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Molecular and morphological evidence for a Pleistocene radiation of laminate-toothed rats (*Otomys*: Rodentia) across a volcanic archipelago in equatorial Africa

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West African Mountains of the Cameroon Volcanic Line harbour two montane-endemic species of laminated-toothed rats (*Otomys*), which represent the most westerly occurrence of the genus. We explore here through mtDNA sequencing and cranial morphometrics the taxonomic status and phylogenetic relationships of *O. burtoni* (Mt Cameroon) and *O. occidentalis* (Mts Oku and Gotel). We conclude that both species are valid and can be discriminated by molecular data, as well as quantitative and qualitative cranial characters. From molecular data, *O. occidentalis* and *O. burtoni* are closest neighbours (p-distance = 7.5–8.5%) and weakly associated sister species (suggesting a single West African radiation) and both are sister clades to a well supported clade of central, East and northeast African members of the *O. typus* s.l. and *O. tropicalis* s.l. species complexes from mountain ranges comprising the East African 'Montane Circle' and Ethiopian Highlands. Re-evaluation of the evolutionary origins of the allopatric *Otomys* populations in equatorial Africa is undertaken in light of fossil evidence of a southern African origin of the genus. We can conclude that *Otomys* reached the Cameroon Volcanic Line via corridors of temperate grasslands during the Late Pliocene. Our data support the hypothesis that, following major peripatric speciation events at around 2.3 to 2.03 Ma (from East Africa into West and North Africa respectively), further speciation occurred across neighbouring mountain ranges in West, Central-East and North-East Africa. Estimated molecular dates of speciation events in *Otomys* reveal close congruence with well-constrained geochronological estimates, pertinently the uplift of the Albertine Rift in the Early Pleistocene. These regional analyses reveal how peripatric speciation events established narrow-range endemics of *Otomys* on principal stratovolcanoes across the East African plateau and Cameroon. © 2014 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **113**, 320–344.

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INTRODUCTION

Analogous to the volcanic highlands of East Africa (Chorowicz 2005; Kingdon *et al*., 2013), the isolated West African mountain archipelagos of Upper Guinea, Nigeria and Cameroon support an exceptional endemism of montane biodiversity. They include rich small mammal assemblages for which new species continue to be discovered (e.g. Petter, 1982; Dieterlen & van der Straeten, 1988, 1992; Van der Straeten & Hutterer, 1986; Hutterer, Dieterlen & Nikolaus, 1992; Dieterlen & Van der Straeten, 1992; Verheyen *et al*., 1997; Fahr *et al*., 2002; Lecompte, Granjon & Denys, 2002; Missoup *et al*., 2012; Monadjem *et al*., 2013a, b; Denys *et al*., 2014). The closest relatives of many of these West African endemics are confined to the mountains of the eastern African Great Rift Valley and the Eastern Arc Mountains, suggesting either ancient forest (Miocene) connections (as suggested for the shrew genus *Congosorex*; Stanley, Rogers & Hutterer, 2005), or possibly more recent dispersal events along historical temperate corridors (e.g. Late Pliocene or Pleistocene glacial periods, when temperate conditions were widespread).

Fahr *et al*. (2002) described a disjunctive pattern between related pairs of horseshoe bats of the *Rhinolophus maclaudi* group occupying the West African highlands of Upper Guinea and East Africa's Albertine Rift. Although their divergence times are unknown, the origin of these groups was attributed to Late Pleistocene climatic changes leading to fragmentation of suitable habitats and survival of relic populations in 'buffered' mountainous habitats (Fahr *et al*., 2002; Kerbis Peterhans *et al*., 2013). Lecompte *et al*. (2002) suggested a sister-group relationship between groups of *Praomys* rodents occupying West African CVL and East African mountain archipelagos, although the relationships among these groups is under debate (Missoup *et al*., 2012).

In describing *Otomys occidentalis* from the Bamenda highlands region (Gotel Mts in Nigeria and Mt Oku in Cameroon), Dieterlen & van der Straeten (1992) postulated, based on a shared dental character (five laminae in the lower first molar, m_1), a close relationship between this species, *O. barbouri* from Mt Elgon (Uganda and Kenya) and *O. lacustris* from the Southern Highlands and Eastern Arc Mountains of Tanzania. The two last-mentioned species were previously considered to be conspecific with *O. anchietae* Bocage, 1882 from the Angolan Highlands, which although much larger-sized, also possesses at least five laminae in m_1 (all other *Otomys* have four or fewer laminae in m_1) (Bohmann, 1952; Misonne, 1974). A second West African species, *O. burtoni* Thomas, 1918 from Mt Cameroon (recognized as a distinct species by Musser & Carleton, 2005) has previously been considered to be conspecific with or related to *O. irroratus* Brants, 1827 (= *tropicalis* Thomas, 1902; Thomas, 1918; Bohmann, 1952; Misonne, 1974), a species distributed in South Africa, Zimbabwe and Mozambique, although Taylor, Denys & Mukerjee (2004) suggested, on the basis of its slit-like petrotympanic foramen, a closer relationship with *O. angoniensis* Wroughton, 1906 (in all other *Otomys* this foramen is distinctly round in shape), a species distributed from S Kenya to SE Botswana and NE South Africa. Subject to testing with taxonomic evidence, these West African *Otomys* from CVL would appear to be narrow-range endemics isolated on respective mountains. Their diversity and biogeographical associations complement similar patterns across the archipelago of Afromontane and Afroalpine habitats on the volcanic mountains of East Africa (Kingdon, 1981; Myers *et al*., 2000; Burgess *et al*., 2005; Lovett & Wasser, 2008).

Congruent with the disjunct West African distribution ranges of *O. occidentalis* and *O. burtoni,* Hutterer *et al*. (1992) demonstrated marked differences in the composition of small mammal faunal assemblages from the southern (e.g. Mt Cameroon) and northern (e.g. Mt Oku and Gotel Mts) mountain archipelagos of Cameroon and Nigeria. This raises the possibility that these montane faunas evolved from two distinct radiations. However, Petter (1982) surmised that *Otomys* may have occurred across the entire Sahel (from East Africa to West Africa), north of the Congo forest block when temperate habitats replaced the current northern savannas during the final Holocene hypothermal period (assuming mean temperatures were 10 °C lower than present; Maley, 1997; Maley & Brenac, 1998). This hypothesis invoked extinction in the subsequent warming period, except where populations retreated to higher altitudes in isolated mountain chains in East and West Africa.

An alternative possibility is that one or both West African montane species of *Otomys* could have originated via a southern dispersal route from an ancestral species, such as *O. angoniensis,* which is capable of colonizing savannas in southern Africa and the foothills of mountains in East and Central Africa. Three recognized species currently occupy the highlands of southeastern Democratic Republic of Congo (DRC; *O. angoniensis*) and the central highlands of Angola, (*O. cuanzensis* Hill & Carter, 1937 and *O. anchietae*), whilst a fourth, *O. maximus* (Roberts, 1924) occurs in lower-lying riverine conditions in Zambia and southern Angola. These species have ranges that are geographically closest to the distribution ranges of the West African species.

Finally, it is important to acknowledge that these mountainous terrains in the Cameroon and East Africa were formed by discrete episodes of Cenozoic volcanism, and in association with regional rifting and epeirogeny (uplift). These epicentres of volcanism elevated the regional relief substantially, evident today in persistent stratovolcanoes (steeply conical volcanoes formed by sequential outpourings of eruptive materials) and volcanic plateaux – exemplified by Mt Cameroon, Mts Elgon, Kenya and Kilimanjaro and the Ethiopian Highlands, where local reliefs exceed 5000 m above sea level (Chorowicz, 2005; Partridge, 2010). This raises poignant questions about the tempo and mode of speciation of *Otomys* across these volcanic archipelagoes, especially how these biotic events relate to ages of respective landforms. Tectonism has persisted into the Late Cenozoic in the Central African Rift Zone that extends west to the north of the Congo Basin (Fairhead & Green, 1989; Guiraud & Maurin, 1992), while the most southern volcanoes in Cameroon exhibit recent activity (Njonfang *et al*., 2011). In contrast, the major volcanism that formed an archipelago of stratovolcanoes across East Africa was focused in the Neogene (Miocene and Pliocene), and then declined in the Late Pliocene; thereafter eruptions and lava flows during the Pleistocene (since 2.57 Ma) were more localized but no less significant. These geographically isolated mountains across East Africa (Chorowicz, 2005) comprise an archipelago of Afromontane islands, of three principal clusters along the Albertine and Gregory Rifts (together with the geologically older Eastern Arc Mountains they comprise East Africa's 'Montane Circle', Taylor *et al*., 2009a). They are remotely isolated from the West African Cameroon Volcanic Line (Fig. 1).

Here we use a synthesis of molecular, morphometric and craniodental evidence to test alternative hypotheses for the origin and phylogenetic relationships of West African *Otomys* populations. If both currently recognized West African species resulted from a single radiation, followed by speciation, we would expect them to be sister species. If, as supposed by Dieterlen & Van der Straeten (1992), *O. occidentalis* forms part of a widespread '*lacustris* group' complex, which underwent vicariance independently from *O. burtoni*, we would expect all species of the former complex including *O. occidentalis* (possessing five or more laminae in m1) to comprise a well supported monophyletic clade based on molecular evidence. Finally, if either or both of the West African species originated from a southern radiation via Angola, we would expect them to show sister species relationships with Angolan-endemic species such as *O. cuanzensis* or *O. anchietae.* As we do not currently possess sequence data for these species, this alternative hypothesis cannot be tested by the current study.

Availability of molecular evidence confers two significant advantages to biogeographical reconstructions (Wen *et al*., 2013). One, molecular dating enables testing of multiple competing hypotheses in a chronobiogeographical framework (cf. references in Goodier *et al*., 2011). Two, phylogeographical evidence broadens insights obtained into palaeoenvironments, no longer constrained by taphonomic restrictions on where fossils are preserved. This means molecular evidence should arguably improve on patchy records of rodent fossils which enabled Denys and coworkers (1986) to reconstruct local palaeoenvironments across the Plio-Pleistocene of East Africa. Here, we exploit phylogeographic evidence, especially its constraints using molecular dating, to evaluate whether patterns and events of diversification in *Otomys* is congruent with episodes of rifting and volcanism and/or climatic change.

We further test two competing mechanisms to explain the biogeography of these montane *Otomys*. (1) Is the largely allopatric distribution of species within the genus the result of palaeoclimatic forcing that alternatively linked and fragmented grassland habitats across Africa's highlands? (2) Was speciation of these grassland rodents a consequence of late Cenozoic landscape evolution (uplift and/or volcanism) that formed an archipelago of significant relief, where Afromontane and Afroalpine biomes expanded?

In summary, the objectives of this study are first, to clarify both the taxonomic status (from morphometric and molecular data) and phylogenetic relationships and origin (from molecular data) of West African populations currently referred to *O. occidentalis* and *O. burtoni*. Second, we use phylogeographical evidence to elucidate the most likely pattern and process of speciation in *Otomys* across Africa. This is informed by the congruent synthesis of geological and molecular dates for key cladogenic events within the geographical context of the volcanic archipelagoes extending from West to East and Northeast Africa.

