

## Review of the *Hylomyscus denniae* complex (Rodentia: Muridae) in Tanzania, with a description of a new species

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*Abstract.*—Based on morphological and morphometric comparisons, a new species of *Hylomyscus*, *H. arcimontensis* (Muridae: Murinae), is identified from Mount Rungwe and the Eastern Arc Mountains of central and eastern Tanzania. The new species is confined to wet montane forests of these mountains and represents another vertebrate endemic to the Tanganyika-Nyasa Montane Forest biotic region (sensu Moreau 1966). It is most closely related to *H. anselli*, a form described from mountains in northern Zambia as a subspecies of *H. denniae* and here elevated to species rank. Morphological evidence supports the view that the nominal species *H. denniae* is a composite of several species whose interrelationships and differentiation patterns indicate two species complexes: the *H. denniae* group centered in Central East African mountains (Burundi, Kenya, Rwanda, Uganda, Zaire) and the *H. anselli* group distributed across more southern mountains (Angola, Malawi, Tanzania, Zambia).

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In his review of East African *Hylomyscus*, Bishop (1979:519) noted that “The species are confined to forest, which in eastern Africa is distributed in isolated patches and is limited to mountain slopes at high altitudes.” He further concluded (p. 529) that “Clearly the history of the distribution of forest habitat in East Africa is [of] considerable importance in the evolution of the group.” One of those forest-dwelling *Hylomyscus* considered by Bishop is *H. denniae*, the Montane Woodland Mouse. As currently understood (e.g., Musser & Carleton 1993), the species is broadly distributed in the highlands of southern and eastern Africa: from the Angolan plateau, through the mountains of northern Zambia and Tanzania; to the Albertine Rift and Central East African systems in easternmost Zaire, Burundi, Rwanda, Uganda, and Kenya. Within this range, the occurrence of the species is highly fragmented, confined to insular moist-forest settings, and size and qualita-

tive character variation among these montane isolates are appreciable (Bishop 1979, Musser & Carleton 1993).

In Tanzania, the local distribution of *Hylomyscus denniae* is similarly patchy, scattered throughout those portions of the Eastern Arc Mountains that have been the focus of recent small mammal surveys (summary in Stanley et al. 1998b). According to Bishop’s (1979) revision, the trinomial *H. denniae anselli*, which he had therein newly named, should apply to the Tanzanian populations. The purposes of our study are threefold: to examine morphometric variation among Tanzanian populations using recent collections; to describe a new species based upon those examinations; and to establish the viewpoint that nominal *denniae* as currently understood is not only a composite of several species but a composite of two species complexes, the *H. denniae* group in the north and the *H. anselli* group in the south. This paper represents another

contribution to improve taxonomic and distributional understanding of small non-volant mammals indigenous to Tanzania's dwindling stands of montane forest (Goodman et al. 1995, Stanley et al. 1996, Stanley et al. 1998a, 1998b, Stanley & Hutterer 2000, Stanley et al. 2000).

### 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); The Natural History Museum, London (BMNH, formerly British Museum of Natural History); 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).

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: 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 g) 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 for Tanzanian samples were recorded in the field by WTS, and those for Ugandan specimens by an FMNH team that included 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, 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).

The following 11 operational taxonomic units (OTUs), listed according to current understanding of species taxonomy, were used to generate the various tabular summaries and undertake descriptive and multivariate analyses. All of these OTUs are allopatric to one another, each restricted to wet montane forest in isolated mountain systems (Fig. 1). We collectively refer to those Tanzanian mountains northeast of the Makambako Gap and trending in a northeasterly direction from the Udzungwas to South Pare as the Eastern Arc Mountains (i.e., sensu Wasser & Lovett, 1993), hereafter abbreviated to EAM. Full provenience and museum registration numbers are provided in the Taxonomic Summary.

*Hylomyscus denniae anselli*: OTU 1—Tanzania, South Pare Mountains, Chome Forest Reserve ( $n = 6$ ); OTU 2—Tanzania, West Usambara Mountains, NW of Korogwe ( $n = 54$ ); OTU 3—Tanzania, East Usambara Mountains, vicinity of Amani ( $n = 24$ ); OTU 4—Nguu Mountains, Nguuru

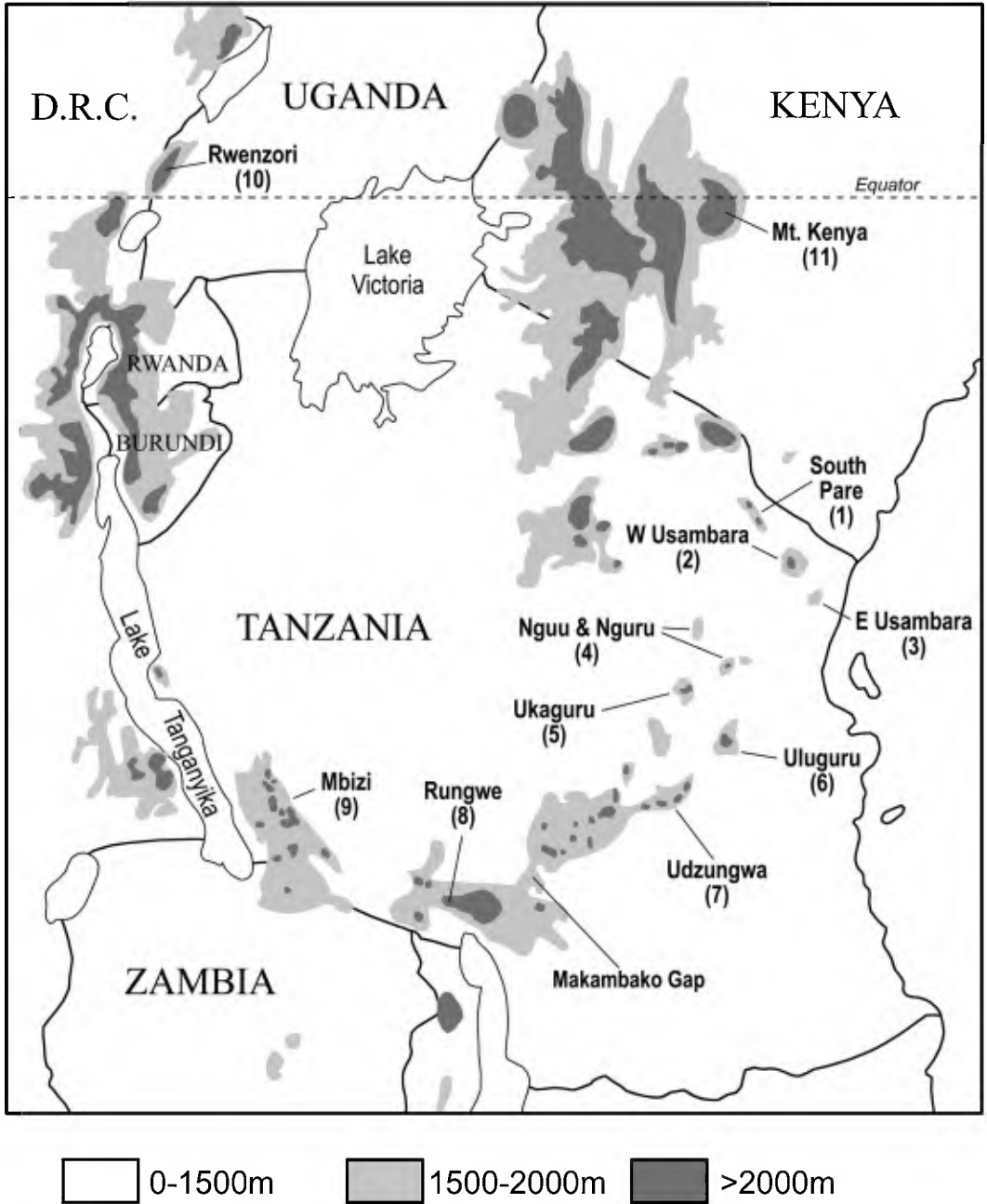


Fig. 1. Mountainous regions of East Africa inhabited by populations of the *Hylomyscus denniae* complex. Numbers in parentheses refer to the 11 geographic samples used in multivariate analyses; see Materials and Methods for localities and sample sizes. The Eastern Arc Mountains (sensu Wasser & Lovett 1993) are those disconnected ranges in Tanzania that trend in a northeastern direction from the Makambako Gap, including the Udzungwa Mountains through the South Pare Mountains.

Table 1.—F values and significance levels derived from two-way analyses of variance of 16 craniodental variables as measured for sex and age cohorts in OTUs of *Hylomyscus denniae denniae* from the Ruwenzori Mts, Uganda (10:  $n = 56$ ; 29 ♂, 27 ♀; 16 Y, 33 A, 7 O), and *H. d. anselli* from the West Usambara Mts., Tanzania (2:  $n = 54$ ; 28 ♂, 26 ♀; 5 Y, 41 A, 8 O).

Variable	Ruwenzori Mts (10)			West Usambara Mts (2)		
	Sex	Age	Interaction	Sex	Age	Interaction
ONL	7.1*	34.6***	0.7	3.3	6.5**	0.7
ZB	0.6	22.7***	1.6	2.1	6.2**	0.5
BBC	0.1	3.3*	1.5	0.0	0.8	0.1
BOC	2.7	14.1***	2.9	0.1	5.7*	3.1
IOB	0.2	0.7	1.5	0.0	0.2	0.3
LR	3.0	21.4***	0.5	1.1	4.3*	0.6
BR	0.0	15.9***	0.1	0.2	2.7	1.3
PPL	6.7*	36.5***	0.6	2.9	2.6	0.1
LBP	2.7	2.9	2.1	1.9	6.3**	4.7*
BBP	0.0	1.4	2.1	0.1	0.2	1.0
LIF	6.9*	26.2***	0.5	2.1	3.2*	0.5
LD	6.8*	62.2***	0.3	3.5	6.1**	0.1
BZP	0.3	5.3**	1.6	0.0	1.9	3.9*
LAB	1.9	6.6**	0.8	0.0	0.1	0.6
CLM	2.3	1.8	1.7	0.1	0.9	0.2
WM1	0.5	0.7	4.0*	0.0	0.0	0.1

\* =  $P \leq 0.05$ ; \*\* =  $P \leq 0.01$ ; \*\*\* =  $P \leq 0.001$ .

North Forest Reserve, and Nguru Mountains, Nguru South Forest Reserve ( $n = 5$ ); OTU 5—Tanzania, Ukaguru Mountains, Mamiwa-Kisara Forest Reserve ( $n = 10$ ); OTU 6—Tanzania, Uluguru Mountains, Uluguru North Forest Reserve ( $n = 16$ ); OTU 7—Tanzania, Udzungwa Mountains, Udzungwa Scarp Forest Reserve ( $n = 18$ ); OTU 8—Tanzania, Mount Rungwe, Rungwe Forest Reserve ( $n = 16$ ); OTU 9—Tanzania, Mbizi Mountains, Mbizi Forest Reserve ( $n = 12$ ).

*Hylomyscus denniae denniae*: OTU 10—Uganda, Ruwenzori Mountains, Kasese District, Mubuku Valley ( $n = 56$ ).

