

**Review of the *Hylomyscus denniae* group (Rodentia: Muridae) in eastern Africa, with comments on the generic allocation of *Epimys endorobae* Heller**

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*Abstract.*—The status and distribution of eastern African populations currently assigned to *Hylomyscus denniae* are reviewed based on morphological and morphometric comparisons. Three species are considered valid, each confined largely to wet montane forest above 2000 meters: *H. denniae* (Thomas, 1906) proper from the Ruwenzori Mountains in the northern Albertine Rift (west-central Uganda and contiguous D. R. Congo); *H. vulcanorum* Lönnberg & Gyldenstolpe, 1925 from mountains in the central Albertine Rift (southwestern Uganda, easternmost D. R. Congo, Rwanda, and Burundi); and *H. endorobae* (Heller, 1910) from mountains bounding the Gregory Rift Valley (west-central Kenya). Although *endorobae* has been interpreted as a small form of *Praomys*, additional data are presented that reinforce its membership within *Hylomyscus* and that clarify the status of *Hylomyscus* and *Praomys* as distinct genus-group taxa. The 12 species of *Hylomyscus* now currently recognized are provisionally arranged in six species groups (*H. aeta*, *H. alleni*, *H. anselli*, *H. baeri*, *H. denniae*, *H. parvus*) based on 8 qualitative characters. Biogeography of the three species of the *H. denniae* group is discussed in the context of broad distributional patterns and area relationships evident among other terrestrial small mammals also confined to the Afromontane biotic region in eastern Africa.

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Until recently, *Hylomyscus denniae*, the Montane Woodland Mouse, was understood to be a highly variable murid species, broadly if patchily distributed in forested highlands across south-central and eastern Africa (e.g., Misonne 1974, Bishop 1979, Musser & Carleton 1993). Carleton & Stanley (2005), however, demonstrated that nominal *denniae* masks a complex of species and perhaps two species groups. Members of the *H. anselli* group occur in mountains of south-central Africa: from the central Angolan

highlands (cf. *anselli* group); through the disconnected mountain chains in northern Zambia and western Tanzania (*anselli*); to Mount Rungwe and the Eastern Arc Mountains of central and eastern Tanzania (*arcimontensis*). In contrast, forms of the *H. denniae* assemblage are centered in eastern African mountains (Fig. 1): the central portion of the Albertine Rift system in easternmost Democratic Republic of Congo, Burundi, Rwanda, and southwestern Uganda (*vulcanorum*); astride the northern section of

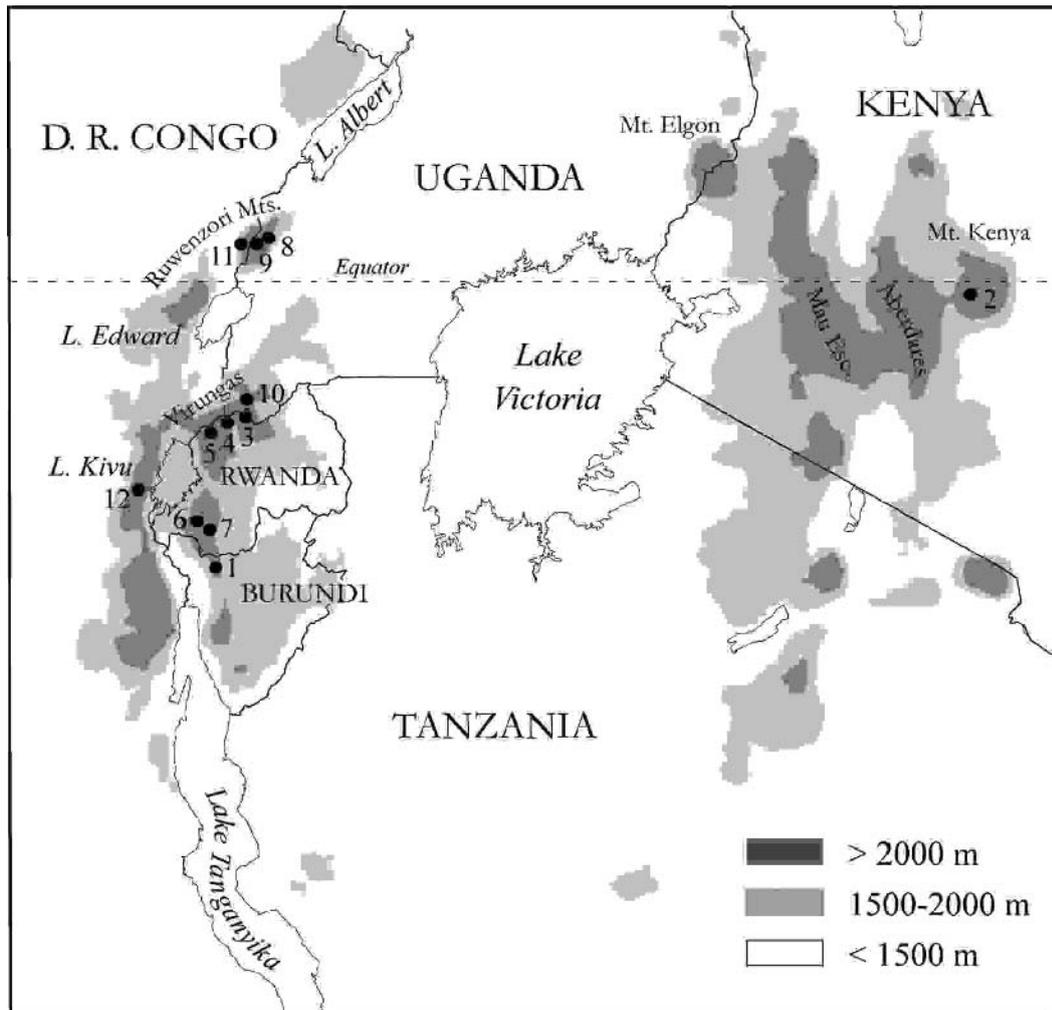


Fig. 1. Mountainous regions of eastern Africa inhabited by populations of the *Hylomyscus denniae* complex, as circumscribed herein. The 12 geographic samples (OTUs) used in multivariate analyses are numbered and generally plotted; see Materials and Methods for specific localities comprising each and sample sizes.

the Albertine Rift in northeastern Democratic Republic of Congo and westernmost Uganda (*denniae*); and mountains surrounding the Gregory Rift Valley in western Kenya (*endorobae*). Members of the two groups differ in three qualitative characters: relative length of the incisive foramina (longer in the *denniae* group, extending between the first molars; shorter in the *anselli* group, terminating about the anterior border of the first molars), patency of the subsquamosal

fenestra (tiny or occluded in the *denniae* group; small to medium size in the *anselli* group), and occurrence of pectoral teats (present in the *denniae* group, total mammae = 8; absent in the *anselli* group, total = 6).

The primary purpose of the current study is to evaluate morphological differentiation among populations of the *H. denniae* complex, as a basis for commenting on the status of the three forms named from wet montane forest in eastern

African mountains—*denniae* Thomas (1906), *endorobae* Heller (1910), and *vulcanorum* Lönnerberg & Gyldenstolpe (1925). Our secondary goal is to review the generic affinity of the Kenyan form *endorobae*, which, although historically considered a form of *Hylomyscus* (e.g., Hatt 1940, Musser & Carleton 1993), has been recently transferred to *Praomys* (Van der Straeten & Robbins 1997).

#### Materials and Methods

Specimens reported herein consist principally of skins with their associated skulls and are contained in the following museum collections: American Museum of Natural History, New York City (AMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM, formerly the U.S. National Museum); Natural History Museum of Los Angeles County, Los Angeles (LACM); The Natural History Museum, London (BMNH, formerly the British Museum of Natural History); and the Rijksuniversitair Centrum, Antwerpen, Belgium (RUCA).

Fourteen cranial and two dental variables were measured by MDC 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 (see Carleton & Van der Straeten 1999 for most landmarks): occipitonasal length (ONL); greatest zygomatic breadth (ZB); breadth of braincase (BBC), measured across the parietal flanges just behind the zygomatic arches; breadth across occipital condyles (BOC); interorbital breadth (IOB); length of rostrum (LR); breadth of rostrum (BR); postpalatal length (PPL); length of bony palate (LBP);

breadth of bony palate (BBP), measured across the maxillary bones above the second molars; length of incisive foramen (LIF); length of diastema (LD); breadth of zygomatic plate (BZP); length of auditory bulla (LAB); coronal length of maxillary toothrow (CLM); width of the upper first molar (WM1). Five external dimensions (to nearest whole mm) and body mass (to nearest 0.5 gm) were transcribed from skin tags or field catalogs as given by the collector: total length (TOTL); head and body length (HBL); tail length (TL); hindfoot length (HFL); ear (pinna) length (EL); and weight (WT). Most external data of the Burundi and Uganda samples were recorded in the field by JKP and WTS, reducing among-collector variability for these big, extremely age-sensitive, dimensions. The large series from Mount Kenya was collected early in the 20<sup>th</sup> century by J. A. Loring and E. A. Mearns (Hollister 1919), and specimens lack field-obtained values for head-and-body length and weight; the former datum was obtained by subtraction of TL from TOTL. Recording of measurements was limited to animals judged to be adult, as based on the possession of fully erupted third molars and adult pelage. Three crude age classes of "adult" specimens were further identified based on degree of upper molar wear, from little (young adult), to moderate (full adult), to heavy (old adult), generally following the patterns of coronal change outlined by Carleton & Martinez (1991). Except for a priori exclusion of juvenile specimens, we did not attempt to remove age-related size effects (post-weaning growth) in portraying the multivariate results. Sexual size dimorphism was statistically unappreciable in large population samples of *H. arcimontensis* and *H. denniae* (Carleton & Stanley 2005); measurements of males and females were accordingly combined in analyses and tables. Throughout the text, we use the abbrevia-

tions M1-3 or m1-m3 to individually reference the upper (maxillary) and lower (dentary) molars, respectively; individual cusps of the M1-3 are referenced using the positional t-system developed by Miller (1912).

The following 12 operational taxonomic units (OTUs) of *Hylomyscus*, arranged according to country of origin, were used to generate the various tabular summaries and undertake descriptive and multivariate analyses. Many of these OTUs are allopatric to one another, restricted to wet montane forest in isolated mountain systems (Fig. 1). Locality numbers correspond to the geographic placenames and coordinates given in Appendix 1; full provenance and museum registration numbers are provided in the Taxonomic Summary. We included a sample of *Praomys delectorum* (Kenya, Taita Hills, Mounts Mbololo and Umengo, N = 29) to assess morphometric discrimination between large-bodied taxa of *Hylomyscus* (i.e., *denniae*, OTU 8, and *endorobae*, OTU 2) and a small form of *Praomys*. Abbreviations are used here and throughout the text for forest reserves (FR), national parks (NP), mount or mountains (Mt, Mts), and Democratic Republic of Congo (D. R. Congo). For consistency, we use the names Albertine Rift Valley (also = Western Rift) and Gregory Rift Valley (also = Eastern Rift or Kenyan Rift) for the western and eastern branches, respectively, of the Great Rift Valley system in eastern Africa.

Burundi: OTU 1—Kibira NP (localities 2–5, 7, 10, 11; N = 38). Kenya: OTU 2—Mt Kenya (localities 25, 28; N = 43). Rwanda: OTU 3—Virunga Volcanoes NP, Gahinga and Gasiza (localities 29, 30; N = 17); OTU 4—Virunga Volcanoes NP, Kinigi (locality 33; N = 14); OTU 5—Virunga Volcanoes NP, Karisoke and Visoke (localities 31, 39) (N = 24); OTU 6—Nyungwe Forest, Routabansougera and Uwinka (localities 37, 38; N = 43); OTU 7—Nyungwe Forest, Kitabi (local-

Table 1.—External and cranial measurements of the holotypes of *Epimys endorobae* Heller and *Epimys taitae* Heller. Although closely similar in size, the former is a large example of the genus *Hylomyscus* (*endorobae*, here considered a valid species) and the latter a small form of *Praomys* (*taitae*, currently a junior synonym of *Praomys delectorum*).

Variable	<i>endorobae</i> (USNM 162858)	<i>taitae</i> (USNM 181797)
TOTL	251.0	243.0
HBL	100.0	105.0
TL	151.0	138.0
HFL	22.5	23.0
EL	19.5	19.0
ONL	28.2	28.5
ZB	13.6	13.1
BBC	12.1	11.5
IOB	4.4	4.3
LR	9.1	9.9
BR	4.9	4.9
PPL	9.6	9.6
LBP	4.6	4.9
BBP	5.3	5.3
LIF	6.0	6.2
LD	7.7	7.9
BZP	2.4	3.0
LAB	4.5	4.6
BOC	6.2	6.0
CLM	4.4	4.2
WM1	1.4	1.3

ity 34; N = 12). Uganda: OTU 8—Ruwenzori Mts, Kasese District, Mubuku Valley, 1890–2670 m (localities 42, 43, 49; N = 56); OTU 9—Ruwenzori Mts, Kasese District, highland localities, 2955–4040 m (localities 40, 41, 45–47; N = 28); OTU 10—Kabale and Kisoro Districts (localities 48, 50–52; N = 38). D. R. Congo: OTU 11—Ruwenzori Mts, Bugongo Ridge and Kalonge (localities 12, 14, 15, 20; N = 30); OTU 12—Kivu District (localities 16, 18, 19; N = 23).

Standard descriptive statistics (mean, range, and standard deviation) were derived for adult specimens (young, full, and old age classes combined) of the 12 OTUs. Means and ranges of external variables are provided as guidance to identification and as a rough index of body size (Tables 1, 2), but were not treated in morphometric analyses. Dis-

Table 2.—External and cranial sample statistics (mean,  $\pm 1$  SD, and observed range) for *Praomys delectorum* (Kenya, Taita Hills, N = 29) and selected OTUs of the *Hylomyscus denniae* species group: *H. vulcanorum* (OTU 1—Burundi, Kibira NP, N = 36); *H. denniae* (OTU 8—Uganda, Ruwenzori Mts, N = 56); and *H. endorobae* (OTU 2—Kenya, Mt Kenya, N = 45).

