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Source: Journal of Mammalogy, 95(3) : 443-454

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/13-MAMM-A-159>

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## A new species of round-eared sengi (genus *Macroscelides*) from Namibia

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While studying the systematics and taxonomy of round-eared sengis (genus *Macroscelides*), we identified an unusual specimen from remote northwestern Namibia in the collection of the California Academy of Sciences. To determine if this represented a different species, we made 9 collecting trips with 5,616 trap-nights of effort that produced 16 voucher specimens (including the original specimen) of the unusual sengi. These specimens are distinguished from other *Macroscelides* species by morphological metrics (they are smaller), external features (rusty-tinged pelage, large subcaudal gland, and lack of dark skin pigment), and by divergence at 3 independently segregating DNA loci. These traits are the basis for the description of a new species of *Macroscelides* that seems to be confined to gravel plains associated with the distinctive reddish colored Etendeka geological formation of northwestern Namibia. The new species appears to be reproductively isolated from congeners, because portions of its distribution are sympatric with that of the Namib round-eared sengi (*M. flavicaudatus*), and we found no evidence of hybrid individuals or gene flow. The new species is allopatric with the Karoo round-eared sengi (*M. proboscideus*), which is found about 500 km to the south. The new species, along with *M. flavicaudatus*, is endemic to Namibia. With this 3rd species in the genus, there are now 19 recognized extant species in the order Macroscelidea.

Key words: elephant-shrew, Etendeka, *Macroscelides*, Namibia, new species, phylogenetics, sengi

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DOI: 10.1644/13-MAMM-A-159

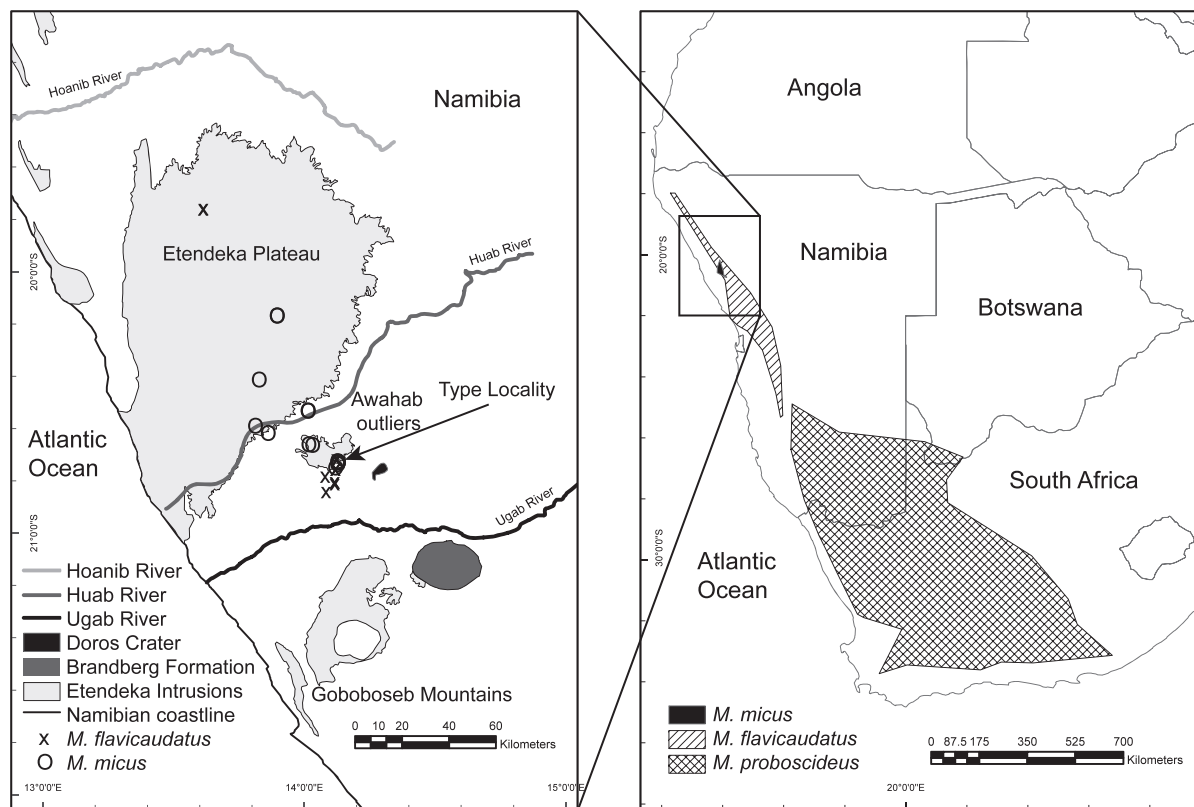
The sengis or elephant-shrews (order Macroscelidea) are a monophyletic clade restricted to Africa with distant phylogenetic affinities to elephants, sea cows, hyraxes, armadillos, golden moles, and tenrecs, which collectively belong to the supercohort Afrotheria (Springer et al. 1999; Seiffert 2007; Meredith et al. 2011). The single family of sengis (Macroscelididae) contains 2 well-defined subfamilies (Corbet and Hanks 1968)—the giant sengis (Rhynchocyoninae), currently with 4 extant species in the genus *Rhynchocyon*, and the soft-furred sengis (Macroscelidinae), with 14 species in 3 genera: *Petrodromus*, *Macroscelides*, and *Elephantulus* (Rathbun 2009; Dumbacher et al. 2012).

Since the publication of the nearly definitive taxonomy by Corbet and Hanks (1968), only 2 completely new taxa have been described: the gray-faced sengi, *Rhynchocyon udzungwensis* (Rovero et al. 2008) and the Karoo rock sengi, *Elephantulus pilicaudus* (Smit et al. 2008). There also are

likely other forms awaiting description (Rathbun 2008; Andanje et al. 2010). Several genetic studies have largely supported the current species taxonomy, although based on phylogenetics the taxonomy of the North African sengi (*E. rozeti*) and the monospecific four-toed sengi (*Petrodromus tetradactylus*) probably will need to be redefined (Douady et al. 2003; Smit et al. 2011). Unusual for small mammal taxonomy, virtually all treatments of the recent species of macroscelids are based mainly on external morphology or molecular genetics, with few analyses of specific cranial and dental features.

Most recently, the 2 subspecies in the monospecific genus *Macroscelides* were raised to full species, the Karoo round-eared sengi (*M. proboscideus*) and the Namib round-eared





**FIG. 1.**—Study area and distribution of *Macroscelides* in Namibia, southwestern Africa. The right map shows the ranges of *Macroscelides proboscideus*, *M. flavicaudatus*, and *Macroscelides* sp. nov. In the left map, specimens of *M. flavicaudatus* and the new form are plotted with respect to major geological features of the region and illustrate broad sympatry, even though they occur in different microhabitats (see text). The 3 major areas of the Etendeka geological formation are noted (Etendeka Plateau, Awahab Outliers, and the Goboboseb Mountains).

sengi (*M. flavicaudatus*—Dumbacher et al. 2012). In the course of reviewing the taxonomy of *Macroscelides*, we encountered an unusual specimen (California Academy of Sciences mammal collections [CAS MAM] 27997) collected in 2006 by MG during a reptile and small mammal collecting expedition in northwestern Namibia. The specimen included a study skin, prepared skull, and tissue samples. This specimen was darker than expected, with a more rusty-colored pelage than other *Macroscelides* specimens in collections from the region. A preliminary genetic assessment (using sequence from cytochrome *b* [Cytb] and 12s ribosomal RNA [rRNA]) suggested that it was distantly related to other *Macroscelides*. With only 1 specimen that lacked external metrics, we sought additional specimens for a thorough analysis. We have since collected an additional series of complete voucher specimens. Here, we describe these as a new species of *Macroscelides* and summarize what is known of its distribution and ecology.