*Hylomyscus denniae endorobae*: OTU 11—Kenya, Mount Kenya, upper western slopes ( $n = 27$ ).

Standard descriptive statistics (mean, range, and standard deviation) were derived for adult specimens (young, full, and old age classes combined) of the 11 OTUs. Means and ranges of external variables are provided as guidance to identification (see Appendix 1) but were not subjected to morphometric comparisons. One- and two-way

analyses of variance, discriminant 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).

#### Morphometric Differentiation among Tanzanian Samples and Comparisons with Ugandan and Kenyan Populations

Consistent age-related size differences are apparent within our two largest OTUs of *Hylomyscus*, those from the Ruwenzori and West Usambara mountains (Table 1), both of which are highly homogeneous in geographic and temporal origin. Furthermore, the anatomical localization of age-re-

lated differences is comparable in those two OTUs: that is, F-ratios are larger and typically highly significant for the biggest skull dimensions (ONL, ZB) and those taken on the facial region (LR, BR, LIF, LD); whereas, this statistic is consistently smaller in value and usually insignificant for variables measured on the neurocranium (BBC, IOB) and the molars (CLM, WM1). Notably more age effects and higher significance levels were derived for the Ruwenzori sample in comparison with that from the West Usambaras, a difference plausibly due to the greater proportion of young adults represented in the former (16 of 56 specimens versus 5 of 54). In contrast, sex and sex-age interaction contribute weakly and infrequently, as indicated by the magnitude and significance of obtained F values, to within-sample variation for the 16 craniodontal dimensions quantified (Table 1). Such patterns of nongeographic variation according to age and sex factors conform closely to those reported for the crania of other murid rodents, whether derived from lab-bred samples controlled for sex and age balance (e.g., Voss et al. 1990) or from field-obtained material in which the mixture of sex and age cohorts is highly variable between samples (e.g., Van der Straeten & Verheyen 1978, Carleton & Martinez 1991, Carleton & Van der Straeten 1997). In the following morphometric comparisons, we combined mensural data from the sexes and, except for a priori exclusion of obviously juvenile specimens, did not attempt to remove age-related size effects (post-weaning growth) in portraying the multivariate results.

Two craniodontal morphologies are clearly revealed in scatter plots of the first two canonical variates derived from discrimination function analysis of the eight Tanzanian samples (Fig. 2): one representing series obtained from the Mbizi Mountains (OTU 9) in westcentral Tanzania; and another representing Mount Rungwe (OTU 8) and the EAM (OTUs 1–7). General size, as indicated by the moderate to large positive correlations of most measurements, ac-

counts for the dispersion of specimen scores along CV1 and the extreme position of the Mbizi sample; especially noteworthy is the influence of their more robust molars (CLM, WM1) as compared with the samples from Mount Rungwe and the EAM (Table 2). On this axis, the Mount Rungwe series and large bodied examples from the EAM, particularly those from the Udzungwa and Uluguru Mountains, approach that from the Mbizi Mountains, and broad mensural overlap in many of their univariate ranges is apparent (Appendix 1). Craniodental proportions of those samples, however, clearly align them with other OTUs drawn from the more northeastern segments of the EAM, notably as reflected in the more constricted interorbital region (IOB), a shorter and narrower rostrum (LR, BR), much shorter bony palate (LBP), and smaller auditory bullae (LAB); all of these variables load heavily and negatively on CV2 (Table 2). The same dimensions in the example from the Mbizi Mountains are appreciably larger relative to skull length and accordingly influence its isolation on CV2. Mahalanobis distances among the nine centroids also disclose the sharp phenetic discontinuity between the Mbizi *Hylomyscus* and all those specimens that originated from Mount Rungwe and the EAM; in 16-dimension morphometric space, the Rungwe series, which represents *Hylomyscus* populations to the southwest of the Makambako Gap, falls within the EAM cluster (Fig. 2). We interpret these results as prima facie evidence that two species occur among Tanzanian populations of *Hylomyscus*.

What names should be applied to these two species is less clear. In his original description, Bishop (1979) reported only three specimens of “*denniae*” from Tanzania, none of them representing populations from mountain systems reported herein, and referred them to the type series of his new subspecies *anselli*. Subsequent systematists have thereafter identified the Tanzanian montane *Hylomyscus* as *H. denniae* (Good-

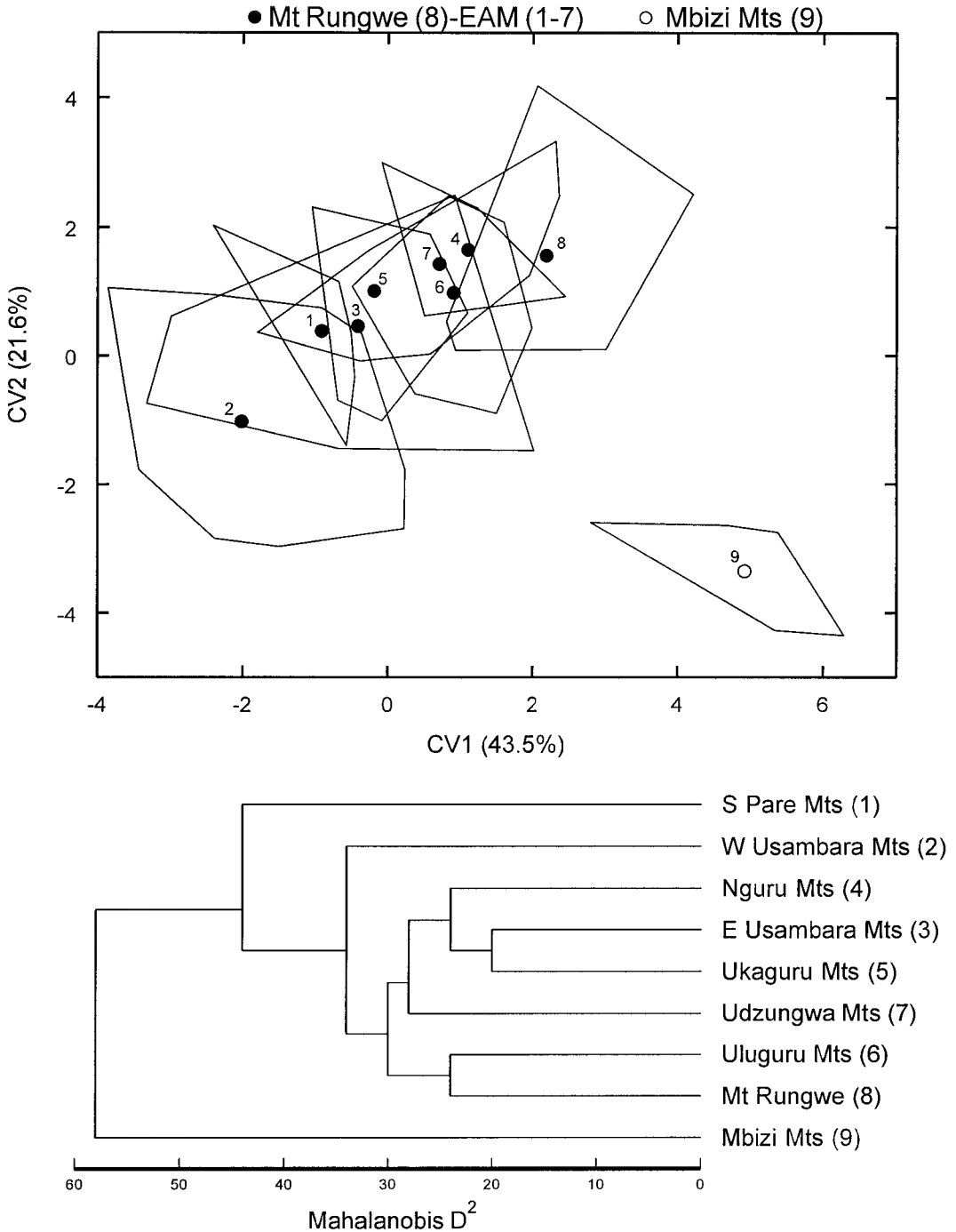


Fig. 2. Results of discriminant function analysis performed on 16 log-transformed craniodental variables as measured on 162 intact specimens representing nine OTUs of Tanzanian *Hylomyscus*. Top, projection of specimen scores on first two canonical variates extracted; irregular polygons represent maximal dispersion of specimen scores around an OTU centroid (numbered circles). Bottom, UPGMA phenogram based on Mahalanobis distances between the nine OTUs. See Table 2.

Table 2.—Results of discriminant function analysis performed on intact specimens ( $n = 162$ ) representing nine OTUs of Tanzanian *Hylomyscus* (see Fig. 2).

Variable	Correlations	
	CV1	CV2
ONL	0.64	-0.33
ZB	0.68	-0.16
BBC	0.70	-0.29
BOC	0.39	-0.22
IOB	0.49	-0.65
LR	0.60	-0.45
BR	0.30	-0.36
PPL	0.50	-0.21
LBP	0.35	-0.62
BBP	0.66	-0.25
LIF	0.67	0.23
LD	0.50	-0.23
BZP	0.30	0.02
LAB	0.44	-0.50
CLM	0.92	-0.12
WM1	0.85	-0.08
Canonical Correlations	0.90	0.82
Eigenvalues	4.16	2.07
Percent variance	43.5	21.6

man et al. 1995, Stanley et al. 1998b), with *anselli* as a synonym of unspecified rank (Musser & Carleton 1993). In the following multivariate analyses, we have included three of Bishop's original type series from Zambia (BMNH 61.944, 73.142, 74.251) in order to assess their affinity to the two Tanzanian phenotypes identified above. One other species-group taxon is critically important to these comparisons: that is nominotypical *denniae*, which Bishop (1979:528) featured in his scant differential diagnosis of *anselli*—"Similar to *denniae denniae* but somewhat smaller with relatively short palatal foramina." In overall size and pelage color, the external similarity of *denniae* proper, described from the Ruwenzori Mountains, to certain samples of Tanzanian *Hylomyscus*, particularly those from the Mbizi Mountains and the western EAM, is indeed striking. Accordingly, we have broadened our taxonomic and geographic perspective by including comparative series of *denniae*, and the equally large bodied *endorobae*,

from the vicinity of their type localities in Uganda and Kenya, respectively.

