Elevational Distribution and Taxonomy of Shrews and Rodents in the Mountains of Northern Tanzania

DISSERTATION

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William T. Stanley

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Dissertation reviewers:

Prof. Dr. Jörg Ganzhorn, University of Hamburg

Dr. Rainer Hutterer, Zoologisches Forschungsmuseum Alexander Koenig, Bonn

Abstract

The ecology of the small mammals living on the mountains of Tanzania is poorly known. In particular, the distribution of species along elevational gradients on these massifs requires detailed surveys to adequately understand the relationship between species diversity and their altitudinal distribution. Two mountains in particular are notable in the paucity of specimen-based surveys that have been undertaken: Mt. Kilimanjaro, the highest mountain of Africa, and Mt. Meru, Tanzania's second highest mountain. Here I document the distribution of shrews and rodents along an elevational gradient on the southeastern versant of these mountains. Five sites were sampled on each mountain, on Kilimanjaro between 2000 and 4000 m and on Meru between 1950 and 3600 m, using a systematic methodology of standard traps and pitfall lines, to inventory the shrews and rodents of the slopes. On Kilimanjaro, 16 species of small mammal were recorded, including six shrew and 10 rodent species, and the greatest diversity for both was found at 3000 m, the elevational midpoint of the transect. On Meru, 10 species of mammal were recorded, including two shrew (one of which is a new taxon) and eight rodent species, and the greatest diversity for both was found at 2300 m. All documented species were previously known from the two massifs. Two rodent genera that occur in the nearby Eastern Arc Mountains (*Hylomyscus* and *Beamys*), were not recorded on the two massifs. Species that are endemic to each mountain (*Myosorex zinki*-Kilimanjaro and *Lophuromys verhageni*-Meru) are widespread across the elevational gradient, and only absent from the lowest site on each gradient. As in other faunal surveys on other mountains of Tanzania using similar methodologies, rainfall influenced the sample success of shrews, but not rodents.

Mt. Kilimanjaro is the type locality for *Crocidura monax* Thomas, a crocidurine shrew for which the taxonomy and detailed distribution has been debated since its description. While some workers maintain that it is restricted to Kilimanjaro, others have suggested it occurs on neighboring montane islands. I assess morphological variation among isolated montane populations of *C. monax* from Tanzania that have been referred to *C. monax*. The montane sites used in this analysis are from two geologically distinct archipelagos (Northern Highlands and the Eastern Arc Mountains) and are a significant component of the Eastern Afromontane Biodiversity Hotspot. Multivariate analyses of morphometric traits suggest two undescribed shrews previously considered *C. monax* occur on these mountains, one on Ngorongoro and another shared by four Eastern Arc Mountains (Rubeho, Ukaguru, Uluguru, and Udzungwa). Similar cranial morphology indicates that *C. monax* is restricted to Mt. Kilimanjaro and North Pare, while *C. tansaniana* is found on the East and West Usambaras, and *C. usambarae* occurs on both the South Pares and the West Usambaras.

Contents

SUMMARY

PUBLICATIONS & MANUSCRIPT

SUMMARY

Introduction

The mountains of Tanzania have fascinated the scientist and romanticist alike for over a century. Obvious and familiar montane icons include Mt. Kilimanjaro and Ngorongoro, which have featured prominently in both popular literature and detailed conservation analyses (Hemingway 1986, Grzimek and Grzimek 1960, Mwasaga 1991, Mduma et al. 1999). Whether a mountain for climbers to conquer, a crater rim for tourists to appreciate, or the type locality of numerous biota, these isolated massifs have been justly celebrated for decades.

The origin of these iconic geographic features is the result of multiple geologic forces over time. The most prominent of these were the vertical movements, resulting in rift valleys and fault block mountains and volcanic eruptions. The mountains we see today resulting from these dynamic geological interactions are part of a broad archipelago of montane islands that stretches from the northeastern to the southwestern and western sectors of the country. They are categorized into four major groups, based primarily on specific geologic origins: the Northern Highlands (including Kilimanjaro, Ngorongoro, and Mt. Meru), which are the result of recent volcanoes; the Eastern Arc Mountains (EAM), which extend from southern Kenya (the Taita Hills) to southern Tanzania (Udzungwa Mountains) and are ancient fault block mountains; the Southern Highlands (including Mt. Rungwe, the Livingstone, and Poroto Mountains), which are the result of both uplift and volcanism; and the Mahale Mountains, which are part of the Albertine Rift (Griffiths 1993; Fig. 1).

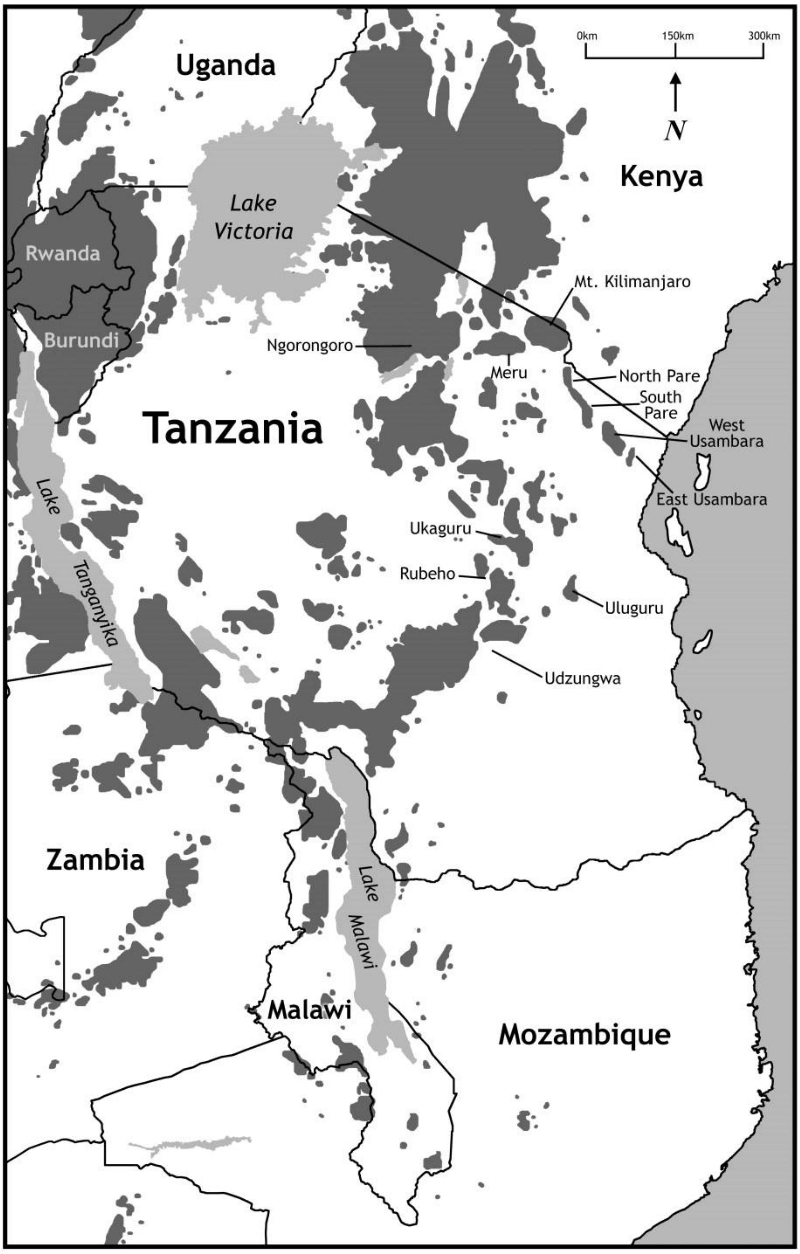

Figure 1. Map of mountainous regions of Tanzania and surrounding countries (adapted from Carleton and Stanley 2005). Areas above 1500 m are shaded. See Methods and Materials for details on specific localities and sample sizes.

The ages of the various fault block mountains that are scattered across Tanzania are a matter of debate. Quennel et al. (1956) suggest the Ulugurus and Usambara Mountains originated no earlier than 25 myr bp, whereas others suggest the Ulugurus may have originated as long as 250 myr bp (Sampson and Wright 1964; Griffiths 1993). However, there is no argument that the fault block mountains are far older than the volcanoes that represent some of the country's most iconic landmarks, and which are estimated to be no older than 1 my (Downie and Wilkinson 1972).

These mountains have been the focus of biological inquiry since the late 1800s and many have been surveyed for a variety of biota and/or are the type locality for numerous plants and animals. Biota investigated include bryophytes (e.g., Pócs 1975, 1985), angiosperms (e.g., Lovett et al. 1988, Lovett 1990, Iversen 1991, Cordeiro and Howe 2003), invertebrates (e.g., Griswold 1991, Hoffman 1993), reptiles and amphibians (e.g., Loveridge 1935, 1937, Menegon et al. 2008), birds (e.g., Stuart 1983, Newmark 1991, 2006, Cordeiro 1998, Lens et al. 2002), small mammals (e.g., Hutterer 1986, Carleton and Stanley 2005, Makundi et al. 2006, Stanley and Hutterer 2007), and larger mammals such as primates (Davenport et al. 2006, Perkin 2007, Rovero et al. 2009), carnivorans (De Luca and Mpunga 2005), and duikers (Rovero et al. 2005).

Because of the establishment of Amani in the East Usambara and Lushoto in the West Usambara Mountains as administrative centers for the German colonial government of Tanzania, the East and West Usambara Massifs are with the longest and most in-depth history of biological investigation (Engler 1893, Barbour and Loveridge 1928, Moreau 1935, Rodgers and Homewood 1982). However, other mountains have been the focus of significant biological analysis and discovery. Examples include the Uluguru Mountains (Allen and Loveridge 1927, Barbour and Loveridge 1928, Jenkins 1984), the Udzungwa Mountains (Homewood and Rodgers 1981, Lovett et al. 1988, Dinesen et al. 1994), and the Southern Highlands (Allen and Loveridge 1933, Gravlund 2002). Ironically, Kilimanjaro and Meru, while the most iconic massifs of the country, have received less attention from naturalists historically than other mountains in Tanzania (but see Heim de Balsac 1957, Demeter and Hutterer 1986, Grimshaw et al. 1995, Hemp 2006). Intensive studies have been conducted on Mt. Kilimanjaro recently (Helbig-Bonitz et al. 2013, Zancolli et al. 2014a, b, Rutten et al. 2015), but Mt. Meru has received much less attention.

Past research notwithstanding, small terrestrial mammals (shrews and rodents) represent one vertebrate group of Tanzanian montane ecosystems that is still poorly understood. This paucity of insight can be attributed to the secretive and, in many cases nocturnal behavior of these mammals, but also to the lack of detailed specimen-based inventories of individual massifs. Understanding the elevational distributions and taxonomy of the locally occurring mammal species, as well as their ecology and biogeography, is reliant on the data generated by such surveys. Such inventories have been conducted on various mountains over the past two decades, but only some of the results have been published (Stanley et al. 1996, 1998, 2005a,b, 2007, 2011a,b, Stanley and Hutterer 2007, Stanley and Goodman 2011). Specifically detailed elevational surveys of shrews and rodents are either sparse or lacking for Kilimanjaro and Meru, both massifs exhibiting the effects of habitat alteration and climate change (Lundgren and Lundgren 1972, Thompson et al. 2009). At the same time, the taxonomy of various mammal species occurring in montane habitats on these and nearby massifs is unresolved. One such taxon is *Crocidura monax*, originally described from specimens collected on Kilimanjaro (Thomas 1910), but purportedly occurring on neighboring mountains (Stanley et al. 2000, Hutterer 2005).

Aim of this study

Although surveys of the distribution along elevational gradients of birds (i.e. Stuart 1983, Stuart et al. 1987), and frogs (i.e. Poynton 2003, Ngalason and Mkonyi 2011, Zancolli et al. 2014a, b) have been conducted recently, there have been few detailed elevational transects sampling shrews and rodents on Tanzanian mountains. Two such studies include those of Stanley and Hutterer (2007) in the Udzungwa Mountains and Mulungu et al. (2008) on Mt. Kilimanjaro. There has been no detailed survey of the mammals of Mt. Meru, Tanzania’s second highest mountain.

The taxonomy and biogeography of Tanzania's montane mammals have received increasing attention in the recent past. For example, the taxonomy of, and relationships among two species of murine rodent genera found in the montane archipelago of the country, *Hylomyscus* and *Praomys* have been the subject of recent publications (Carleton and Stanley 2005, Carleton and Stanley 2012, Bryja et al. 2014). Montane dwelling soricomorph shrews occurring in Tanzania also have received attention from taxonomic and biogeographic studies in recent past. The endemic *Sylvisorex howelli* was described by Jenkins (1984) and the phylogeography was analyzed by Stanley and Olson (2005), a new species of *Congosorex* was described by Stanley et al. (2005b), and Stanley and Esselstyn (2010) assessed the biogeographic and taxonomic relationships of *Myosorex* within Tanzania. The genus *Crocidura* occurring in Tanzania has also received attention historically (Dippenaar 1980, Hutterer 1986). In particular, *C. monax* was first described from specimens collected on Mt. Kilimanjaro. Subsequently this species has been listed as restricted to Kilimanjaro (Burgess et al. 2000) or occurring on mountains within the Northern Highlands and the Eastern Arc (Hutterer 1986, Stanley et al. 2000).

A detailed understanding of the distribution and taxonomy of *Crocidura monax* has important implications for our understanding of the biogeography of the mountains of Tanzania, a significant aspect of the Eastern Afromontane Biodiversity Hotspot (sensu Mittermeier et al. 2004). The biogeographical relationship of vertebrates inhabiting the Northern Highlands and Eastern Arc varies depending on study and particular taxon of focus. For example, Stuart et al. (1993) found faunal affinities among bird taxa occurring on both the Northern Highlands and the northern Eastern Arc. Recent studies on the rodent *Praomys taitae* found affinities among populations spanning the two montane biogeographic entities (Carleton and Stanley 2012, Bryja et al. 2014). Alternatively, another rodent, *Hylomyscus arcimontensis* is broadly distributed along the Eastern Arc (and Southern Highlands) but has yet to be documented in the Northern Highlands (Carleton and Stanley 2005). Among shrews, *Crocidura monax* has been listed as occurring on not only Mt. Kilimanjaro, but also neighboring mountains, including various mountains within the Eastern Arc archipelago. However, no detailed studies of the relationships of the populations of *C. monax* found on these different mountains have been undertaken.

Kingdon (1971) hypothesized two routes that, during past climatic regimes, allowed connections between the montane habitats of central Africa and eastern Africa: one via the mountains of Uganda and Kenya, and the other via the massifs of southern Tanzania and up through the Eastern Arc. The Northern Highlands and the mountains of the northern Eastern Arc lie in the intersection of these two purported avenues.

In this study, I use specimens collected during previous surveys to evaluate the taxonomy of the "*Crocidura monax*" group using morphometric comparisons, and thereby elucidate the biogeographic relationships among populations of this purported species. Is *C. monax* restricted to Kilimanjaro alone (as suggested by Burgess *et al.* [2000]), or is it more broadly distributed per Hutterer (2005)? If the latter is true, are populations of this taxonomic complex within the Northern Highlands distinct from those of the Eastern Arc, or not? In addition, I compare the elevational distributions of shrews and rodents on various Tanzanian mountains. How do distributional and diversity patterns vary among different montane systems? The results of these analyses will elucidate the elevational distributions, community ecology and biogeographical relationships between the small mammal faunas of two geologically distinct sets of montane archipelagos and the intersection of two purported influential biogeographical connections to the montane environments of the Albertine Rift (Kingdon 1971).

Materials and Methods

Elevational Surveys

Field methodology

Small mammals were sampled using a variety of techniques by WTS, in collaboration with other biologists. Notable among these scientists are T. Davenport, S. M. Goodman, K. M. Howell, P. M. Kihaule, M. J. Munissi, W. D. Newmark, and M. Rogers. Most of the field methods involved traps of some form (which are detailed below), but the opportune collection of other specimens found dead or collected by hand, were also added to the analyses.

Pitfall lines

Pitfall lines were installed to capture shrews principally and, in most cases, were positioned on narrow (< 50 cm) trails cut for this purpose. Each pitfall line were comprised of 11 buckets, placed 5 m apart, and buried in the ground so that the top of the bucket was level with the ground. The 15 l buckets measured 26 cm high and with an upper and lower diameter of 26 cm and 24 cm, respectively. The bottoms of the buckets were perforated with small holes to allow water drainage. No bait was placed within the buckets. Each pitfall line had a 50 cm high black vertical plastic drift fence running over the center of each bucket. The objective of these passive traps is that mammals moving on the ground encounter the drift fence and follow it (in either direction of the fence) until they fall into a bucket. The pitfall lines were generally set along straight trails; however, rocks and logs occasionally forced deviations. Indeed, locations involving dead rotting logs were sought, to maximize the potential for shrew captures. This technique has been used with success in other mammalogical surveys (i.e. Stanley et al. 1996, Voss and Emmons 1996). Pitfall lines were examined twice per day, in the early morning and late afternoon.

Trap lines

Trap lines utilized three different kinds of traps: Museum Specials, 14 x 7 cm; Victor Rat Traps (referred to here as Victor Trap), 17.5 x 8.5 cm; and medium-sized

Sherman Traps, 23 x 9.5 x 8 cm. The Museum Specials and Victor Traps were manufactured by Woodstream Corporation, Lititz, Pennsylvania; the Sherman Traps by H.B. Sherman Traps Inc., Tallahassee, Florida. Traps were set primarily for rodents and positioned in terrestrial or arboreal settings, along existing trails, and generally in a straight line. To maximize capture success, traps were set at sites considered likely to be frequented by small mammals, rather than at fixed distances or in a grid system. Consequently, distances between consecutive traps were not constant. Bait for each trap consisted of freshly fried coconut coated in peanut butter, and traps were rebaited each late afternoon. Additional details on this type of trapping technique are presented by Stanley et al. (1998). Trap lines were checked twice each day, in the early morning and mid-afternoon.

Measures of sampling effort and success

Not all traps or buckets were employed for equal amounts of time (some trap lines were set the first day of the survey, others were installed on a subsequent day), so I use the terms “trap night”, “bucket night” and “sample night” to quantify sampling effort. A “trap-night” refers to one trap in operation for a 24 hr period (0700 to 0700 hrs). A “bucket-night” denotes one pitfall bucket in operation for a 24 hr period (0700 to 0700 hrs). The term “sample-night” is used in discussion of overall sampling effort (including the number of trap-nights and bucket-nights). I refer to the success rate of each method as either “trap success” or “bucket success”, and calculate these values by dividing the number of individuals captured by the number of trap-nights or bucket-nights and multiplying by 100. In discussions involving the overall capture success, the term “sample success” refers to the success rate for pitfall and trap methodologies combined. This is calculated by dividing the number of individuals captured by the number of sampling-nights and multiplying by 100.

Systematics

I follow the taxonomy presented for shrews by Hutterer (2005) and for rodents by Carleton and Stanley (2005, 2012), Holden (2005), and Musser and Carleton (2005).

Study Sites

Kilimanjaro

Mt. Kilimanjaro, located in the northeastern section of Tanzania, reaches an elevation of 5895 m. The mountain is the conglomeration of three volcanoes (all extinct): Kibo (the highest, most prominent and familiar), Mawenzi (the second tallest peak of the mountain), and Shira (a plateau) (Sampson 1965). There are numerous paths that originate in the lowlands and run up the side of the mountain, many used by tourists to ascend the mountain (Hanby 1987). Two such routes that are on the southeastern (and wettest) slope are “Marangu” and “Mweka”. Between these two is the “Maua” path, which is currently closed to tourists, and is used by Kilimanjaro National Park (KINAPA) staff to access and service facilities within the park. Between 17 July and 31 August 2002, small mammals (shrews and rodents) were sampled along the Maua route at five different elevations, ranging from roughly 2000 to 4000 m (Fig. 2).

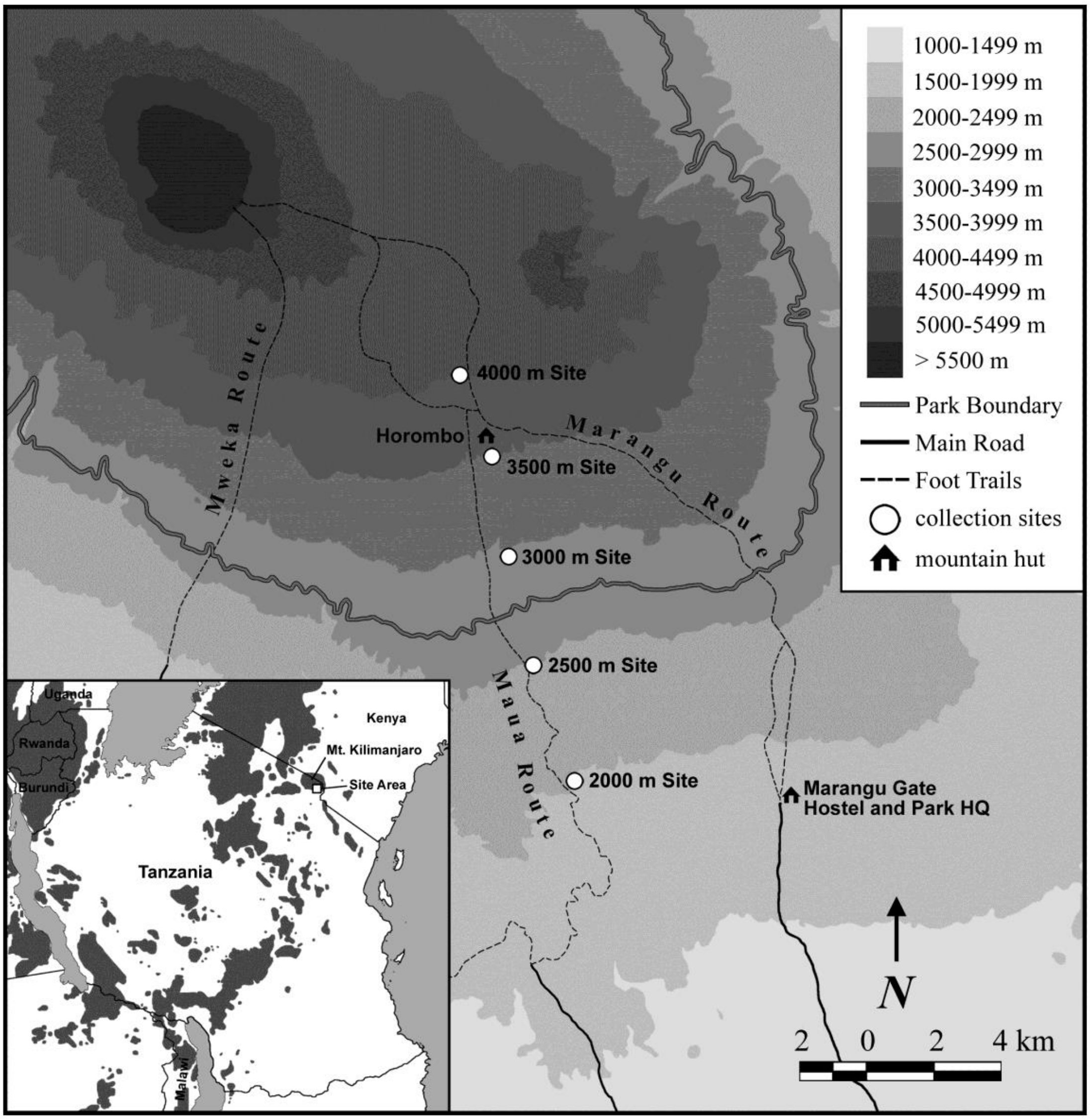

Figure 2. Map of Mt. Kilimanjaro (adapted from Stanley et al. 2014) showing routes, elevational contours, and study sites.

The specific localities, elevations, habitats (sensu Mwasaga 1991), and dates of sampling are presented below. The elevations listed for each site are centered at the associated camp and sampling efforts spanned roughly 100-200 m above and below the camp. For this reason, I labeled each camp at the closest 500 m interval (2043 = 2000 m; 2470 = 2500 m, etc.).

Site 1 - 2000 m. 4 km N, 1.5 km W Maua, 3°14.404' S, 37°27.502' E, 2043 m; lower montane forest; 23-30 August 2002.

Site 2 - 2500 m. 7 km N, 2.5 km W Maua, 3°12.459' S, 37°26.818' E, 2470 m; upper montane forest; 17-25 July 2002.

Site 3 - 3000 m. 10.5 km N, 3.5 km W Maua, 3°10.627' S, 37°26.413' E, 2897 m; ecotone between montane forest and ericaceous zone; 26 July-03 August 2002.

Site 4 - 3500 m. 13.5 km N, 4 km W Maua, 3°08.941' S, 37°26.133' E, 3477 m; ericaceous zone; 4-12 August 2002.

Site 5 - 4000 m. 16 km N, 4.5 km W Maua, 3°07.566' S, 37°25.600' E, 3995 m; ecotone between ericaceous and alpine zones; 13-21 August 2002.

Meru

Mt. Meru is in northeastern Tanzania and reaches an elevation of 4,566 m, and ranks ninth among the highest ten mountains of Africa. An active volcano (the mountain last erupted in 1910), Meru is the centerpiece of Arusha National Park. The mountain is a popular destination for hikers, and there is one path along the southeastern side from the lowlands towards the summit.. Between 16 July and 19 August 2009, we sampled small mammals (shrews and rodents) at five different elevations, ranging from roughly 1950 to 3600 m, along the climbing route on the southeastern slope of Mt. Meru (Fig. 3).

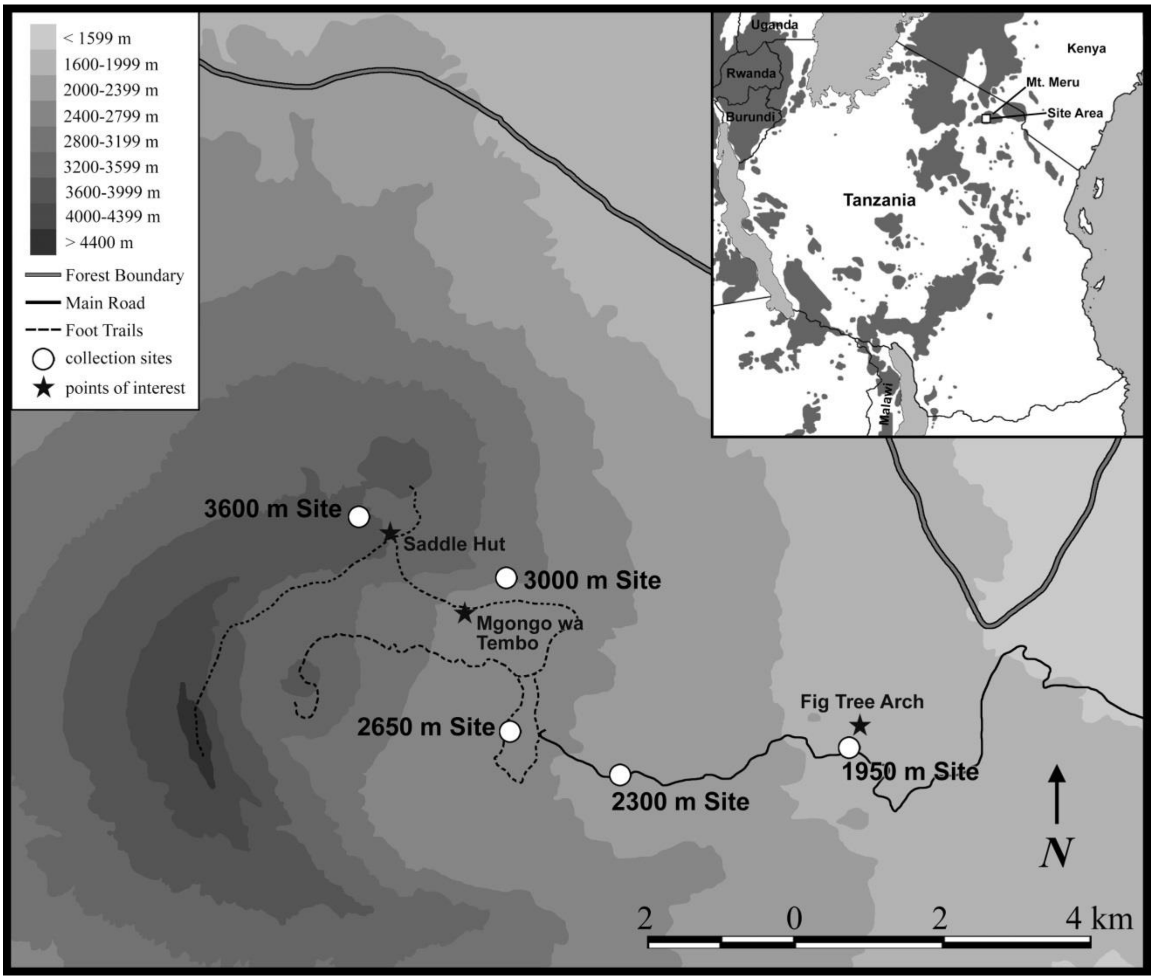

Figure 3. Map of Mt. Meru showing routes, elevational contours, and study sites.

All sampling sites on Mt. Meru were in Arusha National Park, Arumeru District, Arusha Region, Tanzania. The specific localities, elevations, habitats (sensu Demeter and Hutterer 1986), and dates of sampling are listed below. The elevations given for each site are centered at the associated camp and sampling efforts spanned roughly 100-200 m above and below the camp.

Site 1 - 1950 m. Fig Tree Arch, 3.24406° S, 36.82845° E, 1950 m; lower montane forest; 16-23 July 2009.

Site 2 - 2300 m. Site 2, 3.24725° S, 36.80066° E, 2300 m; upper montane forest; 23-30 July 2009.

Site 3 - 2650 m. Meru Crater, 3.242° S, 36.78736° E, 2650 m; ecotone between montane forest and ericaceous zone; 13-19 August 2009.

Site 4 - 3000 m. Mgongo wa Tembo, 3.2235° S, 36.78675° E, 3000 m; ericaceous zone (with some bamboo); 30 July-6 August 2009.

Site 5 - 3600 m. Near Saddle Hut, 3.21609° S, 36.76897° E, 3600 m; ecotone between ericaceous and alpine zones; 6-13 August 2009.

Morphometric study of *Crocidura monax*

Specimens used in the morphometric study of the *C. monax* group were collected in montane habitats on eleven isolated mountains in Tanzania, including (from north to south): Ngorongoro, Mt. Meru, Mt. Kilimanjaro, North Pare, South Pare, West Usambara, East Usambara, Ukaguru, Rubeho, Uluguru, and Udzungwa (Fig. 1; specific localities listed in Appendix 1; sample sizes given in Tables 10,11). Animals were handled following the protocol approved by the American Society of Mammalogists (Sikes et al. 2011). Voucher specimens were prepared as museum study skins with associated skulls and axial skeletons or embalmed in formalin. Tissues for molecular analyses were either flash frozen in liquid nitrogen, or stored in buffer (DMSO).

Standard museum measurements (DeBlase and Martin 1974) were taken by WTS, with the exception of specimens collected in the East and West Usambara and South Pare Mountains by S. M. Goodman. These measurements include: total length (TL; from the tip of the nose to the last caudal vertebrae), head and body length (HB; from the tip of the nose to the junction of the tail and the body), tail length (TV; from the junction of the tail and body to the last caudal vertebrae), hind foot length (HF; from the ankle to the tip of the longest claw; measurements by S. M. Goodman were from ankle to the tip of the longest digit), ear length (EAR; from the notch at the base of the ear to the longest point of the ear), and weight (W). All linear measurements were in millimeters and the weight was measured in grams.

Cranial measurements were taken from adult skulls with hand-held digital calipers by WTS. Adults are defined as animals with fully erupted upper molars and the suture between the basioccipital and basisphenoid bones fused. All voucher specimens are deposited in the Field Museum of Natural History (FMNH), Chicago, and the University of Dar es Salaam (UDSM), Dar es Salaam. FMNH catalogue numbers are presented for voucher specimens.

Statistical analyses

I calculated standard descriptive statistics (mean, range, standard deviation, and coefficient of variation of each character) for each population. I tested for sexual dimorphism in external and cranial variables within each montane population with one-way analyses of variances (ANOVA). To test for geographical variation in morphology, a one-way ANOVA (effect = mountain) was used to identify characters that differed significantly among populations.

Discriminant function analyses of log-transformed craniodental variables were conducted to assess multivariate patterns of variation. Variable loadings are presented as Pearson product-moment correlation coefficients of the derived components with the original cranial measurements. All statistical analyses were conducted using Systat (version 11).

Based on molecular analysis performed by J. Esselstyn and T. Giarla (Stanley et al. in press) that included samples from other *Crocidura* species, populations that were sampled in Tanzania form a mitochondrial clade with two monophyletic groups. Samples from Meru, Kilimanjaro, North Pare, South Pare, and West and East Usambara are monophyletic (but with little support) and sister to a topotypical sample of *C. montis* from Rwenzori. Ngorongoro, Rubeho, Ukaguru, Uluguru, and Udzungwa populations form a clade and are sister to samples of *C. fumosa* (but with little support) from Mt. Kenya (Stanley et al. in press).

Based on these results and the phenotypic dissimilarity of the samples from Meru, which have multiple bristles on the tail as opposed to the naked nature the tail of specimens from other mountains, I constrained subsequent discriminant function analyses of cranial morphometrics to two distinct assemblages: samples from 1) northern populations including Kilimanjaro, North Pare, South Pare, East Usambara, and West Usambara and 2) Ngorongoro, Rubeho, Ukaguru, Uluguru, and Udzungwa.

RESULTS

Elevational Distribution of shrews and rodents on Kilimanjaro and Meru

Over the course of the Kilimanjaro survey, 11,562 sample-nights (8361 trap-nights and 3201 bucket-nights) were accumulated and 612 small mammals, including 319 shrews representing six species, and 293 rodents representing 10 species were trapped (Tables 1, 2, 3). The sum quantity of captures (and overall sample success) at each elevational site ranged from 54 [2.4%] at 3500 m to 151 [6.8%] at 2000 m (Table 1). For shrews, the lowest values were observed at the 4000 m site (34 [1.5%]) and the highest values at the 3000 m site (88 [3.6%]; Tables 1, 2). Rodent captures exhibited the lowest (6 [0.3%]) and highest (87 [3.9%]) totals at the 3500 m and 4000 m sites, respectively (Tables 1, 3). The cumulative number of species trapped reached an asymptote at each site, with the exception of the 2500 m site (Fig. 4), where *Dendromus insignis* and *Otomys angoniensis* were captured on the last day of trapping.

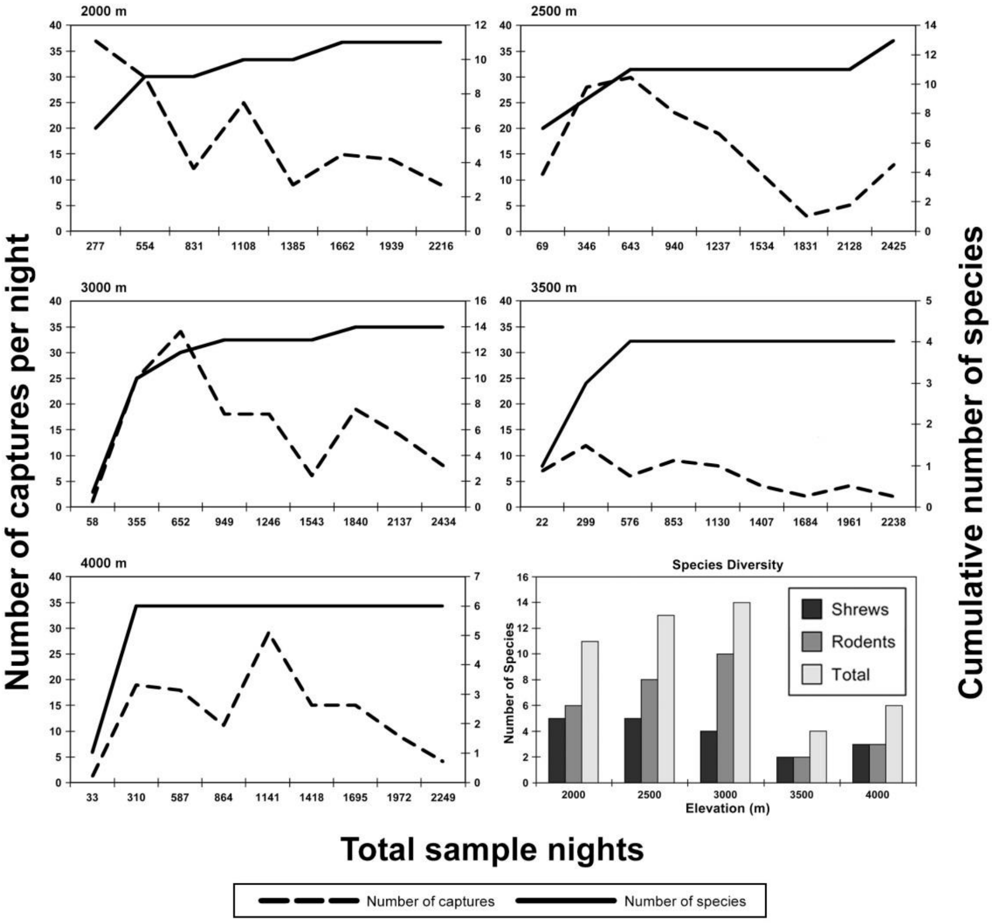

Figure 4. Species accumulation curves (for both pitfall and trap lines combined) for each site on Kilimanjaro. The dashed lines represent the number of captures each day; the solid lines represent the cumulative number of new species for the site observed each day. The graph at the lower right shows the number of specimens of shrew, rodent and mammal captured at each site.

Table 1. Trapping totals for rodents and shrews by trap technique on the southeastern slope of Mt. Kilimanjaro in July-August 2002.

Elevation	2000 m	2500 m	3000 m	3500 m	4000 m	Totals
BUCKETS						
# bucket-nights	616	649	649	638	649	3201
# individuals	84	75	86	51	33	329
(% bucket success)	(13.6)	(11.5)	(13.2)	(8.0)	(5.1)	(10.3)
# species	10	5	7	3	5	13
# shrews	68	74	79	48	30	299
(% bucket success)	(11.0)	(11.4)	(12.2)	(7.5)	(4.6)	(9.3)
# shrew species	5	4	4	2	3	6
# rodents	16	1	7	3	3	30
(% bucket success)	(2.6)	(0.1)	(1.1)	(0.5)	(0.5)	(0.9)
# rodent species	5	1	3	1	2	7
TRAPS						
# trap-nights	1600	1776	1785	1600	1600	8361
# individuals	67	68	57	3	88	283
(% trap success)	(4.2)	(3.8)	(3.2)	(0.2)	(5.5)	(3.4)
# species	5	9	11	2	4	12
# shrews	2	5	9	0	4	20
(% bucket success)	(0.1)	(0.3)	(0.5)		(0.2)	(0.2)
# shrew species	1	2	3	0	1	4
# rodents	65	63	48	3	84	263
(% trap success)	(4.1)	(3.5)	(2.7)	(0.2)	(5.2)	(3.1)
# rodent species	4	7	8	2	3	8
TOTAL						
# sample-nights	2216	2425	2434	2238	2249	11562
# individuals	151	143	143	54	121	612
(% sample success)	(6.8)	(5.9)	(5.9)	(2.4)	(5.4)	(5.3)
# species	11	13	14	4	6	16

Table 2. Elevational distribution of shrew species along the southeastern slope of Mt. Kilimanjaro in July-August 2002. Only specimens caught in traps or buckets are included in totals. [a] presence inferred from occurrence at lower and higher sites.

Elevation	2000 m	2500 m	3000 m	3500 m	4000 m	Totals
Species						
Crocidura allex	24	19	40	45	30	158
Crocidura hildegardeae	7	0	0	0	0	7
Crocidura monax	21	29	26	0	0	76
Crocidura olivieri	2	2	0	0	0	4
Myosorex zinki	0	3	4	3	3	13
Sylvisorex granti	16	26	18	0[a]	1	61
Total # individuals	70	79	88	48	34	319
Total # species	5	5	4	2+1[a]	3	6
Total # sample-nights	2216	2425	2434	2238	2249	11562
Sample success (%)	3.1	3.2	3.6	2.1	1.5	2.7
Total # caught in buckets	68	74	79	48	30	299
Total # bucket-nights	616	649	649	638	649	3201
Bucket success (%) for	11.0	11.4	12.2	7.5	4.6	9.3

Table 3. Elevational distribution of rodent species along the southeastern slope of Mt. Kilimanjaro in July-August 2002. Only specimens caught in traps or buckets are included in totals. [a] presence inferred from occurrence at lower and higher sites.

Elevation	2000 m	2500 m	3000 m	3500 m	4000 m	Totals
Species						
Otomys angoniensis	0	1	1	0	0	2
Otomys tropicalis	0	4	1	0 [a]	7	12
Dendromus insignis	4	1	5	5	21	36
Dendromus melanotis	5	1	4	0	0	10
Grammomys	3	6	6	0	0	15
Lophuromys aquilus	23	25	17	0	0	65
Praomys taitae	37	25	3	0	0	65
Rhabdomys dilectus	0	0	11	1	59	71
Graphiurus murinus	9	1	5	0	0	15
Tachyoryctes daemon	0	0	2	0	0	2
Total # individuals	81	64	55	6	87	293
Total # species	6	8	10	2+1 [a]	3	10
Total # sample-nights	2216	2425	2434	2238	2249	11562
Sample success (%)	3.6	2.6	2.2	0.3	3.9	2.5
Total # caught in traps	65	64	48	3	84	264
Total # trap-nights	1600	1776	1785	1600	1600	8361
Trap success (%)	4.1	3.6	2.7	0.2	5.2	3.1

During the Meru survey, we accumulated 7,111 sample-nights (4592 trap-nights and 2519 bucket-nights) and captured 751 small mammals, including 276 shrews representing two species, and 475 rodents representing eight species (Tables 4, 5, 6). At each elevational site, captures (and overall sample success) ranged from 49 [3.5%] at 3600 m to 257 [18.0%] at 2300 m (Table 4). For shrews, the lowest values were recorded at the 3600 m site (20 [1.4%]) and the highest values at the 3000 m site (87 [6.1%]; Table 5). For rodents, the lowest (29 [2.1%]) and highest (208 [14.6%]) values were observed at the 3600 m and 2300 m sites, respectively (Table 6). The cumulative number of species trapped at a site reached an asymptote at the 1950, 2650 and 3600 sites, but new species (i.e. not yet recorded at a site) were captured at the 2300 (where *Graphiurus murinus* was captured for the first time at that site on the last day of trapping) and 3000 (where *Mus triton* and *Otomys tropicalis* were both captured on the last day) sites. The species accumulations curves (Fig. 5) illustrate these results.

In both surveys, sampling success for shrews was significantly greater in buckets than in traps (X^2 = 695.2 (Kilimanjaro) and X^2 = 61.3 (Meru), P < 0.01 in both cases), and significantly more rodents were caught in traps than in buckets (X^2 = 44.8 (Kilimanjaro) and X^2 = 232.7 (Meru), P < 0.01), a pattern observed in past studies on small mammals of Tanzania (Stanley et al. 1996, 1998, Stanley and Hutterer 2007). Over the course of the two surveys, shrew species caught in traps included *Crocidura allex*, *C. monax*, *C. montis*, *C. olivieri*, and *Myosorex zinki* (weighing between 3.5-51.0 g). While most of the rodents caught in buckets were relatively small (i.e. *Dendromus insignis*; 7-20 g), both specimens of *Tachyoryctes daemon* (240-290 g) captured on Kilimanjaro were found in buckets.

Table 4. Trapping totals for rodents and shrews by trap technique on the southeastern slope of Mt. Meru in July-August 2009.

Elevation	1950 m	2300 m	2650 m	3000 m	3600 m	Totals
BUCKETS						
# bucket-nights	506	506	506	506	495	2519
# individuals	52	24	18	63	13	170
(% bucket success)	(10.3)	(4.7)	(3.6)	(12.3)	(2.6)	(6.7)
# species	3	3	3	4	3	5
# shrews	51	22	17	58	12	160
(% bucket success)	(10.1)	(4.3)	(3.4)	(11.3)	(2.4)	(6.3)
# shrew species	2	2	2	2	2	2
# rodents	1	2	1	5	1	10
(% bucket success)	(0.2)	(0.4)	(0.2)	(1.0)	(0.2)	(0.4)
# rodent species	1	1	1	2	1	3
TRAPS						
# trap-nights	920	920	920	920	912	4592
# individuals	115	233	104	93	36	581
(% trap success)	(12.5)	(25.5)	(11.3)	(9.3)	(3.9)	(12.6)
# species	5	6	8	9	6	9
# shrews	29	27	23	29	8	116
(% bucket success)	(3.2)	(2.9)	(2.5)	(2.8)	(0.9)	(2.5)
# shrew species	2	2	2	2	2	2
# rodents	86	206	81	64	28	465
(% trap success)	(9.3)	(22.6)	(8.8)	(6.5)	(3.1)	(10.1)
# rodent species	3	4	6	7	4	7
TOTAL						
# sample-nights	1426	1426	1426	1426	1407	7111
# individuals	167	257	122	156	49	751
(% sample success)	(11.7)	(18.0)	(8.6)	(10.9)	(3.5)	(10.5)
# species	5	6	9	10	6	10

Table 5. Elevational distribution of shrew species along the southeastern slope of Mt. Meru in July-August 2009. Only specimens caught in traps or buckets are included in totals.

Elevation	1950 m	2300 m	2650 m	3000 m	3600 m	Totals
Species						
Crocidura allex	31	31	18	36	16	132
Crocidura n. sp.	49	18	22	51	4	144
Total # individuals	80	49	40	87	20	276
Total # species	2	2	2	2	2	2
Total # sample-nights	1426	1426	1426	1426	1407	7111
Sample success (%)	5.6	3.4	2.8	6.1	1.4	3.9
Total # caught in buckets	51	22	17	58	12	160
Total # bucket-nights	506	506	506	506	495	2519
Bucket success (%) for	10.1	4.3	3.3	11.5	2.4	6.3

Table 6. Elevational distribution of rodent species along the southeastern slope of Mt. Meru in July-August 2009. Only specimens caught in traps or buckets are included in totals.

Elevation	1950 m	2300 m	2650 m	3000 m	3600 m	Totals
Species						
Otomys tropicalis	0	0	2	1	1	4
Dendromus insignis	0	0	1	7	2	10
Grammomys	3	4	2	4	0	13
Lophuromys	0	18	9	30	2	59
Mus triton	0	0	0	1	0	1
Praomys taitae	79	185	38	4	0	306
Rhabdomys dilectus	0	0	24	7	24	55
Graphiurus murinus	5	1	6	15	0	31
Total # individuals	87	208	82	69	29	475
Total # species	3	4	7	8	4	8
Total # sample-nights	1426	1426	1426	1426	1407	7111
Sample success (%)	6.1	14.6	5.7	4.8	2.1	6.7
Total # caught in traps	86	206	81	64	28	465
Total # trap-nights	920	920	920	920	912	4592
Trap success (%)	9.3	22.4	8.8	6.9	3.1	10.1

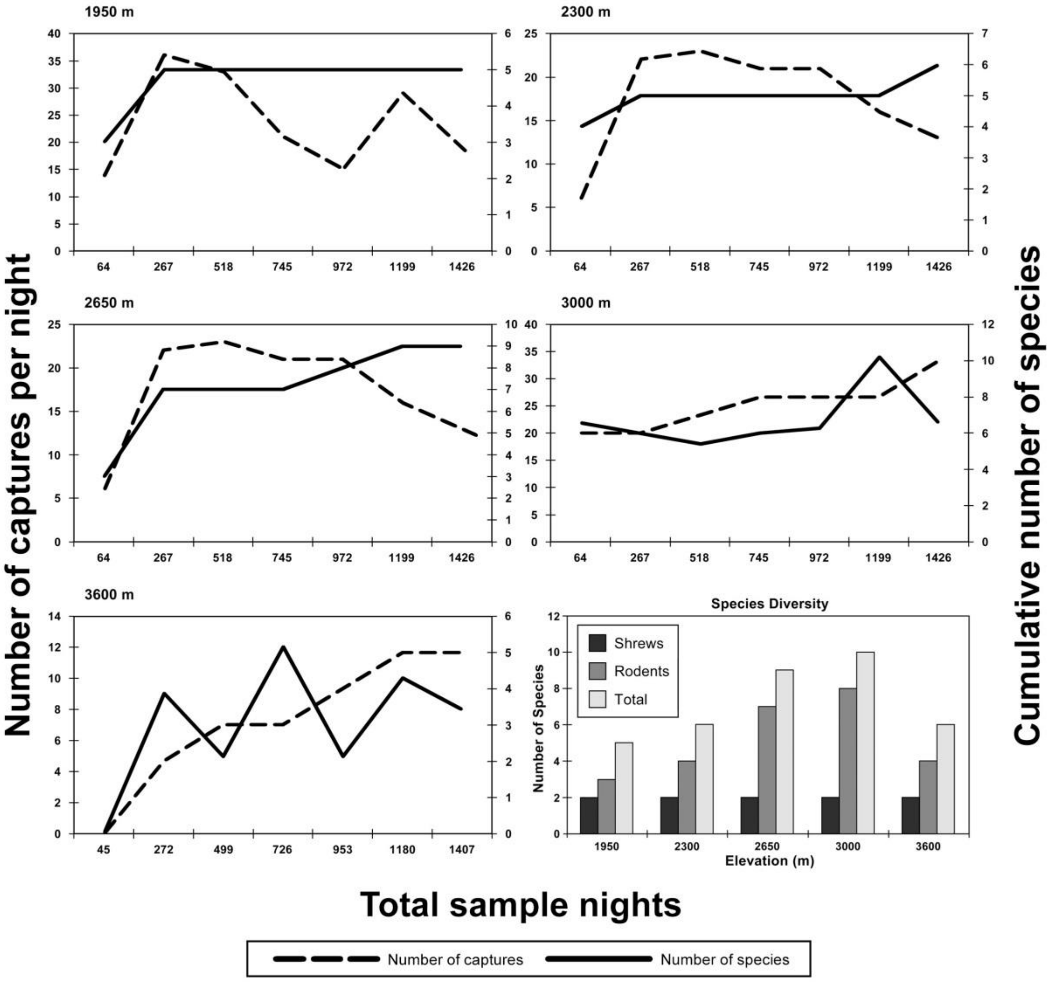

Figure 5. Species accumulation curves (for both pitfall and trap lines combined) for each site on Meru. The dashed lines represent the number of captures each day; the solid lines represent the cumulative number of new species for the site observed each day. The graph at the lower right shows the number of specimens of shrew, rodent, and mammal captured at each site.

As in the survey of montane mammals in the Udzungwa Mountains (Stanley and Hutterer 2007), the relationship between the amount of rainfall and capture of shrews shows a greater correlation than that between rainfall and rodent captures. Over the entire Kilimanjaro transect, the capture of individual shrews in both buckets and traps was significantly correlated with the amount of rainfall each day, but the capture of individual rodents was not (Table 8). A graphic representation of the differences between shrew and rodent captures with respect to the amount of rainfall is presented in Figure 6. During the survey of Mt. Meru, only two sites (1950 and 3000 m) received rain while buckets and traps were in place. The Product-moment correlation coefficients (*r*) of amount of daily rainfall with total captures of shrews (for buckets and traps combined) are 0.60 and 0.55 for the 1950 and 3600 m sites, respectively. For rodents these values were both negative (-0.53 and -0.30, respectively). While none of these *r* values are significant, Figure 7 illustrates the increase in shrew captures during or shortly after measureable rainfall on Meru, a pattern not exhibited by rodent captures. However, the overall relationship between rainfall and captures of shrews was not as strong as in the Udzungwa survey (Stanley and Hutterer 2007).

