Zootaxa 4136 (3): 567–579
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://doi.org/10.11646/zootaxa.4136.3.8
http://zoobank.org/urn:lsid:zoobank.org:pub:1CF2E05A-9A2C-4919-BF77-0AE6FB6B4F6D

Petrosaltator gen. nov., a new genus replacement for the North African sengi *Elephantulus rozeti* (Macroscelidea; Macroscelididae)

JOHN P. DUMBACHER[1,2], ELIZABETH J. CARLEN[1] & GALEN B. RATHBUN[1]

[1] *Institute of Biodiversity Science and Sustainability, California Academy of Sciences, San Francicso, CA 94118 USA*
[2] *Corresponding author. E-mail: jdumbacher@calacademy.org*

Abstract

In 2003, a molecular phylogeny was published that examined the role of the Sahara Desert as a vicariant event in the evolution of sengis (also known as elephant-shrews.) The phylogeny included a single sample from the North African sengi, *Elephantulus rozeti* (Duvernoy, 1833), which was found to be more closely related to the sengi genus *Petrodromus* Peters, 1846 than to other *Elephantulus*. Here we independently test the monophyly of *Elephantulus* using an additional specimen of *E. rozeti* and similar phylogenetic analyses, and discuss additional morphological and behavioral data that support the phylogeny. We propose a revised taxonomy that reflects the current paraphyly of *Elephantulus* and the sister relationship of *E. rozeti* and *Petrodromus*, including a new genus name for the North African sengi, *Petrosaltator rozeti* **gen. nov., nov. comb.** We additionally define two tribes within the subfamily Macroscelidinae, the Macroscelidini (including *Macroscelides*, *Petrodromus*, and *Petrosaltator*), and the Elephantulini (including all other members of *Elephantulus*).

Key words: Sengi, Elephant-shrew, *Petrosaltator*, North African Sengi

Introduction

The sengis or elephant-shrews (Class: Mammalia; Supercohort: Afrotheria; Order: Macroscelidea; Family: Macroscelididae) are a monophyletic clade of endemic African mammals that have a confusing taxonomic history, spanning from their ordinal affiliation down to many species (Corbet & Hanks 1968; Dumbacher *et al.* 2014; Springer *et al.* 2004). There are only 19 recognized extant sengi species, all within the single order and family, but divided into two well-defined subfamilies. The subfamily Rhynchocyoninae (giant sengis) includes a single genus (*Rhynchocyon,* Peters, 1847) and four species (Rovero *et al.* 2008), whereas the subfamily Macroscelidinae (soft-furred sengis) currently includes three genera and 15 species (Dumbacher *et al.* 2014). This diversity of Macroscelididae has been proposed as being remarkably depauperate (Rathbun 2009), especially considering the afrotherians likely have been isolated in Africa for approximately the last 130 million years (Hedges 2001). However, the fossil record indicates additional extinct sengis (about 10 extinct genera with about 20 species, Grossman & Holroyd 2009; Holroyd 2009, 2010; Holroyd & Mussell 2005; Tabuce *et al.* 2012).

Morphological taxonomists have had difficulty resolving phylogenetic relationships and proposing a consistent taxonomy for the extant sengis because of their similar, yet highly specialized, morphology and life history (reviewed by Rathbun 2009). There are relatively few obvious characters distinguishing many of the taxa within each subfamily (Corbet & Hanks 1968; Smit *et al.* 2008) and a relatively scant fossil record (Holroyd 2010; Holroyd & Mussell 2005, Tabuce *et al.* 2012). Corbet and Hanks (1968) and Holroyd (2010) undertook the last major taxonomic revisions of the order. Their treatments were based exclusively on morphology and distribution, and they have mostly withstood the test of time. However, new taxa have been diagnosed using molecular genetics, and new phylogenetic insights have been gained. For example, Smit *et al.* (2008) described a cryptic South African species (*Elephantulus pilicaudus* Smit, 2008, the Karoo rock sengi) that had escaped notice in museum collections. This sengi was discovered based largely on molecular distinctness. More recently, the monospecific genus *Macroscelides* Smith, 1829 from southwestern Africa has been found to be composed of three species (*M.*

Accepted by P. Gaubert: 5 May 2016; published: 7 Jul. 2016

proboscideus [Shaw, 1800], the Karoo round-eared sengi; *M. flavicaudatus* Lundholm, 1955, the Namib round-eared sengi; and *M. micus* Dumbacher & Rathbun, 2014, the Etendeka round-eared sengi), based largely on molecular genetics (Dumbacher *et al.* 2014; Dumbacher *et al.* 2012).

Perhaps most significantly, Douady *et al.* (2003) presented molecular data strongly suggesting that *Elephantulus rozeti* (Duvernoy, 1833), the sengi restricted to the Maghreb region of Africa north of the Sahara (Nyari *et al.* 2010; Rathbun 2015), was more closely related to the monospecific genus *Petrodromus* (with the single species *P. tetradactylus* Peters, 1846, the four-toed sengi), than to any of the other *Elephantulus* taxa (Douady *et al.* 2003; see also a reanalysis of data by Kuntner *et al.* 2011). *Elephantulus rozeti*, the North African sengi, is restricted to the Maghreb region of Africa north of the Sahara (Nyari *et al.* 2010; Rathbun 2015). *Petrodromus* is found only south of the Sahara Desert, along with all other extant sengi taxa, and it is morphologically quite different from the genus *Elephantulus* (Corbet & Hanks 1968). However, there is no existing fossil evidence that independently supports a sister relationship between *E. rozeti* and *Petrodromus*.

The taxonomic history of *Elephantulus* includes misidentifications, lost specimens, and confusing application of names, which are reviewed in depth by Corbet and Hanks (1968). Because of this complexity, a brief synopsis is relevant. The first extant sengi was described in 1800 from the Cape Horn region of South Africa (Shaw 1800), and placed in the genus *Sorex* Linnaeus, 1758. Subsequently, Smith (1829) erected the genus *Macroscelides* for this specimen. Thomas & Schwann (1906) proposed the genera *Elephantulus* and *Nasilio* each to include species that they distinguished from *Macroscelides,* and designated *E. rupestris* (Smith, 1831) as the type species of the new genus *Elephantulus* (Thomas & Schwann 1906). Because the original type specimens of *E. rupestris* (Smith, 1831) were lost, a neotype of *E. rupestris* was designated by Corbet and Hanks (1968). Corbet and Hanks (1968) also eliminated *Nasilio* and placed its taxa into *Elephantulus*. In comparison, the taxonomic status of *P. tetradactylus* and *E. rozeti* is not complicated (Corbet & Hanks 1968). *Elephantulus rozeti* contains two subspecies, *E. r. rozeti* north of the Atlas Mountains and *E. r. deserti* (Thomas, 1901) south of the mountains. The two forms are distinguished by their distributions as well as by the paler pelage and smaller size of *E. r. deserti* (Corbet & Hanks 1968). The monotypic genus *Petrodromus* has a wide distribution in central and eastern Africa (Rathbun 2015), with ten recognized subspecies (Corbet & Hanks 1968; Jennings & Rathbun 2001).