Variable	<i>H. vulcanorum</i>	<i>H. denniae</i>	<i>H. endorobae</i>	<i>P. delectorum</i>
TOTL	227.5 $\pm$ 14.1 206–260	236.1 $\pm$ 14.3 200–266	253.0 $\pm$ 16.8 215–290	229.2 $\pm$ 7.5 218–243
HBL	94.7 $\pm$ 7.0 81–107	101.7 $\pm$ 5.4 90–115	103.8 $\pm$ 7.3 92–120	101.6 $\pm$ 4.7 95–112
TL	132.8 $\pm$ 10.6 117–155	135.7 $\pm$ 8.6 122–157	149.4 $\pm$ 10.8 123–172	127.5 $\pm$ 5.4 118–138
HFL	20.5 $\pm$ 0.9 19–22	21.4 $\pm$ 1.0 19–23	22.8 $\pm$ 1.2 18–26.5	23.0 $\pm$ 0.7 21–24
EL	17.6 $\pm$ 1.2 16–22	19.9 $\pm$ 1.1 18–23	—	19.4 $\pm$ 0.7 18–21
WT	21.5 $\pm$ 4.4 15.5–30.0	31.5 $\pm$ 9.2 17.5–65.0	—	—
ONL	25.0 $\pm$ 0.9 23.1–26.8	26.7 $\pm$ 1.1 24.3–28.7	27.7 $\pm$ 0.9 25.6–29.4	28.3 $\pm$ 0.8 26.9–29.8
ZB	12.6 $\pm$ 0.4 11.6–13.2	13.1 $\pm$ 0.6 11.4–14.5	13.4 $\pm$ 0.4 12.4–14.5	12.9 $\pm$ 0.3 12.3–13.5
BBC	11.3 $\pm$ 0.3 10.7–12.0	11.6 $\pm$ 0.3 11.0–12.2	12.1 $\pm$ 0.3 11.5–12.7	11.4 $\pm$ 0.3 10.8–11.7
IOB	4.1 $\pm$ 0.1 3.9–4.6	4.1 $\pm$ 0.1 3.9–4.4	4.3 $\pm$ 0.1 4.0–4.6	4.4 $\pm$ 0.1 4.2–4.5
LR	7.6 $\pm$ 0.4 6.9–8.3	8.2 $\pm$ 0.4 7.3–9.2	8.7 $\pm$ 0.3 8.1–9.4	9.8 $\pm$ 0.3 9.3–10.5
BR	4.4 $\pm$ 0.3 3.9–5.1	4.5 $\pm$ 0.3 4.0–5.1	4.7 $\pm$ 0.2 4.3–5.3	4.8 $\pm$ 0.2 4.5–5.4
PPL	8.9 $\pm$ 0.6 7.8–10.5	9.6 $\pm$ 0.6 8.1–10.6	9.7 $\pm$ 0.6 8.6–11.0	9.4 $\pm$ 0.4 8.8–10.1
LBP	3.9 $\pm$ 0.2 3.5–4.3	4.1 $\pm$ 0.2 3.6–4.5	4.5 $\pm$ 0.2 4.1–4.8	5.1 $\pm$ 0.3 4.7–6.1
BBP	4.9 $\pm$ 0.1 4.6–5.1	5.1 $\pm$ 0.2 4.6–5.5	5.2 $\pm$ 0.2 4.8–5.5	5.2 $\pm$ 0.1 5.0–5.5
LIF	5.5 $\pm$ 0.3 4.8–6.0	6.0 $\pm$ 0.3 5.3–6.7	6.3 $\pm$ 0.3 5.9–7.0	5.7 $\pm$ 0.3 5.2–6.3
LD	6.8 $\pm$ 0.3 5.8–7.3	7.4 $\pm$ 0.4 6.5–8.5	7.7 $\pm$ 0.4 6.7–8.2	7.7 $\pm$ 0.4 7.1–8.5
BZP	2.2 $\pm$ 0.1 1.9–2.4	2.3 $\pm$ 0.1 1.9–2.7	2.4 $\pm$ 0.2 2.0–3.0	2.9 $\pm$ 0.1 2.7–3.2
LAB	4.3 $\pm$ 0.1 4.0–4.7	4.3 $\pm$ 0.1 3.9–4.6	4.6 $\pm$ 0.2 4.2–4.9	4.5 $\pm$ 0.1 4.2–4.5
BOC	5.8 $\pm$ 0.2 5.4–6.3	6.1 $\pm$ 0.2 5.6–6.4	6.2 $\pm$ 0.2 5.8–6.5	6.0 $\pm$ 0.2 5.6–6.4
CLM	3.94 $\pm$ 0.14 3.64–4.20	4.12 $\pm$ 0.11 3.93–4.43	4.34 $\pm$ 0.13 4.12–4.67	4.14 $\pm$ 0.11 3.83–4.39
WM1	1.17 $\pm$ 0.04 1.07–1.27	1.24 $\pm$ 0.04 1.14–1.32	1.28 $\pm$ 0.05 1.16–1.36	1.26 $\pm$ 0.04 1.17–1.34

criminant function classification and principal component scores were computed using only the 16 craniodental variables, all of which were first transformed to natural logarithms. Principal components

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 with

the original cranial measurements. All analytical procedures were implemented using statistical packages contained in Systat (Version 10.2.01, 2002). Faunal similarities among the mountain systems inhabited by forms of the *H. denniae* group were assessed by means of the Jaccard Index, a matching coefficient for binary data that scales similarity to range from 0 to 1 (Hayek 1994). The indices from the pairwise comparisons were clustered using UPGMA as implemented by Systat.

### Results

*Generic allocation of Epimys endorobae Heller.*—Van der Straeten & Robbins (1997) referred *endorobae* Heller (1910) to *Praomys* based on their principal components analyses of holotypes attributable to *Mastomys* and related genus-group taxa (*Hylomyscus*, *Myomys*, *Myomyscus*, *Praomys*). Heller's (1910) *endorobae* was long associated with *Hylomyscus*, in particular as a subjective synonym of the species *H. denniae* (e.g., Allen 1939, Hatt 1940, Misonne 1974, Musser & Carleton 1993). In the principal component results of Van der Straeten & Robbins (1997), scores for the holotypes of *endorobae* and *taitae*, the latter epithet then and now considered a synonym of *P. delectorum*, plotted closely in multivariate space and influenced their decision to reallocate *endorobae* to *Praomys*. Limited to the holotypes, these results are understandable: not only do the type specimens of *endorobae* and *taitae* resemble one another in size for most craniodental dimensions quantified (Table 1), but homogeneous population samples overlap substantially in most univariate ranges (Table 2). Their similarity in size and possible confusion are also conveyed in the report of Demeter & Hutterer (1986), who initially identified *Hylomyscus* specimens from Mt Meru, Tanzania, as *H. denniae* and speculated that *taitae* from

the Taita Hills, Kenya, is a synonym (the Meru specimens have been subsequently redetermined to be examples of *Praomys delectorum*—R. Hutterer, pers. comm.). In order to evaluate these taxonomic recommendations, we morphometrically compared a population series of *endorobae* from Mt Kenya (OTU 2) with those of a large *Hylomyscus*, *H. denniae* sensu stricto from the Ruwenzori Mts, Uganda (OTU 8), and a small *Praomys*, *P. delectorum taitae* from the Taita Hills, Kenya (We use this trinomial simply as a geographic tag in lieu of any evaluation of infraspecific variation and credible subspecific divisions within *P. delectorum*).

A multivariate perspective discloses that the phenetic affinity of *endorobae* unambiguously lies with *Hylomyscus denniae* and cannot be confused with a small *Praomys* (Fig. 2). Whether principal component or canonical variate, the pronounced separation along the first two factors extracted underscores basic shape differences between a *Hylomyscus* skull and a *Praomys* skull. The cranium of *H. denniae* or *endorobae*, compared with that of *P. delectorum*, is absolutely shorter (ONL) but comparatively broad across the zygomatic arches (ZB) and braincase (BBC, BOC); the interorbital region (IOB) is more constricted; the rostrum is truncate and less robust (LR, BR, LD); the bony palate (LBP) is shorter and the incisive foramina (LIF) correspondingly long; and the zygomatic plate (BZP) is conspicuously narrower (Table 3). Most of these proportional differences are readily apparent in mean univariate contrasts and side-by-side inspection of skulls (Tables 1, 2). Molar dimensions (LM1-3, WM1), on the other hand, contribute little to specimen dispersion along the first factor; indeed, the molar rows of large *Hylomyscus* such as *denniae* and *endorobae* are fully as robust as small *Praomys* (Table 2). In discriminant function classification, the holotypes of *en-*

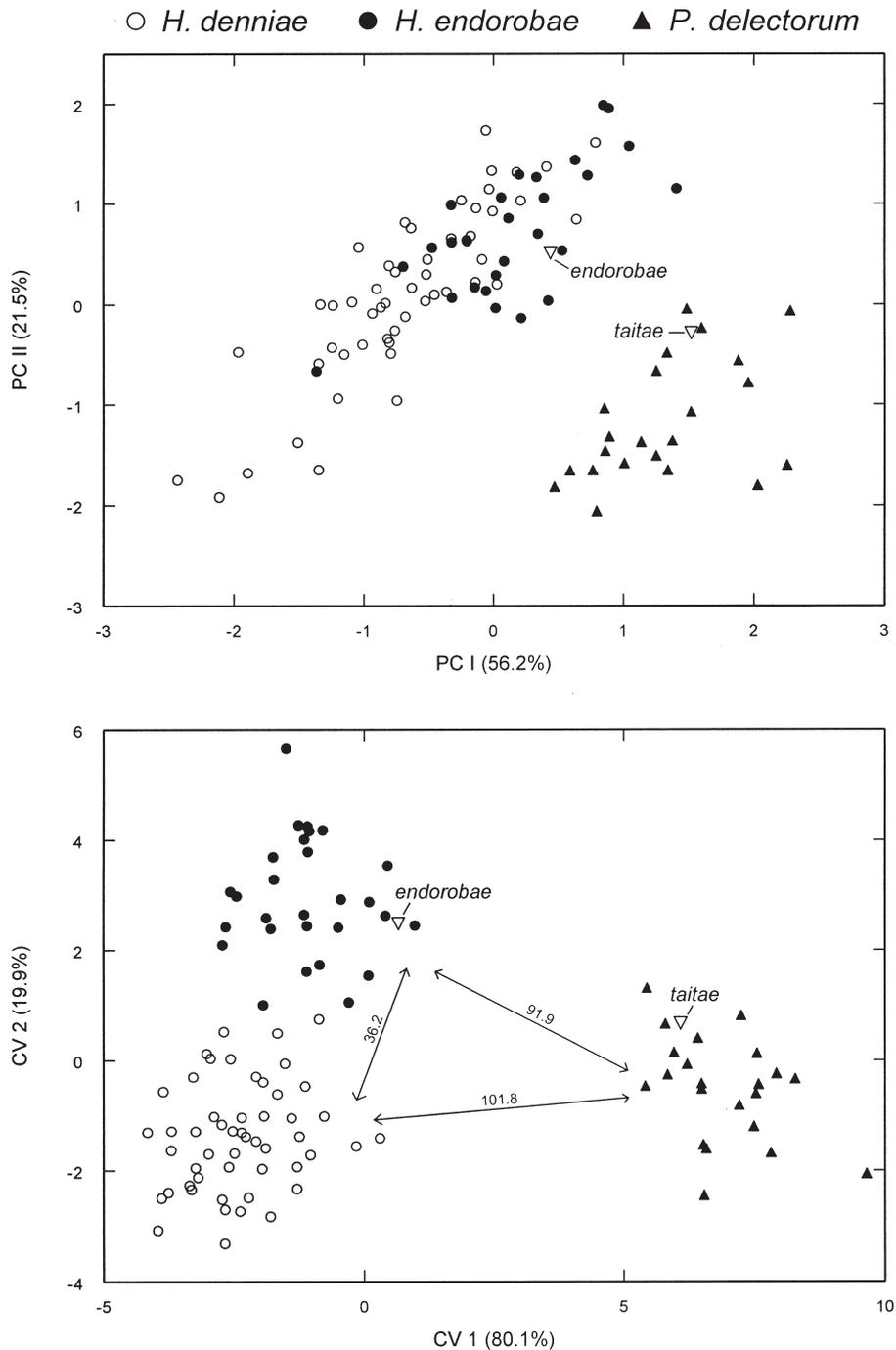


Fig. 2. Results of multivariate ordinations performed on 16 log-transformed craniodental variables as measured on 103 intact specimens representing samples of *Hylomyscus denniae* (OTU 8—Uganda, Ruwenzori Mts), *H. endorobae* (OTU 2—Kenya, Mt Kenya), and *Praomys delectorum taitae* (Kenya, Taita Hills). Open, inverted triangles correspond to the scores of type specimens of *endorobae* (USNM 162858) and *taitaie* (USNM 181797). Top, projection of specimen scores on first two principal components (PC) extracted. Bottom, projection of specimen scores on first two canonical variates (CV) extracted; average between-centroid divergences (Mahalanobis  $D^2$ ) among the three samples are indicated along the two-way arrows. See Table 3 for variable correlations and percent variance explained.

Table 3.—Results of principal component and three-group discriminant function analyses performed on intact specimens (N = 103) representing *Hylomyscus denniae* (OTU 8—Uganda, Ruwenzori Mts), *H. endorobae* (OTU 2—Kenya, Mount Kenya), and *Praomys delectorum taitae* (Kenya, Taita Hills); see Fig. 2 and text for discussion.

Variable	Correlations			
	PCI	PCII	CV1	CV2
ONL	0.90	0.37	0.50	0.41
ZB	0.34	0.79	-0.21	0.35
BBC	0.08	0.70	-0.37	0.72
BOC	0.28	0.65	-0.20	0.37
IOB	0.70	0.01	0.53	0.32
LR	0.95	-0.12	0.86	0.23
BR	0.77	0.34	0.41	0.29
PPL	0.41	0.74	-0.15	0.06
LBP	0.87	-0.39	0.89	0.25
BBP	0.61	0.14	0.37	0.27
LIF	0.13	0.90	-0.40	0.53
LD	0.74	0.57	0.24	0.36
BZP	0.91	-0.22	0.82	0.03
LAB	0.63	0.41	0.29	0.66
CLM	0.23	0.40	-0.10	0.72
WMI	0.30	0.21	0.07	0.40
Canonical correlations	—	—	0.97	0.88
Eigenvalues	0.30	0.01	14.0	3.48
Percent variance explained	56.2	21.5	80.1	19.9

*endorobae* and *taitaie* were entered as unknowns, and each was confidently assigned to their respective species sample, at a level of mathematical certainty ( $P = 1.000$ ) based on the 16 variables we measured and the 3 groups defined a priori.

The pattern of variable correlations lends quantitative validation to fundamental shape contrasts that were visually appreciated by Thomas (1926) in erecting *Hylomyscus* as a genus distinct from *Praomys*. These include the truncated rostrum, relatively expanded braincase, and slender zygomatic plate, which dimensions all weigh heavily (Table 3) in discriminating specimens of *denniae-endorobae* (*Hylomyscus*) from those of *taitaie* (*Praomys*). The shorter and more attenuate muzzle of a *Hylomyscus* versus *Praomys* offers a first clue to generic

identification where members of the two co-occur in the field: the distance between the tip of the nose and eyeball is notably less in the former. In addition to obvious mean differences (BZP—Table 2), Thomas' character of the zygomatic plate is easily grasped in dorsal view, wherein the junction of the anterior zygomatic arch and rostrum in *Praomys* is characterized by a deep and conspicuous dorsal notch, but the notch in *Hylomyscus* is shallow (Fig. 3). Breadth of the zygomatic-plate, in combination with its correlate, depth of the dorsal notch, serves to distinguish species samples of *Hylomyscus* and *Praomys* available to us.

