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New Species of *Scotophilus* (Chiroptera: Vespertilionidae) from Sub-Saharan Africa

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Abstract

A previous phylogenetic study of bats of the genus *Scotophilus* (house bats) showed deep subdivisions and paraphyletic relationships among populations of *S. dinganii* (four distinct clades) and *S. viridis* (two distinct clades). According to the genetic species concept, these clades may represent distinct species. Herein, we assess morphological differences of specimens of four clades representing hypothesized unrecognized species compared to specimens of nominate *S. dinganii* and *S. viridis*. Statistically significant morphological differences provided characters for accurate diagnosis of each clade. Therefore we recognize and formally describe four new species of sub-Saharan African *Scotophilus* (*Scotophilus andrewreborii* sp. nov., *Scotophilus livingstonii* sp. nov., *Scotophilus ejetai* sp. nov., and *Scotophilus trujilloi* sp. nov.).

Key words: Africa, African house bat, cryptic species, phylogeny, *Scotophilus*, Vespertilionidae

Introduction

Bats of the genus *Scotophilus* have a complex and confusing taxonomic history. According to Simmons (2005) and *Mammal Species of the World*, 3rd edition (Wilson and Reeder 2005) the genus is considered to be comprised of 12 species. The distribution of the genus includes Indonesia (*S. celebensis*), mainland Asia (*S. heathi*, *S. kuhlii*), Madagascar (*S. robustus*), Reunion Island (*S. borbonicus*) and mainland Africa (*S. collinus*, *S. dinganii*, *S. leucogaster*, *S. nigrita*, *S. nucella*, *S. nux*, and *S. viridis*). Two additional species have been described from Madagascar (*S. tandrefana* Goodman et al. 2005 and *S. marovaza* Goodman et al. 2006). Grubb et al. (1998) recognized *S. nigritellus* de Winton 1899 as a distinct species whereas Simmons (2005) includes it as a subspecies of *S. viridis*, which brings the current total of recognized species to 15. Sub-Saharan Africa seems to be the most likely origin of the genus given the number of species recorded from this region and the fossil record (Horacek et al. 2006), but this was not confirmed by the most extensive molecular systematic study of Trujillo et al. (2009).

The 15 species listed above do not accurately reflect our current knowledge of *Scotophilus* biodiversity. Trujillo et al. (2009) identified at least three distinct clades based on cytochrome-*b* sequences. The three unrecognized taxa are listed by Trujillo et al. (2009) as *S. dinganii*–like (eastern Africa; Clade 9), *S. dinganii*–like (Ghana to Kakamega; Clade 11), and *S. viridis*–like (eastern Africa; Clade 12). In addition, a fourth unrecognized taxon present in the dataset of Trujillo et al. (2009) is *S. dinganii*-like (Clade 8).

The genetic species concept (Baker and Bradley 2006) is conceptually based on presumptive genetic incompatibilities producing an isolating mechanism in genetically diverged clades. The identification of clades can be based on DNA sequence analysis of mitochondrial and/or nuclear genes and appropriate phylogenetic analysis. Monophyletic clades of sufficient percent sequence divergence are indicative of millions of years of reproductive isolation and may warrant formal taxonomic recognition. Solari et al. (2009) defined operational criteria for the application of the genetic species concept for allopatric monophyletic clades as a divergence value of ≈ 5% in the cytochrome-*b* mitochondrial gene. They point out that the use of the ≈ 5% value is somewhat arbitrary, but this value of divergence is typical for morphologically divergent sister species of mammals. It thus serves as a convenient indicator of the potential for species level distinction. In this paper, sister clades representing hypothetically distinct species differed by 4.2% genetic divergence or greater.

The use of molecular genetics to identify cryptic or unrecognized species is well established in chiropteran systematics including vespertilionids (Baird et al. 2008; Koubínová et al. 2013). For example, the *Rhogeessa tumida* species group consists of 12 species, most of which were recognized based on karyotypic or molecular genetic differences. Typically, genetic differentiation is accompanied by morphological differences, but not always. Multivariate analyses of skull measurements could not differentiate some of the cryptic species of *Rhogeessa* (Baker 1984; Baird et al. 2012). The phenomenon of genetically distinct cryptic species is not unique to mammals. Papenfuss and Parham (2013) described four new species of legless lizards (*Anniella*) which were discovered based on DNA sequences. Three of the new species could be differentiated by morphological characters but one species differed only by gene sequence and karyotype. As Papenfuss and Parham (2013) point out, morphological diagnoses and formal taxonomic descriptions of new species are desirable because they improve our understanding of systematics, biogeography, evolution, biodiversity, and other areas of biology.

As a practical application, systematics guides conservation efforts and incomplete taxonomy impedes our ability to create effective conservation units. The recognition of the genetic and taxonomic diversity within a given complex allows for finer-grained conservation strategies based on the unique habitats occupied by the different species, and their historical biogeography.

The previous molecular study of Trujillo et al. (2009) revealed the presence of four distinct and heretofore unrecognized lineages that we hypothesize to be deserving of species status (Fig. 1). This paper examines specimens of each of these four lineages and uses skull and body measurements to compare specimens of each lineage with specimens representing the appropriate nominate taxon, using specimens of the latter taken from as close to the type locality as possible. In all four cases, statistically significant differences exist between the paired sample groups and thus each of the ostensible new forms is morphologically diagnosable. We therefore describe these four morphologically and genetically unique lineages as new species of *Scotophilus* (*Scotophilus andrewreborii* sp. nov., *Scotophilus livingstonii* sp. nov., *Scotophilus ejetai* sp. nov., and *Scotophilus trujilloi* sp. nov.).

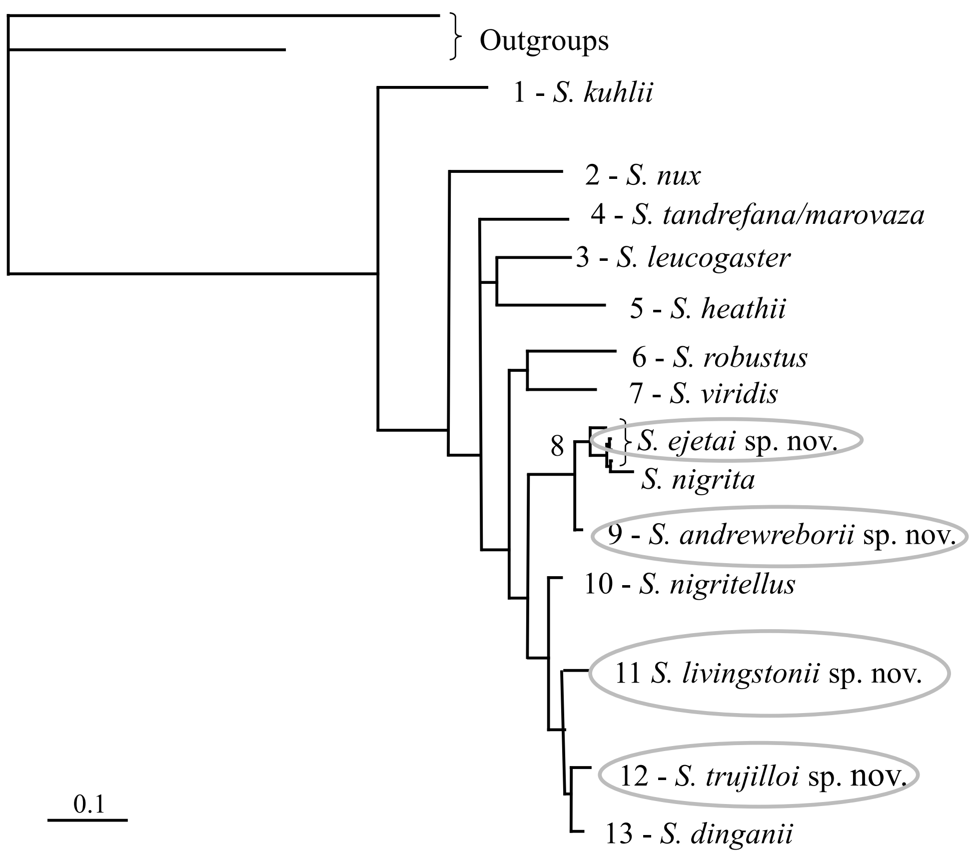

Figure 1. Bayesian phylogram showing the clades and species of *Scotophilus* studied for the mitochondrial cytochrome-*b* gene by Trujillo et al. (2009). The new species described in this paper are circled. This figure is redrawn from Figure 1 of Trujillo et al. (2009) to show the phylogenetic relationships and genetic distances based on cytochrome-*b* sequences among the species of *Scotophilus* including the forms newly described in this paper.

