Craniometric relationships between the Southern African Vlei rat, *Otomys irroratus* (Rodentia, Muridae, Otomyinae) and allied species from North of the Zambezi River

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Introduction

Fourteen species and two genera (*Parotomys* Thomas 1918 – two species, and *Otomys* Cuvier 1823 – 12 species) of laminate-toothed rats (Family Muridae; Subfamily Otomyinae) are currently recognized in Africa, although probably more unrecognized species occur as endemics associated with the isolated East African highlands and volcanoes (MUSSER and CARLETON, 1993). While the two recognized species of *Parotomys* are restricted to the arid and semi-arid regions of southern Africa, the genus *Otomys* includes 64 previously described forms, mostly tied to moist or montane habitats, and discontinuously distributed from the Cape to Mount Cameroun in the West and Ethiopia in the East (DENYS, 1989). Most species of *Otomys* have a uniform vole-like external appearance, with shaggy, dark-brown pelage, and short tail, making taxonomic determination difficult. Moreover, the taxonomy of the group is highly unstable due to variability in diagnostic characters, usually involving the number of laminae in M^3 and M_1, grooving of the incisors, shape of the nasal bone and shape of the petrotympanic foramen (ALLEN and LOVERIDGE, 1933; BOHMANN, 1952; DE GRAAFF, 1981; DIETERLEN and VAN DER STRAETEN, 1992; LAWRENCE and LOVERIDGE, 1953; MEESTER *et al.*, 1986; MISONNE, 1974; THOMAS, 1918).

While species of southern African *Otomys* can for the most part be objectively delimited on morphological, cytogenetic and biochemical grounds (CONTRAFATTO *et al.*, 1992a-c; MEESTER *et al.*, 1992; TAYLOR *et al.*, 1993), the same is not true for West, East and central African taxa (MUSSER and CARLETON, 1993). Critical to delimiting the final number of extant species of *Otomys* is resolving the species and geographical limits of a key southern African species, *O. irroratus* Brants 1827, in relation to several East and West African forms that have in the past been included in this species. PETTER (1982) included *anchietae* Bocage 1882 (which includes *occidentalis* Dieterlen and Van der Straeten 1992, *lacustris* Allen and Loveridge 1933, *barbouri* Lawrence and Loveridge 1953), *tropicalis* Thomas 1902, *typus* Heuglin 1877 and *laminatus* Thomas and Schwann 1905 within a highly polymorphic and widely distributed *O. irroratus* species-complex or "rassenkreis". MISONNE (1974) considered *tropicalis* and *irroratus* together as being possibly conspecific, but distinct from the other above-mentioned species. DIETERLEN and VAN DER STRAETEN (1992), although describing West African *occidentalis* as a distinct species allied to the "*anchietae* group", nevertheless retained *tropicalis* as a synonym of *irroratus*. These authors further recognized *lacustris* (from East Africa) and *barbouri* (from Mount Elgon) to be distinct from *anchietae* (from Angola). Members of the "*anchietae* group" (*anchietae, lacustris, barbouri* and *occidentalis*) are characterized by having five laminae in M_1, as opposed to four or less in other species (with the exception of *O. laminatus* which has 7). While recognizing *occidentalis* to be a good species, MUSSER and CARLETON (1993) retained *lacustris* and *barbouri* in *anchietae*. Based on allozyme and cytogenetic evidence, LAVRENCHENKO *et al.* (1997) suspected that two distinct species should be recognized within *O.* cf. *typus* from the Bale Mountains in Ethiopia.

This paper addresses questions of conspecificity between *O. irroratus* and allied forms, and among members of the "*anchietae* group", using both principal component analysis and discriminant functions analysis based on craniometric data. Since not all the relevant types have been included here (see Appendix), this study is not a final systematic revision of the group in question but rather an evaluation of craniometric relationships which should facilitate a complete systematic revision in the near future. We summarize patterns of variation in dental and cranial diagnostic characters across the subfamily Otomyinae, in order to integrate qualitative and quantitative data. THOMAS (1918) suggested that skull shape would be a more useful feature for separating species of *Otomys* than highly variable key characters such as laminae number. While the present study uses a "traditional" craniometric approach based on linear measurements, further studies in progress are investigating cranial shape relationships between otomyine rodents based on the more recent approach of geometric morphometrics (TAYLOR, KUMIRAI and CONTRAFATTO, unpubl. data).

Materials and methods

Material examined

Quantitative and qualitative cranial measurements were obtained for 285 specimens from all currently recognized species of otomyine rodents except *O. maximus* Roberts 1924 which is not recognized by some authors (e.g., MISONNE, 1974; MEESTER *et al.*, 1986). Skulls were loaned from the following institutions: Amathole Museum (King William's Town), Durban Natural Science Museum, Museum National d'Histoire Naturelle (Paris), and the Natural History Museum (London). Additionally, descriptions and measurements of type specimens of certain species were obtained from the literature, e.g. *O. occidentalis* (DIETERLEN and VAN DER STRAETEN, 1992; type from Staatliches Museum für Naturkunde, Stuttgart - SMNS), *O. lacustris* (ALLEN and LOVERIDGE, 1933; type from Museum of Comparative Zoology, Harvard - MCZ) and *O. barbouri* (LAWRENCE and