## MATERIALS AND METHODS

**Study area.**—Despite past small mammal trapping in northwestern Namibia (M. Griffin and S. J. Eiseb, pers. obs.), including in the Namib Desert, Pro-Namib habitats, and inland highlands, the unusual sengi was not known prior to March 2006. Thus, our trapping efforts focused on the ancient

Etendeka volcanic formation (see habitat section below), where the 1st and all subsequent specimens were captured. This arid area is inland from the coastal Namib Desert between the Ugab and Hoanib rivers (Fig. 1), and because it is relatively remote with few roads or tracks and little or no water, voucher specimens were captured over several carefully planned trapping expeditions.

**Collection of voucher material.**—We trapped in the study area during 9 visits (9 June 2005, 8 April 2006, 2–7 October 2009, 19 December 2009, 4–21 May 2010, 9–12 October 2010, 10–14 November 2010, 12–13 February 2011, and 21–26 September 2011), including the first 2 visits by A. Bauer and M. Griffin, respectively (however, trapping effort and success for these first 2 trips was not recorded). We used Sherman live traps (3 × 3.5 × 9 inches, aluminum folding model LFA; H. B. Sherman Traps, Tallahassee, Florida) baited with a dry mix of peanut butter, whole rolled oats, and Marmite (a yeast spread) set in transects with trap spacing of 10–50 m. Each transect included 20–50 traps, and each night we set a total of 50–200 traps, opening them in late afternoon, and closing them the next morning soon after sunrise. We used handheld global positioning system receivers (Garmin model GPS 60; Garmin International, Inc., Kansas City, Kansas) and Google Earth version 6.1 (Google Inc. 2013) to collect and proof georeferenced locality data.

We prepared specimens as classical study skins and skulls, with fresh muscle, liver, and heart tissues preserved in 95% ethanol for later DNA analyses. We collected standard external body measurements (total length, tail length, hind-foot length with and without claw, ear length from notch to crown, and body mass) from all voucher specimens. We also photographed habitats at capture sites and some live and freshly euthanized specimens prior to preparation. All our work with live specimens was performed in accordance with the standard guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and methods were reviewed and approved by California Academy of Sciences (CAS) Institutional Animal Care and Use Committee.

We examined *Macroscelides* specimens in the collections of the National Museum of Namibia in Windhoek, the Ditsong (Transvaal) National Museum of Natural History in Pretoria (South Africa), the Natural History Museum (British Museum of Natural History) in London, the Los Angeles County Museum of Natural History in California, and the California Academy of Sciences in San Francisco. The location data we used to determine the distributions of *Macroscelides* were based on the 16 voucher specimens we collected, numerous museum holdings, publications, and reports from field biologists (Dumbacher et al. 2012; Rathbun 2012).

*Morphological analyses.*—To assess the morphological distinctness of the new form, we used data from museum skins, photos of live or freshly collected individuals, and prepared skulls. Cranial measurements were taken by JPD and were measured with dial calipers calibrated to 0.1 mm. External features were measured in the field with straight-edge rulers to the nearest 1.0 mm. Characters measured included tail length, hind-foot length (with claw), greatest length of skull, greatest zygomatic breadth, least interorbital breadth, height of rostrum, width of bulla, greatest alveolar length of upper tooththrow, greatest height of skull, greatest alveolar length of mandibular tooththrow, height of mandible, and length of mandible. We compared these 12 measurements with those collected previously from *Macroscelides* (Dumbacher et al. 2012) using principal component analyses and discriminant function analyses in the program Stata 10.0 (StataCorp 2007) for Macintosh computers.

*Genetic analyses.*—To assess the genetic distinctness of the new form and to look for indication of gene flow among *Macroscelides* species, we sequenced mitochondrial loci and 2 independently segregating nuclear genes from the new sengi to compare with other *Macroscelides*. DNA was extracted from fresh specimens using commercially available kits (DNeasy Tissue Kit; Qiagen, Valencia, California). Polymerase chain reaction was performed using several primer sets. For mitochondrial loci, primers F14164 (5' GAAAARYCATCGT TGTAAHTTCAACTA 3') and R15181 (5' ACWGGTTGDC CDCRATTCAKGT 3') were used to amplify a 1,005-base-pair (bp) portion of the *Cytb* gene (Springer et al. 1999). In addition, we amplified a region of approximately 2,650 mitochondrial bases that included 12s rRNA, transfer RNA valine, and 16s rRNA using primers rRNA-aF (AAAGCAAA

RCAGTAAAATGCYTAGATG) and rRNA-eR (TGTTAAG GAGAGGATTTGAACCTCTG) and used multiple internal primers for sequencing (Douady 2001). We also used 2 independently segregating nuclear loci. The 1st was a 962 bp region of the von Willebrand factor locus (vWF) exon 28, amplified and sequenced by primers vWF-A2 (AGCAAGCTG CTGGACCTGGTCTTCTGCTGGA), vWF-B2 (GCAGGGT TTCCTGTGACCATGTAGACCAG), vWF-D2 (GTGATCCC GGTGGGCAT), and vWF-G2 (AAAGGCTTTGTTCTCAG GGGCCTGCTTCTC—Douady 2001). The 2nd nuclear locus was interphotoreceptor retinoid-binding protein (IRBP); 986 bases were amplified from the upstream region of exon 1 using the primers IRBP445 (AACCTTACACAGGAGGAAGTCTG) and IRBP1451 (ACATCTGCAAACCTTGTCAAAGCGCA), and internal primers also were used in sequencing IRBP913 (GCCCTGGACCTCCAGAAGCTGAGGATAGG) and IRBP1046 (AGGGCTTGCTCTGCTGGAG—Douady 2001). Polymerase chain reaction was performed using Invitrogen Taq polymerase and buffers in 25- $\mu$ l reactions with 0.4  $\mu$ M primer concentration, 1.5 mM of MgCl<sub>2</sub>, 0.2 mM of deoxynucleoside triphosphate, and 1 U of Taq polymerase. Primer annealing temperature was 55°C for *Cytb*, rRNA, and IRBP. The vWF polymerase chain reaction used a touchdown protocol with annealing temperature starting at 62°C and dropping 0.5°C per cycle until reaching 55°C, then continuing with 35 additional cycles. Polymerase chain reaction extension was performed at 72°C and was 1 min for *Cytb*, IRBP, and vWF, but was 3 min for rRNA due to the longer region being amplified. Amplicons were cycle sequenced using BigDye Terminator version 3.1 cycle sequencing kit (Life Technologies, Grand Island, New York), and visualized on an ABI 3130 automated sequencer (Life Technologies).

The DNA sequences were edited and assembled and primers were removed using Sequencher 5.0 software (Gene Codes Corporation 2013). Additional published DNA sequences of *M. proboscideus* and *M. flavicaudatus* (Dumbacher et al. 2012) were added to the matrix for comparison, and outgroup sequences from *Petrodromus*, *Rhynchocyon*, and *Elephantulus* were included and sequences were aligned in Sequencher. The rRNA region had multiple insertions and deletions and was highly variable, so to ensure reliable alignments we used ClustalW in Geneious Pro version 5.6.3 software (Biomatters 2013). The software jModelTest2 (Darriba et al. 2012) was used to select appropriate evolutionary models for phylogenetic analyses. PAUP\* (Swofford 2003) and GARLI version 0.96 beta (Zwickl 2006) were used to search for the most likely tree and model parameters. PAUP\* and GARLI were used to run likelihood bootstrap analyses and MrBayes (Ronquist et al. 2011) was used to estimate parameters and posterior probabilities.

## RESULTS

Our fieldwork in northwestern Namibia involved 5,616 trap-nights that yielded 21 *Macroscelides* specimens (Table 1). Fifteen of these *Macroscelides* specimens were morphologi-

cally distinct from the specimens of *M. flavicaudatus* that we collected from the area, and they also were distinct from any other specimens of this genus that we examined or analyzed in collections. These 15 specimens, plus the single specimen (CAS MAM 27997) collected previously, are the only specimens known to us of this distinct sengi, which we define as a new species based upon unique morphological and genetic features.

*Macroscolides micus*, Dumbacher and Rathbun 2014,  
new species  
Etendeka Round-eared Sengi

**Holotype.**—CAS MAM 29679, prepared museum skin; skull and entire postcranial skeleton cleaned of soft tissue; tissue (muscle and liver) preserved in alcohol and frozen.