Table 7. Product-moment correlation coefficients (*r*) of amount of daily rainfall with four parameters of shrew and rodent daily captures on Kilimanjaro. Values in parentheses represent strong but not significant correlations. All captures (both traps and pitfalls) of each group are included. * = $P \leq 0.05$; ** = $P \leq 0.01$

Rainfall amount correlated with (across)	Number of individuals	Number of Species	New species added	Cumulative species
Total, shrews (buckets and traps)	0.385*	0.422**	0.086	(0.277)
Total, rodents (buckets and traps)	0.190	(0.280)	(0.230)	0.053
2000 m, shrews	(0.523)	(0.655)	-0.025	0.262
2000 m, rodents	-0.108	(0.523)	0.424	-0.008
2500 m, shrews	(0.592)	(0.502)	-0.050	0.283
2500 m, rodents	(0.544)	0.201	-0.217	0.096
3000 m, shrews	0.719*	0.199	-0.246	0.187
3000 m, rodents	(0.644)	(0.487)	0.139	0.122
3500 m, shrews	0.363	0.378	-0.357	0.236
3500 m, rodents	-0.267	-0.060	0.286	0.334
4000 m, shrews	(0.629)	(0.652)	0.950**	-0.160
4000 m, rodents	-0.411	-0.086	0.927**	-0.160

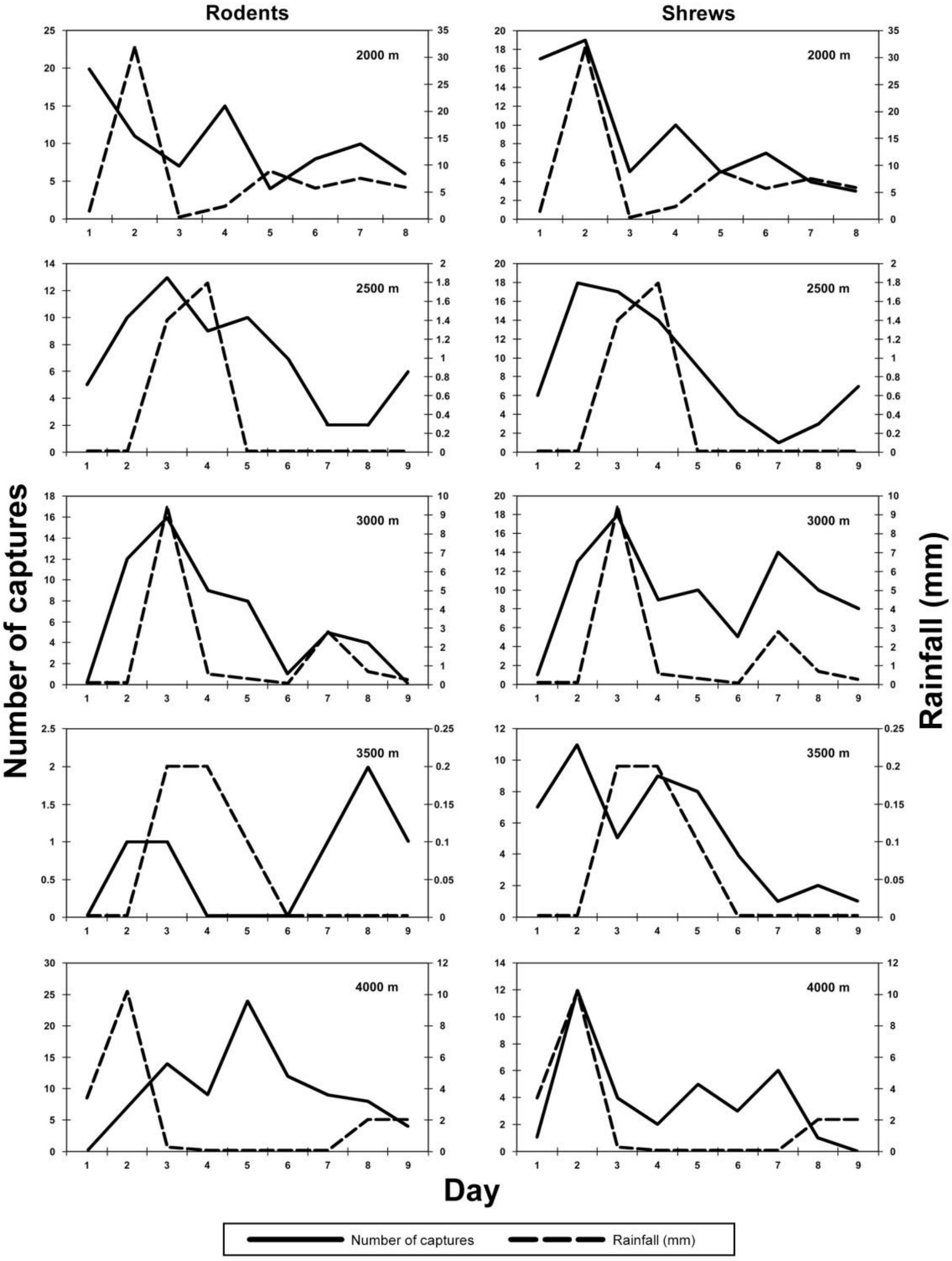

Figure 6. The relationship on Kilimanjaro between numbers of individuals captured each day at each site during the sampling period and rainfall. Rodentia are on the left and Soricomorpha are on the right.

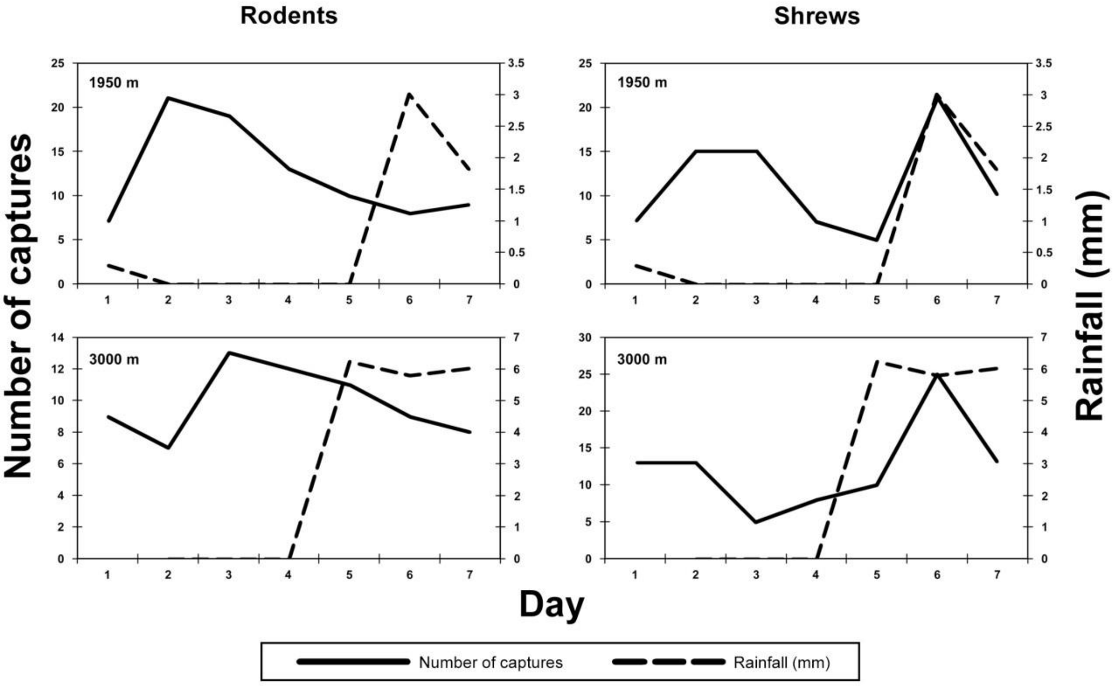

Figure 7. The relationship on Meru between numbers of individuals captured each day at each site during the sampling period and rainfall. Rodentia are on the left and Soricomorpha are on the right.

On Kilimanjaro, a significant negative relationship exists between elevation and the total number of shrew species collected (Table 8). Moreover, elevation was negatively correlated with the total number of individual shrews collected and sample success for shrews, with *r* values high, but not significant. Rodents do not show a similar pattern. The relationship between elevation and total sample success, number of individual mammals, and number of species collected for shrews and rodents combined was generally negative, but not statistically significant. The lowest number of individual mammals and species collected was at the 3500 m site. The greatest number of individuals noted was at the lowest site (2000 m) and the highest species diversity was at the 3000 m site. In most cases, the forested sites showed greater abundance and species diversity than the habitats above tree line (Tables 1,2,3).

The Meru survey exhibited no notable relationship between elevation and number of individuals or species collected, or sample success, for shrews or rodents. A low and relatively constant number of shrew species was observed at all elevations, and the only prominent negative relationship (high but not significant r values) exists in the associations of the total number of individuals and total trap success with elevation (Table 9). The highest species diversity was seen at the 3000 m site and the lowest at the 1950 m site. While the lowest number of individuals collected was at the 3600 m site, the species diversity was higher there (six species) compared to that of the lowest site (five species) that had the second highest sample success of any of the sites (Table 4).

Table 8. Product-moment correlation coefficients (*r*) between elevation and trap success on Kilimanjaro. Values in parentheses represent strong but not significant correlations. Significant relationships ($P < 0.05$) are in bold.

Elevation correlated with	(*r*)	P
Total number of individual mammals collected	-0.59	> 0.05
Total trap success	-0.59	> 0.05
Total number of species collected	-0.68	> 0.05
Total number of shrews collected	(-0.73)	> 0.05
Shrew trap success	(-0.79)	> 0.05
Total number of shrew species collected	**-0.95**	**< 0.05**
Total number of rodents collected	-0.23	> 0.05
Rodent trap success	-0.21	> 0.05
Total number of rodent species collected	-0.56	> 0.05

Table 9. Product-moment correlation coefficients (*r*) between elevation and trap success on Meru. Values in parentheses represent strong but not significant correlations.

Elevation correlated with	(*r*)	P
Total number of individual mammals collected	(-0.75)	> 0.05
Total trap success	(-0.75)	> 0.05
Total number of species collected	0.59	> 0.05
Total number of shrews collected	-0.53	> 0.05
Shrew trap success	-0.52	> 0.05
Total number of shrew species collected	-	-
Total number of rodents collected	-0.62	> 0.05
Rodent trap success	-0.61	> 0.05
Total number of rodent species collected	0.33	> 0.05

During both surveys, most buckets and traps did not catch anything, so captures in any individual trap or bucket were rare events. For example, although there was a 10.3% bucket success with 329 captures on Kilimanjaro, and a 6.7% bucket success and 170 captures on Meru for all mammals captured in 385 buckets (77 buckets installed at each of five sites) in each survey, most buckets captured no animals. Over the entire surveys, 203 out of 385 buckets (Kilimanjaro) and 287 out of 385 (Meru) caught nothing. Similarly, on Kilimanjaro, traps resulted in 3.4% trap success in 1040 individual traps, and 283 captures, with 834 traps not yielding any animals. On Meru there was 12.6% trap success in 750 traps with 581 captures, with only 313 traps capturing at least one animal. Both surveys had individual buckets and traps that caught multiple animals; on Kilimanjaro, a bucket caught 10 animals and a trap secured four animals, and on Meru, 11 animals were found in one bucket and seven animals were obtained in one trap.

To test for "trap competition" and to determine if captures were independent with respect to each other, we compared the observed distribution of captures by bucket and by trap to the Poisson distribution for each individual survey. Neither captures by buckets or traps followed the Poisson distribution (*G*-test for goodness of fit = 84.0 for buckets, 10.0 for traps-Kilimanjaro; 34.0 for buckets, 63.7 for traps-Meru; $P < 0.01$) suggesting a lack of trap or bucket independence. Significantly fewer traps or buckets caught one individual than would have been expected based on the assumption that the frequency of captures follows a Poisson distribution, and significantly more caught 2, or more, than expected (Yu, 1994) .

Morphometrics of *Crocidura monax*

The shrews collected during the Kilimanjaro survey (see above) and referred to *Crocidura monax*, agree with the series used by Thomas (1910) to describe this species, although some specimens having no long bristles on the tail, and others having only a few on the base of the tail. The pelage is wooly and thick and hairs measure approximately 5 mm in length. The color above is blackish-brown, and slightly paler below. External and cranial measurements of these specimens compared to the holotype of *C. monax* (BMNH 10.7.2.58; measured by WTS) and those listed by Thomas support the identification of the recent series sampled from Mt. Kilimanjaro as *C. monax* (Tables 10, 11).

Analyses of external measurements suggested significant sexual dimorphism in total length for the East Usambara and Kilimanjaro samples, where females were shorter than males. The male specimens from the East Usambara, Ukaguru, and Uluguru massifs had longer tails than females, and the East Usambara and South Pare males exhibited a longer hindfoot than the females. The East Usambara and Udzungwa males were heavier than females (Table 10). However, when we applied a Bonferroni correction for multiple tests, no populations show statistically significant dimorphism, with the exception of hindfoot length in the South Pare Mountains. However, this one significant result may be due to the small sample size of females (3) from this population rather than actual dimorphism.

For 17 cranial characters measured, there were significant differences between males and females in six dimensions in the Kilimanjaro sample, four in the East Usambara sample, two in the Uluguru series, and one in the South Pare, West Usambara, and Rubeho samples. These differences were scattered among the dimensions examined and Bonferroni corrections showed that the differences were not significant when the multiple comparisons are considered, with one exception (width of the upper third molar in the South Pare specimens, which included only three females and six males). We combined sexes in all subsequent analyses in the absence of conclusive evidence for sexual dimorphism.

Of the cranial characters measured, the width of the mastoid plate exhibited the highest coefficients of variation within each geographic sample (7-11%; Table 11). We deleted this character in subsequent analyses of geographic variation. F-values produced by the one-way ANOVA to test the null hypothesis of no significant geographic variation were all highly significant ($P < 0.001$). The greatest amount of morphologic heterogeneity was exhibited by those characters associated with the length of the skull, including CI, BL, UTRL, M&I, and LTR. Bimaxillary width was also notably heterogeneous. In general, cranial dimensions were largest in the East Usambara sample (14 of the 16 characters) and the Meru sample was the smallest of the 11 geographic samples measured in 12 of the 16 characters (Table 11).

The discriminant function analysis (DFA) constrained to the Ngorongoro, Rubeho, Ukaguru, Uluguru, and Udzungwa populations correctly classified ≥ 80% of specimens to their respective localities and resulted in the first two components having eigenvalues that all exceeded 1. The first two factors explained 76.3 and 13.9% of the variation. The Ngorongoro population was strikingly small and distinct. The remaining mountain localities all overlapped in canonical variate space, with the Uluguru samples showing the most differentiation along CV2 (Fig. 8).

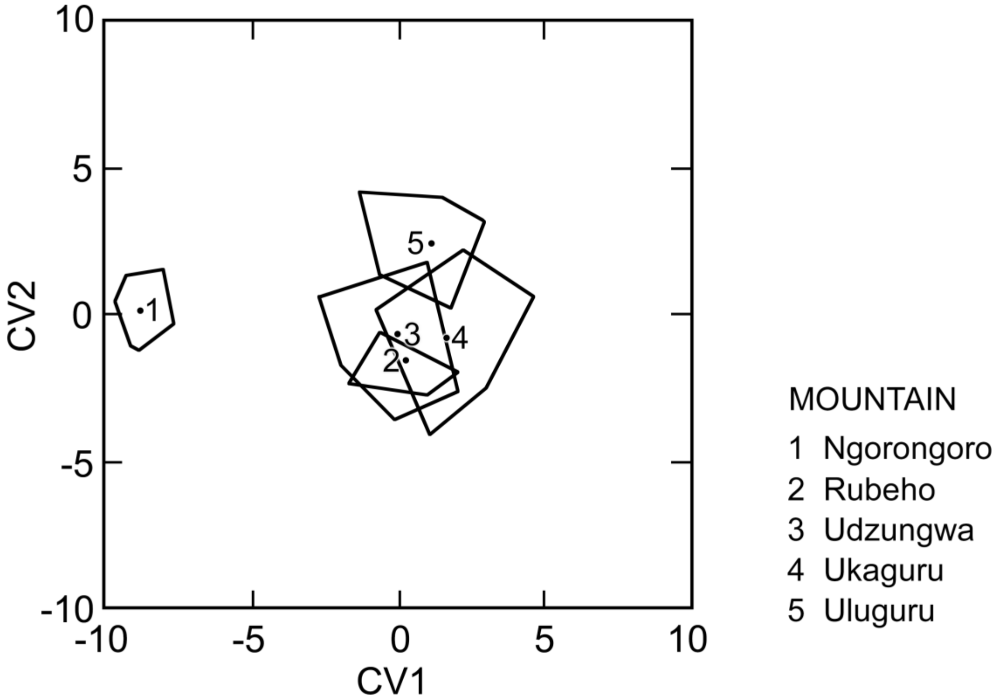

Figure 8. Projection of specimen scores on the first two canonical variates extracted from a discriminant function analysis of 16 log-transformed cranial and dental variables. Measurements were recorded from adult specimens from five populations of *Crocidura* spp. from Ngorongoro (n = 16), Rubeho (n = 10), Udzungwa (n = 31), Ukaguru (n = 68) and Uluguru mountains (n = 34).

Three sets of two overlapping populations each are reflected in the DFA of the Kilimanjaro, North Pare, South Pare, East Usambara, and West Usambara samples, where ≥ 91% of specimens were correctly classified to mountain. The first two factors explained 73.2 and 16.7% of the variation. Overlap in canonical variate space is exhibited between the East and West Usambara samples, Mt. Kilimanjaro, and the North Pare samples, and the South Pare and Magamba samples. The large sizes of both *C. tansaniana* in the East Usambaras, first observed by Hutterer (1986), and the sample from the West Usambaras are reflected in the position of the those two operational taxonomic units (OTUs) along CV1 and the greater PPL of the

Kilimanjaro and North Pare samples relative to the South Pare and Magamba samples is reflected by the dispersion of specimen scores along CV2 (Fig. 9).

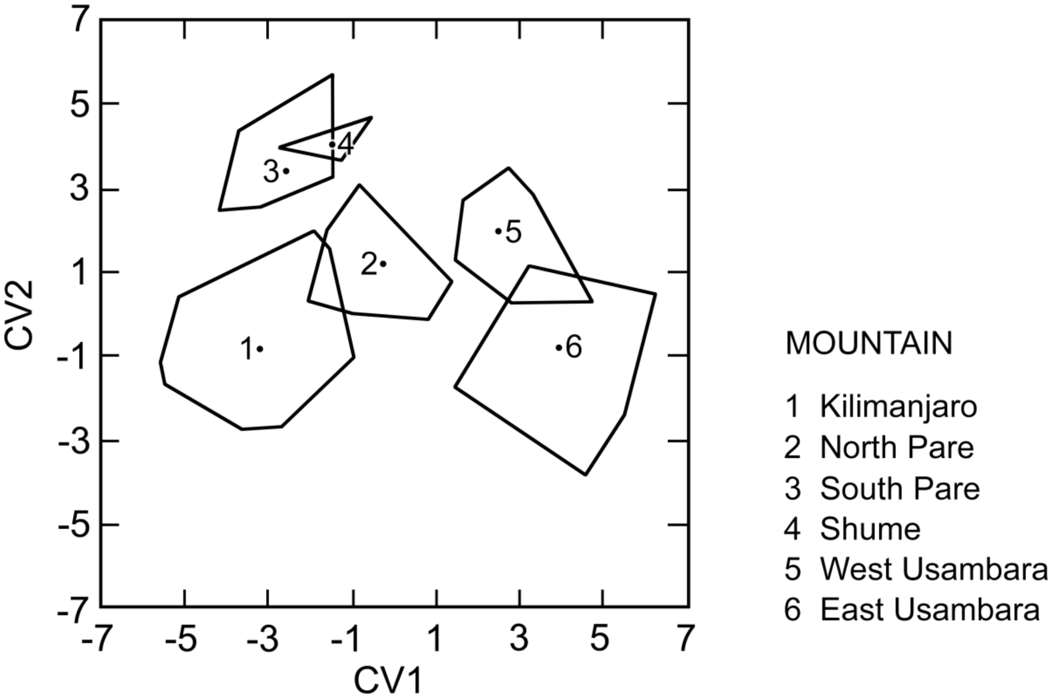

Figure 9. Projection of specimen scores on the first two canonical variates extracted from a discriminant function analysis of 16 log-transformed cranial and dental variables. Measurements were recorded from adult specimens from six populations, including Kilimanjaro (n=55), North Pare (n=11), South Pare (n=9), West Usambara (Shume-Magamba; n=3), West Usambara (Ambangulu; n=17), and East Usambara (n=44). Specimens from Mt. Meru were excluded.

Table 10. External measurements of individuals of *Crocidura* from 11 mountains in Tanzania and four holotypes. All measurements were taken by WTS, with the exception of the West Usambara sample, and those of the holotypes where the measurements were recorded from original skin tags or literature. Mean ± standard deviation, range, sample size, and CV. See text for character definitions.

	TL	HB	TV	HF	EAR	WT
Meru	130.69 ± 6.03 116.00 – 144.00 N = 115 0.05	77.37 ± 3.95 65.00 – 85.00 N = 115 0.05	53.31 ± 3.37 45.00 – 60.00 N = 115 0.06	15.03 ± 0.61 13.00 – 16.00 N = 115 0.04	9.35 ± 0.58 8.00 – 10.00 N = 115 0.06	8.53 ± 1.09 6.00 – 11.00 N = 115 0.13
Ngorongoro	139.38 ± 3.36 134.00 – 145.00 N = 16 0.02	81.69 ± 3.89 76.00 – 91.00 N = 16 0.05	57.69 ± 3.53 52.00 – 65.00 N = 16 0.06	15.38 ± 0.62 14.00 – 16.00 N = 16 0.04	10.63 ± 0.62 9.00 – 11.00 N = 16 0.06	8.61 ± 0.59 7.30 – 9.60 N = 16 0.07
Kilimanjaro	155.58 ± 6.95 141.00 – 172.00 N = 55 0.04	91.49 ± 4.25 83.00 – 101.00 N = 55 0.05	64.09 ± 3.67 55.00 -71.00 N = 55 0.06	17.00 ± 0.67 16.00 -19.00 N = 55 0.04	10.85 ± 0.56 10.00 – 12.00 N = 55 0.05	13.92 ± 1.44 10.00 – 17.00 N = 53 0.10
North Pare	149.80 ± 4.80 140.00 – 158.00 N = 10 0.03	89.90 ± 3.75 84.00– 96.00 N = 10 0.04	60.09 ± 2.21 56.00 – 63.00 N = 11 0.04	16.73 ± 0.47 16.00 – 17.00 N = 11 0.03	10.18 ± 0.40 10.00 – 11.00 N = 11 0.04	11.79 ± 1.72 9.20 – 15.50 N = 11 0.15
South Pare	140.00 ± 5.39 132.00 – 146.00 N = 7 0.04	81.71 ± 3.68 75.00 – 85.00 N = 7 0.05	58.29 ± 3.04 54.00 – 62.00 N = 7 0.05	15.63 ± 0.52 15.00 – 16.00 N = 8 0.03	9.63 ± 0.52 9.00 – 10.00 N = 8 0.05	9.45 ± 0.65 8.40 – 10.50 N = 8 0.07
West Usambara	159.65 ± 5.69 150.00 – 170.00 N = 17 0.04	93.88 ± 3.98 85.00 – 99.00 N = 17 0.04	65.76 ± 2.84 60.00 – 71.00 N = 17 0.04	16.29 ± 0.69 15.00 – 17.00 N = 17 0.04	10.21 ± 0.47 9.50 – 11.00 N = 17 0.05	13.85 ± 1.23 12.00 – 16.50 N = 17 0.09
East Usambara	163.00 ± 8.22 148.00 – 176.00 N = 21 0.05	94.33 ± 6.46 82.00 – 104.00 N = 21 0.07	68.67 ± 3.07 64.00 – 75.00 N = 21 0.04	17.38 ± 0.74 16.00 – 19.00 N = 21 0.04	10.95 ± 0.59 10.00 – 12.00 N = 21 0.05	15.31 ± 2.27 11.00 – 20.00 N = 21 0.15
Ukaguru	173.57 ± 6.59 159.00 – 191.00 N = 68 0.04	94.09 ± 5.20 77.00 – 106.00 N = 68 0.06	79.49 ± 4.74 66.00 – 95.00 N = 68 0.06	17.40 ± 0.65 16.00 – 19.00 N = 68 0.04	12.37 ± 0.54 11.00 – 13.00 N = 68 0.04	15.93 ± 1.56 12.50 – 19.50 N = 68 0.10
Rubeho	177.36 ± 7.59 166.00 – 190.00 N = 11 0.04	93.73 ± 4.22 87.00 – 101.00 N = 11 0.05	83.64 ± 4.78 77.00 – 93.00 N = 11 0.06	17.18 ± 0.75 16.00– 18.00 N = 11 0.04	10.82 ± 0.75 10.00 – 12.00 N = 11 0.07	13.00 ± 1.30 11.00 – 15.00 N =11 0.10
Uluguru	169.82 ± 7.91 158.00 – 187.00 N = 33 0.05	89.12 ± 4.01 82.00 – 97.00 N = 33 0.05	80.94 ± 5.47 70.00 – 95.00 N = 34 0.07	17.03 ± 0.80 16.00 – 19.00 N = 34 0.05	11.15 ± 0.67 10.00 – 13.00 N = 33 0.06	12.32 ± 1.39 9.50 – 15.50 N = 33 0.11
Udzungwa	167.33 ± 8.97 151.00 – 187.00 N = 30 0.05	86.53 ± 6.44 75.00 – 101.00 N = 30 0.07	80.80 ± 3.51 74.00 – 88.00 N = 30 0.04	17.29 ± 0.86 15.00– 19.00 N = 31 0.05	10.90 ± 0.75 9.00 – 12.00 N = 31 0.07	14.32 ± 2.24 10.00 – 19.50 N =31 0.16
C. monax - Holotype		88	66	16.2	10	
C. montis - Holotype		77	61	15	11	
C. tansaniana - Holotype		109	65	17	13	15
C. usambarae - Holotype		80	63	15	8	

Table 11. Cranial measurements of individuals of *Crocidura* from 11 mountains in Tanzania (sexes combined within populations), two holotypes, and one set of paratypes. Mean ± standard deviation, range, sample size, and CV. See text for character definitions.

	CI	BL	PPL	UTRL	LIW	BW	NW	GW	HBC
Ngorongoro	21.49 ± 0.25 21.09 – 21.95 N = 16 0.02	19.30 ± 0.23 18.88 – 19.68 N = 16 0.01	9.89 ± 0.16 9.59 – 10.12 N = 16 0.02	9.14 ± 0.16 8.83 – 9.40 N = 16 0.02	4.59 ± 0.09 4.43 – 4.73 N = 16 0.02	6.28 ± 0.12 6.06 – 6.50 N = 16 0.02	1.98 ± 0.08 1.83 – 2.12 N = 16 0.04	9.80 ± 0.13 9.53 – 10.03 N = 16 0.01	6.55 ± 0.16 6.26 – 6.80 N = 16 0.02
Meru	20.75 ± 0.47 19.50 – 21.58 N = 67 0.02	18.61 ± 0.42 17.49 – 19.43 N = 67 0.02	9.37 ± 0.24 8.61 – 9.91 N = 67 0.03	9.04 ± 0.23 8.52 – 9.55 N = 67 0.03	4.84 ± 0.11 4.58 – 5.08 N = 67 0.02	6.31 ± 0.15 5.91 – 6.62 N = 67 0.02	1.84 ± 0.08 1.63 – 2.01 N = 66 0.04	9.70 ± 0.23 9.22 – 10.15 N = 67 0.02	6.38 ± 0.23 5.73 – 6.86 N = 67 0.04
Kilimanjaro	23.26 ± 0.48 22.32 – 24.15 N = 55 0.02	21.03 ± 0.44 20.32 – 21.89 N = 55 0.02	10.56 ± 0.24 10.02 – 11.08 N = 55 0.02	10.21 ± 0.21 9.71 – 10.58 N = 55 0.02	5.18 ± 0.14 4.84 – 5.51 N = 55 0.03	7.06 ± 0.13 6.77 – 7.30 N = 55 0.02	1.92 ± 0.10 1.65 – 2.11 N = 55 0.05	10.42 ± 0.25 9.86 – 11.01 N = 55 0.02	7.02 ± 0.32 6.36 – 8.04 N = 55 0.05
North Pare	23.05 ± 0.52 22.31 – 23.95 N = 11 0.02	20.99 ± 0.51 20.24 – 21.85 N = 11 0.02	10.41 ± 0.26 10.06 – 10.93 N = 11 0.03	10.33 ± 0.23 9.94 – 10.77 N = 11 0.02	5.06 ± 0.11 4.83 – 5.18 N = 11 0.02	7.16 ± 0.19 6.80 – 7.39 N = 11 0.03	2.12 ± 0.07 2.02 – 2.21 N = 11 0.03	10.27 ± 0.17 9.88 – 10.51 N = 11 0.02	6.76 ± 0.33 6.44 – 7.64 N = 11 0.05
South Pare	22.16 ± 0.36 21.34 – 22.56 N = 9 0.02	19.96 ± 0.34 19.16 – 20.33 N = 9 0.02	9.83 ± 0.19 9.56 – 10.24 N = 9 0.02	9.78 ± 0.18 9.46 – 9.97 N = 9 0.02	5.05 ± 0.10 4.93 – 5.22 N = 9 0.02	6.81 ± 0.16 6.60 – 7.04 N = 9 0.02	1.93 ± 0.09 1.81 – 32.09 N = 9 0.05	9.92 ± 0.23 9.50 – 10.25 N = 9 0.02	6.38 ± 0.18 6.16 –6.62 N = 9 0.03
West Usambara	23.71 ± 0.46 22.92 – 24.70 N = 17 0.02	21.40 ± 0.43 20.86 – 22.36 N = 17 0.02	10.62 ± 0.24 10.23 – 11.11 N = 17 0.02	10.50 ± 0.19 10.26 – 11.01 N = 17 0.02	5.17 ± 0.15 4.87 – 5.37 N = 17 0.03	7.37 ± 0.15 7.14 – 7.64 N = 17 0.02	2.19 ± 0.09 2.01 – 2.36 N = 17 0.04	10.63 ± 0.25 10.06 – 11.04 N = 17 0.02	6.94 ± 0.20 6.51 – 7.39 N = 17 0.03
East Usambara	25.09 ± 0.49 23.82 – 26.12 N = 44 0.02	22.81 ± 0.45 21.85 – 23.95 N = 44 0.02	11.33 ± 0.28 10.85 – 11.94 N = 44 0.02	11.12 ± 0.25 10.75 – 12.05 N = 44 0.02	5.44 ± 0.21 5.00 – 6.04 N = 44 0.04	7.66 ± 0.18 7.25 – 8.04 N = 44 0.02	2.22 ± 0.11 1.99 – 2.54 N =44 0.05	10.88 ± 0.28 10.35 – 11.60 N = 44 0.03	6.97 ± 0.20 6.57 – 7.50 N = 44 0.03

Ukaguru	24.51 ± 0.46 23.38 – 25.76 N = 68 0.02	22.22 ± 0.43 21.11 – 23.32 N = 68 0.02	10.97 ± 0.28 10.08 – 11.4 N = 69 0.03	10.75 ± 0.23 10.15 – 11.29 N = 68 0.02	5.33 ± 0.14 5.05 – 5.75 N = 69 0.03	7.65 ± 0.17 7.23 – 8.06 N = 69 0.02	2.28 ± 0.15 1.99 – 2.56 N = 68 0.07	10.79 ± 0.26 10.10 – 11.47 N = 69 0.02	7.02 ± 0.20 6.63 – 7.70 N = 69 0.03
Rubeho	24.12 ± 0.41 23.49 – 24.63 N = 10 0.02	21.87 ± 0.34 21.27 – 22.27 N = 10 0.02	10.74 ± 0.17 10.46 – 11.05 N = 10 0.02	10.66 ± 0.20 10.32 – 10.93 N = 10 0.02	5.22 ± 0.12 5.02 – 5.40 N = 10 0.02	7.61 ± 0.23 7.21 – 7.89 N = 10 0.03	2.20 ± 0.15 1.97 – 2.38 N = 10 0.07	10.63 ± 0.14 10.30 – 10.78 N = 10 0.01	6.99 ± 0.19 6.68 – 7.32 N = 10 0.03
Uluguru	24.03 ± 0.51 22.70 – 24.89 N = 34 0.02	21.69 ± 0.52 20.21 – 22.60 N = 34 0.02	10.54 ± 0.32 9.65 – 11.15 N =34 0.03	10.65 ± 0.21 10.20 – 11.02 N = 34 0.02	5.30 ± 0.15 4.89 – 5.60 N = 34 0.03	7.30 ± 0.22 6.72 – 7.74 N =34 0.03	2.19 ± 0.10 1.94 – 2.34 N = 34 0.05	10.25 ± 0.22 9.82 – 10.70 N = 33 0.02	6.95 ± 0.23 6.53 – 7.54 N = 33 0.03
Udzungwa	23.78 ± 0.37 23.10 – 24.71 N = 31 0.02	21.45 ± 0.37 20.73 – 22.33 N = 31 0.02	10.60 ± 0.25 10.12 – 11.11 N = 31 0.02	10.52 ± 0.25 10.04 – 10.99 N = 31 0.02	5.28 ± 0.16 4.79 – 5.62 N = 31 0.03	7.54 ± 0.27 6.68 – 8.20 N = 31 0.04	2.24 ± 0.11 2.00 – 2.45 N = 31 0.05	10.55 ± 0.25 9.96 – 11.05 N = 31 0.02	7.24 ± 0.38 6.64 – 8.99 N = 31 0.05
C. usambarae Paratypes	21.98 ± 0.22 21.74 – 22.18 N = 3 0.01	19.93 ± 0.25 19.65 – 20.08 N = 3 0.01	9.99 ± 0.15 9.77 – 10.11 N = 5 0.02	9.76 ± 0.40 9.59 – 9.88 N = 4 0.01	4.94 ± 0.03 4.91 – 4.97 N = 4 0.01	6.89 ± 0.40 6.66 – 7.00 N = 5 0.02	1.97 ± 0.08 1.87 – 2.09 N = 5 0.04	10.14 ± 0.12 10.00 – 10.29 N = 4 0.01	6.50 ± 0.18 6.31 – 6.67 N = 4 0.03
C. monax Holotype	23.67	21.30	10.51	10.60	5.12	7.22	2.24	10.30	6.88
C. tansaniana Holotype	25.36	23.10	11.51	11.20	5.40	7.95	2.32	10.99	6.93

Table 11 (CONTINUED). Cranial measurements of individuals of *Crocidura* from 11 mountains in Tanzania (sexes combined within populations), two holotypes, and one set of paratypes. Mean ± standard deviation, range and sample size, and CV. See text for character definitions.

	I^3–W	C–W	M^3–L	M^3–W	PGW	MP	M&I	LTR
Ngorongoro	0.71 ± 0.03 0.65 – 0.75 N = 16 0.04	0.77 ± 0.03 0.71 – 0.83 N = 16 0.04	1.37 ± 0.05 1.26 – 1.45 N = 16 0.04	0.73 ± 0.03 0.67 – 0.80 N = 16 0.05	6.61 ± 0.12 6.43 – 6.83 N = 16 0.02	1.08 ± 0.14 0.94 – 1.45 N = 16 0.13	13.34 ± 0.17 13.08 – 13.65 N = 16 0.01	8.52 ± 0.14 8.23 – 8.72 N = 16 0.02
Meru	0.69 ± 0.03 0.62 – 0.78 N = 67 0.05	0.73 ± 0.03 0.64 – 0.80 N = 67 0.05	1.45 ± 0.07 1.31 – 1.59 N = 67 0.04	0.77 ± 0.04 0.70 – 0.86 N = 67 0.05	6.55 ± 0.16 5.99 – 6.93 N = 49 0.02	1.04 ± 0.08 0.91 – 1.32 N = 67 0.08	13.05 ± 0.35 12.13 – 13.76 N = 67 0.03	8.35 ± 0.23 7.80 – 8.98 N = 67 0.03
Kilimanjaro	0.80 ± 0.03 0.71 – 0.87 N = 55 0.04	0.90 ± 0.04 0.80 – 0.97 N = 55 0.04	1.57 ± 0.06 1.44 – 1.69 N = 55 0.04	0.84 ± 0.04 0.74 – 0.95 N = 55 0.05	7.06 ± 0.19 6.67 – 7.56 N = 55 0.03	0.99 ± 0.10 0.75 – 1.20 N = 55 0.10	14.80 ± 0.36 14.01 – 15.51 N = 55 0.02	9.51 ± 0.19 9.04 – 9.81 N = 55 0.02
North Pare	0.84 ± 0.04 0.78 – 0.92 N = 11 0.05	0.94 ± 0.04 0.88 – 1.01 N = 11 0.04	1.62 ± 0.06 1.50 – 1.69 N = 11 0.04	0.83 ± 0.04 0.74 – 0.87 N = 11 0.05	6.99 ± 0.15 6.85 – 7.36 N = 11 0.02	1.08 ± 0.08 0.94 – 1.21 N = 11 0.07	14.73 ± 0.34 14.26 – 15.29 N = 11 0.02	9.59 ± 0.20 9.23 – 9.95 N = 11 0.02
South Pare	0.80 ± 0.03 0.76 – 0.84 N = 9 0.04	0.88 ± 0.03 0.82– 0.90 N = 9 0.03	1.49 ± 0.07 1.36 – 1.06 N = 9 0.50	0.77 ± 0.30 0.73 – 0.83 N = 9 0.05	6.81 ± 0.10 6.66 – 6.94 N = 9 0.01	1.14 ± 0.10 0.94 – 1.28 N = 9 0.11	14.04 ± 0.27 13.44 – 14.33 N = 9 0.02	9.07 ± 0.18 8.78 – 9.30 N = 9 0.02
West Usambara	0.97 ± 0.03 0.91 – 1.02 N = 17 0.03	1.01 ± 0.03 0.95 – 1.05 N = 17 0.03	1.71 ± 0.06 1.59 – 1.79 N = 17 0.04	0.87 ± 0.05 0.81 – 0.98 N = 17 0.06	7.28 ± 0.24 6.93 – 7.71 N = 17 0.03	1.20 ± 0.10 1.06 – 1.41 N = 17 0.08	15.08 ± 0.34 14.49 – 15.69 N = 17 0.02	9.74 ± 0.20 9.47 – 10.26 N = 17 0.02
East Usambara	0.98 ± 0.04 0.90 – 1.07 N = 44 0.04	1.01 ± 0.40 0.93 – 1.10 N = 44 0.04	1.72 ± 0.07 1.58 – 1.93 N = 44 0.04	0.87 ± 0.05 0.76 – 0.97 N = 44 0.06	7.50 ± 0.22 7.19 – 8.12 N = 43 0.03	1.23 ± 0.13 0.94 – 1.48 N = 44 0.11	16.04 ± 0.33 15.19 – 16.88 N = 44 0.02	10.29 ± 0.22 9.84 – 11.05 N = 44 0.02

Ukaguru	0.88 ± 0.05 0.74 – 1.07 N = 69 0.06	1.01 ± 0.05 0.88 – 1.10 N = 69 0.04	1.67 ± 0.07 1.50 – 1.80 N = 69 0.04	0.82 ± 0.05 0.68 –0.91 N = 69 0.06	7.61 ± 0.23 7.00 – 8.15 N = 69 0.03	1.01 ± 0.11 0.79 – 1.31 N = 69 0.11	15.51 ± 0.35 14.64 – 16.38 N = 67 0.02	9.96 ± 0.20 9.49 – 10.42 N = 67 0.02
Rubeho	0.86 ± 0.04 0.79 – 0.91 N = 10 0.04	0.97 ± 0.03 0.91 – 1.02 N = 10 0.04	1.65 ± 0.06 1.54 – 1.73 N = 10 0.04	0.87 ± 0.03 0.81 – 0.91 N = 10 0.04	7.28 ± 0.15 7.02 – 7.55 N = 10 0.02	1.22 ± 0.15 0.97 – 1.42 N = 10 0.12	15.12 ± 0.28 14.70 – 15.49 N = 10 0.02	9.81 ± 0.17 9.56 – 10.03 N = 10 0.02
Uluguru	0.87 ± 0.04 0.78 – 0.94 N = 34 0.05	0.98 ± 0.05 0.78 – 1.05 N = 34 0.05	1.63 ± 0.07 1.49 – 1.79 N = 34 0.04	0.79 ± 0.04 0.72 – 0.88 N = 34 0.05	7.21 ± 0.22 6.82 – 7.72 N =34 0.03	1.15 ± 0.13 0.87 – 1.41 N = 34 0.11	15.27 ± 0.36 14.49 – 15.84 N = 34 0.02	9.90 ± 0.17 9.54 – 10.21 N = 34 0.02
Udzungwa	0.88 ± 0.06 0.77 – 0.98 N = 31 0.06	0.97 ± 0.04 0.90 – 1.03 N = 31 0.04	1.66 ± 0.08 1.50 – 1.90 N = 31 0.05	0.83 ± 0.04 0.77 – 0.92 N = 31 0.05	7.42 ± 0.23 6.98 – 7.85 N = 31 0.03	1.06 ± 0.14 0.82 – 1.42 N = 31 0.13	14.93 ± 0.28 14.52 – 15.57 N = 31 0.02	9.76 ± 0.23 9.34 – 10.12 N = 31 0.02
C. usambarae Paratypes	0.90 ± 0.04 0.84 – 0.93 N = 5 0.04	0.91 ± 0.02 0.88 – 0.94 N = 5 0.02	1.64 ± 0.08 1.53 – 1.77 N = 6 0.05	0.82 ± 0.05 0.74 – 0.89 N = 6 0.07	6.82 ± 0.15 6.58 – 6.93 N = 5 0.02	1.05 ± 0.12 0.92 – 1.16 N = 4 0.11	13.87 ± 0.26 13.45 – 14.19 N = 6 0.02	9.03 ± 0.22 8.74 – 9.38 N = 6 0.02
C. monax Holotype	0.88	0.94	1.69	0.85	7.05	1.13	15.12	9.87
C. tansaniana Holotype	0.93	0.99	1.76	0.86	7.51	1.08	16.00	10.30

Conclusion

This study demonstrates that populations of purported "*C. monax*" on discrete mountains within the Northern Highlands and EAM represent different taxa. Of the populations studied, the samples from Ngorongoro were the smallest in cranial characteristics. Based on discriminant function analysis, samples from the following mountain pairs (neighboring each other geographically) overlapped in morphological space: Kilimanjaro and North Pare; South Pare and the northwestern segment of the West Usambaras; and the East Usambaras and the eastern edge of the West Usambaras. Each of these pairs shows modest morphological differentiation between mountain localities. For example, the specimens from Kilimanjaro are generally larger than those from North Pare, shrews from the East Usambaras are larger than in the eastern section of the West Usambaras, and *C. usambarae* from South Pares are subtly larger in some cranial dimensions than the paratypes from the West Usambara Mountains (Table 11). The middle Eastern Arc Mountains (EAM) (Rubeho, Ukaguru, Uluguru, and Udzungwa) also show overlap in morphological space, with the sample from the Uluguru being the most distinct of the four massifs included in the analysis.

Coupled with molecular analyses (Stanley et al. in press), the results indicate that *Crocidura monax* is restricted to Kilimanjaro and North Pare, but is a member of a complex that includes the East and West Usambaras (*C. tansaniana*), the South Pares (*C. usambarae*), Ngorongoro (*Crocidura ndumai*), Meru (*Crocidura newmarki*), and the middle EAM -- Rubeho, Ukaguru, Uluguru, and Udzungwa (*Crocidura munissii*). This geographic distribution of members of the *C. monax* complex is significant as it spans two geologically distinct mountain groups—the Northern Highlands and the EAM, but with significant differences exhibited among discrete populations within both sets of montane archipelagos. For example, three unique forms occur on Ngorongoro, Meru and Kilimanjaro, respectively, within the Northern Highlands. The EAM house distinct forms of the *monax* complex, as well, as evidenced by the differences between crania of specimens from the middle EAM compared to those found in the Pare and Usambara massifs.

The *C. monax* complex as elucidated by this study is another example of soricine shrews that are restricted to subsets of the montane islands of Tanzania and that exhibit a mosaic of distributional and biogeographical patterns. For example, *Congosorex phillipsorum* was described based on specimens from the West Kilombero Scarp forests in the Udzungwa Mountains (Stanley et al. 2005b). To date, no other populations of this species have been discovered and the closest relatives of this taxon are in the Congo basin (Hutterer 2005), at least 2000 km to the west. Thus, this unique shrew represents a remnant of an ancient Miocene connection of forests between central Africa and the EAM (Axelrod and Raven 1978, Stanley et al. 2005b). Other vertebrate species within the same forest area exhibit ancient connections including *Rungwecebus kipunji* (found only in the West Kilimbero forest and the Southern Highlands; Davenport et al. 2006) and *Xenoperdix udzungwensis* (with affinities to taxa in Asia; Dineson et al. 1994,), rendering the Udzungwa Mountains (and the West Kilombero Scarp area) unique among montane habitats within Tanzania.

Sylvisorex howelli is endemic to the northern and central EAM, including the East and West Usambara, Nguru, Nguu, Rubeho, Ukaguru and Uluguru mountains. Stanley and Olson (2005) described the phylogeography and documented the presence of this species on all but one of these mountains (the Rubeho population was discovered subsequent to this analysis). No records exist of this shrew on other mountains, including the Udzungwa massif, the Northern or Southern Highlands, even after intensive sampling of shrews on each. Thus, *S. howelli* is endemic to a subset of the EAM. Like the *C. monax* group in this study, phylogeographic relationships mirrored geographic patterns. For example, based on molecular evidence, the East and West Usambara populations of *S. howelli* were sister to each other, as were the Nguu and Nguru populations. The Ukaguru and Uluguru populations were the most differentiated (Stanley and Olson 2005). The affinities of this species within the Soricidae is under investigation.

Myosorex is represented within Tanzania by three different species, including *M. zinki* (endemic to Mt. Kilimanjaro), *M. geata* (found on central EAM including the Rubeho, Ukaguru and Uluguru mountains) and *M. kihaulei* found on Udzungwa Mountains and the Southern Highlands (Stanley and Esselstyn 2010). In contrast to the present study where a species of the *C. monax* complex spanned the Ruaha River, Stanley and Esselstyn (2010) found a taxonomic separation between populations of *Myosorex* on either side of the Ruaha River (*M. geata* on the northeastern side in the Rubeho, Ukaguru and Uluguru mountains) , and *M. kihaulei* on the southwestern side (in the Udzungwa Mountains and Southern Highlands). As with *S. howelli*, the origins of these isolated populations are still unknown.

The demonstration of distributional patterns of various species of the *C. monax* complex spanning the Northern Highlands and the EAM is concordant with work by Carleton and Stanley (2005) and Bryja *et al.* (2014), who grouped samples of *Praomys* from Kilimanjaro and the northern EAM, such as the Usambaras and South Pare, using both morphologic and molecular analyses. These studies argue against a pervasive influence of the different montane systems on the individual populations contained within each of them or a significant biogeographical boundary between the Northern Highlands and the EAM (sensu Kingdon 1971).

However, because of detailed faunal surveys conducted over the past two decades (Stanley et al. 1996, 1998, 2005a,b, 2007, 2011a,b, Stanley and Hutterer 2007, Stanley and Goodman 2011, W. T. Stanley unpubl. data) there is now multiple evidence that two rodent genera commonly found on EAM and Southern Highlands, *Beamys* and *Hylomyscus,* do not occur on the Northern Highlands (Carleton and Stanley 2005, 2012, Stanley and Goodman 2011, Stanley et al. 2014). This is in contrast to distribution of *Praomys*, as discussed above. While the distribution of *Beamys* is enigmatic because of its presence in lowland coastal forested habitat (Stanley and Goodman 2011), the comparison between the distributions of *Hylomyscus* and *Praomys* (both restricted to submontane or montane forests) is intriguing because one species of the former, *H. arcimontensis*, is distributed along the entire EAM within Tanzania, and throughout the Southern Highlands. *Praomys*, on the other hand, is represented by one species, *P. taitae,* distributed throughout the Northern Highlands, and the EAM, and another, *P. melanotus*, in the Southern Highlands. As Carleton and Stanley (2012) pointed out, based on data generated by faunal surveys, *Hylomyscus* is the more restricted of the two, with regard to elevation. *Praomys* has been recorded as low as 230 m in the East Usambara Mountains, whereas the lowest elevation *Hylomyscus* has been observed is 900 m. In addition, trap success of *Hylomyscus* is much higher than *Praomys* in arboreal settings (Stanley and Goodman 2011, Carleton and Stanley 2012). All of this leads to the suggestion that *Praomys* would be more likely to disperse between montane habitats along lowland corridors produced by conditions allowing the lowering of vegetations belts in the past (Lovett 1993). This might explain the distribution of *Praomys* spanning the EAM and the Northern Highlands, and the absence of *Hylomyscus* on the latter.

However, the reverse situation exists across the gap between the Southern Highlands and the southern end of the EAM, where *Hylomyscus arcimontensis* is found on both montane entities, but *Praomys* is represented by two unique species on each. Thus, the absence of Hylomyscus and Beamys within montane habitats of the Northern Highlands suggests that the distinction between this volcanic island set and the older EAM has some biogeographic influence.

Elevational transects have now been conducted on three mountains in Tanzania, including two from the Northern Highlands: Kilimanjaro and Meru, and one from the EAM: Udzungwa. Because of deforestation, detailed analyses of the natural elevational distribution of montane mammals are not possible on most of the other mountains within the country. All surveys in this study were conducted on the wettest versant of the mountains, which in each case was either the eastern or the southeastern slope, and carried out during the same time of the year, July and August (the dry season) using identical trapping regimes and techniques. Thus, I feel confident making the biogeographic comparisons discussed above, as well as comparisons among surveys to determine similarities or differences in faunal abundance and diversity of the shrews and rodents living on these mountains.

Comparisons constrained to these three mountains illustrate a much richer fauna, but lower abundance, in the Udzungwa Mountains vs. the two massifs of the Northern Highlands. In terms of species diversity, Udzungwa was the richest (23 species), Meru was the most depauperate (10 species), and Kilimanjaro fell midway with 16 species. The reverse was observed for the abundance of mammals, based on sample success. Meru had the greatest abundance (10.5% sample success), followed by Kilimanjaro (5.3% sample success), and Udzungwa (3.3% sample success). This same pattern was seen when taxonomic groups are considered. Udzungwa had the greatest shrew diversity but lowest abundance (three genera, nine species; 1.4% sample success), followed by Kilimanjaro (three genera, six species; 2.7%), and Meru (one genus, two species; 3.9%). Udzungwa also had the highest rodent diversity and lowest abundance (11 genera, 14 species; 2.0%), Kilimanjaro (eight genera, 10 species; 2.5%) and Meru (eight genera, eight species; 6.7%).

A mid-elevational peak in species richness (sensu Heaney and Rickart 1990, McCain 2005) was observed on both Northern Highlands massifs, at 3000 m. Such a pattern was not observed during the Udzungwa survey where the greatest taxonomic diversity was documented at 2000 m (the highest point of the transect). Significantly, the 3000 m sites on each of the Northern Highland sites were at the ecotone between forest and alpine habitats, each with species unique to those habitats (for example, *Praomys* in the forest, and *Rhabdomys* in the alpine grassland). The highest point of the Udzungwa survey was set in montane forest.

