

The status of *Otomys orestes dollmani* Heller, 1912 (Muridae: Otomyinae), a rodent described from the Mathews Range, central Kenya

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Abstract.—Morphological and morphometric comparisons of *Otomys orestes dollmani*, known only from Mount Gargues in the Mathews Range, central Kenya, indicate that the taxon is a valid species distinct from other African forms under which it has been previously synonymized (*O. irroratus*, *O. orestes*, *O. tropicalis*). Based also on these comparisons, the morphological recognition and distribution of *O. orestes* (including *thomasi* Osgood) are further clarified in relation to *O. tropicalis* (including *elgonis* Wroughton) in Kenyan mountains and *O. typus* proper in Ethiopian highlands; another taxon relegated to junior synonymy within *O. typus*, *O. uzunguensis* Lawrence and Loveridge from south-central Tanzania, is resurrected to species. Certain traditional characters used in *Otomys* taxonomy, in particular molar lamination, demonstrate conservative patterns of variation that complement spatial structure derived from morphometric analyses of craniometric data and that vindicate their continued utility in delimiting species. We argue that uncritical emphasis of polytypic species, applied following the biological species concept during the latter 1900s, has led to chronic underestimation of species diversity of *Otomys* confined to the Afromontane Biotic Region in eastern Africa, in particular those populations that inhabit afroalpine environments.

Vlei or laminate-toothed rats of the genus *Otomys* (Muroidea: Muridae) constitute a distinctive morphological and phylogenetic radiation indigenous to the savannas and highlands within Sub-Saharan Africa (Bohmann 1952, Carleton & Musser 1984, Watts & Baverstock 1995, Ducroz et al. 2001, Taylor et al. 2004a). Since the circumscription of the group as a suprageneric taxon (Otomyinae Thomas, 1897), the number of *Otomys* (*sensu lato*) considered to be valid species has vacillated greatly, ranging from 30 (Ellerman 1941) to as few as 8 (Petter 1982) but usually around 12–14 (Misonne 1974,

Honacki et al. 1982, Corbet & Hill 1980, 1986, 1991; Musser & Carleton 1993). Musser & Carleton (2005) recently acknowledged 23 species. In the most considered revisionary study attempted to date, Bohmann (1952) recognized only 11 species, most of them containing from 3 to 5 well-marked subspecies and the exceptionally polymorphic *O. irroratus* embracing 23 geographic races. Much of the indecision over specific diversity has involved populations distributed across eastern African mountains north of the Zambezi River—from the Nyika Plateau and Eastern Arc Mountains, through the ranges and volcanoes fronting the Western and Eastern Rift Valleys, to the Ethiopian Highlands. Within this region,

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named forms have been variously and inconsistently treated as subspecies of *O. irroratus*, *O. tropicalis*, or *O. typus*.

The present study focuses on one such geographically localized population, *Otomys orestes dollmani* Heller (1912), described from Mount Gargues in the Mathews Range, a small and relatively low-elevation range lying to the north of Mount Kenya in central Kenya (Fig. 1). Following its description, *dollmani* has been sequentially referred to *O. orestes* (Dollman 1915, Allen 1939, Ellerman 1941), *O. irroratus* (Bohmann 1952), or *O. tropicalis* (Misonne 1974, Musser & Carleton 1993). Early on, however, Hollister (1919:148) had pointedly raised *dollmani* to species until "actual intergrading specimens are found," a pragmatic viewpoint endorsed by Musser & Carleton (2005). Here, we consolidate morphological and morphometric evidence that decidedly supports the last interpretation.

Materials and Methods

Specimens reported herein consist principally of skins with their associated skulls and are contained in the following North American museum collections: Carnegie Museum of Natural History, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University (MCZ); and the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM, formerly U.S. National Museum).

Relative age was crudely assessed for every specimen examined based on tooth-wear stages, employing a combination of molar eruption and degree of molar abrasion to identify four categories (juveniles, young adult, full adult, old adult). In view of the hypsodont molars characteristic of *Otomys*, we used the appearance of the basal crown-root junction to gauge the degree of molar eruption,

especially the last emerging M3. This junction marks the border of the glossy white enamel of the crown and dull white cementum of the root and is visible as a faint longitudinal line along the base of the tooth (in lateral view). Those individuals whose molars were incompletely erupted, such that the line of the crown-root junction was visible on only the M1 or M1–2, were categorized as juveniles. Adult specimens were identified by the visibility on all molars of the crown-root line, which initially appears approximately even with the maxillary alveoli (young adults); by this growth stage, the occlusal surface of the molar row approximates a horizontal plane. With advancing wear, the crown-root line is progressively displaced above the plane of the maxillary bone, crown height is correspondingly diminished, and dentinal cores of the individual laminae progressively expand in width and length (full and old adults). Our juvenile tooth-wear stage essentially concurs with age classes 1 and 2 as defined by Taylor & Kumirai (2001), and the young, full, and old adult wear stages to their age classes 3, 4, and 5, respectively.

Specimens of *Otomys*, especially those originating from older historically important surveys, complicate study of their craniometric variation because a substantial percentage of skulls encountered in museum collections are damaged. Commonly, nasal bones are dislodged, zygomatic arches broken, or the braincase fractured. Hence, we have taken a robust approach to our definition of operational taxonomic units (OTUs), identifying analytical samples that correspond to mountains or mountain ranges instead of single localities and precise altitudes. Further, rather than eliminate those variables taken on frequently broken cranial parts in order to amplify specimen numbers for multivariate analyses, we have elected to accept smaller sample sizes to capture more fully size and shape differences.

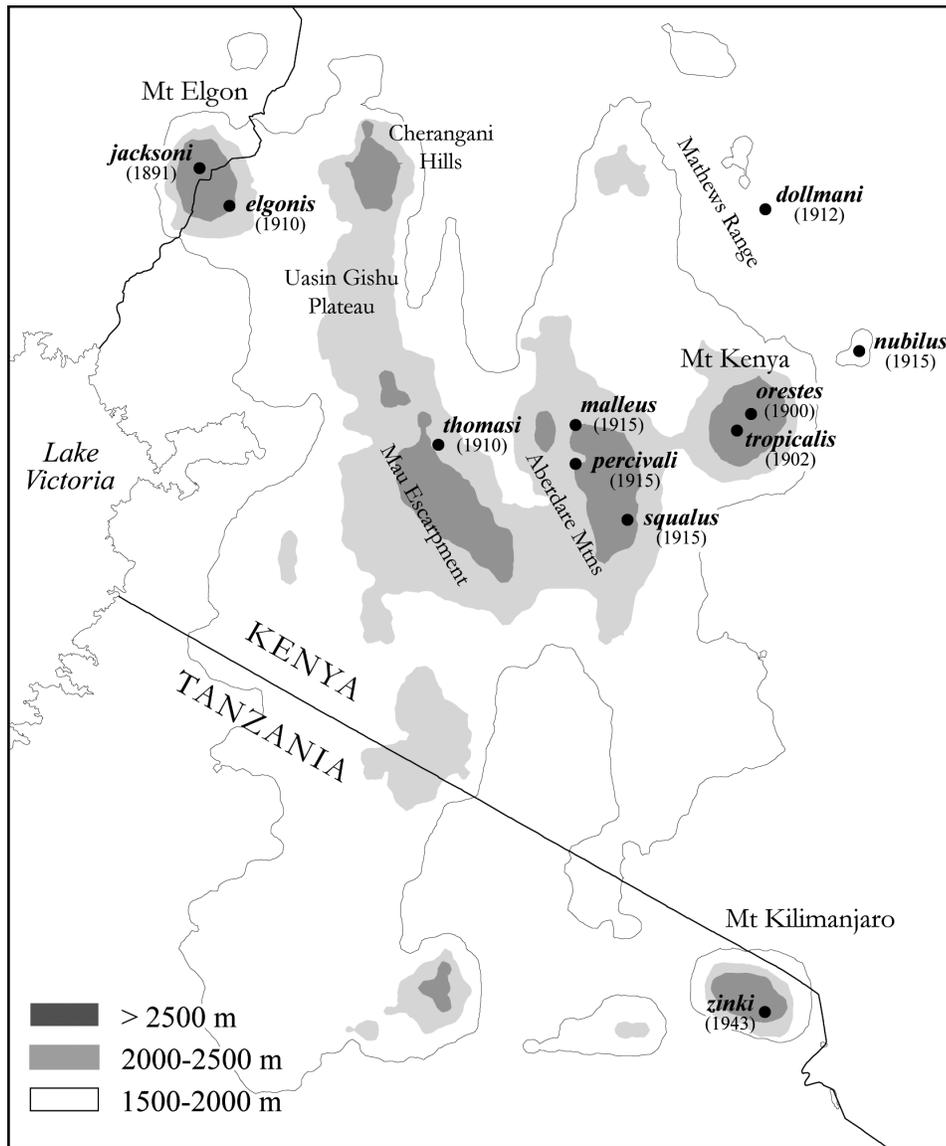


Fig. 1. Mountainous region of eastern Africa inhabited by populations of *Otomys* addressed herein, indicating type localities of relevant taxa and principal geographic features.

Only length of rostrum, a measurement that involves the nasal tips, was conventionally omitted in morphometric comparisons.

Twelve OTUs, their two-letter abbreviations, and sample sizes of crania measured were identified as follows. Provisional species taxonomy observes the arrangement of Musser & Carleton (2005); tri-

nomial species-group taxa of *O. tropicalis* are intended only to convey current synonymy, not to denote any accepted subspecific classification. Full provenance and museum registration numbers are provided either in the Taxonomic Summary or in Appendix 1. Abbreviations are used here and throughout the text for mount or mountains (Mt, Mts).

Otomys dollmani: Kenya, Mt Gargues (MG, $n = 6$, including the holotype USNM 181790).

Otomys irroratus: South Africa, Eastern Cape Province (EC, $n = 21$); Kwa-Zulu-Natal Province (KZ, $n = 17$); Western Cape Province (WC, $n = 32$).

Otomys orestes: Kenya, Aberdare Mts and Mt Kenya (OR, $n = 10$).

Otomys tropicalis elgonis: Kenya, Aberdare Mts (AM, $n = 24$); Uasin Gishu Plateau (UG, $n = 7$); Kaimosi and Kakamega (KA, $n = 21$); Kenya and Uganda, Mt Elgon (ME, $n = 19$).

Otomys tropicalis tropicalis: Kenya, Mt Kenya (MK, $n = 28$).

Otomys typus: Ethiopia, all localities (ET, $n = 14$).

Otomys uzungwensis: Tanzania, Udzungwa Mts (UZ, $n = 14$).

Sixteen cranial and three dental variables were measured to 0.01 mm, using hand-held digital calipers while viewing crania under a stereomicroscope. These measurements, and their abbreviations as used in text and tables, are: condylo-incisive length of skull (CIL), from the occipital condyles to the medial projection of bone (gnathix process) between the incisors (an overall length of skull necessitated by the high incidence of *Otomys* encountered with missing or dislodged nasal bones); greatest zygomatic breadth (ZB), expanse across the zygomatic arches, usually taken at the junction of the jugal bone and zygomatic process of the squamosal; breadth of braincase (BBC), measured on the parietals, with the caliper points placed midway between the glenoid fossa and lambdoidal ridge and just above the squamosal flanges behind the zygomatic arches; depth of skull at the middle orbit (DBO), vertical distance between the lateral ledge of the maxillary above the anterior lamina of M3 and the dorsal surpaorbital crest of the frontal; least interorbital breadth (IOB); breadth across occipital condyles (BOC), distance be-

tween the lateral edge of the upper lobe of the exoccipital condyles; length of rostrum (LR), an oblique line measured from the posterior bevel of the right zygomatic notch to the end of the nasal bones at their midsagittal junction; breadth of rostrum (BR), caliper points on the nasal process of the premaxillaries just inside the dorsal zygomatic notch; postpalatal length (PPL), from the anteriormost bevel of the mesopterygoid fossa to the mid-notch of the basioccipital; length of bony palate (LBP), from the anteriormost bevel of the mesopterygoid fossa to the posterior end of the left incisive foramen; post palatal breadth (PPB), distance across the maxillary bones just behind the third molars; length of incisive foramen (LIF), greatest anterior-posterior expanse measured on the left side; length of diastema (LD), from the inside curvature of the left upper incisor to the crown-root junction (about the gum line) on anterior face of the left M1; breadth of zygomatic plate (BZP), from the rear edge of the right zygomatic plate to its anterior edge, usually near the middle of the plate where it is vertical; length of auditory bulla (LAB), from the posteriormost curve of left ectotympanic bulla to the notch of the eustacian tube (at the seam of the opaque bone of the eustacian tube and translucent bone of the ectotympanic); depth of auditory bulla (DAB), an oblique dimension measured from the dorsal rim of the auditory meatus to the ventralmost curve of the ectotympanic bulla; coronal length of maxillary toothrow (CLM), from the posterior edge of M3 to the crown-root junction on the anterior face of M1, usually at the posterior deflection of the crown; width of the upper first molar (WM1), distance across the edges of the middle lamina (t4-t6); breadth across upper incisors (BIs), outside caliper points on lateral surface of incisors near their tips. In addition, the number of laminae composing the upper third molar (M3) was scored for each cranium measured.

Four external dimensions (to nearest whole mm) were transcribed from skin tags as given by the collector: total length (TOTL), head and body length (HBL), tail length (TL), and hindfoot length (HFL). Most of the specimens we examined originated from the early expeditions to British East Africa (e.g., see Hollister 1919), and collectors of those specimens (E. Heller, J. A. Loring, E. A. Mearns) recorded a head and body length, instead of total length, and measured the hind foot without claw. Thus, TOTL as reported in Table 2 was usually obtained by adding HBL and TL. Means and ranges of external variables are provided as a general index of size and bodily proportions but were not subjected to morphometric comparisons.

Standard descriptive statistics (mean, range, and standard deviation) were derived for adult specimens (young, full, and old age classes combined) of the 12 OTUs. Discriminant function classification, and principal component scores were computed using only the 19 craniodental variables, all of which were first transformed to natural logarithms following the rationale developed by Bookstein et al. (1985:23–26), Marcus (1990:80), and Bookstein (1991:101–102). Principal components (PC) were extracted from the variance-covariance matrix, and variable loadings are expressed as Pearson product-moment correlation coefficients of the derived components or canonical variates (CV) with the original cranial measurements. One-way analyses of variance (ANOVAs), applied to sex or age as group effect, utilized the raw, non-transformed measurements, and Bonferroni's post-hoc multiple comparison test, based on Student's *t* statistic, was employed to isolate between-group significant differences. All analytical procedures were implemented using statistical packages contained in Systat (Version 10.2.01, 2002). Throughout the text, we use the abbreviations M1–3 or m1–m3 to in-

dividually reference the upper (maxillary) and lower (dentary) molars, respectively.

Results and Comparisons

In a sample of *O. tropicalis* from Mt Kenya ($n = 27$), the contribution of secondary sexual dimorphism to within-sample variation is statistically negligible, at least given the unbalanced nature of analyzable material usually consolidated from museum collections. None of the 19 craniodental measurements yielded appreciable differences according to sex (Table 1). Taylor et al. (1993) reported that male *O. irroratus* average slightly larger than females in most cranial dimensions, but that differences were generally not significant. Accordingly, we combined the sexes in composing OTU samples for multi-group discriminant function analysis and in executing principal component analyses.

Size variation within *Otomys* samples, on the other hand, is readily apparent from superficial inspection of crania and their impressive range in gross size, form, rugosity, and definition of sutures. While some of this size range may be attributable to individual variation, much of it certainly reflects age-related size increase (post-weaning growth) and correlates strongly with the three adult age classes based on tooth-wear. Many measurements thus display linear, incremental increases in average size across the three age classes, especially extremal dimensions (CIL, ZB) and those measured on the facial region (LR, BR, LIF, LD); correspondingly, age-class as categorical effect in analyses of variance contributes significantly to non-geographic variation for the majority of variables (Table 1). In nearly all of those age-sensitive variables, the significant differences reside between the young adult and full adult or old adult age classes, but not between the full adult and old adult age classes (according to Bonferroni post-hoc multiple comparison

Table 1.—Arithmetic means of craniodental variables and results of one-way ANOVAs for sex and age cohorts in a sample of adult *Otomys tropicalis* from Mt Kenya ($n = 27$). See Materials and Methods for variable abbreviations.