METHODS

Morphological measurements of museum specimens identified as adult *S. dinganii* (N = 48) and adult *S. viridis* (N = 17) (Appendix) were taken using dial calipers (to the nearest 0.01 mm) by one person (DMB) to help add precision. Adults were recognized by ossified phalanges. Five external measurements included: head-body length (HB), tail length (TL), hind foot length (HF), ear length (EA), and forearm length (FA). Eight cranio-dental measurements included: greatest skull length (SL), zygomatic breadth (ZB), braincase breadth (BB), braincase height (BH), interorbital width (IW), greatest breadth across upper molars (WM), greatest breadth across upper canines (WC), and mandibular length (ML). Morphological terminology followed a slight modification of Siles et al. (2013). All measurements were assessed separately for males and females, as determined by specimen tag data.

Because some type specimens were destroyed during warfare or missing (B. Robbins in lit.) we examined series close to the type localities for comparison. We compared presumed nominate *S. dinganii* (Smith 1833) from Natal (RSA) to specimens from Ethiopia, Kenya's Rift Valley, and Western Kenya and Ghana. Presumed nominate *S. viridis* (Peters 1852) from Mozambique Island (Mozambique) were compared to specimens from coastal Kenya. Cranial measurement variation was assessed for statistical significance using non-parametric Mann-Whitney U tests in light of conservative sample sizes using VassarStats (vassarstats.net).

RESULTS

Comparisons of external measurements (Table 1), male cranio-dental measurements (Table 2), and female cranio-dental measurements (Table 3) between nominate *S. dinganii*, *S. viridis*, and each of the four genetically defined clades are presented.

Clade 9.—Specimens of clade 9 from Kenya's Rift Valley were significantly smaller than specimens of nominate *S. dinganii* from Natal for males in braincase breadth (z = 2.30, P ≤ 0.01; Table 2) and for females in skull length (z = 1.68, P ≤ 0.04), zygomatic breadth (z = 2.08, P ≤ 0.01), braincase height (z = 1.68, P ≤ 0.04), interorbital width (z = 2.32, P ≤ 0.01), greatest breadth across upper molars (z = 2.64, P ≤ 0.004), and greatest breadth across upper canines (z = 2.00, P ≤ 0.02; Table 3).

Clade 11.—Specimens of clade 11 from Ghana and western Kenya showed the least amount of significant variation when compared to specimens of nominate *S. dinganii* from Natal. Skull length in males was significantly smaller (z = 1.93, P ≤ 0.02; Table 2) than Natal populations, whereas mandibular length in females was significantly larger (z = 2.28, P ≤ 0.01; Table 3).

Clade 8.—Specimens of clade 8 from Ethiopia were the most distinct of all comparisons. Males had smaller measurements than specimens of nominate *S. dinganii* from Natal for skull length (z = 1.96, P ≤ 0.02), zygomatic breadth (z = 1.70, P ≤ 0.04), and braincase breadth (z = 1.96, P ≤ 0.02; Table 2). Females had smaller measurements for skull length (z = 2.32, P ≤ 0.01), zygomatic breadth (z = 2.55, P ≤ 0.005), braincase breadth (z = 2.88, P ≤ 0.001), interorbital width (z = 1.84, P ≤ 0.03), greatest breadth across upper molars (z = 2.64, P ≤ 0.004), and greatest breadth across upper canines (z = 2.80, P ≤ 0.002; Table 3).

Clade 12.—In contrast to Clades 8, 9, and 11, which are morphologically similar to *S. dinganii*, specimens of Clade 12 were similar, and provisionally identified in collections, as *S. viridis*. Males of clade 12 from coastal Kenya showed greater differences in measurements than clade 12 females when compared to males and females of nominate *S. viridis* from Mozambique. Clade 12 males were significantly different than nominate *S. viridis* for braincase height (z = 1.74, P ≤ 0.04), but larger for inter-orbital width (z = 1.74, P ≤ 0.04) and greatest width between molars (z = 1.93, P ≤ 0.02; Table 2). Clade 12 females were smaller than nominate *S. viridis* for braincase height (z = 1.67, P ≤ 0.04) and mandibular length (z = 2.64, P ≤ 0.001; Table 3).

Table 1. External measurements for comparison between: Scotophilus dinganii *(Natal, RSA) and* S. andrewreborii *sp. nov. (Rift Valley, Kenya),* S. livingstonii *sp. nov. (W. Kenya/Ghana),* S. ejetai *sp. nov. (Ethiopia); and between* S. viridis *(Mozambique) and* S. trujilloi *sp. nov. (coastal Kenya). Mensural acronyms are as follows: head-body length (HB), tail length (TL), hind foot length (HF), ear length (EA), and forearm length (FA).*

	Males					Females				
	HB	TL	HF	EA	FA	HB	TL	HF	EA	FA
Natal, RSA - *S. dinganii*										
Mean	78.0	42.3	11.2	9.6	51.7	79.1	43.7	10.1	11.4	53.1
R	77.0-79.0	40.8-43.7	10.8-11.5	9.6	50.6-52.8	76.5-81.5	42.0-46.5	9.0-10.9	11.2-11.6	52.5-53.8
N	2	2	2	1	2	3	3	3	3	3
Rift Valley, Kenya - *S. andrewreborii* sp. nov.										
Mean	80.9	47.7	9.4	9.6	52.6	79.6	44.6	9.9	9.5	51.0
R	74.9-85.2	44.2-50.3	9.0-9.9	9.0-10.5	51.0-53.9	76.0-86.5	42.9-48.2	9.4-10.2	8.8-10.8	46.5-54.1
N	5	5	5	4	5	7	7	7	5	7
W. Kenya/Ghana - *S. livingstonii* sp. nov.										
Mean	78.5	45.7	10.2	10.3	53.8	84.3	42.6	11.5	10	54.4
R	74.3-85.4	40.3-48.4	10.0-10.5	9.2-12.0	51.8-54.4	75.5-89.3	32.5-50.6	9.9-12.3	9.2-11.1	51.7-55.6
N	5	5	5	4	5	6	6	6	6	6
Ethiopia - *S. ejetai* sp. nov.										
Mean	76.0	41.8	10.7	11.7	50.4	74.8	42.8	10.7	10.7	50.25
r	76.0	41.8	10.7	11.7	50.4	72.6-77.1	40.4-45.1	9.3-12.1	10.2-11.3	50.2-50.3
N	1	1	1	1	1	2	2	2	2	2
Mozambique - *S. viridis*										
mean	60.9	38.4	9.0	11.3	46.18	63.4	40.3	9.8	11.3	48.82
r	57.2-65.0	33.9-41.6	8.6-9.6	10.4-11.6	44.8-48.0	61.0-65.0	35.5-42.8	9.0-10.1	10.4-12.2	47.4-50.0
N	5	5	5	5	5	5	5	5	5	5
coastal Kenya - *S. trujilloi* sp. nov.										
mean	70.8	37.3	10.3	7.2	44.2	69.4	42.1	10.0	7.6	45.3
r	70.8	37.3	10.3	7.2	44.2	65.4-75.2	39.2-43.8	9.7-10.4	7.5-7.9	43.8-46.2
N	1	1	1	1	1	3	3	3	3	3

Table 2. Male cranio-dental measurements for comparison between: Scotophilus dinganii *(Natal, RSA) and* S. andrewreborii *sp. nov. (Rift Valley, Kenya),* S. livingstonii *sp. nov. (W. Kenya/Ghana),* S. ejetai *sp. nov. (Ethiopia); and between* S. viridis *(Mozambique) and* S. trujilloi *sp. nov. (coastal Kenya). Mensural acronyms are as follows: greatest skull length (SL), zygomatic breadth (ZB), braincase breadth (BB), braincase height (BH), interorbital width (IW), greatest breadth across upper molars (WM), greatest breadth across upper canines (WC), and mandibular length (ML). * P ≤ 0.05, ** P ≤ 0.01.*

