The LINNEAN SOCIETY of London ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2013, **169**, 881–902. With 7 figures

Cryptic diversity in forest shrews of the genus *Myosorex* from southern Africa, with the description of a new species and comments on *Myosorex tenuis*

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Received 31 March 2013; revised 19 August 2013; accepted for publication 19 August 2013

Forest or mouse shrews (*Myosorex*) represent a small but important radiation of African shrews generally adapted to montane and/or temperate conditions. The status of populations from Zimbabwe, Mozambique, and the north of South Africa has long been unclear because of the variability of traits that have traditionally been 'diagnostic' for the currently recognized South African taxa. We report molecular (mitochondrial DNA and nuclear DNA), craniometric, and morphological data from newly collected series of *Myosorex* from Zimbabwe (East Highlands), Mozambique (Mount Gorogonsa, Gorongosa National Park), and the Limpopo Province of South Africa (Soutpansberg Range) in the context of the available museum collections from southern and eastern Africa and published DNA sequences. Molecular data demonstrate close genetic similarity between populations from Mozambique and Zimbabwe, and this well-supported clade (herein described as a new species, ***Myosorex meesteri* sp. nov.**) is the sister group of all South African taxa, except for *Myosorex longicaudatus* Meester & Dippenaar, 1978. Populations of *Myosorex* in Limpopo Province (herein tentatively assigned to *Myosorex* cf. *tenuis*) are cladistically distinct from both *Myosorex varius* (Smuts, 1832) and *Myosorex cafer* (Sundevall, 1846), and diverged from *M. varius* at approximately the same time (2.7 Mya) as *M. cafer* and *Myosorex sclateri* Thomas & Schwann, 1905 diverged (2.4 Mya). Morphometric data are mostly discordant with the molecular data. For example, clearly distinct molecular clades overlap considerably in craniometric variables. On the other hand, extreme size differentiation occurs between genetically closely related populations in the Soutpansberg Range, which coincides with the bissection of the mountain range by the dry Sand River Valley, indicating the potential for strong intraspecific phenotypic divergence in these shrews.

doi: 10.1111/zoj.12083

ADDITIONAL KEYWORDS: cranial morphometrics – mitochondial DNA – *Myosorex* cf. *tenuis* – *Myosorex meesteri* sp. nov. – nuclear DNA.

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INTRODUCTION

Forest or mouse shrews (*Myosorex*) represent a small but interesting sub-Saharan radiation of Afromontane shrews (Hutterer, 2005; Quérouil *et al*., 2007; Willows-Munro & Matthee, 2009; Stanley & Esselstyn, 2010). Recent studies have highlighted new and cryptic lineages within the Cameroon Volcanic Line of West-Central Africa (Hutterer, 2013a, b, c), the Eastern Arc Mountain Range and Mount Kilimanjaro (Stanley & Hutterer, 2000; Stanley & Esselstyn, 2010; Hutterer, 2013d), the Malawi Rift (Kerbis Peterhans *et al*., 2008), the Albertine Rift (Kerbis Peterhans *et al*., 2010, in press; Bober & Kerbis Peterhans, 2013; Dieterlen, 2013; Hutterer, 2013e), and the highlands and temperate coastal regions of southern Africa (Willows-Munro, 2008; Willows-Munro & Matthee, 2011; Baxter & Dippenaar, 2013a, b; Jenkins & Churchfield, 2013).

Because they have very low vagility (R.M. Baxter, unpubl. data), a high metabolism that is very sensitive to temperature (Brown, Hunter & Baxter, 1997), and are restricted to fragile montane and forest ecosystems, forest shrews are sensitive to climate change and human disturbance, and are excellent models to understand the effects of future climate changes on biodiversity; several species are listed by the International Union for Conservation of Nature (IUCN) as vulnerable and endangered (Baxter, 2008a, b, c, d; Howell & Hutterer, 2008a, b). An accurate understanding of their taxonomy, biogeography, and ecology is essential for correctly discerning their conservation status as well as in predicting the impacts of threats, including future climate change.

Southern Africa has typically encompassed four species of *Myosorex*: *Myosorex cafer* (Sundevall, 1846), *Myosorex longicaudatus* Meester & Dippenaar, 1978, *Myosorex sclateri* Thomas & Schwann, 1905, and *Myosorex varius* (Smuts, 1832) (Meester, 1958; Meester & Dippenaar, 1978; Meester *et al*., 1986; Kearney, 1993; Dippenaar, 1995; Skinner & Chimimba, 2005). Based on small cranial size, Roberts (1951) additionally recognized *Myosorex tenuis* Thomas & Schwann, 1905 from the former Transvaal (Mpumalanga and Limpopo provinces) of South Africa and Zimbabwe; although not recognized by Meester *et al*. (1986) or Skinner & Chimimba (2005), this species was tentatively accepted by Hutterer (2005) and Jenkins & Churchfield (2013). Wolhuter (in Smithers, 1983) noted that populations attributable to *M. tenuis* from Wakkerstroom to Entabeni (Soutpansberg Range) comprised a distinct karyotype ($2n = 40$).

It has long been understood that some populations, such as those from the East Zimbabwean Highlands and the north of South Africa, possess variable pelage and cranial diagnostic traits, attributed to both *M. cafer* and *M. varius* (Meester, 1958). Within the *M. cafer* complex, Willows-Munro (2008) demonstrated considerable lineage diversification, with divergent lineages recognized from the Limpopo Province of South Africa and Zimbabwe, whereas within the *M. varius* complex Willows-Munro & Matthee (2011) recognized divergent northern and southern clades.

The aim of the present study is to revise the taxonomy of the *Myosorex* complex in southern Africa with reference to eastern African populations, based on molecular and morphological analysis of recent collections from the Limpopo Province of South Africa, Zimbabwe, and Mozambique, as well as extensive measurements of existing historical collections from the Durban Natural Science Museum, Ditsong National Museum of Natural History (formerly Transvaal Museum), and the Field Museum of Natural History in Chicago. We show that populations from Limpopo Province should be referred to as *M.* cf. *tenuis* (Thomas & Schwann, 1905) pending molecular and detailed morphological analysis of the holotype. Specimens from Zimbabwe plus Mozambique are distinct, and represent a new species, *Myosorex meesteri* sp. nov. We also recognize important patterns of strong (Limpopo) to weak (Zimbabwe–Mozambique) phenotypic variation (in the absence of genotypic differentiation).

MATERIAL AND METHODS

Morphological and molecular sampling

The study focused on recent and historical collections of *Myosorex* from the Limpopo Province of South Africa, the East Highlands of Zimbabwe, and Gorongosa National Park in Mozambique, which were catalogued in the Durban Natural Science Museum (DNSM) and Field Museum of Natural History (FMNH) (Fig. 1). In order to ascertain the identity and relationships of the newly collected samples, we compared them with reference collections of reliably identified species from Tanzania [*Myosorex kihaulei* Stanley & Hutterer, 2000 and *Myosorex geata* (Allen & Loveridge, 1927) in the FMNH] and southern Africa [*M. varius* and *M. cafer* in the DNSM and Ditsong National Museum of Natural History, formerly Transvaal Museum (TM)].

Samples used in the molecular study (Table 1, Fig. 1) were taken from the newly collected material from Limpopo and Mozambique; additional tissue samples (of *M. kihaulei* and *M. geata*) were loaned from the FMNH. Further sequences from Zimbabwe and South Africa were available from the recent

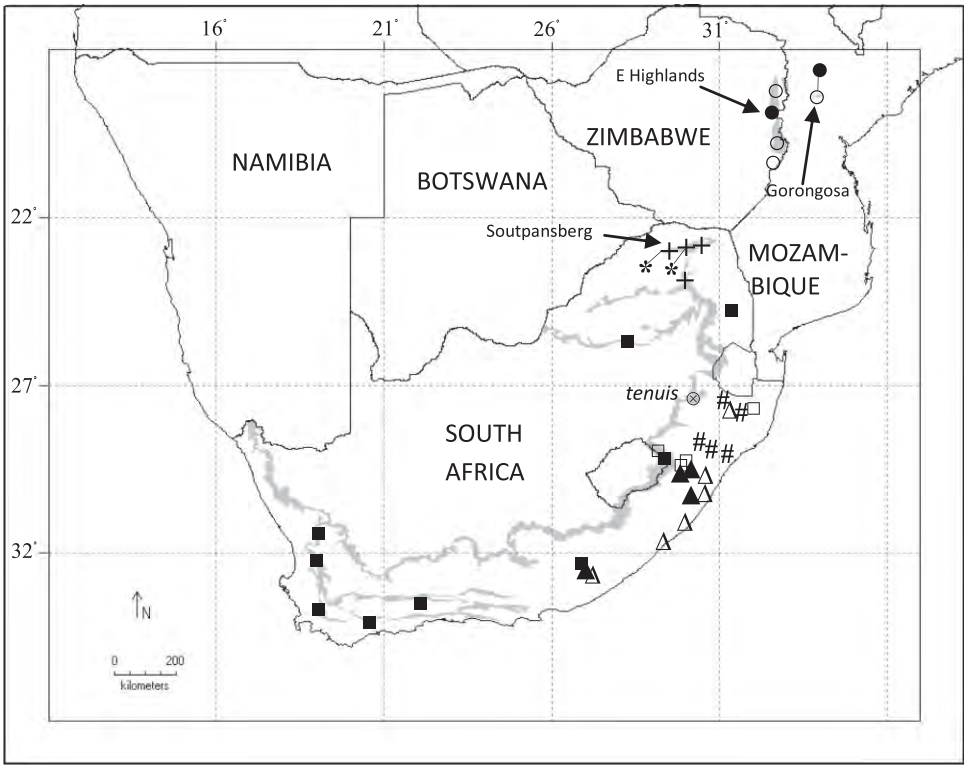


Figure 1. Map of southern Africa showing sampling localities for morphometric and molecular analyses of *Myosorex*. Grey shading represents the Great Escarpment of South Africa and the eastern Zimbabwean montane grassland–forest mosaic ecoregion of Olson *et al*. (2001). (Note: the Gorogosa locality overlies a small isolated patch of this ecoregion.) Symbols indicate recognized and newly defined species as follows: open and closed squares represent morphological and molecular sample localities, respectively, for *Myosorex varius*; open and closed triangles represent morphological and molecular samples, respectively, for *Myosorex cafer*; the hash symbols represent molecular samples of *Myosorex sclateri*; open and closed circles represent morphological and molecular samples, respectively, of ***Myosorex meesteri* sp. nov.**; crosses and asterisks represent morphological and molecular samples, respectively, of *Myosorex* cf. *tenuis*; ⊗, type locality (Zuurbron, Wakkerstroom District, Mpumalanga) of *Myosorex tenuis*. More details of the samples and localities are provided in Table 1 and the Appendix.

studies of Willows-Munro (2008) and Willows-Munro & Matthee (2009, 2011). The sequenced taxa include (where possible) a geographic sample of all recognized representatives of the southern African species: *M. cafer* (*N* = 4), *M. longicaudatus* (*N* = 1), *M. sclateri* (*N* = 5), and *M. varius* (*N* = 9). In addition, three representatives from each of the Limpopo and Zimbabwe–Mozambique populations were included. The *Myosorex blarina* Thomas, 1906 and *M. geata* specimens used in Willows-Munro & Matthee (2009) have recently been reclassified: the *M. blarina* specimen was found to represent *Myosorex zinki* Heim de Balsac and Lamotte, 1956, and the *M. geata* specimen was found to represent *M. kihaulei*. Out-group taxa also included *Congosorex verheyeni* Hutterer, Barrière & Colyn, 2001 from the Democratic Republic of Congo.

