Specific limits and emerging diversity patterns in East African populations of laminate-toothed rats, genus *Otomys* (Muridae: Murinae: Otomyini): Revision of the *Otomys typus* complex

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Abstract

We combined evidence from biogeography, craniodental traits, linear and geometric morphometrics (233 skulls), cytogenetics (karyotypes of 18 individuals) and mitochondrial DNA sequences (44 cytochrome *b* and 21 12S rRNA sequences) to test species limits within *Otomys typus* s.l. (Muridae: Murinae: Otomyini), a complex that is patchily distributed across alpine zones of Ethiopia and East Africa. Our results confirm the specific validity of *O. dartmouthi*, *O. jacksoni*, *O. orestes*, and *O. uzungwensis*, forms recently removed from synonymy under *typus* s.l.; support elevation of four other alpine forms to species (*O. fortior*, *O. helleri*, *O. thomasi*, and *O. zinki*); identify three additional new species (*O. cheesmani* **sp. nov.**, *O. simiensis* **sp. nov.**, *O. yaldeni* **sp. nov.**); and enable redefinition of *O. typus* s.s. as a species restricted to certain mountains west of the Great Rift Valley in Ethiopia (Simien and Guna Mountains in the north, extending to the highlands of the western rim of the Rift Valley). Phylogenetic interpretation of the cytochrome *b* data clearly demonstrates that the alpine morphotype once united under *O. typus* s.l. has originated independently at high elevations on several mountain ranges in eastern and northeastern Africa; although generally adapted to high-elevation vegetation, such alpine species are ecologically segregated from one another. Patterns of morphometric, genetic, and ecological differentiation among populations once misassigned to nominal *O. tropicalis* and *O. typus* more parsimoniously reflect regional cladogenesis along elevational gradients, rather than multiple, successive colonization by different ancestral forms from southern Africa as earlier supposed. Although incomplete and preliminary, information gathered for *O. tropicalis* indicates that it too is a species composite; several lines of research are discussed to redress its polyphyletic content. Our results, together with other recent taxonomic studies of *Otomys*, appreciably elevate the level of endemism within eastern Africa and underscore the significance of Africa's eastern highlands to the continental diversification of Otomyini.

Key words: *Otomys*, geometric morphometrics, cytochrome *b*, 12S rRNA, microendemism, speciation, Afromontane

Résumé

Nous avons combiné un ensemble de données, biogéographiques craniodentaires, morphométriques (linéaires et géométriques; 233 crânes), cytogénétiques (caryotypes de 18 individus) et moléculaires (ADN mitochondrial: 44 séquences de cytochrome *b* et 21 séquences de 12 rRNA) afin d'évaluer les délimitations d'espèces au sein d'*Otomys typus* s.l. (Muridae: Murinae: Otomyini), un complexe d'espèces distribué à travers les zones alpestres de l'Éthiopie et d'Afrique de l'Est. Nos résultats 1) confirment le statut spécifique d'*O. dartmouthi*, *O. jacksoni*, *O. orestes* et *O. uzungwensis*, des formes dont la synonymie avec *typus* s.l. a récemment été infirmée, 2) soutiennent l'élévation au statut d'espèce de quatre autres formes alpestres (*O. fortior*, *O. helleri*, *O. thomasi* et *O. zinki*), 3) permettent d'identifier trois nouvelles espèces supplémentaires (*O. cheesmani* **sp. nov.**, *O. simiensis* **sp. nov.**, *O. yaldeni* **sp. nov.**), et 4) nous permettent de redéfinir O. *typus* s.s. comme une espèce restreinte à certaines montagnes à l'ouest de la Vallée du Rift en Éthiopie (les montagnes Simien et Guna au nord, s'étendant aux pays montagneux du bord occidental de la vallée du Rift). L'interprétation phylogénétique des séquences de cytochrome *b* démontre clairement que la forme alpestre autrefois incluse dans *O. typus* s.l. est apparue de façon indépendante à de hautes altitudes sur plusieurs massifs montagneux en Afrique de l'Est et du Nord-Est. Bien que généralement adaptées à la végétation de haute altitude, de telles espèces alpestres sont écologiquement distinctes les unes des autres. Les différentiations morphométrique, génétique et écologique au sein des populations regroupées de façon incorrecte sous les noms *O. tropicalis* et *O. typus* reflètent plus parcimonieusement une diversification régionale suivant des gradients altitudinaux, plutôt qu'unecolonisation multiple, successive par différentes formes ancestrales d'Afrique du Sud, comme supposé antérieurement. Bien qu'incomplètes et préliminaires, les données obtenues pour *O. tropicalis* indiquent qu'il constitue aussi un complexe d'espèces. Plusieurs lignes de recherche sont envisagées afin de réévaluer son statut polyphylétique. Nos résultats, ajoutés à d'autres études taxinomiques récentes d'*Otomys*, élèvent sensiblement le niveau d'endémisme en l'Afrique de l'Est et soulignent l'importancedes hautes terres de l'est de l'Afrique dans la diversification continentale des Otomyini.

Introduction

Laminate-toothed or "vlei" rats (Tribe Otomyini) are distributed over much of sub-Saharan Africa, where they constitute a small but morphologically distinctive radiation of murine rodents within the continent's savannas and highlands (Bohmann 1952; Carleton & Musser 1984; Taylor *et al.* 2004a; b; 2009a; b). Although southern Africa circumscribes the area of origin of the tribe (Pocock 1976; 1987; Denys 1989; 2003; Senegas & Avery 1998; Senegas 2001), eastern Africa, with its spectacular montane and alpine landscapes, is only beginning to be appreciated for its important role in diversification and endemism of otomyine rodents and other vertebrate taxa (Bowie *et al.* 2004; 2006; Carleton & Stanley 2005; Carleton & Byrne 2006; Carleton *et al.* 2006; Fahr *et al.* 2002; Kerbis Peterhans *et al.* 1998; Kerbis Peterhans & Hutterer, in press; Stanley & Hutterer 2000; Stanley & Olson 2005; Stanley *et al.* 2005; Huhndorf *et al.* 2007; Taylor *et al.* 2009a; Van der Straeten & Kerbis Peterhans 1999). Musser & Carleton (2005:1524) emphasized the need for renewed revision of *Otomys* F. Cuvier (1824) populations that inhabit the rugged East African mountain ranges and volcanoes, and recent studies have elevated several species formerly obscured in synonymy under *O. denti* Thomas (1906), *O. tropicalis* (1902), or *O. typus* Heuglin, (1877) (Carleton & Byrne 2006; Taylor *et al.* 2009a) and identified unnamed cytochrome *b* (cyt *b*) lineages from the Nyika Plateau, Malawi, and the Eastern Arc Mountains, Tanzania (Taylor *et al.* 2009a). The present investigation contributes new information that bears on the status of additional taxa placed within the *O. typus* complex.

Bohmann's (1952) classic revision of *Otomys* established the polytypic arrangement of *O. typus* (Heuglin, 1877) that has prevailed in systematic treatises over the latter 1900s (e.g., Misonne 1974; Honacki *et al.* 1982; Corbet & Hill 1991; Musser & Carleton 1993; see Table 1). Whereas previous authors had restricted *O. typus* to Ethiopia (Dollman 1915; Allen 1939; Ellerman 1941), Bohmann dramatically expanded its morphological and geographic definition to embrace 11 subspecies that range over disjunct alpine settings in eastern Africa (Fig. 1a): nominate O. *typus* Heuglin (1877) and the subspecies *fortior* Thomas (1906a), *helleri* Frick (1914), and *malkensis* Frick (1914) from the Ethiopian highlands; *dartmouthi* Thomas (1906b) from the Ruwenzori Mountains; *jacksoni* Thomas (1891) from Mount Elgon; *orestes* Thomas (1900) from Mount Kenya; *thomasi* Osgood (1910) from the Mau Escarpment; *malleus* Dollman (1915) and *squalus* Dollman (1915) from the Aberdare Mountains; and *zinki* Bohmann (1943) from Mount Kilimanjaro. Soon after Bohmann's (1952) revision, Lawrence and Loveridge (1953) described *O. uzungwensis* from the Udzungwa Mountains, southcentral Tanzania; without presentation of any character data, Misonne (1974) associated the taxon as the southernmost representative of *O. typus*. Bohmann (1952) generally characterized this geographically disparate assemblage as having a pallid dorsal pelage and buffy post-auricular tufts, relatively short tail, an arched cranial profile with narrow interorbit and large auditory bullae, and lower incisors with two deep grooves. In resurrecting *O. orestes* and *O. uzungwensis* as valid species, however, Carleton & Byrne (2006) stressed that such traits do not uniformly describe the taxa that Bohmann subsumed under *O. typus* and that such unique morphologies, isolated on East African mountain tops, exhibit strong morphometric differentiation from *O. typus* proper in Ethiopia. The authors urged continued investigation of taxa allocated to *O. typus* sensu Bohmann (1952) and Misonne (1974).

Based on examination of relevant type specimens and critical historical series in the world's museums, we here integrate evidence from craniodental morphology, linear and geometric morphometry, as well as molecular and cytogenetic data to critically test species limits within the *O. typus* s.l. complex. In particular, we 1) elevate four additional synonyms of *O. typus* s.l. to species (*O. fortior*, *O. helleri*, *O. thomasi*, *O. zinki*); 2) corroborate the specific status of other taxa recently removed from the synonymy of *O. typus* (*O. dartmouthi*, *O. jacksoni*, *O. orestes*, and *O. uzungwensis*); and 3) redefine Ethiopian *typus* as a species complex endemic to the Ethiopian highlands, comprising (based on chromosomal, molecular and morphological grounds) six distinct lineages including *O. typus* s.s., *O. fortior*, *O. helleri*, and three new species (*O. yaldeni* **sp. nov.**, *O. cheesmani* **sp. nov.**, *O. simiensis* **sp. nov.**). Our results decidedly underscore the polyphyletic stature of *typus*, as previously understood by Bohmann and others, and support the independent radiation into alpine environments from different otomyine stocks as conjectured by Carleton & Byrne (2006).

Discrimination of the above species necessarily required extensive comparison with and robust analyses of *Otomys* populations that occupy montane altitudes in eastern African mountains (Fig. 1b), namely forms currently assigned to *O. tropicalis* sensu lato (*tropicalis* Thomas 1902b, *nubilis* Dollman 1915, and *vivax* Dollman 1915 from central Kenyan highlands; *elgonis* Wroughton 1906 from Mount Elgon; *rubeculus* Dollman 1915 and *ghigii* de Beaux 1924 from Uganda; *faradjius* Hatt 1934 and *vulcanis* Lönnberg and Gyldenstolpe 1925 from northern and eastern Democratic Republic of Congo (DRC); and *giloensis* Setzer 1953 from the Imatong Mountains, Sudan). We do not recommend nomenclatural changes within the *tropicalis* complex, but we do provide several profitable lines of inquiry for future research.

TABLE 1. Main classifications of 14 species-group taxa* historically associated with alpine biotopes in eastern Africa (also see Fig. 1). Names in parentheses were allocated as full synonyms to the taxon listed above.

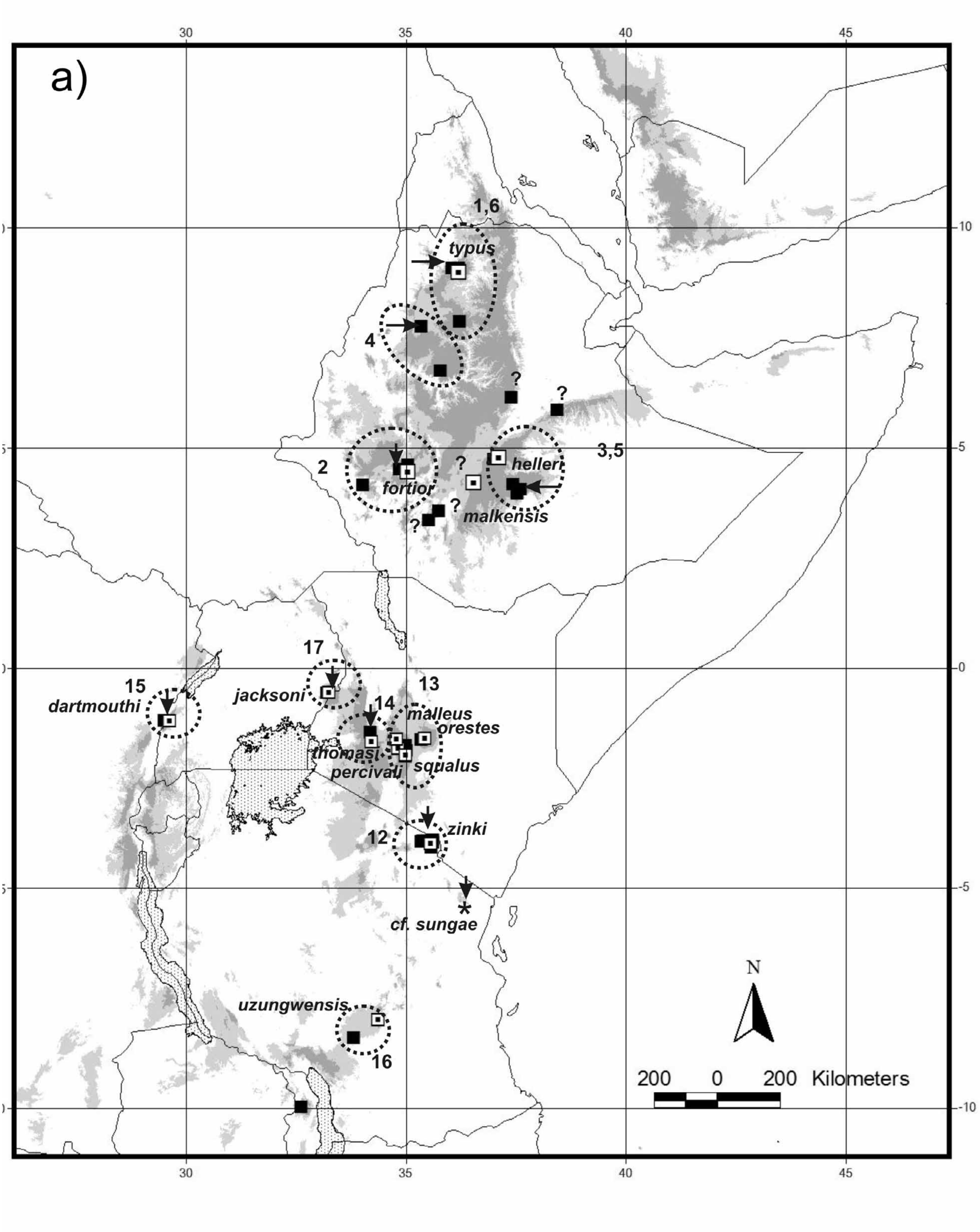
Dollman (1915)	Allen (1939), Ellerman (1941)	Bohmann (1952), Misonne (1974)	Musser & Carleton (2005)
O. dartmouthi	*O. dartmouthi*	*O. typus*	*O. dartmouthi*
		(*degeni*)	
O. fortior	*O. jacksoni*	*O. t. dartmouthi*	*O. jacksoni*
	O. j. helleri	*O. t. fortior*	
O. jacksoni	*O. j. malkensis*	*O. t. helleri*	*O. orestes*
		O. t. jacksoni	(*malleus*)
O. orestes	*O. orestes*	*O. t. malkensis*	(*percivali*)
		O. t. malleus	(*squalus*)
O. percivali	*O. percivali*	(*percivali*)	(*thomasi*)
		O. t. orestes	(*zinki*)
O. thomasi	*O. thomasi*	*O. t. squalus*	
O. t. malleus	*O. t. malleus*	*O. t. thomasi*	*O. typus*
O. t. squalus	*O. t. squalus*	*O. t. uzungwensis*	(*degeni*)
		O. t. zinki	(*fortior*)
O. typus	*O. typus*		(*helleri*)
(*degeni*)	(*degeni*)		(*malkensis*)
	O. t. fortior		
			O. uzungwensis

*Authors and type localities: *dartmouthi* Thomas 1906b—Uganda, Mt Ruwenzori; *degeni* Thomas 1902a—Ethiopia, Gombitchu; *fortior* Thomas 1906a—Ethiopia, Charada Forest; *helleri* Frick 1914—Ethiopia, Chilalo Divide; *jacksoni* Thomas 1891—Uganda, Mt Elgon; *malkensis* Frick 1914—Ethiopia, Malka; *malleus* Dollman 1915—Kenya, Lake Olbollossat; *orestes* Thomas 1910—Kenya, Mt Kenya; *percivali* Dollman 1915—Kenya, 12 mi S Lake Olbollossat; *squalus* Dollman 1915—Kenya, Mt Kinangop; *thomasi* Osgood 1910—Kenya, Molo; *typus* Heuglin 1877—Ethiopia, Simien Mts; *uzungwensis* Lawrence & Loveridge 1953—Tanzania, Udzungwa Mts; *zinki* Bohmann 1943—Tanzania, Mt Kilimanjaro.

Material and methods

Specimens and analytic samples. We examined 321 specimens (skins and skulls) of *Otomys* from eastern Africa and Ethiopia, from the following museum collections: American Museum of Natural History, New York (AMNH); Durban Natural Science Museum (DM); Field Museum of Natural History, Chicago (FMNH); Liverpool Museum, Liverpool (LM); Museum of Comparative Zoology, Harvard University (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Royal Museum of Central Africa, Tervuren, (RMCA); United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Museum für Naturkunde, Stuttgart (SM); The Natural History Museum, London (BM); and the Zoological Museum of the Moscow State University, Russia (ZMMU). Locality data from these specimens were used to map species distributions and to delimit geographically cohesive Operational Taxonomic Units (OTUs) for morphometric analyses (Fig. 1). Photographs of study skins and notes were taken to describe variation in pelage colour. Each skull was assigned to a relative age class from 1 (youngest) to 5 (oldest) based on a combination of tooth wear, skull shape, and degree of suture closure, as described by Taylor & Kumirai (2001). Linear measurements and photographs for geometric morphometric analysis were taken only from intact skulls judged to be "adult" (age classes 4 and 5, as explained below); thus, final multivariate analyses and sample statistics were based only on 247 "adult" (age class 4 and 5) skulls as explained below; of which 128 were *O. typus* s.l., the remainder comprising comparative samples of *O. tropicalis* Thomas

(1902) s.l. (n=67), *O. barbouri* Lawrence & Loveridge (1953) (n=14), *O. lacustris* G. M. Allen & Loveridge (1933) (n=23) and *O. sungae* Bohmann (1943) (n=15) (Table 2). The entire sample was subdivided into 20 OTUs. Full locality information and Museum accession numbers of all specimens examined are provided within Taxonomic Summary and Appendix 1.



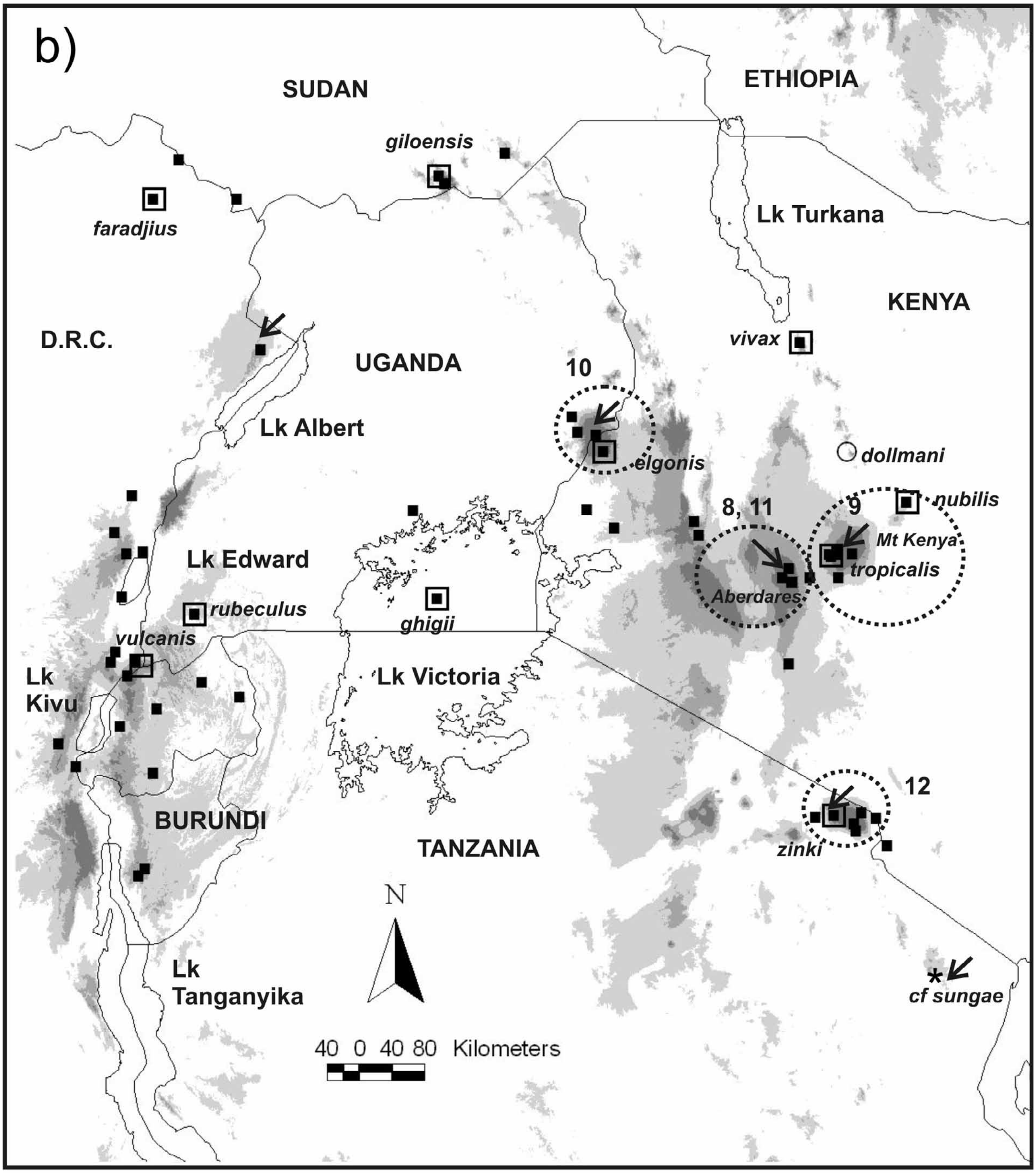


FIGURE 1. Map of east African montane and alpine zones showing distribution of type localities (large, open labeled squares) of forms previously attributed to (a) *Otomys typus* s. l. and (b) *O. tropicalis* s. l. Closed squares represent Museum cranial material examined. Circles enclosed localities assigned to OTU's for this study (in Ethiopia these represent hypothesized taxa based on cytogenetic, molecular and morphological data); numbers indicate OTU numbers in Table 1. Arrows indicate localities from which cytochrome-*b* sequences were available for this study. The asterisk indicates material from a specimen of uncertain identity assigned to cf. *sungae*.

TABLE 2. Summary of east African *Otomys* material included in final morphometric (Lin. = linear variables; Dor. = dorsal landmarks; Lat. = lateral landmarks) and molecular (Mol.) analyses. Latitude (Lat.) and longitude (Long.) are provided in decimal degrees format.

Locality	Lat./ Long.	N Lin.	N Dor.	N Lat.	N Mol.(collector)	Museum holdings
Otomys typus s.l. (Ethiopia): OTUs 1–7						
OTU 1 (n=6): *O. typus s.s.* 2n=58, NFa=58 (Ethiopia: Simien Mts, Guna Mt)						
Simien Mts (TYPE: *typus*)	13.083N 38.2E	-	-	-	-	BM
Guna Mt	11.71N 38.25E	4	-	-	1 (Lavrenchenko)	ZMMU
Chennek area (Simien Mts)	13.25N 38.217E	(2)	-	-	-	ZMMU
Geech Mt, Simien Mts	13.083N 38.2E	2	2	2	-	FMNH
OTU 2 (n=8): *O. fortior*, 2n=58, NFa=58 (Ethiopia: Beletta, Sheko & Charada Forests)						
Kaffa, Charada Forest (TYPE: *fortior*)	7.4167N 36.75E	1	1	1	-	BM
Beletta Forest	7.533N 36.55E	6	-	-	5 (Lavrenchenko)	ZMMU
Sheko Forest	7.067N 35.5E	1	-	-	-	ZMMU
OTU 3 (n=19): *O. typus* Sp.B (= *O. helleri*) 2n=58, NFa=58 (Ethiopia: Bale Mts, Arussi Plateau)						
Arussi, Mt Albasso	7.82N 39.22E	2	1	1	-	USNM, BM
Bale Mts	7.1N 39.77E	17	3	3	2 (Lavrenchenko)	MNHN (4), ZMMU (12), SM (1)
OTU 4 (n=7): *O. typus* Sp.C (= *O. cheesmani* **sp. nov.**) (Ethiopia: Dangila (Lake Tana), Debre Marcos)						
Dangila, Lake Tana	11.583N 37.167E	6	-	-	-	BM
Debre Marcos	10.33N 37.7E	1	-	-	-	BM
OTU 5 (n=4) : *O. typus* Sp. A (= *O. yaldeni* **sp. nov.**), 2n=56, NFa=54 (Ethiopia: Bale Mts)						
Dinsho, Bale Mts	7.1N 39.77E	3	-	-	-	MNHN (1), ZMMU (2)
70 km NW of Kebre-Mengist	6.383N 38.583E	1	-	-	-	BM
OTU 6 (n=5): *O. typus* Sp.D (= *O. simiensis* **sp. nov.**) 2n=54, NF=56 (Ethiopia : Simien Mts)						
Sankaber, Simien Mts	13.233N 38.05E	5	-	-	4(Lavrenchenko)	ZMMU
OTU 7 (n=25) : *O typus*, Ethiopia: unassigned localities						
Chenca, 2700 m	6.333N 37.6667E	9	-	-	-	SM
Chilalo (TYPE: *helleri*)	7.8333N 39.333E	6	-	-	-	SM, CM
Hirna (near), 2520 m	9.2N 41.0167E	2	-	-	-	SM
Jimma, 1750m	7.65N 36.783E	4	-	-	-	USNM
Ankober	9.567N 39.717E	1	-	-	-	SM
Bongke, 3000-3200 m	6.083N 37.383E	2	-	-	-	SM
Malka (TYPE: *malkensis*)	7.117N 38.617E	-	-	-	-	CM
Gombitchu 2450 m (TYPE: *degeni*)	9.333N 38.666E	1	1	-	-	BM
Otomys tropicalis s.l. (East Africa): OTUs 8–11						
OTU 8 (n=19): *O. t. tropicalis* (Aberdares) * = molecular outlier						
"Aberdares"	-0.3167S 36.7E	6	2	1		MRAC(1), USNM(1), BM(4)
"Aberdares, moorland"	-0.4667S 36.733E	3	5	6	4 (E. Verheyen)	MRAC
Aberdare Mts, Changongorra, 7,000 ft (2140 m)	-0.4667S 36.7333E	1	-	-	-	USNM
Mt Kinangop, 2700 m	-0.467S 36.75E	1	-	-	-	MNHN
Nyeri, 16 km E	-0.417S 36.9333E	1	1	1	-	USNM
Ololua Forest Reserve	-1.3667S 36.7E	1	2		1 (E. Verheyen)	MRAC
Aberdares National Park Fishing Lodge, 9500 ft	-0.3167S 36.7E	5	-	-	3 (McLellan)	USNM
Aberdares, Ruhuruini *	-0.4167S 36.6333E	1	-	1	1 (E. Verheyen)	MRAC
OTU 9 (n=25): *O. t. tropicalis* (Mt Kenya)						
Kangaita, 6 mi N Kerugoy	-0.42S 37.25E	3				MNHN
"Mt Kenya"	-0.1500S 37.4E	2				MRAC, USNM

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TABLE 2 Continued

Locality	Lat./ Long.	N Lin.	N Dor.	N Lat.	N Mol.(collector)	Museum holdings
Mt Kenya KWS NM Gate	-0.1667S 37.15E	1	2	1	1 (E. Verheyen)	MRAC
Mt Kenya Met Station	-0.1667S 37.2167E	5	6	6	5 (E. Verheyen)	MRAC
Jomberi Range, NE of Mt Kenya (TYPE: *nubilis*)	0.4127N 38.0E	1				BM
Mt Nyiru, S of Lake Rudolph (TYPE: *vivax*)	2.17N 36.83E	1				BM
Mt Kenya, West Slope, 10,000 ft (3048 m) (TYPE: *tropicalis*)	-0.1667S 37.1667E	1				BM
Mt Kenya, West Slope, 7,000 – 12,000 ft	-0.1667S 37.1667E	8				USNM(7), AMNH(1)
Solai, Mt Kenya	-0.1S 37.23E	3				BM
Mt Kenya, Naro Moru, 10,000 ft	-0.1833S 37.1667E	-			1 (McLellan)	USNM
OTU 10 (n=15) : *O. t. elgonis* (Mt Elgon)						
Mt Elgon, Coletatomoi	?	1	1	1		MCZ
Junction camp at foot of Mt Elgon	1.15N 34.583E	1				MRAC
Mt Elgon. 15km from Chorlim Gate, bamboo zone	1.15N 34.5833E	2	2	2	3 (McLellan)	USNM
Mt Elgon, Bumasola Village	1.18N 34.38E	1			1 (Taylor)	DM
Mt Elgon, Sipi	1.35N 34.3167E	7	6	5		MCZ
S. Elgon	1.15N 34.583E	2				MRAC
Elgonyi, Mt Elgon, 7000 ft (2100 m) (TYPE: *elgonis*)	0.967N 34.6667E	1				BM
OTU 11 (n=11): *O. cf. tropicalis* (m1 with 5 laminae: Aberdares Summit)						
Aberdares	-0.3167S 36.7E	1				BM
Aberdares Mts, summit 11,000 ft	-0.3167S 36.7E	9	7	9		USNM
Mt Kinangop, Aberdares, 2700 m	-0.467S 36.75E	1				MNHN
Otomys typus s.l. (East Africa): OTUs 12–17						
OTU 12 (n=12): *O. orestes zinki* (Mt Kilimanjaro)						
"Kilimanjaro"	-3.0S 37.5E	1				SM
Mt Kilimanjaro NP, 7km N, 2.5km W Maua, 2477 m	-3.2078S 37.4469E	1			1 (Stanley)	FMNH
Kilimanjaro, 16km N, 4.5km W Maua 3995 m	-3.1261S 37.4267E	1		1		FMNH
Mt Kilimanjaro East, Maundi Crater, 3270 m, grassland	-3.0667S 37.5E	6	5	4	4 (E. Verheyen)	MRAC
Mt Kilimanjaro West, Londorosi 2350 m, forest	-3.05S 37.15E	2	3	3		MRAC
Mt Kilimanjaro West, Shira, 3000 m, moorland	-3.0333S 37.2E	1	1	1		MRAC
OTU 13 (n=15): *O. orestes* (Mt Kenya & Aberdares)						
Mt Kenya, Teleki Valley, 13,000 ft (3962 m) (TYPE: *orestes*)	-0.1333S 37.25E	1		1		BM
Aberdare Mts, summit 11,000 ft	-0.3167S 36.7E	2		1		USNM
Aberdares National Park Fishing Lodge, 9000-9500 ft	-0.3167S 36.7E	2		1	2 (McLellan)	USNM
Mt Kenya, 13,500 ft	-0.1667S 37.167E	2		2		USNM
Mt Kenya , 14,600-15,000 ft	-0.1667S 37.167E	3		2		AMNH
Aberdares, 12,500 ft	-0.4667S 36.7333E	1		1		AMNH
Aberdares, moorland	-0.4667S 36.7333E	1	1	1	1 (E. Verheyen)	MRAC
Lake Ol Bolossot, 20 km S, Naivasha District (TYPE: *percivali*)	-0.42S 36.5E	1				BM