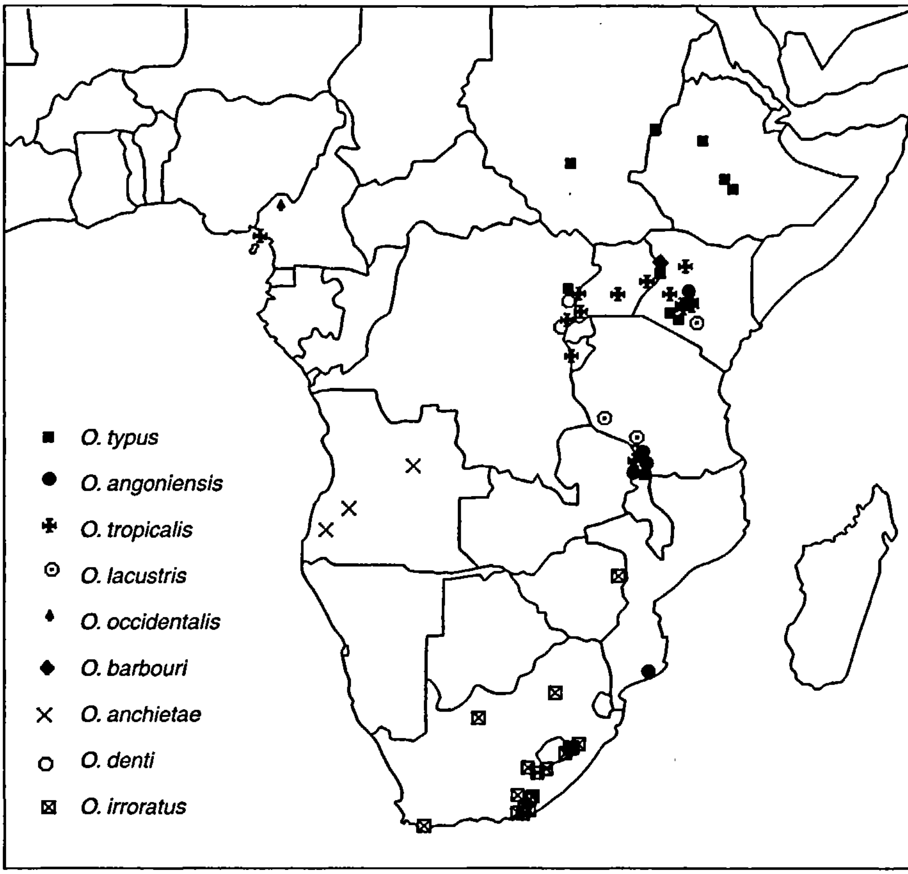


Figure 1
Map of Africa south of Sahara showing distribution of *Otomys irroratus* and related congeneric species occurring north of the Zambezi River, based on material examined.

LOVERIDGE, 1953; type from MCZ). The sample of *O. irroratus* ($n = 105$) was a representative subset of adult skulls (age class 4 and 5) from a larger sample used to analyse morphometric variation within this species (KUMIRAI, unpubl. data). The Appendix provides both a gazetteer of localities and a summary of material examined for each species. Fig. 1 shows the distribution of localities representing material examined for the several species of *Otomys* which were subjected to morphometric analysis, as outlined below.

Qualitative and quantitative measurements

The following qualitative cranial key characters were scored on 285 skulls representing 13 species of *Otomys*:

1) Number of laminae in M^3

2) Number of laminae in M_1

3) Angle of lateral edge of nasal bone at its point of anteriormost expansion – this was scored subjectively as being closest to 90°, 120° or 150°

4) Shape of petrotympanic foramen - slit-like or round

5) Grooving on lower incisors - absent (0), single groove (1), single groove with trace of second (1'), one deep and one faint groove (1+), or two deep grooves (2)

Using Mitutoyo digital calipers with 0.01 mm accuracy, twelve quantitative cranial measurements were taken on the same sample of skulls as mentioned above; however only data from seven species are analysed in the present study, representing southern African *O. irroratus* and extralimital species which have in the past been included in this species. Measurement details are as follows (based on TAYLOR *et al.*, 1993):

GLS - Greatest length of skull measured dorsally (A-B, fig. 2)

PL - Palatal length, from anterior edge of premaxillae to anteriormost point on posterior edge of palate (G-W, fig. 2)

APF - maximum length of anterior palatal foramen (Q-R, fig. 2)

NAW - Nasal width, greatest width across nasals (J-K, fig. 2)

ZYW - Zygomatic width, greatest distance between the outer margins of the zygomatic arches (E-F, fig. 2)

IOC - Interorbital constriction, least distance dorsally between the orbits (C, fig. 2)

BUL - Greatest length of bulla along the longitudinal axis (D, fig. 2)

BUW - Bulla diameter, greatest width of bulla at right angles to main axis of skull (H, fig. 2)

MXTRL - Maxillary tooth row length, distance from anterior edge of first maxillary tooth to posterior edge of last maxillary tooth (I-M, fig. 2)

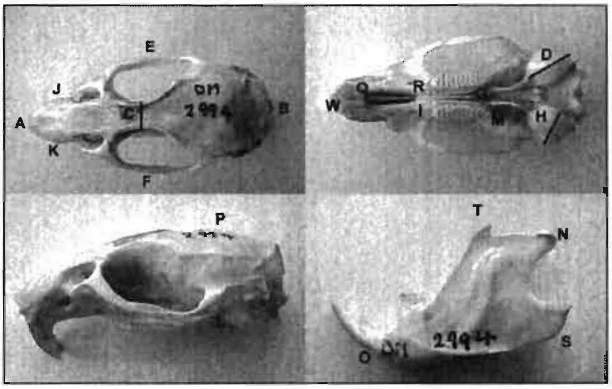


Figure 2
Skull of *Otomys* indicating reference points of 12 cranial variables measured from morphometric analysis. See text for descriptions.