DNA SEQUENCING

Total DNA was extracted using the NucleoSpin Tissue Kit (Macherey-Nagel, Germany). Two mitochondrial DNA (mtDNA) markers and one nuclear intron (ncDNA) marker were amplified using previously published primers and protocols: the hypervariable control region of the mitochondrial genome (CR; Hoelzel, Hancock & Dover, 1991; Shields & Kocher, 1991), *16S* ribosomal RNA (*16S* rRNA; Palumbi *et al*., 1991), and a nuclear intron of the signal transducer and activator of transcription 5A (*STAT*; Matthee *et al*., 2001; Eick, Jacobs & Matthee, 2005). Cycle sequencing was performed using the BigDye kit, and sequencing products were analysed on an ABI automated sequencer (Applied Biosystematics, Perkin Elmer). All heterozygous sites in the nuclear intron

Table 1. Details of specimens included in the molecular analysis

Species	GenBank numbers			Collection numbers	Locality assignment
	CR	*16S* rRNA	*STAT*		
Congosorex verheyeni	EU651995	FJ486968	EU652016	PB R22903	Odzala, Republic of Congo
Myosorex sp.?	EU651996	FJ486974	EU652017	TBP 6315	Rungwe Forest, Tanzania
Myosorex cafer	EU652008	–	EU652029	TM 40491	Stutterheim, South Africa
Myosorex cafer	KC505650	FJ486972	–	FMNH 165585	Boston, South Africa
Myosorex cafer	EU652011	–	EU652032	DM 4815	Hilton, South Africa
Myosorex cafer	EU652010	–	EU652031	NM 917	Umfwalume, South Africa
Myosorex cf. *tenuis*	KC505651	KC505642	KC505660	DM 13638	Buzzard Mountain, South Africa
Myosorex cf. *tenuis*	KC505652	KC505643	–	DM 13559	Lajuma, South Africa
Myosorex cf. *tenuis*	KC505653	KC505644	–	DM 13634	Lajuma, South Africa
Myosorex geata	KC505654	KC505645	KC505661	FMNH 166770	Tanzania
Myosorex kihaulei	–	KC505646	–	FMNH 163555	Tanzania
Myosorex kihaulei	EU651996	FJ486974	EU652017	PB 6315	Tanzania
Myosorex longicaudatus	EU651997	FJ486975	EU652018	KM 687	Humansdorp, South Africa
***Myosorex meesteri* sp. nov.**	KC505655	FJ486970	–	NMZ 83536	Mutare, Zimbabwe
***Myosorex meesteri* sp. nov.**	KC505656	KC505647	KC505662	FMNH 214860	Gorongosa National Park, Mozambique
***Myosorex meesteri* sp. nov.**	KC505657	KC505648	KC505663	FMHN 214629	Gorongosa National Park, Mozambique
Myosorex sclateri	EU652009	–	EU652030	TM 39107	Ngome forest, South Africa
Myosorex sclateri	EU652003	FJ486977	EU652024	DM 1001	Mtunzini, South Africa
Myosorex sclateri	EU651998	FJ486971	EU652019	TM 43301	Hlabisa, South Africa
Myosorex sclateri	EU652005	–	EU652026	DM NK 15	Nkandla forest, South Africa
Myosorex sclateri	KC505658	FJ486979	KC505664	TM 43273	Eshowe, South Africa
Myosorex varius	EU652000	–	EU652021	TM 40904	Belfast, South Africa
Myosorex varius	EU652007	–	EU652028	RB FF 47	Hogsback, South Africa
Myosorex varius	EU651999	KC505649	EU652020	TM 41095	Pretoria, South Africa
Myosorex varius	EU652012	–	EU652033	SU SHREW779	Mooirivier, South Africa
Myosorex varius	EU652013	FJ486973	EU652034	ZM 41335	Grootvadersbos, South Africa
Myosorex varius	EU652006	–	EU652027	AT SWAR543	Oudtshoorn, South Africa
Myosorex varius	EU652001	KC505659	EU652022	TM 6302	Clanwilliam, South Africa
Myosorex varius	EU652004	–	EU652025	SU SHREW281	Niewoudsville, South Africa
Myosorex varius	EU652002	–	EU652023	SU SHREW144	Wellington, South Africa
Myosorex zinki	EU651993	FJ486969	EU652014	TM41428	Mount Kilimanjaro, Tanzania

GenBank accession numbers are provided for the mitochondrial control region (CR), *16S* ribosomal RNA (*16S* rRNA), and the nuclear intron *STAT* sequences data. Collection numbers are those assigned to each specimen by museums (DM, Durban Natural Science Museum; KM, Amatole Museum; NM, Natal Museum; NMZ, National Museum of Zimbabwe; TM, Ditsong National Museum of Natural History; ZM, Iziko Museum), university collections (PB, Paimpont Biological Station, University of Rennes, France; SU, Stellenbosch University), specific projects (TBP, Tanzanian-Belgian Project), or to the collections of other researchers (AT, Andrew Turner; RB, Rod Baxter); –, missing data.

were coded using International Union of Biochemistry (IUB) codes. All sequences were first aligned using ClustalX 2.1 (Larkin *et al*., 2007) and then optimized manually. The aligned data sets for the three markers comprised: CR, 29 taxa and 415 bp (170 variable and 120 parsimony informative); *16S* rRNA, 19 taxa and 466 bp (48 variable and 28 parsimony informative); and *STAT*, 25 taxa and 829 bp (85 variable and 43 parsimony informative). All taxa (except one *M. kihaulei* specimen) were represented in the combined data matrix by at least two molecular markers in order to limit missing data (Table 1). Data for the three molecular markers were initially analysed separately, and all data were then combined into a single concatenated data matrix (30 taxa and 1711 bp). All new sequences were deposited in GenBank (Table 1).

Two approaches were used to infer phylogeny: maximum-likelihood (ML) analyses were conducted using Garli 2.0 (Zwickl, 2006) and Bayesian analyses were performed using MrBayes 3.2 (Ronquist & Huelsenbeck, 2003). In each analysis the best-fitting model of nucleotide substitution for each marker was selected using the Akaike information criterion (AIC) implemented in jModelTest 2 (Darriba *et al*., 2012). For the combined data set, partitioned analyses were conducted, with data partitioned into the three gene regions and model parameters unlinked across partitions. In the ML analyses, each inference was initiated from a random starting tree and nodal support was assessed using 100 bootstrap replicates. In the Bayesian analysis two independent runs were performed, each consisting of four Monte Carlo Markov (MCM) chains and run for 5 million generations (trees sampled every 300th generation). The stationarity of log-likelihood tree scores was determined using the program Tracer 1.5 (Rambaut & Drummond, 2007). Stationarity was assumed when the effective sample size (ESS) reached > 200 for all parameters (as per Drummond *et al*., 2006). A 50% majority rule consensus tree was constructed using the CONSENSE program in the PHYLIP package (Felsenstein, 2005) after the first 20% generations of each simulation were discarded as burn-in.

Divergence dates between clades were estimated from the combined data (CR + *16S* rRNA + *STAT*) using an uncorrelated Bayesian relaxed molecular clock approach (Drummond *et al*., 2006), as implemented in BEAST 1.7.4 (Drummond & Rambaut, 2007). The data were partitioned by gene and given the same substitution models used in the tree inference, with the Yule speciation model as tree prior. Two fossil dates were used to calibrate the tree: oldest fossil assigned to the genus *Myosorex* (12–15 Mya; Butler & Hopwood, 1957; Doben-Florin, 1964) and the oldest record of *M. varius* (0.13–1.6 Mya; Matthews, Denys & Parkington, 2005). To account for the uncertainty associated with fossil calibration points, priors assuming a normal distribution were used to constrain the calibrated nodes: origin of *Myosorex* genus (mean = 13.5 Mya, SD = 0.9 Mya) and origin of *M. varius* lineage (mean = 0.865, stdev = 0.45). In each case the monophyly of these groups were not enforced. Two independent analyses were run, each consisting of 40 million generations, with sampling every 200 generations. These two independent runs were combined using LogCombiner 1.7.4 (available in the BEAST package) to create a single log file comprising 80 million generations, with convergence assessed using Tracer 1.5. After discarding the first 20% of generations as burn-in, the maximum clade credibility tree was obtained using TreeAnnotator 1.7.4 (available in the BEAST package), and then visualized with FigTree 1.3.1 (Rambaut, 2009).