MATERIAL AND METHODS

SAMPLING

The availability of a series of 25 recently collected (by CD, VN, ADM) specimens from Mt Oku, provisionally identified as *O. occidentalis*, and a single *O. burtoni* individual from Mt Cameroon, allowed us to make molecular comparisons with other West, East and Central African *Otomys* taxa. Molecular comparisons were based on available published (Maree, 2002; Taylor *et al*., 2009a; 2011) cyt *b* sequences of 15 East African species and subspecies (*angoniensis*, *barbouri*, *lacustris*, *denti*, *jacksoni*, *tropicalis tropicalis*, *t. elgonis*, *t. faradjius*, *zinki*, *dartmouthi*, *uzungwensis*, *simiensis, fortior, helleri* and *typus*) and four additional southern African species (*Parotomys brantsii*,

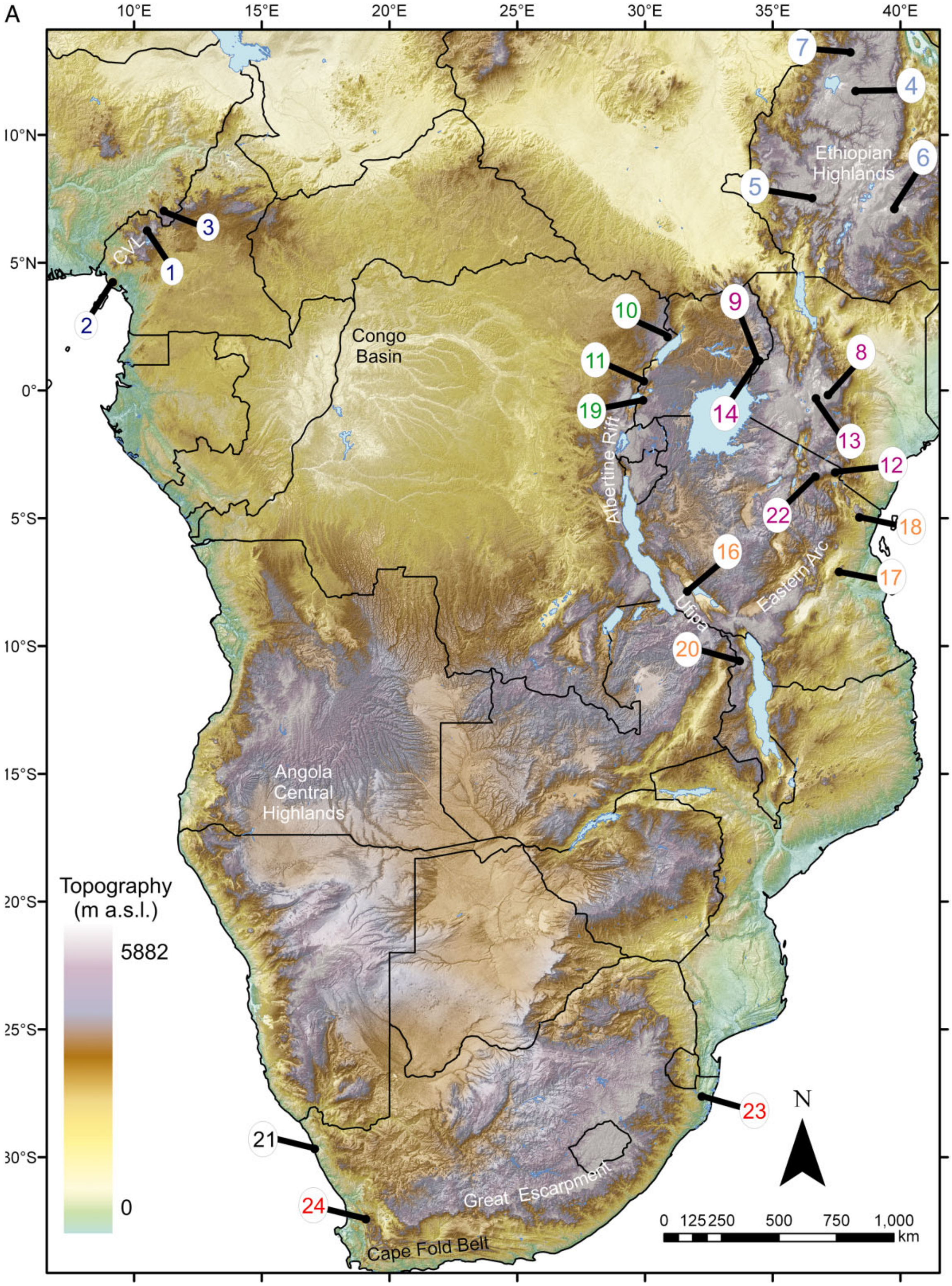


Figure 1. Distribution maps showing collecting localities of all molecular vouchers (A) as well as those of *Otomys occidentalis* (Mts Oku and Gotel) and *O. burtoni* (Mt Cameroon) from the Cameroon Volcanic Line in Cameroon and Nigeria (B). The coloured numbers are coded for the Eastern Arc Mountains (brown), Albertine Rift (green), Cameroon Volcanic Line (dark blue), East African Rift System (purple) and Southern Rift (brown), the Ethiopian Highlands (light blue) and the Southern Escarpment of South Africa (red); colours correspond to those used in Fig. 2. [Colour figure available online.]

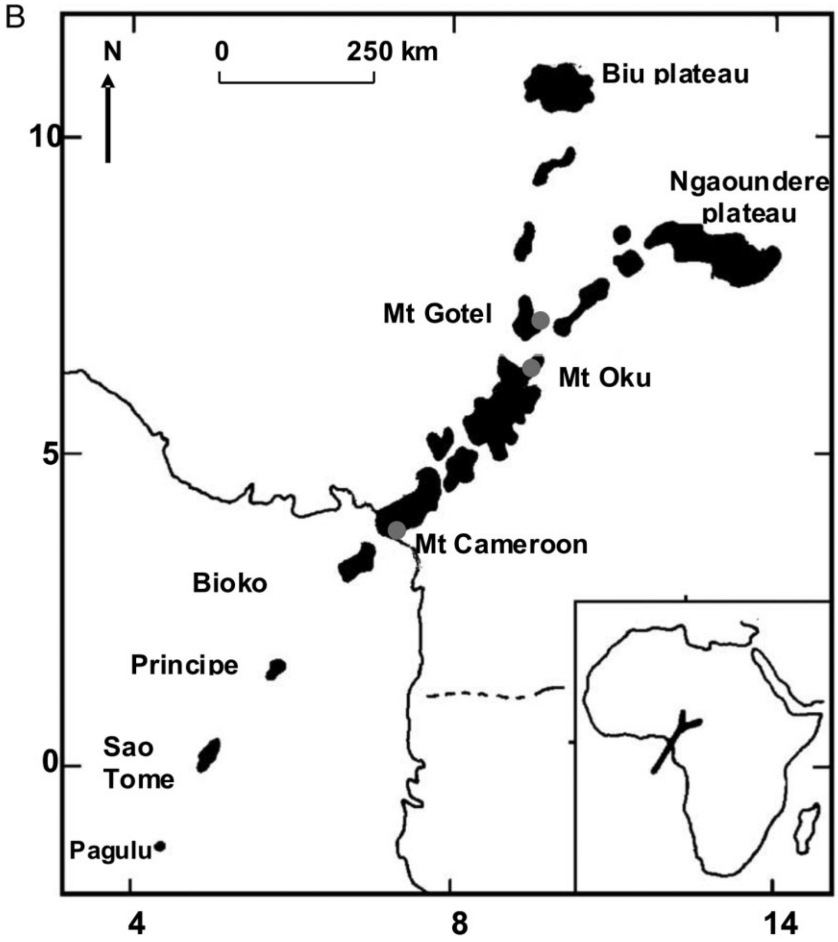


Figure 1. *Continued*

P. littledalei, *O. angoniensis* and *O. irroratus*) (Table 1). Although *Parotomys* is normally regarded as a distinct genus from *Otomys* (Musser & Carleton, 2005), its monophyly has been questioned by Taylor *et al*. (2004). Several new species of *Otomys* have been described recently and we follow the classification and nomenclature of Taylor *et al*. (2011) and Taylor (2013) who recognize 31 species of Otomyinae. Nine murine genera were selected as outgroups (Watrous & Wheeler, 1981) to represent a range of divergent rodent lineages of successive relatedness to the Otomyini, and to include taxa with fossil dates which could be used for calibration as discussed below: *Arvicanthis*, *Aethomys*, *Batomys*, *Lemniscomys*, *Micaelamys*, *Mus*, *Oenomys*, *Phloeomys* and *Rattus* (Table 1; Lecompte *et al*., 2008; Rowe *et al*., 2008).

Craniometric and craniodental comparisons involved almost all known museum specimens of West African *O. occidentalis* and *O. burtoni,* in addition to museum collections of five species samples (*angoniensis*, *anchietae*, *barbouri*, *lacustris* and *tropicalis elgonis*) obtained from geographically restricted regions and selected for being members of species complexes previously affiliated with West African taxa (Appendix). Specimens ($N = 91$) from nine museums were included in the morphometric analysis: Natural History Museum, London, (BM), Ditsong National Museum of Natural History (former Transvaal Museum), Pretoria (TM), Durban Natural Science Museum (DM), Field Museum of Natural History (FMNH), Museum of Comparative Zoology, Harvard (MCZ), Museum national d'Histoire Naturelle, Paris (MNHN), Royal Museum for Central Africa, Tervuren, Belgium (MRAC), Museum für Naturkunde, Stuttgart, Germany (SM), Museum Alexander Koenig (ZFMK) and the Smithsonian Museum of Natural History, Washington DC (USNM).

MOLECULAR ANALYSES

DNA collection and analysis

Total genomic DNA was extracted from frozen or ethanol-preserved soft tissue samples using phenol-chloroform procedures (Sambrook & Maniatis, 1989).

Table 1. Information for voucher specimens included in the molecular phylogenetic analysis based on cytochrome *b* sequences. Latitude (Lat.) and longitude (Long.) are provided in decimal degrees format. Locality numbers correspond with those shown in Figure 1A. The sample from Gotel Mts did not yield sequences for analysis. Abbreviations for museum names explained in text

Species and Geographic Origin	Loc. No.	Lat. & Long.	Collector/ Source	Museum Numbers (field no.)	Genbank Accession No.
Mt Oku, Cameroon	1	06.25N 10.43E	Denys *et al.*	MNHN2011-978 (CAM55)	KJ628257
Mt Oku, Cameroon	1	“ “	Denys *et al.*	CAM100	KJ628258
Mt Oku, Cameroon	1	“ “	Denys *et al.*	MNHN2011-981 (CAM207)	FJ795981
Mt Oku, Cameroon	1	“ “	Denys *et al.*	MNHN2011-982 (CAM360)	KJ628259
Mt Oku, Cameroon	1	“ “	Denys *et al.*	MNHN2011-983 (SPOT10124)	KJ628260
Mt Oku, Cameroon	1	“ “	Denys *et al.*	MNHN2011-984 (SPOT10125)	KJ628261
Mt Oku, Cameroon	1	“ “	Denys *et al.*	MNHN2011-985 (SPOT10146)	KJ628262
Mt Oku, Cameroon	1	“ “	Denys *et al.*	MNHN2011-987 (SPOT10150)	KJ628263
Mt Oku, Cameroon	1	“ “	Eisentraut	ZFMK88140	KJ628264
Mt Oku, Cameroon	1	“ “	Eisentraut/Fülling	ZFMK2003871	KJ628265
Mt Oku, Cameroon	1	“ “	Eisentraut/Fülling	ZFMK2003872	KJ628266
Gotel Mts, Nigeria	2	7.02N 11.18E	Hutterer *et al.*	SM41335, SM41336	N A^{-1}
O. burtoni					
Mt. Cameroon, Cameroon	3	04.23N 9.17E	Eisentraut	ZMFK69214-X	JF796009
O. typus s.l.					
Mt. Guna, Ethiopia	4	11.71N 38.25E	L. A. Lavrenchenko	ZMMU172732 (1110)	JF796016
O. fortior					
Beletta Forest, Jimma, 1750 m, Ethiopia	5	7.53N 36.55E	L. A. Lavrenchenko	ZMMU164962 (47)	JF796010
O. helleri					
Bale Mts, Ethiopia	6	7.10N 39.77E	L. A. Lavrenchenko	ZMMU162597 (232)	JF796014
O. simiensis					
Sankaber, Simien Mts, 3250 m, Ethiopia	7	13.23N 38.05E	L. A. Lavrenchenko	ZMMU178757 (1338)	JF795982
O. tropicalis s.s.					
Mt. Kenya, Naro Moru, 3050 m, Kenya	8	0.18S 37.17E	M. D. Carleton	USNM590000	JF795994
Mt. Elgon, Bumasola	9	1.18N 34.38E	P. J. Taylor	DM6282	JF795999
O. tropicalis faradjius					
Rethy, DRC	10	2.09N 30.89E	A. Laudisoit	RMCA a6.016-M-2034 (CA614)	JF796000
O. dartmouthi					
Bujuku River, Ruwenzori Mts, 3370 m, DRC	11	0.36N 29.96E	J. C. Kerbis-Peterhans	FMNH144327	JF795986
O. zinki					
Mt. Kilimanjaro NP, 2477 m, Tanzania	12	3.21S 37.45E	W. T. Stanley	FMNH174174	JF795989

