ZYGO                                  | POB                                   | MAST                                  | GBW                                   | PAL                                   | LW                                    | MAND                                     |
|---------------------------|--|--|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|--|
| <i>M. sororculus</i>      |  |  |                                       |                                       |                                       |                                       |                                       |                                       |  |
| Holotype FMNH 177259 ♀    | 14.6                                     | 14.1                                     | 8.2                                   | 3.4                                   | 8.1                                   | 7.6                                   | 5.6                                   | 4.7                                   | 10.0                                     |
| Adults                    | 14.5 $\pm$ 0.23,<br>13.8–14.9,<br>n = 34 | 14.0 $\pm$ 0.23,<br>13.5–14.4,<br>n = 35 | 8.1 $\pm$ 0.16,<br>7.7–8.3,<br>n = 35 | 3.4 $\pm$ 0.09,<br>3.2–3.5,<br>n = 36 | 8.0 $\pm$ 0.15,<br>7.7–8.2,<br>n = 35 | 7.4 $\pm$ 0.14,<br>7.1–7.7,<br>n = 36 | 5.5 $\pm$ 0.18,<br>5.2–6.0,<br>n = 32 | 4.7 $\pm$ 0.12,<br>4.5–4.9,<br>n = 37 | 10.0 $\pm$ 0.15,<br>9.7–10.3,<br>n = 25  |
| <i>M. fraterculus</i>     |  |  |                                       |                                       |                                       |                                       |                                       |                                       |  |
| Holotype BMNH 5.5.7.18 ♂  | 14.6                                     | 13.9                                     | 8.2                                   | 3.4                                   | 8.2                                   | 7.6                                   | 5.2                                   | 4.5                                   | 9.9                                      |
| Topotype BMNH 5.5.7.22 ♂  | 14.5                                     | 14.0                                     | 7.9                                   | 3.5                                   | 8.2                                   | 7.5                                   | 5.3                                   | 4.5                                   | 9.9                                      |
| Adults                    | 14.2 $\pm$ 0.15,<br>14.0–14.5,<br>n = 18 | 13.7 $\pm$ 0.14,<br>13.4–14.0,<br>n = 18 | 8.0 $\pm$ 0.19,<br>7.7–8.4,<br>n = 17 | 3.5 $\pm$ 0.09,<br>3.3–3.7,<br>n = 18 | 8.1 $\pm$ 0.10,<br>7.9–8.3,<br>n = 19 | 7.5 $\pm$ 0.19,<br>7.2–8.0,<br>n = 19 | 5.4 $\pm$ 0.16,<br>5.2–5.6,<br>n = 7  | 4.6 $\pm$ 0.16,<br>4.3–5.0,<br>n = 19 | 9.8 $\pm$ 0.15,<br>9.5–10.1,<br>n = 16   |
| <i>M. majori</i>          |  |  |                                       |                                       |                                       |                                       |                                       |                                       |  |
| Holotype BMNH 97.9.1.38 ♀ | 15.7                                     | 15.3                                     | 8.8                                   | 3.7                                   | 8.5                                   | 7.8                                   | 5.9                                   | 5.3                                   | 11.1                                     |
| Adults                    | 15.4 $\pm$ 0.22,<br>14.9–15.8,<br>n = 37 | 15.0 $\pm$ 0.19,<br>14.7–15.4,<br>n = 37 | 8.5 $\pm$ 0.13,<br>8.2–8.8,<br>n = 37 | 3.6 $\pm$ 0.11,<br>3.3–3.8,<br>n = 37 | 8.3 $\pm$ 0.15,<br>7.9–8.7,<br>n = 37 | 7.7 $\pm$ 0.14,<br>7.4–8.0,<br>n = 37 | 5.9 $\pm$ 0.13,<br>5.7–6.3,<br>n = 37 | 5.2 $\pm$ 0.16,<br>4.9–5.5,<br>n = 37 | 10.9 $\pm$ 0.19,<br>10.5–11.2,<br>n = 33 |
| <i>M. natalensis</i>      |  |  |                                       |                                       |                                       |                                       |                                       |                                       |  |
| Adults                    | 15.2 $\pm$ 0.39,<br>14.6–16.2,<br>n = 15 | 14.6 $\pm$ 0.38,<br>14.1–15.5,<br>n = 15 | 8.3 $\pm$ 0.25,<br>8.0–8.9,<br>n = 13 | 3.7 $\pm$ 0.15,<br>3.5–4.0,<br>n = 16 | 8.3 $\pm$ 0.28,<br>7.9–9.0,<br>n = 15 | 7.7 $\pm$ 0.17,<br>7.5–8.1,<br>n = 15 | 5.5 $\pm$ 0.19,<br>5.3–5.9,<br>n = 7  | 5.0 $\pm$ 0.14,<br>4.8–5.3,<br>n = 15 | 10.3 $\pm$ 0.16,<br>10.0–10.4,<br>n = 8  |

*Miniopterus sororculus* is known from several Central Highland regions on the island, generally defined as the region above 800–900 m above sea level, and in all cases these sites are not near native forest formations (Antsampandrano, Manandona, Ibity, and Ambatofinandrahana). This species is known to use rock crevices and deeper caves as day roosts. At

Antsampandrano, this species was found occupying a day roost in the attic of a building occupied by people. Further, it has been obtained in open dry savanna in the central west (Ihosy).

