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Chapter 2

Small Mammal Inventories in the East and West Usambara Mountains, Tanzania. 2. Families Soricidae (Shrews) and Macroscelididae (Elephant Shrews)

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Abstract

Field surveys conducted in the montane forests of the East and West Usambara Mountains between 1991 and 1993 provide data on the species of shrews (Family Soricidae, Subfamily Crocidurinae) and elephant shrews (Family Macroscelididae). In total, 11 species of crocidurine shrew and one elephant shrew were documented on the Usambara Mountains, which include 10 shrew and one elephant shrew species for the East Usambara, and six species of shrew and one elephant shrew in the West Usambara. Information is presented on the captured animals regarding their natural history, distribution, ecology, and reproduction, as well as external and cranio-dental measurements. Species richness and different levels of endemism between the insectivorous small mammal faunas of tropical Africa and Madagascar are compared.

Introduction

The shrews (Family Soricidae, Subfamily Crocidurinae) and elephant shrews (Family Macroscelididae) of the montane areas of Tanzania are a diverse and enigmatic fauna. Recent systematic research is showing ever-increasing levels of diversity and endemism. Three of the four recognized genera within the Macroscelididae occur in Tanzania (the only genus not represented is *Macroscelides*), and the most recently described elephant shrew, *Rhynchocyon udzungwensis*, is endemic to the Udzungwa Mountains in the Eastern Arc Mountains (Schlitter, 2005; Rovero et al., 2008). Over the past century, soricids representing four genera have been described from different Tanzanian massifs, including 11 species endemic to the country, with seven having been described since 1980 (Table 1; Hutterer, 2005; Stanley et al., 2005d). The Usambara Mountains have a particularly rich shrew fauna, with at least one endemic species (*Crocidura tansaniana*; Hutterer, 2005) and one endemic subspecies (*Sylvisorex howelli usambarensis*; Hutterer, 1986).

Although some taxonomic work has been published on the shrews of the Usambaras, no thorough faunal inventory using standard protocols of pitfall trapping is yet available. This method has effectively assessed soricid diversity in other Eastern Arc Mountains, such as the Pares (Stanley et al., 1996, 2005a,b,c) and the Udzungwas (Stanley & Hutterer, 2000, 2007). Here, we report on the shrews and elephant shrews obtained during small mammal inventories in the East and West Usambara Mountains between 1991 and 1993. The principal trapping protocol used for shrews was pitfall traps, but a small percentage was captured in traps set for rodents. Information is also presented on the locally occurring elephant shrews using non-standardized field protocols.

Methodology

The trapping methodology and specifics on research sites and individual trap and pitfall lines are presented in Stanley et al. (this volume). Specimens collected were measured in the field by W.T.S. and S.M.G. External measurements (DeBlase & Martin, 1974) include total length (from the tip of the nose to the last caudal vertebra), head and body length (from the tip of the nose to the junction of the tail and the body), tail length (from the junction of the tail and body to the last caudal vertebra), hind foot length (from the ankle to the tip of the longest claw for W.T.S.; ankle to insertion of claw for S.M.G.), ear length (from the notch at the base of the ear to the longest point of the ear), and weight. All measurements were in millimeters, except weight, which was in grams. W.T.S. measured (with digital calipers to the nearest 0.01 mm) the following cranial and dental variables:

- BL (basal length): From the anterior-most aspect of the upper incisor to the anterior-most border of the foramen magnum.
- BW (bimaxillary width): The greatest breadth across the maxilla.
- CI (condylo-incisive length): From the anterior-most aspect of upper incisor to occipital condyle.
- CW (width of canine): From the most lingual to the most labial aspect of the upper canine.

TABLE 1. Soricid and macroscelidid species and subspecies endemic to different Tanzanian mountains with the site from which they were first discovered and the year of description.

Species	Type locality	Year described
Crocidura desperata	Mt. Rungwe	1991
Crocidura gracilipes	"on the way from the coast to Mt. Kilimanjaro"	1870
Crocidura monax	Mt. Kilimanjaro	1910
Crocidura tansaniana	East Usambara	1986
Crocidura telfordi	Uluguru	1986
Crocidura usambarae	West Usambara	1980
Myosorex geata	Uluguru	1927
Myosorex kihaulei	Udzungwa	2000
Myosorex zinki	Mt. Kilimanjaro	1956
Congosorex phillipsorum	Udzungwa	2005
Sylvisorex howelli	Uluguru	1984
Sylvisorex howelli usambarensis	West Usambara	1986
Rhynchocyon udzungwensis	Udzungwa	2008

- GW (greatest width of the braincase): Greatest breadth of the braincase measured at the posterior insertion of the zygomatic arches.
- HBC (height of the braincase): Measured by placing the cranium on a microscope slide, measuring from the bottom of the slide to the top of the cranium, and subtracting the thickness of the slide.
- I^3W (width of third upper incisor): From the most lingual to the most labial aspect of the third upper incisor.
- LIW (least interorbital width): Shortest distance across the cranium between the orbits.
- LTR (length of lower toothrow): From the anterior aspect of the lower incisor to the posterior aspect of the last tooth in the toothrow.
- MAST (breadth of the mastoid plate): From the posterior-most aspect of the anterior border of the mastoid plate to the anterior-most aspect of the posterior border.
- MI (length of mandible including the incisor): From the anterior aspect of the lower incisor to the posterior aspect of the articular condyle of the dentary.
- M^3L (length of third upper molar): The greatest dimension of the third upper molar.
- M^3W (width of third upper molar): The greatest dimension perpendicular to M^3L.
- NW (nasal width): The greatest breadth of the nasal bones.
- PGW (post-glenoid width): The greatest breadth across the cranium, taken just posterior to the glenoid fossa.
- PPL (post-palatal length): From the posterior border of the palate to anterior-most border of the foramen magnum.
- UTRL (length of entire upper toothrow): From the anterior-most aspect of the upper incisor to the posterior-most border of the third upper molar.

These variables follow Dippenaar (1977), van Zyll de Jong and Kirkland (1989), Carraway (1990), and Stanley and Olson (2005). Only skulls from adults (based on complete fusion between the basioccipital and basisphenoid bones) were measured. Specimens were assigned to one of four tooth wear categories, largely following the definitions of Dippenaar (1977), although we focused largely on the wear of the first upper molar. FMNH 151106, 151110, 151109, and 151117 exemplified categories I, II, III, and IV, respectively (sensu Dippenaar, 1977), and these specimens were subsequently used as a reference series for the tooth wear classification.

Standard descriptive statistics (mean, range, and standard deviation [SD]) were calculated for the different measurements of each taxon. When appropriate, we used one-way analyses of variance (ANOVA) to determine whether sexual dimorphism or geographical variation in skull dimension was significant. Although some of the sample sizes were small, and larger samples in certain cases are needed to confidently test morphological variation, we feel that comparisons of the currently available series from our field specimens are informative and generate hypotheses to be tested with additional samples and study. All statistical analyses were conducted using Systat (version 10, 2002).

Accounts of Species

Eleven species of crocidurine shrew and one elephant shrew were documented in the montane zones of the East and West Usambara Mountains after three survey seasons (see Table 2 for crocidurine shrews). For the East Usambara, 10 shrew and one elephant shrew species were confirmed, and in the West Usambara, six species of shrew were collected. External measurements for animals from both massifs are presented in Table 3. Although subsequent to the surveys reported here, W. D. Newmark found a specimen of *Rhynchocyon* in one of our study sites, and we include this record. Information regarding the natural history, including distribution, ecology and reproduction, specimens examined (including catalog numbers and pitfall lines [PF] and trap lines [TRL], from which each specimen was collected; see Stanley et al., this volume), and, when necessary, other remarks are presented for each species in the following accounts. When citing information on the testes measurements of males, the data are presented as length by width.

Family Soricidae

Subfamily Crocidurinae

Crocidura elgonius Osgood, 1910

DISTRIBUTION—First described from Mt. Elgon (Osgood, 1910), *Crocidura elgonius* is now known to occur in various montane settings in Kenya, Tanzania, and Uganda (Allen & Loveridge, 1942; Aggundey & Schlitter, 1986; Hutterer, 2005). Within Tanzania, this species has been recorded on several massifs, including Malundwe, Nguu, Udzungwa, and the East and West Usambara (Stanley et al., 1998, 2005a,b; Stanley & Hutterer, 2007; Stanley, unpubl. data). Stanley et al. (2005c) documented *C. elgonius* in Kwamgumi Forest Reserve at 300 m at the base of the East Usambara (EU). Near Amani (EU), nine of the 10 specimens collected were in non-forested habitats, eight were taken in tea plantations, and one was found in a swampy area next to a river running between the southwestern section of the EU control site and the tea plantation. The remaining animal was in relatively undisturbed forest in the northeastern section of the EU control site. In the West Usambara (WU), four specimens were trapped in disturbed habitat, including tea and *Eucalyptus*

TABLE 2. Soricomorpha species captured in three seasons of faunal surveys of the East and West Usambara Mountains between 1991 and 1993. Trap success calculated by dividing total captures by total sample-nights (see Stanley et al., this volume).

Species	East Usambara			West Usambara			Total
	1991	1992	1993	1991	1992	1993	
Crocidura elgonius	0	9	1	5	0	0	15
Crocidura fuscomurina	0	1	0	0	0	0	1
Crocidura hildegardeae	2	18	24	0	0	0	44
Crocidura cf. *hirta*	0	30	0	4	0	1	35
Crocidura jacksoni	0	1	0	0	0	0	1
Crocidura cf. *monax*	0	0	0	16	4	0	20
Crocidura olivieri	0	1	1	10	0	0	12
Crocidura tansaniana	2	12	36	0	0	0	50
Crocidura usambarae	0	0	1	0	0	0	1
Suncus megalura	0	1	2	14	3	0	20
Sylvisorex howelli	0	2	0	4	36	22	64
Total no. of individuals	4	75	65	53	43	23	263
Total no. of species	2	9	6	6	3	2	11
Accrued no. of sample-nights	476	8252	2611	5213	1512	499	18,563
Trap success for shrews (%)	0.8	0.9	2.5	1.0	2.8	4.6	1.4

plantations, and one animal was taken in forest at the 37.8-ha site.