If *E. rozeti* is truly the sister species of *Petrodromus*, then a taxonomic revision is required to address the polyphyly of *Elephantulus*. Because Douady *et al.*'s (2003) molecular analysis is based upon a single tissue sample of *E. rozeti*, we wanted to confirm their findings with additional material. Since the publication of the Douady *et al.* (2003) paper, other synapomorphies of *E. rozeti* and *Petrodromus* have been discovered and provide additional independent support for a taxonomic revision. Although other authors have suggested that a revision is needed (Holroyd 2010; Smit *et al.* 2011), to date none has been produced. Here, we test the genetic conclusions of Douady *et al* (2003), consider additional morphological data, and provide a revised taxonomy.

Methods

Specimens. The *E. rozeti* specimen analyzed in the Douady (2001) study was collected near Tadighoust Village, about 50 km west by southwest of Errachida City, at latitude 31.807770°N and longitude 4.958398°W. This specimen is housed in the tissue collections of the Institut des Sciences de l'Evolution de Montpellier (ISEM) at Université de Montpellier (field specimen number V-0778, tissue number T-1456; Rodolphe Tabuce, Pers. Comm.). This locality is south of the Atlas Mountains, and thus should represent the subspecies *E. r. deserti*. The sengi we sequenced from the collection of the California Academy of Sciences (CASMAM 27982) was collected near Salas Village, Morocco, at latitude 31.8278°N and longitude 7.9849°W, which is north of the Atlas Mountains, and thus should represent *E. r. rozeti*. The type specimen (Duvernoy 1833) was collected near Oran, Algeria, which is 35.6970°N / 0.6330°W (US Library of Congress Gazetteer). The coordinates for these three sites are plotted on Fig 1. The distribution polygon of *Elephantulus rozeti* in Fig 1 is based on compiled location data (Rathbun 2015).

Molecular genetics. One mitochondrial locus and two independently segregating nuclear loci were analyzed to assess genetic relationships. Although the loci were the same as those reported earlier (Douady 2001; Douady *et al.* 2003), the samples are different, thus independently verifying those results. For comparison and completeness in our analyses, we include the published sequences of Douady *et al.* (2003) for *E. rozeti* (GenBank records AY310881, AY310888, AY310895) and *Rhynchocyon* (GenBank records AY310880, AY310887, AY310894).

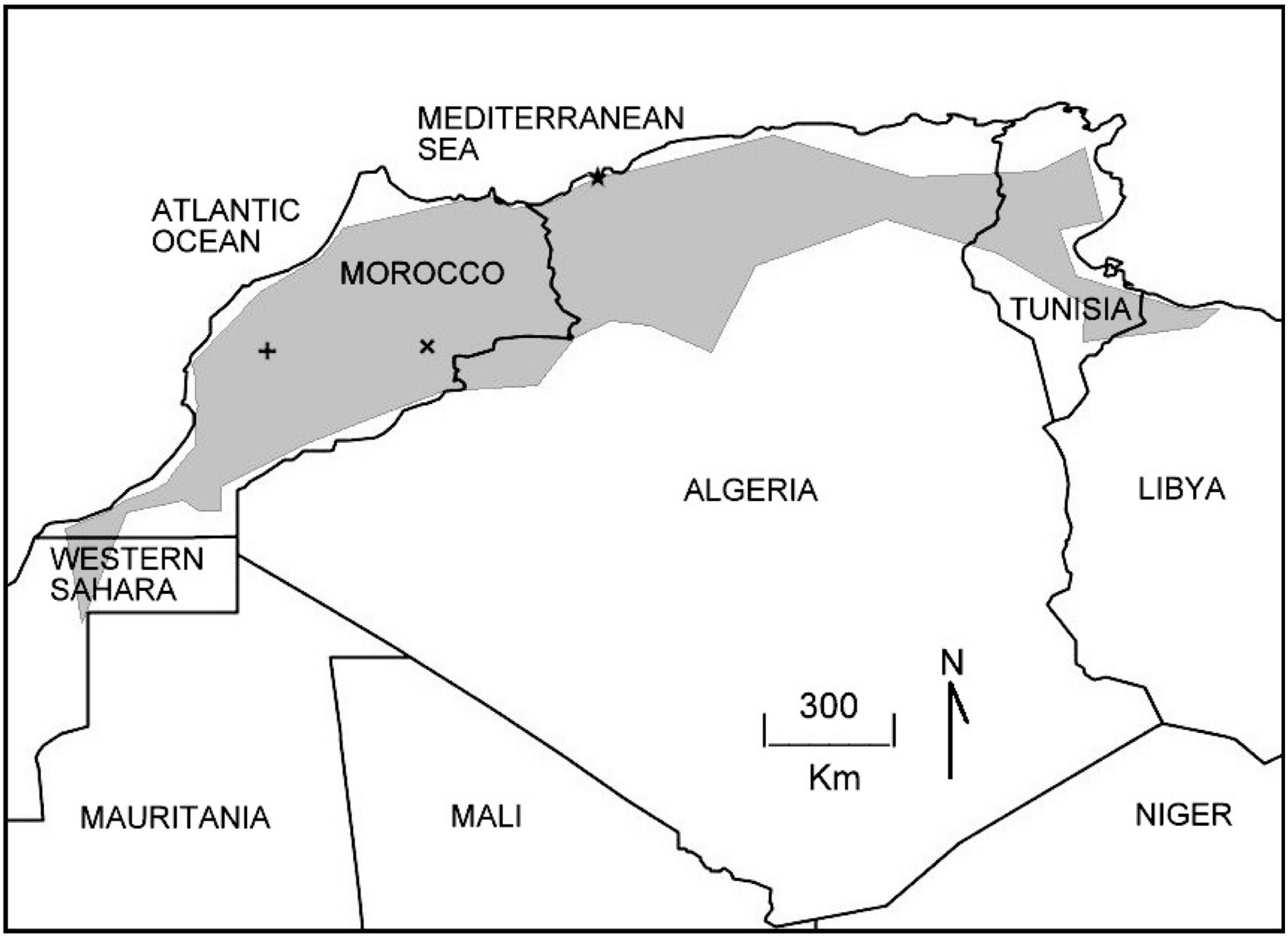

FIGURE 1. North African sengi distribution (shaded area) in the Maghreb region of northern Africa. Distribution based on minimum convex polygon of 203 points with perimeter modified subjectively to avoid unsuitable habitat (Rathbun 2015). Star symbol is approximate location of type specimen, x symbol is approximate location of Douady (2001) voucher specimen, and + symbol is the location of California Academy of Sciences voucher specimen (see Methods and Table 1).