*Etymology.*—The name *sororculus* is derived from the Latin (*sororcula*) and means “small sister.” This epithet was chosen to contrast this taxon with its African counterpart *fraterculus*,

**TABLE 4.**—Dental measurements (in millimeters) of adult *Miniopterus sororculus*, *M. fraterculus*, and *M. natalensis* (both from the eastern and southern portion of South Africa), and *M. majori*. Measurements presented as mean  $\pm$  SD, minimum and maximum measurements, and number of specimens. See “Materials and Methods” for an explanation of variable acronyms.

|                           | I1–M3                                 | C–M3                                  | C1–C1                                 | M3–M3                                 | UPMOLS                                | i1–m3                                 | LWMOLS                                |
|---------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|---------------------------------------|
| <i>M. sororculus</i>      |                                       |                                       |                                       |                                       |                                       |                                       |                                       |
| Holotype FMNH 177259 ♀    | 6.4                                   | 5.4                                   | 4.0                                   | 5.6                                   | 4.5                                   | 6.9                                   | 5.0                                   |
| Adults                    | 6.4 $\pm$ 0.10,<br>6.2–6.8,<br>n = 37 | 5.4 $\pm$ 0.09,<br>5.2–5.6,<br>n = 37 | 4.0 $\pm$ 0.12,<br>3.8–4.2,<br>n = 35 | 5.7 $\pm$ 0.12,<br>5.5–6.0,<br>n = 37 | 4.4 $\pm$ 0.08,<br>4.2–4.5,<br>n = 35 | 6.9 $\pm$ 0.12,<br>6.7–7.1,<br>n = 36 | 5.0 $\pm$ 0.09,<br>4.9–5.3,<br>n = 36 |
| <i>M. fraterculus</i>     |                                       |                                       |                                       |                                       |                                       |                                       |                                       |
| Holotype BMNH 5.5.7.18 ♂  | 6.3                                   | 5.2                                   | 3.8                                   | 5.5                                   | 4.2                                   | 6.7                                   | 5.0                                   |
| Topotype BMNH 5.5.7.22 ♂  | 6.3                                   | 5.3                                   | 3.8                                   | 5.6                                   | 4.3                                   | 6.8                                   | 4.9                                   |
| Adults                    | 6.3 $\pm$ 0.15,<br>6.1–6.6,<br>n = 17 | 5.2 $\pm$ 0.12,<br>5.0–5.4,<br>n = 17 | 3.8 $\pm$ 0.04,<br>3.7–3.8,<br>n = 16 | 5.5 $\pm$ 0.10,<br>5.3–5.6,<br>n = 18 | 4.3 $\pm$ 0.07,<br>4.2–4.4,<br>n = 17 | 6.7 $\pm$ 0.13,<br>6.4–6.9,<br>n = 18 | 4.9 $\pm$ 0.14,<br>4.7–5.2,<br>n = 18 |
| <i>M. majori</i>          |                                       |                                       |                                       |                                       |                                       |                                       |                                       |
| Holotype BMNH 97.9.1.38 ♀ | 7.4                                   | 6.2                                   | 4.5                                   | 6.7                                   | 5.1                                   | 7.9                                   | 5.9                                   |
| Adults                    | 7.1 $\pm$ 0.14,<br>6.9–7.4,<br>n = 37 | 6.0 $\pm$ 0.10,<br>5.8–6.2,<br>n = 37 | 4.4 $\pm$ 0.10,<br>4.2–4.6,<br>n = 36 | 6.5 $\pm$ 0.11,<br>6.3–6.7,<br>n = 37 | 4.9 $\pm$ 0.09,<br>4.7–5.1,<br>n = 37 | 7.5 $\pm$ 0.13,<br>7.2–7.9,<br>n = 37 | 5.6 $\pm$ 0.09,<br>5.4–5.9,<br>n = 36 |
| <i>M. natalensis</i>      |                                       |                                       |                                       |                                       |                                       |                                       |                                       |
| Adults                    | 6.5 $\pm$ 0.21,<br>6.2–6.8,<br>n = 13 | 5.6 $\pm$ 0.18,<br>5.3–5.9,<br>n = 14 | 4.2 $\pm$ 0.17,<br>4.0–4.6,<br>n = 14 | 6.1 $\pm$ 0.21,<br>5.7–6.4,<br>n = 15 | 4.7 $\pm$ 0.16,<br>4.5–5.0,<br>n = 15 | 7.1 $\pm$ 0.25,<br>6.7–7.6,<br>n = 15 | 5.3 $\pm$ 0.20,<br>5.0–5.7,<br>n = 14 |

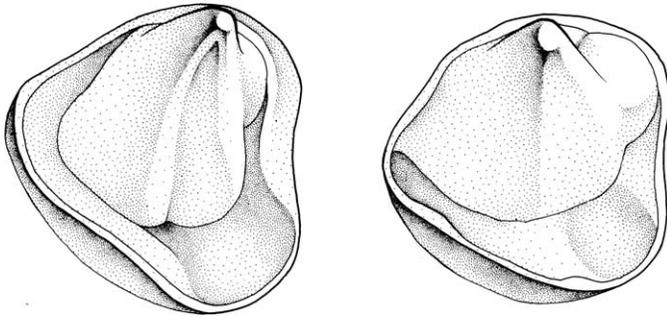


FIG. 6.—View of the 1st upper premolar (P2) in *Miniopterus* from Madagascar and Africa. Left) Holotype of *M. sororculus* (FMNH 177259) from near Ambatofinandrahana. Right) Topotype of *M. fraterculus* (BMNH 5.5.7.22) from near Knysna, South Africa. In *M. sororculus* there is a distinct lingual ledge that is not well developed in *M. fraterculus*.

which means “little brother,” as well as this animal being slightly smaller than *M. majori*, another endemic Malagasy species that occurs in sympatry throughout portions of its range.

**Distribution.**—*Miniopterus sororculus* has been recorded from a variety of localities in the Central Highlands from 950 to 2,200 m (Fig. 1). Malagasy specimens previously assigned to *M. fraterculus* and presumably referable to *Miniopterus* cf. *sororculus* (see Appendix I) have been reported from the Beloha area (Peterson et al. 1995), which is dominated by spiny forest. There also is a report of specimens of *M. fraterculus* in the FMNH from “Antanadava, Isle Sainte Marie” (Peterson et al. 1995). We found 2 specimens in that collection from Antanadava (FMNH 75772, 75773); these are referable to *M. manavi* as it currently is defined.