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TABLE 2 Continued

Locality	Lat./ Long.	N Lin.	N Dor.	N Lat.	N Mol.(collector)	Museum holdings
Lake Ol Bolossot, Naivasha District (TYPE: *malleus*)	-0.1667S 36.45E	1				BM
Mt Kinangop, Aberdares (TYPE: *squalus*)	-0.62S 36.7E	1				BM
OTU 14 (n=5): *O. orestes thomasi* (Mau Escarpment and Uasin Gishu Plateau)						
Molo, Uasin Gishu Plateau	-0.2333S 35.733E	4	4	4		FMNH
Guas Ngishu Plateau, 32 km N of Ravine, 9000 ft	0.05N 35.7167E	1	1			USNM
OTU 15 (n=9): *O. typus dartmouthi* (Ruwenzoris)						
Ruwenzori East, Mubuku Valley, 12,500 ft (TYPE: *dartmouthii*)	0.37N 30.0E	4				BM
Ruwenzori Mts, Lk Bujuku, 11050 13,050 ft	-0.3833S 29.9333E	4	3	3	1 (Kerbis)	FMNH
Wusuwameso, 4380m	0.3833N 29.85	1				MRAC
OTU 16 (n=10): *O. typus uzungwensis* (Eastern Arc Range)						
Kigogo, Udzungwa Mts, 6000 ft	-8.6167S 35.25E	3	2	3		MCZ
Dabaga, Iringa District, Udzungwa Mts, 6000 ft (TYPE: *uzungwensis*)	-8.1167S 35.9167E	6	6	7		MCZ
Nyika Plateau, Malawi, 7000 ft	-10.583S 33.75E	1	1	1		MCZ
OTU 17 (n=3): *O. typus jacksoni* (Mt Elgon)						
Mt Elgon, crater, ca 3300-4200 m (TYPE: *jacksoni*)	1.17N 34.533E	1	1	1		BM
Kaburoni, Mt Elgon	1.167N 34.4833E	1	1	1		MCZ
Mude Cave Camp, Mt Elgon, 3600 m	1.167N 34.4833E	1			1 (Taylor)	DM
OTU 18 (n=13): *O. barbouri* (Mt Elgon)						
Mount Elgon: Mission Delomo	1.17N 34.49E	5	4	2		MNHN
Mude Cave Camp, Mt Elgon, 3600m	1.167N 34.48333E	4			2 (Taylor)	DM
Kaburoni, Mt Elgon (TYPE: *barbouri*)	1.167N 34.4833E	4	5	3		MCZ
OTU 19 (n=18): *O. lacustris* (Eastern Arc Range, S Highlands, Tanzania)						
Madehani, Ukinga Mts, NE end of Lk Nyasa, 7000 ft (2134 m) (TYPE: *lacustris*)	-9.3333S 34.0167E	8	4	7		MCZ(7), FMNH(1)
Ukaguru Mts,Mamiwa-Kisara FR, 1900m	-6.3792S 36.9361E	4	4	4		FMNH
Udzungwa Mts, 4km W, 5km N Chita, 1460 m	-8.475S 35.907E	1	1	1		FMNH
Udzungwa Mts, 19.5km N, 0.5km W Chita, 2000 m	-8.347S 35.939E	1				FMNH
Lucheche River, Abercorn (=Mbala)	-8.76667S 31.4E	1		1		MCZ
Dabaga, Iringa District, Uzungwe Mts, 6000 ft	-8.117S 35.917E	1	1			MCZ
Mt Rungwa Forest Reserve	-9.133S 33.667E	1	1	1		FMNH
Mbizi Mts (Forest Reserve), 0.5km S, 3km E Wipanga, 2300m	-7.875S 31.667E	1				FMNH
Chingombe, Ufipa Plateau	-7.875S 31.667E				1 (Genbank)	MRAC
Bondwa, Uluguru	-7.1S 37.64E				1 (Genbank)	MRAC
Igale, Poroto Mts				1		FMNH
OTU 20 (n=9): *O. sungae* (Usambara Mts, Tanzania)						
Kidunda Forest (2047 m), Kiranga, Usambaras, Tanzania	-4.976S 38.446E	1			1 (Laudisoit)	MRAC
Shume, Lushoto, 7000 ft (2134 m), Tanzania	-4.8S 38.25E	6				USNM(3) TM(3)
Sunga. Usambaras, Tanzania	-4.53S 38.233E	1				USNM
Magamba, Usambaras, Tanzania 5200 ft (1733 m)		1				FMNH

Morphology and morphometrics. Craniodental characters. Four qualitative variables historically applied in *Otomys* alpha taxonomy were scored for 267 skulls representing the 20 OTUs, including both intact skulls and those fragmented crania that suitably preserved the character in question. Character states of those four discrete variables are recognized as follows.

1. The approximate angle of inflexion where the nasal bones expand distally (see Taylor & Kumirai 2001; Taylor *et al.* 2004b; 2009a): 90–99°; 100–119°; 120–149°; >150°.

2. The number of grooves in the anterior face of the lower incisor: single, deep medial groove (1); one medial groove plus faint trace of a second lateral groove (1+t); one medial groove plus a shallow but distinct lateral groove (1+s); two well defined grooves, the lateral and medial corrugations approximately equal in depth (2).

3. The number of laminae in the upper third molar (M3): 6, 7, 8, or 9 complete laminae. The M3 was viewed in lateral aspect to verify that the posteriormost lamina was fully defined from the crown to the base.

4. The number of laminae in the lower first molar (m1): 4 complete laminae; 4+1; 5 complete laminae. The intermediate state (4+1) was encountered infrequently; in this condition, the anterior lamina was subdivided, possessing a small, anteromedial projection (presumptive fifth lamina).

The shape of the petrotympanic (= stapedial) foramen, whether a round hole or a slit-like gutter (illustrated in Meester *et al.* 1986), was also recorded, but a round hole was invariantly observed in all specimens of all OTUs and taxa we examined; only examples of *O. angoniensis* Wroughton (1906), a species not considered herein, exhibit the slit-like condition.

Linear measurements. Ten cranial dimensions, as defined and illustrated in Taylor & Kumirai (2001), were measured using Mitotoyo calipers, with resolution to 0.01 mm and accuracy to 0.1 mm: greatest length of skull (GLS), measured dorsally, equivalent to occipito-nasal length; depth of braincase (BCD), measured vertically at basioccipital; mandible length (MDL), greatest length of the mandible excluding teeth; maximum length of anterior palatal foramen (APF); nasal width (NAW), greatest width across nasals at right angle to skull axis; maxillary tooth row length (MXTRL), distance from anterior edge of first maxillary tooth to posterior edge of last maxillary tooth at crown; interorbital constriction (IOC), least distance dorsally between the orbits; zygomatic width (ZYW), greatest distance between the outer margins of the zygomatic arches; palatal length (PAL), from anterior edge of premaxillae to anterior-most point on posterior edge of palate; greatest length of bulla (BUL), along the longitudinal axis and excluding the eustachian tube.

Almost all the specimens were measured by one of us (PJT). Crania of 15 individuals of *tropicalis* (from Aberdares) and *typus* s.l. (from Beletta Forest, Jimma, Ethiopia) were measured by MDC after calibrating landmarks using specimens measured by both PJT and MDC. Craniometric data for 31 individuals from Ethiopia were collected by LAL whose dataset including 21 variables, seven of which were identical to those defined above (all but GLS and PAL). Comparison of several individuals measured by both LAL and PJT confirmed the accuracy of the landmarks used in these definitions. Based on very significant ($P << 0.001$) correlations obtained between ZYW and both GLS and PAL (in the data set of PJT), we estimated values for these missing variables (GLS and PAL) in the Ethiopian dataset of LAL using regression analysis. In this way we were able to compare data from LAL directly to those obtained by PJT and MDC.

Standard descriptive statistics (mean, range, and standard deviation) were derived for adult specimens (age classes 4 and 5) of all OTUs. To search for patterns among individual variables, Analysis of Variance (ANOVA) was performed using XLSTAT 2008.2.03 (Addinsoft 2008), followed by Tukey's HSD (Honestly Significant Difference) multiple comparison tests where more than two groups were involved. For multivariate analyses, variables were transformed to their natural logarithms in order to correct for size differences (hence unequal contributions to variance matrices) among linear variables (Marcus 1990; Carleton & Byrne 2006). Log-transformed linear data were subjected to exploratory principal component analysis (PCA) to observe relationships between individuals from different sexes, age classes, or geographic samples (OTUs). Canonical variates analysis (CVA) of the log-transformed variables was used to test the significance of and reveal phenotypic patterns between OTUs. Multivariate analyses of linear data were conducted using XLSTAT version 2008.2.03 (Addinsoft 2008) and NTSYS-pc (Rohlf 1997).

Geometric morphometrics. Using a Sony Cybershot DSC-H2 digital camera (6 megapixel; 12x optical zoom, macro function), mounted on a tripod at a fixed distance of approximately 20 cm from the skull (which was always mounted on graph paper), dorsal and lateral images were taken for between 123 (dorsal) and 111 (lateral) skulls from the same OTUs used for linear measurements.

Landmark placement and further analyses were performed using the thin plate spline (TPS) series of programmes. The programme tpsDig version 2.1 (Rohlf 2006) was used to capture landmarks in two dimensions for dorsal (14 landmarks) and lateral (14 landmarks) views (see Figs. 9 and 11 for position of landmarks on lateral and dorsal images respectively). The programme tpsRelw version 1.42 (Rohlf 2005) was used to conduct a Generalised Procrustes Analysis or GPA (Generalised Least Squares, GLS, of Rohlf & Slice 1990), which serves to translate, rotate and scale the landmark configurations, and produces a consensus configuration for the entire suite of specimens in the analysis via a series of iterations. GPA residuals are further decomposed into both non-uniform (non-affine), and uniform (affine) shape components. Non-affine shape expresses localized shape changes, and is represented by the weights matrix, W, of partial warp scores. Affine shape expresses shape changes that affect the entire configuration (i.e. dilation or sheer), and this component is represented by two vectors, U1 and U2. Together, U + W represent total shape. Relative warps analysis performs a principal component analysis of the covariance matrix of the total shape matrix (U + W). The programme tpsRegr version 1.35 (Rohf 2007) was used to perform a two-way MANOVA of the weights matrix to test for significant differences between sexes, and between age classes 3 and 4, in the Tora sample.

For introductions to geometric morphometrics and its application to rodent systematics see Corti (1993), Marcus and Corti (1996), Rohlf (1998), Rohlf and Marcus (1993), Rohlf (2002), and Taylor *et al.* (2004a, 2005, 2009a, b).

Cytogenetic methods. The chromosomal analysis was performed on Ethiopian samples of *O. typus* s.s. (n=1), *O. fortior* (n=6), “Sp. A” (= *O. yaldeni* **sp. nov.**; see Taxonomic Summary) (n=1), “Sp. B” (= *O. helleri*; see Taxonomic Summary) (n=6) and “Sp. D” (= *O. simiensis* **sp. nov.**; see Taxonomic Summary) (n=4). Somatic metaphases were prepared from bone marrow by the usual air-drying technique according to Ford and Hamerton (1956). Slides were stained with 4% Giemsa in phosphate buffer with pH = 7.0.

Molecular methods. Forty-four specimens (Appendix 2) were analyzed representing all but two forms *(thomasi* and *uzungwensis*) recognized within *O. typus* s.l., three forms currently assigned to *O. tropicalis* s.l., three species from eastern Africa (*O. barbouri, O. denti* and *O. lacustris*), two species from West Africa (*O. occidentalis* Dieterlen & Van der Straeten (1992) and *O. burtoni* Thomas (1918)) and three from southern Africa (*O. angoniensis*, *O. irroratus* Brants (1827) and *Parotomys brantsii* A. Smith (1834)). These specimens represent a subset of those analyzed morphologically and cytogenetically (Table 2, Appendix 1) for which appropriate material was available for molecular investigation. Nine species from within the subfamily Murinae but of different levels of relatedness to the Otomyini were selected as outgroups for constructing the phylogeny and for approximating the divergence times of lineages from cyt *b* sequence data (*Batomys granti* Thomas (1895), *Phloeomys sp.*, *Rattus norvegicus* (Berkenhout, 1769), *Mus musculus* Linnaeus (1758), *Micaelamys namaquensis* (A. Smith, 1834), *Aethomys sp.*, *Arvicanthis neumanni* Matschie (1894), *Lemniscomys striatus* (Linnaeus, 1758) and *Oenomys hypoxanthus* (Pucheran, 1855). In addition, a phylogeny was reconstructed from combined cyt *b* and 12S rRNA sequences of 21 Otomyini specimens using *Mus musculus*, *Micaelamys namaquensis*, *Arvicanthis somalicus* and *Lemniscomys striatus* (Linnaeus, 1758) as outgroups (Appendix 2).

Total genomic DNA was extracted from frozen or ethanol-preserved soft tissue samples using phenol-chloroform procedures (Sambrook *et al.* 1989). Polymerase chain reaction (PCR) amplification of the complete mitochondrial cyt *b* gene and a portion of 12S rRNA (small ribosomal subunit, ± 800 bp) followed standard methodology (Saiki *et al.* 1988). Conserved primers used to amplify cyt *b* fragments were L14724 and H15915 (Pääbo & Wilson 1988) and the *Otomys*-specific L15267 (Taylor *et al.* 2009a), and for amplifying 12S rRNA, L82 and H900 (Allard & Honeycutt 1992). Typical cycling conditions were: initial denaturation (2 min at 94 °C); 35 cycles of denaturation (30 s at 94 °C), primer annealing (30 s at 48-55 °C, primer-dependent), DNA extension (35 s at 72 °C); a final extension phase (5 min at 72 °C). Sequences were determined from purified PCR products (High-Pure, Roche) using big dye-terminator chemistry (Sanger *et al.* 1977) on ABI3100/ABI3130 Analyzers (Applied Biosystems). Outgroup sequences were sourced on Genbank™ except for the 12S rRNA sequence for *Micaelamys namaquensis* obtained in this study. Genbank accession numbers for newly sequenced cyt *b* and 12S rRNA gene fragments are provided in Appendix 2

Sequences were aligned in ClustalX (Thompson *et al.* 1997) and the functional reading frame for the protein-coding cyt *b* gene was verified using MacClade version 4.07 (Maddison & Maddison 2000). The 12S rRNA secondary structure model for *Mus* (Damberger & Gutell unpubl. in Sullivan *et al.* 1995) was used to improve the alignment. Phylogenetic tree reconstruction involved model-based maximum likelihood (ML, Felsenstein 1981) and Bayesian inference methods (BPP, Huelsenbeck & Ronquist 2001) as well as parsimony (Kluge & Farris 1969; unweighted and six-parameter-weighted [6PP]: Williams & Fitch 1990; Lanave *et al.* 1984; Rodriguez *et al.* 1990) and distance-based neighbour-joining (NJ, Saitou & Nei 1987) approaches. The best-fit models of sequence evolution for the overall cyt *b* gene (GTR+I+G), 12S rRNA (TrN+I+G), the combined cyt *b* / 12S rRNA data

(GTR+I+G) and the three codon positions of cyt *b* (pos 1: GTR+I+G, pos 2: TrN+I+G, pos 3: TrN+I+G) were estimated using MODELTEST (Posada & Crandall 1998; 2001; Posada 2006). PAUP version 4.0b10 (Swofford 2002) was used for NJ analysis based on uncorrected *p*-distances (Nei 1987) and corrected genetic distances (cyt *b*: GTR+I+G; 12S: TrN+I+G), for executing heuristic parsimony and likelihood searches with TBR branch swapping and random taxon additions (ML: 10; MP: 100) and to produce a 50% majority-rule consensus of minimal-length parsimony trees. Nodal support was assessed by non-parametric bootstrap analysis (Felsenstein 1985; 1000 iterations for NJ, parsimony and ML). Bayesian analysis (MrBayes version 3.1.2, Huelsenbeck & Ronquist 2003) of the independent cyt *b* data (1140 bp) and the concatenated cyt *b* / 12S rRNA sequences (1940 bp) were conducted to empirically determine the posterior probability distribution of trees, branch lengths and substitution parameters using four Markov Chain Monte Carlo chains, each starting from random trees, running simultaneously for $5x10^6$ generations (sampling and recording every 100th generation). The first $5x10^3$ were discarded as "burn-in". The average standard deviation of split frequencies was calculated to assess the similarity between the sets of trees recovered from two independent runs. Alignment gaps in 12S rRNA sequences of the combined data were coded as binary characters (0 gap absent / 1 gap present) according to the "simple indel coding" approach (Simmons & Ochoterena 2000) and added as additional characters to the end of the data matrix, while indels within the matrix were treated as "missing". The binary (restriction) model were specified for the nine binary characters in MrBayes (Command: Lset Coding=Variable).

Divergence date estimation. Given that the assumption of a global molecular clock was rejected for cyt *b* (using criteria outlined by Felsenstein 1988), Bayesian approximation under an uncorrelated, relaxed molecular clock (Drummond *et al.* 2006) was used to estimate mean and 95% confidence limits of divergence dates for the major lineages recovered in the cyt *b* tree. The analysis was executed using BEAST v1.4 package (Drummond & Rambaut 2006a), BEAUTI v1.4 (Drummond & Rambaut 2006b) and TRACER v1.3 (Rambaut & Drummond 2005). The best-fit substitution model for each codon position was assumed and four minimum fossil calibration dates were specified: 3.5 million years (Myr) for the minimum age for the oldest known *Otomys* fossil from southern Africa, *O.* cf. *gracilis* (Pocock 1987; Upper Pliocene, Makapansgat [at least 3.7–3.5 Mya old; Partridge 1973]); 6.0 Myr for the divergence of Arvicanthini and Otomyini lineages (Winkler 2002; Rowe *et al.* 2008); the *Mus-Rattus* lineage split at 11.0 Myr (Jacobs & Downs 1994; Rowe *et al.* 2008) and the divergence of *Batomys* and *Phloeomys* at 12.1 Myr (Rowe *et al.* 2008). To accomplish the date calibrations, we specified a normal prior (minimum estimated fossil age ± 0.1) for each node height. We specified no mean substitution rate and the tree model was selected for root height, so to allow the program to estimate this. FigTree version 1.3.1 was used for visualization of the dated tree.

Ecological methods. Defining bioclimatic niches. We used the programme BIOCLIMAv (Beta 1.1) (Moussalli *et al.* 2003) in ArcView version 3.2a to obtain data for *O. typus s.l.* (n=47 localities) for altitude and eight bioclimatic variables (WORLDCLIM version 1.4: http://biogeo.berkeley.edu/worldclim/; Hijmans *et al.* 2005) reflecting means, extremes and seasonal variation of temperature and precipitation: Bio1 (mean annual temperature), Bio4 (temperature seasonality), Bio5 (maximum temperature of warmest month), Bio6 (minimum temperature of coldest month), Bio12 (annual precipitation), Bio13 (precipitation of wettest month), Bio14 (precipitation of driest month) and Bio15 (precipitation seasonality). The environmental data were set to a spatial grid resolution of 2.5 arc minutes. We used PCA to summarise variation in altitude and bioclimatic variables between localities and OTUs. Given the steep elevational gradients and the imperfect level of precision implicit in determining geographical coordinates from historical localites using maps and gazetteers, we acknowledge that some degree of caution should be exercised when interpreting these results.

Results

Cytogenetic data

At least three distinct karyotypes occur among Ethiopian populations assigned to *Otomys* "*typus*" (see also Lavrenchenko *et al.* 1997). Examples of topotypic *O. typus* s.s. from the alpine zone of Mount Guna (female: ZMMU 172732), of *O. typus fortior* from southwestern Ethiopian forests (4 males: ZMMU 164961, 164962, 164965, 181666; two females: ZMMU 164963, 181667), and of *Otomys helleri* (= "Sp. B") (3 males: ZMMU 162595, 162596, 162601; 3 females: ZMMU 162597, 162599, 162600) from the alpine zone of the Bale Massif share an identical karyotype (2N=58, NFa=58). The chromosomal complement consists of one pair of small metacentrics (1) and a graded series of 27 pairs of acrocentrics (2–28), ranging in size from large to very small (Fig. 2a). The X-chromosome is a medium-sized acrocentric; the acrocentric Y-chromosome is 3/4 of the length of the X-chromosome. In a single specimen of *O. helleri* “Sp. B” (ZMMU 162601), one autosomal pair was heteromorphic, being represented by a submetacentric and two acrocentrics (see Aniskin *et al.* 1998).

A karyotype comprising only acrocentric chromosomes (2N=56, NFa=54), with X and Y similar in size to those of *Otomys helleri* (= “Sp. B”), was found in one individual termed *Otomys* “Sp. A” (= *O. yaldeni* **sp. nov.**; see Taxonomic Summary) (male: ZMMU 162594) from the Bale Massif (Fig. 2b, see also Lavrenchenko *et al.* 1997).

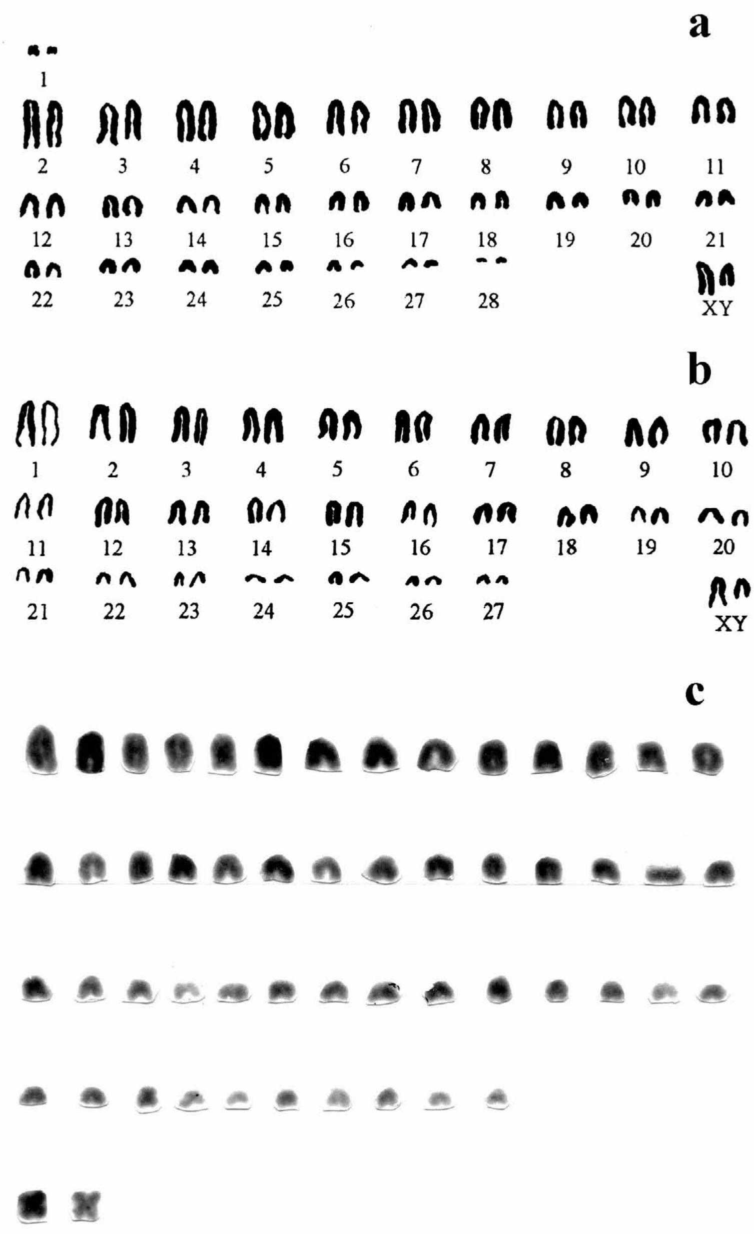

FIGURE 2. Giemsa stained karyotypes of (a) *Otomys helleri* (= “Sp. B”; n=6), *O. fortior* (n=6) and *O.typus* s.s. (n=1) (2n=58, NFa=58), (b) *Otomys yaldeni* **sp. nov.** (= “Sp. A”; n=1; 2n=56, NFa=54), and (c) *Otomys simiensis* **sp. nov.** (= “Sp. D”; n=4; 2n=54, NFa=54).

A third karyotype (2N=54, NF=56), termed "Sp. D" (= O. *simiensis* **sp. nov.**; see Taxonomic Summary), comprising 26 pairs of acrocentrics and one pair of medium-sized metacentrics, was found in four individuals (3 males: ZMMU 178757, 178758, 178759; 1 female: ZMMU 178762) from the Simien Mountains (Fig. 2c). The NFa was not determined because the sex chromosomes could not be identified.

Molecular data

The phylogeny in Fig. 3a reflects the relationships among 44 Otomyini specimens (Appendix 2) as recovered by Bayesian analysis of cyt *b* sequences (1140 bp). Largely similar topologies resulted from neighbor-joining (NJ, uncorrected *p* and GTR+I+G-corrected distances), six-parameter-weighted parsimony (6PP) analysis partitioned by codon position, and maximum likelihood analysis under the best-fit GTR+I+G model (unpartitioned), albeit with varying bootstrap support (bs) for some terminal and deeper relationships (Fig. 3a). Bootstrap support of 70% and above and Bayesian Posterior Probabilities (BPP) of 0.95 and above are considered significant. The topology strongly supports the monophyly of the Otomyini, renders the East African *Otomys* lineages paraphyletic and very prominently demonstrates that neither *O. typus* s.l nor *O. tropicalis* s.l. as traditionally understood are monophyletic. Rather, populations assigned to these two nominal species fall into eight well-supported clades, (annotated on Fig. 3a), some with similarly well-supported subclades (BPP: 0.95–1.00; bs: 83%–100%). Although these clades form a monophyletic group (BPP = 0.99) with *O. occidentalis* and *O. burtoni* from W Africa (Fig. 3a), nodal support for these relationships from ML, parsimony and NJ analyses is statistically insignificant. The eight clades are comprised of the following: Clade 1) an Ethiopian clade whose members conform to the karyotype depicted in Fig. 2a and which taxonomically comprises *O. typus* s.s. (from Mt Guna near the type locality), *O. fortior* from southwestern forests of Ethiopia, and *O. helleri* (= "Sp. B") from the Bale Mts of Ethiopia. Within Clade 1, *typus* s.s. and *O. helleri* group as well-supported sister taxa (BPP= 0.98, MLbs = 83%), but weak genetic distances (Table 3) and absence of statistical nodal support characterize their interrelationships with *O. fortior* from the southwestern Beletta and Inegawa forests (nodes 1c-1e); Clade 2) a taxonomically enigmatic clade (seemingly defined by small-sized individuals; see Morphometrics below). This clade comprises an individual (RMCA a6.016-M-2034) of *O. tropicalis faradjius* from Rethy, DRC; an individual (RMCA a1.008-M-1122) of "*O. tropicalis tropicalis*" from the moorlands of the Aberdares, and two individuals (DM 6282, USNM 590005) of *O. tropicalis elgonis* from Mt Elgon. Within this clade, the Aberdares specimen groups closely [*p* = 1.4%] with the *O. t. elgonis* individuals (node 2b), while the DRC specimen is rather more distant [*p* = 3.2%]; Clade 3) a clade consisting of two well-supported subclades a) *O. orestes* from the Aberdares Mts (USNM 5989997 and RMCA a1.008-M-1123), and b) two outlying *O. tropicalis"elgonis"* individuals (USNM 590004 and 590006) from the sub-alpine bamboo zone of Mt Elgon. A third subclade c) constitutes *O. jacksoni* from the alpine zone of Mt Elgon of which the sister taxon affiliation is unresolved; Clade 4) an individual (RMCA a6.013-M-2031) from the Usambara Mts assigned morphologically to *O. sungae* on cranial and pelage characters (Usambara Mts are also the topotypic source of *sungae*); Clade 5) chromosomally-defined *O. simiensis* **sp. nov.** (= "Sp. D") from the Simien Mts of Ethiopia; Clade 6) *O. zinki* from Mt Kilimanjaro; Clade 7) *O. dartmouthi* from the Albertine Rift (Ruwenzori Mts); Clade 8) *O. tropicalis* s.s, comprising well-supported subclades (separated by distances of around 3%) from Mt Kenya (type locality) and the Aberdares.

TABLE 3. Estimates of mean divergence between Ethiopian *Otomys* taxa given as average uncorrected *p*-distances for cyt *b* (below the diagonal; with standard errors based on 10000 bootstrap replicates given in parentheses). Observed values (average uncorrected *p*-distances followed by standard errors) of intra-taxon sequence variation are given along the diagonal; n = number of sequences within each taxon.

	1 (n=1)	2 (n=5)	3 (n=2)	4 (n=4)
(1) *O. typus* (n=1)	-			
(2) *O. fortior* (n=5)	0.0343 (0.0090)	0.0056 (0.0017)		
(3) *O. helleri* (= "Sp. B") (n=2)	0.0323 (0.0089)	0.0229 (0.0073)	0.0050 (0.0033)	
(4) *O. simiensis* **sp. nov.** (= "Sp. D") (n=4)	0.1045 (0.0160)	0.0880 (0.0089)	0.0871 (0.0139)	0.0000 (0.0000)

Poor support for deeper levels of the cyt *b* phylogeny obscure cladistic relationships of the well-supported eastern African clades to other Otomyini taxa from West Africa (*O. occidentalis* and *O. burtoni*) and southern Africa (*O. irroratus*, *O. angoniensis* and *P. brantsii*) as well as among lineages within each of these regions. Populations once assigned to *O. sungae* s.l. are widely divergent: the topotypic Usambaras population groups closest to *O. orestes* in the eastern African *typus-tropicalis* s.l. clade, whereas the geographically distant population from the Nyika Plateau, Malawi, a putative new species (FMNH 191809), groups within a strongly supported *O. lacustris* clade from the Eastern Arc Mts (FMNH 155623) and the "Southern Rift" (RMCA 96.037-M-5237) sensu Taylor *et al.* (2009a). The relationships of *O. denti denti* from the Albertine Rift remain uncertain.