BCD - Depth of braincase measured vertically at basioccipital (L-P, fig. 2)

GLM - Mandible length, greatest length of the mandible excluding teeth (N-O, fig. 2)

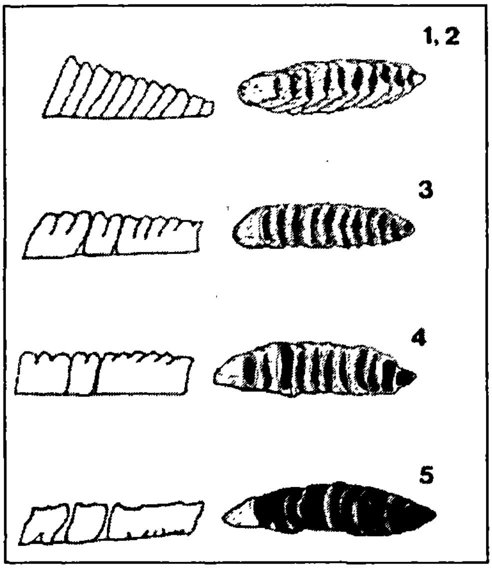
MDH - Mandible height from ventral surface of mandibular ramus to dorsal surface of coronoid process (S-T, fig. 2)

Age variation

Every skull was assigned to a relative age class based on skull size and shape, suture development and tooth wear as follows (after Taylor *et al.* 1993, fig. 3):

Class 1: Occlusal surface of maxillary tooth row sloping in lateral view (higher at M^1 than M^3), lamellae separate; braincase pear-shaped, smooth; tooth wear minimal, with dentine not exposed across full labio-lingual width of molars; fronto-parietal, naso-frontal, naso-maxillary, parieto-interparietal and interparieto-occipital sutures open, distinct; skull conspicuously small (condylobasal length < 30 mm).

Class 2: Occlusal surface of maxillary tooth row as above in lateral view, although one or two anterior lamellae may not be completely separated; braincase oval, interorbital region smooth or slightly ridged; tooth wear either as above, or dentine may be exposed across full labio-lingual width of molars; sutures open; skull noticeably larger (condylobasal length > 30 mm).



I Figure 3
Diagrammatic representation of lateral (left) and occlusal (right) views of upper toothrows of five recognized age classes of *Otomys*. See text for description of toothwear criteria for each class.

Class 3: Occlusal surface of maxillary tooth row almost horizontal in lateral view, molars clearly defined in lateral view but with lamellae of individual molars not fully separated (i.e. divisions extending to over half of the distance from the crown to the cingulum); braincase oval and conspicuously ridged with interorbital and occipital ridges; tooth wear moderate with dentine exposed across full occlusal width of molars, but with enamel faces of lamellae still visible in occlusal view; sutures distinct or becoming indistinct.

Class 4: Occlusal surface of maxillary tooth row horizontal in lateral view, divisions between lamellae extending only to less than half the distance from the crown to the cingulum; braincase oval, sharply ridged; toothwear moderate, with enamel faces of lamellae no longer clearly visible in occlusal view; sutures indistinct.

Class 5: Occlusal surface of maxillary tooth row horizontal, crown-cingulum height much reduced, lamellar divisions no longer visible in lateral view; braincase oval, very strongly ridged; tooth wear severe, with flat occlusal surface composed of exposed dentine and thin transverse enamel bridges, enamel side walls eroded; sutures indistinct or not visible.

Statistical analysis

Due to the broken nature of many skulls and the small sample sizes available for some of the more rarely collected species, principal component analysis of *O. irroratus* and six related East and West African forms (*anchietae, lacustris, barbouri, occidentalis, typus* and *tropicalis*) was performed using only five robust, functionally important and commonly used cranial variables: GLS, NAW, IOC, MXTRL and BUL. Nevertheless, for two-group discriminant analyses involving combinations of the above-mentioned species, in which statistical re-sampling was performed (n = 100 randomizations), 12 or 10 variables were included wherever sample sizes permitted. Multivariate craniometric analysis was restricted only to *O. irroratus* and the six species or forms which have in the past been included in this species.

For most of the species, small sample sizes prohibited detailed non-geographic analysis to investigate the effects of variation due to age and sexual dimorphism. However, a separate study of *O. irroratus* in the Western Cape Province of South Africa (TAYLOR *et al.*, 1993) revealed that, although males tend to have larger crania than females, these differences were generally non-significant, while age classes 3-5 could be considered "adult". Thus, in the present study, males and females were combined and age classes 1 and 2 were not considered for statistical analyses.

Complete discussions of multivariate procedures used in this study can be found in BLACKITH and REYMENT (1971), SNEATH and SOKAL (1973), PIMENTEL (1979), and NEFF and MARCUS (1980). Principal component analysis was performed using NTSYSpc Version 2.01h (ROHLF, 1997). Two-group discriminant analysis, with statistical re-sampling (n = 100 replications), was performed using the programme LINDA (LINear Discriminant Analysis) and Comparison of Multivariate Samples with Randomization Tests, version 5.12; CAVALCANTI, 1999). Hotelling's T-squared, and Wilks Lambda coefficients were calculated, and variance-ratio (F) tests and chi-squared tests respectively were used to test for significant differences between mean vectors.

Results and discussion

Qualitative characters

Table 1 summarises variation in dental and cranial key characters, based on the sample of 285 individuals. The number of laminae in M_1 varied from 3-4 (*Parotomys*) to 7 (*O. laminatus*), but was generally 4, with the exception of members of the "*anchietae* group" which typically have 5 (although this number varied from 4 to 6 in *anchietae*, and a single *O. barbouri* was found to have 4). Laminae number in M^3 varied from 4 (*Parotomys*) to 10 (*O. laminatus*), but was highly variable in both the "*anchietae* group" and *O. typus*. Within the "*anchietae* group", the modal number varied from 6 (*lacustris*) to 7 (*anchietae, barbouri*) to 8 (*occidentalis*), suggesting that this character might prove useful in the future for separating these forms. Within *O. typus* the number of laminae in M^3 appeared to vary geographically, with 6 laminae being recorded from Uganda, 7 from Kenya and Malawi, and 8 or 9 from Ethiopia. In a sample of *O.* cf. *typus* analysed from Bale Mountains in Ethiopia, LAVRENCHENKO *et al.* (1997) noted 6 laminae in M^3 of "*Otomys* sp. A" with a diploid chromosome number of 56, but 7-8 laminae in M^3 of "*Otomys* sp. B" ($2n = 57 - 58$).