**Comparisons.**—Of the 19 species of *Miniopterus* in the world recognized by Simmons (2005), the following species have forearm measurements that fall completely or largely outside the of *M. sororculus* (FA 42–45 mm; Table 1) and do not need to be considered further in the comparisons presented here: *M. africanus* Sanborn, 1936 (FA 45.4–51.7 mm—Peterson et al. 1995); *M. gleni* (FA 47–52 mm—Peterson et al. 1995); *M. inflatus* (FA 45–51 mm—Koopman 1994); *M. macrocneme* Revilliod, 1914 (FA 40.7–41.7 mm—Hill 1983); *M. magnater* Sanborn, 1931 (FA 47–53 mm—Koopman 1994); *M. manavi* (FA 32–40 mm—Koopman 1994); *M. minor* (FA 37–40 mm—Koopman 1994); *M. paululus* Hollister, 1913 (FA 34–38 mm—Koopman 1994); *M. pusillus* Dobson, 1876 (FA 39.6–40.2 mm—Bates and Harrison 1997); *M. robustior* Revilliod, 1914 (FA 39–43 mm—Koopman 1994); and *M. shorridgei* Laurie and Hill, 1957 (FA 34.4–36.6 mm—Hill 1983). The remaining taxa recognized in the genus by Simmons (2005) include: *M. australis* (FA 34–47 mm—Koopman 1994); *M. fraterculus* (FA 41–44 mm—Koopman 1994); *M. fuscus* Bonhote, 1902 (FA 38–45—Koopman 1994); *M. majori* (FA 41.8–46.6 mm—Peterson et al. 1995); *M. medius* Thomas and Wroughton, 1909 (FA 40.8–45.0—Hill 1983); *M. natalensis* (FA 41–49 mm—Koopman 1994); *M. schreibersii* (FA 42–50 mm—Koopman 1994); and *M.*

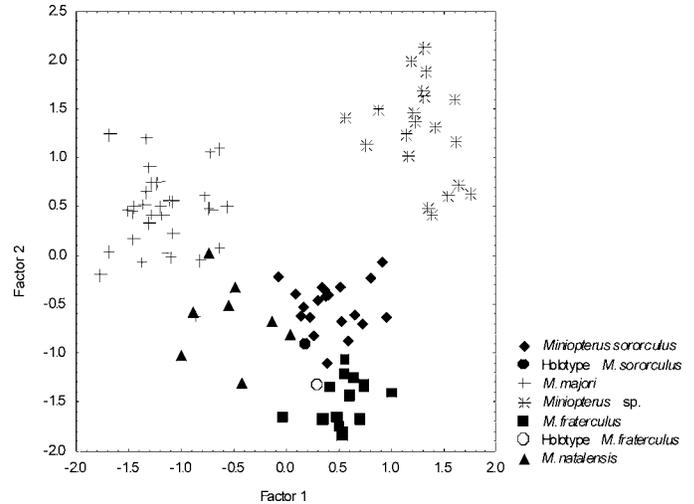


FIG. 7.—Projections of factor 1 (x-axis) and factor 2 (y-axis) in principal component analysis of select cranial measurements of *Miniopterus sororculus*, the unidentified *Miniopterus*, and *M. majori* from Madagascar and *M. natalensis* and *M. fraterculus* from southern and eastern South Africa. The specimens representing the holotypes of *M. sororculus* and *M. fraterculus* are indicated. Loadings of variables on each axis are shown in Table 6.

*tristis* (Waterhouse, 1845) (FA 43–49 mm—Koopman 1994). Given that *M. australis* is known to occur on islands of southeastern Asia to Australia, *M. fuscus* is known from the Japanese Islands, and *M. medius* and *M. tristis* are known from areas of southeastern Asia, the Philippines to New Guinea, and that none of these species have been reported from the Afro-Malagasy region, they are not considered here because of their distant and generally insular distributions. Further, examination of genetic data indicates that African and Asian lineages of this genus are very distinct from one another (Appleton et al. 2004). True *M. schreibersii*, from the Mediterranean, is included in the genetic analyses and differs from *M. sororculus*.

The Malagasy endemic *M. majori* is broadly sympatric with *M. sororculus* across much of its range and the 2 species can be found together in the same day roosts. These 2 species show broad overlap in a range of external morphological characters, although the former is on average larger (Table 2). The easiest way to differentiate these 2 taxa is based on cranial and dental measurements. *M. majori* is on average larger than *M. sororculus* in all cranial measures taken and these show little overlap between the species (Table 3); both taxa show a clear separation in a principal component analysis of cranial characters (Fig. 7). CIL clearly separates these 2 taxa: range in *M. sororculus* is 13.5–14.4 mm and in *M. majori* 14.7–15.4 mm. Further, several dental measurements show complete separation between these 2 taxa (I1–M3, C–M3, M3–M3, and LWMOLS). It has been previously noted that the pelage coloration of “*M. fraterculus*” from Madagascar [= *M. sororculus*] is “gray to grayish brown” and that of *M. majori* is a “grayish brown” (Eger and Mitchell 2003:1296). Based on material available to us, both species have notably dark brown pelage. In *M. sororculus*, the dorsum is generally a rich dark

**TABLE 5.**—Selected cranial and dental measurements (in millimeters) of holotype and topotype of *Miniopterus fraterculus* and South African specimens of *M. natalensis* and *M. fraterculus* for which sequence data are available. See “Materials and Methods” for an explanation of variable acronyms.

