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Biogeography and diversity among montane populations of mouse shrew (Soricidae: *Myosorex*) in Tanzania

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We assess variation in morphological and molecular characters among three species of *Myosorex* (the mouse shrew) – *Myosorex geata*, *Myosorex kihaulei*, and *Myosorex zinki* – as a means to test previously proposed biogeographic hypotheses for Tanzanian 'sky islands' and systematic hypotheses for Tanzanian mouse shrews. We analyse 17 cranial and dental variables using multivariate statistics and perform phylogenetic and phylogeographic analyses on sequences of mitochondrial and nuclear DNA; samples are drawn from every known Tanzanian population of *Myosorex*. Morphometric and phylogenetic analyses reveal that *M. zinki* is distinct, but that currently isolated populations of *M. geata* and *M. kihaulei* are relatively similar to one another, and may not have been isolated over geological time scales. Analyses of molecular variance identify statistically significant, but limited, genetic variation within and between isolated populations of *M. geata* and *M. kihaulei*. Between two putative regional biogeographic boundaries, greater genetic variation is explained by grouping populations on either side of the Ruaha River than by grouping populations on either side of the Makambako Gap. Our results are in agreement with recent studies illustrating the close relationship between faunas of the Southern Highlands and southern Eastern Arc Mountains, diminishing the apparent importance of the Makambako Gap as a historical biogeographic barrier. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **100**, 669–680.

ADDITIONAL KEYWORDS: Eastern Arc Mountains – Makambako Gap – phylogeography – Ruaha River – Southern Highlands.

INTRODUCTION

Geological and climatic processes may alter the distribution and connectivity of habitats, and hence populations, leaving a signature on both morphological and genetic patterns of variation in modern, extant lineages. Deciphering these patterns can therefore lead to insights regarding the effects of abiotic processes on past populations. East African montane archipelagos represent a potentially useful system for understanding the effects of abiotic processes on forest-dependent biodiversity, because the distribution of forests is thought to have been highly dynamic through the Pliocene and Pleistocene, with forests restricted to montane areas during warm dry periods, but expanding to lower elevations during cool, wet periods (Lovett, 1993a).

The mountains of Tanzania are grouped by some workers into categories based primarily on geographic proximity and geologic origin. The Northern Highlands (including Kilimanjaro, Meru, and the Ngorongoro Crater) are volcanic, and were formed within the past million years (Griffiths, 1993). The Eastern Arc Mountains (EAM) is an ancient (*c.* 10–40 Mya) fault block system arranged in a north–south crescent from the Taita Hills of south-eastern Kenya to the Udzungwa Mountains in south-central Tanzania (Fig. 1; Lovett, 1985). South-west of the southern EAM, the Southern Highlands contain Mount

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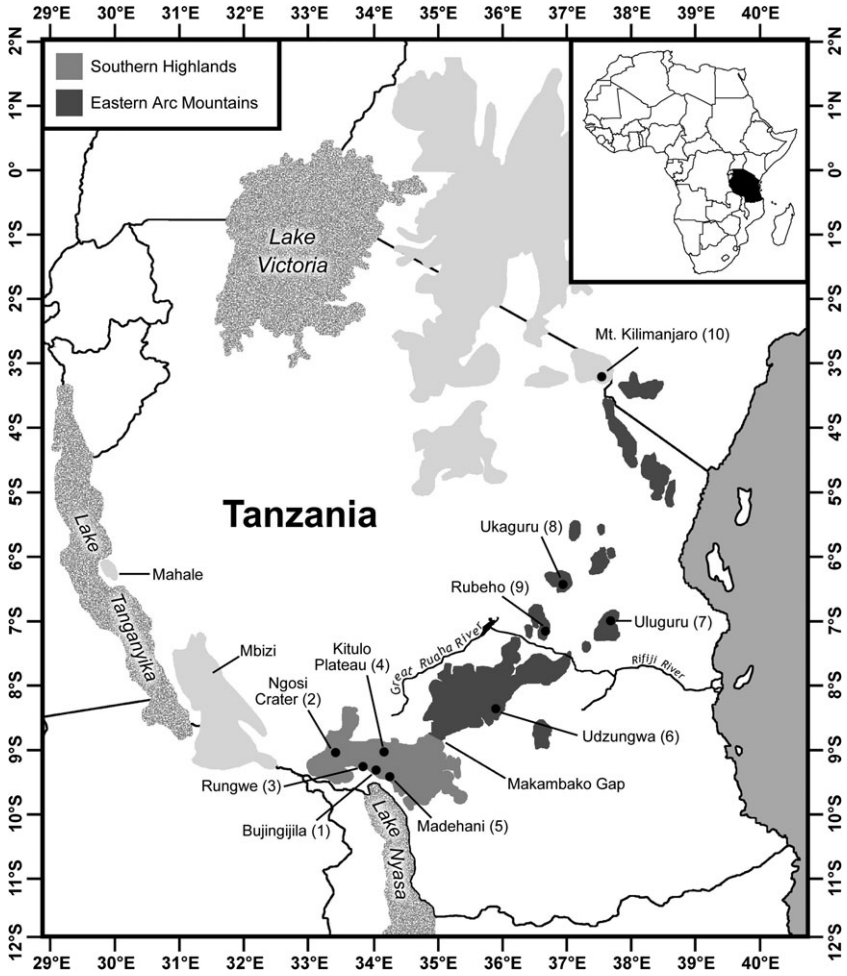

Figure 1. Mountainous regions of Tanzania. Areas above 1500 m a.s.l. are shaded. The Eastern Arc Mountains and Southern Highlands are differentiated. Populations sampled, and sample sizes for this study are indicated. See the Appendix for specific localities and sample sizes.

Rungwe and the Livingstone Mountains (Davenport *et al*., 2008), and are, in part, volcanic in origin (Harkin, 1960). Montane areas resulting from the geological forces that created the Albertine Rift are represented by the Mbizi Mountains on the Ufipa Plateau, and the Mahale Mountains on the western edge of the country.

Although some workers define biogeographic regions to include more than one of these montane clusters (e.g. the Tanganyika–Nyasa Mountain Group; Moreau, 1966), others have postulated that the geologic origins and climatic history of these montane regions led to the generation of distinct, biogeographically partitioned faunas (Lovett, 1985; Wasser & Lovett, 1993). One putative barrier, the Makambako Gap, which divides the EAM from the Southern Highlands, is often cited as a significant biogeographic disjuncture (Burgess *et al*., 2007; Fig. 1). Lovett (1985) first coined the term 'Makambako Gap' to distinguish the EAM from montane regions to the south-west, including the Southern Highlands. However, he presented no evidence of the Makambako Gap having had any biogeographic effect, and the distributions of some vertebrates suggest other potential influences are more prominent. For example, the shrew, *Sylvisorex howelli* Jenkins, 1984 is restricted to the central region of the archipelago, and is not known south of the Ruaha River, despite extensive surveys (Hutterer, 2005; Stanley & Olson, 2005).

Some scientists suggest that forests on these mountains, which are currently restricted to higher altitudes, were found at lower elevations historically, allowing biotic connections among mountains (Lovett, 1993a; Stanley, Rogers & Hutterer, 2005). However, this hypothesis has rarely been tested (but see Bowie *et al*., 2004), and little consideration has been given to the potential effects of large rivers on

the historic connections among montane regions. A few studies have used molecular information from vertebrates to test regional biogeographic scenarios (e.g. Bowie, 2003; Bowie *et al*., 2004; Blackburn & Measey, 2009), but we know of only one that examined small mammals, and that was constrained to relationships within the EAM (Stanley & Olson, 2005).