DENYS (1989) surmised that a relatively low number of 5-6 laminae in M^3 was present in ancestral *Otomys* species, as evidenced by the extinct *O. gracilis* in South Africa (from 1-3.5 Myr deposits), and extinct *O. petteri* from East Africa (from 0.6 - 2 Myr deposits), with a subsequent trend towards an increasing number of laminae in time reflected in extant species. On the basis of a relatively low number of laminae (6), DENYS (1989) assumed *O. saundersiae* Roberts 1929 to be primitive to other extant species of this genus, while "*irroratus - tropicalis*" was said to have 7-8 laminae. Tabl. 2 shows that, while *O. tropicalis* has either 7 (73 individuals) or 8 (10 individuals) laminae, *O. irroratus* invariably possesses 6 (115 out of 116 individuals). Thus, M^3 laminae number appears to provide strong evidence for specific separation between *O. irroratus* and *O. tropicalis*, and *O. irroratus* appears more primitive than presumed by DENYS (1989).

The angle at which the anterior portion of the nasal joins the posterior is highly variable. In most species of *Otomys* the angle is close

	No. of laminae in lower M1					No. of laminae in upper M3							Nasal angle			Petrotympanic		No. grooves in lower incisor				
	3	4	5	6	7	4	5	6	7	8	9	10	90°	120°	150°	Hole	Slit	0	1	1'	1+	2
O. anchietae	-	1	2	4	-	-	-	1	4	1	-	-	-	6	-	5	-	-	4	1	-	-
**O. barbouri*	-	1	7	-	-	-	-	-	6	2	-	-	7	1	-	8	-	-	8	-	-	-
**O. lacustris*	-	-	4	-	-	-	-	3	1	-	-	-	1	3	-	4	-	-	4	-	-	-
O. occidentalis	-	-	7	-	-	-	-	-	2	5	-	-	-	-	-	-	-	-	6	-	-	-
O. angoniensis	-	10	-	-	-	-	-	2	8	-	-	-	3	4	3	-	6	-	-	5	1	-
O. denti	-	2	-	-	-	-	1	1	-	-	-	-	-	2	-	2	-	-	1	1	-	-
O. tropicalis	-	84	-	-	-	-	-	-	73	10	-	-	8	61	14	72	-	-	5	60	11	-
O. typus	-	38	-	-	-	-	-	4	9	15	10	-	32	6	-	36	-	-	-	1	-	28
O. irroratus	-	116	-	-	-	-	-	115	1	-	-	-	74	36	-	116	-	-	-	11	1	-
O. laminatus	-	-	-	-	1	-	-	-	-	-	-	1	1	-	-	1	-	-	-	1	-	-
O. saundersiae karoensis	-	5	-	-	-	-	-	5	-	-	-	-	-	5	-	5	-	-	1	4	-	-
O. unisulcatus	-	2	-	-	-	-	2	-	-	-	-	-	-	-	2	2	-	2	-	-	-	-
O. sloggetti	-	2	-	-	-	1	1	-	-	-	-	-	-	-	2	-	1	2	-	-	-	-
P. brantsii	-	2	-	-	-	3	-	-	-	-	-	-	-	-	3	-	-	1	1	-	-	-
P. littledalei	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-
O. gracilis (E)	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
O. petteri (E)	-	x	-	-	-	-	4%	90%	5%	-	-	-	-	-	-	-	-	-	-	x	-	-

Table 1
Table showing variation of craniodental qualitative characters in laminate-toothed rats of the genera *Otomys* and *Parotomys*, based on specimens examined (Appendix), and from Denys (1989) for the extinct (E) species. Forms marked with asterisks are currently included in the species, *O. anchietae*.

Variable	Species						
	O. irroratus (n=105)	*O. tropicalis* (n=52)	*O. typus* (n=19)	*O. anchietae* (n=5)	**O. barbouri* (n=8)	**O. lacustris* (n=3)	*O. occidentalis* (n=4)
GLS	41.0 ± 2.5 32.6 - 45.9	39.0 ± 2.7 29.0 - 43.5	39.1 ± 3.2 34.3 - 45.9	49.4 ± 3.1 46.2 - 52.8	36.6 ± 2.2 32.4 - 39.0	38.6 ± 1.6 36.8 - 39.9	34.9 ±1.9 32.7 - 36.9
BCD	12.1 ± 0.8 9.5 - 14.0	11.2 ± 0.6 9.2 - 12.4	11.4 ± 0.7 10.5 - 13.1	15.4 ± 1.1 14.6 - 16.6	11.3 ± 0.6 10.5 - 11.8	— (n=2) 10.8 - 12.0	— (n=1) 9.7
MDH	14.8 ± 1.2 10.6 - 17.6	13.5 ± 1.1 9.2 - 16.9	14.0 ±1.3 (25) 12.2 - 16.4	20.0 ± 0.9 (4) 18.9 - 20.9	12.8 ± 0.7 (5) 11.8 - 13.5	— (n=1) 14.6	— (n=1) 10.8
GLM	27.2 ± 2.1 21.7 - 31.5	24.9 ±1.5 20.5 - 28.7	25.6 ± 2.2 22.0 - 30.2	34.4 ± 2.5 31.8 - 37.5	24.4 ± 1.7 21.2 - 27.0	24.6 ± 2.0 22.3 - 25.8	— (n=1) 21.9
APF	7.6 ± 0.8 5.4 - 9.0	6.9 ±0.7 4.5 - 8.4	7.2 ± 0.7 5.8 - 8.6	8.4 ± 0.8 7.3 - 9.3	7.0 ± 0.6 5.9 - 7.7	7.3 ± 0.5 6.6 - 7.9	— (n=2) 5.7 - 6.9
MXTRL	9.7 ± 0.5 8.5 - 11.5	9.2 ± 0.4 8.4 - 10.4	9.6 ±1.0 8.1 - 11.6	12.0 ± 0.5 11.3 - 12.5	8.9 ± 0.2 8.6 - 9.3	8.8 ± 0.3 8.6 - 9.1	8.8 ± 0.5 8.4 - 9.6
NAW	8.0 ± 0.7 6.2 - 9.9	7.0 ± 0.6 4.8 - 7.9	7.0 ± 0.8 6.2 - 9.2	8.8 ± 0.6 8.1 - 9.6	6.6 ± 0.5 5.7 - 7.3	6.5 ± 0.4 6.0 - 6.8	6.2 ±0.2 6.0 - 6.6
IOC	4.6 ±0.2 4.1 - 5.1	4.5 ± 0.2 4.1 - 5.0	4.1 ± 0.3 3.7 - 4.7	5.5 ± 0.4 5.0 - 5.9	4.2 ± 0.3 3.6 - 4.6	4.3 ± 0.1 4.2 - 4.4	4.3 ±0.2 4.1 - 4.4
ZYW	20.5 ± 2.5 (n = 104) 16.8 - 24.1	19.0 ± 1.1 15.0 - 21.8	19.4 ± 1.7 (27) 15.8 - 22.8	26.5 ± 1.5 (4) 25.0 - 28.0	18.5 ±1.0 (10) 16.5 -19.7	— (n=1) 18.9	— (n=1) 17.5
PL	22.8 ± 1.8 18.1 - 27.6	20.7 ± 1.5 15.3 - 24.4	20.8 ± 1.9 17.4 - 24.9	27.1 ± 2.0 25.0 - 29.2	19.6 ± 1.7 16.7 - 21.7	20.2 ± 1.2 18.4 - 21.0	— (n=2) 18.2 - 18.7
BUL	7.0 ± 0.5 5.9 - 8.7	7.6 ± 0.5 6.5 - 9.7	7.6 ± 0.6 6.8 - 8.5	8.8 ± 0.6 7.9 - 9.3	6.7 ± 0.3 6.1 - 7.1	7.0 ± 0.8 6.6 - 7.9	7.1 ± 0.7 6.1 - 7.5
BUW	6.9 ± 0.5 5.8 - 8.4	7.5 ± 0.7 5.5 - 8.8	8.0 ± 0.6 6.8 - 8.9	10.1 ± 0.6 9.2 - 10.9	7.2 ± 0.6 6.1 - 8.0	— (n=2) 7.1 - 8.2	- (n=2) 6.2 - 6.6