Variable	Sex		$F(\text{sex})$	Age			$F(\text{age})$
	M (14)	F (13)		Y (9)	A (14)	O (2)	
CIL	36.9	36.8	0.2	35.2	37.7	38.6	12.5***
ZB	19.1	19.1	0.4	18.8	19.4	—	2.1
BBC	15.6	15.2	1.8	14.9	15.7	15.4	5.2*
IOB	4.3	4.2	2.0	4.3	4.2	4.1	1.9
BOC	8.3	8.3	2.3	8.2	8.3	8.6	1.6
DSO	11.9	11.9	0.0	11.3	12.2	12.7	11.7***
LR	13.2	13.3	0.4	12.7	13.5	14.0	7.3**
BR	7.3	7.3	0.1	7.1	7.4	7.6	3.8*
PPL	13.7	13.7	0.0	13.1	14.0	14.7	10.2**
LBP	9.7	9.8	1.1	9.4	10.0	9.9	8.6**
LIF	7.0	6.8	1.5	6.5	7.1	7.1	6.2**
LD	9.7	9.5	0.1	8.7	10.2	10.3	18.8***
BZP	6.2	6.2	1.6	5.9	6.3	6.4	6.4**
PPB	6.9	7.0	0.3	6.8	6.9	7.5	3.3
LAB	7.5	7.4	0.5	7.3	7.5	7.8	2.4
DAB	7.7	7.7	1.5	7.5	7.8	8.2	4.9*
CLM	9.0	9.0	0.4	9.1	9.0	8.7	1.7
WM1	2.5	2.5	2.5	2.5	2.5	2.5	0.6
BIs	4.3	4.4	0.7	4.1	4.5	4.8	11.0**

* = $P \leq 0.05$;

** = $P \leq 0.01$;

*** = $P \leq 0.001$.

tests). Such a pattern is predicated by sample sizes available for the three age groups and corresponding mean differences. Presumably, the under-representation of the old adult age-class in this OTU diminished the number of dimensions that potentially exhibit significant age effects, as well as lowered the magnitude of F values. Dimensions of the molars (CLM, WM1), which decrease in crown height with occlusal abrasion after eruption, do not grow in length and width, unlike osseous components of the skull; in contrast, the incisors increase in girth with age (Table 1). Other than procedural elimination of juvenile specimens, we did not adjust for size in the following morphometric analyses. Although variation introduced by post-weaning growth may be substantial within samples of *Otomys*, it is typically negligible relative to those extracted factors that emerged as

taxonomically informative (also see Discussion and accompanying Table 9). Furthermore, three of the dimensions that demonstrated no age variation (IOB, CLM, WM1) proved to contribute frequently and strongly to among-sample differentiation in nearly all ordinations performed.

In view of the many taxa addressed, three sets of morphometric comparisons were conducted, emphasizing both the past taxonomic assignments of *dollmani* and different geographic scopes: (1) *dollmani* in relation to *O. irroratus* and *O. tropicalis sensu lato*, the taxa in which *dollmani* has been commonly synonymized; (2) *dollmani* vis-à-vis other taxa found north of the Zambezi River (*elgonis*, *orestes*, *tropicalis*, *typus*), in particular highlighting its divergence with respect to *orestes*, the taxon under which *dollmani* was originally named; and (3) three

Table 2.—External and cranial statistics (mean, ± 1 SD, and observed range) for samples of *Otomys dollmani* (Kenya, Mt Gargues, $n = 6$), *O. orestes* (Kenya, both Mt Kenya, $n = 3$, and Aberdare Mts, $n = 7$), *O. tropicalis* (Kenya, Mt Kenya, $n = 29$), and *O. irroratus* (South Africa, Western Cape Province, $n = 32$). See Materials and Methods for variable abbreviations.

Variable	<i>O. dollmani</i>	<i>O. orestes</i>	<i>O. tropicalis</i>	<i>O. irroratus</i>
TOTL	236.7 \pm 11.7 225–255	232.7 \pm 13.0 212–252	253.1 \pm 16.1 217–284	275.5 \pm 20.2 232–307
HBL	144.7 \pm 5.9 138–150	159.6 \pm 10.6 135–175	169.2 \pm 12.3 137–192	171.0 \pm 12.5 150–192
TL	92.0 \pm 7.2 85–105	73.1 \pm 10.2 61–93	83.9 \pm 5.8 70–96	104.5 \pm 10.2 81–120
HFL	25.1 \pm 1.3 23–27	28.5 \pm 1.6 25–30	31.9 \pm 1.1 29–35	32.5 \pm 1.4 30–35
CIL	33.3 \pm 1.5 31.1–35.1	35.5 \pm 1.5 33.1–38.3	36.8 \pm 1.7 34.1–39.9	38.4 \pm 2.1 34.7–43.4
ZB	17.3 \pm 0.8 16.2–17.9	19.2 \pm 1.0 16.8–20.5	19.2 \pm 0.6 18.2–20.1	19.8 \pm 0.9 18.0–22.3
BBC	13.6 \pm 0.3 13.4–14.1	14.6 \pm 0.5 14.0–15.5	15.4 \pm 0.6 14.5–16.4	15.0 \pm 0.3 14.3–15.5
IOB	4.1 \pm 0.1 4.0–4.3	3.9 \pm 0.3 3.6–4.4	4.3 \pm 0.2 3.9–4.6	4.5 \pm 0.2 4.1–4.9
BOC	7.5 \pm 0.3 7.2–7.9	7.7 \pm 0.2 7.4–8.0	8.3 \pm 0.3 7.7–9.1	8.3 \pm 0.3 7.8–9.3
DSO	10.5 \pm 0.5 9.8–10.9	12.4 \pm 0.7 11.4–13.6	11.9 \pm 0.7 10.7–13.5	12.6 \pm 0.8 11.2–14.5
LR	12.1 \pm 0.7 11.2–13.1	13.3 \pm 0.7 12.5–14.7	13.3 \pm 0.6 12.4–14.6	14.2 \pm 0.9 12.7–16.4
BR	6.9 \pm 0.3 6.6–7.3	6.8 \pm 0.3 6.3–7.3	7.3 \pm 0.3 6.9–7.9	7.5 \pm 0.4 6.4–8.5
PPL	12.5 \pm 0.7 11.5–13.2	13.5 \pm 0.7 12.3–14.6	13.7 \pm 0.8 12.4–15.0	14.9 \pm 0.9 13.5–16.9
LBP	8.6 \pm 0.3 8.2–9.0	9.2 \pm 0.5 8.6–10.3	9.7 \pm 0.4 8.6–10.5	9.9 \pm 0.5 9.0–11.5
LIF	6.1 \pm 0.5 5.4–6.7	6.9 \pm 0.4 6.3–7.5	6.9 \pm 0.4 6.2–7.8	7.4 \pm 0.5 6.5–8.2
LD	8.2 \pm 0.7 7.1–8.9	8.8 \pm 0.6 8.3–9.6	9.6 \pm 0.9 7.9–11.6	9.6 \pm 0.9 7.7–11.5
BZP	5.3 \pm 0.3 4.9–5.5	5.4 \pm 0.5 4.6–6.0	6.2 \pm 0.4 5.4–6.8	6.1 \pm 0.5 5.1–7.0
PPB	6.5 \pm 0.2 6.3–6.9	7.0 \pm 0.2 6.6–7.4	6.9 \pm 0.3 6.4–7.7	7.3 \pm 0.3 6.8–7.8
LAB	6.3 \pm 0.3 5.9–6.9	7.8 \pm 0.3 7.3–8.5	7.4 \pm 0.3 6.8–8.1	7.2 \pm 0.4 6.5–8.0
DAB	6.9 \pm 0.1 6.7–7.0	8.2 \pm 0.3 7.9–8.7	7.7 \pm 0.3 7.2–8.3	7.9 \pm 0.2 7.3–8.3
CLM	8.07 \pm 0.17 7.86–8.34	8.68 \pm 0.21 8.38–8.97	9.00 \pm 0.26 8.46–9.50	9.31 \pm 0.24 8.76–9.81
WM1	2.09 \pm 0.05 2.03–2.18	2.32 \pm 0.11 2.21–2.55	2.52 \pm 0.10 2.37–2.67	2.35 \pm 0.11 2.10–2.57
BIs	3.98 \pm 0.20 3.72–4.29	3.70 \pm 0.30 3.32–4.25	4.32 \pm 0.29 3.68–4.90	4.15 \pm 0.36 3.30–5.01

disjunct highland taxa (*orestes*, *typus*, *uzungwensis*) conventionally grouped within *O. typus*. *Otomys irroratus*, *O. tropicalis*, and *O. typus* are currently

considered valid species (e.g., Taylor & Kumirai 2001, Musser & Carleton 2005); hence, their inclusion in deliberate combinations in the multivariate analyses

provided a comparative yardstick against which to assess the craniometric differentiation of *dollmani*. Further, we routinely employed both discriminant function and principal component analyses to explore patterns of craniodental differentiation for each set. The latter ordination method summarizes covariation patterns based on the log-transformed specimen data itself without prior assumptions about group assignment. Together, the two procedures lend different perspectives to variable covariation and complement one another in supporting taxonomic conclusions.

Morphometric variation.—In discriminant function analysis of the 9 OTUs representing *dollmani* and *irroratus-tropicalis* (including *elgonis*), well-defined phenetic structure is retained for most of the species-group epithets represented (Fig. 2, top). The exceptions are *tropicalis* from Mt Kenya and OTUs of *elgonis*, which overlap substantially in multivariate space and among which a posteriori misclassifications are commonplace (12–47%). Similarly, the three samples of *irroratus* lack unique identity, their CV scores broadly overlapping (29–36% misclassifications among them), but collectively they are set well apart from examples of *elgonis* and *tropicalis* on CV1. Specimens of *irroratus* average larger than those of *tropicalis-elgonis* in most variables (Table 2), an overall size disparity that accounts for some of the separation, but the most heavily weighted variables on CV1 involve the longer and broader palate in *irroratus* (LBP, PPB), its longer basicranial axis (PPL) and deeper skull (DSO), longer but narrower molar rows (CLM, WM1), and broader interorbit (IOB) (Table 3). The conspicuous isolation of *dollmani* issues from its uniformly smaller size, as indicated by variable correlations with CV2, especially its more delicate molars (CLM, WM1) and smaller auditory bullae (LAB, DAB) (Tables 2, 3). The sample of *dollmani* is

equally markedly divergent from those of *irroratus* and *tropicalis-elgonis*, more so than are the latter taxa from one another (Fig. 2, bottom).

Principal component analysis limited to specimens of *irroratus* and those of *tropicalis-elgonis* further corroborates fundamental shape differences between these taxa (Fig. 3). All variables load positively on the first component and most correlations are moderate to strong ($r = 0.55\text{--}0.97$; Table 4). Fewer variables load heavily on PC II, more or less orthogonal to the major axes of the taxon samples, and these emphasize consistent contrasts in shape: the longer (CLM) but narrower (WM1) molar rows in *irroratus*, its relatively smaller ectotympanic bullae (LAB, DAB), and broader interorbital region (IOB) compared with examples of *tropicalis-elgonis* (Table 4). The proportionally smaller bullae and wider interorbit of *O. irroratus* reinforce the morphometric findings obtained by Taylor & Kumirai (2001). Several of these variables are the same as those highlighted on CV 1 derived from the above 9-group discriminant function analysis (CLM, WM1, IOB), but the lack of prior group definitions and removal of *dollmani* specimens divulge other non age-related shape differences, in this instance the relatively greater inflation of the bullae in *tropicalis-elgonis* (LAB, DAB). Although scores of *irroratus* and *tropicalis-elgonis* marginally overlap on the first two components extracted, the major axes of their elliptical spreads are phenetically distinct (Fig. 3), their Y-intercepts being significantly different ($F = 22.7$, $P \leq 0.0001$) while their slopes are statistically inseparable ($F = 0.23$, $P = 0.629$). Juveniles were omitted from our analyses, but age-related size increases (post-weaning growth) still account for much of the elongate scatter observed within the species samples and for the oblique orientation of the group constellations on the first and second principal components. Accordingly, age-

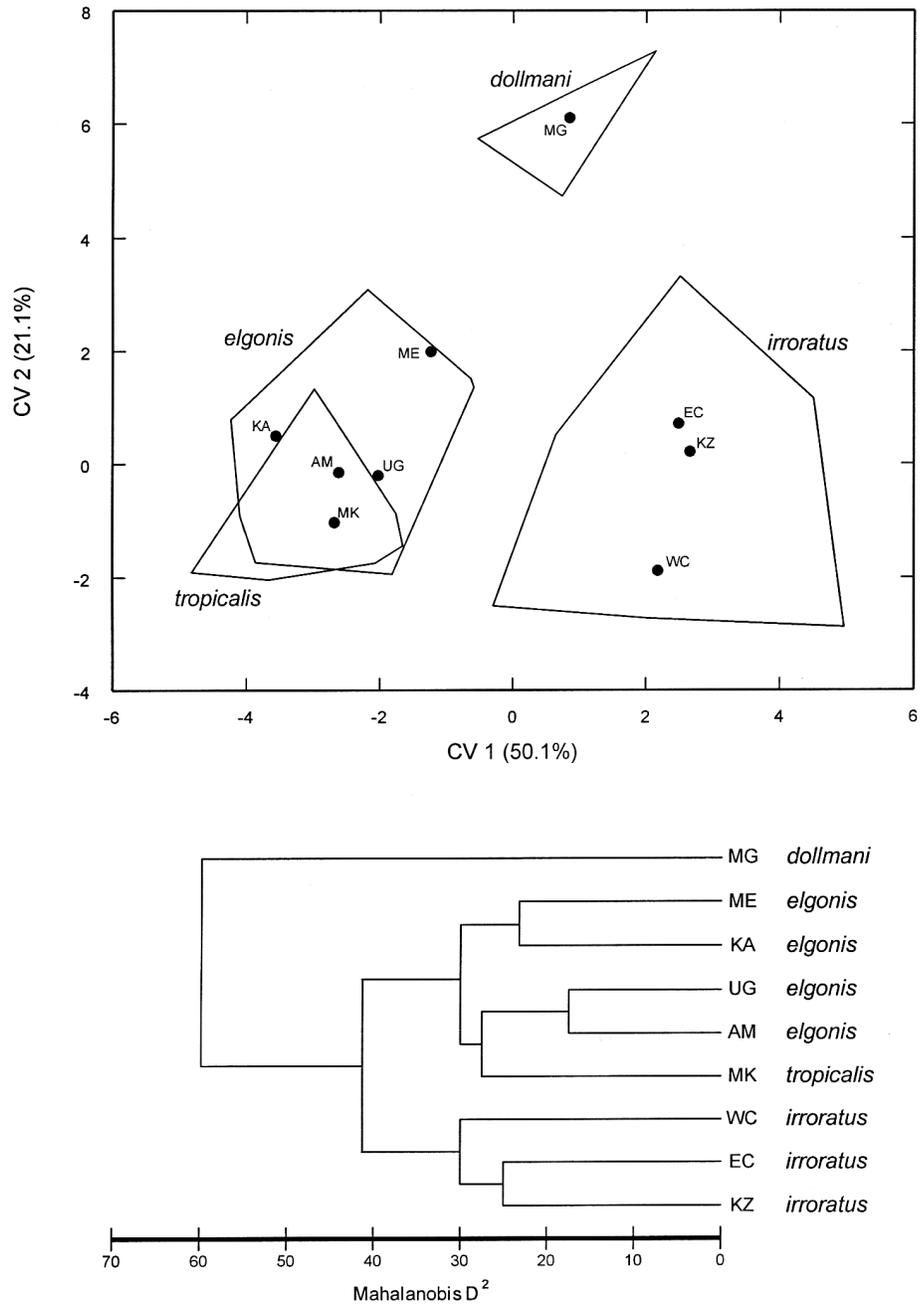


Fig. 2. Results of discriminant function analysis performed on 18 log-transformed craniodental variables as measured on 93 intact specimens representing 9 OTUs of the *Otomys irroratus-tropicalis* complex. Top, scatter plot of specimen scores on first two canonical variates (CV) extracted; irregular polygons enclose maximal dispersion of specimen scores around an OTU centroid (lettered symbols) and species-group taxa are indicated next to the bounding polygons (to avoid visual congestion, polygons surround maximal dispersion for all specimens of the taxa *elgonis* and *irroratus* and only OTU centroids are indicated). Bottom, cluster diagram (UPGMA) based on average Mahalanobis distances between OTU centroids; species-group epithets are indicated for each terminal OTU. See Table 3 for variable correlations and percent variance explained.