Herein, we use isolated populations of mouse shrews of the genus *Myosorex* Gray, 1838 to explore previously proposed biogeographic and systematic hypotheses. *Myosorex* is endemic to sub-Saharan Africa, with 15 species currently recognized (Hutterer, 2005; Kerbis Peterhans *et al*., 2008). Within Tanzania, the genus is represented by populations restricted to montane settings from the north-eastern to the south-western corners of the country (Stanley *et al*., 1998; W.T. Stanley, unpubl. data). Three named taxa are known from these populations: *Myosorex geata* (Allen & Loveridge, 1927) was originally described from the Uluguru Mountains, *Myosorex kihaulei* (Stanley & Hutterer, 2000) was described from the Udzungwa Mountains, and *Myosorex zinki* (Heim de Balsac & Lamotte, 1956) was described from Mount Kilimanjaro. Recent biotic surveys have discovered isolated populations of *Myosorex* in five additional montane areas, including Ukaguru, Rubeho, Livingstone, Mount Rungwe, and the Uporoto Mountains (specifically the Ngozi Crater). The Uluguru, Udzungwa, Ukaguru, and Rubeho mountains are part of the EAM (*sensu* Lovett, 1985), whereas Mount Rungwe and the Livingstone and Uporoto Mountains are part of the Southern Highlands (*sensu* Davenport *et al*., 2008). Our samples from the Livingstone Mountains include the forests near Madehani (an area that has been historically referenced as the Ukinga Mountains, named for the Ukinga people that live in the area) and the Kitulo Plateau. Unlike the forests found on each of the Eastern Arc mountains, the montane habitats of the Southern Highlands either have forest connections among them (Livingstone and Rungwe), or were only recently isolated from each other by habitat modification (Rungwe and Ngozi Crater; T. Davenport, unpubl. data). Thus, given the wide distribution of *Myosorex* across the mountains of Tanzania and its affinity for high-elevation forests, the genus represents a model system for testing the biogeographic significance of both the Makambako Gap and Ruaha River. Herein, we use specimens from montane areas of Tanzania to: (1) identify to species the newly discovered populations of *Myosorex*, (2) infer the phylogenetic/phylogeographic relationships among these populations, and (3) test previously proposed biogeographic hypotheses for montane organisms in Tanzania.

MATERIAL AND METHODS

Morphological analysis

Specimens of *Myosorex* were collected during faunal surveys of montane forests in Tanzania; methodological details of these surveys are presented in Stanley *et al*. (2005). Collection of specimens followed methods approved by the American Society of Mammalogists (Gannon *et al*., 2007). Standard external measurements (DeBlase & Martin, 1974) were taken by WTS from each specimen at the time of collection (Stanley & Hutterer, 2000).

WTS measured (with digital calipers calibrated to the nearest 0.01 mm) the following cranial and dental variables, which follow Dippenaar (1977), van Zyll de Jong & Kirkland (1989), and Carraway (1990): condylo-incisive length (CI), basal length (BL), post-palatal length (PPL), length of entire upper toothrow (UTRL), length of complex teeth in upper toothrow (i.e. the distance from the anterior edge of the fourth upper premolar to the posterior edge of the third upper molar: P4–M3), distance from anterior edge of first upper incisor to anterior edge of the fourth upper premolar, determined by subtracting P4–M3 from UTRL (I–C), least interorbital width (LIW), bimaxillary width (BW), nasal width (NW), greatest width of braincase (GW), height of the braincase (HBC; taken by placing the skull on a microscope slide, measuring from the bottom of the slide to the top of the braincase, and subtracting the thickness of the slide), post-glenoid width (PGW), width of third upper incisor (I3W), width of canine (CW), length of third upper molar (M3L), width of third upper molar (M3W), breadth of the mastoid plate (MAST), length of mandible including the incisor (MI), and length of lower toothrow (LTR). Only adult specimens, as judged by the complete fusion of the basioccipital and basisphenoid bones, and by fully erupted upper molars, were measured.

In all, WTS measured 96 skulls from ten allopatric populations, each restricted to isolated, moist montane forests (Appendix; Fig. 1). We tested for sexual dimorphism with one-way analyses of variance on the three populations with the largest sample size of both sexes [Ukaguru (three females, 12 males), Rungwe (four females, nine males), and Rubeho (four females, five males)] using both external and cranial dimensions. Standard descriptive statistics (mean, range, and standard deviation) were calculated for each population. One-way analyses of variance (effect = locality) were used to test for morphometric variation among populations, and discriminant function analyses of log-transformed craniodental variables were conducted to summarize multivariate patterns of variation. All morphometric analyses were conducted in Systat 10.

Molecular techniques

We amplified and sequenced fragments of the mitochondrial *NADH dehydrogenase subunit 2* (*ND2*) and nuclear *Apolipoprotein B* (*ApoB*) genes. Genomic DNA was isolated following the protocols described in Esselstyn *et al*. (2008). Methods of polymerase chain reaction (PCR) and sequencing follow Esselstyn, Timm & Brown (2009), and relied on the primers Met-1 and Trp-2 for *ND2* (Olson, Goodman & Yoder, 2004), and ApoBf and ApoBr for *ApoB* (Dubey *et al*., 2007). PCR products were sequenced in both directions to minimize errors in base calls. Fragments were assembled and edited using Sequencher 4.1.

Sequences were aligned manually in Se–Al v2.0a11 (Rambaut, 1996). No indels were identified and the alignments are unambiguous. All sequences were deposited in GenBank (GU473388–GU473584); the alignments and resulting trees are available on TreeBase (www.treebase.org; S2610).

Phylogenetic and phylogeographic analyses

We used Bayesian and likelihood methods to infer the phylogeny of Tanzanian *Myosorex*. Alignments were first reduced to a set of unique haplotypes. Appropriate models of sequence evolution were chosen using Akaike's information criterion (AIC), as implemented in MODELTEST 3.7 (Posada & Crandall, 1998). The closest available model with greater complexity was used in MrBayes 3.1 (Ronquist & Huelsenbeck, 2003) and RAxML v7.0 (Stamatakis, 2006). Bayesian analyses included four runs with four chains each and sampled the posterior for 4×10^6 generations. Trees and parameters were sampled every 2000 generations. We lowered the temperature to 0.05 because of a lack of swapping among states with the default temperature (0.2) in preliminary analyses. With the lower temperature setting, runs appeared to converge, based on our examination of trace plots of log-likelihoods and parameter estimates in Tracer (Rambaut & Drummond, 2007), and correlations of pairwise split frequencies in AWTY (Nylander *et al*., 2008). Bayesian analyses were conducted on *ND2* alone, and on a concatenated matrix of *ND2* and *ApoB* sequences. In the latter, each gene was modelled separately. We removed the first 50% of each run as burn-in, leaving 4000 trees (1000 per run) in the posterior distribution for each analysis. Effective sample sizes in each analysis, as estimated by Tracer, were $\geq$800 for all parameters. Likelihood analyses were conducted on the same matrices, but the combined analysis was not partitioned. Each likelihood analysis consisted of 200 searches for a best tree and 1000 bootstrap pseudoreplicates using the rapid hill-climbing algorithm of RAxML v7.0 (Stamatakis, 2006). We used *Crocidura monax* Thomas, 1910 as an outgroup in all analyses, and included specimens of *Suncus* Ehrenberg, 1832 and *Congosorex* Heim de Balsac & Lamotte, 1956 to aid proper rooting.

To test for effects of putative biogeographic barriers (Makambako Gap and Ruaha River), we implemented three-way analyses of molecular variance (AMOVAs). Because we found limited variation in the nuclear *ApoB* gene, we used only the mitochondrial locus for this analysis. AMOVAs were calculated in Arlequin 3.1 (Excoffier, Laval & Schneider, 2005) with 1000 permutations. Sequences were assigned to populations based on their collection locality (all samples within 10 km were assigned to the same population), and populations were grouped on either side of the putative barriers. As another way to address this question, we examined the posterior distribution of trees from Bayesian phylogenetic inferences for the presence of monophyletic groups on either side of the putative biogeographic barriers. We thus filtered the posterior distribution of trees from the combined and *ND2* analyses for consistency with constraint trees that had monophyletic groups on either side of the Ruaha River and Makambako Gap. Filters were implemented in PAUP*4.0b (Swofford, 2002). The proportion of trees in the posterior distribution consistent with the constraint tree is considered an estimate of the posterior probability that the hypothesis is true.