|   | GSKL | CIL  | ZYGO | MAST | C1–C1 | M3–M3 | UPMOLS | LWMOLS |
|---|------|------|------|------|-------|-------|--------|--------|
| <i>M. fraterculus</i>                         |      |      |      |      |       |       |        |        |
| Holotype BMNH 5.5.7.18 ♂                      | 14.6 | 13.9 | 8.2  | 8.2  | 3.8   | 5.5   | 4.2    | 5.0    |
| Topotype BMNH 5.5.7.22 ♂                      | 14.5 | 14.0 | 7.9  | 8.2  | 3.8   | 5.6   | 4.3    | 4.9    |
| Genetically groups with <i>M. fraterculus</i> |      |      |      |      |       |       |        |        |
| TM 41638                                      | 14.2 | 13.6 | 8.0  | 8.1  | 3.8   | 5.5   | 4.4    | 4.7    |
| TM 42120                                      | 14.4 | 13.7 | 7.9  | 7.9  | 3.8   | 5.5   | 4.3    | 4.8    |
| Genetically groups with <i>M. natalensis</i>  |      |      |      |      |       |       |        |        |
| TM 46484                                      | 14.9 | 14.3 | 8.3  | 8.3  | 4.3   | 6.0   | 4.8    | 5.1    |
| TM 46881                                      | 15.0 | 14.5 | 8.2  | 8.4  | 4.1   | 6.0   | 4.6    | 5.2    |
| TM 47622                                      | 15.3 | 14.6 | 8.4  | 8.4  | 4.4   | 6.0   | 4.6    | 5.3    |

brown and the ventrum slightly lighter, whereas in *M. majori* the dorsum is darker, approaching a rich, dark, chocolate brown and the ventrum a slightly paler rich dark brown.

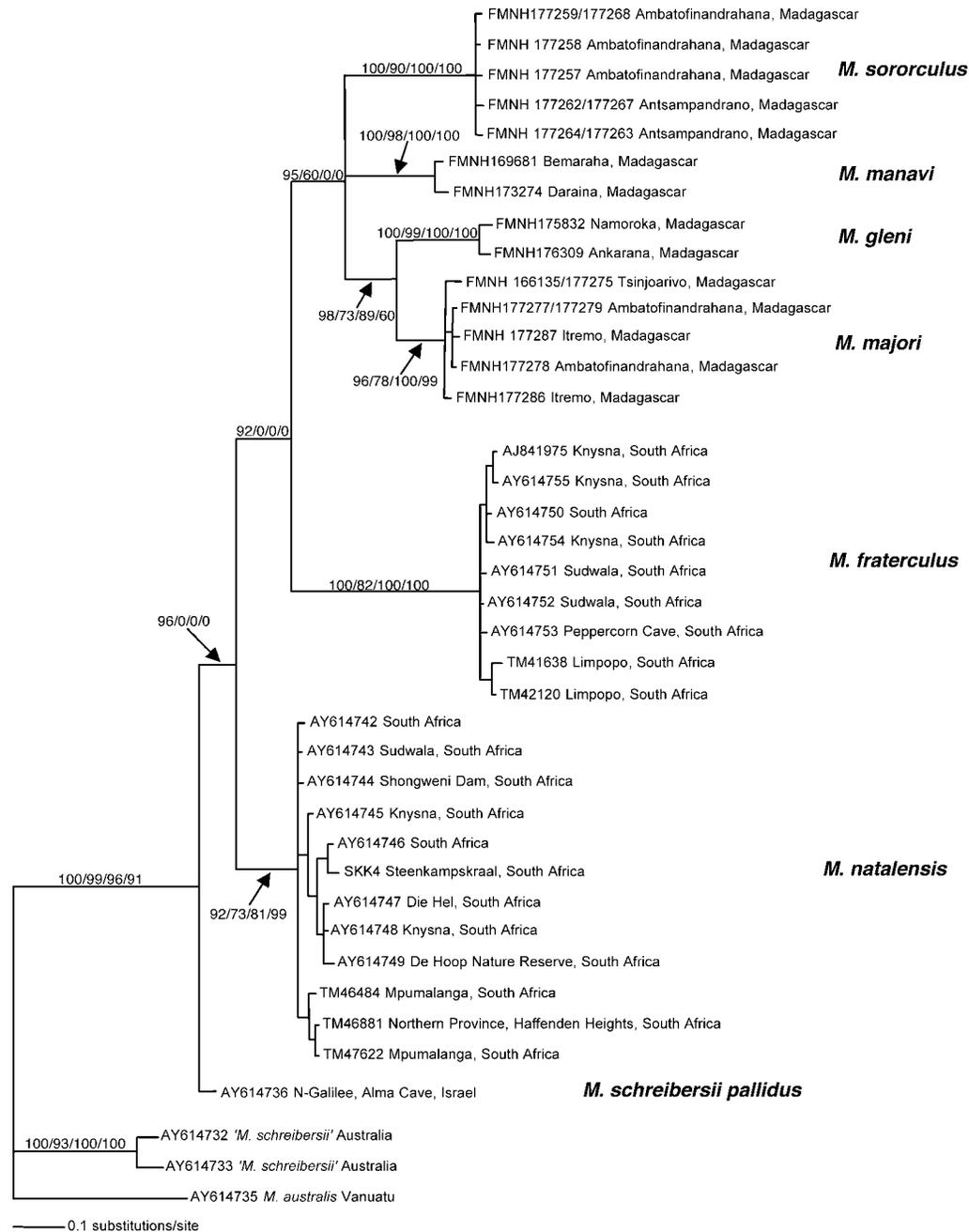
Given that in South Africa, and presumably elsewhere in their ranges, *M. fraterculus* (type locality Knysna) and *M. natalensis* (type locality Durban) are broadly sympatric and are morphologically very similar to one another, it was necessary to conduct some further analyses to identify characters that can be used to distinguish between them and subsequently make the needed comparisons to Malagasy animals formerly referred to *M. fraterculus* (= *M. sororculus*). Stoffberg et al. (2004) presented several cranial and dental measurements that separate these 2 African species, for which *M. natalensis* was on average larger for 8 of 9 characters. One of these characters, which showed no overlap between the 2 species, was the length of skull (from the occipital to alveolus of the canine), which in *fraterculus* was  $14.2 \pm 0.3$  mm (range 13.6–14.3 mm,  $n = 16$ ) and in *M. natalensis* was  $15.1 \pm 0.2$  mm (range 14.7–15.6 mm,  $n = 20$ ). Further, within a key to African species of bats (Roberts 1951), 2 characters were mentioned in the couplets separating *M. natalensis* and *M. fraterculus*—the former has a skull length from the premaxilla of greater than 15 mm and a C–M3 length of 5.6–5.9 mm, whereas these measurements for the latter are <15 mm and 5.3–5.5 mm, respectively.