Other features of the holotype and Mt Kenya series of *endorobae* similarly conform to *Hylomyscus denniae* and differ from the *Praomys delectorum* sample. The fur in specimens of *endorobae* is soft and fine, versus coarser in *P. delectorum*. The tail is absolutely and relatively longer in species of the *H. denniae* group, including *endorobae* (Table 2): tail length relative to head-and-body length averages about 140% versus about 125% in *P. delectorum*. In addition to relative tail length, development of terminal penicillation offers another character to separate eastern African examples of *Praomys* and *Hylomyscus*. In *Praomys*, caudal hairs are short over the entire tail such that scalation remains macroscopically evident even near the tip. In *Hylomyscus*, including specimens of *endorobae*, caudal hairs lengthen over the distal one-quarter to one-fifth of the tail, obscuring the scale pattern to the naked eye and extending beyond the terminal vertebra to form a weak brush or pencil ("the tip rather more hairy"—Thomas, 1926:178). The hindfoot of *endorobae* is relatively short and broad, in metatarsal and phalangeal proportions like those of *H. vulcanorum* and *H. denniae* and unlike the relatively longer and narrower pes of *P. delectorum*. In particular, digit V in *endorobae* is long, its claw reaching nearly to the end of the

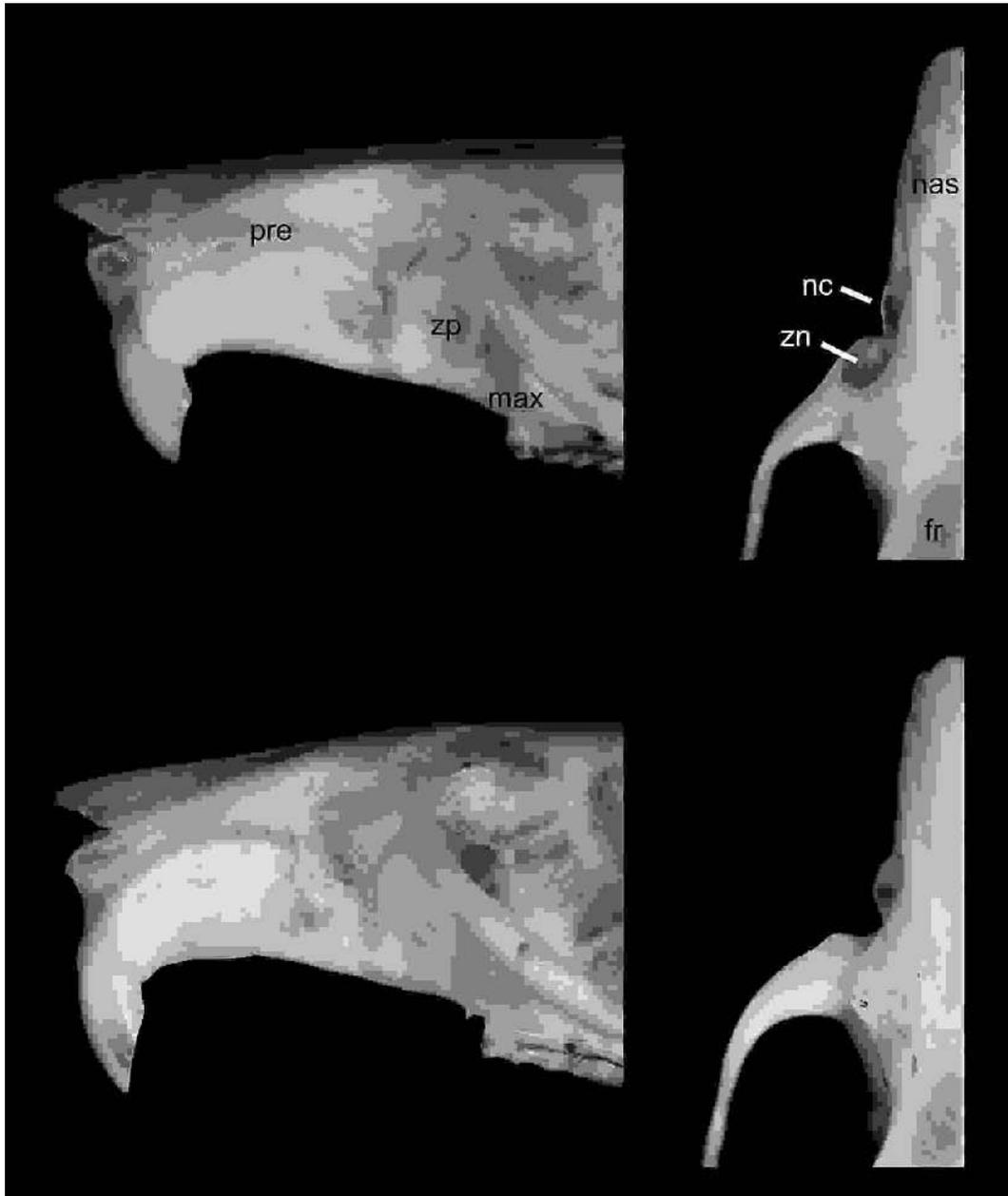


Fig. 3. Lateral (left) and dorsal (right) views of the rostrum and anterior zygomatic arch in species of *Praomys* and *Hylomyscus*: top, *P. delectorum* (FMNH 151303) from Tanzania; bottom, *H. denniae* (FMNH 144611) from Uganda, Ruwenzori Mts. Abbreviations: fr, frontal; max, maxillary; na, nasal; nc, nasolacrimal capsule; pre, premaxillary; zn, zygomatic notch; zp, zygomatic plate.

third or ungual phalanx of digits II–IV; in *P. delectorum*, the fifth digit is notably shorter relative to digits II–IV, extending to the middle of the second phalanx (Fig. 4). This distinction is easily ob-

served in the field or museum and helps to differentiate juveniles of *Hylomyscus* and *Praomys*. The first digit (hallux) is also relatively longer in *Hylomyscus*, extending to the middle of the first

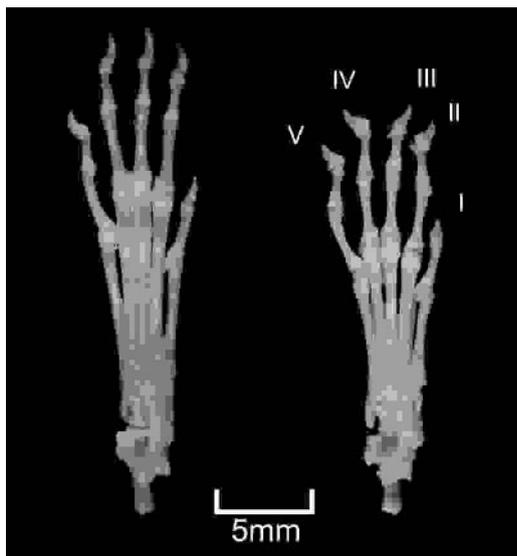


Fig. 4. Dorsal view of metatarsal and phalangeal proportions in the left hind foot of *Praomys* and *Hylomyscus*: left, *P. delectorum* (FMNH 151303; Tanzania); right, *H. denniae* (FMNH 144587; Uganda, Ruwenzori Mts). Roman numerals I through V identify pedal digits one through five. Note the relatively longer digits I and V in *H. denniae* as compared to *P. delectorum*.

phalanx of digit II, but the contrast with *Praomys* is not so visually prominent and less useful for field identification to genus.

The t3 (labial anterocone) of the upper first molar in *endorobae*, as well as that of *H. denniae* and *vulcanorum*, is small and weakly demarcated from the t2 (lingual anterocone). Consequently, the anterior chevron of *Hylomyscus* generally appears narrow with suppressed cuspidation. In the *Praomys jacksoni* and *P. delectorum* complexes (but not *P. tullbergi*—see LeCompte et al. 2002a), the t3 of the M1 constitutes a small but discrete cusp, even in adults with moderately worn molars, and the anterior chevron is correspondingly broader. Contrary to Thomas' (1926) claim—"M1 without antero-external cusplet"—a t3 is not wholly absent in *Hylomyscus* and its development varies among species. In most, its homologous position is usually indicated by a short and shallow indentation on the antero-

lateral face of the M1, as observed in unworn to barely worn molars of juveniles and very young adults. After occlusal wear begins, anatomical demarcation of a t3 is lost, such that it appears as little more than a posterolateral spur from the medial t2. Only in *H. parvus* is the t3 (and t9) of M1 so miniscule that it may be said to be absent; the anterior chevron of this species assumes a very narrow and highly asymmetrical shape. Specimens of *H. aeta* and *H. baeri* possess a relatively large t3, only slightly smaller than the t1, and the first chevron of M1 is basically symmetrical. Still, the t3 in these species of *Hylomyscus* is not as physically well demarcated from the t2 as in the *Praomys jacksoni* and *P. delectorum* complexes and their anterior chevron remains narrower.

A skeletal trait, occurrence of the entepicondylar foramen, also associates *endorobae* as a large *Hylomyscus* instead of a small *Praomys*. Among muroid rodents, an entepicondylar foramen may occur on the distal humerus, above the medial epicondyle, and transmits the median nerve and sometimes the brachial artery (Carleton 1980:Fig. 13, Landry 1958). LeCompte et al. (2002a) documented that this humeral foramen occurs in two species of *Hylomyscus* (*H. aeta*, *H. stella*), and we have found it to be uniformly present in seven other species, including *endorobae* (Table 4). Examples of *P. jacksoni*, type species of the genus, and *P. delectorum* lack an entepicondylar foramen, but the foramen's occurrence varies within the genus as currently arranged—present in species of the *tullbergi* complex and absent in those of the *jacksoni* and *delectorum* complexes (LeCompte et al. 2002a, this study). The latter variability bears on the larger issue of the generic boundaries of *Praomys* proper (see LeCompte et al. 2002a, 2002b for discussion). For our purposes, it is significant that specimens of *endorobae* agree with those of *H. denniae* and other *Hylomyscus* in possessing an entepicon-

Table 4.—Occurrence of the entepicondylar foramen in species of *Hylomyscus* and *Praomys* (see Appendix 2 for localities and specimen numbers).

Species (No. specimens)	Present (+)/Absent (-)
<i>H. aeta</i> (17)	+
<i>H. alleni</i> (2)	+
<i>H. anelli</i> (14)	+
<i>H. arcimontensis</i> (18)	+
<i>H. denniae</i> (20)	+
<i>H. endorobae</i> (5)	+
<i>H. parvus</i> (3)	+
<i>H. stella</i> (20)	+
<i>H. vulcanorum</i> (22)	+
<i>P. degraaffi</i> (21)	-
<i>P. delectorum</i> (27)	-
<i>P. jacksoni</i> (20)	-
<i>P. misonmei</i> (20)	+
<i>P. rostratus</i> (2)	+
<i>P. tullbergi</i> (13)	+

dylar foramen (Fig. 5), a structure that is lacking in a small *Praomys* such as *P. delectorum*.

*Morphometric differentiation among samples of the H. denniae complex.*—Three well defined clusters are evident in plots of specimen scores onto the first two canonical variates extracted from discriminant function analysis of our 12 OTUs (Fig. 6). The largest grouping includes mice that originated from mountains in southwestern Uganda (OTU 10), Burundi (OTU 1), Rwanda (OTUs 3–7), and nearby D. R. Congo (OTU 12); a second consists of those from west-central Uganda (OTUs 8, 9) and contiguous D. R. Congo (OTU 11); and the third is composed of the single sample from Kenya (OTU 2). Each of these three major clusters of eastern African *Hylomyscus* correspond to already named populations—*vulcanorum*, *denniae*, and *endorobae*, respectively—that inhabit isolated mountain systems. Multivariate overlap of specimen scores among individual OTUs within each of the *denniae* and *vulcanorum* clusters is substantial, and a posteriori misclassification of specimens between them is high (typically 40–70%); few individuals, however, were

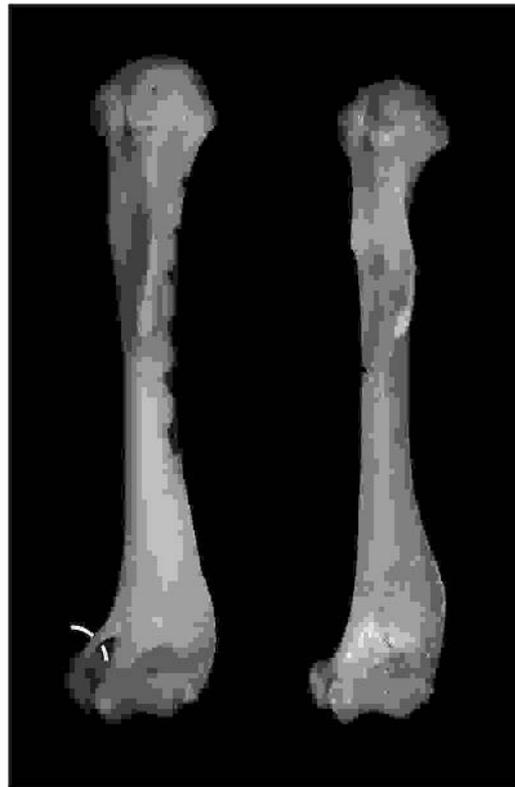


Fig. 5. Frontolateral view of the left humerus in examples of *Hylomyscus denniae* (left—FMNH 144626; Uganda, Ruwenzori Mts) and *Praomys delectorum* (right—FMNH 147314; Tanzania, West Usambara Mts). Note the presence of an entepicondylar foramen above the medial epicondyle in *H. denniae*, a structure found in all *Hylomyscus* species examined but lacking in small *Praomys* (see Table 4).

misallocated among samples of the three taxa (2–7%). Craniodental size plays a predominant role in the dispersion of samples along the first canonical variate (most variable correlations moderate to large and all positive—Table 5), in particular accounting for the separation of the smaller *vulcanorum* from the larger *denniae* and *endorobae*. The closer phenetic association of the latter two relative to *vulcanorum* is similarly reflected in the last clustering division using Mahalanobis distances between group centroids (Fig. 6). Segregation of *endorobae* from *denniae* and *vulcanorum* along CV2 is emphasized by certain weakly correlated