Morphometrics and morphological characters

After calibration using individuals measured by P.J.T. and T.C.K., and using digital calipers calibrated to the nearest 0.01 mm, the following 17 cranial and dental variables were measured (following Dippenaar 1995, Kearney 1993, and Stanley & Esselstyn 2010): BL, basal length; BW, bimaxillary width; CI, condylo-incisive length; CL, length of canine; CW, width of canine; GW, greatest width of braincase; I3L, length of third upper incisor; I3W, width of third upper incisor; LIW, least interorbital width; LTR, length of lower tooth row; m1–m3, the distance from the anterior edge of the lower first molar to the posterior edge of the lower third molar; M3L, length of third upper molar; M3W, width of third upper molar; NW, nasal width; P4–M3, the distance from the anterior edge of the fourth upper premolar to the posterior edge of the third upper molar; PPL, postpalatal length; UTRL, length of entire upper tooth row. Only adult specimens were measured, as indicated by the complete fusion of the basioccipital and basisphenoid bones, and by fully erupted upper molars with some toothwear. Following Kearney (1993), Stanley & Esselstyn (2010), and the Gorongosa series measured here, we found no evidence of sexual dimorphism in *Myosorex*, enabling us to combine males and females. After removing obviously redundant measurements, and those that showed an error variation between observers of > 0.1 mm, ten robust variables remained that were used in all analyses (BW, CI, GW, LIW, LTR, M3L, M3W, P4–M3, PPL, UTR).

A total of 161 adult, complete (unbroken) skulls were measured from 32 distinct localities in South Africa, Zimbabwe, Mozambique, and Tanzania in the collections of DNSM, FMNH, and TM.

The following diagnostic cranial characters were recorded: (1) the extent of overlap between the single medial and paired lateral palatal foramina; (2) the condition of the posterior upper (fourth) unicuspid, whether tiny, intermediate in size, or small, and within a narrow or wide gap between the adjacent teeth. This latter aspect results from the presence or absence of a curved extension of the parastyle of the posterior premolar, leading to a narrow or wider gap, respectively. The following diagnostic pelage characters were recorded: (1) tail bicoloured (dorsal surface distinctly darker than ventral) or unicoloured (no distinction in colour between dorsal and ventral surface); (2) colour of dorsal pelage; (3) colour of ventral pelage; (4) colour of hindfoot (dark or pale). In addition, external measurements were obtained from museum specimen labels, bearing in mind the

inaccuracy that is possible from using data from different observers.

RESULTS

DNA SEQUENCING

As expected, the hypervariable control region contained the highest proportion of variable characters (41%); the mutational rates of the other two markers were more conservative (*16S* rRNA, 10%; *STAT*, 10% variable characters). There was no significant (ML bootstrap > 70%; Bayesian posterior probability > 95%) conflict among the topologies recovered by the independent analysis of the three molecular markers (not shown), and the data were combined. The ML and Bayesian analyses of the combined data (1711 bp) produced similar topologies. The increased taxonomic and character sampling used in the present study is in agreement with results reported previously by Willows-Munro & Matthee (2009). The combined analysis as well as the independent analysis of the three gene regions consistently clustered *Congosorex verheyeni* within the *Myosorex* genus. The inclusion of an additional *C. verheyeni* representative resulted in the same phylogenetic placement (analysis not shown). The South African endemic species *M. longicaudatus* is sister to a clade containing the Tanzanian species *M. geata* and *M. kihaulei* (ML bootstrap, 69; Bayes' posterior probability, 0.95; Fig. 2). The remaining southern African species form a well-supported monophyletic lineage (ML bootstrap, 97; Bayes' posterior probability, 1.00; Fig. 2). Within this lineage the specimens collected from Zimbabwe and Mozambique form a distinct strongly supported clade (ML bootstrap, 100; Bayes' posterior probability, 1.00). The close association between *M. cafer* and *M. sclateri* was supported in the phylogeny (ML bootstrap, 83; Bayes' posterior probability, 1.00). The specimens collected from Limpopo form a distinct lineage (ML bootstrap, 100; Bayes' posterior probability, 1.00) that is only weakly associated with *M. varius* (ML bootstrap, 41; Bayes posterior probability, 0.92). Similar to Willows-Munro & Matthee (2009), the monophyly of the genetically diverse species *M. varius* (Table 2) was not supported in the ML and Bayesian analyses.

On average the uncorrected genetic distances (Table 2) between the Zimbabwe–Mozambique clade (assigned to *M. meesteri* sp. nov.) and the Limpopo clade (assigned to *M.* cf. *tenuis*, based on the morphological similarities discussed below) were greater than that observed between the well-established species *M. cafer* and *M. sclateri*. As expected from previous studies the genetic differentiation within *M. varius* (0.030; Table 2) was much greater than that observed in the other lineages. Surprisingly, given the large morphological differentiation observed (see below), the genetic distance among the three individuals included in the Limpopo clade from Lajuma and Buzzard Mount was the smallest (0.004; Table 2) among the other southern African species.

The BEAST maximum clade probability tree inferred during the dating process did not significantly differ from the topologies generated by GARLI and MrBayes. In the BEAST tree, however, specimens assigned to *M. varius* were recovered as a monophyletic clade: the support for this relationship in the dated phylogeny was modest (BEAST posterior probability: 0.89). The fossil calibrated dating analysis suggests that the southern African taxa (excluding *M. longicaudatus*) last shared a common ancestor *c.* 5.1 Mya. The major lineages within this southern African endemic clade were established during the Pleistocene and Pliocene, between 1 and 3 Mya. The *M. cafer* and *M. sclateri* lineages last shared an ancestor *c.* 2.4 Mya, whereas *M. varius* and the Limpopo lineage (*M.* cf. *tenuis*) diverged on a similar timescale *c.* 2.7 Mya. The molecular clock analysis suggests that *M. meesteri* sp. nov. from Zimbabwe and Mozambique diversified from each other *c.* 1.8 Mya. The node age error bars incorporate the dates of divergence of the major clades, as suggested by previous studies (Willows-Munro & Matthee, 2009, 2011).

MORPHOMETRICS

Analysis of variance (ANOVA) revealed significant variation in all five external variables and ten craniometric variables across the 11 *Myosorex* operational taxonomic units (OTUs) investigated by this study (four recognized taxa and seven additional populations from Zimbabwe, Mozambique, and Limpopo; F values all have $P << 0.001$; Table 3). Principal component analysis (PCA) revealed only slight size variation between specimens from Zimbabwe and Mozambique (*M. meesteri* sp. nov.), but two distinct groups among specimens from Limpopo (*M.* cf. *tenuis*), with specimens from Lajuma (west Soutpansberg) and Woodbush (north Drakensberg) being distinctly smaller than those from Entabeni, Buzzard Mount, Farm Middelfontein, and Hanglip (east Soutpansberg; Fig. 3). In both PCAs separation could be interpreted as predominantly resulting from general cranial size, with all variables having positive values on the first principal component (Tables 4 and 5). Based on these results, and in order to conduct canonical variates analysis (CVA) on homogeneous groups with maximized sample sizes, we combined specimens from Zimbabwe and Mozambique into one OTU, but recognized two Limpopo OTUs. We also combined Tanzanian samples of *M. kihaulei* and

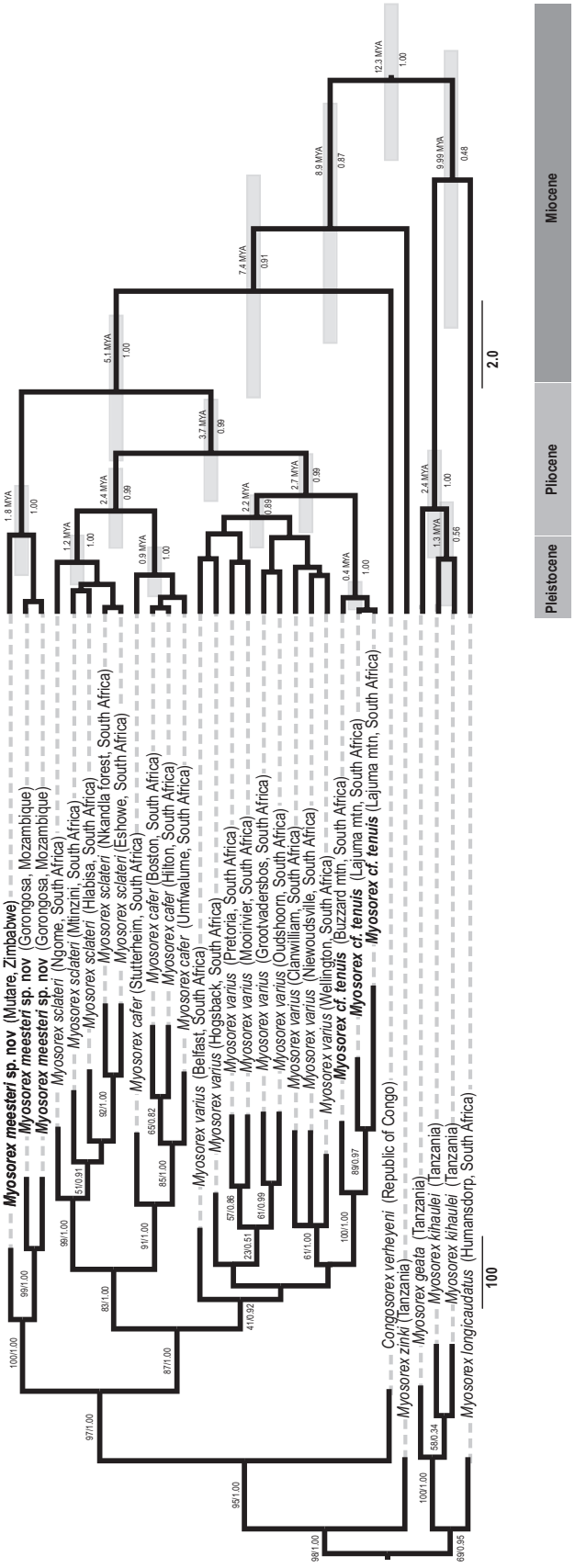


Figure 2. Maximum-likelihood phylogeny (left) and maximum clade probability tree (right), inferred from the combined analysis of molecular data (mitochondrial DNA control region, *16S* rRNA, and the nuclear intron *STAT*). The newly resurrected or described species *Myosorex tenuis* and ***Myosorex meesteri* sp. nov.** are in bold. Maximum-likelihood bootstrap and posterior probability (in that order) values are shown for nodes of the maximum-likelihood tree. Values above nodes of the maximum clade probability tree indicate the posterior mean divergence dates in millions of years before present. Shaded bars indicate the 95% highest posterior density (HPD) credibility intervals. Values below the nodes indicate posterior probability values generated during the BEAST dating analysis.