**Type locality.**—The type locality is latitude and longitude 20.7281°S, 14.1305°E at about 720 m above sea level at the base of rocky outcrops on gently sloping alluvial gravels with scattered cobble-sized reddish colored basalt rocks and stones (Fig. 2) about 10 km south by southwest (200°) of the Mikberg formation, Kunene District, Namibia. The area was arid and dominated by sparse and widely spaced low vegetation composed mostly of perennial bunch grasses, with a few forbs and low bushes.

**Paratypes.**—We collected 5 other specimens at the type locality (within 1 km), some of which will eventually reside at the National Museum of Namibia: CAS MAM 27997, skin with skull (missing field measurements) and tissue in dimethylsulfoxide; CAS MAM 28968, skin, skull, and tissue in ethanol and frozen; CAS MAM 29699, skin, skull, and tissue in ethanol and frozen; CAS MAM 29713, skin with skull and entire postcranial skeleton and muscle in formalin; and CAS MAM 29725, skin, skull, and tissue in ethanol and frozen.

**Etymology.**—The derivation of *micus* is Greek (*mickros*) meaning small, which reflects the diminutive size of this species; indeed, it is the smallest of any known sengi. This epithet continues the practice of using names that reflect distinctive features of each taxon in this genus (see below). We suggest the common name for the new species be Etendeka round-eared sengi (or elephant-shrew), which is based on the widely recognized common name used when the genus was monospecific (round-eared sengi), and incorporates the name of the region in Namibia where it occurs. Etendeka is from the Himba/Otji-Herero language of the Himba people from northwestern Namibia, and refers to the distinctive flat-topped mountains and rust-colored substrates of the region. The other 2 species in the genus are the Karoo round-eared

sengi (*M. proboscideus*) and the Namib round-eared sengi (*M. flavicaudatus*).

**Diagnostic characters.**—Skin of *M. micus* lacks dark pigmentation and results in a pinkish gray coloration. This is most obvious in the external pinnae and legs (Fig. 3), where hair is thinner and shorter and exposes the skin. In the other 2 *Macroscolides* species, the external pinnae and legs are distinctly pigmented and appear nearly black. Thus, the light coloration of the pinnae is a diagnostic trait of *M. micus*.

*Macroscolides micus* has a prominent, dark, hairless gland on the ventrum of the tail, usually starting in the proximal quarter and often extending over halfway to the tip (Fig. 3). Based upon 15 study skins of *M. micus*, the total length of the gland ranged from 20 to 35 mm (mean 29.5 mm), representing 20–40% (mean 32%) of the total tail length. At its widest (typically midlength), the gland occupies nearly the entire width of the ventral side of the tail and results in the tail in this region appearing swollen from all aspects (Fig. 3). The gland in 13 prepared skins of *M. flavicaudatus* was not visible in 8, and in the remaining 5 skins it ranged from 8 to 11 mm and was less than 10% of the tail length in all specimens. The gland in 3 *M. proboscideus* skins ranged from 8 to 12 mm and was less than 10% of the total tail length. Examination of these data indicates that a highly developed subcaudal gland is diagnostic for *M. micus*.

The dorsal and lateral grayish brown pelage of *M. micus* has an obvious rust-colored wash or tinge, most noticeable around the face, on the rump region, and the tail hairs (Fig. 3). The slightly longer, rust-colored, brushlike hairs on the distal portion of the tail also are obvious, although their length is not always notably different than those of *M. flavicaudatus*. The rusty coloration is diagnostic, and most easily distinguished when compared directly with the more typically brown to gray coloration of *M. proboscideus* and the often very light buff coloration of *M. flavicaudatus* (see plate in Dumbacher et al. 2012).

Our principal component analysis of external and cranial characters revealed significant clusters by species, with the new species being the most distinct of the 3 (Fig. 4). Principal component axis 1 explained 67.2% of the variation, and principal component axis 2 explained another 15% of the variation, for a cumulative 82.2% (Table 2). All 12 variables had positive loadings for principal component 1, suggesting that this axis summarized overall size differences among specimens. The primary separation between *M. micus* and the other 2 species was along axis 1, confirming that it is the smallest of the 3, although most characters when considered alone have a size range that overlaps those of the other species.

→

**FIG. 2.**—A) The type locality of *Macroscolides micus* sp. nov. in northwestern Namibia, showing primary physical features, including sparsely vegetated grasses, the lack of shrubs, and the size and dispersal of Etendeka basalt cobbles (GBR photo 3 May 2010). B) Typical habitat of *M. micus* (20°44'56"S, 14°7'12"E; 650 m elevation) on the lower slope (6°) of an outcrop at the southern edge of the Awahab Outliers, about 28 km south of the Huab River in northwestern Namibia. The Sherman trap, just beyond the welwitschia plant in the foreground, is where *M. micus* (CAS MAM 29701) was captured, and a *M. flavicaudatus* (CAS MAM 29700) was captured about 150 m lower on the slope, beyond the trap bag.



Note the rust-colored substrate and arid habitat dominated by the relatively flat gravel surface, scattered rocks, sparse bunch grasses, and near absence of bushes. On the horizon 60 km to the southeast is the Brandberg Massif (approximately 2,600-m granitic mountains) and to the south the Goboboseb Mountains (approximately 1,000 m; GBR photo 10 May 2010).

*Phylogenetics.*—After sequencing the 4 loci, we aligned each and trimmed ends to exclude regions with missing bases. Our analyses included a total of 3,607 aligned mitochondrial DNA bases (2,663 bases in the region from 12s–16s rDNA and 944 from *Cytb*), 976 aligned bases from IRBP, and 883 aligned bases from vWF (GenBank numbers KF742615–KF742671 and KF895103–KF895129). Each of the regions was analyzed separately to give an independent assessment of the phylogeny, but also to provide us with independent tests of gene flow among the species (Fig. 5). Because of alignment difficulties with other sengi taxa, no outgroup was used for the 12s–16s rDNA tree, and a midpoint rooting was used instead.

Every gene provided strong support for the reciprocal monophyly of each of these *Macroscelides* species, with no evidence of gene flow among the species. For every gene, *M. proboscideus* and *M. flavicaudatus* grouped as sister species, with *M. micus* a more distantly related form. We had reasonable sample sizes of *M. flavicaudatus* ( $n = 9$ ), especially from the region where the 2 species were sympatric, and we found no evidence of gene flow or interbreeding among *M. micus* and the other species.

Average pairwise sequence divergence (uncorrected p-distances) at *Cytb* between *M. proboscideus* ( $n = 2$ ) and *M. flavicaudatus* ( $n = 9$ ) was 14.2% (range 13.1–14.9%, *SD* 0.47%), whereas average divergence between *M. micus* ( $n = 16$ ) and these 2 species was 20.4% (range 19.9–21.6%, *SD* 0.39%). The average pairwise *Cytb* sequence divergence among individuals of *M. micus* was 0.2% (range 0–0.3%, *SD* 0.084%). For comparison, the maximum pairwise divergence found within *M. flavicaudatus* was 1.7% and among *M. proboscideus* was 1.8% (Dumbacher et al. 2012).