Table 3.—Results of 9-group discriminant function analysis performed on intact specimens ($n = 93$) representing *dollmani* and taxa of the *irroratus-tropicalis* complex and using 18 log-transformed craniodental variables (excluding LR). See Fig. 2 and Materials and Methods for variable abbreviations.

Variable	Correlations	
	CV1	CV2
CIL	0.35*	-0.51***
ZB	0.34*	-0.51***
BBC	-0.12	-0.62***
IOB	0.46***	-0.25
BOC	0.10	-0.74***
DSO	0.57***	-0.44**
BR	0.36*	-0.34*
PPL	0.38**	-0.49***
LBP	0.47***	-0.45***
LIF	0.33	-0.45***
LD	0.22	-0.30
BZP	0.36*	-0.33
PPB	0.43**	-0.48***
LAB	-0.29	-0.62***
DAB	0.03	-0.60***
CLM	0.46***	-0.71***
WM1	-0.53***	-0.57***
BIs	0.13	-0.11
Canonical correlations	0.94	0.86
Eigenvalues	7.01	2.95
Percent variance	50.1	21.1

* = $P \leq 0.05$;

** = $P \leq 0.01$;

*** = $P \leq 0.001$.

class as a categorical effect in one-way analyses of variance contributes significantly to the spread of specimen scores along PC I ($F = 34.3$, $P \leq 0.0001$) but not PC II ($F = 0.18$, $P = 0.911$); whereas, species as effect contributes substantially to dispersion on both PC I ($F = 13.9$, $P \leq 0.001$) and especially on PC II ($F = 114.1$, $P \leq 0.0001$). The elongate constellations of specimen scores thus revealed and their oblique orientation to PC I and II conform with the now familiar results obtained in multivariate comparisons of other closely related (congeneric) muroid species (Carleton & Martinez 1991, Voss & Marcus 1992).

Discriminant function analysis of *dollmani* and other forms that occur to the

north of the Zambezi River (*elgonis*, *orestes*, *tropicalis*, *typus*) again reveals clearly defined, non-overlapping structure among most taxa (Fig. 4, top). OTUs of *tropicalis* and *elgonis* are extensively congruent on the first two canonical variates extracted (cumulative variation explained = 76.6 %) and are jointly differentiated from samples of *dollmani*, *orestes*, and *typus*. Morphological divergence between *tropicalis* and examples of *elgonis*, as depicted in both the CVA scatter plot and UPGMA phenogram, is unremarkable and questions taxonomic segregation of the two. Instead, the linkage pattern (Fig. 4, bottom), according to inter-centroid Mahalanobis distances among OTUs, preserves some geographic structure, insofar as those OTUs drawn from mountains to the east of the Rift Valley (AM, MK) cluster apart from those to the west of the Rift Valley (KA, ME, UG). Although skulls of *orestes* and *typus* approximate those of *tropicalis-elgonis* in many cranial dimensions (Table 2), certain pronounced shape differences contribute to their separation on CV 1, namely the interorbital constriction (IOB), inflation of the auditory bullae (LAB, DAB), and depth of the cranial vault (DSO) compared with OTUs of *tropicalis-elgonis* (Table 5). Such broad similarities in shape are reflected in the last clustering division, in which *orestes-typus* form a pair-group apart from *dollmani* and *tropicalis-elgonis*. Systematists such as Bohmann (1952) and Missonne (1974) have arranged *orestes* as a subspecies of *typus*, but the morphometric footprints of the two taxa are distinctive, *orestes* being an overall smaller animal than *typus*. According to a posteriori probabilities of group membership, the holotype (FMNH 16698) of *thomasi* Osgood (1910) was classified with the OTU of *orestes* ($P = 0.999$). Once more, small size overridingly influences the morphometric segregation of *dollmani* along CV 2 (Table 5), particularly as

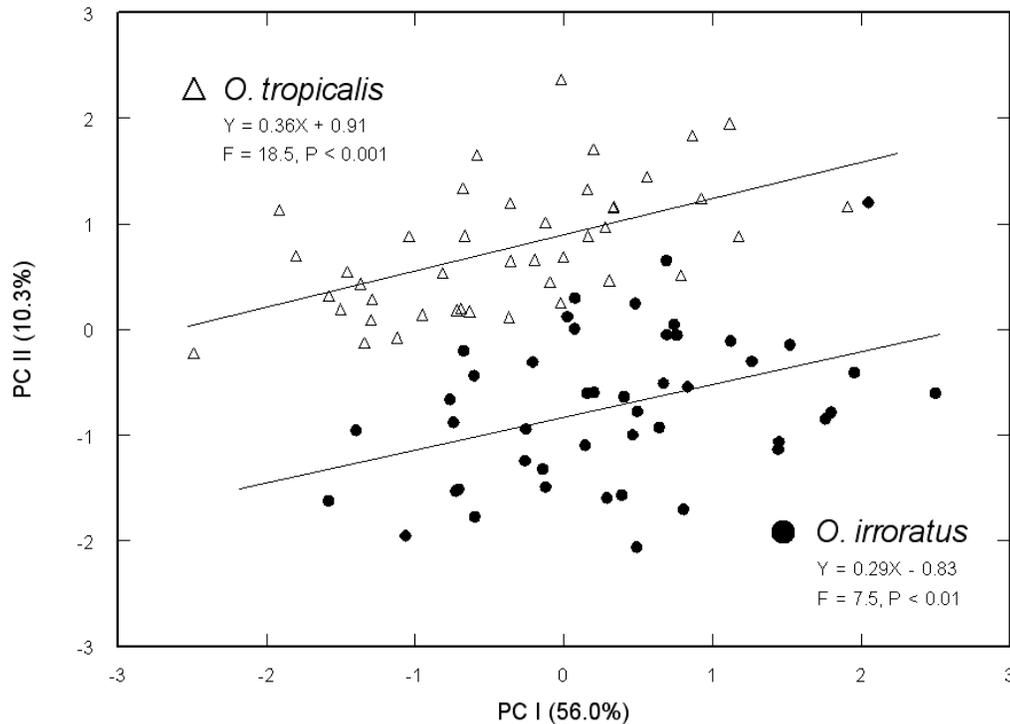


Fig. 3. Scatter plot of specimen scores on the first two principal components (PC) extracted from ordination of 18 log-transformed craniodontal variables as measured on 89 intact specimens representing samples of *Otomys irroratus* and *tropicalis-elgonis*. See Table 4 for variable correlations and percent variance explained.

expressed in its more delicate molar rows (CLM, WM1). As discerned by Hollister (1919), the skull of *dollmani* in fact recalls a small version of *tropicalis-elgonis* and differs from *orestes* and *typus* in the same proportional traits as listed above. The phenetic association of *dollmani* with the *tropicalis-elgonis* group, albeit at a large Mahalanobis distance (Fig. 4, bottom), is consistent with Hollister's observation and contradicts Heller's (1912) original arrangement of the taxon as a subspecies of *orestes*.

Confined only to the large-bodied Kenyan samples, i.e., omitting *dollmani* and *typus*, principal component analysis reaffirms the phenetic intermingling of specimens of *tropicalis* and *elgonis* and suggests their joint discrimination from examples of *orestes* (Fig. 5). Again, post-weaning size increases are captured on the

first component extracted (most variable correlations positive and large—Table 6; ANOVA (age) highly significant— $F = 29.9, P \leq 0.0001$). Variable correlations with the second component convey shape contrasts in select anatomical regions: the narrower interorbital constriction (IOB) in *orestes*, its slimmer molars and incisors (WM1, BIs), narrower zygomatic plate (BZP), and relatively larger bullae (LAB, DAB), compared with individuals of *tropicalis-elgonis* (Table 6). A visual landmark approximately concords with the univariate difference in expanse of the zygomatic plate: the anterodorsal border of the plate in *orestes* is more or less coincident with the premaxillary-maxillary suture, but in *tropicalis-elgonis*, the lead edge of the plate notably overlaps and obscures the middle portion of the suture. Taxon as effect is significantly

Table 4.—Results of principal component analysis performed on 89 intact specimens representing examples of *Otomys irroratus* and *O. tropicalis* (including *elgonis*) and using 18 log-transformed craniodental variables (excluding LR). See Fig. 3 and Materials and Methods for variable abbreviations.

Variable	Correlations	
	PCI	PCII
CIL	0.97***	-0.00
ZB	0.93***	-0.05
BBC	0.55***	0.23
IOB	0.13	-0.70***
BOC	0.62***	0.05
DSO	0.94***	-0.21
BR	0.87***	-0.15
PPL	0.90***	-0.04
LBP	0.84***	-0.24
LIF	0.89***	-0.07
LD	0.93***	0.13
BZP	0.83***	-0.18
PPB	0.66***	-0.16
LAB	0.54***	0.63***
DAB	0.72***	0.43**
CLM	0.35*	-0.51***
WM1	0.01	0.49***
BIs	0.84***	0.17
Eigenvalues	10.1	1.9
Percent variance	56.0	10.3

* = $P \leq 0.05$;

** = $P \leq 0.01$;

*** = $P \leq 0.001$.

reflected in the dispersion of PC II scores ($F = 68.3$, $P \leq 0.0001$), but age-class is not ($F = 0.5$, $P = 0.708$). Scatter of the PC scores, patterns of variable loadings, and ANOVA effects are reminiscent of the PCA results obtained with the larger samples of *irroratus* and *tropicalis-elgonis* (see Fig. 3), but the sparse representation of *orestes* erodes so clear a definition of dual species constellations. The holotype of *thomasi* falls nearer the margin of the *orestes* distribution (Fig. 5).

Specimens of *orestes*, *typus*, and *uzungwensis*, three disjunct highland taxa conventionally viewed as races of a single species, *O. typus* (Bohmann 1952, Missonne 1974), are easily distinguishable in multivariate space, whether derived from principal component or discriminant

function ordinations. In principal components analysis, The Udzungwa Mts form emerges as overall smaller than the northern taxa but with a relatively broader rostrum and incisors and smaller auditory bullae (Fig. 6, top; Table 7). Lawrence and Loveridge (1953:61) remarked on the small skull and relatively heavy rostrum of *uzungwensis* in their description. Specimens of *orestes* are wholly segregated from those of *typus* and *uzungwensis* on PC III (not figured) based on their relatively and absolutely smaller molars (Table 7). Given the unambiguous delineation of the three taxa in scatter-plots of principal components, 3-group discriminant function analysis yields even clearer segregation, grading incrementally in craniodental size along CV 1 (Fig 6, bottom). Narrower incisors (BIs) and smaller auditory bullae (DAB) largely account for divergence of examples of *orestes* on CV 2 (Table 7).

Molar lamination and incisor sulcation.—Counts of laminae on the upper third molar (Table 8) vary intelligibly by taxon and generally concur with patterns already documented (Bohmann 1952, Dollman 1915, Taylor & Kumirai 2001). The modal number of M3 laminae ranges from 6 in *dollmani* and *irroratus* (infrequently 7); to 7 in *elgonis*, *tropicalis*, and *uzungwensis* (infrequently 6 or 8 in each taxon); to 8 in *typus* (infrequently 7 or 9). Within an OTU or species-group taxon, the modal number is pronounced and the range of variation typically spans only two laminae, exceptionally three (e.g., the *elgonis* sample from Mt Elgon).

A notable exception to laminar stability involves the series of *orestes* from Mt Kenya, the area of its type locality. Thomas (1900) diagnosed *orestes* based, in part, on the possession of an M3 with only 6 laminae (citing 4 specimens, which we have not seen), in contrast to a 7-laminated M3 that characterizes *tropicalis* from the middle-upper slopes of Mt Kenya (Thomas 1902). In reporting the

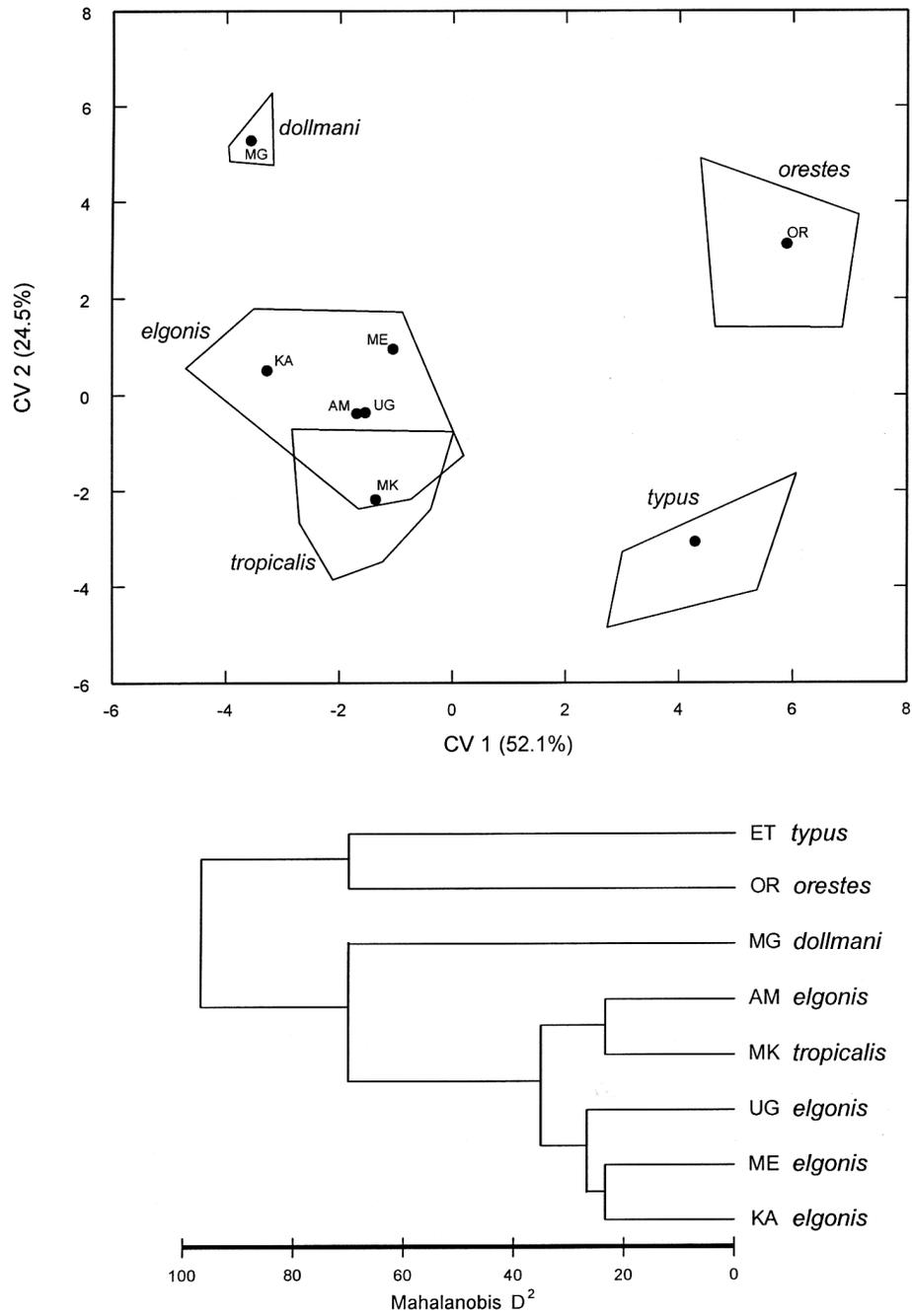


Fig. 4. Results of discriminant function analysis performed on 18 log-transformed craniodental variables as measured on 64 intact specimens representing 8 OTUs of *Otomys* distributed north of the Zambezi River (*dollmani*, *elgonis*, *orestes*, *tropicalis*, *typus*). Top, scatter plot of specimen scores on first two canonical variates (CV) extracted; irregular polygons enclose maximal dispersion of specimen scores around an OTU centroid (lettered symbols), and species-group taxa are indicated next to the bounding polygons (to avoid visual congestion, the polygon surrounds maximal dispersion for all specimens of *elgonis* and only OTU centroids are indicated). Bottom, cluster diagram (UPGMA) based on average Mahalanobis distances between OTU centroids; species-group epithets are indicated for each terminal OTU. See Table 5 for variable correlations and percent variance explained.