	SL	ZB	BB	BH	IW	WM	WC	ML
Natal, RSA - *S. dinganii*								
Mean	19.6	13.9	9.6	8.2	4.8	9.0	6.9	14.1
R	19.2-20.1	13.6-14.2	9.5-9.9	7.9-8.7	4.6-5.0	8.8-9.1	6.7-7.0	13.4-14.8
N	3	2	3	3	3	3	3	3
Rift Valley, Kenya - *S. andrewreborii* sp. nov.								
mean	19.0	13.7	9.1**	8.1	4.6	9.0	6.8	14.2
r	18.1-19.6	13.3-14.0	9.0-9.4	7.6-8.5	4.3-4.8	8.7-9.2	6.6-7.0	13.7-14.7
N	6	5	6	6	6	6	6	6
W. Kenya/Ghana - *S. livingstonii* sp. nov.								
mean	18.9*	14.1	9.4	8.2	4.6	9.3	7.0	14.3
r	18.3-19.4	13.7-14.5	9.2-9.8	7.4-8.8	4.3-4.8	9.0-9.6	6.9-7.2	14.0-14.8
N	8	8	9	9	9	9	8	9
Ethiopia - *S. ejetai* sp. nov.								
mean	18.1*	13*	9.3*	7.8	4.6	8.7	6.7	13.8
r	17.5-18.5	12.5-13.3	9.2-9.3	7.6-8.0	4.5-4.8	8.5-8.9	6.7-6.8	13.7-13.9
N	3	3	3	3	3	3	3	3
Mozambique - *S. viridis*								
mean	16.2	12.0	8.4	7.3	4.3	7.7	5.8	12.8
r	15.9-16.9	11.3-12.3	8.3-8.7	6.8-7.6	4.1-4.5	7.5-7.8	5.5-6.1	12.1-13.3
N	5	4	5	5	5	5	5	5
coastal Kenya - *S. trujilloi* sp. nov.								
mean	16.3	12.2	8.6	6.7*	4.6*	8.0*	6.0	12.1
r	16.2-16.4	12.0-12.3	8.4-8.8	6.5-6.8	4.5-4.7	8.0	5.6-6.4	12.1
N	2	2	2	2	2	1	2	2

Table 3. Female cranio-dental measurements for comparison between: Scotophilus dinganii *(Natal, RSA) and* S. andrewreborii *sp. nov. (Rift Valley, Kenya),* S. livingstonii *sp. nov. (W. Kenya/Ghana),* S. ejetai *sp. nov. (Ethiopia); and between* S. viridis *(Mozambique) and* S. trujilloi *sp. nov. (coastal Kenya). Mensural acronyms are as follows: greatest skull length (SL), zygomatic breadth (ZB), braincase breadth (BB), braincase height (BH), interorbital width (IW), greatest breadth across upper molars (WM), greatest breadth across upper canines (WC), and mandibular length (ML). * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.*

	SL	ZB	BB	BH	IW	WM	WC	ML
Natal, RSA - *S. dinganii*								
mean	19.6	14.2	9.5	8.1	4.8	9.2	6.9	13.9
r	18.4-20.7	13.8-14.6	9.3-9.9	7.8-8.7	4.5-5.0	8.8-9.7	6.7-7.2	13.4-14.7
N	6	4	6	6	6	6	6	6
Rift Valley, Kenya - *S. andrewreborii* sp. nov.								
mean	18.9*	13.5**	9.3	7.8*	4.4**	8.7***	6.7*	13.8
r	18.2-19.6	13.1-13.9	9.0-9.5	7.5-8.4	4.3-4.6	8.5-9.0	6.6-6.9	13.5-14.4
N	6	5	6	6	6	6	6	8
W. Kenya/Ghana - *S. livingstonii* sp. nov.								
mean	18.8	14.0	9.5	7.9	4.6	9.1	7.2	14.6**
r	18.0-19.5	13.3-14.2	9.1-9.8	7.3-8.3	4.4-5.0	8.8-9.3	6.8-7.6	14.0-15.3
N	7	6	7	6	7	6	6	7
Ethiopia - *S. ejetai* sp. nov.								
mean	18.1**	12.9***	8.9***	7.7	4.5*	8.6***	6.5***	13.8
r	17.4-18.8	12.2-13.5	8.6-9.2	7.5-8.0	4.3-4.7	8.4-9.0	6.2-6.7	13.5-14.0
N	6	6	6	6	6	6	6	6
Mozambique - *S. viridis*								
mean	16.5	12.2	8.6	7.2	4.4	7.9	5.7	13.2
r	16.2-16.8	12.2	8.5-8.7	7.0-7.4	4.2-4.5	7.7-8.0	5.5-6.0	12.9-13.5
N	5	1	5	5	5	5	5	5
coastal Kenya - *S. trujilloi* sp. nov.								
mean	16.2	12.2	8.4	6.9*	4.5	7.8	5.5	12.2***
r	16.0-16.4	11.9-12.7	8.1-8.8	6.5-7.4	4.1-4.7	7.6-8.2	5.3-5.8	12.0-12.5
N	5	5	5	5	5	5	5	5

DESCRIPTIONS

In light of concordant morphometric and genetic differences of clades 8, 9, 11, and 12, and nominate *S. dinganii* and *S. viridis*, we describe four new species of *Scotophilus*, as follows:

Family Vespertilionidae Gray 1821
Genus Scotophilus Leach 1821
Genus Pachyotus Gray 1831
***Scotophilus andrewreborii*, new species**
Andrew Rebori's House Bat

Holotype.—Voucher CMNH 98049 (Fig. 2); adult male; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 7 October 1985 by Kimberly Nelson. Prepared by Kimberly Nelson, field number 217. Muscle tissue sample TK 33143. External measurements (mm) are: head-body length 83.0; tail length 50.3; hind foot length 9.0; ear length 9.0; forearm 52.9. Cranial measurements (mm) are: greatest skull length 19.6; zygomatic breadth 13.9; braincase breadth 9.1; braincase height 8.5; interorbital width 4.7; greatest breadth across upper molars 9.2; greatest breadth across upper canines 6.8; mandibular length 14.4.

Type locality.—Kenya: Rift Valley Province, Nakuru District, 12 km S, 4 km E Nakuru (0º24'S, 36º07'E).

Paratypes.—Two additional specimens were collected from Kenya and based on morphological and genetic data are designated as paratypes. The first paratype is voucher CMNH 98048; adult female; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 7 October 1985 by Kimberly Nelson from 12 km S, 4 km E Nakuru (0º24'S, 36º07'E), Nakuru District, Rift Valley Province, Kenya. Prepared by Kimberly Nelson (field number 214). Tissue sample TK 33140. External measurements (mm) are: head-body length 82.8; tail length 48.2; hind foot length 9.8; ear length 8.8; forearm 53.8. Cranial measurements (mm) are: greatest skull length 19.6; zygomatic breadth 13.8; braincase breadth 9.5; braincase height 7.9; interorbital width 4.3; greatest breadth across upper molars 8.8; greatest breadth across upper canines 6.8; mandibular length 13.6.

The second paratype is voucher CMNH 98050; adult male; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 8 October 1985 by Kimberly Nelson from Njoro River, 3 km S, 3 km W Nakuru (0º19'S, 36º03'E), Nakuru District, Rift Valley Province, Kenya. Prepared by Kimberly Nelson (field number 219). Tissue sample TK 33149. External measurements (mm) are: head-body length 83.4; tail length 50.3; hind foot length 9.9; ear length 9.4; forearm 52.0. Cranial measurements (mm) are: greatest skull length 18.7; zygomatic breadth 14.0; braincase breadth 9.0; braincase height 8.4; interorbital width 4.3; greatest breadth across upper molars 8.7; greatest breadth across upper canines 6.8; mandibular length 13.7.

Distribution.—The type series is known from two localities in Kenya, and there are at least five additional Kenyan localities represented by other specimens. Four specimens, CMNH 61497–61500, were collected at Karibiti. CMNH 61501 was collected in the Laikipia District of the Rift Valley Province: Uaso Nyiro River, Nanyuki. CMNH 98042 was collected in the Kwale District of the Coastal Region: Shimba Hills National Reserve, Makandara Picnic Site, 7 km S, 8 km W Kwale (4º15'S, 39º23'E). CMNH 98044, 98045, and 98054 were collected in the Machakos District of the Eastern Province: Bushwackers, 11 km N, 17 km E Kibwezi (2º19'S, 38º07'E). CMNH 102248 and 102249 were collected in the West Pokot District of the Rift Valley Province: Weiwei River bridge, 1.5 km S, 1.5 km E Sigor (1º29'N, 35º29'E; 1030 m). These combined localities encompass a minimum geographic range of approximately 38,653 km^2, with altitude ranging from approximately 332 to 1905 m asl (Fig. 3).

Etymology.—It is our honor to name this species for Andrew N. Rebori (1948–2011). Rebori unknowingly touched the lives and inspired many individuals, including many museum professionals. He always maintained a keen interest in animals, especially bats, which exemplified his spirit and attitude toward life, 'Take flight every new day!'.