ECOLOGY AND REPRODUCTION—In both the East and West Usambara Mountains, only this shrew was captured in tea plantations. Of 15 specimens collected from both massifs, the skulls of 10 were measured (Table 4). In the West Usambara, five specimens were collected in July 1991, which represented 9.4% of the total number of shrews taken that year. Of these, two were female, two were male, and the sex of one was not determined. One male had abdominal testes measuring 4 by 3 mm. One female had small teats, and the other was lactating. All specimens from the East Usambara (captured in the months of July and August in 1992 and 1993) were males; the average testes measurements of examined animals (n = 6) were 3.0 (range = 2–4 mm, SD = 0.6) by 1.8 mm (1–2 mm, 0.4).

REMARKS—External and cranio-dental measurements are given in Tables 3 and 4.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 70—FMNH 151052); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 29—FMNH 149944; PF 31—FMNH 150374); 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 149940–149943, 150373; PF 24—FMNH 149945, 150377); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147194–147196; found dead on the road—FMNH 147351); 14.5 km NW Korogwe, Ambangulu Tea Estate (PF 8—FMNH 147193).

Crocidura fuscomurina (Heuglin, 1865)

DISTRIBUTION—*Crocidura fuscomurina* was described based on a specimen collected in a swampy area at Meshra-el-Req, Sudan. This species has been reported from across much of sub-Saharan Africa. Hutterer (1983) discussed the taxonomy and distribution of this species and cautioned that many references in the literature may involve misidentifications. Hutterer (2005) identifies the known synonyms of this species, including *C. bicolor* Bocage, 1889. Laurie (1971) documented this species (as *C. bicolor*) in Serengeti National Park, and Allen and Loveridge (1942) mentioned specimens from just north of Lindi on the Tanzanian coast. Stanley et al. (2005b) documented *C. fuscomurina* at 1100 m in the Udzungwa Mountains National Park, but it has rarely been recorded in other small mammal surveys in montane habitats of Tanzania (Stanley et al., 1998). However, Oguge et al. (2004) found this species in the Taita Hills (part of the Eastern Arc Mountains) and the Shimba Hills of Kenya.

Our study generated only one specimen, collected in the East Usambara in a pitfall trap on 23 August 1992 in secondary forest dominated by *Maesopsis* trees. Oliver et al. (2002) recorded a specimen, tentatively identified as *C. bicolor* from the Mgambo Forest Reserve, in the northeastern portion of East Usambara at 560 m in open woodland; we have been unable to examine the specimen to verify the species identification.

ECOLOGY AND REPRODUCTION—Information on the ecology of *C. fuscomurina* in Tanzania is limited. The single specimen captured during our study was in a pitfall line in the northeastern section of the EU control site. It was a male found dead and partially eaten by crabs, with the skull damaged. See Table 3 for external measurements. Laurie (1971) found crania and lower jaws of this species in the regurgitated pellets of the Barn Owl (*Tyto alba*) in the Serengeti National Park.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 42—FMNH 150668).

Crocidura hildegardeae Thomas, 1904

DISTRIBUTION—*Crocidura hildegardeae* has been recorded from several areas across eastern and central Africa, including mountains in northern and southern Tanzania. This species has been documented in the North and South Pare Mountains (Stanley et al., 1996, 2007a), Mt. Kilimanjaro (Stanley, unpubl. data), Mt. Meru (Demeter & Hutterer, 1986), and the Udzungwa Mountains (Stanley & Hutterer, 2007) but has not been found during intensive surveys of massifs within the central Eastern Arc Mountains, such as the Nguru, Nguu, Ukaguru, and Uluguru (Stanley et al., 1998; Stanley, unpubl. data). Intensive sampling during the fieldwork of our study found *C. hildegardeae* in the East, but not in the West Usambara, where *Sylvisorex howelli*, a shrew of similar size, was common. Oguge et al. (2004) documented *C. hildegardeae* in many forests of southeastern Kenya, including the Taita Hills.

ECOLOGY AND REPRODUCTION—Forty-four specimens of *C. hildegardeae* were collected in East Usambara over the three years of this study, including two, 18, and 24 individuals in

1991, 1992, and 1993, respectively. The species was generally found in forested habitats. The only animal captured outside of natural forest habitat was in PF 64 (see Stanley et al., this volume), placed at the ecotone between a tea plantation and herbaceous vegetation. It was captured in the same bucket as the rodent *Lophuromys aquilus* (True, 1892). All other *C. hildegardeae* specimens were collected from both disturbed and pristine forested habitats, with 37 of the 43 specimens (86%) coming from the EU control site and six (14%) from one of the fragments (0.2-ha fragment [n = 1], 3.3-ha fragment [n = 1], and 29.4-ha fragment [n = 4]).

In 1992, three females with large teats were captured, neither of the two examined were carrying embryos. All six females captured in 1993 were examined, and three (50%) were pregnant, all with two embryos, one in each uterine horn, and the crown–rump length ranged from 9 to 12 mm (mean = 10.3 mm). In 1991, one male was examined and the testes measured 5 by 4 mm. In 1992, 13 males were inspected and the mean testis measurements were 3.9 (range = 2–5 mm, SD = 0.76) by 2.7 mm (range = 1–5 mm, SD = 0.94). In 1993, 14 males were checked, and the mean testis measurements were 3.9 (range = 2–5 mm, SD = 0.84) by 2.5 mm (range = 1–4 mm, SD = 0.76).

A one-way ANOVA of the cranio-dental measurements of adults indicated males were significantly larger than females in most of the variables (Table 5). A similar pattern of sexual dimorphism was found in this species in the South Pare (Stanley et al., 1996). Hence, we present the external measurements of each sex separately in Table 3.

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 38—149960; PF 39—FMNH 149956; PF 40—FMNH 149954, 150380; PF 41—FMNH 150385; PF 42—FMNH 149953, 149955, 150386; PF 46—FMNH 149957; PF 64—FMNH 151072; PF 65—FMNH 151053, 151075; PF 66—FMNH 151057, 151063, 151074; PF 67—FMNH 151061, 151062; PF 68—FMNH 151058, 151059, 151070, 151071; PF 69—FMNH 151060, 151069, 151073); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 14—FMNH 147197, 147198; PF 33—149950–149952; PF 59—FMNH 151054, 151056, 151067, 151068; PF 60—FMNH 151055, 151065, 151066, 151368; PF 61—FMNH 151064); 6 km NW Amani, Monga Tea Estate (PF 18—FMNH 149947; PF 19—FMNH 149946; PF 26—FMNH 148949; PF 27—FMNH 149948, 149958, 149959).

Crocidura hirta Peters, 1852

Distribution—We tentatively identify the samples listed here as *Crocidura hirta*, although another possible name to apply to the Usambara animals is *C. xantippe* Osgood, 1910, which has also been noted as occurring in the Usambara Mountains (Heim de Balsac & Meester, 1977; Hutterer, 2005). Hutterer (2005) indicated that *C. xantippe* is probably related to *C. hirta*; this is a question that can only be resolved with a series of voucher specimens across a broad geographic range. We have identified specimens as *C. hirta* from sites in other areas of Tanzania (Stanley et al., 1996, 2000, 2005a,b,c, 2007a,b,c). A taxonomic revision of *C. hirta* is needed.

Ecology and Reproduction—Thirty-five specimens referred to *C. hirta* were collected during our study, including 30 from the East and five from the West Usambara Mountains. Most were captured in small forest fragments, in agricultural areas or tea plantations. Only two individuals (6%) were collected in forested areas, in this case, as singletons in the control areas of the East and West Usambara Mountains. Of the remainder, only one (3% of total) was captured in the 29.4-ha East Usambara fragment. In the West Usambara, one and two individuals were trapped in the 0.8- and 1.9-ha fragment, respectively, and one was collected in a *Eucalyptus* plantation. In the East Usambara sites, nine animals were obtained in a tea plantation, three in an agricultural area, and the remainder (16) in forest fragments (all <10 ha in size).

Of the total collected, 34 skulls were aged following Dippenaar (1977); 12 (35%) were juvenile and excluded from analysis of cranio-dental measurements. One skull, the smallest (FMNH 149982), is listed separately in Table 6 and was not included in subsequent analyses. This specimen was captured in the 0.2-ha fragment and is tentatively identified as *C. hirta*. A one-way ANOVA was conducted with the East Usambara sample (the largest) to test for sexual dimorphism in cranial measurements (three females and 13 males), and no significant difference was found. We then combined sexes to test for differences between the samples from the two different mountains, and no significant variation was observed. The descriptive statistics for each external and cranio-dental character measured are given for all samples combined in Tables 3 and 6.

Specimens Examined—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 44—FMNH 149997, 149998, 150006); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 29—FMNH 149984, 150005; PF 31—FMNH 149995); 6 km NW Amani, Monga Tea Estate (PF 16—FMNH 149981, 149988, 150002–150004; PF 17—FMNH 149963, 149964, 149983, 149991, 149992; PF 18—FMNH 149982; PF 19—FMNH 149962, 149966, 149967, 149990; PF 21—FMNH 149965; PF 24—FMNH 149993, 149994; TRL R—FMNH 149989; TRL U—FMNH 149986); 8 km NWN Amani, Bulwa Tea Estate (PF 34—FMNH 150378; PF 36—FMNH 149985; PF 37—FMNH 149987, 149996); **WEST USAMBARA**, 11 km NW Korogwe, Ambangulu Tea Estate (PF 12—FMNH 147359; PF 13—FMNH 147212, 147214; TRL L—FMNH 147213); 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 73—FMNH 151099).

Crocidura jacksoni Thomas, 1904

Distribution—Oguge et al. (2008) include the eastern section of the Democratic Republic of the Congo, Uganda, Kenya, and northern Tanzania in the known distribution of *Crocidura jacksoni*. In Kenya, this species has been documented in the Taita Hills (the northern-most range of the Eastern Arc Mountains), including Mt. Sagala and Mt. Kasigau from elevations ranging from 1300 to 2200 m (Oguge et al., 2004). Similar trapping efforts during the study of Oguge and colleagues did not capture *C. jacksoni* in the volcanic Kyulu Hills, roughly 80 km to the northwest of the Taita Hills. Aggundey and Schlitter (1986) listed a variety of localities across Kenya with voucher specimens of this taxon. Within Tanzania, documented occurrences are few but include specimens from the Tarangire National Park (Stanley et al., 2007c).