Table 5.—Results of 8-group discriminant function analysis performed on intact specimens ($n = 64$) representing *dollmani* and other taxa distributed north of the Zambezi River (*elgonis*, *orestes*, *tropicalis*, *typus*) and using 18 log-transformed craniodental variables (excluding LR). See Fig. 4 and Materials and Methods for variable abbreviations.

Variable	Correlations	
	CV1	CV2
CIL	0.30	-0.43*
ZB	0.39	-0.37
BBC	-0.15	-0.42*
IOB	-0.62***	-0.30
BOC	0.03	-0.75***
DSO	0.68***	-0.22
BR	0.09	-0.43*
PPL	0.25	-0.30
LBP	0.37	-0.55***
LIF	0.38	-0.32
LD	0.22	-0.33
BZP	0.04	-0.57***
PPB	0.43*	-0.25
LAB	0.61***	-0.40
DAB	0.59***	-0.15
CLM	0.45**	-0.79***
WM1	0.22	-0.89***
BIs	-0.17	-0.36
Canonical correlations	0.96	0.93
Eigenvalues	12.7	6.0
Percent variance	52.1	24.5

* = $P \leq 0.05$;

** = $P \leq 0.01$;

*** = $P \leq 0.001$.

large series of *Otomys* recovered by the Smithsonian African Expedition from Mt Kenya, Hollister (1919:147) reinforced the notion that a 6-laminated M3 is diagnostic of *O. orestes*—"The last upper molar has six laminae in all specimens except one (No. 164329) in which there are distinctly seven, the last very small." Hollister referred 16 USNM specimens to *orestes*, leading Bohmann (1952) to assume that he had meant "1 of 16 specimens," but Hollister did not specify how many skulls were available for examination. We have managed to reassemble 13 specimens with skulls from Mt Kenya that were probably studied by Hollister. Among these 13, 7 individuals possess 6

M3 laminae (FMNH 43444, 43446; USNM 164308, 164333, 164334, 164357, 165334) and 6 have 7 laminae (USNM 164293, 164295, 164297, 164304, 164329, 164332). We cannot fully explain the discrepancy between Hollister's and our tallies of M3 laminae. We note that 8 of the 13 specimens are juveniles with unworn M3s, and in many of these, a tiny seventh lamina is set below the occlusal surface. Although visually obscure, it seems evident that initiation of wear in these individuals would have produced a 7-laminated M3, but perhaps Hollister scored their M3s as having 6 laminae. Regardless of the explanation, the notion of 6 M3 laminae as narrowly diagnostic of *orestes* became erroneously entrenched in the literature and influenced the taxonomic arrangements of subsequent authors (Dollman 1915, Bohmann 1952, Setzer 1953), including the description of *dollmani* (which possesses only 6 laminae in all 7 specimens examined) as a subspecies of *O. orestes* (Heller 1912).

Next to molar lamination, the presence and pronouncement of longitudinal grooves (sulci) on the upper and lower incisors have figured prominently in the taxonomy of *Otomys* (Wroughton 1906, Dollman 1915, Thomas 1918, Bohmann 1952). Unlike the variation in upper incisor grooving observed among southern African forms, some of which wholly lack sulci (e.g., *Parotomys littledalei*), eastern African populations considered here are uniform in possessing a deep lateral groove and shallow medial groove. Development of grooves on the lower incisor, however, exhibits appreciable variation among the species-group taxa surveyed.

As reported by many authors, two longitudinal grooves mark the anterior face of the lower incisor in *O. typus sensu stricto* (Dollman 1915, Bohman 1952, Taylor & Kumirai 2001). The sulci are about equal in depth and notch three points (cusps), about equal in height and

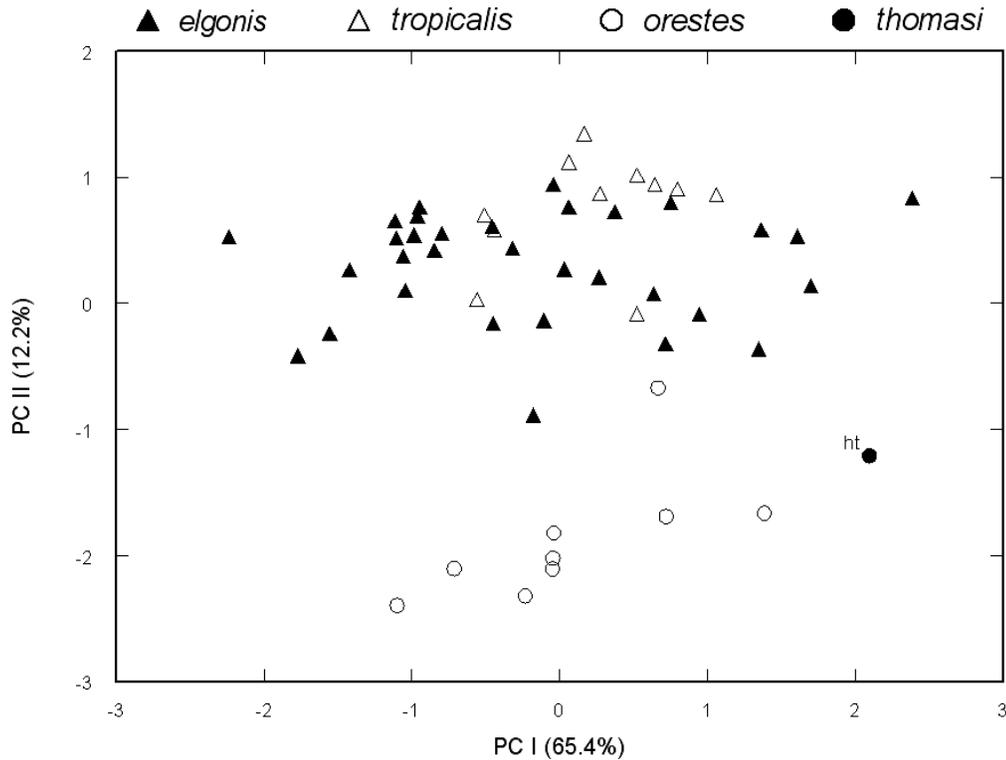


Fig. 5. Scatter plot of specimen scores on the first two principal components (PC) extracted from ordination of 18 log-transformed craniodental measurements as measured on 52 intact specimens representing Kenyan samples of *elgonis*, *orestes*, and *tropicalis*, along with the type specimen of *O. thomasi* Osgood, 1910 (= ht, FMNH 16698 from Molo). See Table 6 for variable correlations and percent variance explained.

width, at the cutting edge of the incisor. The working edge of the lower incisor in *O. typus*, as well as that in *uzungwensis*, thus appears trifurcate or trifid. Among other forms examined here, the tip of the lower incisor is bifurcate or bifid, a deep lateral sulcus clearly inscribing a central point that is wider and set higher than the lateral point. In *dollmani*, *elgonis*, *orestes*, and *tropicalis*, a second, much shallower, longitudinal groove occurs medial to the deep lateral groove. Presumably, this secondary groove is homologous to the deeper medial groove observed in examples of *O. typus* and *O. uzungwensis*, but the indentation is so very shallow that the central incisor point macroscopically appears undivided; that is, the tip of the incisor is functionally bifid. In general,

the secondary medial groove seems to be more strongly expressed in *orestes*, compared with specimens of *dollmani*, *elgonis*, and *tropicalis*, and is usually absent in samples of *irroratus*. This last observation conflicts with the interpretation of most authors, who have characterized *O. irroratus* as possessing one deep lateral and one faint medial groove (e.g., Misonne 1974, Taylor & Kumirai 2001). To us, the configuration of grooves in *O. irroratus* more closely resembles *O. denti*, which (Dollman 1915) described as having only one deep lateral groove and separated it from other eastern African forms with a deep lateral and faint medial groove (i.e., *dollmani*, *elgonis*, *orestes*, *thomasi*, *tropicalis*). Expression of incisor sulcation among otomyine populations is

Table 6.—Results of principal component analysis performed on 52 intact specimens representing Kenyan examples of *elgonis*, *orestes*, and *tropicalis* and using 18 log-transformed craniodental variables (excluding LR). See Fig. 5 and Materials and Methods for variable abbreviations.

Variable	Correlations	
	PCI	PCII
CIL	0.98***	-0.01
ZB	0.88***	-0.08
BBC	0.54**	0.35
IOB	-0.20	0.75***
BOC	0.55**	0.37
DSO	0.87***	-0.38
BR	0.84***	0.34
PPL	0.89***	-0.05
LBP	0.83***	0.12
LIF	0.89***	-0.20
LD	0.96***	0.03
BZP	0.76***	0.40*
PPB	0.57***	-0.23
LAB	0.65***	-0.49**
DAB	0.75***	-0.56***
CLM	0.15	0.21
WMI	0.22	0.54**
BIs	0.81***	0.48*
Eigenvalues	0.049	0.010
Percent variance	64.3	12.7

* = $P \leq 0.05$;

** = $P \leq 0.01$;

*** = $P \leq 0.001$.

extremely subtle, and categorization of specific traits is complicated by the very small size scale. Ultimately, careful scanning electron microscopy must be applied to substantiate our impressions and the incisor descriptions of past authors and to develop a consistent comparative terminology.

Taxonomic Summary

The morphological and morphometric evidence presented above sustains Hollister's (1919) judgment in elevating *dollmani* to a valid species. Our results provide no convincing justification for continuing to treat *dollmani* either as a form of *O. orestes*, as originally described (Heller 1912), or as a subspecies of

O. irroratus or *O. tropicalis*, the species with which it is usually associated (Bohmann 1952, Misonne 1974). The taxa *orestes* (Kenyan highlands), *typus* (Ethiopian plateau), and *uzungwensis* (Udzungwa Mts, Tanzania) comprise three distinctive phenons, each of which is found in widely separated mountain systems. Their union as a single morphogenetic entity, *O. typus* as conventionally arranged (Bohmann 1952, Misonne 1974, Musser & Carleton 1993), should rest on empirical data, not vague preconceptions of intergradation following a polytypic species concept. Clear-cut morphometric delineation of southern African *O. irroratus*, with predominantly 6-laminated M3s, from eastern African *O. tropicalis*, with predominantly 7-laminated M3s, mirrors the multivariate results previously reported by Taylor & Kumirai (2001) and solidifies the judgments of earlier authors, especially Dollman (1915), regarding the specific distinctiveness of the two.

Synonymies of the Kenyan taxa central to this study are presented below and trace name availability and subsequent name combinations as used in major systematic works. As discussed in the respective accounts, full allocation of junior synonyms to *O. orestes* and *O. tropicalis* requires much additional study, including examination of primary types and original descriptive series, as well as incorporation of new specimens and data sources. Specimens examined include all individuals personally seen and identified by us.

Otomys dollmani Heller

Otomys orestes dollmani Heller, 1912:5 (type locality—Kenya, Mathews Range, Mount Gargues [Warges, Uaraguess], 7000 ft [2134 m]; holotype—USNM 181790).—Dollman, 1915:157 (listed as valid subspecies).—Allen, 1939:346 (listed as valid subspecies).—Ellerman, 1941:323 (listed as valid subspecies).—

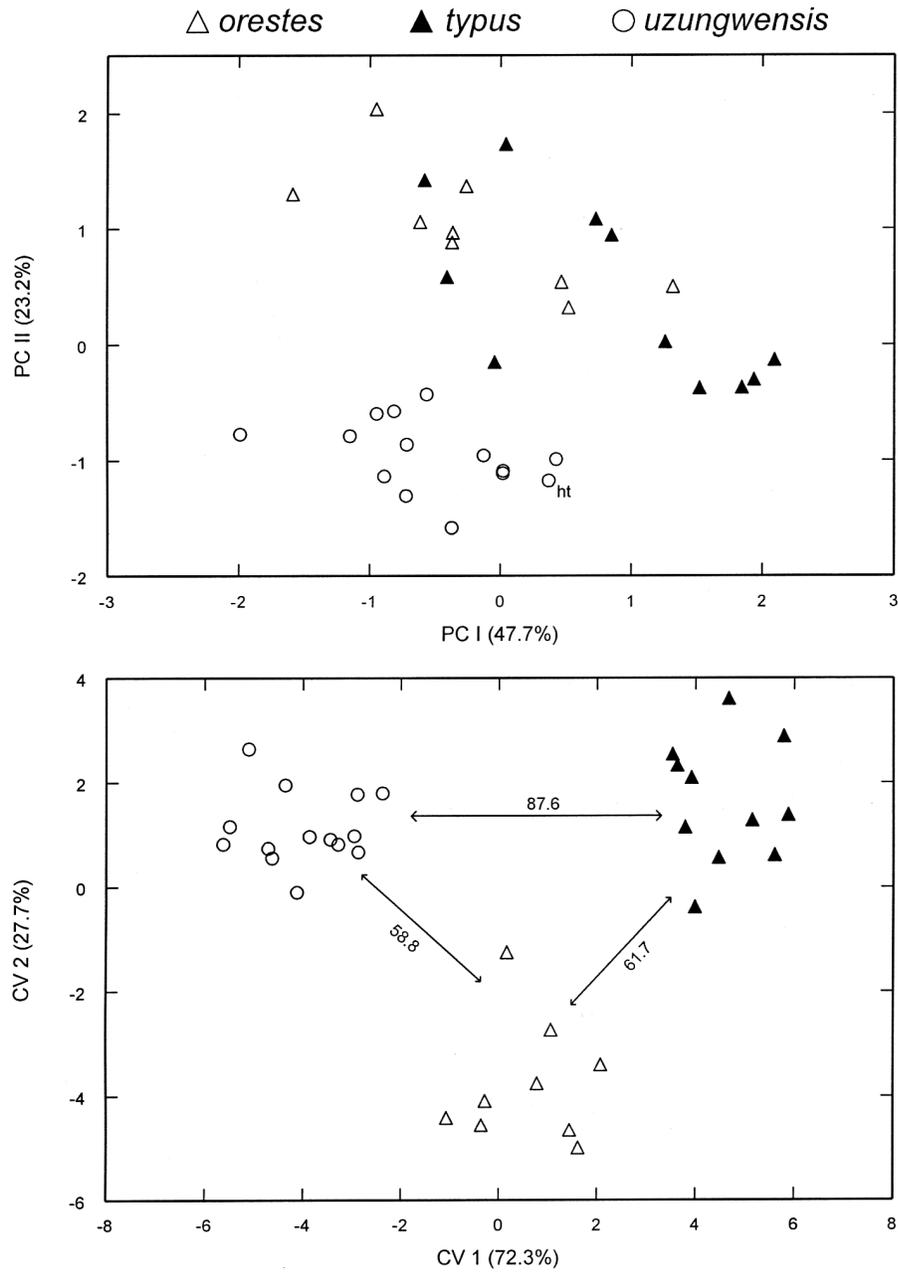


Fig. 6. Ordinations performed on 34 intact specimens representing the disjunct highland taxa *orestes*, *typus*, and *uzungwensis*. Top, projection of specimen scores onto the first two principal components (PC) extracted from factor analysis; the score for the holotype (MCZ 26645) of *O. uzungwensis* Lawrence & Loveridge (1953) is indicated (= ht). Bottom, projection of specimen scores onto the first two canonical variates (CV) extracted from discriminant function analysis; average between-centroid divergences (Mahalanobis D²) among the three samples are indicated along the two-way arrows. See Table 7 for variable correlations and percent variance explained.

Table 7.—Results of principal component and discriminant function analyses performed on 34 intact specimens representing the disjunct highland taxa *orestes*, *typus*, and *uzungwensis* and using 17 log-transformed craniodental variables (excluding LR, DSO). See Fig. 6 and Materials and Methods for variable abbreviations.

