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

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We assess morphological and multilocus genetic variation among 11 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.

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 es-pecially 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, Davenport & Howell, 2011). Nevertheless, the fauna is only coarsely documented, as evidenced by discoveries of new species, including large,

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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, Rogers & Hutterer 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 eight specimens collected near the German mission at Rombo (6000 ft; 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 with *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 & 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 EAM, 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 & 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.* (1998), 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 neighbours Mt Kilimanjaro (Fig. 1), Hutterer (2005) stated that it might occur there. Demeter & 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 geographical variation of populations either identified as *Crocidura monax* or occurring on mountains
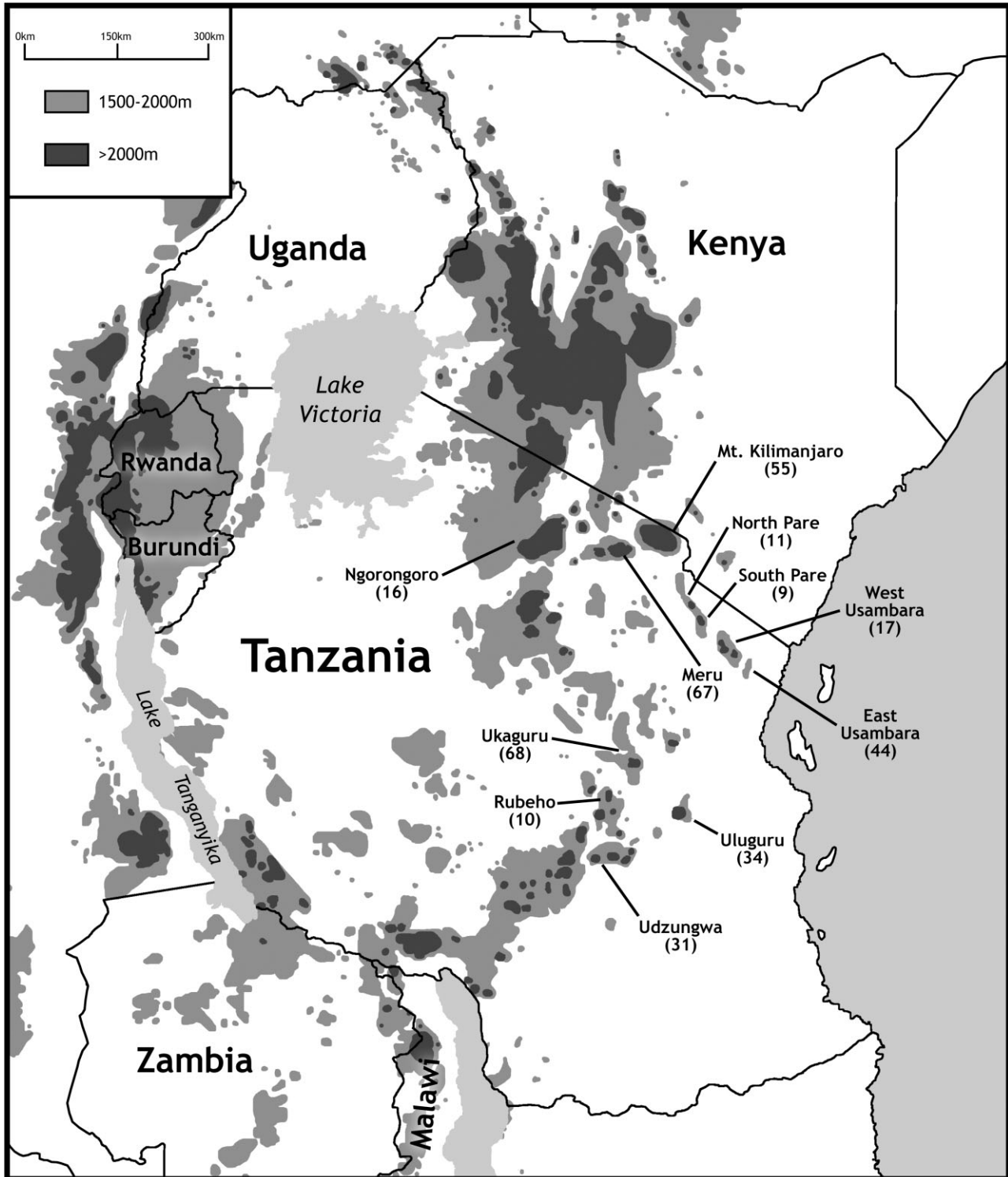
Figure 1. Map of mountainous regions of Tanzania and surrounding countries. Areas above 1500 m are shaded. Populations sampled for this study are indicated with sample sizes for cranial measurements in parentheses. See Material and Methods for details on specific localities and sample sizes.

neighbouring the type locality. Details of many of these surveys have been published elsewhere (Stanley, Goodman & Hutterer, 1996; Stanley *et al*., 1998, 2003; Stanley & Hutterer, 2007; Stanley, Kihaule & Munissi, 2007; Stanley & Esselstyn, 2010; Stanley, Goodman & Newmark, 2011b; Stanley *et al*., 2014). In this paper, we analyse new molecular and morphological data from voucher specimens collected during these surveys to (1) test existing hypotheses of the relationships among the geographically isolated populations of the *C. monax* group (*sensu* Hutterer, 1986); (2) test the specific status of *C. tansaniana*; (3) resolve the identity of the larger shrews on Mt Meru most recently attributed to *C. montis*; and (4) characterize the distribution, geographical variation and biogeographical history of the *C. monax* group.