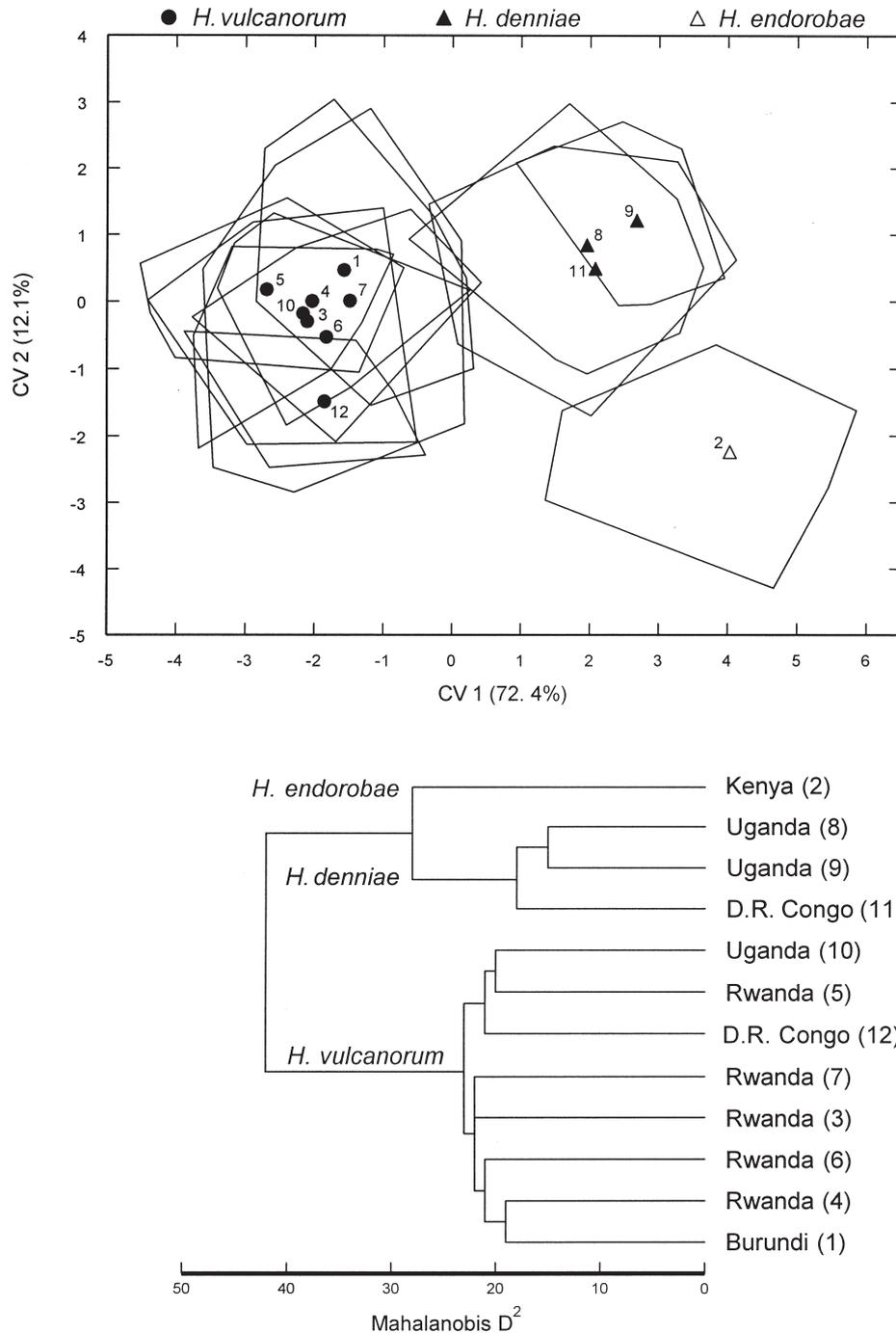


Fig. 6. Results of discriminant function analysis performed on 16 log-transformed craniodental variables as measured on 304 intact specimens representing 12 OTUs of eastern African *Hylomyscus*: *denniae* (8, 9, 11), *endorobae* (2), and *vulcanorum* (1–7, 10, 12). Top, projection of specimen scores onto the first two canonical variates extracted; irregular polygons enclose maximal dispersion of specimen scores around an OTU centroid (numbered symbols). Bottom, UPGMA phenogram based on Mahalanobis distances between the 12 OTUs. See Table 5 for variable correlations and percent variance explained.

Table 5.—Results of discriminant function analysis performed on intact specimens (N = 304) representing 12 OTUs of eastern African *Hylomyscus*; see Fig. 6.

Variable	Correlations	
	CV1	CV2
ONL	0.77	-0.10
ZB	0.52	0.02
BBC	0.73	-0.29
BOC	0.75	0.08
IOB	0.25	-0.28
LR	0.74	-0.16
BR	0.21	-0.24
PPL	0.53	0.11
LBP	0.67	-0.29
BBP	0.73	0.14
LIF	0.62	-0.23
LD	0.68	-0.06
BZP	0.59	-0.01
LAB	0.32	-0.37
CLM	0.81	-0.18
WM1	0.84	-0.10
Canonical Correlations	0.93	0.70
Eigenvalues	5.63	0.93
Percent variance	72.4	12.1

variables that reflect the relatively wider braincase (BBC, IOB), longer bony palate (LBP), and larger bullae (LAB) in specimens of *endorobae* (Tables 2, 5). Although clearly circumscribed in multivariate space, as depicted in our 12-group discriminant function analysis, the generalized distance distinguishing *endorobae* from the three samples of *denniae* ( $MD^2 = 27.5$ ) is a small value in our experience with other African species comparisons, which typically match or exceed that recorded here for *denniae* versus *vulcanorum* ( $MD^2 = 36$ ).

Only modest separation of *denniae* and *endorobae* is also evident in our principal component analyses, both that obtained in comparisons of *denniae-endorobae-tai-tae* (Fig. 2) and that derived only from samples representing *denniae-endorobae* (Fig. 7). Although PCA scores for *Hylomyscus* from the Ruwenzoris (OTUs 8, 9, 11 = *denniae*) and Mt Kenya (OTU 2 = *endorobae*) marginally overlap, the major axes of their elliptical spreads are phenet-

ically discrete, their Y-intercepts being significantly different ( $F = 125.7$ ,  $P < 0.001$ ) while their slopes are comparable ( $F = 0.2$ ,  $P = 0.643$ ). This covariation pattern among the craniodental variables of *denniae* and *endorobae* is a familiar one that resembles multivariate contrasts recovered for other closely related, congeneric species of Muroidea (Voss & Marcus 1992, Voss et al. 1990). Although juveniles were omitted from our analyses, post-weaning growth still accounts 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. Thus, in one-way analyses of variance, age-class as a categorical effect contributes significantly to the spread of specimen scores along PC I ( $F = 78.0$ ,  $P < 0.001$ ) but not PC II ( $F = 1.3$ ,  $P = 0.275$ ); whereas, species (or OTU) as an effect contributes substantially to dispersion on PC II ( $F = 131.5$ ,  $P < 0.001$ ) but much less so on PC I ( $F = 5.9$ ,  $P = 0.017$ ). Predictably, all variables load positively on the first component and most correlations are moderate to large ( $r = 0.50$ – $0.90$ ; Table 6). Those variables that load heavily on PC II, more or less orthogonal to the major axes of the taxon samples, include the same ones highlighted for CV 2 in the discriminant function analysis (BBC, IOB, LBP, LAB), although component correlations are accentuated. Two additional large correlations with PC II emphasize the more robust molars (LM1-3, WM1) observed in examples of *endorobae* as compared with those of *denniae* (Tables 2, 6).

#### Taxonomic Summary

Based on the morphometric and morphological evidence presented above, we continue to view *endorobae* of central Kenya as a constituent form of *Hylomyscus*, one related to *H. denniae* in the

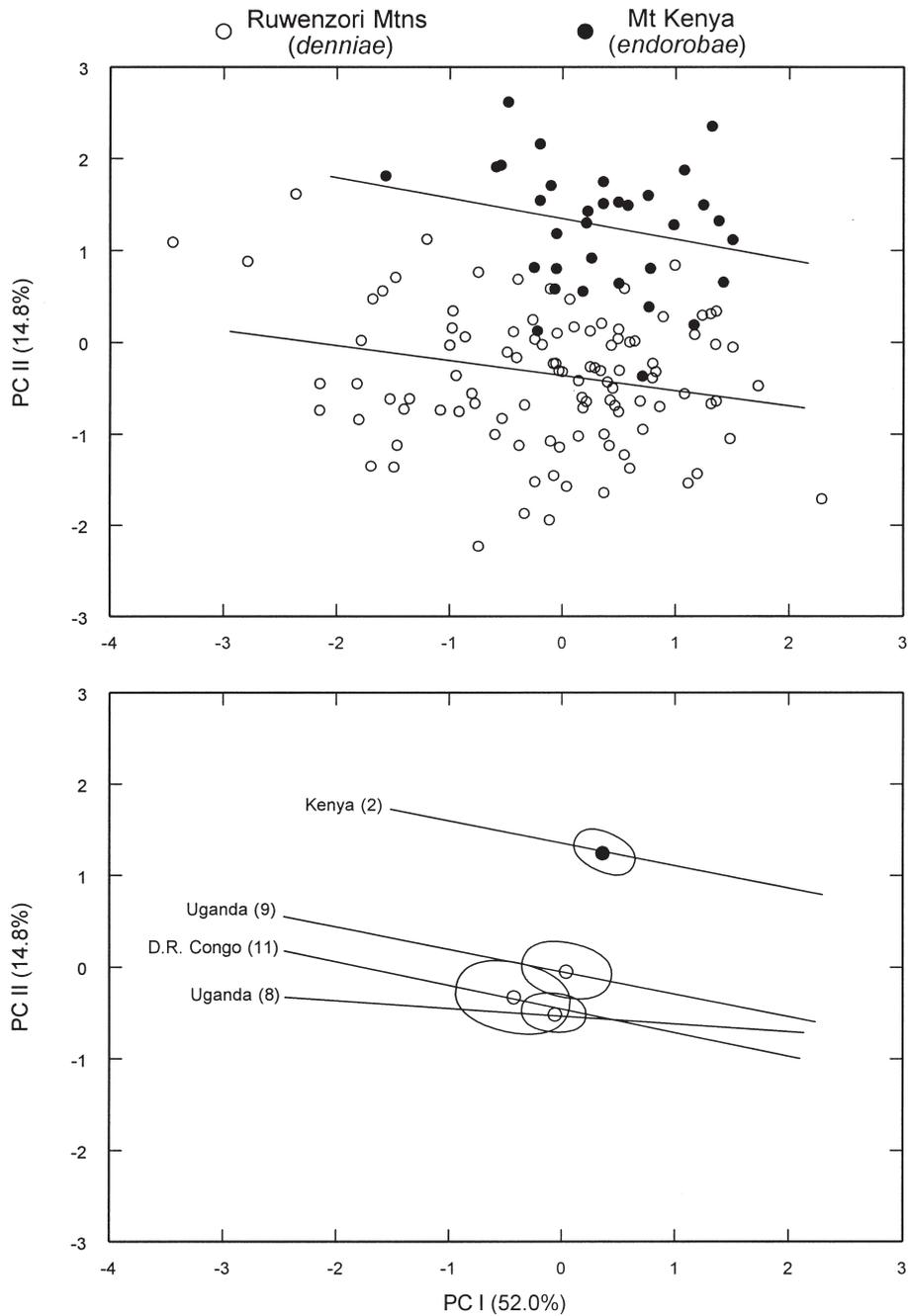


Fig. 7. Results of principal component analysis (Varimax rotation) performed on intact specimens ( $N = 137$ ) representing samples from the Ruwenzori Mountains (OTUs 8, 9, 11) and Mount Kenya (OTU 2). Top, projection of specimen scores onto the first two principal components extracted; regression lines of PC II on PC I indicated for specimens representing each taxon. Bottom, regression lines and centroids as calculated a posteriori for each OTU; ellipses correspond to 95% confidence limits of a group's centroid; individual specimen scores not plotted. See Table 6 for variable correlations and percent variance explained.

Table 6.—Results of principal component analysis (Varimax rotation) performed on intact specimens ( $n = 137$ ) representing samples from the Ruwenzori Mountains (OTUs 8, 9, 11) and Mount Kenya (OTU 2); see Fig. 7.

Variable	Correlations	
	PC I	PC II
ONL	0.90	0.29
ZB	0.83	0.13
BBC	0.49	0.39
BOC	0.56	0.25
IOB	0.42	0.40
LR	0.84	0.35
BR	0.85	0.24
PPL	0.87	-0.05
LBP	0.26	0.86
BBP	0.38	0.36
LIF	0.84	0.17
LD	0.91	0.17
BZP	0.52	0.19
LAB	0.51	0.64
CLM	0.07	0.85
WM1	0.01	0.65
Eigenvalues	0.021	0.006
Percent variance explained	52.0	14.8

Ruwenzori Mts, Uganda. Trenchant features that support this generic assignment include the very long tail, the relatively long fifth digit of the hindfoot, truncate rostrum with slim zygomatic plate, indistinct t3 of M1, and presence of an entepicondylar foramen. Thomas long ago anticipated this conclusion, for in his description of *Mus denniae*, he remarked (1906:145) that “A mouse from Mount Kenya ... would also seem to be assignable to *Mus Denniae*.” The Kenyan populations were soon after formally proposed as a new species, *Epimys endorobae* Heller (1910), and the taxon was subsequently considered either as a full synonym of *Hylomyscus d. denniae* (Hollister 1919, Allen 1939) or as a definable subspecies of *H. denniae* (Hatt 1940). These past allocations more accurately convey the relationship of *endorobae*, although we dispute the taxonomic rank accorded by those authors.