RESULTS

Morphological patterns

Males were significantly heavier than females in the Ukaguru sample ($F = 5.4$; $P < 0.05$; Table 1), but sexual dimorphism was not noted in any other external character. For cranial variables, the only apparent sexual dimorphism was in CI ($F = 6.4$; $P < 0.05$) and PPL ($F = 7.1$; $P < 0.05$) in the Rubeho sample, and M3L ($F = 5.9$; $P < 0.05$) in the Rungwe sample. No other population–dimension combinations were significantly dimorphic, and we note that if we apply a Bonferroni correction for multiple tests, no population X–dimension combinations show statistically significant dimorphism. Similarly, previous studies of *Myosorex* in Tanzania found no significant sexual dimorphism (Stanley & Hutterer, 2000; Stanley *et al*., 2003, 2005). Hence, we combined sexes in all subsequent morphometric analyses.

Myosorex zinki (Kilimanjaro) is significantly larger in total length, head and body length, hindfoot length, and weight, and its tail and ears are shorter than those of all other populations (Table 1). One-way analyses of variance of the other nine populations revealed significant variation among populations for all measurements. Among these nine populations, the

Table 1. External measurements of individuals of *Myosorex* from three species and ten populations in Tanzania (sexes combined)

	M. zinki	*M. geata*			*M. kihaulei*						
	Kilimanjaro ($n = 12$)	Uluguru ($n = 6$†)	Ukaguru ($n = 15$)	Rubeho ($n = 9$)	Udzungwa ($n = 10$)	Madehani ($n = 7$†)	Kitulo ($n = 10$)	Bujingijila ($n = 7$)	Rungwe ($n = 13$†)	Ngosi ($n = 7$)	F (locality)
TL	129.8 ± 5.3	113.2 ± 4.1	120.4 ± 4.0	125.8 ± 3.9	115.6 ± 5.1	125.0 ± 1.6	122.6 ± 4.4	123.4 ± 5.1	120.8 ± 4.2	124.3 ± 5.7	7.2***
	118–137	108–118	113–128	121–132	109–126	123–127	117–132	120–133	116–130	115–132	
HB	93.2 ± 3.9	72.1 ± 2.7	79.2 ± 3.4	79.0 ± 4.1	76.6 ± 3.7	80.2 ± 1.5	79.2 ± 4.1	81.0 ± 2.7	79.1 ± 3.5	81.1 ± 3.1	4.2**
	84–100	68–75	74–87	72–86	70–81	78–82	73–85	78–86	74–85	77–85	
Tail	36.0 ± 2.0	41.0 ± 1.1	41.4 ± 2.1	44.8 ± 2.0	40.4 ± 3.2	44.8 ± 2.2	43.4 ± 2.0	42.4 ± 2.6	41.8 ± 2.2	43.1 ± 3.4	3.5**
	33–40	40–43	38–45	41–47	36–46	42–48	40–47	40–47	38–45	36–47	
HF	16.2 ± 0.8	13.2 ± 1.0	13.6 ± 0.6	14.0 ± 0.5	13.1 ± 0.7	14.3 ± 1.1	14.2 ± 0.6	14.1 ± 1.1	14.1 ± 0.9	13.9 ± 0.4	2.8**
	15–18	12–14	13–15	13–15	12–14	13–16	13–15	12–15	13–16	13–14	
Ear	7.6 ± 0.9	7.2 ± 1.5	8.7 ± 0.9	8.7 ± 0.5	8.4 ± 0.7	8.9 ± 0.7	8.9 ± 0.6	9.4 ± 0.8	9.5 ± 0.5	9.3 ± 0.5	6.5***
	6–9	5–9	7–10	8–9	7–9	8–10	8–10	8–10	9–10	9–10	
WT	16.1 ± 1.8	9.2 ± 1.2	11.5 ± 1.7	10.5 ± 1.1	10.0 ± 1.4	9.2 ± 1.0	9.3 ± 0.9	11.8 ± 1.4	11.7 ± 0.9	10.3 ± 0.9	6.3***
	14.0–19.5	7.6–10.5	8.6–14	8.6–12	8–12	7.4–10	8–11	10–14	9.5–13	9.7–12	

Samples are listed from north-east to south-west. Means ± standard deviations and range are shown. F-values are from one-way ANOVA (effect = locality) analyses involving only *M. geata* and *M. kihaulei*. See text for definitions of morphometric variables.

†$N = 5$ for weight in Uluguru, $N = 5$ for TL and TV in Madehani, and $N = 12$ for head and body in Rungwe.

**$P \leq 0.01$; ***$P \leq 0.001$.

Uluguru and Udzungwa samples generally exhibited the smallest external dimensions, and the Rubeho samples exhibited the largest (Table 1).

Crania also varied significantly among geographic localities. *Myosorex zinki* was larger in nearly all cranial variables, but had the narrowest mastoid plate and a relatively small M3 (Table 2). Given the striking difference in both external and cranial measurements between *M. zinki* and all other samples, we excluded it from subsequent morphological analyses. Most F-values recovered from one-way ANOVAs for the remaining nine populations were significant ($P \leq 0.05$). The mastoid plate, height of braincase, and width of the canine exhibited the greatest heterogeneity. Only four of the nineteen characters examined (P4–M3, BW, LIW, and M3W) did not vary significantly among populations. In general, cranial features were smallest in the Udzungwa sample, and largest in the Rubeho Mountains (Table 2), similar to the pattern noted for external measurements.

Discriminant function analysis (excluding *M. zinki*) correctly classified $\geq 83\%$ of the specimens to their respective mountain localities (Table 3). The first two factors explained 48.4 and 17.1% of the variation. In general, there is striking overlap between the Uluguru and Ukaguru samples, less so for the members of the Southern Highlands, and the Rubeho sample is relatively distinct. The Udzungwa population overlaps populations from the Southern Highlands and Eastern Arc along CV1. A cluster analysis of Mahalanobis distances among population centroids groups Eastern Arc populations separately from Southern Highland populations (Fig. 2). Additional discriminant function analyses (excluding *M. zinki*) were used to classify specimens to their location relative to the Ruaha River and the Makambako Gap (north or south of each). The analyses correctly classified 100 and 94% of the mountains north and south of the Ruaha River, respectively, and 97 and 95% of those mountains north and south of the Makambako Gap, respectively (Table 3).

PHYLOGENETIC AND PHYLOGEOGRAPHIC PATTERNS

Final sequence alignments contained 574 (*ApoB*) and 1041 (*ND2*) nucleotides. Among 98 individuals of *Myosorex* in the *ND2* alignment, 55 unique haplotypes were identified; among 92 individuals in the *ApoB* alignment, 12 unique haplotypes were identified. Models of sequence evolution chosen by AIC were GTR + I + Γ for the combined data (used in likelihood analysis), K81uf + I + Γ for *ApoB* (HKY + I + Γ used for partitioned Bayesian analysis), and GTR + I + Γ for *ND2*.