Table 2
Summary statistics for craniometric variables in seven species of *Otomys*.
Values represent means ± standard deviation, followed by minimum and maximum values.
Forms marked with asterisks are currently included in the species *O. anchietae*.
Where sample size varies from the value shown under each species name, this is indicated in parentheses.

to 90° or 120°. However, this angle is more obtuse (150°) in species of *Parotomys*, and in *O. unisulcatus* Cuvier 1829, *O. sloggetti* Thomas 1902, and *O. saundersiae karoensis*. In 17% of *O. tropicalis*, the nasal angle is 150°, while the modal character state for this species is 120°, as opposed to 90° in *O. irroratus*, providing further support for specific separation of these two species (tabl. 2). DIETERLEN and VAN DER STRAETEN (1992) distinguished *O. occidentalis*, *barbouri* and *lacustris* from "*irroratus*" (= *tropicalis*), based on a more obtuse nasal angle in the latter.

The shape of the petrotympanic foramen is less variable than dental characters and nasal angle, being slit-like in *O. angoniensis* and *O. sloggetti* and consistently round in all other species.

Grooving of lower incisors is absent in *Parotomys* and two species of *Otomys*, *O. unisulcatus* and *O. sloggetti*. Cladistic analyses of allozyme (TAYLOR *et al.*, 1989) and immunoblot data (CONTRAFATTO *et al.*, 1994) provide further support for this clade, and hence for the paraphyly of the genus *Otomys* as currently understood. The presence of two distinct grooves in the lower incisors is diagnostic for *O. typus*. In the present study, this character was relatively consistent, although one individual classified as *O. typus* had an indistinct second groove. Members of the *O. anchietae* group are distinctive in showing generally no trace of a second groove in the lower incisor, a key feature normally used in the identification of *O. denti* Thomas 1906 (MISONNE, 1974), but found in only one of two individuals of *O. denti* examined here (tabl. 1).

Multivariate analysis of craniometric characters

Based on principal component analysis of five cranial variables (fig. 4), the large-skulled *O. anchietae* (see tabl. 2) separates completely from all other species, including other much smaller members of the "*anchietae*-group", *barbouri*, *lacustris* and *occidentalis*. *Otomys irroratus* shows limited or no overlap with the other species with which it has previously been included. Based on variable loadings on each of the

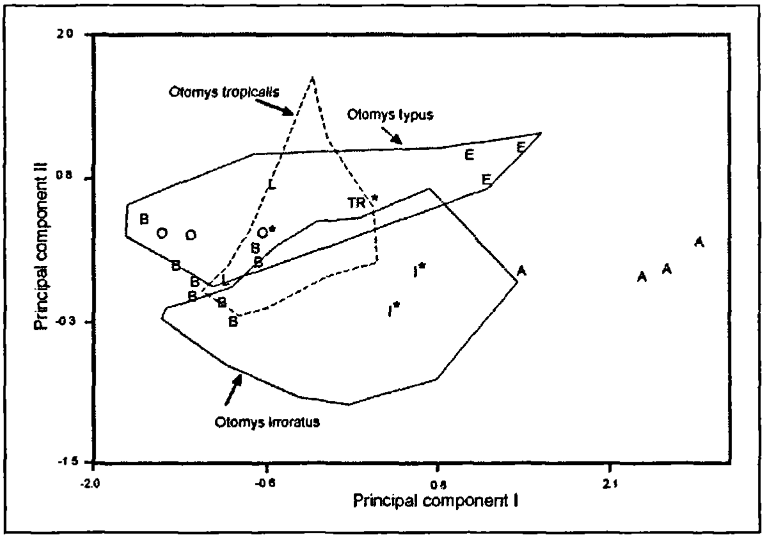


Figure 4
Principal component analysis of five cranial variables in 181 specimens representing seven species of *Otomys*. The first component explained 57.9% of variation, the second 19.2%. Polygons enclose all individuals within the three large species-samples, *O. irroratus*, *O. tropicalis* and *O. typus*. Type specimens of *O. irroratus coensis* from Kuruman, South Africa (I), *O. tropicalis* from Mount Kenya (TR), and *O. occidentalis* from Mount Oku, Cameroon (measurements from literature) are indicated by asterisks. Individuals of the 5-laminate forms are indicated as "A" (*anchietae*), "B" (*barbouri*), "L" (*lacustris*), and "O" (*occidentalis*). Outlying (large) specimens of *O. typus* from Lake Tana in Ethiopia are indicated by "E".