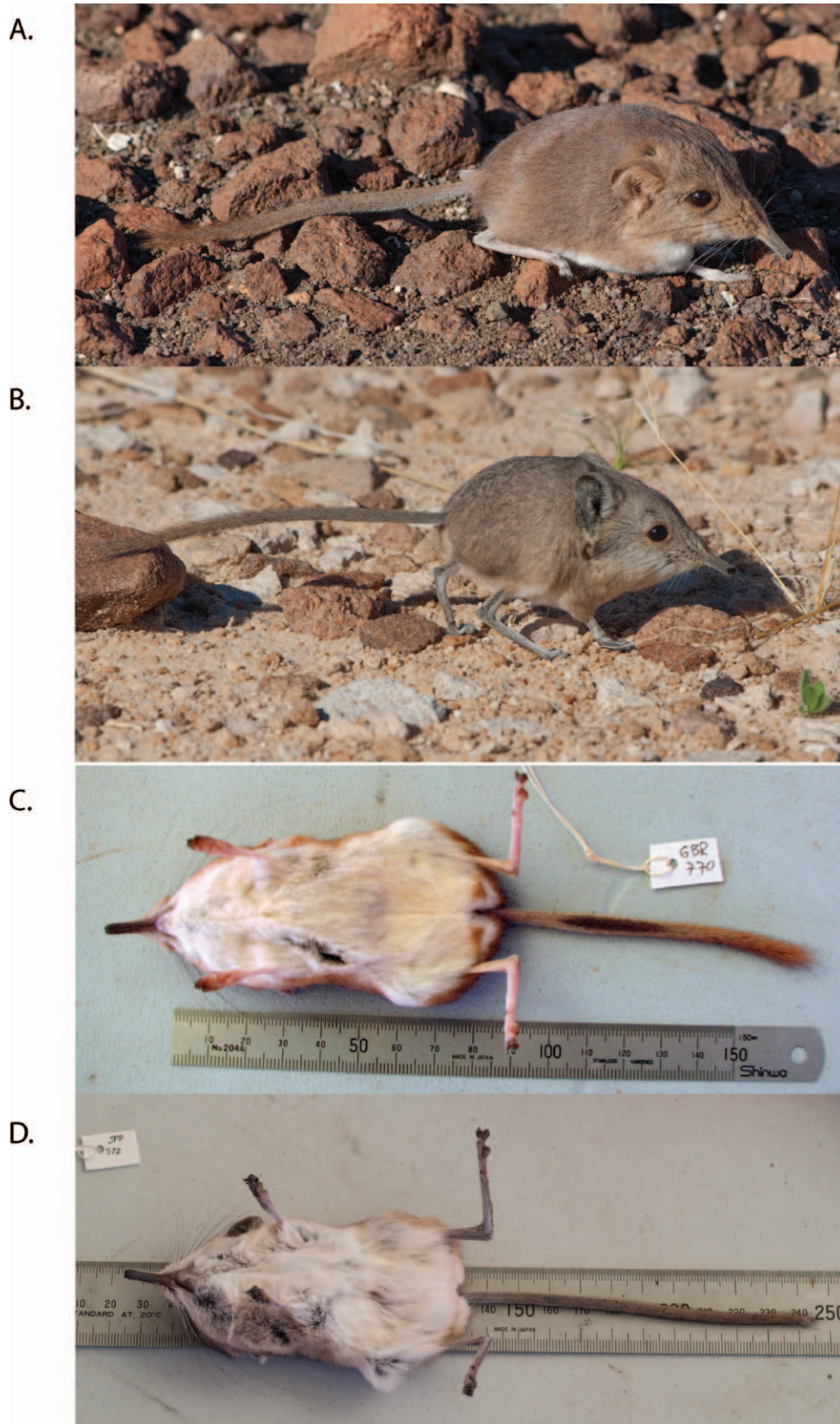
*Description.*—*Macroscelides micus* (Fig. 3) is the smallest member of the extant Macroscelididae, with an average ( $n = 14$ ) adult total length of 186 mm (range 170–195 mm), tail length of 90 mm (range 83–97 mm), and adult body mass of 26.9 g (range 22.3–31.3 g;  $n = 12$  adults, average and range do not include 1 immature with mass of 18.9 g and 2 pregnant females with masses of 36 g and 42.9 g). As with all sengis, *M. micus* has a long, flexible proboscis that extends several millimeters past the mouth, and the tongue can be extended several millimeters beyond the tip of the nose. The proboscis is covered in fine, short hairs, except for the tip surrounding the nostrils. The size of the eye is proportionally smaller than that in other genera in the Macroscelidinae, and there is no eye-ring. The pinnae of *M. micus* are shorter than those of *Elephantulus* and generally shorter than those of the other *Macroscelides*, appearing not to extend above the head, with rounder crowns and a slightly deeper indentation on the posterior margins. The exposed inner surfaces of the pinnae are sparsely covered with short, rust-colored hairs, but the anterior interior edges are fringed with rear-facing 3- to 4-mm-long hairs. External ear surfaces are sparsely covered with fine hair with a slight rust-colored tinge, and the pinkish colored skin is clearly visible through these hairs. Overall, the pelage is dense and soft, with the dorsum being light gray and tinged with a rust color. The ventrum is off-white from the chin to the anus

and extends partly up the sides of the body and onto the upper fore- and hind-limbs, where the hair is shorter and sparser. There is a small patch of rust-colored fur on each side of the perianum. The dorsal hairs are about 10 mm long with slightly rust-colored tips (about 3–4 mm) subtended with dark gray to their bases. Ventral hairs are about 7 mm long with white or off-white tips (3–4 mm) and dark gray to their bases. The tail is nearly naked at the base, but sparsely furred for most of its length. Posterior to the subcaudal gland the rust-colored hairs become denser and longer (4–5 mm), giving the distal half of the tail an almost bushy appearance. The feet are sparsely covered with fine white fur dorsally, whereas the ventral surfaces are mostly naked. The cranium has exceptionally enlarged auditory bullae compared to *Elephantulus* and *Petrodromus*, but very similar to other *Macroscelides*.

*Distribution, habitat, and density.*—The 16 voucher specimens of *M. micus* are restricted to the Etendeka Igneous Province (Fig. 1), which is defined by a volcanic flood that occurred about 133 million years ago, and subsequently was bisected by the breakup of the supercontinent Gondwana that resulted in the creation of South America and Africa (Jerram et al. 1999). In Namibia, there are 3 major and separate extrusions of the Etendeka formation: the Etendeka Plateau and Awahab Outliers are separated by the Huab River, and the Goboboseb Mountains (including the Messum Crater) south of the Ugab River (Fig. 1). Currently, *M. micus* is only known from the lower elevations in the southern half of the Etendeka Plateau and the lower areas of the Awahab Outliers. We did not trap in the northern Etendeka Plateau, the Goboboseb Mountains, or in the western portion of the Etendeka Plateau that lies in Skeleton Coast National Park.

The volcanic rocks and soils associated with the Etendeka formations are rust colored, but where extensive erosion has occurred in the Awahab Outliers and in river valleys, the underlying nearly white sedimentary formations have been exposed. *M. micus* occupies a microhabitat that is characterized by low-gradient rust-colored gravel slopes ( $< 10^\circ$ ) at the bases of outcrops, hills, and mountains in the lower elevations of the Etendeka geological formation. The mountains are as high as 1,400 m in the eastern Etendeka Plateau, although the average trapping elevation for the 16 specimens of *M. micus* was 630 m (range = 340–860 m). The lower elevations where *M. micus* occurred are more xeric and receive 50–100 mm of rain per year (Mendelsohn et al. 2002), whereas the adjacent inland and higher elevations are more mesic. The gravel alluvial fans or plains where we captured *M. micus* had widely spaced shallow washes and scattered fist-sized to cinder-block-sized rocks. The vegetation in these lower elevations comprised widely spaced perennial bunch grasses and forbs with few, if any, bushes that were more than about 30 cm high (Fig. 2).

In contrast to *M. micus*, the 11 *M. flavicaudatus* that we trapped were in a different microhabitat, characterized by light-colored sedimentary substrates exposed in the Awahab Outliers and river valleys, and outside of the Etendeka formations to the south and west (Fig. 2). We captured no *M. proboscideus* in our study area because it occurs about 500 km to the south



**FIG. 3.**—Captive A) *Macroscelides micus* (CAS MAM 29699; JPD photo) and B) *M. flavicaudatus* (CAS MAM 29696; JPD photo), illustrating the diagnostic features of the former: ears that appear pink due to the absence of dark skin pigment; swollen base of tail due to the large subcaudal gland; and rusty pelage of face, dorsum, and tail. Ventral views of C) *M. micus* (CAS MAM 29699; GBR photo) showing the diagnostic subcaudal gland and the light skin color of the legs in contrast to that of D) *M. flavicaudatus* (CAS MAM 29726; GBR photo).