We consider each of the three well circumscribed phena revealed within eastern African “*denniae*” to represent valid species, for which the names *denniae* Thomas (1906), *vulcanorum* Lönnberg & Gyldenstolpe (1925), and *endorobae* Heller (1910) are available and geographically applicable. The three differ predominantly in size (Table 2; Figs. 8, 9)—*H. vulcanorum* the smallest to *H. endorobae* the largest—and more subtly in shape—*H. endorobae* with a broader skull, longer palate, inflated bullae, and larger molars relative to *H. denniae* and *H. vulcanorum*. One could plausibly attribute such differences among isolated populations to geographic variation and interpret their status as subspecies of a highly variable *H. denniae*, as did Hatt (1940) and Bishop (1979 [who did not specifically mention *endorobae*, but attributed Kenyan examples to *H. d. denniae*]). However, morphometric differentiation between populations that represent each epithet is sharply drawn and intimates morphogenetic discontinuity (species) instead of population intergradation (subspecies). Moreover, the degree and pattern of craniodental differentiation among these montane *Hylomyscus* conform to that which has emerged from other multivariate studies of morphologically similar, closely related (congeneric) species of African murids—e.g., those of *Dasymys* (Carleton & Martinez 1991, Verheyen et al. 2003), *Hybomys* (Van der Straeten & Verheyen 1982, Carleton & Robbins 1985), *Lemniscomys* (Van der Straeten 1980, Carleton & Van der Straeten 1997), *Lophuromys* (Verheyen et al. 2002), *Malacomys* (Van der Straeten & Verheyen 1979), and *Praomys* (Van der Straeten & Kerbis Peterhans 1999). In several of the foregoing studies, karyological and-or genetic data are reported that supplement the conventional morphometric results and thereby augment the case for separate species. Such independent data sets should be applied to evaluate our recom-

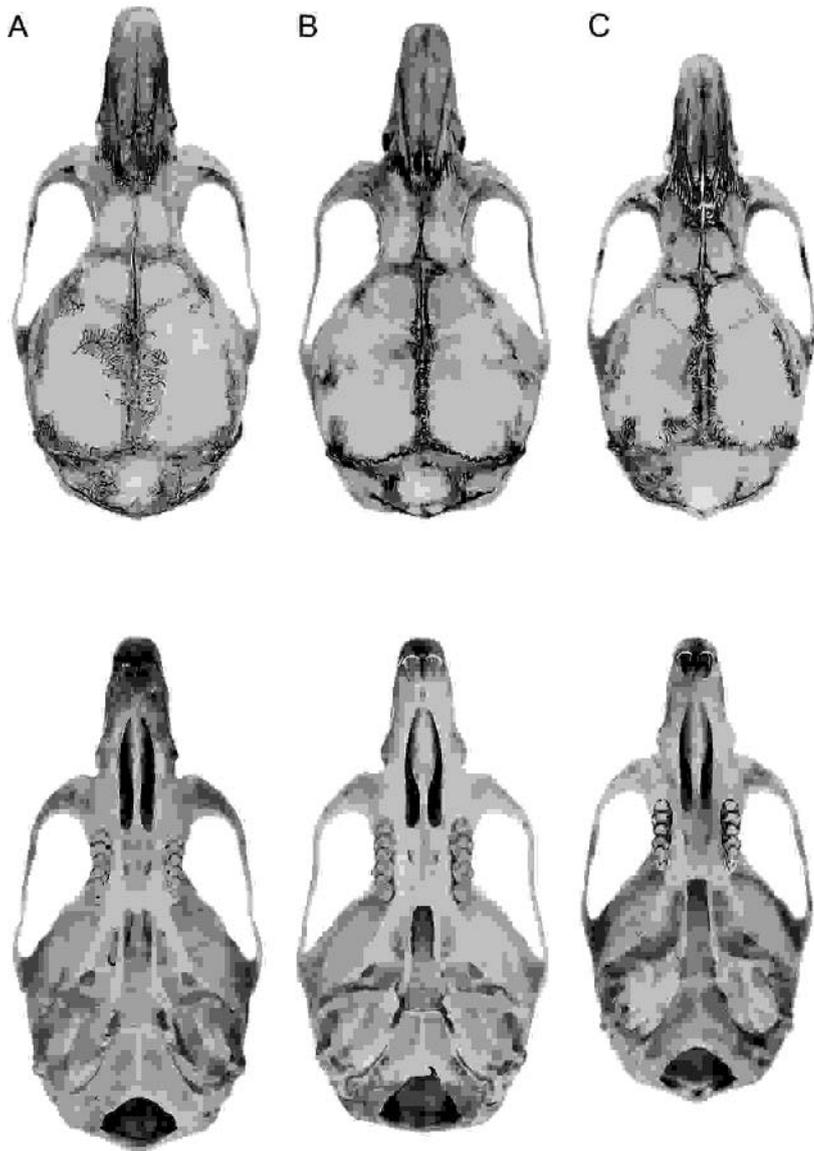


Fig. 8. Dorsal and ventral views (ca.  $2.5\times$ ) of adult crania of: left, *H. denniae* (FMNH 144495; ONL = 28.0 mm), a female from Uganda, Ruwenzori Mts, near the confluence of the Mubuku and Bujuku rivers; middle, *Hylomyscus endorobae* (USNM 163374; ONL = 27.1 mm), a male from Kenya, Mt Kenya, western side; and right, *H. vulcanorum* (FMNH 137661; ONL = 25.5 mm), a female from Burundi, Kibira NP, 2.3 km N and 1.9 km W Teza.

mendation for the specific distinction of *endorobae* and *vulcanorum* from *H. denniae*. In one such preliminary analysis, using two mitochondrial gene fragments (Huhndorf 2001), substantial sequence divergence (4.8–5.8%) was demonstrated between a sample from the Ruwenzoris

(= *H. denniae*) and three others from mountains in the central Albertine Rift (Mgahinga Gorilla NP, Bwindi Impenetrable NP, and Kibira NP = *H. vulcanorum*). Denser geographic representation and wider taxonomic sampling within and among forms of *Hylomyscus* are needed.

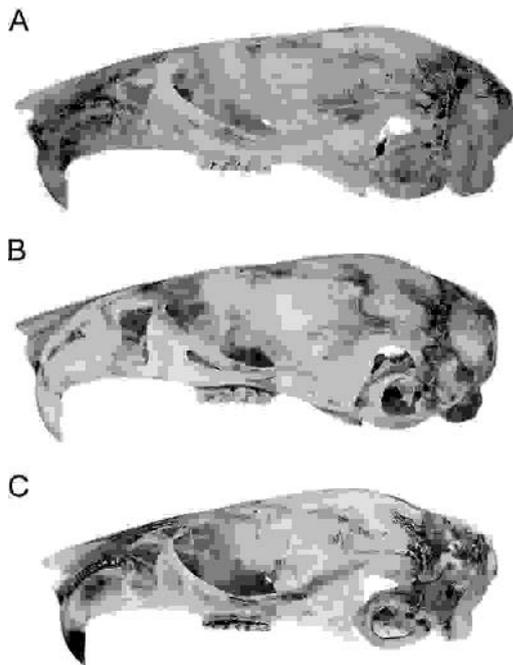


Fig. 9. Lateral views (ca. 2.5 $\times$ ) of adult crania of the same specimens portrayed in Fig. 8: top, *H. denniae*; middle, *Hylomyscus endorobae*; and bottom, *H. vulcanorum*.

The kinship hierarchy among the three species of the *H. denniae* group is ambiguous based on our data. *Hylomyscus denniae* and *H. endorobae* are phenetically most alike, as revealed in ordinations of craniodental variables. On the other hand, the mountain systems inhabited by *H. denniae* and *H. vulcanorum* are geographically much closer to one another, forming the northern and central portions of the Albertine Rift system, respectively, and faunal association between these is much stronger than that with the mountains in west-central Kenya where *H. endorobae* occurs (see Discussion). The geographic context, along with weak similarities in craniodental shape, instead offers circumstantial evidence for closer kinship of *H. denniae* and *H. vulcanorum*. Although the three species appear to be derived from a recent common ancestor, we view their relationship as an unresolved polytomy at this

stage of understanding. A phylogeographic approach using gene-sequence information should decidedly resolve this uncertainty.

Synonymies presented below for the three species of the *H. denniae* group trace earliest identification and first subsequent usage of other name combinations. We have personally examined the holotypes of *denniae* Thomas (1906) and *endorobae* Heller (1910); moreover, in the case of *denniae*, the large series recently collected from the valley of the Mubuku River by FMNH personnel essentially represents topotypic material. The holotype of *vulcanorum* Lönnberg & Gyldenstolpe (1925) was not studied, but the ample material included from other volcanoes in the Virunga mountains supplies confidence in the application of this name to the smallest of the three species. Specimens examined include all individuals personally seen and identified by us; see Appendix 1 for geographic coordinates of principal localities.

#### *Hylomyscus denniae* (Thomas)

*Mus denniae* Thomas, 1906:144 (type locality—Uganda, Ruwenzori East, Mubuku Valley, 7000 ft; holotype—BMNH 6.7.1.137).

*Hylomyscus denniae*, Thomas, 1926:178.

*Hylomyscus denniae denniae*, Allen, 1939:386.

*Rattus (Hylomyscus) denniae denniae*, Ellerman, 1941:209.

*Praomys (Hylomyscus) denniae*, Misonne, 1974:28.

*Praomys (Hylomyscus) denniae denniae*, Delany, 1975:85.

*Distribution*.—Restricted to middle to upper slopes of the Ruwenzori Mts, in both west-central Uganda and contiguous Democratic Republic of Congo (Fig. 10); known elevational range, 1890–4040 m.

*Remarks*.—As we understand the species, *Hylomyscus denniae* is endemic to the

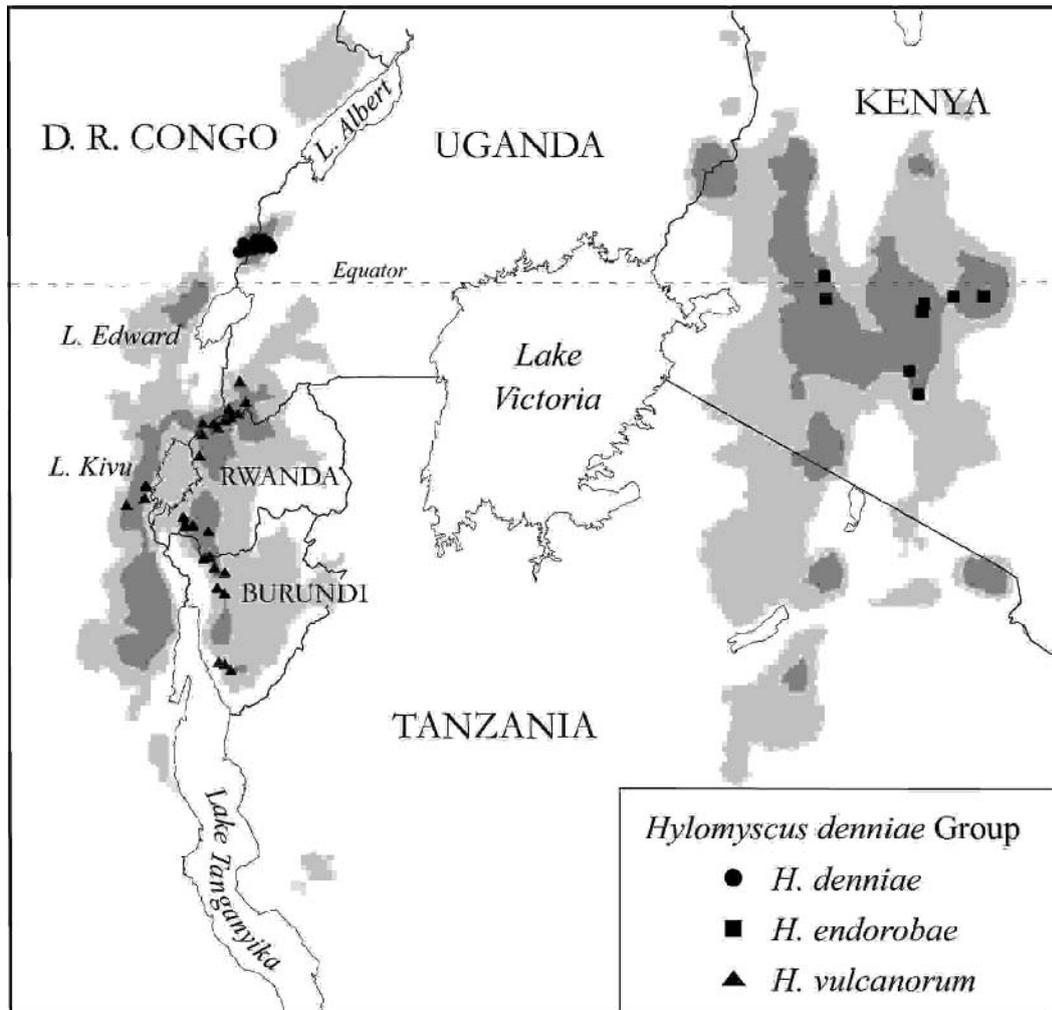


Fig. 10. Known distributions of *Hylomyscus denniae*, *H. endorobae*, and *H. vulcanorum* in eastern Africa, as based on specimens studied by us (see Taxonomic Summary).

Ruwenzori Mountains, but specimens from montane forest on Mt Elgon also have been referenced as *H. denniae* (Clausnitzer & Kityo 2001). Clarification of their species identification is the subject of on-going research (Carleton et al., unpubl.). Although the occurrence of some *denniae*-like form on Mt Elgon seems geographically plausible, the few specimens from the Kenyan slopes that we have examined to date prove to be examples of the *H. anelli* complex (Mt Elgon NP—USNM 589874, 589876, 589879–589881).

Elevational transects along both western (D. R. Congo) and eastern (Uganda) slopes of the Ruwenzoris have documented *H. denniae* from wet montane forest through alpine habitats (Kerbis Peterhans et al. 1998; Misonne 1963). In Uganda, the species was uncommon (4.3–6.6%) relative to other rodents obtained in the forest zone (1920–2100 m) but was more abundant in habitats above 2100 m, including *Podocarpus* forest, bamboo (*Arundinaria alpina*), tree heath and moss, and alpine vegetation characterized by *Senecio* and *Lobelia* (Kerbis Peterhans et

al. 1998). Within *Podocarpus* forest (2700 m), *H. denniae* supplanted *Praomys jacksoni* (*montis*) as the dominant member of the rodent community (32–39% of captures). A similar elevational range (ca. 2000–4500 m), pattern of habitat occupation, and relative abundance of *H. denniae* versus *P. jacksoni* are apparent along the western Ruwenzori slope in D. R. Congo (Heller, 1925 field notes, FMNH archives; Misonne 1963). Misonne (1963) recorded a 1000-m gap between the highest occurrence of *H. stella*, 1000 m in evergreen rainforest, and the lowest capture of *H. denniae*, 2000 m in montane forest, suggesting elevational fidelity to different vegetation zones.

*Specimens examined.*—DEMOCRATIC REPUBLIC OF THE CONGO: Mt Ruwenzori, Bugongo Ridge, 8500 and 9000 ft (AMNH 82448, 82457, 82458, 82467–82469, 82509, 82511; FMNH 26083–26085, 26088, 26089, 96029–96031); Mt Ruwenzori, summit of Bugongo Ridge, 11,000 ft (FMNH 26086); Mt Ruwenzori, Butego Valley, Ibale, 7500 ft (FMNH 26103, 26105–26107, 26109); Mt Ruwenzori, Butagu Valley, Kalonge Village, 7000 ft (FMNH 26026); Mt Ruwenzori, Katahuleko Creek west of Kalonge, 7000 ft (AMNH 82462; FMNH 26096–26099); Mt Ruwenzori, Old Kalonge, 7500 ft (FMNH 26091, 26092); Mt Ruwenzori, Ugongo (= Old Kalonge), 7500 ft (FMNH 26095).

UGANDA: Mt Ruwenzori, Mabuku Valley, east slope, 8500 ft (USNM 172919); Kasese District, Ruwenzori Mts, confluence of Mubuku and Bujuku rivers, Nyabitaba Hut, 8750 ft (FMNH 144475, 144479–144482, 144485–144489, 144491–144495, 144502, 144504, 144505, 144507, 144511, 144513–144515, 144518, 144519, 144522–144525, 144527, 144530–144532, 144536, 144538, 144540–144542, 144550, 144552, 144557, 144558, 144560–144562, 144568, 144571, 144577, 144579, 144580); Kasese District, Ruwenzori Mts,

periphery of Lake Mahoma, 9700 ft (FMNH 144583, 144584); Kasese District, Ruwenzori Mts, left bank Bujuku River, John Mate Camp, 11,050 ft (FMNH 144586, 144587, 144589, 144591–144596, 144598–144605, 144608, 144611); Kasese District, Ruwenzori Mts, right bank Bujuku River, Bigo Hut, 13,000 ft (FMNH 144612); Kasese District, Ruwenzori Mts, above Lake Bujuku, Bujuku Hut, 13,050 ft (FMNH 144613, 144614, 144626–144633, 144642–144645); Kasese District, Ruwenzori Mts, Lower Kitandara Lake, 13,250 ft (FMNH 144646); Kasese District, Ruwenzori Mts, Mubuku Valley, right bank Mubuku River near confluence of Mubuku and Kyoha Rivers, 3 km W Ibanda, 6200 ft (FMNH 144448–144451, 144453–144457); Kasese District, Ruwenzori Mts, Mubuku Valley, confluence of Mubuku and Mahoma rivers, 6900 ft (FMNH 144459–144470).