Variable	Correlations				
	PCI	PCII	PCIII	CV1	CV2
CIL	0.97***	0.03	0.14	0.56*	0.07
ZB	0.78***	0.20	0.45	0.43	-0.27
BBC	0.18	0.59**	-0.01	0.43	-0.32
IOB	0.19	-0.27	-0.07	-0.08	0.24
BOC	0.58**	0.26	-0.36	0.70***	0.16
BR	0.54	-0.72***	0.09	-0.24	0.43
PPL	0.78***	-0.13	0.39	0.24	-0.08
LBP	0.87***	0.17	-0.17	0.66**	0.22
LIF	0.89***	0.10	0.20	0.59**	-0.02
LD	0.93***	0.00	0.19	0.53*	0.07
BZP	0.74***	-0.34	-0.26	0.27	0.53
PPB	0.57*	0.68***	0.01	0.79***	-0.27
LAB	0.48	0.68**	0.21	0.63**	-0.51
DAB	0.43	0.67**	0.29	0.50	-0.57*
CLM	0.59*	0.50	-0.57*	0.91***	0.25
WM1	0.63**	0.21	-0.59*	0.70***	0.45
BIs	0.42	-0.87***	-0.03	-0.33	0.62**
Eigenvalues	0.034	0.017	0.006	14.7	5.6
Percent variance	47.7	23.2	8.1	72.3	27.7

* = $P \leq 0.05$;

** = $P \leq 0.01$;

*** = $P \leq 0.001$.

Setzer, 1953:334 (retained as valid subspecies).

Otomys dollmani: Hollister, 1919:147 (elevation to species).—Musser & Carleton, 2005:1526 (retention as valid species).

Otomys irroratus dollmani: Bohmann, 1952:34 (new name combination, retained as valid subspecies).

Otomys tropicalis [*dollmani*]: Misonne, 1974:34 (new name combination, listed in synonymy without indication of rank).—Musser & Carleton, 1993:681 (listed in synonymy without indication of rank).

Distribution.—Known only from the type locality in central Kenya (Fig. 9).

Emended diagnosis.—A diminutive species of *Otomys*, much smaller than *O. orestes* and *O. tropicalis* in most craniodental and external dimensions quantified; tail relatively and absolutely long;

skull profile relatively flat as per *O. tropicalis* (noticeably arched in *O. orestes*); lower incisor with bifid tip and faint medial sulcus, M3 with 6 laminae.

Remarks.—A key feature of *dollmani* that influenced Heller (1912) to describe it as a subspecies of *O. orestes* is the presence of 6 laminae in the M3, a number considered typical of the latter as diagnosed by Thomas (1900). The occurrence of only 6 M3 laminae is actually less typical of *O. orestes* than appreciated by Thomas; 6 or 7 M3 laminae occur in approximately equal frequency in the small sample of *orestes* proper from Mt Kenya available to us (Table 8). Otherwise the two forms are strikingly dissimilar (Figs. 7, 8), as aptly summarized by Hollister (1919:148), who elevated *dollmani* to species: "It is much darker in color, has a considerably longer tail, and the skull lacks almost entirely any ap-

Table 8.—Counts of laminae in the upper third molars and lower incisor configuration in selected taxa representing the *Otomys irroratus-tropicalis* complex. M3 laminae are tabulated by general locality and incisor morphology is characterized at the level of taxon.

Taxon/Locality	n	M3 laminae				Lower incisor	
		6	7	8	9	tip	medial groove
<i>dollmani</i>						bifid	faint
Mt Gargues	7	7	—	—	—		
<i>elgonis</i>						bifid	faint
Aberdare Mts	32	—	30	2	—		
Uasin Gishu Plateau	9	—	7	2	—		
Kaimosi	15	1	14	—	—		
Kakamega	14	—	14	—	—		
Mt Elgon	23	3	19	1	—		
<i>irroratus</i>						bifid	absent
Eastern Cape	21	21	—	—	—		
KwaZulu-Natal	17	15	2	—	—		
Western Cape	32	29	3	—	—		
<i>orestes</i>						bifid	shallow
Aberdare Mts	10	—	10	—	—		
Mt Kenya	13	7	6	—	—		
<i>tropicalis</i>						bifid	faint
Mt Kenya	59	1	55	3	—		
<i>typus</i>						trifid	deep
Ethiopia	56	—	2	42	12		
<i>uzungwensis</i>						trifid	deep
Tanzania	20	1	18	1	—		

pearance of the highly arched interorbital region or wide spreading zygomata of *orestes*. The skull is in fact almost exactly like skulls of the *tropicalis* group except for small size and the lamina formula.” Tail length of *O. dollmani* is absolutely (Table 2) and relatively longer (TL/HBL \approx 63%) than either *O. orestes* (TL/HBL \approx 46%) or *O. tropicalis* (TL/HBL \approx 50%); in proportional length, it more closely resembles *O. irroratus* (TL/HBL \approx 61%). Hollister’s assessment of cranial size and shape differences is borne out by our multivariate comparisons (Figs. 2, 4), in which the sample of *O. dollmani* is strongly differentiated from examples of *O. irroratus*, *O. orestes*, and *O. tropicalis* (including *elgonis*) (also see Figs. 7, 8).

Bohmann (1952) drew attention to similarities between *dollmani* and *nubilus*

(type locality = Jomberi Range, northeast of Mt Kenya), both of which he treated as subspecies of *O. irroratus*, and emphasized the nearness of their type localities (see Fig. 1) in suggesting their synonymy (he prudently refrained from formally doing so). However, traits of *nubilus* as related in the original description—its dark brown pelage, shorter tail, larger cranial size, and M3 with 7 laminae—to us convey closer resemblance to populations of *elgonis*, as appreciated by the describer Dollman (1915:160): “A very dark race, related to *elgonis* and *tropicalis*.”

Otomys dollmani is so far documented only from Mt Gargues, the type locality. Dollman (1915:157) mentioned additional specimens of *dollmani* from Mt Gargues in the British Museum of Natural Histo-

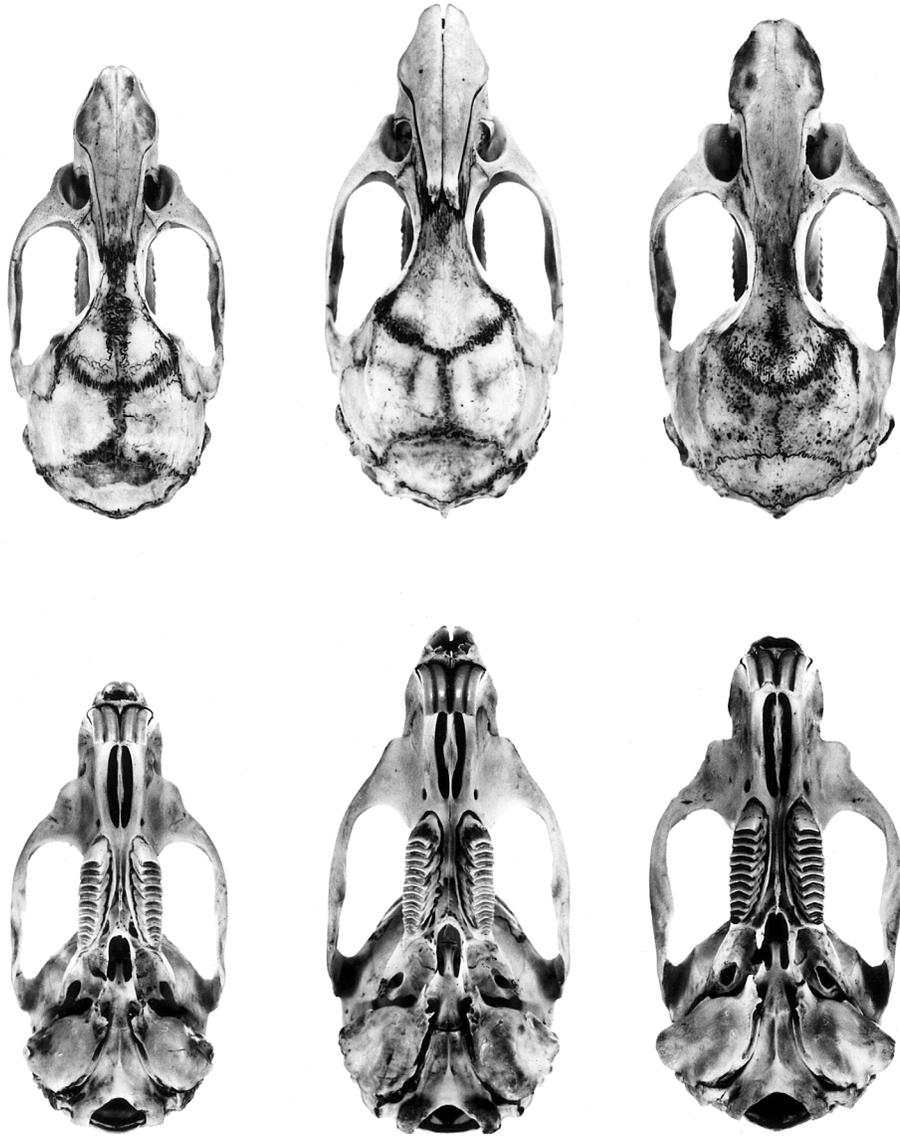


Fig. 7. Dorsal (top) and ventral (bottom) views (ca. 1.75 \times) of adult crania of three species of *Otomys* in Kenya: left, *O. dollmani* (USNM 184046; CIL = 32.7 mm), a female from Mount Gargues; middle, *O. tropicalis (elgonis)* (USNM 184003; CIL = 36.5 mm), a male from Kaimosa Forest; right, *O. orestes* (USNM 164332, CIL = 35.7 mm), a male from Mount Kenya. Heller (1912) described *dollmani* as a subspecies of *O. orestes*, and Misonne (1974) placed it as a synonym of *O. tropicalis*.

ry, collected by Percival, but considered them "too young to be of any systematic use." We have not examined these. New biological surveys should be undertaken to determine whether the species occurs in higher sectors of the Mathews Range, just to the north of Mt Gargues. Minor

discrepancy exists about the altitude of the type locality. Heller (1912) indicated 7000 ft in his description, but as Hollister (1919) observed, all skin tags read 6000 ft. Heller's field notes suggest that either or both altitudes are possible (see next paragraph). Because Heller offered no

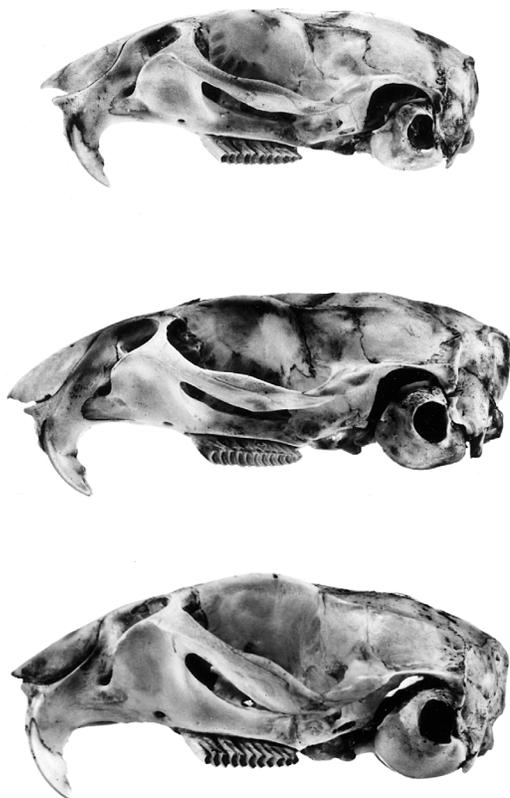


Fig. 8. Lateral views (ca. 1.75 \times) of adult crania of three species of *Otomys* in Kenya (same specimens as illustrated in Fig. 7): top, *O. dollmani*; middle, *O. tropicalis* (*elgonis*); bottom, *O. orestes*.

reason for usage of 7000 ft, we followed Hollister and reported the figure as found on original specimen labels.

In his description of *O. orestes dollmani*, Heller (1912) noted that five specimens were secured in the forest glades at the extreme summit of Mt Gargues. He was slightly more expansive about habitat in his field notes (27 Aug–1 Sep 1911; Mammal Division archives, USNM): “A few *Otomys irroratus* [preliminary field identification] taken at 6300 ft on weedy hillsides. Rarer at 7000 feet.” In his field journal, Heller identified three “floral and faunal zones” along the slopes of Mt Gargues. Specimens of *O. dollmani* originated from the uppermost, which he called the Forest Zone, 5000–7100 ft (summit 8000 ft), and characterized as

“Heavy forest of juniper, *Podocarpus*, olive, croton palms and *Drocaenus*” Within the Forest Zone, he further discerned lower and upper sectors, the lower one forest proper and the upper consisting of “Giant lobelia, date palms, bramble, lupine, lichen and moss.” Although *Otomys* was recorded as an inhabitant peculiar to the Forest Zone of Mt Gargues, Heller did not specify whether they were found in the lower or upper sector, or in both.

Specimens examined.—Kenya, Mathews Range, Mount Gargues, 6000 ft (USNM 181790, 184041–184046).

Otomys orestes Thomas

Otomys irroratus orestes Thomas, 1900:175 (type locality—Kenya, Mount Kenya, Teleki Valley, 13,000 ft [3962 m]).—Wroughton, 1906:275.

Otomys [*orestes*] *orestes*: Dollman, 1915: (elevation to species, de facto arrangement as nominate subspecies).—Hollister, 1919:147 (retention as monotypic species).—Allen, 1939:346 (listed as species and valid subspecies).—Ellerman, 1941:323 (listed as species and valid subspecies).—Setzer, 1953 (retained as valid species and subspecies).—Musser & Carleton, 2005:1528 (retention as species, indication of synonyms).

Otomys typus orestes: Bohmann, 1952:47 (new name combination as valid subspecies).—Misonne, 1974:33 (listed in synonymy without indication of rank).—Musser & Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys thomasi Osgood, 1910: (type locality—Kenya, Molo; type specimen—FMNH 16698).

Otomys [*thomasi*] *thomasi*: Dollman, 1915:153 (listed as species, de facto arrangement as nominate subspecies).—Hollister, 1919:147 (listed as valid species and subspecies).—Allen, 1939:346 (listed as valid species and

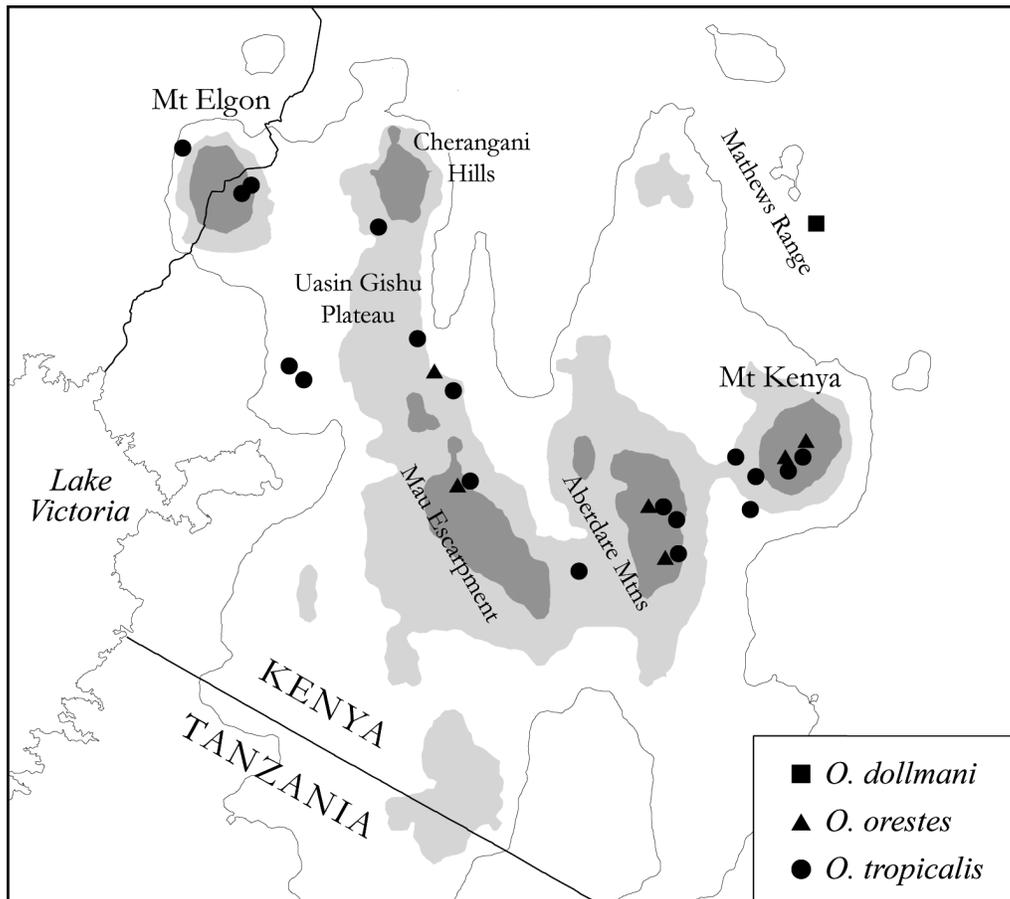


Fig. 9. Distribution of *Otomys dollmani*, *O. orestes*, and *O. tropicalis* in Kenya based on specimens examined by us.

subspecies).—Ellerman, 1941:323 (listed as valid species and subspecies).