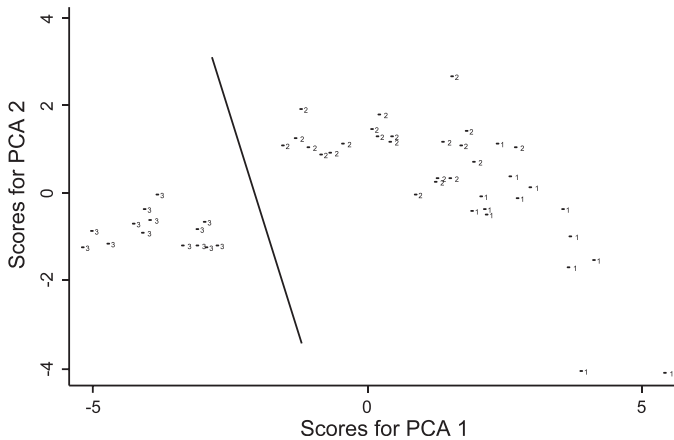


FIG. 4.—Principal component (PC) axes 1 and 2 of 12 morphological variables from specimens of *Macroselides proboscideus* (1), *M. flavicaudatus* (2), and *M. micus* (3). The clear separation along the PC1 axis primarily summarizes size differences.

(Fig. 1). We captured 18 western rock sengis (*Elephantulus rupestris*) in a microhabitat that was dominated by larger rocks and boulders, often higher up the sides of outcrops, hills, and mountains.

Our trapping effort was focused on the microhabitat where we expected to capture specimens of *M. micus*, which resulted in a 0.29% trapping success (5,216 trap-nights, not including any effort or success data from the first 2 trapping field trips, which included 1 *M. micus* and 3 *M. flavicaudatus*) and suggests a very low population density. Trapping successes for other taxa were 0.10% *M. flavicaudatus*, 0.35% *Elephantulus rupestris*, and 7.80% overall for 5 rodent genera (*Desmodillus*, *Gerbillurus*, *Micaelamys*, *Petromus*, and *Petromyscus*).

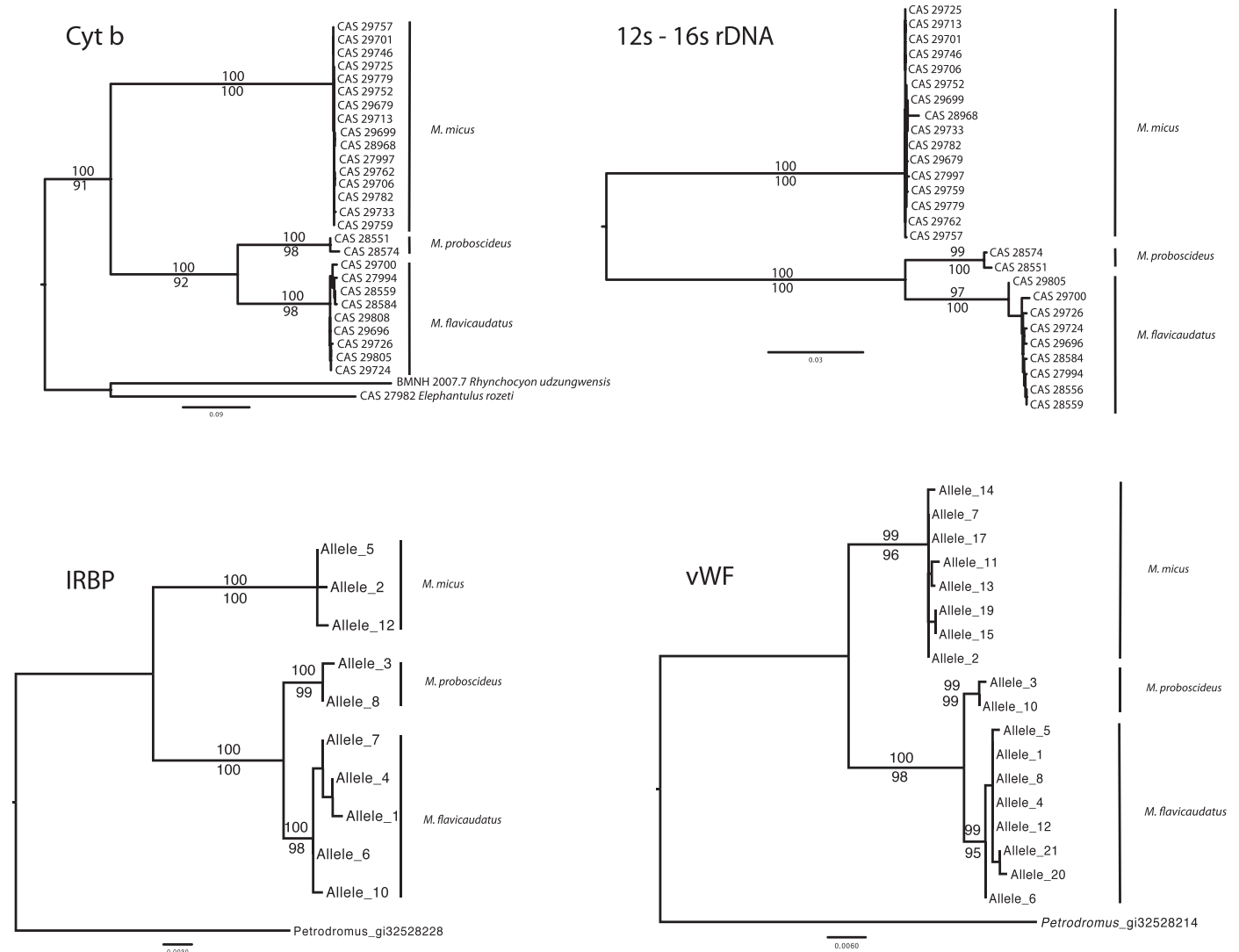
*Natural history.*—Of the 16 voucher specimens of *M. micus* (Table 1), 10 were female, 4 were male, and the sex was not determined for 2 (1 was immature). Of the adult female specimens, 2 were pregnant (February and November) and 1 was lactating (May). The 2 pregnant females each carried twins (28- and 30-mm crown-rump lengths), 1 in each uterine horn.

TABLE 1.—Data from voucher specimens used in describing the new species. In the catalog number column, holotype is indicated with an H, paratypes with a P, specimens including postcranial material with an asterisk (\*), and entire specimen in formalin with a pound sign (#). Reproductive females with embryos are noted with an R. Missing data are shown as a question mark (?). Unless otherwise noted, all catalog numbers are from the California Academy of Sciences mammal collections (CAS MAM). Measurements are in order as follows: total length, tail length, hind-foot length (with claw), and ear length. The animal with catalog number CAS MAM 29713 is likely immature. *E.* = *Elephantulus*; *M.* = *Macroselides*; *R.* = *Rhynchocyon*. M = male; F = female. BMNH = British Museum of Natural History.