As a further aid in our study to make the proper comparisons between African *M. fraterculus* and *M. natalensis* to the Malagasy species, 5 specimens collected in the general vicinity of the South African holotype localities of these 2 taxa were available with both intact skulls and tissue samples. These included TM 41638 and TM 42120 from the Transvaal and TM 46484, TM 46881, and TM 47622 from Mpumalanga. On the basis of measurements from these specimens, we used the following criteria to distinguish between specimens of *Miniopterus* collected in South Africa and falling within the range of *M. natalensis* and *M. fraterculus*:  $CIL \leq 14.0 = fraterculus$ ,  $> 14.5$  mm = *natalensis*;  $C1-C1 \leq 3.8 = fraterculus$ ,  $> 4.1 = natalensis$ ; and  $M3-M3 \leq 5.6 = fraterculus$ ,  $> 6.0$  mm = *natalensis* (Table 5). Details of the genetic relationships of the above mentioned 5 TM specimens are discussed in the next section, but the 2 Transvaal specimens indeed fall within *M.*

*fraterculus* and the Mpumalanga specimens within *M. natalensis*, corroborating the assignment to species based on measurements. Further, measurements of the Transvaal specimens of *M. fraterculus* fall within the range of the type series of *M. fraterculus* in the BMNH and are notably smaller than the 3 specimens of *M. natalensis* from Mpumalanga. It is important to highlight that only 2 of the 5 TM specimens used in this analysis were correctly identified to species and this underlines a general problem in unraveling aspects of systematics of *Miniopterus*. A principal component analysis of cranial measurements shows a clear grouping of the holotype of *M. fraterculus* with other South African specimens we assigned to this taxon and a distinctive separation from *M. natalensis* (Fig. 7).

Notable differences were found in the tragus shapes of *M. fraterculus*, *M. sororculus*, and *M. majori* (Fig. 2). In *M. fraterculus*, the tragus forms a notably small projection, measuring on average 5.3 mm (range 4–8 mm; based on measurements of a variety of field collectors; Table 2). The structure is simply elongated, not notably asymmetric, and terminates in a blunt point. In contrast, *M. sororculus* has a distinctly more elongated tragus, measuring on average 6.7 mm (range 6–8 mm; based on measurements of a single field collector; Table 2). In this taxon, the tragus shows a slight constriction towards the midsection, expands distally into an asymmetric structure, and has a more pointed tip than in *M. fraterculus*. In *M. majori*, the tragus is slightly longer than in *M. sororculus* ( $t = 1.99$ ,  $d.f. = 72$ ,  $P < 0.0001$ ), averaging 7.3 mm (range 7–8 mm; based on measurements of a single field collector; Table 2), has a distinctly broader base, constricts toward the midsection, and then forms a slightly arching structure to a rounded point. Further, in general, ear length in South African *M. fraterculus* is slightly smaller (average 9.2 mm, range 7–10 mm; based on the measurements of different field collectors) as compared to *M. sororculus* (10.7 mm, range 10–12 mm; based on a single field collector; Table 2); these differences are statistically significant ( $t = 1.70$ ,  $d.f. = 29$ ,  $P < 0.0001$ ).

*Molecular phylogenetics.*—Within *M. sororculus*, genetic differentiation is low (0–0.48%) and corresponds with up to 2



**FIG. 8.**—Phylogenetic position of *Miniopterus sororculus* with respect to *M. fraterculus* and *M. natalensis* of South Africa and *M. majori*, *M. manavi*, and *M. gleni* of Madagascar based on the mitochondrial cytochrome-*b* gene. *M. australis* was selected as the outgroup. Tree topology produced using Bayesian analysis as described in the “Materials and Methods.” Posterior probabilities shown as percentages for Bayesian analysis and bootstrap support for maximum-likelihood, neighbor-joining, and maximum-parsimony analyses and are indicated on the major nodes only (Bayesian/maximum likelihood/neighbor joining/maximum parsimony). Labels include collecting locality and catalogue number or sample identification number. Accession numbers are included for those sequences extracted from GenBank. The species identification is included to the right of each clade. Identical sequences for *M. sororculus* are indicated by their museum catalogue numbers.

base changes between cytochrome-*b* haplotypes. In the 8 samples sequenced, 5 haplotypes were found. These results are not unexpected because these samples originated from 2 locations (Ambatofinandrahana, the type locality, and Antsampandrano) about 115 km from one another. However, there appeared to be no geographic structuring of the haplotypes observed. All substitutions were synonymous changes.

The data are presented here in the form of a Bayesian tree (Fig. 8). The maximum likelihood tree had a score of  $-\ln L = 1,947.08821$ . The maximum parsimony analysis showed 288 constant positions and 114 parsimony-informative positions (of the total 414 bp). There were a further 12 variable sites unique to particular taxa. The consensus (of 10 trees) maximum-parsimony tree length was 253 with a consistency index of

0.553 and a retention index of 0.879. All tree-building methods (Bayesian, maximum likelihood, maximum parsimony, and neighbor joining) showed similar topologies. Small differences existed between trees, but the main clades are well supported in each analysis. The Bayesian tree showed good resolution, whereas the bootstrapped maximum-likelihood, maximum-parsimony, and neighbor-joining trees show great confidence in each of the species groups, but there is less resolution of relationships between species.