MATERIAL AND METHODS

FIELDWORK

Specimens were collected during faunal surveys of the mountains of Tanzania by the first author (W.T.S.) and biologists from the University of Dar es Salaam. We collected shrews in montane habitats on 11 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 11 15-L 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*. (2011b). 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). W.T.S. 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 millimetres (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 programme 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 & 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 W.T.S. were included in morphometric analyses. Specimens were assigned to one of four ontogenetic categories of toothwear following the definitions of Dippenaar (1977), 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.

W.T.S. used digital calipers (to the nearest 0.01 mm) to record the following craniodental measurements: condylo-incisive length (CI), basal length (BL), postpalatal 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 & Kirkland (1989) and Carraway (1990) and are illustrated in Stanley & Olson (2005).

W.T.S. 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 the 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 (ANOVAs). 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). 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 the online supporting information (Appendix S1).

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 analysed 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 (MCMC) 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, Smith & Donnelly, 2001) and set the probability threshold to 70%, following Garrick, Sunnucks & Dyer (2010). PHASE files were constructed and interpreted using SeqPhase (Flot, 2010). We used the program BP&P (Yang & 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 Γ (α,β) 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 & 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 & Fujita, 2010; Yang & Rannala, 2010). To assess how prior choice affects our results, we tested six sets of priors previously used by Giarla, Voss & Jansa (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 & Rannala's (2010) algorithms 0 and 1. Next, to minimize the extent to which use of an

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, shallow) and on θ represent two relative mutation-rate-scaled effective population sizes (large, 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	$\theta \sim \Gamma\,(1, 10)$ & $\tau \sim \Gamma\,(2, 2\,000)$
3	Shallow	Large	$\theta \sim \Gamma\,(1, 10)$ & $\tau \sim \Gamma\,(2, 20\,000)$
4	Deep	Small	$\theta \sim \Gamma\,(2, 2000)$ & $\tau \sim \Gamma\,(1, 10)$
5	Moderate	Small	$\theta \sim \Gamma\,(2, 2000)$ & $\tau \sim \Gamma\,(2, 2\,000)$
6	Shallow	Small	$\theta \sim \Gamma\,(2, 2000)$ & $\tau \sim \Gamma\,(2, 20\,000)$

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 five generations and discarding the first 50 000 as burn-in.

RESULTS

ANALYSIS OF MITOCHONDRIAL SEQUENCES

Our phylogenetic analyses of mitochondrial DNA (mtDNA) 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, 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 ten 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 [posterior probability (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 artefact of the small number of individuals we
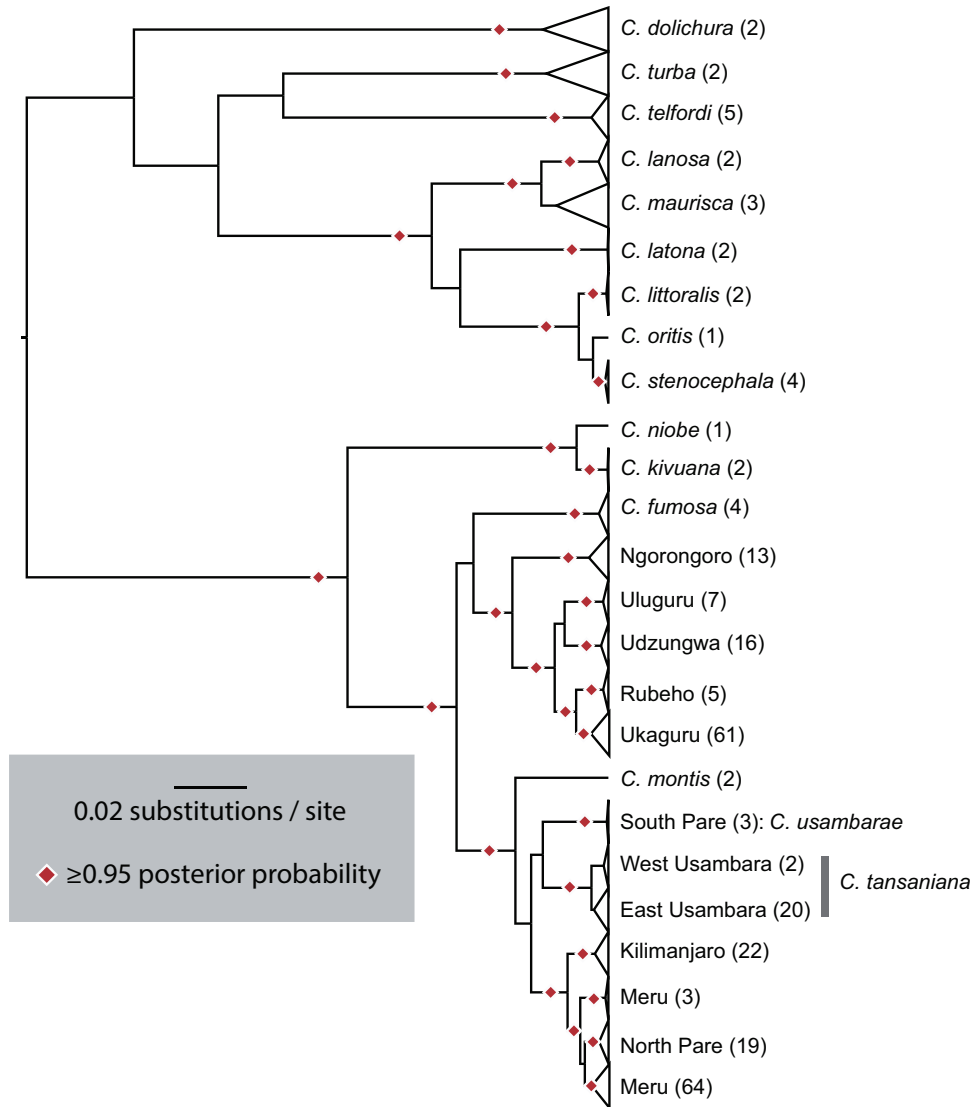
Figure 2. Phylogenetic tree estimated from Bayesian analysis of 267 CytB sequences. Populations/species at tips have been collapsed into triangles where the apex represents the deepest split within the group. Diamonds along branches indicate clades with posterior probabilities greater than, or equal to 0.95, and values in parentheses after names indicate the number of individuals sequenced.