Diagnosis.—*Scotophilus andrewreborii* is distinguished from *S. dinganii* from Natal by a combination

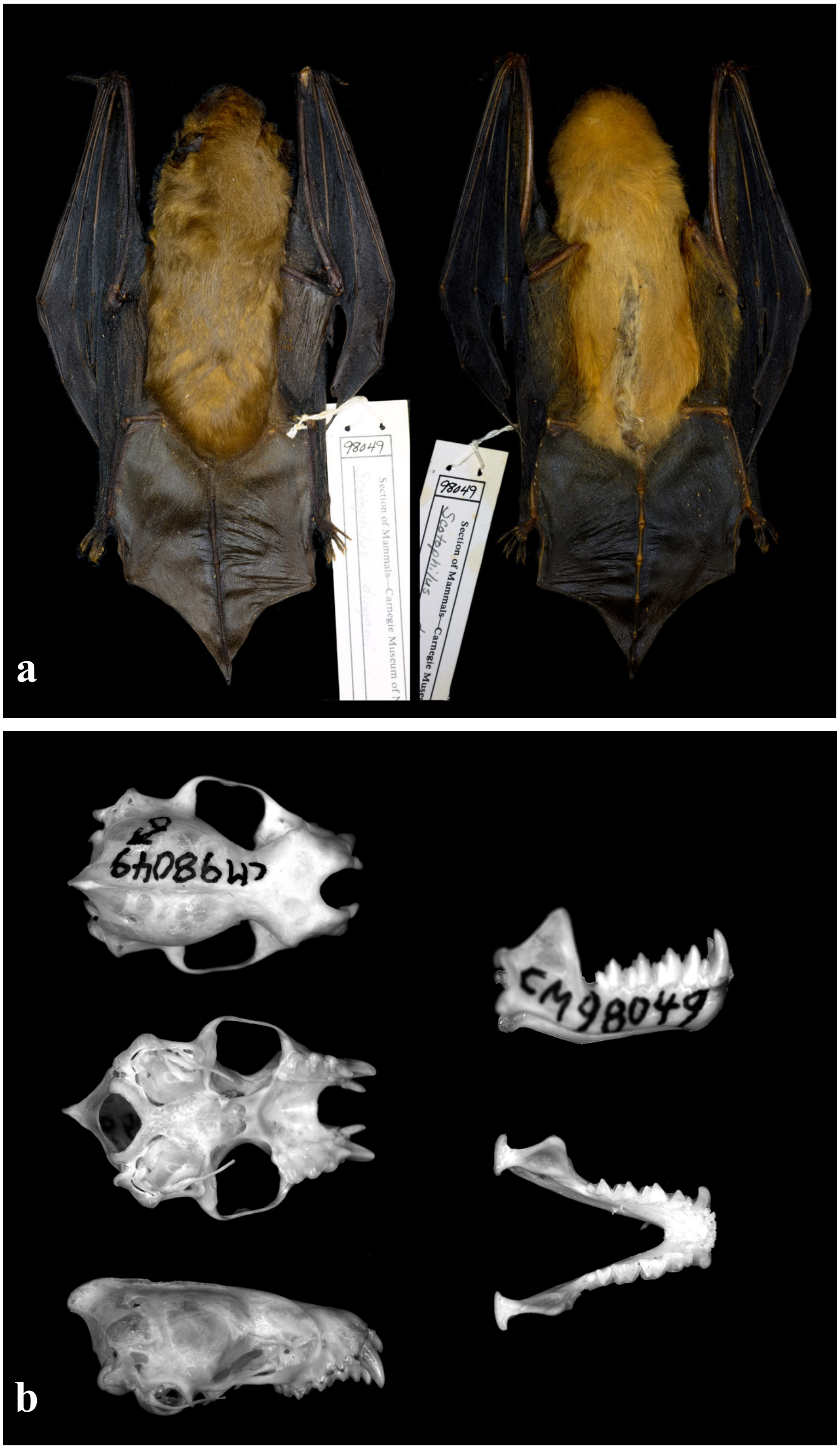

Figure 2. Study skin (a) and cranium and mandible (b) of *Scotophilus andrewreborii* holotype (CMNH 98049).

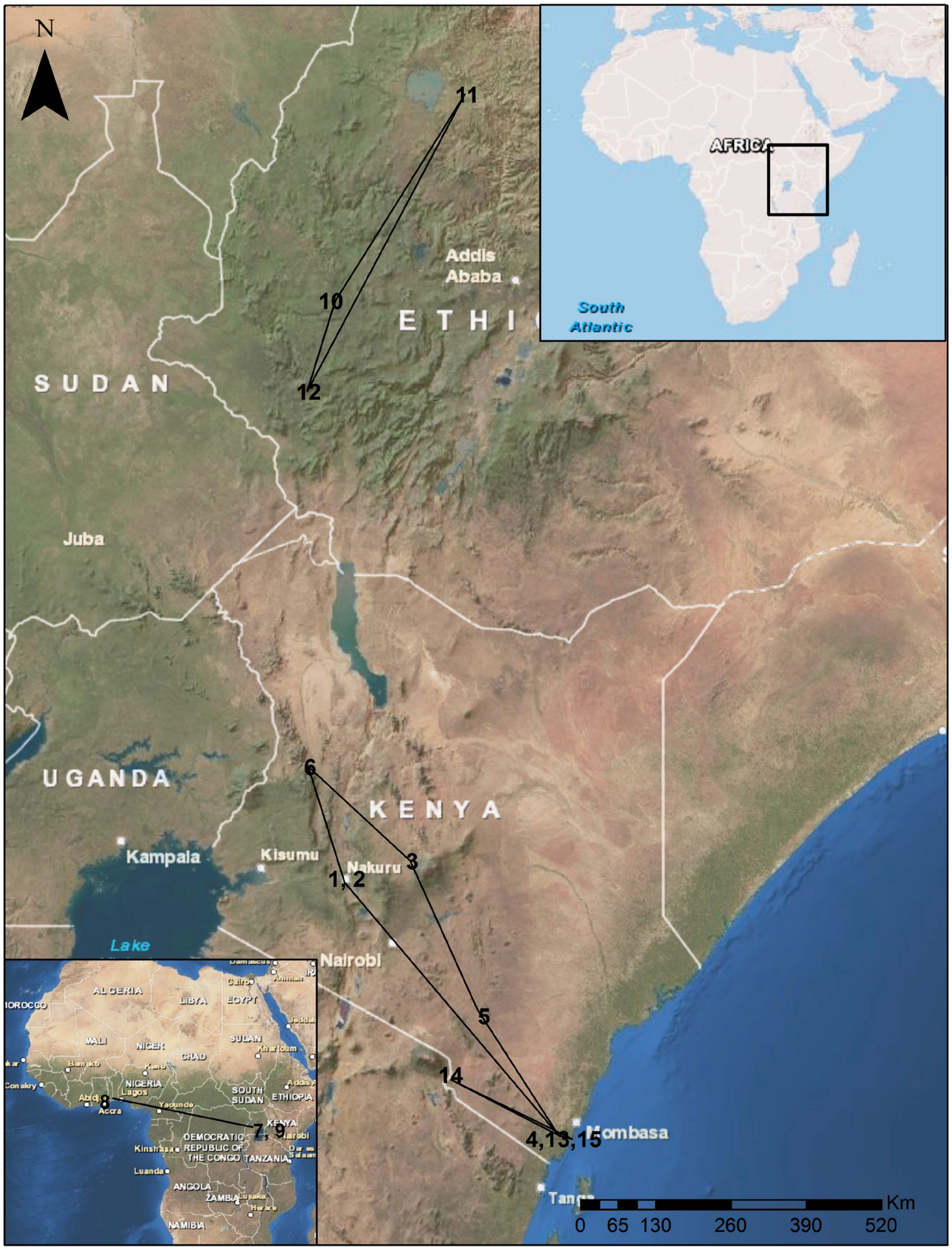

Figure 3. Distributions of the four new species in Africa (top right inset): *Scotophilus andrewreborii*: 1 - (Holotype and Paratype 1) 12 km S, 4 km E Nakuru; 2 - (Paratype 2) Njoro River; 3 - Nanyuki; 4 - Makandara; 5 - Bushwackers; 6 - Weiwei R. bridge. *Scotophilus livingstonii* (bottom left inset): 7 - (Holotype and Paratype 1) Ikuywa R. Bridge; 8 - (Paratype 2) Univ. Ghana Bot. Garden; 9 - 5 km S, 16 km E Kakamega. *Scotophilus ejetai*: 10 - (Holotype and Paratype 2) Dogy R. Bridge; 11 - (Paratype 1) Wereta-Weldiya Rd; 12 - Bishan Waka L. *Scotophilus trujilloi*: 13 - (Holotype and Paratypes) Moana Marine Sta.; 14 - Shimba Hills N.R.; 15 - 3 km E Taveta.

of external and craniodental features. *S. andrewreborii* averages slightly larger in body size for most characters (Table 1). Additionally the dorsal pelage in *S. andrewreborii* is more reddish than the browner dorsal fur of *S. dinganii*, and the ventral pelage in *S. andrewreborii* is orange vs. a much darker grey in *S. dinganii*.