Muscle tissue was taken from carcasses and preserved in 100% ethanol as sengis were being prepared as museum specimens for the California Academy of Sciences. Tissues were stored at -80°C. DNA was extracted from approximately 25 mg of tissue using a Qiagen DNeasy tissue extraction kit (Qiagen, Valencia, CA, USA).

Polymerase chain reaction (PCR) was performed in 25 µL of buffer containing the following: 0.2 units of Invitrogen Taq polymerase, 1X PCR buffer, 1.5 mM magnesium chloride, 0.4 µM forward and reverse primers, 0.2 mM dNTPs, and approximately 50–100 ng DNA template. Multiple primer sets were used to amplify the mitochondrial loci 12s rRNA, valine transfer RNA, and 16s rRNA (hereafter 12s–16s rRNA, 2588 bp), and the nuclear loci interphotoreceptor binding protein (IRBP) exon 1 (969 bp) and von Willebrand Factor (vWF) exon 28 (927 bp), as described in Douady (2001). Primer annealing temperatures were 55°C for 12s–16s rRNA and IRBP, and 63°C for vWF. Polymerase chain reaction extension times were 2–3 minutes for the shorter and longer amplicons respectively. These and other internal primers were used for sequencing the amplification products from 12s–16s rRNA, IRBP, and vWF, and all primers are fully described in Douady (2001).

We visualized PCR products on 1% agarose gels stained with ethidium bromide. Successfully amplified PCR products were purified using the Zymo DNA Clean & Concentrator™-5 kit (Zymo Research, Irvine, CA) and sequenced using BigDye Terminator cycle sequencing kit (version 3.1, Applied Biosystems). We produced the nucleotide sequences on an ABI-3130 automated sequencer (Life Technologies) located at the Center for Comparative Genomics at the California Academy of Sciences.

We edited DNA sequences in Geneious software v7.1.4 (http://www.geneious.com, Kearse *et al.* 2012); primers were removed during the editing process, and consensus sequences were created for each individual. Some individuals were heterozygotes at nuclear loci (e.g. *Macroscelides flavicaudatus* CASMAM29696 at IRBP, and

TABLE 1. Specimens included in molecular analyses with GenBank accession numbers for each locus.

			GenBank Accession Number		
Species	Museum Number	Collection Locality	12s16s	IRBP	vWF
Elephantulus intufi	CASMAM28552	Zwartmodder Farm, Maltahohe District, Hardap Region, Namibia; 24.883933° S, 16.254433° E	KT000006		KT000021
Elephantulus intufi	CASMAM28572	Zwartmodder Farm, Maltahohe District, Hardap Region, Namibia; 24.900° S 16.2439° E	none	KT000012 KT000013	KT000022
Elephantulus rupestris	CASMAM28549	Namib Rand Nature Reserve, Keerweder Farm, Hardap Region, Namibia; 24.9602167° S, 16.0325833° E	KT000007	KT000015 KT000016	KT000023 & KT000024
Petrosaltator rozeti	V-0778 (Université of Montpellier, Institut des Sciences de l'Evolution, Animal tissue collection)	Er-Rachidia (or Errachidia), Morocco, 31.9337°N, 4.4238°W	AY310881	AY310895	AY310888
Petrosaltator rozeti	CASMAM27982	Salas Village, Jhilet Mountains, Marrakech, Morocco; 31.8278° N 7.9849° E	KT000008	KT000017	KT000025
Petrodromus tetradacylus	CASMAM28170	Ndundulu Forest, Udzungwa Mountains, Tanzania; -7.8045° S 36.5059° E	KT000009	KT000018	KT000026 & KT000027
Petrodromus tetradactylus	CASMAM28171	Ndundulu Forest, Udzungwa Mountains, Tanzania; 7.8045° S 36.5059° E	KT000010	KT000019	KT000028 & KT000029
Petrodromus tetradactylus	Douady *et al.* 2003	Chingulungulu region, Tanzania; 10.44° S, 38.33° E	AY310883	AY310897	AY310890
Petrodromus tetradactylus	National Museum, Bloemfontein 12603	Bonamanzi Game Park, Kwazulu Natal, South Africa; 28.05766°S 32.29439°E	EU136156	EU136145	EU136138
Macroscelides flavicaudatus	CASMAM29696	North of Mikberg base camp, road site 2, Khorixas District, Kunene Region, Namibia; 20.71355° S, 14.12369° E	KF895109	KF742662	KF742651

……*continued on the next page*

TABLE 1. (Continued)

			GenBank Accession Number		
Species	Museum Number	Collection Locality	12s16s	IRBP	vWF
Macroscelides flavicaudatus	CASMAM29724	Near Mikberg, Khorixas District, Kunene Region, Namibia; 20.7123° S, 14.12207° E	KF895117	KF742670	KF742654
Macroscelides proboscideus	CASMAM28551	Zwartmodder Farm, Maltahohe District, Hardap Region, Namibia; 24.9136° S 16.2703° E	KF895105	KF742667	KF742646
Macroscelides proboscideus	CASMAM28574	Zwartmodder Farm, Maltahohe District, Hardap Region, Namibia; 24.9136° S 16.2703° E	KF895114	KF742669	KF742652
Macroscelides micus	CASMAM28968	Mikberg base camp, original site, low transect, Khorixas District, Kunene Region, Namibia; 20.727889° S, 14.1303° E	KF895108	KF742664	KF742650
Macroscelides micus	CASMAM27997	Near Mikberg, Khorixas District, Kunene Region, Namibia; 20.72667° S, 14.12833° E	KF895104	KF742665	KF742645
Rhynchocyon udzungwensis	BMNH2007.7	Vikongwa River Valley, Ndundulu Forest, West Kilombero Scarp Forest Reserve, Udzungwa Mountains, Iringa Region, Tanzania; 7148.2690° S, 36130.3550° E	KT000011	KT000020	KF202173
Orycteropus afer	GenBank	GenBank	U97338	U48712	U31617
Procavia capensis	GenBank	GenBank	NC004919	U48586	U31619

Petrodromus tetradactylus CASMAM28170 and *P. tetradactylus* CASMAM28171 at vWF), so an ambiguity code was used at the heterozygous nucleotide in these alignments. Additional sequences from two outgroup taxa (the rock hyrax, *Procavia capensis* and aardvark, *Orycteropus afer*) were included to root the phylogeny. Alignments were done in Geneious using the MAFFT v7.017 alignment plugin (Katoh *et al.* 2002), confirmed by eye, and exported as Nexus files for analysis. Because of the great distance between outgroup and ingroup taxa, the alignment of the 12s–16s ribosomal RNA included regions with complex indels that were excluded from phylogenetic analyses.