Within the Usambara forests, Cunneyworth et al. (1997) report the capture of *C. jacksoni* at the southern edge of Kambai Forest Reserve, a lowland site (about 600 m) with grassy understory. However, no indication was given about the collection of a voucher specimen, which is needed to verify this record.

Ecology and Reproduction—One female specimen was collected on 30 July 1992 in a clump of bamboo in a marshy

TABLE 3. External measurements (mm) and weight (g) of adult shrew and elephant shrew species collected during the 1991–1993 surveys of the East (EU) and West Usambara (WU) Mountains, including total length (TL), head and body length (HB), length of tail vertebrae (TV), hind foot length (HF), ear length (EAR), and weight (WT). Measurements taken by S.M.G. are presented separately from those of W.T.S. (see Stanley et al., this volume). Within these subsets, measurements were subjected to a one-way ANOVA to test for effect of sex or locality (mountain range). If not significant, the samples were pooled to derive the summary statistics. Descriptive statistics are presented as mean ± standard deviation, range, and (sample size).

Species	TL	HB	TV	HF	EAR	WT
Crocidura elgonius EU and WU						
S.M.G.						
Mean ± SD	99.0 ± 5.55	55.8 ± 2.50	39.9 ± 3.48	9.4 ± 0.52	7.1 ± 0.83	3.4 ± 0.41
Range	91–107	53–59	35–45	9–10	6–8	2.5–3.8
n	8	4	8	8	8	8
W.T.S.						
Mean ± SD	92.0 ± 4.64	55.4 ± 3.29	36.2 ± 1.79	10.0 ± 0.71	7.6 ± 0.55	3.3 ± 0.50
Range	86–99	51–59	33–38	9–11	7–8	2.8–4.1
n	5	5	5	5	5	5
Crocidura fuscomurina EU						
S.M.G.	119	73	45	12	—	5.1
Crocidura hildegardeae EU						
S.M.G. females	122	76	49	12	9	5.9
S.M.G. males						
Mean ± SD	123.2 ± 5.04	73.2 ± 5.09	49.3 ± 2.89	12.8 ± 1.77	9.2 ± 0.65	6.8 ± 0.93
Range	109–129	63–81	44–54	8–17	8–10	5.5–8.8
n	18	15	18	18	18	18
W.T.S. Females						
Mean ± SD	116.1 ± 4.85	69.9 ± 5.96	44.4 ± 1.81	12.3 ± 0.46	8.5 ± 0.53	6.1 ± 0.92
Range	108–123	60–77	43–47	12–13	8–19	4.3–7
n	7	8	7	8	8	8
W.T.S. Males						
Mean ± SD	118.2 ± 5.66	71.9 ± 5.23	46.4 ± 3.20	13.1 ± 0.75	8.8 ± 0.66	6.7 ± 1.20
Range	105–126	60–78	37–51	12–14	8–10	4.8–8.7
n	17	17	17	17	17	17
Crocidura hirta EU and WU						
S.M.G.						
Mean ± SD	151.6 ± 13.71	82.1 ± 8.57	62.9 ± 5.29	15.1 ± 1.35	10.4 ± 1.11	10.8 ± 3.11
Range	125–176	66–95	55–72	12–18	8–12	6.1–14.5
n	14	10	14	14	14	14
W.T.S.						
Mean ± SD	147.5 ± 10.00	86.1 ± 6.54	60.9 ± 4.13	15.5 ± 0.98	10.0 ± 0.80	10.9 ± 2.79
Range	127–163	75–98	50–67	14–17	9–11	5.9–14.5
n	20	20	20	20	14	21
Crocidura jacksoni EU						
S.M.G.	147	85	65	15	5	8
Crocidura monax WU						
S.M.G.						
Mean ± SD	159.8 ± 5.84	–	65.7 ± 3.07	16.2 ± 0.73	10.4 ± 0.65	13.9 ± 1.55
Range	150–170		60–71	15–17	9.5–12	10–16.5
n	16		18	18	17	17
W.T.S.						
Mean ± SD	158.5 ± 2.12	–	64.5 ± 2.12	17.0 ± 0.00	10.0 ± 0.00	12.3 ± 0.35
Range	157–160		63–66	17–17	10–10	12–12.5
n	2		2	2	2	2
Crocidura olivieri EU and WU						
S.M.G.						
Mean ± SD	210.9 ± 9.47	113	88.8 ± 4.97	21.1 ± 1.24	11.6 ± 0.92	32.1 ± 7.56
Range	195–224		80–98	19–23	10–13	23.5–45
n	12		12	12	11	12
Crocidura tansaniana						
S.M.G.						
Mean ± SD	167.2 ± 8.52	98.7 ± 5.62	68.8 ± 4.53	16.3 ± 0.74	12.0 ± 1.33	14.6 ± 2.09
Range	151–184	87–110	60–76	15–18	8–14	9.5–20
n	26	18	26	26	26	26
W.T.S.						
Mean ± SD	160.4 ± 11.26	93.5 ± 8.32	67.6 ± 4.70	17.2 ± 0.87	10.7 ± 0.79	14.6 ± 3.02
Range	130–176	73–105	54–75	15–19	9–12	6.6–20
n	25	25	25	25	25	25

TABLE 3. *Continued.*

Species	TL	HB	TV	HF	EAR	WT
Crocidura usambarae EU						
W.T.S. EU	145	84	61	15	10	8.5
Suncus megalura EU & WU						
S.M.G.						
Mean ± SD	165.7 ± 5.46	69.5 ± 3.54	91.7 ± 4.08	15.8 ± 0.66	10.3 ± 1.60	6.2 ± 0.57
Range	157–181	67–72	81–101	15–17	9–16	5–7.5
n	16	2	16	16	16	16
W.T.S.						
Mean ± SD	161.0 ± 4.32	70.8 ± 2.75	92.0 ± 2.16	16.0 ± 0.00	9.5 ± 0.58	6.0 ± 0.97
Range	157–167	68–74	89–94	16–16	9–10	5.2–7.4
n	4	4	4	4	4	4
Sylvisorex howelli EU						
S.M.G.	103	61	45	11	8	3.3
W.T.S.	98	52	41	10	8	3.5
Sylvisorex howelli WU						
S.M.G.						
Mean ± SD	106.2 ± 3.61	65.1 ± 2.56	43.4 ± 2.23	11.1 ± 0.54	8.5 ± 0.65	3.9 ± 0.52
Range	100–112	61–72	39–48	10–13	7.5–10	2.5–5
n	21	21	21	22	22	21
W.T.S.						
Mean ± SD	101.8 ± 5.10	60.6 ± 4.41	40.7 ± 2.17	11.0 ± 0.54	8.3 ± 0.71	3.8 ± 0.36
Range	91–111	52–68	36–46	9–12	8–12	2.9–4.6
n	42	42	42	42	42	42
Petrodromus tetradactylus EU						
S.M.G.	380	—	175	56	37	197

area next to a man-made pond below the Monga Tea Estate factory. The specimen was partially consumed by ants, with damage to the ears (Table 3).

REMARKS—Oguge et al. (2008) mentioned that the species is relatively common and widespread in some portions of its range, without referring to specific localities. Our trapping results in the montane forests of the Usambara Mountains indicate that it is notably uncommon, with the only record being from the East Usambara.

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL W—FMNH 150606).

***Crocidura monax* Thomas, 1910**

DISTRIBUTION—*Crocidura monax* was described from specimens collected on Mt. Kilimanjaro, to the northwest of the Usambara Mountains, and few details are known concerning its geographical range. Burgess et al. (2000) considered this taxon to be restricted to Mt. Kilimanjaro. We trapped this species only on the West Usambara. Conversely, we collected a similarly sized species, *C. tansaniana*, only on the East Usambara. Stanley et al. (1998) tentatively identified medium-sized shrews (10–17 g) obtained during surveys of other

TABLE 4. Cranio-dental measurements of *Crocidura elgonius* from the East and West Usambara Mountains with results of a one-way ANOVA to test for significant differences between mountains.

Measurement	East Usambara (n = 6)		West Usambara (n = 4)		F	P
	Mean ± SD	Range	Mean ± SD	Range		
CI	16.1 ± 0.31	15.6–16.5	15.9 ± 0.12	15.8–16.0	1.21	0.30
BL	14.4 ± 0.32	13.9–14.8	14.2 ± 0.09	14.2–14.3	0.68	0.43
PPL	7.3 ± 0.19	7.1–7.6	7.3 ± 0.05	7.2–7.3	0.38	0.55
UTR	6.8 ± 0.16	6.5–6.9	6.7 ± 0.02	6.6–6.7	1.55	0.24
LIW	3.3 ± 0.09	3.2–3.4	3.4 ± 0.08	3.3–3.5	0.34	0.58
BW	4.7 ± 0.12	4.6–4.9	4.7 ± 0.08	4.6–4.8	0.06	0.82
NW	1.4 ± 0.07	1.3–1.5	1.4 ± 0.09	1.2–1.4	0.91	0.37
GW	7.1 ± 0.13	6.9–7.3	7.1 ± 0.14	6.9–7.3	0.24	0.64
HBC	4.6 ± 0.43	4.1–5.3	4.4 ± 0.20	4.3–4.7	0.40	0.54
I3W	0.5 ± 0.02	0.5–0.5	0.5 ± 0.02	0.4–0.5	4.56	0.06
CW	0.5 ± 0.02	0.5–0.5	0.5 ± 0.03	0.5–0.5	0.47	0.51
M3L	0.9 ± 0.05	0.9–1.0	0.9 ± 0.06	0.8–1.0	0.70	0.42
M3W	0.4 ± 0.04	0.4–0.5	0.4 ± 0.03	0.4–0.4	2.02	0.19
Mast	0.6 ± 0.06	0.5–0.7	0.7 ± 0.05	0.7–0.8	4.23	0.07
MI	9.4 ± 0.23	9.0–9.6	9.3 ± 0.14	9.2–9.5	0.57	0.47
LTR	6.3 ± 0.14	6.1–6.4	6.2 ± 0.03	6.1–6.2	1.15	0.32

TABLE 5. Cranio-dental measurements of male and female *Crocidura hildegardeae* from the East Usambara with results of a one-way ANOVA to test for significant differences between sexes.