Table 1. *Continued*

Species and Geographic Origin	Loc. No.	Lat. & Long.	Collector/ Source	Museum Numbers (field no.)	Genbank Accession No.
O. orestes					
Aberdares NP Fishing lodge, 2743–2895 m, Kenya	13	0.31S 36.70E	M. D. Carleton	USNM589997	JF795990
O. jacksoni					
Mude Cave Camp, Mt. Elgon, 3600 m, Uganda	14	1.16N 34.48E	P. J. Taylor	DM6261	JF795992
O. barbouri					
Mude Cave Camp, Mt. Elgon, 3600 m, Uganda	15	1.16N 34.48E	P. J. Taylor	DM6262	JF795980
O. lacustris					
Chingombe, Ufipa Plateau, 1500 m, Tanzania	16	7.87S 31.66E	W. N. Verheyen†	RMCA 96.037-M-5237 (R13272)	EU874446
Udzungwa Mts, Chita, 1460 m, Tanzania,	17	7.10S 37.64E	W. T. Stanley	FMNH155623	EU874447
O. sungae					
Usambara Mts, Kidunda Forest, 2047 m, Tanzania	18	4.97S 38.44E	A. Laudisoit	RMCA a6.013-M-2031(TE5012)	FJ795993
O. denti					
Mt. Rwenzori, John Mate Camp, 3368 m, Uganda	19	0.38S 29.93E	J. C. Kerbis-Peterhans	FMNH144324	EU874434
Otomys species novo					
Chilinda Camp, Nyika NP, 2230 m, Malawi	20	10.59S 3.71E	J. C. Kerbis-Peterhans	FMNH191809 (MLWM416B)	EU874438?
Parotomys brantsi					
Kleinsee, Northern Cape, South Africa	21	29.68S 17.08E	C. H. Scholtz	TM46133	FJ19561
Parotomys littledalei					
Goegap NR, Springbok, Northern Cape Province	21	29.68S 17.03E	T. P. Jackson	TM46134	AF492732
O. angoniensis					
Mt. Meru, Arusha, Tanzania	22	3.22S 36.38E	B. Jansen van Vuuren	TM46289	AF492728
Mkuze NR, KwaZulu Natal, South Africa	23	27.63S 2.23E	A. Berruti	DM1983	?
O. irroratus					
Cederberg, Northern Cape Province, South Africa	24	32.43S 19.08E	P. J. Taylor	DM4317	FJ19546
OUTGROUPS					
Arvicanthis somalicus					AF004574
Micaelamys namaquensis					AF141215
Aethomys sp.					AF004587
Lemniscomys striatus					AF141211
Oenomys hypoxanthus					EU349769
Mus musculus					V00711
Rattus norvegicus					X14848
Batomys granti					AY324459
Phloeomys sp.					EU349775

Standard polymerase chain reaction (PCR) methodology (Saiki *et al.*, 1988) was followed for amplifying and sequencing (Sanger *et al.*, 1977) the complete cyt *b* gene using L14724 and H15915 end primers (Pääbo & Wilson, 1988) and an *Otomys*-specific internal primer L15267 (Taylor *et al.*, 2009a) using cycling conditions provided in Taylor *et al.* (2011). Sequences were determined by means of Big-Dye$^{\text{TM}}$-terminator chemistry with an ABI3130 Analyzer (Applied Biosystems) and assembled using the associated SeqServe platform (http://www.bi.up.ac.za/software/seqserve/).

Phylogenetic analyses

Nucleotide sequences were aligned using Clustal X version 1.82 (Thompson *et al.*, 1997) and translated into amino acids using MacClade version 4.07 (Maddison & Maddison, 1992) to assess possible ambiguities of the functional reading frame (Arctander, 1995). Phylogenetic tree inference involved model-based Bayesian Posterior Probability (BPP; Huelsenbeck & Ronquist, 2001; Huelsenbeck *et al.*, 2001) and maximum likelihood (ML; Felsenstein, 1981) approaches. The resulting trees were assessed for topological similarity and degree of statistical support (Hillis, 1995; Yang & Rannala, 2012). Maximum likelihood and Bayesian analyses incorporate parameter estimates of the dynamics of nucleotide sequence evolution for phylogenetic inference (Sullivan & Swofford, 1997; Sullivan & Joyce, 2005). Pairwise uncorrected genetic distances (*p*, Nei, 1971) between outgroup taxa and all otomyine taxa included in the study and estimates of sequence variability were calculated in PAUP* 4.0b10 (Swofford, 2003).

Bayesian analyses were executed in MrBayes v3.2.1 (Huelsenbeck & Ronquist, 2003; Ronquist *et al.*, 2012) and we applied the best fitting unpartitioned General Time Reversible (GTR + I + G, Rodriguez *et al.*, 1990; Yang, 1994) and codon-partitioned evolutionary models (1st position – K2 + G (Kimura, 1980; Yang, 1994); 2nd – K2; 3rd – TN93 + I + G (Tamura & Nei, 1993; Yang, 1994) selected under the corrected Akaike Information Criteria (AIC; Akaike, 1974) in MEGA v5.0 (Tamura *et al.*, 2011). Four Markov Chain Monte Carlo chains, each starting from random trees, ran simultaneously for 5×10^6 generations (sampling every 100th tree) of which the first 5×10^3 were discarded as 'burin-in'. Split frequencies between the two independent runs were checked every 1000 generations to test for convergence. Posterior probability values ≥ 0.95 were considered significant. Bayesian trees derived from unpartitioned and partitioned analyses were quantitatively evaluated using Bayes Factors and marginal likelihood and standard error estimates from 1000 bootstrap replicates (Suchard, Weiss & Sinsheimer, 2001) as implemented in Tracer v1.5 (Rambaut & Drummond, 2011).

A rapid heuristic search algorithm implemented in RAxML v7.2.8 (Stamatakis, 2006; Stamatakis *et al.*, 2008) was used for constructing ML trees and computing bootstrap support indices (1000 replicates, Stamatakis, Hoover & Rougemont, 2008). The GTR nucleotide substitution model and parameters (Rodriguez *et al.*, 1990) were estimated under both unpartitioned and codon-partitioned evolutionary models, with incorporation of a gamma-shape-parameter (G) to correct for rate variation among nucleotide sites (Yang, 1994). The likelihood scores for unpartitioned and partitioned analyses were compared using the one-tailed Shimodaira-Hasegawa likelihood ratio test (1000 replicates, Shimodaira & Hasegawa, 1999) in RAxML v7.2.8 (Stamatakis *et al.*, 2008).

Divergence date estimates

As the likelihood ratio test (Felsenstein, 1981) disproved a strict molecular clock model ($P < 0.001$), divergence time estimates, 95% confidence limits and relative substitution rates of lineages within the Otomyini phylogeny were obtained using a Bayesian approach and a relaxed clock model (Rambaut & Bromham, 1998; Drummond *et al.*, 2006) as implemented in BEAST v1.7 (Drummond & Rambaut, 2010; Drummond *et al.*, 2012). The relaxed clock rate, which accommodates substitution rate variation across the tree, was estimated 'unlinked' to allow unique lineage-specific rates for each codon partition under optimal codon-specific evolutionary models (Goldman & Yang, 1994) and a birth-death speciation model (Nee *et al.*, 1994). Fossil-based nodal calibration priors were specified as follows: 10.5 Ma (late Miocene) for the minimum divergence time for the earliest Arvicanthini fossil cf. *Parapelomys* from Ethiopia to calibrate the split of Phloeomyini from other Murinae (11–10 Ma calibration bounds, Jacobs & Downs, 1994; Rowe *et al.*, 2008; Denys & Winkler, in press), 6.5 Ma for the Arvicanthini-Otomyini split (Winkler, 2002; Rowe *et al.*, 2008) assuming a normal prior distribution (7–6 Ma calibration bounds) and the root of the Otomyini radiation between 4.3 Ma (maximum) and 3.7 Ma (minimum) based on two *Euryotomys* specimens from Langebaanweg and Bolt's farm in South Africa (Denys, 2003). Prior distributions for the specified calibrations (tmrca) were set to follow a normal distribution, with the standard deviations set to fall within the minimum and maximum calibration bounds to reduce the variance around the mean (Ho, 2007). The root height of the phylogeny was estimated using the tree model. The average standard deviation of split frequencies was calculated to assess the similarity between the sets of trees recovered from two independent runs.

CRANIODENTAL CHARACTERS

Five craniodental characters were scored on each skull (see Taylor 2013 for illustration and further explanation): (1) the angle of the nasal bone at the point it expands anteriorly; (2) the number of laminae in the third upper molar, M3; (3) the number of laminae in the first lower molar, m1; (4) the shape of the petrotympanic foramen (slit-like or round); and (5) the number of incisor grooves on the lower incisors (one deep groove, one deep and one shallow groove, or two deep grooves).

MORPHOMETRICS

Based on tooth wear, skull shape and degree of closure of sutures, each skull was assigned to a relative age class between 1 and 5 as described by Taylor & Kumirai (2001). Based on previous intra-specific analyses (Taylor, Meester & Kearney, 1993; Taylor & Kumirai, 2001; Taylor, Kumirai & Contrafatto, 2005) that demonstrated lack of significant sexual dimorphism and homogeneity of toothwear classes 4 and 5, we combined males and females and we pooled age classes 4 and 5. In exceptional cases, to boost poor samples, we introduced class 3 individuals but only if their skull length was close to the range of values for classes 4 and 5 (i.e. greatest length > 35 mm) and their potential effect on population differentiation evaluated by *a posteriori* inspection of their distribution in multivariate ordination analyses.

The following ten cranial variables were taken with Mitotoyo calipers to 0.01 mm accuracy, as explained in Taylor & Kumirai (2001): **GLS –** Greatest length of skull measured dorsally; **BCD –** Depth of braincase measured vertically at basioccipital; **MDL –** Mandible length, greatest length of the mandible excluding teeth; **APF –** Maximum length of anterior palatal foramen; **NAW –** Nasal width, greatest width across nasals at right angles to the skull axis; **MXTRL –** Maxillary tooth row length, distance from anterior edge of first maxillary tooth to posterior edge of last maxillary tooth at crown; **IOC –** Interorbital constriction, least distance dorsally between the orbits; **ZYW –** Zygomatic width, greatest distance between the outer margins of the zygomatic arches; **PAL –** Palatal length, from the anterior edge of premaxillae to the anteriormost point on the posterior edge of palate; **BUL –** Greatest length of bulla along the longitudinal axis.