Table 2. Uncorrected pairwise sequence distances among the out-group and the major lineages of the in-group, estimated from the combined data matrix

	M. cafer	*M.* cf. *tenuis*	***M. meesteri* sp. nov.**	***M. sclateri***	***M. varius***	Out-group
Myosorex cafer	**0.010**					
Myosorex cf. *tenuis*	0.057	**0.004**				
***Myosorex meesteri* sp. nov.**	0.072	0.065	**0.019**			
Myosorex sclateri	0.036	0.060	0.065	**0.014**		
Myosorex varius	0.045	0.047	0.071	0.053	**0.030**	
Out-group	0.095	0.089	0.072	0.083	0.083	**0.053**

Averages within lineage pairwise sequence distances are given in bold on the diagonal.

M. geata based on their very close morphological similarity, as demonstrated by Stanley & Esselstyn (2010) and our own results (Table 3). The final CVA analysis of six major OTUs grouped these into two major size clusters, within which there was considerable overlap, but between which overlap was minimal. Specimens from Tanzania, Mozambique/Zimbabwe, and the small Limpopo OTU (comprising Lajuma and Woodbush) formed a smaller-sized group distinct from specimens of *M. cafer*, *M. varius*, and the larger-sized Limpopo OTU (central Soutpansberg) (Figs 4, 5; Table 6). This general pattern could be clearly seen in the summary data for individual variables, particularly in condylobasal skull length, where Tukey's tests indicated homogeneous groups comprising: (1) the smaller Limpopo populations; (2) the larger Limpopo populations, together with *M. varius*; (3) the Tanzanian taxa, together with Zimbabwe and Mozambique; and (4) *M. cafer* on its own (Table 3). Most variables revealed clear size differences with minimal overlap, between Limpopo populations of the small- and large-sized groups (Table 3).

Cranial and pelage characters

Specimens from Zimbabwe, Mozambique, and the Limpopo Province of South Africa showed variability in the traditional characters used to identify *Myosorex* species (Table 7). Whereas most individuals show *M. varius*-like characters such as overlapping palatal foramina, paler dorsal and hindfoot coloration, and a bicoloured tail, some, such as those from Entabeni Forest and Farm Middelfontein, show pelage characters clearly reminiscent of *M. cafer* (blackish dorsal pelage and hindfoot, and unicoloured tail colour). Specimens from Zimbabwe and Mozambique (*M. meesteri* sp. nov.) have a tiny fourth unicuspid tooth bordered by teeth (the third unicuspid and anterior premolar), which are either touching or almost touching (very narrow gap), clearly distinguishing them from *M. cafer*, *M. sclateri*, and *M. varius*, in which the fourth unicuspid is distinctly larger and falls within a substantial gap between the bordering teeth. Limpopo specimens (as well as one individual from Wakkerstroom assigned to *M. tenuis*: TM793) represent a transitional character state, whereby the fourth unicuspid is smaller than in *M. varius* or *M. cafer*, but not quite as tiny as in specimens from Zimbabwe and Mozambique, and it falls within a narrow gap (Fig. 6; Table 7). These differences in the relative gap size seem to arise from the curved projection of the anterolabial edge (parastyle) of the anterior premolar in specimens from Zimbabwe, Mozambique, and Limpopo (and the specimen referred to *M. tenuis* from Wakkerstroom), but not in other, recognized taxa (Fig. 6), rather than from the tooth being more lingually displaced, as supposed by Stanley & Hutterer (2000).

DISCUSSION

Molecular phylogeny

This study confirms the presence of unique radiations of shrews in the southern African region. The molecular data (mtDNA and ncDNA) provide strong evidence in support of the reciprocal monophyly of several lineages within southern African *Myosorex*. In particular, the existence of previously unrecognized clades that we assign here to *M.* cf. *tenuis* (Limpopo) and *M. meesteri* sp. nov. (Zimbabwe and Mozambique) was well supported by the molecular data. The sequence differentiation of the Limpopo and Zimbabwe–Mozambique lineages is comparable with that observed among the other well-established species within the complex (*M. cafer*, *M. sclateri*, and *M. varius*), and it is clear that these two lineages represent distinct evolutionary lineages, having diverged from sister taxa during the late Pliocene.

Table 3. Summary of mass, external body, and craniodental measurements in the *Myosorex* operational taxonomic units (OTUs) defined in this study

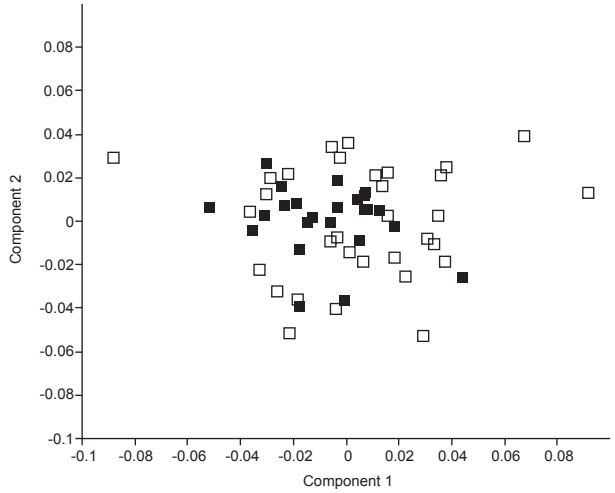
Variable	*M. cafer*	*M. varius*	*M. kihaulei*	*M. geata*	*M. tenuis* type	Limpopo (Hanglip)	Limpopo (Entabeni)	Limpopo (Buzzard + Middel.)	Limpopo (Lajuma)	Limpopo (Woodbush)	Mozambique	Zimbabwe
Total length	$F(9,183) = 25.89$ ($P << 0.001$)											
N	8	2	9	7		–	15	4	11	34	81	22
Min	125	120	111	116	121	–	116	110	107	104	117	109
Max	141	122	130	128		–	139	116	121	125	139	130
Mean	131.4	121.0	120.1	121.4		–	127.1	111.4	113.8	117.3	130.0	119.8
SD	6.7	–	5.2	4.2		–	6.6	3	4.9	4.2	5.2	5.7
Tail length	$F(9,190) = 8.76$ ($P << 0.001$)											
N	8	2	9	7		–	15	4	11	34	81	29
Min	39	34	36	38	45	–	34	30	35	33	34	35
Max	51	38.5	45	46		–	41	39	44	44	49	45
Mean	44.3	36.3	41.6	42.3		–	38.7	35.0	38.7	39.4	42.6	40.4
SD	3.0	–	3.0	2.8		–	2.3	3.7	2.6	2.8	2.7	2.7
Hind foot (CU)	$F(9,183) = 8.23$ ($P << 0.001$)											
N	3	2	9	7		–	14	4	11	33	81	29
Min	14	13.5	13	13	14	–	15	13	11	12	13	10
Max	16	14.5	16	16		–	17	16	15	16	16	15
Mean	15.3	14.0	14.1	14.1		–	15.7	14.25	13.2	14.2	14.9	14.1
SD	1.2	0.7	0.9	0.9		–	0.7	1.5	1.3	0.9	0.6	0.9
Ear length	$F(9,184) = 3.8$ ($P < 0.001$)											
N	6	3	9	7		–	15	4	11	33	81	29
Min	10	9	9	7	9	–	7	9	7	8	8	8
Max	12	12	10	9		–	12	10	11	11	11	14
Mean	10.9	10.3	9.7	8.4		–	10.3	9.75	9.2	9.8	9.7	9.5
SD	0.7	1.5	0.8	0.8		–	1.2	0.5	1.2	1.2	0.8	1.4
Mass	$F(9,170) = 5.92$ ($P << 0.001$)											
N	3	2	9	7		–	14	4	7	34	81	21
Min	10	14	9.5	10		–	9	7.1	8	8	6.9	8
Max	16	14.5	13	12		–	20	9.8	14	13	16.5	20
Mean	14.0	14.25	11.5	11		–	13.8	8.7	10.7	9.8	11.5	13.4
SD	3.5	–	1.1	0.7		–	3.8	1.1	2.3	1.1	2.5	3.3
CI	$F(10,150) = 41.83$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	22.9	21.3	20.0	20.6	21.7	22.0	21.6	22.0	20.9	20.8	20.5	19.6
Max	24.0	23.2	21.4	21.5		23.2	22.9	22.5	21.6	22.1	21.6	22.4
Mean	23.41	22.25	20.69	21.08		22.25	22.31	22.31	21.23	21.29	21.04	20.80
SD	0.35	0.57	0.50	0.34		0.47	0.35	0.20	0.21	0.33	0.31	0.68