Cranial measurements in *S. andrewreborii* are smaller, with non-overlapping measurements for braincase breadth (≤ 9.4 in *S. andrewreborii* vs. ≥ 9.5 mm for *S. dinganii*) for males (Table 2), and shorter mean skull length (18.9 in *S. andrewreborii* vs. 19.6 mm for *S. dinganii*), narrower zygomatic breadth (13.5 vs. 14.2 mm), shorter braincase height (7.8 vs. 8.1 mm), narrower interorbital width (4.4 vs. 4.8 mm), decreased breadth across upper molars (8.7 vs. 9.2 mm), and decreased breadth across upper canines (6.7 vs. 6.9 mm) for females (Table 3).

Description.—*Scotophilus andrewreborii* has a forearm length ranging 46.5–54.1 mm. Dorsal fur is red to mahogany. Ventral fur is tan to orange, darker on the chin and sides of the abdomen. Ears range 8.8–10.8 mm with semi-rounded tips. Ventral plagiopatagium is hairy proximal to body and forearm. Dorsal plagiopatagium, uropatagium, dactylopatagium, tail, legs, and feet are naked.

Premaxillae is deeply notched and wide. Sagittal crest is prominent along entire braincase. Skull is broad with wide orbits. Zygomatic arch is thin. Vomer has a well developed central process. Palatine bones are angled inward anteriorly. Tympanic bullae are round to oval in shape and well developed. Foramen magnum is round. Occipital condyles are developed.

Upper incisors (I1) are bilobate with inner cusp much longer than highly reduced outer cusp. Upper canines (C1) are long and well developed. Paracone of upper premolar (P1) is much longer than metacone, which is longer than hypocone. P1 has a smaller diameter, yet longer paracone than molars M1 and M2. Upper molars M1 and M2 similar in size and structure, ellipsoidal triangular outline in occlusal view, interior edge shortest. Paracone and metacone of M1 and M2 similar in length, both are longer than the hypocone. The last molar (M3) is highly reduced, less than ½ the diameter of M1 and M2 with an ellipsoidal rectangular outline in occlusal view.

Lower incisors (I1–I3) are small. I1 and I2 are well developed trilobate. Lower canine is long and well developed. First lower premolar (P1) is shorter than canine and slightly longer than paracone of M1. Lower molars (M1–M2) are similar in size and structure, with rectangular trapezoid outline in occlusal view, exterior edge shortest. Third lower molar M3 similar to M1–M2 structurally only slightly reduced in size. Paracone of M1–M3 longer than metacone, which is longer than hypocone. All mandibular processes are well developed. Coronoid process is triangular pointing upward. Angular process extends to same level as mandibular condyle.

Comments.—*Scotophilus andrewreborii* was referred to as Clade 9 in Trujillo et al. (2009). It is sister to clade 8, described below, from which it differs by 4.9% sequence difference at cytochrome-*b* which is indicative of species distinction. It differs from nominate *S. dinganii* (represented by clade 13 in Trujillo et al. 2009) by 9.3% sequence difference at cytochrome-*b*.

Scotophilus livingstonii*, new species
Livingstone's House Bat

Holotype.—Voucher CMNH 98051 (Fig. 4); adult male; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 8 November 1985 by Duane Schlitter. Prepared by Duane Schlitter, field number 7394. Muscle tissue sample TK 33534. External measurements (mm) are: head-body length 85.4; tail length 48.4; hind foot length 10.0; ear length 9.2; forearm 51.8. Cranial measurements (mm) are: greatest skull length 18.9; zygomatic breadth 13.9; braincase breadth 9.3; braincase height 8.2; interorbital width 4.4; greatest breadth across upper molars 9.0; greatest breadth across upper canines 6.9; mandibular length 14.4.

Type locality.—Kenya: Western Province, Kakamega District, Ikuywa River Bridge, 6.5 km S, 19 km E Kakamega (0º13'N, 34º55'E).

Paratypes.—Two additional specimens were collected from Kenya and Ghana and based on morphological and genetic data are designated as paratypes. The first paratype is voucher CMNH 98053; adult female; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh,

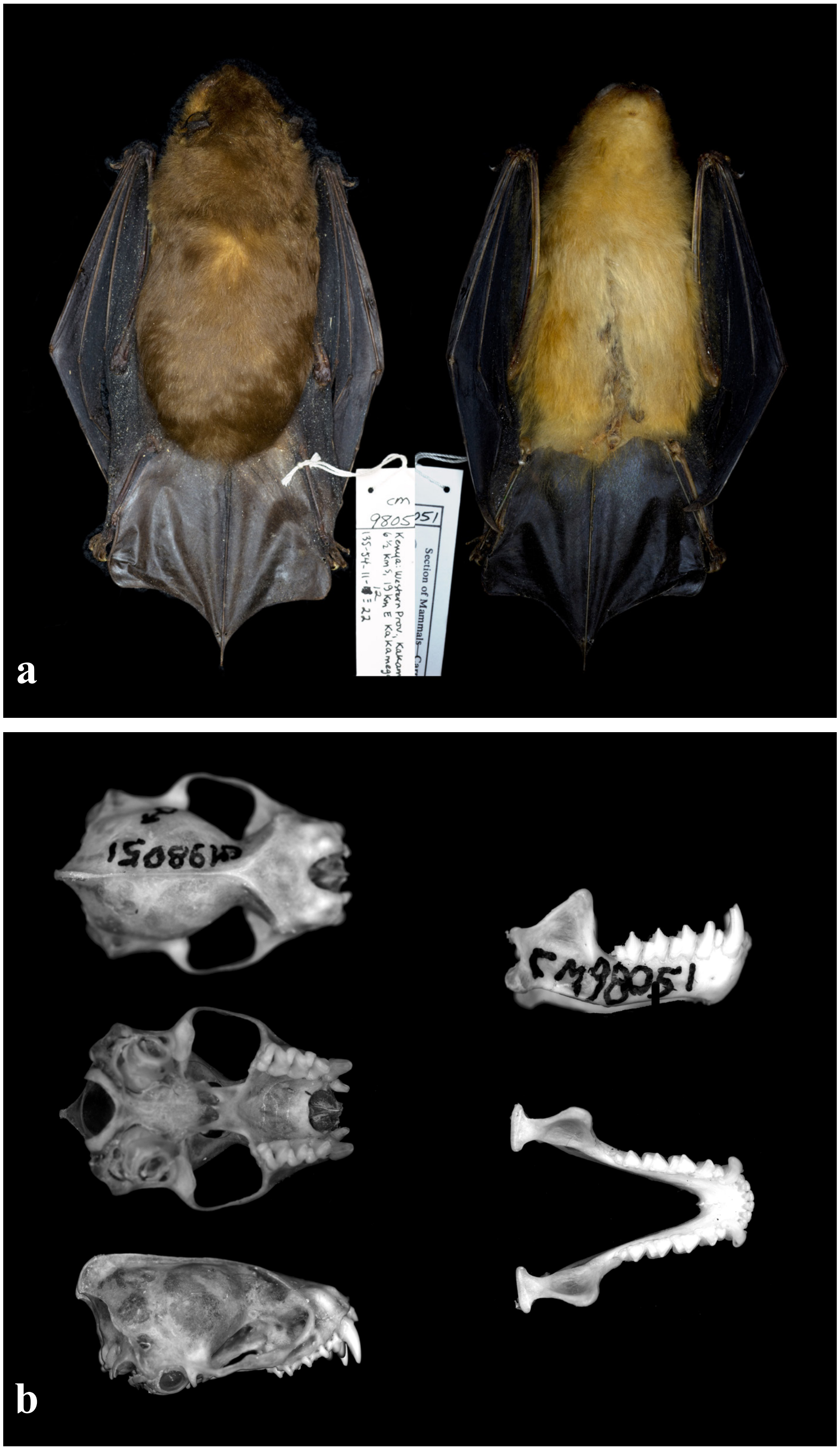

Figure 4. Study skin (a) and cranium and mandible (b) of *Scotophilus livingstonii* holotype (CMNH 98051).