Myosorex contains little genetic diversity relative to other montane groups in the region (e.g. the shrew

Table 2. Cranial measurements of individuals of *Myosorex* from ten mountains in Tanzania (sexes combined within populations)

	M. zinki	*M. geata*			*M. kihaulei*					
	Kilimanjaro	Uluguru	Ukaguru	Rubeho	Udzungwa	Madehani	Kitulo	Bujingijila	Rungwe	Ngosi
CI	22.84 ± 0.60 22.01–23.73 *N* = 11	20.88 ± 0.18 20.66–21.12 *N* = 6	20.76 ± 0.42 20.10–21.39 *N* = 15	20.94 ± 0.26 20.62–21.35 *N* = 9	20.23 ± 0.45 19.70–20.93 *N* = 10	20.57 ± 0.22 20.27–20.87 *N* = 7	20.83 ± 0.33 20.54–21.51 *N* = 10	20.58 ± 0.65 19.60–21.79 *N* = 7	20.54 ± 0.45 19.81–21.31 *N* = 13	20.90 ± 0.24 20.53–21.22 *N* = 7
BL	20.20 ± 0.58 19.24–21.04 *N* = 11	18.65 ± 0.23 18.36–18.91 *N* = 6	18.39 ± 0.36 17.63–18.88 *N* = 15	18.44 ± 0.31 17.98–18.87 *N* = 9	17.97 ± 0.42 17.22–18.49 *N* = 10	18.43 ± 0.20 18.07–18.68 *N* = 7	18.60 ± 0.23 18.36–19.03 *N* = 10	18.42 ± 0.67 17.42–19.38 *N* = 7	18.17 ± 0.42 17.33–18.82 *N* = 13	18.55 ± 0.28 18.08–18.90 *N* = 7
PPL	10.41 ± 0.34 9.74–10.87 *N* = 11	9.19 ± 0.11 9.02–9.34 *N* = 6	9.19 ± 0.24 8.71–9.54 *N* = 15	9.20 ± 0.20 8.87–9.47 *N* = 9	9.05 ± 0.18 8.77–9.32 *N* = 10	9.38 ± 0.22 9.00–9.60 *N* = 7	9.40 ± 0.11 9.26–9.60 *N* = 10	9.40 ± 0.40 8.80–9.99 *N* = 7	9.13 ± 0.26 8.64–9.56 *N* = 13	9.50 ± 0.18 9.13–9.65 *N* = 7
UTRL	9.42 ± 0.19 9.08–9.71 *N* = 12	9.07 ± 0.10 8.97–9.21 *N* = 6	8.87 ± 0.20 8.51–9.23 *N* = 15	8.92 ± 0.09 8.77–9.07 *N* = 9	8.60 ± 0.28 8.01–9.05 *N* = 10	8.78 ± 0.11 8.64–8.96 *N* = 7	8.77 ± 0.14 8.55–9.01 *N* = 10	8.68 ± 0.34 8.19–9.15 *N* = 7	8.64 ± 0.21 8.27–8.90 *N* = 13	8.76 ± 0.24 8.32–9.04 *N* = 7
P4–M3	5.35 ± 0.14 5.15–5.61 *N* = 11	5.38 ± 0.08 5.25–5.47 *N* = 6	5.27 ± 0.10 5.05–5.41 *N* = 13	5.30 ± 0.05 5.24–5.39 *N* = 9	5.21 ± 0.14 4.90–5.41 *N* = 9	5.26 ± 0.12 5.09–5.46 *N* = 7	5.23 ± 0.11 5.06–5.39 *N* = 10	5.21 ± 0.13 5.05–5.41 *N* = 7	5.19 ± 0.15 4.88–5.44 *N* = 13	5.23 ± 0.11 5.05–5.34 *N* = 7
I–C	4.07 ± 0.11 3.92–4.29 *N* = 11	3.69 ± 0.05 3.63–3.74 *N* = 6	3.58 ± 0.12 3.45–3.75 *N* = 13	3.62 ± 0.07 3.53–3.71 *N* = 9	3.40 ± 0.17 3.11–3.64 *N* = 9	3.52 ± 0.07 3.40–3.63 *N* = 7	3.54 ± 0.08 3.39–3.65 *N* = 10	3.47 ± 0.24 3.08–3.79 *N* = 7	3.45 ± 0.10 3.22–3.62 *N* = 13	3.52 ± 0.17 3.27–3.73 *N* = 7
LIW	4.80 ± 0.14 4.58–4.98 *N* = 11	4.39 ± 0.12 4.23–4.55 *N* = 6	4.39 ± 0.16 4.15–4.74 *N* = 15	4.33 ± 0.11 4.13–4.51 *N* = 9	4.25 ± 0.12 4.06–4.38 *N* = 10	4.36 ± 0.17 4.19–4.65 *N* = 7	4.44 ± 0.18 4.22–4.69 *N* = 10	4.38 ± 0.11 4.23–4.54 *N* = 7	4.27 ± 0.13 4.09–4.51 *N* = 13	4.43 ± 0.22 4.07–4.79 *N* = 7
BW	6.52 ± 0.13 6.30–6.77 *N* = 12	6.45 ± 0.07 6.38–6.56 *N* = 6	6.45 ± 0.15 6.14–6.75 *N* = 15	6.40 ± 0.14 6.16–6.55 *N* = 9	6.39 ± 0.10 6.25–6.52 *N* = 10	6.35 ± 0.10 6.20–6.48 *N* = 7	6.38 ± 0.21 6.08–6.66 *N* = 9	6.37 ± 0.16 6.19–6.61 *N* = 7	6.27 ± 0.16 5.93–6.51 *N* = 13	6.39 ± 0.23 6.04–6.60 *N* = 7
NW	2.27 ± 0.07 2.18–2.38 *N* = 12	1.99 ± 0.04 1.92–2.03 *N* = 6	2.12 ± 0.07 2.00–2.28 *N* = 15	2.01 ± 0.09 1.90–2.20 *N* = 9	2.01 ± 0.07 1.90–2.12 *N* = 10	2.00 ± 0.05 1.95–2.08 *N* = 7	2.00 ± 0.11 1.82–2.12 *N* = 10	2.02 ± 0.11 1.88–2.22 *N* = 7	1.95 ± 0.05 1.86–2.02 *N* = 13	2.05 ± 0.06 1.94–2.11 *N* = 7
GW	11.48 ± 0.27 11.13–12.02 *N* = 12	10.57 ± 0.10 10.42–10.67 *N* = 6	10.66 ± 0.17 10.34–10.90 *N* = 15	10.69 ± 0.23 10.38–11.03 *N* = 9	10.42 ± 0.25 9.84–10.68 *N* = 10	10.30 ± 0.12 10.14–10.48 *N* = 7	10.73 ± 0.29 10.38–11.08 *N* = 10	10.47 ± 0.36 9.92–10.88 *N* = 6	10.47 ± 0.23 10.08–10.89 *N* = 13	10.58 ± 0.24 10.30–11.00 *N* = 7
HBC	7.05 ± 0.18 6.69–7.41 *N* = 10	6.61 ± 0.14 6.34–6.75 *N* = 6	6.58 ± 0.17 6.25–6.77 *N* = 15	6.60 ± 0.18 6.32–6.87 *N* = 9	6.45 ± 0.15 6.27–6.80 *N* = 10	6.58 ± 0.14 6.34–6.76 *N* = 7	6.88 ± 0.22 6.61–7.25 *N* = 10	6.67 ± 0.18 6.40–6.88 *N* = 6	6.75 ± 0.08 6.62–6.86 *N* = 13	6.86 ± 0.24 6.53–7.21 *N* = 7
PGW	7.10 ± 0.13 6.69–7.41 *N* = 10	7.14 ± 0.20 6.90–7.46 *N* = 6	7.12 ± 0.15 6.83–7.30 *N* = 15	7.08 ± 0.12 6.89–7.24 *N* = 9	6.86 ± 0.20 6.41–7.10 *N* = 9	6.87 ± 0.19 6.62–7.11 *N* = 7	7.00 ± 0.20 6.68–7.23 *N* = 10	7.16 ± 0.22 6.88–7.52 *N* = 7	6.93 ± 0.16 6.62–7.19 *N* = 13	7.12 ± 0.18 6.95–7.41 *N* = 7
I3–W	0.56 ± 0.03 0.52–0.62 *N* = 12	0.55 ± 0.02 0.53–0.59 *N* = 6	0.54 ± 0.03 0.50–0.60 *N* = 15	0.52 ± 0.03 0.48–0.58 *N* = 9	0.52 ± 0.02 0.48–0.56 *N* = 10	0.52 ± 0.02 0.49–0.54 *N* = 7	0.50 ± 0.04 0.44–0.55 *N* = 10	0.49 ± 0.04 0.43–0.54 *N* = 7	0.47 ± 0.04 0.44–0.53 *N* = 13	0.51 ± 0.03 0.47–0.55 *N* = 7
C–W	0.65 ± 0.04 0.60–0.74 *N* = 12	0.73 ± 0.03 0.71–0.78 *N* = 6	0.71 ± 0.03 0.67–0.76 *N* = 15	0.68 ± 0.04 0.63–0.77 *N* = 9	0.71 ± 0.02 0.68–0.73 *N* = 10	0.69 ± 0.03 0.63–0.73 *N* = 7	0.69 ± 0.03 0.65–0.74 *N* = 10	0.66 ± 0.02 0.63–0.69 *N* = 7	0.65 ± 0.04 0.55–0.71 *N* = 13	0.69 ± 0.03 0.64–0.73 *N* = 7
M3–L	1.47 ± 0.06 1.39–1.57 *N* = 12	1.59 ± 0.05 1.54–1.65 *N* = 6	1.53 ± 0.06 1.42–1.64 *N* = 15	1.46 ± 0.06 1.36–1.55 *N* = 9	1.57 ± 0.04 1.50–1.64 *N* = 10	1.52 ± 0.09 1.38–1.66 *N* = 7	1.50 ± 0.08 1.39–1.67 *N* = 10	1.52 ± 0.07 1.40–1.64 *N* = 7	1.52 ± 0.05 1.38–1.57 *N* = 13	1.54 ± 0.10 1.47–1.74 *N* = 7
M3–W	0.85 ± 0.04 0.78–0.90 *N* = 12	0.92 ± 0.05 0.87–1.00 *N* = 6	0.87 ± 0.04 0.80–0.93 *N* = 15	0.86 ± 0.06 0.76–0.96 *N* = 9	0.90 ± 0.03 0.83–0.93 *N* = 10	0.87 ± 0.06 0.79–0.96 *N* = 7	0.89 ± 0.04 0.83–0.94 *N* = 10	0.88 ± 0.05 0.80–0.96 *N* = 7	0.88 ± 0.06 0.80–0.97 *N* = 13	0.86 ± 0.07 0.80–1.00 *N* = 7
MP	1.35 ± 0.15 1.10–1.49 *N* = 10	1.83 ± 0.16 1.64–2.00 *N* = 6	1.74 ± 0.09 1.56–1.86 *N* = 15	1.76 ± 0.12 1.61–2.03 *N* = 9	1.57 ± 0.10 1.43–1.78 *N* = 9	1.67 ± 0.07 1.55–1.76 *N* = 7	1.65 ± 0.08 1.51–1.79 *N* = 10	1.49 ± 0.13 1.26–1.66 *N* = 7	1.52 ± 0.15 1.18–1.79 *N* = 13	1.51 ± 0.08 1.41–1.63 *N* = 7
M&I	14.09 ± 0.36 13.43–14.62 *N* = 12	13.02 ± 0.07 12.94–13.14 *N* = 6	12.95 ± 0.30 12.38–13.40 *N* = 15	12.96 ± 0.21 12.59–13.25 *N* = 9	12.54 ± 0.22 12.18–12.83 *N* = 10	12.73 ± 0.11 12.57–12.88 *N* = 7	12.85 ± 0.24 12.49–13.20 *N* = 10	12.84 ± 0.44 12.11–13.33 *N* = 7	12.66 ± 0.33 12.05–13.21 *N* = 13	12.90 ± 0.30 12.39–13.23 *N* = 7
LTR	8.59 ± 0.19 8.30–8.86 *N* = 12	8.20 ± 0.09 8.10–8.32 *N* = 6	8.08 ± 0.18 7.78–8.42 *N* = 15	8.13 ± 0.09 7.95–8.21 *N* = 9	7.85 ± 0.25 7.33–8.30 *N* = 10	8.02 ± 0.08 7.91–8.16 *N* = 7	8.01 ± 0.14 7.84–8.21 *N* = 10	7.90 ± 0.26 7.50–8.23 *N* = 7	7.93 ± 0.18 7.53–8.13 *N* = 12	8.03 ± 0.21 7.66–8.27 *N* = 7