Table 3. *Continued*

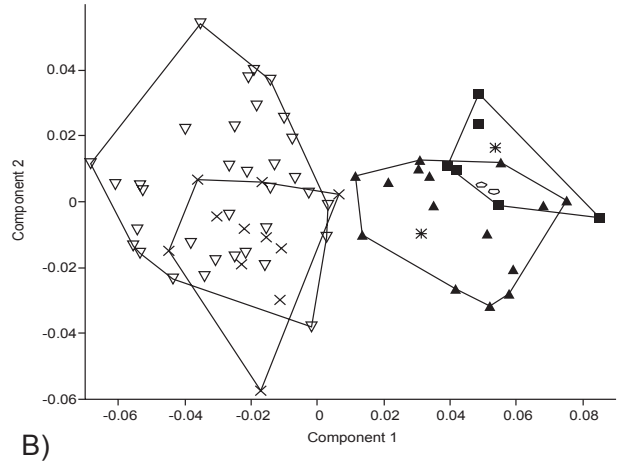
Variable	*M. cafer*	*M. varius*	*M. kihaulei*	*M. geata*	*M. tenuis* type	Limpopo (Hanglip)	Limpopo (Entabeni)	Limpopo (Buzzard + Middel.)	Limpopo (Lajuma)	Limpopo (Woodbush)	Mozambique	Zimbabwe
Tukey	D	A	C	C		A	A	A	B	B	C	C
PPL	$F(10,150) = 18.04$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	10.1	9.6	9.1	9.1	9.3	9.9	9.4	9.8	9.2	9.2	9.3	9.0
Max	11.1	10.4	9.8	9.9		10.8	10.4	10.5	9.8	10.0	9.9	10.2
Mean	10.60	9.96	9.54	9.52		10.15	9.95	10.04	9.53	9.60	9.52	9.55
SD	0.34	0.27	0.20	0.28		0.34	0.30	0.35	0.21	0.22	0.17	0.35
UTRL	$F(10,148) = 47.88$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	9.6	8.7	8.3	8.7	9.5	9.1	9.1	9.4	8.7	8.5	8.4	8.2
Max	10.5	9.9	8.9	9.2		9.7	9.7	9.8	9.3	9.4	9.0	9.4
Mean	10.10	9.46	8.69	9.00		9.40	9.52	9.57	9.03	8.96	8.70	8.75
SD	0.31	0.34	0.23	0.17		0.21	0.19	0.18	0.17	0.18	0.19	0.27
LIW	$F(10,150) = 8.92$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	4.4	4.1	4.2	4.3	4.2	4.4	4.3	4.5	4.3	4.0	4.1	3.8
Max	4.9	4.5	4.6	4.7		4.6	4.7	4.8	4.6	5.0	4.5	4.6
Mean	4.59	4.30	4.40	4.50		4.53	4.46	4.64	4.45	4.28	4.27	4.30
SD	0.16	0.14	0.11	0.16		0.10	0.14	0.13	0.09	0.17	0.09	0.18
BW	$F(10,150) = 25.77$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	6.8	6.4	6.0	6.2	6.3	6.6	6.4	6.6	6.2	6.1	6.2	6.0
Max	7.4	7.1	6.5	6.6		7.0	7.0	6.8	6.5	6.7	6.7	6.9
Mean	7.02	6.75	6.25	6.46		6.79	6.74	6.70	6.43	6.32	6.38	6.53
SD	0.15	0.20	0.16	0.16		0.17	0.16	0.10	0.08	0.14	0.13	0.21
GW	$F(10,150) = 10.48$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	10.6	10.3	10.1	10.4	10.2	10.4	10.5	10.3	10.1	10.1	10.0	9.8
Max	11.4	11.5	10.9	11.1		11.1	11.1	11.0	10.6	10.9	10.8	11.0
Mean	11.16	10.74	10.46	10.67		10.71	10.77	10.72	10.37	10.47	10.52	10.43
SD	0.25	0.41	0.26	0.23		0.23	0.19	0.32	0.13	0.20	0.17	0.28

LTR	$F(10,150) = 47.32$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	8.7	7.8	7.7	7.7	8.8	8.4	8.3	8.6	8.0	7.9	7.7	7.4
Max	9.4	8.9	8.2	8.4		9.2	8.9	8.7	8.5	8.5	8.2	8.3
Mean	9.11	8.54	7.97	8.18		8.69	8.68	8.64	8.28	8.16	7.94	7.90
SD	0.23	0.33	0.20	0.21		0.31	0.16	0.06	0.16	0.15	0.16	0.24
M3L	$F(10,150) = 4.94$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	1.5	1.4	1.4	1.4	1.7	1.6	1.5	1.5	1.3	1.4	1.4	1.5
Max	1.7	1.7	1.8	1.8		1.7	1.6	1.7	1.5	1.7	1.6	1.8
Mean	1.62	1.58	1.55	1.54		1.61	1.53	1.59	1.47	1.50	1.49	1.55
SD	0.09	0.09	0.11	0.11		0.04	0.05	0.06	0.06	0.07	0.05	0.07
M3W	$F(10,150) = 5.56$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	0.8	0.8	0.8	0.9	0.8	0.8	0.8	0.88	0.8	0.8	0.8	0.7
Max	1.1	1.0	1.0	1.0		1.0	0.9	0.95	0.9	1.0	0.9	1.0
Mean	0.93	0.90	0.90	0.91		0.88	0.86	0.93	0.83	0.83	0.85	0.86
SD	0.09	0.06	0.08	0.04		0.07	0.05	0.04	0.04	0.05	0.04	0.05
P4–M3	$F(10,150) = 29.34$ ($P << 0.001$)											
N	9	10	9	7		6	15	4	11	34	24	32
Min	5.5	5.1	4.9	5.2	5.5	5.6	5.4	5.5	5.1	5.0	4.9	4.9
Max	6.1	5.8	5.4	5.4		5.8	5.8	5.6	5.4	5.5	5.4	5.7
Mean	5.82	5.57	5.23	5.29		5.65	5.61	5.53	5.27	5.26	5.15	5.21
SD	0.23	0.22	0.15	0.07		0.08	0.11	0.03	0.11	0.11	0.12	0.18

F values (with degrees of freedom in parentheses) represent results of ANOVA for all OTUs. Results of Tukey's pairwise comparison tests shown only for CI; letters indicate non-significant (homogeneous) subsets of OTUs. As a result of the low sample sizes of two nearby localities, and morphometric similarity between them (see Fig. 3), samples from Farm Middelfontein (Middel.) ($N = 2$) and Buzzard Mountain ($N = 2$) were pooled for the ANOVA. External body measurements and measurements for CI, GW, and UTR for the holotype of *Myosorex tenuis* from the Natural History Museum, London (BM 4.9.1.22) were obtained from Thomas & Schwann (1905); the balance of cranial measurements were taken on the holotype by Paulina Jenkins. For a list of the abbreviations, see the Material and methods section.



A)



B)

Figure 3. Principal component analyses (PCA) of ten log-transformed craniometric variables in *Myosorex* samples from: (A) Zimbabwe (filled squares) and Mozambique (open squares); and (B) Limpopo Province, South Africa (■, Hanglip; ▲, Entabeni; △, Woodbush; ×, Lajuma; *, Buzzard Mount; ○, Middelfontein Farm). The first two principal components explained 40.8, 23.0, 62.5, and 16.1% of the total variance, respectively, for (A) and (B).

Table 4. Character loadings for the first three principal components (PCs) principal component analysis (PCA) of specimens from Zimbabwe and Mozambique

	PC 1	PC 2	PC 3
CI	0.2417	0.1684	0.4267
PPL	0.186	0.2999	0.3541
UTRL	0.326	0.09307	0.1914
LIW	0.3301	0.1438	−0.1276
BW	0.277	0.1358	−0.3401
GW	0.1072	0.2004	0.2221
LTR	0.25	0.07301	0.2681
M3L	0.4632	0.1787	−0.6111
M3W	0.4245	−0.8655	0.1125
P4-M3	0.3826	0.08617	0.1293

For a list of the abbreviations, see the Material and methods section.

Table 5. Character loadings for the first three principal components (PCs) principal component analysis (PCA) of specimens from Limpopo Province of South Africa

	PC1	PC2	PC3
CI	0.2816	−0.05958	−0.09753
PPL	0.2792	−0.1031	0.01692
UTRL	0.3439	−0.05005	−0.2116
LIW	0.2927	−0.3505	0.8145
BW	0.3609	−0.1416	0.09949
GW	0.1739	−0.08475	0.03271
LTR	0.3368	0.005465	−0.2582
M3L	0.2525	0.9128	0.316
M3W	0.388	−0.00143	−0.2285
P4-M3	0.388	−0.00143	−0.2285

For a list of the abbreviations, see the Material and methods section.

The placement of *Congosorex verheyeni* within the genus *Myosorex* has been suggested previously (Willows-Munro, 2008), and the higher-level taxonomy will need to be investigated in the future using increased taxonomic coverage of the subfamily Myosoricinae.

Taxonomic conclusions

In describing *M. kihaulei* from the Eastern Arc, Stanley & Hutterer (2000) emphasized the diagnostic importance of the 'tiny, lingually displaced' fourth upper unicuspid tooth. In spite of its variability, we confirmed the relatively 'tiny' size in both *M. geata* and *M. kihaulei* from Tanzania, as well as in virtually all specimens from Zimbabwe and Mozambique (*M. meesteri* sp. nov.). Together with the small cranial size of specimens from Zimbabwe and Mozambique, which is a character shared with the Eastern Arc forms (*M. geata* and *M. kihaulei*), these data suggest a closer phylogenetic relationship between populations from Zimbabwe and Mozambique with eastern African populations, rather than with South African populations. This morphological similarity between Zimbabwe and Eastern Arc *M. geata* was realized long ago by Heim de Balsac (1967), who suggested that Zimbabwean *Myosorex* may be conspecific with

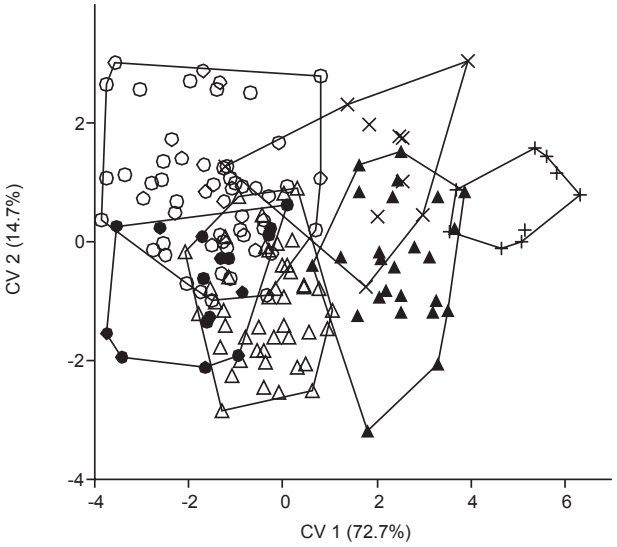


Figure 4. Canonical variate analysis (CVA) of ten log-transformed craniometric variables in six operational taxonomic units (OTUs) of *Myosorex* from southern and eastern Africa; ○, Zimbabwe–Mozambique; ●, *Myosorex kihaulei* and *Myosorex geata* (Tanzania); ▲, east Soutpansberg; △, north Drakensberg + west Soutpansberg; ×, *Myosorex varius*; +, *Myosorex cafer* (topotypic). The first two canonical vectors explained 72.7 and 14.7%, respectively, of the total variance.

M. geata; however, Heim de Balsac & Meester (1977) later considered that *M. geata* could be distinguished from Zimbabwean populations by its darker pelage, and that Zimbabwean populations should thereafter be assigned to *M. cafer*. The hypothesis of a close phylogenetic relationship between Zimbabwean–Mozambiquan and Eastern Arc forms based on morphological similarity is directly refuted by our molecular evidence, which indicates a strongly supported sister-group relationship between *Myosorex* from Zimbabwe–Mozambique and *Myosorex* from South Africa: these two clades diverged 5.1 Mya (Fig. 2). Eastern African *Myosorex* diverged from southern African clades much earlier, at 8.9 Mya for *M. zinki* from Mount Kilimanjaro, and at 12.3 Mya for the Eastern Arc taxa (Fig. 2).