Pennsylvania, USA). Collected on 8 November 1985 by Duane Schlitter from Ikuywa River Bridge, 6.5 km S, 19 km E Kakamega (0º13'N, 34º55'E), Kakamega District, Western Province, Kenya. Prepared by Duane Schlitter (field number 7396). Tissue sample TK 33536. External measurements (mm) are: head-body length 85.7; tail length 50.6; hind foot length 9.9; ear length 9.2; forearm 51.7. Cranial measurements (mm) are: greatest skull length 18.9; zygomatic breadth 13.9; braincase breadth 9.1; braincase height 8.0; interorbital width 4.4; greatest breadth across upper molars 9.0; greatest breadth across upper canines 6.8; mandibular length 14.4.

The second paratype is voucher NMNH 412150; adult female; standard skin and skull deposited at the National Museum of Natural History (Smithsonian Institution, Washington, DC, USA). Collected on 22 July 1967 by Bruce Hayward at University of Ghana Botanical Garden (5º40'N, 10º12'W), Legon, Eastern (Greater Accra) Region, Ghana. Prepared by Bruce Hayward (field number 4135). External measurements (mm) are: head-body length 87.4; tail length 45.3; hind foot length 12.3; ear length 10.0; forearm 54.0. Cranial measurements (mm) are: greatest skull length 18.7; zygomatic breadth 14.2; braincase breadth 9.2; braincase height 8.3; interorbital width 4.5; greatest breadth across upper molars 9.3; greatest breadth across upper canines 7.2; mandibular length 14.8.

Distribution.—The specimens are known from two international localities in southeast Ghana and southwest Kenya spanning approximately 3941 km (Fig. 3) with respective altitudes ranging from approximately 100 to 1530 m asl. Two additional specimens (skulls only), CMNH 102250 and 102251, were collected at a nearby locality in the Kakamega District of Kenya: 5 km S, 16 km E Kakamega (0º14'N, 34º54'E).

Etymology.—It is our honor to name this species for the late David Livingstone (1813–1873). At a time when most of Africa was barely known compared to today, Livingstone, a young Scot of humble means, explored central Africa. Between 1841 and his death in 1873, Livingstone made several expeditions into the interior of the continent, mapping uncharted lands and searching for navigable waterways.

Diagnosis.—Scotophilus livingstonii is distinguished from *S. dinganii* from Natal by a combination of external and craniodental features. *S. livingstonii* averages larger overall in body size (Table 1). Additionally the dorsal pelage in *S. livingstonii* is more reddish-mahogany than the browner dorsal fur of *S. dinganii*, and the ventral abdominal pelage in *S. livingstonii* is light buff vs. a much darker grey in *S. dinganii*.

Scotophilus livingstonii is also distinguished from *S. dinganii* from Natal by cranio-dental measurements. Male *S. livingstonii* have a shorter mean skull length (18.9 in *S. livingstonii* vs. 19.6 for *S. dinganii*; Table 2), and females have a longer mean mandibular length (14.6 in *S. livingstonii* vs. 13.9 mm for *S. dinganii*) (Table 3).

Description.—Scotophilus livingstonii has a forearm length ranging 51.7–55.6 mm. Dorsal fur is reddish brown. Ventral fur is buff with darker orange hue on throat and lower abdominal sides. Ears range 9.2–12.0 mm with rounded tips. Ventral plagiopatagium is hairy proximal to forearm. Dorsal plagiopatagium, uropatagium, dactylopatagium, tail, legs, and feet are naked.

Premaxillae deeply notched and wide. Sagittal crest is prominent along entire braincase. Skull is broad with wide orbits. Zygomatic arch is thin. Vomer is wide. Tympanic bullae are spherical and well developed. Foramen magnum is round to slightly oval. Occipital condyles are well developed.

Upper incisors (I1) are bilobate with inner cusp longer than outer cusp. Upper canines (C1) are long and well developed. Paracone of upper premolar (P1) is much longer than metacone, which is longer than hypocone. P1 has a similar diameter and metacone length as molars M1 and M2. Upper molars M1 and M2 similar in size and structure, with triangular outline in occlusal view, interior edge shortest. Metacone of M1 and M2 similar in length to paracone, and both longer than the hypocone. The last molar (M3) is highly reduced, similar in appearance to metacone and proximal hypocone of M2 with an ellipsoidal outline in occlusal view.

Lower incisors (I1–I3) are small. I1 and I2 present poorly developed bilobate. Lower canine is long and well developed. First lower premolar (P1) is shorter than canine. Lower molars (M1–M3) are similar in size and structure, with trapezoid outline in occlusal view, exterior edge shortest. Paracone of

M1–M3 longer than metacone, which is longer than hypocone. All mandibular processes are well developed. Coronoid process is triangular pointing upward. Angular process extends to same level as mandibular condyle.

Comments.—*S. livingstonii* was identified as clade 11 by Trujillo et al. (2009). Clade 11 is sister to a clade that includes clade 12 (see below) and nominate *S. dinganii* (clade 13). Clade 11 included two monophyletic lineages (11A and 11B) that corresponded to specimens from Ghana and Kenya, respectively. These lineages differ by 2.8% in cytochrome-*b* sequences and they differ from nominate *S. dinganii* by 5.5% (clade 11A) and 5.2% (clade 11B) which are indicative of species level distinction. The 2.8% difference between the Ghana and Kenya populations indicates these two lineages could be distinct taxa as well (species or subspecies), but more data are required to determine this.

***Scotophilus ejetai*, new species**
Ejeta's House Bat

Holotype.—Voucher BRTC 57970 (Fig. 5); adult male; standard skin and skull deposited at the Texas Cooperative Wildlife Collection (Texas A&M University, College Station, Texas, USA). Collected on 23 February 2001 by Duane Schlitter. Prepared by Duane Schlitter, field number 10310. Muscle tissue sample AK 21235. External measurements (mm) are: head-body length 76.0; tail length 41.8; hind foot length 10.7; ear length 11.7; forearm 50.4. Cranial measurements (mm) are: greatest skull length 17.5; zygomatic breadth 13.1; braincase breadth 9.2; braincase height 7.7; interorbital width 4.6; greatest breadth across upper molars 8.9; greatest breadth across upper canines 6.7; mandibular length 13.7.

Type locality.—Ethiopia: Orimaya Region, Dogy River Bridge (8º21'43"N, 35º53'02"E). Collected at 1390 m asl.

Paratypes.—Two additional specimens were collected from Ethiopia and based on morphological and genetic data are designated as paratypes. The first paratype is voucher CMNH 114043; adult female; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 2 April 1995 by Duane Schlitter from 7 km N, 10 km W Debre Tabor, Wereta-Weldiya Rd (11°55'N, 37°55'E; 2100 m), Gondar Province, Ethiopia. Prepared by Duane Schlitter (field number 9986). Tissue sample SP 13027. External measurements (mm) are: head-body length 77.1; tail length 40.4; hind foot length 12.1; ear length 10.2; forearm 50.3. Cranial measurements (mm) are: greatest skull length 18.8; zygomatic breadth 13.3; braincase breadth 9.2; braincase height 7.9; interorbital width 4.7; greatest breadth across upper molars 8.4; greatest breadth across upper canines 6.2; mandibular length 13.7.

The second paratype is voucher BRTC 57954; adult female; standard skin and skull deposited at the Texas Cooperative Wildlife Collection (Texas A&M University, College Station, Texas, USA). Collected on 21 February 2001 by Duane Schlitter at Dogy River Bridge (8º21'43"N, 35º53'02"E; 1390 m), Orimaya Region, Ethiopia. Prepared by Duane Schlitter (field number 10292). Tissue sample AK 21213. External measurements (mm) are: head-body length 72.6; tail length 45.1; hind foot length 9.3; ear length 11.3; forearm 50.2. Cranial measurements (mm) are: greatest skull length 17.4; zygomatic breadth 12.2; braincase breadth 8.6; braincase height 7.6; interorbital width 4.3; greatest breadth across upper molars 9.0; greatest breadth across upper canines 6.7; mandibular length 13.5.

Distribution.—The specimens are known from two localities in Ethiopia ranging from 1390 to 2100 m asl. An additional specimen, BRTC 57927 (skull only) was collected at a different locality in the Orimaya Region: E sideshore Bishan Waka Lake (07º18'01"N 35º16'24"E; 1402 m). These combined localities encompass a minimum geographic range of approximately 8580 km^2 (Fig. 3).

Etymology.—This species is named in honor of Dr. Gebisa Ejeta, Distinguished Professor of Plant Breeding & Genetics and International Agriculture at Purdue University, who was born and raised in the village of Wollonkomi, west-central Ethiopia. Dr. Ejeta is a plant breeder and geneticist who received the 2009 World Food Prize for his research and development of improved sorghum hybrids resistant to drought and Striga weed. The results of his work have dramatically enhanced the food supply of hundreds of millions of people in sub-Saharan Africa.