The vast majority of the species documented during these surveys are either endemic or restricted to montane habitats within eastern Africa. Importantly, with one exception, there were no commensals documented on the Northern Highlands, and only one specimen of *Rattus rattus* was observed in the Udzungwa survey (Stanley and Hutterer 2007). This is in contrast to patterns documented by Goodman and Carleton (1997) in Madagascar where *Rattus* was abundant in montane forests far from human settlements.

The relatively high diversity of small terrestrial mammals on the ancient fault block mountain (Udzungwa) relative to the more recent volcanoes may be due to the geologic origin or the age of the mountain. Surveys of the shrews over a three year period in the East and West Usambara Mountains (of the same geologic category as Udzungwa) exhibited three genera and 10 species, and three genera and six species, respectively (Stanley et al. 2011a). While these surveys were in one general elevational range (roughly 1000 to 1300 m), and included habitat mosaics including agricultural land as well as disturbed forest, so may not reflect the overall diversity of small mammals along the extent of the elevational range of the massif, the comparison is interesting in that the East and West housed shrew diversity that either exceeded that of the Udzungwas (in the case of the East Usambaras), or equaled that of Kilimanjaro (West Usambaras). For rodents, both the East and West Usambaras exhibited greater rodent diversity than the Udzungwas (10 genera and 12 species in the East and nine genera and 10 species in the West Usambaras; Stanley and Goodman 2011a). Thus, the small mammal diversity in each of these larger northern EAM is consistently equal to, or greater than that of the Northern Highlands.

Meru remains enigmatic in the notable low shrew diversity, with only two species, recovered during the survey of that mountain, compared to six on Kilimanjaro and nine on Udzungwa. When placed in a broader context, this level of diversity is lower than any of the 18 individual sites spanning the Afro-Malagasy region cited by Stanley and Goodman (2011), where the diversity values ranged from three to 17 species and involved independently evolved taxonomic groups of insectivorous mammals (tenrecs and soricid shrews). The reasons for such a striking low diversity on Meru are unknown. Volcanic activity on the mountain has been recent in comparison to Kilimanjaro (Guest and Leedal 1953), but it seems unlikely that eruptions and associated destruction of natural habitat would have contributed to extinction of taxa once existing on Meru.

In conclusion, this study has elucidated the distribution and taxonomy of the the *C. monax* group across two distinct montane sets of islands and adds three new endemic shrews to the montane system of Tanzania. While the distribution of the *C. monax* group suggests the biogeographic influence of the boundary between the Northern Highlands and the EAM is minimal, the absence of rodents such as *Hylomyscus* in the Northern Highlands indicates otherwise. Faunal surveys along elevational transects of mountains of differing geologic compositions indicate greater diversity on the EAM relative to the Northern Highlands, and highlight Mt. Meru as a massif with low soricid diversity.

Literature

Allen, G. M., and Loveridge, A. (1927) Mammals from the Uluguru and Usambara Mountains, Tanganyika Territory. *Proceedings of the Boston Society of Natural History* **38:** 413-431.

Allen, G. M., and Loveridge, A. (1933) Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika Territory. *Bulletin of the Museum of Comparative Zoology at Harvard* **75:** 47-140.

Axelrod, D. I. and Raven, P. H. (1978) Late Cretaceous and Tertiary vegetation history of Africa. In: Werger, M. J. A. (Ed.) *Biogeography and Ecology of Southern Africa*, pp. 77-130. The Hague, Junk.

Barbour, T., and Loveridge, A. (1928) A comparative study of the herpetological fauna of the Uluguru and Usambara Mountains, Tanganyika. *Memoirs of the Museum of Comparative Zoology of Harvard College* **50:** 87-265.

Bryja, J., Mikula, O., Patzenhauerová, H., Oguge, N. O., Šumbera, R., and Verheyen, E. (2014) The role of dispersal and vicariance in the Pleistocene history of an East African mountain rodent, *Praomys delectorum*. *Journal of Biogeography* **41:** 196–208.

Burgess, N. D, Kock, D., Cockle, A., FitzGibbon, C., Jenkins, P. and Honess, P. (2000) Mammals. In: Burgess N. D., and Clarke, G. P. (Eds.) *Coastal forests of eastern Africa*, pp. 173-190 and 401-406. I.U.C.N., Gland and Cambridge.

Carleton, M. D., and Stanley, W. T. (2005) Review of the *Hylomyscus arcimontensis* complex (Rodentia: Muridae) in Tanzania, with description of a new species. *Proceedings of the Biological Society of Washington* **118:** 619-646.

Carleton, M. D., and Stanley, W. T. (2012) Species limits within the *Praomys delectorum* group (Rodentia: Muridae: Murinae) of East Africa: A morphometric reassessment and biogeographic implications. *Zoological Journal of the Linnean Society* **165**: 420-469.

Cordeiro, N. J. (1998) Preliminary analysis of the nestedness patterns of montane forest birds of the Eastern Arc Mountains. *Journal of East African Natural History* **87:** 101-118.

Cordeiro, N. J., and Howe, H. F (2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences* **100:** 14052-14056.

Davenport, T. R. B., Stanley, W. T., Sargis, E. J., De Luca, D. W., Mpunga, N. E., Machaga, S. J., and Olson, L. E. (2006) A new genus of African monkey, *Rungwecebus*: Morphology, ecology, and molecular phylogenetics. *Science* **312:** 1378-1381.

DeBlase, A. F., and Martin, R. E. (1974) *A manual of mammalogy with keys to the families of the world.* Wm. C. Brown Company Publishers, Dubuque, Iowa.

De Luca, D. W., and Mpunga, N. E. (2005) Small carnivores of the Udzungwa Mountains: Presence, distributions and threats. *Small Carnivore Conservation* **32:** 1-7.

Demeter, A, and Hutterer, R. (1986) Small mammals from Mt. Meru and its environs (Northern Tanzania). *Cimbebasia* **8:** 199-207.

Dinesen, L., Lehmberg, T.,Svendsen, J. O.,Hansen, L. A., and Fjeldså, J. (1994) A new genus and species of perdicine bird (Phasianidae, Perdicini) from Tanzania; a relict form with Indo-Malayan affinities. *Ibis* **136:** 3-11.

Dippenaar N. J. (1980) New species of *Crocidura* from Ethiopia and northern Tanzania (Mammalia: Soricidae). *Annals of the Transvaal Museum* **32**:125-154.

Downie, C. and Wilkinson, P. (1972) *The geology of Kilimanjaro*. Sheffield: Geological Survey of Tanzania and Department of Geology, Sheffield University.

Engler, A. (1893) Über die Flora des Gebirgslandes von Usambara, auf Grund der von Herrn Carl Hölst das elbst gemachten Sammlungen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* **17:** 156-168.

Goodman, S. M., and Carleton, M. D. (1998) The rodents of the Réserve Spéciale d'Anjanaharibe-Sud. In Goodman, S. M. (Ed.) *A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation*. Fieldiana: Zoology, n.s., **90:** 201-221.

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, C. J. (1993) The geological evolution of East Africa. In: Lovett, J. C., and Wasser, S. K. (Eds.) *Biogeography and Ecology of the Rain Forests of Eastern Africa*, pp. 9-21. Cambridge University Press, Cambridge.

Grimshaw, J., Cordeiro, N., and Foley, C. (1995) The mammals of Kilimanjaro. *Journal of the East African Natural History* **84:** 105-139.

Griswold, C. E. (1991) Cladistic biogeography of Afromontane spiders. *Australian Systematic Botany* **4:** 73-89.

Grzimek, B., and Grzimek, M. (1960) *Serengeti Shall Not Die*. London: Hamish Hamilton.

Guest, N. J., and Leedal, G. P. (1953) Volcanic activity of Mt. Meru. *Records of the Geological Survey of Tanganyika* **3:** 40-46.

Hanby, J. (1987) Kilimanjaro National Park. Tanzania National Parks/Africa Wildlife Foundation.

Heaney, L. R., and Rickart, E. A. (1990) Correlations of clades and clines: Geographic, elevational, and phylogenetic distribution patterns among Philippine mammals. In: Peters, G., and Hutterer, R. (Eds.) *Vertebrates in the Tropics*, pp. 321-332. Museum Alexander Koenig, Bonn.

Heim de Balsac, H. (1957) Insectivores de la famille des Soricidae de l'Afrique orientale. *Zoologischer Anzeiger* **158:** 144-153.

Helbig-Bonitz M., Rutten G., Kalko E. K. V. (2013) Fruit bats can disperse figs over different landuse types on Mount Kilimanjaro, Tanzania. *African Journal of Ecology* **52:** 122-125.

Hemingway, E. (1986) The snows of Kilimanjaro, and other stories (1st Scribner classic/Collier ed.). New York: Collier Books.

Hemp, A. (2006) Continuum or zonation? Altitudinal gradients in the forest vegetation of Mt. Kilimanjaro. *Plant Ecology* **184:** 27-42.

Hoffman, R. L. (1993) Biogeography of east African montane forest millipedes, In: Lovett, J. C., and Wasser, S. K. (Eds.) *Biogeography and Ecology of the Rain Forests of Eastern Africa,* pp. 103-115. Cambridge University Press, Cambridge.

Holden, M. E. (2005) Family Gliridae. In: Wilson, D. E., and Reeder, D. M. (Eds.) *Mammal Species of the World: A Taxonomic and Geographic Reference,* 3rd edition, pp. 819-841. Johns Hopkins University Press, Baltimore.

Homewood, K. M., and Rodgers, W. A. (1981) A previously undescribed mangabey from southern Tanzania. *International Journal of Primatology* **2:** 47-55.

Hutterer, R. (1986) Diagnosen neuer Spitzmäuse aus Tansania (Mammalia: Soricidae). *Bonner Zoologische Beiträge* **37:** 23-33.

Hutterer, R. (2005) Order Soricomorpha. In: Wilson, D. E., and Reeder, D. M. (Eds.) *Mammal Species of the World: A Taxonomic and Geographic Reference, 3rd edition*, pp. 220-311. Johns Hopkins University Press, Baltimore.

Iversen, S. T. (1991) The Usambara Mountains, NE Tanzania: Phytogeography of the vascular plant flora. *Acta Universitatis Upsaliensis Symbolae Botanicae Upsalienses* **29:** 1-234.

Jenkins, P. (1984) Description of a new species of *Sylvisorex* (Insectivora: Soricidae) from Tanzania. *Bulletin of the British Museum (Natural History), Zoology* **47:** 65-76.

Kingdon, J. (1971) East African mammals: An atlas of evolution in Africa. Academic Press, London, **1:** 1-446.

Lens, L., Dongen, D.V., Norris, K., Githuri, K. M., and Matthysen, E. (2002) Avian persistence in fragmented rainforest. *Science*, **298:** 1236-1238.

Loveridge, A. (1935) Scientific results of an expedition to rain forest regions in eastern Africa. I. New reptiles and amphibians from East Africa. *Bulletin of the Museum of Comparative Zoology at Harvard*, **79:** 3-19.

Loveridge, A. (1937) Scientific results of an expedition to rain forest regions in eastern Africa. IX. Zoogeography and itinerary. *Bulletin of the Museum of Comparative Zoology at Harvard,* **79:** 481-541.

Lovett, J. C. (1990) Altitudinal variation in large tree community associations on the West Usambara Mountains, In: Hedberg, I, and Persson, E. (Eds.) Research for Conservation of Tanzania Catchment Forests, pp. 48-53. Uppsala Universitet, Uppsala.

Lovett, J. C. (1993) Climatic history and forest distribution in eastern Africa. In: Lovett J. C., Wasser S. K. (Eds) *Biogeography and ecology of the rain forests of eastern Africa.* pp. 23–32. Cambridge: Cambridge University Press,

Lovett, J. C., Bridson, D. M., and Thomas, D. W. (1988) A preliminary list of the moist forest angiosperm flora of the Mwanihana forest reserve, Tanzania. *Annals of the Missouri Botanical Garden* **75:** 874-888.

Lundgren,B., and Lundgren, L. (1972) Comparison of some soil properties in one forest and two grassland ecosystems on Mount Meru, Tanzania *Geografiska Annaler. Series A, Physical Geography Vol. 54, No. 3/4, Studies of Soil Erosion and Sedimentation in Tanzania* pp. 227-240

Makundi, R. H., Massawe, A. W., and Mulungu, L. S. (2006) Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *African Journal of Ecology,* **45:** 17-21.

McCain, C. M. (2005) Elevational gradients in diversity of small mammals. *Ecology* **86:** 366-372.

Mduma, S. A. R., Sinclair, A. R. E., and Hilborn, R. (1999) Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology* **68**: 1101-1122.

Menegon, M., Doggart, N., and Owen, N. (2008) The Nguru Mountains of Tanzania, an outstanding hotspot of herpetofaunal diversity. *Acta Herpetologica*, **3:** 107-127.

Mittermeier, R. A., Robles-Gil, P., Hoffmann, M., Pilgrim, J. D., Brooks, T. B., Mittermeier, C. G., Lamoreux, J. L. & Fonseca, G. A. B. (2004). Hotspots revisited: Earth’s biologically richest and most endangered terrestrial ecoregions. Conservation International, 241–273.

Moreau, R. E. (1935) A synecological study of Usambara, Tanganyika Territory with particular reference to birds. *Journal of Ecology,* **23:** 1-43.

Mulungu, L.S., Makundi, R.H., Massawe, A.W., Machang’u, R.S., and Mbije, N.E. (2008) Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Mammalia,* **72:** 178-185.

Musser, G. G., and Carleton, M. D. (2005) Superfamily Muroidea. In: Wilson, D. E., and Reeder, D. M. (Eds.) *Mammal Species of the World: A Taxonomic and Geographic Reference,* 3rd edition, pp. 894-1531. Johns Hopkins University Press, Baltimore.

Mwasaga, B.C. (1991) The natural forest of Mount Kilimanjaro. In: Newmark, WD, (Ed.) *The Conservation of Mount Kilimanjaro,* pp. 111-114. IUCN, Gland, Switzerland and Cambridge, UK.

Newmark, W. D. (1991) Tropical forest fragmentation and the local extinction of understory birds in the Eastern Usambara Mountains, Tanzania. *Conservation Biology*, **5:** 67-78.

Newmark, W. D. (2006) A 16-year study of forest disturbance and understory bird community structure and composition in Tanzania. *Conservation Biology* **20:** 122-134.

Ngalason, W., and Mkonyi, F. J. (2011) Herpetofauna of montane areas of Tanzania. 3. Altitudinal distribution of amphibians on the Uluguru South Mountains. In: Stanley, W. T., (Ed) Studies of montane vertebrates of Tanzania. pp. 81-89. *Fieldiana: Life and Earth Sciences* Vol. **4**.

Perkin, A. W. (2007) Comparative penile morphology of East African galagos of the genus *Galagoides* (Family Galagidae): Implications for taxonomy. *International Journal of Primatology*, **69:** 16-26.

Pócs, T. (1975) Affinities between the bryoflora of East Africa and Madagascar. *Boissiera*, **24:** 125-128.

Pócs, T. (1985) East African bryophytes, VIII. The Hepaticae of the Usambara rain forest project expedition, 1982. *Acta Botanica Hungarica*, **24:** 113-133.

Poynton, J. C. (2003) Altitudinal species turnover in southern Tanzania shown by anurans: Some zoogeographical considerations. *Systematics and Biodiversity*, **1:** 117-126.

Quennel, A. M., McKinlay, A. C. M., and Aitken, W. G. (1956) Summary of the geology of Tanganyika, Part I. Introduction and stratigraphy. *Geological Survey of Tanganyika Memoir* 1. Dar es Salaam: Government Printer.

Rodgers, W. A., and Homewood, K. M. (1982) Species richness and endemism in the Usambara mountain forests, Tanzania. *Biological Journal of the Linnean Society* **18:** 197-242.

Rovero, F., Jones, T., and Sanderson, J. (2005) Notes on Abbott’s duiker (*Cephalophus spadix* True 1890) and other forest antelopes of Mwanihana Forest, Udzungwa Mountains, Tanzania, as revealed by camera-trapping and direct observations. *Tropical Zoology*, **18:** 13-23.

Rovero, F., Marshall, A. R., Jones, T., and Perkin, A. (2009) The primates of the Udzungwa Mountains: Diversity, ecology and conservation. *Journal of Anthropological Sciences*, **87:** 93-126.

Rutten G., Ensslin A., Hemp A., Fischer M. (2015) Forest structure and composition of previously selectively logged and non-logged montane forests at Mt. Kilimanjaro. *Forest Ecology and Management* **337:** 61-66.

Sampson, D. N. (1965) The geology, volcanology and glaciology of Kilimanjaro. *Tanzanian Notes and Records*, **64:** 118-124.

Sampson, D. N., and Wright, A. E. (1964) *The geology of the Uluguru Mountains*. Geological Survey of Tanzania Bulletin **37**. Dar es Salaam: Government Printer.

Sikes, R. S., Gannon, W. L., and the Animal Care and Use Committee of the American Society of Mammalogists (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, **92:** 235-253.

Stanley, W.T., and Esselstyn, J.A. (2010) Biogeography and diversity among montane populations of mouse shrew (Soricidae: *Myosorex*) in Tanzania. *Biological Journal of the Linnaean Society*, **100:** 669-680.

Stanley, W. T., and Goodman, S. M. (2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 4. Rodentia. In: Stanley, W. T., (Ed) Studies of montane vertebrates of Tanzania. pp. 53-73. *Fieldiana: Life and Earth Sciences* Vol. **4**.

Stanley, W. T., Goodman, S. M., and Hutterer, R. (1996) Notes on the insectivores and elephant shrews of the Chome Forest, South Pare Mountains, Tanzania. (Mammalia: Insectivora et Macroscelidea). *Zoologische Abhandlugen Staatliches Museum für Tierkunde Dresden*, **49:** 131-147.

Stanley, W. T., Goodman, S. M., and Hutterer, R. (2011a) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 2. Families Soricidae (shrews) and Macroscelididae (elephant shrews), In: Stanley, W. T., (Ed) Studies of montane vertebrates of Tanzania. pp. 18-33. *Fieldiana: Life and Earth Sciences* Vol. **4**.

Stanley, W. T., Goodman, S. M., and Kihaule, P. M. (1998) Results of two surveys of rodents in the Chome Forest Reserve, South Pare Mountains, Tanzania (Mammalia: Rodentia). *Zoologische Abhandlugen Staatliches Museum für Tierkunde Dresden*, **50:** 145-160.

Stanley, W. T., Goodman, S. M., and Newmark, W. D. (2011b) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 1. Study areas, methodologies, and general results, In: Stanley, W. T., (Ed) Studies of montane vertebrates of Tanzania. pp. 1-17. *Fieldiana: Life and Earth Sciences* Vol. **4**.

Stanley, W. T., Gunn, J., and Kihaule, P. M. (2005a) Results of a preliminary small mammal survey of Malundwe Mountain, Mikumi National Park, Tanzania. *Journal of East African Natural History*, **94:** 213-222.

Stanley, W. T., and Hutterer, R. (2007) Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. *Acta Theriologica*, **52:** 261-275.

Stanley, W. T., Hutterer, R., Giarla, T. C., and Esselstyn, J. A. (In press) Phylogeny, phylogeography and geographical variation in the *Crocidura monax* (Soricidae) species complex from the montane islands of Tanzania, with descriptions of three new species. Zoological Journal of the Linnean Society

Stanley W. T., Kihaule, P. M., Howell, K. M., and Hutterer, R. (2000) Small mammals of the Eastern Arc Mountains, Tanzania. *Journal of East African Natural History,* **87:** 91-100.

Stanley, W. T., Kihaule, P. M., and Munissi, M. J. (2007) Small mammals of two forest reserves in the North Pare Mountains, Tanzania. *Journal of East African Natural History*, **96:** 215-226.

Stanley, W. T., and Olson, L. E. (2005) Phylogeny, phylogeography, and geographic variation of *Sylvisorex howelli* (Family Soricidae), an endemic shrew of the Eastern Arc Mountains, Tanzania. *Journal of Zoology*, **266:** 341-354.

Stanley, W. T., Rogers, M. A., and Hutterer, R. (2005b) A new species of *Congosorex* from the Eastern Arc Mountains, Tanzania, with significant biogeographical implications. *Journal of Zoology,* **265:** 269-280.

Stanley, W. T., Rogers, M. A., Kihaule, P. M., Munissi, M. J. (2014) Elevational distribution and ecology of small mammals on Africa's highest mountain. *PLOS ONE* **9**(11): e109904.

Stuart, S. N. (1983) Biogeographical and ecological aspects of forest bird communities in Eastern Tanzania. Ph.D. dissertation, University of Cambridge.

Stuart, S.N., Jensen, F. P., and Brøgger-Jensen, S. (1987) Altitudinal zonation of the avifauna in Mwanihana and Magombera Forests, eastern Tanzania. *Gerfaut,* **77:** 165-186.

Stuart, S. N., Jensen, F. P., Brøgger-Jensen, S, and Miller, R. I. (1993) The zoogeography of the montane forest avifauna of eastern Tanzania. In: Lovett, J. C., and Wasser, S. K. (Eds.) *Biogeography and Ecology of the Rain Forests of Eastern Africa*, pp. 203–228. Cambridge University Press, Cambridge.

Thomas, O. (1910) List of mammals from Mount Kilimanjaro, obtained by Mr. Robin Kemp, and presented to the British Museum by Mr. C. D. Rudd. *Annals and Magazine of Natural History,* **8(6):** 308-316.

Thompson, L. G., Brecher, H. H., Mosley-Thompson, E., Hardy, D. R., and Mark, B. G. (2009) Glacier loss on Kilimanjaro continues unabated. *Proceedings of the National Academy of Sciences*, **106:** 19770-19775.

Voss, R., and Emmons, L. H.(1996) Mammalian diversity in Neotropical lowland rainforest: A preliminary assessment. *Bulletin of American Museum of Natural History,* **230:** 3-115.

Yu, H. T. (1994) Distribution and abundance of small mammals along a subtropical elevational gradient in central Taiwan. Journal of Zoology, **234**: 577-600.

Zancolli, G., Steffan-Dewenter, I., and Rödel, M. O. (2014a) Amphibian diversity on the roof of Africa: Unveiling the effects of habitat degradation, altitude and biogeography. Diversity and Distributions, **20**: 297-308.

Zancolli G., Rödel M. O., Steffan-Dewenter I., and Storfer A. (2014b) Comparative landscape genetics of two river frog species occurring at different elevations on Mount Kilimanjaro. Molecular Ecology, **23**: 4989-5002.

Appendix I – Specimens examined for morphometric analysis of *Crocidura monax* complex.

Specimens used in this study are housed at the Field Museum of Natural History (FMNH).

Ngorongoro

Tanzania, Arusha Region, Ngorongoro District, Ngorongoro Conservation Area, Ngorongoro Crater rim, near Pongo Ranger Post, 3.24407° S, 35.65040° E, 2064 m:

FMNH 211272, 211314-211315, 211317, 211320, 211322-211323, 211327-211328, 211331-211332.

Tanzania, Arusha Region, Ngorongoro District, Ngorongoro Conservation Area, Ngorongoro Crater Rim, near Lamala Gate, 3.14255° S, 35.68669° E, 2372 m:

FMNH 211058-211059, 211124, 211131-211132, 211134.

Kilimanjaro

Tanzania, Kilimanjaro Region, Moshi District, 4 km N, 1.5 km W Maua, 3°14.404' S (or 3.24007° S), 37°27.502' E (or 37.45837° E), 2043 m:

FMNH 173788-173789, 173796, 174103-174110, 174112.

Tanzania, Kilimanjaro Region, Moshi District, 7 km N, 2.5 km W Maua, 3°12.459' S, 37°26.818' E, 2470 m:

FMNH 173770-173771, 173774-173778, 174066-174080.

Tanzania, Kilimanjaro Region, Moshi District, 10.5 km N, 3.5 km W Maua, 3°10.627' S, 37°26.413' E, 2897 m:

FMNH 173784, 174081-174102.

North Pare

Tanzania, Kilimanjaro Region, Mwanga District, North Pare Mts, Kindoroko Forest Reserve, 3.76039° S, 37.64726° E, 1688 m:

FMNH 192663-192669
Tanzania, Kilimanjaro Region, Mwanga District, North Pare Mts, Minja Forest Reserve, 3.58149° S, 37.6773° E, 1572 m:

FMNH 192670-192671, 192673-192674

Udzungwa

Tanzania, Morogoro Region, Kilombero District, Udzungwa Mts, 19.5 km N, 0.5 km W Chita, 8.3472° S, 35.9389° E, 2000 m:

FMNH 155308-155309, 155312, 155314-155318, 155320, 155322-155329, 155490-155501.

Tanzania, Morogoro Region, Kilombero District, Udzungwa Mts, 4 km W, 5 km N Chita, 8.475° S, 35.9069° E, 1460 m:

FMNH 155485-155487.

Ukaguru

Tanzania, Morogoro Region, Kilosa District, Ukaguru Mts, Mamiwa-Kisara Forest Reserve, 1 km E, 0.75 km S Mount Munyera, 6.3792° S, 36.9361° E, 1900 m:

FMNH 166569, 166690-166691, 166693-166700, 166702-166717, 166720-166721.

Tanzania, Morogoro Region, Kilosa District, Ukaguru Mts, Mamiwa-Kisara Forest Reserve, 1 km E, 1.5 km S Mt Munyera, 6.3889° S, 36.95° E, 1840 m:

FMNH 166578, 166723, 166725-166741, 166744-166748, 166750-166759, 166761-166762, 166764-166766.

Rubeho

Tanzania, Dodoma Region, Mpwapwa District, Rubeho Mts, Mwofwomero Forest Reserve, near Chugu Peak, 6.8337° S, 36.57198° E, 1900 m:

FMNH 197657-197659

Tanzania, Morogoro Region, Kilosa District, Rubeho Mts, Ilole Forest, 7.43774° S, 36.72729° E, 1878 m:

FMNH 197403-197404, 197660-197665

Uluguru

Tanzania, Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North Forest Reserve, 3 km W, 1.3 km N Tegetero, 6.9292° S, 37.7056° E, 1345 m:

FMNH 158280-158283, 158286.

Tanzania, Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North Forest Reserve, 5.1 km W, 2.3 km N Tegetero, 6.92° S, 37.6833° E, 1535 m:

FMNH 158287-158291, 158293-158297, 158392-158396,158399-158400, 158402-158403, 158405-158408, 158572.

Tanzania, Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North Forest Reserve, 6 km W, 3 km N Tegetero, 6.9167° S, 37.675° E, 1850 m:

FMNH 158409-158413.

Meru

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, Fig Tree Arch, 3.24406° S, 36.82845° E, 1950 m:

FMNH 207914, 207978, 207981, 207986, 208384-208388, 208390-208392, 208394-208395, 208397-208398, 208401-208408, 208410-208411.

Tanzania, Arusha Region, Arumeru District, Mt Meru, Arusha National Park, 3.24725°S, 36.80066°E, 2300 m:

FMNH 208415-208416.

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, Meru Crater, 3.24200° S, 36.78736° E, 2652 m:

FMNH 208045-208048, 208050, 208443-208451, 208453, 208456-208457.

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, Mgongo wa Tembo, 3.22350° S, 36.78675° E, 3000 m:

FMNH 208012, 208016-208017, 208022-208025, 208027-208028, 208032-208035, 208422-208424, 208426-208433, 208435-208436.

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, near Saddle Hut, 3.21609° S, 36.76897° E, 3600 m:

FMNH 208042, 208439, 208440

West Usambara-Ambangulu Forest

Tanzania, Tanga Region, Korogwe District, West Usambara Mts, 12.5 km NW Korogwe, Ambangulu Tea Estate, 5.07° S, 38.42° E, 1300 m:

FMNH 147203-147209, 147353-147354, 147357-147358, 147376, 149979-149980, 149999-150000, 151099.

Tanzania, Tanga Region, Korogwe District, West Usambara Mts, West Usambara Mts, 14.5 km NW Korogwe, Ambangulu Tea Estate, 5.05° S, 38.38° E, 1250 m:

FMNH 147210

East Usambara

Tanzania, Tanga Region, Muheza District, East Usambara Mts, 4.5 km ESE Amani, Monga Tea Estate, 5.1° S, 38.6° E, 1000 m:

FMNH 149973-149975, 149977-149978, 150376, 151112-151118, 151126, 151129-151134.

Tanzania, Tanga Region, Muheza District, East Usambara Mts, East Usambara Mts, 4.5 km NW Amani, Monga Tea Estate, 5.07° S, 38.62° E, 1100 m:

FMNH 147211, 147360.

Tanzania, Tanga Region, Muheza District, East Usambara Mts, 4.5 km WNW Amani, Monga Tea Estate, 5.1° S, 38.6° E, 1000 m:

FMNH 149969-149972, 149976, 151106-151107, 151109-151111, 151120-151125, 151376-151381.

South Pare

Tanzania, Kilimanjaro Region, Same District, South Pare Mts, Chome Forest Reserve, 3 km E, 0.7 km N Mhero, 4.28° S, 37.9278° E, 2000 m:

FMNH 153844, 153918-153922.

Tanzania, Kilimanjaro Region, Same District, South Pare Mts, Chome Forest Reserve, 7 km S Bombo, 4.33° S, 38° E, 1100 m:

FMNH 151137-151138, 151375.

West Usambara-Shume Magamba

Tanzania, Tanga Region, Lushoto District, West Usambara Mts, Magamba, 4.66667° S, 38.25° E, 1585 m:

FMNH 27424-27430

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Elevational distribution and ecology of small mammals on Africa's highest mountain

WILLIAM T. STANLEY[1], MARY ANNE ROGERS[1], PHILIP M. KIHAULE[2], and MAIKO J. MUNISSI[3]

[1] The Field Museum of Natural History, Department of Science and Education, Chicago, Illinois, United States of America; email:bstanley@fieldmuseum.org
[2] University of Dar es Salaam, Department of Zoology, Dar es Salaam, Tanzania;
[3]Southern Highlands Conservation Programme, Mbeya, Tanzania

ABSTRACT

Mt Kilimanjaro is Africa's highest mountain, and an icon for a country famous for its mammalian fauna. The distribution and abundance of small mammals on the mountain are poorly known. Here we document the distribution of shrews and rodents along an elevational gradient on the southeastern versant of Kilimanjaro. Five sites were sampled with elevational center points of 2000, 2500, 3000, 3500 and 4000 m, using a systematic methodology of standard traps and pitfall lines, to inventory the shrews and rodents of the slope. Sixteen species of mammal were recorded, including 6 shrew and 10 rodent species, and the greatest diversity of both was found at 3000 m, the elevational midpoint of the transect. No species previously unrecorded on Kilimanjaro were observed. Two genera of rodents that occur in nearby mountains (*Hylomyscus* and *Beamys*) were not recorded. *Myosorex zinki,* the only mammal endemic to Mt. Kilimanjaro, which previously was known by only a few specimens collected in the ericaceous or moorland habitat, was found in all but one (the lowest) of the sites sampled, and was one of the most widespread species of small mammal along the gradient. Two shrews (*Crocidura allex* and *Sylvisorex granti*) and one rodent (*Dendromus insignis*) were found throughout the entire transect, with *Dendromus* being observed at our highest trap point (4240 m). As in similar faunal surveys on other mountains of Tanzania, rainfall influenced the sample success of shrews, but not rodents. Trap success for rodents at 3500 m was notably low. This study contributes further justification for the conservation of the forest habitat of Mt. Kilimanjaro.

ADDITIONAL KEYWORDS: Mt. Kilimanjaro – shrews – rodents – *Myosorex* – Tanzania

INTRODUCTION

Knowing the distribution of organisms along an elevational gradient is critical to understanding the evolution and ecology of montane biotic systems, and to designing conservation strategies to maintain them. These reasons have motivated elevational surveys of small mammals in various areas of the world including Chile [1], Costa Rica [2], Malaysia [3], Philippines [4], [5], [6], Taiwan [7], and Tanzania [8]. Goodman, Ganzhorn & Rakotondravony [9] summarize some of the important biotic inventories along elevational gradients in Madagascar. Each of these studies elucidate both specific and broadly general patterns that help explain the mechanisms influencing the distributions of mammals along such gradients with significant implications for biogeographic analysis and conservation priorities [10]. Indeed, such surveys have served as vital baselines for comparison to subsequent inventories in testing the influence of climatic vicissitudes or habitat alteration. For example, range shifts in various mammalian species were documented in Yosemite Valley, California, with two similar surveys separated by almost a century [11].

Knowledge of the ecology and behavior of the targeted faunas help frame considerations of the results of systematic sampling along gradients. For example, Stanley & Hutterer [8] documented patterns of distribution along an altitudinal gradient in the Udzungwa Mountains of Tanzania that differed between shrews and rodents, and suggested that the amount of coincident rainfall influenced shrew, but not rodent, capture rates. Such observations must be factored into deciphering the results of systematic sampling along elevational gradients, and surveys using identical methodologies on other mountains should help to reveal whether such observations are unique to particular sites or more common across multiple gradients.

Mt. Kilimanjaro is the highest mountain in Africa and an icon for a region renowned for its unique mammalian fauna. Ironically, the mammals that inhabit the habitats of this volcano are relatively unknown, with most historical attention focused on larger species, leading to calls for complete inventories of the fauna of the mountain [12]. To date, the most comprehensive summary of our overall understanding of the mammalian fauna of Kilimanjaro remains that presented by Grimshaw, Cordeiro & Foley [13], who provided a faunal list of the mountain, and described past studies of Kilimanjaro’s mammalian fauna. Few studies employing systematic sampling have taken place on Kilimanjaro [14] and only one [15] used a systematic survey to document the presence and distribution of small rodents and shrews along elevational gradients on the mountain. The lack of detailed biotic vertebrate surveys, such as those of small mammals, hampers efforts to monitor ecological change over time on the mountain. Thompson *et al*. [16] suggest that climate change is affecting the habitat and ecology of Kilimanjaro, and baseline data for the distribution and abundance of various plants and animals are needed to judge the effect of such changes, as has been done elsewhere [11].

Using a standardized sampling regime that has been utilized in several other montane sites of Tanzania over the past two decades [8], [17], [18], [19] we surveyed the small mammals (shrews and rodents) at five different elevations and habitats along the southeastern versant of Mt. Kilimanjaro. Our study had three principal goals: 1) to initiate intensive surveys of the elevational distribution and abundance of small mammals along the transect sampled; 2) to test for differences between rodents and shrews in their relationship to elevation and response to different trapping methodologies; and 3) to compare the generated results to similar studies on Kilimanjaro and other mountains of Tanzania.

MATERIALS AND METHODS

Study Site

Mt. Kilimanjaro is in northeastern Tanzania and reaches an elevation of 5895 m. An extinct volcano, the mountain is the conglomeration of three volcanoes: Kibo (the highest, most prominent and familiar), Mawenzi (the second peak of the mountain), and Shira (a plateau) [20]. Because the mountain is a popular destination for climbers, there are numerous paths that originate in the lowlands and run up the side of the mountain [21]. Two such routes that are on the southeastern (and wettest) versant are “Marangu” and “Mweka”. Between these two is the “Maua” path which is currently closed to tourists, and is used by Kilimanjaro National Park (KINAPA) staff to access and maintain facilities within the park. Between 17 July and 31 August 2002, we sampled the small mammals (shrews and rodents) at five different elevations, ranging from roughly 2000 to 4000 m, along the “Maua” route on the southeastern slope of Mt. Kilimanjaro (Figure 1).

The specific localities, elevations, habitats (sensu Mwasaga [22]) and dates of sampling are listed below. The elevations given for each site are centered at the associated camp and sampling efforts spanned roughly 100-200 m above and below the camp. For this reason, we labeled each camp at the closest 500 m interval (2043 = 2000 m; 2470 = 2500 m, etc.). Temperature and rainfall for each site (measured at camp) are listed in Table 1:

Site 1 - 2000 m). 4 km N, 1.5 km W Maua, 3°14.404' S, 37°27.502' E, 2043 m; lower montane forest; 23-30 August 2002.

Site 2 - 2500 m). 7 km N, 2.5 km W Maua, 3°12.459' S, 37°26.818' E, 2470 m; upper montane forest; 17-25 July 2002.

Site 3 - 3000 m). 10.5 km N, 3.5 km W Maua, 3°10.627' S, 37°26.413' E, 2897 m; ecotone between montane forest and ericaceous zone; 26 July-03 August 2002.

Site 4 - 3500 m). 13.5 km N, 4 km W Maua, 3°08.941' S, 37°26.133' E, 3477 m; ericaceous zone; 4-12 August 2002.

Site 5 - 4000 m). 16 km N, 4.5 km W Maua, 3°07.566' S, 37°25.600' E, 3995 m; ecotone between ericaceous and alpine zones; 13-21 August 2002.

Trapping Procedure

We used identical sampling techniques to those employed in similar small mammal surveys in other Tanzanian forests [8], [19], [23], [24], [25], [26], [27], [28]. Pitfall and trap lines were set in different microhabitats at each site, to sample shrews and small rodents (< 200 g). Each pitfall line consisted of 11, 15 l buckets spaced 5 m apart, and placed so the upper rim was flush with the ground level. A 50 cm high vertical plastic fence was placed over the buckets, bisecting the openings. Most shrews and very small rodents were captured with this technique. Trap lines were installed using three types of traps: Museum Special traps, 14 x 7 cm; Victor rat traps, 17.5 x 8.5 cm (both manufactured by Woodstream Corporation, Lititz, Pennsylvania, USA); and medium-sized Sherman live traps, 23 x 9.5 x 8 cm (H.B. Sherman Traps Inc., Tallahassee, Florida, USA). Each line was composed of between 20 to 70 traps, with the Museum Special and Victor traps making up approximately 85% of each line. Traps were baited with pieces of freshly fried coconut coated in peanut butter, which was renewed each afternoon. Further details are outlined in Stanley, Goodman & Newmark [29].

All traps and buckets were checked once in the early morning and again in the late afternoon. Not all traps or buckets were employed for equal amounts of time (some trap lines were set the first day of the survey, others were installed on the second), so we use the measures “trap-night” and “bucket-night” (one trap or bucket in operation for one 24 hr period-0700 to 0700 hrs) to quantify sampling effort. We refer to the success rate of each method as either “trap success” or “bucket success”, and calculate these values by dividing the number of individuals captured by the number of trap-nights or bucket-nights and multiplying by 100. In discussions involving the two trapping methodologies combined, the term “sampling-night” refers to either one trap-night or one bucket-night, and “sample success” refers to the success rate for the two methodologies combined. The latter is calculated by dividing the number of individuals captured by the number of sampling-nights and multiplying by 100.

Standard external measurements and reproductive status were recorded for each specimen, which was then either prepared as a study skin and skeleton or preserved in 10% formalin, and later transferred to 70% EtOH. Specimens are deposited in the Field Museum of Natural History (FMNH) with a portion to be returned to Museum of Zoology, University of Dar es Salaam (UDSM). We follow the taxonomy of Carleton & Stanley [30], Holden [31], Hutterer [32], and Musser & Carleton [33].

ETHICS STATEMENT

Permits for the collection and export of specimens were provided by the Tanzania Commission for Science and Technology (Ref# 2002-232-ER-90-172), the Tanzania Ministry of Natural Resources and Tourism (Wildlife Division; Ref# GD/R.40/1/22), and the Tanzania National Parks (Ref # TNP A44). Import of specimens into USA was approved by the US Fish and Wildlife Service (3177-W10214-9/18/02). Shrews and rodents were euthanized following the protocol approved by the American Society of Mammalogists [34], and the study was approved by the Field Museum of Natural History.

RESULTS

During the survey, we accumulated 11,562 sample-nights (8361 trap-nights and 3201 bucket-nights) and trapped 612 small mammals, including 319 shrews representing 6 species, and 293 rodents representing 10 species (Tables 2, 3, 4).

Sampling success for shrews was significantly greater in buckets than in traps (X^2 = 695.2, P < 0.05), and significantly more rodents were caught in traps than in buckets (X^2 = 44.8, P < 0.05), a pattern observed in past studies on small mammals of Tanzania [8], [23], [24]. In 8361 trap-nights, 283 mammals were captured for an overall trap success of 3.4%. Of the mammals caught in traps, 263 were rodents (3.1% trap success for rodents) and 20 were shrews (0.2% trap success). In the 3201 bucket-nights, 329 mammals were captured for a total bucket success of 10.3%. Of these, 299 were shrews (9.3% success) and 30 were rodents (0.9% success). This striking pattern was evident not only across the entire survey, but also at each of the five sites sampled (Table 2). Shrew species caught in traps included *Crocidura allex*, *C. monax*, *C. olivieri*, and *Myosorex zinki* (weighing between 3.6-51.0 g). While most of the rodents caught in buckets were relatively small (i.e. *Dendromus insignis*; 7-20 g), both specimens of *Tachyoryctes daemon* (240-290 g) were captured in buckets. Other rodent species captured in buckets included *Grammomys dolichurus*, *Graphiurus murinus*, *Praomys taitae*, and *Rhabdomys dilectus*.

The number of captures (and overall sample success) at each elevational site ranged from 54 [2.4%] at 3500 m to 151 [6.8%] at 2000 m (Table 2). For shrews alone, the lowest values were observed at the 4000 m site (34 [1.5%]) and the highest values at the 3000 m site (88 [3.6%]; Tables 2, 3). For rodents, the lowest (6 [0.3%]) and highest (87 [3.9%]) values were observed at the 3500 m and 4000 m sites, respectively (Tables 2, 4). The cumulative number of species trapped reached an asymptote at all sites except 2500 m site (Figure 2), where *Dendromus insignis* and *Otomys angoniensis* were captured on the last day of trapping.

We examined the relationship of four daily capture parameters (number of individuals, number of species, number of new species [i.e. previously unsampled at a given site], and cumulative number of species) with cumulative sample-nights for both type of trapping methodology (Table 5) and mammalian order (Table 6). We chose cumulative sample-nights instead of day of sampling period because of the differences in sampling effort among sites (Table 2). Based on correlation analysis, there was a significant positive correlation between cumulative sample-nights and cumulative species across all sites for trap lines, bucket lines and both sampling methods combined (Table 5). The same pattern was generally evident at each site, although, in some cases, correlation values were high, but not significant. The correlation of the cumulative number of shrew species caught in buckets with cumulative number of bucket nights was significant at the 2500 m site, and high at all other sites. For both shrews and rodents, there was generally a negative correlation between cumulative sampling effort and new species captured. Notable exceptions include trap lines at the 3000 and 3500 m sites. There was no notable correlation between the number of species and cumulative sampling effort across the entire transect or at each site, with the exception of shrew species captured in buckets at the 2000 m site. The correlation between number of individuals and sampling effort varied among sites. There was a significantly negative pattern exhibited by pitfall lines and both trap and pitfall lines combined at the 3500 m site, but no such relationship exhibited at the 3000 and 4000 m sites. Table 6 presents the same analyses as Table 5, but is focused on the taxonomic groups sampled, and the patterns are similar.

The effect of rainfall on captures is presented in Table 7. Generally, there was a stronger and more positive correlation between rainfall and daily captures of shrews, than there was for rodents. Over the entire transect, the capture of individual shrews in both buckets and traps was significantly correlated with the amount of rainfall each day, but the capture of individual rodents was not. A graphic representation of the differences between shrew and rodent captures with respect to rainfall amount is presented in Figure 3. The overall relationship between rainfall and captures of shrews was not as strong as in other elevational surveys of mammals in Tanzania [8].

There was a significantly negative relationship between elevation and the total number of shrew species collected (Table 8). Additionally, elevation was negatively correlated with total number of individual shrews collected and sample success for shrews, with *r* values high, but not significant. Rodents showed no such notable pattern. The relationship between elevation and total sample success, number of individual mammals, and number of species collected for shrews and rodents combined was generally negative, but not significant. The least number of mammals, and species collected was at the 3500 m site. The greatest number of individuals noted was at the lowest site (2000 m), and the highest species diversity was observed at the 3000 m site. In most cases, the forested sites showed greater abundance and species diversity than the habitats above tree line (Tables 2, 3, 4).

Captures in any individual trap or bucket were rare events. Although there was a 10.3% bucket success for all mammals captured, and 329 animals (299 shrews and 30 rodents) were collected in 385 buckets (77 buckets installed at each of five sites), most buckets captured no animals. Over the entire survey, 203 buckets caught nothing, 100 took one animal, 43 trapped two, 26 captured three, 7 caught four animals, 3 collected five animals, 2 trapped six animals, and ten animals were found in one bucket. Traps showed a similar pattern with 3.4% trap success in 1040 individual traps, and 283 captures (263 rodents and 20 shrews), but 834 traps caught nothing, 148 one, 42 two, 13 three and 3 four. To test for "trap competition" and to determine if captures were independent with respect to each other, we compared the observed distribution of captures by bucket and by trap to the Poisson distribution. Neither captures by buckets or traps followed the Poisson distribution (G-test for goodness of fit = 84.0 for buckets, 10.0 for traps; $p< 0.01$) suggesting a lack of trap or bucket independence. Significantly fewer traps or buckets caught one individual than would have been expected based on the assumption that the frequency of captures follows a Poisson distribution, and significantly more caught 2, or more, than expected [7].

DISCUSSION

Sixteen species of mammal (6 shrews and 10 rodents) were recorded along an elevational transect from roughly 2000 to 4000 m on the southeastern slope of Mt. Kilimanjaro (images of select taxa are presented in Figure 4). Only one of these (*Myosorex zinki*) is endemic to the massif, and none were introduced taxa. The other species have broader distributions, to varying degrees. For example, among the soricomorphs, *Crocidura monax* has been recorded in neighboring mountains within the Eastern Arc Mountains to the southeast of Kilimanjaro, including the North Pare and West Usambara Mountains. *Crocidura allex* is known from other mountains of the northern highlands of Tanzania (Meru, Ngorongoro) and the highlands of Kenya (Kenya, Aberdares). *Crocidura hildegardeae* and *Sylvisorex granti* are distributed across Kenya and the montane habitats of the Albertine Rift. Finally, *Crocidura olivieri* is broadly distributed across much of the African continent [32]. Among the ten species of rodents recorded, most are variably distributed across eastern Africa, and some range over larger regions of Africa. For example, *Tachyoryctes daemon* is restricted to northern Tanzania, but murines such as *Grammomys dolichurus* and *Rhabdomys dilectus* range across much of eastern and southern Africa, as does the dormouse, *Graphiurus murinus* [31], [33]. However, many taxonomists have cautioned that some of these soricomorph and rodent taxa are almost certainly species complexes, and work in progress may alter our taxonomic understanding of these groups [31], [32], [33].

We found no species not previously documented on the mountain. There are several published faunal lists for Kilimanjaro, the most complete being that of Grimshaw *et al.* [13], who evaluated the accuracy of previous published records, and developed a working list of likely residents of the mountain. While this list includes every species we documented, there are other small mammals listed by Grimshaw *et al.* [13] that we did not document. For example, among shrews, we have no record of *Crocidura luna*. This species was listed by Grimshaw *et al.* [13] based on voucher specimens at the FMNH, collected at 1400 m, an elevation below our lowest sampling site (2000 m). Similarly, many rodent species listed by Grimshaw *et al.* [13] occur at elevations lower than the range of this study. Examples include genera such as *Aethomys, Arvicanthis, Lemniscomys*, *Mastomys*, *Pelomys* and *Tatera*. One rodent historically recorded in our elevation sampling range but absent from animals we captured is *Otomys typus* (= *O. orestes zinki*; [35]). The holotype of *O. zinki* Bohmann 1943 was collected at Horombo Hut [36], [37], but the only two species of *Otomys* we documented were *O. angoniensis* and *O. tropicalis*. Two other rodents are notably absent from our inventory: *Beamys hindei* and *Hylomyscus arcimontensis*. Both are residents in forests of the Eastern Arc (including the North Pare Mountains roughly 50 km SE of Kilimanjaro) and Southern Highlands [38], [39], but no voucher specimen is known for either species from Kilimanjaro, or other northern highland sites. The type locality of *Beamys hindei* is Taveta, Kenya [40], and Dieterlen [41] identified a skull collected by C.G. Schillings in 1903 at Moshi as *Beamys*. Both localities are at, or near the base of Mt. Kilimanjaro. While this is not the most common species recorded in recent surveys of montane habitats of Tanzania across the elevational range from 600 to 2000 m [8], [19], given the number of trap nights expended during this survey, we anticipate the capture of *Beamys* if it occurs in the forests of southeastern Kilimanjaro. Records of *Hylomyscus* on Meru [42] and Ngorongoro [43] are now attributed to *Praomys taitae* [30], [38]. Recent surveys of both Meru and Ngorongoro using techniques identical to this study did not record either *Beamys* or *Hylomyscus* (Stanley, unpubl. data). All of this leads us to the conclusion that neither *Beamys* nor *Hylomyscus* currently occur in the forests of Mt. Kilimanjaro.

The trap success for rodents was highest at 4000 m and lowest at the 3500 m site (Table 4). The very low number of rodent captures at 3500 m (three in 1600 trap nights; Table 2) was striking, and is the lowest trap success recorded in similar surveys in montane habitats of Tanzania [8], [19], [24], [39]. Shore & Garbett [14] trapped at 3500 m, roughly the same elevation as our fourth site, but on the Shira Plateau on the western slopes of Kilimanjaro. The species they documented (*Crocidura allex, Myosorex blarina zinki* [= *M. zinki*], *Dendromus mesomelas kilimandjari* [= *D. insignis*] and *Rhabdomys pumilio diminutus* [= *R. dilectus*] were the same as in our study at the 3500 m site. One species (*Otomys tropicalis*) recorded by Shore & Garbett at 3500 m was not trapped by us at that elevation, but was collected at sites both lower and higher than 3500 m. Notably, their trap success for small mammals (2.7%; 81 captures in 2995 trap nights) was much higher that of the 3500 m site in this study (0.2%; 3 captures in 1600 trap nights), although the period of the surveys (mid-July to early August) was similar in both studies and trapping extended over several days at each site. The bait used by Shore & Garbett [14] included fried coconut and peanut butter (as in our procedure) but also fish, nuts and oats. However, the 3500 m site in our study was in stark contrast to lower and higher sites along the same transect, leading us to hypothesize that different bait is not the explanation for the lower rodent trap success at 3500 m in this study compared to the patterns documented by Shore & Garbett [14]. One potential explanation might be the proximity of Horombo Hut (3°8'20"S, 37°26'18"E) which was approximately 600 m from our trap lines (no other sites in this study were close to human habitation). The buildings and discarded flour and other foodstuffs generated by people occupying this touristic camp provide shelter and food for rodents. Indeed, while visiting Horombo on 8 and 10 August, we saw many *Rhabdomys* moving between buildings. Both repeating our sampling methodology at our site, and sampling with the same techniques at, and at increasing distances from Horombo would be illustrative of the influence of human habitation on the abundance of native rodents in the environs of Kilimanjaro.

Mulungu *et al.* [15] published the results of two elevational transects of Kilimanjaro (along the Shira and Marangu routes) that focused on shrews and rodents.

While total trapping effort was less than half of the current study (3600 vs 8361 trap nights), the recorded trap success was much higher (up to 36%). We attribute the higher success of Mulungu *et al.* [15] to the fact that traps were in place for only two nights at each site, and thus a reduction in capture rates typical of longer periods of time was not observed. The soricomorph and rodent species documented by Mulungu *et al.* [15] were identical to this study, with the exception of *Mus triton*, which they recorded at 2300 and 3270 m. *Lophuromys aquilus* was recorded at 3200 and 3590 m by Mulungu *et al.* [15] but our study did not record this rodent above 3000 m. However, one *Lophuromys* was brought to us by a Tanzanian National Parks employee who captured it at Horombo Hut (3760 m). The presence of other species at various elevations documented by Mulungu *et al.* [15] mirrored patterns observed during this study.