This suggests that cranial size and dental characters are subject to strong convergent evolution, and may have little phylogenetic significance, a thesis that is strongly supported by the existence of two divergent size groups within Limpopo. Within the Soutpansberg of north Limpopo, the dry Sand River Valley longitudinally bisects the mountain range, separating the small-sized Lajuma population in the drier, far western Soutpansberg from distinctly larger-sized populations in the moister environments of the central and eastern Soutpansberg (Fig. 5). As these populations are genetically closely related and are estimated to have diverged only 0.4 Mya (Fig. 2), this provides compelling evidence for strong selection and intraspecific morphological divergence within geologically recent time frames. This discordance between molecular and morphological characters justifies caution in making taxonomic judgements in this group of shrews based on morphology alone. On the other hand, populations from Zimbabwe and Mozambique, which were estimated to have diverged 1.8 Mya, are indistinguishable through our morphometric analysis (Fig. 3; Table 3).

The combined mitochondrial and nuclear DNA sequences, taken together with small cranial size and the presence of the tiny fourth upper unicuspid in a narrow or non-existent gap in the tooth row, is sufficient to justify recognizing populations from Zimbabwe and Mozambique as a unique evolutionary species distinct from South African taxa (which we name below as *M. meesteri* sp. nov.). However, the situation with respect to the Limpopo populations is more enigmatic, given the discordance between morphological and molecular data, as well as the uncertain relationship between Limpopo populations and *M. tenuis* described from Zuurbron, Wakkerstroom District, Mpumalanga Province (Thomas & Schwann, 1905). Nevertheless, divergent lines of evidence support recognition of Limpopo populations as a distinct evolutionary species, which can be provisionally assigned to *M. tenuis* based on small cranial size. This was recognized long ago by Roberts (1951), who demonstrated craniometric similarity between the holotype of *M. tenuis* from Wakkerstroom in Mpumalanga Province and a series of *Myosorex* from Woodbush and Entabeni Forest (Soutpansberg) in Limpopo Province.

Firstly, the dated molecular tree indicates that Limpopo populations diverged from *M. varius* in the late Pliocene, some 2.7 Mya, which was a time of considerable faunal turnover in Africa (Vrba, 1985), and is the same time that *M. cafer* diverged from *M. sclateri*. Palaeoclimatic and tectonic forcing in the late Pliocene, leading to the conversion of forests into open woodland (Partridge, 2010; Cotterill & de Wit, 2011), has been invoked as driving speciation in African mammals, including antelope (Moodley & Bruford, 2007), bats (Taylor *et al*., 2012), and rodents (Taylor *et al*., 2009).

Furthermore, given that Limpopo populations were formerly assigned to *M. cafer* (Baxter & Dippenaar, 2013a), traits that are diagnostic for *M. cafer* (such as blackish dorsal pelage, unicoloured tail, dark hindfoot, and non-overlapping medial and lateral palatal foramina) are completely variable within the Limpopo populations. Thus, whereas palatal

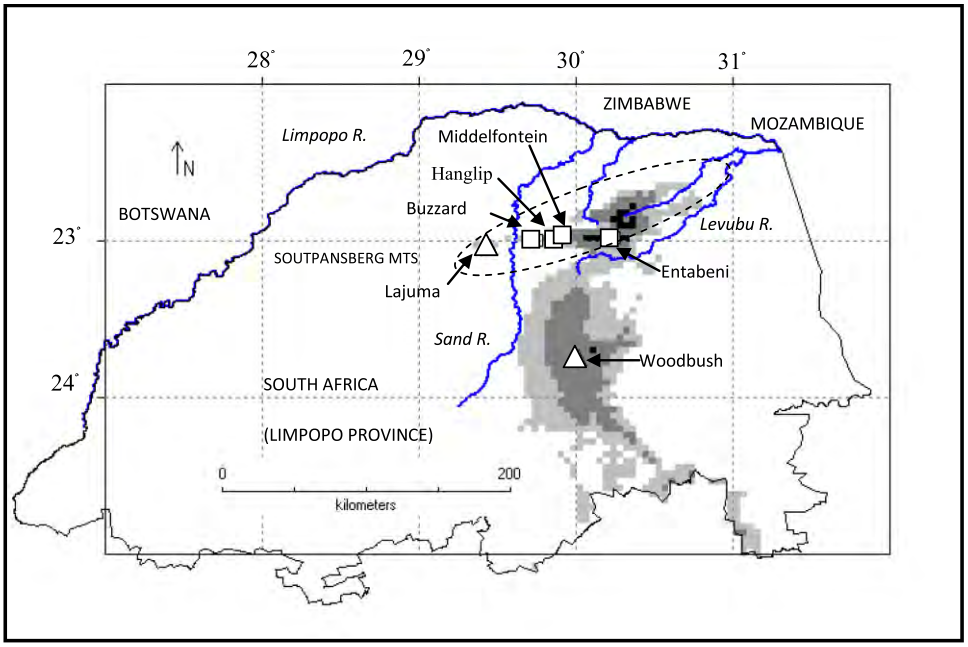


Figure 5. Map showing distribution of two distinct morphological groups in the Soutpansberg Mountains and northern Drakensberg Mountains of Limpopo Province in relation to a map of annual precipitation (AP) for the region (pale-grey shading indicates AP of 800–1000 mm; dark-grey shading indicates AP of 1000–1300 mm; black indicates AP > 1300 mm). Open triangles represent the smaller-sized morph (from Woodbush and Lajuma), whereas open squares indicate the large-sized populations from east of the Sand River in the Soutpansberg (Buzzard Mount, Hanglip, Farm Middelfontein, and Entabeni Forest). The dashed line outlines the extent of the Soutpansberg Mountains.

Table 6. Character loadings for canonical variates analysis (CVA) of all *Myosorex* operational taxonomic units (OTUs) included in the study

	CV1	CV2	CV3
CI	33.596	15.475	89.026
PPL	16.202	2.188	−25.249
UTRL	21.29	−5.4503	53.493
LIW	−5.7288	−49.053	−34.97
BW	25.924	85.197	23.748
GW	−13.17	26.087	−62.29
LTR	48.572	−48.84	−34.249
M3L	−3.2299	9.7843	−4.2751
M3W	−7.7276	14.766	−20.635
P4-M3	−3.7645	−15.998	−47.132

For a list of the abbreviations, see the Material and methods section.

foramina are frequently overlapping in Limpopo (e.g. in 84% of Woodbush individuals), they are sometimes non-overlapping or barely overlapping (e.g. in 25% of Lajuma individuals), and in some cases (4/72 Limpopo individuals) the medial foramen is absent, a characteristic frequently found in Tanzanian specimens, but never in southern African *M. varius* and *M. cafer* (Table 7). The colour of the hind foot varies from dark (e.g. in most Entabeni animals) to pale (in Lajuma and most Woodbush animals).

Roberts (1951) regarded the small cranial size (CI 21.6 mm) of the *M. tenuis* holotype from the Natural History Museum in London (BM 4.9.1.22) from Zuurbron (near Wakkerstroom) in Mpumalanga Province to be a character linking it with populations from Limpopo and Zimbabwe (Table 3). Our study further shows that the condition of the fourth uncuspid in Limpopo specimens (and one Wakkerstroom specimen in the TM assigned to *M. tenuis*; TM 793) is more similar to the condition in Zimbabwe and Mozambique (*M. meesteri* sp. nov.) than it is to specimens of *M. cafer*, *M. sclateri*, and *M. varius* (Fig. 6; Table 7). This apparent similarity (in cranial size and fourth unicuspid morphology) between *M.* cf. *tenuis* and *M. meesteri* sp. nov. is not indicative of phylogenetic relatedness, as shown from the molecular data (Fig. 2), suggesting once again that these characters may be convergent amongst *Myosorex* lineages. Nevertheless, in combination with other traits and molecular and biogeographical evidence, they may serve as useful diagnostic traits for individual

Table 7. Variation in craniodental and pelage diagnostic traits in different *Myosorex* operational taxonomic units (OTUs)

		Arrangement of palatal foramina			Fourth upper unicuspid				Hindfoot colour		Tail	
Taxon & OTU	*N*	Overlap	No overlap	Medial absent	Tiny, gap absent or very narrow	Small, narrow gap	Small–medium, wider gap	Absent	Dark	Pale	Bicolour	Unicolour
M. cafer	9	1	8	–	–	–	9	–	9	–	–	9
M. varius	11	10	1	–	–	–	11	–	–	4	4	–
M geata	7	3	1	3	7	–	–	–	7	–	2	5
M. kihaulei	10	6	1	3	7	3	–	–	8	2	5	5
Zimbabwe	39	29	5	3	37	1	–	1	–	17	17	–
Mozambique	25	25	–	–	25	–	–	–	–	102	102	–
Limpopo, Woodbush	38	32	2	1	1	35	–	3	–	36	35	1
Limpopo, Entabeni	16	12	–	2	2	13	–	–	13	3	15	1
Limpopo, Hanglip	4	3	1	–	–	4	–	–	–	–	–	–
Limpopo, Buzzard Mount	2	2	–	–	–	2	–	–	–	2	2	–
Limpopo, Lajuma	12	8	3	1	–	11	–	–	–	4	4	–
Limpopo, Middelfontein Farm	2	2	–	–	–	2	–	–	2	–	–	2

