

Craniometric relationships

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 (MUSSEY 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, MUSSEY and CARLETON (1993) retained *lacustris* and *barbouri* in *anchietae*. Based on allozyme and cytogenetic evidence, LAVRENCHEKOV *et al.* (1997) suspected that two distinct species should be recognized within *O. cf. typus* from the Bale Mountains in Ethiopia.

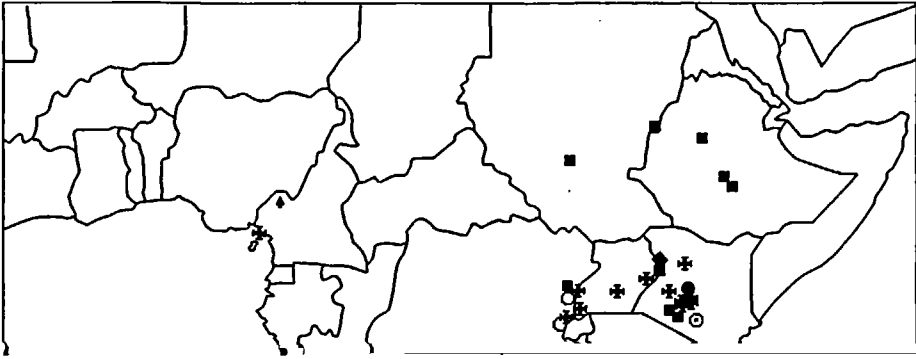
This paper addresses questions of conspecificity between *O. irrortatus* and allied forms, and among members of the “*anchietae* group”, using both principal component analysis and discriminant functions analysis based on craniometric data. Since not all the relevant types have been included here (see 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



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 anal

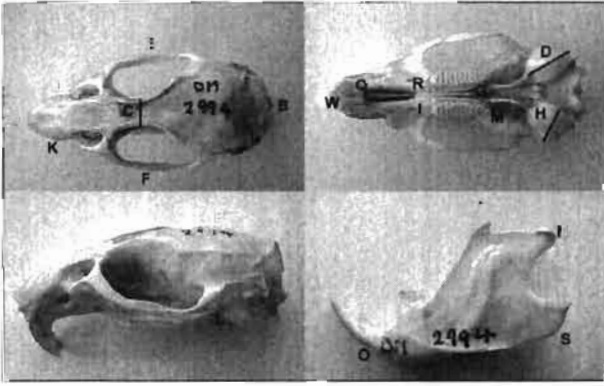




Figure 3
Diagrammatic
representation of lateral

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

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 (*anchi-*

etae, 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, LAVRENCENKO *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			Petrotympic		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
<i>O. anchietae</i>	-	1	2	4	-	-	-	1	4	1	-	-	-	6	-	5	-	-	4	1	-	-
* <i>O. barbouri</i>	-	1	7	-	-	-	-	-	6	2	-	-	7	1	-	8	-	-	8	-	-	-
* <i>O. leucurus</i>	-	-	4	-	-	-	-	3	1	-	-	-	1	3	-	4	-	-	4	-	-	-
<i>O. occidentalis</i>	-	-	7	-	-	-	-	-	2	5	-	-	-	-	-	-	-	-	6	-	-	-
<i>O. angoniensis</i>	-	10	-	-	-	-	-	2	8	-	-	-	3	4	3	-	6	-	-	5	1	-
<i>O. denti</i>	-	2	-	-	-	-	1	1	-	-	-	-	-	2	-	2	-	-	1	1	-	-
<i>O. tropicalis</i>	-	64	-	-	-	-	-	-	73	10	-	-	8	61	14	72	-	-	5	60	11	-
<i>O. typus</i>	-	38	-	-	-	-	-	4	9	15	10	-	32	6	-	36	-	-	-	1	-	28
<i>O. irroratus</i>	-	116	-	-	-	-	-	115	1	-	-	-	74	36	-	116	-	-	-	11	1	-
<i>O. laminatus</i>	-	-	-	-	1	-	-	-	-	-	1	-	1	-	-	1	-	-	-	1	-	-
<i>O. saundersae keroensis</i>	-	5	-	-	-	-	-	5	-	-	-	-	-	5	-	5	-	-	1	4	-	-
<i>O. unisulcatus</i>	-	2	-	-	-	-	2	-	-	-	-	-	-	-	2	2	-	2	-	-	-	-
<i>O. sloggettii</i>	-	2	-	-	-	1	1	-	-	-	-	-	-	-	2	-	1	2	-	-	-	-
<i>P. brantsii</i>	-	2	-	-	-	3	-	-	-	-	-	-	-	-	3	-	-	1	1	-	-	-
<i>P. littledalei</i>	1	-	-	-	-	1	-	-	-	-	-	-	-	-	1	1	-	1	-	-	-	-
<i>O. gracilis</i> (E)	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>O. petterii</i> (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						
	<i>O. irroratus</i> (n=105)	<i>O. tropicalis</i> (n=52)	<i>O. typos</i> (n=19)	<i>O. anchietae</i> (n=5)	* <i>O. barbouri</i> (n=8)	* <i>O. lacustris</i> (n=3)	<i>O. occidentalis</i> (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