Otomys typus thomasi: Bohmann, 1952:41 (new name combination as valid subspecies).—Misonne, 1974:33 (listed in synonymy without indication of rank).

—Musser and Carleton, 1993:682 (listed in synonymy without indication of rank).

Otomys orestes [thomasi]: Musser & Carleton, 2005:1529 (*thomasi* allocated as synonym without indication of rank).

Distribution.—Discontinuous in alpine settings, ca. 2700–4200 m, from western and central Kenya (Fig. 9), presumably to northeastern Tanzania (Grimshaw et al. 1995, reported as *O. typus zinki*).

Emended diagnosis.—Compared with *O. tropicalis*, post-auricular patches present, tail relatively and absolutely shorter, hindfoot smaller. Skull strongly arched (flatter profile in *O. tropicalis*); rostrum narrower, nasal tips not so abruptly flared toward tips; interorbit more narrowly constricted; zygomatic arches expanded anteriorly, somewhat boxy (bowed and widest in middle and slightly convergent anteriorly in *O. tropicalis*), maxillary process of zygoma deeper and zygomatic plate shorter; parapterygoid fossa deeper, more cavernous, anterior portion slightly undercutting hard palate; bullae relatively and absolutely larger. Molar rows and incisors narrower; M3

with 6–7 laminae (8–9 in *O. typus*); lower incisor tip bifid (trifid in *O. typus*), with medial groove consistently expressed albeit shallow (not deep as per *O. typus*; wider, shallower, more facet-like in *O. tropicalis*).

Remarks.—Thomas (1900) differentially compared *O. irroratus orestes* from the alpine zone of Mt Kenya (13,000 ft) to a then unnamed form from lower slopes (8000–10,000 ft) on the same mountain, not to *O. irroratus sensu stricto* from southern African. Shortly thereafter, he (1902) named the other Mt Kenyan form *tropicalis*, which he also described as a subspecies of *O. irroratus*. Our morphometric results support Thomas' discernment of two forms along the upper slopes of Mt Kenya, one present in alpine settings (*orestes*) and the other (*tropicalis*) in the montane forest-bamboo zone, and add weight to the subtle cranial features that he visually appreciated in separating them (Figs. 7, 8). The more strongly arched skull (DSO) of *O. orestes*, its narrower interorbit (IOB), and narrower molars (WM1) are dimensions that all contribute prominently to segregating *orestes* from OTUs of *tropicalis* in morphometric space (see Figs. 4, 5; Tables 5, 6); to these size and shape contrasts may be added the narrower incisors (BIs) of *O. orestes*, its relatively and absolutely larger ectotympanic bullae (LAB, DAB), and shorter zygomatic plate (BZP), which also contribute significantly to morphometric segregation but which were not mentioned by Thomas (1900). The smaller hindfoot in *O. orestes* and its noticeably shorter tail, as quantified in Table 2, are also consistent with the diagnostic contrasts mentioned by Thomas. None of our measured variables reflects the differences in depth of the zygomatic arch (see Fig. 8) and area of the parapterygoid fossa, apparent to us and mentioned in the emended diagnosis; presumably a geometric morphometric approach could better analyze the consis-

tency of these contrasts and their taxonomic value.

Although some systematists have viewed the status of *orestes* as a distinct species, following the taxonomic action of Dollman (1915; also Hollister 1919, Setzer 1953, Musser & Carleton 2005), others have treated it as a subjective synonym of *O. typus*, observing the precedent introduced by Bohmann (1952; also Misonne 1974, Musser & Carleton 1993). This synonymy is unsupported by our analyses, which unambiguously reveal *orestes* to be as distinct from *O. typus* in Ethiopia as it is from contiguous populations of *O. tropicalis* in Kenya. Coupled with the singular morphometric footprint of *orestes*, its historical inclusion as a subspecies of *O. typus* is questioned by qualitative differences in M3 lamination (6–7 laminae in *O. orestes* versus 8–9 in *O. typus*) and lower incisor sulcation (1 deep and 1 shallow groove in *O. orestes* versus 2 deep creases in *O. typus*) and by the pronounced disjunction of alpine habitats in the Ethiopian Highlands and those on high mountains that border the Eastern Rift Valley (see Discussion).

Which other species-group taxa belong as junior synonyms of *O. orestes*? Musser & Carleton (2005) listed five (*malleus* Dollman 1915, *percivali* Dollman 1915, *squalus* Dollman 1915, *thomasi* Osgood 1910, *zinki* Bohmann 1943) based on original descriptions, comparisons conducted by early workers (Dollman 1915, Hollister 1919, Bohmann 1952), and biogeographic plausibility. Of those five, we have examined only the holotype (FMNH 16698) and referred specimens (FMNH 16694, 16699) of *O. thomasi* from Molo, Kenya. Curiously, Osgood (1910) contrasted his new species only with *O. irroratus tropicalis*, but the qualitative features he noted for *thomasi*—narrow nasals, conspicuously arched skull, and creamy buff post-auricular patches—recall those of *O. orestes*, as

later stressed by Dollman (1915), Bohmann (1952), and Lawrence & Loveridge (1953) in their taxonomic comparisons. The type is a large individual (Bohmann [1952] considered it very old, but we graded it as full adult), but the other two specimens (skulls incomplete) fit within the range of size variation of the series of *O. orestes* from the Aberdare Mts. Entered as an unknown in 8-group discriminant function analysis, the type was indisputably assigned as a member of the *orestes* OTU ($P = 0.999$), in contrast to the 7 other OTU options available among *dollmani*, *elgonis*, *tropicalis*, and *typus*; in our principal component results, the score of the specimen fell at the margin of PC I variation for *orestes*, consistent with Bohmann's interpretation of its advanced age, and outside the sphere of dispersion of *elgonis* and *tropicalis* specimens (Fig. 5). Although these results support allocation of *thomasi* Osgood to the synonymy of *O. orestes*, given the data at hand, we stress that sample sizes are abysmally small. The specific union of the taxon (*thomasi*) named from highlands to the west of the Rift Valley in Kenya with those (*orestes*, *malleus*, *percivali*, *squalus*) described from mountains to the east must be tested with fresh material and other information bases.

Our specimens from the summit of the Aberdare Mts may essentially represent topotypes of Dollman's (1915) *O. thomasi squalus* (type locality—Mt Kinangop, Aberdare Mts, 12,000 ft), as the series was reported by Hollister (1919), but we have not studied the type specimen itself. Examination of that type, along with those of *malleus* and *percivali*, original type series, and, as importantly, fresh topotypic material, is required to certainly resolve the synonymy of these epithets described from the Aberdare Mts. Of the synonyms attributed by Musser & Carleton (2005), *O. typus zinki* Bohmann (1943), described from Mt Kilimanjaro at 3800 m, especially merits reconsidera-

tion based on its isolation from Afroalpine zones in Eastern Rift mountains of central Kenya (Fig. 1) and on the distinctive pelage colors recounted by Bohmann (1952).

The concept of *O. orestes* advanced here essentially circumscribes Dollman's (1915) *Otomys* Division B, Section I, to which he assigned the species *O. thomasi* (including *malleus* and *squalus*) and *O. orestes* (including *dollmani*). He considered the two to be morphologically highly similar but emphasized the difference in M3 laminae, 7 in *thomasi* and 6 in *orestes*, in maintaining them as separate species. As detailed in the Results and Comparisons, 6 or 7 laminae occur in equal frequency within our small sample of *orestes* proper from Mt Kenya; 7 laminae uniformly characterize the M3s in samples from the Aberdare Mts and Uasin Gishu Plateau, including the type and topotypes of *thomasi*. The constancy of laminae counts, however, must be viewed cautiously given our small locality samples, an insufficiency that once again prescribes new material. We are impressed that Dollman's (1915) and Bohmann's (1952) taxonomic comparisons regularly featured *orestes* vis-à-vis *thomasi*, *squalus*, and *malleus*, and were it not for the mistaken acceptance of laminar difference, we suspect that they would have considered those taxa even more closely related, if not synonymous. All such populations of *O. orestes* inhabit open habitats above treeline and exhibit a characteristic morphology. At lower altitudes within the Aberdare Mts and on Mt Kenya, examples of *O. orestes* have been collected in sympatry with *O. tropicalis* (see respective Specimens examined). Whether such instances reflect occupation of the same biotope or whether alpine and montane forest elements are intermixed at those elevations cannot be deduced from the collectors' field journals. Long term ecological studies and elevational surveys, such as those con-

ducted by Clausnitzer (2001) and Clausnitzer & Kityo (2001) on Mt Elgon, are needed.

Specimens examined.—Kenya: Aberdare Mts, summit, 11,000 ft (USNM 184033–184035); Aberdare National Park, Fishing Lodge, 8760, 9000, and 9500 ft (USNM 589995–589997); Uasin Gishu Plateau, 20 mi N Eldama Ravine, 9000 ft (USNM 164290); Molo (FMNH 16694, 16698, 16699; type and original topotypes of *O. thomasi* Osgood, 1910); Mt Kenya, 10,700 ft (FMNH 43444; USNM 164308, 164346, 164357, 164358), 13,500 ft (USNM 164293–164295, 164297, 164329, 164332–164334), 13,700 ft (FMNH 43445, 43446; USNM 164300–164305, 164344, 164345).

Otomys tropicalis Thomas

Otomys irroratus tropicalis Thomas, 1902:314 (type locality—Kenya, western slope of Mt Kenya, 10,000 ft).—Wroughton, 1906:274 (listed as valid subspecies).—Bohmann, 1952:33 (retained as valid subspecies); Delany, 1975:53 (listed as synonym without indication of rank).—Honacki et al., 1982:445 (given as synonym without indication of rank).

Otomys [tropicalis] tropicalis: Dollman, 1915:157 (elevation to species, de facto arrangement as nominate subspecies).—Hollister, 1919:148 (listed as valid species and subspecies).—Allen, 1939:347 (listed as valid species and subspecies).—Ellerman, 1941:322 (listed as valid species and subspecies).—Misonne, 1974:34 (listed as species, indication of synonyms).—Corbet & Hill, 1980:159 (listed as species).—Corbet & Hill, 1986:178 (listed as species).—Corbet & Hill, 1991:167 (listed as species).—Musser & Carleton, 1993:681 (listed as species, indication of synonyms).—Musser & Carleton, 2005:1529 (listed as species, indication of synonyms).

Distribution.—As currently understood, highlands in eastern Africa, mostly 1800

to 3200 m, from southern Sudan and Ethiopia, through eastern D. R. Congo, Uganda, and western Kenya, to Rwanda and northeastern Tanzania.

Remarks.—Together with *O. irroratus orestes*, *O. i. tropicalis* was the second kind of vlei rat that Thomas (1902) recognized as dwelling on the upper western slopes of Mt Kenya. He (1902:314) pithily characterized *tropicalis* as “The northern strong-coloured form of *O. irroratus*, with seven laminae to the last upper molar,” and considered it to be the widespread *Otomys* in “Eastern Tropical Africa, from British East Africa [Uganda, Kenya] to Nyasaland [Malawi].” Wroughton (1906) considered the Zambezi River to be the geographic divide that separated northern (*tropicalis*) and southern (*irroratus*) forms of the *O. irroratus* complex, but Dollman (1915:149) accentuated its importance when he raised *tropicalis* to species: “... *tropicalis* taking the place of *irroratus*, which species, on account of its cranial structure and lamina formula, is not considered a near enough relative for the name to be used in connection with the East-African forms; in this manner, we confine *irroratus* and its subspecies to the country south of the Zambesi.” In spite of a workable diagnosis and persuasive biogeographic context, mammalogists thereafter dithered over treatment of *tropicalis* as a race of *O. irroratus* (Bohmann 1952, Delany 1972) or as a distinct species (Allen 1939, Hatt 1940, Misonne 1974, Musser & Carleton 1993). The recent study of Taylor & Kumirai (2001) brings decisive illumination to this issue in demonstrating that clear cranio-metric differentiation accompanies the qualitative dental and pelage contrasts between *O. irroratus* and *O. tropicalis* long ago appreciated by Thomas, Wroughton, and Dollman. Our results reinforce the conclusion of Taylor & Kumirai (2001) apropos the specific distinction of *O. tropicalis* from *O. irroratus* in southern Africa and additionally provide evidence

for segregation of *O. tropicalis* from *O. dollmani*, *O. orestes*, and *O. typus sensu stricto* in eastern Africa.

As with *O. orestes*, the legitimacy of synonyms allocated to *O. tropicalis* and refinement of its geographic distribution invite future studies that pose specific taxonomic hypotheses within critical regional contexts, that amplify field surveys and sample sizes, and that incorporate new data bases. Musser & Carleton (2005) assigned eight species-group taxa to *O. tropicalis*—*elgonis* Wroughton 1910 (Elgonyi, Mt Elgon, Kenya), *faradjius* Hatt 1934 (Faradje, D. R. Congo), *ghigii* de Beaux 1924 (Bugala, Uganda), *giloensis* Setzer 1953 (Gilo, Imatong Mts, Sudan), *nubilus* Dollman 1915 (Jomberi Range, Kenya), *rubeculus* Dollman 1915 (Kagambah, Uganda), *vivax* Dollman 1915 (Mt Nyiro, Kenya), *vulcanis* Lönnberg and Gyldenstolpe 1925 (Mt Sabinio, D. R. Congo)—based on the comparative context given in many of the original descriptions, which recurringly referenced *tropicalis* or *elgonis* or both. They further identified three morphological assemblages among these epithets that may merit specific status: *tropicalis* proper on Mt Kenya, *elgonis* (provisionally including *faradjius*, *ghigii*, *giloensis*, *nubilus*, *vivax*), and *rubeculus* (provisionally including *vulcanis*). Wroughton (1910) described *elgonis* as being most similar to *tropicalis*, except for smaller size and darker pelage color, a resemblance robustly sustained by results of our morphometric analyses (Figs. 2, 4, 5). The usual overlap in multivariate space among examples of *tropicalis* and *elgonis* contradicts the speculation of Musser and Carleton and justifies their continued synonymy. Although the type specimens of *tropicalis* and *elgonis* were not consulted, we are confident that our samples from the slopes of Mt Kenya and Mt Elgon comprehensively represent, respectively, the morphologies intended by Thomas (1902) and Wroughton (1910).