Measurement	Females (n = 6)		Males (n = 25)		F
	Mean ± SD	Range	Mean ± SD	Range	
CI	18.5 ± 0.29	18.0–18.8	19.2 ± 0.36	18.1–19.6	22.8***
BL	16.7 ± 0.23	16.4–17.1	17.3 ± 0.31	16.4–17.8	19.9***
PPL	8.4 ± 0.17	8.2–8.7	8.7 ± 0.19	8.2–9.0	12.4**
UTR	7.9 ± 0.13	7.8–8.1	8.2 ± 0.13	7.9–8.4	22.7***
LIW	3.9 ± 0.03	3.9–3.9	4.0 ± 0.11	3.8–4.2	2.8
BW	5.7 ± 0.08	5.6–5.8	5.8 ± 0.13	5.5–6.1	4.5*
NW	1.5 ± 0.06	1.4–1.6	1.6 ± 0.06	1.4–1.7	1.5
GW	8.6 ± 0.15	8.4–8.7	8.8 ± 0.15	8.4–9.1	9.7**
HBC	5.5 ± 0.19	5.3–5.8	5.6 ± 0.16	5.2–5.9	1.2
I3W	0.6 ± 0.02	0.5–0.6	0.6 ± 0.02	0.5–0.6	5.8*
CW	0.6 ± 0.02	0.6–0.6	0.6 ± 0.02	0.6–0.7	4.1
M3L	1.2 ± 0.02	1.2–1.2	1.2 ± 0.04	1.2–1.3	0.9
M3W	0.6 ± 0.02	0.5–0.6	0.6 ± 0.03	0.6–0.7	5.2*
Mast	0.9 ± 0.08	0.9–0.6	1.0 ± 0.11	0.7–1.2	0.3
MI	11.2 ± 0.10	11.0–11.3	11.6 ± 0.22	11.0–12.0	21.4***
LTR	7.3 ± 0.13	7.1–7.5	7.5 ± 0.12	7.3–7.7	17.3***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

montane habitats in Tanzania as *C. monax*, pending a thorough analysis of this material with specimens from the type locality.

ECOLOGY AND REPRODUCTION—Sixteen specimens were collected in 1991 (12 males and four females) and four males in 1992. One female was examined for reproductive activity and was nulliparous. From the 1991 and 1992 collections, the reproductive condition of four males was examined each year. In 1991, the average testis measurement was 4.2 mm (range = 4–5 mm) by 3.0 mm (2–4 mm) and in 1992, 5.2 mm (3–6 mm) by 3.0 mm (2–4 mm). All the specimens, except two, came from the WU control site and the balance from the 37.8-ha and 1.5-ha fragments of that massif.

REMARKS—A one-way ANOVA found no significant difference between sexes in cranio-dental measurements. Hence, the sexes were pooled to compare cranio-dental differences between specimens from the West Usambara and those recently collected from Mt. Kilimanjaro. In all but three measurements (post-palatal length, least interorbital width, and height of the braincase), the West Usambara sample was significantly larger than that from Mt. Kilimanjaro (Table 7). The taxonomic implications of these differences are under study, including samples of "*monax*" from other mountains in Tanzania (see Remarks under *C. tansaniana*).

SPECIMENS EXAMINED—**WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 1—FMNH 147205, 147206, 147352; PF 2—FMNH 147354; PF 5—FMNH 147204, 147207–147209, 147356–147358; PF 48—FMNH 149979, 149980; PF 49—FMNH 149999; PF 53—FMNH 150000; TRL B—FMNH 147355; TRL H—FMNH 147353; TRL J—FMNH 147203, 147376); 14.5 km NW Korogwe, Ambangulu Tea Estate (PF 7—FMNH 147210).

Crocidura olivieri (Lesson, 1827)

DISTRIBUTION—*Crocidura olivieri* is distributed from Egypt to South Africa, and this large-bodied shrew (average weight 35 g) is found in various habitats across its range. Within eastern Africa, *C. olivieri* has been reported from numerous sites, including the Taita Hills, Mt. Kilimanjaro, and the South Pare, North Pare, Nguru, Nguu, Uluguru, Ukaguru, Udzungwa, Rungwe, and Mahale Mountains (Stanley et al., 1996, 1998, 2007b; Oguge et al., 2004; Stanley & Hutterer, 2007). Cunneyworth et al. (1997) captured this species in Kambai Forest Reserve, between 500 and 800 m, on the East Usambara.

ECOLOGY AND REPRODUCTION—We collected 12 specimens of *C. olivieri* in the Usambaras, with 10 (83%) at West Usambara sites—six were taken in the WU control and two in the 37.8-ha and one each in the 1.9-ha and 1.5-ha fragments. The two specimens from the East Usambara were taken in the EU control site. Singleton females from each mountain were examined for reproductive condition; neither was pregnant. One male collected 5 August 1992 had testes that measured 6 by 4 mm with convoluted epididymides. Three males from the

TABLE 6. Cranio-dental measurements of *Crocidura hirta* from the East and West Usambara Mountains. FMNH 149982 is listed separately (see text).

Measurement	*C. hirta* (n = 21)		FMNH 149982
	Mean ± SD	Range	
CI	22.8 ± 0.46	21.7–23.9	20.4
BL	20.6 ± 0.44	19.6–21.6	18.8
PPL	10.0 ± 0.27	9.5–10.5	9.5
UTRL	9.9 ± 0.23	9.3–10.5	8.9
LIW	4.7 ± 0.15	4.4–5.0	4.4
BW	7.0 ± 1.80	6.7–7.3	6.6
NW	1.9 ± 0.12	1.7–2.2	1.9
GW	9.8 ± 0.28	9.4–10.7	9.2
PMH	6.2 ± 0.21	5.9–6.7	5.7
PGW	6.8 ± 0.19	6.6–7.2	6.2
M&I	13.9 ± 0.37	13.2–14.9	12.6
LTR	9.1 ± 0.23	8.6–9.7	8.3
I3W	0.80 ± 0.06	0.7–1.0	0.7
CW	0.80 ± 0.06	0.7–1.0	0.7
M3L	1.5 ± 0.09	1.4–1.7	1.4
M3W	0.7 ± 0.05	0.6–0.9	0.6
MAST	1.1 ± 0.12	0.9–1.4	0.8

TABLE 7. Comparison of cranio-dental measurements between samples of *Crocidura monax* from Mt. Kilimanjaro and the West Usambara, with results of a one-way ANOVA to test for significant differences between localities.

	Mt. Kilimanjaro (n = 54)		West Usambara (n = 18)		F
	Mean ± SD	Range	Mean ± SD	Range	
CI	23.2 ± 0.48	22.3–24.1	23.7 ± 0.46	22.9–24.7	11.084**
BL	21.0 ± 0.43	20.3–21.9	21.4 ± 0.44	20.8–22.4	8.844**
PPL	10.6 ± 0.24	10.0–11.1	10.6 ± 0.28	10.0–11.1	1.101
UTRL	10.2 ± 0.20	9.7–10.6	10.5 ± 0.23	10.0–11.0	20.458***
LIW	5.2 ± 0.14	4.8–5.5	5.1 ± 0.19	4.6–5.4	0.590
BW	7.1 ± 0.13	6.8–7.3	7.3 ± 0.16	7.1–7.6	59.597***
NW	1.9 ± 0.10	1.6–2.1	2.1 ± 0.11	1.8–2.3	51.505***
GW	10.4 ± 0.25	9.9–11.0	10.6 ± 0.29	10.0–11.0	6.109*
PMH	7.0 ± 0.32	6.4–8.0	6.9 ± 0.25	6.3–7.4	1.434
M&I	14.8 ± 0.35	14.0–15.5	15.0 ± 0.42	14.0–15.7	5.178*
LTR	9.5 ± 0.18	9.0–9.8	9.7 ± 0.24	9.1–10.3	13.907***
I3W	0.80 ± 0.03	0.71–0.87	0.96 ± 0.05	0.80–1.02	243.089***
CW	0.90 ± 0.04	0.80–0.97	1.00 ± 0.06	0.80–1.05	65.281***
M3L	1.57 ± 0.06	1.44–1.69	1.71 ± 0.06	1.59–1.79	72.453***
M3W	0.84 ± 0.04	0.74–0.95	0.87 ± 0.06	0.75–0.98	6.547*
MAST	1.00 ± 0.11	0.75–1.31	1.19 ± 0.09	1.06–1.40	40.712***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

West Usambara sites (all collected in July) were examined: the testes ranged from 2 to 6 by 3 to 4 mm, and only one had convoluted epididymides. See Table 3 for external measurements.

No significant morphological variation was found between samples from the East and West Usambara Mountains. This species is the largest shrew in Tanzania and one of the largest in Africa. Although we have no direct evidence, we strongly suspect that it is able, on occasion, to climb out of our 15-liter pit-fall buckets. Hence, we do not include this species in comparisons of pitfall results among forest fragments.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site (TRL X—FMNH 149968; TRL AO—FMNH 151101). **WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 1—FMNH 147199; PF 3—FMNH 147361; PF 5—FMNH 147362, 147363; TRL A—FMNH 147200, 147201); 14.5 km NW Korogwe, Ambangulu Tea Estate (TRL C—FMNH 147364, 147365); 11 km NW Korogwe, Ambangulu Tea Estate (TRL D—FMNH 147202; TRL E—FMNH 147366).

Crocidura tansaniana Hutterer, 1986

DISTRIBUTION—*Crocidura tansaniana* was described based on a specimen collected near Amani, East Usambara (Hutterer, 1986). This species was quite common in the forests we sampled in the East Usambara, but, during our study, it was not documented in the West Usambara. *Crocidura monax*, which is similar in size (10–20 g) to *C. tansaniana*, was common in the West Usambara forests (see under that taxon).