Strongly defined morphometric structure is again apparent in the canonical variate plot based on discriminant function analysis of all 11 OTUs (Fig. 3). On the first canonical axis, greater size is generally indicated for the separation of samples from the Ruwenzori Mountains and Mount Kenya from those in Tanzania. Noteworthy are the strong correlations of three dimensions—those of the molars (CLM, WM1) and length of the incisive foramen (LIF)—with this variate (Table 3). In his bivariate ratio comparisons, Bishop (1979) highlighted both the size of the incisive foramen and upper molar row, relative to occipitonasal length, in his subspecific separation of populations in Uganda and Kenya (as *denniae denniae*) from those in Zambia and Tanzania (as *denniae anselli*). In all ordinations involving all 11 OTUs, whether in principal component (not figured) or discriminant function analyses, these three variables repeatedly weight prominently on the first axis and reinforce Bishop's appreciation of their taxonomic significance from a multivariate perspective. Covariation patterns on CV2 emphasize the nonoverlap of the Mbizi Mountains sample and those from Rungwe-EAM and only marginal overlap of the Ugandan and Kenyan specimen scores. Greater size of the Mbizi and Kenyan *Hylomyscus* is indicated by the negative correlations of nearly all variables with CV2. As in discriminant analysis of the Tanzanian populations alone, a wider interorbital region (IOB), longer bony palate (LBP), and larger auditory bulla (LAB) weight most strongly on the second canonical variate (Table 3) and contribute heavily to the peripheral position of the Mbizi series on this axis. The pronounced phenetic separation of Bishop's *denniae denniae* (Ugandan and Kenyan OTUs) from his *denniae anselli* (Tanzanian OTUs) is reflected in the first clustering division based on Mahalanobis' distances between group centroids (Fig. 3). Within those two major clusters,

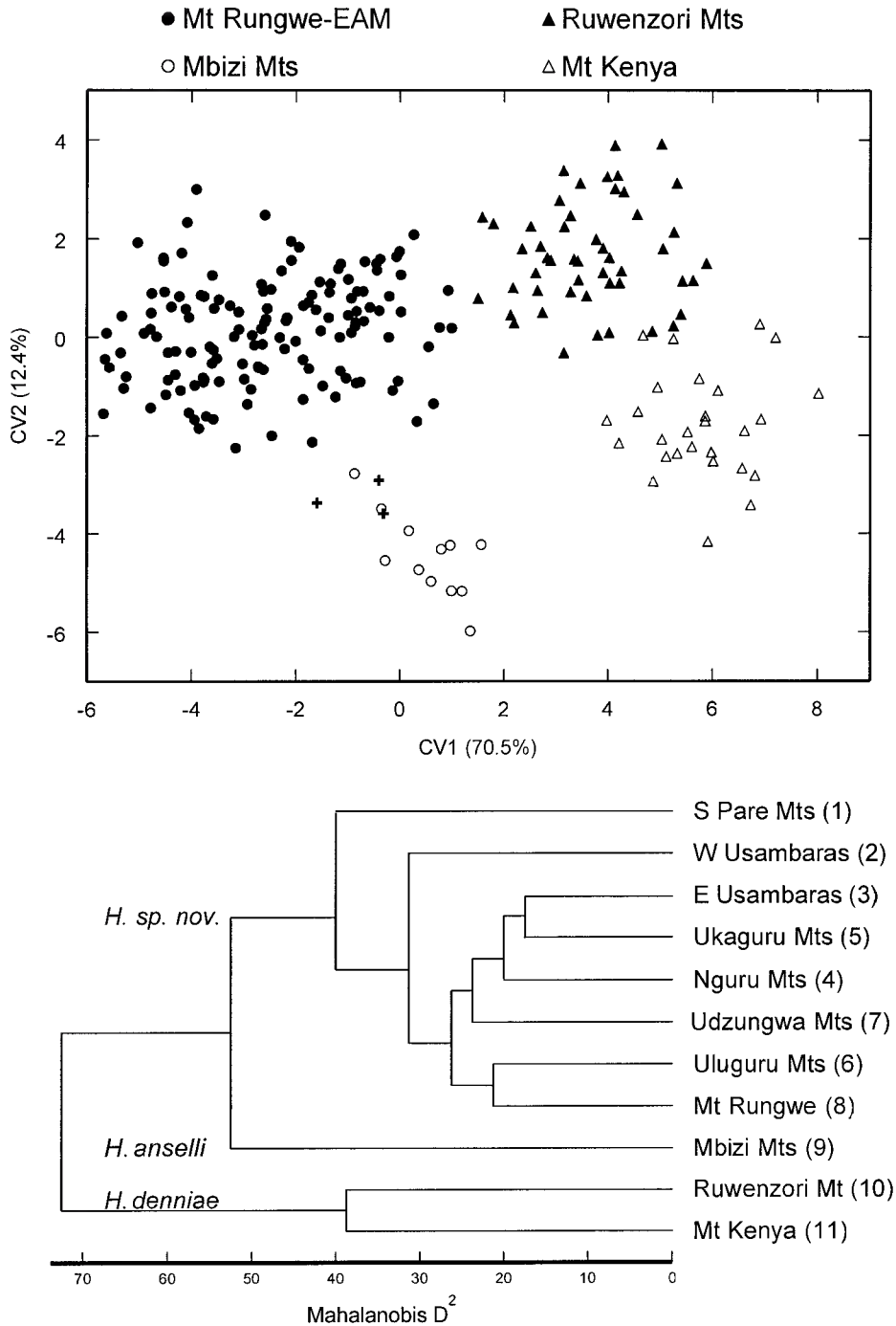


Fig. 3. Results of discriminant function analysis performed on 16 log-transformed craniodental variables as measured on 242 intact specimens representing nine OTUs of Tanzanian *Hylomyscus* (1–9) and samples of *H. denniae* from Uganda (10) and Kenya (11). Top, projection of specimen scores on first two canonical variates extracted. The three small crosses interspersed among specimens from the Mbizi Mountains, Tanzania, represent members of Bishop’s (1979) original type series of *Praomys (Hylomyscus) denniae ansellii* from Zambia. Bottom, UPGMA phenogram based on Mahalanobis distances between the 11 OTUs. See Table 3.



Table 3.—Results of discriminant function analysis performed on intact specimens ( $n = 242$ ) representing nine OTUs of Tanzanian *Hylomyscus* and one each of *H. demniae demniae* (Ruwenzori Mountains, Uganda) and *H. d. endorobae* (Mount Kenya, Kenya); see Fig. 3.

Variable	Correlations	
	CV1	CV2
ONL	0.73	-0.33
ZB	0.59	-0.29
BBC	0.76	-0.41
BOC	0.40	-0.33
IOB	-0.10	-0.71
LR	0.66	-0.43
BR	0.36	-0.37
PPL	0.68	-0.04
LBP	-0.03	-0.76
BBP	0.58	-0.34
LIF	0.91	0.01
LD	0.51	-0.35
BZP	0.33	-0.17
LAB	0.50	-0.57
CLM	0.92	-0.24
WMI	0.87	-0.18
Canonical Correlations	0.96	0.83
Eigenvalues	12.6	2.2
Percent variance	70.5	12.4

the divergence of samples drawn from the Ruwenzori Mountains (*denniae* proper) and Mount Kenya (*endorobae*), while appreciable (Mahalanobis  $D^2 = 36.9$ ), is much less than that which characterizes the segregation of Mbizi animals from those on Mount Rungwe and the EAM (Mahalanobis  $D^2 = 53.1$ ).

The three examples of *Zambian anselli*, entered as unknowns in the 11-group discriminant function analysis, are clearly aligned with the spread of scores representing specimens from the Mbizi Mountains, Tanzania (Fig. 3). According to posterior probabilities of classification, two of these (BMNH 73.142, 74.251) were definitely assigned to the Mbizi sample ( $P = 1.00$ ); whereas, the third, a young adult (BMNH 61.944), was equivocally associated with two EAM OTUs at low levels of probability (OTUs 5 and 8 at  $P = 0.55$  and  $0.44$ , respectively). The affinity of the third

Zambian specimen is unequivocal as revealed in principal component analysis, an ordination method that conveys covariation patterns based on the log-transformed specimen data itself without a priori assumptions about group assignment. In this analysis (Fig. 4), the three *Zambian* specimens are again phenetically intermingled with specimens from the Mbizi Mountains (OTU 9), in contrast to others representing Mount Rungwe (OTU 8) and the larger-bodied examples from the EAM (OTUs 6, 7). 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). Other variables that account for the separation of the Mbizi *Hylomyscus*, not so clearly expressed in the discriminant function analyses, include the comparatively narrow zygomatic plate (BZP) and their shorter incisive foramina (LIF) relative to a longer bony palate (LBP) (Table 4).

#### Taxonomic Summary

On the basis of the results presented above, we conclude (1) that mice from the Mbizi Mountains represent an eastern population of *anselli* Bishop (1979) and (2) that samples from Mount Rungwe and the EAM represent a new species of *Hylomyscus*, *H. arcimontensis* as described below, indigenous to those Tanzanian highlands and their wet montane forests.

As a third general conclusion, we elevate *H. anselli* Bishop (1979) to a full species distinct from *H. demniae* (Thomas 1906) and underscore the qualitative distinctions of the two as exemplars of two species groups within *Hylomyscus*. The conspicuously longer length of the incisive foramina in *H. demniae* proper in comparison with *anselli* was first appreciated by Ansell (1960) and later quantified by Bishop (1979) in his description of the latter as a

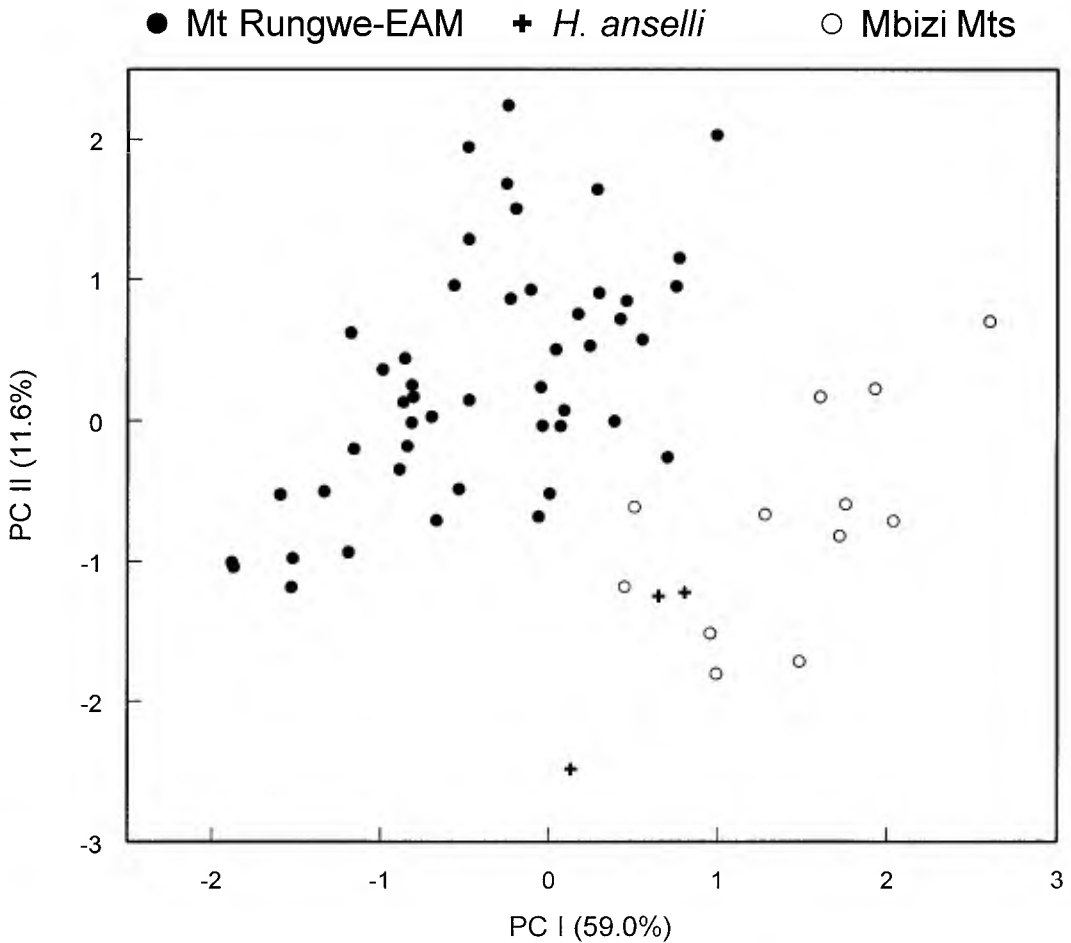


Fig. 4. Scatter plot of first and second principal components extracted from ordination of 16 log-transformed craniodental variables as measured on 66 intact specimens representing large-bodied samples (OTUs 6–9) from western Tanzania. The three small crosses associated with specimens from the Mbizi Mountains, Tanzania, represent members of Bishop's (1979) original type series of *Praomys (Hylomyscus) denniae anelli* from Zambia. See Table 4.