Figure 5. Study skin (a) and cranium and mandible (b) of *Scotophilus ejetai* holotype (BRTC 57970).

Diagnosis.—*Scotophilus ejetai* is distinguished from *S. dinganii* from Natal by a combination of external and craniodental features. *S. ejetai* averages smaller overall in body size, with females presenting non-overlapping forearm length (≤ 50.3 in *S. ejetai* vs. ≥ 52.5 mm for *S. dinganii*; Table 1). Additionally the ventral pelage in *S. ejetai* has an orange hue, whereas the ventral fur is buff with a greyish abdomen in *S. dinganii*.

Cranial measurements in *S. ejetai* are smaller, with non-overlapping measurements for skull length (≤ 18.5 in *S. ejetai* vs. ≥ 19.2 mm for *S. dinganii*), zygomatic breadth (≤ 13.3 vs. ≥ 13.6 mm) and braincase breadth (≤ 9.3 vs. ≥ 9.5 mm) for males (Table 2), and zygomatic breadth (≤13.5 vs. ≥ 13.8 mm) and braincase breadth (≤ 9.2 vs. ≥ 9.3 mm) for females (Table 3).

Description.—*Scotophilus ejetai* has a forearm length ranging 50.2–50.4 mm. Dorsal fur is dark reddish mahogany. Ventral fur is orange with a grayish hue on the abdomen. Ears range 10.2–11.7 mm with rounded tips. Ventral plagiopatagium is hairy proximal to forearm. Dorsal plagiopatagium, uropatagium, dactylopatagium, tail, legs, and feet are naked.

Premaxillae deeply notched and wide. Sagittal crest is prominent along entire braincase. Orbits are wide ventrally with square outline and rounded corners. Zygomatic arch is thin. Palatine bones are angled inward anteriorly. Tympanic bullae are well developed and spherical to conical in shape with anterior projection. Foramen magnum is slightly oval. Occipital condyles are well developed.

Upper incisors (I1) are bilobate with inner cusp much longer than highly reduced outer cusp. Upper canines (C1) are long and well developed. Paracone of upper premolar (P1) is much longer than metacone, which is longer than hypocone. P1 has a smaller diameter, yet longer paracone than molars M1 and M2. Upper molars M1 and M2 similar in size and structure, with trapezoid outline in occlusal view, interior edge shortest. Metacone of M1 and M2 longer than paracone, which is longer than the hypocone. The last molar (M3) is highly reduced, half the length of M1 and M2 with a rectangular outline in occlusal view.

Lower incisors (I1–I3) are small. I1 and I2 present trilobate. Lower canine is long and well developed. Lower premolar (P1) paracone is shorter than canine. Lower molars (M1–M3) are similar in size and structure, with trapezoid outline in occlusal view, exterior edge shortest. Paracone of M1–M3 longer than metacone, which is longer than hypocone. M3 is more reduced than M1 and M2. All mandibular processes are well developed. Coronoid process is low. Angular process extends to same level as mandibular condyle.

Comments.—*S. ejetai* was identified by Trujillo et al. (2009) as clade 8 which is a paraphyletic cytochrome-*b* lineage including *S. ejetai* haplotypes as well as a single haplotype of *S. nigrita*. There is a distinct size difference between the two species, and the sharing of similar haplotypes is likely due to past hybridization, mtDNA capture, or incomplete lineage sorting. Clade 8 is sister to *S. andrewreborii* (clade 9) and is 4.9% different in sequence of cytochrome-*b*. It is 9.4% different from nominate *S. dinganii* (clade 13) which is indicative of species level divergence.

***Scotophilus trujilloi*, new species**
Trujillo's House Bat

Holotype.—Voucher CMNH 98038 (Fig. 6); adult male; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 18 October 1985 by Duane Schlitter. Prepared by Duane Schlitter, field number 7086. Muscle tissue sample TK 33263. External measurements (mm) are: head-body length 70.8; tail length 37.3; hind foot length 10.3; ear length 7.2; forearm 44.2. Cranial measurements (mm) are: greatest skull length 16.4; zygomatic breadth 12.0; braincase breadth 8.8; braincase height 6.5; interorbital width 4.7; greatest breadth across upper molars 8.0; greatest breadth across upper canines 5.6; mandibular length 12.1.

Type locality.—Kenya: Coastal Province, Kwale District, Moana Marine Station, 1 km S, 2 km E Ukunda (4º18'S, 39º35'E).

Paratypes.—Two additional specimens were collected from the type locality in Kenya and based on morphological and genetic data are designated as paratypes. The first paratype is voucher CMNH 98040;

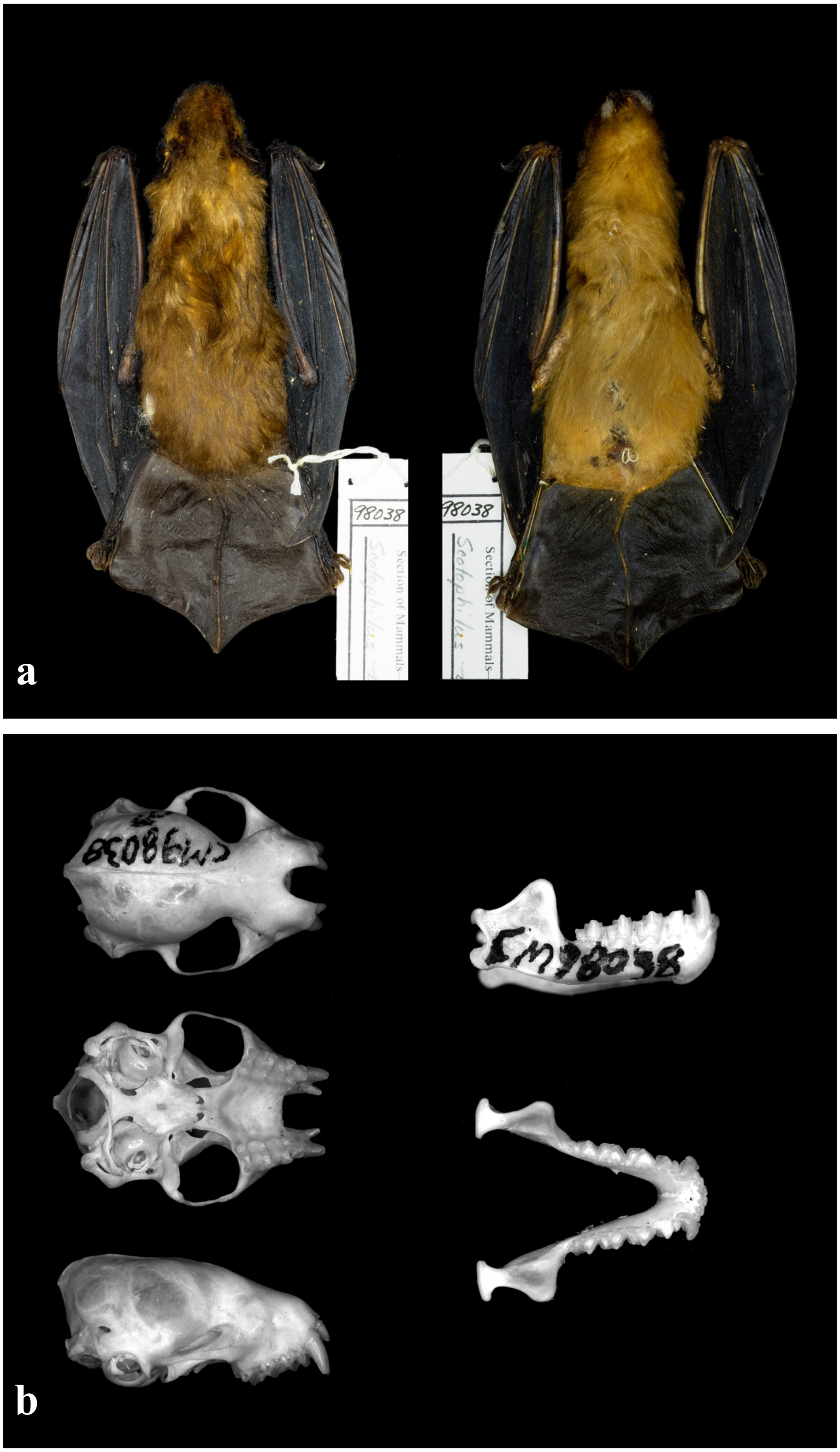

Figure 6. Study skin (a) and cranium and mandible (b) of *Scotophilus trujilloi* holotype (CMNH 98038).

adult female; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 18 October 1985 by Duane Schlitter from Moana Marine Station, 1 km S, 2 km E Ukunda (4º18'S, 39º35'E), Kwale District, Coastal Province, Kenya. Prepared by Duane Schlitter (field number 7089). Tissue sample TK 33266. External measurements (mm) are: head-body length 75.2; tail length 39.2; hind foot length 10.4; ear length 7.5; forearm 45.9. Cranial measurements (mm) are: greatest skull length 16.4; zygomatic breadth 12.2; braincase breadth 8.5; braincase height 6.7; interorbital width 4.7; greatest breadth across upper molars 7.6; greatest breadth across upper canines 5.4; mandibular length 12.5.