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, 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;

Table 2. Alignment characteristics for all nuclear genes included in this study

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

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 θ priors.

Churchfield, Hutterer & Dudu, 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 with *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, Hutterer & Asher, 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 renders *C. maurisca* as smaller than any operational taxonomic units (OTUs) except Ngorongoro (Bober & 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 ANOVA 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 non-significant 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, 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 ANOVA 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 woolly and hairs measure approximately 5 mm in length at mid-dorsum. The colour is blackish brown above and only slightly paler below. External and cranial measurements of specimens recently collected compared with the holotype (BMNH 10.7.2.58; measured by W.T.S.) 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
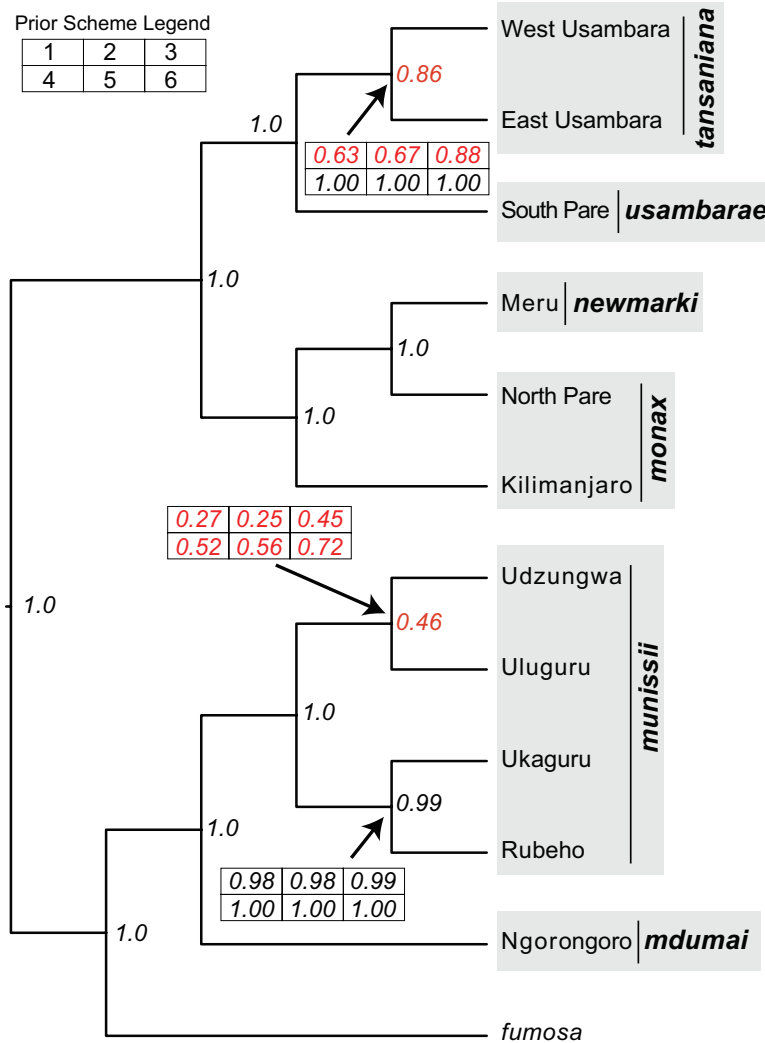
Figure 3. Results from guide-tree-based BP&P analysis for 12 putative species. The guide tree is based on the CytB topology (Fig. 2), but excludes *Crocidura montis* from the Rwenzoris, for which no nuclear sequences were obtained. The posterior probability that a given split represents a speciation 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 grey boxes according to our taxonomic conclusions.