first three principal components (tabl. 3), which cumulatively explain 91.5% of the variation, the first component is influenced by overall size (positive high loadings for all variables), while the second component is a "shape axis" contrasting bulla length with nasal and interorbital widths (high scores represent individuals having relatively inflated bulla and narrow nasals and interorbital region). The third component contrasts interorbital constriction (negative) with nasal width; since it explains only 14.4% of the variation, it is not regarded further. Clearly, *O. irroratus* is distinguished mostly from its allies on the basis of the second principal component, in having proportionately

Variable	PC 1	PC 2	PC 3
Greatest skull length (GLS)	0.93	0.06	0.14
Maxillary toothrow length (MXTRL)	0.89	0.07	0.14
Nasal width (NAW)	0.83	– 0.30	0.33
Interorbital constriction (IOC)	0.54	– 0.47	– 0.69
Bulla length (BUL)	0.50	0.80	– 0.30

Table 3
Standardized coefficients from five-variable, principal components analysis of seven species of laminate-toothed rats, *Otomys*. The first three components explained 57.9%, 19.2% and 14.4% respectively of the total variation.

smaller bullae and wider nasals and interorbital region. The extreme range in size variation (first component) in *O. typus* is due to the presence of three outlying, large specimens from Lake Tana in Ethiopia (marked as "E" in fig. 2). As noted above, Ethiopian specimens typically have nine laminae in M^3, as opposed to 6 to 8 further south, confirming the observation of larger size. It is likely that this species probably represents a composite of two or more species. Generally, individuals of this species plot towards the left of the first component (small skulls) and higher on the second component (larger bullae and narrower nasals and interorbital region).

Two-group discriminant analyses involving the same species as mentioned above generally resulted in limited overlap (low percentage of misclassifications) and significant differences between species mean vectors (based on both Hotelling's T-squared and Wilk's Lamda tests) (tabl. 4).

A 12-variable discriminant analysis of *O. irroratus* and *O. tropicalis* resulted in misclassification of 15.4% of *O. irroratus* and only 3.8% of *O. tropicalis*. The three variables showing the greatest percentage contribution to the total multivariate distance (i.e. greatest relative importance) were palatal length (38%), and bulla length (32%) and width (13%). From summary data (tabl. 2), *O. tropicalis* tends to be slightly smaller than *O. irroratus* in most cranial dimensions but to have disproportionately larger bullae and a disproportionately shortened palate.

Species	Number of variables	Hotelling T-squared	Wilks Lambda	% mis-classified	Variables contributing strongly (> 20% contribution)
irroratus (n = 105) vs. *tropicalis* (n = 52)	12	259.9**	0.37**	15.4; 3.8	PL, BUL
irroratus (n = 105) vs. *typus* (n = 19)	10	237.8**	0.34**	2.9; 5.3	BUW, PL, IOC
irroratus (n = 105) vs. *anchietae* (n = 5)	10	382.7**	0.22**	0.0; 0.0	BUW, GLM, MXTRL
irroratus (n = 105) vs. *barbouri* (n = 8)	10	102.9**	0.52**	1.9; 0.0	GLS, NAW
anchietae (n = 5) vs. *occidentalis* (n = 4)	5	102.2	0.06*	0.0; 0.0	MXTRL, NAW
anchietae (n = 5) vs. *barbouri* (n = 8)	10	1903*	0.01**	0.0;0.0	GLS, GLM
occidentalis (n = 4) vs. *barbouri* (n = 12)	5	10.8	0.56	25.0; 16.7	BUL, NAW
barbouri (n = 12) vs. *lacustris* (n = 3)	5	28.2*	0.32*	0.0; 0.0	GLS
tropicalis (n = 52) vs. *typus* (n = 19)	10	65.9**	0.51**	11.5; 21.1	IOC, APF

I Table 4
Results of selected two-group discriminant analyses, with re-sampling (*n* = 100 randomizations), to test conspecificity between *O. irroratus* and related species-groups, and between members of the "*anchietae* - group". Asterisks indicate statistical significance (** – $p < 0.01$; * – $p < 0.05$)) of Hotelling T-squared and Wilks Lambda coefficients based on variance ratio (F) and Chi-squared tests respectively.

A 10-variable discriminant analysis of *O. irroratus* and *O. typus* resulted in misclassification of 2.9% of *O. irroratus* and 5.3% of *O. typus* (tabl. 4). Bulla width contributed most strongly to this separation (41%), followed by palatal length (26.2%) and interorbital constriction (25.7%). As also reported for *O. tropicalis*, *O. typus* has a cranium which is smaller in overall size compared to *O. irroratus*, but with disproportionately inflated bullae and shortened palate (tabl. 2). As would be predicted from the above, *O. tropicalis* and

O. typus show greater morphometric overlap (11.5% of *O. tropicalis* and 21.1% of *O. typus* misclassified) than when either species is compared with *O. irroratus*. However, craniometric differences between these two species are still significantly different in multivariate space (tabl. 4).

As was evidenced from the principal component analysis (fig. 2), the much larger (tabl. 2) *O. anchietae* separates clearly in two-group discriminant analysis from both *O. irroratus* (0% misclassified), as well as additional forms previously included in the "*anchietae*-group" such as *O. occidentalis* and *O. barbouri* (0% misclassified; tabl. 4). Greater morphometric overlap occurs between the smaller members of the "*anchietae*-group" (*barbouri, lacustris, occidentalis*). For example, differences between mean vectors of *O. occidentalis* and *O. barbouri* are not statistically significant ($p > 0.05$), and 18.8% of individuals are misclassified.