ECOLOGY AND REPRODUCTION—Between 1991 and 1993, 50 specimens were collected comprising 20 females and 30 males, including two males in 1991, three females and nine males in 1992, and 17 females and 18 males in 1993. The higher number of captures of this species in 1993 may reflect more extensive sampling effort in the northeastern and southwestern portions of the EU control site, where most specimens were collected. The only exception was an animal obtained in the 3.3-ha fragment near Monga. Of 102 shrews trapped between 1991 and 1993 at the EU control site, 48 were *C. tansaniana* (47%). There were yearly fluctuations in the number of *C. tansaniana* captured relative to other shrew species—in 1991, four of eight shrews obtained were *C. tansaniana,* and the other half were *C. hildegardeae*; in 1992, *C. tansaniana* made up 35% of the shrews captured (12/34); and in 1993, *C. tansaniana* constituted 55% of the shrews trapped (35/64). In 1993, 12 of the 35 *C. tansaniana* specimens (34%) came from one pitfall line (PF 69). This line was installed in primary forest in the southeastern portion of the EU control site and was positioned across a valley where the soil was very fine and clay-like.

Of the 18 males examined over the three-year study for reproductive condition, the average testis measurements were 4.4 mm (range = 3–6 mm) by 2.4 mm (1.5–4 mm). Measurements of examined males for each year include: 1991, one with testes 6 by 4 mm; 1992, seven males with mean measurements of 4.3 by 2.1 mm; and 1993, nine males with mean measurements of 4.6 by 2.6 mm. In 1992, two females were examined: one was pregnant with a single embryo in each uterine horn and the largest embryo measuring 14 mm in crown–rump length. In 1993, 11 females were dissected, and only a single animal was pregnant, with one embryo in each uterine horn and the largest embryo measuring 8 mm in crown–rump length. Over the two years, 17 females were examined for teat condition—eight were noted as small, seven large, and two lactating.

REMARKS—Hutterer (1986) considered *C. tansaniana* to be part of the *C. monax* group but differentiated the former from *C. monax* sensu stricto in being larger, with a more robust skull, and a more prominent third upper molar; no statistical comparisons of these parameters were presented in his description. With the increased sample sizes associated with our inventories, including new material of *C. monax* from Mt. Kilimanjaro (type locality), such statistical comparisons are now possible. A one-way ANOVA found few significant differences between sexes in cranio-dental characters for *C. monax* from Mt. Kilimanjaro (16 females, 48 males) and for *C. tansaniana* (12 females, 15 males); the significant values were for nasal width and mastoid plate, which may be best allocated

TABLE 8. Comparison of cranio-dental measurements between samples of *Crocidura monax* from Mt. Kilimanjaro and West Usambara and *C. tansaniana* from East Usambara, with results of a one-way ANOVA to test for significant differences among localities.

	KILI			WU			EU			F
	Mean ± SD	Range	n	Mean ± SD	Range	n	Mean ± SD	Range	n	
CI	23.2 ± 0.48	22.3–24.1	54	23.7 ± 0.46	22.9–24.7	18	25.1 ± 0.48	23.8–26.1	35	164.1**
BL	21.0 ± 0.43	20.3–21.9	54	21.4 ± 0.44	20.8–22.4	18	22.8 ± 0.41	21.8–23.5	35	193.1**
PPL	10.6 ± 0.24	10.0–11.1	54	10.6 ± 0.28	10.0–11.1	18	11.4 ± 0.27	10.9–12.1	36	124.5**
UTRL	10.2 ± 0.20	9.7–10.6	54	10.5 ± 0.23	10.0–11.0	18	11.1 ± 0.21	10.7–11.5	36	192.7**
LIW	5.2 ± 0.14	4.8–5.5	54	5.1 ± 0.19	4.6–5.4	18	5.4 ± 0.23	5.0–6.0	37	29.7**
BW	7.1 ± 0.13	6.8–7.3	54	7.3 ± 0.16	7.1–7.6	18	7.7 ± 0.19	7.2–8.0	37	165.2**
NW	1.9 ± 0.10	1.6–2.1	54	2.1 ± 0.11	1.8–2.3	18	2.2 ± 0.10	2.0–2.4	35	91.0**
GW	10.4 ± 0.25	9.9–11.0	54	10.6 ± 0.29	10.0–11.0	18	10.9 ± 0.28	10.3–11.6	36	38.7**
PMH	7.0 ± 0.32	6.4–8.0	54	6.9 ± 0.25	6.3–7.4	18	7.0 ± 0.20	6.6–7.5	36	0.9
M&I	14.8 ± 0.35	14.0–15.5	54	15.0 ± 0.42	14.0–15.7	18	16.0 ± 0.32	15.2–16.7	37	136.1**
LTR	9.5 ± 0.18	9.0–9.8	54	9.7 ± 0.24	9.1–10.3	18	10.3 ± 0.18	9.9–10.7	37	183.2**
I3W	0.80 ± 0.03	0.71–0.87	54	0.96 ± 0.05	0.80–1.02	18	0.98 ± 0.04	0.90–1.07	37	281.7**
CW	0.90 ± 0.04	0.80–0.97	54	1.00 ± 0.06	0.80–1.05	18	1.01 ± 0.04	0.93–1.10	37	86.4**
M3L	1.57 ± 0.06	1.44–1.69	54	1.71 ± 0.06	1.59–1.79	18	1.71 ± 0.06	1.60–1.93	37	73.4**
M3W	0.84 ± 0.04	0.74–0.95	54	0.87 ± 0.06	0.75–0.98	18	0.86 ± 0.05	0.74–0.97	37	4.3*
MAST	1.00 ± 0.11	0.75–1.31	54	1.19 ± 0.09	1.06–1.40	18	1.23 ± 0.12	0.90–1.42	36*	50.8**

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

to type II error. Hence, in both species the sexes were pooled for comparisons between the East Usambara (*C. tansaniana*) and the West Usambara/Mt. Kilimanjaro (*C. monax*). As noted above (see account of *C. monax*), animals from the West Usambara are significantly larger in most cranial dimensions than those from Mt. Kilimanjaro.

Table 8 lists the summary statistics of cranio-dental measurements for each of the three localities (East and West Usambaras and Mt. Kilimanjaro) and the F values for a one-way ANOVA to test for significant differences among populations. F values used to test the null hypothesis of no significant difference among the three localities were all highly significant (Table 8), with the greatest amount of morphological heterogeneity exhibited by characters of the upper toothrow and individual teeth. The highest F value exhibited was for the width of the third upper incisor (I^3-W). *Crocidura tansaniana* was the largest in every character measured, except width of the third upper molar (M^3W), which, for the West Usambara population of *C. monax,* was slightly larger. Hutterer's (1986) appreciation for the more robust nature of the skull in *C. tansaniana* was borne out in our analyses. The taxonomic implications of these observations are currently being examined using samples of *C.* cf. *monax* from other Tanzanian montane localities (Stanley, unpubl. data).

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (PF 19—FMNH 149961); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 14—FMNH 147211, 147360; PF 31—FMNH 149976; PF 32—149969, 149971, 149972, 150375; PF 33—FMNH 149970; PF 58—FMNH 151106, 151108, 151376, 151380; PF 60—FMNH 151124; PF 61—FMNH 151121; PF 62—FMNH 151109, 151110, 151379, 151382; PF 63—FMNH 151107, 151123, 151125, 151377, 151378, 151381; TRL AO—FMNH 151111, 151120, 151122); 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 39—FMNH 149973; PF 42—FMNH 149974, 149975, 149978; PF 46—FMNH 149977; PF 65—FMNH 151112; PF 67—FMNH 151113, 151127; PF 68—FMNH 151132; PF 69—FMNH 151114–151116, 151118, 151119, 151126, 151128–151131, 151133, 151134; TRL AG—FMNH 150376; TRL AP—FMNH 151117).

Crocidura usambarae Dippenaar, 1980

DISTRIBUTION—*Crocidura usambarae* was described by Dippenaar (1980) based on specimens collected in the Shume and Magamba Forest Reserves of the West Usambara Massif, in the elevational range of 1580–1830 m. Two specimens without skulls from the Ngozi Crater, Poroto Mountains, in the Southern Highlands of Tanzania were tentatively referred to this species by Dippenaar (1980) based on pelage. The presence of this species in the Southern Highlands needs to be confirmed.

ECOLOGY AND REPRODUCTION—The type locality for *C. usambarae* is the West Usambara, in a zone between 1580 and 1830 m. During our study of small mammals of this massif, working sites between 1170 and 1300 m, we did not trap a single individual of this species during an accrued 7224 sample-nights. The only specimen we obtained was at 1050 m in the East Usambara, based on 11,339 sample-nights. This may be associated with this species' apparent preference for higher elevations. Stanley et al. (1996) documented more than twice as many individuals of this taxon at 2000 m than at 1100 m in the Chome Forest Reserve of the South Pare Massif, a site about 80 km from the holotype locality and separated by a valley descending to 400 m. The East Usambara specimen was taken in an overgrown agricultural area between a tea plantation and a stream running along the edge of the southeastern portion of the EU control area. It was a nulliparous sub-adult female.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 70—FMNH 151135).

Suncus megalura (Jentink, 1888)

DISTRIBUTION—*Suncus megalura* is found throughout tropical Africa, including savannah habitats (Hutterer, 2005). Oguge et al. (2004) documented this species at 2200 m in the

TABLE 9. Testis length and width for *Sylvisorex howelli* captured in the West Usambara between 1991 and 1993.

		1992 (n = 17)		1993 (n = 11)		Total (n = 29)	
	1991 (n = 1)	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Testes length (mm)	5	3.6 ± 0.50	3–4	3.6 ± 0.44	3–4	3.6 ± 0.53	3–5
Testes width (mm)	3	2.2 ± 0.39	2–3	2.0 ± 0.00	2–2	2.1 ± 0.35	2–3

isolated Mbololo Massif of the Taita Hills, but did not find it in other forests of that Kenyan mountain range.