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 (three) 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 nonsignificant, 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 geographical sample (7–11%; Table 4), so we deleted this character in subsequent analyses of geographical variation. *F*-values produced by the

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

Population (Cont'd) 1	2	1	2	3	4	5	6
Kilimanjaro	Ukaguru	1	1	1	1	1	1
Kilimanjaro	Uluguru	1	1	1	1	1	1
Kilimanjaro	West Usambara	1	1	0.98	1	1	1
Meru	Ngorongoro	1	1	1	1	1	1
Meru	North Pare	0.98	1	1	1	1	1
Meru	Rubeho	1	1	1	1	1	1
Meru	South Pare	1	1	1	1	1	1
Meru	Udzungwa	1	1	1	1	1	1
Meru	Ukaguru	1	1	1	1	1	1
Meru	Uluguru	1	1	1	1	1	1
Meru	West Usambara	1	1	1	1	1	0.99
Ngorongoro	North Pare	1	1	1	1	1	1
Ngorongoro	Rubeho	1	1	1	1	1	1
Ngorongoro	South Pare	1	1	1	1	1	1
Ngorongoro	Udzungwa	1	1	1	1	1	1
Ngorongoro	Ukaguru	1	1	1	1	1	1
Ngorongoro	Uluguru	1	1	1	1	1	1
Ngorongoro	West Usambara	1	1	0.99	1	1	1
North Pare	Rubeho	1	1	1	1	1	1
North Pare	South Pare	0.05	0.84	0.85	0.95	1	1
North Pare	Udzungwa	1	1	1	1	1	1
North Pare	Ukaguru	1	1	1	1	1	1
North Pare	Uluguru	1	1	1	1	1	1
North Pare	West Usambara	0.94	1	0.94	1	1	1
Rubeho	West Usambara	1	1	1	1	1	0.99
Rubeho	South Pare	1	1	1	1	1	1
South Pare	Udzungwa	1	1	1	1	1	1
South Pare	Ukaguru	1	1	1	1	1	1
South Pare	Uluguru	1	1	1	1	1	1
South Pare	West Usambara	0.83	0.97	0.64	1	1	0.99
Udzungwa	West Usambara	1	1	1	1	1	1
Ukaguru	West Usambara	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 12 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 grey boxes.

one-way ANOVAs to test the null hypothesis of no significant geographical 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 geographical 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 (CV) 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,

Table 3. External measurements of individuals of *Crocidura* from 11 mountains in Tanzania (listed in geographical order from north to south) and three holotypes

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

Sexes are combined within populations. All measurements were taken by W.T.S., 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 are given. See text for character definitions.

Table 4. Cranial measurements of individuals of *Crocidura* from 11 mountains in Tanzania (sexes combined within populations), two holotypes and one set of paratypes