All sequences from South African populations of *M. fraterculus*, including those from the vicinity of the terra typica, form a single clade. All sequences from populations of *M. sororculus* also form a well-supported and distinct lineage. Clearly, based on the molecular data, *M. sororculus* warrants recognition at the species level. Mean genetic differentiation of 14.28% between *M. sororculus* and *M. fraterculus* is as expected for separate species in this genus (Appleton et al. 2004; Cardinal and Christidis 2000; Miller-Butterworth et al. 2005). The 2 species are not closely related on the phylogenetic tree and they are at least as divergent from each other as they are from other African and Malagasy species. The genetic distance between *M. sororculus* and all other African *Miniopterus* species was 9.5–15.5%, which is a value widely recognized as being likely to indicate separate species (Baker and Bradley 2006). Monophyly of *M. fraterculus* and *M. sororculus* (topological constraints enforced in PAUP\*; data not shown) requires 22 additional steps and results in at least 10 times more equally parsimonious trees and a significant permutation tail probability (PTP) test ( $P = 0.01$ ) indicating that monophyly of these clades is unlikely.

As mentioned in the morphology section of this paper, 5 samples from the Transvaal Museum (TM) were included in the genetic analysis. These 5 samples were labeled as *M. fraterculus*. However, as can be seen in the phylogenetic tree, only TM 42120 and TM 41638 group with the other sequences of *M. fraterculus*. In contrast, TM 46484, TM 46881, and TM 47622 from Mpumalanga clearly align with the sequences from specimens of *M. natalensis*. This result supported the independently conducted morphological analysis.

## DISCUSSION

Malagasy specimens previously assigned to *M. fraterculus*, a relatively widespread species in eastern and southern Africa, represent a previously undescribed species, which is named here as *M. sororculus*. The process of reaching this conclusion has been complicated by the fact that morphologically similar species occur in sympatry with *M. fraterculus* in Africa and *M. sororculus* on Madagascar. Although this question has been resolved using classical morphological studies of museum specimens, supporting earlier suggestions that African and Malagasy populations of “*fraterculus*” showed size differences (Eger and Mitchell 2003; Peterson et al. 1995), parallel work using molecular methods has provided corroborating evidence. In a genus such as *Miniopterus*, which shows remarkable levels of convergence in taxa that are not closely related to one

another, molecular phylogenetic studies are of considerable importance to unravel numerous questions.

The genus *Miniopterus* shows notable taxonomic complexity and caution should be given to field identifications of released individuals without associated voucher specimens. The case of *M. natalensis* and *M. fraterculus* from southern and eastern South Africa mentioned in the “Comparisons” section is a case in point, with only 40% of specimens used in 1 of the analyses correctly identified. On Madagascar, recent field inventories and study of associated specimens have disclosed a considerable number of taxa new to science and several others remain to be described. Voucher specimens with associated tissue samples are of considerable importance for documenting the results of these surveys and also helping to unravel other systematic questions associated with the taxonomy and evolutionary history of the island’s chiropteran fauna. In a group such as *Miniopterus*, where cryptic species are not uncommon and where morphologically similar species occur in sympatry, the need for specimen documentation with associated tissue samples is essential.

On Madagascar, it previously has been proposed that *M. “fraterculus”* is restricted to the eastern region, within the elevational range of 500 to 2,000 m, and *M. majori* largely in the eastern region with some records from the south and west, within the elevational range from sea level to 1,000 m (Eger and Mitchell 2003; Peterson et al. 1995). A number of field surveys have been conducted on Malagasy bats in recent years based on captured–released individuals and recordings of their calls. As demonstrated here with a cryptic species of *Miniopterus* new to science, the creation of dictionaries of different bat calls based on nonvouchered specimens (e.g., Bennett and Russ 2001) in a group such as *Miniopterus*, where morphologically difficult to distinguish species occur in sympatry, clearly has its shortfalls. Certainly, once the genetics of this genus on Madagascar are completely resolved, small tissue samples from wing-punches (Wilmer and Barratt 1996), and associated laboratory analyses should be enough to corroborate the majority of field identifications.

A principal component analysis of cranial variables shows clear separation of *M. majori* and *M. sororculus* on Madagascar and *M. fraterculus* and *M. natalensis* in South Africa (Fig. 7; Table 6). Further, in this analysis specimens formerly assigned to *M. fraterculus* from Madagascar show 2 different groupings: animals defined herein as *M. sororculus* from the Central Highlands above 900 m (including the holotype) and individuals collected in lowland areas from Montagne d’Ambre in the north to the Tolagnaro area in the extreme southeast that are currently referred to as *M. cf. sororculus* (Appendix I). Currently we do not have tissue samples available for molecular studies of the lowland population and we defer any decision about their taxonomic status until these samples are available.

*Problems of parphyly in Miniopterus.*—The genus *Miniopterus* initially was described in 1837 and more taxa have been steadily named over the years. The difficulties of understanding the species’ relationships of this genus based on morphological grounds are embodied in Dobson’s

**TABLE 6.**—Factor loadings from principal component analysis of cranial measurements of specimens of *Miniopterus sororculus*, *M. fraterculus*, *M. natalensis*, and *Miniopterus* sp. A graphical representation of the first 2 factors is presented in Fig. 7. See “Materials and Methods” for an explanation of variable acronyms.

| Variable                                    | Factor 1 | Factor 2 | Factor 3 |
|---|----------|----------|----------|
| GSKL  | -0.900   | 0.355    | 0.094    |
| CIL   | -0.941   | 0.283    | 0.078    |
| ZYGO  | -0.948   | -0.118   | 0.133    |
| POB   | -0.781   | -0.536   | -0.222   |
| MAST  | -0.889   | -0.368   | 0.125    |
| GBW   | -0.848   | -0.468   | 0.062    |
| LW  | -0.870   | 0.295    | -0.357   |
| MAND  | -0.826   | 0.499    | 0.044    |
| Explained variance                          | 6.153    | 1.198    | 0.289    |
| Proportion of total explained variation (%) | 76.9     | 91.9     | 94.7     |

(1878:348) statement of nearly 130 years ago: “The species of this genus are so very closely allied that almost the only differences noticeable are size, relative lengths of parts, and the distribution of the fur.” With some regularity, species taxonomy of *Miniopterus* has been reviewed by a long list of researchers. Invariably, the species-level relationships have changed with each review. For many years, this problem was exacerbated by the similarity of form across the genus and the many overlapping external and skull measurements found in species descriptions. As highlighted herein, many of the specimens currently held in museums are incorrectly identified. More recently, detailed morphological and genetic research has shown that many of the long-standing species and often broadly distributed taxa are actually paraphyletic species complexes (Appleton et al. 2004; Cardinal and Christidis 2000; Eger and Mitchell 2003; Miller-Butterworth et al. 2005; Peterson et al. 1995). Research is steadily uncovering new examples where slight morphological differences translate into substantial genetic differentiation. Suggestions of further parphyly in Malagasy members of this genus include recent morphological analyses, which have provided evidence that the species currently recognized as *M. manavi* may represent several different taxa (Eger and Mitchell 2003; Peterson et al. 1995).