ECOLOGY AND REPRODUCTION—Hutterer (2005) stated that this species is common at forest edges and in forested savannas. Our data support these habitat preferences, in that most specimens were captured in thick vegetation at the ecotone between forest and agricultural land. Only male *S. megalura* were trapped in the East Usambara (n = 3), and 12 of the 17 individuals collected in the West Usambara were male. Of the remaining five specimens, four were female and the sex of one was not determined. Three of the females were examined for reproductive condition; two were pregnant, each with a single embryo and crown–rump lengths of 16 mm (25 July 1991) and 3 mm (29 August 1992).

SPECIMENS EXAMINED—**EAST USAMBARA**, 6 km NW Amani, Monga Tea Estate (TRL W—FMNH 150379); 4.5 km WNW Amani, Monga Tea Estate, EU control site (PF 62—FMNH 151156); 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 70—FMNH 151157); **WEST USAMBARA**, 14.5 km NW Korogwe, Ambangulu Tea Estate (PF 6—FMNH 147373); 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 1—FMNH 147188, 147189, 147367–147369, 147372; PF 2—FMNH 147371; PF 3—FMNH 147190, 147390; PF 48—FMNH 150037–150039); 11 km NW Korogwe, Ambangulu Tea Estate (PF 10—FMNH 147191, 147374; PF 13—FMNH 147192, 147375).

Sylvisorex howelli **Jenkins, 1984**

DISTRIBUTION—Jenkins (1984) described *Sylvisorex howelli* based on specimens obtained in the Uluguru Mountains. Subsequently, Hutterer (1986) named the subspecies *S. h. usambarae* from the West Usambara. Stanley et al. (1998), Stanley and Olson (2005), and Stanley (unpubl. data) added five massifs to the known distribution of this shrew, endemic to the Eastern Arc—East Usambara, Nguru, Ukaguru, Nguu, and Rubeho Mountains. Thus, *S. howelli* is found only in the center massifs of the Eastern Arc Mountains. Even after extensive small mammal surveys with pitfall lines in the South and North Pare Mountains, the Udzungwa Mountains, and the Southern Highlands (Stanley et al., 1996, 2005b, 2007b; Stanley & Hutterer, 2007; Stanley, unpubl. data), this species is unknown south of the Ruaha River and north of the West Usambara.

ECOLOGY AND REPRODUCTION—*Sylvisorex howelli* has only been found in montane forests. In most cases, this species is among the most commonly collected shrews during faunal inventories (Stanley & Olson, 2005; Stanley, unpubl. data)—for example, 66.0% of the total trapped shrews in the West Usambara Mountains between 1991 and 1993. In contrast, two individuals of this species (1.4% of total shrews captured) were captured in the East Usambara over this three-year study. The ratio of females to males in the West Usambara was 2/2, 14/22, and 8/14, for 1991, 1992, and 1993, respectively. Of 16 females examined over three years, only one obtained in 1992 was pregnant, with a single embryo in each uterine horn, the largest of which had a crown–rump length of 3 mm. Table 9 reports testis measurements of *S. howelli*.

REMARKS—Stanley and Olson (2005) found that specimens from the East Usambara were smaller than those from the West Usambara, Nguru, Nguu, Uluguru, and Ukaguru Mountains. This pattern was not concordant in the concomitant molecular study based on mitochondrial DNA. The genetic data indicate that the East and West Usambara populations are sister groups, relative to all other Eastern Arc Mountain populations. Stanley and Olson (2005) hypothesized that the co-occurrence of *S. howelli* and the similar sized *Crocidura hildegardeae* in the East Usambara caused character displacement that led to smaller skulls in the local population of *S. howelli*.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km ESE Amani, Monga Tea Estate, EU control site (PF 40—FMNH 150023; PF 45—FMNH 150008); **WEST USAMBARA,** 12.5 km NW Korogwe, Ambangulu Tea Estate (PF 5—FMNH 147184–147187; PF 49—FMNH 150009, 150013, 150018, 150026, 150032, 150034, 150035; PF 50—FMNH 150001, 150010, 150016, 150017, 150020, 150021, 150031, 150033, 150036, 150382, 150383; PF 51—FMNH 150011, 150012, 150014, 150015, 150019, 150024, 150025, 150381, 150384; PF 52—FMNH 150007, 150022, 150027–150029, 150387–150389; PF 53—FMNH 150030; PF 71—151144, 151151, 151387; PF 72—FMNH 151139, 151145, 151146, 151148, 151152, 151155; PF 73—151141, 151143, 151147, 151153, 151383, 151385, 151386; PF 74—FMNH 151140, 151142, 151149, 151150, 151154, 151384).

Macroscelididae

Petrodromus tetradactylus **Peters, 1846**

DISTRIBUTION—The genus *Petrodromus* is represented by a single species, *P. tetradactylus*, and is distributed from southeastern Kenya to northeastern South Africa (Schlitter, 2005). Kingdon (1974) lists two subspecies occurring in Tanzania: *rovumae* and *tetradactylus*. In contrast, Jennings and Rathbun (2001) list three subspecies for the country—*rovumae*, *sultan*, and *zanzibaricus*—and illustrate a zone of overlap and possible hybridization between *P. t. sultan* and *P. t. rovumae* in northeastern Tanzania. Pelage characteristics identify the specimen collected during this study as *P. t. sultan*. Specifically, the reddish-brown dorsal stripe is clearly defined, distinct from the more lateral gray pelage, and the mid-ventral caudal bristles are long (4–5 mm) and all knobbed (Corbet & Neal, 1965).

ECOLOGY AND REPRODUCTION—This species is typically associated with dense vegetation, in both xeric and mesic habitats. In montane areas, *P. tetradactylus* is restricted to drier forests and is not found above approximately 1400 m (Jennings & Rathbun, 2001). It is often sympatric with the macroscelidid *Rhynchocyon petersi* Bocage, 1880, and we found both species in sympatry in the East Usambara. One female *P. tetradactylus* was collected 6 August 1993 at 0930 h at the edge of the northeastern portion of the EU control site and in the ecotone between forest and tea plantation. External measurements are given in Table 3.

REMARKS—Field workers from Frontier-Tanzania obtained a female (FMNH 182578) and a skull (FMNH 187089) 24 October 1996 in the Kwamgumi Forest Reserve, a lowland forest at 300 m near the base of the East Usambara Mountains and approximately 25 km NE of Amani (Doggart et al., 1999). N. J. Cordeiro collected a female and a male in the Bombo East I Forest Reserve at approximately 400 m between 17 and 21 September 1996 (FMNH 163412, 163413). These specimens also possess the knobbed long bristles on the ventral side of the tail and distinct dorsal brown stripe of *P. t. sultan*.

SPECIMENS EXAMINED—**EAST USAMBARA**, 4.5 km WNW Amani, Monga Tea Estate, EU control site (collected by hand—FMNH 151459).

Rhynchocyon petersi Bocage, 1880

DISTRIBUTION—The genus *Rhynchocyon* is more restricted in its distribution than the often-sympatric genus *Petrodromus*. *Rhynchocyon petersi* is documented from various localities across northeastern Tanzania, including the Nguru, East and West Usambara, and North and South Pare Mountains (Stanley et al., 1996, 2007b; Stanley, unpubl. data).

ECOLOGY AND REPRODUCTION—Although *R. petersi* was not directly observed during the Usambara Mountain surveys of 1991–1993, a male was found dead in 1996 by W. D. Newmark in a snare set near the site of trap line A in the WU control area.

REMARKS—Field workers from Frontier-Tanzania found a dead male on the road near the Kwamgumi Forest Reserve (FMNH 158851), a lowland forest at 300 m near the foot of the East Usambara Mountains, approximately 25 km NE Amani.

SPECIMENS EXAMINED—**WEST USAMBARA**, 12.5 km NW Korogwe, Ambangulu Tea Estate (proximity of TRL A—FMNH 158276).

Discussion

Faunistics

THE SORICID FAUNA OF THE EAST AND WEST USAMBARA MOUNTAINS—The shrew fauna of both the East and West Usambara Mountains is diverse, especially in relation to other regional montane localities (see below). On each massif of the Usambaras, we collected species that occurred almost exclusively in forested habitats and others that were found predominately in more open or very disturbed forest habitats. Examples of species found almost exclusively in forest include *Crocidura hildegardeae*, *C. monax*, *C. tansaniana*, and *Sylvisorex howelli*. The single exception was a *C. hildegardeae* caught in a pitfall line set between a tea plantation and thick herbaceous/woody vegetation along a stream bank. This site was less than 30 m from the edge of the EU control site forest. Not only were these species generally restricted to forest sites, but also 98%, 88%, 98%, and 100% of specimens captured for *C. hildegardeae*, *C. monax*, *C. tansaniana*, and *S. howelli*, respectively, came from the control sites of the East and West Usambaras. Hence, these species are generally not present in the small forest parcels falling into the same elevation ranges as the control sites.

Conversely, other species (*C. elgonius*, *C. hirta*, and *C. jacksoni*) were found almost exclusively in non-forest habitats, including tea plantations, agricultural land, and secondary vegetation. Only one of the nine *C. elgonius* collected in the East Usambara was in relatively undisturbed forest; the rest were taken in tea plantations and agricultural habitat. In the West Usambara, four *C. elgonius* were collected in tea and *Eucalyptus* plantations, and only one specimen was taken in forest, in this case in the 37.8-ha site. This species was the most common of the mammals collected in tea plantations. *Crocidura hirta* was found in tea plantations, agricultural areas, and disturbed forest within fragments of less than 10 ha, with one exception in the East Usambara in the 29.4-ha fragment. The single record of *C. jacksoni* documented during this survey was in bamboo of a marshy area with some agricultural activities. This species is known from drier habitats in Tanzania, such as Tarangire National Park (Stanley et al., 2007c). All non-forested habitats sampled during our surveys were the result of human alteration of the natural vegetation. No natural savannah or other drier habitats occur in the portions of the Usambara Mountains we inventoried. Thus, we hypothesize that species such as *C. elgonius* and *C. hirta* arrived in the specific sampled areas after human modification of natural habitats. Whether the agent was natural colonization from more lowland areas or physical introduction by humans will require further study.