	CI	BL	PPL	UTRL	LIW	BW	NW	GW	HBC	I³-W	C-W	M³-L	M³-W	PGW	MP	M&I	LTR
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	0.71 ± 0.03	0.77 ± 0.03	1.37 ± 0.05	0.73 ± 0.03	6.61 ± 0.12	1.08 ± 0.14	13.34 ± 0.17	8.52 ± 0.14
	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	0.65–0.75	0.71–0.83	1.26–1.45	0.67–0.80	6.43–6.83	0.94–1.45	13.08–13.65	8.23–8.72
	N = 16	N = 16	N = 16	N = 16	N = 16	N = 16	N = 16	N = 16	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	0.04	0.04	0.04	0.05	0.02	0.13	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	0.69 ± 0.03	0.73 ± 0.03	1.45 ± 0.07	0.77 ± 0.04	6.55 ± 0.16	1.04 ± 0.08	13.05 ± 0.35	8.35 ± 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	0.62–0.78	0.64–0.80	1.31–1.59	0.70–0.86	5.99–6.93	0.91–1.32	12.13–13.76	7.80–8.98
	N = 67	N = 67	N = 67	N = 67	N = 67	N = 67	N = 66	N = 67	N = 67	N = 67	N = 67	N = 67	N = 67	N = 49	N = 67	N = 67	N = 67
	0.02	0.02	0.03	0.02	0.02	0.02	0.04	0.02	0.04	0.05	0.05	0.04	0.05	0.02	0.08	0.03	0.03
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	0.80 ± 0.03	0.90 ± 0.04	1.57 ± 0.06	0.84 ± 0.04	7.06 ± 0.19	0.99 ± 0.10	14.80 ± 0.36	9.51 ± 0.19
	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	0.71–0.87	0.80–0.97	1.44–1.69	0.74–0.95	6.67–7.56	0.75–1.20	14.01–15.51	9.04–9.81
	N = 55	N = 55	N = 55	N = 55	N = 55	N = 55	N = 55	N = 55	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	0.04	0.04	0.04	0.05	0.03	0.10	0.02	0.02
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	0.84 ± 0.04	0.94 ± 0.04	1.62 ± 0.06	0.83 ± 0.04	6.99 ± 0.15	1.08 ± 0.08	14.73 ± 0.34	9.59 ± 0.20
	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	0.78–0.92	0.88–1.01	1.50–1.69	0.74–0.87	6.85–7.36	0.94–1.21	14.26–15.29	9.23–9.95
	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11	N = 11
	0.02	0.02	0.02	0.02	0.02	0.02	0.03	0.02	0.05	0.04	0.04	0.04	0.05	0.02	0.07	0.02	0.02
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	0.80 ± 0.03	0.88 ± 0.03	1.49 ± 0.07	0.77 ± 0.30	6.81 ± 0.10	1.14 ± 0.10	14.04 ± 0.27	9.07 ± 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	0.76–0.84	0.82–0.90	1.36–1.06	0.73–0.83	6.66–6.94	0.94–1.28	13.44–14.33	8.78–9.30
	N = 9	N = 9	N = 9	N = 9	N = 9	N = 9	N = 9	N = 9	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	0.05	0.05	0.04	0.04	0.05	0.01	0.11	0.02	0.02
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	0.97 ± 0.03	1.01 ± 0.03	1.71 ± 0.06	0.87 ± 0.05	7.28 ± 0.24	1.20 ± 0.10	15.08 ± 0.34	9.74 ± 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	0.91–1.02	0.95–1.05	1.59–1.79	0.81–0.98	6.93–7.71	1.06–1.41	14.49–15.69	9.47–10.26
	N = 17	N = 17	N = 17	N = 17	N = 17	N = 17	N = 17	N = 17	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	0.03	0.03	0.04	0.06	0.03	0.08	0.02	0.02
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	0.98 ± 0.04	1.01 ± 0.40	1.72 ± 0.07	0.87 ± 0.05	7.50 ± 0.22	1.23 ± 0.13	16.04 ± 0.33	10.29 ± 0.22
	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	0.90–1.07	0.93–1.10	1.58–1.93	0.76–0.97	7.19–8.12	0.94–1.48	15.19–16.88	9.84–11.05
	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 44	N = 43	N = 44	N = 44	N = 44
	0.02	0.02	0.02	0.02	0.04	0.02	0.05	0.03	0.03	0.04	0.04	0.04	0.06	0.03	0.11	0.02	0.02
Ukaguru	24.51 ± 0.46	22.22 ± 0.43	10.97 ± 0.26	10.75 ± 0.23	5.33 ± 0.14	7.65 ± 0.17	2.28 ± 0.15	10.79 ± 0.26	7.02 ± 0.20	0.88 ± 0.05	1.01 ± 0.05	1.67 ± 0.07	0.82 ± 0.05	7.61 ± 0.23	1.01 ± 0.11	15.51 ± 0.35	9.96 ± 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	0.74–1.07	0.88–1.10	1.50–1.80	0.68–0.91	7.00–8.15	0.79–1.31	14.64–16.38	9.49–10.42
	N = 68	N = 68	N = 69	N = 68	N = 69	N = 69	N = 68	N = 69	N = 69	N = 69	N = 69	N = 69	N = 69	N = 69	N = 69	N = 67	N = 67
	0.02	0.02	0.02	0.02	0.03	0.02	0.07	0.03	0.03	0.06	0.04	0.04	0.06	0.03	0.11	0.02	0.02
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	0.86 ± 0.04	0.97 ± 0.03	1.65 ± 0.06	0.87 ± 0.03	7.28 ± 0.15	1.22 ± 0.15	15.12 ± 0.28	9.81 ± 0.17
	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	0.79–0.91	0.91–1.02	1.54–1.73	0.81–0.91	7.02–7.55	0.97–1.42	14.70–15.49	9.56–10.03
	N = 10	N = 10	N = 10	N = 10	N = 10	N = 10	N = 10	N = 10	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	0.04	0.04	0.04	0.04	0.02	0.12	0.02	0.02
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	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
	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	0.78–0.94	0.78–1.05	1.49–1.79	0.72–0.88	6.82–7.72	0.87–1.41	14.49–15.84	9.54–10.21
	N = 34	N = 34	N = 34	N = 34	N = 34	N = 34	N = 34	N = 33	N = 33	N = 34	N = 34	N = 34	N = 34	N = 34	N = 34	N = 34	N = 34
	0.02	0.02	0.03	0.02	0.03	0.03	0.05	0.02	0.03	0.05	0.05	0.04	0.05	0.03	0.11	0.02	0.02
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	0.88 ± 0.06	0.97 ± 0.04	1.66 ± 0.08	0.83 ± 0.04	7.42 ± 0.23	1.06 ± 0.14	14.93 ± 0.28	9.76 ± 0.23
	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	0.77–0.98	0.90–1.03	1.50–1.90	0.77–0.92	6.98–7.85	0.82–1.42	14.52–15.57	9.34–10.12
	N = 31	N = 31	N = 31	N = 31	N = 31	N = 31	N = 31	N = 31	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	0.06	0.04	0.05	0.05	0.03	0.13	0.02	0.02
***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	0.90 ± 0.04	0.91 ± 0.02	1.64 ± 0.08	0.82 ± 0.05	6.82 ± 0.15	1.05 ± 0.12	13.87 ± 0.26	9.03 ± 0.22
	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	0.84–0.93	0.88–0.94	1.53–1.77	0.74–0.89	6.58–6.93	0.92–1.16	13.45–14.19	8.74–9.38
	N = 3	N = 3	N = 5	N = 4	N = 4	N = 5	N = 5	N = 5	N = 4	N = 5	N = 5	N = 6	N = 6	N = 5	N = 4	N = 6	N = 6
	0.01	0.01	0.02	0.01	0.01	0.02	0.04	0.01	0.03	0.04	0.02	0.05	0.07	0.02	0.11	0.02	0.02
***C. monax* Holotype**	23.67	21.30	10.51	10.60	5.12	7.22	2.24	10.30	6.88	0.88	0.94	1.69	0.85	7.05	1.13	15.12	9.87
***C. tansaniana* Holotype**	25.36	23.10	11.51	11.20	5.40	7.95	2.32	10.99	6.93	0.93	0.99	1.76	0.86	7.51	1.08	16.00	10.30