As in past studies within Tanzania, the combination of traps and pitfall lines were effective in sampling non-volant small mammal communities at different elevations on Mt. Kilimanjaro [8]. In general, species accumulation curves reached a plateau at each site, with the exception of the 2500 site where we captured *Dendromus insignis* and *Otomys angoniensis* for the first time during the last 24-hours of trapping. Notwithstanding the 2500 m pattern, we are confident that we documented almost all of the species of shrews and small rodents occurring at each site, and thus feel justified in comparing results among different elevational sites of this transect, as well as to results of similar surveys within Tanzania [8].

There was a significantly negative correlation between elevation and shrew species diversity at each site, and while not significant, there was generally lower abundance (as measured by sample success) for shrews as elevation increased (Table 8). However, rodents showed no notable correlation with elevation, either in diversity or abundance. This is in contrast to the patterns observed in the Udzungwa Mountains [8], where diversity and abundance of rodents were positively and significantly correlated with elevation. The same trends were not observed for shrews in the Udzungwas. Another difference between the Udzungwa and Kilimanjaro studies was seen in the overall measures of sample success in relation to elevation. Stanley & Hutterer [8] found either significant or high positive correlations between elevation and total sample success, number of individual mammals, and number of species collected for shrews and rodents combined. Such a relationship on Mt. Kilimanjaro was negative but not statistically significant. Whereas there was no mid-elevational peak (sensu McCain [10]) in the Udzungwa study, the greatest diversity of shrews and rodents on Kilimanjaro was at 3000 m, in the middle of our transect. Indeed, this site was situated at the ecotone between forest and heathland, and species typical of both habitats were present. For example, this was the highest, and lowest site where *Praomys taitae* and *Rhabdomys dilectus*, respectively, were documented and the only site where the two species were found together. In general, there was more species diversity for both shrews and rodents in forest habitats than above treeline (Tables 2,3,4).

Rainfall generally influenced the capture of shrews, but not rodents as was observed in the faunal inventories in the Udzungwa Mountains [8]. Thus, rainfall amounts while sampling shrew diversity or abundance should be considered. In addition, there was a lack of capture independence among traps and buckets across the entire transect and at each site. Stanley & Hutterer [8] documented similar results in the Udzungwa Mountains, and hypothesized that multiple captures are influenced by the placement of individual traps and buckets. More specifically, while traps cannot catch more than one animal, generally, buckets can capture more than one on a given bucket-night. The possibility exists that the presence of a captured animal in a bucket may attract other animals into that bucket.

The only endemic mammal, as currently understood, on Mt. Kilimanjaro is *Myosorex zinki* [44]. Until this survey, and that of Mulungu *et al*. [15], *M. zinki* was only known from a few specimens captured in the moorland habitats above tree line [14]. This species was documented across the elevational range of 2500 to 4000 m in this survey [45] and between 2500 to 2600 m by Mulungu *et al.* [15]. Thus, this endemic shrew extends across several different habitats on the mountain. *Myosorex zinki* was not observed at our lowest sampling site (2000 m). Stanley *et al.* [45] suggest that human impact on the forests at 2000 m on the Maua route may be responsible for the absence of this endemic mammal, but this hypothesis has not been adequately tested.

Three species (2 shrews and 1 rodent) were found at all sites sampled and occur across the range from roughly 2000 to 4000 m: *Crocidura allex*, *Sylvisorex granti*, and *Dendromus insignis*. The latter was found in the highest trap set in the survey (3° 6.481’ S, 37° 25.312’ E, 4240 m, on the ridge leading to West Lava Hill), and four individuals of this species were collected in this single trap (a Museum Special). How high small mammals extend on Kilimanjaro remains unanswered.

Wild dog (*Lycaon pictus*) is the only mammal (other than *Homo sapiens*) recorded at the summit (5895 m; [46]). However no small mammal surveys have been conducted above 4000 m, and such efforts would help elucidate the upper ranges of shrews and rodents on this unique and iconic mountain, and would further our understanding of its faunistic dynamics.

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REFERENCES

1. Patterson BD, Meserve PL, Lang BK (1989) Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. J Mammal 70: 67-78.

2. McCain CM (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. J Biogeogr 31: 19-31.

3. Md Nor S (2001) Elevational diversity patterns of small mammals on Mount Kinabalu, Malaysia. Glob Ecol Biogeogr 10: 41-62.

4. Heideman PD, Heaney LR, Thomas RL, Erickson KR (1987) Patterns of faunal diversity and abundance of non-volant small mammals on Negros Island, Philippines. J Mammal 68: 884-888.

5. Heaney LR, Heideman PD, Rickart EA, Utzurrum RB, Klompen JSH (1989) Elevational zonation of mammals in the central Philippines. J Trop Ecol 5: 259-280.

6. Rickart EA, Heaney LR, Utzurrum RB (1991) Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. J Mammal 72: 458-469.

7. Yu HT (1994) Distribution and abundance of small mammals along a subtropical elevational gradient in central Taiwan. J Zool 234: 577-600.

8. Stanley WT, Hutterer R (2007) Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. Acta Theriol 52: 261–275.

9. Goodman SM, Ganzhorn JU, Rakotondravony D (2003) Introduction to the Mammals. In: Goodman, SM, Benstead, JP, editors. The Natural History of Madagascar. Chicago: The University of Chicago Press. Pp. 1159-1186.

10. McCain CM (2005) Elevational gradients in diversity of small mammals. Ecology 86: 366-372.

11. Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. Science 322: 261-264.

12. Newmark, WD (1991) Priorities for the conservation of Mount Kilimanjaro. In: Newmark, WD, editor. The Conservation of Mount Kilimanjaro. IUCN, Gland, Switzerland and Cambridge, UK. pp. 111-114.

13. Grimshaw J, Cordeiro N, Foley C (1995) The mammals of Kilimanjaro. J East Afr Nat Hist 84: 105–139.

14. Shore RF, Garbett SD (1991) Notes on the small mammals of the Shira Plateau, Mt. Kilimanjaro. Mammalia 55: 601-607.

15. Mulungu LS, Makundi RH, Massawe AW, Machang'u, RS, Mbije, NE (2008) Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. Mammalia 72: 178-185.

16. Thompson LG, Brecher HH, Mosley-Thompson E, Hardy DR, Mark BG (2009) Glacier loss on Kilimanjaro continues unabated. Proc Natl Acad Sci USA 106: 19770-19775.

17. Goodman SM, Newmark WD, Stanley WT, Howell KM (1995) The Ambangulu Forest, West Usambara Mountains, Tanzania: a threatened Eastern Arc forest. Oryx 29: 212–214.

18. Stanley WT, Kihaule PM, Howell KM, Hutterer R (1998) Small mammals of the Eastern Arc Mountains, Tanzania. J East Afr Nat Hist 87: 91–100.

19. Stanley WT, Goodman SM (2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 4. Rodentia. In: Stanley WT, editor. Studies of Montane Vertebrates of Tanzania. Fieldiana Life Earth Sci 4: 53–73.

20. Sampson, DN (1965) The geology, volcanology and glaciology of Kilimanjaro. Tanzan Notes Rec 64: 118-124.

21. Hanby, J (1987) Kilimanjaro National Park. Tanzania National Parks/Africa Wildlife Foundation.

22. Mwasaga, BC (1991) The natural forest of Mount Kilimanjaro. In: Newmark, WD, editor. The Conservation of Mount Kilimanjaro. IUCN, Gland, Switzerland and Cambridge, UK. pp. 111-114.

23. Stanley WT, Goodman SM, Hutterer R (1996) Notes on the insectivores and elephant shrews of the Chome Forest, South Pare Mountains, Tanzania (Mammalia: Insectivora and Macroscelidea). Zool Abh 49: 131–148.

24. Stanley WT, Goodman SM, Kihaule PM (1998) Results of two surveys of rodents in the Chome Forest Reserve, South Pare Mountains, Tanzania (Mammalia: Rodentia). Zool Abh 50: 145–160.

25. Stanley WT, Goodman SM, Kihaule PM, Howell KM (2000) A survey of the small mammals of the Gonja Forest Reserve, Tanzania. J East Afr Nat Hist 89: 73–83.

26. Stanley WT, Nikundiwe AM, Mturi FA, Kihaule PM, Moehlman PD (2005) Small mammals collected in the Udzungwa Mountains National Park, Tanzania. J East Afr Nat Hist 94: 203–212.

27. Stanley WT, Rogers MA, Howell KM, Msuya CA (2005) Results of a survey of small mammals in the Kwamgumi Forest Reserve, East Usambara Mountains, Tanzania. J East Afr Nat Hist 94: 223–230.

28. Stanley WT, Goodman SM, Hutterer R (2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 2. Families Soricidae (Shrews) and Macroscelididae (Elephant Shrews). In: Stanley WT, editor. Studies of Montane Vertebrates of Tanzania. Fieldiana Life Earth Sci 4: 18–33.

29. Stanley WT, Goodman SM, Newmark WD 2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 1. Study areas, methodologies, and general results. In: Stanley WT, ed. Studies of Montane Vertebrates of Tanzania. Fieldiana Life Earth Sci 4: 1–17.

30. Carleton MD, Stanley WT (2012) Species limits within the *Praomys delectorum* group (Rodentia: Muridae: Murinae) of East Africa: A morphometric reassessment and biogeographic implications. Zool J Linn Soc 165: 420-469.

31. Holden ME (2005) Family Gliridae. In: Wilson DE, Reeder DM, editors. Mammal species of the world: A taxonomic and geographic reference, Third Edition. Baltimore: Johns Hopkins University Press, pp. 819–841.

32. Hutterer R (2005) Order Soricomorpha. In: Wilson DE, Reeder DM, editors. Mammal species of the world: A taxonomic and geographic reference, Third Edition. Baltimore: Johns Hopkins University Press, pp. 220–299.

33. Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE, Reeder DM, editors. Mammal species of the world: A taxonomic and geographic reference, Third Edition. Baltimore: Johns Hopkins University Press, pp. 894–1531.

34. Sikes RS, Gannon WL and the Animal Care and Use Committee of the American Society of Mammalogists. (2011) Guidelines of the American

Society of Mammalogists for the use of wild mammals in research. J Mammal 92: 235-253.

35. Carleton MD, Schaefer Byrne E (2006) The status of *Otomys orestes dollmani* Heller, 1912 (Muridae: Otomyinae), a rodent described from the Mathews Range, central Kenya. Proc Biol Soc Wash 119: 477–515.

36. Swynnerton GH, Hayman RW (1951) A checklist of the land mammals of the Tanganyika Territory and Zanzibar Protectorate. J East Afr Nat Hist 20: 274–392.

37. Child GS (1965) Some notes on the mammals of Kilimanjaro. Tanzan Notes Rec 64: 77-89.

38. Carleton MD, Stanley WT (2005) Review of the *Hylomyscus denniae* complex in Tanzania, with description of a new species. Proc Biol Soc Wash 118: 619–646.

39. Stanley WT, Kihaule PM, Munissi MJ (2007) Small mammals of two forest reserves in the North Pare Mountains, Tanzania. J East Afr Nat Hist 96: 215–226.

40. Thomas, O (1909) New African small Mammals in the British Museum Collection. Ann Mag Nat Hist 8: 98-112.

41. Dieterlen, F. (1979) Der früheste Fund der afrikanischen Kleinen Hamsterratte (*Beamys hindei*) (Cricetomyinae; Cricetidae; Rodentia) Stuttgarter Beitr zur Naturk ser. A 330: 1-3.

42. Demeter A, Hutterer R (1986) Small mammals from Mt. Meru and its environs (Northern Tanzania). Cimbebasia 8: 199–207.

43. Bishop IR (1979) Notes on *Praomys* (*Hylomyscus*) in eastern Africa. Mammalia 43: 521–530.

44. Stanley WT, Rogers MA, Hutterer R (2005) A morphological assessment of *Myosorex zinki*, an endemic shrew on Mount Kilimanjaro. Belg J Zool 135 Supplement: 141–144.

45. 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.

46. Thesiger, W (1970) Wild Dog at 5894 metres. E Afr Wildl J 8: 202.

FIGURE LEGENDS

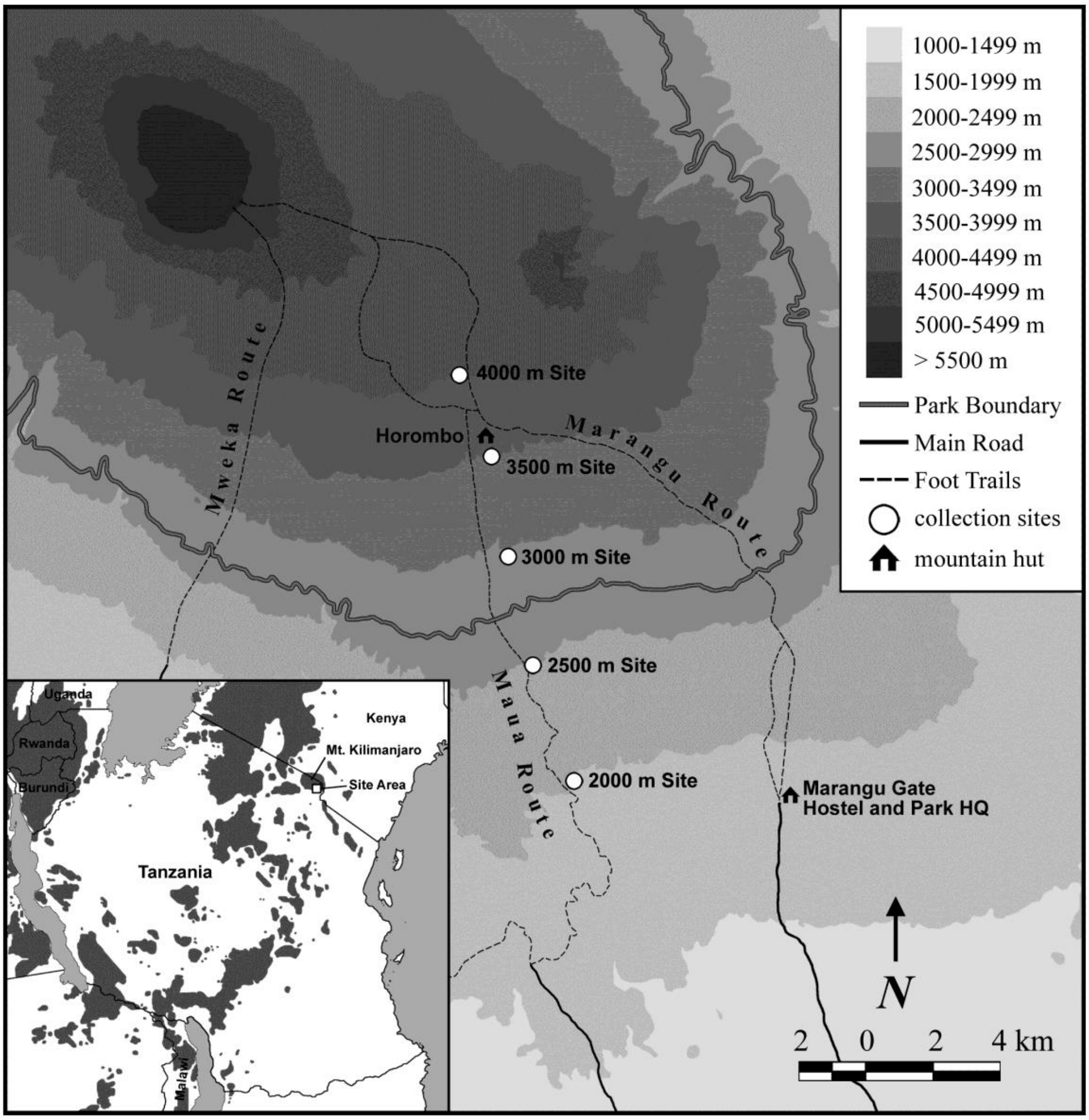

Figure 1. Map of Mt. Kilimanjaro showing routes, elevational contours and study sites.

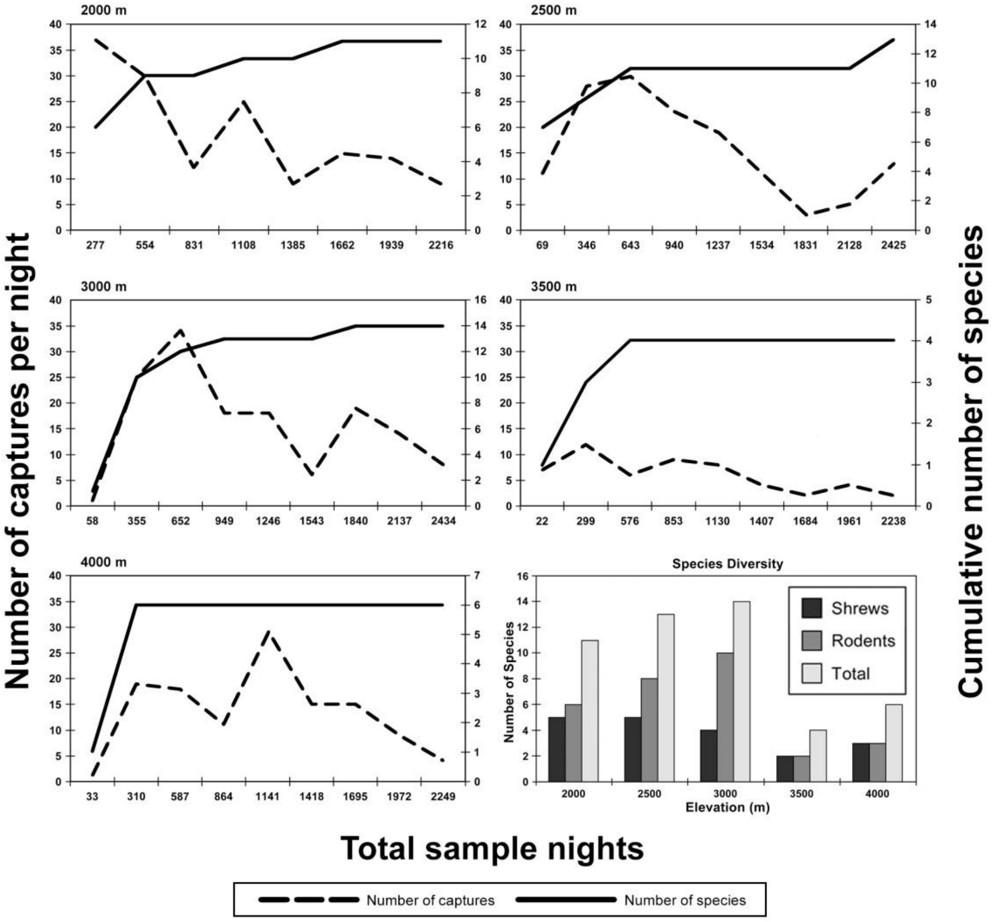

Figure 2. Species accumulation curves (for both pitfall and trap lines combined) for each site. The dashed lines represent the number of captures each day; the solid lines represent the cumulative number of new species for the site observed each day. The graph at the lower right shows the number of specimens of shrew, rodent and mammal captured at each site.

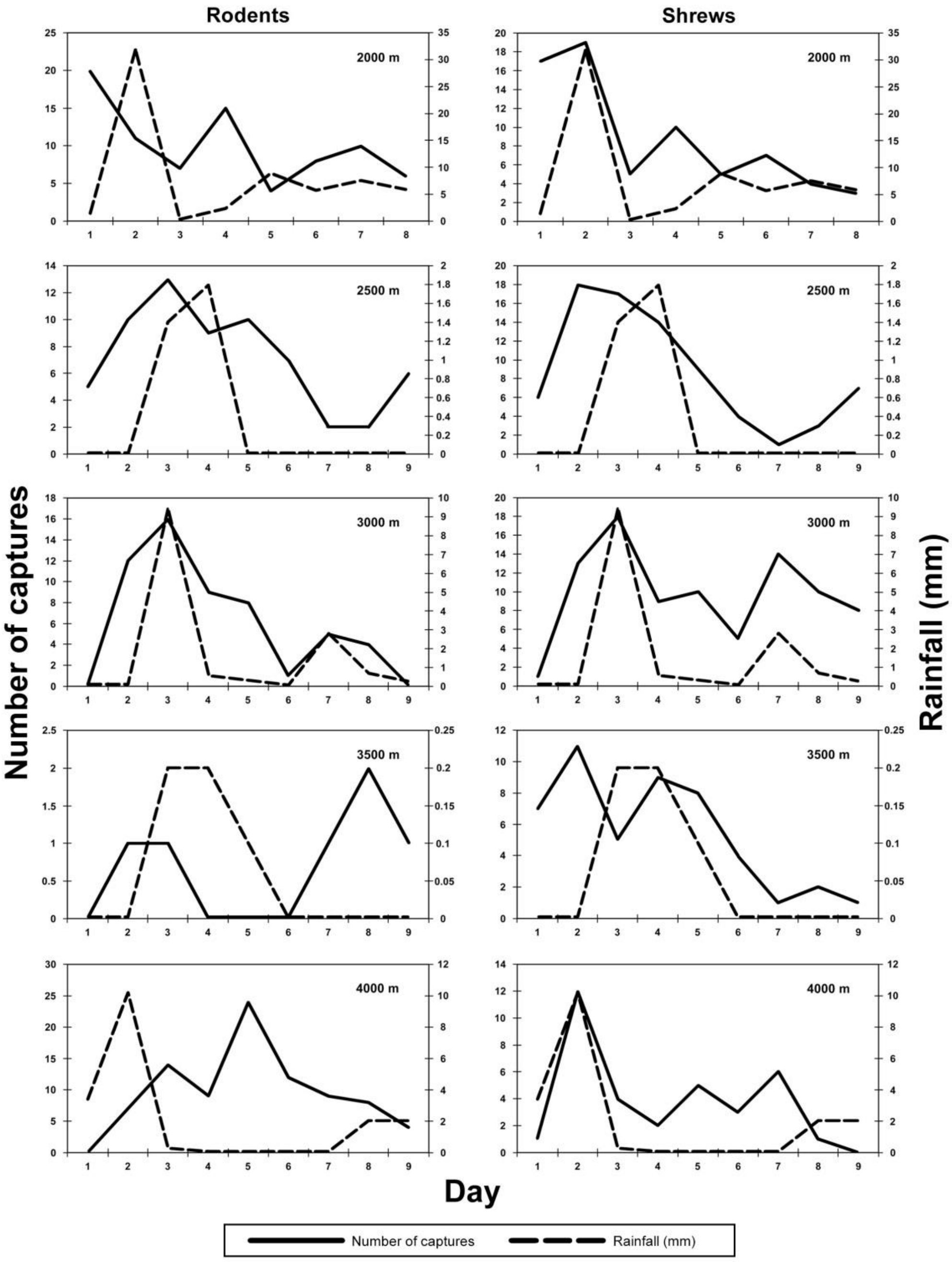

Figure 3. The relationship between numbers of individuals captured each day of the sampling period, and rainfall, at each site. Rodentia are on the left and Soricomorpha are on the right.

Table 1. Climatic data for each of the sites sampled on Mt. Kilimanjaro in July-August, 2002. Totals given as mean ± standard deviation, range and sample size (number of days measured). Sample size for rainfall is given as number of days monitored and (number of days with rain).

Elevation (m)	Daily Minimum Temperature (º C)	Daily Maximum Temperature (º C)	Daily rainfall (mm)
2000	8.5° ± 1.7 5 – 10º N = 9	14.1° ± 2.1 12 – 18° N = 8	4.2 ± 3.0 0 – 9 N = 9 (8)
2500	3.6° ± 2.2 1 – 6.5º N = 9	11.6° ± 1.9 9 – 15° N = 9	1.6 ± 0.3 0 – 1.8 N = 8 (2)
3000	2.2° ± 2.5 -2 – 5º N = 9	9.3° ± 2.5 6 – 12° N = 8	1.5 ± 3.1 0 – 9.5 N = 9 (6)
3500	-0.9° ± 1.2 -3 – 1º N = 9	12.3° ± 3.5 7.5 – 17° N = 8	0.1 ± 0.1 0 – 0.2 N = 8 (3)
4000	-6.8° ± 3.6 -12 – -1º N = 9	20.5° ± 5.9 11 – 25.5° N = 8	1.5 ± 3.4 0 – 10.2 N = 9 (3)

Table 2. Trapping totals for rodents and shrews by trap technique on the southeastern slope of Mt. Kilimanjaro in July-August, 2002.

Elevation	2000 m	2500 m	3000 m	3500 m	4000 m	Totals
BUCKETS						
# bucket-nights	616	649	649	638	649	3201
# individuals	84	75	86	51	33	329
(% bucket success)	(13.6)	(11.5)	(13.2)	(8.0)	(5.1)	(10.3)
# species	10	5	7	3	5	13
# shrews	68	74	79	48	30	299
(% bucket success)	(11.0)	(11.4)	(12.2)	(7.5)	(4.6)	(9.3)
# shrew species	5	4	4	2	3	6
# rodents	16	1	7	3	3	30
(% bucket success)	(2.6)	(0.1)	(1.1)	(0.5)	(0.5)	(0.9)
# rodent species	5	1	3	1	2	7
TRAPS						
# trap-nights	1600	1776	1785	1600	1600	8361
# individuals	67	68	57	3	88	283
(% trap success)	(4.2)	(3.8)	(3.2)	(0.2)	(5.5)	(3.4)
# species	5	9	11	2	4	12
# rodents	65	63	48	3	84	263
(% trap success)	(4.1)	(3.5)	(2.7)	(0.2)	(5.2)	(3.1)
# rodent species	4	7	8	2	3	8
# shrews	2	5	9	0	4	20
(% bucket success)	(0.1)	(0.3)	(0.5)		(0.2)	(0.2)
# shrew species	1	2	3	0	1	4
TOTAL						
# sample-nights	2216	2425	2434	2238	2249	11562
# individuals	151	143	143	54	121	612
(% sample success)	(6.8)	(5.9)	(5.9)	(2.4)	(5.4)	(5.3)
# species	11	13	14	4	6	16

Table 3. Elevational distribution of Soricomorpha species along the southeastern slope of Mt. Kilimanjaro in July-August, 2002. Only specimens caught in traps or buckets are included in totals. [a] presence inferred from occurrence at lower and higher sites.

Elevation	2000 m	2500 m	3000 m	3500 m	4000 m	Totals
Species						
Crocidura allex	24	19	40	45	30	158
Crocidura hildegardeae	7	0	0	0	0	7
Crocidura monax	21	29	26	0	0	76
Crocidura olivieri	2	2	0	0	0	4
Myosorex zinki	0	3	4	3	3	13
Sylvisorex granti	16	26	18	0 [a]	1	61
Total # individuals	70	79	88	48	34	319
Total # species	5	5	4	2+1 [a]	3	6
Total # sample-nights	2216	2425	2434	2238	2249	11562
Sample success (%)	3.1	3.2	3.6	2.1	1.5	2.7
Total # caught in buckets	68	74	79	48	30	299
Total # bucket-nights	616	649	649	638	649	3201
Bucket success (%) for	11.0	11.4	12.2	7.5	4.6	9.3

Table 4. Elevational distribution of rodent species along the southeastern slope of Mt. Kilimanjaro in July-August, 2002. Only specimens caught in traps or buckets are included in totals. [a] presence inferred from occurrence at lower and higher sites.

Elevation	2000 m	2500 m	3000 m	3500 m	4000 m	Totals
Species						
Otomys angoniensis	0	1	1	0	0	2
Otomys tropicalis	0	4	1	0 [a]	7	12
Dendromus insignis	4	1	5	5	21	36
Dendromus melanotis	5	1	4	0	0	10
Grammomys	3	6	6	0	0	15
Lophuromys aquilus	23	25	17	0	0	65
Praomys taitae	37	25	3	0	0	65
Rhabdomys dilectus	0	0	11	1	59	71
Graphiurus murinus	9	1	5	0	0	15
Tachyoryctes daemon	0	0	2	0	0	2
Total # individuals	81	64	55	6	87	293
Total # species	6	8	10	2+1 [a]	3	10
Total # sample-nights	2216	2425	2434	2238	2249	11562
Sample success (%)	3.6	2.6	2.2	0.3	3.9	2.5
Total # caught in traps	65	64	48	3	84	264
Total # trap-nights	1600	1776	1785	1600	1600	8361
Trap success (%)	4.1	3.6	2.7	0.2	5.2	3.1

Table 5. Product-moment correlation coefficients (*r*) of cumulative sample-nights with four parameters of trap/bucket captures. Results are given for each sampling method for both targeted groups and everything captured. Values in parentheses represent strong but not significant correlations. * = $P \leq 0.05$; ** = $P \leq 0.01$

Daily cumulative sample-nights correlated with (across)	Number of individuals	Number of Species	New Species added	Cumulative species
Total				
traps (rodents only)	0.099	-0.131	-0.428**	0.713**
traps (all captures)	0.068	-0.168	-0.491**	0.778**
buckets (shrews only)	(-0.249)	-0.085	-0.161	0.673**
buckets (all captures)	-0.149	0.168	(-0.217)	0.875**
traps and buckets combined (all captures)	-0.049	-0.100	-0.404**	0.798**
2000 m				
traps (rodents only)	(-0.698)	0.231	(-0.540)	0.865**
traps (all captures)	-0.746*	-0.066	(-0.605)	(0.577)
buckets (shrews only)	-0.800*	(-0.668)	(-0.684)	(0.577)
buckets (all captures)	-0.698	0.126	-0.882**	0.900**
traps and buckets combined (all captures)	-0.786*	-0.425	-0.752*	0.883**
2500 m				
traps (rodents only)	(-0.541)	-0.353	-0.376	0.727*
traps (all captures)	-0.455	-0.262	(-0.515)	0.776*
buckets (shrews only)	(-0.660)	-0.374	(-0.542)	1.000**
buckets (all captures)	(-0.657)	-0.429	(-0.611)	0.722*
traps and buckets combined (all captures)	(-0.604)	-0.442	(-0.591)	0.819**
3000 m				
traps (rodents only)	-0.424	-0.287	-0.452	0.809**
traps (all captures)	-0.342	-0.177	-0.401	0.826**
buckets (shrews only)	-0.020	0.164	(-0.585)	(0.548)
buckets (all captures)	0.060	-0.137	-0.666*	0.730*
traps and buckets combined (all captures)	-0.213	-0.220	(-0.539)	0.747*
3500 m				
traps (rodents only)	0.169	0.169	-0.126	0.907**
traps (all captures)	0.169	0.169	0.247	0.907**
buckets (shrews only)	0.809**	-0.365	-0.725*	(0.548)
buckets (all captures)	-0.760*	0.000	(-0.645)	(0.548)
traps and buckets combined (all captures)	-0.776*	-0.274	-0.754*	0.675*
4000 m				
traps (rodents only)	-0.310	-0.252	(-0.577)	1.000**
traps (all captures)	-0.309	-0.314	(-0.577)	1.000**
buckets (shrews only)	-0.465	-0.438	(-0.645)	(0.548)
buckets (all captures)	-0.439	-0.259	(-0.628)	0.903**
traps and buckets combined (all captures)	-0.108	-0.030	(-0.523)	(0.548)

Table 6. Product-moment correlation coefficients (*r*) of shrew and rodent captures with four parameters of trap success. Values in parentheses represent strong but not significant correlations. * = $P \leq 0.05$; ** = $P \leq 0.01$.

Shrew and rodent captures correlated with (across)	Number of individuals	Number of Species	New species added	Cumulative species
Total, shrews	(-0.273)	-0.187	(-0.268)	0.726**
Total, rodents	0.074	-0.158	-0.496**	0.730**
2000 m, shrews	(-0.821)	(-0.668)	(-0.684)	(0.577)
2000 m, rodents	(-0.620)	0.063	0.724*	0.924**
2500 m, shrews	(-0.615)	-0.407	(-0.611)	0.722*
2500 m, rodents	(-0.539)	-0.412	-0.466	0.804**
3000 m, shrews	0.064	0.246	(-0.585)	(0.548)
3000 m, rodents	-0.440	-0.355	(-0.488)	0.794*
3500 m, shrews	-0.803**	-0.365	-0.725*	(0.548)
3500 m, rodents	0.452	0.000	(-0.518)	0.710*
4000 m, shrews	-0.398	-0.438	(-0.645)	(0.548)
4000 m, rodents	0.081	0.405	-0.411	(0.548)

Table 7. Product-moment correlation coefficients (*r*) of amount of daily rainfall with four parameters of shrew and rodent daily captures. All captures (both traps and pitfalls) of each group are included. * = $P \leq 0.05$; ** = $P \leq 0.01$

Rainfall amount correlated with (across)	Number of individuals	Number of Species	New species added	Cumulative species
Total, shrews (buckets and traps)	0.385*	0.422**	0.086	(0.277)
Total, rodents (buckets and traps)	0.190	(0.280)	(0.230)	0.053
2000 m, shrews	(0.523)	(0.655)	-0.025	0.262
2000 m, rodents	-0.108	(0.523)	0.424	-0.008
2500 m, shrews	(0.592)	(0.502)	-0.050	0.283
2500 m, rodents	(0.544)	0.201	-0.217	0.096
3000 m, shrews	0.719*	0.199	-0.246	0.187
3000 m, rodents	(0.644)	(0.487)	0.139	0.122
3500 m, shrews	0.363	0.378	-0.357	0.236
3500 m, rodents	-0.267	-0.060	0.286	0.334
4000 m, shrews	(0.629)	(0.652)	0.950**	-0.160
4000 m, rodents	-0.411	-0.086	0.927**	-0.160

Table 8. Product-moment correlation coefficients (*r*) between elevation and trap success. Values in parentheses represent strong but not significant correlations. Significant relationships (P < 0.05) are in bold.

Elevation correlated with	(*r*)	P
Total number of individual mammals collected	-0.59	> 0.05
Total trap success	-0.59	> 0.05
Total number of species collected	-0.68	> 0.05
Total number of shrews collected	(-0.73)	> 0.05
Shrew trap success	(-0.79)	> 0.05
Total number of shrew species collected	**-0.95**	**< 0.05**
Total number of rodents collected	-0.23	> 0.05
Rodent trap success	-0.21	> 0.05
Total number of rodent species collected	-0.56	> 0.05

Phylogeny, phylogeography, and geographic variation in the *Crocidura monax* (Soricidae) species complex from the montane islands of Tanzania, with descriptions of three new species

IN PRESS IN ZOOLOGICAL JOURNAL OF LINNEAN SOCIETY

WILLIAM T. STANLEY[1]*, RAINER HUTTERER[2], THOMAS C. GIARLA[3], and JACOB A. ESSELSTYN[3]

[1] *Science and Education, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, IL 60605 USA*
[2] *Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany.*
[3] *Museum of Natural Science and Department of Biological Sciences, Louisiana State University, 119 Foster Hall, Baton Rouge, LA 70803 USA*

*Corresponding author. William T. Stanley, Science and Education, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605 USA. E–mail: bstanley@fieldmuseum.org

Running head: Systematics of *Crocidura monax*

ABSTRACT

We assess morphological and multilocus genetic variation among eleven isolated montane populations of white-toothed shrews from Tanzania that have been referred to either *Crocidura monax* Thomas or *C. montis* Thomas. The montane sites we sampled represent “sky-islands” from two geologically distinct archipelagos (Northern Highlands and the Eastern Arc Mountains) and are a significant component of the Eastern Afromontane Biodiversity Hotspot. We used multivariate analyses of morphometric traits and phylogenetic and species-delimitation analyses of multilocus DNA sequence data to assess species-level diversity. Our species delimitation analyses included a novel, pairwise validation approach that avoids potential biases associated with specifying a guide tree. These analyses reveal several distinct lineages, which we treat as six allopatric species. Each species is restricted to one, two or four mountains. We use available names to recognize *C. monax, C. tansaniana* Hutterer, and *C. usambarae* Dippenaar, while naming and describing three new species. Our results demonstrate the effectiveness of combining morphological and genetic data to uncover and describe hidden diversity in a cryptic mammalian system.

ADDITIONAL KEYWORDS: *Crocidura* – Eastern Arc Mountains – Northern Highlands – Soricomorpha – species delimitation – taxonomy – morphometrics

INTRODUCTION

Integrative systematic studies of small mammals continue to document the common failure of taxonomic hypotheses to reflect evolutionary history, especially among the small mammal faunas of montane tropical regions (Carleton & Goodman, 1998; Taylor *et al.*, 2009; Heaney *et al.*, 2011). The diversity of some groups, such as shrews (order Soricomorpha), has proven especially difficult to untangle because of an apparently conservative morphology at broad taxonomic scales. Taxonomic resolution in groups such as these can often be greatly enhanced by combining morphological and genetic data to infer relationships and delimit species.

The montane vertebrates of Tanzania have been the focus of biological study for over a century, gaining increased attention in the past three decades (Moreau, 1966; Bowie *et al*., 2004; Davenport *et al*., 2006; Lawson, 2010; Menegon *et al*., 2011). Nevertheless, the fauna is only coarsely documented, as evidenced by discoveries of new species, including large, charismatic mammals (e.g. Davenport *et al.* 2006). Shrews inhabit montane and submontane environments (sensu Lovett, 1993) in Tanzania and show the highest level of endemism and the most restricted distributions among mammals of these habitats. Examples include *Myosorex zinki* Heim de Balsac & Lamotte (Mt. Kilimanjaro only), *Congosorex phillipsorum* Stanley, Rogers & Hutterer (Udzungwa Mountains only), *Crocidura telfordi* Hutterer (Uluguru and Udzungwa Mountains only) and *Sylvisorex howelli* Jenkins (Eastern Arc Mountains [EAM] only; Hutterer, 2005; Stanley & Olson, 2005; Stanley *et al.*, 2005). Several other shrew species in the region are considered more widespread (e.g. *Crocidura hildegardeae* Thomas, *C. luna* Dollman, and *C. monax* Thomas), but it is not clear whether these broad distributions are real or reflect a lack of taxonomic resolution.

Crocidura monax was described from a series of 8 specimens collected near the German mission at Rombo (6000'; 1829 m), on the eastern slope of Mt. Kilimanjaro. The description emphasized the “almost bristleless tail” with only a “few scattered ones [bristles] on the basal third” (Thomas, 1910). The author compared the new species to *C. turba* Dollman (stating that *C. turba* had many more bristles on the tail), *C. fumosa* Thomas (*C. fumosa* is smaller and has more bristles on the tail) and *C. maurisca* Thomas (*C. maurisca* is smaller). Subsequently, *C. monax* has been considered part of the *C. littoralis* Heller species complex (Heller, 1910; Heim de Balsac & Meester, 1977; Dieterlen & Heim de Balsac, 1979; Hutterer, 2005), together with *C. oritis* Hollister and *C. ultima* Dollman. Dieterlen and Heim de Balsac (1979) differentiated *C. monax* from *C. littoralis* based on the larger upper molars and premolars of the former. Hutterer (2005) included *C. oritis* within *C. littoralis*. Dollman (1915) differentiated *C. monax*, with its similarly sized second and third upper unicuspids from *C. ultima*, which has a second unicuspid much smaller than its third unicuspid.

Dippenaar (1980) defined the "*C. monax-dolichura* complex" as having low pilosity on the tail, with hairs restricted to the basal section. He included *C. monax, C. ultima, C. maurisca, C. littoralis, C. lanosa* Heim de Balsac, *C. kivuana* Heim de Balsac, *C. niobe* Thomas, *C. dolichura* Peters and *C. latona* Hollister in his study. However, the tail of *C. dolichura* is longer than the head and body, a condition not seen in the other species listed above (including *C. monax*). Moreover select cranial measurements of *C. kivuana, C. niobe*, and *C. latona* fall well below those of *C. monax* (Thomas, 1906; Hollister, 1916; Heim de Balsac, 1968). In addition, *C. lanosa* has a thicker pelage and larger skull than *C. monax* according to Heim de Balsac (1968), suggesting that Dippenaar's grouping was overly inclusive.

As part of his work on the *monax-dolichura* group, Dippenaar (1980) also described *C. usambarae* Dippenaar from the Lushoto (Shume and Magamba) area of the West Usambara Mountains. *Crocidura monax* and *C. usambarae,* as defined by Dippenaar, are allopatric, with *C. monax* on Kilimanjaro and *C. usambarae* in the West Usambaras. The two forms are not distinguishable in external proportions, but the cranium of *C. usambarae* is smaller (Dippenaar, 1980). Dippenaar (1980) also distinguished *usambarae* from *C. littoralis, C. maurisca* and *C. ultima* based on differences in various cranial dimensions.

Subsequently, Hutterer (1986) described *C. tansaniana* Hutterer from the East Usambara Mountains, showing that it was larger in cranial characteristics (especially the third upper molar) than *C. monax*. He described the *C. monax* group as containing *C. monax, C. tansaniana*, and *C. usambarae* and suggested that *C. monax* was found on mountains other than Kilimanjaro, a hypothesis repeated later when he stated that the distribution of *C. monax* is "montane forests in Northern Tanzania" (Hutterer, 2005). He also described *C. telfordi* Hutterer as endemic to the Eastern Arc Mountains, but, based on morphological characters, stated that this species is more closely related to *C. lanosa* than to *C. monax*.

Hutterer's (1986) suggestion that *Crocidura monax* is distributed more widely is consistent with some, but not all taxonomic delineations. Heim de Balsac and Meester (1977) regarded *C. ultima* as a subspecies of *C. monax* and thus included western Kenya in its range, but Jenkins (in Burgess *et al*., 2000) restricted *C. monax* to the type locality. Stanley *et al*. (2000b), in agreement with Hutterer (1986), stated that it occurred on a number of mountains within the Eastern Arc "archipelago" in Tanzania, including the East and West Usambara, Nguru, Uluguru and Udzungwa Mountains (Fig. 1).

Although *Crocidura monax* has never been explicitly recorded from Mt. Meru, which neighbors Mt. Kilimanjaro (Fig. 1), Hutterer (2005) stated that it might occur there. Demeter and Hutterer (1986) listed the small mammals of Mt. Meru and identified the larger shrews of the fauna as *Crocidura montis* Thomas. This form exhibits extensive pilosity on the tail, in stark contrast to the nearly naked tail of *C. monax*. However, the phylogenetic relationship of the Meru population to topotypical *C. montis* (Rwenzori Mountains) has never been assessed. Given the proximity of Meru to Kilimanjaro and other ranges that have records of *C. monax*, the relationship of the Meru shrews to those identified tentatively as *C. monax* deserves attention.

Over the past two decades, numerous inventories of wild mammals in montane habitats of Tanzania have produced series of specimens that now allow investigation of the phylogeny, phylogeography, and geographic variation of populations either identified as *Crocidura monax* or occurring on mountains neighboring the type locality. Details of many of these surveys have been published elsewhere (Stanley *et al*., 1996; Stanley *et al*., 1998; Stanley *et al*, 2003; Stanley *et al*., 2007; Stanley & Hutterer, 2007; Stanley & Esselstyn, 2010; Stanley *et al*., 2011b; Stanley, Rogers, Kihaule, & Munissi, 2014). In this paper, we analyze new molecular and morphological data from voucher specimens collected during these surveys to a) test existing hypotheses of the relationships among the geographically isolated populations of the *C. monax* group (sensu Hutterer, 1986); b) test the specific status of *C. tansaniana*; c) resolve the identity of the larger shrews on Mt. Meru most recently attributed to *C. montis*; and d) characterize the distribution, geographic variation, and biogeographic history of the *C. monax* group.

METHODS AND MATERIALS

Fieldwork

Specimens were collected during faunal surveys of the mountains of Tanzania by the first author (WTS) and biologists from the University of Dar es Salaam. We collected shrews in montane habitats on eleven isolated mountains in Tanzania, including (from north to south): Ngorongoro, Mt. Meru, Mt. Kilimanjaro, North Pare, South Pare, West Usambara, East Usambara, Ukaguru, Rubeho, Uluguru and Udzungwa (Fig. 1). Shrews were collected using pitfall lines consisting of eleven 15-liter buckets buried in the ground such that the top of the bucket was flush with the soil surface. Details are presented in Stanley *et al*. (2011). All specimens were handled in accordance with American Society of Mammalogists guidelines (Sikes *et al.*, 2011). Voucher material was prepared as skins, skulls and skeletons or in fluid and was deposited in the Field Museum of Natural History, Chicago. Heart, kidney, and liver tissues were frozen in liquid nitrogen or buffered in dimethyl sulfoxide (DMSO). WTS took external measurements from each specimen at the time of collection, which include total length (TL, tip of nose to last caudal vertebra), head and body (HB, tip of nose to where tail inserts on body), tail vertebrae length (TV, from where tail inserts on body to last caudal vertebra), hind foot (HF, from heel to tip of claw), ear (EAR, notch to tip of ear) and weight (WT; DeBlase & Martin, 1974). The only exceptions were some specimens from the West Usambara sample that were measured in the same manner by S. M. Goodman. All linear measurements are in millimeters (mm) and weight is in grams (g).

We obtained tissues of taxa referenced in previous taxonomic treatments of *C. monax* from the FMNH collection of tissues; most were collected as part of the long-term program of Julian Kerbis Peterhans (Kerbis Peterhans *et al.*, 2008; 2009; 2010) in montane habitats of the Albertine Rift.

Morphology

We studied external morphology on fluid specimens and dry skins under magnification. Details of skulls and teeth were examined with the aid of a dissecting microscope and drawings were made with a camera lucida attached to a microscope. The terminology follows Brown and Yalden (1973) for external features and Meester (1963) for cranial and dental characters.

Morphometrics

Skulls from adults (with complete fusion between the basioccipital and basisphenoid bones) collected by WTS were included in morphometric analyses.

Specimens were assigned to one of four ontogenetic categories of toothwear following the definitions of Dippenaar (1997), with a focus on the wear of the first upper molar. FMNH 151118, 151125, 151109, and 147205 exemplified categories I (youngest), II, III, and IV (oldest), respectively, and we used these as a reference series.

WTS used digital calipers (to the nearest 0.01 mm) to record the following craniodental measurements: condylo-incisive length (CI), basal length (BL), post-palatal length (PPL), length of entire upper toothrow (UTRL), least interorbital width (LIW), bimaxillary width (BW), nasal width (NW), greatest width of the braincase (GW), height of the braincase (PMH; measured by placing the skull on a microscope slide, measuring from the ventral surface of the slide to the highest point of the cranium and then subtracting the thickness of the slide from that measurement; J. Patton, pers. comm.), post-glenoid width (PGW), width of third upper incisor (I^3-W), width of upper canine (C-W), length of third upper molar (M^3-L), width of third upper molar (M^3-W), least distance across the maxillary plate parallel to the alveolar line (MP), length of mandible including the first incisor (M&I) and length of mandibular toothrow including first incisor (LTR). These variables follow Dippenaar (1977), van Zyll de Jong and Kirkland (1989), and Carraway (1990) and are illustrated in Stanley & Olson (2005).

WTS measured the variables detailed above in specimens of putative *Crocidura monax* from across Tanzania, putative *C. montis* from Mt. Meru, as well as type material of various taxa held in the FMNH, British Museum (Natural History), London (BMNH) and the Alexander Koenig Museum, Bonn (ZFMK). Additional specimens, collected during Tanzanian-Belgian rodent projects, were studied in the museum collections of Royal Museum for Central Africa, Tervuren (RMCA) and ZFMK. We calculated standard descriptive statistics (mean, range, standard deviation and coefficient of variation of each character) for each population. We tested for sexual dimorphism in external and cranial variables within each montane population with one-way analyses of variances (ANOVA). To test for geographical variation in morphology, a one-way ANOVA (effect = mountain) was used to identify characters that differed significantly among populations. Discriminant function analyses of log-transformed craniodental variables were conducted to assess multivariate patterns of variation. Variable loadings are presented as Pearson product-moment correlation coefficients of the derived components with the original cranial measurements. All statistical analyses were conducted using Systat (version 11).

DNA sequencing and analysis

We extracted, amplified, and sequenced various fragments of DNA from montane populations of the *Crocidura monax* species complex and several potentially related taxa. Laboratory protocols followed those of Esselstyn *et al.* (2009, 2013). We first sequenced 684 bp from the 3′ end of cytochrome b (CytB) in 267 specimens (APPENDIX I.). Initial phylogenetic analyses of these data indicated that *C. monax* is not a close relative of *C. dolichura*, *C. turba*, *C. telfordi*, *C. maurisca*, *C. latona*, *C. littoralis*, *C. oritis*, *C. kivuana*, or *C. niobe*. We therefore focused subsequent sequencing of nuclear DNA on *C. fumosa*, C. *monax*, *C. montis*, C. *tansaniana* and *C. usambarae*. We sequenced the nuclear exons breast cancer susceptibility 1 (BRCA), growth hormone receptor 10 (GHR) and von Willebrand factor 28 (vWF) in 84 specimens drawn from each montane population of these putative species. The three exons were subsequently used in species delimitation analyses (see below). We also sequenced fragments of apolipoprotein B (ApoB), brain derived neurotrophic factor (BDNF), mast cell growth factor (MCGF), prostaglandin E4 receptor (PTGER) and recombination activating gene 1 (RAG) from a subset of 17 individuals to provide independent estimates of the population-scaled mutation rate (θ) to guide prior probability selection in species delimitation analyses. A table of GenBank accession numbers (KP061859-KP062422) for all individuals sequenced is provided in online supporting information.

We estimated mitochondrial gene tree relationships with our CytB alignment, which contained sequences from 267 individuals. Sixteen sequences were incomplete at one or both ends of the alignment, but the matrix was 99.0% complete. We analyzed these data as a single partition. An appropriate model of sequence evolution was chosen among 88 candidates using the Bayesian information criterion and a fixed BIONJC tree in jModeltest 2.1.4 (Guindon & Gascuel 2003; Darriba *et al.* 2012). We estimated phylogenetic relationships and branch lengths in a Bayesian context using BEAST v. 2.1.3 (Bouckaert *et al.* 2014). We ran four independent Markov chain Monte Carlo analyses of 2×10^7 generations, with parameters sampled every 2000 generations. We applied a log-normal relaxed clock (mean = 1.0) model to account for rate heterogeneity among branches (Drummond *et al.* 2006). We applied a constant population size coalescent model to the topological inference. We examined convergence diagnostics, including the trends, distributions, and effective sample sizes of parameters, including the likelihood, in Tracer v1.5. We chose an appropriate burn-in based on this analysis.

We resolved nuclear DNA sequences to their constituent haplotypes with the PHASE software package (Stephens *et al.* 2001) and set the probability threshold to 70%, following Garrick *et al.* (2010). PHASE files were constructed and interpreted using SeqPhase (Flot 2010). We used the program BP&P (Yang and Rannala 2010) to test possible species limits among 12 geographically isolated populations within *C. fumosa*, C. *monax*, *C. montis*, C. *tansaniana*, and *C. usambarae*. BP&P can be thought of as testing species limits under the framework of the biological species concept because regular gene flow between two populations would lead to the analytical conclusion that they are the same species. Because we formulated our initial hypotheses based on geography and mitochondrial sequence variation, we used only nuclear exon sequences (BRCA, GHR, and vWF) to test the extent to which geographically isolated populations represent independently evolving lineages. BP&P requires that users define three priors: θ (mutation-rate-scaled effective population sizes), τ (the root divergence time), and a guide tree that the BP&P algorithm collapses and resolves in proportion to the posterior probability that a node in the guide tree represents a speciation event. In BP&P, gamma distributions $\Gamma(\alpha,\beta)$ are used to model priors for θ and τ, where the mean = α/β and variance = α/β^2. We chose the most appropriate θ prior by calculating Watterson's estimator, θ_W, in DnaSP v5 (Librado and Rozas 2009) from five nuclear loci not otherwise included in the BP&P analyses (four exons: ApoB, BDNF, PTGER, and RAG1; one intron: MCGF). These loci were sampled from a subset of 17 individuals included in the BP&P analyses.