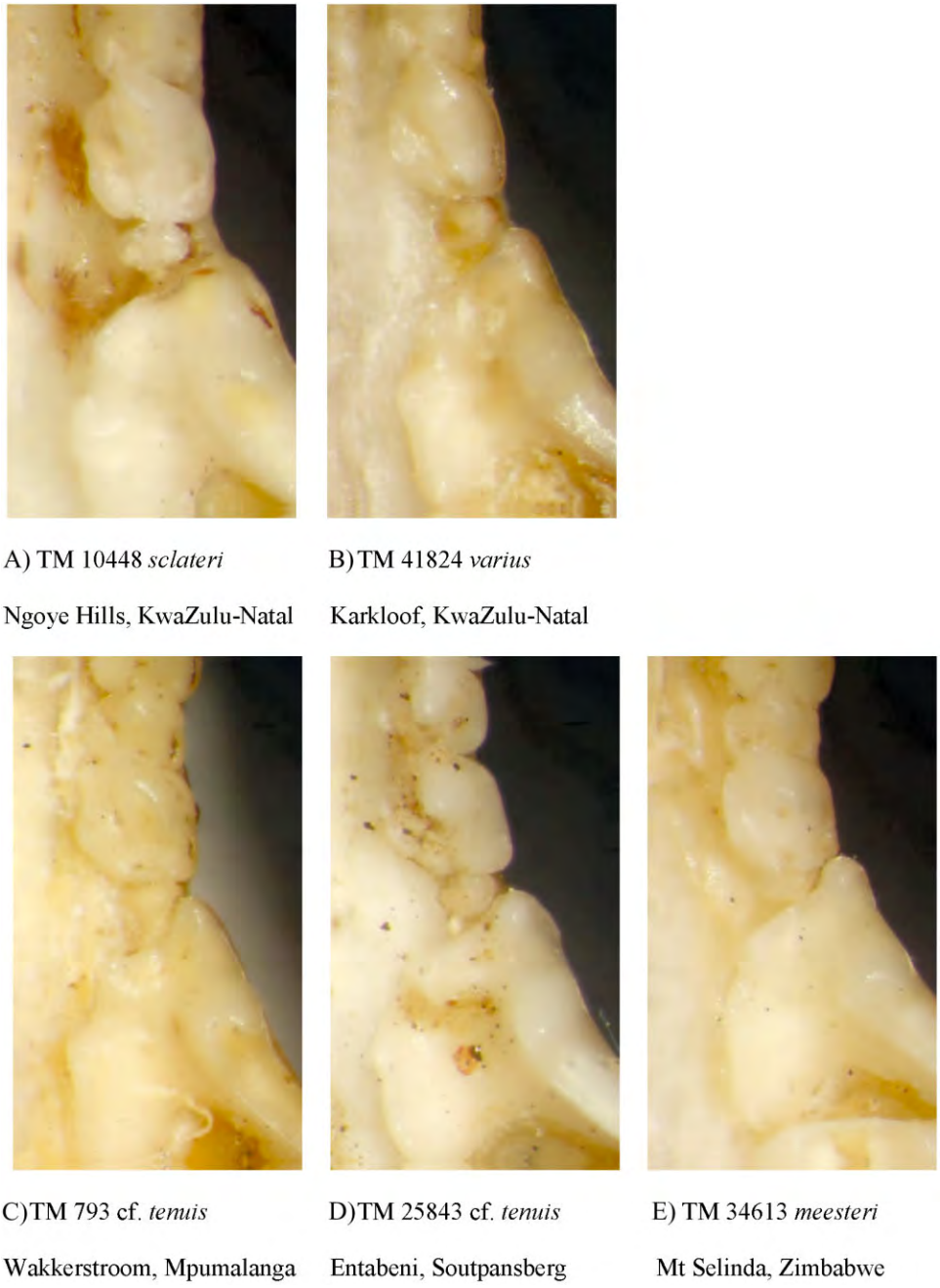


Figure 6. Photographs of the fourth unicuspid and adjacent molars in the upper tooth rows of: (A) TM 10448, *Myosorex sclateri* (Ngoye Hills, KwaZulu-Natal); (B) TM 41824, *Myosorex varius* (Karkloof, KwaZulu-Natal); (C) TM 793, *Myosorex* cf. *tenuis* (Wakkerstroom, Mpumalanaga); (D) TM 25843, *Myosorex* cf. *tenuis* (Entabeni, Soutpansberg Range, Limpopo); (E) TM 34613, ***Myosorex meesteri* sp. nov.** (Mount Selinda, Chirinda Forest, Zimbabwe).

species. In order to finally resolve the suitability of *M. tenuis* as the correct name for the Limpopo lineage, here defined on molecular grounds, further research is needed based on detailed analysis and comparisons of dental, morphometric, and molecular characters of the holotype of *M. tenuis*. Pending such analysis, we provisionally assign Limpopo populations to *M.* cf. *tenuis*.

DESCRIPTION AND RE-DEFINITION OF SPECIES

FAMILY SORICIDAE G. FISCHER, 1814
GENUS *MYOSOREX* GRAY, 1838
***MYOSOREX MEESTERI* SP. NOV.**
MEESTER'S FOREST SHREW

Holotype
DM 4693, an adult female collected by Teresa Kearney, Albert Kumirai, Peter Taylor, and Peter Wright on 10 December 1995. The specimen is represented by a skin and skull in good condition. The external measurements are as follows (in mm): total length 120; tail length 40, hindfoot length (*cum unguis*) 15; ear 10. Body mass was 12 g. The extremely small cranial size is indicated by cranial measurements (in mm) as follows (see abbreviations under Material and methods): CI 20.6; PPL 9.46; UTR 8.82, LIW 4.05; BW 6.22; GW 10.3; LTR 8.1; M3L 1.48; M3W 0.8; P4–M3 5.11. The skull, dentition, and mandible are illustrated in Figure 7. The anterior margin of the medial palatal foramen overlaps with the posterior margins of the two lateral foramina (Fig. 7). The fourth upper unicuspid is tiny and bordered by teeth, which are almost touching because of the curved extension of the parastyle of the third upper unicuspid (Fig. 7). The pelage coloration is brownish rather than blackish above and below, with pale hindfoot and bicoloured tail, similar to *M. varius*.

Type locality
Chingamwe Estates, 15 km south-east of Juliasdale, Inyanga Mountains, eastern Zimbabwe (18.4625°S, 32.753°E). The specimen was trapped with a Sherman trap in tall grassland bordering a young pine plantation.

Paratypes
An additional 21 shrews were collected from the same series (DM: 4641, 4642, 4643, 4644, 4645, 4646, 4647, 4648, 4651, 4652, 4655, 4656, 4664, 4665, 4678, 4679, 4680, 4688, 4694, 5003, 5004).

Referred specimens: See the Appendix.

Etymology
This species is named after J.A.J. 'Waldo' Meester who made a significant contribution to African mammalogy, most particularly through his authorship of two landmark volumes: *Mammals of Africa: an Identification Manual* (1971–1977) and *Classification of Southern African Mammals* (1986). He was a shrew specialist whose early work drew attention to

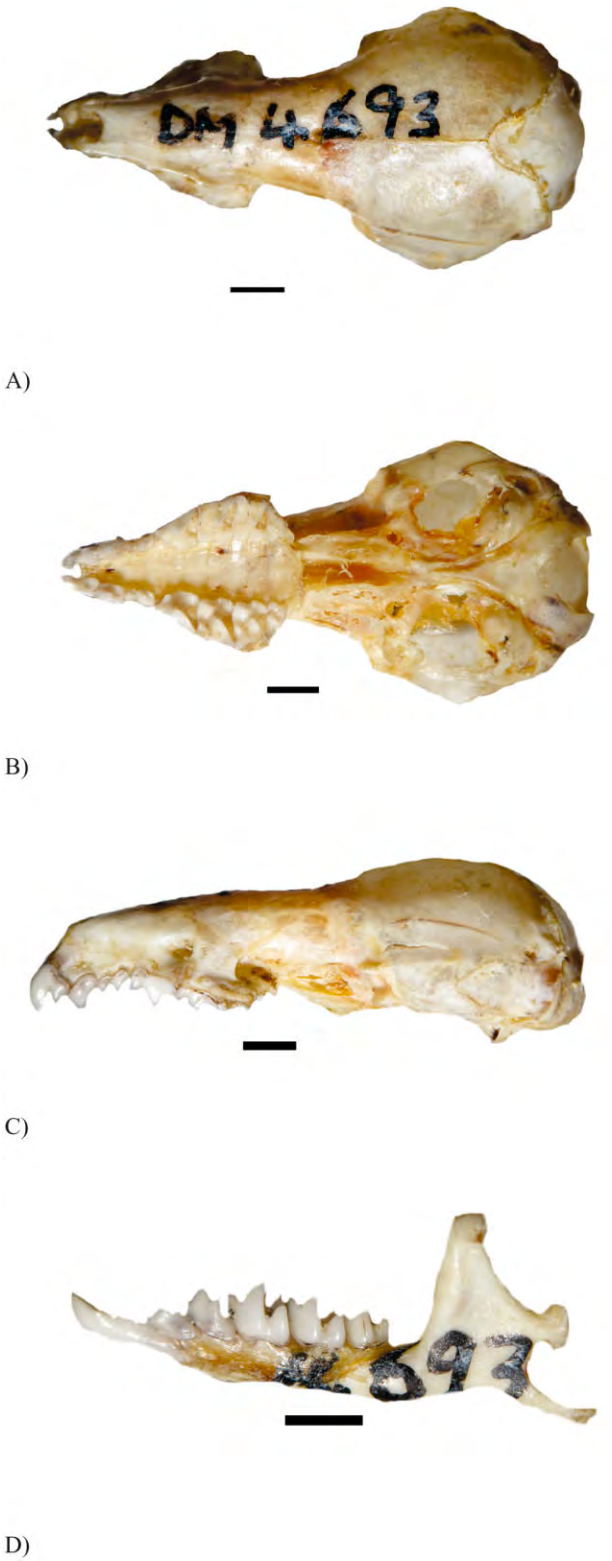


Figure 7. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of the holotype of ***Myosorex meesteri* sp. nov.** (DM 4693). Scale bar: 2 mm.

the enigmatic taxonomic status of *Myosorex* from Zimbabwe (Meester, 1958), which we now name in his honour.

Diagnosis
Individuals of this species can be readily distinguished from South African *Myosorex* species by the presence of a 'tiny' fourth upper unicuspid tooth, bordered by teeth that are touching or almost touching because of a curved extension of the parastyle of the anterior premolar (Fig. 6; Table 7). This feature, together with small cranial size (Fig. 4; Table 3), is shared with Tanzanian species (*M. geata* and *M. kihaulei*); however, *M. meesteri* sp. nov. is clearly distinguished on molecular and biogeographical grounds from the Tanzanian species (Fig. 2).

Description
This is a small species of *Myosorex*, particularly in cranial dimensions (Table 3). In its pelage colour it is most like *M. varius*, having brownish rather than blackish dorsal pelage and relatively pale hindfeet and a bicoloured tail. Similarly, in its predominantly overlapping medial and lateral palatal foramina it is most like *M. varius*; however, in a few cases (13%) the foramina do not overlap or the medial foramina may be missing (8%; Table 7).