Large cyt *b* genetic distances characterise those taxa formerly assigned to *Otomys typus* by Bohmann (1952) and Misonne (1975). The Mt Kilimanjaro population (*O. zinki*) herein, elevated to full species status, forms a well-supported clade separated from all other *Otomys* specimens by uncorrected cyt *b* distances of 6.6–13.6%. Although based on fewer specimens, large genetic distances also characterize specimens referred to *O. dartmouthi* (6.6–12.7%), *O. orestes* (4.6–13.0%), and *O. jacksoni* (7.3–12.9%). According to the cyt *b* data, each of these four taxa has cladistic affinity to different Kenyan samples currently assigned to *O. tropicalis* s.l., not to those from Ethiopia (*O. typus* s.s., *O. fortior*, *O. helleri* (= "Sp. B"), *O. simiensis* **sp. nov.** (= "Sp. D")). Divergence dates obtained for the major clades from Bayesian approximation in BEAST using cyt *b* data partitioned by codon positions are shown in Fig. 3a and discussed further below.

Bayesian, maximum likelihood, parsimony and NJ analyses of combined 12S rRNA and cyt *b* sequences for a reduced taxon sample of *Otomys* (n=20) and *Parotomys brantsii* (n=1) proved valuable for clarifying some deeper level associations among eastern, western and southern African lineages (Fig. 3b). Notwithstanding the unresolved position of *O. barbouri* (Mt Elgon) and *Parotomys brantsii* (South Africa) in the Otomyini clade, two well-supported main clades emerged. The first (Clade 1; node 6), exclusively eastern African clade unites *O. denti denti* (Albertine Rift; FMNH 157807), the putative new species from the Nyika Plateau (FMNH 191809) and *O. lacustris* (Eastern Arc Mts and "Southern Rift"). The second well-supported main clade (defined by node 10 in Fig. 3b) contains southern, western and eastern African lineages (Clade 2). Herein, the sister taxon affiliations of the South African *O. irroratus* and *O. angoniensis* and *O. fortior* (Beletta Forest, Jimma, Ethiopia, part of cyt *b* clade 1) remain unresolved, but *O. occidentalis* from western Africa is supported (on Bayesian probabilities although not consistently with bootstrap support) as the sister taxon of a larger clade comprising two unresolved taxa (*O. zinki* and *O. dartmouthi*) and two well supported subclades: a) constituting two distinct and well supported lineages, one involving *O. jacksoni*, the divergent *O. tropicalis "elgonis"* lineage (Mt Elgon) and *O. orestes* from Aberdares NP (part of cyt *b* clade 3 subclades a, b, and c), and the second comprising *O. t. elgonis* from Mt Elgon (part of cyt *b* clade 2 in Fig. 3a); b) a well-supported clade confirming the monophyly of *O. tropicalis* s.s.from the Aberdares (moorlands) and Mt Kenya (cyt *b* clade 8).

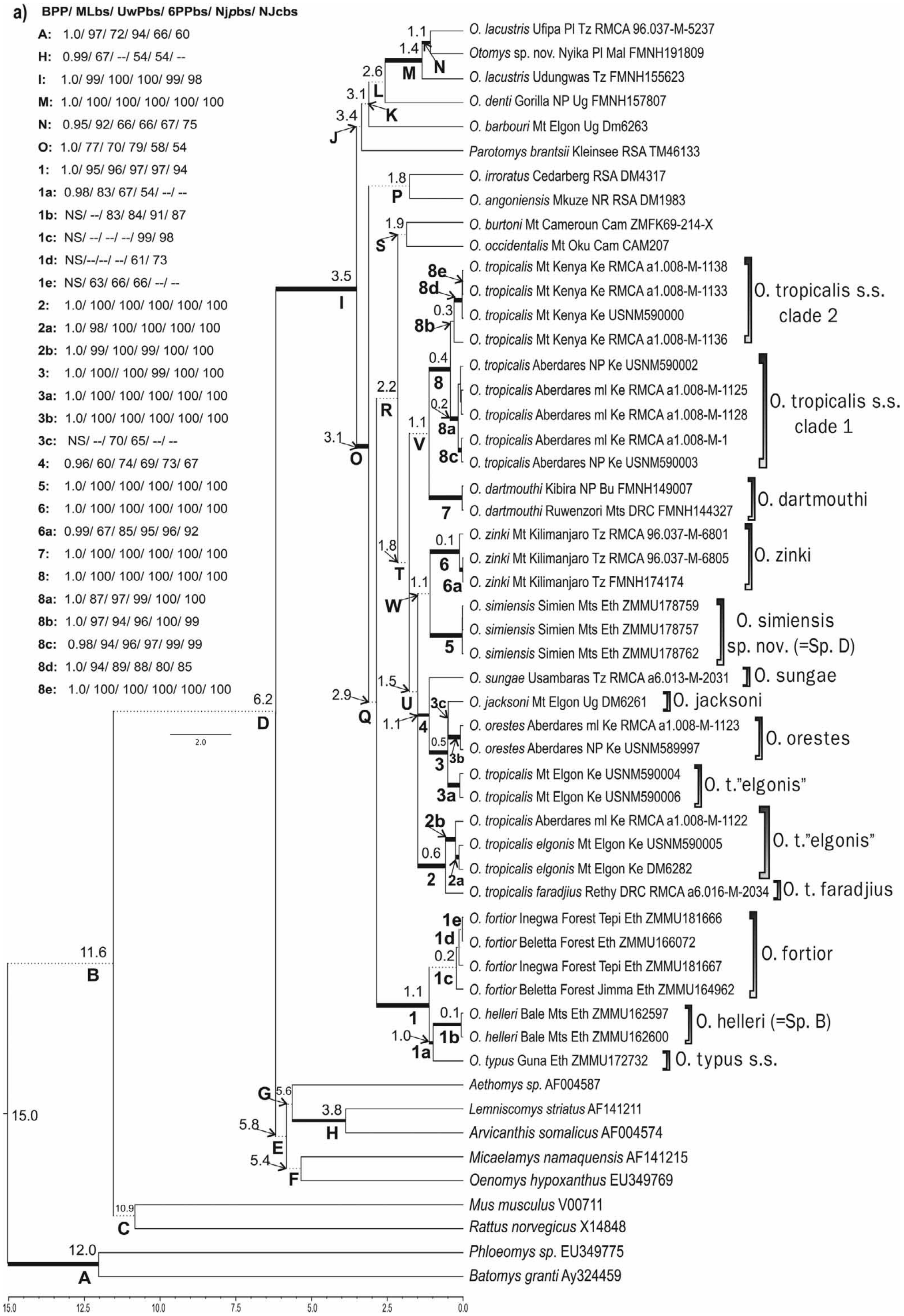

FIGURE 3a. Bayesian phylogeny inferred from cyt *b* sequences partitioned by codon position for 34 East African specimens of *O. typus* s.l. and *O. tropicalis* s.l. in relation to representatives of seven *Otomys* species and *Parotomys brantsii* from eastern, western and southern Africa. Representatives of nine murine taxa served as outgroups (see Appendix 1). Nodal support indices for the main clades (annotated 1 to 8) and subclades (a, b, c, d and e), as well as supported deeper nodes (A, H, I, M, N, O) are given beside the phylogram in the following order: Bayesian posterior probabilities (BPP)/ bootstrap support from 1000 replicates for maximum likelihood (MLbs), under an unpartitioned GTR+I+G model/ unweighted parsimony (UwPbs), six-parameter-weighted parsimony partitioned by codon positions (6PPbs)/ neighbour-joining using uncorrected *p*-distances (Njpbs)/ neighbour-joining using GTR+I+G-corrected distances (Njcbs). Estimated divergence dates (Myr) for the major lineages identified in the cyt *b* phylogeny are indicated to the left of each node. Bayesian estimation of divergence times was conducted under a relaxed clock model using BEAST v.1.4. Four well established murine fossil calibration points were specified (Pocock 1987; Rowe *et al.* 2008, see text).

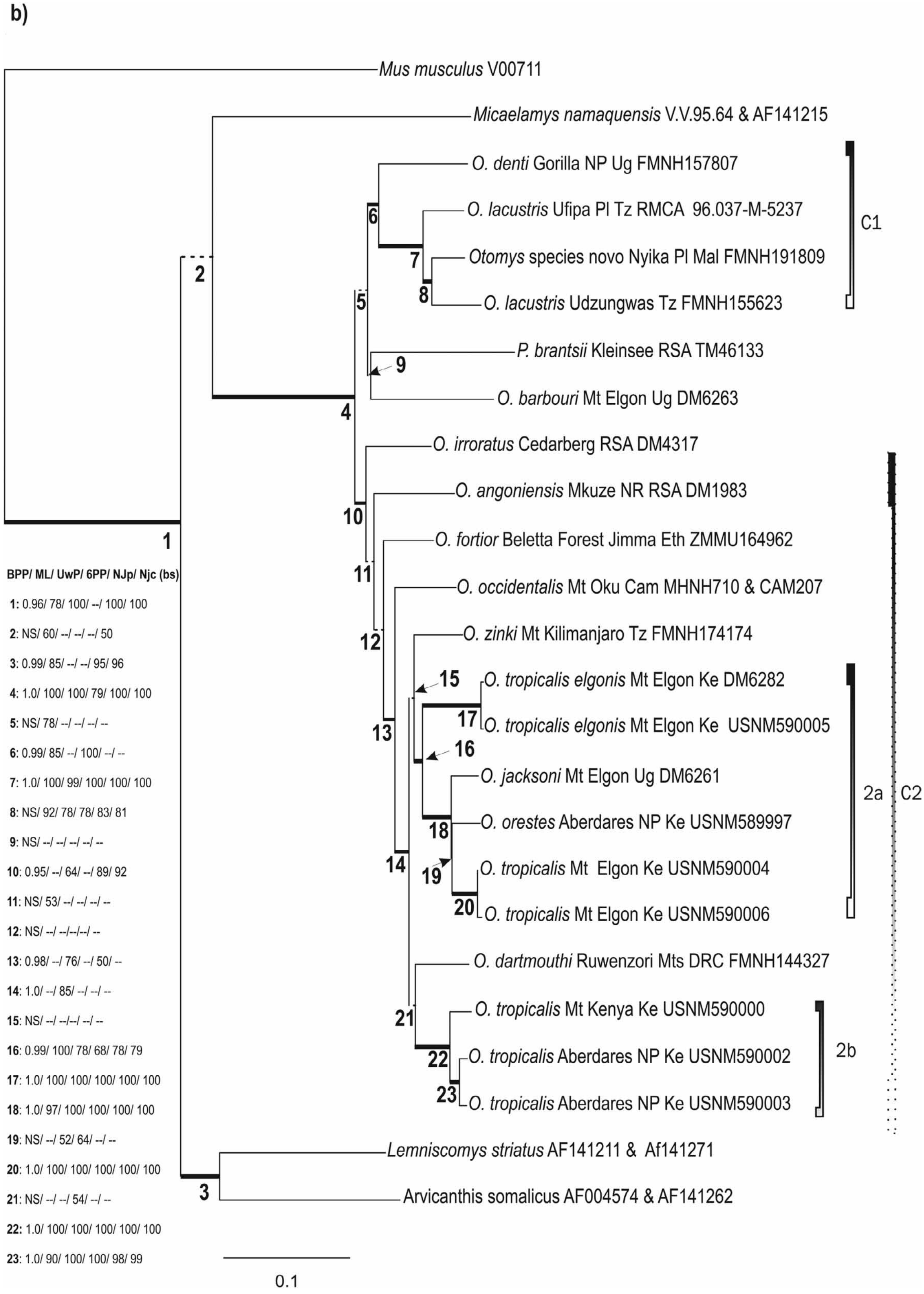

FIGURE 3b. Maximum likelihood phylogram constructed from combined cyt *b* and 12S rRNA sequences for 20 *Otomys* specimens, one representative of *Parotomys brantsii* and four murine outgroups under the best-fit GTR+I+G model. Support indices for each node (1 – 23) are given beside the phylogram (BPP/ MLbs/ UwPbs/ 6PPbs/ NJpbs/ Njcbs). For both phylogenies (Figure 3a and 3b), the relative branch thickness indicates significant nodal support from the phylogenetic reconstruction methods employed herein (four to six methods—thick lines; two methods—intermediate lines). Dashed lines show unsupported relationships; Abbreviations and symbols: NS - BPP < 0.95; "-" indicates that the node was not present in the relevant analysis, or percentage bootstrap support below 50%.

Craniodental characters

Of the five characters traditionally used to define species and supra-specific groupings in *Otomys*, two (number of m1 laminae and shape of petrotympanic foramen) are typically invariant intraspecifically whilst the other three tend to be highly variable both within and between taxa historically assigned to *typus* s.l. or *tropicalis* s.l. (Table 4). A population of *tropicalis* from the summit of the Aberdares, Kenya, is exceptional in possessing five well defined m1 laminae in six out of ten specimens (another three contained an incipient fifth lamina), a character state otherwise not found in any other east African *Otomys* populations except for *O. barbouri* from Mt Elgon (Kenya/ Uganda border) and *O. lacustris* from the Southern Highlands and Eastern Arc Range of Tanzania (Table 4). Additional specimens from Aberdares possess five m1 laminae, including one generally labeled "Aberdares" (BM 10.5.3.480), one from Mt Kinangop, Aberdares (MNHN1913_216A), and a third from Aberdare National Park Fishing Lodge (USNM 590014).

Modal numbers of the OTU samples are instructive for the more variable craniodental characters. Thus in OTUs representing *tropicalis* s.l., the angle of anterior expansion of the nasal bones is typically >120°, whilst in the alpine forms representing *typus* s.l. (*O. dartmouthi*, *O. jacksoni*, *O. orestes*, *O. thomasi*, *O. typus* s.s., *O. uzungwensis* and *O. zinki*), the modal angle is <100°. The presence of two equally deep grooves on the lower incisors characterizes all forms from Ethiopia (*O. typus* s.s., *O. fortior, O. yaldeni* **sp. nov.** (= "Sp. A"), *O. helleri* (= "Sp. B"), *O. cheesmani* **sp. nov.** (= "Sp. C"), *O. simiensis* **sp. nov.** (= "Sp. D")) and the alpine taxa from the Ruwenzoris (*dartmouthi*), Mt Elgon (*jacksoni*) and the Tanzanian Highlands (*uzungwensis*); in contrast, alpine forms from the Kenyan Highlands (*orestes* and *thomasi*) and Mt Kilimanjaro (*zinki*) possess one deep and one shallow groove, with the exception of the type specimens of *malleus* and *squalus* from the Aberdares which have two deep grooves. Strangely, two deep grooves in i1 characterize two individuals from *O. tropicalis elgonis* from Mt Elgon, including the holotype of *elgonis*. Discrete craniodental characters provide a reliable means to distinguish certain forms previously grouped as synonyms within *O. typus*; e.g., the M3 of *dartmouthi* individuals consistently comprise only six laminae (n=13), individuals of *uzungwensis* (n=19) and *jacksoni* (n=3) comprise seven, whereas those from Ethiopia are much more variable, usually comprising eight or more (47 of 50 individuals scored). Interestingly, the Ethiopian populations of the chromosomally defined *O. yaldeni* **sp. nov.** (= "Sp. A") and *O. simiensis* **sp. nov.** (= "Sp. D") possess a modal number of seven laminae as opposed to eight in other populations from Ethiopia (Table 4).

TABLE 4A. Variation in the nasal angle and development of lower incisor grooves in OTUs of *Otomys* from eastern Africa. See text for explanation of character states.

		Nasal angle				Lower incisor grooves			
Taxon and OTU	*N*	90–99°	100–119°	120–149°	>150°	1	1+t	1+s	2
O. typus s.l. (Cytotype 1) (incl. *fortior* + "Sp. B" + "Sp. C") OTU 1-4 (Ethiopia)	50	18	5	–	–	–	–	–	50
O. typus s.l. (Cytotypes 2, 3) (incl. "Sp. A" + "Sp. D") OTU 5-7 (Ethiopia)	9	3	3	–	–	–	–	–	9

continued next page

TABLE 4A. (continued)

Taxon and OTU	*N*	Nasal angle 90–99°	100–119°	120–149°	>150°	Lower incisor grooves 1	1+t	1+s	2
O. typus s.l.									
OTU 7 (un-assigned localities)									
Chilalo	6	5	1	–	–	–	–	–	6
Chenca	10	10	–	–	–	–	–	–	7
Bongke	2	2	–	–	–	–	–	–	–
Jimma	8	8	–	–	–	–	–	–	2
Ankober	1	1	–	–	–	–	–	–	1
Hirna	2	–	–	–	–	–	–	–	2
Arussi Plateau	6	2	–	–	–	–	–	–	2
O. tropicalis									
OTU 8 (Aberdares)	11	2	1	7	–	–	–	8	0
OTU 9 (Mt Kenya)	22	4	4	11	3	5	3	10	–
OTU 10 (Mt Elgon)	15	–	4	11	–	–	1	11	2
OTU 11 (Aberdares Summit)	10	9	1	–	–	5	2	3	–
O. zinki									
OTU 12 (Mt Kilimanjaro)	9	6	3	–	–	1	8	–	–
O. orestes									
OTU 13 (Mt Kenya & Aberdares)	14	7	2	3	1	–	–	11	2
O. thomasi OTU 14 (Mau Escarpment)	5	3	2	–	–	–	–	5	–
O. dartmouthi OTU 15 (Ruwenzoris)	13	5	4	3	–	–	–	–	13
O. uzungwensis OTU 16 (Eastern Arc)	19	14	5	–	–	–	–	–	19
O. jacksoni OTU (Mt Elgon)	3	1	1	1	–	–	–	–	3
O. barbouri OTU 18 (Mt Elgon)	14	12	1	1	–	2	4	–	–
O. lacustris OTU 19 (Eastern Arc)	23	2	2	11	8	21	2	–	–
O. sungae OTU 20 (Usambaras)	15	–	2	5	–	9	5	–	–

TABLE 4B. Number of laminae in the upper third molar (M3) and lower first molar (m1) in OTUs of *Otomys* from eastern Africa. See text for explanation of character states.

		M3 laminae				m1 laminae		
Taxon and OTU	*N*	6	7	8	9	4	4+1	5
O. typus s.l. (Cytotype 1) (incl. *fortior* + “Sp. B” + “Sp. C”) OTU 1-4 (Ethiopia)	50	–	3	35	12	50	–	–

continued next page

TABLE 4B. (continued)

		M3 laminae				m1 laminae		
Taxon and OTU	*N*	6	7	8	9	4	4+1	5
O. typus s.l. (Cytotypes 2, 3)	9	1	8	–	–	9	–	–
(incl. “Sp. A” + “Sp. D”)								
OTU 5-6 (Ethiopia)								
O. typus s.l.								
OTU 7 (un-assigned localities)								
Chilalo	6	–	1	5	–	6	–	–
Chenca	10	–	1	5	4	3	–	–
Bongke	2	–	–	2	–	2	–	–
Jimma	8	–	–	8	–	8	–	–
Ankober	1	–	1	–	–	1	–	–
Hirna	2	–	1	1	–	2	–	–
Arussi Plateau	6	–	–	5	1	3	–	–
O. tropicalis								
OTU 8 (Aberdares)	11	–	9	2	–	10	–	–
OTU 9 (Mt Kenya)	22	2	18	2	–	22	–	–
OTU 10 (Mt Elgon)	15	2	13	–	–	15	–	–
OTU 11 (Aberdares Summit)	10	–	8	2	–	1	3	6
O. zinki								
OTU 12 (Mt Kilimanjaro)	9	–	9	–	–	8	–	–
O. orestes								
OTU 13 (Mt Kenya & Aberdares)	14	2	11	–	–	13	–	–
O. thomasi	5	–	4	1	–	5	–	–
OTU 14 (Mau Escarpment)								
O. dartmouthi	13	13	–	–	–	13	–	–
OTU 15 (Ruwenzoris)								
O. uzungwensis	19	–	19	–	–	19	–	–
OTU 16 (Eastern Arc)								
O. jacksoni	3	–	3	–	–	3	–	–
OTU (Mt Elgon)								
O. barbouri	14	–	12	2	–	1	–	13
OTU 18 (Mt Elgon)								
O. lacustris	23	3	19	1	–	1	2	20
OTU 19 (Eastern Arc)								
O. sungae	15	3	7	–	–	9	5	–
OTU 20 (Usambaras)								

Morphometric data

Non-geographic variation. On average, males have slightly larger crania than females in all linear variables, but this was only significant (and only at the 5% level) in the case of anterior palatal length and maxillary toothrow (Table 5). Age classes differed significantly in linear and shape variables (Table 5; Fig. 4). Only one variable, interorbital constriction showed absence of significant ontogenetic variation, with mean values increasing from toothwear class 2 to class 3 and then decreasing in class 4 individuals (Table 5). In other variables, toothwear class explained between 42% and 86% of total variance; in six variables, all means differed significantly from each other, whilst in three, toothwear classes 3 and 4 formed homogeneous subsets. By comparison, sex explained only between 0.3% and 9% of the total variance. Multivariate analysis of variance (MANOVA) of the weights matrix from dorsal landmarks revealed significant differences between age classes 3 and 4 at the 5% probability level (Wilks lambda = 0.129, d.f. = 18, 9; p = 0.03). MANOVA of a pooled sample of age classes 3 and 4 individuals from Tora revealed lack of significant sexual dimorphism in shape (Wilks lambda = 0.106, d.f. = 18, 6; p > 0.05). Based on these results, further analyses combined the sexes, but were restricted to toothwear class 4 and 5 individuals (the latter refer to very old individuals with heavily worn teeth, which are very rare in collections), except in the case of types or other critical specimens where occasionally toothwear class 3 individuals were included.

TABLE 5. Means and two-way ANOVAs of craniometric variables for age classes 2–4 of male (*N* = 19) and female (*N* = 20) *Otomys tropicalis* from Tora, Burundi.

Variable	Age Class (*N*): Male 2(2)	3(10)	4(7)	Age Class (*N*): Female 2(2)	3(7)	4(11)	%SS; F Sex	Age	Sex×Age	Age Subsets (Tukey HSD)
GLS	30.3	38.2	41.0	30.5	37.7	40.2	0.7; 1.7	85.6; 105.0**	0.2; 0.2	AS
BCD	9.6	11.1	11.7	9.8	11.0	11.2	2.2; 1.6	49.8; 18.1**	2.4; 0.9	(2):(3-4)
GLM	20.0	23.9	25.9	20.0	23.4	25.2	2.0; 3.5	79.0; 69.6**	0.3; 0.3	AS
APF	4.8	6.5	7.3	4.9	6.3	6.7	4.4; 4.8*	64.6; 37.1**	2.2; 1.2	AS
MXTRL	8.3	9.3	9.4	8.5	9.0	9.1	8.9; 5.8*	42.2; 15.1**	3.5; 1.2	(2):(3-4)
NAW	5.6	6.8	7.4	5.5	6.7	7.3	0.6; 1.1	80.6; 70.6**	0.0; 0.1	AS
IOC	4.5	4.6	4.5	4.4	4.5	4.5	3.5; 1.3	1.7; 0.3	0.3; 0.1	NS
ZYW	13.7	18.1	19.3	15.6	18.2	19.3	0.5; 0.8	77.5; 68.0**	3.2; 2.8	AS
PL	15.6	19.8	21.5	16.2	19.7	21.1	0.3; 0.7	84.7; 97.4**	0.8; 0.9	AS
BL	6.5	7.5	7.7	6.5	7.4	7.5	2.2; 1.8	56.2; 22.6**	0.6; 0.2	(2):(3-4)

* = P ≤ 0.05; ** = P ≤ 0.01; AS = All pair-wise comparisons significantly different; NS = Not significant.

Geographic and taxonomic variation. Ethiopian sample. Based on combined cytogenetic, molecular, dental and craniometric data (Lavrenchenko 1997, unpublished; Figs. 2, 3, 5–7), we propose the existence of six *Otomys* lineages in Ethiopia (represented by OTUs 1–6 in Fig. 1, Tables 2 and 4). Unassigned populations (from additional Museum collections) were arbitrarily assigned to OTU 7. Figure 5 shows the results of PCA of nine craniometric variables of specimens from the six hypothesized taxa. Specimens from Dangila (near Lake Tana) and Debra Marcos ("Sp. C"; described as *O. cheesmani* **sp. nov.** under Taxonomic Summary) are clearly distinguished by their larger cranial size (higher non-overlapping scores on PC1; Fig 5 and Table 6). Specimens belonging to the distinct chromosomal forms "Sp. A" (from Bale Mts; described as *O. yaldeni* **sp. nov.** under Taxonomic Summary) and "Sp. D" (Simien Mts; described as *O. simiensis* **sp. nov.** under Taxonomic Summary) are distinguished by their smaller size (low scores on PC 1; Fig. 5 and Table 6); they are further distinguished from each other by shape characteristics (PC2 versus PC3: Fig. 5b) whereby *O. simiensis* sp. nov (= "Sp. D") (OTU 6) has lower scores on PC2 and PC3 representing a narrower interorbital constriction and shallower braincase (Table 6), than *O. yaldeni* **sp. nov.** (= "Sp. A") (OTU 5). These same shape dimensions distinguish populations from the southwestern forests (Charada, Sheko, Beletta) of Ethiopia (encompassing the form *fortior*) from those from the alpine zone of the Bale Massif ("Sp. B" or *O. helleri*; see discussion below) (Fig. 5b) whereby the former have a narrower interorbital constriction and shallower braincase. Topotypic specimens from the alpine zone of the Simien Mts and Mt Guna (*typus* s.s.) are intermediate in shape between those of *fortior* (including the type specimen marked with asterisk in Fig. 5) and *O. helleri* (= "Sp. B"). The position of the type specimen of *degeni* from Gombitchu in central Ethiopia (not far from the capital of Addis Ababa) on the PCA plots is somewhat peripheral to other Ethiopian specimens but not clearly distinct (Fig. 5). No other specimens attributable to this taxon were available for analysis.

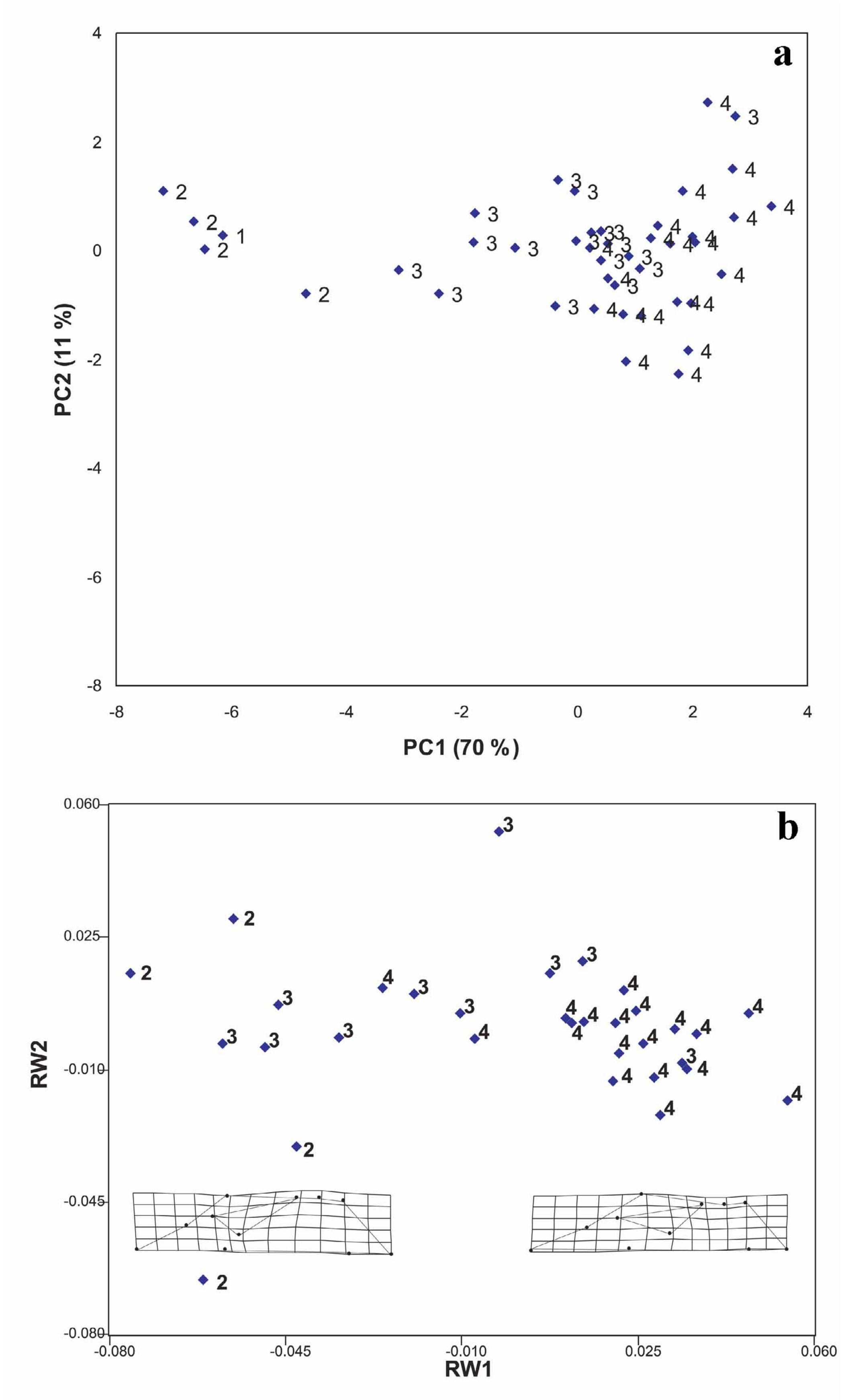

FIGURE 4. Principal component analysis (PCA) of nine linear craniometric variables (a) and relative warps analysis (RWA) of dorsal landmarks (b) showing dispersion of relative age classes in one population of *O. tropicalis* from Tora, Burundi.