Mean ± standard deviation, range and sample size are shown. See text for character definitions.

Table 3. Results of discriminant function analysis performed on 77 crania representing nine populations of *Myosorex* across Tanzania. Sample size (*N*) and percentage of sample that was accurately classified to their respective population are shown

Population	*N*	% correctly classified
Uluguru	6	83
Ukaguru	13	100
Rubeho	9	100
Udzungwa	8	88
Madehani	7	100
Kitulo	9	100
Bujingijila	6	83
Rungwe	12	83
Ngosi	7	100
Mountains north of river	28	100
Mountains south of river	49	94
Mountains north of Gap	36	97
Mountains south of Gap	41	95

Table 4. Mean uncorrected *p*-distances within and between species of *Myosorex*

Comparison	*ND2*	*ApoB*
Within *M. zinki*	0.0006	0.0000
Within *M. geata*	0.0010	0.0016
Within *M. kihaulei*	0.0150	0.0027
Between *M. zinki* and *M. geata*	0.1314	0.0065
Between *M. zinki* and *M. kihaulei*	0.1329	0.0066
Between *M. geata* and *M. kihaulei*	0.0247	0.0029

Sylvisorex howelli; Stanley & Olson, 2005, the frog *Arthroleptis xenodactyloides* Hewitt, 1933, Blackburn & Measey, 2009). Uncorrected mitochondrial *p*-distances are highest between *M. zinki* and other species (~0.13), but relatively little genetic divergence was noted among other populations (≤ 0.03; Table 4). Phylogenetic analyses of the combined data and mitochondrial sequences demonstrate that *M. zinki* is distinct from all other populations, but the divergences among populations from the EAM and Southern Highlands are fairly shallow (Fig. 3). Individuals from the neighbouring mountains of Rubeho, Ukaguru, and Uluguru formed a monophyletic group in analyses of mitochondrial and combined sequence data, but node support for this clade was weak (Fig. 3). In general, most populations were not inferred to have monophyletic gene trees. Two exceptions are provided by populations from the Uporoto and Uluguru Mountains, both of which were inferred to be monophyletic in all analyses.

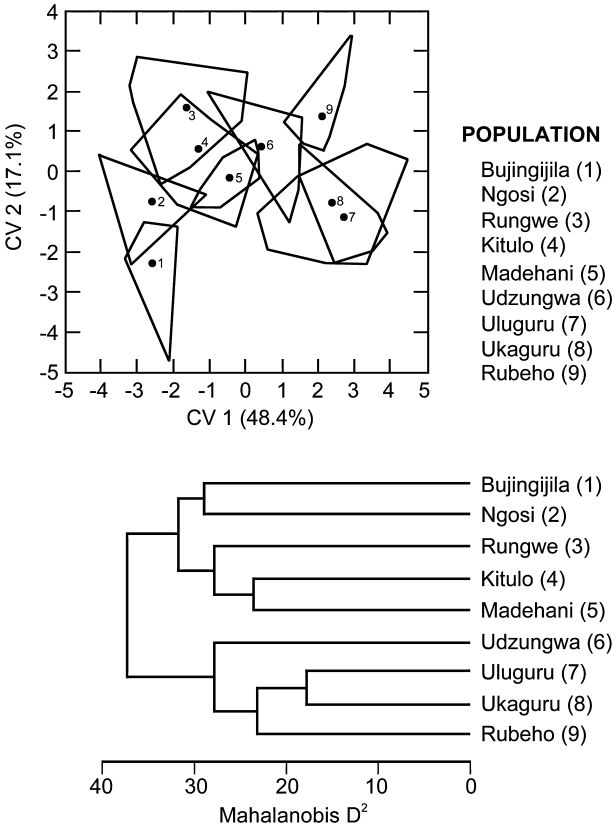

Figure 2. Results of discriminant function analysis of 19 log-transformed cranial and dental variables recorded from 84 adult specimens from nine populations of *Myosorex* [specimens from Mount Kilimanjaro (*Myosorex zinki*) were excluded]. Upper panel shows the projection of scores on the first two canonical variates. Polygons outline the dispersion of specimen scores around population centroids (numbered circles). Lower panel shows unweighted pair group method with arithmetic mean (UPGMA) clustering of Mahalanobis' distances among the nine population centroids of *Myosorex*. Specimens from the Eastern Arc Mountains cluster independently of those from the Southern Highlands (see Figure 1 for localities). Locality names used here are defined in Figure 1.