Use of inappropriate priors or an incorrect guide tree in BP&P can bias posterior probabilities of species delimitation, potentially yielding false positives (Leaché and Fujita 2010; Yang and Rannala 2010). In order to assess how prior choice affects our results, we tested six sets of priors previously used by Giarla *et al.* (2014) that represent a range of effective population sizes and divergence times (Table 1). First, we conducted a series of replicated analyses using a guide tree based on the topology from the CytB phylogeny. For each of the six prior schemes, we conducted the analysis twice: once each with Yang and Rannala's (2010) algorithms 0 and 1. Next, to minimize the extent to which use of an incorrect guide tree might impact results, we conducted a series of BP&P analyses on subsets of the three-exon dataset. We constructed 66 pair-wise datasets, one for each potential population-pair of the 12 populations in the guide tree. For each pair-wise dataset, we conducted six analyses to explore each of the six prior schemes. For all of our BP&P analyses, we ran the MCMC chain for 550,000 generations, sampling every 5 generations and discarding the first 50,000 as burn-in.

RESULTS

Analysis of mitochondrial sequences

Our phylogenetic analyses of mitochondrial DNA appeared to converge within the first 2×10^6 generations and we discarded these as burn-in. Remaining samples were combined in LogCombiner (part of the BEAST package) from all four runs to generate the posterior distribution. Effective sample sizes for the posterior were >400 for all parameters. The resulting topology clearly separated populations within the *Crocidura monax* species complex from *C. dolichura*, *C. kivuana*, *C. lanosa*, *C. latona*, *C. littoralis*, *C. maurisca*, *C. niobe*, *C. oritis*, *C. stenocephala*, *C. telfordi* and *C. turba* (Fig. 2). Populations that comprise the *C. monax* complex form a mitochondrial clade with *C. fumosa*, *C. montis*, *C. tansaniana*, and *C. usambarae*. Within this clade, we found two monophyletic groups. Samples from Meru, (those currently referred to *C. montis*), Kilimanjaro, North Pare, South Pare (*C. usambarae*) and West and East Usambara (*C. tansaniana*) are monophyletic (but with little support) and sister to a topotypical sample of *Crocidura montis* from Rwenzori. Ngorongoro, Rubeho, Ukaguru, Uluguru and Udzungwa populations form a clade and are sister to samples of *Crocidura fumosa* (but with little support) from Mt. Kenya.

Species delimitation in BP&P

Sequence characteristics for the nuclear loci included in BP&P are reported in Table 2. Our guide-tree-based and pairwise BP&P results (Figs. 3 and 4, respectively) largely agree, but the two suites of analyses differ in notable areas. Those that rely on the guide tree (Fig. 3) support the recognition of 10 distinct groups, with only two pairs of populations receiving inconsistent or low support for distinctiveness across a range of prior schemes (West Usambara + East Usambara and Udzungwa + Uluguru). In the pairwise BP&P analyses (Fig. 4), three of the pairs receive low support across all prior schemes (Rubeho vs. Uluguru, Rubeho vs. Udzungwa, and Udzungwa vs. Uluguru), whereas 55 comparisons receive strong support for species distinctiveness ($PP > 0.90$) across all prior schemes. Eight pairwise comparisons show inconsistent results that apparently depend on the prior scheme used (i.e., a mixture of PPs above and below 0.90).

Our θ_W estimates (derived from an independent sample of five distinct nuclear loci not included in the BP&P analyses; Table 2) suggest that the prior schemes that assume large population sizes (Schemes 1–3) are not biologically realistic. Estimates for θ_W ranged from 0.0034 to 0.0052 (Table 2), values on the same order of magnitude as the mean of θ for the "small" population size priors (Schemes 4–6; θ prior with a mean equal to 0.001) and two orders of magnitude smaller than the mean of the "large" population size gamma distribution (Schemes 1–3; θ prior with a mean equal to 0.1). If we only consider Schemes 4–6, the South Pare, Meru, and Ngorongoro populations receive strong support as distinct species across all pairwise combinations (Fig. 4), and we ultimately assign each of those populations to their own species (see below). *Crocidura fumosa* is found to be distinct from all other populations across biologically realistic prior schemes 4, 5 and 6 in all comparisons but one. For the pairwise test between *C. fumosa* and the West Usambara population, application of Prior Scheme 6 (relatively shallow divergence and small population sizes) does not support each population as distinct. This result is surprising, because no previous assessment has suggested that these populations are closely related; we posit that this result may be an artifact of the small number of individuals we sequenced for *C. fumosa* and the West Usambara population (4 and 1, respectively). Given the morphological distinctiveness of *C. fumosa* and its divergent position in the CytB tree (Fig. 2), we do not consider this one BP&P result as compelling evidence for grouping *C. fumosa* with West Usambara.

Integrating morphological and molecular results

As we pointed out previously, certain phenotypic characters (e.g., pilosity of the tail, tail length relative to the length of the head and body, length of hairs in pelage, and cranial characters) argue against hypotheses of close relationships among some of the taxa historically associated with *C. monax* (Tables 3 and 4). For example, in contrast to the specimens representing the *C. monax* group of this study, *C. fumosa* and *C. turba* exhibit extreme pilosity over most of the tail and *C. dolichura* has a tail that is much longer than the length of the head and body. *Crocidura lanosa* has a longer hind foot (mean = 19.3 mm) and much denser, woolier pelage than the *C. monax* populations considered here (Dieterlen, 2013). *Crocidura latona* and *C. niobe* are both smaller in cranial measurements than *C. monax* (Table 4; Bober & Kerbis Peterhans, 2013; Churchfield *et al.*, 2013). The combination of CI, UTRL and BW render *C. kivuana* smaller than any *C. monax* population considered here (Heim de Balsac, 1968). *Crocidura ultima* has a relatively large second upper unicuspid (Dollman, 1915), which overlaps with the third upper unicuspid (in position along the antero-posterior axis); these phenotypic characters lead us to exclude *C. ultima* from further comparison to *C. monax*. *Crocidura gracilipes* Peters was described based on a specimen taken somewhere between the coast and Mt. Kilimanjaro and is only known from the type (Zoologisches Museum Berlin 3905; Turni *et al*., 2007). Based on the measurements of the upper toothrow (8.7 mm given in the type description), this is a smaller specimen than any of the forms discussed herein, and we exclude it from further consideration. The combination of CI, UTRL and BW render *C. maurisca* as smaller than any OTU's except Ngorongoro (Bober and Kerbis Peterhans, 2013), but our phylogenetic analyses of mitochondrial sequences show it to be a distant relative to *C. monax* (Fig. 2). Other East African montane species that fall within the range of external and cranial measurements of *C. monax* are *C. littoralis* (including *oritis*) and *C. stenocephala*, but again our phylogenetic analyses of mtDNA sequences suggest these are not close relatives of *C. monax.*

Shrews from Mt. Meru have previously been identified as *C. montis* (Demeter & Hutterer, 1986), and exhibit phenotypic characters such as extensive pilosity of the tail and a cranial profile reminiscent of topotypical *C. montis* from the Rwenzoris. However, the samples from Mt. Meru formed a clade of closely related haplotypes with the Kilimanjaro/North Pare populations (maximum uncorrected mitochondrial *p*-distance = 0.025) as mentioned above. To evaluate the inferred mitochondrial relationships, where samples previously identified as *C. montis* from the Rwenzoris and Meru were not monophyletic with respect to *C. monax*, we conducted a one-way analysis of variance to test for significant cranial differences between each of these localities. The Meru skulls were significantly ($P < 0.001$) smaller in 13 of 16 cranial characters, with the only nonsignificant variables being least interorbital width (LIW), width of the third upper molar (M^3-W), and width of maxillary plate (MP; Table 5). In addition, the topotypical *C. montis* from the Rwenzoris had a much higher tail pilosity value than the samples from Meru (Table 6). These observations, combined with our species delimitation analyses of nuclear DNA sequences (Figs. 3 and 4), lead us to conclude that the specimens from Mt. Meru represent an undescribed species that exhibits phenotypic characters quite different from those exhibited by the *C. monax* populations studied here (see below) and modestly different from true *C. montis*.

Given the relatively close relationship (although with little support) of *C. fumosa* to the Ngorongoro sample in the CytB analysis, and the general similarity in cranial dimensions we observed, a one-way analysis of variance was conducted to test for significant cranial differences between the *C. fumosa* (from Mt. Kenya) and the sample from Ngorongoro. The Ngorongoro specimens had significantly shorter upper and lower toothrows, narrower maxillary and nasal breadths, and narrower upper unicuspids (Table 7). The last upper molar was also significantly shorter than those of *C. fumosa*. We conclude that the samples from Ngorongoro represent an undescribed species.

Morphological patterns within the **monax** *group*

The recently collected series from Kilimanjaro (Stanley *et al.*, 2014) is similar to the series of Thomas (1910), with some specimens having no long bristles on the tail and others having only a few on the very proximal base of the tail (Table 6). The pelage is thick and wooly and hairs measure approximately 5 mm in length at mid-dorsum. The color is blackish-brown above and only slightly paler below. External and cranial measurements of specimens recently collected compared to the holotype (BMNH 10.7.2.58; measured by WTS) and those measured by Thomas support the identification of the recent series sampled from Mt. Kilimanjaro as *C. monax* (Tables 3, 4).

Analyses of external measurements suggested significant sexual dimorphism in total length for the East Usambara and Kilimanjaro samples, where males were longer than females. The male specimens from the East Usambara, Ukaguru and Uluguru localities had longer tails than females, and the East Usambara and South Pare males exhibited a longer hindfoot than the females. The East Usambara and Udzungwa males were heavier than females. However, when we applied a Bonferroni correction for multiple tests, no populations show statistically significant dimorphism, with the exception of hindfoot length in the South Pare Mountains. This one significant result may reflect the small sample size of females (3) from this population rather than actual dimorphism. For 17 cranial characters measured, there were significant differences between males and females in six dimensions in the Kilimanjaro sample, four in the East Usambara sample, two in the Uluguru sample, and one in the South Pare, West Usambara, and Rubeho samples. These differences were scattered among the dimensions examined, and Bonferroni corrections relegated all results as non-significant, with one exception (width of the upper third molar in the South Pare specimens, which included only three females and six males). We regard these results as an absence of conclusive evidence for sexual dimorphism, and we therefore combined sexes in all subsequent analyses.

Of the cranial characters measured, the width of the maxillary plate exhibited the highest coefficients of variation within each geographic sample (7–11%; Table 4), so we deleted this character in subsequent analyses of geographic variation. F-values produced by the one-way ANOVAs to test the null hypothesis of no significant geographic variation were all highly significant ($P < 0.001$). The greatest amount of morphological heterogeneity was exhibited by those characters associated with the length of the skull, including CI, BL, UTRL, M&I, and LTR. Bimaxillary width was also notably heterogeneous. In general, cranial dimensions were largest in the East Usambara sample (14 of the 16 characters) and the Meru sample was the smallest of the 11 geographic samples measured in 12 of the 16 characters (Table 4).

Based on both the results of the molecular analyses and the general morphological patterns that emerged from the morphological assessment, including the phenotypic distinction of the Meru sample, we constrained subsequent analyses of cranial morphometrics to two distinct assemblages: samples from 1) northern populations including Kilimanjaro, North Pare, South Pare, East Usambara, and West Usambara and 2) Ngorongoro, Rubeho, Ukaguru, Uluguru and Udzungwa.

The discriminant function analysis (DFA) constrained to the Ngorongoro, Rubeho, Ukaguru, Uluguru and Udzungwa populations correctly classified ≥ 80% of specimens to their respective localities and resulted in the first two components having eigenvalues that all exceeded 1. The first two factors explained 76.3 and 13.9% of the variation. The Ngorongoro population was strikingly small and distinct. The remaining mountain localities all overlapped in canonical variate space, with the Uluguru samples showing the most differentiation along CV2 (Fig. 5).

Three sets of two overlapping populations each are reflected in the DFA of the Kilimanjaro, North Pare, South Pare, East Usambara, and West Usambara samples, where ≥ 91% of specimens were correctly classified to mountain. The first two factors explained 73.2 and 16.7% of the variation. Overlap in canonical variate space is exhibited between the East and West Usambara samples, Mt. Kilimanjaro and the North Pare samples, and the South Pare and Magamba samples. The large sizes of both *C. tansaniana* in the East Usambaras, first observed by Hutterer (1986), and the sample from the West Usambaras are reflected in the position of the those two operational taxonomic units (OTUs) along CV1 and the greater PPL of the Kilimanjaro and North Pare samples relative to the South Pare and Magamba samples is reflected by the dispersion of specimen scores along CV2 (Fig. 6).

Based on mitochondrial gene tree relationships, nuclear species delimitation analyses, and morphological characters, we conclude that *C. monax* is restricted to Mt. Kilimanjaro and North Pare Mountains, *C. tansaniana* is found on both the East and West Usambaras, and *C. usambarae*, originally described from the Shume-Magamba forests in the northwestern segment of the West Usambaras, is also found in the montane forests of the South Pare Mountains. Populations on Ngorongoro, Meru, and the middle Eastern Arc Mountains (Rubeho, Ukaguru, Uluguru and Udzungwa) each represent undescribed species.

DESCRIPTIONS OF EXISTING AND NEW SPECIES

Crocidura monax Thomas, 1910 (Figs 7–9; Tables 3,4,6)

Holotype. – BMNH10.7.2.58, an adult female preserved as a skin and skull (field number 1161) collected on 11 June 1910.

Paratypes. – Thomas (1910) mentioned seven additional specimens, six of which are deposited in the British Museum (4 males: BMNH 1910.7.2.54–1910.7.2.57; and 2 females: BMNH 1910.7.2.59–1910.7.2.60). Field number 1164 mentioned by Thomas

(1910) was not located at the BMNH. Additional specimens studied are listed in Appendix 1.

Type locality. – "Rombo", 6000 ft., Mt. Kilimanjaro, Tanzania.

Measurements of holotype. – External measurements presented as listed by Thomas (1910); cranial measurements taken by WTS. See Methods and Materials for character definitions. HB: 88; TV: 66; HF (without claws): 16.2; E: 10; WT: unknown; CI: 23.67; BL: 21.30; PPL: 10.51; PGW: 7.05; UTRL: 10.60; LIW: 5.12; BW: 7.22; NW: 2.24; GW: 10.30; HBC: 6.88; I^3-W: 0.88; CW: 0.94; M^3-L: 1.69; M^3-W: 0.85; MP: 1.13; MI: 15.12; LTR: 9.87.

Diagnosis. – "Size large, colour dark, tail nearly without bristles. Size about as in *C. turba*, or rather larger. Fur thick, close and wooly; hairs on back 4.5-5.0 mm in length. General colour dark slaty, very much as in *turba* and *fumosa*, scarcely lighter below. Ears, hands, feet, and tail uniform dark brown. Tail longer than usual, slender, practically without longer bristles, a few scattered ones present on the basal third – in this respect like *C. maurisca*. Skull rather broader and flatter than in *C. turba*." (Thomas, 1910).

Emended diagnosis and description. – Large shrew with a head and body length of 83–101 mm, tail of 55–71 mm, and mass of 10.0 –17.0 g (Table 3). The ear pinnae are short but prominent. The longest mystacial vibrissae are 20 mm in length. Typically there are a few short bristles (4 mm) on the basal 9–32% of the tail (which is 67–70% of the length of head and body), but occasionally long bristles are completely absent. The dorsum and venter are both a rich brown color, hairs of the back are 4 mm in length at mid-dorsum. The hairs of the dorsum are steel gray with brown tips. The tail is equally brown. Front and hind feet are slightly paler than the body, and covered by short brown hairs. The hindfoot is rather long and wide; digit 5 is slightly longer than digit 1. The inner plantar surface is largely glandular, covered by numerous small wart-like structures (Fig. 7), while the surface behind the thenar and hypothenar pads is smooth.

The cranium is wedge-shaped, with a narrow rostrum, a short, broad interorbital region and a wide, somewhat angular braincase (Fig. 8). The dorsal profile of the skull is curved, with a slightly domed braincase. The maxillary plate is rather wide and bears a large lachrymal foramen. The lambdoid crest is relatively prominent. The first upper incisor is of medium size (Figs. 8, 9) and extends beyond the tip of the short second upper incisor. The upper incisors are wide and have narrow cingula (Fig 9).

Comparisons. – *C. monax* is larger than *C. usambarae*, *C. mdumai* (a new species described below) and *C. newmarki* (a new species described below), but smaller than *C. tansaniana* and *C. munissii* (a new species described below) in external measurements (Table 3). The length of the tail is 67–70% of the head and body length, as in the other species on neighboring mountains in northern Tanzania. The proportional length of the tail pilosity (c. 15%) is greater than that in *C. usambarae*, *C. tansaniana* and *C. munissii*, but shorter than in the remaining species (Table 6). The CI, UTRL and BW are all absolutely larger than in *C. usambarae*, *C. mdumai* and *C. newmarki*, but smaller (with some overlap) than *C. tansaniana* and the southern Eastern Arc Mountain samples (Table 4). The first upper incisors are almost equal in length to those of *C. usambarae*, but the second incisor of *C. monax* is shorter. The upper unicuspids and complex cheekteeth are similar to those of *C. usambarae*, but wider and more robust than in *C. mdumai* and *C. newmarki*.

Distribution. – Known from forest habitats of Mt Kilimanjaro and North Pare. Child (1965) mentioned a specimen of *C. maurisca* from Kilimanjaro, which may represent *C. monax*, but we were unable to examine this specimen.

Etymology. – Not given by Thomas (1910) but most likely derived from Latin *mons* (mountain), *monax* thus meaning 'from the mountain'.

Ecological notes. – *Crocidura monax* was recorded between 2000 to 3000 m on the Maua route along the southeastern slope of Mt. Kilimanjaro in July and August, 2002, where it made up 30–40% of the shrews observed at each elevational site (Stanley *et al.*, 2014). *Crocidura monax* is syntopic with *C. allex*, *C. hildegardeae*, *C. olivieri* (Lesson), *Myosorex zinki* and *Sylvisorex granti* Thomas. *Crocidura monax* was not found in moorland habitats above treeline on Kilimanjaro, and we know of no records of this species below 2000 m. During a survey along the Maua route of Mt. Kilimanjaro females and males made up 29 and 71% of the total (76), respectively. Twelve females were examined for reproductive status, and four (33%) were pregnant with the largest embryo measuring 20 mm crown to rump. While *C. monax* is sympatric with two other soricid genera on Mt. Kilimanjaro, *Crocidura* is the only genus of shrew in the North Pare Mountains, and *C. monax* made up 51% of the shrews recorded by Stanley *et al.* (2007), where it was found with *C. hildegardeae* and *C. olivieri*. In the North Pare Mountains, females made up 32% of the total (28). Only two females were examined for reproductive status, and neither was pregnant.

Crocidura usambarae Dippenaar, 1980 (Figs 7,9,10; Tables 3,4,6)

Holotype. – Transvaal Museum TM 16810. Skin and skull of male in good condition. Collected 24 May 1965 by C.A. Hubbard (Field no. 2458).

Type locality. – "Shume, 16 m n Lushoto, Tanzania" on original label (Dippenaar 1980: 128), = Tanzania, Tanga Region, Lushoto District, West Usambara Mts, Magamba, 4.67° S, 38.25° E, 1585 m.

Paratypes. – FMNH 27424–27430 (3 females, 4 males, skins and skulls); WTS measured the paratypes with complete crania (FMNH 27425, 27429 and 27430); other paratypes not examined in this study include TM 14986 and 16130. See Appendix 1 for additional specimens examined.

Measurements of holotype. – Measurements are presented as listed by Dippenaar (1980), who listed only a subset of the measurements used in this study. TL: 143; HB: 80; TV: 63; tail pilosity: 23%; HF: 15; EAR: 8; CI: 22.4; UTRL: 9.9; LIW: 5.1; BW: 6.8; NW: 3.2; GW: 10.4; HBC: 5.6; I^3-W: 0.95; CW: 0.93; M^3-L: 1.67; M^3-W: 0.82; MI: 14.3; LTR: 9.1.

Diagnosis. – (modified from Dippenaar 1980), dark slate grey to dark brownish-grey above, slightly paler ventrally. Feet brown to dark reddish brown. Tail long, on average 73% of head and body length, proximal 20–30% covered in long bristle hairs. Medium sized (CI: mean 22.1, range 21.8–22.4), with wide interorbital region, moderately robust rostrum, wide braincase, very robust unicuspids and robust M^3.

Emended diagnosis and description. – Medium sized shrew with a head and body length of 75–93 mm, tail of 54–62 mm, and mass of 8.4–10.5 g (Table 3). The ear pinnae are short but protrude beyond the pelage. The longest mystacial vibrissae are 17 mm in length. There are sparse short bristles (3 mm) on the basal 10–25% of the tail (which is 70% of the length of head and body); one specimen from South Pare (FMNH 151138) has fewer than ten bristles at the very base of the tail. The dorsum and venter are both a rich brown color and the hairs of the back are 4 mm in length at mid-dorsum. The hairs of the dorsum are steel gray with brown tips. Both the front and back feet are slightly paler than the body, and cloaked in short hairs, some of which are brown and others translucent.

The cranium is relatively short and dorso-ventrally compressed. There is a short broad interorbital region and a stout, globose braincase with angular superior articular facets (Fig. 10). The maxillary plate is narrow and bears a large lachrymal foramen. The lambdoidal crest is relatively prominent. The first upper incisor is short and stout (Fig. 9, 10), barely longer than the second upper incisor. The upper incisors are wide in occlusal view, with narrow cingula (Fig. 9).

Comparisons.- *Crocidura usambarae* is larger than *C. mdumai* and *C. newmarki*, but smaller in external measurements than all other Tanzanian members of the *C. monax* group (Table 3). As with other northern Tanzanian populations, the length of the tail is ≤ 75% of the head and body length, compared to ≥ 80% in the southern EAM populations. The greatest length of the skull, length of the upper toothrow and maxillary width are all absolutely larger than in *C. mdumai* and *C. newmarki*, but smaller than the southern EAM samples and the East and West Usambaras (Table 4). The first upper incisors, while stout, barely extend below the occlusal surface of the second upper incisor, in contrast to those of *C. monax*, which are larger in general. There is only slight overlap between *C. usambarae* and *C. monax* in both CI and UTRL (Table 4). The upper unicuspids and complex cheekteeth are narrower and less robust than those of *C. monax.*

Crocidura usambarae from South Pare has a narrower third upper incisor (Table 4), and a more elongate skull generally than *C. usambarae* from Magamba, particularly with regard to the region of the skull bearing the upper unicuspids. The tail of *C. usambarae* from South Pare also has fewer bristle hairs than the Magamba population (Table 6).

Distribution. – The typical form of *C. usambarae* is only known from the type series from Magamba and Shume collected between 1580 and 1830 m a.s.l. (Dippenaar 1980), and from two additional specimens from Shume/Magamba and Mazumbai (both in Lushoto District) subsequently reported by Howell & Jenkins (1984). We also refer the population from the Chome Forest Reserve of the South Pare Mountains above 1100 m to this species (Stanley *et al.* 1996).

Etymology. – Name derived from the Usambara Mountains.

Ecological notes. – This species was the most common shrew observed in the Chome Forest Reserve, South Pare Mountains in montane forests (sensu Lovett & Pocs, 1993) at 2000 m (Stanley *et al.*, 1996), where it made up 70% of the shrews captured. The only other shrew recorded at this elevation was *C. hildegardeae*. At lower (and drier) habitats (1100 m), *C. usambarae* was much less common and made up only 8% of the shrew species recorded, which included *C. hildegardeae*, *C. hirta* and *C. olivieri*. One female found dead at 1100 m had five embryos, the largest of which has a crown-rump length of 6 mm (Stanley *et al*., 1996).

Crocidura tansaniana Hutterer, 1986 (Figs 7,9,11; Tables 3,4,6)

Holotype. – Zoologisches Forschungsmuseum Alexander Koenig, ZFMK 85.194, adult male, skin and skull, collected by S.R. Telford on 17 June 1984: field number SRT-TZ-12078. Skin and skull in good condition.

Type locality. – Tanzania, Tanga Region, East Usambara Mts., Amani (05.06S, 38.38E).

Measurements of holotype. – Measurements are listed as presented by Hutterer (1986), who listed only a subset of the measurements used in this study. TL: 174; HB: 109; TV: 65; tail pilosity: 35%; HF: 17; EAR: 13; WT: 15 g; CI: 25.5; UTRL: 11.3; LIW: 5.5; BW: 8.1; GW: 11.1; HBC: 6.4; M^3-L: 1.80; M^3-W: 0.96; LTR: 10.2.

Diagnosis. – “Large species of the *Crocidura monax* group, comparable to *C. monax* Thomas, 1910 and *C. littoralis* Heller, 1910, however skull considerably larger and more robust; teeth more robust, particularly the upper M3.” (Hutterer, 1986).

Emended diagnosis and description. – Large sized shrew with a head and body length of 82–108 mm, tail of 60–76 mm, and mass of 11–20 g (Table 3). Ear pinnae short but prominent. The longest mystacial vibrissae are 20 mm in length. The tail is equipped with numerous long bristles (6 mm) along the basal 24–48% of its length. The tail length is 70–71% of the length of head and body. Dorsal and ventral pelage is rich brown; hairs of the back are 6 mm in length at mid-dorsum. The hairs of the dorsum are brownish-gray with reddish-brown tips. The tail is equally brown. Front and hind feet are only slightly paler on the dorsal surface than the color of the body, and covered by short brown hairs.

The cranium is long and stout, with a wide maxillary, a broad interorbital and a wide, angular braincase (Fig. 11). The dorsal profile of the skull is rather flat with only a slight angle between braincase and rostrum. The maxillary plate is massive and bears a lachrymal foramen near the anterior rim. The lambdoidal crest is well developed. The first upper incisor forms a long hook (Figs. 9, 11) and extends far lower than the tip of the second upper incisor, and even the tip of P^4. The upper unicuspids are wide and have broad cingula (Fig. 9).

***Comparisons.* –** *C. tansaniana* is larger than all other Tanzanian species, except for *C. munissii*, in external measurements (Table 3). Relative length of the tail (70–71%) is similar to the other species, except for *C. munissii*, which has a tail that is above 85% the length of the head and body (Table 6). The pilosity of the tail (30–35%) is greater than in all other species, except for *C. mdumai* (43%) and *C. newmarki* (67%; Table 6). The large values for greatest length of the skull, length of the upper toothrow and maxillary width are only met by *C. munissii* (Table 4), which differs by its longer tail and lesser pilosity. The large first upper incisors are similar only to those of *C. munissii*; all other species have smaller incisors. Wide upper unicuspids and cheekteeth are also shared with *C. munissii*. *Crocidura tansaniana* has the longest M^3 of all species examined (Table 4).

***Distribution*.** – East and West Usambara Mountains. In the West Usambara Mountains, known only from the Ambangulu Forest above 1100 m in elevation. Although not yet recorded, we suspect that it occurs in other forested habitats of the West Usambara Mountains.

***Etymology.* –** Named for the country of Tanzania.

Ecological notes. – Other shrews recorded in sympatry with *C. tansaniana* include *C. elgonius* Osgood, *C. fuscomurina*, *C. hildegardeae*, *C. hirta*, *C. olivieri*, *Suncus megalura,* and *Sylvisorex howelli.* Although both *C. tansaniana* and *C. usambarae* have been recorded from the West Usambara Mountains, there are no records of the two species occurring in sympatry. Stanley *et al*. (2013) documented the distribution of *C. tansaniana* in forest fragments in the East and West Usambaras (reported as *C. monax* in the West) where this shrew was found predominantly in the largest fragments of (> 500 ha) relatively undisturbed montane forest, and only 3 individuals (4% of total captures) were observed in fragments of disturbed forest that were smaller than 40 ha.

***Crocidura newmarki* sp. nov.** (Figs 7,9,12; Tables 3,4,6)

Holotype.- FMNH 208439, an adult male, with slightly worn molars (age class II; see methods and materials), prepared as a round skin, skull, skeleton, and frozen tissue (liver); collected by M. J. Munissi (original field number WTS 9955) on 9 August 2009. The condition of the skin, skull and skeleton are good.

Paratypes. – We designate as paratypes five females and four males: FMNH 208440, collected at the type locality (see below) at 3600 m elevation; FMNH 208444 and

208447 collected at Mt Meru, Arusha National Park, Meru Crater, 3.24200° S, 36.78736° E, 2652 m. FMNH 208435 and 208436 collected at Mt Meru, Arusha National Park, Mgongo wa Tembo, 3.22350° S, 36.78675° E, 3000 m. FMNH 208415 and 208416 collected at Mt Meru, Arusha National Park, 3.24725° S, 36.80066° E, 2300 m. FMNH 208406 and 208411 collected at Mt Meru, Arusha National Park, Fig Tree Arch, 3.24406° S, 36.82845° E, 1950 m. All type materials are preserved as skins, skulls and either fluid preserved post-cranial bodies, or cleaned post-cranial skeletons.

Type locality. – Tanzania, Arusha Region, Arumeru District, Mt Meru, Arusha National Park, near Saddle Hut, 3.21609° S, 36.76897° E, 3600 m.

Measurements of holotype. **–** Measurements were all recorded by WTS and are in millimeters and weight in grams: TL: 131; HB: 81; TV: 50; tail pilosity: 67%; HF: 16; EAR: 9; WT: 8.5 g; CI: 20.59; BL: 18.44; PPL: 9.20; PGW: 6.53; UTRL: 8.98; LIW: 4.95; BW: 6.34; NW: 1.79; GW: 9.67; HBC: 6.63; I^3-W: 0.68; CW: 0.68; M^3-L: 1.53; M^3-W: 0.79; MP: 0.92; MI: 13.06; LTR: 8.34.

Diagnosis. – *Crocidura newmarki* is a medium-sized, dark shrew similar to *Crocidura montis* Thomas, 1906 from Rwenzori Mountains, but with a less hairy tail (pilosity 67% versus 81% in *C. montis*; Table 6); head and body length 65–85 mm, tail 45–60 mm, and mass 6 –11 g (Table 3). It is smaller than any of the other shrews allied to *C. monax* in Tanzania, except *C. mdumai*. The proximal two-thirds of the tail bears numerous long, translucent bristles (up to 7 mm in length); the rest of the tail is covered in short, dark brown applied hairs. The pelage is dark brown on the dorsum and is only slightly more grayish brown on the venter; hairs of the back are 6–7 mm in length at mid-dorsum. The dorsal surfaces of both the front and back feet are slightly paler than the rest of the body. The longest vibrissae emanating from the snout are 15 mm in length.

The skull of *C. newmarki* is small and wedge-shaped with a rounded braincase, smaller than any of the other OTUs considered in this study, except for *C. mdumai*, which is even smaller (Fig. 12; Table 4). The lateral profile of the skull is straight and slightly rounded towards the braincase. The first upper incisor is short and slender (Figs. 9, 12), barely reaching as low as the tip in I^2. The upper unicuspids are narrow, with small cingula (Fig. 9).

Description and comparisons. – *Crocidura newmarki* is a medium sized shrew with long wooly fur. The head and body length range is 65–85 mm, tail length, 45–60 mm, the length of the hindfoot 13–16 mm, and mass 6 –11 g. Fifty eight to ninety five percent (mean 67.2%) of the tail is covered by long bristle hairs. However, bristles are scattered and less numerous than in *C. montis* (Table 6). Vibrissae extend up to 15 mm in length. The ear conch is stout. The hairs of the dorsal and ventral pelage, which are 6–7 mm long, are grey but the tips are a rich brown. The dorsal aspects of the feet are paler than the body and there are nearly translucent hairs sparsely distributed along the length of each foot. The hindfoot is smaller and narrower than in *C. monax*; digit 5 is only slightly longer than digit 1. The inner plantar surface is covered by numerous small tubercles (Fig. 7), as in *C. monax*.

The skull of *C. newmarki* is small (Table 4) and wedge-shaped with a rounded braincase and a moderate lambdoidal crest. It is smaller than any of the other OTUs considered in this study, except for *C. mdumai*. It is also considerably smaller than true *C. montis* from Rwenzori Mountains (Table 5). The lateral profile of the skull is straight and slightly rounded towards the braincase. The first upper incisor is short and slender, barely reaching as low as the tip in I^2. The upper unicuspids are narrow and have small cingula. The last upper molar (M^3) is robust, but smaller than in *C. montis* (Table 5).

Distribution.- Known only from Mt. Meru, Tanzania (Demeter & Hutterer, 1986, Dippenaar & Meester, 1989), at elevations between 1800 and 3600 m. Dippenaar & Meester (1989) and Hutterer and Dieterlen (1981) listed specimens from Kilimanjaro (West) and various places in Kenya and Sudan as *C. montis*, but these have to be restudied. The distribution maps of *C. montis* in Dippenaar & Meester (1989) and Hutterer (2013) apparently include more than one species.

Etymology.-The species is named in honour of Dr. William D. Newmark in recognition of his tireless conservation efforts and long term study of the Tanzanian biota, with an emphasis on the East and West Usambara Mountains. We suggest the common name Newmark's Shrew.

Ecological notes. – *Crocidura newmarki* is syntopic with *C. allex* and *C. hildegardeae* in the montane habitats of the eastern slopes of Mt. Meru. Interestingly, the soricid species diversity appears to be much lower on Mt. Meru than similar habitats in neighboring Mt. Kilimanjaro (Stanley, unpubl. data), where at least five different species, and three different genera occur (see *C. monax* account). In a faunal survey in 2009 (Stanley, unpubl. data), *Crocidura newmarki* was found between 1950 to 3600 m in habitats ranging from submontane forest to ericaceous zone above treeline. Females made up 38% of the total number of *C. newmarki* sampled in 2009 along the southeastern slope of Mt. Meru.

Crocidura mdumai **sp. nov.** (Figs 7,9,13; Tables 3,4,6)

Holotype. – FMNH 211323, an adult male with slightly worn molars (age class II; see methods and materials), prepared as a round skin, skull and body embalmed in formalin and now in 70% ethanol, and frozen tissue (liver); collected by M. J. Munissi (original field number WTS 10842). The condition of the skin, skull and preserved post-cranial body are good.

Paratypes. – We designate as paratypes three females and four males, FMNH 211131, 211132, 211134, 211322, 211327, 211328, and 211332, all collected at two localities on the Ngorongoro Crater rim in 2010 (see Type locality). All paratypes are preserved as skins, skulls and fluid-preserved post-cranial bodies, with the exception of FMNH 211134, which is preserved as a skin, skull and post-cranial skeleton. See Appendix 1 for additional specimens examined.

Type locality. – Tanzania, Arusha Region, Ngorongoro District, Ngorongoro Conservation Area, Ngorongoro Crater rim, near Pongo Ranger Post, 3.24407° S, 35.64040° E, 2064 m asl. Paratypes were collected at this locality (FMNH 211322, 211327, 211328, 211332) and: Tanzania, Arusha Region, Ngorongoro District, Ngorongoro Conservation Area, Ngorongoro Crater rim, near Lamala Gate, 3.14255° S, 35.68669° E, 2372 m asl (FMNH 211131, 211132, 211134).

Measurements of holotype. **–**TL: 140; HB: 81; TL: 59; tail pilosity: 29%; HF: 15; EAR: 11; WT: 8.3 g; CI: 21.64; BL: 19.27; PPL: 9.98; PGW: 6.53; UTRL: 9.04; LIW: 4.60; BW: 6.25; NW: 2.00; GW: 9.75; HBC: 6.46; I^3-W: 0.70; CW: 0.76; M^3-L: 1.39; M^3-W: 0.67; MP: 0.94; MI: 13.26; LTR: 8.42.

Diagnosis. – *Crocidura mdumai* is a medium-sized, but robust shrew with a head and body length of 76–91 mm, tail of 52–65 mm, and mass of 7.3–9.6 g (Table 3). It is smaller than any of the other species of this study, except for *C. newmarki*. It is the smallest of any of the specimens with low levels of pilosity on the tail (Table 6). There is low pilosity on the proximal 43% of the tail (which is 70% of the length of head and body and slightly bicolored). The long bristles (4 mm) at the base of the tail are translucent; the rest of the tail is covered in short, dark brown applied hairs. The dark brown pelage of the dorsum contrasts slightly with the dark gray of the venter.

The hairs of the back are 5 mm in length. The dorsal surfaces of both the front and back feet are paler than the rest of the body. The longest vibrissae emanating from the snout are 19 mm in length.

The skull is smaller and rounder with less angular anterior corners of the braincase than in those of any of the other species considered in this study (Fig. 13; Table 4). The lateral profile of the skull exhibits a depression between the braincase and the rostrum, which has a slightly rounded lateral profile. The first upper incisor is short and slender (Figs. 9, 13), and the upper canine is longer and broader than the third upper incisor.

Description and comparisons. – *Crocidura mdumai* is a medium sized, but robust shrew with the pilosity of the tail restricted to the proximal third, and the slightly bicolored (dorso-ventrally) tail is roughly 70% the length of the head and body (Table 3, 6). Mystacial vibrissae range from 15 to 19 mm long (mean = 17.3 mm, n = 10). The ear conch is stout. The proximal 3/4 of the hairs of the dorsal pelage, which are 4–5 mm long, is grey but the tips are a rich brown. The hairs of the ventral pelage are the same length, but the color is a more uniform grey-brown from base to tip. The claws on the back feet are slightly longer than those of the front. The dorsal aspects of the feet are lighter in color than the body and there are almost translucent hairs sparsely distributed along the length of each foot. The hindfoot is small and narrow and similar to that of *C. newmarki*.

The cranium is medium-sized (Table 4), with a moderate lambdoidal crest. The lateral profile of the cranium reveals a depression between the rostrum and braincase (Fig. 13). The first upper incisors are short and slender, exceeding the length of the second upper incisor, which is large. The canine is larger than the third upper incisor and rectangular in shape (Fig. 13), and the last upper molar is robust. Among the OTUs defined for this study, *C. mdumai* is the smallest in external dimensions (Table 3). While there is some overlap in various measures of the cranium between *C. mdumai* and *C. usambarae*, the UTRL, LIW, and BW for *C. mdumai* all exhibit a range below that of *C. usambarae*, including specimens from South Pare (Table 4). The upper unicuspids and complex cheekteeth are also more slender and less robust (Fig. 13). The phylogenetically closer (according to our mitochondrial gene tree) *Crocidura fumosa* Thomas, 1904 from Mt. Kenya has greater tail pilosity (c. 80%) and is larger in skull measurements; in 7 out of 17 cranial measurements the new species significantly differs from *C. fumosa*, which also has a much narrower infraorbital bridge than the new species (Tables 7).

Distribution. – *Crocidura mdumai* is known only from the forests of Ngorongoro Crater above 2000 m.

Etymology. – The species is named in honour of Dr. Simon Mduma in recognition of his contributions to conservation efforts and long-term study of the biota of the Serengeti ecosystem. We suggest the common name Mduma's Shrew.

Ecological notes. – Other soricid species in the Ngorongoro crater forest are *Crocidura allex*, *C. hildegardeae* and *Suncus megalura* [Jentink] (Howell & Jenkins, 1984; W. T. Stanley, unpubl. data). Habitat includes montane forest on the rim of the Ngorongoro caldera (2370 m), and slightly drier forests at 2000 m on the southeastern slope. Females made up 37% of the total *C. mdumai* observed in 2010 during a faunal survey of the montane forests of Ngorongoro (n = 16).

Crocidura munissii **sp. nov.** (Figs 7,9,14; Tables 3,4,6)

Holotype. – FMNH 158290, an adult male with slightly worn molars (age class II; see methods and materials), prepared as a round skin, skull and skeleton, and frozen tissue (liver, heart, and kidney) collected by W. T. Stanley (original field number WTS 2651) on 11 August 1996. The condition of the skin, skull and post-cranial skeleton are good.

Paratypes. – We designate nine specimens from Tanzania as paratypes: Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North Forest Reserve, 3 km W, 1.3 km N Tegetero, 6.9292° S, 37.7056° E, 1345 m (FMNH 158280-158281, 158283); Uluguru Mts, Uluguru North Forest Reserve, 5.1 km W, 2.3 km N Tegetero, 6.92° S, 37.6833° E, 1535 m (FMNH 158287-158289); Uluguru Mts, Uluguru North Forest Reserve, 6 km W, 3 km N Tegetero, 6.9167° S, 37.675° E, 1850 m (FMNH 158410-158412). See Appendix 1 for additional specimens examined.

Type locality. – Tanzania, Morogoro Region, Morogoro District, Uluguru Mts., Uluguru North Forest Reserve, 5.1 km W, 2.3 km N Tegetero, 6.92° S, 37.6833° E, 1535 m.

Measurements of holotype. – TL: 166; HB: 86; TV: 80; tail pilosity: 11%; HF: 17; EAR: 10; WT: 11.5 g; CI: 24.69; BL: 22.37; PPL: 10.91; PGW: 7.24; UTRL: 10.91;

LIW: 5.14; BW: 7.21; NW: 2.19; GW: 10.25; HBC: 6.88; I^3-W: 0.88; CW: 0.98; M^3-L: 1.58; M^3-W: 0.83; MP: 1.15; MI: 15.62; LTR: 10.06.

Diagnosis. – Large *Crocidura* with a long tail (91% of HB in the Uluguru population) covered by only a few bristle hairs over 8–15% of its basal length (Table 6); hindfoot long and narrow (17–19 mm), distance between thenar and interdigital pad 1 relatively larger (Fig 7) than in *C. monax*, *C. usambarae* and *C. tansaniana*; skull large (CI 22.7–25.8), braincase long with pronounced anterior facets; first upper incisor long and hook-like.

Description. **–** Large shrews with a head and body length of 75–106 mm, a long tail of 66–95 mm, and mass of 9.5–19.5 g (Table 3). Ear pinnae are short, as in other species of this study. The longest mystacial vibrissae are about 24 mm in length. There are very few short bristles (3 mm) on the basal 8–15% of the tail (which is 85–93% of the length of head and body; Table 6). Dorsal and ventral pelage is rich brown in color and hairs of the back are 6–7 mm in length. The hairs of the dorsum are steel gray with brown tips (with the exception of FMNH 166739 from Ukaguru which represents a light gray color variant). The tail is equally brown. Front and hind feet are slightly paler, and covered by short brown to whitish hairs. The hindfoot of *C. munissii* differs from all other taxa treated here by its slenderness; it is rather long but narrow; digit 5 is longer than digit 1. The medial plantar surface is only glandular in its anterior part; there is more space between the thenar and the interdigital pad 1, and the interdigital pads 1–4 are situated more closely together than in *C. monax* and the other species (Fig. 7).

The cranium is long (CI 22.70–25.76) as in *C. tansaniana*, but slightly smaller and narrower, with a narrow maxillary, a short broad interorbital region and a squarish braincase with prominent superior articular facets (Fig. 14). The dorsal profile of the skull is flat from the rostrum to the interorbital region, but slightly domed over the braincase. The maxillary plate is large and bears a large foramen at its anterior rim. The lambdoidal crest is well developed. The first upper incisor is a long hook (Figs. 9, 14) and extends beyond the tip of the second upper incisor and the fourth upper premolar. The upper unicuspids are wide, with broad cingula (Fig. 14).

Comparisons. **–** *C. munissii* is best distinguished from all other Tanzanian species of the *C. monax* group by its relatively long tail (84–94% of HB), in combination with a low pilosity (means of 7–15% in all four populations; Table 6). The few scattered bristles are short. In overall size *C. munissii* equals *C. tansaniana*; both species are larger than all other taxa of this study (Table 1). The hindfoot measurements of all four populations average larger than all other species, but there is overlap with *C. monax* and *C. tansaniana* (Table 3). The hindfoot of *C. munissii* differs by the close arrangement of the plantar pads (Fig. 7).

In skull size, *C. munissii* resembles *C. tansaniana*, although East Usambara populations of the latter species tend to be larger (Table 4). The length of the third upper molar is also larger in *C. tansaniana*. The first upper incisors are very long in all four populations of *C. munissii*, but are similar to those of *C. tansaniana*. The upper unicuspids are wide with broad cingula.

Distribution. – The species occurs on four southern mountains of the Eastern Arc: Rubeho, Udzungwa, Ukaguru, and Uluguru Mountains.

Etymology. – The species is named in honour of Maiko J. Munissi in recognition of his contribution to our understanding of the natural history of montane mammals in Tanzania. This study, and many others, could not have happened without Munissi's tireless efforts during faunal inventories of each of the mountains covered here. We suggest the common name Munissi's Shrew.

Ecological notes. – *Crocidura munissii* is found in submontane and montane habitats (sensu Lovett & Pocs, 1993) of the Rubeho, Udzungwa, Ukaguru and Uluguru Mountains. Syntopic soricids include *Crocidura hildegardeae*, *C. desperata*, *C. elgonius*, *C. olivieri*, *C. telfordi*, *Myosorex geata* and *M. kihaulei*, *Suncus lixus*, *S. megalura* and *Sylvisorex howelli*. Stanley & Hutterer (2007) documented *C. munissii* (reported as *C. monax*) in habitats above 1450 m in the Udzungwa Scarp forests, but not below in drier forests.

DISCUSSION

Although the larger and more visible biota of Tanzania has been the focus of taxonomic study for over a century, the smaller mammals remain poorly known. This is particularly true of the montane faunas spread across the country in the Northern and Southern Highlands and the Eastern Arc Mountains. However, recent studies have begun to shed light on the taxonomy and biogeography of various montane vertebrate groups, including frogs (Lawson, 2010; Loader *et al.* 2010), snakes (Gravlund, 2002; Menegon, Davenport & Howell, 2011), and birds (Dinesen *et al.*, 1994; Bowie *et al.*, 2004). Among mammals, diversity has been investigated within various groups of rodents, including *Hylomyscus* (Carleton & Stanley, 2005) and *Praomys* (Carleton & Stanley 2012; Bryja *et al.*, 2014). The shrews of Tanzanian mountains, including *Sylvisorex howelli* (Stanley & Olson, 2005) and various species in the genus *Myosorex* (Stanley & Esselstyn 2010), also have received some attention. The genus *Crocidura* is far more species-rich, but nevertheless has received relatively scant attention, with most studies relying exclusively on morphological variation (e.g., Hutterer, 1986). Here we used initial inferences of mitochondrial gene tree relationships to formulate plausible taxonomic hypotheses, which we subsequently tested with multi- and uni-variate analyses of continuous morphological characters, qualitative examination of discrete morphological characters, and coalescent-based species validation approaches. Remarkably, the results we obtained from these approaches were largely congruent and we recognized species where a majority of our approaches suggested the same conclusion.

In our species validation analyses, we were concerned that an incorrect guide tree would bias our results (Leaché and Fujita, 2010) and conclusions. We therefore completed 66 pairwise analyses in an attempt to eliminate the potential for guide-tree misspecification bias. Presumably, these pairwise analyses are biased toward recognizing distinct species when we compare non-sister populations, but they should be unbiased when comparing sister populations. Although we cannot be certain of which populations are necessarily sister to one another, several pairwise comparisons showed little or inconsistent support for recognizing two species (Fig. 4). Consistent support or rejection across all prior schemes implies that a strong signal underlies the data and prior assumptions are not affecting species delimitation conclusions. In situations where the support for species recognition was inconsistent across different prior assumptions, justification for choosing the results based on one set of priors over another must be based on some external source of information (Yang and Rannala, 2010). In this case, we used $\square_{W}$ estimates from unlinked loci not included in species validation approaches, and these suggest that our prior schemes 1–3, which assumed large $\square$ values, were not realistic. Nevertheless, many of the pairwise comparisons yielded consistent results across all prior schemes, with most analyses giving a posterior probability of 1.0 that the two populations represent different species. Results varied in the comparisons between populations we treat as conspecific within *C. munissii*, *C. monax*, and *C. tansaniana*, as well as the comparison between *C. fumosa* and the West Usambara population of *C. tansaniana*. With the exception of this latter comparison, these results were consistent with patterns of overlap in multivariate morphometric space (Figs. 5, 6), where we observed broad overlap between the four populations of *C. munissii*, and modest overlap between the populations of *C. monax* and *C. tansaniana*.

As a whole, our pairwise comparisons offer a conservative approach to testing species limits with BP&P. The guide-tree-based results could be interpreted to support the recognition of nearly all of the sky island populations as distinct species, but this was inconsistent with our pairwise comparisons and morphometric variation, which suggests that the guide tree approach may be artificially inflating posterior probabilities by placing distantly related populations close together in the guide tree. Other authors have discussed this bias (Yang and Rannala, 2010; Leaché and Fijita, 2010), but our study is the first we are aware of to introduce a systematic means by which to eliminate it.

This study reveals three new species within *Crocidura* that are endemic to Tanzanian mountains. Two of the taxa named here are restricted to individual mountains (*C. mdumai* on Ngorongoro and *C. newmarki* on Mt. Meru), similar to *Myozorex zinki* and *Congosorex phillipsorum*, which are restricted to Mt. Kilimanjaro and the Udzungwa Mountains, respectively. Three taxa included in this study are found on only two mountains (*C. monax* on Kilimanjaro and North Pare; *C. usambarae* on South Pare and West Usambara; and *C. tansaniana* on West and East Usambara). Each of these pairs shows modest morphological differentiation between mountain localities. For example, the specimens of *C. monax* from Kilimanjaro are generally larger than those from North Pare, *C. tansaniana* is bigger on the East Usambaras than in the West Usambaras, and *C. usambarae* from South Pares are subtly larger in some cranial dimensions than the paratypes from the West Usambara Mountains (Table 4). However, neither molecular nor morphological analyses show clear distinction between members of these populations (Fig. 6) and we therefore treat each pair as a single species. *Crocidura munissii* is found on four mountains within the Eastern Arc, and also shows modest differentiation among the isolated populations. For example, the population from the Udzungwa Mountains is generally smaller than the other three (Fig. 5; Table 4), but again, the overlap among all four populations is too great to distinguish among them at a species level (Fig. 5).

The geographic distribution of *C. monax* s.s. is interesting as it spans two geologically distinct mountain groups—the Northern Highlands and the Eastern Arc

Mountains (Griffiths, 1993). Carleton and Stanley (2005) and Bryja *et al.* (2014) grouped samples of *Praomys* from Kilimanjaro and the northern Eastern Arc Mountains, such as the Usambaras and South Pare, using both morphologic and molecular analyses. In contrast, *Hylomyscus arcimontensis* is distributed throughout the Southern Highlands and the Eastern Arc all the way up to the North Pares, but it has never been found in the Northern Highlands. The distributional difference between *Hylomyscus* on one hand and *C. monax* and *Praomys* on the other is striking and suggests that ancient geological events have not had a fixed effect on diversity patterns in various groups of organisms.

The West Usambara range has two species of closely related shrew living within its montane habitats: *Crocidura usambarae*, originally described from specimens collected in the Shume-Magamba forests in the north-western corner of the West Usambara and subsequently recorded in Mazumbai near Lushoto, and *Crocidura tansaniana*, known from the Ambangulu forest at the south-eastern corner of the range facing the East Usambara across the Lwengera Valley. Determining the entire distribution of these two species across the West Usambara is important, as it is currently unknown whether these two species occur in sympatry, or, if not, where the boundary between the two species is situated.