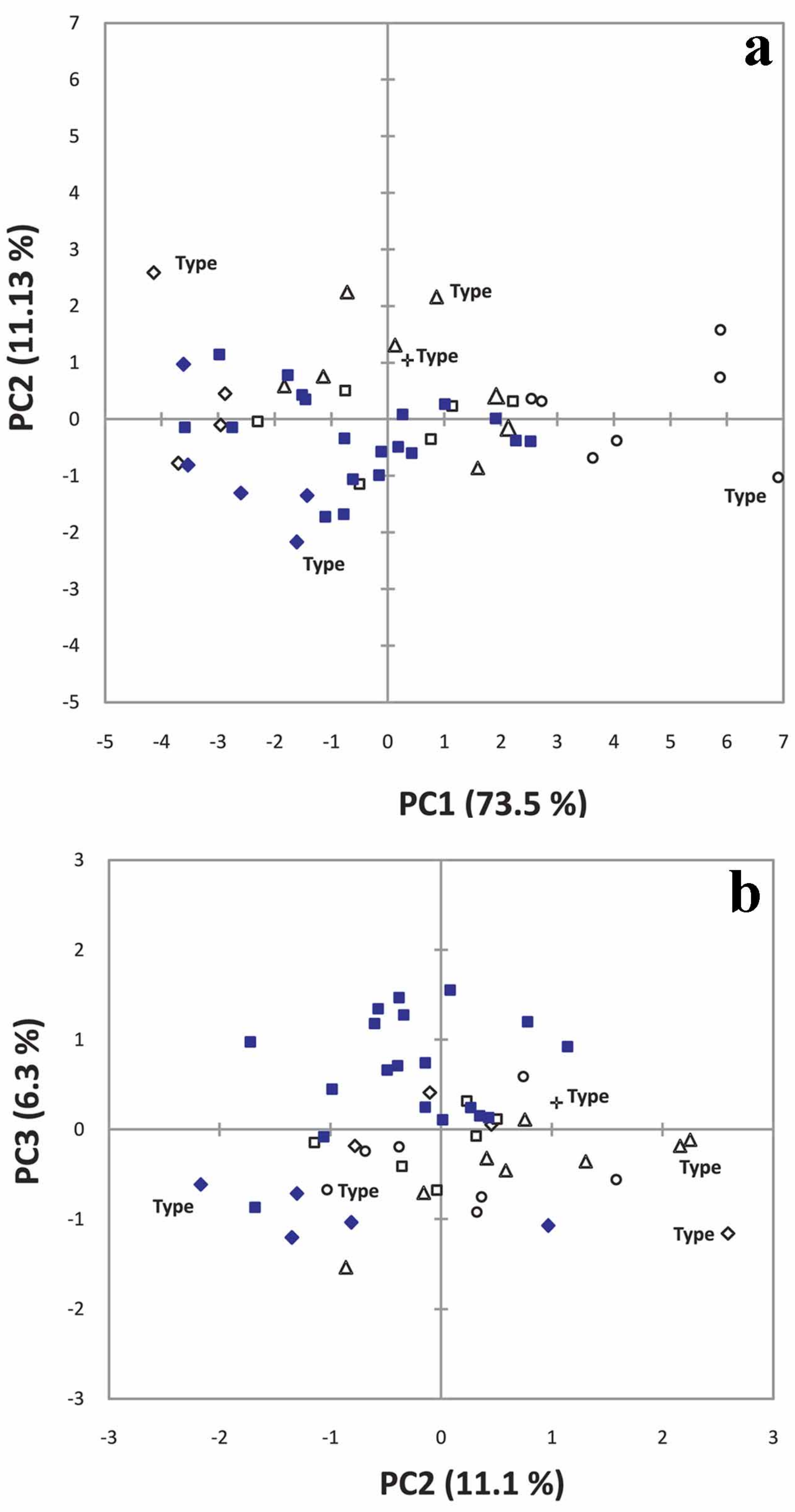

FIGURE 5. Principal components analysis (PCA) based on nine craniometric variables indicating scatter of individuals on PC1 and PC2 (a) and PC2 and PC3 (b) from six pre-defined taxon-groups of Ethiopian *Otomys* in relation to existing type specimens of *fortior* and *degeni* and new holotypes designated for new species (see Taxonomic Summary). Open squares = *O. typus* s.s., open triangles = *O. fortior*; open diamonds = *O. yaldeni* **sp. nov.** (= Sp. A); closed squares = *O. helleri* (= Sp. B); open circles = *O. cheesmani* **sp. nov.** (= Sp.C); closed diamonds = *O. simiensis* **sp. nov.** (= Sp. D); cross = *degeni*. Type specimens indicated; normal font indicates existing holotypes; bold font represents newly designated holotypes (see Taxonomic Summary).

TABLE 6. Eigenvectors (PCA) and Canonical Variates Analysis (CVA) of linear craniometric data from different data subsets of the *O. typus* species complex.

	Ethiopian Highlands (Fig. 5, 6)					Kenyan Highlands (Fig. 8a)		*O. orestes* versus *O. thomasi* (Fig. 8b)	
	PC1	PC2	PC3	CV1	CV2	PC1	PC2	PC1	PC2
GLS	0.374	-0.092	-0.259	0.849	0.035	0.454	0.038	0.498	-0.165
BCD	0.300	0.048	0.684	0.603	0.499	0.266	-0.433	0.067	0.669
APF	0.363	0.088	0.080	0.771	0.112	0.390	-0.147	0.421	0.117
MXTRL	0.355	0.016	0.052	0.935	0.236	0.272	0.022	0.291	0.489
NAW	0.354	0.045	-0.357	0.899	-0.214	0.330	0.475	0.362	-0.029
IOC	0.082	0.972	-0.034	0.317	-0.128	0.085	0.598	0.148	0.116
ZYW	0.372	-0.101	-0.222	0.821	0.067	0.390	-0.056	0.439	-0.021
PL	0.374	-0.091	-0.249	0.827	0.026	0.385	0.223	0.305	-0.508
BL	0.320	-0.129	0.466	0.629	0.507	0.282	-0.391	0.217	0.014

continued.

	Forms with 5 laminae in m1 (Fig. 10)				*O. typus* s.l. (Fig. 12)	
	PC1	PC2	CV1	CV2	CV1	CV2
GLS	0.411	0.017	0.565	0.422	0.250	0.741
BCD	0.264	-0.112	0.352	0.150	0.233	0.766
APF	0.367	0.147	0.317	0.509	0.251	0.557
MXTRL	0.235	-0.529	0.827	-0.357	0.049	0.360
NAW	0.272	0.288	0.073	0.033	0.164	0.678
IOC	0.143	0.745	-0.217	0.659	-0.191	0.411
ZYW	0.372	0.041	0.569	0.588	0.249	0.451
PL	0.342	-0.095	0.541	0.178	-0.105	0.768
BL	0.312	-0.186	0.664	0.275	0.677	0.541

Morphometric separation of the six hypothesized taxa was further emphasized by canonical variates analysis (CVA) as shown in Fig. 6. CVA resulted in 100% correct classification of four of the six hypothesized species: *fortior* (OTU 2), *O. yaldeni* **sp. nov.** (= “Sp. A”) (OTU 5), *O. cheesmani* **sp. nov.** (= “Sp. C”; see Taxonomic Summary) (OTU 4) and *O. simiensis* **sp. nov.** (= “Sp. D”) (OTU 6). In *O. typus* s.s. three of four specimens (75%) were correctly identified, as were 18 of 19 specimens (95%) of *O. helleri* (= “Sp. B”) (OTU 3).

Specimens from unassigned (“unknown”) localities (OTU 7) were plotted on the canonical variates plot shown in Fig. 6 and their affiliations predicted a posteriorly from the CVA. Thus, for example, specimens from Jimma, although very close geographically to the type locality of *fortior* (Charada Forest; Fig. 1), grouped with *O. cheesmani* **sp. nov.** (= “Sp. C”); statistically, three of the four specimens were classified as *O. cheesmani* **sp. nov.** (= “Sp. C”) while the fourth was classified as *O. typus* s.s. The same process was repeated with all the specimens listed in OTU 7 (Table 2; results not shown). At three localities all or most of the specimens were assigned by CVA to “Sp. B”: Ankober (n=1; 100%), Bongke (n=2; 100%), and Chilalo n=6; 83%). The last-mentioned locality is the type locality of *helleri*; thus the name *helleri* can be equated with the taxon “Sp. B” of Lavrenchenko *et al.* (1997). The assignment of specimens from other unassigned localities was more ambiguous; thus Hirna comprises specimens assigned to both *typus* s.s. (n=1) and “Sp. B” (n=1) whilst Chenca includes specimens assigned to *typus* s.s. (n=2), *fortior* (n=2), *O. helleri* (= “Sp. B”) (n=4) and *O. yaldeni* **sp. nov.** (= “Sp A”) (n=1).

Relative warps analysis (RWA) of dorsal landmarks on a subset of crania (Fig. 7) indicated shape differences between topotypic specimens of *typus* s.s. from Simien Mts, specimens of *O. helleri* (“Sp. B”) from the Bale Massif and neighbouring Arussi Plateau and the type specimen of *fortior* from Charada Forest.

East African Highlands sample. In spite of minor overlap, specimens of *tropicalis* from East Africa show a trend of increasing cranial size from Mt Elgon (smallest; low scores on PC1) to the Aberdare Mts (intermediate) to

Mt Kenya (largest; high scores on PC1) (Fig. 8a; Table 6). Specimens classified as *orestes* from the Aberdares and Mt Kenya overlap in size with *tropicalis* but are almost completely distinguished from *tropicalis* on skull shape (PC2) by having narrower interorbit and nasals, a deeper cranium and larger bullae (Fig. 8a; Table 6).

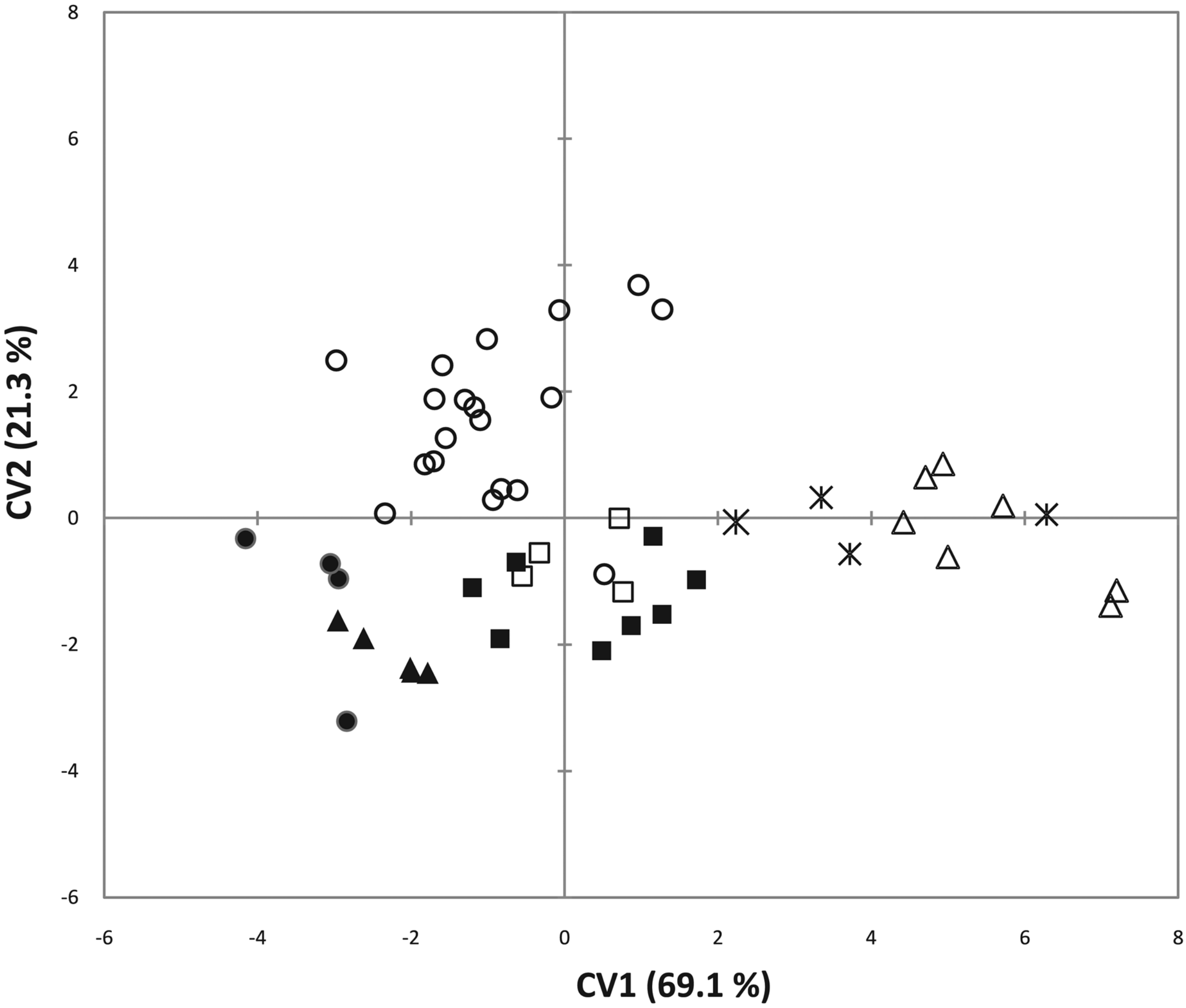

FIGURE 6. Canonical variates analysis (plot of first two canonical variates) of six defined taxon-groups of Ethiopian *Otomys* based on nine craniometric variables. Position of individuals form "unknown" sample from Oromiya, Jimma (asterisks) predicted *a posteriori*. Open squares = *O. typus* s.s. (Mt Guna); Closed squares = *O. fortior*; open circles = *O. helleri* (= "Sp. B"); closed circles = *O. yaldeni* **sp. nov.** (= "Sp. A"); open triangles = *O. cheesmani* **sp. nov.** (= "Sp. C"); closed triangles = *O. simiensis* **sp. nov.** (= "Sp. D").

Specimens from the summit of the Aberdares having five laminae in m1 (OTU 11 indicated as open circles in Fig. 8a) overlap in cranial size and shape with *O. tropicalis* from Aberdares (closed circles) and Mt Kenya (open diamonds). One *O. tropicalis* specimen from the Aberdares (RMCA a1.008-M-1122; Field No. R28198) which formed a distinct clade from topotypic *O. tropicalis* based on its cyt *b* sequences (grouping closest to a specimen of *O. tropicalis elgonis* from Mt Elgon), was distinctly smaller than all other Aberdares specimens and grouped with smaller-sized specimens from Mt Elgon. Another Aberdares specimen initially classified as *O. tropicalis* (RMCA a1.008-M-1123; Field No. R28205) which grouped genetically with *O. orestes* (Fig. 3) clustered morphometrically with *O. orestes*, confirming its identification.

The holotypes of *O. percivali*, *malleus* and *squalus* from the Aberdares Range all fall within the cluster represented by *O. orestes* (Figs. 8a and 8b), whereas a series of four specimens from the type locality of *O. thomasi* (Molo on the Mau Escarpment), and one individual from the Guas Ngishu Plateau (USNM 164290) fall mostly (with one exception) outside the size range (PC1 scores) of *O. orestes* (due to their larger size: PC1 scores -3.6 to 1.1 in *O. orestes* compared to 0.2 to 3.1 in *thomasi*) but within the shape range of *O. orestes* (PC2 scores) (Fig. 8b; Table 6).

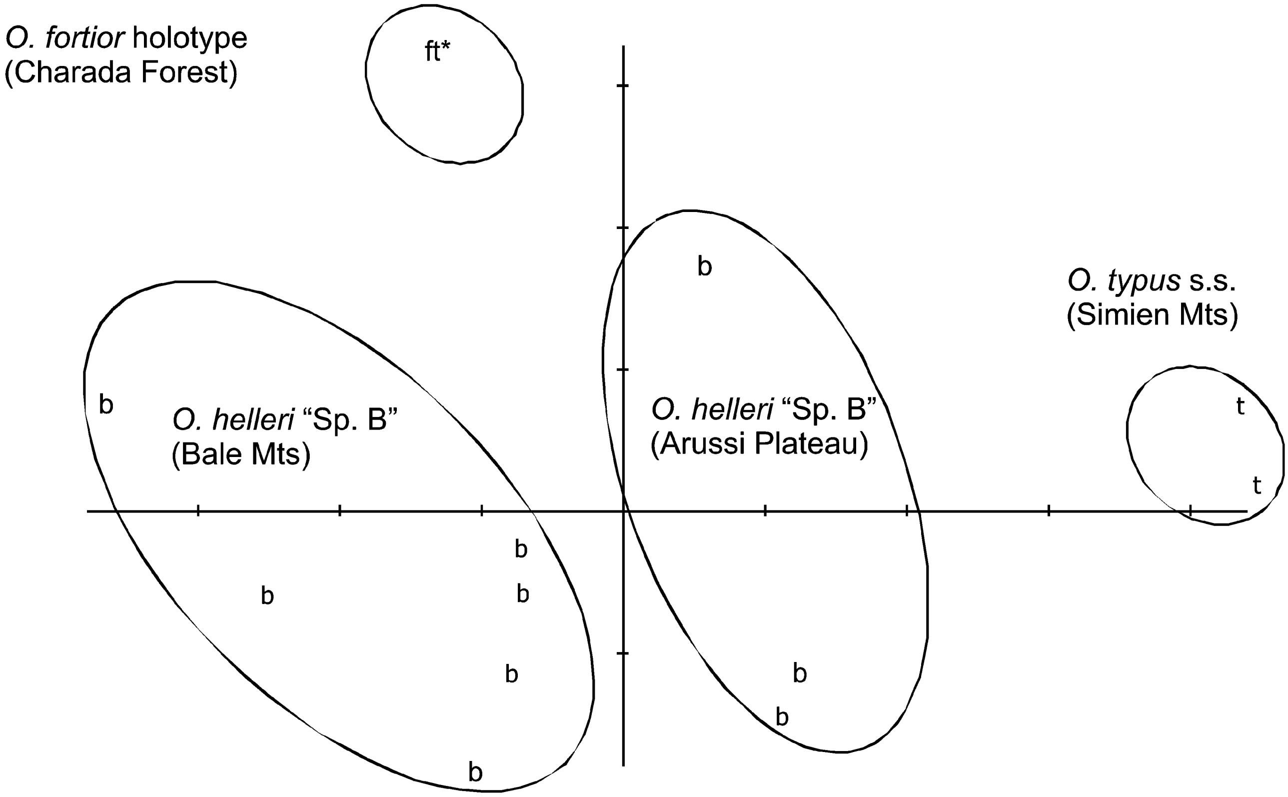

FIGURE 7. Relative warps analysis (RW) of 14 dorsal landmarks from 12 Ethiopian individuals assigned to *O. typus* s.s. from Simien Mts ("t"), *O. helleri* (= Sp. B: "b"; Dinsho and Arussi Plateau) and *O. fortior* ("ft*"; type specimen from Charada Forest).

The deeper, more arched cranial profile of *O. orestes* and *O. thomasi* relative to *O. tropicalis* is clearly reflected in the thin plate splines associated with Relative Warp 1 in RWA of lateral landmarks (Fig. 9). This analysis also confirms the overlap in cranial shape between *O. tropicalis* specimens from the Aberdares having either 4 or 5 m1 laminae.

The Aberdares summit sample having 5 m1 laminae is distinguished on linear variables from other East Africa taxa having five laminae in m1 (Fig. 10), by having a narrower interorbit than *O. lacustris* (low scores on PC2: see Table 6 for eigenvector loadings), and being larger in size than *O. barbouri* (high scores on PC1). CVA confirms the complete separation between the three taxa. Completely separable from *O. lacustris* on dorsal shape, based on its broader and shorter cranial form and more abrupt angle of anterior expansion of the nasal (RW1), the Aberdares summit *tropicalis* population is partly distinguished from *O. barbouri* on RW2, based on wider separation of the three landmarks defining the internal and external angles of the posterior roots of the zygomatic arch and the dorsal extension of the mastoid (Fig. 11).

Regional relationships

Univariate results. Table 7 documents ANOVA results and multiple range tests for the *typus* s.l. group. This complex is characterized by significant inter-OTU differences in all variables; these differences tend to explain high proportions of the total variance (44–75%). Within the *typus* group, *jacksoni* is smallest in most variables whilst "Sp. C" is largest in all but one variable (interorbital constriction); in three variables (GLS, MXTRL and NAW), "Sp. C" occupies a unique significant subset indicating distinctive morphometric separation from all other species. Apart from Ethiopian "Sp. C", *O. thomasi* usually displays the highest mean values. Exceptions include maxillary toothrow length (MTR) where *typus* s.s., *fortior* and "Sp. B" display the greatest mean values (due to their higher modal number of eight laminae in M3; Table 4), and greatest braincase depth (BCD) and maximum zygomatic arch (ZYW) where *thomasi* and *orestes* display the greatest mean values (due to their arched lateral profile and "boxy"

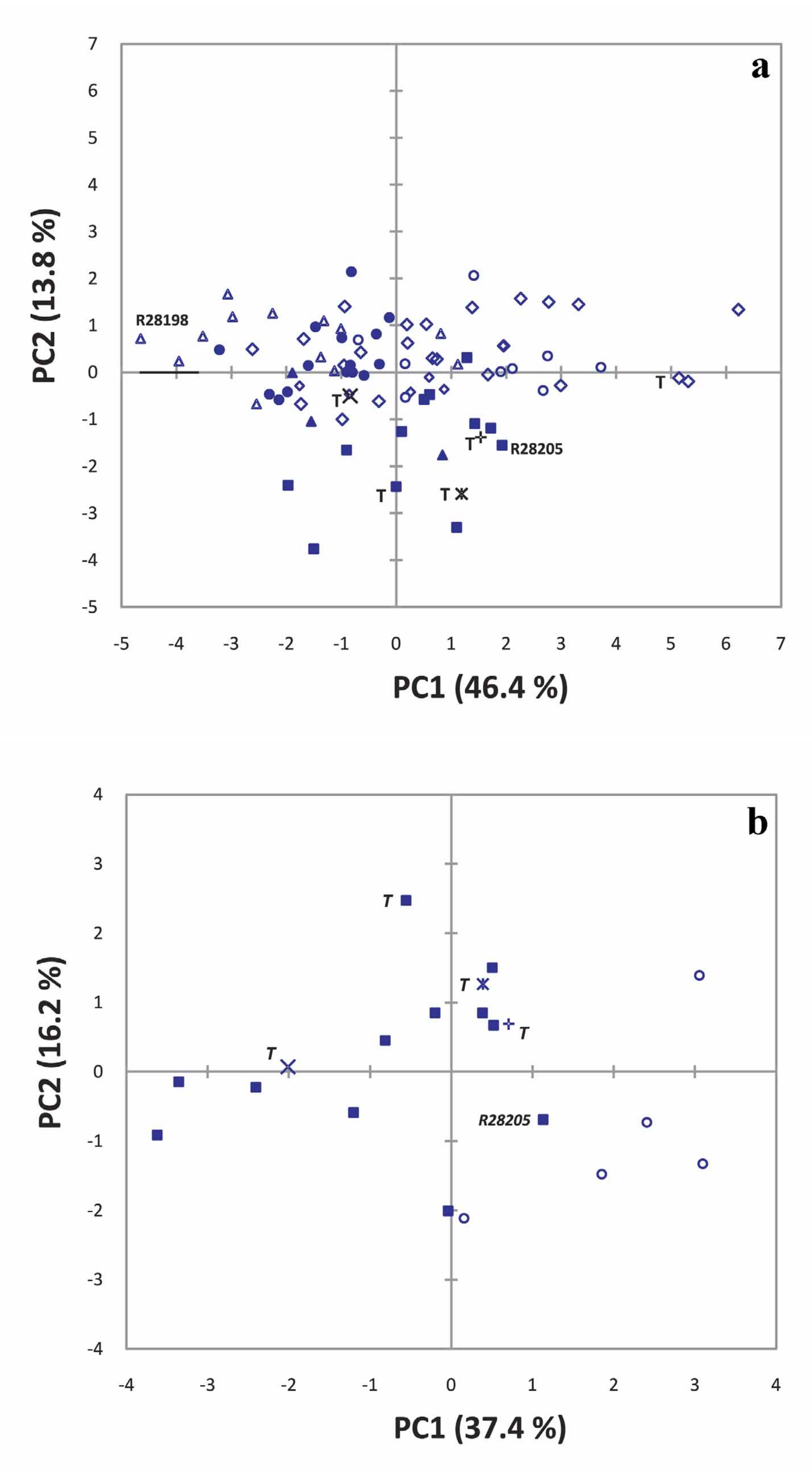

FIGURE 8. PCA of nine linear variables comparing *O. orestes* (closed squares) with: (a) East African populations of *O. tropicalis* from Aberdares (closed and open circles representing samples with 4 and 5 laminae in lower M1 respectively), Mt Elgon (open triangles) and Mt Kenya (open diamond) and (b) topotypic specimens of *O. thomasi* (open circles) from Molo in the Guas Ngishu Plateau. Position of type specimens of *O. tropicalis* (open diamond), *O. orestes* (closed square), *percivali* (asterisk), *malleus* (X) and *squalus* (cross) indicated by "T". RMCA specimens R28198 and R28205 representing divergent cyt *b* lineages indicated.

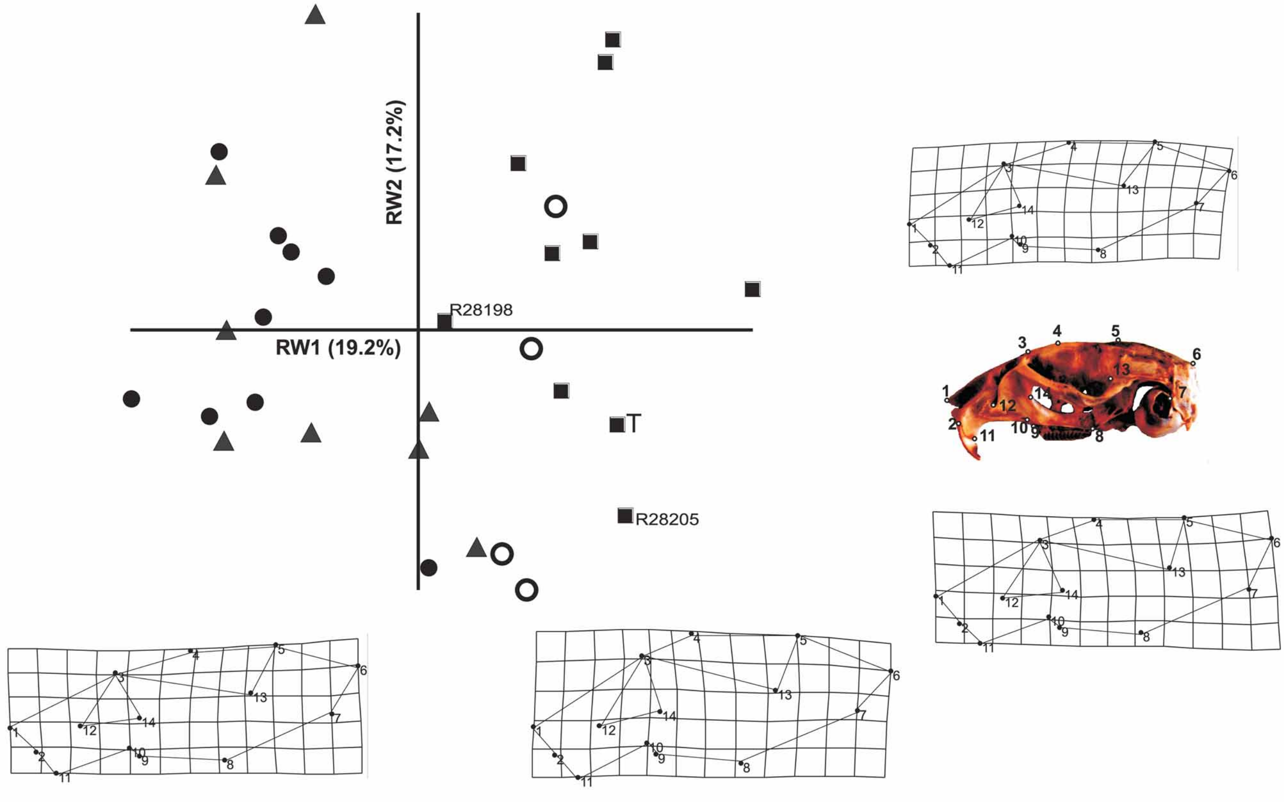

FIGURE 9. RWA of lateral landmarks showing variation in samples from the Aberdares Range of Kenya, between *O. orestes* (closed squares), *O. tropicalis* (closed triangles) and the population from the Aberdares summit having 5 laminae in m1 (closed circles). Topotypic specimens of *thomasi* from Molo in the Guas Ngishu Plateau indicated by open circles; RMCA specimens R28198 and R28205 representing divergent cyt *b* lineages indicated. Position of type specimen indicated by "T".

divergent zygomata). Between one and five overlapping homogeneous groups are present. Whilst most groups overlap indicating clinal variation, exceptions are GLS, MXTRL, NAW where "Sp. C" forms a non-overlapping distinct subgroup.

TABLE 7. ANOVA of selected cranial variables for 12 proposed taxa of *O. typus* s.l. Homogeneous groups represent Tukey's honestly significant subsets.

Occipito-nasal skull length (GLS)						
OTU	N	Mean	Groups			
jacksoni	3	35.1	A			
yaldeni **sp. nov.** (= "Sp. A")	4	35.2	A			
simiensis **sp. nov.** (= "Sp. D")	5	37.0	A	B		
uzungwensis	10	37.3	A	B		
dartmouthi	9	37.8	A	B	C	
helleri (= "Sp. B")	25	38.2	A	B	C	
orestes	14	38.4	A	B	C	
typus s.s.	6	38.8	A	B	C	
zinki	12	39.4		B	C	
fortior	8	39.6		B	C	
thomasi	5	40.8			C	
cheesmani **sp. nov.** (= "Sp. C")	7	45.1				D
F = 15.02 (p<<0.001); Explained SS = 63.2%						

continued.

Brain case depth (BCD)

OTU	N	Mean	Groups		
simiensis **sp. nov.** (= “Sp. D”)	5	10.1	A		
yaldeni **sp. nov.** (= “Sp. A”)	4	10.6	A	B	
fortior	8	10.8	A	B	
typus s.s	6	10.9	A	B	
dartmouthi	9	11.0	A	B	
jacksoni	3	11.0	A	B	C
uzungwensis	10	11.2		B	C
helleri (= “Sp. B”)	25	11.2		B	C
zinki	12	11.5		B	C
thomasi	5	11.5		B	C
orestes	14	11.8			C
cheesmani **sp. nov.** (= “Sp. C”)	7	11.9			C

F = 7.01 (p<<0.001); Explained SS = 44.5%

continued.

Maxillary tooth row length (MXTRL)

OTU	N	Mean	Groups				
jacksoni	3	8.4	A				
yaldeni **sp. nov.** (= “Sp. A”)	4	8.4	A				
dartmouthi	9	8.8	A	B			
simiensis **sp. nov.** (= “Sp. D”)	5	8.8	A	B			
uzungwensis	10	9.1	A	B			
zinki	12	9.2	A	B			
orestes	14	9.3		B	C		
thomasi	5	9.4		B	C		
helleri (= “Sp. B”)	25	9.7			C	D	
fortior	8	9.8			C	D	
typus s.s.	6	10.2				D	
cheesmani **sp. nov.** (= “Sp. C”)	7	11.3					E

F = 26.05 (p<<0.001); Explained SS = 74.9%

continued.

Nasal width (NAW)

OTU	N	Means	Groups			
yaldeni **sp. nov.** (= “Sp. A”)	4	6.1	A			
jacksoni	3	6.4	A	B		
helleri (= “Sp. B”)	25	6.6	A	B		
simiensis **sp. nov.** (= “Sp. D”)	5	6.6	A	B	C	
dartmouthi	9	6.8	A	B	C	
orestes	14	6.9	A	B	C	
typus s.s	6	7.1		B	C	
zinki	12	7.1		B	C	
thomasi	5	7.1		B	C	
uzungwensis	10	7.2		B	C	
fortior	8	7.3			C	
cheesmani **sp. nov.** (= “Sp. C”)	7	8.6				D

F = 18.77 (p<<0.001); Explained SS = 68.2%

continued.