*Hylomyscus endorobae* (Heller)

*Mus Denniae*, Thomas, 1906:145 (in part—referral of Mt Kenya specimen).

*Epimys endorobae* Heller, 1910:3 (type locality—Kenya, western edge of Mau Forest, 25 mi N Eldoma [= Eldama] Ravine, 8600 ft; holotype—USNM 162888).

*Rattus denniae*, Hollister, 1919:79 (allocated as junior synonym).

*Hylomyscus denniae denniae*, Allen, 1939:386 (considered full synonym of nominate race, following Hollister's [1919] action).

*Hylomyscus denniae endorobae*, Hatt, 1940:536 (reinstated as a valid subspecies).

*Rattus (Hylomyscus) denniae denniae*, Ellerman, 1941:209 (generic reallocation).

*Praomys (Hylomyscus) denniae*, Misonne, 1974:28 (listed in synonymy without indication of rank).

*Distribution.*—Highlands of west-central Kenya (Fig. 10), including Mt Kenya,

the Aberdare Mts, and Mau Escarpment; extent of geographic range uncertain; known elevational range, 2135–3260 m.

*Remarks.*—Heller (1910) considered his new species *endorobae* to be a close ally of *H. denniae*, “distinguished by much darker coloration, smaller ears, and larger molars.” We appreciate his first and third differentiating features but cannot quantitatively substantiate the smaller pinnae of *H. endorobae*. The direction of the mean difference is supportive ( $\bar{x} \approx 20$  mm in *H. denniae* versus  $\bar{x} \approx 18$  mm in *H. endorobae*), but sample size of *H. endorobae* with reliable ear measurements was too small ( $N = 5$ ) to tabulate and statistically contrast.

Detailed ecological information is lacking for *H. endorobae*, although most examples can be generally associated with montane forest. At the type locality (25 mi N Eldama Ravine, 2620 m) in the Mau Escarpment, Heller (1910) reported that his new species was found only in montane forest, commonly in association with *Praomys jacksoni*. In his field notes, Heller (27 Nov 1909) further characterized the habitat as “vegetation in forest, juniper, yew, and bamboo with gray olive and *Hypericum* on margin.” The extensive series from Mt Kenya was obtained at five collecting camps sited within the forest zone, approximately from 2135 to 3260 m. Most specimens were collected in a “belt composed mainly of bamboo [*Arundinaria*] and yellowwood [*Afrocarpus*],” 2590–3260 m, but some were obtained from a lower forest belt composed of cedars (*Juniperus*) and various hardwood trees, 2135–2590 m (Mearns, in Roosevelt 1910:489). Again, *Praomys jacksoni* was often taken in sympatry with *H. endorobae* on Mt Kenya, especially at the 3050-m and 3260-m camps (Loring, in Roosevelt 1910:484). No *H. endorobae* was recorded around the highest and only collecting station established in afroalpine habitat proper (4175 m—“a zone of

giant heath, mixed with giant groundsels and shrubs”; Mearns, in Roosevelt, 1910:489).

In addition to *H. endorobae*, at least three other species of *Hylomyscus* occur in Kenya, *H. aeta*, *H. stella* (*kaimosae*), and *H. cf. anselli*. The lone sample of *H. aeta* so far recorded is from the Kakamega FR (CM 98254) in extreme west-central Kenya. Examples of *H. stella* are known to us from Kaimosi (USNM 183182–183184) and Kakamega FR (CM 98251–98253, 98256, 98257, 102459–102461; USNM 589877, 589878), nearby localities again in far west-central Kenya. Examples of *H. cf. anselli* are found on the eastern slopes of Mt Elgon (see *H. denniae* account), the Guas Ngishu Plateau (USNM 163349—reported as *endorobae* by Hollister 1919), and from 4 mi E Molo (USNM 437428, 437468). In places, the species may prove to be sympatric with *H. endorobae*; e.g., the species we identify from Molo is *H. endorobae* (FMNH 17024) and that from 4 mi E Molo is *H. cf. anselli*. Additional collecting, especially along designed elevational transects, is required to illuminate the number, distribution, and ecology of *Hylomyscus* species in Kenya.

*Specimens examined.*—KENYA: Aberdare Mts, 10,000 and 10,500 ft (USNM 163348, 183312); Aberdare Mts NP, Fishing Lodge, 9000 ft (USNM 589869); Aberdare Mts, Bamboo Camp, 8650 ft (AMNH 114025); Nasin Gishu District, 7500 ft (AMNH 34789); western edge of Mau Forest, 25 mi N Eldama Ravine, 8600 ft (USNM 162888, holotype); west side of Mt Kenya, various elevations from 7000 to 10,700 ft (AMNH 80984; CM 2843, 2856; FMNH 43454–43457; USNM 163347, 163357–163362, 163364, 163365, 163367–163377, 163379–163384, 163386, 1163387, 163389, 163390, 163395–163401); Mt Kenya, east slope, 10,300 ft (AMNH 82452, 82453); Mt Kenya, Naro Moru, 9000 and 10,000 ft (USNM 589870–589873, 589875); Kikuyu, Mu-

gaga North, ca. 7200 ft (FMNH 86322, 86335); Kijabe (FMNH 16987, 16989, 17013); Rift Valley Province, Nakuru District, Molo (FMNH 17024); Nyeri District, South Laikipia Forest, 6 mi W Bellevue, 10,000 ft (AMNH 187595).

*Hylomyscus vulcanorum* (Lönnerberg & Gyldenstolpe, 1925), new rank

*Rattus (Praomys) denniae vulcanorum* Lönnerberg & Gyldenstolpe, 1925:4 (type locality—Belgian Congo [= D. R. Congo], Birunga [= Virunga] Volcanoes, Mount Karisimbi, 3800 m).

*Hylomyscus denniae vulcanorum*, Allen, 1939:386.

*Rattus (Hylomyscus) denniae vulcanorum*, Ellerman, 1941:209.

*Praomys (Hylomyscus) denniae*, Misonne, 1974:28 (listed in synonymy without indication of rank).

*Praomys (Hylomyscus) denniae vulcanorum*, Bishop, 1979:528.

*Distribution*.—Mountains bordering the central Albertine Rift valley, from southwestern Uganda and east-central Democratic Republic of Congo, through Rwanda, to southern Burundi (Fig. 10); known elevational range, 1670–3100 m.

*Remarks*.—As herein documented, *H. vulcanorum* occurs as far south as 4°S latitude in southern Burundi, in mountain chains to the west and east of Lake Kivu in the central Albertine Rift. Along the southern portion of the Albertine Rift, mountains to the east of Lake Tanganyika, in western Tanzania (Mahale Mts, ca. 06°30'S, and Mbizi Mts, ca. 07°50'S; specimens in FMNH), harbor forms of the *H. anselli* group (Carleton & Stanley 2005, this study); mountains at comparable latitudes to the west of Lake Tanganyika, in southeastern D. R. Congo (Itombwe, Marungu, Mt Kabobo), have been little surveyed for small mammals and their *Hylomyscus* remain unknown. To the north, *H. vulcanorum* ranges into SW Uganda at least as far as Bwindi

Impenetrable NP, about 1°S latitude. Bishop (1979) also referred specimens from the Cherengani Hills, Kenya, and Mt Elgon, Uganda, to his *Praomys denniae vulcanorum*. We have not yet examined these specimens but question their identification as *H. vulcanorum* proper. As noted in the *H. denniae* account, those high-elevation occurrences of *Hylomyscus* on Mt Elgon seen by us are a species referable to the *H. anselli* complex. Perhaps Bishop's series also represent this species, which in aspects of general size recalls *H. vulcanorum* sensu stricto.

At Bwindi Impenetrable NP in southwestern Uganda, *H. vulcanorum* occurs at 2350 m (Ruhizha), but at lower sites (FMNH collections) it is replaced by its congeners *H. stella* (e.g., at Omubiyanja Swamp, 1850 m; Nteko Parish, 1600 m; Byumba, 1540 m; Buhoma, 1500 m) or *H. aeta* (also at Nteko Parish, 1600 m), an elevational replacement analogous to distributions of *Hylomyscus* on the slopes of the Ruwenzori Mts. In montane forests of Burundi and Uganda, *H. vulcanorum* was commonly obtained in traps placed above ground, averaging about 20% in arboreal captures (Kerbis, unpubl.).

*Specimens examined*.—BURUNDI: Bubanza Province, Kibira NP, Ntamba Zone, Kubutare Colline, Ruhondo, 2000, 2020, and 2030 m (FMNH 148455, 148469–148471, 148474); Bubanza Province, Kibira NP, Rugazi Commune, Kabanga Colline, Nyabikona River, 1950 m (FMNH 148458); Bubanza Province, Bururi FR, Nyagatarugwa River Valley, 1800 m (FMNH 148462); Cibitoke Province, Bukinanyana Commune, Kibira NP, Ndoro zone, Kwogofe Colline, 2200 m (FMNH 148463, 148472); Cibitoke Province, Bukinanyana Commune, Kibira NP, Ndoro zone, Giserama Colline, Ruvyirame River, 2.1 km N Kirumura, 1670 m (FMNH 149084–149086, 149088); Cibitoke Province, Bukinanyana Commune, Kibira

NP, Ndora zone, Giserama Colline, Gatara Stream, 1.9 km N Kirumura, 1950 m (FMNH 149090, 149091, 149094, 149095); Kayanza Province, Matongo Commune, Kibira NP, Abris Kivuso, 2430 m (FMNH 148464); Kayanza Province, Muruta Commune, Kibira NP, Gitenge River, 2177 m (FMNH 148465–148468); Muryamuya Province, Kibira NP, 2.9 km N and 1.4 km W Teza, 2480 and 2520 m (FMNH 137657, 137658); Muryamuya Province, Kibira NP, 2.3 km N and 1.9 km W Teza, 2330–2390 m (FMNH 137659–137662, 137699); Muryamuya Province, Kibira NP, 3.5 km S and 2.6 km W Teza, 1970–2050 m (FMNH 137663–137671); Muryamuya Province, Bukeye Commune, Kibira NP, Nyamugari Colline, Teza, 2080 m; 03 14 S, 29 34 E (FMNH 148473); Bururi Province, Bururi FR, Mumushwizi Valley, 1880 m (FMNH 155981, 155982, 155984–155990); Bururi Province, Bururi FR, Ruhinga Hill, 2170 m (FMNH 155991, 155992).

**DEMOCRATIC REPUBLIC OF THE CONGO:** Kivu District, Kalehe, Lemera (USNM 375361, 375365, 375367, 375368); Kivu District, Bukavu, Mugaba (USNM 375348); Tshibati (RUCA 812, 1023, 1122, 1163, 1223, 1124, 1218, 1230, 1478, 1507, 2055, 2210, 2215, 2279, 2293, 2298, 2327, 2328); Kivu District, Mount Mikeno, northwest slope, 7900 ft (AMNH 82512).

**RWANDA:** Gahinga Volcano (RUCA 4894–4896, 4935, 4936, 4992, 5004, 5055–5057, 5082, 5084); Gasiza Volcano, 2360 m (5178, 5179, 5188, 5195, 5226); Karisoke, 3100 m (RUCA 3659, 3662, 3682, 3706, 3720); Kayove (RUCA 5279); Kinigi, 2250 m (RUCA 2407, 2410, 2417, 2419, 2488, 2653, 2667, 2669, 2687, 2740, 2763, 2764, 2825, 2836, 2837, 2855, 3010, 3881, 3882); Kitabi, 2200 m (RUCA 853, 863, 864, 887–889, 892–896, 903, 1006, 1015); Mutura, 2200 m (RUCA 670); Pindura (RUCA 150); Routabansougera, 1750 m (RUCA 214–216, 220, 221, 225,

228, 266, 4145, 4152, 4153, 4173, 4230, 4282, 4331); Uwinka, 2450 m (RUCA 161, 163, 164, 168, 173, 178, 191, 199, 201, 206, 207, 2061, 2129, 2130, 2136, 2137, 2139, 2147, 2166, 2173, 2190, 2198, 2252, 2260, 2319; USNM 340837, 340839, 340841, 340842, 340848, 340850, 340859); Visoke Volcano, 2700 m (RUCA 2849, 2850, 2949–2957, 3027–3034, 3049, 3050, 3742, 3903).

**UGANDA:** Virunga Volcanoes, pass between Mt Sabinio and Mt Mgahinga, 8000–8500 ft (FMNH 26124, 26125, 26128, 26521–26525); Kigezi, Kabale District, Bwindi Impenetrable NP, Ruhizha, 2350 m (FMNH 157903–157907, 160502; LACM 35608); Kabale District, Bwindi Impenetrable NP, Mubwindi Swamp, 2070 m (LACM 53328, 53329); Kabale District, Bwindi Impenetrable NP, Itama area, 1615 m (LACM 35610); Kigezi, Kisoro District, Mgahinga Gorilla NP, saddle between Mts Muhavura and Mgahinga, 2980 m (FMNH 157511–157513); Kigezi, Kisoro District, Mgahinga Gorilla NP, edge of encroached area along pipeline, 2680 m (FMNH 157515, 157516, 157518, 157521, 157524, 157527, 157528, 157530); Kigezi, Rubanda District, Echuya FR, 2380 m (FMNH 161049, 161050).

#### Discussion

*Generic and specific taxonomy.*—The taxonomic status of *Hylomyscus* as genus or subgenus has vascillated since its description. Thomas (1926) expressly created the taxon as a genus (*H. aeta*, type species) to segregate certain small African murines that had been associated with *Praomys*, and considered the two genera to be closely related, species of *Hylomyscus* exhibiting more arboreal adaptations. Allen (1939) and Hatt (1940) acknowledged Thomas' generic distinction, but Ellerman (1941) reduced *Hylomyscus*, along with *Mastomys* and *Praomys*, to subgenera of a broadly de-

finer *Rattus*. Misonne (1969) effectively argued the in situ African origin of *Praomys* and kin, including *Hylomyscus*, and their distant phylogenetic relationship to *Rattus sensu stricto*, although he maintained them in separate generic groupings within his *Rattus* Division. Recent molecular studies of informative taxonomic breadth decidedly sustain the exclusion of *Praomys*, *Hylomyscus*, and *Mastomys* from *Rattus* proper (Watts & Baverstock 1995, LeCompte et al. 2002b, Jansa & Weksler 2004). Aside from *Rattus*, *Hylomyscus* has been considered a subgenus of *Praomys* by some systematists (Davis 1965, Misonne 1969, 1974, Delany 1975). This taxonomic stature too has been rejected by recent authorities (Rosevear 1969, Robbins et al. 1980, Musser & Carleton 1993), and phylogenetic evaluations of morphological or molecular data portray *Hylomyscus* both as monophyletic and as cladistically removed from *Praomys* and related taxa (Fadda et al. 2001, LeCompte et al. 2002a, 2002b). Within the radiation of African murines, this clade of six genera—*Heimyscus*, *Hylomyscus*, *Mastomys*, *Myomyscus*, *Praomys*, *Stenocephalemys*—has been identified as the *Praomys* group (LeCompte et al. 2002b) or *Stenocephalemys* Division (Musser & Carleton 2005).