subspecies. In the *denniae* complex, the incisive foramina span approximately 80–85% of diastemal length, versus 70–75% in the *anselli* group; the length of the foramina relative to the hard palate is correspondingly greater in the *denniae* group, 1.4–1.6 times longer as compared with 1.1–1.3 times in the *anselli* group (Fig. 5). According to anatomical landmarks, the shorter incisive foramina in individuals of the *anselli* complex terminate in front of the anterior roots of the first molars or end approximately equal with them; in examples of the

*denniae* complex, the foramina project between the anterior roots to the level of the t2 (lingual anterocone) or even the t1 (anterostyle). Two qualitative traits concord with the distinctions in the relative length of the incisive foramen. For one, the opening of the subsquamosal fenestra is consistently smaller in examples of the *H. denniae* complex examined (*denniae*, *endorobae*, and the small-bodied *vulcanorum*), and the hamular process is correspondingly shorter and broader. In many individuals, the fenestra is so minute as to be function-

Table 4.—Results of principal component analysis performed on intact specimens ( $n = 64$ ) representing *Hylomyscus* from the Mbizi Mountains (OTU 9), Mount Rungwe (OTU 8), westernmost samples from the Eastern Arc Mountains (OTUs 6, 7), and original type material of *H. denniae anselli* from Zambia; see Fig. 4.

Variable	Correlations	
	PCI	PCII
ONL	0.94	0.09
ZB	0.87	0.08
BBC	0.78	-0.24
BOC	0.72	0.07
IOB	0.81	-0.18
LR	0.85	-0.03
BR	0.80	0.34
PPL	0.87	0.31
LBP	0.82	-0.38
BBP	0.82	-0.02
LIF	0.49	0.39
LD	0.84	0.23
BZP	0.45	0.67
LAB	0.67	-0.25
CLM	0.71	-0.39
WMI	0.63	-0.46
Eigenvalues	0.019	0.004
Percent variance	59.0	11.7

ally closed. In specimens of the *H. anselli* complex, this temporal opening is always patent and more spacious, forming about one-third to one-half the area of the contiguous postglenoid foramen; the hamular process, which forms the anterior margin of the fenestra, is longer and more slender (Fig. 6). For another, based on lactating females for which counts could be reliably determined, members of the *H. denniae* group possess a pectoral mammary pair, the teat number totaling eight. Females of the *H. anselli* group lack the pectoral pair, the teat count equaling six, a contrast also remarked by Ansell (1960).

The geographic complementarity of these morphologies suggests a biogeographic pattern that may prove to reflect vicariant effects associated with older orogenic events and climatic changes (e.g., see Griffiths 1993 and Lovett 1993a, 1993b for general introduction). Members of the *H. anselli* assemblage occur in more southern African

mountains: from the central Angolan highlands (*H. c.f. anselli* group); through the disconnected mountains in northern Zambia and western Tanzania (*H. anselli*); to Mount Rungwe and the Eastern Arc Mountains of central and eastern Tanzania (*H. arcimontensis*, new species). Forms of the *H. denniae* group are centered in eastern African mountains: in the southern portion of the Albertine Rift system in Burundi, Rwanda, easternmost Zaire, and southwestern Uganda (*vulcanorum*); the northern section of the Albertine Rift in northeastern Zaire and westernmost Uganda (*denniae*); and the Central East African mountains in easternmost Uganda and western Kenya (*endorobae*).

Formal enactment of our taxonomic recommendations follows for the two species of the *H. anselli* group central to the present investigation. Synonymies presented for these two trace earliest identification and subsequent name combinations; specimens examined include all individuals personally seen and identified by us. Determination of species limits within the *H. denniae* group is under study and will be reported in a companion paper (Carleton, Kerbis-Peterhans, & Stanley, in preparation). The synonymy given is therefore short and lists only the primary synonyms according to current taxonomic understanding; specimens examined include only those used in the analyses and tabular summaries.

*Hylomyscus arcimontensis*, new species  
(Fig. 7; Appendix 1)

*Hylomyscus weileri* (part), Allen & Loveridge 1933:108.

*Rattus (Hylomyscus) carillus weileri* (part), Swynnerton & Hayman 1951:316.

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

*Hylomyscus denniae* (part), Musser & Carleton 1993:599.—Stanley et al. 1998a:156.—Stanley et al. 1998b:95.

*Holotype*.—Field Museum of Natural History 151251, an adult male prepared as

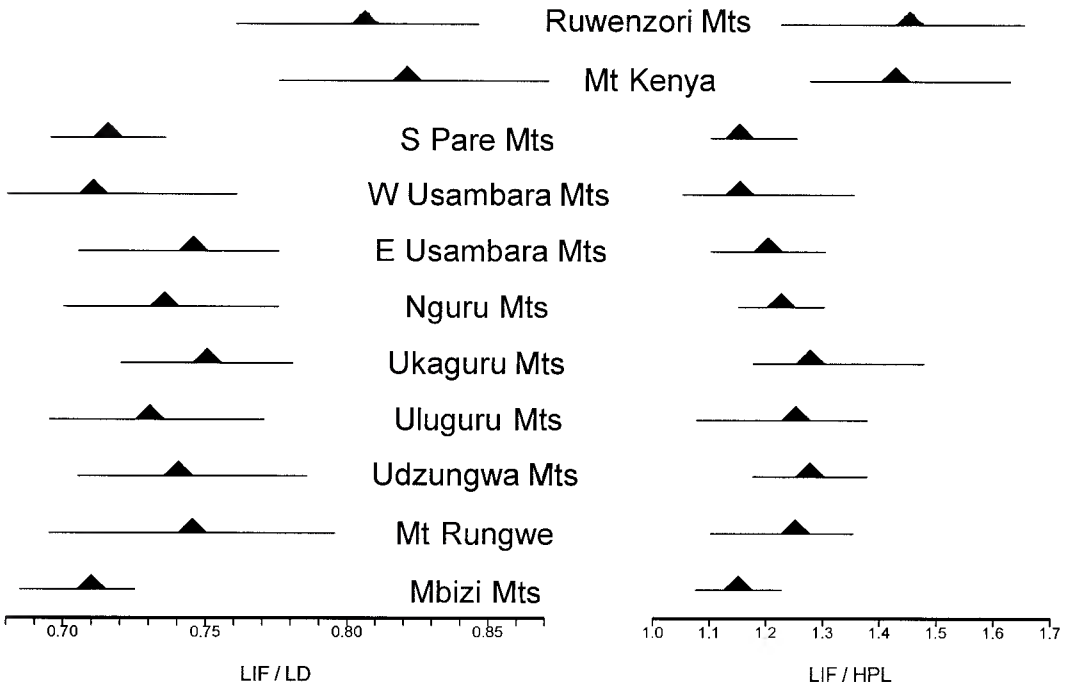


Fig. 5. Variation in relative length of the incisive foramen among ten samples of montane *Hylomyscus* as illustrated by simple ratios. Left, length of incisive foramen (LIF) relative to length of diastema (LD); right, length of incisive foramen relative (LIF) to hard palatal length (HPL). Solid triangles indicate the ratio mean of the 11 montane samples and horizontal lines the range. Both ratio comparisons convey the proportionally longer incisive foramen in *Hylomyscus* from northern mountains in Uganda and Kenya (*H. denniae* group) as compared with those from southern ranges in Tanzania (*H. anselii* group).

skin, skull, partial skeleton, and frozen tissue (liver); collected 5 August 1993 by William T. Stanley (original number WTS 1316).

The general condition of the round skin is good and the skull excellent. External data recorded on the skin tag include: TOTL, 240 mm; HBL, 100 mm; TL, 140 mm; HFL, 22 mm; EL, 18 mm; and WT, 29 g. The testes (15 × 7 mm) were noted as scrotal in position, with convoluted epididymides. The phallus was everted in preparation and remains attached to the skin.

*Type locality*.—Tanzania, Tanga Region, Muheza District, East Usambara Mountains, 4.5 km WNW Amani, Monga Tea Estate, control site; elevation 900 m; geographic coordinates, as recorded by the collector, 05°06'S–38°36'E.

*Diagnosis*.—A species of the *Hylomys-*

*cus anselii* group characterized by small size (HBL ≈ 85–100 mm; ONL ≈ 24.5–26.5 mm; CLM ≈ 3.6–4.0 mm). As in *H. anselii*, subsquamosal fenestra well defined, about one-third to one-half the area of the postglenoid foramen, and pectoral pair of teats absent (mammary total = 6 versus 8 in the *H. denniae* complex). Smaller in most external and cranial measurements than *H. anselii* proper, notably as expressed in the more delicate molars, narrower interorbit, shorter rostrum and smaller auditory bullae (Appendix 1); incisive foramina, however, relatively longer, bony palate correspondingly shorter, and zygomatic plate broader.