Inter-orbital constriction (IOC)				
OTU	N	Means	Groups	
simiensis **sp. nov.** (= “Sp. D”)	5	3.6	A	
jacksoni	3	3.8	A	B
helleri (= “Sp. B”)	25	3.8	A	B
typus s.s	6	3.9	A	B
yaldeni **sp. nov.** (= “Sp. A”)	4	3.9	A	B
cheesmani **sp. nov.** (= “Sp. C”)	7	4.0	A	B
uzungwensis	10	4.0		B
orestes	14	4.1		B
thomasi	5	4.1		B
fortior	8	4.1		B
zinki	12	4.2		B
dartmouthi	9	4.2		B
F = 5.95 (p<<0.001); Explained SS = 40.5%				

continued.

Greatest zygomatic width (ZYW)							
OTU	N	Means	Groups				
jacksoni	3	17.5	A				
yaldeni **sp. nov.** (= “Sp. A”)	4	17.6	A				
uzungwensis	10	18.2	A	B			
simiensis **sp. nov.** (= “Sp. D”)	5	18.4	A	B	C		
helleri (= “Sp. B”)	25	19.0	A	B	C		
typus s.s.	6	19.2	A	B	C		
dartmouthi	9	19.2	A	B	C		
zinki	12	19.2	A	B	C		
fortior	8	19.4		B	C	D	
orestes	14	19.5			C	D	
thomasi	5	20.8				D	E
cheesmani **sp. nov.** (= “Sp. C”)	7	21.5					E
F = 11.8 (p<<0.001); Explained SS = 57.5%							

continued.

Maximum bulla length (BUL)					
OTU	N	Means	Groups		
yaldeni **sp. nov.** (= “Sp. A”)	4	6.6	A		
jacksoni	3	7.0	A	B	
simiensis **sp. nov.** (= “Sp. D”)	5	7.0	A	B	
dartmouthi	9	7.0	A	B	
uzungwensis	10	7.2	A	B	
typus s.s.	6	7.7		B	C
fortior	8	7.8		B	C
helleri (= “Sp. B”)	25	7.8			C
orestes	14	7.9			C
zinki	12	8.0			C
thomasi	5	8.3			C
cheesmani **sp. nov.** (= “Sp. C”)	7	8.3			C
F = 11.92 (p<<0.001); Explained SS = 57.8%					

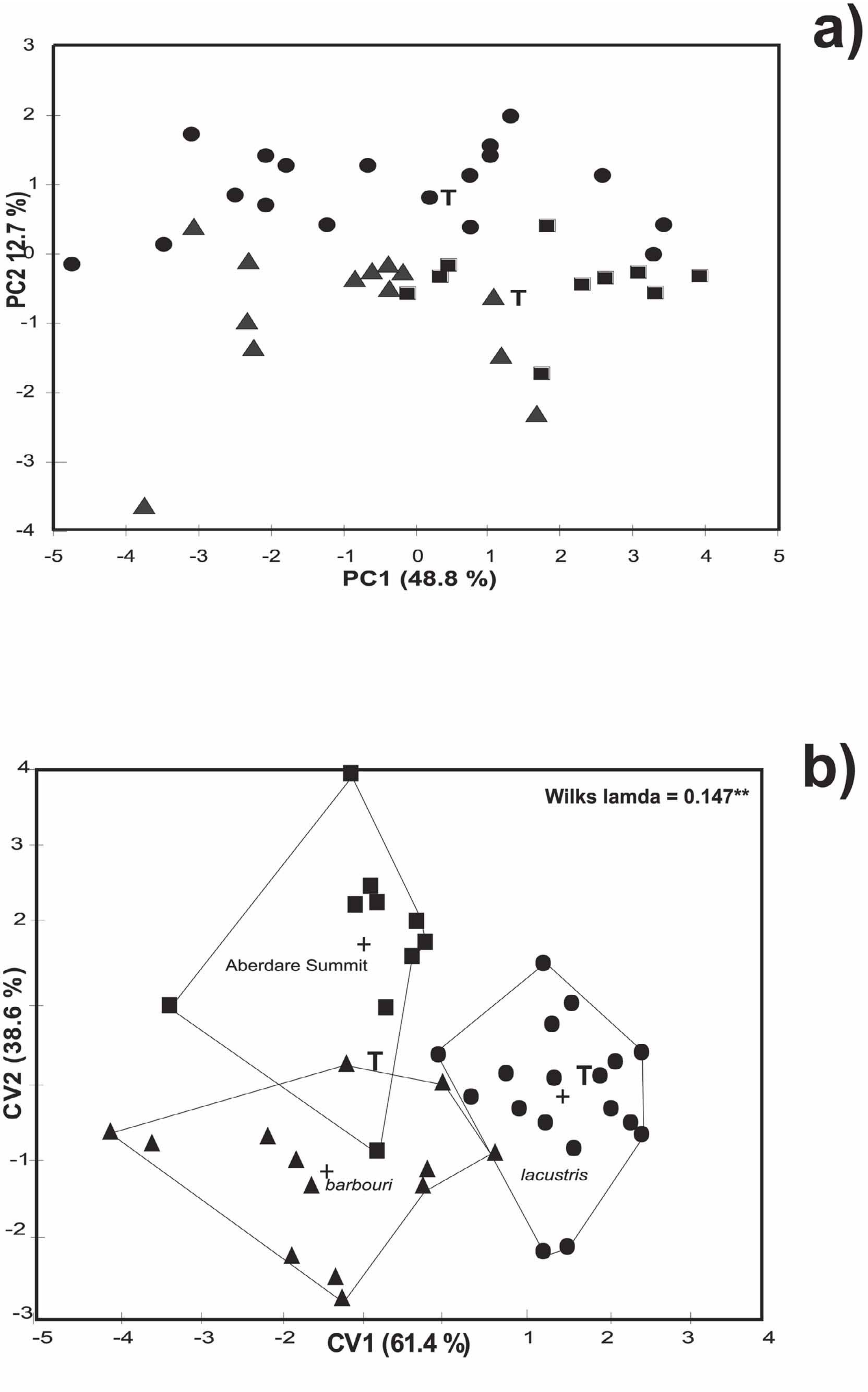

FIGURE 10. PCA (a) and CVA (b) of linear variables showing craniometric separation between the population from Aberdares summit (closed squares) and other eastern African species sharing five laminae in m1 (*O. barbouri*, closed triangles, and *O. lacustris*, closed circles). Positition of type specimens indicated by "T".

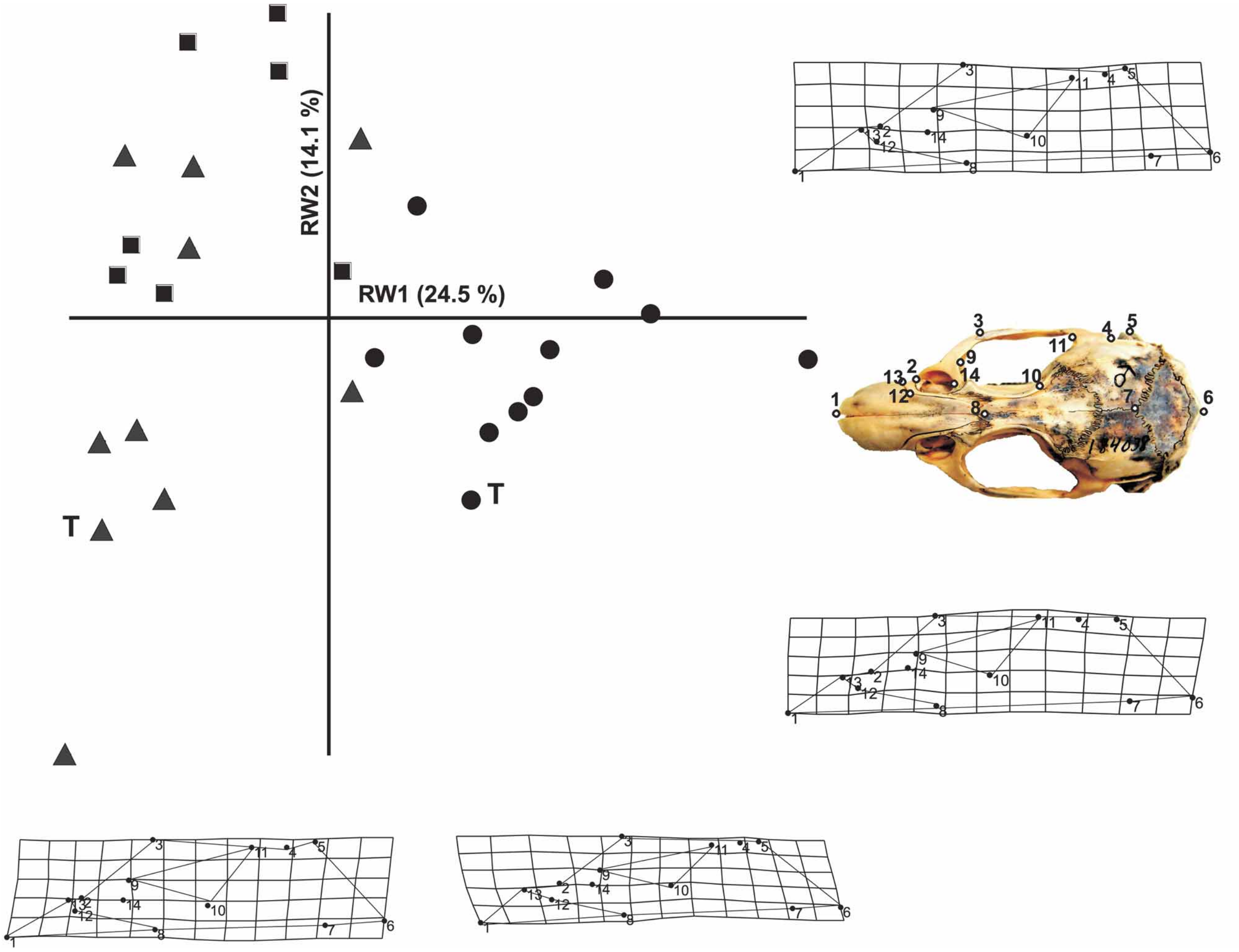

FIGURE 11. RWA of dorsal landmarks showing craniometric separation between east African species sharing five laminae in m1 (*O. barbouri*, closed triangles, *O. lacustris*, closed circles, Aberdares Summit population, closed squares). Position of type specimens indicated by "T".

Multivariate results. Broader morphometric relationships amongst alpine zone *Otomys* forms in Ethiopia, East and Central Africa are shown in Figs. 12–14. The most distinct form is "Sp. C" from the Lake Tana region of western Ethiopia (highest CV1 scores; Fig. 12, Table 6, and forming a highly divergent branch on the phenogram of Mahalanobis distances between group means). Apart from "Sp. C", Ethiopian and east African alpine forms overlap widely in cranial linear dimensions. As summarized by Mahalanobis phenogram (Fig. 12b), notwithstanding "Sp. C" there are two morphometric groups representing larger-sized (*typus* s.s., *fortior*, "Sp. B", *orestes*, *thomasi*, *zinki*) and smaller-sized taxa ("Sp. A", "Sp. D", *dartmouthi*, *jacksoni*, *uzungwensis*).

Alpine forms were even less well resolved by landmark data (Figs. 13, 14) compared with the linear data. However, on dorsal landmarks, specimens of *O. orestes* and from the alpine Mt Kilimanjaro population (*zinki*) are mostly separated from other forms in having a marked forward shear (more acutely angled) of the shorter anterior zygomatic arch (Fig. 13). In lateral profile, individuals of *O. orestes* and *O. thomasi* separate partially from other alpine forms on RW2, having a more pronounced lateral arching, in particular a deeper cranium at the level of the orbit (the "ram's head" described by Dollman 1915 as being most pronounced in *thomasi*) and a longer, more downward-angled parietal outline (between landmarks 4 and 5) (Fig. 14). RW2 also tends to separate *uzungwensis* (more pronounced arching) from *dartmouthi* (less pronounced).

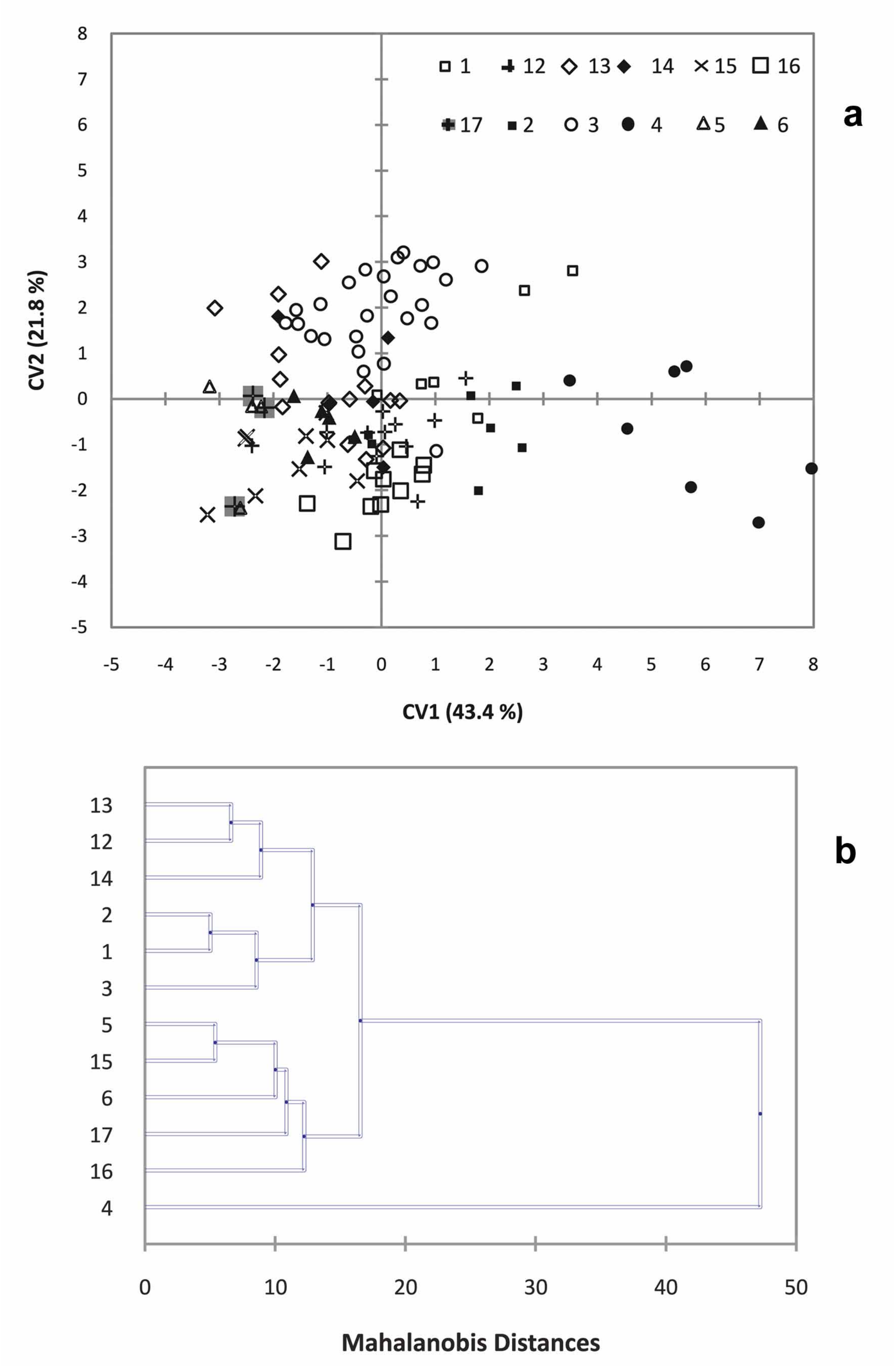

FIGURE 12. CVA (a) of linear variables showing craniometric separation between regional groups of specimens assigned to *typus* s.l. and phenogram (b) based on Mahalanobis distances between OTUs. Numbers represent OTU numbers in Table 2.

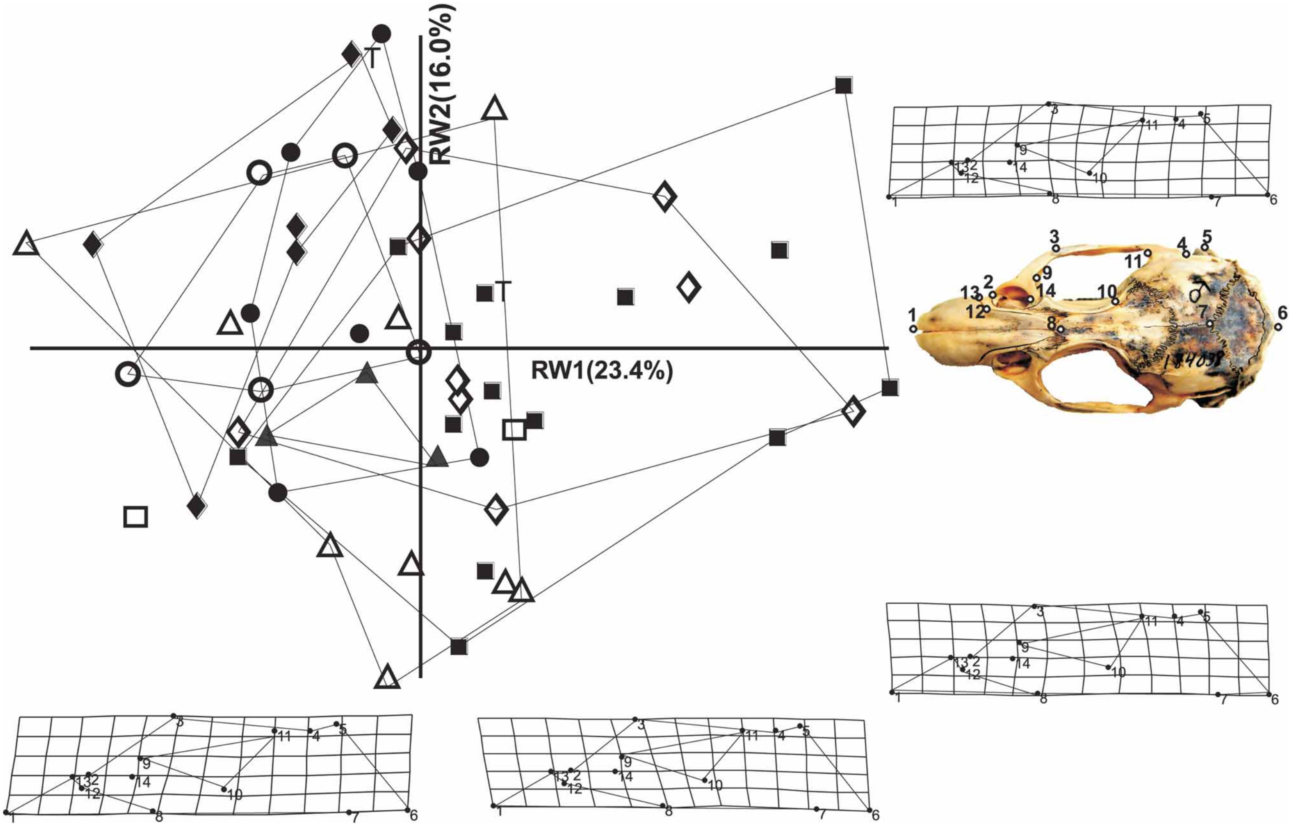

FIGURE 13. Relative warps analysis of dorsal landmarks showing craniometric separation between regional groups of specimens from alpine habitats assigned to *typus* s.l. Closed squares = *orestes*; closed circles = Aberdare summit; closed triangles = *dartmouthi*, closed diamonds = *typus* s.1. (Ethiopia); open squares = *jacksoni*; open circles = *thomasi*; open triangles = *uzungwensis*; open diamonds = *zinki*.

Ecological data

PCA of bioclimatic variables. Based on PCA of nine bioclimatic variables, Fig. 15 summarises ecological relationships between localities representing *O. typus* s.l. (47 localities: Fig. 15; Table 8). Populations of most alpine forms of *O. typus* s.l. are notably segregated ecologically. This is particularly marked in the case of the Ethiopian forms; thus *typus* s.s. (Simien Mts), *O. cheesmani* **sp. nov.** (= “Sp. C”) (Lake Tana Region), and *O. yaldeni* **sp. nov.** (= “Sp. A”) (lower altitudes within the Bale Mts) occupy unique bioclimatic niches quite distinct from each other and from *O. helleri* (= “Sp. B”) (higher altitudes within the Bale Mts, Arussi Plateau), *thomasi* (from Uasin Gishu Plateau in Kenya) and *fortior* (sub-alpine forests of southwestern Ethiopia). However, *helleri* (= “Sp. B”), *thomasi* and *fortior* overlap ecologically.

Forms of *typus* s.l. separate on PC1 on the basis of an inverse relationship between altitude/precipitation and temperature (see eigenvectors: Table 8; high positive scores indicating higher elevation, colder and wetter climates), and on PC2 on the basis of seasonality in temperature and precipitation. On PC2, populations further north or south from the equator (Simien Mts (*typus* s.s.), Kilimanjaro (*zinki*) and the Eastern Arc and Nyika Plateau (*uzungwensis*)) show greater seasonality compared to those from the more equatorial Kenyan Highlands, Mt Elgon and the Albertine Rift. Albertine Rift (*dartmouthi*) occupies the most seasonally equitable bioclimatic niche. Whilst *orestes*, *fortior*, *jacksoni* and “Sp. B” have intermediate values on PC2 (“seasonality”), *jacksoni* differs clearly from the others on PC1 (low scores indicating relatively low precipitation and high temperatures, possibly due to its proximity to the equator).

The positions of Ethiopian localities of uncertain taxonomic affiliation (lacking molecular and chromosomal data) are shown on Fig. 15. Not surprisingly, Chilalo, the type locality of *helleri*, which is located on the Arussi Plateau, shares a similar climatic niche to geographically close localities of Mt Albasso on the Arussi Plateau and Dinsho in the Bale Mts. Likewise, Jimma, which is situated 30 km from Charada Forest (type locality of *fortior*) in southwestern Ethiopia groups close ecologically to localities assigned to *fortior*, and the localities Gombitchu (type locality of *degeni*) and Ankober which are situated 120 km apart in the central Ethiopia highlands west of the Rift Valley group with geographically close localities assigned to *O. cheesmani* **sp. nov.** (="Sp. C") (e.g. these two localities are situated 150 – 250 km from Debra Marcos). The remaining unassigned localities are not grouped ecologically with any particular taxon: these include Chencha and Bongke in the southern highlands, Hirna in the northern highlands east of the Rift, 250 km north of the Arussi Plateau, and Malka (type locality of *malkensis*), east of the Rift and 110 km south of the Arussi Plateau.

TABLE 8. Eigenvectors from PCA of altitude and bioclimatic variables from 47 localities assigned to the *O. typus* s.l. species complex.

Climate variables	PC1	PC2	PC3
Altitude (m)	0.408	0.081	-0.238
Bio_1_MAT	-0.405	-0.162	0.237
Bio_12_AP	0.330	0.230	0.484
Bio_13_MaxP_Wettest_Mth	0.024	0.583	0.436
Bio_14_MinP_Driest_Mth	0.332	-0.179	0.492
Bio_15_P_Season	-0.284	0.468	-0.213
Bio_4_T_Season	-0.262	0.511	-0.043
Bio_5_MaxT_Warmest_Mth	-0.404	-0.183	0.183
Bio_6_MinT_Coldest_Mth	-0.370	-0.173	0.374

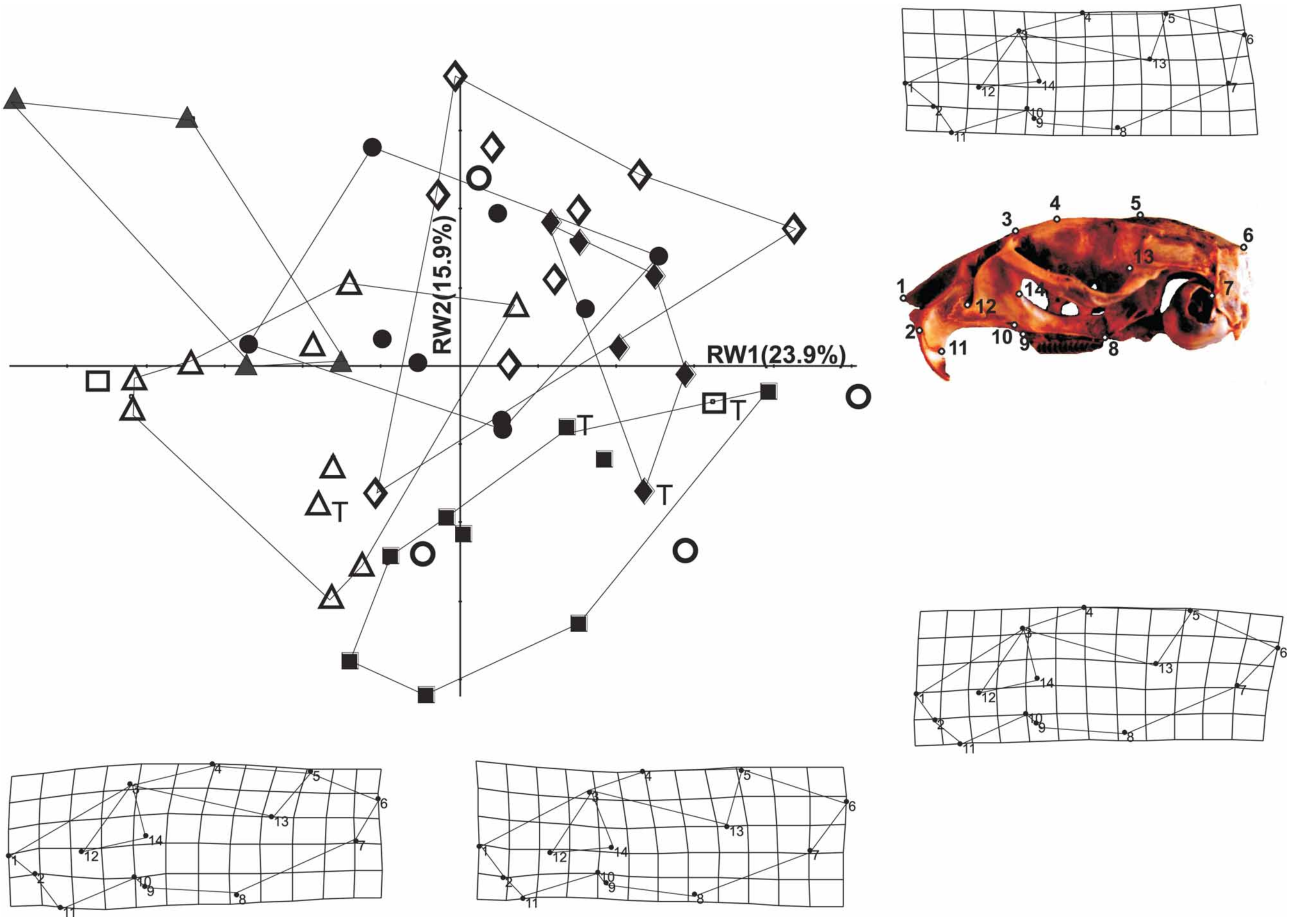

FIGURE 14. Relative warps analysis of lateral landmarks showing craniometric separation between regional groups of specimens from alpine habitats assigned to *typus* s.l. Closed squares = *orestes*; closed circles = Aberdare summit; closed triangles = *dartmouthi*, closed diamonds = *typus* s.1. (Ethiopia); open squares = *jacksoni*; open circles = *thomasi*; open triangles = *uzungwensis*; open diamonds = *zinki*.

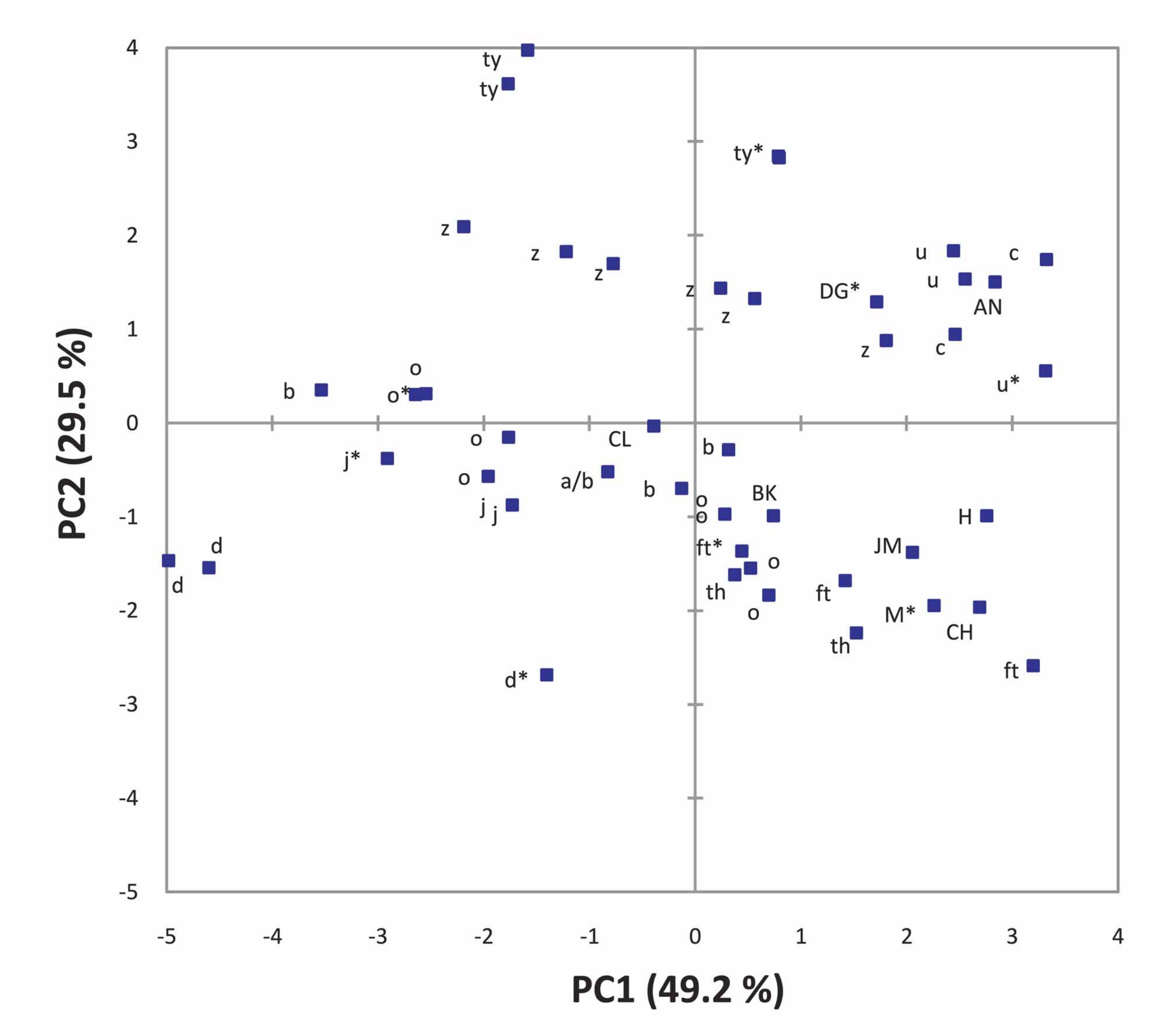

FIGURE 15. PCA summarizing variation in altitude and eight bioclimatic variables in localities of O. *typus* s.l. (48 localities). Asterisks denote type localities. Symbols of localities assigned to revised taxa given in lower case as follows: "ty" = *typus* s.s. (Ethiopia: Simien Mts, Mt Guna); "a" = *yaldeni*: Sp. A (Ethiopia: Bale Mts); "ft" = *fortior* (Ethiopia: Charada (type locality), Beletta and Sheka Forests); "b" = *helleri*: Sp B (Ethiopia: Bale Mts, Arussi Plateau); "c" = *cheesmani*: Sp. C (Ethiopia: Dangila – Debra Marcos); "d" = *dartmouthi* (Ruwenzori Range); "j" = *jacksoni* (Mt Elgon); "o" = *orestes* (Kenya: Aberdares and Mt Kenya); "th" = *thomasi* (Kenya: Uasin Gisho Plateau); "u" = *uzungwensis* (Malawi: Nyika Plateau and Tanzania: Southern Rift and Eastern Arc); "z" = *zinki* (Mt Kilimanjaro). Symbols of localities from Ethiopia, which could not be unambiguously assigned to revised taxa are labelled in upper case as follows: AN = Ankober; BK = Bongke; CH = Chenca; CL = Chilalo (type locality of *helleri*); H = Hirna; M = Malka (type locality of *malkensis*); JM = Oromiya, Jimma.