Stanley *et al*. (1998) stated that *C. monax* occurs on the Nguru and Nguu Mountains in the middle of the Eastern Arc archipelago, but these specimens were not closely related to *C. monax* in preliminary analyses of mitochondrial diversity (Esselstyn, Hutterer, and Stanley, unpubl. data). Rather, they have historically been identified as *C. luna* (Dippenaar & Meester, 1989). Further study is needed to confirm this identification and the biogeography of the shrews in these mountains.

Crocidura monax was included in the “dolichura group” by Dollman (1916), in the “naked-tailed” group by Heim de Balsac (1968), and in the “monax-dolichura” complex by Dippenaar (1980), together with several other taxa, because of the relatively low pilosity on the tail. Whether or not this phenotypic character state provides phylogenetic signal has not been critically analyzed, but our results suggest it is highly plastic within *Crocidura*. Closely related species often differ in the relative amounts of bristles on the tail. For example *C. newmarki*, *C. monax*, *C. usambarae* and *C. tansaniana* especially, but also *C. mdumai* and *C. munissii* differ widely in the extent of tail bristles, but are phylogenetically closely related. Determination of the function (if any) of these bristles may help explain how this variation arises. Possible adaptive functions for these bristles include that they provide tactile sensory instruments or disseminate scent from glands near the anus.

In combination, these new species limits reveal a finer geographic scale of endemism than has been previously considered for many Tanzanian mammals. While rodents such as *Otomys* and *Lophuromys* have been recently shown to contain microendemics (Verheyen et al., 2002; Taylor et al. 2009, 2011), the restricted distribution of many of these shrew taxa contrast with murine rodent taxa that share the same habitats. The montane murine rodents of Tanzania that have been critically examined morphologically exhibit distributional patterns spanning several massifs throughout the country. For example *Hylomyscus arcimontensis* ranges from the North Pare Mountains to the Southern Highlands (Carleton & Stanley, 2005). *Praomys taitae* is distributed from the Taita Hills of Kenya, across the northern Highlands, south to the Udzungwa Mountains (Carleton & Stanley, 2012); Bryja *et al.* (2014) published molecular evidence showing only modest divergence in mitochondrial DNA sequences between the middle-southern Eastern Arc and the Northern Highlands-Northern Eastern Arc populations.

Why shrews exhibit greater species diversity and more restricted ranges than murine rodents has yet to be addressed adequately. Future studies, including systematic analysis of other soricid taxa and comparisons to paleobotanical datasets, should significantly augment efforts to understand the biogeographic history of these unique montane archipelagos.

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Bober SO, Kerbis-Peterhans JC. 2013. *Crocidura niobe* Niobe's Shrew ; pp 116-117 in Happold, M. & Happold, D.C.D. (eds) 2013. *Mammals of Africa*: *Volume IV.* Bloomsbury Publishing, London.

Bouckaert, R, Heled, J, Kühnert, D, Vaughan, TG, Wu, C-H, Xie, D, Suchard, MA, Rambaut, A, Drummond, A. 2014. A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **10**:e1003537.

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.

Brown, JC, Yalden, DW. 1973. The description of mammals-2 Limbs and locomotion of terrestrial mammals. *Mammal Review* **3**: 107-134.

Bryja, J, Mikula, O, Patzenhauerová, H, Oguge, NO, Šumbera, R, Verheyen, E. 2014. The role of dispersal and vicariance in the Pleistocene history of an East African mountain rodent, *Praomys delectorum*. *Journal of Biogeography* **41**: 196-208.

Burgess ND, Kock D, Cockle A, FitzGibbon C, Jenkins P, Honess P. 2000. Mammals. Pp. 173-190 and 401-406, *in* Coastal forests of eastern Africa. (N. D. Burgess and G. P. Clarke, eds.). I.U.C.N., Gland and Cambridge, 443 pp.

Carleton MD, Goodman SM. 1998. New taxa of nesomyine rodents (Muroidea: Muridae) from Madagascar's northern highlands, with taxonomic comments on previously described forms, pp. 163-200 (M. D. Carleton & SMG) in in "A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar, with reference to elevational variation. Fieldiana: Zoology, new series, no. **90**: 1-246.

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.

Child GS. 1965. Some notes on mammals of Kilimanjaro. *Tanganyika Notes and Records*, **64**: 77-89.

Churchfield S, Hutterer R, Dudu A. 2013. *Crocidura latona* Latona Shrew ; p 95 in Happold, M. & Happold, D.C.D. (eds) 2013. *Mammals of Africa*: *Volume IV.* Bloomsbury Publishing, London.

Darriba, D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9:** 772.

Davenport TRB, Stanley WT, Sargis EJ, De Luca DW, Mpunga NE, Machaga SJ, Olson LE. 2006. A new genus of African monkey, *Rungwecebus*: morphology, ecology, and molecular phylogenetics. *Science* **312:** 1378–1381.

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

Demeter A, Hutterer R. 1986. Small mammals from Mt. Meru and its environs (Northern Tanzania). *Cimbebasia* **8:** 199–207.

Dieterlen F, Heim de Balsac H. 1979. Zur Ökologie und Taxonomie der Spitzmäuse (Soricidae) des Kivu-Gebietes. *Säugetierkundliche Mitteilungen* **27**: 241-287.

Dinesen L, Lehmberg T, Svendsen TO, Hansen LA, Fjeldså J. 1994. A new genus and species of perdicine bird (Phasianidae, Perdicini) from Tanzania ; a relict form with Indo-Malayan affinites. *Ibis* **136**: 2-11.

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.

Dippenaar NJ. 1980. New species of *Crocidura* from Ethiopia and northern Tanzania (Mammalia: Soricidae). *Annals of the Transvaal Museum* **32**:125-154.

Dippenaar NJ, Meester JAJ. 1989. Revision of the luna-fumosa complex of Afrotropical Crocidura Wagler, 1832 (Mammalia: Soricidae). *Annals of the Transvaal Museum,* **35**: 1-47.

Dollman, G. 1915. On the African shrews belonging to the genus *Crocidura*. – V. *Annals and Magazine of Natural History* **8 (16)**: 507-527.

Dollman, G. 1916. On the African shrews belonging to the genus *Crocidura*. – VII. Annals and Magazine of Natural History **8 (17):** 188-209.

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. **2006.** Relaxed phylogenetics and dating with confidence. *PLoS Biology* **4**:e88.

Drummond, AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology, **7(1)**: 214.

Esselstyn JA, Maharadatunkamsi, Achmadi AS, Siler CD, Evans BJ. 2013. Carving out turf in a biodiversity hotspot: multiple, previously unrecognized shrew species co-occur on Java Island, Indonesia. *Molecular Ecology* **22**: 4972–4987.

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.

Flot J-F. 2010. Seqphase: A web tool for interconverting phase input/output files and fasta sequence alignments. Molecular Ecology Resources **10**: 162–166.

Garrick RC, Sunnucks P, Dyer RJ. 2010. Nuclear gene phylogeography using PHASE: dealing with unresolved genotypes, lost alleles, and systematic bias in parameter estimation. BMC Evolutionary Biology **10**: 118.

Giarla TC, Voss RS, Jansa SA. 2014. Hidden diversity in the Andes: Comparison of species delimitation methods in montane marsupials. Molecular Phylogenetics and Evolution **70**: 137–151.

Gotch AF. 1979. *Mammals - Their Latin Names Explained*: A guide to animal classification. Blandford.

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.

Guindon S., Gascuel O. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology* **52:** 696–704.

Heaney LR, Rickart EA, Balete DS, Duya MV, Duya MR, Steppan S. 2011. Seven new species and a new subgenus of forest mice (Rodentia: Muridae: *Apomys*) from Luzon Island. *Fieldiana Life and Earth Sciences,* **2**: 1-60.

Heim de Balsac H. 1968. Considérations préliminaires sur le peuplement des montages Africaines par les Soricidae. *Biologia Gabonica,* **4**: 299-323.

Heim de Balsac H, Meester J. 1977. Order Insectivora. Part 1. In: Meester J, Setzer HW, eds. The mammals of Africa: An identification manual.Smithsonian Institution Press, Washington, D.C., [not continuously paginated], 1-29.

Heller E. 1910. New species of insectivores from British East Africa, Uganda and Sudan. *Smithsonian Miscellaneous Collections* **56:** 1-5.

Hollister N. 1916. Shrews collected by the Congo expedition of the American Museum. *Bulletin of the American Museum of Natural History* **35:** 663-667.

Howell KM Jenkins PD. 1984. Records of shrews from Tanzania. *African Journal of Ecology* **22**: 67-68.

Hutterer R. 1986. Diagnosen neuer Spitzmäuse aus Tansania (Mammalia: Soricidae). *Bonner Zoologische Beiträge* **37:** 23–33.

Hutterer R. 2005. Order Soricomorpha. In: Wilson DE, Reeder DM, eds. *Mammal Species of the World: a Taxonomic and Geographic Reference,* third ed. Baltimore: Johns Hopkins University Press, 220–311.

Hutterer R. 2013. *Crocidura montis* Montane Shrew (Montane White-toothed Shrew); pp. 108-109 in Happold, M. & Happold, D. C. D. (eds) 2013. Mammals of Africa: Volume IV. Bloomsbury Publishing, London.

Hutterer, R. & Dieterlen, F. 1981. Weitere Erstnachweise von Kleinsaeugerarten fuer den Sudan. *African Small Mammal Newsletter* **6**: 1-3.

Kerbis Peterhans JC, Hutterer R, Kaliba P, Mazibuko L. 2008. The 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.

Kerbis Peterhans JC, Stanley WT, Hutterer R, Demos TC, Agwanda B. 2009. A new species of Surdisorex Thomas, 1906 (Mammalia, Soricidae) from western Kenya. Bonner Zoologische Beiträge **56:** 175-183.

Kerbis Peterhans JC, Hutterer R, Mwanga J, Ndara B, Davenport L, Karhagomba IB, Udelhoven J. 2010. African shrews endemic to the Albertine Rift: two new species of *Myosorex* (Mammalia, Soricidae) from Burundi and the Democratic Republic of Congo. *Journal of East African Natural History* **99**: 103-128.

Lawson LP. 2010. The discordance of diversification: evolution in the tropical-montane frogs of the Eastern Arc Mountains of Tanzania. *Molecular Ecology* **19**: 4046-4060.

Leaché AD, Fujita MK. 2010. Bayesian species delimitation in West African forest geckos (*Hemidactylus fasciatus*). Proceedings of the Royal Society B: Biological Sciences **277**: 3071–3077.

Librado P, Rozas J. 2009. DnaSP v5: A software for comprehensive analysis of

DNA polymorphism data. Bioinformatics **25**: 1451–1452.

Loader SP, Gower DJ, Ngalason W, Menegon M. 2010. Three new species of *Callulina* (Amphibia: Anura: Brevicipitidae) highlight local endemism and conservation plight of Africa's Eastern Arc forests. *Zoological Journal of the Linnean Society* **160:** 496-514.

Lovett JC. 1993. 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.

Lovett JC, Pocs T. 1993. Assessment of the condition of the Catchment Forest Reserves, a botanical appraisal. Catchment Forestry Report 93.3. Dar es Salaam.

Meester, J. 1963. A systematic revision of the shrew genus *Crocidura* in Southern Arica. *Transvaal Museum Memoir* **13**: 1-127.

Menegon M, Davenport TRB, Howell KM. 2011. Description of a new and critically endangered species of *Atheris* (Serpentes: Viperidae) from the Southern Highlands of Tanzania, with an overview of the country's tree viper fauna. *Zootaxa* **3120:** 43-54.

Moreau RE. 1966. *The Bird Faunas of Africa and its Islands*. London: Academic Press.

Sikes RS, Gannon WL and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **92**: 235-253.

Stanley WT. 2013. *Crocidura monax* Kilimanjaro Shrew (Rombo Shrew); pp. 107-108 in Happold, M. & Happold, D. C. D. (eds) 2013. Mammals of Africa: Volume IV. Bloomsbury Publishing, London.

Stanley WT., Kihaule PM, Howel KM, Hutterer R. 2000. Small mammals of the Eastern Arc Mountains, Tanzania. Journal of East African Natural History, **87**: 91-100.

Stanley WT, Esselstyn JA. 2010. Biogeography and diversity among montane populations of mouse shrew (Soricidae: *Myosorex*) in Tanzania. *Biological Journal of the Linnaean Society* **100**: 669-680.

Stanley WT, Goodman SM, Hutterer R. 1996. Notes on the insectivores and elephant shrews of the Chome Forest, South Pare Mountains, Tanzania.

(Mammalia: Insectivora et Macroscelidea). *Zoologische Abhandlugen Staatliches Museum für Tierkunde* Dresden **49**: 131-147.

Stanley WT, Goodman SM, Newmark WD. 2011. Small mammal inventories in the East and West Usambara Mountains, Tanzania. 1. Study areas, methodologies, and general results, pp. 1-17. In Stanley WT, ed. Studies of Montane Vertebrates of Tanzania. *Fieldiana: Life and Earth Sciences*, vol. 4. Field Museum of Natural History, Chicago.

Stanley, WT, Hutterer, R. 2007. Differences in abundance and species richness between shrews and rodents along an elevational gradient in the Udzungwe Mountains, Tanzania. *Acta Theriologica* **52**: 259-273.

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, Munissi MJ. 2007. Small mammals of two forest reserves in the North Pare Mountains, Tanzania. *Journal of East African Natural History* **96**: 215-226.

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

Stanley WT, Rogers MA, Hutterer R. 2005. A new species of *Congosorex* from the Eastern Arc Mountains (Tanzania), with significant biogeographical implications. *Journal of Zoology* **265**: 269-280.

Stanley WT, Rogers MA, Kihaule PM, Munissi MJ. 2014. Elevational distribution and ecology of small mammals on Africa's highest mountain. *PloS One* **9(11):** e109904.

Stephens M, Smith NJ, Donnelly P. 2001. A new statistical method for haplotype reconstruction from population data. American Journal of Human Genetics **68**: 978–989.

Taylor PJ, Lavrenchenko LA, Carleton MD, Verheyen E, Bennett NC, Oosthuizen CJ, Maree S. 2011. Specific limits and emerging diversity patterns in East African populations of laminate-toothed rats, genus *Otomys* (Muridae: Murinae: Otomyini): Revision of the *Otomys typus* complex. *Zootaxa* **3024**: 1-66.

Taylor PJ, Maree S, van Sandwyk J, Kerbis Peterhans JC, Stanley WT, Verheyen E, Kaliba P, Verheyen W, Kaleme P, Bennett NC. 2009. Speciation mirrors geomorphology and palaeoclimatic history in African laminate-toothed rats (Muridae: Otomyini) of the *Otomys denti* and *Otomys lacustris* species-complexes in the “Montane Circle” of East Africa. *Biological Journal of the Linnean Society* **96**: 913–941.

Thomas, O. 1906. Descriptions of new mammals from Mount Ruwenzori. *Annals and Magazine of Natural History,* **7 (18)**: 136-147.

Thomas O. 1910. List of mammals from Mount Kilimanjaro, obtained by Mr. Robin Kemp, and presented to the British Museum by Mr. C. D. Rudd. *Annals and Magazine of Natural History,* **8 (6):** 308-316.

Turni H, Hutterer R, Asher R. 2007. Type specimens of “insectivoran” mammals at the Museum für Naturkunde, Berlin. *Zootaxa* **1470**: 1 – 33.

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.

Verheyen WN, Hulselmans JLJ, Dierckx T, Verheyen E. 2002. The *Lophuromys flavopunctatus* Thomas 1888 species complex: A craniometric study, with the description and genetic characterization of two new species (Rodentia-Muridae-Africa). *Bulletin de L’Institut Royal des Sciences Naturelles de Belgique, Biologie* **73**: 27-71.

Yang Z, Rannala B. 2010. Bayesian species delimitation using multilocus sequence data. *Proceedings of the National Academy of Sciences* **107**: 9264-9269

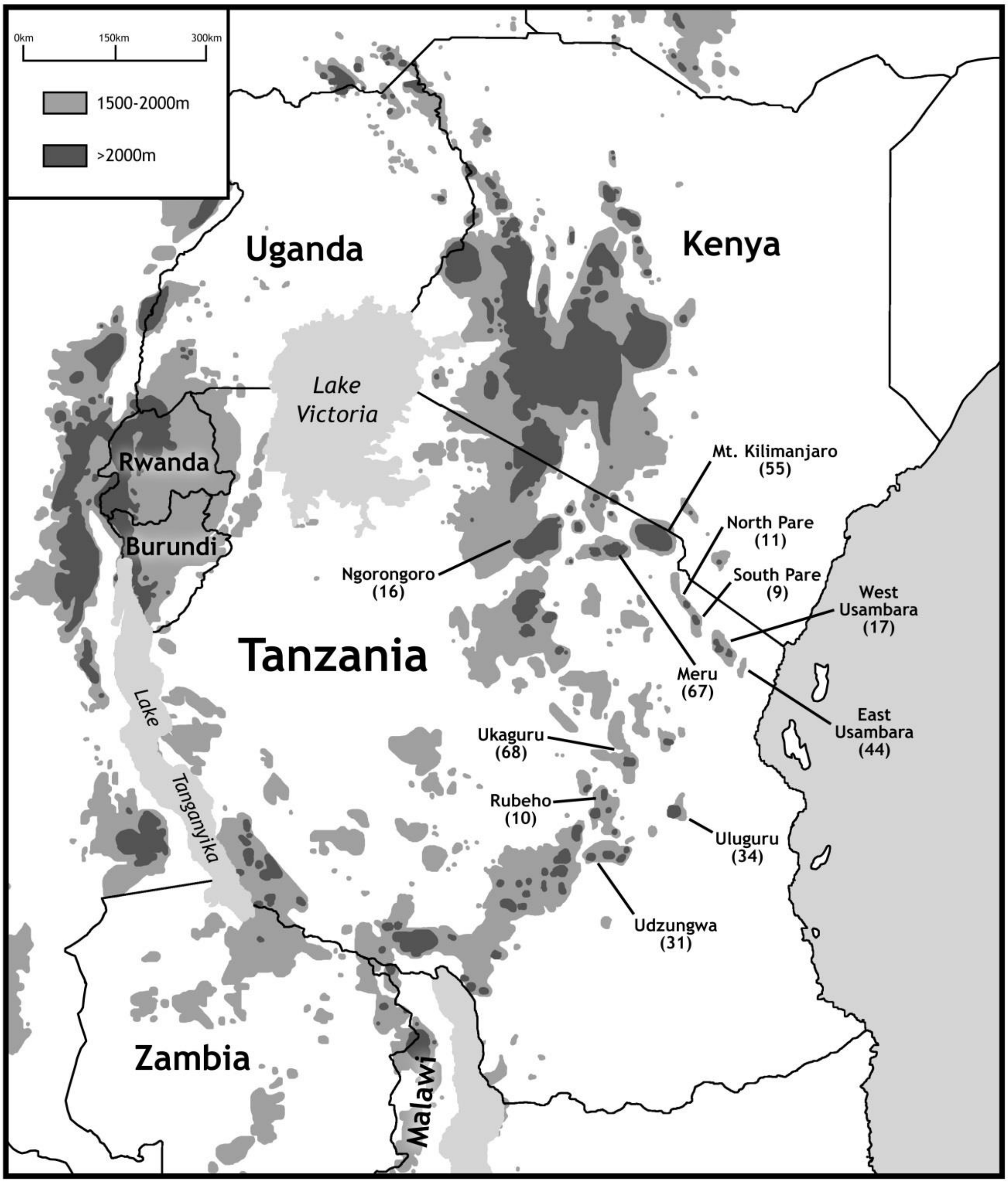


Figure 1. Map of mountainous regions of Tanzania and surrounding countries. Areas above 1500 m are shaded. Populations sampled for this study are indicated with sample sizes for cranial measurements in parentheses. See Methods and Materials for details on specific localities and sample sizes.

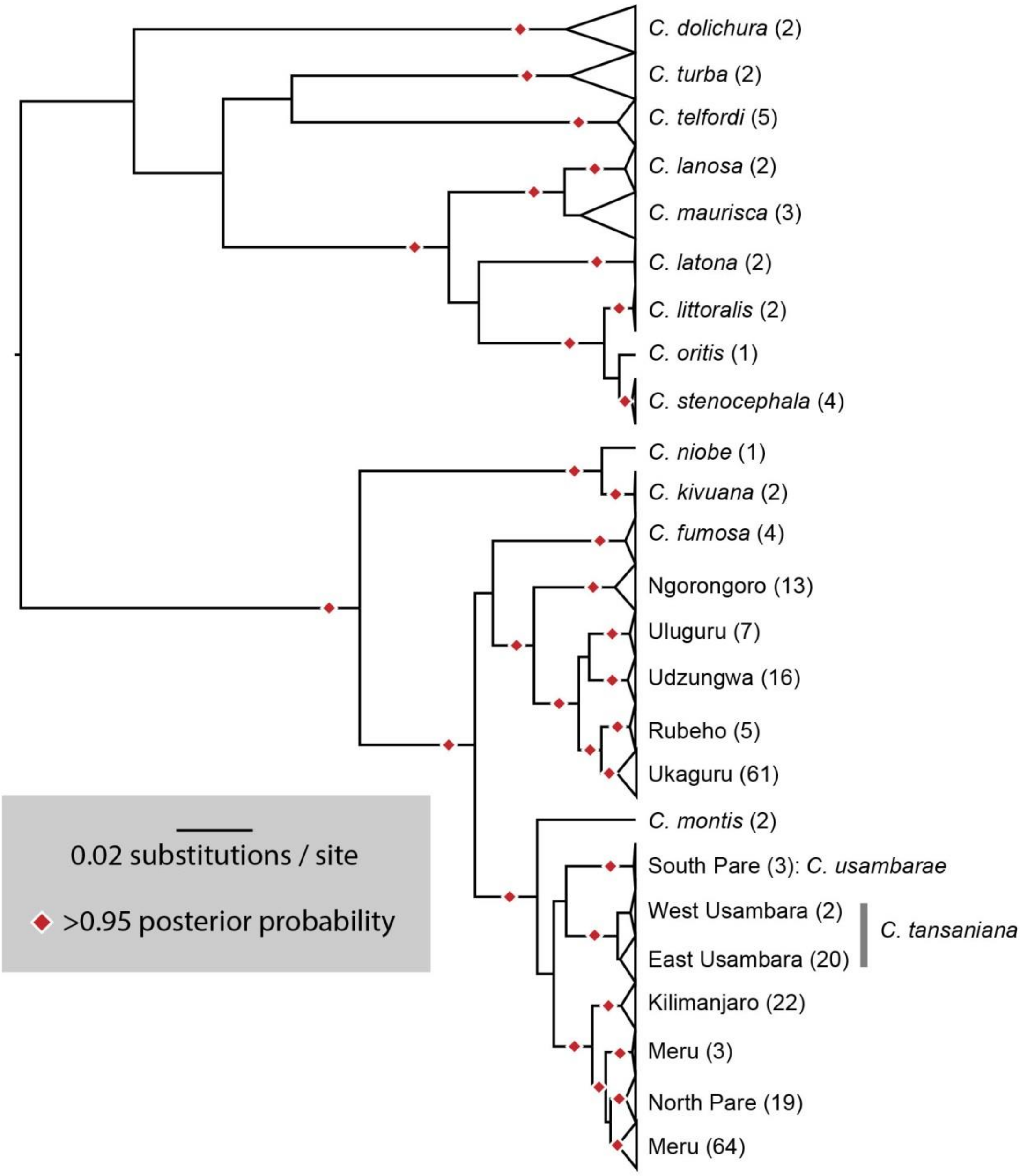


Figure 2. Phylogenetic tree estimated from Bayesian analysis of 267 cytochrome b sequences. Populations/species at tips have been collapsed into triangles where the apex represents the deepest split within the group. Diamonds along branches indicate clades with posterior probabilities greater than 0.95, and values in parentheses after names indicate the number of individuals sequenced.

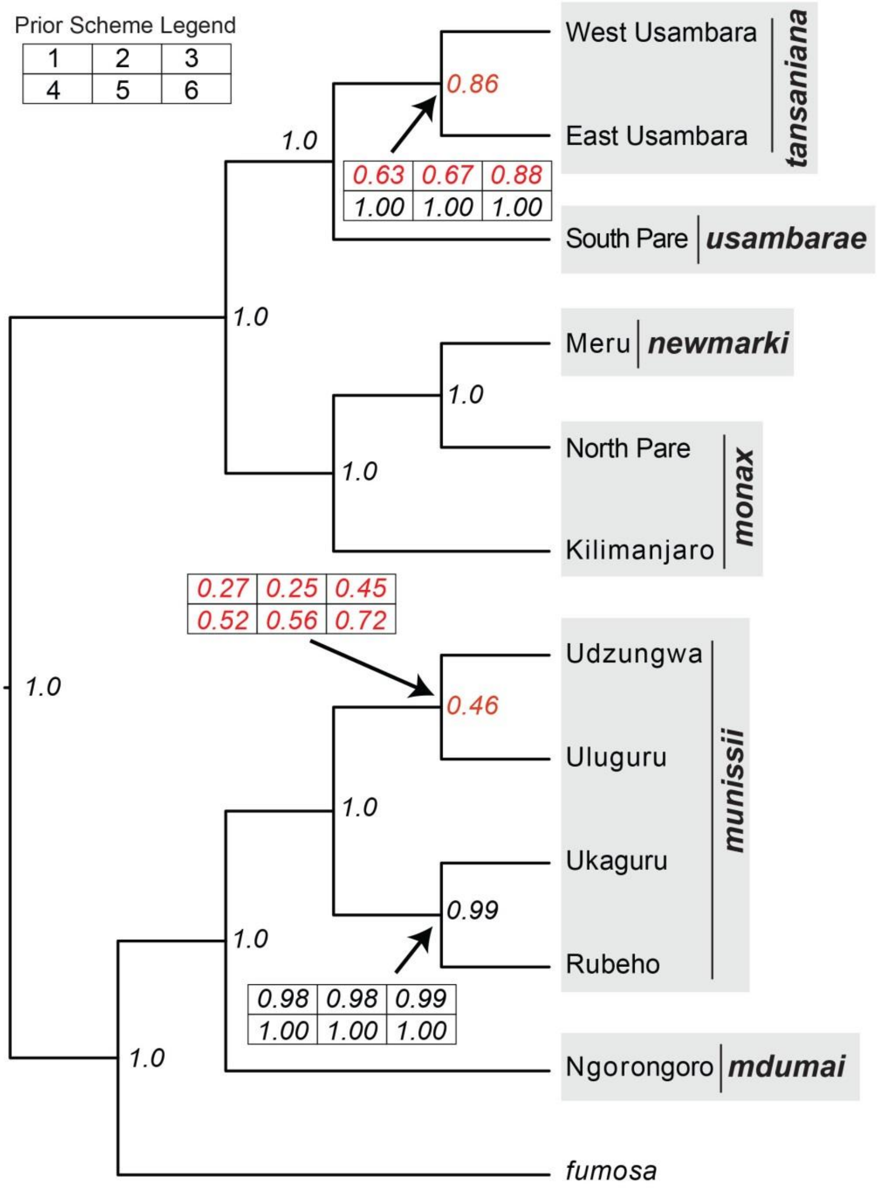
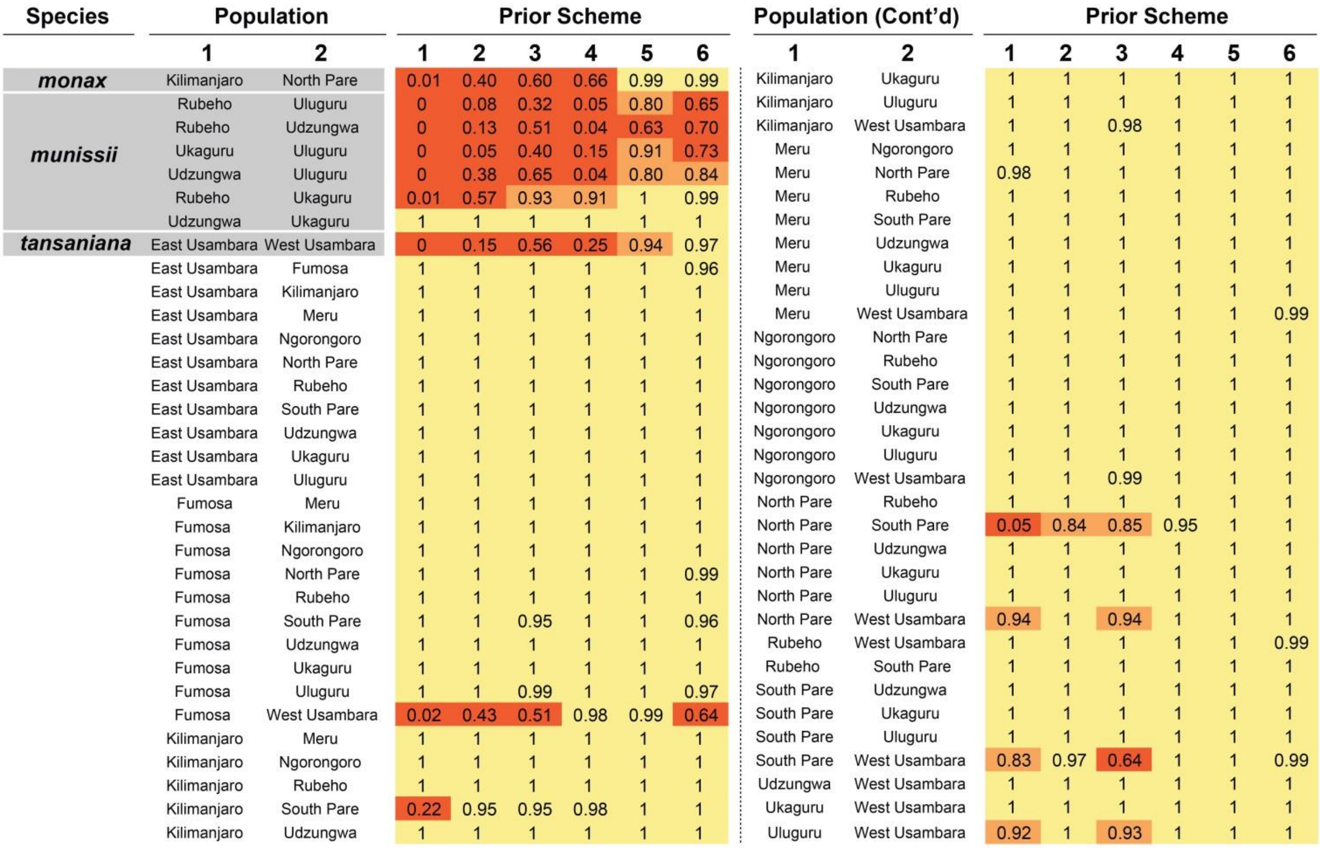


Figure 3. Results from guide-tree-based BP&P analysis for 12 putative species. The guide tree is based on the Cytb topology (Fig. 2), but excludes *Crocidura montis* from the Rwenzoris, for which no nuclear sequences were obtained. The posterior probability that a given split represents a speciation event is given at each node, averaged across all six prior schemes (Table 1). For the three nodes that exhibited variation across different prior schemes, the full results are illustrated in grids. Populations are grouped in gray boxes according to our taxonomic conclusions.



Species	Population		Prior Scheme						Population (Cont'd)		Prior Scheme					
	1	2	1	2	3	4	5	6	1	2	1	2	3	4	5	6
monax	Kilimanjaro	North Pare	0.01	0.40	0.60	0.66	0.99	0.99	Kilimanjaro	Ukaguru	1	1	1	1	1	1
munissii	Rubeho	Uluguru	0	0.08	0.32	0.05	0.80	0.65	Kilimanjaro	Uluguru	1	1	1	1	1	1
	Rubeho	Udzungwa	0	0.13	0.51	0.04	0.63	0.70	Kilimanjaro	West Usambara	1	1	0.98	1	1	1
	Ukaguru	Uluguru	0	0.05	0.40	0.15	0.91	0.73	Meru	Ngorongoro	1	1	1	1	1	1
	Udzungwa	Uluguru	0	0.38	0.65	0.04	0.80	0.84	Meru	North Pare	0.98	1	1	1	1	1
	Rubeho	Ukaguru	0.01	0.57	0.93	0.91	1	0.99	Meru	Rubeho	1	1	1	1	1	1
	Udzungwa	Ukaguru	1	1	1	1	1	1	Meru	South Pare	1	1	1	1	1	1
tansaniana	East Usambara	West Usambara	0	0.15	0.56	0.25	0.94	0.97	Meru	Udzungwa	1	1	1	1	1	1
	East Usambara	Fumosa	1	1	1	1	1	0.96	Meru	Ukaguru	1	1	1	1	1	1
	East Usambara	Kilimanjaro	1	1	1	1	1	1	Meru	Uluguru	1	1	1	1	1	1
	East Usambara	Meru	1	1	1	1	1	1	Meru	West Usambara	1	1	1	1	1	0.99
	East Usambara	Ngorongoro	1	1	1	1	1	1	Ngorongoro	North Pare	1	1	1	1	1	1
	East Usambara	North Pare	1	1	1	1	1	1	Ngorongoro	Rubeho	1	1	1	1	1	1
	East Usambara	Rubeho	1	1	1	1	1	1	Ngorongoro	South Pare	1	1	1	1	1	1
	East Usambara	South Pare	1	1	1	1	1	1	Ngorongoro	Udzungwa	1	1	1	1	1	1
	East Usambara	Udzungwa	1	1	1	1	1	1	Ngorongoro	Ukaguru	1	1	1	1	1	1
	East Usambara	Ukaguru	1	1	1	1	1	1	Ngorongoro	Uluguru	1	1	1	1	1	1
	East Usambara	Uluguru	1	1	1	1	1	1	Ngorongoro	West Usambara	1	1	0.99	1	1	1
	Fumosa	Meru	1	1	1	1	1	1	North Pare	Rubeho	1	1	1	1	1	1
	Fumosa	Kilimanjaro	1	1	1	1	1	1	North Pare	South Pare	0.05	0.84	0.85	0.95	1	1
	Fumosa	Ngorongoro	1	1	1	1	1	1	North Pare	Udzungwa	1	1	1	1	1	1
	Fumosa	North Pare	1	1	1	1	1	0.99	North Pare	Ukaguru	1	1	1	1	1	1
	Fumosa	Rubeho	1	1	1	1	1	1	North Pare	Uluguru	1	1	1	1	1	1
	Fumosa	South Pare	1	1	0.95	1	1	0.96	North Pare	West Usambara	0.94	1	0.94	1	1	1
	Fumosa	Udzungwa	1	1	1	1	1	1	Rubeho	West Usambara	1	1	1	1	1	0.99
	Fumosa	Ukaguru	1	1	1	1	1	1	Rubeho	South Pare	1	1	1	1	1	1
	Fumosa	Uluguru	1	1	0.99	1	1	0.97	South Pare	Udzungwa	1	1	1	1	1	1
	Fumosa	West Usambara	0.02	0.43	0.51	0.98	0.99	0.64	South Pare	Ukaguru	1	1	1	1	1	1
	Kilimanjaro	Meru	1	1	1	1	1	1	South Pare	Uluguru	1	1	1	1	1	1
	Kilimanjaro	Ngorongoro	1	1	1	1	1	1	South Pare	West Usambara	0.83	0.97	0.64	1	1	0.99
	Kilimanjaro	Rubeho	1	1	1	1	1	1	Udzungwa	West Usambara	1	1	1	1	1	1
	Kilimanjaro	South Pare	0.22	0.95	0.95	0.98	1	1	Ukaguru	West Usambara	1	1	1	1	1	1
	Kilimanjaro	Udzungwa	1	1	1	1	1	1	Uluguru	West Usambara	0.92	1	0.93	1	1	1

Figure 4. BP&P results from 66 pairwise comparisons between all twelve populations considered in this study. Each pairwise comparison was made with six different prior schemes (Table 1). Strong support for species delimitation (PP > 0.9) is coded in yellow and low support (PP < 0.9) is coded in red. Three sets of populations are ultimately grouped into three distinct species (*Crocidura monax*, *C. munissii*, and *C. tansaniana*) based on these results and our morphological analyses; comparisons involving only those populations are grouped together in gray boxes.

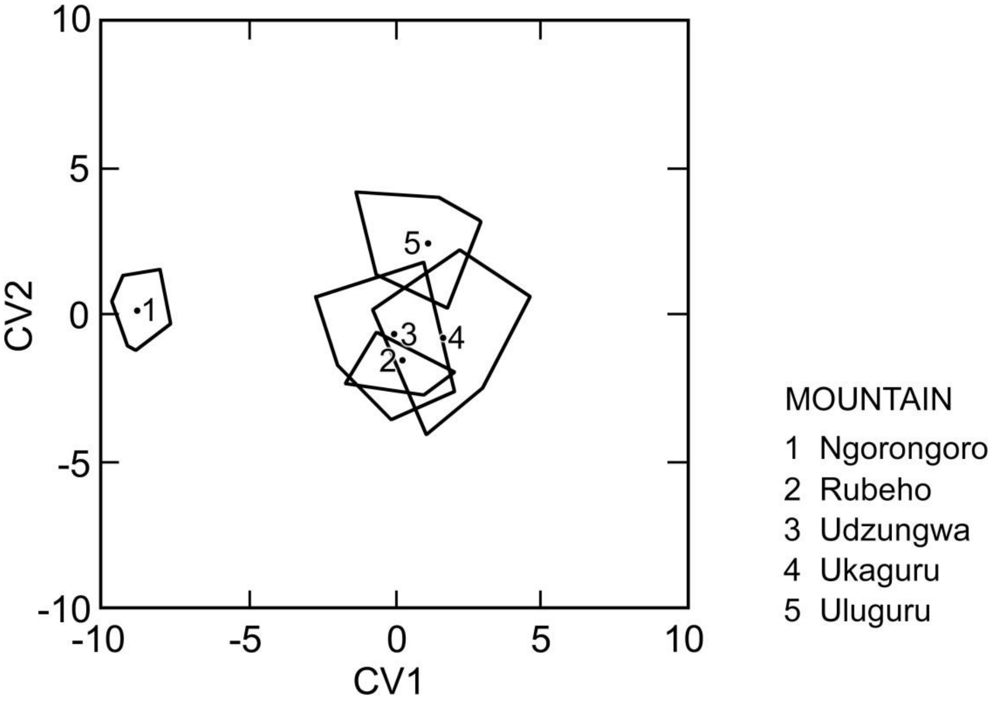


Figure 5. Projection of specimen scores on the first two canonical variates extracted from a discriminant function analysis of 16 log-transformed cranial and dental variables. Measurements were recorded from adult specimens from 5 populations of *Crocidura* from Ngorongoro, Rubeho, Udzungwa, Ukaguru and Uluguru Mountains.

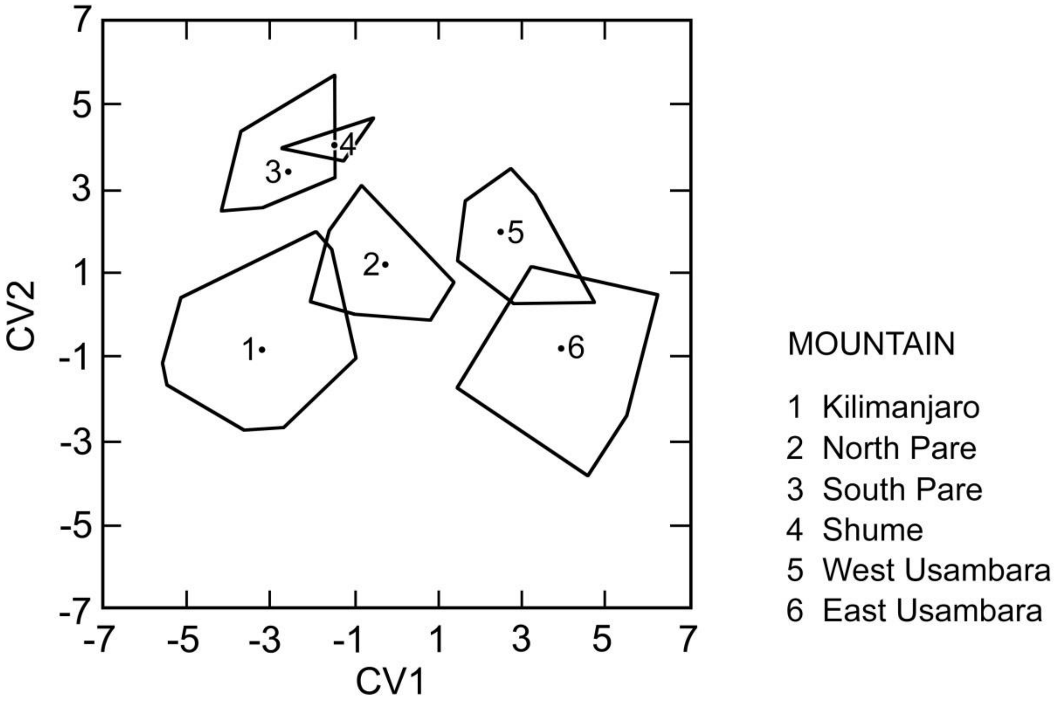


Figure 6. Projection of specimen scores on the first two canonical variates extracted from a discriminant function analysis of 16 log-transformed cranial and dental variables. Measurements were recorded from adult specimens from 6 populations, including Kilimanjaro, North Pare, South Pare, West Usambara (Shume-Magamba), West Usambara (Ambangulu) and East Usambara (specimens from Mt. Meru [*C. newmarki*] were excluded).

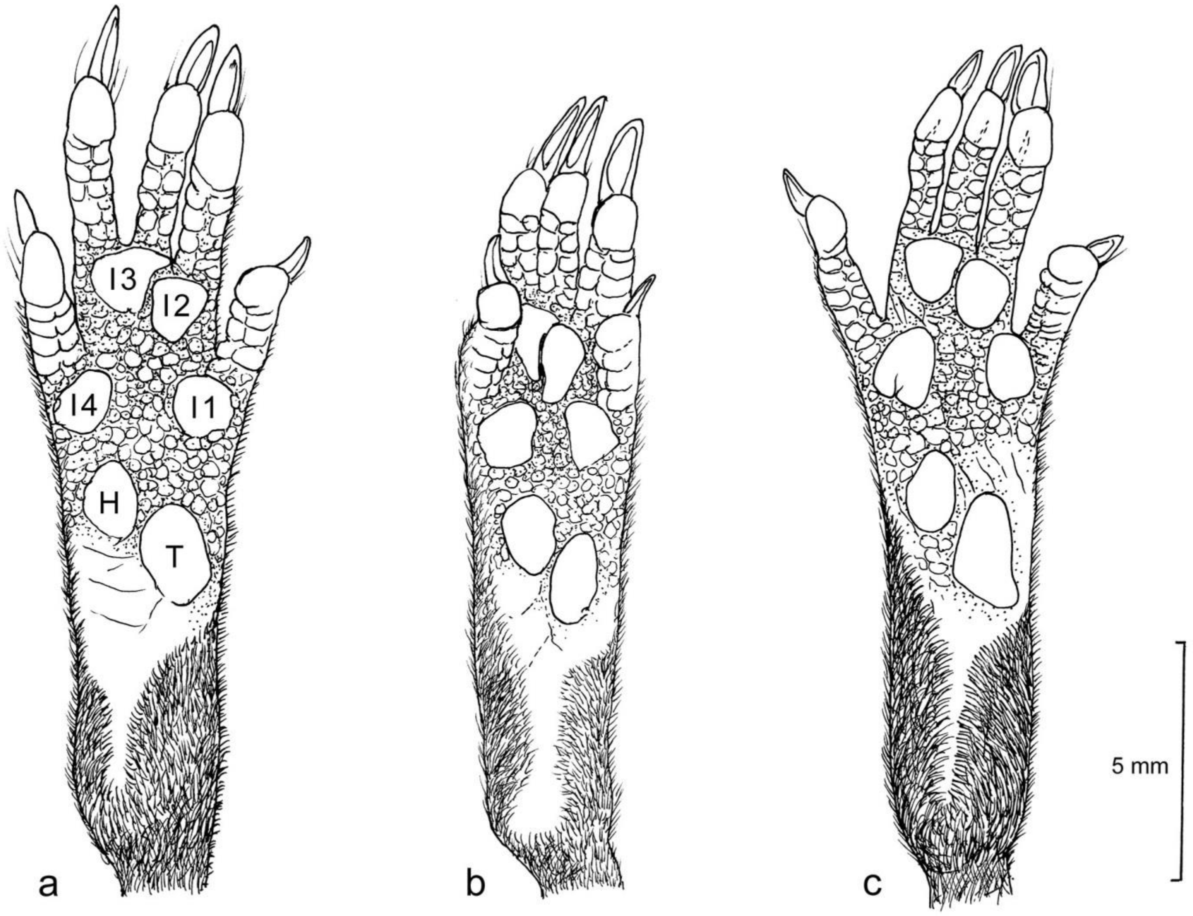


Figure 7. Plantar view of the right hindfoot of (a) *Crocidura monax* (FMNH 173789), (b) *C. newmarki* sp. nov. (FMNH 208012), and (c) *C. munissii* sp. nov. (FMNH 158407); scale is 5 mm. Note differences in the relative distance between thenar (T), hypothenar (H), and interdigital pads (I1-4).

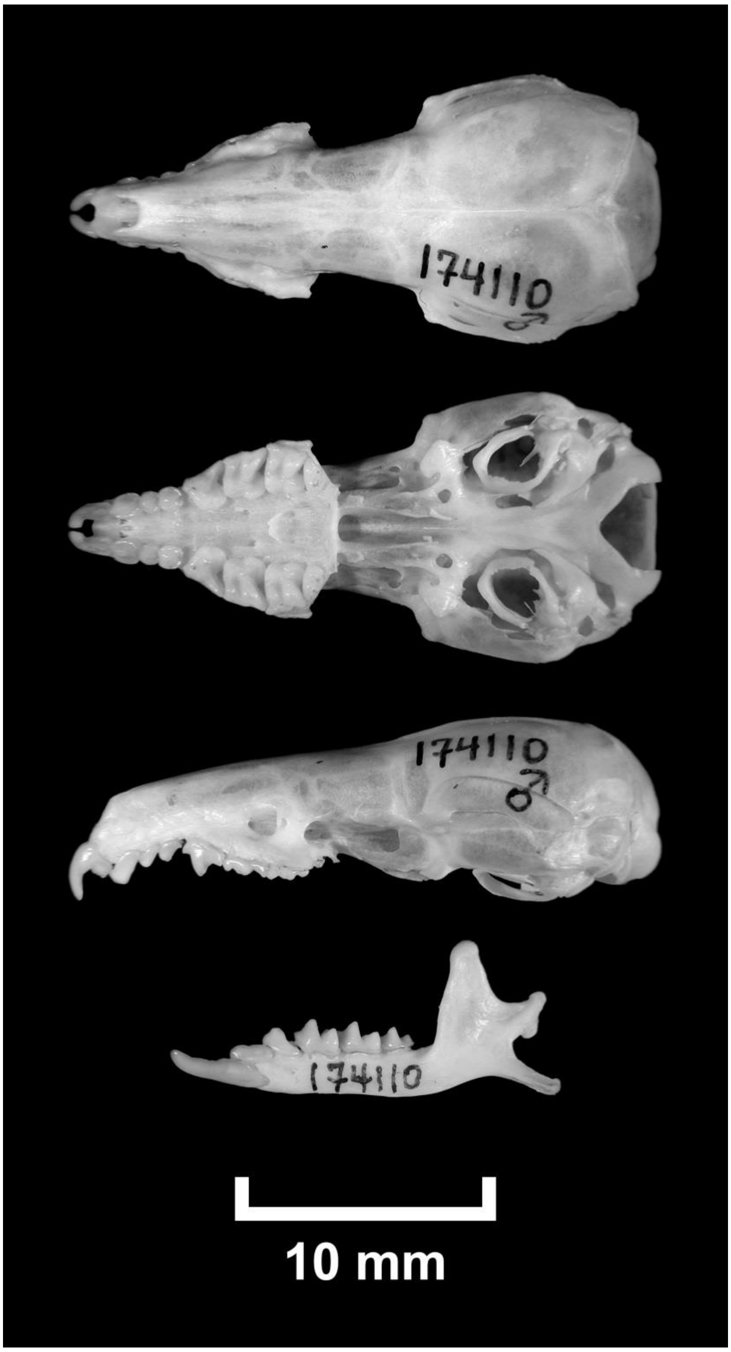


Figure 8. Dorsal, ventral and lateral views of adult cranium and mandible of *Crocidura monax* (FMNH 174110; CI = 23.04 mm), a male from 4 km N, 1.5 km W Maua on Mt. Kilimanjaro (2000 m).

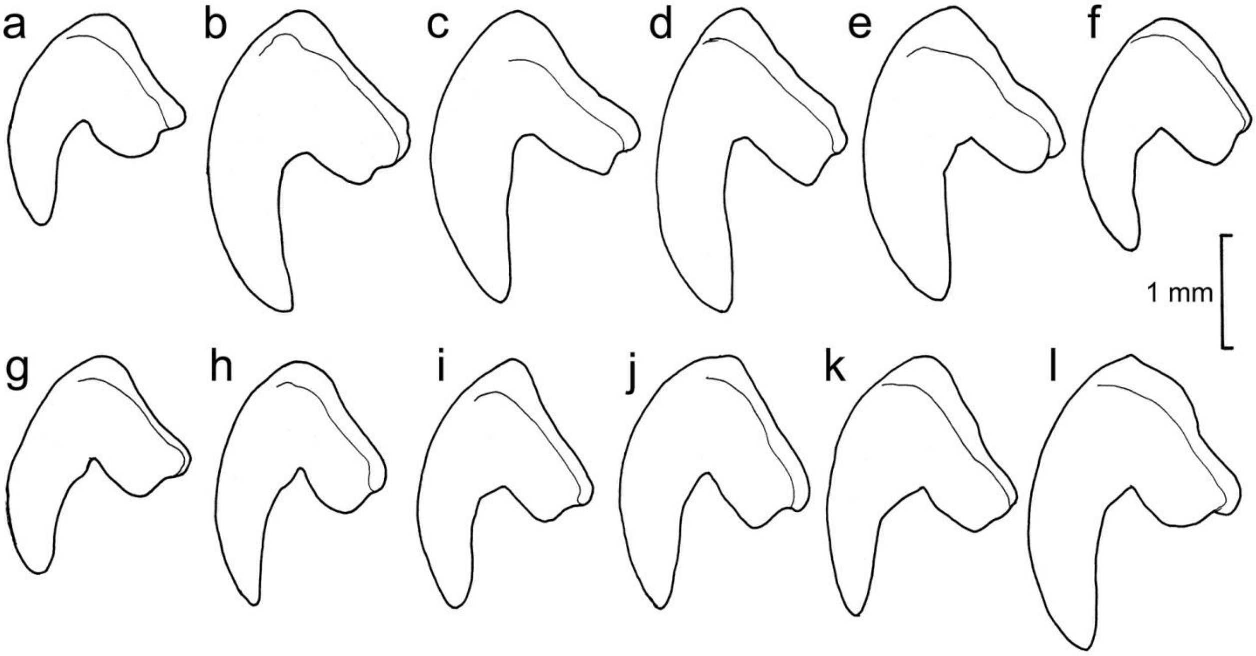


Figure 9. Lateral views of the first upper incisor of populations of the *C. monax* species group; scale is 1 mm: (a) Ngorongoro FMNH 211332 (= *C. mdumai* sp. nov.), (b) Uluguru FMNH 158280 (= *C. munissii* sp. nov.), (c) Udzungwa FMNH 155501 (= *C. munissii* sp. nov.), (d) Ruhebo FMNH 197660 (= *C. munissii* sp. nov.), (e) Ukaguru FMNH 166705 (= *C. munissii* sp. nov.), (f) Meru FMNH 208424 (= *C. newmarki* sp. nov.), (g) Kilimanjaro FMNH 174109, (h) North Pare FMNH 192665 (= *C. monax*), (i) South Pare FMNH 153918, (j) Magamba FMNH 27429 (= *C. usambarae*), (k) West Usambara FMNH 151099, and (l) East Usambara FMNH 149970 (= *C. tansaniana*).