| Catalog no. | Date              | Species                 | Latitude (°S) | Longitude (°E) | Body mass (g) | Measurements (mm) | Sex |
|-------------|-------------------|-------------------------|---------------|----------------|---------------|-------------------|-----|
| 27982       | 18 July 2005      | <i>E. rozeti</i>        | −31.828       | 7.985          | 31.0          | 250-133-35-26     | M   |
| 27991       | 9 June 2005       | <i>M. flavicaudatus</i> | −20.778       | 14.080         | 24.0          | 217-113-33-23     | F   |
| 27993       | 28 March 2006     | <i>M. flavicaudatus</i> | −20.807       | 14.117         | 22.0          | 195-98-33-22      | F   |
| 27994       | 28 March 2006     | <i>M. flavicaudatus</i> | −20.800       | 14.117         | 34.0          | 218-112-33-24     | F   |
| 27995       | 28 March 2006     | <i>M. flavicaudatus</i> | −20.800       | 14.117         | 39.0          | 235-127-34-24     | F   |
| 27996       | 28 March 2006     | <i>M. flavicaudatus</i> | −20.837       | 14.083         | 23.0          | 201-104-34-21     | M   |
| 29696       | 7 May 2010        | <i>M. flavicaudatus</i> | −20.714       | 14.124         | 30.8          | 224-118-35.5-23   | M   |
| 29700       | 10 May 2010       | <i>M. flavicaudatus</i> | −20.750       | 14.119         | 32.0          | 228-124-37-32     | F   |
| 29724       | 8 May 2010        | <i>M. flavicaudatus</i> | −20.712       | 14.122         | 32.0          | 228-119-36.5-26   | F   |
| 29726 *     | 10 May 2010       | <i>M. flavicaudatus</i> | −20.751       | 14.119         | 33.5          | 233-130.5-38-28.5 | M   |
| 29805       | 22 September 2011 | <i>M. flavicaudatus</i> | −19.754       | 13.615         | 24.6          | 199-105-33.5-20   | M   |
| 29808       | 22 September 2011 | <i>M. flavicaudatus</i> | −19.756       | 13.613         | 27.9          | 207-105-32-20     | M   |
| 28551 *     | 10 June 2007      | <i>M. proboscideus</i>  | −24.914       | 16.270         | 37.5          | 236-122-37-22     | M   |
| 28556 *     | 12 June 2007      | <i>M. proboscideus</i>  | −25.27        | 15.932         | 28            | 226-122-35-21     | M   |
| 28559 *     | 12 June 2007      | <i>M. proboscideus</i>  | −25.292       | 15.923         | 26.5          | 224-119-35-22     | M   |
| 28574 *     | 10 June 2007      | <i>M. proboscideus</i>  | −24.914       | 16.270         | 34.0          | 225-116-35-24     | M   |
| 28584 *     | 12 June 2007      | <i>M. proboscideus</i>  | −25.27        | 15.932         | 26            | 235-127-35-26.5   | M   |
| 27997 P     | 8 April 2006      | <i>M. micus</i>         | −20.727       | 14.128         | ?             | ?                 | ?   |
| 28968 P     | 3 May 2010        | <i>M. micus</i>         | −20.728       | 14.130         | 24.9          | 184-96-28.5-19.5  | F   |
| 29679 H *   | 5 October 2009    | <i>M. micus</i>         | −20.728       | 14.131         | 25.7          | 195-97-30-17      | F   |
| 29699 P     | 9 May 2010        | <i>M. micus</i>         | −20.725       | 14.128         | 28.8          | 193-94-30-20.5    | F   |
| 29701 *     | 10 May 2010       | <i>M. micus</i>         | −20.749       | 14.120         | 24.8          | 189-89-29-28      | F   |
| 29706 *     | 16 May 2010       | <i>M. micus</i>         | −20.531       | 14.014         | 25.7          | 187-92-28.5-19    | M   |
| 29713 P #   | 3 May 2010        | <i>M. micus</i>         | −20.727       | 14.130         | 18.9          | 167-82-28-19.5    | ?   |
| 29725 P *   | 9 May 2010        | <i>M. micus</i>         | −20.736       | 14.129         | 22.3          | 188-92.5-30.5-21  | M   |
| 29733 *     | 16 May 2010       | <i>M. micus</i>         | −20.531       | 14.015         | 27.2          | 193-95-28.5-21.5  | F   |
| 29746       | 10 October 2010   | <i>M. micus</i>         | −20.617       | 13.862         | 31.3          | 191-94-28-18      | F   |
| 29752 *     | 10 November 2010  | <i>M. micus</i>         | −20.589       | 13.813         | 30.8          | 185-89-28-18      | F   |
| 29757 *     | 13 November 2010  | <i>M. micus</i>         | −20.662       | 14.032         | 29.0          | 177-85-28-17      | M   |
| 29759 *     | 13 November 2010  | <i>M. micus</i>         | −20.660       | 14.017         | 29.0          | 180-83-29-19      | F   |
| 29762 R     | 14 November 2010  | <i>M. micus</i>         | −20.413       | 13.828         | 42.9          | 191-93-29-19      | F   |
| 29779 * R   | 13 February 2011  | <i>M. micus</i>         | −20.167       | 13.897         | 36.0          | 185-87-28-17      | F   |
| 29782 *     | 13 February 2011  | <i>M. micus</i>         | −20.168       | 13.896         | 22.9          | 170-84-27.5-17    | M   |
| BMNH 2007.7 | 23 March 2006     | <i>R. udzungwensis</i>  | −7.805        | 36.506         | ?             | ?                 | M   |

**TABLE 2.**—Principal component (PC) analyses of morphological characters, with variable loadings for each component axis. The bottom portion of the table provides eigenvalues and proportion of variation explained by each axis.

| Variable                                    | PC1     | PC2     | PC3     | PC4      | PC5      | PC6      |
|---|---------|---------|---------|----------|----------|----------|
| Tail length                                 | 0.2063  | 0.4803  | -0.1462 | 0.6439   | 0.2379   | 0.3016   |
| Hind-foot length                            | 0.2856  | 0.3142  | -0.1045 | 0.3356   | -0.2792  | -0.3979  |
| Skull length                                | 0.341   | -0.0065 | -0.0988 | -0.1985  | -0.1307  | 0.2678   |
| Zygomatic breadth                           | 0.3413  | 0.0335  | -0.0171 | -0.1327  | -0.2956  | -0.0019  |
| Interorbital width                          | 0.2826  | 0.2865  | 0.1159  | -0.3605  | 0.5974   | -0.3273  |
| Height of rostrum                           | 0.1432  | 0.1848  | 0.9357  | 0.0247   | -0.0986  | 0.1054   |
| Width of bulla                              | 0.2912  | 0.2806  | -0.2375 | -0.4314  | 0.04     | 0.2063   |
| Upper tooththrow length                     | 0.3102  | -0.3009 | 0.055   | 0.069    | -0.037   | 0.234    |
| Greatest height of skull                    | 0.3418  | -0.0006 | -0.0904 | -0.122   | -0.1527  | -0.0578  |
| Mandibular tooththrow length                | 0.2554  | -0.4329 | 0.0233  | 0.1764   | 0.4968   | 0.3162   |
| Height of mandible                          | 0.2818  | -0.3614 | 0.0149  | 0.2035   | 0.1587   | -0.5987  |
| Length of mandible                          | 0.3166  | -0.2566 | 0.0176  | 0.0827   | -0.31    | 0.0419   |
| <b>PC axes summary</b>                      |         |         |         |          |          |          |
| Eigenvalue                                  | 8.06444 | 1.79571 | 0.87216 | 0.419271 | 0.277234 | 0.168596 |
| Proportion of variance explained            | 0.672   | 0.1496  | 0.0727  | 0.0349   | 0.0231   | 0.014    |
| Cumulative proportion of variance explained | 0.672   | 0.8217  | 0.8944  | 0.9293   | 0.9524   | 0.9665   |



**FIG. 5.**—Maximum-likelihood phylogenetic trees for mitochondrial DNA haplotypes and alleles at 2 nuclear loci. Numbers above each node indicate Bayesian posterior probabilities times 100, and the numbers below the node indicate likelihood bootstrap values.

Of the 16 captures, 3 pairs were caught in close proximity to each other on the same trapline, and 2 of these pairs were of opposite sex, whereas the 3rd pair was a female and immature. We found no paths or burrows that would suggest the presence of *M. micus*. We collected unidentified ticks and mites from several *M. micus* and *M. flavicaudatus*, but found no fleas nor lice, despite our focused combings.

*Status and conservation.*—Because of the species' low density and restricted range, there may be some conservation concern. Direct human impacts are relatively rare within the range and are limited to low-impact game hunting and viewing by tourists.

## DISCUSSION

*Macrosclides micus* clearly qualifies as a new species by every definition or criteria. It is morphologically distinct and easily diagnosable, examination of all available genetic data suggests it is reproductively isolated from sympatric *M. flavicaudatus* without any indication of hybrid forms or gene flow, and it forms a reciprocally monophyletic clade with respect to all other members of its genus. In addition, genetically *M. micus* is remarkably divergent from other *Macrosclides* at every locus examined.