The core distribution of *O. tropicalis* occupies the highlands of western and central Kenya (Fig. 9), but the limits of its range, to the north, south and west, are poorly documented. We have examined the type and referred series of *Otomys orestes giloensis* Setzer, 1953 (type locality—Sudan, Gilo, 6500 ft), known from the Imatong Mts in southern Sudan (FMNH 73901, 79456–79463, 108207, 108208). Setzer contrasted his new Sudanese subspecies with the Kenyan taxa *orestes dollmani* (sensu Heller 1912) and *o. orestes* (sensu Dollman 1915), a narrow scope of comparison shaped by his interpretation of 6 laminae on the M3 of his type series. Our examination of those specimens uniformly revealed a 7-laminated M3, a discrepancy that must reflect different criteria for scoring laminae. In view of the affinity and rank supposed by its describer, along with Bohmann's (1952) union of *orestes* with *typus*, *giloensis* was afterwards swept under the synonymy of *O. typus sensu lato* (Misonne 1974, Musser & Carleton 1993). Nevertheless, in 8-group discriminant function analysis including samples of *elgonis*, *orestes*, *tropicalis*, and *typus*, the holotype of *giloensis* (FMNH 73901) was associated with two of the smaller-bodied OTUs of *elgonis*, at comparable levels of a posteriori probabilities (KA, $P = 0.466$; ME, $P = 0.398$), not with the samples of *O. orestes* from Kenya or *O. typus* from Ethiopia. This analytical consignment concurs with our estimation of its affinity derived from inspection of skins and skulls: *giloensis* is a darkly colored animal, slightly smaller and more uniformly chocolate brown than typical *elgonis*, but it possesses the cranial shape, lower incisor grooving, and 7-laminated M3 that otherwise recall the *elgonis* morph. The presence of *O. tropicalis* in southwestern Ethiopia was reported by Musser & Carleton (2005), who noted it (FMNH 28165) as altitudinally parapatric with *O. "typus"* on Mount Albasso.

The kinds, detailed distribution, and ecology of *Otomys* in Ethiopia invite wholesale revision (also see Lavrenchenko et al. 1997).

Towards the south, the material reported from Mts Meru and Kilimanjaro in northeastern Tanzania plausibly represents *O. tropicalis* (Demeter & Hutterer 1986, Grimshaw et al. 1995), based on the authors' descriptions of morphology and/or elevational range and habitats. A small series from the West Usambara Mts, a range forming the eastern portion of the Eastern Arc Mts, also fits with *O. tropicalis* (Shume, 6000–7000 ft [USNM 381484–381487]; Sunga [USNM 340800]). Sunga is the type locality of *O. denti sungae*, which Bohmann (1943) named as an outlier subspecies to the main distribution of *O. denti* in Western Rift mountains (type locality = Uganda, Mt Ruwenzori, 6000 ft). Compared with *O. denti* proper, however, these specimens exhibit more spatulate-shaped nasals, a broader zygomatic plate that partially covers the premaxillary-maxillary suture (thus a deeper zygomatic notch), larger otic capsules, broader upper incisors, lower incisors with a faint medial groove, and M3 with 7 laminae [Bohmann (1943) reported 6 laminae based on the type and 1 other specimen in the BMNH]. All of these traits are indicative of *O. tropicalis*, in particular the *elgonis* morphology. The rich blackish-brown pelage in these 5 specimens favorably compares to Bohmann's (1943, 1952) description of *O. denti sungae*, but such a dark tone is approached by other taxa currently associated with *O. tropicalis*—e.g., more strongly saturated examples of *elgonis* and the type series of *giloensis* and *nubilus* (Dollman 1915, Setzer 1953), taxa also described from lower mountains near the distributional periphery of *O. tropicalis*. If the USNM specimens prove to be representative of *sungae* proper, future investigation should determine whether the taxon is a junior synonym of *O. tropicalis*

or whether it is a valid species endemic to the Eastern Arc Mountains and related to the *O. tropicalis* complex. At whichever rank, such a phyletic affinity is biogeographically as persuasive as its present classification under *O. denti*, otherwise known from mountains along the upper Western Rift Valley.

To the west, the synonymy of *rubeculus* Dollman (1915) and *vulcanis* Lönnberg & Gyldenstolpe (1925), from southwestern Uganda and northernmost Rwanda, respectively, under *O. tropicalis* or with one another should be objectively demonstrated. One can only suspect, for instance, that much of the confusing variation that Dieterlen (1968) encountered within *O. "irroratus"* from mountains around Lake Kivu indicated the presence of two or more species, one of which should bear the regional epithet *vulcanis*. Furthermore, the morphological and genetic homogeneity of populations represented by these epithets, described from mountains rising astride the Western Rift Valley, with *O. tropicalis* and others named from Afromontane highlands bordering the Eastern Rift Valley, must be viewed skeptically based alone on geographic occurrence and on the pronounced biotic discontinuity established between the two mountain systems (e.g., see Moreau 1966, White 1978, Dowsett 1986, Carleton et al. 2006).

Specimens examined.—Kenya: Aberdare Mts, 10,500 ft (USNM 164279, 164280), summit, 11,000 ft (USNM 184025–184032, 184037–184340); Aberdare Mts, Changongorra, 7000 ft (USNM 184019–184023); Aberdare National Park, Fishing Lodge, 8760, 9000, and 9500 ft (USNM 589998, 589999, 590002, 590003, 590012–590015); 12 mi N Eldama Ravine, 8800 ft (USNM 164281); Uasin Gishu Plateau, 30 mi N Ravine, 8600 ft (USNM 164286–164289); Uasin Gishu Plateau, Nzoia River, 6000 ft (USNM 164282–164285); Kaimosi Forest (USNM 184003–184017); Kakamega (MCZ

31375, 31416–31420, 31432–31437, 31439, 31440; USNM 184018); Molo (FMNH 16693, 16695); Mt Elgon National Park, 15 km from Chorlim Gate towards Koi-tobos Peak (USNM 590004–590006, 590011); Mt Kenya, west slope, 7000–13,700 ft (CM 2836, 2837; FMNH 43819–43822; USNM 164277, 164291–164293, 164296, 164298, 164299, 164307, 164309–164312, 164314–164324, 164326, 164330, 164331, 164337–164343, 164347–164350, 164353, 164354, 164356, 164359–164363, 164365–164373, 164375); Mt Kenya, Naro Moru, 10,000 ft (USNM 590000, 590001); Mt Kenya, Naro Moru Gate, Meteorological Station, 10,000 ft (USNM 590007–590010); Naivasha Plains, Nalsitichu River (USNM 184036); 10 mi E Nyeri (USNM 164278). Uganda: Mt Elgon, Sipi (MCZ 31269–31272, 31373, 31374, 31377–31381, 31426–31432).

Discussion

The biological species narrative and current underestimation of diversity within Otomyinae.—By the close of the fertile era of taxonomic discovery of African Rodentia (ca. 1880–1930), 28 or 30 species of otomyines were recognized (Allen 1939, Ellerman 1941). Emergence of the New Systematics (Huxley 1940) and biological species concept (Mayr 1942) in the middle 1900s profoundly influenced how mammalogists treated and nomenclaturally conveyed interpopulation variation. Specific taxa based on supposedly minor features of size and pelage during the early descriptive phase were routinely reconsidered as geographic variants or subspecies, often with little or no presentation of supportive data. Examination of the pivotal reasoning for some of these synonymies is instructive. For example, Ellerman et al. (1953:307), aligned *angoniensis* as a subspecies of *O. irroratus*, contra Roberts (1951) who maintained the two as distinct based on distal nasal shape, because “this seems

altogether too slight a character on which to base species” In this particular instance, quantitative comparisons of the degree of nasal flaring have proven helpful for discrimination of closely related species of *Otomys* (Taylor & Kumirai 2001, Taylor et al. 2005). For Ellerman and other taxonomists of the middle 1900s, however, certain classes of characters, especially subtle size and shape distinctions, were a priori viewed as indicative of geographic variation and deemed useful only for recognition of subspecies.

Bohmann’s (1952) study appeared at the crest of this new “population thinking” and constituted the watershed publication in applying this research paradigm to patterns of inter- and intraspecific variation among named forms of *Otomys* (He recognized the single genus *Otomys* and no subgenera; most authors have retained *Parotomys* as generically distinct.). Eleven species, nearly all polytypic and some of these morphologically highly heterogeneous, were recognized by Bohmann. His construct of an exceptionally polymorphic *O. irroratus*, distributed over much of Sub-Saharan Africa, was successively broadened to subsume three forms that he had maintained as species—*anchietae*, *lamina-tus*, and *typus*—further decreasing the number of species to only 8 (Dieterlen 1968, Petter 1982). Unfortunately, the recommendations in the latter contributions lacked the synoptic regional and taxonomic perspective developed by Bohmann and compounded his underestimation of otomyine diversity. By the late 1900s, when taxonomic listings of mammalian species became popular, the number of valid species had stabilized at 12 or 13 (Misonne 1974, Corbet & Hill 1980, 1986, 1991; Honacki et al. 1982, Musser & Carleton 1993—The departure from Bohmann’s recognition of 11 reflected the tendency in these works to maintain eastern African *tropicalis* as distinct.). Classifica-

tory consensus over the past 30 yr should not be confused with systematic understanding: repetition without recourse to new data or new methods of evaluating old data does little to advance it.

Given such systematic quiescence, the notion has passively entered the recent literature that differentiating traits relied upon in the pioneering studies of otomyines are too highly variable to be taxonomically useful at the species level. Lawrence & Loveridge (1953:60), for example, remarked that “the grooving on the lower incisors and the lamina formula of M3/ in *Otomys* are highly plastic.” More recently, Taylor and Kumorai (2001:162) prefaced their cranio-metric study by observing that “the taxonomy of the group is highly unstable due to variability in diagnostic characters, usually involving the number of laminae in M3 and M1, grooving of the incisors....” That these characters are inordinately variable and extremely plastic is implicit in the disparate synonymies and heterogeneous morphologies that Bohmann (1952) submerged under the “species” *O. irroratus* and *O. typus*, but his study did not constitute an empirical demonstration of such variability. A proponent of Rensch’s (1929) rassenkreis concept, the intellectual predecessor to Mayr’s (1942) polytypic species, and intent on identifying geographically replacing subspecies, Bohmann’s revision remains an insightful narrative of evolutionary and biogeographic diversification within *Otomys*, but it less critically addressed among-population variation and character intergradation as bases for delimiting species. In consequence of the immense amount of inter-population variation embraced by his permissive definitions of species limits, it was a small step for Dieterlen (1968) and Petter (1982) to rationalize the morphological boundaries of *O. irroratus* as also embracing *anchietae*, *laminatus*, and *typus*. In hindsight, a curious circularity has pervaded the

alpha-level systematics of otomyine rodents in the latter 1900s: in aggregating so many more or less distinctive forms as supposedly intergrading subspecies, as was impelled by the persuasive orthodoxy of the biological species concept, taxonomists could afterwards only lament the immense plasticity of morphological traits and their insufficiency as diagnostic characters at the species level.

That perception may have stemmed from the words of the illustrious taxonomist Oldfield Thomas (1918:204), who considered “the grooves on the incisors, and the numbers of the molar laminae, used so effectively by Wroughton and Dollman for the sorting of species, are so plastic, and show so wide a range of variation, that, however useful for specific distinction, they have to be used with great caution when generic divisions are in question.” Careful rereading of his comments, however, indicates that he readily acknowledged the utility of these features for species-level systematics—“however useful for specific distinction”—but not for genus-group arrangements. Thomas’ statement was meant to introduce his emphasis of other cranial features (bullar size, nasal expansion, interorbital constriction), in a paper expressly designed to revise the classification of Otomyinae and to define new genera and subgenera (e.g., *Anchotomys*, *Myotomys*, *Parotomys*), not to reevaluate specific limits. His observations on the morphological plasticity and extraordinary variation of otomyine dentitions have been taken out of context as they bear on species-level questions.

Notwithstanding Thomas’ (1918) depreciation of molar lamination and incisor grooves for delineating major lineages among otomyine species (genera and subgenera), it is tellingly ironic that he was nonetheless obliged to rely on these very same characters in his taxonomic key and genus-group diagnoses. Indeed, we find it noteworthy that traits

of molar lamination and incisor sulcation have regularly served in identification keys to otomyine species, whether employed in taxonomic or faunal works (Wroughton 1906, Dollman 1915, Ellerman et al. 1953, Misonne 1974, Delany 1975, Smithers 1983, Meester et al. 1986, Taylor 1998). The practical application of these characters issues from their pronounced modal development within population samples distributed over broad geographic regions, which is the actual pattern of variation so far documented for otomyines (Table 8; Dollman 1915, Bohmann 1952, Taylor & Kumirai 2001). Numbers of M3 laminae do not range from 4 to 10 within populations and modal counts do not vary randomly among geographic samples. Such usefulness in keys, in and by itself, controverts the notions of inordinate plasticity and uninformative variation, particularly in a rodent superfamily wherein morphological differences among closely related species usually rest upon minimally perceptible features of size, shape, and pelage texture or color. A combination of continuous and qualitative features is typically necessary for workable definition and recognition of taxa at the species level in Muroidea. Considered against this experience, readily grasped meristic characters such as molar laminae are a boon not to be casually dismissed.

And in point of fact, variation in M3 laminae regularly complements spatial structure evident in the multivariate summaries of craniodental covariation. Although number of laminae was scored for each specimen used in our various morphometric comparisons, we emphasize that it was not entered as an analytical variable. Still, post hoc tests of M3 number as categorical effect in analyses of variance typically disclosed significant mean differences among the extracted factors, whether principal component or canonical variate (Table 9). The magnitude of F values seldom

exceeded those of taxon or OTU as a post hoc grouping variable (especially in DFAs wherein OTU was procedurally inherent to the computation), but the significance level attained by M3 laminae often matched those broader group effects. Furthermore, all three of those group effects conventionally dwarfed the contribution of sex and age cohorts to dispersion of factor scores. A notable, and predictable, exception to this generalization involved the influence of age-class upon first principal component scores extracted in two of the three factor analyses (see explanation under Results); in these instances, taxon, OTU, and-or M3 laminae emerged as important categorical effects on the second component derived (Table 9). In summary, differences in number of M3 laminae covary intelligibly with unambiguous discrimination of otomyine populations and species in morphometric space, and these patterns intimate a significant degree of morphogenetic integration and ontogenetic canalization. Applied in concert with such continuous variables and other discrete traits, molar lamination is a taxonomically informative and highly useful character system for distinguishing otomyine species.

Of the taxa considered herein, Bohmann (1952) had allocated some to *O. irroratus* (23 subspecies, including *dollmani*, *elgonis*, and *tropicalis*) and some to *O. typus* (11 subspecies, including *orestes* and *thomasi*). Taylor & Kumirai (2001) have previously cemented the morphometric argument for separation of southern African *O. irroratus* from eastern African *O. tropicalis sensu lato* and from *O. typus sensu lato* (i.e., according to Bohmann 1952, Misonne 1974). We regard the retention of *O. dollmani*, *O. orestes* (including *thomasi*), *O. tropicalis* (including *elgonis*), and *O. uzungwensis* as valid species, distinct from *O. irroratus* and *O. typus*, as a rough first-glimpse to the species diversity yet to be uncovered

Table 9.—One-way ANOVAs generated for various group effects on results of discriminant function (DFA) and principal component (PCA) analyses of *Otomys*: 9-group DFA (see Fig. 2); 8-group DFA (see Fig. 4); 3-group DFA (see Fig. 6); PCA of samples of *O. irroratus* and *O. tropicalis* (including *elgonis*; see Fig. 3); PCA of samples of *O. orestes* and *O. tropicalis* (including *elgonis*; see Fig. 5); and PCA of samples of *O. orestes*, *O. typus*, and *O. uzungwensis* (see Fig. 6).

Variable	<i>F</i> (taxon)	<i>F</i> (OTU)	<i>F</i> (sex)	<i>F</i> (age)	<i>F</i> (M3 laminae)
DFA: 9 OTUs					
CV 1 scores	170.1***	73.7***	0.3	3.2*	80.1***
CV 2 scores	31.3***	30.9***	3.5	0.1	1.3
DFA: 8 OTUs					
CV 1 scores	134.9***	101.6***	1.9	1.3	6.7**
CV 2 scores	75.6***	47.8***	0.8	0.1	19.3***
DFA: 3 Highland OTUs					
CV 1 scores	228.1***	—	3.1	2.7	14.2***
CV 2 scores	87.3***	—	0.0	0.8	4.1*
PCA: <i>O. irroratus</i> - <i>O. tropicalis</i>					
PC I scores	13.9***	5.7***	0.5	34.3***	4.5*
PC II scores	114.1***	24.4***	0.3	0.2	30.8***
PCA: <i>O. orestes</i> - <i>O. tropicalis</i>					
PC I scores	2.1	3.5**	1.8	29.9***	1.6
PC II scores	68.3***	44.6***	0.0	0.5	3.3*
PCA: <i>O. orestes</i> - <i>O. typus</i> - <i>O. uzungwensis</i>					
PC I scores	9.0**	—	1.9	1.7	4.9**
PC II scores	38.1***	—	3.7*	7.8**	1.5

* = $P \leq 0.05$;

** = $P \leq 0.01$;

*** = $P \leq 0.001$.

in eastern Africa. As remarked in the above taxonomic summaries, the homogeneity of *O. orestes* and *O. tropicalis* as arranged herein are highly questionable. *Otomys typus*, even with removal of *O. orestes* and *O. uzungwensis* and as restricted to Ethiopian plateaus, remains a composite (see Lavrenchenko et al. 1997, Musser & Carleton 2005). The stature of *O. dartmouthi* and *O. jacksoni*, viewed as species by earlier authors and Musser & Carleton (2005) or classified under *O. typus* by Bohmann (1952) and others, still requires validation. Synonyms attributed to *O. denti* (*kempi* and *sungae*) deserve reevaluation. New species will likely emerge from the upper elevations of other mountains in eastern Africa that have yet to receive thorough field survey. And so on. Redressing these inadequa-

cies, coupled with continued investigation of *Otomys* found south of the Zambezi River (e.g., see Taylor et al. 2004b), will surely restore the diversity within Otomyinae at least to the level of 28–30 species, although doubtfully the same ones enumerated by Allen (1939) and Ellerman (1941).