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

Table 5. Comparison of cranial measurements (mm) for *Crocidura montis* from Rwenzori Mountains and *Crocidura newmarki* from Mt Meru

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**

Mean ± standard deviation, sample size and range are given. *F* values result from a one-way ANOVA on the populations from Meru and Rwenzori (Holotype not included). **$P \leq 0.01$. See text for character definitions.

first observed by Hutterer (1986), and the sample from the West Usambaras are reflected in the position of the two 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 the West Usambaras, and *C. usambarae*, originally described from the Shume-Magamba forests in the north-western segment of the West Usambaras, is also found in the montane forests of the South Pare Mountains. Populations on Ngorongoro, Meru and the middle EAM (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.

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* sp. nov.**
Uluguru	12	14.6	9–20	few, short	90.8	***C. munissii* sp. nov.**
Ukaguru	43	8.1	4–27	very few, short	84.5	***C. munissii* sp. nov.**
Rubeho	5	7.5	6–8	very few, short	89.2	***C. munissii* sp. nov.**
Udzungwa	15	12.1	7–18	few, short	93.4	***C. munissii* sp. nov.**
Meru	10	67.2	58–95	many, long	68.9	***C. newmarki* sp. 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*

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 the Appendix.

Type locality: 'Rombo', 6000 ft, Mt Kilimanjaro, Tanzania.

Measurements of holotype: External measurements presented as listed by Thomas (1910); cranial measurements taken by W.T.S.. 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 colour, and hairs of the back are 4 mm in length at mid-dorsum. The hairs of the dorsum are steel grey 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: *Crocidura 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 neighbouring 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*,

SYSTEMATICS OF *CROCIDURA MONAX*   199

Table 7. Comparison of cranial measurements (mm) for *Crocidura fumosa* from Mt Kenya and *Crocidura* from Ngorongoro

| 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**

Mean ± standard deviation, sample size and range are given. F values result from one-way ANOVA. *$P \leq 0.05$; **$P \leq 0.01$. See text for character definitions.

but shorter than in the remaining species (Table 6). 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 EAM 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*.
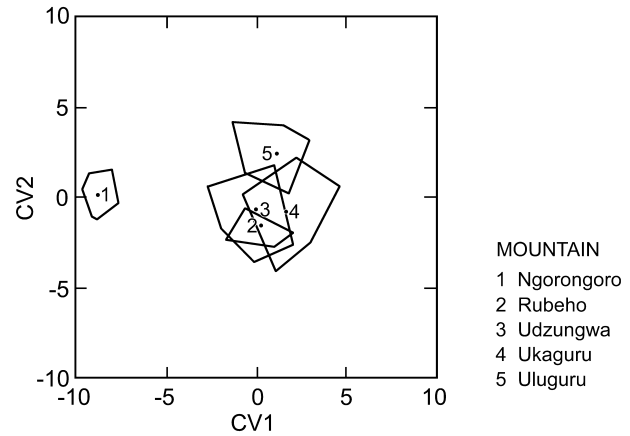
Figure 5. Projection of specimen scores on the first two canonical variates extracted from a discriminant function analysis of 16 log-transformed cranial and dental variables. Measurements were recorded from adult specimens from five populations of *Crocidura* from Ngorongoro, Rubeho, Udzungwa, Ukaguru and Uluguru Mountains.
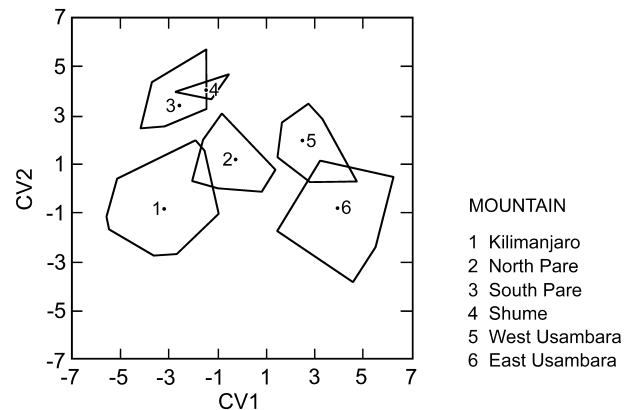
Figure 6. Projection of specimen scores on the first two canonical variates extracted from a discriminant function analysis of 16 log-transformed cranial and dental variables. Measurements were recorded from adult specimens from six populations, including Kilimanjaro, North Pare, South Pare, West Usambara (Shume-Magamba), West Usambara (Ambangulu) and East Usambara [specimens from Mt Meru (*C. newmarki*) were excluded].