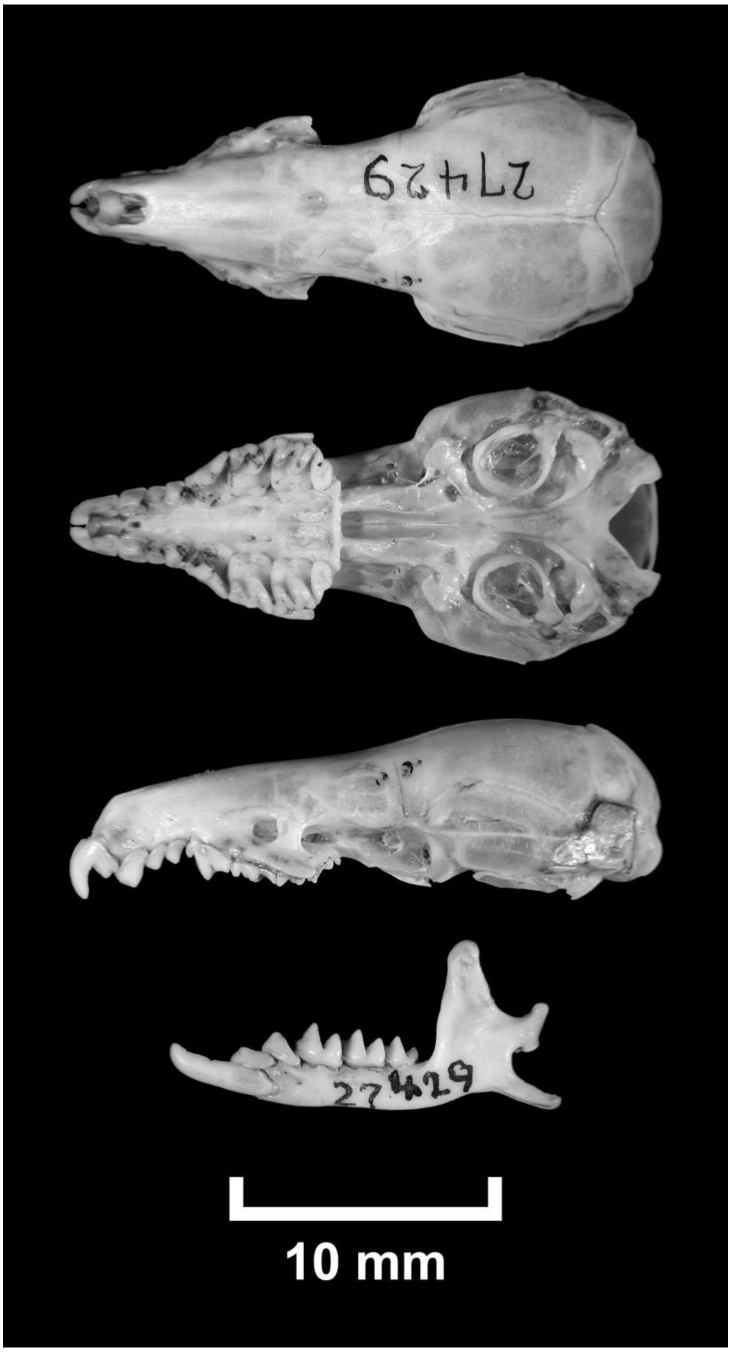


Figure 10. Dorsal, ventral and lateral views of adult cranium and mandible of *Crocidura usambarae* [FMNH 27429; (paratype); CI = 22.02 mm], a male from Magamba, West Usambara Mountains.

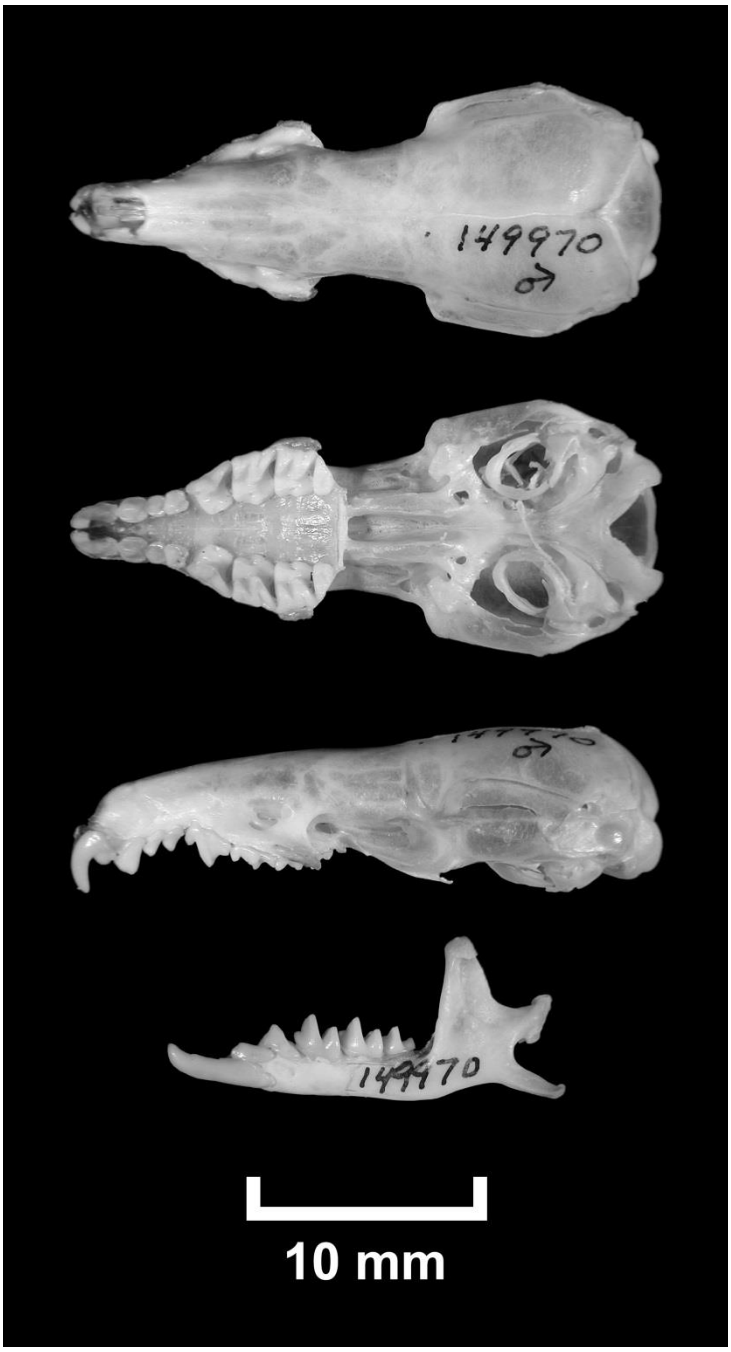


Figure 11. Dorsal, ventral and lateral views of adult cranium and mandible of *Crocidura tansaniana* (FMNH 149970; CI = 25.24 mm), a male from 4.5 km WNW Amani, Monga Tea Estate in the East Usambara Mountains.

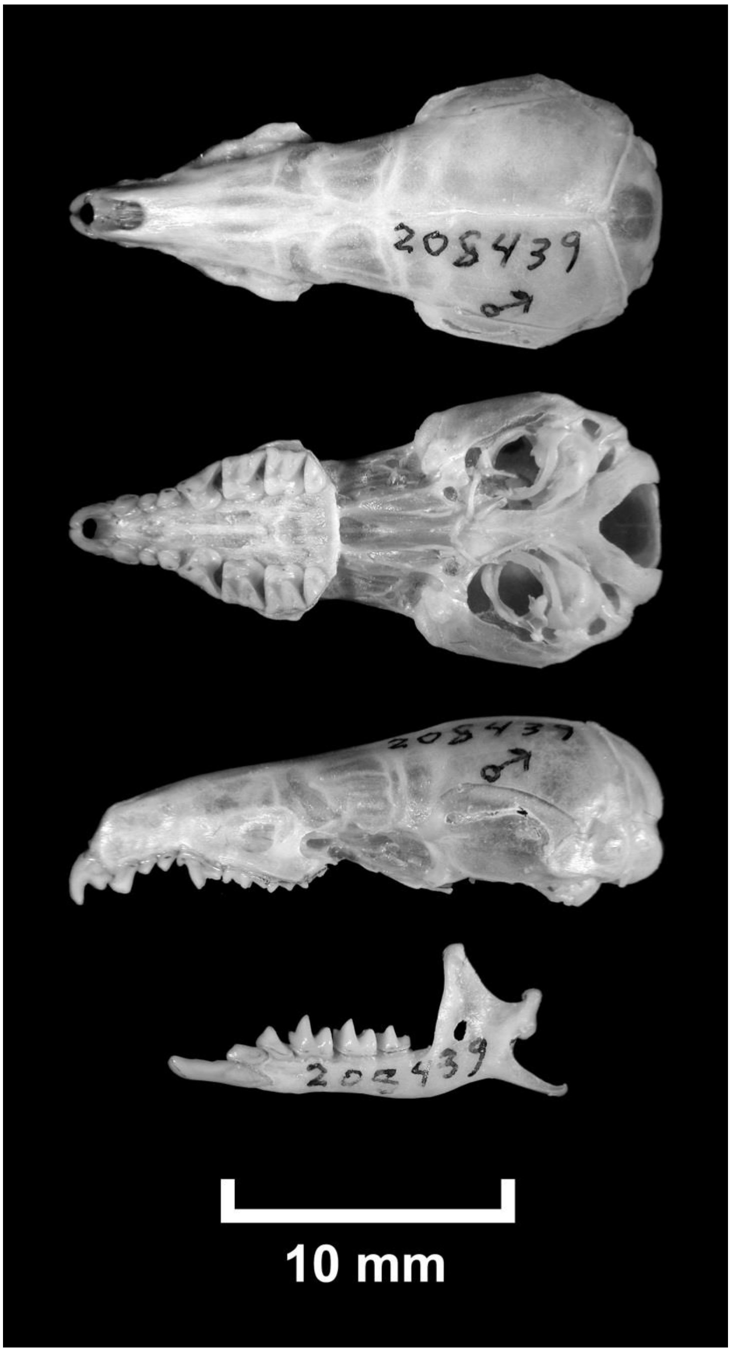


Figure 12. Dorsal, ventral and lateral views of adult cranium and mandible of *Crocidura newmarki* [FMNH 208439 (holotype); CI = 20.59 mm], a male from Mt Meru, Arusha National Park, near Saddle Hut (3600 m).

Figure 13. Dorsal, ventral and lateral views of adult cranium and mandible of *Crocidura mdumai* [FMNH 211323 (holotype); CI = 21.64 mm], a male from Ngorongoro Conservation Area, Ngorongoro Crater rim, near Pongo Ranger Post (2064 m).

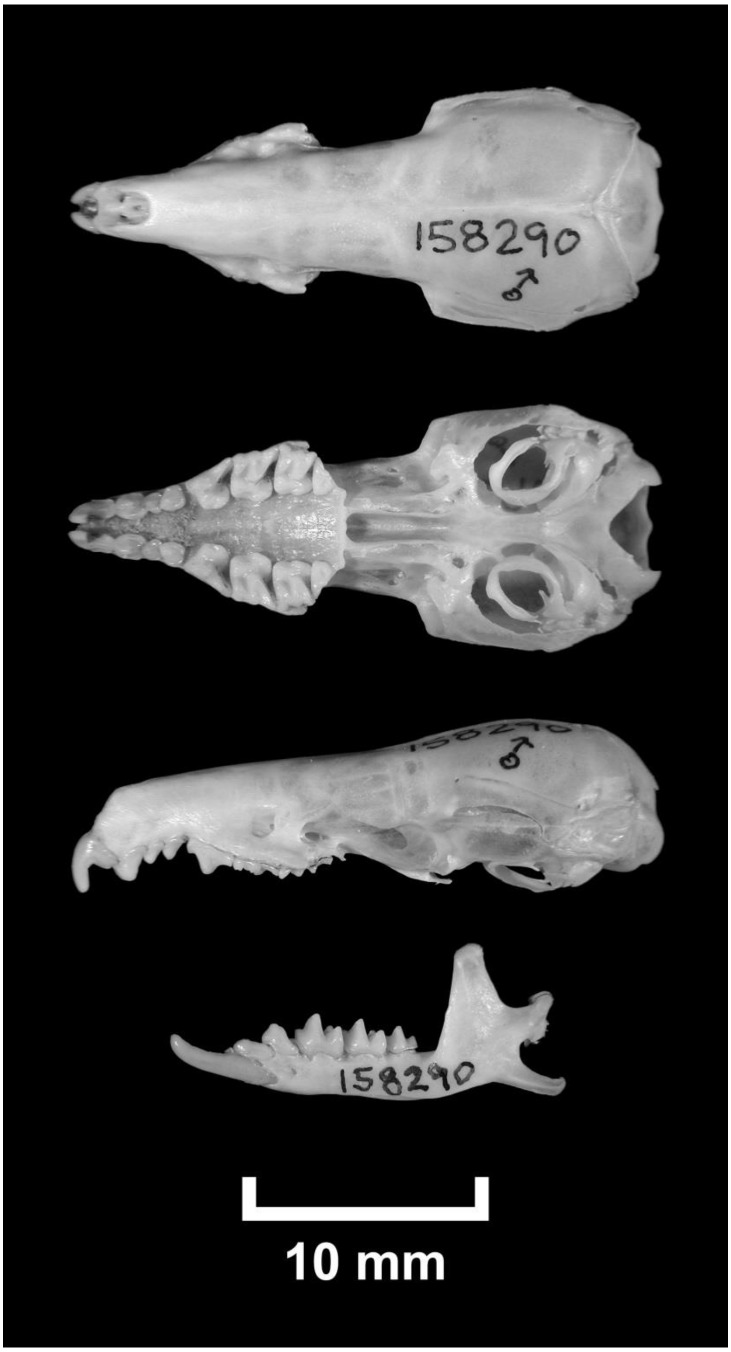


Figure 14. Dorsal, ventral and lateral views of adult cranium and mandible of *Crocidura munissii* [FMNH 158290 (holotype); CI = 24.69 mm], a male from 5.1 km W, 2.3 km N Tegetero in the Uluguru Mountains (1535 m).

Table 1. Prior schemes used in guide-tree-based and pairwise BP&P analyses. Prior distributions on τ represent three relative divergence depths (deep, moderate, and shallow) and on θ represent two relative mutation-rate-scaled effective population sizes (large and small).

Prior scheme	Divergence depth	Effective pop. size	Gamma distribution for prior
1	Deep	Large	$\theta \sim \Gamma(1, 10)$ & $\tau \sim \Gamma(1, 10)$
2	Moderate	Large	$\theta \sim \Gamma(1, 10)$ & $\tau \sim \Gamma(2, 2000)$
3	Shallow	Large	$\theta \sim \Gamma(1, 10)$ & $\tau \sim \Gamma(2, 20000)$
4	Deep	Small	$\theta \sim \Gamma(2, 2000)$ & $\tau \sim \Gamma(1, 10)$
5	Moderate	Small	$\theta \sim \Gamma(2, 2000)$ & $\tau \sim \Gamma(2, 2000)$
6	Shallow	Small	$\theta \sim \Gamma(2, 2000)$ & $\tau \sim \Gamma(2, 20000)$

Table 2. Alignment characteristics for all nuclear genes included in this study. The first three loci listed were included in BP&P analyses. The other five loci were not included in BP&P analyses but rather were used to make independent estimates of the population-scaled mutation parameter θ across a subset of individuals, allowing an evaluation of the validity of our chosen □ priors.

Locus	Individuals Sampled	Locus Length	θ_W
BRCA	77	588	0.0059
GHR	74	531	0.0042
VWF	68	627	0.0108
APOB	15	559	0.0035
BDNF	16	403	0.0034
MCGF	15	594	0.0052
PTGER	16	482	0.0033
RAG1	16	563	0.0047

Table 3. External measurements of individuals of *Crocidura* from 11 mountains in Tanzania (listed in geographic order from north to south). and three holotypes. Sexes are combined within populations. All measurements were taken by WTS, with the exception of the West Usambara sample, and those of the holotypes where the measurements were recorded from original skin tags or literature. Mean ± standard deviation, range, sample size and CV. See text for character definitions.

	TL	HB	TV	HF	EAR	WT
Meru	130.69 ± 6.03 116.00 – 144.00 N = 115 0.05	77.37 ± 3.95 65.00 – 85.00 N = 115 0.05	53.31 ± 3.37 45.00 – 60.00 N = 115 0.06	15.03 ± 0.61 13.00 – 16.00 N = 115 0.04	9.35 ± 0.58 8.00 – 10.00 N = 115 0.06	8.53 ± 1.09 6.00 – 11.00 N = 115 0.13
Ngorongoro	139.38 ± 3.36 134.00 – 145.00 N = 16 0.02	81.69 ± 3.89 76.00 – 91.00 N = 16 0.05	57.69 ± 3.53 52.00 – 65.00 N = 16 0.06	15.38 ± 0.62 14.00 – 16.00 N = 16 0.04	10.63 ± 0.62 9.00 – 11.00 N = 16 0.06	8.61 ± 0.59 7.30 – 9.60 N = 16 0.07
Kilimanjaro	155.58 ± 6.95 141.00 – 172.00 N = 55 0.04	91.49 ± 4.25 83.00 – 101.00 N = 55 0.05	64.09 ± 3.67 55.00 -71.00 N = 55 0.06	17.00 ± 0.67 16.00 -19.00 N = 55 0.04	10.85 ± 0.56 10.00 – 12.00 N = 55 0.05	13.92 ± 1.44 10.00 – 17.00 N = 53 0.10
North Pare	149.80 ± 4.80 140.00 – 158.00 N = 10 0.03	89.90 ± 3.75 84.00– 96.00 N = 10 0.04	60.09 ± 2.21 56.00 – 63.00 N = 11 0.04	16.73 ± 0.47 16.00 – 17.00 N = 11 0.03	10.18 ± 0.40 10.00 – 11.00 N = 11 0.04	11.79 ± 1.72 9.20 – 15.50 N = 11 0.15
South Pare	140.00 ± 5.39 132.00 – 146.00 N = 7 0.04	81.71 ± 3.68 75.00 – 85.00 N = 7 0.05	58.29 ± 3.04 54.00 – 62.00 N = 7 0.05	15.63 ± 0.52 15.00 – 16.00 N = 8 0.03	9.63 ± 0.52 9.00 – 10.00 N = 8 0.05	9.45 ± 0.65 8.40 – 10.50 N = 8 0.07
West Usambara	159.65 ± 5.69 150.00 – 170.00 N = 17 0.04	93.88 ± 3.98 85.00 – 99.00 N = 17 0.04	65.76 ± 2.84 60.00 – 71.00 N = 17 0.04	16.29 ± 0.69 15.00 – 17.00 N = 17 0.04	10.21 ± 0.47 9.50 – 11.00 N = 17 0.05	13.85 ± 1.23 12.00 – 16.50 N = 17 0.09
East Usambara	163.00 ± 8.22 148.00 – 176.00 N = 21 0.05	94.33 ± 6.46 82.00 – 104.00 N = 21 0.07	68.67 ± 3.07 64.00 – 75.00 N = 21 0.04	17.38 ± 0.74 16.00 – 19.00 N = 21 0.04	10.95 ± 0.59 10.00 – 12.00 N = 21 0.05	15.31 ± 2.27 11.00 – 20.00 N = 21 0.15
Ukaguru	173.57 ± 6.59 159.00 – 191.00 N = 68 0.04	94.09 ± 5.20 77.00 – 106.00 N = 68 0.06	79.49 ± 4.74 66.00 – 95.00 N = 68 0.06	17.40 ± 0.65 16.00 – 19.00 N = 68 0.04	12.37 ± 0.54 11.00 – 13.00 N = 68 0.04	15.93 ± 1.56 12.50 – 19.50 N = 68 0.10
Rubeho	177.36 ± 7.59 166.00 – 190.00 N = 11 0.04	93.73 ± 4.22 87.00 – 101.00 N = 11 0.05	83.64 ± 4.78 77.00 – 93.00 N = 11 0.06	17.18 ± 0.75 16.00– 18.00 N = 11 0.04	10.82 ± 0.75 10.00 – 12.00 N = 11 0.07	13.00 ± 1.30 11.00 – 15.00 N =11 0.10
Uluguru	169.82 ± 7.91 158.00 – 187.00 N = 33 0.05	89.12 ± 4.01 82.00 – 97.00 N = 33 0.05	80.94 ± 5.47 70.00 – 95.00 N = 34 0.07	17.03 ± 0.80 16.00 – 19.00 N = 34 0.05	11.15 ± 0.67 10.00 – 13.00 N = 33 0.06	12.32 ± 1.39 9.50 – 15.50 N = 33 0.11
Udzungwa	167.33 ± 8.97 151.00 – 187.00 N = 30 0.05	86.53 ± 6.44 75.00 – 101.00 N = 30 0.07	80.80 ± 3.51 74.00 – 88.00 N = 30 0.04	17.29 ± 0.86 15.00– 19.00 N = 31 0.05	10.90 ± 0.75 9.00 – 12.00 N = 31 0.07	14.32 ± 2.24 10.00 – 19.50 N =31 0.16
C. monax Type		88	66	16.2	10	
C. montis Type		77	61	15	11	
C. tansaniana Type		109	65	17	13	15
C. usambarae Type		80	63	15	8	

Table 4. Cranial measurements of individuals of *Crocidura* from 11 mountains in Tanzania (sexes combined within populations), two holotypes, and one set of paratypes. Mean ± standard deviation, range, sample size and CV. See text for character definitions.

	CI	BL	PPL	UTRL	LIW	BW	NW	GW	HBC
Ngorongoro	21.49 ± 0.25	19.30 ± 0.23	9.89 ± 0.16	9.14 ± 0.16	4.59 ± 0.09	6.28 ± 0.12	1.98 ± 0.08	9.80 ± 0.13	6.55 ± 0.16
	21.09 – 21.95	18.88 – 19.68	9.59 – 10.12	8.83 – 9.40	4.43 – 4.73	6.06 – 6.50	1.83 – 2.12	9.53 – 10.03	6.26 – 6.80
	N = 16	N = 16	N = 16	N = 16	N = 16	N = 16	N = 16	N = 16	N = 16
	0.02	0.01	0.02	0.02	0.02	0.02	0.04	0.01	0.02
Meru	20.75 ± 0.47	18.61 ± 0.42	9.37 ± 0.24	9.04 ± 0.23	4.84 ± 0.11	6.31 ± 0.15	1.84 ± 0.08	9.70 ± 0.23	6.38 ± 0.23
	19.50 – 21.58	17.49 – 19.43	8.61 – 9.91	8.52 – 9.55	4.58 – 5.08	5.91 – 6.62	1.63 – 2.01	9.22 – 10.15	5.73 – 6.86
	N = 67	N = 67	N = 67	N = 67	N = 67	N = 67	N = 66	N = 67	N = 67
	0.02	0.02	0.03	0.03	0.02	0.02	0.04	0.02	0.04
Kilimanjaro	23.26 ± 0.48	21.03 ± 0.44	10.56 ± 0.24	10.21 ± 0.21	5.18 ± 0.14	7.06 ± 0.13	1.92 ± 0.10	10.42 ± 0.25	7.02 ± 0.32
	22.32 – 24.15	20.32 – 21.89	10.02 – 11.08	9.71 – 10.58	4.84 – 5.51	6.77 – 7.30	1.65 – 2.11	9.86 – 11.01	6.36 – 8.04
	N = 55	N = 55	N = 55	N = 55	N = 55	N = 55	N = 55	N = 55	N = 55
	0.02	0.02	0.02	0.02	0.03	0.02	0.05	0.02	0.05
North Pare	23.05 ± 0.52	20.99 ± 0.51	10.41 ± 0.26	10.33 ± 0.23	5.06 ± 0.11	7.16 ± 0.19	2.12 ± 0.07	10.27 ± 0.17	6.76 ± 0.33
	22.31 – 23.95	20.24 – 21.85	10.06 – 10.93	9.94 – 10.77	4.83 – 5.18	6.80 – 7.39	2.02 – 2.21	9.88 – 10.51	6.44 – 7.64
	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11
	0.02	0.02	0.03	0.02	0.02	0.03	0.03	0.02	0.05
South Pare	22.16 ± 0.36	19.96 ± 0.34	9.83 ± 0.19	9.78 ± 0.18	5.05 ± 0.10	6.81 ± 0.16	1.93 ± 0.09	9.92 ± 0.23	6.38 ± 0.18
	21.34 – 22.56	19.16 – 20.33	9.56 – 10.24	9.46 – 9.97	4.93 – 5.22	6.60 – 7.04	1.81 – 32.09	9.50 – 10.25	6.16 –6.62
	N = 9	N = 9	N = 9	N = 9	N = 9	N = 9	N = 9	N = 9	N = 9
	0.02	0.02	0.02	0.02	0.02	0.02	0.05	0.02	0.03
West Usambara	23.71 ± 0.46	21.40 ± 0.43	10.62 ± 0.24	10.50 ± 0.19	5.17 ± 0.15	7.37 ± 0.15	2.19 ± 0.09	10.63 ± 0.25	6.94 ± 0.20
	22.92 – 24.70	20.86 – 22.36	10.23 – 11.11	10.26 – 11.01	4.87 – 5.37	7.14 – 7.64	2.01 – 2.36	10.06 – 11.04	6.51 – 7.39
	N = 17	N = 17	N = 17	N = 17	N = 17	N = 17	N = 17	N = 17	N = 17
	0.02	0.02	0.02	0.02	0.03	0.02	0.04	0.02	0.03
East Usambara	25.09 ± 0.49	22.81 ± 0.45	11.33 ± 0.28	11.12 ± 0.25	5.44 ± 0.21	7.66 ± 0.18	2.22 ± 0.11	10.88 ± 0.28	6.97 ± 0.20
	23.82 – 26.12	21.85 – 23.95	10.85 – 11.94	10.75 – 12.05	5.00 – 6.04	7.25 – 8.04	1.99 – 2.54	10.35 – 11.60	6.57 – 7.50
	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N =44	N = 44	N = 44
	0.02	0.02	0.02	0.02	0.04	0.02	0.05	0.03	0.03
Ukaguru	24.51 ± 0.46	22.22 ± 0.43	10.97 ± 0.28	10.75 ± 0.23	5.33 ± 0.14	7.65 ± 0.17	2.28 ± 0.15	10.79 ± 0.26	7.02 ± 0.20
	23.38 – 25.76	21.11 – 23.32	10.08 – 11.4	10.15 – 11.29	5.05 – 5.75	7.23 – 8.06	1.99 – 2.56	10.10 – 11.47	6.63 – 7.70
	N = 68	N = 68	N = 69	N = 68	N = 69	N = 69	N = 68	N = 69	N = 69
	0.02	0.02	0.03	0.02	0.03	0.02	0.07	0.02	0.03
Rubeho	24.12 ± 0.41	21.87 ± 0.34	10.74 ± 0.17	10.66 ± 0.20	5.22 ± 0.12	7.61 ± 0.23	2.20 ± 0.15	10.63 ± 0.14	6.99 ± 0.19
	23.49 – 24.63	21.27 – 22.27	10.46 – 11.05	10.32 – 10.93	5.02 – 5.40	7.21 – 7.89	1.97 – 2.38	10.30 – 10.78	6.68 – 7.32
	N = 10	N = 10	N = 10	N = 10	N = 10	N = 10	N = 10	N = 10	N = 10
	0.02	0.02	0.02	0.02	0.02	0.03	0.07	0.01	0.03
Uluguru	24.03 ± 0.51	21.69 ± 0.52	10.54 ± 0.32	10.65 ± 0.21	5.30 ± 0.15	7.30 ± 0.22	2.19 ± 0.10	10.25 ± 0.22	6.95 ± 0.23
	22.70 – 24.89	20.21 – 22.60	9.65 – 11.15	10.20 – 11.02	4.89 – 5.60	6.72 – 7.74	1.94 – 2.34	9.82 – 10.70	6.53 – 7.54
	N = 34	N = 34	N =34	N = 34	N = 34	N =34	N = 34	N = 33	N = 33

	0.02	0.02	0.03	0.02	0.03	0.03	0.05	0.02	0.03
Udzungwa	23.78 ± 0.37	21.45 ± 0.37	10.60 ± 0.25	10.52 ± 0.25	5.28 ± 0.16	7.54 ± 0.27	2.24 ± 0.11	10.55 ± 0.25	7.24 ± 0.38
	23.10 – 24.71	20.73 – 22.33	10.12 – 11.11	10.04 – 10.99	4.79 – 5.62	6.68 – 8.20	2.00 – 2.45	9.96 – 11.05	6.64 – 8.99
	N = 31	N = 31	N = 31	N = 31	N = 31	N = 31	N = 31	N = 31	N = 31
	0.02	0.02	0.02	0.02	0.03	0.04	0.05	0.02	0.05
C. usambarae Paratypes	21.98 ± 0.22	19.93 ± 0.25	9.99 ± 0.15	9.76 ± 0.40	4.94 ± 0.03	6.89 ± 0.40	1.97 ± 0.08	10.14 ± 0.12	6.50 ± 0.18
	21.74 – 22.18	19.65 – 20.08	9.77 – 10.11	9.59 – 9.88	4.91 – 4.97	6.66 – 7.00	1.87 – 2.09	10.00 – 10.29	6.31 – 6.67
	N = 3	N = 3	N = 5	N = 4	N = 4	N = 5	N = 5	N = 4	N = 4
	0.01	0.01	0.02	0.01	0.01	0.02	0.04	0.01	0.03
C. monax Holotype	23.67	21.30	10.51	10.60	5.12	7.22	2.24	10.30	6.88
C. tansaniana Holotype	25.36	23.10	11.51	11.20	5.40	7.95	2.32	10.99	6.93

Table 4 (CONTINUED). Cranial measurements of individuals of *Crocidura* from 11 mountains in Tanzania (sexes combined within populations), two holotypes, and one set of paratypes. Mean ± standard deviation, range and sample size and CV. See text for character definitions.

	I^3–W	C–W	M^3–L	M^3–W	PGW	MP	M&I	LTR
Ngorongoro	0.71 ± 0.03 0.65 – 0.75 N = 16 0.04	0.77 ± 0.03 0.71 – 0.83 N = 16 0.04	1.37 ± 0.05 1.26 – 1.45 N = 16 0.04	0.73 ± 0.03 0.67 – 0.80 N = 16 0.05	6.61 ± 0.12 6.43 – 6.83 N = 16 0.02	1.08 ± 0.14 0.94 – 1.45 N = 16 0.13	13.34 ± 0.17 13.08 – 13.65 N = 16 0.01	8.52 ± 0.14 8.23 – 8.72 N = 16 0.02
Meru	0.69 ± 0.03 0.62 – 0.78 N = 67 0.05	0.73 ± 0.03 0.64 – 0.80 N = 67 0.05	1.45 ± 0.07 1.31 – 1.59 N = 67 0.04	0.77 ± 0.04 0.70 – 0.86 N = 67 0.05	6.55 ± 0.16 5.99 – 6.93 N = 49 0.02	1.04 ± 0.08 0.91 – 1.32 N = 67 0.08	13.05 ± 0.35 12.13 – 13.76 N = 67 0.03	8.35 ± 0.23 7.80 – 8.98 N = 67 0.03
Kilimanjaro	0.80 ± 0.03 0.71 – 0.87 N = 55 0.04	0.90 ± 0.04 0.80 – 0.97 N = 55 0.04	1.57 ± 0.06 1.44 – 1.69 N = 55 0.04	0.84 ± 0.04 0.74 – 0.95 N = 55 0.05	7.06 ± 0.19 6.67 – 7.56 N = 55 0.03	0.99 ± 0.10 0.75 – 1.20 N = 55 0.10	14.80 ± 0.36 14.01 – 15.51 N = 55 0.02	9.51 ± 0.19 9.04 – 9.81 N = 55 0.02
North Pare	0.84 ± 0.04 0.78 – 0.92 N = 11 0.05	0.94 ± 0.04 0.88 – 1.01 N = 11 0.04	1.62 ± 0.06 1.50 – 1.69 N = 11 0.04	0.83 ± 0.04 0.74 – 0.87 N = 11 0.05	6.99 ± 0.15 6.85 – 7.36 N = 11 0.02	1.08 ± 0.08 0.94 – 1.21 N = 11 0.07	14.73 ± 0.34 14.26 – 15.29 N = 11 0.02	9.59 ± 0.20 9.23 – 9.95 N = 11 0.02
South Pare	0.80 ± 0.03 0.76 – 0.84 N = 9 0.04	0.88 ± 0.03 0.82– 0.90 N = 9 0.03	1.49 ± 0.07 1.36 – 1.06 N = 9 0.50	0.77 ± 0.30 0.73 – 0.83 N = 9 0.05	6.81 ± 0.10 6.66 – 6.94 N = 9 0.01	1.14 ± 0.10 0.94 – 1.28 N = 9 0.11	14.04 ± 0.27 13.44 – 14.33 N = 9 0.02	9.07 ± 0.18 8.78 – 9.30 N = 9 0.02
West Usambara	0.97 ± 0.03 0.91 – 1.02 N = 17 0.03	1.01 ± 0.03 0.95 – 1.05 N = 17 0.03	1.71 ± 0.06 1.59 – 1.79 N = 17 0.04	0.87 ± 0.05 0.81 – 0.98 N = 17 0.06	7.28 ± 0.24 6.93 – 7.71 N = 17 0.03	1.20 ± 0.10 1.06 – 1.41 N = 17 0.08	15.08 ± 0.34 14.49 – 15.69 N = 17 0.02	9.74 ± 0.20 9.47 – 10.26 N = 17 0.02
East Usambara	0.98 ± 0.04 0.90 – 1.07 N = 44 0.04	1.01 ± 0.40 0.93 – 1.10 N = 44 0.04	1.72 ± 0.07 1.58 – 1.93 N = 44 0.04	0.87 ± 0.05 0.76 – 0.97 N = 44 0.06	7.50 ± 0.22 7.19 – 8.12 N = 43 0.03	1.23 ± 0.13 0.94 – 1.48 N = 44 0.11	16.04 ± 0.33 15.19 – 16.88 N = 44 0.02	10.29 ± 0.22 9.84 – 11.05 N = 44 0.02
Ukaguru	0.88 ± 0.05 0.74 – 1.07 N = 69 0.06	1.01 ± 0.05 0.88 – 1.10 N = 69 0.04	1.67 ± 0.07 1.50 – 1.80 N = 69 0.04	0.82 ± 0.05 0.68 –0.91 N = 69 0.06	7.61 ± 0.23 7.00 – 8.15 N = 69 0.03	1.01 ± 0.11 0.79 – 1.31 N = 69 0.11	15.51 ± 0.35 14.64 – 16.38 N = 67 0.02	9.96 ± 0.20 9.49 – 10.42 N = 67 0.02
Rubeho	0.86 ± 0.04 0.79 – 0.91 N = 10 0.04	0.97 ± 0.03 0.91 – 1.02 N = 10 0.04	1.65 ± 0.06 1.54 – 1.73 N = 10 0.04	0.87 ± 0.03 0.81 – 0.91 N = 10 0.04	7.28 ± 0.15 7.02 – 7.55 N = 10 0.02	1.22 ± 0.15 0.97 – 1.42 N = 10 0.12	15.12 ± 0.28 14.70 – 15.49 N = 10 0.02	9.81 ± 0.17 9.56 – 10.03 N = 10 0.02
Uluguru	0.87 ± 0.04	0.98 ± 0.05	1.63 ± 0.07	0.79 ± 0.04	7.21 ± 0.22	1.15 ± 0.13	15.27 ± 0.36	9.90 ± 0.17

	0.78 – 0.94 N = 34 0.05	0.78 – 1.05 N = 34 0.05	1.49 – 1.79 N = 34 0.04	0.72 – 0.88 N = 34 0.05	6.82 – 7.72 N =34 0.03	0.87 – 1.41 N = 34 0.11	14.49 – 15.84 N = 34 0.02	9.54 – 10.21 N = 34 0.02
Udzungwa	0.88 ± 0.06 0.77 – 0.98 N = 31 0.06	0.97 ± 0.04 0.90 – 1.03 N = 31 0.04	1.66 ± 0.08 1.50 – 1.90 N = 31 0.05	0.83 ± 0.04 0.77 – 0.92 N = 31 0.05	7.42 ± 0.23 6.98 – 7.85 N = 31 0.03	1.06 ± 0.14 0.82 – 1.42 N = 31 0.13	14.93 ± 0.28 14.52 – 15.57 N = 31 0.02	9.76 ± 0.23 9.34 – 10.12 N = 31 0.02
C. usambarae Paratypes	0.90 ± 0.04 0.84 – 0.93 N = 5 0.04	0.91 ± 0.02 0.88 – 0.94 N = 5 0.02	1.64 ± 0.08 1.53 – 1.77 N = 6 0.05	0.82 ± 0.05 0.74 – 0.89 N = 6 0.07	6.82 ± 0.15 6.58 – 6.93 N = 5 0.02	1.05 ± 0.12 0.92 – 1.16 N = 4 0.11	13.87 ± 0.26 13.45 – 14.19 N = 6 0.02	9.03 ± 0.22 8.74 – 9.38 N = 6 0.02
C. monax Holotype	0.88	0.94	1.69	0.85	7.05	1.13	15.12	9.87
C. tansaniana Holotype	0.93	0.99	1.76	0.86	7.51	1.08	16.00	10.30

Table 5. Comparison of cranial measurements (mm) for *Crocidura montis* from Rwenzori Mountains and *Crocidura newmarki* from Mt. Meru, given as mean, ± standard deviation, sample size and range. F values result from a one-way analysis of variance on the populations from Meru and Rwenzori (Holotype not included). ** = P ≤ 0.01. See text for character definitions.

Character	*Crocidura* Meru (*n* =67)	*C. montis* Rwenzori (n = 8)	*C. montis* Holotype (n = 1)	*F*
CI	20.75 ± 0.47 19.50 – 21.58	22.20 ± 0.55 21.31 – 22.97	21.57	65.5**
BL	18.61 ± 0.42 17.49 – 19.43	19.86 ± 0.54 18.94 – 20.62	19.31	58.8**
PPL	9.37 ± 0.24 8.61 - 9.91	9.98 ± 0.32 9.36 - 10.34	9.58	42.7**
UTRL	9.04 ± 0.23 8.52 - 9.55	9.77 ± 0.30 9.44 - 10.25	9.49	67.2**
LIW	4.84 ± 0.11 4.58 - 5.08	4.88 ± 0.09 4.78 - 5.05	5.11	1.0
BW	6.31 ± 0.15 5.91 - 6.62	6.92 ± 0.23 6.63 - 7.23	6.58	100.7**
NW	1.84 ± 0.08 1.63 - 2.01	2.08 ± 0.12 1.85 - 2.20	2.10	56.8**
GW	9.70 ± 0.23 9.22 - 10.15	10.16 ± 0.30 9.66 - 10.66	9.90	27.4**
PMH	6.38 ± 0.23 5.73 - 6.86	6.93 ± 0.09 6.80 - 7.10	6.86	44.0**
I^3-W	0.69 ± 0.03 0.62 - 0.78	0.83 ± 0.04 0.77 - 0.88	0.73	112.0**
C-W	0.73 ± 0.03 0.64 - 0.80	0.84 ± 0.03 0.79 - 0.90	0.74	69.8**
M^3-L	1.45 ± 0.07 1.31 - 1.59	1.60 ± 0.06 1.53 - 1.68	1.42	34.7**
M^3-W	0.77 ± 0.04 0.70 - 0.86	0.79 ± 0.04 0.72 - 0.84	0.72	2.6
MP	1.04 ± 0.08 0.91 - 1.32	1.04 ± 0.16 0.81 - 1.21	1.14	0.01
M&I	13.05 ± 0.35 12.13 – 13.76	13.93 ± 0.42 13.48 – 14.54	13.54	42.7**
LTR	8.35 ± 0.23 7.80 - 8.98	9.02 ± 0.26 8.73 - 9.43	8.64	59.8**

Table 6. Pilosity (%) and tail length relative to head and body length (Rel TL) in the populations studied, based on FMNH specimens.

Population	N	Pilosity mean	Range	Bristles	Rel TL	Taxon name
Kilimanjaro	40	15.9	0–32	few, long	70.0	*C. monax*
North Pare	10	15.3	9–26	few, short	66.8	*C. monax*
South Pare	7	10.1	7–21	few, short	70.7	*C. usambarae*
Magamba	7	24.5	22–28	few, short	73.2	*C. usambarae*
West Usambara	11	35.4	29–48	many, long	70.0	*C. tansaniana*
East Usambara	35	29.5	24–41	many, long	71.2	*C. tansaniana*
Ngorongoro	11	42.7	29–46	many, long	70.6	*C. mdumai* nov.
Uluguru	12	14.6	9–20	few, short	90.8	*C. munissii* nov.
Ukaguru	43	8.1	4–27	very few, short	84.5	*C. munissii* nov.
Rubeho	5	7.5	6–8	very few, short	89.2	*C. munissii* nov.
Udzungwa	15	12.1	7–18	few, short	93.4	*C. munissii* nov.
Meru	10	67.2	58–95	many, long	68.9	*C. newmarki* nov.
Rwenzori	11	81.3	70–86	many, long	75.7	*C. montis*
Mt Kenya	10	79.8	51–86	many, long	72.3	*C. fumosa*

Table 7. Comparison of cranial measurements (mm) for *Crocidura fumosa* from Mt. Kenya and *Crocidura* from Ngorongoro, given as mean, ± standard deviation, sample size and range. F values result from one-way analysis of variance. ** = $P \leq 0.01$. See text for character definitions.

Character	*Crocidura* Ngorongoro (*n* =16)	*C. fumosa* Mt. Kenya (n = 10)	*F*
CI	21.49 ± 0.25 21.09 – 21.95	21.56 ± 0.58 20.25 – 22.24	0.2
BL	19.30 ± 0.23 18.88 – 19.68	19.34 ± 0.57 18.10 – 20.05	0.1
PPL	9.89 ± 0.16 9.59 – 10.12	9.68 ± 0.35 9.96 – 10.08	4.2
UTRL	9.14 ± 0.16 8.83 – 9.40	9.44 ± 0.25 8.89 – 9.73	13.9**
LIW	4.59 ± 0.09 4.43 – 4.73	4.62 ± 0.13 4.43 – 4.77	0.5
BW	6.28 ± 0.12 6.06 – 6.50	6.43 ± 0.16 6.19 – 6.66	6.0*
NW	1.98 ± 0.08 1.83 – 2.12	2.06 ± 0.09 1.92 – 2.19	4.9*
GW	9.80 ± 0.13 9.53 – 10.03	9.88 ± 0.24 9.48 – 10.20	1.2
PMH	6.55 ± 0.16 6.26 – 6.80	6.66 ± 0.13 6.40 – 6.79	3.1
I^3-W	0.71 ± 0.03 0.65 – 0.75	0.78 ± 0.03 0.74 – 0.82	34.9**
C-W	0.77 ± 0.03 0.71 – 0.83	0.83 ± 0.05 0.75 – 0.89	15.0**
M^3-L	1.37 ± 0.05 1.26 – 1.45	1.42 ± 0.05 1.35 – 1.52	6.9*
M^3-W	0.73 ± 0.03 0.67 – 0.80	0.72 ± 0.03 0.69 – 0.76	1.5
MP	1.08 ± 0.14 0.94 – 1.45	1.00 ± 0.13 0.81 – 1.24	1.7
PGW	6.61 ± 0.12 6.43 – 6.83	6.59 ± 0.14 6.27 – 6.78	0.1
M&I	13.34 ± 0.17 13.08 – 13.65	13.51 ± 0.40 12.65 – 14.05	2.3
LTR	8.52 ± 0.14 8.23 – 8.72	8.80 ± 0.14 8.63 – 9.07	23.2**

Appendix I – Specimens Examined.

Most specimens used in this study are housed at the Field Museum of Natural History; numbers below are FMNH catalogue numbers. Other specimens are from museums in Bonn (ZFMK), Tervuren (RMCA) and Copenhagen (ZMUC).

Crocidura fumosa

Mt. Kenya

Kenya, Eastern Province, Meru South District, Mt. Kenya National Reserve, near Meru Bandas, 0.16263° S, 37.44621° E, 2980 m:

FMNH 216870-216874, 216876, 216878, 216881.

Kenya, Eastern Province, Meru South District, Mt. Kenya National Reserve, 0.20677° S, 37.49867° E, 2410 m:

FMNH 216892.

Crocidura mdumai

Ngorongoro

Tanzania, Arusha Region, Ngorongoro District, Ngorongoro Conservation Area, Ngorongoro Crater rim, near Pongo Ranger Post, 3.24407° S, 35.65040° E, 2064 m:

FMNH 211272, 211314-211315, 211317, 211320, 211322-211323, 211327-211328, 211331-211332.

Tanzania, Arusha Region, Ngorongoro District, Ngorongoro Conservation Area, Ngorongoro Crater rim, near Lamala Gate, 3.14255° S, 35.68669° E, 2372 m:

FMNH 211058-211059, 211124, 211131-211132, 211134.

Crocidura monax

Kilimanjaro

Tanzania, Kilimanjaro Region, Moshi District, 4 km N, 1.5 km W Maua, 3°14.404' S (or 3.24007° S), 37°27.502' E (or 37.45837° E), 2043 m:

FMNH 173788-173789, 173796, 174103-174110, 174112.

Tanzania, Kilimanjaro Region, Moshi District, 7 km N, 2.5 km W Maua, 3°12.459' S, 37°26.818' E, 2470 m:

FMNH 173770-173771, 173774-173778, 174066-174080.

Tanzania, Kilimanjaro Region, Moshi District, 10.5 km N, 3.5 km W Maua, 3°10.627' S, 37°26.413' E, 2897 m:

FMNH 173784, 174081-174102.

Tanzania, Kilimanjaro Region, Moshi District, Sothern slope, Mweka trail, Rombo, 3°08' S, 37°20' E, 3200 m:
RMCA 96.037-M-5797 - 96.037-M-5801, 96.037-M-7123 – 96.037-M-7127, ZFMK 2014.500.

North Pare

Tanzania, Kilimanjaro Region, Mwanga District, North Pare Mts, Kindoroko Forest Reserve, 3.76039° S, 37.64726° E, 1688 m

FMNH 192663-192669
Tanzania, Kilimanjaro Region, Mwanga District, North Pare Mts, Minja Forest Reserve, 3.58149° S, 37.6773° E, 1572 m

FMNH 192670-192671,192673-192674

Crocidura montis

Rwenzori

Democratic Republic of the Congo, Kivu, Ituri, Rwenzori Mts., SW slope, Butagu drainage, Bugongo Ridge, 2743 m:

FMNH 26244

Democratic Republic of the Congo, Kivu, Ituri, Rwenzori Mts, Butagu River Valley, Katahuleko Creek, W of Kalonge, 2134 m:

FMNH 26247, 26261, 26265, 26267, 26269

Democratic Republic of the Congo, Kivu, Ituri, Rwenzori Mts, Ibale, 2286 m:

FMNH 26270, 26272

Crocidura munissii

Udzungwa

Tanzania, Morogoro Region, Kilombero District, Udzungwa Mts, 19.5 km N, 0.5 km W Chita, 8.3472° S, 35.9389° E, 2000 m:

FMNH 155308-155309, 155312, 155314-155318, 155320, 155322-155329, 155490-155501.

Tanzania, Morogoro Region, Kilombero District, Udzungwa Mts, 4 km W, 5 km N Chita, 8.475° S, 35.9069° E, 1460 m:

FMNH 155485-155487.

Tanzania, Morogoro Region, Iringa Region, Kilombero District, Udzungwa Mts, Mufindi, 8.38° S, 35.22° E, 1940 m:

ZFMK 2014.0481.

Ukaguru

Tanzania, Morogoro Region, Kilosa District, Ukaguru Mts, Mamiwa-Kisara Forest Reserve, 1 km E, 0.75 km S Mount Munyera, 6.3792° S, 36.9361° E, 1900 m:

FMNH 166569, 166690-166691, 166693-166700, 166702-166717, 166720-166721.

Tanzania, Morogoro Region, Kilosa District, Ukaguru Mts, Mamiwa-Kisara Forest Reserve, 1 km E, 1.5 km S Mt Munyera, 6.3889° S, 36.95° E, 1840 m:

FMNH 166578, 166723, 166725-166741, 166744-166748, 166750-166759, 166761-166762, 166764-166766.

Rubeho

Tanzania, Dodoma Region, Mpwapwa District, Rubeho Mts, Mwofwomero Forest Reserve, near Chugu Peak, 6.8337° S, 36.57198° E, 1900 m:

FMNH 197657-197659

Tanzania, Morogoro Region, Kilosa District, Rubeho Mts, Ilole Forest, 7.43774° S, 36.72729° E, 1878 m:

FMNH 197403-197404,197660-197665

Uluguru

Tanzania, Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North Forest Reserve, 3 km W, 1.3 km N Tegetero, 6.9292° S, 37.7056° E, 1345 m:

FMNH 158280-158283, 158286.

Tanzania, Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North Forest Reserve, 5.1 km W, 2.3 km N Tegetero, 6.92° S, 37.6833° E, 1535 m:

FMNH 158287-158291, 158293-158297, 158392-158396,158399-158400, 158402-158403, 158405-158408, 158572.

Tanzania, Morogoro Region, Morogoro District, Uluguru Mts, Uluguru North Forest Reserve, 6 km W, 3 km N Tegetero, 6.9167° S, 37.675° E, 1850 m:

FMNH 158409-158413.

Tanzania, Morogoro Region, Morogoro District, Uluguru, Bondwa Peak, 6.54 S,, 37.40 E.

ZFMK 2014.0482; RMCA 96.037-M-6787, 96.037-M-7136, 96.037-M-7137.

Tanzania, Morogoro Region, Morogoro District, Uluguru N Forest Reserve, Morningside,6.53 S, 37.40 E.

RMCA 96.037-M-7121, 96.037-M-7122; ZFMK 2014.499.

Tanzania, Morogoro Region, Morogoro District, Uluguru, Mbete, 6.53 S, 37.41 E.

RMCA 96.037-M-7120

Tanzania, Morogoro Region, Morogoro District, Uluguru East, Lupanga, 1300 m.

ZMUC 1747.

Crocidura newmarki

Meru

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, Fig Tree Arch, 3.24406° S, 36.82845° E, 1950 m:

FMNH 207914, 207978, 207981, 207986, 208384-208388, 208390-208392, 208394-208395, 208397-208398, 208401-208408, 208410-208411.

Tanzania, Arusha Region, Arumeru District, Mt Meru, Arusha National Park, 3.24725°S, 36.80066°E, 2300 m:

FMNH 208415-208416.

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, Meru Crater, 3.24200° S, 36.78736° E, 2652 m:

FMNH 208045-208048, 208050, 208443-208451, 208453, 208456-208457.

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, Mgongo wa Tembo, 3.22350° S, 36.78675° E, 3000 m:

FMNH 208012, 208016-208017, 208022-208025, 208027-208028, 208032-208035, 208422-208424, 208426-208433, 208435-208436.