Sequences were imported into PAUP* v4.0b10 (Swofford 2003), partitioned by gene and codon position, and we used MrModeltest v2.3 (Nylander *et al.* 2004) to determine the best fit model using the Akaike Information Criterion (Akaike 1992). We analyzed each of the three independently segregating loci separately using both maximum-likelihood analysis and Bayesian analysis. We used PAUP* for Maximum-likelihood searches and MrBayes v3.1.2 for Bayesian analyses (Ronquist *et al.* 2011). Because the resulting trees were identical for each gene, all genes were concatenated and analyzed as a single data matrix. Support for each node was estimated using parsimony and maximum likelihood bootstrap analyses in PAUP* and Bayesian posterior probabilities in MrBayes.

Results

Molecular systematics. MrModeltest software provided best-fit nucleotide substitution models, as follows: GTR+I+G for 12s, HKY+G for tRNA valine, GTR+I+G for 16s, GTR for IRBP1 codon position 1, GTR+I for IRBP1 codon position 2, GTR+G for IRBP1 codon position 3, HKY+I for vWF codon position 1, HKY+G for vWF codon position 2, and HKY+G for codon position 3. Maximum likelihood phylogenies for 12s–16s, IRBP, and vWF were congruent, so data were combined, MrModeltest software re-run, and the data reanalyzed using the recommended model, GTR+I+G, for the entire matrix. The maximum likelihood tree is shown in Fig 2, and nodes with bootstrap values over 90% and Bayesian posterior probabilities over 0.95 were considered significant. Average pairwise genetic distances among taxa are presented in Table 2.

TABLE 2. Average uncorrected genetic distances (%) among Macroscelididae taxa in this study. Pairwise distances at the nuclear loci (IRBP/vWF) are presented above the diagonal and mitochondrial 12s–16s distances are below the diagonal.

	Rhyncho-cyon	*E. intufi*	*E. rupestris*	*E. rozeti*	*P. tetradactylus*	*M. flavicaudatus*	*M. proboscideus*	*M. micus*
Rhynchocyon		14.7/13.9	15.4/14.2	15.3/15.0	14.8/15.0	15.9/14.3	15.9/14.2	15.8/13.4
E. intufi	22.7		1.9/2.0	6.2/7.5	5.1/7.8	5.0/6.4	5.3/6.4	5.2/6.0
E. rupestris	22.1	13.6		6.5/7.6	5.5/8.1	5.5/7.0	5.7/6.7	5.8/5.9
E. rozeti	21.9	18.7	18.3		3.7/3.8	4.9/6.0	5.2/5.9	5.1/5.8
P. tetradactylus	22.4	19.6	19.3	15.7		4.2/6.8	4.4/6.6	4.1/6.0
M. flavicaudatus	21.1	19.3	18.9	16.9	17.6		1.0/0.8	3.3/3.2
M. proboscideus	20.7	18.9	19.1	17.1	17.3	6.3		3.6/3.0
M. micus	21.3	19.9	18.7	17.9	18.3	16.9	16.4	

Our total evidence phylogenetic tree strongly supported relationships among most genera and major clades. The phylogeny showed *Elephantulus* as polyphyletic, with *E. rozeti* more closely related to *Petrodromus* than to *Elephantulus* representatives (*E. intufi* or *E. rupestris*). The *E. rozeti* plus *Petrodromus* clade is sister to the genus *Macroscelides*, and the clade containing *E. rozeti*, *Petrodromus,* and *Macroscelides* is sister to *Elephantulus*. Our results are consistent with those of other genetic studies (Douady *et al.* 2003; Kuntner *et al.* 2011; Smit *et al.* 2011), independently confirming that *Elephantulus* is polyphyletic and *E. rozeti* belongs in a clade with *Petrodromus*.

Rationale for erecting a new genus for the North African sengi. While our genetic results confirm the affiliation of *E. rozeti* with *Petrodromus* (Douady *et al.* 2003; Smit *et al.* 2011) we disagree with the taxonomic suggestion of Smit *et al.* (2011) to subsume all members of the subfamily (including *Petrodromus* and *Macroscelides)* into a single genus, *Elephantulus*. This artificially lumps many distinct morphological, ecological, and phylogenetic forms under one genus and obscures much of its diversity. Furthermore, if the taxa were to be combined into a single genus, it would be *Macroscelides* and not *Elephantulus*, as the former is the older of the two available generic names.

There are two remaining options for bringing sengi taxonomy into conformity with the phylogenetic, morphological and distributional data. One is to subsume *E. rozeti* into the genus *Petrodromus*; the other is to erect a new genus for *E. rozeti*. We favor the latter because this action better recognizes the great genetic, morphological, ecological, and biogeographical distinction of these genera, especially *Petrodromus*, which is the most highly morphologically distinct genus within the Macroscelidinae. Recognizing the distinctness of both *E. rozeti* and *Petrodromus* at the generic level more accurately reflects the diversity of these sengis.