AMOVAs reveal statistically significant genetic variation within and between populations. In addition, they determine that between the two putative biogeographic barriers, the Ruaha River contains more explanatory power than the Makambako Gap (Fig. 4). Between-group variation was statistically significant at 38% ($P = 0.017$) for the Ruaha River, but only 21% ($P = 0.077$) for the Makambako Gap. The posterior distributions of trees contained no replicates with clades on each side of the Makambako Gap, but a few trees were consistent with the Ruaha River being a barrier, with posterior probabilities of 0.0685 and 0.0613 in the combined and *ND2* data sets, respectively.

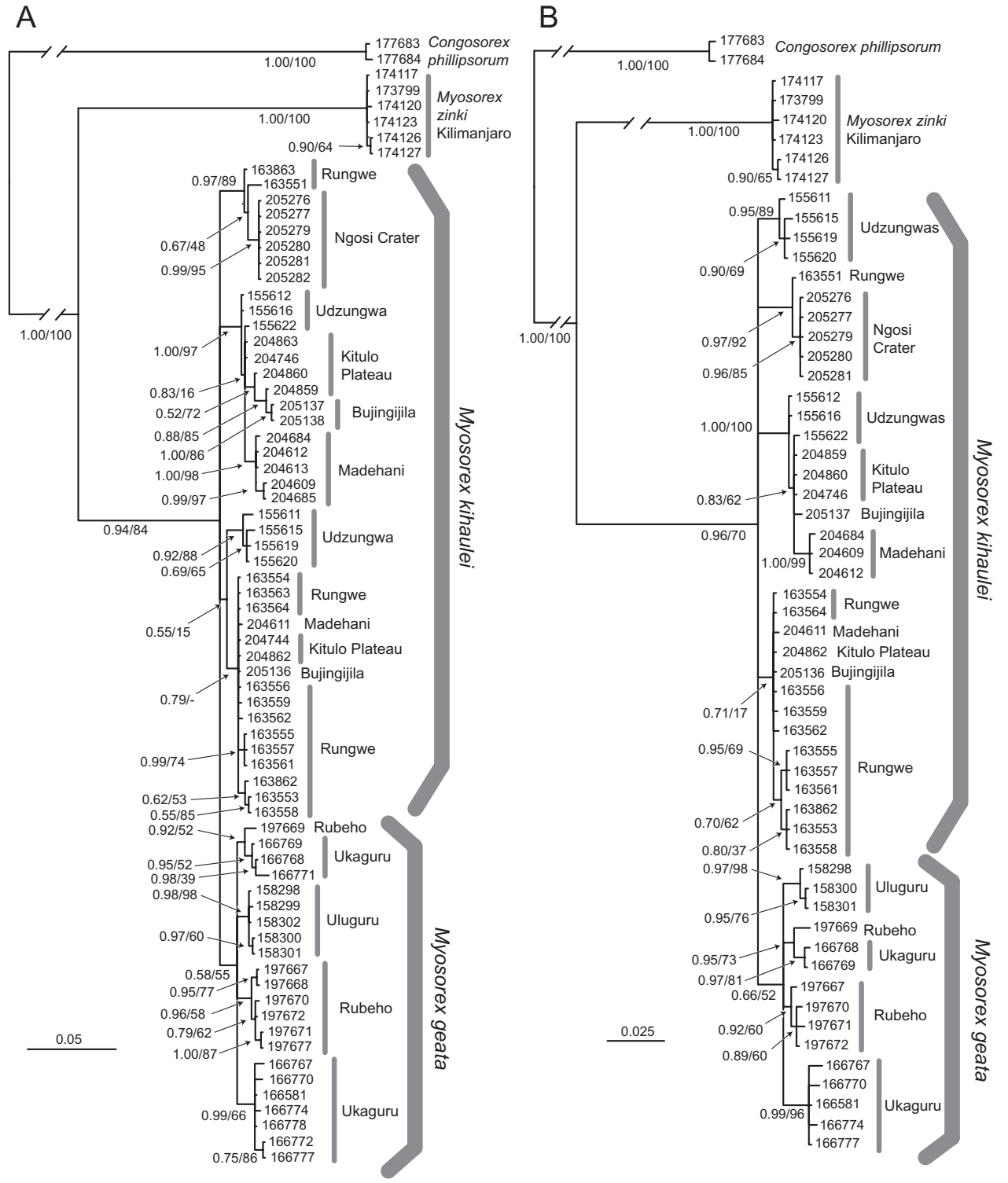

Figure 3. Bayesian majority rule consensus trees for Tanzanian *Myosorex*. A, results of a combined analysis of mitochondrial and nuclear DNA sequence data. B, results of an analysis restricted to mitochondrial data. Bayesian posterior probabilities are followed by maximum likelihood bootstrap support at the nodes. Terminal branches are labelled with Field Museum catalogue numbers, collection localities, and taxonomic identities. Outgroups (*Crocidura monax* and *Suncus lixus*) have been removed and branches broken by hash marks have been shortened for ease of presentation. The locality names used here are defined in Figure 1.

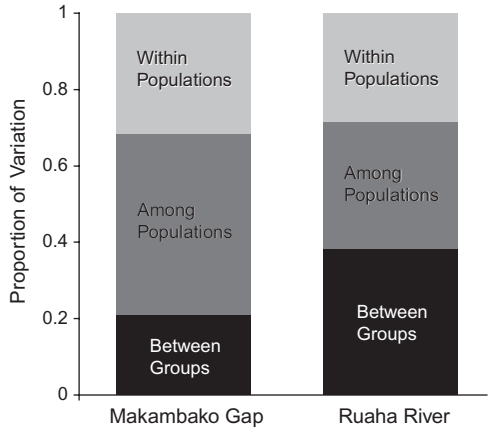

Figure 4. Analyses of molecular variance grouping populations of *Myosorex* on either side of the Makambako Gap and Ruaha River show that the latter has greater ability to explain variation in mitochondrial DNA sequences. Individuals from all known Tanzanian localities south of Mount Kilimanjaro were included. All levels of the analyses of molecular variance (AMOVAs), except the between-group category in the Makambako analysis, were statistically significant, with P-values < 0.05.

DISCUSSION

Among populations of *Myosorex* in Tanzania, *M. zinki* on Mount Kilimanjaro is the most distinctive, from both a morphological and molecular perspective. These results confirm that *M. zinki* occurs only on Mount Kilimanjaro. Variation among other populations is limited, and much less than that noted in other montane-restricted vertebrates in the region, including rodents (*Hylomyscus*, Carleton & Stanley, 2005), sunbirds (*Nectarinia*, Bowie *et al*., 2004), snakes (*Crotaphopeltis*, Gravlund, 2002), and other shrews (*Sylvisorex*, Stanley & Olson, 2005).