Tanzania, Arusha Region, Arumeru District, Mt. Meru, Arusha National Park, near Saddle Hut, 3.21609° S, 36.76897° E, 3600 m:

FMNH 208042, 208439, 208440

Tanzania, Kilimanjaro Region, Moshi District, Mount Meru, 6000 ft.

FMNH 86059-86068

Tanzania, Kilimanjaro Region, Moshi District, Mount Meru; Meru East and Meru West (Olkokola), 2550-2750 m.

ZFMK 60.018 – 60.025; 63.015 - 63.032

Crocidura tansaniana

West Usambara-Ambangulu Forest

Tanzania, Tanga Region, Korogwe District, West Usambara Mts, 12.5 km NW Korogwe, Ambangulu Tea Estate, 5.07° S, 38.42° E, 1300 m:

FMNH 147203-147209, 147353-147354, 147357-147358, 147376, 149979-149980, 149999-150000, 151099.

Tanzania, Tanga Region, Korogwe District, West Usambara Mts, West Usambara Mts, 14.5 km NW Korogwe, Ambangulu Tea Estate, 5.05° S, 38.38° E, 1250 m:

FMNH 147210

East Usambara

Tanzania, Tanga Region, Muheza District, East Usambara Mts, 4.5 km ESE Amani, Monga Tea Estate, 5.1° S, 38.6° E, 1000 m

FMNH 149973-149975, 149977-149978, 150376, 151112-151118, 151126, 151129-151134.

Tanzania, Tanga Region, Muheza District, East Usambara Mts, East Usambara Mts, 4.5 km NW Amani, Monga Tea Estate, 5.07° S, 38.62° E, 1100 m:

FMNH 147211, 147360

Tanzania, Tanga Region, Muheza District, East Usambara Mts, 4.5 km WNW Amani, Monga Tea Estate, 5.1° S, 38.6° E, 1000 m

FMNH 149969-149972, 149976, 151106-151107, 151109-151111, 151120-151125, 151376-151381.

Tanzania, Tanga Region, Muheza District, East Usambara Mts, Amani, primary forest

ZFMK 85.194 (holotype)

Crocidura usambarae

South Pare

Tanzania, Kilimanjaro Region, Same District, South Pare Mts, Chome Forest Reserve, 3 km E, 0.7 km N Mhero, 4.28° S, 37.9278° E, 2000 m

FMNH 153844, 153918-153922

Tanzania, Kilimanjaro Region, Same District, South Pare Mts, Chome Forest Reserve, 7 km S Bombo, 4.33° S, 38° E, 1100 m

FMNH 151137-151138, 151375.

West Usambara-Shume Magamba

Tanzania, Tanga Region, Lushoto District, West Usambara Mts, Magamba, 4.66667° S, 38.25° E, 1585 m

FMNH 27424-27430

Elevational distribution and ecology of small mammals Tanzania’s second highest mountain

William T. Stanley[1], Philip M. Kihaule[2]

[1] *The Field Museum of Natural History, Department of Science and Education, Chicago, Illinois, United States of America; email:bstanley@fieldmuseum.org*
[2] *University of Dar es Salaam, Department of Zoology, Dar es Salaam, Tanzania*

ABSTRACT

Mt Meru is Tanzania's second highest mountain, and the ninth highest in Africa. The distribution and abundance of small mammals on the mountain are poorly known. Here we document the distribution of shrews and rodents along an elevational gradient on the southeastern versant of Meru. Five sites were sampled with elevational center points of 1950, 2300, 2650, 3000 and 3600 m, using a systematic methodology of standard traps and pitfall lines, to inventory the shrews and rodents of the slope. 10 species of mammal were recorded, including 2 shrew and 8 rodent species, and the greatest diversity of both was found at 2300 m. No species previously unrecorded on Meru were observed. Two genera of rodents that occur in nearby Eastern Arc Mountains (*Hylomyscus* and *Beamys*) were not recorded. *Lophuromys verhageni* and a new species of *Crocidura* are the only endemic mammals on Mt. Meru, and were widespread across the elevational gradient. As in similar faunal surveys on other mountains of Tanzania, rainfall influenced the sample success of shrews, but not rodents. This study contributes further justification for the conservation of the forest habitat of Mt. Meru. Comparisons are made to similar surveys of other mountains in Tanzania.

ADDITIONAL KEYWORDS: Mt. Meru – shrews – rodents – *Crocidura* – Tanzania

INTRODUCTION

Mammalian distribution along elevational gradients is of increasing interest and, as a result, the efforts to document the montane faunas of various massifs around the world have intensified over the past few decades. Climate change has recently increased this curiosity and the need for detailed investigations. Documenting the present elevational distribution of organisms will facilitate the monitoring of that biota during times of climatic perturbation or habitat alteration. Biogeographic, ecological and evolutionary studies are also informed by comprehension of montane biotic systems. Examples of elevational surveys of small mammals in montane localities on various continents using systematic sampling protocols include Chile [1], Costa Rica [2], Madagascar [3], Malaysia [4], Philippines [5], Taiwan [6] and U.S.A. [7]. Each of these studies produces a more complete understanding of both specific and broadly general patterns of mammalian elevational distribution, and the mechanisms that led to such an array [8]. The utility of these studies in monitoring impacts of environmental changes cannot be overstated. For example, in Yosemite Valley, California, a survey along an elevational transect documented significant range shifts in various mammalian species since an identical survey was conducted along the same transect a century earlier [7].

The montane mammals of sub-Saharan Africa have been studied for over a century, and studies of the elevational distributions of mammals on some massifs of the continent are documented [9], [10]. Published results from detailed systematic inventories of mammals on mountains of eastern Africa include, Kerbis Peterhans et al. [11] for Rwenzori Mountains, Stanley and Hutterer [12] for Udzungwa Mountains, Mulungu et al. [13] and Stanley et al. [14] for Kilimanjaro. Various other massifs, although significant geologic entities, remain enigmatic with regard to the mammals occurring on them.

Mt. Meru, Tanzania’s second highest mountain, and the ninth highest in Africa, is a case in point. While its neighbor, Kilimanjaro, has been the subject of mammalian study [13], [14], [15], [16], Meru has been understudied. While some aspects of the ecology of the mountain have been documented [17], small mammals of the mountain have not been systematically studied. The most complete analysis of the fauna of Meru is that of Demeter and Hutterer [18]. The need for detailed knowledge of this mountain has been emphasized by the results of other studies such as Thompson *et al*. [19] who implied that climate change is affecting the ecology and habitat of neighboring Kilimanjaro. Baseline data for small mammals of Meru will allow future analyses of the impact of climate change on the ecology of this volcano.

We used a standardized methodology that has been recently employed in myriad other montane sites of Tanzania [12], [20], [21], [22] to survey the small mammals (shrews and rodents) at five different elevations and habitats along the southeastern slope of Mt. Meru. Our study had three principal goals: 1) to conduct the first intensive survey of the presence and abundance of small mammals along an elevational gradient on the mountain; 2) to test for differences between rodents and shrews in their relationship to elevation, response to different trapping methodologies and relationship of captures to rainfall; and 3) to compare the generated results to similar studies other mountains of Tanzania.

MATERIALS AND METHODS

Study Site

Mt. Meru is in northeastern Tanzania and reaches an elevation of 4,566 m (14,977 ft) m, and ranks ninth among the highest ten mountains of Africa. An active volcano (the mountain last erupted in 1910), Meru is the centerpiece of Arusha National Park. The mountain is a popular destination for climbers, and there is one path that originates in the lowlands and runs up the southeastern side of the mountain [18]. Between 16 July and 19 August 2009, we sampled the small mammals (shrews and rodents) at five different elevations, ranging from roughly 1950 to 3600 m, along the climbing route on the southeastern slope of Mt. Meru (Figure 1).

All sampling sites were on Mt. Meru in Arusha National Park, Arumeru District, Arusha Region, Tanzania. The specific localities, elevations, habitats (sensu Demeter and Hutterer, [18]) and dates of sampling are listed below. The elevations given for each site are centered at the associated camp and sampling efforts spanned roughly 100-200 m above and below the camp. Temperature and rainfall for each site (measured at camp) are listed in Table 1:

Site 1 - 1950 m). Fig Tree Arch, 3.24406° S, 36.82845° E, 1950 m; lower montane forest; 16-23 July 2009.

Site 2 - 2300 m). Site 2, 3.24725° S, 36.80066° E, 2300 m; upper montane forest; 23-30 July 2009.

Site 3 - 2650 m). Meru Crater, 3.242° S, 36.78736° E, 2650 m; ecotone between montane forest and ericaceous zone; 13-19 August 2009.

Site 4 - 3000 m). Mgongo wa Tembo, 3.2235° S, 36.78675° E, 3000 m; mix of forest, ericaceous plants and some bamboo); 30 July-6 August 2009.

Site 5 - 3600 m). near Saddle Hut, 3.21609° S, 36.76897° E, 3600 m; ecotone between ericaceous and alpine zones; 6-13 August 2009.

Field methodology

Pitfall lines and traplines were installed to capture principally shrews and rodents, respectively. Each pitfall line were comprised of 11 buckets, placed 5 m apart, and buried in the ground so that the top of the bucket was level with the ground. Each of these 15 l buckets was 26 cm high and had an upper and lower diameter of 26 cm and 24 cm, respectively. Each pitfall line had a 50 cm high black plastic drift fence running over the center of each bucket. This technique has been used with success in other mammalogical surveys.

Trap lines utilized three different kinds of traps: Museum Specials, 14 x 7 cm; Victor Rat Traps (referred to here as Victor Trap), 17.5 x 8.5 cm; and medium-sized Sherman Traps, 23 x 9.5 x 8 cm. To maximize capture success, traps were set at sites considered likely to be frequented by small mammals, rather than at fixed distances or in a grid. Consequently, distances between consecutive traps were not constant. Bait for each trap consisted of freshly fried coconut coated in peanut butter, and traps were rebaited each late afternoon. Additional details on this type of trapping technique are presented by Stanley et al. [22]. Both pitfall and trap lines were checked twice each day, in the early morning and mid-afternoon.

Not all traps or buckets were employed for equal amounts of time (some trap lines were set the first day of the survey, others were installed on a subsequent day), so we use the terms “trap night”, “bucket night” and “sample night” to quantify sampling effort. A “trap-night” refers to one trap in operation for a 24 hr period (0700 to 0700 hrs). A “bucket-night” denotes one bucket in operation for a 24 hr period (0700 to 0700 hrs). The term “sample-night” is used in discussion of overall sampling effort (including the number of trap-nights and bucket-nights). We refer to the success rate of each method as either “trap success” or “bucket success”, and calculate these values by dividing the number of individuals captured by the number of trap-nights or bucket-nights and multiplying by 100. In discussions involving the overall capture success, the term “sample success” refers to the success rate for pitfall and trap methodologies combined. This is calculated by dividing the number of individuals captured by the number of sampling-nights and multiplying by 100.

Animals were handled following the protocol approved by the American Society of Mammalogists [23]. Voucher specimens were prepared as either museum study skins with associated skulls and axial skeletons or embalmed in formalin. Standard museum measurements [24] were taken by WTS, and tissues including heart, liver, kidney and/or muscle were extracted from select specimens and frozen in liquid nitrogen, or saved in dimethyl sulfoxide buffer (DMSO) at ambient temperature. All voucher specimens are deposited in the Field Museum of Natural History (FMNH), Chicago, and the University of Dar es Salaam (UDSM), Dar es Salaam, and all tissue samples are in liquid nitrogen storage in the FMNH. We follow the taxonomy presented for shrews by Hutterer [25]; rodents by Carleton and Stanley [26],[27], Holden [28], Musser and Carleton [29].

RESULTS

Over the course of the survey, we accumulated 7,111 sample-nights (4592 trap-nights and 2519 bucket-nights) and captured 751 small mammals, including 276 shrews representing 2 species, and 475 rodents representing 8 species (Tables 2, 3, 4). Significantly more shrews were captured in buckets than in traps ($X^2 = 61.3$, $P < 0.05$), and significantly more rodents were caught in traps than in buckets ($X^2 = 232.7$, $P < 0.05$), a pattern observed in past studies within Tanzania [12], [14], [30]. In 4592 trap-nights, 581 mammals were captured for an overall trap success of 12.6%. Of the mammals caught in traps, 465 were rodents (10.1% trap success for rodents) and 116 were shrews (2.5% trap success). In the 2519 bucket-nights, 170 mammals were captured for a total bucket success of 6.7%. Of these, 160 were shrews (6.3% success) and 10 were rodents (0.4% success). This conspicuous pattern was evident both across the entire survey, and at each of the five sites sampled (Table 2). Both shrew species found during the survey were caught in traps (weighing between 3.5-11 g). Ten rodents representing 3 species (*Dendromus insignis*, *Mus triton*, and *Praomys taitae*) were caught in buckets and ranged in weight (10-27 g). Interestingly, of the total ten *Dendromus* captured, the lightest (10-13 g; n = 6) were captured in buckets, and the heaviest 4 (14-22.5 g) were captured in traps. The animals caught in buckets were adults based on the presence of fused cranial sutures.

At each elevational site, captures (and overall sample success) ranged from 49 [3.5%] at 3600 m to 257 [18.0%] at 2300 m (Table 2). For shrews, the lowest values were recorded at the 3600 m site (20 [1.4%]) and the highest values at the 3000 m site (87 [6.1%]; Table 3). For rodents, the lowest (29 [2.1%]) and highest (208 [14.6%]) values were observed at the 3600 m and 2300 m sites, respectively (Tables 4). The cumulative number of species trapped at a site reached an asymptote at the 1950, 2650 and 3600 sites, but new species (i.e. not yet recorded at a site) were captured at the 2300 (where *Graphiurus murinus* was captured for the first time at that site on the last day of trapping) and 3000 (where *Mus triton* and *Otomys tropicalis* were both captured on the last day) sites. The species accumulations curves (Figure 2) illustrate these results.

As in past surveys of montane mammals in Tanzania [12], [14], the relationship between the amount of rainfall and capture of shrews is more positive than that between rainfall and rodent captures. During the survey of Mt. Meru, only two sites (1950 and 3000 m) received rain while buckets and traps were in place. The Product-moment correlation coefficients (*r*) of amount of daily rainfall with total captures of shrews (for buckets and traps combined) are 0.60 and 0.55 for the 1950 and 3600 m sites, respectively. For rodents these values were both negative (-0.53 and -0.30, respectively). While none of these *r* values are significant, Figure 3 illustrates the increase in shrew captures during or shortly after measureable rainfall, a pattern not exhibited by rodent captures.

The correlation of four daily capture parameters (number of individuals, number of species, number of new species [i.e. previously unsampled at a given site], and cumulative number of species) with cumulative sample-nights was analyzed for both type of trapping methodology (Table 5) and mammalian order (Table 6). Because only two species of shrews were recorded during the entire survey (Table 2, 3), and these both were caught on either the first, or every day, correlation analysis between cumulative sampling effort and some parameters is not applicable. For example, the cumulative number of shrew species captured by buckets was two the first day of the survey and remained the same throughout the entire survey. Other comparisons revealed differing patterns. The correlation between sampling effort and number of individuals fluctuated among elevations and the number of species captured each day was not correlated with cumulative sampling effort. For all taxa, a negative correlation existed between new species captured and cumulative sampling effort, but the correlation was significant in only five cases across the transect and not consistently with one parameter. Correlation analysis revealed a significant positive correlation between cumulative sample-nights and cumulative species across all sites for trap lines, bucket lines (for captures of both shrews and rodents) and both sampling methods combined. Each site exhibited the same general pattern, although not in all parameters examined. For example, there was no strong relationship between cumulative sample nights and cumulative shrew species captured in buckets at the 2650 and 3600 m sites (Table 5). Table 6 illustrates the same general pattern when the analysis is focused on mammalian order. Again the low number of shrew species influences the analysis, and the strongest relationship is that of cumulative species of rodents with cumulative sampling effort.

The relationship between elevation and number of individuals or species collected, or sample success was not notable. The low and relatively constant number of shrew species was observed at all elevations, and the only prominent negative relationship (high but not significant r values) exists in the associations of the total number of individuals and total trap success with elevation (Table 7). The highest species diversity was seen at the 3000 m site, and the lowest at the 1950 m site. While the lowest number of individuals collected was at the 3600 m site, the species diversity was higher there (6 species) compared to that of the lowest site (5 species) that had the second highest sample success of any of the sites (Table 2).

There was a 6.7% bucket success for all animals captured, and 170 mammals (160 shrews and 10 rodents) were collected in 385 buckets (77 buckets installed at each of five sites), but most buckets captured no animals. Over the entire survey, 287 buckets caught nothing, and only 98 buckets (25% of total installed) captured animals. Of the buckets that captured animals, 61 caught one animal, 20 collected two, 10 captured three, 3 caught four animals, 3 collected five animals, and eleven animals were found in one bucket. A similar pattern was exhibited by traps; although there was 12.6% trap success in 750 traps with 581 captures, only 313 traps (42% of total employed) caught at least one animal. A total of 166 traps caught only one animal, 74 trapped two, 43 three, 18 four, 8 five, 2 six, and one trap caught seven animals while in place. Neither of these values followed the Poisson distribution (G-test for goodness of fit = 34.0 for buckets, 63.7 for traps; $p< 0.01$) indicating a lack of trap independence.

DISCUSSION

Ten mammal species (2 shrews and 8 rodents) were documented along an elevational transect from roughly 1950 to 3600 m on the eastern slope of Mt. Meru, none of which are introduced taxa. With the exception of *Crocidura newmarki* and *Lophuromys verhageni*, which are endemic to Mt. Meru [31], [32], all species have broad distributions, to different extents. One shrew is found on other mountains within eastern Africa: *Crocidura allex* on Kilimanjaro, Ngorongoro, Kenya and Aberdares [25]. Among the rodents, the species with the broadest distribution are *Grammomys dolichurus*, *Rhabdomys dilectus* and *Graphiurus murinus*, all of which are distributed in eastern and southern Africa [28], [29]. The rodent species with the most restricted distribution (other than *Lophuromys verhageni*) was *Praomys taitae* which occurs from southeastern Kenya through eastern Tanzania [27].

The faunal list of Demeter and Hutterer [18] represents the heretofore most complete list of shrews and rodents known to occur on Meru, and their list contained species not observed during this survey. Some of these taxa are larger and not the subjects of the methodology employed during this study (i.e. *Paraxerus*, *Thryonomys*, and *Tachyoryctes*) and are not considered further here. The elevational range of the study of Demeter and Hutterer [18] was 1200 m to 2750 m and included towns and villages such as Arusha and Tengeru, and habitats other than forest such as savanna. Some of the taxa listed include taxa typically found at elevations and habitats below forest on Meru, including *Mastomys natalensis* and *Pelomys fallax*. However, some taxa listed from forest localities that we did not observe are worthy of discussion here, including *Crocidura hildegardeae*, *C. luna*, *Aethomys kaiseri*, *Hylomyscus denniae*, *Lemniscomys striatus*, *Mus gratus*, *Rattus rattus*, and *Otomys irroratus*, The two species of *Crocidura* were collected at elevations of 1700 m, or lower, below the elevational range of the current study. *Crocidura hildegardeae* has been recorded at 2000 m, and *C. luna* at 1400 m on Mt. Kilimanjaro [14], [15]. Thus, we conclude that these two species were not present in the sites we sampled. The specimens of *Aethomys kaiseri Lemniscomys striatus*, and *Rattus rattus* cited by Demeter and Hutterer [18] came from habitats below 2000 m, with the exception of specimens from ”House Mgondah” at 2000 m. The authors suggest *Aethomys* and *Rattus* may have occurred at this locality because of human influence. Certainly, *Rattus* is a known commensal [29]. While the vast majority of our efforts were in primary habitat, we did place traps around the dwellings of Saddle Hut (not included in analysis above) to collect rodents living under the buildings. As a result we collected *Crocidura allex, Lophuromys verhageni, Rhabdomys dilectus* but no *Aethomys, Lemniscomys* or *Rattus*. We saw no evidence of these species in forested habitats of the mountain, and hypothesize that all three genera were found at this locality either having been introduced by human activities, or supported by habitat alteration associated with the dwelling. Demeter and Hutterer [18] list *Mus gratus* among the taxa occurring on Meru. While one locality (“Forest House”; 1700 m) was below the range of our study area, another (Meru East: 1550-2750 m) does overlap with our elevational range. Given there was no specific elevation of the collection sites of these specimens of *M. gratus*, we cannot definitely determine that they were collected in forest. We saw no evidence of this species, and only one specimen of *M. bufo*. The records of *Otomys irroratus* listed by Demeter and Hutterer [18] (now *O. angoniensis* [29]) are interesting to us because there are also specimens in the Field Museum collected by B. Cooper in 1938 from the crater of Mt. Meru at roughly 2900 m (FMNH 48610-48619). We recorded *O. tropicalis* from the same crater and at elevations ranging from 2650 – 3600 m, but saw no evidence of *O. angoniensis*. Temporal differences (1938 vs. 2009) or seasonal differences (January vs. July/August) may explain the difference, but additional surveys of the mountain are needed to determine the current presence and distributional extent of both species. Finally, the records of *Hylomyscus* on Meru [18] (and Ngorongoro [33]) are now referred to *Praomys taitae* [26], [27]. Another rodent that is found on northern Eastern Arc Mountains and the Southern Highlands [29], and has been recorded from Moshi (Dieterlen [34]), is *Beamys hindei,* and this taxon was not recorded on Meru by us, or past work. In addition to the survey of Meru, similar detailed faunal surveys have been conducted on Kilimanjaro [14] and Ngorongoro (WT Stanley, unpubl. data) and neither *Hylomyscus* nor *Beamys* have been recorded on any of these Northern Highland Mountains during these transects, suggesting they do not occur in these locals. Assuming this to be correct, this supports the hypothesis that the establishment of these two rodent taxa on the mountains where they are found was via a southern route. We suspect establishment via a northern route from Kenya would have resulted in populations of both of these rodents on some, if not all of the Northern Highlands.

The combination of traps and pitfall lines were effective in sampling non-volant small mammal communities at different elevations on Mt. Meru, as in past studies in Tanzania [12], [14], [22], [30], [35]. However, species accumulation curves failed to reach a plateau at every site: the 2300 and 3000 m site had one and two species, respectively, captured on the last 24-hour period of trapping at the site. While we are confident that we documented almost all of the species of shrews and small rodents occurring at each site, and thus feel justified in comparing results among different elevational sites of this transect, as well as to results of similar surveys within Tanzania [12], [14], we suggest additional surveys are needed to be determine with certainty the complete list of small mammals in different elevation zones of Mt. Meru.

The results of this survey differ in several ways when compared to surveys of other mountains in Tanzania using identical techniques [12], [14]. The most striking difference is the low diversity of shrews on Meru. Restricting comparisons to only lists generated by our surveys of the other mountains, Meru had one genus (*Crocidura*) and two species (*C. allex*, *C. newmarki*); Kilimanjaro had three genera (*Crocidura*, *Myosorex*, and *Sylvisorex*) and six species (*C. allex*, *C. hildegardeae*, *C. monax*, *C. olivieri*, *M. zinki* and *S. granti*); and Udzungwa had three genera (*Crocidura*, *Myosorex*, and *Sylvisorex*) and nine species (*C. hildegardeae*, *C. desperata*, *C. elgonius*, *C. munissii*, *C. olivieri*, *C. telfordi*, *M. kihaulei*, *S. lixus*, and *S. megalura*). The Udzungwa survey included dry forest near the base of the scarp at 600 m. If species recorded there, and no higher in the Udzungwas are removed from consideration, the Udzungwa list shrinks from nine to seven species. Even after this, the Meru list stands in stark contrast to the list of a nearby mountain of similar origins and a range of different geologic composition. The reasons for such a striking low diversity on Meru are unknown. Volcanic activity on the mountain has been recent in comparison to Kilimanjaro [36], but it seems unlikely that eruptions would have contributed to extinction of taxa once existing on Meru.

Unlike Kilimanjaro and Udzungwa elevation was not significantly correlated with captures or diversity of either shrews or rodents. In the Udzungwas rodent diversity and abundance increased with elevation [12], and on Kilimanjaro shrew abundance and diversity decreased with elevation [14]. Similar patterns, or any influence of elevation on abundance or diversity were not seen on Meru. As in Kilimanjaro [14], the greatest diversity of shrews and rodents on Meru was at 3000 m, and not at the top of the transect as in Udzungwa [12], and the greatest diversity was documented within forested habitats and not above treeline (Tables 2,3,4).

Similarities among the three transects were observed in the effect rainfall had on the capture of shrews, but not rodents. The Meru survey adds additional support to the idea that the amount of rainfall during a sampling period should be considered while sampling shrew diversity or abundance. Also, there was a lack of capture independence among traps and buckets across the entire transect and at each site on Meru, as in surveys of Kilimanjaro and Udzungwas [12], [14]. As in those studies, we hypothesize that the presence of a captured animal in a bucket may attract other animals into that bucket and placement of traps influences the chances of multiple captures over time by one trap.

Although this may change with future taxonomic studies, the only endemic mammal on Mt. Meru is *Lophuromys verhageni* [31]. This species was found at all sites but the lowest (1950 m), which was unexpected, as *Lophuromys aquilus* is found in moist habitats on Mt. Kilimanjaro at 2000 m [14]. While the habitat at the 1950 m site on Meru appeared suitable for *Lophuromys* based on our experience of trapping this mammal on different mountains in Tanzania [12], [14], [37] there may be some element that prohibits *Lophoromys* from occurring at this elevation on the mountain. No rodent species were recorded at all sites during the Meru survey, but both species of shrew were. Also, as in the Kilimanjaro survey [14], the highest elevation that mammals natural extend to (other than *Homo sapiens*) remains unknown. Additional surveys are needed to determine this and to further elucidate the natural history of the mammals of Meru.

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REFERENCES

1. Patterson BD, Meserve PL, Lang BK (1989) Distribution and abundance of small mammals along an elevational transect in temperate rainforests of Chile. J Mammal 70: 67-78.
2. McCain CM (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. J Biogeogr 31: 19-31.
3. Goodman SM, Ganzhorn JU, Rakotondravony D (2003) Introduction to the Mammals. In: Goodman, SM, Benstead, JP, editors. The Natural History of Madagascar. Chicago: The University of Chicago Press. Pp. 1159-1186.
4. Md Nor S (2001) Elevational diversity patterns of small mammals on Mount Kinabalu, Malaysia. Glob Ecol Biogeogr 10: 41-62.
5. Rickart EA, Heaney LR, Utzurrum RB (1991) Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. J Mammal 72: 458-469.
6. Yu HT (1994) Distribution and abundance of small mammals along a subtropical elevational gradient in central Taiwan. J Zool 234: 577-600.
7. Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a Century of Climate Change on Small-Mammal Communities in Yosemite National Park, USA. Science 322: 261-264.
8. McCain CM (2005) Elevational gradients in diversity of small mammals. Ecology 86: 366-372.
9. Happold DCD, Happold M (1989) Biogeography of small montane mammals in Malawi, Central Africa. J. Biogeogr 16: 353-367.
10. Yalden DW (1988) Small mammals of the Bale mountains, Ethiopia. Afr J Ecol 26: 281-294.
11. Kerbis Peterhans JC, Kityo RM, Stanley WT, Austin PK (1998) Small mammals along an elevational gradient in Rwenzori Mountains National Park, Uganda. Pp. 149-171 In: Osmaston H, Tukahirwa J, Basalirwa C, Nyakaana J, editors. The Rwenzori Mountains National Park, Uganda. Exploration, environment and biology. Conservation, management and community. Makerere University, Kampala.
12. Stanley WT, Hutterer R (2007) Differences in abundance and species richness

between shrews and rodents along an elevational gradient in the Udzungwa Mountains, Tanzania. Acta Theriol 52: 261–275.

13. Mulungu LS, Makundi RH, Massawe AW, Machang'u, RS, Mbije, NE (2008) Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. Mammalia 72: 178-185.

14. Stanley WT, Rogers MA, Kihaule PM, Munissi MJ. 2014. Elevational distribution and ecology of small mammals on Africa's highest mountain. *PLOS ONE* 9(11): e109904. DOI: 10.1371/journal.pone.0109904

15. Grimshaw J, Cordeiro N, Foley C (1995) The mammals of Kilimanjaro. J East Afr Nat Hist 84: 105–139.

16. Shore RF, Garbett SD (1991) Notes on the small mammals of the Shira Plateau, Mt. Kilimanjaro. Mammalia 55: 601-607.

17. Lundgren B, Lundgren L (1972) Comparison of Some Soil Properties in One Forest and Two Grassland Ecosystems on Mount Meru, Tanzania *Geografiska Annaler. Series A, Physical Geography* Vol. 54, No. 3/4, Studies of Soil Erosion and Sedimentation in Tanzania pp. 227-240

18. Demeter A, Hutterer R (1986) Small mammals from Mt. Meru and its environs (Northern Tanzania). Cimbebasia 8: 199–207.

19. Thompson LG, Brecher HH, Mosley-Thompson E, Hardy DR, Mark BG (2009) Glacier loss on Kilimanjaro continues unabated. Proc Natl Acad Sci USA 106: 19770-19775.

20. Goodman SM, Newmark WD, Stanley WT, Howell KM (1995) The Ambangulu Forest, West Usambara Mountains, Tanzania: a threatened Eastern Arc forest. Oryx 29: 212–214.

21. Stanley WT, Kihaule PM, Howell KM, Hutterer R (1998) Small mammals of the Eastern Arc Mountains, Tanzania. J East Afr Nat Hist 87: 91–100.

22. Stanley WT, Goodman SM, Newmark WD (2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 1. Study areas, methodologies, and general results. In: Stanley WT, ed. Studies of Montane Vertebrates of Tanzania. Fieldiana Life Earth Sci 4: 1–17.

23. Sikes RS, Gannon WL and the Animal Care and Use Committee of the American Society of Mammalogists. (2011) Guidelines of the American

Society of Mammalogists for the use of wild mammals in research. J Mammal 92: 235-253.

24. DeBlase AF, Martin RE (1974) A Manual of Mammalogy with Keys to the Families of the World. Wm. C. Brown Company Publishers, Dubuque, Iowa.

25. Hutterer R (2005) Order Soricomorpha. In: Wilson DE, Reeder DM, editors. Mammal species of the world: A taxonomic and geographic reference, Third Edition. Baltimore: Johns Hopkins University Press, pp. 220–299.

26. Carleton MD, Stanley WT (2005) Review of the *Hylomyscus denniae* complex in Tanzania, with description of a new species. Proc Biol Soc Wash 118: 619–646.

27. Carleton MD, Stanley WT (2012) Species limits within the *Praomys delectorum* group (Rodentia: Muridae: Murinae) of East Africa: A morphometric reassessment and biogeographic implications. Zool J Linn Soc 165: 420-469.

28. Holden ME (2005) Family Gliridae. In: Wilson DE, Reeder DM, editors. Mammal species of the world: A taxonomic and geographic reference, Third Edition. Baltimore: Johns Hopkins University Press, pp. 819–841.

29. Musser GG, Carleton MD (2005) Superfamily Muroidea. In: Wilson DE, Reeder DM, editors. Mammal species of the world: A taxonomic and geographic reference, Third Edition. Baltimore: Johns Hopkins University Press, pp. 894–1531.

30. Stanley WT, Goodman SM, Hutterer R (2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 2. Families Soricidae (Shrews) and Macroscelididae (Elephant Shrews). In: Stanley WT, editor. Studies of Montane Vertebrates of Tanzania. Fieldiana Life Earth Sci 4: 18–33.

31. Verheyen W, Hulselmans JLJ, Dierckx T, Verheyen E (2002) The *Lophuromys flavopunctatus* Thomas 1888 species complex: A craniometric study, with the description and genetic characterization of two new species (Rodentia-Muridae-Africa). Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Biologie 72:141-182.

32. Stanley, W. T., Hutterer, R., Giarla, T. C., and Esselstyn, J. A. (In press) Phylogeny, phylogeography and geographical variation in the *Crocidura monax* (Soricidae) species complex from the montane islands of Tanzania, with descriptions of three new species. Zoological Journal of the Linnean Society

33. Bishop IR (1979) Notes on *Praomys* (*Hylomyscus*) in eastern Africa. Mammalia 43: 521–530.

34. Dieterlen, F. (1979) Der früheste Fund der afrikanischen Kleinen Hamsterratte (*Beamys hindei*) (Cricetomyinae; Cricetidae; Rodentia) Stuttgarter Beitr zur Naturk ser. A 330: 1-3.

35. Stanley WT, Kihaule PM, Munissi MJ (2007) Small mammals of two forest reserves in the North Pare Mountains, Tanzania. J East Afr Nat Hist 96: 215–226.

36. Guest NJ, Leedal GP (1953) Volcanic activity of Mt. Meru. Records of the Geological Survey of Tanganyika 3: 40-46.

37. Stanley WT, Goodman SM (2011) Small mammal inventories in the East and West Usambara Mountains, Tanzania. 4. Rodentia. In: Stanley WT, editor. Studies of Montane Vertebrates of Tanzania. Fieldiana Life Earth Sci 4: 53–73.

FIGURE LEGENDS

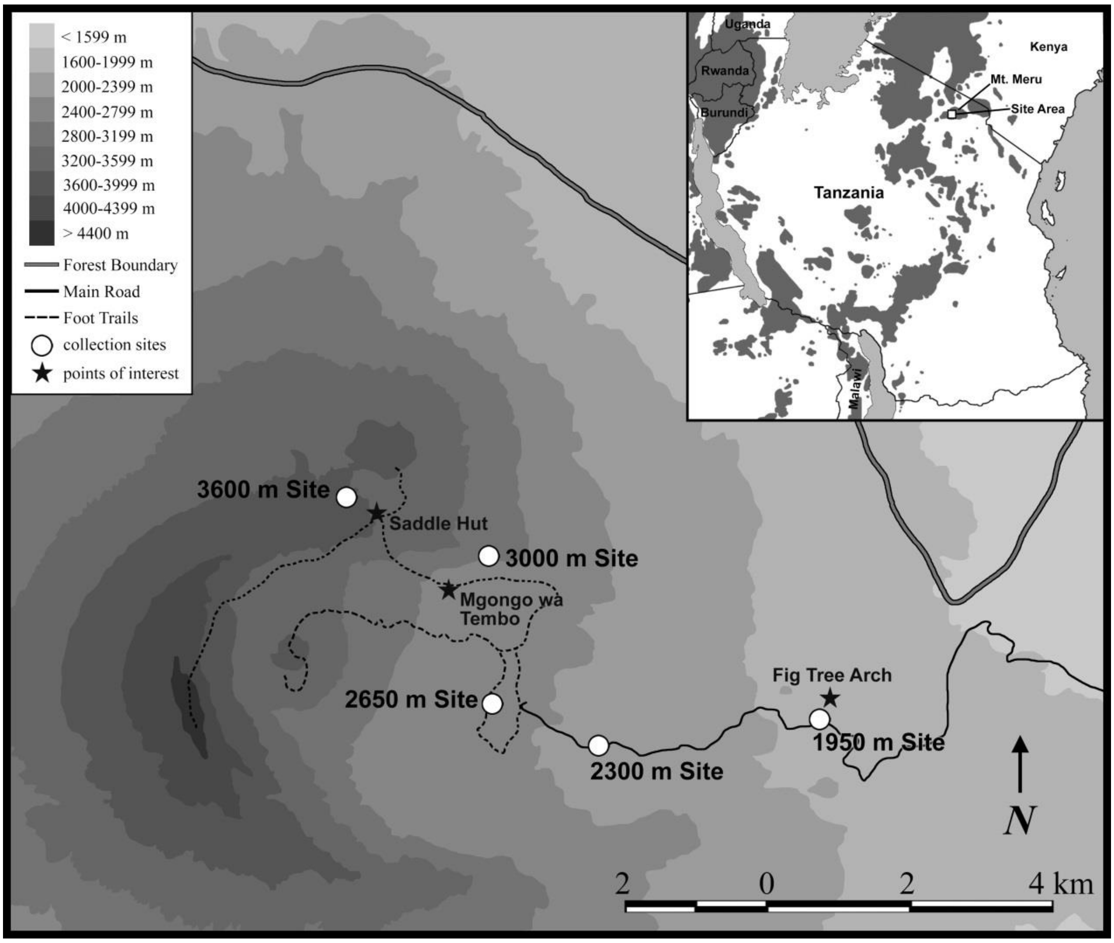

Figure 1. Map of Mt. Meru showing routes, elevational contours and study sites.

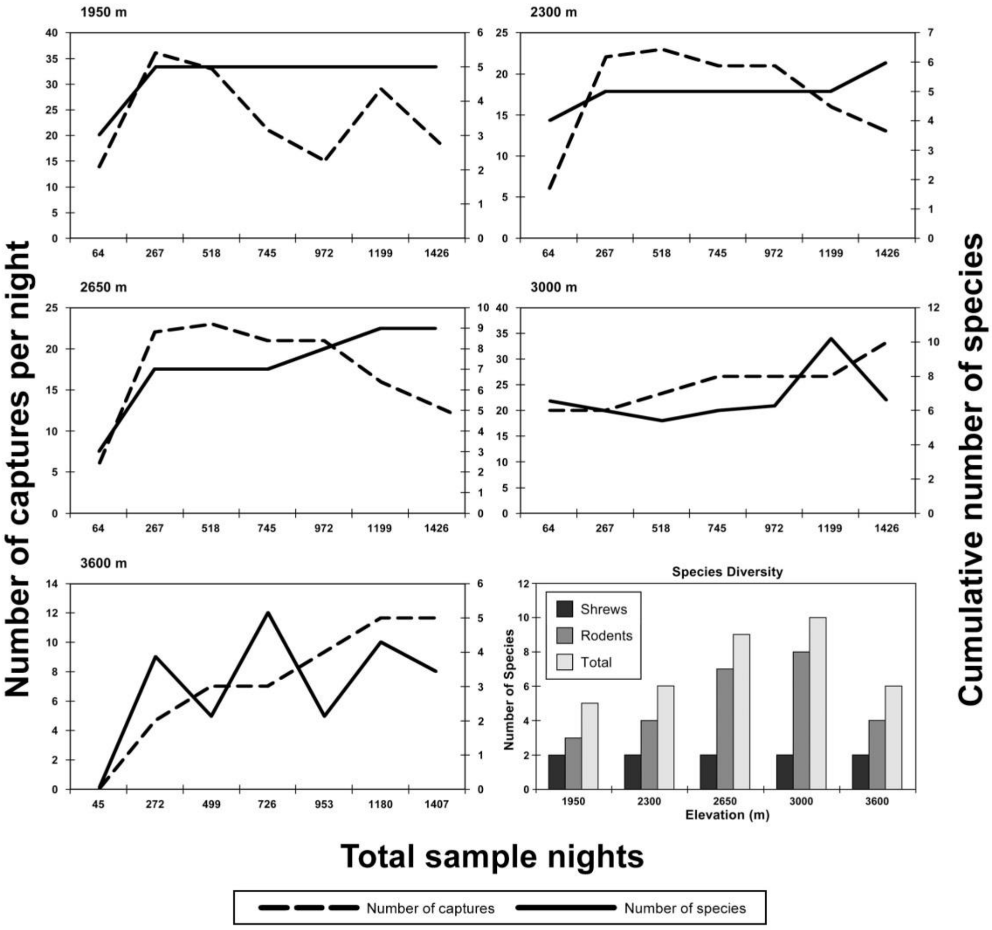

Figure 2. Species accumulation curves (for both pitfall and trap lines combined) for each site. The dashed lines represent the number of captures each day; the solid lines represent the cumulative number of new species for the site observed each day. The graph at the lower right shows the number of specimens of shrew, rodent and mammal captured at each site.

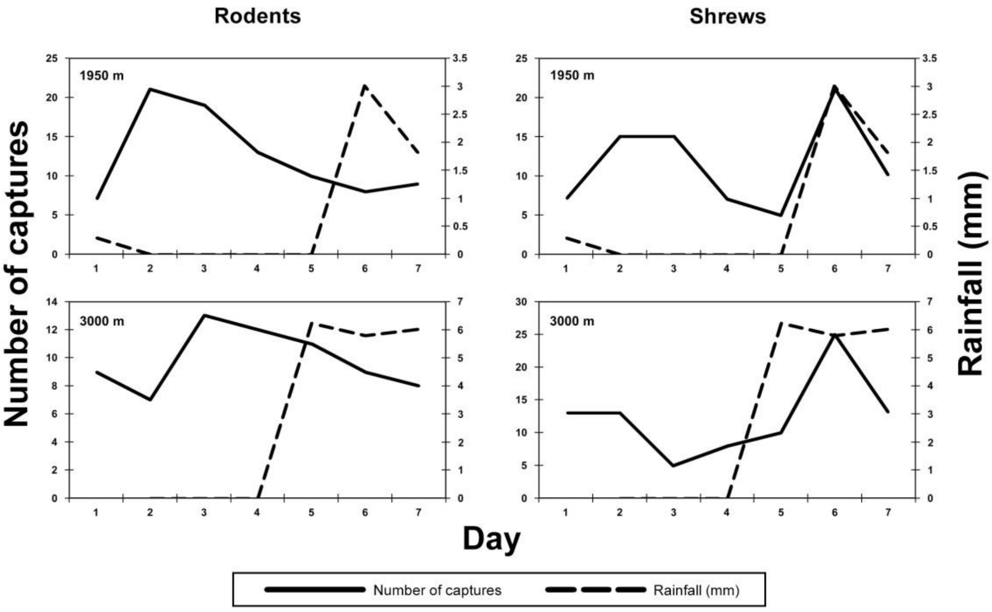

Figure 3. The relationship between numbers of individuals captured each day of the sampling period, and rainfall, at each site. Rodentia are on the left and Soricomorpha are on the right.

Table 1. Climatic data for each of the sites sampled on Mt. Meru in July-August, 2009. Totals given as mean ± standard deviation, range and sample size (number of days measured). Sample size for rainfall is given as number of days monitored and (number of days with rain).

Elevation (m)	Daily Minimum Temperature (° C)	Daily Maximum Temperature (° C)	Daily rainfall (mm)
1950	10.2° ± 0.4 10 – 11° N = 7	16.7° ± 1.0 16 – 18° N = 6	0.7 ± 1.2 0 – 3 N = 7 (2)
2300	7.9° ± 0.9 6.5 – 9.0° N = 7	14.2° ± 1.8 11.5 – 16° N = 6	0 N = 6
2650	6.2° ± 0.7 5.5 – 7.5° N = 6	13.1° ± 2.7 10 – 18° N = 6	0 N = 6
3000	4.3° ± 0.9 3 – 5° N = 7	13.8° ± 3.4 9.0 – 16.5° N = 6	3.0 ± 3.3 0 – 6.2 N = 6 (3)
3600	2.1° ± 1.4 0 – 4° N = 7	16.3° ± 1.6 14.5 – 18.0° N = 6	0 N = 6

Table 2. Trapping totals for rodents and shrews by trap technique on the southeastern slope of Mt. Meru in July-August, 2009.

Elevation	1950 m	2300 m	2650 m	3000 m	3600 m	Totals
BUCKETS						
# bucket-nights	506	506	506	506	495	2519
# individuals	52	24	18	63	13	170
(% bucket success)	(10.3)	(4.7)	(3.6)	(12.3)	(2.6)	(6.7)
# species	3	3	3	4	3	5
# shrews	51	22	17	58	12	160
(% bucket success)	(10.1)	(4.3)	(3.4)	(11.3)	(2.4)	(6.3)
# shrew species	2	2	2	2	2	2
# rodents	1	2	1	5	1	10
(% bucket success)	(0.2)	(0.4)	(0.2)	(1.0)	(0.2)	(0.4)
# rodent species	1	1	1	2	1	3
TRAPS						
# trap-nights	920	920	920	920	912	4592
# individuals	115	233	104	93	36	581
(% trap success)	(12.5)	(25.5)	(11.3)	(9.3)	(3.9)	(12.6)
# species	5	6	8	9	6	9
# rodents	86	206	81	64	28	465
(% trap success)	(9.3)	(22.6)	(8.8)	(6.5)	(3.1)	(10.1)
# rodent species	3	4	6	7	4	7
# shrews	29	27	23	29	8	116
(% bucket success)	(3.2)	(2.9)	(2.5)	(2.8)	(0.9)	(2.5)
# shrew species	2	2	2	2	2	2
TOTAL						
# sample-nights	1426	1426	1426	1426	1407	7111
# individuals	167	257	122	156	49	751
(% sample success)	(11.7)	(18.0)	(8.6)	(10.9)	(3.5)	(10.5)
# species	5	6	9	10	6	10

Table 3. Elevational distribution of shrew species along the southeastern slope of Mt. Meru in July-August, 2009. Only specimens caught in traps or buckets are included in totals.

Elevation	1950 m	2300 m	2650 m	3000 m	3600 m	Totals
Species						
Crocidura allex	31	31	18	36	16	132
Crocidura newmarki	49	18	22	51	4	144
Total # individuals	80	49	40	87	20	276
Total # species	2	2	2	2	2	2
Total # sample-nights	1426	1426	1426	1426	1407	7111
Sample success (%)	5.6	3.4	2.8	6.1	1.4	3.9
Total # caught in buckets	51	22	17	58	12	160
Total # bucket-nights	506	506	506	506	495	2519
Bucket success (%) for	10.1	4.3	3.3	11.5	2.4	6.3

Table 4. Elevational distribution of rodent species along the southeastern slope of Mt. Meru in July-August, 2009. Only specimens caught in traps or buckets are included in totals.

Elevation	1950 m	2300 m	2650 m	3000 m	3600 m	Totals
Species						
Otomys tropicalis	0	0	2	1	1	4
Dendromus insignis	0	0	1	7	2	10
Grammomys	3	4	2	4	0	13
Lophuromys	0	18	9	30	2	59
Mus triton	0	0	0	1	0	1
Praomys taitae	79	185	38	4	0	306
Rhabdomys dilectus	0	0	24	7	24	55
Graphiurus murinus	5	1	6	15	0	31
Total # individuals	87	208	82	69	29	475
Total # species	3	4	7	8	4	8
Total # sample-nights	1426	1426	1426	1426	1407	7111
Sample success (%)	6.1	14.6	5.7	4.8	2.1	6.7
Total # caught in traps	86	206	81	64	28	465
Total # trap-nights	920	920	920	920	912	4592
Trap success (%)	9.3	22.4	8.8	6.9	3.1	10.1

Table 5. Product-moment correlation coefficients (*r*) of cumulative sample-nights with four parameters of trap/bucket captures. Results are given for each sampling method for both targeted groups and everything captured.Values in parentheses represent strong but not significant correlations. * = *P*≤ 0.05; ** = *P*≤ 0.01

Daily cumulative sample-nights correlated with (across)	Number of individuals	Number of Species	New Species added	Cumulative species
Total				
traps (rodents only)	-0.425**	0.060	(-0.317)	0.943**
traps (all captures)	-0.448**	0.001	-0.388*	0.920**
buckets (shrews only)	-0.254	(-0.311)	(-0.293)	-
buckets (all captures)	-0.226	-0.176	(-0.255)	0.910**
traps and buckets combined (all captures)	-0.479**	-0.011	-0.350*	0.962**
1950 m				
traps (rodents only)	-0.403	0.119	(-0.697)	(0.605)
traps (all captures)	0.071	0.671	(-0.636)	0.785*
buckets (shrews only)	-0.453	(-0.611)	(-0.605)	-
buckets (all captures)	-0.464	-0.677	-0.784*	0.605
traps and buckets combined (all captures)	-0.159	0.119	-0.802*	0.605
2300 m				
traps (rodents only)	-0.350	0.009	-0.491	0.796*
traps (all captures)	-0.260	0.429	(-0.691)	0.846*
buckets (shrews only)	-0.888**	-0.774*	-0.605	-
buckets (all captures)	-0.851	(-0.693)	(-0.677)	0.796*
traps and buckets combined (all captures)	-0.385	-0.210	-0.576	0.796*
2650 m				
traps (rodents only)	0.221	0.546	(-0.707)	0.812*
traps (all captures)	0.336	0.627	-0.633	0.751*
buckets (shrews only)	-0.823*	(-0.676)	-0.796*	0.605
buckets (all captures)	-0.779*	-0.413	-0.438	0.889**
traps and buckets combined (all captures)	0.081	(0.667)	(-0.682)	0.866**
3000 m				
traps (rodents only)	0.071	0.484	-0.523	0.935**
traps (all captures)	0.551	0.636	-0.831*	0.912**
buckets (shrews only)	0.129	0.200	-0.605	-
buckets (all captures)	0.090	0.293	-0.401	0.611
traps and buckets combined (all captures)	0.453	0.255	-0.458	0.941**
3600 m				
traps (rodents only)	0.285	0.588	0.144	0.975**
traps (all captures)	0.416	(0.670)	0.000	0.971**
buckets (shrews only)	0.309	0.224	-0.408	0.612
buckets (all captures)	0.368	0.378	-0.196	0.849*
traps and buckets combined (all captures)	0.501	(0.688)	-0.289	0.927**

Table 6. Product-moment correlation coefficients (*r*) of cumulative sample-nights with four parameters of trap success shrew and rodent captures. Values in parentheses represent strong but not significant correlations. * = *P*≤ 0.05; ** = *P*≤ 0.01.

Shrew and rodent captures correlated with (across)	Number of individuals	Number of Species	New species added	Cumulative species
Total, shrews	(-0.290)	-0.346*	(-0.293)	-
Total, rodents	-0.421**	0.141	-0.252	0.969**
1950 m, shrews	0.141	-	-0.605	-
1950 m, rodents	-0.414	0.119	(-0.697)	(0.605)*
2300 m, shrews	-0.769*	-0.408	-0.605	-
2300 m, rodents	-0.341	-0.009	-0.491	0.796*
2650 m, shrews	-0.275	0.605	-0.796*	0.605
2650 m, rodents	-0.203	0.628	-0.611	0.900**
3000 m, shrews	0.351	-	-0.725*	-
3000 m, rodents	0.011	0.629	-0.605	0.941**
3600 m, shrews	0.644	0.408	-0. 408	0.612
3600 m, rodents	0.339	0.784*	0.000	0.980**

Table 7. Product-moment correlation coefficients (*r*) between elevation and trap success. Values in parentheses represent strong but not significant correlations.

Elevation correlated with	(*r*)	P
Total number of individual mammals collected	(-0.75)	> 0.05
Total trap success	(-0.75)	> 0.05
Total number of species collected	0.59	> 0.05
Total number of shrews collected	-0.53	> 0.05
Shrew trap success	-0.52	> 0.05
Total number of shrew species collected	-	-
Total number of rodents collected	-0.62	> 0.05
Rodent trap success	-0.61	> 0.05
Total number of rodent species collected	0.33	> 0.05

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Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe nur unter Verwendung der angeführten Literatur angefertigt habe.

Signature

____

William Stanley

Erklärung zum Promotionsvorhaben Hiermit erkläre ich, dass ich zuvor noch keiner Promotionsprüfung unterzogen wurde, sowie ich mich noch um keine Zulassung an der Universität Hamburg bzw. einer anderen Universität beworben habe.
Weiterhin habe ich noch keiner Universität oder ähnlichen Einrichtung eine Dissertation vorgelegt.

William Stanley

WAIVER

The manuscripts included as part of this thesis include taxonomic descriptions that are part of a manuscript currently in press with the *Zoological Journal of the Linnean Society*. Any names proposed in this thesis should not be considered official and will be formally presented in the forthcoming publication in the *Zoological Journal of the Linnean Society*.

William T. Stanley
19 February 2015