Distribution and biology
The species is endemic to the Eastern Zimbabwean montane forest–grassland mosaic ecoregion of the Eastern Highlands of Zimbabwe and of Mount Gorongosa, Gorongosa National Park of Mozambique. The type series from Inyanga Mountains of Zimbabwe were all collected in moist grasslands, sometimes bordering a dam or pine plantations, but never in forest. On Mount Gorongosa, it was by far the most common small terrestrial mammal caught, comprising almost 50% of all captures. It is restricted to the moist montane forest (1120–1580 m a.s.l) and alpine meadows (1680–1700 m a.s.l.), and is not found in the drier scrubbier areas, nor even amid the gallery forest below (elevation 790–940 m a.s.l.).

Myosorex cf. *tenuis* Thomas & Schwann 1905
Thin forest shrew or Transvaal forest shrew

Holotype
BM 4.9.1.22. External and cranial measurements are shown in Table 3. Type locality is Zuurbron, near Wakkerstroom in Mpumalanga Province, South Africa (indicated in Fig. 1).

Referred material: See the Appendix.

Diagnosis
This species is clearly differentiated genetically and biogeographically from all other southern and eastern African species of *Myosorex*; however, it is difficult to diagnose morphologically as pelage, craniodental, and size characters vary considerably within the species. Nevertheless, from series examined in this study, the condition and position of the fourth unicispid (most particularly the pronounced extension of the parastyle of the upper anterior premolar, which results in a narrow gap between this tooth and the upper third unicuspid) is similar to that found in *M. meesteri* sp. nov., and clearly differentiates *M.* cf. *tenuis* from other South African species (Fig. 6; Table 7). The consistency of this character should be tested from larger and geographically broader samples. Typically, specimens from north Drakensberg (Wakkerstroom, Woodbush) and west Soutpansberg are easily distinguished by their small cranial size, with CI usually 20–22 mm, as opposed to > 22 mm in *M. varius* and *M. cafer* (Table 3). The Zuubron, Wakkerstroom type specimen is sympatric with the larger-sized *M. varius* (Thomas & Schwann, 1905); however, populations from Woodbush and Soutpansberg occur allopatrically. Populations from east Soutpansberg are larger in size, and overlap in cranial and external measurements with *M. varius*; however, these populations are genetically associated with *M.* cf. *tenuis* from western Soutpansberg rather than with *M. varius* (Fig. 2), and they tend to have a darker hindfoot colour and unicoloured tail more typical of *M. cafer* (from which they are also distinguished genetically). Roberts (1951) indicated clearly that *M. tenuis* was a dark-footed form and included Wakkerstroom and Woodbush in its range; however, examination of a large series from Woodbush indicate that they are all relatively pale-footed (Table 7). Wolhuter (in Smithers, 1983) pointed out that specimens from the type locality of *M. tenuis* had a karyotype ($2n = 40$) that was distinct from those of *M. cafer* ($2n = 38$) and *M. varius* ($2n = 42$), and that was found in populations from 'about Wakkerstroom' to as far north as Entabeni in the central Soutpansberg. These data provide additional support for the existence of *M. tenuis* occurring from Wakkerstroom to Entabeni (Soutpansberg); however, the resolution of the correct name for this lineage awaits detailed molecular and morphological analysis of the holotype of *M. tenuis* in the London Natural History Museum, in comparison with critical historical and recent collections.

Description
Pelage colour varies considerably, from individuals (e.g. from Entabeni) that are dark (almost blackish) in dorsal colour, and with dark feet, like *M. cafer*, to others with brownish dorsal pelage and paler

hindfeet, more like *M. varius* (Table 7). Likewise, body and particularly cranial size varies dramatically with populations, falling into two divergent size classes (with minimal overlap between them): smaller-sized individuals from western Soutpansberg and the northern Drakensberg Escarpment, and larger-sized individuals from eastern Soutpansberg (Figs 3B, 4, 5). Palatal foramina are mostly overlapping (as in *M. varius*), but are sometimes (8%) non-overlapping or with the medial foramina absent (6%; Table 7).

Biology and distribution

Based on the material examined in this study, *M.* cf. *tenuis* is mostly restricted to the Limpopo Province of South Africa from the Soutpansberg Range to the northern extension of the Great Escarpment of South Africa, extending southwards to the type locality of *M. tenuis* (Zuurbron, Wakkerstroom District), which is located some 400 km south of Woodbush on the border between Mpumalanga and KwaZulu-Natal provinces (Figs 1, 5). It is strange that few or no museum specimens in the intervening northern Drakensberg region of Mpumalanga Province have been assigned unequivocally to *M. tenuis*, with collections from this region from the TM being referred mostly to *M. varius* (or apparently in error to *M. cafer*). An accurate understanding of the distribution limits of *M.* cf. *tenuis* awaits a critical analysis of historical and recent collections (in the TM and NHM) of *Myosorex* from the Mpumalanga Drakensberg.

It appears that phenotypic and possibly genotypic differentiation is continuing in this species, as evidenced by the large morphological gap between populations west (Lajuma) and east (Buzzard Mount, Entabeni, Middelfontein, and Hanglip) of the Sand River Valley, which bisects the Soutpansberg from north to south. From recent Soutpansberg collections, these shrews were almost always collected in wetlands and moist grasslands, although a couple of individuals were collected from the margin of mistbelt forests. This habitat association further emphasizes the ecological separation between this species and the forest specialist *M. cafer*, with which it was until recently associated.

ACKNOWLEDGEMENTS

The authors would like to thank Patrick Barriére, Ian Gaigher, Denise Hamerton, Aubrey Munyai, Tshifhiwa Nemakhavani, Aluwani Nengovhela, Lilian Ogony, Ethinah Sibanda, Andrew Turner, and F.P.D. (Woody) Cotterill for assistance with sampling. Some of the molecular data used in the study was generated during S.W.M.'s PhD at Stellenbosch University under the supervision of Conrad Matthee. Funding was provided to P.J.T. by the National Research Foundation (NRF) and the University of Venda. Paula Jenkins from the Natural History Museum in London is thanked for providing cranial measurements of the holotype of *M. tenuis*. Fieldwork on Mount Gorongosa, Mozambique, was sponsored by the Gorongosa Restoration Project (funded by the Carr Foundation), with field assistance from A. Short, T. Castigo, and L. Oliviera. Additional support came from the Field Museum's Barbara Brown Fund and the Emerging Pathogens Project, funded by the Davee Foundation and the Dr Ralph and Mariam Falk Medical Research Trust. We also acknowledge the Museu de História Natural (Mozambique, Maputo) and curator Carlos Bento. W.T. Stanley (FMNH) loaned crucial specimens of *Myosorex*, providing geographic and taxonomic context.

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APPENDIX

DETAILS OF MUSEUM SPECIMENS USED IN MORPHOMETRIC AND MORPHOLOGICAL ANALYSES

Species	Country	Locality	Latitude	Longitude	Specimens
Myosorex cafer	South_Africa	Transkei, Port St Johns	–31.6333	29.55	DM 156–158
Myosorex cafer	South_Africa	Pirie	–32.77	27.25	DM 159
Myosorex cafer	South_Africa	Hillcrest	–29.77	30.75	DM 778
Myosorex cafer	South_Africa	Ngome	–27.8333	31.4	DM 1003
Myosorex cafer	South_Africa	Clearwater Farm	–31.033	30.1667	DM 1121
Myosorex cafer	South_Africa	Umtamvuna Reserve	–31.0667	30.1667	DM 1124
Myosorex cafer	South_Africa	Renishaw	–30.2667	30.7556	DM 1851
Myosorex varius	South_Africa	Karkloof	–29.3333	30.1833	TM 41824–26, 43838
Myosorex varius	South_Africa	Drakensberg, Cathedral_Peak	–28.9333	29.23333	TM 42213, 15
Myosorex varius	South_Africa	Dargle, Kilgobbin	–29.4667	30.05334	TM 42229
Myosorex varius	South_Africa	Hluhluwe Game Reserve	–28.0333	32.1167	TM 44400, 44401, 44383
Myosorex kihaulei	Tanzania	Rungwe Forest Reserve	–9.1805	33.65277	FMNH 163554–57, 59–63
Myosorex geata	Tanzania	Ukaguru Mountains, Mamiwa-Kisara Forest Reserve	–6.39583	35.93611	FMNH 166767–70, 197670–72
***Myosorex meesteri* sp. nov.**	Mozambique	Gorongosa National Park	–18.4593	34.05538	FMNH 214623, 24, 26, 28–30, 33–35, 40, 42, 43, 59, 71, 80, 85–87, 214840–42, 44, 60, 64
***Myosorex meesteri* sp. nov.**	Zimbabwe	Chingamwe Estates	–18.45	32.75	DM 4641–48, 51, 53, 55, 65, 78–80, 93, 5003, 5004
***Myosorex meesteri* sp. nov.**	Zimbabwe	Inyanga	–18.4333	32.78333	TM 10474, 75, 79, 82, 83, 85, 89, 92, 34720, 34749
***Myosorex meesteri* sp. nov.**	Zimbabwe	Sawerombi	–19.7667	32.81667	TM 13556
***Myosorex meesteri* sp. nov.**	Zimbabwe	Mount Selinda, Chirinda Forest	–20.4333	32.7	TM 34611, 13, 32, 55
Myosorex cf. *tenuis*	South Africa	Hanglip, Soutpansberg	–22.9833	29.8833	DM 7279–80, 7301, 2, 5, 8
Myosorex cf. *tenuis*	South Africa	Entabeni State Forest, Soutpansberg	–22.9833	30.25	TM 25843–46, 58–61, 68, 70, 71, 73, 30473–75
Myosorex cf. *tenuis*	South Africa	Woodbush Forest Reserve	–23.75	30.0167	TM 30079–87, 89–99, 30101, 30104–11
Myosorex cf. *tenuis*	South Africa	Buzzard Mount Retreat, Soutpansberg	–22.9997	29.7536	DM 13638–9
Myosorex cf. *tenuis*	South Africa	Lajuma Mountain Reserve, Soutpansberg	–23.0357	29.4276	DM 13455–6, 13512, 13559, 13629–31, 13633–4, 13643–44
Myosorex cf. *tenuis*	South Africa	Farm Middelfontein, Soutpansberg	–22.9754	29.9521	DM 13641–42