In light of resurgent assessments of species limits within Otomyinae (Dieterlen & Van der Straeten 1992, Taylor & Kumirai 2001, this study), Guy Dollman's (1915) classification of *Otomys* in eastern Africa earns a retrospective salute for its modern outlook. His study elevated to species many forms treated as subspecies of *O. irroratus* by Thomas (1900, 1902) and Wroughton (1906)—e.g., *O. angoniensis*, *O. denti*, *O. orestes*, and *O. tropicalis*—and following the

retrograde interlude in the middle 1900s when the stature of most was again buried under *O. irroratus*, their validity as species is gaining renewed appreciation. Dollman further underscored the biogeographic significance of the Zambezi River in separating eastern and southern species complexes of *Otomys*. Of the several patronyms associated with the genus, *O. dollmani* Heller (1912) is among the most appropriate and deserved.

Montane biotopes in eastern Africa and the diversification of Otomys.—The Kenyan species of *Otomys* central to this study are restricted to moist montane environments in eastern Africa (Fig. 9), the majority of localities falling within an elevational belt covering 1800 to 4000 m. Two species are found in middle to upper montane zones, one narrowly (*O. dollmani*) and one more broadly distributed (*O. tropicalis*), and one occurs higher in ericaceous vegetation and tropical alpine habitats (*O. orestes*). Based on such ecological occurrences and a naturally discontinuous highland setting, these species comprise elements endemic to the Afromontane Biotic Region. The region is sometimes used in a broad sense to include both wet montane forests and open habitats above continuous tree canopy (i.e., following White 1978, 1981); others consider the capstone afroalpine vegetation to comprise a separate biotic region (Hedberg 1986, Clausnitzer 2001). According to either definitional scope, the Afromontane Region of Sub Sahara Africa is highly disjunct and archipelago-like in its occurrence, consisting of several mountain ranges and highland blocks that are diverse in geological age and orogenic formation; these nonetheless share a characteristic and largely stenotopic high-altitude flora and fauna. Within the Afromontane Region (*sensu lato*), both botanical and ornithological biogeographers have distilled distributional patterns and foci of endemism to denote seven major mountainous

groups (Moreau 1966, Dowsett 1986, White 1978, 1981), most of which are congruent but which differ between the disciplines in exact limits and in name. *Otomys dollmani* and *O. orestes*, as understood here, fall within the Kenya montane group (according to the ornithological designation). *Otomys tropicalis*, as currently arranged, is found in the Kenya and East Congo montane groups but may extend to the periphery of the Ethiopian Plateau and Tanganyika-Nyasa Ranges. The endemism levels and localized distributional patterns exhibited by other plants and animals that inhabit these same mountain systems expose the probable composite nature of this provisional arrangement of *O. tropicalis* (White 1978, Dowsett 1986, Stuart et al. 1993, Bowie et al. 2004, 2006; Carleton et al. 2006.).

In our view, the conceptual approach to understanding specific radiation of *Otomys*, especially in eastern African highlands, has been misdirected, hindered by the historical preference for large, broadly distributed polytypic species and implicit reliance on a model of geographic (allopatric) speciation. Bohmann's (1952) definition of *O. typus*, as expanded by Misonne (1974) and currently accepted in most systematic works, exemplifies our point. The species' distribution was decidedly patchy, extending from the Ethiopian plateaus (nominate *O. typus* and the subspecies *fortior*, *helleri*, and *malleus*), across the highest mountain tops in eastern African—Ruwenzori Mts (*dartmouthi*), Mt Elgon (*jacksoni*), Mau Escarpment (*thomasi*), northern and southern sectors of the Aberdare Mts (*malleus* and *squalus*), Mt Kenya (*orestes*), and Mt Kilimanjaro (*zinki*)—to as far south as Mt Rungwe and the Udzungwa Mts in western Tanzania (*uzungwensis*). Observing the tenets of a polytypic species, Bohmann was forced to assume that the isolated populations indicated the past general distribution of *O. typus* in

eastern Africa and former interconnections among afroalpine biotopes, presumably during pluvial maxima of the Pleistocene.

Botanical evidence for such past connections of afroalpine zones has not been forthcoming. Hedberg (1986:457) remarked that "... intermountain contacts may have been established for the montane forest belt, but such contacts are unlikely to have been possible for the ericaceous and afroalpine belts," and that "... there is no evidence of any large-scale Pleistocene intermountain dispersal of afroalpine vascular plants." Working with giant senecios (*Dendrosenecio*, Asteraceae), a spectacular genus iconographic of afroalpine habitats, Knox & Palmer (1995:10350) observed that "The current geographic distribution is insular and would have remained almost entirely so, even given the response of the vegetation to the estimated extremes of past climates" Instead, these authors have invoked long distance seed dispersal by wind and by birds (in feathers or mud on feet) to partly account for colonization of afroalpine zones and chorological similarities in their plant communities. Still, endemism levels within the afroalpine flora are exceedingly high in the mountains of eastern Africa and Ethiopia, and many plant endemics are restricted to a single mountain (Hedberg 1986). Furthermore, the geologically young age of some eastern African volcanoes (ca. 1 million years old—e.g., Mts Kilimanjaro and Meru; Griffiths 1993) indicates that heights sufficient to support an alpine zone have been attained only recently, a spatiotemporal consideration that also disputes notions of the former connectivity of their uppermost plant zones with those in more northern and southern mountains.

Bohmann (1952), of course, perceived real morphological similarities that persuaded him to group these taxa under a widely distributed *Otomys typus*. This

afroalpine morphotype may be sketched as having a deeper and more luxuriant pelage with pale post-auricular patches, a relatively short tail, a more conspicuously arched cranium and constricted interorbit, narrower rostrum with less expansive nasal tips, relatively larger auditory bullae, M3 with more laminae, and lower incisors with two grooves. Such an idealized morphology involves tendencies of character development, but when examined in detail within geographically cohesive regions, not all of these qualitative characteristics are equally expressed in the taxa that Bohmann gathered under *typus*. That is to say, development of incisor grooving, numbers of M3 laminae, and presence-absence of post-auricular patches occur in different and unique combinations (this study, Bohmann 1952, also see Musser & Carleton 2005). Moreover, pronounced morphometric divergence in size and shape demonstrably accompanies such qualitative contrasts, at least in *typus*, *orestes*, and *uzungwensis*, and together, these discontinuities more convincingly argue specific boundaries, not subspecific intergradation. The same pattern is apparent for certain taxa confined to the Afromontane zone proper, i.e., *O. dollmani* and *O. tropicalis*, and additional study of the latter will likely divulge other instances of specific differentiation within Afromontane environments coincident with major mountain systems.

Rather than a classical model of allopatric speciation, the possibility of multiple independent originations (speciation) of otomyines in afroalpine environments on eastern African mountaintops deserves to be tested as an alternative hypothesis to explain their diversification. Phylogenetic results recently obtained for other organisms confined to moist montane environments within tropical latitudes offer instructive analogies. Giant senecios (*Dendrosenecio*), for example, are prominent members of afroalpine floras

in eastern Africa where populations of *Otomys* co-occur. Knox & Palmer (1995:10349) summarized that the diversification of giant senecios "... primarily involved repeated altitudinal radiation, both up and down the mountains, leading to morphological parallelism in both directions." In a genus of Neotropical butterfly, Hall (2005:5) concluded that "The overwhelming pattern discernable in *Ithomiola* is of vertical speciation, ..., one elevational band at a time, following or concomitant with orogenic cycles of uplift." Recent molecular studies of African birds have disclosed complex vicariance patterns, bursts of speciation, and the concentration of evolutionarily young species in montane regions of eastern Africa, concomitant with pronounced vegetational, climatic, and geological changes during the Quaternary (Fjelds  & Lovett 1997, Roy et al. 1997, 1998; Bowie et al. 2006). In light of the dynamic biogeography and prolific phylogenetic diversification that have attended the Pleistocene history of other montane organisms, the apparent evolutionary stasis of a terrestrial rodent of low vagility, as reflected in the conventional taxonomies and wide distributions of *O. tropicalis* and *O. typus*, is difficult to reconcile if not patently absurd.

The above examples represent only circumstantial evidence and do not specifically improve understanding of the phyletic radiation of otomyine rodents in eastern African mountains. The striking morphological differentiation evident among taxa (*O. dollmani*, *O. orestes*, *O. tropicalis*, *O. uzungwensis*) once considered to be subspecies of widely ranging species, namely *O. irroratus* or *O. typus*, is not circumstantial and provides a framework for future phylogenetic investigation. A pattern of regionally localized cladogenesis, situated within the major Afromontane physiographic groups identified for other organisms, and independent evolution of the afroalpine morpho-

type may be anticipated. In addition to forms once synonymized under *typus*, denser sampling of populations and taxa currently placed within *O. denti* and especially *O. tropicalis* will prove crucial to exploring these possibilities.

A paleontological coda.—Otomyine rodents are thought to have evolved from an arvicanthine-like stock sometime in the late Miocene, a hypothesis robustly supported by morphological, paleontological, and molecular studies (Pocock 1976, 1987; Carleton & Musser 1984, Chevret et al. 1993, S n gas & Avery 1998, Ducroz et al. 2001, S n gas 2001). Furthermore, southern Africa is believed to encompass the area of origin of the subfamily, as indicated by the presence of the oldest known fossils (Pocock 1976, 1987; Denys 1989, S n gas & Avery 1998, S n gas 2001), including the annectant fossil genus *Euryotomys* (Mio-Pliocene, South Africa), and by the geographic distribution of morphological apomorphies (Bohmann 1952, Denys 1989). Earliest fossil species of *Otomys* proper date from the middle to late Pliocene (2–3.5 million years ago) in southern Africa (S n gas & Avery 1998, S n gas 2001) and from the early Pleistocene (1–2 million years ago) in eastern Africa (Denys 1989). As with the later appearance of fossils, the distribution of apomorphies within *Otomys*—notably the greater incidence of taxa with a 7-, 8-, or 9-laminated M3s (*O. laminatus* of southern Africa is a conspicuous exception), lower incisors with dual sulci, and prominently arched cranial vaults—also suggest that more highly derivative lineages are localized within eastern Africa highlands. *Otomys petteri*, an extinct species named from Olduvai Bed I, early Pleistocene of Tanzania (Denys 1989), warrants comment in this regard and apropos the evolutionary significance of *O. dollmani*.

Key diagnostic characters of *O. petteri*—its relatively small size, 6-laminated M3, and lower incisors with a deep lateral groove and shallow medial groove are the

same traits that recall *O. dollmani*. In contrasting the fossil *O. petteri* with living *Otomys*, Denys (1989:714) mistakenly attributed 7–8 laminae as characteristic of the M3 in the “*tropicalis-irroratus* group.” The possession of 6 M3 laminae by southern African *O. irroratus* was long ago appreciated by Thomas (1902), who emphasized this contrast in his definition of *tropicalis* (as a subspecies of *O. irroratus*). The characteristic modal contrast in M3 laminae between southern *irroratus* and eastern *tropicalis* was also acknowledged by other authors in early classifications of *Otomys*, whether as separate subspecies (Wroughton 1906) or species (Dollman 1915). Along with *O. irroratus* proper, *O. dollmani* emerges as another member of the “*tropicalis-irroratus* group,” as currently understood, whose M3 possesses only 6 laminae. Reevaluation of the Olduvai sample is required to determine whether *O. petteri* more closely resembles *O. irroratus* or *O. dollmani*, instead of *O. angoniensis* as highlighted by Denys in her comparisons with recent *Otomys*. Owing to our different measuring protocols—one focused on crania, the other on individual molars—we cannot critically contrast size of *O. dollmani* and *O. petteri*. Still, certain characteristics of *O. petteri* noted by Denys—the low crown height and incomplete fusion of cusps in the posterior M3 laminae—do not suggest examples of *O. dollmani*. In our view, *O. dollmani* represents an in situ differentiation unique to the Mathews Range, Kenya, and is certainly a species distinct from *O. petteri* as known from the early Pleistocene of northern Tanzania (If demonstrated to be synonymous, *dollmani* has priority over *petteri*). The retention of 6 M3 laminae in *O. dollmani* intimates that it is a relict surviving from the early cladogenesis of *Otomys* in eastern Africa. According to this interpretation, *O. dollmani* is predicted to be a cladistically primitive outlier relative to eastern Afri-

can forms with 7 or 8 M3 laminae, i.e., *O. tropicalis* (including *elgonis*), *O. orestes*, and *O. typus*. Phylogenetic studies applying gene-sequence analyses should explore this possibility.

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Appendix 1

Listed below are additional specimens of *Otomys* that formed the basis for the morphological comparisons, sample statistics, morphometric analyses, and counts of M3 laminae presented herein.

Otomys irroratus.—South Africa: Western Cape Province, 2 mi N Clanwilliam (USNM 343731–343735); Goudveld, 10 mi N Knysna (USNM 343761–343776); Klein Brakrivier, 9 km N Mosselbaai (USNM 343743–343761); Kluitjieskraal, 7 mi SW Swellendam (USNM 343741, 343742); Pakhuis

Pass (USNM 343739, 343740); 6 mi WNW Redelinghuys (USNM 469704–469707); 22 mi SW Worcester (USNM 469695–469703). South Africa: Eastern Cape Province, 19 mi S Aliwal North (USNM 344783–344788); Coloniesplaats, 28 mi N Graaf Reinet (USNM 344795, 344796); 2 mi E Houtbosdorp (USNM 382365–382373); Kenkel Bosch (USNM 221390–221399, 221400, 221401, 221415); Pirie, 12 mi NW King Williams Town (USNM 344774–344782); 4 mi W Port St. Johns (USNM 381220–381228); 5 mi W Somerset East (USNM 452460–452462). South Africa: KwaZulu-Natal Province, 2 mi W Drakensberg Gardens (USNM 381185–381187, 381207–381219); Kilgobbin, 8 mi W Dargle Station (USNM 381195–381197); Sani Pass (USNM 381198–381206).

Otomys typus.—Ethiopia: Arussi Plateau, Albasso (USNM 259506); Gojam, N'jabara (USNM 259507); Bale Mts, Dinsho (MCZ 57319); Simien Mts, Mt Geech, 11,200 ft (MCZ 26992); Simien Mts, 10,000 ft (MCZ 34372); Simien Mts, Devark, 9200 ft (MCZ 34373); Arussi (FMNH 28125, 28126, 28129, 28132–28139, 28159–28164); Gojam (FMNH 28141–28143, 28172–28177, 28179); Shou (FMNH 28140); Sidamo, (FMNH 28167); Simien Mts (FMNH 28146–28151, 28153–28158).

Otomys uzungwensis.—Malawi: Nyika Plateau, 7000 ft (MCZ 43947, 43950). Tanzania: Udzungwa Mts, Kigoro (MCZ 26637, 26638, 26640–26644); Udzungwa Mts, Dabaga (MCZ 26645 [holotype], 26646, 26648–26653, 26655, 26656, 26664); Poroto Mts, Mbeya, 9000 ft (MCZ 51147).