*Distribution*.—Forested highlands from the Misuku Mountains, northern Malawi; to Mount Rungwe and contiguous highlands, southwestern Tanzania; eastwards through the Eastern Arc Mountain chain to the South Pare Mountains, northeastern Tanza-

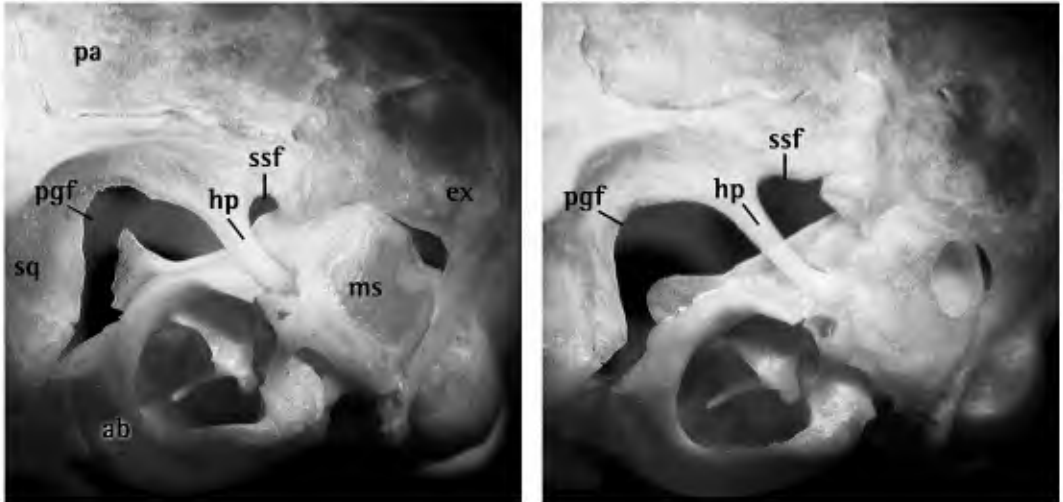


Fig. 6. Otic-temporal region (approximately 9.5x) and associated foramina in species of *Hylomyscus*. Left, *H. denniae* (FMNH 144532; Uganda, Ruwenzori Mts, Mubuku River Valley, Nyabitaba Hut); right, *H. arcimontensis*, new species (FMNH 158348; Tanzania, Uluguru Mts., 3 km W & 1.3 km N Tegetero). Abbreviations: ab, auditory (ectotympanic) bulla; ex, exoccipital; hp, hamular process of squamosal; ms, mastoid bulla; pa, parietal; pgf, postglenoid foramen; sq, squamosal; ssf, subsquamosal fenestra. In *Hylomyscus* from northern mountain ranges (*H. denniae* group), the subsquamosal fenestra is small or nearly occluded and the hamular process short as compared with those from southern mountains (*H. ansellii* group).

nia (Fig. 9); known altitudinal range, 900–2410 m.

**Description.**—Pelage soft and fine in texture, short (6–8 mm over middle rump) and closely appressed to body. Dorsal body hairs medium to dark plumbeous gray over most of their length, tipped with bright buff; guard hairs brownish, little longer than body fur except over rump. General effect of dorsum a lusterless, somber dark brown; somewhat more vivid along flanks where tips of body hairs are more ochraceous-buff; blackish-brown over rostrum and around eyes. Ventral hairs a brighter plumbeous gray over basal two-thirds of length, distal third bright white. General effect of ventrum a whitish-gray, variably medium to dark in tone between individuals and among populations. Dorsal-ventral pelage contrast well marked. Pinnae dusky brown, generally blending with the muted dark tones of the dorsum. Tail notably longer than head and body (TL  $\approx$  142–148% of HBL); color dusky-brown, dark all around circumference; caudal scales finely

textured and hairs short, about 1.5–2 annuli in length; tail thus appearing naked over most of its length, fine hairs becoming macroscopically visible toward the tip; caudal hairs brown to end of tail in most individuals, becoming white at the very tip in a few. Tops of fore and hind feet pale brown over the metapodials and dirty white over the phalanges; unguis tufts silvery white. Hind feet short and narrow as per the genus; digit 5 nearly as long as digits 2–4; plantar surface naked, with six well-formed and cushiony pads. Mammae number six, distributed as one post-axial and two inguinal pairs.

Cranium overall delicate in build, an impression conveyed by small size, a short, attenuate rostrum, thin zygoma, and absence of temporal-lambdoidal ridging. Braincase smooth, cranial vault notably arched, especially over the parietals-interparietal. Rostral processes of premaxillaries terminate more or less equal with the rear border of the nasals; frontal-parietal suture bluntly acute or evenly bowed; interparietal



Fig. 7. Dorsal, ventral, and lateral views of adult crania and mandibles of: left, *Hylomyscus denniae* (FMNH 144449; ONL = 27.5 mm), a male from the confluence of the Mubuku and Kyoha Rivers, Ruwenzori Mountains, Uganda; and right, *Hylomyscus arcimontensis*, new species (FMNH 151251 [holotype]; ONL = 27.0 mm), a male from 4.5 km WNW Amani, East Usambara Mountains, Tanzania.

deep anteriorly-posteriorly and wide, but not laterally contacting the squamosals. Interorbit relatively narrow, lacking supra-orbital ridging or beading; interorbital borders mostly amphoral in shape, post-orbital shelving weakly expressed in full and old adults. Zygomatic arches parallel-sided or slightly convergent rostrally; zygomatic plate medium in width, anterior edge more or less straight and perpendicular, dorsal notch shallow. Incisive foramina moderately long (LIF  $\approx$  70–75% of LD), posteriorly terminating just short of or equal with the anterior root of the first molars; foramina broader over their anterior portion, narrowing slightly over posterior half. Hard palate

smooth, slightly concave dorsally; posterior palatal foramina a single pair, set within the premaxillary-maxillary suture at the level of the third lamina of M1. Mesopterygoid fossa narrow and elongate, its anterior border squared or weakly rounded; parapterygoid fossae shallow, only slightly broader than mesopterygoid fossa. Alisphenoid strut present; tegmen tympani reduced, not contacting the squamosal, postglenoid foramen thus communicating with middle lacerate fissure; subsquamosal foramen small (one-third to one-half area of postglenoid foramen) but consistently present, hamular process of squamosal well delineated. Ectotympanic bullae moderately inflated for the

genus, mostly obscuring the periotic in ventral view. Coronoid process of dentary short and pointed, about same in height as condylar process; sigmoid notch shallow, angular notch broad and moderately incised.

Upper incisors mostly orthodont, enamel face yellow-orange. Lower incisor posteriorly terminating below the sigmoid notch, producing a low mound on the lateral mandibular ramus but no protruding process; enamel of lower incisors pale yellow. Upper molar row about as long as the hard palate, toothrows nearly parallel. On M1, t3 of first chevron small and poorly defined, obscured after little wear; t9 indistinct, present as a short spur from the t8; t3 on M2 tiny, set above the occlusal plane and noticeably smaller than t1; M3 small, about half the length and less than half the occlusal area of M2. On m1, anteroconid typically bilobate, but much narrower than contiguous middle chevron (protoconid-metaconid); posterolateral cusplet typically present on the m1 and m2, other accessory cusps absent.

*Comparisons.*—As described above, *H. arcimontensis* shares certain qualitative traits with *H. anselli* that implicate the two as very closely related, perhaps sister species. These include conformation of the incisive foramina and bony palate (Fig. 5), patency of the subsquamosal fenestra (Fig. 6), and absence of pectoral mammae (total = 6). Specimens of *H. arcimontensis* and *H. anselli* can be unambiguously separated from those of the *H. denitiae* group (*denitiae*, *endorobae*, *vulcanorum*) based on these features.

Discrimination of *H. arcimontensis* from *H. anselli* rests principally on the larger size of the latter, as reflected in nearly all cranial and external dimensions quantified (Appendix 1) and as demonstrated by its singular definition in multivariate space (Figs. 2, 3). Univariate contrasts between the two species are particularly strong for total and tail lengths, lengths of the skull, rostrum, and hard palate, interorbital breadth, and size of the ectotympanic bullae, all of them sub-

stantially greater in *H. anselli* compared with *H. arcimontensis*. Proportional cranial contrasts do exist but are inherently subtle to appreciate in side-by-side observations of the skulls. Noteworthy are the longer incisive foramina in *H. arcimontensis* relative to the bony palate (Fig. 5), its relatively broader zygomatic plate, and less inflated auditory bullae. Although not visually impressive, such proportional differences contribute significantly to multivariate distinction of the two species (Figs. 2, 4; Tables 2, 4). We caution that the consistency of the aforementioned contrasts should be verified with better series of *H. anselli* from Zambia.

*Ecological notes.*—*Hylomyscus arcimontensis* is restricted to submontane, montane, and upper montane habitats (sensu Lovett 1993b) of Mount Rungwe and the EAM. The arboreal nature of this climbing mouse is well suited for the many shrubs and vines found in these cool moist habitats. It is commonly caught in traps set on thin vines and limbs (< 5 mm diameter), but is also frequently captured in ground sets. In the South Pare Mountains, capture success for *Hylomyscus* was significantly higher in upper montane forest at 2000 m than at 1100 m (Stanley et al. 1998a). An elevational transect (600–2000 m) in the Udzungwa Scarp Forest Reserve documented a significantly greater abundance of *H. arcimontensis* at the 910 and 1460 m sites than was expected based on the null hypothesis of equal distribution along the transect. No *Hylomyscus* were documented in drier forest at the lowest site (600 m) during the survey, and the abundance of the species in the moist bamboo habitat at the highest site (2000 m) did not depart significantly from the null expectation (Stanley et al. 1998b).

Individuals of *H. arcimontensis* occur sympatrically with other murine rodents, the two most common being *Lopluromys flavopunctatus* and *Praomys delectorum* (also restricted to montane forests where it occurs in Tanzanian mountains). In the

EAM archipelago, *H. arcimontensis* is the most abundant arboreal small rodent in montane forests, sharing this habitat with *Dendromus mesomelas*, *Beamys hindei*, *Grammomys ibeanus*, *G. macmillani*, and *Graphiurus murinus* (Stanley et al. 1998b).

The biotic surveys that produced most specimens of *H. arcimontensis* reported here were conducted in the dry season, July through September of 1991–2003. The vast majority of specimens collected were adult, based on evidence of molar wear and pelage condition. Of 78 adult females examined, roughly 20% were pregnant, their embryos averaging 8.2 mm in crown-rump length (range = 1.5–20 mm,  $n = 15$ ). The number of embryos in a single uterine horn ranged from 1 to 4; for both uterine horns combined, the number of embryos ranged from 2 to 4, with an average litter size of 3.1 ( $n = 15$ ). Among 97 adult males examined, roughly 80% had convoluted epididymides and their testes averaged 6.8 mm in width (range = 2–10 mm) and 12.4 mm in length (range = 3–17 mm).

*Taxonomic and biogeographic remarks.*—The apparently earliest records of the new species were collected from the Uluguru Mountains by Arthur Loveridge in October, 1926, for the Museum of Comparative Zoology, Harvard College. These were at first mistakenly reported as *Praomys delectorum* (Allen & Loveridge 1927) until the sympatry of *P. delectorum* and a smaller murine, identified as *Hylomyscus weileri*, was later recognized within the Uluguru series (Allen & Loveridge 1933). All of the latter MCZ specimens, and those called *H. weileri* from the Udzungwa and Ukinga mountains (Allen & Loveridge 1933, Swynnerton & Hayman 1951), are examples of *H. arcimontensis*, not the larger *H. aeta* with its distinctive skull that bears weakly beaded supraorbital ridging. Populations of *P. delectorum* and *H. arcimontensis* broadly co-occur in wet montane forests throughout the EAM of Tanzania (Stanley et al. 1998b, reported as *H. deninae*).