*Ecology and conservation concerns.*—*Miniopterus sororculus* is known from several sites on the island, many of which are in heavily degraded habitats and considerable distances from natural forest habitats. Across its currently known distribution, it has an elevational range from about 950 to 2,200 m. The vast majority of specimens used in this study were captured free-flying individuals and only on a few occasions has this species been found occupying day roosts; such sites include limestone caves, rock overhangs, and an attic of a house occupied by people.

Peterson et al. (1995) noted that specimens they collected of *M. sororculus*, which were identified originally as *M. fraterculus* (ROM), in a cave at 2,200 m, above the village of Manandona, on 16 May 1967, were torpid. This is a zone of the island where during the austral winter the minimum

temperature drops to near freezing. Given the date and location of these observations it can be assumed that such populations actually hibernate. To our knowledge, this is the only record of a bat hibernating on the island. However, given the elevational range of *M. majori* it is presumed that at least upland populations might exhibit a similar adaptation during the austral winter.

At numerous sites across the range of *M. sororculus*, it is known to occupy the same day roosts as other species of *Miniopterus*. We have found this species together with *M. majori* in a limestone cave close to Ambatofinandrahana. There also are reports of *M. “fraterculus”* (= *sororculus*) occurring sympatrically with *M. manavi* and *M. majori* at Imasindry (20°17'S, 47°31'E—Jenkins and Carleton 2005). It is presumed that these records are of individuals obtained in day roosts.

Given the relatively broad distribution of *M. sororculus* on Madagascar, spanning various portions of the Central Highlands, and the fact that this species is not necessarily associated with relatively intact native forests, the long-term future of this species seems rather favorable. Human pressures on day roost sites, particularly caves and rock overhangs, might have an impact on local populations of this animal. Further research is needed on this species to understand aspects of its natural history and distribution, particularly fascinating aspects concerning its physiological capacity to enter torpor.

## RÉSUMÉ

Une nouvelle espèce de chauve-souris dans le genre *Miniopterus* est décrite de Madagascar à partir d'une série de spécimens récoltés sur les Hautes Terres du Centre de l'île. Cette nouvelle espèce était préalablement identifiée en tant que *M. fraterculus*, qui est largement distribuée dans certaines régions d'Afrique orientale et méridionale. Les comparaisons entre ces deux taxons se heurtaient à de nouvelles complications car une partie de l'aire de distribution de *M. fraterculus* chevauche celle de *M. natalensis*, qui est une espèce morphologiquement proche et qui vit en sympatrie avec la précédente. À partir de spécimens et d'échantillons de tissus associés de matériels récoltés près des localités de récolte des types de *M. natalensis* et *M. fraterculus* mais aussi en ayant accès à certains des spécimens type déterminants, nous avons procédé à des analyses morphologiques et moléculaires pour déterminer si les animaux malgaches qui étaient antérieurement assignés à *M. fraterculus* représentaient une nouvelle espèce endémique de l'île ou non. Dans la mesure où l'habitat fréquenté par *Miniopterus* sp. nov. n'est pas forcément lié à la forêt autochtone, que cette chauve-souris présente une vaste répartition sur les Hautes Terres et qu'elle a été rencontrée dans des situations synanthropiques, l'espèce n'est pas considérée comme menacée.

## ACKNOWLEDGMENTS

We are grateful to the Direction des Eaux et Forêts and Association National pour la Gestion des Aires Protégées for issuing permits to conduct faunal surveys on Madagascar; specimens collected during these field projects were important to resolve the taxonomic identity of

the new species described herein. For access to specimen material under their care we are indebted to N. Simmons, American Museum of Natural History, New York; P. Jenkins, The Natural History Museum, London; P. Taylor, Durban Natural Science Museum, Durban; J. L. Eger, Royal Ontario Museum, Toronto; T. Kearney, Transvaal Museum, Pretoria; and M. Carleton and L. Gordon, National Museum of Natural History, Washington, D.C. For access to tissues, we are grateful to C. Miller-Butterworth and T. Kearney. Prof. O. Ramilijaona and Dr. D. Rakotondravony helped with numerous administrative details. L. Wilmé kindly prepared Fig. 1 and the French résumé; J. Weinstein prepared Fig. 3; and R. Kramer prepared Figs. 2, 4, 5, and 6. Field research associated with this paper has been generously supported by WWF-Madagascar, Ellen Thorne Smith Fund of the Field Museum of Natural History, John D. and Catherine T. MacArthur Foundation, National Geographic Society (6637–99 and 7402–03), and the Volkswagen Foundation. SMG's visit to the Natural History Museum, London, was financed by a SYNTHESYS grant from the European Union. A portion of the molecular study associated with this project was funded by Biodiversity Conservation Madagascar, through the generosity of O. Griffiths, and the University of Melbourne Collaborative Grants Scheme. We are grateful to 2 anonymous reviewers of an earlier version of this paper, as well as the associate editors, for their insightful comments.

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Submitted 23 August 2006. Accepted 17 January 2007.

Associate Editors were Jesús E. Maldonado and Robert D. Bradley.

## APPENDIX I

*Specimens examined*.—All specimens used in this study are listed below and are housed in museums, for which the acronyms are given in the “Materials and Methods” section. Two specimens collected by SMG and deposited, but not catalogued yet, at Université d’Antananarivo, Département de Biologie Animale (UADBA) are cited by their field catalog numbers. In most cases, locality data were recorded directly from collectors’ field catalogs.