Consensual recognition of *Hylomyscus* as genus has thus returned full circle. In retrospect, this rank most effectively captures the conservative nature and diagnostic value of the traits originally emphasized by Thomas (1926:178): fur soft and fine; tail relatively long with fine caudal scales and a weak terminal pencil; hind feet small but relatively broad, digit V relatively long; skull with a diminutive rostrum, expanded brain-case, and narrow zygomatic plate; and t3 of the M1 weakly or not defined. Our comparisons of craniodental morphometry and morphology, in concert with the cladistic results of LeCompte et al. (2002a, 2002b), serve only to support his insights

on generic boundaries among these endemic African murines. In essence, the disagreement over *endorobae* as small *Praomys* (Van der Straeten & Robbins 1997) or large *Hylomyscus* (Musser & Carleton 1993, 2005; this study) represents just another context that underscores the basic shape differences that characterize the crania of these two genus-group taxa, again as first appreciated by Thomas (1926). Principal component ordination of covariation among continuous variables has proven to be a sensitive technique for discerning subtle cranial size and shape differences between closely related (congeneric) species populations of murid rodents (e.g., Voss & Marcus 1992). In our view, application of principal component analysis solely to holotypes in order to delimit murid generic boundaries (as per Van der Straeten and Robbins 1997), taxonomic entities historically founded on qualitative traits, overextends the power and purpose of the method.

At the time Thomas (1926) erected *Hylomyscus*, he allocated six species as generic members: *H. aeta* (type species), *H. alleni*, *H. carillus*, *H. denniae*, *H. schoutedeni*, and *H. stella*. Five of these are still considered valid, and subsequent descriptions and revisions have raised the number of *Hylomyscus* species to 12, a small but distinctive murine radiation characteristic of moist lowland and montane forests in Sub-Saharan Africa (see Musser & Carleton 2005 for taxonomic updates; also Carleton & Stanley 2005, this study). With increase in the number of species recognized, certain themes or patterns of morphological affinity among them are becoming apparent. Six species groups are provisionally arranged here (Table 7), four of them (*aeta*, *alleni*, *baeri*, and *parvus*) distributed within sectors of lowland rainforest in West and Central Africa, and two (*anselli* and *denniae*) confined to wet montane forest in south-central and eastern Africa. Within spe-

Table 7.—Provisional species groupings<sup>1</sup> discernable within *Hylomyscus* and distribution of certain character states (see Discussion).

Character	Species Groups					
	<i>H. aeta</i>	<i>H. alleni</i>	<i>H. anelli</i>	<i>H. baeri</i>	<i>H. denniae</i>	<i>H. parvus</i>
Pectoral mammae <sup>2</sup> (total)	absent (6)	present (8)	Absent (6)	present? (8)	present (8)	absent? (6)
Upper incisors	opisthodont	orthodont, weakly proodont	opisthodont	opisthodont	opisthodont	proodont
T3 on M1 <sup>3</sup>	large	medium	medium	large	medium	Minute
T9 on M1	distinct	indistinct	indistinct	distinct	indistinct	Absent
Interorbital condition <sup>4</sup>	shelf with bead	amphoral	weak shelf	shelf	weak shelf	amphoral
Rostral length	medium	short	medium	medium	long	short
Incisive foramen <sup>5</sup>	medium	short	medium	medium	long	short
Subsquamosal foramen <sup>6</sup>	medium	medium	medium	medium	tiny, absent	medium

<sup>1</sup> *Hylomyscus aeta* group = *H. aeta* (Thomas, 1911), *H. grandis* Eisentraut, 1969. *Hylomyscus alleni* group = *H. alleni* (Waterhouse, 1838), *H. carillus* (Thomas, 1904), *H. stella*, (Thomas 1911). *Hylomyscus anelli* group = *H. anelli* Bishop, 1979, *H. arcimontensis* Carleton & Stanley, 2005. *Hylomyscus baeri* group = *H. baeri* Heim de Balsac & Aellen, 1965. *Hylomyscus denniae* group = *H. denniae* (Thomas, 1906), *H. endorobae* (Heller, 1910), *H. vulcanorum* Lönnberg & Gyldenstolpe, 1925. *Hylomyscus parvus* group = *H. parvus* Brosset, Dubois, & Heim de Balsac, 1965.

<sup>2</sup> In general, counts are based on many females with enlarged mammae (near-term pregnancy or nursing) surveyed per species. The count for *H. baeri* is based on a single young adult (USNM 450446); typical condition uncertain. Only two suitable females of *H. parvus* were located (FMNH 167829, 167830), one of which possessed a pair of small pectoral mammae in addition to prominently swollen post-axial and two inguinal pairs; typical condition needs verification.

<sup>3</sup> Size and distinctiveness relative to t1: large = area of t3 subequal to t1, physically discrete only in juveniles-young adults, anterior chevron approximately symmetrical; medium = t3 smaller than t1, physically discrete only in juveniles and indistinct in adults, anterior chevron moderately asymmetrical; minute = t3 minute relative to t1, indistinct or seemingly absent even in juveniles, anterior chevron highly asymmetrical.

<sup>4</sup> Amphoral = no supraorbital shelf present, rear edges of orbit more or less smoothly contoured, shape hourglass-like; weak shelf = rear edges of orbit squared, forming weak supraorbital shelf in older animals, shape hourglass-like; shelf = rear edges of orbit squared, distinct supraorbital shelf evident even in young animals, shape weakly cuneate; shelf with bead = supraorbital shelf present at rear of orbit, lateral shelf edges dorsally reflected (beaded), shape moderately cuneate.

<sup>5</sup> Posteriormost extent of incisive foramina: short = terminates short of or even with anterior root of the M1s; medium = extends to middle of anterior root or even with t2 of M1s; long = extends to the level of the t2-t1 of M1s.

<sup>6</sup> Area and hamular process: medium = foramen present, one-third to one-half the area of the contiguous postglenoid foramen, hamular process thin and long; tiny = foramen distinctly less than one-third the area of the postglenoid foramen or occluded, hamular process thick and short or indistinct if foramen occluded.

ciouse muroid genera, species groups or complexes have traditionally emerged, following the early phase of discovery and description, as phenetic foci or tendencies of character variation and lack a persuasive phylogenetic perspective to sustain their monophyly (other than the overall morphological similarity exhibited by the constituent species). So it is with the six groups identified here: many of

their character “differences” consist of crude verbalizations of subtle size and shape variation of continuous variables (Table 7), and few of these differences can be objectively systematized as cladistically informative transformation series.

Other data sets must be mustered to test the naturalness of these six groups and to place their phylogenetic diversification within the context of broad geo-

graphic patterns. Several questions invite immediate attention in this regard. For example, although *H. parvus* is morphologically distinctive within the genus (Brosset et al. 1965), certain characteristics of the *alleni* group approach the conditions observed in *H. parvus* and suggest that it should belong in the same species group. Certainly, this is the conclusion indicated by the cladistic hierarchy (*H. stella* (*H. alleni*-*H. parvus*)) disclosed by the cytochrome-b analyses of Lecompte et al. (2002b). However, their representation within *Hylomyscus* is limited, geographically and taxonomically, and merger of the two groups should be argued more substantially. *Hylomyscus baeri* is a species endemic to far West Africa and seemingly is not closely related to the broadly distributed West African congener, *H. alleni*. By virtue of its relatively large t3 on M1 and distinctive post-orbital shelf (albeit not beaded), is *H. baeri* the West African vicar to *H. aeta* of the Congo Basin? Are the *H. anselli* and *H. denniae* species groups, which occupy isolates of wet montane forest in south-central and eastern Africa, respectively, derived from a common ancestor, as implied by their former inclusion under the broadly ranging, polytypic construct of *H. denniae* (e.g., sensu Bishop 1979)? Or did each originate from different species groups that inhabit lowland rainforest via independent dispersions into mountainous settings? The distribution of our few character states speaks inconclusively to these questions (Table 7). In view of the singular development of an interorbital bead and relatively large t3 on M1, does the *H. aeta* group form a basal kinship group to all other *Hylomyscus*? For the traits Thomas (1926) emphasized in his diagnosis of *Hylomyscus*, in particular the weak expression of a t3, he curiously selected an exceptional species to serve as the standard of his new genus (Table 7). The monophyly of the genus, as its specific contents are currently

understood, remains a legitimate issue that deserves stronger resolution based on expanded species sampling within *Hylomyscus* and among related genera. Such phylogenetic and biogeographic issues will simultaneously profit from continued alpha taxonomic revision and documentation of distributions, which are especially required for three of the groups (*aeta*, *alleni*, *anselli*). This much-needed attention will undoubtedly further increase the species diversity within *Hylomyscus*.

*Biogeographic remarks.*—The three species of the *Hylomyscus denniae* group are restricted to moist montane environments in eastern Africa, the majority of localities falling within an elevational belt covering 1800–3400 m. The species are common in middle to upper elevation montane forests, including bamboo zones, but also occur higher into ericaceous vegetation and tropical alpine habitats (Misonne 1963, Kerbis Peterhans et al. 1998, this study). On the basis of such an ecological occurrence and naturally discontinuous mountain setting, the *H. denniae* group qualifies as an element of the Afromontane biotic region, here used in the broad sense to connote both wet montane forests and afroalpine habitats above continuous tree canopy (i.e., following White 1978, 1981, although the afroalpine is considered a separate region by some—e.g., Hedberg 1986, Clausnitzer 2001). By its nature, the Afromontane region of Sub Sahara Africa is highly disjunct, consisting of several mountain ranges and highlands that are diverse in geological age and orogenic formation; these nonetheless share a characteristic and largely stenotopic high-altitude flora and fauna. Ornithological biogeographers have denoted seven physiographic groups within the Afromontane region (Moreau 1966, Dowsett 1986), and species of the *H. denniae* group occupy portions of two of these, the East Congo (*H. denniae*, *H. vulcanorum*) and Kenya (*H. endorobae*)

Table 8.—List of terrestrial small mammals (orders Soricomorpha and Rodentia) known from afromontane habitats in eastern Africa. (E) = probable endemic; (?) = occurrence uncertain, not used for statistical summaries.

	Albertine rift		Gregory rift	
	Ruwenzoris	Kivu Mts	Mt Elgon	Aberdares-Mt Kenya
Soricomorpha				
<i>Crocidura elgonius</i>			X	X
<i>Crocidura fumosa</i>				X (E)
<i>Crocidura kivuana</i>		X (E)		
<i>Crocidura lanosa</i>		X (E)		
<i>Crocidura maurisca</i>		X (E)		
<i>Crocidura montis</i>	X		X	X
<i>Crocidura nigrofusca</i>		X	X	X
<i>Crocidura niobe</i>	X	X		
<i>Crocidura stenocephala</i>		X (E)		
<i>Crocidura tarella</i>		X (E)		
<i>Myosorex babaulti</i>		X (E)		
<i>Myosorex blarina</i>	X (E)			
<i>Paracrocidura maxima</i>	X	X		
<i>Ruwenzorisorex suncoides</i>	X	X		
<i>Scutisorex somereni</i>	X	X		
<i>Surdisorex norae</i>				X (E)
<i>Surdisorex polulus</i>				X (E)
<i>Sylvisorex granti</i>	X	X	X	X
<i>Sylvisorex lunaris</i>	X	X		
<i>Sylvisorex vulcanorum</i>	(?)	X		
Rodentia				
<i>Funisciurus carruthersi</i>	X	X		
<i>Heliosciurus ruwenzorii</i>	X	X		
<i>Tachyoryctes audax</i>				X (E)
<i>T. rex</i>				X (E)
<i>T. ruandae</i>		X (E)		
<i>T. ruddi</i>		X	X	
<i>Cricetomys ansorgei</i>			X	X
<i>C. kivuensis</i>		X (E)		
<i>Delanymys brooksi</i>		X (E)		
<i>Dendromus insignis</i>	X	X	X	X
<i>D. kahuziensis</i>		X (E)		
<i>D. nyasae</i>	X	X		
<i>Lophuromys aquilus</i>	X	X	X	
<i>L. medicaudatus</i>		X (E)		
<i>L. rahmi</i>		X (E)		
<i>L. woosnami</i>	X	X		
<i>L. zena</i>				X (E)
<i>Colomys goslingi</i>	X	X	X	
<i>Dasymys incomtus</i>	X	X	X	X
<i>D. montanus</i>	X (E)			
<i>D. rwandae</i>		X (E)		
<i>Grammomys dryas</i>	X	X		
<i>G. gigas</i>				X (E)
<i>G. dolichurus</i>			X	X
<i>G. ibeanus</i>				X
<i>Hybomys lunaris</i>	X (E)			
<i>Hylomyscus cf. anselli</i>			X	X
<i>H. denniae</i>	X (E)			
<i>H. endorobae</i>				X (E)

Table 8.—Continued.

	Albertine rift		Gregory rift	
	Ruwenzoris	Kivu Mts	Mt Elgon	Aberdares-Mt Kenya
<i>H. vulcanorum</i>		X (E)		
<i>Mus bufo</i>	X	X		
<i>M. triton</i>	X	X	X	X
<i>Praomys degraaffi</i>		X (E)		
<i>P. jacksoni</i>	X	X	X	X
<i>Rhabdomys dilectus</i>			X	X
<i>Thamnomys kemp</i>		X (E)		
<i>T. major</i>		X (E)		
<i>T. venustus</i>	X	X		
<i>Otomys barbouri</i>			X (E)	
<i>O. dartmouthi</i>	X (E)			
<i>O. denti</i>	X	X		
<i>O. jacksoni</i>			X (E)	
<i>O. orestes</i>				X (E)
<i>O. tropicalis</i>	X	X	X	X
# species	27	41	18	23
# endemics	5	17	2	9
% endemism	18.5	41.5	11.1	39.1

montane groups. We judge the southern geographic extent of *H. denniae* to be well delimited, but additional collecting in the mountains west of Lake Albert may extend its northern limits. Similarly, the ranges of *H. vulcanorum* and *H. endorobae* may reach slightly farther south than presently documented within their principal montane groups (see remarks under Taxonomic Summary). Notwithstanding such local distributional refinements, we doubt that members of the *H. denniae* group will be found to occur in the Ethiopian Plateau or Cameroon Highlands, farther to the north and west, respectively. Nor are members of the *H. denniae* species group so far known from Afromontane zones to the south and southwest, in the Tanganyika-Nyasa ranges or Angola Plateau where examples of the *H. anselli* group are found (Carleton & Stanley 2005). As discussed above, whether the two species groups of *Hylomyscus* indigenous to montane settings share a recent common ancestor relative to those in the Guinean-Congo lowlands merits investigation.