*Hylomyscus* has not been previously reported for Malawi (e.g., Ansell & Dowsett 1988, Musser & Carleton 1993). We base its presence in extreme northern Malawi on a juvenile specimen (MCZ 44253) from the Misuku Mountains, just to the north of the Nyika Plateau; although originally reported as *Praomys jacksoni delectorum* (Lawrence & Loveridge 1953), we provisionally refer the specimen to *H. arcimontensis*. While biogeographically plausible, the occurrence of *H. arcimontensis* in the Misuku Mountains, and potentially on the Nyika Plateau and farther south in Malawi, should be documented with better material and more samples.

Among Tanzanian samples that we identify as *H. arcimontensis*, slight decrease in size is apparent along a southwestern to northeastern transect, from larger animals in the Rungwe and Uluguru samples to smaller in the West Usambara and South Pare mountains. Such a geographic trend is suggested by mean differences along the first principal component extracted (Fig. 8), an axis that generally captures variation in size. Although our samples from Mount Rungwe occur to the west of the Makambako Gap and therefore outside of the EAM as usually defined (Wasser & Lovett 1993), those specimens fit with EAM samples and broadly overlap them in morphometric space (Figs. 3, 4). We are impressed by the morphometric divergence of the animals from the South Pare Mountains, at the northeastern periphery of the Eastern Arc chain, but our sample size is regrettably small as are sample sizes of some other OTUs. Perhaps in part because of such insufficiencies, the correspondence of geographic proximity of mountain ranges to phenetic similarity among the mice inhabiting them is, at best, rough. Anomalous pair-groups formed include samples from East Usambara-Ukaguru and Uluguru-Rungwe systems (Figs. 2, 3); three of these four mountains are geographically well isolated within the Rungwe-EAM archipelago, and the East Usambaras are actually closest



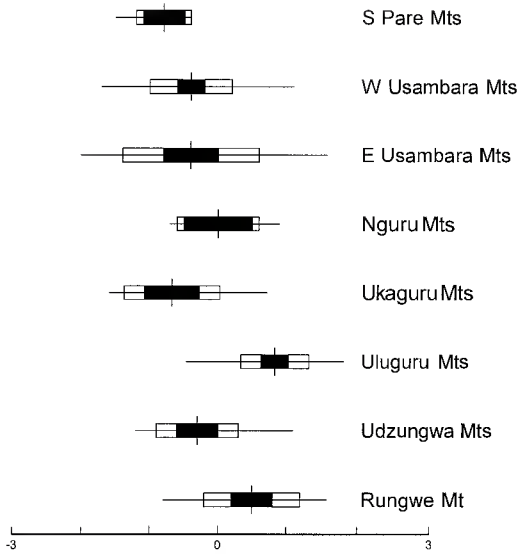


Fig. 8. Dice-Leraas diagrams of first principal component parameters for eight population samples of *Hylomyscus arcimontensis*, arranged in a southwesterly direction from eastcentral to southwestern Tanzania. For each bar, the vertical line corresponds to the sample mean, the horizontal line the sample range, the open rectangle  $\pm$  one standard deviation, and the close rectangle  $\pm$  two standard errors of the mean. As indexed by this multivariate statistic, animals in the northeastern portion of the EAM are smaller and irregularly trend through the southwestern EAM toward larger size on Mount Rungwe.

to the West Usambaras. Firm estimation of genetic relatedness among Tanzanian populations and its correspondence to geographic connectivity will require evaluation with other information sources.

*Hylomyscus arcimontensis* is yet another organism that is endemic to Moreau's (1966) Tanganyika-Nyasa Montane Forest Group. Other vertebrates that share roughly the same distribution are represented by *Arthroleptis reichei* (frogs), *Crotaphopeltis tornieri* (snakes), and *Sheppardia sharpie* (birds) (Burgess et al. 1998). *Hylomyscus arcimontensis* is the first small rodent to be formally recognized as a member of this faunal association, but further surveys and taxonomic studies may reveal other muroids with congruent distributions. Several shrews are known to be restricted to the Eastern Arc Mountains (i.e. *Crocidura tan-*

*saniata*, *C. telfordi*, *Myosorex geata*, *M. kihalei*, and *Sylvisorex howelli*), but their distribution covers only a fraction of the broader range of *H. arcimontensis*. Instead, each of these insectivores is more narrowly restricted to a specific mountain group or groups within the EAM (see Stanley et al. 1998b, Stanley & Hutterer 2000). The question remains why various shrew species are locally endemic within this region whereas *H. arcimontensis*, and possibly other rodents, are not. Should future research bear out the perceived variation between the distributional patterns of insectivores and rodents in the EAM, a unifying biogeographic explanation must be advanced to account for such an intriguing difference.

*Etymology.*—The specific epithet *arcimontensis* (arc[us]-i-montensis) is intended to evoke the principal distribution of the new species, the Eastern Arc Mountains, and to suggest the areal configuration of its known range, tracing a wide arc across central Tanzania, from the South Pare Mountains to Mount Rungwe.

*Referred specimens.*—MALAWI: Misuku Mountains, Matipa-Wilindi Ridge, 6000 ft (MCZ 44253). TANZANIA: Kilimanjaro Region, South Pare Mountains, Chome Forest Reserve, 7 km S Bombo, 1100 m, 04°20'S–38°00'E (FMNH 151253); Kilimanjaro Region, South Pare Mountains, Chome Forest Reserve, 3 km E and 0.7 km N Mhero, 2000 m, 04°17'S–37°55'40"E (FMNH 153946, 153947, 153949–153951); Tanga Region, Korogwe District, West Usambara Mountains, 12.5 km NW Korogwe, 1300 m, 05°04' S–38°25'E (FMNH 147252–147254, 147256, 147258, 147260–147262, 147264–147266, 147268–147270, 147272–147274, 147276, 147277, 150127–150129, 150131, 150132, 150135–150137, 150154–150156, 150160–150162, 150164, 150166, 150168–150170, 150439, 150442, 150446, 150451, 151244, 151245); Tanga Region, Korogwe District, West Usambara Mountains, 14.5 km NW Korogwe, 1250 m, 05°03'S–38°23'E (FMNH 147278–147280, 147282–147284, 147286–147288);

Tanga Region, Muheza District, East Usambara Mountains, 4.5 km WNW Amani, 1100 m, 05°46'S–38°36'E (FMNH 147290, 147291); Tanga Region, Muheza District, East Usambara Mountains, 6 km NW Amani, 1100 m, 05°04'S–38°36'E (FMNH 150118, 150119, 150139); Tanga Region, Muheza District, East Usambara Mountains, 4.5 km ESE Amani, 900 m, 05°06'S–38°36'E (FMNH 150121–150124, 150140–150142, 150144–150146, 150148–150150, 150152, 150153, 150433, 151248, 151250–151252); Tanga Region, Handeni District, Nguu Mountains, Nguru North Forest Reserve, 5.6 km S and 3 km E Gombero, 1180 m, 05°28'40"S–37°28'30"E (FMNH 168175); Tanga Region, Handeni District, Nguu Mountains, Nguru North Forest Reserve, 4.7 km S and 3.6 km E Gombero, 1430 m, 05°28'10"S–37°28'55"E (FMNH 168176); Morogoro Region, Morogoro District, Nguru Mountains, Manyangu Forest Reserve, 8 km N and 3 km W Mhonda, 1000 m, 06°02'50"S–37°32'50"E (FMNH 161270, 161271); Morogoro Region, Morogoro District, Nguru Mountains, Nguru South Forest Reserve, 6 km N and 6 km W Mhonda, 1500 m, 06°03'50"S–37°31'25"E (FMNH 161272); Morogoro Region, Morogoro District, Uluguru Mountains, Uluguru North Forest Reserve, 3 km W and 1.3 km N Tegetero, 1345 m, 06°55'45"S–37°42'20"E (FMNH 158343–158354, 158495, 158500, 158573); Morogoro Region, Morogoro District, Uluguru Mountains, Uluguru North Forest Reserve, 5.1 km W and 2.3 km N Tegetero, 1535 m, 06°55'12"S–37°41'00"E (FMNH 158355, 158505); Uluguru Mountains, Vituri (MCZ 22505, 22507, 22508, 22510, 22511); Morogoro Region, Kilosa District, Ukaguru Mountains, Mamiwa-Kisara Forest Reserve, 1 km E and 0.75 km S Mount Munyera, 1900 m, 06°22'45"S–36°56'10"E (FMNH 166916–166923); Morogoro Region, Kilosa District, Ukaguru Mountains, Mamiwa-Kisara Forest Reserve, 1 km E and 1.5 km S Mt. Munyera, 1840 m, 06°23'20"S–36°57'00"E (FMNH 166923–

166925); Morogoro Region, Kilombero District, Udzungwa Mountains, Udzungwa Scarp Forest Reserve, 3.5 km W and 1.7 km N Chita, 910 m, 08°30'20"S–35°54'30"E (FMNH 155555–155563); Morogoro Region, Kilombero District, Udzungwa Mountains, Udzungwa Scarp Forest Reserve, 4 km W and 5 km N Chita, 1460 m, 08°20'30"S–35°54'25"E (FMNH 155390, 155564–155570); Morogoro Region, Kilombero District, Udzungwa Mountains, Udzungwa Scarp Forest Reserve, 0.5 km W and 19.5 km N Chita, 2000 m, 08°20'50"S–35°56'20"E (FMNH 155392, 155571–155573); Udzungwa Mountains, Kigogo (MCZ 26499); Iringa Region, Iringa District, Ndundulu Mountains, West Kilombero Scarp Forest Reserve, 9 km E Udekwa, 1900 m, 7°45.117'S–36°27.803'E (FMNH 177698–177703); Ukinga Mountains, Madehani (MCZ 26406, 26409, 26410–26417); Mbeya Region, Rungwe District, Mount Rungwe, Rungwe Forest Reserve, 5 km E Iloilo, 1870 m, 09°10'05"S–33°38'15"E (FMNH 163584–163593); Mbeya Region, Rungwe District, Mount Rungwe, Rungwe Forest Reserve, 6 km E and 1.2 km N Iloilo, 2140 m, 09°10'50"S–33°39'10"E (FMNH 163594–163597); Mbeya Region, Rungwe District, Mount Rungwe, Rungwe Forest Reserve, 7 km E and 2.5 km N Iloilo, 2410 m, 09°11'30"S–33°39'25"E (FMNH 163598–163600); Rungwe, 5000 & 5800 ft (AMNH 81371–81374).

*Hylomyscus anselli* (Bishop, 1979),  
new rank

*Praomys denniae* subsp., Ansell, 1960: 393.—Ansell, 1973:15.—Ansell, 1978: 82.

*Praomys (Hylomyscus) denniae anselli* Bishop, 1979:528 (type locality—Zambia, Mwinilunga District, Jimbe Stream, 10°57'S–24°05'E; holotype—BMNH 74.250).

*Hylomyscus denniae* [anselli], Musser & Carleton, 1993:599 (listed as a species-

group synonym without indication of rank).

*Emended diagnosis.*—A species of *Hylomyscus* characterized by medium size (HBL  $\approx$  95–110 mm; ONL  $\approx$  26.5–28.5 mm; CLM  $\approx$  3.9–4.3 mm), a well defined subsquamosal fenestra, and a total of six mammary glands (pectoral pair of teats absent; present and total = 8 in the *H. denniae* group); larger in most external and cranial measurements than *H. arcimontensis*, especially as observed in the more robust molars, wider interorbital region, longer and broader rostrum, and larger auditory bullae (Appendix 1); incisive foramina, however, relatively shorter and the bony palate notably longer; zygomatic plate absolutely as wide as in *H. arcimontensis*, relatively narrower.