In order to correct for size differences (hence unequal contributions to variance matrices) among linear variables, for multivariate analyses we used the $\log_{10}$ transformation (Marcus, 1990; Carleton & Byrne, 2006). These data were subjected to exploratory principal component analysis (PCA) as well as Canonical Variates Analysis (CVA) to observe morphometric patterns between individuals from all seven taxa (OTUs), as described above (under *Sampling*). As the extreme size of *O. anchietae* individuals obscured variation among other taxa which overlapped considerably in size (as reflected in CVA), we repeated the CVA excluding *O. anchietae*. Multivariate analyses of linear data were conducted using PAST version 2.11 (Hammer, Harper & Ryan, 2001).

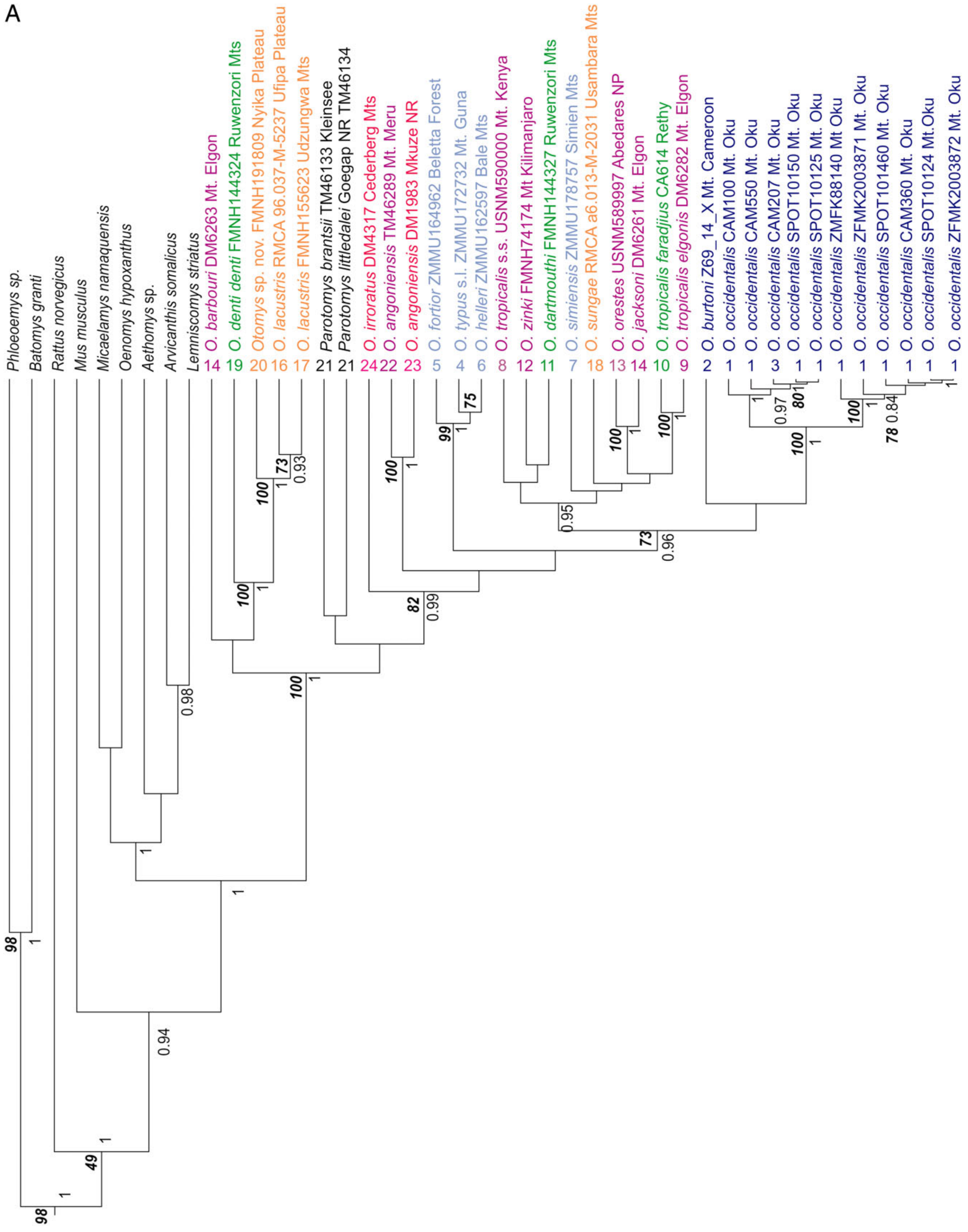
RESULTS

MOLECULAR

Alignment of cyt *b* sequences for 34 *Otomys* taxa and nine outgroups (Table 1) resulted in a functional mtDNA reading frame when translated to amino acids. Estimates of sequence variability yielded 385 parsimony informative, 415 variable and 628 constant characters across 1143 nucleotide sites.

Largely similar tree topologies were retrieved across phylogenetic inference methods and partition schemes (unpartitioned or codon-partitioned). The inconsistencies found in the branching order of some deep and terminal lineages always concern unsupported nodes (bootstrap support < 70% and Bayesian Posterior probabilities < 0.95; Fig. 2A). Bayesian analysis yielded a

Figure 2. (A) Bayesian phylogram based on 1143 base pairs (except for *O. burtoni* with 440 base pairs) of the cytochrome *b* gene showing relationships of *O. occidentalis* and *O. burtoni* to other eastern and southern African *Otomys* and *Parotomys* species. Bootstrap support values from maximum likelihood (bold italics) and Bayesian probabilities (normal font) analyses are also shown; (B) Dated Bayesian ultrametric phylogram based on a relaxed clock model and three fossil-based calibration points showing estimated divergence times for *O. occidentalis* and *O. burtoni* from West Africa and other eastern and southern African *Otomys* and *Parotomys* species. Outgroups not shown. Colours of taxon names indicate the major biogeographic regions mapped in Figure 1. Major episodes of volcanism are indicated (see text for referenced authorities) along with major changes to global climate through the Late Cenozoic, including final scale changes in sea surface temperature (Benthic ^{18}O plotted from Lisiecki & Raymo, 2005, middle panel), highlighting the overall cooling trend in global climate (left panel) and Africa's orbital shift since the Late Pliocene (modified from Kingston, 2007). Major episodes of uplift and rifting include the rapid uplift of the Albertine horsts (discussed in main text) and late Neogene epeirogeny across south-central Africa, focused on the Ufipa Plateau and Malawi, and extending southwest of the Albertine Rift from Tanganyika and northern Zambia (Cotterill & de Wit, 2011) to Katanga (Decrée *et al*., 2010). [Colour figure available online.]


A
Phloeoemys sp.
Batomys granti
Rattus norvegicus
Mus musculus
Micaelamys namaquensis
Oenomys hypoxanthus
Aethomys sp.
Arvicanthis somalicus
Lemniscomys striatus
14 *O. barbouri* DM6263 Mt. Elgon
19 *O. denti denti* FMNH144324 Ruwenzori Mts
20 *Otomys* sp. nov. FMNH191809 Nyika Plateau
16 *O. lacustris* RMCA 96.037-M-5237 Ufipa Plateau
17 *O. lacustris* FMNH155623 Udzungwa Mts
21 *Parotomys brantsii* TM46133 Kleinsee
21 *Parotomys littledalei* Goegap NR TM46134
24 *O. irroratus* DM4317 Cederberg Mts
22 *O. angoniensis* TM46289 Mt. Meru
23 *O. angoniensis* DM1983 Mkuze NR
5 *O. fortior* ZMMU164962 Beletta Forest
4 *O. typus* s.l. ZMMU172732 Mt. Guna
6 *O. helleri* ZMMU162597 Bale Mts
8 *O. tropicalis* s.s. USNM590000 Mt. Kenya
12 *O. zinki* FMNH74174 Mt Kilimanjaro
11 *O. dartmouthi* FMNH144327 Ruwenzori Mts
7 *O. simiensis* ZMMU178757 Simien Mts
18 *O. sungae* RMCA a6.013-M-2031 Usambara Mts
13 *O. orestes* USNM589997 Abedares NP
14 *O. jacksoni* DM6261 Mt. Elgon
10 *O. tropicalis faradjius* CA614 Rethy
9 *O. tropicalis elgonis* DM6282 Mt. Elgon
2 *O. burtoni* Z69_14_X Mt. Cameroon
1 *O. occidentalis* CAM100 Mt. Oku
1 *O. occidentalis* CAM550 Mt. Oku
3 *O. occidentalis* CAM207 Mt. Oku
1 *O. occidentalis* SPOT10150 Mt. Oku
1 *O. occidentalis* SPOT10125 Mt. Oku
1 *O. occidentalis* ZMFK88140 Mt Oku
1 *O. occidentalis* ZFMK2003871 Mt. Oku
1 *O. occidentalis* SPOT101460 Mt. Oku
1 *O. occidentalis* CAM360 Mt. Oku
1 *O. occidentalis* SPOT10124 Mt.Oku
1 *O. occidentalis* ZFMK2003872 Mt. Oku
98
1
98
1
49
1
0.94
1
1
0.98
100
1
100
1
100
1
73
1
0.93
82
0.99
100
1
99
1
75
0.95
73
0.96
100
1
100
1
100
1
1
0.97
80
1
100
1
78
0.84
1