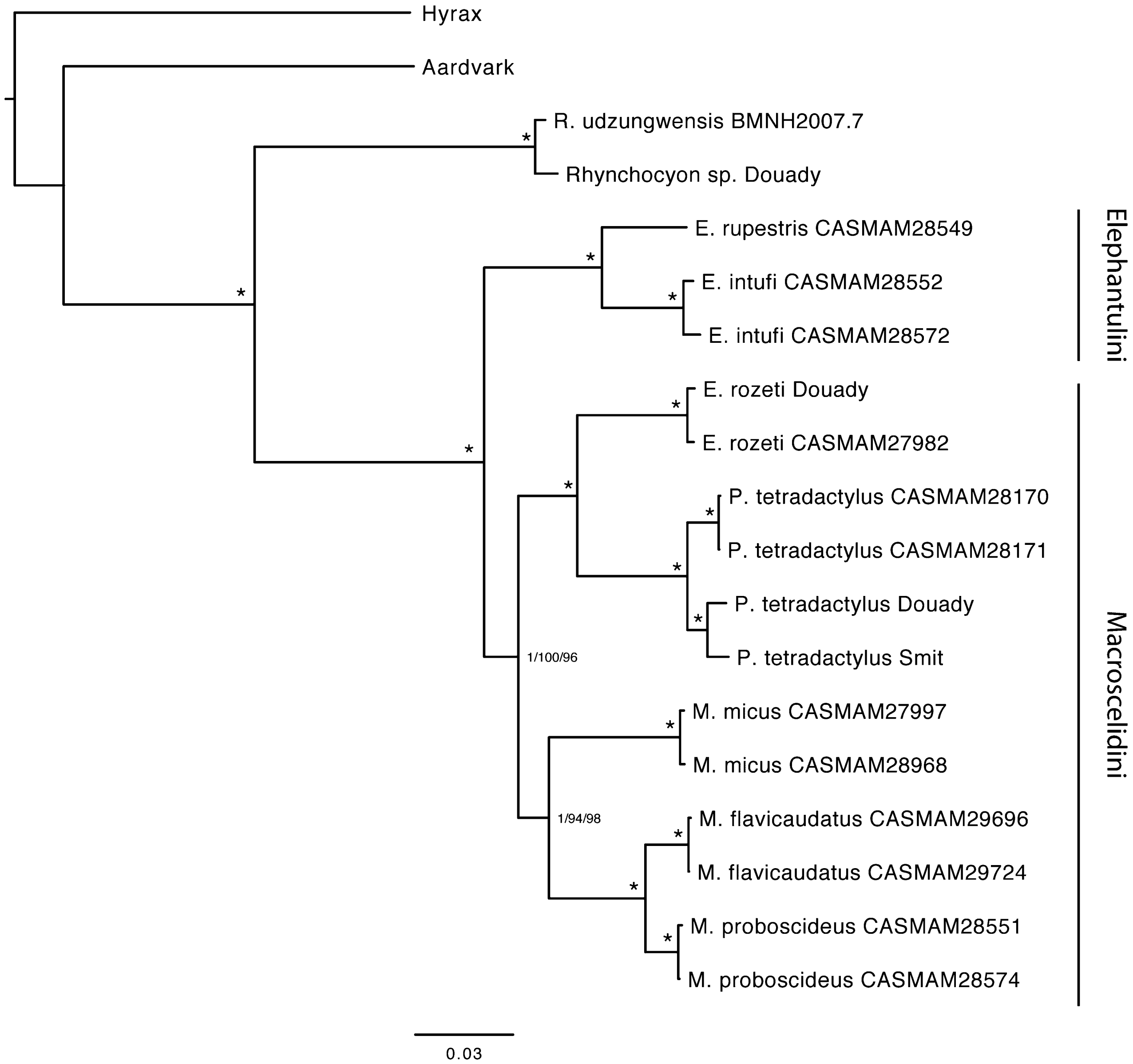

FIGURE 2. Molecular phylogeny of *E. rozeti* and related taxa showing the proposed delimitation of the subfamily Macroscelidinae into two tribes. Branch support is shown as Bayesian posterior probabilities / parsimony bootstrap values / maximum likelihood bootstrap values. Nodes with best possible support (1/100/100) are denoted with an asterisk. Scale bar represents corrected (GTR+G+I) distances.

Petrosaltator Rathbun and Dumbacher, new genus

Fig. 3

Type species: *Petrosaltator rozeti* (Duvernoy, 1833)

Holotype. The type specimen is located at Musée Zoologique de la ville de Strasbourg, France; specimen number MZSMAM03685.

Geographic distribution. *Petrosaltator* has a unique range, and is currently the only species of the family Macroscelididae that occurs north of the Sahara Desert. It is known from the Maghreb Region of northern Africa, in Mediterranean, sub-desert, and montane zones from near sea level to 2725m elevation (Fig. 1) (Corbet & Hanks 1968; Cuzin & Séguignes 1990).

Diagnosis and description. The genus *Petrosaltator* is monotypic (*P. rozeti*) (Corbet & Hanks 1968; Duvernoy 1833; Perrin & Rathbun 2013). Features that distinguish the genus from all other Macroscelidinae are rare (see below), thus explaining why it was included in *Elephantulus* by earlier workers. Genetic data are among the most useful diagnostic characters, and have been used here and elsewhere to identify *P. rozeti* and clearly align it with *Petrodromus* and *Macroscelides* (Douady *et al.* 2003; Kuntner *et al.* 2011; Smit *et al.* 2011).

Petrosaltator measurements include head and body 90–130mm, tail 95–140mm, hind foot 29–37mm, upper tooth row 16–19mm, with larger individuals from north of the Atlas mountains belonging to the nominate forms, *P. r. rozeti*, and smaller individuals south of the Atlas mountains belonging to *P. r. deserti* (Corbet & Hanks 1968).

Despite overall morphological similarity, *Petrosaltator* differs from *Elephantulus* in the following characters. In penis morphology, *Petrosaltator* has two lateral lobes and a tapering distal end, whereas *Elephantulus* species have a bulbous tip of the glans penis (Woodall 1995b). In superficial male mammary morphology, *Petrosaltator* males have small nipples which are absent in *Elephantulus* (Olbricht & Stanley 2009). Finally, *Petrosaltator* has an ossified stapediofacial tube that corresponds to the bony enclosure of the path of the facial nerve within the bulla (Benoit *et al.* 2013).

Corbet & Hanks (1968) additionally identify three morphological characters that distinguish *Petrosaltator* from *Elephantulus* (see Corbet & Hanks 1968, Table 1, page 49). Character states shared by *Petrosaltator* and *Macroscelides* include a large tragus and highly rugose interdigital pads (Corbet & Hanks 1968). Synapomorphies of *Petrosaltator* and *Petrodromus* include the double root on the third upper incisor (I^3). Corbet & Hanks (1968, Table 1) identify no single morphological character that has a unique character state in *Petrosaltator rozeti* (Corbet & Hanks 1968).

Petrosaltator can additionally be distinguished from *Macroscelides* in having significantly smaller mastoids and auditory bullae, smaller supratragus, and slightly less-silky pelage (Corbet & Hanks 1968). *Petrosaltator* differs from *Petrodromus* in being smaller overall, having the hallux present, having three rows of mammae (vs. two in *Petrodromus*), and having no facial markings (vs. *Petrodromus* having a prominent dark spot behind the eye), having caudal hair on distal dorsal tail surface (dorsal tail surface is essentially naked in *Petrodromus*), and the eye and pinnae are proportionally smaller in *Petrosaltator* in comparison to overall head size,

Etymology. The roots of *Petrosaltator* (masculine gender) are Greek (*petro*) and Latin (*saltator*), together meaning "rockdancer". This genus name reflects the habitats occupied by this species, which are dominated by rocks and boulders (Séguignes 1988). *Petrosaltator* also alludes to the phylogenetic relationship with *Petrodromus* (meaning rockrunner with Greek roots), although oddly *Petrodromus tetradactylus* is not specifically a petrophile (Jennings & Rathbun 2001). We suggest that the common name of *Petrosaltator rozeti* continue to be the North African Sengi or Elephant-shrew.

Specimens examined. Our work is based primarily on molecular analyses, and specimens sequenced are listed in Table 1. The two *P. rozeti* specimens sequenced were *P. rozeti rozeti* (CASMAM27982 from north of the Atlas Mountains) and *P. r. deserti* [from Douady *et al.* (Douady *et al.* 2003), south of the Atlas Mountains]. Based on the divergence level between these two specimens (Fig. 2, uncorrected p-distance at 12s–16s rDNA = 1.09% divergence), recognizing two subspecies of *P. rozeti* could be justified, although the lack of morphometrics, our minimal sample size, and analysis of only one genetic region precludes any definitive determination.