We must address the status of the enigmatic *Macrosclides melanotis* (Ogilby 1838) because of several irregularities surrounding the collection and naming of the type specimen, and the possibility that this name might be available for the new species described herein. We examined the type specimen and high-quality photographs of the type from the Natural History Museum in London (BMNH 38.3.8.2). It was putatively collected from Damaraland (at the time of Ogilby, this was an interior region of northern Namibia between 19°S and 23°S; part of this large region is now more formally called Khorixas District—J. Irish, pers. comm.). Ogilby's description is short, and primarily compares the type of *M. melanotis* with a 2nd specimen (*Macrosclides alexandri* Ogilby, 1838) that is now recognized as *Elephantulus intufi* (Corbet and Hanks 1968). We argue that the type specimen of *M. melanotis*, and the published description, are unrecognizable and represent a nomen dubium, for the following reasons.

First, the holotype is data depauperate and incomplete. No field measurements were taken (total length, tail length, hind foot, ear, or mass) and these cannot be recovered from prepared skins. The tail and most skull elements are completely missing, with the exception of the rostrum, which currently provides no diagnostic characters. The skin is tattered, the darker gray bases of the hairs are exposed resulting in an unnatural look and color, and there is some indication that the specimen had been preserved in fluid (Corbet and Hanks 1968), and this may have affected the pelage and skin color in unknown ways. The most phylogenetically useful characters for *Macrosclides* (Dumbacher et al. 2012) are the genetic sequence characters, but the initial fluid preservation has likely affected their usefulness. Additionally, the Natural History Museum in London, where the holotype of *M. melanotis* is presently stored, has a policy

prohibiting destructive sampling of any type specimens, and therefore, we were not able to obtain tissues for DNA extraction. These factors render the type of *M. melanotis* currently useless for taxonomic comparison, but this may change if new technology provides methods for distinguishing the known taxa or if the museum changes its policy on destructive sampling.

Second, the type specimen does not match the original imprecise description of *M. melanotis*, which follows: "Of a rather larger size than [*E. intufi*], with large head, dark brown or black ears, rather sandy under lip, dunnish white throat and abdomen, but pale reddish brown chest; color of the upper parts much the same, but rather more ashy; tarsi light brown; tail mutilated; length 6 inches" (Ogilby 1838: pg 5). The reported pale, reddish brown chest color is not visible on the specimen, nor is the dunnish white abdomen or throat. The characters noted are not specific enough to be taxonomically useful for *Macrosclides*, although the dark brown or black ears may eliminate the possibility that *M. micus* could be synonymous with *M. melanotis*.

Third, *M. melanotis* has a confusing history and application. After the voucher was collected and described from Damaraland in 1838, the name was applied to South African specimens from Port Nolloth, Steinkopf, and Naroep in Namaqualand (Sclater 1901), and Klipfontein (Thomas and Schwann 1904). New diagnoses of *M. melanotis* were based on series of these Namaqualand specimens (Roberts 1951). Apart from the holotype specimen of *M. melanotis*, *Macrosclides* was unknown from Namibia north of Berseba, and so the type locality of "Damaraland" was questioned (Shortridge 1942; Corbet and Hanks 1968), and Shortridge (1942) fixed the type locality as Berseba, Namibia, without designating a neotype. Thus, newer species diagnoses, as well as geographic ranges, were based upon populations of *M. proboscideus* from Namaqualand, and not the ambiguous type specimen or the locality of *M. melanotis*. Corbet and Hanks (1968) argued that the *M. melanotis* type was unidentifiable, and found no consistent differences between Namaqualand populations of *M. melanotis* and specimens of *M. p. proboscideus*, and thus treated *M. melanotis* as synonymous with *M. proboscideus*. In conclusion, the status of *M. melanotis* is uncertain and thus constitutes a potential threat to taxonomic stability, so we recommend treating it as nomen dubium.

All sengi species have similar morphology, resulting in their taxonomy being based largely on relatively minor morphological differences (Corbet and Hanks 1968). For example, morphologically distinguishing *M. proboscideus* from *M. flavicaudatus* involves subtle differences (Dumbacher et al. 2012) and the recently described *E. pilicaudus* was only discovered with genetic analysis (Smit et al. 2008). Remarkably, the unique gross diagnostic morphological features of *M. micus* make it one of the most easily distinguished species of Macrosclidinae.

One of the most prominent features of *M. micus* that we found was the subcaudal gland. Various dermal glands are found in nearly all sengi taxa (Corbet and Hanks 1968; Faurie

and Perrin 1995), but few are proportionately as large as that of *M. micus*. The subcaudal gland's function in *M. micus* is unknown; however, based on studies of other sengis, it likely produces scents used for intraspecific communication and structuring social interactions (Rathbun 1979, 2008; Rathbun and Redford 1981; Koontz 1984; Koontz et al. 1999) that likely include monogamy. Social monogamy is characteristic of its congeners (Sauer 1973; Schubert et al. 2009) as well as several other sengis (Rathbun 1979; Rathbun and Rathbun 2006), and some type of social pairing was also suggested by our trapping results, especially considering the low densities that we encountered.

Several other observations deserve short note. Our low trapping success could have been due to trap shyness, but more likely it is the result of the harsh arid habitat. In this respect, *M. micus* is probably similar to *M. flavicaudatus*, which has home ranges in the Namib Desert of up to 1 km (Sauer 1973). To cover these long distances, *M. flavicaudatus* uses trails across the gravel desert (Sauer 1973; Rathbun 2009), which undoubtedly are associated with its highly cursorial gait, small size, and the coarse structure of the desert surface. In contrast, trail use has not been documented for *M. proboscideus* (Dumbacher et al. 2012), and we did not find trails where we captured *M. micus*, which is perplexing given that *M. micus* is the smallest sengi species and was found on substrates that were similarly coarse to those of *M. flavicaudatus*, which uses trails.

Based on the taxonomy of Corbet and Hanks (1968), more recent changes to sengi taxonomy (Rovero et al. 2008; Smit et al. 2008; Dumbacher et al. 2012), and the addition of *M. micus*, there are only 19 species of extant Macroscelidea, which are endemic to Africa, but absent from the Sahara Desert and far western Africa (Rathbun 2012). Within this vast area, sengis occur in habitats as diverse as coastal and montane deserts to lowland and montane forests. Despite this wide spatial diversity and their ancient and highly unique phylogeny (Meredith et al. 2011), the lack of extant species diversity continues to be remarkable (Rathbun 2009). It also might seem remarkable that *M. micus* escaped detection for more than 100 years since the 1st sengis were being described (Corbet and Hanks 1968), but it occurs in a small and remote arid area that is difficult to access and has only recently been explored by small-mammal biologists. Because of the restricted distribution of *M. micus*, it joins several other endemic Namibian mammals (Griffin 1998), including *M. flavicaudatus*, in contributing to the unique biodiversity of the region (Barnard 1998).

#### ACKNOWLEDGMENTS

P. Jenkins and L. Tomsett generously provided GBR photographs and access to the collection of sengis at the Natural History Museum in London, as did T. Kearney at the Ditsong National Museum of Natural History in Pretoria, and J. Dines at the Los Angeles County Museum. We thank A. M. Bauer for his initial collecting efforts in the Gai As region. We appreciate M. Flannery's help with import permits and cataloging specimens at CAS, and L. Osborne and L. Rathbun for assistance with fieldwork. Laboratory assistance at CAS was provided

by A. Bifolk, Z. Hanna, M. McDonald, and L. Carlen. We greatly enjoyed the pre- and postexpedition fellowship and hospitality of R. Fussell and L. van den Bosch of Big Sky Lodges in Windhoek. R. Fryer from Integrated Rural Development and Nature Conservation allowed us access to Wêreldsend, Wilderness Safaris gave us permission to trap on the Palmwag concession, and Damaraland Camp kindly provided us trapping access to their concession in the Huab River valley, as well as a night of luxury after 2 weeks in the desert. We thank the Namibia Ministry of Environment and Tourism for research permits and associated export permits: 1023/2006, 1131/2007, 1225/2008, 1394/2009, 1531/2010, 1531/2011, 1737/2012, and 1812/2013. We received with appreciation partial funding from numerous contributors that responded to a mobile phone campaign. J. Irish helped us with the etymology of local names. R. Swart provided information on the geology of the study area, and B. Brell of Save The Rhino Trust assisted us with his knowledge of the region. We thank H. Smit-Robinson and an anonymous reviewer for helpful comments on the manuscript.