DIFFERENCES BETWEEN THE EAST AND WEST USAMBARAS—More shrew species were documented in the East Usambara Mountains (10) than in the West Usambara Mountains (6). In certain cases, a given taxon occurred on one massif and not the other, or was seemingly rare on one massif compared with the other based on our trap captures. For example, *C. monax* was only found in the West Usambara, and *C. hildegardeae*, *C. tansaniana*, and *C. usambarae* were found only in the East Usambara. *Sylvisorex howelli* was ubiquitous in the WU control area, but only collected twice (2% of all *S. howelli* captured) in the East Usambara. Most of the *C. hirta* we trapped came from disturbed habitats in the East Usambara. Differences in the shrew faunas between the two massifs may relate to elevational zonation, as most of our trapping efforts in the West Usambara were around 1300 m and in the East Usambara between 900 and 1100 m.

REGIONAL DIFFERENCES OF THE TANZANIAN NORTHERN MASSIFS—The shrew fauna of the East and West Usambara Mountains is rich and diverse relative to those of other regional mountains, both geographically close (e.g., North and South Pares, Mt. Kilimanjaro) or geologically similar, with the same base rock composition (Uluguru). Surveys in the South and North Pare Mountains, using the same methodology during the same season, documented four and three shrew species, respectively, in the elevational range of 1100–2000 m (Stanley et al., 1996, 2007b). Despite a broader elevational range, this is less than 50% of the shrew species in the East Usambara and less than 70% of those in the West Usambara. There were also differences in measured abundance of some species. *Crocidura usambarae* made up 8.1% and 21.3% of the total number of shrews collected at 1100 and 2000 m, respectively, in the survey of the South Pare (Stanley et al., 1996), but it comprised only 0.7% of the total shrews taken in the East Usambara and was not trapped in the West Usambara Mountains.

Comparisons within and between Different Communities of Insectivorous Small Mammals in the Afrotropics and Madagascar

Over the past few decades, S.M.G. and W.T.S. have performed detailed inventories of insectivorous small mammals in the Afro-Malagasy region using comparable field methods, particularly pitfall lines, and similar styles of installation and maintenance. Sufficient data are now available to make some first-order comparisons of species richness and diversity among different sites in the Afrotropics and Madagascar, with particular emphasis on levels of endemicity (Table 10). Madagascar sites are all in the eastern humid forests; those from the Afrotropics range from montane forest habitats to lower lying, less mesic forests.

On Madagascar, most insectivorous small mammals are of the endemic Family Tenrecidae (Order Afrosoricida), with the most speciose group being the shrew tenrecs, genus *Microgale*, of the Subfamily Oryzorictinae. This family contains 32 living species, most weighing less than 45 g (Goodman et al., 2008; Olson et al., 2009). In addition, two species of the Family Soricidae occur on Madagascar; one is introduced, and the indigenous status of the other is ambiguous (Hutterer & Trainer, 1990; Hutterer, 2005). Across the Afrotropics, the principal group of insectivorous small mammals are shrews Family Soricidae, with approximately 150 species known in this zone (Hutterer, 2005; Hutterer et al., 2009; Hutterer & Montermann, 2009; Kerbis Peterhans et al., 2008, 2009; Kerbis Peterhans & Hutterer, 2009; Mukinzi et al., 2009).

Notably, the insectivorous small mammal communities, soricid shrews for the Afrotropics and tenrecs for Madagascar, are not phylogenetically closely related (Murphy et al., 2001). Each lineage represents a separate adaptive radiation (although there is some paraphyly within Afrotropical soricids [Dubey et al., 2008]), and there are extraordinary levels of morphological convergence between the two groups. Hence, the Afro-Malagasy comparisons presented here allow an assessment of the evolution of ecological constraints between independently evolved lineages of insectivorous small mammals, with regards to models of speciation, the number of sympatrically occurring taxa, and patterns of endemism.

Although the Afro-Malagasy comparisons are insightful concerning the evolution and levels of speciation in these different insectivorous small mammal communities, some caveats are needed. Madagascar, with a total surface area of 581,500 km^2, has been isolated from other large landmasses for well over 120 million years (de Wit, 2003), and it has been estimated that the colonizing ancestor of the Tenrecidae arrived between 42 and 25 million years ago (Poux et al., 2005). In contrast, tropical Africa is a vast expanse of about 20 million km^2 (Baccini et al., 2008), with a very complex geological history (e.g., Moore & Cotterill, 2010), resulting in different patterns of isolation and subsequent speciation of soricid shrews. This group apparently evolved in the Upper Miocene, is of Palearctic-Oriental origin, and colonized the African continent an estimated 1–5 million years ago (Dubey et al., 2008).

Given the different evolutionary histories of shrews and tenrecs, as well as the contrasting surface area and geological history of tropical Africa and Madagascar, meaningful comparisons using estimates of endemism can be problematic. To address these issues, we use three different measures here: (1) species endemic to a specific massif (=micro-endemic), (2) those restricted to a geographical region involving only a few neighboring massifs, and (3) those restricted to a specific phytogeographical zone (see Table 10, footnote 1). The sites chosen for Madagascar are massifs with montane forest that are isolated from one another by other types of lower lying forest formations and, hence, are in parallel with the definition number 2 presented above. Finally, with one exception (Central African Republic), the data used in these comparisons came solely from surveys designed and conducted by W.T.S. or S.M.G., who employed largely consistent field methodologies (Table 10).

Intra-Afrotropical comparisons—In comparing the species richness among various small insectivore communities (shrews) within the Afrotropics, several patterns emerge (Table 10). The submontane and montane (sensu Lovett & Pócs, 1993) forests of the Eastern Arc Mountains in northern Tanzania (East and West Usambara and South and North Pare Mountains), spanning the latitudinal range from 3°S to 5°S, show notable differences in species richness; the Usambaras have 6–10 species and the Pares 3–4 species. The elevational range each massif presents and its distance to the coast may in part explain the differences in species richness; elsewhere, both factors, as well as aspect, affect orographic precipitation and the length of the dry season (Basist et al., 1994; Abebe & Savenije, 1995). The summits of the East and West Usambara Mountains reach 1506 and 2200 m, respectively, and these massifs are 50 and 100 km, respectively, from the Indian Ocean coast. In contrast, the South and North Pares have summits at 2463 and 2113 m, respectively, and are 150 and 220 km, respectively, from the coast. The Pares are, in part, in the rain shadow of the Usambara Mountains and, to a smaller extent, in that of the Taita Hills of southern Kenya. Mount Kilimanjaro, with a different geological origin, composition, and age, with six species of small insectivorous animals and several different types of natural habitats, is a further example of this pattern; this massif lies to the northwest of the Pares and rises to 5895 m, and the eastern flank is 275 km from the coast.

In contrast to species diversity, insectivore endemism is largely consistent across these four Eastern Arc Mountains, based on the phytogeographical zone endemism classification (see Table 10, footnote 1) with respect to the Tanganyika Montane Forest Group. They range from 25% in the South Pare, to 30% in the East Usambara, to 33% in the North Pare and West Usambara. The shrew fauna of Mt. Kilimanjaro shows 33% endemism based on this definition. From a regional perspective, the percentage of species found on these mountains, and only a few other nearby montane localities, ranged from 0% on the North Pare to 25% on the South Pare; figures for the Usambaras and Mt. Kilimanjaro are intermediate (Table 10).

In the southern Eastern Arc Mountains, across the latitudinal gradient from 6.5°S to 8.5°S, shrew species richness is reduced, with four and five taxa per massif in the Uluguru and Ukaguru, respectively. The summits of these mountains are at 2400 and 2250 m, respectively, and the distances to the coast are 180 and 220 km, respectively. The exception to the relatively low shrew taxonomic diversity in the southern Eastern Arc Mountains is the Udzungwa Massif. This massif, with 10 species, rises to 2580 m, and the eastern flank is 300 km from the coast. Differences in species richness among these three massifs appear to correlate with their position relative to the Indian Ocean and general topography, which in turn would be associated with orographic precipitation, surface area of each massif, and the elevational range sampled. Relative to the Uluguru and Ukaguru, the Udzungwa Massif is the largest of the Eastern Arc Mountains, and no other geological feature blocks the passage of weather systems arriving from the Indian Ocean. Contrasting insectivore

TABLE 10. Comparisons of patterns of species richness of insectivorous small mammals at different sites in the Afro-Malagasy region. Habitat classifications are based on Lovett and Pócs (1993) for the Afrotropics and Du Puy and Moat (1996) for Madagascar. Site names in bold are part of the Eastern Arc Mountains (Lovett, 1990).