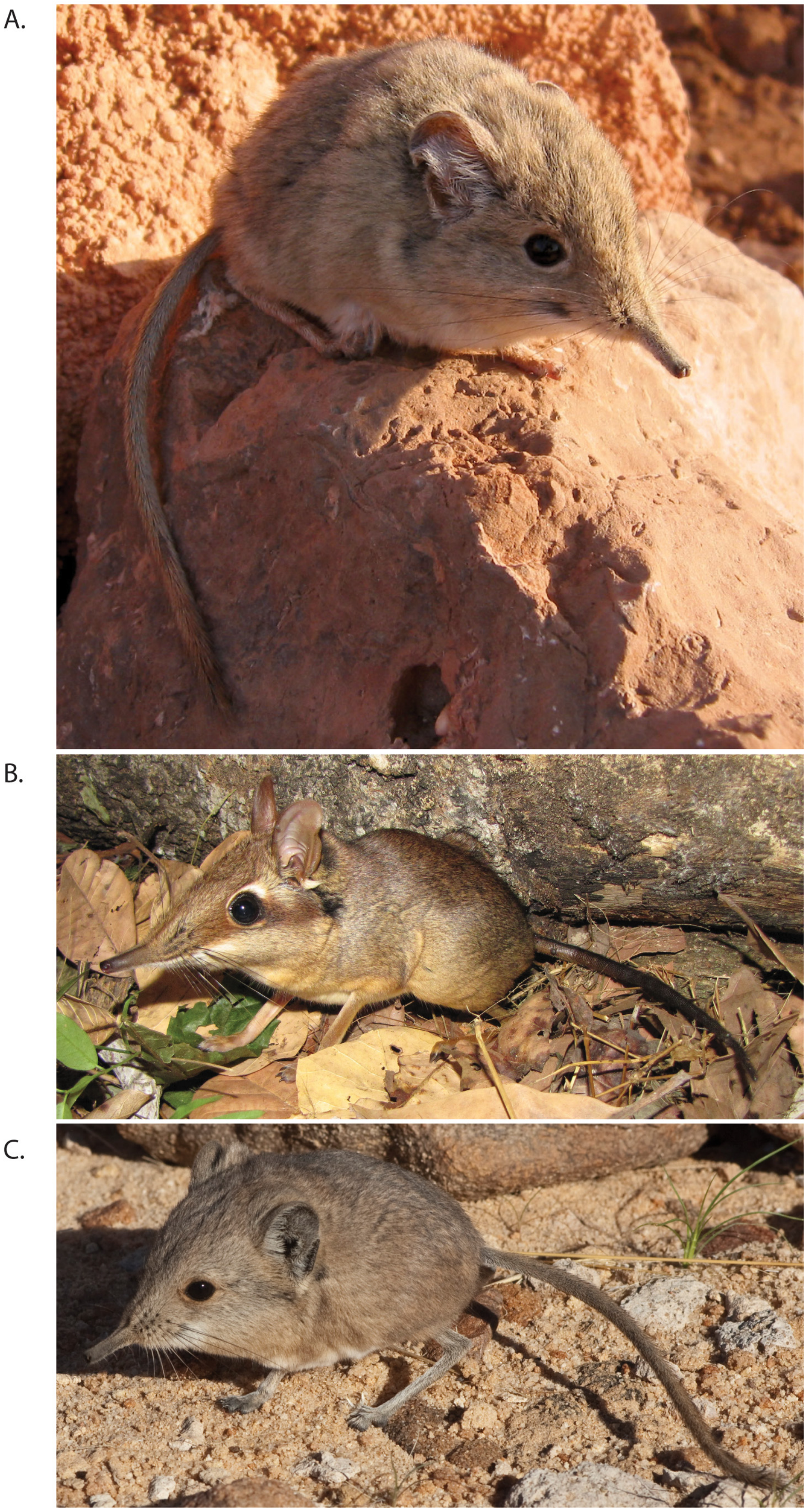

FIGURE 3. Images of the three genera of the tribe Macroscelidini. A. Basking North African sengi (*Petrosaltator rozeti*). Adult male near Salas village, Jhilet Mountains, Marrakesh, Morocco on 18 July 2005, specimen number CAS MAM 27982. Photo G. Rathbun. B. The four-toed sengi (*Petrodromus tetradactylus*), Mareja Community Reserve, Pemba, northern Mozambique, 17 June 2011, specimen number CAS MAM 29347, Photo G. Rathbun. C. The Namib round-eared sengi (*Macroscelides flavicaudatus*), south of the Micberg formation, Kunene Region, Khorixas District, 7 May 2010, specimen number CAS MAM 29700, photo J.P. Dumbacher.

Discussion

The remarkable and unexpected genetic relationship shared by *E. rozeti* and *Petrodromus* is supported by several relatively cryptic morphological characters, including penis morphology (Woodall 1995a), occurrence of male nipples (Olbricht & Stanley 2009), skull morphology (Panchetti *et al.* 2008; Scalici & Panchetti 2011), and inner-ear structure (Benoit *et al.* 2013). Additionally, Smit *et al.* (2011) presented chromosomal data that support the grouping affinities of these two taxa, with the addition of *Macroscelides*.

Scalici & Panchetti (2011) informally proposed the name '*Panelephantulus*' for the clade including *E. rozeti*, *Petrodromus*, and *Macroscelides*, however there is some confusion regarding whether "*Panelephantulus*" was suggested as a new genus (as suggested by their use of italics) or as a higher unranked taxonomic name (as interpreted by Benoit *et al.* 2013). Furthermore, their intention is made unclear by the name Panelephantulus itself, which translates to "all *Elephantulus*", however the group appears to include all Macroscelidinae *except* for the members of *Elephantulus*.

Hence, we propose the following tribe-level classification for the subfamily Macroscelidinae. We designate type genera and provide short descriptions to ensure that the tribe names are made available as per chapter 8 article 35.3 of the International Code of Zoological Nomenclature for family group names.