#### LITERATURE CITED

- ANDANJE, S., B. R. AGWANDA, G. W. NGARUIYA, R. AMIN, AND G. B. RATHBUN. 2010. Sengi (elephant-shrew) observations from northern coastal Kenya. *Journal of East African Natural History* 99:1–8.
- BARNARD, P. 1998. Biological diversity in Namibia: a country study. Namibian National Biodiversity Task Force, Windhoek, Namibia.
- BIOMATTERS. 2013. Geneious software, version 5.6.3. Biomatters, Auckland, New Zealand. <http://www.geneious.com/>.
- CORBET, G. B., AND J. HANKS. 1968. A revision of the elephant-shrews, family Macroscelididae. *Bulletin of the British Museum (Natural History)* Zoology 16:47–111.
- DARRIBA, D., G. L. TABOADA, R. DOALLO, AND D. POSADA. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9:772.
- DOUADY, C. J. G. 2001. Molecular phylogenetics of the Insectivora. Ph.D. dissertation, The Queen's University of Belfast, Belfast, Ireland.
- DOUADY, C. J., F. CATZEFLIS, J. RAMAN, M. S. SPRINGER, AND M. J. STANHOPE. 2003. The Sahara as a vicariant agent, and the role of Miocene climatic events, in the diversification of the mammalian order Macroscelidea (elephant shrews). *Proceedings of the National Academy of Sciences USA* 100:8325–8330.
- DUMBACHER, J. P., G. B. RATHBUN, H. A. SMIT, AND S. J. EISEB. 2012. Phylogeny and taxonomy of the round-eared sengis or elephant-shrews, genus *Macroscelides* (Mammalia, Afrotheria, Macroscelidea). *PLoS ONE* 7:e32410.
- FAURIE, A. S., AND M. R. PERRIN. 1995. A histological investigation of the structure and distribution of scent glands in four species of elephant-shrews. *Mammal Review* 25:95–96.
- GENE CODES CORPORATION. 2013. Sequencher® version 5.0 sequence analysis software, Gene Codes Corporation, Ann Arbor, Michigan. <http://www.genecodes.com>.
- GOOGLE INC. 2013. Google Earth version 6.0. <http://www.google.com/earth/>. Accessed 24 June 2013.
- GRIFFIN, M. 1998. The species diversity, distribution and conservation of Namibian mammals. *Biodiversity and Conservation* 7:483–494.
- JERRAM, D., N. MOUNTNEY, F. HOLZFORSTER, AND H. STOLLHOFEN. 1999. Internal stratigraphic relationships in the Etendeka Group in the Huab Basin, NW Namibia: understanding the onset of flood volcanism. *Journal of Geodynamics* 28:393–418.
- KOONTZ, F. W. 1984. Sternal gland scent communication in the rufous elephant-shrew, *Elephantulus rufescens* Peters, with additional

- observations on behavior and reproduction in captivity. Ph.D. dissertation, University of Maryland, College Park, Maryland.
- KOONTZ, F. W., J. L. WELLINGTON, AND P. J. WELDON. 1999. The sternal gland of the rufous elephant-shrew, *Elephantulus rufescens* (Macroscelidea, Mammalia): anatomy, maturation, and secretion composition. Pp. 163–171 in *Advances in chemical signals in vertebrates* (R. E. Johnson, D. Muller-Schwarze, and P. W. Sorenson, eds.). Plenum Publishers, New York.
- MENDELSON, J., A. JARVIS, C. ROBERTS, AND T. ROBERTSON. 2002. *Atlas of Namibia; a portrait of the land and its people*. David Philip Publishers, Cape Town, South Africa.
- MEREDITH, R. W., ET AL. 2011. Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334:521–524.
- OGILBY, W. 1838. A selection of the Mammalia procured by Captain Alexander during his recent journey into the country of the Damaras on the south west coast of Africa. *Proceedings of the Zoological Society of London* 1838:5–6.
- RATHBUN, G. B. 1979. The social structure and ecology of elephant-shrews. *Zeitschrift für Tierpsychologie, Supplement* 20:1–77.
- RATHBUN, G. B. 2008. Tales of sengi tails. *Afrotherian Conservation—Newsletter of the IUCN-SCC Afrotheria Specialist Group* 6:8–10.
- RATHBUN, G. B. 2009. Why is there discordant diversity in sengi (Mammalia: Afrotheria: Macroscelidea) taxonomy and ecology? *African Journal of Ecology* 47:1–13.
- RATHBUN, G. B. 2012. Distribution map of *Macroscelides* spp. <http://www.sengis.org/distribution-macroscelides.php>. Accessed 16 March 2013.
- RATHBUN, G. B., AND C. D. RATHBUN. 2006. Social structure of the bushveld sengi (*Elephantulus intufi*) in Namibia and the evolution of monogamy in the Macroscelidea. *Journal of Zoology (London)* 269:391–399.
- RATHBUN, G. B., AND K. REDFORD. 1981. Pedal scent-marking in the rufous elephant-shrew, *Elephantulus rufescens*. *Journal of Mammalogy* 62:635–637.
- ROBERTS, A. 1951. *The mammals of South Africa*. Central News Agency, Cape Town, South Africa.
- RONQUIST, F., ET AL. 2011. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:1–4.
- ROVERO, F., ET AL. 2008. A new species of giant sengi or elephant-shrew (genus *Rhynchocyon*) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. *Journal of Zoology (London)* 274:126–133.
- SAUER, E. G. F. 1973. Zum sozialverhalten der kurzohrigen elefantenspitzmaus, *Macroscelides proboscideus*. *Zeitschrift für Säugetierkunde* 38:65–97.
- SCHUBERT, M., C. SCHRADIN, H. G. RODEL, N. PILLAY, AND D. RIBBLE. 2009. Male mate guarding in a socially monogamous mammal, the round-eared sengi: on costs and trade-offs. *Behavioral Ecology and Sociobiology* 64:257–264.
- SCLATER, W. L. 1901. *Rodentia, Chiroptera, Insectivora, Cetacea and Edentata*. R. H. Porter, London, England.
- SEIFFERT, E. R. 2007. A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. *BMC Evolutionary Biology* 7:224.
- SHORTTRIDGE, G. C. 1942. Field notes on the first and second expedition of the Cape Museum's mammal survey of the Cape Province. *Annals of the South African Museum* 36:27–100.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SMIT, H. A., B. Jansen van Vuuren, P. C. M. O'Brien, M. Ferguson-Smith, F. Yang, and T. J. Robinson. 2011. Phylogenetic relationships of elephant-shrews (Afrotheria, Macroscelididae). *Journal of Zoology (London)* 284:133–143.
- SMIT, H. A., T. J. ROBINSON, J. WATSON, AND B. JANSEN VAN VUUREN. 2008. A new species of elephant-shrew (Afrotheria: Macroscelidea: *Elephantulus*) from South Africa. *Journal of Mammalogy* 89:1257–1269.
- SPRINGER, M. S., H. M. AMRINE, A. BURK, AND M. J. STANHOPE. 1999. Additional support for Afrotheria and Paenungulata, the performance of mitochondrial versus nuclear genes, and the impact of data partitions with heterogeneous base compounds. *Systematic Biology* 48:65–75.
- STATA CORP. 2007. *Stata statistical software: release 10*. StataCorp LP, College Station, Texas.
- Swofford, D. L. 2003. *PAUP\*: phylogenetic analysis using parsimony (\*and other methods)*. Version 4. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- THOMAS, O., AND H. SCHWANN. 1904. On a collection of mammals from British Namaqualand, presented to the national museum by Mr. C.D. Rudd. *Proceedings of the Zoological Society of London* 1904:171–183.
- ZWICKL, D. J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin, Austin.

Submitted 21 July 2013. Accepted 22 December 2013.

Associate Editor was Burton Lim.