*Distribution.*—Documented from highlands in northern Zambia and westernmost Tanzania (Ufipa Plateau); known altitudinal range, 1220–2300 m.

*Remarks.*—The geographic range of *H. anselli* sensu stricto needs refinement. Most specimens that Bishop (1979) referred to *anselli* originated from mountains in northwestern Zambia (Mwinilunga and Solunezi Districts), but Ansell (1960, 1973, 1978) also documented it, as *Praomys denniae* subsp., from mountains in north-central Zambia (Senenje, Mpika, and Kasama Districts). The species likely occurs in comparable habitat of the same mountain systems where they extend into southeastern Zaire. We have not seen (and did not plot) the three Tanzanian specimens that Bishop (1979) allocated to his new subspecies *anselli*. Two are from Ngorongoro and the third from Tengeru, both sites in highlands to the northwest of the EAM. These should be reexamined to determine whether they represent true *H. anselli* or *H. arcimontensis*; we are suspicious of either allocation based simply on biogeographic considerations. A third and biogeographically plausible alternative is that populations in these northern Tanzanian mountains are members

of the *H. denniae* complex as known in western Kenya. In that same region of northern Tanzania, Demeter and Hutterer (1986) had reported *Hylomyscus* specimens from Mount Meru as *H. denniae*, but these have been subsequently redetermined to be examples of *Praomys delectorum* (R. Hutterer, pers. comm.). The isolated populations in Angola, which Musser & Carleton (1993) drew attention to under *H. denniae* sensu lato, also belong to the *H. anselli* complex, but their status is undergoing assessment (Carleton et al., in preparation).

In summary, *Hylomyscus anselli* proper is so far definitely known only from mountains in northern Zambia and contiguous westcentral Tanzania (Fig. 9). In those Zambian ranges and on the Ufipa Plateau, Tanzania, *H. anselli* generally overlaps the range of *Praomys jacksoni* (Ansell 1978, Stanley unpubl.). The latter species has not been recorded in the western reaches of the Nyika Plateau, northeastern Zambia, where instead the smaller *Praomys*, *P. delectorum*, is found (Ansell & Ansell 1973, Ansell 1978). This is the *Praomys* species that broadly co-occurs with *H. arcimontensis* throughout the Mount Rungwe-EAM ranges in Tanzania (Stanley et al. 1998b, this study).

*Specimens examined.*—TANZANIA: Rukwa Region, Sumbawanga District, Mbi-zi Forest Reserve, 0.5 km N and 4 km E Wipanga, 2200 m, 07°51'50"S–31°40'10"E (FMNH 171358, 171359, 171364, 171367); 0.5 km S and 3 km E Wipanga, 2300 m, 07°52'30"S–31°40'00"E (FMNH 171342, 171345, 171346, 171349, 171350, 171352–171354). ZAMBIA: Mpika District, Danger Hill, Luitikila Stream, 11°36' S–31°34' E (BMNH 73.142); Mwinilunga District, Sakeji Stream (BMNH 61.944); Solunezi District, Nyansule Stream (BMNH 74.251).

*Hylomyscus denniae* (Thomas, 1906)

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

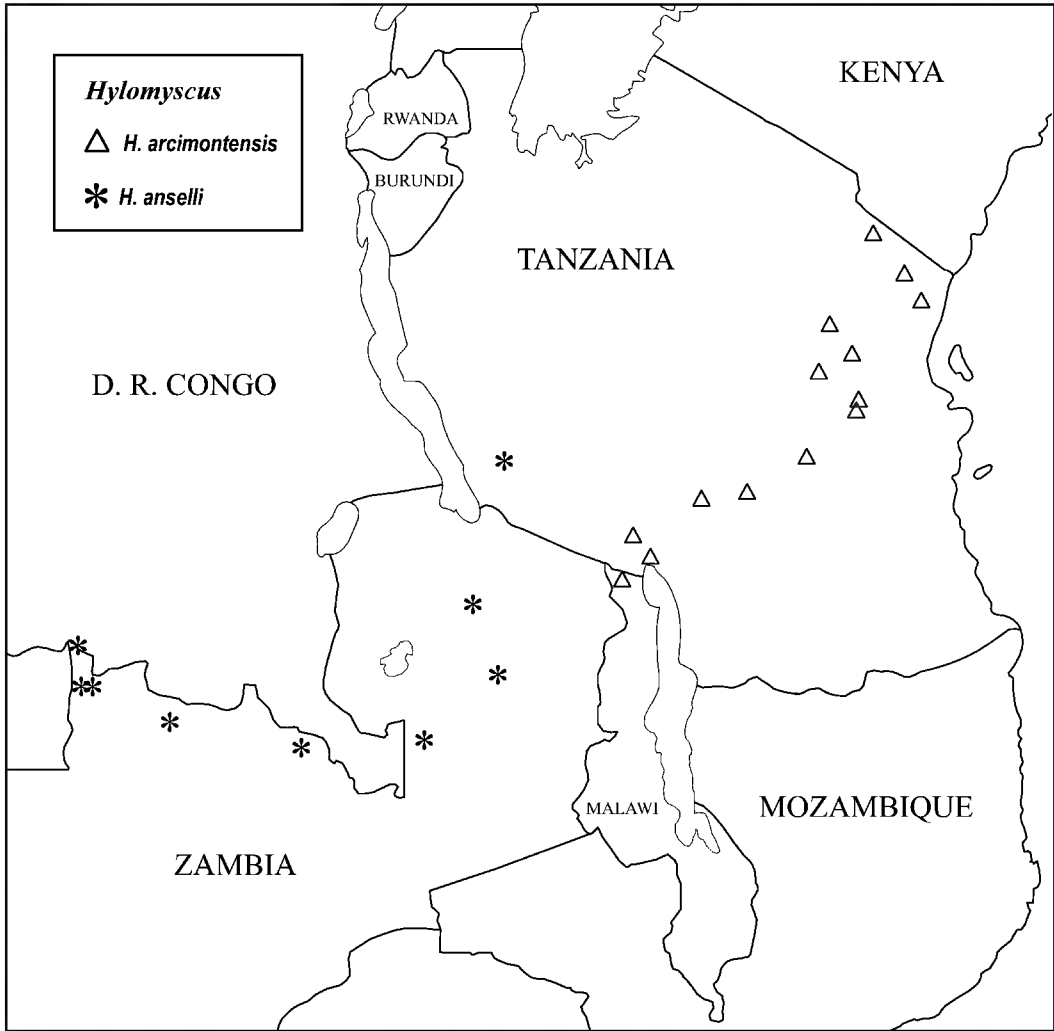


Fig. 9. Known distributions of *Hylomyscus anelli* and *H. arcimontensis* in southeastern Africa. Localities of *H. anelli* are based both on specimens studied by us (see Specimens examined) and those reported by Ansell (1960, 1964, 1973, 1978); all localities of *H. arcimontensis* reflect specimens documented herein.

*Epimys endorobae* Heller, 1910: 3 (type locality—Kenya, 25 mi N Eldoma Ravine, western edge of Mau Forest, 8600 ft).

*Praomys (Hylomyscus) denniae vulcanorum* Lönnberg & Gyldenstolpe, 1925: 4 (type locality—Belgian Congo, Birunga Volcanoes, Mount Karisimbi, 3800 m).

*Specimens examined.*—KENYA: west side of Mt. Kenya, 7000, 8500, 9000, 10,000, and 10,700 ft (CM 2843, 2856; FMNH 43454, 43456, 43457; USNM

163347, 163358, 163361, 163362, 163365, 163367, 163369–163377, 163379, 163381, 163382, 163384, 1163387, 163396, 163398). UGANDA: Kasese District, Ruwenzori's confluence with Mubuku and Bujuku rivers, Nyabitaba Hut, 8750 ft (FMNH 144475, 144479–144482, 144485–144489, 144491–144495, 144502, 144513, 144515, 144519, 144523, 144527, 144530–144532, 144536, 144538, 144540–144542, 144550, 144552, 144557, 144558, 144561, 144568,

144571, 144577; Kasese District, Ruwenzori Mountains, Mubuku Valley, right bank Mubuku River, 3 km W Ibanda, 6200 ft (FMNH 144448–144451, 144453, 144454); Kasese District, Ruwenzori Mountains, Mubuku Valley, confluence of Mubuku and Mahoma rivers, 6900 ft (FMNH 144459–144461, 144466, 144467, 144469, 144470).

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Appendix 1.—External and craniodental sample statistics for selected OTUs of *Hylomyscus*.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Total length				
<i>H. arcimontensis</i>				
South Pare Mts (1)	4	217	208–222	6.2
W Usambara Mts (2)	51	223	190–249	11.8
Uluguru Mts (6)	16	231	225–241	4.9
Udzungwa Mts (7)	16	217	196–245	13.2
Mt Rungwe (8)	15	217	199–240	10.8
<i>H. anseli</i>				
Mbizi Mts (9)	12	246	238–264	7.4
<i>H. denniae</i>				
Ruwenzori Mts (10)	25	235	200–266	14.5
Mt Kenya (11)	36	253	222–290	15.7
Head and body length				
<i>H. anseli</i>				
South Pare Mts (1)	4	93	90–95	2.1
W Usambara Mts (2)	52	90	80–105	5.7
Uluguru Mts (6)	16	96	90–102	3.1
Udzungwa Mts (7)	16	89	75–102	6.8
Mt Rungwe (8)	15	93	85–100	4.9
<i>H. anseli</i>				
Mbizi Mts (9)	12	101	95–109	7.4
<i>H. denniae</i>				
Ruwenzori Mts (10)	25	100	76–115	7.5
Mt Kenya (11)	35	104	92–120	6.8
Tail length				
<i>H. arcimontensis</i>				
South Pare Mts (1)	4	127	120–130	4.6
W Usambara Mts (2)	51	134	110–151	7.3
Uluguru Mts (6)	16	137	132–144	3.1
Udzungwa Mts (7)	16	131	121–145	7.5
Mt Rungwe (8)	15	127	109–141	8.1
<i>H. anseli</i>				
Mbizi Mts (9)	12	146	141–159	5.0
<i>H. denniae</i>				
Ruwenzori Mts (10)	25	135	122–157	8.7
Mt Kenya (11)	35	150	130–172	10.1
Hindfoot length				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	20	19–21	0.7
W Usambara Mts (2)	53	20	18–22	1.0
Uluguru Mts (6)	16	21	19–22	0.8
Udzungwa Mts (7)	15	20	19–21	0.6
Mt Rungwe (8)	15	20	19–21	0.6
<i>H. anseli</i>				
Mbizi Mts (9)	12	21	20–22	0.7
<i>H. denniae</i>				
Ruwenzori Mts (10)	25	21	19–23	1.0
Mt Kenya (11)	38	23	18–26	1.3