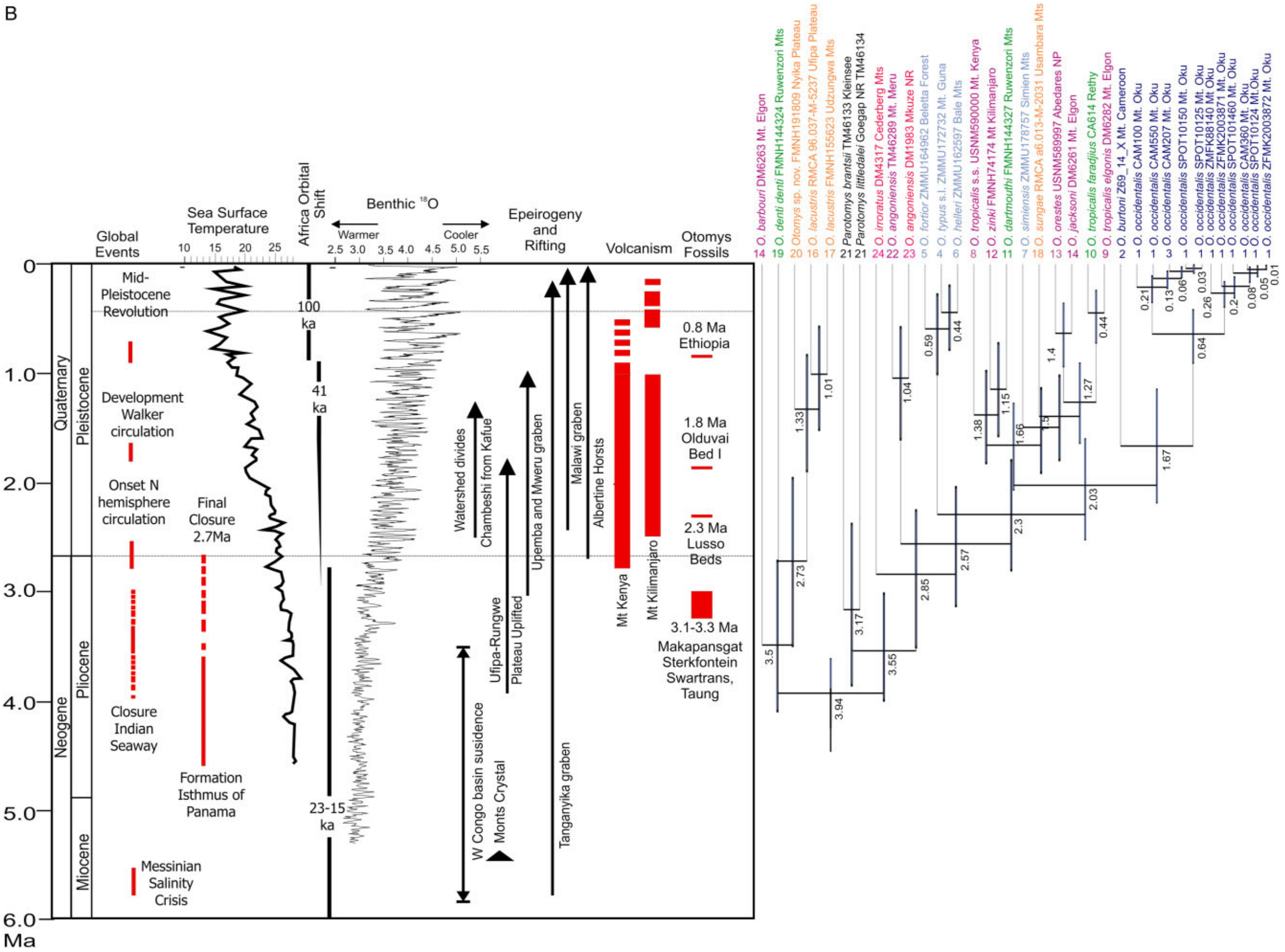


Figure 2. *Continued*

codon-partitioned evolutionary model with a score, which was higher (log L = −10371.140 ± 0.194) than that of the tree based on an unpartitioned model (log L = −10861.815 ± 0.119). Maximum likelihood analyses yielded similar results (codon model, best log L = −10313.369 versus unpartitioned model log L = −10894.910).

The 11 *O. occidentalis* specimens from Mt Oku formed two well supported sister clades (*p*-distance = 2.9-5.8%, Fig. 2A). The closest lineage to Mt Oku, in terms of genetic distance, is from Mt Cameroon and presumed to be *O. burtoni* (*p*-distance = 7.5–8.5%; based on 402 base pairs of sequence), but the sister relationship received only weak support (BPP = 0.86). These two West African *Otomys* species formed a broader monophyletic group (BPP = 0.96, ML = 65%) with a well supported East African clade (BPP = 0.95, ML = 62%). The latter includes taxa formerly assigned to *O. tropicalis* s.l and *O. typus* s.l. (from the Albertine Rift, Mt Elgon, Kenyan Rift, Mt Kilimanjaro, northern Eastern Arc Range and the Simien Mts of Ethiopia) (Fig. 2A, B). Whilst the sister relationships of certain species were reliably supported, e.g., the *denti-lacustris-sungae* and *fortior-typus-helleri* clades (found previously by Taylor *et al*., 2009a; 2011), relationships among some eastern and southern African species and subspecies remain unresolved. Figure 2B shows the estimated divergence times of lineages within the Otomyini phylogeny (and 95% confidence intervals) obtained under a relaxed clock model with three internal nodes calibrated against the fossil record.

MORPHOLOGY

All the 28 *O. occidentalis* skulls examined, including 25 recently collected from Mt Oku as well as the holotype (SM 41336) and co-type (SM 41335), had five laminae in m_1, confirming their identification as *O. occidentalis*, although, in six cases, a minute additional appendage was present on the fifth lamina. Out of 28 crania where the number of laminae in M^3 was observed, eight had seven distinct laminae, six had eight laminae, and 14 had seven plus an additional highly reduced appendage. Twelve of 28 skulls (including the holotype and co-type) had nasals which expanded at a sharp angle, c. 95° to 100°; in 16 cases the angle was more obtuse and varied from c. 120° to 150°. There was no association of the angle of the nasal expansion observed in voucher specimens and their molecular relationships (or clade membership); in three voucher specimens within Clade 1 (see below for definition of molecular clades), the angle varied from 95° to 135°, and similarly so in four vouchers grouping within Clade 2. In all cases ($n = 25$) where the petrotympanic (PT) foramen was visible (including the holotype), it was slit-like in shape, although in one case this character was scored as 'small hole'.

Of seven *O. burtoni* skulls examined, five had slit-like PT foramena; of the remaining two, the foramen shape was not clear in one specimen and in the other it was scored (perhaps erroneously) as a small hole. Of three *O. burtoni* specimens in which dental characters were observed, all had four laminae in m_1 and either six (in the type specimen BM 7.1.1.196) or seven ($N = 2$) in M^3. The angle of expansion of the nasal varied from 90° (in the holotype) to 130°.

Examination of nine East African *O. angoniensis* skulls confirmed the slit-like shape of the PT foramen in all eight cases where it was visible. All other *Otomys* species examined had round PT foramena. Thus, the two West African species examined here, together with *O. angoniensis* are unique in sharing a slit-like PT foramen (see also Taylor & Kumirai, 2001).

As confirmed by CVA (Fig. 3), and from summary statistics of craniometric variables (Table 2), our morphometric sample included the smallest (*occidentalis*) and largest (*anchietae*) *Otomys* species. Apart from the much larger-sized *O. anchietae* (Fig. 3A; Table 3), no other species can be distinguished morphometrically (Fig. 3A). When *O. anchietae* was excluded (Fig. 3B), greater separation was achieved between species on the first two axes. In particular, *O. occidentalis* was completely separated craniometrically from all other species. Based on character loadings on the first canonical variate, separation was mostly due to variation in greatest skull length, bulla length, nasal width and palatal length whereby *O. occidentalis* was smaller in respect of these variables, but with a proportionately longer palate (Table 4; see also Table 2).

PCA of specimens of *O. occidentalis* revealed no distinct craniometric differences between animals from the Gotel Mts and Mt Oku, as well as no craniometric, dental or external differentiation between individuals identified from Clade 1 and Clade 2 in the molecular analysis (Fig. 4A, B, C).

DISCUSSION

BIOGEOGRAPHIC AND SPECIATION SCENARIOS

Utility of phylogenetic conclusions based on cyt b *gene trees in Otomys*

Whilst caution should be exercised in interpreting gene trees (particularly from mtDNA) as species trees, previous studies in the *Otomys* group have demonstrated considerable congruence between mtDNA sequences (cyt *b* and 12S rRNA genes), chromosomal, morphometric, morphological and ecological data in defining specific lineages (e.g. Maree, 2002; Taylor *et al*., 2009a, b; 2011). In particular, Taylor *et al*. (2011) analysed both cyt *b* and 12S sequences from a similar set of taxa to those here presented (at least with respect to the *typus s.l and tropicalis s.l.* complexes), resulting in very similar phylogenetic conclusions to those presented here. Since 12S gene sequences did not improve resolution or node support when combined with cyt *b* in the study of Taylor *et al*. (2011), we did not re-analyse them in the present study. Maree (2002) analysed a single 12S sequence of *O. maximus* from Botswana and found it to be very close in genetic distance to South African examples of *O. angoniensis*. Based on this, we assume for the present study that *maximus* is conspecific with *angoniensis*.

Origins of West African taxa

Our data clearly refute the hypothesis of Dieterlen & Van der Straeten (1992) that *O. occidentalis* is phylogenetically related to the '*lacustris* group' (*O. anchietae*, *O. lacustris*, *O. occidentalis*, *O. barbouri*) defined by possession of five or more laminae in m_1. As shown also by Taylor *et al*. (Taylor *et al*., 2009a; 2011), *lacustris* and *denti* are sister species whilst *barbouri* is a distant relative whose relationship with other *Otomys* or *Parotomys* taxa is poorly defined (Fig. 2A, B). No molecular data are yet available for *O. anchietae* from the Angolan Highlands. Albeit, founded only on a single partial sequence of *O. burtoni*, the most parsimonious explanation based on cyt *b* sequences is that a single colonization event around 2.03 Ma (95% range: 2.53–1.6 Ma) gave rise to both recognized West African taxa (*O. occidentalis* and *O. burtoni*), which are clearly distinct from a well supported Central–East–Northeast African (hereafter termed northern equatorial) sister group whose descendants comprise distinct populations spanning the Albertine Rift mountains, Mt Elgon, the Kenyan Rift mountains, Mt Kilimanjaro, the Usambara Mts

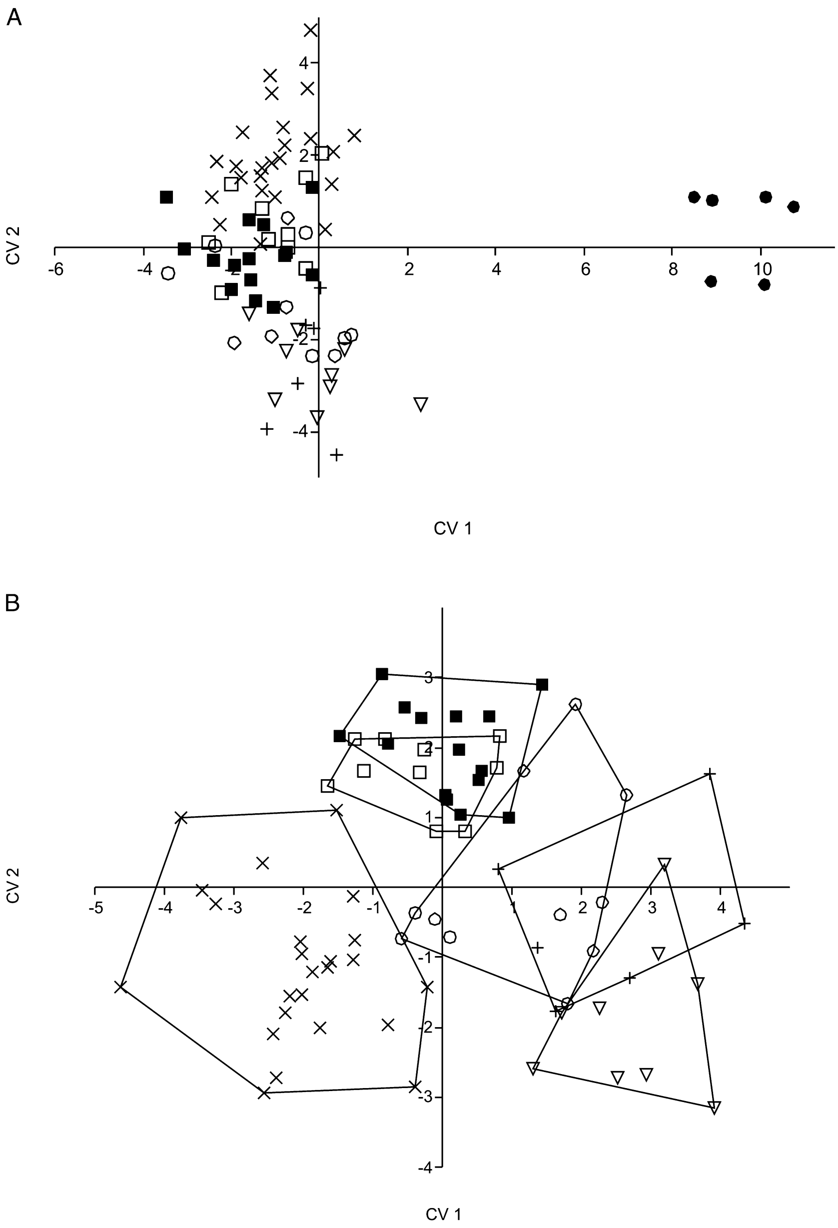


Figure 3. Results of Canonical Variates Analysis (CVA) of ten craniometric variables in *Otomys* from: (A) seven putative taxa including those from the Cameroon Volcanic Line (*O. occidentalis* and *O. burtoni*) and an additional five taxa which have been associated with *O. occidentalis* or *O. burtoni* in the past; and (B) six taxa (as above but excluding *O. anchietae*). Symbols as follows: X's = *occidentalis*; pluses = *burtoni*; open squares = *barbouri*; closed squares = *lacustris*; open circles = *tropicalis elgonis*; closed circles = *anchietae*; open triangles = *angoniensis*. CV1 and CV2 explain 63.3% and 18.0% of the variance in (A) and 48.7% and 32.9% of the variance in (B) respectively.