Our analyses of morphological and molecular data weakly support the distinction between *M. kihaulei* and *M. geata*. Whereas the Udzungwa sample (including the holotype of *M. kihaulei*) shows an affiliation with *M. geata* in morphometric analyses, there is a weak genetic affinity of the Udzungwa population with other shrews from the Southern Highlands. We therefore recommend that populations north and east of the Ruaha River (in the Ukaguru, Uluguru, and Rubeho mountains) be recognized as *M. geata*, and those south and west of the river (in the Udzungwa Mountains and Southern Highlands) be recognized as *M. kihaulei*. However, the contradictory results depicted for the relationship of the Udzungwa sample and weak genetic differentiation revealed between *M. geata* and *M. kihaulei* warrant additional study and firmer taxonomic resolution. *Myosorex geata*, as we define it here, was inferred to be monophyletic in the phylogenetic analyses of *ND2* and the combined data, although clade support was limited. *Myosorex kihaulei* contains many haplotypes, all of which are inferred to be paraphyletic. However, considering the limited degree of divergence observed among populations from across Tanzania, we consider it likely that incomplete lineage sorting is obscuring the relationships among populations. Paraphyletic gene trees are expected in recently diverged species (Knowles & Carstens, 2007). On-going gene flow among these populations could generate the same pattern, and may be occurring among some populations in the Southern Highlands, but seems unlikely between Southern Highland and Udzungwa populations, given the wide expanses of drier habitats in lower altitudes that probably isolate current populations of these montane, forest-dwelling shrews.

The term 'Eastern Arc Mountains' (EAM) was coined by Lovett (1985), and refers to a group of ancient crystalline mountains in eastern Tanzania and south-eastern Kenya. The EAM is under the climatic influence of the Indian Ocean and exhibits remarkable levels of diversity and endemism. Lovett (1985) described the southern limit of this archipelago as the Mufindi escarpment, and cited the Makambako Gap as the dividing line between the EAM and mountains to the south. Others have agreed, treating the Makambako Gap as a biogeographically important entity (e.g. Burgess *et al*., 2007). As a result, many biodiversity studies have been restricted to the EAM (e.g. Newmark, 1998; Pócs, 1998; Stanley *et al*., 1998). Some have concluded that levels of endemism are higher in the EAM than in the 'Southern Rift' forests south-east of the Makambako Gap (Lovett, 1993b; Burgess *et al*., 2004a, b; Burgess *et al*., 2007). Our genetic results suggest that the Makambako Gap was of little significance in the historical biogeography of *Myosorex*, echoing conclusions of other recent studies of montane organisms. For example, Carleton & Stanley (2005) found little variation among populations on either side of the gap in a morphological assessment of the relationships among isolated populations of a murid rodent (*Hylomyscus arcimontensis*, Carleton & Stanley, 2005). Similarly, Stuart *et al*. (1993) conducted cluster analyses of avifaunas in Tanzania and Malawi, and found commonality among populations on the Nyika Plateau, Mount Rungwe, and the southern Udzungwas, with no evidence of the Makambako Gap having a biogeographic influence. Based on surveys of spiders, Scharff (1993) concluded that although each of the Eastern Arc Mountains contains a unique suite of species, the EAM as a biogeographic entity is artificial.

Our results suggest that the Ruaha River had a greater, although perhaps recent, influence on the biogeographical history of populations of *Myosorex*

than the Makambako Gap. The geographic proximity of the Rubeho and Udzungwa mountain populations, separated by the Ruaha River, is noteworthy in light of both the morphological and molecular distinctness exhibited by these two populations, relative to others in the study. However, analyses of some other vertebrate groups, such as birds, do not support the Ruaha River as a biogeographic boundary (Stuart *et al*., 1993; Bowie *et al*., 2004).

The distribution of *Myosorex* across montane islands in Tanzania is enigmatic. There are no records of the genus in the areas of Tanzania influenced by the Albertine Rift (Mahale Mountains and the Mbizi forests, for example), despite extensive surveys (W.T. Stanley, unpubl. data). Interestingly, *Myosorex schalleri* Heim de Balsac, 1966 does occur in the Itombwe Mountains of the Albertine Rift system of the Democratic Republic of the Congo, west of Lake Tanganyika (Hutterer, 2005). *Myosorex zinki* occurs on Mount Kilimanjaro, but no myosoricine species have been recorded on neighbouring Mount Meru, again after similar sampling efforts (W.T. Stanley, unpubl. data). Potential explanations for the apparent absence of the genus on some mountains include extinction and a lack of colonization; determining which process is responsible and the associated causal circumstances would advance our understanding of the biogeography of the region.

The relatively low level of divergence in *ND2* sequences among isolated populations of *Myosorex* (uncorrected *p*–distance ≤ 0.03 within the *M. geata* + *M. kihaulei* clade; Table 4) contrasts with the results of Stanley & Olson (2005), in which populations of *Sylvisorex howelli*, endemic to the EAM, have much greater divergence in sequences of the same gene (0.011–0.089). Given that *Myosorex* and *Sylvisorex* probably have similar generation times, effective population sizes, metabolic rates, and other features that may affect substitution rates, it seems reasonable to assume that the observed differences in the extent of divergence among populations in the EAM represent real differences in the timing of isolation. We therefore suggest that past genetic exchange among currently allopatric populations of *Myosorex* in the EAM and Southern Highlands was more recent than among populations of *Sylvisorex howelli* in the EAM. Future research on the relationships among other montane, forest-dwelling organisms may illuminate factors responsible for the variation in patterns observed in these recent studies.

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REFERENCES

Allen GM, Loveridge A. 1927. Mammals from the Uluguru and Usambara mountains, Tanganyika territory. *Proceedings of the Boston Society of Natural History* **38:** 413–441.

Blackburn DC, Measey GJ. 2009. Dispersal to or from an African biodiversity hotspot? *Molecular Ecology* **18:** 1904–1915.

Bowie RCK. 2003. Birds, molecules, and evolutionary patterns among Africa's Islands in the sky. Ph.D. thesis, University of Cape Town, South Africa.

Bowie RCK, Fjeldså J, Hackett SJ, Crowe TM. 2004. Systematics and biogeography of the double–collared sunbirds of the Eastern Arc Mountains, Tanzania. *Auk* **121:** 660–681.

Burgess ND, Butynski TM, Cordeiro NJ, Doggart NH, Fjeldså J, Howell KM, Kilahama FB, Loader SP, Lovett JC, Mbilinyi B, Menegon M, Moyer DC, Nashanda E, Perkin A, Rovero F, Stanley WT, Stuart SN. 2007. The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation* **134:** 209–231.

Burgess ND, D'Amico Hales J, Underwood E, Dinerstein E, Olson D, Itoua Il, Schipper J, Ricketts T, Newman K. 2004b. *Terrestrial ecoregions of Africa and Madagascar: A continental assessment*. Washington, DC: Island Press.

Burgess ND, Lovett JC, Rodgers A, Kilahama FB, Nashanda E, Davenport TRB, Butynski TM. 2004a. Eastern Arc Mountains and Southern Rift. In: Mittermeier RA, Robles–Gil P, Hoffmann M, Pilgrim JD, Brooks TM, Mittermeier CG, Lamoreux JL, Fonseca GAB, eds. *Hotspots revisited: earth's biologically richest and most endangered ecoregions*, 2nd edn. Mexico: Cemex, 244–255.

Carleton MD, Stanley WT. 2005. Review of the *Hylomyscus denniae* complex (Rodentia: Muridae) in Tanzania, with description of a new species. *Proceedings of the Biological Society of Washington* **118:** 619–646.

Carraway LN. 1990. A morphologic and morphometric analysis of the '*Sorex vagrans* species complex' in the Pacific coast region. *Special Publications of the Museum of Texas Tech University* **32:** 1–76.

Davenport TRB, De Luca DW, Jones T, Mpunga NE, Machaga SJ, Kitegile A, Picton Phillipps G. 2008. The Critically Endangered kipunji *Rungwecebus kipunji* of southern Tanzania: first census and assessments of distribution and conservation status. *Oryx* **42:** 352–359.

DeBlase AF, Martin RE. 1974. *A manual of mammalogy with keys to the families of the world*. Dubuque: W. C. Brown.

Dippenaar NJ. 1977. Variation in *Crocidura mariquensis* (A. Smith, 1844) in southern Africa, Part 1 (Mammalia: Soricidae). *Annals of the Transvaal Museum* **30:** 163–206.

Dubey S, Salamin N, Ohdachi SD, Barrière P, Vogel P. 2007. Molecular phylogenetics of shrews (Mammalia: Soricidae) reveal timing of transcontinental colonizations. *Molecular Phylogenetics and Evolution* **44:** 126–137.