The taxonomic hierarchy for the subfamily Macroscelidinae follows:

- Class: Mammalia Linneus, 1758
  - Supercohort: Afrotheria Stanhope *et al.*, 1998
    - Order: Macroscelidea Butler, 1956
      - Family: Macroscelididae Bonaparte, 1838
        - Subfamily: Macroscelidinae Bonaparte, 1838
          - Tribe: Macroscelidini, **new tribe**
            - Genus: *Macroscelides* A. Smith 1829
            - Genus: *Petrodromus* Peters 1846
            - Genus: *Petrosaltator*, **new genus**
          - Tribe: Elephantulini, **new tribe**
            - Genus: *Elephantulus* Thomas & Schwann 1906

Macroscelidini, New Tribe

Type genus: *Macroscelides* A. Smith 1829

Description: The tribe is defined primarily by the genera included—*Macroscelides, Petrodromus,* and *Petrosaltator*. Synapomorphies recovered from genetic analyses include portions of vWF, IRBP, and mtDNA 12s–16s ribosomal RNA loci, which are all consistent with the monophyly of the tribe. Morphological synapomorphies for the group are not easy to discern, although these may include a penis with two lateral lobes and a narrowing end (Woodall 1995b) and the presence of a fully ossified stapediofacial tube (Benoit *et al.* 2013). Analyses of basal skull morphometrics also appear to support the monophyly of Macroscelidini (Scalici & Panchetti 2011).

Elephantulini, New Tribe

Type Genus: *Elephantulus* Thomas and Schwann, 1906, by monotypy

Description: The tribe provisionally includes only members of the genus *Elephantulus* (not including *Petrosaltator rozeti*) and is supported primarily by genetic synapomorphies. All members have three pairs of mammae, hallux present, auditory bullae not grossly inflated (Corbet & Hanks 1968), and penis morphology in which the urethra does not extend beyond the lateral lobes (Woodall 1995b). Not all members of the genus *Elephantulus* have been included in phylogenetic studies, so we include all members provisionally.

In addition to the placement of *P. rozeti* with *Petrodromus* and *Macroscelides* into the tribe Macroscelidini, our genetic data suggest a possible phylogenetic split within *Petrodromus tetradactylus*, with one population in the Udzungwa Mountains of Tanzania (CASMAM28170 and CASMAM28171) and another occurring from at least southeastern Tanzania (Douady *et al.* 2003) to KwaZulu Natal in South Africa (GenBank numbers EU136156, EU136145, and EU136138), at the southern end of the current distribution of the genus (Rathbun 2015). Divergence within *Petrodromus tetradactylus* suggests that more research is needed to understand subspecies diversity in this monotypic genus.

With our renaming of *Petrosaltator*, the subfamily Macroscelidinae now contains four genera (*Elephantulus*, *Macroscelides*, *Petrosaltator*, and *Petrodromus*). The number of extant species in the order, however, remains the same at 19 (Dumbacher *et al.* 2014). The diversity of extant taxa within the order continues to slowly increase with a better understanding of the underlying phylogenetics. Although this trend may continue as we learn more, extant species diversity in the order Macroscelidea remains remarkably low compared to other non-Afrotherian mammalian radiations in Africa (Kingdon *et al.* 2013; Rathbun 2009).

Acknowledgements

We thank Sarah Werning for suggesting the new genus name *Petrosaltator*. David Germano and Larry Saslaw assisted GBR in capturing CASMAM27982, and Mohammed Znari facilitated export of the specimen. We thank Patricia Holroyd for discussions and advice regarding naming the new genus. We thank Alfred L. Gardner, Ryan Norris, and Rodolphe Tabuce for comments on earlier versions of this paper.

References

Akaike, H. (1992) Information theory and an extension of the maximum likelihood principle. *In:* Kotz, S. & Johnson, N.L. (Eds.), *Breakthroughs in Statistics. Vol. I. Foundations and Basic Theory*. Springer-Verlag, New York, pp. 610–624. http://dx.doi.org/10.1007/978-1-4612-0919-5_38

Benoit, J., Crumpton, N., Merigeaud, S. & Tabuce, R. (2013) Petrosal and bony labyrinth morphology supports paraphyly of *Elephantulus* within Macroscelididae (Mammalia, Afrotheria). *Journal Mammalian Evolution*, 21, 173–193. http://dx.doi.org/10.1007/s10914-013-9234-5

Corbet, G.B. & Hanks, J. (1968) A revision of the elephant-shrews, Family Macroscelididae. *Bulletin of the British Museum (Natural History) Zoology*, 16, 47–111.

Cuzin, F. & Séguignes, M. (1990) Capture d'*Elephantulus rozeti* (Macroscelidae, Macroscelididae) dans le Haut-Atlas marocain au dessus de 2700 m. *Mammalia*, 54, 164–165.

Douady, C.J. (2001) *Molecular phylogenetics of the Insectivora*. Ph.D. dissertation, The Queen's University of Belfast, Belfast, Ireland. 205 pp.

Douady, C.J., Catzeflis, F., Raman, J., Springer, M.S. & Stanhope, M.J. (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. http://dx.doi.org/10.1073/pnas.0832467100

Dumbacher, J.P., Rathbun, G.B., Osborne, T.O., Griffin, M. & Eiseb, S.J. (2014) A new species of round-eared sengi (genus *Macroscelides*) from Namibia. *Journal of Mammalogy*, 95, 443–454. http://dx.doi.org/10.1644/13-MAMM-A-159

Dumbacher, J.P., Rathbun, G.B., Smit, H.A. & Eiseb, S.J. (2012) Phylogeny and taxonomy of the round-eared sengis or elephant-shrews, genus *Macroscelides* (Mammalia, Afrotheria, Macroscelidea). *PLOS ONE*, 7, e32410. http://dx.doi.org/10.1371/journal.pone.0032410

Duvernoy, G.L. (1833) Description d'un Macroscelide d'Alger. *Mémoires de la Société d'Histoire Naturelle de Strasbourg*, 1, 1–25.

Grossman, A. & Holroyd, P.A. (2009) *Miosengi butleri*, gen. et sp. nov., (Macroscelidea) from the Kalodirr Member, Lothidok Formation, early Miocene of Kenya. *Journal of Vertebrate Paleontology*, 29, 957–960. http://dx.doi.org/10.1671/039.029.0318

Hedges, S.B. (2001) Afrotheria: Plate tectonics meets genomics. *Proceedings of the National Academy of Sciences USA*, 98, 1–2. http://dx.doi.org/10.1073/pnas.98.1.1

Holroyd, P.A. (2009) Past records of *Elephantulus* and *Macroscelides*: geographic and taxonomic issues. *Afrotherian Conservation - Newsletter of the IUCN-SCC Afrotheria Specialist Group*, 7, 3–7.

Holroyd, P.A. (2010) Macroscelidea. *In:* Werdelin, L. & Sanders, J. (Eds.), *Cenozoic Mammals of Africa*. University of California Press, Berkeley, pp. 89–98. http://dx.doi.org/10.1525/california/9780520257214.003.0008

Holroyd, P.A. & Mussell, J.C. (2005) Macroscelidea and Tubulidentata. *In:* Rose, K.D. & Archibald, J.D. (Eds.), *The Rise of Placental Mammals*. The Johns Hopkins University Press, Baltimore, pp. 71–83.