(northern Eastern Arc Range) and the Simien Mts (Ethiopian Highlands). This molecular date concords well with the first known East African appearance of *Otomys* fossils in the Albertine Rift at ~2.3 Ma (Denys, 2003) as well as with the rapid, pronounced uplift (by 1000–1500 m) of the Albertine Rift during the Late Pliocene and Early Pleistocene (Pickford, 1990; Partridge, Wood & DeMenocal, 1995; Bauer *et al.*, 2010, 2012). This rapid uplift is assumed to have transformed tropical rain forests (or savanna) into montane habitats, which heralded the first arrival of other montane taxa such as the mountain gorilla (Pickford, 1990; Ackermann & Bishop, 2009).

Our data do not resolve the actual route by which *Otomys* colonized West Africa from East Africa (south

Table 2. Summary statistics for ten craniometric variables in seven *Otomys* taxa

Taxon	GLS	BCD	GLM	APF	MXTRL	NAW	IOC	ZYW	PL	BL
O. occidentalis (*N* = 24):										
Mean ± SD	36.6 ± 1.27	10.8 ± 0.47	22.6 ± 1.33	6.4 ± 0.53	9.1 ± 0.34	6.7 ± 0.31	4.3 ± 0.20	18.4 ± 0.55	20.8 ± 1.09	6.5 ± 0.29
Range	34.5–38.7	10.2–12.1	20.6–26.8	5.3–7.4	8.2–9.8	6.1–7.4	3.9–4.8	17.5–19.4	19.1–22.5	6.0–7.1
O. burtoni (*N* = 6):										
Mean ± SD	38.4 ± 0.78	10.7 ± 0.47	23.3 ± 1.02	6.5 ± 0.29	9.0 ± 0.22	7.1 ± 0.37	4.4 ± 0.07	18.4 ± 0.29	20.3 ± 0.67	7.6 ± 0.10
Range	37.2–39.0	10.0–11.5	22.0–24.7	6.1–7.0	8.7–9.3	6.6–7.5	4.3–4.4	18.1–18.7	19.3–20.9	7.5–7.8
O. barbouri (*N* = 10):										
Mean ± SD	37.9 ± 0.85	11.4 ± 0.46	24.2 ± 1.53	7.3 ± 0.51	9.0 ± 0.27	6.8 ± 0.31	4.2 ± 0.16	18.6 ± 0.66	20.9 ± 0.77	6.8 ± 0.31
Range	36.4–39.0	10.5–11.8	21.8–27.0	6.1–7.7	8.4–9.3	6.4–7.3	4.0–4.5	17.5–19.7	19.7–22.4	6.4–7.4
O. lacustris (*N* = 15):										
Mean ± SD	38.7 ± 1.39	11.2 ± 0.59	22.8 ± 1.04	7.3 ± 0.44	9.0 ± 0.28	6.8 ± 0.27	4.5 ± 0.20	18.6 ± 0.82	21.4 ± 1.00	6.9 ± 0.39
Range	36.3–40.7	10-5–12.3	21.6–25.6	6.6–8.3	8.6–9.5	6.2–7.2	4.2–4.9	17.0–19.9	19.8–23.7	6.0–7.6
O. t. elgonis (*N* = 11):										
Mean ± SD	38.7 ± 2.16	11.2 ± 0.67	23.3 ± 1.42	7.1 ± 0.67	9.1 ± 0.48	7.1 ± 0.42	4.3 ± 0.25	18.8 ± 1.09	21.4 ± 1.35	7.3 ± 0.47
Range	36.0–42.8	10.4–12.7	21.6–25.9	6.4–8.5	8.2–9.9	6.7–8.2	4.0–4.8	17.5–21.1	20.0–24.4	6.7–8.2
O. angoniensis (*N* = 9):										
Mean ± SD	39.3 ± 1.95	11.8 ± 0.63	23.9 ± 1.3	7.1 ± 0.47	9.5 ± 0.44	7.8 ± 0.52	4.4 ± 0.18	19.4 ± 0.96	21.4 ± 1.11	7.4 ± 0.45
Range	36.1–43.2	11.2–12.9	21.8–26.0	6.5–7.9	9.0–10.5	7.2–9.0	4.1–4.7	18.4–21.3	19.8–23.6	6.5–8.0
O. anchietae (*N* = 7):										
Mean ± SD	48.7 ± 2.98	15.0 ± 1.06	33.3 ± 2.9	8.2 ± 0.78	11.9 ± 0.48	8.6 ± 0.67	5.5 ± 0.34	25.5 ± 1.72	26.8 ± 1.73	8.8 ± 0.47
Range	45.2–52.8	14.0–16.6	29.5–37.5	7.3–9.3	11.3–12.5	7.6–9.6	5.0–5.9	23.2–28.0	25.0–29.2	7.0–9.3

Table 3. Character loadings for canonical variates from CVA of ten craniometric variables in *Otomys* from seven taxa including those from the Cameroon Volcanic Line (*O. occidentalis* and *O. burtoni*) and an additional five taxa which have been associated with *occidentalis* or *burtoni* in the past

	CV 1	CV 2	CV 3	CV 4	CV 5	CV 6
GLS	27.518	–41.573	–94.962	–60.521	–12.068	–43.615
BCD	15.6	3.052	–3.2806	30.684	2.9763	–1.5304
GLM	13.231	18.022	–9.1256	14.068	–36.597	–14.388
APF	–21.574	–11.892	–24.061	23.952	13.169	0.63633
MXTRL	42.682	18.804	15.027	10.556	–6.0257	–9.7651
NAW	–21.795	–41.379	52.196	20.582	23.376	–13.091
IOC	–2.4012	–4.5139	–7.2515	–20.849	26.426	–26.761
ZYW	19.346	11.534	25.295	7.9172	11.512	28.818
PL	–10.041	60.199	33.333	–20.21	17.231	54.171
BL	9.2148	–31.456	7.2587	–14.525	–15.184	24.198

Table 4. Character loadings for canonical variates from CVA of 10 craniometric variables in *Otomys* from six taxa including those from the Cameroon Volcanic Line (*O. occidentalis* and *O. burtoni*) and an additional four taxa (excluding the much larger-sized *anchietae*) which have been associated with *occidentalis* or *burtoni* in the past

	CV 1	CV 2	CV 3	CV 4	CV 5
GLS	39.541	80.496	–56.02	16.324	–54.847
BCD	1.1603	0.13709	31.945	–1.5073	–3.4151
GLM	–12.884	5.9629	18.917	35.931	–16.264
APF	11.913	29.11	21.202	–14.633	4.3148
MXTRL	–15.072	–25.769	11.269	10.576	–16.457
NAW	37.802	–43.068	17.068	–29.363	–6.6031
IOC	3.8695	8.5797	–21.299	–26.368	–25.868
ZYW	–4.72	–29.348	10.78	–8.477	27.801
PL	–61.83	–28.849	–19.271	–17.36	52.746
BL	30.902	–7.552	–16.365	16.859	24.498

or north of the Congo forest block). Nevertheless, the biochronological constraints reveal this may have occurred soon after the first arrival of ancestral lineages in East Africa. As *Otomys* is a specialized grazer, we assume that East Africa was colonized from the southern African ancestral lineages following grassland or savanna corridors, and that the extensive Congo forest block would have been an effective barrier to simultaneous dispersal to West Africa. Petter (1982) considered that *Otomys* colonized West Africa from East Africa via the northern savanna corridor but this hypothesis cannot be tested with the available data. If the subsequent dispersal route from East to West Africa was along the highlands and central plateaux of Angola, south of the Congo forest block, we would have expected one of the Angolan species (*O. cuanzensis*, *O. anchietae*) to have been the sister group of all West African *Otomys*. This is still to be robustly tested; unfortunately, there are no molecular or palaeontological data for the two Angolan lineages.

Diversification of northern equatorial lineage

Significantly, the well supported northern equatorial clade, whose members diverged within the last 1.67 million years (95% range: 2.07–1.28 Ma), comprised multiple instances where distantly related taxa occupy the same or adjacent mountain ranges. Thus, both *O. tropicalis elgonis* and *O. jacksoni* occur on Mt Elgon, with the former distributed on lower slopes below the montane forest line, and the latter occurring in alpine meadows above the bamboo forest line. These two species are clearly diagnosable from each other on morphological grounds. Similarly, two clearly recognized species, *O. tropicalis tropicalis* (at lower elevations) and *O. orestes* (at higher elevations) are distributed throughout the Kenyan Rift mountains (including Mt Kenya and the Aberdare Mts), and *O. tropicalis faradjius* and *O. dartmouthi* are found on the mountains of the Albertine Rift (including the Rwenzori Mts) at lower and higher elevations, respectively. When considering the northern equatorial clade together with the adjacent clade comprising