## Appendix 1.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Ear length				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	18	18–19	0.4
W Usambara Mts (2)	53	18	16–21	1.0
Uluguru Mts (6)	15	18	17–19	0.8
Udzungwa Mts (7)	15	18	16–20	1.1
Mt Rungwe (8)	15	19	18–21	1.0
<i>H. anseli</i>				
Mbizi Mts (9)	12	20	19–21	0.5
<i>H. denniae</i>				
Ruwenzori Mts (10)	25	20	18–23	1.1
Mt Kenya (11)	4	18	17–19	0.8
Weight				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	18.5	14.0–22.0	2.6
W Usambara Mts (2)	52	19.0	13.5–28.5	4.0
Uluguru Mts (6)	15	26.5	21.0–31.0	2.6
Udzungwa Mts (7)	17	19.0	13.5–26.0	3.5
Mt Rungwe (8)	15	22.0	18.0–27.5	2.6
<i>H. anseli</i>				
Mbizi Mts (9)	12	28.5	22.0–34.5	3.1
<i>H. denniae</i>				
Ruwenzori Mts (10)	25	30.3	17.5–39.0	6.1
Occipitonasal length				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	25.1	24.5–25.7	0.5
W Usambara Mts (2)	54	25.1	23.9–26.6	0.7
Uluguru Mts (6)	16	26.1	25.3–27.0	0.5
Udzungwa Mts (7)	17	25.3	24.2–26.3	0.6
Mt Rungwe (8)	16	25.6	24.3–26.9	0.7
<i>H. anseli</i>				
Mbizi Mts (9)	12	27.4	26.3–28.6	0.7
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	26.7	24.3–28.7	1.1
Mt Kenya (11)	32	27.8	25.6–29.4	0.9
Zygomatic breadth				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	12.8	12.3–13.0	0.3
W Usambara Mts (2)	54	12.4	11.7–13.1	0.7
Uluguru Mts (6)	16	12.8	12.1–13.2	0.3
Udzungwa Mts (7)	17	12.6	11.8–13.5	0.4
Mt Rungwe (8)	16	13.0	12.3–13.5	0.3
<i>H. anseli</i>				
Mbizi Mts (9)	12	13.5	12.9–13.7	0.2
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	13.1	11.4–14.5	0.6
Mt Kenya (11)	34	13.4	12.4–14.4	0.4



## Appendix 1.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Breadth of braincase				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	11.2	11.0–11.4	0.1
W Usambara Mts (2)	54	11.1	10.8–11.7	0.2
Uluguru Mts (6)	16	11.4	11.1–11.8	0.2
Udzungwa Mts (7)	17	11.2	10.9–11.5	0.1
Mt Rungwe (8)	16	11.4	11.0–11.8	0.2
<i>H. anselli</i>				
Mbizi Mts (9)	12	11.9	11.5–12.3	0.2
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	11.6	11.0–12.2	0.3
Mt Kenya (11)	34	12.1	11.6–12.7	0.3
Breadth across occipital condyles				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	5.7	5.5–5.8	0.1
W Usambara Mts (2)	54	6.0	5.5–6.3	0.2
Uluguru Mts (6)	16	6.1	5.9–6.4	0.1
Udzungwa Mts (7)	17	5.8	5.6–6.2	0.2
Mt Rungwe (8)	16	6.2	5.9–6.5	0.1
<i>H. anselli</i>				
Mbizi Mts (9)	12	6.2	5.9–6.5	0.1
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	6.1	5.6–6.4	0.2
Mt Kenya (11)	33	6.2	5.8–6.5	0.2
Interorbital breadth				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	4.2	4.0–4.3	0.1
W Usambara Mts (2)	54	4.3	4.1–4.5	0.1
Uluguru Mts (6)	16	4.3	4.1–4.4	0.1
Udzungwa Mts (7)	17	4.1	4.0–4.3	0.1
Mt Rungwe (8)	16	4.3	4.1–4.5	0.1
<i>H. anselli</i>				
Mbizi Mts (9)	12	4.6	4.5–4.8	0.1
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	4.1	3.9–4.4	0.1
Mt Kenya (11)	34	4.3	4.0–4.6	0.1
Length of rostrum				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	7.8	7.5–8.2	0.2
W Usambara Mts (2)	54	7.7	7.1–8.4	0.3
Uluguru Mts (6)	16	7.9	7.5–8.2	0.2
Udzungwa Mts (7)	17	7.8	7.3–8.1	0.2
Mt Rungwe (8)	16	7.7	7.0–8.2	0.3
<i>H. anselli</i>				
Mbizi Mts (9)	12	8.7	8.3–9.1	0.3
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	8.2	7.3–9.2	0.4
Mt Kenya (11)	33	8.7	8.1–9.4	0.3

## Appendix 1.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Breadth of rostrum				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	4.3	4.0–4.4	0.1
W Usambara Mts (2)	54	4.4	4.2–4.9	0.1
Uluguru Mts (6)	16	4.7	4.2–4.9	0.2
Udzungwa Mts (7)	17	4.3	3.9–4.7	0.2
Mt Rungwe (8)	16	4.5	3.9–4.7	0.3
<i>H. anselli</i>				
Mbizi Mts (9)	12	4.7	4.5–5.0	0.2
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	4.5	4.0–5.1	0.3
Mt Kenya (11)	30	4.7	4.3–5.3	0.2
Postpalatal length				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	8.6	8.1–9.1	0.4
W Usambara Mts (2)	54	8.7	7.9–9.4	0.4
Uluguru Mts (6)	16	9.1	8.5–9.5	0.3
Udzungwa Mts (7)	17	8.7	8.0–9.5	0.4
Mt Rungwe (8)	16	8.8	8.3–9.3	0.3
<i>H. anselli</i>				
Mbizi Mts (9)	12	9.5	8.9–10.1	0.4
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	9.6	8.1–10.6	0.6
Mt Kenya (11)	33	9.6	8.6–11.0	0.6
Length of bony palate				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	4.4	4.0–4.4	0.1
W Usambara Mts (2)	54	4.3	4.0–4.7	0.2
Uluguru Mts (6)	16	4.4	4.0–4.9	0.3
Udzungwa Mts (7)	17	4.1	4.0–4.4	0.1
Mt Rungwe (8)	16	4.3	4.1–4.6	0.2
<i>H. anselli</i>				
Mbizi Mts (9)	12	4.8	4.5–5.0	0.2
<i>H. denniae</i>				
Ruwenzori Mts (10)	54	4.1	3.6–4.5	0.2
Mt Kenya (11)	34	4.5	4.2–4.7	0.2
Breadth of bony palate				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	4.8	4.7–5.0	0.1
W Usambara Mts (2)	54	4.9	4.7–5.1	0.1
Uluguru Mts (6)	16	5.1	4.9–5.2	0.1
Udzungwa Mts (7)	17	4.9	4.6–5.1	0.1
Mt Rungwe (8)	16	5.0	4.8–5.2	0.1
<i>H. anselli</i>				
Mbizi Mts (9)	12	5.2	5.1–5.4	0.1
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	5.1	4.7–5.5	0.1
Mt Kenya (11)	34	5.1	4.8–5.5	0.2

## Appendix 1.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Length of incisive foramen				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	5.1	4.9–5.3	0.2
W Usambara Mts (2)	54	5.0	4.6–5.5	0.2
Uluguru Mts (6)	16	5.5	5.1–5.8	0.2
Udzungwa Mts (7)	17	5.3	5.1–5.5	0.1
Mt Rungwe (8)	16	5.4	5.1–5.8	0.2
<i>H. anseli</i>				
Mbizi Mts (9)	12	5.5	5.3–5.8	0.1
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	6.0	5.3–6.7	0.3
Mt Kenya (11)	34	6.3	5.9–7.0	0.2
Length of diastema				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	7.1	6.8–7.3	0.2
W Usambara Mts (2)	54	7.1	6.4–7.8	0.3
Uluguru Mts (6)	16	7.5	6.9–7.9	0.3
Udzungwa Mts (7)	17	7.1	6.6–7.6	0.3
Mt Rungwe (8)	16	7.3	6.8–7.7	0.3
<i>H. anseli</i>				
Mbizi Mts (9)	12	7.7	7.4–8.4	0.3
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	7.4	6.5–8.5	0.4
Mt Kenya (11)	34	7.7	6.8–8.2	0.3
Breadth of zygomatic plate				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	2.13	2.04–2.24	0.07
W Usambara Mts (2)	54	2.28	2.10–2.64	0.10
Uluguru Mts (6)	16	2.41	2.11–2.64	0.12
Udzungwa Mts (7)	17	2.33	2.10–2.63	0.15
Mt Rungwe (8)	16	2.34	2.15–2.52	0.08
<i>H. anseli</i>				
Mbizi Mts (9)	12	2.38	2.18–2.60	0.14
<i>H. denniae</i>				
Ruwenzori Mts (10)	51	2.35	1.95–2.68	0.13
Mt Kenya (11)	34	2.44	2.02–3.02	0.18
Length of auditory bulla				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	3.9	3.7–4.1	0.1
W Usambara Mts (2)	54	4.2	3.9–5.0	0.2
Uluguru Mts (6)	16	4.2	4.0–4.5	0.1
Udzungwa Mts (7)	17	4.3	4.1–4.4	0.1
Mt Rungwe (8)	16	4.2	4.0–4.5	0.1
<i>H. anseli</i>				
Mbizi Mts (9)	12	4.6	4.5–4.7	0.1
<i>H. denniae</i>				
Ruwenzori Mts (10)	50	4.3	3.9–4.6	0.1
Mt Kenya (11)	34	4.6	4.2–4.9	0.2

## Appendix 1.—Continued.

Species and OTU	<i>n</i>	Mean	Range	<i>SD</i>
Coronal length of maxillary toothrow				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	3.53	3.47–3.56	0.03
W Usambara Mts (2)	54	3.62	3.41–3.89	0.09
Uluguru Mts (6)	16	3.88	3.66–4.07	0.10
Udzungwa Mts (7)	17	3.76	3.56–3.93	0.11
Mt Rungwe (8)	16	3.93	3.77–4.09	0.09
<i>H. anselli</i>				
Mbizi Mts (9)	12	4.16	3.87–4.28	0.11
<i>H. denniae</i>				
Ruwenzori Mts (10)	55	4.12	3.93–4.43	0.12
Mt Kenya (11)	37	4.33	4.12–4.67	0.13
Width of first upper molar				
<i>H. arcimontensis</i>				
South Pare Mts (1)	6	1.08	1.05–1.11	0.02
W Usambara Mts (2)	54	1.10	0.98–1.16	0.03
Uluguru Mts (6)	16	1.16	1.13–1.21	0.03
Udzungwa Mts (7)	18	1.13	1.06–1.20	0.03
Mt Rungwe (8)	16	1.20	1.15–1.27	0.03
<i>H. anselli</i>				
Mbizi Mts (9)	12	1.24	1.17–1.29	0.04
<i>H. denniae</i>				
Ruwenzori Mts (10)	55	1.24	1.14–1.31	0.04
Mt Kenya (11)	38	1.27	1.16–1.36	0.05