Within the East Congo and Kenya Afromontane groups, the geographic

distribution of each *Hylomyscus* species is more narrowly congruent with local mountain systems: *H. denniae* in the Ruwenzori Mts of the northern Albertine (Western) Rift; *H. vulcanorum* in mountains rimming Lake Kivu of the central Albertine Rift; and *H. endorobae* in the Mau Escarpment, Aberdare Mts, and Mt Kenya along the Gregory (Eastern) Rift Valley (Fig. 10). Based on shrew and rodent distributions, the specific richness and amount of endemism of the Ruwenzori-Kivu sectors of the Albertine Rift are jointly impressive (Table 8), and the historical role of the Ruwenzoris as a lesser area of endemism is clearly appreciable, as previously remarked by Kerbis Peterhans et al. (1998). The total number of species found in the Kenya Afromontane group is notably less, but the level of endemism is still high, especially for shrew and rodent species that inhabit the Aberdare Mts-Mt Kenya subregion (Table 8). Few species occur across all four mountain systems, and some that do—such as *Sylvisorex granti*, *Praomys jacksoni*, and *Otomys tropicalis*—are believed to represent species composites in need of careful taxonomic

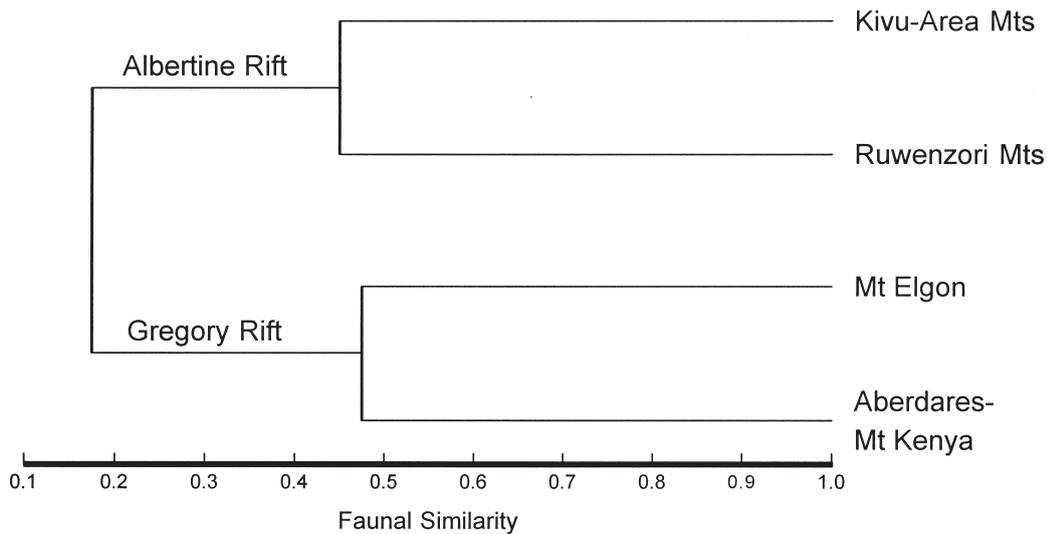


Fig. 11. Area relationships based on the geographic occurrences of small terrestrial mammals restricted to Afromontane habitats in eastern Africa (see Table 8); phenogram of faunal similarity produced from UPGMA clustering of Jaccard's Index (coefficient of cophenetic correlation = 0.98,  $P < 0.001$ ).

revision (see Hutterer 2005, Musser & Carleton 2005, for comments). Others, such as *Dendromus insignis* and *Mus triton*, lack a current revisionary standard employing morphometric and-or molecular analyses. A pronounced faunal discontinuity is predictably recorded between mountains of the Albertine Rift (Ruwenzoris-Kivu) and those of the Gregory Rift (Mt Elgon-Aberdares-Mt Kenya) (Fig. 11). Such a division among small terrestrial mammals follows from comparable biogeographic patterns exhibited by other animals, notably birds (Dowsett 1986, Stuart et al. 1993); from geographic proximity and topographic connectivity of the mountain ranges; and from the probable former continuity of montane forests among those ranges, especially during cooler and moister stadia of the Pleistocene (White 1981, Lovett 1993, DeBusk 1998).

Confidence in the above area relationships, foci of endemism, and inferred vicariance zones suffers from several glaring weaknesses in our systematic framework: (1) inadequacy of biological inventory to convincingly vouch specific

distributions and of long-term site study to assess their ecological fidelity to afromontane environments; (2) need for improved taxonomic understanding of many genera and species; and (3) the general lack of credible interspecific phylogenies to implicate historical geographic events in the genesis of kinship patterns. All three facets require concerted attention to enhance comprehension of the biogeography of shrews and rodents found in Afromontane landscapes.

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#### Appendix 1

The 52 principal localities (in bold face) used in preparation of distribution maps (Figs. 1, 10). Most geographic coordinates were obtained from collec-

tors' skin tags and-or field catalogs (C), some from USBGN gazetteers (G), faunal publications (P), or topographic maps (M). Publications consulted include Aggundey & Schlitter (1984), Davis & Misonne (1964), Delany (1975), Hutterer et al. (1987), and Verheyen et al. (2002). See *Specimens examined* for full locality data.

## BURUNDI

1. **Abris Kivuso**, Kayanza Prov., Kibira NP, 2430 m: 03°00'S, 29°32.5'E C.
2. **Gitenge River**, Kayanza Prov., Kibira NP, 2177 m: 02°57'S, 29°30'E C.
3. **Kirumura, 1.9 km N**, Cibitoke Prov., Kibira NP, Gatere Stream, 1950 m: 02°51'S, 29°24'E M.
4. **Kirumura, 2.1 km N**, Cibitoke Prov., Kibira NP, Ruvyirame River, 1670 m: 02°51'S, 29°23'E M.
5. **Kwogofe Hill**, Cibitoke Prov., Kibira NP, 2170–2250 m: 02°50'S, 29°25'E C.
6. **Mumushwizi Valley**, Bururi Prov., Bururi FR, 1880 m: 03°55'11"S, 29°35'01"E M.
7. **Nyabikona River**, Bubanza Prov., Kibira NP, 1950–2140 m: 03°10'S, 29°32'E C.
8. **Nyagatarugwa River Valley**, Bubanza Prov., Bururi FR, 1795 m: 03°55'36"S, 29°35'14"E C.
9. **Ruhinga Hill**, Bururi Prov., Bururi FR, 2170–2250 m: 03°55'13"S, 29°35'18"E M.
10. **Ruhondo**, Bubanza Prov., Kibira NP, 2040 m: 02°56'S, 29°29'E C.
11. **Teza and vicinity**, Muramuruzi Prov., Kibira NP, 2120 m: 03°13'S, 29°34'E C.

## DEMOCRATIC REPUBLIC OF THE CONGO

12. **Bugongo Ridge**, 2745–3350 m: ca. 00°20'N, 29°48'E P.
13. **Ibale**, 2285 m: 00°20'N, 29°46'E M.
14. **Kalonge Village**, Butagu Valley, 2100 m: 00°20'N, 29°48'E C.
15. **Katahuleko Creek**, west of Kalonge: 00°20'N, 29°48'E C.
16. **Lemera**, 2100 m: 02°08'S, 28°49'E P.
17. **Mt Mikeno**, Kivu District, 2410 m: 01°29'S, 29°23'E P.
18. **Mugaba**, 2200 m: 02°18'S, 28°36'E P.
19. **Tshibati**: 02°14'S, 28°48'E P.
20. **Ugongo** (= Old Kalonge), 2285 m: 00°20'N, 29°49'E M.

## KENYA

21. **Aberdare Mts**, 2635–3200 m: 00°19'S, 36°42'E P.
22. **Bellevue**, 6 mi W, Nyeri Dist., 3048 m: 00°14'S, 36°43'E G.

23. **Eldama Ravine**, 2620 m: 00°03'N, 35°43'E P.
24. **Kijabe**, 2652 m: 00°56'S, 36°34'E P.
25. **Mt Kenya**, 2135–3325 m: 00°10'S, 37°20'E P.
26. **Molo**, 2438 m: 00°15'S, 35°44'E P.
27. **Muguga**, 2195 m: 01°11'S, 36°39'E P.
28. **Naro Moru**, 2740 m: 00°10'S, 37°01'E G.

## RWANDA

29. **Gahinga Volcano**, up to 2700 m: 01°24'S, 29°40'E P.
30. **Gasiza Volcano**, 2360 m: 01°25'S, 29°40'E P.
31. **Karisoke**, 3100 m: 01°28'S, 29°29'E P.
32. **Kayove**, 2000 m: 01°48'S, 29°21'E P.
33. **Kinigi**, 2250 m: 01°26'S, 29°36'E P.
34. **Kitabi**, 2200 m: 02°34'S, 29°26'E P.
35. **Mutura**, 2200 m: 01°34'S, 29°22'E P.
36. **Pindura**: 02°28'54"S, 29°13'56"E G.
37. **Routabansougera**, 1750 m: 02°26'S, 29°11'E P.
38. **Uwinka**, 2450 m: 02°29'S, 29°12'E P.
39. **Visoke Volcano**, 2700 m: 01°27'S, 29°30'E P.

## UGANDA

40. **Bigo Hut**, Kasese Dist., Ruwenzori Mts, 3420 m: 00°23'N, 29°55'E C.
41. **Bujuku Hut**, Lake Bujuku, Kasese Dist., Ruwenzori Mts, 3980 m: 00°23'N, 29°53'E C.
42. **Ibanda, 3 km W**, Kasese Dist., confluence of Mubuku and Kyoha Rivers, Ruwenzori Mts, 1890 m: 00°21'47"N, 30°00'40"E C.
43. **Confluence of Mubuku and Mahoma Rivers**, Kasese Dist., Ruwenzori Mts, 2105 m: 00°22'N, 30°00'E C.
44. **Echuya FR**, Rubanda Dist., 2380 m: 01°14'40"S, 29°48'38"W C.
45. **John Mate Camp**, Kasese Dist., Ruwenzori Mts, 3370 m: 00°23'N, 29°56'E C.
46. **Lake Mahoma**, Kasese Dist., Ruwenzori Mts, 2960 m: 00°21'N, 29°58'E C.
47. **Lower Kitandara Lake**, Kasese Dist., Ruwenzori Mts, 4040 m: 00°22'N, 29°53'E C.
48. **Mgahinga Gorilla NP**, between Mts Mgahinga and Muhavura, Kisoro Dist., 2680 m: 01°22'S, 29°39'E C.
49. **Nyabitaba Hut**, Kasese Dist., Ruwenzori Mts, 2670 m: 00°22'N, 29°59'E C.
50. **Pass between Mts Sabinio and Mgahinga**, 2440–2590 m: 01°22'S, 29°37'E M.
51. **Ruhizha**, Kabale Dist., Bwindi Impenetrable NP, 2350 m: 01°02'S, 29°45'E C.
52. **Saddle between Mts Mgahinga and Muhavura**, Kisoro Dist., Mgahinga Gorilla NP, 2980 m: 01°23'S, 29°39'E M.

## Appendix 2

Specimens with post-cranial skeletons used to confirm the occurrence of the entepicondylar foramen on the humerus (See Table 4, Fig. 5).

*Hylomyscus aeta* (N = 17).—Burundi, Kibira NP (FMNH 149064); Ruvyirame River (FMNH 149066–149071, 149078, 149079); Gatare Stream (FMNH 149082, 149098). Gabon, Mount Doudou (FMNH 167682). Uganda, Bwindi-Impenetrable NP, Nteko Parish (FMNH 160492–160496).

*H. alleni* (N = 2).—Ivory Coast, Haute Dodo Forest (USNM 583911, 583915).

*H. anseli* (N = 14).—Tanzania, Rukwa Region, Mbizi Mountains FR (FMNH 171342, 171344–171356).

*H. arcimontensis* (N = 18).—Tanzania, West Usambaras, Ambangulu Tea Estate (FMNH 150126–150132, 150135–150138, 150154–150156, 150159–150162).

*H. demniae* (N = 20).—Uganda, Ruwenzori Mountains NP, Mubuku-Kyoha Rivers (FMNH 144448–144451, 144453–144457); Mubuku-Mahoma Rivers (FMNH 144459–144469).

*H. endorobae* (N = 5).—Kenya, Aberdare NP (USNM 589869); Mount Kenya (USNM 589870–589873).

*H. parvus* (N = 3).—Gabon, Maritime Province, Ogoue (USNM uncataloged).

*H. stella* (N = 20).—Democratic Republic of Congo, Epula Zone, Ituri Forest (USNM 548741, 548742, 548745, 548751–548754, 548756, 548757, 548759, 548760, 548765, 548766, 548769, 548770, 548773, 548775, 548779). Kenya, Kakamega Forest Reserve (USNM 589877, 589878).

*H. vulcanorum* (N = 22).—Burundi, Bururi Forest, Mumushwizi Valley (FMNH 155981, 155982, 155984–155988, 155990; Ruhinga Hill (FMNH 155991, 155992). Uganda, Bwindi-Impenetrable NP, Ruhizha (FMNH 157903–157905, 160502); Mgahinga-Gorilla NP, saddle between Mts Muhavura and Mgahinga (FMNH 157511, 157512); Mgahinga-Gorilla NP, slope of Mt Muhavura (FMNH 157515, 157516, 157518, 157528); Echuya FR (FMNH 161049, 161050).

*P. degraaffi* (N = 21).—Burundi, Kibira NP, near Teza (FMNH 138037, 138039–138052, 138059, 138060, 138073, 138074, 138076, 138081).

*Praomys delectorum* (N = 27).—Tanzania, South Pare Mountains, Chome FR (FMNH 151311, 151313–151315, 151317–151319, 151321–151323, 151325–151327, 151329); Udzungwa Mts (FMNH 155624–155636).

*P. jacksoni* (N = 20).—Burundi, Kibira NP, Kwogofe Colline (FMNH 148795, 148796, 148799–148802, 148806–148808, 148810, 148811, 148813, 148816, 148821). Uganda, Bwindi-Impenetrable NP, Omubianja Swamp (FMNH 160870–160874); Bwindi-Impenetrable NP, Buhoma (FMNH 160875).

*P. misonnei* (N = 20).—Democratic Republic of Congo, Ituri Forest, Epulu (FMNH 149570, 149574, 149576, 149594, 149595–149602). Uganda, Budongo Forest (FMNH 165316–165319, 165327–165330).

*P. rostratus* (N = 2).—Ivory Coast, Siahe (USNM 583925); Zagne (USNM 583926).

*P. tullbergi* (N = 13).—Liberia, Tars Town (USNM 481923). Sierra Leone, Outamba-Kilimi National Park (USNM 547393, 547397, 547399, 547400, 547409, 547413, 547417, 547418, 547426, 547434, 547435, 547437).