Discussion

Intraspecific variation. Based on data from two African rodent genera, Abdel-Rahman *et al.* (2009) showed that ontogenetic and secondary sexual variation, although often overlooked in systematic studies, can confound taxonomic decisions based on morphometric results. Previous intra-population analyses of southern African populations of *Otomys* (Taylor *et al.* 1993, 2005; Taylor & Kumirai 2001) demonstrated lack of significant sexual dimorphism and homogeneity of toothwear classes 4 and 5. Our results (Fig. 4; Table 5) confirm absence of significant sexual dimorphism and presence of significant ontogenetic variation in an East African population of *O. tropicalis*, where age classes 2, 3 and 4 differ significantly from each other both in size (linear variables) and shape (dorsal landmarks). Individuals of Class 2 and most Class 3 individuals display a "juvenile" skull shape with proportionately wide braincase and short facial region (Fig. 2). For this reason, with a few exceptions (e.g. type specimens), further analyses were based on pooled sexes for age class 4 and 5 individuals only.

Taxonomic conclusions. A multi-disciplinary approach emphasizes integration of biogeographic, morphometric, genetic, and ecological evidence and positions us to delimit species under the Cohesion Species Concept (Templeton 1998), which holds that species are "evolutionary lineages, with the lineage boundaries that define species arising from the forces that create reproductive communities (i.e. cohesion mechanisms)". These cohesion mechanisms are genetic exchangeability (absence of barriers to gene flow) and ecological interchangeability (occupancy of the same niche). Whilst phylogeographic data can elucidate barriers to gene flow or genetic non-exchangeability (Avise 2009), ecological non-interchangeability (occupancy of different niches) can be elucidated by adaptive morphological divergence or, in the case of cryptic species, ecological niche models (see Bond & Stockman 2008; Stockman & Bond 2007). In this study, we regard "good" species as those showing both genetic non-exchangeability (inferred from molecular and/or morphometric data) and ecological non-interchangeability (based on ordination of bioclimatic variables and/or adaptive morphometric trends). A weakness of this holistic approach to species definitions, particularly as it bears on practical issues of *Otomys* taxonomy, is that we lack full complementarity of morphometric, genetic, and ecological information across all analytical samples.

Principal components analysis of altitude and eight bioclimatic variables disclosed that eastern African alpine taxa formerly classified as subspecies of *O. typus* are mostly ecologically distinct in their ranges compared with *O. typus* s.s. from the Simien Mts of Ethiopia (Fig. 15), as well as from each other, and occupy distinct niches that are also geographically widely separated. In particular, *O. dartmouthi* (Ruwenzori Mts), *O. jacksoni* (Mt Elgon), *O. uzungwensis* (Udzungwa Mts), and *O. zinki* (Mt Kilimanjaro) showed no overlap in their bioclimatic niches. The wide geographic lowlands that isolate these "sky islands" of Afro-alpine habitat, coupled with evidence for adaptive morphometric and/or genetic (p = 8–9%) divergence between them (see **Results**), substantiate their specific status. Genetic data are so far unavailable for *O. uzungwensis*, but this species can be clearly demarcated on morphometric as well as ecological grounds, as discussed above and as also demonstrated by Carleton & Byrne (2006).

The status of *O. thomasi* and *zinki* in relation to *O. orestes* requires further comment. Carleton & Byrne (2006) tentatively placed both in synonymy with *O. orestes*. In the case of *zinki*, those authors lacked topotypic examples of *zinki* and based their synonymy on literature descriptions and geographic proximity. Our evidence decisively portrays this form as a genetically and ecologically divergent lineage that merits species status. Although overlapping with *O. orestes* in some morphological aspects, *O. zinki* clearly lacks the arched lateral skull profile that typifies *O. orestes*.

The case for species recognition of *thomasi* is more tenuous. Sample size is small, genetic data are lacking, and the range of this form on the Mau Escarpment and Uasin Gishu Plateau overlaps ecologically with the lower altitudinal reaches of the alpine form, *O. orestes* on Mt Kenya and the Aberdares. Nevertheless, whereas type specimens of *malleus*, *percivali* and *squalus* from the Aberdares (east of the eastern Rift Valley) clustered within the range of variation of *O. orestes*, the topotypic series of *thomasi* from Molo in the Mau Escarpment (western rim of the eastern Rift Valley) falls almost completely outside the range of variation of *O. orestes*, owing principally to their larger size (easily evidenced by external variables; Table 9; Fig. 16b). Furthermore, specimens of *thomasi* have an overall paler buffy pelage when compared to those of *O. orestes* and from our observations, lack the pale aural tufts of the latter (Fig. 16b). In view of the geographical barrier imposed by the eastern Rift Valley, separating alpine habitats on mountains to the east (Mt Kenya and Aberdares) and west (Uasin Gishu Plateau and Mau Escarpment), the observed size and colour differences between *O. orestes* and *thomasi* may indicate adaptive divergence and hence ecological non-interchangeability. Given the large genetic distances that distinguish other isolated East African alpine forms— e.g., on Mt Elgon (*O. jacksoni*), the Ruwenzoris (*O. dartmouthi*), and Mt Kilimanjaro (*O. zinki*)— we predict that high genetic divergence will be found to separate *thomasi* from *O. orestes*. Pending availability of such data, we consider it parsimonious to provisionally recognize *O. thomasi* as a distinct evolutionary lineage and valid species, as it was initially described by Osgood (1910).

The situation in Ethiopia is also ambiguous. A very deep genetic divergence separates the chromosomally distinct *O. simiensis* **sp. nov.** (= "Sp. D") from Simien Mts (with 2n=54, NFa=54) from populations having the common karyotype of 2n=58, NFa=58 (*O. typus* s.s., O. *fortior*, and *O. helleri* (= "Sp. B")). Although the last-mentioned three forms differ only by around 3% (uncorrected *p*-distance), the ecological and biogeographic separation of these forms argues for species status. Populations of *O. helleri* from the Bale Mts and Arussi Plateau occur east of the Rift Valley (a major barrier to dispersal) and are morphometrically distinct from other Ethiopian populations,

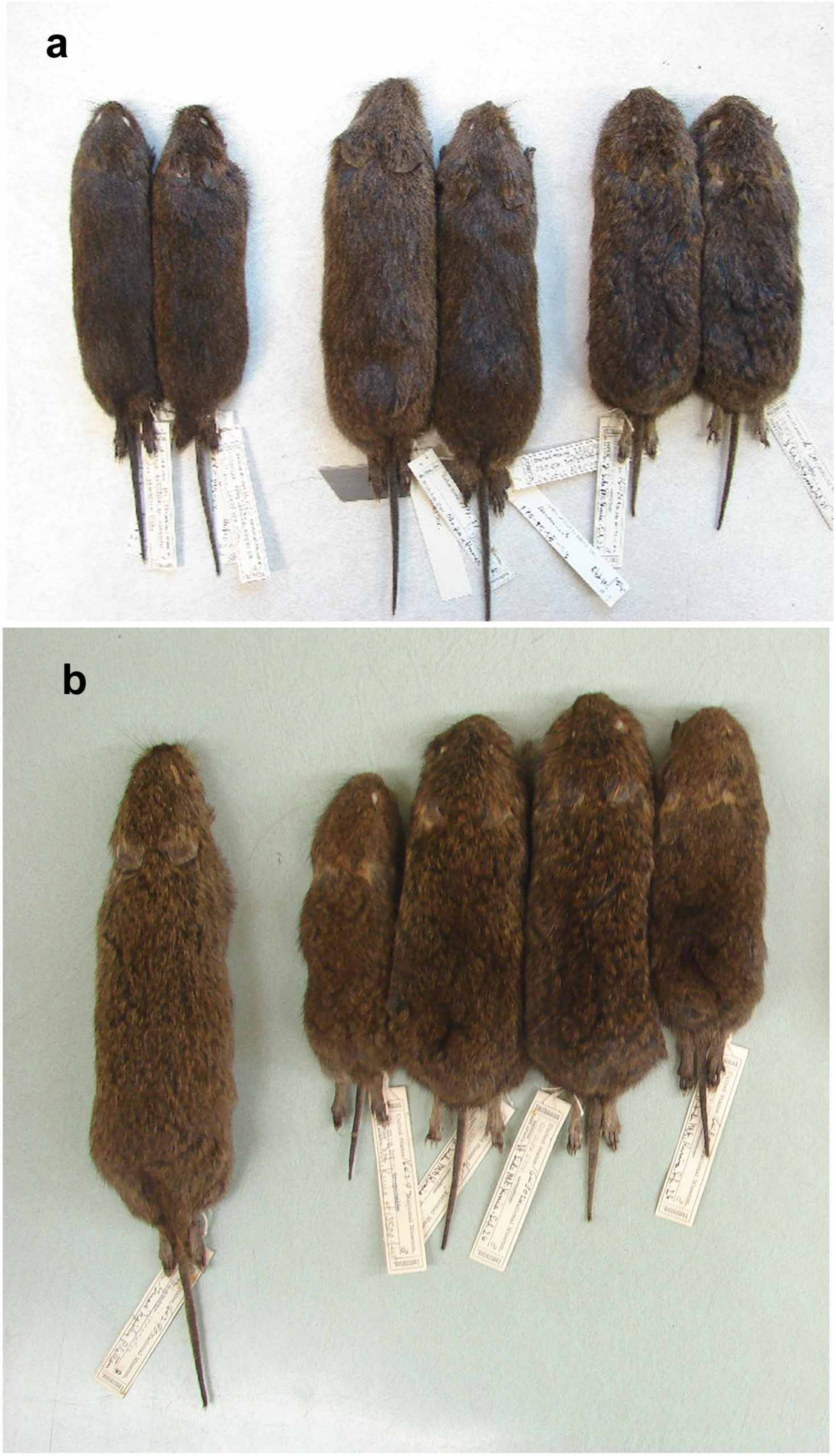

FIGURE 16. Photographs a) comparing pairs of study skins from three populations in the Aberdares: *O. tropicalis* (from mid-altitudes, two skins on left, and summit, two skins in middle) and *O. orestes* (two skins on right); and (b) comparing *O. thomasi* (left) with series of *O. orestes* (right). Apparent differences in size are not due to over-stuffing of specimens but more or less indicative of real size difference as can be verified from inspection of means of head and body length of relevant taxa in Table 9

whilst *O. typus* s.s. and *O. fortior* occur to the west of the Rift valley. Whilst *O. typus* s.s. is known from alpine moorlands, *fortior* occupies lower-lying forests in the southwestern parts of Ethiopia and is almost completely differentiated morphometrically from *O. typus* s.s. populations. Lavrenchenko *et al*. (1997) already demonstrated the genetic distinctness (on allozyme data) of *O. yaldeni* **sp. nov.** (= "Sp. A") occurring sympatrically with *O. helleri* (= "Sp. B") on the Bale Mountains. Thus, we feel justified in recognised six distinct species in Ethiopia on a combination of karyotypic, molecular, craniodental, morphometric, biogeographic and ecological data (see Taxonomic Summary below).

Our study was not intended to focus upon the *O. tropicalis* species complex as currently understood (i.e., *sensu* Musser & Carleton 2005; Carleton & Byrne 2006). Although long confused as a subspecies of *O. irroratus* (Thomas, 1902b; Bohmann, 1952), subsequent studies drawing upon morphological, morphometric, and genetic information have underscored that *O. tropicalis* of eastern Africa is specifically distinct from *O. irroratus* of southern Africa (Taylor & Kumirai 2001; Carleton & Byrne 2006; Taylor *et al*. 2009a; see Fig. 3a, b). Nonetheless, these latter studies and results presented herein reveal that *O. tropicalis* actually refers to a complex of species. Taxonomic problems encountered and some profitable lines of inquiry follow.

At least three divergent "*tropicalis*" cyt *b* clades are apparent (Fig. 3a). One includes topotypic series of *tropicalis* from Mt Kenya, as well as slightly divergent (genetically and morphometrically) Aberdares populations; a heterogenous mixture of forms from Ruhuruini in the Aberdares (*O. t. tropicalis*?), from Mt Elgon (*O. t. elgonis*?), and from Rethy in the northeastern DRC (*O. t. faradjius*) comprises a second; and a third unites individuals from the bamboo zone of Mt Elgon (*O. t. elgonis*?). Although our results are preliminary, we note that these different moieties within "*tropicalis*" link at various levels of kinship with taxa formerly classified as subspecies under *O. typus* (*O. dartmouthi*, *O. jacksoni*, *O. orestes*). To resolve the *tropicalis* complex properly will require further molecular and morphometric studies that broaden geographical sampling, survey elevational transects on a finer scale, and incorporate topotypic material in deliberate taxonomic comparisons. Our study notably lacks genetic data for populations that inhabit mountains along the Albertine Rift (*rubeculus*, *vulcanis*), the Imatong Mts in southern Sudan (*giloensis*, reallocated to *O. tropicalis* s.l. by Carleton & Byrne 2006), or ranges that outlie the core highlands bordering the eastern Rift Valley (*nubilus*, *vivax*). Specimens obtained from detailed transects along the slopes of East Africa's higher mountains would do much to illuminate the status of taxa currently assigned to *O. tropicalis*, in particular the middle elevation form *elgonis*. Specimens nominally referrable to the latter form are scattered in the gene tree produced from cyt *b* sequences (Fig. 3a), a result that leaves us uncertain about which ones actually represent *O. tropicalis elgonis* proper as known from its type locality (Elgonyi, Mt Elgon).

The variable occurrence of 5 m1 laminae in certain localities of *O. tropicalis* from the Aberdare Mts is a surprizing finding in view of the remarkable stability of this character observed in most species of *Otomys* (4 m1 laminae), including taxa synonymized under *O. tropicalis* s.l. (Table 4). The occasional report of *O. lacustris* in central Kenya (Taylor & Kumirai 2001) is based on one of these exceptional specimens with a 5-laminated m1 (BM 10.5.3.480). Possession of a lower first molar with 5 laminae figured prominently in the diagnoses of other east African species (i.e., *O. barbouri*, *O. lacustris*), but the Aberdares sample (OTU 11) is morphometrically well differentiated from those forms (Fig. 10). Instead, it morphologically and morphometrically fits with other OTUs here referred to *O. tropicalis* and as earlier identified by others (Hollister 1919; Carleton & Byrne 2006). Two specimens (USNM 590002, 590003) from one locality where m1 variation was encountered (Aberdares National Park, Fishing Lodge) genetically clustered with other *O. tropicalis* from the Aberdare Mts and Mt Kenya (Fig. 3a, b); unfortunately, both retain the common 4-laminated m1 character state. Do individuals with 5 m1 laminae form a cryptic species that is otherwise morphometrically indistinguishable from *O. tropicalis*, or do they represent population variation which may or may not be indicative of incipient speciation, paralleling the evolution of forms with 5 m1 laminae on Mt Elgon (*O. barbouri*) and the Eastern Arc Mountains (*O. lacustris*)? Answers to these questions must incorporate fresh material collected along carefully designed elevational transects in the Aberdare Mts.

In discussing the southern geographic limits of *O. tropicalis*, Carleton & Byrne (2006) suggested that *sungae*, described from the Usambara Mts of the northern Eastern Arc Mts and previously assigned to the *O. denti* group based on morphology (see Taylor *et al*. 2009a), could as reasonably be assigned to the *tropicalis* group on biogeographical and morphological grounds. Cytochrome *b* data unequivocally support this hypothesis (Fig. 3a), grouping near-topotypic *O. sungae* within a clade comprising *O. jacksoni*, *O. orestes*, and the small-sized molecular clade of *tropicalis* s.l. discussed above. As already proposed by Taylor *et al.* (2009a), *O. sungae* is a good species; however, the topotypic population from the Usambaras is clearly genetically remote from the lineage from the

Nyika Plateau formerly assigned to *O. denti sungae* (Musser & Carleton 2005, Fig. 3 a, b). Taylor *et al.* (2009a) already raised this possibility based on biogeographical and morphometric data but, pending molecular data, refrained from formally describing this lineage. The evidence at hand, from this study and that of Taylor *et al.*, (2009a), makes it abundantly clear that the name *O. sungae* should be reserved only for the Usambaras population and that the lineage from the Nyika Plateau (which groups genetically with two divergent lineages of *O. lacustris*) should be formally described as new (with no available names in the literature).

Speciation, adaptive divergence, and patterns of microendemism. Palaeontological data support a South African origin and early Pliocene radiation of Otomyini (Denys 1989, 1999, 2003; Pocock 1976, 1987; Senegas 2001; Senegas & Avery 1998). Two fossil species of *Euryotomys* from South Africa, *E. pelymoides* (Pocock 1976; 3.7–5 Myr; Denys *et al.* 1989) and *E. bolti* (Senegas & Avery 1998; 4-5 Myr; Senegas 2001), provide evidence for the murine origin of Otomyini. The oldest fossils of true *Otomys* appear around 3–3.7 Myr in South Africa (*O.* cf. *gracilis* and *O.* cf. *sloggetti*) but not until 2.3 Myr in the western Rift Valley (eastern DRC; *Otomys* sp.) and 1.5–2.0 Myr in East Africa (*O. petteri* and *O.* cf. *petteri*; Denys 1989, 2003), despite excellent micromammal fossil records from older sequences in east Africa.

As discussed in depth by Taylor *et al.* (2004b), Bohmann's (1952) adaptive scenarios emphasized the evolutionary trend towards increasing lamina number in M3 in successively derived taxa, surmising that multiple south-north African radiations occurred that coincided with cooler Pleistocene “pluvial” (glacial) periods. Specifically, Bohmann (1952) proposed that *O. sloggetti* radiated north to give rise to *O. denti* in the western (Albertine) Rift highlands during an early Pleistocene pluvial, South African *O. saundersiae* radiated north to give rise to Ethiopian *O. typus* during a subsequent pluvial, whereas South African *O. irroratus* gave rise to east African *O. tropicalis* during a third pluvial cycle. On the other hand, based on palaeontological evidence, Denys (2003) postulated a single northern dispersal of the extinct *O.* cf. *gracilis* first to the western Rift mountains (*Otomys* sp; 2.3 Myr) and then subsequent *in situ* speciation in East Africa, giving rise *inter alia* to the extinct *O. petteri* (from 1.8 Myr at Olduvai) and *O.* cf. *angoniensis* (0.3 Myr).

The earliest diversification within Otomyini estimated at around 3.5 Myr (Fig. 3a), which separates East African *O. denti-lacustris*, *O. barbouri* and South African *P. brantsii* from other southern, western, northern and eastern lineages, is consistent with the earliest fossil appearance of *Otomys* (*O.* cf. *gracilis*) in the Upper Pliocene deposits at Makapansgat (3.5–3.7 Myr; Pocock 1987), possibly indicative of a single or multiple simultaneous northwards, westward and eastwards dispersals from South Africa as predicted by Denys (2003). Two events dated at around 3.1 Mya resulted in splits in the former clade between the *denti-lacustris* clade and *O. barbouri* and *P. brantsii*; and in the latter clade, the split between *O. angoniensis* and *O. irroratus* from South Africa and all other East and West African taxa (*occidentalis, burtoni, tropicalis* s.l., *typus* s.l., *sungae*). At approximately 2.8 Myr ago the Ethiopian *O. typus* s.l. clade diverged from the remaining East and West African clades followed by the split around 1.8 Myr between *O. occidentalis* and *O. burtoni*, and between a clade comprising *O. tropicalis* s.s., *O. tropicalis* (Aberdares) and *O. dartmouthi* (Burundi and DRC) from a clade constituting *O. zinki* (Mt Kilimanjaro), *O. simiensis* **sp. nov.** (Simien Mts), *O. sungae* (Usambaras), *O. jacksoni* (Mt Elgon), *O. orestes* (Abedares moorland), the two divergent clades of *O. tropicalis “elgonis”* (Mt. Elgon) and *O. t. faradjius* from the DRC. Divergence of a number of more terminal lineages: 1) *tropicalis* s.s from *dartmouthi*; 2) *O. zinki* from *O. typus* s.l. [*O. simiensis* **sp. nov.**]; 3) *O. sungae* from a clade comprising *O. jacksoni, O. tropicalis “elgonis* “ and *O. t. faradjius,* took place close to 1 Mya, a time which corresponds closely with a hypothesized period of aridification in the region. Congruent speciation pulses are apparent in the *O. denti-lacustris* clade, the Ethiopian clade (*O. typus* s.s. and *O. helleri*) and these lineages splitting off from *O. fortior* (southwestern forests) as well as in other mammal and bird taxa (Bowie *et al*. 2004, 2006; DeMenocal 1995, 2004; Huhndorf *et al*. 2007; Taylor *et al*. 2009a).

As anticipated by Denys (2003) and Carleton & Byrne (2006), patterns of morphometric, genetic and ecological divergence amongst East African populations of the *O. tropicalis* s.l. and *O. typus* s.l. complexes are more parsimoniously explained by regional cladogenesis along elevational gradients, rather than by multiple successive continental colonisations of different ancestral forms as supposed by Bohmann (1952). Clearly the “alpine morph” of *O. typus* s.l. has evolved independently at very high elevations on several mountain ranges in eastern and north-eastern Africa. The strong support for monophyly of two divergent lineages (*O. jacksoni* from the alpine zone and one sub-alpine/montane lineage assigned previously to *O. tropicalis elgonis*) occurring on Mt Elgon provides direct corroboration of this hypothesis of *in situ* speciation along an elevational gradient. *Otomys orestes* from the Kenyan Highlands is also included in this clade (Clade 3b of Fig. 3a), suggesting continuity of habitats between Mt

Elgon and the Kenyan Highlands at around 0.5 Myr (based on dating estimates from BEAST; Fig. 3a). On the other hand, the existence of a divergent "elgonis" clade in Clade 2 (Fig. 3a) and the unresolved but basal position within Otomyini of another Mt Elgon endemic, *O. barbouri*, suggests that independent radiations on Mt Elgon have occurred widely separated in time. However, it should be noted that the combined 12S rRNA/ cyt *b* tree (Fig. 3b) provides strong support for monophyly of the two divergent *O. t. elgonis* clades, which form separate clades based only on cyt *b* sequences (Fig. 3a). Thus, further molecular data may indeed more strongly validate the hypothesis of multiple speciation events occurring *in situ* along elevational transects on Mt Elgon.

As in the case of *O. barbouri*, members of the *O. denti-lacustris* complex from the Albertine Rift, Southern Rift and Eastern Arc Mts—all characterised by ancestral morphological characters, such as fewer M3 laminae, blackish coloration, and single-grooved lower incisors—seem to occupy a more basal origin in the radiation of eastern African species (Fig. 3a, b; see also Taylor *et al*. 2009a).

As reasoned by Carleton & Byrne (2006:504–510), the biodiversity of Otomyini within eastern Africa has been chronically underestimated since Bohmann's (1952) revision. The results of this study appreciably elevate the number of endemic *Otomys* species (of the *O. typus* s.l. and *O. tropicalis* s.l. complexes) known from eastern and northeastern Africa: Ethiopian Highlands (six taxa including *O. fortior*, *O. helleri*, *O. typus* s.s., and the three new species described formally below, *O. cheesmani* **sp. nov.**, *O. simiensis* **sp. nov.** and *O. yaldeni* **sp. nov.**); Eastern Arc Mts and Southern Highlands of Tanzania and Nyika Plateau of Malawi (*O. uzungwensis*, two lineages obscured within *O. lacustris, O. sungae,* and the Nyika population previously assigned to *O. denti sungae*); Ruwenzori Mts (*O. dartmouthi, O. denti, O. tropicalis* s.l.); Mt Elgon (*O. jacksoni, O. barbouri,* and perhaps two unnamed lineages previously assigned to *O. tropicalis elgonis*); the Mau Escarpment and Uasin Gishu Plateau (*O. thomasi*, *O. tropicalis* s.l.); Aberdares and Mt Kenya (*O. orestes*, *O. tropicalis* s.s.); the Mathews Range (*O. dollmani*; see Carleton & Byrne 2006); and Mt Kilimanjaro (*O. zinki*). Detailed molecular, cytogenetic, and morphological analyses of populations belonging to the *O. angoniensis* complex, distributed on lower mountain slopes in Kenya and Tanzania, may reveal other geographically restricted species of *Otomys* that would enhance estimates of species richness and endemism within the region.

Given the highly microendemic status of most of the above-mentioned species and their restriction to localized alpine or subalpine habitats, threats such as climate change and/or anthropogenic effects (e.g., extensive fires caused by poachers in the alpine zone of Mt Elgon; PJT personal observation) may result in high extinction risks and red-listing as Endangered or Critically Endangered taxa.

Taxonomic summary

The following accounts formalize our results and taxonomic recommendations that involve species-group epithets formerly classified within *O. typus* sensu Bohmann (1952), Misonne (1974), and others. In view of the many forms herein considered and inconsistent interpretations of their status and affinity by past systematists, we present full synonymies that trace earliest identifications, primary synonyms, and subsequent name combinations as used in major classifications, faunal reports, and taxonomic revisions and compendia. Specimens examined include all individuals personally seen and identified by us. More detailed diagnoses and descriptions are provided for the three species herein described: *O. yaldeni* **sp. nov.**, *O. cheesmani* **sp. nov.** and *O. simiensis* **sp. nov.**

Otomys cheesmani new species

Figs 5, 6, 17; Table 9
Cheesman's Vlei Rat

Holotype. BMNH 1937.2.24.84; adult male, dry skin and skull, collector's number 7400; collected by R.E. Cheesman, 20 October 1937.

Type locality. Ethiopia, vicinity of Dangila, 66 km S Lake Tana, 2100 m; 11°16'N, 36°51'E.

Diagnosis. The largest representative of the *Otomys typus* species complex, differing from all other members by its distinctly larger and more robust skull with short and broad nasal bones, broad, angular and thickened zygomatic arches, very well developed supraorbital and parietal ridges and relatively very narrow interorbital region (referred to "Sp. C" above; see Figs 5, 6, 17 and Tables 7, 9).

Paratypes. BMNH 28.1.11.117 (adult female, dry skin and skull, collector's number 6040), BMNH 28.1.11.174 (adult male; dry skin and skull, collector's number 6078), BMNH 28.1.11.175 (subadult male, dry skin and skull), BMNH 28.1.11.176 (subadult male, dry skin and skull, collector's number 6366), BMNH 28.1.11.177 (adult female; dry skin and skull, collector's number 6040), BMNH 28.1.11.178 (adult female, dry skin and skull, collector's number 6070), BMNH 28.1.11.179 (adult female, dry skin and skull, collector's number 6165), BMNH 1937.2.24.82 (adult male, dry skin and skull, collector's number 7383), BMNH 1937.2.24.83 (adult male, dry skin and skull, collector's number 7387), BMNH 1937.2.24.85 (adult male, dry skin and skull, collector's number 7404), BMNH 1937.2.24.86 (adult female, dry skin and skull)—all 11 from the type locality, collected by R.E. Cheesman between 1926 and 1937; BMNH 70.657 (Ethiopia, Gojam, Debra Marcos, 2500 m; 10°20'N, 37°46'E; collected by Great Abbai Expedition, 19 August 1968).

Description. The dorsal pelage of *O. cheesmani* is bright brown with a reddish shade. Ventral pelage is pale yellowish-grey, the individual hairs yellow tipped and grey at the base. The ears are blackish, their inner surface covered with short rufous hairs. The dorsal surface of the forefeet and hindfeet is dark grey; the claws are grey. The tail is relatively short (49.3% of HB). The caudal hairs are blackish on the upper surface and pale yellowish on the lower surface; however, the tail does not appear distinctly bicoloured.

The robust skull of *O. cheesmani* (Fig. 17) is reflected in the large means recorded for most cranial dimensions, which exceed those of all other representatives of the *O. typus* complex except for interorbital width (Table 9). Although the observed ranges of certain external and cranial variables overlap, four cranial variables do not overlap in size: GLS (43.3–48.2 mm versus 34.3–43.3 mm); MXTL (11.0–12.0 mm versus 8.1–10.5 mm); NAW (8.0–9.0 mm versus 5.8–8.0 mm); PL (23.6–26.2 mm versus 16.7–23.6 mm) (Table 9). The anterior face of the lower incisor has two well defined and equally deep grooves. The upper third molar has 8 or 9 complete laminae (9 in the holotype) and the lower first molar 4 complete laminae.

Distribution. Known only from two localities in northwestern Ethiopia, 2100–2500 m (see above).

Ecology. The type locality currently represents a true agricultural landscape, presumably much transformed from the time when Cheesman collected the series. The holotype and paratypes of *O. cheesmani* were supposedly collected in an intrazonal wetland habitat. The specimen from Debra Marcos (BMNH 70.657) was captured in low *Acacia* scrub. *Otomys cheesmani* occupies lower elevations (2100–2500 m) than other Ethiopian *Otomys* (excluding the rainforest dweller *O. fortior*). Nevertheless, habitat requirements of this new species remain unclear.

Etymology. We selected the specific epithet to recognize Robert E. Cheesman (1878–1962), who collected the holotype and topotypic series of this distinctive species of *Otomys*. Cheesman was a British military and diplomatic officer in the Middle East, Arabian Peninsula, and nearby Africa, and like many other professionals of this era, he developed broad interests in the geography and natural history of the lands where he worked. During his service as Consul in North-West Abyssinia, Cheesman not only explored the source of the Blue Nile and surveyed its course from Lake Tana to the Sudan border (*Lake Tana and the Blue Nile: An Abyssinian Quest* by R. E. Cheesman, 1936; Macmillan: London, 400 pp.), but also found time to collect bird and mammal specimens for the British Museum. The species name combines the surname Cheesman and genitive singular case-ending "i" indicative of masculine gender.

Otomys dartmouthi Thomas, 1906b

Otomys dartmouthi; Thomas, 1906b:141 (type locality—Uganda, Ruwenzori East, Mubuku Valley, 12,500 ft [3810 m]; holotype—BMNH 6.7.1.64); Dollman, 1915:166 (taxonomic revision, retained as species); Allen, 1939:344 (listed as valid species); Ellerman, 1941:322 (listed as valid species); Musser & Carleton, 2005:1526 (reinstated as valid species).