The second paratype is voucher CMNH 98041; adult female; standard skin and skull deposited at the Carnegie Museum of Natural History (Pittsburgh, Pennsylvania, USA). Collected on 18 October 1985 by Duane Schlitter from Moana Marine Station, 1 km S, 2 km E Ukunda (4º18'S; 39º35'E), Kwale District, Coastal Province, Kenya. Prepared by Duane Schlitter (field number 7090). Tissue sample TK 33267. External measurements (mm) are: head-body length 67.6; tail length 43.3; hind foot length 9.7; ear length 7.5; forearm 46.2. Cranial measurements (mm) are: greatest skull length 16.4; zygomatic breadth 11.9; braincase breadth 8.4; braincase height 6.9; interorbital width 4.5; greatest breadth across upper molars 7.8; greatest breadth across upper canines 5.3; mandibular length 12.2

Distribution.—The specimens are known from the type locality in Kenya, with three additional specimens (skulls only) representing two additional localities in Coastal Province, Kenya. CMNH 102240 was also collected in Kwale District of Kenya: Shimba Hills National Reserve, 7 km S, 8 km W Kwale (4º15'S, 39º23'E). CMNH 102241 and 102242 were collected in Taita District of Kenya: 3 km E Taveta (3º23'S, 37º42'E; 760 m). These combined localities encompass a minimum geographic range of approximately 543 km^2, with altitude ranging from approximately 0 to 760 m asl (Fig. 3)

Etymology.—It is our honor to name this species for Dr. Robert Trujillo (b. 1975), who's ground-breaking doctoral dissertation on the molecular systematics of *Scotophilus* paved the way for the description of the four cryptic species described in this paper (Trujillo 2005; Trujillo et al. 2009). Dr. Trujillo's dedication to science and environmental stewardship are reflected in his outstanding career in the US Forest Service.

Diagnosis.—*Scotophilus trujilloi* is distinguished from *S. viridis* from Mozambique Island by a combination of external and craniodental features. *S. trujilloi* averages larger in body size and shorter in forearm length, with females presenting non-overlapping head-body (≥ 65.4 in *S. trujilloi* vs. ≤ 65.0 mm for *S. viridis*) and forearm lengths (≤ 46.2 in *S. trujilloi* vs. ≥ 47.4 mm for *S. viridis*; Table 1). Additionally the dorsal pelage in *S. trujilloi* is mahogany, whereas the dorsal fur is brown in *S. viridis*. The ventral pelage in *S. trujilloi* is orange with a greyish abdomen, whereas the ventral fur is grayish-brown grizzled whitish abdominally in *S. viridis*.

Cranial measurements in *S. trujilloi* differ from *S. viridis*, with shorter mean braincase height in males (6.7 in *S. trujilloi* vs. 7.3 mm for *S. viridis*, Table 2); and females (6.9 vs. 7.2 mm), as well as non-overlapping mandibular length (≤ 12.5 in *S. trujilloi* vs. ≥ 12.9 mm for *S. viridis*) in females (Table 3).

Description.—*Scotophilus trujilloi* has a forearm length ranging 43.8–46.2 mm. Dorsal fur is reddish-mahogany. Ventral fur is orange with a greyish abdomen. Ears range 7.2–7.9 mm with semi-rounded tips. Ventral plagiopatagium is hairy proximal to body and forearm. Dorsal plagiopatagium, uropatagium, dactylopatagium, tail, legs, and feet are naked.

Premaxillae deeply notched. Sagittal crest presents along entire braincase. Skull is broad with rounded orbits. Zygomatic arch is thin. Vomer has a well developed central process. Tympanic bullae are spherical and well developed. Foramen magnum is round. Occipital condyles are well developed.

Upper incisors (I1) are bilobate with inner cusp longer and wider than outer cusp. Upper canines (C1) are very large and well developed. Paracone of upper premolar (P1) is much longer than metacone, which is longer than hypocone. P1 has a smaller diameter but similar metacone length compared to molars M1 and M2. Upper molars M1 and M2 similar in size and structure, with triangular outline that is notched exteriorly in occlusal view, interior edge shortest. Metacone of M1 and M2 slightly longer than paracone, and both longer than the hypocone. The last molar (M3) is highly reduced, similar in appearance to metacone and proximal hypocone of M2 with an ellipsoidal outline narrowing exteriorly in occlusal view.

Lower incisors (I1–I3) are small. I1 and I2 present weakly developed trilobate. Lower canine is long and well developed. First lower premolar (P1) is shorter than canine. Lower molars (M1–M3) are similar in structure, with trapezoid outline in occlusal view, exterior edge shortest. Paracone of M1–M3 longer than metacone, which is longer than hypocone. M1 and M2 are similar in size and wider in diameter than M3. All mandibular processes are well developed. Coronoid process is low and triangular shaped. Angular process extends to same level as mandibular condyle.

Comments.—*S. trujilloi* was identified as clade 12 by Trujillo et al. (2009). Clade 12 is sister to *S. dinganii* (clade 13) with which it differs by 4.2%, which is indicative of species level divergence. It differs from nominate *S. viridis* (clade 7) by 11.5%.

DISCUSSION

Recognizing four new cryptic species of African *Scotophilus* reinforces the already well accepted concept that chiropteran, and mammalian, biodiversity is not always accurately depicted in our current taxonomy. Genetic diversity is far greater than previously believed, and morphology often shows greater plasticity as demonstrated herein. Of the four new species, three were inaccurately designated previously as *S. dinganii* (*S. andrewreborii*, *S. livingstonii*, and *S. ejetai*) and one as *S. viridis* (*S. trujilloi*). However, phylogenetic analysis shows the most closely related species to *S. dinganii* is *S. trujilloi*. Therefore, general morphological similarity does not accurately predict underlying genetic relationships in this lineage.

The description of these four species does not indicate a finish to biodiversity discovery in African *Scotophilus*. Indeed, indications of additional undescribed taxa have been reported based on echolocation (Jacobs et al. 2006) and genetics (Vallo et al. 2013), and *Scotophilus* in many parts of the African continent have not yet been well collected or assessed by modern methods. Continued efforts to better understand the systematics of African bats will contribute to better understanding of biodiversity and evolutionary history. In tandem with these components, better conservation plans for this ecologically important group of mammals may be built upon a better-known taxonomy (Fenton and Rautenbach 1998).

Scotophilus species boundaries can be elucidated with increased collection across the entire range, especially in Southeast Asia, coupled with molecular systematic studies. The tremendous variation in altitude and habitat types that *Scotophilus* inhabits suggests that more cryptic species coming to light is possible.

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Appendix

Gazeteer of specimens examined at different institutions with their respective catalogue numbers. Institutional acronyms are as follows: AMNH = American Museum of Natural History; BRTC = Biodiversity and Research Teaching Collection, Texas A&M University; CMNH = Carnegie Museum of Natural History; FMNH = Field Museum of Natural History; NMNH = National Museum of Natural History.

S. dinganii (N = 48).–SOUTH AFRICA: Natal (AMNH 81885–66, FMNH 152822–4, NMNH 351382, CMNH 41069, 41071–2); KENYA: Rift Valley Province (CMNH 61501, 98048–50, 102248–9; Coast Region – CMNH 98042); Karibiti (CMNH 61497–500); Eastern Province (CMNH 98044–5, 98054); Western Province (CMNH 98051, 98053, 102250–1); GHANA: Eastern Region (NMNH 412146, 412150–2, 412155–6, 429522–3, 429526); Greater Accra Region (CMNH 113641–3); ETHIOPIA: Gondar Province (CMNH 114043); Orimaya Region (BRTC 57927, 57954–6, 57958, 57969–70, 58657).

S. viridis (N = 17).–MOZAMBIQUE: Tete (NMNH 365414–9, 365421–2, 365425–6); KENYA: Coast Region (CMNH 98038–41, 102240–42).

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