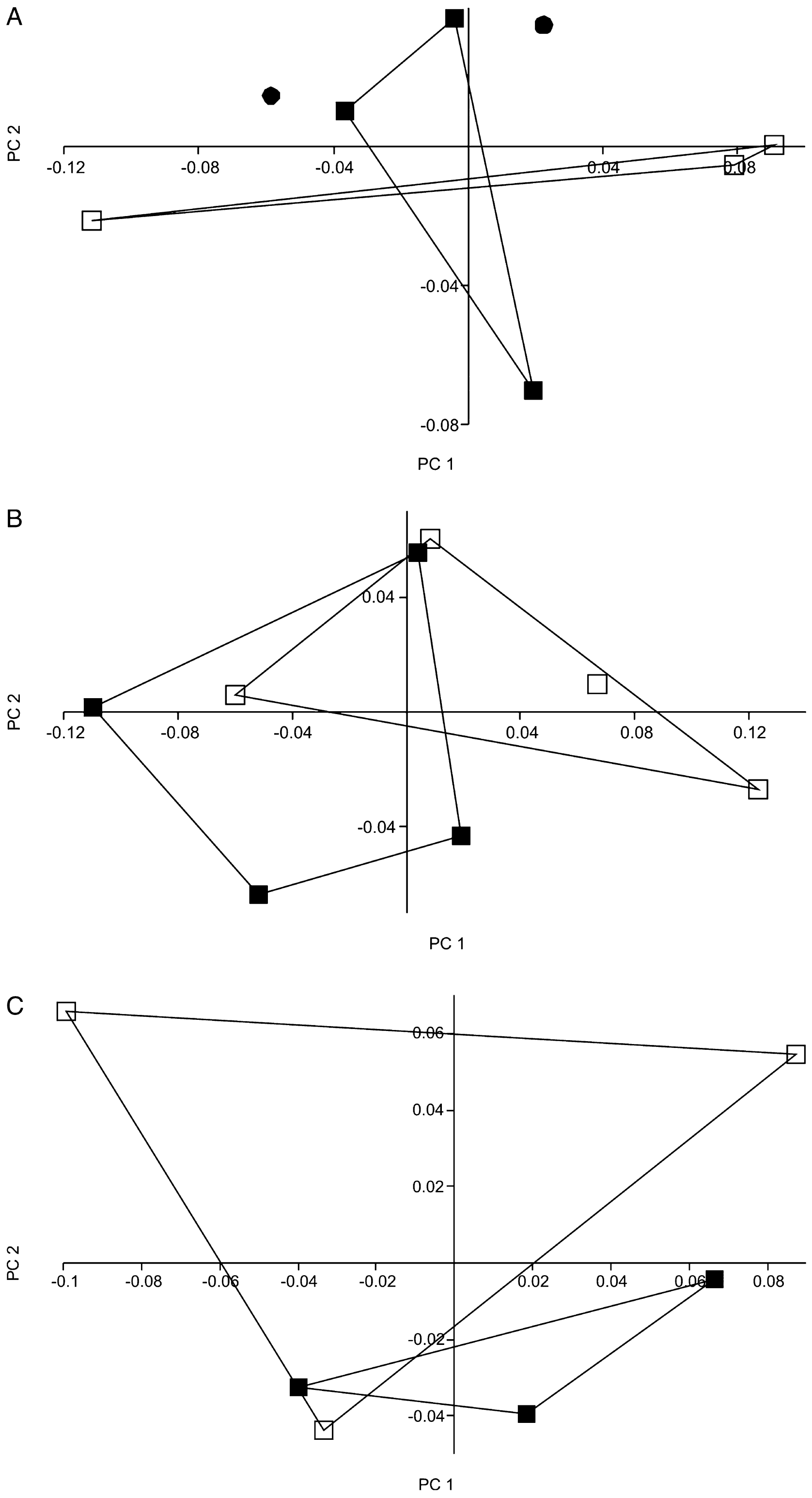


Figure 4. Results of Principal Components Analysis (PCA) of voucher specimens from Mt Oku (squares) and Gotel Mts (closed circles) belonging two molecular clades (denoted as open and closed squares). PCAs were based on log-transformed craniodental (A: ten variables), dental (B: four variables) and external (C: four variables) variables. PC1 and PC2 explain 61.3% and 15.6% of the variance in (A); 63.2% and 22.2% of the variance in (B) and 58.9% and 28.1% of the variance in (C) respectively.

three Ethiopian species (Fig. 2A, B), both *O. simiensis* and *O. typus* are found in the Simien Mts and adjacent Guna Mts of northern Ethiopia (see also Taylor *et al.*, 2011). As these sympatric lineages are *not* sister species, the hypothesis of Carleton & Byrne (2006) of recent *in situ* speciation along elevational gradients is not supported by our molecular data. A similar result was reported by Missoup *et al.* (2012) concerning two murine (Praomyini) species from high and low elevations in the same mountain range in the CVL which were not sister species and did not *diverge in situ*.

On the other hand, when considering all the above-mentioned clades from West, Central-East and Northeast Africa, it is significant that well supported sister species occupy adjacent mountain ranges. The following examples of sister species pairs or trios are instructive: (1) *burtoni* (Mt Cameroon) and *occidentalis* (Mt Oku); (2) *orestes* (Mt Kenya) and *jacksoni* (Mt Elgon); (3) *t. faradjius* (Albertine Rift) and *t. elgonis* (Mt Elgon); (4) *zinki* (Mt Kilimanjaro), *t. tropicalis* (Mt Kenya) and *dartmouthi* (Albertine Rift); and (5) *helleri* (Bale Mts, east of Ethiopian Rift), *fortior* (Beletta Forest, southeast of Ethiopian Rift) and *typus* (Guna Mts, northeast of Ethiopian Rift).

This overall pattern points to multiple cases of allopatric or peripatric speciation, whereby colonization and expansion first occurred on individual ranges followed by later founder events colonizing adjacent ranges (or near-simultaneous colonization of montane-alpine archipelagos occurred from an ancestral species). Given the occurrence of multiple, divergent species on individual landforms, it appears that the vicissitudes of palaeoclimate or tectonism (as expounded below) may have resulted in multiple (at least two) colonization events of the same mountain ranges by common progenitors. In such cases, interspecific competition resulted in elevational segregation whereby successive colonizers were forced to occupy niches distinct from that of the original colonizer.

Peripatric events entailed colonization of discrete mountains in the CVL. If the original colonization of West Africa occurred between 2.03 and 1.67 Ma during a cold wet climate phase then allopatric speciation during a subsequent arid phase (e.g. at around 1.7 Ma (DeMenocal, 1995, 2004) may have given rise to *O. occidentalis* and *O. burtoni* on Mts Oku and Gotel, and Mt Cameroon, respectively. A subsequent drier period may have resulted in contraction of the range of *O. occidentalis* to cause divergence in isolated populations trapped either in different elevational zones or even on neighbouring peaks (e.g. on Mt Oku and Gotel Mts). A following mesic episode can explain secondary contact (sympatry) between the two *occidentalis* lineages, as currently evident from our study (Fig. 2A, B).

Congruence of biochronological and geochronological dating

Here we underscore how the robust geochronology constraining the timing of comparatively rapid uplift across the Albertine Rift since the Late Pliocene (Bauer *et al.*, 2010, 2012), exhibits close congruence with molecular dating of *Otomys* cladogenic events (Fig. 2B). Ideally, a comprehensive reconstruction of the palaeoenvironmental dynamics of the CVL and the EARS needs to account for all episodes of volcanism, and also requires more precise dates for uplift events at a finer spatial scale. Such an exercise is beyond the scope of this paper. Nevertheless, we highlight encouraging evidence for tight congruence between our biochronological (molecular) dates and pertinent geochronological (geological) ages of key landforms. The former recovers episodes of peripatric speciation through the Pleistocene, which can be explained by colonization by *Otomys* of recently formed stratovolcanoes across the East African plateau. This followed on widespread Neogene volcanism across the Ethiopian and Gregory Rifts (Nagaoka *et al.*, 2005; WoldeGabriel *et al.*, 2005); for example, the most recent main-vent eruption of Mt Kenya at ~2.8 Ma was the penultimate event in the recurrent eruptions, whose lavas built this large stratovolcano through the late Neogene (Veldkamp *et al.*, 2012). Pertinently, *O. orestes* then colonized Mt Kenya in the Early Pleistocene. Interestingly, our molecular dating constrains speciation of the endemic *O. zinki* at 1.15 Ma (95% range: 1.58–0.73 Ma) on Mt. Kilimanjaro, formed by recurring volcanism from 2.5–1 Ma; colonization by *O. zinki* followed on final episodes of more localized volcanism in the Middle Pleistocene, which coincided with initiation of glaciers on Mt. Kilimanjaro (Nonnotte *et al.*, 2008). Overall, these peripatric speciation events in *Otomys* can be interpreted as invasion of fertile montane habitats established on young lava soils, derived from the massive lava flows that built these mountains.

The entire East African plateau has also experienced recurring uplift since the Late Miocene, and the extensive mountain ranges it generated are focused along the principal rift flanks (Abebe, Balestrieri & Bigazzi, 2010; Speigel *et al.*, 2010; Bruhn *et al.*, 2011). The stratovolcanoes formed the highest nodes of relief across this East African plateau (see above). Our biogeographical reconstruction reveals *Otomys* to be a relatively recent (Pleistocene) arrival on this landscape, in the light of earlier first appearances and dispersal events in the Afrotemperate flora, which appear to have begun in the Miocene (Galley *et al.*, 2007; Bonnefille, 2010; Feakins *et al.*, 2013). We suggest the global Late Pliocene cooling event (~2.8

Ma, deMenocal, 1995, 2004) was the inaugural trigger that enabled expansion of *Otomys* into equatorial Africa (Fig. 2B). This would have fragmented forests with concomitant grassland expansion, and these small mammals exploited availability of this montane grassland-forest mosaic niche. This is in agreement with the palaeontological data that dates first appearance of *Otomys* at ~2.3 Ma in the Lusso Beds (eastern Congo basin), at ~1.7 Ma in Olduvai Bed I (Tanzania) and finally at ~0.8 Ma in Ethiopia (out of south temperate habitats into equatorial Africa (Denys, 2003). Given the inferred ancestral origin of Afromontane plants (Galley *et al*., 2007), and assuming that *Otomys* followed similar dispersal routes, source populations of *Otomys* likely dispersed from the Cape Fold Belt and Drakensberg Maluti Mountains along the eastern fringing escarpments of southern Africa. Triggered by global cooling, this inaugural event opened up the new Afroalpine adaptive zone, which complemented mesic grasslands around wetlands. At the regional scale, this comprised patches of meadow grasslands at the highest altitudes on now quiescent equatorial volcanoes. Thereafter, expansion of lowland forests during interglacials would have isolated founder populations of *Otomys* across this Afroalpine archipelago. The sympatric species of endemic *Otomys* on Mts Elgon and Kenya, and along the Albertine Rift (Fig. 2A, B) point to repeated dispersals that have successfully colonized these Afromontane islands.

These recurrent events are reminiscent of the variable climatic record forcing invoked to explain phylogeographic diversity of Afromontane plants (Janssens *et al*., 2009; Kadu *et al*., 2013). This phylogeographic evidence for *Otomys* reveals the first direct evidence for how rodents responded to the availability of Afromontane environments (montane forest plus grasslands) over the Pleistocene. It expands on previous fossil evidence restricted to the environs of Plio-Pleistocene rift lakes (Denys, Chorowicz & Jaeger, 1985; Denys, Chorowicz & Tiercelin, 1986), which represent *Otomys* occurring in wetland margins. Our phylogeographic evidence further demonstrates the greatly expanded geographical resolution of evidence from the genomic record, which is not constrained by taphonomic conditions that restrict fossil preservation. Nevertheless, fossils remain crucial to constrain molecular date estimates, as applied in this study using ~2.3 Ma old Lusso fossils of *Otomys*. So, as argued by Cotterill & de Wit (2011) this study demonstrates how combining molecular clocks and phylogeographic evidence provides a powerful tool, which exploits extant biotic indicators to reconstruct palaeoenvironmenal dynamics, which can be integrated with the fossil record (which is distinctly patchy in the case of these rodents). Molecular date estimates are especially informative where scenario testing can identify which individual dispersal events contributed to biotic assembly (in this case, where the southern Africa lineage occupied equatorial landscapes). In contrast, fossils can only estimate the first appearance of a lineage.

Deeper relationships in the Otomyini radiation

We conclude that the northern equatorial radiation of *Otomys*, explored in this paper, was seeded from southern Africa, and inaugurated by Late Pliocene global cooling. We propose that *O. angoniensis* and *O. irroratus* are the surviving representatives of the founding southern ancestral lineage, because both are the extant sister species of the northern equatorial radiation (BPP = 0.99, ML = 77%; Fig. 2A, B). Peripatric speciation events were seeded from ancestral populations of southern African laminate-toothed rats; these dispersals into equatorial Africa invaded new Afroalpine habitats establishing on quiescent stratovolcanoes, originally formed through the Neogene across the Ethiopian and Gregory Rift zones. Complementary peripatric dispersals by *Otomys* similarly responded to Afroalpine habitats as they began to form on the Albertine Rift during its uplift in the Early Pleistocene.

The base of our molecular tree is poorly resolved; apart from the above-mentioned clades, two clades remain. The first *Parotomys* clade (a southern African radiation of arid-adapted 'whistling rats') groups with southern African (*O. irroratus* and *O. angoniensis*) and northern equatorial lineages (albeit with uncertain sister affiliation), and the second, constitute *O. barbouri* (Mt. Elgon) and the East African *denti-lacustris* clade of Taylor *et al*. (2009a). The divergence of the last-mentioned clade at 2.73 Ma (95% range: 3.51–1.97 Ma) separates Albertine Rift *denti* from the *lacustris* group from the southern Eastern Arc, Southern Highlands of Tanzania and the Nyika Plateau in Malawi. Diversification within this southern equatorial (*denti-lacustris*) clade ~2.7 Ma predates that of the northern equatorial clade discussed above (which split from the West African lineage at 2.03 Ma), but is still concordant with the uplift of the Albertine Rift at 2.5 to 2.8 Ma.