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'.
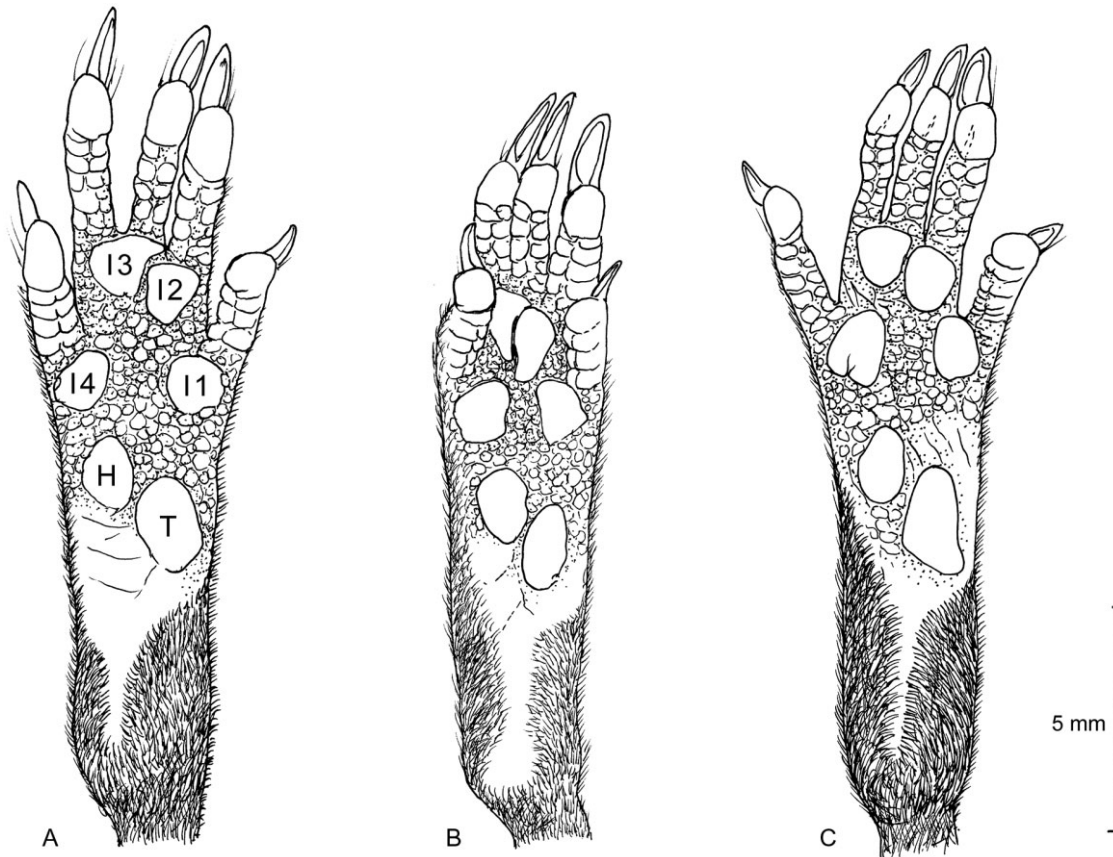
Figure 7. Plantar view of the right hindfoot of (A) *Crocidura monax* (FMNH 173789), (B) ***C. newmarki* sp. nov.** (FMNH 208012) and (C) ***C. munissii* sp. nov.** (FMNH 158407); scale is 5 mm. Note differences in the relative distance between thenar (T), hypothenar (H) and interdigital pads (I1–4).

Ecological notes: Crocidura monax was recorded between 2000 and 3000 m on the Maua route along the south-eastern 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 the 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); W.T.S. 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 for additional specimens examined.
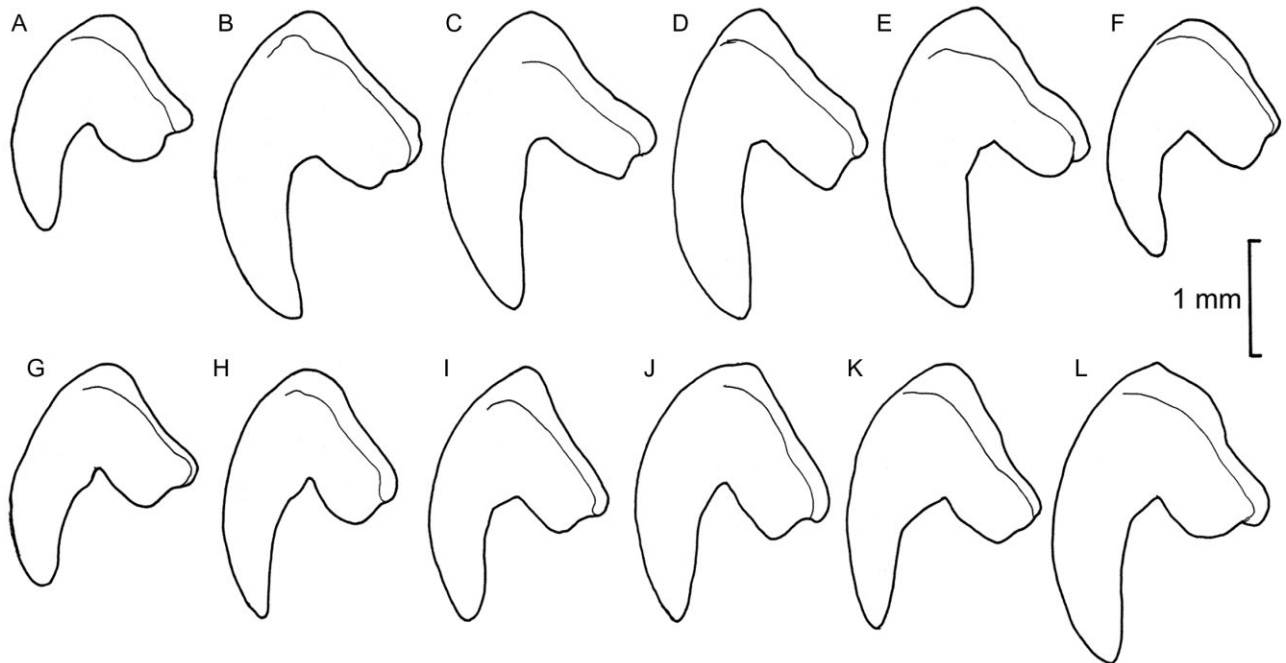
region, moderately robust rostrum, wide braincase, very robust unicuspids and robust M^3.