Values represent means ± standard deviation, followed by minimum and maximum values. Forms marked with asterisks are currently included.

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

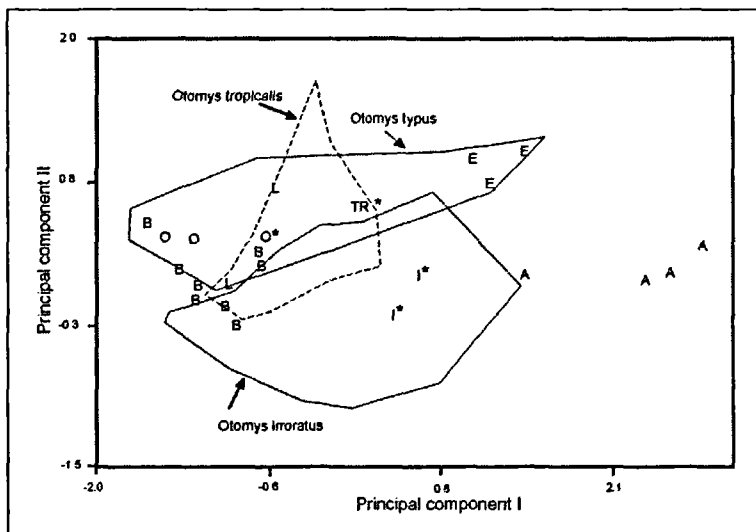


Figure 4

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".

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 M³, 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 Lambda 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)
<i>irroratus</i> (n = 105) vs. <i>tropicalis</i> (n = 52)	12	259.9**	0.37**	15.4; 3.8	PL, BUL
<i>irroratus</i> (n = 105) vs. <i>typus</i> (n = 19)	10	237.8**	0.34**	2.9; 5.3	BUW, PL, IOC
<i>irroratus</i> (n = 105) vs. <i>anchietae</i> (n = 5)	10	382.7**	0.22**	0.0; 0.0	BUW, GLM, MXTRL
<i>irroratus</i> (n = 105) vs. <i>barbouri</i> (n = 8)	10	102.9**	0.52**	1.9; 0.0	GLS, NAW
<i>anchietae</i> (n = 5) vs. <i>occidentalis</i> (n = 4)	5	102.2	0.06*	0.0; 0.0	MXTRL, NAW
<i>anchietae</i> (n = 5) vs. <i>barbouri</i> (n = 8)	10	1903*	0.01**	0.0; 0.0	GLS, GLM
<i>occidentalis</i> (n = 4) vs. <i>barbouri</i> (n = 12)	5	10.8	0.56	25.0; 16.7	BUL, NAW
<i>barbouri</i> (n = 12) vs. <i>lacustris</i> (n = 3)	5	28.2*	0.32*	0.0; 0.0	GLS
<i>tropicalis</i> (n = 52) vs. <i>typus</i> (n = 19)	10	65.9**	0.51**	11.5; 21.1	IOC, APF

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

The situation regarding the 5-laminate-M₁ “*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 Gotele 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

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I 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).

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