Otomys typus dartmouthi; Bohmann, 1952:43 (taxonomic revision, new name combination, retention as valid subspecies).

Otomys typus [*dartmouthi*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys irroratus [*dartmouthi*]; Delany, 1975:53 (faunal work, new name combination, listed in synonymy without indication of rank).

Distribution. Alpine habitats, ca. 3300–4400 m, of the Ruwenzori Mountains, southwestern Uganda and contiguous eastern D.R. Congo.

Specimens examined. D.R. CONGO: Blanc (RMCA 1095); Kalindera Masereka (RMCA 82011-M827); Virungas, Albert National Park, Wusuwameso, 4380 m (RMCA 82011-M830, 82011-M831). UGANDA: Ruwenzori East, Mubuku Valley, 12,500 ft (3810 m) (BMNH 6.7.1.62–6.7.1.65); Kasese District, Ruwenzoris, left bank Bujuku River, 11,050 ft (3368.04 m) (**FMNH 144327**, 144328, 144330); Kasese District, Ruwenzoris, above Lake Bujuku, 13,050 ft (3977.64 m) (FMNH 144334–144336, 144338, 144341, 144342).

Otomys fortior Thomas, 1906a

Otomys typus fortior; Thomas, 1906a:302 (type locality—Ethiopia, Kaffa, Charada Forest, 6000 ft [1829 m]; holotype—BMNH 6.11.1.29); Allen, 1939:348 (listed as valid subspecies); Ellerman, 1941:321 (listed as valid subspecies); Bohmann, 1952:45 (taxonomic revision, retained as valid subspecies).

Otomys fortior; Dollman, 1915:170 (taxonomic revision, elevation to species).

Otomys typus [*fortior*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Yalden *et al.*, 1976:56 (faunal work, listed in synonymy without indication of rank); Musser & Carleton, 1993:682, 2005:1530 (listed in synonymy without indication of rank).

Distribution. Restricted to montane evergreen forests in the southwestern regions of Ethiopia (see OTU 2 in Fig. 1a). Although specimens from Jimma are assigned provisionally to *O. fortior* based on geographic and ecological proximity, we note that morphometrically this series is characterized by large cranial size making them comparable with specimens from "Sp. C" from the Lake Tana region of central Ethiopia.

Specimens examined. ETHIOPIA: Kaffa, Charada Forest, 6,000 ft (1828.8 m) (BMNH 6.11.1.29); Beletta Forest (ZMMU 164960–164965, 166072); Sheko Forest (ZMMU 167310); Oromiya, Jimma, 1750 m (USNM 515058–515064, 516317, 516507); Inegawa Forest, 20 km N of Tepi, 2340 m (ZMMU 181665–181667).

Otomys helleri Frick, 1914, new rank

Otomys jacksoni helleri; Frick, 1914:10 (type locality—Abyssinia [Ethiopia], Chilalo Divide Camp, 9000 ft [2743 m]; holotype—CM 3519); Allen, 1939:345 (listed as valid subspecies); Ellerman, 1941:322 (listed as valid subspecies).

Otomys typus helleri; Bohmann, 1952:44 (taxonomic revision, new name combination, retained as valid subspecies).

Otomys typus [*helleri*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Yalden *et al.*, 1976:56 (faunal work, listed in synonymy without indication of rank); Musser & Carleton, 1993:682, 2005:1530 (listed in synonymy without indication of rank).

Otomys jacksoni malkensis; Frick, 1914:11 (type locality—Abyssinia [Ethiopia], Sidamo, Malka; holotype—CM 3433); Allen, 1939:345 (listed as valid subspecies); Ellerman, 1941:322 (listed as valid subspecies).

Otomys typus malkensis; Bohmann, 1952:43 (taxonomic revision, new name combination, retained as valid subspecies).

Otomys typus [*malkensis*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Yalden *et al.*, 1976:56 (faunal work, listed in synonymy without indication of rank); Musser & Carleton, 1993:682, 2005:1530 (listed in synonymy without indication of rank).

Distribution. Alpine habitats in Bale Mountains and Arussi Plateau, possibly extending southwards to include localities such as Malka (see OTU 3 in Fig. 1a).

Specimens examined. ETHIOPIA: Arussi Plateau, Mount Albasso (BMNH 29.11.7.82, 29.11.7.83; FMNH 28125, 28126, 28129, 28132–28139, 28159–28164; USNM 259506); Bale Mountains (BMNH 72.1229, 72.1300, 72.1302, 72.1304, 72.1307, 72.1308; LM 1986-212-6; SM 23340; ZMMU 162595–162601); Bale Mountains, Dinsho (MNHN 1972.218–1972.228; MCZ 57319); Chilalo (SM 35868, 35876, 35877, 35879, 35883, 35887).

Otomys jacksoni Thomas, 1891

Otomys jacksoni; Thomas, 1891:184 (type locality—Uganda, crater of Mount Elgon, 13,200 ft [4023 m]; holotype—BMNH 93.2.3.34); Wroughton, 1906: 276 (retained as valid species); Dollman, 1915:167 (taxonomic revision, retained as valid species); Lawrence & Loveridge, 1953:59 (faunal report, recognition as valid species); Musser & Carleton, 2005:1527 (reinstated as valid species).

Otomys jacksoni jacksoni; Allen, 1939:345 (listed as valid species and subspecies); Ellerman, 1941:322 (listed as valid species and subspecies).

Otomys typus jacksoni; Bohmann, 1952:43 (taxonomic revision, new name combination, retained as valid subspecies)

Otomys typus [*jacksoni*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Yalden *et al.*, 1976:56 (faunal work, listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys irroratus [*jacksoni*]; Delany, 1975:53 (faunal work, new name combination, listed in synonymy without indication of rank).

Distribution. Alpine zone, 3300–4200 m, of Mount Elgon, straddling the border of southeastern Uganda-westcentral Kenya.

Specimens examined. UGANDA: Mount Elgon, crater, 3300–4200 m (BMNH 93.2.3.34, 2.9.9.19, 35.2.22.37, 35.2.22.38); Mount Elgon, Kaburomi (MCZ 31368); Mount Elgon, Mude Cave camp, 3600 m (DM 6261).

Otomys orestes Thomas, 1900

Otomys irroratus orestes; Thomas, 1900:175 (type locality—Kenya, Mount Kenya, Teleki Valley, 13,000 ft [3962 m]; holotype—BMNH 1900.2.1.21); Wroughton, 1906:275 (listed as valid subspecies).

Otomys orestes orestes; Dollman, 1915: (new name combination, elevation to species, *de facto* arrangement as nominate subspecies); Allen, 1939:346 (listed as valid species and subspecies); Ellerman, 1941:323 (listed as valid species and subspecies); Setzer, 1953:334 (taxonomic description, retained as valid species and subspecies).

Otomys orestes; Hollister, 1919:147 (faunal report, retained as monotypic species); Musser & Carleton, 2005:1528 (reinstated as species, indication of synonyms); Carleton & Byrne, 2006:497 (taxonomic revision, retained as species).

Otomys typus orestes; Bohmann, 1952:41 (taxonomic revision, new name combination, retained as valid subspecies).

Otomys typus [*orestes*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys thomasi malleus; Dollman, 1915:154 (type locality—British East Africa [Kenya], Naivasha Province, Lake Olbollossat; holotype—BMNH 12.7.1.431); Allen, 1939:346 (listed as valid subspecies); Ellerman, 1941:323 (listed as valid subspecies).

Otomys typus malleus; Bohmann, 1952:42 (new name combination, retained as valid subspecies).

Otomys typus [*malleus*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys orestes [*malleus*]; Musser & Carleton, 2005:1529 (new name combination, listed in synonymy without indication of rank).

Otomys percivali; Dollman, 1915:168 (type locality—British East Africa [Kenya], Naivasha District, 12 mi S Lake Olbollossat, 8700 ft [2652 m]; holotype—BMNH 12.7.1.424); Allen, 1939:346 (listed as valid species); Ellerman, 1941: 322 (listed as valid species).

Otomys typus malleus; Bohmann, 1952:42 (taxonomic revision, new name combination, *percivali* allocated as full synonym, invalid as subspecies).

Otomys typus [*percivali*]; Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys orestes [*percivali*]; Musser & Carleton, 2005:1529 (new name combination, listed in synonymy without indication of rank).

Otomys thomasi squalus; Dollman, 1915:155 (type locality—British East Africa [Kenya], Aberdare Range, Mount Kinangop, 12,000 ft [3658 m]; holotype—BMNH 10.5.3.41); Hollister, 1919:147 (faunal report, listed as valid subspecies); Allen, 1939:347 (listed as valid subspecies); Ellerman, 1941:323 (listed as valid subspecies).

Otomys typus squalus; Bohmann, 1952:41 (taxonomic revision, new name combination, retained as valid subspecies).

Otomys typus [*squalus*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys orestes [*squalus*]; Musser & Carleton, 2005:1529 (new name combination, listed in synonymy without indication of rank).

Distribution. Discontinuous in alpine settings, ca. 2700–4200 m, on Mount Kenya and the Aberdare Mountains, central Kenya.

Specimens examined. KENYA: Aberdare Mountains, summit, 11,000 ft (USNM 184033–184035), 12,500 ft (3810 m) (AMNH 80995); Aberdare Mountains, moorland (RMCA a1.008-M-1123); Aberdares, Mount Kinangop, 12,000 ft (3658 m) (BMNH 10.5.3.41); Aberdare National Park, Fishing Lodge, 8,760, 9,000, and 9,500 ft (2670, 2743, and 2896 m) (USNM 589995–589997); Naivasha District, Lake Ol Bolossot (BMNH 12.7.1.431); Naivasha District, 12 mi S Lake Ol Bolossot, 8,700 ft (2652 m) (BMNH 12.7.1.424); Mount Kenya, Teleki Valley, 13,000 ft (3962 m) (BMNH 1900.2.1.21); Mount Kenya, west side, 10,700 ft (3261 m) (FMNH 43819, 43444; USNM 164308, 164346, 164357, 164358), 13,500 ft (4115 m) (USNM 164293–164295, 164297, 164329, 164332–

164334), 13,700 ft (4157 m) (FMNH 43445, 43446; USNM 164300–164305, 164344, 164345), 14,600 ft (4450 m) (AMNH 80993), 15,000 ft (4572 m) (AMNH 82605–82607).

Otomys simiensis new species

Figs. 2c, 5, 6, 17; Table 9

Simien Vlei Rat

Holotype. ZMMU 178757; adult male, dry skin and skull, collector's number 1338; collected by L.A. Lavrenchenko, 4 May 2005.

Type locality. Ethiopia, Simien Mountains National Park, vicinity of Sankaber campsite, 3250 m; 13°14'N, 38°03'E (GPS reading by collector).

Diagnosis. A small-sized representative of the *O. typus* species complex (referred to "Sp. D" above; see Figs. 5, 6, 17 and Tables 7, 9). Similar to *O. yaldeni* but considerably larger externally (HB mean 155 mm in *simiensis*, cf. 143 in *yaldeni*; tail means 83 mm and 72 mm respectively); skull having a narrower interorbital region, less pronounced supraorbital ridges, relatively longer nasal bones, and braincase with flatter dorsal profile (Fig. 17); karyotype distinctive (2N=54, NF=56).

Paratypes. ZMMU 178756 (adult female, dry skin and skull, collector's number 1336); ZMMU 178758 (adult male, dry skin and skull, collector's number 1352); ZMMU 178759 (adult male, dry skin and skull, collector's number 1353); ZMMU 178762 (adult female, dry skin and skull, collector's number 1429); all four specimens from the type locality, collected by L.A. Lavrenchenko between 4 and 20 May 2005.

Description. The dorsal pelage is dark brown, with individual hairs having a blackish base, rufous subterminal band, and relatively narrow black tip. Among the guard hairs (17 mm), there are longer bristles (26 mm) that produce the effect of the double-layered fur. Ventral pelage is pale grey, the individual hairs grey at the base and tipped with pale whitish. The ears are blackish, their inner surface covered with short rufous hairs. Dorsal surfaces of the forefeet and hindfeet are dark grey, and the claws are grey. The tail is moderately long (53.4% of HB) and appears distinctly bicoloured, the dorsal caudal hairs relatively long and blackish in contrast to the white ventral hairs.

The skull resembles most other members of the *O. typus* complex, having a relatively narrow interorbital region, reduced supraorbital ridges, shallow braincase, and short anterior palatal foramen (Table 9). Anterior face of the lower incisor has two well defined and equally deep grooves. The upper third molar possesses 7 complete laminae; the lower first molar possesses 4 complete laminae.

The chromosomal complement of *O. simiensis* consists of 2N=54, NF=56; 2m + 52a (Fig. 2c).

Otomys simiensis differs from other Ethiopian *Otomys* (excluding *yaldeni*) by the lower number of laminae in the upper third molar (7 versus 8–9) and the double-layered dorsal fur. Amongst other members of *typus* s.l., *simiensis* is most like *jacksoni* which is similar in skull size and shape (Table 9) and also has 7 laminae in the third upper molar and a similar dark brown colour (Bohmann 1952); however, *jacksoni* is much smaller in external dimensions (HB mean 141 mm in *jacksoni* cf. 155 mm in *simiensis*) and has a proportionately shorter tail (45.4% in *jacksoni* cf. 53.4% in *simiensis*). Furthermore molecular data (Fig. 3) clearly demonstrate the genetic separation of these taxa.

Distribution. Known only from the type locality in the Simien Mountains, northern Ethiopia (see above).

Ecology. The holotype and paratypes of *O. simiensis* were captured in tree-heather forest (trees: *Erica arborea*, *Hypericum revolutum*; shrub: *Rosa abyssinica*) with open grassy patches. At higher altitudes, this species is replaced by *O. typus* s.s., a common inhabitant of the afroalpine zone in the Simien Mountains National Park (e.g., Chennek area, 13°15'N, 38°13'E, 3800 m).

Etymology. The rugged Simien Mountains, to which the new species is apparently endemic, dominate the northern plateau of Ethiopia and contain its highest peaks. The name combines the stem Simien with the Latin suffix "ensis," meaning "native of" or "characteristic of" the place indicated by the stem.

Otomys thomasi Osgood, 1910

Otomys thomasi; Osgood, 1910:9 (type locality—British East Africa [Kenya], Molo; holotype—FMNH 16698).

Otomys thomasi thomasi; Dollman, 1915:153 (taxonomic revision, retained as species, *de facto* arrangement as nominate subspecies); Hollister, 1919:147 (faunal report, listed as valid species and subspecies); Allen, 1939:346 (listed as valid species and subspecies); Ellerman, 1941:323 (listed as valid species and subspecies).

Otomys typus thomasi; Bohmann, 1952:41 (taxonomic revision, new name combination, retained as valid subspecies).

Otomys typus [*thomasi*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys orestes [*thomasi*]; Musser & Carleton, 2005:1529 (new name combination, listed in synonymy without indication of rank); Carleton & Byrne, 2006:497 (taxonomic revision, retention of *thomasi* as junior synonym).

Distribution. High plateau and mountains that form the western border of the Rift Valley (eastern branch), central Kenya; elevational range ca. 2450–2750 m.

Specimens examined. KENYA: Uasin Gishu Plateau, 32 km N Eldama Ravine, 9,000 ft (2743 m) (USNM 164290); Molo (FMNH 16693–16695, 16698, 16699).

Otomys typus (Heuglin, 1877)

Oreomys typus; Heuglin, 1877:76; Thomas, 1891:185 (new species description of *Otomys*, retention of *typus* in separate genus).

Otomys degeni; Thomas, 1902a:311 (type locality—Abyssinia [Ethiopia], Shoa, Gombitchu, 8,000 ft (2438 m); holotype—BMNH 2.9.9.19).

Otomys typus; Wroughton, 1906:276 (new name combination, listed as valid species); Thomas, 1906a:302 (listed as valid species, including *degeni* Thomas, 1902a as full synonym); Dollman, 1915:169 (listed as valid species, including *degeni* Thomas, 1902a as full synonym); Misonne, 1974:33 (listed as valid species, allocation of synonyms without indication of rank); Yalden *et al.*, 1976:56 (faunal work, listed as valid species, allocation of synonyms without indication of rank); Corbet & Hill, 1980:159, 1986:178, 1991:167 (listed as valid species, no indication of synonyms); Honacki *et al.*, 1982:445 (listed as valid species, no indication of synonyms); Musser & Carleton, 1993:682, 2005:1530 (listed as valid species, allocation of synonyms without indication of rank); Yalden *et al.*, 1996:119 (faunal work, listed as valid species, no indication of synonyms).

Otomys typus typus; Allen, 1939:348 (listed as valid subspecies, including *degeni* Thomas, 1902a as full synonym); Ellerman, 1941:321 (listed as valid subspecies, including *degeni* Thomas, 1902a as full synonym); Bohmann, 1952:44 (taxonomic revision, arranged as valid subspecies, including *degeni* Thomas, 1902a as full synonym).

Otomys irroratus [*typus*]; Delany, 1975:53 (faunal work, new name combination, listed in synonymy without indication of rank); Petter, 1982:219 (allocated to synonymy without indication of rank).

Distribution. Simien Mts, Ethiopia extending eastwards to the highlands of the western rim of the Ethiopian Rift.

Specimens examined. ETHIOPIA: Ankober (SM 23838); Bonke (SM 23349, 23351); Chenca (SM 23320–23322, 23325, 23326, 23328, 23333–23335, 23337); Gojam (FMNH 28141–28143, 28172–28177, 28179); Gojam, N'jabara (USNM 259507); Mount Guna (ZMMU 172728–**172732**); Hirna (SM 23842, 23844); Simien Mountains, 10,000 ft (3048 m) (FMNH 28146–28151, 28153–28158; MCZ 34372; SM 1051); Simien Mountains, Debark, 9,200 ft (2804 m) (MCZ 34373); Simien Mountains, Mount Geech, 11,200 ft (3414 m) (MCZ 26992; FMNH 28147, 28154); Shou (FMNH 28140); Sidamo, (FMNH 28167).

Otomys uzungwensis Lawrence and Loveridge, 1953

Otomys percivali; Allen & Loveridge, 1933:119 (faunal report, preliminary identification); Swynnerton and Hayman, 1951:322 (faunal work, listed as species per Allen & Loveridge, 1933).

Otomys uzungwensis; Lawrence & Loveridge, 1953:61 (type locality—Tanganyika Territory [Tanzania], Iringa District, Uzungwe Mountains, Dabaga; holotype—MCZ 26645); Musser & Carleton, 2005:1530 (reinstated as valid species); Carleton & Byrne, 2006:492 (taxonomic revision, retained as valid species).

Otomys typus [*uzungwensis*]; Misonne, 1974:33 (new name combination, listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys typus uzungwensis; Ansell, 1978:78 (faunal work, listed as valid subspecies); Ansell & Dowsett, 1988:102 (faunal work, listed as valid subspecies).

Distribution. Udzungwa Mountains in westcentral Tanzania to the Nyika Plateau, northern Malawi and contiguous Zambia; elevational range ca. 1800–2750 m.

FIGURE 17(a–c). Photographs comparing dorsal, ventral and lateral views of the skulls of holotype of *Otomys yaldeni* (ZMMU 162594).

FIGURE 17(d–f). Photographs comparing dorsal, ventral and lateral views of the skulls of holotype of *O. simiensis* (ZMMU 178757).

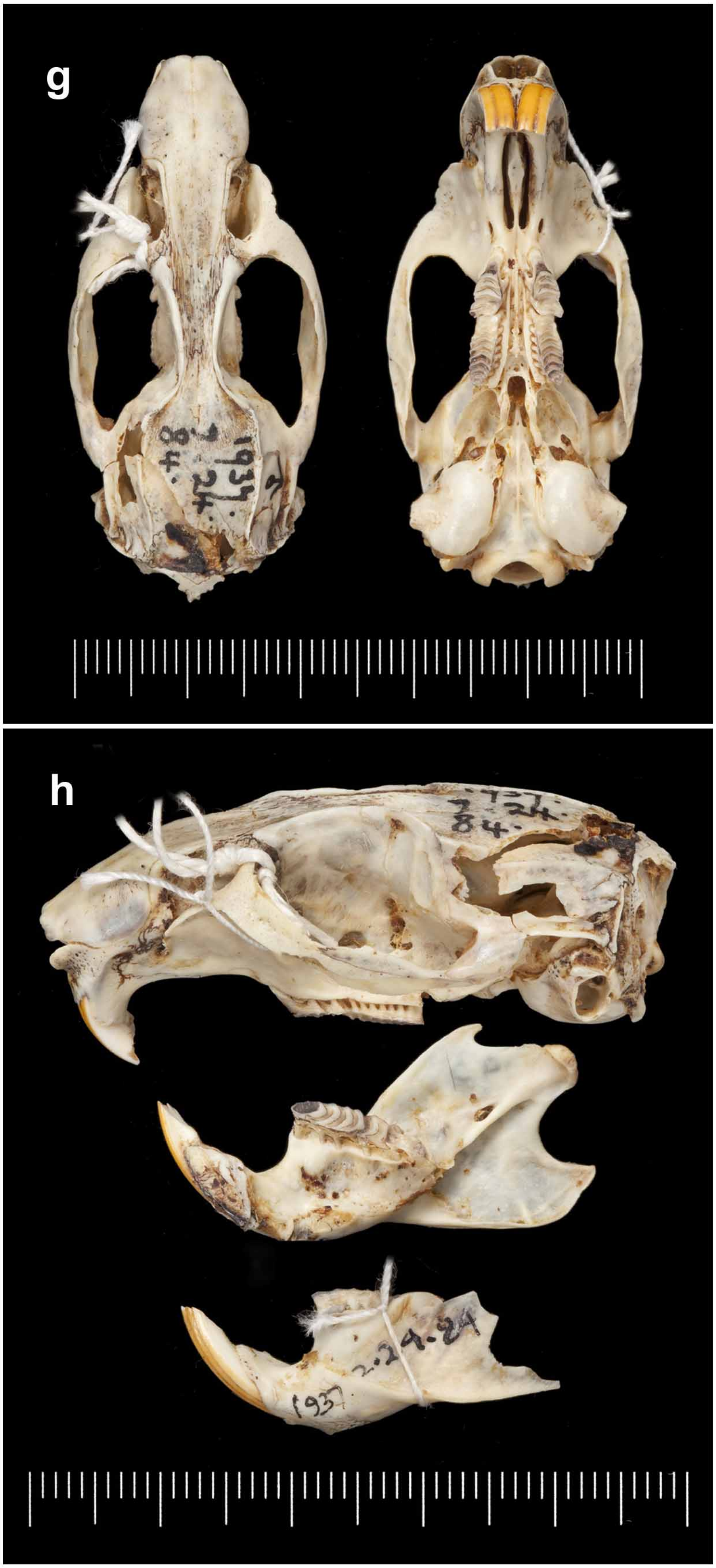

FIGURE 17(g–h). Photographs comparing dorsal, ventral and lateral views of the skulls of holotype of *Otomys cheesmani* (BMNH 1937.2.24.84). © The Natural History Museum, London.

Specimens examined. MALAWI: Nyika Plateau, Chelinda (BMNH 62.337, 66.1094, 78.2722); Nyika Plateau, 7,000 ft (2133.6 m) (MCZ 43947, 43950); (FMNH 192029, 192030). TANZANIA: Udzungwe Mountains, Kigoro (MCZ 26637, 26638, 26640–26644); Udzungwe Mountains, Iringa District, Dabaga, 6,000 ft (1828.8 m) (MCZ 26645, 26646, 26648–26653, 26655, 26656, 26664); Poroto Mountains, Mbeya, 9,000 ft (2743.2 m) (MCZ 51147).

***Otomys yaldeni* new species**

Figs. 2b, 5, 6, 17; Table 9
Yalden's Vei Rat

Otomys sp. A: Lavrenchenko *et al*. 1997: 222.
Otomys typus A: Aniskin *et al*. 1998: 230.

Holotype. ZMMU 162594; adult male, dry skin and skull, collector's number 132; collected by L.A. Lavrenchenko, 17 February 1995.

Type locality. Ethiopia, Bale Mountains, vicinity of Dinsho, 3170 m; 07°06'N, 39°47'E (interpolated from topographic map).

Diagnosis. The smallest representative of the *Otomys typus* complex (excluding *O. jacksoni* on Mt Elgon). Similar to *O. simiensis*, but considerably smaller in external and craniodental size, possessing a wider interorbital region, more pronounced supraorbital ridges, relatively smaller rostral region (clearly shortened nasal bones), more rounded and deeper braincase (Fig. 17), and distinct karyotype (2N=56, NF=56, NFa=54).

Paratypes. BMNH 76.114 (Ethiopia, 70 km NW Kebre Mengist, 2650 m; 06°23'N, 38°35'E; adult male, dry skin and skull, collector's number 121; collected by D.W. Yalden, P.A. Morris & M.J. Largen, 13 April 1975); BMNH 76.115 (Ethiopia, Bale Mountains, 17 km SE of Goba, 3800 m; 06°53'N, 40°03'E; adult female, dry skin and skull, collector's number 201; collected by D.W. Yalden, P.A. Morris & M.J. Largen, 19 April 1975); BMNH 76.116 (Ethiopia, Bale Mountains, 10 km SE of Goba, 3300 m; 06°57'N, 40°03'E; adult female, dry skin and skull, collector's number 175; collected by D.W. Yalden, P.A. Morris & M.J. Largen, 18 April 1975).

Description. A small-sized *Otomys* with a relatively short tail. The dorsal pelage is drab brown, the hairs are greyish at base and yellow-rufous in distal part. Among the guard hairs (11–12 mm), there are longer bristles (20 mm) that produce the effect of double-layered fur. Ventral pelage is pale grey, individual hairs grey at the base and tipped with pale whitish. The ears are blackish, their inner surface covered with short rufous hairs. The dorsal surface of the forefeet and hind feet is dark grey; the claws are grey. The tail is relatively short (49.9% of HB), with blackish caudal hairs on the upper surface and nearly white hairs on the lower; however, given its shortness, the bicoloration of the tail does not appear as well defined as in *O. simiensis*.

The small skull features a relatively wide interorbital region, markedly well-developed supraorbital ridges, very small rostral region with narrow nasals, short anterior palatal foramen, and small tympanic bullae (Fig. 17; Table 9). Anterior face of the lower incisor is scored by two well defined and equally deep grooves. The upper third molar possesses 6 or 7 complete laminae; the lower first molar possesses 4 complete laminae.

Otomys yaldeni averages smaller than all other species formerly obscured under *O. typus* except for *O. jacksoni* (Table 9). However it can be easily distinguished from *O. jacksoni* on the basis of skull shape. Compared with *O. yaldeni*, the holotype of *O. jacksoni* displays a much narrower interorbital region, with weakly developed supraorbital ridges, and does not possess such conspicuously shortened nasal bones (Fig. 17). *Otomys yaldeni* differs from other Ethiopian *Otomys* (excluding *O. simiensis*) by the lower number of laminae in the upper third molar (6–7 vs. 8–9) and by its double-layered dorsal fur.

The chromosomal set of *O. yaldeni* consists of $2n = 56$, NF=56, NFa=54, acrocentrics with an acrocentric X and Y (Fig. 2b). Allozymic investigation of 18 enzymatic and non-enzymatic proteins (*Adh*, *Alb*, *Gdc*, *Hbb*, *Got-1*, *Got-2*, *G-6-pd*, *Dia-1*, *Dia-2*, *Idh-1*, *Ldh-A*, *Ldh-B*, *Mdh-1*, *Mdh-2*, *Me-1*, *Sdh*, *Sod-1*, *Sod-2*) revealed that non-overlapping allele spectra in four loci (*G-6-pd*, *Dia-2*, *Alb* and *Got-2*) discriminated *O. yaldeni* and *O. helleri*, which are partially sympatric in the Bale Mountains (Lavrenchenko *et al*. 1997).

Distribution. Documented from the northern (Dinsho and Goba areas) and south-western (70 km NW Kebre Mengist) slopes of the Bale Massif, southeastern Ethiopia.

Ecology. All known specimens of *O. yaldeni* were collected in mosaic habitats of grassland and forest between 2650 and 3800 m. The holotype was captured at the edge of typical undifferentiated afromontane forest with *Junipe-*

rus procera, *Hypericum revolutum*, *Maytenus arbutifolia*, *Rosa abyssinica* and open grassy patches with *Euphorbia dumalis*, *Festuca abyssinica*, *Koeleria capensis*, *Poa schimperana*, *Exotheca abyssinica*. The paratypes were captured in afromontane forest with *Hagenia abyssinica* and bamboo patches with *Arundinaria alpine* (BMNH 76.114), in moorland with *Erica trimera* and *Helichrysum citrispinum* (BMNH 76.115), in open woodland with *Hypericum revolutum* and *Helichrysum citrispinum* (BMNH 76.116).

Etymology. The species name acknowledges the substantial contributions of Derek W. Yalden to our understanding of Ethiopia's indigenous mammals. His museum and field efforts, published over some 20 years in faunal reports and taxonomic catalogues (e.g., Yalden *et al.* 1976, 1996), meaningfully advanced specimen-based knowledge of species and their distributions, thereby underscoring the exceptional endemism that characterizes the mammal fauna of the Ethiopian highlands. *Otomys yaldeni* appropriately represents another of those endemics. The species name combines the surname Yalden and genitive singular case-ending "i" indicative of masculine gender.

Otomys zinki Bohmann, 1943

Otomys typus zinki; Bohmann, 1943:153 (type locality—German East Africa [Tanzania], Kilimanjaro, Peters Hut, 3800 m; holotype—not seen; listed as "No. 548" in his private collection by Bohmann, 1943); Swynnerton and Hayman, 1951:321 (faunal report, listed as valid subspecies); Bohmann, 1952:41 (taxonomic revision, retained as valid subspecies).

Otomys typus [*zinki*]; Misonne, 1974:33 (listed in synonymy without indication of rank); Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys orestes [*zinki*]; Musser & Carleton, 2005:1528 (new name combination, listed in synonymy without indication of rank).

Distribution. The species is limited in its distribution to Mt Kilimanjaro.

Specimens examined. TANZANIA: Kilimanjaro (SM 4270, 4272, 4278, 4280); Mount Kilimanjaro East, Maundi Crater, grassland, 3270 m (RMCA 96.037.M-6801, 96.037.M-6802, 96.037.M-6803, 96.037.M-6804, 96.037.M-6805, 96.037.M-6801); Mount Kilimanjaro West, Londorosi, forest, 2350 m (96.037.M-6807, 96.037.M-6810); Mount Kilimanjaro West, Shira, moorland, 3000 m (96.037.M-6809); Mount Kilimanjaro, Kilimanjaro National Park, 13,100 ft (3993 m) (FMNH 174178–174180); Mount Kilimanjaro, Kilimanjaro National Park, 7 km N and 2.5 km W Maua, 8,100 ft (2469 m) (FMNH 174173, 174174).

TABLE 9. Summary statistics for taxa recognised by this study.