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 colour and the hairs of the back are 4 mm in length at mid-dorsum. The hairs of the dorsum are steel grey with brown tips. Both the front and the 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 (Figs 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 with ≥ 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).

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 north, 1.5 km west of Maua on Mt Kilimanjaro (2000 m).

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

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; L, East Usambara FMNH 149970 (= *C. tansaniana*).

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 (05.06°S, 38.38°E).

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 shrew with a head and body length of 82–108 mm, tail of

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.

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 middorsum. The hairs of the dorsum are brownish grey with reddish brown tips. The tail is equally brown. Front and hind feet are only slightly paler on the dorsal surface than the colour 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 brain-case (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: Crocidura tansaniana is larger than all other Tanzanian species, except *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 M³ 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 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, Goodman & Hutterer (2011a) 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 (> 500 ha) of relatively undisturbed montane forest, and only three 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 W.T.S. 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,

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).

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 W.T.S. and are in millimetres 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 greyish 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 the 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 woolly fur. The head and body length range is 65–85 mm, tail length is 45–60 mm, the length of the hindfoot is 13–16 mm, and mass is 6–11 g. In total, 58–95% (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 & 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 neighbouring 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 and 3600 m in habitats ranging from submontane forest to the ericaceous zone above the treeline. Females made up 38% of the total number of *C. newmarki* sampled in 2009 along the south-eastern 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 W.T.S. 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 for additional specimens examined.

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).

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 a.s.l. 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 a.s.l. (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 bicoloured). 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 grey of the venter. The hairs of the back are 5 mm in length. The dorsal surfaces of both the front and the 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 bicoloured (dorso-ventrally) tail is roughly 70% the length of the head and body (Tables 3, 6). Mystacial vibrissae range from 15 to 19 mm long (mean = 17.3 mm, $N = 10$). The ear conch is stout. The proximal three-quarters 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 colour 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 colour 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*, 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 seven of 17 cranial measurements the new species differs significantly from *C. fumosa*, which also has a much narrower infraorbital bridge than the new species (Table 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 W.T.S. 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 for additional specimens examined.

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 west, 2.3 km north of Tegetero in the Uluguru Mountains (1535 m).

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 colour and hairs of the back are 6–7 mm in length. The hairs of the dorsum are steel grey with brown tips (with the exception of FMNH 166739 from Ukaguru which represents a light grey colour 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: Crocidura 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). Mean hindfoot measurements of all four populations are 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 EAM. 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 *et al*., 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 univariate 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 & 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 & Rannala, 2010). In this case, we used θ_W estimates from unlinked loci not included in species validation approaches, and these suggest that our prior schemes 1–3, which assumed large θ values, were not realistic. Nevertheless, many of the pairwise comparisons yielded consistent results across all prior schemes, with most analyses giving a PP 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 ap-

proach may be artificially inflating posterior probabilities by placing distantly related populations close together in the guide tree. Other authors have discussed this bias (Leaché & Fujita, 2010; Yang & Rannala, 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 geographical distribution of *C. monax s.s.* is interesting as it spans two geologically distinct mountain groups – the Northern Highlands and the EAM (Griffiths, 1993). Carleton & Stanley (2005) and Bryja *et al.* (2014) grouped samples of *Praomys* from Kilimanjaro and the northern EAM, such as the Usambaras and South Pare, using both morphological 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 the 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 this phenotypic character state provides phylogenetic signal has not been critically analysed, 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* in particular, 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 geographical 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 mtDNA 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 with palaeobotanical datasets, should significantly augment efforts to understand the biogeographical history of these unique montane archipelagos.

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APPENDIX

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, Bodwa 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, Mornigside, 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, 208050, 208443–208451, 208453, 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.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. List of new GenBank accession records.
Appendix S2. Top left: *C. newmarkii* FMNH 208406. Top right: *C. mdumai* FMNH 211320. Bottom left: *C. munissii* FMNH 197665. Bottom right: *C. monax* FMNH 192518.