*Miniopterus fraterculus*.—SOUTH AFRICA: Cape Province, Knysna, BMNH 5.5.7.18 (holotype), 5.5.7.22.; Gauteng Province [ex. Transvaal], Uitkomst Farm, 32 miles W of Pretoria, USNM 342641; Kwa-Zulu Natal Province, Shongweni Dam, 29°51’S, 30°43’E, DM 3513, 7031–7034; Enseleni Nature Reserve, DM 5604; Melmoth Area, Mooi-plas Plantation, DM 5108; Pietermaritzburg, Town Bush Cave, AMNH 245203, 245204, 245206, 245207; Limpopo Province, Entabeni State Forest, 23°00’45”S, 30°15’50”E, TM 41638; Tzaneen, 15 km W of De Hoek Forest Station, 23°49’S, 30°01’E, TM 42120. SWAZILAND: Ngwenya-Oshoek, Byrhytes Mine, 26°13’S, 31°02’E, DM 5785; Nottinghill Mine, TM 8050; Pigg’s Peak Mine, DM 8043; Wylesdale, DM 8048.

*Miniopterus majori*.—MADAGASCAR: Province d’Antananarivo, 10 km SE de Tsinjoarivo, 19°40.7’S, 47°46.2’E, 1,550 m, FMNH 166135, 166188–166192, UADBA uncatalogued (SMG 10453, 10454); Province d’Antsiranana, Parc National de la Montagne d’Ambre, 5.5 km SW de Joffreville (Ambohitra), Station des Roussettes, 12°31’S, 49°10’E, 1,000 m, FMNH 154553; Province de Fianarantsoa, Imasindry [= Masindry, 20°17’S, 47°31’E, approximately 1,000–1,500 m (Jenkins and Carleton 2005)], BMNH 97.9.1.38 (holotype), 97.9.1.44, 2000.82–2000.84; Itremo (village), 20°35.630’S, 46°37.090’E, 1,450 m, FMNH 166051, 166052; 2.5 km W d’Itremo, 20°35.631’S, 46°37.072’E, 1,400 m, FMNH 177285–

177292; 3 km S d’Ambatofinandrahana, in unnamed cave, 20°34.321’S, 46°48.531’E, 1,450 m, FMNH 177275–177284; near Cascade Sahanalatra, just outside PN de Ranomafana, 21°14’14.9”S, 47°23’52.0”E, 1,100 m, FMNH 187652–187661; Fianarantsoa, 21°27.535’S, 47°04.604’E, 1,190 m, FMNH 184469.

*Miniopterus natalensis*.—KENYA: Makindu, Upper Cave, ROM 81216; 30 km E of Voi, Maungu, ROM 68676; Tsavo National Park, Kilaguni Lodge, ROM 36403; Simba, Kiboko River, ROM 36401. SOUTH AFRICA: Gauteng Province [ex. Transvaal], Uitkomst Farm, 32 miles W of Pretoria, USNM 342640; Pretoria Fountains, USNM 376759, 376761; Kwa-Zulu Natal Province, Pietermaritzburg, Town Bush Cave, AMNH 245201, 245202, 245205; Makatini Reserve Village, near Jozini Dam, DM 6963; Mpumalanga Province, Sterkspruit, 24°35.5’S, 30°37’E, TM 46484; Haffenden Heights, 24°07’S, 30°00’30”E, TM 46481; Malelane, Old Mine Shaft, 25°31.867’S, 31°32.111’E, TM 47622; 4 miles E of, 2 miles S of Nelspruit, USNM 381620. ZIMBABWE: Triumph Mine, near Lake McIlwaine, ROM 64503; Calcite Cave, Netridge Farm, ROM 70849.

*Miniopterus sororculus*.—MADAGASCAR: Province d’Antananarivo, granite caves of Angavokely, approximately 1,770 m, BMNH 1982.529–1982.531; Station Forestière d’Antsampsandrano, 26 km SE de Faratsiho, 19°36.720’S, 47°03.770’E, 1,850 m, FMNH 177261–177274, 177293; Caves of Manandona, high on mountain side, 6,600 feet [= 2,200 m], ROM 42628, 42719, 42721, 42723, 42725, 42727, 42729, 42731, 42733, 42735; Province de Fianarantsoa, Ibity Massif, Tombamboanjo, 1,725 m, FMNH 179402, 179403; 3 km S d’Ambatofinandrahana, in unnamed cave, 20°34.321’S, 46°48.530’E, 1,450 m, FMNH 177255–177258, 177259 (holotype), 177260; Ihosy commune rurale, Ankily, Grotte d’Andranomilitary, 22°23.111’S, 46°03.385’E, 950 m, FMNH 184467, 184468.

*Miniopterus* cf. *sororculus*.—MADAGASCAR: Province d’Antsiranana, 6 km S de Joffreville, Montagne d’Ambre, USNM 341722, 341723, 341725–341730, 341733; Parc National de la Montagne d’Ambre, 5.5 km SW de Joffreville (Ambohitra), 12°31’S, 49°10’E, 1,000 m, FMNH 156307; Province de Fianarantsoa, Vatovavy, 9 km ESE de Kianjavato, 21°24’S, 47°57’E, 150 m, USNM 449203, 449204; 2 km NE Andrambovato, 21°30’S, 47°27’E, 550 m, USNM 449205; Province de Toliara, Analalava, 24°13.5’S, 47°19’E, approximately 20 m, USNM 577126; approximately 21 km NW de Tolagnaro, Itapera, 24°52’S, 47°07’E, 10 m, USNM 577128; Nahampoana, 24°58’S, 46°58’E, 40 m, USNM 577109–577116; Manantantely, 24°59’S, 46°54’E, 60 m, USNM 577096–577101; 20 km WNW de Ranopiso, Itaranta, 25°01’S, 46°30’E, 40 m, 1990 m, USNM 577072, 577073, 577122.