Species	N	Mean	Range	Standard deviation
Head and Body Length				
O. tropicalis s.s	37	159.0	125–205	17.6
O. typus s.s.	4	163.2	155–178	10.1
O. fortior	8	160.2	145–182	13.4
O. yaldeni **sp. nov.** (= "Sp. A")	3	143.3	125–155	16.1
O. helleri (= "Sp. B")	12	151.6	123–185	20.9
O. cheesmani **sp. nov.** (= "Sp. C")	6	188.8	165–210	17.5
O. simiensis **sp. nov.** (= "Sp. D")	5	155.2	135–172	15.0
O. zinki	16	161.6	135–186	13.7
O. orestes	9	156.7	135–172	11.0
O. thomasi	3	170.7	162–182	10.3
O. dartmouthi	1	-	150	-
O. uzungwensis	-	-	-	-
O. jacksoni	1	-	141	-
Length of Tail				
O. tropicalis s.s.	37	86.7	52–102	9.5

continued next page

TABLE 9. (continued)

Species	N	Mean	Range	Standard deviation
O. typus s.s.	4	83.7	77–92	7.6
O. fortior	8	93.7	85–98	4.0
O. yaldeni **sp. nov.** (= "Sp. A")	3	71.5	70–73	2.1
O. helleri (= "Sp. B")	12	80.8	68–95	8.4
O. cheesmani **sp. nov.** (= "Sp. C")	6	93.0	77–106	9.6
O. simiensis **sp. nov.** (= "Sp. D")	5	82.8	77–88	4.3
O. zinki	15	84.1	60–108	12.1
O. orestes	9	79.8	69–93	6.9
O. thomasi	3	88.3	84–93	4.5
O. dartmouthi	1	-	93	-
O. uzungwensis	-	-	-	-
O. jacksoni	1	-	64	-
Length of Hind Foot				
O. t. tropicalis s.s.	36	29.9	26–34	2.6
O. typus s.s.	4	26.0	25–27	0.8
O. fortior	8	28.8	28–30	0.9
O. yaldeni **sp. nov.** (= "Sp. A")	3	23.7	22–25	1.5
O. helleri (= "Sp. B")	12	27.0	23–30	2.0
O. cheesmani **sp. nov.** (= "Sp. C")	6	30.2	28–31	1.3
O. simiensis **sp. nov.** (= "Sp. D")	5	25.0	24–26	0.6
O. zinki	16	27.9	24–32	2.1
O. orestes	9	27.1	23–31	2.6
O. thomasi	3	30.3	30–31	0.6
O. dartmouthi	1	-	26.5	-
O. uzungwensis	-	-	-	-
O. jacksoni	1	-	21	-
Length of Ear				
O. t. tropicalis s.s.	30	21.9	17–25	1.9
O. typus s.s.	4	21.8	20–25	2.2
O. fortior	8	21.3	20–26	2.0
O. yaldeni **sp. nov.** (= "Sp. A")	3	19.2	18.5–20	1.1
O. helleri (= "Sp. B")	12	21.8	20–24.5	1.4
O. cheesmani **sp. nov.** (= "Sp. C")	6	23.2	22–24	0.8
O. simiensis **sp. nov.** (= "Sp. D")	5	19.4	17.5–21.8	1.6
O. zinki	–	–	–	–
O. orestes	5	22.0	21–25	1.7
O. thomasi	3	21.3	20–22	1.2
O. dartmouthi	1	-	25	-
O. uzungwensis	-	-	-	-
O. jacksoni	1	-	21	-

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TABLE 9. (continued)

Species	N	Mean	Range	Standard deviation
Occipitonasal Length				
O. tropicalis s.s.	124	39.6	35.8–44.0	1.9
O. typus s.s.	4	38.3	37.1–40.2	1.4
O. fortior	8	39.6	36.6–42.6	2.4
O. yaldeni **sp. nov.** (= "Sp. A")	3	35.2	34.7–35.5	0.4
O. helleri (= "Sp. B")	12	38.7	34.6–43.3	3.0
O. cheesmani **sp. nov.** (= "Sp. C")	6	45.3	43.3–48.2	1.8
O. simiensis **sp. nov.** (= "Sp. D")	5	37.0	35.2–39.2	1.7
O. zinki	12	39.4	36.6–42.4	1.7
O. orestes	14	38.4	37.3–39.5	0.8
O. thomasi	5	40.8	40.2–41.4	0.6
O. dartmouthi	9	37.8	36.6–39.1	0.7
O. uzungwensis	10	37.3	36.0–38.9	1.0
O. jacksoni	3	35.1	34.3–35.5	0.7
Depth of Braincase				
O. tropicalis s.s.	124	11.4	10.2–12.9	0.6
O. typus s.s.	4	10.9	10.5–11.1	0.2
O. fortior	8	10.8	10.0–11.3	0.5
O. yaldeni **sp. nov.** (= "Sp. A")	3	10.5	9.9–10.7	0.4
O. helleri (= "Sp. B")	12	11.2	10.3–11.8	0.5
O. cheesmani **sp. nov.** (= "Sp. C")	6	12.0	11.3–13.1	0.6
O. simiensis **sp. nov.** (= "Sp. D")	5	10.1	9.6–10.6	0.4
O. zinki	12	11.5	10.9–12.5	0.6
O. orestes	14	11.8	10.6–12.6	0.5
O. thomasi	5	11.5	10.6–12.9	0.9
O. dartmouthi	9	11.0	10.6–11.5	0.3
O. uzungwensis	10	11.2	10.5–11.6	0.3
O. jacksoni	3	11.0	10.8–11.2	0.2
Length of Anterior Palatal Foramen				
O. tropicalis s.s.	124	7.0	5.9–9.2	0.5
O. typus s.s.	4	6.7	5.9–7.3	0.6
O. fortior	8	7.2	6.5–7.8	0.4
O. yaldeni **sp. nov.** (= "Sp. A")	3	6.0	5.6–6.5	0.4
O. helleri (= "Sp. B")	12	6.7	5.6–7.5	0.7
O. cheesmani **sp. nov.** (= "Sp. C")	6	8.2	7.5–8.9	0.6
O. simiensis **sp. nov.** (= "Sp. D")	5	6.2	5.6–6.6	0.4
O. zinki	12	7.3	6.7–8.2	0.5
O. orestes	14	7.2	6.5–7.7	0.4
O. thomasi	5	7.4	7.1–7.5	0.2

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TABLE 9. (continued)

Species	N	Mean	Range	Standard deviation
O. dartmouthi	9	6.9	6.2–7.4	0.4
O. uzungwensis	10	6.7	6.2–7.2	0.3
O. jacksoni	3	6.3	5.8–6.8	0.5
Length of Maxillary Toothrow				
O. tropicalis s.s.	124	9.3	8.2–10.4	0.4
O. typus s.s.	4	9.8	9.3–10.0	0.3
O. fortior	8	9.8	9.2–10.3	0.5
O. yaldeni **sp. nov.** (= “Sp. A”)	3	8.4	8.1–8.6	0.3
O. helleri (= “Sp. B”)	12	9.6	9.0–10.5	0.4
O. cheesmani **sp. nov.** (= “Sp. C”)	6	11.4	11.0–12.0	0.3
O. simiensis **sp. nov.** (= “Sp. D”)	5	8.8	8.6–8.9	0.1
O. zinki	12	9.2	8.3–10.0	0.4
O. orestes	14	9.3	8.8–9.8	0.3
O. thomasi	5	9.4	9.2–9.7	0.2
O. dartmouthi	9	8.8	8.1–9.4	0.4
O. uzungwensis	10	9.1	8.6–9.5	0.3
O. jacksoni	3	8.4	8.2–8.5	0.2
Greatest Width Across Nasals				
O. tropicalis s.s.	124	7.2	6.4–8.6	0.4
O. typus s.s.	4	7.0	6.5–7.5	0.4
O. fortior	8	7.3	6.8–8.0	0.5
O. yaldeni **sp. nov.** (= “Sp. A”)	3	6.2	6.1–6.2	0.1
O. helleri (= “Sp. B”)	12	6.5	5.8–7.0	0.4
O. cheesmani **sp. nov.** (= “Sp. C”)	6	8.8	8.0–9.7	0.7
O. simiensis **sp. nov.** (= “Sp. D”)	5	6.6	6.3–6.9	0.3
O. zinki	12	7.1	6.4–7.5	0.3
O. orestes	14	6.9	6.3–7.4	0.4
O. thomasi	5	7.2	6.8–7.6	0.3
O. dartmouthi	9	6.8	6.5–7.1	0.2
O. uzungwensis	10	7.2	6.9–7.5	0.2
O. jacksoni	3	6.4	6.2–6.8	0.3
Interorbital Constriction				
O. tropicalis s.s.	124	4.4	3.7–5.0	0.2
O. typus s.s.	4	3.8	3.6–4.0	0.2
O. fortior	8	4.1	3.8–4.5	0.2
O. yaldeni **sp. nov.** (= “Sp. A”)	3	4.0	3.6–4.5	0.4
O. helleri (= Sp. B)	12	3.8	3.4–4.1	0.2
O. cheesmani **sp. nov.** (= “Sp. C”)	6	4.0	3.8–4.4	0.2
O. simiensis (= “Sp. D”)	5	3.6	3.3–4.1	0.3
O. zinki	12	4.2	3.8–4.5	0.2

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TABLE 9. (continued)

Species	N	Mean	Range	Standard deviation
O. orestes	14	4.1	3.7–4.7	0.3
O. thomasi	5	4.1	4.0–4.4	0.2
O. dartmouthi	9	4.2	3.9–4.4	0.2
O. uzungwensis	10	4.0	3.9–4.2	0.1
O. jacksoni	3	3.8	3.7–3.8	0.1
Zygomatic Width				
O. tropicalis s.s.	124	19.3	17.3–21.8	0.9
O. typus s.s.	4	18.9	18.4–19.7	0.6
O. fortior	8	19.5	18.2–20.7	1.0
O. yaldeni **sp. nov.** (= “Sp. A”)	3	17.6	17.4–17.8	0.2
O. helleri (= “Sp. B”)	12	19.0	17.4–21.0	1.2
O. cheesmani **sp. nov.** (= “Sp. C”)	6	21.5	20.5–22.8	0.8
O. simiensis **sp. nov.** (= “Sp. D”)	5	18.4	17.6–19.3	0.7
O. zinki	12	19.2	17.6–21.1	1.0
O. orestes	14	19.6	19.0–20.7	0.5
O. thomasi	5	20.8	19.7–21.5	0.8
O. dartmouthi	9	19.2	18.3–19.7	0.5
O. uzungwensis	10	18.2	16.9–19.2	0.8
O. jacksoni	3	17.5	17.5–17.6	0.1
Palatal Length				
O. tropicalis s.s.	124	21.5	18.6–24.6	1.2
O. typus s.s.	4	20.9	20.2–21.9	0.7
O. fortiori	8	21.6	19.9–23.2	1.3
O. yaldeni **sp. nov.** (= “Sp. A”)	3	19.2	18.9–19.3	0.2
O. helleri (= Sp. B)	12	21.1	18.8–23.6	1.6
O. cheesmani **sp. nov.** (= “Sp. C”)	6	24.8	23.6–26.2	0.9
*O. simiensis***sp. nov.** (= “Sp. D”)	5	20.2	19.2–21.3	0.9
O. zinki	12	21.2	19.3–22.8	1.0
O. orestes	14	20.3	16.7–21.7	1.2
O. thomasi	5	22.2	21.4–22.7	0.6
O. dartmouthi	9	20.2	19.6–21.5	0.6
O. uzungwensis	10	20.4	19.8–21.7	0.7
O. jacksoni	3	18.2	17.4–19.2	0.9
Length of Auditory Bulla				
O. tropicalis s.s.	124	7.5	6.4–9.1	0.4
O. typus s.s.	4	7.4	6.8–7.7	0.4
O. fortior	8	7.8	7.4–8.2	0.3
O. yaldeni **sp. nov.** (= “Sp. A”)	3	6.5	6.3–6.8	0.3
O. helleri (= “Sp. B”)	12	7.9	7.2–9.2	0.6
O. cheesmani **sp. nov.** (= “Sp. C”)	6	8.4	7.6–8.8	0.4

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TABLE 9. (continued)

Species	N	Mean	Range	Standard deviation
O. simiensis **sp. nov.** (= “Sp. D”)	5	7.0	6.6–7.2	0.2
O. zinki	12	8.0	7.2–8.9	0.6
O. orestes	14	7.9	7.4–8.5	0.3
O. thomasi	5	8.3	7.7–8.7	0.4
O. dartmouthi	9	7.0\	6.7–7.6	0.3
O. uzungwensis	10	7.2	6.7–7.5	0.2
O. jacksoni	3	7.0	6.8–7.0	0.1

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APPENDIX 1. Supplementary specimens of eastern African *Otomys* were broadly examined for morphological and morphometric comparisons with taxa traditionally classified under *O. typus* s.l. Those of *O. tropicalis* are listed as trinomials to convey their regional origin and historical usage, not (!) to endorse formal subspecific divisions. Voucher specimens that were used in the molecular analysis are indicated in bold face.

Otomys barbouri. UGANDA: Mount Elgon, Kuburomi (MCZ 31369 [holotype], 31371, 31422–31424, 31438); Mount Elgon, Mission Deloma (MNHN 1933.2758–1933.2760, 1933.2762–1933.2766); Mount Elgon, Mude Camp, 3600 m (DM 6262, **6263**, 6275, 6280, 6281).

Otomys dollmani. KENYA: Mathews Range, Mount Gargues, 6,000 ft (1828.8 m) (USNM 181790 [holotype], 184041–184046).

Otomys lacustris. TANZANIA: Ufipa Plateau, Mbizi Forest (BMNH 58.355, 58.356, 58.358, **RMCA 96037**); Mbizi Mountains Forest Reserve, 0.5 km S and 3 km E Wipanga, 2300 m (FMNH 171302); Poroto Mountains, east of Mbeya (BMNH 58.363); Mount Rungwa Forest Reserve (FMNH 163761); Udzungwa Mountains, 4 km W and 5 km N Chita, 1460 m (**FMNH 155623**); Udzungwa Mountains, 19.5 km N and 0.5 km W [where?], 2000 m (FMNH 155461); Udzungwa Mountains, Iringa District Dabaga, 6,000 ft (1828.8 m) (MCZ 26654); Ukaguru Mountains, Mamiwa-Kisara Forest Reserve, 1 km E and 0.75 km S Mount Munyera, 1900 m (FMNH 166648, 166907–166909); Ukinga Mountains, Madehani, northeast end of Lake Nyasa, 7,000 ft (2133.6 m) (FMNH 44411; MCZ 26345–26348, 26352–26354, 26358 [holotype]). ZAMBIA: Lucheche River, Abercorn (MCZ 51146).

Otomys tropicalis elgonis. D.R. CONGO: S. Elgon (RMCA 5185, 5253) [???]. KENYA: 12 mi N Eldama Ravine, 8,800 ft (2682.24 m) (USNM 164281); Uasin Gishu Plateau, 30 mi N Ravine, 8,600 ft (2621.28 m) (USNM 164286–164289); Uasin Gishu Plateau, Nzoia River, 6,000 ft (1828.8 m) (USNM 164282–164285); Kaimosi Forest (USNM 184003–184017); Kakamega (MCZ 31375, 31416–31420, 31432–31437, 31439, 31440; USNM 184018); Molo (FMNH 16693, 16695); Molo, Londiani Forest Camp, 2400 m (RMCA 38950, 38951); Mount Elgon, Coletatomoi (MCZ 31366); Mount Elgon National Park, 15 km from Chorlim Gate towards Koitobos Peak, bamboo zone (**USNM 590004–590006**, 590011); Junction camp at foot of Mount Elgon (RMCA 5249). UGANDA: Mount Elgon, Mission Delomo (MNHN1933.2763); Mount Elgon, Sipi (MCZ 31269–31272, 31373, 31374, 31377–31381, 31426-31432); Bumasola, Mt Elgon (DM 6282).

Otomys tropicalis faradjius. D.R. CONGO: Djugu, 1650 m (RMCA10714); Upper Uele District, Faradje (AMNH 50357 [holotype]; RMCA 12995); Mongbwalu, 1300 m (RMCA 15564); Parc Nacional Garambo (RMCA 7834-M167, 7834-M169, 7834-M173, 7834-M174, 7834-M176, 7834-M179, 7834-M187, 7834-M189, 7834-M191, 7834-M192, 7839-M165, 8934-M193).

Otomys tropicalis ghigii. UGANDA: Masaka, Bugala Island, Kalangala, 1180 m (FMNH 138125–138127).

Otomys tropicalis giloensis. SUDAN: "South" (SM 36564–36566); Imatong Mountains, Gilo (FMNH 179460; SM 27163–27165, 27539, 27543, 27544, 27546, 27552, 27554, 27556, 27557, 27561, 27567, 27568, 27762); 5 mi S Gilo (FMNH 108207); Mount Kinyeti (SM 29985, 29986, 30186); Nagishot, Didinga (SM 29990, 29992, 29994).

Otomys tropicalis nubilus. KENYA: northeast of Mount Kenya, Jombeni Range, 6,000 ft (1228.8 m) (BMNH 11.12.2.4 [holotype]).

Otomys tropicalis rubeculus. UGANDA: Gitebe (MNHN 1960.459); Kagambah, 1600 m (BMNH 11.12.3.87); Kampala (MNHN 1985.199).

Otomys tropicalis tropicalis. KENYA: Aberdare Mountains (BMNH 10.5.3.46–10.5.3.48, 10.5.3.52, 10.5.3.54, 10.5.3.56), 10,500 ft (3200.4 m) (USNM 164279, 164280); Aberdare Mountains, summit, 11,000 ft (3352.8 m) (USNM 184024–184032, 184037–184340); Aberdare Mountains, moorland (**RMCA a1.008-M-1125 (R28216)**, **a1.008-M-1126 (R28217)**, **a1.008-M-1128 (R28222)**, a1.008-M-1130 (28234)); Aberdare Mountains, Changongorra, 7,000 ft (2133.6 m) (USNM 184019–184023); Aberdare National Park, Fishing Lodge, 8,760, 9,000, and 9,500 ft (2670.048,2743.2, and 2895.6 m) (**USNM** 589998, 589999, **590002**, **590003**, 590012–590015); Aberdare Range, Mount Kinangop, 2700 m (MNHN 1913.216a); Aberdares, Ruhuruini (a1.008-M-1122 (R 28198)); Mount Kenya (RMCA 5031; R 28138; USNM 165324, 165326, 165327, 165335), west slope, 7,000–13,700 ft (2133.6-4175.76 m)(AMNH 80992; BMNH 0.2.1.20 [holotype]; CM 2836, 2837; FMNH 43819–43822; USNM 164277, 164291–164293, 164296, 164298, 164299, 164307, 164309–164312, 164314–164324, 164326, 164330, 164331, 164337–164343, 164347–164350, 164353, 164354, 164356, 164359–164363, 164365–164373, 164375), 4000 m (MNHN 1913.215a); Mount Kenya, Naro Moru, 10,000 ft (**USNM 590000**, 590001); Mount Kenya, Naro Moru Gate, Meteorological Station, 10,000 ft (3048 m) (USNM 590007–590010); Mount Kenya, Meteorological Station (R 28369, 28380, 28385, 28388, 28394, 28398); Mount Kenya, Solai (BMNH 11.4.7.37, 11.12.8.40, 11.12.8.43); Kangaita, 6 mi N Kerugoy (MNHN 1961.24–1961.27); Naivasha Plains, Nalsitichu River (USNM 184036); 10 mi E Nyeri (USNM 164278); Ololua (R 28117); Thompson Falls Forest (SM 23887).

Otomys tropicalis vivax. KENYA: Mount Nyiru, south of Lake Rudolph (BMNH 12.7.1.425 [holotype]).

Otomys tropicalis vulcanis. BURUNDI: Ntentamaza (MNHN 1993.2332–1993.2337, 1993.2340–1993.2345); Tora (MNHN 1993.2147, 1993.2151, 1993.2300–1993.2321, 1993.2322a, 1993.2322b, 1993.2323–1993.2331, 1993.2338–1993.2340, 1993.2346–1993.2352). D.R. CONGO: Astrida (RMCA 20173, 20494, 20567, 21211, 21219, 27623); Beni (RMCA 16354, 16355); Blukwa (RMCA 9598, 9601, 12824); Bukavo (RMCA 82001-M1–82001-M3); Sud Kivu, Fomilac (USNM 535913); Gala (RMCA 8024); Gitebe (RMCA 82011-M872, 82011-M912); Kabara (RMCA 82011-M916); Kaberanyuma (RMCA 82011-M877); Kabira (RMCA 30421); Sud Kivu, Kahungu (USNM 535910, 535911); Kahuzi (RMCA 30418); Kalindera Masereka (RMCA 82011-M917); Kambekla (Butembo), 1800 m (RMCA 74024-M3, 74024-M4); Kasali (RMCA 82011-M879); Sud Kivu, Kayandja (USNM 535912); Kundhuru (RMCA 16689); Lake Ganda (RMCA 16690, 16692); Sud Kivu, Bogamanda, Lemera (USNM 535907); Sud Kivu, Lushala (USNM 535914); Lushebere (RMCA 30423); Lwege (RMCA 30411); Lwiro (RMCA 32454); Magera, 2000 m (RMCA 82011-M885); Sud Kivu, Bukuvu, Mugaba, 2300 m (USNM 375509–375513, 498739); Musai, 20 km S Butembo (RMCA 13146, 13147); Mutsora, 1200 m (RMCA 82011-M891); Muvo (RMCA 82011-M893); Nyambasha (RMCA 30413); Nyamirwa (RMCA 21847); Nyamlagira (RMCA 82011-M896, 82011-M923); Nyragongo (RMCA 82011-M905). Rukumi, 3500 m (RMCA 82011-M926, 82011-M927, 82011-M929–82011-M931); Rumangaba, 1600 m (RMCA 82011-M932, 82011-M933); Rutshuru (RMCA 15208, 17029, 17030, 82011-M934, 82011-M935); Rwindi (RMCA 82011-M908, 82011-M938); Albert National Park, northern Virungas, Tshamugussa, 2250 m (RMCA 82011-M939–82011-M941, 82011-M943 , 82011-M944); Tusi Tsiaberimu (RMCA 82011-M945); Winka, near station (RMCA 32810); locality unknown (RMCA 33450). RWANDA: Butare INRS (RMCA 74020-M1062); Gaminga (RMCA 82011-M867); Gasarenda (RMCA 74020-M616, 74020-M617, 74020-M621, 74020-M624, 74020-M626); Gitesi (RMCA 74020-M630); Kagano [Kataka] (RMCA 74020-M1065); Kibuye (RMCA 74020-M1074); Kigombe (RMCA 74020-M684); Mamba (RMCA 74020-M498, 74020-M499, 74020-M992); Masaka (RMCA 74020-M645); Mukanda (RMCA 5023); Murene (RMCA 74020-M651); Musi Milsi (RMCA 74020-M618); Mutura (RMCA 74020-M679); Nkuli (RMCA 74020-M685); Nyamikenke (RMCA 74020-M635); Nyarubuye (RMCA 74020-M680); Rwanda (RMCA 74020-M1078); Uinka, Cyangugu (USNM 340922, 340923). UGANDA: Ruwenzori (MNHN 1911.734).

APPENDIX 2. Information of voucher specimens included in the molecular phylogenetic analysis. Latitude (Lat.) and longitude (Long.) are provided in decimal degrees format. The asterisk (*) indicate vouchers of which 12S rRNA were sequenced.

Species & Geographic Origin	Lat. & Long.	Collector	Museum numbers (field number)	Genbank Accession numbers (cyt *b*)	Genbank Accession numbers (12S rRNA)
O. typus s.s.					
Mt Guna, Ethiopia	11.71N 38.25E	L. Lavrenchenko	ZMMU 172732 (1110)	JF796016	-
O. fortior					
Beletta Forest, Jimma, Ethiopia, 1750 m	7.53N 36.55E	L. Lavrenchenko	ZMMU 164962* (47)	JF796010	JF795968
Beletta Forest, Ethiopia			ZMMU 166072 (798)	JF796011	
Inegwa Forest, 20 km N of Tepi, Ethiopia, 2340 m		L. Lavrenchenko	ZMMU 181666 (1625)	JF796012	-
			ZMMU 181667 (1629)	JF796013	-
O. helleri **sp. nov.** (= “Sp. B”)					
Bale Mts, Ethiopia	7.10N 39.77E	L. Lavrenchenko	ZMMU 162597 (232)	JF796014	-
			ZMMU 162600 (338)	JF796015	-
O. simiensis **sp. nov.** (= “Sp. D”)					
Sankaber, Simien Mts, Ethiopia, 3250 m	13.23N 38.05E	L. Lavrenchenko	ZMMU 178757 (1338)	JF795982	-
			ZMMU 178759 (1353)	JF795983	-
			ZMMU 178762 (1429)	JF795984	-
O. tropicalis					
Aberdares, moorland, Kenya	-0.47S 36.73E	W. N. Verheyen†	RMCA a1.008-M-1125 (R28216)	JF796002	-
			RMCA a1.008-M-1126 (R28217)	JF796004	-
			RMCA al.008-M-1128 (R28222)	JF796005	-
Aberdares NP Fishing lodge, Kenya, 9,500 ft (2900 m)	-0.32S 36.70E	L. J. McLellan	USNM 590002*	JF795995	JF795973
			USNM 590003*	JF796003	JF795974
Ruhuruini, Aberdares Mts, Kenya	-0.42S 36.63E	W. N. Verheyen†	RMCA al.008-M-1122 (R28198)	JF796001	-
O. tropicalis s.s.					
Mt Kenya KWS NM Gate, Kenya	-0.17S 37.15E	W. N. Verheyen†	RMCA a1.008-M-1138 (R28423)	JF796008	-
			RMCA a1.008-M-1133 (R28380)	JF796006	-
			RMCA a1.008-M-1136 (R28394)	JF796007	-
Mt Kenya, Naro Moru, Kenya, 10,000 ft (3050 m)	-0.18S 37.17E	L. J. McLellan	USNM 590000*	JF795994	JF795976
O. tropicalis “elgonis”					
Mt Elgon, 15km from Chorlim Gate, bamboo zone	1.15N 34.58E	L. J. McLellan	USNM 590004*	JF795996	JF795977
			USNM 590005*	JF795997	JF795970
			USNM 590006*	JF795998	JF795978
Mt Elgon, Bumasola Village	1.18N 34.38E	P. J. Taylor	DM 6282*	JF795999	JF795969

continued next page

APPENDIX 2. (continued)

Species & Geographic Origin	Lat. & Long.	Collector	Museum numbers (field number)	Genbank Accession numbers (cyt *b*)	Genbank Accession numbers (12S rRNA)
O. tropicalis faradjius					
Rethy, DRC	2.09N 30.89E	A. Laudisoit	RMCA a6.016-M-2034 (CA614)	JF796000	-
O. dartmouthi					
Kibira NP, Ndora Zone, Giseram, Burundi, 1950m	-2.85S 29.40E	J. C. Kerbis-Peterhans	FMNH149007	JF795985	-
Bujuju River, Ruwenzori Mts, Kasese Dist., DRC, 11,050 ft (3370m)	0.36N 29.96E	J. C. Kerbis-Peterhans	FMNH 144327*	JF795986-	JF795975
O. zinki					
Mt Kilimanjaro NP, 7km N, 2.5km W Maua, Tanzania, 2477m	-3.21S 7.45E	W. T. Stanley	FMNH 174174*	JF795989	JF795972
Mt Kilimanjaro East, Maundi Crater grassland, Tanzania, 3270m	-3.07S 37.50E	W. N. Verheyen†	RMCA 96.037-M-6801 (CTZ1764)	JF795987	-
			RMCA 96.037-M-6805 (CTZ1902)	JF795988	-
O. orestes					
Aberdares National Park Fishing lodge, 9,000-9,500 ft (2743-2895 m)	-0.31S 36.70E	L. J. McLellan	USNM 589997 *	JF795990	JF795979
Aberdares, moorland, Kenya	-0.46S 36.73E	W. N. Verheyen†	RMCA a1.008-M-1123 (R28205)	JF795991	-
O. jacksoni					
Mude Cave Camp, Mt Elgon, 3600m	1.16N 34.48E	P. J. Taylor	DM 6261*	JF795992	JF795971
O. barbouri					
Mude Cave Camp, Mt Elgon, 3600m	1.16N 34.48E	P. J. Taylor	DM 6263*	JF795980	JF795964
O. lacustris					
Chingombe, Ufipa Plateau, Tanzania, 1500m	-7.87S 31.66E	W. N. Verheyen†	RMCA 96.037-M-5237 (R13272) *	EU874446	JF795965
Udzungwa Mts, Chita, Tanzania, 1460m	-7.10S 37.64E	W. T. Stanley	FMNH 155623*	EU874447	JF795966
O. sungae					
Usambara Mts, Kidunda Forest, Tanzania, 2047m	-4.97S 38.44E	A. Laudisoit	RMCA a6.013-M-2031(TE5012)	FJ795993	-
O. denti					
Saddle between Mgahinga & Muhavura Mts, Mgahinga Gorilla NP, Uganda, 2980m	01,38S 29,63E	J. C. Kerbis-Peterhans	FMNH 157807*	EU874435	JF795959
Otomys species novo					
Chilinda Camp Dam, Nyika NP, Nyika Plateau, Malawi, 2230m	10.59S 33.71E	J. C. Kerbis-Peterhans	FMNH 191809*	EU874438	FJ795967
Parotomys brantsi					
Kleinsee, Northern Cape Province, South Africa	29.68S 17.08E	C. H. Scholtz	TM 46133*	FJ19561	JF795962

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APPENDIX 2. (continued)

Species & Geographic Origin	Lat. & Long.	Collector	Museum numbers (field number)	Genbank Accession numbers (cyt *b*)	Genbank Accession numbers (12S rRNA)
O. angoniensis					
Mkuze NR, KwaZulu Natal, South Africa	27.63S 32.23E	A. Berruti	DM 1983	Genbank	JF795961
O. irroratus					
Cedarberg, Northern Cape Province, South Africa	32.43S 19.08E	P. J. Taylor	DM 4317*	FJ19546	JF795960
O. occidentalis					
Mt. Oku, Cameroun	06.25N 19.43E	C. Denys	CAM 207	FJ795981	-
Mt. Oku, Cameroun	06.25N 19.43E	F. Lamotte	MNHN 710*	-	JF795963
O. burtoni					
Mt. Cameroun, Cameroun	04.23N 9.17E	W. N. Verheyen†	ZMFK 69-214-X	JF796009	-
OUTGROUPS					
Arvicanthis somalicus				AF004574	AF141262
Micaelamys namaquensis				AF141215	-
Itala NR, KwaZulu Natal, South Africa	28.51S 31.03E	L. Granjon	V.V.95.64	-	JF795958
Aethomys sp.				AF004587	-
Lemniscomys striatus				AF141211	AF141271
Oenomys hypoxanthus				EU349769	-
Mus musculus				V00711	V00711
Rattus norvegicus				X14848	-
Batomys granti				AY324459	-
Phloeomys sp.				EU349775	-