Site (Country)	Elevation (m) (range of survey)	Trapping type and effort			Habitat type	Latitude (centroid)	Species richness	Different measures of % endemism[1]	Source of data[2]
		Bucket-nights	Trap-nights	Sample-nights					
East Usambara (Tanzania)	900–1110	3314	8025	11,339	Submontane forest	5°3′S	10	10–20–30	1
West Usambara (Tanzania)	1120–1300	1924	5300	7224	Submontane forest	5°3′S	6	0–16–33	1
South Pare (Tanzania)	1100–2000	1364	3794	5158	Submontane forest	4°18′S	4	0–25–25	2
North Pare (Tanzania)	1550–1700	1089	2286	3375	Submontane forest, with some fragmentation	3°34′S	3	0–0–33	3
Udzungwa (Tanzania)	600–2000	2893	7448	10,341	Dry submontane to montane forest	8°23′S	10	10–30–50	4
Minziro (Tanzania)	1150	550	1505	2055	Guineo-Congolian lowland forest	1°1′S	6	0–0–0	5
Uluguru (Tanzania)	1350–1850	1739	5620	7359	Submontane to montane forest	6°55′S	4	0–75–100	6
Ukaguru (Tanzania)	1800–1900	1727	3134	4861	Submontane to montane forest	6°22′S	5	0–60–80	6
Mt. Kilimanjaro (Tanzania)	2000–4000	3201	8361	11,562	Submontane forest to alpine desert	3°10′S	6	17–17–33	6, 7
Mt. Mulanje (Malawi)	1000–1850	1320	2608	3928	Submontane forest to montane grassland	15°58′S	3	0–0–0	6
Minkébé (Gabon)	600	330	1500	1830	Guineo-Congolian lowland forest	2°5′S	11	0–0	8
Mt. Doudou (Gabon)	110–625	726	1650	2376	Lowland rain forest to mid-elevation rain forest	2°15′S	9	0–0	9
Dzanga-Sangha and Dzanga-Ndoki forests (Central African Republic)	300–650	All identified species were identified from remains in small carnivoran scats.			Semi-deciduous	2°30′N	17	6.5–13	10
Anjanaharibe-Sud (Madagascar)	875–1550	814	1646	2460	Undisturbed lowland and montane forest	14°45′S	11	9–73	11
Marojejy (Madagascar)	775–1625	726	2100	2826	Undisturbed lowland and montane forest	14°30′S	14	7–79	12
Tsinjoarivo (Madagascar)	1400–1550	396	1200	1596	Montane forest slight degradation and some fragmentation	19°45′S	15	0–87	13
Ambohitantely (Madagascar)	1450–1660	627	1750	2377	Fragmented montane forest	18°20′S	10	0–70[3]	14
Andringitra (Madagascar)	810–1625	902	1925	2827	Undisturbed lowland and montane forest	22°15′S	13	0–77	15

[1] We provide three separate measures of endemism, which are, in order: (1) micro-endemics or strict endemic, which refers to a species not known outside of the specific site or massif; (2) regional endemics, which is defined as taxa that have limited geographical ranges, including the specific study site (such as certain massifs in the Eastern Arc Mountains and nearby massifs). For Madagascar, these comparisons are limited to the eastern humid forests; (3) phytogeographical zone endemics, for Eastern Arc Mountains and some other sites ranging from Tanzania to southern Malawi, shrews endemic to the Tanganyika Montane Forest Group (sensu Moreau, 1966), and Mt. Kilimanjaro. This phytogeographical region has been picked to make comparisons between this zone and Madagascar more equitable with regard to several different parameters.

[2] Data sources: 1 = herein; 2 = Stanley et al. (1996, 1998); 3 = Stanley et al. (2007b); 4 = Stanley and Hutterer (2007); 5 = Stanley and Foley (2008); 6 = W. T. Stanley (unpubl. data); 7 = Stanley et al. (2003); 8 = Goodman et al. (2001); 9 = Goodman and Hutterer (2004), Nicolas et al. (2004); 10 = Ray and Hutterer (1995), Lunde (2007); 11 = Goodman and Jenkins (1998); 12 = Goodman and Jenkins (2000); 13 = Goodman et al. (2000); 14 = Goodman and Rakotondravony (2000), Olson et al. (2004); 15 = Jenkins et al. (1996), Goodman and Rasolonandrasana (2001).

[3] This includes *Suncus madagascariensis*, which may not be endemic to Madagascar, but an introduced form of *S.* "*etruscus.*"

endemism based on phytogeographical regions (see Table 10, footnote 1), the Uluguru (100%) and Ukaguru (80%) have notably high levels of small mammal endemism within the Tanganyika Montane Forest Group. In contrast, this value for the Udzungwa Mountains is only 50%. The regional endemics made up 60% and 75% of the Ukaguru and Uluguru samples, respectively, but only 30% of the Udzungwa samples.

Comparing other regional mountains with submontane forest to the Eastern Arc Mountains, sites such as Mt. Mulanje, summit at 3002 m in southern Malawi and forming the southern limit of the Tanganyika Montane Forest Group, has few shrew species and no regional endemics (Table 10). In the Guineo-Congolian forests near Minziro, in northwestern Tanzania, six species of shrew were recorded, none endemic. Portions of central western Africa, represented in our data set by Minkébé, Monts Doudou, and the Dzangha-Sangha/Dzanga-Ndoki complex, have high species richness, ranging from 9 to 16 taxa, with regional endemism ranging from 0% to 13%.

The highest measure of shrew species richness (Table 10) is the Dzangha-Sangha/Dzanga-Ndoki complex in the Central

African Republic, part of the Congo River basin. Here, where a marked dry season extends from December to March, 17 species of shrew were identified from small carnivore scats and some limited field surveys (Ray & Hutterer, 1995; Lunde, 2007). Whether Dzangha-Sangha/Dzanga-Ndoki has an exceptional diversity of small insectivorous animals or the lower measures of species richness at the other sites mentioned in Table 10 using the pitfall and trap techniques are artifacts of sampling techniques will require further research. Sites in Gabon within the same elevational range and habitat types as Dzangha-Sangha/Dzanga-Ndoki sampled by pitfall traps have notably lower measures of shrew species richness.

Intra-Malagasy comparisons—Five sites from the eastern humid formations of Madagascar, spanning the latitudinal range from about 14°S to 22°S, were compared with the Afrotropical sites (Table 10); four of these sites are large massifs that form separate montane forest islands, and the fifth is an isolated and fragmented series of forest parcels. In the four intact sites, where tenrec surveys were conducted in the same elevational range and forest type, species richness varied from 11 taxa at Anjanaharibe-Sud to 15 at Tsinjoarivo. The lowest species richness of the five sites was 10, recorded at Ambohitantely, the locality with heavy anthropogenic fragmentation. Only two of the five sites had micro-endemic taxa of tenrecs (Anjanaharibe-Sud and Marojejy Massifs), with values ranging from 7% to 9% of the total local fauna. Levels of endemism for each of these sites within the broader regional eastern humid forests ranged from 70% (Ambohitantely) to 87% (Tsinjoarivo).

Inter-Afrotropical–Malagasy comparisons—Except for two sites, more tenrec species occurred in the intact montane sites on Madagascar than did shrews in similar habitats in the Eastern Arc Mountains (Table 10). The exceptions are the East Usambara and Udzungwa Mountains; each had the same number of species as did Ambohitantely, the least diverse (10 taxa) of the Malagasy sites used in these comparisons. Ambohitantely is a fragmented montane forest with blocks ranging from 0.64 to 1250 ha and the local insectivorous small mammal community forms a nested subset, presumed to have undergone faunal collapse (Goodman & Rakotondravony, 2000). Notably, trapping effort was between four to five times greater at the East Usambara and Udzungwa Mountains than at Ambohitantely.

Table 10 presents several measures of endemism. The number of strict micro-endemics in the Eastern Arc Mountain and Malagasy montane forest sites differ little; the former ranges from 0% to 10% of the local insectivorous small mammal fauna being restricted to a specific massif and the latter from 0% to 9%. For the different surveyed sites in the Eastern Arc Mountains, the percentage of endemic species in the local community, when measured at the regional level, ranges from 16% to 75%, with the exception of the North Pare (0%). The comparisons at the phytogeographical level of the expanded Tanganyika Montane Forest Group show levels ranging from 30% to 100%. At several sites, such as the Uluguru and Ukaguru Mountains, species are relatively few, but most taxa are regional endemics. Probably the best comparison of these measures of endemism between the Eastern Arc Mountains and Madagascar is the number of species at a given site that are restricted to the eastern humid forest, where the values range from 70% to 87% (Table 10). Hence, at a regional level, the Tenrecidae show similar percentages of endemic taxa as the Soricidae in the Eastern Arc Mountains, despite tenrecs having been in place five times as long as the latter. Why faunas of significantly different geological ages show comparable endemism is not apparent and bears further investigation. Intervening habitats (humid forests versus drier woodland habitats), geological history, and timing of climatic perturbations and past connectivity of sites need to be taken into account. Another important consideration is the notable advancement of taxonomic work on tenrecs in the recent decades compared with Afrotropical soricids, particularly in this case, Eastern Arc shrews, which are still under scrutiny, and new species may be uncovered by ongoing molecular and morphological analyses.

As mentioned earlier, all of the members of the Tenrecidae are endemic to Madagascar. In the humid forests of the central and eastern portion of the island, most members of this family have broad distributions; few taxa are micro-endemics. An exception associated with the sites chosen here for comparison is *Microgale monticola*, which is only known from the Anjanaharibe-Sud and Marojejy Massifs (Goodman & Jenkins, 2000). At virtually all of the Malagasy sites inventoried, the number of sample nights exceeds 2300, which should provide a relatively precise measure of local species richness. The exception is at Tsinjoarivo, with slightly less than 1600 sample-nights, and the Malagasy site with the highest measure of species richness. The lowest species count is from the heavily fragmented forests of Ambohitantely. Across an assortment of different dry forests of western Madagascar, species richness of Tenrecidae is generally two to five species, but one site, Kirindy (CFPF), holds seven taxa (Soarimalala, 2008), notably less than the most species poor montane site in the east.

On the Tanzanian side, three species of shrew are known only from one mountain range (*Crocidura tansaniana*—East Usambara; *Congosorex phillipsorum*—Udzungwa; *Myosorex zinki*—Mt. Kilimanjaro). In addition, five species are restricted to a subset of mountain ranges within the Eastern Arc (*Crocidura desperata*, *C. telfordi*, *M. kihaulei*, *M. geata*, and *Sylvisorex howelli*). These distributions have been documented with intense surveys involving more than 3500 sample-nights at different montane sites. The one lowland Tanzanian site included in our comparisons is Minziro in the northwestern corner of the country and composed of Guinea-Congo habitat. In slightly more than 2000 sample-nights accrued at this sight, six species were documented, not one of which is locally endemic or regionally restricted.

Conservation

Tanzanian endemics such as *Crocidura monax*, *C. tansaniana*, and *Sylvisorex howelli* were found only in the forests of the control areas of the Usambara Mountains. These forest blocks are under constant threat from illegal logging and other influences, such as wind damage, invasive tree species (e.g., *Maesopsis*), and a variety of other human-induced pressures. Given that species such as *C. tansaniana* are found only in relatively pristine forest on the East Usambara Massif, and that the forests we sampled on the West Usambara Massif are the lowest remaining montane forests of that range, all remaining forest patches need to be conserved. The Amani Nature Reserve is a good example of the type of conservation actions that are regionally required to preserve the remaining montane forest habitats of the East and West Usambaras.

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