Conclusions

The hypothesis put forward by PETTER (1982), that *O. irroratus* comprises a highly polymorphic species with Pan African distribution, including the forms *anchietae, occidentalis, lacustris, barbouri, tropicalis,* and *typus,* can be refuted based on the craniometric results presented here. *Otomys irroratus* can be reliably separated from all of the above East and West African forms, using discriminant analysis of cranial variables. Furthermore, in spite of the plasticity of some cranial and dental qualitative characters, *O. irroratus* can be convincingly separated from *O. tropicalis* based on the consistent occurrence of 6 laminae in M^3 in *O. irroratus*, as opposed to 7 or 8 in *O. tropicalis*, as well as by the acute angle of the nasal bone in *O. irroratus*, compared to a much less acute angle in *O. tropicalis* (see also THOMAS, 1918). *Otomys typus* can be clearly separated from all other species, including *O. irroratus*, due to the unique and consistent presence of two grooves in the upper incisor (present in 28 out of 29 skulls examined), thus validating the usefulness of this key character for this species.

The situation regarding the 5-laminate-M_1 "*anchietae* - group" (*anchietae, barbouri, occidentalis* and *lacustris*) is less clearcut. While *anchietae* from Angola separates very clearly from all other otomyines in its much larger cranial size (GLS > 46 mm), the smaller forms (hereafter termed "*lacustris* - group") show varying degrees of morphometric overlap. These forms tend to be restricted to isolated mountain chains, e.g. *occidentalis* to the Gotel Mts and mont Oku in West Africa, *O. barbouri* to Mount Elgon in Uganda/Kenya, and *O. lacustris* to the Uzungwe Mts, Ukinga Mts, Ufipa Plateau and Poroto Mts in Tanzania, and the Aberdare Range in Kenya. Based on the information presented above, and given the disjunct nature of the distribution of these taxa, it is best to follow the example of VAN DER STRAETEN and DIETERLEN (1992), and to recognize *anchietae, barbouri, lacustris* and *occidentalis* as full species pending a thorough review.

Further studies including all the relevant type specimens, and using morphometric, cytogenetic and molecular characters, are required before the correct number of species of *Otomys* can be finally established. Cytogenetic, biochemical or molecular data are available for *O. barbouri, O. tropicalis*, and *O. typus* from Mount Elgon (TAYLOR, KUMIRAI, CONTRAFATTO and CAMPBELL, unpubl. data), *O. typus* from Ethiopia (LAVRENCHENKO *et al.*, 1997), and many of the southern African otomyine taxa (CONTRAFATTO *et al.*, 1992a-c; MEESTER *et al.*, 1992; RAMBAU *et al.*, 1997; ROBINSON and ELDER, 1987; S. MAREE in litt.), but are urgently required for most species occurring north of the Zambesi River.

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Appendix

Gazetteer of localities and summary of material examined from nine species of *Otomys*. Type localities are indicated; in most case type specimens were examined in the collection of the Natural History Museum, London. Location, descriptions and/or measurements of type specimens of *O. occidentalis*, *O. lacustris* and *O. barbouri* were obtained from the literature (DIETERLEN and VAN DER STRAETEN, 1992; ALLEN and LOVERIDGE, 1933; and LAWRENCE and LOVERIDGE 1953, respectively). Acronyms for museums are explained in the text. Acronyms for South African province names as follows: ECP (Eastern Cape), GTP (Gauteng), KZN (KwaZulu-Natal), NWP (Northwest).

Species	Locality	Coordinates	Specimens examined
Otomys anchietae	Angola: Alto Chicapa	10° 56'S 19° 12'E	BM (5)
Otomys anchietae	Angola: Caconda (TYPE)	13° 42; S 15° 03'E	? Not seen
Otomys anchietae	Angola: Huila (incl. P. Campana?)	15° 06'S 13° 33'E	MNHN (2)
Otomys angoniensis	Kenya: Menengai (East) – 2333 m	0° 12'S 36° 46'E	MNHN (3)
Otomys angoniensis	Malawi: Nthungwa	11° 42'S 33° 50'E	BM (1)
Otomys angoniensis nyikae	Malawi: Nyika Plateau (TYPE)	10° 6'S 33° 42'E	BM (1)
Otomys angoniensis	Malawi: Matipa Forest, 2100 m (= M'Kombhuie) (TYPE)	9° 39'S 33° 26'E	BM (2)
Otomys angoniensis rowleyi	Mozambique: « Coguus » (= Coguna), Inhambane (TYPE)	24° 23'S 34° 32'E	BM (1)*
Otomys barbouri	Uganda: Kaburomi, Mt Elgon, 3150 m (TYPE)	1° 14'N 34° 31'E	MCZ—not seen
Otomys barbouri	Uganda: Mount Elgon: Mission Delomo	1° 10'N 34° 29'E	MNHN (8)
Otomys barbouri	Uganda: Mude Cave Camp, Mt Elgon, 3600 m	1° 10'N 34° 29'E	DM (5)
Otomys denti	Uganda: Ruwenzori E, Mubuku Valley, 1800 m (TYPE)	0° 22'N 30° 02'E	BM (1)
Otomys denti kempi	Rwanda: Burunga, Mt Mikeno, 1800 m (TYPE)	1° 29'S 29° 21'E	BM (1)
Otomys irroratus	South Africa: ECP: Albany, Grahamstown	33° 18'S 26° 30'E	KM (8), DM (1)
Otomys irroratus	South Africa: ECP: 37.5 km west of Alexandria	33° 40'S 26° 00'E	KM (4)
Otomys irroratus	South Africa: ECP: 2.1 km west of Alexandria	33° 45'S 26° 23'E	KM (4)
Otomys irroratus	South Africa: ECP: Alice	32° 47'S 26° 50'E	DM (5), KM (1)
Otomys irroratus	South Africa: ECP: Aliwal North	30° 42'S 26° 42'E	KM (2)
Otomys irroratus	South Africa: ECP: Barkly East, Tushielaw	30° 47'S 27° 57'E	KM (1)
Otomys irroratus	South Africa: ECP: 23 km west of Barkly	31° 02'S 27° 21'E	KM (1)
Otomys irroratus	South Africa: ECP: Bathurst State Forest	33° 32'S 26° 47'E	KM (5)
Otomys irroratus	South Africa: ECP: Bedford, Lyndock	32° 31'S 26° 01'E	KM (1)