Jennings, M.R. & Rathbun, G.B. (2001) *Petrodromus tetradactylus*. *American Society of Mammalogists, Mammalian Species*, 682, 1–6. http://dx.doi.org/10.1644/1545-1410(2001)682%3C0001:PT%3E2.0.CO;2

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, 30, 3059–3066.
http://dx.doi.org/10.1093/nar/gkf436

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *BioInformatics*, 28, 1647–1649.
http://dx.doi.org/10.1093/bioinformatics/bts199

Kingdon, J., Seiffert, E.R., Hedges, S.B. & Rathbun, G. (2013) Supercohort Afrotheria. *In:* Kingdon, J., Happld, D., Hoffmann, M., Butynski, T., Happold, M. & Kalina, J. (Eds.), *Mammals of Africa. Vol. I.* Bloombury, London, pp. 143–146.

Kuntner, M., May-Collado, L.J. & Agnarsson, I. (2011) Phylogeny and conservation priorities of afrotherian mammals (Afrotheria, Mammalia). *Zoologica Scripta*, 40, 1–15.
http://dx.doi.org/10.1111/j.1463-6409.2010.00452.x

Nyari, A.S., Peterson, A.T. & Rathbun, G.B. (2010) Late Pleistocene potential distribution of the North African sengi or elephant-shrew *Elephantulus rozeti* (Mammalia: Macroscelidea). *African Zoology*, 45, 330–339.
http://dx.doi.org/10.3377/004.045.0212

Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P. & Nieves-Aldrey, J.L. (2004) Bayesian phylogenetic analysis of combined data. *Systematic Biology*, 53, 47–67.
http://dx.doi.org/10.1080/10635150490264699

Olbricht, G. & Stanley, W.T. (2009) The topographic distribution of the penis and mammary glands in sengis (Macroscelidea) and its usefulness for taxonomic distinctions. *Zoosystematics and Evolution*, 85, 297–303.
http://dx.doi.org/10.1002/zoos.200900007

Panchetti, F., Scalici, M., Carpaneto, G.M. & Gibertini, G. (2008) Shape and size variation in the cranium of elephant-shrews: a morphometric contribution to a phylogenetic debate. *Zoomorphology*, 127, 69–82.
http://dx.doi.org/10.1007/s00435-007-0053-1

Perrin, M. & Rathbun, G.B. (2013) Species accounts: Order Macroscelidea, Family Macroscelididae, Genus *Elephantulus*, *E. edwardii*, *E. intufi*, *E. myurus*, *E. rozeti*, *E. rufescens*; Genus *Macroscelides*; species account *M. proboscideus*. *In:* Kingdon, J., Happld, D., Hoffmann, M., Butynski, T., Happold, M. & Kalina, J. (Eds.), *Mammals of Africa. Vol. I.* Bloombury, London, pp. 261–278.

Rathbun, G.B. (2009) Why is there discordant diversity in sengi (Mammalia: Afrotheria: Macroscelidea) taxonomy and ecology? *African Journal of Ecology*, 47, 1–13.
http://dx.doi.org/10.1111/j.1365-2028.2009.01102.x

Rathbun, G.B. (2015) Distribution map of sengis extracted from Sengis.org.

Ronquist, F., Teslenko, M., Mark, P.V.d., Ayres, D.L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2011) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice across a Large Model Space. *Systematic Biology*, 61, 1–4.

Rovero, F., Rathbun, G.B., Perkin, A., Jones, T., Ribble, D., Leonard, C., Mwakisoma, R.R. & Doggart, N. (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.
http://dx.doi.org/10.1111/j.1469-7998.2007.00363.x

Scalici, M. & Panchetti, F. (2011) Morphological cranial diversity contributes to phylogeny in soft-furred sengis (Afrotheria, Macroscelidea). *Zoology*, 114, 85–94.
http://dx.doi.org/10.1016/j.zool.2010.09.005

Séguignes, M. (1988) Facteurs de repartition d'*Elephantulus rozeti* (Macroscelidea, Macroscelididae) en Afrique du nord. *In: Académie de Montpellier*. Université des Sciences et Techniques du Languedoc, Montpellier, pp. 326

Shaw, G. (1800) *General zoology or systematic natural history. Vol. I. Part 2. Mammalia*. Printed for G. Kearsley, London, xiii + 552 pp.
http://dx.doi.org/10.5962/bhl.title.53459

Smit, H.A., Robinson, T.J., Watson, J. & Jansen van Vuuren, B. (2008) A new species of elephant-shrew (Afrotheria: Macroscelidea: *Elephantulus*) from South Africa. *Journal of Mammalogy*, 89, 1257–1269.
http://dx.doi.org/10.1644/07-MAMM-A-254.1

Smit, H.A., Van Vuuren, B.J., O'Brian, P.C.M., Ferguson-Smith, M.A., Yang, F. & Robinson, T.J. (2011) Phylogenetic relationships of elephant-shrews (Afrotheria, Macroscelididae). *Journal of Zoology, London*, 284, 133–143.
http://dx.doi.org/10.1111/j.1469-7998.2011.00790.x

Smith, A. (1829) Contributions to the natural history of South Africa. *Zoological Journal of London*, 4, 433–444.

Springer, M.S., Stanhope, M.J., Madsen, O. & De Jong, W.W. (2004) Molecules consolidate the placental mammal tree. *Trends in Ecology and Evolution*, 19, 430–438.
http://dx.doi.org/10.1016/j.tree.2004.05.006

Stamatakis, A. (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *BioInformatics*, 30, 1312–1313.
http://dx.doi.org/10.1093/bioinformatics/btu033

Swofford, D.L. (2003) *Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Sinauer Associates, Sunderland, Massachusetts. [software]

Tabuce, R., Jaeger, J.-J., Marivaux, L., Salem, M., Bilal, A.A., Benammi, M., Chaimanee, Y., Coster, P., Marandat, B., Valentin, X. & Brunet, M. (2012) New stem elephant-shrews (Mammalia, Macroscelidea) from the Eocene of Dur At-Talah, Libya. *Palaeontology*, 55, 945–955.
http://dx.doi.org/10.1111/j.1475-4983.2012.01163.x

Thomas, O. & Schwann, H. (1906) The Rudd exploration of South Africa - V. List of mammals obtained by Mr. Grant in North East Transvaal. *Proceedings of the Zoological Society of London*, 1906, 575–591.

Woodall, P.F. (1995a) The male reproductive system and the phylogeny of elephant-shrews (Macroscelidea). *Mammal Review*, 25, 87–93.
http://dx.doi.org/10.1111/j.1365-2907.1995.tb00441.x

Woodall, P.F. (1995b) The penis of elephant shrews (Mammalia: Macroscelididae). *Journal of Zoology, London*, 237, 399–410.
http://dx.doi.org/10.1111/j.1469-7998.1995.tb02770.x