Esselstyn JA, Garcia HJD, Saulog MG, Heaney LR. 2008. A new species of *Desmalopex* (Pteropodidae) from the Philippines, with a phylogenetic analysis of the Pteropodini. *Journal of Mammalogy* **89:** 815–825.

Esselstyn JA, Timm RM, Brown RM. 2009. Do geological or climatic processes drive speciation in dynamic archipelagos? The tempo and mode of diversification in Southeast Asian shrews. *Evolution* **63:** 2595–2610.

Excoffier L, Laval G, Schneider S. 2005. Arlequin ver. 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* **1:** 47–50.

Gannon WL, Sykes RS, the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **88:** 809–823.

Gravlund P. 2002. Molecular phylogeny of Tornier's cat snake (*Crotaphopeltis tornieri*), endemic to East African mountain forests: biogeography, vicariance events and problematic species boundaries. *Journal of Zoological Systematics and Evolutionary Research* **40:** 46–56.

Griffiths CJ. 1993. The geological evolution of East Africa. In: Lovett JC, Wasser SK, eds. *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge: Cambridge University Press, 9–21.

Harkin DA. 1960. The Rungwe Volcanics at the Northern End of Lake Nyasa. Geological Survey of Tanganyika. Government Printer, Dar es Salaam. pp. 172.

Heim de Balsac H, Lamotte M. 1956. Evolution et phylogénie des Soricidés africains. *Mammalia* **20:** 140–167.

Hutterer R. 2005. Order Soricomorpha. In: Wilson DE, Reeder DM, eds. *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Baltimore: Johns Hopkins University Press, 220–311.

Kerbis Peterhans JC, Hutterer R, Kaliba P, Mazibuko L. 2008. First record of *Myosorex* (Mammalia: Soricidae) from Malawi with description as a new species, *Myosorex gnoskei*. *Journal of East African Natural History* **97:** 19–32.

Knowles LL, Carstens BC. 2007. Delimiting species without monophyletic gene trees. *Systematic Biology* **56:** 887–895.

Lovett JC. 1985. Moist forests of Tanzania. *Swara* **8:** 8–9.

Lovett JC. 1993a. Climatic history of eastern Africa. In: Lovett JC, Wasser SK, eds. *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge: Cambridge University Press, 23–29.

Lovett JC. 1993b. Eastern Arc moist forest flora. In: Lovett JC, Wasser SK, eds. *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge: Cambridge University Press, 33–55.

Moreau RE. 1966. *The bird faunas of Africa and its islands*. London: Academic Press.

Newmark WD. 1998. Forest area, fragmentation, and loss in the Eastern Arc Mountains: implications for the conservation of biological diversity. *Journal of East African Natural History* **87:** 29–36.

Nylander JAA, Wilgenbusch JC, Warren DL, Swofford DL. 2008. AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* **24:** 581–583.

Olson LE, Goodman SM, Yoder AD. 2004. Illumination of cryptic species boundaries in long–tailed shrew tenrecs (Mammalia: Tenrecidae; *Microgale*): New insights into geographic variation and distributional constraints. *Biological Journal of the Linnean Society* **83:** 1–22.

Pócs T. 1998. Bryophyte diversity along the Eastern Arc. *Journal of East African Natural History* **87:** 75–84.

Posada D, Crandall KA. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14:** 817–818.

Rambaut A. 1996. Se–Al: sequence alignment editor. Available at http://evolve.zoo.ox.ac.uk/. [Accessed October 10, 2006].

Rambaut A, Drummond AJ. 2007. Tracer v1.4. Available at http://beast.bio.ed.ac.uk/Tracer. [Accessed December 15, 2007].

Ronquist F, Huelsenbeck JP. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19:** 1572–1574.

Scharff N. 1993. The Linyphiid spider fauna (Araneae: Linyphiidae) of mountain forests in the Eastern Arc Mountains. In: Lovett JC, Wasser SK, eds. *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge: Cambridge University Press, 115–132.

Stamatakis A. 2006. RAxML–VI–HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22:** 2688–2690.

Stanley WT, Hutterer R. 2000. A new species of *Myosorex* Gray, 1832 (Mammalia: Soricidae) from the Eastern Arc Mountains, Tanzania. *Bonner Zoologische Beiträge* **49:** 19–29.

Stanley WT, Kihaule PM, Hutterer R, Howell KM. 1998. Small mammals of the Eastern Arc Mountains, Tanzania. *Journal of East African Natural History* **87:** 91–100.

Stanley WT, Kihaule PM, Rogers MA, Makwetta AJ. 2003. Elevational distribution and ecology of the endemic *Myosorex zinki* (Insectivora: Soricidae) along the southeastern slope of Mount Kilimanjaro, Tanzania. Tanzania Wildlife Research Institute. Proceedings of the third annual scientific conference, Arusha, Dec 3–5, 2002.

Stanley WT, Olson LE. 2005. Phylogeny, phylogeography, and geographic variation of *Sylvisorex howelli* (Family Sori-

cidae), an endemic shrew of the Eastern Arc Mountains, Tanzania. *Journal of Zoology* **266:** 341–354.

Stanley WT, Rogers MA, Hutterer R. 2005. A morphological assessment of *Myosorex zinki*, an endemic shrew on Mt Kilimanjaro. *Belgian Journal of Zoology* **135** (supplement)**:** 141–144.

Stuart SN, Jensen FP, Brøgger–Jensen S, Miller RI. 1993. The zoogeography of the montane forest avifaunas of eastern Tanzania. In: Lovett JC, Wasser SK, eds. *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge: Cambridge University Press, 203–228.

Swofford DL. 2002. *PAUP*. Phylogenetic analysis using parsimony (*and other methods)*, 4.0 edn. Sunderland, MA: Sinauer Associates.

van Zyll de Jong CG, Kirkland Jr GL. 1989. A morphometric analysis of the *Sorex cinereus* group in central and eastern North America. *Journal of Mammalogy* **70:** 110–122.

Wasser SK, Lovett JC. 1993. Introduction to the biogeography and ecology of the rain forests of eastern Africa. In: Lovett JC, Wasser SK, eds. *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge: Cambridge University Press, 3–7.

APPENDIX

Populations sampled for morphological and/or molecular analyses. Specimens included in the morphometric analyses are shown in bold; those used in molecular analyses are indicated with an asterisk; HSUVM, Humboldt State University Vertebrate Museum. All numbers not prefixed with a museum abbreviation represent specimens catalogued at the Field Museum of Natural History (FMNH).

Myosorex zinki: Mount Kilimanjaro, Kilimanjaro National Park, 173799*, **174117***–**174121***, 174122*, **174123***–**174128***.

Myosorex geata: Uluguru Mountains, Uluguru North Forest Reserve, **158298***–**158302***, **158487**; Ukaguru Mountains, Mamiwa–Kisara Forest Reserve **166767***–**166779***, **166581*, HSUVM 7584**; Rubeho Mountains, Mwofomero and Ilole forests, 197407*, **197667***, 197668*, **197669***–**197674***, **197676–197677***.

Myosorex kihaulei: Udzungwa Mountains, Udzungwa Scarp Forest Reserve, **155459***, **155611***, 155612*, **155457*–155458***, **155615*–155617***, **155618**, **155619***–**155620***; Madehani, Livingstone Mountains, **204684***–**204685***, **204609***–**204613***; Kitulo Plateau, Kitulo National Park, Numbe Forest **204856***–**204863***, **204744***–**204745***, 204746*; Mount Rungwe, Rungwe Forest Reserve, **163551***, 163552*–163554*, **163555***–**163557***, 163558*, **163559***–**163565***, **163862***–**163863***; Bujingijila corridor between Livingstone Mountains and Mount Rungwe, **205025**, 205026*, **205133–205134**, **205135***–**205138***; Uporoto Mountains, Ngozi Crater, 205242*, **205276***–**205282***.