Otomys irroratus	South Africa: ECP: 8.1 km west of Bredasdorp	34° 32'S 19° 57'E	KM (2)
Otomys irroratus	South Africa: ECP: Hogsback	32° 36'S 27° 01'E	DM (8)
Otomys irroratus	South Africa: GTP: Rietvlei Nature Reserve	25° 49'S 28° 32'E	DM (2)
Otomys irroratus	South Africa: KZN: Garden Castle Nature Reserve	29° 45'S 29° 13'E	DM (3)
Otomys irroratus	South Africa: KZN: Kamberg Nature Reserve	29° 24'S 29° 40'E	DM (5)
Otomys irroratus	South Africa: KZN: Karkloof Forest	29° 10'S 30° 05'E	DM (37)
Otomys irroratus	South Africa: KZN: Loteni Nature Reserve	29° 27'S 29° 32'E	DM (3)
Otomys irroratus	South Africa: NWP: Kuruman	27° 27'S 23° 26'E	DM (5)
Otomys irroratus	Zimbabwe: Nyanga Mts	18° 12'S 32° 40'E	KM (10)
Otomys lacustris	Kenya: Aberdares	0° 20'S 36° 37'E	BM (1)
Otomys lacustris	Tanzania: Madehani, Ukinga Mts (TYPE)	9° 20'S 34° 01'E	*MCZ—not seen*
Otomys lacustris	Tanzania: Mbizi Forest, Ufipa Plateau	7° 52'S 31° 43'E	BM (3)
Otomys lacustris	Tanzania: Poroto Mts, E. of Mbeya	9° 00'S 33° 44'E	BM (1)
Otomys occidentalis	Cameroon: Mt Oku, 2700-2900m (TYPE)	6° 12'N 10° 31'E	SMNS—not seen, MNHN (3)
Otomys tropicalis	Burundi: Tora	3° 42'S 29° 33'E	MNHN (45)
Otomys tropicalis	Burundi: Ntentamaza	?	MNHN (12)
Otomys tropicalis	Kenya: Aberdares	0° 20'S 36° 37'E	BM (5)
Otomys tropicalis nubilis	Kenya: Jambeni (TYPE)	0° 20'N 35° 50'E	BM (1)
Otomys tropicalis	Kenya: Kangaita, 6mi N Kerugoy	0° 25'S 37° 15'E	BM (4)
Otomys tropicalis	Kenya: Mt Kenya, W slope, 3000 m (TYPE)	0° 10'S 37° 10'E	BM (1)
Otomys tropicalis	Kenya: Mt Kinangop, 2700 m	0° 37'S 36° 42'E	MNHN (1)
Otomys tropicalis	Kenya: Mt Kenya, 4000 m	0° 10'S 37° 10'E	MNHN (1)
Otomys tropicalis vivax	Kenya: Mt Nyiru (TYPE)	2° 10'N 36° 50'E	BM (1)
Otomys tropicalis	Kenya: Solai, Mt Kenya	0° 05'S 37° 14'E	BM (3)
Otomys tropicalis	Malawi: Nyika Plateau	10° 36'S 33° 42'E	BM (1)
Otomys tropicalis burtoni	Nigeria: Onyanga, E. Mt Cameroon (TYPE)	4° 14'N 9° 10'E	BM (1)
Otomys tropicalis	Uganda: Bumasola, Mt Elgon	1° 11'N 34° 23'E	DM (1)
Otomys tropicalis	Uganda: Gitebe	1° 21'S 29° 15'E	MNHN (1)
Otomys tropicalis	Uganda: Kagambah, 1600 m	0° 49'S 30° 10'E	BM (1)
Otomys tropicalis	Uganda: Kampala	0° 19'N 32° 34'E	MNHN (1)
Otomys tropicalis	Uganda: Ruwenzori	0° 22'N 30° 02'E	MNHN (1)
Otomys typus	Ethiopia: Arussl, Albasso	7° 49'N 39° 13'E	BM (2)
Otomys typus fortior	Ethiopia: Dangila, Lk Tana (TYPE)	11° 17'N 34° 56'E	BM (11)
Otomys typus	Ethiopia: Dinsho	7° 06'N 39° 46'E	MNHN (11)
Otomys typus	Ethiopia: Gojjam, Debra Marcos	10° 20'N 37° 42'E	BM (1)
Otomys typus	Ethiopia: Shoa Province (TYPE)	9° 00'N 29° 30'E	?—not seen
Otomys typus thomasi	Kenya: Mt Kinangop, Aberdares (TYPE)	0° 37'S 36° 42'E	BM (1)
Otomys typus percivali	Kenya: Naivasha (TYPE)	0° 43'S 36° 26'E	BM (2)
Otomys typus jacksoni	Kenya/Uganda: Mt Elgon, 3960 m (TYPE)	1° 10'N 34° 29'E	BM (1)
Otomys typus uzungwensis	Malawi: Chelinda, Nyika Plateau (TYPE)	10° 36'S 33° 48'E	BM (3)
Otomys typus	Uganda: Mude Cave Camp, Mt Elgon, 3600 m	1° 10'N 34° 29'E	DM (1)
Otomys typus dartmouthi	Uganda: Ruwenzori East, 3750 m (TYPE)	0° 22'N 30° 00'E	BM (3)