In conclusion, these refined insights obtained for the *Otomys* radiation highlights the informative role of biotic indicators, especially where their ecological specializations inform the quest to understand origins of biomes. The pulse of Early Pleistocene speciation events focused across equatorial Africa constrains the first appearance of the Afromontane and Afroalpine biomes along the Albertine and Gregory Rifts. Although Cameroon volcanism began to form the CVL in the Late Miocene (Fig. 2B), *Otomys* only colonized these mountains in the Pleistocene (in contrast to the late Neogene speciation of *Phrynobatrachus* endemics across the CVL, Zimkus & Gvoždík, 2013). These younger dates are interesting, given that the first known fossils of the Afroalpine fossorial rodent *Tachyoryctes* are constrained to the Late Miocene with a pulse of morpho-species diversification at ~4.1 Ma. These events were all confined to the Ethiopian Plateau (López-Antonãnzasa, Flynn & Knoll, 2013). Complementary phylogeographic studies of *Lobelia, Tachyoryctes* and other representative Afroalpine endemics can be expected to refine these insights revealed by *Otomys* across the volcanic archipelago of equatorial Africa.

TAXONOMIC CONCLUSIONS

Unlike the case in the *Otomys denti-lacustris* complex where morphometric data revealed marked adaptive phenotypic divergence between different groups of species from different East African mountain ranges (Eastern Arc and Albertine Rift) defined by both molecular and ecological characters (Taylor *et al*., 2009a), our current study revealed morphological conservatism between sister-group populations from the CVL and the East African 'Montane Circle'. Nevertheless, our combined morphological and morphometric data clearly support the diagnosis of both *O. occidentalis* and *O. burtoni* as distinct West African species which are not conspecific with each other or any other taxa known from eastern and southern Africa. The two taxa can easily be distinguished from each other by a range of morphological and morphometric characters, including the possession of five laminae on m1 in *occidentalis* (four in *burtoni*) and the distinctly smaller cranial size of *occidentalis* (see also Dieterlen & Van der Straeten, 1992). Whilst *O. occidentalis* can be distinguished craniometrically from all other *Otomys* based on its smaller cranial size, *O. burtoni* shows morphometric overlap between *O. angoniensis* and *O. tropicalis* (Fig. 3B). However, molecular data clearly exclude the possibility of conspecificity with either of these taxa; morphometric similarity is therefore entirely convergent in nature, as is the possession of a slit-like petrotympanic foramen in *burtoni*, *occidentalis* and *angoniensis*. Such convergent evolution, and the dependency on just very few craniodental characters which are themselves subject to convergence, together with a rigid adherence to the Biological Species Concept in the past, led to previous classifications which accepted only a few, highly polytypic and very widespread species of Otomyini (e.g. Bohmann, 1952; Misonne, 1974). As a result of several recent studies employing an integrated systematic approach, at least 31 species of Otomyini have been shown to exist (Taylor, 2013).

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APPENDIX

Specimens examined for morphometric analyses. Acronyms for museums explained in text. In the case of recent Mt Oku collections, both Museum and collectors' numbers (in parentheses) are included

Museum Catalogue No.	Species	Sex	Country	Locality
DM6281	*Otomys barbouri*	M	Uganda	Mude Cave Camp, Mt Elgon, 3600 m
DM6280	*Otomys barbouri*	F	Uganda	Mude Cave Camp, Mt Elgon, 3600 m
DM6263	*Otomys barbouri*	F	Uganda	Mude Cave Camp, Mt Elgon, 3600 m
MNHN1933-2762	*Otomys barbouri*	M	Uganda	Mount Elgon: Mission Delomo
DM6262	*Otomys barbouri*	M	Uganda	Mude Cave Camp, Mt Elgon, 3600 m
MNHN1933_2760	*Otomys barbouri*	M	Uganda	Mount Elgon: Mission Delomo
MCZ31422	*Otomys barbouri*	M	Uganda	Kaburomi, Mt Elgon
MNHN1933_2758	*Otomys barbouri*	X	Uganda	Mount Elgon: Mission Delomo
MCZ31369	*Otomys barbouri*	M	Uganda	Kaburomi, Mt Elgon
MCZ31371	*Otomys barbouri*	?	Uganda	Kaburomi, Mt Elgon
MCZ31423	*Otomys barbouri*	F	Uganda	Kaburomi, Mt Elgon
CG1933_2764	*Otomys barbouri*	M	Uganda	Mount Elgon: Mission Delomo
MCZ31424	*Otomys barbouri*	F	Uganda	Kaburomi, Mt Elgon
SM5513	*Otomys burtoni*	M	Cameroon	Mt. Cameroon
BM7.1.1.196	*Otomys burtoni*	F	Cameroon	Cameroon Mts, 7000 ft
FMNH106575	*Otomys burtoni*	M	Cameroon	SW Province: Buea Station
BM34.6.6.4	*Otomys burtoni*	X	Cameroon	Onyanga, E. Mt Cameroon
SM6479	*Otomys burtoni*	F	Cameroon	Mt. Cameroon
SM5511	*Otomys burtoni*	M	Cameroon	Mt. Cameroon
BM58.356	*Otomys lacustris*	M	Tanzania	Mbizi Forest, Ufipa Plateau
BM58.355	*Otomys lacustris*	M	Tanzania	Mbizi Forest, Ufipa Plateau
FMNH166909	*Otomys lacustris*	M	Tanzania	Ukaguru Mts, Mamiwa-Kisara FR, 1kE, 0.75 kS Mt Munyera, 1900 m
MCZ51146	*Otomys lacustris*	M	Zambia	Lucheche River, Abercorn (= Mbala)
MCZ26654	*Otomys lacustris*	F	Tanzania	Dabaga, Iringa District, Udzungwa Mts, 6000 ft
MCZ26352	*Otomys lacustris*	F	Tanzania	Madehani, Ukinga Mts, NE end of Lk Nyasa, 2134 m
MCZ26347	*Otomys lacustris*	M	Tanzania	Madehani, Ukinga Mts, NE end of Lk Nyasa, 2134 m
FMNH155623	*Otomys lacustris*	M	Tanzania	Udzungwa Mts, 4km W, 5km N Chita, 1460 m
MCZ26345	*Otomys lacustris*	F	Tanzania	Madehani, Ukinga Mts, NE end of Lk Nyasa, 2134 m
FMNH163761	*Otomys lacustris*	M	Tanzania	Mt Rungwa Forest Reserve
MCZ26358	*Otomys lacustris*	F	Tanzania	Madehani, Ukinga Mts, NE end of Lk Nyasa, 2134 m
FMNH44411	*Otomys lacustris*	F	Tanzania	Ukinga Mts, Madehani
FMNH155461	*Otomys lacustris*	F	Tanzania	Udzungwa Mts, 2000 m
FMNH166648	*Otomys lacustris*	M	Tanzania	Ukaguru Mts, Mamiwa-Kisara FR, 1900 m
FMNH166908	*Otomys lacustris*	M	Tanzania	Ukaguru Mts,Mamiwa-Kisara FR, 1900 m
FMNH166907	*Otomys lacustris*	M	Tanzania	Ukaguru Mts,Mamiwa-Kisara FR, 1900 m
FMNH171302	*Otomys lacustris*	F	Tanzania	Mbizi Mts (Forest Reserve), 0.5k S, 3k E Wipanga, 2300 m
MNHN1980-60	*Otomys occidentalis*	F	Cameroon	Mt Oku, 2700–2900 m, Clade ?
CAM169	*Otomys occidentalis*		Cameroon	Mt Oku, 2500–2700 m, Clade?
MNHN2011-988 (SPOT 10155)	*Otomys occidentalis*	F	Cameroon	Mt Oku, 2500–2700 m, Clade?
MNHN2011-985 (CAM10146)	*Otomys occidentalis*	M	Cameroon	Mt Oku, 2500–2700 m, Clade?

APPENDIX *Continued*

Museum Catalogue No.	Species	Sex	Country	Locality
MNHN2011-981 (CAM54)	*Otomys occidentalis*	M	Cameroon	Mt Oku, 2500–2700 m, Clade?
MNHN2011-981 (CAM207)	*Otomys occidentalis*	F	Cameroon	Mt Oku, 2500–2700 m, Clade1
MNHN2011-982 (CAM360)	*Otomys occidentalis*	F	Cameroon	Mt Oku, 2500–2700 m, Clade1
SM41336	*Otomys occidentalis*	M	Nigeria	Gotel Mts, Chappal Waddi
SM41335	*Otomys occidentalis*	F	Nigeria	Gotel Mts, Chappal Waddi
MNHN2011-986 (SPOT10148)	*Otomys occidentalis*	F	Cameroon	Mt Oku, 2500–2700 m, Clade2
MNHN2011-987 (SPOT10150)	*Otomys occidentalis*	M	Cameroon	Mt Oku, 2500–2700 m, Clade2
MNHN2011-984 (SPOT10125)	*Otomys occidentalis*	M	Cameroon	Mt Oku, 2500–2700 m, Clade2
BM10.4.1.78	*Otomys tropicalis elgonis*	M	Kenya	Mt Elgon, 2133 m
MRAC5185	*Otomys t. elgonis*	F	Uganda	S. Elgon
MRAC5249	*Otomys t. elgonis*	F	Kenya	Junction camp at foot of Mt Elgon
MRAC5253	*Otomys t. elgonis*	M	Uganda	S. Elgon
MCZ31381	*Otomys t. elgonis*	F	Uganda	Mt Elgon, Sipi
MCZ31366	*Otomys t. elgonis*	F	Kenya	Coletatomoi, Mt Elgon
MCZ31270	*Otomys t. elgonis*	F	Uganda	Mt Elgon, Sipi
MCZ31271	*Otomys t. elgonis*	M	Uganda	Mt Elgon, Sipi
MCZ31427	*Otomys t. elgonis*	M	Uganda	Mt Elgon, Sipi
MCZ31378	*Otomys t. elgonis*	M	Uganda	Mt Elgon, Sipi
SI590005	*Otomys t. elgonis*	F	Kenya	Mt Elgon, 15km from Chorlim Gate
SI318086	*Otomys angoniensis*	M	Kenya	Njoro
SI437517	*Otomys angoniensis*	M	Kenya	Molo, 4miles E, Nakuru district
SI437518	*Otomys angoniensis*	F	Kenya	Molo, 4 miles E, Nakuru district
SI437515	*Otomys angoniensis*	F	Kenya	Nakuru, 10 miles NE
SI318087	*Otomys angoniensis*	F	Kenya	Njoro
SI318084	*Otomys angoniensis*	F	Kenya	Njoro
FMNH174176	*Otomys angoniensis*	M	Tanzania	Kilimanjaro NP
FMNH48616	*Otomys angoniensis*	M	Tanzania	Mt Meru, E Crater
FMNH48613	*Otomys angoniensis*	M	Tanzania	Mt Meru, E Crater
TM5159	*Otomys anchietae*	F	Angola	Mombola
BM63.1124	*Otomys anchietae*	M	Angola	Alto Chicapa
BM92.1.9.12	*Otomys anchietae*	M	Angola	Alto Chicapa
BM63.1127	*Otomys anchietae*	F	Angola	Alto Chicapa
TM5160	*Otomys anchietae*	F	Angola	Mombola
BM63.1125	*Otomys anchietae*	M	Angola	Alto Chicapa
BM63.1126	*Otomys anchietae*	F	Angola	Alto Chicapa